Propagation properties in a multi-species SIR reaction-diffusion system

Romain Ducasse¹ · Samuel Nordmann²

Received: 22 October 2022 / Revised: 5 June 2023 / Accepted: 10 June 2023 / Published online: 23 June 2023
© The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2023

Abstract
We consider a multi-species reaction-diffusion system that arises in epidemiology to describe the spread of several strains, or variants, of a disease in a population. Our model is a natural spatial, multi-species, extension of the classical SIR model of Kermack and McKendrick. First, we study the long-time behavior of the solutions and show that there is a “selection via propagation” phenomenon: starting with \( N \) strains, only a subset of them - that we identify - propagates and invades space, with some given speeds that we compute. Then, we obtain some qualitative properties concerning the effects of the competition between the different strains on the outcome of the epidemic. In particular, we prove that the dynamics of the model is not characterized by the usual notion of basic reproduction number, which strongly differs from the classical case with one strain.

Keywords Reaction-diffusion systems · SIR models · Spreading speed · Multi-species models · Epidemiology · Threshold phenomenon

Mathematics Subject Classification 35B36 · 35B40 · 35K10 · 35K40 · 35K57 · 92D30

1 Introduction

1.1 Problem under consideration

In 1927, Kermack and McKendrick (1991, 1932, 1933) introduced several deterministic models designed to describe the temporal development of a disease in a population,
among which the celebrated SIR model, which became a cornerstone of mathematical epidemiology. In this model, the population under consideration is divided into three compartments: the susceptible (who are not infected), the infectious (who have the disease and can transmit it to the susceptible) and the recovered (who had the disease and are now immune, or dead). The original SIR model consists in the following system of ODEs:

\[
\begin{align*}
\dot{S}(t) &= -\alpha SI, & t > 0, \\
\dot{I}(t) &= \alpha SI - \mu I, & t > 0, \\
\dot{R}(t) &= \mu I, & t > 0.
\end{align*}
\] (1.1)

The functions \( S(t), I(t), R(t) \) represent the densities of susceptible, infectious or recovered individuals respectively, at time \( t > 0 \). The susceptible individuals are infected by the infectious, according to a law of mass-action, with a rate \( \alpha I \), where \( \alpha > 0 \) is a constant parameter that accounts for the transmission efficiency of the disease. The infected individuals cease to be infectious at some recovery rate \( \mu > 0 \) (then, \( \frac{1}{\mu} \) is the mean duration of the infection), and then become recovered. In this model the recovered individuals cannot become susceptible again, hence the equations on \( S, I \) are decoupled from the one on \( R \).

We review the main results on (1.1) in Sect. 1.2. For now, let us mention that a serious drawback of this model is that it is purely temporal: spatial effects (migrations and distribution of individuals for instance) are not taken into account. Spatial effects are now recognized as being of first importance in the description of epidemics. Many models were introduced to bridge this gap. A classical way to build a spatial model is to add diffusion terms to the equations. The simplest diffusive SIR model is the following (originally introduced by Källén 1984):

\[
\begin{align*}
\partial_t S(t, x) &= -\alpha SI, & t > 0, \ x \in \mathbb{R}, \\
\partial_t I(t, x) &= d\Delta I + \alpha SI - \mu I, & t > 0, \ x \in \mathbb{R}, \\
\partial_t R(t, x) &= \mu I, & t > 0, \ x \in \mathbb{R}.
\end{align*}
\] (1.2)

Now, \( S, I, R \) do not only depend on the time \( t \) but also on a space variable \( x \in \mathbb{R} \). The presence of a diffusion operator on the equation for \( I \) accounts for the fact that the infectious individuals move randomly, following a Brownian motion, and therefore can bring the disease into places were it was not present before, potentially leading to a spatial spread. We briefly review this model, and mention others, in Sect. 1.2. One may find natural to add diffusion on the \( S \) and \( R \) individuals also. It turns out that doing so in the equation for \( R \) does not change much, but doing so in the equation for \( S \) makes the analysis much more intricate. We give more details about that in Sect. 1.2.

The goal of this paper is to answer the following natural question:

**What happens when there are several strains?**
To answer this, we consider the following spatial and multi-species SIR model:

\[
\begin{align*}
\partial_t S &= -S \left( \sum_{k=1}^{N} \alpha_k I_k \right), \quad t > 0, \ x \in \mathbb{R}, \\
\partial_t I_k &= d_k \Delta I_k + (\alpha_k S - \mu_k) I_k, \quad t > 0, \ x \in \mathbb{R}, \ k \in [1, N], \\
\partial_t R_k &= \mu_k I_k, \quad t > 0, \ x \in \mathbb{R}, \ k \in [1, N].
\end{align*}
\]

(1.3)

Here \( N \in \mathbb{N} \) is a positive integer, and the system is therefore made of \( 2N + 1 \) equations. The parameters \( \alpha_1, \ldots, \alpha_N, \mu_1, \ldots, \mu_N, d_1, \ldots, d_N \) are strictly positive constants. The unknowns are the \( 2N + 1 \) functions \( (S(t, x), I_1(t, x), \ldots, I_N(t, x), R_1(t, x), \ldots, R_N(t, x)) \). Being an evolution problem, (1.3) has to be completed with \( 2N + 1 \) initial data.

This paper is concerned with the long-time behavior of solutions to (1.3) - our main interests are the convergence to an equilibrium and the speed of propagation of the solutions. For the sake of clarity, we consider the case where the spatial domain is \( \mathbb{R} \), but our proofs and results hold true with minor adjustments to \( \mathbb{R}^d, d > 1 \).

System (1.3) describes the spread of \( N \) traits (or strains, or variants) of a disease in a population. In the following, we will always use the generic term *trait*. For \( k \in [1, N] \), \( I_k \) represents the density of individuals infected by the trait \( k \). They can transmit this trait to the susceptible individuals with rate \( \alpha_k \), they recover with rate \( \mu_k \), and when recovering they turn into individuals of type \( R_k \). The individuals \( I_k \) diffuse with rate \( d_k \).

The model (1.3) is probably the simplest and most natural spatial multi-species SIR model one could come up with: the only phenomena taken into account are infection and remission. There is no waning of immunity, there are no vital dynamics (arrival of new individuals, birth and death of individuals), and there can not be multiple infections: individuals who were infected by the trait \( k \) will not be infected by any other trait. Yet, as we shall prove, this model exhibits some interesting behaviors.

The main result of this paper, presented in Sect. 1.3 as Theorem 1.3, is that there is a *selection via propagation* phenomenon that appears: only a given subset of all the traits (possibly empty) propagates, all the other traits vanish. Such a phenomenon can be seen as an emergent property of the model: there is no *a priori* selection mechanism in the equations.

In addition to finding the traits that survive, and to computing their limits, we also identify at which speed and how these traits spread across space. As we will see, the system generates spatial traveling patterns such as *pulses* and *terraces*.

With this result at hand, we obtain some qualitative properties on the model. More precisely, we study how the parameters of the model (the infection, remission, and diffusion rates, and the initial densities) influence the outcome of the epidemic. In this paper, we highlight how our model with several strains differs from the case with one strain by focusing on three properties.

First, we show that the so-called *basic reproduction number* (whose definition is recalled after) is not a good predictor of the dynamics of the model: we exhibit situations where the strains that have the larger basic reproduction number do not propagate while those with the smaller basic reproduction number do. This is somewhat
counter-intuitive, as the basic reproduction number is in many classical situations an adequate criterion to predict the evolution of the disease.

The second property we investigate concerns the infection and remission rates of each trait that propagates. More precisely, we show that each trait that spreads is less contagious and has a lower recovery rate than all the traits that have propagated before.

Third, we study how the final density of susceptible individuals (that is, the density of surviving/untouched individuals) depends on the initial conditions. When there is only one strain that propagates, it is known that the density of surviving individuals is a decreasing function of the initial density of susceptible individuals. When there are several strains, we will see that this may be false.

Let us mention that some models with several strains were previously introduced in different contexts, sometimes in connection with evolutionary issues, we refer for instance to Bichara et al. (2014); Osnas et al. (2015) and the references therein. However, these models do not exhibit the same behaviors as the one we consider here: either only one trait propagates, or all the traits propagate - there is either no selection, or a very strong one. This is because the models usually considered in the literature take into account other effects (as internal dynamics, such as reproduction, for instance), which somehow impose a given dynamics to the system and strongly change its outcome.

To conclude this introduction, let us mention that the system (1.3) is a reaction-diffusion system. Although there is a wide literature on this topic, there are very few results dealing with general systems with more than 2 components. A key difficulty is the lack of comparison principles for such systems. Also, the convergence to an equilibrium for reaction-diffusion systems is, in general, a rather intricate question.

Before presenting our results, we give a quick review on the one-species SIR models (1.1) and (1.2). This will give a first intuition on how to study the dynamics of (1.3).

### 1.2 SIR models: review and basic results

As we mentioned already, the original SIR model is the ODE system (1.1). The main result on this system, proved by Kermack and McKendrick (1991), is that there is a threshold phenomenon:

- If \( \frac{\alpha S_0}{\mu} > 1 \), the disease propagates, in the sense that there is \( \eta > 0 \) such that, no matter how small \( I_0 > 0 \) is, \( \lim_{t \to +\infty} S(t) < S_0 - \eta \).
  In other words, the epidemic outburst grows to a significant size regardless of how few infectious individuals there were at initial time.
- If \( \frac{\alpha S_0}{\mu} \leq 1 \), the disease fades out, i.e., \( \lim_{t \to +\infty} S(t) \) can be made arbitrarily close to \( S_0 \) by decreasing \( I_0 > 0 \).

This celebrated result led to introduce the so-called basic reproduction number

\[ R_0 := \frac{\alpha S_0}{\mu}, \]

whose value dictates the behavior of the disease. This notion is now a cornerstone of mathematical epidemiology, and has been extended to several other contexts.
As we mentioned, a natural way to turn the ODE system into a spatial system is to add diffusion terms to it. This leads to the system

\begin{align}
\partial_t S(t, x) &= d_S \Delta S - \alpha SI, & t > 0, & x \in \mathbb{R}, \\
\partial_t I(t, x) &= d_I \Delta I + \alpha SI - \mu I, & t > 0, & x \in \mathbb{R}, \\
\partial_t R(t, x) &= \mu I, & t > 0, & x \in \mathbb{R}.
\end{align}

(1.4)

We refer to Murray (2003) for more details on this model. Observe that this system does not feature any diffusion on the $S$ individuals - this would not change the analysis, nor the results. The diffusion on $I$, on the other hand, rises many complications. For instance, the boundedness of solutions is not clear at all (when $d_S = d_I$, one could sum the equations for $S$ and $I$ and apply the parabolic comparison principle, but in general, the question is rather intricate, see Ducrot (2021) for instance).

For this reason, we consider here only the case where $d_S = 0$, that is, the susceptible individuals do not move, and then (1.4) boils down to (1.2). In this case, the threshold phenomenon of Kermack and McKendrick can be extended in the following form: consider (1.2) and take for initial data $S(0, x) = S_0 \in \mathbb{R}_+$ (i.e., the susceptible population is initially uniformly distributed), $I(0, x) = I_0(x)$ where $I_0$ is non-negative, non-zero, and compactly supported (the infectious individuals are initially localized), and take $R(0, x) = 0$.

First, if $\frac{\alpha S_0}{\mu} \leq 1$, then the epidemic fades out in the sense that, for every $I_0$ non-negative and compactly supported, one has

$$
\lim_{|x| \to +\infty} \lim_{t \to +\infty} R(t, x) = 0 \quad \text{and} \quad \lim_{|x| \to +\infty} \lim_{t \to +\infty} S(t, x) = S_0.
$$

This means that the densities of recovered and susceptible individuals are unchanged after the spread of the disease (in the limit $t \to +\infty$), at least far away in space (in the limit $|x| \to +\infty$): far away from the initial focus of infection (the support of $I_0$ say), no infection occurred. Of course, in the vicinity of the initial focus of infection, even when the disease does not propagate, $\lim_{t \to +\infty} S$ and $\lim_{t \to +\infty} R$ can be arbitrarily small (resp. large), depending on the initial datum $I_0$. This is natural: even if a disease does not propagate, at least the individuals who were infectious at initial time will eventually recover.

Now, if $\frac{\alpha S_0}{\mu} > 1$, the disease propagates with speed $c^* := 2\sqrt{d(\alpha S_0 - \mu)}$ and has asymptotic value $\rho > 0$, in the sense that

$$
\sup_{|x| > ct} R(t, x) \longrightarrow 0, \quad \forall c > c^* \quad \text{and} \quad \sup_{\delta < |x| < ct} |R(t, x) - \rho| \longrightarrow 0, \quad \forall c < c^*.
$$

This means that infections occur everywhere in space asymptotically in time, even far away from the support of $I_0$. The number $\rho$ represents the number of casualties, and one can show that $\rho$ is the unique positive solution of the transcendent equation $S_0(1 - e^{-\frac{\rho}{\mu}}) = \rho$. Observe that it is independent of $I_0$. 

@Springer
The propagation can also be seen in the evolution of the density of susceptible individuals $S(t, x)$:

$$\sup_{|x|>ct} |S(t, x) - S_0| \xrightarrow{t \to +\infty} 0, \quad \forall c > c^* \quad \text{and} \quad \sup_{\delta<|x|<ct} |S(t, x) - S_1| \xrightarrow{t \to +\infty} 0, \quad \forall c < c^*,$$

where $S_1 := S_0 e^{\frac{\alpha}{\mu} \rho} < S_0$.

Again, saying that the disease propagates is relevant only for large values of $|x|$, hence the $\delta$ in the above suprema.

A crucial observation is that the dynamics far away from the support of $I_0$ will be independent of $I_0$ itself.

The above result means that, when $\frac{\alpha S_0}{\mu} > 1$, then $R$ develops into two traveling waves that connect 0 to $\rho$, one traveling to the right and one to the left, and $S$ develops into two waves that connect $S_0$ to $S_1$. The $I$ density develops into two traveling pulses (one going to the right, one going to the left). The dynamics at a given time is represented in the following drawing, where $I$ is represented with a dashed line, and $S$, $R$ with solid lines.

The proof of this result relies on the fact that $R(t, x)$ solves

$$\partial_t R(t, x) = d_I \Delta R(t, x) + f(R(t, x)) + \mu I_0(x), \quad t > 0, \quad x \in \mathbb{R}, \quad (1.5)$$

where $f(z) = \mu S_0 (1 - e^{-\frac{\alpha}{\mu} z}) - \mu z$.

This equation is obtained by doing some easy algebraic manipulations on the equations (we will present them in the sequel). The resulting equation (1.5) is a KPP reaction-diffusion equation, whose name refers to Kolmogorov, Petrovski and Piskunov, who proved some crucial results on such equations, see Kolmogorov et al. (1937). The threshold phenomenon and the speed of propagation we mentioned before are then direct consequences of some now classical results from reaction-diffusion equation theory (that we will present below in the course of our proof). In particular, $R$ converges to a stationary solution of (1.5), that is, $R(t, x) \xrightarrow{t \to +\infty} R_\infty(x)$, where $R_\infty$ solves

$$d_I \Delta R_\infty(x) + f(R_\infty(x)) + \mu I_0(x) = 0, \quad x \in \mathbb{R}.$$
Moreover, one can show that $\lim_{|x| \to +\infty} R_\infty(x) = \rho$, where $\rho \in \mathbb{R}$ satisfies the stationary equation “far away” in space, i.e., where $I_0$, which is compactly supported, has no influence. More precisely, $\rho$ is solution of
\[
f(\rho) = 0.
\]

It is easy to see that there is a unique positive $\rho$ solution of this equation if and only if $f'(0) = \alpha S_0 - \mu > 0$.

Let us briefly mention some related works. Here, we build spatial models from the ODE model by adding diffusion terms. One could also consider models where infections occurs at distance. This was first suggested by Kendall Kendall (1957, 1965), and such models were studied in the homogeneous case by Diekmann and Thieme, see Diekmann (1978, 1979); Thieme (1977, 1979a, b); Thieme and Zhao (2003), and in the heterogeneous case by the first author, see Ducasse (2022). Heterogeneous diffusive SIR models were also considered, see Ducasse (2018); Ducrot and Giletti (2014). Let us also mention the work Berestycki et al. (2021) where the authors consider the influence of networks on similar models. Finally, the system (1.4) with $d_S > 0$ was considered by Hosono and Ilyas (1995), who proved the existence of traveling fronts, and also in Ducrot (2021), where the Cauchy problem is considered (under a more general form).

### 1.3 Results of the paper

Before presenting our main results, let us mention that the existence and uniqueness of classical solutions for (1.3) (that is, solutions that are $C_1^1 C_2$ for $I, R$ and $C_1^1 C_0^0$ for $S$) is standard, see Henry (1981) for instance.

We start with defining what it means for a trait to propagate, and what is the speed of propagation.

**Definition 1.1 (Propagation)** Let $(S, I_1, \ldots, I_N, R_1, \ldots, R_N)$ be the solution of (1.3) arising from the initial datum $(S_0, I_0^1, \ldots, I_0^N, 0, \ldots, 0)$, where $S_0$ is a positive constant and $I_0^1, \ldots, I_0^N$ are continuous, non-zero, non-negative and compactly supported functions.

- We say that the $k$-th trait, $k \in [1, N]$, has **asymptotic value** $\rho_k$ if
  \[
  \rho_k = \lim_{|x| \to +\infty} \left( \lim_{t \to +\infty} R_k(t, x) \right).
  \]

- We say that the $k$-th trait **propagates** if
  \[\rho_k > 0.\]

If $\rho_k = 0$, we say that **the trait vanishes**.
When the $k$-th trait, $k \in [1, N]$, propagates, we say that it propagates with speed $c^* > 0$ if
\[
\left( \sup_{|x| > ct} R_k(t, x) \right) \longrightarrow 0, \quad \text{for every } c > c^*,
\]
and
\[
\left( \sup_{\delta < |x| < c t} |R_k(t, x) - \rho_k| \right) \longrightarrow 0, \quad \text{for every } 0 < c < c^*.
\]

Observe that, in the system (1.3), we have that $\partial_t R_k(t, x) \geq 0$, hence, $\lim_{t \to +\infty} R_k(t, x)$ exists. The existence of $\rho_k$ will be established in the proof.

Let us now introduce some notations. For $N$ fixed (the number of traits that exist at initial time), for $(\alpha_k)_{[1, N]}$, $(\mu_k)_{[1, N]}$, $(d_k)_{[1, N]}$ given, we define some functions $c_k(\sigma)$, $f_k(\rho, \sigma)$ and $\rho_k(\sigma)$, of variables $\rho \in \mathbb{R}$ and $\sigma \in \mathbb{R}^+$. 

- The speed function $c_k(\sigma)$ is defined for $\sigma \geq 0$ by
  \[
c_k(\sigma) := \begin{cases} 
  2\sqrt{d_k(\alpha_k \sigma - \mu_k)}, & \text{when } \alpha_k \sigma - \mu_k \geq 0, \\
  0, & \text{otherwise}.
\end{cases}
\]

- The reaction function $f_k(\rho, \sigma)$, defined for $\rho \in \mathbb{R}$, $\sigma \geq 0$, is given by
  \[
f_k(\rho, \sigma) := \sigma \mu_k \left( 1 - e^{-\frac{\alpha_k}{\mu_k} \rho} \right) - \mu_k \rho.
\]

- For $\sigma > 0$ given, the equation $f_k(\cdot, \sigma) = 0$ has a unique positive solution if and only if $\frac{\alpha_k \sigma}{\mu_k} > 1$. When it exists, we denote this positive solution $\rho_k(\sigma)$.

According to what we recalled in the previous section concerning the model (1.2) with one strain, we see that $c_k(\sigma)$, $f_k(\rho, \sigma)$ and $\rho_k(\sigma)$ would be respectively the speed of propagation, the nonlinear reaction term and the asymptotic value for the $k$-th trait, provided it were the only trait present in the model and if the initial density of susceptible individuals were $\sigma$.

We can now explain the heuristics underlying the results we are about to present. When there is only one trait, the result we mentioned in the previous section says that either it vanishes, or it propagates with some speed. If it propagates, the trait infects a certain proportion of the susceptible population. When there are several traits, we can expect the competition between the traits to be negligible at first, and then each trait would start to propagate at the speed it would have provided it were alone: the trait $k$ would propagate with speed $c_k(S_0)$. The idea is that the fastest trait, that is, the trait with the largest $c_k(S_0)$, will indeed do so. While it propagates, this fastest trait will infect a proportion of the susceptible population. Therefore all the other traits will
have to propagate in an environment where there are fewer susceptible individuals, which will hinder their propagation.

For instance, assume that $c_1(S_0) > c_k(S_0)$ for all $k \neq 1$. Then, the trait 1 would start to propagate, and it would leave behind a density of susceptible individuals equal to $S_1 := S_0 e^{-\frac{a_1}{\mu_1} \rho_1}$ (this is the case if it is the only trait present, as explained before). Then all the other traits would be left in an environment where the density of susceptible individuals is equal to $S_1$, not $S_0$. One can expect the above dynamics to continue this way: the trait $j \neq 1$ that maximizes $c_j(S_1)$ should propagate, and infect a proportion of the susceptible population, and the dynamics should go on until either there are not enough susceptible individuals left for the remaining traits to propagate, or all the traits have propagated.

The situation at a given time is depicted below, when 2 traits propagate (we only represent the right-hand side of space, the dynamics is similar on the left-hand side):

We will prove the heuristics under some extra hypotheses. We shall require the speeds of each trait that propagate to be distinct enough, so that we could control the interactions between the different traits. The result may be false without this hypothesis, see the remark after the statement of Theorem 1.3.

To formalize the heuristics, we introduce the following:

**Definition 1.2** Let $N \in \mathbb{N}^*$ and $S_0 > 0$ be fixed, and let $(d_k, \alpha_k, \mu_k)_{k \in [1,N]}$ be strictly positive real numbers. We define the propagation sequences as four (finite) sequences $(k_i)_{i \in [1,p]}$, $(c_i)_{i \in [1,p]}$, $(\rho_i)_{i \in [1,p]}$ and $(S_i)_{i \in [0,p]}$ as follows: first, we take $S_{i=0} = S_0$, and then we define recursively:

- $k_i := \arg\max_{z \in [1,N] \setminus \{k_1, \ldots, k_{i-1}\}} \{c_z(S_{i-1}) \text{ such that } c_z(S_{i-1}) > 0\}$. For now, we assume that the argmax is well defined (that is, there is a unique $z$ that maximizes $c_z(S_{i-1})$). When stating our results, we will actually need a stronger hypothesis. If the above set is empty, then $k_i$ is not defined and the sequence stops here.
- $c_i := c_{k_i}(S_{i-1})$.
- $\rho_i := \rho_{k_i}(S_{i-1})$.
- $S_i := S_{i-1} e^{-\frac{a_{k_i}}{\mu_{k_i}} \rho_i}$.

These definitions allow us to state precisely our heuristics: the traits $k_1, \ldots, k_p$ should propagate, with speed $c_1, \ldots, c_p$, and each trait should have asymptotic value $\rho_1, \ldots, \rho_p$ respectively.
Moreover, for any trait $k_i$ that propagates, with $i = 1, \ldots, p$, then there will be $S_{i-1}$ susceptible individuals just before this trait propagates, and $S_i$ susceptible individuals after.

We are now in position to state our main result:

**Theorem 1.3** Let $(S, I_1, \ldots, I_N, R_1, \ldots, R_N)$ be the solution of (1.3) arising from the initial datum $(S_0, I_1^0, \ldots, I_N^0, 0, \ldots, 0)$, where $S_0 \in \mathbb{R}^+$ and the $I_i^0$ are continuous non-negative, non-zero, compactly supported initial data, for all $i \in [1, N]$.

Let $(k_i)_{i \in [1, p]}, (c_i)_{i \in [1, p]}, (\rho_i)_{i \in [1, p]}, (S_i)_{i \in [0, p]}$ be the propagation sequences given in Definition 1.2.

Assume that, for all $i \in [1, p - 1]$, \[ c_k(S_{i-1}) + c_k(S_i) < c_i, \quad \text{for all } k \neq k_1, \ldots, k_p, \] and that \[ \alpha_k S_p - \mu_k < 0, \quad \text{for all } k \neq k_1, \ldots, k_p. \] (1.6) (1.7)

Then, the traits $k_1, \ldots, k_p$ propagate in the sense of Definition 1.1, with speeds $c_1, \ldots, c_p$, and have asymptotic values $\subset_1, \ldots, \rho_p$. All the other traits do not propagate and vanish.

Let us give some remarks on this theorem. First, if one finds that $p = 0$ or $p = 1$ when computing the propagation sequences, then the hypothesis (1.6) is void, and the theorem only requires (1.7). Similarly, if one finds that $p = N$, then the hypothesis (1.7) is void and only (1.6) is required.

When $N = 1$ and $p = 0$, observe that our theorem does not completely boil down to the result on the model with a single trait recalled in Sect. 1.2. Indeed, we still need (1.7) while the classical result recalled in Sect. 1.2 says that $\alpha_1 S_0 - \mu_1 \leq 0$ is sufficient.

We emphasize that, although $\lim_{t \to +\infty} R_k(t, x)$ depends on the values of the initial data $I_1^0, \ldots, I_N^0$, the quantity $\rho_k$ does not. Moreover, whether a trait propagates does not depend on the initial data, under the hypotheses of the theorem. In particular, if some initial datum is not compactly supported, the result may be false. Also, if some $I_k^0$ is everywhere equal to 0, one has to remove it and consider the problem with $N - 1$ traits.

We define the final density of susceptible individuals

$$ S_\infty := \lim_{|x| \to +\infty} \left( \lim_{t \to +\infty} S(t, x) \right). $$

It represents the density of individuals that have survived to all the traits. When our theorem applies, we have

$$ S_\infty = S_p.$$

Springer
where $p$ is given by the propagation sequences.

Now, as we can see, Theorem 1.3 proves our heuristics under (1.6) and (1.7). These assumptions are actually necessary in the sense that the result may be false without them. Indeed, hypothesis (1.6) says that when a trait propagates, the speed of the other traits that could propagate are “sufficiently” smaller. If two traits have almost equal speeds, then the two fronts that should arise could interfere, and the slower front could accelerate. This phenomenon was observed for instance in the papers (Girardin and Lam 2019; Liu et al. 2021), in the case of competition models. In our case, this might indeed change the speed of propagation of each trait, and this might lead to a different selection phenomenon. We leave this question for later studies.

Theorem 1.3 is a “selection” result. It indicates which traits propagate, and which traits do not. Let us point out that the model does not feature any explicit selection mechanism: it emerges as a by-product.

This result allows to study some qualitative properties of the model. More precisely, we will be interested in understanding how the parameters influence the dynamics. To do so, we need to compute the propagation sequences, which is a complicated task, as these sequences are implicitly defined.

We dedicate the last section of this paper to establishing three properties that shed light on some aspects of the system (1.3).

- We prove in Corollary 3.1 that, when several strains can propagate, the basic reproduction number of each strain does not indicate which one can propagate. More precisely, we construct examples with two traits, where the trait with the smallest basic reproduction number propagates, while the other vanishes.
- We show in Corollary 3.2 that, when several traits propagate, each one is less contagious (i.e., it has a lower infection rate $\alpha_i$) and has a lesser recovery rate $\mu_i$, than each trait that propagates before.
- We study in Corollary 3.3 how the final density of susceptible individuals depends on the initial density of susceptible. We consider the case with two traits. The picture here is rather different from the case with a single trait.

We give the precise statements and the proofs of these three properties in Sect. 3. First, we dedicate the next Sect. 2, to the proof of Theorem 1.3.

2 Proof of Theorem 1.3

2.1 Outline of the proof

This section is dedicated to the proof of our main result, Theorem 1.3. In this section, the parameters $S_0$, $(\alpha_i)_{i\in[1,N]}$, $(\mu_i)_{i\in[1,N]}$, $(d_i)_{i\in[1,N]}$ are fixed, strictly positive constants, and $(k_i)_{i\in[1,p]}$, $(c_i)_{i\in[1,p]}$, $(\rho_i)_{i\in[1,p]}$, $(S_i)_{i\in[0,p]}$ denote the propagation sequences given in Definition 1.2. We also assume that the initial data for the $(I_i)_{i\in[1,N]}$, denoted $(I_i^0)_{i\in[1,N]}$, are continuous, non-zero, non-negative and compactly supported.
We prove Theorem 1.3 by (finite) induction. For \( j \in \llbracket 0, p \rrbracket \), we denote \((H_j)\) the induction hypothesis:

The traits \( k_1, \ldots, k_j \) propagate with speeds \( c_1, \ldots, c_j \) and asymptotic values \( \rho_1, \ldots, \rho_j \).

\((H_j)\)

When \( j = 0 \), we use the convention that the hypothesis \((H_0)\) is empty (that is, when we write: assume \((H_j)\), when \( j = 0 \), we have nothing to assume).

To prove Theorem 1.3, we will prove first that \((H_p)\) holds true, and then that every trait \( k \neq k_1, \ldots, k_p \) does not propagate. A key point in the proof will be to obtain suitable exponential estimates on the functions \( I_k, R_k \), for all \( k \). This is the object of the following:

**Proposition 2.1** Let \((S, I_1, \ldots, I_N, R_1, \ldots, R_N)\) be the solution of (1.3) arising from the initial datum \((S_0, I_{01}, \ldots, I_{0N}, 0, \ldots, 0)\).

Assume that (1.6) holds true and that the induction hypothesis \((H_j)\) is verified for some \( j \in \llbracket 0, p \rrbracket \).

Then, for all \( k \neq k_1, \ldots, k_j \), for all \( \varepsilon > 0 \) small enough, there are \( A_{k,j}^{\varepsilon}, B_{k,j}^{\varepsilon} > 0 \) such that

\[
I_k(t, x) \leq A_{k,j}^{\varepsilon} e^{-\frac{(c_k(S_j)+\varepsilon)}{2d_k}(|x|-c_k(S_j)+\varepsilon)t)}, \quad \text{for all } t > 0, \ x \in \mathbb{R},
\]

and

\[
R_k(t, x) \leq B_{k,j}^{\varepsilon} e^{-\frac{(c_k(S_j)+\varepsilon)}{2d_k}(|x|-c_k(S_j)+\varepsilon)t)}, \quad \text{for all } t > 0, \ x \in \mathbb{R}.
\]

This proposition will allow us to obtain upper bounds on the speed of propagation.

Observe that the estimates on the functions \( R_k \) are a consequence of the estimates on the \( I_k \). Indeed, we have \( \partial_t R_k = \mu_k I_k \), hence, integrating the estimate on \( I_k \) yields the same estimate on \( R_k \) with \( B_{k,j}^{\varepsilon} = \mu_k A_{k,j}^{\varepsilon} \frac{2d_k}{(c_k(S_k)+\varepsilon)^2} \).

In the above Proposition 2.1, it is possible to have \( c_k(S_j) = 0 \) for some \( k, j \). In this case, the exponential in the proposition travels with a speed \( \varepsilon > 0 \) as small as we want.

The proof of Proposition 2.1 is done in several steps, each one being a lemma presented in Sect. 2.2. First, we rewrite the system (1.3) under a different form that involves only the functions \( R_k \), \( k \in \llbracket 1, N \rrbracket \). This is the object of Lemma 2.2.

Then, we show in Lemma 2.4 that the functions \( I_k, R_k \) are respectively subsolutions and supersolutions of some equations. Combining these two lemmas with another technical result (Lemma 2.5), we will finally get Proposition 2.1.

We then use this proposition to show that, if \((H_j)\) is verified for some \( j \in \llbracket 0, p - 1 \rrbracket \), then \((H_{j+1})\) also holds true. This is the object of Proposition 2.6 below. Eventually, this yields that \((H_p)\) holds true.

Finally, we prove in Proposition 2.8 that the traits \( k \neq k_1, \ldots, k_p \) do not propagate, and this will conclude the proof of Theorem 1.3.
2.2 Proof of the exponential estimates, Proposition 2.1

We start with rewriting the system (1.3). The next lemma strongly relies on the fact that there is no diffusion on the susceptible individuals.

**Lemma 2.2** Let \((S, I_1, \ldots, I_N, R_1, \ldots, R_N)\) be the solution of (1.3) arising from the initial datum \((S_0, I_0^1, \ldots, I_0^N, 0, \ldots, 0)\).

- The function \(S(t, x)\) can be written as
  \[
  S(t, x) = S_0 \prod_{i=1}^{N} e^{-\frac{\alpha_i}{\mu_i} R_i(t, x)}, \quad \forall t > 0, \ x \in \mathbb{R}.
  \]

- For any \(k \in [1, N]\), for \(t > 0, x \in \mathbb{R}\), we have
  \[
  \partial_t R_k = d_k \Delta R_k + \mu_k I_k^0 - \mu_k R_k + \alpha_k S_0 \int_0^t e^{-\frac{\alpha_k}{\mu_k} R_k} \partial_t R_k \left( \prod_{i \neq k} e^{-\frac{\alpha_i}{\mu_i} R_i} \right) d\tau.
  \]

**Proof** The proof follows from the simple observation that the first equation in (1.3), giving \(S(t, x)\), can be rewritten, using the equations for \(R_1, \ldots, R_N\), as
  \[
  \frac{\partial_t S}{S} = -\sum_{i=1}^{N} \frac{\alpha_i}{\mu_i} \partial_t R_i.
  \]

Integrating this relation directly gives the result.

To get the second point, we simply replace \(S(t, x)\) by the expression we just found in the equation giving \(I_k\), thus obtaining
  \[
  \partial_t I_k = d_k \Delta I_k + \left( \alpha_k S_0 \prod_{i=1}^{N} e^{-\frac{\alpha_i}{\mu_i} R_i} - \mu_k \right) I_k.
  \]

Then, we multiply by \(\mu_k\) and we integrate over the \(t\) variable, from 0 to some \(t > 0\). Remembering that \(\partial_t R_k = \mu_k I_k\), we find the result. \(\square\)

Using the above lemma we obtain the uniform boundedness of all the functions appearing in the system.

**Corollary 2.3** Let \((S, I_1, \ldots, I_N, R_1, \ldots, R_N)\) be the solution of (1.3) arising from the initial datum \((S_0, I_0^1, \ldots, I_0^N, 0, \ldots, 0)\).

Then, there is \(C > 0\) such that
  \[
  S(t, x) \leq C, \quad I_k(t, x) \leq C, \quad R_k(t, x) \leq C, \quad \text{for all } t > 0, \ x \in \mathbb{R}, \ k \in [1, N],
  \]

and \(C\) depends only on the coefficients of the system and on the initial data.
Proof The boundedness of $S$ is direct: we have $0 \leq S(t, x) \leq S_0$.

Let $k \in \llbracket 1, N \rrbracket$ be chosen. The second point of Lemma 2.2 (together with $R_i \geq 0$, $\partial_t R_i \geq 0$ for all $i \in \llbracket 1, N \rrbracket$) implies that

$$
\partial_t R_k \leq d_k \Delta R_k + \mu_k I_k^0 - \mu_k R_k + \alpha_k S_0 \int_0^t e^{-\frac{\alpha_k}{\mu_k} \partial_t R_k d \tau} = d_k \Delta R_k + f_k(S_0, R_k) + \mu_k I_k^0,
$$

where $z \mapsto f_k(S_0, z)$ is the reaction function defined in Sect. 1.3. Because $f_k(S_0, z) \xrightarrow{z \to +\infty} -\infty$, the parabolic comparison principle implies indeed that $R_k$ is bounded uniformly in $t, x$.

The boundedness of $I_k$ comes from usual regularity theory results. Indeed, $I_k$ is solution of a parabolic equation with bounded coefficients. Therefore, owing to the Harnack inequality, there is $A > 0$ such that, for all $t \geq 1$, $x \in \mathbb{R}$, we have $I_k(t, x) \leq A \inf_{\tau \in [t+1, t+2]} I_k(\tau, x)$, and then

$$
I_k(t, x) \leq A \int_{t+1}^{t+2} I_k(\tau, x) d\tau \leq \frac{2A}{\mu_k} \|R_k\|_{L^\infty_{t,x}}.
$$

This proves that $I_k$ is uniformly bounded for $t \geq 1$, $x \in \mathbb{R}$. For $t \leq 1$, observe that

$$
\partial_t I_k \leq d_k \Delta I_k + (\alpha_k S_j \theta - \mu_k)I_k
$$

implies, thanks to the parabolic comparison principle again, that $I_k(t, x) \leq \|I_k^0\|_{L^\infty(\mathbb{R})} e^{(\alpha_k S_0 - \mu_k) t}$ for $t \leq 1$, $x \in \mathbb{R}$, which concludes the proof. $\square$

The next lemma builds on the previous one, and shows that the functions $I_k$, $R_k$, $k \in \llbracket 1, N \rrbracket$, are respectively subsolutions/supersolutions of some parabolic equations on some domains.

Lemma 2.4 Let $(S, I_1, \ldots, I_N, R_1, \ldots, R_N)$ be the solution of (1.3) arising from the initial datum $(S_0, I_0^1, \ldots, I_0^N, 0, \ldots, 0)$.

Assume that the induction hypothesis $(H_j)$ holds true for some $j \in \llbracket 0, p \rrbracket$. Then, the following inequalities hold true:

- For every $\theta > 1$, $\varepsilon > 0$, there are $L$, $T > 0$ such that
  $$
  \partial_t I_k \leq d_k \Delta I_k + (\alpha_k S_j \theta - \mu_k)I_k, \quad \text{for } t > T, \quad L < |x| < (c_j - \varepsilon)t, \quad k \in \llbracket 1, N \rrbracket.
  $$

- For $k \neq k_1, \ldots, k_j$, for any $\omega \in (0, 1)$, there is $L > 0$ such that
  $$
  \partial_t R_k \geq d_k \Delta R_k + f_k(R_k, \omega S_j) - \mu_k S_j \left( \sum_{i \neq k, k_1, \ldots, k_j} \frac{\alpha_i}{\mu_i} R_i \right) R_k, \quad \text{for } t > 0, \quad |x| > L.
  $$
When \( j = 0 \), the first point in the above lemma is not well-written (\( c_j \) is not defined when \( j = 0 \)). In this case, we use the convention that the first point should read: for every \( \theta > 1, \varepsilon > 0 \), there is \( T > 0 \) such that

\[
\partial_t I_k \leq d_k \Delta I_k + (\alpha_k S_0 \theta - \mu_k) I_k, \quad \text{for } t > T, \quad k \in \llbracket 1, N \rrbracket,
\]

that is, there are no restrictions on \( x \). Observe that this is actually a direct consequence of the fact that \( \partial_t S(t, x) \leq 0 \), which implies that \( S(t, x) \leq S_0 \) for all \( t > 0, x \in \mathbb{R} \) (one can even take \( \theta = 1 \) and \( T = 0 \) in this case, but not for the other indices \( j \)).

The second point reads similarly when \( j = 0 \), the sum in the right hand term simply runs on all \( i \in \llbracket 1, N \rrbracket \setminus k \).

**Proof** Let \( j \in [0, p] \) be fixed and assume that \( (H_j) \) holds true. We denote \( K_j := \{k_1, \ldots, k_j\} \) and \( K_j^c := \llbracket 1, N \rrbracket \setminus K_j \) (if \( j = 0 \), then \( K_j = \emptyset \)).

**First point.** Let \( \theta > 1, \varepsilon > 0 \) be fixed. We already know from Lemma 2.2 that, for all \( k \in \llbracket 1, N \rrbracket \),

\[
\partial_t I_k = d_k \Delta I_k + \left( \alpha_k S_0 \prod_{i \in K_j} e^{-\frac{\alpha_i}{\mu_i} R_i(t)} \right) \left( \prod_{i \in K_j^c} e^{-\frac{\alpha_i}{\mu_i} R_i} - \mu_k \right) I_k.
\]

Owing to \( (H_j) \), the traits \( i \in K_j \) all propagate, with speed at least \( c_j \) (because \( c_1 > c_2 > \ldots > c_j \)), hence, for every \( \eta > 0 \), there are \( L, T > 0 \) such that

\[
R_i(t, x) \geq \rho_i - \eta, \quad \text{for all } i \in K_j, \ t > T, \ L < |x| < (c_j - \varepsilon)t.
\]

Then, for \( t > T, \ L < |x| < (c_j - \varepsilon)t \), we have

\[
\prod_{i \in K_j} e^{-\frac{\alpha_i}{\mu_i} R_i(t, x)} \leq \prod_{i \in K_j} e^{-\frac{\alpha_i}{\mu_i} \rho_i} \prod_{i \in K_j} e^{\frac{\alpha_i}{\mu_i} \eta}.
\]

Take \( \eta > 0 \) small enough so that \( \prod_{i \in K_j} e^{\frac{\alpha_i}{\mu_i} \eta} \leq \theta \). On the other hand, we bound from above \( \prod_{i \in K_j} e^{-\frac{\alpha_i}{\mu_i} R_i(t, x)} \) by 1 and we recall that, by definition, \( S_j = S_0 \prod_{i \in K_j} e^{-\frac{\alpha_i}{\mu_i} \rho_i} \), to get

\[
\partial_t I_k \leq d_k \Delta I_k + (\alpha_k S_j \theta - \mu_k) I_k, \quad \text{for } t > T, \ L < |x| < (c_j - \varepsilon)t.
\]

**Second point.** Let us take \( k \neq k_1, \ldots, k_j \). Owing to Lemma 2.2, we have

\[
\partial_t R_k = d_k \Delta R_k + \mu_k I_k^0 - \mu_k R_k + \alpha_k S_0 \int_0^t e^{-\frac{\alpha_k}{\mu_k} R_k} \partial_t R_k \left( \prod_{i \neq k} e^{-\frac{\alpha_i}{\mu_i} R_i} \right) d\tau.
\]
Because all the \( R_i \) are non-decreasing with respect to \( t \), we find that

\[
\partial_t R_k \geq d_k \Delta R_k + \mu_k I^0_k - \mu_k R_k + \alpha_k S_0 \left( \prod_{i \neq k} e^{-\frac{\alpha_i}{\mu_i} R_i(t,x)} \right) \int_0^t e^{-\frac{\alpha_k}{\mu_k} R_k} \partial_t R_k \, d\tau \\
\geq d_k \Delta R_k - \mu_k R_k + \mu_k S_0 \left( \prod_{i \neq k} e^{-\frac{\alpha_i}{\mu_i} R_i(t,x)} \right) \left( 1 - e^{-\frac{\alpha_k}{\mu_k} R_k} \right)
\]

Now, owing to \((H_j)\), for \( i \in K_j \), we know that \( R_i \) propagates and has asymptotic value \( \rho_i \). Therefore (because \( R_i \) is time-non-decreasing), for every \( \eta > 0 \), there is \( L > 0 \) such that

\[
R_i(t,x) \leq \rho_i + \eta, \quad \text{for } t > 0, \ |x| > L, \ i \in K_j.
\]

This allows us to derive a lower bound on \( \prod_{i \neq k} e^{-\frac{\alpha_i}{\mu_i} R_i(t,x)} \) for \( t > 0 \) and \( |x| > L \) (recall that \( k \notin K_j \)):

\[
\prod_{i \neq k} e^{-\frac{\alpha_i}{\mu_i} R_i(t,x)} = \prod_{i \in K_j} e^{-\frac{\alpha_i}{\mu_i} R_i(t,x)} \prod_{i \in K_j \setminus k} e^{-\frac{\alpha_i}{\mu_i} R_i(t,x)} \\
\geq \left( \prod_{i \in K_j} e^{-\frac{\alpha_i}{\mu_i} \rho_i} \right) \left( \prod_{i \in K_j} e^{-\frac{\alpha_i}{\mu_i} \eta} \right) \left( 1 - \sum_{i \in K_j \setminus k} \frac{\alpha_i}{\mu_i} R_i(t,x) \right) 
\]

Hence, up to taking \( \eta \) small enough so that \( \prod_{i \in K_j} e^{-\frac{\alpha_i}{\mu_i} \eta} > \omega \), we get, for \( t > 0 \), \( |x| > L \),

\[
\partial_t R_k \geq d_k \Delta R_k - \mu_k R_k + \mu_k S_0 \omega \prod_{i \in K_j} e^{-\frac{\alpha_i}{\mu_i} \rho_i} \left( 1 - \sum_{i \in K_j \setminus k} \frac{\alpha_i}{\mu_i} R_i(t,x) \right) \left( 1 - e^{-\frac{\alpha_k}{\mu_k} R_k} \right) \\
\geq d_k \Delta R_k - \mu_k R_k + \mu_k \omega S_j \left( 1 - \sum_{i \in K_j \setminus k} \frac{\alpha_i}{\mu_i} R_i(t,x) \right) \left( 1 - e^{-\frac{\alpha_k}{\mu_k} R_k} \right) \\
\geq d_k \Delta R_k + f_k(R_k, \omega S_j) - \mu_k S_j \omega \left( \sum_{i \in K_j \setminus k} \frac{\alpha_i}{\mu_i} R_i(t,x) \right) \left( 1 - e^{-\frac{\alpha_k}{\mu_k} R_k} \right) \\
\geq d_k \Delta R_k + f_k(R_k, \omega S_j) - \alpha_k S_j \left( \sum_{i \in K_j \setminus k} \frac{\alpha_i}{\mu_i} R_i(t,x) \right) R_k,
\]

hence the result. \( \square \)
Now, in order to prove Proposition 2.1, we need the following technical lemma:

**Lemma 2.5** Let \( d, r > 0 \) and let \( u(t, x) \geq 0 \) be \( C^1_x \) and bounded, such that:

- There are \( c_1, A > 0 \) such that, for all \( t > 0, x \in \mathbb{R} \), we have
  \[
  u(t, x) \leq Ae^{-\frac{c_1}{2d}(x-c_1t)}.
  \]

- There are \( L, T, c_2 > 0 \) such that, for all \( t > T, L < |x| < c_2t \), we have
  \[
  \partial_t u - d\Delta u \leq ru.
  \]

In addition, define

\[
  c_3 := 2\sqrt{rd}.
  \]

Assume that

\[
  c_1 > c_3 \quad \text{and} \quad c_2 > c_1 + c_3. \tag{2.8}
  \]

Then, there is \( B > 0 \) such that, for \( t > 0, x \in \mathbb{R} \),

\[
  u(t, x) \leq Be^{-\frac{c_3}{2d}(x-c_3t)}.
  \]

Observe that in this lemma, we need an hypothesis on \( c_1, c_2, c_3 \), namely (2.8). When applying this lemma later, this requirement will force us to assume the separation hypothesis (1.6) on the speeds of each trait.

**Proof** For \( B > \max \{ A, \sup_{t,x} u \} \) to be chosen large enough later, define

\[
  w(t, x) := Be^{-\frac{c_3}{2d}(x-c_3t)}.
  \]

Observe first that, for \( t > 0, x > c_2t \), we have thanks to (2.8), \( Ae^{-\frac{c_1}{2d}(x-c_1t)} \leq w(t, x) \), and then \( w \geq u \) in this region. For \( t > 0, x < -c_2t \), we have \( w(t, x) \geq B \), and then \( w \geq u \) also in this region. Up to taking \( B \) large enough, we can also ensure that \( w \geq u \) in the bounded domain \( \{ (t, x) \ t \in (0, T), \ |x| < c_2T \} \) and in the region \( \{ (t, x) \ t > 0, \ |x| < L \} \).

It remains to prove that \( w \geq u \) on the domain \( E := \{ (t, x) \ t > T, \ L < |x| < c_2T \} \). To do so, we use the parabolic comparison principle (see Protter and Weinberger 1967).

We have

\[
  \partial_t w - d\Delta w = rw, \quad \text{for } t > 0, x \in \mathbb{R}.
  \]

By hypothesis, we know that \( u \) is subsolution of this equation on the domain \( E \).

To apply the parabolic comparison principle, we need that \( w \geq u \) on \( \partial E \), that is, we need to have \( w(T, x) \geq u(T, x) \) for \( |x| \leq c_2T \) and \( w(t, x) \geq u(t, x) \) for \( t > T \) and \( |x| = c_2t \) and \( |x| = L \). This last point, for \( t > T \) and \( |x| = L \) is already guaranteed.
Because \( u \) is bounded, taking \( B \) large enough guarantees that the first requirement is verified. For the second requirement, it is sufficient to have

\[
Be^{-\frac{c_3}{2d}(c_2-c_3)t} \geq Ae^{-\frac{c_1}{2d}(c_2-c_1)t}, \quad \text{for } t > T.
\]

Up to increasing \( B \), this is true if \( \frac{c_3}{2d}(c_2-c_3) < \frac{c_1}{2d}(c_2-c_1) \), which is guaranteed by (2.8). Then, we can apply the parabolic comparison theorem to \( u, w \) on \( E \) to get the result. \( \square \)

We can now finally turn to the proof of Proposition 2.1.

**Proof of Proposition 2.1** We will prove that, under the hypotheses of Proposition 2.1, we have, for \( \varepsilon > 0 \) small enough,

\[
I_k(t, x) \leq A^\varepsilon_k, j e^{-\frac{(c_k(S_j)+\varepsilon)^2}{2d_k}(x-(c_k(S_j)+\varepsilon)t)}, \quad \text{for all } t > 0, \ x \in \mathbb{R}.
\]

This is not exactly was is required, because we do not have the absolute value on the \( x \) in the exponential. To get it, one can either redo the same arguments with supersolution moving toward the left (that is, supersolutions of the form \( e^{\lambda(x+ct)} \), or, equivalently, one can do a change of variable \( x \rightarrow -x \), that does not change the equations in (1.3) and apply the results to these new equations.

We argue by induction. In this proof, the induction hypothesis is denoted \((P_j)\), for \( j \in [0, p] \) and is the following:

\[(H_j) \quad \implies \quad \forall k \neq k_1, \ldots, k_j, \ \forall \varepsilon > 0 \ \text{small enough, } \exists A^\varepsilon_k, j > 0 \ \text{such that} \quad I_k(t, x) \leq A^\varepsilon_k, j e^{-\frac{(c_k(S_j)+\varepsilon)^2}{2d_k}(x-(c_k(S_j)+\varepsilon)t)}, \quad \text{for all } t > 0, \ x \in \mathbb{R}. \quad (P_j)\]

When \( j = 0 \), by convention \((H_0)\) is the void hypothesis, it is always true. Therefore, \((P_0)\) would hold true if we can prove the upper bounds on the \( I_k \) functions, for all \( k \in [1, N] \), unconditionally.

To do so, we start with observing that \( S(t, x) \leq S_0 \). This implies that, for every \( k \in [1, N] \), \( I_k \) satisfies

\[
\partial_t I_k \leq d_k \Delta I_k + (\alpha_k S_0 - \mu_k) I_k, \quad t > 0, \ x \in \mathbb{R}. \quad (2.9)
\]

For any \( \varepsilon > 0 \), the function

\[
w(t, x) = A e^{-\frac{(c_k(S_0)+\varepsilon)^2}{2d_k}(x-(c_k(S_0)+\varepsilon)t)}
\]

is supersolution of (2.9). Indeed, \( \partial_t w - d_k \Delta w = \frac{(c_k(S_0)+\varepsilon)^2}{4d_k} w \geq (\alpha_k S_0 - \mu_k) w \). Hence, provided \( A \) is large enough so that \( w(0, \cdot) \geq I_k^0 \), the parabolic comparison principle yields the result.
Now, assume the property \((P_j)\) is verified for some \(j \in [0, p - 1]\), and let us show that \((P_{j+1})\) is true.

To do so, we assume that \((H_{j+1})\) holds true. Therefore, \((H_j)\) is also verified, and then \((P_j)\) tells us that for all \(k \neq k_1, \ldots, k_j\), for \(\varepsilon > 0\) small enough, there is \(A_{k,j}^\varepsilon > 0\) such that \(I_k(t, x) \leq A_{k,j}^\varepsilon e^{-\frac{(c_k(S_j)+\varepsilon)}{2d_k}(x-(c_k(S_j)+\varepsilon)t)}, \) for all \(t > 0, \ x \in \mathbb{R}.\)

In addition, because \((H_{j+1})\) is assumed to hold, we can apply Lemma 2.4, to get that, for \(\theta > 1, \ \eta > 0, \) there are \(L, T > 0\) such that \(\partial_t I_k \leq d_k \Delta I_k + (\alpha_k S_{j+1} - \mu_k) I_k, \) \(t > T, \ L < |x| < (c_{j+1} - \eta)t, \ k \in [1, N].\)

Define \(r := \frac{(c_k(S_{j+1})+\varepsilon)^2}{4d_k}\). Then, up to taking \(\theta\) close enough to 1, we can ensure that \(\alpha_k S_{j+1} \theta - \mu_k \leq r, \) and then
\[
\partial_t I_k \leq d_k \Delta I_k + r I_k, \quad t > T, \quad L < |x| < (c_{j+1} - \eta)t, \quad k \in [1, N].
\]

Now, define \(c_1 = c_k(S_j) + \varepsilon, \ c_2 = c_{j+1} - \eta, \ c_3 = c_k(S_{j+1}) + \varepsilon.\)

Then, up to taking \(\varepsilon, \ \eta > 0\) small enough, we can ensure that \(c_1 + c_3 < c_2,\) thanks to the hypothesis (1.6). We always have \(c_1 > c_3,\) because \(S_{j+1} < S_j.\) Then, we can apply Lemma 2.5 and this yields the result. \(\square\)

### 2.3 Conclusion. Proof of Theorem 1.3

We now use Proposition 2.1 to prove that the hypothesis \((H_p)\) is true, that is, the traits \(k_1, \ldots, k_p\) computed by the propagation sequences indeed propagate, with their prescribed speeds to their prescribed asymptotic values. To prove this, we argue by induction again, this is the object of the following:

**Proposition 2.6** Let \((S, I_1, \ldots, I_N, R_1, \ldots, R_N)\) be the solution of (1.3) arising from the initial datum \((S_0, I_1^0, \ldots, I_N^0, 0, \ldots, 0).\)

Assume that \((H_j)\) holds true for some \(j \in [0, p - 1]\). Then the trait \(k_{j+1}\) propagates with speed \(c_{j+1}\) and has asymptotic value \(\rho_{j+1}\), that is, \((H_{j+1})\) also holds true.

We start with the following lemma, that uses Proposition 2.1 to improve Lemma 2.4.

**Lemma 2.7** Let \((S, I_1, \ldots, I_N, R_1, \ldots, R_N)\) be the solution of (1.3) arising from the initial datum \((S_0, I_1^0, \ldots, I_N^0, 0, \ldots, 0).\)
• Assume that \((H_j)\) holds true for some \(j \in [0, p-1]\). Let \(\tilde{c} = \max_{i \neq k_1, \ldots, k_{j+1}} c_i(S_j)\). For any \(\eta > 0\), \(\omega \in (0, 1)\) and for every \(c > \tilde{c}\), there is \(T > 0\) such that, for \(t > T\) and \(|x| > ct\),

\[
\partial_t R_{k_{j+1}} \geq d_{k_{j+1}} \Delta R_{k_{j+1}} + f_{k_{j+1}}(R_{k_{j+1}}, \omega S_j) - \eta R_{k_{j+1}}.
\] (2.10)

• Assume that \((H_j)\) holds true for some \(j \in [0, p]\). For any \(\theta > 1\), for any \(k \neq k_1, \ldots, k_j\), for any \(c \in (0, c_j]\), there are \(C, q, L, T > 0\) such that, for \(t > T\) and \(L < |x| < ct\),

\[
\partial_t R_k \leq d_k \Delta R_k + \mu_k I_k^0 + C e^{-q|x|} + f_k(R_k, \theta S_j).
\] (2.11)

**Proof** First point. \(R_{k_{j+1}}\) is supersolution of a reaction-diffusion equation.

Let \(j \in [0, p-1]\) be fixed and assume that \((H_j)\) holds true. Owing to Lemma 2.4, we know that, for any \(\omega \in (0, 1)\), there is \(L > 0\) such that \(R_{k_{j+1}}\) satisfies, for \(t > 0\), \(|x| > L\),

\[
\partial_t R_{k_{j+1}} \geq d_{k_{j+1}} \Delta R_{k_{j+1}} + f_{k_{j+1}}(R_{k_{j+1}}, \omega S_j) - \mu_{k_{j+1}} S_j \left( \sum_{i \neq k_1, \ldots, k_{j+1}} \frac{\alpha_i}{\mu_i} R_i \right) R_{k_{j+1}}.
\]

For \(i \neq k_1, \ldots, k_j\), for \(\varepsilon > 0\) small enough, the bounds provided by Proposition 2.1 tell us that \(R_i(t, x) \leq B_{i, j}^\varepsilon e^{-\frac{(c_i(S_j)+\varepsilon)c_j(S_j)+\varepsilon}{d_i} |x|-(c_i(S_j)+\varepsilon)t}\), for some \(B_{i, j}^\varepsilon > 0\). Hence, for \(t > 0\), \(|x| > L\),

\[
\partial_t R_{k_{j+1}} \geq d_{k_{j+1}} \Delta R_{k_{j+1}} + f_{k_{j+1}}(R_{k_{j+1}}, \omega S_j) - \mu_{k_{j+1}} S_j \left( \sum_{i \neq k_1, \ldots, k_{j+1}} \frac{\alpha_i}{\mu_i} B_{i, j}^\varepsilon e^{-\frac{(c_i(S_j)+\varepsilon)c_j(S_j)+\varepsilon}{d_i} |x|-(c_i(S_j)+\varepsilon)t} \right) R_{k_{j+1}}.
\]

Let \(c > \max_{i \neq k_1, \ldots, k_{j+1}} c_i(S_j) = \tilde{c}\). Up to taking \(\varepsilon\) smaller if needed, we ensure that \(\tilde{c} + \varepsilon < c\). Hence, for \(|x| > ct\), for all \(i \neq k_1, \ldots, k_{j+1}\), we have

\[
\frac{(c_i(S_j)+\varepsilon)c_j(S_j)+\varepsilon}{d_i} |x|-(c_i(S_j)+\varepsilon)t \leq \frac{(c_i(S_j)+\varepsilon)(c-\tilde{c}-\varepsilon)t}{d_i}.
\]

Therefore, for any \(\eta > 0\), there is \(T > 0\) large enough so that

\[
\partial_t R_{k_{j+1}} \geq d_{k_{j+1}} \Delta R_{k_{j+1}} + f_{k_{j+1}}(R_{k_{j+1}}, \omega S_j) - \eta R_{k_{j+1}}, \quad \text{for } t > T, \ ct < |x|.
\]

(observe that, up to increasing \(T\) so that \(T > cL\), the condition \(|x| > L\) disappears).

Second point. \(R_k\) is subsolution of a reaction-diffusion equation.
Let \( j \in [0, p] \) be fixed and assume that \((H_j)\) holds true. Let \( k \notin K_j = \{k_1, \ldots, k_j\} \) be chosen. Owing to Lemma 2.2, we know that \( R_k \) satisfies

\[
\partial_t R_k \leq d_k \Delta R_k + \mu_k I_k^0 - \mu_k R_k + \alpha_k S_0 \int_0^t e^{-\frac{\alpha_k}{\mu_k} R_k} \partial_t R_k \left( \prod_{i \in K_j} \frac{1}{e^{-\frac{\alpha_i}{\mu_i} R_i}} \right) d\tau.
\]

Let \( c \in [0, c_j) \) be chosen. We take \( \bar{c} \) such that \( \bar{c} \in (\max\{c, c_{j+1}\}, c_j) \) (with the convention that, if \( j = p \), then \( c_{p+1} := 0 \)).

The hypothesis \((H_j)\) yields that, for any \( \eta > 0 \), there are \( L, T > 0 \) such that, for all \( i \in K_j = \{k_1, \ldots, k_j\} \), we have \( R_i(t, x) \geq \rho_i - \eta \) for \( t > T \) and \( L < |x| < \bar{c} t \).

Denote \( \theta = \prod_{i \in K_j} e^{\bar{c} x t} \). Assume that \( t > T \) and \( L < |x| < c t \). Then, \( |x| < \bar{c} t \) and we have

\[
\int_0^t e^{-\frac{\alpha_k}{\mu_k} R_k} \partial_t R_k \left( \prod_{i \in K_j} \frac{1}{e^{-\frac{\alpha_i}{\mu_i} R_i}} \right) d\tau \\
\leq \int_0^{\frac{|x|}{c}} \partial_t R_k d\tau + \int_{\frac{|x|}{c}}^t e^{-\frac{\alpha_k}{\mu_k} R_k} \partial_t R_k \left( \prod_{i \in K_j} \frac{1}{e^{-\frac{\alpha_i}{\mu_i} R_i}} \right) d\tau \\
\leq \int_0^{\frac{|x|}{c}} \partial_t R_k d\tau + \theta \left( \prod_{i \in K_j} \frac{1}{e^{-\frac{\alpha_i}{\mu_i} \rho_i}} \right) \int_0^{\frac{|x|}{c}} e^{-\frac{\alpha_k}{\mu_k} R_k} \partial_t R_k d\tau \\
\leq R_k \left( \frac{|x|}{c}, x \right) + \theta \left( \prod_{i \in K_j} \frac{1}{e^{-\frac{\alpha_i}{\mu_i} \rho_i}} \right) \int_0^t e^{-\frac{\alpha_k}{\mu_k} R_k} \partial_t R_k d\tau.
\]

Therefore, for \( t > T \) and \( L < |x| < c t \), we have

\[
\partial_t R_k \leq d_k \Delta R_k + \mu_k I_k^0 - \mu_k R_k + \mu_k \theta S_j (1 - e^{-\frac{\alpha_k}{\mu_k} R_k}) + \alpha_k S_0 R_k \left( \frac{|x|}{c}, x \right).
\]

Now, using again Proposition 2.1, for \( \epsilon > 0 \) small enough, we have \( R_k(t, x) \leq B_{k,j}^\epsilon e^{-(c_k(S_j)+\epsilon t)(|x|-(c_k(S_j)+\epsilon) t)} \). Up to taking \( \epsilon \) smaller if needed so that \( \bar{c} > c_k(S_j) + \epsilon \), this implies that

\[
R_k \left( \frac{|x|}{c}, x \right) \leq B_{k,j}^\epsilon e^{-\frac{(c_k(S_j)+\epsilon)}{2d_k \epsilon} (\bar{c}-(c_k(S_j)+\epsilon))|x|}.
\]

In the end, taking \( q := \frac{(c_k(S_j)+\epsilon)}{2d_k \epsilon} (\bar{c}-(c_k(S_j)+\epsilon)) \) and \( C := \alpha_k S_0 B_{k,j}^\epsilon \), we indeed find (2.11).

We are now in position to prove Proposition 2.6.
Proof of Proposition 2.6  We assume that \((H_j)\) holds true. Let us prove that \((H_{j+1})\) is verified, that is, let us prove that, for all \(c > c_{j+1}\),
\[
\lim_{t \to +\infty} \sup_{t < |x|} |R_{k_{j+1}}(t, x)| = 0,
\]
(2.12)
and that, for all \(c \in (0, c_{j+1})\),
\[
\lim_{\delta, t \to +\infty} \sup_{\delta < |x| < ct} |R_{k_{j+1}}(t, x) - \rho_{j+1}| = 0.
\]
(2.13)

Step 1. Proof of (2.12).
Owing to Proposition 2.1, for \(\varepsilon > 0\) small enough, there is \(B > 0\) such that
\[
R_{k_{j+1}}(t, x) \leq B e^{-\frac{(c_{j+1} + \varepsilon)(S_j) + \varepsilon}{2d_{k_{j+1}}}} |x| - (c_{j+1} + \varepsilon) t, \quad \text{for all } t > 0, \ x \in \mathbb{R}.
\]
Then, for any \(c > c_{j+1} + \varepsilon = c_{k_{j+1}}(S_j) + \varepsilon\), we have
\[
\sup_{|x| > ct} R_{k_{j+1}}(t, x) \leq B e^{-\frac{(c_{j+1} + \varepsilon)(c - c_{j+1} - \varepsilon)}{2d_{k_{j+1}}}} |x| - (c_{j+1} + \varepsilon) t \to 0.
\]
Then, because we can take \(\varepsilon\) as close to zero as we want, (2.12) holds true.

Step 2. Upper bound.
The remaining steps are dedicated to prove (2.13). This particular step is dedicated to prove that, for any \(\eta > 0\), there are \(M, \varepsilon > 0\) such that
\[
R_{k_{j+1}}(t, x) \leq \rho_{j+1} + \eta + Me^{-\varepsilon|x|}.
\]
(2.14)
This will imply in particular that, for any \(c > 0\),
\[
\lim_{t \to +\infty} \sup_{\delta, t \to +\infty} \sup_{\delta < |x| < ct} \left( R_{k_{j+1}}(t, x) - \rho_{j+1} \right) \leq 0.
\]
The remaining step below will prove that this is also true with \(\rho_{j+1}\) and \(R_{k_{j+1}}\) reversed (but then we will have to restrict to \(c < c_{j+1}\)).

First, let us take \(c \in (c_{j+1}, c_j)\). Observe that, owing to (2.11) from Lemma 2.7, we have that, for any \(\theta > 1\), there are \(C, q, T, L > 0\) such that, for \(t > T\) and \(L < |x| < ct\),
\[
\partial_t R_{k_{j+1}} \leq d_{k_{j+1}} \Delta R_{k_{j+1}} + \mu_{k_{j+1}} I_{k_{j+1}}^0 + Ce^{-q|x|} + f_{k_{j+1}}(R_{k_{j+1}}, \theta S_j).
\]
We denote \(\rho(\theta)\) the unique positive solution of the equation \(f_{k_{j+1}}(\rho(\theta), \theta S_j) = 0\) (this solution exists because \(z \mapsto f_{k_{j+1}}(z, \theta S_j)\) is concave and vanishes at \(z = 0\).
where it has a strictly positive derivative, and goes to $-\infty$ as $z \to +\infty$). We have $\rho(\theta) \to \rho_{j+1}$ as $\theta \to 1$.

Let us define the function

$$u(t, x) = \rho(\theta) + Me^{-ex}$$

Because the function $f_{k_{j+1}}(\cdot, \theta S_j)$ is concave, we have $f_{k_{j+1}}(u, \theta S_j) \leq f'_{k_{j+1}}(\rho(\theta), \theta S_j)Me^{-ex}$. Therefore, for $t > 0$, $x \in \mathbb{R}$,

$$\partial_t u - dk_{j+1} \Delta u - f_{k_{j+1}}(u, \theta S_j) \geq Me^{-ex}(-dk_{j+1}e^2 - f'_{k_{j+1}}(\rho(\theta), \theta S_j)).$$

Up to taking $M > 0$ large enough and $\varepsilon > 0$ small enough, we can guarantee that $M(-dk_{j+1}e^2 - f'_{k_{j+1}}(\rho(\theta), \theta S_j)) \geq (\mu_{k_{j+1}}I^0_{k_{j+1}} + Ce^{-q|x|})e^{ex}$, indeed, $f'_{k_{j+1}}(\rho(\theta), \theta S_j) < 0$ and $I^0_{k_{j+1}}$ is compactly supported.

Therefore, $u$ and $R_{k_{j+1}}$ are respectively supersolution and subsolution of the same parabolic equation on the domain $t > T$, $L < |x| < ct$ ($u$ is actually supersolution everywhere in space and time). Up to choosing $M$ large enough, we can ensure that $u(T, \cdot) \geq R_{k_{j+1}}(T, \cdot)$. To apply the parabolic comparison principle, we need to have, for $t > T$, $R_{k_{j+1}}(t, \pm L) \leq u(t, \pm L)$, which can be ensured up to choosing $M$ larger if needed, and we also need $R_{k_{j+1}}(t, \pm ct) \leq u(t, \pm ct)$, but this comes again from the exponential estimates of Proposition 2.1, up to taking $M$ large enough (and because we took $c > c_{j+1}$).

Doing the same reasoning with the supersolution $\rho(\theta) + Me^{ex}$, we finally find, thanks to the parabolic comparison principle, that

$$R_{k_{j+1}}(t, x) \leq \rho(\theta) + Me^{-e|x|}, \quad t > T, \ L < |x| < ct.$$  

Up to increasing $M > 0$ if needed and taking $\theta$ close enough to 1 we get that (2.14) is verified at least for $t > 0$, $|x| < ct$, but because $R_{k_{j+1}}$ is non-decreasing with respect to $t$, this is actually true for all $t > 0$, $x \in \mathbb{R}$.

**Step 3. Lower bound.**

It now remains to prove that, for $c \in (0, c_{j+1})$, we have

$$\limsup_{\delta \to +\infty} \sup_{\delta < |x| < ct} (\rho_{j+1} - R_{k_{j+1}}(t, x)) \leq 0,$$

or, equivalently, that

$$\liminf_{\delta \to +\infty} \inf_{\delta < |x| < ct} R_{k_{j+1}}(t, x) \geq \rho_{j+1}. \quad (2.15)$$

To do so, we use (2.10) from Lemma 2.7. Let us take $\zeta, \bar{c} \in (\max(\tilde{c}, c), c_{j+1})$ (where $\tilde{c}$ is from Lemma 2.7), such that $\zeta < \bar{c}$. 

\[\text{Springer}\]
Let us take \( \eta > 0 \) small enough and \( \omega \in (0, 1) \) close enough to 1 such that
\[
2\sqrt{d_{k_{j+1}}(\omega\alpha_{k_{j+1}}S_j - \mu_{k_{j+1}} - \eta)} > \overline{c},
\]
which is possible because \( 2\sqrt{d_{k_{j+1}}(\alpha_{k_{j+1}}S_j - \mu_{k_{j+1}})} = c_{j+1} > \overline{c} \). The equation (2.10) from Lemma 2.7 then implies that there is \( T > 0 \) such that
\[
\partial_t R_{k_{j+1}} \geq d_{k_{j+1}} \Delta R_{k_{j+1}} + f_{k_{j+1}}(R_{k_{j+1}}, \omega S_j) - \eta R_{k_{j+1}}, \quad \text{for } t > T, \ |x| > cT.
\]
Let us now define \( u(t, x) \) as the solution of the equation
\[
\partial_t u = d_{k_{j+1}} \Delta u + f_{k_{j+1}}(u, \omega S_j) - \eta u, \quad \text{for } t > T, \ |x| > cT,
\]
with (moving) Dirichlet boundary condition \( u(t, \pm cT) = 0 \) for \( t > T \), and with initial condition at time \( t = T \) given by \( u(T, \cdot) = R_{k_{j+1}}(T, \cdot) \).

Then, applying the parabolic comparison principle on the domain \( E := \{(t, x) \mid t > T, \ |x| > cT\} \), we find that \( R_{k_{j+1}}(t, x) \geq u(t, x) \) for \( (t, x) \in E \).

Now, because \( R_{k_{j+1}}(t, x) \) is non-decreasing with respect to \( t \), and by continuity, for any \( \delta, t > 0 \), we can find \( x_t^\delta \) such that \( \delta \leq |x_t^\delta| \leq ct \) that satisfies
\[
\inf_{\delta < |x| < ct} R_{k_{j+1}}(t, x) = R_{k_{j+1}}(t, x_t^\delta) \geq R_{k_{j+1}}(\frac{|x_t^\delta|}{c}, x_t^\delta).
\]
Observe that we used the fact that \( \overline{c} > c > \underline{c} \) here.

Now, for \( \delta, t \) large enough, we have \( \left( \frac{|x_t^\delta|}{c}, x_t^\delta \right) \in E \). Hence, for \( \delta, t \) large, we have
\[
\inf_{\delta < |x| < ct} R_{k_{j+1}}(t, x) \geq u \left( \frac{|x_t^\delta|}{c}, x_t^\delta \right).
\]

Now, owing to classical results from reaction-diffusion equations theory, we have
\[
u(t, \pm c\overline{c}t) \to \rho_{j+1}(\omega, \eta),
\]
where \( \rho_{j+1}(\omega, \eta) \) is the unique positive solution of
\[
f_{k_{j+1}}(\rho_{j+1}(\omega, \eta), \omega S_j) - \eta \rho_{j+1}(\omega, \eta) = 0.
\]
This solution exists and is unique provided \( \eta, \omega \) are small enough and close enough to 1 respectively. Clearly, we have \( \rho_{j+1}(\omega, \eta) \to \rho_{j+1} \) as \( \eta \) goes to zero and \( \omega \) goes to 1, which yields (2.15), and concludes the proof. \( \square \)

To conclude the proof of Theorem 1.3, we need the following:

**Proposition 2.8** Let \((S, I_1, \ldots, I_N, R_1, \ldots, R_N)\) be the solution of (1.3) arising from the initial datum \((S_0, I_1^0, \ldots, I_N^0, 0, \ldots, 0)\).

Assume that \((H_p)\) holds true. Then, for every \( k \neq k_1, \ldots, k_p \), the trait \( k \) vanishes.
Proof Let $k \neq k_1, \ldots, k_p$ be chosen. Using (2.11) from Lemma 2.7, we know that, for $\theta > 1$, for $c < c_p$, there are $C, q, T, L > 0$ such that
\[
\partial_t R_k \leq d_k \Delta R_k + \mu_k I^0_k + C e^{-q|x|} + f_k(R_k, \theta S_p), \quad \text{for } t > T, \ L < |x| < ct.
\]

By definition of the propagation sequence, up to taking $\theta$ close enough to 1 and thanks to hypothesis (1.7), we can guarantee that $-\eta := \alpha_k \theta S_p - \mu_k < 0$. Hence, by concavity of $z \mapsto f_k(z, \theta S_p)$, and because $f_k'(0, \theta S_p) = -\eta$, we have
\[
\partial_t R_k \leq d_k \Delta R_k + \mu_k I^0_k + C e^{-q|x|} - \eta R_k, \quad \text{for } t > T, \ L < |x| < ct.
\]

Now, owing to the estimates from Proposition 2.1, we know that, for every $\varepsilon > 0$, we have (remember that $c_k(S_p) = 0$)
\[
R_k(t, x) \leq B^\varepsilon_{k, p} e^{-\frac{\varepsilon}{\sigma_k}(|x| - \varepsilon t)}, \quad \text{for all } t > 0, \ x \in \mathbb{R}.
\]

Let now $M, \lambda > 0$ be fixed, and define $w(t, x) := M e^{-\lambda x}$. We have
\[
\partial_t w - d_k \Delta w + \eta w = (-d_k \lambda^2 + \eta) M e^{-\lambda x} \geq \mu_k I^0_k + C e^{-q|x|},
\]
provided $\lambda$ is small enough and $M$ is large enough. Moreover, up to decreasing $\lambda$ and increasing $M$ if needed, we have
\[
M e^{-\lambda ct} \geq B^\varepsilon_{k, p} e^{-\frac{\varepsilon}{\sigma_k}(c-\varepsilon)t}.
\]
Therefore, $R_k(t, \pm ct) \leq w(t, \pm ct)$. Up to increasing $M$ if needed, we can ensure that $R_k(t, \pm L) \leq w(t, \pm L)$. Hence, we can apply the parabolic comparison principle to get that
\[
R_k(t, x) \leq M e^{-\lambda x}, \quad \text{for } t > T, \ L < |x| < ct.
\]

Because $R_k(t, x)$ is non-decreasing with respect to $t$, then this is actually true for all $t > 0, \ x \in \mathbb{R}$ (up to increasing $M$ again if needed). Therefore, the $k$-th trait does not propagate, hence the result. \(\square\)

3 Qualitative properties

Now that we have proved Theorem 1.3, we use it to study some qualitative properties of our model (1.3). More precisely, Theorem 1.3 tells us that the dynamics of the system is characterized by the propagation sequences from Definition 1.2. Hence, understanding how the propagation sequences depend on the parameters of the model will yield further qualitative properties.

As we already mentioned, the propagation sequences depend on the parameters in a complex way. Our goal here is not to give a complete and detailed analysis, but rather
to highlight some salient properties of the model by focusing on the three properties mentioned at the end of Sect. 1.3. These three properties are stated as the three following results, that are corollaries of Theorem 1.3.

First, we show that the basic reproduction numbers, introduced in Sect. 1.2 as the ratio $\frac{\alpha S_0}{\mu}$, fail to describe properly the dynamics of the system.

**Corollary 3.1** Consider system (1.3) with $N = 2$. Take $d_1 = d_2 = 1$. Then, one can choose $\alpha_1, \alpha_2, \mu_1, \mu_2$ and $S_0$ such that

$$1 < \frac{\alpha_1 S_0}{\mu_1} < \frac{\alpha_2 S_0}{\mu_2},$$

but where the trait 1 propagates while the trait 2 vanishes.

This corollary claims that there exist instances where the trait with the lower basic reproduction number propagates, while the trait with the larger basic reproduction number vanishes. This is in contrast with the intuition one could have built from the model with one single trait. We mention that this result can be adapted to the case where $N \geq 2$.

The second property we prove claims that each trait that propagates is less contagious, and has a lower recovery rate, than the traits that have propagated before. This is not a direct consequence of Theorem 1.3, which only implies that each trait that propagates has a smaller speed than the traits that have propagated before.

**Corollary 3.2** Consider system (1.3) with $d_1 = \cdots = d_N$. Assume that the coefficients satisfy the hypotheses of Theorem 1.3 (in particular (1.6) and (1.7)).

Let $(k_i)_{i \in [1, p]}$ be the sequence of the indices of the traits that propagate, given in Definition 1.2.

Then, for all $i \in [1, p - 1]$, one has

$$\alpha_{k_{i+1}} < \alpha_{k_i} \quad \text{and} \quad \mu_{k_{i+1}} < \mu_{k_i}.$$ 

To conclude, we present a result concerning the final density of susceptible individuals. This result can also be interpreted as a result on the number of casualties. We denote $S_\infty := \lim_{|x| \to +\infty} \lim_{t \to +\infty} S(t, x)$.

As we already mention in Sect. 1.3, under the assumptions of Theorem 1.3, we have $S_\infty = S_p$, where $S_p$ is given by the propagation sequences.

As we recalled in Sect. 1.2, when $N = 1$, and when $\frac{\alpha S_0}{\mu} \leq 1$, the single trait does not propagate, and $S_\infty = S_0$, whereas when $\frac{\alpha S_0}{\mu} > 1$, the trait propagates, and $S_\infty = S_0 e^{-\frac{a}{\mu} \rho}$, were $\rho$ solves $S_0(1 - e^{-\frac{a}{\mu} \rho}) = \rho$. 

\( \square \) Springer
A straightforward computation allows to reformulate this by saying that $S_\infty$ is the smallest positive solution of

$$S_0 - \frac{\mu}{\alpha} \ln(S_0) = S_\infty - \frac{\mu}{\alpha} \ln(S_\infty).$$

Note that the function $f(z) = z - \frac{\mu}{\alpha} \ln(z)$ is strictly convex, goes to $+\infty$ as $z$ goes to 0 or to $+\infty$, and has a unique minimum, reached at $z = \frac{\mu}{\alpha}$.

Observe that we necessarily have $S_0 e^{-\frac{\mu}{\alpha} \rho} < \frac{\mu}{\alpha}$ when $S_0 > \frac{\mu}{\alpha}$ (this implies that, when a disease propagates, the final density of susceptible individuals is too small for this disease to propagate again). We will use this fact several times in the following proofs.

The following figure depicts $S_\infty$ as a function of $S_0$ in this case $N = 1$.

Our next corollary shows how the final density of susceptible individuals $S_\infty$ depends on the initial density of susceptible individuals $S_0$ when $N = 2$. We recall that the quantities $\rho_1(S_0), \rho_2(S_0), \rho_1(S_1)$ that appear in the statement of the corollary are defined at the beginning of Sect. 1.3, after Definition 1.1.

**Corollary 3.3** Consider the system (1.3) with $N = 2$. We denote $S_\infty := \lim_{|x|\to+\infty} \lim_{t\to+\infty} S(t, x)$.

Without loss of generality, assume that

$$\frac{\mu_1}{\alpha_1} < \frac{\mu_2}{\alpha_2},$$

Then, there are $0 < r \leq \bar{r}$ such that

- If

$$\frac{d_2}{d_1} < r,$$

the situation is the same as if there were only the trait \(\lambda\) in the model:
– When $S_0 < \frac{\mu_1}{\alpha_1}$, we have $S_\infty = S_0$.
– When $S_0 > \frac{\mu_1}{\alpha_1}$, only the trait 1 propagates, and $S_\infty$ is the smallest solution of

\[ S_\infty - \frac{\mu_1}{\alpha_1} \ln(S_\infty) = S_0 - \frac{\mu_1}{\alpha_1} \ln(S_0). \]

• If

\[ \frac{d_2}{d_1} > \bar{r}, \]

there are $S, \bar{S}$ that verify $\frac{\mu_1}{\alpha_1} < \frac{\mu_2}{\alpha_2} < S < \bar{S}$ and \( \varepsilon \geq 0 \) such that

– When $S_0 < \frac{\mu_1}{\alpha_1}$, no trait propagates, and $S_\infty = S_0$.
– When $S_0 \in \left( \frac{\mu_1}{\alpha_1}, S \right)$, only the trait 1 propagates, and then $S_\infty = S_0 e^{-\frac{\mu_1}{\alpha_1} \rho_1(S_0)}$.
– When $S_0 \in \left( S, S + \varepsilon \right)$, we can not apply Theorem 1.3 (hypothesis (1.6) is not verified).
– When $S_0 \in \left( S + \varepsilon, \bar{S} \right)$, then the traits 2 and 1 propagate, and $S_\infty = S_1 e^{-\frac{\mu_2}{\alpha_2} \rho_2(S_1)}$, where $S_1 = S_0 e^{-\frac{\mu_1}{\alpha_1} \rho_1(S_0)}$.
– When $S_0 > \bar{S}$, then only the trait 2 propagates, and $S_\infty = S_0 e^{-\frac{\mu_2}{\alpha_2} \rho_2(S_0)}$.

In addition, we have that $S \rightarrow \frac{\mu_2}{\alpha_2}$ and $\varepsilon \rightarrow 0$ as $\frac{d_2}{d_1} \rightarrow +\infty$, and $\bar{S}$ does not depend on $d_1, d_2$.

Let us give here some remarks concerning this corollary. The most interesting situation is when $d_1 \ll d_2$. In this case, plotting $S_\infty$ as a function of $S_0$ would give

![Graph](image)

The dashed zone, for $S_0 \in \left( S, S + \varepsilon \right)$, corresponds to the zone where we can not apply our theorem ((1.6) is not verified there). However, this zone can be made as small as we want up to increasing $d_2$ or decreasing $d_1$.

We now turn to the proofs of these results.

**Proof of Corollary 3.1** We take $d_1 = d_2 = 1$ and $\alpha_1, \mu_1, S_0$ fixed in such a way that

\[ \frac{\alpha_1 S_0}{\mu_1} > 1. \]
Now, let \( S_1 = S_0 e^{-\frac{\alpha_1}{\mu_1} \rho_1} \), where \( \rho_1 \) is the unique positive solution of \( f_1(\rho_1, S_0) = 0 \). We have
\[
\frac{\alpha_1 S_1}{\mu_1} < 1.
\]
Take \( \lambda \in \left( \frac{\alpha_1}{\mu_1}, \frac{1}{S_1} \right) \) and define \( \alpha_2 = \varepsilon \lambda \) and \( \mu_2 = \varepsilon \), for \( \varepsilon > 0 \). Then
\[
\frac{\alpha_1 S_0}{\mu_1} < \lambda S_0 = \frac{\alpha_2 S_0}{\mu_2}.
\]
Moreover, up to taking \( \varepsilon > 0 \) small enough, we ensure that
\[
\alpha_2 S_0 - \mu_2 = \varepsilon (\lambda S_0 - 1) < \alpha_1 S_0 - \mu_1.
\]
We also have
\[
\alpha_2 S_1 - \mu_2 = \varepsilon (\lambda S_1 - 1) < 0.
\]
We can compute the propagation sequence associated with these parameters: we find \( p = 1 \) and \( k_1 = 1 \). Moreover, the hypotheses of Theorem 1.3 are verified, then only the trait 1 propagates and the trait 2 vanishes.

We now turn to the proof of the second qualitative property.

**Proof of Corollary 3.2** By definition of the propagation sequences, we know that, for all \( i \in \llbracket 1, p - 1 \rrbracket \),
\[
c_{k_{i+1}}(S_{i-1}) < c_{k_i}(S_{i-1}),
\]
that is (recall that we assume that the diffusion coefficients are equal),
\[
\alpha_{k_{i+1}} S_{i-1} - \mu_{k_{i+1}} < \alpha_{k_i} S_{i-1} - \mu_{k_i},
\]
hence
\[
(\alpha_{k_{i+1}} - \alpha_{k_i}) S_{i-1} < \mu_{k_{i+1}} - \mu_{k_i}.
\]
In addition, because the trait \( k_{i+1} \) propagates, we necessarily have
\[
\alpha_{k_{i+1}} S_i - \mu_{k_{i+1}} > 0.
\]
Moreover, by definition of \( S_i \), we have
\[
\alpha_{k_i} S_i - \mu_{k_i} < 0.
\]
Combining (3.16), (3.17) and (3.18) yields

\[(\alpha_{k_{i+1}} - \alpha_{k_i})S_{i-1} < (\alpha_{k_{i+1}} - \alpha_{k_i})S_i.\]

Now, because \(S_{i-1} > S_i\), we have

\[\alpha_{k_{i+1}} < \alpha_{k_i}.\]

Combining this again with (3.17) and (3.18) yields

\[\mu_{k_{i+1}} < \mu_{k_i},\]

and this concludes the proof. \(\square\)

We now prove our third qualitative property.

**Proof of Corollary 3.3** We define

\[r := \frac{\alpha_1}{\alpha_2}.\]

Then, when \(\frac{d_2}{d_1} \leq r\), we have \(d_2 \alpha_2 \leq d_1 \alpha_1\) and we can verify that, for all \(S_0 > 0\),

\[c_1(S_0) \geq c_2(S_0),\]

and this inequality is strict as soon as \(c_1(S_0) > 0\) (indeed, we have \(c_1(S_0) = c_2(S_0) = 0\) if \(S_0 \leq \frac{\mu_1}{\alpha_1}\), then \(c_1(S_0) > 0 = c_2(S_0)\) if \(S_0 \in \left(\frac{\mu_1}{\alpha_1}, \frac{\mu_2}{\alpha_2}\right]\), and \(c_1(S_0) > c_2(S_0) > 0\) for \(S_0 > \frac{\mu_2}{\alpha_2}\).

If \(S_0 < \frac{\mu_1}{\alpha_1}\), then \(\alpha_2 S_0 - \mu_2 < 0\) and \(\alpha_1 S_0 - \mu_1 < 0\). We can compute the propagation sequences: we find \(p = 0\), the sequences are empty. We can apply Theorem 1.3 to get that no trait propagates, and then \(S_\infty = S_0\).

If \(S_0 > \frac{\mu_1}{\alpha_1}\), then \(c_1(S_0) > 0\). Computing the propagation sequence, we find that \(k_1 = 1, S_1 = S_0 e^{-\frac{\alpha_1}{\mu_1} \rho_1(S_0)} < \frac{\mu_1}{\alpha_1}\). This implies that \(S_1 < \frac{\mu_2}{\alpha_2}\), then \(\alpha_2 S_1 - \mu_2 < 0\), hence \(p = 1\). We can apply Theorem 1.3 to find that only the trait 1 propagates, and \(S_\infty = S_1\).

Now, we let \(\bar{r} > 0\) be a real number to be taken sufficiently large later (unlike \(r\), it will not be explicit). We assume for now that \(\bar{r} > \frac{\alpha_1}{\alpha_2}\).

If \(S_0 < \frac{\mu_1}{\alpha_1}\), the situation is the same as above, no trait propagates and \(S_\infty = S_0\).

Now, let

\[S := \frac{d_2 \mu_2 - d_1 \mu_1}{d_2 \alpha_2 - d_1 \alpha_1}.\]

Because we assumed that \(\bar{r} > \frac{\alpha_1}{\alpha_2}\), an easy computation shows that \(S > \frac{\mu_2}{\alpha_2}\), and, for \(S_0 \in \left(\frac{\mu_1}{\alpha_1}, S\right]\), we have \(c_1(S_0) > c_2(S_0)\).
Hence, computing the propagation sequence, we find that \( k_1 = 1 \) and \( S_1 = S_0 e^{-\frac{\alpha_1}{\mu_1} \rho_1(S_0)} \). We have \( S_1 < \frac{\mu_1}{\alpha_1} < \frac{\mu_2}{\alpha_2} \), then \( d_2(\alpha_2 S_1 - \mu_2) < 0 \), and we find \( p = 1 \).

We can apply Theorem 1.3, we find that only the trait 1 propagates and \( S_\infty = S_1 = S_0 e^{-\frac{\alpha_1}{\mu_1} \rho_1(S_0)} \).

Now, let \( \overline{S} \) be the largest solution of

\[
\overline{S} - \frac{\mu_2}{\alpha_2} \ln(\overline{S}) = \frac{\mu_1}{\alpha_1} - \frac{\mu_2}{\alpha_2} \ln \left( \frac{\mu_1}{\alpha_1} \right).
\]

We recall that the function \( f(z) = z - \frac{\mu_2}{\alpha_2} \ln(z) \) is convex, goes to \(+\infty\) as \( z \) goes to 0 and \(+\infty\) and reaches its minimum at \( \frac{\mu_2}{\alpha_2} \). This implies that \( \overline{S} > \frac{\mu_2}{\alpha_2} \).

On the one hand, \( \overline{S} \) does not depend on \( d_1, d_2 \). On the other hand, it is readily seen that \( S \) is a decreasing function of \( \frac{\alpha_2}{\alpha_1} \) and that, when \( \frac{d_2}{d_1} \to +\infty \), we have \( S \to \frac{\mu_2}{\alpha_2} \). We assume from now on that \( \overline{F} \) is large enough so that, for \( \frac{d_2}{d_1} > \overline{F} \), we have \( S > \overline{S} \).

We find that, for \( S_0 > \overline{S} \), we have

\[
c_1(S_0) < c_2(S_0).
\]

Computing the propagation sequence, we find \( k_1 = 2 \), and \( S_1 = S_0 e^{-\frac{\alpha_2}{\mu_2} \rho_2(S_0)} \). If \( S_0 \in (\overline{S}, \overline{S}) \), owing to our choice of \( \overline{S} \), we have \( S_1 > \frac{\mu_1}{\alpha_1} \), and then

\[
c_1(S_1) > 0.
\]

Then, we find \( p = 2 \), and \( S_\infty = S_2 = S_1 e^{-\frac{\alpha_1}{\mu_1} \rho_1(S_1)} \).

Now, to apply Theorem 1.3, we need to verify that (1.6) holds true, i.e., we can apply the theorem only when \( S_0 \) is such that

\[
c_1(S_0) + c_1(S_1) < c_2(S_0).
\]

Unfortunately, this can not be always satisfied (indeed, \( c_2(S_0) - c_1(S_0) \to 0 \) when \( S_0 \to \overline{S} \)). Finding an explicit formula for the smallest \( S_0 \) that satisfies this condition is rather intricate (\( S_1 \) is a function of \( S_0 \)). However, let us observe that

\[
c_1(S_0) + c_1(S_1) < 2c_1(S_0) = 4\sqrt{d_1(\alpha_1 S_0 - \mu_1)}.
\]

Up to increasing \( \overline{F} \) so that \( \overline{F} > 4\frac{\alpha_1}{\alpha_2} \), it is easy to see that

\[
4\sqrt{d_1(\alpha_1 S_0 - \mu_1)} < 2\sqrt{d_2(\alpha_2 S_0 - \mu_2)} \iff S_0 > \overline{S} + \varepsilon,
\]

where \( \varepsilon = \frac{3d_2 d_1 (\mu_2 \alpha_1 - \mu_1 \alpha_2)}{(d_2 \alpha_2 - 4d_1 \alpha_1)(d_2 \alpha_2 - d_1 \alpha_1)} \) indeed vanishes when \( \frac{d_2}{d_1} \to +\infty \).

Now, when \( S_0 > \overline{S} \), we still have \( c_2(S_0) > c_1(S_0) \), but now \( \alpha_1 S_1 - \mu_1 < 0 \). Hence, the propagation sequence contains one element, \( p = 1 \), and we can apply Theorem 1.3 to find that only the trait 2 propagates, and \( S_\infty = S_1 = S_0 e^{-\frac{\alpha_2}{\mu_2} \rho_2(S_0)} \). \( \square \)
References

Berestycki H, Roquejoffre J-M, Rossi L (2021) Propagation of epidemics along lines with fast diffusion. Bull Math Biol 83(1):34
Bichara D, Iggidr A, Sallet G (2014) Global analysis of multi-strains SIS, SIR and MSIR epidemic models. J Appl Math Comput 44:273–292
Diekmann O (1978) Thresholds and travelling waves for the geographical spread of infection. J Math Biol 6(2):109–130
Diekmann O (1979) Run for your life. A note on the asymptotic speed of propagation of an epidemic. J Differ Equ 33(1):58–73
Ducasse R (2022) Threshold phenomenon and traveling waves for heterogeneous integral equations and epidemic models. Nonlinear Anal Theory Methods Appl Ser A Theory Methods 218:34
Ducasse R (2018) Qualitative properties of spatial epidemiological models. Preprint
Ducrot A, Giletti T (2014) Convergence to a pulsating travelling wave for an epidemic reaction-diffusion system with non-diffusive susceptible population. J Math Biol 69(3):533–552
Ducrot A (2021) Spreading speed for a KPP type reaction-diffusion system with heat losses and fast decaying initial data. J Differ Equ 270:217–247
Girardin L, Lam K-Y (2019) Invasion of open space by two competitors: spreading properties of monostable two-species competition-diffusion systems. Proc Lond Math Soc 119(5):1279–1335
Henry D (1981) Geometric theory of semilinear parabolic equations, vol 840. Lecture Notes in Mathematics. Springer, Berlin
Hosono Y, Ilyas B (1995) Traveling waves for a simple diffusive epidemic model. Math Models Methods Appl Sci 5(7):935–966
Källén A (1984) Thresholds and travelling waves in an epidemic model for rabies. Nonlinear Anal Theory Methods Appl. 8:851–856
Kendall D (1957) Discussion of “measles periodicity and community size” by ms bartlett. J R Stat Soc A 120:64–76
Kendall DG (1965) Mathematical models of the spread of infection. Math Comput Sci Biol Med, pp 213–225
Kermack WO, McKendrick AG (1991) Contributions to the mathematical theory of epidemics. I. Bull Math Biol 53(1–2):33–55
Kermack WO, McKendrick AG (1932) Contributions to the mathematical theory of epidemics II. The problem of endemicity. Proc R Soc Lond A 138(834):55–83
Kermack WO, McKendrick AG (1933) Contributions to the mathematical theory of epidemics III further studies of the problem of endemicity. Proc R Soc Lond A 141(843):94–122
Kolmogorov AN, Petrovskii IG, Piskunov NS (1937) Étude de l’équation de la diffusion avec croissance de la quantité de matière et son application à un problème biologique. Bull. Univ. Etat. Moscow Ser. Int Math Mech Sect A 1:1–26
Liu S, Liu Q, Lam K-Y (2021) Asymptotic spreading of interacting species with multiple fronts. II Exponentially decaying initial data. J Differ Equ 303:407–455
Murray JD (2003) Mathematical biology. II, volume 18 of Interdisciplinary Applied Mathematics. Springer, New York, third edition, 2003. Spatial models and biomedical applications
Osnas EE, Hurtado PJ, Dobson AP (2015) Evolution of pathogen virulence across space during an epidemic. Am Nat 185(3):332–342
Protter MH, Weinberger HF (1967) Maximum principles in differential equations. Prentice-Hall Inc., Englewood Cliffs, NJ
Thieme HR (1977) A model for the spatial spread of an epidemic. J Math Biol 4(4):337–351
Thieme HR (1979) Asymptotic estimates of the solutions of nonlinear integral equations and asymptotic speeds for the spread of populations. J Reine Angew Math 306:94–121
Thieme HR (1979) Density-dependent regulation of spatially distributed populations and their asymptotic speed of spread. J Math Biol 8(2):173–187
Thieme HR, Zhao X-Q (2003) Asymptotic speeds of spread and traveling waves for integral equations and delayed reaction-diffusion models. J Differ Equ 195(2):430–470

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.
Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.