ASYMPTOTIC SPEED OF SPREAD FOR A NONLOCAL EVOLUTIONARY-EPIDEMIC SYSTEM

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Abstract. We investigate spreading properties of solutions for a spatially distributed system of equations modelling the evolutionary epidemiology of plant-pathogen interactions. In this work the mutation process is described using a non-local convolution operator in the phenotype space. Initially equipped with a localized amount of infection, we prove that spreading occurs with a definite spreading speed that coincides with the minimal speed of the travelling wave solutions discussed in [1]. Moreover, the solution of the Cauchy problem asymptotically converges to some specific function for which the moving frame variable and the phenotype one are separated.

1. Introduction. In this note we investigate the long time behaviour and asymptotic speed of spread for the following spatially structured epidemic system of equations

\[
\begin{aligned}
\frac{\partial u}{\partial t}(t,x) &= \Lambda - \mu u(t,x) - u(t,x) \int_{\mathbb{R}^M} \beta(z) w(t,x,z) dz, \\
\frac{\partial v}{\partial t}(t,x,y) &= \beta(y) u(t,x)w(t,x,y) - \mu v(t,x,y), \\
\delta w(t,x,y) - D \frac{\partial^2 w}{\partial x^2}(t,x,y) &= \int_{\mathbb{R}^M} J(y - y') r(y') v(t,x',y') dy',
\end{aligned}
\]

posed for time \( t \in \mathbb{R}^+ \), spatial location \( x \in \mathbb{R} \) and phenotypic trait value \( y \in \mathbb{R}^M \), for some fixed integer \( M \geq 1 \). The above system is supplemented with some non negative initial conditions

\[
u(0,x) = u_0(x), \quad v(0,x,y) = v_0(x,y),
\]

whose specific properties are detailed in Section 2 below.

The above system of equations describes the spatial evolutionary epidemiology of a fungal disease within a spatially distributed plant population.

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In [10], a similar non spatial but more detailed model has been introduced to investigate the gain achieved by the deployment of a crop variety resistant to the disease before this resistance is overcome. The model makes it possible to predict the evolution of some phenotypic traits of the pathogen such as the spore infection efficiency in response to the resistance of the plant host. More recently, a spatially explicit stochastic simulation model has been devised to achieve the same study in [20] allowing various deployment strategies in space and time and taking into account realistic landscapes.

Model (1)-(2) describes the spatio-temporal dynamic of healthy plant density $u(t, x)$ with respect to time $t$ and spatial location $x \in \mathbb{R}$, of infected plant density $v(t, x, y)$ (i.e. the plant surface density bearing spore colonies) where $y \in \mathbb{R}^M$ is the phenotypic trait of the disease variant, and of density of spores produced in the environment $w(t, x, y)$.

The parameters of the model are the following. The vital dynamics parameters are $\Lambda > 0$ the influx of healthy plant density while $\mu > 0$ and $\mu_v > 0$ are the healthy and infected plant death rates respectively. The disease transmission rate depends on the trait value $y$ and is denoted by $\beta(y)$. Contamination of the plant occurs due to the deposition on the foliar surface of the spores released in the environment by the fungal colonies. The production rate of spores by the colonies denoted by $r(y)$ is the second parameter that depends on the phenotypic trait. Spores produced by a colony associated to a trait value $y'$ may mutate to trait $y$ with respect to the probability kernel $J(y - y')$. We have assumed that the spores dispersal obeys a rapid diffusion process of coefficient $D$ before settling on the plant surface with deposition rate $\delta$.

Before going further, we simplify this model using parameter rescaling by setting $\delta = D = \mu = 1$. Let $K = K(x)$ denotes the fundamental solution of the elliptic operator $(1 - \frac{\partial^2}{\partial x^2})$, that is

$$K(x) = \frac{1}{2} e^{-|x|}, \quad x \in \mathbb{R},$$

then system (1) rewrites as the following nonlocal system

$$\begin{align*}
\frac{\partial u}{\partial t}(t, x) &= \Lambda - u(t, x) - u(t, x) \int_{\mathbb{R}^M} \beta(z) w(t, x, z) dz, \\
\frac{\partial v}{\partial t}(t, x, y) &= \beta(y) u(t, x) w(t, x, y) - \mu_v v(t, x, y),
\end{align*}
$$

wherein we have set

$$w(t, x, y) = \int_{\mathbb{R}} \int_{\mathbb{R}^M} K(x - x') J(y - y') r(y') v(t, x', y') dx' dy'.
$$

In a previous work, see [1], the authors studied the existence of travelling solutions for the above system of equations, namely (1) or equivalently (4). Introducing the so-called basic reproduction number $R_0$ given by

$$R_0 = \frac{\lambda_1 \Lambda}{\mu_v},$$

where $\lambda_1 > 0$ is the principal eigenvalue of some linear operator related to the mutation kernel $J$, the authors proved the existence of a unique endemic steady state if and only if $R_0 > 1$ as well as the existence of travelling wave solutions connecting
the disease free steady state \((u, v) = (\Lambda, 0)\) and this unique endemic steady state, for any wave speed \(c\) greater than some minimal speed \(c^* > 0\). Furthermore, the authors also proved that any travelling wave solutions (with speed \(c\)) exhibit a simple shape, separating the moving frame spatial variable, \(x-ct\), from the phenotype trait variable, \(y \in \mathbb{R}^M\).

As mentioned above, the aim of the work is to study the long time behaviour of (2)-(4) as well as the asymptotic speed of spread of infection, when the initial amount of infection, \(v_0 = v_0(x, y) \geq 0\), is a compactly supported function with respect to the \(x\)-variable. Roughly speaking in that case and when \(R_0 > 1\), we shall show that the infection spreads with the speed \(c^*\), the minimal wave speed of the travelling waves. Furthermore the profile of infection, \(v = v(t, x, y)\), asymptotically decouples the spatio-temporal variables, \((t, x)\), from the phenotype trait variable, \(y \in \mathbb{R}^M\).

To analyse the spatial spread for System (4), one may notice that the comparison principle does not directly apply to the system and one has to overcome this difficulty. Such a lack of comparison principle typically arises when studying predator-prey interaction and epidemic systems, such as the one we consider in this work.

The description of spatial propagation for diffusive predator-prey systems and epidemic problems has a long history. In particular, travelling wave solutions have been exhibited for a wide range of systems. As far as epidemic problems are concerned, we refer for instance to [21] for a survey, and to [8, 11] and the references therein for recent results on reaction-diffusion systems with mutations.

The spreading dynamics for such non-monotone problems has been scarcely studied in the literature and as far as we know no general method has been developed. Quite recently analysis of the spreading properties for the solutions of non-cooperative and non-competitive systems (of epidemic and predator-prey type) has been performed. We refer the reader to [4, 6, 9, 12, 14, 18, 19, 25] for system with local diffusion, to [7, 28] for non-monotone systems with nonlocal diffusion. We also refer to [5, 26] for studies of the spreading behaviour for three interacting (competitive coupled with predator-prey interactions) species.

In this note, our spreading speed analysis extends to nonlocal diffusion some dynamical system ideas used in [4, 5, 6] for systems with local diffusion to overcome the lack of comparison principle. More specifically our analysis is mostly based on ideas coming from the uniform persistence theory for semiflows, for which we refer the reader to [13, 16, 23] and the references cited therein. Next the asymptotic shape (separation of the variables) as \(t \to \infty\) of the solution of the Cauchy Problem (2)-(4) is obtained by a careful comparison of the projections of the solution over all the eigenmodes of the mutation kernel operator.

This work is organized as follows: Section 2 is devoted to the assumptions and to the main result of this work, namely Theorem 2.1. We also briefly state some results on the spectral properties of some nonlocal operator involved in the modelling of the mutations. Section 3 deals with preliminary results needed for the proof of Theorem 2.1. In particular we prove the well-posedness and asymptotic compactness properties of the solutions of Model (4). The next sections contain the proofs of our main result. In Section 4, we prove the outer spreading property while the inner spreading one is handled in Section 5. Finally, Section 6 is concerned with the proof of the asymptotic variables separation result.
2. Assumptions and main results. In this section we state and discuss the main results that will be proved in this manuscript. Before going to our main spreading result, Theorem 2.1 below, we first introduce our main assumptions, preliminary materials and useful notations.

We first deal with the phenotype trait specific functions, $J$, $r$ and $\beta$. Along this note we assume the following set of hypothesis

**Assumption 1.** We assume that

a) the mutation kernel $J$ is positive, continuous and $J \in L^1(\mathbb{R}^M) \cap L^\infty(\mathbb{R}^M)$. Also $J$ symmetric with respect to the origin, that is $J(-y) = J(y)$ for all $y \in \mathbb{R}^M$, and it has a unit mass, that is $\int_{\mathbb{R}^M} J(y)dy = 1$.

Moreover for every $R > 0$, the function $y \mapsto \sup_{\|y'\| \leq R} J(y + y')$ belongs to $L^1(\mathbb{R}^M)$.

b) Functions $r, \beta: \mathbb{R}^M \to \mathbb{R}$ are both continuous, non-negative. They enjoy the following behaviour: $(r(y), \beta(y)) \to (0, 0)$ as $\|y\| \to \infty$. In particular, they are bounded and uniformly continuous.

The product function $y \mapsto r(y)\beta(y)$ belongs to $L^1(\mathbb{R}^M)$ and is not identically zero.

We now turn to the assumptions we shall impose for the initial data $(u_0,v_0)$ arising in (2). To do so, for each ordered Banach space $X$, with positive cone $X^+$, we denote by $C^0_b(I; X)$ and $C^0_b(I; X^+)$ the space of bounded continuous functions on the non empty set $I$ into $X$ and $X^+$, respectively, supplemented with the $L^\infty$-norm.

We now make the following assumption on the initial conditions of problem system (4).

**Assumption 2.** Denoting by $L^1_+(\mathbb{R}^M)$ the cone of the non-negative function in $L^1(\mathbb{R}^M)$, we assume that $(u_0,v_0) \in C^0_b(\mathbb{R}; X^+) \times C^0_b(\mathbb{R}; L^1_+(\mathbb{R}^M))$ satisfies

(i) $0 \leq u_0(x) \leq \Lambda$ for all $x \in \mathbb{R}$;

(ii) the function $x \mapsto \int_{\mathbb{R}^M} v_0(x,y)dy$ is compactly supported, $\int_{\mathbb{R}^M} r(y)v_0(x,y)dy \neq 0$ and there exists some constant $c_0 > 0$ such that

$0 \leq v_0(x,y) \leq c_0\beta(y)$ a.e. for $y \in \mathbb{R}^M$ and for all $x \in \mathbb{R}$.

First note that for any $(u_0, v_0) \in C^0_b(\mathbb{R}; X^+) \times C^0_b(\mathbb{R}; L^1_+(\mathbb{R}^M))$, System (4) admits a unique non negative and globally defined solution $t \mapsto (u(t), v(t))$ that is continuously differentiable from $[0, \infty)$ into $C^0_b(\mathbb{R}; X^+) \times C^0_b(\mathbb{R}; L^1_+(\mathbb{R}^M))$ (see Proposition 2 in the next section).

Now, let us consider $\Omega \subset \mathbb{R}^M$ the non empty open set (see Assumption 1 b)) defined as

$\Omega = \{y \in \mathbb{R}^M, r(y)\beta(y) > 0\}$. \hfill (7)

Let $\gamma: \mathbb{R}^M \to \mathbb{R}^+$ be the non negative function defined as

$\gamma(y) = \frac{r(y)}{\beta(y)}$ if $\beta(y) > 0$, and 0 elsewhere.

Note that the support of the continuous function $\gamma$ is the closure of $\Omega$. Now let $L^2_+(\mathbb{R}^M)$ be the weighted $L^2$-space defined as the set of measurable functions on $\mathbb{R}^M$ such that $\int_{\mathbb{R}^M} f^2(y)\gamma(y)dy < \infty$. In particular we have

$f \in L^2_+(\mathbb{R}^M)$ if $f$ is measurable and $f\sqrt{\gamma} \in L^2(\mathbb{R}^M)$. 


The norm of $L^2_\gamma(\mathbb{R}^M)$, denoted by $\| \cdot \|_{2,\gamma}$, is given by
\[
\| f \|_{2,\gamma} = \left( \int_{\mathbb{R}^M} f^2(y)\gamma(y)dy \right)^{1/2}, \quad \forall f \in L^2_\gamma(\mathbb{R}^M).
\]
Before going to our main spreading result, we need to introduce the mutation operator as well as some spectral properties. Consider the bounded linear mutation operator $\mathcal{L} \in \mathcal{L} (L^1(\mathbb{R}^M))$ defined as follows
\[
\mathcal{L}[\varphi](y) = \int_{\mathbb{R}^M} \beta(y)J(y-y')r(y')\varphi(y')dy', \quad \forall \varphi \in L^1(\mathbb{R}^M),
\]
as well as its formal adjoint operator, $\mathcal{L}^* \in \mathcal{L} (L^1(\mathbb{R}^M))$, given by
\[
\mathcal{L}^*[\varphi](y) = \int_{\mathbb{R}^M} r(y)\beta(y')J(y-y')\varphi(y')dy', \quad \forall \varphi \in L^1(\mathbb{R}^M).
\]
Then these two positive operators enjoy the following Perron-Frobenius property.

**Proposition 1.** Let $\lambda_1 = \rho(\mathcal{L})$ denote the spectral radius of the operator $\mathcal{L}$. Then the following assertions hold true

(i) $\rho(\mathcal{L}) > 0$ and there exists a non negative eigenfunction $\varphi_1 \in C_b(\mathbb{R}^M) \cap L^2_\gamma(\mathbb{R}^M) \cap L^p_\gamma(\mathbb{R}^M)$, for all $p \in [1, \infty]$, associated to $\lambda_1$. In the sequel it is normalized so that $\| \varphi_1 \|_{2,\gamma} = 1$. Moreover, $\varphi_1$ is positive on $\Omega$.

(ii) $\rho(\mathcal{L}^*) = \rho(\mathcal{L})$ and there exists a non negative eigenfunction $\varphi_1^* \in C_b(\mathbb{R}^M) \cap L^p_\gamma(\mathbb{R}^M)$ for all $p \in [1, \infty]$ of $\mathcal{L}^*$ associated to $\rho(\mathcal{L})$. Moreover it is positive on $\Omega$.

As recalled in the introduction, we define $\mathcal{R}_0$ as in (6) where $\lambda_1 = \rho(\mathcal{L})$ and throughout that work we assume that $\mathcal{R}_0 > 1$.

This assumption biologically means that the disease will spread. The above condition is always assumed and not recalled. Now we define the minimal wave speed $c_\ast$ as in [1] by
\[
c_\ast := \inf_{0 < \lambda < 1} \frac{\mu_v}{\lambda} \left( \frac{\mathcal{R}_0}{1 - \lambda^2} - 1 \right).
\]
Note that $c_\ast$ is related to the function $\mathcal{K}(c, \lambda)$ defined by
\[
\mathcal{K}(c, \lambda) := (1 - \lambda^2)(c\lambda + \mu_v) - \mu_v\mathcal{R}_0.
\]
through the following characterisation: $c_\ast$ satisfies the following assertions
\[
\begin{cases}
\forall c \in (0, c_\ast), \quad \forall \lambda \in (0, 1), \quad \mathcal{K}(c, \lambda) < 0, \\
\mathcal{K}(c_\ast, \lambda) = 0 \text{ has a unique solution in } (0, 1), \\
\forall c > c_\ast, \quad \mathcal{K}(c, \lambda) = 0 \text{ has two solutions in } (0, 1).
\end{cases}
\]
This property will also be used in our analysis.

We are now able to state the main spreading result we shall prove in this note, that reads as follows.

**Theorem 2.1.** Let Assumptions 1 and 2 be satisfied. Then the solution $(u, v)$ of (4) with initial conditions $(u_0, v_0)$ satisfies the following properties.

Let $v_1 = v_1(t, x)$ be defined as
\[
v_1(t, x) = \int_{\mathbb{R}^M} v(t, x, y)\varphi_1^*(y)dy,
\]
where $\varphi_1^*$ is related to the function $\varphi_1$ and $\lambda_1$ as in (8) below.

\[
\begin{align*}
\int_{\mathbb{R}^M} v(t, x, y)\varphi_1^*(y)dy &= \int_{\mathbb{R}^M} v(t, x, y)\varphi_1(y)dy \\
&= \int_{\mathbb{R}^M} v(t, x, y)\varphi_1^*(y)dy \\
&= \int_{\mathbb{R}^M} v(t, x, y)\varphi_1^*(y)dy \\
&= \int_{\mathbb{R}^M} v(t, x, y)\varphi_1^*(y)dy.
\end{align*}
\]
then $v_1$ enjoys the following asymptotic speed of spread behaviour

(i) **Outer spreading property:** For all $c > c_\star$ it holds that
$$\lim_{t \to \infty} \sup_{|x| \geq ct} v_1(t, x) = 0.$$

(ii) **Inner spreading property:** For all $0 \leq c < c_\star$ it holds that
$$\lim_{t \to \infty} \inf_{|x| \leq ct} v_1(t, x) > 0.$$

Furthermore the solution $v$ looks like $v_1 \varphi_1$ for the large time, in the sense that it satisfies the following asymptotic behaviour

(iii) **Separation of variables for large times:** The function $v$ belongs to the space $C_0^b([0, \infty) \times \mathbb{R}; L_2^\gamma(\mathbb{R}^M))$ and as $t$ goes to infinity, the $v$-component of the solution converges towards its projection on the eigenspace spanned by $\varphi_1$ in the following sense
$$\lim_{t \to \infty} \sup_{x \in \mathbb{R}} \|v(t, x, \cdot) - v_1(t, x) \varphi_1(\cdot)\|_{2, \gamma} = 0.$$

The above convergence also holds in $L^1(\mathbb{R}^M)$, uniformly for $x \in \mathbb{R}$.

Note that the above result shows that $v(t, x, y) \approx v_1(t, x) \varphi_1(y)$ for $t \gg 1$, uniformly for $x \in \mathbb{R}$ and some strong topology in $y$, while $v_1$ spreads at the speed $c_\star$. As a consequence the epidemics propagates with the spreading speed $c_\star$ as time goes to infinity. Moreover in the phenotype trait space, the distribution of the persistent strains of the disease follows the shape of the principle eigenvector $\varphi_1 = \varphi_1(y)$. This shape strongly depends on the three functions $J$, $r$ and $\beta$. Sufficient conditions for this eigenfunction to be unimodal, and thus for the population to be roughly monomorphic, have been discussed in [3] in the case where the mutation kernel is narrow.

The proof of (i) makes use of a suitable super-solution while the proof of (ii) is based on a careful examination of the translates of the solution in suitable moving frames coupled with the construction of a suitable sub-solution on some moving interval. Finally the proof of (iii) follows from a refined analysis of the projection of the solution on the eigenspace decomposition associated with the operator $L$.

Here our analysis strongly relies on the spreading properties of the function $v_1$, (i) and more importantly (ii), to compare the projection of the solution on the higher eigenmodes and $v_1$.

3. **Preliminary results.**

3.1. **Well-posedness of model (4).** To prove the existence of the solutions of the Cauchy Problem (2)-(4), we rewrite the system as an abstract ODE in a suitable Banach space. To that aim, let us recall the definition of $\mathcal{L}$ in (8) and of the spatial kernel $K$ in (3). Next, let us consider the bounded linear operator $\widehat{\mathcal{L}} : C_0^b(\mathbb{R}, L^1(\mathbb{R}^M)) \to C_0^b(\mathbb{R}, L^1(\mathbb{R}^M))$ given by
$$\widehat{\mathcal{L}}[\psi](x, \cdot) = \beta(\cdot) \int_{\mathbb{R}^M} K(x - x') J(\cdot - y') r(y') \psi(x', y') \, dx' \, dy', \quad (13)$$
as well as $\widetilde{\mathcal{L}} \in \mathcal{L}(C_0^b(\mathbb{R}, L^1(\mathbb{R}^M)); C_0^b(\mathbb{R}))$ by
$$\widetilde{\mathcal{L}}[\psi](\cdot) = \int_{\mathbb{R}^M} \widehat{\mathcal{L}}[\psi](\cdot, y) \, dy. \quad (14)$$
Using the above bounded operators, we now turn to the well-posedness of the Cauchy problem associated to (4). To do so consider the Banach space $E = C^0_0([0, T_{\text{max}}]) \times C^0_0([-\infty, \infty])$ and its positive cone $E_+ = C^0_0([0, T_{\text{max}}]) \times C^0_0([-\infty, \infty])$. Consider the map $F : E \to E$ given by

$$F(X) = \left( \begin{array}{c} \Lambda - u - u\tilde{L}[v] \\ u\tilde{L}[v] - \mu_v v \end{array} \right), \quad \forall X = \left( \begin{array}{c} u \\ v \end{array} \right) \in E.$$ 

Hence, setting $X(t) = (u(t, \cdot), v(t, \cdot))^T \in E$, Problem (2)-(4) rewrites as the following ODE on the Banach space $E$:

$$\frac{dX(t)}{dt} = F(X(t)), \quad t \geq 0 \text{ with } X(0) = (u_0, v_0)^T \in E_+. \quad (15)$$

Next the following well-posedness result holds.

**Proposition 2.** The following assertions hold

(i) Let $X(0) = (u_0, v_0)^T \in E_+$ be given. Then System (4) with initial data $(u_0, v_0)$ (or equivalently (15)) admits a unique globally defined solution $X(t) = (u(t), v(t)) \in C^1([0, \infty), E_+)$, that is furthermore uniformly bounded in $E$ while $u$ satisfies

$$\liminf \inf_{t \to \infty} \inf_{x \in \mathbb{R}} u(t, x) > 0.$$

(ii) Let $(u_0, v_0) \in E_+$ be some initial data satisfying Assumption 2. Then the associated solution solution $(u, v)$ satisfies

$$0 \leq u(t, x) \leq \Lambda, \quad \forall t \geq 0, \quad x \in \mathbb{R},$$

and there exists some constant $M > 0$ such that

$$0 \leq v(t, x, y) \leq M\beta(y), \quad (t, x) \in \mathbb{R}^+ \times \mathbb{R} \text{ and a.e. } y \in \mathbb{R}^M.$$

**Proof.** First note that the map $F$ is locally Lipschitz continuous on $E$ so that (15) admits a unique maximal solution in $X \in C^0([0, T_{\text{max}}], E)$ for some $T_{\text{max}} > 0$.

Now let $M > 0$ be given. Then for $\lambda = \max(\mu_v, 1 + \|\beta\|_\infty \|r\|_\infty M)$ we have $F(X) + \lambda X \in E_+$ for all $X \in E_+$ with $\|X\|_E \leq M$. As a consequence the local solution $X$ belongs to $C^0([0, T_{\text{max}}], E_+)$ for all initial data $X_0 \in E_+$.

Next we prove the boundedness of the solution, let $X_0 = (u_0, v_0)^T \in E_+$ be given and let $(u, v)$ denote the corresponding maximal solution. First note that since $v \geq 0$ then $u$ satisfies

$$\partial_t u \leq \Lambda - u(t, x),$$

that is, for all $t$ and $x$

$$u(t, x) \leq \Lambda + (u_0(x) - \Lambda)e^{-t}.$$ 

(16)

This shows that $u$ is bounded. Now set

$$n(t, x) = u(t, x) + \int_{\mathbb{R}^M} v(t, x, z)dz.$$ 

Then, integrating the $v-$equation in (4) with respect to the variable $y$ and adding-up the $u-$equation yields

$$\partial_t n(t, x) = \Lambda - u(t, x) - \mu_v \int_{\mathbb{R}^M} v(t, x, z)dz,$$

which implies

$$\partial_t n(t, x) \leq \Lambda - \min(1, \mu_v)n(t, x).$$
This yields
\[
n(t, x) \leq n(0, x) e^{-\min(1, \mu_v)} + \frac{\Lambda}{\min(1, \mu_v)} \left(1 - e^{-\min(1, \mu_v)} \right), \quad \forall t \geq 0, \ \forall x \in \mathbb{R}.
\]
This ensures that the positive solutions of (15) are globally bounded in time, and thus globally defined. Now since \( v(t, \cdot, \cdot) \) is uniformly bounded in \( C^0_b(\mathbb{R}; L^1(\mathbb{R}^M)) \), there exists some constant \( N > 0 \) such that
\[
\bar{L}[v(t, \cdot, \cdot)](x) \leq N, \quad \forall t \geq 0, \ \forall x \in \mathbb{R}.
\]
We now infer from the \( u \)-equation that
\[
\partial_t u(t, x) \geq \Lambda - (1 + N) u(t, x),
\]
so that, for all \( t \geq 0 \) and \( x \in \mathbb{R} \), we get
\[
u(t, x) \geq \frac{\Lambda}{1 + N} + \left( u_0(x) - \frac{\Lambda}{1 + N} \right) e^{-(1+N)t},
\]
and (i) follows.

To check (ii), first note that the estimate for \( u \) directly follows from (16). Let us now complete the proof for the \( v \)-estimate. To see this recall that Problem (4) writes for the non-negative \( v \)-component
\[
\partial_t v(t, x, y) = \beta(y) u(t, x) K * x J * y (rv)(t, x, y) - \mu_v v(t, x, y).
\]
Herein we have used \( *_x \) and \( *_y \) to denote the convolution product with respect to \( x \in \mathbb{R} \) and \( y \in \mathbb{R}^M \), respectively. Next since \( 0 \leq u \leq \Lambda \) and \( J * y (rv) \) is bounded uniformly for \( t \in \mathbb{R}^+ \), \( x \in \mathbb{R} \) and \( y \in \mathbb{R}^M \), there exists some constant \( M_1 > 0 \) such that
\[
\forall (t, x, y) \in \mathbb{R}^+ \times \mathbb{R} \times \mathbb{R}^M, \quad \partial_t v(t, x, y) \leq M_1 \beta(y) - \mu_v v(t, x, y),
\]
hence we get
\[
0 \leq v(t, x, y) \leq \frac{M_1}{\mu_v} \beta(y) + e^{-\mu_v t} v_0(x, y).
\]
Finally since, \( v_0(x, y) \) is bounded by \( c_0 \beta(y) \) (see Assumption 2 (ii)), the estimate for \( v \) follows, which concludes the proof of the proposition.

**Remark 1.** Under Assumption 2 and more precisely recalling that one has \( x \mapsto \int_{\mathbb{R}^M} r(y) v_0(x, y) dy \neq 0 \) and since \( J > 0 \) and \( K > 0 \) one readily obtains that the solution \((u, v)\) satisfies
\[
v(t, x, y) > 0, \quad \text{for all } t > 0, \ x \in \mathbb{R} \ \text{and a.e. for } y \in \{ \beta > 0 \}.
\]

Hence \( v > 0 \) on \((0, \infty) \times \mathbb{R} \times \Omega \), where \( \Omega \) is defined in (7). On the other hand when the function \( x \mapsto \int_{\mathbb{R}^M} r(y) v_0(x, y) dy \equiv 0 \) then we have \( \int_{\mathbb{R}^M} r(y) v(t, x, y) dy \equiv 0 \) on \([0, \infty) \times \mathbb{R} \) and thus \( v(t, x, y) = 0 \) for all \((t, x) \in (0, \infty) \times \mathbb{R} \) and a.e. for \( y \in \Omega \).

3.2. **Compactness properties of the solutions.** In this section, we investigate asymptotic compactness for the positive solutions of (4), provided by Proposition 2. We start by deriving some estimates for the operator \( \mathcal{L} \) defined in (8).

**Lemma 3.1.** Under Assumption 1 the linear bounded operator \( \mathcal{L} \) is compact in \( L^1(\mathbb{R}^M) \). It indeed enjoys the following estimates:
Lemma 3.2

(i) For all $\varphi \in L^1(\mathbb{R}^M)$ and $h \in \mathbb{R}^M$ one has

$$\|\tau_h \mathcal{L}[\varphi] - \mathcal{L}[\varphi]\|_1 \leq \|r\|_{\infty} \|\tau_h \beta - \beta\|_{\infty} \|\varphi\|_1 + \|\beta\|_{\infty} \|\tau_h J - J\|_1 \|\varphi\|_1,$$

wherein $\tau_h$ denotes the translation operator in $L^1(\mathbb{R}^M)$, $\tau_h f(\cdot) = f(\cdot + h)$ for $h \in \mathbb{R}^M$ and $f \in L^1(\mathbb{R}^M)$.

(ii) Let $R, R' > 0$ be given. Then for all $\varphi \in L^1(\mathbb{R}^M)$ one has

$$\|\mathcal{L}[\varphi]\|_{L^1(\|y\| \geq R)} \leq \sup_{\|y\| \geq R} \beta(y) \left(\|r\|_{\infty} \int_{\|y\| \geq R} \sup_{\|y'\| \leq R' + 1} J(y + y') dy + \sup_{\|y'\| \geq R'} r(y')\right) \|\varphi\|_1.$$

Proof. All assertions but (ii) are straightforward using Young inequality for convolution products. For assertion (ii) we consider for $R' > 0$ a smooth and non-negative function $\chi_{R'} \leq 1$ satisfying

$$\chi_{R'}(y) = \begin{cases} 1, & \text{if } \|y]\| \leq R', \\ 0, & \text{if } \|y\| \geq R' + 1. \end{cases}$$

Then, for $R > 0$ and $\varphi \in L^1(\mathbb{R}^M)$ one has

$$\|\mathcal{L}[\varphi]\|_{L^1(\|y\| \geq R)} = \int_{\|y\| > R} \int_{\mathbb{R}^M} \beta(y) J(y - y') r(y') |\varphi(y')| (\chi_{R'}(y') + (1 - \chi_{R'}(y'))) dy'dy.$$

On the one hand we have

$$\int_{\|y\| > R} \int_{\mathbb{R}^M} \beta(y) J(y - y') r(y') |\varphi(y')| \chi_{R'}(y') dy'dy$$

$$\leq \sup_{\|y\| \geq R} \beta(y) \|r\|_{\infty} \int_{\|y\| \geq R} \sup_{\|y'\| \leq R' + 1} J(y + y') dy \|\varphi\|_1,$$

while on the other hand

$$\int_{\|y\| > R} \int_{\mathbb{R}^M} \beta(y) J(y - y') r(y') |\varphi(y')| (1 - \chi_{R'}(y')) dy'dy,$$

$$\leq \sup_{\|y\| \geq R} \beta(y) \sup_{\|y'\| \geq R'} r(y') \int_{\mathbb{R}^M} \int_{\mathbb{R}^M} J(y - y') |\varphi(y')| dy'dy$$

$$\leq \sup_{\|y\| \geq R} \beta(y) \sup_{\|y'\| \geq R'} r(y') \|\varphi\|_1,$$

and (ii) follows. \hfill \Box

Lemma 3.2 (Regularity estimates). Let $(u_0, v_0) \in E_+ \text{ be given, such that } u_0 \leq \Lambda$. Let $(u(t), v(t))$ denote the corresponding solution for $t \geq 0$. Then there exists some constant $M > 0$ such that for all $t \geq 0$, for all $x, h \in \mathbb{R}$ we have

$$|u(t, x + h) - u(t, x)| \leq |u_0(x + h) - u_0(x)| e^{-\frac{1}{2}t} + M \|K(h + \cdot) - K(\cdot)\|_{L^1(\mathbb{R})},$$

$$\|v(t, x + h, \cdot) - v(t, x, \cdot)\|_{L^1(\mathbb{R}^M)} \leq \|v_0(x + h, \cdot) - v_0(x, \cdot)\|_{L^1(\mathbb{R}^M)} e^{-\mu_0 t} + \alpha(t) M |u_0(x + h) - u_0(x)| + M \|K(h + \cdot) - K(\cdot)\|_{L^1(\mathbb{R})},$$

(18)

where $\alpha(t)$ is a positive function tending to $0$ as $t \to \infty$.

Moreover there exists some constant $M'$ such that for all $t \geq 0$ and $x \in \mathbb{R}$

$$|\partial_t u(t, x)| \leq M' \text{ and } \|\partial_t v(t, x, \cdot)\|_{L^1(\mathbb{R}^M)} \leq M'.$$
Corollary 1 (Asymptotic compactness of the orbits). Let \((u_0, v_0) \in E_+\) be given such that \(u_0 \leq \Lambda\). Let \((u(t), v(t))\) denotes the corresponding solution for \(t \geq 0\). Let \((t_j)_{j \geq 0}\) be a sequence of positive numbers tending to \(\infty\) as \(j \to \infty\) and \((x_j)_{j \geq 0} \subset \mathbb{R}\) be a given sequence. Then the sequence of function \((u_j, v_j) \subset E\) given for \(t \geq -t_j\) and \(x \in \mathbb{R}\) by

\[
u_j(t, x) = u(t + t_j, x + x_j) \quad \text{and} \quad v_j(t, x, \cdot) = v(t + t_j, x + x_j, \cdot),
\]
is relatively compact in \(C_{\text{loc}}(\mathbb{R}^2) \times C_{\text{loc}}(\mathbb{R}^2, L^1(\mathbb{R}^M))\).

Proof of Lemma 3.2. To prove the lemma, we make use of some ideas developed in [24] (see Theorem 4.2 in this paper). First recall that \(\hat{L}\) and \(\hat{\mathcal{L}}\) are defined in (13) and (14), respectively. Let \((u_0, v_0) \in E_+\) be given with \(u_0 \leq \Lambda\), and let \((u(t), v(t))\) denote the corresponding solution of (4). Since \(t \mapsto (u(t), v(t))\) is uniformly bounded in \(E\), we readily obtain the following preliminary regularity estimate: there exists some constant \(M_1 > 0\) such that for all \(t \geq 0\), \(x, z \in \mathbb{R}\), one has

\[
\|\hat{\mathcal{L}}[v](t, z, \cdot) - \hat{L}[v](t, x, \cdot)\|_{L^1(\mathbb{R}^M)} \leq M_1 \|K(z + \cdot) - K(x + \cdot)\|_{L^1(\mathbb{R})}. \tag{19}
\]

Next the function \(u = u(t, x)\) satisfies the following equation

\[
\partial_t u(t, x) = \Lambda - u(t, x) - u(t, x)\hat{L}[v](t, x).
\]

Then, for any \(t \geq 0\) and \(x, z \in \mathbb{R}\) one has

\[
\partial_t ((u(t, z) - u(t, x))^2) = 2(u(t, z) - u(t, x)) \left(-u(t, z) + u(t, x) - u(t, z)\hat{L}[v](t, z) + u(t, x)\hat{L}[v](t, x)\right),
\]

that rewrites as

\[
\partial_t ((u(t, z) - u(t, x))^2) = -2(u(t, z) - u(t, x))^2 - 2(u(t, z) - u(t, x))^2\hat{L}[v](t, x) - 2u(t, z)(u(t, z) - u(t, x)) \left(\hat{L}[v](t, z) - \hat{L}[v](t, x)\right).
\]

Since \(\hat{L}[v] \geq 0\), this implies

\[
\partial_t ((u(t, z) - u(t, x))^2) \leq -2(u(t, z) - u(t, x))^2 - 2u(t, z)(u(t, z) - u(t, x)) \left(\hat{L}[v](t, z) - \hat{L}[v](t, x)\right).
\]

Now since \(u_0 \leq \Lambda\) one has \(u \leq \Lambda\) and Young inequality ensures that

\[
\partial_t ((u(t, z) - u(t, x))^2) \leq -(u(t, z) - u(t, x))^2 + \Lambda^2 \left(\hat{L}[v](t, z) - \hat{L}[v](t, x)\right)^2.
\]

Next integrating this inequality with respect to time between \(0\) to \(t\) for some \(t \geq 0\) leads us to

\[
(u(t, z) - u(t, x))^2 \leq (u_0(z) - u_0(x))^2 e^{-t} + \Lambda^2 \sup_{0 \leq \tau \leq t} \left(\hat{L}[v](\tau, z) - \hat{L}[v](\tau, x)\right)^2,
\]

combined with (19), it yields the first estimate in (18).

Next we similarly prove that functions \(v(t, x, \cdot)\) satisfies the second estimate in (18). To that aim, recall that for \(t \geq 0\), \(x, y \in \mathbb{R}\) and \(y \in \mathbb{R}^M\) one has

\[
\partial_t (v(t, x, y) - v(t, z, y)) = -\mu_v (v(t, x, y) - v(t, z, y)) + u(t, x)\hat{L}[v](t, x, y) - u(t, z)\hat{L}[v](t, z, y).
\]
Hence, integrating the above equation from 0 to \( t \geq 0 \) yields
\[
v(t, x, y) - v(t, z, y) = (v_0(x, y) - v_0(z, y)) e^{-\mu v t} \\
+ \int_0^t e^{-\mu v (t-s)} \big[ u(s, x) \hat{L}[v](s, x, y) - u(s, z) \hat{L}[v](s, z, y) \big] \, ds.
\]
Then taking the \( L^1(\mathbb{R}^M) \)-norm with respect to \( y \) leads to
\[
\|v(t, x, \cdot) - v(t, z, \cdot)\|_{L^1(\mathbb{R}^M)} \leq \|v_0(x, \cdot) - v_0(z, \cdot)\|_{L^1(\mathbb{R}^M)} e^{-\mu v t} \\
+ \int_0^t e^{-\mu v (t-s)} \|u(s, x) \hat{L}[v](s, x, \cdot) - u(s, z) \hat{L}[v](s, z, \cdot)\| \, dy \, ds \\
\leq \|v_0(x, \cdot) - v_0(z, \cdot)\|_{L^1(\mathbb{R}^M)} e^{-\mu v t} \\
+ \int_0^t e^{-\mu v (t-s)} \|u(s, x) - u(s, z)\| \|\hat{L}[v](s, x, \cdot)\|_{L^1(\mathbb{R}^M)} \, ds \\
+ \frac{A}{\mu v} \sup_{s \geq 0} \|\hat{L}[v](s, x, \cdot) - \hat{L}[v](s, z, \cdot)\|_{L^1(\mathbb{R}^M)}.
\]
By coupling (19) with first estimate in (18) we obtain
\[
\|v(t, x, \cdot) - v(t, z, \cdot)\|_{L^1(\mathbb{R}^M)} \leq \|v_0(x, \cdot) - v_0(z, \cdot)\|_{L^1(\mathbb{R}^M)} e^{-\mu v t} \\
+ \|u_0(x) - u_0(z)\| \int_0^t e^{-\mu v (t-s)} e^{-\frac{1}{2} \hat{L}[v](s, x, \cdot)} \|\hat{L}[v](s, x, \cdot)\|_{L^1(\mathbb{R}^M)} \, ds \\
+ M \|K(z + \cdot) - K(x + \cdot)\|_{L^1(\mathbb{R})} \int_0^t e^{-\mu v (t-s)} \|\hat{L}[v](s, x, \cdot)\|_{L^1(\mathbb{R}^M)} \, ds \\
+ \frac{A}{\mu v} M_1 \|K(z + \cdot) - K(x + \cdot)\|_{L^1(\mathbb{R})}.
\]
Finally thanks to the uniform bound for \( v \) provided in Proposition 2, the term \( \|\hat{L}[v](t, x, \cdot)\|_{L^1(\mathbb{R}^M)} \) is also uniformly bounded for \( t \geq 0 \) and \( x \in \mathbb{R} \). Hence we readily obtain that there exist some constants \( M_2 > 0 \) and \( M_3 > 0 \) such that for all \( t \geq 0 \), \( x \) and \( z \in \mathbb{R} \) we have
\[
\|v(t, x, \cdot) - v(t, z, \cdot)\|_{L^1(\mathbb{R}^M)} \leq \|v_0(x, \cdot) - v_0(z, \cdot)\|_{L^1(\mathbb{R}^M)} e^{-\mu v t} \\
+ \alpha(t) M_2 \|u_0(x) - u_0(z)\| + M_3 \|K(z + \cdot) - K(x + \cdot)\|_{L^1(\mathbb{R})}
\]
with \( \alpha(t) := \int_0^t e^{-\mu v (t-s)-\frac{1}{2}} \, ds \), satisfying \( \alpha(t) \to 0 \) as \( t \to +\infty \).

To conclude note that the bound for the time derivatives directly follows from the equations for \( u \) and \( v \) together with the uniform bound provided in Proposition 2. The lemma is proved.

**Proof of Corollary 1.** We apply Arzelà-Ascoli theorem. Let \( A > 0 \) be given and \( j_0 \geq 0 \) large enough such that \( t_j \geq A \), for all \( j \geq j_0 \). Next, since \( t_j \to \infty \) as \( j \to \infty \), we infer from Lemma 3.2 that the sequence \( (u_j, v_j)_{j \geq j_0} \) is equi-continuous for \( (t, x) \in [-A, A]^2 \) in \( \mathbb{R} \times L^1(\mathbb{R}^M) \). Hence, to complete the proof of the corollary, it is sufficient to show that for all \( (t, x) \in [-A, A]^2 \), the sequence \( (v_j(t, x, \cdot))_{j \geq j_0} \) is relatively compact in \( L^1(\mathbb{R}^M) \). By integrating the \( v \)-equation, we obtain
\[
v_j(t, x, y) = v_0(x + x_j, y) e^{-\mu v (t+j)} + K_j(t, x, y),
\]
with \( K_j(t, x, y) := \int_{-t_j}^t e^{-\mu v (t-s)} u(s, x + x_j) \hat{L}[v_j(s, x, \cdot)](y) \, ds.\)
For any \((t, x) \in [-A, A]^2\), since \(v_0(x, y)e^{-\mu_1(t+\tau)} \to 0\) as \(j \to \infty\) in \(L^1(\mathbb{R}^M)\) it is sufficient to show that the sequence \(\{K_j(t, x, \cdot)\}_{j \geq j_0}\) is relatively compact in \(L^1(\mathbb{R}^M)\) applying Fréchet-Kolmogorov theorem. Thanks to the boundedness property of the solutions (Proposition 2) and the operator estimate of Lemma 3.1 (ii) we firstly have, for any \(R, R' > 0\)

\[
\int_{\|y\| \geq R} K_j(t, x, y)dy \leq \Lambda \int_{-t_j}^{t} e^{-\mu_1(t-s)} \int_{\|y\| \geq R} \hat{\mathcal{L}}[v_j(s, x, \cdot)](y)dy \, ds
\]

\[
\leq M \sup_{\|y\| \geq R} \beta(y) \left( \|r\|_{\infty} \int_{\|y\| \geq R} \sup_{\|y'\| \leq R+1} J(y + y')dy + \sup_{\|y'\| \geq R} r(y') \right),
\]

for some constant \(M > 0\) independent of \(j \geq j_0\). This implies thanks to Assumption 1 that

\[
\lim_{R \to \infty} \int_{\|y\| \geq R} K_j(t, x, y)dy = 0 \text{ uniformly with respect to } j \geq 0.
\]

Next, let \(h \in \mathbb{R}^M\) be given. Due to Lemma 3.1 (i) and the boundedness property of the solutions, there exists some constant \(M'\) such that, for all \(j \geq j_0\) one has

\[
\|\tau_h K_j(t, x, \cdot) - K_j(t, x, \cdot)\| \leq M' \|r\|_{\infty} \left( \|\tau_h \beta - \beta\|_{\infty} + \|\beta\|_{\infty} \|\tau_h J - J\|_1 \right),
\]

which implies thanks to Assumption 1 as \(J \in L^1(\mathbb{R}^M)\) and \(\beta\) is uniformly continuous that

\[
\lim_{h \to 0} \|\tau_h K_j(t, x, \cdot) - K_j(t, x, \cdot)\|_1 = 0.
\]

The proof of the Corollary is complete. □

3.3. Spectral properties of \(\mathcal{L}\). In this subsection, we prove Proposition 1. Thanks to Lemma 3.1 the operator \(\mathcal{L}\) is compact. Let us recall that \(\Omega = \{y \in \mathbb{R}^M, r(y)\beta(y) > 0\}\). Let \(\mathcal{M}\) the compact operator defined as the restriction of \(\mathcal{L}\) to \(L^1(\Omega)\), that is

\[
\mathcal{M}[f](y) = \int_{\Omega} \beta(y)J(y - y')r(y')f(y')dy', \quad f \in L^1(\Omega).
\]

We have \(\beta(y)J(y - y')r(y') > 0\), \(\forall y, y' \in \Omega\). Therefore, thanks to Theorem 6.6 in [22], \(\mathcal{M}\) is irreducible and admits a principal eigenpair \((\lambda_1, \psi_1) \in \mathbb{R}^+ \times L^1_+(\Omega)\) with \(\lambda_1 = \rho(\mathcal{M}) > 0\) and \(\psi_1(y) > 0\), \(a.e.\) in \(\Omega\).

Next, the function \(\varphi_1 \in L^1_+(\mathbb{R}^M)\) defined as

\[
\varphi_1(y) = \begin{cases} 
\psi_1(y) & \text{if } y \in \Omega, \\
\frac{\beta(y)}{\lambda_1} \int_{\Omega} J(y - y')r(y')\psi_1(y')dy' & \text{if } y \in \mathbb{R}^M \setminus \Omega,
\end{cases}
\]

satisfies \(\mathcal{L}[\varphi_1] = \lambda_1 \varphi_1\) on \(\mathbb{R}^M\). Indeed notice that \(r \varphi_1 = 0\) on \(\mathbb{R}^M \setminus \Omega\) so that

\[
\int_{\Omega} J(y - y')r(y')\psi_1(y')dy' = \int_{\mathbb{R}^M} J(y - y')r(y')\varphi_1(y')dy'.
\]

Thanks to this identity, \(\mathcal{M}[\psi_1] = \lambda_1 \psi_1\) implies that \(\mathcal{L}[\varphi_1] = \lambda_1 \varphi_1\) holds true on \(\Omega\), while the definition of \(\varphi_1\) yields the result on \(\mathbb{R}^M\setminus\Omega\).

Moreover, as \(r \in L^{\infty}(\mathbb{R}^M)\), \(J \in C_0^0(\mathbb{R}^M)\) and \(\beta \in C_0^0(\mathbb{R}^M)\), \(\varphi_1 = \frac{1}{\lambda_1} \beta J \ast_y (r \varphi_1)\) implies that \(\varphi_1 \in C_0^0(\mathbb{R}^M) \cap L^p_+(\mathbb{R}^M)\) for all \(p \geq 1\) and \(\varphi_1 > 0\) on \(\Omega\). Then, since \(\varphi_1^2 \gamma \varphi_1 = \frac{\gamma}{\lambda_1} J \ast_y (r \varphi_1)^2\), we readily prove that \(\varphi_1 \in L^2_+(\mathbb{R}^M)\) and we choose the eigenfunction \(\varphi_1\) to satisfy \(\|\varphi_1\|_{2, \gamma} = 1\).

Let us now prove that \(\rho(\mathcal{L}) = \rho(\mathcal{M})\). We first have that \(\rho(\mathcal{L}) \geq \rho(\mathcal{M}) > 0\). Next, using compactness of \(\mathcal{L}\) (cf. Lemma 4.2.10 in [17]), \(\mathcal{L}\) has a positive
eigenfunction $\phi \in L^1(\Omega)$ associated to $\rho(\mathcal{L})$, i.e. $\mathcal{L}\phi = \rho(\mathcal{L})\phi$. Then, the restriction of $\phi$ to $L^1(\Omega)$ is a positive eigenfunction of $\mathcal{M}$, hence $\rho(\mathcal{L})$ is a positive eigenvalue of $\mathcal{M}$ associated to a positive eigenfunction. However Corollary 4.2.15 (Frobenius Theorem) in [17] implies that for any eigenvalue $\mu$ of $\mathcal{M}$ with $|\mu| < \rho(\mathcal{M})$, the corresponding eigenfunction $\psi$ does not have a constant sign, therefore $\rho(\mathcal{L}) = \rho(\mathcal{M})$.

Recall that $\mathcal{L}^*: L^1(\mathcal{R}^M) \rightarrow L^1(\mathcal{R}^M)$, the formal adjoint of $\mathcal{L}$, is defined in (9). By swapping $r$ and $\beta$, we readily prove that this operator is compact as for the proof of Lemma 3.1. Moreover, as $J$ is symmetric, the following identity holds

$$\int_{\mathcal{R}^M} f(y)\mathcal{L}[g](y)dy = \int_{\mathcal{R}^M} \mathcal{L}^*[f](y)g(y)dy, \quad \forall f, g \in L^1(\mathcal{R}^M) \cap L^\infty(\mathcal{R}^M). \tag{20}$$

Next similarly to the definition of $\varphi_1$ set

$$\varphi_1^*(y) = \left\{ \begin{array}{ll} \gamma(y)\psi_1(y) & \text{if } y \in \Omega, \\
\frac{\gamma(y)}{\lambda_1} \int_{\Omega} J(y-y')\beta(y')\gamma(y')\psi_1(y')dy' & \text{if } y \in \mathcal{R}^M \setminus \Omega. \end{array} \right. $$

with $\beta\gamma\psi_1 = r\psi_1$. We have $r\varphi_1 = \beta\varphi_1^*$ on $\Omega$ with $r\varphi_1 = \beta\varphi_1^* = 0$ on $\mathcal{R}^M \setminus \Omega$. Then, $\mathcal{L}[\varphi_1] = \lambda_1\varphi_1$ on $\Omega$ writes

$$\beta(y)\int_{\mathcal{R}^M} J(y-y')r(y')\varphi_1(y')dy' = \lambda_1\varphi_1(y), \quad \forall y \in \Omega,$n

and multiplying this identity by $\gamma(y)$ directly yields $\mathcal{L}^*[\varphi_1^*] = \lambda_1\varphi_1^*$ on $\Omega$. Next, $\mathcal{L}^*[\varphi_1^*] = \lambda_1\varphi_1^*$ also holds on $\mathcal{R}^M \setminus \Omega$ as a consequence of the definition of $\varphi_1^*$ and of the identity

$$\int_{\Omega} J(y-y')\beta(y')\gamma(y')\psi_1(y')dy' = \int_{\mathcal{R}^M} J(y-y')\beta(y')\varphi_1^*(y')dy'.$$

Moreover from the identity $\mathcal{L}^*[\varphi_1^*] = \lambda_1\varphi_1^*$ we infer that for all $y \in \mathcal{R}^M$

$$\varphi_1^*(y) = \frac{r(y)}{\lambda_1} \int_{\mathcal{R}^M} J(y-y')r(y')\varphi_1(y')dy',$$

so that $\varphi_1^* \in C_c^0(\mathcal{R}^M) \cap L^1(\mathcal{R}^M)$ for all $p \geq 1$ and $\varphi_1^*(y) = 0 \iff r(y) = 0$.

Next, as above the restriction of the operator $\mathcal{L}^*$ to $L^1(\Omega)$ is also irreducible and since $\varphi_1^*$ is non negative, we obtain that $(\lambda_1, \varphi_1^*)$ is a principal eigenpair of $\mathcal{L}^*$ with $\lambda_1 = \rho(\mathcal{L}) = \rho(\mathcal{L}^*)$.

4. Proof of Theorem 2.1 (i). To prove Theorem 2.1 (i), we construct a suitable super-solution $\tilde{v}_1$.

First notice that due to the symmetry of the kernel $K$ (see (3) and (5)) if $(u(t,x), v(t,x,y))$ is some solution of (4) then $(u(t,-x), v(t,-x,y))$ is also solution of (4) for the initial condition $(u_0(-x), v_0(-x,y))$. Therefore, in this proof it suffices to consider the case $x \geq ct$, for some $c > c_*$, the case where $x \leq -ct$ can be handled similarly.

Next let $(u,v)$ be a solution of (4) with initial data $(u_0, v_0)$ satisfying Assumption 2. Let us recall that the operator $\mathcal{L}$ is defined in (8). Now recalling that $u_0 \leq \Lambda$ (see Assumption 2) using assertion (ii) of Proposition 2 ensures that $u(t,x) \leq \Lambda$ for all $t \geq 0$ and $x \in \mathcal{R}$. As a consequence we have

$$\partial_t v(t,x,y) = u(t,x)K *_x \mathcal{L}[v(t,x,\cdot)](y) - \mu v(t,x,y),$$

$$\leq \Lambda K *_x \mathcal{L}[v(t,x,\cdot)](y) - \mu v(t,x,y).$$
Recalling the definition of \( v_1 = v(t,x) \) in (12), multiplying this inequality by \( \varphi_1^*(y) \geq 0 \) and integrating over \( \mathbb{R}^M \) we readily find

\[
\partial_t v_1(t,x) \leq \Lambda K \ast_x \left( \int_{\mathbb{R}^M} \mathcal{L}[v(t,x,\cdot)](y)\varphi_1^*(y)dy \right) - \mu_v v_1(t,x), \quad \forall t \geq 0, \ x \in \mathbb{R}.
\]

Then due to (20) we get

\[
\partial_t v_1(t,x) \leq \Lambda K \ast_x \left( \int_{\mathbb{R}^M} \mathcal{L}^\ast [\varphi_1^*](y)v(t,x,y)dy \right) - \mu_v v_1(t,x),
\]

then it follows that

\[
\partial_t v_1(t,x) \leq \lambda_1 \Lambda K \ast_x (v_1(t,\cdot)(x) - \mu_v v_1(t,x)), \quad \forall t \geq 0, \ \forall x \in \mathbb{R}. \quad (21)
\]

Let us recall that \( K \) (defined in (3)) is non-negative. Let \( c > c_* \) be given and fixed. We now look for a super-solution of (21) of the form \( \bar{v}_1(t,x) = \phi_0 e^{-\lambda(x-ct)} \), for some positive constant \( \phi_0 > 0 \) and \( \lambda \in (0,1) \), to be chosen later. Note that, for all \( t \in \mathbb{R} \) and \( x \in \mathbb{R} \) one has

\[
\partial_t \bar{v}_1(t,x) - \lambda_1 \Lambda K \ast_x \bar{v}_1(t,\cdot)(x) + \mu_v \bar{v}_1(t,x) = \phi_0 e^{-\lambda(x-ct)} \left[ c\lambda + \mu_v - \frac{\lambda_1 \Lambda}{1 - \lambda^2} \right].
\]

Now recall that \( K(c,\lambda) = (1 - \lambda^2)(c\lambda + \mu_v) - \mu_v \mathcal{R}_0 \) with \( \mu_v \mathcal{R}_0 = \lambda_1 \Lambda \) (see (10)). Hence, since \( c > c_* \), due to (11) there exists \( \lambda_0 \in (0,1) \) such that \( K(c,\lambda_0) = 0 \). We now choose \( \lambda = \lambda_0 \) so that the function \( \bar{v}_1 \) satisfies

\[
\partial_t \bar{v}_1(t,x) - \lambda_1 \Lambda K \ast_x \bar{v}_1(t,\cdot)(x) + \mu_v \bar{v}_1(t,x) = 0, \quad \forall (t,x) \in \mathbb{R}^2.
\]

Finally as \( x \mapsto \int_{\mathbb{R}^M} v_0(x,y)dy \) is compactly supported, the function \( x \mapsto v_1(0,x) \) is also compactly supported, and we choose \( \phi_0 \) large enough such that

\[
\bar{v}_1(0,x) = \phi_0 e^{-\lambda_0 x} \geq v_1(0,x), \quad \forall x \in \mathbb{R}.
\]

Hence \( \bar{v}_1 \) becomes a super-solution and we end up with the following upper-bound

\[
v_1(t,x) \leq \bar{v}_1(t,x) = \phi_0 e^{-\lambda_0 (x-ct)}, \quad \forall x \in \mathbb{R}, \ t \geq 0.
\]

Now let \( c_1 \) be any real such that \( c_1 > c > c_* \). Then,

\[
\sup_{x \geq c_1 t} \bar{v}_1(t,x) = \phi_0 e^{-\lambda_0 (c_1 - c)t} \to 0, \quad \text{as } t \to \infty,
\]

therefore as \( c > c_* \) can be chosen arbitrarily close to \( c_* \). Theorem 2.1 (i) holds true in the case \( x \geq ct \) and consequently for \( |x| \geq ct \) as well. This concludes the proof of Theorem 2.1 (i).

5. **Proof of Theorem 2.1 (ii).** This section will present the behaviour for \( t \gg 1 \) of the solution in the region \( |x| \leq ct \) for some \( 0 \leq c < c_* \). Here we only focus on the region of the form \( 0 \leq x \leq ct \) for \( c \in [0,c_*) \) since the case where \( -ct \leq x \leq 0 \) can be handled similarly like in the proof of Theorem 2.1 (i).

Throughout this section we fix an initial data \((u_0,v_0)\) satisfying Assumption 2 and we denote by \((u,v)\) the corresponding solution of (4). We also denote by \( v_1 = v_1(t,x) \) the function defined for \( t \geq 0 \) and \( x \in \mathbb{R} \) by (12). Since \( r(y)v_0(x,y) \neq 0 \) on \( \mathbb{R} \times \mathbb{R}^M \) (see Assumption 2 (ii)) then, according to Remark 1 one has \( v_1 > 0 \) on \((0,\infty) \times \mathbb{R} \). Recall also that throughout this section, we assume that \( \mathcal{R}_0 > 1 \).

The main purpose of this section is to prove that \( v_1 = v_1(t,x) \) remains uniformly positive in the large time in the region of the form \( 0 \leq x \leq ct \) for \( c \in [0,c_*) \).
In order to state our results let us introduce some useful notations and remarks that will be used along in this section. We define $\mathcal{T} \subset C^0_b(\mathbb{R}^2; \mathbb{R}^+ \times C^0_b(\mathbb{R}^2; L^1_+(\mathbb{R}^M)))$ the set of the limits of the translates of the orbit $(u, v)$ as

$$(\bar{u}, \bar{v}) \in \mathcal{T} \iff \text{there exist a sequence } (t_n)_{n \geq 0} \text{ with } t_n \to \infty$$

and a sequence $(x_n)_{n \geq 0} \subset \mathbb{R}$ such that

$$(\bar{u}(t, x), \bar{v}(t, x, \cdot)) = \lim_{n \to \infty} (u(t + t_n, x + x_n), v(t + t_n, x + x_n, \cdot)),$$

for the topology of $C_{\text{loc}}(\mathbb{R}^2) \times C_{\text{loc}}(\mathbb{R}^2; L^1(\mathbb{R}^M)).$

Due to Lemma 3.2 (and Corollary 1), observe that $\mathcal{T}$ is non empty and is a compact set when endowed with the topology of $C_{\text{loc}}(\mathbb{R}^2) \times C_{\text{loc}}(\mathbb{R}^2; L^1(\mathbb{R}^M))$. Note that since $(u_0, v_0)$ satisfies Assumption 2, Proposition 2 ensures that there exists $M > \Lambda^{-1}$ large enough such that for all $(\bar{u}, \bar{v}) \in \mathcal{T}$ one has

$$M^{-1} \leq \bar{u}(t, x) \leq \Lambda \text{ and } 0 \leq \int_{\mathbb{R}^M} \bar{v}(t, x, y)dy \leq M, \forall (t, x) \in \mathbb{R}^2,$$

$$0 \leq \bar{v}(t, x, y) \leq M \beta(y), \forall (t, x) \in \mathbb{R}^2 \text{ and a.e. for } y \in \mathbb{R}^M.$$

Note also that any $(\bar{u}, \bar{v}) \in \mathcal{T}$ becomes a non-negative entire solution of the system (4).

As a consequence we obtain the following separation property: for any $(\bar{u}, \bar{v}) \in \mathcal{T}$, it holds that

either $(\bar{u}, \bar{v}) \in \mathcal{T} \equiv (\Lambda, 0)$, or, $\int_{\mathbb{R}^M} \bar{v}(\cdot, \cdot, y)\phi_1^*(y)dy > 0$ on $\mathbb{R} \times \mathbb{R}$.

To see this let $(\bar{u}, \bar{v}) \in \mathcal{T}$ be given. Assume that there exists $(t_0, x_0) \in \mathbb{R} \times \mathbb{R}$ such that

$$\int_{\mathbb{R}^M} \bar{v}(t_0, x_0, y)\phi_1^*(y)dy = 0.$$

Then $\bar{v}(t_0, x_0, y) = 0$ a.e. for $y \in \Omega$. Next since $(\bar{u}, \bar{v})$ is an entire solution of (4) then the function $\bar{v}_1(t, x) := \int_{\mathbb{R}^M} \bar{v}(t, x, y)\phi_1^*(y)dy$ satisfies

$$\partial_t \bar{v}_1(t, x) = \lambda_1 \bar{u}(t, x)K *_{\chi} \bar{v}_1(t, \cdot, x) - \mu_v \bar{v}_1(t, x), \forall (t, x) \in \mathbb{R} \times \mathbb{R},$$

with $\bar{v}_1(t_0, x_0) = 0$. Since $\bar{u} > 0$ and $K > 0$ we infer that $\bar{v}_1(t, x) \equiv 0$ on $\mathbb{R} \times \mathbb{R}$.

Then as $\phi_1^*$ and $r$ have the same support (see section 3.3), then $r\bar{v} \equiv 0$ on $\mathbb{R}^2 \times \mathbb{R}^M$. The equation for $\bar{v}$ reads

$$\partial_t \bar{v}(t, x, y) = \beta(y)\bar{u}(t, x)K *_{\chi} J *_y (r\bar{v})(t, x, y) - \mu_v \bar{v}(t, x, y), \forall (t, x, y) \in \mathbb{R}^2 \times \mathbb{R}^M,$$

and becomes

$$\partial_t \bar{v}(t, x, y) = -\mu_v \bar{v}(t, x, y), \forall (t, x, y) \in \mathbb{R}^2 \times \mathbb{R}^M,$$

so that $\bar{v} \in C^0(\mathbb{R}^2; L^1_+(\mathbb{R}^M))$ is identically equal to 0 on $\mathbb{R}^2 \times \mathbb{R}^M$ and thus $\bar{u} = \Lambda$. The separation property follows.

This separation property allows us to split the set $\mathcal{T}$ as the following disjoint union

$$\mathcal{T} = \partial \mathcal{T} \cup \bar{\mathcal{T}} \text{ with } \partial \mathcal{T} \cap \bar{\mathcal{T}} = \emptyset,$$

wherein we have set $\partial \mathcal{T} = \{ (\Lambda, 0) \}$ and

$$\bar{\mathcal{T}} = \{ (\bar{u}, \bar{v}) \in \mathcal{T}, \bar{v} \neq 0 \} = \left\{ (\bar{u}, \bar{v}) \in \mathcal{T}, \int_{\mathbb{R}^M} \bar{v}(\cdot, \cdot, y)\phi_1^*(y)dy > 0 \text{ on } \mathbb{R} \times \mathbb{R} \right\}.$$

Now to prove Theorem 2.1 (ii) we closely follow the methodology developed in [6] and we split our argument into three steps. We first study pointwise weak spreading
property before dealing with pointwise strong spreading, to finally conclude to the uniform spreading, as stated in Theorem 2.1 (ii).

5.1. First step: Pointwise weak spreading. In this subsection we aim at proving the following lemma.

**Lemma 5.1.** Let \( \eta \in (0, c_\ast) \) be given. Then there exists \( \varepsilon = \varepsilon(\eta) > 0 \) such that for all \((\hat{u}, \hat{v}) \subset \mathcal{T}\) it holds that

\[
\limsup_{t \to \infty} \hat{v}_1(t, ct) \geq \varepsilon(\eta), \quad \forall c \in [0, c_\ast - \eta].
\]

Herein \( \hat{v}_1 = \hat{v}_1(t, x) \) is given by

\[
\hat{v}_1(t, x) = \int_{\mathbb{R}^M} \hat{v}(t, x, y) \varphi_1^1(y) dy, \quad \forall (t, x) \in \mathbb{R}^2.
\]

**Remark 3.** The proof of the above lemma given below also applies to the original solution \((u, v)\) due to the asymptotic compactness of the solution (see Corollary 1). Hence for each \( \eta \in (0, c_\ast) \) there exists \( \varepsilon = \varepsilon(\eta) > 0 \) such that

\[
\limsup_{t \to \infty} v_1(t, ct) \geq \varepsilon(\eta), \quad \forall c \in [0, c_\ast - \eta],
\]

with \( v_1(t, x) = \int_{\mathbb{R}^M} v(t, x, y) \varphi_1^1(y) dy, \quad \forall (t, x) \in \mathbb{R}^+ \times \mathbb{R} \).

**Proof.** To prove the lemma, we argue by contradiction by assuming that there exist a sequence \((\hat{u}^n, \hat{v}^n) \subset \mathcal{T}\), a sequence \((t_n)_{n \geq 1} \), with \( t_n \to +\infty \) as \( n \to +\infty \) and a sequence \((c_n)_{n \geq 1} \) with \( 0 \leq c_n \leq c_\ast - \eta, \quad \forall n \geq 1 \) such that

\[
\forall n \in \mathbb{N}^*, \quad \forall t \geq 0, \quad \hat{v}^n_1(t_n + t, c_n(t_n + t)) \leq \frac{1}{n}.
\]

Below, up to a subsequence, we assume that \( c_n \to c_\infty \) with \( 0 \leq c_\infty \leq c_\ast - \eta \) as \( n \to \infty \).

Now we make the following claim

**Claim 5.2.** Up to a subsequence, one has

\[
\limsup_{n \to \infty} \hat{v}_1^n(t_n + t, x + c_n(t_n + t)) = 0,
\]

uniformly for \( t \geq 0 \) and locally uniformly for \( x \in \mathbb{R} \).

To prove this claim we argue again by contradiction by assuming that there exist a bounded sequence \((x_n)_{n \geq 1} \subset \mathbb{R}\), with \( x_n \to x_\infty \in \mathbb{R} \) as \( n \to \infty \) and a sequence of positive numbers \((s_n)_{n \geq 1} \) such that

\[
\limsup_{n \to \infty} \hat{v}_1^n(t_n + s_n, x_n + c_n(t_n + s_n)) > 0.
\]

Now we let

\[
(\hat{u}^n(t, x), \hat{v}^n(t, x, y)) := (\hat{u}^n(t + t_n + s_n, x + c_n(t_n + s_n)), \hat{v}^n(t + t_n + s_n, x + c_n(t_n + s_n), y))
\]

and

\[
\hat{v}_1^n(t, x) := \int_{\mathbb{R}^M} \hat{v}^n(t, x, y) \varphi_1^1(y) dy\]

so that \((\hat{u}^n, \hat{v}^n) \in \mathcal{T}\), \( \forall n \geq 1 \). Since \( \mathcal{T} \) is compact one may assume that, up to a subsequence, there exists some \((\hat{u}_\infty, \hat{v}_\infty)\) such that \((\hat{u}^n, \hat{v}^n) \rightharpoonup (\hat{u}_\infty, \hat{v}_\infty) \in \mathcal{T}\). For the topology of \(C_{loc}(\mathbb{R}^2) \times C_{loc}(\mathbb{R}^2; L^1(\mathbb{R}^M))\) while \( \hat{v}_1^n(t, x) \rightharpoonup \hat{v}_1^\infty(t, x) \) in \(C_{loc}(\mathbb{R}^2)\) with \( \hat{v}_1^\infty(t, x) := \int_{\mathbb{R}^M} \hat{v}_1^\infty(t, x, y) \varphi_1^1(y) dy\).
Next observe that (24) ensures that $\hat{v}_1(0, 0) = 0$ and thus $\hat{v}_1 \equiv 0$ due to the separation property (23) while (26) ensures that $\hat{v}_1(0, x_\infty) > 0$, a contradiction that completes the proof of our claim.

Moreover using the same arguments we obtain that along a subsequence, we have

$$\lim_{n \to \infty} \tilde{u}^n(t + t_n, x + c_n(t + t_n)) = \Lambda,$$

uniformly for $t \geq 0$ and locally uniformly for $x \in \mathbb{R}$.

Thanks to (11), we can fix $\varepsilon > 0$ such that for all $0 \leq c \leq c_* - \eta$ we have

$$\max_{0 \leq \lambda \leq 1} \left( (1 - \lambda^2)(c_\lambda + \mu_v) - \mu_v \lambda (1 - \varepsilon) \right) < 0.$$

Now let $Q_{R,c}$ defined as

$$Q_{R,c}[\varphi](x) := c\varphi'(x) + \lambda_1 \Lambda(1 - \varepsilon) \int_{-R}^{R} K(x - x') \varphi(x') dx' - \mu_v \varphi(x).$$

The following lemma holds true. It is a slight variant of lemma 3.6 in [1] where $c$ is replaced with $-c$ and that takes into account the dependence of $Q_{R,c}$ with respect to the variable $c$. We also refer to [2, 15] where compactly supported sub-solutions for linear nonlocal problems have been constructed.

**Lemma 5.3.** For $\alpha \in (-1, 1)$ define

$$\varphi_{R,\alpha}(x) := e^{\alpha x} \cos \left( \frac{\pi x}{2R} \right), \forall x \in (-R, R).$$

For any $c_0 \in [0, c_* - \eta]$, there exist some positive constants $M_0, R_0$ and $\delta$ such that for all $(R, c) \in (R_0, \infty) \times ((c_0 - \delta, c_0 + \delta) \cap [0, c_* - \eta])$ there exists $\alpha_{R,c} \in (-1, 1)$ such that the function $\varphi_{R,\alpha_{R,c}}$ satisfies

$$\forall x \in (-R, R), Q_{R,c}[\varphi_{R,\alpha_{R,c}}](x) \geq M_0 \varphi_{R,\alpha_{R,c}}(x).$$

We apply Lemma 5.3 with $c_0 = c_\infty$, which defines some $M_0, R_0, \delta$ and the family of functions $\varphi_{R,\alpha_{R,c}}$. Let $R$ some constant such that $R > R_0$. Using (27) there exists $n_0$ large enough such that $c_{n_0} \in (c_0 - \delta, c_0 + \delta)$ and for $(\tilde{u}^{n_0}, \tilde{v}^{n_0}) \in \mathcal{T}$ we have

$$\tilde{u}^{n_0}(t + t_{n_0}, x + c_{n_0}(t + t_{n_0})) \geq \Lambda(1 - \varepsilon), \forall t \geq 0, \forall x \in [-R, R],$$

so that $\forall t \geq t_{n_0}, \forall x \in [-R + c_{n_0}t, R + c_{n_0}t], \forall y \in \Omega,$

$$\partial_t \tilde{u}^{n_0}(t, x, y) = \beta(y) \tilde{u}^{n_0}(t, x)[K * \hat{J} * (r \tilde{u}^{n_0})](t, x, y) - \mu_v \tilde{v}^{n_0}(t, x, y)$$

$$\geq \Lambda(1 - \varepsilon) \beta(y)[K * \hat{J} * (r \tilde{v}^{n_0})](t, x, y) - \mu_v \tilde{v}^{n_0}(t, x, y),$$

thus multiplying this equation by $\varphi_1^*$ and integrating over $\Omega$ gives for all $t \geq t_{n_0}$ and $x \in [-R + c_{n_0}t, R + c_{n_0}t]$

$$\partial_t \tilde{v}^{n_0}_1(t, x) \geq \lambda_1 \Lambda(1 - \varepsilon) \hat{J} * \tilde{v}^{n_0}_1(t, x) - \mu_v \tilde{v}^{n_0}_1(t, x).$$

By setting $\psi(t, x) := e^{\lambda_1 t} \varphi_{R,\alpha_{R,c_{n_0}}}(x)$, we have for all $t \in \mathbb{R}$ and $x \in (-R, R)$

$$\partial_t \psi(t, x) \leq c_{n_0} \partial_x \psi(t, x) + \lambda_1 \Lambda(1 - \varepsilon) \int_{-R}^{R} K(x - x') \psi(t, x') dx' - \mu_v \psi(t, x).$$
Now let \( \tilde{\psi}(t,x) := \psi(t,x - c_n t) \), we have \( \forall t \geq t_{n_0}, \forall x \in (-R + c_n t_{n_0}, R + c_n t_{n_0}) \)
\[
\partial_t \tilde{\psi}(t,x) = \partial_t \psi(t,x - c_n t) - c_n \partial_x \psi(t,x - c_n t)
\]
\[
\partial_t \tilde{\psi}(t,x) \leq \lambda_1 \Lambda(1 - \varepsilon) \int_{-R}^R K(x - c_n t - x') \psi(t,x') dx' - \mu \tilde{\psi}(t,x)
\]
\[
\partial_t \tilde{\psi}(t,x) \leq \lambda_1 \Lambda(1 - \varepsilon) \int_{-R+c_n t}^{R+c_n t} K(x-z) \tilde{\psi}(t,z) dz - \mu \tilde{\psi}(t,x).
\]

As \( (\tilde{v}^n_0, \tilde{v}^n_1(t_{n_0}, x) \) is positive for all \( x \in \mathbb{R} \) and there exists \( \kappa > 0 \) such that
\[
\tilde{v}^n_1(t_{n_0}, x) \geq \kappa \tilde{\psi}(t_{n_0}, x), \forall x \in (-R + c_n t_{n_0}, R + c_n t_{n_0}).
\]

Let us define the function \( w = w(t,x) \) on \( [t_{n_0}, \infty) \times \mathbb{R} \) by
\[
w(t,x) = \begin{cases} 
\tilde{v}^n_1(t_{n_0}, x) - \kappa \tilde{\psi}(t_{n_0}, x) & \text{for } (t,x) \in [t_{n_0}, \infty) \times (-R + c_n t, R + c_n t), \\
\tilde{v}^n_1(t,x) & \text{for } t \geq t_{n_0} \text{ and } x \not\in (-R + c_n t, R + c_n t).
\end{cases}
\]

We thus have
\[
w(t_{n_0}, x) \geq 0, \forall x \in [-R + c_n t_{n_0}, R + c_n t_{n_0}],
\]
moreover
\[
w(t,x) = \tilde{v}^n_1(t_{n_0}, x) \geq 0, \forall x \not\in (-R + c_n t, R + c_n t), \forall t \geq t_{n_0},
\]
while for all \( t \geq t_{n_0} \) and \( x \in (-R + c_n t, R + c_n t) \)
\[
\partial_t w(t,x) \geq \lambda_1 \Lambda(1 - \varepsilon) \int_{-R+c_n t}^{R+c_n t} K(x-z) w(t,z) dz - \mu w(t,x).
\]

Then we use a comparison lemma to prove that \( w \) is non-negative. The following lemma is inspired from Lemma 4.7 in [27].

**Lemma 5.4.** Assume that \( K \in L^1_1(\mathbb{R}) \). Let \( d > 0 \) and \( \mu \in \mathbb{R} \) be given. For any \( t_0 \) and \( T > t_0 \), assume that \( f \) is a continuous function on \([t_0,T] \times \mathbb{R} \) that is absolutely continuous in respect to \( t \in [t_0,T] \) for any \( x \in \mathbb{R} \). Assume that \( X,Y \) are continuous functions on \([t_0,T]\) with \( X < Y \). If \( f \) satisfies
\[
\begin{align*}
\partial_t f(t,x) &\geq d K x f(t,x) - \mu f(t,x), \forall t \in [t_0,T], \forall x \in (X(t),Y(t)), \\
f(t,x) &\geq 0, \forall t \in (t_0,T], \forall x \in \mathbb{R} \setminus (X(t),Y(t)), \\
f(t_0,x) &\geq 0, \forall x \in [X(t_0),Y(t_0)],
\end{align*}
\]
then
\[
f(t,x) \geq 0, \forall t \in [t_0,T], \forall x \in [X(t),Y(t)].
\]

**Proof.** Let \( \mu' > \mu \) and \( m = \mu' - \mu > 0 \). Let \( g(t,x) = e^{\mu' t} f(t,x) \). Denote \( \Omega_T = \{(t,x) \in \mathbb{R}^2, t \in (t_0,T], x \in (X(t),Y(t))\} \). Then we have
\[
\partial_t g(t,x) \geq d K x g(t,x) + m g(t,x), \forall (t,x) \in \Omega_T.
\]

Let \( T_* \leq \min\left(T, t_0 + \frac{1}{4(d_1 K z dz + m)}\right) \). We aim to prove that \( g \geq 0 \) on \( \Omega_{T_*} \).

Assuming that this assertion is false, then \( g(t,x) < 0 \) for some \( (t,x) \in \Omega_{T_*} \). We are able to define \( g_{inf} = \inf_{(t,x) \in \Omega_{T_*}} g(t,x) < 0 \) as \( g \) is a bounded function on the
closure of $\Omega_T$. Let $(t_n, x_n)$ a sequence of $\Omega_T$ such that $g(t_n, x_n) \to g_{inf}$ as $n \to \infty$. Integrating (32) we find

$$g(t_n, x_n) = g(t_0, x_n) + d \int_{t_0}^{t_n} \int_{y \in \mathbb{R} \setminus (X(s), Y(s))} K(x_n - y)g(s, y)dyds + d \int_{t_0}^{t_n} \int_{X(s)} K(x_n - y)g(s, y)dyds + m \int_{t_0}^{t_n} g(s, x_n)ds,$$

so that thanks to (30) the two first terms of the right-hand side of this equality are non-negative and

$$g(t_n, x_n) \geq \left( d \int_{\mathbb{R}} K(z)dz + m \right) (t_n - t_0)g_{inf} > \frac{1}{2} g_{inf}.$$

As $n \to \infty$, we obtain $g_{inf} > \frac{1}{2} g_{inf}$, which contradicts $g_{inf} < 0$. Hence $g$ and $f$ are non-negative functions on $\Omega_T$. The same argument can be repeated until $T_s = T$. This concludes the proof of the lemma.

Applying the above lemma, we find that

$$\forall x \in [-R + c_n t, R + c_n t], \forall t \geq t_0, \tilde{v}_1^n(t, x) \geq \epsilon \tilde{v}(t, x),$$

and it follows that $\tilde{v}_1^n(t, c_n t) \to \infty$ as $t \to \infty$. This contradicts the boundedness of the solution and completes the proof of Lemma 5.1.

5.2. Second step: Pointwise strong spreading. We now turn to the proof of the pointwise strong spreading property, that reads as follows.

**Lemma 5.5.** Let $\eta \in (0, c_*)$ be given. Then there exists $\epsilon = \epsilon(\eta)$ such that for all $(\tilde{u}, \tilde{v}) \in T$, we have

$$\liminf_{t \to \infty} \tilde{v}_1(t, ct) > \epsilon(\eta), \forall c \in [0, c_* - \eta].$$

(33)

Herein, as in the previous subsection, $\tilde{v}_1$ is given by $\tilde{v}_1(t, x) = \int_{\mathbb{R}^M} \tilde{v}(t, x, y)\varphi_1^*(y)dy$.

**Remark 4.** Here again, the proof of the above lemma given below also applies to the original solution $(u, v)$. Hence for each $\eta \in (0, c_*)$ there exists $\epsilon = \epsilon(\eta) > 0$ such that

$$\liminf_{t \to \infty} v_1(t, ct) > \epsilon(\eta), \forall c \in [0, c_* - \eta],$$

with $v_1(t, x) = \int_{\mathbb{R}^M} \tilde{v}(t, x, y)\varphi_1^*(y)dy, \forall(t, x) \in \mathbb{R}^+ \times \mathbb{R}$.

**Proof.** We argue again by contradiction by assuming that there exist a sequence $(\tilde{u}^n, \tilde{v}^n)_{n \geq 1} \in T$ and a converging sequence $(c_n)_{n \geq 1}$ with $0 \leq c_n \leq c_* - \eta$ and $c_n \to c \in [0, c_* - \eta]$ as $n \to \infty$ such that

$$\liminf_{t \to \infty} \tilde{v}_1^n(t, c_n t) < \frac{1}{n}.$$

Thanks to Lemma 5.1, there exists $\epsilon(\eta) > 0$ such that for all $n \geq 1$

$$\limsup_{t \to +\infty} \tilde{v}_1^n(t, c_n t) \geq \epsilon(\eta),$$

(34)
therefore there exist a sequence \( (t_n)_{n \geq 1} \), that tends to \( \infty \) as \( n \to \infty \), and a sequence \( (h_n)_{n \geq 1} \) of positive numbers such that, for any \( n \geq 1 \),

\[
\begin{align*}
\hat{v}_n^1(t_n, c_n t_n) &= \frac{\epsilon(n)}{2}, \\
\hat{v}_n^1(t, c_n t) &\leq \frac{\epsilon(n)}{2} - \epsilon_t \in [t_n, t_n + h_n], \\
\hat{v}_n^1(t_n + h_n, c_n (t_n + h_n)) &\leq \frac{\epsilon(n)}{2}.
\end{align*}
\] (35)

One may observe that the sequence of positive numbers \( (h_n) \) arising in (35) is unbounded. Indeed, by contradiction we assume that \( (h_n) \) is bounded and converges towards \( h \) up to a subsequence. Then let us define the following functions

\[
(\hat{u}^n(t, x), \hat{v}^n(t, x, y)) = \begin{cases}
\hat{u}^n(t + t_n + h_n, x + c_n(t_n + h_n), y), & y \in \mathcal{T} \\
\hat{v}^n(t + t_n + h_n, x + c_n(t_n + h_n), y), & y \notin \mathcal{T}
\end{cases}
\]

that up to a subsequence converges towards \((\hat{u}^\infty, \hat{v}^\infty)\) for the open compact topology of \( C_{\text{loc}}(\mathbb{R}^2) \times C_{\text{loc}}(\mathbb{R}^2; L^1(\mathbb{R}^M)) \) due to the compactness properties of \( \mathcal{T} \). The third inequality in (35) yields

\[
\hat{v}_1^n(0, 0) \leq 1 - \frac{1}{n}, \quad \forall n \geq 1,
\]

so that \( \hat{v}_1^\infty(0, 0) = 0 \) and \( \hat{v}_1^\infty \in \mathcal{T} \setminus \mathcal{F} = \partial \mathcal{T} \), hence \( \hat{v}_1^\infty \equiv 0 \) and thus \( \hat{v}_1^\infty \equiv 0 \). Now as \( \hat{v}_1^n(-h_n, -c_n h_n) = \epsilon(n)/2 \) for all \( n \), we have \( \hat{v}_1^n(-h, -c h) = \epsilon(n)/2 > 0 \), a contradiction with \( \hat{v}_1^\infty \equiv 0 \).

Next, let us define the sequence of functions in \( \mathcal{T} \), also denoted by \((\hat{u}^n, \hat{v}^n)\) for simplicity, as follows

\[
\hat{u}^n(t, x) = \hat{u}^n(t_n + t_n + c_n t_n, x), \\
\hat{v}^n(t, x, y) = \hat{v}^n(t_n + t_n + c_n t_n, x, y),
\]

that possibly along a subsequence converges towards \((\hat{u}^\infty, \hat{v}^\infty)\) for the topology of \( C_{\text{loc}}(\mathbb{R}^2) \times C_{\text{loc}}(\mathbb{R}^2; L^1(\mathbb{R}^M)) \). Observe that by (35) we can ensure \( \hat{v}_1(0, 0) = \epsilon(n)/2 \) so that \((\hat{u}, \hat{v}) \in \mathcal{T} \). Moreover, we have

\[
\hat{v}_1^n(t_n + t_n + c_n(t_n + t_n)) \leq \epsilon(n)/2, \quad \forall t \in [0, h_n],
\]

with, possibly along a subsequence, \( h_n \to \infty \) as \( n \to \infty \) and \( c_n \to c \in [0, c_* - \eta] \). Therefore thanks to the locally uniform convergence one obtains letting \( n \to \infty \) that

\[
\hat{v}_1^\infty(t, ct) \leq \epsilon(n)/2, \quad \forall t \geq 0,
\]

so that in particular we have \( \limsup_{t \to \infty} \hat{v}_1^\infty(t, ct) \leq \epsilon(n)/2 \). Next since \( \hat{v}_1(0, 0) = \epsilon(n)/2 \), one also has \((\hat{u}, \hat{v}) \in \mathcal{T} \) and \( 0 \leq c \leq c_* - \eta \). This contradicts Lemma 5.1 and completes the proof of Lemma 5.5.

5.3. Third step: Uniform spreading. In Lemma 5.5, we showed that some pointwise – strong – spreading property occurs locally in any moving frame with constant speed \( 0 \leq c < c_* \). We prove now that this spreading is uniform for \( 0 \leq x \leq ct \), with \( 0 < c < c_* \). As already mentioned above, the case where \( x \) is negative can be handled similarly using the symmetry of the kernel function \( K \).

Lemma 5.6. Let \( \eta \in (0, c_*) \), then there exists \( \epsilon(\eta) > 0 \) such that

\[
\liminf_{t \to \infty} \inf_{0 \leq x \leq (c_* - \eta) t} \int_{\mathbb{R}^M} v(t, x, y) \varphi_1^y(y) dy \geq \epsilon(\eta).
\]
Proof. The proof is inspired by the proof of Lemma 5.7 in [6].

Let \( v_1(t, x) = \int_{\mathbb{R}^N} v(t, x, y) \psi_1(y) dy \). Assume by contradiction that there exist a sequence \( (t_n)_{n \geq 1} \) that tends to \( \infty \) as \( n \to \infty \) and a converging sequence \( (c_n) \in [0, c_* - \eta] \) with \( c_n \to \infty \in [0, c_* - \eta] \) as \( n \to \infty \) such that

\[
\lim_{n \to \infty} v_1(t_n, c_n t_n) = 0.
\]

(36)

Let \( \delta > 0 \) and \( \eta' > 0 \) be such that \( c_\infty + \delta < c_* - \eta' \). Let us introduce the sequence of times \( (t'_n)_{n \geq 1} \) by

\[
t'_n = \frac{c_n t_n}{c_\infty + \delta} \in [0, t_n).
\]

Let us first observe that the sequence \( (c_n t_n) \) cannot have a bounded subsequence. Indeed if a subsequence were bounded then (36) implies that possibly along a subsequence

\[
v_1(t_n + t, x) \to \hat{v}_1^\infty(t, x) \equiv 0 \text{ locally uniformly with respect to } t, x.
\]

In particular, \( v_1(t_n, 0) \to 0 \) as \( n \to \infty \), which contradicts Remark 4 with \( r = 0 \).

Hence \( c_n t_n \to \infty \) and equivalently \( t'_n \to \infty \) as \( n \to \infty \). Due to Remark 4, there exists \( \varepsilon(\eta') > 0 \) such that for large enough

\[
v_1(t'_n, c_n t_n) = v_1(t'_n, (c_\infty + \delta)t'_n) \geq \varepsilon(\eta').
\]

Since \( t'_n \leq t_n \) and \( v_1(t_n, c_n t_n) \to 0 \) (due to (36)), we define for all \( n \) large enough the time \( \tilde{t}_n \) by

\[
\tilde{t}_n := \sup \left\{ t \in (t'_n, t_n), \ v_1(t, c_n t_n) \geq \frac{\varepsilon(\eta')}{2} \right\} \in (t'_n, t_n).
\]

Next define for all \( n \) large enough the sequence of functions

\[
u^n(t, x) = u(\tilde{t}_n + t, c_n t_n + x), \ v^n(t, x, y) = v(\tilde{t}_n + t, c_n t_n + x, y)
\]

\[
v^n_1(t, x) = v_1(\tilde{t}_n + t, c_n t_n + x),
\]

so that, for all \( n \) large enough one has

\[
\begin{cases}
 v^n_1(0, 0) = \frac{\varepsilon(\eta')}{2}, \\
 v^n_1(t, 0) \leq \frac{\varepsilon(\eta')}{2}, \forall t \in [0, t_n - \tilde{t}_n] \\
 v^n_1(t_n - \tilde{t}_n, 0) \to 0 \text{ as } n \to \infty.
\end{cases}
\]

Choose a subsequence such that \( (u^n, v^n) \to (u^\infty, v^\infty) \) in \( C_{\text{loc}}(\mathbb{R}^2) \times C_{\text{loc}}(\mathbb{R}^2; L^1(\mathbb{R}^M)) \) so that the first condition above ensures that \( (u^\infty, v^\infty) \in \mathcal{F} \), while the third condition ensures, as for the proof of Lemma 5.5, that \( t_n - \tilde{t}_n \to \infty \). We finally end up with

\[
v^\infty_1(t, 0) \leq \frac{\varepsilon(\eta')}{2}, \forall t \geq 0,
\]

that contradicts Lemma 5.5. This concludes the proof of Lemma 5.6.

\[\square\]

6. Proof of Theorem 2.1 (iii). Along this section recall that Assumptions 1 and 2 are satisfied. Then we define the function \( \theta : \mathbb{R}^M \to \mathbb{R}^+ \) by

\[
\theta = \sqrt{r \beta}.
\]

Let us recall that due to Assumption 1, one has \( \theta(y) \in L^2(\mathbb{R}^M) \).

Throughout this section let \( (u, v) \) denotes the solution of (4) with an initial data \((u_0, v_0)\) satisfying Assumption 2. Now recalling the estimate for \( v \) provided in Proposition 2 (ii), note that \( v = v(t,x,y) \in C^1([0,\infty),C^0_b(\mathbb{R},L^2_c(\mathbb{R}^M))) \) and
Supp \( v(t, x, \cdot) \subset \text{Supp} \beta \) for all \((t, x) \in [0, \infty) \times \mathbb{R}\). Moreover there exists some constant \(c_\nu > 0\) such that
\[
\sqrt{\gamma(y)}v(t, x, y) \leq c_\nu^2 \theta(y), \quad \forall (t, x) \in \mathbb{R}^+ \times \mathbb{R}, \text{ a.e. } y \in \mathbb{R}^M. \tag{37}
\]
Due to the above remark, let us define
\[
\hat{v} := \sqrt{\gamma}v \in C^1([0, \infty), C_0^0(\mathbb{R}, L^2(\mathbb{R}^M))),
\]
and since Supp \(v(t, x, \cdot)\subset \text{Supp} \beta\) for all \((t, x) \in \mathbb{R}^+ \times \mathbb{R}\), then \(rv = \theta \hat{v}\) and we readily retrieve that \(\hat{v}\) satisfies the following equation
\[
\partial_t \hat{v} = u \theta K_x J_y (\theta \hat{v}) - \mu v, \quad t \geq 0, \quad x \in \mathbb{R}, \quad y \in \mathbb{R}^M,
\]
\[
\hat{v}(0, x, y) = \sqrt{\gamma(y)}\nu_0(x, y), \quad x \in \mathbb{R}, \quad y \in \mathbb{R}^M.
\tag{38}
\]
Let us recall that \(\Omega = \{y \in \mathbb{R}^M, \theta(y) > 0\}\) (see (7)), so that Supp \(\hat{v}(t, x, \cdot) \subset \Omega\) for all \(t, x\).

Next we define the linear operator \(\mathcal{M}_2 \in \mathcal{L}(L^2(\Omega))\) by
\[
\mathcal{M}_2[f](y) = \theta(y) \int_{\Omega} J(y - y') \theta(y') f(y') dy', \quad \forall f \in L^2(\Omega).
\]
As in the proof of Proposition 1, we can prove that the operator \(\mathcal{M}_2\) is irreducible and compact on \(L^2(\Omega)\). Moreover as \(J\) is symmetrical, \(\mathcal{M}_2\) is self-adjoint. Therefore it admits a spectral decomposition with positive eigenvalues \(\{\lambda_k\}_{k \geq 1}\) such that
\[
\lambda_1 = \rho(\mathcal{M}) = \rho(\mathcal{M}_2) \quad \text{and} \quad \lambda_1 > \lambda_2 \geq \cdots \geq \lambda_k \geq \cdots \geq 0 \text{ with } \lim_{k \to \infty} \lambda_k = 0,
\]
see also [1, 3] for more details. The corresponding eigenvectors \(\{\phi_k\}_{k \geq 1}\) form a Hilbert basis of \(L^2(\Omega)\). We have \(\phi_1 > 0\) while the other eigenvectors for \(k \geq 2\) have no constant sign. Actually we have a correspondence between the eigenfunctions \(\phi_1\) of the operators \(\mathcal{M}_2\) and \(\psi_1\) of \(\mathcal{M}\): \(\phi_1 = \kappa_1 \sqrt{\gamma} \psi_1\) with some constant \(\kappa_1\) such that \(\|\phi_1\|_{L^2(\Omega)} = 1\). Since the principal eigenfunction \(\psi_1\) of \(\mathcal{L}\) was chosen to satisfy the normalization condition \(\|\psi_1\|_{2, \gamma} = 1\) and since \(\gamma^{1/2} \varphi_1 = \gamma^{1/2} \psi_1\) on \(\Omega\) with Supp \(\gamma = \Omega\), we have \(\kappa_1 = 1\). Next, the eigenfunction \(\varphi_1^* = \gamma^{1/2} \phi_1\) of the operator \(\mathcal{L}^*\) satisfies \(\varphi_1^* = \gamma^{1/2} \phi_1\) on \(\Omega\).

Here again we use the definition of the set of the limit shifted orbits, \(\mathcal{T}\), defined in the previous section. Recall that for each sequence \((t_n) \subset \mathbb{R}^+\) with \(t_n \to \infty\) as \(n \to \infty\) and sequence \((x_n) \subset \mathbb{R}\), Corollary 1 implies that, up to a subsequence, the sequence of functions \((t, x, y) \to (u(t + t_n, x + x_n), v(t + t_n, x + x_n, y))\) converges towards some function \((t, x, y) \to (U(t, x), V(t, x, y)) \in \mathcal{T}\) with respect to the topology of \(C_{\text{loc}}(\mathbb{R}^2) \times C_{\text{loc}}(\mathbb{R}^2; L^2(\mathbb{R}^M))\). As already noticed above, \(\hat{v} = \sqrt{\gamma}v \in C^1([0, \infty), C_0^0(\mathbb{R}, L^2(\mathbb{R}^M)))\) and (37) holds so that Lebesgue convergence theorem ensures that the sequence of functions \((t, x, y) \to (u(t + t_n, x + x_n), \hat{v}(t + t_n, x + x_n, y))\) converges towards the complete orbit \((t, x, y) \to (U(t, x), \hat{V}(t, x, y))\), with \(\hat{V}(t, x, y) := \sqrt{\gamma(y)}V(t, x, y)\), with respect to the topology of \(C_{\text{loc}}(\mathbb{R}^2) \times C_{\text{loc}}(\mathbb{R}^2; L^2(\mathbb{R}^M))\).

Now let \(\hat{v}_k\) be the projection of \(\hat{v}\) with respect to the eigenvector \(\phi_k\), i.e.
\[
\hat{v}_k(t, x) = \int_{\Omega} \hat{v}(t, x, y) \phi_k(y) dy.
\]
Since \( \hat{v} = \gamma^{1/2}v \) and \( \phi_1^* = \gamma^{1/2}\phi_1 \) on \( \Omega \), the following equality holds

\[
\hat{v}_1(t, x) = \int_{\mathbb{R}^d} v(t, x, y) \phi_1^*(y) dy = v_1(t, x). \tag{39}
\]

By projecting the equation (17) we obtain the following infinite system of ODEs for \( k \geq 1 \) and \( (t, x) \in \mathbb{R}^+ \times \mathbb{R} \)

\[
\partial_t \hat{v}_k(t, x) = \lambda_k u(t, x) K * \hat{v}_k(t, x) - \mu_v \hat{v}_k(t, x), \tag{40}
\]

while any limit orbit \( (U, V) \) satisfies for any \( k \geq 1 \) and for any \( (t, x) \in \mathbb{R}^2 \)

\[
\partial_t \hat{V}_k(t, x) = \lambda_k U(t, x) K * \hat{V}_k(t, x) - \mu_v \hat{V}_k(t, x), \tag{41}
\]

wherein we have set \( \hat{V}_k(t, x) = \int_\Omega \hat{v}(t, x, y) \phi_k(y) dy \).

To prove Theorem 2.1 \((iii)\) we shall show that for all \( (U, V) \in \mathcal{T} \) one has

\[
\hat{V}_k(t, x) \equiv 0 \text{ on } \mathbb{R}^2, \forall k \geq 2.
\]

To proceed let us first prove that for all \( (U, V) \in \mathcal{T} \) one has \( \hat{V}_k(t, x) \equiv 0 \) for all \( k \geq 2 \) large enough. To do so, since \( \lambda_k \to 0 \) as \( k \to \infty \) and since \( \mathcal{R}_0 = \lambda_1 \Lambda \mu_v > 1 \), let us define the integer \( k_0 \geq 2 \) by

\[
k_0 := \min\{k \geq 2 : \mu_v - \lambda_k \Lambda > 0\}. \tag{42}
\]

Our first result reads as follows.

**Lemma 6.1.** For each \( (U, V) \in \mathcal{T} \) one has, for all \( k \geq k_0 \),

\[
\hat{V}_k(t, x) \equiv 0, \forall (t, x) \in \mathbb{R}^2.
\]

**Proof.** Set \( \alpha > 0 \)

\[
\alpha := \mu_v - \lambda_k \Lambda.
\]

Let \( (U, V) \in \mathcal{T} \) and \( k \geq k_0 \) be given. Let us show that \( \hat{V}_k \equiv 0 \). To that aim, recall that \( \hat{V}_k \) is bounded by some constant \( M_k > 0 \). Then consider the function \( \hat{V}_k(t, x) = M_k e^{-\alpha t} \). Note that, since \( U \leq \Lambda \) and \( \int_\mathbb{R} K(x) dx = 1 \), one has, for all \( s \in \mathbb{R} \) and \( t \geq 0 \)

\[
\partial_t \hat{V}_k(t, x) - \lambda_k U(s + t, x) K * \hat{V}_k(t, x) + \mu_v \hat{V}_k(t, x) = M_k e^{-\alpha t} \left[ -\alpha - \lambda_k U(s + t, x) + \mu_v \right] \geq M_k e^{-\alpha t} \left[ -\alpha - \lambda_k \Lambda + \mu_v \right] \geq M_k e^{-\alpha t} \left[ \lambda_k - \lambda_k \Lambda \right] \geq 0.
\]

From the above estimate and recalling that \( |\hat{V}_k| \leq M_k \) and that \( \hat{V}_k \) satisfies (41), the comparison principle applies and ensures that

\[
|\hat{V}_k(s + t, x)| \leq M_k e^{-\alpha t}, \forall t \geq 0, \forall (s, x) \in \mathbb{R}^2.
\]

This proves that \( \hat{V}_k \equiv 0 \). This ends the proof of the lemma.

Note that if \( k_0 = 2 \) then the proof of Theorem 2.1 \((iii)\) is over. Indeed, in that case, one has for any \( (U, V) \in \mathcal{T} \) and all \( (t, x) \in \mathbb{R}^2 \)

\[
\sqrt{\gamma(\cdot)} V(t, x, \cdot) = \sum_{k=1}^{\infty} \hat{V}_k(t, x) \phi_k(\cdot) \text{ in } L^2(\Omega),
\]

that reads as \( V(t, x, \cdot) = V_1(t, x) \phi_1(\cdot) \). To complete this section, we investigate the case where \( k_0 \geq 3 \) and we shall also prove that each projection of the solution \( v \) onto the eigenvalues \( \lambda_2 \geq \cdots \geq \lambda_{k_0-1} \) vanishes in the large time, uniformly in space.
To go further in our analysis, let us define
\[ R_1 = \frac{\lambda_2 \Lambda}{\mu_v} < R_0. \]
Note that since \( k_0 \geq 3 \) one has
\[ 1 \leq R_1 < R_0. \]
And, similarly to the definition of \( c_* \), we define \( c_{**} \in [0, c_*) \) as
\[ c_{**} := \inf_{0 < \lambda < 1} \frac{R_1}{\lambda} \left( 1 - \frac{\lambda}{\lambda^2} - 1 \right). \]
Using these notations, we split our argument into two parts. We first inquire of
the behaviour of \( \hat{v}_k \) for \( |x| \geq ct \) for \( c > c_{**} \) and \( t \gg 1 \), before going to the region
\( |x| \leq ct \) for some speed \( c \in [0, c_*) \) and \( t \gg 1 \).

First the following result holds.

**Lemma 6.2.** For all \( k \in \{2, \cdots, k_0 - 1\} \) and \( c > c_{**} \), it holds that
\[ \lim_{t \to +\infty} \sup_{|x| \geq ct} |\hat{v}_k(t, x)| = 0. \]

**Proof.** Fix \( k \in \{2, \cdots, k_0 - 1\} \) and \( c > c_{**} \). We only consider the case \( x \geq ct \),
while the case \( x \leq -ct \) can be handled similarly. Similarly to the proof of Theorem
2.1 (i), we look for a super solution \( \bar{x} \) such that \( c_{**} \leq \bar{x} < c_\ast \) and
\( t \gg 1 \), before going to the region \( |x| \leq ct \) for some speed \( c \in [0, c_*) \) and \( t \gg 1 \).

To that aim, we fix \( \tilde{v}_k \) in (40), one obtains
\[ \partial_t \tilde{v}_k(t, x) - \lambda_k u(t, x)K \ast \tilde{v}_k(t, x) + \mu_v \tilde{v}_k(t, x) \]
\[ = M_k e^{-\mu(x-ct)} \left[ c \mu + \mu_v - \lambda_k u(t, x) \frac{1}{1 - \mu^2} \right], \forall (t, x) \in \mathbb{R}^+ \times \mathbb{R}. \]

Since \( c > c_{**} \), there exists \( \mu \in (0, 1) \) such that
\[ c \mu + \mu_v = \frac{\lambda_2 \Lambda}{1 - \mu^2}. \]
Hence, since \( u \leq \Lambda \) (see Proposition 2), we obtain
\[ \partial_t \tilde{v}_k(t, x) - \lambda_k u(t, x)K \ast \tilde{v}_k(t, x) + \mu_v \tilde{v}_k(t, x) \geq 0, \forall (t, x) \in \mathbb{R}^+ \times \mathbb{R}. \]

Moreover, since \( v_0 \) is compactly supported with respect to \( x \), there exists \( M_k \) such that
\[ |\tilde{v}_k(0, x)| = \int_{\Omega} \sqrt{\gamma(y)} v_0(x, y) \phi_k(y) dy \leq M_k e^{-\mu x}, \forall x \in \mathbb{R}. \]

With this choice of \( \mu \) and \( M_k \), \( \tilde{v}_k \) is a super solution of \( |\tilde{v}_k| \). The result follows as
in the proof of Theorem 2.1 (i). \( \square \)

To complete the proof of Theorem 2.1 (iii), we investigate the large time behaviour of \( \tilde{v}_k \) in some region \( |x| \leq ct \) for some \( c \in (c_{**}, c_\ast) \). To that aim, we fix
\( c_1 \in (c_{**}, c_\ast) \) and we consider the set \( T_1 \subset T \) by
\[ (U, V) \in T_1 \iff \text{there exist a sequence } (t_n)_{n \geq 0} \text{ with } t_n \to \infty \]
and a sequence \((x_n)_{n \geq 0}\) with \(|x_n| \leq c_1 t_n\) such that
\[ (U, V) = \lim_{n \to \infty} \left( u(t + t_n, x + x_n), v(t + t_n, x + x_n) \right), \]

for the topology of \( C_{\text{loc}}(\mathbb{R}^2) \times C_{\text{loc}}(\mathbb{R}^2; L^1(\mathbb{R}^M)) \).

Now, since \( c_1 > c_{**} \), to complete the proof of Theorem 2.1 (iii), it is sufficient to prove the following lemma.
Lemma 6.3. For any $(U, V) \in T_1$ and all $k \in \{2, \cdots, k_0 - 1\}$ it holds that
\[
\hat{V}_k(t, x) = 0, \forall (t, x) \in \mathbb{R}^2.
\]

The above lemma roughly follows from the spreading property for $v_1$, as stated in Theorem 2.1 (ii) coupled with a suitable comparison argument.

Proof. Let $(U, V) \in T_1$ be given. We first claim that

Claim 6.4. One has
\[
\inf_{(t, x) \in \mathbb{R}^2} V_1(t, x) = \inf_{(t, x) \in \mathbb{R}^2} \hat{V}_1(t, x) > 0.
\]

Proof of Claim 6.4. First recall that due to (39) one has $V_1 = \hat{V}_1$. Next let $c' \in (c_1, c_*)$ be given. Then Lemma 5.6 implies that there exists $\varepsilon' > 0$ such that
\[
\liminf_{t \to \infty} \inf_{|x| \leq c't} \int_{M} \rho(t, x, y) \rho_1^*(y) dy = \liminf_{t \to \infty} \inf_{|x| \leq c't} \int_{\Omega} \rho(t, x, y) \rho_1(y) dy \geq \varepsilon'.
\]

This rewrites as
\[
\liminf_{t \to \infty} \inf_{|x| \leq c't} \hat{v}_1(t, x) \geq \varepsilon' > 0. \tag{43}
\]

Let $(t_n) \subseteq \mathbb{R}^+$ and $(x_n) \subseteq \mathbb{R}$ be two sequences such that $t_n \to \infty$, $|x_n| \leq c_1 t_n$ and
\[
(U, V) = \lim_{n \to \infty} \left( u(t + t_n, x + x_n), v(t + t_n, x + x_n) \right),
\]

for the topology of $C_{\text{loc}}(\mathbb{R}^2) \times C_{\text{loc}}(\mathbb{R}^2; L^1(\mathbb{R}^M))$.

Now (43) implies that there is some $T > 0$ such that for all $t, x \in \mathbb{R}$ that satisfy $t + t_n \geq T$ and $|x + x_n| \leq c'(t + t_n)$, one has
\[
\hat{v}_1(t + t_n, x + x_n) \geq \varepsilon'/2.
\]

Then, passing to the limit $n \to \infty$ we retrieve that $\forall t, x \in \mathbb{R}$, $\hat{V}_1(t, x) \geq \varepsilon'/2$ and the claim is proved.

Thanks to (37), the projections $\hat{V}_k$ are uniformly bounded for all $k \geq 1$. Now fix $k \in \{2, \cdots, k_0 - 1\}$. Due to the uniform positivity of $\hat{V}_1$ provided in Claim 6.4, there exists some positive constant $C_1$ such that
\[
K * x \hat{V}_1(t, x) \geq C_1 \hat{V}_1(t, x), \forall (t, x) \in \mathbb{R}^2.
\]

Since $\hat{V}_k$ is uniformly bounded, for any $s \in \mathbb{R}$, there exists a constant $M_k > 0$ such that
\[
|\hat{V}_k(s, x)| \leq M_k \hat{V}_1(s, x), \forall (s, x) \in \mathbb{R}^2. \tag{44}
\]

Next due to Proposition 2, there exists $\varepsilon > 0$ such that $U(t, x) \geq \varepsilon$ for all $(t, x) \in \mathbb{R}^2$.

Let $\alpha$ be some positive constant to be chosen later. Let $s \in \mathbb{R}$ be given and set
\[
\hat{v}_1(t, x) := M_k e^{-\alpha t} \hat{V}_1(s + t, x).
\]

Then we readily compute that, for any $(t, x) \in \mathbb{R}^2$,
\[
\begin{align*}
\partial_t \hat{v}_1(t, x) - \lambda_k U(t + s, x) K * x \hat{v}_1(t, x) + \mu_v \hat{v}_1(t, x) \\
= M_k e^{-\alpha t} \left( -\alpha \hat{V}_1(s + t, x) + (\lambda_1 - \lambda_k) U(s + t, x) K * x \hat{V}_1(s + t, x) \right) \\
\geq M_k e^{-\alpha t} \hat{V}_1(s + t, x) \left( -\alpha + C_1 \varepsilon (\lambda_1 - \lambda_k) \right) \\
\geq M_k e^{-\alpha t} \hat{V}_1(s + t, x) \left( -\alpha + C_1 \varepsilon (\lambda_1 - \lambda_2) \right).
\end{align*}
\]
Hence since $\lambda_1 > \lambda_2$, we fix $\alpha$ small enough (independent of $s \in \mathbb{R}$) such that $-\alpha + C_1\varepsilon(\lambda_1 - \lambda_2) > 0$. With such a choice of the parameter $\alpha > 0$ we obtain
\[
\partial_t \bar{v}_1(t, x) - \lambda_k U(t + s, x)K \ast_x \bar{v}_1(t, x) + \mu_x \bar{v}_1(t, x) \geq 0, \forall (t, s) \in \mathbb{R}^2.
\]
Recalling (44), the comparison principle applies and ensures
\[
|\bar{V}_k(s + t, x)| \leq M_k e^{-\alpha t} \bar{V}_1(s + t, x), \forall (s, x) \in \mathbb{R}^2 \text{ and } t \in \mathbb{R}^+.
\]
Setting $l = t + s$ and letting $t \to \infty$ we obtain that $\forall (l, x) \in \mathbb{R}^2$, $\bar{V}_k(l, x) = 0$ and this completes the proof of the lemma. \qed

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