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Spreading speeds and traveling wave solutions of diffusive vector-borne disease models without monotonicity

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Vector-borne diseases, such as chikungunya, dengue, malaria, West Nile virus, yellow fever and Zika, pose a major global public health problem worldwide. In this paper we investigate the propagation dynamics of diffusive vector-borne disease models in the whole space, which characterize the spatial expansion of the infected hosts and infected vectors. Due to the lack of monotonicity, the comparison principle cannot be applied directly to this system. We determine the spreading speed and minimal wave speed when the basic reproduction number of the corresponding kinetic system is larger than one. The spreading speed is mainly estimated by the uniform persistence argument and generalized principal eigenvalue. We also show that solutions converge locally uniformly to the positive equilibrium by employing two auxiliary monotone systems. Moreover, it is proven that the spreading speed is the minimal wave speed of travelling wave solutions. In particular, the uniqueness and monotonicity of travelling waves are obtained. When the basic reproduction number of the corresponding kinetic system is not larger than one, it is shown that solutions approach to the disease-free equilibrium uniformly and there is no travelling wave solutions. Finally, numerical simulations are presented to illustrate the analytical

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1. Introduction

Vector-borne diseases, such as chikungunya, dengue, malaria, West Nile virus, yellow fever and Zika, posed a major global public health problem worldwide. For instance, dengue is endemic in more than 100 countries with 100–400 million infections occur yearly (WHO [55]). In 2014–2015, an outbreak of chikungunya

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originating on the Indian Ocean islands spread, via viremic travelers, to the Americas with a total of 1,071,696 and 635,955 suspected cases (including 169 and 82 deaths) in 2014 and 2015, respectively (PAHO [39]). In 2013–2014, a large-scale Zika outbreak was reported in Pacific islands and spread to Brazil and other countries and territories in the Americas, including the United States, with a total of 515,348 suspected cases in 2015–2016 (PAHO [40]).

For many vector-borne diseases, mosquitoes are the vectors. For example, Aedes mosquitoes are the primary vectors for transmitting chikungunya, dengue and Zika viruses (Gao et al. [18], WHO [56]). In modern time, humans travel more frequently on scales from local to global. Such movements can spread disease pathogens over long distances and can threaten public health (Lounibos [31]). It has been observed that human movement is essential for the spread of vector-borne diseases (Stoddard et al. [46, 47]). Thus, it is crucial to consider the influence of host and vector movements on the transmission dynamics and spatial spread of vector-borne diseases.

Reaction-diffusion equations have been frequently used to model the spreading of some vector-borne diseases, see Favier et al. [14], Fitzgibbon et al. [17], Lewis et al. [24], Wang and Zhao [49], and the reviews by Fitzgibbon and Langlais [15] and Ruan and Wu [43]. In order to provide a qualitative description of the Zika outbreak in Rio de Janeiro in 2015–2016, Fitzgibbon et al. [16] proposed and investigated the following vector-borne epidemic model with spatial dependence:

$$\begin{cases} \partial_t V_s = \nabla \cdot (d_1(x)\nabla V_s) + (V_s + V_i)[\beta(x) - \mu(x)V_s] - \sigma_1(x)H_iV_s, & x \in \Omega, \ t > 0, \\ \partial_t V_i = \nabla \cdot (d_1(x)\nabla V_i) + \sigma_1(x)H_iV_s - \mu(x)(V_s + V_i)V_i, & x \in \Omega, \ t > 0, \\ \partial_t H_i = \nabla \cdot (d_2(x)\nabla H_i) + \sigma_2(x)H_s(x)V_i - \rho(x)H_i, & x \in \Omega, \ t > 0 \end{cases}$$

$$(1.1)$$

with homogeneous Neumann boundary conditions and initial conditions

$$\begin{cases} \frac{\partial}{\partial \mathbf{n}} V_s(x,t) = \frac{\partial}{\partial \mathbf{n}} V_i(x,t) = \frac{\partial}{\partial \mathbf{n}} H_i(x,t) = 0, & x \in \partial \Omega, \ t > 0, \\ V_s(x,0) = V_{s,0}(x), \ V_i(x,0) = V_{i,0}(x), \ H_i(x,0) = H_{i,0}(x), & x \in \Omega, \end{cases}$$

where $\Omega \subset \mathbb{R}^2$ is a smooth, bounded domain, and \mathbf{n} is the outer normal vector, $V_s(x,t), V_i(x,t)$ and $H_i(x,t)$ represent the densities of uninfected vectors, infected vectors and infected hosts in location x and at time t, respectively, $H_s(x)$ is the density of uninfected hosts, $\beta(x)$ formulates the breeding rate of vectors, $\mu(x)$ is the loss rate of vectors due to the environmental crowding, $\rho(x)$ denotes the loss rate of infected hosts, $\sigma_1(x)$ and $\sigma_2(x)$ are the transmission rates of uninfected vectors and uninfected hosts, respectively, $d_1(x)$ and $d_2(x)$ reflect the diffusion rates of vectors and infected hosts, respectively.

The simulation results in [16] indicate that the location and magnitude of local outbreaks of the epidemic at the beginning of the season can have significant impact on the spatial development and final size at the end of the season. Recently, there has been further investigation on reaction-diffusion model (1.1). Magal et al. [33, 34] considered the global dynamics of solutions, redefined and investigated the basic reproduction number for this spatial epidemic model. When all parameters in (1.1)

are positive constants, Cai et al. [5] studied global stability of the positive equilibrium. Recently, Li and Zhao [26] studied the global dynamics of a modified model of (1.1) by including the effect of seasonality.

Based on the extinction or persistence of vector-borne diseases formulated in [5, 16, 33, 34], we plan to explore how fast the infected vectors and hosts expand when they are locally introduced into the whole space occupied by uninfected vectors. For this purpose, we first consider the asymptotic spreading of the following rescaled Cauchy problem as all parameters of (1.1) are spatially homogeneous

$$\begin{cases} \partial_{t}V_{s} = \partial_{xx}V_{s} + \beta(V_{s} + V_{i}) - \mu(V_{s} + V_{i})V_{s} - \sigma_{1}H_{i}V_{s}, & x \in \mathbb{R}, \ t > 0, \\ \partial_{t}V_{i} = \partial_{xx}V_{i} + \sigma_{1}H_{i}V_{s} - \mu(V_{s} + V_{i})V_{i}, & x \in \mathbb{R}, \ t > 0, \\ \partial_{t}H_{i} = d\partial_{xx}H_{i} + \sigma_{2}H_{s}V_{i} - \rho H_{i}, & x \in \mathbb{R}, \ t > 0, \\ V_{s}(x, 0) = V_{s,0}(x) = \frac{\beta}{\mu}, \ V_{i}(x, 0) = V_{i,0}(x), \ H_{i}(x, 0) = H_{i,0}(x), & x \in \mathbb{R}, \end{cases}$$

$$(1.2)$$

in which parameters and initial conditions satisfy the following hypotheses

- (H1) d, σ_1 , σ_2 , ρ , β , μ , H_s are positive constants;
- (H2) $V_{i,0}(x)$, $H_{i,0}(x)$ are nonnegative, bounded, continuous functions, and $V_{i,0}(x) + H_{i,0}(x)$ admits nonempty compact support in $x \in \mathbb{R}$.

We then study the existence and nonexistence of travelling wave solutions. Here, a travelling wave solution is a special entire positive solution taking the form

$$V_s(x,t) = \phi(\xi), \quad V_i(x,t) = \varphi(\xi), \ H_i(x,t) = \psi(\xi), \ \xi = x + ct,$$

in which c is the wave speed while ϕ, φ, ψ are wave profiles. By the definition, c and (ϕ, φ, ψ) must satisfy the following wave profile system

$$\begin{cases}
c\phi'(\xi) = \phi''(\xi) + [\phi(\xi) + \varphi(\xi)][\beta - \mu\phi(\xi)] - \sigma_1\phi(\xi)\psi(\xi), \\
c\varphi'(\xi) = \varphi''(\xi) + \sigma_1\phi(\xi)\psi(\xi) - \mu\varphi(\xi)[\phi(\xi) + \varphi(\xi)], \\
c\psi'(\xi) = d\psi''(\xi) + \sigma_2H_s\varphi(\xi) - \rho\psi(\xi)
\end{cases} (1.3)$$

for $\xi \in \mathbb{R}$. Due to the biological background, the wave profile also satisfies

$$\begin{cases} \lim_{\xi \to -\infty} \phi(\xi) = \frac{\beta}{\mu}, & \lim_{\xi \to -\infty} \varphi(\xi) = \lim_{\xi \to -\infty} \psi(\xi) = 0, \\ \lim\inf_{\xi \to +\infty} \phi(\xi) > 0, & \liminf_{\xi \to +\infty} \varphi(\xi) > 0, & \liminf_{\xi \to +\infty} \psi(\xi) > 0. \end{cases}$$
(1.4)

In this paper, we answer the above questions by estimating the speed at which the hosts and vectors expand spatially by the asymptotic speed of spreading (for short, the spreading speed) and the minimal wave speed of travelling wave solutions. For monotone semiflows, these two propagation thresholds have been widely studied in different parabolic type equations or systems [1, 2, 4, 27, 28, 32, 51, 52, 54]. Moreover, these two propagation thresholds of nonmonotone systems that can be controlled by two monotone systems admitting the same propagation threshold have been investigated in [21, 25, 48, 53, 62].

Modeling the spatial propagation of infectious diseases by spreading speed and travelling wave solutions is an important topic in mathematical epidemiology [37, 41, 44, 64]. When the travelling wave solutions of epidemic models are concerned, there are many important and classical results, and we may refer to some monographs including [37, 41, 44, 64]. For the spreading speed of non-cooperative epidemic models, Ducrot [9] obtained the speed by using the idea of uniform persistence for a classical epidemic model, Lin et al. [30] established the speed of a delayed epidemic model. Ducrot and his co-authors [8, 10, 11] studied the spreading speed of several predator-prey reaction-diffusion systems, Lin et al. [29] investigated the spreading speed in an integrodifference predator-prey system without comparison principle. We also refer to [6, 19, 36, 38, 58] and references therein for other non-cooperative systems.

Evidently, (1.2) is not even quasi-monotone, which leads to the lack of comparison principle for this system and the above results do not work directly to this system. To estimate the propagation threshold, we use the idea in Ducrot [9] to obtain the lower bound of the spreading speed. During this process, we further study the principal eigenvalue problem of a weakly coupled elliptic system in a bounded domain by applying the corresponding generalized principal eigenvalue problem in the whole space [19]. In addition, we introduce a limiting system to estimate the principal eigenvalue and then achieve our desired results by taking a limiting procedure. Furthermore, we construct two auxiliary monotone systems and apply the theory of monotone dynamical systems to prove the convergence to the positive equilibrium. Finally, we find the spreading speed is the minimal wave speed of travelling wave solutions or the threshold such that (1.3)–(1.4) has a positive solution. As a by-product, we obtain the monotonicity and uniqueness in the sense of phase shift of positive solutions to (1.3)–(1.4).

The rest of this paper is organized as follows. We start in $\S 2$ with some preliminaries and our main results. Section 3 is devoted to estimating the upper and lower bounds of the spreading speed. In $\S 4$, we obtain the convergence of solutions. The minimal wave speed of travelling wave solutions is investigated in $\S 5$. We give some numerical simulations in $\S 6$ and present a discussion in $\S 7$.

2. Preliminaries and main results

Before stating the main results of this paper, we give some preliminaries as follows. A matrix $\mathbf{A} = (a_{i,j})_{n \times n}$ is essentially nonnegative if $\mathbf{A} - \min_{1 \leq i \leq n} (a_{i,i}) \mathbf{I}_n$ is nonnegative, where \mathbf{I}_n is the $n \times n$ identity matrix. Let the Banach space

$$X := BUC(\mathbb{R}, \mathbb{R}^3)$$

denote the space of all bounded and uniformly continuous functions from \mathbb{R} into \mathbb{R}^3 , which is equipped with the usual supremum norm $\|\cdot\|_X$.

Let $m:=\max\{\sup_{x\in\mathbb{R}}V_{i,0}(x),\sup_{x\in\mathbb{R}}H_{i,0}(x)\}>0$ be given. Define the set of initial data $Y\subset X$ as

$$Y = \{ (V_{s,0}, V_{i,0}, H_{i,0}) \in X \mid V_{s,0} = \beta/\mu, \quad 0 \leqslant V_{i,0}, H_{i,0} \leqslant m, \ V_{i,0}, H_{i,0} \not\equiv 0 \}.$$

We first recall a convergence result of the scalar Fisher-KPP equation [45, 61].

Lemma 2.1. Consider the Fisher-KPP equation

$$\begin{cases}
\partial_t v = \partial_{xx} v + v(\beta - \mu v), & x \in \mathbb{R}, \ t > 0, \\
v(x,0) = v_0(x), & x \in \mathbb{R},
\end{cases}$$
(2.1)

where β , $\mu > 0$ are constants and $v_0(x) \ge 0$ is a bounded, continuous function satisfying $\liminf_{|x| \to \infty} v_0(x) > 0$. Then

$$\lim_{t \to \infty} v(x,t) = \frac{\beta}{\mu} \quad uniformly \ in \ x \in \mathbb{R}.$$

Moreover, assume that $v(x,t) = \zeta(x+ct)$ is a positive bounded travelling wave solution of (2.1) such that

$$\liminf_{\xi \to -\infty} \zeta(\xi) > 0, \quad \liminf_{\xi \to +\infty} \zeta(\xi) > 0,$$

then $\zeta(\xi) = \frac{\beta}{\mu}, \ \xi \in \mathbb{R}$.

Applying lemma 2.1 to the equation of $V_s + V_i$, we obtain the following boundedness result.

LEMMA 2.2. For any initial data $(V_{s,0}, V_{i,0}, H_{i,0}) \in Y$, system (1.2) admits a globally classical, positive and bounded solution; i.e. there exists a constant M > 0 independent of (x,t) such that

$$||(V_s, V_i, H_i)(\cdot, t; V_{s,0}, V_{i,0}, H_{i,0})||_X \le M, \quad t \in [0, \infty).$$

Proof. The local existence of (1.2) is evident. For any given $A \geqslant \frac{\beta}{\mu}$, we define B, C > 0 by

$$\sigma_1 AC = \mu B^2, \quad \sigma_2 H_s B = \rho C.$$

Clearly, $A \to \infty$ implies that $B \to \infty, C \to \infty$. Then (0,0,0) and (A,B,C) are a pair of generalized upper-lower solutions of (1.2) by selecting $A \ge \beta/\mu$ large enough such that the initial condition holds. Then there exists a constant M(m) > 0 such that $0 \le V_s, V_i, H_i \le M$ and the main result is clear.

Moreover, we show further bounds of solutions. For given m > 0, adding the V_s -equation to the V_i -equation implies that $V_s + V_i$ satisfies

$$\begin{cases} \partial_t (V_s + V_i) = \partial_{xx} (V_s + V_i) + (V_s + V_i) [\beta - \mu(V_s + V_i)], & x \in \mathbb{R}, t > 0, \\ \frac{\beta}{\mu} \leqslant (V_{s,0} + V_{i,0})(x) \leqslant \frac{\beta}{\mu} + m, & x \in \mathbb{R}. \end{cases}$$

Lemma 2.1 ensures that

$$\lim_{t \to \infty} (V_s + V_i)(x, t) = \frac{\beta}{\mu} \text{ uniformly in } x \in \mathbb{R},$$
 (2.2)

$$\frac{\beta}{\mu} \leqslant (V_s + V_i)(x, t) \leqslant \frac{\beta}{\mu} + m \quad \text{for all } (x, t) \in \mathbb{R} \times [0, \infty).$$
 (2.3)

From the V_s -equation, we also have

$$0 \leqslant V_s(x,t) \leqslant \frac{\beta}{\mu} \quad \text{for all } (x,t) \in \mathbb{R} \times [0,\infty).$$
 (2.4)

The proof is complete.

Based on the boundedness of solutions and the standard estimates in [23], we have the following uniform estimates:

LEMMA 2.3. Assume that (V_s, V_i, H_i) is the solution of (1.2) satisfying $|V_s|$, $|V_i|$, $|H_i| \leq M_0$ for some constant $M_0 > 0$. Then there exists a constant $M_1 > 0$ such that

$$|\partial_t u(x,t)|, |\partial_x u(x,t)|, |\partial_{tt} u(x,t)|, |\partial_{xx} u(x,t)|, |\partial_{xxx} u(x,t)| \leq M_1,$$

where $u \in \{V_s, V_i, H_i\}, x \in \mathbb{R}, t \geqslant 1$.

In the corresponding kinetic system of (1.2), the threshold

$$\mathcal{R}_0 = \frac{H_s \sigma_1 \sigma_2}{\rho \mu}$$

is called the basic reproduction number [16, 33]. If $\mathcal{R}_0 \leq 1$, then there exists a disease-free equilibrium $E_1 = (\beta/\mu, 0, 0)$. When $\mathcal{R}_0 > 1$, it also admits a positive equilibrium [16, 33]

$$E^* = (V_s^*, V_i^*, H_i^*) = \left(\frac{\beta}{\mu \mathcal{R}_0}, \frac{\beta(\mathcal{R}_0 - 1)}{\mu \mathcal{R}_0}, \frac{\beta(\mathcal{R}_0 - 1)}{\sigma_1}\right).$$

To state our conclusion, we consider the following cooperative system

$$\begin{cases}
\partial_t v_i = \partial_{xx} v_i + \sigma_1 h_i \left(\frac{\beta}{\mu} - v_i\right) - \beta v_i, & x \in \mathbb{R}, \ t > 0, \\
\partial_t h_i = d\partial_{xx} h_i + \sigma_2 H_s v_i - \rho h_i, & x \in \mathbb{R}, \ t > 0, \\
(v_i, h_i)(x, 0) = (\psi_1, \psi_2)(x) := \Psi, & x \in \mathbb{R},
\end{cases} \tag{2.5}$$

where $\psi_i(i=1,2)$ are bounded, uniformly continuous functions, and $0 \le \psi_1 \le V_i^*$, $0 \le \psi_2 \le H_i^*$. Note that (2.5) is a cooperative, irreducible system such that it generates a monotone semiflow. Thus the result in Liang and Zhao [28] implies that (2.5) has the following propagation properties.

LEMMA 2.4. If $\mathcal{R}_0 > 1$, then there is a constant $c^* > 0$ that is the spreading speed and minimal wave speed of (2.5) in the following sense:

(i) Spreading speed: if $v_i(x,0) + h_i(x,0)$ admits nonempty compact support, then

$$\limsup_{t\to\infty} \sup_{|x|\geqslant ct} \left[v_i(x,t) + h_i(x,t) \right] = 0 \quad \text{for any } c > c^*,$$

$$\limsup_{t \to \infty} \sup_{|x| \le ct} (|v_i(x,t) - V_i^*| + |h_i(x,t) - H_i^*|) = 0 \quad \text{for any } 0 < c < c^*,$$

(ii) Minimal wave speed: (2.5) admits a monotone travelling wave solution $(\widetilde{\varphi}, \widetilde{\psi})(\xi)$ with $\xi = x + ct$, c > 0, connecting (0,0) to (V_i^*, H_i^*) if and only if $c \geqslant c^*$.

We now analyse the definition of c^* in order to estimate it in applications. Since the system also satisfies the subhomogeneous property, results in Liang and Zhao [28, sections 3 and 5] imply that c^* is determined by the following linear system

$$\begin{cases} \partial_t v_i = \partial_{xx} v_i + \frac{\sigma_1 \beta}{\mu} h_i - \beta v_i, & x \in \mathbb{R}, \ t > 0, \\ \partial_t h_i = d \partial_{xx} h_i + \sigma_2 H_s v_i - \rho h_i, & x \in \mathbb{R}, \ t > 0. \end{cases}$$

For such a linear cooperative system, the threshold c^* has been investigated in several studies, see e.g., Hsu and Yang [20], Wu and Hsu [57]. To determine c^* , we further consider the following eigenvalue problem

$$\lambda(\gamma) \begin{pmatrix} \varphi_1 \\ \varphi_2 \end{pmatrix} = \begin{bmatrix} \gamma^2 \begin{pmatrix} 1 & 0 \\ 0 & d \end{pmatrix} + \begin{pmatrix} -\beta & \frac{\beta \sigma_1}{\mu} \\ \sigma_2 H_s & -\rho \end{bmatrix} \end{bmatrix} \begin{pmatrix} \varphi_1 \\ \varphi_2 \end{pmatrix}$$
$$=: (\gamma^2 \mathbf{D} + \mathbf{L}) \begin{pmatrix} \varphi_1 \\ \varphi_2 \end{pmatrix}.$$

From [28], c^* is the threshold such that

$$\lambda(\gamma) \begin{pmatrix} \varphi_1 \\ \varphi_2 \end{pmatrix} = c\gamma \begin{pmatrix} \varphi_1 \\ \varphi_2 \end{pmatrix}$$

has a positive eigenvector $(\varphi_1, \varphi_2)^T$ if $c \geqslant c^*$.

Note that **L** and $\mathbf{A}(\gamma) := (\gamma^2 \mathbf{D} + \mathbf{L})$ are essentially nonnegative and irreducible matrices, we can estimate c^* by using the idea in [19, pp. 110]. Calculating the above eigenvalue problem, for any given $\gamma \geq 0$, the larger eigenvalue or the so-called Perron-Frobenius eigenvalue (see [19]) of $\mathbf{A}(\gamma)$ is given by

$$\begin{split} \lambda(\gamma) &:= \frac{(d+1)\gamma^2 - (\beta+\rho) + \sqrt{\left[(d-1)\gamma^2 - \rho + \beta\right]^2 + 4\beta\rho\mathcal{R}_0}}{2} \\ &\geqslant \lambda(0) = \frac{-(\beta+\rho) + \sqrt{(\beta-\rho)^2 + 4\beta\rho\mathcal{R}_0}}{2} \\ &\geqslant \frac{-(\beta+\rho) + \sqrt{(\beta-\rho)^2 + 4\beta\rho}}{2} = 0, \quad \gamma \geqslant 0. \end{split}$$

Moreover, $\lambda(\gamma)$ is simple and has a positive eigenvector $(\varphi_1, \varphi_2)^T$. In fact, $(\varphi_1, \varphi_2)^T$ is also the corresponding eigenvector of the principal eigenvalue (the larger

eigenvalue) of the following irreducible and positive matrix

$$\mathbf{A}(\gamma) + \left(\begin{array}{cc} \beta + \rho & 0 \\ 0 & \beta + \rho \end{array} \right),$$

for which we can use the Perron-Frobenius theorem. Evidently, regarding γ as the unique variable, there exists $\gamma' > 0$ such that

$$\frac{d^2[\lambda(\gamma)]}{d\gamma^2} > \frac{d+1}{2}, \gamma > \gamma',$$

which further implies that

$$\lim_{\gamma \to 0} \frac{\lambda(\gamma)}{\gamma} = \lim_{\gamma \to \infty} \frac{\lambda(\gamma)}{\gamma} = +\infty.$$

Using these two limits, we know that

$$c^* := \min_{\gamma > 0} \frac{\lambda(\gamma)}{\gamma} = \min_{\gamma > 0} \frac{(d+1)\gamma^2 - (\beta+\rho) + \sqrt{[(d-1)\gamma^2 - \rho + \beta]^2 + 4\beta\rho\mathcal{R}_0}}{2\gamma}$$
(2.6)

is positive and finite, which is also attained for some finite $\gamma^* > 0$. By direct calculation, we know that $\frac{\lambda(\gamma)}{\gamma}$ is strictly convex (also see [19, lemma 6.2]), so $\gamma^* > 0$ is unique.

At the same time, due to the special form of travelling wave solutions, (2.5) has a travelling wave solution $(\widetilde{\varphi}, \widetilde{\psi})$ if and only if $\widetilde{\varphi}$ satisfies the following quasimonotone equation

$$c\widetilde{\varphi}'(\xi) = \widetilde{\varphi}''(\xi) + \sigma_1(\beta/\mu - \widetilde{\varphi}(\xi))(J * \widetilde{\varphi})(\xi) - \beta\widetilde{\varphi}(\xi)$$
(2.7)

with $\widetilde{\varphi}(-\infty) = 0$, $\widetilde{\varphi}(\infty) = V_i^*$, where

$$\widetilde{\psi}(\xi) = \sigma_2 H_s \int_0^\infty \frac{e^{-\rho t}}{\sqrt{4\pi dt}} \int_{\mathbb{R}} e^{-\frac{y^2}{4dt}} \widetilde{\varphi}(\xi - ct - y) dy dt := (J * \widetilde{\varphi})(\xi)$$
 (2.8)

is obtained by using the elementary solution of heat equations.

Linearizing (2.7) at zero and plugging $e^{\gamma\xi}$ into it, we obtain the corresponding characteristic equation

$$\Lambda(\gamma, c) := \gamma^2 - c\gamma - \beta - \frac{\beta \rho \mathcal{R}_0}{d\gamma^2 - c\gamma - \rho} = 0, \quad \gamma \in [0, \gamma^+), \tag{2.9}$$

where $\gamma^+ = \frac{c + \sqrt{c^2 + 4d\rho}}{2d}$. By direct calculation, we obtain that $\Lambda(0,c) = \beta(\mathcal{R}_0 - 1) > 0$, $\Lambda(\gamma,c) \to \infty$ for any $c \geqslant 0$ as $\gamma \to \gamma^+ -$, and $\partial_{\gamma\gamma}\Lambda(\gamma,c) > 0$ for any $c \geqslant 0$, $\gamma \in [0,\gamma^+)$, which implies that $\Lambda(\gamma,c)$ is convex in $\gamma \in [0,\gamma^+)$. Moreover, since $\partial_c \Lambda(\gamma,c) < 0$ for any given $\gamma \in [0,\gamma^+)$, $\Lambda(\gamma,c)$ is continuous and strictly decreasing in $c \in [0,\infty)$ such that for any $\gamma \in [0,\gamma^+)$, $\Lambda(\gamma,0) \geqslant \beta(\mathcal{R}_0 - 1) > 0$,

 $\lim_{c\to\infty} \Lambda(\gamma,c) = -\infty$. We now define the following bounded constant

$$c^* := \inf \{c > 0 \mid \Lambda(\gamma, c) = 0 \text{ has exact one positive root for } \gamma \in [0, \gamma^+) \}, (2.10)$$

which is the minimal wave speed of (2.7) ([60, 65]). Since the travelling wave in lemma 2.4 is equivalent to that of (2.7), lemma 2.4 implies that the two definitions of c^* are equivalent.

With the above constants, we now state our main results as follows.

THEOREM 2.5. Suppose that $\mathcal{R}_0 > 1$ holds. Then the solution of (1.2) satisfies the following spreading properties:

(i) For any given $c > c^*$, one has

$$\limsup_{t \to \infty} \sup_{|x| \ge ct} \left[\left| V_s(x,t) - \frac{\beta}{\mu} \right| + V_i(x,t) + H_i(x,t) \right] = 0;$$

(ii) For any given $0 < c < c^*$, one has

$$\limsup_{t \to \infty} \sup_{|x| \le ct} (|V_s(x,t) - V_s^*| + |V_i(x,t) - V_i^*| + |H_i(x,t) - H_i^*|) = 0.$$

Moreover, (1.3)–(1.4) has a monotone solution if and only if $c \ge c^*$. In particular, if (1.3)–(1.4) has a monotone solution, then it must satisfy

$$\lim_{\xi \to \infty} \phi(\xi) = V_s^*, \quad \lim_{\xi \to \infty} \varphi(\xi) = V_i^*, \quad \lim_{\xi \to \infty} \psi(\xi) = H_i^*$$
 (2.11)

and it is unique in the sense of phase shift; that is, if $(\phi_1(\xi), \varphi_1(\xi), \psi_1(\xi))$ is a positive solution of (1.3)–(1.4), then there exists $h \in \mathbb{R}$ such that

$$(\phi(\xi), \varphi(\xi), \psi(\xi)) = (\phi_1(\xi+h), \varphi_1(\xi+h), \psi_1(\xi+h)), \quad \xi \in \mathbb{R}.$$

In addition, $\phi(\xi)$ is strictly decreasing in ξ while $\varphi(\xi)$, $\psi(\xi)$ are strictly increasing in ξ .

REMARK 2.6. Theorem 2.5 implies that c^* is the spreading speed of the infected population and the minimal wave speed of travelling wave solutions describing disease spreading.

When $\mathcal{R}_0 \leq 1$, we state the following result on the convergence of solutions and the nonexistence of travelling waves.

THEOREM 2.7. If $\mathcal{R}_0 \leqslant 1$, then the solution of (1.2) satisfies

$$\lim_{t\to\infty} (V_s, V_i, H_i)(x, t) = \left(\frac{\beta}{\mu}, 0, 0\right) \text{ uniformly in } x \in \mathbb{R}.$$

Moreover, (1.3)-(1.4) does not have a positive solution for any $c \in \mathbb{R}$.

3. Spreading properties

In this section, we are devoted to proving the main part of theorem 2.5 if $\mathcal{R}_0 > 1$. To complete the proof of theorem 2.5 (i), we use an auxiliary system as the upper control system, and establish our results by constructing an upper solution and applying the comparison principle. We deal with theorem 2.5 (ii) in a weak sense by using the idea of uniform persistence [9] from dynamical system theory [35]. In this procedure, we introduce the generalized principal eigenvalue problem [19] of a weakly coupled elliptic system in the whole space to estimate the lower bounds of the spreading speed.

3.1. Upper bounds on the spreading speed

In this subsection, we prove theorem 2.5 (i) by showing the following lemma.

LEMMA 3.1. For any given $\epsilon > 0$, the solution of (1.2) satisfies

$$\limsup_{t \to \infty} \sup_{|x| \ge (c^* + \epsilon)t} \left[\left| V_s(x, t) - \frac{\beta}{\mu} \right| + V_i(x, t) + H_i(x, t) \right] = 0.$$

Proof. It follows from lemma 2.2, (2.3)–(2.4) that $V_i(x,t)$ and $H_i(x,t)$ satisfy

$$\begin{cases} \partial_t V_i(x,t) \leqslant \partial_{xx} V_i(x,t) + \frac{\beta \sigma_1}{\mu} H_i(x,t) - \beta V_i(x,t), & x \in \mathbb{R}, \ t > 0, \\ \partial_t H_i(x,t) = d \partial_{xx} H_i(x,t) + \sigma_2 H_s V_i(x,t) - \rho H_i(x,t), & x \in \mathbb{R}, \ t > 0, \\ (V_i, H_i)(x,0) = (V_{i,0}(x), H_{i,0}(x)), & x \in \mathbb{R}. \end{cases}$$
(3.1)

Let $c^*, \gamma^*, \varphi^* = (\varphi_1, \varphi_2)^T$ be given in § 2, we define a positive vector function

$$(\overline{V_i}, \overline{H_i})(x, t) = \min \left\{ e^{\gamma^*(x + c^*t + t_1)}, \ e^{\gamma^*(-x + c^*t + t_1)} \right\} \varphi^*,$$

where $t_1 > 0$ is sufficiently large such that $(\overline{V_i}, \overline{H_i})(x, 0) \ge (V_i, H_i)(x, 0)$. Based on the above arguments, we verify that if $(\overline{V_i}, \overline{H_i})(x, t)$ is differentiable, then

$$\begin{cases}
\partial_t \overline{V_i}(x,t) = \partial_{xx} \overline{V_i}(x,t) + \frac{\beta \sigma_1}{\mu} \overline{H_i}(x,t) - \beta \overline{V_i}(x,t), & x \in \mathbb{R}, \ t > 0, \\
\partial_t \overline{H_i}(x,t) = d\partial_{xx} \overline{H_i}(x,t) + \sigma_2 H_s \overline{V_i}(x,t) - \rho \overline{H_i}(x,t), & x \in \mathbb{R}, \ t > 0, \\
(\overline{V_i}, \overline{H_i})(x,0) = \min \left\{ e^{\gamma^*(x+t_1)}, \ e^{\gamma^*(-x+t_1)} \right\} \varphi^*, & x \in \mathbb{R}
\end{cases}$$
(3.2)

and (V_i, H_i) is a lower solution of (3.2). Applying the classical parabolic comparison principle [45, 61] to the cooperative system (3.2), we obtain

$$\limsup_{t\to\infty}\sup_{|x|\geqslant (c^*+\epsilon)t}(V_i+H_i)(x,t)\leqslant \limsup_{t\to\infty}\sup_{|x|\geqslant (c^*+\epsilon)t}(\overline{V_i}+\overline{H_i})(x,t)=0$$

for any $\epsilon > 0$.

Next we show the convergence of V_s by contradiction. Assume that for any $\epsilon > 0$, there exist $\delta > 0$, a sequence $\{t_n\}_{n \geq 0}$ tending to infinity, and a sequence $\{x_n\}_{n \geq 0}$

 \mathbb{R} such that

$$|x_n| \ge (c^* + \epsilon)t_n$$
, $\left| V_s(x_n, t_n) - \frac{\beta}{\mu} \right| \ge \delta$ for all $n \ge 0$.

Consider a sequence of functions

$$(V_{s,n}, V_{i,n}, H_{i,n})(x,t) = (V_s, V_i, H_i)(x + x_n, t + t_n).$$

By lemma 2.3 and the parabolic estimates, we obtain that $(V_{s,n}, V_{i,n}, H_{i,n})$ has a subsequence, still denoted by $(V_{s,n}, V_{i,n}, H_{i,n})$, converging to some entire solution $(V_{s,\infty}, V_{i,\infty}, H_{i,\infty})$ of (1.2) locally uniformly. Thus $V_{s,\infty}$ satisfies

$$\left| V_{s,\infty}(0,0) - \frac{\beta}{\mu} \right| \geqslant \delta. \tag{3.3}$$

Due to the convergence of V_i and H_i , we have $(V_{i,\infty}, H_{i,\infty})(0,0) = (0,0)$. Then the strong maximum principle implies that $(V_{i,\infty}, H_{i,\infty})(x,t) \equiv (0,0)$. Thus

$$(V_s + V_i)(x + x_n, t + t_n) \to V_{s,\infty}(x, t), \quad n \to \infty.$$

By (2.2), we have $(V_s + V_i)(x + x_n, t + t_n) \to \frac{\beta}{\mu}$ as $n \to \infty$, which further implies that $V_{s,\infty} \equiv \frac{\beta}{\mu}$ by the uniqueness of the entire solution for the scalar Fisher-KPP equation [4]. It contradicts (3.3) and completes the proof.

3.2. Lower bounds on the spreading speed

In this subsection, we first prove a lemma as a weak version of (theorem 2.5(ii), which relies on the uniform persistence theory in dynamical systems. The final convergence in theorem 2.5(ii) will be completed in § 4.

LEMMA 3.2. Suppose that $\mathcal{R}_0 > 1$. Then for any given $0 < c < c^*$, the solution of (1.2) satisfies

$$0 < \liminf_{t \to \infty} \inf_{|x| \leqslant ct} V_s(x, t) \leqslant \limsup_{t \to \infty} \sup_{|x| \leqslant ct} V_s(x, t) < \frac{\beta}{\mu},$$

$$0 < \liminf_{t \to \infty} \inf_{|x| \leqslant ct} V_i(x,t), \quad 0 < \liminf_{t \to \infty} \inf_{|x| \leqslant ct} H_i(x,t).$$

In what follows, we divide the proof of the above lemma into three steps: (1) pointwise weak spreading property, (2) point-wise spreading property, and (3) uniform spreading property. Throughout this subsection, we assume that c^0 is an arbitrarily fixed constant such that $0 \le c^0 < c^*$.

3.2.1. An eigenvalue problem. In order to prove the weak point-wise spreading property, we first investigate an eigenvalue problem of weakly coupled elliptic systems by the corresponding generalized principal eigenvalue. For 0 < R, $0 < \eta < \beta$, and $c \in \mathbb{R}$, we consider the following eigenvalue problem:

$$\begin{cases} \lambda \psi_{1} = -\partial_{xx}\psi_{1} - c\partial_{x}\psi_{1} + (\beta + \eta)\psi_{1} - \sigma_{1}(\frac{\beta - \eta}{\mu})\psi_{2}, & x \in (-R, R), \\ \lambda \psi_{2} = -d\partial_{xx}\psi_{2} - c\partial_{x}\psi_{2} - \sigma_{2}H_{s}\psi_{1} + \rho\psi_{2}, & x \in (-R, R), \\ \psi_{1}(x) = \psi_{2}(x) = 0, & x \in \{-R, R\}. \end{cases}$$
(3.4)

LEMMA 3.3. For any given $|c| < c^*$, there exist $\eta_c > 0$ small enough and $\overline{R}_c > 0$ large enough such that the principal eigenvalue of (3.4) satisfies $\Lambda_R(\eta) < 0$ for any $R \geqslant \overline{R}_c$ and $0 \leqslant \eta \leqslant \eta_c$.

Proof. Since this weak coupled elliptic system is cooperative and irreducible, the celebrated Krein-Rutman theorem [7] implies that there exists a unique principal eigenvalue $\Lambda_R(\eta)$ associated with a positive eigenfunction pair (ψ_1, ψ_2) for (3.4).

We first consider the case $0 \le c < c^*$. From [19, theorem 4.2], we obtain that as $R \to +\infty$, $\Lambda_R(\eta)$ converges to a generalized principal eigenvalue of the operator

$$\mathcal{L}[\psi_1, \psi_2] := \begin{pmatrix} -\partial_{xx}\psi_1 - c\partial_x\psi_1 + (\beta + \eta)\psi_1 - \sigma_1\left(\frac{\beta - \eta}{\mu}\right)\psi_2\\ -d\partial_{xx}\psi_2 - c\partial_x\psi_2 - \sigma_2H_s\psi_1 + \rho\psi_2 \end{pmatrix},$$

in which the generalized principal eigenvalue is defined by

$$\Lambda_1(\eta) := \sup \left\{ \lambda \in \mathbb{R} \mid \exists (\psi_1, \psi_2) \in C^2(\mathbb{R}, \mathbb{R}^2_+), \quad \mathcal{L}[\psi_1, \psi_2] \geqslant \lambda[\psi_1, \psi_2] \right\},\,$$

where $C^2(\mathbb{R}, \mathbb{R}^2_+)$ represents the space of all positive twice continuously differentiable vector functions. It follows from [19, lemma 6.4] that

$$\lim_{R \to \infty} \Lambda_R(\eta) = \Lambda_1(\eta) = \max_{\gamma \ge 0} [-\lambda(\gamma, \eta) + c\gamma],$$

where $\lambda(\gamma, \eta)$ denotes the unique Perron-Frobenius eigenvalue of the matrix

$$\mathbf{A}(\gamma,\eta) := \begin{pmatrix} \gamma^2 - (\beta + \eta) & \frac{\sigma_1(\beta - \eta)}{\mu} \\ \sigma_2 H_s & d\gamma^2 - \rho \end{pmatrix}.$$

Recalling the first definition of c^* in §2, $\mathbf{A}(\gamma,0)$ is essentially nonnegative and irreducible, and admits the unique Perron-Frobenius eigenvalue $\lambda(\gamma,0) > 0$ associated with a positive eigenvector (see [19]). Moreover,

$$c^* = \min_{\gamma > 0} \frac{\lambda(\gamma, 0)}{\gamma} > 0.$$

For any given $c \in [0, c^*)$, one obtains that there exist $\eta_c > 0$ small enough and \overline{R}_c large enough such that

$$\Lambda_R(\eta) < 0, \quad R \in [\overline{R}_c, \infty), \quad \eta \in [0, \eta_c].$$

By a symmetric argument on -x and the uniqueness of this eigenvalue, the conclusion for the case $-c^* < c \le 0$ follows. This completes the proof.

3.2.2. The first step: point-wise weak spreading property

LEMMA 3.4. There exists $\varepsilon_1(c^0) > 0$ such that for any $c \in [0, c^0]$ and $x \in \mathbb{R}$, the solution (V_s, V_i, H_i) of (1.2) with initial data in Y satisfies

$$\limsup_{t \to \infty} (V_i + H_i)(x + ct, t) \geqslant \varepsilon_1(c^0). \tag{3.5}$$

Proof. Suppose by contradiction that there exist sequences

$$\{(V_{s,0}^n, V_{i,0}^n, H_{i,0}^n)(x)\}_{n\geqslant 0} \subset Y, \quad \{c_n\}_{n\geqslant 0} \subset [0, c^0], \quad \{x_n\}_{n\geqslant 0} \subset \mathbb{R}$$

such that the solution (V_s^n, V_i^n, H_i^n) of (1.2) with initial data $(V_{s,0}^n, V_{i,0}^n, H_{i,0}^n)$ satisfies

$$\limsup_{t \to \infty} (V_i^n + H_i^n)(x_n + c_n t, t) \leqslant \frac{1}{n+1} \text{ for all } n \geqslant 0.$$

Then it implies that there exists $\{t_n\}_{n\geqslant 0}\subset [0,\infty)$ tending to ∞ , and

$$\max\{V_i^n(x_n + c_n t, t), H_i^n(x_n + c_n t, t)\} \leqslant \frac{2}{n+1} \text{ for all } t \geqslant t_n.$$
 (3.6)

By (3.6), we claim that for any R > 0, there exists a sequence $t'_n \geqslant t_n$ such that

$$\lim_{n \to \infty} \sup_{t \ge 0, |x| \le R} \left| V_s^n(x_n + c_n(t_n' + t) + x, t_n' + t) - \frac{\beta}{\mu} \right| = 0.$$
 (3.7)

In fact, it suffices to verify (3.7) with $\{t'_n = t_n\}$. We suppose by contradiction that there exist $\delta > 0$, sequences $s_n \geqslant t_n, c_n \to c_\infty \in [0, c^0]$ and $x'_n \to x'_\infty \in [-R, R]$ such that

$$\left| V_s^n(x_n + c_n s_n + x_n', s_n) - \frac{\beta}{\mu} \right| \geqslant \delta.$$

Using lemma 2.3, the standard parabolic estimates imply that up to a subsequence,

$$(V_s^n, V_i^n, H_i^n)(x_n + c_n(s_n + t) + x, s_n + t) \rightarrow (u_\infty, v_\infty, w_\infty)(x, t)$$
 as $n \rightarrow \infty$

locally uniformly for $(x,t) \in \mathbb{R}^2$, where $(u_{\infty}, v_{\infty}, w_{\infty})$ is an entire solution of

$$\begin{cases} (\partial_t - \partial_{xx} - c_\infty \partial_x) u_\infty = (u_\infty + v_\infty)(\beta - \mu u_\infty) - \sigma_1 u_\infty w_\infty, \\ (\partial_t - \partial_{xx} - c_\infty \partial_x) v_\infty = \sigma_1 u_\infty w_\infty - \mu (u_\infty + v_\infty) v_\infty, \\ (\partial_t - d\partial_{xx} - c_\infty \partial_x) w_\infty = \sigma_2 H_s v_\infty - \rho w_\infty. \end{cases}$$

Note that (3.6) yields $(v_{\infty}, w_{\infty})(0, 0) = (0, 0)$. Applying the strong maximum principle, we obtain that $(u_{\infty}, v_{\infty}, w_{\infty})(x, t) \equiv (\beta/\mu, 0, 0)$. However, since the sequence $\{x'_n\} \subset [-R, R]$ is relatively compact, $u_{\infty}(x, t) \equiv \frac{\beta}{\mu}$ contradicts the fact that

$$\left| u_{\infty}(x_{\infty}', 0) - \frac{\beta}{\mu} \right| \geqslant \delta,$$

which proves (3.7).

Now we return to prove lemma 3.4. Consider a sequence of functions (u_n, v_n, w_n) with moving frames defined by

$$(u_n, v_n, w_n)(x, t) := (V_s^n, V_i^n, H_i^n)(x_n + c_n(t_n + t) + x, t_n + t),$$

then (3.6) becomes

$$\max\{v_n(0,t), w_n(0,t)\} \leqslant \frac{2}{n+1} \text{ for all } n \geqslant 0, \ t \geqslant 0.$$
 (3.8)

Let us fix small $\eta > 0$ and large R > 0 such that lemma 3.3 holds for c^0 . It follows from (2.3) and (3.7) that for any n large enough, one has

$$u_n(x,t) \geqslant \frac{\beta - \eta}{\mu}, \quad \frac{\beta}{\mu} \leqslant (u_n + v_n)(x,t) \leqslant \frac{\beta + \eta}{\mu} \text{ for all } t \geqslant 0, \ |x| \leqslant R.$$

Then $(v_n, w_n)(x, t)$ satisfies

$$\begin{cases} (\partial_t - \partial_{xx} - c_n \partial_x) v_n \geqslant \sigma_1 \frac{\beta - \eta}{\mu} w_n - (\beta + \eta) v_n, & t \geqslant 0, \ |x| \leqslant R, \\ (\partial_t - d\partial_{xx} - c_n \partial_x) w_n \geqslant \sigma_2 H_s v_n - \rho w_n, & t \geqslant 0, \ |x| \leqslant R. \end{cases}$$

Thus the comparison principle yields that

$$(v_n, w_n)(x, t) \geqslant \tau e^{-\Lambda_R t}(\psi_1, \psi_2)(x)$$
 for all $|x| \leqslant R$, $t \geqslant 0$,

where Λ_R and (ψ_1, ψ_2) are the principal eigenvalue and the associated positive eigenfunction pair defined in lemma 3.3, $\tau > 0$ is small enough so that $(v_n, w_n)(x, 0) \ge \tau(\psi_1, \psi_2)(x)$ for all $|x| \le R$.

Using lemma 3.3, we have $\Lambda_R < 0$ since η is small enough and R is large enough. Thus, $v_n(0,t) \ge \tau e^{-\Lambda_R t} \psi_1(0) \to \infty$ as $t \to \infty$, which contradicts (3.8). The proof is complete.

3.2.3. The second step: point-wise strong spreading property In the following lemma, we shall improve the weak spreading properties stated in the previous subsection.

LEMMA 3.5. There exists $\varepsilon_2(c^0) > 0$ such that for any $c \in [0, c^0]$ and $x \in \mathbb{R}$, the solution (V_s, V_i, H_i) of (1.2) with initial data in Y satisfies

$$\lim_{t \to \infty} \inf(V_i + H_i)(x + ct, t) \geqslant \varepsilon_2(c^0). \tag{3.9}$$

Proof. We prove (3.9) by contradiction. Assume that there exist sequences

$$\{(V_{s,n}^0, V_{i,n}^0, H_{i,n}^0)(x)\}_{n\geqslant 0} \subset Y, \quad \{c_n\}_{n\geqslant 0} \subset [0, c^0], \quad \{x_n\}_{n\geqslant 0} \subset \mathbb{R}$$

such that

$$\liminf_{t \to \infty} (V_{i,n} + H_{i,n})(x_n + c_n t, t) < \frac{1}{n+1}, \quad n \in \mathbb{N}.$$

Without loss of generality, we further assume that $c_n \to c^{\infty} \in [0, c^0]$ as $n \to \infty$. Lemma 3.4 implies that there exist two sequences $t_n \to \infty$ and $\tau_n \in \mathbb{R}_+$ such that for each $n \ge 0$

$$[V_{i,n} + H_{i,n}](x_n + c_n t_n, t_n) = \frac{\varepsilon_1(c^0)}{2},$$

$$[V_{i,n} + H_{i,n}](x_n + c_n t, t) \leqslant \frac{\varepsilon_1(c^0)}{2}, \quad t \in [t_n, t_n + \tau_n],$$

$$[V_{i,n} + H_{i,n}](x_n + c_n (t_n + \tau_n), t_n + \tau_n) = \frac{1}{n+1},$$

where $\varepsilon_1(c^0)$ is given in lemma 3.4.

By lemma 2.3, standard parabolic estimates and up to a sequence, we have

$$(V_{s,n}, V_{i,n}, H_{i,n})(x_n + c_n t_n + x, t_n + t) \to (V_s^{\infty}, V_i^{\infty}, H_i^{\infty})(x, t)$$

locally uniformly in $(x,t) \in \mathbb{R}^2$ as $n \to \infty$, where $(V_s^{\infty}, V_i^{\infty}, H_i^{\infty})$ is an entire solution of (1.2). Due to the choice of t_n , we have

$$V_i^{\infty}(0,0) + H_i^{\infty}(0,0) = \frac{\varepsilon_1(c^0)}{2},$$

which further yields $V_i^{\infty}(x,t) + H_i^{\infty}(x,t) > 0$ by the strong maximum principle.

We find that $\tau_n \to \infty$ as $n \to \infty$. Indeed, suppose by contradiction that its subsequence converges to some $t_0 \in \mathbb{R}_+$, then one has

$$(V_i^{\infty} + H_i^{\infty})(c^{\infty}t_0, t_0) = 0.$$

Then it follows that $V_i^{\infty}(c^{\infty}t_0,t_0)=H_i^{\infty}(c^{\infty}t_0,t_0)=0$ since these solutions are nonnegative. The strong maximum principle implies that $V_i^{\infty}=H_i^{\infty}\equiv 0$, a contradiction. Hence by the second construction we have

$$V_i^{\infty}(c^{\infty}t,t) + H_i^{\infty}(c^{\infty}t,t) \leqslant \frac{\varepsilon_1(c^0)}{2}$$
 for all $t \geqslant 0$,

and it contradicts (3.5) in lemma 3.4 as x = 0 and $c = c^{\infty}$. This completes the proof.

3.2.4. The third step: uniform spreading property

Lemma 3.6. For any $c \in [0, c^0]$, the solution of (1.2) with initial data in Y satisfies

$$\liminf_{t \to \infty} \inf_{0 \leqslant x \leqslant ct} V_i(x, t) > 0, \quad \liminf_{t \to \infty} \inf_{0 \leqslant x \leqslant ct} H_i(x, t) > 0, \tag{3.10}$$

$$0 < \liminf_{t \to \infty} \inf_{0 \le x \le ct} V_s(x, t) \le \limsup_{t \to \infty} \sup_{0 \le x \le ct} V_s(x, t) < \frac{\beta}{\mu}. \tag{3.11}$$

Proof. We first prove that

$$\liminf_{t \to \infty} \inf_{0 \le x \le ct} (V_i + H_i)(x, t) > 0.$$
(3.12)

For any given $\hat{c} \in (0, c^0)$, we suppose by contradiction that there exist sequences $t_n \to \infty$ and $c_n \in [0, \hat{c})$ such that

$$\lim_{n \to \infty} (V_i + H_i)(c_n t_n, t_n) = 0.$$

Up to a subsequence, we assume, without loss of generality, that $c_n \to \widetilde{c}_\infty \in [0, \widehat{c}]$ as $n \to \infty$. Select c' > 0 such that $\widetilde{c}_\infty < c' \leqslant c^0$, and define the sequence

$$t'_n := \frac{c_n t_n}{c'} \in [0, t_n)$$
 for all $n \geqslant 0$.

We first consider the case that the sequence $\{c_n t_n\}_{n\geqslant 0}$ is bounded, which may occur if $\widetilde{c}_{\infty}=0$. Up to a subsequence, it follows from the strong maximum principle that as $n\to\infty$, $c_n t_n\to x_{\infty}$ and

$$(V_i + H_i)(c_n t_n + x, t_n + t) \to 0$$
 locally uniformly for $(x, t) \in \mathbb{R}^2$.

This implies in particular that $(V_i + H_i)(0, t_n) \to 0$ as $n \to \infty$, which contradicts the case c = 0 in lemma 3.5. Thus $\widetilde{c}_{\infty} > 0$ implies that the sequence $\{c_n t_n\}$ has no bounded subsequence.

Now we assume that $t'_n \to \infty$ as $n \to \infty$. Since $c' \in (0, c^0]$, lemma 3.5 implies that

$$(V_i + H_i)(c_n t_n, t'_n) = (V_i + H_i)(c't'_n, t'_n) \geqslant \varepsilon_2(c^0)$$

for each n large enough.

Now we define the third time sequence $\{t''_n\}$ as follows

$$t_n'' := \inf \left\{ t \leqslant t_n \mid (V_i + H_i)(c_n t_n, s) \leqslant \frac{\min\{\varepsilon_1(c^0), \varepsilon_2(c^0)\}}{2} \text{ for any } s \in (t, t_n) \right\},$$

then $t''_n \in (t'_n, t_n)$. Since $(V_i + H_i)(c_n t_n, t_n) \to 0$ as $n \to \infty$, we have

$$(V_i + H_i)(c_n t_n, t_n'') = \frac{\min\{\varepsilon_1(c^0), \varepsilon_2(c^0)\}}{2}.$$

By using a similar limiting argument and a strong maximum principle, one also has

$$t_n - t_n'' \to \infty$$
 as $n \to \infty$.

Then by lemma 2.3 and standard parabolic estimates and up to a subsequence, we obtain that

$$(V_s, V_i, H_i)(c_n t_n + x, t_n'' + t) \to (\widetilde{u}_\infty, \widetilde{v}_\infty, \widetilde{w}_\infty)(x, t), \quad n \to \infty$$

locally uniformly in (x, t) such that

$$(\widetilde{v}_{\infty} + \widetilde{w}_{\infty})(0,0) > 0,$$

$$(\widetilde{v}_{\infty} + \widetilde{w}_{\infty})(0, t) \leqslant \frac{\min\{\varepsilon_1(c^0), \varepsilon_2(c^0)\}}{2}$$
 for all $t \geqslant 0$,

which contradicts (3.9) in lemma 3.5 as c = 0 and x = 0. Thus (3.12) holds.

Next we show (3.10) by contradiction. Assume that there exist sequences $t_n \to \infty$ and $0 \le x_n \le ct_n$ such that $V_i(x_n, t_n) \to 0$ as $n \to \infty$, then up to a subsequence, lemma 2.3, parabolic estimates and the strong maximum principle imply that as $n \to \infty$,

$$(V_s, V_i, H_i)(x + x_n, t + t_n) \to (u^{\infty}, 0, w^{\infty})(x, t)$$
 locally uniformly in $(x, t) \in \mathbb{R}^2$,

where $(u^{\infty}, 0, w^{\infty})$ is an entire solution of (1.2). But (3.12) yields $w^{\infty} > 0$, which contradicts (1.2). Then it follows that for any $c \in [0, c^0]$,

$$\liminf_{t \to \infty} \inf_{0 \le x \le ct} V_i(x, t) > 0.$$

Thus we finish the proof of (3.10) by using a similar argument for H_i .

To deal with (3.11), we first assume by contradiction that there exist sequences $t_n \to \infty$ and $0 \le x_n \le ct_n$ such that $V_s(x_n, t_n) \to \frac{\beta}{\mu}$ as $n \to \infty$, then $(V_s, V_i, H_i)(x + x_n, t + t_n)$ converges to an entire solution $(u_\infty, v_\infty, w_\infty)(x, t)$ of (1.2), which satisfies $u_\infty(0,0) = \frac{\beta}{\mu}$. Using the strong maximum principle, $u_\infty \equiv \frac{\beta}{\mu}$ follows. However, it follows from (3.10) that $w_\infty > 0$, which contradicts (1.2). For the remaining part, if $V_s(x_n, t_n) \to 0$ as $n \to \infty$, then $V_i(x_n, t_n) \to 0$ as $n \to \infty$, which contradicts (3.10). This completes the proof.

Recall that the aforementioned three lemmas addressed the rightward speed case of lemma 3.2, the leftward part of spreading follows by using a symmetric argument. Thus lemma 3.2 is proved.

4. Convergence of solutions

In this section, we show some convergence results to complete the proofs of theorem 2.5 (ii) and theorem 2.7. If $\mathcal{R}_0 > 1$, we show that the solution converges to the positive equilibrium locally uniformly, which gives the final convergence in theorem 2.5 (ii). Then the disease will persist eventually. If $\mathcal{R}_0 \leq 1$, then the solution tends to the disease-free equilibrium, which indicates that the vector-borne disease will die out.

Before proving the final convergence in theorem 2.5 (ii), we state a convergence result for the bounded, persistent entire solutions of (1.2), which is established by constructing two auxiliary monotone systems.

LEMMA 4.1. Suppose that $\mathcal{R}_0 > 1$. If (V_s, V_i, H_i) is a bounded entire solution of (1.2) such that

$$\inf_{(x,t)\in\mathbb{R}^2} V_s(x,t) > 0, \quad \inf_{(x,t)\in\mathbb{R}^2} V_i(x,t) > 0, \quad \inf_{(x,t)\in\mathbb{R}^2} H_i(x,t) > 0, \tag{4.1}$$

then $(V_s, V_i, H_i)(x, t) \equiv (V_s^*, V_i^*, H_i^*)$ for all $(x, t) \in \mathbb{R}^2$.

Proof. We set $V = V_s + V_i$, then V(x,t) satisfies the following Cauchy problem

$$\begin{cases} \partial_t V(x,t) = \partial_{xx} V(x,t) + V(x,t) [\beta - \mu V(x,t)], & x \in \mathbb{R}, \ t > 0, \\ V(x,0) = (V_s + V_i)(x,0) > 0, & x \in \mathbb{R}. \end{cases}$$
(4.2)

It follows from (2.2) that for any $\varepsilon > 0$, there exists T > 0 such that

$$\left| (V_s + V_i)(x, t) - \frac{\beta}{\mu} \right| < \varepsilon, \quad t \geqslant T, \ x \in \mathbb{R}.$$

Due to (4.1), we reset the initial function as $V(x,0) = (V_s + V_i)(x, -t_0)$ for any $t_0 > 0$, we similarly have

$$\left| (V_s + V_i)(x, t - t_0) - \frac{\beta}{\mu} \right| < \varepsilon, \quad t \geqslant T, \ x \in \mathbb{R}.$$

Taking $t_0 \to \infty$, since the problem (4.2) is autonomous, we actually obtain that

$$\left| (V_s + V_i)(x, t+T) - \frac{\beta}{\mu} \right| < \varepsilon, \quad t \in \mathbb{R}, \ x \in \mathbb{R}.$$

Due to the arbitrariness of ε , the above inequality implies that $V_s + V_i \equiv \frac{\beta}{\mu}$ for all $(x,t) \in \mathbb{R}^2$. Thus the bounded entire solution (V_s,V_i,H_i) satisfies the following subsystem:

$$\begin{cases}
\partial_t V_i = \partial_{xx} V_i + \sigma_1 H_i(\frac{\beta}{\mu} - V_i) - \beta V_i, & x \in \mathbb{R}, \ t > 0, \\
\partial_t H_i = d\partial_{xx} H_i + \sigma_2 H_s V_i - \rho H_i, & x \in \mathbb{R}, \ t > 0, \\
(V_i, H_i)(x, 0) = (V_{i,0}, H_{i,0})(x), & x \in \mathbb{R},
\end{cases} \tag{4.3}$$

where the initial data $(V_{i,0}(x), H_{i,0}(x))$ satisfies

$$\inf_{x \in \mathbb{R}} V_{i,0}(x) > 0, \quad \inf_{x \in \mathbb{R}} H_{i,0}(x) > 0.$$

Now we deal with the long time behaviour of a spatial homogeneous solution to (4.3). Let $(\underline{v}, \underline{h})(t)$ be the solution of

$$\begin{cases}
\frac{\mathrm{d}\underline{v}(t)}{\mathrm{d}t} = \sigma_{1}\underline{h} \left(\frac{\beta}{\mu} - \underline{v}\right) - \beta\underline{v}, & t > 0, \\
\frac{\mathrm{d}\underline{h}(t)}{\mathrm{d}t} = \sigma_{2}H_{s}\underline{v} - \rho\underline{h}, & t > 0, \\
(\underline{v},\underline{h})(0) = (\inf_{x \in \mathbb{R}} |V_{i,0}(x)|, \inf_{x \in \mathbb{R}} |H_{i,0}(x)|),
\end{cases}$$
(4.4)

then $(\underline{v},\underline{h})(t)$ is a spatially homogeneous lower solution of (4.3). Since (4.4) is cooperative and $\mathcal{R}_0 > 1$ holds, it is evident that

$$(v,h)(t) \to (V_i^*, H_i^*), \quad t \to \infty.$$
 (4.5)

Similarly, we consider a spatial homogeneous upper solution $(\overline{v}, \overline{h})(t)$ of (4.3) with initial data $(\sup_{x \in \mathbb{R}} |V_{i,0}(x)|, \sup_{x \in \mathbb{R}} |H_{i,0}(x)|)$. Since $\mathcal{R}_0 > 1$, we have

$$(\overline{v}, \overline{h})(t) \to (V_i^*, H_i^*), \quad t \to \infty.$$
 (4.6)

It follows from (4.5)–(4.6) and the comparison principle that for any $\tilde{\epsilon} > 0$, there exists $\tilde{T} > 0$ such that

$$|V_i(x,t) - V_i^*| + |H_i(x,t) - H_i^*| < \widetilde{\varepsilon}, \quad t \geqslant \widetilde{T}, \ x \in \mathbb{R}.$$

Applying a similar argument as at the beginning of the proof to (4.3), we actually obtain that

$$\left|V_i(x,t+\widetilde{T})-V_i^*\right|+\left|H_i(x,t+\widetilde{T})-H_i^*\right|<\widetilde{\varepsilon},\quad t\in\mathbb{R},\ x\in\mathbb{R}.$$

Due to the arbitrariness of $\widetilde{\varepsilon}$, the above inequality together with $V_s + V_i \equiv \frac{\beta}{\mu}$ yields that $(V_s, V_i, H_i) \equiv (V_s^*, V_i^*, H_i^*)$ for all $(x, t) \in \mathbb{R}^2$, which completes the proof. \square

Proof of the convergence in theorem 2.5 (ii): We suppose by contradiction that there exist $c \in [0, c^*)$, a sequence $\{t_n\}_{n \geqslant 0} \subset (0, \infty)$ tending to $+\infty$, a sequence $\{x_n\}_{n \geqslant 0} \subset \mathbb{R}$ and a $\delta > 0$ such that

$$|x_n| \le ct_n$$
, $|V_s(x_n, t_n) - V_s^*| + |V_i(x_n, t_n) - V_i^*| + |H_i(x_n, t_n) - H_i^*| > \delta$, $n \ge 0$.

(4.7)

Let us define a sequence of functions (V_s, V_i, H_i) as follows:

$$(V_s^n, V_i^n, H_i^n)(x, t) := (V_s, V_i, H_i)(x + x_n, t + t_n).$$

We fix c' > 0 such that $c < c' < c^*$. Note that (V_s, V_i, H_i) is bounded, it follows from lemma 3.2 that there exist $T_1 > 0$ large enough and $\epsilon > 0$ small enough such that for all $n \ge 0$, $(x,t) \in \mathbb{R}^2$, if $t + t_n \ge T_1$ and $|x| \le c't + (c'-c)t_n$, then

$$\epsilon \leqslant V_s^n(x,t) \leqslant \frac{1}{\epsilon}, \quad \epsilon \leqslant V_i^n(x,t) \leqslant \frac{1}{\epsilon}, \ \epsilon \leqslant H_i^n(x,t) \leqslant \frac{1}{\epsilon}.$$
 (4.8)

Due to lemma 2.3 and the parabolic estimates, up to a subsequence, one has

$$(V_s^n,V_i^n,H_i^n)(x,t)\to (V_s^\infty,V_i^\infty,H_i^\infty)(x,t)$$
 locally uniformly for $(x,t)\in\mathbb{R}^2$

as $n \to \infty$, where $(V_s^{\infty}, V_i^{\infty}, H_i^{\infty})$ is a bounded entire solution of (1.2). Moreover, (4.8) yields

$$\inf_{(x,t)\in\mathbb{R}^2}V_s^\infty>0,\quad \inf_{(x,t)\in\mathbb{R}^2}V_i^\infty>0,\quad \inf_{(x,t)\in\mathbb{R}^2}H_i^\infty>0.$$

Therefore, lemma 4.1 implies that $(V_s^{\infty}, V_i^{\infty}, H_i^{\infty})(x, t) \equiv (V_s^*, V_i^*, H_i^*)$ for all $(x, t) \in \mathbb{R}^2$.

But (4.7) implies that

$$|V_s^{\infty}(0,0) - V_s^*| + |V_i^{\infty}(0,0) - V_i^*| + |H_i^{\infty}(0,0) - H_i^*| > \delta$$

which is a contradiction. This completes the proof of theorem 2.5 (ii).

To prove theorem 2.7, we show another convergence result for bounded entire solutions of (1.2) when $\mathcal{R}_0 \leq 1$.

LEMMA 4.2. Suppose that $\mathcal{R}_0 \leqslant 1$. If (V_s, V_i, H_i) is a bounded entire solution of (1.2), then $(V_s, V_i, H_i)(x, t) \equiv (\frac{\beta}{\mu}, 0, 0)$ for all $(x, t) \in \mathbb{R}^2$.

Proof. Since the solution is bounded and nonnegative, there exists a sequence $\{(x_n,t_n)\}_{n\geqslant 0}\subset \mathbb{R}^2$ such that

$$\lim_{n \to \infty} V_s(x_n, t_n) = \inf_{(x,t) \in \mathbb{R}^2} V_s(x,t) \geqslant 0.$$

Then we consider the sequence of functions

$$(V_s^n, V_i^n, H_i^n)(x, t) := (V_s, V_i, H_i)(x + x_n, t + t_n).$$

By the parabolic estimates and up to a subsequence, one has

$$(V_s^n, V_i^n, H_i^n)(x,t) \to (\widehat{V}_s, \widehat{V}_i, \widehat{H}_i)(x,t)$$
 locally uniformly for $(x,t) \in \mathbb{R}^2$

as $n \to \infty$, where $(\hat{V}_s, \hat{V}_i, \hat{H}_i)$ is a bounded entire solution of (1.2) and satisfies

$$\begin{cases}
\partial_t \widehat{V}_s = \partial_{xx} \widehat{V}_s + (\widehat{V}_s + \widehat{V}_i)(\beta - \mu \widehat{V}_s) - \sigma_1 H_i \widehat{V}_s, & (x, t) \in \mathbb{R}^2, \\
\partial_t \widehat{V}_i = \partial_{xx} \widehat{V}_i + \sigma_1 \widehat{H}_i \widehat{V}_s - \mu (\widehat{V}_s + \widehat{V}_i) \widehat{V}_i, & (x, t) \in \mathbb{R}^2, \\
\partial_t \widehat{H}_i = d\partial_{xx} \widehat{H}_i + \sigma_2 H_s \widehat{V}_i - \rho \widehat{H}_i, & (x, t) \in \mathbb{R}^2.
\end{cases} \tag{4.9}$$

The definition of (x_n, t_n) implies that

$$\widehat{V}_s(0,0) = \inf_{(x,t) \in \mathbb{R}^2} V_s(x,t).$$

Note that $0 \leqslant \hat{V}_s \leqslant \frac{\beta}{\mu}$ for all $(x,t) \in \mathbb{R}^2$. Then we apply the strong comparison principle to the \hat{V}_s -equation and obtain that

$$\widehat{V}_s(x,t) \equiv \inf_{(x,t) \in \mathbb{R}^2} V_s(x,t) := V_s^0 \geqslant 0, \tag{4.10}$$

which is a constant.

Next we consider two cases: (i) $V_s^0 = 0$, (ii) $V_s^0 > 0$. For case (i), $V_s^0 = 0$ implies that $\hat{V}_s(x,t) = \hat{V}_i(x,t) = \hat{H}_i(x,t) \equiv 0$ for all $(x,t) \in \mathbb{R}^2$. But lemma 2.1 yields that $(V_s + V_i)(x,t)$ with initial data $(V_{s,0} + V_{i,0})(x) \geqslant \frac{\beta}{\mu}$ converges to $\frac{\beta}{\mu}$ uniformly in $x \in \mathbb{R}$ as $t \to \infty$. It is a contradiction. Thus $V_s^0 = 0$ is impossible.

For case (ii), $V_s^0 > 0$ ensures that $\inf_{(x,t) \in \mathbb{R}^2} (V_s + V_i)(x,t) > 0$. Applying [4, proposition 1.8] to $V_s + V_i$ satisfying a classical Fisher-KPP equation, we immediately obtain that $(V_s + V_i)(x,t) \equiv \frac{\beta}{\mu}$ for all $(x,t) \in \mathbb{R}^2$, which implies $\widehat{V}_s + \widehat{V}_i \equiv \frac{\beta}{\mu}$. Together with (4.9)–(4.10), one obtains that $(\widehat{V}_s, \widehat{V}_i, \widehat{H}_i)(x,t) \equiv (V_s^0, V_i^0, H_i^0)$ satisfies the system of stationary equations

$$\begin{cases} (V_s^0 + V_i^0)(\beta - \mu V_s^0) - \sigma_1 H_i^0 V_s^0 = 0, \\ \sigma_1 H_i^0 V_s^0 - \mu (V_s^0 + V_i^0) V_i^0 = 0, \\ \sigma_2 H_s V_i^0 - \rho H_i^0 = 0. \end{cases}$$

Due to $\mathcal{R}_0 \leq 1$, $(V_s^0, V_i^0, H_i^0) = (\frac{\beta}{\mu}, 0, 0)$ follows. Combining (4.10) with the fact $0 \leq V_s \leq \frac{\beta}{\mu}$ for all $(x, t) \in \mathbb{R}^2$, we obtain $(V_s, V_i, H_i) \equiv (\frac{\beta}{\mu}, 0, 0)$, which completes the proof of this lemma.

Proof of theorem 2.7: Note that the travelling wave solution is also a special entire solution of (1.2), lemma 4.2 directly shows that if $\mathcal{R}_0 \leq 1$, (1.3) and (1.4) does not have a positive solution for any $c \in \mathbb{R}$.

Now we prove that when $\mathcal{R}_0 \leq 1$, the solution of (1.2) goes to the disease-free equilibrium as time tending ∞ . Suppose by contradiction that there exist a constant $\widetilde{\delta} > 0$, a sequence $\{(x_n, t_n)\}_{n \geq 0}$ with $t_n \to \infty$, and $x_n \in \mathbb{R}$ such that

$$\left| V_s(x_n, t_n) - \frac{\beta}{\mu} \right| + \left| V_i(x_n, t_n) \right| + \left| H_i(x_n, t_n) \right| \geqslant \widetilde{\delta}, \quad n \geqslant 0.$$
 (4.11)

We consider the sequence of functions (V_s, V_i, H_i) as follows:

$$(V_s^n, V_i^n, H_i^n)(x, t) := (V_s, V_i, H_i)(x + x_n, t + t_n).$$

By lemma 2.3 and the parabolic estimates, up to a subsequence, one has

$$(V_s^n, V_i^n, H_i^n)(x,t) \to (u, v, h)(x,t)$$
 locally uniformly for $(x,t) \in \mathbb{R}^2$

as $n \to \infty$, where (u, v, h) is a bounded entire solution of (1.2). Moreover, it follows from (4.11) that

$$\left| u(0,0) - \frac{\beta}{\mu} \right| + |v(0,0)| + |h(0,0)| \geqslant \tilde{\delta} > 0.$$
 (4.12)

However, due to $\mathcal{R}_0 \leq 1$, lemma 4.2 implies that $(u, v, h)(x, t) \equiv (\frac{\beta}{\mu}, 0, 0)$ for all $(x, t) \in \mathbb{R}^2$, which contradicts (4.12). We complete the proof of theorem 2.7.

5. Minimal wave speed

In this section, we prove the travelling wave results given in theorem 2.5. Let $\chi(\xi) = \phi(\xi) + \varphi(\xi)$, then

$$c\chi'(\xi) = \chi''(\xi) + \chi(\xi) [\beta - \mu \chi(\xi)], \quad \xi \in \mathbb{R}$$

such that

$$\liminf_{\xi \to -\infty} \chi(\xi) > 0, \quad \liminf_{\xi \to \infty} \chi(\xi) > 0$$

by (1.4). From lemma 2.1, we have the following conclusion.

Lemma 5.1. A solution of (1.3) and (1.4) must satisfy

$$\phi(\xi) + \varphi(\xi) = \beta/\mu, \quad \phi(\xi), \varphi(\xi) \in (0, \beta/\mu), \ \xi \in \mathbb{R}.$$

By lemma 5.1, it suffices to study the monotone solutions of the following coupled system

$$\begin{cases}
c\varphi'(\xi) = \varphi''(\xi) + \sigma_1(\beta/\mu - \varphi(\xi))\psi(\xi) - \beta\varphi(\xi), \\
c\psi'(\xi) = d\psi''(\xi) + \sigma_2 H_s \varphi(\xi) - \rho\psi(\xi), \\
\lim_{\xi \to -\infty} (\varphi(\xi), \psi(\xi)) = (0, 0), \quad \liminf_{\xi \to \infty} \varphi(\xi) > 0, \quad \liminf_{\xi \to \infty} \psi(\xi) > 0.
\end{cases} (5.1)$$

Note that (5.1) is the wave profile system of (2.5). It directly follows from lemma 2.4 that the existence, nonexistence and monotonicity of solutions for (5.1) are obtained if $\mathcal{R}_0 > 1$.

To better show the uniqueness of travelling wave solutions and provide a simple method to compute c^* , we further reduce the problem (5.1) to a scalar equation. Since a travelling wave solution is a special entire solution, it follows that $\psi(\xi) := (J * \varphi)(\xi)$ satisfies (2.8). Therefore, $\varphi(\xi)$ satisfies the following differential-integral equation

$$c\varphi'(\xi) = \varphi''(\xi) + \sigma_1(\beta/\mu - \varphi(\xi))(J * \varphi)(\xi) - \beta\varphi(\xi). \tag{5.2}$$

From the second definition of c^* in § 2, we recall

$$c^*:=\inf\left\{c>0:\Lambda(\gamma,c)=0\text{ has exact one positive root if}\right.$$

$$\gamma\in\left(0,(c+\sqrt{c^2+4d\rho})/(2d)\right)\right\},$$

where $\Lambda(\gamma, c)$ is defined by (2.9).

Due to the equivalence between (5.1) and (5.2), it suffices to solve (5.2) with asymptotic boundary condition $\lim_{\xi \to -\infty} \varphi(\xi) = 0$, $\liminf_{\xi \to \infty} \varphi(\xi) > 0$. By the theory of travelling wave solutions in nonlocal delayed equations [13, 42, 50, 60, 65], we immediately have the following existence, nonexistence, monotonicity and uniqueness of travelling wave solutions (for very recent results, see [60, theorems 2.1 and 2.2]).

LEMMA 5.2. Suppose that $\mathcal{R}_0 > 1$. For any $c \ge c^*$, (5.2) has a positive solution $\varphi(\xi)$ with

$$\lim_{\xi \to -\infty} \varphi(\xi) = 0, \quad \lim_{\xi \to \infty} \varphi(\xi) = V_i^*. \tag{5.3}$$

In particular, such a travelling wave solution is strictly increasing and unique in the sense of phase shift. For any $0 < c < c^*$, (5.2) has no positive solution $\varphi(\xi)$ satisfying (5.3). Moreover, c^* is the minimal wave speed of (5.2) and (5.3).

Combining lemmas 5.1 and 5.2 with (5.1), we obtain the existence, nonexistence, uniqueness and monotonicity of (ϕ, ψ) . This completes the proof of travelling wave problem in theorem 2.5.

6. Numerical simulations

In this section, we illustrate the above theoretical results by performing numerical simulations in two examples. We select $\beta = \mu = H_s = 1$ and consider the following

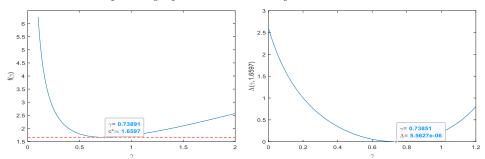


Figure 1. The plot of the functions $f(\gamma)$ and $\Lambda(\gamma, 1.6597)$.

system

$$\begin{cases} \partial_{t}V_{s} = \partial_{xx}V_{s} + (V_{s} + V_{i})(1 - V_{s}) - \sigma_{1}H_{i}V_{s} & x \in \mathbb{R}, \ t > 0, \\ \partial_{t}V_{i} = \partial_{xx}V_{i} + \sigma_{1}H_{i}V_{s} - (V_{s} + V_{i})V_{i}, & x \in \mathbb{R}, \ t > 0, \\ \partial_{t}H_{i} = d\partial_{xx}H_{i} + \sigma_{2}V_{i} - \rho H_{i}, & x \in \mathbb{R}, \ t > 0, \\ V_{s}(x, 0) = 1, & V_{i}(x, 0) = H_{i}(x, 0) = \mathbf{1}_{x \in [-5, 0]}, & x \in \mathbb{R}. \end{cases}$$

$$(6.1)$$

By results in $\S 2$, we obtain that

$$\mathcal{R}_0 = \frac{\sigma_1 \sigma_2}{\rho}, \quad (V_s^*, V_i^*, H_i^*) = \left(\frac{\rho}{\sigma_1 \sigma_2}, \ 1 - \frac{\rho}{\sigma_1 \sigma_2}, \frac{\sigma_2}{\rho} - \frac{1}{\sigma_1}\right), \quad E_1 = (1, 0, 0).$$

Example 6.1. Consider the following special case of (6.1)

$$\begin{cases} \partial_t V_s = \partial_{xx} V_s + (V_s + V_i)(1 - V_s) - 1.5H_i V_s & x \in \mathbb{R}, \ t > 0, \\ \partial_t V_i = \partial_{xx} V_i + 1.5H_i V_s - (V_s + V_i) V_i, & x \in \mathbb{R}, \ t > 0, \\ \partial_t H_i = 1.2\partial_{xx} H_i + 1.2V_i - 0.5H_i, & x \in \mathbb{R}, \ t > 0. \end{cases}$$
(6.2)

We have

$$\mathcal{R}_0 = 3.6 > 1, \quad c^* \approx 1.6597, \ (V_s^*, V_i^*, H_i^*) \approx (0.2778, 0.7222, 1.7333),$$

where c^* is defined by (see Fig. 1)

$$c^* := \min_{\gamma > 0} \frac{2.2\gamma^2 - 1.5 + \sqrt{\left[0.2\gamma^2 + 0.5\right]^2 + 7.2}}{2\gamma} := \min_{\gamma > 0} f(\gamma)$$

and

$$\begin{split} c^* := \inf \left\{ c > 0 : \Lambda(\gamma,c) = \gamma^2 - c\gamma - 1 - \frac{1.8}{(1.2\gamma^2 - c\gamma - 0.5)} = 0 \right. \\ \text{has exact one positive root if } \gamma \in \left(0, (c + \sqrt{c^2 + 2.4})/2.4\right) \right\}. \end{split}$$

Figure 2 shows the spatial-temporal evolution of V_s , V_i and H_i defined by (6.2). We show the distributions of three components at t = 200 in the first figure of

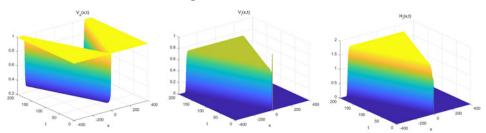


Figure 2. The spatio-temporal plots of the solution (V_s, V_i, H_i) of system (6.2).

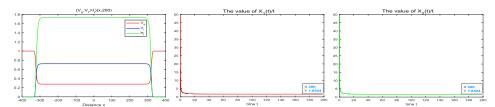


Figure 3. The graphs of the solution $(V_s, V_i, H_i)(x, 200)$, $X_1(t)/t$ and $X_2(t)/t$ for (6.2).

Table 1. Numerical speed c_{num} vs. theoretical speed c^*

| | $c_{num}^{V_i}$ | $c_{num}^{H_i}$ | c^* | $c_{num}^{V_i} - c^*$ | $c_{num}^{H_i} - c^*$ |
|-------------|-----------------|-----------------|--------|-----------------------|-----------------------|
| Example 6.1 | 1.6524 | 1.6524 | 1.6597 | -0.0073 | -0.0073 |

figure 3. From figure 2, we find that V_i , H_i almost invade at a constant speed. In order to estimate the invasion speed, we introduce the level set to describe the expansion speed of fronts. Denote

$$\begin{split} X_1(t) &= \sup \left\{ x \mid V_i(x,t) > 0.005 \right\}, \quad X_2(t) = \sup \left\{ x \mid H_i(x,t) > 0.005 \right\}, \\ c_{num}^{V_i} &:= X_1(200)/200, \quad c_{num}^{H_i} := X_2(200)/200. \end{split}$$

We estimate the invasion speeds of V_i and H_i by $X_1(t)/t$ and $X_2(t)/t$ in figure 3, which indicates that if t is large, then $X_1(t)/t$, $X_2(t)/t$ are close to c^* (see table I). From figures 2–3, we also see the solution (V_s, V_i, H_i) on any compact interval converges to (V_s^*, V_i^*, H_i^*) , which illustrates theorem 2.5.

EXAMPLE 6.2. Consider the following special case of (6.1)

$$\begin{cases} \partial_t V_s = \partial_{xx} V_s + (V_s + V_i)(1 - V_s) - 1.5H_i V_s & x \in \mathbb{R}, \ t > 0, \\ \partial_t V_i = \partial_{xx} V_i + 1.5H_i V_s - (V_s + V_i) V_i, & x \in \mathbb{R}, \ t > 0, \\ \partial_t H_i = 1.8\partial_{xx} H_i + 1.5V_i - \rho H_i, & x \in \mathbb{R}, \ t > 0. \end{cases}$$
(6.3)

We have two cases.

(i) When $\rho = 2.5$, $\mathcal{R}_0 = 0.9 < 1$. Simulations of this case are presented in figures 4 and 5.

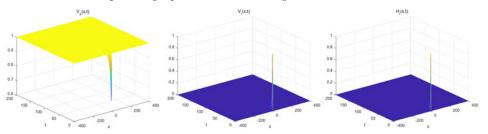


Figure 4. The spatio-temporal plots of the solution (V_s, V_i, H_i) of (6.3) with $\rho = 2.5$.

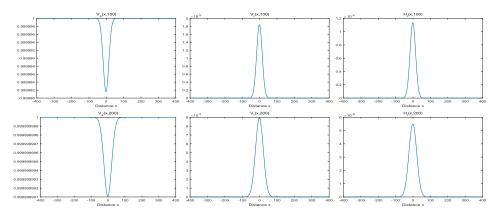


Figure 5. The spatial plots of the solution (V_s, V_i, H_i) of (6.3) with $\rho = 2.5$ when t = 100, 200.

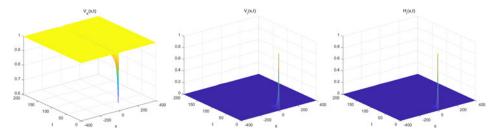
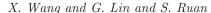


Figure 6. The spatio-temporal plots of the solution (V_s, V_i, H_i) of (6.3) with $\rho = 2.25$.

(ii) When $\rho = 2.25$, $\mathcal{R}_0 = 1$. Simulations of this case are presented in figures 6 and 7.

Figures 4–7 simulate the spatial-temporal evolutions of V_s , V_i and H_i defined by (6.3). They show the spatial distributions of the three components, which demonstrate that when the basic reproduction number $\mathcal{R}_0 \leq 1$, V_i and H_i cannot invade successfully and will vanish as t tends to infinity. This illustrates theorem 2.7.



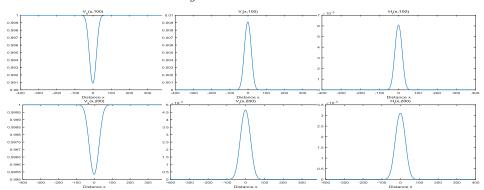


Figure 7. The spatial plots of the solution (V_s, V_i, H_i) of (6.3) with $\rho = 2.25$ when t = 100, 200.

7. Discussion

26

In the present paper, we mainly investigated the spreading speed and travelling wave solutions of the diffusive vector-borne disease model (1.2). The lack of comparison principle for this model makes it nontrivial to estimate the bounds of the spreading speed. To overcome this difficulty, we combined the idea of uniform persistence [9] from dynamical system theory [35] with the generalized principal eigenvalue problem of a weakly coupled elliptic system. From the definition of spreading speed, this could help us to identify the factors that affect the disease spreading. Additionally, when the disease invades successfully, we further showed that solutions converge to a unique positive steady state by constructing two control systems and using monotone dynamical system arguments in Zhao [64]. Note that a similar convergence result was obtained by employing Lyapunov approach in [5]. However, the convergence in Cai et al. [5] requires that $1 < \mathcal{R}_0 < 3$, whereas our method removes this restriction such that it is possible to improve their conclusions.

Returning to the original model (1.1) proposed in Fitzgibbon et al. [16], their main goal was to illustrate the influences on the dynamics of an outbreak, in both the geographical spread and the final size of the epidemic caused by the spatial heterogeneity of vectors and hosts. Recently, Li and Zhao [26] considered a time-periodic model based on (1.1) and obtained the global dynamics. Their numerical results showed that the neglect of seasonality underestimates the value of \mathcal{R}_0 and the maximum carrying capacity affects the spread of the Zika virus. In [3, 4, 12, 22, 59, 63], the propagation dynamics of spatial heterogeneity models have been widely studied. Motivated by the phenomena in these studies, the propagation dynamics of the following system

$$\begin{cases} \partial_t V_s = \nabla \cdot (d_1(x,t) \nabla V_s) \\ + (V_s + V_i) [\beta(x,t) - \mu(x,t) V_s] - \sigma_1(x,t) H_i V_s, & x \in \mathbb{R}, t > 0, \\ \partial_t V_i = \nabla \cdot (d_1(x,t) \nabla V_i) + \sigma_1(x,t) H_i V_s - \mu(x,t) (V_s + V_i) V_i, & x \in \mathbb{R}, t > 0, \\ \partial_t H_i = \nabla \cdot (d_2(x,t) \nabla H_i) + \sigma_2(x,t) H_s(x,t) V_i - \rho(x,t) H_i, & x \in \mathbb{R}, t > 0, \\ V_s(0,x) = V_{s,0}(x), \ V_i(0,x) = V_{i,0}(x), \ H_i(0,x) = H_{i,0}(x), & x \in \mathbb{R} \end{cases}$$

$$(7.1)$$

deserves further investigation, in which all the coefficients are space-time dependent functions and have the same epidemiological meanings as in (1.1). We believe that more complicated dynamics will arise in (7.1). In fact, even if in scalar equations with spatio-temporal dependent coefficients, the propagation dynamics may be richer comparing with the case of constant coefficients. There might exist generalized transition waves [3] that are quite different from classical travelling waves. For space-time periodic habitat, there might occur a gap between the lower bound and upper bound of the spreading speed caused by spatial heterogeneity [12, 22], which is different from that of (1.2). Investigating the effects of spatial heterogeneity and seasonality on spreading speed, pulsating wave speed and \mathcal{R}_0 may provide us some constructive suggestions to prevent the spread of the Zika virus. Before studying generalized transition waves, pulsating waves, and spreading speeds, we first need to explore the steady state problems including the existence and stability. However, the lack of comparison principle and the heterogeneous habitat make it more difficult to investigate the existence and stability of some desirable space-time periodic entire solutions, estimate the spreading speed and establish the existence of generalized transition waves or pulsating waves. These are challenging problems and deserve further consideration.

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References

- 1 D. G. Aronson and H. F. Weinberger, Nonlinear diffusion in population genetics, combustion, and nerve pulse propagation. In *Partial Differential Equations and Related Topics* (ed. J.A. Goldstein), Lecture Notes in Math, Vol. 446, pp. 5–49 (Springer, Berlin, 1975).
- 2 D. G. Aronson and H. F. Weinberger. Multidimensional nonlinear diffusion arising in population dynamics. *Adv. Math.* **30** (1978), 33–76.
- H. Berestycki and F. Hamel. Generalized transition waves and their properties. Comm. Pure Appl. Math. 65 (2012), 592–648.
- 4 H. Berestycki, F. Hamel and G. Nadin. Asymptotic spreading in heterogeneous diffusive excitable media. J. Funct. Anal. 255 (2008), 2146–2189.
- 5 Y. Cai, K. Wang and W. Wang. Global transmission dynamics of a Zika virus model. Appl. Math. Lett. 92 (2019), 190–195.
- 6 X. Chen and J. C. Tsai. Spreading speed in a farmers and hunter-gatherers model arising from Neolithic transition in Europe. J. Math. Pures Appl. 143 (2020), 192–207.
- 7 Y. Du. Order Structure and Topological Methods in Nonlinear Partial Differential Equations: Maximum Principles and Applications (New Jersey: World Scientific, 2006).
- 8 A. Ducrot. Convergence to generalized transition waves for some Holling-Tanner preypredator reaction-diffusion system. J. Math. Pures Appl. 100 (2013), 1–15.
- A. Ducrot. Spatial propagation for a two component reaction-diffusion system arising in population dynamics. J. Differ. Equ. 260 (2016), 8316–8357.
- A. Ducrot, T. Giletti, J.-S. Guo and M. Shimojo. Asymptotic spreading speeds for predatorprey system with two predators and one prey. *Nonlinearity* 34 (2021), 669–704.

- A. Ducrot, T. Giletti and H. Matano. Spreading speeds for multidimensional reactiondiffusion systems of the prey-predator type. Calc. Var. Partial Differ. Equ. 58 (2019), 137.
- 12 J. Fang, X. Yu and X.-Q. Zhao. Traveling waves and spreading speeds for time-space periodic monotone systems. J. Funct. Anal. 272 (2017), 4222–4262.
- 13 J. Fang and X.-Q. Zhao. Existence and uniqueness of traveling waves for non-monotone integral equations with applications. J. Differ. Equ. 248 (2010), 2199–2226.
- 14 C. Favier, D. Schmit, C. D. M. M. Graf, B. Cazelles, N. Degallier, B. Mondet and M. A. Dubois. Influence of spatial heterogeneity on an emerging infectious disease: the case of dengue epidemics. *Proc. R. Soc. B* 272 (2005), 1171–1177.
- W. E. Fitzgibbon and M. Langlais, Simple models for the transmission of microparasites between host populations living on non coincident spatial domain. In Structured Population Models in Biology and Epidemiology (eds. P. Magal and S. Ruan), Lecture Notes in Math. Vol. 1936, 115–164 (Springer-Verlag, Berlin, 2008).
- W. E. Fitzgibbon, J. J. Morgan and G. F. Webb. An outbreak vector-host epidemic model with spatial structure: the 2015-2016 Zika outbreak in Rio De Janeiro. Theor. Biol. Med. Modell. 14 (2017), 2–17.
- W. E. Fitzgibbon, M. E. Parrott and G. F. Webb. Diffusion epidemic models with incubation and crisscross dynamics. *Math. Biosci.* 128 (1995), 131–155.
- D. Gao, Y. Lou, D. He, T. C. Porco, Y. Kuang, G. Chowell and S. Ruan. Prevention and control of Zika as a mosquito-borne and sexually transmitted disease: a mathematical modeling analysis. Sci. Rep. 6 (2016), 28070.
- L. Girardin. Non-cooperative Fisher-KPP systems: traveling waves and long-time behavior. Nonlinearity 31 (2018), 108–164.
- 20 C.-H. Hsu and T.-S. Yang. Existence, uniqueness, monotonicity and asymptotic behaviour of travelling waves for epidemic models. *Nonlinearity* 26 (2013), 121–139.
- 21 S.-B. Hsu and X.-Q. Zhao. Spreading speeds and traveling waves for nonmonotone integrodifference equations. SIAM J. Math. Anal. 40 (2008), 776–789.
- 22 L. Kong, N. Rawal and W. Shen. Spreading speeds and linear determinacy for two species competition systems with nonlocal dispersal in periodic habitats. *Math. Model. Nat. Phenom.* 10 (2015), 113–141.
- O. A. Ladyženskaya, V. A. Solonnikov and N. N. Ural'ceva, Linear and Quasilinear Equation of Parabolic Type, AMS Translations of Mathematical Monographs (Providence, RI. 1968).
- 24 M. A. Lewis, J. Renclawowicza and P. van den Driessche. Traveling waves and spread rates for a West Nile virus model. Bull. Math. Biol. 68 (2006), 3–23.
- B. Li, M. A. Lewis and H. F. Weinberger. Existence of traveling waves for integral recursions with nonmonotone growth functions. J. Math. Biol. 58 (2009), 323–338.
- 26 F. Li and X.-Q. Zhao. Global dynamics of a reaction-diffusion model of Zika virus transmission with seasonality. Bull. Math. Biol. 83 (2021), 43.
- 27 X. Liang, Y. Yi and X.-Q. Zhao. Spreading speeds and traveling waves for periodic evolution systems. J. Differ. Equ. 231 (2006), 57–77.
- 28 X. Liang and X.-Q. Zhao. Asymptotic speeds of spread and traveling waves for monotone semiflows with applications. *Comm. Pure Appl. Math.* **60** (2007), 1–40.
- 29 G. Lin, Y. Niu, S. Pan and S. Ruan. Spreading speed in an integrodifference predator-prey system without comparison principle. Bull. Math. Biol. 82 (2020), 53.
- 30 G. Lin, S. Pan and X.-P. Yan. Spreading speeds of epidemic models with nonlocal delays. Math. Biosci. Eng. 16 (2019), 7562–7588.
- 31 L. P. Lounibos. Invasions by insect vectors of human disease. Annu. Rev. Entomol. 47 (2002), 233–266.
- 32 R. Lui. Biological growth and spread modeled by systems of recursions. I. mathematical theory. *Math. Biosci.* **93** (1989), 269–295.
- 33 P. Magal, G. Webb and Y. Wu. On a vector-host epidemic model with spatial structure. Nonlinearity 31 (2018), 5589–5614.
- 34 P. Magal, G. Webb and Y. Wu. On the basic reproduction number of reaction-diffusion epidemic models. SIAM J. Appl. Math. 79 (2019), 284–304.

- 35 P. Magal and X.-Q. Zhao. Global attractors and steady states for uniformly persistent dynamical systems. SIAM J. Math. Anal. 37 (2005), 251–275.
- 36 N. A. Maidana and H. M. Yang. Spatial spreading of West Nile virus described by traveling waves. J. Theoret. Biol. 258 (2009), 403–417.
- 37 J. D. Murray. Mathematical Biology II. Spatial Models and Biomedical Applications, 3rd ed. (Springer-Verlag, New York, 2003).
- 38 S. Pan. Invasion speed of a predator-prey system. Appl. Math. Lett. 74 (2017), 46–51.
- 39 Pan American Health Organization (PAHO), Chikungunya, www.paho.org/hq/index.php? option=com_topics&view=article&id=343&Itemid=40931&lang=en.
- 40 PAHO, Zika virus infection, www.paho.org/hq/index.php?option=com_content&view= article&id=11585&Itemid=41688&lang=en.
- 41 L. Rass and J. Radcliffe, Spatial Deterministic Epidemics, Math. Surveys Monogr. Vol. 102 (Amer. Math. Soc., Providence, PI, 2003).
- 42 S. Ruan and D. Xiao. Stability of steady states and existence of travelling waves in a vector-disease model. *Proc. Roy. Soc. Edinburgh Sect. A* **134** (2004), 991–1011.
- 43 S. Ruan and J. Wu, Modeling spatial spread of communicable diseases involving animal hosts. In *Spatial Ecology* (eds. S. Cantrell, C. Cosner and S. Ruan), pp. 293–316 (Chapman & Hall/CRC, Boca Raton, FL, 2009).
- 44 N. Shigesada and K. Kawasaki. Biological Invasions: Theory and Practice (Oxford, New York, 1997).
- J. Smoller. Shock Waves and Reaction Diffusion Equations, (Springer-Verlag, New York, 1994).
- 46 S. T. Stoddard, B. M. Forshey, A. C. Morrison, V. A. Paz-Soldan, G. M. Vazquez-Prokopec et al. House-to-house human movement drives dengue virus transmission. Proc. Natl. Acad. Sci. USA 110 (2009), 994–999.
- 47 S. T. Stoddard, A. C. Morrison, G. M. Vazquez-Prokopec, V. Paz Soldan, T. J. Kochel et al.The role of human movement in the transmission of vector borne pathogens. PLoS Negl. Trop. Dis. 3 (2009), e481.
- 48 H. Wang. Spreading speeds and traveling waves for non-cooperative reaction-diffusion systems. J. Nonlinear Sci. 21 (2011), 747–783.
- 49 W. Wang and X.-Q. Zhao. A nonlocal and time-delayed reaction-diffusion model of dengue transmission. SIAM J. Appl. Math. 71 (2011), 147–168.
- 50 Z.-C. Wang, W.-T. Li and S. Ruan. Traveling fronts in monostable equations with nonlocal delayed effects. J. Dynam. Differ. Equ. 20 (2008), 573–607.
- 51 H. F. Weinberger. Long-time behavior of a class of biological model. SIAM J. Math. Anal. 13 (1982), 353–396.
- 52 H. F. Weinberger. On spreading speeds and traveling waves for growth and migration models in a periodic habitat. *J. Math. Biol.* **45** (2002), 511–548.
- 53 H. F. Weinberger, K. Kawasaki and N. Shigesada. Spreading speeds for a partially cooperative 2-species reaction-diffusion model. *Discrete Contin. Dyn. Syst.* 23 (2009), 1087–1098.
- 54 H. F. Weinberger, M. A. Lewis and B. Li. Analysis of linear determinacy for spread in cooperative models. J. Math. Biol. 45 (2002), 183–218.
- World Health Organization (WHO), Dengue and severe dengue, Updated 23 June 2020. https://www.who.int/news-room/fact-sheets/detail/dengue-and-severe-dengue.
- 56 WHO, Zika virus. Updated 20 July 2018. https://www.who.int/news-room/fact-sheets/detail/zika-virus.
- 57 S.-L. Wu and C.-H. Hsu. Existence of entire solutions for delayed monostable epidemic models. Trans. Amer. Math. Soc. 368 (2016), 6033–6062.
- 58 D. Xiao and R. Mori. Spreading properties of a three-component reaction-diffusion model for the population of farmers and hunter-gatherers. Ann. Inst. H. Poincaré Anal. Non Linéaire 38 (2021), 911–951.
- 59 J. Xin. Front propagation in heterogeneous media. SIAM Rev. 42 (2000), 161–230.
- 60 Z. Xu and D. Xiao. Spreading speeds and uniqueness of traveling waves for a reaction diffusion equation with spatio-temporal delays. J. Differ. Equ. 260 (2016), 268–303.

X. Wang and G. Lin and S. Ruan

30

- 61 Q. Ye, Z. Li, M. Wang and Y. Wu. Introduction to Reaction-Diffusion Equations, 2nd ed. (Science Press, Beijing, 2011).
- 62 T. Yi, Y. Chen and J. Wu. Unimodal dynamical systems: comparison principles, spreading speeds and travelling waves. J. Differ. Equ. 254 (2013), 3538–3572.
- 63 X. Yu and X.-Q. Zhao. Propagation phenomena for a reaction-advection-diffusion competition model in a periodic habitat. J. Dynam. Differ. Equ. 29 (2017), 41–66.
- 64 X.-Q. Zhao. Dynamincal Systems in Population Biology, 2nd ed. (Springer, New York, 2017).
- 65 X.-Q. Zhao and D. Xiao. The asymptotic speed of spread and traveling waves for a vector disease model. J. Dynam. Differ. Equ. 18 (2006), 1001–1019.