Long time evolution of populations under selection and vanishing mutations

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Abstract: In this paper, we Consider a long time and vanishing mutations limit of an integro-differential model describing the evolution of a population structured with respect to a continuous phenotypic trait. We show that the asymptotic population is a steady-state of the evolution equation without mutations, and satisfies an evolutionary stability condition.

1 Introduction

1.1 The model

We consider a population $f(t,\cdot)$ structured by a phenotypic trait $x \in X \subset \mathbb{R}^d$. We denote by $f(t,x)$ the density of the population of trait $x \in X$, at time $t \geq 0$. The population evolves through a process of mutations and selection, according to the integro-differential model (see [17, 4, 7, 8]):

$$\begin{cases} f(0,x) &= f^0(x), \quad x \in X, \\ \partial_t f(t,x) &= s[f(t,\cdot)](x) f(t,x) + \int_X m(x-y) f(t,y)\, dy, \quad t \geq 0,\, x \in X, \end{cases} \tag{1}$$

where $s[\mu](x)$ denotes the fitness of individuals of trait x living among a population $\mu \in M^1_+(\mathbb{R})$, that is the birth rate minus the death rate of those individuals. $\int_X m(\cdot - y) f(t,y)\, dy$ represents mutations (see [7, 21, 5]), with $m : X - X \to \mathbb{R}_+$. In this paper, we consider that the fitness $s[\mu]$ is of logistic type (see [1]), and more precisely that:

$$s[\mu](x) := a(x) - \int_X b(x,y)\mu(y)\, dy, \tag{2}$$

where $a(x)$ is the fitness of an individual of trait $x \in X$ without competition. In this article, we consider that the competition between two individuals depends on their respective traits, we thus consider a competition kernel $b(\cdot,\cdot) > 0$. Throughout this article, we will write abusively $\int_X b(x,y)\mu(y)\, dy$ instead of the correct $\int_X b(x,y) d\mu(y)$.

We introduce a parameter $\varepsilon > 0$, that represents the frequency of mutations (see [10, 21]):

$$\partial_t f(t,x) = s[f(t,\cdot)](x) f(t,x) + \varepsilon (m *_x f)(t,x). \tag{3}$$

Since mutations are rare (especially those affecting the phenotype $x \in X$), we are interested in the limit case $\varepsilon \to 0$. More precisely, we are interested in the long-time behavior of (3) when $\varepsilon \to 0$, we thus rescale the time variable: $\tilde{t} = \varepsilon t$. (3) then becomes:

$$\partial_t f^\varepsilon(t,x) = \frac{1}{\varepsilon} s[f^\varepsilon(t,\cdot)](x) f^\varepsilon(t,x) + (m *_x f^\varepsilon)(t,x). \tag{4}$$

Remark 1. *Notice that the scaling we chose is different from the scaling usually considered for such equations (see [21, 2, 22]): the usual one would be $\tilde{t} = \sqrt{\varepsilon} t$. Eq. (3) rescaled then becomes (with $\varepsilon' := \sqrt{\varepsilon}$):*

$$\partial_t f^\varepsilon(t,x) = \frac{1}{\varepsilon} s[f^\varepsilon(t,\cdot)](x) f^\varepsilon(t,x) + \varepsilon (m *_x f^\varepsilon)(t,x). \tag{5}$$

Since our timescale is faster than the usual one, we expect that the limit f of solutions f^ε of (4) when $\varepsilon \to 0$ will be constituted of steady-states of (1) without mutations (that is with $m = 0$). Indeed, we will even show, in Prop. 4 that for a.e. $t \geq 0$, $f(t,\cdot)$ is a stable (in the sense that it is an ESD, see Def. 1) steady-state of (1) with $m = 0$. This result is the main result of this paper.

In evolution theory, and in particular in Adaptive Dynamics (see [15, 20, 13, 9]), the notion of Evolutionary Stable Strategies (ESS) plays an important role for the evolutionary stability of a population (see [19, 3, 9]). However, this notion is not well-adapted for general measure-valued populations, for which one should consider the following extension of the notion of ESS (see [8, 16]):

Definition 1. *$\bar{f} \in M^1(X)$ is called an Evolutionary Stable Distribution of (2) if*

$$\forall x \in supp(\bar{f}), \quad s[\bar{f}](x) = 0, \tag{6}$$

$$\forall x \in X, \quad s[\bar{f}](x) \leq 0. \tag{7}$$

We make the following basic assumptions:

Assumption 1: $X \subset \mathbb{R}^d$ compact, $f^0 \in M^1_+(X)$, $f^0 \neq 0$, and

- $a \in W^{1,\infty}(X)$, $\mathcal{O} := \{x; a(x) > 0\} \neq \emptyset$;
- $b \in W^{1,\infty}(X \times X)$, $\inf_{x,y\in Y} b(x,y) > 0$;

- $m \in W^{1,\infty}(X-X) \cap L^1(X-X)$, $m \geq 0$, $m(0) > 0$.

If Assumption 1 is satisfied, then there exists a unique solution $f \in C([0,\infty); M^1_+(X))$ of (1) (see Thm 2.1 of [8]). We also recall the uniform bound on $\|f(t,\cdot)\|_{M^1(X)}$ obtained in [8]:

$$\|f\|_{L^\infty(\mathbb{R}_+, M^1(X))} \leq \frac{\max_{x\in X} a(x) + \max_{x,y\in X} m(x-y)}{\inf_{x,y\in X} b(x,y)} < \infty. \tag{8}$$

Moreover, we make the following assumption on m and X:

Assumption 2: There exists $I \in \mathbb{N}$ and $C > 0$, such that for any $x, y \in X$,

$$\left(*_{i=1}^I m\right)(x-y) > C > 0,$$

where $*_{i=1}^I m = m * (m * (\cdots * (m)\dots))$.

Since we assumed in Assumption 1 that $m(0) > 0$, Assumption 2 holds for compact set $X \subset \mathbb{R}^d$ such that $\operatorname{Int} X$ is connected.

In this work, we will often use the integral formulation of f^ε, following an idea from [10]: for $t \geq 0$, $x \in X$,

$$f^\varepsilon(t,x) = f^0(x) e^{\frac{1}{\varepsilon}\int_0^t s[f^\varepsilon(\tau,\cdot)](x)\,d\tau} + \int_0^t (m *_x f^\varepsilon)(\sigma,x) e^{\frac{1}{\varepsilon}\int_\sigma^t s[f^\varepsilon(\tau,\cdot)](x)\,d\tau}\,d\sigma. \tag{9}$$

By a slight modification of Thm 3.1 from [8], one obtains that f^ε converges (up to an extraction) to a limit measure in the sense that:

Proposition 1. *Assume that Assumptions 1 and 2 are satisfied, and for $\varepsilon > 0$, let $f^\varepsilon \in C([0,\infty); M^1_+(X))$ be the solution of (4) given by [8]. Then, there exists a subsequence of $(f^\varepsilon)_\varepsilon$, that we still denote $(f^\varepsilon)_\varepsilon$, and $f \in L^\infty([0,T], M^1(X))$ such that:*

$$f^\varepsilon \to_{\varepsilon\to 0} f \quad L^\infty\left(\omega * [0,T], \sigma(M^1, C_b)(X)\right), \tag{10}$$

and for every $\sigma, t \in [0,T]$,

$$\int_\sigma^t s[f^\varepsilon(\tau,\cdot)]\,d\tau \to \int_\sigma^t s[f(\tau,\cdot)]\,d\tau \quad L^\infty\left([0,T]\times X\right). \tag{11}$$

In Subsection 1.3, we state the results of this paper, the main result being Prop. 4. In subsection 1.4, we first discuss the interplay between previous results on asymptotics for (1) and the results of this paper, then, we state two corollaries of Prop 4 that we find particularly interesting. Finally, in Section 2, we proove the results stated in Subsection 1.3.

1.2 The results

1.3 Statement of the results

The main objective of this article is to characterize a limit $f \in L^\infty([0,T], M^1_+(X))$ of the solutions $f^\varepsilon \in C([0,\infty); M^1_+(X))$ to (4) given by Prop. 1. As mentioned in the introduction, we expect $f(t,\cdot)$ to be an ESD (see Def. 1) for a.e. $t \geq 0$. To show this property of f, the first step is to show that $f(t,\cdot)$ satisfies (7) for a.e. $t \geq 0$:

Proposition 2. *Assume that Assumptions 1 and 2 are satisfied. For $\varepsilon > 0$, let $f^\varepsilon \in C([0,\infty); M^1_+(X))$ be the solution of (4) given by [8], and $f \in L^\infty([0,T], M^1(X))$ be an asymptotic population density given by Prop. 1.*

Then, for a.e. $t \in \mathbb{R}_+$,

$$\forall x \in X, \quad s[f(t,\cdot)](x) \leq 0.$$

To show Prop. 2, we will need the following Lemma, which provides a (non-uniform in ε) lower bound on f^ε:

Lemma 1. *Assume that Assumptions 1 and 2 are satisfied, and for $\varepsilon > 0$, let $f^\varepsilon \in C([0,\infty); M^1_+(X))$ be the solution of (4) given by [8].*

Then, there exists C, $\kappa > 0$ such that for all $\varepsilon > 0$ small enough,

$$f^\varepsilon(t,x) \geq C\,\varepsilon^\kappa, \quad \text{for } t \geq 0,\ x \in X.$$

The second step is to show that $f(t,\cdot)$ satisfies (6) for a.e. $t \geq 0$:

Proposition 3. *Assume that Assumptions 1 and 2 are satisfied. For $\varepsilon > 0$, let $f^\varepsilon \in C([0,\infty); M^1_+(X))$ be the solution of (4) given by [8], and $f \in L^\infty([0,T], M^1(X))$ be an asymptotic population density given by Prop 1.*

Then, for a.e. $t \in \mathbb{R}_+$,

$$\forall x \in \text{supp } f(t,\cdot), \quad s[f(t,\cdot)](x) = 0. \tag{12}$$

To show Prop. 3, we will use the following Lemma:

Lemma 2. *Assume that Assumptions 1 and 2 are satisfied. For $\varepsilon > 0$, let $f^\varepsilon \in C([0,\infty); M^1_+(X))$ be the solution of (4) given by [8], and $f \in L^\infty([0,T], M^1(X))$ be an asymptotic population density given by Prop. 1.*

If η, $\bar\delta > 0$, there exists $\bar\kappa \in (0,\eta)$ such that for any $\bar x \in X$ and $\bar t$ a Lebesgue point of $t \mapsto s[f(t,\cdot)](\bar x)$ satisfying

$$s[f(\bar t,\cdot)](\bar x) < -\eta,$$

there exists t_1, $t_2 \in \mathbb{Q}$, $t_2 - t_1 \leq 1$, such that $\bar t \in (t_1,t_2)$ and:

$$\frac{1}{|t_1 - t_2|\,|B(\bar x,\bar\kappa)|}\int_{[t_1,t_2]}\int_{B(\bar x,\bar\kappa)} f(t,x)\,dt\,dx \leq Cst\,\bar\delta,$$

where Cst is a constant depending only on a, b, and m.

Finally, if we combine the results of Prop. 2 and Prop 3, we obtain the main result of this paper (thanks to Def. 1):

Proposition 4. *Assume that Assumptions 1 and 2 are satisfied. For $\varepsilon > 0$, let $f^\varepsilon \in C([0,\infty); M^1_+(X))$ be the solution of (4) given by [8], and $f \in L^\infty([0,T], M^1(X))$ be the asymptotic population density given by Prop 1.*

Then, for a.e. $t \in \mathbb{R}_+$, $f(t,.)$ is an ESD of (2).

Note that in general, the limit population f given by Prop. 4 depends on the time variable t, and on the subsequence of $(f^\varepsilon)_\varepsilon$ extracted in Prop. 1.

Remark 2. *For the sake of Proofs readability, we wrote our results under the non-optimal assumptions 1 and 2. One can probably generalize our results to non-compact phenotypic trait spaces X, provided that $a(x)$ decreases fast enough when $x \to \infty$. One can also consider mutation kernels that depend resonably on ε.*

1.4 Comments on our results and previous results

In the case when (2) admits a unique ESD $\bar f = \bar\rho\delta_{\bar x}$ ($\bar x$ is then called ESS of the system), the convergence of the solution f of (1) to $\bar f$ under an asymptotic of large time and small mutations has been studied e.g. in [5, 6]. For competition kernels of the type $b(x,y) = b_1(x)b_2(y)$, the dynamics of the population can indeed be well understood using the scaling (5), see [10, 21, 2].

For more general competition kernels such as we consider in this article (and that are widely used in theoretical biology, see e.g. [17, 11, 24, 12]), the scaling (5) still can be used (see [22]), but the asymptotic population f cannot be explicitly described, and we don't know then any result on the long-time properties of the population.

If mutations are neglected in (1), that is when $m \equiv 0$, (1) has been studied in [8, 23, 16]. In [8, 23], the local stability of some ESD of (2) for (1) without mutations have been proven. More precisely, it is shown that an ESD $\bar f = \sum_{i=1}^n \bar\rho_i\delta_{\bar x_i}$ of (2) is a locally (in the sense of the W_∞ Wasserstein distance on measures) stable steady-state of (1) (with $m \equiv 0$) if $(\bar x_i)_i$ is an Evolutionary Attractor, which is a stronger stability notion than ESD (see [14, 18, 23]).

The case where mutations are neglected has also been studied in [16], under an assumption on the competition kernel, which corresponds to $b(x,y) = B(x-y)$ and the Fourier transform of B is positive. Then, under the additional assumption that there exists an ESD $\bar f$ of (2), it is shown in [16] that $f(t,\cdot) \rightharpoonup \bar f$ (see [16] for a precise statement). Cor. 1 below shows that this last assumption is always satisfied (under reasonable assumptions on X, a and b, see also Rem 2).

We emphasize two important corollaries of the main result of this article (Prop. 4), which are of particular interest:

The first corollary states that for any coefficients a, b satisfying Assumption 1, there exists at least one ESD of (2):

Corollary 1. *If Assumption 1 is satisfied, then there exists an ESD* $\bar{f} \in M^1(X)$ *of* (2).

To prove this result, one may choose for instance a mutation kernel $m(x) := 1$, and apply Prop. 4.

The second corollary states that if (2) admits only one ESD $\bar{f}$, then the solutions (f^ε) of (4) converge asymptotically to $\bar{f}$

Corollary 2. *Assume that Assumptions 1 and 2 are satisfied, and for* $\varepsilon > 0$*, and let* $f^\varepsilon \in C([0,\infty); M^1_+(X))$ *be the solution of* (4) *given by [8].*

If (2) *admits a unique ESD* $\bar{f} \in M^1(X)$ *of* (2)*, then*

$$f^\varepsilon \to_{\varepsilon\to 0} \bar{f} \quad L^\infty\left(\omega * [0,T], \sigma(M^1, C_b)(X)\right).$$

This corollary is a direct consequence of Prop. 4 and Prop 1. Notice that in evolution theory, and in particular in Adative Dynamics theory, one often assume (usually implicitly) that a unique ESS (ESD being a generalization of the notion of ESS) of the system exists. Cor. 2 then identifies the asymptotic behaviour of the population, with very few assumptions on the initial population and on a, b, m.

2 Proofs of the results.

2.1 Proof of Lemma 1

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Step 1: We show that there exists $C_1 > 0$ such that for any $t > 0$, $x \in X$, if $\varepsilon > 0$ is small enough, then $f^\varepsilon(t,x) \geq C_1 \varepsilon^I \inf_{\sigma\in[t-I\varepsilon,t]} \|f(\sigma,\cdot)\|_{L^1(X)}$.

Let $t > 0$, $x \in X$. If $\varepsilon > 0$ is small enough, $t - I\varepsilon \geq 0$, and then we get from (9):

$$\begin{aligned} f^\varepsilon(t,x) &\geq \int_{t-\varepsilon}^t (m *_x f^\varepsilon)(\sigma,x) e^{\frac{1}{\varepsilon}\int_\sigma^t s[f^\varepsilon(\tau,\cdot)](x)\,d\tau}\,d\sigma, \\ &\geq e^{-\frac{\varepsilon}{\varepsilon}\|s\|_{L^\infty(X)}} \left[m *_x \left(\int_{t-\varepsilon}^t f^\varepsilon(\sigma,\cdot)\,d\sigma\right)\right](x), \end{aligned}$$

and further,

$$\begin{aligned}
f^\varepsilon(t,x) &\geq e^{-\|s\|_{L^\infty(X)}} m *_x \left(\int_{t-\varepsilon}^t \left(\int_{\sigma-\varepsilon}^\sigma m *_x f^\varepsilon(\tilde\sigma,x) e^{\frac{1}{\varepsilon}\int_{\tilde\sigma}^\sigma s[f^\varepsilon(\tau,\cdot)](x)\,d\tau}\,d\tilde\sigma\right) d\sigma\right)\\
&\geq e^{-\|s\|_{L^\infty(X)}} \left(e^{-\frac{\varepsilon\|s\|_{L^\infty(X)}}{\varepsilon}}\right) m *_x \left(\int_{t-\varepsilon}^t \int_{\sigma-\varepsilon}^\sigma m *_x f^\varepsilon(\tilde\sigma,\cdot)\,d\tilde\sigma\,d\sigma\right)(x)\\
&\geq \frac{\varepsilon}{2}\left(e^{-\|s\|_{L^\infty(X)}}\right)^2 m * m *_x \left(\int_{t-\frac{3}{2}\varepsilon}^{t-\frac{1}{2}\varepsilon} f^\varepsilon(\sigma,\cdot)\,d\sigma\right)(x).
\end{aligned}$$

Iterating this estimation, we get, for $I \in \mathbb{N}$:

$$\begin{aligned}
f^\varepsilon(t,x) &\geq \left(\frac{\varepsilon}{2}\right)^{I-1}\left(e^{-\|s\|_{L^\infty(X)}}\right)^I \left(*_{i=1}^I m\right) *_x \left(\int_{t-\frac{I+1}{2}\varepsilon}^{t-\frac{I-1}{2}\varepsilon} f^\varepsilon(\sigma,\cdot)\,d\sigma\right)(x),\\
&\geq \left(\frac{\varepsilon}{2}\right)^{I-1}\left(e^{-\|s\|_{L^\infty(X)}}\right)^I \min_{y\in X}\left(*_{i=1}^I m\right)(y) \int_{t-\frac{I+1}{2}\varepsilon}^{t-\frac{I-1}{2}\varepsilon} \|f^\varepsilon(\sigma,\cdot)\|_{L^1(X)}\,d\sigma.
\end{aligned}$$

Thanks to Assumption 2, we get:

$$\begin{aligned}
f^\varepsilon(t,x) &\geq C\left(\frac{\varepsilon}{2}\right)^{I-1}\left(e^{-\|s\|_{L^\infty(X)}}\right)^I \int_{t-\frac{I+1}{2}\varepsilon}^{t-\frac{I-1}{2}\varepsilon} \|f^\varepsilon(\sigma,\cdot)\|_{L^1(X)}\,d\sigma\\
&\geq C_1\,\varepsilon^I \inf_{\sigma\in[t-I\varepsilon,t]} \|f(\sigma,\cdot)\|_{L^1(X)}.
\end{aligned}$$

Step 2: We show that there exists C, $\kappa>0$ such that for $t>0$, if $\varepsilon>0$ is small enough, then, $\|f^\varepsilon(t,\cdot)\|_{L^1} \geq C\,\varepsilon^\kappa$.

Let C_1 be the constant of Step 1, and $X_1 := \left\{x\in x; a(x) \geq \frac{1}{2}\max_{y\in X} a(x)\right\}$. Let:

$$\begin{aligned}
&\Delta T := \frac{4\varepsilon}{\max a}\ln\left(\frac{2}{C_1|X_1|\varepsilon^I}\right),\\
&\Lambda := \min\left\{\|f^0\|_{L^1(X)} e^{-\|s\|_\infty I},\ \frac{\max a}{4\|b\|_\infty} e^{\frac{-\|s\|_\infty \Delta T}{\varepsilon}}\right\},\\
&T := \inf\left\{t>0; \|f^\varepsilon(t,\cdot)\|_{L^1(X)} \leq \Lambda\right\},
\end{aligned}$$

where $\|s\|_\infty<\infty$ denotes the uniform bound on $s[f^\varepsilon](\cdot)$ (see Assumption 1 and (8)):

$$\|s\|_\infty = \|a\|_\infty + \|b\|_\infty \max\left(\frac{\max_{x\in X} a(x) + \max_{x,y\in X} m(x-y)}{\inf_{x,y\in X} b(x,y)}, \|f^0\|_{M^1(X)}\right).$$

We want to show that $T=\infty$, using a reductio ab absurdum argument.

If $t \leq I\varepsilon$, thanks to (9),

$$\|f^\varepsilon(t,\cdot)\|_{L^1(X)} \geq \|f^0\|_{L^1(X)} e^{\frac{-\|s\|_\infty I\varepsilon}{\varepsilon}} \geq \Lambda,$$

and then, $T \geq I\varepsilon$.

Assume now that $T \geq 2\Delta T$ is finite. Then, $[T - I\varepsilon, T] \subset \mathbb{R}_+$, and we can apply the result of step 1: for $x \in X$,

$$f^\varepsilon(T - \Delta T, x) \geq C_1 \varepsilon^I \inf_{\sigma \in [t - I\varepsilon, t]} \|f^\varepsilon(\sigma,\cdot)\|_{L^1(X)} \geq C_1 \varepsilon^I \Lambda. \tag{13}$$

Moreover, using the definition of ΔT, we can bound $\|f^\varepsilon(t,\cdot)\|_{L^1(X)}$ from above using an integral formulation of f similar to (9): for $t \in [T - \Delta T, T]$ and $x \in X$,

$$\begin{aligned} f^\varepsilon(T,x) &\geq f^\varepsilon(t,x) e^{\frac{1}{\varepsilon}\int_t^T s[f^\varepsilon(\tau,\cdot)](x)\,d\tau} \\ &\geq f^\varepsilon(t,x) e^{\frac{-\|s\|_\infty}{\varepsilon}\Delta T}. \end{aligned}$$

Thus, thanks to an integration over X, we get for $t \in [T - \Delta T, T]$:

$$\begin{aligned} \|f^\varepsilon(t,\cdot)\|_{L^1(X)} &\leq \Lambda e^{\frac{1}{\varepsilon}\|s\|_\infty \Delta T} \\ &\leq \frac{\max a}{4\|b\|_\infty}, \end{aligned}$$

and then, for $t \in [T - \Delta T, T]$ and $x \in X_1$,

$$\begin{aligned} \partial_t f^\varepsilon(t,x) &\geq \frac{1}{\varepsilon}\left(\frac{1}{2}\max a - \|b\|_\infty \|f^\varepsilon(t,\cdot)\|_{L^1(X)}\right) f^\varepsilon(t,x) \\ &\geq \frac{\max a}{4\varepsilon} f^\varepsilon(t,x). \end{aligned} \tag{14}$$

Then, $f^\varepsilon(T,x) \geq f^\varepsilon(T - \Delta T, x) e^{\frac{\max a}{4\varepsilon}\Delta T}$, and thanks to (13), we get for $x \in X_1$:

$$f^\varepsilon(T,x) \geq C_1 \varepsilon^I \Lambda e^{\frac{\max a}{4\varepsilon}\Delta T},$$

and then,

$$\|f^\varepsilon(T,\cdot)\|_{L^1(X)} \geq \|f^\varepsilon(T,\cdot)\|_{L^1(X_1)} \geq C_1 |X_1| \varepsilon^I \Lambda e^{\frac{\max a}{4\varepsilon}\Delta T},$$

which implies, thanks to the definition of ΔT that $\|f^\varepsilon(T,\cdot)\|_{L^1(X)} > 2\Lambda$, which is absurd. Then, necessarily, $T = \infty$, which proves Step 2, since for $t \geq 0$, $\|f^\varepsilon(t,\cdot)\|_{L^1(X)} \geq \Lambda$ and Λ can be bound from below by a polynomial in ε:

$$\begin{aligned} \Lambda &= \min\left\{\|f^0\|_{L^1(X)} e^{-\|s\|_\infty I}, \frac{\max a}{4\|b\|_\infty} e^{\frac{-\|s\|_\infty \Delta T}{\varepsilon}}\right\} \\ &= \min\left\{\|f^0\|_{L^1(X)} e^{-\|s\|_\infty I}, \frac{\max a}{4\|b\|_\infty}\left(\frac{C_1 |X_1| \varepsilon^I}{2}\right)^{\frac{4\|s\|_\infty}{\max a}}\right\} \end{aligned}$$

Finally, the combination on of Step 1 and Step 2 proves Lem. 1.

2.2 Proof of Prop. 2

We assume that there exists $\bar{x} \in Int(X)$ and a Lebesgue point $\bar{t} > 0$ of $t \mapsto s[f(t,\cdot)](\bar{x})$ such that:

$$s[f(\bar{t},\cdot)](\bar{x}) > 0. \tag{15}$$

Step 1: We will show that this assumption leads to a contradiction.

Since $\bar{t}$ is a Lebesgue point of $t \mapsto s[f(t,\cdot)](\bar{x})$,

$$\frac{1}{\delta}\int_{\bar{t}-\delta}^{\bar{t}} s[f(\tau,\cdot)](\bar{x})\,d\tau \to_{\delta\to 0} s[f(\bar{t},\cdot)](\bar{x}) > 0.$$

Then, there exists $\bar{\delta} > 0$ such that:

$$\int_{\bar{t}-\bar{\delta}}^{\bar{t}} s[f(\tau,\cdot)](\bar{x})\,d\tau > Cst > 0. \tag{16}$$

Thanks to the limit (11), (16) implies that there exists $\bar{\varepsilon} > 0$ such that:

$$\forall \varepsilon \in (0,\bar{\varepsilon}), \quad \int_{t-\bar{\delta}}^{\bar{t}} s[f^\varepsilon(\tau,\cdot)](\bar{x})\,d\tau > Cst > 0. \tag{17}$$

Finally, $\left(x \mapsto \int_{t_1}^{\bar{t}} s[f^\varepsilon(\tau,\cdot)](\bar{x})\,d\tau\right)_\varepsilon$ is uniformly Lipschitz-continuous thanks to Assumption 1, and then, there exists $\bar{\kappa} > 0$ such that:

$$\forall \varepsilon \in (0,\bar{\varepsilon}), \forall x \in B(\bar{x},\bar{\kappa}), \quad \int_{t_1}^{\bar{t}} s[f^\varepsilon(\tau,\cdot)](x)\,d\tau > Cst > 0,$$

where $B(\bar{x},\bar{\kappa}) := \{x \in X, |x-\bar{x}| < \bar{\kappa}\}$. Then, using an integral formulation of f^ε (see (9)), we get:

$$\begin{aligned} f^\varepsilon(\bar{t},x) &\geq e^{\frac{1}{\varepsilon}\int_{\bar{t}-\bar{\delta}}^{\bar{t}} s[f^\varepsilon(\sigma,\cdot)](x)\,d\sigma} f^\varepsilon(\bar{t}-\bar{\delta},x) \\ &\geq e^{\frac{Cst}{\varepsilon}\bar{\delta}} f^\varepsilon(\bar{t}-\bar{\delta},x), \end{aligned} \tag{18}$$

where $Cst > 0$. Thanks to Lem. 1,if $\bar{\varepsilon} > 0$ is small enough,

$$\forall \varepsilon \in (0,\bar{\varepsilon}), \forall x \in B(\bar{x},\bar{\kappa}), \quad f^\varepsilon(\bar{t}-\bar{\delta},x) \geq e^{\frac{Cst}{\varepsilon}\bar{\delta}} C\varepsilon^\kappa$$

where Cst, $\kappa > 0$, and then,

$$\|f^\varepsilon(\bar{t},\cdot)\|_{L^1(X)} = \int_{B(\bar{x},\bar{\kappa})} f^\varepsilon(\bar{t},x)\,dx \geq C\,|B(\bar{x},\bar{\kappa})|\,\varepsilon^\kappa e^{\frac{Cst}{\varepsilon}\bar{\delta}} \to_{\varepsilon\to 0} \infty,$$

which is in contradiction with the uniform a priori bound (8) on f^ε.

Step 2: We will show that Step 1 implies Prop. 2.

Let $\eta > 0$. Since X is bounded, there exists $N \in \mathbb{N}$ and $x_1, \ldots, x_N \in X$ such that

$$X \subset \cup_{i=1}^N B(x_i, \eta). \tag{19}$$

For $i \in \{1, \ldots, N\}$, there exists a negligeable set $N_i \subset \mathbb{R}_+$ (that is $|N_i| = 0$), such that any $t \in \mathbb{R}_+ \setminus N_i$ is a Lebesgue point of $s[f(t,\cdot)](x_i)$, and then, thanks to Step 1, $s[f(t,\cdot)](x_i) \leq 0$. Since this is true for $i = 1, \ldots, N$,

$$\forall i = 1, \ldots, N,\ \forall t \in \mathbb{R}_+ \setminus \left(\cup_{i=1}^N N_i\right), \quad s[f(t,\cdot)](x_i) \leq 0. \tag{20}$$

Since $\{x_1, \ldots, x_N\}$ satisfies (19) and $\|\partial_x s[f]\|_{L^\infty(\mathbb{R}_+\times X)} \leq \|a'\| + \|\partial_1 b\|_\infty \|f\|_{L^\infty(\mathbb{R}_+, M^1(X))} < \infty$, we get from (20):

$$\forall t \in \mathbb{R}_+ \setminus \left(\cup_{i=1}^N N_i\right),\ \forall x \in X, \quad s[f(t,\cdot)](x_i) \leq Cst\,\eta,$$

that is $|\{t \in \mathbb{R}_+;\ \exists x \in X,\ s[f(t,\cdot)](x) \geq Cst\,\eta\}| = 0$, and since this is true for any $\eta > 0$, Prop. 2 follows.

2.3 Proof of Lem. 2

Since $\bar t > 0$ is a Lebesgue point of $t \mapsto s[f(t,\cdot)](\bar x)$, then

$$\frac{1}{\delta}\int_{\bar t-\delta}^{\bar t} s[f(\tau,\cdot)](\bar x)\,d\tau \rightarrow_{\delta\to 0} s[f(\bar t,\cdot)](\bar x) \leq -\eta < 0,$$

and therefore, there exists $\delta \in (0, \bar\delta)$ such that:

$$\int_{\bar t-\delta}^{\bar t} s[f(\tau,\cdot)](\bar x)\,d\tau \leq -\frac{1}{2}\,\eta\,\delta < 0. \tag{21}$$

Thanks to the limit (11), (21) implies that for some $\bar\varepsilon > 0$, we have:

$$\forall \varepsilon \in (0, \bar\varepsilon), \quad \int_{\bar t-\delta}^{\bar t} s[f^\varepsilon(\tau,\cdot)](\bar x)\,d\tau \leq -\frac{1}{4}\,\eta\,\delta < 0.$$

Since $\|\partial_x s[f^\varepsilon]\|_{L^\infty(\mathbb{R}_+\times X)} \leq \|a'\| + \|\partial_1 b\|_\infty \|f^\varepsilon\|_{L^\infty(\mathbb{R}_+, M^1(X))} < \infty$ is uniformly bounded, for $\varepsilon \in (0, \bar\varepsilon)$,

$$\begin{aligned}\int_{\bar t-\delta}^{t} s[f^\varepsilon(\tau,\cdot)](x)\,d\tau &= \int_{\bar t-\delta}^{\bar t} s[f^\varepsilon(\tau,\cdot)](\bar x)\,d\tau + O(\delta|x-\bar x|) + O(|t-\bar t|)\\ &\leq \left(-\frac{1}{4}\eta + \|\partial_x s[f^\varepsilon]\|_{L^\infty(\mathbb{R}_+\times X)}\,|x-\bar x|\right)\delta + O(|t-\bar t|).\end{aligned}$$

Let $\bar\kappa := \min\left(\frac{\eta}{8\|\partial_x s[f^\varepsilon]\|_{L^\infty(\mathbb{R}_+\times X)}}, \eta\right)$. Then, there exists t_1, $t_2 \in \mathbb{Q}\cap\mathbb{R}_+$, $t_2 - t_1 \le 1$, such that $t \in (t_1, t_2)$, and :

$$\forall\varepsilon\in(0,\bar\varepsilon),\,\forall(t,x)\in(t_1,t_2)\times B(\bar x,\bar\kappa)\cap(\mathbb{R}_+\times X),\quad \int_{t-\delta}^t s[f^\varepsilon(\tau,\cdot)](x)\,d\tau \le -Cst < 0. \tag{22}$$

Notice that $|t_2-t_1|$ depends on δ, it is thus impossible to control uniformly $|t_2-t_1|$ from below, as we do for $\bar\kappa$.

Let $t\in(t_1,t_2)$, and $x\in B(\bar x,\bar\kappa)$. Thanks to (9),

$$\begin{aligned} f^\varepsilon(t,x) &= f^0(x)e^{\frac{1}{\varepsilon}\int_0^t s[f^\varepsilon(\tau,\cdot)](x)\,d\tau} + \int_0^{t-\delta} m *_x f^\varepsilon(\sigma,x)e^{\frac{1}{\varepsilon}\int_\sigma^t s[f^\varepsilon(\tau,\cdot)](x)\,d\tau}\,d\sigma \\ &\quad + \int_{t-\delta}^t m *_x f^\varepsilon(\sigma,x)e^{\frac{1}{\varepsilon}\int_0^t s[f^\varepsilon(\tau,\cdot)](x)\,d\tau}\,d\sigma. \end{aligned}$$

For $\sigma \le t-\delta$, we use Prop. 2 and (22) to estimate:

$$\begin{aligned} \int_\sigma^t s[f^\varepsilon(\tau,\cdot)](x)\,d\tau &= \int_\sigma^{t-\delta} s[f^\varepsilon(\tau,\cdot)](x)\,d\tau + \int_{t-\delta}^t s[f^\varepsilon(\tau,\cdot)](x)\,d\tau \\ &\le 0 - Cst < 0, \end{aligned}$$

and if $\sigma > t-\delta$, thanks to Prop. 2, $\int_\sigma^t s[f^\varepsilon(\tau,\cdot)](x)\,d\tau \le 0$. Then,

$$\begin{aligned} f^\varepsilon(t,x) &\le f^0(x)e^{\frac{-Cst}{\varepsilon}} + \int_0^{t-\delta} \|m\|_{L^\infty(X-X)}\|f^\varepsilon(\sigma,\cdot)\|_{L^1(X)}e^{\frac{-Cst}{\varepsilon}}\,d\sigma \\ &\quad + \|m\|_{L^\infty(X-X)}\|f^\varepsilon\|_{L^\infty(L^1(X))}\int_{t-\delta}^t e^0\,d\sigma, \\ &\le o_\varepsilon(1) + Cst\,\bar\delta, \end{aligned}$$

where the constant Cst only depends on a, b and m.

Let now $\phi\in C_c(X)$ be a test-function such that:

$$0\le\phi\le1,\quad \mathrm{supp}(\phi)\subset B(\bar x,\bar\kappa),\quad \phi|_{B(\bar x,\frac{\bar\kappa}{2})}\equiv 1. \tag{23}$$

Then:

$$\begin{aligned} \int_{t_1}^{t_2}\int_X f^\varepsilon\phi &\le \int_{t_1}^{t_2}\int_{B(\bar x,\bar\kappa)} f^\varepsilon \\ &\le \int_{t_1}^{t_2}\int_{B(\bar x,\bar\kappa)} \left(o_\varepsilon(1)+Cst\,\bar\delta\right) \\ &\le |t_1-t_2|\,|B(\bar x,\bar\kappa)|\left(o_\varepsilon(1)+Cst\,\bar\delta\right). \end{aligned} \tag{24}$$

Thanks to (23), if we let $\varepsilon \mapsto 0$, we get from (24) and (10):

$$\frac{1}{|t_1 - t_2|\,|B(\bar{x}, \bar{\kappa})|} \int_{t_1}^{t_2} \int_{B(\bar{x}, \frac{\bar{\kappa}}{2})} f \leq Cst\,\bar{\delta}.$$

Note that the constant Cst does not depend on $\bar{\delta}$, but only on a, b and m.

2.4 Proof of Prop. 3

Let $T > 0$, $\eta > 0$, $\bar{\delta} > 0$, and $\bar{\kappa}$ the constant appearing in Lem. 2. We will show that $\int_0^T \int_X f(t,x) \mathbb{1}_{s[f(t,\cdot)](x)<0}\,dx\,dt = 0$.

Since X is bounded, there exists $N \in \mathbb{N}$ and $x_1, \ldots, x_N \in X$ such that

$$X \subset \cup_{i=1}^N B(x_i, \bar{\kappa}). \tag{25}$$

For $i \in \{1, \ldots, N\}$, there exists a negligeable set $N_i \subset [0,T]$ such that any $t \in [0,T] \backslash N_i$ is a Lebesgue point of $s[f(t,\cdot)](x_i)$. We define $N := \cup_{i=1}^N N_i$.

If $\bar{x} \in X$ and a Lebesgue point $\bar{t} \in [0,T] \setminus N$ of $t \mapsto s[f(t,\cdot)](\bar{x})$ are such that $s[f(\bar{t},\cdot)](\bar{x}) < -\eta - \bar{\kappa}\,\|\partial_x s[f]\|_{L^\infty(\mathbb{R}_+ \times X)}$, then there exists $i \in \{1, \ldots, N\}$ such that $|\bar{x} - x_i| \leq \bar{\kappa}$, and then, thanks to the definition (25) of $x_1, \ldots, x_N$,

$$s[f(\bar{t},\cdot)](x_i) \leq s[f(\bar{t},\cdot)](\bar{x}) + \bar{\kappa}\|\partial_x s[f]\|_{L^\infty(\mathbb{R}_+ \times X)} \leq -\eta.$$

Then,

$$\begin{aligned} \big\{(t,x) \in ([0,T] \setminus N) \times X;\, s[f(t,\cdot)](x) \leq -\eta - \bar{\kappa}\|\partial_x s[f]\|_{L^\infty(\mathbb{R}_+ \times X)}\big\} \\ \subset \cup_{i=1}^N \mathcal{T}_i \times B(x_i, \bar{\kappa}) \end{aligned} \tag{26}$$

where $\mathcal{T}_i := \{t \in \mathbb{R}_+ \setminus N;\, s[f(\bar{t},\cdot)](x_i) < -\eta\}$.

Lem. 2 applies to (t, x_i) for $i \in \{1, \ldots, N\}$ and $t \in \mathcal{T}_i$: there exists $t_1^{t,i}$, $t_2^{t,i} \in \mathbb{Q}$, $t \in (t_1^{t,i}, t_2^{t,i})$ such that

$$\frac{1}{|t_1^{t,i} - t_2^{t,i}|\,|B(\bar{x}, \bar{\kappa})|} \int_{[t_1^{t,i}, t_2^{t,i}]} \int_{B(\bar{x}, \bar{\kappa})} f(t,x)\,dt\,dx \leq Cst\,\bar{\delta}. \tag{27}$$

Let consider a fixed $i \in \{1, \ldots, N\}$. Since $t_1^{t,i}$, $t_2^{t,i} \in \mathbb{Q}$ (see Lem. 2), the set $\{(t_1^{t,i}, t_2^{t,i}) \in [0,T]^2; t \in \mathcal{T}_i\}$ is indeed countable. There exits then an increasing sequence $(\Omega^k)_{k \in \mathbb{N}}$ of finite subsets of $\{(t_1^{t,i}, t_2^{t,i}) \in [0,T]^2; t \in \mathcal{T}_i\}$ such that $\cup_{K=0}^\infty \Omega^k = \{(t_1^{t,i}, t_2^{t,i}); t \in \mathcal{T}_i\}$. Thanks to the monotone convergence theorem,

$$\int_{\mathcal{T}_i}\int_{B(x_i,\bar\kappa)} f(t,x)\,dx\,dt \le \int_{\cup_{t\in\mathcal{T}_i}[t_1,t_2]}\int_{B(x_i,\bar\kappa)} f(t,x)\,dx\,dt \tag{28}$$

$$\le \lim_{k\to\infty}\int_{\cup_{(t_1,t_2)\in\Omega^k}[t_1,t_2]}\int_{B(x_i,\bar\kappa)} f(t,x)\,dx\,dt. \tag{29}$$

Before using estimate (27), we modify the finite sets Ω^k so that intervals $\{[t_1,t_2];(t_1,t_2)\in\Omega^k\}$ do not intersect too much. To do so, we proceed as follows:

- We order $\Omega^k=\{(t_1^1,t_2^1),\,(t_1^2,t_2^2),\,\dots\}$ so that (t_1^l) is increasing.
- For $l\ge 1$, if $t_2^{l+1}\le t_2^l$, we remove (t_1^{l+1},t_2^{l+1}) from Ω^k.
  If $t_2^{l+1}\le t_2^l$, then $[t_1^{l+1},t_2^{l+1}]\subset[t_1^l,t_2^l]$, and $\cup_{(t_1,t_2)\in\Omega^k}[t_1,t_2]\times B(x_i,\bar\kappa)$ is not affected by the removal of (t_1^{l+1},t_2^{l+1}) from Ω^k.
  We repeat this procedure as often as required, starting from $l=1$.
- For $l\ge 1$, if $t_1^{l+2}\le t_2^l$, we remove (t_1^{l+1},t_2^{l+1}) from Ω^k.
  If $t_1^{l+2}\le t_2^l$, thanks to the preceding step, $t_2^{l+2}>t_2^{l+1}$, and then,

  $$[t_1^{l+1},t_2^{l+1}]\subset[t_1^l,t_2^{l+2}]=[t_1^l,t_2^l]\cup[t_1^{l+2},t_2^{l+2}].$$

  $\cup_{(t_1,t_2)\in\Omega^k}[t_1,t_2]\times B(x_i,\bar\kappa)$ is thus not affected by the removal of (t_1^{l+1},t_2^{l+1}).
  We repeat this procedure as often as required, starting from $l=1$.

Finally, we end up with a finite family of intervals $\tilde\Omega^k=\{(t_1^1,t_2^1),\,(t_1^2,t_2^2),\,\dots\}$ such that $t_1^{l+2}>t_2^l$ for any $l\ge 1$. Then, only consecutive intervals $[t_1,t_2]$, $[t_1',t_2']$ can intersect, and thus:

$$\begin{aligned}\sum_{(t_1,t_2)\in\tilde\Omega^k}|t_1-t_2| &= |\cup_{(t_1,t_2)\in\tilde\Omega^k}[t_1,t_2]|+\sum_l|[t_1^l-t_2^l]\cap[t_1^{l+1}-t_2^{l+1}]|\\ &\le 2|\cup_{(t_1,t_2)\in\tilde\Omega^k}[t_1,t_2]|\\ &\le 2T+2.\end{aligned}$$

(Since $t_2-t_1\le 1$, see Lem 2). Moreover, $\cup_{(t_1,t_2)\in\tilde\Omega^k}[t_1,t_2]\times B(x_i,\bar\kappa)=\cup_{(t_1,t_2)\in\Omega^k}[t_1,t_2]\times B(x_i,\bar\kappa)$.

Thanks to the modified family $\tilde{\Omega}^k$ constructed above, we can estimate, using (27):

$$\begin{aligned}
\int_{\cup_{(t_1,t_2)\in\Omega^k}[t_1,t_2]}\int_{B(x_i,\bar\kappa)} f(t,x)\,dx\,dt &= \int_{\cup_{(t_1,t_2)\in\tilde\Omega^k}[t_1,t_2]}\int_{B(x_i,\bar\kappa)} f(t,x)\,dx\,dt \\
&\leq \sum_{(t_1,t_2)\in\tilde\Omega^k}\int_{[t_1,t_2]}\int_{B(x_i,\bar\kappa)} f(t,x)\,dx\,dt \\
&\leq \sum_{(t_1,t_2)\in\tilde\Omega^k} Cst\,\bar\delta\,|t_1-t_2||B(\bar x,\bar\kappa)| \\
&\leq Cst\,\bar\delta|B(\bar x,\bar\kappa)|\sum_{(t_1,t_2)\in\tilde\Omega^k}|t_1-t_2| \\
&\leq Cst\,\bar\delta.
\end{aligned}$$

where Cst does not depend on k or $\bar\delta$. Since this bound is uniform in k, we get from (29):

$$\int_{\mathcal{T}_i}\int_{B(x_i,\bar\kappa)} f(t,x)\,dx\,dt \leq Cst\,\bar\delta,$$

and then, combining this inequality (which holds for any $i\in\{1,\dots,N\}$) with (26), we get:

$$\begin{aligned}
&\int_0^T\int_X f(t,x)\mathbb{1}_{\left\{(t,x);\,s[f(t,\cdot)](x)\leq-\eta-\bar\kappa\,\|\partial_x s[f]\|_{L^\infty(\mathbb{R}_+\times X)}\right\}}(x)\,dx\,dt \\
&\quad= \int_{[0,T]\setminus N}\sum_{i=1}^N\int_{B(x_i,\bar\kappa)} f(t,x)\mathbb{1}_{\left\{(t,x);\,s[f(t,\cdot)](x)\leq-\eta-\bar\kappa\,\|\partial_x s[f]\|_{L^\infty(\mathbb{R}_+\times X)}\right\}}(x)\,dx\,dt \\
&\quad\leq \sum_{i=1}^N\int_{\mathcal{T}_i}\int_{B(x_i,\bar\kappa)} f(t,x)\,dx\,dt \\
&\quad\leq Cst\,\bar\delta.
\end{aligned}$$

Since this is true for any $\bar\delta>0$ (we recall also that $f\geq 0$),

$$\int_0^T\int_X f(t,x)\mathbb{1}_{\left\{(t,x);\,s[f(t,\cdot)](x)\leq-\eta-\bar\kappa\,\|\partial_x s[f]\|_{L^\infty(\mathbb{R}_+\times X)}\right\}}(x)\,dx\,dt = 0,$$

and since this true for any $\eta>0$,

$$\int_0^T\int_X f(t,x)\mathbb{1}_{\{x\in X; s(t,x)<0\}}\,dx\,dt = 0,$$

and then for a.e. $t \geq 0$ (since $T > 0$ can be choosen arbitrarly large), $\int_X f(t,x)\mathbb{1}_{\{x\in X; s(t,x)<0\}} = 0$. It follows that for a.e. $t \geq 0$,

$$\forall x \in \text{supp } f(t,\cdot), \quad s[f(t,\cdot)](x) = 0.$$

which proves Prop. 3.

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