

## NONTRIVIAL TRAVELING WAVES OF PHAGE-BACTERIA MODELS IN DIFFERENT MEDIA TYPES\*

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**Abstract.** Phages are ubiquitous in nature, but many essential factors of host-phage biology have not yet been integrated into mathematical models. In this paper, we investigate a spatial phage-bacteria model to describe the propagation of phages and bacteria in different types of nutrient media. Unlike existing models, we construct a more realistic reaction-diffusion model that incorporates inoculum and bacterial growth and movement, then rigorous mathematical analysis is challenging. We study traveling wave solutions and obtain complete information about the existence and nonexistence of nontrivial traveling wave solutions. The threshold conditions for the existence and nonexistence of traveling wave solutions are obtained by using Schauder's fixed point theorem, limiting argument, and one-sided Laplace transform. Considering different propagation media, we extend the existence of traveling wave solutions from liquid nutrition model to agar model. Moreover, in the absence of bacterial mortality, we obtain the existence of a new traveling wave solution describing phage invasion. We attempt to explain the occurrence of co-transport by the existence and nonexistence of traveling waves, and screen out the key parameters affecting the co-transport of phages and bacteria according to the definition of critical wave speed. Finally, we provide numerical simulations to verify the theoretical results and reveal the effects of key parameters on the propagation of phages and bacteria.

**Key words.** phage-bacteria model, traveling wave solution, critical wave speed, bacterial infection, phage invasion, co-transport

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**1. Introduction.** Phages, viruses which infect and destroy bacteria, have been referred to as bacterial parasites, with each phage type replicating on a specific strain of host bacteria. There are two types of phage infection that are lytic and lysogenic. The lytic life cycle is where phages infect and rapidly kill their infected host cells, thereby shaping bacterial population dynamics and occasionally assisting in their long-term evolution via generalized transduction. The lysogenic life cycle, in contrast, is where phages, instead of directly killing their hosts, integrate into their host genome, or exist as plasmid within their host cell. Lysogenic phages can also sometimes break away from the host DNA and enter the lytic cycle, where they replicate and multiply within the host cell to produce many progeny phages and eventually lyse bacteria [32]. A plaque, also known as a negative colony, is a transparent circular spot formed

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on the surface of culture medium by phage infection of bacterial cells resulting in lysis and death of host cells. The rate of phage invasion can often be described by looking at the rate of negative colony expansion.

Phages have long been of interest to scientists as tools for understanding fundamental molecular biology, as vectors for horizontal gene transfer, as drivers of bacterial evolution, as sources of diagnostic and genetic tools, and as novel therapeutics [4]. The specificity of phages is a potential disadvantage for phage therapy when the particular species of infecting bacteria is unidentified [22]. However, the specificity of phages reduces the chance that probiotics will be killed. From this point of view, the safety of phage therapy is assured. The establishment of a suitable phage-bacteria model is helpful to understand the relationship between phages and their hosts.

In the absence of bacterial movement, some results have been found in the study of phage-bacteria PDE models. Jones et al. [15] proposed a delayed reaction-diffusion system for virus diffusion on immobilized bacteria, and gave the first mathematically rigorous proof of the spread of infection and of the existence of traveling wave solutions representing an expanding plaque. In [13], Jones, Smith, and Thieme modified the model in [15] by incorporating all virus removal terms including adsorption to bacteria and decay of unabsorbed virus into a single linear loss rate. In this case they showed that the spreading speed is also the minimum wave speed of the traveling wave solution. The traveling wave profile for phage is pulse-like, and virus levels are low well in front of the wave and well behind the wave. The profile for bacteria connects the virus-free value to a significantly lower one. In [14], they extended earlier results on the spread of virus and on the existence of traveling wave solutions when the basic reproductive number for virus exceeds one, and compared these results with those in [15, 13]. The above works assume that host bacteria do not grow or spread, but in reality, we cannot ignore the growth and movement of bacteria. For example, if a cyanophage-cyanobacteria model ignores the growth and movement of cyanobacteria, the model will not play a role in describing the expansion of cyanobacteria and the invasion of cyanophage.

The movement of bacteria is key to their survival. Bacteria explore their environment by alternating between different swimming patterns. Wei et al. [37] showed that bacteria with flagella and other mechanisms that push in random directions have a competitive advantage over bacteria that move only in response to external forces. Recently, Tian et al. [33] found a new swimming mode of singly flagellated bacteria, namely, the wrap mode, which can randomly change the swimming direction of bacteria and make bacteria evenly distributed in space, thus greatly improving the efficiency of bacteria exploring the environment. Random movement of bacteria can keep bacteria away from each other and thus gain a greater share of resources in the environment. This is why bacteria have evolved to retain a pattern of random diffusion. In the case of bacterial mobility, the matter state and nutrient concentration of the medium greatly influence the pattern of bacterial colony formation [25, 34].

Combining the ideas in [25, 33, 34, 37, 39], we assume that bacteria are able to grow by breaking down nutrients and diffuse randomly in the culture medium. Using these assumptions, we construct a more realistic reaction-diffusion model that incorporates nutrients explicitly and bacterial growth and movement. A minimum mathematical model for phage-bacteria interactions in the liquid base is

$$\begin{cases} \frac{\partial N}{\partial t} = D_N \Delta N - \frac{1}{\gamma} h(N) B, \\ \frac{\partial B}{\partial t} = D_B \Delta B + h(N) B - k B V - d B, \\ \frac{\partial V}{\partial t} = D_V \Delta V + \beta k B V - \delta V, \end{cases}$$

where  $\Delta$  is a Laplacian, and  $D_N$ ,  $D_B$ ,  $D_V$  are diffusion coefficients of nutrients, bacteria, and phages, respectively.  $N(t, x)$ ,  $B(t, x)$ ,  $V(t, x)$  represent the density of nutrient, host bacteria, and phage population at position  $x$  and  $t$ , respectively. Parameter  $k > 0$  is the infection rate,  $\beta > 1$  is the burst size,  $\delta > 0$  is the mortality rate of phage, and  $d$  is the mortality rate of bacteria. Bacteria multiply via binary fission at a per capita rate that is a function of the resource concentration in the petri dish, and  $\gamma < 1$  is the yield constant. We assume that the nutrient uptake function  $h$  satisfies  $h(0) = 0$ ,  $h'(N) > 0$ ,  $h''(N) \leq 0$ ; an example being the Monod function  $h(N) = \frac{\alpha N}{K+N}$ , where  $\alpha > 0$  is a maximum specific growth rate, and  $K > 0$  is the half saturation constant. The model has initial and homogeneous Neumann boundary (zero flux) conditions:  $N(0, x) = N_0$ ,  $B(0, x) = B_0$ , and  $V(0, x) = V_0$  for  $x \in \Omega$ ;  $\nabla N \cdot \vec{n} = \nabla B \cdot \vec{n} = \nabla V \cdot \vec{n} = 0$  on  $\partial\Omega$ , where  $\vec{n}$  is an outward normal vector to the boundary  $\partial\Omega$ .

Compared to bacteria, phages themselves are almost immobile, so their dispersal relies on either free diffusion or transport by their hosts. However, diffusion is inefficient for covering long distances. An increasing number of microbiologists are concerned about the co-transport of phages and bacteria. Existing experiments and data show that phages are able to hitchhike with expanding bacterial populations by repeatedly reinfected cells in an expanding bacterial front [19, 28]. To the best of our knowledge, the mechanism of hitchhiking, whether biological or mathematical, is not clear. The most obvious manifestation of this hitchhiking mechanism is that phages and bacteria move at the same speed. It is worth noting that the traveling wave solution is a special solution of the system, in which all components move at the same speed, which is consistent with the hitchhiking mechanism of phages and bacteria. The existence and nonexistence of traveling wave solutions can well explain whether the co-transport occurs. To obtain a theoretical understanding, on the basis of the work in [15, 13, 14, 31], we modify and extend an existing reaction-diffusion model of bacteria-phage interaction incorporating nutrient explicitly. We assume that the bacteria and phage can diffuse, while nutrients may or may not diffuse. Mathematically, without loss of generality, we only study the propagation dynamics of bacteria and phages in one dimensional spatial domain  $\mathbb{R}$ .

This paper is organized as follows. In section 2, we consider a bacteria-phage model in liquid medium, convert the existence of traveling wave solutions into the existence of fixed points for a certain operator, and provide full information about the existence and nonexistence of traveling wave solutions for a bacterial-phage liquid medium model. In section 3, we extend the conclusions in section 2 to other variant models. Considering a class of agar models, the existence of traveling wave solutions for a class of partially degenerate systems is proven. Then we consider the model without mortality of bacteria, and prove the existence of a traveling wave solution, which describes the spread of phages. In section 4, we simulate the propagation phenomena of bacteria and phages, and explain the influence of some parameters in the model on the propagation dynamics of the system. In section 5, we conclude and discuss our findings.

**2. Mathematical results.** In this section, we assume that the environment is a kind of soup in which nutrients, bacteria, and phages all diffuse. We restrict the space domain to the real line and describe the propagation dynamics via traveling wave solutions. To consider the propagation dynamics of the following model:

$$(2.1) \quad \begin{cases} \frac{\partial N}{\partial t} = D_N \frac{\partial^2 N}{\partial x^2} - \frac{1}{\gamma} h(N)B, \\ \frac{\partial B}{\partial t} = D_B \frac{\partial^2 B}{\partial x^2} + h(N)B - kBV - dB, \\ \frac{\partial V}{\partial t} = D_V \frac{\partial^2 V}{\partial x^2} + \beta kBV - \delta V, \end{cases}$$

we first consider the corresponding ODE model

$$(2.2) \quad \begin{cases} \frac{dN}{dt} = -\frac{1}{\gamma} h(N)B, \\ \frac{dB}{dt} = h(N)B - kBV - dB, \\ \frac{dV}{dt} = \beta kBV - \delta V, \end{cases}$$

with initial conditions  $N(0) = N_0, B(0) = B_0, V(0) = V_0$ .

For spatially uniform steady states where solutions are independent of time and space, we have the following algebraic equations:

$$(2.3) \quad \begin{cases} h(N)B = 0, \\ (h(N) - kV - d)B = 0, \\ k\beta BV - \delta V = 0. \end{cases}$$

The first equation of (2.3) implies  $B = 0$  or  $N = 0$ .

*Case 1:  $d > 0$ .*

Let  $N = 0$ . If  $B \neq 0$ , then by the second equation of (2.3), we have  $V = -\frac{d}{k} < 0$ . Thus,  $B = 0$  and  $V = 0$ , that is,  $(0, 0, 0)$  is a steady state.

If  $N > 0$ , then  $B = 0$  and  $V = 0$ . Thus,  $(N_s, 0, 0)$  with  $N_s \geq 0$  are steady states.

*Case 2:  $d = 0$ .*

If  $N > 0$ , then  $B = 0$  and  $V = 0$ , that is,  $(N_s, 0, 0)$  with  $N_s > 0$  are steady states.

If  $N = 0$ , then  $V = 0$  and  $B = B_s \geq 0$ . Therefore,  $(0, B_s, 0)$  with  $B_s \geq 0$  are steady states.

**2.1. Equivalent form.** Here, we consider a system of reaction-diffusion equations

$$(2.4) \quad \frac{\partial U}{\partial t} = DU_{xx} + F(U) \text{ for } x \in \mathbb{R}, t \geq 0,$$

where  $U = (N, B, V)$ ,  $D = (D_N, D_B, D_V)$  with  $D_i > 0$  for  $i = N, B, V$  and  $D_B \geq D_V$ . The reaction function is given by

$$F(U) = (f_N(U), f_B(U), f_V(U)).$$

We seek a traveling wave solution of the form  $U(x+ct)$  with  $c$  being the traveling speed. Substituting  $U(x, t) = U(x+ct)$  into (2.4) and letting  $\xi = x+ct$ , we obtain the following system:

$$(2.5) \quad \begin{cases} cN' = D_N N'' - \frac{1}{\gamma} h(N)B, \\ cB' = D_B B'' + h(N)B - kBV - dB, \\ cV' = D_V V'' + \beta kBV - \delta V, \end{cases}$$

where the symbol ' denotes derivative with respect to the variable  $\xi$ . Then system (2.5) can be reduced to the following system:

$$(2.6) \quad DU''(\Xi) - cU'(\Xi) + F(U(\Xi)) = 0 \text{ for } \Xi \in \mathbb{R}.$$

Now, we seek a solution of the form  $(U_i) = (e^{\lambda \xi} \eta_\lambda^i)$ ,  $\lambda > 0$ ,  $\eta_\lambda = (\eta_\lambda^i) \gg 0$  (i.e.,  $\eta_\lambda^i > 0$ ) for the linearization of (2.6) at an initial equilibrium  $E_0$ , and arrive at the following system:

$$\text{diag}(D_i \lambda^2 - c\lambda) \eta_\lambda + F'(E_0) \eta_\lambda = 0,$$

which can be rewritten as the eigenvalue problem  $\frac{1}{\lambda} A_\lambda \eta_\lambda = c \eta_\lambda$ , where  $A_\lambda = (a_\lambda^{i,j}) = \text{diag}(D_i \lambda^2) + F'(E_0)$ .

Let  $\Psi(A_\lambda)$  be the principal eigenvalue of  $A_\lambda$  for  $\lambda \in [0, \infty)$ , and define  $\Phi(\lambda) := \frac{1}{\lambda} \Psi(A_\lambda) > 0$ .

From a biological perspective, we are interested in a traveling wave solution connecting from one bacteria-free state  $E_0(N^*, 0, 0)$  to another bacteria-free state  $E_1(N_*, 0, 0)$ . These traveling waves describe the propagation of the bacteria as a wave with a fixed shape and a fixed speed. Linearizing the equations of  $B$  and  $V$  of (2.1) at  $E_0(N^*, 0, 0)$ , we obtain

$$(2.7) \quad \begin{cases} cB' = D_B B'' + h'(N^*)B - dB, \\ cV' = D_V V'' - \delta V. \end{cases}$$

For  $\lambda \geq 0$ , two eigenvalues of the matrix

$$A_\lambda = \begin{pmatrix} D_B \lambda^2 + h(N^*) - d & 0 \\ 0 & D_V \lambda^2 - \delta \end{pmatrix}$$

are  $D_B \lambda^2 + h(N^*) - d, D_V \lambda^2 - \delta$ . A threshold speed can be defined as

$$c^* := \inf_{\lambda > 0} \Phi(\lambda) = \inf_{\lambda > 0} \frac{D_B \lambda^2 + h(N^*) - d}{\lambda} = 2\sqrt{D_B(h(N^*) - d)}.$$

We set that  $R_B := h(N^*)/d > 1, c^* = 2\sqrt{D_B(h(N^*) - d)}$ . It is noted that  $R_B$  is the basic reproduction number of bacteria for the ordinary differential system without diffusion. Moreover, linearizing the equation for  $B$  and  $V$  at the point  $(N^*, 0, 0)$  gives the characteristic function

$$(2.8) \quad f(\lambda) := -D_B \lambda^2 + c\lambda - (h(N^*) - d), \quad \tilde{f}(\lambda) := -D_V \lambda^2 + c\lambda + \delta.$$

Then

$$(2.9) \quad \lambda_0 := \frac{c - \sqrt{c^2 - 4D_B(h(N^*) - d)}}{2D_B} > 0, \quad \lambda_1 := \frac{c + \sqrt{c^2 + 4D_V \delta}}{2D_V} > 0$$

are the minimum positive roots of  $f(\lambda)$  and  $\tilde{f}(\lambda)$ , and  $\lambda_0 < \lambda_1$ .

Let  $\alpha_N, \alpha_B$ , and  $\alpha_V$  be three sufficiently large constants, and we define the second-order differential operator  $\mathfrak{D}_i$  with  $i = N, B, V$  by

$$(2.10) \quad \mathfrak{D}_i g := -D_i g'' + c g' + \alpha_i g$$

for any  $g \in C^2(\mathbb{R})$ . Let

$$(2.11) \quad \lambda_i^\pm = \frac{c \pm \sqrt{c^2 + 4D_i \alpha_i}}{2D_i}, \quad (\lambda_i^- < 0 < -\lambda_i^- < \lambda_i^+)$$

be the two roots of the function

$$(2.12) \quad f_i(\lambda) := -D_i \lambda^2 + c \lambda + \alpha_i.$$

Denote

$$(2.13) \quad \rho_i = D_i(\lambda_i^+ - \lambda_i^-) = \sqrt{c^2 + 4D_i \alpha_i}.$$

The inverse operator  $\mathfrak{D}_i^{-1}$  is given by the following integral representation:

$$(2.14) \quad (\mathfrak{D}_i^{-1} g)(\xi) := \frac{1}{\rho_i} \int_{-\infty}^{\xi} e^{\lambda_i^-(\xi-s)} g(s) ds + \frac{1}{\rho_i} \int_{\xi}^{\infty} e^{\lambda_i^+(\xi-s)} g(s) ds$$

for  $g \in C_{\mu^-, \mu^+}(\mathbb{R})$  with  $\mu^- > \lambda_i^-$  and  $\mu^+ < \lambda_i^+$ , where

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

It is readily seen from its integral representation in (2.13) that  $\mathfrak{D}_i^{-1} g$  is differentiable and

$$(2.15) \quad (\mathfrak{D}_i^{-1} g)'(\xi) = \frac{\lambda_i^-}{\rho_i} \int_{-\infty}^{\xi} e^{\lambda_i^-(\xi-s)} g(s) ds + \frac{\lambda_i^+}{\rho_i} \int_{\xi}^{\infty} e^{\lambda_i^+(\xi-s)} g(s) ds,$$

$$(2.16) \quad (\mathfrak{D}_i^{-1} g)''(\xi) = \frac{(\lambda_i^-)^2}{\rho_i} \int_{-\infty}^{\xi} e^{\lambda_i^-(\xi-s)} g(s) ds + \frac{(\lambda_i^+)^2}{\rho_i} \int_{\xi}^{\infty} e^{\lambda_i^+(\xi-s)} g(s) ds - \frac{g(\xi)}{D_i}.$$

We choose  $\alpha_i$  to be sufficiently large such that  $|\lambda_i^-| = -\lambda_i^- > \lambda_1 > 0$  for  $i = N, B, V$ . Given  $\mu > \lambda_1 > 0$  such that  $\mu < -\lambda_i^-$  for all  $i = N, B, V$ , we have  $\lambda_1 < \mu < -\lambda_i^- < \lambda_i^+$  and  $\lambda_i^- < -\mu < \mu < \lambda_i^+$ .

Define the Banach space  $B_\mu(\mathbb{R}, \mathbb{R}^3) := C_{-\mu, \mu}(\mathbb{R}) \times C_{-\mu, \mu}(\mathbb{R}) \times C_{-\mu, \mu}(\mathbb{R})$  equipped with the norm

$$(2.17) \quad \|u\|_\mu := \sup_{\xi \in \mathbb{R}} e^{-\mu|\xi|} \|u(\xi)\|_{\mathbb{R}^3},$$

where  $u = (N, B, V) \in B_\mu(\mathbb{R}, \mathbb{R}^3)$ . Then, we define a map  $G = (G_N, G_B, G_V)$  on the space  $B_\mu(\mathbb{R}, \mathbb{R}^3)$ :

$$(2.18) \quad \begin{aligned} G_N(N, B, V) &:= \mathfrak{D}_N^{-1} \left[ \alpha_N N - \frac{1}{\gamma} h(N) B \right], \\ G_B(N, B, V) &:= \mathfrak{D}_B^{-1} [\alpha_B B + h(N) B - k B V - dB], \\ G_V(N, B, V) &:= \mathfrak{D}_V^{-1} [\alpha_V V + \beta k B V - \delta V]. \end{aligned}$$

The following lemma shows that the fixed point of the map  $G$  is indeed a traveling wave solution.

LEMMA 2.1. Let  $(N, B, V) \in B_\mu(\mathbb{R}, \mathbb{R}^3)$  be a fixed point of the map  $G$ , then  $(N, B, V)$  satisfies the traveling wave equations (2.5).

*Proof.* Set  $g_1(N, B, V) := \alpha_N N - \frac{1}{\gamma} h(N)B$ . Since  $(N, B, V)$  is a fixed point of  $G$ , it follows that  $N = G_N(N, B, V) = \mathfrak{D}_N^{-1} g_1$ , that is  $\mathfrak{D}_N N = \mathfrak{D}_N \circ \mathfrak{D}_N^{-1} g_1$ . According to [35, Lemma 3.1], we have  $\mathfrak{D}_N \circ \mathfrak{D}_N^{-1} g_1 = -D_N(\mathfrak{D}_N^{-1} g_1)'' + c(\mathfrak{D}_N^{-1} g_1)' + \alpha_N(\mathfrak{D}_N^{-1} g_1) = g_1$ . Thus, we obtain  $-D_N N'' + cN' = -\frac{1}{\gamma} h(N)B$ . Similarly, we can show that the other two equations in (2.5) are also satisfied.  $\square$

**2.2. Preliminary.** To obtain the existence of traveling wave solutions of (2.5), we construct an auxiliary system

$$(2.19) \quad \begin{cases} cN' = D_N N'' - \frac{1}{\gamma} h(N)B, \\ cB' = D_B B'' + h(N)B - kBV - dB - \epsilon B^2, \\ cV' = D_V V'' + \beta kBV - \delta V - \epsilon V^2, \end{cases}$$

where  $\epsilon$  is a positive constant. Systems (2.19) and (2.5) have the same linearized system at the equilibrium point  $(N^*, 0, 0)$ . Accordingly, we define a map  $G^\epsilon = (G_N, G_B, G_V)$  as follows:

$$\begin{aligned} G_N(N, B, V) &:= \mathfrak{D}_N^{-1} \left[ \alpha_N N - \frac{1}{\gamma} h(N)B \right], \\ G_B(N, B, V) &:= \mathfrak{D}_B^{-1} [\alpha_B B + h(N)B - kBV - dB - \epsilon B^2], \\ G_V(N, B, V) &:= \mathfrak{D}_V^{-1} [\alpha_V V + \beta kBV - \delta V - \epsilon V^2]. \end{aligned}$$

Set the upper and lower solutions as follows:

$$(2.20) \quad \bar{N}(\xi) := N^*, \quad \underline{N}(\xi) := \max\{N^*(1 - M_1 e^{\varepsilon_1 \xi}), 0\},$$

$$(2.21) \quad \bar{B}(\xi) := \min\{e^{\lambda_0 \xi}, K_1\}, \quad \underline{B}(\xi) := \max\{e^{\lambda_0 \xi}(1 - M_2 e^{\varepsilon_2 \xi}), 0\},$$

$$(2.22) \quad \bar{V}(\xi) := \min\{e^{\lambda_1 \xi} + \varrho_1 e^{\lambda_0 \xi}, K_2\}, \quad \underline{V}(\xi) := 0,$$

where  $M_1, M_2, M_3, K_1, K_2, \varepsilon_1, \varepsilon_2, \varepsilon_3, \varrho_1$  are positive constants to be determined. Define that  $\xi_i (i = 1, 2, 3, 4, 5)$  satisfy  $M_i e^{\varepsilon_i \xi_i} = 1 (i = 1, 2, 3)$ ,  $e^{\lambda_0 \xi_4} = K_1$ , and  $e^{\lambda_1 \xi_5} + \varrho_1 e^{\lambda_0 \xi_5} = K_2$ .

LEMMA 2.2. For appropriately given parameters, the following inequalities hold:

$$(2.23) \quad D_N \underline{N}'' - c \underline{N}' - \frac{1}{\gamma} h(\underline{N}) \bar{B} \geq 0 \text{ for any } \xi \in \mathbb{R} \setminus \{\xi_1\};$$

$$(2.24) \quad D_B \underline{B}'' - c \underline{B}' + h(\underline{N}) \underline{B} - k \underline{B} \bar{V} - d \underline{B} - \epsilon \underline{B}^2 \geq 0 \text{ for any } \xi \in \mathbb{R} \setminus \{\xi_2\};$$

$$(2.25) \quad D_V \underline{V}'' - c \underline{V}' + \beta k \underline{B} \underline{V} - \delta \underline{V} - \epsilon \underline{V}^2 \geq 0 \text{ for any } \xi \in \mathbb{R};$$

$$(2.26) \quad D_N \bar{N}'' - c \bar{N}' - \frac{1}{\gamma} h(\bar{N}) \underline{B} \leq 0 \text{ for any } \xi \in \mathbb{R};$$

$$(2.27) \quad D_B \bar{B}'' - c \bar{B}' + h(\bar{N}) \bar{B} - k \bar{B} \underline{V} - d \bar{B} - \epsilon \bar{B}^2 \leq 0 \text{ for any } \xi \in \mathbb{R} \setminus \{\xi_4\};$$

$$(2.28) \quad D_V \bar{V}'' - c \bar{V}' + \beta k \bar{B} \bar{V} - \delta \bar{V} - \epsilon \bar{V}^2 \leq 0 \text{ for any } \xi \in \mathbb{R} \setminus \{\xi_5\}.$$

*Proof.* If  $\xi > \xi_1 = -\varepsilon_1^{-1} \ln M_1$ , then  $\underline{N}(\xi) = 0$  and inequality (2.23) holds. Given a constant  $M_0 := \max\{\frac{1}{\gamma}h(\underline{N})\} > 0$ . To prove inequality (2.23) for  $\xi < \xi_1$ , we need only prove that  $D_N \underline{N}'' - c \underline{N}' - M_0 \bar{B} \geq 0$ . Choose a sufficiently small  $\varepsilon_1 > 0$  such that  $\varepsilon_1 < \min\{\lambda_0, c/D_N\}$ . It is easy to get  $M_1^{-\frac{\lambda_0 - \varepsilon_1}{\varepsilon_1}} \rightarrow 0$  as  $M_1 \rightarrow +\infty$ . Then for  $M_1$  large enough, we have

$$\begin{aligned} D_N \underline{N}'' - c \underline{N}' - M_0 \bar{B} &\geq e^{\varepsilon_1 \xi} \left[ N^* M_1 \varepsilon_1 (c - D_N \varepsilon_1) - M_0 e^{(\lambda_0 - \varepsilon_1) \xi} \right] \\ &\geq e^{\varepsilon_1 \xi} \left[ N^* M_1 \varepsilon_1 (c - D_N \varepsilon_1) - M_0 M_1^{-(\lambda_0 - \varepsilon_1)/\varepsilon_1} \right] \\ &\geq 0. \end{aligned}$$

If  $\xi > \xi_2 = -\ln M_2/\varepsilon_2$ , then  $\underline{B}(\xi) = 0$  and the inequality (2.24) holds. Choose a sufficiently small  $\varepsilon_2 \in (0, \varepsilon_1)$  such that  $f(\lambda_0 + \varepsilon_2) > 0$ . Set  $\tau = \max_{N \in [0, N^*]} \{h'(N)\}$ . For  $\xi < \xi_2 < \xi_1 < 0$ ,  $\underline{N}(\xi) = N^*(1 - M_1 e^{\varepsilon_1 \xi}) > 0$ ,  $\underline{B}(\xi) = e^{\lambda_0 \xi} (1 - M_2 e^{\varepsilon_2 \xi}) > 0$ . To prove inequality (2.24), it is enough to show  $e^{-\lambda_0 \xi} [D_B \underline{B}'' - c \underline{B}' + h(\underline{N}) \underline{B} - k \underline{B} \bar{V} - d \underline{B} - \epsilon \underline{B}^2] \geq 0$ . In fact,

$$\begin{aligned} &e^{-\lambda_0 \xi} [D_B \underline{B}'' - c \underline{B}' + h(\underline{N}) \underline{B} - k \underline{B} \bar{V} - d \underline{B} - \epsilon \underline{B}^2] \\ &= e^{-\lambda_0 \xi} [D_B \underline{B}'' - c \underline{B}' + h(N^*) \underline{B} - d \underline{B} - h(N^*) \underline{B} + h(\underline{N}) \underline{B} - k \underline{B} \bar{V} - \epsilon \underline{B}^2] \\ &\geq M_2 f(\lambda_0 + \varepsilon_2) e^{\varepsilon_2 \xi} - M_1 N^* \tau e^{\varepsilon_1 \xi} (1 - M_2 e^{\varepsilon_2 \xi}) - k(1 - M_2 e^{\varepsilon_2 \xi}) (e^{\lambda_1 \xi} + \varrho_1 e^{\lambda_0 \xi}) \\ &\quad - \epsilon e^{\lambda_0 \xi} (1 - M_2 e^{\varepsilon_2 \xi})^2 \\ &= e^{\varepsilon_2 \xi} [M_2 f(\lambda_0 + \varepsilon_2) - M_1 N^* \tau e^{(\varepsilon_1 - \varepsilon_2) \xi} (1 - M_2 e^{\varepsilon_2 \xi}) \\ &\quad - k(1 - M_2 e^{\varepsilon_2 \xi}) (e^{(\lambda_1 - \varepsilon_2) \xi} + \varrho_1 e^{(\lambda_0 - \varepsilon_2) \xi}) - \epsilon e^{(\lambda_0 - \varepsilon_2) \xi} (1 - M_2 e^{\varepsilon_2 \xi})^2]. \end{aligned}$$

Since  $0 \leq 1 - M_2 e^{\varepsilon_2 \xi} \leq 1$ ,  $0 \leq e^{(\varepsilon_1 - \varepsilon_2) \xi} \leq 1$ ,  $0 \leq e^{(\lambda_1 - \varepsilon_2) \xi} \leq 1$ , and  $0 \leq e^{(\lambda_0 - \varepsilon_2) \xi} \leq 1$ , then we need only prove  $M_2 f(\lambda_0 + \varepsilon_2) \geq M_1 N^* \tau + k(1 + \varrho_1) + \epsilon$ . By  $f(\lambda_0 + \varepsilon_2) > 0$ , the above inequality holds if  $M_2 > \frac{M_1 N^* \tau + k(1 + \varrho_1) + \epsilon}{f(\lambda_0 + \varepsilon_2)}$ .

Inequality (2.25) is obviously true if  $\underline{V}(\xi) = 0$ . Now we intend to prove inequalities (2.26)–(2.28). Since  $\bar{N}(\xi)$  is a constant function, inequality (2.26) is obviously true. If  $\xi > \xi_6$ , then  $\bar{B}(\xi) = K_1$  and  $h(\bar{N}) \bar{B} - k \bar{B} \underline{V} - d \bar{B} - \epsilon \bar{B}^2 \leq (h(N^*) - d - \epsilon K_1) K_1 < 0 = -D_B \bar{B}'' + c \bar{B}'$  provided that  $K_1 > \frac{h(N^*) - d}{\epsilon}$ . If  $\xi < \xi_6$ , then  $\bar{B}(\xi) = e^{\lambda_0 \xi}$  and  $h(\bar{N}) \bar{B} - k \bar{B} \underline{V} - d \bar{B} - \epsilon \bar{B}^2 \leq h(N^*) \bar{B} - d \bar{B} = -D_B \bar{B}'' + c \bar{B}'$ .

If  $\xi > \xi_7$ , then  $\bar{V}(\xi) = K_2$  and  $\beta k \bar{B} \bar{V} - \delta \bar{V} - \epsilon \bar{V}^2 \leq (\beta k K_1 - \delta - \epsilon K_2) K_2 < 0 = -D_V \bar{V}'' + c \bar{V}'$  provided that  $K_2 > \frac{\beta k K_1 - \delta}{\epsilon}$ . Then, we assume  $\varrho_1 > K_2/K_1$  such that  $\xi_7 < \xi_6$  holds. If  $\xi < \xi_7$ , then  $\bar{V}(\xi) = e^{\lambda_1 \xi} + \varrho_1 e^{\lambda_0 \xi}$  and

$$\begin{aligned} &D_V \bar{V}'' - c \bar{V}' + \beta k \bar{B} \bar{V} - \delta \bar{V} - \epsilon \bar{V}^2 \\ &\leq -\varrho_1 \tilde{f}(\lambda_0) e^{\lambda_0 \xi} + \beta k e^{\lambda_0 \xi} K_2 \\ &< 0 \end{aligned}$$

provided that  $\varrho_1 > \max\{\beta k K_2 / \tilde{f}(\lambda_0), K_2 / K_1\}$ . The proof is completed. □

With the upper and lower solutions, we define a convex set  $\Gamma$  as

$$(2.29) \quad \Gamma := \{(N, B, V) \in B_\mu(\mathbb{R}, \mathbb{R}^3) : \underline{N} \leq N \leq \bar{N}, \underline{B} \leq B \leq \bar{B}, \underline{V} \leq V \leq \bar{V}\}.$$

Since  $\mu > \lambda_1 > 0$ , it is easily seen that  $\Gamma$  is uniformly bounded with respect to the norm  $|\cdot|_\mu$  defined in (2.17). To verify the Schauder fixed point theorem, the following lemmas are given. The proofs of some lemmas are not novel, but for completeness, we include the proofs in the appendix.



LEMMA 2.3. *The operator  $G^\epsilon = (G_N, G_B^\epsilon, G_V^\epsilon)$  maps  $\Gamma$  into  $\Gamma$ .*

LEMMA 2.4. *The operator  $G^\epsilon = (G_N, G_B^\epsilon, G_V^\epsilon)$  is continuous and compact with respect to the norm  $|\cdot|_\mu$ .*

LEMMA 2.5. *Assume that  $R_B > 1$ . Then for any  $c > c^*$ , auxiliary system (2.19) admits a nontrivial traveling wave solution  $(N(\xi), B(\xi), V(\xi)), \xi = x + ct$  satisfying*

$$(2.30) \quad \lim_{\xi \rightarrow -\infty} (N(\xi), B(\xi), V(\xi)) = (N^*, 0, 0), \quad \lim_{\xi \rightarrow +\infty} (N(\xi), B(\xi), V(\xi)) = (N_*, 0, 0).$$

*Proof.* Combining the Schauder fixed point theorem, Lemmas 2.3 and 2.4 imply that (2.19) has a nonnegative solution  $(N(\cdot), B(\cdot), V(\cdot)) \in \Gamma$ , and  $\underline{N}(\xi) \leq N(\xi) \leq \overline{N}(\xi)$ ,  $\underline{B}(\xi) \leq B(\xi) \leq \overline{B}(\xi)$ , and  $\underline{V}(\xi) \leq V(\xi) \leq \overline{V}(\xi)$ , which follow

$$\lim_{\xi \rightarrow -\infty} (N(\xi), B(\xi), V(\xi)) = (N^*, 0, 0).$$

Applying the L'Hospital rule to the map  $G^\epsilon$ , it is easy to show that

$$\lim_{\xi \rightarrow -\infty} (N'(\xi), B'(\xi), V'(\xi)) = (0, 0, 0).$$

Next, we investigate the asymptotic behavior of  $(N(\xi), B(\xi), V(\xi))$  as  $\xi \rightarrow +\infty$ . We then show that  $N(\xi)$  is monotonically decreasing in  $\xi \in \mathbb{R}$ . Indeed, in view of the facts  $\lim_{\xi \rightarrow -\infty} N(\xi) = N^*$  and  $\lim_{\xi \rightarrow -\infty} N'(\xi) = 0$ , integrating the two sides of the first equation of (2.19) from  $-\infty$  to  $\xi$  follows:

$$(2.31) \quad D_N N'(\xi) = c(N(\xi) - N^*) + (1/\gamma) \int_{-\infty}^{\xi} h(N)B ds.$$

We now claim the integral  $\int_{-\infty}^{+\infty} h(N)B ds < +\infty$ . If not, noting that the fact  $0 \leq N(\xi) \leq N^*$  for all  $\xi \in \mathbb{R}$ , we then conclude that there exists  $\delta_0 > 0$  such that  $N'(\xi) > \delta_0$  for all large  $\xi > 0$ , which implies that  $\lim_{\xi \rightarrow +\infty} N(\xi) = +\infty$ , this is a contradiction. Hence, the integral  $\int_{-\infty}^{+\infty} h(N)B ds$  converges, i.e.,  $\int_{-\infty}^{+\infty} h(N)B ds =: Q_0 < +\infty$ . As a result, it follows that  $N'(\xi)$  is uniformly bounded for all  $\xi \in \mathbb{R}$ . Note that the first equation of (2.19) implies that  $(e^{-\frac{c\xi}{D_N}} N')' = \frac{1}{\gamma D_N} e^{-\frac{c\xi}{D_N}} h(N)B \forall \xi \in \mathbb{R}$ . Integrating the equality from  $\xi$  to  $+\infty$  yields  $N'(\xi) = -\frac{1}{\gamma D_N} e^{\frac{c\xi}{D_N}} \int_{\xi}^{+\infty} e^{-\frac{cs}{D_N}} h(N)B ds \forall \xi \in \mathbb{R}$ , which, together with the fact that  $N(\xi) \geq 0$  and  $B(\xi) \geq 0$  are continuous and not identically zero in  $\xi \in \mathbb{R}$ , implies  $N'(\xi) < 0$  for all  $\xi \in \mathbb{R}$ . Thus,  $N(\xi)$  is monotonically decreasing in  $\xi \in \mathbb{R}$ , and let  $N_* := \lim_{\xi \rightarrow +\infty} N(\xi)$ , and then,  $N^* > N_* \geq 0$ .

Set  $g_2(N, B, V) := \alpha_B B + h(N)B - kBV - dB - \epsilon B^2$ . From (2.19), we have

$$(2.32) \quad B(\xi) = \frac{1}{\rho_B} \int_{-\infty}^{\xi} e^{\lambda_B^-(\xi-s)} g_2(s) ds + \frac{1}{\rho_B} \int_{\xi}^{+\infty} e^{\lambda_B^+(\xi-s)} g_2(s) ds,$$

where  $\lambda_B^\pm := \frac{c \pm \sqrt{c^2 + 4D_B \alpha_B}}{2D_B}$  and  $\rho_B := D_B (\lambda_B^+ - \lambda_B^-) = \sqrt{c^2 + 4D_B \alpha_B}$ . Note that  $\lambda_B^- < 0 < \lambda_0 < \lambda_B^+$  and  $\lambda_B^\pm$  are the two roots of the following equation:  $-D_B \lambda^2 + c\lambda + \alpha_B = 0$ . Since  $h(N)B$  is integrable on  $\mathbb{R}$ , it follows from the integral equation (2.32) and Fubini's theorem that  $B$  is also integrable on  $\mathbb{R}$ , and

$$\int_{-\infty}^{+\infty} B(\xi) d\xi \leq \frac{1}{d} \int_{-\infty}^{+\infty} h(N(\xi))B(\xi) d\xi, \quad \int_{-\infty}^{+\infty} B(\xi)V(\xi) d\xi \leq \frac{1}{k} \int_{-\infty}^{+\infty} h(N(\xi))B(\xi) d\xi.$$

Furthermore,

$$(2.33) \quad B'(\xi) = \frac{\lambda_B^-}{\rho_B} \int_{-\infty}^{\xi} e^{\lambda_B^-(\xi-s)} g_2(s) ds + \frac{\lambda_B^+}{\rho_B} \int_{\xi}^{\infty} e^{\lambda_B^+(\xi-s)} g_2(s) ds.$$

From  $\lambda_B^- < 0 < \lambda_B^+, \rho_B = D_B(\lambda_B^+ - \lambda_B^-)$  and  $g_2 \leq (\alpha_B + h(N^*) - d)B =: L_1 B$ , we have  $|B'(\xi)| \leq \frac{L_1}{D_B} \int_{-\infty}^{\infty} B(\xi) d\xi$ . Since  $B'(\xi)$  is uniformly bounded and  $B \geq 0$  is integrable on  $\mathbb{R}$ , it is easily seen that  $B(\xi) \rightarrow 0$  as  $\xi \rightarrow \infty$ ; otherwise, we can find a number  $\varepsilon > 0$ , a sequence  $\xi_n \rightarrow \infty$ , and a number  $\kappa > 0$  such that  $B(\xi) > \varepsilon$  for all  $|\xi - \xi_n| < \kappa$ , which contradicts the integrability of  $B$  on  $\mathbb{R}$ . Similarly, we can obtain  $\int_{-\infty}^{\infty} V(\xi) d\xi = \frac{\beta k}{\delta} \int_{-\infty}^{\infty} B(\xi) V(\xi) d\xi$  and  $|V'(\xi)| \leq \frac{L_2}{D_V} \int_{-\infty}^{\infty} V(\xi) d\xi$ , where  $L_2 := \alpha_V - \delta$ . It is seen that  $V(\xi) \rightarrow 0$  as  $\xi \rightarrow \infty$ , and hence  $B(\xi)$  and  $V(\xi)$  are bounded. According to the selected definition of  $\underline{B}(\xi)$ , we obtain that  $B(\xi) > 0$  for all  $\xi \in \mathbb{R}$  by using the Harnack inequality.

Combining the results obtained before, we can get  $\lim_{\xi \rightarrow +\infty} (N(\xi), B(\xi), V(\xi)) = (N_*, 0, 0)$ , where  $N_* \in [0, N^*)$ . □

Our results show that different components of the system have different types of traveling waves, namely wavefront and pulse wave. Such pulse wave profiles imply the boundedness of traveling waves, and the uniform upper bound of traveling waves does not depend on the selection of upper solutions. However, it is not easy to determine the boundedness of traveling wave solutions in general. More details can be found in [16]. Unfortunately, we cannot rule out the case of  $V(\xi) \equiv 0$ , since we have not found a nonzero  $\underline{V}(\xi)$ . It is worth noting that a function  $v(\xi) = \varepsilon e^{-\mu|\xi - \xi_0|}$  cannot be used as a lower solution because  $v'_+(\xi_0) < v'_-(\xi_0)$ ; see [24]. For such a noncooperative system, constructing a nonzero lower solution is difficult and remains an open problem.

**2.3. Existence of traveling waves when  $c > c^*$ .** We now extend the existence of traveling waves from the auxiliary system to the original system (2.1) by a limiting argument.

**THEOREM 2.6.** *Assume that  $R_B > 1$ . Then for any  $c > c^*$ , system (2.1) admits a nontrivial traveling wave solution  $(N(\xi), B(\xi), V(\xi)), \xi = x + ct$  satisfying*

$$\lim_{\xi \rightarrow -\infty} (N(\xi), B(\xi), V(\xi)) = (N^*, 0, 0), \quad \lim_{\xi \rightarrow +\infty} (N(\xi), B(\xi), V(\xi)) = (N_*, 0, 0).$$

*Proof.* For  $c > c^*$ . Let  $\{\epsilon_n\}$  be a sequence such that  $0 < \epsilon_{i+1} < \epsilon_i < 1$  and  $\epsilon_n \rightarrow 0$  as  $n \rightarrow \infty$ . By Lemma 2.5, there exists a solution  $U_n(\xi) = (N_n(\xi), B_n(\xi), V_n(\xi))$  of (2.19) for  $\epsilon = \epsilon_n$  satisfying the conclusion of Lemma 2.5, and  $|N'_n(\xi)|, |B'_n(\xi)|, |V'_n(\xi)|$  are uniformly bounded for  $\xi \in \mathbb{R}$ . By (2.19), there exists a positive constant  $\bar{L}$  independent of  $\xi$  such that  $|N''_n(\xi)|, |B''_n(\xi)|, |V''_n(\xi)|, |N'''_n(\xi)|, |B'''_n(\xi)|, |V'''_n(\xi)| \leq \bar{L} \forall \xi \in \mathbb{R}$ . Thus,  $\{U_n(\xi)\}, \{U'_n(\xi)\}$ , and  $\{U''_n(\xi)\}$  are uniformly bounded and equi-continuous in  $\mathbb{R}$ . By Arzela-Ascoli's theorem, it follows that there exists a subsequence of  $\{\epsilon_n\}$ , still denoted by  $\{\epsilon_n\}$ , such that  $\lim_{n \rightarrow \infty} \epsilon_n = 0$  and

$$U_n(\xi) \rightarrow U(\xi), \quad U'_n(\xi) \rightarrow U'(\xi), \quad U''_n(\xi) \rightarrow U''(\xi)$$

uniformly on every bounded and closed interval when  $n \rightarrow \infty$ , and pointwise on  $\mathbb{R}$ , where  $U(\xi) = (u, v, w)$ . By Lebesgue's dominated convergence theorem, letting  $n \rightarrow \infty$  in (2.19), we obtain

$$\begin{cases} cu' = D_N u'' - \frac{1}{\gamma} h(u)v, \\ cv' = D_B v'' + h(u)v - kvw - dv, \\ cw' = D_V w'' + \beta kvw - \delta w. \end{cases}$$

Therefore,  $U(\xi) = (u(\xi), v(\xi), w(\xi))$  is a solution of (2.5) satisfying  $\lim_{\xi \rightarrow -\infty} U(\xi) = (N^*, 0, 0)$ ,  $\lim_{\xi \rightarrow +\infty} U(\xi) = (N_*, 0, 0)$ .  $\square$

**2.4. Existence of traveling waves when  $c = c^*$ .** In this subsection, we prove the existence of the traveling wave solutions to the system (2.1) with the critical wave speed  $c = c^*$ .

**THEOREM 2.7.** *If  $R_B > 1$  and  $c = c^*$ , then system (2.1) admits a nontrivial traveling wave solution  $(N(x + c^*t), B(x + c^*t), V(x + c^*t))$ ,  $\xi = x + c^*t$  satisfying*

$$\lim_{\xi \rightarrow -\infty} (N(\xi), B(\xi), V(\xi)) = (N^*, 0, 0), \quad \lim_{\xi \rightarrow +\infty} (N(\xi), B(\xi), V(\xi)) = (N_*, 0, 0).$$

*Proof.* In the case where  $c = c^*$ , we use a limiting argument. Choose the sequence  $\{c_m\}_{m \geq 1} \subset (c^*, \infty)$  such that  $\lim_{m \rightarrow \infty} c_m = c^*$ . We have known that for each  $c_m$ , there exists a traveling wave  $(N^m, B^m, V^m)$ . Let  $U_m(\xi) = (N^m(\xi), B^m(\xi), V^m(\xi))$  be the positive solution of (2.1) obtained in Theorem 2.6 with  $c = c_m$ , where  $c_m > c^*$  and  $c_m \rightarrow c^*$ . Since system (2.1) is autonomous,  $N^m(\xi)$  is decreasing, and  $N^m(+\infty) < N^* - \epsilon_0$  for some positive constant  $\epsilon_0 > 0$ , we can suppose by a possible translation that  $N^m(0) = N^* - \epsilon_0/2, N^m(\xi) > N^* - \epsilon_0/2$  for  $\epsilon_0 > 0$  and for any  $\xi < 0$  and  $m$ . Since  $\{U_m(\cdot)\}$  is uniformly bounded, the elliptic estimate shows that  $U_m(\cdot) \rightarrow U^*(\cdot)$  in  $C^2_{loc}(\mathbb{R})$  norm by passing to a subsequence, where  $U^*(\xi) := (N_{c^*}(\xi), B_{c^*}(\xi), V_{c^*}(\xi))$  is a nonnegative solution of (2.5) with  $c = c^*$  and satisfies  $N_{c^*}(\xi) \geq N^* - \epsilon_0/2$  for  $\xi \leq 0$ .  $N_{c^*}(\xi)$  is decreasing with respect to  $\xi \in \mathbb{R}$  since  $N^m(\xi)$  is decreasing. A similar argument as in the proof of existence theorem shows that this fixed point actually satisfies  $B_{c^*}(\pm\infty) = V_{c^*}(\pm\infty) = 0$ . And then we need to show that the limit is nontrivial because we have infinity many equilibria and the standard argument as in [45] fails.

Suppose there exists some  $\xi_a$  such that  $N_{c^*}(\xi_a) = 0$ , then  $N'_{c^*}(\xi_a) = 0$ . According to the first equation of (2.5), we can get  $N''_{c^*}(\xi_a) = 0$ , which implies  $N_{c^*}(\xi) = 0$  for all  $\xi \in \mathbb{R}$ . This is in contradiction with  $N_{c^*}(0) = N^* - \epsilon_0/2$ . Thus,  $N_{c^*}(\xi) > 0$ .

Suppose that  $B_{c^*}(\xi) \equiv 0$ . It follows from the first equation of (2.5) that  $c^* N'_{c^*}(\xi) = D_N N''_{c^*}(\xi), \xi \in \mathbb{R}$ . It is easy to obtain  $N_{c^*}(\xi) = C_1 + C_2 e^{\frac{c^*}{D_N} \xi}$  for some positive constants  $C_1$  and  $C_2$ . Since  $0 < N_{c^*}(\xi) \leq N^*$  and  $N_{c^*}(0) = N^* - \epsilon_0/2$ , we have  $N_{c^*}(\xi) \equiv N^* - \epsilon_0/2$  at each point  $\xi \in \mathbb{R}$ . This contradicts the monotonicity of  $N_{c^*}(\xi)$ . Therefore, there exists  $\xi_0$  such that  $B_{c^*}(\xi_0) > 0$ , by using Harnack inequality on  $[-L, L]$ , it follows that  $B_{c^*}(\xi) > 0$  for all  $\xi \in [-L, L]$ . We then obtain that  $B_{c^*}(\xi) > 0$  for all  $\xi \in \mathbb{R}$  since  $L > 0$  is arbitrarily chosen. Similarly, from  $\int_{-\infty}^{\infty} V_{c^*}(\xi) d\xi = \frac{\beta k}{\delta} \int_{-\infty}^{\infty} B_{c^*}(\xi) V_{c^*}(\xi) d\xi$ , we can obtain  $V_{c^*}(\xi) > 0$  for all  $\xi \in \mathbb{R}$  unless  $V_{c^*}(\xi) \equiv 0$ .

If  $N_{c^*}(\xi_b) = N^*$ , then it follows that  $N'_{c^*}(\xi_b) = 0, N''_{c^*}(\xi_b) \leq 0$  since  $N_{c^*}(\xi) \leq N^*$  for any  $\xi \in \mathbb{R}$ . From the first equation of (2.5), we have

$$D_N N''_{c^*}(\xi_b) = \frac{1}{\gamma} h(N_{c^*}(\xi_b)) B_{c^*}(\xi_b),$$

it means  $B_{c^*}(\xi_b) = 0$ , a contradiction, which implies  $N_{c^*}(\xi) < N^*$  for any  $\xi \in \mathbb{R}$ .

Next, we will prove that  $N_{c^*}(-\infty) = N^*$ .  $N_{c^*}(-\infty)$  exists since  $N_{c^*}(\xi)$  is decreasing with respect to  $\xi$ . The boundedness of  $N''_{c^*}(\xi)$  on  $\mathbb{R}$  yields  $N'_{c^*}(-\infty) = 0$ . Similar to the derivation of (2.31), we have

$$(2.34) \quad D_N N^{m'}(\xi) = c_m (N^m(\xi) - N^*) + (1/\gamma) \int_{-\infty}^{\xi} h(N^m(s)) B^m(s) ds.$$

Setting  $m \rightarrow \infty$  yields that  $D_N N_{c^*}'(\xi) = c^*(N_{c^*}(\xi) - N^*) + (1/\gamma) \int_{-\infty}^{\xi} h(N_{c^*}(s)) B_{c^*}(s) ds$ . Setting  $\xi \rightarrow -\infty$  gives  $0 = c^*(N_{c^*}(-\infty) - N^*)$ . It follows that  $N_{c^*}(-\infty) = N^*$ . Similar to the proof of Lemma 2.5, we can show  $(N_{c^*}(+\infty), B_{c^*}(+\infty), V_{c^*}(+\infty)) = (N_*, 0, 0)$ .  $\square$

**2.5. Nonexistence of traveling wave solutions.** In this subsection, we will establish the nonexistence of traveling wave solution for system (2.1) either  $R_B > 1$  and  $0 < c < c^*$  or  $R_B \leq 1$ .

**THEOREM 2.8.** *If  $R_B > 1$  and  $0 < c < c^*$ , then system (2.1) has no traveling wave solution  $(N(\xi), B(\xi), V(\xi)), \xi = x + ct$  satisfying*

$$(2.35) \quad \lim_{\xi \rightarrow -\infty} (N(\xi), B(\xi), V(\xi)) = (N^*, 0, 0), \quad \lim_{\xi \rightarrow +\infty} (N(\xi), B(\xi), V(\xi)) = (N_*, 0, 0).$$

*Proof.* We will prove this theorem by a contradiction. Suppose that (2.1) has a positive solution  $(N(\xi), B(\xi), V(\xi))$  satisfying (2.35). It is evident that  $c < c^*$  is equivalent to  $c < 2\sqrt{D_B(h(N^*) - d)}$ . Then it follows by stable manifold theorem in [27] (see also the proof of [46, Lemma 3.1]) that there exists a positive constant  $\omega$  such that

$$(2.36) \quad \sup_{\xi < 0} \{B(\xi)e^{-\omega\xi}\} < +\infty, \quad \sup_{\xi < 0} \{|B'(\xi)|e^{-\omega\xi}\} < +\infty, \quad \sup_{\xi < 0} \{|B''(\xi)|e^{-\omega\xi}\} < +\infty.$$

Next, we introduce the definition of the negative one-sided Laplace transform

$$\mathcal{B}(\lambda) = \mathcal{N}[B(\cdot)](\lambda) := \int_{-\infty}^0 e^{-\lambda\xi} B(\xi) d\xi$$

for  $\lambda \geq 0$ . By this definition we know that  $\mathcal{B}(\lambda)$  is increasing on  $[0, \lambda^*)$ , where  $\lambda^* = +\infty$  or  $\lambda^* < +\infty$  with  $\lim_{\lambda \rightarrow \lambda^* -} \mathcal{B}(\lambda) = +\infty$ . It follows from (2.36) that  $\lambda^* \geq \omega$ .

According to [45, Lemma 3.7], there exists a constant  $M_c > 0$  such that

$$\int_{-\infty}^0 e^{-\lambda\xi} |B'(\xi)| d\xi \leq M_c \int_{-\infty}^0 e^{-\lambda\xi} B(\xi) d\xi < +\infty$$

implying that  $\int_{-\infty}^0 e^{-\lambda\xi} B'(\xi) d\xi$  is convergent. Then it follows from  $[e^{-\lambda\xi} B(\xi)]' = e^{-\lambda\xi} B'(\xi) - \lambda e^{-\lambda\xi} B(\xi)$  that

$$B(0) - e^{-\lambda\xi} B(\xi) = \int_{\xi}^0 e^{-\lambda s} B'(s) ds - \lambda \int_{\xi}^0 e^{-\lambda s} B(s) ds.$$

We obtain that  $\lim_{\xi \rightarrow -\infty} e^{-\lambda\xi} B(\xi)$  exists since the right-hand side of above equality is convergent if  $\xi \rightarrow -\infty$ . Then  $\lim_{\xi \rightarrow -\infty} e^{-\lambda\xi} B(\xi) = 0$  since  $\lim_{\xi \rightarrow -\infty} e^{-\lambda\xi} B(\xi) \neq 0$  implies that  $\int_{-\infty}^0 e^{-\lambda\xi} B(\xi) d\xi$  is divergent. It can be similarly shown that

$$\lim_{\xi \rightarrow -\infty} e^{-\lambda\xi} B'(\xi) = 0.$$

Then we can verify that  $\mathcal{N}[\cdot]$  satisfies

$$\begin{aligned}\mathcal{N}[B'(\cdot)](\lambda) &= \lambda \mathcal{B}(\lambda) + B(0) - \lim_{\xi \rightarrow -\infty} e^{-\lambda \xi} B(\xi) = \lambda \mathcal{B}(\lambda) + B(0), \\ \mathcal{N}[B''(\cdot)](\lambda) &= \lambda^2 \mathcal{B}(\lambda) + \lambda B(0) + B'(0) - \lim_{\xi \rightarrow -\infty} e^{-\lambda \xi} B'(\xi) - \lambda \lim_{\xi \rightarrow -\infty} e^{-\lambda \xi} B(\xi) \\ &= \lambda^2 \mathcal{B}(\lambda) + \lambda B(0) + B'(0)\end{aligned}$$

for all  $\lambda \in [0, \lambda^*)$ . Let  $L[B(\cdot)](\xi) := D_B B''(\xi) - cB'(\xi) + (h(N^*) - d)B(\xi)$ . Then  $L[B(\cdot)](\xi) = [h(N^*) - h(N) + kV]B(\xi)$ . Define  $\sigma := \min\{P(\lambda) : \lambda \geq \omega\}$ , where  $P(\lambda) = D_B \lambda^2 + c\lambda + h(N^*) - d$ . It follows from condition  $c < c^*$  that  $\sigma > 0$ . Since (2.5) is autonomous, for any  $a \in \mathbb{R}$ ,  $(N(\xi - a), B(\xi - a), V(\xi - a))$  is also a solution of (2.5) satisfying  $\lim_{\xi \rightarrow -\infty} N(\xi - a) = N^*$ ,  $\lim_{\xi \rightarrow -\infty} B(\xi - a) = 0$ , and  $\lim_{\xi \rightarrow -\infty} V(\xi - a) = 0$ . By using the fact that  $(N(-\infty), B(-\infty), V(-\infty)) = (N^*, 0, 0)$ , we obtain that  $N^* - N(\xi)$ ,  $B(\xi)$ , and  $V(\xi)$  can be small enough when  $\xi$  is negatively large. We then choose some  $a_0 \in \mathbb{R}$  such that  $N(\xi - a_0)$ ,  $B(\xi - a_0)$ ,  $V(\xi - a_0)$  satisfy

$$h(N^*) + kV(\xi - a_0) - h(N(\xi - a_0)) < \frac{\sigma}{2} \quad \forall \xi \leq 0.$$

Consequently, without losing generality, we assume  $h(N^*) + kV(\xi) - h(N(\xi)) < \frac{\sigma}{2}$  for all  $\xi \leq 0$ , which implies  $L[B(\cdot)](\xi) \leq \frac{\sigma}{2}B(\xi)$ . Applying the operator  $\mathcal{N}[\cdot]$  to this inequality, we have  $\frac{\sigma}{2}\mathcal{B}(\lambda) \geq \mathcal{N}[L[B(\cdot)](\cdot)](\lambda) = P(\lambda)\mathcal{B}(\lambda) + q(\lambda)$ , where  $q(\lambda) = B'(0) + (\lambda - c)B(0)$ . Thus, we have  $\mathcal{H}(\lambda) := [P(\lambda) - \frac{\sigma}{2}]\mathcal{B}(\lambda) + q(\lambda) \leq 0$ . If  $\lambda^* < +\infty$ , then  $\lim_{\lambda \rightarrow \lambda^*} \mathcal{B}(\lambda) = +\infty$ , and hence,  $\lim_{\lambda \rightarrow \lambda^*} \mathcal{H}(\lambda) = +\infty$ , which is a contradiction. If  $\lambda^* = +\infty$ , we have that  $\lim_{\lambda \rightarrow +\infty} \mathcal{H}(\lambda) = +\infty$  by the monotonicity of  $\mathcal{B}(\lambda)$  and the definitions of  $P(\lambda)$  and  $q(\lambda)$ , which is still a contradiction. The proof is completed.  $\square$

**THEOREM 2.9.** *If  $R_B = h(N^*)/d \leq 1$ , then there does not exist a nontrivial and nonnegative traveling wave solution of system (2.1) such that  $N(-\infty) = N^*$ ,  $N(+\infty) < N^*$ ,  $B(\pm\infty) = 0$ , and  $V(-\infty) = 0$ .*

*Proof.* We prove by contradiction. Let  $(N, B, V)$  be a nontrivial and nonnegative solution to (2.5). Based on the argument in subsection 2.2, and

$$B'(\xi) = \frac{\lambda_B^-}{\rho_B} \int_{-\infty}^{\xi} e^{\lambda_B^-(\xi-s)} g_2(s) ds + \frac{\lambda_B^+}{\rho_B} \int_{\xi}^{\infty} e^{\lambda_B^+(\xi-s)} g_2(s) ds,$$

by the L'Hospital rule, we have  $B(\pm\infty) = 0$ ,  $B'(\pm\infty) = 0$ ,  $B''(\pm\infty) = 0$ . If  $R_B = h(N^*)/d \leq 1$ , then  $h(N(\xi)) \leq h(N^*) \leq d$  for all  $\xi \in \mathbb{R}$ . Thus,

$$\frac{d}{d\xi} \left[ e^{-(c/D_B)\xi} \frac{d}{d\xi} B(\xi) \right] = -\frac{1}{D_B} e^{-(c/D_B)\xi} [h(N(\xi))B(\xi) - kB(\xi)V(\xi) - dB(\xi)] \geq 0.$$

It implies that the function  $e^{-(c/D_B)\xi} B'(\xi)$  is nondecreasing. Since  $B'(+\infty) = 0$  and  $e^{-(c/D_B)\xi} \rightarrow 0$  as  $\xi \rightarrow +\infty$ , it follows that  $B'(\xi) \leq 0$  for all  $\xi \in \mathbb{R}$ . By  $B(\pm\infty) = 0$ , we obtain  $B(\xi) \equiv 0$  for all  $\xi \in \mathbb{R}$ . This is a contradiction.  $\square$

**3. Extensions.** We obtain full information about the existence and nonexistence of traveling wave solutions for a general class of bacterial-phage liquid medium model, and the threshold dynamics for spatial spread of the bacterial by constructing an invariant cone and applying Schauder fixed point theorem. Our results on traveling waves for such models are the basis for several possible extensions.

**3.1. General agar model.** For agar media, nutrients cannot diffuse, while bacteria and phages can. We remove the nutrient diffusion term from system (2.1) to obtain a generic agar model:

$$(3.1) \quad \begin{cases} \frac{\partial N}{\partial t} = -\frac{1}{\gamma}h(N)B, \\ \frac{\partial B}{\partial t} = D_B \frac{\partial^2 B}{\partial x^2} + h(N)B - kBV - dB, \\ \frac{\partial V}{\partial t} = D_V \frac{\partial^2 V}{\partial x^2} + \beta kBV - \delta V. \end{cases}$$

In general, a system is said to be nondegenerate if each diffusion coefficient  $D_i$  is positive, such as system (2.1), and partially degenerate if some but not all diffusion coefficients are zero, such as system (3.1).

Define a sequence  $D_N^j$  such that  $D_N^j \rightarrow 0$  as  $j \rightarrow \infty$ . We construct the following nondegenerate system:

$$(3.2) \quad \begin{cases} \frac{\partial N}{\partial t} = D_N^j \frac{\partial^2 N}{\partial x^2} - \frac{1}{\gamma}h(N)B, \\ \frac{\partial B}{\partial t} = D_B \frac{\partial^2 B}{\partial x^2} + h(N)B - kBV - dB, \\ \frac{\partial V}{\partial t} = D_V \frac{\partial^2 V}{\partial x^2} + \beta kBV - \delta V. \end{cases}$$

According to Theorems 2.6 and 2.7, for any  $j \geq 1$ , if  $R_B > 1$  and  $c \geq c^*$ , then system (3.2) admits a nontrivial traveling wave solution  $(N^j(x + ct), B(x + ct), V(x + ct))$  satisfying

$$\lim_{\xi \rightarrow -\infty} (N^j(\xi), B(\xi), V(\xi)) = (N^*, 0, 0), \quad \lim_{\xi \rightarrow +\infty} (N(\xi), B(\xi), V(\xi)) = (N_*, 0, 0),$$

where  $\xi = x + ct$ , and the wave speed  $c$  does not depend on the diffusion coefficient  $D_N^j$ . Suppose  $c > 0$ ,  $\alpha_N > 0$  such that  $g_1(N, B, V) := \alpha_N N + f_N(N, B, V)$  is nondecreasing in  $N$ , where  $f_N(N, B, V) = -\frac{1}{\gamma}h(N)B$ . From (2.10)–(2.14), we know that  $N^j$  satisfies the wave profile equation  $D_N^j(N^j)'' - c(N^j)' + f_N(N^j, B, V) = 0$ , which is equivalent to the following integral system:

$$N^j(\xi) = \frac{1}{\rho_N^j} \left( \int_{-\infty}^{\xi} e^{\lambda_N^{j-}(\xi-s)} g_1(N^j(s)) ds + \int_{\xi}^{\infty} e^{\lambda_N^{j+}(\xi-s)} g_1(N^j(s)) ds \right)$$

with  $\rho_N^j = \sqrt{c^2 + 4D_N^j \alpha_N}$ ,  $\lambda_N^{j-} = \frac{c - \sqrt{c^2 + 4D_N^j \alpha_N}}{2D_N^j}$ ,  $\lambda_N^{j+} = \frac{c + \sqrt{c^2 + 4D_N^j \alpha_N}}{2D_N^j}$ . By direct computation, we obtain  $\rho_N = \lim_{j \rightarrow \infty} \rho_N^j = \lim_{j \rightarrow \infty} \sqrt{c^2 + 4D_N^j \alpha_N} = c \neq 0$ ,  $\lambda_N^- := \lim_{j \rightarrow \infty} \lambda_N^{j-} = \lim_{j \rightarrow \infty} \frac{c - \sqrt{c^2 + 4D_N^j \alpha_N}}{2D_N^j} = -\frac{\alpha_N}{c}$ , and  $\lambda_N^+ := \lim_{j \rightarrow \infty} \lambda_N^{j+} = \lim_{j \rightarrow \infty} \frac{c + \sqrt{c^2 + 4D_N^j \alpha_N}}{2D_N^j} = +\infty$ . By the Lebesgue dominated convergence theorem, it then follows that  $N(\xi) = \frac{1}{\rho_N} \left( \int_{-\infty}^{\xi} e^{\lambda_N^-(\xi-s)} g_1(N(s)) ds + \int_{\xi}^{\infty} e^{\lambda_N^+(\xi-s)} g_1(N(s)) ds \right)$ , which is equivalent to  $-cN' + f_N(N, B, V) = 0$ . Here, the expressions of  $\mathfrak{D}_N$  and  $\mathfrak{D}_N^{-1}$  are reduced to  $\mathfrak{D}_N g := cg' + \alpha_N g$ , and  $(\mathfrak{D}_N^{-1} g)(x) := \frac{1}{c} \int_{-\infty}^x e^{-\frac{\alpha_N}{c}(x-y)} g(y) dy$ . Let  $G_N(N, B, V) := \mathfrak{D}_N^{-1}[\alpha_N N - \frac{1}{\gamma}h(N)B]$ , we can verify  $\underline{N} \leq G_N(N, B, V) \leq \bar{N}$ , and map  $G_N$  is uniformly bounded and equi-continuous. Similar to the discussion in the previous section, we can prove the existence of traveling wave solutions.

**THEOREM 3.1.** *Assume that  $R_B > 1$ . Then for any  $c \geq c^*$ , system (3.1) admits a nontrivial traveling wave solution  $(N(\xi), B(\xi), V(\xi)), \xi = x + ct$  satisfying*

$$\lim_{\xi \rightarrow -\infty} (N(\xi), B(\xi), V(\xi)) = (N^*, 0, 0), \quad \lim_{\xi \rightarrow +\infty} (N(\xi), B(\xi), V(\xi)) = (N_*, 0, 0).$$

**3.2. General minimum model without mortality of bacteria.** In this section, we assume that the environment is a kind of soup in which nutrients, bacteria, and phages all diffuse. Hence, the model becomes

$$(3.3) \quad \begin{cases} \frac{\partial N}{\partial t} = D_N \frac{\partial^2 N}{\partial x^2} - \frac{1}{\gamma} h(N)B, \\ \frac{\partial B}{\partial t} = D_B \frac{\partial^2 B}{\partial x^2} + h(N)B - kBV - dB, \\ \frac{\partial V}{\partial t} = D_V \frac{\partial^2 V}{\partial x^2} + \beta kBV - \delta V. \end{cases}$$

Let  $d = 0$ . If  $N > 0$ , then  $B = 0$  and  $V = 0$ , that is,  $(N_s, 0, 0)$  with  $N_s > 0$  are steady states. Similar to the argument before, we can get that system (3.3) has a traveling wave solution connecting from one bacteria-free state  $E_0(N^*, 0, 0)$  to another bacteria-free state  $E_1(N_*, 0, 0)$ . If  $N = 0$ , then  $V = 0$  and  $B = B_s \geq 0$ . Therefore,  $(0, B_s, 0)$  with  $B_s \geq 0$  are steady states. The important thing is to show the invasion of phage, we are interested in a traveling wave solution connecting from one phage-free state  $E_2(0, B^*, 0)$  to another bacteria-free state  $E_3(0, B_*, 0)$ . Linearizing the equations of  $B$  and  $V$  of (3.3) at  $E_2(0, B^*, 0)$ , we get

$$(3.4) \quad \begin{cases} \frac{\partial B}{\partial t} = D_B \frac{\partial^2 B}{\partial x^2} - kBV, \\ \frac{\partial V}{\partial t} = D_V \frac{\partial^2 V}{\partial x^2} + \beta kBV - \delta V. \end{cases}$$

We set  $R_V := \beta kB^*/\delta$ . It is noted that  $R_V$  is the basic reproduction number of bacteria for the corresponding ordinary differential system. The minimum wave speed can be defined as  $c^{**} := \inf_{\lambda > 0} \frac{D_V \lambda^2 + \beta kB^* - \delta}{\lambda} = 2\sqrt{D_V(\beta kB^* - \delta)}$ .

The value  $c^{**}$  denotes the spreading speed of the phage  $V$  in the absence of nutrients, i.e.,  $N \equiv 0$ . Note that  $R_V > 1$  if and only if  $B^* > B_{cri}$ , where  $B_{cri} = \frac{\delta}{\beta k}$ .

**THEOREM 3.2.** *Assume  $B^*$  is a positive constant. If  $B^* > B_{cri}$ , then there exists a positive constant  $c^{**}$  such that system (3.4) has a positive traveling wave solution  $(B(\xi), V(\xi)), \xi = x + ct, c > 0$  satisfying*

$$(B(-\infty), V(-\infty)) = (B^*, 0), \quad (B(+\infty), V(+\infty)) = (B_*, 0)$$

*if and only if  $c \geq c^{**}$ , where  $B_*$  is a nonnegative constant depending on  $c$ . If  $B^* \leq B_{cri}$  or  $c < c^{**}$ , (3.4) has no traveling wave solution with wave speed  $c$  for any  $c > 0$ .*

**4. Numerical simulations.** In this section, we use a numerical simulation to illustrate and complement our theoretical results. We verify the existence of traveling waves in different nutrient media and simulate the effects of key parameters on the propagation dynamics of bacteria and phages. We estimate reasonable parameter ranges from the literature (see Table 4.1). We select proper parameter values from these ranges to run simulations.

TABLE 4.1  
Variables and parameters.

Var/Par	Definition	Unit	Value	Reference
$B$	Density of bacteria	$\mu g(cm)^{-3}$	-	-
$V$	Density of phage	$\mu g(cm)^{-3}$	-	-
$N$	Density of nutrient	$\mu g(cm)^{-3}$	-	-
$D_B$	Diffusion coefficient of bacteria	$(cm)^2 h^{-1}$	0 – 0.03	[12]
$D_V$	Diffusion coefficient of phage	$(cm)^2 h^{-1}$	0 – 0.002	[12]
$D_N$	Diffusion coefficient of nutrient	$(cm)^2 h^{-1}$	0 – 10	[12]
$\alpha$	Resource uptake rate	$h^{-1}$	0.7 – 0.8	[2, 12, 17]
$\delta$	Phage mortality rate	$h^{-1}$	0.003 – 0.03	[2]
$\gamma$	Yield constants	-	0.5	-
$K$	Half-saturation constant	$\mu g(cm)^{-3}$	4 – 5	[2, 17]
$\beta$	Burst size	-	50 – 150	[15, 17, 36]
$k$	Infection rate	$h^{-1}$	$(6.24)10^{-8} - (6.24)10^{-6}$	[2, 36]
$d$	Decompose rate	$h^{-1}$	0 – 0.01	-

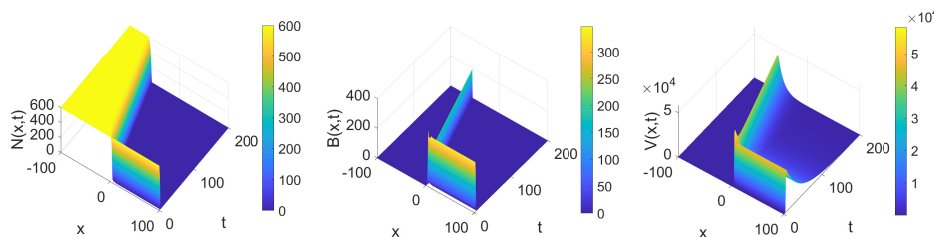


FIG. 4.1. Densities over time and space in general minimum model case.

**4.1. General minimum model.** By Theorem 2.6, system (2.1) admits traveling wave solutions whose components have the same wave speed but different waveforms. The parameter values are given in Table 4.1:  $\alpha = 0.75$ ,  $K = 5$ ,  $k = 0.0000624$ ,  $\beta = 150$ ,  $d = 0.008$ ,  $\delta = 0.03$ ,  $\gamma = 0.5$ ,  $D_N = 0.5$ ,  $D_B = 0.02$ ,  $D_V = 0.0002$ , and the initial conditions are

$$N_0(x) = 600, B_0(x) = \begin{cases} 0, & x < 0, \\ 4x, & 0 \leq x \leq 10, \text{ and } V_0(x) = 10. \\ 40, & x > 10, \end{cases}$$

The evolution of the solution is shown in Figure 4.1. Our simulation result shows the propagation dynamics of bacteria in the culture medium with phages. A bacterial front composed of the fastest migrating bacteria, which carry a hitchhiking phage population, is trailed by a secondary phage front where bacteria collapse under infection pressure. From the observation, bacteria propagate in the form of a pulse wave at a low concentration, and the bacterial density at both ends of the wave is almost zero, respectively representing the state that is not invaded by bacteria and the state that has been decomposed into bacteriophage plaque. It can also be seen from the simulation that bacteria and phages cannot persist in a given location. This shows that early release of phages in the culture medium can effectively ward off bacterial invasion.

**4.2. General agar model.** Here we consider the general agar model (3.1), in which nutrients cannot diffuse while bacteria can. Nutrient media vary from liquid to agar by changing the nutrient diffusion rate. We choose the same parameters as



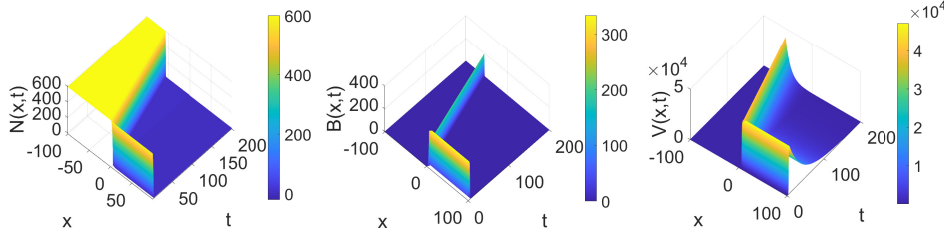


FIG. 4.2. Densities over time and space in the general agar model case.

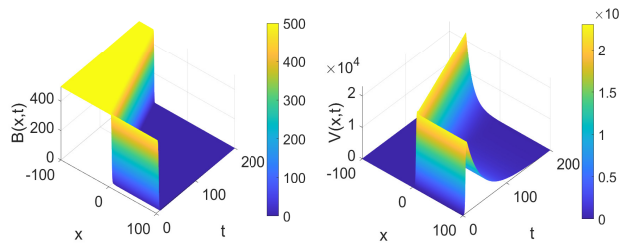


FIG. 4.3. Densities over time and space in general minimum model case. The chosen values of the parameters are  $\alpha = 0.75$ ,  $K = 5$ ,  $k = 0.0000624$ ,  $\beta = 150$ ,  $d = 0$ ,  $\delta = 0.03$ ,  $\gamma = 0.5$ ,  $D_N = 0.2$ ,  $D_B = 0.02$ ,  $D_V = 0.0002$ .

in the previous simulation, except for the diffusion coefficient of nutrients  $D_N = 0$ . Compared to the system (2.1), the agar model has similar results (see Figure 4.2). The density of nutrients is propagated by wave fronts, while the density of bacteria and phages is propagated by pulse waves. The smoothness of the nutrient wavefront in the agar model is weaker than that in the liquid model.

**4.3. General minimum model without mortality of bacteria.** In this subsection, we consider system (2.1) with  $d = 0$ , and choose the initial functions

$$N_0(x) = 0, \quad B_0(x) = 500, \quad \text{and} \quad V_0(x) = \begin{cases} 0, & x < 0, \\ 0.4x, & 0 \leq x \leq 10, \\ 4, & x > 10. \end{cases}$$

A new class of steady state solutions appears when the mortality of bacteria  $d = 0$ . Our simulation depicts the state of phage invasion of bacteria when all nutrients are consumed and the bacterial density has stabilized. The density of bacteria is propagated by wave fronts, while the density of phages is propagated by pulse waves (see Figure 4.3).

**4.4. Impact of diffusion coefficient.** To explain the influence of the diffusivity of each component on the propagation dynamics. We select parameter values from ranges given in Table 4.1:  $\alpha = 0.75$ ,  $K = 5$ ,  $k = 0.000624$ ,  $\beta = 150$ ,  $d = 0.01$ ,  $\delta = 0.03$ ,  $\gamma = 0.5$ , and the initial conditions:  $N_0(x) = 600$ ,  $V_0(x) = 10$ , and

$$B_0(x) = \begin{cases} 0, & x < -10, \\ 3 \cos(\pi x/20), & -10 \leq x \leq 10, \\ 0, & x > 10. \end{cases}$$

The diffusion coefficient of nutrients could not change the spreading speed of bacteria and phage (see Figures 4.4 and 4.5), but the diffusion coefficient of bacteria could

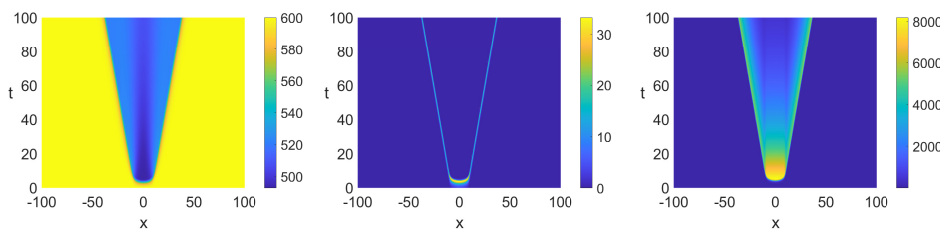


FIG. 4.4. Densities evolve over time and space when  $D_N = 0.5$ ,  $D_B = 0.02$ ,  $D_V = 0.002$ .

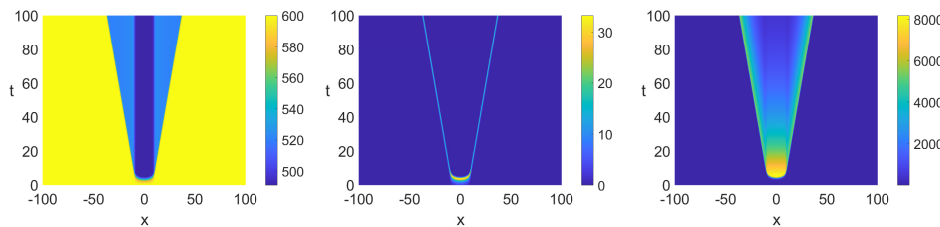


FIG. 4.5. Densities evolve over time and space when  $D_N = 0$ ,  $D_B = 0.02$ ,  $D_V = 0.002$ .

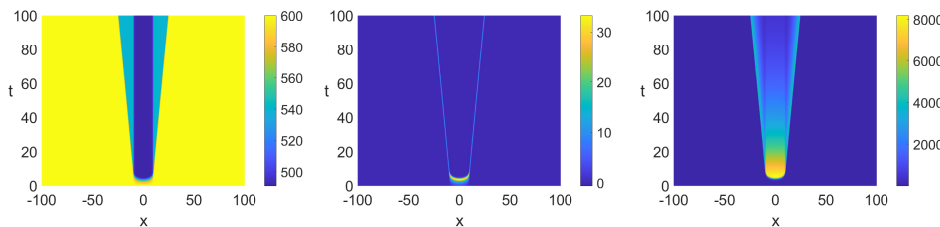


FIG. 4.6. Densities evolve over time and space when  $D_N = 0$ ,  $D_B = 0$ ,  $D_V = 0.002$ .

obviously change the spreading speed of bacteria and phage (see Figures 4.5 and 4.6). Our results provide some insight into the long-term preservation of phages in bounded region by a strategy of reducing bacterial diffusion to slow the removal of phages from the environment.

**4.5. Impact of burst size.** In this subsection, we explain the effects of different burst sizes on bacterial and phage propagation. We select the following parameter values:  $\alpha = 0.75$ ,  $K = 5$ ,  $k = 0.0000624$ ,  $\delta = 0.03$ ,  $\gamma = 0.5$ ,  $d = 0$ ,  $D_N = 0.2$ ,  $D_B = 0.02$ ,  $D_V = 0.002$  and the initial conditions:  $N_0(x) = 50$ ,  $V_0(x) = 2$ , and

$$B_0(x) = \begin{cases} 0, & x < -1, \\ 30 \cos(\pi x/2), & -1 \leq x \leq 1, \\ 0, & x > 1. \end{cases}$$

We increase the burst size  $\beta$  from 50 to 140 to see its impact on the density of bacteria.

Our results show that as  $\beta$  increases, the spread of bacteria remains constant, the expansion speed of plaque increases, and the living space of bacteria becomes narrow. This means that bacteria and plaque can spread at different speeds. The lower burst size can take a longer time to infect and remove bacteria (see Figure 4.7). Therefore, the bacteria will be controlled if the burst size of phage is greater than a certain threshold. This provides a theoretical basis for the rapid control of bacteria.

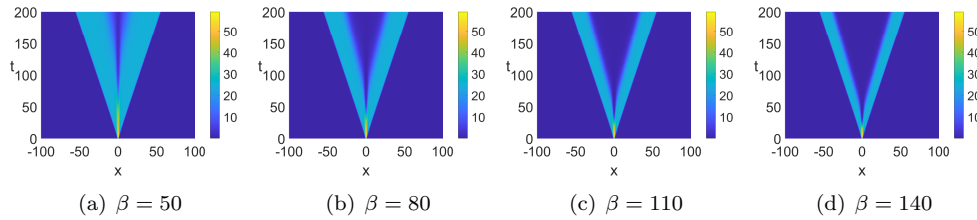


FIG. 4.7. Impact of the burst size on density of bacteria over time and space.

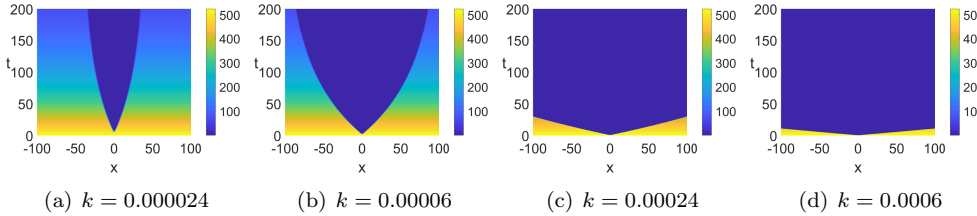


FIG. 4.8. Impact of the infection rate on density of bacteria over time and space.

**4.6. Impact of infection rate.** We then explain the effects of different burst sizes on bacterial and phage propagation. We select parameter values:  $\alpha = 0.75$ ,  $K = 5$ ,  $\beta = 140$ ,  $\delta = 0.03$ ,  $\gamma = 0.5$ ,  $d = 0.01$ ,  $D_N = 0.2$ ,  $D_B = 0.02$ ,  $D_V = 0.002$  and the initial conditions:

$$N_0(x) = 50, \quad B_0(x) = 500, \quad \text{and} \quad V_0(x) = \begin{cases} 0, & x < -1, \\ 3 \cos(\pi x/2), & -1 \leq x \leq 1, \\ 0, & x > 1. \end{cases}$$

We increase the infection rate  $k$  from 0.000024 to 0.0006 to see its impact on the density of bacteria.

Our simulation shows that the removal rate of bacteria depends heavily on the infection rate. With the increase of infection rate, bacteria will be removed quickly (see Figure 4.8). In addition, the expansion of plaque produced by phage invasion may have variable speed, which is a new phenomenon compared to the traditional predator-prey system.

**4.7. Propagating terraces and multipulse waves.** In this subsection, we explain the effects of impact of the nutrient concentration on bacterial and phage propagation. We select the following parameter values:  $\alpha = 0.75$ ,  $K = 5$ ,  $k = 0.0000624$ ,  $\delta = 0.03$ ,  $\beta = 150$ ,  $\gamma = 0.5$ ,  $d = 0.005$ ,  $D_N = 0.2$ ,  $D_B = 0.02$ ,  $D_V = 0.002$  and the initial conditions:  $V_0(x) = 0.01$ , and

$$B_0(x) = \begin{cases} 0, & x < -1, \\ \cos(\pi x/2), & -1 \leq x \leq 1, \\ 0, & x > 1. \end{cases}$$

We increase the nutrient concentration  $N_0(x)$  from 500 to 2000 to investigate the distribution pattern of bacteria. As the concentration of nutrients increases, bacteria and phages experience multiple outbreaks, manifested as a series of multipulse waves. According to our Theorem 2.6, nutrient  $N(\xi)$  may generate a front connecting the initial concentration  $N^*$  and the final concentration  $N_*$ . However,  $N_*$  may still satisfy the condition  $h(N_*)/d > 1$ . Our simulation supplements this setting (see Figures 4.9

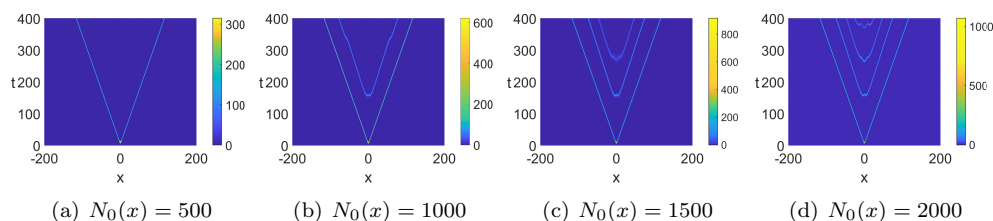


FIG. 4.9. Impact of the nutrient concentration on density of bacteria over time and space.

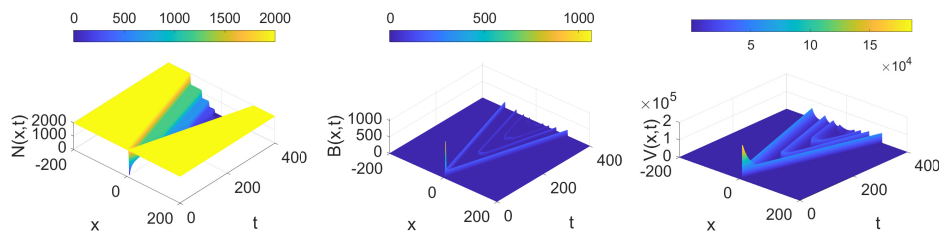


FIG. 4.10. Propagating terraces and multipulse waves phenomenon when  $N_0(x) = 2000$ .

and 4.10). It can be observed that there is a pair of traveling waves for components  $B$  and  $V$  propagating in opposite directions, which are multipulse waves. At the same time, it can be observed that the waveform of  $N$  evolves into a terrace.

**5. Discussion.** Substrate quantified by nutrient concentration is one key factor regulating the distribution of bacterial colonies. However, previous studies rarely considered the role of nutrients in bacteriophage invasion on culture medium. Focusing on the lytic phage life cycle rather than the lysogenic cycle, we introduce a group of reaction-diffusion models to describe possible elimination of bacteria by phage. The main feature of our theoretical framework is to incorporate the nutrient explicitly for bacterial consumption and growth.

There is evidence that some immobile microbes use cross-species hitchhiking to travel through their environment. Carrier bacteria (host or nonhost) can expand the migration range of the phage, thus improving the chances of infecting the host bacteria [26, 42, 43]. Specific adsorption allows phages to hitch a ride with an expanding bacterial population by repeatedly reinfecting cells in the front of the expanding bacteria [28]. The main feature of this hitchhiking mechanism is that the phage and bacteria move at the same speed. This is consistent with the traveling wave solution definition of the system. Therefore, this paper attempts to explain the occurrence of co-transport by the existence and nonexistence of traveling wave, and screen out the key parameters affecting the co-transport of phages and bacteria according to the definition of critical wave speed.

Mathematically, a large number of literature papers have been devoted to the study of traveling wave solutions. At present, there is a relatively uniform treatment method for cooperative (i.e., the principle of comparison holds) systems (see [8, 20, 21, 23, 38]). However, for noncooperative systems, there is no unified theoretical framework to prove the existence of traveling wave solutions (see [5, 6, 7, 10, 18, 35, 40, 41, 47, 48]). In our model, for a class of noncooperative systems with nonisolated equilibrium states, we obtain complete information about the existence and nonexistence of nontrivial traveling wave solutions. The threshold conditions for the existence

and nonexistence of traveling wave solutions are obtained by using Schauder's fixed point theorem, limiting argument, and one-sided Laplace transform. Furthermore, we extend the related results from reaction-diffusion systems to partially degenerate reaction-diffusion systems to describe the propagation dynamics of systems in different media. Moreover, without considering nutrients and mortality of bacteria, our conclusion is similar to that in [15, 13, 14], we have proved that the system has a traveling wave solution, in which the bacterial component  $B(\cdot)$  is monotonically decreasing (front type), but the phage components  $V(\cdot)$  is not monotone (pulse wave). However, considering the system with nutrients and mortality of bacteria, bacteria and phages propagate in the form of pulse waves.

From the perspective of invasion ecology, the traveling wave solution of our system has a different ecological interpretation from the classical traveling wave solution. For the classical traveling wave solution, it can be seen that the population density in some fixed sites is always greater than zero, and such areas show an expanding trend, that is, invasive species has local persistence. However, the invasion phenomenon described in our work is a different matter. The first type of traveling waves (described in Theorems 2.6 and 3.1) that our paper focuses on is that the bacteriophages are placed in the culture medium (liquid or agar) in advance to resist bacterial invasion, thus the bacterial population cannot establish a permanent population, and bacterial invasion fails. The pulsed wave phenomenon indicates that the bacteria only spread geographically but cannot establish colonies at any given location, thus the bacterial population is weakly persistent rather than locally persistent. We also find that the traveling wave of phage invasion cannot be observed if the bacterial mortality  $d$  is not equal to zero. It should be noted that the topology of the system will change when the mortality rate of bacteria  $d$  equals zero. The system may have a second type of traveling waves (described in Theorem 3.2), which represent the phage invading bacteria and removing bacteria after the bacteria have established a colony, and the phage is also extirpated due to a lack of hosts to be infected. Both types of traveling waves suggest that phages propagate at the same speed with bacteria through some kind of hitchhiking mechanism. The key parameters affecting the existence of traveling wave solutions have certain enlightening effect on the study of co-transport mechanism in microbiology.

Traveling waves are not only an important mechanism for species invasion and transmission, but also reflect the temporal and spatial evolution of the genetic structure of expanding populations to some extent [9, 25, 34]. Roughly speaking, traveling waves can be divided into pulled and pushed waves depending on whether the critical wave speed of a system is equal to the minimum wave speed of a linear system (see [1, 30]). For the pulled waves, only the very tip of the expansion contributes to reproduction. On the contrary, the organisms at the forefront of the push wave have almost no offspring, and the population mainly descends from the organisms in the high growth area. This shift in the spatial patterns of ancestry is closely related to the diversity of genes, and has a profound impact on the evolution of species [3, 11, 29]. The transition from a pulled wave to a pushed wave has usually been associated with increased cooperativity between individuals. Our numerical simulations verify that when the bacterial diffusion coefficient is zero, the spreading speed (greater than zero) of the system is not equal to the minimum wave speed (equal to zero) of the linearized system, that is, the pulled wave of the system transforms into a pushed wave. Genetically, our results provide insight into the evolution of spatial patterns tracing the ancestors of bacteria and phages.

As an important concept to describe the dynamics of population propagation, the asymptotic spreading speed has not been fully studied in the multispecies model.

Considering the spreading speed for solutions of our model that the initial values of phage and bacteria components have compact support is quite meaningful. However, our numerical simulations show that even if the initial function of only one component is compact supported, there will be unusual propagation phenomena, such as two components propagate at different speeds (see Figure 4.7) or the propagation speed is time-varying (see Figure 4.8). Therefore, the analysis of the spreading speed is a challenging and open problem. By setting the initial concentration of nutrients, we observed propagating terraces and multipulse waves (see Figures 4.9 and 4.10). Exploring further why multipulse waves occur is another interesting question. We leave these questions for future investigation.

**Appendix.**

*Proof of Lemma 2.3.* From Lemma 2.2, it follows that  $\alpha_N N - \frac{1}{\gamma} h(N)B \geq \alpha_N \underline{N} - \frac{1}{\gamma} h(\underline{N})\underline{B} \geq \alpha_N \underline{N} - D_N \underline{N}'' + c \underline{N}'$  ( $\xi \neq \xi_1$ );  $\alpha_B B + h(N)B - kBV - dB - \epsilon B^2 \geq \alpha_B \underline{B} + h(\underline{N})\underline{B} - kB\underline{V} - d\underline{B} - \epsilon \underline{B}^2 \geq \alpha_B \underline{B} - D_B \underline{B}'' + c \underline{B}'$  ( $\xi \neq \xi_2$ );  $\alpha_V V + \beta kBV - \delta V - \epsilon V^2 \geq \alpha_V \underline{V} + \beta k \underline{B} \underline{V} - \delta \underline{V} - \epsilon \underline{V}^2 \geq \alpha_V \underline{V} - D_V \underline{V}'' + c \underline{V}'$  ( $\xi \neq \xi_4, \xi_5$ );  $\alpha_N N - \frac{1}{\gamma} h(N)B \leq \alpha_N \bar{N} = \mathfrak{D}_N \bar{N}$ ;  $\alpha_B B + h(N)B - kBV - dB - \epsilon B^2 \leq \alpha_B \bar{B} + h(\bar{N})\bar{B} - k \bar{B} \bar{V} - d \bar{B} - \epsilon \bar{B}^2 \leq \alpha_B \bar{B} - D_B \bar{B}'' + c \bar{B}'$  ( $\xi \neq \xi_6$ );  $\alpha_V V + \beta kBV - \delta V - \epsilon V^2 \leq \alpha_V \bar{V} + \beta k \bar{B} \bar{V} - \delta \bar{V} - \epsilon \bar{V}^2 \leq \alpha_V \bar{V} - D_V \bar{V}'' + c \bar{V}'$  ( $\xi \neq \xi_7$ ). Thus, for any  $(N, B, V) \in \Gamma$  such that  $\underline{N} \leq N(\xi) \leq \bar{N}, \underline{B} \leq B(\xi) \leq \bar{B}, \underline{V} \leq V(\xi) \leq \bar{V}$ , we can obtain  $\underline{N} \leq \mathfrak{D}_N^{-1}(\mathfrak{D}_N \underline{N}) \leq G_N(N, B, V) \leq \mathfrak{D}_N^{-1}(\mathfrak{D}_N \bar{N}) \leq \bar{N}$ ;  $\underline{B} \leq \mathfrak{D}_B^{-1}(\mathfrak{D}_B \underline{B}) \leq G_B^e(N, B, V) \leq \mathfrak{D}_B^{-1}(\mathfrak{D}_B \bar{B}) \leq \bar{B}$ ;  $\underline{V} \leq \mathfrak{D}_V^{-1}(\mathfrak{D}_V \underline{V}) \leq G_V^e(N, B, V) \leq \mathfrak{D}_V^{-1}(\mathfrak{D}_V \bar{V}) \leq \bar{V}$ .

*Proof of Lemma 2.4.* For any  $(N_1, B_1, V_1) \in \Gamma$  and  $(N_2, B_2, V_2) \in \Gamma$ , it is easy to see that there exists a constant  $z_1 > 0$  such that  $|(\alpha_N N_1 - \frac{1}{\gamma} h(N_1)B_1) - (\alpha_N N_2 - \frac{1}{\gamma} h(N_2)B_2)| \leq z_1(|N_1 - N_2| + |B_1 - B_2|)$ . Consequently, we obtain

(A.1)

$$|G_N(N_1, B_1, V_1)(\xi) - G_N(N_2, B_2, V_2)(\xi)| e^{-\mu|\xi|} \leq \frac{z_1}{\rho_N} (|N_1 - N_2|_\mu + |B_1 - B_2|_\mu) C(\xi),$$

where  $C(\xi) := e^{-\mu|\xi|} [\int_{-\infty}^\xi e^{\lambda_N^-(\xi-s)+\mu|s|} ds + \int_\xi^\infty e^{\lambda_N^+(\xi-s)+\mu|s|} ds]$ ,  $N_1 - N_2 \in C_{-\mu, \mu}(\mathbb{R}) = B_\mu(\mathbb{R}, \mathbb{R})$  and  $|N_1 - N_2|_\mu = \sup_{\xi \in \mathbb{R}} e^{-\mu|\xi|} |N_1(\xi) - N_2(\xi)|$ . Since  $\lambda_N^- < -\mu < \mu < \lambda_N^+$ , the direct calculations show that

$$C(-\infty) = \frac{1}{\mu + \lambda_N^+} - \frac{1}{\mu + \lambda_N^-}, \quad C(\infty) = \frac{1}{\lambda_N^+ - \mu} + \frac{1}{\mu - \lambda_N^-}.$$

Hence,  $C(\xi)$  is uniformly bounded on  $\mathbb{R}$ , which follows from (A.1) that the operator  $G_N$  is continuous with respect to the norm  $|\cdot|_\mu$ . Similarly, we also can show that operators  $G_B^e$  and  $G_V^e$  are continuous with respect to the norm  $|\cdot|_\mu$ . Consequently,  $G^e$  is a continuous operator on  $\Gamma$  with respect to the norm  $|\cdot|_\mu$ .

Since  $G^e$  maps  $\Gamma$  into  $\Gamma$ , it is obvious that  $G^e$  is uniformly bounded. Next, we will show that  $G^e$  is equi-continuous. Set  $g_2(N, B, V) = \alpha_B B + h(N)B - kBV - dB - \epsilon B^2$ . From the definition of  $G_B^e$  and integral representation for the derivative of  $\mathfrak{D}_B^{-1}$ ,

$$G_B^e'(N, B, V)(\xi) = (\mathfrak{D}_B^{-1} g_2)'(x) = \frac{\lambda_B^-}{\rho_B} \int_{-\infty}^\xi e^{\lambda_B^-(\xi-s)} g_2(s) ds + \frac{\lambda_B^+}{\rho_B} \int_\xi^\infty e^{\lambda_B^+(\xi-s)} g_2(s) ds.$$

Then we have

$$\begin{aligned} |G_B^{\epsilon'}(N, B, V)(\xi)|_\mu &\leq \frac{-\lambda_B^-}{\rho_B} |g_2(N, B, V)(\xi)|_\mu \sup_{\xi \in R} e^{\lambda_B^- \xi - \mu|\xi|} \int_{-\infty}^{\xi} e^{-\lambda_B^- s} e^{\mu|s|} ds \\ &\quad + \frac{\lambda_B^+}{\rho_B} |g_2(N, B, V)(\xi)|_\mu \sup_{\xi \in R} e^{\lambda_B^+ \xi - \mu|\xi|} \int_{\xi}^{\infty} e^{-\lambda_B^+ s} e^{\mu|s|} ds \\ &\leq \frac{1}{\rho_B} \left( \frac{\lambda_B^-}{\mu + \lambda_B^-} + \frac{\lambda_B^+}{\lambda_B^+ - \mu} \right) |g_2(N, B, V)(\xi)|_\mu. \end{aligned}$$

In fact, note that  $u = (N, B, V) \in \Gamma$ . It is easy to see that  $|g_2(u)|_\mu$  is bounded by a positive number. Therefore, there exists a constant  $K_0$  such that  $|G_B^{\epsilon'}(N, B, V)(\xi)|_\mu \leq K_0$ . Similarly,  $|G_N^{\epsilon'}(N, B, V)(\xi)|_\mu$  and  $|G_V^{\epsilon'}(N, B, V)(\xi)|_\mu$  are also bounded, which shows that  $G^\epsilon(\Gamma)$  is uniformly bounded and equi-continuous with respect the norm  $|\cdot|_\mu$  in any compact interval. Moreover, for fixed positive integer  $n$ . Then we define

$$G^{\epsilon n}(N, B, V)(\xi) = \begin{cases} G^\epsilon(\phi, \varphi, \psi)(\xi), & \xi \in [-n, n], \\ G^\epsilon(\phi, \varphi, \psi)(n), & \xi \in (n, \infty), \\ G^\epsilon(\phi, \varphi, \psi)(-n), & \xi \in (-\infty, -n). \end{cases}$$

Then, for each  $n \geq 1$ ,  $G^{\epsilon n}$  is also equi-continuous and uniformly bounded. Now, in the interval  $[-n, n]$ , it follows from the Ascoli–Arzela theorem that  $G^{\epsilon n}$  is compact. Since

$$|G_B^{\epsilon n}(N, B, V)(\xi)| \leq \frac{H_0}{\rho_B} \left[ \int_{-\infty}^{\xi} e^{\lambda_B^-(\xi-s)} ds + \int_{\xi}^{+\infty} e^{\lambda_B^+(\xi-s)} ds \right] = \frac{H_0}{D_B |\lambda_B^-| \lambda_B^+}.$$

Then

$$\begin{aligned} &\sup_{\xi \in R} |G_B^{\epsilon n}(N, B, V)(\xi) - G_B^\epsilon(N, B, V)(\xi)| e^{-\mu|\xi|} \\ &= \sup_{\xi \in (-\infty, -n) \cup (n, \infty)} |G_B^{\epsilon n}(N, B, V)(\xi) - G_B^\epsilon(N, B, V)(\xi)| e^{-\mu|\xi|} \\ &\leq 2 \frac{H_0}{D_B |\lambda_B^-| \lambda_B^+} e^{-\mu n} \rightarrow 0, \quad n \rightarrow \infty. \end{aligned}$$

Similarly, we can prove that  $|G_N^{\epsilon n} - G_N^\epsilon| \rightarrow 0$ ,  $|G_V^{\epsilon n} - G_V^\epsilon| \rightarrow 0$ , when  $n \rightarrow +\infty$ . Thus,  $|G^{\epsilon n} - G^\epsilon| \rightarrow 0$  when  $n \rightarrow +\infty$ . By [44, Proposition 2.12], we have that  $G^\epsilon : \Gamma \rightarrow \Gamma$  is compact.

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