

## A *Wolbachia* infection model with free boundary

Yunfeng Liu<sup>a,b</sup>, Zhiming Guo<sup>a</sup>, Mohammad El Smaily<sup>c</sup> and Lin Wang<sup>d</sup>

<sup>a</sup>School of Mathematics and Information Sciences, Guangzhou University, Guangzhou, People's Republic of China; <sup>b</sup>School of Mathematics & Statistics, Qiannan Normal University for Nationalities, Duyun, People's Republic of China; <sup>c</sup>Department of Mathematics & Statistics, University of Northern British Columbia, Prince George, Canada; <sup>d</sup>Department of Mathematics & Statistics, Statistics, University of New Brunswick, Fredericton, Canada

### ABSTRACT

Scientists have been seeking ways to use *Wolbachia* to eliminate the mosquitoes that spread human diseases. Could *Wolbachia* be the determining factor in controlling the mosquito-borne infectious diseases? To answer this question mathematically, we develop a reaction-diffusion model with free boundary in a one-dimensional environment. We divide the female mosquito population into two groups: one is the uninfected mosquito population that grows in the whole region while the other is the mosquito population infected with *Wolbachia* that occupies a finite small region. The mosquito population infected with *Wolbachia* invades the environment with a spreading front governed by a free boundary satisfying the well-known one-phase Stefan condition. For the resulting free boundary problem, we establish criteria under which spreading and vanishing occur. Our results provide useful insights on designing a feasible mosquito releasing strategy that infects the whole mosquito population with *Wolbachia* and eradicates the mosquito-borne diseases eventually.

### ARTICLE HISTORY

Received 17 July 2018  
Accepted 6 June 2020

### KEYWORDS

*Wolbachia* infection;  
reaction-diffusion systems;  
free boundary;  
spreading-vanishing  
dichotomy

## 1. Introduction

Recently, several public health projects were launched in China [27], USA [1] and France [22], with an aim to fight mosquito populations that transmit Zika virus, Dengue fever and Chikungunya. All of these projects involve the release of male *Aedes aegypti* mosquitoes infected with the *Wolbachia* bacteria to the wild. For instance, 20000 male *Aedes aegypti* mosquitoes carrying *Wolbachia* bacteria were released on Stock Island of the Florida Keys in the week of April 20, 2017. Google's Verily is about to release 20 million machine-reared *Wolbachia*-infected mosquitoes in Fresno (see [1]). A factory in Southern China is manufacturing millions of 'mosquito warriors' (male *Aedes aegypti* mosquitoes carrying *Wolbachia* bacteria) to combat epidemics transmitted by mosquitoes [27].

The science behind these projects is based on the following two facts: (i) *Wolbachia* often induces cytoplasmic incompatibility (CI) which leads to early embryonic death when *Wolbachia*-infected males mate with uninfected females and (ii) *Wolbachia*-infected females

**CONTACT** Z. Guo  [guozm@gzhu.edu.cn](mailto:guozm@gzhu.edu.cn)

produce viable embryos after mating with either infected or uninfected males, resulting in a reproductive advantage over uninfected females. In practice, *Wolbachia* has been successfully transferred into *Aedes aegypti* or *Aedes albopictus* by embryonic microinjections, and the injected infection has been stably maintained with complete CI and nearly perfect maternal transmission [2,16,17,23,31,32,34]. Thus, the bacterium is expected to invade host population easily driving the host population to decline. Successful *Wolbachia* invasion in *Aedes aegypti* has been observed by Xi et al. in the laboratory caged population within seven generations [33].

By releasing *Aedes albopictus* mosquitoes infected with *Wolbachia* bacteria into the wild, it is expected that over a long time period, the wild *Aedes aegypti* mosquito population would decline drastically and hopefully be completely replaced by infected mosquitoes so that the mosquito-borne infectious diseases such as Zika, Dengue fever and Chikungunya would be eradicated. To qualitatively examine if *Wolbachia* can effectively invade the wild uninfected mosquito population, Zheng, Tang and Yu [38] considered the following model:

$$\begin{aligned} \frac{du}{dt} &= u[b_1 - \delta_1(u + v)] && \text{for } t > 0, \\ \frac{dv}{dt} &= v \left[ \frac{b_2v}{u + v} - \delta_2(u + v) \right] && \text{for } t > 0, \end{aligned} \tag{1}$$

where  $u$  denotes the number of reproductive infected insects and  $v$  denotes uninfected ones,  $b_1$  and  $b_2$  denote half of the constant birth rates for the infected and uninfected insects respectively. The parameter  $\delta_1$  (resp.  $\delta_2$ ) denotes the density-dependent death rate for the infected (resp. uninfected) population. The birth rate of uninfected mosquitoes is diminished by the factor  $v/(u + v)$  due to the sterility caused by cytoplasmic incompatibility (CI) for mating between infected males and uninfected females.

Let us now recall the origin of system (1) with some details. Let  $r_f$  and  $r_m$  denote the number of released female mosquitoes and the number of released males, respectively, and suppose the released mosquitoes were infected with *Wolbachia*. Also, assume that  $r_f$  and  $r_m$  satisfy

$$\begin{aligned} \frac{dr_f}{dt} &= -\delta_1 r_f T(t), && t > 0, \\ \frac{dr_m}{dt} &= -\delta_1 r_m T(t), && t > 0, \end{aligned} \tag{2}$$

where

$$T(t) = r_f + r_m + I_f + I_m + U_f + U_m$$

denotes the total population size, with  $U_f$ ,  $U_m$ ,  $I_f$  and  $I_m$  standing for the numbers of uninfected reproductive females, uninfected reproductive males, and infected reproductive females and males other than those from releasing, respectively. Let  $b_I$  (resp.  $b_U$ ) be the natural birth rate of the infected (resp. uninfected) mosquitos and  $0 \leq \delta \leq 1$  be the proportion of mosquitos born female. Then the proportion of mosquitos born male is  $1 - \delta$ .

**Table 1.** Strong CI, × means ‘no offspring’.

mate	$U_m$	$I_m$
$U_f$	$U_f$ or $U_m$	×
$I_f$	$I_f$ or $I_m$	$I_f$ or $I_m$

With complete CI (see Table 1) and perfect maternal transmission, we have

$$\begin{aligned}
 \frac{dI_f}{dt} &= \delta b_I [I_f + r_f] - \delta_1 I_f T(t), & t > 0, \\
 \frac{dI_m}{dt} &= (1 - \delta) b_I [I_f + r_m] - \delta_1 I_m T(t), & t > 0, \\
 \frac{dU_f}{dt} &= \delta b_U \left[ U_f \frac{U_m}{r_m + I_m + U_m} \right] - \delta_2 U_f T(t), & t > 0, \\
 \frac{dU_m}{dt} &= (1 - \delta) b_U \left[ U_f \frac{U_m}{r_m + I_m + U_m} \right] - \delta_2 U_m T(t), & t > 0.
 \end{aligned}
 \tag{3}$$

One can easily verify that both  $r_f$  and  $r_m$  approach 0 as  $t \rightarrow +\infty$ . We denote by

$$u(t) = I_f + I_m \quad \text{and} \quad v(t) = U_f + U_m.
 \tag{4}$$

Assuming equal determination case, which means that  $\delta = 1/2$ ,  $I_f = I_m$  and  $U_f = U_m$ , then system (1) can be obtained by setting  $b_1 = b_I/2$  and  $b_2 = b_U/2$ . In order to obtain the spatiotemporal dynamics of (1), Huang et al. [14,15] studied the following reaction-diffusion system:

$$\begin{aligned}
 \frac{\partial u}{\partial t} &= d_1 \Delta u + u(b_1 - \delta_1(u + v)), & t > 0, \quad x \in \Omega, \\
 \frac{\partial v}{\partial t} &= d_2 \Delta v + v \left( \frac{b_2 v}{u + v} - \delta_2(u + v) \right), & t > 0, \quad x \in \Omega, \\
 \frac{\partial u}{\partial \nu} &= \frac{\partial v}{\partial \nu} = 0, & t > 0, \quad x \in \partial\Omega, \\
 u(0, x) &= u_0(x), \quad v(0, x) = v_0(x), & x \in \Omega.
 \end{aligned}
 \tag{5}$$

In (5),  $d_1$  and  $d_2$  are the diffusion rates,  $\Delta$  denotes the Laplace operator in the spatial variable  $x$ , and  $\nu$  denotes the unit outward normal vector to the boundary of  $\Omega$ . We mention that (5) is obtained from a delay differential equation model in [38] after ignoring the delay factor and incorporating the spatial inhomogeneity. Similarly, there has been several mathematical models formulated to describe the *Wolbachia* spreading dynamics [13,35,36,39]. These models focused on studying the subtle relation between the threshold releasing level for *Wolbachia*-infected mosquitoes and several important parameters including the CI intensity and the fecundity cost of *Wolbachia* infection.

We also note that female *Aedes aegypti* mosquitoes infected with the *Wolbachia* bacteria were initially released at a specific site. Hence, the infected female mosquitoes initially occupy only a small region, while the wild uninfected females are distributed over the whole area.

To model the spatial spreading of *Wolbachia* in the wild mosquito population and explore the possibility that the infection can indeed occupy the whole region, it is natural to consider system (5) under the setting of a free boundary problem.

In this work, we consider the following free boundary problem in one-dimensional space:

$$\begin{aligned}
 \frac{\partial u}{\partial t} &= d_1 u_{xx} + u(b_1(x) - \delta_1(u + v)), & t > 0, & 0 < x < h(t), \\
 \frac{\partial v}{\partial t} &= d_2 v_{xx} + v \left( \frac{b_2(x)v}{u + v} - \delta_2(u + v) \right), & t > 0, & x > 0, \\
 u_x(t, 0) &= v_x(t, 0) = 0, u(t, h(t)) = 0, & t > 0, & \\
 h'(t) &= -\mu u_x(t, h(t)), & t > 0, & \\
 h(0) &= h_0, & & \\
 u(0, x) &= u_0(x), & x \in [0, h_0], & \\
 v(0, x) &= v_0(x), & x \in [0, +\infty). &
 \end{aligned}
 \tag{6}$$

The equation governing the movement of the spreading front  $x = h(t)$  is deduced in a manner similar to that in Section 1.3 of [3]. It is known as the one-phase Stefan condition in the literature. This type of free boundary condition has been widely used in previous work such as [5–7,10,18–20,24,28–30].

We will first analyse system (6) with constant birth rates  $b_1$  and  $b_2$  in Section 3. Environmental variables such as available water surfaces and humidity have huge impacts on birth rates [8]. This is why we also extend our study to the case with space-dependent birth rates  $b_1(x)$  and  $b_2(x)$  in Section 4, while we assume that the natural death rate is spatially independent for simplicity.

Throughout this paper, we assume that  $b_1(x)$  and  $b_2(x)$  satisfy the following conditions, unless otherwise stated:

$$\begin{cases} \exists \theta \in (0, 1) \text{ such that } b_i \in C^{0,\theta}([0, +\infty)) \cap L^\infty([0, +\infty)), \\ b_i \geq 0, i = 1, 2. \end{cases}
 \tag{B_1}$$

$C^{0,\theta}([0, +\infty))$  is the Hölder space with Hölder exponent  $\theta$ . The initial conditions  $u_0$  and  $v_0$  are assumed to be bounded and satisfy

$$\begin{aligned}
 u_0 &\in C^2([0, h_0]), \\
 u'_0(0) &= u_0(h_0) = 0, \\
 u_0(x) &> 0 \text{ for all } x \in (0, h_0), \\
 v_0 &\in C^2[0, \infty) \cap L^\infty[0, \infty) \text{ and } v_0 > 0.
 \end{aligned}
 \tag{7}$$

For the free boundary problem (6)–(7), the main question we are concerned about is whether the infected population can eventually occupy the whole space or not.

**Definition 1.1 (The notion of vanishing and spreading):** If the infected population eventually occupies the whole space, i.e.

$$\lim_{t \rightarrow \infty} h(t) = +\infty,$$

we say *spreading* occurs; otherwise, we say *vanishing* occurs.

The main goal of this work is to derive conditions under which the spreading occurs. If spreading occurs, then the whole mosquito population will become infected with *Wolbachia* bacteria and this leads to the *extinction* of the mosquito population and eventually the eradication of mosquito-borne diseases.

**Organization of the paper.** The paper is organized as follows. We first establish the global existence and uniqueness of solutions to the free boundary problem (6) in Section 2. In Section 3, we present a detailed analysis of a specific case of model (6). In Section 4, we study the population dynamics of infected mosquitoes in a heterogeneous environment with a free boundary condition. In order to better understand the effects of dispersal and spatial variations on the outcome of the competition, we study system (6) over a bounded domain with Neumann boundary conditions. We summarize our results in the last section.

## 2. Global existence of smooth solutions

Using arguments that are similar to those in [11], we can establish the following result concerning the existence and uniqueness of solutions to system (6)–(7).

**Theorem 2.1 (Local existence):** *Consider system (6) with initial conditions (7). Assume that  $b_1$  and  $b_2$  satisfy  $(B_1)$ . Then, there exists  $T > 0$  such that (6) admits a unique solution  $(u, v, h(t))$  satisfying*

- (i)  $(u, v, h) \in C^{(1+\theta)/2, 1+\theta}(Q) \times C^{(1+\theta)/2, 1+\theta}(Q^\infty) \times C^{1+\theta/2}([0, T])$ ,
- (ii)  $\|u\|_{C^{(1+\theta)/2, 1+\theta}(Q)} + \|v\|_{C^{(1+\theta)/2, 1+\theta}(Q^\infty)} + \|h\|_{C^{1+\theta/2}([0, T])} \leq K$ ,

where  $0 < \theta < 1$  is the Hölder exponent in  $(B_1)$ ,

$$Q = \{(t, x) \in \mathbb{R}^2, \text{ such that } t \in [0, T] \text{ and } x \in [0, h(t)]\},$$

$$Q^\infty = \{(t, x) \in \mathbb{R}^2, \text{ such that } t \in [0, T] \text{ and } x \in [0, +\infty)\},$$

$K$  and  $T$  are constants that depend only on  $h_0, \theta, \|u_0\|_{C^2([0, h_0])}$  and  $\|v_0\|_{C^2([0, +\infty))}$ .

The next result provides some bounds on the solutions to system (6) with initial conditions (7).

**Lemma 2.1:** *Let  $(u, v, h)$  be a solution of (6) for  $t \in [0, T]$  for some  $T > 0$ . Then,*

- (i)  $0 < u(t, x) \leq M_1$  for all  $t \in (0, T]$  and  $x \in [0, h(t))$ , where

$$M_1 := \max \left\{ \frac{\|b_1\|_{L^\infty([0, \infty))}}{\delta_1}, \|u_0\|_{L^\infty([0, h_0])} \right\}.$$

- (ii)  $0 < v(t, x) \leq M_2$  for all  $t \in (0, T]$  and  $x \in [0, +\infty)$ , where

$$M_2 := \max \left\{ \frac{\|b_2\|_{L^\infty([0, \infty))}}{\delta_2}, \|v_0\|_{L^\infty([0, +\infty))} \right\}.$$

- (iii)  $0 < h'(t) \leq \Lambda$  for all  $t \in (0, T]$ , where  $\Lambda > 0$  depends on  $\mu, d_1, \|u_0\|_{L^\infty([0, h_0])}$  and  $\|u'_0\|_{C[0, h_0]}$ .

**Proof:** The strong maximum principle yields that  $u(t, x) > 0$  for all  $t \in (0, T]$  and  $x \in [0, h(t))$ , and  $v(t, x) > 0$  for all  $t \in (0, T]$  and  $x \in [0, +\infty)$ . Note that  $u(t, h(t)) = 0$  yields that

$$u_x(t, h(t)) < 0 \quad \text{for all } t \in (0, T].$$

Thus,  $h'(t) > 0$  for  $t \in (0, T]$ . Next, we consider the initial value problem

$$\begin{aligned} u'(t) &= u(t)(\|b_1\|_{L^\infty([0,\infty))} - \delta_1 u(t)), \text{ for } t > 0, \\ u(0) &= \|u_0\|_{L^\infty([0,h_0])}. \end{aligned} \tag{8}$$

From the comparison principle, we know that

$$u(t, x) \leq \max \left\{ \frac{\|b_1\|_{L^\infty([0,\infty))}}{\delta_1}, \|u_0\|_{L^\infty([0,h_0])} \right\}.$$

Similarly, we can show that

$$v(t, x) \leq \max \left\{ \frac{\|b_2\|_{L^\infty([0,\infty))}}{\delta_2}, \|v_0\|_{L^\infty([0,+\infty))} \right\}.$$

To prove (iii), we first consider the auxiliary function

$$\omega_1(t, x) := M_1 [2M(h(t) - x) - M^2(h(t) - x)^2] \tag{9}$$

for  $t \in [0, T]$  and  $x \in [h(t) - M^{-1}, h(t)]$ , where

$$M = \max \left\{ \frac{1}{h_0}, \sqrt{\frac{\|b_1\|_{L^\infty([0,\infty))}}{2d_1}}, \frac{\|u'_0\|_{C[0,h_0]}}{M_1} \right\}.$$

We have

$$\begin{aligned} \omega_{1t} - d_1 \omega_{1xx} &\geq 2d_1 M_1 M^2 \geq b_1 M_1 \\ &\geq u[b_1 - \delta_1(u + v)] = u_t - d_1 u_{xx}, \\ \omega_1(t, h(t)) &= 0 = u(t, h(t)), \\ \omega_1(t, h(t) - M^{-1}) &= M_1 \geq u(t, h(t) - M^{-1}). \end{aligned} \tag{10}$$

We also note that

$$u_0(x) = - \int_x^{h_0} u'_0(s) ds \leq (h_0 - x) \|u'_0\|_{C[0,h_0]}$$

and

$$\omega_1(0, x) = M_1 M(h_0 - x)[2 - M(h_0 - x)] \geq M_1 M(h_0 - x), \quad \text{for } x \in [h_0 - M^{-1}, h_0].$$

Thus,  $\omega_1(0, x) \geq u(0, x)$ . Applying the comparison principle, we get

$$\omega_1(t, x) \geq u(t, x), \quad \text{for } t \in [0, T] \quad \text{and} \quad x \in [h(t) - M^{-1}, h(t)].$$

Since  $\omega_1(t, h(t)) = 0 = u(t, h(t))$ , we then have

$$u_x(t, h(t)) \geq \omega_{1x}(t, h(t)) = -2MM_1.$$

Consequently,  $h'(t) = -\mu u_x(t, h(t)) \leq \Lambda$  with  $\Lambda := 2\mu MM_1$ . ■

Bearing the above result in mind, we can show that the local solution obtained in Theorem 2.1 can indeed be extended to all  $t > 0$ .

**Theorem 2.2 (Global existence and uniqueness):** *System (6)–(7) admits a unique solution for  $t \in [0, \infty)$ .*

**Proof:** Let  $[0, T_{\max})$  be the maximal time interval in which the unique solution exists. We will show that  $T_{\max} = \infty$ . Suppose to the contrary that  $T_{\max} < \infty$ . In view of Lemma 2.1, there exists positive constants  $M_1, M_2$  and  $\Lambda$ , independent of  $T_{\max}$ , such that for  $t \in [0, T_{\max}]$ ,

$$0 < u(t, x) \leq M_1, \quad 0 < v(t, x) \leq M_2 \quad \text{and} \quad 0 < h'(t) \leq \Lambda.$$

Fix  $\delta \in (0, T_{\max})$  and  $K > T_{\max}$ . Using the standard  $L^p$  estimates together with the Sobolev embedding theorem and the Hölder estimates for parabolic equations (see Lunardi [21] for eg.), we can find  $M_3$  depending only on  $\delta, K, M_1$  and  $M_2$  such that

$$\|u(t, \cdot)\|_{C^{1+\theta}[0, h(t)]} \leq M_3 \quad \text{and} \quad \|v(t, \cdot)\|_{C^{1+\theta}[0, +\infty)} \leq M_3 \quad \text{for all } t \in [\delta, T_{\max}),$$

where we used the convention that  $u(t, x) = 0$  for  $x \geq h(t)$ . By virtue of the proof of Theorem 2.1 in [11], there exists a  $\tau > 0$  depending only on  $M_1, M_2$  and  $M_3$  such that the solution of (6) with the initial time  $T_{\max} - \tau/2$  can be extended uniquely to the time  $T_{\max} + \tau/2$ , which contradicts the definition of  $T_{\max}$ . Thus,  $T_{\max} = +\infty$  and the proof is complete. ■

### 3. The special case of constant birth rates

System (5) was investigated in [14,15] for two disjoint cases. Namely, the fitness benefit case and the fitness cost case. Define  $\kappa_1$  and  $\kappa_2$  as  $\kappa_1 = b_1/\delta_1$  and  $\kappa_2 = b_2/\delta_2$ . *Wolbachia* is said to have the fitness benefit if  $\kappa_1 > \kappa_2$ , which means that the local area is more (or at least equally) favourable for infected mosquitoes. The fitness cost case is represented by  $\kappa_1 < \kappa_2$ , see [38].

In this section, we assume that  $b_i(x) = b_i$  for  $i = 1, 2$ , where  $b_i$  are positive constants. In other words, we have the constant-coefficient free boundary problem given by

$$\begin{aligned} \frac{\partial u}{\partial t} &= d_1 u_{xx} + u(b_1 - \delta_1(u + v)), & t > 0, \quad 0 < x < h(t), \\ \frac{\partial v}{\partial t} &= d_2 v_{xx} + v \left( \frac{b_2 v}{u + v} - \delta_2(u + v) \right), & t > 0, \quad x > 0, \\ u_x(t, 0) &= v_x(t, 0) = 0, \quad u(t, h(t)) = 0, & t > 0, \\ h'(t) &= -\mu u_x(t, h(t)), & t > 0, \\ h(0) &= h_0, \\ u(0, x) &= u_0(x), \quad x \in [0, h_0], \\ v(0, x) &= v_0(x), \quad x \in [0, +\infty). \end{aligned} \tag{11}$$

System (11) is essentially a competition model. For the fitness benefit case,  $\kappa_1 > \kappa_2$ ,  $u$  is the so-called superior competitor and  $v$  the inferior competitor (see [11]). For the fitness

cost case,  $\kappa_1 < \kappa_2$ , (11) represents a strong competition [25]. Throughout this section, we always assume  $u$  is a superior competitor. That is, the *Wolbachia* infection has a fitness benefit. The strong competition case is usually more complicated to be studied mathematically. To the best of our knowledge, results for competition models with a free boundary are very limited in strong competition case. Further details can be seen in [41,42].

We organize this section as follows. In Subsection 3.1 we present some preliminary results, which play a role in proving our main results. Subsection 3.2 is devoted to the vanishing case. The invasion dynamics is studied in detail in Subsection 3.3. A rough estimation of asymptotic spreading speed of *Wolbachia* invasion is given in Subsection 3.4.

### 3.1. Preliminary results

Consider the system

$$\begin{aligned} \frac{\partial u}{\partial t} &= d_1 u_{xx}(t, x) + u(t, x)(b_1 - \delta_1 u(t, x)), \quad t > 0, \quad 0 < x < L, \\ u_x(t, 0) &= u(t, L) = 0, \quad t \in (0, \infty). \end{aligned} \tag{12}$$

The following result holds.

**Lemma 3.1:** *Let  $L^* = \pi/2\sqrt{d_1/b_1}$  and  $d_* = 4b_1L^2/\pi^2$ . Then,*

- (i) *if  $L \leq L^*$ , all positive solutions of (12) tend to zero in  $C([0, L])$  as  $t \rightarrow +\infty$ .*
- (ii) *If  $L > L^*$ , there exists a unique positive stationary solution  $\phi$  of (12) such that all positive solutions of (12) approach  $\phi$  in  $C([0, L])$  as  $t \rightarrow +\infty$ .*

**Proof:** (i) and (ii) follow from Propositions 3.1, 3.2 and 3.3 of [4]. ■

We recall the following comparison principle.

**Lemma 3.2 (Comparison principle [11]):** *Assume that  $0 \leq T_0 < T < +\infty$  and  $\bar{h}, \underline{h} \in C^1([T_0, T])$ . Denote by*

$$G_T = \{(t, x) \in \mathbb{R}^2 : t \in (T_0, T], x \in (0, \underline{h})\}$$

and

$$G_T^1 = \{(t, x) \in \mathbb{R}^2 : t \in (T_0, T] \text{ and } x \in (0, \bar{h})\}.$$

Let

$$\underline{u} \in C(\overline{G_T}) \cap C^{1,2}(G_T), \quad \bar{u} \in C(\overline{G_T^1}) \cap C^{1,2}(G_T^1)$$

and

$$\bar{v}, \underline{v} \in L^\infty \cap C([T_0, T] \times [0, +\infty)) \cap C^{1,2}((T_0, T] \times [0, +\infty)).$$



Suppose that

$$\begin{aligned}
 \frac{\partial \bar{u}}{\partial t} - d_1 \bar{u}_{xx} &\geq \delta_1 \bar{u}(\kappa_1 - \bar{u} - \underline{v}), \quad T_0 < t \leq T, \quad 0 < x < \bar{h}(t), \\
 \frac{\partial \underline{u}}{\partial t} - d_1 \frac{\partial^2 \underline{u}}{\partial x^2} &\leq \delta_1 \underline{u}(\kappa_1 - \underline{u} - \bar{v}), \quad T_0 < t \leq T, \quad 0 < x < \underline{h}(t), \\
 \frac{\partial \bar{v}}{\partial t} - d_2 \bar{v}_{xx} &\geq \delta_2 \bar{v} \left( \frac{\kappa_2 \bar{v}}{\underline{u} + \bar{v}} - \bar{v} - \underline{u} \right), \quad T_0 < t \leq T, \quad x > 0, \\
 \frac{\partial \underline{v}}{\partial t} - d_2 \frac{\partial^2 \underline{v}}{\partial x^2} &\leq \delta_2 \underline{v} \left( \frac{\kappa_2 \underline{v}}{\bar{u} + \underline{v}} - \underline{v} - \bar{u} \right), \quad T_0 < t \leq T, \quad x > 0,
 \end{aligned}
 \tag{13a}$$

$$\begin{aligned}
 \underline{h}'(t) &\leq -\mu \underline{u}_x(t, \underline{h}(t)), T_0 < t \leq T, \\
 \bar{h}'(t) &\geq -\mu \bar{u}_x(t, \bar{h}(t)), T_0 < t \leq T,
 \end{aligned}
 \tag{13b}$$

and

$$\begin{aligned}
 \bar{u}_x(t, 0) &\leq 0, \quad \bar{u}(t, \bar{h}(t)) = 0, \quad T_0 < t \leq T, \\
 \partial_x \underline{u}(t, 0) &\geq 0, \quad \underline{u}(t, \underline{h}(t)) = 0, \quad T_0 < t \leq T, \\
 \bar{v}_x(t, 0) &\leq 0, \quad \underline{v}_x(t, 0) \geq 0, \quad T_0 < t \leq T, \\
 \underline{h}(T_0) &\leq h(T_0) \leq \bar{h}(T_0), \\
 \underline{u}(T_0, x) &\leq u(T_0, x) \leq \bar{u}(T_0, x), \quad 0 \leq x \leq h(T_0), \\
 \underline{v}(T_0, x) &\leq v(T_0, x) \leq \bar{v}(T_0, x), \quad x \geq 0.
 \end{aligned}
 \tag{13c}$$

Let  $(u, v, h)$  be the unique solution of (11). Then,

- (i)  $h(t) \leq \bar{h}(t)$ ,  $u(t, x) \leq \bar{u}(t, x)$  and  $v(t, x) \geq \underline{v}(t, x)$  for all  $(t, x)$  in  $(T_0, T] \times [0, +\infty)$ .
- (ii)  $h(t) \geq \underline{h}(t)$ ,  $u(t, x) \geq \underline{u}(t, x)$  and  $v(t, x) \leq \bar{v}(t, x)$  for all  $(t, x)$  in  $(T_0, T] \times [0, +\infty)$ .

The following follows from Lemmas A.2 and A.3 in [37].

**Lemma 3.3:** (a) Let  $a, b$  and  $q$  be fixed positive constants. For any given  $\varepsilon > 0$  and  $L > 0$ , there exists

$$l > \max \left\{ L, \frac{\pi}{2} \sqrt{\frac{d}{a}} \right\}$$

such that, if the continuous and non-negative function  $U(t, x)$  satisfies

$$\begin{aligned}
 U_t - dU_{xx} &\geq U(a - bU), \quad t > 0, \quad 0 < x < l, \\
 U_x(t, 0) = 0, \quad U(t, l) &\geq q, \quad t > 0, \quad (q \geq 0),
 \end{aligned}
 \tag{14}$$

with  $U(0, x) > 0$  for all  $x \in [0, l]$ , then

$$\liminf_{t \rightarrow +\infty} U(t, x) > \frac{a}{b} - \varepsilon \text{ uniformly on } [0, L].$$

(b) Let  $a, b$  and  $q$  be fixed positive constants. For any given  $\varepsilon > 0$  and  $L > 0$ , there exists  $l > \max\{L, \pi/2\sqrt{d/a}\}$  such that

$$\limsup_{t \rightarrow +\infty} V(t, x) < \frac{a}{b} + \varepsilon \text{ uniformly on } [0, L],$$

where  $V(t, x)$  is a continuous and non-negative function satisfying

$$\begin{aligned} V_t - dV_{xx} &\leq V(a - bV), \quad t > 0, \quad 0 < x < l, \\ V_x(t, 0) = 0, \quad V(t, l) &\leq q, \quad t > 0, \quad (q \geq 0), \end{aligned} \tag{15}$$

and  $V(0, x) > 0$  for all  $x \in [0, l]$ .

We are now in the position to present part of our main results.

### 3.2. The vanishing case

We consider the vanishing case in this subsection.

**Theorem 3.1:** Let  $(u, v, h)$  be the solution of system (11) with initial data (7). If  $h_\infty < +\infty$ , then

$$\lim_{t \rightarrow +\infty} \|u(t, \cdot)\|_{C[0, h(t)]} = 0 \quad \text{and} \quad \lim_{t \rightarrow +\infty} v(t, x) = \kappa_2$$

uniformly in any bounded subset of  $[0, +\infty)$ .

**Proof:** Theorem 2.1 yields that for  $\theta \in (0, 1)$ , there is a constant  $\hat{C}$  depending on  $\theta, (u_0, v_0), h_0$  and  $h_\infty$  such that

$$\|u\|_{C^{(1+\theta)/2, 1+\theta}(G)} + \|v\|_{C^{(1+\theta)/2, 1+\theta}(G)} + \|h(t)\|_{C^{1+\theta/2}([0, \infty))} \leq \hat{C}, \tag{16}$$

where

$$G := \{(t, x) \in [0, \infty) \times [0, h(t)]\}.$$

Suppose that

$$\limsup_{t \rightarrow +\infty} \|u(t, \cdot)\|_{C([0, h(t)])} = \varepsilon > 0.$$

Then, there exists a sequence  $(t_k, x_k)$  in  $(0, \infty) \times [0, h(t)]$ , where  $t_k \rightarrow \infty$  as  $k \rightarrow \infty$ , such that

$$u(t_k, x_k) \geq \frac{\varepsilon}{2} \text{ for all } k \in \mathbb{N}.$$

Note that  $0 \leq x_k < h(t_k) < h_\infty < \infty$ . By passing to a subsequence if necessary, it follows that  $x_k \rightarrow x_0 \in (0, h_\infty)$  as  $k \rightarrow \infty$ . Define

$$u_k(t, x) := u(t + t_k, x) \quad \text{and} \quad v_k(t, x) = v(t + t_k, x)$$

for  $t \in (-t_k, \infty)$  and  $x \in [0, h(t + t_k)]$ . It follows from (16) and standard parabolic regularity that  $\{(u_k, v_k)\}$  has a subsequence  $\{(u_{k_i}, v_{k_i})\}$  satisfying  $(u_{k_i}, v_{k_i}) \rightarrow (\tilde{u}, \tilde{v})$  as  $k_i \rightarrow \infty$ ,

where  $(\tilde{u}, \tilde{v})$  is the solution to the following system

$$\begin{aligned} \frac{\partial \tilde{u}}{\partial t} &= d_1 \tilde{u}_{xx} + \tilde{u} [b_1 - \delta_1(\tilde{u} + \tilde{v})], & (t, x) \in (-\infty, +\infty) \times (0, h_\infty), \\ \frac{\partial \tilde{v}}{\partial t} &= d_2 \tilde{v}_{xx} + \tilde{v} \left[ \frac{b_2 \tilde{v}}{\tilde{u} + \tilde{v}} - \delta_2(\tilde{u} + \tilde{v}) \right], & (t, x) \in (-\infty, +\infty) \times (0, h_\infty), \end{aligned} \tag{17}$$

with  $\tilde{u}(t, h_\infty) = 0$  for all  $t \in \mathbb{R}$ . Since

$$\tilde{u}(0, x_0) = \lim_{k_i \rightarrow \infty} u_{k_i}(0, x_{k_i}) = \lim_{k_i \rightarrow \infty} u(t_{k_i}, x_{t_{k_i}}) \geq \frac{\varepsilon}{2},$$

the maximum principle implies that  $\tilde{u} > 0$  in  $(-\infty, +\infty) \times (0, h_\infty)$ . Hence, we can apply Hopf Lemma at the point  $(0, h_\infty)$  to obtain  $\tilde{u}_x(0, h_\infty) < 0$ . Therefore, we have  $u_x(t_{k_i}, h(t_{k_i})) = \partial_x u_{k_i}(0, h(t_{k_i})) < 0$  for large  $i$ . This, together with the Stefan condition, implies that  $h'(t_{k_i}) > 0$ .

On the other hand,  $h_\infty < +\infty$  implies  $h'(t) \rightarrow 0$  as  $t \rightarrow \infty$  (see Lemma 3.3 in [12]). This is a contradiction. Thus,

$$\lim_{t \rightarrow +\infty} \|u(t, \cdot)\|_{C[0, h(t)]} = 0.$$

Next, we prove that  $\lim_{t \rightarrow +\infty} v(t, x) = \kappa_2$ . Having  $\lim_{t \rightarrow +\infty} \|u(t, \cdot)\|_{C[0, h(t)]} = 0$  implies that, for any  $\varepsilon \in (0, 1)$ , there exists  $T > 0$  such that  $0 \leq u(t, x) \leq \varepsilon$  for all  $t > T$  and  $x \in (0, +\infty)$ . Thus,

$$\begin{aligned} \frac{\partial v}{\partial t} &\geq d_2 v_{xx} + v \left[ \frac{b_2 v}{\varepsilon + v} - \delta_2(\varepsilon + v) \right], & t > T, \quad x > 0, \\ v_x(t, 0) &= 0, \quad v(t, +\infty) \geq 0, & t > T, \\ v(T, x) &> 0. \end{aligned} \tag{18}$$

By Lemma 3.3 and the arbitrariness of  $\varepsilon$ , we have  $\liminf_{t \rightarrow +\infty} v(t, x) \geq b_2/\delta_2 = \kappa_2$  uniformly in any bounded subset of  $[0, +\infty)$ . This, together with the fact  $\limsup_{t \rightarrow +\infty} v(t, x) \leq \kappa_2$ , shows that  $\lim_{t \rightarrow +\infty} v(t, x) = \kappa_2$ . ■

### 3.3. The invasion dynamics

**Theorem 3.2:** *Suppose  $(u, v, h)$  is the solution of system (11) under conditions (7). If  $h_\infty = +\infty$ , then  $\lim_{t \rightarrow +\infty} u(t, x) = \kappa_1$  and  $\lim_{t \rightarrow +\infty} v(t, x) = 0$  uniformly in any compact subset of  $[0, +\infty)$ .*

**Proof:** Consider the system

$$\begin{aligned} \tilde{u}'(t) &= \delta_1 \tilde{u}(\kappa_1 - \tilde{u}), & t > 0, \\ \tilde{u}(0) &= \|u_0\|_{L^\infty([0, h_0])}. \end{aligned} \tag{19}$$

Then,  $\lim_{t \rightarrow +\infty} \tilde{u}(t) = \kappa_1$  and  $u(t, x) \leq \tilde{u}(t)$ . Consequently, we have

$$\limsup_{t \rightarrow +\infty} u(t, x) \leq \kappa_1 \text{ uniformly for } x \in [0, +\infty).$$

In a similar manner, we can obtain that

$$\limsup_{t \rightarrow +\infty} v(t, x) \leq \kappa_2 \text{ uniformly for } x \in [0, +\infty).$$

Since  $\kappa_1 > \kappa_2$  then, for  $\delta = (\kappa_1 - \kappa_2)/2$ , there exists  $T_1 > 0$  such that  $v(t, x) \leq \kappa_2 + \delta$  for all  $t > T_1$  and  $x \geq 0$ . If  $h_\infty = +\infty$ , then for any given  $L$ , there exists  $l > \{L, \pi/2\sqrt{d_1/\delta_1\delta}\}$  such that  $u$  satisfies

$$\begin{aligned} \frac{\partial u}{\partial t} &\geq d_1 u_{xx} + \delta_1 u(\delta - u), & t > T_1, & \quad 0 < x < l, \\ u_x(t, 0) &= 0, u(t, l) \geq 0, & t > T_1, & \\ u(T_1, x) &> 0, & 0 < x < l. & \end{aligned} \tag{20}$$

By Lemma 3.3, we know that for sufficiently small  $\varepsilon > 0$ ,  $\liminf_{t \rightarrow +\infty} u(t, x) > \delta - \varepsilon$  uniformly in any compact subset of  $[0, L]$ . Since  $h_\infty = +\infty$ , there exists  $T_2 > T_1$  such that  $h(T_2) > L$  and  $u(t, x) \geq \delta/2$  for all  $t > T_2$  and  $0 \leq x < L$ . Then,  $(u, v)$  satisfies

$$\begin{aligned} \frac{\partial u}{\partial t} &= d_1 u_{xx} + u[b_1 - \delta_1(u + v)], & t > T_2, & \quad 0 < x < L, \\ \frac{\partial v}{\partial t} &= d_2 v_{xx} + v \left[ \frac{b_2 v}{u + v} - \delta_2(u + v) \right], & t > T_2, & \quad 0 < x < L, \\ u_x(t, 0) &= v_x(t, 0) = 0, & t > T_2, & \\ u(T_2, x) &\geq \frac{\delta}{2}, \quad v(T_2, x) \leq \kappa_2 + \delta, & 0 < x < L. & \end{aligned} \tag{21}$$

Let  $(\underline{u}, \bar{v})$  be the solution to the following problem:

$$\begin{aligned} \frac{\partial \underline{u}}{\partial t} &= d_1 \underline{u}_{xx} + \underline{u}[b_1 - \delta_1(\underline{u} + \bar{v})], & t > T_2, & \quad 0 < x < L, \\ \frac{\partial \bar{v}}{\partial t} &= d_2 \bar{v}_{xx} + \bar{v} \left[ \frac{b_2 \bar{v}}{\underline{u} + \bar{v}} - \delta_2(\underline{u} + \bar{v}) \right], & t > T_2, & \quad 0 < x < L, \\ \partial_x \underline{u}(t, 0) &= \bar{v}_x(t, 0) = 0, & t > T_2, & \\ \underline{u}(t, L) &= \frac{\delta}{2}, \quad \bar{v}(t, L) = \kappa_2 + \delta, & t > T_2, & \\ \underline{u}(T_2, x) &= \frac{\delta}{2}, \quad \bar{v}(T_2, x) = \kappa_2 + \delta, & 0 \leq x \leq L. & \end{aligned} \tag{22}$$

It follows from the comparison principle that

$$u(t, x) \geq \underline{u}(t, x) \quad \text{and} \quad v(t, x) \leq \bar{v}(t, x) \quad \text{for } t > T_2 \quad \text{and} \quad 0 \leq x \leq L.$$

By Corollary 3.6 of [26], we have

$$\lim_{t \rightarrow +\infty} \underline{u}(t, x) = \underline{u}_L(x) \quad \text{and} \quad \lim_{t \rightarrow +\infty} \bar{v}(t, x) = \bar{v}_L(x) \quad \text{uniformly in } [0, L].$$

Here,  $(\underline{u}_L, \bar{v}_L)$  satisfies

$$\begin{aligned}
 d_1 \partial_{xx} \underline{u}_L + \underline{u}_L [b_1 - \delta_1(\underline{u}_L + \bar{v}_L)] &= 0, & 0 < x < L, \\
 d_2 \partial_{xx} \bar{v}_L + \bar{v}_L \left[ \frac{b_2 \bar{v}_L}{\underline{u}_L + \bar{v}_L} - \delta_2(\underline{u}_L + \bar{v}_L) \right] &= 0, & 0 < x < L, \\
 \partial_x \underline{u}_L(0) = \partial_x \bar{v}_L(0) &= 0, \\
 \underline{u}_L(L) = \frac{\delta}{2}, \quad \bar{v}_L(L) &= \kappa_2 + \delta.
 \end{aligned} \tag{23}$$

Letting  $L \rightarrow +\infty$ , it follows from standard elliptic regularity and a diagonal procedure that  $(\underline{u}_L(x), \bar{v}_L(x))$  converges to  $(\underline{u}_\infty(x), \bar{v}_\infty(x))$  uniformly on any compact subset of  $[0, +\infty)$ , where  $(\underline{u}_\infty, \bar{v}_\infty)$  satisfies

$$\begin{aligned}
 d_1 \partial_{xx} \underline{u}_\infty + \underline{u}_\infty [b_1 - \delta_1(\underline{u}_\infty + \bar{v}_\infty)] &= 0, & x > 0 \\
 d_2 \partial_{xx} \bar{v}_\infty + \bar{v}_\infty \left[ \frac{b_2 \bar{v}_\infty}{\underline{u}_\infty + \bar{v}_\infty} - \delta_2(\underline{u}_\infty + \bar{v}_\infty) \right] &= 0, & x > 0 \\
 \partial_x \underline{u}_\infty(0) = \partial_x \bar{v}_\infty(0) &= 0, \\
 \underline{u}_\infty(x) \geq \frac{\delta}{2}, \quad \bar{v}_\infty(x) \leq \kappa_2 + \delta, & & 0 < x < +\infty.
 \end{aligned} \tag{24}$$

We consider now the following system:

$$\begin{aligned}
 \frac{du_1}{dt} &= u_1(b_1 - \delta_1(u_1 + v_1)), & t > 0, \\
 \frac{dv_1}{dt} &= v_1 \left( \frac{b_2 v_1}{u_1 + v_1} - \delta_2(u_1 + v_1) \right), & t > 0, \\
 u_1(0) = \frac{\delta}{2}, \quad v_1(0) &= \kappa_2 + \delta.
 \end{aligned} \tag{25}$$

Since  $\kappa_1 > \kappa_2$ , then  $(u_1, v_1) \rightarrow (\kappa_1, 0)$  as  $t \rightarrow +\infty$  (see Lemma 2.2 of [38], for e.g.). Then, the solution  $(U, V)$  of the problem

$$\begin{aligned}
 \frac{\partial U}{\partial t} &= d_1 U_{xx} + U(b_1 - \delta_1(U + V)), & t > 0, \quad x \geq 0, \\
 \frac{\partial V}{\partial t} &= d_2 V_{xx} + V \left( \frac{b_2 V}{U + V} - \delta_2(U + V) \right), & t > 0, \quad x \geq 0, \\
 U_x(t, 0) = V_x(t, 0) &= 0, & t > 0, \\
 U(0, x) = \frac{\delta}{2}, \quad V(0, x) &= \kappa_2 + \delta, & x \geq 0.
 \end{aligned} \tag{26}$$

satisfies  $(U(t, x), V(t, x)) \rightarrow (\kappa_1, 0)$ , as  $t \rightarrow +\infty$ , uniformly in  $x \in [0, +\infty)$ . By the comparison principle, we have  $\underline{u}_\infty \geq U$  and  $\bar{v}_\infty \leq V$  for  $t \geq 0$ , which immediately yields that

$$\lim_{t \rightarrow +\infty} u(t, x) = \kappa_1 \quad \text{and} \quad \lim_{t \rightarrow +\infty} v(t, x) = 0.$$

The criteria for spreading and vanishing are given in the following theorem. ■

**Theorem 3.3:** *If  $h_0 \geq \pi/2\sqrt{d_1/\delta_1(\kappa_1 - \kappa_2)} := h_0^*$ , then  $h_\infty = +\infty$ .*

**Proof:** Note that  $h(t)$  is nondecreasing. We only need to show that  $h_\infty < +\infty$  implies  $h_\infty \leq h_0^*$ . It follows from Theorem 3.1 that  $h_\infty < +\infty$  implies

$$\lim_{t \rightarrow +\infty} \|u(t, \cdot)\|_{C[0, h(t)]} = 0 \quad \text{and} \quad \lim_{t \rightarrow +\infty} v(t, x) = \kappa_2$$

uniformly in any bounded subset of  $[0, +\infty)$ . Assume that  $h_\infty > h_0^*$ . Then for sufficiently small  $\varepsilon > 0$ , there exists  $T > 0$  such that

$$h(t) > \frac{\pi}{2} \sqrt{\frac{d_1}{\delta_1(\kappa_1 - \kappa_2) - \varepsilon}} \quad \text{and} \quad v(t, x) \leq \kappa_2 + \frac{\varepsilon}{\delta_1} \quad \text{for } t \geq T \quad \text{and} \quad x \in [0, +\infty).$$

Let  $\underline{u}$  be the solution of the following problem

$$\begin{aligned} \frac{\partial \underline{u}}{\partial t} - d_1 \underline{u}_{xx} &= \delta_1 \underline{u} \left( \kappa_1 - \kappa_2 - \frac{\varepsilon}{\delta_1} - \underline{u} \right), & t > T, \quad 0 < x < h(T), \\ \underline{u}_x(t, 0) = 0 &= \underline{u}(t, h(T)), & t > T, \\ \underline{u}(T, x) &= u(T, x), & 0 < x < h(T). \end{aligned} \tag{27}$$

By the comparison principle, we have  $\underline{u}(t, x) \leq u(t, x)$  for all  $t \geq T$  and  $x \in [0, h(T)]$ . Since  $h(t) > \pi/2\sqrt{d_1/\delta_1(\kappa_1 - \kappa_2) - \varepsilon}$  for  $t > T$  then, by Lemma 3.1, we know that  $\lim_{t \rightarrow +\infty} \underline{u} = \underline{U} > 0$  uniformly in any compact subset of  $(0, h(T))$ , where  $\underline{U}$  is the unique positive solution of

$$\begin{aligned} -d_1 \underline{U}_{xx} &= \delta_1 \underline{U} \left[ \kappa_1 - \kappa_2 - \frac{\varepsilon}{\delta_1} - \underline{U} \right], & 0 < x < h(T), \\ \underline{U}_x(t, 0) = 0 &= \underline{U}(t, h(T)). \end{aligned} \tag{28}$$

Thus,

$$\liminf_{t \rightarrow +\infty} u(t, x) \geq \lim_{t \rightarrow +\infty} \underline{u}(t, x) = \underline{U}(x) > 0,$$

which is a contradiction. Therefore,  $h_\infty \leq h_0^*$  and this completes the proof. ■

**Theorem 3.4:** *If  $h_0 < h_0^*$ , then there exists  $\bar{\mu} > 0$  such that  $h_\infty = +\infty$  as  $\mu \geq \bar{\mu}$ .*

**Proof:** Since  $\limsup_{t \rightarrow +\infty} v(t, x) \leq \kappa_2 + \varepsilon$  uniformly for  $x \in [0, +\infty)$ , then there exists  $T_1 > 0$  such that  $v(t, x) \leq \kappa_2$  when  $t > T_1$ . So,  $(u, h)$  satisfies

$$\begin{aligned} \frac{\partial u}{\partial t} &\geq d_1 u_{xx} + \delta_1 u[\kappa_1 - \kappa_2 - u], & t > T_1, \quad 0 < x < h(t), \\ h'(t) &= -\mu u_x(t, h(t)), & t > T_1, \\ u_x(t, 0) = 0, u(t, h(t)) &= 0, & t > T_1, \\ u(T_1, x) &> 0, & 0 < x < h(T_1). \end{aligned} \tag{29}$$

Note that,  $u(T_1, x)$  depends on  $\mu$ . So, we consider the following problem.

$$\begin{aligned}
 \frac{\partial \tilde{u}(t, x)}{\partial t} &= d_1 \tilde{u}_{xx} + \tilde{u}(b_1 - \delta_1(\tilde{u} + \tilde{v})), & t > 0, \quad 0 < x < h_0, \\
 \frac{\partial \tilde{v}(t, x)}{\partial t} &= d_2 \tilde{v}_{xx} + \tilde{v} \left( \frac{b_2 \tilde{v}}{\tilde{u} + \tilde{v}} - \delta_2(\tilde{u} + \tilde{v}) \right), & t > 0, \quad 0 < x < h_0, \\
 \tilde{u}_x(t, 0) = \tilde{v}_x(t, 0) &= 0, & t > 0, \\
 \tilde{u}(t, h_0) &= 0, & t > 0, \\
 \tilde{u}(0, x) &= u_0(x), & 0 < x < h_0, \\
 \tilde{v}(0, x) &= \max \{ \kappa_2, \|v_0\|_{L^\infty([0, +\infty))} \}, & 0 < x < h_0, \\
 \tilde{v}_x(t, h_0) &= \max \{ \kappa_2, \|v_0\|_{L^\infty([0, +\infty))} \}, & t > 0.
 \end{aligned} \tag{30}$$

It follows from the comparison principle that

$$u(T_1, x) \geq \tilde{u}(T_1, x) \quad \text{for all } (t, x) \in [0, +\infty) \times [0, h_0].$$

Clearly,  $\tilde{u}(T_1, x)$  is independent of  $\mu$ . Now, we consider the following system.

$$\begin{aligned}
 \frac{\partial \underline{u}}{\partial t} - d_1 \underline{u}_{xx} &= \delta_1 \underline{u} [\kappa_1 - \kappa_2 - \underline{u}], & t > T_1, \quad 0 < x < \underline{h}(t), \\
 \underline{u}_x(t, 0) = 0 &= \underline{u}(t, \underline{h}(t)), & t > T_1, \\
 \underline{h}'(t) &= -\mu \underline{u}_x(t, \underline{h}(t)), & t > T_1, \\
 \underline{u}(T_1, x) &= \tilde{u}(T_1, x), & x \in [0, h_0], \\
 \underline{h}(T_1) &= h_0.
 \end{aligned} \tag{31}$$

By Lemma 3.2, we know that  $\underline{h}(t) \leq h(t)$  for  $t > T_1$ . It follows from [10, Lemma 3.7] that  $\underline{h}_\infty = +\infty$  if  $\mu \geq \bar{\mu}$ , where

$$\bar{\mu} := \max \left( 1, \frac{\|\tilde{u}(T_1, x)\|_\infty}{\kappa_1 - \kappa_2} \right) \frac{d_1 (h_0^* - h_0)}{\int_0^{h_0} \tilde{u}(T_1, x) \, dx}.$$

This implies that  $h_\infty = +\infty$ . ■

By Theorems 3.3 and 3.4, we can also derive spreading criteria in terms of the diffusion coefficient  $d_1$ , for any fixed  $h_0$ .

**Theorem 3.5 (Spreading criteria):** *Let  $d_1^* = 4\delta_1(\kappa_1 - \kappa_2)h_0^2/\pi^2$ , where  $h_0$  is any prefixed positive constant. Then, spreading occurs provided that either*

- (1)  $0 < d_1 \leq d_1^*$  or
- (2)  $d_1 > d_1^*$  and  $\mu \geq \bar{\mu}$ .

Our next result is a criterion on ‘vanishing’.

**Theorem 3.6:** Assume that

$$h_0 < \frac{\pi}{2} \sqrt{\frac{d_1}{b_1}} = \frac{\pi}{2} \sqrt{\frac{d_1}{\delta_1 \kappa_1}} < h_0^*.$$

Then, there exists  $\underline{\mu} > 0$  such that  $h_\infty < +\infty$ , whenever  $\mu \leq \underline{\mu}$ .

**Proof:** Consider the following problem

$$\begin{aligned} \bar{u}_t - d_1 \bar{u}_{xx} &= \bar{u}(b_1 - \delta_1 \bar{u}), & t > 0, & \quad 0 < x < \bar{h}(t), \\ \bar{u}_x(t, 0) &= 0, \quad \bar{u}(t, \bar{h}(t)) = 0, & t > 0, & \\ \bar{h}'(t) &= -\mu u_x(t, \bar{h}(t)), & t > 0, & \\ u(0, x) &= u_0(x), \quad \bar{h}(0) = h_0, & x \in [0, h_0]. & \end{aligned} \tag{32}$$

Lemma 3.2 applies and yields that

$$h(t) \leq \bar{h}(t) \quad \text{and} \quad u(t, x) \leq \bar{u}(t, x) \quad \text{for } t > 0 \quad \text{and} \quad 0 \leq x \leq h(t).$$

Furthermore, by Lemma 3.8 of [10], there exists  $\underline{\mu} > 0$  such that  $\bar{h}_\infty < +\infty$  in the case  $\mu \leq \underline{\mu}$ , where

$$\underline{\mu} = \frac{\tilde{\delta} \tilde{\gamma} h_0^2}{4\tilde{M}}, \quad \tilde{\gamma} = \frac{1}{2} \left[ \left( \frac{\pi}{2} \right)^2 \frac{d_1}{h_0^2} - b_1 \right],$$

and  $\tilde{\delta}, \tilde{M}$  are such that

$$\left( \frac{\pi}{2} \right)^2 \frac{d_1}{(1 + \tilde{\delta})^2 h_0^2} - b_1 = \tilde{\gamma}$$

and

$$u_0(x) \leq \tilde{M} \cos \left( \frac{\pi}{2} \frac{x}{h_0(1 + \tilde{\delta}/2)} \right), \quad \text{for } x \in [0, h_0].$$

Therefore,  $h_\infty < +\infty$ . ■

### 3.4. The spreading speed

If spreading occurs, it is important to estimate the spreading speed of  $h(t)$ . Following an idea in [12], one can obtain a rough estimate of the spreading speed as stated in the following theorem.

**Theorem 3.7 ([12]):** Suppose that  $\kappa_1 > \kappa_2$  and let  $(u, v, h)$  be the solution of (11). If  $h_\infty = +\infty$ ,  $u_0(x) \leq \kappa_1$  in  $[0, h_0]$ ,  $v_0(x) > 0$  in  $[0, +\infty)$  and  $\liminf_{x \rightarrow +\infty} v_0(x) \geq \kappa_2$ , then

$$\limsup_{t \rightarrow +\infty} \frac{h(t)}{t} \leq s_*,$$

where  $s_*$  is the minimal speed of the travelling waves to the problem related with (11) in the entire space. This estimation of the spreading speed is independent of  $\mu$ .



However, in the fitness benefit case, we can derive an estimate better than the one in Theorem 3.4. We first recall Proposition 5.1 of [11].

**Proposition 3.1 ([11]):** For any given constants  $d_1 > 0$ ,  $b_1 > 0$ ,  $\delta_1 > 0$  and  $\beta \in [0, 2\sqrt{b_1 d_1})$ , the problem

$$\begin{aligned} -d_1 U'' + \beta U' &= b_1 U - \delta_1 U^2 \quad \text{for } x \in (0, \infty), \\ U(0) &= 0, \end{aligned} \tag{33}$$

admits a unique positive solution  $U = U_\beta$ , which depends on  $d_1, b_1, \delta_1, \beta$ , and satisfies  $U_\beta(x) \rightarrow \kappa_1$  as  $x \rightarrow +\infty$ . Moreover,  $U'(x) > 0$  for  $x \geq 0$ , and for each  $\mu > 0$ , there exists a unique  $\beta_0 = \beta_0(\mu, d_1, b_1, \delta_1) \in (0, 2\sqrt{b_1 d_1})$  such that  $\mu U'_{\beta_0}(0) = \beta_0$ .

Our result reads:

**Theorem 3.8:** Assume  $\kappa_1 > \kappa_2$ . If  $h_\infty = +\infty$ , then

$$\beta_0(\mu, \kappa_1 - \kappa_2, d_1) \leq \liminf_{t \rightarrow +\infty} \frac{h(t)}{t} \leq \limsup_{t \rightarrow +\infty} \frac{h(t)}{t} \leq \beta_0(\mu, b_1, \delta_1, d_1),$$

where  $\beta_0$  is determined by Proposition 3.1.

**Proof:** Note that

$$\begin{aligned} \frac{\partial u}{\partial t} - d_1 u_{xx} &= u[b_1 - \delta_1(u + v)] \leq u(b_1 - \delta_1 u), & t > 0, \quad 0 < x < h(t), \\ u_x(t, 0) &= 0, \quad u(t, h(t)) = 0, & t > 0, \\ h'(t) &= -\mu u_x(t, h(t)), & t > 0, \\ u(0, x) &= u_0(x), & x \in [0, h_0]. \end{aligned} \tag{34}$$

Thus, the pair  $(u, h)$  is a subsolution to the problem

$$\begin{aligned} \frac{\partial \bar{u}}{\partial t} - d_1 \bar{u}_{xx} &= \bar{u}(b_1 - \delta_1 \bar{u}), & t > 0, \quad 0 < x < \bar{h}(t), \\ \bar{u}_x(t, 0) &= 0, \quad \bar{u}(t, \bar{h}(t)) = 0, & t > 0, \\ \bar{h}'(t) &= -\mu \bar{u}_x(t, \bar{h}(t)), & t > 0, \\ \bar{u}(0, x) &= u_0(x), \quad \bar{h}(0) = h_0, & x \in [0, h_0]. \end{aligned} \tag{35}$$

By the comparison principle,  $h(t) \leq \bar{h}(t)$  for  $t > 0$ . Theorem 4.2 of [10] yields that

$$\lim_{t \rightarrow +\infty} \frac{\bar{h}(t)}{t} = \beta_0(\mu, b_1, \delta_1, d_1).$$

Hence

$$\limsup_{t \rightarrow +\infty} \frac{h(t)}{t} \leq \beta_0(\mu, b_1, \delta_1, d_1).$$

Note that  $\limsup_{t \rightarrow +\infty} v(t, x) \leq \kappa_2$  uniformly for  $x \in [0, +\infty)$  and  $h_\infty = +\infty$ . Then, there exists  $T_\varepsilon > 0$  such that  $v(t, x) \leq \kappa_2 + \varepsilon$  and

$$h(T_\varepsilon) > \frac{\pi}{2} \sqrt{\frac{d_1}{\kappa_1 - \kappa_2 - \varepsilon}} \quad \text{when } t > T_\varepsilon.$$

Next, we consider the following problem

$$\begin{aligned}
 \frac{\partial \underline{u}}{\partial t} - d_1 \frac{\partial^2 \underline{u}}{\partial x^2} &= \underline{u}(\kappa_1 - \kappa_2 - \varepsilon - \underline{u}), & t > T_\varepsilon, & 0 < x < \underline{h}(t), \\
 \underline{u}_x(t, 0) = 0, \underline{u}(t, \underline{h}(t)) &= 0, & t > T_\varepsilon, & \\
 \underline{h}'(t) &= -\mu \underline{u}_x(t, \underline{h}(t)), & t > T_\varepsilon, & \\
 \underline{u}(T_\varepsilon, x) &= u(T_\varepsilon, x), & x \in [0, h(T_\varepsilon)]. &
 \end{aligned}
 \tag{36}$$

By the comparison principle, we obtain  $h(t) \geq \underline{h}(t)$  for  $t > T_\varepsilon$ . From Theorem 3.3, we know that  $\underline{h}(\infty) = +\infty$ . Using a similar argument as above, we have  $\lim_{t \rightarrow +\infty} (\underline{h}(t)/t) = \beta_0(\mu, \kappa_1 - \kappa_2, d_1)$ . Therefore,

$$\liminf_{t \rightarrow +\infty} \frac{h(t)}{t} \geq \beta_0(\mu, \kappa_1 - \kappa_2, d_1). \quad \blacksquare$$

#### 4. The free boundary problem with a heterogeneous birth rate

In this section, we consider the free boundary problem (6)–(7) with the heterogeneous birth rates  $b_1(x)$  and  $b_2(x)$ .

##### 4.1. Some useful lemmas

In this subsection, we first study a related eigenvalue problem:

$$\begin{aligned}
 d\phi_{xx} + b(x)\phi + \lambda\phi &= 0, & x \in (0, h_0), \\
 \phi_x(0) = \phi(h_0) &= 0.
 \end{aligned}
 \tag{37}$$

Problem (37) admits a positive principal eigenvalue  $\lambda_1$  determined by

$$\lambda_1 = \inf_{\phi \in W^{1,2}([0, h_0])} \left\{ \int_0^{h_0} [d\phi_x^2 - b(x)\phi^2] dx, \phi_x(0) = \phi(h_0) = 0, \int_0^{h_0} \phi^2 dx = 1 \right\}.
 \tag{38}$$

We state two hypotheses that we refer to when needed. We use a generic symbol  $B(x)$  in the statement of the hypotheses. The function  $B(x)$  will be replaced accordingly (by  $b, b_1$  or  $b_2$ ) in the rest of this Section.

$$B(x) \in C^1([0, +\infty)) \cap L^\infty([0, +\infty)) \text{ and } B(x) \text{ is positive somewhere in } (0, h_0). \tag{B_2}$$

$$\left\{ \begin{aligned}
 &B(x) \in C^1([0, +\infty)) \text{ and } \underline{b} < B(x) < \bar{b} \text{ for all } x \in [0, +\infty), \\
 &\text{where } \underline{b} \text{ and } \bar{b} \text{ are two positive constants.}
 \end{aligned} \right. \tag{B_3}$$

**Remark 4.0.1:** In order to compare the principal eigenvalues  $\lambda_1$  associated with different parameters, we denote the principal eigenvalue  $\lambda_1$  by  $\lambda_1(d, h_0)$ . When we fix  $h_0$  and study the property of  $\lambda_1$  as  $d$  varies, we write  $\lambda_1 = \lambda_1(d)$ . Similarly, we write  $\lambda_1 = \lambda_1(h_0)$  when  $d$  is fixed while  $h_0$  varies.

We gather the following known results about the dependance of  $\lambda_1$  on  $d$  and  $h$ .

**Lemma 4.1** ([40]): *Suppose that  $b(x)$  satisfies  $(B_2)$ , where  $B(x)$  is replaced by  $b(x)$ . Then,  $\lambda_1 = \lambda_1(d)$  has the following properties:*

- (i)  $\lambda_1(d)$  is increasing with respect to  $d$ .
- (ii)  $\lambda_1(d) \rightarrow +\infty$  as  $d \rightarrow +\infty$  and  $\lambda_1(d) \rightarrow -\max_{x \in [0, l]} b(x) < 0$  as  $d \rightarrow 0$ .
- (iii) For any fixed  $h_0 > 0$ , there exists  $d = d^* > 0$  such that
  - $\lambda_1(d) < 0$  for  $0 < d < d^*$ ,
  - $\lambda_1(d) > 0$  for  $d > d^*$ , and
  - $\lambda_1(d) = 0$  for  $d = d^*$ .

**Lemma 4.2** ([40]): *Assume that  $(B_3)$  holds, where  $B(x)$  is replaced by  $b(x)$ . Then,  $\lambda_1 = \lambda_1(h_0)$  has the following properties:*

- (i)  $\lambda_1(h_0)$  is monotone decreasing with respect to  $h_0$ .
- (ii)  $\lambda_1(h_0) \rightarrow +\infty$  as  $h_0 \rightarrow 0$  and  $\lim_{h_0 \rightarrow +\infty} \lambda_1(h_0) < 0$ .
- (iii) For any fixed  $d > 0$ , there exists  $h_0 = h_0^* > 0$  such that
  - $\lambda_1(h_0) > 0$  for  $0 < h_0 < h_0^*$ ,
  - $\lambda_1(h_0) < 0$  for  $h_0 > h_0^*$ ,
  - $\lambda_1(h_0) = 0$  for  $h_0 = h_0^*$ .

For the reader’s convenience, we also recall some facts related to the following problem

$$\begin{aligned} \frac{\partial v}{\partial t} &= d_2 v_{xx} + v(b_2(x) - \delta_2 v), & t > 0, \quad x > 0, \\ v_x(t, 0) &= 0, & t > 0, \\ v(0, x) &= v_0(x), & x \in [0, +\infty). \end{aligned} \tag{39}$$

The proof of the next lemma follows from Lemma 5.2 and Lemma 6.2 of [40].

**Lemma 4.3:** *Assume that  $b_2(x)$  satisfies  $(B_3)$ , where  $B(x)$  is replaced by  $b_2(x)$ . Let  $v(t, x)$  be the unique solution of (39) with an initial condition*

$$v_0 \in C^2[0, \infty) \cap L^\infty[0, \infty) \quad \text{and} \quad v_0 > 0.$$

Then,

$$\lim_{t \rightarrow +\infty} v(t, \cdot) = \phi_{v^*} \text{ uniformly in any compact subset of } [0, \infty),$$

where  $\phi_{v^*}$  is the unique positive solution of the following elliptic problem

$$\begin{aligned} d_2 v_{xx} + v(b_2(x) - \delta_2 v) &= 0, \quad x > 0, \\ v_x(0) &= 0. \end{aligned} \tag{40}$$

### 4.2. Sharp criteria for spreading and vanishing

Let us first consider the vanishing case.

**Theorem 4.1:** Let  $(u, v, h)$  be the solution of system (6) subject to initial conditions (7). If  $h_\infty < +\infty$  and  $b_2$  satisfies  $(B_3)$ , where we replace  $B(x)$  by  $b_2(x)$ , then

$$\lim_{t \rightarrow +\infty} \|u(t, \cdot)\|_{C[0, h(t)]} = 0 \quad \text{and} \quad \lim_{t \rightarrow +\infty} v(t, x) = \phi_{v^*}$$

uniformly in any bounded subset of  $[0, +\infty)$ .

The proof is similar to that of Theorem 3.1, above.

In order to obtain sharp criteria for spreading, we require stronger conditions on  $b_1(x)$  and  $\delta_1$ . Namely, we assume that

$$b_1(x) - \delta_1 \phi_{v^*} \text{ is positive somewhere in } [0, h_0]. \tag{41}$$

Our assumption (41) is not excessive in the sense that, when  $b_i$  and  $\delta_i (i = 1, 2)$  are constant, we have  $\phi_{v^*} = b_2/\delta_2$ . Consequently,  $b_1 - \delta_1 \phi_{v^*}$  is a positive constant over the interval  $[0, +\infty)$ .

**Theorem 4.2:** Assume that  $b_1(x) - \delta_1 \phi_{v^*}(x)$  satisfies  $(B_2)$  and  $b_2(x)$  satisfies  $(B_3)$  (where  $B$  is replaced accordingly). If  $0 < d_1 < d_1^*$ , then spreading occurs.

**Proof:** First, we consider the following equation:

$$\begin{aligned} \frac{\partial \bar{v}}{\partial t}(t, x) &= d_2 \bar{v}_{xx} + \bar{v}(b_2(x) - \delta_2 \bar{v}), \quad t > 0, \quad x > 0, \\ \bar{v}_x(t, 0) &= 0, \quad t > 0, \\ \bar{v}(0, x) &= v_0(x). \end{aligned} \tag{42}$$

Since  $b_2(x)$  satisfies the hypotheses of Lemma 4.3, all solutions of (42) with non-trivial non-negative initial values converge to  $\phi_{v^*}$  as  $t \rightarrow \infty$ .

It follows, from the comparison principle, that  $v \leq \bar{v}$  for all  $t > 0$  and  $x > 0$ . Since  $\lim_{t \rightarrow +\infty} \bar{v}(t, x) = \phi_{v^*}$  uniformly in any compact subset of  $[0, \infty)$ , then, for any  $\varepsilon > 0$ , there exists  $T > 0$  such that  $v(t, x) \leq \phi_{v^*} + \varepsilon$ , for  $t \geq T$ .

Consider the following eigenvalue problem:

$$\begin{aligned} d_1 \varphi_{xx} + \varphi(b_1(x) - \delta_1(\phi_{v^*} + \varepsilon)) + \lambda \varphi &= 0, \quad x \in (0, h_0), \\ \varphi_x(0) = \varphi(h_0) &= 0. \end{aligned} \tag{43}$$

It is well known that the principal eigenvalue  $\lambda_1$  can be characterized by

$$\lambda_1 = \inf_{\varphi \in H^1(0, h_0)} \left\{ \int_0^{h_0} d_1 \varphi_x^2 - (b_1(x) - \delta_1(\phi_{v^*} + \varepsilon)) \varphi^2, \int_0^{h_0} \varphi^2 = 1 \right\}.$$

Using (iii) of Lemma 4.1, for any fixed  $h_0$ , there exists  $d_1^*$  such that

$$\begin{aligned} \lambda_1(d_1) < 0 & \text{ for all } 0 < d_1 < d_1^*, \quad \lambda_1(d_1) = 0 \text{ for } d_1 = d_1^*, \quad \text{and} \\ \lambda_1(d_1) > 0 & \text{ for } d_1 > d_1^*. \end{aligned}$$

In this theorem, we have  $0 < d_1 < d_1^*$ . Let us set  $\underline{u} = \delta\varphi_1(x)$ , for  $t \geq T$  and  $x \in [0, h_0]$  (here  $\varphi_1(x)$  is the corresponding eigenfunction of  $\lambda_1$ ). Choose  $\delta > 0$ , small enough, so that

$$\delta\varphi_1(x) \leq \min \left\{ -\frac{\lambda_1}{\delta_1}, u(T, x) \right\} \quad \text{for } x \in [0, h_0].$$

A straightforward calculation leads to

$$\begin{aligned} & \frac{\partial \underline{u}}{\partial t} - d_1 \underline{u}_{xx} - \underline{u}(b_1(x) - \delta_1(\phi_{v^*} + \varepsilon) - \delta_1 \underline{u}) \\ &= \delta\varphi_1(x)(\lambda_1 + \delta_1\delta\varphi_1(x)) \leq 0 \quad \text{for } t > T, \quad 0 < x < h_0, \\ & \underline{u}_x(t, 0) = 0, \quad t > T, \\ & \underline{u}(t, h_0) = 0, \quad t > T, \\ & \underline{u}(0, x) = \delta\varphi_1 \leq u(T, x), \quad 0 \leq x \leq h_0. \end{aligned} \tag{44}$$

By the comparison principle, we have  $u \geq \underline{u}$ , for  $t \geq T$  and  $x \in [0, h_0]$ . Thus,

$$\liminf_{t \rightarrow \infty} \|u(t, \cdot)\|_{C[0, h_0]} \geq \delta\varphi_1(0) > 0.$$

By Theorem 4.1, we have  $h_\infty = +\infty$ . Therefore, spreading occurs. ■

**Theorem 4.3:** *Suppose that  $b_1(x) - \delta_1\phi_{v^*}(x)$  satisfies  $(B_3)$  and  $b_2(x)$  satisfies the hypotheses of Lemma 4.3. If  $h_0 > h^*$ , then  $h_\infty = +\infty$  (i.e. the species  $u$  spreads eventually).*

**Proof:** Similarly, we consider the following equation

$$\begin{aligned} & \frac{\partial \bar{v}}{\partial t} = d_2 \bar{v}_{xx} + \bar{v}(b_2(x) - \delta_2 \bar{v}), \quad t > 0, \quad x > 0, \\ & \bar{v}_x(t, 0) = 0, \quad t > 0, \\ & \bar{v}(0, x) = v_0(x). \end{aligned} \tag{45}$$

Since  $b_2(x)$  satisfies the hypotheses of Lemma 4.3, all solutions of (45) with nontrivial and nonnegative initial conditions converge to  $\phi_{v^*}$  as  $t \rightarrow \infty$ .

It follows from the comparison principle that  $v \leq \bar{v}$  for  $t > 0, x > 0$ . Since  $\limsup_{t \rightarrow +\infty} \bar{v}(t, x) = \phi_{v^*}$  uniformly in any compact subset of  $[0, \infty)$ . So for any  $\varepsilon > 0$ , there exists  $T > 0$  such that  $v(t, x) \leq \phi_{v^*} + \varepsilon$  for  $t \geq T$ .

Consider the following eigenvalue problem:

$$\begin{aligned} & d_1\varphi_{xx} + \varphi(b_1(x) - \delta_1(\phi_{v^*} + \varepsilon)) + \lambda\varphi = 0, \quad x \in (0, h_0), \\ & \varphi_x(0) = \varphi(h_0) = 0. \end{aligned} \tag{46}$$

The principal eigenvalue  $\lambda_1$  is characterized by

$$\lambda_1 = \inf_{\varphi \in H^1(0, h_0)} \left\{ \int_0^{h_0} d_1\varphi_x^2 - (b_1(x) - \delta_1(\phi_{v^*} + \varepsilon))\varphi^2, \int_0^{h_0} \varphi^2 = 1 \right\}.$$

Since  $b_1(x) - \delta_1\phi_{v^*}$  satisfies the hypotheses of  $(B^3)$ . Then by Lemma 4.2, for any fixed  $d_1$ , there exists  $h^*$  such that  $\lambda_1(h_0) < 0$  for all  $h_0 > h^*$ ,  $\lambda_1(h_0) = 0$  for  $h_0 = h^*$ , and  $\lambda_1(h_0) > 0$  for  $h_0 < h^*$ .

If  $h_0 > h^*$ , then we set  $\underline{u} = \delta\varphi_1(x)$ , for  $t \geq T$ ,  $x \in [0, h_0]$  (here  $\varphi_1(x)$  is the corresponding eigenfunction of  $\lambda_1$ ). Choose  $\delta > 0$  small enough so that  $\delta\varphi_1(x) \leq \min\{-\lambda_1/\delta_1, u(T, x)\}$  for  $x \in [0, h_0]$ . After a straightforward calculation, we obtain

$$\begin{aligned} & \frac{\partial \underline{u}}{\partial t} - d_1 \frac{\partial^2 \underline{u}}{\partial x^2} - \underline{u}(b_1(x) - \delta_1(\phi_{v^*} + \varepsilon) - \delta_1 \underline{u}) \\ &= \delta\varphi_1(x)(\lambda_1 + \delta_1\delta\varphi_1(x)) \leq 0, & t > T, \quad 0 < x < h_0, \\ & \partial_x \underline{u}(t, 0) = 0, & t > T, \\ & \underline{u}(t, h_0) = 0, & t > T, \\ & \underline{u}(0, x) = \delta\varphi_1 \leq u(T, x), & 0 \leq x \leq h_0. \end{aligned} \tag{47}$$

By the comparison principle, we have  $u \geq \underline{u}$  for  $t \geq T$ ,  $x \in [0, h_0]$ . Hence,

$$\liminf_{t \rightarrow \infty} \|u(t, \cdot)\|_{C[0, h_0]} \geq \delta\varphi_1(0) > 0.$$

Similarly, we have  $h_\infty = +\infty$ ; hence, spreading occurs. ■

**Theorem 4.4:** *If  $d_1 > d_1^*$  and  $u_0$  is small enough, then ‘vanishing’ occurs.*

**Proof:** We consider the following problem as an auxiliary to the first equation of (6):

$$\begin{aligned} & \frac{\partial u}{\partial t} = d_1 u_{xx} + u(b_1(x) - \delta_1 u), \quad t > 0, \quad 0 < x < h_0, \\ & u_x(t, 0) = u(t, h_0) = 0, \quad t > 0, \\ & u(0, x) = u_0(x), \quad x \in [0, h_0]. \end{aligned} \tag{48}$$

Denote the principal eigenvalue  $\lambda_1$  and the corresponding positive eigenfunction  $\phi_1$  satisfy

$$\begin{aligned} & d_1 \phi_{xx} + \phi b_1(x) + \lambda \phi = 0, \quad 0 < x < h_0, \\ & \phi_x(0) = \phi(h_0) = 0. \end{aligned} \tag{49}$$

One can verify that there exists  $d_1^*$  such that  $\lambda_1 > 0$ , when  $d_1 > d_1^*$ . Furthermore, it follows, from Theorem 4.2 in [40], that there exists a constant  $\mathcal{B}$  such that  $\phi_1'(x) \leq 2h_0\mathcal{B}\phi_1(x)$  for all  $x \in [0, h_0]$ . Now, we can use the following auxiliary functions, which were constructed in [40]. Let

$$\begin{aligned} & \bar{h}(t) = h_0 \left( 1 + \alpha - \frac{\alpha}{2} e^{-\alpha t} \right), \quad \text{for } t \geq 0 \quad \text{and} \\ & \bar{u}(t, x) = \beta e^{-\alpha t} \phi_1 \left( \frac{xh_0}{\bar{h}(t)} \right), \quad \text{for } t \geq 0 \quad \text{and} \quad 0 \leq x \leq \bar{h}(t). \end{aligned}$$

The conditions on  $\alpha$  and  $\beta$  will be determined later. If we let  $0 < \alpha \leq 1$ , direct calculations show that

$$\begin{aligned} \left| \frac{h_0^2}{\bar{h}^2(t)} b_1 \left( \frac{xh_0}{\bar{h}(t)} \right) - b_1(x) \right| &\leq \frac{h_0^2}{\bar{h}^2(t)} \left| b_1 \left( \frac{xh_0}{\bar{h}(t)} \right) - b_1(x) \right| + \left| \left( \frac{h_0^2}{\bar{h}^2(t)} - 1 \right) b_1(x) \right| \\ &\leq \left| b_1 \left( \frac{xh_0}{\bar{h}(t)} \right) - b_1(x) \right| + \|b_1\|_{C([0,2h_0])} \left| \frac{h_0^2}{\bar{h}^2(t)} - 1 \right| \\ &\leq 2 \left[ h_0 \|b_1\|_{C^1([0,2h_0])} + \|b_1\|_{C([0,2h_0])} \right] \left| \frac{h_0}{\bar{h}(t)} - 1 \right|. \end{aligned}$$

Since  $\bar{h}(t) \rightarrow h_0$  as  $\alpha \rightarrow 0$ , we can find sufficiently small  $\alpha_1$ , such that

$$\left| \frac{h_0^2}{\bar{h}^2(t)} b_1 \left( \frac{xh_0}{\bar{h}(t)} \right) - b_1(x) \right| \leq \frac{\lambda_1}{4} \quad \text{for } \alpha \leq \alpha_1.$$

Moreover, there exists  $\alpha_2 > 0$ , small enough, such that

$$2h_0^2 \mathcal{B}\alpha \leq \frac{1}{4} \lambda_1 \quad \text{and} \quad \frac{1}{(1 + \alpha)^2} \geq \frac{3}{4}, \quad \text{for } \alpha \leq \alpha_2.$$

Let  $\alpha = \min\{1, \lambda_1/4, \alpha_1, \alpha_2\}$ . Direct calculation leads to

$$\begin{aligned} \bar{u}_t - d_1 \bar{u}_{xx} - b_1(x) \bar{u} &= -\alpha \bar{u} - \beta e^{-\alpha t} \phi_1' \left( \frac{xh_0}{\bar{h}} \right) \frac{xh_0 \bar{h}'(t)}{\bar{h}^2(t)} \\ &\quad - \beta e^{-\alpha t} d_1 \phi_1'' \left( \frac{xh_0}{\bar{h}(t)} \right) \frac{h_0^2}{\bar{h}^2(t)} - b_1(x) \bar{u} \\ &= -\alpha \bar{u} - \beta e^{-\alpha t} \phi_1' \left( \frac{xh_0}{\bar{h}} \right) \frac{xh_0 \bar{h}'(t)}{\bar{h}^2(t)} \\ &\quad + \left[ \frac{h_0^2}{\bar{h}^2(t)} b_1 \left( \frac{xh_0}{\bar{h}(t)} \right) - b_1(x) \right] \bar{u} + \frac{h_0^2}{\bar{h}^2(t)} \lambda_1 \bar{u} \\ &\geq -\alpha \bar{u} - 2h_0^2 \mathcal{B}\alpha^2 \bar{u} - \frac{\lambda_1 \bar{u}}{4} + \frac{\lambda_1 \bar{u}}{(1 + \alpha)^2} \\ &\geq \bar{u} \left( \frac{-\lambda_1}{4} + \frac{-\lambda_1}{4} + \frac{-\lambda_1}{4} + \frac{3\lambda_1}{4} \right) = 0. \end{aligned}$$

Furthermore, we choose  $0 < \beta \leq -h_0 \alpha^2 / 2\mu \phi_1'(h_0)$ . Then,

$$\begin{aligned} -\mu \bar{u}_x(t, \bar{h}(t)) &= -\beta \mu e^{-\alpha t} \phi_1'(h_0) \frac{h_0}{\bar{h}(t)} \\ &\leq -\beta \mu e^{-\alpha t} \phi_1'(h_0) \\ &\leq \frac{h_0 \alpha^2}{2} e^{-\alpha t} = \bar{h}'(t). \end{aligned}$$

In order to apply the comparison principle, we choose  $u_0$  small enough such that

$$u_0(x) \leq \beta\phi_1\left(\frac{x}{1 + \frac{\alpha}{2}}\right), \quad \text{for } x \in [0, h_0].$$

Thus, we have

$$\begin{aligned} \frac{\partial \bar{u}}{\partial t} - d_1 \bar{u}_{xx} - \bar{u}(b_1(x) - \delta_1 \bar{u}) &\geq 0, & t > 0, & \quad 0 < x < \bar{h}(t), \\ \bar{u}_x(t, 0) = \bar{u}(t, h(t)) &= 0, & t > 0, \\ \bar{h}'(t) &\geq -\mu \bar{u}_x(t, \bar{h}(t)), & t > 0, \\ \bar{u}(0, x) = \beta\phi_1\left(\frac{x}{1 + \frac{\alpha}{2}}\right) &\geq u_0(x), & x \in [0, h_0], \\ \bar{h}(0) &= h_0\left(1 + \frac{\alpha}{2}\right) > h_0. \end{aligned} \tag{50}$$

Form the comparison principle, we have  $h(t) \leq \bar{h}(t)$  for  $t > 0$  and

$$u(t, x) \leq \bar{u}(x, t) \quad \text{for } t > 0 \quad \text{and} \quad x \in [0, h(t)].$$

So,  $h_\infty \leq \lim_{t \rightarrow +\infty} \bar{h}(t) = h_0(1 + \alpha) < +\infty$ . This implies that vanishing occurs. ■

Moreover, we can derive vanishing criteria in terms of the coefficient  $\mu$  when  $d_1 > d_1^*$ .

**Theorem 4.5:** *Suppose that  $d_1 > d_1^*$ . For any given  $u_0$ , there exists  $\mu_*$  depending on  $u_0$  and  $h_0$ , such that vanishing occurs whenever  $\mu \leq \mu_*$ .*

**Proof:** As in the proof of the Theorem 4.4, let  $\lambda_1$  and  $\phi_1$  satisfy Equation (49). We still define  $\bar{u}, \bar{h}(t)$  as follows

$$\begin{aligned} \bar{u}(t, x) &= \beta_1 e^{-\alpha t} \phi_1\left(\frac{x h_0}{\bar{h}(t)}\right), & \text{for } t \geq 0, & \quad 0 \leq x \leq \bar{h}(t). \\ \bar{h}(t) &= h_0\left(1 + \alpha - \frac{\alpha}{2} e^{-\alpha t}\right), & \text{for } t \geq 0. \end{aligned}$$

Here, we also let  $\alpha = \min\{1, \frac{1}{4}\lambda_1, \alpha_1, \alpha_2\}$  and choose  $\beta_1 > 0$  large enough such that

$$u_0(x) \leq \beta_1 \phi_1\left(\frac{x}{1 + \frac{\alpha}{2}}\right), \quad \text{for } x \in [0, h_0].$$

For this fixed  $\beta_1$ , we choose

$$0 < \mu \leq -\frac{h_0 \alpha^2}{2\beta_1 \phi_1'(h_0)} =: \mu_*$$



such that

$$\begin{aligned} -\mu \bar{u}_x(t, \bar{h}(t)) &= -\beta_1 \mu e^{-\alpha t} \phi_1'(h_0) \frac{h_0}{\bar{h}(t)} \\ &\leq -\beta_1 \mu e^{-\alpha t} \phi_1'(h_0) \\ &\leq \frac{h_0 \alpha^2}{2} e^{-\alpha t} = \bar{h}'(t). \end{aligned}$$

Then, we have

$$\begin{aligned} \frac{\partial \bar{u}}{\partial t} - d_1 \bar{u}_{xx} - \bar{u}(b_1(x) - \delta_1 \bar{u}) &\geq 0, \quad t > 0, \quad 0 < x < \bar{h}(t), \\ \bar{u}_x(t, 0) = \bar{u}(t, h(t)) &= 0, \quad t > 0, \\ \bar{h}'(t) &\geq -\mu \bar{u}_x(t, \bar{h}(t)), \quad t > 0, \\ \bar{u}(0, x) = \beta_1 \phi_1 \left( \frac{x}{1 + \frac{\alpha}{2}} \right) &\geq u_0(x), \quad x \in [0, h_0], \\ \bar{h}(0) = h_0 \left( 1 + \frac{\alpha}{2} \right) &> h_0. \end{aligned} \tag{51}$$

Form the comparison principle, we have  $h(t) \leq \bar{h}(t)$ , for  $t > 0$ , and

$$u(t, x) \leq \bar{u}(x, t), \quad \text{for } t > 0 \quad \text{and} \quad x \in [0, h(t)].$$

Thus,

$$h_\infty \leq \lim_{t \rightarrow +\infty} \bar{h}(t) = h_0(1 + \alpha) < +\infty.$$

This implies that vanishing occurs. ■

Next, we will prove the following conclusions.

**Theorem 4.6:** *Assume that  $b_1(x)$  satisfies  $(B_3)$ , where  $B(x)$  is replaced by  $b_1(x)$ . If  $h_\infty \leq h_*$ , then the species  $u$  vanishes eventually.*

**Proof:** Choose  $l \in [h_\infty, h_*]$ . Consider the following equation:

$$\begin{aligned} \frac{\partial \bar{u}}{\partial t} - d_1 \bar{u}_{xx} + \bar{u}(b_1(x) - \delta_1 \bar{u}) &= 0, \quad t > 0, \quad 0 < x < l, \\ \bar{u}_x(t, 0) = \bar{u}(t, l) &= 0, \quad t > 0, \\ \bar{u}(0, x) = u_0(x), & \quad x \in [0, h_0], \\ \bar{u}(0, x) = 0, & \quad x \in [h_0, l]. \end{aligned} \tag{52}$$

It follows from the comparison principle that  $0 \leq u \leq \bar{u}$  for  $t > 0$  and  $x \in (0, l)$ . Since  $l \leq \pi/2\sqrt{d_1/\max_{x \in [0, +\infty)} b_1(x)} =: h_*$ , Proposition 3.1 of [4] yields that

$$\lim_{t \rightarrow +\infty} \|\bar{u}(t, \cdot)\|_{C[0, l]} = 0.$$

Consequently,  $\lim_{t \rightarrow +\infty} \|u(t, \cdot)\|_{C[0, l]} = 0$ . ■

Under some assumptions, stated below, we can obtain the asymptotic spreading speed from Theorem 3.6 of [9].

**Theorem 4.7:** Assume that  $b_1(x)$  satisfies  $(B_3)$ , where  $B(x)$  is replaced by  $b_1(x)$ . If  $h_\infty = +\infty$ , then

$$\limsup_{t \rightarrow +\infty} \frac{h(t)}{t} \leq \beta_0 \left( \mu, \max_{x \in [0, +\infty)} b_1(x), \delta_1, d_1 \right).$$

Furthermore, if  $b_1(x) - \delta_1 \phi_{v^*}$  satisfies  $(B_3)$ , then

$$\liminf_{t \rightarrow +\infty} \frac{h(t)}{t} \geq \beta_0 \left( \mu, \min_{x \in [0, +\infty)} (b_1(x) - \delta_1 \phi_{v^*}), \delta_1, d_1 \right).$$

### 5. Summary and conclusions

We studied a reaction-diffusion model with a free boundary in one-dimensional environment. The model is developed to better understand the dynamics of *Wolbachia* infection under the assumptions supported by recent experiments such as perfect maternal transmission and complete CI.

In the special case of constant birth rates, we only considered the fitness benefit case. For the fitness benefit case, where the environment is more favourable for infected mosquitoes, our results show that the spreading of *Wolbachia* infection occurs if either the size of the initial habitat of infected population  $h_0$  is large enough, say  $h_0 \geq h_0^*$  (Theorem 3.3), or the boundary moving coefficient  $\mu$  is sufficiently large ( $\mu \geq \bar{\mu}$ ) in case of  $h_0 < h_0^*$  (Theorem 3.4). A rough estimate on the spreading speed of  $h(t)$  is also provided. Moreover, if  $h_0 < \pi/2\sqrt{d_1/b_1} < h_0^*$  and  $\mu \leq \bar{\mu}$ , then the infection cannot spread and  $h_\infty < +\infty$ .

The case of inhomogeneous (spatially dependent) birth rates is treated in Section 4. Detailed criteria for spreading and vanishing are derived in Subsection 4.2 with the aid of spectral properties of relevant eigenvalue problems.

### Acknowledgments

The authors wish to thank the anonymous reviewers for their valuable comments and suggestions, which greatly helped us improve the presentation of this work. Y. Liu and Z. Guo were supported by National Science Foundation of China (No. 11371107, 11771104), Program for Chang Jiang Scholars and Innovative Research Team in University (IRT-16R16). Y. Liu was supported by the National Natural Science Foundation of China under Grant No.11271093 and the Innovation Research for the Postgraduates of Guangzhou University under Grant No.2017GDJC-D05. M. El Smailly and L. Wang acknowledge partial support received through NSERC-Discovery grants from the Natural Sciences and Engineering Research Council of Canada (NSERC).

### Disclosure statement

No potential conflict of interest was reported by the author(s).

### Funding

The authors wish to thank the anonymous reviewers for their valuable comments and suggestions, which greatly helped us improve the presentation of this work. Y. Liu and Z. Guo were supported by

National Science Foundation of China (No. 11371107, 11771104), Program for Chang Jiang Scholars and Innovative Research Team in University (IRT-16R16). Y. Liu was supported by the National Natural Science Foundation of China under Grant No.11271093 and the Innovation Research for the Postgraduates of Guangzhou University under Grant No.2017GDJC-D05. M. El Smailly and L. Wang acknowledge partial support received through NSERC-Discovery grants from the Natural Sciences and Engineering Research Council of Canada (NSERC).

## References

- [1] S.Y. Mukherjee, *Why Google's verily is unleashing 20 million bacteria-infected mosquitoes in Fresno*. Available at <http://fortune.com/2017/07/14/google-verily-zika-mosquitoes/>.
- [2] G. Bian, Y. Xu, P. Lu, Y. Xie, Z. Xi and D. S. Schneider, *The endosymbiotic bacterium wolbachia induces resistance to dengue virus in aedes aegypti*, PLoS Pathog 6 (2010), p. e1000833.
- [3] G. Bunting, Y. Du and K. Krakowski, *Spreading speed revisited: analysis of a free boundary model*, Netw. Het. Media 7 (2012), pp. 583–603.
- [4] R. Cantrell, C. Cosner, *Spatial Ecology Via Reaction-Diffusion Equations*, John Wiley & Sons, Chichester, 2003.
- [5] J. Cao, W. Li and M. Zhao, *A nonlocal diffusion model with free boundaries in spatial heterogeneous environment*, J. Math. Anal. Appl. 449 (2017), pp. 1015–1035.
- [6] W. Ding, Y. Du and X. Liang, *Spreading in space-time periodic media governed by a monostable equation with free boundaries, part 1: continuous initial functions*, J. Differ. Equ. 262 (2017), pp. 4988–5021.
- [7] W. Ding, R. Peng and L. Wei, *The diffusive logistic model with a free boundary in a heterogeneous time-periodic environment*, J. Differ. Equ. 263 (2017), pp. 2736–2779.
- [8] N.C. Dom, A.H. Ahmad and R. Ismail, *Habitat characterization of Aedes Sp. breeding in Urban hotspot area*, Procedia 85 (2013), pp. 100–109.
- [9] Y. Du and Z. Guo, *Spreading-vanishing dichotomy in a diffusive logistic model with a free boundary II*, J. Differ. Equ. 250 (2011), pp. 4336–4366.
- [10] Y. Du and Z. Lin, *Spreading-vanishing dichotomy in the diffusive logistic model with a free boundary*, SIAM J. Math. Anal. 42 (2010), pp. 377–405.
- [11] Y. Du and Z. Lin, *The diffusive competition model with a free boundary: invasion of a superior or inferior competitor*, Discrete Contin. Dyn. Syst. Ser. B 19 (2014), pp. 3105–3132.
- [12] J. Guo and C. Wu, *On a free boundary problem for a two-species weak competition system*, J. Dynam. Differ. Equ. 24 (2012), pp. 873–895.
- [13] M. Huang, J. Luo, L. Hu, B. Zheng and J. Yu, *Assessing the efficiency of Wolbachia driven aedes mosquito suppression by delay differential equations*, J. Theoret. Biol. 440 (2018), pp. 1–11.
- [14] M. Huang, M. Tang and J. Yu, *Wolbachia infection dynamics by reaction-diffusion equations*, Sci. China Math. 58 (2015), pp. 77–96.
- [15] M. Huang, J. Yu, L. Hu and B. Zheng, *Qualitative analysis for a wolbachia infection model with diffusion*, Sci. China Math. 59 (2016), pp. 1249–1266.
- [16] I. Iturbe-Ormaetxe, T. Walker and S.L. O'Neill, *Wolbachia and the biological control of mosquito-borne disease*, EMBO Rep. 12 (2011), pp. 508–518.
- [17] H. Laven, *Cytoplasmic inheritance in culex*, Nature 177 (1956), pp. 141–142.
- [18] F. Li, X. Liang and W. Shen, *Diffusive KPP equations with free boundaries in time almost periodic environments: II. spreading speeds and semi-wave solutions*, J. Differ. Equ. 261 (2016), pp. 2403–2445.
- [19] Z. Lin, *A free boundary problem for a predator-prey model*, Nonlinearity 20 (2007), pp. 1883–1892.
- [20] Z. Lin and H. Zhu, *Spatial spreading model and dynamics of West Nile virus in birds and mosquitoes with free boundary*, J. Math. Biol. (2017), pp. 1–29.
- [21] A. Lunardi, *Schauder theorems for linear elliptic and parabolic problems with unbounded coefficients in  $\mathbb{R}^N$* , Studia Math. 128(2) (1998), pp. 171–198.
- [22] E. Marris, *Bacteria could be key to freeing South Pacific of mosquitoes*, Nature 548(7665) (2017), pp. 17–18. doi:10.1038/548017a.

- [23] C.J. McMeniman, R.V. Lane, B.N. Cass, A.W.C. Fong, M. Sidhu, Y.-F. Wang and S.L. O'Neill, *Stable introduction of a life-shortening wolbachia infection into the mosquito aedes aegypti*, *Science* 323 (2009), pp. 141–144.
- [24] H. Monobe and C. Wu, *On a free boundary problem for a reaction-diffusion-advection logistic model in heterogeneous environment*, *J. Differ. Equ* 261 (2016), pp. 6144–6177.
- [25] H. Ninomiya, *Separatrices of competition-diffusion equations*, *J. Math. Kyoto Univ.* 35 (1995), pp. 539–567.
- [26] H. Smith, *Monotone Dynamical Systems*, American Math Society, Providence, 1995.
- [27] L. Song. (2017). *China Focus: China's mosquito warriors fight global epidemic*. Available at [http://news.xinhuanet.com/english/2017-06/29/c\\_136403687.htm](http://news.xinhuanet.com/english/2017-06/29/c_136403687.htm).
- [28] C. Tian and S. Ruan, *A free boundary problem for aedes aegypti mosquito invasion*, *Appl. Math. Model.* 46 (2017), pp. 203–217.
- [29] M. Wang, *On some free boundary problems of the prey-predator model*, *J. Differ. Equ.* 256 (2014), pp. 3365–3394.
- [30] L. Wei, G. Zhang and M. Zhou, *Long time behavior for solutions of the diffusive logistic equation with advection and free boundary*, *Calc. Var. Partial Differ. Equ.* 55 (2016), pp. 1–34.
- [31] Z. Xi, J. Dean, C. Khoo and S. Dobson, *Generation of a novel wolbachia infection in aedes albopictus (asian tiger mosquito) via embryonic microinjection*, *Insect Biochem. Mol. Biol.* 35 (2005), pp. 903–910.
- [32] Z. Xi and S. Dobson, *Characterization of wolbachia transfection efficiency by using microinjection of embryonic cytoplasm and embryo homogenate*, *Appl. Environ. Microbiol.* 71 (2005), pp. 3199–3204.
- [33] Z. Xi, C. Khoo and S. Dobson, *Wolbachia establishment and invasion in an aedes aegypti laboratory population*, *Science* 310 (2005), pp. 326–328.
- [34] Z. Xi, C. Khoo and S. Dobson, *Interspecific transfer of wolbachia into the mosquito disease vector aedes albopictus*, *Proc. Biol. Sci.* 273 (2006), pp. 1317–1322.
- [35] J. Yu, *Modeling mosquito population suppression based on delay differential equations*, *SIAM J. Appl. Math.* 78 (2018), pp. 3168–3187.
- [36] J. Yu and B. Zheng, *Modeling Wolbachia infection in mosquito population via discrete dynamical model*, *J. Differ. Equ. Appl.* (2019) Available at <https://doi.org/10.1080/10236198.2019.1669578>.
- [37] Y. Zhang and M. Wang, *A free boundary problem of the ratio-dependent prey-predator model*, *Appl. Anal.* 94 (2015), pp. 2147–2167.
- [38] B. Zheng, M. Tang and J. Yu, *Modeling wolbachia spread in mosquitoes through delay differential equations*, *SIAM J. Appl. Math.* 74 (2014), pp. 743–770.
- [39] B. Zheng and J. Yu, *Characterization of Wolbachia enhancing domain in mosquitoes with imperfect maternal transmission*, *J. Biol. Dyn.* 12 (2018), pp. 596–610.
- [40] P. Zhou and D. Xiao, *The diffusive logistic model with a free boundary in heterogeneous environment*, *J. Differ. Equ.* 256 (2014), pp. 1927–1954.
- [41] L. Zhou, S. Zhang and Z. Liu, *An evolutionary free-boundary problem of a reaction-diffusion-advection system*, *Proc. Roy. Soc. Edinburgh Sect. A* 147 (2017), pp. 615–648.
- [42] L. Zhou, S. Zhang and Z. Liu, *Pattern formations for a strong interacting free boundary problem*, *Acta Appl. Math.* 148 (2017), pp. 121–142.