GLOBAL DYNAMICS AND TRAVELLING WAVE SOLUTIONS FOR A CLASS OF NON-COOPERATIVE REACTION-DIFFUSION SYSTEMS WITH NONLOCAL INFECTIONS

WEI WANG AND WANBIAO MA

Department of Applied Mathematics, School of Mathematics and Physics
University of Science and Technology Beijing, Beijing 100083, China

(Communicated by Yuan Lou)

Abstract. We consider a class of non-cooperative reaction-diffusion system, which includes different types of incidence rates for virus dynamical models with nonlocal infections. Threshold dynamics are expressed by basic reproduction number $R_0$ in the following sense, if $R_0 < 1$, the infection-free steady state is globally attractive, implying infection becomes extinct; while if $R_0 > 1$, virus will persist. To study the invasion speed of virus, the existence of travelling wave solutions is studied by employing Schauder’s fixed point theorem. The method of constructing super-solutions and sub-solutions is very technical. The mathematical difficulty is the problem constructing a bounded cone to apply the Schauder’s fixed point theorem. As compared to previous mathematical studies for diffusive virus dynamical models, the novelty here is that we successfully establish the general existence result of travelling wave solutions for a class of virus dynamical models with complex nonlinear transmissions and nonlocal infections.

1. Introduction. Mathematical models have been shown to be an effective and valuable approach to understand virus infection dynamics in the within-host environment. The dynamical properties of human immunodeficiency virus-1 (HIV-1), hepatitis B virus (HBV) and human T-cell leukemia type-1 (HTLV-1) infections have been discussed with the help of mathematical models. Most of these works are based on the assumption that cells and viruses are well mixed.

Spatial structure is important to understand the dynamical behaviour of virus infection. In [38], Wang and Wang proposed a model to simulate the HBV infection with spatial dependence. They assume that target cells and infected cells cannot move, while virus can move according to Fickian diffusion. For this model, the non-existence of travelling wave solutions is studied by employing the geometric singular perturbation method. The existence of travelling wave solutions is observed numerically. In [53], Xu and Ma made a further investigation for the HBV model with saturation response. Global dynamics for steady states were discussed by constructing the coupled lower-upper solution. In [61], a diffusive HBV model

---

2010 Mathematics Subject Classification. Primary: 34D20, 35C07; Secondary: 35Q92, 92D3.

Key words and phrases. Reaction-diffusion system, nonlinear transmissions, threshold dynamics, travelling wave solutions, nonlocal infections.

The research is partly supported by the China Scholarship Council for W. Wang, the National Natural Science Foundation of China (11471034) and National Key R-D Program of China (2017YFF0207400-0207403) for W. Ma.
with delayed Beddington-DeAngelis response was proposed. Global dynamics and travelling wave solutions were investigated, only considering the diffusion of virus. Some further developments have been performed on diffusive virus dynamical models (see, [44, 45]).

Some recent studies reveal that high concentration of infected cells can promote the diffusion of virus [9]. [26] established a diffusive virus model to study the repulsion effect of super-infecting virions by infected cells (see, also [46]). Numerical computations of the spreading speed have shown that the repulsion of super-infecting virions can promote the spread of virus (see, [26, 46]).

As is known to all, the process of productive infection of CD$^4^+$ T cell with HIV-1 is very complicated, which can be decomposed into several steps: entry of virus into the cell, reverse transcription of virus RNA to DNA, and integration of viral DNA into the host-cell genome [1]. In the past few years, it has been realized that the decreasing of CD$^4^+$ T cells induced by two factors: one is the natural death, and the other is apoptosis which has been considered as the main pathway to cause the decreasing of CD$^4^+$ T cells (see, for example, [2, 29]). However, recent studies in [1] and [4] reveal that only 5% of CD$^4^+$ T cells die due to caspase-3-mediated apoptosis. Most of CD$^4^+$ T cells die due to the caspase-1-mediated pyroptosis in non-activated CD$^4^+$ T cells that have undergone abortive infection [1, 8]. Dying infected CD$^4^+$ T cells can release inflammatory signals which attract more uninfected CD$^4^+$ T cells to die [4]. [51] firstly proposed the following virus infection dynamical model with the caspase-1-mediated pyroptosis

\[
\begin{align*}
\frac{\partial U(x, t)}{\partial t} &= D_0 \Delta U + \xi - \beta U(x, t) \omega(x, t) \frac{1 + a \omega(x, t)}{1 + b M(x, t)} - \frac{q U(x, t) M(x, t)}{1 + b M(x, t)}, \\
\frac{\partial V(x, t)}{\partial t} &= D_0 \Delta V + \int_{\Omega} \Gamma(\tau, x, y) \beta U(y, t - \tau) \omega(y, t - \tau) \frac{1 + a \omega(y, t - \tau)}{1 + b M(y, t - \tau)} dy - d_V V(x, t) - \alpha_1 V(x, t), \\
\frac{\partial M(x, t)}{\partial t} &= D_1 \Delta M + \alpha_2 V(x, t) - d_M M(x, t), \\
\frac{\partial \omega(x, t)}{\partial t} &= D_2 \Delta \omega + k V(x, t) - d_\omega \omega(x, t). 
\end{align*}
\]

(1)

In model (1), $U(x, t)$, $V(x, t)$, $M(x, t)$ and $\omega(x, t)$ describe the concentrations of uninfected cells, infected cells, inflammatory cytokines IL-1 and virus at time $t$ and location $x$, respectively. $\xi$ is the target cell production rate. $\beta$ is the infection rate. $k$ is the virus production rate. $\alpha_1$ is the death rate of infected CD$^4^+$ T cells which are caused by pyroptosis. $\alpha_2$ is the production rate of inflammatory cytokines IL-1 released from infected cells. Inflammatory cytokines IL-1 is assumed to induce the death of uninfected CD$^4^+$ T cells $q U M / (1 + b M)$. The natural death rates of uninfected cells, infected cells, inflammatory cytokines and virus are $d_U$, $d_V$, $d_M$ and $d_\omega$. The diffusion rates of uninfected cells, infected cells, inflammatory cytokines and virus are $D_0$, $D_0$, $D_1$ and $D_2$. Time delay $\tau$ is the average incubation period. Here $\Gamma$ is the Green function associated with $\Delta$ and zero-flux boundary conditions, which satisfies $\int_{\Omega} \Gamma(\tau, x, y) dy = 1, \forall x \in \Omega, \tau > 0$. $\Gamma(\tau, x, y) = \Gamma(\tau, y, x)$ and $\Gamma(\tau, x, y) > 0 \forall x, y \in \Omega, x \neq y, \tau > 0$ (see, [10]). All the parameters in model (1) are assumed to be positive constants.

Usually, an infectious case is firstly found at one location and then the virus spreads to other areas. Thus, an important question for virus infection is: what is the spreading speed? In general, it is challenging to compute the asymptotic
spreading speed. For most of cooperative systems, the asymptotic speed equals the minimal wave speed [19]. However, for some non-cooperative systems, it is challenging to obtain the asymptotic spreading speed, especially for diffusive SIR models and virus models. Travelling wave solutions are an important tool which can be used to describe the spreading speed of population [6, 15, 7, 14, 22, 56, 59, 16, 54, 43, 17, 18, 57, 3, 14, 49, 62, 30].

[20] and [36] have developed the general theory on the existence of travelling wave solutions for monotonic (or cooperative) systems. Obviously, this method can not be applied to the non-monotonic model (1). In the recent years, many methods for the existence of travelling wave solutions for non-cooperative systems have been established. Shooting method is firstly proposed by Dunbar in [6] to investigate the existence of travelling wave solutions for the Lotka-Volterra predator-prey system (non-monotonic). Recently, [17] developed a geometric method to study the existence of travelling wave solutions for a class of non-monotonic systems consisting of two equations with general functions. In [18], Huang made a further investigation for the model proposed in [17] to abandon the restriction condition on the diffusion coefficients. The Schauder’s fixed point theorem is also widely applied to show the existence of travelling wave solutions connecting two steady states [15, 7, 22, 59, 54, 43, 25, 17, 18, 57, 3]. In [57], Zhang et al. developed another method to show the existence of weak travelling wave solutions for a class of non-cooperative systems, which allows us to avoid the difficulties in studying the detailed final state (i.e., steady states, periodic solutions, etc.)

The non-cooperative models in above literatures mostly consist of two equations. To the best of our knowledge, there are few literatures about the existence result of minimal wave speed for non-cooperative systems consisting of more than three equations with complicated nonlinear interaction functions. In [58], Zhang investigated the existence of weak travelling wave solutions for a class of non-cooperative reaction-diffusion systems consisting of three equations. However, the results obtained in [58] cannot be directly applied to study the existence of travelling wave solutions for a class of non-cooperative reaction-diffusion systems with a discrete delay and spatial non-locality. Thus, it is important and necessary to establish the general result for travelling wave solutions for the non-cooperative system with complicated nonlinear interaction functions and a discrete delay and spatial non-locality, which is constituted by more than three equations.

In this paper, we further consider threshold dynamics and travelling wave solutions for the following virus dynamical model with more complex, nonlinear transmissions and nonlocal infections, which is constituted by four equations

\[
\begin{aligned}
\frac{\partial U(x,t)}{\partial t} &= D_0 \Delta U + \xi - f(U(x,t),\omega(x,t))\omega(x,t) - d_U U(x,t) - g(M(x,t))U(x,t), \\
\frac{\partial V(x,t)}{\partial t} &= D_0 \Delta V + \int_{\Omega} \Gamma(y,x)V(y,t-\tau)f(U(y,t-\tau)\omega(y,t-\tau))\omega(y,t-\tau)dy - d_V V(x,t) - \alpha_1 V(x,t), \\
\frac{\partial M(x,t)}{\partial t} &= D_1 \Delta M + g_1(V(x,t)) - d_M M(x,t), \\
\frac{\partial \omega(x,t)}{\partial t} &= D_2 \Delta \omega + g_2(V(x,t)) - d_\omega \omega(x,t).
\end{aligned}
\]

The general functions \(f(U,\omega), g(M), g_1(V)\) and \(g_2(V)\) satisfy the following hypotheses:
(C1) \( f(\cdot, \cdot) \in C^1(\text{cl}(R^2_+)), \overline{f}(\cdot, \cdot) \in C^1(\text{cl}(R^2_+)) \), where \( R^2_+ := \{(U, \omega) : U > 0, \omega > 0\} \)

and \( \overline{f}(U, \omega) = f(U, \omega) \omega, \text{cl}(R^2_+) \) is the closure of \( R^2_+ \) and \( C^1(\text{cl}(R^2_+)) \) is the continuously differentiable function space defined from \( \text{cl}(R^2_+) \) to \( R \).

(C2) \( f(0, \omega) = 0, f_U(U, \omega) \geq 0, \overline{f}_\omega(U, \omega) \geq 0 \) and \( f_\omega(U, \omega) \leq 0 \) for any \( (U, \omega) \in R^2_+ \).

For any positive constant \( \eta \), there exists a positive constant \( K_2 \) such that

\[
\max_{0 \leq U \leq U_0, 0 \leq \omega \leq \eta} \left\{ \overline{f}_U(U, \omega), \overline{f}_\omega(U, \omega) \right\} \leq K_2.
\]

(C3) \( \frac{U}{f(U, \omega)} \) is increasing with respect to \( U \) for \( (U, \omega) \in R^2_+ \).

(C4) \( g(0) = 0, g'(y) \geq 0 \) for \( y \geq 0 \), \( g'(y) \) is non-increasing for \( y \geq 0 \), \( g''(y) \) is continuous for \( y \geq 0 \).

(C5) \( g_i(0) = 0, g_i'(y) \geq 0 \) for \( y \geq 0 \), \( g_i'(y) \) is non-increasing for \( y \geq 0 \). \( g_i''(y) \) is continuous for \( y \geq 0 \), \( i = 1, 2 \).

The above hypotheses (C1 – C3) about \( f(U, \omega) \omega \) can be satisfied by different types of functions including the mass action, the Holling type II function, the saturation incidence, Beddington-DeAngelis incidence function, Crowley-Martin incidence function, and the more generalized incidence functions \([38, 53, 61, 55, 60, 48]\). Obviously, \( g(M) = qM/(1+bM) \), \( g_1(V) = \alpha_2 V \) and \( g_2(V) = kV \) for model (1) satisfying hypotheses (C4) and (C5).

In this paper, we use zero-flux boundary conditions

\[
\frac{\partial U(x, t)}{\partial \nu} = \frac{\partial V(x, t)}{\partial \nu} = \frac{\partial M(x, t)}{\partial \nu} = \frac{\partial \omega(x, t)}{\partial \nu} = 0, \quad x \in \partial \Omega, \ t > 0, \tag{3}
\]

where \( \nu \) is the outward normal to \( \partial \Omega \), and the initial conditions

\[
U(x, \theta) = \phi_1(x, \theta) \geq 0, \ V(x, \theta) = \phi_2(x, \theta) \geq 0, \ M(x, \theta) = \phi_3(x, \theta) \geq 0, \ \omega(x, \theta) = \phi_4(x, \theta) \geq 0, \quad \theta \in [-\tau, 0]. \tag{4}
\]

The purpose of the paper is to discuss global dynamics of model (2) in the case of a bounded domain and the existence of travelling wave solutions of model (2) in the case of an unbounded domain.

The remainder of the paper is organised as follows. In Section 2, we establish global dynamics for virus dynamical models with nonlinear transmissions and nonlocal infections in the case of a bounded spatial domain. In Section 3, the existence of travelling wave solutions is studied in the case of an unbounded domain. Finally, some discussions and conclusions are given in Section 4.

2. In a bounded spatial domain-threshold dynamics. Denoting \( X = C(\Omega, R^4) \) is a Banach space of continuous functions with supremum norm \( \| \cdot \|_X \). We denote the positive cone as \( X_+ = C(\Omega, R^4_+) \). We denote \( Y := C(\Omega, R) \) and \( Y_+ = C(\Omega, R_+) \). Define \( \mathbb{C} = C([-\tau, 0], X) \) with the norm \( \| \phi \| = \sup_{\theta \in [-\tau, 0]} \| \phi(\theta) \|_X \) and \( \mathbb{C}_+ = C([-\tau, 0], X_+) \). Supposing \( M_1(t), M_2(t), M_3(t) \) and \( M_4(t) \) are the strongly continuous semigroups associated with \( D_0 \Delta - d_U, D_0 \Delta - (d_V + \alpha_1), D_1 \Delta -(d_V + \alpha_1) \).
Proof. For any given \( \phi \in \mathbb{C}_+ \), there exists a unique mild solution \( u(t, \cdot, \phi) \) of model (2) defined on its maximal interval of existence \([0, t_\phi)\) with \( u_0 = \phi \), where \( t_\phi \leq \infty \). Further, \( u(t, \cdot, \phi) \in \mathbb{C}_+ \) for all \( t \in [0, t_\phi) \) and \( u(t, \cdot, \phi) \) is a classical solution of model (2) for all \( t > \tau \).
Thus, \( \phi + \dot{k}F(\phi)(x) \in \mathbb{C}_+ \). This implies \( \lim_{k \to +\infty} \frac{1}{k} \text{dist}(\phi + \dot{k}F(\phi)(x), \mathbb{C}_+) = 0 \), for all \( \phi \in \mathbb{C}_+ \). From Corollary 4 in [27] (see, also [52], Corollary 8.1.3), we obtain the conclusion stated in Lemma 2.1. The proof is completed.

We are now in the position to study the well-posedness of model (2) in the sense of the following theorem.

**Theorem 2.2.** For any \( \phi = (\phi_1, \phi_2, \phi_3, \phi_4) \in \mathbb{C}_+ \), model (2) has a unique solution \( u(t, \cdot, \phi) \) on \([0, \infty)\) with \( u_0 = \phi \). Moreover, the solution semiflow \( \Phi(t) = u(t, \cdot, \phi) : \mathbb{C}_+ \to \mathbb{C}_+ \) is compact for \( t \geq 0 \) and has a compact global attractor.

**Proof.** We find that model (2) defines a semiflow: \( \Phi(t) := u_t(\cdot) : \mathbb{C}_+ \to \mathbb{C}_+ \) by

\[
(\Phi(t)\phi)(\theta, x) = u(t + \theta, x, \phi), \quad \forall \theta \in [-\tau, 0], \ x \in \overline{\Omega}.
\]

Let \( \phi = (\phi_1, \phi_2, \phi_3, \phi_4) \in \mathbb{C}_+ \to \mathbb{C}_+ \) and let \( H = U + V \). From model (2), we obtain

\[
\frac{\partial H(x, t)}{\partial t} \leq D_0 \Delta H + \xi - r_1 H,
\]

where \( r_1 = \min\{d_V, d_V + \alpha_1\} \).

From [21], we have that \( \frac{\xi}{r_1} \) is the globally attractive steady state for the parabolic equations

\[
\begin{align*}
\frac{\partial H(x, t)}{\partial t} &= D_0 \Delta H(x, t) + \xi - r_1 H(x, t), \quad x \in \Omega, \ t > 0, \\
\frac{\partial H(x, t)}{\partial \nu} &= 0, \quad x \in \partial \Omega, \ t > 0.
\end{align*}
\]

The comparison principle implies there exists \( t_1(\phi) > 0 \) such that \( H(x, t) \leq \frac{2\xi}{r_1} =: B_1 \) for \( t > t_1 \). Thus, there exists \( t_2(\phi) > 0 \) such that \( M(x, t) \leq \frac{2\xi(B_1)}{d_M} =: B_2 \) for \( t > t_2 \). There exists \( t_3(\phi) > 0 \) such that \( \omega(x, t) \leq \frac{2\xi(B_1)}{d_M} =: B_3 \) for \( t > t_3 \).

Hence, the existence of solutions \( u(t, \cdot, \phi) \) of model (2) claimed in Lemma 2.1 is indeed global (i.e., \( t_\phi = \infty \)). The solution semiflow is point dissipative. According to Theorem 2.2.6 in [52], we get that \( \Phi(t) \) is compact for any \( t \geq 0 \). Thus, from Theorem 3.4.8 in [13], we know that \( \Phi(t) \) has a compact global attractor in \( \mathbb{C}_+ \).

In the following, we establish the threshold-type result on the extinction and uniform persistence of the virus in terms of the basic reproduction number for model (2) in a bounded spatial domain.

Obviously, it is easy to see that model (2) always exists a unique infection-free steady state \( E_0 = (U_0, 0, 0, 0) \), where \( U_0 = \frac{\xi}{d_M} \). Linearizing model (2) at the infection-free steady state \( E_0 \), we obtain that

\[
\begin{align*}
\frac{\partial u_1}{\partial t} &= D_0 \Delta u_1 - d u_1 - g'(0) U_0 u_3 - f(U_0, 0) u_4, \\
\frac{\partial u_2}{\partial t} &= D_0 \Delta u_2 + \int_{\Omega} \Gamma(x, y) f(U_0, 0) u_4 (t - \tau, y) dy - (d_V + \alpha_1) u_2, \\
\frac{\partial u_3}{\partial t} &= D_1 \Delta u_3 + g'_1(0) u_2 - d_M u_3, \\
\frac{\partial u_4}{\partial t} &= D_2 \Delta u_4 + g'_2(0) u_2 - d_\omega u_4,
\end{align*}
\]

satisfying the following boundary conditions

\[
\frac{\partial u_1}{\partial \nu} = \frac{\partial u_2}{\partial \nu} = \frac{\partial u_3}{\partial \nu} = \frac{\partial u_4}{\partial \nu} = 0, \ \forall x \in \partial \Omega, \ t > 0.
\]
We consider the nonlocal eigenvalue problem of model (5) associated with

\[ \lambda \phi_1(x) = D_0 \Delta \phi_1(x) + e^{-\lambda t} \int_\Omega \Gamma(\tau, x, y) f(U_0, 0) \phi_2(y) dy - (d_\nu + \alpha_1) \phi_1(x), \]

\[ \lambda \phi_2(x) = D_2 \Delta \phi_2(x) + g_2'(0) \phi_1(x) - d_\omega \phi_2(x), \]  

\[ \frac{\partial \phi_1(x)}{\partial \nu} = \frac{\partial \phi_2(x)}{\partial \nu} = 0, \ \forall x \in \partial \Omega, \ t > 0, \ \phi = (\phi_1, \phi_2) \in Y \times Y. \]  

We firstly consider the following model

\[
\begin{aligned}
\frac{\partial u_1}{\partial t} &= D_0 \Delta u_1 - du_1 - g'(0) U_0 u_3 - f(U_0, 0) u_4, \\
\frac{\partial u_2}{\partial t} &= D_0 \Delta u_2 + \int_\Omega \Gamma(\tau, x, y) f(U_0, 0) u_4(t, y) dy - (d_\nu + \alpha_1) u_2, \\
\frac{\partial u_3}{\partial t} &= D_1 \Delta u_3 + g_1'(0) u_2 - d_M u_3, \\
\frac{\partial u_4}{\partial t} &= D_2 \Delta u_4 + g_2'(0) u_2 - d_\omega u_4.
\end{aligned}
\]  

Substituting \( u_2(x, t) = e^{M \phi_1(x)} \) and \( u_4(x, t) = e^{M \phi_2(x)} \) into equations of \( u_2 \) and \( u_4 \), we have the following eigenvalue problem of model (7)

\[
\begin{aligned}
\lambda \phi_1(x) &= D_0 \Delta \phi_1(x) + \int_\Omega \Gamma(\tau, x, y) f(U_0, 0) \phi_2(y) dy - (d_\nu + \alpha_1) \phi_1(x), \\
\lambda \phi_2(x) &= D_2 \Delta \phi_2(x) + g_2'(0) \phi_1(x) - d_\omega \phi_2(x), \\
\frac{\partial \phi_1(x)}{\partial \nu} &= \frac{\partial \phi_2(x)}{\partial \nu} = 0, \ \forall x \in \partial \Omega, \ t > 0, \ \phi = (\phi_1, \phi_2) \in Y \times Y.
\end{aligned}
\]  

By the similar argument to Theorem 7.6.1 in [32], eigenvalue problem (8) has a principal eigenvalue \( \lambda_0 \) with a positive eigenfunction.

From Theorem 2.2 in [34], we get the following result.

**Lemma 2.3.** The eigenvalue problem (6) has a principal eigenvalue \( \lambda_0 \) with a strictly positive eigenfunction, and for any \( \tau \geq 0 \), \( \lambda_0 \) has the same sign as \( \lambda_0 \).

From Theorem 2.3 in [47] (see, also [5, 35, 37, 11]), we can show that the basic reproduction number \( R_0 \) of model (2) equals the spectral radius of the following \( 2 \times 2 \) matrix

\[
\begin{pmatrix}
0 & \frac{f(U_0, 0)}{d_\nu + \alpha_1} \\
g_2'(0) & 0
\end{pmatrix},
\]

and hence

\[ R_0 = \sqrt{g_2'(0) f(U_0, 0)} / (d_\omega (d_\nu + \alpha_1)). \]

By Theorem 3.1 (i) in [37], we then obtain the following Lemma.

**Lemma 2.4.** \( R_0 - 1 \) has the same sign as \( \lambda_0 \).

**Theorem 2.5.** If \( R_0 < 1 \), then the infection-free steady state \( E_0 \) is globally attractive for model (2).

If \( R_0 > 1 \), then model (2) has at least one coexistence steady state and there exists \( \zeta > 0 \) such that any nonnegative solution \( u(t, x, \phi) \) with \( \phi_2(0) \neq 0 \) and \( \phi_4(0) \neq 0 \) such that

\[ \liminf_{t \to \infty} V(x, t) \geq \zeta, \ \liminf_{t \to \infty} \omega(x, t) \geq \zeta, \]
uniformly for all \( x \in \overline{\Omega} \).

**Proof.** From Lemma 2.4, we obtain \( \lambda_0(U_0) < 0 \) when \( R_0 < 1 \). Since \( \lim_{t \to 0} \lambda_0(U_0 + \varepsilon) = \lambda_0(U_0) < 0 \), there exists \( \varepsilon_0 > 0 \) sufficiently small such that \( \lambda_0(U_0 + \varepsilon_0) < 0 \). Applying the comparison theorem to the first equation in model (2), one obtains

\[
\limsup_{t \to \infty} U(x,t) \leq U_0 + \varepsilon_0 \quad \text{for all } t \geq T_2, x \in \overline{\Omega}.
\]

Thus, for fixed \( \varepsilon_0 > 0 \), there exists \( T_2 > 0 \) such that \( U(x,t) \leq U_0 + \varepsilon_0 \) for all \( t \geq T_2, x \in \overline{\Omega} \). Therefore, for all \( t \geq T_2 \), we obtain the following

\[
\begin{cases}
\frac{\partial V}{\partial t} &\leq D_0 \Delta V + \int_{\Omega} \Gamma(\tau,x,y) f(U_0 + \varepsilon_0,0) \omega(y,t-\tau) dy - (\alpha_1 + d_V) V, \\
\frac{\partial M}{\partial t} &\leq D_1 \Delta M + g_1'(0) V - d_M M, \\
\frac{\partial u}{\partial t} &\leq D_2 \Delta u + g_2'(0) V - d_u u, \\
\frac{\partial \omega}{\partial t} &\leq \alpha e \omega - d_\omega \omega.
\end{cases}
\]

By Lemma 2.4, \( \lambda_0(U_0 + \varepsilon_0) < 0 \), and there exists a strongly positive eigenfunction \( \psi_0 \) corresponding to \( \lambda_0(U_0 + \varepsilon_0) < 0 \). It then obtains the following linear system

\[
\begin{cases}
\frac{\partial u_2}{\partial t} & = D_0 \Delta u_2 + \int_{\Omega} \Gamma(\tau,x,y) f(U_0 + \varepsilon_0,0) u_2(y,t-\tau) dy - (\alpha_1 + d_V) u_2, \\
\frac{\partial u_3}{\partial t} & = D_1 \Delta u_3 + g_1'(0) u_2 - d_M u_3, \\
\frac{\partial u_4}{\partial t} & = D_2 \Delta u_4 + g_2'(0) u_2 - d_u u_4, \\
\frac{\partial \omega}{\partial t} & = \alpha \omega - d_\omega \omega = 0, \quad x \in \overline{\Omega},
\end{cases}
\]

admits a solution \( u(t,x) = e^{\lambda_0(U_0+\varepsilon_0)t} \psi_0(x) \). Then for any given \( \phi \in C_+ \), there exists \( \hat{\alpha} > 0 \) such that \( (V(t,\cdot,\phi), M(t,\cdot,\phi), \omega(t,\cdot,\phi)) \leq \hat{\alpha} u(t,\cdot), \quad t \in [T_2-\tau, T_2] \). The comparison principle yields

\[
(V(t,x,\phi), M(t,x,\phi), \omega(t,x,\phi)) \leq \hat{\alpha} e^{\lambda_0(U_0+\varepsilon_0)t} \psi_0(x), \quad \forall t \geq T_2.
\]

Then \( \lim_{t \to \infty} (V(t,x,\phi), M(t,x,\phi), \omega(t,x,\phi)) = 0 \) uniformly for \( x \in \overline{\Omega} \). Thus, in view of [21], we obtain that \( \lim_{t \to \infty} U(t,x,\phi) = U_0 \) uniformly for \( \forall x \in \overline{\Omega} \). Then, the infection-free steady state \( E_0 \) of model (2) is globally attractive if \( R_0 < 1 \).

For \( R_0 > 1 \), we employ the persistence theory developed in [31] to study uniform persistence of model (2). From model (2), (C3) and (C4), we get that

\[
\frac{\partial U(x,t)}{\partial t} = D_0 \Delta U + \xi - f(U(x,t),\omega(x,t)) \omega(x,t) - d_U U(x,t) - g(M(x,t)) U(x,t),
\]

\[
\geq D_0 \Delta U + \xi - (B_3 \lim_{U \to 0} \frac{f(U,B_3)}{U} + d_U + g(B_2)) U(x,t)
\]

\[
= D_0 \Delta U + \xi - (B_3 f_U(0,B_3) + d_U + g(B_2)) U(x,t).
\]

The comparison theorem yields that \( U(x,t) \) is bounded ([32] Theorem 7.3.4).

Define

\[
\mathcal{X}_0 = \{ \phi = (\phi_1, \phi_2, \phi_3, \phi_4) \in C_+ : \phi_2(0) \neq 0 \text{ and } \phi_4(0) \neq 0 \}.
\]

Clearly, we have that

\[
\partial \mathcal{X}_0 := C_+ \setminus \mathcal{X}_0 = \{ \phi \in C_+ : \phi_2(0) \equiv 0 \text{ or } \phi_4(0) \equiv 0 \}.
\]

We easily obtain that \( \mathcal{X}_0 \) is positively invariant for the solution semiflow \( \Phi(t) \). Define

\[
G_0 := \{ \phi \in C_+ : \Phi(t) \phi \in \partial \mathcal{X}_0, \forall t \geq 0 \}.
\]
Let $\omega(\phi)$ be the omega limit set of the orbit of $\Phi(t)$ through $\phi \in \mathbb{C}_+$, and set

$$G_1 := \{(U_0, 0, 0, 0)\}.$$

**Claim 1.** $\bigcup_{\phi \in G_0} \omega(\phi) \subset G_1$.

For any given $\phi \in G_0$, we have $u_t(\phi) \in \partial X_0$. Due to $u_t(\phi) = u(t, \cdot, \phi)$, we easily get that for each $t \geq 0$ either $V(t, \cdot, \phi) = 0$ or $\omega(t, \cdot, \phi) \equiv 0$. For the case where $V(t, \cdot, \phi) \equiv 0$, $\forall t \geq 0$, from model (2), it can be seen that $\lim_{t \to +\infty} M(t, \cdot, \phi) = 0$ and

$$\lim_{t \to +\infty} \omega(t, \cdot, \phi) = 0 \text{ uniformly for } x \in \overline{\Omega}.$$

The theory of asymptotically autonomous semiflows in [33] yields $\lim_{t \to +\infty} U(t, x) = U_0$ uniformly for $x \in \overline{\Omega}$. In the case where $V(t, \cdot, \phi) \not\equiv 0$ for some $t_0 > 0$, we have that $V(t, \cdot, \phi) > 0$ for all $t > t_0$ and $x \in \overline{\Omega}$. Thus, we have $\omega(t, \cdot, \phi) \equiv 0$ for all $t \geq t_0$. From model (2), we obtain that $\lim_{t \to +\infty} V(t, \cdot, \phi) = 0$ uniformly for $x \in \overline{\Omega}$. Similarly, $\lim_{t \to +\infty} M(t, x) = 0$ and $\lim_{t \to +\infty} U(t, x) = U_0$ uniformly for $x \in \overline{\Omega}$. Hence, we get $\bigcup_{\phi \in G_0} \omega(\phi) \subset G_1$.

**Claim 2.** $E_0$ is a uniform weak repeller for in the sense that

$$\limsup_{t \to +\infty} \| u(t, \cdot, \phi) - (U_0, 0, 0, 0) \|_{\mathbb{C}_+} \geq \tau_1.$$

For any $\phi \in \mathbb{C}_+$ with $\phi_2(0) \neq 0$ and $\phi_4(0) \neq 0$, parabolic maximum principle yields

$$V(t, x) > 0, \ M(x, t) > 0, \ \omega(t, x) > 0, \ \forall t > 0, \ x \in \overline{\Omega}.$$  \hspace{1cm} (9)

From Lemma 2.3, we get $\overline{x}_0 > 0$ if $R_0 > 1$. Then, there exists a sufficiently large positive number $T_1$ such that

$$U_0 - \tau_1 < U(t, x), \ t < U_0 + \tau_1, \ V(t, x) < \tau_1, \ \omega(t, x) < \tau_1, \ \forall t \geq T_1, \ x \in \overline{\Omega}.$$

Let $\psi$ be the positive eigenfunction associated with $\overline{x}_0(U_0 - \tau_1)$. It then follows that

$$\begin{cases}
\frac{\partial u_2}{\partial t} = D_0 \Delta u_2 + \int_{\Omega} \Gamma(\tau, x, y)f(U_0 - \tau_1, \tau_1)u_4(y, t - \tau)dy - (\alpha_1 + dV)u_2, \\
\frac{\partial u_4}{\partial t} = D_2 \Delta u_4 + g_2'(\tau_1)u_2 - d_\omega u_4.
\end{cases}$$

admits a solution $u(t, x) = e^{\overline{x}_0(U_0 - \tau_1)t} \psi_1(x), \psi_2(x))$. Since $u(t, x, \phi) > 0$ for all $t > 0$ and $x \in \overline{\Omega}$, there exists $\chi > 0$ such that

$$(V(t, x), \omega(t, x)) \geq \chi(u_2(t, x), u_4(t, x)), \ \forall t \in [T_1 - \tau, T_1], \ x \in \overline{\Omega}.$$  \hspace{1cm} (V)

The comparison principle yields

$$(V(t, x), \omega(t, x)) \geq \chi e^{\overline{x}_0(U_0 - \tau_1)t} \psi_1(x), \psi_2(x)), \ \forall t > T_1, \ x \in \overline{\Omega},$$

where $\chi > 0$. Since $\lambda_0(U_0 - \tau_1) > 0$, then $\lim_{t \to +\infty} V(t, x) = \infty, \lim_{t \to +\infty} \omega(t, x) = \infty,$ which is a contradiction. We complete the proof of Claim 2.

Define a continuous function $p : \mathbb{C}_+ \to \mathbb{R}^+$ by

$$p(\phi) = \min\{\min_{x \in \Omega} \phi_2(0)(x), \ \min_{x \in \Omega} \phi_4(0)(x)\}, \ \forall \phi \in \mathbb{C}_+.$$  \hspace{1cm} (p)

Clearly, we obtain that $p^{-1}(0, +\infty) \subset \overline{x}_0$. By (9), $p$ has the property that if either $p(\phi) = 0$ and $\phi \in \overline{x}_0$, or $p(\phi) > 0$, then $p(\Phi(t)(\phi)) > 0$. From Theorem 3 in [31], it then follows that $G_1$ is isolated invariant set in $\mathbb{C}_+$ and $W^u(G_1) \cap \overline{x}_0 = \emptyset$, where $W^u(G_1)$ is the stable set of $G_1$. By Theorem 3 in [31], it can be concluded that there exists $\zeta > 0$ such that $\min\{p(\psi) : \psi \in \omega(\phi)\} > \zeta$ for any $\phi \in \overline{x}_0$. 

Non-Cooperative Reaction-Diffusion Systems 3221
3. In 1-D whole space-travelling wave solutions for model (2). In this section, we investigate the existence of travelling wave solutions when $R_0 > 1$ in an unbounded domain ([36, 15, 7, 22, 56, 59, 54, 43, 25, 17, 18, 57, 3]). For convenience, we assume that $D_0 = D_1 = D_2 = D$. In such a special case, following the same derivation in [50], we can obtain the particular form for the kernel $\Gamma(t, x)$:

$$
\Gamma(t, x) = \frac{1}{\sqrt{4\piDt}} e^{-\frac{x^2}{4Dt}}.
$$

Let $\hat{U} = \frac{x}{dt} - U$. Thus, model (2) is transformed into (omitting the hats on $U$ for simplicity)

$$
\begin{cases}
\frac{\partial U(x, t)}{\partial t} = D\Delta U + f(U_0 - U, \omega)\omega - d_U U + g(M)(U_0 - U), \\
\frac{\partial V(x, t)}{\partial t} = D\Delta V + \int_\Omega \Gamma(t, x - y) f(U_0 - U(y, t - \tau), \omega(y, t - \tau))\omega(y, t - \tau)dy \\
- d_V V - \alpha V, \\
\frac{\partial M(x, t)}{\partial t} = D\Delta M + g_1(V) - d_M M, \\
\frac{\partial \omega(x, t)}{\partial t} = D\Delta \omega + g_2(V) - d_\omega \omega.
\end{cases}
$$

(10)

We study the existence of travelling wave solutions of model (10), which has the form $U(x, t) = \phi(x + ct), V(x, t) = \varphi(x + ct), M(x, t) = \psi(x + ct), \omega(x, t) = \gamma(x + ct)$, where $\phi, \varphi, \psi, \gamma \in C^2(R, R^4)$ and $c > 0$ is the wave speed. Denoting the travelling wave coordinate $x + ct$ still by $t$, we derive from model (10) that

$$
\begin{cases}
D\ddot{\phi} - c^2\dot{\phi} + f_{c_1}(\phi_t, \varphi_t, \psi_t, \gamma_t) = 0, \\
D\ddot{\varphi} - c^2\dot{\varphi} + f_{c_2}(\phi_t, \varphi_t, \psi_t, \gamma_t) = 0, \\
D\ddot{\psi} - c^2\dot{\psi} + f_{c_3}(\phi_t, \varphi_t, \psi_t, \gamma_t) = 0, \\
D\ddot{\gamma} - c^2\dot{\gamma} + f_{c_4}(\phi_t, \varphi_t, \psi_t, \gamma_t) = 0,
\end{cases}
$$

(11)

where

$$
\begin{align*}
\left. f_{c_1}(\phi_t, \varphi_t, \psi_t, \gamma_t) = f(U_0 - \phi(t), \gamma(t))\gamma(t) - d_U \phi(t) + g(\psi(t))(U_0 - \phi(t)), \\
\left. f_{c_2}(\phi_t, \varphi_t, \psi_t, \gamma_t) = \int_\Omega \Gamma(t, y) f(U_0 - \phi(t - y - ct), \gamma(t - y - ct))\gamma(t - y - ct)dy \\
- d_V \varphi(t) - \alpha \varphi(t), \\
\left. f_{c_3}(\phi_t, \varphi_t, \psi_t, \gamma_t) = g_1(\varphi(t)) - d_M \psi(t), \\
\left. f_{c_4}(\phi_t, \varphi_t, \psi_t, \gamma_t) = g_2(\varphi(t)) - d_\omega \gamma(t).
\end{align*}
$$

Based on the ideas of [24] (see, also [39]), linearizing (11) at $E_0(0, 0, 0, 0)$ yields

$$
\begin{cases}
D\ddot{\phi} - c^2\dot{\phi} + f(U_0, 0)\gamma(t) - d_U \phi(t) + g'(0)U_0\varphi(t) = 0, \\
D\ddot{\varphi} - c^2\dot{\varphi} + f(U_0, 0)\int_\Omega \Gamma(t, y)\gamma(t - y - ct)dy - (\alpha_1 + d_V)\varphi(t) = 0, \\
D\ddot{\psi} - c^2\dot{\psi} + g'_1(0)\varphi(t) - d_M \psi(t) = 0, \\
D\ddot{\gamma} - c^2\dot{\gamma} + g'_2(0)\varphi(t) - d_\omega \gamma(t) = 0.
\end{cases}
$$

(12)

Plugging $(\phi(t), \varphi(t), \psi(t), \gamma(t)) = (\eta_1, \eta_2, \eta_3, \eta_4)e^{\lambda t}$ into (12), it then follows that

$$
A(\lambda, c)\eta = 0,
$$

(13)
where \( \eta = (\eta_1, \eta_2, \eta_3, \eta_4)^T \),

\[
A(\lambda, c) = \begin{pmatrix}
h_1(\lambda, c) & 0 & g'(0)U_0 & f(U_0, 0) \\
0 & h_2(\lambda, c) & 0 & f(U_0, 0)e^{\xi(\lambda^2 - c\lambda)} \\
0 & g_1(0) & h_3(\lambda, c) & 0 \\
0 & g_2(0) & 0 & h_4(\lambda, c)
\end{pmatrix}
\]

and

\[
h_1(\lambda, c) = D\lambda^2 - c\lambda - d_U, \quad h_2(\lambda, c) = D\lambda^2 - c\lambda - (d_V + \alpha_1), \\
h_3(\lambda, c) = D\lambda^2 - c\lambda - d_M, \quad h_4(\lambda, c) = D\lambda^2 - c\lambda - d_\omega.
\]

It is easy to see that (13) can be rewritten as \( \mathcal{M}(\lambda, c)\eta = \eta \), where

\[
\mathcal{M}(\lambda, c) = \begin{pmatrix}
0 & 0 & -g'(0)U_0 & -f(U_0, 0) \\
0 & 0 & 0 & -f(U_0, 0)e^{\xi(\lambda^2 - c\lambda)} \\
0 & -g_1(0) & 0 & 0 \\
0 & -g_2(0) & 0 & 0
\end{pmatrix}.
\]

By the assumptions on the related nonlinear functions and the fact that \( h_i(\lambda, c) < 0 \) for \( \lambda \in [0, \frac{c}{2D}] \), it is seen that \( \mathcal{M}(\lambda, c) \) is a non-negative matrix. Hence, by the Perron-Frobenius Theorem, the spectral radius of \( \mathcal{M}(\lambda, c) \), denoted by \( \rho(\mathcal{M}(\lambda, c)) \), is a simple eigenvalue of \( \mathcal{M}(\lambda, c) \). Direct calculations give

\[
\rho(\mathcal{M}(\lambda, c)) = \sqrt{\frac{g_2(0)f(U_0, 0)e^{\xi(\lambda^2 - c\lambda)}}{h_2(\lambda, c)h_4(\lambda, c)}}, \quad \lambda \in [0, \frac{c}{2D}].
\]

Letting \( \lambda = \frac{c}{2D} \), we get that

\[
\rho(\mathcal{M}(\frac{c}{2D}, c)) = \sqrt{\frac{g_2(0)f(U_0, 0)e^{\xi\frac{c^2}{2D}}}{h_2(\frac{c}{2D}, c)h_4(\frac{c}{2D}, c)}}.
\]

Since \( h_i(\frac{c}{2D}, c)(i = 2, 4) \) is strictly decreasing in \( c \in [0, +\infty) \), then \( \rho(\mathcal{M}(\frac{c}{2D}, c)) \) is strictly decreasing in \( c \in [0, +\infty) \). It is easy to see that

\[
\rho(\mathcal{M}(0, 0)) = R_0 > 1, \quad \rho(\mathcal{M}(\frac{c}{2D}, c)) \rightarrow 0, \quad c \rightarrow +\infty.
\]

Consequently, there exists a unique \( c^* > 0 \) such that

\[
\rho(\mathcal{M}(\frac{c}{2D}, c)) \begin{cases} > 1, & c \in [0, c^*), \\
= 1, & c = c^*, \\
< 1, & c \in (c^*, +\infty) \end{cases}
\]

Fixing \( c > c^* \), we have that \( \rho(\mathcal{M}(\lambda, c)) \) is strictly decreasing in \( \lambda \in [0, \frac{c}{2D}] \). Then

\[
\rho(\mathcal{M}(0, c)) = \rho(\mathcal{M}(0, 0)) > 1, \quad \rho(\mathcal{M}(\frac{c}{2D}, c)) < 1.
\]

Therefore, there exists a unique \( \lambda_c \in (0, \frac{c}{2D}) \) such that

\[
\rho(\mathcal{M}(\lambda, c)) \begin{cases} > 1, & \lambda \in [0, \lambda_c), \\
= 1, & \lambda = \lambda_c, \\
< 1, & \lambda \in (\lambda_c, +\infty) \end{cases}
\]
Based on the analysis above, we have the following Lemma.

**Lemma 3.1.** If $R_0 > 1$, there exists $c^* > 0$ such that for any $c > c^*$, there is $\lambda_c \in (0, \frac{c}{2\pi})$ and $\eta = (\eta_1, \eta_2, \eta_3, \eta_4)$ with $\eta_i > 0$, $i = 1, 2, 3, 4$, satisfying (13) and (14). Moreover, for any $\varepsilon \in (0, \frac{c}{2\pi} - \lambda_c)$, $h_i(\lambda_c + \varepsilon, c) < h_i(\lambda_c, c) < 0$ for any $c > c^*$, $i = 1, 2, 3, 4$.

Main result about travelling wave solutions for model (10) is stated as follows.

**Theorem 3.2.** Let $R_0 > 1$ hold. For every $c > c^*$, model (10) admits travelling wave solutions

$$(U(x, t), V(x, t), M(x, t), \omega(x, t)) = (\phi(t), \varphi(t), \psi(t), \gamma(t)) := \Xi(t),$$

with speed $c$ satisfying

$$\lim_{t \to -\infty} \Xi(t) = 0.$$

Moreover, $\lim_{t \to -\infty} \Xi(t) = 0$, and

$$\lim_{t \to -\infty} \Xi(t) e^{-\lambda_c t} = (\eta_1, \eta_2, \eta_3, \eta_4), \quad \lim_{t \to -\infty} \Xi'(t) e^{-\lambda_c t} = \lambda_c (\eta_1, \eta_2, \eta_3, \eta_4).$$

3.1. **Super-solutions and sub-solutions.** To construct the profile set $\Pi$, we need to define two functions $\Phi(t) = (\overline{\phi}(t), \overline{\varphi}(t), \overline{\psi}(t), \overline{\gamma}(t))$ and $\Psi(t) = (\underline{\phi}(t), \underline{\varphi}(t), \underline{\psi}(t), \underline{\gamma}(t))$ as follows

$$\overline{\phi}(t) = \min\{U_0, \eta_1 e^{\lambda_c t}\}, \quad \overline{\varphi}(t) = \eta_2 e^{\lambda_c t}, \quad \overline{\psi}(t) = \eta_3 e^{\lambda_c t}, \quad \overline{\gamma}(t) = \eta_4 e^{\lambda_c t},$$

$$\underline{\phi}(t) = \max\{0, \eta_1 e^{\lambda_c t} (1 - Q e^t)\}, \quad \underline{\varphi}(t) = \max\{0, \eta_2 e^{\lambda_c t} (1 - Q e^t)\}, \quad \underline{\psi}(t) = \max\{0, \eta_3 e^{\lambda_c t} (1 - Q e^t)\}, \quad \underline{\gamma}(t) = \max\{0, \eta_4 e^{\lambda_c t} (1 - Q e^t)\},$$

where $\eta_i > 0$ ($i = 1, 2, 3, 4$), $\lambda_c > 0$ and $\varepsilon > 0$ are given in Lemma 4.1. By choosing $Q > 1$ large so that $\frac{1}{\lambda_c} \ln \frac{k}{\eta_i} > -\frac{1}{2} \ln Q$, it follows that $\underline{\phi}(t) \leq \overline{\phi}(t)$ for all $t \in \mathbb{R}$.

**Lemma 3.3.** The function $\Phi(t) = (\overline{\phi}(t), \overline{\varphi}(t), \overline{\psi}(t), \overline{\gamma}(t))$ satisfies

$$D^2 \overline{\phi}(t) - c^2 \overline{\phi}(t) + f(U_0 - \overline{\phi}(t), \overline{\gamma}(t)) \overline{\gamma}(t) - d_U \overline{\phi}(t) + g(\overline{\psi}(t))(U_0 - \overline{\phi}(t)) \leq 0,$$

$a.e.$ in $\mathbb{R}$,

$$D^2 \overline{\varphi}(t) - c^2 \overline{\varphi}(t) + \int_{\Omega} \Gamma(\tau, y) f(U_0 - \overline{\phi}(t - y - c\tau), \overline{\gamma}(t - y - c\tau)) \overline{\gamma}(t - y - c\tau) dy$$

$$- d_U \overline{\varphi}(t) - \alpha_1 \overline{\varphi}(t) \leq 0, \quad a.e.$ in $\mathbb{R}$,

$$D^2 \overline{\psi}(t) - c^2 \overline{\psi}(t) + g_1(\overline{\varphi}(t)) - d_M \overline{\psi}(t) \leq 0, \quad a.e.$ in $\mathbb{R}$,

$$D^2 \overline{\gamma}(t) - c^2 \overline{\gamma}(t) + g_2(\overline{\varphi}(t)) - d_M \overline{\gamma}(t) \leq 0, \quad a.e.$ in $\mathbb{R}$.

**Proof.** If $t > \frac{1}{\lambda_c} \ln \frac{k}{\eta_1}$, the conclusion is obvious. If $t \leq \frac{1}{\lambda_c} \ln \frac{k}{\eta_1}$, $\overline{\phi}(t) = \eta_1 e^{\lambda_c t}$.

From (C1), (C2), (C4) and the mean value theorem, we get that

$$D^2 \overline{\phi}(t) - c^2 \overline{\phi}(t) + f(U_0 - \overline{\phi}(t), \overline{\gamma}(t)) \overline{\gamma}(t) - d_U \overline{\phi}(t) + g(\overline{\psi}(t))(U_0 - \overline{\phi}(t))$$

$$\leq e^{\lambda_c t} \left( \eta_1 D \lambda_c^2 - \eta_1 c \lambda_c - \eta_1 d_U + f(U_0, 0) \eta_4 + g'(0) U_0 \eta_3 \right) = 0.$$
For $\varphi(t) = \eta_2 e^{\lambda_1 t}$, from (C1) and (C2), we obtain that
\[
D\varphi(t) - c\varphi(t) + \int_{\Omega} \Gamma(\tau, \gamma) f(U_0 - \phi(t - \gamma t), \gamma(t - \gamma t)) dy \\
- dV \varphi(t) - \alpha_1 \varphi(t) \\
\leq e^{\lambda_1 t} \left( \eta_2 D\lambda_c^2 - \eta_2 c\lambda_c - (\alpha_1 + dV)\eta_2 + f(U_0, 0)\eta_4 e^{\tau(D\lambda_c^2 - c\lambda_c)} \right) = 0.
\]
For $\psi(t) = \eta_3 e^{\lambda_1 t}$, from (C5), we get that
\[
D\psi(t) - c\psi(t) + g_1(\varphi(t)) - d_M \psi(t) \leq D\psi(t) - c\psi(t) + g_1(0)\varphi(t) - d_M \psi(t) \\
\leq e^{\lambda_1 t} \left( \eta_3 D\lambda_c^2 - \eta_3 c\lambda_c - d_M \eta_3 + g_1(0)\eta_2 \right) = 0.
\]
For $\gamma(t) = \eta_4 e^{\lambda_1 t}$, from (C5), we have that
\[
D\gamma(t) - c\gamma(t) + g_2(\varphi(t)) - d_\omega \gamma(t) \leq D\gamma(t) - c\gamma(t) + g_2(0)\varphi(t) - d_\omega \gamma(t) \\
\leq e^{\lambda_1 t} \left( \eta_4 D\lambda_c^2 - \eta_4 c\lambda_c - d_\omega \eta_4 + g_2(0)\eta_2 \right) = 0.
\]
This completes the proof.

**Lemma 3.4.** The function $\Psi(t) = (\phi(t), \varphi(t), \psi(t), \gamma(t))$ satisfies
\[
D\phi(t) - c\phi(t) + f(U_0 - \phi(t), \varphi(t), \gamma(t))(U_0 - \phi(t)) \geq 0,
\]
a.e. in $R$,
\[
D\varphi(t) - c\varphi(t) + \int_{\Omega} \Gamma(\tau, \gamma) f(U_0 - \phi(t - \gamma t), \gamma(t - \gamma t)) \gamma(t - \gamma t) dy \\
- dV \varphi(t) - \alpha_1 \varphi(t) \geq 0, \text{ a.e. in } R,
\]
\[
D\psi(t) - c\psi(t) + g_1(\varphi(t)) - d_M \psi(t) \geq 0, \text{ a.e. in } R,
\]
\[
D\gamma(t) - c\gamma(t) + g_2(\varphi(t)) - d_\omega \gamma(t) \geq 0, \text{ a.e. in } R.
\]

**Proof.** From the definition of super-solutions and sub-solutions, we have that
\[
\lim_{t \to -\infty} (U_0 - \phi(t)) = U_0, \quad \lim_{t \to -\infty} \gamma(t) = 0.
\]
Thus, there exists a positive constant $Q_0$ such that
\[
\left( U_0 - \phi(t), \gamma(t) \right) \in \mathcal{U} \left( U_0, 0, \frac{U_0^2}{2} \right) := \{(U, \omega) : (U - U_0)^2 + \omega^2 \leq \frac{U_0^2}{4} \}
\]
for all $t \leq t_0 := \frac{1}{\varepsilon} \ln \frac{1}{Q_0}$. Similarly, we have that
\[
\lim_{t \to -\infty} (U_0 - \phi(t)) = U_0, \quad \lim_{t \to -\infty} \gamma(t) = 0.
\]
Thus, there exists a positive constant $Q_1$ such that
\[
\left( U_0 - \phi(t), \gamma(t) \right) \in \mathcal{U} \left( U_0, 0, \frac{U_0^2}{2} \right) := \{(U, \omega) : (U - U_0)^2 + \omega^2 \leq \frac{U_0^2}{4} \}
\]
for all $t \leq t_1 := \frac{1}{\varepsilon} \ln \frac{1}{Q_1}$.

If $t > -\frac{1}{\varepsilon} \ln Q$, then $\phi(t) = 0$. It is easy to obtain the result. In the following, we set $Q > \max\{Q_0, Q_1\}$ and $t \leq \min\{t_0, t_1\}$. If $t \leq -\frac{1}{\varepsilon} \ln Q \leq t_0$, then
\[
\dot{\phi}(t) = \eta_1 (\lambda_c e^{\lambda_1 t} - Q(\lambda_c + \varepsilon) e^{(\lambda_c + \varepsilon)t}), \quad \dot{\gamma}(t) = \eta_1 (\lambda_c^2 e^{\lambda_1 t} - Q(\lambda_c + \varepsilon) e^{(\lambda_c + \varepsilon)t}).
\]
Thus, we obtain that
\[
e^{-\lambda_\epsilon t} \left( D \hat{\phi}(t) - c \hat{\phi}(t) + f(U_0 - \hat{\phi}(t), \lambda_\epsilon(t)) \lambda_\epsilon(t) - dV \hat{\phi}(t) + g(\psi(t))(U_0 - \hat{\phi}(t)) \right)
\geq D\eta \lambda_\epsilon^2 - D\eta Q(\lambda_\epsilon + \epsilon)^2 e^{\epsilon t} - c\eta \lambda_\epsilon + c\eta Q(\lambda_\epsilon + \epsilon) e^{\epsilon t} - dV \eta_1 + dV \eta_1 Q e^{\epsilon t}
+ \left\{ f(U_0, 0) - \left( f(U(P)) \eta_4 e^{\lambda_\epsilon t}(1 - Q e^{\epsilon t}) - f_\omega(P) \right) \eta_4(1 - Q e^{\epsilon t})
+ e^{-\lambda_\epsilon t} \left( g'(0)U_0\hat{\phi}(t) - g'(0)U_0\psi(t) + g(\psi(t))(U_0 - \phi(t)) \right) \right\}
\geq -g'(0)\eta_1 \eta_3 e^{\lambda_\epsilon t} + g''(\theta_1) U_0 \eta_3^2 e^{\lambda_\epsilon t}
+ Q \left( -D\eta \lambda_\epsilon^2 + c\eta \lambda_\epsilon + c\eta Q(\lambda_\epsilon + \epsilon) - f(U_0, 0) \eta_4 + dV \eta_1 - g'(0)U_0 \eta_3 \right) e^{\epsilon t}
- \eta_4 \left( f(U(P)) \eta_1 e^{\lambda_\epsilon t}(1 - Q e^{\epsilon t}) - f_\omega(P) \right)
+ \eta_4 Q \left( f(U(P)) \eta_1 e^{\lambda_\epsilon t}(1 - Q e^{\epsilon t}) - f_\omega(P) \right) e^{\epsilon t}
= \left( -g'(0)\eta_1 \eta_3 e^{(\lambda_\epsilon - \epsilon)t} + g''(\theta_1) U_0 \eta_3^2 e^{(\lambda_\epsilon - \epsilon)t}
- Q \left( h_1(\lambda_\epsilon + \epsilon) \eta_1 + f(U_0, 0) \eta_4 + g'(0)U_0 \eta_3 \right)
- \eta_4 f(U(P)) \eta_4 e^{(\lambda_\epsilon - \epsilon)t}(1 - Q e^{\epsilon t}) + \eta_4 f_\omega(P) \eta_4 e^{(\lambda_\epsilon - \epsilon)t}(1 - Q e^{\epsilon t}) \right) e^{\epsilon t}
+ \eta_4 Q \left( f(U(P)) \eta_1 e^{(\lambda_\epsilon - \epsilon)t}(1 - Q e^{\epsilon t}) - f_\omega(P) \right) e^{\epsilon t}.
\]
In the first equality, the mean value theorem is used and \( P = (U_0 - \theta \hat{\phi}, \theta \hat{\gamma}), \ 0 < \theta < 1 \). It is obvious that \( P \in U \left( (U_0, 0), \frac{U_0}{\sqrt{\theta}} \right) \). Since \( f_U(U, \omega) \geq 0 \) and \( f_\omega(U, \omega) \leq 0 \), we only need to show
\[-Q \left( h_1(\lambda_\epsilon + \epsilon) \eta_1 + f(U_0, 0) \eta_4 + g'(0)U_0 \eta_3 \right) \geq g'(0)\eta_1 \eta_3 + K_4 U_0 \eta_3^2 + \eta_4 K_1 + \eta_2^2 K_1.\]
Since
\[0 \leq f_U(P) < K_1, \quad 0 \leq -f_\omega(P) < K_1, \quad 0 \leq g''(\theta_1) < K_4\]
and
\[0 \leq 1 - Q e^{\epsilon t} \leq 1, \quad 0 \leq e^{(\lambda_\epsilon - \epsilon)t} \leq 1,\]
it is sufficient to show
\[-Q \left( h_1(\lambda_\epsilon + \epsilon) \eta_1 + f(U_0, 0) \eta_4 + g'(0)U_0 \eta_3 \right) \geq g'(0)\eta_1 \eta_3 + K_4 U_0 \eta_3^2 + \eta_4 K_1 + \eta_2^2 K_1.\]

Thanks to \( t \leq \frac{1}{\epsilon} \ln \frac{1}{Q_0} \), then we need to show
\[Q \geq \frac{g'(0)\eta_1 \eta_3 + K_4 U_0 \eta_3^2 + \eta_4 K_1 + \eta_2^2 K_1}{\left( h_1(\lambda_\epsilon + \epsilon) \eta_1 + f(U_0, 0) \eta_4 + g'(0)U_0 \eta_3 \right)},\]
where
\[K_1 = \max_{(U, \omega) \in U(U(t_0, 0), \omega)} \left\{ f_U(U, \omega), -f_\omega(U, \omega) \right\}, \quad K_4 = \max_{\theta \in [0, \eta_3]} \{-g''(\theta)\}.
\]
If \( t \leq \frac{1}{\epsilon} \ln Q \leq t_1 \), then
\[
\hat{\phi}(t) = \eta_2(\lambda_\epsilon e^{\lambda_\epsilon t} - Q(\lambda_\epsilon + \epsilon)e^{(\lambda_\epsilon + \epsilon)t}), \quad \hat{\psi}(t) = \eta_2(\lambda_\epsilon^2 e^{\lambda_\epsilon t} - Q(\lambda_\epsilon + \epsilon)^2 e^{(\lambda_\epsilon + \epsilon)t}).
\]
Hence, we have that
\[ e^{-\lambda c t} \left( D_2\tilde{\omega}(t) - c_2\tilde{\omega}(t) \right) + \int_\Omega \Gamma(\tau, y) f(U_0 - \varphi(t - y - cr), \gamma(t - y - cr)) \gamma(t - y - cr) dy \\
- dV\gamma(t) - \alpha_1\gamma(t) \right) \\
\geq D\eta_2^2 - D\eta_2 Q(\lambda c + \varepsilon) e^{t} - cr_2\lambda c + cr_2 Q(\lambda c + \varepsilon) e^{t} - (dV + \alpha_1)\eta_2 + (dV + \alpha_1)\eta_2 Q e^{t} \\
+ \int_\Omega \Gamma(\tau, y) e^{\lambda c (t - y - cr)} \left\{ f(U_0, 0) - f_{U}(P_{11}\eta_1 e^{\lambda c (t - y - cr)} - f_{U}(P_{11}\gamma_2) \right\} \eta_4(1 - Q e^{e(t - y - cr)}) dy \\
\geq \left( - Q(h_2(\lambda c + \varepsilon)\eta_2 + f(U_0, 0)e^{\tau(D\lambda c^2 - c\lambda c)} \eta_4) - \eta_4 e^{\tau(D\lambda c^2 - c\lambda c)} f_{U}(P_{11}\eta_1 e^{(\lambda c - \theta_1))} \right. \\
\left. + \eta_4^2 e^{\tau(D\lambda c^2 - c\lambda c)} f_{U}(P_{11}) e^{(\lambda c - \theta_1))} (1 - Q e^{e(t - y - cr)}) \right) e^{t}.
\]

In the first equality, the mean value theorem is used and \( P_{11} = (U_0 - \theta_2\phi, \theta_2\gamma), \)
\( 0 < \theta_2 < 1. \) Obviously, \( P_{11} \in \mathcal{U}\left((U_0, 0), \frac{t_0}{2} \right). \) Since \( f_{U}(U, \omega) \geq 0 \) and \( f_{\omega}(U, \omega) \leq 0, \)
\[ 0 \leq f_{U}(P_{11}) < K_1, \]
\[ 0 \leq -f_{\omega}(P_{11}) < K_1, \]
it is sufficient to show
\[ -Q\left(h_2(\lambda c + \varepsilon)\eta_2 + f(U_0, 0)e^{\tau(D\lambda c^2 - c\lambda c)} \eta_4\right) \geq e^{\tau(D\lambda c^2 - c\lambda c)}(\eta_4 K_1 + \eta_4^2 K_1). \]

We need to show
\[ Q \geq \frac{e^{\tau(D\lambda c^2 - c\lambda c)} (\eta_4 K_1 + \eta_4^2 K_1)}{-\left(h_2(\lambda c + \varepsilon)\eta_2 + f(U_0, 0)e^{\tau(D\lambda c^2 - c\lambda c)} \eta_4\right)}. \]

If \( t > -\frac{1}{\varepsilon} \ln Q, \) then \( \psi(t) = 0. \) It is easy to obtain the result. If \( t \leq -\frac{1}{\varepsilon} \ln Q, \)
\[ \tilde{\omega}(t) = \eta_3(\lambda c e^{\lambda c t} - Q(\lambda c + \varepsilon) e^{(\lambda c + \varepsilon) t}), \]
\[ \tilde{\omega}(t) = \eta_3(\lambda c e^{\lambda c t} - Q(\lambda c + \varepsilon) e^{(\lambda c + \varepsilon) t}), \]
and
\[ D\tilde{\omega}(t) - c\tilde{\omega}(t) + \alpha_2\tilde{\omega}(t) - dV\tilde{\omega}(t) \]
\[ \geq -\left(Q\left(h_3(\lambda c + \varepsilon)\eta_3 + g_1'(0)\eta_2\right) - g_1''(0)\eta_2^2 e^{(\lambda c + \varepsilon) t}\right) e^{(\lambda c + \varepsilon) t} \]
\[ \geq -\left(Q\left(h_3(\lambda c + \varepsilon)\eta_3 + g_1'(0)\eta_2\right) + K_5\eta_2^2\right) e^{(\lambda c + \varepsilon) t} \]
\[ \geq 0. \]

If \( t > -\frac{1}{\varepsilon} \ln Q, \) then \( \bar{\gamma}(t) = 0. \) It is easy to obtain the result. If \( t \leq -\frac{1}{\varepsilon} \ln Q, \)
\[ \bar{\gamma}(t) = \eta_4(\lambda c e^{\lambda c t} - Q(\lambda c + \varepsilon) e^{(\lambda c + \varepsilon) t}), \]
\[ \bar{\gamma}(t) = \eta_4(\lambda c e^{\lambda c t} - Q(\lambda c + \varepsilon) e^{(\lambda c + \varepsilon) t}). \]

Hence, we get that
\[ D\bar{\gamma}(t) - c\bar{\gamma}(t) + k\bar{\gamma}(t) - dV\bar{\gamma}(t) \]
\[ \geq -\left(Q\left(h_4(\lambda c + \varepsilon)\eta_4 + g_2'(0)\eta_2\right) + K_6\eta_2^2\right) e^{(\lambda c + \varepsilon) t} \]
\[ \geq 0, \]
where
\[ K_5 = \max_{\theta \in [0, \eta_2]} \{-g_1''(\theta)\}, \]
\[ K_6 = \max_{\theta \in [0, \eta_2]} \{-g_2''(\theta)\}. \]

This completes the proof.
3.2. Existence of travelling wave solutions. In this subsection, we study the existence of travelling wave solutions for model (10). Choosing four positive constants $\beta_1 \geq dV + g'(\bar{h})\mu + \eta_4 K_2$, $\beta_2 \geq \alpha_1 + dV + g'(\bar{h})\nu_3$, $\beta_3 \geq d_M$, $\beta_4 \geq d_\omega$ and define $H = (H_1, H_2, H_3, H_4)$ by

$$H_1(\phi, \varphi, \psi, \gamma) = f_{c_1}(\phi_t, \varphi_t, \psi_t, \gamma_t) + \beta_1 \phi(t),$$
$$H_2(\phi, \varphi, \psi, \gamma) = f_{c_2}(\phi_t, \varphi_t, \psi_t, \gamma_t) + \beta_2 \varphi(t),$$
$$H_3(\phi, \varphi, \psi, \gamma) = f_{c_3}(\phi_t, \varphi_t, \psi_t, \gamma_t) + \beta_3 \psi(t),$$
$$H_4(\phi, \varphi, \psi, \gamma) = f_{c_4}(\phi_t, \varphi_t, \psi_t, \gamma_t) + \beta_4 \gamma(t).$$

Now, we define the second-order differential operator $D_i$ with $i = 1, 2, 3, 4$ as follows

$$D_i h := -Dh + ch + \beta_i h, \quad \text{for any } h \in C^2(R).$$

Let

$$\lambda_{i1} = \frac{c - \sqrt{c^2 + 4\beta_i D}}{2D}, \quad \lambda_{i2} = \frac{c + \sqrt{c^2 + 4\beta_i D}}{2D}, \quad i = 1, 2, 3, 4,$$

be the two roots of the function

$$f_i(\lambda) := -D\lambda^2 + c\lambda + \beta_i.$$

Here $\lambda_{i1} < 0 < -\lambda_{i1} < \lambda_{i2}$. The inverse operator $D_i^{-1}$ is given as follows

$$(D_i^{-1} h)(t) := \frac{1}{\rho_i} \left( \int_{-\infty}^{t} e^{\lambda_{i1}(t-s)} h(s) ds + \int_{t}^{\infty} e^{\lambda_{i2}(t-s)} h(s) ds \right),$$

for $h \in C_{\mu-\mu+}(R)$ with $\mu > \lambda_{i1}$ and $\mu^+ < \lambda_{i2}$, where

$$C_{\mu-\mu+}(R) := \left\{ h \in C(R) : \sup_{t \leq 0} |h(t)e^{-\mu^- t}| + \sup_{t \geq 0} |h(t)e^{-\mu^+ t}| < \infty \right\},$$

and

$$\rho_i := D(\lambda_{i2} - \lambda_{i1}) = \sqrt{c^2 + 4D\beta_i}, \quad i = 1, 2, 3, 4.$$

Choosing $\beta_i$ sufficiently large such that $|\lambda_{i1}| = -\lambda_{i1} > \lambda_c > 0$. Given $\mu > \lambda_c > 0$ such that $\mu < -\lambda_{i1}$ for $i = 1, 2, 3, 4$, we have $\lambda_c < \mu < -\lambda_{i1} < \lambda_{i2}$, and $\lambda_{i1} < -\mu < \mu < \lambda_{i2}$, $i = 1, 2, 3, 4$. We define the Banach space as follows

$$B_{\mu}(R, R^d) := C_{-\mu,\mu}(R) \times C_{-\mu,\mu}(R) \times C_{-\mu,\mu}(R) \times C_{-\mu,\mu}(R)$$

equipped with the norm

$$|u|_\mu := \max_{1 \leq i \leq 4} \sup_{t \in R} e^{-\mu|t|} |u_i(t)|,$$

where $u = (u_1, u_2, u_3, u_4) \in B_{\mu}(R, R^4)$. We define a map $F = (F_1, F_2, F_3, F_4)$ on the space $B_{\mu}(R, R^4)$ as

$$F_i(u_1, u_2, u_3, u_4) := D_i^{-1} H_i(u_1, u_2, u_3, u_4), \quad i = 1, 2, 3, 4.$$ (15)

We find travelling wave solutions in the following profile set:

$$\Pi := \left\{ (\phi, \varphi, \psi, \gamma) \in B_{\mu}(R, R^4) \mid \phi \leq \phi \leq \bar{\phi}, \quad \varphi \leq \varphi \leq \bar{\varphi}, \quad \psi \leq \psi \leq \bar{\psi}, \quad \gamma \leq \gamma \leq \bar{\gamma} \right\}.$$

Due to $\mu > \lambda_c > 0$, then $\Pi$ is uniformly bounded with respect to the norm $| \cdot |_\mu$ and $\Pi$ is a closed and convex subset of $B_{\mu}(R, R^4)$. Based on the idea in [42], we show that the convex set $\Pi$ is invariant under the map $F = (F_1, F_2, F_3, F_4)$.

**Lemma 3.5.** $F(\Pi) \subset \Pi$. 
Proof. For any \((\phi, \varphi, \psi, \gamma) \in B_\mu(R, R^4)\) such that
\[
\bar{\phi} \leq \phi \leq \underline{\phi}, \quad \varphi \leq \varphi \leq \overline{\varphi}, \quad \psi \leq \psi \leq \overline{\psi}, \quad \gamma \leq \gamma \leq \overline{\gamma}.
\]
Then it is sufficient to prove
\[
\bar{\phi} \leq F_1(\phi, \varphi, \psi, \gamma) \leq \underline{\phi}, \quad \varphi \leq F_2(\phi, \varphi, \psi, \gamma) \leq \overline{\varphi},
\]
\[
\psi \leq F_3(\phi, \varphi, \psi, \gamma) \leq \overline{\psi}, \quad \gamma \leq F_4(\phi, \varphi, \psi, \gamma) \leq \overline{\gamma}.
\]
By [40] and simple computations, we obtain that
\[
\beta_1 \phi(t) + f(U_0 - \phi(t), \gamma(t)) \gamma(t) - d_U \phi(t) + g(\psi(t))(U_0 - \phi(t))
\]
\[
\leq \beta_1 \overline{\phi}(t) + f(U_0 - \overline{\phi}(t), \gamma(t)) \gamma(t) - d_U \overline{\phi}(t) + g(\overline{\psi}(t))(U_0 - \overline{\phi}(t))
\]
\[
\leq \beta_1 \overline{\phi}(t) - D \overline{\phi}(t) + c \overline{\phi}(t).
\]
For \(t > \frac{1}{\lambda_1} \ln \frac{\delta}{\delta_0} = t_{11}\), in view of (15) and by using integration of parts twice, we have that
\[
F_1(\phi, \varphi, \psi, \gamma)(t) = \frac{1}{\rho_1} \left[ \int_{-\infty}^{t} e^{\lambda_1 (t-s)} H_1(\phi, \varphi, \psi, \gamma)(s) ds
+ \int_{t}^{\infty} e^{\lambda_1 (t-s)} H_1(\phi, \varphi, \psi, \gamma)(s) ds \right]
\]
\[
\leq \overline{\phi}(t) + \frac{1}{\lambda_1 - \lambda_1} e^{\lambda_1 (t-t_5)} \left( \frac{\overline{\phi}(t_5) + 0}{\overline{\phi}(t_5) - 0} \right)
\]
\[
\leq \overline{\phi}(t).
\]
By employing the similar method, we can prove \(F_1(\phi, \varphi, \psi, \gamma)(t) \leq \overline{\phi}(t)\) for \(t \leq t_{11}\).

Thus, for any \(t \geq 0\), we have that \(F_1(\phi, \varphi, \psi, \gamma)(t) \leq \overline{\phi}(t)\). If \(t < t^*\), we have that
\[
\beta_1 \phi(t) + f(U_0 - \phi(t), \gamma(t)) \gamma(t) - d_U \phi(t) + g(\psi(t))(U_0 - \phi(t))
\]
\[
\geq \beta_1 \overline{\phi}(t) - d_U \overline{\phi}(t) + f(U_0 - \overline{\phi}(t), \gamma(t)) \gamma(t) + g(\overline{\psi}(t))(U_0 - \overline{\phi}(t))
\]
\[
\geq \beta_1 \overline{\phi}(t) - D \overline{\phi}(t) + c \overline{\phi}(t)
\]
\[
= D_1 \overline{\phi}(t).
\]

If \(t \geq t^*\), then we get that
\[
\beta_1 \phi(t) + f(U_0 - \phi(t), \gamma(t)) \gamma(t) - d_U \phi(t) + g(\overline{\psi}(t))(U_0 - \overline{\phi}(t))
\]
\[
\geq (\beta_1 - d_U) \phi(t)
\]
\[
= 0
\]
\[
= D_1 \phi(t).
\]

Therefore, we obtain that \(F_1(\phi, \varphi, \psi, \gamma) \geq D^{-1}_1(D_1 \phi(t)) \geq \phi(t)\). From the discussions above, for any \(t \geq 0\), we easily obtain that \(\overline{\phi}(t) \leq F_1(\phi, \varphi, \psi, \gamma) \leq \overline{\phi}(t)\).

Similarly, we can show that \(\varphi \leq F_2(\phi, \varphi, \psi, \gamma) \leq \overline{\varphi}, \overline{\psi} \leq F_3(\phi, \varphi, \psi, \gamma) \leq \overline{\psi}, \gamma \leq F_4(\phi, \varphi, \psi, \gamma) \leq \overline{\gamma}\). This ends the proof of the lemma.

**Lemma 3.6.** The operator \(F\) is continuous with the norm \(|.|\) in \(B_\mu(R, R^4)\).

**Proof.** Introduce notations
\[
\mathcal{P} = \theta(U_1, \omega_1) + (1 - \theta)(U_2, \omega_2), \quad 0 < \theta < 1,
\]
\[
K_3 = \sup_{0 \leq U \leq U_0, 0 \leq \omega \leq \eta_4} \left( |f_U(U, \omega) + f_\omega(U, \omega)| \right).
\]
In fact, for any $\Phi_1, \Psi_1 \in C(R, R^4)$, it then follows that
\[
|H_1(\Phi_1)(t) - H_1(\Psi_1)(t)| e^{-\mu|t|} \\
\leq (d_U + \beta_1)|\phi_1(t) - \phi_2(t)| e^{-\mu|t|} \\
+ \left| \overline{f}_U(\mathcal{P})(\phi_1(t) - \phi_2(t)) + \overline{f}_\omega(\mathcal{P})(\gamma_1(t) - \gamma_2(t)) \right| e^{-\mu|t|} \\
+ U_0 g'(0)(1 + U_0)|\psi_1(t) - \psi_2(t)| e^{-\mu|t|} + g'(0)\eta_3 e^{\lambda_3 t}|\phi_1(t) - \phi_2(t)| e^{-\mu|t|} \\
= (d_U + \beta_1 + K_3 + U_0 g'(0)(1 + U_0) + g'(0)\eta_3 e^{\lambda_3 t})|\Phi_1(t) - \Psi_1(t)| e^{-\mu|t|}.
\]
By employing the method similar to [28], Lemma 2.4 (see, also, [23] Lemma 3.4, and [12] Lemma 3.4), we have that
\[
|F_1(\Phi_1(\cdot))(t) - F_1(\Psi_1(\cdot))(t)| e^{-\mu|t|} \\
\leq \frac{e^{-\mu|t|}}{\rho_1} \left( \int_{-\infty}^t e^{\lambda_1(t-s)}|H_1(\Phi_1)(s) - H_1(\Psi_1)(s)|\, ds \\
+ \int_t^\infty e^{\lambda_2(t-s)}|H_1(\Phi_1)(s) - H_1(\Psi_1)(s)|\, ds \right) \\
\leq \frac{P_1 e^{-\mu|t|}}{\rho_1} \left[ \int_{-\infty}^t e^{\lambda_1(t-s)+\mu|s|}\, ds + \int_t^\infty e^{\lambda_2(t-s)+\mu|s|}\, ds \right] |\Phi_1(t) - \Psi_1(t)| e^{-\mu|t|},
\]
where $P_1 = d_U + \beta_1 + K_3 + U_0 g'(0)(1 + U_0) + g'(0)\eta_3 e^{\lambda_3 t}$. If $t < 0$, it follows that
\[
|F_1(\Phi_1(\cdot))(t) - F_1(\Psi_1(\cdot))(t)| e^{-\mu|t|} \\
\leq \frac{P_1}{\rho_1} \left( \frac{1}{-\lambda_1 - \mu + \frac{\lambda_1}{\lambda_2 + \mu} + \frac{1}{\lambda_2 - \mu}} \right) |\Phi_1(t) - \Psi_1(t)| e^{-\mu|t|},
\]
where $P_1 = d_U + \beta_1 + K_3 + U_0 g'(0)(1 + U_0) + g'(0)\eta_3$. If $t \geq 0$, we have that
\[
|F_1(\Phi_1(\cdot))(t) - F_1(\Psi_1(\cdot))(t)| e^{-\mu|t|} \\
\leq \frac{P_1}{\rho_1} \left( \frac{1}{-\lambda_1 - \mu + \frac{\mu}{\lambda_1} + \frac{1}{\lambda_2 - \mu}} \right) |\Phi_1(t) - \Psi_1(t)| e^{-\mu|t|}.
\]
Hence, it then follows that
\[
|F_1(\Phi_1(\cdot))(t) - F_1(\Psi_1(\cdot))(t)| \mu \leq P_2|\Phi_1 - \Psi_1|_\mu,
\]
where
\[
P_2 = \frac{P_1}{\rho_1} \max \left\{ \frac{1}{-\lambda_1 - \mu + \frac{\lambda_1}{\lambda_2 + \mu} + \frac{1}{\lambda_2 - \mu}}, \frac{1}{-\lambda_1 - \mu + \frac{\mu}{\lambda_1} + \frac{1}{\lambda_2 - \mu}} \right\}.
\]
Similarly, we can prove that $F_2, F_3$ and $F_4$ are continuous with respect to the norm $|.|$ in $B_\mu(R, R^4)$. The proof is completed.

**Lemma 3.7.** The operator $F : \Pi \rightarrow \Pi$ is compact with the norm $|.|$ in $B_\mu(R, R^4)$.

**Proof.** For any $(\phi, \varphi, \psi, \gamma) \in \Pi$, we have that
\[
||F_1(\phi, \varphi, \psi, \gamma)||'(t) \leq \frac{-\lambda_1}{\rho_1} \int_{-\infty}^t e^{\lambda_1(t-s)}|H_1(s)|\, ds + \frac{\lambda_1}{\rho_1} \int_t^\infty e^{\lambda_2(t-s)}|H_1(s)|\, ds \\
\leq \frac{e^{\lambda_1 t}Q_1}{\rho_1} \left( \frac{-\lambda_1}{\lambda_c - \lambda_1} + \frac{\lambda_1}{\lambda_1 - \lambda_c} \right),
\]
where \( O_1 = (\beta_1 - d_U)\eta_1 + f(U_0, 0)\eta_4 + g'(0)U_0\eta_3 \). By simple computation, we get

\[
||F_2(\phi, \varphi, \psi, \gamma)(t)|| \leq \frac{\lambda_{21}}{\rho_2} \int_{-\infty}^{t} e^{\lambda_{21}(t-s)}|H_2(s)|ds + \frac{\lambda_{22}}{\rho_2} \int_{t}^{\infty} e^{\lambda_{22}(t-s)}|H_2(s)|ds
\]

\[
\leq e^{\lambda_1 t}O_2 \left( \frac{-\lambda_{21}}{\lambda_c - \lambda_{21}} + \frac{\lambda_{22}}{\lambda_{12} - \lambda_c} \right),
\]

where \( O_2 = (\beta_2 - d_U - \alpha_1)\eta_2 + f(U_0, 0)\eta_4 \). Thus, we have that \( \frac{\partial}{\partial t} F_1(\Phi(\cdot))(\cdot) \) and \( \frac{\partial}{\partial t} F_2(\Phi(\cdot))(\cdot) \) are bounded. Similarly, we get that \( \frac{\partial}{\partial t} F_3(\Phi(\cdot))(\cdot) \) and \( \frac{\partial}{\partial t} F_4(\Phi(\cdot))(\cdot) \) are bounded, which shows that \( F(\Pi) \) is uniformly bounded and equicontinuous with respect to the norm \( | \cdot |_\mu \).

Furthermore, for any positive integer \( n \), we define

\[
F^n(\Phi(\cdot))(t) = \begin{cases} 
F(\Phi(\cdot))(t), & t \in [-n, n], \\
F(\Phi(\cdot))(-n), & t \in (-\infty, -n], \\
F(\Phi(\cdot))(n), & t \in [n, +\infty).
\end{cases}
\]

We easily obtain that \( F^n : \Pi \to B_\mu(R, R^4) \) is continuous. Furthermore, \( F^n(\Pi) \) is uniformly bounded and equicontinuous with respect to the norm \( | \cdot |_\mu \) in \( B_\mu(R, R^4) \), which implies that \( F^n : \Pi \to B_\mu(R, R^4) \) is compact operator. Since

\[
||F_1(\Phi(\cdot))(t)|| \leq \frac{O_1}{\rho_1} \int_{-\infty}^{t} e^{\lambda_{11}(t-s)}ds + \frac{O_1}{\rho_1} \int_{t}^{\infty} e^{\lambda_{12}(t-s)}ds
\]

\[
= e^{\lambda_1 t}O_1 \left( \frac{1}{\lambda_c - \lambda_{11}} + \frac{1}{\lambda_{12} - \lambda_c} \right),
\]

it then follows that

\[
||F^n_1(\Phi(\cdot))(\cdot) - F_1(\Phi(\cdot))(\cdot)||_\mu = \sup_{t \in R} ||F^n_1(\Phi(\cdot))(\cdot) - F_1(\Phi(\cdot))(\cdot)|| e^{-\mu t}
\]

\[
\leq 2O_1 \rho_1 \left( \frac{1}{\lambda_c - \lambda_{11}} + \frac{1}{\lambda_{12} - \lambda_c} \right) e^{(\lambda_\mu - \mu)n} \to 0
\]

as \( n \to +\infty \). Similarly, we have that

\[
||F^n_2(\Phi(\cdot))(\cdot) - F_2(\Phi(\cdot))(\cdot)||_\mu \to 0,
\]

\[
||F^n_3(\Phi(\cdot))(\cdot) - F_3(\Phi(\cdot))(\cdot)||_\mu \to 0,
\]

\[
||F^n_4(\Phi(\cdot))(\cdot) - F_4(\Phi(\cdot))(\cdot)||_\mu \to 0,
\]

as \( n \to +\infty \). Thus, \( ||F^n(\Phi(\cdot))(\cdot) - F(\Phi(\cdot))(\cdot)||_\mu \to 0 \), as \( n \to +\infty \). By Proposition 2.12 in [63], we get \( F : \Pi \to B_\mu(R, R^4) \) is compact. The proof is completed.

### 3.3. Proof of the main result stated in Theorem 3.2

Based on the Lemmas 3.2-3.6, we show the existence result of travelling wave solutions stated in Theorem 3.2.

**Proof of Theorem 3.2.** For any \( c > c^* \), combining Lemmas 3.2-3.6 with Schauder’s fixed point theorem, it then follows that \( F \) has a fixed point \((\phi(t), \varphi(t), \psi(t), \gamma(t)) : = \Xi(t) \in \Pi \). Furthermore, we have that

\[
(0, 0, 0, 0) \leq (\phi(t), \varphi(t), \psi(t), \gamma(t)) \leq (\phi(t), \varphi(t), \psi(t), \gamma(t)) \leq (\bar{\phi}(t), \bar{\varphi}(t), \bar{\psi}(t), \bar{\gamma}(t)).
\]

Note that

\[
\eta_4 e^{\lambda_4 t} (1 - Qe^{\varepsilon t}) \leq \Xi(t) \leq \eta_4 e^{\lambda_4 t},
\]
for $t > 0$, which follows that

$$
\lim_{t \to -\infty} \Xi(t)e^{-\lambda_c t} = (\eta_1, \eta_2, \eta_3, \eta_4).
$$

Note that $\Xi \in \Pi$ is a fixed point of the operator of $F$. By employing L'Hôpital rule to the maps $F_i$, ($i = 1, 2, 3, 4$), it then follows that $\lim_{t \to -\infty} \Xi(t) = 0$. Integrating both sides of the first equation of (12) from $-\infty$ to $t$ gives

$$
D\phi'(t) = c\phi(t) - \int_{-\infty}^{t} f(U_0 - \phi(s), \gamma(s))\gamma(s)ds + dU\int_{-\infty}^{t} \phi(s)ds
$$

$$
- \int_{-\infty}^{t} g(\psi(s))(U_0 - \phi(s))ds.
$$

Recall that $\lim_{t \to -\infty} \Xi(t)e^{-\lambda_c t} = (\eta_1, \eta_2, \eta_3, \eta_4)$ and $\lim_{t \to -\infty} \Xi(t) = 0$, we get that

$$
\lim_{t \to -\infty} e^{-\lambda_c t}\phi'(t) = \frac{e^{-\lambda_c t}}{D}\lim_{t \to -\infty} [c\phi(t) - \int_{-\infty}^{t} f(U_0 - \phi(s), \gamma(s))\gamma(s)ds]
$$

$$
+ dU\int_{-\infty}^{t} \phi(s)ds - \int_{-\infty}^{t} g(\psi(s))(U_0 - \phi(s))ds
$$

$$
= \lambda_c\eta_1.
$$

Similarly, we obtain that

$$
\lim_{t \to -\infty} \psi'(t)e^{-\lambda_c t} = \lambda_c\eta_2, \quad \lim_{t \to -\infty} \psi'(t)e^{-\lambda_c t} = \lambda_c\eta_3, \quad \lim_{t \to -\infty} \gamma'(t)e^{-\lambda_c t} = \lambda_c\eta_4.
$$

The proof of the main result stated in Theorem 3.2 is completed.

**Remark 1.** Generally speaking, it is a challenging problem to study the existence of travelling wave solutions by constructing suitable super-solutions and sub-solutions connecting two steady states for the applications of Schauder’s fixed point theorem. In Theorem 3.2, the profile of travelling wave solutions has the infection-free steady state as its limit as $-\infty$. However, we cannot show the asymptotic property of profile in the other end $+\infty$ in mathematics. However, in [24], Li and Zou first offer an algorithm for numerically computing travelling wave solutions for spatially non-local equations which is very challenging. By employing the method proposed in [24], numerically, we find that the profile of travelling wave solutions has the infection steady state as its limit as $+\infty$ for model (1) (see, [51] Section 6).

4. **Discussions and conclusions.** In this paper, we study a class of non-cooperative reaction-diffusion system, which includes different types of incidence rates for virus dynamical models with nonlinear transmissions and nonlocal infections. In Theorem 2.5, we have obtained the threshold-type result in a bounded domain. Our threshold-type result (Theorem 2.5) shows that basic reproduction number $R_0$ may be used to design the control strategies of the disease transmission and to estimate the infection level. In the case where $R_0 > 1$, we may obtain an approximate value of the infection level from the persistence of model (2), and then change some parameters to drive $R_0 < 1$ so that the disease can be eradicated ultimately.

To study the invasion speed of virus, in Theorem 3.2, we investigate the existence of travelling wave solutions by employing Schauder’s fixed point theorem. To the best of our knowledge, there are few literatures about the existence result of minimal wave speed for non-cooperative systems consisting of more than three equations with complicated nonlinear interaction functions and nonlocal infection.
The mathematical difficulty in the proof of Theorem 3.2 is the problem constructing a bounded cone to apply the Schauder’s fixed point theorem. Thanks for Lemma 3.1, we construct two continuous functions $\Phi(t)$ and $\Psi(t)$, which are useful for constructing the profile set. Then the bounded cone is achieved through a pair of super-solutions and sub-solutions. This approach is very technical, and has been proven successfully in establishing the general existence result of travelling wave solutions for virus dynamical models with more complex nonlinear transmissions and nonlocal infection.

As a final remark, we should point out that, in the present paper, we did not derive whether $c^*$ is the minimal wave speed, that is, there do not exist travelling wave solutions for $0 < c < c^*$. A detailed analysis of this problem will be challenging and we leave this as a further project.

Acknowledgments. The authors thank the editor and anonymous reviewers for their helpful and valuable comments.

REFERENCES

[1] A. L. Cox and R. F. Siliciano, HIV: Not-so-innocent bystanders, Nature, 505 (2014), 492–493.
[2] N. W. Cummins and A. D. Badley, Mechanisms of HIV-associated lymphocyte apoptosis, Cell Death and Disease, 1 (2010), 1–9.
[3] Y.-Y. Chen, J.-S. Guo and C.-H. Yao, Traveling wave solutions for a continuous and discrete diffusive predator-prey model, J. Math. Anal. Appl., 445 (2017), 212–239.
[4] G. Doitsh, et al., Pyroptosis drives CD4 T-cell depletion in HIV-1 infection, Nature, 505 (2014), 509–514.
[5] O. Diekmann, J. Heesterbeek and J. Metz, On the definition and the computation of the basic reproduction ratio $R_0$ in the models for infectious disease in heterogeneous populations, J. Math. Biol., 28 (1990), 365–382.
[6] S. R. Dunbar, Travelling wave solutions of diffusive Lotka-Volterra equations, J. Math. Biol., 17 (1983), 11–32.
[7] A. Ducrot and M. Langlais, Traveling waves in invasion processes with pathogens, Math. Models Methods Appl. Sci., 18 (2008), 325–349.
[8] G. A. Doitsh, et al., Abortive HIV infection mediates CD4 T cell depletion and inflammation in human lymphoid tissue, Cell, 143 (2010), 789–801.
[9] V. Doceul, M. Hollinshead, L. van der Linden and G. Smith, Repulsion of superinfecting virions: A mechanism for rapid virus spread, Science, 327 (2010), 873–876.
[10] A. Friedman, Partial Differential Equations of Parabolic Type, Prentice-Hall, Englewood Cliffs, 1964.
[11] Z. Guo, F. Wang and X. Zou, Threshold dynamics of an infective disease model with a fixed latent period and non-local infections, J. Math. Biol., 65 (2012), 1387–1410.
[12] Q. Gan, R. Xu and P. Yang, Travelling waves of a hepatitis B virus infection model with spatial diffusion and time delay, IMA J. Appl. Math., 75 (2010), 392–417.
[13] J. K. Hale, Asymptotic Behavior of Dissipative Systems, American Mathematical Society, Providence, RI, 1988.
[14] Y. Hosono and B. Ilyas, Traveling waves for a simple diffusive epidemic model, Math. Models Methods Appl. Sci., 5 (1995), 935–966.
[15] J. Huang and X. Zou, Existence of traveling wavefronts of delayed reaction diffusion systems without monotonicity, Discrete Contin. Dyn. Syst. Ser. A, 9 (2003), 925–936.
[16] C. Hsu, C. Yang, T. Yang and T. Yang, Existence of traveling wave solutions for diffusive predator-prey type systems, J. Differ. Equ., 252 (2012), 3040–3075.
[17] W. Huang, Traveling wave solutions for a class of predator-prey systems, J. Dyn. Diff. Equat., 24 (2012), 633–644.
[18] W. Huang, A geometric approach in the study of traveling waves for some classes of non-monotone reaction-diffusion systems, J. Differ. Equ., 260 (2016), 2190–2224.
[19] B. Li, H. F. Weinberger and M. A. Lewis, Spreading speeds as slowest wave speeds for cooperative systems, Math. Biosci., 196 (2005), 82–98.
[20] X. Liang and X. Zhao, Asymptotic speeds of spread and traveling waves for monotone semiflows with applications, *Comm. Pure Appl. Math.*, 60 (2007), 1–40.
[21] Y. Lou and X. Zhao, A reaction-diffusion malaria model with incubation period in the vector population, *J. Math. Biol.*, 62 (2011), 543–568.
[22] X. Lin, P. Weng and C. Wu, Traveling wave solutions for a predator-prey system with sigmoidal response function, *J. Dyn. Diff. Equat.*, 23 (2011), 903–921.
[23] W. Li, G. Lin and S. Ruan, Existence of traveling wave solutions in delayed reaction-diffusion models with applications to diffusion-competition models, *Nonlinearity*, 19 (2006), 1253–1273.
[24] J. Li and X. Zou, Modeling spatial spread of infectious diseases with a fixed latent period in a spatially continuous domain, *Bull. Math. Biol.*, 71 (2009), 2048–2079.
[25] G. Lin, W. Li and M. Ma, Traveling wave solutions in delayed reaction diffusion systems with applications to multi-species models, *Discrete Contin. Dyn. Syst. Ser. B*, 13 (2010), 393–414.
[26] R. H. Martin and H. L. Smith, Abstract functional differential equations and reaction-diffusion systems, *Trans. Amer. Math. Soc.*, 321 (1990), 1–44.
[27] S. Ma, Traveling wavefronts for delayed reaction-diffusion models via a fixed point theorem, *J. Differ. Equ.*, 171 (2001), 294–314.
[28] C. A. Muro-Cacho, G. Pantaleo and A. S. Fauci, Analysis of apoptosis in lymph nodes of HIV-infected persons. Intensity of apoptosis correlates with the general state of activation of the lymphoid tissue and not with stage of disease or viral burden, *J. Immunol.*, 154 (1995), 5555–5566.
[29] X. Ren, Y. Tian, L. Liu and X. Liu, A reaction-diffusion within-host HIV model with cell-to-cell transmission, *J. Math. Biol.*, 76 (2018), 1831–1872, https://doi.org/10.1007/s00285-017-1202-x.
[30] H. L. Smith and X. Zhao, Robust persistence for semidynamical systems, *Nonlinear Anal.*, 47 (2001), 6169–6179.
[31] H. R. Thieme and X. Zhao, A non-local delayed and diffusive predator-prey model, *Nonlinear Anal. Real Word Appl.*, 2 (2001), 145–160.
[32] H. R. Thieme and X. Zhao, Convergence results and Poincar’e-Bendixson trichotomy for asymptotically autonomous differential equations, *J. Math. Biol.*, 30 (1992), 755–763.
[33] H. R. Thieme and X. Zhao, Repulsion effect on superinfecting virions by infected cells, *Bull. Math. Biol.*, 76 (2014), 2806–2833.
[34] H. Wang and W. Ma, Travelling wave solutions for a nonlocal dispersal HIV infection dynamical model, *J. Dyn. Diff. Equat.*, 28 (2016), 143–166.
[35] H. Wang and W. Wang, Propagation of HBV with spatial dependence, *Math. Biosci.*, 179 (2002), 73–107.
[36] H. Wang and W. Wang, Travelling wave solutions for a nonlocal dispersal HIV infection dynamical model, *J. Math. Anal. Appl.*, 457 (2018), 868–889.
[37] H. Wang and X. Wang, Traveling wave phenomena in a Kermack-McKendrick SIR model, *J. Dyn. Diff. Equat.*, 28 (2016), 2312–2329.
[38] H. Wang, Y. Huang and X. Zou, Global dynamics of a PDE in-host viral model, *Appl. Anal.*, 93 (2014), 2312–2329.
[39] J. Wang, J. Yang and T. Kuniya, Dynamics of a PDE viral infection model incorporating cell-to-cell transmission, *J. Math. Anal. Appl.*, 444 (2016), 1542–1564.
[46] W. Wang, W. Ma and X. Lai, Repulsion effect on superinfecting virions by infected cells for virus infection dynamic model with absorption effect and chemotaxis, *Nonlinear Anal. Real World Appl.*, 33 (2017), 253–283.

[47] W. Wang and X. Zhao, A nonlocal and time-delayed reaction-diffusion model of dengue transmission, *SIAM J. Appl. Math.*, 71 (2011), 147–168.

[48] W. Wang, W. Ma and X. Lai, A diffusive virus infection dynamic model with nonlinear functional response, absorption effect and chemotaxis, *Commun. Nonlinear Sci. Numer. Simulat.*, 42 (2017), 585–606.

[49] W. Wang and W. Ma, Block effect on HCV infection by HMGB1 released from virus-infected cells: An insight from mathematical modeling, *Commun. Nonlinear Sci. Numer. Simulat.*, 59 (2018), 488–514.

[50] W. Wang and W. Ma, Hepatitis C virus infection is blocked by HMGB1: A new nonlocal and time-delayed reaction-diffusion model, *Appl. Math. Comput.*, 320 (2018), 633–653.

[51] W. Wang and T. Zhang, Caspase-1-mediated pyroptosis of the predominance for driving CD4$^+$ T cells death: A nonlocal spatial mathematical model, *Bull. Math. Biol.*, 80 (2018), 540–582.

[52] J. Wu, *Theory and Applications of Partial Functional Differential Equations*, (Springer-Verlag, New York, 1996).

[53] R. Xu and Z. Ma, An HBV model with diffusion and time delay, *J. Theor. Biol.*, 257 (2009), 499–509.

[54] Z. Yu and R. Yuan, Travelling wave solutions in non-local convolution diffusive competitive-cooperative systems, *IMA J. Appl. Math.*, 76 (2011), 493–513.

[55] T. Zhang, X. Meng and T. Zhang, Global dynamics of a virus dynamical model with cell-to-cell transmission and cure rate, *Comput. Math. Methods Med.*, 2015 (2015), Article ID 758362, 8pp.

[56] T. Zhang and W. Wang, Existence of traveling wave solutions for influenza model with treatment, *J. Math. Anal. Appl.*, 419 (2014), 469–495.

[57] T. Zhang, W. Wang and K. Wang, Minimal wave speed for a class of non-cooperative diffusion-reaction system, *J. Differ. Equ.*, 260 (2016), 2763–2791.

[58] T. Zhang, Minimal wave speed for a class of non-cooperative reaction-diffusion systems of three equations, *J. Differ. Equ.*, 262 (2017), 4724–4770.

[59] G. Zhang, W. Li and Z. Wang, Spreading speeds and traveling waves for nonlocal dispersal equations with degenerate monostable nonlinearity, *J. Differ. Equ.*, 252 (2012), 5096–5124.

[60] T. Zhang, X. Meng and T. Zhang, Global analysis for a delayed SIV model with direct and environmental transmissions, *J. Appl. Anal. Comput.*, 6 (2016), 479–491.

[61] Y. Zhang and Z. Xu, Dynamics of a diffusive HBV model with delayed Beddington-DeAngelis response, *Nonlinear Anal. Real World Appl.*, 15 (2014), 118–139.

[62] X. Zhao, *Dynamical Systems in Population Biology*, Springer, New York, 2003.

[63] E. Zeidler, *Nonlinear Functional Analysis and Its Applications I*, Springer, New York, 1986.

Received December 2017; revised March 2018.

*E-mail address*: weiw10437@gmail.com; wei_wang0163.com

*E-mail address*: wanbiao_ma@ustb.edu.cn (Corresponding author)