

Epidemic models in measure spaces: persistence, concentration and oscillations

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Abstract

We investigate the long-time dynamics of a SIR epidemic model in the case of a population of pathogens infecting a homogeneous host population. The pathogen population is structured by a genotypic variable. 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. Finally, we provide an example of a pathological situation in which the distribution never reaches a stationary distribution but oscillates forever around the set of fitness maxima.

1 Introduction

In this article we investigate the large time behavior of the SIR epidemic model

$$\begin{cases} S_t(t) = \Lambda - \theta S(t) - S(t) \int_X \beta(x) I(t, dx), \\ I_t(t, dx) = \beta(x) S(t) I(t, dx) - \gamma(x) I(t, dx), \\ R_t(t) = \int_X \gamma(x) I(t, dx), \end{cases} \quad (1.1a)$$

with the initial data

$$S(0) = S_0 \in (0, +\infty), \quad I(0, dx) = I_0(dx) \in \mathcal{M}_+(X), \quad R(0) = R_0 \in (0, +\infty), \quad (1.1b)$$

where X is a Polish space and $\mathcal{M}_+(X)$ is the set of nonnegative Borel measures on X .

This model describes the evolution of a population of hosts that can be, at any time $t > 0$, either free of infection ($S(t)$, the susceptible population), infected by a pathogen of type $x \in X$ ($I(t, dx)$, the infected population of type x) or removed from the system ($R(t)$, the recovered population), the latter class including two possible outcomes of the infection, complete immunity or death. The parameter $\Lambda > 0$ models a constant influx of susceptible hosts, $\theta > 0$ the death rate of the hosts in the absence of infection, $\beta(x)$ the transmission parameter of the pathogen of type x , and $\gamma(x)$ the recovery rate of a pathogen of type x . Both $\beta(x)$ and $\gamma(x)$ are bounded continuous functions. SIR models are ubiquitous in the literature concerning mathematical epidemiology and have been extensively studied. Without the pretention of reconstructing the entire history of the model, let us cite the works of Kermack and McKendrick [29] that might well be its first occurrence in the literature, and was immediately applied to a plague outbreak in the island of Bombay.

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In this article we consider that the phenotype of the pathogen (that is, the values of $\beta(x)$ and $\gamma(x)$) depends on an underlying variable $x \in X$, where X is a set of attainable values that possesses a few mathematical properties. This variable x may be a collection of quantitative phenotypic traits involved the mechanism of transmission, reproduction or replication of the pathogen (expression of surface protein at the cellular or viral level, impact on the host's behavior, ...) or the underlying genes that determine the values of $\beta(x)$ and $\gamma(x)$. We do not specify the particular mechanisms that link the underlying variable $x \in X$ and the phenotype $(\beta(x), \gamma(x))$ but focus on the dynamics of the population under (1.1) conditionally to the knowledge of these mechanisms. By analogy, because it stands for a hidden process that determines an observable quantity, x will be called the *genotypic variable*, even if it could well stand for hidden quantitative phenotypic variables. We do not take mutations into account and consider that the pathogen is asexual; therefore, (1.1) can be considered a pure competition model where the pathogens compete for a single resource (the susceptible hosts).

When $I_0(dx)$ is a finite collection of Dirac masses,

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

our problem is reduced to a system of ordinary differential equations,

$$\begin{cases} \frac{d}{dt} S(t) = \Lambda - \theta S(t) - S(t)(\beta_1 I^1(t) + \beta_2 I^2(t) + \dots + \beta_n I^n(t)) \\ \frac{d}{dt} I^1(t) = \beta_1 S(t) I^1(t) - \gamma_1 I^1(t) \\ \vdots \\ \frac{d}{dt} I^n(t) = \beta_n S(t) I^n(t) - \gamma_n I^n(t), \end{cases} \quad (1.2a)$$

with the initial data

$$S(0) = S_0 \in (0, +\infty), \quad I^1(0) = I_0^1 \in (0, +\infty), \quad \dots, \quad I^n(0) = I_0^n \in (0, +\infty), \quad (1.2b)$$

where $\beta_i = \beta(x_i)$, $\gamma_i = \gamma(x_i)$ and $I(t, dx) = \sum_{i=1}^n I^i(t) \delta_{x_i}(dx)$. In this context, Hsu [24] and Hsu, Hubbell, and Waltman [25] showed for closely related systems of ordinary differential equations that the solution eventually converges to an equilibrium which may not be unique but is always concentrated on the equations that maximize the fitness β_i/γ_i . One of the objectives of the current article is to establish an equivalent result in the context of measure-valued initial conditions that are not necessarily finite sums of Dirac masses (this will be given by Theorem 2.2).

In a recent work [10] we clarified the asymptotic behavior of an extension of (1.2) in the case of an infinite number of equations. This discrete setting is a particular case of the results that we present here, and we provide a number of illuminating examples that give a glimpse of the diversity of different behaviors that can be expected for solutions to (1.1). In particular, we show that, when the assumptions of Proposition 2.7 are not satisfied, it is possible to construct exotic initial data for which the total mass of pathogen $\int_X I(t, dx)$ does not converge to a limit but oscillates between distinct values. We refer to [10] for details.

The problem of several species competing for a single resource has received a lot of attention in the literature. 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 [22]. 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 [24] and Hsu, Hubbell, and Waltman [25] followed by Armstrong and McGehee [2], Butler and Wolkowicz [12], Hsu, Smith, and Waltman [23], Li [30], Rapaport and Veruete [39], Wolkowicz and Lu [41], and Wolkowicz and Xia [42], to cite a few – and also disproved in other contexts, for instance in fluctuating environments, see Cushing [13] and Smith [40]. 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.

In our model, the fitness of a pathogen with genotype x is given by the formula $\mathcal{R}_0(x) = \frac{\Lambda \beta(x)}{\theta \gamma(x)} = \frac{\Lambda}{\theta} \alpha(x)$, where $\alpha(x) := \frac{\beta(x)}{\gamma(x)}$; the competitive exclusion principle implies that the only genotypes that eventually remain are the ones that maximize $\mathcal{R}_0(x)$. When $\mathcal{R}_0(x)$ has a unique maximum then it is clear that $I(t, x)$ converges to a Dirac distribution concentrated at the maximum. But if $\mathcal{R}_0(x)$ attains its maximum at a more complex set – from two isolated maxima to an entire line segment – then the eventual weight of each fitness maximum in the population is less clear. We will give a partial description of this distribution here, that depends on the initial repartition of infected as well as the repartition of the phenotypic value $\gamma(x)$ in the vicinity of the set of fitness maxima. 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 genotypic value but several 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 method 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 Day and Gandon [14], it has been observed that a strain 1 with a higher value of γ and a slightly lower $\mathcal{R}_0$ value than a strain 2 may nevertheless be dominant for some time (we reproduce such a behavior numerically in Figure 5). These borderline cases shed light on our understanding of the transient dynamics, see also Burie, Djidjou-Demasse, and Ducrot [8] where we explicit transient dynamics for a related evolutionary model depending on the local flatness of the fitness function.

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 [3, 4, 6, 16, 18, 21, 28, 33–36, 38]. In this context, and this has been remarked before [16, 32], concentration on the maximum level set of the fitness function $\mathcal{R}_0(x)$ means that the classical mathematical framework of functions is not sufficient to describe accurately the dynamics of the solutions to (1.1). In this article, we will therefore extend our analysis to the case of Radon measures. Note that it is also natural to consider measures as initial data in epidemic models with an age of infection structure to model cohorts of patients, see Demongeot et al. [15].

When $X = \mathbb{R}^N$, System (1.1) arises naturally as the limit of a mutation-selection model of spore-producing pathogen proposed by [31] and studied mathematically by Burie, Djidjou-Demasse, and Ducrot [8, 9], Burie et al. [11], Djidjou-Demasse, Ducrot, and Fabre [17], and Fabre et al. [19] when the dynamics of the spores is very fast. The system (1.1) corresponds to the case of no mutations at all or, equivalently, the case of a fully concentrated kernel (equal to a Dirac mass at 0).

Despite our efforts, we were unable to find a precise description of the behavior of the solutions of (1.1) in the literature when the initial condition $I_0(dx)$ is a Radon measure. Here we remark that the vector field of (1.1) is locally Lipschitz continuous in the space $\mathbb{R} \times \mathcal{M}_+(X) \times \mathbb{R}$ (when $\mathcal{M}(X)$ is equipped with the total variation norm), so the existence of solutions is not the main difficulty. The solution $I(t, dx)$ can be written as

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

so the solution is always a bounded continuous function multiplied by the initial data $I_0(x)$ at any finite time $t > 0$. But to describe what happens as $t \rightarrow +\infty$ is not at all trivial. In Theorem 2.2, we distinguish two typical situations. When there is a positive initial mass on the set of maximal fitness ($\int_{\alpha(x)=\alpha^*} I_0(dx) > 0$, where $\alpha^* = \sup_{x \in \text{supp } I_0} \alpha(x)$) and we recall that $\alpha(x) = \beta(x)/\gamma(x)$, then we can show that the distribution of pathogens converges to a stationary distribution that we can compute explicitly. This is done with the help of a Lyapunov function that is essentially the same as the one used by Hsu [24]. This is point i) of Theorem 2.2. The case when there is no initial mass on the set of maximal fitness ($\int_{\alpha(x)=\alpha^*} I_0(dx) = 0$) is less clear. We compactify the orbits by using the weak-* topology of measures and use this compactness to show the uniform persistence of the population thanks to a general argument from Magal and Zhao [37]. Then we show that the population on the sets of high fitness always grows faster than the one on sets of low fitness, and this allows us to control uniformly the Kantorovitch-Rubinstein distance between the solution $I(t, dx)$ and the space of measures that are concentrated on the set of maximal fitness, $\mathcal{M}_+(\{\alpha(x) = \alpha^*\})$. Thus in this case also we can prove that the solution eventually concentrates on the set that maximizes the fitness. This is point ii) of Theorem 2.2.

In general, it is not true that the distribution $I(t, dx)$ eventually reaches a stationary distribution. We construct a counterexample in Section 2.3. By carefully choosing the initial data and the fitness function $\alpha(x) = \beta(x)/\gamma(x)$, we construct a solution of (1.1) with $I(t, dx dy)$ that approaches the unit circle of $\mathbb{R}^2$ but never stops turning around it. This fact is illustrated numerically in Section 3.3. We prove in Claim 2.14 that the ω -limit set of the integral of $I(t, dx dy)$ on the upper-half plane, $\int_{\mathbb{R} \times \mathbb{R}^+} I(t, dx dy)$, contains at least two values, therefore $I(t, dx dy)$ does not converge to a stationary distribution. We also refer to [10] where we construct an exemple in a discrete setting where the total mass $\int_X I(t, dx)$ does not converge to a single value but oscillates between several values.

With some additional assumption we improve the description of the asymptotic behavior of $I(t, dx)$ compared to Theorem 2.2 in case ii). In Assumption 2.5 we impose a condition on the disintegration of $I_0(dx)$ with respect to $\alpha(x)$ to impose that the distribution of $I_0(dx)$ is uniformly positive around the maximum of $\gamma(x)$, $\gamma^* := \sup_{\alpha(x)=\alpha^*} \gamma(x)$. Under this assumption, in Proposition 2.7, we refine the localization of the asymptotic concentration set of $I(t, dx)$ and we prove that the total mass of $I(t, dx)$, $\int_X I(t, dx)$, converges to a limit value. We also focus on the special case when the fitness function $\alpha(x)$ attains a finite number of interior regular maxima in the interior of $\text{supp } I_0$, and when $X = \mathbb{R}^N$. In Theorem 2.10, we show that the initial distribution around the maxima of the fitness function plays a crucial role in the asymptotic behavior of the solution. We show that the fitness maxima that keep a non-zero asymptotic population are the ones that maximize an ad-hoc score that involves the value of $\gamma(x)$ but also the dimension of the Euclidean space and the polynomial decay of the initial data around the fitness maximum.

The structure of the paper is as follows. In section 2 we present our main results. More precisely, we state our results for persistence and concentration in section 2.1, we give precise statements of our results concerning fitness

functions with a finite number of regular maxima in section 2.2, and in section 2.3 we provide a counterexample to the convergence of the distribution $I(t, dx)$ when the initial mass of fitness maxima is negligible. In section 3 we illustrate our results with numerical simulations. The corresponding figures are added at the end of the article. 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 statements on the systems with a fitness function $\alpha(x)$ having a finite number of regular maxima (corresponding to the statements in section 2.2).

Data availability Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

2 Main results

Without loss of generality, the system (1.1) can be rewritten as

$$\begin{cases} S_t(t) = \Lambda - \theta S(t) - S(t) \int_X \alpha(x) \gamma(x) I(t, dx), \\ I_t(t, dx) = (\alpha(x) S(t) - 1) \gamma(x) I(t, dx), \quad x \in X, \end{cases} \quad (2.1a)$$

with the initial data

$$S(0) = S_0 \in (0, +\infty), \quad I(0, dx) \in \mathcal{M}_+(X), \quad (2.1b)$$

by setting $\alpha(x) := \beta(x)/\gamma(x)$, and removing the third equation, which has no impact on the dynamics of the system. In the rest of the article we will study the system (2.1) instead of (1.1).

Before going to our results, we introduce some notations that will be used along this work. We work on a Polish space X (*i.e.* a metrizable space which is separable and complete for at least one metric) equipped with a complete distance d . We denote by $\mathcal{M}(X)$ the set of finite signed Radon measures on X . Recall that $\mathcal{M}(X)$ is a Banach space when endowed with the *total variation norm* given by:

$$\|\mu\|_{TV} = |\mu|(X) = \int_X |\mu|(dx), \quad \forall \mu \in \mathcal{M}(X).$$

This fact is proved for instance in Bogachev [5, Vol. I, Theorem 4.6.1 p. 273]. When X is compact, it is possible to identify $\mathcal{M}(X)$ with the dual of the space of continuous functions over X , $C(X)$. This is the Riesz representation theorem [5, Vol. II, Theorem 7.10.4 p.111]. When X is an arbitrary Polish space, while it is true that every measure $\mu \in \mathcal{M}(X)$ yields a continuous linear functional on $BC(X)$ (the space of bounded continuous functions), the converse is no longer true [5, Vol. II, Example 7.10.3 p.111].

We denote by $\mathcal{M}_+(X)$ the set of the finite nonnegative measures on X . Observe that one has $\mathcal{M}_+(X) \subset \mathcal{M}(X)$ and $\mathcal{M}_+(X)$ is a closed subset of $\mathcal{M}(X)$ for the norm topology of $\|\cdot\|_{TV}$. An alternate topology on $\mathcal{M}(X)$ can be defined by the Kantorovitch-Rubinstein norm [5, Vol. II, Chap. 8.3 p. 191],

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

wherein we have set

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

Let us recall [5, Theorem 8.3.2] that the metric generated by $\|\cdot\|_0$ on $\mathcal{M}_+(X)$ is equivalent to the weak-* topology generated by tests against bounded continuous test functions. Note however that this equivalence is true only for $\mathcal{M}_+(X)$ and cannot be extended to $\mathcal{M}(X)$ since the latter space is not (in general) complete for the metric generated by $\|\cdot\|_0$. We denote by d_0 this metric on $\mathcal{M}_+(X)$, that is

$$d_0(\mu, \nu) := \|\mu - \nu\|_0 \text{ for all } \mu, \nu \in \mathcal{M}_+(X). \quad (2.2)$$

About the parameters arising in (2.1) 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 bounded and continuous from X into $\mathbb{R}$ and there exist positive constants α^∞ and $\gamma_0 < \gamma^\infty$ such that

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

We let $S_0 > 0$ be given and $I_0(dx) \neq 0$ be a finite nonnegative Radon measure and $S_0 > 0$ be given. We define the two quantities $\alpha^* \geq 0$ and $\mathcal{R}_0(I_0)$ by

$$\alpha^* := \sup_{x \in \text{supp } I_0} \alpha(x) \text{ and } \mathcal{R}_0(I_0) := \frac{\Lambda}{\theta} \alpha^*. \quad (2.3)$$

We finally assume that the set

$$L_\varepsilon(I_0) := \{x \in X : \alpha(x) \geq \alpha^* - \varepsilon\} \cap \text{supp } I_0 = \{x \in \text{supp } I_0 : \alpha(x) \geq \alpha^* - \varepsilon\} \quad (2.4)$$

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

Let us observe that if $S_0 \geq 0$ then (2.1) equipped with the initial data $S(0) = S_0$ and $I(0, dx) = I_0(dx)$ has a unique solution $S(t) \geq 0$ and $I(t, dx) \in \mathcal{M}_+(X)$ for all $t \geq 0$. This is a direct application of the Cauchy-Lipschitz Theorem in the Banach space $\mathbb{R} \times \mathcal{M}(X)$. It is not difficult to show that $S(t)$ and $I(t, dx)$ are *a priori* bounded (this will be proved in Lemma 4.1), hence the solution is global. In addition I is given by a quasi-explicit formula:

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

The above formula ensures that $\text{supp } I(t, \cdot) = \text{supp } I_0$ for all $t \geq 0$.

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 (2.1) when I_0 is an arbitrary Radon measure. We show that $I(t, dx)$ concentrates on the points that maximize both α and γ . 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 initial measure with respect to Lebesgue measure and a finite set $\{\alpha(x) = \alpha^*\}$. In that setting we are able to fully characterize the points where the measure $I(t, dx)$ concentrates as $t \rightarrow \infty$.

2.1 Persistence and concentration

As mentioned above this subsection is concerned with the large time behavior of the solution (S, I) of (2.1) 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 and suppose that $\mathcal{R}_0(I_0) > 1$. Let $(S(t), I(t, dx))$ be the solution of (2.1) equipped with the initial data $S(0) = S_0$ and $I(0, dx) = I_0(dx)$. We distinguish two cases depending on the measure of the set $\{\alpha(x) = \alpha^*\}$ with respect to I_0 :*

i) *If $\int_{\alpha(x)=\alpha^*} I_0(dx) > 0$, then one has*

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

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

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

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

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

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

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

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

where d_0 is the Kantorovitch-Rubinstein distance.

In the statement of the Theorem 2.2 and in the rest of the paper, we stress for clarity that $\mathcal{M}_+(\{\alpha(x) = \alpha^*\})$ is the set of finite positive measures on the closed set $\{x \in X : \alpha(x) = \alpha^*\}$. This set is naturally embedded as a subset of the space $\mathcal{M}_+(X)$, which is closed for the topology induced by the total variation norm $\|\cdot\|_{TV}$ and also the one induced by the Kantorovitch-Rubinstein distance d_0 .

Theorem 2.2 can be interpreted as follows. In case i), when the set of pathogens with maximal fitness is “already populated”, the behavior of the dynamical system is no different from the case of a finite system: it converges to an equilibrium which is concentrated on the set of maximal fitness. The case ii), when the maximal fitness is not attained for the population but can only be reached asymptotically, is more intricate and we can only prove that the population of pathogens is uniformly persistent and asymptotically concentrated on the set of maximal fitness. We cannot prove the convergence to an equilibrium distribution in general; in fact, it is false, see the example in section 2.3 below and also the counterexamples in [10]. In fact, as shown in the latter reference, it is not even true in general that the total mass of pathogen $\int_X I(t, dx)$ converges to a limit.

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 $\{\alpha(x) = \alpha^*\}$ that also maximize the function γ .

The additional assumption for the initial measure $I_0(dx)$ are expressed in term of some properties of its disintegration measure with respect to the function α on $L_\varepsilon(I_0)$ with ε sufficiently small. We refer to the book of Bourbaki [7, VI, §3, Theorem 1 p. 418] for a proof of the disintegration Theorem which is recalled in the Appendix, Theorem C.4.

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

$$\text{supp } I_0(y, dx) \subset \{x \in X : \alpha(x) = y\}, \quad \int_{\alpha(x)=y} I_0(y, dx) = 1 \text{ and } I_0(dx) = \int I_0(y, dx) A(dy) \quad (2.5)$$

wherein the last equality means that

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

Note that, by definition, the measure A is supported on the set $\alpha(\text{supp } I_0)$. The measure A is called the *pushforward* measure of I_0 under the mapping α . Note that the disintegration is unique up to a redefinition on an A -negligible set of fibers, see the disintegration theorem recalled in the Appendix, Theorem C.4.

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 γ , as follows

$$I_0(y, dx) = \int_{\mathbb{R}} I_0^{\alpha, \gamma}(y, z, dx) I_0^\alpha(y, dz),$$

where $I_0^{\alpha, \gamma}(y, z, dx)$ is concentrated on the set $\{x : \alpha(x) = y \text{ and } \gamma(x) = z\}$. This allows to the following reformulation of $I_0(dx)$:

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

Remark 2.3 (Explicit disintegration in Euclidean spaces). Suppose that $X = \mathbb{R}^N$ and $I_0 \in L^1(\mathbb{R}^N)$. 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 α is Lipschitz continuous on $\mathbb{R}^N$ and that

$$\frac{I_0(x)}{|\nabla \alpha(x)|} \in L^1(\mathbb{R}^N). \quad (2.6)$$

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

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

where $\mathcal{H}_{N-1}(dx)$ is the $(N-1)$ -dimensional Hausdorff measure (see Federer [20, §3.2]).

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

$$\int_{\mathbb{R}^N} f(x) I_0(x) dx = \int_{\mathbb{R}} \int_{\alpha(x)=y} f(x) \frac{I_0(x)}{|\nabla \alpha(x)|} \mathcal{H}_{N-1}(dx) dy, \quad (2.7)$$

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

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

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

$$A(dy) = \int_{\alpha(x)=y} \frac{I_0(x)}{|\nabla \alpha(x)|} \mathcal{H}_{N-1}(dx) dy \quad (2.8)$$

and (recalling (2.7)) we deduce the following explicit disintegration of I_0 :

$$I_0(y, dx) = \frac{\mathbb{1}_{\{x | \alpha(x)=y\}} \frac{I_0(x)}{|\nabla \alpha(x)|} \mathcal{H}_{N-1}(dx)}{\int_{\alpha(x)=y} \frac{I_0(z)}{|\nabla \alpha(z)|} \mathcal{H}_{N-1}(dz)}. \quad (2.9)$$

Equations (2.8) and (2.9) give an explicit formula for the disintegration introduced in (2.5).

Remark 2.4. In particular, if α 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 the assumption (2.6) above 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 (2.6) with $I_0 \in L^\infty(\mathbb{R}^N)$ should involve I_0 vanishing sufficiently fast in the neighborhood of each maximum of α .

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

Assumption 2.5 (Regularity with respect to α, γ). Let us define $\gamma^* > 0$ by

$$\gamma^* := \sup_{\alpha(x)=\alpha^*} \gamma(x). \quad (2.10)$$

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

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

Remark 2.6. The assumption 2.5 means that the initial measure $I_0(dx)$ is uniformly positive in a small neighborhood of $\{\alpha(x) = \alpha^*\} \cap \{\gamma(x) = \gamma^*\}$. For instance, if the assumptions (2.6) is satisfied and if there exists an open set U containing $\{\alpha(x) = \alpha^*\} \cap \{\gamma(x) = \gamma^*\}$ 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 $\{x \in X : \alpha(x) = \alpha^* \text{ and } \gamma(x) = \gamma^*\}$.

Proposition 2.7. Let Assumption 2.1 hold, and suppose that $\mathcal{R}_0(I_0) > 1$. Assume moreover that $\int_{\alpha(x)=\alpha^*} I_0(dx) = 0$ and that Assumption 2.5 holds, then:

i) The measure $I(t, dx)$ concentrates on the set $\{\alpha(x) = \alpha^*\} \cap \{\gamma(x) = \gamma^*\}$:

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

ii) The total mass of $I(t, dx)$ converges to a limit value:

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

iii) If there exists a Borel set $U \subset X$ such that $U \cap \{x : \alpha(x) = \alpha^* \text{ and } \gamma(x) = \gamma^*\} \neq \emptyset$ and

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

then the following persistence occurs

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

Here the notation $\text{ess inf}_K^{\mu(dy)}$ denotes the essential infimum taken on the set K and relatively to the measure μ (i.e. up to redefinition on μ -negligible sets). The condition on the set U in iii) means that the distribution of the population does not vanish in a neighborhood of $\{x : \alpha(x) = \alpha^* \text{ and } \gamma(x) = \gamma^*\}$ in U ; the existence of a set U cannot be guaranteed in general, in particular, no such U exists in the case of the counterexample given in subsection 2.3.

2.2 Refined concentration estimates: regular fitness maxima in Euclidean spaces

We now deepen our analysis of (2.1) set on $X = \mathbb{R}^N$ when the fitness function has a finite number of regular maxima. We will not discuss here the case of a unique global maximum, in which the precise asymptotic behavior can be completely determined: see the Appendix for a statement of what we obtain. Rather, we describe the large time behavior of the solutions when the function α 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 α^* in (2.3), 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 2.8. We assume that:

- (i) the set $\{\alpha(x) = \alpha^*\}$ 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

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

- (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 α and γ 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 2.9. 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 η 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 2.10. *Let Assumption 2.8 be satisfied. Then the function $\eta = \eta(t)$ satisfies the following asymptotic expansion*

$$\eta(t) = \varrho \frac{\ln t}{t} + O\left(\frac{1}{t}\right), \text{ as } t \rightarrow \infty. \quad (2.11)$$

wherein we have set

$$\varrho := \min_{i=1, \dots, p} \frac{N + \kappa_i}{2\gamma(x_i)}. \quad (2.12)$$

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

$$\int_{|x - x_i| \leq \varepsilon} I(t, dx) \asymp t^{\gamma(x_i)\varrho - \frac{N + \kappa_i}{2}} \text{ as } t \rightarrow \infty. \quad (2.13)$$

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

$$J := \left\{ i = 1, \dots, p : \frac{N + \kappa_i}{2\gamma(x_i)} = \varrho \right\}. \quad (2.14)$$

The above theorem states that the function $I(t, dx)$ concentrates on the set of points $\{x_i, i \in J\}$ (see Corollary 2.12 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 therefore the measure I concentrates on $\{\alpha(x) = \alpha^*\}$ as predicted by Theorem 2.2, but not necessarily on $\{\alpha(x) = \alpha^*\} \cap \{\gamma(x) = \gamma^*\}$ as would have been given by Proposition 2.7. In Figure 6 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 (4.1).

Corollary 2.11. *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 $t \rightarrow \infty$:*

$$t^{\frac{N}{2}} \int_{\mathbb{R}^N} f\left((x - x_i)\sqrt{t}\right) I(t, dx) \asymp t^{\gamma(x_i)\varrho - \frac{N + \kappa_i}{2}} \int_{\mathbb{R}^N} f(x) |x|^{\kappa_i} \exp\left(\frac{\gamma(x_i)}{2\alpha^*} D^2\alpha(x_i) x^2\right) dx. \quad (2.15)$$

Our next corollary relies on some properties of the ω -limit set of the solution $I(t, dx)$. Using the estimates of the mass around x_i given in (2.13), it readily follows that any limit measures of $I(t, dx)$ belongs to a linear combination of δ_{x_i} with $i \in J$ and strictly positive coefficients of each of these Dirac masses. This reads as follows.

Corollary 2.12. *Under the same assumptions as in Theorem 2.10, the ω -limit set $\overline{\mathcal{O}}(I_0)$ as defined in Lemma 4.6 satisfies that there exist $0 < A < B$ such that*

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

2.3 Oscillations

Here we construct a counterexample which shows that, in general, it is hopeless to expect convergence of the genotypic distribution to a stationary measure on $X = \mathbb{R}^2$. Such a counterexample is new in the case of “continuous” spaces; we provided some counterexamples in the case of discrete spaces in [10].

Fix $L > 0$ and let Ω be the parametric curve described as

$$\Omega := \left\{ \omega(\tau) := (1 - e^{-\tau}) \left(\cos\left(\frac{\pi}{L}\tau\right), \sin\left(\frac{\pi}{L}\tau\right) \right) : \tau \in \mathbb{R}^+ \right\},$$

and define $I_0(dx dy) \in \mathcal{M}(\mathbb{R}^2)$ as the pushforward of the measure $e^{-\tau} \mathbb{1}_{\tau \geq 0} d\tau$ by ω . That is to say,

$$\int_{\mathbb{R}^2} \varphi(x, y) I_0(dx dy) = \int_{\mathbb{R}^+} e^{-\tau} \varphi \left((1 - e^{-\tau}) \cos\left(\frac{\pi}{L}\tau\right), (1 - e^{-\tau}) \sin\left(\frac{\pi}{L}\tau\right) \right) d\tau, \text{ for all } \varphi \in BC(\mathbb{R}^2).$$

Then we select

$$\alpha(x, y) := 1 - \left| 1 - \sqrt{x^2 + y^2} \right|, \quad \gamma(x, y) \equiv 1.$$

In this setting, α attains its global maximum on the unit circle in $\mathbb{R}^2$, while the support of I_0 (the curve Ω) approaches the unit circle from the inside with an exponentially decreasing mass as the radius converges to 1. We are thus in the situation described in case ii) of Theorem 2.2; in particular, it is true that $\bar{S}(t) = \frac{1}{t} \int_0^t S(s) ds \rightarrow 1$ as $t \rightarrow +\infty$. Yet, explicit computations show that

$$I(t, dx dy) = e^{(1-e^{-\tau}) \int_0^t S(s) ds - t} I_0(\tau) \omega(d\tau) = e^{(1-e^{-\tau}) t \bar{S}(t) - t - \tau} \omega(d\tau) =: I(t, \tau) \omega(d\tau),$$

where we denote $\omega(d\tau)$ the pushforward of the Lebesgue measure on $\mathbb{R}^+$ onto Ω and, with a small abuse of notation, $I_0(\tau) = e^{-\tau} \mathbb{1}_{\tau \geq 0}$. More precisely,

$$\int_{\mathbb{R}^2} \varphi(x, y) I(t, dx dy) = \int_{\mathbb{R}^+} I(t, \tau) \varphi \left((1 - e^{-\tau}) \cos\left(\frac{\pi}{L}\tau\right), (1 - e^{-\tau}) \sin\left(\frac{\pi}{L}\tau\right) \right) d\tau, \text{ for all } \varphi \in BC(\mathbb{R}^2).$$

Now by using explicit computations, we establish the following claim.

Claim 2.13. The function $I(t, \tau)$ is, up to a multiplicative error of order zero, a solitary wave whose position behaves like $\tau_0(t) := \ln(t)$:

$$I(t, \tau) = e^{u(\tau - \tau_0(t)) + o(1)}, \tag{2.16}$$

where $u(\tau) = \ln(\mathcal{I}^\infty) - e^{-\tau} - \tau$ and $\mathcal{I}^\infty := \frac{\theta}{\alpha^*} (\mathcal{R}_0 - 1)$ is given by Proposition 2.7.

We now prove the claim. We note that Assumption 2.5 is clearly satisfied since $\gamma \equiv 1$ therefore, by Proposition 2.7, we have $\int_0^{+\infty} I(t, \tau) d\tau = \mathcal{I}^\infty + o(1)$ with $\mathcal{I}^\infty := \theta \left(\frac{\Delta}{\theta} \alpha^* - 1 \right) > 0$. By computing the integral of $I(t, \tau)$, we will now obtain a precise description of the behavior of $\bar{S}(t)$ as $t \rightarrow +\infty$. Indeed,

$$\begin{aligned} \int_0^{+\infty} I(t, \tau) d\tau &= \frac{e^{t\bar{S}(t)-t}}{t\bar{S}(t)} \int_0^{+\infty} t\bar{S}(t) e^{-\tau} e^{-t\bar{S}(t)e^{-\tau}} d\tau = \frac{e^{t\bar{S}(t)-t}}{t\bar{S}(t)} \left[e^{-t\bar{S}(t)e^{-\tau}} \right]_0^{+\infty} \\ &= \frac{e^{t\bar{S}(t)-t}}{t\bar{S}(t)} \left(1 - e^{-t\bar{S}(t)} \right) = \frac{e^{t\bar{S}(t)-t}}{t\bar{S}(t)} - \frac{e^{-t}}{t\bar{S}(t)} = \frac{e^{t\bar{S}(t)-t}}{t\bar{S}(t)} + o(1), \end{aligned}$$

therefore, recalling $\bar{S}(t) = 1 + o(1)$, we have $e^{t\bar{S}(t)-t} = t\mathcal{I}^\infty + o(t)$, and finally

$$\bar{S}(t) = 1 + \frac{\ln(t)}{t} + \frac{\ln(\mathcal{I}^\infty)}{t} + o\left(\frac{1}{t}\right).$$

We deduce that

$$\begin{aligned}
I(t, \tau + \tau_0(t)) &= \exp \left((1 - e^{-(\tau + \tau_0(t))}) (t + \ln(t) + \ln(\mathcal{I}^\infty) + o(1)) - t - (\tau + \tau_0(t)) \right) \\
&= \exp \left(\left(1 - \frac{e^{-\tau}}{t}\right) (\ln(t) + \ln(\mathcal{I}^\infty) + o(1)) - t e^{-(\tau + \tau_0(t))} - (\tau + \tau_0(t)) \right) \\
&= \exp (\ln(t) + \ln(\mathcal{I}^\infty) + o(1) + e^{-\tau} - \tau - \ln(t)) \\
&= \exp (\ln(\mathcal{I}^\infty) - e^{-\tau} - \tau + o(1)),
\end{aligned}$$

which proves the claim.

Note that the above computations and in particular the result of Claim 2.13 are completely independent of the parameter L . We see that $I(t, dx dy)$ is asymptotically equivalent to a rotating mass which becomes concentrated on the unit circle and does not converge to a static distribution. We illustrate this fact in numerical simulations in section 3.3. We can also prove that the distribution does not reach stationarity when the rotation speed of the spiral (which behaves like L^{-1}) is very slow. Indeed, the integral in the upper half-space never reaches a stationary value, as we show in the following Claim.

Claim 2.14. There exists a function $\varepsilon(L) \geq 0$ such that $\varepsilon(L) \rightarrow 0$ as $L \rightarrow \infty$, and two sequences $t_n^1 := e^{(2n+1/2)L} \rightarrow +\infty$ and $t_n^2 := e^{(2n+3/2)L} \rightarrow +\infty$ such that

$$\liminf_{n \rightarrow +\infty} \int_{\mathbb{R} \times \mathbb{R}^+} I(t_n^1, dx dy) \geq \mathcal{I}^\infty - \varepsilon(L) \quad (2.17)$$

and

$$\limsup_{n \rightarrow +\infty} \int_{\mathbb{R} \times \mathbb{R}^+} I(t_n^2, dx dy) \leq \varepsilon(L). \quad (2.18)$$

Indeed, we have

$$\begin{aligned}
\int_{\mathbb{R} \times \mathbb{R}^+} I(t, dx dy) &= \sum_{k=0}^{+\infty} \int_{2kL}^{(2k+1)L} I(t, \tau) d\tau = \sum_{k=0}^{+\infty} \int_{2kL}^{(2k+1)L} e^{u(\tau - \tau_0(t)) + o(1)} d\tau \\
&= (1 + o(1)) \sum_{k=0}^{+\infty} \int_{2kL - \tau_0(t)}^{(2k+1)L - \tau_0(t)} e^{u(\tau)} d\tau = (1 + o(1)) \sum_{k=0}^{+\infty} \int_{2kL - \tau_0(t)}^{(2k+1)L - \tau_0(t)} \mathcal{I}^\infty e^{-e^{-\tau} - \tau} d\tau \\
&= (1 + o(1)) \sum_{k=0}^{+\infty} \mathcal{I}^\infty \left(\exp \left(-e^{-(2k+1)L + \tau_0(t)} \right) - \exp \left(-e^{-2kL + \tau_0(t)} \right) \right), \quad (2.19)
\end{aligned}$$

so when $t = t_n^1 = e^{(2n+1/2)L}$ we have

$$\begin{aligned}
\int_{\mathbb{R} \times \mathbb{R}^+} I(t_n^1, dx dy) &= (1 + o(1)) \sum_{k=0}^{+\infty} \mathcal{I}^\infty \left(\exp \left(-e^{-(2k+1)L + (2n+1/2)L} \right) - \exp \left(-e^{-2kL + (2n+1/2)L} \right) \right) \\
&= \mathcal{I}^\infty (1 + o(1)) \sum_{k=-n}^{+\infty} e^{-e^{-2kL - L/2}} - e^{-e^{-2kL + L/2}}
\end{aligned}$$

We note that $e^{-e^{-(2k+1/2)L}} \leq e^{-(2k-1/2)L}$ as $L \rightarrow \infty$ when $k \leq -1$, and that for $k \geq 1$ we have by a Taylor expansion:

$$|e^{-e^{-(2k-1/2)L}} - e^{-e^{-(2k+1/2)L}}| \leq C e^{-(2k-1/2)L},$$

for some constant $C > 0$ independent of L and k . Therefore by the dominated convergence theorem we have

$$\lim_{L \rightarrow +\infty} \left(\sum_{k=-\infty}^{-1} + \sum_{k=1}^{+\infty} \right) |e^{-e^{-2kL - L/2}} - e^{-e^{-2kL + L/2}}| = 0.$$

Now for $k = 0$ we have $e^{-e^{-2kL - L/2}} - e^{-e^{-2kL + L/2}} = e^{-e^{-L/2}} - e^{-e^{L/2}} \rightarrow 1$ as $L \rightarrow +\infty$. We have shown

$$\liminf_{L \rightarrow +\infty} \liminf_{n \rightarrow +\infty} \int_{\mathbb{R} \times \mathbb{R}^+} I(t_n^1, dx dy) \geq \mathcal{I}^\infty,$$

which proves (2.17). Now (2.19) with $t = t_n^2 = e^{(2n+3/2)L}$ leads us to

$$\begin{aligned}
\int_{\mathbb{R} \times \mathbb{R}^+} I(t_n^2, dx dy) &= (1 + o(1)) \sum_{k=0}^{+\infty} \mathcal{I}^\infty \left(\exp \left(-e^{-(2k+1)L + (2n+3/2)L} \right) - \exp \left(-e^{-2kL + (2n+3/2)L} \right) \right) \\
&= \mathcal{I}^\infty (1 + o(1)) \sum_{k=-n}^{+\infty} e^{-e^{-2kL + L/2}} - e^{-e^{-2kL + 3L/2}}.
\end{aligned}$$

Note that we have

$$\lim_{L \rightarrow +\infty} \left(\sum_{k=-\infty}^{-1} + \sum_{k=1}^{+\infty} \right) \left| e^{-e^{-2kL+L/2}} - e^{-e^{-2kL+3L/2}} \right| = 0.$$

by the dominated convergence theorem and, for $k = 0$, $e^{-e^{-2kL+L/2}} - e^{-e^{-2kL+3L/2}} = e^{-e^{L/2}} - e^{-e^{3L/2}} \rightarrow 0$ as $L \rightarrow \infty$. This shows

$$\limsup_{L \rightarrow +\infty} \limsup_{n \rightarrow +\infty} \int_{\mathbb{R} \times \mathbb{R}^+} I(t_n^2, dx dy) \leq 0,$$

which finishes the proof of Claim 2.14.

3 Comments and numerical illustrations

3.1 Numerical illustrations: the main Theorem

In this section we provide numerical illustrations to some of our results. Note however that the figures are included at the end of the manuscript.

We start with an illustration of the long-time behavior of the solution to (2.1) when the initial mass of the fitness maximum is positive ($I_0(\{\alpha(x) = \alpha^*\}) > 0$) in Figure 1. 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 $L^1(\mathbb{R}^2)$ function. We provide a plot of the fitness function which is proportional to α (top left sub-figure) and the initial data (top right). The fitness function attains its maximum on the union of a rectangle $[0.2, 0.5] \times [-0.5, 0.5]$ with a line segment $\{-0.3\} \times [-0.5, 0.5]$ and the support of the initial data intersects this set with non-negligible intersection. We plot the time evolution of the converging function $S(t)$ (bottom left) and a snapshot of the distribution $I(t, dx)$ at $t = 50$ (bottom right). 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 precise distribution 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 2 we present four snapshots of the distribution $I(t, dx)$ to monitor the time evolution of this distribution with the same initial distribution.

Next, we consider the case when the initial mass of the fitness maximum is equal to zero ($I_0(\{\alpha(x) = \alpha^*\}) = 0$) in Figure 3. Again, we provide a plot of the fitness function (top left) and of the initial data (top right). The fitness function attains its maximum on the line segment $\{0.35\} \times [-0.5, 0.5]$. The time evolution of $S(t)$ (bottom left) and a snapshot of the distribution $I(t, dx)$ at $t = 100$ (bottom right) are also displayed. The distribution $I(t, dx)$ at $t = 100$ is already concentrated on the maximum of the fitness. Figure 4 consists of four snapshots of the example presented in Figure 3.

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 local maxima situation (corresponding to Theorem 2.10), 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 5 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

$$\alpha(x) = 0.95 \times \mathbb{P}_{[x_1-\delta, x_1+\delta]}(x) + \mathbb{P}_{[x_2-\delta, x_2+\delta]}(x) \text{ with } \delta = 0.2. \quad (3.1)$$

The function $I_0(x)$ is chosen as

$$I_0(x) = \min\left(1, 4(x - x_1)^2\right) \min\left(1, 4(x - x_2)^2\right) \mathbb{1}_{[-1, 1]}(x), \quad (3.2)$$

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

$$\gamma(x) = \frac{1}{1 + \mathbb{P}_{[x_1-\delta, x_1+\delta]}(x) + 3\mathbb{P}_{[x_2-\delta, x_2+\delta]}(x)} \quad (3.3)$$

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 2.10 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 5) that the distribution first concentrates on x_1 on a transient time scale, before the dynamics on x_2 takes precedence. We refer to Burie, Djidjou-Demasse, and Ducrot [8] for a related model with mutations where these transient behaviors are analytically characterized.

Figure 3 illustrates the case when the maximal fitness is negligible for the initial measure (Point ii) of Theorem 2.2). We provide a plot of the fitness function (top left-hand side) and the initial data (top 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. We also plot the time evolution of $S(t)$ (bottom 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 (bottom right-hand side). 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 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

$$\alpha(x) = \mathbb{P}_{[x_1 - \delta, x_1 + \delta]}(x) + \mathbb{P}_{[x_2 - \delta, x_2 + \delta]}(x), \quad (3.4)$$

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

$$I_0(x) = \min \left(1, 1024 (x - x_1)^8 \right) \min \left(1, 4 (x - x_2)^2 \right) \mathbb{1}_{[-1, 1]}(x), \quad (3.5)$$

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

$$\gamma(x) = \frac{1}{1 + \mathbb{P}_{[x_1 - \delta, x_1 + \delta]}(x) + 3\mathbb{P}_{[x_2 - \delta, x_2 + \delta]}(x)} \quad (3.6)$$

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

3.3 Numerical illustration: Oscillations

In Figure 7 we present a numerical simulation that illustrates the example provided in section 2.3. The parameter L is set to 1. A supplementary movie is also available ([spiraling.avi](#)).

3.4 Comments

We have studied the asymptotic behavior of a simple epidemiological model whose originality is that the population is structured by a continuous genotypic variable. Thus the population is divided into a compartment of susceptible and infected by a certain strain of pathogen. The duration of the infectious period ($1/\gamma$) and the basic reproduction number (α , up to a multiplicative constant) of the disease depend on the trait considered.

In this work, the pathogen population does not mutate and therefore if a trait is absent from the initial pathogen population, it cannot appear in the population afterwards.

Assuming that the basic reproduction number has a maximum strictly greater than one for at least one phenotypic trait of the initial population, we have shown the convergence of the solution of this model towards an endemic equilibrium. Firstly, in the case where the maximum value of the basic reproduction number is reached on a continuum of phenotypic traits of the initial population, we can completely describe the asymptotic number of susceptible as well as the distribution of the infected population with respect to the different variants.

Secondly, in the case where the maximum of $\mathcal{R}_0$ is reached on a set of zero measure, we have shown the persistence of the infectious population and its asymptotic concentration on a subset of the set of the traits maximizing both the $\mathcal{R}_0$ and the additional mortality rate due to the pathogen (or in other words minimizing the infectious period).

To go further in the analysis, we then considered the case of a finite number of traits maximizing the $\mathcal{R}_0$. In this case, we were able to describe more precisely the set of traits around which the population of infected (and therefore of pathogens) is concentrated, as well as the profile of the asymptotic distribution of infected around these traits.

In particular, we observed that even if there are no infected individuals with a trait maximizing the $\mathcal{R}_0$ initially, the population can concentrate around this trait (but not on this trait since there is no mutation in this model). The selection of traits around which the population concentrates thus depends not only on the value of $\mathcal{R}_0$ and the additional mortality rate, but also on the initial population distribution around the trait. A non-standard behavior may thus appear where the selected strain no longer maximizes γ , the virulence. The question arises whether such a configuration can be observed in vivo.

4 Measure-valued solutions and proof of Theorem 2.2

In this section we derive general properties of the solution of (2.1) equipped with the given and fixed initial data $S(0) = S_0 \in [0, \infty)$ and $I_0(dx) \in \mathcal{M}_+(X)$. Recall that α^* and $\mathcal{R}_0(I_0)$ are both defined in (2.3). Next for $\varepsilon > 0$ we recall that $L_\varepsilon(I_0)$ is the following superlevel set (defined by (2.4) in Assumption 2.1):

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

Recall also that the existence and uniqueness of a solution $(S(t), I(t, dx)) \in \mathbb{R} \times \mathcal{M}(X)$ corresponding to (S_0, I_0) in the Banach space $\mathbb{R} \times \mathcal{M}(X)$ (where $\mathcal{M}(X)$ is equipped with the norm $\|\cdot\|_{TV}$) follow directly from the Cauchy-Lipschitz Theorem.

The following lemma holds true.

Lemma 4.1. *Let Assumption 2.1 hold. Denote $(S(t), I(t, dx)) \in \mathbb{R} \times \mathcal{M}(X)$ be the corresponding solution of the ordinary differential equation (2.1). Then $(S(t), I(t, dx))$ is defined for all $t \geq 0$ and*

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

$$\limsup_{t \rightarrow +\infty} \int_X I(t, dx) \leq \frac{\Lambda}{\min(\theta, \gamma_*)} < +\infty,$$

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

$$\frac{d}{dt} \left(S(t) + \int_X I(t, dx) \right) \leq \Lambda - \theta S(t) - \gamma_* \int_X I(t, dx),$$

therefore

$$S(t) + \int_X I(t, dx) \leq \frac{\Lambda}{\min(\theta, \gamma_*)} + \left(S_0 + \int_X I_0(dx) - \frac{\Lambda}{\min(\theta, \gamma_*)} \right) e^{-\min(\theta, \gamma_0)t}.$$

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

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

Next we return to the S -component of equation (2.1) and let $\varepsilon > 0$ be given. We have, for t_0 sufficiently large and $t \geq t_0$,

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

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. □

Lemma 4.2. *Let Assumption 2.1 hold. Let $(S(t), I(t, dx))$ be the corresponding solution of (2.1). Then*

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

where α^* is given in (2.3).

Proof. Let us remark that the second component of (2.1) can be written as

$$\begin{aligned} I(t, dx) &= I_0(dx) e^{\gamma(x)(\alpha(x) \int_0^t S(s) ds - t)}, \\ &= I_0(dx) \exp \left(\gamma(x) \int_0^t S(s) ds \left[\alpha(x) - \frac{t}{\int_0^t S(s) ds} \right] \right). \end{aligned} \quad (4.1)$$

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 map $x \mapsto \alpha(x)$ 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

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

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

An important tool in later proofs is that the mass of $I(t, dx)$ vanishes on any set sufficiently far away from I_0 when the Cesàro mean $\bar{S}(t) = \frac{1}{t} \int_0^t S(s) ds$ of S is sufficiently close to α^* , which we prove now.

Lemma 4.3. *Let Assumption 2.1 hold and $(S(t), I(t, dx))$ be the corresponding solution of (2.1). Let $\{t_\tau\}$ be a net $t_\tau \rightarrow \infty$ and $\varepsilon > 0$ be such that we have eventually*

$$\bar{S}(t_\tau) = \frac{1}{t_\tau} \int_0^{t_\tau} S(s) ds \leq \frac{1}{\alpha^* - \varepsilon} \text{ for all } \tau. \quad (4.2)$$

Then for any $p > 1$ we have

$$\int_{\{\alpha(x) \leq \alpha^* - p\varepsilon\}} I(t_\tau, dx) \xrightarrow{t_\tau \rightarrow +\infty} 0. \quad (4.3)$$

Proof. Indeed, we can write

$$\begin{aligned} \int_{\{\alpha(x) \leq \alpha^* - p\varepsilon\}} I(t_\tau, dx) &= \int_{\{\alpha(x) \leq \alpha^* - p\varepsilon\}} \exp \left[\gamma(x) t_\tau \bar{S}(t_\tau) \left(\alpha(x) - \frac{1}{\bar{S}(t_\tau)} \right) \right] I_0(dx) \\ &\leq \int_{\{\alpha(x) \leq \alpha^* - p\varepsilon\}} \exp \left[\gamma(x) t_\tau \bar{S}(t_\tau) \left(\alpha^* - p\varepsilon - \frac{1}{\bar{S}(t_\tau)} \right) \right] I_0(dx) \\ &\leq \int_{\{\alpha(x) \leq \alpha^* - p\varepsilon\}} \exp [\gamma(x) t_\tau \bar{S}(t_\tau) (1 - p)\varepsilon] I_0(dx). \end{aligned}$$

Since $p > 1$ and $\liminf \bar{S}(t_\tau) > 0$ by Lemma 4.1, the argument of the exponential converges to $-\infty$ as $t_\tau \rightarrow +\infty$ therefore

$$\int_{\{\alpha(x) \leq \alpha^* - p\varepsilon\}} I(t_\tau, dx) \xrightarrow{t_\tau \rightarrow +\infty} 0.$$

The Lemma is proved. $\square$

The following weak persistence property holds.

Lemma 4.4. *Let Assumption 2.1 hold and suppose that $\mathcal{R}_0(I_0) > 1$. Let $(S(t), I(t, dx))$ be the corresponding solution of (2.1). Then*

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

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

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

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

with $\eta' > 0$.

As a consequence of Lemma 4.2 we have

$$\liminf_{t \rightarrow +\infty} S(t) \leq \limsup_{T \rightarrow +\infty} \frac{1}{T} \int_0^T S(t) dt \leq \frac{1}{\alpha^*}. \quad (4.4)$$

Let $\underline{S} := \liminf_{t \rightarrow +\infty} S(t)$. Let $(t_n)_{n \geq 0}$ be a sequence that tends to ∞ 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 $\int_X I(t_n, dx) \leq \eta'$ for n large enough we deduce from the equality

$$S'(t_n) = \Lambda - \theta S(t_n) - S(t_n) \int_X \alpha(x) \gamma(x) I(t_n, dx),$$

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 η

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

which contradicts (4.4). $\square$

Let us remind that $\mathcal{M}_+(X)$, equipped with the Kantorovitch-Rubinstein metric d_0 defined in (2.2), is a complete metric space.

Lemma 4.5 (Compactness of the orbit and concentration). *Let Assumption 2.1 hold and Let $(S(t), I(t, dx))$ be the corresponding solution of (2.1). Then, the closure of the orbit of (S_0, I_0) ,*

$$\overline{\mathcal{O}}(S_0, I_0) := \left\{ (s, \mu) \in \mathbb{R} \times \mathcal{M}_+(X) : \text{there exists } (t_n) \text{ such that } d_0(I(t_n, dx), \mu) \xrightarrow{n \rightarrow +\infty} 0 \text{ and } |S(t_n) - s| \xrightarrow{n \rightarrow +\infty} 0 \right\},$$

is compact.

Moreover $\mathcal{R}_0(I_0) > 1$ and $t_n \rightarrow +\infty$ is an arbitrary sequence along which

$$\liminf_{n \rightarrow +\infty} \int_X I(t, dx) > 0, \quad (4.5)$$

then one can extract from (t_n) a subsequence (t_{n_k}) such that the shifted orbits

$$t \mapsto (S(t + t_{n_k}), I(t + t_{n_k}, dx))$$

converge weak-* pointwise to a complete orbit $(S^\infty, I^\infty(t, dx))$ satisfying the following properties:

$$\int_X I^\infty(t, dx) > 0 \text{ for all } t \in \mathbb{R}, \quad (4.6)$$

and

$$\int_{\alpha(x) < \alpha^*} I^\infty(t, dx) = 0. \quad (4.7)$$

Finally the convergence $S(t + t_{n_k}) \rightarrow S^\infty(t)$ holds locally uniformly in $C^1(\mathbb{R})$.

Proof. First of all let us remark that

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

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 α^* defined in (2.3). We prove that the family $\{I(t, dx), t \geq 0\}$ is uniformly tight. Let $\varepsilon > 0$ be sufficiently small, so that the set $L_\varepsilon(I_0)$ is compact. By Lemma 4.3 and Lemma 4.2 we have

$$\limsup_{t \rightarrow +\infty} \int_{X \setminus L_\varepsilon(I_0)} I(t, dx) = 0.$$

Thus given any threshold $\nu > 0$, there is T_ν such that $I(t, X \setminus L_\varepsilon(I_0)) \leq \nu$ for all $t \geq T_\nu$, and since I_0 is Radon there exists a compact set $K_\nu \subset X$ such that $I_0(X \setminus K) \leq \nu e^{-\gamma^\infty T_\nu \alpha^\infty \sup_{0 \leq s \leq T_\nu} \bar{S}(s)}$ so that

$$\int_{X \setminus K} I(t, dx) \leq \int_{X \setminus K} I_0(dx) e^{\gamma^\infty T_\nu (\alpha^\infty \sup_{0 \leq s \leq T_\nu} \bar{S}(s) - 1)} \leq \nu.$$

Thus for all $t \geq 0$ we have $I(t, X \setminus (K_\nu \cup L_\varepsilon(I_0)))$. The set $\{I(t, dx) : t \geq 0\}$ is uniformly tight. Moreover it is bounded in the total variation norm (see Lemma 4.1) in the complete separable metric space X , therefore precompact for the weak topology by Prokhorov's Theorem [5, Theorem 8.6.2, Vol. II p. 202].

Next let (t_n) be an arbitrary sequence along which (4.5) holds. Thanks to the compactness of the orbit, we extract from $(S(t_n), I(t_n, dx))$ a subsequence still denoted t_n , such that $S(t_n) \rightarrow S^\infty$ and $I(t_n, dx) \rightarrow I^\infty(dx)$ weakly. Clearly $S'(t + t_n)$ is bounded independently on n ; differentiating the first line in (2.1a) we see that $S''(t + t_n)$ is also bounded independently on n when t is in an arbitrary compact set. Thus, up to a diagonal extraction, we may assume that both $S(t + t_n)$ and $S'(t + t_n)$ converge locally uniformly in t to a limit $S^\infty(t)$ and $(S^\infty)'(t)$. This proves the final statement of the Lemma. We can now take the weak-* limit in the formula

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

which shows that, for fixed but arbitrary $t \in \mathbb{R}$, we have that $I(t_n + t, dx)$ converges weakly to

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

In particular $(S^\infty(t), I^\infty(t, dx))$ is a complete orbit of the equation (2.1). Since $1 \in BC(X)$ we have that

$$\int_X I^\infty(dx) = \int_X 1 I^\infty(dx) = \lim_{n \rightarrow +\infty} \int_X 1 I(t + t_n, dx) > 0,$$

which shows (4.6).

Next it follows from Lemma 4.2 that $\limsup_{n \rightarrow +\infty} \frac{1}{t_n} \int_0^{t_n} S(s) ds \leq \frac{1}{\alpha^*}$ and thus by Lemma 4.3 that

$$\int_{\alpha(x) \leq \alpha^* - \frac{1}{k}} I^\infty(dx) = \lim_{n \rightarrow +\infty} \int_{\alpha(x) \leq \alpha^* - \frac{1}{k}} I(t_n, dx) = 0, \text{ for all } k \in \mathbb{N}.$$

Thus by Fatou's Lemma

$$\int_{\alpha(x) < \alpha^*} I^\infty(dx) \leq \lim_{k \rightarrow +\infty} \int_{\alpha(x) \leq \alpha^* - \frac{1}{k}} I^\infty(dx) = 0.$$

This proves (4.7) and completes the proof of Lemma 4.5. $\square$

Next we show the weak uniform persistence property if $\mathcal{R}_0(I_0) > 1$.

Lemma 4.6 (Uniform persistence). *Let Assumption 2.1 hold and suppose that $\mathcal{R}_0 > 1$. Let $(S(t), I(t, dx))$ be the corresponding solution of (2.1). Then*

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

Proof. We adapt here the argument of Magal and Zhao [37, Proposition 3.2] to our context. Suppose by contradiction that there exists a sequence $t_n \rightarrow +\infty$ such that

$$\lim_{n \rightarrow +\infty} \int_X I(t_n, dx) = 0.$$

By Lemma 4.1 we know that $S(t_n) \geq \underline{S} > 0$ for all $n \in \mathbb{N}$. By Lemma 4.4, for each $n \in \mathbb{N}$ sufficiently large, there exists $s_{< t_n}$ such that

$$\int_X I(s_n, dx) = \frac{\theta}{2\alpha^* \gamma^*} (\mathcal{R}_0(I_0) - 1) \text{ and } \int_X I(t, dx) \leq \frac{\theta}{2\alpha^* \gamma^*} (\mathcal{R}_0(I_0) - 1) \text{ for all } s_n \leq t \leq t_n. \quad (4.8)$$

Up to replacing t_n by a subsequence, we will assume without loss of generality that $t_{n-1} < s_n < t_n$ for all $n \in \mathbb{N}$. Thanks to Lemma 4.5 and up to a further extraction, the shifted orbits $(S(t+s_n), I(t+s_n, dx))$ converge to a complete orbit $(S^\infty(t), I^\infty(t, dx))$ which satisfies $0 < \underline{S} \leq S^\infty(t) \leq \frac{\Lambda}{\theta}$ and $\int_X I^\infty(t, dx) > 0$ for all $t \in \mathbb{R}$. Moreover $I^\infty(t, dx)$ is concentrated on the set $\{x : \alpha(x) = \alpha^*\}$, and in particular $\mathcal{R}_0(I^\infty(0, dx)) = \mathcal{R}_0(I_0) > 1$. By Lemma 4.4 we have therefore

$$\limsup_{t \rightarrow +\infty} \int_X I^\infty(t, dx) \geq \frac{\theta}{\alpha^* \gamma^*} (\mathcal{R}_0(I_0) - 1). \quad (4.9)$$

Next we investigate the time $T_n := t_n - s_n$. Up to extracting a subsequence, there are two options.

- $T_n \rightarrow T$ as $n \rightarrow +\infty$. In that case we have $\int_X I^\infty(T, dx) = 0$ so $I^\infty(T, dx) \equiv 0$, and by the uniqueness of the solution to (2.1) we have $I^\infty(t, dx) \equiv 0$ for all $t \geq T$. This contradicts (4.9).
- $T_n \rightarrow +\infty$ as $n \rightarrow +\infty$. In that case, recalling (4.8), we have $\int_X I^\infty(t, dx) \leq \frac{\theta}{2\alpha^* \gamma^*} (\mathcal{R}_0(I_0) - 1)$ for all $t \geq 0$, and this also contradicts (4.9).

This completes the proof of Lemma 4.6. $\square$

Lemma 4.7. *Let Assumption 2.1 hold. Let $(S(t), I(t, dx))$ be the corresponding solution of (2.1). Assume that $\mathcal{R}_0(I_0) > 1$. Then*

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

with α^* given in (2.3).

Proof. 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 ε is sufficiently small. Therefore by Lemma 4.3 we have

$$\liminf_{t \rightarrow +\infty} \int_X I(t, dx) \leq \liminf_{n \rightarrow +\infty} \int_X I(T_n, dx) = 0,$$

which is in contradiction with Lemma 4.6. This proves the Lemma. $\square$

Remark 4.8. By combining Lemma 4.2 and Lemma 4.7 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 4.9. *Let Assumption 2.1 hold. Let $(S(t), I(t, dx))$ be the corresponding solution of (2.1). Then one has*

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

Proof. Let $\varepsilon > 0$ be as in the statement of Lemma 4.9. By Lemma 4.2, there exists $T \geq 0$ such that for all $t \geq T$ we have

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

Hence Lemma 4.3 implies that

$$\int_{X \setminus L_\varepsilon(I_0)} I(t, dx) \xrightarrow{t \rightarrow +\infty} 0.$$

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

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

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

$$\limsup_{t \rightarrow +\infty} \int_X I(t, dx) \leq \frac{\Lambda}{\min(\theta, \gamma_*)},$$

so that for t sufficiently large, we have

$$\int_X I(t, dx) \leq 2 \frac{\Lambda}{\min(\theta, \gamma_*)}.$$

Finally by using Proposition B.5 (proved in the Appendix), we have

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

Since

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

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

Lemma 4.10. *Let Assumption 2.1 hold and suppose moreover that $\alpha(x) \equiv \alpha^*$ for all $x \in \text{supp } I_0$ and that $\mathcal{R}_0(I_0) > 1$. Let $(S(t), I(t, dx))$ be the corresponding solution of (2.1) and let $S^* := \frac{1}{\alpha^*}$ and $i^*(x) := e^{\tau \gamma(x)}$ where $\tau \in \mathbb{R}$ is the unique solution of the equation*

$$\int_X \gamma(x) e^{\tau \gamma(x)} I_0(dx) = \frac{\theta}{\alpha^*} (\mathcal{R}_0 - 1). \quad (4.10)$$

Define $g(x) := x - \ln(x)$ and let

$$D(V) := \left\{ (S, i(x)) \in \mathbb{R} \times L_{i^*}^\infty(I_0) : S > 0 \text{ and } \text{ess inf}_{i^*} \frac{I_0(dx)}{i^*(x)} > 0 \right\},$$

where $L_{i^*}^\infty(I_0)$ is the weighted L^∞ space equipped with the norm $\|i\|_{L_{i^*}^\infty(I_0)} := \|\frac{i}{i^*}\|_{L^\infty(I_0)}$. Then $D(V)$ is open in $\mathbb{R} \times L_{i^*}^\infty(I_0)$ and the functional

$$V(S, i) := S^* g\left(\frac{S}{S^*}\right) + \int_X i^*(x) g\left(\frac{i(x)}{i^*(x)}\right) I_0(dx)$$

is well-defined and continuous on $D(V)$. Moreover if $i(t, x)$ is the Radon-Nikodym derivative of $I(t, dx)$ with respect to I_0 (in other words, $I(t, dx) = i(t, x) I_0(dx)$), then $t \mapsto V(S(t), i(t, x))$ is of class C^1 and we have

$$\frac{d}{dt} V(S(t), i(t, x)) \leq -\theta \frac{(S(t) - S^*(t))^2}{S(t)} \text{ for all } t \in \mathbb{R}. \quad (4.11)$$

Proof. The well-definition of τ is clear since the left-hand side of (4.10) is strictly increasing and connects 0 when $\tau \rightarrow -\infty$, to $+\infty$ when $\tau \rightarrow +\infty$. The openness of $D(V)$, the well-definition and continuity of $V(S, i)$ are also clear.

Let us check (4.11). We first remark that $i(t, x) = e^{t\gamma(x)(\alpha(x)\bar{S}(t)-1)}$, so it is clear that $i(t, x) \in D(V)$ and that $t \mapsto V(S(t), i(t, x)) \in C^1(\mathbb{R})$.

We show (4.11). Let us write $V_1(S) = S^* g\left(\frac{S(t)}{S^*}\right)$ and $V_2(t) = \int_X i^*(x) g\left(\frac{i(t,x)}{i^*(x)}\right) I_0(dx)$, then we have

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

and

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

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

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

Since

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

which stems from the inequality $a + b \geq 2\sqrt{ab}$, we have indeed proved that (4.11) holds. $\square$

Next we can determine the long-time behavior when the initial measure I_0 puts a positive mass on the set of maximal fitness.

Lemma 4.11. *Let Assumption 2.1 hold. Assume that $\mathcal{R}_0(I_0) > 1$ and suppose that $I_0(\{\alpha(x) = \alpha^*\}) > 0$, or in other words,*

$$\int_{\alpha(x)=\alpha^*} I_0(dx) > 0.$$

Let $\eta(t) := \alpha^ \bar{S}(t) - 1$, then there exists a constant $\bar{\eta}$ such that*

$$-\infty < -\bar{\eta} \leq t\eta(t) \leq \bar{\eta} < +\infty, \tag{4.12}$$

for all $t \geq 0$. If moreover $\liminf_{t \rightarrow -\infty} \int_{\alpha(x)=\alpha^} I(t, dx) > 0$, then up to changing the constant $\bar{\eta}$, (4.12) holds for all $t \in \mathbb{R}$.*

Proof. We first remark that $I(t, dx)$ can be written as

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

By Jensen's inequality we have

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

so that

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

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 $X \setminus \{\alpha(x) = \alpha^*\}$, so that by Lebesgue's dominated convergence theorem, we have

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

Next it follows from Lemma 4.7 that $\liminf_{t \rightarrow +\infty} I(t, dx) > 0$, so that

$$\liminf_{t \rightarrow +\infty} \int_{\alpha(x)=\alpha^*} I(t, dx) = \liminf_{t \rightarrow +\infty} \int_X I(t, dx) > 0.$$

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

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

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,

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

This completes the proof of Lemma 4.11. $\square$

Finally we prove that any complete orbit that is already concentrated on $\{\alpha(x) = \alpha^*\}$ is constant, provided the mass can be bounded when $t \rightarrow -\infty$. This is a kind of LaSalle principle, since we have a partial Lyapunov functional by Lemma 4.10.

Lemma 4.12. *Let Assumption 2.1 hold and assume that $\alpha(x) \equiv \alpha^*$ for all $x \in \text{supp } I_0$. Suppose that $(S(t), I(t, dx))$ is a complete orbit of (2.1) with initial data $(S_0, I_0(dx))$, and assume that*

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

Then

$$S(t) \equiv \frac{1}{\alpha^*}, \text{ for all } t \in \mathbb{R}.$$

Proof. Thanks to our assumption and the results of Lemma 4.11, we know that $t\eta(t)$ is bounded for $t \in \mathbb{R}$; moreover by Lemma 4.10, the functional $V(S(t), i(t, x))$ is well-defined and decreasing along the orbit $(S(t), i(t, x)), t \in \mathbb{R}$. Since $V(S(t), i(t, x))$ is bounded and decreasing there exists $V^\infty \in \mathbb{R}$ such that

$$V(S(t), i(t, x)) \xrightarrow{t \rightarrow -\infty} V^\infty.$$

Let $t_n \rightarrow -\infty$ be a sequence with $S(t_n) \rightarrow S^{-\infty}$ and $t_n\eta(t_n) \rightarrow \eta^{-\infty}$ when $t_n \rightarrow -\infty$, so that $I(t_n, dx) = e^{t_n\eta(t_n)\gamma(x)} I_0(dx)$ converges when $t \rightarrow -\infty$ to $I_0^{-\infty}(dx) := e^{\eta^{-\infty}} I_0(dx)$. Then the shifted orbits $(S(t+t_n), I(t+t_n, dx))$ converge, as $t_n \rightarrow -\infty$, to a complete orbit $(S^{-\infty}(t), I^{-\infty}(t, dx))$ with $I^{-\infty}(0, dx) = I_0^{-\infty}(dx) = e^{\eta^{-\infty}} I_0(dx)$. By the continuity of V , along the new orbit $(S^{-\infty}(t), I^{-\infty}(t, dx))$, we have that

$$V(S^{-\infty}(t), I^{-\infty}(t, dx)) \equiv V^{-\infty}$$

is a constant. Thus $\frac{d}{dt} V(S^{-\infty}(t), I^{-\infty}(t, dx)) = 0$ and, by (4.11),

$$S^{-\infty}(t) \equiv S^* = \frac{1}{\alpha^*} \text{ and } (S^{-\infty})'(t) \equiv 0 \text{ for all } t \in \mathbb{R}.$$

Then it follows from the first line in (2.1a) that

$$0 = \Lambda - \theta S^* - S^* \int_X \alpha^* \gamma(x) I^{-\infty}(t, dx) \text{ for all } t \in \mathbb{R},$$

therefore in particular

$$\int_X \gamma(x) e^{\eta^\infty \gamma(x)} I_0(dx) = \frac{\theta}{\alpha^*} (\mathcal{R}_0 - 1).$$

Thus $\eta^{-\infty}$ is a solution of (4.10) and, by the uniqueness of the solution, we have $\eta^{-\infty} = \tau$ and $I_0^{-\infty}(dx) = i^*(x) I_0(dx)$. Thus

$$V^{-\infty} = V(S^{-\infty}, e^{\eta^{-\infty} \gamma(x)}) = V(S^*, i^*(x)) = 0.$$

Thus $V^{-\infty}$ is the smallest possible value of $V(S, i(x))$. Since $t \mapsto V(S(t), i(t, x))$ is nonincreasing, we have therefore

$$V(S(t), i(t, x)) \equiv 0, \frac{d}{dt} V(S(t), i(t, x)) \equiv 0, \text{ for all } t \in \mathbb{R}.$$

By (4.11), we have therefore

$$S(t) \equiv S^* = \frac{1}{\alpha^*} \text{ for all } t \in \mathbb{R},$$

which completes the proof of Lemma 4.12. $\square$

Lemma 4.13. *Let Assumption 2.1 hold. Assume that $\mathcal{R}_0(I_0) > 1$ and suppose that $I_0(\{\alpha(x) = \alpha^*\}) > 0$, or in other words,*

$$\int_{\alpha(x)=\alpha^*} I_0(dx) > 0.$$

Then

$$S(t) \xrightarrow[t \rightarrow +\infty]{} \frac{1}{\alpha^*} \text{ and } \|I(t, dx) - I^\infty(dx)\|_{TV} \xrightarrow[t \rightarrow +\infty]{} 0,$$

where we have the following formula for $I^\infty(dx)$, with τ being the unique solution of (4.10),

$$I^\infty(dx) = e^{\tau \gamma(x)} \mathbb{1}_{\alpha(x)=\alpha^*} I_0(dx).$$

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

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

By Lemma 4.5, the shifted orbits $(S(t + t_n), I(t + t_n, dx))$ converge to a complete orbit $(S^\infty(t), I^\infty(t, dx))$ with $I(t_n, dx) \xrightarrow[t \rightarrow +\infty]{} e^{\gamma(x)\eta^*} \mathbb{1}_{\alpha(x)=\alpha^*} I_0(dx) = I^\infty(t, dx)$. We know that $\text{supp } I^\infty(t, dx) \subset \{\alpha(x) = \alpha^*\}$ and by Lemma 4.4 we have

$$\int_X I^\infty(t, dx) \geq \liminf_{s \rightarrow +\infty} \int_X I(s, dx) > 0 \text{ for all } t \in \mathbb{R}.$$

Thus we can apply Lemma 4.12 which shows that

$$S^\infty(t) \equiv \frac{1}{\alpha^*} \text{ for all } t \in \mathbb{R}.$$

Thus $(S^\infty)'(t) \equiv 0$ and by using the first line in (2.1a) we find that

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

This is (4.10) which has a unique solution $\eta^* = \tau$. Since we can extract from any sequence $t_n \rightarrow +\infty$ a subsequence with $t_n \eta(t_n) \rightarrow \tau$, we conclude that $\lim_{t \rightarrow +\infty} t \eta(t) = \tau$ therefore

$$I(t, dx) \xrightarrow[t \rightarrow +\infty]{\|\cdot\|_{TV}} e^{\tau \gamma(x)} \mathbb{1}_{\alpha(x)=\alpha^*} I_0(dx).$$

We show similarly that $S(t) \rightarrow \frac{1}{\alpha^*}$ as $t \rightarrow +\infty$. $\square$

When the set of maximal fitness $\{\alpha(x) = \alpha^*\}$ 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 4.14. *Let Assumption 2.1 hold. Assume that $\mathcal{R}_0(I_0) > 1$. Suppose that $I_0(\{\alpha(x) = \alpha^*\}) = 0$ and set*

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

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

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

which is in contradiction with Lemma 4.6. We conclude that $t\eta(t) \rightarrow +\infty$ as $t \rightarrow +\infty$. $\square$

We are now in the position to prove Theorem 2.2.

Proof of Theorem 2.2. The convergence of $S(t)$ and $I(t, dx)$ in case i) was proved in Lemma 4.13.

Let us focus on case ii), that is to say, we assume

$$\int_{\alpha(x)=\alpha^*} I_0(dx) = 0.$$

The uniform persistence of $I(t, dx)$ is a consequence of 4.6. The concentration on the maximal fitness was proved in Lemma 4.9. Let us show that $S(t) \rightarrow \frac{1}{\alpha^*}$. Suppose by contradiction that it is not the case, then there exists $\varepsilon > 0$ and a sequence $t_n \rightarrow +\infty$ with $|S(t_n) - \frac{1}{\alpha^*}| \geq \varepsilon$. By Lemma 4.5 we can extract t_n a subsequence such that the shifted orbits $(S(t+t_n), I(t+t_n, dx))$ converge to $(S^\infty(t), I^\infty(t, dx))$. We have $\int_{\alpha(x) < \alpha^*} I^\infty(t, dx) = 0$, $\int_X I^\infty(t, dx) > 0$, and

$$\liminf_{t \rightarrow -\infty} \int_X I^\infty(t, dx) \geq \liminf_{t \rightarrow +\infty} \int_X I(t, dx) > 0,$$

so by Lemma 4.12 we have

$$\lim_{n \rightarrow +\infty} S(t_n) = S^\infty(0) = \frac{1}{\alpha^*}.$$

This is obviously a contradiction. Theorem 2.2 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 α and γ . This property is summarized in the next lemma.

Lemma 4.15. *Let Assumptions 2.5 hold. Assume that $\mathcal{R}_0(I_0) > 1$ and that $I_0(\{\alpha(x) = \alpha^*\}) = 0$. Recalling the definition of α^* in (2.3) and γ^* in Assumption 2.5, set $\Gamma_0(I_0)$ be the set of maximal points of γ on $\{\alpha(x) = \alpha^*\}$, defined by*

$$\Gamma_0(I_0) := \{x : \gamma(x) = \gamma^* \text{ and } \alpha(x) = \alpha^*\}.$$

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 $\|\cdot\|_{TV}$. That is to say,

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

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 $\mathbb{1}_{\alpha(x)\bar{S}(t) < 1} I(t, dx) = \mathbb{1}_{\alpha(x)\bar{S}(t) < 1} e^{\gamma(x)(\alpha(x)\bar{S}(t)-1)t} I_0(dx)$ is uniformly bounded. On the other hand, since $I_0(\{\alpha(x) = \alpha^*\}) = 0$ 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

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

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 $\bar{\gamma} < \gamma^*$. Recall that A is the pushforward measure of I_0 by the continuous map α . Note that $I_0(\{\alpha(x) = \alpha^*\}) = 0$ implies that $A(\{\alpha^*\}) = 0$ and remark that one has

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

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

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

wherein $m > 0$ is the constant associated with $\bar{\gamma}$ in Assumption 2.5 and we used the Landau notation $o(1)$ to collect terms that converges to 0 as $t \rightarrow +\infty$. Recalling the upper bound for $I(t, dx)$ from Lemma 4.1, we have

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

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 $0 < \varepsilon \leq \frac{\gamma^* - \bar{\gamma}}{2}$. Then we have

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

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

$$\begin{aligned} \int_{\gamma(x) \leq \bar{\gamma} \text{ and } \alpha(x) \geq 1/\bar{S}(t)} I(t, dx) &\leq \left(\int_{\min(\alpha^*, 1/\bar{S}(t))}^{\alpha^*} \left(e^{-\varepsilon(y\bar{S}(t)-1)t} \right)^{\frac{\bar{\gamma}}{\varepsilon}} e^{\bar{\gamma}(y\bar{S}(t)-1)t} A(dy) \right)^{\frac{\varepsilon}{\bar{\gamma}}} \\ &\quad \times \left(\int_{\min(\alpha^*, 1/\bar{S}(t))}^{\alpha^*} \left(\int_{\alpha(x)=y} I_0(y, dx) \right)^{\frac{\bar{\gamma}}{\bar{\gamma}-\varepsilon}} e^{\bar{\gamma}(y\bar{S}(t)-1)t} A(dy) \right)^{1-\frac{\varepsilon}{\bar{\gamma}}} \\ &\leq \left(\int_{\min(\alpha^*, 1/\bar{S}(t))}^{\alpha^*} A(dy) \right)^{\frac{\varepsilon}{\bar{\gamma}}} \left(\int_{\min(\alpha^*, 1/\bar{S}(t))}^{\alpha^*} e^{\bar{\gamma}(y\bar{S}(t)-1)t} A(dy) \right)^{1-\frac{\varepsilon}{\bar{\gamma}}} \\ &= I_0(L_{\alpha^* - \min(\alpha^*, 1/\bar{S}(t))}(I_0))^{\frac{\varepsilon}{\bar{\gamma}}} \left(\int_{\min(\alpha^*, 1/\bar{S}(t))}^{\alpha^*} e^{\bar{\gamma}(y\bar{S}(t)-1)t} A(dy) \right)^{1-\frac{\varepsilon}{\bar{\gamma}}}. \quad (4.13) \end{aligned}$$

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

$$\int_{\gamma(x) \leq \bar{\gamma} \text{ and } \alpha(x) \geq 1/\bar{S}(t)} I(t, dx) \xrightarrow{t \rightarrow +\infty} 0,$$

and this completes proof of Lemma 4.15. $\square$

Proof of Proposition 2.7. The concentration of the distribution to $\mathcal{M}_+(\{\alpha(x) = \alpha^*\} \cap \{\gamma(x) = \gamma^*\})$ was shown in Lemma 4.15.

Next we prove the asymptotic mass. Pick a sequence $t_n \rightarrow +\infty$. By the compactness of the orbit (proved in Lemma 4.6) 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,

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

By the concentration result in Lemma 4.15, I^∞ is concentrated on $\{\alpha(x) = \alpha^*\} \cap \{\gamma(x) = \gamma^*\}$. Therefore

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

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

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

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 (4.13) that

$$\int_{\gamma(x) \leq \bar{\gamma} \text{ and } \alpha(x) \geq 1/\bar{S}(t)} I(t, dx) \xrightarrow{t \rightarrow +\infty} 0,$$

therefore

$$f(t) = \int_{\min(\alpha^*, 1/\bar{S}(t))}^{\alpha^*} \int_{\bar{\gamma}}^{\gamma^*} \int_{\{\gamma(x)=z\}} e^{z(y\bar{S}(t)-1)t} I_0^{\alpha, \gamma}(y, z, dx) I_0^\alpha(z, dy) A(dy) = \int_{\bar{\gamma} \leq \gamma(x) \leq \gamma^* \text{ and } \alpha(x) \geq 1/\bar{S}(t)} I(t, dx)$$

satisfies

$$0 < \liminf_{t \rightarrow +\infty} \int I(t, dx) = \liminf_{t \rightarrow +\infty} \left[\int_{\gamma(x) \leq \bar{\gamma} \text{ and } \alpha(x) \geq 1/\bar{S}(t)} I(t, dx) + f(t) \right] \leq \liminf_{t \rightarrow +\infty} f(t)$$

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 γ^* , where

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

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 a finite number of regular maxima

In this section we prove Theorem 2.10. To that aim, we shall make use of the following formula

$$I(t, dx) = \exp \left(\gamma(x) \left(\alpha(x) \int_0^t S(s) ds - t \right) \right) I_0(dx). \quad (5.1)$$

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 2.10. 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 $\{\alpha(x) = \alpha^*\}$.

Upper bound:

Let $i = 1, \dots, p$ be given. Recall that $\nabla \alpha(x_i) = 0$. Now due to (iii) in Assumption 2.8 there exist $m > 0$ and $T > \varepsilon_0^{-2}$ large enough such that for all $t \geq T$ and for all $y \in B(0, t^{-\frac{1}{2}})$ 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 (5.1) and the lower estimate of I_0 around x_i given in Assumption 2.8 (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

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

Now, since γ and α 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 $t \gg 1$

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

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

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

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

$$\eta(t) \leq \varrho \frac{\ln t}{t} + O\left(\frac{1}{t}\right) \text{ as } t \rightarrow \infty, \quad (5.2)$$

where ϱ is defined in (2.12).

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 2.8 (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

$$|\Gamma(x) - \gamma(x_k) - \nabla\gamma(x_k) \cdot (x - x_k)| \leq M|x - x_k|^2. \quad (5.3)$$

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

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

so that we get, using Assumption 2.8 (ii), that

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

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 4.14 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 (5.2) 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

$$\int_{|x-x_i| \leq \varepsilon} I(t, dx) \leq C' t^{-\frac{N+\kappa_i}{2}} e^{t\eta(t)\gamma(x_i)}, \quad \forall t \gg 1. \quad (5.4)$$

Since $I(t, dx)$ concentrates on $\{\alpha(x) = \alpha^*\}$, 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 (5.4) ensures that there exists $c > 0$ and $T > 0$ such that

$$0 < c \leq \sum_{i=1}^p e^{\gamma(x_i) \left(t\eta(t) - \frac{N+\kappa_i}{2\gamma(x_i)} \ln t \right)}, \quad \forall t \geq T. \quad (5.5)$$

Now recalling the definition of ϱ and J in (2.12) and (2.14), the upper bound for $\eta(t)$ provided in (5.2) 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 (5.5) 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

$$\eta(t) \geq \varrho \frac{\ln t}{t} + O\left(\frac{1}{t}\right) \text{ as } t \rightarrow \infty. \quad (5.6)$$

Then (2.11) follows coupling (5.2) and (5.6).

Estimate of the masses: In this last step we turn to the proof of (2.13). Observe first that the upper estimate directly follows from the asymptotic expansion of $\eta(t)$ in (2.11) together with (5.4). Next, the proof for the lower estimate follows from similar inequalities as the one derived in the second step above. $\square$

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] R. A. Armstrong and R. McGehee. Competitive exclusion. *Amer. Natur.* **115.2** (1980), pp. 151–170. DOI: 10.1086/283553.
- [3] 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.
- [4] 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.
- [5] 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.
- [6] 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.
- [7] N. Bourbaki. *Elements of Mathematics. Integration I*. Springer, Berlin, Heidelberg, 2004. DOI: 10.1007/978-3-642-59312-3.
- [8] 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.

- [9] 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.
- [10] J.-B. Burie, A. Ducrot, and Q. Griette. Asymptotic behavior of an epidemic model with infinitely many variants (2023). DOI: 10.48550/arXiv.2305.05699.
- [11] 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.
- [12] 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.
- [13] J. M. Cushing. Two species competition in a periodic environment. *J. Math. Biol.* **10.4** (1980), pp. 385–400. DOI: 10.1007/BF00276097.
- [14] 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.
- [15] J. Demongeot, Q. Griette, Y. Maday, and P. Magal. A Kermack-McKendrick model with age of infection starting from a single or multiple cohorts of infected patients (2022). DOI: 10.48550/ARXIV.2205.15634.
- [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] A. Ducrot, Q. Griette, Z. Liu, and P. Magal. *Differential equations and population dynamics I. Introductory approaches*. Lecture Notes on Mathematical Modelling in the Life Sciences. With forewords by Jacques Demongeot and Glenn Webb. Springer, Cham, 2022, pp. xx+458. DOI: 10.1007/978-3-030-98136-5.
- [19] 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.
- [20] 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.
- [21] 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.
- [22] G. Hardin. The competitive exclusion principle. *Science* **131.3409** (1960), pp. 1292–1297.
- [23] 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.
- [24] S.-B. Hsu. Limiting behavior for competing species. *SIAM J. Appl. Math.* **34.4** (1978), pp. 760–763. DOI: 10.1137/0134064.
- [25] 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.
- [26] 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.
- [27] 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.
- [28] 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.
- [29] W. O. Kermack and A. G. McKendrick. A Contribution to the Mathematical Theory of Epidemics. *Proceedings of the Royal Society of London A: Mathematical, Physical and Engineering Sciences* **115.772** (1927), pp. 700–721. DOI: 10.1098/rspa.1927.0118.
- [30] 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.
- [31] 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.
- [32] 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.

- [33] 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.
- [34] 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.
- [35] 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.
- [36] 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.
- [37] 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.
- [38] 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.
- [39] 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.
- [40] H. L. Smith. Competitive coexistence in an oscillating chemostat. *SIAM J. Appl. Math.* **40.3** (1981), pp. 498–522. DOI: 10.1137/0140042.
- [41] 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.
- [42] 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.

Appendix

A The case of a unique fitness maximum

If the function $\alpha(x)$ has a unique global maximum in the support of 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 A.1 (The case of a unique global maximum). *Let Assumption 2.1 be satisfied. Suppose that the function $\alpha = \alpha(x)$ has a unique maximum α^* 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

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

B Existence of a regular metric projection

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 B.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*

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

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

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

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_∞ is not empty. However we see that, by definition of K_∞ , 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 σ -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 B.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 B.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 B.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 define $B_H(C, R)$ 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

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

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 σ -algebra, P_K is indeed Borel measurable. The Lemma is proved. $\square$

Theorem B.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 B.3 Proposition B.2. $\square$

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

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

Proof. Indeed, let us choose a Borel measurable metric projection P_K on K as in Theorem B.4. Let μ^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 $f \in BC(M)$ we have

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

Let $f \in \text{Lip}_1(M)$, then we have

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

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

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

The Proposition is proved. $\square$

C Disintegration of measures

C.1 Bourbaki's disintegration theorem

We recall the disintegration theorem as stated in [7, 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 [26, 27].

Let us first we recall some background on adequate families. This is adapted from [7, 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 C.1 (Scalarly essentially integrable family). Let $\Lambda : t \mapsto \lambda_t$ be a mapping from T into $\mathcal{M}_+(X)$. Λ is *scalarly essentially integrable* for the measure μ 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 ν , which is the *integral* of the family Λ , and we denote

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

Recall that every positive Borel measure μ 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 μ is a positive bounded linear functional on $C_c(X)$, there are two canonical ways to define a measure on the Borel σ -algebra.

1. Outer-regular construction. Let $U \subset X$ be an 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 [7, 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 [7, V.1, §1].

It is always true that $\mu^\bullet \leq \mu^*$, however it may happen that $\mu^* \neq \mu^\bullet$ when μ^* is not finite, see e.g. [5, II§7.11 p.113] or [7, V.1, §1]. If μ is a Borel measure, then we define the corresponding notions of $\mu^\bullet$ and μ^* associated with the linear functional $f \mapsto \int_X f(x) \mu(dx)$. Note that if μ is Radon, then $\mu^* = \mu = \mu^\bullet$.

Definition C.2 (Pre-adequate and adequate families). We follow [7, Definition 1, V.17§3]. Let $\Lambda : t \mapsto \lambda_t$ be a scalarly essentially μ -integrable mapping from T into $\mathcal{M}_+(X)$, ν the integral of Λ .

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

The last notion we need to define is the one of μ -proper function.

Definition C.3 (μ -proper function). We say that a function $p : T \rightarrow X$ is μ -proper if it is μ -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 μ is Radon, in particular, then every μ -measurable mapping $p : T \rightarrow X$ (X being equipped with the Borel σ -algebra) is μ -proper. The following Theorem is taken from [7, Theorem 1, VI.41 No.1, §3].

Theorem C.4 (Disintegration of measures). *Let T and X be two locally compact spaces having countable bases, μ be a positive measure on T , p be a μ -proper mapping of T into X , and $\nu = p(\mu)$ the image of μ under p . There exists a ν -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) λ_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 ν -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 ν .

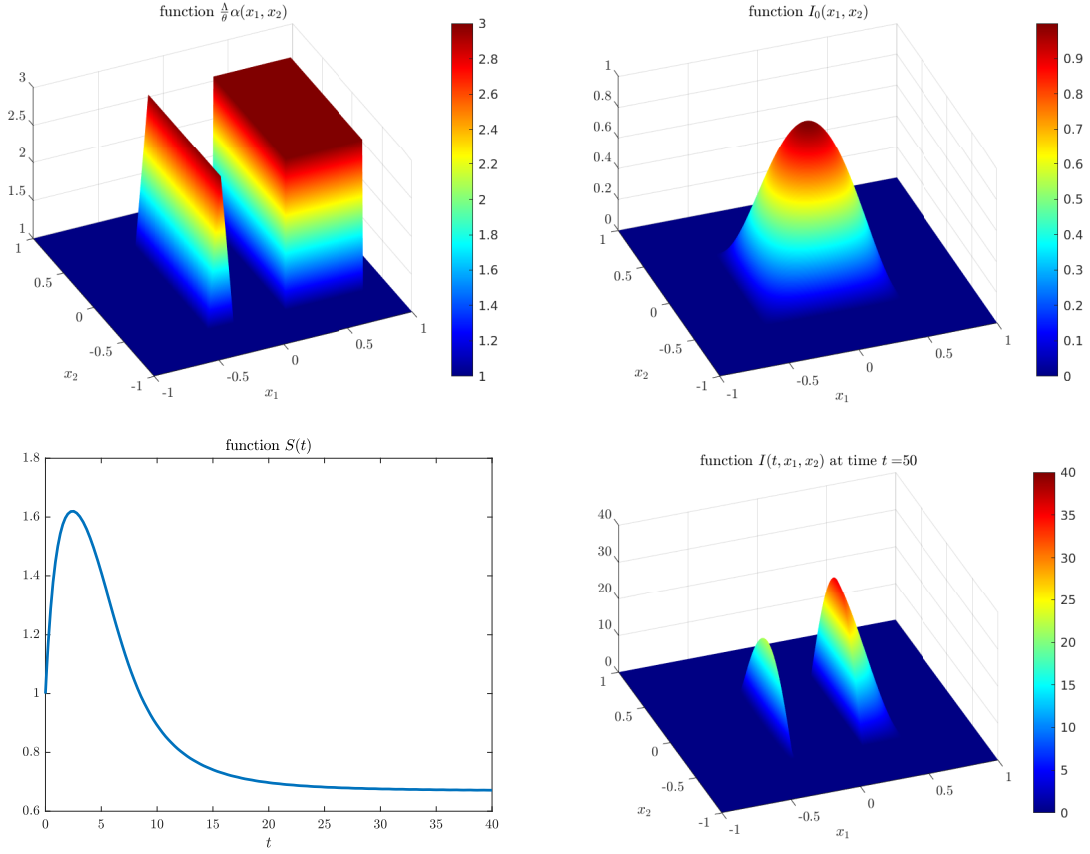


Figure 1: Illustration of Theorem 2.2 in the case i), *i.e.*, when $I_0(\{\alpha(x) = \alpha^*\}) > 0$. Parameters of this simulation are: $\Lambda = 2$, $\theta = 1$, $\alpha(x) = 0.5 + (\mathbb{T}_{[-0.4, -0.2]}(x_1) + \mathbb{1}_{[0.2, 0.8]}(x_1)) \mathbb{1}_{[-0.6, 0.6]}(x_2)$ where $x = (x_1, x_2) \in \mathbb{R}^2$ 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 $\{\alpha(x) = \alpha^*\} = (\{-0.3\} \cup [0.2, 0.5]) \times [-0.5, 0.5]$. 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 $\{\alpha(x) = \alpha^*\} = (\{-0.3\} \cup [0.2, 0.5]) \times [-0.5, 0.5]$.

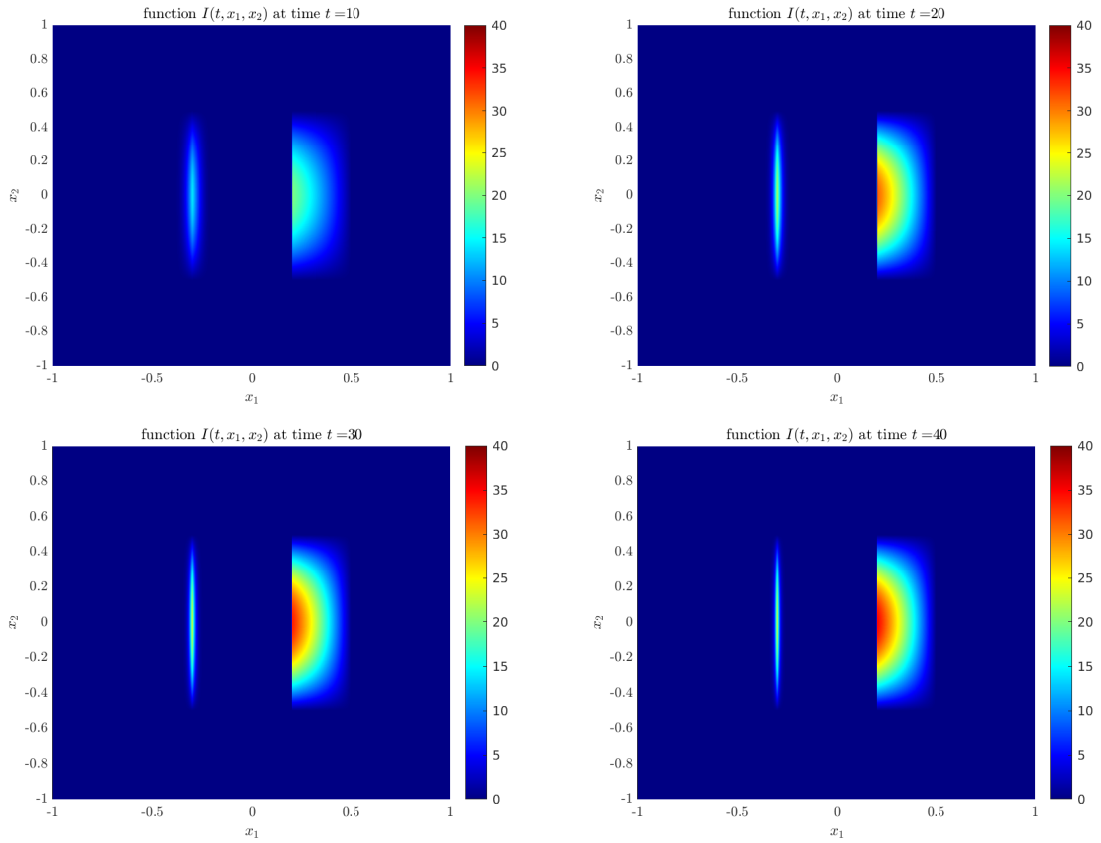


Figure 2: Illustration of Theorem 2.2 in the case i), *i.e.*, when $I_0(\{\alpha(x) = \alpha^*\}) > 0$. Function $x \rightarrow I(t, x)$ at time $t = 10, 20, 30$ and 40 . The function I remains bounded in this case.

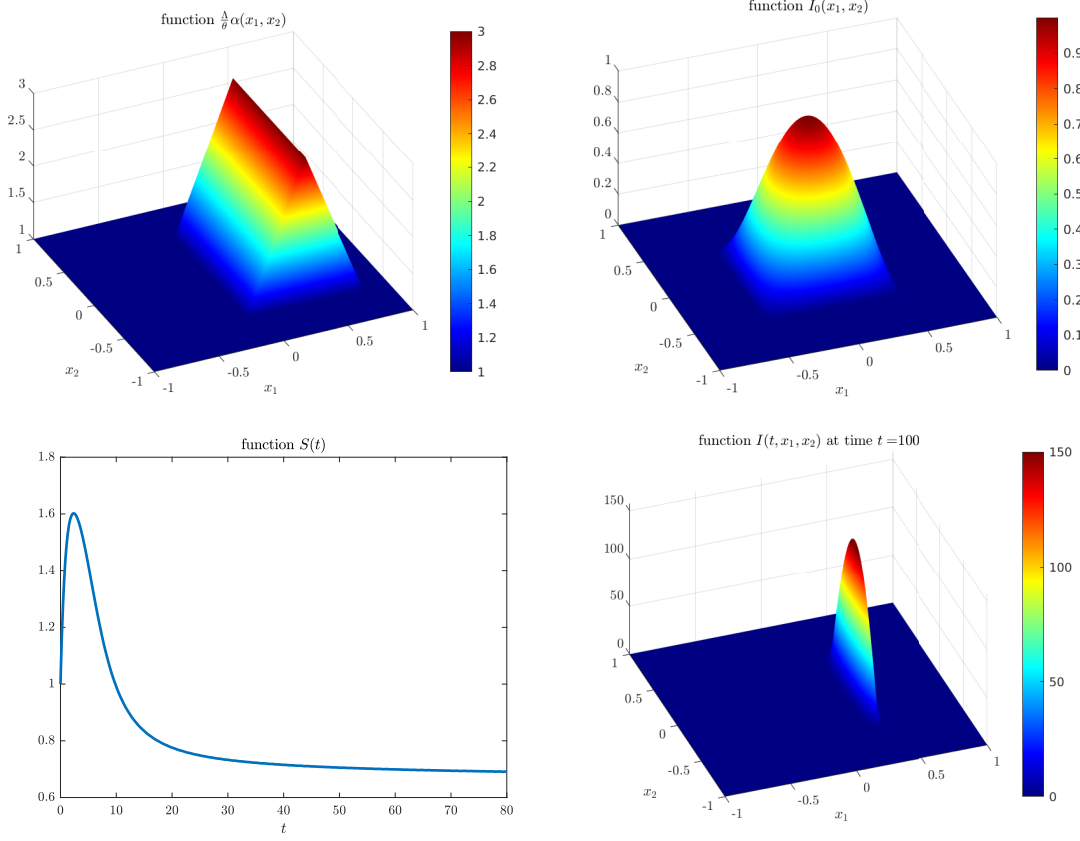


Figure 3: Illustration of Theorem 2.2 in the case ii), *i.e.*, when $\int_{\alpha(x)=\alpha^*} I_0(dx) = 0$. Parameters of this simulation are: $\Lambda = 2$, $\theta = 1$, $\alpha(x) = 0.5 + \mathbb{T}_{[-0.1, 0.8]}(x_1) \mathbb{1}_{[-0.5, 0.5]}(x_2)$ where $x = (x_1, x_2) \in \mathbb{R}^2$ and $\mathbb{T}_{[-0.1, 0.5]}$ 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 $\{\alpha(x) = \alpha^*\} = \{0.35\} \times [-0.5, 0.5]$. The function $t \rightarrow S(t)$ converges towards $1/\alpha^* = 2/3$. The function $x \rightarrow I(t, x)$ at time $t = 100$ is asymptotically concentrated on $\{\alpha(x) = \alpha^*\} = \{0.35\} \times [-0.5, 0.5]$.

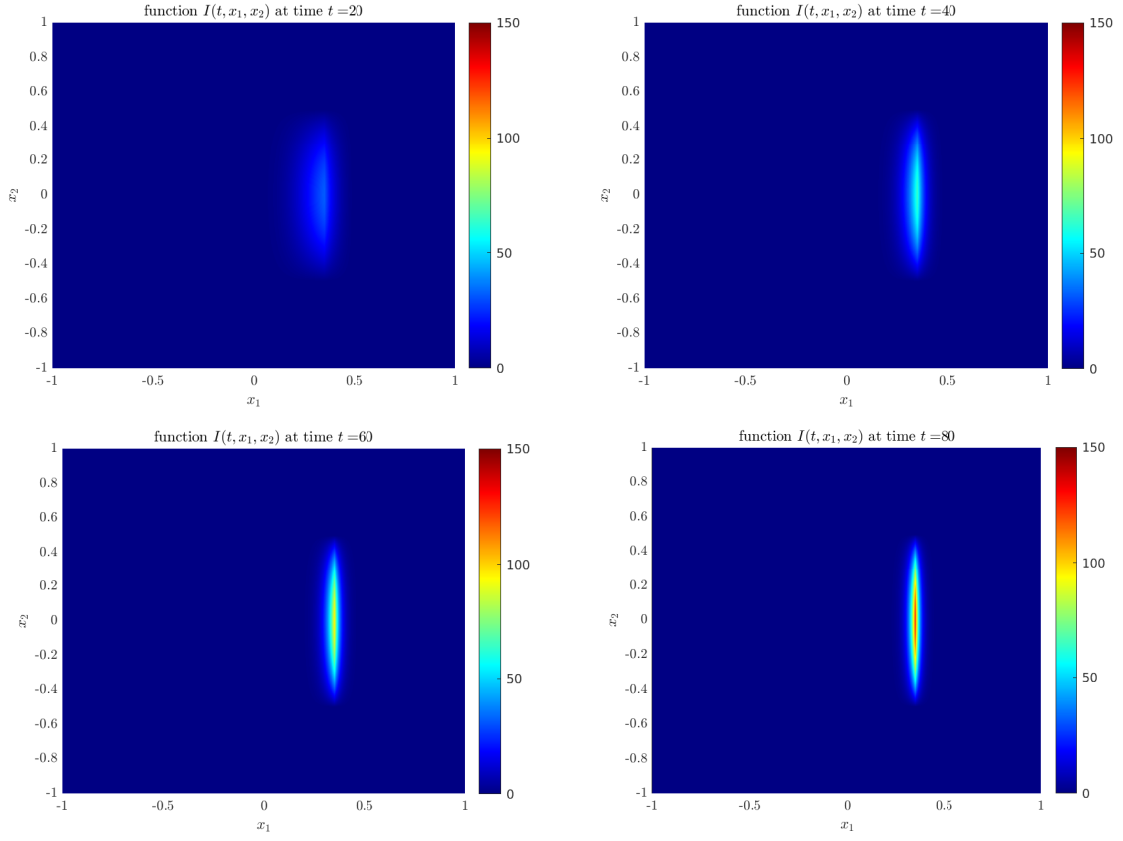


Figure 4: Illustration of Theorem 2.2 in the case ii), *i.e.*, when $I_0(\{\alpha(x) = \alpha^*\}) = 0$. Function $x \rightarrow I(t, x)$ at time $t = 20, 40, 60$ and 80 . The function I asymptotically converges towards a singular measure.

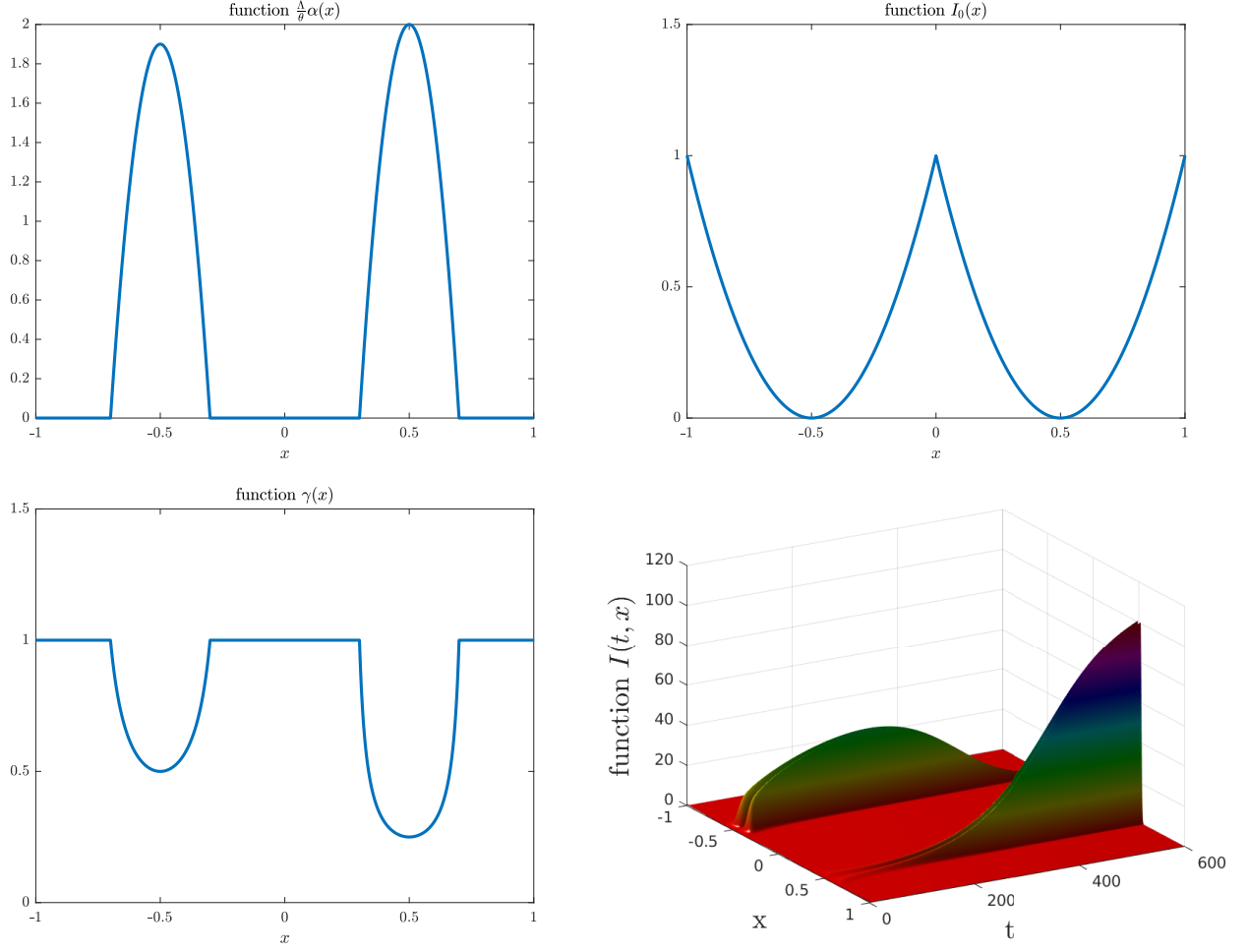


Figure 5: Illustration of a transient behavior for (2.1). Parameters of this simulation are: $\Lambda = 2$, $\theta = 1$, $\alpha(x)$ is given by (3.1), $I_0(x)$ by (3.2) and $\gamma(x)$ by (3.3). In particular, $\alpha^* = 1$, $\{\alpha(x) = \alpha^*\} = \{x_2\}$ with $x_1 = -0.5$, $x_2 = 0.5$. Other 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 α^* , observe that the distribution $I(t, x)$ first concentrates around x_1 before the global maximum x_2 becomes dominant (bottom right plot).

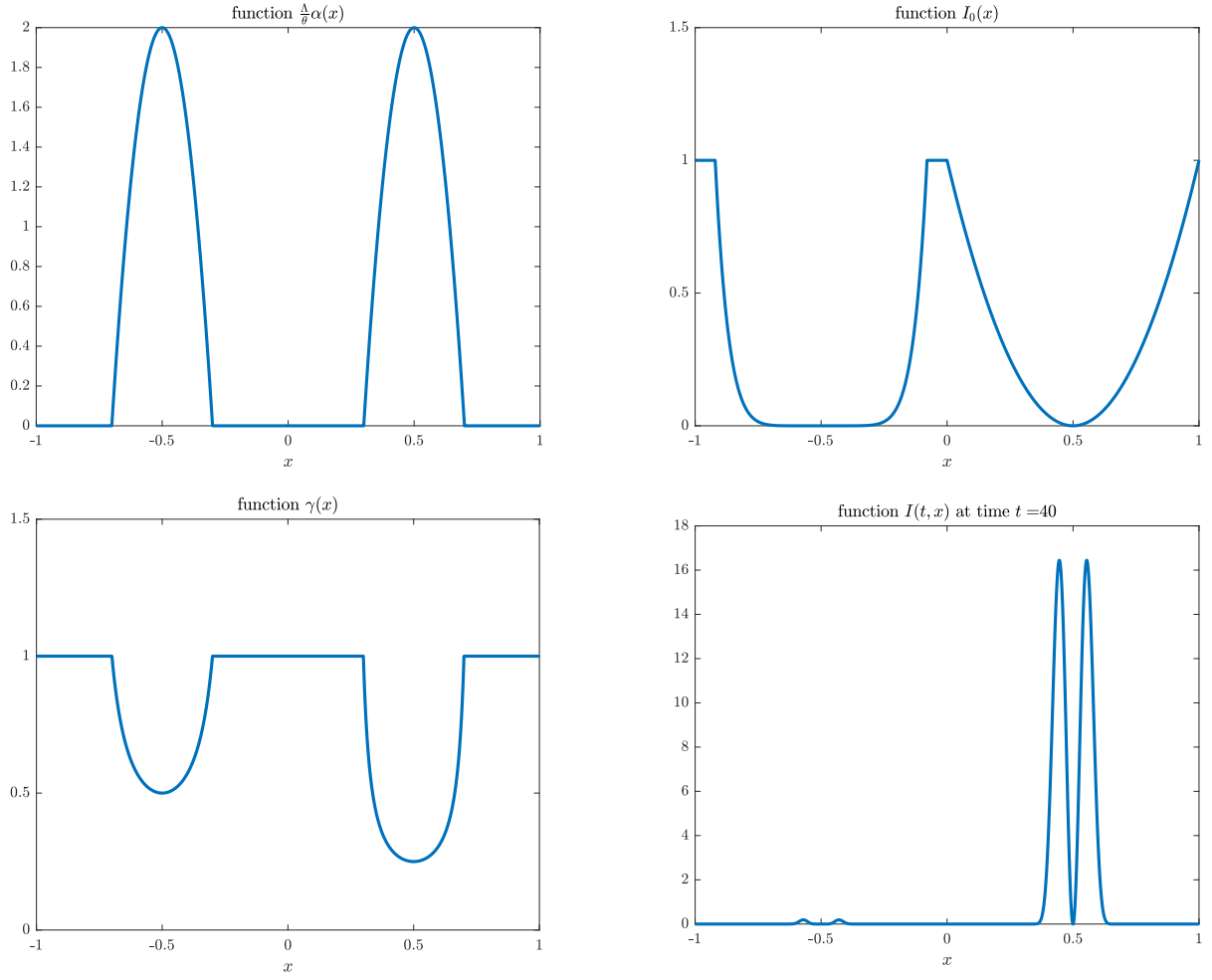


Figure 6: Illustration of Theorem 2.10 and Corollary 2.11. Parameters of this simulation are: $\Lambda = 2$, $\theta = 1$, $\alpha(x)$ is given by (3.4), $I_0(x)$ by (3.5) and $\gamma(x)$ by (3.6). In particular, $\alpha^* = 1$, $\{\alpha(x) = \alpha^*\} = \{x_1, x_2\}$ with $x_1 = -0.5$, $x_2 = 0.5$, $\kappa_1 = 8$, $\kappa_2 = 2$, $\gamma(x_1) = 1/2$, $\gamma(x_2) = 1/4$, $\rho = 6$ 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 ∞ , even though $\gamma(x_1) > \gamma(x_2)$, while around x_2 it takes the shape given by expression (2.11).

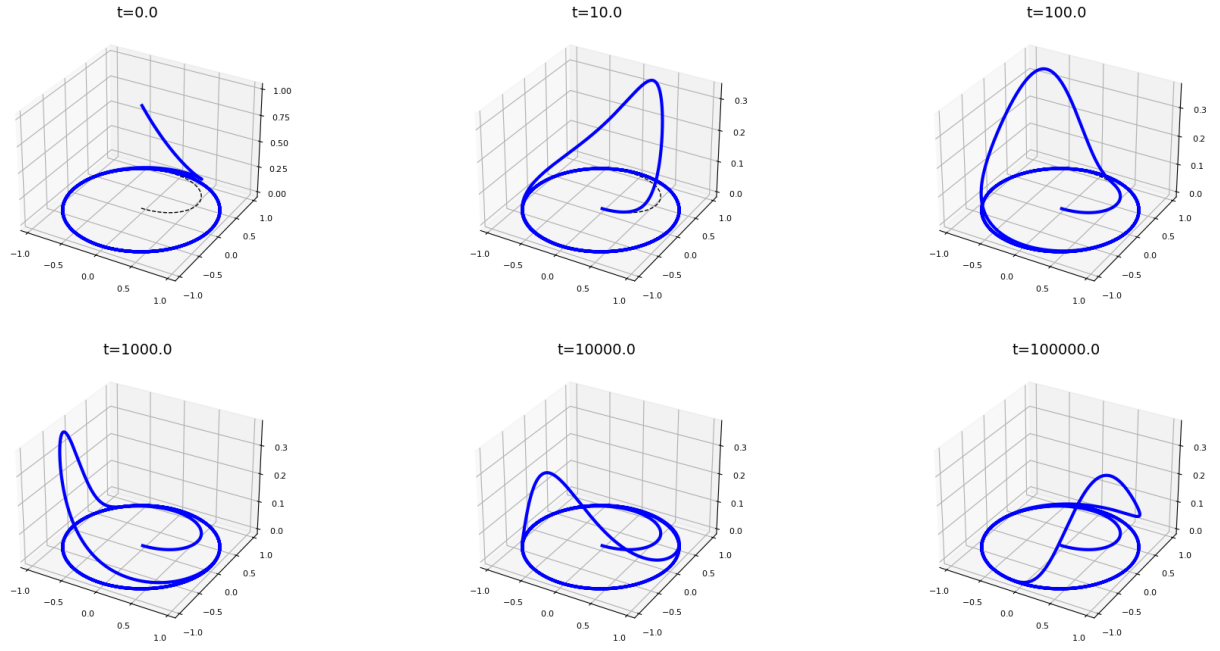


Figure 7: Numerical solution of the example provided in Section 2.3 of the main text with $L = 1$. The x, y axes correspond to the underlying physical space and we plot $I(t, \tau)$ on the z axis at every $x = (1 - e^{-\tau}) \cos(\tau)$ and $y = (1 - e^{-\tau}) \sin(\tau)$. The observation times are spaced exponentially from one another ($t = 0, 10, 10^2, 10^3, 10^4, 10^5$) to observe constant shifts of the fixed asymptotic profile. These plots are snapshots of the supplementary movie `spiraling.avi`.