PROPAGATION PHENOMENA FOR A CRISS-CROSS INFECTION MODEL WITH NON-DIFFUSIVE SUSCEPTIBLE POPULATION IN PERIODIC MEDIA

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ABSTRACT. This paper is concerned with propagation phenomena for an epidemic model describing the circulation of a disease within two populations or two subgroups in periodic media, where the susceptible individuals are assumed to be motionless. The spatial dynamics for the cooperative system obtained by a classical transformation are investigated, including spatially periodic steady state, spreading speeds and pulsating travelling fronts. It is proved that the minimal wave speed is linearly determined and given by a variational formula involving linear eigenvalue problem. Further, we prove that the existence and non-existence of travelling wave solutions of the model are entirely determined by the basic reproduction ratio $R_0$. As an application, we prove that if the localized amount of infectious individuals are introduced at the beginning, then the solution of such a system has an asymptotic spreading speed in large time and that is exactly coincident with the minimal wave speed.

1. Introduction. Infectious diseases are the primary causes of species extinction and endangering human health because infections with viruses are incurable and prone to recurrence, even worse, some ancient infectious disease pathogens continue to mutate and change, and new pathogens are still emerging in endlessly. Since the celebrated work of Kermack and Mckendrick [20], various mathematical models have been proposed to describe the dynamics of all kinds of viral infections, such as HIV, FIV, Dengue, Malaria, Rabies, Bilharzia, Zika viruses in Rio De Janerio, and so on [46, 17, 16, 37, 25]. In particular, criss-cross models described by differential equations have been widely utilized to depict the circulation of viral infections between vectors and hosts or among multiple groups. We refer to the excellent monograph of Murray [28], the works of Fitzgibbon et al. [16, 17], Ducrot et al. [13], Magal and McCluskey [26], Zhao et al. [47, 48] and references therein.

Recently, many studies provide ample evidence to support the view that the effect of spatial heterogeneity on the spread of the viral infections and ecological modelling cannot be ignored [2, 17, 25, 9, 10, 37, 46, 34]. As stated in these literatures, natural environment are generally heterogeneous, which may be a consequence of the presence of highly differentiated zones, such as forests, fields, roads, cities, etc. This indicates that real environments are assembled by more complex patterns, but

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periodic spaces, as a simple approximation to unbounded heterogeneous spaces, still capture the key features of habitats for many species and pathogens well. Therefore, based on the pioneering works of Fisher [15], Kolmogorov et al. [21] and Aronson and Weinberger [4], growing attention has been paid to the travelling waves and spreading speeds for various evolution systems in heterogeneous media (see, e.g. [6, 31, 43] and references therein), which are of great significance to disease control and ecological balance.

Typically, Shigesada et al. [32, 31] first introduced a reaction-diffusion model to study the biological invasions in a patchy habitat with periodic variations in mobility and growth rate via numerical simulations. Later, Berestycki et al. studied the stationary problem in [9] and pulsating travelling fronts (monotone) in [10] for a scalar reaction-diffusion equation in periodic environments and analyzed the influence of heterogeneity; besides, the speed of propagation for KPP type problems is also investigated in more general media [7, 8]. Nadin replenished in detail the discussion about the effect of heterogeneity on spreading speeds in [30, 29]. In another way, a general theory of spreading speeds and travelling waves in a periodic habitat has been developed by Weinberger [40] with an order-preserving compact operator; Liang and Zhao [24] established the monotone semiflows with “interval-\(\alpha\)-contraction” compactness and monostable structure, and further, this compactness is weakened to be “point-\(\alpha\)-contraction” by Fang and Zhao [14]. These abstract results can be applied to various evolution systems to study their spatial dynamics, mainly for the monotone systems. For instance, Yu and Zhao [44] recently studied the propagation phenomena for a Lotka-Volterra weakly competitive model in a periodic habitat by means of the abstract results in [14] and [24]. However, there is little research on spreading speeds and pulsating travelling waves (non-monotone) for the non-monotone problems in periodic media, especially for the epidemic models. The main difficulties are the lack of the comparison principle and the combination of unboundedness and heterogeneity. But it is worth mentioning that Wang et al. [39, 45] established the existence and non-existence of time-periodic travelling waves for a SIR epidemic model with standard and bilinear incidence infection mechanism. More generally, the generalized travelling waves for a non-autonomous reaction-diffusion system of epidemic type have been recently treated in [3].

In this paper we study the spatial dynamics of a criss-cross infection model in periodic media with non-diffusive susceptible population. More precisely, the model assumes that an infectious disease spreads within two populations or a population of two groups, and in each group, population is divided into three subclasses: the susceptible class \(S\) which is capable of becoming infected, the infective class \(I\) transmitting the disease to others, and the removed class \(R\) consisting of individuals which have died from the infection and recovered due to the treatment, thereby becoming immune. Denoting the potential evolution among three subclasses by “\(\leftarrow, \rightarrow\)” and the infection mechanism by “\(\leftarrow, \Rightarrow, \uparrow, \downarrow\)” then the circulation of the disease can be represented by the following illustration:

\[
\begin{align*}
\text{Susceptible I} & \quad \Rightarrow \quad \text{Infective I} \quad \rightarrow \quad \text{Removed I} \\
\text{Removed II} & \quad \leftarrow \quad \text{Infective II} \quad \leftarrow \quad \text{Susceptible II}
\end{align*}
\]

Besides, we suppose that the susceptible individuals are motionless. Then the corresponding mathematical formulation is the following spatially heterogeneous
reaction-diffusion system

\[
\begin{align*}
\frac{\partial S_i}{\partial t} &= -[\beta_{11}(x)I_1 + \beta_{12}(x)I_2]S_i, \\
\frac{\partial I_i}{\partial t} &= d_i(x) \frac{\partial^2 I_i}{\partial x^2} + [\beta_{11}(x)I_1 + \beta_{12}(x)I_2]S_i - \delta_i(x)I_i, \\
\frac{\partial S_2}{\partial t} &= -[\beta_{21}(x)I_1 + \beta_{22}(x)I_2]S_2, \\
\frac{\partial I_2}{\partial t} &= d_2(x) \frac{\partial^2 I_2}{\partial x^2} + [\beta_{21}(x)I_1 + \beta_{22}(x)I_2]S_2 - \delta_2(x)I_2
\end{align*}
\]

posed for \((t, x) \in (0, +\infty) \times \mathbb{R}\). Here the functions \(S_i = S_i(t, x)\) (resp. \(I_i = I_i(t, x)\)) denote the density of susceptible (resp. infected) individuals that belong to the \(i\)th group at time \(t > 0\) and spatial location \(x \in \mathbb{R}\), and the nonnegative functions \(d_i\) and \(\delta_i\) are diffusion and mortality (or recovery) rates due to the infection, \(i = 1, 2\). Besides, the contamination process follows the usual mass-action incidence with the inter- and intra-specific contact rates \(\beta_{ij}\), respectively, \(1 \leq i, j \leq 2\). System (1.1) is supplemented together with some nonnegative initial data

\[
\begin{align*}
S_1(0, x) &= S_1^0(x) \neq 0, \quad I_1(0, x) = I_1^0(x) \neq 0, \quad \forall \ x \in \mathbb{R}, \\
S_2(0, x) &= S_2^0(x) \neq 0, \quad I_2(0, x) = I_2^0(x) \neq 0, \quad \forall \ x \in \mathbb{R}.
\end{align*}
\]

(1.2)

This model incorporates spatial heterogeneity, criss-cross mechanism and individual mobility due to contagious diseases. If the disease in consideration spreads only in a single population, then (1.1)-(1.2) becomes

\[
\begin{align*}
\partial_t S &= -\beta(x)SI, \quad t > 0, \ x \in \mathbb{R}, \\
\partial_t I &= d(x)\partial_x I + \beta(x)SI - \delta(x)I, \quad t > 0, \ x \in \mathbb{R}, \\
S(0, x) &= S_0(x), \ I(0, x) = I_0(x), \ x \in \mathbb{R}.
\end{align*}
\]

(1.3)

The spatio-temporal dynamics of (1.3) are investigated by Ducrot and Giletti [12] for arbitrary dimensional space and \(d(x) \equiv 1\). As already pointed out in [12], this problem has been first proposed by Kallen et al. [19] with constant coefficients to model the spatial spread of rabies epizootic in foxes across Europe. Because rabid foxes exhibit an abnormal movement during migration and the fox family occupies the new territory and settles on a time scale that is very slow relative to the movement of rabid foxes, then the model assumes that susceptible foxes are motionless and the diffusion is caused by the disease. A more detailed explanation about the spatial spread of this disease sees the Sections 13.4 and 13.5, Volume II in the monograph of Murray [28] or the recent work of Alanazi et al. [1]. However, the fox is not the only virus vector and contact between animals (such as raccoons, wolves, dogs) for prey or territorial competition may also lead to viral infection. Therefore, criss-cross infection cannot be ignored. Indeed, many infectious diseases, especially sexually transmitted diseases (STDs), are all criss-cross [28].

The goal of this work is to study the propagation dynamics of the partially degenerate reaction-diffusion system (1.1)-(1.2) under a periodic framework. Many studies on criss-cross infection models with a spatially heterogeneous medium only focus on threshold dynamics of the epidemic (see, e.g. [25, 26, 37]). Although there are a few results on the existence of travelling wave solutions (see, e.g. [13, 48, 47]), the media under consideration are spatially homogeneous. We may also mention the works on partially degenerate system in [38, 42] where the spreading speeds and
pulsating travelling waves are investigated, but unlike those, system (1.1) is non-monotone. In this work, our core idea is to introduce the accumulative distribution function of the infection such that (1.1) can be transformed into a cooperative system. Further, we will prove that it is a monostable system with periodicity conditions. This will enable us to apply the abstract results of Liang and Zhao [24] to obtain the existence of travelling waves for the model (1.1). Nevertheless, it is not an easy task to study the spreading speed for the Cauchy problem (1.1)-(1.2). This is because such a cooperative system is no longer monostable and periodic provided that infectious individuals are introduced at the beginning. In addition, another difficulty, that the nonlinearity of this cooperative system changes sign, hinders the use of a well-known comparison theorem for principal eigenvalues when we analyze the effect of spatial heterogeneity and diffusion rates \(d_i\) on the spreading speed. Unlike the discussions of numerical simulation in many articles, we will address this issue in subsequent article.

This work is organized as follows: Section 2 is devoted to transform the model (1.1) into a cooperative system and to set the mathematical framework. In Section 3, we first introduce the basic reproduction ratio \(R_0\) for the model (1.1) and provide a mathematical approach to calculate \(R_0\). Next, we establish the threshold dynamics for this cooperative system with general initial data. Finally, we consider spreading speeds, pulsating travelling fronts, as well as the linear determinacy and some variational characterizations of the minimal wave speed. Section 4 is concerned with some spreading properties for the Cauchy problem (1.1)-(1.2) under suitable conditions.

2. Preliminaries. We begin with some notations. For any vectors \(a = (a_1, \ldots, a_n)\) and \(b = (b_1, \ldots, b_n) \in \mathbb{R}^n\), we write \(a \geq b (a \gg b)\) provided \(a_i \geq b_i (a_i > b_i)\), \(\forall i = 1, \ldots, n\), and \(a > b\) provided \(a \geq b\) but \(a \neq b\). We equip \(\mathbb{R}^n\) with the usual Euclid norm \(|\cdot|\). Let \(L\) be a positive constant and \(\mathbb{R}_+ = [0, +\infty)\). Throughout this paper, we make the following assumption:

(H) Assume that all coefficients of model (1.1) satisfy the following conditions:

(a) \(d_i(x + L) = d_i(x)\) for all \(x \in \mathbb{R}\) and \(d_i \in C^\gamma(\mathbb{R})\), where \(C^\gamma(\mathbb{R})\) is a Hölder continuous function space with the exponent \(\gamma \in (0, 1)\); the operators \(d_i(x)\frac{\partial^2}{\partial x^2}\) are uniformly elliptic in the sense that there exists a positive number \(\alpha_0\) such that \(d_i(x) \geq \alpha_0\) for any \(x \in \mathbb{R}, i = 1, 2\).

(b) The functions \(\delta_i\) and \(\beta_{ij}\) are \(L\)-periodic in \(x\) and of class \(C^\gamma, 1 \leq i, j \leq 2\). Moreover, \(\delta_i(x) > 0, \beta_{ii}(x) \geq 0\) and \(\beta_{ij}(x) > 0 (i \neq j)\) for any \(x \in \mathbb{R}\).

Motivated by the idea of Ducrot and Giletti in [12] (see also the work of Beaumont et al. in [5]), we will introduce a new vector-valued function that satisfies an equation with similar properties to the standard scalar KPP reaction-diffusion equation. Specifically, the integrations of the first and third equations of (1.1) yield

\[
S_1(t, x) = S_1^0(x) e^{-\left(\int_0^t \beta_{11}(s) I_1(s, x) ds + \beta_{12}(s) I_2(s, x) ds\right)},
\]

\[
S_2(t, x) = S_2^0(x) e^{-\left(\int_0^t \beta_{21}(s) I_1(s, x) ds + \beta_{22}(s) I_2(s, x) ds\right)},
\]

and by setting

\[
u_i(t, x) = \int_0^t I_i(s, x) \, ds, \quad i = 1, 2,
\]
the second and fourth equations can be rewritten as
\[
\frac{\partial I_1(t,x)}{\partial t} = d_1(x) \frac{\partial^2 I_1(t,x)}{\partial x^2} - \delta_1(x) I_1(t,x) - S^0_1(x) \frac{\partial}{\partial t} \left( \beta_{11}(x) u_1(t,x) + \beta_{12}(x) u_2(t,x) \right),
\]
\[
\frac{\partial I_2(t,x)}{\partial t} = d_2(x) \frac{\partial^2 I_2(t,x)}{\partial x^2} - \delta_2(x) I_2(t,x) - S^0_2(x) \frac{\partial}{\partial t} \left( \beta_{21}(x) u_1(t,x) + \beta_{22}(x) u_2(t,x) \right).
\]
Hence one gets that \((u_1, u_2)\) satisfies
\[
\begin{align*}
\frac{\partial u_1}{\partial t} &= d_1(x) \frac{\partial^2 u_1}{\partial x^2} + I_1^0(x) + f_1(x, u_1, u_2), \quad t > 0, \ x \in \mathbb{R}, \\
\frac{\partial u_2}{\partial t} &= d_2(x) \frac{\partial^2 u_2}{\partial x^2} + I_2^0(x) + f_2(x, u_1, u_2), \quad t > 0, \ x \in \mathbb{R}, \\
u_1(0, x) = 0, \ u_2(0, x) = 0, \quad x \in \mathbb{R},
\end{align*}
\] (2.1)

where the functions \(f_1 \) and \(f_2 : \mathbb{R} \times [0, +\infty) \times [0, +\infty) \rightarrow \mathbb{R}\) are defined by
\[
\begin{align*}
f_1(x, u_1, u_2) &= S^0_1(x) \left[ 1 - e^{-\left( \beta_{11}(x) u_1 + \beta_{12}(x) u_2 \right)} \right] - \delta_1(x) u_1, \\
f_2(x, u_1, u_2) &= S^0_2(x) \left[ 1 - e^{-\left( \beta_{21}(x) u_1 + \beta_{22}(x) u_2 \right)} \right] - \delta_2(x) u_2.
\end{align*}
\] (2.2)

Consequently, if the terms \(I_i^0\) are neglected, (2.1) becomes the following reaction-diffusion system
\[
\begin{align*}
\frac{\partial u_1}{\partial t} &= d_1(x) \frac{\partial^2 u_1}{\partial x^2} + f_1(x, u_1, u_2), \quad t > 0, \ x \in \mathbb{R}, \\
\frac{\partial u_2}{\partial t} &= d_2(x) \frac{\partial^2 u_2}{\partial x^2} + f_2(x, u_1, u_2), \quad t > 0, \ x \in \mathbb{R},
\end{align*}
\] (2.3)

and further, \(u_i(t,x) \equiv 0\) provided \(u_i(0, \cdot) = 0\), \(i = 1, 2\).

Recalling (2.2), the initial values \(S^0_i\) play a crucial role in the reaction term and the functions \(u_i\) represent the accumulations of the infection at each spatial location \(x \in \mathbb{R}\). In order to deal with subsequent issues, we will make the following additional assumptions:

(A1) The functions \(S^0_i \in C^\gamma(\mathbb{R})\) are \(L\)-periodic in \(x\) and positive, \(i = 1, 2\).

(A2) (a) The functions \(I_i^0 \in C(\mathbb{R}) \setminus \{0\}\) are nonnegative and bounded, \(i = 1, 2\).

(b) Furthermore, the functions \(I_i^0\) are compactly supported.

Remark 2.1. As a result of the point of Kallen et al. [19] and actual situation with regard to the spread of disease, it can be reasonable to assume that the susceptible population is motionless in (1.1). Therefore, \(E_0 = (S^0_1(x), 0, S^0_2(x), 0)\) can be considered as the steady state of the population before the introduction of the disease. Further, its periodicity in (A1) is a reasonable hypothesis in the spatially periodic framework.

For the sake of convenience, we express (2.1) and (2.3) in the more concise form
\[
\begin{align*}
\partial_t U &= D(x) \partial_{xx} U + I_0(x) + F(x, U), \quad t > 0, \ x \in \mathbb{R}, \\
U(0, x) &= 0, \quad x \in \mathbb{R}
\end{align*}
\] (2.4)

and
\[
\partial_t U = D(x) \partial_{xx} U + F(x, U), \quad t > 0, \ x \in \mathbb{R},
\] (2.5)

where \(U = (u_1, u_2), I_0(x) = (I_1^0(x), I_2^0(x)), F(x, U) = (f_1(x, u_1, u_2), f_2(x, u_1, u_2))\) and \(D(x) = \text{diag} \{d_1(x), d_2(x)\}\) in \(\mathbb{R}\). Under assumptions (H) and (A1), it is easy to verify that for the reaction term \(F\), the following properties hold:
(P1) The functions \( f_i : \mathbb{R} \times \mathbb{R}^2_+ \to \mathbb{R} \) are of class \( C^7 \) in \( x \) locally in \( u_i \), locally Lipschitz-continuous with respect to \( u_i \), and \( L \)-periodic in \( x \). Moreover, \( f_i(x, u_1, u_2) \) are second-order differentiable with respect to \( u_i \); \( \partial_{u_i} f_i(x, u_1, u_2) \) are continuous and \( L \)-periodic in \( x \); \( f_i(x, 0, 0) \equiv 0 \), \( 1 \leq i, j \leq 2 \).

(P2) There exists a strictly positive vector \( M = (M_1, M_2) \in \mathbb{R}^2 \) such that for any \( x \in \mathbb{R} \) and \( u_i \geq M_i \), \( f_i(x, u_1, u_2) \leq 0 \), \( i = 1, 2 \).

(P3) \( \partial_{u_1} f_1(x, u_1, u_2) \geq 0 \) and \( \partial_{u_2} f_2(x, u_1, u_2) \geq 0 \) for any \( x \in \mathbb{R} \) and \( U \in \mathbb{R}^2_+ \).

(P4) The reaction term \( F(x, U) \) is strongly subhomogeneous on \( \mathbb{R}^2_+ \) in the sense that \( F(x, \theta U) \gg \theta F(x, U) \) for any \( x \in \mathbb{R} \), \( \theta \in (0, 1) \) and \( U \gg 0 \).

(P5) The vector-valued function \( F(x, U) \) satisfies

\[
F(x, U) \leq DF(x, 0)U, \quad \forall x \in \mathbb{R}, \quad U \in \mathbb{R}^2_+.
\]

where \( DF(x, 0) \) is the Jacobian matrix of \( F(x, U) \) at \( U = 0 \) and equality holds if and only if \( U \equiv 0 \).

In particular, (P3) means that \( (2.5) \) is a cooperative system. Furthermore, due to assumptions (H)(b) and (A1), there exists some \( x_0 \in \mathbb{R} \) such that the off-diagonal elements of the Jacobian matrix \( DF(x_0, U) \) are positive for any \( U \geq 0 \), which indicates that system \( (2.5) \) is irreducible. Besides, (P5) can be directly derived by (P3) and (P4). As a consequence, \( (2.4) \) is a localized spatial perturbation of \( (2.5) \) under assumption (A2), while the latter is a cooperative and irreducible system and shares structural similarities with a scalar Fisher-KPP equation. For the sake of clarity in the following, \( (2.4) \) is called a *perturbed system*, whereas \( (2.5) \) is an *unperturbed system*. In next section, we first investigate the propagation dynamics for the unperturbed system \( (2.5) \) in a periodic framework.

3. Spatial dynamics of the unperturbed system. Let \( \mathbb{P} = PC(\mathbb{R}, \mathbb{R}^2) \) be the set of all \( L \)-periodic and continuous functions from \( \mathbb{R} \) to \( \mathbb{R}^2 \) and \( \mathbb{P}_+ = \{ \varphi \in \mathbb{P} : \varphi(x) \geq 0, \forall x \in \mathbb{R} \} \). Then, \( \mathbb{P}_+ \) is a closed cone of \( \mathbb{P} \) and induces a partial ordering on \( \mathbb{P} \). We equip \( \mathbb{P} \) with the maximum norm \( \| \cdot \|_\mathbb{P} \), i.e. \( \| \varphi \|_\mathbb{P} = \max_{x \in \mathbb{R}} |\varphi(x)| \). It then follows that \( (\mathbb{P}, \mathbb{P}_+, \| \cdot \|_\mathbb{P}) \) is an ordered Banach lattice.

3.1. Threshold dynamics. In this section, we mainly focus on the existence and uniqueness of a strongly positive and periodic steady state for the unperturbed system \( (2.5) \) and the large time behavior of the Cauchy problem \( (2.5) \) with the bounded and continuous initial data. These results are expressed by a condition on the sign of the principal eigenvalue of a linearized problem associated with system \( (2.5) \) in a periodic framework.

Linearizing system \( (2.5) \) at the trivial steady state \((0, 0)\), we obtain the following system of equations

\[
\begin{align*}
\frac{\partial u_1}{\partial t} &= d_1(x) \frac{\partial^2 u_1}{\partial x^2} + (\beta_{11}(x)S_1^0(x) - \delta_1(x)) u_1 + \beta_{12}(x)S_1^0(x)u_2, & t > 0, & x \in \mathbb{R}, \\
\frac{\partial u_2}{\partial t} &= d_2(x) \frac{\partial^2 u_2}{\partial x^2} + \beta_{21}(x)S_2^0(x)u_1 + (\beta_{22}(x)S_2^0(x) - \delta_2(x)) u_2, & t > 0, & x \in \mathbb{R}. \\
\end{align*}
\]

Set

\[
B(x) = \begin{pmatrix}
\beta_{11}(x)S_1^0(x) & \beta_{12}(x)S_1^0(x) \\
\beta_{21}(x)S_2^0(x) & \beta_{22}(x)S_2^0(x)
\end{pmatrix}
\quad \text{and} \quad
V(x) = \begin{pmatrix}
\delta_1(x) & 0 \\
0 & \delta_2(x)
\end{pmatrix}, \quad \forall x \in \mathbb{R}.
\]

(3.2)
Substituting \( u_t(x) = e^{-\lambda t} u(x) \) into (3.1), one gets the following periodic eigenvalue problem

\[
\begin{align*}
\lambda \phi &= -D(x)\phi'' - DF(x,0)\phi, & x \in \mathbb{R}, \\
\phi(x + L) &= \phi(x), & x \in \mathbb{R},
\end{align*}
\]

(3.3)

where \( \phi(x) = (\phi_1(x), \phi_2(x)) \) and \( DF(x,0) = B(x) - V(x) \).

Notice that (H)(b) and (A1) imply that \( DF(x_0,0) \) is irreducible for some \( x_0 \in \mathbb{R} \), i.e. system (3.1) is cooperative and irreducible. By [49, Theorem 11.3.1 and Remark 11.3.2], (3.3) admits an algebraically simple eigenvalue \( \lambda_0 \) (principal eigenvalue) associated with a principal eigenfunction \( \phi_0 \in \mathbb{P} \) and \( \phi_0(x) = (\phi_0^1(x), \phi_0^2(x)) \gg 0 \) for all \( x \in \mathbb{R} \).

On the other hand, from the expression (2.2) of \( F \), it is not hard to check that the components of \( F = (f_1, f_2) : \mathbb{R} \times \mathbb{R}^2_+ \rightarrow \mathbb{R}^2 \) satisfy

\[
f_i(x, u_1, u_2) \geq 0 \quad \text{whenever} \quad x \in \mathbb{R}, \quad U \in \mathbb{R}^2_+ \quad \text{and} \quad u_i = 0.
\]

(3.4)

It then follows that for any \( \varphi \in \mathbb{P} \), (2.5) has a unique classical solution \( U(t, \cdot; \varphi) \in \mathbb{P} \) defined on \([0, \infty)\). Moreover, for any \( \varphi \in \mathbb{P}_+ \), we have \( U(t, x + L; \varphi) = U(t, x; \varphi) \) and \( U(t, x; \varphi) \geq 0 \) for all \( t \geq 0 \) and \( x \in \mathbb{R} \) (see, e.g. [33, Corollary 7.3.2]).

Next, we adopt the approaches of [36] and [49, Section 11] to identify the basic reproduction ratio \( R_0 \) of model (1.1). Let \( A = D(\cdot) \frac{\partial^2}{\partial x^2} - \mathcal{V} \) and \( B \) be the linear operators on \( \mathbb{P} \) where \( \mathcal{B} \) and \( \mathcal{V} \) are the multiplication operators by \( B(x) \) and \( V(x) \) in (3.2). It is easy to check that \( A + B \) and \( A \) are resolvent-positive, \( s(A) < 0 \) (it is the spectral bound of \( A \)) and \( A + B \) is a positive perturbation of \( A \). Following the ideas of the next generation operator, the basic reproduction ratio is defined as \( R_0 = r(-BA^{-1}) \), where \( r(-BA^{-1}) \) is the spectral radius of \( -BA^{-1} \). Furthermore, by [36, Theorem 3.5] and similar arguments to those of [49, Theorems 11.3.3-11.3.4], we immediately have the following result:

**Lemma 3.1.** 1 – \( R_0 \) has the same sign as \( \lambda_0 \). Furthermore, \( R_0 \) can be characterized by

\[
R_0 = r(-BA^{-1}) = r(-A^{-1}B) = 1/\mu_0
\]

(3.5)

where \( \mu_0 \) is the principal eigenvalue of the elliptic eigenvalue problem

\[
\begin{align*}
-D(x)\phi'' + V(x)\phi &= \mu B(x)\phi, & x \in \mathbb{R}, \\
\phi(x + L) &= \phi(x), & x \in \mathbb{R}.
\end{align*}
\]

Now, we are in a position to describe the globally spatial dynamics of system (2.5) in terms of the basic reproduction ratio \( R_0 \). The proof is based on some ideas in [9] and a general threshold dynamics theory in [49, Section 2.2-2.3] of which applications may refer to [41, Theorem 3.2] and [42, Theorem 2.4].

**Theorem 3.2.** Assume that (H) and (A1) hold. Let \( \varphi \) be any bounded and continuous functions such that \( \varphi(x) \geq 0 \), \( \varphi \not\equiv 0 \) for all \( x \in \mathbb{R} \), and \( U(t, x; \varphi) \) be the solution of (2.5) with initial datum \( U(0, x) = \varphi(x) \). Then the following statements are valid:

(i) If \( R_0 > 1 \), then there exists a unique and \( L \)-periodic steady state \( P \) of (2.5) such that \( \mathbf{0} \ll P \ll \mathbf{M} \) and for any \( \varphi \) satisfying \( \inf_{x \in \mathbb{R}} \varphi(x) > 0 \), we have

\[
\lim_{t \to \infty} |U(t, x; \varphi) - P(x)| = 0
\]

uniformly for all \( x \in \mathbb{R} \).
(ii) If $R_0 \leq 1$, then there are no any positive and bounded steady states of (2.5), i.e. $0$ is the only nonnegative and bounded steady state of (2.5). Moreover, we have
\[
\lim_{t \to \infty} U(t, x; \varphi) = 0
\]
uniformly for all $x \in \mathbb{R}$.

Proof. Note that under assumptions (H) and (A1), the nonlinearity $F$ of (2.5) satisfies (P1)-(P5). As such, applying [49, Theorem 2.3.4] to the solution semiflow generated by (2.5) with any initial data $\varphi \in [0, M]$ can readily obtain that if $R_0 > 1$, (2.5) admits a unique and $L$-periodic steady state $P(x)$ such that $0 \ll P \leq M$ and for any $\varphi \in [0, M] \setminus \{0\} := \{\varphi \in \mathbb{R} : 0 < \varphi \leq M\}$, $U(t, x; \varphi)$ converges to $P(x)$ as $t \to +\infty$ uniformly for all $x \in \mathbb{R}$; if $R_0 \leq 1$, then for any $\varphi \in [0, M]$, $U(t, x; \varphi) \to 0$ as $t \to +\infty$ uniformly for all $x \in \mathbb{R}$.

Now, suppose $R_0 > 1$ and let $\varphi$ be a bounded and continuous initial datum with $\inf_{x \in \mathbb{R}} \varphi(x) > 0$. Then, one can choose some vector-valued function $\hat{\varphi} \in \{0, M\} \setminus \{0\}$ with $\inf_{x \in \mathbb{R}} \hat{\varphi}(x) = \inf_{x \in [0, L]} \hat{\varphi}(x) = 0$ and take $M' \in \mathbb{R}_+^2$ ($M' > M$) large enough such that
\[
0 < \hat{\varphi}(x) \leq \varphi(x) \leq M', \quad \forall x \in \mathbb{R}.
\]
Consider the following Cauchy problem
\[
\begin{cases}
\partial_t U = D(x)\partial_{xx} U + F(x, U), & t > 0, \; x \in \mathbb{R}, \\
U(0, x) = M', & x \in \mathbb{R}.
\end{cases}
\] (3.6)

From the property (P2) of $F$, $M'$ is a supersolution of (2.5), whence $U(t, x; M')$ is nonincreasing in $t$. Therefore, from the comparison principle, we have
\[
0 < U(t, x; \hat{\varphi}) \leq U(t, x; \varphi) \leq U(t, x; M') \leq M', \quad \forall \ t \geq 0, \; x \in \mathbb{R}.
\] (3.7)

On the other hand, since $U(t, x; M')$ is nonincreasing in $t$, standard parabolic estimates imply that $U(t, \cdot ; M')$ converges in $C^2_{\text{loc}}(\mathbb{R}, \mathbb{R}^2)$ to a bounded and nonnegative steady state $U_\infty$ of (2.5). As carried above, we know either $U_\infty \equiv 0$ or $U_\infty \equiv P$. Since $U(t, x; \hat{\varphi}) \to P(x)$ as $t \to +\infty$ uniformly for all $x \in \mathbb{R}$, it follows from (3.7) that $U_\infty \equiv P$, and that $U(t, x; \varphi)$ converges to $P(x)$ in $C^2_{\text{loc}}(\mathbb{R}, \mathbb{R}^2)$ as $t \to +\infty$, and further, the convergence is uniformly in $x$. Indeed, since $D(x)$ and $F(x, U)$ are $L$-periodic and the solution at $t = 0$, $M'$, is $L$-periodic, $U(t, x; M')$ is $L$-periodic in $x$ at each $t \geq 0$. It then follows from (3.7) that $U(t, x; \varphi)$ converges to $P(x)$ uniformly as $t \to +\infty$.

When $R_0 \leq 1$, we have $U_\infty \equiv 0$. Hence, using similar arguments above, it is not hard to check that for any bounded and continuous initial data $\varphi \geq 0$, $U(t, x; \varphi)$ converges to $0$ uniformly as $t \to +\infty$. This ends the proof of Theorem 3.2. \hfill \Box

3.2. Spreading speeds and travelling waves. In this section we investigate the spreading speeds and pulsating travelling fronts for the unperturbed system (2.5). The key point is to apply a general theory about monotone semiflows developed in [24] for abstract monostable evolution systems in a periodic habitat, together with some ideas in [40], to the following general initial value problem
\[
\begin{cases}
\partial_t U = D(x)\partial_{xx} U + F(x, U), & t > 0, \; x \in \mathbb{R}, \\
U(0, x) = \varphi(x), & x \in \mathbb{R}.
\end{cases}
\] (3.8)
To this end, we suppose that $R_0 > 1$ throughout this subsection. By Theorem 3.2, system (3.8) always has a unique steady state $P \in P$ and $P \geq 0$.

Let $C$ be the set of all bounded and continuous functions from $R$ to $R^2$. For any $u = (u_1, u_2), v = (v_1, v_2) \in C$, we write $u \geq v(u \gg v)$ provided $u_i(x) \geq v_i(x) (u_i(x) > v_i(x))$ for all $x \in R$, and $u > v$ provided $u \geq v$ but $u \neq v$. Let $C_+ = \{ \varphi \in C : \varphi(x) \geq 0, \forall x \in R \}$ and $C_P = \{ \varphi \in C : 0 \leq \varphi(x) \leq P(x), \forall x \in R \}$ be the subsets of $C$. Moreover, we introduce a norm on $C$ by

$$
\|u\|_C = \sum_{k=1}^{\infty} \max_{x \in R, |x| \leq k} \frac{|u(x)|}{2^k}, \forall u \in C.
$$

and the compact open topology in the sense that $u^n \to u$ in $C$ means that the sequence of functions $u^n(x)$ converges to $u(x)$ in $R^2$ uniformly for $x$ in every compact set. It then follows that $(C, \| \cdot \|_C)$ is a normed vector lattice and $C_P$ is a uniformly bounded subset of $C$. By [24, Proposition 2.2], the topology generated by the norm $\| \cdot \|_C$ and the compact open topology on $C$ are equivalent on $C_P$. Furthermore, $C_P$ is a complete metric space.

Let $\mathcal{B} = BC(R, R)$ be the set of all bounded and continuous functions from $R$ to $R$ and $T_i(t)$ be the $C_0$-semigroup on $\mathcal{B}$ generated by $A_i := d_i(\cdot) \frac{\partial^2}{\partial x^2} - \delta_i(\cdot)$ defined on

$$
D(A_i) := \left\{ \psi \in C : A_i \psi \in \mathcal{B} \text{ and } \lim_{t \to 0^+} \frac{T_i(t) \psi - \psi}{t} = A_i \psi \right\}, \quad i = 1, 2.
$$

It then follows that for each $t > 0$, $T_i(t) : \mathcal{B} \to \mathcal{B}$ are strongly positive and compact with respect to the compact open topology (see, e.g. [33, Corollary 7.2.3] and [41]). Therefore, $T(t) := (T_1(t), T_2(t)) : C \to C$ is a $C_0$-semigroup generated by the operator $A := (A_1, A_2)$ defined on $D(A) := D(A_1) \times D(A_2)$. Moreover, $T(t)$ is compact for each $t > 0$ and $T(t)C_+ \subset C_+$ for all $t \geq 0$. Next, define $\mathcal{F} = (\mathcal{F}_1, \mathcal{F}_2) : C_P \to C$ by

$$
\mathcal{F}_1(\varphi)(x) = S_1^0(x) \left[ 1 - e^{-(\beta_1(x)\varphi_1 + \beta_2(x)\varphi_2)} \right]
$$

and

$$
\mathcal{F}_2(\varphi)(x) = S_2^0(x) \left[ 1 - e^{-(\beta_1(x)\varphi_1 + \beta_2(x)\varphi_2)} \right]
$$

for any $x \in R$ and $\varphi = (\varphi_1, \varphi_2) \in C_P$. Then system (3.8) can be rewritten as the following integral equation form:

$$
\begin{align*}
U(t) = & T(t)U(0) + \int_0^t T(t-s)\mathcal{F}(U(s))ds, \; t > 0, \\
U(0) = & \varphi \in C_P.
\end{align*}
$$

(3.9)

In general, a solution of (3.9) is called a mild solution if it is continuous and satisfies (3.9). Since $\mathcal{F}(\varphi)$ is Lipschitz continuous on $C_P$, it follows that for any $\varphi \in C_P$, system (3.9) admits a unique mild solution $U(t, \cdot) \in C_P$ with $U(0, \cdot) = \varphi$ and $U(t, \cdot; \varphi) \in C_P$ for all $t \geq 0$. Further, the mild solution is also a classical solution of (3.8).

Let us recall that a function $W(x - ct, x)$ is said to be a $L$-periodic rightward travelling wave (or rightward pulsating wave) of system (3.8) if $W(\cdot + a, \cdot) \in C_P$, $\forall a \in R$, $U(t, x; W(\cdot, \cdot)) = W(x - ct, x)$, $\forall t \geq 0$, and $W(\xi, x)$ is a $L$-periodic function in $x$ for any fixed $\xi := x - ct \in R$. Moreover, we say that $W(\xi, x)$ connects a positive periodic state $P$ to the trivial solution $0$ with speed $c > 0$ provided that
\[ \lim_{\xi \to -\infty} W(\xi, x) = P(x) \quad \text{and} \quad \lim_{\xi \to \infty} W(\xi, x) = 0 \]

uniformly for all \( x \in \mathbb{R} \). The leftward pulsating wave \( W(x + ct, x) \) can be similarly defined.

Note that the reaction term \( F \) of (3.8) is cooperative and irreducible, and satisfies (3.4). Combining [42, Lemma 2.1] and [33, Theorem 7.4.1], we can establish the following comparison principle for system (3.8).

**Lemma 3.3.** (Comparison Principle). Let \( \varphi, \psi \in C_+ \) satisfy \( \varphi \leq \psi \) and let \( U(t, x; \varphi) \) and \( U(t, x; \psi) \) be the solutions of (3.8) with initial values \( U(0, \cdot; \varphi) = \varphi \) and \( U(0, \cdot; \psi) = \psi \), respectively. Then \( U(t, x; \varphi) \leq U(t, x; \psi) \) holds for all \( x \in \mathbb{R} \) and \( t \geq 0 \). Furthermore, if \( \varphi < \psi \), then \( U(t, x; \varphi) \ll U(t, x; \psi) \) holds for all \( x \in \mathbb{R} \) and \( t > 0 \).

In fact, this result is a special version of [33, Theorem 7.4.1 and Corollary 7.4.2] in a periodic framework. We can find a weaker version in [38], omitting its proof here.

Define a family of operators \( \{Q_t\}_{t \geq 0} \) on \( C_P \) by

\[ Q_t(\varphi)(x) := U(t, x; \varphi), \quad \forall \varphi \in C_P, \ x \in \mathbb{R}, \]

where \( U(t, \cdot; \varphi) \) is the solution of system (3.8) with \( U(0, \cdot) = \varphi \in C_P \). By Lemma 3.3, \( \{Q_t\}_{t \geq 0} \) is a monotone semiflow on \( C_P \). Then, from the properties of semiflow, the solution maps \( Q_t : \mathbb{R}_+ \times C_P \to C_P \) satisfy that \( Q_t(\varphi) \) is jointly continuous in \( (t, \varphi) \in \mathbb{R}_+ \times C_P \) and \( Q_0 = I, \ Q_t \circ Q_s = Q_{t+s}, \forall t, s \geq 0 \).

Let \( \mathcal{H} = \mathbb{R}, \ r = L, \ \mathcal{H} = \mathbb{R}^2, \ X = Y = \mathbb{R}^2, \ \beta = P, \ \mathcal{D} = \mathcal{C} \) and \( \mathcal{M} = \mathcal{C}_P \) in Section 5 of the literature [24]. Further, we have the following observation.

**Proposition 3.4.** Let (H) and (A1) hold, and assume further that \( R_0 > 1 \). Then for each \( t > 0 \), \( Q_t \) satisfies the hypotheses (E1)-(E5) in the Section 5 of [24]. In addition, \( \{Q_t\}_{t \geq 0} \) is a strongly subhomogeneous semiflow on \( C_P \).

**Proof.** Note that if \( U(t, x; \varphi) \) is a solution of (3.8), so is \( U(t, x-a; \varphi), \forall a \in \mathbb{Z} \). This implies that (E1) is true. Since \( T(t) \) is compact with the compact open topology for each \( t > 0 \), (E2) and (E3) follow from the same arguments as in [27, Theorem 8.5.2]. In other words, \( Q_t(C_P) \subset \mathcal{D} \) is uniformly bounded and precompact in \( C_P \) with respect to the compact open topology, and \( \{Q_t\}_{t \geq 0} \) is a continuous-time semiflow on \( C_P \). By Lemma 3.3, (3.8) generates a monotone semiflow \( \{Q_t\}_{t \geq 0} \) on \( C_P \), which indicates that (E4) is true. From the part (i) of Theorem 3.2, we know that for each \( t > 0 \), (E5) holds for \( Q_t \).

Next, let us verify that \( \{Q_t\}_{t \geq 0} \) is a strongly subhomogeneous semiflow on \( C_P \). In other words, we need to show that \( Q_t(\theta \varphi) \geq \theta Q_t(\varphi) \) holds for all \( \theta \in [0, 1] \) and \( \varphi \in C_P \). To this end, we set \( \overline{U} = U(t, x; \theta \varphi) \) and \( \underline{U} = \theta U(t, x; \varphi) \). Due to the strongly subhomogeneous property (P4) of \( F, \overline{U} \) and \( \underline{U} \) satisfy

\[
\begin{align*}
\partial_t \overline{U} &= D(x) \partial_{xx} \overline{U} + F(x, \overline{U}), & t > 0, & x \in \mathbb{R}, \\
\overline{U}(0, x) &= \theta \varphi(x), & x \in \mathbb{R}
\end{align*}
\]

and

\[
\begin{align*}
\partial_t \underline{U} &= D(x) \partial_{xx} \underline{U} + \theta F(x, U) \\
&\ll D(x) \partial_{xx} \underline{U} + F(x, \underline{U}), & t > 0, & x \in \mathbb{R}, \\
\underline{U}(0, x) &= \theta \varphi(x), & x \in \mathbb{R}
\end{align*}
\]
respectively. Therefore, \( \overline{U} \) and \( U \) are upper and lower solutions of system (3.8) with \( \overline{U}(0, x) = \overline{U}(0, x) \) for all \( x \in \mathbb{R} \). By Lemma 3.3, one gets that \( U(t, x) \geq \overline{U}(t, x) \) for all \( t > 0 \) and \( x \in \mathbb{R} \). Further, (P4) and the above strict inequality imply that \( Q_t(\theta \varphi) \gg \theta Q_t(\varphi) \) for all \( \theta \in (0, 1) \) and \( \varphi \gg 0 \). Thus, \( \{Q_t\}_{t \geq 0} \) is a strongly subhomogeneous semiflow on \( \mathcal{C}_P \).

Eventually, in combination with Theorem 3.2, Proposition 3.4 and [24, Theorems 5.2-5.3], we can obtain the main results of this section. Notice that part (ii) of Theorem 5.2 in [24] needs the condition \( c^*_+ + c^-_* > 0 \). For convenience, we first state the main results, and it will be verified in subsequent Theorem 3.9.

**Theorem 3.5.** Let (H) and (A1) hold, and assume further that \( \mathcal{R}_0 > 1 \). Then there exist \( c^*_+ \) and \( c^-_* \), denoting the rightward and leftward spreading speeds of \( Q_1 \), respectively, such that the following statements are valid:

(i) For any \( c > c^*_+ \) and \( c' > c^-_* \), if \( \varphi \in \mathcal{C}_P \) with \( 0 \leq \varphi \leq \overline{x} \) for some \( \overline{x} \in \mathcal{P} \) and \( \varphi \ll P \), and \( \varphi(x) = 0 \) for \( x \) outside a bounded interval, then

\[
\lim_{t \to \infty, x \geq ct} U(t, x; \varphi) = 0 \quad \text{and} \quad \lim_{t \to \infty, x \leq -c(t)} U(t, x; \varphi) = 0.
\]

(ii) For any \( c < c^*_+ \), \( c' < c^-_* \), if \( \varphi \in \mathcal{C}_P \) with \( \varphi \neq 0 \), then

\[
\lim_{t \to \infty, -c(t) \leq x \leq ct} |U(t, x; \varphi) - P(x)| = 0.
\]

**Theorem 3.6.** Let (H) and (A1) hold, and assume further that \( \mathcal{R}_0 > 1 \). Let \( c^*_+ \) and \( c^-_* \) be the rightward and leftward spreading speeds of \( Q_1 \), respectively. Then the following statements are valid:

(i) For any \( c \geq c^*_+ \), system (3.8) admits a \( L \)-periodic rightward travelling wave \( W(x - ct, x) \) connecting \( P \) to \( 0 \), with wave profile components \( w_1(\xi, x) \) and \( w_2(\xi, x) \) being continuous and non-increasing in \( \xi \), while for any \( c < c^*_+ \), there are no such solutions connecting \( P \) to \( 0 \).

(ii) For any \( c \geq c^-_* \), system (3.8) admits a \( L \)-periodic leftward travelling wave \( W(x + ct, x) \) connecting \( 0 \) to \( P \), with wave profile components \( w_1(\xi, x) \) and \( w_2(\xi, x) \) being continuous and non-decreasing in \( \xi \), while for any \( c < c^-_* \), there are no such solutions connecting \( 0 \) to \( P \).

### 3.3. Characterization of the minimal wave speed

This section is concerned with the proof of the variational characterization of the minimal wave speed. Note that due to the property (P5) of \( F \), we may actually prove that the spreading speed is determined by the linearization of system (3.8) at \( 0 \). For this purpose, we follow the schemes as in [23, 40] to give a formula of \( c^*_+ \). In addition, another equivalent characterization of \( c^-_* \) will be obtained.

Consider the linearized system of (3.8) at its zero solution:

\[
\begin{aligned}
\partial_t U &= D(x)\partial_{xx}U + DF(x, 0)U, \quad t > 0, \ x \in \mathbb{R}, \\
U(0, \cdot) &= \varphi \in \mathcal{C}.
\end{aligned}
\]

(3.10)

Let \( \{L(t)\}_{t \geq 0} \) be the linear solution semigroup generated by (3.10), that is, \( L(t)\varphi = U_t(\varphi) \), where \( U(t, x; \varphi) \) is the unique solution of (3.10). For any given \( \mu \in \mathbb{R} \), substituting \( U(t, x) = e^{-\mu t}V(t, x) \) into (3.10), we find that for any \( \varphi \in \mathcal{C} \), \( V(t, x) \)
satisfies
\[
\begin{align*}
\partial_t V &= D(x)\partial_{xx} V - 2\mu D(x)\partial_x V + \mu^2 D(x)V + DF(x,0)V, \quad t > 0, \ x \in \mathbb{R},
\partial_x V(0)(x) &= \varphi(x)e^{\mu x}, \quad x \in \mathbb{R}.
\end{align*}
\]
(3.11)

Similarly, let \(\{L_\mu(t)\}_{t \geq 0}\) be the linear solution maps associated with (3.11), that is, \(L_\mu(t)\varphi = V_t(\varphi)\), where \(V(t,x;\varphi)\) is the unique solution of (3.11). It then follows that
\[
\begin{align*}
L(t)[e^{-\mu x}\varphi](x) &= e^{-\mu x}L_\mu(t)[\varphi](x), \quad \forall \ t \geq 0, \ x \in \mathbb{R}, \ \varphi \in \mathcal{C}.
\end{align*}
\]
(3.12)

Letting \(V(t,x) = e^{\lambda t}\phi(x)\), we obtain the following periodic eigenvalue problem
\[
\begin{align*}
\{\lambda\phi &= D(x)\phi'' - 2\mu D(x)\phi' + \mu^2 D(x)\phi + DF(x,0)\phi, \quad x \in \mathbb{R},
\phi(x + L) &= \phi(x), \quad x \in \mathbb{R}.
\end{align*}
\]
(3.13)

From the Krein-Rutman Theorem, we can readily derive the following conclusion:

**Proposition 3.7.** Let (H) and (A1) hold. Then for any \(\mu \in \mathbb{R}\), (3.13) has an algebraically simple eigenvalue \(\lambda(\mu)\) associated with a strongly positive and \(L\)-periodic eigenfunction \(\phi(x;\mu)\) for all \(x \in \mathbb{R}\). Moreover, if \(\lambda(\mu)\) is any other eigenvalues of (3.13), then \(\Re(\lambda(\mu)) < \lambda(\mu)\).

**Remark 3.1.** It follows from Proposition 3.7 that \(L_\mu(t) : \mathbb{P} \rightarrow \mathbb{P}\) is strongly positive and compact for each \(t > 0\), and \(K\phi(\cdot;\mu) = \lambda(\mu)\phi(\cdot;\mu)\). The Krein-Rutman Theorem applies to \(L_\mu(t)\) as well, which derives such a result that the spectral radius \(\rho(L_\mu(t))\) is the principal eigenvalue of \(L_\mu(t)\) and \(\rho(L_\mu(t)) = e^{\lambda(\mu)t} > 0\).

**Proposition 3.8.** Let (H) and (A1) hold. Then the function \(\mu \mapsto \lambda(\mu)\) is convex on \(\mathbb{R}\). Furthermore, the function \(\mu \mapsto \lambda(\mu)/\mu\) is continuous on \((0, \infty)\) and
\[
\lim_{\mu \rightarrow 0^+} \frac{\lambda(\mu)}{\mu} = +\infty, \quad \lim_{\mu \rightarrow \infty} \frac{\lambda(\mu)}{\mu} = +\infty.
\]
(3.14)

**Proof.** From [40, Lemma 6.2] (see also [23, Lemma 3.7]), it is not hard to check that the function \(\mu \mapsto \lambda(\mu)\) is convex, whence \(\mu \mapsto \lambda(\mu)/\mu\) is continuous on \((0, \infty)\).

Let us now turn to the proof of (3.14). Recalling that \(\lambda_0 = -\lambda(0)\) is the principal eigenvalue of (3.3), then by continuity, one easily gets that \(\lambda(\mu)/\mu \rightarrow \infty\) as \(\mu \rightarrow 0^+\).

As for the limit at infinity, by Proposition 3.7 and (P3), it is clear that for each \(\mu \in \mathbb{R}\)
\[
\lambda(\mu) \geq \frac{d_1(x)\phi'' - 2\mu d_1(x)\phi'}{\phi_1} + \mu^2 d_1(x) + (\beta_{11}(x)S^0_1(x) - \delta_1(x)), \quad \forall \ x \in \mathbb{R},
\]
(3.15)
where \(\phi_1(\cdot;\mu) > 0\) is the first component of the principal eigenfunction \(\phi(\cdot;\mu)\) associated with \(\lambda(\mu)\). Let \(\kappa(\mu)\) be the principal eigenvalue of the elliptic operator
\[
L_\mu \psi := d_1(x)\psi'' - 2\mu d_1(x)\psi' + \mu^2 d_1(x)\psi + (\beta_{11}(x)S^0_1(x) - \delta_1(x)) \psi
\]
with \(L\)-periodic conditions. Utilizing a result of [6, Proposition 5.7 (ii)], we obtain that
\[
\kappa(\mu) = \min_{\psi \in \hat{E}} \sup_{x \in \mathbb{R}} \left\{ \frac{d_1(x)\psi'' - 2\mu d_1(x)\psi'}{\psi} + \mu^2 d_1(x) + (\beta_{11}(x)S^0_1(x) - \delta_1(x)) \right\},
\]
where \(\hat{E} := \{ \psi \in C^2(\mathbb{R}) : \psi > 0 \text{ and } \psi \text{ is } L\text{-periodic} \} \). From the positivity of \(\phi_1(\cdot;\mu)\) and (3.15), we have \(\lambda(\mu) \geq \kappa(\mu)\) for any \(\mu \in \mathbb{R}\). On the other hand, by the proof of [10, Lemma 3.1], we know that \(\kappa(\mu)\) is convex in \(\mu\) and \(\kappa'(0) = 0\) (\(\kappa(\mu)\)
Remark 3.2. If all coefficients separately. Furthermore, \( c \) the condition \( c^*_+ + c^-_* > 0 \) in Theorem 3.5.

**Theorem 3.9.** Let (H) and (A1) hold, and assume further that \( R_0 > 1 \). Let \( c^*_+ \) and \( c^-_* \) denote the rightward and leftward spreading speeds of \( Q_1 \), respectively. Then

\[
    c^*_+ = \inf_{\mu > 0} \frac{\lambda(\mu)}{\mu}, \quad c^-_* = \inf_{\mu > 0} \frac{\lambda(-\mu)}{\mu}.
\]

Furthermore, \( c^*_+ + c^-_* > 0 \).

The proof is similar to that of [24, Proposition 7.4] and will not be detailed separately.

**Remark 3.2.** If all coefficients \( d_i(x), \beta_{ij}(x), \delta_i(x) \) of model (1.1) and the initial susceptible distributions \( S^0_i(x) \) are even functions in \( x \in \mathbb{R} \), it is easy to check that the principal eigenvalue \( \lambda(\mu) \) is also an even function of \( \mu \in \mathbb{R} \). Therefore, the rightward spreading speed equals the leftward one, i.e. \( c^*_+ = c^-_* \).

**Remark 3.3.** If the diffusion term of (3.8) is replaced by the divergence form \( D(x)U_x \) and assume that \( D(x) \) is of the class \( C^{1,\gamma} \), then \( \lambda(\mu) \) is still an even function of \( \mu \) on \( \mathbb{R} \) even though all coefficients of (1.1) and the initial functions \( S^0_i \) are asymmetrical, that is, \( c^*_+ = c^-_* \). Indeed, for any given \( \mu \in \mathbb{R} \), suppose that \( \phi = (\phi_1, \phi_2), \psi = (\psi_1, \psi_2) \in \mathbb{P} \) are the eigenfunctions associated with \( \lambda(\mu) \) and \( \lambda(-\mu) \), respectively. As argued above, it is clear that \( \phi \) and \( \psi \) satisfy

\[
\begin{align*}
    \lambda(\mu) \phi &= (D(x)\phi')' - 2\mu D(x)\phi' + \left[ \mu^2 D(x) - \mu D'(x) + DF(x,0) \right] \phi, \quad x \in \mathbb{R}, \\
    \phi(x + L) &= \phi(x) \gg 0,
\end{align*}
\]

and

\[
\begin{align*}
    \lambda(-\mu) \psi &= (D(x)\psi')' + 2\mu D(x)\psi' + \left[ \mu^2 D(x) + \mu D'(x) + DF(x,0) \right] \psi, \quad x \in \mathbb{R}, \\
    \psi(x + L) &= \psi(x) \gg 0,
\end{align*}
\]

From the periodicity conditions and using an integration by parts over \([0, L]\), a direct calculation yields that

\[
\lambda(\mu) \int_0^L \phi_i(x)\psi_i(x)dx = \lambda(-\mu) \int_0^L \phi_i(x)\psi_i(x)dx, \quad i = 1, 2.
\]

Therefore, by the strong positivity of \( \phi \) and \( \psi \), we have \( \lambda(\mu) = \lambda(-\mu) \) for all \( \mu \in \mathbb{R} \). In particular, if the diffusion coefficients \( d_i \) are constants, it is clear that \( c^*_+ = c^-_* \).

In what follows, another way to define the minimal wave speeds \( c^*_+ \) will be given. We only focus on the characterization of \( c^*_+ \), and \( c^-_* \) can be similarly defined.

From Theorem 3.6, a rightward pulsating wave of system (3.8) means that a particular solution \( U(t, x) = W(\xi, x) \) \( (\xi := x - ct) \) of (3.8) is \( L \)-periodic in \( x \) and nonincreasing in \( \xi \), and subjects to the boundary conditions

\[
\lim_{\xi \to -\infty} W(\xi, x) = P(x) \quad \text{and} \quad \lim_{\xi \to \infty} W(\xi, x) = 0
\]
uniformly for all $x \in \mathbb{R}$. Owing to the biological significance, it is more reasonable to expect a nonnegative pulsating travelling front. Thus, we assume that $W$ converges to zero with exponential decay and utilize the following ansatz

$$W(\xi, x) \sim e^{-\mu \xi} \psi(x) \quad \text{as} \quad \xi \to \infty$$

with the decay rate $\mu > 0$ and a given vector-valued function $\psi > 0$, both of which are dependent on the wave speed $c$. Plugging (3.17) into (3.8) yields

$$D(x)\psi'' - 2\mu D(x)\psi' + \left[\mu^2 D(x) - \mu c I + DF(x, 0)\right] \psi = 0,$n

where $I$ is a $2 \times 2$ identity matrix. Consider the following eigenvalue problem

$$\begin{cases}
L_{c, \mu} \phi = \Lambda_c(\mu) \phi \quad \text{in} \quad \mathbb{R}, \\
\phi \quad \text{is} \quad L\text{-periodic},
\end{cases}$$

where the operator $L_{c, \mu}$ is defined by

$$L_{c, \mu} \psi := D(x)\psi'' - 2\mu D(x)\psi' + \left[\mu^2 D(x) - \mu c I + DF(x, 0)\right] \psi$$

with $L$-periodic conditions. Letting $B^*_\mu(x) := \mu^2 D(x) - \mu c I + DF(x, 0)$ and applying Proposition 3.7 to (3.19), we know that (3.19) admits a principal eigenvalue, denoted as $\Lambda_c(\mu)$ without confusion, associated with a strongly positive and $L$-periodic eigenfunction $\psi$. It is clear that $\Lambda_c(\mu)$ is dependent on the parameters $c$ and $\mu$. In particular, $\Lambda_c(0) = -\lambda_0 > 0$. Further, we have the following observation.

**Corollary 3.10.** Let (H) and (A1) hold, and assume further that $R_0 > 1$. Then the function $\mu \mapsto \Lambda_c(\mu)$ is convex on $\mathbb{R}$ and $\lim_{\mu \to \infty} \Lambda_c(\mu) > 0$ for all $c \in \mathbb{R}$. Moreover, the function $c \mapsto \Lambda_c(\mu)$ is decreasing for any $\mu > 0$.

**Proof.** From Proposition 3.1 and Remark 3.1 in [35], $\Lambda_c(\mu)$ can be represented by

$$\Lambda_c(\mu) = \inf_{\phi \in E} \sup_{1 \leq i \leq 2} \sup_{x \in \mathbb{R}} \frac{(L_{c, \mu} \phi)_i(x)}{\phi_i(x)},$$

where $E := \{\phi \in C^2(\mathbb{R}, \mathbb{R}^2) : \phi \gg 0 \quad \text{and} \quad \phi \text{ is } L\text{-periodic}\}$. Let $E_\mu$ be the set defined by

$$E_\mu = \{\phi \in C^2(\mathbb{R}, \mathbb{R}^2) : \exists \psi \in E \text{ with } \phi(x) = e^{-\mu x} \psi\}$$

$$= \left\{\bar{\phi} \in C^2(\mathbb{R}, \mathbb{R}^2) : \bar{\phi}e^{\mu x} \text{ is } L\text{-periodic and } \bar{\phi} \gg 0\right\}.$$n

Then, the principal eigenvalue $\Lambda_c(\mu)$ can be rewritten as $\Lambda_c(\mu) = \lambda(\mu) - c\mu$ with

$$\lambda(\mu) = \inf_{\phi \in E_\mu} \sup_{1 \leq i \leq 2} \sup_{x \in \mathbb{R}} \frac{(D(x)\phi'' + DF(x, 0)\phi)_i}{\phi_i}.$$n

From Proposition 3.8, it is clear that $\Lambda_c(\mu)$ is a convex function of $\mu$ on $\mathbb{R}$. Furthermore, by (3.14), it is not hard to check that $\Lambda_c(+\infty)$ lies above zero for all $c \in \mathbb{R}$.

Finally, it follows from the monotonicity properties of the principal eigenvalue of cooperative systems (see [22, Proposition 3.4]) that $c \mapsto \Lambda_c(\mu)$ is decreasing for any $\mu > 0$. \hfill \Box

Note that (3.18) implies that 0 is the principal eigenvalue of (3.20). Thus, by Corollary 3.10, the minimal wave speed is the smallest of such $c$ that (3.18) holds for any $\mu > 0$. 
Remark 3.4 (An equivalent formula). It is easy to verify that the minimal wave speed can be defined as follows

\[ c^*_\mu = \min\{\lambda \in \mathbb{R} : \exists \lambda > 0, \text{ such that } \Lambda_c(\lambda) = 0\}. \]  

(3.21)

Indeed, from the proof of Corollary 3.10, the wave speed can be defined by \( c = \lambda(\mu)/\mu \). Moreover, equation

\[ \lambda(\mu) - c^*_\mu = 0 \]  

(3.22)

has a unique solution \( \mu^* \) if and only if \( \mu^* \) is the unique root of \( \Lambda c^*_\mu(\mu) = 0 \). As a result, the first formula of (3.16) is coincident with (3.21).

At the end of this subsection, we give a result on monotonicity of the minimal wave speed with respect to the Jacobian matrix of the nonlinearity \( B \) at 0. For convenience, we set \( B(\cdot) := DF(\cdot, 0) \) and denote the minimal wave speed \( c^*_\mu(B) \) given in Theorem 3.9 and Remark 3.4 by \( c^*_\mu(B) \) in order to emphasize its dependence on parameters. The other notations below are similar intentions.

Theorem 3.11. Let (H) and (A1) hold, and assume further that \( R_0 > 1 \). If \( B(x) \leq \hat{B}(x) \) for all \( x \in \mathbb{R} \), then \( c^*_\mu(B) \leq c^*_\mu(\hat{B}) \). Furthermore, if there exists some \( x_0 \in [0, L] \) such that \( B(x_0) < \hat{B}(x_0) \), then \( c^*_\mu(B) < c^*_\mu(\hat{B}) \).

Proof. For any \( \mu > 0 \), let \( \lambda(\mu; B) \) and \( \lambda(\mu; \hat{B}) \) be the principal eigenvalues of the following problem

\[ \begin{cases} \lambda(\mu) \phi = D(x) \phi'' - 2\mu D(x) \phi' + \mu^2 D(x) \phi + \Upsilon(x) \phi, & x \in \mathbb{R}, \\ \phi(x + L) = \phi(x), & x \in \mathbb{R} \end{cases} \]  

(3.23)

with \( \Upsilon = B \) and \( \Upsilon = \hat{B} \), respectively (the existence of the principal eigenvalue is guaranteed by Proposition 3.7). From the comparison theorem for principal eigenvalues of cooperative systems (see, e.g., [22, Proposition 3.4]), it is clear that \( \lambda(\mu; B) \leq \lambda(\mu; \hat{B}) \). By Theorem 3.9, one gets \( c^*_\mu(B) \leq c^*_\mu(\hat{B}) \).

We now proceed to establish the strict inequality under the extra assumption \( B(x_0) < \hat{B}(x_0) \) for some \( x_0 \in \mathbb{R} \). Firstly, by Theorem 3.9 and (3.14), we can choose some \( \mu_0 > 0 \) such that \( c^*_\mu(\hat{B}) = \lambda(\mu_0; \hat{B})/\mu_0 \). Next, we claim that

\[ \lambda(\mu_0; B) < \lambda(\mu_0; \hat{B}). \]  

(3.24)

To show (3.24), assume by contradiction that \( \lambda(\mu_0; B) \geq \lambda(\mu_0; \hat{B}) \). Let \( \phi_B \) and \( \phi_{\hat{B}} \) be the strongly positive and \( L \)-periodic eigenfunctions of (3.23) with \( \mu = \mu_0 \) associated with the principal eigenvalues \( \lambda(\mu_0; B) \) and \( \lambda(\mu_0; \hat{B}) \), respectively. From the proof of Theorem 3.2, there exists some \( \gamma > 0 \) such that \( \phi_B \leq \gamma \phi_{\hat{B}} \) in \( \mathbb{R} \). Set

\[ V(x) := \phi_B(x) - \gamma \phi_{\hat{B}}(x), \forall x \in \mathbb{R}. \]  

Then, \( V \leq 0 \) in \([0, L] \) with equality somewhere. Moreover, the function \( V \) satisfies

\[ D(x)V'' = 2\mu_0 D(x)V' + [\mu_0^2 D(x) + \lambda(\mu_0; B) + B(x)]V \]

\[ = (\lambda(\mu_0; B) - \lambda(\mu_0; \hat{B})) \gamma \phi_{\hat{B}} + (\hat{B}(x) - B(x)) \gamma \phi_{\hat{B}}, \quad x \in \mathbb{R}. \]

Since \( B(x_0) < \hat{B}(x_0) \), at least one of the components of \( V \), \( v_1 \) satisfies

\[ d_1(x)v''_1 = 2\mu_0 d_1(x)v'_1 + [\mu_0^2 d_1(x) + \lambda(\mu_0; B) + \beta_{11}(x) S_1^0(x) - \beta_1(x)] v_1 \geq (\neq) 0 \]

(3.25)

for any \( x \in \mathbb{R} \) without loss of generality. However, we know that \( v_1 \leq 0 \) in \([0, L] \) with equality somewhere. Therefore, it follows from the strong maximum principle.
that \( v_1 \equiv 0 \) in \( \mathbb{R} \), which is a contradiction that the left-hand side of (3.25) is not identically zero. This proves \( \lambda(\mu_0; B) < \lambda(\mu_0; \hat{B}) \), whence we have
\[
\lambda(\mu_0; B) \leq \frac{\lambda(\mu_0; B)}{\mu_0} < \frac{\lambda(\mu_0; \hat{B})}{\mu_0} = \lambda^*_+(\hat{B}).
\]
That completes the proof of Theorem 3.11.

Before going further on, let us review and comment on some of the results above. Coming back to model (1.1), from the standard parabolic estimates and the fact that for any \((t, x) \in (0, \infty) \times \mathbb{R} \) and \( i, j \in \{1, 2\}, \)
\[
I_i(t, x) = \partial_t u_i(t, x) \quad \text{and} \quad S_i(t, x) = S_i^0(x) e^{-[\beta_{ij}(x) u_i(t, x) + \beta_{ji}(x) u_j(t, x)]}, \quad i \neq j, \quad (3.26)
\]
we can deduce the following corollary from Theorem 3.6 and Theorem 3.2:

Corollary 3.12. Let (H) and (A1) hold. If \( R_0 > 1 \), then for any \( c \geq c^*_+ \), system (1.1) admits a rightward travelling wave solution \((S_1(\xi, x), I_1(\xi, x), S_2(\xi, x), I_2(\xi, x))\) with \( \xi := x - ct \) which satisfies that for any \( x \in \mathbb{R} \) and \( \xi \in \mathbb{R} \),
\[
S_i(\xi, x + L) = S_i(\xi, x), \quad I_i(\xi, x + L) = I_i(\xi, x) \geq (\neq) 0, \quad \partial_\xi S_i(\xi, \cdot) \geq 0,
\]
\[
I_1(\pm \infty, \cdot) = 0, \quad S_1(-\infty, \cdot) = S_1^0(\cdot) e^{-[\beta_{11}(\cdot) p_1(\cdot) + \beta_{12}(\cdot) p_2(\cdot)]}, \quad S_1(+\infty, \cdot) = S_1^0(\cdot),
\]
\[
I_2(\pm \infty, \cdot) = 0, \quad S_2(-\infty, \cdot) = S_2^0(\cdot) e^{-[\beta_{21}(\cdot) p_1(\cdot) + \beta_{22}(\cdot) p_2(\cdot)]}, \quad S_2(+\infty, \cdot) = S_2^0(\cdot),
\]
while for any \( c < c^*_+ \), system (1.1) has no such solutions. If \( R_0 \leq 1 \), there are no such travelling wave solutions as well.

The leftward pulsating travelling waves \((\xi := x + ct)\) can be similarly obtained. Here \( R_0 \) reflects the infection risk, while \( c^*_+ \) quantifies the speed of disease transmission after the disease invaded. In addition, the functions \( S_i(-\infty, \cdot) \) depict the state of susceptible individuals of the ith group after the epidemic and \( 0 < S_i(-\infty, x) < S_i^0(x) \) for any \( x \in \mathbb{R} \).

In particular, by Theorem 3.11, we see that the greater coupling strength (namely criss-cross mechanism) of the unperturbed system (2.5) implies a higher value of the minimal wave speed. Biologically, this suggests that the high infection rates between sub-groups and sufficiently large density of susceptible individuals can be favourable factors in terms of the disease transmission. Thus, if the different types of patients or carriers of the source are isolated in time, then the disease will be potentially eliminated.

4. Spreading speed in the Cauchy problem. This section is concerned with the spreading speed of system (1.1)-(1.2) under suitable conditions, especially if (A2)(b) is satisfied. From an epidemiological point of view, we focus on the spatial propagation phenomena of the disease after the localized amount of infectious individuals are introduced at the beginning.

Let us start with the existence and uniqueness of some positive steady state for the perturbed system (2.4).

Lemma 4.1. Let (H), (A1) and (A2)(a) hold. Assume further that \( R_0 > 1 \). Then the elliptic system of equations
\[
D(x) \phi'' + I_0(x) + F(x, \phi) = 0, \quad x \in \mathbb{R}
\]
(4.1)
admits a unique positive and bounded solution \( P_0 = (p_0^1, p_0^2) \) such that \( P_0(x) \gg P(x) \) for all \( x \in \mathbb{R} \). Furthermore, if (A2)(b) is satisfied, then \( P_0(x) - P(x) \to 0 \) as \( |x| \to \infty \).
Note that (2.4) only differs from (2.5) by a spatially localized perturbation. Thus we expect that large time behaviour of the Cauchy problem (2.4) will strongly depend on the spreading properties of the unperturbed system (2.5). The following result indicates that the solution of the Cauchy problem (2.4) has a leftward spreading speed and a rightward spreading speed in large time which are exactly equal to \( c^*_+ \) and \( c^*_- \) defined in Theorem 3.9, respectively, where \( c^*_+ + c^*_- > 0 \) by Theorem 3.9.

**Theorem 4.2.** Let (H) and (A1)-(A2) hold, and assume further that \( R_0 > 1 \). Then the solution \( U(t,x) \) of the Cauchy problem (2.4) spreads to the right at the speed \( c^*_+ \) and to the left at the speed \( c^*_- \) in the sense that

1. for any \( c > c^*_+ \) and \( c' > c^*_- \), we have
   \[
   \lim_{t \to \infty} \sup_{x \geq ct} U(t,x) = 0 \quad \text{and} \quad \lim_{t \to \infty} \sup_{x \leq -c't} U(t,x) = 0;
   \]
2. for any \( c < c^*_+ \) and \( c' < c^*_- \) satisfying \( c + c' > 0 \), we have
   \[
   \lim_{t \to \infty} \sup_{x \in [c't, c't]} |U(t,x) - P_0(at)| = 0.
   \]

Coming back to the Cauchy problem (1.1)-(1.2), by (3.26), we see that Lemma 4.1 provides the limiting state towards which propagation does occur. Using standard parabolic estimates and Theorem 4.2, we have the following observations.

**Theorem 4.3.** Let (H) and (A1)-(A2) hold, and assume further that \( R_0 > 1 \). Then the solution \( (S_1, I_1, S_2, I_2) \) of (1.1)-(1.2) spreads to the right at the speed \( c^*_+ \) and to the left at the speed \( c^*_- \) in the sense that

1. for any \( c > c^*_+ \) and \( c' > c^*_- \), we have
   \[
   \lim_{t \to \infty} \sup_{x \geq ct} |S_1(t,x) - S_1^0(x)| = 0, \quad \lim_{t \to \infty} \sup_{x \geq ct} I_1(t,x) = 0,
   \]
   \[
   \lim_{t \to \infty} \sup_{x \geq ct} |S_2(t,x) - S_2^0(x)| = 0, \quad \lim_{t \to \infty} \sup_{x \geq ct} I_2(t,x) = 0
   \]
   and
   \[
   \lim_{t \to \infty} \sup_{x \leq -c't} |S_1(t,x) - S_1^0(x)| = 0, \quad \lim_{t \to \infty} \sup_{x \leq -c't} I_1(t,x) = 0,
   \]
   \[
   \lim_{t \to \infty} \sup_{x \leq -c't} |S_2(t,x) - S_2^0(x)| = 0, \quad \lim_{t \to \infty} \sup_{x \leq -c't} I_2(t,x) = 0;
   \]
2. for any \( c < c^*_+ \) and \( c' < c^*_- \) satisfying \( c + c' > 0 \), we have
   \[
   \lim_{t \to \infty} \sup_{-c't \leq \alpha \leq c} \left| S_1(t,\alpha) - S_1^0(\alpha) e^{-\beta_1(\alpha) p_1^0(\alpha) + \beta_2(\alpha) p_2^0(\alpha)} \right| = 0,
   \]
   \[
   \lim_{t \to \infty} \sup_{-c't \leq \alpha \leq c} \left| S_2(t,\alpha) - S_2^0(\alpha) e^{-\beta_1(\alpha) p_1^0(\alpha) + \beta_2(\alpha) p_2^0(\alpha)} \right| = 0,
   \]
   \[
   \lim_{t \to \infty} \sup_{-c't \leq \alpha \leq c} I_1(t,\alpha) = 0 \quad \text{and} \quad \lim_{t \to \infty} \sup_{-c't \leq \alpha \leq c} I_2(t,\alpha) = 0;
   \]
3. (Uniform persistence of the disease) The functions \( I_1 \) and \( I_2 \) satisfy
   \[
   \liminf_{t \to \infty} \sup_{x \in \mathbb{R}} I_1(t,x) > 0 \quad \text{and} \quad \liminf_{t \to \infty} \sup_{x \in \mathbb{R}} I_2(t,x) > 0.
   \]

**Theorem 4.4.** Let (H), (A1) and (A2)(a) hold. Assume further that \( R_0 < 1 \). Then the functions \( I_1 \) and \( I_2 \) satisfy

\[
\lim_{t \to \infty} I_1(t,x) = 0 \quad \text{and} \quad \lim_{t \to \infty} I_2(t,x) = 0
\]
uniformly for all \( x \in \mathbb{R} \).
Remark 4.1. Note that the initial contributions $I_0^i$ of infected populations play an important role in the steady state $P_0$ of the perturbed system (2.4) stated by Lemma 4.1. However, whether propagation occurs is determined by $R_0$ which depends on the initial susceptible numbers $S_0^i$ instead of $I_0^i$. Furthermore, from Subsection 3.3., we see that $c^*_\pm$ are accurately described by the linearization of the unperturbed system (2.5) at zero steady state. Thus, the spreading speeds $c^*_\pm$ of the initial value problem (1.1)-(1.2) are also independent on $I_0^i$, at least as long as the initial infected populations $I_0^i$ are compactly supported.

Biological interpretation: The results stated by Theorems 4.3-4.4 and Remark 4.1 suggest that the disease persistence or extinction is fully determined by $R_0$, and the initial introduction of the localized amount of infectious individuals not only causes more healthy individuals to die from the disease, but also contributes to the disease persistence. In other words, because of the lack of the supplement of new members, these species may eventually die out provided that there is no effective treatment.

The proofs of these results will closely rely on the previous discussion about the spatial dynamics for the unperturbed system (2.5), and the basic ideas are inspired by those arguments of Ducrot and Giletti in [12].

4.1. Stationary states of the perturbed system (2.4). The aim of this subsection is to prove Lemma 4.1.

Proof of Lemma 4.1. From the positivity of $\delta_1$ and $\delta_2$ (see (H)(b)), the boundedness of $I_0$ (see (A2)(a)) and (P2), there exists some vector $\hat{M} \in \mathbb{R}^2$ whose all components are positive such that

$$I_0(x) + F(x,H) \ll 0, \quad \forall x \in \mathbb{R}, \quad H \geq \hat{M}.$$  

Thus, $0$ and $\hat{M}$ are strict subsolution and supersolution of (4.1), respectively. Let us set

$$\hat{F}(x,U) := (f_1(x,u_1,u_2) + I_0^1(x), f_2(x,u_1,u_2) + I_0^2(x)), \quad \forall x \in \mathbb{R}.$$  

Then, the components of $\hat{F}$ also satisfy

$$\frac{\partial \hat{f}_i}{\partial u_j}(x,U) \geq 0, \quad i \neq j, \quad \forall x \in \mathbb{R}, \quad U \in [0,\hat{M}].$$

Furthermore, we see that $\hat{f}_i$ are locally Lipschitz continuous with respect to the last two variables and $\partial_{u_j} \hat{f}_i$ are uniformly continuous with respect to $(x,U)$ on $\mathbb{R} \times [0,\hat{M}]$. Hence, we can get the existence of a positive and bounded steady state for system (2.4) via a classical monotone iteration, denoted as $P_0 = (p_0^1, p_0^2)$.

Now, we prove that any such solutions satisfy $P_0(x) \gg P(x)$ for all $x \in \mathbb{R}$. Let us consider the solution $V = (v_1, v_2)$ of the following Cauchy problem

$$\begin{cases} 
\partial_t V = D(x)\partial_{xx}V + F(x,V), \quad t > 0, \quad x \in \mathbb{R}, \\
V(0,x) = P_0(x), \quad x \in \mathbb{R}.
\end{cases}$$  

(4.2)

Due to the nonnegativity of $I_0$, $P_0$ becomes a supersolution of (4.2). Therefore, $v_i$ is decreasing in $t$ for each fixed $x \in \mathbb{R}$ and

$$\lim_{t \to \infty} V(t,x) = V_\infty(x) \leq P_0(x), \quad \forall x \in \mathbb{R},$$
where $V_\infty$ is some steady state for system (4.2). On the other hand, from the spreading property stated by Theorem 3.5, it is clear to see that $V_\infty \geq P$. Then, we have $\inf_{\mathbb{R}} P_0 \gg 0$. Applying the statement (i) of Theorem 3.2 to (4.2), it follows that $V_\infty \equiv P \leq P_0$, i.e.

$$p_1(x) \leq p_0^0(x), \quad p_2(x) \leq p_0^0(x), \quad \forall \, x \in \mathbb{R}. \quad (4.3)$$

Further, we have

$$-d_1(x) \left( p_1^0 - p_1 \right) + \delta_1(x) \left( p_1^0 - p_1 \right) = I_1^0(x) + S_1^0(x) \left[ e^{-\left( \beta_{11}(x) p_1 + \beta_{12}(x) p_2 \right)} - e^{-\left( \beta_{11}(x) p_1^0 + \beta_{12}(x) p_2^0 \right)} \right] \geq (\neq) 0, \quad x \in \mathbb{R}.$$

From the strong maximum principle, the above inequality (4.3) is actually strict, i.e. $p_1^0(x) > p_1(x), \quad \forall \, x \in \mathbb{R}$. Similarly, we can also show that $p_2^0 > p_2$. Therefore, we obtain that $P_0(x) \gg P(x)$ for all $x \in \mathbb{R}$.

Next, it remains to prove its uniqueness. From the classical super/subsolution method of the quasimonotone systems, there exist the minimal solution $P_0 = (p_1^0, p_2^0)$ and the maximal solution $Q_0 = (q_1^0, q_2^0)$ for (4.1) which satisfy

$$P(x) \ll P_0(x) \ll Q_0(x) \ll \hat{M}, \quad \forall \, x \in \mathbb{R}. \quad (4.4)$$

Thus, it suffices to show that $P_0(x) \geq Q_0(x)$ for all $x \in \mathbb{R}$. Since $Q_0$ is bounded and $\inf_{\mathbb{R}} P_0 \geq \inf_{[0, L]} P \gg 0$, we have $\theta P_0 \gg Q_0$ for $\theta$ large enough. Therefore, we can define

$$\theta^* = \inf \{ \theta > 0 : \theta P_0(x) \gg Q_0(x), \quad \forall \, x \in \mathbb{R} \}.$$

Since $P_0$ is bounded and $\inf_{\mathbb{R}} Q_0 \geq \inf_{[0, L]} P \gg 0$, we see $\theta^* \geq 1$.

Assume now that $\theta^* > 1$. From the definition of $\theta^*$, we know that either

$$\inf_{x \in \mathbb{R}} \left( \theta^* p_1^0(x) - q_1^0(x) \right) = 0 \quad (4.5)$$

or

$$\inf_{x \in \mathbb{R}} \left( \theta^* p_2^0(x) - q_2^0(x) \right) = 0. \quad (4.6)$$

If (4.5) holds, we see that $\theta^* p_1^0(x) \geq q_1^0(x)$ for all $x \in \mathbb{R}$. Since $P = (p_1, p_2)$ is $L$-periodic and $\inf P \gg 0$, we have

$$\inf_{x \in \mathbb{R}} \left( \theta^* p_1^0(x) - p_1^0(x) \right) \geq (\theta^* - 1) \inf_{x \in [0, L]} p_1(x) > 0.$$

It then follows from the strongly subhomogeneous property (P4) of $F$ that

$$\inf_{x \in \mathbb{R}} \left[ \theta^* f_1 \left( x, p_1^0(x), p_2^0(x) \right) - f_1 \left( x, \theta^* p_1^0(x), \theta^* p_2^0(x) \right) \right] > 0,$$

that is,

$$\theta^* f_1 \left( x, p_1^0(x), p_2^0(x) \right) \geq f_1 \left( x, \theta^* p_1^0(x), \theta^* p_2^0(x) \right) + \varepsilon, \quad \forall \, x \in \mathbb{R}. \quad (4.7)$$

Besides, for any $x \in \mathbb{R}$, we have

$$d_1(x) \left( \theta^* p_1^0(x) - q_1^0(x) \right) + (\theta^* - 1) I_1^0(x) + \theta^* f_1 \left( x, p_1^0(x), p_2^0(x) \right) - f_1 \left( x, q_1^0(x), q_2^0(x) \right) = 0, \quad x \in \mathbb{R}.$$

Therefore, it follows from (4.7) that

$$d_1(x) \left( \theta^* p_1^0(x) - q_1^0(x) \right) + (\theta^* - 1) I_1^0(x) + f_1 \left( x, \theta^* p_1^0(x), \theta^* p_2^0(x) \right) - f_1 \left( x, q_1^0(x), q_2^0(x) \right) \leq -\varepsilon < 0, \quad x \in \mathbb{R}. \quad (4.8)$$
Furthermore, due to the quasimonotonicity (P3) of $F$ and the fact that $f_1$ is of class $C^1$ in $\mathbb{R} \times [0, k_1] \times [0, k_2]$ (see (P1)), we obtain
\[
\begin{align*}
&f_1 (x, \theta^* p^0_1(x), \theta^* p^0_2(x)) - f_1 (x, q^0_1(x), q^0_2(x)) \\
&= \hat{b}_1(x) (\theta^* p^0_1(x) - q^0_1(x)) + \hat{b}_2(x) (\theta^* p^0_2(x) - q^0_2(x)) \\
&\geq \hat{b}_1(x) (\theta^* p^0_1(x) - q^0_1(x)), \quad \forall x \in \mathbb{R},
\end{align*}
\]

where $\hat{b}_1$ and $\hat{b}_2$ are bounded functions in $\mathbb{R}$ and $\hat{b}_2 \geq 0$. Since $I^0_1$ is a nonnegative function and $\theta^* > 1$, it follows from (4.8) that
\[
-d_1(x) (\theta^* p^0_1(x) - q^0_1(x))'' - \hat{b}_1(x) (\theta^* p^0_1(x) - q^0_1(x)) \geq \varepsilon > 0, \quad x \in \mathbb{R}.
\]

Thus, from a strong maximum principle for strict super-solutions (see [11, Lemma 2.1]), one gets $\inf_{\mathbb{R}} (\theta^* p^0_1 - q^0_1) > 0$, which is a contradiction with our hypothesis (4.5). Similarly, if (4.6) holds, we also obtain a contradiction.

Consequently, we conclude that $\theta^* = 1$, i.e. $P_0 \geq Q_0$. One has shown the uniqueness.

Finally, let us show $P_0(x) \to P(x)$ as $|x| \to \infty$ under further assumption (A2)(b).

Assume contradiction that there exist some $\varepsilon_0 > 0$ and a sequence $\{x_n\} \in \mathbb{R}$ satisfying $|x_n| \to \infty$ as $n \to \infty$ such that $P_0(x_n) - P(x_n) \geq \varepsilon_0$ for any $n \in \mathbb{N}$. Set $x_n = l_n L + \pi_n$, where $l_n \in \mathbb{Z}$ and $\{\pi_n\} \subset [0, L]$. Then, up to the extraction of some subsequence, one can assume that there exists $\pi_{\infty} \in [0, L]$ such that $\pi_n \to \pi_{\infty}$ as $n \to \infty$. Define $P^0_n(x) = P_0(x + l_n L)$, $\forall x \in \mathbb{R}$, $n \in \mathbb{N}$. From standard elliptic estimates, one gets that up to the extraction of some subsequence, $P^0_n$ converges in $C^2_c(\mathbb{R})$ to a nonnegative and bounded function $P_{\infty}$ as $n \to \infty$. Since $I_0$ is compactly supported and $P_0(x) > P(x)$ for any $x \in \mathbb{R}$, then by the periodicity of $D$ and $F$, we further obtain that $P_{\infty}$ satisfies
\[
D(x)P_{\infty}'' + F(x, P_{\infty}) = 0, \quad x \in \mathbb{R}
\]

and $P_{\infty}(x) \geq P(x)$ for any $x \in \mathbb{R}$. Consequently, it follows from the uniqueness of a positive and bounded steady state of (2.5) that $P_{\infty} \equiv P$ in $\mathbb{R}$. On the other hand, it follows from the inequality $P_0(x_n) - P(x_n) \geq \varepsilon_0 > 0$ for any $n \in \mathbb{N}$ that $P_{\infty}(\pi_{\infty}) - P(\pi_{\infty}) \geq \varepsilon_0 > 0$, whence a contradiction has been achieved. This ends the proof of Lemma 4.1. \hfill \Box

4.2. **Spreading speed of the perturbed system (2.4).** This subsection is devoted to the proof of spreading speed for system (2.4). We split the arguments into two parts.

**Proof of Theorem 4.2.** (1) Outer spreading speed. For any given $c > c^*_+, c_0 \in (c^*_+, c)$. From the definition of $c^*_+$ (see Remark 3.4), there exists some $\mu > 0$ such that $\Lambda_{c_0}(\mu) = 0$. Thus, by (3.22), one gets
\[
\lambda(\mu) - c_0 \mu = 0. \tag{4.9}
\]

Let us define the following vector-valued function
\[
\hat{U}(t, x) = \begin{pmatrix} \hat{u}_1(t, x), \hat{u}_2(t, x) \end{pmatrix} = e^{-\mu(x-c_0t)} \left( \phi^\mu_1(x), \phi^\mu_2(x) \right),
\]

where $\phi^\mu = \begin{pmatrix} \phi^\mu_1, \phi^\mu_2 \end{pmatrix} \gg 0$ is the principal eigenfunction of (3.13) corresponding to the principal eigenvalue $\lambda(\mu)$. From the property (P5) of $F$ and (4.9), we can easily check that $\hat{U}$ is a supersolution of (2.5). Moreover, since $I_0$ is compactly
supported, we can choose some vector $\mathbf{K} = (K_1, K_2) \gg \phi^\mu$ sufficiently large such that $U = (\pi_1, \pi_2)$ defined by

$$\pi_i(t, x) := \inf \left\{ p_i^0(x), K_i e^{-\mu(x-ct)} \right\}, \forall t > 0, x \in \mathbb{R}$$

is a supersolution of (2.4). Note that $P_0 = (p_1^0, p_2^0)$ is the unique steady state of (2.4). From the proof of Lemma 4.1, we see that the parabolic comparison principle is still valid for system (2.4). Therefore, it follows that the solution $U = (u_1, u_2)$ of the Cauchy problem (2.4) satisfies

$$U(t, x) \leq (K_1, K_2) e^{-\mu(x-ct)}, \forall t > 0, x \in \mathbb{R}. \quad (4.10)$$

With $\tau \geq c$ and $x = \tau t$, one gets $x \geq ct > c_0 t$. Passing to the limit $t \to \infty$ on both sides of (4.10), we obtain

$$\lim_{t \to \infty} \sup_{x \geq ct} U(t, x) = 0.$$ 

Similarly, we can also obtain the desired limit for any $c' > c^*_\star$.

(2) Inner spreading speed. Let us recall that

$$\partial_t u_i(t, x) = I_i(t, x) > 0, \forall t > 0, x \in \mathbb{R}, i = 1, 2$$

and $\partial_t u_i(t, x) = I_i(t, x) \to 0$ as $t \to +\infty$. Moreover, it follows from the comparison principle that

$$U(t, x) = (u_1(t, x), u_2(t, x)) \leq P_0(x), \forall t > 0, x \in \mathbb{R}.$$ 

Thus, it is clear that $U$ converges locally uniformly to a positive steady state of (2.4). By Lemma 4.1, the uniqueness of a positive steady state for system (2.4) implies that this limit is equals to $P_0$, that is, $U$ converges locally uniformly to $P_0$ as $t \to \infty$.

Next, let us consider a moving frame with speed $-c^*_\star < -c' < c < c^*_\star$. We will prove that the solution $U(t, ct)$ of the Cauchy problem (2.4) converges to $P(ct)$ as $t \to \infty$. For this purpose, we first consider the following Cauchy problem

$$\begin{cases}
\partial_t U = D(x) \partial_x U + F(x, U), & t > 0, x \in \mathbb{R}, \\
U(0, x) = U(1, x), & x \in \mathbb{R}.
\end{cases}$$

From the comparison principle, we obtain

$$\overline{U}(t, ct) \leq U(t + 1, ct) \leq P_0(ct), \forall t \geq 0. \quad (4.11)$$

Note that due to the nonnegativity of $I_0$ and the diffusion, we have $U(1, x) \gg 0$. Therefore, it follows from the statement (ii) of Theorem 3.5 that $\overline{U}$ spreads asymptotically to the right and left at least with the speeds $c^*_\star$ and $c^*_\star$, so that for any $-c^*_\star < -c' < c < c^*_\star$,

$$\lim_{t \to \infty, -c't \leq x \leq ct} |\overline{U}(t, x) - P(x)| = 0.$$ 

Besides, from Lemma 4.1, we see that $\limsup_{|x| \to \infty} |P_0(x) - P(x)| = 0$. It then follows that for any $c < c^*_\star$,

$$\lim_{t \to +\infty} |U(t, ct) - P(ct)| = 0. \quad (4.12)$$

Now, let $\varepsilon > 0$ small enough be given. Since $U$ converges locally uniformly to $P_0$ as $t \to \infty$ and thanks to assumption (A2), we can choose some $T > 0$ sufficiently large and some $D > 0$ large enough such that

$$|U(t, x) - P_0(x)| \leq \varepsilon, \forall |x| \leq D, t \geq T.$$
that locally bounded in $W$ uniform persistence of the disease. Theorem 4.2. Hence, it suffices to show that the statement (iii) holds, namely $0$ and a sequence $\varepsilon > 0$ as $k \rightarrow \infty$ such that
\[ |P_0(x) - P(x)| \leq \varepsilon, \forall |x| \geq D. \]
Consequently, by (4.11) and (4.12), it readily follows that for any $c < c^*_+$,
\[ \lim_{t \rightarrow \infty} \sup_{\alpha \leq c} |U(t, \alpha t) - P_0(\alpha t)| \leq \varepsilon. \]
Similarly, for any $c' > c^*_+$, we can get the desired limit for any $\alpha \geq -c'$. This ends the proof of Theorem 4.2. \hfill \Box

4.3. Spreading speed of system (1.1)-(1.2). This subsection is concerned with the proofs of Theorem 4.3 and Theorem 4.4.

Proof of Theorem 4.3. Due to (3.26) and using the fact that the functions $u_i$ are locally bounded in $W^{2,p}$ for any $p \geq 1$, thus the convergence to any $\omega$-limit must hold in $C^{1,\gamma}$ for $0 \leq \gamma \leq 1$, we easily deduce the statements (i) and (ii) from Theorem 4.2. Hence, it suffices to show that the statement (iii) holds, namely uniform persistence of the disease.

Assume by contradiction that there exists a sequence $t_k \rightarrow \infty$ as $k \rightarrow \infty$ such that
\[ \lim_{k \rightarrow \infty} \sup_{x \in \mathbb{R}} I_1(t_k, x) = 0 \quad \text{and} \quad \lim_{k \rightarrow \infty} \sup_{x \in \mathbb{R}} I_2(t_k, x) = 0. \tag{4.13} \]
Therefore, from the spreading property stated by Theorem 3.5, there exist some $\varepsilon > 0$ and a sequence $r_k \rightarrow \infty$ as $k \rightarrow \infty$ such that
\[ \varepsilon I \ll U(t_k, r_k) \ll \inf_{x \in \mathbb{R}} P(x) - \varepsilon I, \forall k \geq 0. \tag{4.14} \]
Without loss of generality, we can write $r_k = n_k L + s_k$ where $n_k$ is an integer and the sequence $s_k \in (0, L)$ converges to $s_\infty$ (up to extraction of some subsequence). Now, let us consider the sequence $U_k(x) = U(t_k, x + n_k L)$. Its components $u_{ik}$ satisfy
\[
\begin{cases}
I_1(t_k, x + n_k L) = d_1(x) \partial_{xx} u_{1k} + f_1(x, u_{1k}, u_{2k}), & \forall x \in \mathbb{R}, \\
I_2(t_k, x + n_k L) = d_2(x) \partial_{xx} u_{1k} + f_2(x, u_{1k}, u_{2k}), & \forall x \in \mathbb{R}.
\end{cases}
\tag{4.15}
\]
From standard elliptic $L^p$-estimates, $u_{ik}$ is bounded in $W^{2,p}_{loc}(\mathbb{R})$ for all $1 < p < \infty$, $i = 1, 2$. Thus, due to the fact that $W^{2,p}_{loc}(\mathbb{R})$ ($1 < p < \infty$) is a reflexive Banach space, we can assume that $u_{ik}$ converges to some function $u_{i\infty}$ weakly in $W^{2,p}_{loc}(\mathbb{R})$ for all $1 < p < \infty$. Further, the compact imbedding
\[ W^{2,p}_{loc}(\mathbb{R}) \hookrightarrow C^{1,\theta}_{loc}(\mathbb{R}), \quad 0 < \theta \leq 1 - \frac{1}{p} \]
indicates that $u_{ik}$ converges to $u_{i\infty}$ strongly in $C^{1,\theta}_{loc}(\mathbb{R})$ for all $0 \leq \theta < 1$. It then follows from (4.14) that
\[ \varepsilon I \ll U_{\infty}(s_\infty) \ll P(s_\infty) - \varepsilon I. \tag{4.16} \]
Passing to the limit $k \rightarrow \infty$ on both sides of two equations of (4.15), thanks to (4.13), (4.16) and the fact that $I_0 = (I_1^0, I_2^0)$ is compactly supported, it then follows that the function $U_\infty$ satisfies
\[ 0 = D(x) \partial_{xx} U_\infty + F(x, U_\infty), \quad U_\infty(0) \in \left(0, \inf_{x \in \mathbb{R}} P(x)\right). \]
However, Theorem 3.2 asserts that $P$ is the unique positive solution of the above equation, whence a contradiction has been achieved.

Proof of Theorem 4.4. From the first and third equations of (1.1), we can easily check that $S_i(t,x) \leq S_0^i(x)$ for any $(t,x) \in \mathbb{R}_+ \times \mathbb{R}$, $i = 1, 2$. It then follows that

\[
\begin{cases}
\partial_t I_1 \leq d_1(x) \partial_{xx} I_1 + \beta_{11}(x) S_1^0(x) I_1 + \beta_{12}(x) S_0^i(x) I_2 - \delta_1(x) I_1, & t > 0, \ x \in \mathbb{R}, \\
\partial_t I_2 \leq d_2(x) \partial_{xx} I_2 + \beta_{21}(x) S_2^0(x) I_1 + \beta_{22}(x) S_0^i(x) I_2 - \delta_2(x) I_2, & t > 0, \ x \in \mathbb{R}.
\end{cases}
\]

(4.17)

Suppose now that $\mathcal{R}_0 < 1$. By Lemma 3.1, we see that $\lambda_0 > 0$ and the corresponding eigenfunction $\phi_0 = (\phi_0^1, \phi_0^2)$ is $L$-periodic and strongly positive in $\mathbb{R}$. We normalize $\phi_0$ such that $\|\phi_0\|_{\infty} = 1$. Next, let us consider the following linear system

\[
\begin{cases}
\partial_t v_1 = d_1(x) \partial_{xx} v_1 + \beta_{11}(x) S_1^0(x) v_1 + \beta_{12}(x) S_0^i(x) v_2 - \delta_1(x) v_1, & t > 0, \ x \in \mathbb{R}, \\
\partial_t v_2 = d_2(x) \partial_{xx} v_2 + \beta_{21}(x) S_2^0(x) v_1 + \beta_{22}(x) S_0^i(x) v_2 - \delta_2(x) v_2, & t > 0, \ x \in \mathbb{R}, \\
v_1(0,x) = \|I_1^0\|_{\infty} \phi_0^1(x), \ v_2(0,x) = \|I_2^0\|_{\infty} \phi_0^2(x), & x \in \mathbb{R}.
\end{cases}
\]

(4.18)

It is not hard to check that (4.18) admits a solution

\[
(v_1(t,x), v_2(t,x)) = (\|I_1^0\|_{\infty} e^{-\lambda_0^i t} \phi_0^1(x), \|I_2^0\|_{\infty} e^{-\lambda_0^i t} \phi_0^2(x)).
\]

Due to the periodicity conditions and $\|\phi_0\|_{\infty} = 1$, we have $v_i(t,x) \leq \|I_i^0\|_{\infty} e^{-\lambda_0^i t}$ for any $t \geq 0$ and $x \in \mathbb{R}$. Therefore, by (4.17), we can readily verify that for any $S_i \leq S_0^i$, $\overline{T}_i(t,x) = \|I_i^0\|_{\infty} e^{-\lambda_0^i t}$ is a supersolution for the Eq.(1.1) satisfied by $I_i$, $i = 1, 2$. Since $I_i^0$ are nonnegative and bounded, then we have

\[
\lim_{t \to \infty} (I_1(t,x), I_2(t,x)) \leq \lim_{t \to \infty} (\overline{T}_1(t,x), \overline{T}_2(t,x)) = 0
\]

uniformly for all $x \in \mathbb{R}$. This ends the proof of Theorem 4.4.

5. Discussion. Our results describe in detail the propagation phenomena for the criss-cross infection model with non-diffusive susceptible population (1.1)-(1.2). On the one hand, we have captured the complete information about the existence and non-existence of pulsating travelling waves of model (1.1) in Corollary 3.12 in terms of $\mathcal{R}_0$. On the other hand, the spreading speed of the Cauchy problem (1.1)-(1.2) has also been obtained in Theorem 4.3. To be specific, we have proved that the infected populations have some pulse-like asymptotic shape and there are only two possible outcomes: either the disease dies out when $\mathcal{R}_0 < 1$, or if $\mathcal{R}_0 > 1$ and the initial infected populations $I_i^0$ are compactly supported, then the disease spreads in two directions with different speeds $c_{i+}$ and $c_{i-}$, which coincide with the minimal speeds of the leftward pulsating travelling wave and the rightward one. Such a dichotomy implies that this threshold $\mathcal{R}_0 > 1$ is almost optimal for spreading to occur.

Besides, we have obtained two equivalent characterizations of $c_{i+}$ in Theorem 3.9 and Remark 3.21, together with a mathematical approach (3.5) to calculate $\mathcal{R}_0$. It is worth pointing out that $\mathcal{R}_0$ and $c_{i\pm}$ depend on all coefficients of (1.1) and the initial density of susceptible populations, but not on the initial density of infected populations. Furthermore, the higher infection rates between sub-groups and the more susceptible individuals will lead to the disease to overspread faster.

Because of space constraints, the impact of various factors on $\mathcal{R}_0$ and $c_{i\pm}$ is not exhaustively analyzed in the current paper. Those formulae given by (3.16), (3.21) and (3.5) will be exploited in the future work to elaborate the dependence
of $\mathcal{R}_0$ and $c^*_{\pm}$ on the model ingredients, in particular on the criss-cross mechanism, diffusion rates and spatially periodic heterogeneity. Mathematically, it amounts to investigate the various properties of the principal eigenvalue for a fully coupled elliptic system, such as its monotonicity and asymptotic behaviour with respect to some parameters.

Let us mention the difficulties encountered in these issues. For those models with simple structures, $\mathcal{R}_0$ can be accurately formulated via the Rayleigh formula of the principal eigenvalue for a single equation [2]. However, $\mathcal{R}_0$ of model (1.1) is related to the principal eigenvalue of an elliptic system and hard to visualize, which makes it more difficult to explore the impact of spatial heterogeneity and the large or small diffusions. As for $c^*_{\pm}$, those dependence results between the spreading speed and the coefficients of a periodic Fisher-KPP equation in [7, 10, 30, 29] can be extended to the single-group model (1.3), but not directly to our framework. A serious obstacle towards this extension is the fully coupled interaction between components of system (3.13), namely the irreducibility of system (2.5). Another difficulty is that the nonlinearity of (2.5) changes sign, which hinders the use of a well-known comparison theorem for principal eigenvalues in [22] when we study the effect of the amplitude of the reaction term on $c^*_{\pm}$.

On the other hand, the result of the spreading speed for (1.1)-(1.2), that is stated by part (ii) of Theorem 4.3, only depicts what happens between $-c^t$ and $ct$ for any $c^t < c^*_{\pm}$ and $c < c^*_{\pm}$. For the single-group model, Ducrot and Giletti have exhibited a more detailed description for the asymptotic behaviour in the one dimensional setting (see [12, Theorem 1.7]), where the convergence of the profile of the solutions of (1.3) to that of the pulsating travelling wave with minimal speed was proved. It is natural to ask whether such observations can be extended to our framework. But in fact it is not an easy task. This is because the realization of their result strongly relies on the generalization of a classical result, namely the solution of a KPP type equation in the spatially periodic environment, associated with some fast decaying initial data, converges to the profile of the pulsating travelling wave with minimal speed (see [18, Theorem 1.3]). Unfortunately, such a stronger link between spreading speed and pulsating wave has not yet been established for the unperturbed system (2.5) similar to a scalar KPP type equation. This problem is very challenging but essential in the propagation dynamics of reaction-diffusion equations. Thus, we leave it as a future work in order to give a more complete picture of the large time behaviour for the Cauchy Problem (1.1)-(1.2).

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