Dynamics of a kinetic model describing protein exchanges in a cell population

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Abstract

We consider a cell population structured by a positive real number, describing the number of P-glycoproteins carried by the cell. We are interested in the effect of those proteins on the growth of the population: those proteins are indeed involved in the resistance of cancer cells to chemotherapy drugs. To describe this dynamics, we introduce a kinetic model. We then introduce a rigorous hydrodynamic limit, showing that if the exchanges are frequent, then the dynamics of the model can be described by a system of two coupled differential equations. Finally, we also show that the kinetic model converges to a unique limit in large times. The main idea of this analysis is to use Wasserstein distance estimates to describe the effect of the kinetic operator, combined to more classical estimates on the macroscopic quantities.

1 Introduction

In this study, we are interested a population of cells structured by a trait $x \in \mathbb{R}_+$, which measures the quantity of P-glycoprotein (P-gp) carried by the cell. We assume that cells create pairs with a given probability, and that those pairs proceed to an exchange, after which the links between the two cells disappear. During the exchange phase, each cell gives a portion of its protein to the other. We want to describe the dynamics of the density of individuals along the trait space, driven by those exchanges. The P-gp are membrane proteins, which play an important role in tumours. The cells can exchange their P-gp through nanotubes [13, 19, 20], and experiments show that those exchanges have a significant effect on the number of P-gp that the cells carry. The goal of this article is to study the effect of the exchanges on the number of P-gp that are carried by cells.

In this study, we assume that all the cells are genetically identical cells. The trait corresponds to the quantity of P-gp at the surface of the cells. This quantity is measured by using the fluorescence of membrane-tagged antibody. We assume that the trait of new born cells are drawn from a given distribution independent from the trait of the parent (we discuss possible generalisations of this model in the discussion section). In other words, we assume that there is no heritability of the trait. We will however assume that the trait of an individual has an effect on its reproduction rate. This is indeed the case when some chemotherapy drugs are present in the environment of the cells: the P-gp are membrane proteins that can pump several chemicals out of the cells, and which are in particular able to pump cytotoxic drugs out of the cells [21]. The P-gp thus play an important role in the emergence of chemotherapy resistance in tumour cell populations: cancer cells which carry a large number of P-gp are less susceptible to the drugs.

Notice that the exchange phenomenon that we will model and analyse here is related to several of other biological phenomena (see the discussion section), and we believe that the development of new mathematical methods for these phenomena will enable us to better understand their effect.

This article is structured as follows: in Section 2, we derive the model (2.8) from biological phenomena. We detail in particular the derivation of the exchange operator. Then, in Section 3, we state the two
results of this study: a hydrodynamic limit of our kinetic model, and the long time convergence of the solutions of the kinetic model. We also recall the definition of Wasserstein distances, and some properties of those metric that we will use throughout this study. In section 3 we the first result of our study, that is Theorem 3.1. The proof is based on the contracting property of the exchange operator for the $W_2$–Wasserstein distance. Finally, Section 5 is devoted to the second main result of this study, that is Theorem 5.3. The proof of this second result is based on the $W_1$–Wasserstein distance.

2 Modelling

2.1 Derivation of the exchange operator

The model we consider here is based on the assumption that when two cells (the cell 1 and the cell 2) interact, no information is exchanged: the cell 1 does not know how many P-gp the cell 2 carries. The number of P-gp the cell 1 sends to the cell 2 then only depends on its own number of P-gp. If we denote by $x_i$ (resp. $x'_i$) the number of P-gp the cell $i$ contains before (resp. after) the exchange, and $X_i$ the number of P-gp the cell $i$ sends to the other cell, we have the relation:

\[ x'_i = x_i - X_1 + X_2. \] (2.1)

We have assumed that the number of pumps the cell 1 sends to the cell 2 only depends on $x_1$, so that the density of probability $x \to B(x, x_1)$ of $X_1$ only depends on $x_1$. Notice that to be consistent biologically, a cell cannot give a negative number of pumps, or more pumps that it originally had, that is:

\[ \forall x_1 \in \mathbb{R}^+, \quad \text{supp } B(\cdot, x_1) \subset [0, x_1]. \] (2.2)

Note that we will be more precise on the dependency of $B$ in $x_1$ later on. We can relate the law of $x'_1$, that we denote $K(x, x_1, x_2) dx$, to the probability laws of $X_1$ and $X_2$, thanks to (2.1):

\[ \int_0^x K(x, x_1, x_2) dx = \mathbb{P}(x'_1 \leq x | x_1, x_2) = \int_0^\infty \int_0^{x-x_1+y} B(z, x_2) dz B(y, x_1) dy. \]

That is, thanks to a derivation in $x$:

\[ K(x, x_1, x_2) = \int_0^{\infty} B(w, x_1) B(x - x_1 + w, x_2) dw. \]

The above integral is well defined as a convolution. Moreover

\[ \int_0^{\infty} K(x, x_1, x_2) dx = \int_0^{\infty} B(w, x_1) \int_0^{\infty} B(x - x_1 + w, x_2) dx dw = \int_0^{\infty} B(w, x_1) \int_0^{\infty} B(x - x_1 + w, x_2) dx dw = \int_0^{\infty} B(w, x_1) \int_0^{\infty} B(\tilde{w}, x_2) d\tilde{w} dw, \]

therefore

\[ \int_0^{\infty} K(x, x_1, x_2) dx = 1. \]

Since the problem is symmetric, the law of $x'_2$ is $K(x, x_2, x_1)$, and the collision operator can be written, for $u \in \mathcal{P}_2(\mathbb{R})$:

\[ K(u)(x) := \int \frac{1}{2} \left( K(x, x_1, x_2) + K(x, x_2, x_1) \right) u(x_1) u(x_2) dx_1 dx_2 - u(x), \]

which can also be written, thanks to a change of variable $(\tilde{x}_1, \tilde{x}_2) \to (x_2, x_1)$:

\[ K(u)(x) := \int \int K(x, x_1, x_2) u(x_1) u(x_2) dx_1 dx_2 - u(x). \]

If we assume that the law of the number of P-gp the cell 1 (resp. 2) sends to the cell 2 (resp. 1) is proportional to the number of P-gp it originally contained, that is

\[ B(y, x) = \frac{1}{x} B \left( \frac{y}{x} \right), \] (2.3)
For the death term, we assume that the death rate \( \beta n \) is given by
\[
K(x, x_1, x_2) = \frac{1}{x_1 x_2} \int_0^\infty \int_0^\infty \delta_{x=x_1-y_1+y_2} B \left( \frac{y_1}{x_1} \right) B \left( \frac{y_2}{x_2} \right) dy_1 dy_2,
\]
that is
\[
\int_0^\infty K(x, x_1, x_2) h(x) dx = \frac{1}{x_1 x_2} \int_0^\infty \int_0^\infty h(x_1 - y_1 + y_2) B \left( \frac{y_1}{x_1} \right) B \left( \frac{y_2}{x_2} \right) dy_1 dy_2,
\]
for any test function \( h \in L^\infty(\mathbb{R}_+) \). In our study, we will assume that
\[
\int_{(0,1)} B(x) dx = 1.
\]

### 2.2 Derivation of the model

We consider a well-mixed population of cells, and assume that all the cells are genetically identical. Although genetically identical, the cell can differ by the number of P-gp they carry. The population is thus structured by a trait \( x \), where
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During its life, each cell will proceed to exchanges at a rate \( \alpha \), that the traits have no influence on the selection of the exchange partner, which is chosen uniformly among the population. Moreover, we assume that the birth rate of a cell depends on its trait \( x \): as described in the introduction, the P-gp are membrane proteins that pump chemotactic drugs out of the cell. If some drugs are present in the cell culture, the fitness of an individual will directly depend on the number of pumps it carries. We assume that the fitness of an individual is given by \( r + \alpha(x) \), where \( \alpha \in W^{1,\infty}(\mathbb{R}_+) \). The birth is then
\[
\left( \int (r + \alpha(y)) n(t, y) dy \right) n_b(\cdot) = \left( r + \int \alpha(y) \frac{n(t, y)}{N(t)} dy \right) N(t) n_b(\cdot),
\]
where
\[
N(t) := \int n(t, x) dx.
\]

For the death term, we assume that the death rate \( \beta N(t) \) of the cells does not depend on their trait \( x \), and is proportional to the total population. This assumption leads to the classical logistic regulation model, with the following death term:
\[
-\beta N(t) n(t, \cdot).
\]

During its life, each cell will proceed to exchanges at a rate \( \gamma > 0 \) independent of the size of the population (we assume that finding exchange partners is not a limiting factor). Moreover, we assume that the traits have no influence on the selection of the exchange partner, which is chosen uniformly among the population. Considering the exchange operator described in Subsection 2.1, the effect of the exchanges can then be represented as follows:
\[
\gamma \left( \frac{1}{N(t)} \int \int K(\cdot, x_1, x_2) n(t, x_1) n(t, x_2) dx_1 dx_2 - n(t, \cdot) \right).
\]

Bringing all those terms together, we obtain the following model:
\[
\partial_t n(t, x) = \left( r + \int \alpha(y) \frac{n(t, y)}{N(t)} \right) \left( \int n(t, y) dy \right) n_b(x) - \beta N(t) n(t, x) + \gamma \left( \frac{1}{N(t)} \int \int K(x, x_1, x_2) n(t, x_1) n(t, x_2) dx_1 dx_2 - n(t, x) \right),
\]
where \( r, \beta, \gamma > 0, \alpha \in W^{1,\infty}(\mathbb{R}_+) \), \( K \) is defined by (2.4), and the population size \( N(t) \) is given by (2.7).

In this study, we have chosen to focus our attention on the dynamics of solutions, rather than their existence and uniqueness, for which we refer to [2]. The kinetic exchange term indeed induces some difficulties to show the existence of solutions. If \( \text{supp } B \subset [\delta, 1] \), for some \( \delta > 0 \), and \( n_b(\cdot) \) is smooth, then the proof of Lemma 3.1 from [3] can be reproduced to show the existence of solutions of (2.8). In the manuscript, we will formulate our result for any solution \( n = n(t, x) \in L^\infty_{\text{loc}}(\mathbb{R}_+, L^\infty(\mathbb{R}_+)) \) of (2.8).
3 Main results and comments

3.1 Main results

Our analysis will be based on Wasserstein distances, and more precisely, the $W_p$-Wasserstein distances (for $p = 1$ or $p = 2$). We refer to [10] for a description of those distances. Let us recall the properties of these metrics. The distance $W_p$ is defined on the set $\mathbb{R}^+$ of measures with a finite $p$-moment:

$$\mathcal{P}_p(\mathbb{R}^+) := \left\{ \mu \geq 0 \text{ a probability measure over } \mathbb{R}^+, \text{ such that } \int x^p \, d\mu(x) < \infty \right\}.$$ 

for two such probability measures $\mu, \nu \in \mathcal{P}_p(\mathbb{R})$, we define

$$W_p(\mu, \nu) := \left( \sup_{\pi \in \Pi(\mu, \nu)} \int (x - y)^p \, d\pi(x, y) \right)^{\frac{1}{p}},$$

(3.9)

where $\Pi(\mu, \nu)$ is the set on measures on $\mathbb{R}^+_2$ with marginals $\mu$ and $\nu$, that is, for any measurable set $\omega \subset \mathbb{R}^+$,

$$\mu(\omega) = \pi(\omega \times \mathbb{R}^+), \quad \nu(\omega) = \pi(\mathbb{R}^+ \times \omega).$$

For $\mu, \nu \in \mathcal{P}_p(\mathbb{R})$, the Kantorovich formula states that

$$W_p(\mu, \nu)^p = \sup_{(\varphi, \psi) \in \Phi_p} \left( \int \varphi(x) \, d\mu(x) + \int \psi(X) \, d\nu(X) \right),$$

(3.10)

where the supremum is taken over all functions

$$(\varphi, \psi) \in \Phi_p : = \{ (\varphi, \psi) \in C_b(\mathbb{R}) ; \varphi(x) + \psi(X) \leq |x| \}.$$  

Finally, for $p = 1$, (3.10) can be written as the so-called Kantorovich-Rubinstein formula:

$$W_1(\mu, \nu) = \sup_{\|\varphi\|_{\infty} \leq 1} \left( \int \varphi(x) \, d\mu(x) - \int \varphi(x) \, d\nu(x) \right).$$

(3.12)

Our first result is a hydrodynamic limit of the model (2.8): we show that when $\gamma > 0$ is large, it is possible to describe the dynamics of the macroscopic quantities $n(t) = \int n(t, x) \, dx$ and $Z(t, x) = \int \frac{n(t, x)}{\bar{N}(t)} \, dx$, which behave like solutions of the following ordinary differential equation:

$$\begin{cases}
\dot{\bar{N}}(t) = (r + \int \alpha(x) \bar{u}_Z(t, x) \, dx - \beta \bar{N}(t)) \bar{N}(t), \\
\dot{\bar{Z}}(t) = (r + \int \alpha(x) \bar{u}_Z(t, x) \, dx) \left( \int n_0(x) \, dx - \bar{Z}(t) \right).
\end{cases}$$

(3.13)

We also show that the microscopic profile $n(t, x)$ is then characterized by $n(t, x) \sim \bar{N}(t) \bar{u}_Z(t, x)$, where $\bar{u}_Z$ is the unique solution of

$$\bar{u}_Z(x) = \int \int K(x, x_1, x_2) \bar{u}_Z(x_1) \bar{u}_Z(x_2) \, dx_1 \, dx_2, \quad x \in \mathbb{R}^+, \quad (3.14)$$

such that $\int x \bar{u}_Z(x) \, dx = Z$.

Theorem 3.1. Let $M > 0$ as in (2.3), with $B \in \mathcal{P}_2(\mathbb{R}^+)$ satisfying (2.6), $\alpha \in W^{1, \infty}(\mathbb{R}^+)$, $\beta > 0$ and $n_0 \in \mathcal{P}_1(\mathbb{R}^+)$ such that $\int n_0(x) \, dx < M$. For $Z \in \mathbb{R}^+$, let $\bar{u}_Z \in \mathcal{P}_2(\mathbb{R}^+)$ be the unique solution of (3.14), such that $\int x \bar{u}_Z(x) \, dx = Z$. We define $t \mapsto (\bar{N}(t), \bar{Z}(t)) \in (\mathbb{R}^+)^2$ as the solution of (3.13), with

$$(\bar{N}(0), \bar{Z}(0)) = \left( \int n_0^0(x) \, dx, \frac{\int n_0^0(x) \, dx}{\int n_0(x) \, dx} \right).$$

There exists $C > 0$ and $\nu > 0$ such that if $n = n(t, x) \in L^\infty_{loc}(\mathbb{R}^+, L^\infty(\mathbb{R}^+))$ is a solution of (2.8) with initial value $n^0$, then, for $t \geq 0$,

$$W_2 \left( \frac{n(t, \cdot)}{\bar{N}(t)}, \bar{u}_Z(t) \right) + \left| \bar{N}(t) - \bar{N}(t) \right| \leq \frac{C}{\gamma^2},$$

(3.15)

where $N$ is defined by (2.4).
Remark 3.2. To study this problem, we will need to first consider a simpler model, where only exchanges are present (see [1,24]). The estimates we derive on the exchange operator (Section 4.1) and on the pure exchange model (Section 4.2) have been considered for related models in e.g. [12] and [2], using different methods (either Fourier transform techniques, or probabilist tools). To improve the readability of our study, we have derived all the necessary estimates using Wasserstein distance methods.

Our second result is the long-time convergence of solutions of (2.8) to a unique steady-state, involving both the exchanges and the birth-death process:

**Theorem 3.3.** Let $M > 0$, $K$ as in (2.4), with $B \in \mathcal{P}_2(\mathbb{R}^+) \text{ satisfying (2.6)}$, $\alpha \in W^{1,\infty}(\mathbb{R}^+)$, $\beta, \gamma > 0$ and $n_b \in \mathcal{P}_1(\mathbb{R}^+)$ such that $\int x n_b(x) \, dx < M$. If

$$\kappa := r + \min_{x \in \mathbb{R}^+} \alpha(x) - 6M \|\alpha'\|_{\infty} > 0,$$

then there exists a unique measure $x \mapsto \bar{N}(x)$, with $\bar{n} \in \mathcal{P}_1(\mathbb{R}^+)$, such that all solutions $n = n(t, x) \in L^\infty_{\text{loc}}(\mathbb{R}^+, L^\infty(\mathbb{R}^+))$ of (2.8) converge to $\bar{n}$ as $t \to \infty$ for the weak-* topology of measures over $\mathbb{R}^+$, provided $\int x n(0, x) \, dx < M$. More precisely, there exists a constant $C > 0$ such that

$$W_1\left(\frac{n(t, \cdot)}{\int n(t, x) \, dx}, \bar{n}\right) \leq C e^{-\kappa t},$$

$$\left|\int n(t, x) \, dx - \bar{N}\right| \leq C e^{-\min(\kappa, \frac{M\gamma}{\beta}) t}.$$

### 3.2 Related works and discussion

In [12], a model was proposed to model the exchange of P-gp in a cell population. The analysis was based on a strong assumption on the nature of exchanges: the result of an exchange between two cells carrying $x_1, x_2 \in \mathbb{R}^+$ P-gp originally, was an equilibration of those traits: after the exchange, the cells traits are respectively $x_1' = x_1 + f(x_2 - x_1)$ and $x_2' = x_2 - f(x_2 - x_1)$, for some $f \in (0, 1)$. After the derivation of this exchange operator, the authors show the existence of solutions for the model (where only exchanges are present), and prove that all solutions converge to a Dirac mass (that is all the individuals ultimately carry the same number of P-gp). The exchange operator derived in Section 2.1 is an extension of their exchange model (Section 4.2) have been considered for related models in e.g. [3] and [2], using different respect to both the exchanges and the birth-death process:

3.2 Related works and discussion

In 1978, Tanaka introduced a new entropy functional for the Boltzmann equation. This functional described a contracting effect of the equation’s flow, and allowed the author to describe the long-time convergence of solutions. In [17], this idea was extended to the inelastic Boltzmann equation. We show in this article that the methods developed in the two articles mentioned above can be used to study the dynamics of the solutions of (2.8). The main idea is to consider the Wasserstein distance between two solutions of the equation. It is then possible to show that the exchange operator tends to decrease the distance between solutions: in the case of the $W_2$–Wasserstein distance, the operator decreases the distance between solutions, while for the $W_1$–Wasserstein distance, the operator cannot increase the distance between solutions (eventhough it is not a strict contraction). The $W_2$–Wasserstein distance then provides a powerful contraction, which we use to derive a hydrodynamic limit of the equation, Theorem 3.1. However, the $W_2$–Wasserstein distance does not behave very well when the birth-death process plays a role as important as the exchange process. The $W_1$–Wasserstein distance is then better adapted to the analysis, and it allowed us to prove the long time convergence of solutions of the kinetic model (2.8), see Theorem 3.3.

The Tanaka functional and the wasserstein distance methods employed in our study are indeed related to another set of distances between probability measures, based on the Fourier transform. Those methods

![Image](image_url)
were introduced in [5, 6], and we refer to [10] for a description of the links existing between those metrics and Wasserstein distances. Those Fourier-based arguments have proven useful to study the properties of the Boltzmann equation in the Maxwellian case, and they could probably also be used to study the dynamics of (2.8). The Fourier-based distance was used to study a range of models from econometrics [3] and opinion formation theory. Let us finally mention [2], where probabilist methods are used to prove the contractivity of a large class of kinetic operators.

Another important ingredient of our model is the birth and deaths of individuals, which is impacted by the trait $x$ of individuals. It is a priori difficult to use the tools described above in this context: the solutions are no longer probability measures, and the birth/death are of a different nature than the effect of exchanges (or collision in the case of the Boltzmann equation), which merely moves the mass along the trait $x$. Our strategy is to introduce the size $N(t)$ of the population, and the normalized population $\hat{n}(t, x) := \frac{n(t, x)}{N(t)}$. In the special case where $\alpha(x) = ax + b$, it is possible to derive closed equations on $N(t)$ and $Z(t) = \int \hat{n}(t, x) x \, dx$, and the problem is then very close to the situation where only the exchanges are considered (see Theorem 4.4 and Remark 4.5). In more general situations, the dynamics of $N$ and $\hat{n}$ are coupled. We show however that the contracting effects of the exchange operator (discussed above) and the simple dynamics of the macroscopic quantities $N$ and $Z$ can be combined to study the dynamics of solutions of (2.8).

In this article, we focus our attention on the exchange phenomena: we believe that the exchange term derived in Subsection 2.1 is biologically convincing model for P-gp transfers happening through nanotubes (see [19]). Concerning the birth-death process however, many other modelling choices are possible. We decided to consider a simple situation, to avoid additional difficulties to the analysis (although we avoided artificially simple situations, see Remark 4.5). Here are the some generalizations that could be interesting in terms of biological applications:

- If a parent cell carrying $x$ P-glycoproteins gives rise to a daughter cell, we could assume that the traits $x'$ and $y'$ of the parent and daughter cells are given by $x' = y' = x + x_0$, where $x_0$ is drawn from a distribution $x_0$.
- A natural extension of this work would be to assume that the P-gp are continuously created by living cells, rather than created at birth only.
- In this study, we have considered cytotoxic drugs, that are toxic to cells because they increase their death rate. It would also be interesting to consider cytostatic drugs, that affect their birth rates.
- The exchanges described by (2.8) happen through nanotubes between cells (see [19]). P-gp are indeed also known to be exchanged through the release of microparticles. Those micro-particles, that contain a certain number of P-gp, are then captured by any other cell. This second mechanism could probably be included in the model (2.8) thanks to a BGK-type operator.

Finally, to study the effect of exchanges on the emergence and propagation of resistance in tumors, one would like to consider several types of cells (with different genotypes), with exchanges happening across the different types. We believe the methods develop here will be helpful to consider those more complicated situations.

Finally, let us mention two biological problems linked to the present article. The first class of biological problematic is cooperation in biological populations. Cooperation is a widespread behaviour: it exists at all levels of life, and appearance and stability of such phenomena is a challenging problem, and we refer to [14, 18, 1]. One of the mechanisms of cooperation is the exchange of goods. These exchanges could be modelled with an operator similar to the one we derived in Section 2.1. The second class of problems is linked to sexual reproduction, where the formation of gametes and recombinations implies that the DNA of the offspring is a combination of the genomes of both parents. A model used in biology to describe the effect of those events on a given phenotype is the so-called infinitesimal model, see [8, 9]. The properties of the operator appearing in this model are similar to the exchange operator described in Section 2.1. We believe the analysis methods developed here could also be useful in those two other contexts. In particular, they could be an interesting step towards a rigorous mathematical description of the hydrodynamic limits introduced in [16].
4 A Hydrodynamic limit for the model (2.8)

4.1 Contraction of the exchanges in the $W_2$-distance

The following lemma details the effect of an exchange on the $W_2$-Wasserstein distance between two cells:

**Lemma 4.1.** Let $x_1, x_2, x'_1, x'_2 \in \mathbb{R}_+^*$, and $K$ as in (2.4). We define $\lambda_1, \lambda_2 \in [0, 1]$ as

$$
\lambda_1 := \int x B(x) \, dx, \quad \lambda_2 := \int x^2 B(x) \, dx.
$$

We have

$$
W^2_2\left(K(\cdot, x_1, x_2), K(\cdot, x'_1, x'_2)\right) \leq (1 + \lambda_2 - 2\lambda_1)(x_1 - x'_1)^2 + \lambda_2(x_2 - x'_2)^2
+ 2(1 - \lambda_1)\lambda_1(x_1 - x'_1)(x_2 - x'_2).
$$

**Proof of Lemma 4.1.** To estimate the Wasserstein distance $W^2_2\left(K(\cdot, x_1, x_2), K(\cdot, x'_1, x'_2)\right)$, we will use the Kantorovich dual formula. We consider $(\varphi, \psi) \in \Phi_2$ (see (3.11)), and estimate

$$
I = \int \varphi(x)K(x, x_1, x_2) \, dx + \int \psi(X)K(X, x'_1, x'_2) \, dX
= \int \varphi(x) \int \int \delta_{x=x_1-y_1+y_2} \frac{1}{x_1x_2} B \left(\frac{y_1}{x_1}\right) B \left(\frac{y_2}{x_2}\right) \, dy_1 \, dy_2 \, dx
+ \int \psi(X) \int \int \delta_{x=x'_1-y'_1+y'_2} \frac{1}{x'_1x'_2} B \left(\frac{y'_1}{x'_1}\right) B \left(\frac{y'_2}{x'_2}\right) \, dy'_1 \, dy'_2 \, dX
= \int \int \varphi(x_1 - y_1 + y_2) \frac{1}{x_1x_2} B \left(\frac{y_1}{x_1}\right) B \left(\frac{y_2}{x_2}\right) \, dy_1 \, dy_2
+ \int \int \psi(x'_1 - y'_1 + y'_2) \frac{1}{x'_1x'_2} B \left(\frac{y'_1}{x'_1}\right) B \left(\frac{y'_2}{x'_2}\right) \, dy'_1 \, dy'_2.
$$

and then, thanks to the changes of variable $\tilde{y}_i = \frac{y_i}{x_i}$ and $\tilde{y}'_i = \frac{y'_i}{x'_i}$ for $i = 1, 2$, we get

$$
I = \int \int \varphi(x_1 - x_1y_1 + x_2y_2)B \left(\frac{y_1}{x_1}\right) B \left(\frac{y_2}{x_2}\right) \, dy_1 \, dy_2
+ \int \int \psi(x'_1 - x'_1y'_1 + x'_2y'_2)B \left(\frac{y'_1}{x'_1}\right) B \left(\frac{y'_2}{x'_2}\right) \, dy'_1 \, dy'_2
= \int \int (\varphi(x_1 - x_1y_1 + x_2y_2) + \psi(x'_1 - x'_1y'_1 + x'_2y'_2))B \left(\frac{y_1}{x_1}\right) B \left(\frac{y_2}{x_2}\right) \, dy_1 \, dy_2.
$$

We can now use the fact that $(\varphi, \psi) \in \Phi_2$ (see (3.11)), and thus

$$
I \leq \int \int |(x_1 - x_1y_1 + x_2y_2) - (x'_1 - x'_1y'_1 + x'_2y'_2)|^2 \, dy_1 \, dy_2
$$

$$
= \int \int |(x_1 - x'_1)(1 - y_1) + (x_2 - x'_2)y_2|^2 \, dy_1 \, dy_2
$$

$$
= \int \int \left((x_1 - x'_1)^2(1 - y_1)^2 + (x_2 - x'_2)^2y_2^2 + 2(x_1 - x'_1)(x_2 - x'_2)(1 - y_1)y_2\right)B \left(\frac{y_1}{x_1}\right) B \left(\frac{y_2}{x_2}\right) \, dy_1 \, dy_2
$$

$$
= (x_1 - x'_1)^2 \int (1 - y_1)^2B \left(\frac{y_1}{x_1}\right) \, dy_1 + (x_2 - x'_2)^2 \int y_2^2B \left(\frac{y_2}{x_2}\right) \, dy_2
$$

$$
+ 2(x_1 - x'_1)(x_2 - x'_2) \left(\int (1 - y_1)B \left(\frac{y_1}{x_1}\right) \, dy_1 \right) \left(\int y_2B \left(\frac{y_2}{x_2}\right) \, dy_2\right),
$$

and then, with the notations (4.16),

$$
I \leq (x_1 - x'_1)^2(1 + \lambda_2 - 2\lambda_1) + (x_2 - x'_2)^2\lambda_2 + 2(x_1 - x'_1)(x_2 - x'_2)(1 - \lambda_1)\lambda_1.
$$
Since this is true for any \((\varphi, \psi) \in \Phi_2\) (see (3.11)), we can use this estimate and (3.10) to show that
\[
W_2^2 \left( K(\cdot, x_1, x_2), K(\cdot, x_1', x_2') \right) = \max_{(\varphi, \psi) \in \Phi_2} I
\leq (1 + \lambda_2 - 2\lambda_1)(x_1 - x_1')^2 + \lambda_2(x_2 - x_2')^2 + 2(1 - \lambda_1)\lambda_1(x_1 - x_1')(x_2 - x_2').
\]

\[\square\]

We now show that the exchange dynamics has a contraction effect on the population, in the sense of the \(W_2\)-distance:

**Lemma 4.2.** Let \(K\) defined by (2.4), with \(B \in \mathcal{P}_2(\mathbb{R}_+)\) satisfying (2.10). Then, for any \(u_1, u_2 \in \mathcal{P}_2(\mathbb{R}_+)\) such that
\[
\int xu_1(x) \, dx = \int xu_2(x) \, dx,
\]
we have
\[
W_2(u_1', u_2') \leq \left( 1 + 2 \int x(x - 1)B(x) \, dx \right)^\frac{1}{2} W_2(u_1, u_2),
\]
where \(u_i'(x) := \int K(x, x_1, x_2)u_i(x_1)u_i(x_2) \, dx_1 \, dx_2\) for \(i = 1, 2\). Moreover,
\[
\left( 1 + 2 \int x(x - 1)B(x) \, dx \right)^\frac{1}{2} < 1.
\]

**Proof of Lemma 4.2.** We want to estimate the \(W_2\) distance between \(u'_1\) and \(u'_2\) thanks to (4.10). We consider \((\varphi, \psi) \in \Phi_2\), and estimate
\[
I = \int \varphi(x)u'_1(x) \, dx + \int \psi(X)u'_2(X) \, dX
= \int \varphi(x) \int \int K(x, x_1, x_2)u_1(x_1)u_1(x_2) \, dx_1 \, dx_2 \, dx
+ \int \psi(X) \int \int K(X, x_1', x_2')u_2(x_1')u_2(x_2') \, dx_1' \, dx_2' \, dX
= \int \int \left( \int \varphi(x)K(x, x_1, x_2) \, dx \right) u_1(x_1)u_1(x_2) \, dx_1 \, dx_2
+ \int \int \left( \int \psi(X)K(X, x_1', x_2') \, dX \right) u_2(x_1')u_2(x_2') \, dx_1' \, dx_2'.
\]

Remember that \(u_1, u_2 \in \mathcal{P}_2(\mathbb{R}_+)\) implies \(\int u_1(x) \, dx = \int u_2(x) \, dx = 1\). It follows that
\[
I = \int_{\mathbb{R}_+} \left( \int \varphi(x)K(x, x_1, x_2) \, dx + \int \psi(X)K(X, x_1', x_2') \, dX \right) u_1(x_1)u_1(x_2)u_2(x_1')u_2(x_2') \, dx_1 \, dx_2 \, dx_1' \, dx_2'.
\]

Let now \(\pi_t \in \Pi(u_1, u_2)\) (see (3.9)). The above equality can be rewritten as follow
\[
I = \int_{\mathbb{R}_+^4} \left( \int \varphi(x)K(x, x_1, x_2) \, dx + \int \psi(X)K(X, x_1', x_2') \, dX \right) d\pi_t(x_1, x_1', x_2, x_2')
\leq \int_{\mathbb{R}_+^4} W_2^2 \left( K(\cdot, x_1, x_2), K(\cdot, x_1', x_2') \right) d\pi_t(x_1, x_1') d\pi_t(x_2, x_2'),
\]
where we have used the fact that \((\varphi, \psi) \in \Phi_2\) as in formula (4.10). We now use the result of Lemma 4.1.
We notice next that thanks to (4.19),

\[ I \leq \int \int \left( (1 + \lambda_2 - 2\lambda_1)(x_1 - x'_1)^2 + \lambda_2(x_2 - x'_2)^2 + 2(1 - \lambda_1)\lambda_1(x_1 - x'_1)(x_2 - x'_2) \right) \]
\[ d\pi_t(x_1, x'_1) d\pi_t(x_2, x'_2) \]
\[ \leq (1 + \lambda_2 - 2\lambda_1) \int \left( \int (x_1 - x'_1)^2 d\pi_t(x_1, x'_1) \right) d\pi_t(x_2, x'_2) \]
\[ + \lambda_2 \int \left( \int (x_2 - x'_2)^2 d\pi_t(x_2, x'_2) \right) d\pi_t(x_1, x'_1) \]
\[ + 2(1 - \lambda_1)\lambda_1 \left( \int (x_1 - x'_1) d\pi_t(x_1, x'_1) \right) \left( \int (x_2 - x'_2) d\pi_t(x_2, x'_2) \right). \]  
(4.22)

We notice next that thanks to (4.19),

\[ \int (x - x') d\pi_t(x, x') = - \int xu_1(x) dx - \int xu_2(x) dx = 0, \]  
(4.23)

and then, since this estimate holds for any \((\varphi, \psi) \in \Phi_2\), thanks to the Kantorovich dual formula (3.10),

\[ W^2_2(u'_1, u'_2) \leq (1 + 2\lambda_2 - 2\lambda_1) \int (x_1 - x'_1)^2 d\pi_t(x_1, x'_1). \]

Since this inequality holds for any \(\pi_1 \in \Pi(u_1, u_2)\) (with the notation of (4.24)), we can take the minimum over such \(\pi_t\), and get

\[ W^2_2(u'_1, u'_2) \leq (1 + 2\lambda_2 - 2\lambda_1)W^2_2(u_1, u_2) \]
\[ = \left( 1 + 2 \int x(x - 1)B(x) dx \right) W^2_2(u_1, u_2). \]

Finally, \((1 + 2 \int x(x - 1)B(x) dx)^{\frac{1}{2}} < 1\) is a direct consequence of (2.6). \(\square\)

### 4.2 Steady-states of the pure exchange model

We consider a model where the population is only affected by exchanges, that is

\[ \partial_t u(t, x) = \int \int K(x, x_1, x_2)u(t, x_1)u(t, x_2) dx_1 dx_2 - u(t, x), \]  
(4.24)

where \(K\) is defined by (4.23). The first result on this model is the existence of steady-states:

**Theorem 4.3.** Let \(K\) defined by (4.23), with \(B \in \mathcal{P}_2(\mathbb{R}^+)\) satisfying (2.6), and \(Z \in \mathbb{R}^+\). There is a unique steady-state \(\bar{u}\) of (4.24) such that \(\int x\bar{u}(x) dx = Z\).

Moreover, there exists \(C > 0\) such that for any \(Z_1, Z_2 \geq 0\),

\[ W_2(\bar{u}_{Z_1}, \bar{u}_{Z_2}) \leq C|Z_1 - Z_2|. \]  
(4.25)

**Proof of Theorem 4.3.** Notice that \(\{u \in \mathcal{P}_2(\mathbb{R}^+); \int xu(x) dx = Z\}\) is a closed subset of \(\mathcal{P}_2(\mathbb{R}^+)\) for \(W_2\), and then \(\{u \in \mathcal{P}_2(\mathbb{R}^+); \int xu(x) dx = Z\}\) is a complete metric space (see e.g. [24]). Let

\[ T : u \in \mathcal{P}_2(\mathbb{R}^+) \mapsto \left( \int \int K(\cdot, x_1, x_2)u(x_1)u(x_2) dx_1 dx_2 \right). \]  
(4.26)

More precisely, for any \(h \in L^\infty(\mathbb{R}^+)\), thanks to (2.5),

\[ \int h(x)T(u)(x) dx := \int \left( \int \left( \int h(x_1 - y_1 + y_2)B \left( \frac{y_1}{x_1} \right) dy_1 \right) B \left( \frac{y_2}{x_2} \right) dy_2 \right) u(x_1) dx_1 \]
\[ \leq ||h||_{L^\infty}, \]
and
\[
\int x^2 T(u)(x) \, dx = \int \int \left( \int x^2 K(x, x, x) \, dx \right) u(x_1) u(x_2) \, dx_1 \, dx_2
\]
\[
= \int \int \left( \int \left( x_1 - y_1 + y_2 \right) B \left( \frac{y_1}{x_1} \right) B \left( \frac{y_2}{x_2} \right) \, dy_1 \, dy_2 \right) u(x_1) u(x_2) \, dx_1 \, dx_2
\]
\[
= \int \int \left( x_1^2 (1 + \lambda_2 - 2 \lambda_1) + x_2^2 \lambda_2 + 2 x_1 x_2 \left( \lambda_1 - \lambda_2^2 \right) \right) u(x_1) u(x_2) \, dx_1 \, dx_2
\]
\[
= \left( \int x^2 u(x) \, dx \right) \left( 1 + 2 \lambda_2 - 2 \lambda_1 \right) + 2 \lambda_2^2 \left( \lambda_1 - \lambda_2^2 \right) < \infty.
\]

Note that for any \( x_1, x_2 \geq 0 \), \( \text{supp} \, K(\cdot, x_1, x_2) \) is bounded, the unbounded test function \( x \mapsto x^2 \) can thus be modified to become an \( L^\infty \) test function, for which \( \int x^2 K(x, x, x) \, dx \) is well defined. The computation above is thus valid. We can thus define \( T \) as an operator mapping \( \mathcal{P}(\mathbb{R}^+) \) into itself. Moreover, for any \( u \in \{ u \in \mathcal{P}(\mathbb{R}^+); \int xu(x) \, dx = Z \} \),
\[
\int x T(u)(x) \, dx = \int \int \left( \int x K(x, x, x) \, dx \right) u(x_1) u(x_2) \, dx_1 \, dx_2
\]
\[
= \int \int \left( \int \left( x_1 - y_1 + y_2 \right) B \left( \frac{y_1}{x_1} \right) B \left( \frac{y_2}{x_2} \right) \, dy_1 \, dy_2 \right) u(x_1) u(x_2) \, dx_1 \, dx_2
\]
\[
= \int \int \left( x_1 - x_1 \lambda_1 + x_2 \lambda_1 \right) u(x_1) u(x_2) \, dx_1 \, dx_2
\]
\[
= \int xu(x) \, dx = Z,
\]
so that the application \( T \) maps \( \{ u \in \mathcal{P}(\mathbb{R}^+); \int xu(x) \, dx = Z \} \) into itself. Finally, thanks to Lemma 4.2, the application is a strict contraction on this set. We can then apply the Banach fixed point Theorem, to show that there exists then a unique measure \( \bar{u} \in \{ u \in \mathcal{P}(\mathbb{R}^+); \int xu(x) \, dx = Z \} \), such that
\[
\forall x \in \mathbb{R}^+, \quad \bar{u} = T(\bar{u}).
\]
\( \bar{u} \) is then the unique steady-state of (4.23) such that \( \int xu(x) \, dx = Z \).

We can reproduce the proof of Lemma 4.2 until (4.22) with \( u_1 := \bar{u}_{Z_1} \) and \( u_2 := \bar{u}_{Z_2} \). Here, (4.23) becomes
\[
\int (x - x') \, d\pi_t(x, x') = \int xu_1(x) \, dx - \int xu_2(x) \, dx = Z_1 - Z_2,
\]
and then, since this estimate holds for any \( (\varphi, \psi) \in \Phi_2 \), thanks to the Kantorovich dual formula (3.10),
\[
W_2^2(u_1', u_2') \leq (1 + 2 \lambda_2 - 2 \lambda_1) \int (x_1 - x'_1)^2 \, d\pi_t(x_1, x'_1) + 2(1 - \lambda_1) \lambda_1 |Z_1 - Z_2|^2.
\]
Since this inequality holds for any \( \pi_t \in \Pi(u_1, u_2) \) (with the notation of (3.9)), we can take the minimum over such \( \pi_t \), and get
\[
W_2^2(u_1', u_2') \leq (1 + 2 \lambda_2 - 2 \lambda_1) W_2^2(u_1, u_2) + 2(1 - \lambda_1) \lambda_1 |Z_1 - Z_2|^2.
\]
Now, \( u_1 = \bar{u}_{Z_1} \) and \( u_2 = \bar{u}_{Z_2} \) are steady-points of \( T \), and then, \( u_1' = u_1, u_2' = u_2 \). Thus,
\[
W_2^2(\bar{u}_{Z_1}, \bar{u}_{Z_2}) \leq \frac{(1 - \lambda_1) \lambda_1}{\lambda_1 - \lambda_2} |Z_1 - Z_2|^2.
\]
4.3 Dynamics of the pure exchange model

We show here that the equation (4.24) induces a contraction for the $W_2$-distance, which implies in particular that all solutions converge to the steady-state given by Theorem 4.3.

**Theorem 4.4.** Let $K$ defined by (2.24), with $B \in \mathcal{P}_2(\mathbb{R}_+)$ satisfying (2.6), and $Z \in \mathbb{R}_+$.

Let two non negative solutions $u = u(t, x) \in L^\infty_{loc}(\mathbb{R}_+, L^\infty(\mathbb{R}_+))$ and $v = v(t, x) \in L^\infty_{loc}(\mathbb{R}_+, L^\infty(\mathbb{R}_+))$ of (4.24) such that

$$Z = \int xu(0, x) \, dx = \int xv(0, x) \, dx.$$  

Then, $u$ and $v$ satisfy

$$W_2^2(u(t, \cdot), v(t, \cdot)) \leq W_2^2(u(0, \cdot), v(0, \cdot)) e^{-ct},$$  

(4.27)

with $c = \int x(1 - x)B(x) \, dx > 0$.

In particular, any solution $u = u(t, x)$ of (4.24) such that $\int xu(0, x) \, dx = Z$ converges to the steady-state $\bar{u}$ defined in Theorem 4.3.

$$W_2^2(u(t, \cdot), \bar{u}) \leq W_2^2(u(0, \cdot), \bar{u}) e^{-ct},$$  

(4.28)

where $c = \int x(1 - x)B(x) \, dx > 0$.

**Remark 4.5.** If $\alpha(x) = ax + b$, the dynamics of $N(t)$ and $Z(t) = \int z \frac{n(t, z)}{N(t)} \, dz$ only depends on $N$ and $Z$, and not on the detailed distribution $n$ of the population. It is then possible to show that $N$ and $Z$ converge exponentially to a limit $(N, Z)$. We can then use the contracting properties of the exchange operator, just as in the proof of Theorem 4.4 to prove the convergence of the solution $n$ to a unique limit. If $\alpha(\cdot)$ is more complicated however, it is not possible to write closed equations on $N$ and $Z$, and to describe the long-time dynamics of the solution then, we will need to use a different metric, namely the $W_1$-Wasserstein distance, see Theorem 3.3.

**Proof of Theorem 4.4.** We now consider solutions $t \mapsto u(t, \cdot) \in \mathcal{P}_2(\mathbb{R}_+)$ of (4.24), which write

$$u(t, x) = e^{-t}u(0, x) + \int_0^t e^{-(t-s)} \int K(x, x_1, x_2)u(t, x_1)u(t, x_2) \, dx_1 \, dx_2.$$  

Let $u$ and $v$ be two solutions of (4.24) with respective initial conditions $u_0$, $v_0$. We want to estimate the $W_2$ distance between $u$ and $v$ thanks to (3.10). We then consider $(\varphi, \psi) \in \Phi_2$, and estimate

$$I = \int \varphi(x)u(t, x) \, dx + \int \psi(X)v(t, X) \, dX$$

$$= e^{-t} \left( \int \varphi(x)u(0, x) \, dx + \int \psi(X)v(0, X) \, dX \right)$$

$$+ \int_0^t e^{-(t-s)} \left[ \int \varphi(x) \int K(x, x_1, x_2)u(t, x_1)u(t, x_2) \, dx_1 \, dx_2 \right.$$

$$+ \int \psi(X) \int K(X, x'_1, x'_2)v(t, x'_1)v(t, x'_2) \, dx'_1 \, dx'_2 \, dX \right] \, ds$$

$$\leq e^{-t} W_2^2(u(0, \cdot), v(0, \cdot)) + \int_0^t (1 + 2\lambda_2 - 2\lambda_1) W_2^2(u(s, \cdot), v(s, \cdot)) \, ds,$$

thanks to the Kantorovich formula (3.10) and Lemma 4.2. Since this holds for any $(\varphi, \psi) \in \Phi_2$ (see (3.10)), we can pass to the supremum over such functions to show that

$$W_2^2(u(t, \cdot), v(t, \cdot)) \leq e^{-t} W_2^2(u(0, \cdot), v(0, \cdot)) + (1 + 2\lambda_2 - 2\lambda_1) \int_0^t e^{s-t} W_2^2(u(s, \cdot), v(s, \cdot)) \, ds.$$

This estimate can be written

$$y(t) \leq W_2^2(u(0, \cdot), v(0, \cdot)) + \kappa \int_0^t y(s) \, ds,$$
where \( y(t) := e^{tW_2^2(u(t,\cdot),v(t,\cdot))} \). Then, thanks to the Gronwall inequality, \( y(t) \leq W_2^2(u(0,\cdot),v(0,\cdot)) e^{(1+2\lambda_2-2\lambda_1)t} \), and (4.27) follows. Finally, when \( v = \tilde{u} \), a steady-state of (4.24), (4.27) proves the exponential convergence of any solution (such that \( \int xu(0,x) \, dx = Z \)) of (4.24) to \( \tilde{u} \). The proof of Theorem 4.3 is then complete. 

4.4 Proof of Theorem 3.1

Step 1: Equations on \( N(t) \), \( Z(t) \), and \( \frac{u(t,\cdot)}{N(t)} \)

For \( t \geq 0 \), we define \( N(t) \) by (2.7), and \( Z(t) \) as

\[
Z(t) := \int x \frac{n(t,x)}{N(t)} \, dx. \tag{4.29}
\]

We can integrate the equation (2.8) to get the following equation on \( N \):

\[
\frac{d}{dt} N(t) = \left( r + \int \alpha(x) \frac{n(t,x)}{N(t)} \, dx - \beta N(t) \right) N(t), \tag{4.30}
\]

which implies that for all \( t \geq 0, \, 0 \leq N(t) \leq \max \left( N(0), \frac{r+\beta\|\alpha\|_{L^\infty}}{\beta} \right) \), and

\[ \|N'(t)\|_{L^\infty} \leq C, \]

where the constant \( C > 0 \) is independent of \( \gamma > 0 \). If we derive \( Z \), we get

\[
\frac{d}{dt} Z(t) = \frac{1}{N(t)} \int x \frac{\partial_t n(t,x)}{N(t)} \, dx - \frac{N'(t)}{N(t)^2} \int x n(t,x) \, dx
\]

\[
= \left( r + \int \alpha(x) \frac{n(t,x)}{N(t)} \, dx \right) Z_b - \beta N(t) Z(t)
\]

\[
- \left( r + \int \alpha(x) \frac{n(t,x)}{N(t)} \, dx - \beta N(t) \right) Z(t)
\]

\[
= \left( r + \int \alpha(x) \frac{n(t,x)}{N(t)} \, dx \right) (Z_b - Z(t)), \tag{4.31}
\]

where \( Z_b := \int x n_b(x) \, dx \). Since \( \alpha \geq 0 \), we have that for all \( t \geq 0, \, 0 \leq Z(t) \leq \max \left( \int x \frac{n_0(x)}{N(0)} \, dx, Z_b \right) \), and

\[ \|Z'(t)\|_{L^\infty} \leq C, \]

where the constant \( C > 0 \) is independent of \( \gamma > 0 \).

We introduce the following normalized population:

\[
\tilde{n}(t,x) := \frac{n(t,x)}{N(t)}, \tag{4.32}
\]

which satisfies

\[
\frac{\partial_t \tilde{n}(t,x)}{N(t)} = \frac{1}{\int n(t,y) \, dy} - \frac{n(t,x)}{\int n(t,y) \, dy} \frac{d}{dt} \int n(t,x) \, dx
\]

\[
= \left( r + \int \alpha(y) \tilde{n}(t,y) \, dy \right) n_b(x) - \beta n(t,x)
\]

\[
+ \frac{\gamma}{N(t)^2} \int \int K(x,x_1,x_2) \tilde{n}(t,x_1) n(t,x_2) \, dx_1 \, dx_2
\]

\[
- \frac{\gamma}{N(t)} n(t,x)
\]

\[
- \left[ \left( r + \int \alpha(y) \tilde{n}(t,y) \, dy \right) - \beta N(t) \right] \frac{n(t,x)}{N(t)},
\]
that is
\[
\partial_t \tilde{n}(t, x) = \left( r + \int \alpha(y) \tilde{n}(t, y) \, dy \right) (n_0(x) - \tilde{n}(t, x)) \\
+ \gamma \left[ \int \int K(x, x_1, x_2) \tilde{n}(t, x_1) \tilde{n}(t, x_2) \, dx_1 \, dx_2 - \tilde{n}(t, x) \right].
\] (4.33)

**Step 2: uniform bound on the second moment of \( n(t, \cdot) \)**

\( \tilde{n} \) satisfies
\[
\tilde{n}(t, x) = \tilde{n}(0, x)e^{-\gamma t} \\
+ \int_0^t e^{-\gamma (t-s)} \left[ \left( r + \int \alpha(y) \tilde{n}(s, y) \, dy \right) (n_0(x) - \tilde{n}(s, x)) \\
+ \gamma T(\tilde{n}(s, \cdot)) \right] \, ds,
\]

and then
\[
\int \tilde{n}(t, x)^2 \, dx = \left( \int \tilde{n}(0, x)^2 \, dx \right) e^{-\gamma t} \\
+ \int_0^t e^{-\gamma (t-s)} \left[ \left( r + \int \alpha(y) \tilde{n}(s, y) \, dy \right) \left( \int \tilde{n}_b(x)^2 \, dx - \int \tilde{n}(s, x)^2 \, dx \right) \\
+ \gamma \int T(\tilde{n}(s, \cdot))(x)^2 \, dx \right] \, ds.
\] (4.34)

We use Lemma 12 to estimate the last term: since \( Z(t) \) is uniformly bounded,
\[
\sqrt{\int x^2 T(\tilde{n}(s, \cdot))(x) \, dx} = W_2(T(\tilde{n}(s, \cdot)), \delta_0) \leq W_2(T(\tilde{n}(s, \cdot)), T(u_{Z(s)})) + W_2(u_{Z(s)}, \delta_0)
\]
\[
\leq \left( 1 + 2 \int x(x-1)B(x) \, dx \right) W_2(\tilde{n}(s, \cdot), u_{Z(s)}) + C
\]
\[
\leq \left( 1 + 2 \int x(x-1)B(x) \, dx \right) \sqrt{\int x^2 \tilde{n}(s, x) \, dx} + C,
\]

and then \( \int x^2 T(\tilde{n}(s, \cdot))(x) \, dx \leq \kappa \int x^2 \tilde{n}(s, x) \, dx + C \), for some \( \kappa \in (0, 1) \). If we inject this estimate in (4.33), we get
\[
\int \tilde{n}(t, x)^2 \, dx \leq C + \int_0^t e^{-\gamma (t-s)} \kappa\gamma \left( \int \tilde{n}(s, x)^2 \, dx \right) \, ds
\]
\[
\leq C + \kappa \sup_{s \in [0,t]} \int \tilde{n}(s, x)^2 \, dx \left( \gamma \int_0^t e^{-\gamma (t-s)} \, ds \right)
\]
\[
\leq C + \kappa \sup_{s \in [0,t]} \int \tilde{n}(s, x)^2 \, dx.
\]

Thus, for all \( t \geq 0 \),
\[
\int \tilde{n}(t, x)^2 \, dx \leq \max \left( \int \tilde{n}(0, x)^2 \, dx, \frac{C}{1 - \kappa} \right).
\] (4.35)

Note that this bound implies also a bound on \( W_2^2(\tilde{n}(t, \cdot), \delta_0) = \int \tilde{n}(t, x)^2 \, dx \). Finally, we notice that this argument can be reproduced for the equation \( 12 \), with the initial condition \( u(0, \cdot) = \delta_Z \). Then \( \tilde{n}(t, x)^2 \) becomes \( \int u(t, x)^2 \, dx \leq \max \left( Z^2, \frac{C}{1 - \kappa} \right) \), and since \( u \) converges to \( \bar{u}_Z \) thanks to Theorem 4.3 we get
\[
\int u_Z(x)^2 \, dx \leq C(Z^2 + 1),
\] (4.36)
which, here also, is equivalent to $W_2(\tilde{n}(t, \cdot), \delta_0) \leq C(Z + 1)$

**Step 3: Estimates on $W_2(\tilde{n}(t, \cdot), \tilde{u}_{Z(t)})$** For $0 \leq t < t + \tau$, $\tilde{n}$ can be written

$$\tilde{n}(t + \tau, x) = \tilde{n}(t, x) e^{-\gamma \tau} + \int_t^{t+\tau} e^{-\gamma(s-t)} \left[ \left( r + \int \alpha(y) \tilde{n}(s, y) dy \right) (n_b(x) - \tilde{n}(s, x)) + \gamma T(\tilde{n}(s, \cdot)) \right] ds,$$

where we have used the notation $T$ introduced in (4.20). Since $\tilde{u}_{Z(t)}$ is a steady-state of (4.24), it satisfies

$$\tilde{u}_{Z(t)}(x) = \tilde{u}_{Z(t)}(x) e^{-\gamma \tau} + \int_t^{t+\tau} e^{-\gamma(s-t)} \gamma T(\tilde{u}_{Z(t)})(x) ds.$$

We consider $(\varphi, \psi) \in \Phi_2$, and estimate

$$I = \int \varphi(x) \tilde{n}(t + \tau, x) dx + \int \psi(X) \tilde{u}_{Z(t)}(X) dX = e^{-\gamma \tau} \left( \int \varphi(x) \tilde{n}(t, x) dx + \int \psi(X) \tilde{u}_{Z(t)}(X) dX \right) + \int_t^{t+\tau} e^{-\gamma(s-t)} \left( \int \varphi(x) \left( r + \int \alpha(y) \tilde{n}(s, y) dy \right) (n_b(x) - \tilde{n}(s, x)) ds \right) + \int_t^{t+\tau} e^{-\gamma(s-t)} \gamma \left( \int \psi(X) T(\tilde{n}(s, \cdot)) + \int \varphi(x) T(\tilde{u}_{Z(t)})(X) dX \right) ds.$$

We can now use the formula (4.10) to get:

$$I \leq e^{-\gamma \tau} W_2^2 (\tilde{n}(t, \cdot), \tilde{u}_{Z(t)}) + \int_t^{t+\tau} e^{-\gamma(s-t)} \left( \int \varphi(x) \left( r + \int \alpha(y) \tilde{n}(s, y) dy \right) (n_b(x) - \tilde{n}(s, x)) ds \right) + \int_t^{t+\tau} e^{-\gamma(s-t)} \gamma W_2^2 \left( T(\tilde{n}(s, \cdot)), T(\tilde{u}_{Z(t)}) \right) ds. \quad (4.37)$$

To estimate the second term of this expression, we notice that for any couple $(\varphi, \psi) \in \Phi_2$, we have $-\varphi(y) \leq \psi(y)$, and then,

$$\int \varphi(x) (n_b(x) - \tilde{n}(s, x)) dx \leq \int \varphi(x) n_b(x) dx + \int \psi(X) \tilde{n}(s, X) dX \leq W_2^2 (n_b, \tilde{n}(s, \cdot)) \leq \int x^2 n_b(x) dx + \int x^2 \tilde{n}(s, x) dx \leq C,$$

thanks to the uniform bound (4.36) obtained in Step 2. We can use this estimate as well as Lemma (4.2) to estimate (4.37), and if we additionally pass to the supremum over $(\varphi, \psi) \in \Phi_2$, we obtain

$$W_2^2 (\tilde{n}(t + \tau, \cdot), \tilde{u}_{Z(t)}) \leq e^{-\gamma \tau} W_2^2 (\tilde{n}(t, \cdot), \tilde{u}_{Z(t)}) + C(r + \|\alpha\|_\infty) \int_t^{t+\tau} e^{-\gamma(s-t)} ds + (1 + 2\lambda_2 - 2\lambda_1) \gamma \int_t^{t+\tau} e^{-\gamma(s-t)} W_2^2 (\tilde{n}(s, \cdot), \tilde{u}_{Z(t)}) ds.$$

We can then introduce, for $\sigma \geq 0$, $y(t + \sigma) := e^{\gamma \sigma} W_2^2 (\tilde{n}(t + \sigma, \cdot), \tilde{u}_{Z(t)})$, that satisfies

$$y(t + \tau) \leq y(t) + \frac{C}{\gamma} + (1 + 2\lambda_2 - 2\lambda_1) \gamma \int_0^\tau y(t + s) ds,$$

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and then, thanks to the Gronwall inequality,

\[ y(t + \tau) \leq \left( y(t) + \frac{C}{\gamma} \right) e^{(1+2\lambda_2-2\lambda_1)\gamma\tau}, \]

that is

\[ W_2^2 \left( \tilde{n}(t + \tau, \cdot), \bar{u}_{Z(t)} \right) \leq \left( W_2^2 \left( \tilde{n}(t, \cdot), \bar{u}_{Z(t)} \right) + \frac{C}{\gamma} \right) e^{2(\lambda_1-\lambda_2)\gamma\tau}, \]

or

\[ W_2 \left( \tilde{n}(t + \tau, \cdot), \bar{u}_{Z(t)} \right) \leq \left( W_2 \left( \tilde{n}(t, \cdot), \bar{u}_{Z(t)} \right) + \frac{C}{\gamma} \right) e^{-(\lambda_1-\lambda_2)\gamma\tau}. \quad (4.38) \]

We notice next that thanks to Step 1, \(|Z(t + \tau) - Z(t)| \leq C\tau\), which, combined to Theorem 4.3 implies

\[ W_2 \left( \bar{u}_{Z(t+\tau)}, \bar{u}_{Z(t)} \right) \leq C\tau. \quad (4.39) \]

Then,

\[ W_2 \left( \tilde{n}(t + \tau, \cdot), \bar{u}_{Z(t+\tau)} \right) \leq \left( W_2 \left( \tilde{n}(t, \cdot), \bar{u}_{Z(t)} \right) + \frac{C}{\gamma} \right) e^{-(\lambda_1-\lambda_2)\gamma\tau} + C\tau. \]

If we choose \( \tau := \frac{1}{\gamma} \), we get

\[ W_2 \left( \tilde{n} \left( t + 1/\gamma, \cdot \right), \bar{u}_{Z(t+1/\gamma)} \right) \leq e^{-(\lambda_1-\lambda_2)}W_2 \left( \tilde{n}(t, \cdot), \bar{u}_{Z(t)} \right) + \frac{C}{\gamma}, \]

where \( e^{-(\lambda_1-\lambda_2)} < 1 \). As soon as

\[ W_2 \left( \tilde{n}(t, \cdot), \bar{u}_{Z(t)} \right) \geq \frac{2}{1 - e^{-(\lambda_1-\lambda_2)}} \frac{C}{\gamma} = C_1, \quad (4.40) \]

we have

\[ W_2 \left( \tilde{n} \left( t + 1/\gamma, \cdot \right), \bar{u}_{Z(t+1/\gamma)} \right) \leq \frac{1 + e^{-(\lambda_1-\lambda_2)}}{2} W_2 \left( \tilde{n}(t, \cdot), \bar{u}_{Z(t)} \right). \]

As long as \( (4.40) \) is satisfied for \( W_2 \left( \tilde{n} \left( t + k/\gamma, \cdot \right), \bar{u}_{Z(t+k/\gamma)} \right) \), we iterate this estimate, we get that for \( k \in \mathbb{N}^* \),

\[ W_2 \left( \tilde{n} \left( t + k/\gamma, \cdot \right), \bar{u}_{Z(t+k/\gamma)} \right) \leq \left( \frac{1 + e^{-(\lambda_1-\lambda_2)}}{2} \right)^k W_2 \left( \tilde{n}(t, \cdot), \bar{u}_{Z(t)} \right) \leq C \left( \frac{1 + e^{-(\lambda_1-\lambda_2)}}{2} \right)^k, \]

where we have used the estimate \( W_2 \left( \tilde{n}(t, \cdot), \bar{u}_{Z(t)} \right) \leq W_2 \left( \tilde{n}(t, \cdot), \delta_0 \right) + W_2 \left( \delta_0, \bar{u}_{Z(t)} \right) \leq C \), thanks to \( (4.35) \) and \( (4.36) \). Since \( e^{-(\lambda_1-\lambda_2)} < 1 \), we can choose \( k \) such that \( C \left( \frac{1 + e^{-(\lambda_1-\lambda_2)}}{2} \right)^k < \frac{C_1}{\gamma} \), where \( C_1 \) is the constant defined in \( (4.40) \). There exists thus some \( k \in \{0, \ldots, \bar{k}\} \) such that \( (4.40) \) does not hold for \( W_2 \left( \tilde{n} \left( t + k/\gamma, \cdot \right), \bar{u}_{Z(t+k/\gamma)} \right) \). Since this holds for any \( t \geq 0 \), we have shown that for any \( t \geq \frac{k}{\gamma} \),

\[ \min_{s \in [t, t+k/\gamma]} W_2 \left( \tilde{n}(s, \cdot), \bar{u}_{Z(s)} \right) \leq \frac{C_1}{\gamma}. \]

This estimate combined to \( (4.38) \) implies that there is a constant \( C > 0 \) such that for all \( t \geq \frac{k}{\gamma} \),

\[ W_2 \left( \tilde{n}(t, \cdot), \bar{u}_{Z(t)} \right) \leq \frac{C}{\gamma}. \quad (4.41) \]

**Step 4: Estimates on \(|Z(t) - \bar{Z}(t)|\)**

Thanks to \( (3.13) \) and \( (4.31) \), for \( t \geq 0 \),

\[ |Z(t) - Z_b| \leq |Z(0) - Z_b|e^{-rt}, \quad |Z(t) - Z_b| \leq |Z(0) - Z_b|e^{-rt}, \quad (4.42) \]
and then
\[ |\bar{Z} - Z(t)| \leq \frac{1}{\gamma}, \tag{4.43} \]
for any \( t \in [C \ln \gamma, \infty) \). We then simply need to estimate \(|\bar{Z} - Z(t)|\) on \([0, C \ln \gamma]\). We estimate:
\[
Z(t) - \bar{Z}(t) = (Z(t) - Z_b) - (\bar{Z}(t) - Z_b)
\]
\[
= (Z(0) - Z_b)e^{-\int_0^t (r + f \alpha(x)\bar{n}(s,x)) \, dx} - (Z(0) - Z_b)e^{-\int_0^t (r + f \alpha(x)u_{Z(s)}(x(x))) \, dx}
\]
\[
= (Z(0) - Z_b) \left( e^{-\int_0^t (f \alpha(x)(\bar{n}(s,x) - u_{Z(s)}(x))) \, dx} - 1 \right) e^{-\int_0^t (r + f \alpha(x)u_{Z(s)}(x)) \, dx}. \tag{4.44}\]
To estimate the first term in this expression, we use the duality formula for \( W_1 \) (see (3.12)):
\[
\left| \int \alpha(x) (\bar{n}(s,x) - \bar{u}_{Z(s)}(x)) \, dx \right| \leq \|\alpha\|_\infty W_1 (\bar{n}(s,\cdot), \bar{u}_{Z(s)})
\]
\[
\leq \|\alpha\|_\infty W_2 (\bar{n}(s,\cdot), \bar{u}_{Z(s)})
\]
\[
\leq \|\alpha\|_\infty (W_2 (\bar{n}(s,\cdot), \bar{u}_{Z(s)}) + W_2 (\bar{u}_{Z(s)}, \bar{u}_{Z(s)})), \tag{4.45}\]
where the second inequality can be easily obtained from the definition (3.9) of Wasserstein distances thanks to a Cauchy-Schwarz inequality. We can now apply the result of the previous step as well as Lemma 4.4 to get
\[
\left| \int \alpha(x) (\bar{n}(s,x) - \bar{u}_{Z(s)}(x)) \, dx \right| \leq \|\alpha\|_\infty \left( \frac{C}{\gamma} + C|Z(s) - \bar{Z}(s)| \right), \tag{4.46}\]
for any \( t \geq \frac{C}{\gamma} \), while \( \int_0^{C/\gamma} |f \alpha(x) (\bar{n}(s,x) - \bar{u}_{Z(s)}(x)) \, dx| \, ds \leq \frac{C}{\gamma} \) and \( \int_0^{C/\gamma} |Z(s) - \bar{Z}(s)| \, ds \leq \frac{C}{\gamma} \).
(4.43) then becomes
\[
\left| Z(t) - \bar{Z}(t) \right| \leq (Z(0) - Z_b) \left( e^{\frac{C}{\gamma} + \int_0^{C/\gamma} |Z(s) - \bar{Z}(s)| \, ds} - 1 \right) e^{-\int_0^t (r + f \alpha(x)u_{Z(s)}(x)) \, dx}
\]
\[
\leq C \left( \frac{1 + t}{\gamma} + \int_0^t |Z(s) - \bar{Z}(s)| \, ds \right) e^{-rt},
\]
As long as
\[
\frac{1}{\gamma} + \int_0^t \left| Z(s) - \bar{Z}(s) \right| \, ds \leq 1. \tag{4.47}\]
y(t) = e^{rt} |Z(t) - \bar{Z}(t)| then satisfies
\[
y(t) \leq \frac{C(1 + t)}{\gamma} + \int_0^t C e^{-rs} y(s) \, ds.
\]
We apply the Gronwall inequality to obtain
\[
y(t) \leq \frac{C(1 + t)}{\gamma} e^{\int_0^t e^{-rs} \, ds},
\]
and then
\[
\left| Z(t) - \bar{Z}(t) \right| \leq \frac{C(1 + t)}{\gamma^r} e^{-rt}. \tag{4.48}\]
For \( t \in [0, C \ln \gamma] \), we have then
\[
\frac{1 + t}{\gamma} + \int_0^t \frac{C(1 + s)}{\gamma^r} e^{-rs} \, ds \leq \frac{1 + C \ln \gamma}{\gamma^r} + \int_0^{C \ln \gamma} \frac{C(1 + s)}{\gamma^r} e^{-rs} \, ds
\]
\[
\leq \frac{1 + C \ln \gamma}{\gamma^r} + \frac{C(1 + s)}{\gamma^r} < 1,
\]
provided \( \gamma > 0 \) is large enough. Then (4.47) is satisfied for all \( t \in [0, C \ln \gamma] \), and (4.48) holds for \( t \in [0, C \ln \gamma] \), which, combined to (4.43), shows that if \( \gamma > 0 \) is large enough, then for any \( t \geq 0 \),
\[
\left| Z(t) - \bar{Z}(t) \right| \leq \frac{C}{\gamma}. \tag{4.49}\]
If we combine (4.40) to (4.41) and (4.25), we can show that for all $t \geq \frac{C}{\gamma}$,

$$W_2(\tilde{n}(t, \cdot), \tilde{u}_{Z(t)}) \leq W_2(\tilde{n}(t, \cdot), \tilde{u}_{Z(t)}) + W_2(\tilde{u}_{Z(t)}, \tilde{u}_{Z(t)}) \leq \frac{C}{\gamma} + C|Z(t) - Z(t)| \leq \frac{C}{\gamma}.$$  \hspace{1cm} (4.50)

**Step 4: Estimates on $|N(t) - \tilde{N}(t)|$**

Let us first notice that $N'(t) \geq (r - \beta N(t)) N(t)$, and thus, for $t \geq 0$,

$$N(t) \geq \min \left( N(0), \frac{r}{\beta} \right).$$  \hspace{1cm} (4.51)

We define $\tilde{N} := \frac{1}{\beta} \left( r + \int \alpha(x) \tilde{u}_{Z}(x) \, dx \right)$, and estimate:

$$N - \tilde{N}(t) = \left( r + \int \alpha(x) \tilde{n}(t, x) \, dx - \beta N(t) \right) N(t)$$

$$= \left( \int \alpha(x) (\tilde{n}(t, x) - \tilde{u}_{Z}(x)) \, dx - \beta \left( N(t) - \tilde{N}(t) \right) \right) N(t),$$

To estimate the first term, we use an argument similar to the one used in (4.45), and then estimates (4.41), (4.49), (4.42) and Lemma 4.2 to shows that for $t \geq \frac{C}{\gamma}$,

$$\left| \int \alpha(x) (\tilde{n}(t, x) - \tilde{u}_{Z}(x)) \, dx \right| \leq \| \alpha \|_{\infty} \left( W_2(\tilde{n}(t, \cdot), \tilde{u}_{Z(t)}) + W_2(\tilde{u}_{Z(t)}, \tilde{u}_{Z(t)}) \right)$$

$$\leq C \left( \frac{1}{\gamma} + e^{-rt} \right),$$

provided $\gamma > 0$ is large enough. Then, for $t \geq \ln(\gamma)$ and $\gamma > 0$ large enough, $\left| \int \alpha(x) (\tilde{n}(t, x) - \tilde{u}_{Z}(x)) \, dx \right| \leq \frac{C}{\gamma}$, and then, thanks to (4.51),

$$\frac{d}{dt} \left| N - \tilde{N}(t) \right| \leq \left( \frac{C}{\gamma} - \beta \left| N(t) - \tilde{N}(t) \right| \right) N(t)$$

$$\leq -\frac{1}{C} \left| N(t) - \tilde{N}(t) \right|,$$

provided $\left( N - \tilde{N} \right)(t) \geq \frac{C}{\gamma}$ and $t \geq \ln(\gamma)$. Since moreover $\left( N - \tilde{N} \right)(\ln(\gamma))$ is bounded uniformly in $\gamma$ (see Step 1), we have, for $t \geq \ln(\gamma)$,

$$\left| N - \tilde{N}(t) \right| \leq \max \left( C e^{\frac{\gamma}{2}}, \frac{C}{\gamma} \right),$ \hspace{1cm} (4.52)

Finally, we compute

$$\left( N - \tilde{N} \right)'(t) = \left( r + \int \alpha(x) \tilde{n}(t, x) \, dx - \beta N(t) \right) \left( N(t) - \tilde{N}(t) \right)$$

$$+ \left( \int \alpha(x) (\tilde{u}_{Z(t)}(x) - \tilde{n}(t, x)) \, dx - \beta \left( \tilde{N}(t) - N(t) \right) \right) \tilde{N}(t),$$

and then,

$$\left( N - \tilde{N} \right)(t) = \int_0^t \left( \int \alpha(x) (\tilde{u}_{Z(s)}(x) - \tilde{n}(s, x)) \, dx \right) \tilde{N}(s)$$

$$\exp \left[ \int_0^t \left( r + \int \alpha(x) \tilde{n}(s, x) \, dx - \beta (\tilde{N}(s) + N(s)) \right) \, ds \right] \, ds,$$
Thanks to an argument similar to the one used to obtain (4.45), and then (4.41), (4.49) and Lemma 1.2, we can show that for $t \geq \frac{C}{\gamma}$,
\[
\left| \int \alpha(x) \left( \tilde{u}_{Z(t)}(x) - \tilde{n}(t, x) \right) dx \right| \\
\leq \|\alpha'\|_{\infty} \left( W_2 \left( \tilde{n}(t, \cdot), \tilde{u}_{Z(t)} \right) + W_2 \left( \tilde{u}_{Z(t)}, \tilde{u}_{Z(t)} \right) \right) \leq \frac{C}{\gamma},
\]
and since moreover $N, \tilde{N}$ are bounded (see Step 1) and $\alpha$ is Lipschitz continuous, we get
\[
(N - \tilde{N})(t) \leq C \int_0^1 \left( 1_{s \in [0, C/\gamma]} + \frac{1}{\gamma} \right) e^{C(t-s)} ds \leq \frac{C}{\gamma} e^{Ct},
\]
and then, if we combine this estimate for $t \leq \frac{\ln \gamma}{\gamma}$ to (4.52) for $t \geq \frac{\ln \gamma}{\gamma}$, we get
\[
|N(t) - \tilde{N}(t)| \leq \max \left( C e^{\frac{-\ln \gamma}{\gamma}} \frac{C}{\sqrt{\gamma}} \right),
\]
that is
\[
|N(t) - \tilde{N}(t)| \leq C \gamma^{-\nu}, \tag{4.53}
\]
for some $\nu > 0$. Brought together, (4.49), (4.53) and (4.50) conclude the proof of Theorem 3.1.

\section{Convergence of the solution to a unique steady-state}

\subsection{Contraction of the exchanges in the $W_1$-distance}

\textbf{Lemma 5.1.} Let $x_1, x_2, x'_1, x'_2 \in \mathbb{R}_+^\ast$, and $K$ as in $(2.4)$. We define $\lambda_1, \lambda_2 \in [0,1]$ as in $(4.10)$. We have
\[
W_1 \left( K(\cdot, x_1, x_2), K(\cdot, x'_1, x'_2) \right) \leq (1 - \lambda_1)|x_1 - x'_1| + \lambda_1|x_2 - x'_2|. \tag{5.54}
\]

\textit{Proof of Lemma 5.1.} The proof of the first part of Lemma 4.1 can be reproduced for $(\varphi, \psi) \in \Phi_1$ until (4.18). Similarly, we can use the fact that $(\varphi, \psi) \in \Phi_1$ (see (3.11)) to get
\[
I \leq \left| (x_1 - x_1 y_1 + x_2 y_2) - (x'_1 - x'_1 y_1 + x'_2 y_2) \right| B \left( y_1 \right) B \left( y_2 \right) dy_1 dy_2 \\
\leq |x_1 - x'_1| \int (1 - y_1) B \left( y_1 \right) dy_1 + |x_2 - x'_2| \int y_2 B \left( y_2 \right) dy_2
\]
and then, with the notations (4.10),
\[
I \leq |x_1 - x'_1|(1 - \lambda_1) + |x_2 - x'_2|\lambda_1.
\]
Since this is true for any $(\varphi, \psi) \in \Phi_1$ (see (3.11)), we can use this estimate and (3.10) to show that
\[
W_1 \left( K(\cdot, x_1, x_2), K(\cdot, x'_1, x'_2) \right) = \max_{(\varphi, \psi) \in \Phi_1} I \\
\leq |x_1 - x'_1|(1 - \lambda_1) + |x_2 - x'_2|\lambda_1.
\]

\subsection{Proof of Theorem 3.3}

\textit{Step 1: Rough estimate on the first moment of $\tilde{n}(t, \cdot)$}

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We recall the notation \( \tilde{n}(t, x) = \frac{n(t, x)}{N(t)} \), as well as the equation [4.31] satisfied by \( Z(t) = \int x \tilde{n}(t, x) \, dx \).

For \( t \geq 0, \)

\[
\left| Z(t) - \int x n_b(x) \, dx \right| \leq \left| Z(0) - \int x n_b(x) \, dx \right| \\
\leq \int x n(0, x) \, dx + \int x n_b(x) \, dx,
\]

and in particular,

\[
W_1(n_b, n(t, \cdot)) \leq W_1(n_b, \delta_0) + W_1(\delta_0, n(t, \cdot)) \\
\leq W_1(n_b, \delta_0) + \int x \tilde{n}(t, x) \, dx \\
\leq 2 \int x n(0, x) \, dx + \int x n_b(x) \, dx. \tag{5.55}
\]

**Step 2: The contraction argument**

Let \( n_1, n_2 \) be two solutions of \( \mathcal{E} \), associated to two initial solutions \( n_{10}^0, n_{20}^0 \). We denote \( \tilde{n}_1, \tilde{n}_2 \) the two corresponding renormalized measures, and

\[
\omega(t) := r + \frac{1}{2} \left( \int \alpha(y) \tilde{n}_1(t, y) \, dy + \int \alpha(y) \tilde{n}_2(t, y) \, dy \right). \tag{5.56}
\]

Thanks to [4.33], \( \tilde{n}_i \), for \( i = 1, 2 \) can be written

\[
\tilde{n}_i(t, x) = \tilde{n}_i^0(x)e^{-f_i^o + \omega(s) + \gamma ds} \\
+ \int_0^t e^{-f_i^o + \omega(s) + \gamma ds} \left[ \left( r + \int \alpha(y) \tilde{n}_i(s, y) \, dy \right) n_b(x) \\
+ \left( \int \alpha(y) \tilde{n}_i(s, y) - \tilde{n}_i(s, y) \right) \tilde{n}_i(s, y) \\
+ \gamma \int K(x, x_1, x_2) \tilde{n}_i(s, x_1) \tilde{n}_i(s, x_2) \, dx_1 \, dx_2 \right] \, ds,
\]

where \( i^c = 1 \) if \( i = 2 \), and \( i^c = 2 \) if \( i = 1 \). We consider \( (\varphi, \psi) \in \Phi_1 \), and estimate:

\[
I = \int \varphi(x) \tilde{n}_1(t, x) \, dx + \int \psi(X) \tilde{n}_2(t, X) \, dX \\
= e^{-f_i^o + \omega(s) + \gamma ds} \int \varphi(x) \tilde{n}_i^0(x) \, dx + \int \psi(X) \tilde{n}_i^0(X) \, dX \\
+ \int_0^t e^{-f_i^o + \omega(s) + \gamma ds} \left[ \int \varphi(x) \left( r + \int \alpha(y) \tilde{n}_1(s, y) \, dy \right) n_b(x) \\
+ \left( \int \alpha(y) \tilde{n}_2(s, y) - \tilde{n}_1(s, y) \right) \tilde{n}_1(s, x) \right] \, dx \\
+ \int \psi(X) \left( \left( r + \int \alpha(y) \tilde{n}_2(s, y) \, dy \right) n_b(X) \\
+ \left( \int \alpha(y) \tilde{n}_1(s, y) - \tilde{n}_2(s, y) \right) \tilde{n}_2(s, X) \right] dX \right] ds \\
+ \gamma \int_0^t e^{-f_i^o + \omega(s) + \gamma ds} \left[ \int \varphi(x) \left( \int K(x, x_1, x_2) \tilde{n}_1(s, x_1) \tilde{n}_1(s, x_2) \, dx_1 \, dx_2 \right) \, dx \\
+ \int \psi(X) \left( \int K(x, x_1, x_2) \tilde{n}_2(s, x_1) \tilde{n}_2(s, x_2) \, dx_1 \, dx_2 \right) \, dX \right] ds \tag{5.57}
\]

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To estimate the first term of this expression, we simply use the formula (3.10) to obtain:

\[
\int \varphi(x)\tilde{n}_1^0(x) \, dx + \int \psi(X)\tilde{n}_0^0(X) \, dX \leq W_1(\tilde{n}_1^0, \tilde{n}_2^0).
\] (5.58)

Let

\[
\theta(t) := \int \alpha(y)\frac{\tilde{n}_1(t, y) - \tilde{n}_2(t, y)}{2} \, dy.
\]

We estimate the second term of (5.57) as follows:

\[
J = \omega(s) \left( \int \varphi(x)n_b(x) \, dx + \int \psi(X)n_b(X) \, dX \right)
+ \theta(s) \left( \int (\varphi(x) - \psi(x))n_b(x) \, dx \right)
- \theta(s) \left( \int \varphi(x)\tilde{n}_1(s, x) \, dx - \int \psi(X)\tilde{n}_2(s, X) \, dX \right)
= \omega(s) \left( \int \varphi(x)n_b(x) \, dx + \int \psi(X)n_b(X) \, dX \right)
+ \theta(s) \left( \int \varphi(x)n_b(x) \, dx + \int \psi(x)\tilde{n}_2(X) \, dX \right)
- \theta(s) \left( \int \varphi(x)\tilde{n}_1(s, x) \, dx + \int \psi(X)n_b(X) \, dX \right)
\]

Since \((\varphi, \psi) \in \Phi, \varphi(x) + \psi(x) = 0\), and combining this property to the formula (3.10), we get

\[
J \leq |\theta(s)| \left( W_1(n_b, \tilde{n}_1(s, \cdot)) + W_1(n_b, \tilde{n}_2(s, \cdot)) \right),
\]

and then, thanks to (5.55) and the definition of \(\theta(\cdot)\) and (3.10),

\[
J \leq C_1 \|\alpha'\|_{\infty} W_1(\tilde{n}_1(s, \cdot), \tilde{n}_2(s, \cdot)),
\] (5.59)

where

\[
C_1 := 4 \int n_b(x) \, dx + \int \tilde{n}_1(0, x) + \tilde{n}_2(0, x) \, dx.
\] (5.60)

Finally, to estimate the last term of (5.57), we reproduce the method employed in (4.21), but with \((\varphi, \psi) \in \Phi_1\) for any \(\pi_s \in \Pi(\tilde{n}_1(s, \cdot), \tilde{n}_2(s, \cdot))\) (see (3.11)),

\[
L = \int \varphi(x) \left( \int \int K(x, x_1, x_2)\tilde{n}_1(s, x_1)\tilde{n}_1(s, x_2) \, dx_1 \, dx_2 \right) \, dx
+ \int \psi(X) \left( \int \int K(X, x_1, x_2)\tilde{n}_2(s, x_1)\tilde{n}_2(s, x_2) \, dx_1 \, dx_2 \right) \, dX
\leq \int \int \left( \varphi(x)K(x, x_1, x_2) \, dx + \psi(X)K(X, x', x'_2) \, dX \right) \, d\pi(x_1, x_1') \, d\pi(x_2, x'_2)
\leq \int \int W_1(K(\cdot, x_1, x_2), K(\cdot, x'_1, x'_2)) \, d\pi(x_1, x_1') \, d\pi(x_2, x'_2)
\]

We can now use the second estimate of Lemma (4.1) to get

\[
L \leq \int \left( 1 - \lambda_1 \right) |x_1 - x'_1| + \lambda_1 |x_2 - x'_2| \, d\pi(x_1, x_1') \, d\pi(x_2, x'_2)
= \int |x_1 - x'_1| \, d\pi(x_1, x'_1),
\]

and since this estimate holds for any \(\pi_s \in \Pi(\tilde{n}_1(s, \cdot), \tilde{n}_2(s, \cdot))\), we get (see (3.59)):

\[
L \leq W_1(\tilde{n}_1(s, \cdot), \tilde{n}_2(s, \cdot)).
\] (5.61)
Finally, (5.54) becomes

\[ I \leq e^{-\int_0^t \omega(s) + \gamma ds} W_1(\tilde{n}_1(0), \tilde{n}_2(0)) + \int_0^t e^{-\int_0^r \omega(s) + \gamma ds} C_1 ||\alpha'||_{\infty} W_1(\tilde{n}_1(s, \cdot), \tilde{n}_2(s, \cdot)) \, ds + \gamma \int_0^t e^{-\int_0^r \omega(s) + \gamma ds} W_1(\tilde{n}_1(s, \cdot), \tilde{n}_2(s, \cdot)) \, ds. \]

Since this estimate is independent of \((\varphi, \psi) \in \Phi_1\), we can apply (3.10) to get

\[ W_1(\tilde{n}_1(t, \cdot), \tilde{n}_2(t, \cdot)) \leq e^{-\int_0^t \omega(s) + \gamma ds} W_1(\tilde{n}_1(0), \tilde{n}_2(0)) + \int_0^t e^{-\int_0^r \omega(s) + \gamma ds} (C_1 ||\alpha'||_{\infty} + \gamma) W_1(\tilde{n}_1(s, \cdot), \tilde{n}_2(s, \cdot)) \, ds. \]

and then \(g(t) := e^{\int_0^t \omega(s) + \gamma ds} W_1(\tilde{n}_1(t, \cdot), \tilde{n}_2(t, \cdot))\) satisfies:

\[ g(t) \leq W_1(\tilde{n}_1(0), \tilde{n}_2(0)) + \int_0^t (C_1 ||\alpha'||_{\infty} + \gamma) g(s) \, ds, \]

and then, thanks to the Gronwall inequality,

\[ g(t) \leq W_1(\tilde{n}_1(0), \tilde{n}_2(0)) e^{(C_1 ||\alpha'||_{\infty} + \gamma) t}, \]

that is

\[ W_1(\tilde{n}_1(t, \cdot), \tilde{n}_2(t, \cdot)) \leq W_1(\tilde{n}_1(0), \tilde{n}_2(0)) e^{C_1 ||\alpha'||_{\infty} t - \int_0^t \omega(s) \, ds}. \]

Thanks to the definition (5.50) of \(\omega\), \(\omega \geq \tau + \min_{x \in \mathbb{R}_+} \alpha(x)\), and then,

\[ W_1(\tilde{n}_1(t, \cdot), \tilde{n}_2(t, \cdot)) \leq W_1(\tilde{n}_1(0), \tilde{n}_2(0)) e^{- (r + \min_{x \in \mathbb{R}_+} \alpha(x) - C_1 ||\alpha'||_{\infty}) t}. \]

(5.62)

Step 4: Convergence of \(\tilde{n}\)

To show that (4.33) admits a steady-state, let \(n(t, \cdot) \in \mathcal{P}_1(\mathbb{R}_+)\) be a solution of (2.8), and \(\tilde{n}\) the corresponding normalized solution. For any \(0 \leq \sigma \leq \tau\), we use the estimate (5.62) with \(\tilde{n}_1(t, x) = \tilde{n}(t, x)\), \(\tilde{n}_2(t, x) = \tilde{n}(\tau - x + t, x)\), to get

\[ W_1(\tilde{n}_1(t, \cdot), \tilde{n}_2(t, \cdot)) \leq W_1(\tilde{n}_1(0, \cdot), \tilde{n}(\tau - x + t, \cdot)) e^{- (r + \min_{x \in \mathbb{R}_+} \alpha(x) - C_1 ||\alpha'||_{\infty}) \sigma} \leq (W_1(\tilde{n}_1(0, \cdot), 0) + W_1(0, \tilde{n}(\tau - x, \cdot)) e^{- (r + \min_{x \in \mathbb{R}_+} \alpha(x) - C_1 ||\alpha'||_{\infty}) \sigma} \leq C_1 e^{- (r + \min_{x \in \mathbb{R}_+} \alpha(x) - C_1 ||\alpha'||_{\infty}) \sigma}. \]

(5.63)

Thanks to the estimate (5.56) and the definition (5.60) of \(C_1\). It follows that for any sequence \(t_n \to \infty\), \((\tilde{n}(t_n, \cdot))_n\) is a Cauchy sequence in the complete metric space \((\mathcal{P}_1(\mathbb{R}_+), W_1)\), and thus converge to a limit. Thanks to (5.63), this limit is indeed independent of the sequence \((t_n)\), so that there exists a limit \(\tilde{n} \in \mathcal{P}_1(\mathbb{R}_+)\) such that \(\tilde{n}(t, \cdot) \to_{t \to \infty} \tilde{n}(x)\) in \((\mathcal{P}_1(\mathbb{R}_+), W_1)\). It follows that \(\tilde{n}(t, \cdot)\) is a steady-state of (4.33).

Let now \(n(t, x)\) be any solution of (2.8), and \(\tilde{n}\) defined as in (4.32). With the steady-state \(\tilde{n}\) of (4.33) at hand, we can use (5.62) with \(\tilde{n}_1(t, x) = n(t, x)\) and \(\tilde{n}_2 = \tilde{n}\), to show that \(\tilde{n}\) converges exponentially fast to \(n\):

\[ W_1(\tilde{n}(t, \cdot), \tilde{n}) \leq C_1 e^{- (r + \min_{x \in \mathbb{R}_+} \alpha(x) - C_1 ||\alpha'||_{\infty}) t}. \]

(5.64)

Step 5: Convergence of \(N\) and \(n\)

Thanks to the definition (4.32) of \(\tilde{n}\), we simply need to show that \(N(t, x) = \int n(t, x) \, dx\) converges to the following limit:

\[ \bar{N} := \frac{1}{\beta} \left( r + \int \alpha(x) \tilde{n}(x) \, dx \right). \]
Thanks to (5.64), \( N \) satisfies:

\[
N'(t) = \left( \int \alpha(x) (\bar{n} - \bar{n}(t, x)) \, dx - \beta(N(t) - \bar{N}) \right) N(t),
\]

where

\[
\left| \int \alpha(x) (\bar{n} - \bar{n}(t, x)) \, dx \right| \leq \|\alpha'\|_{\infty} W_1(\bar{n}, n(t, \cdot))
\]

\[
\leq C_1 \|\alpha'\|_{\infty} e^{-\left(r + \min_{s \in \mathbb{R}_+} \alpha(x) - C_1 \|\alpha'\|_{\infty}\right) t},
\]

thanks to (5.64). Thanks to this estimate, there exists \( T > 0 \) such that for any \( t \geq T, \left| \int \alpha(x) (\bar{n} - \bar{n}(t, x)) \, dx \right| \leq \frac{N}{2} \), and then, for \( t > T, \)

\[
N'(t) \geq -\beta N(t) \left( N(t) - \frac{N}{2} \right),
\]

and then \( N(t) \geq \frac{N}{4} \) for any \( t > T' \). Then, for \( t > T' \),

\[
|N(t) - \bar{N}| \leq \left| N(T') - \bar{N} \right| e^{-\beta \int_{T'}^t N(s) \, ds}
\]

\[
+ \int_{T'}^t \left| \int \alpha(x) (n - \bar{n}(s, x)) \, dx \right| e^{-\beta \int_{s}^t N(s) \, ds} \, ds
\]

\[
\leq \frac{3N}{4} e^{-\frac{\beta}{C_1} \left( t - T' \right)}
\]

\[
+ C_1 \|\alpha'\|_{\infty} \int_{T'}^t e^{-\left(r + \min_{s \in \mathbb{R}_+} \alpha(x) - C_1 \|\alpha'\|_{\infty}\right) s} e^{-\frac{\beta}{C_1} (t - s)} \, ds
\]

\[
\leq C e^{-\min_{s \in \mathbb{R}_+} \left( r + \min_{s \in \mathbb{R}_+} \alpha(x) - C_1 \|\alpha'\|_{\infty} \right) \frac{\beta}{C_1} t}. \tag{5.65}
\]

Finally, we check that the convergence of \( \bar{n} \) and \( N \) implies the convergence of \( n \), for the weak-* topology of measures. Let \( \varphi \in C^0(\mathbb{R}_+) \) and any \( \varepsilon > 0 \). Thanks to the density of \( C^1(\mathbb{R}_+) \) in \( C^0(\mathbb{R}_+) \), there exists \( \tilde{\varphi} \in C^1(\mathbb{R}_+) \) such that \( \|\tilde{\varphi}'\|_{\infty} < \infty \), and \( \|\varphi - \tilde{\varphi}\|_{\infty} \leq \varepsilon \). Then,

\[
\left| \int \varphi(x) (n(t, x) - \bar{N} \bar{n}(x)) \, dx \right| \leq \|\varphi - \tilde{\varphi}\|_{\infty} \left( \|n(t, \cdot)\|_{L^1} + \bar{N} \|\bar{n}\|_{L^1} \right)
\]

\[
+ \left| \int \tilde{\varphi}(x) (N(t, x) \bar{n}(t, x) - \bar{N} \bar{n}(x)) \, dx \right|
\]

\[
\leq C \varepsilon + \|N(t) - \bar{N}\|_{\infty} + \bar{N} \|\tilde{\varphi}'\|_{\infty} W_1(\bar{n}(t, \cdot), \bar{n})
\]

\[
\leq (C + 1) \varepsilon,
\]

provided \( t \) is large enough, thanks to (5.64) and (5.65). This estimates with (5.64) and (5.65) conclude the proof of Theorem 5.3.3.

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