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Global behavior of N competing species with strong diffusion: diffusion leads to exclusion

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Abstract

It is known that the competitive exclusion principle holds for a large kind of models involving several species competing for a single resource in an homogeneous environment. Various works indicate that the coexistence is possible in an heterogeneous environment. We propose a spatially heterogeneous system modeling the competition of several species for a single resource. If spatial movements are fast enough, we show that our system can be well approximated by a spatially homogeneous system, called aggregated model, which can be explicitly computed. Moreover, we show that if the competitive exclusion principle holds for the aggregated model, it holds for the spatially heterogeneous model too.

Key words Reaction-diffusion systems, Heterogeneous environment, Global behavior, Chemostat

2010 Mathematics Subject Classification 35J55, 35J61, 92D40.

1 Introduction

In this paper, we are interested in a reaction-diffusion system in a smooth domain $\Omega \subset \mathbb{R}^p$ modeling the interaction of N species competing for a single resource in a heterogeneous environment

$$\begin{cases} \frac{\partial}{\partial t} R^\varepsilon = I - \sum_{i=1}^N \frac{1}{\lambda_i} f_i(R^\varepsilon) V_i^\varepsilon - m_0 R^\varepsilon + \frac{1}{\varepsilon} A_0 R^\varepsilon & & \text{on } \Omega \\ \frac{\partial}{\partial t} V_i^\varepsilon = (f_i(x, R^\varepsilon) - m_i(x)) V_i^\varepsilon + \frac{1}{\varepsilon} A_i V_i^\varepsilon & i = 1..N & \text{on } \Omega \\ \partial_n R^\varepsilon = 0 & & \text{on } \partial\Omega \\ \partial_n V_i^\varepsilon = 0 & i = 1, .., N & \text{on } \partial\Omega \\ R^\varepsilon(t=0) = R^0 \geq 0 & & \\ V_i^\varepsilon(t=0) = V_i^0 \geq 0 & i = 1, \cdots, N & \end{cases} \tag{1.1}$$

where, for $i = 0, \cdots, N$, $A_i = div(a_i(x)\nabla\cdot)$, with $a_i \in C^1(\overline{\Omega})$ is positive, and $\partial_n = \nabla \cdot \vec{n}$ denotes the normal derivative on $\partial\Omega$, and, at any position $x \in \Omega$ and instant $t \geq 0$,

- $R^\varepsilon(x,t)$ is the concentration of resource,
- $I(x) \geq 0$ is the input of substrate,
- $m_0(x) > 0$ is a natural decreasing factor modeling phenomena as sedimentation and dilution,
- $V_i^\varepsilon(x,t)$ is the concentration of the species i,
- $f_i(R)(x,t) = f_i(x, R(x,t))$ is the consumption rates of the species i on the resource R,
- $\lambda_i \in (0, +\infty)$ is the growth yield of the species i,
- $m_i(x) > 0$ is the mortality rates of the species i,
- $\frac{1}{\varepsilon} \in (0, +\infty)$ is the common diffusion rate.

The resource is the only limiting factor in this model and species interact indirectly through their respective consumption of the resource. Without spatial structure, this model is known as the well stirred chemostat which has received considerable attention [20, 27, 28, 32, 33]. In the well stirred chemostat it is known that generically, all (nonnegative) steady states are of the form $(r, u_1, \cdots, u_n)$ where at most one u_i is positive and exactly one of these steady states is stable. Under some additional assumptions on the parameters this only stable steady state is a global attractor. In other words, the competitive exclusion principle (CEP) holds: at most one species survives as $t \to +\infty$. In this perspective, our model is motivated by the following question. *Can the spatial heterogeneity permits the long term coexistence of many species.*
The influence of spatial heterogeneity in population dynamics has received considerable attention. We refer to the review of Lou [21] and references therein. Most of the time, spatial heterogeneity is considered in prey-predator system or Lotka-Volterra competing system. There is very few consideration of spatial heterogeneity in systems of species competing for a single resource.

Waltman *et al.* [19, 31] studied this kind of system for two species in one spatial dimension with $A_i = \partial_{xx}$ for $i = 0, 1, 2$ and $m_i \equiv 0$, $I \equiv 0$ with Michaelis-Menten consumption rates *independent on* x and Robin boundary conditions. Wu [34] generalized this system in any spatial dimensions and showed the existence of positive stationary solution for two species. Recently Nie and Wu [22] show uniqueness and global stability properties for this stationary solution under some technical assumptions.
The above mentioned works use strongly a monotone method which holds only for *two species* and under the additional condition that both the diffusion rates a_i *do not depend on* i. The other cases has been very little studied. Waltman *et al.* [14] treat the case of two species and different but close enough diffusion rates, by using a perturbation method. For more than two species, Baxley and Robinson [4] show the existence of a stationary solution *near a bifurcation point* for general elliptic operators $A_i - m_i$ and Michaelis-Menten type consumption functions.

Our system is slightly different from the above cited works since here, the spatial heterogeneity takes place directly on the reaction terms rather than on the boundary conditions. If a similar analysis can be done for two species in the case of operators $A_i - m_i$ which do not depend on i, this different formulation allows us to take Neumann boundary conditions. This make possible to investigate phenomena occurring when the diffusion rates $\frac{1}{\varepsilon}$ varies, in a situation wherethe operator $A_i - m_i$ are *species dependent.* Stationary solution of this system for two species and any diffusion rates has been investigated by Castella and Madec in [9] using global bifurcation methods. For any number of species, the stationary solutions has been studied by Ducrot and Madec in [13] when the diffusion rates $\frac{1}{\varepsilon}$ tends to 0. The present paper focuses on the opposite case $\frac{1}{\varepsilon} \to +\infty$ and investigates both the stationary solutions and the global dynamic.

The purpose of this article is to show that the dynamics of the system is well described by the dynamics of an associated averaged system, called aggregated system, if the diffusion rate is large enough. In particular, we show that if the CEP holds for the aggregated problem, then the CEP holds for the original problem for small enough ε. Note that the model of homogeneous chemostat is based on the assumption that the chemostat is well mixed. This study makes the validity of this assumption more precise and clarifies the parameters of the associated homogeneous problem.

Here, we investigate a fast migration problem:

$$\frac{d}{dt}\boldsymbol{W}^\varepsilon(x,t) = \mathcal{F}(x, \boldsymbol{W}^\varepsilon(x,t)) + \frac{1}{\varepsilon} K \boldsymbol{W}^\varepsilon(x,t) \tag{1.2}$$

where $\boldsymbol{W}^\varepsilon(t) := \boldsymbol{W}^\varepsilon(\cdot, t)$ is a vector with $N+1$ components both belonging to a well chosen Banach space. The demography is described by the reaction terms $\mathcal{F}(\boldsymbol{W}^\varepsilon)$ and the operator K models the spatial movements. Such a complex system, involving $N+1$ partial derivatives equations, appears naturally when one considers phenomena acting on different time scales. It is well known (see for instance, Conway, Hoff and Smoller [11], Hale and Carvalho [7] and references therein) that systems like (1.2) are well described, with an $O(\varepsilon)$ error term, by the averaged system

$$\frac{d}{dt}\boldsymbol{w}^\varepsilon(t) = \frac{1}{|\Omega|}\int_\Omega \mathcal{F}\left(x, \boldsymbol{w}^\varepsilon(t)\right) dx \text{ where } \boldsymbol{w}^\varepsilon(t) = \frac{d}{dt}\frac{1}{|\Omega|}\int_\Omega \boldsymbol{W}^\varepsilon(x,t)dx \tag{1.3}$$

as soon ε is small enough. In fact, in the case of *homogeneous* reaction-terms, the asymptotic profiles are given *exactly* by the system (1.3), while for *spatially dependent* reaction-terms, the $O(\varepsilon)$ error term remains.
Hence, we use here an alternative approach using the invariant manifold theory (see [6]) which provides precise estimates on the error between (1.3) and (1.2). These estimates are useful to describe *exactly* the long time dynamic of (1.2) for small enough ε.

Basically, the central manifold theorem allows to reduce the study of (1.2) to this of the aggregated system (1.3) involving only $N+1$ differential equations. Many authors use this approach in populations dynamics. We refer to Poggiale, Auger and Sanchez [3, 25, 26] for results on this subject in differential systems, Arino *et al* [1] for age-structured model and most recently, Castella *et al.* [8] and Sanchez *et al.* [30] in problems involving functional space.

The essential features for this approach to be valid is that the solution space $\mathcal{H}$ admits a decomposition on the form $\mathcal{H} = E \oplus F$ where $E = ker(K)$ and F is invariant under K while the real part of the spectrum of $K_{|F}$ belongs to $(-\infty, -\alpha)$ for some $\alpha > 0$. Note that such is the case for Δ with zero flux boundary conditions. Under this conditions, projecting the system S_ε on E and F and denoting X^ε and Y^ε the projections of $\boldsymbol{W}^\varepsilon$ on E and F respectivly, leads to the following "slow-fast" system

$$\begin{cases} \partial_t X^\varepsilon(t) = \mathcal{F}_0(X^\varepsilon(t), Y^\varepsilon(t)) \\ \partial_t Y^\varepsilon(t) = \mathcal{G}_1(X^\varepsilon(t), Y^\varepsilon(t)) + \frac{1}{\varepsilon} K Y^\varepsilon(t). \end{cases} . \tag{1.4}$$

Here, $X^\varepsilon \in E$ is the slow variable and $Y^\varepsilon \in F$ is the fast variable.

In essence, the central manifold theorem asserts the existence of an invariant manifold $\mathcal{M}^\varepsilon = (X^\varepsilon, h(X^\varepsilon, \varepsilon)) \in E \times F$ verifying $h(X^\varepsilon, \varepsilon) = O(\varepsilon)$ as $\varepsilon \to 0$ and attracting exponentially fast any trajectories. Thus, the complex dynamics of S_ε may be approach, up to exponentially small error term, by the dynamics reduced to $\mathcal{M}^\varepsilon$, which is described by only $N+1$ differential equations rather than $N+1$ partial differential equations. This reduced system reads shortly

$$\begin{cases} \frac{d}{dt} X^\varepsilon(t) = \mathcal{F}_0(X^\varepsilon, h(X^\varepsilon, \varepsilon)) \\ Y^\varepsilon(t) = h(X^\varepsilon, \varepsilon), \end{cases} . \tag{1.5}$$

Generaly, the central manifold $\mathcal{M}^\varepsilon$ can not be explicitly computed. Explicit approximations of $h(x, \varepsilon)$ can though be computed at any order ε^l. This allows to describe the dynamic of the reduced system up to an additional polynomial small error term of order ε^{l+1}. In this works, we concentrate our study on the order 0 reduced system, called the aggregated system, which reads

$$\frac{d}{dt} X^{\varepsilon,[0]}(t) = \mathcal{F}_0(X^{\varepsilon,[0]}, 0),\ Y^{\varepsilon,[0]}(t) = h(X^{\varepsilon,[0]}(t), \varepsilon). \tag{1.6}$$

Explicit calculation shows that the system (1.6) is a simple homogeneous chemostat system. It follows that long time behavior of its solutions is completely known for a large choice of function $\mathcal{F}_0$. The aim of this work is to transfer qualitative properties of (1.6) to the original system S_ε.

This article is organized as follow. In the second section, we precise the assumptions on the model and we state a theorem assuring the existence and uniqueness of classical solutions which are uniformly bounded independently on t and ε. We then restate the system on a slow-fast form allowing to apply the central manifold theorem. In the end of the second section, we state our two main results: Theorems 2.7 and 2.10. In the third section, we beging to state the central manifold Theorem 3.1 and a Theorem describing the exponential convergence towards the central manifold 3.2. Next, we use these two Theorems to prove several general results on slow-fast systems. In the fourth section, we use these general results to prove the Theorems 2.7 and 2.10. The main result (Theorem 2.10) states that, if the CEP holds for the aggregated system, then it holds for the original system too, for small enough ε. Hence, only one species can win the competition, namely the best competitor in average. This best competitor in average can be explicitly computed. In the fith section, we discuss through some examples three important phenomena determining which species is the best competitor in averaged. These phenomena give good informations on how a heterogeneous environment may promote the coexistence for an intermediate diffusion rate. The sixth section concludes the paper.

2 Model and main results

2.1 The model

First, by denoting $U_i^\varepsilon(x,t) = \lambda_i^{-1} V_i^\varepsilon(x,t)$ we see that $(R^\varepsilon, V_1^\varepsilon, \cdots, V_N^\varepsilon)(x,t)$ is a solution of the system (1.1) if and only if $(R^\varepsilon, U_1^\varepsilon, \cdots, U_N^\varepsilon)(x,t)$ is a solution of

$$S_\varepsilon : \begin{cases} \dfrac{d}{dt} R^\varepsilon(x,t) = I(x) - \displaystyle\sum_{i=1}^N f_i(x, R^\varepsilon(x,t)) U_i^\varepsilon - m_0(x) R^\varepsilon(x,t) + \dfrac{1}{\varepsilon} A_0 R^\varepsilon(x,t) & & \text{on } \Omega \\ \dfrac{d}{dt} U_i^\varepsilon(x,t) = (f_i(x, R^\varepsilon(x,t)) - m_i(x)) U_i^\varepsilon(x,t) + \dfrac{1}{\varepsilon} A_i U_i^\varepsilon(x,t) & i = 1, \cdots, N & \text{on } \Omega \\ \partial_n R^\varepsilon(x,t) = 0 & & \text{on } \partial\Omega \\ \partial_n U_i^\varepsilon(x,t) = 0 & i = 1, \cdots, N & \text{on } \partial\Omega \\ R^\varepsilon(x,0) \geq 0 & & \\ U_i^\varepsilon(x,0) \geq 0 & i = 1, \cdots, N & . \end{cases}$$

This system can be shortly written as

$$\begin{cases} \frac{d}{dt} \boldsymbol{W}^\varepsilon(x,t) = \mathcal{F}(x, \boldsymbol{W}^\varepsilon(x,t)) + \frac{1}{\varepsilon} K \boldsymbol{W}^\varepsilon(x,t) & t > 0 \text{ et } x \in \Omega, \\ \partial_n(\boldsymbol{W}^\varepsilon)(x,t) = 0, & t > 0 \text{ et } x \in \partial\Omega \\ \boldsymbol{W}^\varepsilon(x,0) = \left(R^0(x), U_1^0(x), \cdots, U_N^0(x)\right), & x \in \Omega \end{cases} \tag{2.7}$$

where

- $\boldsymbol{W}^\varepsilon(x,t) = (R^\varepsilon(x,t), U_1^\varepsilon(x,t), .., U_n^\varepsilon(x,t))^T$,
- $\mathcal{F}(x, \boldsymbol{W}^\varepsilon(x,t)) = \begin{pmatrix} I(x) - m_0(x) R^\varepsilon(x,t) - \displaystyle\sum_{i=1}^N U_i^\varepsilon(x,t) f_i(x, R^\varepsilon(x,t)) \\ \left(f_1(x, R^\varepsilon(x,t)) - m_1(x)\right) U_1^\varepsilon(x,t) \\ \vdots \\ \left(f_N(x, R^\varepsilon(x,t)) - m_N(x)\right) U_N^\varepsilon(x,t) \end{pmatrix}$,
- $K = diag(A_i)$.

In the sequel, the *same* symbol $\mathcal{F}$ is used to refer to the Nemitski operator $\boldsymbol{W} \mapsto \mathcal{F}(\boldsymbol{W})$ where

$$\mathcal{F}(\boldsymbol{W})(x) = \mathcal{F}(x, \boldsymbol{W}(x)).$$

Remark 2.1 *All the results of this works hold true for any uniform elliptic operators A_i, or integral operators verifying some property (see [8]). One can also investigate gradostat-like models by taking $\Omega = \{1, \cdots, P\}$ and $A_i \in \mathbb{R}^{P \times P}$ an irreducible matrix with nonnegative off diagonal entries such that the sum of each column is 0. The results proved here hold as well in this case.*

In the sequel, we make the two following assumptions insuring that the system S_ε admits an unique global classical positive solution which is uniformly bounded in $C^0\left(\overline{\Omega}\right)$.

Assumption 2.2 (Assumption on the parameters)

- *$I \in C^1(\overline{\Omega}, \mathbb{R}^+)$ and $I \not\equiv 0$.*
- *For $i = 0, \cdots, N$, $m_i \in C^1(\overline{\Omega})$ and $m_i(x) > 0$.*
- *For $i = 0, \cdots, N$, $a_i \in C^1(\overline{\Omega})$ and for all $x \in \overline{\Omega}$, we have $a_i(x) > 0$.*

The assumption $I \not\equiv 0$ means that there is always an input of resource in the system. If $I \equiv 0$, then $(0, \cdots, 0) \in \mathbb{R}^{N+1}$ is a global attractor and the problem is trivial.

Assumption 2.3 (Assumptions on the consumption functions) *For each $i = 1, \cdots, N$, we assume*

- *$\forall R \in \mathbb{R}^+$, $f_i(\cdot, R) : x \mapsto f_i(x, R)$ belongs to $C^1(\overline{\Omega})$ and take values in $\mathbb{R}^+$,*
- *$\forall x \in \Omega$, $f_i(x, \cdot) : R \mapsto f_i(x, R)$ belongs to $C^1(\mathbb{R}^+)$ and is increasing. Moreover, $R \mapsto D_R f_i(x, R)$ is locally Lipschitz.*
- *$\forall x \in \Omega$, $f_i(x, 0) = 0$.*

Remark 2.4 *The monotonicity of $R \mapsto f_i(x,R)$ is not fundamental in our analysis. Indeed, our results hold true if $\int_\Omega f_i(x,r)dx = \int_\Omega m_i(x)dx$ has at most one solution r_i^* and if the conclusions of the proposition 2.9 are verified. However, in order to avoid technical difficulties, we restrict ourself to the case of increasing consumption functions.*

It is classical that the system S_ε conserves the positive quadrant and admits an unique solution for a time τ small enough. Moreover, the maximum principle implies that R^ε verifies for any $t > 0$ the uniform bound $\|R^\varepsilon(\cdot,t)\| \leq M$ for some $M > 0$ independent of the time t. It follows, using standard results on parabolic systems (see [15, 23]), that the solution is well defined and classical globally in time. Finally, it can be proven by a L^p estimates method[1] (Hollis *et al.* [16]), that the system S_ε admits a unique classical positive solution which is uniformly bounded in time in $\left(C^0(\overline{\Omega})\right)^{N+1}$. More precisely, the following theorem[2] holds (see [29] chapter III for this specific case).

Theorem 2.5 *Assume that $W^\varepsilon(0) \in (C^0(\overline{\Omega}))^{N+1}$ is nonnegative. For each $\varepsilon > 0$, the system S_ε admits an unique solution $\boldsymbol{W}^\varepsilon = (R^\varepsilon, U_1^\varepsilon, .., U_N^\varepsilon) \in C^1\left(]0,+\infty[; (C^0(\overline{\Omega}))^{N+1}\right)$ which is nonnegative. Moreover, for each $\varepsilon_0 > 0$ and $\varepsilon \in (0,\varepsilon_0)$, there exists a constant $M(\varepsilon_0)$ independent on t and ε such that*

$$\|R^\varepsilon(\cdot,t)\|_\infty + \sum_{i=1}^N \|U_i^\varepsilon(\cdot,t)\|_\infty \leq M(\varepsilon_0).$$

Armed with this Theorem, we are in position to analyze the asymptotic behavior of the dynamic of S_ε as $\varepsilon \to 0$.

2.2 Slow Fast Form

When seen as an operator on $L^2(\Omega)$, the operator $A_i^2 := div(a_i(x)\nabla\cdot)$ with homogeneous Neumann boundary conditions is defined as

$$D(A_i^2) := \left\{U \in H^1(\Omega)\ \exists V \in L^2(\Omega),\ \forall \phi \in H^1(\Omega),\ \int_\Omega a_i(x)\nabla U(x)\nabla\phi(x)dx = -\int_\Omega V(x)\phi(x)\right\}.$$

$$A_i^2 U := V,\ \forall U \in D(A_i^2).$$

In order to obtain uniform estimates, we prefer to focus on the operator $A_i^\infty := div(a_i(x)\nabla\cdot)$ when acting on the set of continuous function $(C^0(\overline{\Omega}), \|\cdot\|_\infty)$ where $\|f\|_\infty = \sup_{x\in\overline{\Omega}}(|f(x)|)$. Hence, we define

$$D(A_i^\infty) = \left\{U \in D(A_i^2) \cap C^0(\overline{\Omega}),\ A_i^2 U \in C^0(\overline{\Omega})\right\},$$

$$A_i^\infty U = A_i^2 U,\ \forall U \in D(A_i^\infty)$$

We have

$$ker(A_i^\infty) = span(1) = \mathbb{R} \text{ and } \widetilde{F} := Im(A_i^\infty) = \left\{U \in C^0(\overline{\Omega}),\ \int_\Omega U = 0\right\}.$$

One gets clearly $C^0(\overline{\Omega}) = ker(A_i^\infty) \oplus Im(A_i^\infty)$. Now, we define the Banach space $\left(C^0(\overline{\Omega})\right)^{N+1}$ together with the norm

$$\|(U_0, \cdots, U_N)\|_\infty = \sum_{i=0}^N \|U_i\|_\infty.$$

and the operator $K^\infty = diag(A_i^\infty)$ acting on $\left(C^0(\overline{\Omega})\right)^{N+1}$. The Kernel and the range of K^∞ are respectively[3]

$$E := ker(K^\infty) = \mathbb{R}^{N+1} \text{ and } F := Im(K^\infty) = \widetilde{F}^{N+1}.$$

The spaces E and F are cleary two complete subspaces of $\left(C^0(\overline{\Omega})\right)^{N+1}$ and one has

$$\left(C^0(\overline{\Omega})\right)^{N+1} = E \oplus F.$$

[1]The key to apply this method is as follows. 1. There is a L^1 control on the solutions uniformly in time $\|\boldsymbol{W}^\varepsilon(\cdot,t)\|_1 \leq C$. 2. The system has a particular structure. For our system, the system is triangular since the U_i^ε are coupled indirectly through R^ε. 3. There is a uniform bound for a (well chosen) component of $\boldsymbol{W}^\varepsilon$. Here, $\|R^\varepsilon(\cdot,t)\| \leq M$.

[2]The theorem 2.5 holds true with an initial condition $W^\varepsilon(0) \in (L^\infty(\Omega))^{N+1}$. However, since $W^\varepsilon(t)$ belongs to $\left(C^0(\overline{\Omega})\right)^{N+1}$ for any $t > 0$, one reduce ourself to the case of continuous initial data. This will simplify the statement of the main results. Finally, the solution is more regular since $\boldsymbol{W}^\varepsilon \in C^1((0,+\infty), W^{2,p})$ for any $p > 1$.

[3]In the case of most general operator (see remark 2.1), one has $ker(A_i^\infty) = span(\phi_i)$ for some positive function ϕ_i and $\widetilde{F}_i = ker(A_i)^\perp$. For the sake of simplicity we reduce ourself to the case of operator A_i^∞ s.t. $\phi_i = 1$ and $\widetilde{F}_i = span(1)^\perp$ do not depends on i.

The projections of $\left(C^0(\overline{\Omega})\right)^{N+1}$ on E and F, denoted by Π_E and Π_F respectively, are given explicitly by

$$\Pi_E(V_0,\cdots,V_N)=\frac{1}{|\Omega|}\left(\int_\Omega V_0,\cdots,\int_\Omega V_N\right) \text{ and } \Pi_F=I_d-\Pi_E.$$

The restrictions of the norm $\|\cdot\|_\infty$ on E and F are noted respectivly

$$\|(u_0,\ldots,u_N)\|_E=\sum_{i=0}^N|u_i|,\qquad \|(U_0,\ldots,U_N)\|_F=\sum_{i=0}^N\|U_i\|_\infty.$$

Finally, let us define the norm $\|\cdot\|_{E\times F}$ on the Banach space $E\times F$ by

$$\forall(u,V)\in E\times F,\quad \|(u,V)\|_{E\times F}=\|u\|_E+\|V\|_F.$$

One verifies easily that the map $E\times F\to\left(C^0(\overline{\Omega})\right)^{N+1}=E\oplus F\ :\ (u,v)\mapsto u+v$ defines an isomorphism between the banach spaces $(E\times F,\|\cdot\|_{E\times F})$ and $\left(\left(C^0(\overline{\Omega})\right)^{N+1},\ \|\cdot\|_\infty\right)$. Thus, it is equivalent to obtain estimates on $E\times F$ and on $\left(C^0(\overline{\Omega})\right)^{N+1}$.

The above considerations permits to restate the system S_ε on an equivalent "slow-fast" form by projecting S_ε on E and F respectivly. Let $\boldsymbol{W}^\varepsilon(t)$ be a solution of S_ε. The slow variable $X^\varepsilon:=\Pi_E(\boldsymbol{W}^\varepsilon)\in E$ is the vector of the mean mass of resource and species. More precisely,

$$X^\varepsilon=\left(\frac{1}{|\Omega|}\int_\Omega R^\varepsilon,\frac{1}{|\Omega|}\int_\Omega U_1^\varepsilon,..,\frac{1}{|\Omega|}\int_\Omega U_N^\varepsilon\right)\in\mathbb{R}^{N+1}.$$

The fast variable is simply $Y^\varepsilon:=\Pi_F\boldsymbol{W}^\varepsilon=\boldsymbol{W}^\varepsilon-X^\varepsilon\in F$.
Furthermore, thanks to the boundary conditions, we have $\Pi_E(K^\infty\boldsymbol{W}^\varepsilon)=0$ and $\Pi_F(K^\infty\boldsymbol{W}^\varepsilon)=K^\infty\Pi_F\boldsymbol{W}^\varepsilon=KY^\varepsilon$ where we have note $K:=K^\infty_{|F}$ the restriction of K^∞ to F.
Projecting the system S_ε on E and F yields to the equivalent system

$$\left(S_\varepsilon^{sf}\right)\ :\quad\begin{cases}\frac{d}{dt}X^\varepsilon(t)=\mathcal{F}_0(X^\varepsilon,Y^\varepsilon)\\ \frac{d}{dt}Y^\varepsilon(t)=\mathcal{G}_1(X^\varepsilon,Y^\varepsilon)+\frac{1}{\varepsilon}KY^\varepsilon\\ \partial_nX^\varepsilon=0\\ \partial_nY^\varepsilon=0\\ X^\varepsilon(0)=\Pi_E(\boldsymbol{W}(0))\\ Y^\varepsilon(0)=\Pi_F(\boldsymbol{W}(0))\end{cases}$$

where $\mathcal{F}_0(X^\varepsilon,Y^\varepsilon)=\Pi_E\mathcal{F}(X^\varepsilon+Y^\varepsilon)$ and $\mathcal{G}_1(X^\varepsilon,Y^\varepsilon)=\mathcal{F}(X^\varepsilon+Y^\varepsilon)-\mathcal{F}_0(X^\varepsilon,Y^\varepsilon)$.

In its slow-fast form, the system describes on the one hand the *slow* dynamics on the kernel E of K^∞, and on the other hand the *fast* dynamics on the orthogonal F of E. These two dynamics are coupled which results in complex dynamics of S_ε^{sf}. However, this complex dynamics may be completly understood using the central manifold theory.

Basically (see section 3.1 for a precise statement), this theory asserts that there exists a manifold $\mathcal{M}^\varepsilon=\{(x,h(x,\varepsilon)),\ x\in E\}\in E\times F$ which is invariant for S_ε^{sf}. It verifies moreover $h(x^\varepsilon,\varepsilon)=O(\varepsilon)$ and $\mathcal{M}^\varepsilon$ attracts any trajectory exponentially fast in time. The system on $\mathcal{M}^\varepsilon$ reads

$$\left(S_\varepsilon^{[\infty]}\right),\quad \frac{d}{dt}X^{\varepsilon,[\infty]}(t)=\mathcal{F}_0(X^{\varepsilon,[\infty]}(t),h(X^{\varepsilon,[\infty]}(t),\varepsilon)),\ Y^{\varepsilon,[\infty]}(t)=h(X^{\varepsilon,[\infty]}(t),\varepsilon).\tag{2.8}$$

Since $h(x^\varepsilon,\varepsilon)=O(\varepsilon)$ as $\varepsilon\to0$, one obtains the following system, as a first approximation.

$$\left(S_\varepsilon^{[0]}\right),\quad \frac{d}{dt}X^{[0]}(t)=\mathcal{F}_0(X^{[0]}(t),0),\ Y^{\varepsilon,[0]}(t)=h(X^{\varepsilon,[0]}(t),\varepsilon).\tag{2.9}$$

An important fact in the sequel is that the dynamic of $S_\varepsilon^{[\infty]}$ is completely determined by its first equation: the following $O.D.E$ system

$$\left(S_\varepsilon^c\right),\quad \frac{d}{dt}X^{\varepsilon,[\infty]}(t)=\mathcal{F}_0(X^{\varepsilon,[\infty]}(t),h(X^{\varepsilon,[\infty]}(t),\varepsilon))\tag{2.10}$$

In many cases, S_ε^c can be seen as a *regular perturbation* of the first equation of $S_\varepsilon^{[0]}$, that is

$$\left(S_0^c\right),\quad \frac{d}{dt}X^{[0]}(t)=\mathcal{F}_0(X^{[0]}(t),0)\tag{2.11}$$

2.3 Main results

The general strategy to prove our results is as follow.
When S_ε^c can be seen as a regular perturbation of S_0^c, many properties of S_0^c can be transfer to S_ε^c which infers properties of $S_\varepsilon^{[\infty]}$. The system $S_\varepsilon^{[\infty]}$ is exaclty the slow-fast system S_ε^{sf} reduced to the invariant manifold $\mathcal{M}_\varepsilon$. Since $\mathcal{M}_\varepsilon$ attracts exponentially fast in time any trajectectory of $S_\varepsilon^{[sf]}$, many properties of $S_\varepsilon^{[\infty]}$ yield properties for $S_\varepsilon^{[sf]}$ which is equivalent to the original system S_ε. This strategy may be summarized as follow.

$$\boxed{S_0^c} \xrightarrow[\text{perturbation}]{\text{regular}} \boxed{S_\varepsilon^c} \leftrightarrow \boxed{S_\varepsilon^{[\infty]}} \xrightarrow[\text{of } \mathcal{M}_\varepsilon]{\text{fast attraction}} \boxed{S_\varepsilon^{[sf]}} \leftrightarrow \boxed{S_\varepsilon}$$

The essential difficulties in the proofs appear in transfering some properties from $S_\varepsilon^{[\infty]}$ to $S_\varepsilon^{[sf]}$. This part uses strongly theorem 3.2.

In order to apply the above mentioned strategy, the first step is to study S_0^c. In the case of our system, S_0^c reads explicitly

$$\begin{cases} \frac{d}{dt} r = \widetilde{I} - \widetilde{m_0} r - \sum\limits_{i=1}^{N} \widetilde{f}_i(r) u_i, \\ \frac{d}{dt} u_i = \left(\widetilde{f}_i(r) - \widetilde{m_i} \right) u_i, \ i = 1, \cdots, N. \end{cases} \tag{2.12}$$

where $\widetilde{I} = \frac{1}{|\Omega|} \int_\Omega I(x)dx$, $\widetilde{m_0} = \frac{1}{|\Omega|} \int_\Omega m_0(x)dx$ and for $1 \le i \le N$,

$$\widetilde{m_i} = \frac{1}{|\Omega|} \int_\Omega m_i(x)dx \ \text{ and } \ \widetilde{f}_i(r) = \frac{1}{|\Omega|} \int_\Omega f_i(x,r)dx.$$

One defines $r_0^* = \widetilde{I}/\widetilde{m_0}$. For any $i \in \{1, \cdots, N\}$, since $f_i(x, \cdot)$ is increasing, $\widetilde{f}_i(\cdot)$ is an increasing function and one may define the number r_i^* as shown in the figure 1.

$$r_i^* = \begin{cases} \widetilde{f}_i^{-1}(\widetilde{m_i}) & \text{if } \lim\limits_{r \to +\infty} \widetilde{f}_i(r) > \widetilde{m_i}, \\ +\infty \text{ else.} \end{cases}$$

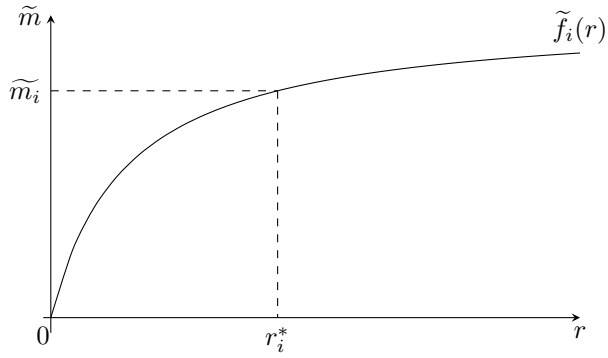

Figure 1: Definition of r_i^*.

The nonnegative stationary solutions of S_0^c are well known and are described in the following proposition.

Proposition 2.6 (Stationnary solutions of the aggregated system S_0^c (see [28])) *Under the assumptions 2.2 and 2.3,we have.*

(i) The system S_0^c always admits the stationary solution $p_0^* = (r_0^*, 0, \cdots, 0)$. This solution is hyperbolic[4] if $r_0^* \neq r_i^*$ for any $i \ge 1$.
If moreover $r_0^* < r_i^*$ for all $i \ge 1$. Then p_0^* is the only nonnegative stationary solution of S_0^c and is (linearly) asymptotically stable[5].

(ii) Let $i \in \{1, \cdots, N\}$ and suppose that $r_i^* < r_0^*$ and $r_i^* \neq r_j^*$ for all $j \in \{1, \cdots, N\} \setminus \{i\}$. Then the system S_0^c has one non-negative stationary solution

$$p_i^* = (r_i^*, 0, \cdots, 0, u_i^*, 0, \cdots, 0) \quad \text{where } u_i^* = \frac{\widetilde{m_0}}{\widetilde{m_i}} (r_i^* - r_0^*) > 0.$$

Moreover, this solution is hyperbolic and is asymptoticaly stable if $r_i^* < r_j^*$ for all $j \in \{0, \cdots, N\} \setminus \{i\}$ and unstable else.

[4]That is, 0 is not an eigenvalue of $D_X \mathcal{F}_0(X^*, 0)$.
[5]An hyperbolic solution X^* is say to be (linearly) asymptotically stable (resp. unstable) if the real part of all the eigenvalue of $D_X \mathcal{F}_0(X^*, 0)$ is negative (resp. if the real part of almost one eigenvalue is positive). In the sequel, we do not precise (linearly).

(iii) Suppose that $r_i^* \neq r_j^*$ for all $i \neq j$ and $r_i^* < r_0^*$ for all $i \geq 1$. Then the system S_0^c has exactly $N+1$ non-negative stationary solutions: p_i^*, $i = 0, \cdots, N$. Moreover, all these solutions are hyperbolic and exactly one of these is stable: $p_{i_0}^*$ where $r_{i_0}^* = \min\{r_0^*, \cdots, r_N^*\}$.

The knowledge of the stationary solutions of S_0^c permits to completely describe the stationary solutions of S_ε. This yields our firth main result, which is proved in section 4.

Theorem 2.7 (Stationary solutions of the original system S_ε) *There exist two positive scalars ε_0 and C such that for all $\varepsilon \in (0, \varepsilon_0)$ the following holds.*

(i) Suppose that $r_0^* < r_i^*$ for all $i \geq 1$. Then the system S_ε has only one nonnegative stationary solution $W_0^\varepsilon(x) = (R_0^\varepsilon(x), 0, \cdots, 0)$ which is hyperbolic and stable and verifies,

$$\|R_0^\varepsilon(\cdot) - r_0^*\|_\infty \leq C\varepsilon.$$

(ii) Let $i \in \{1, \cdots, N\}$ and suppose that $r_i^* < r_0^*$ and $r_i^* \neq r_j^*$ for all $j \in \{1, \cdots, N\} \setminus \{i\}$. Then the system S_ε has (at least) one non-negative stationary solution

$$W_i^\varepsilon(x) = (R_i^\varepsilon(x), 0, \cdots, 0, U_i^\varepsilon(x), 0, \cdots, 0) \text{ which verifies } \|R_i^\varepsilon(\cdot) - r_i^*\|_\infty + \|U_i^\varepsilon(\cdot) - u_i^*\|_\infty \leq C\varepsilon.$$

Moreover, W_i^ε is hyperbolic and is stable if $r_i^* < r_j^*$ for all $j \in \{0, \cdots, N\} \setminus \{i\}$ and unstable else.

(iii) Suppose that $r_i^* \neq r_j^*$ for all $i \neq j$ and $r_i^* < r_0^*$ for all $i \geq 1$. Then the system S_ε has exactly $N+1$ non-negative stationary solutions: $W_i^\varepsilon(x)$, $i = 0, \cdots, N$. Moreover, all these solutions are hyperbolic and exactly one of them is stable: $W_{i_0}^\varepsilon$ where $r_{i_0}^* = \min\{r_0^*, \cdots, r_N^*\}$.

If in addition, the global dynamics of S_0^c is known, then so is the global dynamics of S_ε. The system S_0^c being a homogeneous chemostat model, for a large choice of functions $\widetilde{f}_i$, it verifies the Competitive Exclusion Principle (CEP).
More precisely, it is known that if $r_i^* > r_0^*$ then $u_i(t) \to 0$ as $t \to +\infty$, therefore if $r_0^* < r_i^*$ for all $i \geq 1$, then the only steady state $(r_0^*, 0, \cdots, 0)$ of S_0^c is a global attractor (in the nonnegative cadrant $\mathbb{R}_+^{N+1}$).
If for some $i \geq 1$ one has $r_i^* < r_0^*$ then the global dynamics of S_0^c is known under some additional assumptions. Here, we make the following assumption on S_0^c which is sufficient[6] to ensure that S_0^c satisfies the CEP.

Assumption 2.8 *One assumes that $\widetilde{f}_i$ is increasing and that either*

(i) For each $i \in \{1, \cdots, N\}$ one has $\widetilde{m_i} = \widetilde{m_0} > 0$.

(ii) For each $i \in \{1, \cdots, N\}$, $\widetilde{f}_i$ reads $\widetilde{f}_i(r) = c_i f(r)$ for some (increasing) function f and positive constant c_i.

(iii) For each $i \in \{1, \cdots, N\}$, $\widetilde{f}_i$ reads $\widetilde{f}_i(r) = \frac{c_i r}{k_i + r}$ for some positive constants c_i and k_i.

Under this assumption, the asymptotic dynamics of S_0^c (and all its sub-systems) are known in the following sense (see [28] for a proof).

Proposition 2.9 (CEP for the aggregated system S_0^c (see [28])) *Assume that the assumption (2.8) holds true. Let $(r(t), u_1(t), \cdots, u_N(t))$ be a solution of S_0^c with nonnegative initial conditions.*
Define the set $J = \{0\} \cup \{j \in \{1, \cdots, N\},\ u_j(0) > 0,\ r_j^* < r_0^*\}$ and the number $\widehat{r} = \min_{j \in J}(r_j^*)$. We have

(i) $\lim_{t \to +\infty} r(t) = \widehat{r}$ and $\forall i \notin J$, $\lim_{t \to +\infty} u_i(t) = 0$.

(ii) In particular, if $J = \{0\}$ then $p_0^* := (r_0^*, 0, \cdots, 0)$ is a global attractor in $\mathbb{R}_+^{N+1}$.

(iii) If for some $j_1 \in J \setminus \{0\}$ one has $r_{j_1}^* < r_j^*$ for any $j \in J \setminus \{j_1\}$ then

$$\lim_{t \to +\infty} u_{j_1}(t) = \frac{\widetilde{m_0}}{\widetilde{m_{j_1}}}\left(r_0^* - r_{j_1}^*\right) \text{ and } \lim_{t \to +\infty} u_j(t) = 0,\ \forall j \in J \setminus \{0, j_1\}$$

[6] The proposition 2.9 holds true under more general hypothesis, see the monograph of Smith and Waltmann [28]. Indeed, a well known conjecture asserts that the CEP holds true under the simpler hypothesis of monotonicity of the functions f_i. This result is proven for equal mortalities in Amstrong and McGehee [2] (1980). In the case of different mortalities, this result is proven using Lyapunov functionals when the functions $\widetilde{f}_i$ verify some additional assumption. We refers to Hsu [18] (1978), Wolkowicz and Lu [32] (1992), Wolkowicz and Xia [33] (1997) and Li [20] (1998) for historical advances on this topic. See also Sari and Mazenc [27] (2011) for recent results on this subject.

Note that, from the assumption 2.3, $\widetilde{f}_i$ is increasing. In practice, one has to compute the functions $\widetilde{f}_i$ explicitly to verify the assumption 2.8. Here are some explicit examples ensuring that the assumption 2.8 holds true.

(i) Assume that $m_i(x) = m_0(x)$ for any $x \in \Omega$. Then the case (i) of the assumption 2.8 occurs.

(ii) Assume that $f_i(x, R) = C_i(x)f(R)$ for some smooth positive functions $C_i : \Omega \to \mathbb{R}^+$ and $f : \mathbb{R}_+ \to \mathbb{R}_+$. Then

$$\widetilde{f}_i(r) = c_i f(r), \quad \text{where } c_i = \frac{1}{|\Omega|}\int_\Omega C_i(x)dx$$

and the case (ii) of the assumption 2.8 occurs.

(ii') Assume that for each $i \geq 2$, $f_i(x, R) = c_i f_1(x, R)$ for some positive constant c_i. Then $\widetilde{f}_i(r) = c_i \widetilde{f}_1(r)$ and the case (ii) of the assumption 2.8 occurs.

(iii) Assume that $f_i(R, x) = \frac{C_i(x)R}{k_i+R}$ where k_i is a positive constant. Then

$$\widetilde{f}_i(r) = \frac{c_i r}{k_i + r} \quad \text{where } c_i = \frac{1}{|\Omega|}\int_\Omega C_i(x)dx$$

and the cases (iii) of the assumption 2.8 occurs.

Now, we are in position to state our main result. Let us denote the non-negative cadrant of $\left(C^0(\overline{\Omega})\right)^{N+1}$ by

$$Q = \left\{V(\cdot) \in C^0(\overline{\Omega}),\ V(x) \geq 0,\ \forall x \in \overline{\Omega}\right\}^{N+1}.$$

Thanks to the crucial uniform boudedness result (theorem 2.5), one obtains the global dynamics in Q for small ε.

Theorem 2.10 (CEP for the original system S_ε) *Assume that the assumptions (2.2) and (2.3) hold true. For each i, denote $\boldsymbol{W}_i^\varepsilon(x)$ the stationary solution of S_ε as defined in the Theorem 2.7. There exists $\varepsilon_0 > 0$ such that for all $\varepsilon \in (0, \varepsilon_0)$ and initial data $\boldsymbol{W}^\varepsilon(\cdot, 0) \in Q$, one has the following properties.*

(i) Let $i \in \{1, \cdots, N\}$. If $r_i^* > r_0^*$ then $\lim\limits_{t\to\infty} \|U_i^\varepsilon(\cdot, t)\|_\infty = 0$.

(ii) Assume that $r_0^* < r_i^*$ for all $i \geq 1$. Then every solution $\boldsymbol{W}^\varepsilon(x, t)$ of S_ε verifies

$$\lim_{t\to+\infty} \|\boldsymbol{W}^\varepsilon(\cdot, t) - \boldsymbol{W}_0^\varepsilon(\cdot)\|_\infty = 0.$$

(iii) Assume that $r_1^* < r_i^*$ for all $i \neq 1$ and that the assumption 2.9 holds. Then every solution $\boldsymbol{W}^\varepsilon(x, t)$ of S_ε with nonnegative initial data verifying $U_1^\varepsilon(x, 0) > 0$ for some $x \in \Omega$ verifies

$$\lim_{t\to+\infty} \|\boldsymbol{W}^\varepsilon(\cdot, t) - \boldsymbol{W}_1^\varepsilon(\cdot)\|_\infty = 0.$$

3 General results for slow-fast system

In this section we state precisly the Central manifold Theorem 3.1 and the Theorem of convergence towards the central manifold 3.2. These theorems may be proved following [8]. Next, we state and prove two general results for fast-slow systems: propositions 3.7 and 3.8. These propositions are used in section 4 to prove the Theorems 2.7 and 2.10.

3.1 Central Manifold Theorem

Let us begin by a version of the central manifold Theorem used in this paper. This Theorem claims the existence of an invariant manifold for the slow-fast system which allows to defined several reduced systems.

Theorem 3.1 (Central manifold Theorem) *Let E and F be two Banach spaces. Define $\mathcal{F}_0(X, Y) \in C^1(E\times F; E)$ and $\mathcal{G}_0(X, Y) \in C^1(E \times F; F)$. One assumes that $\mathcal{F}_0$ and $\mathcal{G}_1$ are uniformly bounded as well than there first derivatives. Let K be an operator with domain $\mathcal{D}(K) \subset F$. One assumes that K generates an analytical semi-group $exp(tK)$ of linearly operators on F and that there exists $\mu > 0$ such that*

$$\forall t \geq 0, \quad \forall \varepsilon \in (0, 1], \quad \left\| exp\left(\frac{t}{\varepsilon}K\right) Y \right\|_F \leq C\|Y\|_F exp\left(-\mu\frac{t}{\varepsilon}\right).$$

For all initial condition $(x_0, y_0) \in E \times F$ and, for all $\varepsilon \in (0,1]$, on defines $X^\varepsilon(t, x_0, y_0) \equiv X^\varepsilon(t)$ and $Y^\varepsilon(t, x_0, y_0) \equiv Y^\varepsilon(t)$ the solution, for $t \geq 0$, of the differential system

$$S_\varepsilon^{sf} \quad \begin{cases} \frac{d}{dt} X^\varepsilon(t) = \mathcal{F}_0(X^\varepsilon(t), Y^\varepsilon(t)), \\ \frac{d}{dt} Y^\varepsilon(t) = \mathcal{G}_1(X^\varepsilon(t), Y^\varepsilon(t)) + \frac{1}{\varepsilon} K Y^\varepsilon(t) \\ X^\varepsilon(0) = x_0, \quad Y^\varepsilon(0) = y_0. \end{cases}$$

Then, there exists $\varepsilon_0 > 0$ such that, for all $\varepsilon \in (0, \varepsilon_0)$, the system S_ε^{sf} admit a central manifold $\mathcal{M}^\varepsilon$ in the following sense.

There exists a function $h(X, \varepsilon) \in C^1(E \times [0, \varepsilon_0]; F)$ such that, for all $\varepsilon \in]0, \varepsilon_0]$, the set $\mathcal{M}^\varepsilon = \{(X, h(X, \varepsilon)); X \in E\}$ is invariant under the semi flow generated by S_ε^{sf} for $t \geq 0$. Moreover,

$$\|h(\cdot, \varepsilon)\|_{L^\infty(E,F)} = O(\varepsilon) \text{ as } \varepsilon \to 0.$$

This Theorem provides the existence of a manifold $\mathcal{M}^\varepsilon$ which is invariant for the system S_ε^{sf} and parametrized by the slow variable $X^\varepsilon \in E$. In our application, E is finite dimensional so that the system *on* $\mathcal{M}_\varepsilon$ is a finite dimensional system. After showing that the solutions are close to the central manifold, up to an exponentially small error term, we can reduce the study to a system *on* the invariant manifold $\mathcal{M}^\varepsilon$. This finite dimensional system approach, in a sense that we specify below, the original problem.
More precisely, let us define the following reduced system. We do not precise the initial data at this step.

$$\left(S_\varepsilon^{[\infty]}\right) \quad \frac{d}{dt} X^{\varepsilon,[\infty]}(t) = \mathcal{F}_0(X^{\varepsilon,[\infty]}(t), h(X^{\varepsilon,[\infty]}(t), \varepsilon)), \quad Y^{\varepsilon,[\infty]}(t) = h(X^{\varepsilon,[\infty]}(t), \varepsilon)$$

When the original data lies on this manifold, $S_\varepsilon^{[\infty]}$ describes the exact dynamics of S_ε^{sf}. In general $Y^\varepsilon(0) \neq h(X^\varepsilon(0), \varepsilon)$ and the real solutions do not belong to $\mathcal{M}^\varepsilon$. However, the next theorem state that, up to slightly modify the initial datum, the solution of S_ε^{sf} are exponentially close to the solution of $S_\varepsilon^{[\infty]}$.

The exact calculation of the cental manifold is usually out of reach. A practical idea is to make approximate calculations. Theorem 3.1 ensures that $h(X, \varepsilon) = O(\varepsilon)$. So, as a first approximation[7], $h(X, \varepsilon) \approx 0$ and we obtain the following reduced system

$$\left(S_\varepsilon^{[0]}\right) \quad \frac{d}{dt} X^{\varepsilon,[0]}(t) = \mathcal{F}_0(X^{\varepsilon,[0]}(t), 0), \quad Y^{\varepsilon,[0]}(t) = h(X^{\varepsilon,[0]}(t), \varepsilon).$$

In addition to the exponentially small error term between the solutions of S_ε^{sf} and the central manifold $\mathcal{M}^\varepsilon$, the following Theorem describes the error (more precisly a shadowing principle) between the reduced systems $S_\varepsilon^{[\infty]}$ and $S_\varepsilon^{[0]}$ and the original system S_ε^{sf}.

Theorem 3.2 (error bounds between the reduced systems and the original system) *Under the assumptions and the notations of the Theorem 3.1, for any exponant $0 < \mu' < \mu$ and any initial data $(X_0, Y_0) \in E \times F$, the following assertions hold true.*

(i) **Exponential convergence towards the central manifold.**
There exists a constant $C > 0$ such that

$$\forall t \geq 0, \quad \|Y^\varepsilon(t) - h(X^\varepsilon(t), \varepsilon)\|_F \leq C exp\left(-\mu' \frac{t}{\varepsilon}\right).$$

(ii) **Shadowing principle for $\left(S_\varepsilon^{[\infty]}\right)$.**
For any $T > 0$, there exist an initial data X_0^ε, depending on T and ε-close to X_0 and a constant $C_T > 0$, such that the solution of the reduced system $S_\varepsilon^{[\infty]}$, with initial data $X^{\varepsilon,[\infty]}(0) = X_0^\varepsilon$ and $Y^{\varepsilon,[\infty]}(0) = h(X_0^\varepsilon, \varepsilon)$, satisfies the following error estimate

$$\forall t \in [0, T], \quad \|X^\varepsilon(t) - X^{\varepsilon,[\infty]}(t)\|_E + \|Y^\varepsilon(t) - Y^{\varepsilon,[\infty]}(t)\|_F \leq C_T exp\left(-\mu' \frac{t}{\varepsilon}\right),$$

where $C_T > 0$ is independent of $t \geq 0$ and ε. If moreover there exists $M > 0$ independent of t and ε such that, for all $t > 0$, $\|X^\varepsilon(t)\|_E \leq M$, then we can take $T = +\infty$.

[7] Indeed, $h(X, \varepsilon)$ admits an asymptotic expansion of the form $h(X, \varepsilon) = \sum_{k=1}^r \varepsilon^k h_k(X) + O(\varepsilon^{r+1})$ which is explicitly calculable provided the functions $\mathcal{F}_0$ and $\mathcal{G}_0$ have C^{r+1} smoothness. The approximate $h(X, \varepsilon) \approx \sum_{k=1}^r \varepsilon^k h_k(X)$ leads to the writing of reduced systems of order r (see [8]). This paper focus only on the case $r = 0$.

(iii) **Shadowing principle for $\left(S_\varepsilon^{[0]}\right)$.**
For any $T > 0$, there exist an initial data X_0^ε, depending on T and ε-close to X_0 and a constant $C_T > 0$, such that the solution of the reduced system $S_\varepsilon^{[0]}$, with $X^{\varepsilon,[0]}(0) = X_0^\varepsilon$, satisfies the following error estimate

$$\forall t \in [0,T], \quad \|X^\varepsilon(t) - X^{\varepsilon,[0]}(t)\|_E + \|Y^\varepsilon(t) - Y^{\varepsilon,[0]}(t)\|_F \leq C_T \left(\varepsilon + exp\left(-\mu' \frac{t}{\varepsilon}\right)\right),$$

where $C_T > 0$ is independent of $t \geq 0$ and ε. If moreover there exists $M > 0$ independent of t and ε such that, for all $t > 0$, $\|X^\varepsilon(t)\|_E \leq M$, then we can take $T = +\infty$.

This Theorem means that, up to slightly modify the initial datum, the original system is well described by the reduced systems when ε is small enough. This allows us to study the qualitative behavior of solutions of the original system by working on finite dimensional systems.

Remark 3.3 *The initial data X_0^ε is constructed as follows.*
First for a fixed $T > 0$, one chooses $X_0^\varepsilon(T) = X_T^{\varepsilon,[0]}(0)$ as the only initial conditions such that the solution of $\frac{d}{dt}X_T^{\varepsilon,[0]}(t) = \mathcal{F}_0(X_T^{\varepsilon,[0]}(t), 0)$ verifies $X_T^{\varepsilon,[0]}(T) = X^\varepsilon(T)$.
Now if X^ε is uniformly bounded in E, independently of t and ε, then $X_T^{\varepsilon,[0]}$ and $\frac{d}{dt}X_T^{\varepsilon,[0]}$ are bounded as well. By the Ascoli Theorem, one can choose a sequence of trajectories $X_T^{\varepsilon,[0]}$ which converges as $T \to +\infty$. This allows us to define $X_0^\varepsilon = lim_{T\to\infty} X_T^{\varepsilon,[\infty]}(0)$.
As a consequence, if S_ε^{sf} conserves the line $X_i = 0$, then for any initial data satisfying $X_i^\varepsilon(0) \geq 0$ one see that $X_i^{\varepsilon,[0]}(T) := X_i^\varepsilon(T) \geq 0$ for any fixed $T > 0$. If in addition, $S_\varepsilon^{[0]}$ conserves the line $X_i = 0$, this implies that the ith componant $X_{0,i}^\varepsilon(T) := X_{T,i}^{\varepsilon,[0]}(0)$ is nonnegative. This fact remains obviously true by passing to the limit $T \to +\infty$. In conclusion, if $X_i^\varepsilon(0) \geq 0$ then one has $X_{0,i}^\varepsilon \geq 0$. This fact is essential in order to deal with global dynamics in the positive cone.

3.2 General consequences

The aim of this section is to prove the two below stated general results on slow-fast system: propositions 3.7 and 3.8. These propositions are the key in the proofs of our main results, theorems 2.7 and 2.10. In order to prove these two propositions, we start by the three following lemmas.
The first lemma uses the invariance of the central manifold and is already noted in [6].

Lemma 3.4 *Each stationary solution of S_ε^{sf} lies on $\mathcal{M}^\varepsilon$.*

Proof. Let $P^\varepsilon = (X^\varepsilon, Y^\varepsilon) \in E \times F$ be a stationary solution of S_ε^{sf}. The invariance of the central manifold implies that $(X^\varepsilon, h(X^\varepsilon, \varepsilon))$ is a stationary solution of S_ε^{sf}. By the theorem 3.2, it comes

$$\|Y^\varepsilon - h(X^\varepsilon, \varepsilon)\|_F \leq Cexp(-\mu \frac{t}{\varepsilon})$$

and so, by passing to the limit $t \to +\infty$,

$$Y^\varepsilon = h(X^\varepsilon, \varepsilon).$$

■

Hence, the complete description of the stationary solutions of the *finite dimensional system*

$$S_\varepsilon^c \ : \ \frac{d}{dt}X^{\varepsilon,[\infty]}(t) = \mathcal{F}_0(X^{\varepsilon,[\infty]}(t), h(X^{\varepsilon,[\infty]}(t), \varepsilon))$$

provides a complet description of the stationary solutions of the slow-fast system S_ε^{sf}.

Despite the fact that the system S_ε^c is finite dimensional, it is not explicit and difficult to study directly. But it can generically be seen as a regular perturbation of S_0^c and stationary solutions can then be easily reconstructed by local inversion.

Lemma 3.5 *Assume that p^0 is a stationary asymptotically linearly stable (unstable) solution of S_0^c. Then there exists $\varepsilon_1 > 0$ such that for all $\varepsilon \in [0, \varepsilon_1]$, there exists a stationary point $p^\varepsilon \in E$ of S_ε^c which is asymptotically linearly stable (resp. unstable) and $\varepsilon \mapsto p^\varepsilon$ is a C^1 function from $[0, \varepsilon_1]$ to E. Moreover, p^ε is the only stationary solutions of S_ε^c in a neighborhood of p^0.*

Proof. A simple application of the implicit function theorem on the function $(X,\varepsilon) \mapsto \mathcal{F}_0(X, h(X,\varepsilon))$ shows both the existence of the C^1 map $\varepsilon \mapsto p^\varepsilon$ and the uniqueness. The systems S^c_ε being finite dimensional, a simple perturbation argument shows that p^ε is asymptotically linearly stable (unstable). ■

Thanks to the regularity of $\mathcal{F}_0$, linear asymptotic stability implies asymptotic stability. Hence, if p^0 is linearly asymptotically stable, then p^ε is asymptotically stable. In fact, a stronger result holds : the size of the basin of attraction can be chosen independently on ε. This is used strongly in the sequel to deduce both local and global stability properties of the stationary solutions of S_ε from the corresponding results for S^c_0.

Lemma 3.6 *Define $S^\varepsilon(t)$ the one-parameter group associated to S^c_ε. That is*

$$S^\varepsilon(t)X_0 = X^\varepsilon(t)$$

where $X^\varepsilon(t)$ is the only solution of S^c_ε with initial data X_0.
If p^0 is linearly asymptotically stable for S^c_0, then

$$\exists \varepsilon_0 > 0,\ \exists r > 0,\ \forall \varepsilon \in [0,\varepsilon_0],\ \forall w_0 \in B(p^\varepsilon, r),\ \lim_{t\to+\infty} \|S^\varepsilon(t)w_0 - p^\varepsilon\| = 0$$

Proof.
Since the linear stability implies the (local) stability, the lemma 3.5 yields that for all $\varepsilon \in (0,\varepsilon_1)$ there exists $r > 0$ such that

$$X_0 \in B(p^\varepsilon, r) \Rightarrow \lim_{t\to+\infty} \|S(t)X_0 - p^\varepsilon\|_E = 0.$$

So one can define

$$r_\varepsilon = sup\{r > 0, \forall w \in B(p^\varepsilon, r),\ \text{s.t.}\ \lim_{t\to+\infty} \|S^\varepsilon(t)w - p^\varepsilon\|_E = 0\}. \tag{3.13}$$

The lemma holds true if $\liminf_{\varepsilon\to 0} r_\varepsilon > 0$. Let us argue by contradiction.

Suppose that $\liminf_{\varepsilon\to 0} r_\varepsilon = 0$, then there exists three sequences $\varepsilon_n \to 0$, $r_{\varepsilon_n} \to 0$ and $w_n \in E$ verifying

$$r_{\varepsilon_n} \le \|w_n - p^{\varepsilon_n}\|_E \le 2r_{\varepsilon_n}, \tag{3.14}$$

such that

$$\limsup_{t\to+\infty} \|S^{\varepsilon_n}(t)w_n - p^{\varepsilon_n}\|_E > 0. \tag{3.15}$$

We claim that

$$\forall t \ge 0, \quad \|S^{\varepsilon_n}(t)w_n - p^{\varepsilon_n}\|_E \ge r_{\varepsilon_n}. \tag{3.16}$$

Indeed, arguing by contradiction, assume that there exists $t_0 \ge 0$ such that

$$\|S^{\varepsilon_n}(t_0)w_n - p^{\varepsilon_n}\|_E < r_{\varepsilon_n}$$

Therefore one gets for each $t > t_0$,

$$\|S^{\varepsilon_n}(t)w_n - p^{\varepsilon_n}\|_E = \|S^{\varepsilon_n}(t-t_0)S^{\varepsilon_n}(t_0)w_n - p^{\varepsilon_n}\|_E$$

So that, by (3.13),

$$\lim_{t\to+\infty} \|S^{\varepsilon_n}(t)w_n - p^{\varepsilon_n}\|_E = 0,$$

which contradicts (3.15). It follows that (3.16) holds.
Now, denote $h_n = w_n - p^{\varepsilon_n}$ and remark that $S^\varepsilon(t)p^\varepsilon = p^\varepsilon$. One gets for all $t \ge 0$,

$$r_{\varepsilon_n} \le \|S^{\varepsilon_n}(t)h_n\|_E \le \|S^{\varepsilon_n}(t)h_n - S^0(t)h_n\|_E + \|S^0(t)h_n\|_E \tag{3.17}$$

Take any $T > 0$, the Gronwall Lemma together with global Lipschitz property of $\mathcal{F}_0$ and h yields for all $t \in [0,T]$

$$\|S^\varepsilon(t)X_0 - S^0(t)X_0\|_E \le \varepsilon C_T \|X_0\|_E \tag{3.18}$$

for some positive constant C_T independent on t and X_0. Therefore

$$\|S^{\varepsilon_n}(t)h_n\|_E \le \varepsilon_n C_T \|h_n\|_E + \|S^0(t)h_n\|_E.$$

Divide (3.17) by $\|h_n\|_E$, using (3.14) and passing, up to a subsequence, to the limit $n \to +\infty$, one obtains

$$\forall t \in (0,T), \quad \frac{1}{2} \le \lim_{n\to+\infty} \frac{1}{\|h_n\|_E} \|S^0(t)h_n\|_E \le \||e^{tA}\|| \tag{3.19}$$

where $A = D_X\mathcal{F}_0(p^0, 0)$.

The asymptotic linear stability of p^0, reads $\sigma(A) \subset \{\lambda \in \mathbb{C},\ \Re(\lambda) \in]-\infty, -\beta]\}$ for some $\beta > 0$ so that

$$\lim_{t\to+\infty} |||e^{tA}||| = 0$$

which yields to a contradiction by taking T and t big enough in (3.19). ■

One can now state the first proposition describing completly the stationary solutions of S_ε^{sf}.

Proposition 3.7 *Under the assumptions of theorem 3.1, there exists $\varepsilon_0 > 0$ such that for each $\varepsilon \in (0, \varepsilon_0)$ the following holds true.*

(i) Assume that S_0^c has one stationary solution p^0 which is hyperbolic.Then S_ε^{sf} has one stationary solution $P^\varepsilon := (p^\varepsilon, h(p^\varepsilon, \varepsilon))$ which is hyperbolic and verifies $\lim_{\varepsilon\to 0} \|p^\varepsilon - p^0\|_E = 0$.
P^ε is called the stationary solution corresponding to p^0.

(ii) Assume that S_0^c has one linearly asymptotically stable (resp. unstable) solution. Then the corresponding stationary solution of S_ε^{sf} is linearly asymptotically stable (resp. unstable).

(iii) If all the stationary solution of S_0^c are hyperbolic, then S_0^c has a finite number m of stationary solution and S_ε^{sf} has exactly m stationary solutions.

Proof. Proof of (i). By the lemma 3.5, one knows that there exists p^ε an hyperbolic stationary solution of S_ε^c. It follows that $P^\varepsilon := (p^\varepsilon, h(p^\varepsilon, \varepsilon))$ is a stationary solution of S_ε^{sf}.
Proof of (ii). Assume that p^0 is a linearly asymptotically stable (resp. unstable) stationary solution of S_0^c. By the lemma 3.5, p^ε is a linearly asymptotically stable (resp. unstable) stationary solution of S_ε^c. It remains to proof that if p^ε is stable (resp. unstable) for S_ε^c then so is P^ε for S_ε^{sf}. If p^ε is an unstable stationary solution of S_ε^c, then P^ε is obviously an unstable stationary solution of S_ε^{sf}.
Let us show that, if p^ε is a stable stationary solution of S_ε^c, then P^ε is a stable stationary solution of S_ε^{sf}. This is the main difficulties of this proof. We solve this problem[8] by using lemma 3.6.
Denote $Z^\varepsilon(t) = (X^\varepsilon(t), Y^\varepsilon(t))$ the only solution of S_ε^{sf} with initial data $Z^\varepsilon(0) = (X_0, Y_0)$ in a neighborhood (remaining to determine) of P^ε in $E \times F$ and $Z^{\varepsilon,[\infty]}(t) = (X^{\varepsilon,[\infty]}(t), h(^{\varepsilon,[\infty]}(t), \varepsilon))$ the only solution of $S_\varepsilon^{[\infty]}$ with initial data $Z^{\varepsilon,[\infty]}(0) = (X_0^\varepsilon, h(X_0^\varepsilon, \varepsilon))$ given in the Theorem 3.2- (iii). Recall that $\|X_0^\varepsilon - X_0\|_E = O(\varepsilon)$. One gets

$$\begin{aligned}\|Z^\varepsilon(t) - P^\varepsilon\|_{E\times F} &:= \|X^\varepsilon(t) - p^\varepsilon\|_E + \|Y^\varepsilon(t) - h(p^\varepsilon, \varepsilon)\|_F \\ &\le \|Z^\varepsilon(t) - Z^{\varepsilon,[\infty]}(t)\|_{E\times F} + \|Z^{\varepsilon,[\infty]}(t) - P^\varepsilon\|_{E\times F}.\end{aligned}$$

Let $r > 0$ be the size of the basin of attraction define in the lemma 3.6. r is independent of ε. If $\|Z^\varepsilon(0) - P^\varepsilon\|_{E\times F} \le r/3$, then one gets

$$\|X_0^\varepsilon - p^\varepsilon\|_{E\times F} = \|X_0^\varepsilon - X_0\|_E + \|X_0 - p^\varepsilon\|_F \le r/2$$

for small enough ε.
Therefore, Lemma 3.6 yields

$$\lim_{t\to+\infty} \|X^{\varepsilon,[\infty]}(t) - p^\varepsilon\|_E = 0$$

and then by continuity of h,

$$\lim_{t\to+\infty} \|Z^{\varepsilon,[\infty]}(t) - P^\varepsilon\|_{E\times F} = 0.$$

Finally, by the Theorem 3.2, for some positive constants C and μ', one gets

$$\|Z^\varepsilon(t) - Z^{\varepsilon,[\infty]}(t)\|_{E\times F} \le Cexp(-\mu'\frac{t}{\varepsilon}) \to 0 \text{ as } t \to +\infty,$$

which shows that

$$\|Z^\varepsilon(t) - P^\varepsilon\|_{E\times F} \to 0 \text{ as } t \to +\infty,$$

and end the proof of the stability of P^ε for S_ε^{sf}. ■

[8] Indeed, this is a general fact for central manifold as point out by Carr [6].

The last result of this section describes the *asymptotic dynamics* of S_ε^{sf} when the global dynamics of S_0^c is known.

Proposition 3.8 *Suppose that the assumption of the theorem 3.1 are verified. Set $\varepsilon_0 > 0$ the (small) scalar such that for all $\varepsilon \in (0, \varepsilon_0)$ the conclusion of theorems 3.1 and 3.2 occur.*
Let $\varepsilon \in (0, \varepsilon_0)$ and for any initial condition $Z_0 = (X_0, Y_0) \in E \times F$, define $X_0^\varepsilon(Z_0) \in E$ be a modified initial data appearing in the theorem (3.2)-(iii).
Assume that there exists three set $\mathcal{Q} \in E$, $Q_E \in E$ and $Q_F \in F$ satisfying the three following assumptions.

(i) S_0^c admits one hyperbolic stationary solution $p^0 \in \mathcal{Q}$ which is a global attractor in $\mathcal{Q}$ for the dynamic of S_0^c.

Let $P^\varepsilon := (p^\varepsilon, h(p^\varepsilon, \varepsilon)) \in E \times F$ be the corresponding stationnary solution for S_ε^{sf}.

(ii) For any initial condition $Z_0 = (X_0, Y_0) \in Q_E \times Q_F$, the modified initial data $X_0^\varepsilon(Z_0)$ belongs to $\mathcal{Q}$.

Then, for any initial condition $Z_0 \in Q_E \times Q_F$, one have $\|\boldsymbol{W}^\varepsilon(\cdot, t) - P^\varepsilon(\cdot)\|_{E\times F} \to 0$ as $t \to +\infty$.

Remark 3.9 *Since the modified initial data X_0^ε is ε-close to X_0, if $Q_E \subset int(\mathcal{Q})$, then for ε small enough, the assumption (ii) is satisfied. The only difficulty in the application is when $Q_E \cap \partial\mathcal{Q} \neq \emptyset$ which may occur when we deal with dynamics in the nonnegative cadrant, see lemma 4.6.*

Proof. Let p^0 be an linearly asymptotically stable stationary solution of S_0^c. By the Theorem 3.7, the steady state $P^\varepsilon = (p^\varepsilon, h(p^\varepsilon, \varepsilon))$ exists and is a local attractor. Besides, by the lemma 3.5 and the smoothness of h, one gets for some positive constant C' independent on ε,

$$\|p^\varepsilon - p^0\|_E + \|h(p^\varepsilon, \varepsilon) - h(p^0, \varepsilon)\|_F \leq C'\varepsilon. \tag{3.20}$$

Let $Z^\varepsilon(t) = (X^\varepsilon(t), Y^\varepsilon(t))$ be the solution of S_ε^{sf} with initial data $(X_0, Y_0) \in Q_E \times Q_F$ and $Z^{\varepsilon,[0]}(t) = (X^0(t), h(X^0(t), \varepsilon))$ be the solution of $S_\varepsilon^{[0]}$ with initial data $Z^{\varepsilon,[0]}(0) := (X_0^\varepsilon, h(X_0^\varepsilon, \varepsilon))$ given in the Theorem 3.2. By Theorem 3.2, it comes for some positive constants C and μ' and any $t \geq 0$ and small enough ε, the bound

$$\|Z^\varepsilon(t) - Z^{\varepsilon,[0]}\|_{E\times F} \leq C(\varepsilon + exp(-\mu'\frac{t}{\varepsilon})). \tag{3.21}$$

Let $r > 0$ be the size of the basin of attraction given in the lemma 3.6. By the assumption (ii), $X_0^\varepsilon \in \mathcal{Q}$ and by the assumption (i), p^0 is a global attractor of S_0^c in $\mathcal{Q}$. This implies

$$\exists T > 0, \forall t \geq T, \|X^0(t) - p^0\|_E \leq r/4.$$

By the continuity of $X \mapsto h(X, \varepsilon)$, this yields

$$\exists T > 0, \forall t \geq T, \|Z^{\varepsilon,[0]}(t) - P^0\|_{E\times F} := \|X^0(t) - p^0\|_E + \|h(X^0(t), \varepsilon) - h(p^0, \varepsilon)\|_F \leq r/3. \tag{3.22}$$

Besides, for all $t \geq 0$,

$$\|Z^\varepsilon(t) - P^\varepsilon\|_{E\times F} \leq \|Z^\varepsilon(t) - Z^{\varepsilon,[0]}(t)\|_{E\times F} + \|Z^{\varepsilon,[0]}(t) - P^0\|_{E\times F} + \|P^0 - P^\varepsilon\|_{E\times F}$$

The inequalities 3.20, 3.21 and 3.22, imply that there exists a constant C'' independent of ε and of r such that,

$$\exists T > 0, \forall t \geq T, \|Z^\varepsilon(t) - P^\varepsilon\|_{E\times F} \leq C''(\varepsilon + exp(-\mu\frac{t}{\varepsilon})) + r/3. \tag{3.23}$$

Choosing ε small enough such that $C''(\varepsilon + exp(-\mu\frac{T}{\varepsilon})) \leq r/6$, (3.23) yields

$$\exists T > 0, \forall t \geq T, \|Z^\varepsilon(t) - P^\varepsilon\|_{E\times F} \leq r/2. \tag{3.24}$$

Arguing as in the proof of the Theorem 3.7, if ε is small enough, (3.24) implies $\|Z^\varepsilon(t) - P^\varepsilon\|_{E\times F} \to 0$ as needed. ■

4 Proofs of Theorems 2.7 and 2.10

In this section, we begin by showing that the Theorems 3.1 and 3.2 apply to our particular system S_ε. Then we give the proof of the main results

4.1 Application of the Central Manifold theorem

The precise definitions of the operators A_i^∞ and $K^\infty = diag(A_i^\infty)$ are given in section 2.2 as well as the definitions of the banach spaces $E = ker(K^\infty) = \mathbb{R}^{N+1}$ and $F = Im(K^\infty)$. In the case of the system S_ε, one gets explicitly, with the notation of the section 2.2,

$$X^\varepsilon := (r^\varepsilon, u_1^\varepsilon \ldots, u_N^\varepsilon) = \Pi_E\left(R^\varepsilon, U_1^\varepsilon, \cdots, U_N^\varepsilon\right) := \left(\frac{1}{|\Omega|}\int_\Omega R^\varepsilon, \frac{1}{|\Omega|}\int_\Omega U_1^\varepsilon, \cdots, \frac{1}{|\Omega|}\int_\Omega U_N^\varepsilon\right)$$

$$Y^\varepsilon(x) := (Y_0^\varepsilon(x), \ldots, Y_N^\varepsilon(x)) = \Pi_F\left(R^\varepsilon, U_1^\varepsilon, \cdots, U_N^\varepsilon\right)(x) := (R^\varepsilon(x) - r^\varepsilon, U_1^\varepsilon(x) - u_1^\varepsilon, \ldots, U_N^\varepsilon(x) - u_N^\varepsilon).$$

Of course, with these notations, one has $X^\varepsilon + Y^\varepsilon = (R^\varepsilon, U_1^\varepsilon, \cdots, U_N^\varepsilon)$. Finally, for any $x \in \Omega$,

$$\mathcal{F}(X^\varepsilon + Y^\varepsilon)(x) = \begin{pmatrix} I(x) - m_0(x)\big(r^\varepsilon + Y_0^\varepsilon(x)\big) - \sum_{i=1}^N f_i(r^\varepsilon + Y_0^\varepsilon(x), x)\big(u_i^\varepsilon + Y_i^\varepsilon(x)\big) \\ \Big(f_1(r^\varepsilon + Y_0^\varepsilon(x), x) - m_1(x)\Big)\big(u_1^\varepsilon + Y_1^\varepsilon(x)\big) \\ \vdots \\ \Big(f_N(r^\varepsilon + Y_0^\varepsilon(x), x) - m_N(x)\Big)\big(u_N^\varepsilon + Y_N^\varepsilon(x)\big) \end{pmatrix}$$

and

$$\mathcal{F}_0(X^\varepsilon, Y^\varepsilon) = \Pi_E\mathcal{F}(X^\varepsilon + Y^\varepsilon) \text{ and } \mathcal{G}_1(X^\varepsilon, Y^\varepsilon)(x) = \Pi_F\mathcal{F}(X^\varepsilon + Y^\varepsilon)(x).$$

Note that

$$\mathcal{F}_0 \ : \ E \times F \to E \ \text{ and } \ \mathcal{G}_1 \ : \ E \times F \to F.$$

We first show that the operator $K = diag(A_i)$ define a C^0 semi-group of contraction on F.

The assumed smoothness of $\partial\Omega$ implies that the operator A_i^∞ generates a C^0 semi-group of contraction on $C^0(\overline{\Omega})$ (see [5]). Denoting $exp(tA_i^\infty)$ this semi-group, this reads

$$\forall t \geq 0, \ \|exp\left(tA_i^\infty\right)v\|_\infty \leq \|v\|_\infty.$$

The following lemma is a well know result using the gap between the two first eigenvalues of A_i^∞.

Lemma 4.1 *The restriction A_i of A_i^∞ to the subspace $\widetilde{F} := \{u \in C^0(\overline{\Omega}), \int_\Omega u = 0\}$ is the generator of a C^0 semi-group of strict contraction $exp(tA_i)$ on $\widetilde{F}$ verifying for some $\mu_i > 0$*

$$\forall v \in \widetilde{F}, \ \|exp(tA_i)v\|_\infty \leq e^{-\mu_i t}\|v\|_\infty. \tag{4.25}$$

Proof. $\widetilde{F}$ is closed in $C^0(\overline{\Omega})$ and is clearly invariant under $exp(tA_i^\infty)$. It follows (Pazy [23] p. 123) that A_i is the generator of a C^0 semi-group of contraction on $\widetilde{F}$.
It is well known that the spectrum $\sigma(-A_i^\infty)$ is a sequence of real nonnegative scalars

$$0 = \lambda_0 < \lambda_1 \leq \cdots$$

Since $\sigma(A_i) \subset \sigma(A_i^\infty)$ and $0 \notin \sigma(A_i)$ one see that $\sigma(A_i) \subset]-\infty, -\lambda_1]$ and an application of the Theorem 4.3 p 118 in Pazy [23] end the proof. ■

Noting $\mu = \min\{\mu_0, \cdots, \mu_N\}$ where μ_i is as in (4.25) and $K := diag(A_i)$, and $F = \widetilde{F}^{N+1}$, the lemma 4.1 implies directly

Proposition 4.2 *K is the generator of a C^0 semi-group $exp(tK)$ on F verifying*

$$\|exp(tK)v\|_F \leq e^{-\mu t}\|v\|_F.$$

Now, we show that the functions $\mathcal{F}_0 = \Pi_E\mathcal{F}$ and $\mathcal{G}_1 = \Pi_F\mathcal{F}$ are smooth enough.

Lemma 4.3 *The functions $\mathcal{F}_0$ and $\mathcal{G}_1$ have C^1 smoothness when acting on $E \times F$.*

Proof. By assumption 2.1 and 2.2, $\mathcal{F}$ is C^1 from $E \oplus F$ into itself. The only difficulty is the presence of the linear operators Π_E and Π_F. Since $\mathcal{G}_1 = \mathcal{F} - \mathcal{F}_0$ it suffices to prove lemma for $\mathcal{F}_0$. These functions have $N+1$ components. Denote $\mathcal{F}^i$ and $\mathcal{F}_0^i$ the ith component of $\mathcal{F}$ and $\mathcal{F}_0$. Taking (X, Y) and (X', Y') both belonging to some compact subset $\mathcal{K} \subset E \times F$, one gets for all $x \in \overline{\Omega}$ and $i = 0, \cdots, N$, using the fact that $\mathcal{F}^i(\cdot, x)$ is locally Lipschitz and $\mathcal{F}^i(X + Y, \cdot)$ is smooth,

$$|\mathcal{F}^i(x, X + Y(x)) - \mathcal{F}^i(x, X' + Y'(x))| \leq C(\mathcal{K})\left(\|X - X'\|_E + \|Y - Y'\|_F\right)$$

where $C(\mathcal{K})$ is a positive constant depending on $\mathcal{K}$. Since $\mathcal{F}_0^i = \frac{1}{|\Omega|}\int_\Omega \mathcal{F}^i$, this yields

$$|\mathcal{F}_0^i(X,Y) - \mathcal{F}_0^i(X',Y')| \leq C(\mathcal{K})\left(\|X-X'\|_E + \|Y-Y'\|_F\right)$$

for all $i = 0, \cdots, N$. It follows

$$\|\mathcal{F}_0(X,Y) - \mathcal{F}_0(X',Y')\|_E \leq (N+1)C(\mathcal{K})\left(\|X-X'\|_E + \|Y-Y'\|_F\right)$$

which proves that $\mathcal{F}_0$ is C^0 from $E \times F$ into E and so is $\mathcal{G}_1$ from $E \times F$ into F.

Since $R \mapsto f_i(R,x)$ is assumed to be C^1 with locally Lipschitz derivative, the proof of the C^1 smoothness follows the same lines and we omit it.

■

The theorem 3.1 also requires that $\mathcal{F}_0$ and $\mathcal{G}_1$ as well than their derivatives are bounded independently on ε. Obviously, this boundedness assumption does not hold in general. However, by theorem 2.5, one already knows that every solution is bounded in $(C^0(\overline{\Omega}))^{N+1}$ independently on ε and t. It follows with the definition of the norm $E \times F$ that, for some large enough $M > 0$, we have

$$\|X^\varepsilon(t)\|_E + \|Y^\varepsilon(t)\|_F \leq M.$$

It then suffices to conveniently truncate $\mathcal{F}_0$ and $\mathcal{G}_1$ outside the set $\{(X,Y) \in E \times F,\ \|X(t)\|_E + \|Y(t)\|_F \leq M\}$.

It follows that Theorems 3.1 and 3.2 as well as propositions 3.7 and 3.8 apply to the system S_ε^{sf} (defined in section 2.2).

4.2 Proof of the Theorem 2.7 and 2.10

Now, we apply the propositions 3.7 and 3.8 to the case of S_ε^{sf}.
Since we are interested in biologically relevant solutions, we are only interested in nonnegative solutions which leads to some additional difficulties. Let us start with the following lemma with is the key to deal with the positive quadrant near the boundaries.

Lemma 4.4 *Let $\mathcal{M}^\varepsilon = \{(X, h(X,\varepsilon)), X \in E\}$ be a central manifold for S_ε^{sf} defined in Theorem 3.1. Denote $h(X,\varepsilon) = (h_i(X,\varepsilon))_{0\leq i\leq N} \in F$ and $X = (r, u_1, \cdots, u_N) \in E$.*
Then there exists a function $g \in C^0(E \times [0,1]; F)$ such that for any $i = 1, \cdots, N$ one has

$$h_i(X,\varepsilon) = u_i g_i(X,\varepsilon).$$

Proof. Since the nonnegative quadrant is invariant for S_ε and since $\mathcal{M}^\varepsilon$ is invariant for S_ε^{sf}, one sees that for any $X = (r, u_1, \cdots, u_N) \in \mathbb{R}_+^{N+1}$, one has for any $i = 1, \cdots, N$ and $x \in \Omega$, $u_i + h_i(X,\varepsilon)(x) \geq 0$. In particular, if $u_i = 0$ it follows by the continuity of $h(\cdot,\varepsilon)$ from E to F that for all $x \in \Omega$, $h_i(X_{|u_i=0},\varepsilon)(x) \geq 0$.
Besides, since $h(X,\varepsilon) \in F$, one gets $\int_\Omega h_i(X_{|u_i=0},\varepsilon)(x)dx = 0$ and then $h_i(X_{|u_i=0},\varepsilon) \equiv 0$.
Now, since $h(\cdot,\varepsilon) \in C^1(E;F)$, one sees that $\frac{1}{u_i}h_i(X,\varepsilon)$ converges in F as $u_i \to 0$ and we are able to write

$$h_i(X,\varepsilon) = u_i g_i(X,\varepsilon).$$

Since $h \in C^1(E \times [0,1]; F)$, the regularity of g follows. ■

The following lemma ensures that the stationary solutions of S_ε^{sf}, constructed in the proposition 3.7, correspond to nonnegative stationary solutions of S_ε.

Lemma 4.5 *Assume that the system S_0^c admits a nonnegative hyperbolic stationary solution denoted by*

$$p^0 = (r^0, u_1^0, \cdots, u_N^0) \in \mathbb{R}_+^{N+1}.$$

Let $P^\varepsilon(x) = (p^\varepsilon, h(p^\varepsilon,\varepsilon)(x))$ be the stationary solution of S_ε^{sf} defined in the Theorem 3.7. The corresponding stationary solution of S_ε is denoted by

$$\boldsymbol{W}^\varepsilon(x) = p^\varepsilon + h(p^\varepsilon,\varepsilon)(x) := (R^\varepsilon(x), U_1^\varepsilon(x), \cdots, U_N^\varepsilon(x)).$$

Then for small enough $\varepsilon > 0$ one gets $R^\varepsilon(x) > 0$ for all $x \in \overline{\Omega}$ and

$$u_i^0 > 0 \Rightarrow U_i^\varepsilon(x) > 0,\ \forall x \in \overline{\Omega} \ \text{ and } u_i^0 = 0 \Rightarrow U_i^\varepsilon \equiv 0.$$

Proof. Since $h(p^\varepsilon,\varepsilon)(x)=O(\varepsilon)$, and $p^\varepsilon\to p^0$ as $\varepsilon\to 0$, if a component of p^0 is positive, so is the corresponding component of $W^\varepsilon(x)$ for small enough ε. It is clear that $r^0>0$ and then $R^\varepsilon(x)>0$ for all $x\in\overline{\Omega}$. Now, up to a rearrangement, suppose that $p^0=(r^0,u_1^0,\cdots,u_{N-1}^0,0)$. One knows that there exists a stationary solutions $W^\varepsilon(x)=p^\varepsilon+h(p^\varepsilon,\varepsilon)(x)$ of S_ε. We now show that $U_N^\varepsilon\equiv 0$. Thanks to the lemma 4.4, it suffices to show that $u_N^\varepsilon:=p_N^\varepsilon=0$. Hence, define $\widetilde{S}_\varepsilon^c$ the subsystem without the species N similarly to the corresponding systems, S_ε^c. Since p^0 is a hyperbolic stationary nonnegative solution of S_0^c, $\widetilde{p^0}=(r^0,u_1^0,\cdots,u_{N-1}^0)$ is a hyperbolic stationary non negative solution of $\widetilde{S}_0^c$. Lemma 3.5 applied to $\widetilde{S}_\varepsilon^c$ allows to define a stationary solution $\widetilde{p^\varepsilon}$ of $\widetilde{\mathcal{S}}_\varepsilon$. It follows that $(\widetilde{p^\varepsilon},0)$ is a stationary solution of S_ε^c and the uniqueness of p^ε in the neighborhood of p^0 yields to $p^\varepsilon=(\widetilde{p^\varepsilon},0)$, that is $u_N^\varepsilon=0$ which end the proof. ■

Proof of the Theorem 2.7. This theorem follows directly from the theorem 2.6 together with the proposition 3.7 and the lemma 4.5. ■

The proof of theorem 2.10 uses strongly proposition 3.8. The following lemma ensures that the assumption (i) of this proposition is satisfied.

Lemma 4.6 *Define the two subsets of $\mathbb{R}^{N+1}$:*

$$\mathcal{Q}=\mathbb{R}_+^{N+1},\qquad \mathcal{Q}_1=\{(r,u_1,\dots,u_N)\in\mathcal{Q},\ u_1>0\}$$

and, for any positive scalar α, define the two subsets of $\left(C^0(\overline{\Omega})\right)^{N+1}$

$$Q(\alpha):=\{(R,U_1,\dots,U_N)\in C^0(\overline{\Omega}),\ \forall x\in\Omega,\ R(x)\geq\alpha \text{ and for each } i\geq 1,\ U_i(x)\geq 0\}$$

$$Q_1(\alpha):=\{(R,U_1,\dots,U_N)\in Q(\alpha),\ \exists x\in\Omega,\ U_1(x)>0\}.$$

For any initial data $\boldsymbol{W}(0):=(R(0),U_1(0),\dots,U_N(0))\in Q(\alpha)$, one notes $\Pi_E\boldsymbol{W}(0)=(r(0),u_1(0),\cdots,u_N(0))$, $Z_0=(\Pi_E\boldsymbol{W}(0),\Pi_F\boldsymbol{W}(0))\in E\times F$ and $X_0^\varepsilon(Z_0)=(r^\varepsilon(0),u_1^\varepsilon(0),\cdots,u_N^\varepsilon(0))$ the modified initial data defined in the theorem 3.2-(iii).
For any α, there exists $\varepsilon(\alpha)>0$ such that for each $\varepsilon\in(0,\varepsilon(\alpha))$, the following holds true.

(i) For any initial data $\boldsymbol{W}(0)\in Q(\alpha)$ one gets $X_0^\varepsilon(Z_0)\in\mathcal{Q}$.

(ii) Assume that $r_1^*<r_j^*$ for any $j\neq 1$. Then, for any initial data $\boldsymbol{W}(0)\in Q_1(\alpha)$ one gets $X_0^\varepsilon(Z_0)\in\mathcal{Q}_1$.

Proof. Let $\alpha>0$ be fixed and take $\boldsymbol{W}(0)\in Q(\alpha)$. From $\|\Pi_E(\boldsymbol{W}(0))-X_0^\varepsilon(Z_0)\|_E\leq C\varepsilon$, we deduce $r^\varepsilon(0)=r(0)+O(\varepsilon)\geq\alpha+O(\varepsilon)>0$ provided ε is small enough. Moreover, the conservation of the line $U_i\equiv 0$ by both the system S_ε and S_0^c implies $u_i^\varepsilon(0)\geq 0$ (see the remark 3.3) which proves the point (i).

The only difficulty in proving (ii) is that, *a priori*, taking an initial data $\boldsymbol{W}(0)\in Q_1(\alpha)$ can provide a modified initial data $X_0^\varepsilon(Z_0)\notin\mathcal{Q}_1$, i.e. such that $u_1^\varepsilon(0)=0$. We show that this can not hold by contradiction[9]. Assume that $\boldsymbol{W}(0)\in Q_1(\alpha)$ and that $X_0^\varepsilon(Z_0)$ verifies $u_1^\varepsilon(0)=0$. Denote $X^{\varepsilon,[0]}(t):=(r^{\varepsilon,0}(t),u_1^{\varepsilon,0}(t),\cdot,u_N^{\varepsilon,0}(t))$ the solution of S_0^c with $X^{\varepsilon,[0]}(0)=X_0^\varepsilon(Z_0)$.
The line $u_1=0$ being invariant for S_0^c, one has

$$\forall t\geq 0,\quad u_1^{\varepsilon,[0]}(t)=0 \tag{4.26}$$

and then, by the proposition 2.9,

$$\lim_{t\to+\infty} r^{\varepsilon,[0]}(t)=\widehat{r}\text{ where }\widehat{r}=r_k^*\text{ for some }k\neq 1. \tag{4.27}$$

Now, let $X^{\varepsilon,[\infty]}(t)=(r^{\varepsilon,\infty}(t),u_1^{\varepsilon,\infty}(t),\dots,u_N^{\varepsilon,\infty}(t))$ be a solution of S_ε^c whis initial data $X^{\varepsilon,[\infty]}(0)$ given by Theorem 3.2-(ii). We claim that $u_1^{\varepsilon,[\infty]}=0$. Indeed, from (4.26) and (4.27), this theorem implies

$$\forall t>0,\ 0\leq u_1^{\varepsilon,\infty}(t)\leq C\varepsilon \tag{4.28}$$

and for t large enough,

$$|r^{\varepsilon,\infty}(t)-\widehat{r}|\leq C\varepsilon. \tag{4.29}$$

[9] Let us remarks at this step that one gets $u_1(0):=\frac{1}{\Omega}\int_\Omega U_1^\varepsilon(0,x)dx+O(\varepsilon)$ so that for any initial data $U_1(x,0)>0$, one gets $u_1^\varepsilon(0)>0$ for small enough ε *depending on* $\boldsymbol{W}(0)$. It follows directly that the global asymptotic behavior holds true when $\boldsymbol{U}_1^\varepsilon(0)$ is far enough from the boundary. One can also reformulate this by saying that for any compact subset $\mathcal{K}$ of $Q_1(\alpha)$, there exists $\varepsilon(\mathcal{K})$ such that for any $\varepsilon\in(0,\varepsilon(\mathcal{K}))$, the global asymptotic behaviors holds.
The only problem occurs when $U_1=O(\varepsilon)$ which can very hold in $Q_1(\alpha)$.

Thus, by lemma 4.4, and smoothness of h and f_1, one gets for t large enough

$$\frac{d}{dt}u_1^{\varepsilon,\infty} = u_1^{\varepsilon,\infty}\left(\widetilde{f_1}(\widehat{r}) - \widetilde{m_1} + O(\varepsilon)\right)(1+O(\varepsilon)).$$

Moreover, since $r_1^* < r_k^*$ for all $k \neq 1$, one has $\widehat{r} > r_1^*$ and then, if ε is small enough (depending only on the gap $\widetilde{f_1}(\widehat{r}) - \widetilde{m_1}$), one gets

$$\left(\widetilde{f_1}(\widehat{r}) - \widetilde{m_1} + O(\varepsilon)\right) > 0.$$

It follows that if $u_1^{\varepsilon,\infty}(0) > 0$, then $\lim\limits_{t\to+\infty} u_1^{\varepsilon,\infty}(t) = +\infty$ a contradiction with (4.28).
Thus $u_1^{\varepsilon,\infty}(0) = 0$ and then $u_1^{\varepsilon,\infty}(t) = 0$ for all $t \geq 0$. It follows by the Theorem 3.2 that, for some positive constants C and μ',

$$\|U_1^\varepsilon(\cdot,t)\|_\infty \leq Ce^{-\mu'\frac{t}{\varepsilon}}, \tag{4.30}$$

and from (4.27) we deduce for large enough $t > 0$,

$$\|R^\varepsilon(\cdot,t) - \widehat{r}\|_\infty \leq C\varepsilon. \tag{4.31}$$

On the other hand, for any $t > 0$ and $x \in \Omega$, the real (component of the) solution $U_1^\varepsilon(x,t)$ is positive and verifies

$$\begin{aligned}\partial_t U_1^\varepsilon(x,t) &= U_1^\varepsilon(x,t)\left(f_1(x,R^\varepsilon(x,t)) - m_1(x)\right) + \frac{1}{\varepsilon}A_i U_1^\varepsilon(x,t)\\ &= U_1^\varepsilon(x,t)\left(f_1(x,\widehat{r}) - m_1(x) + O(\varepsilon)\right) + \frac{1}{\varepsilon}A_i U_1^\varepsilon(x,t)\end{aligned} \tag{4.32}$$

It is well known that the operator $(f_1(x,\widehat{r}) - m_1(x)) + \frac{1}{\varepsilon}A_i$ has a principal eigenvalue λ_ε and a corresponding function $\phi_\varepsilon > 0$. Moreover (see for instance [12]) λ_ε tends continuously to $\widetilde{f_1}(\widehat{r}) - \widetilde{m_1} > 0$ as $\varepsilon \to 0$. Multiplying (4.32) by ϕ_ε and integrating over Ω, one obtains for large enough $t > 0$,

$$\partial_t \int_\Omega U_1^\varepsilon(t,x)\phi_\varepsilon(x)dx = (\lambda_\varepsilon + O(\varepsilon))\int_\Omega U_1^\varepsilon(t,x)\phi_\varepsilon(x)dx.$$

If ε is small enough (depending only on $\widetilde{f_1}(\widehat{r}) - \widetilde{m_1}$), it follows that $t \mapsto \int_\Omega U_1^\varepsilon(t,x)\phi_\varepsilon(x)dx$ is a positive increasing function for t large enough which contradicts (4.30). It follows that $u_1^\varepsilon(0) > 0$ and the point (ii) is proved. ■

Proof of the Theorem 2.10. Take $\boldsymbol{W}(.,0) \in Q$. By the theorem 2.5, one has for some constant $M > 0$

$$\partial_t R^\varepsilon(x,t) - \frac{1}{\varepsilon}A_0 R^\varepsilon(x,t) \geq I(x) - m_0(x)R^\varepsilon(x,t) - M\sum_{i=1}^N f_i(x,R^\varepsilon(x,t),\ t>0,\ x\in\Omega. \tag{4.33}$$

The comparison principle in parabolic equations shows that $R^\varepsilon(x,t) > \underline{R}(x,t)$ where $\underline{R}(x,t)$ is a solution of (4.33) with an equality, together with zero flux boundary conditions and the initial values $\underline{R}(x,0) = R(x,0)$. A lower-upper solution method shows that $\underline{R}(x,t) \to \Phi(x)$ as $t \to +\infty$ where $\Phi(x)$ is the only stationary solution of (4.33) (with equality). From $I \not\equiv 0$ and the strong maximum principle, we deduce $\Phi(x) > 0$ for all $x \in \overline{\Omega}$. As a consequences, there exists a scalar $0 < \alpha < \min_{x\in\overline{\Omega}}\Phi(x)$ and a time $t_0 \geq 0$ such that $R^\varepsilon(t_0,x) > \alpha$ for any $t > t_0$. Since S_ε conserve the positive quadrant, it follows that $W(\cdot,t) \in Q(\alpha)$ for $t \geq t_0$ Hence, without loss of generality, one may assume that $\boldsymbol{W}(\cdot,0) \in Q(\alpha)$ resp. $Q_1(\alpha)$). It follows from lemma 4.6 that all the perturbed initial data appearing in theorem 3.2 lies on $\mathcal{Q} := \mathbb{R}_+^{N+1}$ (resp. $\mathcal{Q}_1$). Now, by the proposition 3.8, the points (ii) and (iii) of the theorem follow from the points (ii) and (iii) of the proposition 2.9. It remains to prove the point (i).

Let $i \in \{1,\cdots,N\}$. First, it is well known (and easy to check) that for any initial data $X(0) \in \mathcal{Q}$, one gets $\limsup_t r(t) \leq r_0^*$. Arguing as in the proof of the lemma 4.6, one deduces that for large enough t,

$$\partial_t u_i^{\varepsilon,[\infty]}(t) \leq u_i^{\varepsilon,[\infty]}(t)(\widetilde{f_i}(r_0^*) - \widetilde{m_i} + O(\varepsilon))(1+O(\varepsilon)).$$

The inequality $r_0^* < r_i^*$ reads exactly $\widetilde{f_i}(r_0^*) - \widetilde{m_i} < 0$. It follows that $u_i^{\varepsilon,[\infty]}(t) \to 0$ for small enough ε and any initial data $X_0^\varepsilon \in \mathcal{Q}$. By virtue of the theorem 3.2, for some initial data $X_0^\varepsilon \in \mathcal{Q}$, one has

$$\|U_i^\varepsilon(\cdot,t) - u_i^{\varepsilon,[\infty]}(t)\|_\infty \leq Ce^{-\mu'\frac{t}{\varepsilon}}$$

and $\|U_i^\varepsilon(\cdot,t)\|_\infty \to 0$ follows.

■

5 The best competitor in average

Rougly speaking, the Theorem 2.10 may be summarized as follow. If the diffusion rate is large enough, then the CEP holds for the system S_ε. At most one species survives namely *the best competitors in average*, that is the species associated with the smallest r_i^*. Inversely, looking at the system S_ε without diffusion, one defines for each $x \in \Omega$, $R_0^*(x) = I(x)/m_0(x)$ and $R_i^*(x)$ the only solution of $f_i(R_i(x), x) = m_i(x)$ if it exists and $R_i^*(x) = +\infty$ else. We say that the ith species is a strong local competitor if there exists $x \in \Omega$ such that $R_i^*(x) < R_j^*(x)$ for all $j \neq i$. We say that the ith species is *a weak local competitor* if for all $x \in \Omega$, there exists j such that $R_i^*(x) > R_j^*(x)$. A weak local competitor can not survive to the competition without diffusion[10].

This has two implications. Fistly, this highlights that different competitive strategies may be selected depending if the environment is well-mixed or not. Secondly, this indicates that for *intermediate* diffusion rates, several competitive strategies may yield *coexistence*.

Thus, the below detailled phenomena are indicators of the possibility of a given environement to promote coexistence by mixing both the *local* aspects and the *global* ones. This type of local/global duality has been discussed within a different framework in [10] for instance.

We now discuss on precise examples three phenomena showing that the best competitor in average can be a weak local competitor.

For a given function $g \in C^0(\Omega)$, (resp. a vector g if Ω is finite), denote E the average of g. The number r_i^* (defined in figure 1) reads

$$r_i^* = E(R_i^*) + J_i + H_i$$

wherein we have set

$$J_i = \widetilde{f_i}^{-1}\big(E(m_i)\big) - E\big(\widetilde{f_i}^{-1}((m_i))\big) \text{ and } H_i = E\big(\widetilde{f_i}^{-1}(m_i)\big) - E\big(f_i^{-1}(m_i)\big).$$

The biological interpretation of each term is as follows.

- **The (averaged) local competitive strength** is represented by $E(R_i^*)$. The stronger local competitor the species i is, the smaller is $E(R_i^*)$.
  This phenomena is of particular interest in a *three species (or more) situation* since a generalist (a species which is a weak local competitor but with a small $E(R_i^*)$) may lose the competition on each patche but win the competition in average.
  From a coexistence point of view, this permits to several (three or more) species to coexiste for an intermediate diffusion rate, while they can not coexist neither for a small nor a large diffusion rate.

- **The non linear effect** is represented by J_i. This term is null if either $\widetilde{f_i}$ is linear or m_i is constant. Usually, the consumption function $\widetilde{f_i}$ is increasing and concave so that $\widetilde{f_i}^{-1}$ is convex. In this case, due to the Jensen inequality, J_i is negative.
  Hence, *the nonlinear effect improves the competition strength of species.*
  From a coexistence point of view and for intermediate diffusion rate, this is the phenomena which permits coexistence in the classical unstirred chemostat [19, 34] or in the classical gradostat [28].

- **The heterogeneous effect of the consumption** is represented by H_i. Basically, it represents the effect of the heterogeneity of the consumption function $f_i(x, \cdot)$ and it is null if $f_i = \widetilde{f_i}$.
  The larger the consumption $f_i(j, \cdot)$ is at location $j \in \Omega$ where $R_i^*(j)$ is large, the smaller is H_i.
  Hence, *a fast dynamics on the sites where $R_i^*(j)$ is small improves the averaged competitive strenght of the species.*
  From a coexistence point of view and for intermediate diffusion rate, this phenomena increase the possibility of coexistence in the generalised chemostat (or gradostat), see [9].

Now, we illustrate this three phenomena on examples. To simplify the discution, we focus here on the case of a two patches model: $\Omega = \{1, 2\}$ and $A_i \in \mathbb{R}^{2\times 2}$ defined for each i as $A = A_i = \begin{bmatrix} -1 & 1 \\ 1 & -1 \end{bmatrix}$. Besides, we assume that $R_i^*(j)$ is well defined for all $j = 1, 2$. Here, for $g = (g(1), g(2))$, one has $E(g) = \frac{1}{2}(g(1) + g(2))$.

5.1 The local competitive strength

Define the special case of S_ε (in $\Omega = \{1, 2\}$) for three species (with positive initial data)

$$\begin{cases} d_t R(j,t) = 1 - R(j,t) - \sum U_i(j,t) R(j,t) + \frac{1}{\varepsilon}(AR)(j,t), \\ d_t U_i(j,t) = (R(j,t) - m_i(j)) U_i(j,t) + \frac{1}{\varepsilon}(AU_i)(j,t), \quad i = 1,2,3 \end{cases} \quad j = 1, 2 \tag{5.34}$$

[10] Numerical evidence show that a weak local competitor can no survive to the competition for small enough diffusion rates. As it is proved in [13], a rigourous studied of *stationnary* solutions for small diffusion supporte these evidences.

For $j = \{1, 2\}$, one gets $R_0^*(j) = 1$ and $R_i^*(j) = m_i(j)$ for $i = 1, 2, 3$. We also assume that $1 > R_i^*(j)$ for $i = 1, 2, 3$ and $j = 1, 2$. Here, r_i^* reads $r_i^* = \frac{1}{2}(m_i(1) + m_i(2))$.

One claims that it is possible to find three vector m_i such that $R_3^*(j) > min(R_1^*(j), R_2^*(j))$. for all $j \in \{1, 2\}$ and $r_3^* < \min(r_1^*, r_2^*)$. It suffices to choose m_i such that for instance $m_1(1) < m_3(1) < m_2(1)$ and $m_2(2) < m_3(2) < m_1(2)$ and $m_3(1) + m_3(2) < m_i(1) + m_i(2)$ for $i = 1, 2$. The vectors $m_1 = {}^t(0.1, 0.9)$, $m_2 = {}^t(0.9, 0.1)$ and $m_3 = {}^t(0.4, 0.4)$ suit.
Biologically, an interpretation is that the first and second species are specialists (the best competitor on one site and the weakest on the other site) whereas the third species is a generalist (a weak competitor but the weakest on no site)

Hence, according to Theorem 2.10, the third species is the best averaged competitor but a weak local competitor. Hence, **without migration the first species survives on the site 1, the second on the site 2 and the third nowhere, while for fast migration, the two first species do not survive and the third is the only survivor.**

For an intermediate diffusion rate, we guess that the three species may eventually coexiste (even if it means increasing the number of sites[11]).

in the sense that the species 1 and 2 are good only on the sites 1 and 2 respectivly, while the species 3

5.2 The non linear effect

Here we assume that the consumption function f_i is homogeneous so that $H_i = 0$. One discuss the particular cases of Holling type II functions : $f_i(R) = \frac{R}{k_i + R}$. The nonlinear effect is more important if the function f_i is very nonlinear. For Holling type II functions, this can be measured by the number k_i:

$$J_i = k_i \left[\frac{E(m_i)}{1 - E(m_i)} - E\left(\frac{m_i}{1 - m_i} \right) \right]. \tag{5.35}$$

Due to the Jensen's inequality, J_i is non positive and is null if and only if m_i is constant.

As a consequence one can constructed an explicit example of two species competing for the same resource R such that the species 1 is the best local competitor on each site while the second species is the best competitor in average. An explicit example is the following

$$\begin{cases} d_t R(j,t) = 10 - R(j,t) - \frac{R(j,t)}{1+R(j,t)} U_1(j,t) - \frac{R(j,t)}{0.25+R(j,t)} U_2(j,t) + \frac{1}{\varepsilon}(AR)(j,t), \\ d_t U_1(j,t) = (\frac{R(j,t)}{1+R(j,t)} - m_i(j)) U_1(j,t) + \frac{1}{\varepsilon}(AU_1)(j,t), \\ d_t U_2(j,t) = (\frac{R(j,t)}{0.25+R(j,t)} - m_i(j)) U_2(j,t) + \frac{1}{\varepsilon}(AU_2)(j,t), \end{cases} \tag{5.36}$$

where $m_1 = {}^t(0.38, 34/41)$ and $m_2 = {}^t(0.75, 20/21)$. Explicite computations give $R_1^* = {}^t(0.6129, 4.8571)$ and $R_2^* = {}^t(0.75, 5)$ while $r_1^* \approx 1.5293$ and $r_2^* = 1.43$.

As a consequence, **the first species is the only survivor for slow migration will the species 2 will be the only survivor for fast enough migration.**
One can also build an example of a single species and we obtain: **due to the nonlinear effect, a species which is able to survives on no site without migration can survive for fast enough migration.**

5.3 The heterogeneous effect of the consumption

In the previous discussion, the heterogeneity take place only on the mortality. If the consumption function itself is heterogeneous, a third phenomenon occurs. Here, we discuss the case of a linear consumption function so that J_i is null. Let take

$$f_i(j, R) = C_i(j) R.$$

We illustrate this phenomena on the following two species system

$$\begin{cases} d_t R(j,t) = 1 - R(j,t) - \sum C_i(j) U_i(j,t) R(j,t) + \frac{1}{\varepsilon}(AR)(j,t), \\ d_t U_i(j,t) = (C_i(j) R(j,t) - m_i(j)) U_i(j,t) + \frac{1}{\varepsilon}(AU_i)(j,t), \quad i = 1, 2 \end{cases} \tag{5.37}$$

We will see that *the best competitor in average can be the weakest competitor everywhere* in that case.
This phenomena is similar to the Fitness-density covariance in heterogeneous environment stress by Chesson *et al.* [10]. Indeed, noting $cov(f, g) = E(fg) - E(f)E(g)$, one get $r_i^* = E(R_i^*) + cov(\frac{C_i}{E(C_i)}, R_i^*)$ and

[11] As it is shown in [17], stationary coexistence of N species in P sites is generically impossible. Thus, 3 species can not coexist in less than 3 patches.

$r_0^* = E(R_0^*) + cov(\frac{m_0}{E(m_0)}, R_0^*)$.

A species may be the weakest local competitor and the best competitor in average. Indeed, $r_1^* > r_2^*$ if and only if $cov(\frac{C_2}{E(C_2)}, R_2^*) - cov(\frac{C_1}{E(C_1)}, R_1^*) < E(R_1^*) - E(R_2^*)$ which implies

Proposition 5.1 *(Competitive covariance in heterogeneous environment)*
$r_2^* < r_1^*$ if and only if $cov(\frac{C_2}{E(C_2)}, R_2^*) - cov(\frac{C_1}{E(C_1)}, R_1^*) < E(R_1^*) - E(R_2^*)$. In particular, one may have $R_1^*(j) < R_2^*(j)$ for each $j \in \Omega$.

If $R_1^*(j) < R_2^*(j)$ for each $j \in \Omega$, then it is necessary that $cov(c_2, R_2^*) - cov(c_1, R_1^*)$ is negative and small enough. This means that either the best local competitor as maximal consumption rate on bad site (where $R_1^*(j)$ is large), or the weak local competitor has maximal consumption rate on good site,(where $R_2^*(j)$ is small).
The following result give a necessary and sufficient condition on R_i^* for this phenomena may happen.

Proposition 5.2 *Suppose that the first species is the best competitors everywhere, that is $R_1^*(j) < R_2^*(j)$ for all $j \in \Omega$.*
If $\max_{j\in\Omega} R_2^*(j) < \min_{j\in\Omega} R_1^*(j)$, then there exists two smooth positive vectors C_1 and C_2 such that $r_1^* > r_2^*$

Proof. $R_1^*(j)$ and $R_2^*(j)$ being fixed, one gets $r_i^* = \frac{C_i(j)R_i^*(j)}{C_i(j)}$. It suffices to find two vectors such that $E(C_1R_1^*)EC_2) < E(C_2R_2^*)E(C_1)$. Denoting j_1 and j_2 such that $\min_{j\in\Omega} R_1^*(j) = R_1^*(j_1)$ and $\max_{j\in\Omega} R_2^*(j) = R_2^*(j_2)$, it suffices to choose two vectors, such that for $i = 1, 2$, $C_i(j) \approx \delta(j = j_i)$. It comes $r_i^* \approx R_i^*(j_i)$ which end the proof. ■

According to the Theorem 2.10, the second species is the only survivor if ε is small enough. Numerical simulations indicate that, as expected, the first species is the only survivor for large ε, the second is the only survivor for small ε, and the two species coexist for an intermediate value of ε. Similiar arguments on single species models show that a species may not survive locally but survive globaly or conversely. In conclusion **a fast dynamics on good sites increases the averaged competitive strenght of a species.**
This underline the importance of the spatial heterogeneity together with the value of the diffusion rates on coexistence phenomena.

6 Conclusion

In this text, we have studied a system of N species competing for a single resource where populations and resource depend both on time and space. The demography is described *at each site* by a chemostat model, assuming increasing consumption functions and constant yields. The diffusions are assumed *fast* which induces an average effect on the spatial repartition of the populations. Our results are as follows.

We show that the dynamics is asymptotically well described, up to an exponentially small error term, by a system involving $N + 1$ equations instead of $N + 1$ equations *per site*, describing the dynamics of the total number of individual. In turn, this reduced system is well described, up to an order one small error term, by a standard homogeneous chemostat system, called the aggregated system, which can be *explicitly computed*.

The main result of this work is that, if the aggregated system verifies the CEP, then the original system verifies the CEP, *for fast enough diffusions*.
This result give a justification to "well-mixed" assumption done in the statement of homogeneous chemostat models. Besides, the parameters of the aggregated system can be explicitly computed.

In particular, we show that the only survivor is the best competitor *in average*. Moreover, we note that the best competitor in average can be *the best competitor nowhere*, and indeed, if the heterogeneity concern both the mortalities and the consumption functions or if the consumptions function are non linear, the best competitor in average can be *the weakest competitor everywhere* (see section 5 for a definition of weak/best competitors).
Moreover, these results give indication about the possibility that a heterogeneous environment promotes coexistence for intermediate diffusion rates. Note that all the results of this work hold for a gradostat model, replacing the continuous space Ω by a finite number of sites, and the diffusion operators by a migration matrix assuming to be irreducible. In that case, the Perron-Frobenius Theorem give all the spectral information and the central manifold Theorem state in [8] apply directly leading to the similar results.

Several ways of future investigation can extend this study.
First, Theorems 2.7 and 2.10 assume that the stationary solution of the aggregated problem are hyperbolic, that is the numbers r_i^* are different. In an homogeneous chemostat (together with some additional assumption), the

global dynamics can be described even if the r_i^* are equal. The global attractor is then a family of non isolated stationary solutions instead of a unique stationary solution, and several species can survive [28]. The Theorem 3.2 gives directly some informations on the dynamics of the original system S_ε, up to an error in ε. However, the stationary solution being degenerate, the local inversion Theorem can no longer apply, and the construction of section 4 fails to describe completely the dynamics of the original system. In order to study more precisely this case, we have to calculate the reduced system at a higher order (up to an order 2 error term). This new system is still a system of $N+1$ differential equations, but with additional terms of order ε. The dynamics of this systems is not known to our knowledge. Such a study can give several information of the ways the coexistence can happens and even on the way large diffusion leads to exclusion.

Secondly, our study is restricted to the case of increasing consumption functions and constant yields. These assumptions are indeed used only from the the section 4. Various results are known in the case of an homogeneous chemostat with non monotone consumption functions [20, 32, 33] or variable yields [24, 27]. An aggregated system can be compute for such case and determined which of this results can be applies.

References

[1] O. Arino, E. Sanchez, R. Bravo de la Parra, and P. Auger. *A singular perturbation in an age-structured population model*, SIAM J. Appl. Math., **60** No. 2 (1999), 408–436

[2] R. A. Armstrong and R. McGehee. *Competitive exclusion*, American Naturalist **170** (1980), 115–151

[3] P. Auger and J. C. Poggiale. *Aggregation and emergence in systems of ordinary differential equations* Aggregation and emergence in population dynamics. Math. Comput. Modelling, **27** No. 4 (1998) 1–21

[4] J. V. Baxley and S. B. Robinson. *Coexistence in the unstirred chemosat* Applied Math. And Comput., **39** (1998) 41–65

[5] Markus Biegert. *The neumann laplacian on spaces of continuous functions* Note di Matematica, **22** (2003), 65–74

[6] J. Carr. *Applications of Center Manifold Theory* Applied Mathematical Sciences **35** Springer-Verlag, New York, 1981.

[7] A.N. Carvalho and J.K. Hale. *Large diffusion with dispersion* Nonlinear Analysis, **17** (1991) 1139–1151

[8] F. Castella, J. P. Hoffbeck, and Y. Lagadeuc. *A reduced model for spatially structured predator-prey systems with fast spatial migrations and slow demographic evolutions* Asymptot. Anal., **61** No. 3-4 (2009) 125–175

[9] F. Castella and S. Madec. *Coexistence phenomena and global bifurcation structure in a chemostat-like model with species-dependent diffusion rates*, J. Math. Bio., **68** No.1-2 (2014), 377–415

[10] P. Chesson. *General theory of competitive coexistence in spatially-varying environments*, Theoret. Pop. Biol.,, **58** (2000), 211–237

[11] E. Conway, D. Hoff and J. Smoller. *Large time behavior of solutions of systems of nonlinear reaction-diffusion equations*, SIAM J. Appl. Math., **35**, 1–16 (1978)

[12] J. Dockery, V. Hutson, K. Mischaikow, and M. Pernarowski. *The evolution of slow dispersal rates: a reaction diffusion model* J. Math. Biol, **37** (1998), 61–83

[13] A. Ducrot and S. Madec. *Singularly perturbed elliptic system modeling the competitive interactions for a single resource*, Math. Models Methods Appl. Sci., **23**, No. 11 (2013), pp. 1939–1977

[14] J. L. Dung, H. L. Smith, and P. Waltman. *Growth in the unstirred chemostat with different diffusion rates* Fields institute communications, **21** (1999) 131–142.

[15] D. Henry. *Geometric theory of semilinear parabolic equations* Lecture Notes in Mathematics **840**, Springer-Verlag, New York, 1981.

[16] S. L. Hollis, R. H. Martin, and M. Pierre. *Global existence and boundedness in reaction- diffusion systems* SIAM J. Math. Anal., **18** No. 3 (1987), 744–761.

[17] J. Hofbauer and J. W.-H. So. *Competition in the gradostat: the global stability problem* Nonlinear Analysis: Theory, Methods and Applications, **22** (1994), 1017–1031.

[18] S. B. Hsu. *Limiting behavior for competing species*, SIAM J. Appl. Math., **34** (1978), 760–763

[19] S. B. Hsu and P. Waltman. *On a system of reaction-diffusion equations arising from competition in an unstirred chemostat*, SIAM J. Appl. Math., **53** (1993), 1026–1044

[20] B. Li. *Global asymptotic behavior of the chemostat : general response functions and differ- ential removal rates*,SIAM J. Appl. Math., **59** (1998), 411–422

[21] Y. Lou. *Some challenging mathematical problems in evolution of dispersal and population dynamics* In A. Friedman, editor, Tutor. Math. Biosci., volume IV: Evolution and Ecology of Lect. Notes Mathematics, pages 171–205. Springer, 2007.

[22] H. Nie and J.Wu. *Uniqueness and stability for coexistence solutions of the unstirred chemostat model* Applicable Analysis, **89(7)** (2010), 1151–1159

[23] A. Pazy. *Semigroups of linear operators and applications to partial differential equations*, Applied Math. Sciences, 44, Springer-Verlag, New York, 1983.

[24] S. Pilyugin and P. Waltman. *Multiple limit cycles in the chemostat with variable yield math- ematical biosciences*, J. Theoret. Biol., **182** No2 (2003), 151–166

[25] J. C. Poggiale. *From behavioural to population level: growth and competition. Aggregation and emergence in popuation dynamics*, Math. Comput. Modelling, **27** No4 (1998), 41–49

[26] J. C. Poggiale. *Predator-prey models in heterogeneous environment: emergence of functional response*, Math. Comput. Modelling, **27** No4 (1998), 63–71

[27] T. Sari and F. Mazenc. *Global dynamics of the chemostat with different removal rates and variable yields*, Mathematical Biosciences And Engineering, **8(3)** (2011),827–840

[28] H. L. Smith and P. Waltman. *The theory of the Chemostat*, Cambridge university press, 1995.

[29] S. Madec, *Hétérogénéité spatiale en dynamique des populations*, Phd Thesis (in french)

[30] E. Sanchez, P. Auger, and J.-C. Poggiale. *Two-time scales in spatially structured models of population dynamics: A semigroup approach*, Journal of Mathematical Analysis and Applications, **375** (2010) 149–165

[31] J. So and P. Waltman. *A nonlinear boundary value problem arising from competition in the chemostat*, Appl. math. Camp., **32** (1989), 169–183

[32] G. S. K. Wolkowicz and Z. Lu. *Global dynamics of a mathematical model of competition in the chemostat : general response functions and differential death rates*, SIAM J. Appl. Math., **52** (1992), 222–233

[33] G. S. K. Wolkowicz and H. Xia. *Global asymptotic behavior of a chemostat model with discrete delays*, SIAM J. Appl. Math., **57** (1997), 1019–1043

[34] J. H. Wu. *Global bifurcation of coexistence state for the competition model in the chemostat*, Nonlinear Analysis, **39** (2000) 817–835