



**HAL**  
open science

# Long-time dynamics of a competition-selection model in the space of measures: persistence and concentration

Jean-Baptiste Burie, Arnaud Ducrot, Quentin Griette

## ► To cite this version:

Jean-Baptiste Burie, Arnaud Ducrot, Quentin Griette. Long-time dynamics of a competition-selection model in the space of measures: persistence and concentration. 2021. hal-03286220v2

**HAL Id: hal-03286220**

**<https://hal.science/hal-03286220v2>**

Preprint submitted on 15 Dec 2021 (v2), last revised 2 Jun 2023 (v4)

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

# Long-time dynamics of a competition-selection model in the space of measures: persistence and concentration

Jean-Baptiste Burie<sup>a</sup>, Arnaud Ducrot<sup>b</sup>, and Quentin Griette<sup>a,\*</sup>

December 15, 2021

<sup>a</sup> *Institut de Mathématiques de Bordeaux, Université de Bordeaux, CNRS, IMB, UMR 5251, 351, cours de la Libération, F-33400 Talence, France.*

<sup>b</sup> *Normandie Univ, UNIHAVRE, LMAH, FR-CNRS-3335, ISCN, 76600 Le Havre, France.*

## Abstract

We investigate the long-time dynamics of a competition-selection model in the case of a continuously distributed initial population. We introduce an epidemic model of pathogen species competing for a single resource, whose efficiency is encoded by a continuous variable (the “trait variable”) living in a Euclidean space. The differential equation is solved in a space of measures to allow the observation of the natural concentration of the distribution on specific traits. We show the concentration of the distribution on the maximizing set of the fitness function in the sense of the Kantorovitch-Rubinstein metric. When the initial mass of the maximal fitness set is positive, we give a precise description of the convergence of the orbit, including a formula for the asymptotic distribution. We also investigate precisely the case of a finite number of regular global maxima and show that the initial distribution may have an influence on the support of the eventual distribution. In particular, the natural process of competition is not always selecting a unique species, but several species may coexist as long as they maximize the fitness function. In many cases it is possible to compute the eventual distribution of the surviving competitors. In some configurations, species that maximize the fitness may still get extinct depending on the shape of the initial distribution and some other parameter of the model, and we provide a way to characterize when this unexpected extinction happens.

## 1 Introduction

In this paper we investigate the large time behavior of the system

$$\begin{cases} S_t(t) = \Lambda - \theta S(t) - S(t) \int_{\mathbb{R}^N} \alpha(x) \gamma(x) I(t, dx), & x \in \mathbb{R}^N, \\ I_t(t, dx) = (\alpha(x) S(t) - 1) \gamma(x) I(t, dx), \end{cases} \quad (1)$$

equipped with suitable non-negative initial data. This system of equations intervenes in theoretical ecology, in epidemiology and in genetics. In ecology, it describes the evolution of a population of individuals with density  $I$  that compete for a single limited resource with density  $S = S(t)$ . In epidemiology, this system describes the evolution of the number of susceptible  $S$  and of the density of infected individuals  $I$  who have been contaminated by different pathogen variants of some disease. In both cases, the density of individuals  $I$  is represented by a measure on the space  $\mathbb{R}^N$ , for some integer  $N > 0$ , of phenotypic traits. Representing the density  $I$  by a measure is natural in this context as one expects concentration properties of the density on one or several optimal traits as time goes to infinity. Note also that this model does not take into account mutations but only pure competition (or selection). In the context of ecology, phenotypical traits are related to the competitors and how they interact with the resource via the continuous functions  $\alpha$  and  $\gamma$ , while the last two parameters  $\Lambda > 0$  and  $\theta > 0$  are positive constants which encode the renewal and disappearance rates of the resource.

**AMS subject classifications (2020).** 34D05, 92D25, 34D05, 37L15, 37N25

**Keywords.** ordinary differential equations, asymptotic behavior, population dynamics, Radon measure, evolution.

\*Corresponding author. e-mail: [quentin.griette@u-bordeaux.fr](mailto:quentin.griette@u-bordeaux.fr)

System (1) arises naturally as the limit of a mutation-selection model of spore-producing pathogen,

$$\begin{cases} S_t(t) = \Lambda - \theta S(t) - S(t) \int_{\mathbb{R}^N} \beta(y) A(t, y) dy, \\ I_t(t, x) = S(t) \int_{\mathbb{R}^N} \beta(y) A(t, y) dy - d(x) I(t, x), & t > 0, \quad x \in \mathbb{R}^N, \\ A_t(t, x) = -\delta A(t, x) + \int_{\mathbb{R}^N} r(y) m^\varepsilon(x - y) A(t, y) dy, & t > 0, \quad x \in \mathbb{R}^N, \end{cases} \quad (2)$$

when the mutation kernel is a Dirac mass. The above system describes the evolution of a pathogen producing spores in a heterogeneous plant population. The host population does not represent individual plants, but rather leaf area densities [34]. The function  $S(t)$  denotes the healthy tissue density,  $I(t, x)$  represents the density of tissue infected by pathogen with phenotypic trait value  $x \in \mathbb{R}^N$ , and  $A(t, x)$  describes the density of airborne spores of pathogens with phenotypic trait value  $x \in \mathbb{R}^N$ . The positive parameters  $\Lambda, \theta, \delta$  respectively denote the influx of total new healthy tissue, the death rate of host tissue and the death rate of the spores. Note that in the absence of the disease, namely when  $I = A = 0$ , the density of tissue at equilibrium is equal to  $\Lambda/\theta$ .

The phenotypic traits of the pathogen considered in the model are supposed to influence the functions  $r, \beta$  and  $\gamma$  that respectively denote the spores production rates, the infection efficiencies and the infectious periods of the pathogen. Those parameters depend on the phenotypic value  $x \in \mathbb{R}^N$ . The function  $m^\varepsilon(x) := \frac{1}{\varepsilon^N} m(\frac{x}{\varepsilon})$  is a probability kernel that characterises the mutations arising during the reproduction process. More precisely, given tissue infected by a mother spore with phenotypic value  $y$ ,  $m^\varepsilon(x - y)$  stands for the probability that a produced spore has a phenotypic value  $x$ . The shape of the probability kernel  $m(x)$  is a fixed  $L^1(\mathbb{R}^N) \cap L^\infty(\mathbb{R}^N)$  function while  $\varepsilon > 0$  is a parameter that quantifies the concentration of the kernel  $m^\varepsilon$ . The parameter  $\varepsilon$  is linked to the variance of the mutation kernel.

The above problem supplemented with an age of infection structure has been investigated by Fabre *et al.* [18] using formal asymptotic expansions and numerical simulations. A refined mathematical analysis of the stationary states has been carried out in [17] with a particular emphasis on the concentration property for  $\varepsilon \ll 1$ . We also refer to [10, 11] for the study of the dynamical behaviour and the transient regimes of a corresponding simplified Cauchy problem. Burie, Ducrot, Griette and Richard [12] also studied a similar model with two hosts.

Here we focus on the fully concentrated kernel, that is to say, the case  $\varepsilon = 0$  with no mutation, or equivalently  $m_0(x) = \delta_0(dx)$ . We aim at giving a precise description of what happens in this singular limit case as a first approximation of the transient dynamics of the system (2) with  $\varepsilon > 0$  small but positive. Notice that, for simplicity, we placed ourselves in the fast spores dynamics regime for simplicity (this amounts to equating the left-hand side of the third equation of (2) to zero). We also changed the name of the coefficients to highlight the important quantities in the understanding of the dynamics of (1). As we will see, the use of possibly singular Radon measures as initial data arises as a necessity to include (1) in the framework of dynamical systems and, in particular, to apply the uniform persistence theory of Magal and Zhao [40], which is one of the key elements in our analysis.

While our principal motivation is the understanding of the weak mutation regime for the epidemiological model (2), our system (1) can also be viewed as an abstract ecological model for a continuum of species competing for a single resource. In this context, the ‘‘Competitive exclusion principle’’ states that ‘‘Complete competitors cannot coexist’’, which in particular means that given a number of species competing for the same resource in the same place, only one can survive in the long run. This idea was already present to some extent in the book of Darwin, and is sometimes referred to as Gause’s law [21]. One aim of the present paper is to investigate this principle in the case of a continuously distributed initial population. We will show in particular that, while it is true that the species have to maximize the fitness function in order to survive, the natural process of competition is not selecting a unique species but several species may coexist as long as they maximize the fitness function. In many cases it is possible to compute the eventual repartition of the surviving competitors. In some cases, species that maximize the fitness may still get extinct if the initial population is not sufficient, and we provide a way to characterize when this unexpected extinction happens. Considering a situation where  $\mathcal{R}_0$  has more than one maximum at the same exact level may appear artificial but is not without biological interest. Indeed, the long-time behavior that we observe in these borderline cases can persist in transient time upon perturbing the function  $R_0$ . For example in the epidemiological context of [15], it has been observed that a strain 1 with a higher value of  $\gamma$  and a slightly lower  $\mathcal{R}_0$  value than a strain 2 may nevertheless be dominant for some time, see Figure 8. These borderline cases shed light on our understanding of the transient dynamics, see also [10] where we explicit transient dynamics for a related evolutionary model depending on the local flatness of the fitness function.

This problem of survival of competitors has attracted the attention of mathematicians since the ’70s and many studies have proved this property in many different contexts – let us mention the seminal works of Hsu, Hubbell and Waltman [24] and Hsu [23], followed by Armstrong and McGehee [3], Butler and Wolkowicz [13],

Wolkowicz and Lu [49], Hsu, Smith and Waltman [22], Wolkowicz and Xia [50], Li [33], and more recently Rapaport and Veruete [45], to cite a few – and also disproved in other contexts, for instance in fluctuating environments, see Cushing [14] and Smith [46]. Ackleh and Allen [1] study the competitive exclusion in an epidemic model with a finite number of strains, and describe how different species can coexist in some cases.

A common feature of the above-mentioned studies on the competitive exclusion principle is that they all focus on *finite* systems representing the different species competing for the resource. Yet quantitative traits such as the virulence or the transmission rate of a pathogen, the life expectancy of an individual and more generally any observable feature such as height, weight, muscular mass, speed, size of legs, etc. are naturally represented using continuous variables. Such a description of a population seems highly relevant and has been used mostly in modelling studies involving some kind of evolution [39, 38, 5, 4, 36, 37, 7, 43, 20]

A few studies actually focus on pure competition for a continuously structured population. Let us mention the work of Desvillettes, Mischler, Jabin and Raoul [16], and later Jabin and Raoul [27] and Raoul [44], who studied the logistic equation

$$\partial_t f(t, x) = \left( a(x) - \int b(x, y) f(y) \right) f(t, x), \quad (3)$$

and more precisely the asymptotic behavior of the solutions  $f = f(t, x)$  when the initial condition is a Radon measure. Lorenzi and Pouchol [35] study the concentration dynamics of a logistic equation with nonlocal competition, similar to (3) with  $b(x, y) \equiv 1$  and involving a finite number of fitness maxima, as the vanishing viscosity limit of a diffusion problem. Ackleh, Cleveland and Thieme devoted a part of their study [2] to purely competitive dynamics. Here the focus are equations of the type

$$\mu'(t)(E) = \int_E [B(\bar{\mu}(t), q) - D(\bar{\mu}(t), q)] \mu(t)(dq),$$

where  $\mu$  is a Radon measure on a space of strategies  $Q$  and  $\bar{\mu}(t) = \mu(t)(Q)$ . They show a persistence property for such a model and give more precise statements on the asymptotic behavior of the total mass; under the assumption that a unique strategy maximizing the carrying capacity, they show the convergence in the sense of measures to a Dirac mass concentrated on this strategy.

An important example of a biological system which allows the experimenter to observe the competitive exclusion principle is the so-called *chemostat*, a device in which living organisms (like cells, yeasts, bacteria...) are cultivated in a controlled environment where the in- and outflow of nutrients are monitored. Systems of the same type as (1) (as most systems in the literature cited above) are particularly well-adapted to the modeling of a population in a chemostat. We refer to the monograph of Smith and Waltman [48] for a detailed work on mathematical models for the chemostat. Recently, a lot of interest has been given to chemostat models as a mean to study the Darwinian evolution of a population, that is, the changes in frequency of common characteristics due to the processes of selection and mutation. An important difference of chemostat models is that they usually assume Michaelis-Menten functional response, contrary to our system where the functional response is linear.

The connections between chemostat and epidemic models has been remarked in [47], where an extensive review of the literature is conducted. A competitive exclusion principle for epidemic models has been established by Bremermann and Thieme [9]. The asymptotic behavior of epidemic models of SIR type has been investigated by Korobeinikov and Wake [32], Korobeinikov and Maini [31], Korobeinikov [28, 29, 30], McCluskey [41, 42], in the context of systems of ordinary differential equations.

We add to the existing literature on systems related to (1) by considering the case when the initial condition  $I_0(dx)$  is a Radon measure. We consider measures as initial data is because they appear naturally in the long-time behavior of the equation. Indeed as we will show in Theorem 2.2, initial conditions in the usual space  $L^1(\mathbb{R}^N)$  will converge, in many cases, towards a singular Radon measure. Therefore it is necessary to study the equation in a space of measures in order to investigate the long-time behavior of the solutions to (1). By doing so we were able to include the case of finite systems of ODE into our framework, see Section 2.2 below. Those results are extended to the case of countably many equations under the structural requirement that the coefficients converge to a limit. The system behaves as predicted and the density  $I$  converges towards a Dirac measure at some  $x^*$  when the basic reproduction number (fitness) associated to the phenotypic value  $x$  defined as  $\mathcal{R}_0(x) := \frac{\lambda}{\theta} \alpha(x)$  has a unique maximum on the support of  $I_0$  and the initial data has a positive mass on the maximizing value  $x^*$ , see Section 2.3.

Yet considering the flow generated by (1) in the space of Radon measures is not without difficulty. Indeed (1) has a lot of different stationary solutions in this space: any subset of  $\{\alpha(x) = \alpha_0\}$  is the support of a stationary measure, provided the basic reproduction number associated with  $\alpha_0$  is greater than 1. Thus the stationary solutions for (1) form a continuum and it is not necessarily easy to figure out the one that is selected by an initial condition.

While the case of a positive initial mass on the fitness maxima  $I_0(\{\alpha^{-1}(\alpha^*)\})$  is rather well-understood, when this assumption is removed, it is not even clear that  $I(t, dx)$  converges to a stationary distribution. In

spite of this difficulty, we were able to show that  $I(t, dx)$  is eventually concentrated on the set of maximal fitness. We found that the mass  $\int_{\mathbb{R}^N} I(t, dx)$  does converge to a limit when a stronger assumption is made on the initial distribution  $I_0(x)$ . The asymptotic behavior of the solution strongly depends on the initial condition  $I_0$ . When the fitness function has a finite number of regular maxima, we can study the local behavior of the solutions  $I(t, dx)$  in the vicinity of each fitness maximum, and give a sharp criterion to determine which fitness maximum will keep some mass at  $+\infty$  and which will have a vanishing mass (see Section 2.3). This extinction phenomenon at some fitness maxima is new, to the extent of our knowledge, and shows that the dynamics of the system with continuous phenotypic traits  $x \in \mathbb{R}^N$  is far more rich than the one of discrete models.

The structure of the paper is as follows. In section 2 we present our main results. More precisely, we state our results for general initial measure data in section 2.1, in section 2.2 we show how our results apply to the simpler cases of finite and countably infinite systems, and in section 2.3 we give precise statements of our results concerning fitness functions with a finite number of regular maxima. In section 3 we illustrate our results with numerical simulations and explore the transient dynamics of our system. In section 4 we prove our results concerning general measure initial data (corresponding to the statements in section 2.1). In section 5 we prove our results concerning general measure initial data (corresponding to the statements in section 2.2). In section 6 we prove our statements on the systems with a fitness function  $\alpha(x)$  having a finite number of regular maxima (corresponding to the statements in section 2.3).

## 2 Main results

In this section we state and discuss the main results we shall prove in this note related to the large time behavior of (1). Before going to our results, we introduce some notations that will be used along this work. For a Borel set  $K \subset \mathbb{R}^N$ , we denote by  $\mathcal{M}(K)$  the set of the signed Radon measures on  $K$  of finite mass. Recall that  $\mathcal{M}(K)$  is a Banach space when endowed with the *absolute variation norm* given by:

$$\|\mu\|_{AV} = |\mu|(K), \quad \forall \mu \in \mathcal{M}(K).$$

We also denote by  $\mathcal{M}_+(K)$  the set of the finite nonnegative measures on  $K$ . Observe that one has  $\mathcal{M}_+(K) \subset \mathcal{M}(K)$  and  $\mathcal{M}_+(K)$  is a closed subset of  $\mathcal{M}(K)$  for the norm topology of  $\|\cdot\|_{AV}$ . An alternate topology on  $\mathcal{M}(K)$  can be defined by the so-called Kantorovitch-Rubinstein norm (see [6, Vol. II, Chap. 8.3 p. 191]),

$$\|\mu\|_0 := \sup \left\{ \int f d\mu : f \in \text{Lip}_1(K), \sup_{x \in K} |f(x)| \leq 1 \right\},$$

wherein we have set

$$\text{Lip}_1(K) := \{f \in BC(K) : |f(x) - f(y)| \leq \|x - y\|, \forall (x, y) \in K^2\}.$$

Here (and below)  $BC(K)$  denotes the set of the continuous and bounded functions from  $K$  into  $\mathbb{R}$ . Let us recall (see for instance [6, Theorem 8.3.2]) that the metric generated by  $\|\cdot\|_0$  on  $\mathcal{M}_+(K)$  is equivalent on this set to the weak topology obtained by identifying  $\mathcal{M}(K)$  to the dual space of  $BC(K)$ . Note however that this equivalence is true only for  $\mathcal{M}_+(K)$  and cannot be extended to  $\mathcal{M}(K)$  since the latter space is not (in general) complete for the metric generated by  $\|\cdot\|_0$ . We denote by  $d_0$  this metric on  $\mathcal{M}_+(K)$ , that is

$$d_0(\mu, \nu) := \|\mu - \nu\|_0 \text{ for all } \mu, \nu \in \mathcal{M}_+(K). \quad (4)$$

Now along this note we fix  $I_0 = I_0(dx) \in \mathcal{M}_+(\mathbb{R}^N)$ .

About the parameters arising in (1) our main assumption reads as follows.

**Assumption 2.1.** The constants  $\Lambda > 0$  and  $\theta > 0$  are given. The functions  $\alpha(x)$  and  $\gamma(x)$  are continuous from  $\mathbb{R}^N$  into  $\mathbb{R}$  and there exist positive constants  $\alpha^\infty$  and  $\gamma_0 < \gamma^\infty$  such that

$$\alpha(x) \leq \alpha^\infty, \quad 0 < \gamma_0 \leq \gamma(x) \leq \gamma^\infty \quad \text{for all } x \in \mathbb{R}^N.$$

Finally, define  $\alpha^* := \sup_{x \in \text{supp } I_0} \alpha(x)$ . We assume that the set

$$\begin{aligned} L_\varepsilon(I_0) &:= \{\alpha \geq \alpha^* - \varepsilon\} \cap \text{supp } I_0 \\ &= \{x \in \text{supp } I_0 : \alpha(x) \geq \alpha^* - \varepsilon\} \end{aligned}$$

is bounded when  $\varepsilon > 0$  is sufficiently small.

Let us observe that if  $S_0 \geq 0$  then (1) equipped with the initial data  $S(0) = S_0$  and  $I(0, dx) = I_0(dx)$  has a unique globally defined solution  $S(t) \geq 0$  and  $I(t, dx) \in \mathcal{M}_+(\mathbb{R}^N)$  for all  $t \geq 0$ . In addition  $I$  is given by

$$I(t, dx) = \exp\left(\gamma(x) \left(\alpha(x) \int_0^t S(s) ds - t\right)\right) I_0(dx).$$

The above formula ensures that  $\text{supp } I(t, \cdot) = \text{supp } I_0$  for all  $t \geq 0$ . And to describe the large time behavior of  $I$ , we will use the values of  $\alpha$  and  $\gamma$  on the support of  $I_0$ . Due to the above remark and since  $I_0$  is given and fixed, along this paper, for any  $y \in \mathbb{R}$  we write

$$\alpha^{-1}(y) = \{x \in \text{supp}(I_0) : \alpha(x) = y\} \subset \text{supp}(I_0). \quad (5)$$

We also define the two quantities  $\alpha^* \geq 0$  and  $\mathcal{R}_0(I_0)$  by

$$\alpha^* =: \sup_{x \in \text{supp } I_0} \alpha(x) \text{ and } \mathcal{R}_0(I_0) := \frac{\Lambda}{\theta} \alpha^*. \quad (6)$$

We now split our main results into several parts. We first derive very general results about the large time behavior of the solution  $(S, I)$  of (1) when  $I_0$  is an arbitrary Radon measure. We roughly show that  $I(t, dx)$  concentrates on the points that maximize both  $\alpha$  and  $\gamma$ . We then apply this result to consider the case where  $I_0(dx)$  is a finite or countable sum of Dirac masses. We continue our investigations with an absolutely continuous (with respect to Lebesgue measure) initial measure and a finite set  $\alpha^{-1}(\alpha^*)$ . In that setting we are able to fully characterize the points where the measure  $I(t, dx)$  concentrates as  $t \rightarrow \infty$ .

## 2.1 General results for measure-valued initial data

As mentioned above this subsection is concerned with the large time behavior of the solution  $(S, I)$  of (1) where the initial measure  $I_0(dx)$  is an arbitrary Radon measure. Using the above notations our first result reads as follows.

**Theorem 2.2** (Asymptotic behavior of measure-valued initial data). *Let Assumption 2.1 be satisfied. Let  $S_0 \geq 0$  be given and denote by  $(S(t), I(t, dx))$  the solution of (1) equipped with the initial data  $S(0) = S_0$  and  $I(0, dx) = I_0(dx)$ . Recalling (6), suppose that  $\mathcal{R}_0(I_0) > 1$ . We distinguish two cases depending on the measure of this set w.r.t.  $I_0$ :*

i) *If  $I_0(\alpha^{-1}(\alpha^*)) > 0$ , then one has*

$$S(t) \xrightarrow[t \rightarrow +\infty]{} \frac{1}{\alpha^*} \text{ and } I(t, dx) \xrightarrow[t \rightarrow +\infty]{} I_\infty^*(dx) := \mathbb{1}_{\alpha^{-1}(\alpha^*)}(x) e^{\tau\gamma(x)} I_0(dx),$$

where  $\tau \in \mathbb{R}$  denotes the unique solution of the equation

$$\int_{\mathbb{R}^N} \gamma(x) \mathbb{1}_{\alpha^{-1}(\alpha^*)}(x) e^{\tau\gamma(x)} I_0(dx) = \frac{\theta}{\alpha^*} (\mathcal{R}_0 - 1).$$

The convergence of  $I(t, dx)$  to  $I_\infty^*(dx)$  holds in the absolute variation norm  $\|\cdot\|_{AV}$ .

ii) *If  $I_0(\alpha^{-1}(\alpha^*)) = 0$ , then one has  $S(t) \rightarrow \frac{1}{\alpha^*}$  and  $I(t, dx)$  is uniformly persistent, namely*

$$\liminf_{t \rightarrow +\infty} \int_{\mathbb{R}^N} I(t, dx) > 0.$$

Moreover  $I(t, dx)$  is asymptotically concentrated as  $t \rightarrow \infty$  on the set  $\alpha^{-1}(\alpha^*)$ , in the sense that

$$d_0(I(t, dx), \mathcal{M}_+(\alpha^{-1}(\alpha^*))) \xrightarrow[t \rightarrow +\infty]{} 0,$$

where  $d_0$  is the Kantorovitch-Rubinstein distance.

We continue our general result by showing that under additional properties for the initial measure  $I_0$ , the function  $I(t, dx)$  concentrates in the large times on the set of the points in  $\alpha^{-1}(\alpha^*)$  that maximize the function  $\gamma = \gamma(x)$ .

The additional hypothesis for the initial measure  $I_0(dx)$  are expressed in term of some properties of its disintegration measure with respect to the function  $\alpha$ . We refer to the book of Bourbaki [8, VI, §3, Theorem 1 p. 418] for a proof of the disintegration Theorem B.4 which is recalled in Appendix B.

Let  $A(dy)$  be the image of  $I_0(dx)$  under the continuous mapping  $\alpha : \mathbb{R}^N \rightarrow \mathbb{R}$ , then there exists a family of nonnegative measures  $I_0(y, dx)$  (the disintegration of  $I_0$  with respect to  $\alpha$ ) such that for almost every  $y \in \alpha(\text{supp } I_0)$  with respect to  $A$  we have:

$$\text{supp } I_0(y, dx) \subset \alpha^{-1}(y), \quad \int_{\alpha^{-1}(y)} I_0(y, dx) = 1 \text{ and } I_0(dx) = \int I_0(y, dx)A(dy) \quad (7)$$

wherein the last equality means that

$$\int_{\mathbb{R}^N} f(x)I_0(dx) = \int_{y \in \mathbb{R}} \int_{\alpha^{-1}(y)} f(x)I_0(y, dx)A(dy) \text{ for all } f \in BC(\mathbb{R}^N).$$

Note that, by definition, the measure  $A$  is supported on the set  $\alpha(\text{supp } I_0)$ .

**Remark 2.3** (Important example). Suppose that  $I_0 \in L^1(\mathbb{R}^n)$ . Since we restrict to measures which are absolutely continuous with respect to the Lebesgue measure here, with a small abuse of notation we will omit the element  $dx$  when the context is clear. Assume that  $\alpha$  is Lipschitz continuous on  $\mathbb{R}^N$  and that

$$\frac{I_0(x)}{|\nabla\alpha(x)|} \in L^1(\mathbb{R}^N). \quad (8)$$

The coarea formula implies that, for all  $g \in L^1(\mathbb{R}^N)$ , we have

$$\int_{\mathbb{R}^N} g(x)|\nabla\alpha(x)|dx = \int_{\mathbb{R}} \int_{\alpha^{-1}(y)} g(x)\mathcal{H}_{N-1}(dx)dy,$$

where  $\mathcal{H}_{N-1}(dx)$  is the  $(N-1)$ -dimensional Hausdorff measure (see Federer [19, §3.2]).

Therefore if  $g(x) = f(x) \frac{I_0(x)}{|\nabla\alpha(x)|}$  we get

$$\int_{\mathbb{R}^N} f(x)I_0(x)dx = \int_{\mathbb{R}} \int_{\alpha^{-1}(y)} f(x) \frac{I_0(x)}{|\nabla\alpha(x)|} \mathcal{H}_{N-1}(dx)dy, \quad (9)$$

and if moreover  $f(x) = \varphi(\alpha(x))$  we get

$$\int_{\mathbb{R}} \varphi(y)A(dy) = \int_{\mathbb{R}^N} \varphi(\alpha(x))I_0(x)dx = \int_{\mathbb{R}} \varphi(y) \int_{\alpha^{-1}(y)} \frac{I_0(x)}{|\nabla\alpha(x)|} \mathcal{H}_{N-1}(dx)dy,$$

where we recall that  $A(dy)$  is the image measure of  $I_0(dx)$  through  $\alpha$ . Therefore we have an explicit expression for  $A(dy)$ :

$$A(dy) = \int_{\alpha^{-1}(y)} \frac{I_0(x)}{|\nabla\alpha(x)|} \mathcal{H}_{N-1}(dx)dy \quad (10)$$

and (recalling (9)) we deduce the following explicit disintegration of  $I_0$ :

$$I_0(y, dx) = \frac{\mathbb{1}_{x \in \alpha^{-1}(y)} \frac{I_0(x)}{|\nabla\alpha(x)|} \mathcal{H}_{N-1}(dx)}{\int_{\alpha^{-1}(y)} \frac{I_0(z)}{|\nabla\alpha(z)|} \mathcal{H}_{N-1}(dz)}. \quad (11)$$

Equations (10) and (11) give an explicit formula for the disintegration introduced in (7).

**Remark 2.4.** Suppose that  $\alpha$  is a  $C^2$  function with no critical point in  $\text{supp } I_0$  except for a finite number of regular maxima (in the sense that the bilinear form  $D^2\alpha(x)$  is non-degenerate at each maximum). This is a typical situation. Then assumption (8) in Remark 2.3 is automatically satisfied if  $N \geq 3$  and  $I_0 \in L^\infty(\mathbb{R}^N)$ . If  $N = 2$  then a sufficient condition to satisfy (8) with  $I_0 \in L^\infty(\mathbb{R}^N)$  should involve  $I_0$  vanishing sufficiently fast in the neighborhood of each maximum of  $\alpha$ .

We shall also make use, for all  $y$   $A$ -almost everywhere, of the disintegration measure of  $I_0(y, dx)$  with respect to the function  $\gamma$ , as follows

$$I_0(y, dx) = \int_{z \in \gamma(\alpha^{-1}(y))} I_0^{\alpha, \gamma}(y, z, dx) I_0^\alpha(y, dz),$$

that allows to the following reformulation of  $I_0(dx)$ :

$$I_0(dx) = \int_{y \in \mathbb{R}} \int_{z \in \gamma(\alpha^{-1}(y))} I_0^{\alpha, \gamma}(y, z, dx) I_0^\alpha(y, dz) A(dy).$$

Now equipped with this disintegration of  $I_0$  with respect to  $\alpha$  we are now able to state our regularity assumption to derive more refine concentration information in the case where  $I_0(\alpha^{-1}(\alpha^*)) = 0$ .

**Assumption 2.5** (Regularity with respect to  $\alpha, \gamma$ ). Recalling (5), assume that  $\alpha^{-1}(\alpha^*) \neq \emptyset$  and define  $\gamma^* > 0$  by

$$\gamma^* := \sup_{x \in \alpha^{-1}(\alpha^*)} \gamma(x). \quad (12)$$

We assume that, for each value  $\bar{\gamma} < \gamma^*$  there exist constants  $\delta > 0$  and  $m > 0$  such that

$$m \leq \int_{\gamma^{-1}([\bar{\gamma}, \gamma^*]) \cap \alpha^{-1}(y)} I_0(y, dx) \text{ for } A\text{-almost every } y \in (\alpha^* - \delta, \alpha^*].$$

**Remark 2.6.** The above assumption means that the initial measure  $I_0(dx)$  is uniformly positive in a small neighborhood of  $\alpha^{-1}(\alpha^*)$ . For instance, if the assumptions of Remark 2.3 are satisfied and if there exists an open set  $U$  containing  $\alpha^{-1}(\alpha^*) \cap \gamma^{-1}(\gamma^*)$  on which  $I_0(x)$  is almost everywhere uniformly positive, then Assumption 2.5 is automatically satisfied.

The next proposition ensures that, when the initial measure  $I_0$  satisfies Assumption 2.5, then the function  $I(t, dx)$  concentrates on  $\alpha^{-1}(\alpha^*) \cap \gamma^{-1}(\gamma^*)$ .

**Proposition 2.7.** *Under the same assumptions as in Theorem 2.2, assume that  $I_0(\alpha^{-1}(\alpha^*)) = 0$  and let us furthermore assume that Assumption 2.5 holds, then recalling that  $\gamma^*$  is defined in (12) one has*

$$d_0(I(t, dx), \mathcal{M}_+(\alpha^{-1}(\alpha^*) \cap \gamma^{-1}(\gamma^*))) \xrightarrow{t \rightarrow +\infty} 0,$$

as well as the following asymptotic mass

$$\int_{\mathbb{R}^N} I(t, dx) \xrightarrow{t \rightarrow +\infty} \frac{\theta}{\alpha^* \gamma^*} (\mathcal{R}_0(I_0) - 1).$$

Let  $U \subset \mathbb{R}^N$  be a Borel set such that  $U \cap \alpha^{-1}(\alpha^*) \cap \gamma^{-1}(\gamma^*) \neq \emptyset$  and

$$\liminf_{\varepsilon \rightarrow 0} \operatorname{ess\,inf}_{\alpha^* - \varepsilon \leq y \leq \alpha^* \gamma^* - \varepsilon} \int_U I_0^{\alpha, \gamma}(y, z, dx) > 0,$$

then the following persistence occurs

$$\liminf_{t \rightarrow \infty} \int_U I(t, dx) > 0.$$

We now explore some numerical computations of (1) with various configurations.

## 2.2 The case of discrete systems

In this subsection we propose an application of the general result, namely Theorem 2.2, to the case of discrete systems. We start with the case of *finite* systems, *i.e.*, the case when system (1) can be written as follows:

$$\begin{cases} \frac{d}{dt} S(t) = \Lambda - \theta S(t) - S(t)(\alpha_1 \gamma_1 I^1(t) + \alpha_2 \gamma_2 I^2(t) + \dots + \alpha_n \gamma_n I^n(t)) \\ \frac{d}{dt} I^1(t) = (\alpha_1 S(t) - 1) \gamma_1 I^1(t) \\ \frac{d}{dt} I^2(t) = (\alpha_2 S(t) - 1) \gamma_2 I^2(t) \\ \vdots \\ \frac{d}{dt} I^n(t) = (\alpha_n S(t) - 1) \gamma_n I^n(t). \end{cases} \quad (13)$$

For the above system, we can completely characterize the asymptotic behavior of the population. To that aim we define the basic reproductive number (in the ecological or epidemiological sense) for species  $i$  as follows:

$$\mathcal{R}_0^i := \frac{\Lambda}{\theta} \alpha_i, \quad i = 1, \dots, n.$$

Then we can show that the only species that do not get extinct are the ones for which  $\mathcal{R}_0^i$ ,  $i = 1, \dots, n$ , is maximal and strictly greater than one.

In the case when several species have the same basic maximal reproductive number, then these species all survive and the asymptotic distribution can be computed explicitly as a function of the initial data  $I_0^i$  and of the values  $\gamma_i$ .



**Theorem 2.8** (Asymptotic behavior of finite systems). *Let  $n \geq 1$  and  $\alpha_1, \dots, \alpha_n$  and  $\gamma_1 > 0, \dots, \gamma_n > 0$  be given. Set*

$$\alpha^* := \max\{\alpha_1, \dots, \alpha_n\},$$

and assume that

$$\mathcal{R}_0^* := \frac{\Lambda}{\theta} \alpha^* = \max\{\mathcal{R}_0^1, \dots, \mathcal{R}_0^n\} > 1.$$

Then, for any initial data  $S_0 \geq 0, I_0^1 > 0, \dots, I_0^n > 0$ , the corresponding solution to (13) converges in the large times to  $(S_\infty, (I_\infty^1, \dots, I_\infty^n))$  given by

$$S_\infty = \frac{1}{\alpha^*} \text{ and } I_\infty^i = \begin{cases} 0 & \text{if } \mathcal{R}_0^i < \mathcal{R}_0^*, \\ e^{\tau\gamma_i} I_0^i & \text{if } \mathcal{R}_0^i = \mathcal{R}_0^*, \end{cases} \text{ for all } i = 1, \dots, n,$$

wherein the constant  $\tau \in \mathbb{R}$  is defined as the unique solution of the equation:

$$\sum_{\{i: \mathcal{R}_0^i = \mathcal{R}_0^*\}} \gamma_i I_0^i e^{\tau\gamma_i} = \frac{\theta}{\alpha^*} (\mathcal{R}_0 - 1).$$

Note that in the case when the interaction of the species with the resource is described by the Michaelis-Menten kinetics instead of the mass action law, or when the growth of the resource obeys a logistic law (Hsu [23]), a similar result was already present in Hsu, Hubbell and Waltman [24] and Hsu [23], including the case when several species have the exact same reproduction number (or fitness)  $\mathcal{R}_0^i$ .

In the case of a countable system we can still provide a complete description when both  $\alpha$  and  $\gamma$  converge to a limit near  $+\infty$ . We now investigate the following system

$$\begin{cases} \frac{d}{dt} S(t) = \Lambda - \theta S(t) - S(t) \sum_{i \in \mathbb{N}} \alpha_i \gamma_i I_i(t), \\ \frac{d}{dt} I^i(t) = (\alpha_i S(t) - 1) \gamma_i I^i(t), \end{cases} \text{ for } i \in \mathbb{N}, \quad (14)$$

supplemented with some initial data

$$S(0) = S_0 > 0 \text{ and } I^i(0) = I_0^i > 0, \forall i \in \mathbb{N} \text{ with } \sum_{i \in \mathbb{N}} I_0^i < \infty. \quad (15)$$

Since components of (14) starting from a zero initial data will stay equal to zero in positive time, they can be removed from the system without impacting the dynamics and we may without loss of generality assume that  $I_0^i > 0$  for all  $i \in \mathbb{N}$  (as we did in (15)).

In the sequel we denote by  $(S(t), I^i(t))$  be the corresponding solution to (14) with initial data  $S(0) = S_0$  and  $I^i(0) = I_0^i$  for all  $i \in \mathbb{N}$ .

**Theorem 2.9** (Asymptotic behavior of discrete systems). *Let  $(\alpha_i)_{i \in \mathbb{N}}$  and  $(\gamma_i)_{i \in \mathbb{N}}$  be bounded sequences with  $\gamma_i > 0$  for all  $i \in \mathbb{N}$ . Set*

$$\alpha^* := \sup\{\alpha_i, i \in \mathbb{N}\},$$

and assume that

$$\mathcal{R}_0^* := \frac{\Lambda}{\theta} \alpha^* > 1.$$

We distinguish two cases.

- i) *If the set  $\{i \in \mathbb{N} : \alpha_i = \alpha^*\}$  is not empty, then  $(S(t), I^i(t))$  converges to the following asymptotic stationary state*

$$S_\infty = \frac{1}{\alpha^*}, \text{ and } I_\infty^i = \begin{cases} 0 & \text{if } \mathcal{R}_0^i < \mathcal{R}_0^*, \\ e^{\tau\gamma_i} I_0^i & \text{if } \mathcal{R}_0^i = \mathcal{R}_0^*, \end{cases} \text{ for all } i \in \mathbb{N} \cup \{\infty\}.$$

where the constant  $\tau \in \mathbb{R}$  is the unique solution of the equation:

$$\sum_{\{i \in \mathbb{N} : \mathcal{R}_0^i = \mathcal{R}_0^*\}} \gamma_i I_0^i e^{\tau\gamma_i} = \frac{\theta}{\alpha^*} (\mathcal{R}_0^* - 1).$$

- ii) If the set  $\{i \in \mathbb{N} : \alpha_i = \alpha^*\}$  is empty, then one has  $S(t) \rightarrow \frac{1}{\alpha^*}$  and  $I^i(t) \rightarrow 0$  for all  $i \in \mathbb{N}$  as  $t \rightarrow \infty$ , while

$$\liminf_{t \rightarrow +\infty} \sum_{i \in \mathbb{N}} I^i(t) > 0.$$

If moreover one has  $\alpha_n \rightarrow \alpha^*$  and  $\gamma_n \rightarrow \gamma_\infty > 0$  as  $n \rightarrow \infty$  with  $n \in \mathbb{N}$  then the total mass converges to a positive limit

$$\lim_{t \rightarrow +\infty} \sum_{i \in \mathbb{N}} I^i(t) = \frac{\theta}{\alpha^* \gamma_\infty} (\mathcal{R}_0^* - 1). \quad (16)$$

Note that for more complex countable systems, such as if the  $\omega$ -limit set of  $\alpha_n$  or  $\gamma_n$  contains two or more distinct values, then it is no longer possible in general to state a result independent of the initial data. We will discuss a similar phenomenon for measures with a density with respect to the Lebesgue measure in Section 2.3

### 2.3 The case when $\alpha(x)$ has a finite number of regular maxima

We now go back to our analysis of (1) set on  $\mathbb{R}^N$ . If the function  $\alpha(x)$  has a unique global maximum which is accessible to the initial data, then our analysis leads to a complete description of the asymptotic state of the population. This may be the unique case when the behavior of the orbit is completely known, independently on the positivity of the initial mass of the fitness maximizing set  $\{\alpha(x) = \alpha^*\}$ .

**Theorem 2.10** (The case of a unique global maximum). *Let Assumption 2.1 be satisfied. Let  $S_0 \geq 0$  and  $I_0(dx) \in \mathcal{M}_+(\mathbb{R}^N)$  be a given initial data. Suppose that the function  $\alpha = \alpha(x)$  has a unique maximum  $\alpha^*$  on the support of  $I_0$  attained at  $x^* \in \text{supp } I_0$ , and that*

$$\mathcal{R}_0(I_0) := \frac{\Lambda}{\theta} \alpha^* > 1.$$

Then it holds that

$$S(t) \xrightarrow{t \rightarrow +\infty} \frac{1}{\alpha^*}, \quad d_0(I(t, dx), I^\infty \delta_{x^*}(dx)) \xrightarrow{t \rightarrow +\infty} 0,$$

where  $\delta_{x^*}(dx)$  denotes the Dirac measure at  $x^*$  and

$$I^\infty := \frac{\theta}{\alpha^* \gamma(x^*)} (\mathcal{R}_0(I_0) - 1).$$

Next we describe the large time behavior of the solutions when the function  $\alpha$  has a finite number of maxima on the support of  $I_0(dx)$ . We consider an initial data  $(S_0, I_0) \in [0, \infty) \times \mathcal{M}_+(\mathbb{R}^N)$  with  $I_0$  absolutely continuous with respect to the Lebesgue measure  $dx$  in  $\mathbb{R}^N$  (in other words and with a small abuse of notation,  $I_0 \in L^1(\mathbb{R}^N)$ ) in a neighborhood of the maxima of the fitness function. Recalling the definition of  $\alpha^*$  in (6), throughout this section, we shall make use of the following set of assumptions.

By a small abuse of notation, we will identify in this section the function  $I_0 \in L^1(\mathbb{R}^N)$  and the associated measure  $I_0(x)dx \in \mathcal{M}_+(\mathbb{R}^N)$  when the context is clear.

**Assumption 2.11.** We assume that:

- (i) the set  $\alpha^{-1}(\alpha^*)$  (given in (5)) is a finite set, namely there exist  $x_1, \dots, x_p$  in the interior of  $\text{supp}(I_0)$  such that  $x_i \neq x_j$  for all  $i \neq j$  and

$$\alpha^{-1}(\alpha^*) = \{x_1, \dots, x_p\} \text{ and } \mathcal{R}_0 := \frac{\Lambda \alpha^*}{\theta} > 1.$$

- (ii) There exist  $\varepsilon_0 > 0$ ,  $M > 1$  and  $\kappa_1 \geq 0, \dots, \kappa_p \geq 0$  such that for all  $i = 1, \dots, p$  and for almost all  $x \in B(x_i, \varepsilon_0) \subset \text{supp}(I_0)$  one has

$$M^{-1}|x - x_i|^{\kappa_i} \leq I_0(x) \leq M|x - x_i|^{\kappa_i}.$$

Here and along this note we use  $|\cdot|$  to denote the Euclidean norm of  $\mathbb{R}^N$ .

- (iii) The functions  $\alpha$  and  $\gamma$  are of class  $C^2$  and there exists  $\ell > 0$  such that for each  $i = 1, \dots, p$  one has

$$D^2\alpha(x_i)\xi^2 \leq -\ell|\xi|^2, \quad \forall \xi \in \mathbb{R}^N.$$

**Remark 2.12.** Let us observe that since  $x_i$  belongs to the interior of  $\text{supp}(I_0)$  then  $D\alpha(x_i) = 0$ .

In order to state our next result, we introduce the following notation: we write  $f(t) \asymp g(t)$  as  $t \rightarrow \infty$  if there exists  $C > 1$  and  $T > 0$  such that

$$C^{-1}|g(t)| \leq |f(t)| \leq C|g(t)|, \quad \forall t \geq T.$$

According to Theorem 2.2 (ii), one has  $\alpha^* S(t) \rightarrow 1$  as  $t \rightarrow \infty$ , and as a special case we conclude that

$$\bar{S}(t) = \frac{1}{t} \int_0^t S(l) dl \rightarrow \frac{1}{\alpha^*} \text{ as } t \rightarrow \infty.$$

As a consequence the function  $\eta(t) := \alpha^* \bar{S}(t) - 1$  satisfies  $\eta(t) = o(1)$  as  $t \rightarrow \infty$ . To describe the asymptotic behavior of the solution  $(S(t), I(t, dx))$  with initial data  $S_0$  and  $I_0$  as above, we shall derive a precise behavior of  $\eta$  for  $t \gg 1$ . This refined analysis will allow us to characterize the points of concentration of  $I(t, dx)$ . Our result reads as follows.

**Theorem 2.13.** *Let Assumption 2.11 be satisfied. Then the function  $\eta = \eta(t)$  satisfies the following asymptotic expansion*

$$\eta(t) = \varrho \frac{\ln t}{t} + O\left(\frac{1}{t}\right), \text{ as } t \rightarrow \infty. \quad (17)$$

wherein we have set

$$\varrho := \min_{i=1, \dots, p} \frac{N + \kappa_i}{2\gamma(x_i)}. \quad (18)$$

Moreover there exists  $\varepsilon_1 \in (0, \varepsilon_0)$  such that for all  $0 < \varepsilon < \varepsilon_1$  and all  $i = 1, \dots, p$  one has

$$\int_{|x-x_i| \leq \varepsilon} I(t, dx) \asymp t^{\gamma(x_i)\varrho - \frac{N+\kappa_i}{2}} \text{ as } t \rightarrow \infty. \quad (19)$$

As a special case, for all  $\varepsilon > 0$  small enough and all  $i = 1, \dots, p$  one has

$$\int_{|x-x_i| \leq \varepsilon} I(t, dx) \begin{cases} \asymp 1 & \text{if } i \in J \\ \rightarrow 0 & \text{if } i \notin J \end{cases} \text{ as } t \rightarrow \infty,$$

where  $J$  is the set defined as

$$J := \left\{ i = 1, \dots, p : \frac{N + \kappa_i}{2\gamma(x_i)} = \varrho \right\}. \quad (20)$$

The above theorem states that the function  $I(t, dx)$  concentrates on the set of points  $\{x_i, i \in J\}$  (see Corollary 2.15 below). Here Assumption 2.5 on the uniform positiveness of the measure  $I_0(dx)$  around the points  $x_i$  is not satisfied in general, and the measure  $I$  concentrates on  $\alpha^{-1}(\alpha^*)$  as predicted by Theorem 2.2, but not necessarily on  $\alpha^{-1}(\alpha^*) \cap \gamma^{-1}(\gamma^*)$  as would have been given by Proposition 2.7. In Figure 7 we provide a precise example of this non-standard behavior.

In addition, the precise expansion of  $\eta = \eta(t)$  provided in the above theorem allows us obtain the self-similar behavior of the solution  $I(t, dx)$  around the maxima of the fitness function. This asymptotic directly follows from (29).

**Corollary 2.14.** *For each  $i = 1, \dots, p$  and  $f \in C_c(\mathbb{R}^N)$ , the set of the continuous and compactly supported functions, one has as  $t \rightarrow \infty$ :*

$$t^{\frac{N}{2}} \int_{\mathbb{R}^N} f\left((x-x_i)\sqrt{t}\right) I(t, dx) \asymp t^{\gamma(x_i)\varrho - \frac{N+\kappa_i}{2}} \int_{\mathbb{R}^N} f(x)|x|^{\kappa_i} \exp\left(\frac{\gamma(x_i)}{2\alpha^*} D^2 \alpha(x_i) x^2\right) dx. \quad (21)$$

Our next corollary relies on some properties of the  $\omega$ -limit set of the solution  $I(t, dx)$ . Using the estimates of the mass around  $x_i$  given in (19), it readily follows that any limit measures of  $I(t, dx)$  belongs to a linear combination of  $\delta_{x_i}$  with  $i \in J$  and strictly positive coefficients of each of these Dirac masses. This reads as follows.

**Corollary 2.15.** *Under the same assumptions as in Theorem 2.13, the  $\omega$ -limit set  $\bar{\mathcal{O}}(I_0)$  as defined in Lemma 4.4 satisfies that there exist  $0 < A < B$  such that*

$$\bar{\mathcal{O}}(I_0) \subset \left\{ \sum_{i \in J} c_i \delta_{x_i} : (c_i)_{i \in J} \in [A, B]^J \right\}.$$

### 3 Comments and numerical illustrations

#### 3.1 Numerical illustrations

In this section we provide numerical illustrations to some of our results. We start with an illustration of the long-time behavior of the solution to (1) when the initial mass of the fitness maximum is positive ( $I_0(\alpha^{-1}(\alpha^*)) > 0$ ). To help with the visual representation, in our example,  $I_0$  is chosen absolutely continuous with respect to the Lebesgue measure, *i.e.* carried by a  $L^1(\mathbb{R}^N)$  function. In Figure 1 we provide a plot of the fitness function (left-hand side) and the initial data (right-hand side). The fitness function attains its maximum on a rectangle with positive Lebesgue measure and the support of the initial data intersects this rectangle with non-negligible intersection.

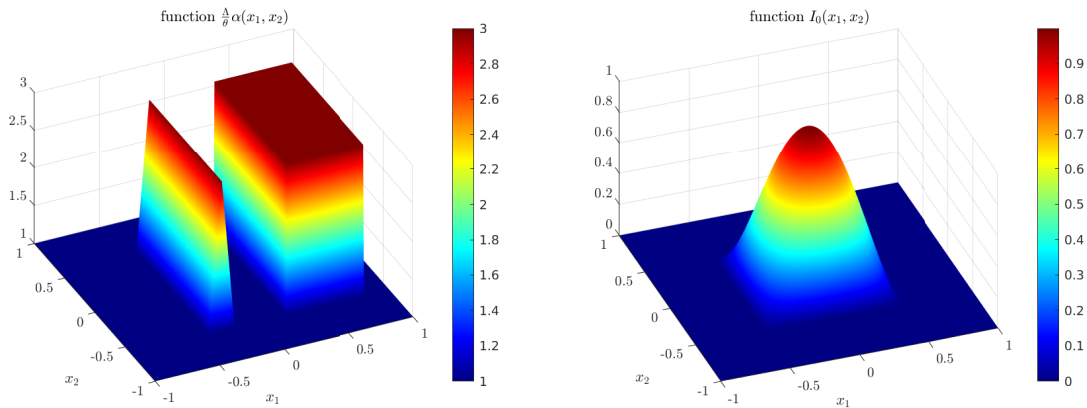


Figure 1: Illustration of Theorem 2.2 in the case i), *i.e.*, when  $I_0(\alpha^{-1}(\alpha^*)) > 0$ . Parameters of this simulation are:  $\Lambda = 2$ ,  $\theta = 1$ ,  $\alpha(x) = 0.5 + (\mathbb{T}_{[-0.4, -0.2]}(x_1) + \mathbb{1}_{[0.2, 0.8]}(x_1)) \mathbb{1}_{[-0.6, 0.6]}(x_2)$  where  $x = (x_1, x_2) \in \mathbb{R}^2$  and  $\mathbb{T}_{[-0.4, -0.2]}$  is the triangular function of height one and support  $[-0.4, -0.2]$ , and  $\gamma = \frac{1}{2\alpha}$ . Initial condition is given by  $I_0(dx) = I_0(x_1, x_2) dx$  where  $I_0(x_1, x_2) = \mathbb{1}_{[-0.5, 0.5]}(x_1) \cos(\pi x_1) \mathbb{1}_{[-0.5, 0.5]}(x_2) \cos(\pi x_2)$ . In particular, we have  $\alpha^* = 3/2$  and  $\alpha^{-1}(\alpha^*) = (\{-0.3\} \cup [0.2, 0.5]) \times [-0.5, 0.5]$ .

In Figure 2 we plot the time evolution of  $S(t)$  (left-hand side) and a snapshot of the distribution  $I(t, x)$  at  $t = 50$ . We observe that the mass that was initially located outside of the fitness maximum has vanished. What remains is a distribution of mass in the initial rectangle of maximal fitness (according to Theorem 2.2, the distribution precise can be computed). The distribution located at  $\{x_1 = -0.3\}$  is still positive, but is negligible with respect to the Lebesgue measure and does not contribute to the mass. In Figure 3 we present four snapshots of the distribution  $I(t, x)$  to monitor the time evolution of this distribution with the same initial distribution.

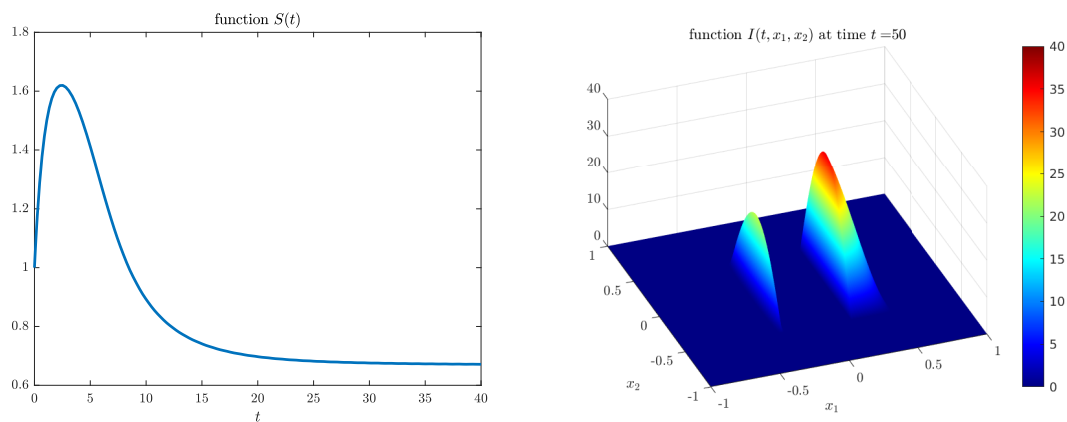


Figure 2: (continued from Fig. 1) Illustration of Theorem 2.2 in the case i), *i.e.*, when  $I_0(\alpha^{-1}(\alpha^*)) > 0$ . Function  $t \rightarrow S(t)$  converges towards  $1/\alpha^* = 2/3$  and function  $x \rightarrow I(t, x)$  at time  $t = 50$  is asymptotically concentrated on  $\alpha^{-1}(\alpha^*) = (\{-0.3\} \cup [0.2, 0.5]) \times [-0.5, 0.5]$ .

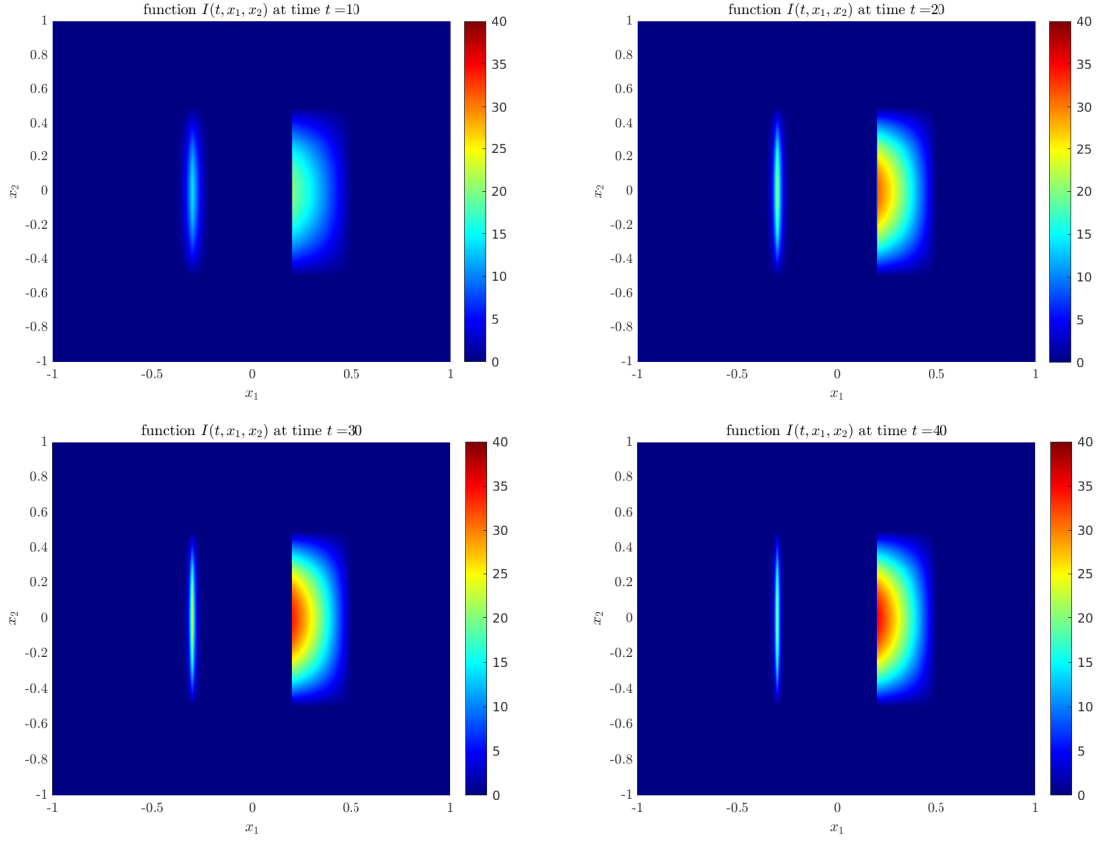


Figure 3: Illustration of Theorem 2.2 in the case i), *i.e.*, when  $I_0(\alpha^{-1}(\alpha^*)) > 0$ . Function  $x \rightarrow I(t, x)$  at time  $t = 10, 20, 30$  and  $40$ . The function  $I$  remains bounded in this case.

Figures 4, 5, and 6 illustrate the case when the maximal fitness is negligible for the initial measure (Point ii) of Theorem 2.2). In Figure 4 we provide a plot of the fitness function (left-hand side) and the initial data (right-hand side). The fitness function attains its maximum on a rectangle with positive Lebesgue measure and the support of the initial data intersects this rectangle with non-negligible intersection.

In Figure 5 we plot the time evolution of  $S(t)$  (left-hand side) and a snapshot of the distribution  $I(t, x)$  at  $t = 100$ . We observe that the mass that was initially located outside of the fitness maximum has vanished. What remains is a distribution of mass around the initial line of maximal fitness, which is negligible for the initial data; however the distribution takes very high values. In Figure 6 we present four snapshots of the distribution  $I(t, x)$  to monitor the time evolution of this distribution with the same initial distribution.

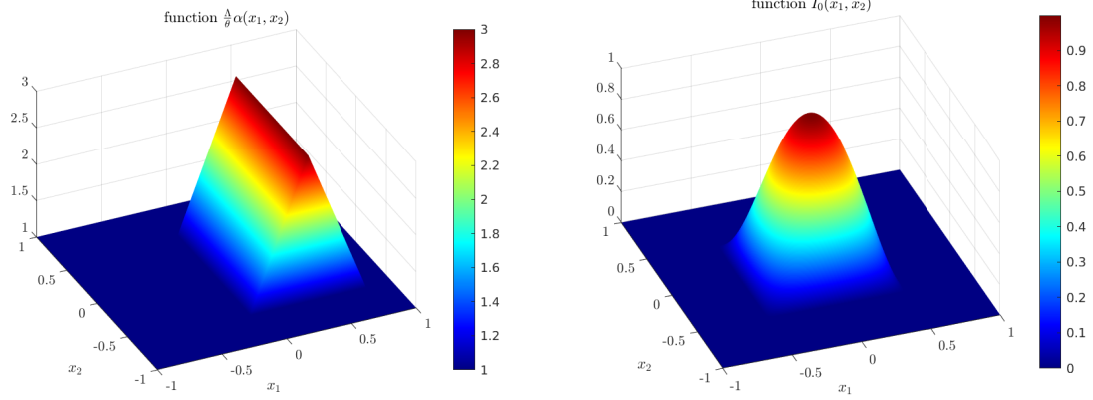


Figure 4: Illustration of Theorem 2.2 in the case ii), *i.e.*, when  $I_0(\alpha^{-1}(\alpha^*)) = 0$ . Parameters of this simulation are:  $\Lambda = 2$ ,  $\theta = 1$ ,  $\alpha(x) = 0.5 + \mathbb{T}_{[-0.1, 0.8]}(x_1) \mathbb{1}_{[-0.5, 0.5]}(x_2)$  where  $x = (x_1, x_2) \in \mathbb{R}^2$  and  $\mathbb{T}_{[-0.1, 0.5]}$  is the triangular function of height one and support  $[-0.1, 0.5]$ ,  $\gamma = \frac{1}{2\alpha}$ . Initial condition is given by  $I_0(dx) = I_0(x_1, x_2) dx$  where  $I_0(x) = \mathbb{1}_{[-0.5, 0.5]}(x_1) \cos(\pi x_1) \mathbb{1}_{[-0.5, 0.5]}(x_2) \cos(\pi x_2)$ . In particular,  $\alpha^* = 3/2$  and  $\alpha^{-1}(\alpha^*) = \{0.35\} \times [-0.5, 0.5]$ .

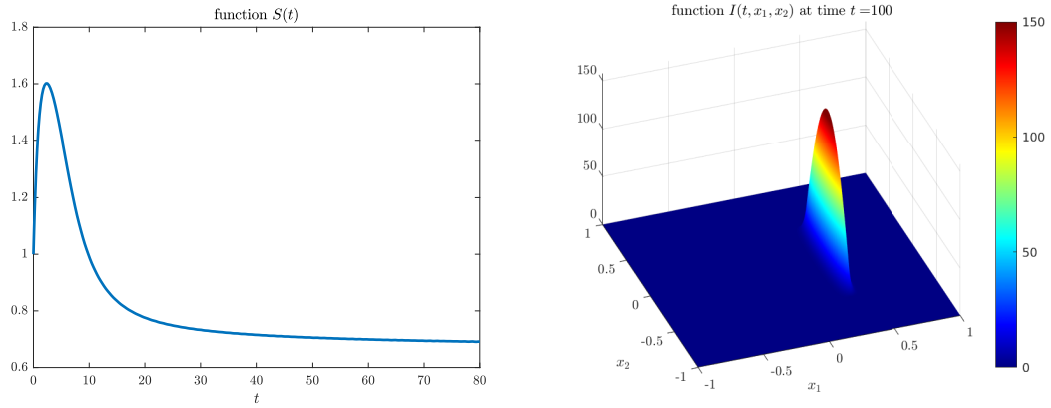


Figure 5: (continued from Fig. 4) Illustration of Theorem 2.2 in the case ii), *i.e.* when  $I_0(\alpha^{-1}(\alpha^*)) = 0$ . Function  $t \rightarrow S(t)$  converges towards  $1/\alpha^* = 2/3$ . Function  $x \rightarrow I(t, x)$  at time  $t = 100$  is asymptotically concentrated on  $\alpha^{-1}(\alpha^*) = \{0.35\} \times [-0.5, 0.5]$ .

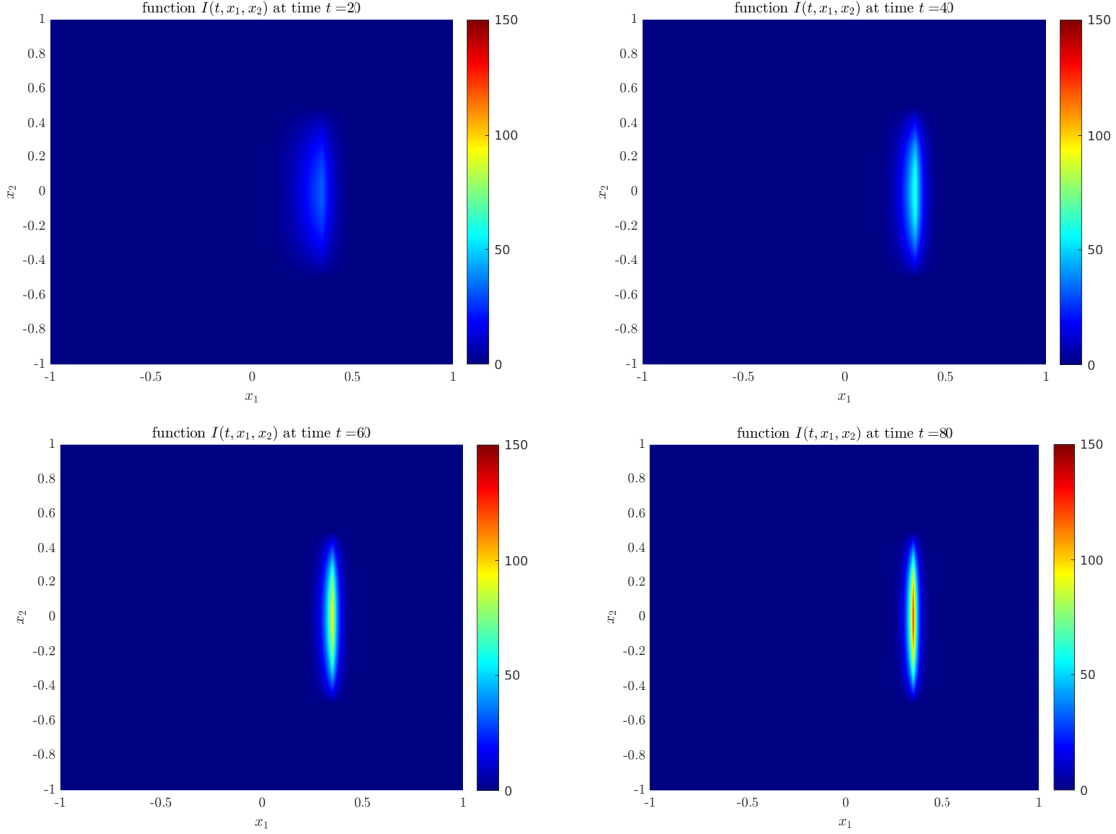


Figure 6: Illustration of Theorem 2.2 in the case ii), *i.e.*, when  $I_0(\alpha^{-1}(\alpha^*)) = 0$ . Function  $x \rightarrow I(t, x)$  at time  $t = 20, 40, 60$  and  $80$ . The function  $I$  asymptotically converges towards a singular measure.

In Figure 7 we provide a precise example of this non-standard behavior. The function  $\alpha(x)$  is chosen to have two maxima  $x_1 = -0.5$  and  $x_2 = 0.5$ ; the precise definition of  $\alpha(x)$  is

$$\alpha(x) = \mathbb{P}_{[x_1-\delta, x_1+\delta]}(x) + \mathbb{P}_{[x_2-\delta, x_2+\delta]}(x), \quad (22)$$

where

$$\mathbb{P}_{[a,b]}(x) := \max\left(1 - \frac{(a+b-2x)^2}{(a-b)^2}, 0\right)$$

is the downward parabolic function of height one and support  $[a, b]$  and  $\delta = 0.2$ . The function  $\alpha(x)$  has the exact same local behavior in the neighborhood of  $x_1$  and  $x_2$ . The function  $I_0(x)$  is chosen as

$$I_0(x) = \min\left(1, 1024(x-x_1)^8\right) \min\left(1, 4(x-x_2)^2\right) \mathbb{1}_{[-1,1]}(x), \quad (23)$$

so that  $\kappa_1 = 8$  and  $\kappa_2 = 2$ . Finally we take

$$\gamma(x) = \frac{1}{1 + \mathbb{P}_{[x_1-\delta, x_1+\delta]}(x) + 3\mathbb{P}_{[x_2-\delta, x_2+\delta]}(x)} \quad (24)$$

so that  $\gamma(x_1) = \frac{1}{2}$  and  $\gamma(x_2) = \frac{1}{4}$ . Summarizing, we have

$$\frac{N + \kappa_1}{2\gamma(x_1)} = 9 > 6 = \frac{N + \kappa_2}{2\gamma(x_2)},$$

so that Theorem 2.13 predicts that the mass  $I(t, dx)$  will vanish near  $x_1 = \alpha^{-1}(\alpha^*) \cap \gamma^{-1}(\gamma^*)$  and concentrate on  $x_2$ .

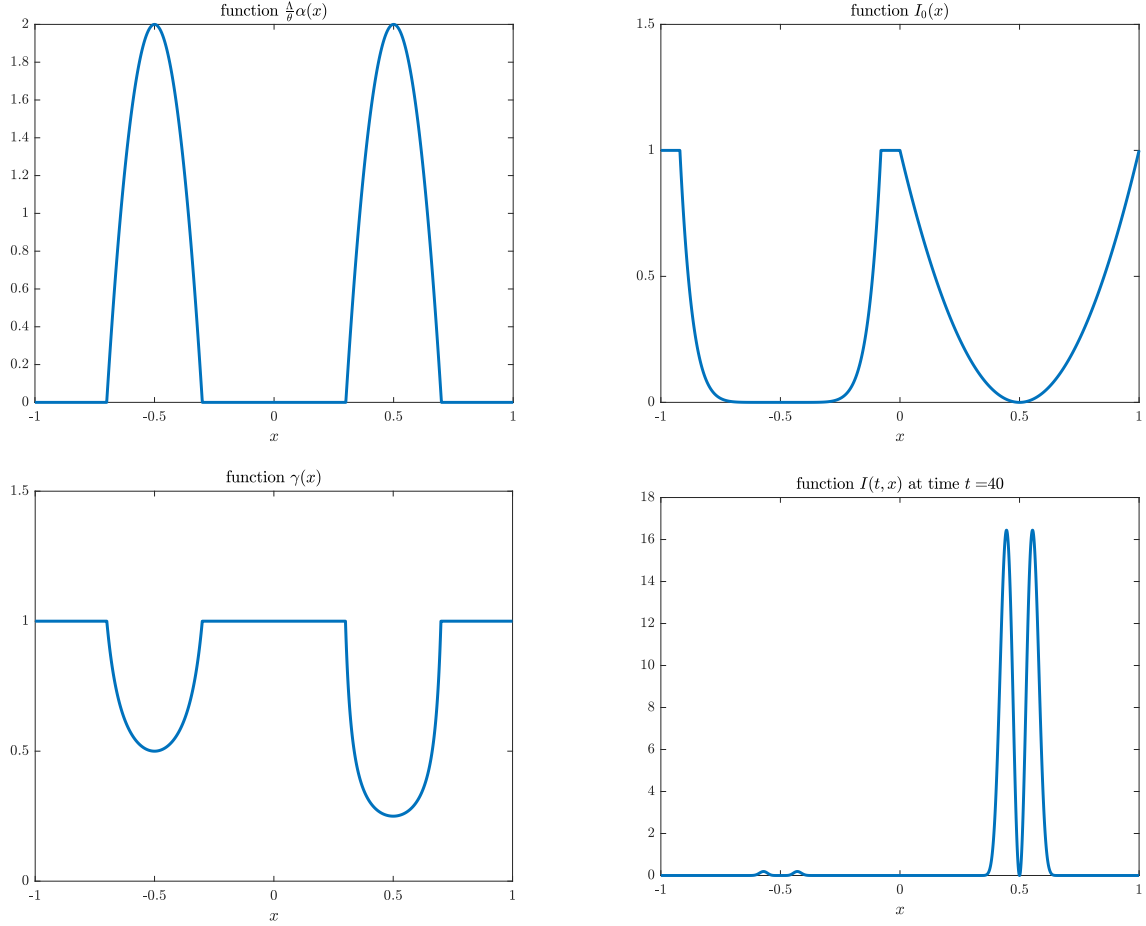


Figure 7: Illustration of Theorem 2.13 and Corollary 2.14. Parameters of this simulation are:  $\Lambda = 2$ ,  $\theta = 1$ ,  $\alpha(x)$  is given by (22),  $I_0(x)$  by (23) and  $\gamma(x)$  by (24). In particular,  $\alpha^* = 1$ ,  $\alpha^{-1}(\alpha^*) = \{x_1, x_2\}$  with  $x_1 = -0.5$ ,  $x_2 = 0.5$ ,  $\kappa_1 = 8$ ,  $\kappa_2 = 2$ ,  $\gamma(x_1) = 1/2$ ,  $\gamma(x_2) = 1/4$ ,  $\rho = 6$  and  $J = \{2\}$ . The initial condition  $I_0$  vanishes more rapidly around  $x_1$  than  $x_2$  so that the solution  $I(t, x)$  vanishes around  $x_1$  as  $t$  goes to  $\infty$ , even though  $\gamma(x_1) > \gamma(x_2)$ , while around  $x_2$  it takes the shape given by expression (2.14).

### 3.2 Transient dynamics on local maxima: a numerical example

In many biologically relevant situations it may be more usual to observe situations involving a fitness function with one global maximum and several (possibly many) local maxima, whose values are not exactly equal to the global maximum but very close. In such a situation, while the long-term distribution will be concentrated on the global maximum, one may observe a transient behavior in which the orbits stay close to the equilibrium of the several global maxima situation (corresponding to Theorem 2.13), before it concentrates on the eventual distribution. We leave the analytical treatment of such a situation open for future studies, however, we present a numerical experiment in Figure 8 which shows such a transient behavior.

In this simulation, we took a fitness function presenting one global maximum at  $x_2 = +0.5$  and a local maximum at  $x_1 = -0.5$ , whose value is close to the global maximum. The precise definition of  $\alpha(x)$  is

$$\alpha(x) = 0.95 \times \mathbb{P}_{[x_1 - \delta, x_1 + \delta]}(x) + \mathbb{P}_{[x_2 - \delta, x_2 + \delta]}(x) \text{ with } \delta = 0.2. \quad (25)$$

The function  $I_0(x)$  is chosen as

$$I_0(x) = \min\left(1, 4(x - x_1)^2\right) \min\left(1, 4(x - x_2)^2\right) \mathbb{1}_{[-1, 1]}(x), \quad (26)$$

so that  $\kappa_1 = 2$  and  $\kappa_2 = 2$ . Finally,

$$\gamma(x) = \frac{1}{1 + \mathbb{P}_{[x_1 - \delta, x_1 + \delta]}(x) + 3\mathbb{P}_{[x_2 - \delta, x_2 + \delta]}(x)} \quad (27)$$

so that  $\gamma(x_1) = \frac{1}{2}$  and  $\gamma(x_2) = \frac{1}{4}$ . Summarizing, we have

$$\frac{N + \kappa_1}{2\gamma(x_1)} = 3 < 6 = \frac{N + \kappa_2}{2\gamma(x_2)}.$$



If  $\alpha(x)$  had two global maximum at the same level, Theorem 2.13 would predict that the mass  $I(t, dx)$  vanishes near  $x_2$  and concentrates on  $x_1$ . Since the value of  $\alpha(x_2)$  is slightly higher than the value of  $\alpha(x_1)$ , however, it is clear that the eventual distribution will be concentrated on  $x_2$ . We observe numerically (see Figure 8) that the distribution first concentrates on  $x_1$  on a transient time scale, before the dynamics on  $x_2$  takes precedence. We refer to [10] for a related model with mutations where these transient behaviors are analytically characterized.

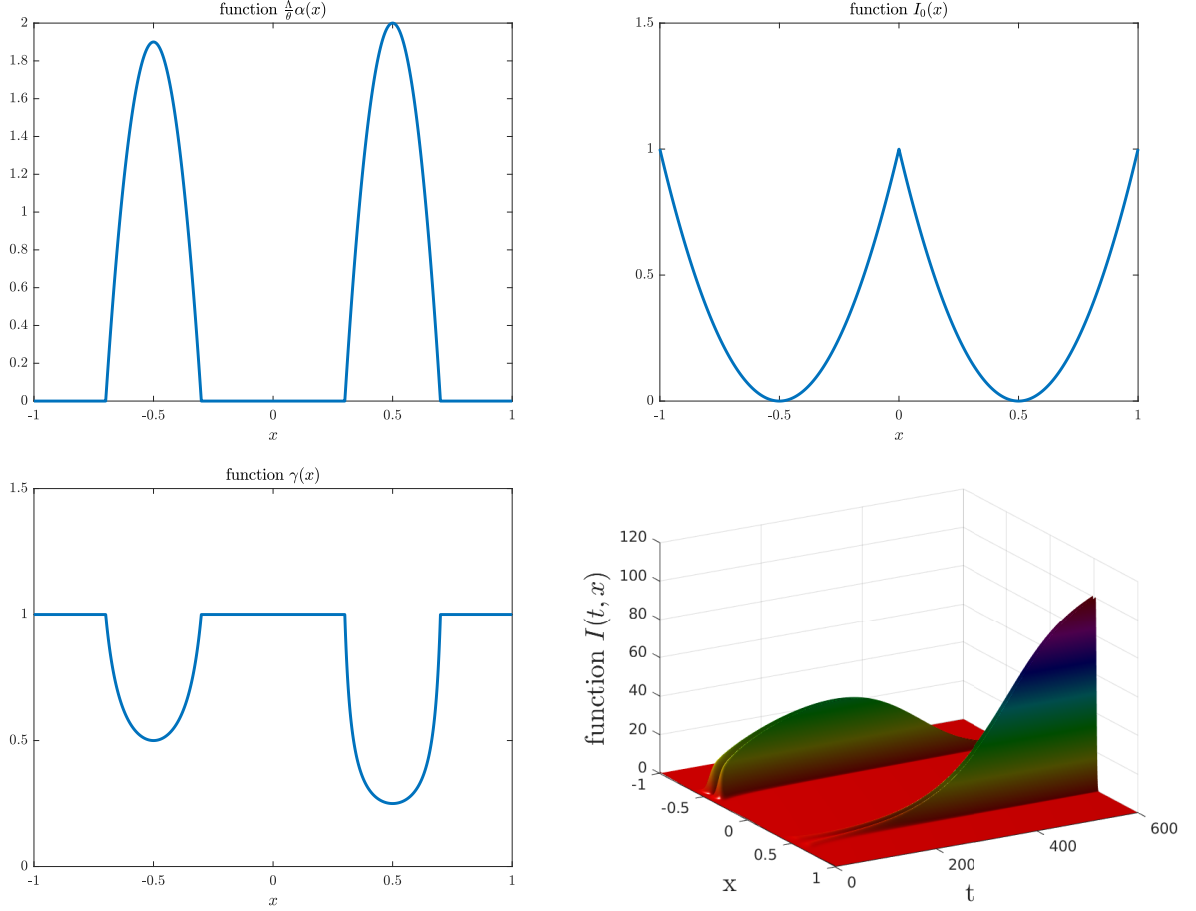


Figure 8: Illustration of a transient behavior for (1). Parameters of this simulation are:  $\Lambda = 2$ ,  $\theta = 1$ ,  $\alpha(x)$  is given by (25),  $I_0(x)$  by (26) and  $\gamma(x)$  by (27). In particular,  $\alpha^* = 1$ ,  $\alpha^{-1}(\alpha^*) = \{x_2\}$  with  $x_1 = -0.5$ ,  $x_2 = 0.5$ . Other parameters are  $\kappa_1 = 2$ ,  $\kappa_2 = 2$ ,  $\gamma(x_1) = 1/2$ ,  $\gamma(x_2) = 1/4$ . The value of the local maximum at  $x_1$ ,  $\alpha(x_1) = 0.95$ , being very close to  $\alpha^*$ , observe that the distribution  $I(t, x)$  first concentrates around  $x_1$  before the global maximum  $x_2$  becomes dominant (bottom right plot).

## 4 Measure-valued solutions and proof of Theorem 2.2

In this section we derive general properties of the solution of (1) equipped with the given and fixed initial data  $S(0) = S_0 \in [0, \infty)$  and  $I_0(dx) \in \mathcal{M}_+(\mathbb{R}^N)$ . Recall that  $\alpha^*$  and  $\mathcal{R}_0(I_0)$  are both defined in (6). Next for  $\varepsilon > 0$  let us denote by  $L_\varepsilon(I_0)$  the following superlevel set:

$$L_\varepsilon(I_0) := \{x \in \text{supp } I_0 : \alpha(x) \geq \alpha^* - \varepsilon\} = \bigcup_{\alpha^* - \varepsilon \leq y \leq \alpha^*} \alpha^{-1}(y). \quad (28)$$

Then the following lemma holds true.

**Lemma 4.1.** *Let Assumption 2.1 hold and let  $(S_0, I_0(dx)) \in \mathbb{R}^+ \times \mathcal{M}_+(\mathbb{R}^N)$  be a given initial condition. Denote  $(S(t), I(t, dx))$  the corresponding solution of (1). Then  $(S(t), I(t, dx))$  is defined for all  $t \geq 0$  and*

$$0 < \frac{\min(\theta, \gamma_*)}{\theta \Lambda \min(\theta, \gamma_*) + \alpha^* \gamma^*} \leq \liminf_{t \rightarrow +\infty} S(t) \leq \limsup_{t \rightarrow +\infty} S(t) \leq \frac{\Lambda}{\theta} < +\infty,$$

$$\limsup_{t \rightarrow +\infty} \int_{\mathbb{R}^N} I(t, dx) \leq \frac{\Lambda}{\min(\theta, \gamma_*)} < +\infty,$$

where  $\gamma_* := \inf_{x \in \text{supp } I_0} \gamma(x)$ ,  $\gamma^* := \sup_{x \in \text{supp } I_0} \gamma(x)$  and  $\alpha^* := \sup_{x \in \text{supp } I_0} \alpha(x)$ .

*Proof.* We remark that

$$\frac{d}{dt} \left( S(t) + \int_{\mathbb{R}^N} I(t, dx) \right) \leq \Lambda - \theta S(t) - \gamma_* \int_{\mathbb{R}^N} I(t, dx),$$

therefore

$$S(t) + \int_{\mathbb{R}^N} I(t, dx) \leq \frac{\Lambda}{\min(\theta, \gamma_*)} + \left( S_0 + \int_{\mathbb{R}^N} I_0(dx) - \frac{\Lambda}{\min(\theta, \gamma_*)} \right) e^{-\min(\theta, \gamma_*)t}.$$

In particular  $I(t, dx)$  is uniformly bounded in  $\mathcal{M}(\mathbb{R}^N)$  and therefore we have the global existence of the solution as well as

$$\limsup_{t \rightarrow +\infty} \int_{\mathbb{R}^N} I(t, dx) \leq \frac{\Lambda}{\min(\theta, \gamma_*)} \text{ and } \limsup_{t \rightarrow +\infty} S(t) \leq \frac{\Lambda}{\min(\theta, \gamma_*)}.$$

Next we return to the  $S$ -component of equation (1) and let  $\varepsilon > 0$  be given. We have, for  $t_0$  sufficiently large and  $t \geq t_0$ ,

$$S_t = \Lambda - \left( \theta + \int_{\mathbb{R}^N} \alpha(x) \gamma(x) I(t, dx) \right) S(t) \geq \Lambda - \left( \theta + \alpha^* \gamma^* \frac{\Lambda}{\min(\theta, \gamma_*)} + \varepsilon \right) S(t),$$

therefore

$$S(t) \geq e^{-\left(\theta + \frac{\Lambda \alpha^* \gamma^*}{\min(\theta, \gamma_*)} + \varepsilon\right)(t-t_0)} S(t_0) + \frac{\Lambda \min(\theta, \gamma_*)}{(\theta + \varepsilon) \min(\theta, \gamma_*) + \Lambda \alpha^* \gamma^*} \left( 1 - e^{-\left(\theta + \frac{\Lambda \alpha^* \gamma^*}{\min(\theta, \gamma_*)} + \varepsilon\right)(t-t_0)} \right),$$

so that finally by letting  $t \rightarrow +\infty$  we get

$$\liminf_{t \rightarrow +\infty} S(t) \geq \frac{\min(\theta, \gamma_*) \Lambda}{(\theta + \varepsilon) \min(\theta, \gamma_*) + \Lambda \alpha^* \gamma^*}.$$

Since  $\varepsilon > 0$  is arbitrary we have shown

$$\liminf_{t \rightarrow +\infty} S(t) \geq \frac{\min(\theta, \gamma_*) \Lambda}{\theta \min(\theta, \gamma_*) + \Lambda \alpha^* \gamma^*}.$$

The Lemma is proved.  $\square$

**Lemma 4.2.** *Let Assumption 2.1 hold and let  $(S_0, I_0(dx)) \in \mathbb{R}^+ \times \mathcal{M}_+(\mathbb{R}^N)$  be a given nonnegative initial condition. Let  $(S(t), I(t, dx))$  be the corresponding solution of (1). Then*

$$\limsup_{T \rightarrow +\infty} \frac{1}{T} \int_0^T S(t) dt \leq \frac{1}{\alpha^*},$$

where  $\alpha^*$  is given in (6).

*Proof.* Let us remark that the second component of (1) can be written as

$$\begin{aligned} I(t, dx) &= I_0(dx) e^{\gamma(x)(\alpha(x) \int_0^t S(s) ds - t)}, \\ &= I_0(dx) \exp \left( \gamma(x) \int_0^t S(s) ds \left[ \alpha(x) - \frac{t}{\int_0^t S(s) ds} \right] \right). \end{aligned} \quad (29)$$

Assume by contradiction that the conclusion of the Lemma does not hold, *i.e.* there exists  $\varepsilon > 0$  and a sequence  $T_n \rightarrow +\infty$  such that

$$\frac{1}{T_n} \int_0^{T_n} S(t) dt \geq \frac{1}{\alpha^*} + \varepsilon.$$

Then

$$\frac{T_n}{\int_0^{T_n} S(t) dt} \leq \frac{1}{\frac{1}{\alpha^*} + \varepsilon} \leq \alpha^* - \varepsilon',$$

where  $\varepsilon' = (\alpha^*)^2 \varepsilon + o(\varepsilon)$ . Since the mapping  $x \mapsto \alpha(x)$  is continuous, the set  $L_\nu(I_0) = \{x \in \text{supp } I_0 : \alpha(x) \geq \alpha^* - \nu\}$  has positive mass with respect to the measure  $I_0(dx)$  for all  $\nu > 0$ , *i.e.*  $\int_{L_\nu(I_0)} I_0(dx) > 0$ . This is true,

in particular, for  $\nu = \frac{\varepsilon'}{2}$ , therefore

$$\begin{aligned} \int_{L_{\varepsilon'/2}(I_0)} I(T_n, dx) &= \int_{L_{\varepsilon'/2}(I_0)} \exp \left( \gamma(x) \int_0^{T_n} S(s) ds \left[ \alpha(x) - \frac{T_n}{\int_0^{T_n} S(s) ds} \right] \right) I_0(dx) \\ &\geq \int_{L_{\varepsilon'/2}(I_0)} \exp \left( \gamma_* \int_0^{T_n} S(s) ds \cdot \frac{\varepsilon'}{2} \right) I_0(dx) \\ &= \int_{L_{\varepsilon'/2}(I_0)} I_0(dx) \exp \left( \frac{\varepsilon' \gamma_*}{2} \int_0^{T_n} S(s) ds \right), \end{aligned}$$

where  $\gamma_* = \inf_{x \in \text{supp } I_0} \gamma(x)$ . Since  $\int_{L_{\varepsilon'/2}(I_0)} I_0(dx) > 0$  and  $\int_0^{T_n} S(t) dt \rightarrow +\infty$  when  $n \rightarrow +\infty$ , we have therefore

$$\limsup_{t \rightarrow +\infty} \int_{\mathbb{R}^N} I(t, dx) \geq \limsup_{n \rightarrow +\infty} \int_{L_{\varepsilon'/2}(I_0)} I(T_n, dx) = +\infty,$$

which is a contradiction since  $I(t, dx)$  is bounded in  $\mathcal{M}(\mathbb{R}^N)$  by Lemma 4.1. This completes the proof of the Lemma.  $\square$

The following kind of weak persistence property holds.

**Lemma 4.3.** *Let Assumption 2.1 hold and let  $(S_0, I_0(dx)) \in \mathbb{R}^+ \times \mathcal{M}_+(\mathbb{R}^N)$  be a given nonnegative initial condition. Let  $(S(t), I(t, dx))$  be the corresponding solution of (1). Recalling the definition of  $\alpha^*$  in (6), assume that*

$$\mathcal{R}_0(I_0) = \frac{\Lambda}{\theta} \alpha^* > 1.$$

Then

$$\limsup_{t \rightarrow +\infty} \int_{\mathbb{R}^N} I(t, dx) \geq \frac{\theta}{\alpha^* \gamma^*} (\mathcal{R}_0(I_0) - 1) > 0,$$

where  $\gamma^* := \sup_{x \in \text{supp } I_0} \gamma(x)$ .

*Proof.* Assume by contradiction that for  $t_0$  sufficiently large we have

$$\int_{\mathbb{R}^N} I(t, dx) \leq \eta' < \eta =: \frac{\theta}{\alpha^* \gamma^*} (\mathcal{R}_0(I_0) - 1) \text{ for all } t \geq t_0,$$

with  $\eta' > 0$ .

As a consequence of Lemma 4.2 we have

$$\liminf_{t \rightarrow +\infty} S(t) \leq \limsup_{T \rightarrow +\infty} \frac{1}{T} \int_0^T S(t) dt \leq \frac{1}{\alpha^*}. \quad (30)$$

Let  $\underline{S} := \liminf_{t \rightarrow +\infty} S(t)$ . Let  $(t_n)_{n \geq 0}$  be a sequence that tends to  $\infty$  as  $n \rightarrow \infty$  and such that  $\lim_{n \rightarrow +\infty} S'(t_n) = 0$  and  $\lim_{n \rightarrow +\infty} S(t_n) = \underline{S}$ . As  $\int_{\mathbb{R}^N} I(t_n, dx) \leq \eta'$  for  $n$  large enough we deduce from the equality

$$S'(t_n) = \Lambda - \theta S(t_n) - S(t_n) \int_{\mathbb{R}^N} \alpha(x) \gamma(x) I(t_n, dx),$$

that

$$0 \geq \Lambda - \theta \underline{S} - \underline{S} \alpha^* \gamma^* \eta'$$

so that

$$\underline{S} \geq \frac{\Lambda}{\theta + \alpha^* \gamma^* \eta'} > \frac{\Lambda}{\theta + \alpha^* \gamma^* \eta}$$

and by definition of  $\eta$

$$\underline{S} > \frac{\Lambda}{\theta \mathcal{R}_0} = \frac{1}{\alpha^*},$$

which contradicts (30).  $\square$

Let us remind that  $\mathcal{M}_+(\mathbb{R}^N)$ , equipped with the Kantorovitch-Rubinstein metric  $d_0$  defined in (4), is a complete metric space.

**Lemma 4.4** (Compactness of the orbit and uniform persistence). *Let Assumption 2.1 hold and let  $(S_0, I_0(dx)) \in \mathbb{R}^+ \times \mathcal{M}_+(\mathbb{R}^N)$  be a given nonnegative initial condition. Let  $(S(t), I(t, dx))$  be the corresponding solution of (1). Assume that there exists  $\varepsilon > 0$  such that the superlevel set  $L_\varepsilon(I_0)$  (defined in (28)) is bounded. Then, the closure of the orbit of  $I_0$ ,*

$$\overline{\mathcal{O}}(I_0) := \left\{ \mu \in \mathcal{M}_+(\mathbb{R}^N) : \text{there exists a sequence } t_n \geq 0 \text{ such that } d_0(I(t_n, dx), \mu) \xrightarrow{n \rightarrow +\infty} 0 \right\},$$

*is compact for the topology induced by  $d_0$  (i.e. the weak topology of measures).*

*If moreover  $\mathcal{R}_0(I_0) > 1$ , then it holds*

$$\liminf_{t \rightarrow +\infty} \int_{\mathbb{R}^N} I(t, dx) > 0.$$

*Proof.* First of all let us remark that

$$I(t, dx) = e^{(\int_0^t S(s) ds \alpha(x) - t) \gamma(x)} I_0(dx),$$

and therefore the orbit  $t \mapsto I(t, dx)$  is continuous for the metric  $d_0$ .

By Lemma 4.2 we have

$$\limsup_{T \rightarrow +\infty} \frac{1}{T} \int_0^T S(s) ds \leq \frac{1}{\alpha^*},$$

where  $\alpha^*$  defined in (6). Let  $\varepsilon > 0$  be sufficiently small, so that the set  $L_\varepsilon(I_0)$  is bounded and let  $R := \sup_{x \in L_\varepsilon(I_0)} \|x\|$ . Then there exists  $T_0 = T_0(\varepsilon)$  such that

$$\frac{T}{\int_0^T S(t) dt} \geq \alpha^* - \frac{\varepsilon}{2} \text{ for all } T \geq T_0.$$

Therefore if  $T \geq T_0$ , we have

$$\begin{aligned} \int_{\|x\| \geq R} I(T, dx) &= \int_{\|x\| \geq R} e^{\gamma(x) \int_0^T S(t) dt \left( \alpha(x) - \frac{T}{\int_0^T S(t) dt} \right)} I_0(dx) \\ &\leq \int_{\|x\| \geq R} e^{\gamma(x) \int_0^T S(t) dt \left( \alpha(x) - \alpha^* + \frac{\varepsilon}{2} \right)} I_0(dx) \\ &\leq \int_{\|x\| \geq R} e^{-\frac{\varepsilon}{2} \gamma(x) \int_0^T S(t) dt} I_0(dx) \xrightarrow{T \rightarrow +\infty} 0. \end{aligned}$$

In particular, the set  $\{I(t, dx) : t \geq 0\}$  is tight and bounded in the absolute variation norm (see Lemma 4.1), therefore precompact for the weak topology by Prokhorov's Theorem [6, Theorem 8.6.2, Vol. II p. 202].

Next we show the weak uniform persistence property if  $\mathcal{R}_0(I_0) > 1$ . Let  $t_n \rightarrow +\infty$  be such that  $I(t_n, dx) \xrightarrow{n \rightarrow +\infty} I^\infty(dx)$ . Then, for  $\varepsilon > 0$  sufficiently small we will be fixed in the rest of the proof, we have

$$\inf_{x \in L_\varepsilon(I_0)} \frac{\Lambda}{\theta} \alpha(x) > 1. \quad (31)$$

By Lemma 4.2 we have

$$\frac{t_n}{\int_0^{t_n} S(t) dt} \geq \alpha^* - \frac{\varepsilon}{2} \text{ for all } T \geq T_0,$$

for some  $T_0 = T_0(\varepsilon)$ . Therefore we get

$$\begin{aligned} \int_{\mathbb{R}^N \setminus L_\varepsilon(I_0)} I(t_n, dx) &= \int_{\mathbb{R}^N \setminus L_\varepsilon(I_0)} e^{\gamma(x) \int_0^{t_n} S(t) dt \left( \alpha(x) - \frac{t_n}{\int_0^{t_n} S(t) dt} \right)} I_0(dx) \\ &\leq \int_{\mathbb{R}^N \setminus L_\varepsilon(I_0)} e^{\gamma(x) \int_0^{t_n} S(t) dt \left( \alpha(x) - \alpha^* + \frac{\varepsilon}{2} \right)} I_0(dx) \\ &\leq \int_{\mathbb{R}^N \setminus L_\varepsilon(I_0)} e^{-\frac{\varepsilon}{2} \gamma(x) \int_0^{t_n} S(t) dt} I_0(dx) \xrightarrow{t_n \rightarrow +\infty} 0. \end{aligned}$$

In particular we have  $\int_{\mathbb{R}^N \setminus L_\varepsilon(I_0)} I^\infty(dx) = 0$ . Recall that, as a consequence of (31), we have  $\mathcal{R}_0(I^\infty) := \sup_{x \in \text{supp}(I^\infty)} \frac{\Lambda}{\theta} \alpha(x) \geq \frac{\Lambda}{\theta} \inf_{x \in L_\varepsilon(I_0)} \alpha(x) > 1$ . By Lemma 4.3 we have the alternative:

$$\text{either } I(dx) \equiv 0 \text{ or } \int_{\mathbb{R}^N} I^\infty(dx) \geq \frac{\theta}{\alpha^* \gamma^*} (\mathcal{R}_0(I^\infty) - 1) \geq \frac{\theta}{\alpha^* \gamma^*} \left( \frac{\Lambda}{\theta} \inf_{x \in L_\varepsilon(I_0)} \alpha(x) - 1 \right) > 0.$$

This is precisely the weak uniform persistence in the metric space  $(\overline{\mathcal{O}}(I_0), d_0)$ , which is complete. As a consequence of [40, Proposition 3.2] in the complete (and compact) metric space  $M = \overline{\mathcal{O}}(I_0) \cup \{0\}$  equipped with the metric  $d_0$ , with  $M_0 = \overline{\mathcal{O}}(I_0) \setminus \{0\}$ ,  $\partial M_0 = \{0\}$  and

$$\rho(\mathcal{I}) = \int_{\mathbb{R}^N} \mathcal{I}(dx) = \langle \mathcal{I}, 1 \rangle_{\mathcal{M}(\mathbb{R}^N), BC(\mathbb{R}^N)},$$

the Poincaré map is uniformly persistent, where the chevron  $\langle \cdot, \cdot \rangle_{\mathcal{M}(\mathbb{R}^N), BC(\mathbb{R}^N)}$  denotes the canonical bilinear mapping on  $\mathcal{M}(\mathbb{R}^N) = BC(\mathbb{R}^N)^* \times BC(\mathbb{R}^N)$ . Hence this yields

$$\liminf_{t \rightarrow +\infty} \int_{\mathbb{R}^N} I(t, dx) > 0,$$

and the Lemma is proved.  $\square$

**Lemma 4.5.** *Let Assumption 2.1 hold and let  $(S_0, I_0(dx)) \in \mathbb{R}^+ \times \mathcal{M}_+(\mathbb{R}^N)$  be a given nonnegative initial condition. Let  $(S(t), I(t, dx))$  be the corresponding solution of (1). Assume that  $\mathcal{R}_0(I_0) > 1$  and that  $L_\varepsilon(I_0)$  (defined in (28)) is bounded for  $\varepsilon > 0$  sufficiently small. Then*

$$\liminf_{T \rightarrow +\infty} \frac{1}{T} \int_0^T S(t) dt \geq \frac{1}{\alpha^*},$$

with  $\alpha^*$  given in (6).

*Proof.* As in the proof of Lemma 4.5, we write

$$\begin{aligned} I(t, dx) &= I_0(dx) e^{(\alpha(x) \int_0^t S(s) ds - t) \gamma(x)}, \\ &= I_0(dx) \exp \left( \gamma(x) \int_0^t S(s) ds \left[ \alpha(x) - \frac{t}{\int_0^t S(s) ds} \right] \right). \end{aligned}$$

Assume by contradiction that the conclusion of the Lemma does not hold, *i.e.* there exists  $\varepsilon > 0$  and a sequence  $T_n \rightarrow +\infty$  such that

$$\frac{1}{T_n} \int_0^{T_n} S(t) dt \leq \frac{1}{\alpha^*} - \varepsilon.$$

Then

$$\frac{T_n}{\int_0^{T_n} S(t) dt} \geq \frac{1}{\frac{1}{\alpha^*} - \varepsilon} \geq \alpha^* + \varepsilon',$$

where  $\varepsilon' = (\alpha^*)^2 \varepsilon + o(\varepsilon)$ , provided  $\varepsilon$  is sufficiently small. Therefore

$$\begin{aligned} \int_{\mathbb{R}^N} I(T_n, dx) dx &= \int_{\mathbb{R}^N} \exp \left( \gamma(x) \int_0^{T_n} S(s) ds \left[ \alpha(x) - \frac{T_n}{\int_0^{T_n} S(s) ds} \right] \right) I_0(dx) \\ &\leq \int_{\mathbb{R}^N} \exp \left( -\gamma_0 \int_0^{T_n} S(s) ds \cdot \varepsilon' \right) I_0(dx) \\ &= \exp \left( -\varepsilon' \gamma_0 \int_0^{T_n} S(s) ds \right) \int_{\mathbb{R}^N} I_0(dx), \end{aligned}$$

We have therefore

$$\liminf_{t \rightarrow +\infty} \int_{\mathbb{R}^N} I(t, dx) \leq \liminf_{n \rightarrow +\infty} \int_{\mathbb{R}^N} I(T_n, dx) = 0,$$

which is in contradiction with Lemma 4.4. This completes the proof of the Lemma.  $\square$

**Remark 4.6.** By combining Lemma 4.2 and Lemma 4.5 we obtain that  $\frac{1}{T} \int_0^T S(t) dt$  admits a limit when  $T \rightarrow +\infty$  and

$$\lim_{T \rightarrow +\infty} \frac{1}{T} \int_0^T S(t) dt = \frac{1}{\alpha^*}.$$

**Lemma 4.7.** *Let Assumption 2.1 hold and let  $(S_0, I_0(dx)) \in \mathbb{R}^+ \times \mathcal{M}_+(\mathbb{R}^N)$  be a given nonnegative initial condition. Let  $(S(t), I(t, dx))$  be the corresponding solution of (1). Assume that  $L_\varepsilon(I_0)$  (defined in (28)) is bounded for  $\varepsilon > 0$  sufficiently small. Then one has*

$$d_0(I(t, dx), \mathcal{M}_+(\alpha^{-1}(\alpha^*))) \xrightarrow{t \rightarrow +\infty} 0.$$

*Proof.* Let  $\varepsilon > 0$  be as in the statement of Lemma 4.7. By Lemma 4.2, there exists  $T \geq 0$  such that for all  $t \geq T$  we have

$$\frac{t}{\int_0^t S(s)ds} \geq \alpha^* - \frac{\varepsilon}{2},$$

where  $\alpha^* := \sup_{x \in \text{supp } I_0} \alpha(x)$ . Hence for  $t \geq T$  we have

$$\begin{aligned} \int_{\mathbb{R}^N \setminus L_\varepsilon(I_0)} I(t, dx) &= \int_{\mathbb{R}^N \setminus L_\varepsilon(I_0)} \exp\left(\gamma(x) \int_0^t S(s)ds \left(\alpha(x) - \frac{t}{\int_0^t S(s)ds}\right)\right) I_0(dx) \\ &\leq \int_{\mathbb{R}^N \setminus L_\varepsilon(I_0)} \exp\left(\gamma(x) \int_0^t S(s)ds \left(\alpha^* - \varepsilon - \frac{t}{\int_0^t S(s)ds}\right)\right) I_0(dx) \\ &\leq \int_{\mathbb{R}^N \setminus L_\varepsilon(I_0)} e^{-\frac{\varepsilon}{2}\gamma(x) \int_0^t S(s)ds} I_0(dx) \xrightarrow{t \rightarrow +\infty} 0. \end{aligned}$$

In particular, if  $I(t, dx)|_{L_\varepsilon(I_0)}$  denotes the restriction of  $I(t, dx)$  to  $L_\varepsilon(I_0)$ , we have  $\|I(t, dx) - I(t, dx)|_{L_\varepsilon(I_0)}\|_{AV} \xrightarrow{t \rightarrow +\infty} 0$  and hence

$$d_0(I(t, dx), I(t, dx)|_{L_\varepsilon(I_0)}) \leq d_{AV}(I(t, dx), I(t, dx)|_{L_\varepsilon(I_0)}) \xrightarrow{t \rightarrow +\infty} 0.$$

Here  $\varepsilon > 0$  can be chosen arbitrarily small. By Lemma 4.1 we know moreover that

$$\limsup_{t \rightarrow +\infty} \int_{\mathbb{R}^N} I(t, dx) \leq \frac{\Lambda}{\min(\theta, \gamma_*)},$$

so that for  $t$  sufficiently large, we have

$$\int_{\mathbb{R}^N} I(t, dx) \leq 2 \frac{\Lambda}{\min(\theta, \gamma_*)}.$$

Finally by using Proposition A.5, we have

$$\begin{aligned} d_0(I(t, dx), \mathcal{M}_+(\alpha^{-1}(\alpha^*))) &\leq d_0(I(t, dx), I(t, dx)|_{L_\varepsilon(I_0)}) + d_0(I(t, dx)|_{L_\varepsilon(I_0)}, \mathcal{M}_+(\alpha^{-1}(\alpha^*))) \\ &\leq d_0(I(t, dx), I(t, dx)|_{L_\varepsilon(I_0)}) + 2 \frac{\Lambda}{\min(\theta, \gamma_*)} \sup_{x \in L_\varepsilon(I_0)} d(x, \alpha^{-1}(\alpha^*)). \end{aligned}$$

Since

$$\sup_{x \in L_\varepsilon(I_0)} d(x, \alpha^{-1}(\alpha^*)) \xrightarrow{\varepsilon \rightarrow 0} 0,$$

the Kantorovitch-Rubinstein distance between  $I(t, dx)$  and  $\mathcal{M}(\alpha^{-1}(\alpha^*))$  can indeed be made arbitrarily small as  $t \rightarrow +\infty$ . This proves the Lemma.  $\square$

**Lemma 4.8.** *Let Assumption 2.1 hold and let  $(S_0, I_0(dx)) \in \mathbb{R}^+ \times \mathcal{M}_+(\mathbb{R}^N)$  be a given nonnegative initial condition. Let  $(S(t), I(t, dx))$  be the corresponding solution of (1). Assume that  $\alpha(x) \equiv \alpha^*$  is a constant function on  $\text{supp } I_0$  such that  $\mathcal{R}_0(I_0) > 1$ . There exists a stationary solution  $(S^*, i^*) \in \mathbb{R}^+ \times L^1(I_0)$  such that*

$$\begin{aligned} S(t) &\xrightarrow{t \rightarrow +\infty} S^* = \frac{1}{\alpha^*}, \\ I(t, dx) &\xrightarrow{t \rightarrow +\infty} i^*(x) I_0(dx). \end{aligned}$$

$i^*$  is a Borel-measurable function on  $\mathbb{R}^N$ , which is unique up to a negligible set with respect to  $I_0(dx)$ . Moreover it satisfies  $i^*(x) = e^{\tau\gamma(x)}$ , where  $\tau$  is the unique solution to the equation

$$\int_{\mathbb{R}^N} \gamma(x) e^{\tau\gamma(x)} I_0(dx) = \frac{\theta}{\alpha^*} (\mathcal{R}_0 - 1). \quad (32)$$

*Proof.* First we check that the proposed stationary solution is indeed unique and a stationary solution. By Lemma 4.2–4.5,  $S^* = \frac{1}{\alpha^*}$  is the only possible choice for  $S^*$ . Next, we remark that the map

$$\tau \mapsto \int_{\mathbb{R}^N} \gamma(x) e^{\tau\gamma(x)} I_0(dx)$$

is strictly increasing and maps  $\mathbb{R}$  onto  $(0, +\infty)$ , therefore (32) has a unique solution  $\tau$  and the corresponding function  $i^*(x) I_0(dx) := e^{\tau\gamma(x)} I_0(dx)$  satisfies

$$\int_{\mathbb{R}^N} \gamma(x) i^*(x) I_0(dx) = \frac{\theta}{\alpha^*} (\mathcal{R}_0 - 1).$$

Therefore it is not difficult to check that  $(S^*, i^*(x)I_0(dx))$  is a stationary solution to the system of differential equations

$$\begin{cases} S'(t) = \Lambda - \theta S(t) - \int_{\mathbb{R}^N} \alpha^* \gamma(x) I(t, dx) \\ I'(t, dx) = \gamma(x) (\alpha^* S(t) - 1) I(t, dx), \end{cases}$$

which is equivalent to (1) on  $\text{supp } I_0$ .

Next we show the convergence of an initial condition to  $(S^*, I^*)$  where  $I^*(dx) = i^*(x)I_0(dx)$ . To that aim we introduce the Lyapunov functional

$$V(S, I) := S^* g\left(\frac{S}{S^*}\right) + \int_{\mathbb{R}^N} i^*(x) g\left(\frac{I(x)}{i^*(x)}\right) I_0(dx),$$

where  $g(s) = s - \ln(s)$ .  $V(S, I)$  is well-defined when  $\ln(I(x)) \in L^1(I_0)$ . Let us denote  $I(t, dx) = i(t, x)I_0(dx)$  and remark that  $V(S(t), i(t, x))$  is always well-defined since  $i(t, x) = e^{\alpha(x)\bar{S}(t) - \gamma(x)t}$ . We claim that  $V'(S(t), i(t, \cdot)) \leq 0$ . Indeed, writing  $V_1(S) = S^* g\left(\frac{S(t)}{S^*}\right)$  and  $V_2(t) = \int_{\mathbb{R}^N} i^*(x) g\left(\frac{i(t, x)}{i^*(x)}\right) I_0(dx)$ , we have

$$\begin{aligned} V_1'(t) &= S^* \frac{S'(t)}{S^*} g'\left(\frac{S(t)}{S^*}\right) = \left(\Lambda - \theta S(t) - S(t) \int_{\mathbb{R}^N} \alpha^* \gamma(x) i(t, x) I_0(dx)\right) \left(1 - \frac{S^*}{S(t)}\right) \\ &= \left(\Lambda - \theta S(t) - S(t) \int_{\mathbb{R}^N} \alpha^* \gamma(x) i(t, x) I_0(dx) - \Lambda + \theta S^* + S^* \int_{\mathbb{R}^N} \alpha^* \gamma(x) i^*(x) I_0(dx)\right) \left(1 - \frac{S^*}{S(t)}\right) \\ &= -\theta \frac{(S(t) - S^*)^2}{S(t)} + \left(S^* \int_{\mathbb{R}^N} \alpha^* \gamma(x) i^*(x) I_0(dx) - S(t) \int_{\mathbb{R}^N} \alpha^* \gamma(x) i(t, x) I_0(dx)\right) \left(1 - \frac{S^*}{S(t)}\right), \\ &= -\theta \frac{(S(t) - S^*)^2}{S(t)} + S^* \int_{\mathbb{R}^N} \alpha^* \gamma(x) i^*(x) I_0(dx) - \frac{(S^*)^2}{S(t)} \int_{\mathbb{R}^N} \alpha^* \gamma(x) i^*(x) I_0(dx) \\ &\quad - S(t) \int_{\mathbb{R}^N} \alpha^* \gamma(x) i(t, x) I_0(dx) + S^* \int_{\mathbb{R}^N} \alpha^* \gamma(x) i(t, x) I_0(dx), \end{aligned}$$

and

$$\begin{aligned} V_2'(t) &= \int_{\mathbb{R}^N} i^*(x) \frac{i_t(t, x)}{i^*(x)} g'\left(\frac{i(t, x)}{i^*(x)}\right) I_0(dx) = \int_{\mathbb{R}^N} \gamma(x) (\alpha^* S(t) - 1) i(t, x) \left(1 - \frac{i^*(x)}{i(t, x)}\right) I_0(dx) \\ &= \int_{\mathbb{R}^N} \gamma(x) (\alpha^* S(t) - 1) (i(t, x) - i^*(x)) I_0(dx) \\ &= \int_{\mathbb{R}^N} \gamma(x) \alpha^* S(t) i(t, x) I_0(dx) - \int_{\mathbb{R}^N} \gamma(x) i(t, x) I_0(dx) - \int_{\mathbb{R}^N} \gamma(x) \alpha^* S(t) i^*(x) I_0(dx) \\ &\quad + \int_{\mathbb{R}^N} \gamma(x) i^*(x) I_0(dx). \end{aligned}$$

Recalling  $S^* = \frac{1}{\alpha^*}$ , we have therefore

$$\begin{aligned} \frac{d}{dt} V(S(t), i(t, \cdot)) &= \frac{d}{dt} V_1(t) + \frac{d}{dt} V_2(t) \\ &= -\theta \frac{(S(t) - S^*)^2}{S(t)} + 2 \int_{\mathbb{R}^N} \gamma(x) i^*(x) dx - \frac{(S^*)^2}{S(t)} \int_{\mathbb{R}^N} \alpha^* \gamma(x) i^*(x) I_0(dx) \\ &\quad - \int_{\mathbb{R}^N} \alpha^* \gamma(x) S(t) i^*(x) I_0(dx). \end{aligned}$$

Since

$$\int_{\mathbb{R}^N} \alpha^* \gamma(x) i^*(x) \left(S(t) + \frac{(S^*)^2}{S(t)}\right) I_0(dx) \geq \int_{\mathbb{R}^N} \alpha^* \gamma(x) i^*(x) \times 2S^* I_0(dx),$$

which stems from the inequality  $a + b \geq 2\sqrt{ab}$ , we have proved that

$$\frac{d}{dt} V(S(t), i(t, \cdot)) \leq 0.$$

It then follows from classical arguments that  $S(t) \rightarrow S^*$  and  $i(t, \cdot) \rightarrow i^*(\cdot)$  as  $t \rightarrow +\infty$  (where the last limit holds in  $L^1(I_0)$ ). The Lemma is proved.  $\square$

Next we can determine the long-time behavior when the initial measure  $I_0$  puts a positive mass on the set of maximal fitness. Recall that  $\alpha^{-1}(\alpha^*)$  (see (5) and (6)) is the set of points in the support of  $I_0$  that have maximal fitness, *i.e.*

$$\alpha^{-1}(\alpha^*) = \bigcap_{\varepsilon > 0} L_\varepsilon(I_0) = \{x \in \text{supp } I_0 : \alpha(x) \geq \alpha(y) \text{ for all } y \in \text{supp } I_0\}.$$

**Lemma 4.9.** *Assume that  $L_\varepsilon(I_0)$  is bounded for  $\varepsilon > 0$  sufficiently small and that  $\mathcal{R}_0(I_0) > 1$ . Suppose that  $I_0(\alpha^{-1}(\alpha^*)) > 0$ , or in other words,*

$$\int_{\alpha^{-1}(\alpha^*)} I_0(dx) > 0.$$

*Then the limit of  $I(t, dx)$  is completely determined by the part of  $I_0$  in  $\alpha^{-1}(\alpha^*)$ , that is to say,*

$$d_0(I(t, dx), I_\infty^*(dx)) \xrightarrow{t \rightarrow +\infty} 0,$$

*where  $I_\infty^*(dx)$  is the stationary measure given by Lemma 4.8 associated with the initial condition  $I_0^*(dx) := I_0|_{\alpha^{-1}(\alpha^*)}(dx)$ , the restriction of  $I_0(dx)$  to the set  $\alpha^{-1}(\alpha^*)$ .*

*Proof.* First, let us define  $\alpha^* := \sup_{x \in \text{supp } I_0} \alpha(x)$  (so that  $\alpha(x)$  is a constant equal to  $\alpha^*$  on  $\alpha^{-1}(\alpha^*)$ ) and

$$\eta(t) := \alpha^* \bar{S}(t) - 1, \text{ with } \bar{S}(t) = \frac{1}{t} \int_0^t S(s) ds.$$

Then  $I(t, dx)$  can be written as

$$I(t, dx) = \exp\left(\gamma(x)t \left[\eta(t) + (\alpha(x) - \alpha^*) \frac{1}{t} \int_0^t S(s) ds\right]\right) I_0(dx).$$

We remark that the function  $t \mapsto t\eta(t)$  is bounded. Indeed, by Jensen's inequality we have

$$\exp\left(\int_{\alpha^{-1}(\alpha^*)} \gamma(x)t\eta(t) \frac{I_0(dx)}{\int_{\alpha^{-1}(\alpha^*)} I_0(dx)}\right) \leq \int_{\alpha^{-1}(\alpha^*)} e^{\gamma(x)t\eta(t)} \frac{I_0(dx)}{\int_{\alpha^{-1}(\alpha^*)} I_0(dx)},$$

so that

$$t\eta(t) \leq \frac{\int_{\alpha^{-1}(\alpha^*)} I_0}{\int_{\alpha^{-1}(\alpha^*)} \gamma(x) I_0(dx)} \ln\left(\int_{\mathbb{R}^N} e^{\gamma(x)t\eta(t)} \frac{I_0(dx)}{\int_{\mathbb{R}^N} I_0(dx)}\right) = \frac{\int_{\alpha^{-1}(\alpha^*)} I_0}{\int_{\alpha^{-1}(\alpha^*)} \gamma(x) I_0(dx)} \ln\left(\frac{1}{\int_{\alpha^{-1}(\alpha^*)} I_0} \int_{\alpha^{-1}(\alpha^*)} I(t, dx)\right).$$

Applying Lemma 4.1,  $I(t, dx)$  is bounded and we have indeed an upper bound for  $t\eta(t)$ . Next, writing

$$I(t, dx) = \exp\left(\gamma(x)t\eta(t) + (\alpha(x) - \alpha^*) \int_0^t S(s) ds\right) I_0(dx)$$

and recalling that  $\int_0^t S(s) ds \rightarrow +\infty$  as  $t \rightarrow +\infty$ , the function  $\exp\left(\gamma(x)t\eta(t) + (\alpha(x) - \alpha^*) \int_0^t S(s) ds\right)$  converges almost everywhere (with respect to  $I_0$ ) to 0 on  $\mathbb{R}^N \setminus \alpha^{-1}(\alpha^*)$ , so that by Lebesgue's dominated convergence theorem, we have

$$\lim_{t \rightarrow +\infty} \int_{\mathbb{R}^N \setminus \alpha^{-1}(\alpha^*)} I(t, dx) = \int_{\mathbb{R}^N \setminus \alpha^{-1}(\alpha^*)} \lim_{t \rightarrow +\infty} \exp\left(\gamma(x)t\eta(t) + (\alpha(x) - \alpha^*) \int_0^t S(s) ds\right) I_0(dx) = 0.$$

Next it follows from Lemma 4.5 that  $\liminf_{t \rightarrow +\infty} I(t, dx) > 0$ , so that

$$\liminf_{t \rightarrow +\infty} \int_{\alpha^{-1}(\alpha^*)} I(t, dx) = \liminf_{t \rightarrow +\infty} \int_{\mathbb{R}^N} I(t, dx) > 0.$$

Assume by contradiction that there is a sequence  $(t_n)$  such that  $t_n\eta(t_n) \rightarrow -\infty$ , then

$$\int_{\alpha^{-1}(\alpha^*)} I(t, dx) = \int_{\alpha^{-1}(\alpha^*)} e^{\gamma(x)t_n\eta(t_n)} I_0(dx) \leq \int_{\alpha^{-1}(\alpha^*)} e^{\gamma_* t_n\eta(t_n)} I_0(dx) = e^{\gamma_* t_n\eta(t_n)} \int_{\alpha^{-1}(\alpha^*)} I_0(dx) \xrightarrow{t \rightarrow +\infty} 0,$$

where  $\gamma_* := \inf_{x \in \text{supp } I_0} \gamma(x) > 0$ . This is a contradiction. Therefore there is a constant  $\underline{\eta} > 0$  such that

$$t\eta(t) \geq -\underline{\eta} > -\infty.$$



In particular, the function  $t \mapsto t\eta(t)$  is bounded by two constants,

$$-\infty < -\underline{\eta} \leq t\eta(t) \leq \bar{\eta} < +\infty.$$

Suppose that there exists a sequence  $t_n \rightarrow +\infty$  and  $\eta^* \in [-\underline{\eta}, \bar{\eta}]$  such that

$$\lim_{n \rightarrow +\infty} t_n \eta(t_n) = \eta^*.$$

Upon replacing  $t_n$  by a subsequence, the function  $S(t_n)$  converges to a limit  $S_0^*$  and therefore the shifted orbits satisfy

$$(S(t + t_n), I(t + t_n, dx)) \xrightarrow[n \rightarrow +\infty]{} (S^*(t), I^*(t, dx))$$

locally uniformly in time. The resulting orbit  $(S^*(t), I^*(t, dx))$  is a solution to (1), defined for all times  $t \in \mathbb{R}$ , and satisfying

$$\begin{aligned} S^*(0) &= S_0, \\ I^*(0, dx) &= e^{\gamma(x)\eta^*} I_0^*(dx), \end{aligned}$$

where we recall that  $I_0^*(dx)$  is the restriction of  $I_0(dx)$  to  $\alpha^{-1}(\alpha^*)$ . By Lemma 4.8, this implies that  $S_0^* = \frac{1}{\alpha^*}$  and  $I^*(0, dx) = e^{\tau\gamma(x)} I_0^*(dx)$ , where  $\tau$  is uniquely defined by (32) (and independent of the sequence  $t_n$ ). Therefore  $\eta^* = \tau$ . We conclude that

$$\lim_{t \rightarrow +\infty} t\eta(t) = \tau,$$

where  $\tau$  is the constant uniquely defined by (32) with the initial measure  $I_0^*(dx)$ . This ends the proof of the Lemma.  $\square$

When the set of maximal fitness  $\alpha^{-1}(\alpha^*)$  is negligible for  $I_0$ , it is more difficult to obtain a general result for the long-time behavior of  $I(t, dx)$ . We start with a short but useful estimate on the rate  $\eta(t)$

**Lemma 4.10.** *Assume that  $L_\varepsilon(I_0)$  is bounded for  $\varepsilon > 0$  sufficiently small and that  $\mathcal{R}_0(I_0) > 1$ . Suppose that  $I_0(\alpha^{-1}(\alpha^*)) = 0$  and set*

$$\eta(t) := \alpha^* \bar{S}(t) - 1, \quad \text{with } \bar{S}(t) = \frac{1}{t} \int_0^t S(s) ds,$$

where  $\alpha^* := \sup_{x \in \text{supp } I_0} \alpha(x)$ . Then it holds

$$t\eta(t) \xrightarrow[t \rightarrow \infty]{} +\infty.$$

*Proof.* Assume by contradiction that there exists a sequence  $t_n \rightarrow +\infty$  such that  $t_n \eta(t_n)$  has a uniform upper bound as  $t_n \rightarrow +\infty$ , then observe that the quantity

$$e^{\gamma(x)(\alpha(x)\bar{S}(t_n)-1)t_n} = e^{\gamma(x)(\alpha(x)-\alpha^*)\bar{S}(t_n)t_n + \gamma(x)\eta(t_n)t_n}$$

is uniformly bounded in  $t_n$  and vanishes as  $t_n \rightarrow +\infty$  almost everywhere with respect to  $I_0(dx)$ . By a direct application of Lebesgue's dominated convergence Theorem, we have therefore

$$\int_{\mathbb{R}^N} I(t_n, dx) = \int_{\mathbb{R}^N} e^{\gamma(x)(\alpha(x)\bar{S}(t_n)-1)t_n} I_0(dx) \xrightarrow[t_n \rightarrow +\infty]{} 0,$$

which is in contradiction with Lemma 4.4. We conclude that  $t\eta(t) \rightarrow +\infty$  as  $t \rightarrow +\infty$ .  $\square$

We can now state our convergence result for measures which vanish on  $\alpha^{-1}(\alpha^*)$ , provided the behavior of  $I_0$  at the boundary is not too pathological. Basically, it says that the selection filters the low values of  $\gamma(x)$  near boundary points  $x \in \alpha^{-1}(\alpha^*)$ .

We are now in the position to prove Theorem 2.2.

*Proof of Theorem 2.2.* To show the convergence of  $S(t)$  to  $\frac{1}{\alpha^*}$  (which is present in both i) and ii)), we first remark that

$$\bar{S}(t) = \frac{1}{t} \int_0^t S(s) ds \xrightarrow[t \rightarrow +\infty]{} \frac{1}{\alpha^*}, \quad (33)$$

as a consequence of Lemma 4.2 and 4.5. Next, let  $t_n \rightarrow +\infty$  be an arbitrary sequence, then by the compactness of the orbit proved in Lemma 4.4 we can extract from  $S(t_n)$  a subsequence which converges to a number  $S^*$ . It follows from (33) that  $S^* = \frac{1}{\alpha^*}$ .

The convergence of  $I(t, dx)$  in case i) was proved in Lemma 4.9.

The uniform persistence of  $I(t, dx)$  in case ii) is a consequence of 4.4. The concentration on the maximal fitness was proved in Lemma 4.7. The Theorem is proved.  $\square$

We now turn to the proof of Proposition 2.7 and we first prove that  $I(t, dx)$  concentrates on the set of points maximizing both  $\alpha$  and  $\gamma$ . This property is summarized in the next lemma.

**Lemma 4.11.** *Assume that  $L_\varepsilon(I_0)$  is bounded for  $\varepsilon > 0$  sufficiently small and that  $\mathcal{R}_0(I_0) > 1$ . Suppose that  $I_0(\alpha^{-1}(\alpha^*)) = 0$  and that Assumption 2.5 holds. Recalling the definition of  $\alpha^*$  in (6) and  $\gamma^*$  in Assumption 2.5, set  $\Gamma_0(I_0)$  be the set of maximal points of  $\gamma$  on  $\alpha^{-1}(\alpha^*)$ , defined by*

$$\Gamma_0(I_0) := \{x \in \alpha^{-1}(\alpha^*) : \gamma(x) \geq \gamma(y) \text{ for all } y \in \alpha^{-1}(\alpha^*)\} = \gamma^{-1}(\{\gamma^*\}) \cap \alpha^{-1}(\alpha^*).$$

Then one has

$$d_0(I(t, dx), \mathcal{M}_+(\Gamma_0(I_0))) \xrightarrow{t \rightarrow +\infty} 0.$$

*Proof.* We decompose the proof in several steps.

**Step 1: We show that  $I(t, dx)$  and  $\mathbb{1}_{\alpha(x)\bar{S}(t) \geq 1} I(t, dx)$  are asymptotically close in  $\|\cdot\|_{AV}$ .** That is to say,

$$\|I(t, dx) - \mathbb{1}_{\alpha(\cdot)\bar{S}(t) \geq 1} I(t, dx)\|_{AV} \xrightarrow{t \rightarrow +\infty} 0.$$

Indeed we have

$$I(t, dx) - \mathbb{1}_{\alpha(x)\bar{S}(t) \geq 1} I(t, dx) = \mathbb{1}_{\alpha(x)\bar{S}(t) < 1} I(t, dx) = \mathbb{1}_{\alpha(x)\bar{S}(t) < 1} e^{\gamma(x)(\alpha(x)\bar{S}(t)-1)t} I_0(dx).$$

First note that the function  $\mathbb{1}_{\alpha(x)\bar{S}(t) < 1} I(t, dx) = \mathbb{1}_{\alpha(x)\bar{S}(t) < 1} e^{\gamma(x)(\alpha(x)\bar{S}(t)-1)t}$  is uniformly bounded. On the other hand, since  $I_0(\alpha^{-1}(\alpha^*)) = 0$  recall that  $\bar{S}(t) \rightarrow \frac{1}{\alpha^*}$  for  $t \rightarrow \infty$ , so that  $\mathbb{1}_{\alpha(x)\bar{S}(t) < 1} \rightarrow 0$  as  $t \rightarrow \infty$  almost everywhere with respect to  $I_0$ . It follows from Lebesgue's dominated convergence Theorem that

$$\int_{\mathbb{R}^N} \mathbb{1}_{\alpha(x)\bar{S}(t) < 1} e^{\gamma(x)(\alpha(x)\bar{S}(t)-1)t} I_0(dx) \xrightarrow{t \rightarrow +\infty} 0.$$

**Step 2: We show that the measure  $\mathbb{1}_{\bar{S}(t)y \geq 1} e^{\bar{\gamma}(y\bar{S}(t)-1)t} A(dy)$  is bounded when  $t \rightarrow \infty$  for all  $\bar{\gamma} < \gamma^*$ .**

Note that  $I_0(\alpha^{-1}(\alpha^*)) = 0$  implies that  $A(\{\alpha^*\}) = 0$  and remark that one has

$$\int_{\mathbb{R}^N} \mathbb{1}_{\alpha(x)\bar{S}(t) \geq 1} I(t, dx) = \int_{\min(\alpha^*, 1/\bar{S}(t))}^{\alpha^*} \int_{\{x \in \alpha^{-1}(y)\}} e^{\gamma(x)(y\bar{S}(t)-1)t} I_0(y, dx) A(dy),$$

so, according to Step 1, for  $t$  sufficiently large one has

$$\begin{aligned} \int_{\gamma^{-1}([\bar{\gamma}, \gamma^*])} I(t, dx) &= \int_{\min(\alpha^*, 1/\bar{S}(t))}^{\alpha^*} \int_{x \in \alpha^{-1}(y) \cap \gamma^{-1}([\bar{\gamma}, \gamma^*])} e^{\gamma(x)(y\bar{S}(t)-1)t} I_0(y, dx) A(dy) + o(1) \\ &\geq \int_{\min(\alpha^*, 1/\bar{S}(t))}^{\alpha^*} \int_{\{\alpha(x)=y\} \cap \gamma^{-1}([\bar{\gamma}, \gamma^*])} e^{\bar{\gamma}(y\bar{S}(t)-1)t} I_0(y, dx) A(dy) + o(1) \\ &= \int_{\min(\alpha^*, 1/\bar{S}(t))}^{\alpha^*} \int_{\{\alpha(x)=y\} \cap \gamma^{-1}([\bar{\gamma}, \gamma^*])} I_0(y, dx) e^{\bar{\gamma}(y\bar{S}(t)-1)t} A(dy) + o(1) \\ &\geq m \int_{\min(\alpha^*, 1/\bar{S}(t))}^{\alpha^*} e^{\bar{\gamma}(y\bar{S}(t)-1)t} A(dy) + o(1), \end{aligned}$$

wherein  $m > 0$  is the constant associated with  $\bar{\gamma}$  in Assumption 2.5. Recalling the upper bound for  $I(t, dx)$  from Lemma 4.1, we have

$$\limsup_{t \rightarrow +\infty} \int_{\min(\alpha^*, 1/\bar{S}(t))}^{\alpha^*} e^{\bar{\gamma}(y\bar{S}(t)-1)t} A(dy) \leq \limsup_{t \rightarrow +\infty} \frac{1}{m} \int_{\mathbb{R}^N} I(t, dx) \leq \frac{\Lambda}{m \min(\theta, \gamma_0)} < +\infty.$$

This implies that

$$\limsup_{t \rightarrow +\infty} \int_{\alpha(\text{supp}(I_0))} e^{\bar{\gamma}(y\bar{S}(t)-1)t} A(dy) < \infty.$$

Note that, if the constant  $m$  is independent of  $\bar{\gamma}$ , then the above estimate does not depend on  $\bar{\gamma}$  either.

**Step 3: We show that**  $\int \mathbb{1}_{\gamma(x) < \bar{\gamma}} \mathbb{1}_{\bar{S}(t)\alpha(x) \geq 1} I(t, dx)$  **vanishes whenever**  $\bar{\gamma} < \gamma^*$ .

Fix  $\bar{\gamma} < \gamma^*$  and let  $\varepsilon := \frac{\gamma^* - \bar{\gamma}}{2}$ . Then we have

$$\begin{aligned} \int_{\gamma^{-1}((-\infty, \bar{\gamma})) \cap \alpha^{-1}([1/\bar{S}(t), \infty))} I(t, dx) &= \int_{\min(\alpha^*, 1/\bar{S}(t))}^{\alpha^*} \int_{x \in \gamma^{-1}((-\infty, \bar{\gamma})) \cap \alpha^{-1}(y)} e^{\gamma(x)(y\bar{S}(t)-1)t} I_0(y, dx) A(dy) \\ &\leq \int_{\min(\alpha^*, 1/\bar{S}(t))}^{\alpha^*} \int_{x \in \gamma^{-1}((-\infty, \bar{\gamma})) \cap \alpha^{-1}(y)} I_0(y, dx) e^{(\gamma^* - 2\varepsilon)(y\bar{S}(t)-1)t} A(dy) \\ &\leq \int_{\min(\alpha^*, 1/\bar{S}(t))}^{\alpha^*} \int_{x \in \alpha^{-1}(y)} I_0(y, dx) e^{-\varepsilon(y\bar{S}(t)-1)t} e^{\bar{\gamma}(y\bar{S}(t)-1)t} A(dy). \end{aligned}$$

Reducing  $\varepsilon$  if necessary we may assume that  $\frac{\bar{\gamma}}{\varepsilon} > 1$ . Therefore it follows from Hölder's inequality that

$$\begin{aligned} \int_{\gamma^{-1}((-\infty, \bar{\gamma})) \cap \alpha^{-1}([1/\bar{S}(t), \infty))} I(t, dx) &\leq \left( \int_{\min(\alpha^*, 1/\bar{S}(t))}^{\alpha^*} \left( e^{-\varepsilon(y\bar{S}(t)-1)t} \right)^{\frac{\bar{\gamma}}{\varepsilon}} e^{\bar{\gamma}(y\bar{S}(t)-1)t} A(dy) \right)^{\frac{\varepsilon}{\bar{\gamma}}} \\ &\quad \times \left( \int_{\min(\alpha^*, 1/\bar{S}(t))}^{\alpha^*} \left( \int_{\alpha(x)=y} I_0(y, dx) \right)^{\frac{\bar{\gamma}}{\bar{\gamma}-\varepsilon}} e^{\bar{\gamma}(y\bar{S}(t)-1)t} A(dy) \right)^{1-\frac{\varepsilon}{\bar{\gamma}}} \\ &\leq \left( \int_{\min(\alpha^*, 1/\bar{S}(t))}^{\alpha^*} A(dy) \right)^{\frac{\varepsilon}{\bar{\gamma}}} \left( \int_{\min(\alpha^*, 1/\bar{S}(t))}^{\alpha^*} e^{\bar{\gamma}(y\bar{S}(t)-1)t} A(dy) \right)^{1-\frac{\varepsilon}{\bar{\gamma}}} \\ &= I_0(L_{\alpha^* - \min(\alpha^*, 1/\bar{S}(t))}(I_0))^{\frac{\varepsilon}{\bar{\gamma}}} \left( \int_{\min(\alpha^*, 1/\bar{S}(t))}^{\alpha^*} e^{\bar{\gamma}(y\bar{S}(t)-1)t} A(dy) \right)^{1-\frac{\varepsilon}{\bar{\gamma}}}. \end{aligned} \tag{34}$$

Since  $\bar{S}(t) \rightarrow 1/\alpha^*$  as  $t \rightarrow \infty$ ,  $I_0(L_\varepsilon(I_0)) \xrightarrow{\varepsilon \rightarrow 0} 0$  and by the boundedness of  $\int_{\min(\alpha^*, 1/\bar{S}(t))}^{\alpha^*} e^{\bar{\gamma}(y\bar{S}(t)-1)t} A(dy)$  shown in Step 2, we have indeed

$$\int_{\gamma^{-1}((-\infty, \bar{\gamma})) \cap \alpha^{-1}([1/\bar{S}(t), \infty))} I(t, dx) \xrightarrow{t \rightarrow +\infty} 0, \quad \square$$

and this completes proof of Lemma 4.11.

*Proof of Proposition 2.7.* The concentration of the distribution to  $\mathcal{M}_+(\alpha^{-1}(\alpha^*) \cap \gamma^{-1}(\gamma^*))$  was shown in Lemma 4.11.

Next we prove the asymptotic mass. Pick a sentence  $t_n \rightarrow +\infty$ . By the compactness of the orbit (proved in Lemma 4.4) we can extract from  $t_n$  a subsequence  $t'_n$  such that there exists a Radon measure  $I^\infty(dx)$  with

$$d_0(I(t, dx), I^\infty(dx)) \xrightarrow{t \rightarrow +\infty} 0,$$

and since  $S(t) \rightarrow \frac{1}{\alpha^*}$  and upon further extraction,  $S'(t'_n) \rightarrow 0$ . Therefore,

$$\int_{\mathbb{R}^N} \alpha(x)\gamma(x)I(t'_n, dx) = \frac{\Lambda - S_t(t'_n)}{S(t'_n)} - \theta \xrightarrow{n \rightarrow +\infty} \alpha^* \Lambda - \theta = \theta(\mathcal{R}_0(I_0) - 1).$$

By the concentration result in Lemma 4.11,  $I^\infty$  is concentrated on  $\alpha^{-1}(\alpha^*) \cap \gamma^{-1}(\gamma^*)$ . Therefore

$$\alpha^* \gamma^* \int I^\infty(dx) = \int \alpha(x)\gamma(x)I^\infty(dx) = \lim_{n \rightarrow +\infty} \int \alpha(x)\gamma(x)I(t'_n, dx) = \theta(\mathcal{R}_0(I_0) - 1),$$

so that

$$\lim_{n \rightarrow +\infty} \int I(t'_n, dx) = \int I^\infty(dx) = \frac{\theta}{\alpha^* \gamma^*} (\mathcal{R}_0(I_0) - 1).$$

Since the limit is independent of the sequence  $t_n$ , we have indeed shown that

$$\lim_{t \rightarrow +\infty} \int_{\mathbb{R}^N} I(t, dx) = \frac{\theta}{\alpha^* \gamma^*} (\mathcal{R}_0(I_0) - 1).$$

To prove the last statement, set

$$f(t) := \int_{\min(\alpha^*, 1/\bar{S}(t))}^{\alpha^*} \int_{\bar{\gamma}}^{\gamma^*} e^{z(y\bar{S}(t)-1)t} I_0^\alpha(y, dz) A(dy),$$

where  $\bar{\gamma} < \gamma^*$ . It follows from (34) that

$$\int_{\gamma^{-1}((-\infty, \bar{\gamma}]) \cap \alpha^{-1}([1/\bar{S}(t), \infty))} I(t, dx) \xrightarrow{t \rightarrow +\infty} 0,$$

therefore

$$f(t) = \int_{\min(\alpha^*, 1/\bar{S}(t))}^{\alpha^*} \int_{\bar{\gamma}}^{\gamma^*} \int_{\{\gamma(x)=z\}} e^{z(y\bar{S}(t)-1)t} I_0^{\alpha, \gamma}(y, z, dx) I_0^\alpha(z, dy) A(dy) = \int_{\gamma^{-1}([\bar{\gamma}, \gamma^*]) \cap \alpha^{-1}([1/\bar{S}(t), \infty))} I(t, dx)$$

satisfies

$$0 < \liminf_{t \rightarrow +\infty} \int I(t, dx) = \liminf_{t \rightarrow +\infty} \int_{\gamma^{-1}((-\infty, \bar{\gamma}]) \cap \alpha^{-1}([1/\bar{S}(t), \infty))} I(t, dx) \leq \liminf_{t \rightarrow +\infty} f(t)$$

Remark that

$$\begin{aligned} \int \mathbb{1}_U(x) \mathbb{1}_{\gamma \geq \bar{\gamma}} \mathbb{1}_{S(t)y \geq 1} I(t, dx) &= \int_{\min(\alpha^*, 1/\bar{S}(t))}^{\alpha^*} \int_{\bar{\gamma}}^{\gamma^*} \int_{\{\gamma(x)=z\}} \mathbb{1}_U(x) e^{z(yS(t)-1)t} I_0^{\alpha, \gamma}(y, z, dx) I_0^\alpha(y, dz) A(dy) \\ &= \int_{\min(\alpha^*, 1/\bar{S}(t))}^{\alpha^*} \int_{\bar{\gamma}}^{\gamma^*} \int_{\{\gamma(x)=z\}} \mathbb{1}_U(x) I_0^{\alpha, \gamma}(y, z, dx) e^{z(yS(t)-1)t} I_0^\alpha(y, dz) A(dy) \\ &\geq \int_{\min(\alpha^*, 1/\bar{S}(t))}^{\alpha^*} \int_{\bar{\gamma}}^{\gamma^*} \frac{m}{2} e^{z(yS(t)-1)t} I_0^\alpha(y, dz) A(dy) \\ &\geq f(t) \frac{m}{2}, \end{aligned}$$

provided  $t$  is sufficiently large and  $\bar{\gamma}$  is sufficiently close to  $\gamma^*$ , where

$$m := \liminf_{\varepsilon \rightarrow 0} \operatorname{ess\,inf}_{\alpha^* - \varepsilon \leq y \leq \alpha^*} \operatorname{ess\,inf}_{\gamma^* - \varepsilon \leq z \leq \gamma^*} \int \mathbb{1}_{x \in U} I_0^{\alpha, \gamma}(y, z, dx) > 0.$$

Therefore

$$\liminf_{t \rightarrow +\infty} \int_U I(t, dx) \geq \frac{m}{2} \liminf_{t \rightarrow +\infty} f(t) > 0.$$

This completes proof of Proposition 2.7.  $\square$

## 5 The case of discrete systems. Proof of Theorem 2.8 and 2.9

In this section we show how the theory for discrete systems can be included in the theory for measure-valued solutions to (1) in  $\mathbb{R}^N$ . Rather than doing a direct proof of the results, we show how the general results from Section 4 can be applied to prove Theorem 2.8 and 2.9. In particular, we rely heavily on Theorem 2.2, which has been proven in Section 4 (independently of Theorem 2.8 and 2.9).

*Proof of Theorem 2.8.* Let us choose  $n$  distinct real numbers  $x_1, \dots, x_n$ . Then there exist continuous functions  $\alpha(x)$  and  $\gamma(x)$  such that

$$\alpha(x_i) = \alpha_i \text{ and } \gamma(x_i) = \gamma_i \text{ for all } i = 1, \dots, n.$$

There are many ways to construct  $\alpha(x)$  and  $\gamma(x)$ ; for instance one can work with Lagrange polynomials and interpolate with a constant value outside of a ball and when the values of  $\gamma(x)$  become close to 0. In particular one can impose that  $\alpha(x)$  and  $\gamma(x)$  are bounded and that  $\gamma(x) > 0$  for all  $x \in \mathbb{R}^N$ , thus meeting Assumption 2.1. Now define the initial data

$$I_0(dx) := \sum_{i=1}^n I_0^i \delta_{x_i}.$$

Clearly, the solution  $(S(t), I(t, dx))$  to (1) can be identified with the solution  $(S(t), I^i(t))$  to (13) by the formula

$$I(t, dx) = \sum_{i=1}^n I^i(t) \delta_{x_i}.$$

Since the set  $\{x : \alpha(x) = \alpha^*\}$  has non-zero measure for  $I_0$ , we are in the situation i) of Theorem 2.2 and Theorem 2.8 can therefore be deduced from Theorem 2.2.  $\square$

*Proof of Theorem 2.9.* As in the proof of Theorem 2.8, we identify the solutions to (14) with the solutions  $I(t, dx)$  to (1) through the formula

$$I_0(dx) := \sum_{i=1}^{+\infty} I_0^i \delta_{x_i}, \quad I(t, dx) = \sum_{i=1}^{+\infty} I^i(t) \delta_{x_i},$$

only this time we choose  $x_i = (\alpha_i, \gamma_i) \in \mathbb{R}^2$ . Because of this particular choice, it is fairly easy to construct  $\alpha(x)$  and  $\gamma(x)$  by the formula

$$\alpha(x_1, x_2) := \alpha^\infty f\left(\frac{x_1}{\alpha^\infty}\right), \quad \gamma(x_1, x_2) := \left| \gamma^\infty f\left(\frac{x_2 - \gamma_0}{\gamma^\infty}\right) \right| + \gamma_0,$$

where  $\alpha^\infty := \sup |\alpha_i|$ ,  $\gamma^\infty := \sup |\gamma_i|$ ,  $\gamma_0 = \inf \gamma_i$  and  $f(x) := \min(\max(x, -1), 1)$ . Then the conclusions of Theorem 2.9 in case i) are given by a direct application of Theorem 2.2. Suppose that the set  $\{i : \alpha_i = \alpha^*\}$  is empty, then we are in case ii) of Theorem 2.2, and we can readily conclude that

$$S(t) \xrightarrow{t \rightarrow +\infty} \frac{1}{\alpha^*} \text{ and } \liminf_{t \rightarrow +\infty} \sum_{i=1}^{+\infty} I^i(t) = \liminf_{t \rightarrow +\infty} \int_{\mathbb{R}^2} I(t, dx) > 0.$$

If we assume moreover that  $\alpha_n \rightarrow \alpha^*$  and  $\gamma_n \rightarrow \gamma^*$ , then the maximum of  $\alpha(x)$  on  $\text{supp } I_0$  is attained at a single point  $(\alpha^*, \gamma^*)$  and we can apply Theorem 2.10 to find that

$$I(t, dx) \xrightarrow{t \rightarrow +\infty} I^\infty \delta_{(\alpha^*, \gamma^*)},$$

where  $I^\infty = \frac{\theta}{\gamma^*} (\mathcal{R}_0^* - 1)$ . This finishes the proof of Theorem 2.9.  $\square$

## 6 The case of a finite number of regular maxima

In this section we prove Theorem 2.13. To that aim, we shall make use of the following formula

$$I(t, dx) = \exp\left(\gamma(x) \left(\alpha(x) \int_0^t S(s) ds - t\right)\right) I_0(dx). \quad (35)$$

Recall also the definition of  $\eta(t)$ :

$$\eta(t) = \alpha^* \frac{1}{t} \int_0^t S(s) ds - 1 = \alpha^* \bar{S}(t) - 1.$$

*Proof of Theorem 2.13.* We split the proof of this result into three parts. We first derive a suitable upper bound. We then derive a lower bound in a second step and we conclude the proof of the theorem by estimating the large time asymptotic of the mass of  $I$  around each point of  $\alpha^{-1}(\alpha^*)$ .

### Upper bound:

Let  $i = 1, \dots, p$  be given. Recall that  $\nabla \alpha(x_i) = 0$ . Now due to (iii) in Assumption 2.11 there exist  $m > 0$  and  $T > \varepsilon_0^{-2}$  large enough such that for all  $t \geq T$  and for all  $y \in B\left(0, t^{-\frac{1}{2}}\right)$  we have

$$\alpha(x_i + y) - \alpha^* \leq -\alpha^* m \|y\|^2.$$

As a consequence, setting

$$\Gamma(x) = \gamma(x) \frac{\alpha(x)}{\alpha^*},$$

we infer from (35) and the lower estimate of  $I_0$  around  $x_i$  given in Assumption 2.11 (ii), that for all  $t > T$

$$\int_{\|x_i - x\| \leq t^{-\frac{1}{2}}} I(t, dx) \geq M^{-1} \int_{|y| \leq t^{-\frac{1}{2}}} |y|^{\kappa_i} \exp[t\eta(t)\Gamma(x_i + y) - t\gamma(x_i + y)m|y|^2] dy.$$

Next since the function  $I = I(t, dx)$  has a bounded mass, there exists some constant  $C > 0$  such that

$$\int_{\mathbb{R}^N} I(t, dx) \leq C, \quad \forall t \geq 0.$$

Coupling the two above estimates yields for all  $t > T$

$$\int_{|y| \leq t^{-\frac{1}{2}}} |y|^{\kappa_i} \exp [t\eta(t)\Gamma(x_i + y) - t\gamma(x_i + y)m|y|^2] dy \leq MC.$$

Hence setting  $z = y\sqrt{t}$  into the above integral rewrites as

$$\int_{|z| \leq 1} t^{-\frac{\kappa_i}{2}} |z|^{\kappa_i} \exp [t\eta(t)\Gamma(x_i + t^{-\frac{1}{2}}z) - \gamma(x_i + t^{-\frac{1}{2}}z)m|z|^2] \frac{dz}{t^{N/2}} \leq MC, \forall t > T.$$

Now, since  $\gamma$  and  $\alpha$  are both smooth functions, we have uniformly for  $|z| \leq 1$  and  $t \gg 1$ :

$$\begin{aligned} \Gamma(x_i + t^{-\frac{1}{2}}z) &= \gamma(x_i) + O\left(t^{-\frac{1}{2}}\right), \\ \gamma(x_i + t^{-\frac{1}{2}}z) &= \gamma(x_i) + O\left(t^{-\frac{1}{2}}\right). \end{aligned}$$

This yields for all  $t \gg 1$

$$\begin{aligned} \int_{|z| \leq 1} t^{-\frac{\kappa_i}{2}} |z|^{\kappa_i} \exp [t\eta(t) \left( \gamma(x_i) + O\left(t^{-\frac{1}{2}}\right) \right) - \gamma(x_i)m|z|^2] \frac{dz}{t^{N/2}} &\leq CM, \\ t^{-\frac{\kappa_i}{2} - \frac{N}{2}} e^{t\eta(t) \left( \gamma(x_i) + O\left(t^{-\frac{1}{2}}\right) \right)} \int_{|z| \leq 1} |z|^{\kappa_i} e^{-\gamma(x_i)m|z|^2} dz &\leq CM, \end{aligned}$$

that also ensures the existence of some constant  $c_1 \in \mathbb{R}$  such that

$$t\eta(t) \left( \gamma(x_i) + O\left(t^{-\frac{1}{2}}\right) \right) - \frac{N + \kappa_i}{2} \ln t \leq c_1, \forall t \gg 1,$$

or equivalently

$$\eta(t) \leq \frac{N + \kappa_i}{2\gamma(x_i)} \frac{\ln t}{t} + O\left(\frac{1}{t}\right) \text{ as } t \rightarrow \infty.$$

Since the above upper-bound holds for all  $i = 1, \dots, p$ , we obtain the following upper-bound

$$\eta(t) \leq \varrho \frac{\ln t}{t} + O\left(\frac{1}{t}\right) \text{ as } t \rightarrow \infty, \quad (36)$$

where  $\varrho$  is defined in (18).

**Lower bound:**

Let  $\varepsilon_1 \in (0, \varepsilon_0)$  small enough be given such that for all  $i = 1, \dots, p$  and  $|y| \leq \varepsilon_1$  one has

$$\alpha(x_i + y) \leq \alpha^* - \frac{\ell}{2}|y|^2.$$

Herein  $\ell > 0$  is defined in Assumption 2.11 (iii). Next define  $m > 0$  by

$$m = \frac{\ell}{2} \min_{i=1, \dots, p} \min_{|y| \leq \varepsilon_1} \gamma(x_i + y) > 0.$$

Recall that  $\Gamma(x) = \frac{\alpha(x)\gamma(x)}{\alpha^*}$  and  $\nabla\Gamma(x) = \frac{1}{\alpha^*} (\alpha(x)\nabla\gamma(x) + \gamma(x)\nabla\alpha(x))$ . Consider  $M > 0$  such that for all  $k = 1, \dots, p$  and all  $|x - x_k| \leq \varepsilon_1$  one has

$$|\Gamma(x) - \gamma(x_k) - \nabla\gamma(x_k) \cdot (x - x_k)| \leq M|x - x_k|^2. \quad (37)$$

Next fix  $i = 1, \dots, p$  and  $\varepsilon \in (0, \varepsilon_1)$ . Then one has for all  $t > 0$

$$\begin{aligned} \int_{|x - x_i| \leq \varepsilon} I(t, dx) &\leq \int_{|x - x_i| \leq \varepsilon} \exp [t\eta(t)\Gamma(x) - tm|x - x_i|^2] I_0(dx) \\ &\leq e^{t\eta(t)\gamma(x_i)} \int_{|x - x_i| \leq \varepsilon} \exp [t(\eta(t)\nabla\gamma(x_i) \cdot (x - x_i) - (m + O(\eta(t))|x - x_i|^2))] I_0(dx). \end{aligned}$$

Now observe that for all  $t \gg 1$  one has

$$\eta(t)\nabla\gamma(x_k) \cdot (x - x_i) - (m + O(\eta(t)))|x - x_i|^2 = -(m + O(\eta(t))) \left| x - x_i - \frac{\eta(t)\nabla\gamma(x_i)}{2(m + O(\eta(t)))} \right|^2 + \frac{\eta(t)^2 \|\nabla\gamma(x_i)\|^2}{4(m + O(\eta(t)))},$$

so that we get, using Assumption 2.11 (ii), that

$$\begin{aligned} \int_{|x-x_i|\leq\varepsilon} I(t, dx) &\leq e^{t\eta(t)\gamma(x_i)+\frac{t\eta(t)^2\|\nabla\gamma(x_i)\|^2}{4(m+O(\eta(t)))}} \int_{|x-x_i|\leq\varepsilon} \exp\left[-(m+O(\eta(t)))t\left|x-x_i-\frac{\eta(t)\nabla\gamma(x_i)}{2(m+O(\eta(t)))}\right|^2\right] I_0(dx) \\ &\leq M e^{t\eta(t)\gamma(x_i)+\frac{t\eta(t)^2\|\nabla\gamma(x_i)\|^2}{4(m+O(\eta(t)))}} \\ &\quad \times \int_{|x-x_i|\leq\varepsilon} |x-x_i|^{\kappa_i} \exp\left[-(m+O(\eta(t)))t\left|x-x_i-\frac{\eta(t)\nabla\gamma(x_i)}{2(m+O(\eta(t)))}\right|^2\right] dx. \end{aligned}$$

We now make use of the following change of variables in the above integral

$$z = \sqrt{t}\left(x-x_i-\frac{\eta(t)\nabla\gamma(x_i)}{2(m+O(\eta(t)))}\right),$$

so that we end up with

$$\int_{|x-x_i|\leq\varepsilon} I(t, dx) \leq t^{-\frac{N+\kappa_i}{2}} e^{t\eta(t)\gamma(x_i)+\frac{t\eta(t)^2\|\nabla\gamma(x_i)\|^2}{4(m+O(\eta(t)))}} C(t),$$

with  $C(t)$  given by

$$C(t) := M \int_{|z|\leq\sqrt{t}(\varepsilon+O(\eta(t)))} |z+\sqrt{t}O(\eta(t))|^{\kappa_i} e^{-\frac{m+O(\eta(t))}{2}|z|^2} dz.$$

Now let us recall that Lemma 4.10 ensures that

$$\lim_{t\rightarrow\infty} t\eta(t) = \infty.$$

Hence one already knows that  $\eta(t) \geq 0$  for all  $t \gg 1$ . Moreover (36) ensures that

$$\lim_{t\rightarrow\infty} \sqrt{t}\eta(t) = 0,$$

so that Lebesgue convergence theorem ensures that

$$C(t) \rightarrow C_\infty := M \int_{\mathbb{R}^N} |z|^{\kappa_i} e^{-\frac{m}{2}|z|^2} dz \in (0, \infty) \text{ as } t \rightarrow \infty.$$

As a conclusion of the above analysis, we have obtained that there exists some constant  $C'$  such that for all  $\varepsilon \in (0, \varepsilon_1)$  and all  $i = 1, \dots, p$  one has

$$\int_{|x-x_i|\leq\varepsilon} I(t, dx) \leq C' t^{-\frac{N+\kappa_i}{2}} e^{t\eta(t)\gamma(x_i)}, \quad \forall t \gg 1. \quad (38)$$

Since  $I(t, dx)$  concentrates on  $\alpha^{-1}(\alpha^*)$ , then for all  $\varepsilon \in (0, \varepsilon_1)$  one has

$$\int_{\mathbb{R}^N} I(t, dx) = \sum_{i=1}^p \int_{|x-x_i|\leq\varepsilon} I(t, dx) + o(1) \text{ as } t \rightarrow \infty.$$

Using the persistence of  $I$  stated in Theorem 2.2 (see Lemma 4.1), we end-up with

$$0 < \liminf_{t\rightarrow\infty} \int_{\mathbb{R}^N} I(t, dx) \leq \liminf_{t\rightarrow\infty} \sum_{i=1}^p \int_{|x-x_i|\leq\varepsilon} I(t, dx),$$

so that (38) ensures that there exists  $c > 0$  and  $T > 0$  such that

$$0 < c \leq \sum_{i=1}^p e^{\gamma(x_i)\left(t\eta(t)-\frac{N+\kappa_i}{2\gamma(x_i)}\ln t\right)}, \quad \forall t \geq T. \quad (39)$$

Now recalling the definition of  $\varrho$  and  $J$  in (18) and (20), the upper bound for  $\eta(t)$  provided in (36) implies

$$\sum_{i \notin J} e^{\gamma(x_i)\left(t\eta(t)-\frac{N+\kappa_i}{2\gamma(x_i)}\ln t\right)} \rightarrow 0 \text{ as } t \rightarrow \infty,$$

and (39) rewrites as

$$0 < \frac{c}{2} \leq \sum_{i \in J} e^{\gamma(x_i)(t\eta(t) - \varrho \ln t)}, \quad \forall t \gg 1.$$

This yields

$$\liminf_{t \rightarrow \infty} (t\eta(t) - \varrho \ln t) > -\infty,$$

that is

$$\eta(t) \geq \varrho \frac{\ln t}{t} + O\left(\frac{1}{t}\right) \text{ as } t \rightarrow \infty. \quad (40)$$

Then (17) follows coupling (36) and (40).

**Estimate of the masses:** In this last step we turn to the proof of (19). Observe first that the upper estimate directly follows from the asymptotic expansion of  $\eta(t)$  in (17) together with (38). Next, the proof for the lower estimate follows from similar inequalities as the one derived in the second step above.  $\square$



# APPENDIX

## A Measure theory on metric spaces

In this Section we let  $(M, d)$  be a complete metric space. Let  $\mathcal{K}(M)$  be the set of compact subsets in  $M$  and let  $K \in \mathcal{K}(M)$ . We first recall that we can define a kind of frame of reference, internal to  $K$ , which allows to identify each point in  $K$ .

Let us denote  $\mathcal{K}(M)$  the set formed by all compact subsets of  $M$ . Recall that  $(\mathcal{K}(M), d_H)$  is a complete metric space, where  $d_H$  is the Hausdorff distance

$$d_H(K_1, K_2) = \max \left( \sup_{x \in K_1} d(x, K_2), \sup_{x \in K_2} d(x, K_1) \right).$$

**Proposition A.1** (Metric coordinates). *There exists a finite number of points  $x_1, \dots, x_n \in K$  with the property that each  $y \in K$  can be identified uniquely by the distance between  $y$  and  $x_1, \dots, x_n$ . In other words the map*

$$y \xrightarrow{c_K} \begin{pmatrix} d(y, x_1) \\ \vdots \\ d(y, x_n) \end{pmatrix} \in \mathbb{R}_+^n,$$

is one-to-one. Moreover  $c_K$  is continuous and its reciprocal function  $c_K^{-1} : c_K(K) \rightarrow K$  is also continuous.

*Proof.* Let us choose  $x_1 \in K$  and  $x_2 \in K$  such that  $x_1 \neq x_2$ . We recursively construct a sequence  $x_n$  and a compact set  $K_n$  such that

$$\begin{aligned} K_n &= \{y \in K : d(y, x_i) = d(y, x_1) \text{ for all } 1 \leq i \leq n\}, \\ x_{n+1} &\in K_n, \end{aligned}$$

the choice of  $x_{n+1}$  being arbitrary. Clearly  $K_n$  is a compact set and  $K_{n+1} \subsetneq K_n$ . Suppose by contradiction that  $K_n \neq \emptyset$  for all  $n \in \mathbb{N}$ , then (because  $K$  is compact) one can construct a sequence  $x_{\varphi(n)}$ , extracted from  $x_n$ , and which converges to a point

$$x = \lim_{n \rightarrow +\infty} x_{\varphi(n)} \in \bigcap_{n \in \mathbb{N}} K_n =: K_\infty.$$

In particular  $K_\infty$  is not empty. However we see that, by definition of  $K_\infty$ , we have  $d(x, x_n) = d(x, x_1) > 0$  for all  $n \in \mathbb{N}$ , which contradicts the fact that

$$\lim_{n \rightarrow +\infty} d(x, x_{\varphi(n)}) = 0.$$

Hence we have shown by contradiction that there exists  $n_0 \in \mathbb{N}$  such that  $K_{n_0} = \emptyset$  and  $K_{n_0-1} \neq \emptyset$ . This is precisely the injectivity of the map  $c_K : K \rightarrow \mathbb{R}^{n_0}$ .

To show the continuity, we remark that  $c_K$  is continuous, and therefore for each closed set  $F \subset K$ ,  $F$  is compact so that  $c_K(F)$  is compact and therefore closed. Therefore  $(c_K^{-1})^{-1}(F) = c_K(F)$  is closed in  $c_K(K)$ . The proposition is proved.  $\square$

Recall that the Borel  $\sigma$ -algebra  $\mathcal{B}(M)$  is the closure of the set of all open sets in  $\mathfrak{P}(M) = 2^M$  under the operations of complement and countable union. A function  $\varphi : M \rightarrow N$  is Borel measurable if the reciprocal image of any Borel set is Borel, *i.e.*  $\varphi^{-1}(B) \in \mathcal{B}(M)$  for all  $B \in \mathcal{B}(N)$ .

**Proposition A.2** (Borel function of choice). *There exists a Borel measurable map  $c : (\mathcal{K}(K), d_H) \rightarrow (K, d)$  such that*

$$c(K') \in K' \text{ for all } K' \in \mathcal{K}(K).$$

*Proof.* Let  $c_K : K \rightarrow \mathbb{R}^{n_0}$  be the map constructed in Proposition A.1. For a compact  $K' \subset K$  we define

$$c(K') := c_K^{-1} \left( \min_{y \in c_K(K')} y \right),$$

where the minimum is taken with respect to the lexicographical order in  $\mathbb{R}^{n_0}$  (which is a total order and therefore identifies a unique minimum for each  $K' \in \mathcal{K}(K)$ ). Since the map  $\tilde{K} \subset \mathbb{R}^{n_0} \rightarrow \min_{y \in \tilde{K}} y$  is Borel for the topology on  $\mathcal{K}(\mathbb{R}^{n_0})$  induced by the Hausdorff metric, so is  $c$ . The proposition is proved.  $\square$

**Proposition A.3** (Borel measurability of the metric projection). *Let  $K \subset M$  be compact. The map  $P_K : M \rightarrow \mathcal{K}(K)$  defined by*

$$P_K(x) = \{y \in K : d(x, y) = d(x, K)\},$$

*is Borel measurable.*

*Proof.* First we remark that the map

$$P_K(x) := \{y \in K : d(x, y) = d(x, K)\} \in \mathcal{K}(M),$$

is well-defined for each  $x \in M$ , and therefore forms a mapping from  $M$  into  $\mathcal{K}(K) \subset \mathcal{K}(M)$ . Indeed  $P_K(x)$  is clearly closed in the compact space  $K$ , therefore is compact.

To show the Borel measurability of  $P_K$ , we first remark that, given a compact space  $K' \subset K$ , the set

$$\widetilde{P_K^{-1}}(K') := \{x \in M : P_K(x) \cap K' \neq \emptyset\}$$

is closed. Indeed let  $x_n \rightarrow x$  be a sequence in  $\widetilde{P_K^{-1}}(K')$ , then by definition there exists  $y_n \in K'$  such that  $d(x_n, y_n) = d(x_n, K)$ . By the compactness of  $K'$ , there exists  $y \in K'$  and a subsequence  $y_{\varphi(n)}$  extracted from  $y_n$  such that  $y_{\varphi(n)} \rightarrow y$ . Because of the continuity of  $z \mapsto d(z, K)$ , we have

$$d(x, y) = \lim_{n \rightarrow +\infty} d(x_{\varphi(n)}, y_{\varphi(n)}) = \lim_{n \rightarrow +\infty} d(x_{\varphi(n)}, K) = d(x, K),$$

therefore  $y \in P_K(x) \cap K'$ , which shows that  $x \in \widetilde{P_K^{-1}}(K')$ . Hence  $\widetilde{P_K^{-1}}(K')$  is closed.

We are now in a position to show the Borel regularity of  $P_K$ . Let  $C \in \mathcal{K}(K)$  and  $R > 0$  be given. We defined  $B_H(C, R)$  the ball of center  $C$  and radius  $R$  in the Hausdorff metric:

$$B_H(C, R) = \{C' \in \mathcal{K}(K) : d_H(C, C') \leq R\}.$$

Then

$$P_K^{-1}(B_H(C, R)) = \{x \in M : d_H(P_K(x), C) \leq R\} = B_1 \cap B_2,$$

where

$$\begin{aligned} B_1 &:= \{x \in M : d(y, C) \leq R \text{ for all } y \in P_K(x)\}, \text{ and} \\ B_2 &:= \{x \in M : d(z, P_K(x)) \leq R \text{ for all } z \in C\}. \end{aligned}$$

It can be readily seen that  $B_1$  is a Borel set by writing

$$B_1 = \widetilde{P_K^{-1}}(V_R(C)) \cap \bigcap_{n \geq 1} \left( M \setminus \left( \widetilde{P_K^{-1}}(K \setminus V_{R+\frac{1}{n}}(C)) \right) \right),$$

where  $V_R(C) := \{y \in K : d(y, C) \leq R\}$ . To see that  $B_2$  is a Borel set, we choose a sequence  $z_n$  which is dense in  $C$  and write

$$B_2 = \bigcap_{k \geq 1} \bigcap_{n \geq 1} \widetilde{P_K^{-1}}(B(z_n, R + 1/k)).$$

Indeed if  $x \in B_2$  then  $P_K(x)$  intersects every ball of radius  $R$  and center  $z \in C$ ; in particular  $P_K(x)$  intersects every ball of radius  $R + 1/k$  and center  $z_n$ . Conversely suppose that  $P_K(x)$  intersects every ball  $B(z_n, R + 1/k)$  for  $n \geq 1$  and  $k \geq 1$ . If  $z \in C$  then there is a sequence  $z_{\varphi(k)}$  such that  $z = \lim z_{\varphi(k)}$ , and (by assumption) we have  $P_K(x) \cap B(z_{\varphi(k)}, R + 1/k) \neq \emptyset$ . Therefore

$$d(z, P_K(x)) = \lim_{k \rightarrow +\infty} d(z_{\varphi(k)}, P_K(x)) \leq \lim_{k \rightarrow +\infty} R + \frac{1}{k} = R.$$

Thus  $x \in B_2$ . The equality is proved.

We conclude that  $P_K^{-1}(B_H(C, R))$  is a Borel set for all  $C \in \mathcal{K}(K)$  and  $R > 0$ , and since those sets form a basis of the Borel  $\sigma$ -algebra,  $P_K$  is indeed Borel measurable. The Lemma is proved.  $\square$

**Theorem A.4** (Existence of a regular metric projection). *Let  $K \subset M$  be compact. There exists a Borel measurable map  $P_K : M \rightarrow K$  such that*

$$d(x, P_K(x)) = d(x, K).$$

*Proof.* The proof is immediate by combining Proposition A.3 Proposition A.2.  $\square$

**Proposition A.5** (Metric projection on measure spaces). *Let  $K \in \mathcal{K}(\mathbb{R}^N)$  be a given compact set. Let  $\mu \in \mathcal{M}_+(K)$  be a given nonnegative measure on  $K$ . Then the Kantorovich-Rubinstein distance between  $\mu$  and  $\mathcal{M}_+(K)$  can be bounded by the distance between  $K$  and the furthest point in  $\text{supp } \mu$ :*

$$d_0(\mu, \mathcal{M}_+(K)) \leq \|\mu\|_{AV} \sup_{x \in \text{supp } \mu} d(x, K).$$

*Proof.* Indeed, let us choose a Borel measurable metric projection  $P_K$  on  $K$  as in Theorem A.4. Let  $\mu^K$  be the image measure defined on  $\mathcal{B}(K)$  by

$$\mu^K(B) := \mu(P_K^{-1}(B)), \text{ for all } B \in \mathcal{B}(K).$$

Then in particular for all  $f \in BC(\mathbb{R}^N)$  we have

$$\int_{\mathbb{R}^N} f(P_K(x)) d\mu(x) = \int_K f(x) d\mu^K(x).$$

Let  $f \in \text{Lip}_1(\mathbb{R}^N)$ , then we have

$$\begin{aligned} \int_{\mathbb{R}^N} f(x) d(\mu - \mu^K)(x) &= \int_{\mathbb{R}^N} f(x) d\mu(x) - \int_{\mathbb{R}^N} f(x) d\mu^K(x) \\ &= \int_{\mathbb{R}^N} f(x) d\mu(x) - \int_{\mathbb{R}^N} f(P_K(x)) d\mu(x) \\ &= \int_{\mathbb{R}^N} f(x) - f(P_K(x)) d\mu(x) \\ &\leq \int_{\text{supp } \mu} |x - P_K(x)| d\mu(x) \\ &\leq \sup_{y \in \text{supp } \mu} d(y, K) \int_{\text{supp } \mu} 1 d\mu = \|\mu\|_{AV} \sup_{x \in \text{supp } K} d(x, K). \end{aligned}$$

Therefore  $d_0(\mu, \mu^K) \leq \|\mu\|_{AV} \sup_{x \in \text{supp } K} d(x, K)$  and, since  $\mu^K \in \mathcal{M}_+(K)$ ,

$$d_0(\mu, \mathcal{M}_+(K)) \leq d_0(\mu, \mu^K) \leq \|\mu\|_{AV} \sup_{x \in \text{supp } \mu} d(x, K).$$

The Proposition is proved. □

## B Disintegration of measures

We recall the disintegration theorem as stated in [8, VI, §3, Theorem 1 p. 418]. We use Bourbaki's version, which is proved by functional analytic arguments, for convenience, although other approaches exist which are based on measure-theoretic arguments and may be deemed more intuitive. We refer to Ionescu Tulcea and Ionescu Tulcea for a disintegration theorem resulting from the theory of (strong) liftings [25, 26].

Let us first we recall some background on adequate families. This is adapted from [8, V.16 §3] to the context of finite measures of  $\mathbb{R}^N$ . We let  $T$  and  $X$  be locally compact topological spaces and  $\mu \in \mathcal{M}_+(T)$  be a fixed Borel measure.

**Definition B.1** (Scalarly essentially integrable family). Let  $\Lambda : t \mapsto \lambda_t$  be a mapping from  $T$  into  $\mathcal{M}_+(X)$ .  $\Lambda$  is *scalarly essentially integrable* for the measure  $\mu$  if for every compactly supported continuous function  $f \in C_c(X)$ , the function  $t \mapsto \int_X f(x) \lambda_t(dx)$  is in  $L^1(\mu)$ . Setting  $\nu(f) = \int_T \int_X f(x) \lambda_t(dx) \mu(dt)$  defines a linear form on  $C_c(X)$ , hence a measure  $\nu$ , which is the *integral* of the family  $\Lambda$ , and we denote

$$\int_T \lambda_t \mu(dt) := \nu.$$

Recall that every positive Borel measure  $\mu$  on a locally compact space  $X$  defines a positive bounded linear functional on  $C_c(X)$  equipped with the inductive limit of the topologies on  $C_c(K)$  when  $K$  runs over the compact subsets of  $X$ . Conversely if  $\mu$  is a positive bounded linear functional on  $C_c(X)$ , there are two canonical ways to define a measure on the Borel  $\sigma$ -algebra.

1. Outer-regular construction. Let  $U \subset X$  be a open, then one can define

$$\mu^*(U) := \sup \{ \mu(f) : f \in C_c(X), 0 \leq f(x) \leq \mathbb{1}_U(x) \},$$

then for an arbitrary Borel set  $B$ ,

$$\mu^*(B) := \inf \{ \mu^*(U) : U \text{ open}, B \subset U \}.$$

This notion corresponds to that of the *upper integral* discussed in [8, IV.1 §1].

2. Inner-regular construction. If  $U \subset X$  is open, we define  $\mu^\bullet(U) := \mu^*(U)$  and similarly if  $K \subset X$  is compact, then  $\mu^\bullet(K) := \mu^*(K)$ . Then for an arbitrary Borel set  $B$  which is contained in an open set of finite measure:  $B \subset U$  with  $\mu^\bullet(U) < +\infty$ , we define

$$\mu^\bullet(B) := \sup\{\mu^\bullet(K) : K \text{ compact, } K \subset B\}.$$

Else  $\mu^\bullet(B) = +\infty$ . This corresponds to the *essential upper integral* discussed in [8, V.1, §1].

It is always true that  $\mu^\bullet \leq \mu^*$ , however it may happen that  $\mu^* \neq \mu^\bullet$  when  $\mu^*$  is not finite, see e.g. [6, II§7.11 p.113] or [8, V.1, §1]. If  $\mu$  is a Borel measure, then we define the corresponding notions of  $\mu^\bullet$  and  $\mu^*$  associated with the linear functional  $f \mapsto \int_X f(x)\mu(dx)$ . Note that if  $\mu$  is Radon, then  $\mu^* = \mu = \mu^\bullet$ .

**Definition B.2** (Pre-adequate and adequate families). We follow [8, Definition 1, V.17§3]. Let  $\Lambda : t \mapsto \lambda_t$  be a scalarly essentially  $\mu$ -integrable mapping from  $T$  into  $\mathcal{M}_+(X)$ ,  $\nu$  the integral of  $\Lambda$ .

We say that  $\Lambda$  is  $\mu$ -pre-adequate if, for every lower semi-continuous function  $f \geq 0$  defined on  $X$ , the function  $t \mapsto \int f(x)\lambda_t^\bullet(dx)$  is  $\mu$ -measurable on  $T$  and

$$\int_X f(x)\nu^\bullet(dx) = \int_T \int_X f(x)\lambda_t^\bullet(dx)\mu^\bullet(dt).$$

We say that  $\Lambda$  is  $\mu$ -adequate if  $\Lambda$  is  $\mu'$ -pre-adequate for every positive Borel measure  $\mu' \leq \mu$ .

The last notion we need to define is the one of  $\mu$ -proper function.

**Definition B.3** ( $\mu$ -proper function). We say that a function  $p : T \rightarrow X$  is  $\mu$ -proper if it is  $\mu$ -measurable and, for every compact set  $K \subset X$ , the set  $p^{-1}(K)$  is  $\mu^\bullet$ -measurable and  $\mu^\bullet(p^{-1}(K)) < +\infty$ .

If  $\mu$  is Radon, in particular, then every  $\mu$ -measurable mapping  $p : T \rightarrow X$  ( $X$  being equipped with the Borel  $\sigma$ -algebra) is  $\mu$ -proper. The following Theorem is taken from [8, Theorem 1, VI.41 No.1, §3].

**Theorem B.4** (Disintegration of measures). *Let  $T$  and  $X$  be two locally compact spaces having countable bases,  $\mu$  be a positive measure on  $T$ ,  $p$  be a  $\mu$ -proper mapping of  $T$  into  $X$ , and  $\nu = p(\mu)$  the image of  $\mu$  under  $p$ . There exists a  $\nu$ -adequate family  $x \mapsto \lambda_x$  ( $x \in X$ ) of positive measures on  $T$ , having the following properties:*

- a)  $\|\lambda_x\| = 1$  for all  $x \in p(T)$ ;
- b)  $\lambda_x$  is concentrated on the set  $p^{-1}(\{x\})$  for all  $x \in p(T)$ , and  $\lambda_x = 0$  for  $x \notin p(T)$ ;
- c)  $\mu = \int \lambda_x \nu(dx)$ .

Moreover, if  $x \mapsto \lambda'_x$  ( $x \in X$ ) is a second  $\nu$ -adequate family of positive measures on  $T$  having the properties b) and c), then  $\lambda'_x = \lambda_x$  almost everywhere in  $B$  with respect to the measure  $\nu$ .

## References

- [1] A. S. Ackleh and L. J. S. Allen. Competitive exclusion and coexistence for pathogens in an epidemic model with variable population size. *J. Math. Biol.* **47.2** (2003), pp. 153–168. DOI: 10.1007/s00285-003-0207-9.
- [2] A. S. Ackleh, J. Cleveland, and H. R. Thieme. Population dynamics under selection and mutation: long-time behavior for differential equations in measure spaces. *J. Differential Equations* **261.2** (2016), pp. 1472–1505. DOI: 10.1016/j.jde.2016.04.008.
- [3] R. A. Armstrong and R. McGehee. Competitive exclusion. *Amer. Natur.* **115.2** (1980), pp. 151–170. DOI: 10.1086/283553.
- [4] G. Barles, S. Mirrahimi, and B. Perthame. Concentration in Lotka-Volterra parabolic or integral equations: a general convergence result. *Methods Appl. Anal.* **16.3** (2009), pp. 321–340. DOI: 10.4310/MAA.2009.v16.n3.a4.
- [5] G. Barles and B. Perthame. Concentrations and constrained Hamilton-Jacobi equations arising in adaptive dynamics. In: *Recent developments in nonlinear partial differential equations*. Vol. 439. Contemp. Math. Amer. Math. Soc., Providence, RI, 2007, pp. 57–68. DOI: 10.1090/conm/439/08463.
- [6] V. I. Bogachev. *Measure theory. Vol. I, II*. Springer-Verlag, Berlin, 2007, Vol. I: xviii+500 pp., Vol. II: xiv+575. DOI: 10.1007/978-3-540-34514-5.
- [7] E. Bouin et al. Invasion fronts with variable motility: phenotype selection, spatial sorting and wave acceleration. *C. R. Math. Acad. Sci. Paris* **350.15-16** (2012), pp. 761–766. DOI: 10.1016/j.crma.2012.09.010.

- [8] N. Bourbaki. *Elements of Mathematics. Integration I*. Springer, Berlin, Heidelberg, 2004. DOI: 10.1007/978-3-642-59312-3.
- [9] H.-J. Bremermann and H. R. Thieme. A competitive exclusion principle for pathogen virulence. *J. Math. Biol.* **27.2** (1989), pp. 179–190. DOI: 10.1007/BF00276102.
- [10] J.-B. Burie, R. Djidjou-Demasse, and A. Ducrot. Asymptotic and transient behaviour for a nonlocal problem arising in population genetics. *European J. Appl. Math.* **31.1** (2020), pp. 84–110. DOI: 10.1017/s0956792518000487.
- [11] J.-B. Burie, R. Djidjou-Demasse, and A. Ducrot. Slow convergence to equilibrium for an evolutionary epidemiology integro-differential system. *Discrete Contin. Dyn. Syst. Ser. B* **25.6** (2020), pp. 2223–2243. DOI: 10.3934/dcdsb.2019225.
- [12] J.-B. Burie, A. Ducrot, Q. Griette, and Q. Richard. Concentration estimates in a multi-host epidemiological model structured by phenotypic traits. *J. Differential Equations* **269.12** (2020), pp. 11492–11539. DOI: 10.1016/j.jde.2020.08.029.
- [13] G. J. Butler and G. S. K. Wolkowicz. A mathematical model of the chemostat with a general class of functions describing nutrient uptake. *SIAM J. Appl. Math.* **45.1** (1985), pp. 138–151. DOI: 10.1137/0145006.
- [14] J. M. Cushing. Two species competition in a periodic environment. *J. Math. Biol.* **10.4** (1980), pp. 385–400. DOI: 10.1007/BF00276097.
- [15] T. Day and S. Gandon. Applying population-genetic models in theoretical evolutionary epidemiology. *Ecology Letters* **10.10** (2007), pp. 876–888. DOI: 10.1111/j.1461-0248.2007.01091.x.
- [16] L. Desvillettes, P.-E. Jabin, S. Mischler, and G. Raoul. On selection dynamics for continuous structured populations. *Commun. Math. Sci.* **6.3** (2008), pp. 729–747.
- [17] R. Djidjou-Demasse, A. Ducrot, and F. Fabre. Steady state concentration for a phenotypic structured problem modeling the evolutionary epidemiology of spore producing pathogens. *Math. Models Methods Appl. Sci.* **27.2** (2017), pp. 385–426. DOI: 10.1142/S0218202517500051.
- [18] F. Fabre et al. An epi-evolutionary model to predict spore-producing pathogens adaptation to quantitative resistance in heterogeneous environments. *bioRxiv* (2021). DOI: 10.1101/423467.
- [19] H. Federer. *Geometric measure theory*. Die Grundlehren der mathematischen Wissenschaften, Band 153. Springer-Verlag New York Inc., New York, 1969, pp. xiv+676. DOI: 10.1007/978-3-642-62010-2.
- [20] Q. Griette. Singular measure traveling waves in an epidemiological model with continuous phenotypes. *Trans. Amer. Math. Soc.* **371.6** (2019), pp. 4411–4458. DOI: 10.1090/tran/7700.
- [21] G. Hardin. The competitive exclusion principle. *Science* **131.3409** (1960), pp. 1292–1297.
- [22] S. B. Hsu, H. L. Smith, and P. Waltman. Competitive exclusion and coexistence for competitive systems on ordered Banach spaces. *Trans. Amer. Math. Soc.* **348.10** (1996), pp. 4083–4094. DOI: 10.1090/S0002-9947-96-01724-2.
- [23] S.-B. Hsu. Limiting behavior for competing species. *SIAM J. Appl. Math.* **34.4** (1978), pp. 760–763. DOI: 10.1137/0134064.
- [24] S.-B. Hsu, S. Hubbell, and P. Waltman. A mathematical theory for single-nutrient competition in continuous cultures of micro-organisms. *SIAM J. Appl. Math.* **32.2** (1977), pp. 366–383. DOI: 10.1137/0132030.
- [25] A. Ionescu Tulcea and C. Ionescu Tulcea. On the lifting property. IV. Disintegration of measures. *Ann. Inst. Fourier (Grenoble)* **14.fasc. 2** (1964), pp. 445–472. DOI: 10.5802/aif.182.
- [26] A. Ionescu Tulcea and C. Ionescu Tulcea. *Topics in the theory of lifting*. Ergebnisse der Mathematik und ihrer Grenzgebiete, Band 48. Springer-Verlag New York Inc., New York, 1969, pp. x+190. DOI: 10.1007/978-3-642-88507-5.
- [27] P.-E. Jabin and G. Raoul. On selection dynamics for competitive interactions. *J. Math. Biol.* **63.3** (2011), pp. 493–517. DOI: 10.1007/s00285-010-0370-8.
- [28] A. Korobeinikov. Lyapunov functions and global stability for SIR and SIRS epidemiological models with non-linear transmission. *Bull. Math. Biol.* **68.3** (2006), pp. 615–626. DOI: 10.1007/s11538-005-9037-9.
- [29] A. Korobeinikov. Global properties of infectious disease models with nonlinear incidence. *Bull. Math. Biol.* **69.6** (2007), pp. 1871–1886. DOI: 10.1007/s11538-007-9196-y.
- [30] A. Korobeinikov. Global properties of SIR and SEIR epidemic models with multiple parallel infectious stages. *Bull. Math. Biol.* **71.1** (2009), pp. 75–83. DOI: 10.1007/s11538-008-9352-z.

- [31] A. Korobeinikov and P. K. Maini. A Lyapunov function and global properties for SIR and SEIR epidemiological models with nonlinear incidence. *Math. Biosci. Eng.* **1.1** (2004), pp. 57–60. DOI: 10.3934/mbe.2004.1.57.
- [32] A. Korobeinikov and G. C. Wake. Lyapunov functions and global stability for SIR, SIRS, and SIS epidemiological models. *Appl. Math. Lett.* **15.8** (2002), pp. 955–960. DOI: 10.1016/S0893-9659(02)00069-1.
- [33] B. Li. Global asymptotic behavior of the chemostat: general response functions and different removal rates. *SIAM J. Appl. Math.* **59.2** (1999), pp. 411–422. DOI: 10.1137/S003613999631100X.
- [34] G Lo Iacono, F van den Bosch, and N Paveley. The evolution of plant pathogens in response to host resistance: factors affecting the gain from deployment of qualitative and quantitative resistance. *J. Theoret. Biol.* **304** (2012), pp. 152–163. DOI: 10.1016/j.jtbi.2012.03.033.
- [35] T. Lorenzi and C. Pouchol. Asymptotic analysis of selection-mutation models in the presence of multiple fitness peaks. *Nonlinearity* **33.11** (2020), pp. 5791–5816. DOI: 10.1088/1361-6544/ab9bad.
- [36] A. Lorz and B. Perthame. Long-term behaviour of phenotypically structured models. *Proc. R. Soc. Lond. Ser. A Math. Phys. Eng. Sci.* **470.2167** (2014), pp. 20140089, 10. DOI: 10.1098/rspa.2014.0089.
- [37] A. Lorz, B. Perthame, and C. Taing. Dirac concentrations in a chemostat model of adaptive evolution. *Chin. Ann. Math. Ser. B* **38.2** (2017), pp. 513–538. DOI: 10.1007/s11401-017-1081-x.
- [38] P. Magal. Mutation and recombination in a model of phenotype evolution. *J. Evol. Equ.* **2.1** (2002), pp. 21–39. DOI: 10.1007/s00028-002-8078-x.
- [39] P. Magal and G. F. Webb. Mutation, selection, and recombination in a model of phenotype evolution. *Discrete Contin. Dynam. Systems* **6.1** (2000), pp. 221–236. DOI: 10.3934/dcds.2000.6.221.
- [40] P. Magal and X.-Q. Zhao. Global attractors and steady states for uniformly persistent dynamical systems. *SIAM J. Math. Anal.* **37.1** (2005), pp. 251–275. DOI: 10.1137/S0036141003439173.
- [41] C. C. McCluskey. Lyapunov functions for tuberculosis models with fast and slow progression. *Math. Biosci. Eng.* **3.4** (2006), pp. 603–614. DOI: 10.3934/mbe.2006.3.603.
- [42] C. C. McCluskey. Global stability for a class of mass action systems allowing for latency in tuberculosis. *J. Math. Anal. Appl.* **338.1** (2008), pp. 518–535. DOI: 10.1016/j.jmaa.2007.05.012.
- [43] G. Raoul. Long time evolution of populations under selection and vanishing mutations. *Acta Appl. Math.* **114.1-2** (2011), pp. 1–14. DOI: 10.1007/s10440-011-9603-0.
- [44] G. Raoul. Local stability of evolutionary attractors for continuous structured populations. *Monatsh. Math.* **165.1** (2012), pp. 117–144. DOI: 10.1007/s00605-011-0354-9.
- [45] A. Rapaport and M. Veruete. A new proof of the competitive exclusion principle in the chemostat. *Discrete Contin. Dyn. Syst. Ser. B* **24.8** (2019), pp. 3755–3764. DOI: 10.3934/dcdsb.2018314.
- [46] H. L. Smith. Competitive coexistence in an oscillating chemostat. *SIAM J. Appl. Math.* **40.3** (1981), pp. 498–522. DOI: 10.1137/0140042.
- [47] H. L. Smith and H. R. Thieme. Chemostats and epidemics: competition for nutrients/hosts. *Math. Biosci. Eng.* **10.5-6** (2013), pp. 1635–1650. DOI: 10.3934/mbe.2013.10.1635.
- [48] H. L. Smith and P. Waltman. *The theory of the chemostat*. Vol. 13. Cambridge Studies in Mathematical Biology. Dynamics of microbial competition. Cambridge University Press, Cambridge, 1995, pp. xvi+313. DOI: 10.1017/CB09780511530043.
- [49] G. S. K. Wolkowicz and Z. Q. Lu. Global dynamics of a mathematical model of competition in the chemostat: general response functions and differential death rates. *SIAM J. Appl. Math.* **52.1** (1992), pp. 222–233. DOI: 10.1137/0152012.
- [50] G. S. K. Wolkowicz and H. Xia. Global asymptotic behavior of a chemostat model with discrete delays. *SIAM J. Appl. Math.* **57.4** (1997), pp. 1019–1043. DOI: 10.1137/S0036139995287314.