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A control strategy for Sterile Insect Techniques using exponentially decreasing releases to avoid the hair-trigger effect

Alexis Leculier¹, Nga Nguyen²

Abstract

In this paper, we introduce a control strategy for applying the Sterile Insect Technique (SIT) to eliminate the population of *Aedes* mosquitoes which are vectors of various deadly diseases like dengue, zika, chikungunya... in a wide area. We use a system of reaction-diffusion equations to model the mosquito population and study the effect of releasing sterile males. Without any human intervention, and due to the so-called *hair-trigger effect*, the introduction of only a few individuals (eggs or fertilized females) can lead to the invasion of mosquitoes in the whole region after some time. To avoid this phenomenon, our strategy is to keep releasing a small number of sterile males in the treated zone and move this release forward with a negative forcing speed c to push back the invasive front of wild mosquitoes. By using traveling wave analysis, we show in the present paper that the strategy succeeds in repulsing the population while consuming a finite amount of mosquitoes in any finite time interval even though we treat a moving half-space $\{x > ct\}$. Moreover, we succeed in constructing a ‘forced’ traveling wave for our system moving at the same speed as the releases. We also provide some numerical illustrations for our results.

Keywords: sterile insect technique, hair-trigger effect, traveling waves

1 Introduction

1.1 The biological motivation

Pest and disease vector controls have become a global issue because of the spread of these species all around the world causing crop losses and disease epidemics. For example, the oriental fruit fly is a serious pest of a wide variety of fruit crops in Asia and has also invaded a number of other countries and is a very damaging pest wherever it occurs (PMP-FFM, 2004). It was first detected in French Polynesia in 1996 and invaded Africa in 2004. Few individuals have been detected in Italy in 2018 and hence southern Europe is at high risk. Similarly, according to the World Health Organization, the global incidence of dengue has grown dramatically with about half of the world’s population now at risk. It was first identified in the 1950s during dengue epidemics in Philippines and Thailand due to the travel and invasion of its vectors, female mosquitoes of the species *Aedes aegypti* and *Ae. albopictus*. They

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are also vectors of chikungunya, yellow fever, Zika viruses..., and, until now, there is neither effective treatment nor vaccine for these diseases. So pest/vector controls play an important role in getting rid of these problems. The classical control method based on insecticides induces resistance, which reduces its own efficiency and is detrimental to the environment. Among others, the Sterile Insect Technique (SIT) aiming at reducing the size of the insect population recently gathered much attention. The SIT is a biological method where people release sterile individuals (modified in laboratories) of pest species to introduce sterility into the wild population, and thus control it (see [14] for an overall presentation of SIT). It is a promising control method against many agricultural pests and disease vectors, most notably screw worms and fruit flies (see [14]), and recently mosquitoes of genus *Aedes*. This technique has been applied successfully for *Aedes* mosquitoes in the field in many different countries, for instance, in Italy [12], Cuba [16], and China [32]. In our work, we focus on applying SIT in a vast region using the idea of the ‘‘rolling carpet’’: a large number of sterile insects are released near the front of the invasion, and as soon as this area is free from wild insects, we move the front of release and continue to release a few sterile individuals in the already treated area (see [14]). The purpose of these small releases at the back is to prevent reinvasion by the so-called *hair-trigger effect* (where the existence of just a few individuals leads to the total invasion of the territory). The notion of ‘hair-trigger’ was first introduced in [7] to refer to the persistence in long-time of the solution with respect to any non-trivial initial data. In our case, it has been observed in [14] that the mosquitoes reinvade the treated territory without this small amount of releases of sterile males. By implementing such a process, we succeed in eradicating wild insects, preventing reinvasion, and keeping the number of released sterile insects below a threshold in a finite time interval $[0, T]$. It is in our interest to consume as few sterile males as possible since it is one of the main costs of the strategy. We propose in the present work to study a mathematical model of such release strategy used in the field for *Aedes* mosquitoes.

1.2 Our model and the spreading results

Following ideas in e.g. [4], [27], we model the mosquito population by a partially degenerate reaction-diffusion system for time $t > 0$, position $x \in \mathbb{R}$:

$$\begin{cases} \partial_t E & = \beta F \left(1 - \frac{E}{K}\right) - (v_E + \mu_E)E, \\ \partial_t F - D\partial_{xx}F & = r v_E E \frac{M}{M + \gamma M_s} - \mu_F F, \\ \partial_t M - D\partial_{xx}M & = (1 - r)v_E E - \mu_M M, \\ \partial_t M_s - D\partial_{xx}M_s & = \Lambda(t, x) - \mu_s M_s, \\ (E, F, M, M_s)(t = 0, x) & = (E^0, F^0, M^0, M_s^0)(x). \end{cases} \quad (1)$$

In this system, we have:

- E , M , M_s and F denote respectively the number of mosquitoes in the aquatic phase, adult males, sterile adult males and fertilized adult females depending on time t and position x ;
- $\Lambda(t, x)$ is the number of sterile mosquitoes that are released at position x and time t ;
- the fraction $\frac{M}{M + \gamma M_s}$ corresponds to the probability that a female mates with a fertile male, and parameter γ models the competitiveness of sterile males;
- $\beta > 0$ is a birth rate; $\mu_E > 0$, $\mu_M > 0$, and $\mu_F > 0$ denote the death rates for the mosquitoes in the aquatic phase, for adult males and for adult females, respectively;

- K is an environmental capacity for the aquatic phase, accounting also for the intraspecific competition;
- $v_E > 0$ is the rate of emergence;
- $D > 0$ is the diffusion rate;
- $r \in (0, 1)$ is the probability that a female emerges, then $(1 - r)$ is the probability that a male emerges;
- the initial data $(E^0, F^0, M^0, M_s^0) \geq (0, 0, 0, 0)$ (component by component).

We introduce the basic offspring number as follows

$$\mathcal{R}_0 = \frac{\beta r v_E}{\mu_F (v_E + \mu_E)}. \quad (2)$$

When there is no regulation of sterile males, our model becomes

$$\begin{cases} \partial_t E = \beta F \left(1 - \frac{E}{K}\right) - (v_E + \mu_E)E, \\ \partial_t F - D \partial_{xx} F = r v_E E - \mu_F F, \\ \partial_t M - D \partial_{xx} M = (1 - r) v_E E - \mu_M M, \end{cases} \quad (3)$$

It is obvious that $(0, 0, 0)$ is an equilibrium of (3). When the basic offspring number $\mathcal{R}_0 > 1$, this system has a second equilibrium (E^*, F^*, M^*) where

$$\begin{aligned} E^* &= K \frac{\beta r v_E - \mu_F (v_E + \mu_E)}{\beta r v_E} > 0, \\ F^* &= K \frac{\beta r v_E - \mu_F (v_E + \mu_E)}{\beta \mu_F} > 0, \\ M^* &= K \frac{1 - r}{r} \frac{\beta r v_E - \mu_F (v_E + \mu_E)}{\beta \mu_M} > 0. \end{aligned} \quad (4)$$

Note that, the positive equilibrium (E^*, F^*, M^*) is stable and $(0, 0, 0)$ is unstable. Thus, in the case without sterile males, the following result shows the spread of the population toward the positive equilibrium and provides the existence of the spreading speed for the solution of the system (3).

Proposition 1. *If the basic offspring number $\mathcal{R}_0 > 1$, then there exists a spreading speed $c^* > 0$ such that for any positive ε , the solution (E, F, M) of system (3) satisfies*

- *if the initial data (E^0, F^0, M^0) is compactly supported and $0 \leq (E^0, F^0, M^0) < (E^*, F^*, M^*)$, then*

$$\lim_{t \rightarrow +\infty} \left[\max_{|x| \geq t(c^* + \varepsilon)} \max(E, F, M)(t, x) \right] = 0, \quad (5)$$

- *if the initial data $(E^0, F^0, M^0) < (E^*, F^*, M^*)$ and if there exists a set with a positive measure $\Omega \subset \mathbb{R}$, such that $\max_{x \in \Omega} (\min E^0, \min F^0) > 0$ then*

$$\lim_{t \rightarrow +\infty} \left[\max_{|x| \leq t(c^* - \varepsilon)} \max(E^* - E, F^* - F, M^* - M)(t, x) \right] = 0. \quad (6)$$

We present in Appendix A a proof for this result based on the result in the work of Lui [23] with an extension for reaction-diffusion system in Weinberger et al. [31] for a monostable system. We also underline that, with only females at the initial time (i.e. $E^0 \equiv 0$, $M^0 \equiv 0$, and $F^0 > 0$ in some ball), invasion still occurs. This is due to the fact that in our model we consider F to be the fertilized females. Therefore, if $F^0 > 0$ on a set with a positive measure, then the same holds for the aquatic phase at any $t > 0$ in the whole domain \mathbb{R} , and the dynamics of invasion start to occur.

The main result in the present work shows that when a release function of sterile males Λ moving with a certain speed $c < 0$ is imposed in the system, we can succeed in suppressing the mosquitoes and in avoiding reinvasion. In the present work, we consider the release function

$$\Lambda(t, x) = \begin{cases} 0 & \text{for } x - ct \leq 0, \\ Ae^{-\eta(x-ct)} & \text{for } x - ct > 0, \end{cases} \quad (7)$$

with constants $A > 0$, $\eta > 0$.

Theorem 2. *If the basic offspring number $\mathcal{R}_0 > 1$, $(E^0, F^0, M^0) \leq (E^*, F^*, M^*)$, $(E^0, F^0, M^0)|_{\mathbb{R}_+} = (0, 0, 0)$ and $M_s^0 \geq \phi_s$, where ϕ_s is the solution of*

$$-c\phi_s' - \phi_s'' = Ae^{-\eta x} 1_{\{x>0\}} - \mu_s \phi_s \quad \text{and} \quad \phi_s(\pm\infty) = 0$$

then for any speed $c < 0$, there exist $\tilde{A}_c > 0$, $\tilde{\eta}_c > 0$ such that for any $A \geq \tilde{A}_c$, $0 < \eta \leq \tilde{\eta}_c$, we have the solution (E, F, M, M_s) of system (1) and (7) satisfies

$$\lim_{t \rightarrow +\infty} \sup_{x > ct} \max(E, F, M)(t, x) = 0.$$

From this result, we can see that if the initial data is compactly supported in \mathbb{R}_- and below (E^*, F^*, M^*) , the invasion does not occur: the equilibrium $(0, 0, 0)$ invades the positive equilibrium (E^*, F^*, M^*) . We also remark that the number of sterile males released in the field in a finite time interval $[0, T]$ is $T \times \frac{A}{\eta}$ finite even though the space is infinite. However, if $T \rightarrow +\infty$, the total amount of released mosquitoes also tends to $+\infty$. Finally, we point out that in the above results, the number of sterile males released (A, η) depends on the speed c of the rolling carpet. This can be observed more precisely in the proof in section 4 and discussed in section 2 with some numerical illustrations. However, finding A, η that minimizes the number of released mosquitoes each time remains a challenge.

1.3 State of the art

Based on biological knowledge, mathematical modeling and numerical simulations can be additional and useful tools to prevent failures, improve protocols, and test assumptions before applying the SIT strategy in the field. Many works have been done using mean-field temporal models to assess the SIT efficiency for a long-term period (see e.g. [10], [27] and references therein).

Only a few works exist modeling explicitly the spatial component due to the lack of knowledge about vectors in the field. Moreover, from the mathematical point of view, the studies of spatial-temporal models are more sophisticated. A reaction-diffusion equation was first used in [24] to model the spreading of a pest in the SIT model. Then, the model was completed by considering the release of sterile females in [22]. In this article, the author assumed that the same amount of sterile insects is released in the whole field (i.e. $\Lambda \equiv \text{constant}$). It follows that if the number of released sterile insects is large enough, the reaction term becomes strictly negative, and the extinction of the wild population follows. However, this hypothesis is unrealistic in a large area since the number of sterile insects to release tends to infinity as the size of the domain increases. The main contribution of our work is to tackle this problem by following what has been done in the field experiment: we assume that the releases are not homogeneous. By

considering only releases supported in \mathbb{R}_+ with exponential decay, the amount of sterile males released in a finite time interval is constant.

In [25], the authors studied SIT control with barrier effect using a system of two reaction-diffusion equations for the wild and the sterile populations. Recently, a sex-structured system including the aquatic phase of mosquitoes has been studied in [5]. Using the theory of traveling waves, the authors proved, for a similar system to (1), the existence of natural invading traveling wave when $\{M_s = 0\}$ and the system is either monostable or bistable. They also provide some numerical implementation of the SIT but only for the bistable case.

In the bistable case, one can release the mosquitoes in a compact set since the equilibrium 0 is stable. The main result in [4] shows that if the initial wild mosquitoes distribution behaves as $1_{\mathbb{R}_-}$ and we release enough sterile males in some compact set $(ct, L + ct)$ with a speed $c < 0$, then the wild population remains close to 0 in the set $\{x > L + ct\}$ thanks to the assumed natural dynamics of the mosquitoes. We also quote [1, 2], which was done before [4] where the authors studied the analogous system of reaction-diffusion equations to (1) in a bistable context taking into account the strong Allee effects. They proved that for large enough constant releases in a bounded interval, there exists a barrier that blocks the invasion of mosquitoes. However, for the monostable case, they obtain numerically that there is no blocking. The so-called ‘‘hair-trigger effect’’ makes the monostable case become more complicated since one can not rely on the natural dynamics of the mosquitoes. So the main purpose of the present work is to study an efficient strategy for the SIT to deal with the difficulty in this case.

The control of sterile insect techniques in a bistable context in a bounded domain is studied in [29, 28]. We also quote [11, 3] that focus on the optimal form to stop or repulse an invading traveling wave by spreading a killing agent (such as insecticide). In [11] the authors study the optimal shape of spreading in order to repulse an invasion. In [3], the authors study the optimal shape of spreading in order to block an invasion but consider more constraints on the spreading area than in [11]. The key argument in these works is to consider that the reaction term is bistable. In the present work, we propose a way to deal with the difficulty of the monostable case with a finite amount of control agents (such as sterile insects or insecticides, or other kinds of control) in any finite time interval.

1.4 The traveling wave results

Another natural question that arises in the study of our model of reaction-diffusion equations is the existence of a traveling wave solution. First, we study the traveling wave problem for the system (3) in which there are no sterile male. Then, by imposing a control function Λ that moves with a speed $c < 0$, we will construct a traveling wave for the main system (1) moving with the same speed.

Recall that a traveling wave solution of (3) with any speed c is the pair (U, c) where $U = (E, F, M)^T$ and $U(x - ct)$ is a nontrivial and bounded solution of (3). We say (U, c) is a wavefront if $U(\pm\infty)$ exist and $U(-\infty) \neq U(+\infty)$. The existence of such wavefronts for reaction-diffusion systems has been studied widely in the literature. In our case, the nonlinearity is monostable and it is well-known that there exists a minimal speed such that the monostable system admits traveling wave solutions with any speed larger than this minimum value. For example, in the book [30], the authors studied the existence of minimal speed and the stability of wavefronts for the non-degenerate system. However, our systems are partially degenerate because the first stage E is quiescent (does not diffuse). The paper [15] studied monotone wavefronts for partially degenerate systems and they proved that the spreading speed of the solution is the minimal wave speed of monotone wavefronts in the monostable cooperative case. The authors of [5] proved the same result for a similar system to (3) and for the sake of completeness, we present it in the following

Proposition 3. *Let c^* be defined in Proposition 1, then for each $c_+ \geq c^*$, system (3) has a nonincreasing wavefront $U(x - c_+t)$ connecting (E^*, F^*, M^*) and $(0, 0, 0)$. While for any $c_+ \in (0, c^*)$, there is no wavefront connecting (E^*, F^*, M^*) and $(0, 0, 0)$.*

The general system (1) (with $M_s > 0$) is not cooperative at first glance. Some works in the recent literature have tackled the lack of comparison principle for non-cooperative Fisher-KPP systems (see e.g. [17, 18, 19]). However, due to the fact that the system (1) in the present paper is partially degenerate, that is, it does not satisfy that $\min \mathbf{D}_{ii} > 0$ where \mathbf{D} is the diffusive matrix, we can not apply these results in our work. Fortunately, the system (1) can be put in the setting of cooperative systems by the change of variable ($\tilde{M}_s = C - M_s$ with C a large constant). With this change of variable, we define a new order for the solutions (E, F, M, M_s) of (1) such that $(E^1, F^1, M^1, M_s^1) \geq (E^2, F^2, M^2, M_s^2)$ if $E^1 \geq E^2$, $F^1 \geq F^2$, $M^1 \geq M^2$, $M_s^1 \leq M_s^2$. In section 4.1, we present more precisely the comparison principle used in our problem.

One of the main interests of this article is the establishment of a ‘forced’ traveling wave solution for (1) with a control function Λ as in (7). Dealing with the whole system of ODE-PDE like (1) is by no means an easy task, so our first idea is to try to simplify the system to a single reaction-diffusion equation by adding some assumptions and then find a general strategy to study the full model. When we assume that the equilibrium of the aquatic phase is attained instantaneously (i.e. $\partial_t E = 0$) then from the first equation of (1), one has $E = \frac{\beta F}{\beta \frac{F}{K} + \nu_E + \mu_E}$. Thus, if the number of females F is equal to the number of males M , and the sterile males are assumed to be equal to Λ in the treating time interval $[0, T]$, using the second equation of (1), we end up with only a single equation :

$$\partial_t F - D \partial_{xx} F = \frac{F}{F + \Lambda} \frac{\beta F}{\beta \frac{F}{K} + \nu_E + \mu_E} - \mu_F F. \quad (8)$$

The model of a scalar reaction-diffusion equation was used widely in the literature studying SIT (see e.g. [22], [33]) or in other contexts, for e.g. in climate change [8], [9]. In our case, the source term $\Lambda(t, x)$ moving with a certain speed $c < 0$, we can construct the ‘forced’ traveling wave solution of (8) moving with the same speed. Equation (8) having the form $\partial_t u - \partial_{xx} u = f(x - ct, u)$ with $f(s, u) : \mathbb{R} \times \mathbb{R}_+ \rightarrow \mathbb{R}$ is asymptotic of F-KPP type as $s \rightarrow \pm\infty$ and was studied in the literature (see e.g. [9] and references therein). In the present work, even if it has been already studied, we provide in Section 3 an explicit construction of the ‘forced’ wave for (8) which can help to grasp the general idea of the proof for the whole system.

Indeed, back to the main model of the present paper, we infer from the scalar model that the main difficulty lies in the construction of the super-solution of (1). The forced wave has the form $(E, F, M, M_s)(t, x) = (\phi_E, \phi_F, \phi_M, \phi_s)(x - ct)$, where $c < 0$ is the forced speed and $(\phi_E, \phi_F, \phi_M, \phi_s)$ is the profile satisfying

$$\begin{cases} -c\phi'_E & = \beta\phi_F \left(1 - \frac{\phi_E}{K}\right) - (\nu_E + \mu_E)\phi_E, \\ -c\phi'_F - D\phi''_F & = r\nu_E\phi_E \frac{\phi_M}{\phi_M + \gamma\phi_s} - \mu_F\phi_F, \\ -c\phi'_M - D\phi''_M & = (1-r)\nu_E\phi_E - \mu_M\phi_M, \\ -c\phi'_s - D\phi''_s & = \phi - \mu_s\phi_s, \end{cases} \quad (9)$$

where $\phi(x - ct) = \Lambda(t, x)$ in (7). To overcome the difficulty of the construction of the super-solution, we use the fact that the dynamic is governed, in some sense, by F . Thanks to what was observed for the scalar equation, we have a natural candidate to be the super-solution for F . More in detail, by denoting $\overline{\phi}_E, \overline{\phi}_F, \overline{\phi}_M$ respectively the super-solution of ϕ_E, ϕ_F, ϕ_M , we proceed as follows:

- **Step 1.** Fix $\phi_s = \overline{\phi}_s = C_s e^{-\eta x} 1_{\{x > 0\}}$. We insert $\overline{\phi}_F = F_* (1_{\{x \leq 0\}} + 1_{\{x > 0\}} e^{-\lambda x})$ in the first equation of (9),
- **Step 2.** We prove that with such a $\overline{\phi}_F$ the associated ϕ_E satisfies $\phi_E \leq C e^{-\lambda x}$ for x large enough,
- **Step 3.** We insert $\overline{\phi}_E = E_* (1_{\{x \leq 0\}} + 1_{\{x > 0\}} e^{-\lambda x})$ in the third equation of (9),

- **Step 4.** We prove that with such a $\overline{\phi_E}$ the associated ϕ_M satisfies $\phi_M \leq Ce^{-\lambda x}$ for x large enough
- **Step 5.** We define $\overline{\phi_M} = M_* (1_{\{x \leq 0\}} + 1_{\{x > 0\}} e^{-\lambda x})$,
- **Step 6.** We prove that $(\overline{\phi_E}, \overline{\phi_F}, \overline{\phi_M}, \phi_s)$ is a super-solution of (9), where ϕ_s is the solution of the last equation with $\phi_s(\pm\infty) = 0$.

We present precisely this construction of a super-solution in section 4.3 and we also construct a sub-solution in section 4.4. Therefore, we obtain the main result:

Theorem 4. *If the basic offspring number $\mathcal{R}_0 > 1$, then for any speed $c < 0$, there exist $\tilde{A}_c > 0$, $\tilde{\eta}_c > 0$ such that for any $A \geq \tilde{A}_c$, $0 < \eta \leq \tilde{\eta}_c$, system (9) with $\phi(x-ct) = \Lambda(t, x)$ defined in (7) admits a solution $(\phi_E, \phi_F, \phi_M, \phi_s)$ such that (ϕ_E, ϕ_F, ϕ_M) converges to (E^*, F^*, M^*) at $-\infty$ and to $(0, 0, 0)$ at $+\infty$.*

We underline that to obtain the exact limits at $-\infty$ is technical since the sterile males diffuse, $\phi_s > 0$ everywhere and the system is not heterogeneous in \mathbb{R}^- (contrary to the super-solutions). Using a perturbation of the equilibrium (E^*, F^*, M^*) , we succeed in obtaining a sub-solution $(\underline{\phi_E}, \underline{\phi_F}, \underline{\phi_M}, \underline{\phi_s})$. However, this sub-solution satisfies $\lim_{x \rightarrow -\infty} (\underline{\phi_E}, \underline{\phi_F}, \underline{\phi_M}, \underline{\phi_s}) = (E^* - \varepsilon_E, F^* - \varepsilon_F, M^* - \varepsilon_M, \varepsilon_0)$ (where $\varepsilon_{E,F,M,0}$ are small positive constants) so we can not deduce directly the limit of $(\phi_E, \phi_F, \phi_M, \phi_s)$ at $-\infty$. We prove that the solution of (9) satisfies the desired limit at $-\infty$ by contradiction (see Section 4.5).

1.5 Outline of the paper

The outline of the rest of this paper is the following: section 2 is devoted to showing some numerical illustrations to support our theoretical results. Next, in section 3 we provide the technical details for the results stated for the simplified model. Finally, section 4 is devoted to the technical details that allow proving Theorems 2 and 4. As mentioned in the introduction, the results for the case without any sterile males (Propositions 1 and 3) are applications of former works. For the sake of completeness, we present the proofs in Appendix A.

2 Numerical illustrations

2.1 The numerical scheme

In this section, we present some numerical illustrations for our theoretical results using a simple finite difference scheme. Since we study the model in one-dimensional space, we use a semi-implicit second-order scheme for space discretization, and a first-order explicit scheme for time discretization, with the time step following a CFL condition. We use Neumann boundary conditions on the boundary of a very large spatial interval. It is well-known that such a spatial domain approximates correctly \mathbb{R} , or at least regarding spreading properties of reaction–diffusion systems.

2.2 Observations

The values of parameters are chosen following [13] for mosquitoes of species *Aedes albopictus* and presented in Table 1. With these parameters, we first verify that the basic offspring number $\mathcal{R}_0 \approx 30.77 > 1$, thus the condition in our theorems is satisfied. The positive equilibrium is $(E^*, F^*, M^*) \approx (193.5, 77.4, 55.3)$.

In our plots, the time unit is a day, space unit is 1 km. We consider the domain $[-50, 50]$ of width 100 km discretized by 500 points, with a 60-day time interval. We show in Figure 1 the dynamics of the female population over time and space. In this simulation, the initial data are taken as compactly

Table 1: Parameters for the numerical illustration

Parameters	β	K	v_E	μ_E	μ_F	μ_M	μ_s	γ	r	D
Values	10	200	0.08	0.05	0.1	0.14	0.14	1	0.5	0.5

supported functions. When there is no SIT control, the wave of mosquitoes invades the space (see Figure 1a) and approaches the steady state $F^* = 77.4$. This illustrates the invasion phenomenon in Proposition 1.

To stop this invasion, we keep releasing sterile mosquitoes over time with a release function that decays exponentially on half of the space $\Lambda(t, x) = Ae^{-\eta(x-ct)} \mathbf{1}_{\{x>ct\}}$.

In practice, the number of sterile males to release is usually fixed and one can adjust the speed of the releases to obtain the best result. To illustrate our result, first, we fix $A = 600$, $\eta = 0.2$ and vary the speeds $c \leq 0$ to observe the dynamics of mosquitoes while applying SIT. When we do not move the release ($c = 0$), we observe in Figure 1b that the wave is blocked near $x = 0$ and cannot pass through the release zone. Then, by moving this release domain to the left with velocity $c = -0.3$, we succeed to push back the wave to the left (see Figure 1c), and there is no mosquito behind the releases which illustrates the main result in Theorems 4 and 2. However, we observe in Figure 1d that if we move the releases faster to the left with velocity $c = -0.7$, there is a reinvasion on the right of the zone. It seems that the faster we move the release domain, the faster we push back the mosquito waves, but we need to release more sterile males in the treated zone to prevent reinvasion. Indeed, when the speed $c = -0.7$ is fixed and the number of sterile males is increased by taking $A = 800$ (see 1e), and $\eta = 0.1$ (see 1f), one can see that the reinvasion in the treated zone gets slower and disappears.

3 Study of the simplified model

3.1 The simplified model

From (8) we study in this section the following scalar equations:

$$\begin{cases} \partial_t u - \partial_{xx} u = \frac{u}{u + \Lambda} \frac{\beta u}{\frac{\beta u}{K} + \delta} - \mu u, & \text{for } x \in \mathbb{R}, t > 0, \\ u(t = 0, x) = u_0(x). \end{cases} \quad (10)$$

where β, δ, μ, K are parameters, u is the density of mosquitoes, and the function $\Lambda(t, x)$ is the control (i.e. the number of sterile males released). In order to ensure the existence of a non-trivial steady state, we need the following assumption:

Assumptions 1. *The parameters β, δ, μ, K are positive and $\beta - \mu\delta > 0$.*

We first treat briefly the case without any control (i.e. $\Lambda = 0$) and then we explain how to obtain a similar result to Theorem 2.

3.1.1 The case without control

In this case, when Assumption 1 holds, the equation has two equilibria $u_0 = 0$ and $u_* = \frac{K(\beta - \mu\delta)}{\beta\mu} > 0$.

The reaction term $f(u) := \frac{\beta u}{\frac{\beta u}{K} + \delta} - \mu u > 0$ for any $u \in (0, u_*)$, $f'(0) = \frac{\beta}{\delta} - \mu > 0$, and $f(u) < \frac{\beta u}{\delta} -$

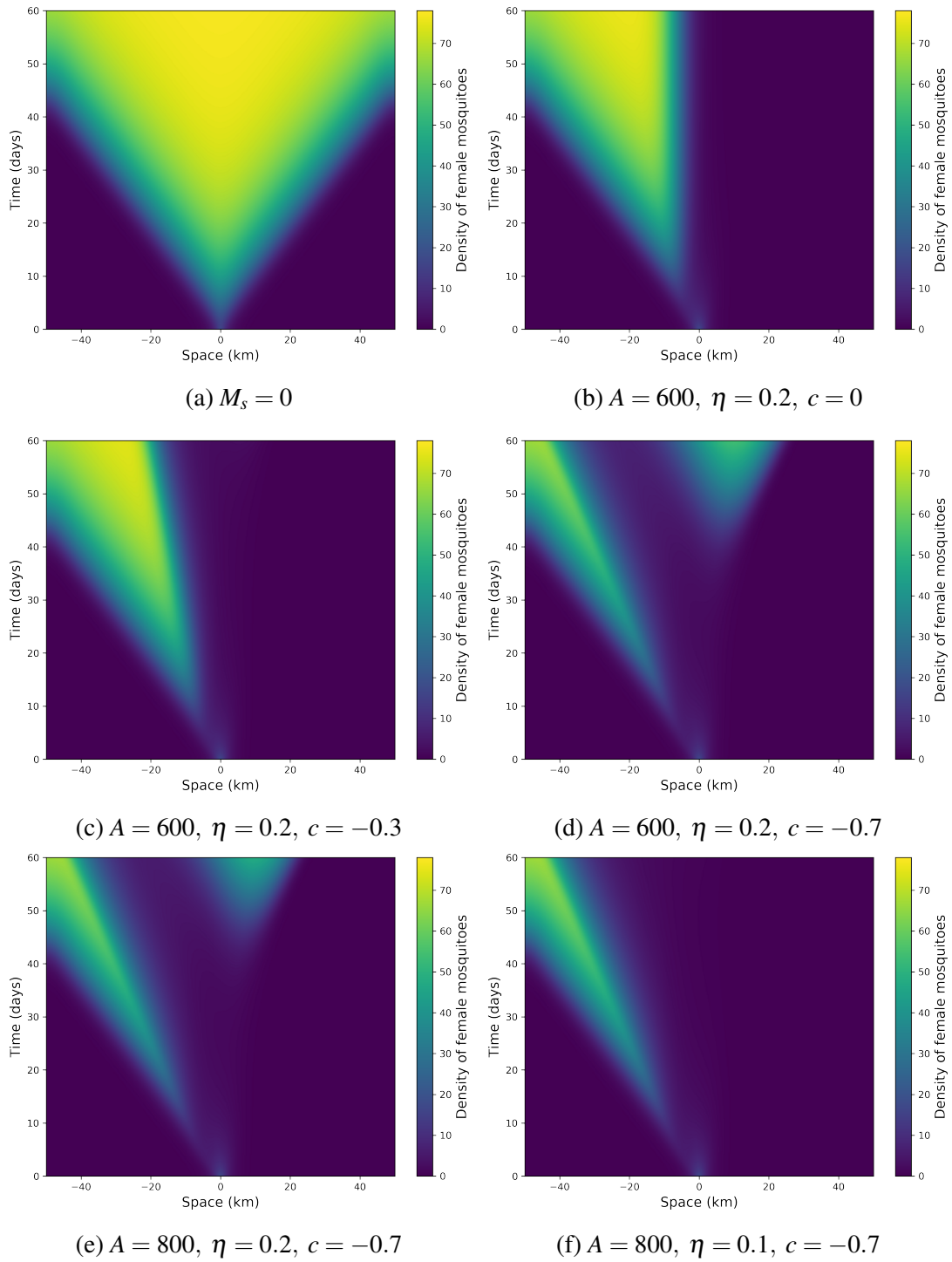


Figure 1: Dynamics of the female density in system (1).

$\mu u = f'(0)u$. Then, from the result in [21], there exists a number $c_* > 0$ such that (10) possesses “natural” traveling wave solutions $u(t, x) = v_N(x - c_+ t)$ for all speed $c_+ \geq c_*$ with v_N solutions of

$$\begin{cases} -c_+ v'_N - v''_N = \frac{\beta v_N}{\frac{\beta v_N}{K} + \delta} - \mu v_N, \\ v_N(-\infty) = u_*, \quad v_N(+\infty) = 0. \end{cases}$$

Hence, when $t \rightarrow +\infty$, the positive state $u = u_*$ invades the extinction state $u = 0$ (see [6, Theorem 4.1] for more details). We recall the following classical result

Proposition 5. [6, Theorem 4.1] *For any positive initial data u_0 , the solution of (10) with $\Lambda \equiv 0$ satisfies*

$$\forall c_+ \geq c_*, \quad \lim_{t \rightarrow +\infty} \sup_{|x| < c_+ t} |u(t, x) - u_*| = 0, .$$

Remark 1. *Depending on the initial data, the front can go faster and even accelerate (see [20]). But, in any case, the steady-state u_* invades the steady state 0 at least with a speed c_* .*

3.1.2 The controlled case

In this case, function Λ is considered as in (7), and we prove the existence of a forced traveling wave moving with the same speed as Λ satisfying

$$\begin{cases} -c v' - v'' = \frac{v}{v + \phi} \frac{\beta v}{\frac{\beta v}{K} + \delta} - \mu v, \\ v(-\infty) = u_*, \quad v(+\infty) = 0, \end{cases} \quad (11)$$

with $\phi(x - ct) = \Lambda(t, x)$ and speed c negative. The result is the following:

Theorem 6. *For any $c < 0$, there exists constants $\tilde{A}, \tilde{\eta} > 0$ such that for any $A \geq \tilde{A}, 0 < \eta \leq \tilde{\eta}$, and the release function $\phi(x - ct) = \Lambda(t, x)$ defined in (7), problem (11) admits a solution v .*

Then, we have the following result for the space-time model (10) (which is an analog to Theorem 2):

Theorem 7. *For any initial data $u_0 \geq 0$ with $u_0 \leq u_*$ and $u_0|_{\mathbb{R}_+} = 0$ and $c \leq 0$, there exist constants $\tilde{A}, \tilde{\eta} > 0$ such that for any $A \geq \tilde{A}, 0 < \eta \leq \tilde{\eta}$, and the release function $\phi(x - ct) = \Lambda(t, x)$, one has that the solution u of (10) satisfies, with any $\varepsilon > 0$, that*

$$\lim_{t \rightarrow +\infty} \sup_{x > (c+\varepsilon)t} u(t, x) = 0.$$

By imposing a control with exponential decay, we succeed in suppressing the insects in the region behind the release. It is contrary to what happens naturally (when the stable steady state u_* invades the unstable steady state 0). Notice that the hypothesis on the initial data u_0 takes into account any positive and compactly supported initial data bounded by u_* (up to a translation of the support in \mathbb{R}_-).

In the following section, we construct a super-solution for (11) in Proposition 8, then we can apply this result to prove Theorem 7. The existence of a sub-solution of (11) is presented in Proposition 10 in section 3.3. Finally, by using comparison principle for a scalar reaction-diffusion equation, we prove Theorem 6.

3.2 Construction of a super-solution for the simplified model

The existence of super-solution for (11) is shown in the following proposition

Proposition 8. For any fixed speed c and any fixed parameter $\alpha \in \left(0, \frac{\delta\mu}{\beta}\right)$, there exists a constant $r(\alpha) < 0$ depending on α, c such that the function

$$\bar{w}(x) = \begin{cases} u_* & \text{when } x < 0, \\ u_* e^{r(\alpha)x} & \text{when } x \geq 0, \end{cases} \quad (12)$$

is a super-solution of (11) with $\phi(x-ct) = \Lambda(t, x)$ for any $\eta \in [0, -r(\alpha)]$ and $A \geq \frac{u_*}{\alpha} - u_* > 0$.

Proof of Proposition 8. For a constant $c < 0$, we study the following problem

$$\begin{cases} -c\bar{w}' - \bar{w}'' = \left(\frac{\alpha\beta}{\delta} - \mu\right)\bar{w} & \text{on } [0, +\infty), \\ \bar{w} > 0 \text{ on } [0, +\infty), \quad \bar{w}(+\infty) = 0. \end{cases} \quad (13)$$

Consider the characteristic polynomial $r^2 + cr + \frac{\alpha\beta}{\delta} - \mu = 0$, since $\frac{\alpha\beta}{\delta} - \mu < 0$ then for any $c < 0$, the

polynomial admits two distinct roots $r_{\pm} = \frac{-c \pm \sqrt{c^2 - 4\left(\frac{\alpha\beta}{\delta} - \mu\right)}}{2}$ where $r_+ > 0$ and $r_- < 0$.

Since we look for a solution w of (13) with $w(+\infty) = 0$, then the solution of (13) is

$$\bar{w}(x) = u_* e^{r(\alpha)x} \quad \text{for } x > 0, \quad (14)$$

with $r(\alpha) = r_- = \frac{-c - \sqrt{c^2 - 4\left(\frac{\alpha\beta}{\delta} - \mu\right)}}{2} < 0$.

Now, remarking that Assumption 1 provides $\frac{\delta\mu}{\beta} \leq 1$, it follows for any $\alpha \in (0, \frac{\delta\mu}{\beta})$ and any constant $\eta \in [0, -r(\alpha)]$ and $A \geq \frac{u_*}{\alpha} - u_* > 0$, one defines $\phi(x-ct) = \Lambda(t, x)$ as in (7), then for all $x \in [0, \infty)$, one

has $\frac{\bar{w}(x)}{\bar{w}(x) + \phi(x)} = \frac{u_* e^{r(\alpha)x}}{u_* e^{r(\alpha)x} + A e^{-\eta x}} = \frac{u_*}{u_* + A e^{-(\eta+r(\alpha))x}} \leq \alpha$. We deduce that

$$-c\bar{w}' - \bar{w}'' - \frac{\bar{w}}{\bar{w} + \phi} \frac{\beta\bar{w}}{\frac{\beta\bar{w}}{K} + \delta} + \mu\bar{w} \geq -c\bar{w}' - \bar{w}'' - \left(\frac{\alpha\beta}{\delta} - \mu\right)\bar{w} = 0.$$

For any $x < 0$, one has $\bar{w}(x) = u_*$ and

$$-c\bar{w}' - \bar{w}'' - \frac{\bar{w}}{\bar{w} + \phi} \frac{\beta\bar{w}}{\frac{\beta\bar{w}}{K} + \delta} + \mu\bar{w} = -\frac{\beta u_*}{\frac{\beta u_*}{K} + \delta} + \mu u_* = 0.$$

Moreover, we have $\lim_{x \rightarrow 0^-} \bar{w}'(x) = 0 > r(\alpha)u_* = \lim_{x \rightarrow 0^+} \bar{w}'(x)$. Hence, function \bar{w} as in (12) is a super-solution of (11) with any $\phi(x-ct) = \Lambda(t, x)$ of the form in (7). \square

From the existence of this super-solution we have the following proof of Theorem 7:

Proof of Theorem 7. Let $\bar{u}(t, x) = \bar{w}(x-ct)$, $\Lambda(t, x) = \phi(x-ct)$, and \bar{w}, ϕ provided by Proposition 8 with a certain speed $c < 0$. It is clear that with such a choice of $\Lambda(t, x)$, we have that \bar{u} is a super-solution of (10). Thanks to the definition of \bar{w} , we have $u_0(x) \leq \bar{u}(t=0, x)$, therefore, the comparison principle implies that for any $t > 0$, $x \in \mathbb{R}$, $u(t, x) \leq \bar{u}(t, x)$. For any $\varepsilon > 0$, $x > (c + \varepsilon)t$, one has $\bar{u}(t, x) \leq u_* e^{r(\alpha)\varepsilon t} \rightarrow 0$ when $t \rightarrow +\infty$, then the result follows. \square

3.3 Construction of a sub-solution for the simplified model

We are going to construct this sub-solution by part. In the part where $\phi \equiv 0$, we recall $f(s) = \frac{\beta s}{\frac{\beta s}{K} + \delta} - \mu s$ which corresponds to the reaction term of (11) with $\phi \equiv 0$. Consider the following system

$$\begin{cases} -w'' = f(w) & \text{in } \mathbb{R}_-, \\ w(0) = 0; \quad \lim_{x \rightarrow 0^-} w'(x) = -\sqrt{2 \int_0^{u_*} f(s) ds}. \end{cases} \quad (15)$$

We have the following Lemma

Lemma 9. *System (15) admits a solution $w \geq 0$ such that for any $x < 0$ $w'(x) < 0$ and $\lim_{x \rightarrow -\infty} w(x) = u_*$.*

Proof. By Cauchy-Lipschitz theorem, problem (15) admits a solution $w \geq 0$ in $[-L_0, 0)$ for some $L_0 \in (0, +\infty]$. Multiplying the first equation of (15) by w' and integrating in $(-L, 0)$ for some $L \in (0, L_0]$, we have

$$-\int_{-L}^0 \left[\frac{(w')^2}{2} \right]' dx = \int_{-L}^0 f(w) w' dx,$$

then

$$\frac{w'(-L)^2}{2} - \frac{w'(0)^2}{2} = -\int_0^{w(-L)} f(s) ds.$$

From (15), we have $w'(0)^2 = 2 \int_0^{u_*} f(s) ds$ then

$$\frac{w'(-L)^2}{2} = \int_{w(-L)}^{u_*} f(s) ds. \quad (16)$$

Since f is monostable, then $w'(-L) = 0$ if and only if $w(-L) = u_*$.

Define

$$L := \inf\{x > 0 : w'(-x) = 0\} = \inf\{x > 0 : w(-x) = u_*\} \leq +\infty. \quad (17)$$

If $L < +\infty$, from the definition of L one has $w'(-L) = 0$ and $w(-L) = u_*$. However, u_* is a stable equilibrium of equation $-w'' = f(w)$, so $w(-L) = u_*$ implies that $w \equiv u_*$. This is contradictory to the fact that $w(0) = 0$.

Hence, $L = +\infty$. So we have $w'(x) < 0$ and $w(x) < u_*$ for any $x < 0$. We can deduce from this bound that w converges when $x \rightarrow -\infty$. Since $\lim_{x \rightarrow -\infty} w(x) < w(0) = 0$, then w converges to u_* . \square

Now, we can use the solution w of (15) to construct a sub-solution of (11).

Proposition 10. *For any $c < 0$, problem (11) has a sub-solution \underline{w} which is defined as follows*

$$\underline{w}(x) = \begin{cases} w(x) & \text{when } x < 0, \\ 0 & \text{when } x \geq 0, \end{cases} \quad (18)$$

with $\phi(x - ct) = \Lambda(t, x)$.

Proof. For any $c < 0$, for any $x < 0$, one has $\phi(x) = 0, \underline{w}(x) = w(x), \underline{w}'(x) < 0$, then

$$-c\underline{w}' - \underline{w}'' - \frac{\underline{w}}{\underline{w} + \phi} \frac{\beta \underline{w}}{\frac{\beta \underline{w}}{K} + \delta} + \mu \underline{w} = -c\underline{w}' - \underline{w}'' - f(\underline{w}) = -c\underline{w}' < 0.$$

Moreover, $\lim_{x \rightarrow 0^-} \underline{w}(x) = -\sqrt{2 \int_0^{u_*} f(s) ds} < 0 = \lim_{x \rightarrow 0^+} \underline{w}(x)$. Hence, \underline{w} is a sub-solution of (11). \square

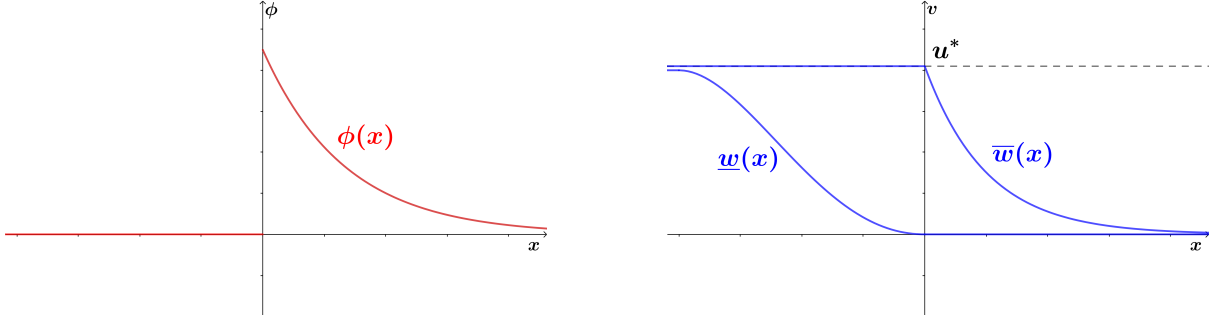


Figure 2: Control function ϕ and super-, sub-solutions.

3.4 Construction of a traveling wave solution for the simplified model

We construct a solution from the above sub- and super-solutions.

Proof of Theorem 6. According to Propositions 8 and 10, for the control function $\phi(x - ct) = \Lambda(t, x)$, problem (11) has the super-solution \bar{w} as in (12) and the sub-solution \underline{w} as in (15). Moreover, the sub- and super-solutions are well-ordered : $\underline{w} \leq \bar{w}$ (see Figures 2). By applying the classical technique of sub- and super-solution (see e.g. [26]), there exists a classical solution of (11). Moreover, we have

$$\int_{\mathbb{R}} \phi(x) dx = C_s \int_0^{+\infty} e^{-\lambda x} dx = \frac{C_s}{\lambda} < +\infty. \quad \square$$

4 Study of the whole system

In subsection 4.1, we provide some preliminary results such as a comparison principle adapted to system (1). In subsection 4.2, we prove the main Theorem 2 by introducing a super-solution. The proof of the result which states that it is indeed a super-solution is postponed to subsection 4.3. Subsection 4.4 is devoted to the establishment of a sub-solution of (9). Finally, in subsection 4.5, we provide the proof of Theorem 4.

4.1 Preliminary results

In this part, we focus on studying the existence of traveling wave solutions for system (1) and then apply it to prove Theorem 2. In the rest of the paper, we study this system in the subset $\{E \leq K\}$ of the positive cone since we have the following property.

Lemma 11. *On the positive cone $\{E \geq 0, F \geq 0, M \geq 0, M_s \geq 0\}$, the subset $\{E \leq K\}$ is time invariant, that is, if $0 \leq E^0 \leq K$, then $E(t, \cdot) \leq K$ for all $t > 0$.*

Proof. Assume that there exists a time $t_0 > 0$ such that $E(t_0, x) > K$ for some x . Since $0 \leq E^0 \leq K$, and E is continuous over time, we can deduce that there exists a time $t_1 \in (0, t_0)$ such that $E(t_1, x) > 0$ and $\partial_t E(t_1, x) > 0$. However, we also have $\partial_t E(t_1, x) = \beta F(t_1, x) \left(1 - \frac{E(t_1, x)}{K}\right) - (\nu_E + \mu_E)E(t_1, x) < 0$. This contradiction proves the result. \square

We recall that in the subset $\{E \leq K\}$, system (1) is not cooperative due to the introduction of sterile males $M_s > 0$. Indeed, from the second equation of (1), we have the reaction term

$$g(E, F, M, M_s) := r\nu_E E \frac{M}{M + \gamma M_s} - \mu_F F,$$

and $\frac{\partial g}{\partial M_s} = -\frac{\gamma r v_E E M}{(M + \gamma M_s)^2} < 0$ on the positive cone. Hence, we introduce a new comparison principle that can be applied to system (1) in the following part. We first define the nonlinear vector-valued function

$$\mathbf{f}(E, F, M; \psi) = \begin{bmatrix} f_1(E, F, M) \\ f_2(E, F, M) \\ f_3(E, F, M) \end{bmatrix} = \begin{bmatrix} \beta F \left(1 - \frac{E}{K}\right) - (v_E + \mu_E)E \\ r v_E E \frac{M}{M + \gamma \psi} - \mu_F F \\ (1 - r)v_E E - \mu_M M \end{bmatrix}, \quad (19)$$

where $\psi(t, x)$ is a fixed function. Denote $U(t, x) = (E, F, M)(t, x) \in \mathbb{R}_+^3$ then we obtain the following system

$$\partial_t U - D \partial_{xx} U = \mathbf{f}(U; \psi). \quad (20)$$

Next, we introduce the following theorem

Theorem 12 (Comparison principle for (1)). *Consider two functions $M_s^1, M_s^2 \in L_{\text{loc}}^1((0, +\infty) \times \mathbb{R})$ such that $0 \leq M_s^2(t, x) \leq M_s^1(t, x)$ for all $t \geq 0, x \in \mathbb{R}$. Suppose that*

- (E^1, F^1, M^1) is a sub-solution of system (20) with $\psi \equiv M_s^1$,
- (E^2, F^2, M^2) is a super-solution of system (20) with $\psi \equiv M_s^2$,
- $(E^1, F^1, M^1)(t = 0) \leq (E^2, F^2, M^2)(t = 0)$, for any $x \in \mathbb{R}$,

then

$$(E^1, F^1, M^1)(t, x) \leq (E^2, F^2, M^2)(t, x),$$

for all $t > 0, x \in \mathbb{R}$.

Proof. Recall that system (20) with $\psi(t, x)$ fixed is a cooperative system. Indeed,

$$\begin{aligned} \frac{\partial f_1}{\partial F} &= \beta \left(1 - \frac{E}{K}\right) > 0, & \frac{\partial f_1}{\partial M} &= 0, \\ \frac{\partial f_2}{\partial E} &= r v_E \frac{M}{M + \gamma \psi} > 0, & \frac{\partial f_2}{\partial M} &= \frac{\gamma \psi r v_E E}{(M + \gamma \psi)^2} > 0, \end{aligned}$$

and

$$\frac{\partial f_3}{\partial E} = (1 - r)v_E > 0, \quad \frac{\partial f_3}{\partial F} = 0.$$

On the other hand, from the assumption of Theorem 12, one has $0 \leq M_s^2(t, x) \leq M_s^1(t, x)$ for any $t > 0, x \in \mathbb{R}$, we deduce that $\mathbf{f}(U; M_s^1) \leq \mathbf{f}(U; M_s^2)$ for any $U \in \mathbb{R}_+^3$. Hence, recalling that $U^1 = (E^1, F^1, M^1)$ is a sub-solution of system (20) with $\psi \equiv M_s^1$, it follows

$$\partial_t U^1 - D \partial_{xx} U^1 - \mathbf{f}(U^1; M_s^2) \leq \mathbf{f}(U^1; M_s^1) - \mathbf{f}(U^1; M_s^2) \leq 0.$$

This inequality deduces that U^1 is also a sub-solution of system (20) with $\psi \equiv M_s^2$. From assumptions in Theorem 12, we also have $U^2 = (E^2, F^2, M^2)$ is a super-solution of this system. Moreover, $U^1(t = 0) \leq U^2(t = 0)$. Therefore, by applying the comparison principle for this cooperative system (see e.g. [30], Chapter 5, §5), we obtain that $(E^1, F^1, M^1)(t, x) \leq (E^2, F^2, M^2)(t, x)$ for any $t > 0, x \in \mathbb{R}$. \square

Next, we will use Theorem 12 for studying system (1) and prove the main result in Theorem 2.

4.2 Proof of Theorem 2

Before treating the main system, we first fix the distribution of sterile males by assuming that the sterile males neither die nor diffuse, and we assign $M_s(t, x) = \bar{\phi}_s(x - ct)$ where

$$\bar{\phi}_s(x) = \begin{cases} 0 & \text{for } x < 0, \\ C_s e^{-\eta x} & \text{for } x \geq 0, \end{cases} \quad (21)$$

with constants $C_s > 0$, $\eta > 0$. We consider the traveling wave solution $(E, F, M)(t, x) = (\phi_E, \phi_F, \phi_M)(x - ct)$ where (ϕ_E, ϕ_F, ϕ_M) satisfies the following system

$$\begin{cases} -c\phi_E' = \beta\phi_F\left(1 - \frac{\phi_E}{K}\right) - (v_E + \mu_E)\phi_E, \\ -c\phi_F' - D\phi_F'' = r v_E E \frac{\phi_M}{\phi_M + \gamma\phi_s} - \mu_F\phi_F, \\ -c\phi_M' - D\phi_M'' = (1-r)v_E\phi_E - \mu_M\phi_M, \\ (\phi_E, \phi_F, \phi_M)(-\infty) = (E^*, F^*, M^*), \quad (\phi_E, \phi_F, \phi_M)(+\infty) = (0, 0, 0). \end{cases} \quad (22)$$

with speed $c < 0$. Note that, system (22) is cooperative on the positive cone $\{E \geq 0, F \geq 0, M \geq 0\}$, thus we can apply directly the comparison principle for a cooperative system (see e.g. [30], Chapter 5, §5). Our idea is to construct a super-solution for the system (22) where the sterile males' distribution is fixed and then deduce a super-solution for the main system (9). First, we need to show that the solution ϕ_s of (9) is larger than $\bar{\phi}_s$ in the whole \mathbb{R} . It will follow that the solution $M_s(t, x)$ of the Cauchy problem with appropriate initial data is also larger than $\bar{\phi}_s$.

Lemma 13. *For a certain speed $c < 0$ and function $\phi(x - ct) = \Lambda(t, x)$ defined in (7), there exists a solution ϕ_s of equation*

$$-c\phi_s' - D\phi_s'' = \phi - \mu_s\phi_s, \quad \phi_s(\pm\infty) = 0,$$

such that for $A > C_s$ large enough and $\eta > 0$ small enough, one has $\bar{\phi}_s \leq \phi_s$ in \mathbb{R} .

Moreover, if $M_s^0 \geq \phi_s$ then the solution M_s of

$$\begin{cases} \partial_t M_s - D\partial_{xx} M_s = \Lambda - \mu_s M_s, \\ M_s(t=0) = M_s^0 \end{cases} \quad (23)$$

satisfies $M_s(t, x) \rightarrow \phi_s(x - ct)$ uniformly with respect to time and $M_s(t, x) \geq \bar{\phi}_s(x - ct)$.

Proof. Denote $\sigma_{\pm} = \frac{-c \pm \sqrt{c^2 + 4D\mu_s}}{2D}$ two roots of the characteristic polynomial of equation $-c\phi_s' - D\phi_s'' + \mu_s\phi_s = 0$, then we have $\sigma_- < 0 < \sigma_+$. Assume that $0 < \eta < -\sigma_-$, and define $A_s := \frac{A}{-D\eta^2 + c\eta + \mu_s}$, then we have solution

$$\phi_s(x) = \begin{cases} B_+ e^{\sigma_+ x} + B_- e^{\sigma_- x} & \text{for } x \leq 0, \\ A_+ e^{\sigma_+ x} + A_- e^{\sigma_- x} + A_s e^{-\eta x} & \text{for } x > 0, \end{cases}$$

for some A_{\pm} , B_{\pm} . Since we have $\phi_s(\pm\infty) = 0$, then $B_- = A_+ = 0$. To ensure that ϕ_s is \mathcal{C}^1 , we need $B_+ = A_- + A_s$, $\sigma_+ B_+ = \sigma_- A_- + \eta A_s$. Hence, we obtain that

$$A_- = \frac{\eta + \sigma_+}{\sigma_- - \sigma_+} A_s < 0, \quad B_+ = \frac{\eta + \sigma_-}{\sigma_- - \sigma_+} A_s > 0,$$

since $0 < \eta < -\sigma_-$. Now for any $x \leq 0$, one has $\phi_s(x) = \frac{\eta + \sigma_-}{\sigma_- - \sigma_+} \frac{A}{-D\eta^2 + c\eta + \mu_s} e^{\sigma_+ x} > 0 = \bar{\phi}_s(x)$. Otherwise, if $x > 0$, one has $\phi_s(x) = \frac{\eta + \sigma_+}{\sigma_- - \sigma_+} A_s e^{\sigma_- x} + A_s e^{-\eta x} > \frac{\eta + \sigma_-}{\sigma_- - \sigma_+} \frac{A}{-D\eta^2 + c\eta + \mu_s} e^{-\eta x} > C_s e^{-\eta x}$ if $A > C_s$ large enough.

For the second claim, we split the solution M_s into two parts: $M_s = M_s^1 + M_s^2$ solutions of

$$\begin{cases} \partial_t M_s^1 - D\partial_{xx} M_s^1 = -\mu_s M_s^1, \\ M_s^1(t=0) = M_s^0 - \phi_s \end{cases} \quad \text{and} \quad \begin{cases} \partial_t M_s^2 - D\partial_{xx} M_s^2 = \Lambda - \mu_s M_s^2, \\ M_s^2(t=0) = \phi_s \end{cases}$$

By linearity, it is clear that $M_s^1 + M_s^2$ is a solution of (23). Moreover, we have $M_s^1 = [H * (M_s^0 - \phi_s)] e^{-ct}$ (where H stands for the heat kernel in $\mathbb{R} \times [0, +\infty[$ and $*$ stands for the convolution) and $M_s^2(x-ct) = \phi_s(x-ct)$. Since $(M_s^0 - \phi_s) \in C_b^0(\mathbb{R}) \cap L^1(\mathbb{R})$ we deduce that M_s^1 converges uniformly to 0 as $t \rightarrow +\infty$. Finally, remarking that $(M_s^0 - \phi_s) \geq 0$ we deduce that $M_s^1 \geq 0$ and $M_s \geq \phi_s > \bar{\phi}_s$. \square

The next Proposition shows that we can construct a super-solution of (9) by studying system (22)

Proposition 14. *Assume that the basic offspring number $\mathcal{R}_0 > 1$, then for any speed $c < 0$ and the control function $\bar{\phi}_s$ defined in (21) with $C_s > 0$ large enough and $\eta > 0$ small enough, there exists a non-negative super-solution $(\bar{\phi}_E, \bar{\phi}_F, \bar{\phi}_M)$ of system (22) such that $\bar{\phi}_E \leq E^*$, $\bar{\phi}_F \leq F^*$, $\bar{\phi}_M \leq M^*$, and when $x \rightarrow +\infty$, $(\bar{\phi}_E, \bar{\phi}_F, \bar{\phi}_M)$ converges to $(0, 0, 0)$.*

Hence, we deduce that $(\bar{\phi}_E, \bar{\phi}_F, \bar{\phi}_M, \phi_s)$ is a super-solution of (9) where ϕ_s is defined in Lemma 13.

The proof of Proposition 14 is long and technical therefore, we postpone it to section 4.3. We finally provide the details of the proof of Theorem 2.

Proof of Theorem 2. We define $(\bar{E}, \bar{F}, \bar{M})(t, x) = (\bar{\phi}_E, \bar{\phi}_F, \bar{\phi}_M)(x - c't)$ where $c' < c < 0$, $(\bar{\phi}_E, \bar{\phi}_F, \bar{\phi}_M)$ is defined in Proposition 14 with a speed c' . It is clear that $(\bar{E}, \bar{F}, \bar{M})$ is a super-solution of system (20) with $\psi(t, x) = \bar{\phi}_s(x - ct)$ and $\bar{\phi}_s$ defined in (21). Denote (E, F, M, M_s) solution of system (1) with Λ defined in (7). Then (E, F, M) is a sub-solution of system (20) with $\psi \equiv M_s$. From Lemma 13, we can choose $A > C_s$ such that $M_s(t, x) \geq \bar{\phi}_s(x - ct)$ for any $t > 0$ and $x \in \mathbb{R}$. Moreover, by the construction of $(\bar{\phi}_E, \bar{\phi}_F, \bar{\phi}_M)$ in Proposition 14 (see Section 4.3), we have $(E^0, F^0, M^0)(x) \leq (\bar{E}, \bar{F}, \bar{M})(t=0, x)$. Now, we apply the comparison principle in Theorem 12 and we obtain that $(E, F, M)(t, x) \leq (\bar{E}, \bar{F}, \bar{M})(t, x)$ for any time $t > 0$ and $x \in \mathbb{R}$. Since $(\bar{\phi}_E, \bar{\phi}_F, \bar{\phi}_M)(x) \rightarrow (0, 0, 0)$ when $x \rightarrow +\infty$, we conclude that

$$\begin{aligned} \limsup_{t \rightarrow +\infty, x < ct} (E, F, M)(x, t) &\leq \limsup_{t \rightarrow +\infty, x < ct} (\bar{E}, \bar{F}, \bar{M})(x, t) \\ &= \limsup_{t \rightarrow +\infty, x < ct} (\bar{\phi}_E, \bar{\phi}_F, \bar{\phi}_M)(x - c't) \\ &\leq \lim_{t \rightarrow +\infty} C e^{(c-c')t} (1, 1, 1) = (0, 0, 0). \end{aligned}$$

\square

In the following parts, we construct super- and sub-solutions for (9), then conclude by proving Theorem 4.

4.3 Construction of a super-solution for (9)

We first remark that if $(\bar{\phi}_E, \bar{\phi}_M, \bar{\phi}_F)$ is a super-solution of (22) then $(\bar{\phi}_E, \bar{\phi}_M, \bar{\phi}_F, \phi_s)$ is a super-solution of (9). Indeed, by applying Lemma 13, we have $\phi_s \geq \bar{\phi}_s$ in \mathbb{R} , thus, we have

$$-c\bar{\phi}_F' - D\bar{\phi}_F'' - r\nu_E \bar{\phi}_E \frac{\bar{\phi}_M}{\bar{\phi}_M + \gamma\phi_s} + \mu_F \bar{\phi}_F \geq -c\bar{\phi}_F' - D\bar{\phi}_F'' - r\nu_E \bar{\phi}_E \frac{\bar{\phi}_M}{\bar{\phi}_M + \gamma\phi_s} + \mu_F \bar{\phi}_F \geq 0.$$

Following the idea we used with the simplified model, we construct super-solutions for (22) established by two parts, a constant part on $(-\infty, x_*]$ and a tail on $(x_*, +\infty)$ that decays to 0 at $+\infty$, with some $x_* \geq 0$. We start by considering $\overline{\phi}_F$ as follows

$$\overline{\phi}_F(x) = \begin{cases} F^* & \text{when } x \leq 0, \\ F^* e^{-\lambda x} & \text{when } x > 0, \end{cases} \quad (24)$$

with some $\lambda > 0$. Next, we construct the tails for $\overline{\phi}_E$ and $\overline{\phi}_M$, and clarify the value of x_* . After that, we provide proof of Proposition 14.

• **Construction of function $\overline{\phi}_E$:** First, on \mathbb{R}_+ , we consider function $\widetilde{\phi}_E(x)$ such that

$$\begin{cases} -c\widetilde{\phi}_E' = \beta F^* e^{-\lambda x} \left(1 - \frac{\widetilde{\phi}_E}{K}\right) - (v_E + \mu_E)\widetilde{\phi}_E, \\ \widetilde{\phi}_E > 0, \quad \lim_{x \rightarrow +\infty} \widetilde{\phi}_E = 0, \quad \widetilde{\phi}_E(0) = E^*. \end{cases} \quad (25)$$

Hence, for any $x \geq 0$, we obtain $\widetilde{\phi}_E$ of the form

$$\widetilde{\phi}_E(x) = e^{\delta(x)} \left(-\frac{\beta F^*}{c} \int_0^x e^{-\lambda s - \delta(s)} ds + E^* \right) > 0, \quad (26)$$

where $\delta(x) = -\frac{\beta F^*}{\lambda c K} e^{-\lambda x} + \frac{v_E + \mu_E}{c} x + \frac{\beta F^*}{\lambda c K}$. One has $\delta(0) = 0$ and $\lim_{x \rightarrow +\infty} \delta(x) = -\infty$. We have the following lemma

Lemma 15. *Assume that $\lambda + \frac{v_E + \mu_E}{c} < 0$, then there exists a constant $C_E > E^*$ such that $\widetilde{\phi}_E(x) \leq C_E e^{-\lambda x}$ for any $x \geq 0$.*

Proof. Since $\lambda + \frac{v_E + \mu_E}{c} < 0$ and $c < 0$, for any $x \geq 0$, we obtain that $\delta(x) \leq \frac{v_E + \mu_E}{c} x \leq -\lambda x$. Therefore, $e^{\delta(x)} \leq e^{\frac{v_E + \mu_E}{c} x} \leq e^{-\lambda x}$. On the other hand, one has

$$e^{\delta(x)} \int_0^x e^{-\lambda s - \delta(s)} ds \leq e^{\frac{v_E + \mu_E}{c} x} \int_0^x e^{-\lambda s - \frac{v_E + \mu_E}{c} s} e^{-\frac{\beta F^*}{c \lambda K} (1 - e^{-\lambda s})} ds \leq \frac{e^{-\frac{\beta F^*}{c \lambda K}}}{\lambda + \frac{v_E + \mu_E}{c}} e^{-\lambda x}.$$

Then one has $C_E := E^* + \frac{\beta F^*}{c} \frac{e^{-\frac{\beta F^*}{c \lambda K}}}{\lambda + \frac{v_E + \mu_E}{c}} > E^*$. This induces the result of the lemma. \square

From Lemma 15, we can deduce that $\lim_{x \rightarrow +\infty} \widetilde{\phi}_E(x) = 0$. Moreover, we define

$$x_E := \sup\{x \geq 0 : \widetilde{\phi}_E(x) = E^*\} < +\infty, \quad (27)$$

and $\widetilde{\phi}_E(x) < E^*$ for any $x > x_E$. We define function $\overline{\phi}_E$ as follows

$$\overline{\phi}_E(x) = \begin{cases} E^* & \text{when } x \leq x_E \\ \widetilde{\phi}_E(x) & \text{when } x > x_E. \end{cases} \quad (28)$$

Then for any x , we have $\overline{\phi}_E(x) \leq \min\{E^*, C_E e^{-\lambda x}\}$, $\lim_{x \rightarrow +\infty} \overline{\phi}_E(x) = 0$, and $\lim_{x \rightarrow x_E^-} \overline{\phi}_E'(x) = 0 \geq \widetilde{\phi}_E'(x_E) = \lim_{x \rightarrow x_E^+} \overline{\phi}_E'(x)$.

• **Construction of function $\overline{\phi}_M$:** Next, on \mathbb{R}_+ , we consider function $\widetilde{\phi}_M$ which satisfies

$$\begin{cases} -c\widetilde{\phi}_M' - D\widetilde{\phi}_M'' = (1-r)v_E C_E e^{-\lambda x} - \mu_M \widetilde{\phi}_M, \\ \widetilde{\phi}_M(x) > 0, \quad \lim_{x \rightarrow +\infty} \widetilde{\phi}_M(x) = 0, \quad \widetilde{\phi}_M(0) = M^*. \end{cases} \quad (29)$$

Consider the characteristic polynomial $-D\delta^2 - c\delta + \mu_M = 0$ with two roots $\delta_{\pm} = \frac{-c \pm \sqrt{c^2 + 4D\mu_M}}{2D}$, where $\delta_+ > 0, \delta_- < 0$. Then any solution of (29) has the form $\widetilde{\phi}_M(x) = C_M e^{-\lambda x} + C_1 e^{\delta_- x} + C_2 e^{\delta_+ x}$, where

$$C_M = \frac{(1-r)v_E C_E}{-D\lambda^2 + c\lambda + \mu_M}. \quad (30)$$

Since we look for $\lim_{x \rightarrow +\infty} \widetilde{\phi}_M(x) = 0$, then $C_2 = 0$. Moreover, $M^* = \widetilde{\phi}_M(0) = C_M + C_1$, thus $C_1 = M^* - C_M$.

Assume that $\lambda + \delta_- < 0$, so we have $\mu_M > -D\lambda^2 + c\lambda + \mu_M > 0$ and

$$C_M > \frac{(1-r)v_E C_E}{\mu_M} = M^* \frac{C_E}{E^*} \geq M^*.$$

Moreover, since $\delta_- < -\lambda$, then for any $x > 0$, we have

$$C_M e^{-\lambda x} > \widetilde{\phi}_M(x) = C_M e^{-\lambda x} + (M^* - C_M) e^{\delta_- x} > M^* e^{\delta_- x} > 0.$$

and we have $\lim_{x \rightarrow +\infty} \widetilde{\phi}_M(x) = 0$, so $\widetilde{\phi}_M$ is a solution of problem (29). We define

$$x_M = \sup\{x \geq 0 : \widetilde{\phi}_M(x) = M^*\} < +\infty, \quad (31)$$

and

$$\overline{\phi}_M(x) = \begin{cases} M^* & \text{when } x \leq x_M \\ \widetilde{\phi}_M(x) & \text{when } x > x_M. \end{cases} \quad (32)$$

Again we have $\overline{\phi}_M(x) \leq \min\{M^*, C_M e^{-\lambda x}\}$ for any x , $\lim_{x \rightarrow +\infty} \overline{\phi}_M(x) = 0$, and $\lim_{x \rightarrow x_M^+} \overline{\phi}_M'(x) = 0 \geq \widetilde{\phi}_M'(x_M) = \lim_{x \rightarrow x_M^+} \overline{\phi}_M'(x)$.

Now we prove that for C_s large enough, $(\overline{\phi}_E, \overline{\phi}_F, \overline{\phi}_M)$ defined as above is a super-solution of (22).

Proof of Proposition 14. Fix a positive parameter α such that $\alpha < \frac{\mu_F F^*}{r v_e C_E} = \frac{E^*}{C_E} < 1$. Then, we choose a positive constant λ such that

$$\lambda \leq \min \left\{ -\frac{v_E + \mu_E}{c}, \frac{c + \sqrt{c^2 + 4D\mu_M}}{2D}, \frac{c + \sqrt{c^2 + 4D\mu_F (1 - \alpha \frac{C_E}{E^*})}}{2D} \right\}. \quad (33)$$

Recalling C_M defined respectively in (30), we take $\eta < \lambda$ and C_s large enough such that $\frac{C_s}{C_M} \geq \frac{1}{\gamma} \left(\frac{1}{\alpha} - 1 \right)$.

Then for any $x > 0$, $\frac{\overline{\phi}_s}{\overline{\phi}_M} \geq \frac{C_s e^{-\eta x}}{C_M e^{-\lambda x} + (M^* - C_M) e^{\delta_- x}} \geq \frac{C_s e^{-\eta x}}{C_M e^{-\lambda x}} \geq \frac{C_s}{C_M}$, thus we obtain that $\frac{\overline{\phi}_M}{\overline{\phi}_M + \gamma \overline{\phi}_s} = \frac{1}{1 + \gamma \frac{\overline{\phi}_s}{\overline{\phi}_M}} \leq \alpha$.

We now check that $(\overline{\phi}_E, \overline{\phi}_F, \overline{\phi}_M)$ is a super-solution of (22).

◦ **Checking for $\overline{\phi_E}$:** For any $x \leq x_E$, since $\overline{\phi_E}(x) = E^*$, $\overline{\phi_F}(x) \leq F^*$, then

$$-c\overline{\phi_E}' - \beta\overline{\phi_F} \left(1 - \frac{\overline{\phi_E}}{K}\right) + (v_E + \mu_E)\overline{\phi_E} \geq -\beta F^* \left(1 - \frac{E^*}{K}\right) + (v_E + \mu_E)E^* = 0,$$

and for $x > x_E > 0$, one has

$$-c\overline{\phi_E}' - \beta\overline{\phi_F} \left(1 - \frac{\overline{\phi_E}}{K}\right) + (v_E + \mu_E)\overline{\phi_E} = -c\widetilde{\phi_E}' - \beta F^* e^{-\lambda x} \left(1 - \frac{\widetilde{\phi_E}}{K}\right) + (v_E + \mu_E)\widetilde{\phi_E} = 0.$$

◦ **Checking for $\overline{\phi_F}$:** For any $x \leq 0$, we have $\overline{\phi_F} = F^*$, $\overline{\phi_E} \leq E^*$, then

$$-c\overline{\phi_F}' - D\overline{\phi_F}'' - r v_E \overline{\phi_E} \frac{\overline{\phi_M}}{\overline{\phi_M} + \gamma\phi_s} + \mu_F \overline{\phi_F} \geq -r v_E E^* + \mu_F F^* = 0.$$

For any $x > 0$, we have $\overline{\phi_E}(x) \leq C_E e^{-\lambda x}$, $\overline{\phi_F}(x) = F^* e^{-\lambda x}$, $\frac{\overline{\phi_M}}{\overline{\phi_M} + \gamma\phi} \leq \alpha$.

From (4), we note that $\frac{\mu_F F^*}{E^*} = r v_E$, thus

$$-c\overline{\phi_F}' - D\overline{\phi_F}'' - r v_E \overline{\phi_E} \frac{\overline{\phi_M}}{\overline{\phi_M} + \gamma\phi_s} + \mu_F \overline{\phi_F} \geq F^* e^{-\lambda x} \left(-D\lambda^2 + c\lambda - \mu_F \alpha \frac{C_E}{E^*} + \mu_F\right) \geq 0$$

since $0 < \lambda \leq \frac{c + \sqrt{c^2 + 4D\mu_F(1 - \alpha \frac{C_E}{E^*})}}{2D}$.

◦ **Checking for $\overline{\phi_M}$:** For any $x \leq x_M$, one has $\overline{\phi_M}(x) = M^*$, $\overline{\phi_E}(x) \leq E^*$, thus

$$-c\overline{\phi_M}' - D\overline{\phi_M}'' - (1-r)v_E \overline{\phi_E} + \mu_M \overline{\phi_M} \geq -(1-r)v_E E^* + \mu_M M^* = 0.$$

On the other hand, when $x > x_M$, one has $\overline{\phi_E}(x) \leq C_E e^{-\lambda x}$, $\overline{\phi_M}(x) = \widetilde{\phi_M}(x)$ with $\widetilde{\phi_M}$ defined in (29) thus

$$-c\overline{\phi_M}' - D\overline{\phi_M}'' - (1-r)v_E \overline{\phi_E} + \mu_M \overline{\phi_M} \geq -c\widetilde{\phi_M}' - D\widetilde{\phi_M}'' - (1-r)v_E C_E e^{-\lambda x} + \mu_M \widetilde{\phi_M} = 0.$$

In conclusion, for $\lambda > 0$ small such that (33) holds, $(\overline{\phi_E}, \overline{\phi_F}, \overline{\phi_M})$ defined as above is a super-solution of (22) where C_s is large enough and $0 < \eta < \lambda$. Then, we deduce that $(\overline{\phi_E}, \overline{\phi_F}, \overline{\phi_M}, \phi_s)$ is a super-solution of (9). \square

4.4 Construction of a sub-solution for (9)

First, we remark that the sub-solution is established only to prove Theorem 4. Therefore, according to Theorem 12, we need to establish $(\underline{\phi_E}, \underline{\phi_F}, \underline{\phi_M}, \underline{\phi_s})$ such that

$$\underline{\phi_s} \geq \phi_s \quad \text{and} \quad \begin{cases} -c\underline{\phi_E}' \leq \beta\underline{\phi_F} \left(1 - \frac{\underline{\phi_E}}{K}\right) - (v_E + \mu_E)\underline{\phi_E}, \\ -c\underline{\phi_F}' - D\underline{\phi_F}'' \leq r v_E \frac{\underline{\phi_M}}{\underline{\phi_M} + \gamma\underline{\phi_s}} \underline{\phi_E} - \mu_F \underline{\phi_F}, \\ -c\underline{\phi_M}' - D\underline{\phi_M}'' \leq (1-r)v_E \underline{\phi_E} - \mu_M \underline{\phi_M}. \end{cases}$$

The first difficulty is that the sterile males diffuse so $\phi_s > 0$ on \mathbb{R} . It is clear that $\phi_s(x) \xrightarrow{|x| \rightarrow +\infty} 0$ uniformly.

Therefore, we deduce that

$$\forall \varepsilon > 0, \exists x_\varepsilon = \inf\{x \in \mathbb{R} : \phi_s(x) < \varepsilon\} \quad \text{and} \quad x_\varepsilon < +\infty.$$

Moreover, taking ε small enough, we can consider $x_\varepsilon \leq 0$. Then, we take

$$\underline{\phi}_s(x) = \begin{cases} \varepsilon & \text{for } x < x_\varepsilon, \\ \phi_s & \text{for } x > x_\varepsilon. \end{cases} \quad (34)$$

The second difficulty is that (E^*, F^*, M^*) is no more an equilibrium if we impose $\underline{\phi}_s(-\infty) = \varepsilon$. Nevertheless, thanks to the implicit function theorem, we obtain

Proposition 16. *There exists $\varepsilon_0 > 0$ such that for any $\varepsilon \in [0, \varepsilon_0)$, there exists a strictly positive solution $(E_\varepsilon^*, F_\varepsilon^*, M_\varepsilon^*)$ of*

$$\begin{cases} \beta F_\varepsilon^* \left(1 - \frac{E_\varepsilon^*}{K}\right) - (v_E + \mu_E) E_\varepsilon^* = 0, \\ r v_E E_\varepsilon^* \frac{1}{1+\varepsilon} - \mu_F F_\varepsilon^* = 0, \\ (1-r) v_E E_\varepsilon^* - \mu_M M_\varepsilon^* = 0. \end{cases} \quad (35)$$

Moreover, one has $(E_\varepsilon^*, F_\varepsilon^*, M_\varepsilon^*)$ is decreasing continuously with respect to ε , and $(E_0^*, F_0^*, M_0^*) = (E^*, F^*, M^*)$.

Proof. We define

$$\mathbf{f}_2(E, F, M, \varepsilon) = \begin{pmatrix} \beta F \left(1 - \frac{E}{K}\right) - (v_E + \mu_E) E \\ r v_E E \frac{1}{1+\varepsilon} - \mu_F F \\ (1-r) v_E E - \mu_M M \end{pmatrix}.$$

According to the explicit writing of (E^*, F^*, M^*) in (4) and since $\mathcal{R}_0 > 1$, we have that

$$\det(D_{E,F,M} \mathbf{f}_2(E^*, F^*, M^*, 0)) = -\mu_M [\beta r v_E - \mu_F (\mu_E + v_E)] < 0.$$

Then, the implicit function theorem provides the existence of ε_0 . Still thanks to the implicit function theorem, there holds

$$\begin{aligned} \begin{pmatrix} \partial_\varepsilon E_\varepsilon^* \\ \partial_\varepsilon F_\varepsilon^* \\ \partial_\varepsilon M_\varepsilon^* \end{pmatrix} &= - (D_{E,F,M} \mathbf{f}_2)^{-1} \cdot \nabla_\varepsilon \mathbf{f}_2(E_\varepsilon^*, F_\varepsilon^*, M_\varepsilon^*, \varepsilon) \\ &= \frac{r v_E E_\varepsilon^*}{(1+\varepsilon)^2 (\det D_{E,F,M} \mathbf{f}_2(E_\varepsilon^*, F_\varepsilon^*, M_\varepsilon^*, \varepsilon))} \begin{pmatrix} \beta \left(1 - \frac{E_\varepsilon^*}{K}\right) \mu_M \\ \left(\frac{\beta F_\varepsilon^*}{K} + \mu_E + v_E\right) \mu_M \\ \left(\frac{\beta F_\varepsilon^*}{K} + \mu_E + v_E\right) \mu_F \end{pmatrix}. \end{aligned}$$

Recalling, that $\det(D_{E,F,M} \mathbf{f}_2(E^*, F^*, M^*, 0)) < 0$, we deduce by continuity that $\begin{pmatrix} \partial_\varepsilon E_\varepsilon^* \\ \partial_\varepsilon F_\varepsilon^* \\ \partial_\varepsilon M_\varepsilon^* \end{pmatrix} < \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}$ and

the conclusion follows. \square

Because of our choice of $\underline{\phi}_s$, we construct a subsolution that converges to $(E_\varepsilon, F_\varepsilon, M_\varepsilon)$ for some positive ε . We construct a sub-solution $(\underline{\phi}_E, \underline{\phi}_F, \underline{\phi}_M)$ for system (22) by two parts. The first part of $(\underline{\phi}_E, \underline{\phi}_F, \underline{\phi}_M)$ is equal to 0 on $[x_\varepsilon, +\infty)$ and the second part on $(-\infty, x_\varepsilon)$ converges to $(E_\varepsilon^*, F_\varepsilon^*, M_\varepsilon^*)$ when $x \rightarrow -\infty$. The construction of the sub-solution on $(-\infty, x_\varepsilon)$ is the third difficulty. To cope with this problem, we use the fact that $\underline{\phi}_E \leq E_\varepsilon$. We present the result of the existence of a sub-solution as follows

Proposition 17. *For a speed $c < 0$, there exists $\varepsilon_1 \in (0, \varepsilon_0)$ and $\varepsilon < \varepsilon_1$ a constant small enough such that for the control function $\psi = \underline{\phi}_s$ defined in (34), there exists a non-negative sub-solution $(\underline{\phi}_E, \underline{\phi}_F, \underline{\phi}_M)$ of system (22) such that $\underline{\phi}_E \leq E_{\varepsilon_1}^*$, $\underline{\phi}_F \leq F_{\varepsilon_1}^*$, $\underline{\phi}_M \leq M_{\varepsilon_1}^*$. Moreover, when $x \rightarrow -\infty$, $(\underline{\phi}_E, \underline{\phi}_F, \underline{\phi}_M)(x)$ converges to $(E_{\varepsilon_1}^*, F_{\varepsilon_1}^*, M_{\varepsilon_1}^*)$.*

Proof. We fix $c < 0$ and $\varepsilon_1 \in (0, \varepsilon_0)$ (where ε_0 is defined in Proposition 16). Then, we consider $(\hat{E}, \hat{F}, \hat{M})$ a solution of the following linear system in \mathbb{R}_-

$$\begin{cases} -c\hat{E}' = \beta\hat{F}\left(1 - \frac{E_{\varepsilon_1}^*}{K}\right) - (v_E + \mu_E)\hat{E}, \\ -c\hat{F}' - D\hat{F}'' = \frac{rv_E}{1+\varepsilon_1}\hat{E} - \mu_F\hat{F}, \\ -c\hat{M}' - D\hat{M}'' = (1-r)v_E\hat{E} - \mu_M\hat{M}, \end{cases} \quad (36)$$

with $\hat{E}(-\infty) = E_{\varepsilon_1}^*$, $\hat{F}(-\infty) = F^*$, $\hat{M}(-\infty) = M^*$.

Now, we will study this linear system by denoting $U = \begin{pmatrix} \hat{E} \\ \hat{F} \\ \hat{M} \\ \hat{F}' \\ \hat{M}' \end{pmatrix}$. Then system (36) becomes $U' = BU$

where $B = \begin{pmatrix} \frac{v_E + \mu_E}{c} & -\frac{\mu_F(v_E + \mu_E)}{\beta rv_E/(1+\varepsilon_1)} & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 1 \\ -\frac{rv_E}{D(1+\varepsilon_1)} & \frac{\mu_F}{D} & 0 & -\frac{c}{D} & 0 \\ -\frac{(1-r)v_E}{D} & 0 & \frac{\mu_M}{D} & 0 & -\frac{c}{D} \end{pmatrix}$, since $1 - \frac{E_{\varepsilon_1}^*}{K} = \frac{\mu_F(v_E + \mu_E)}{\beta rv_E/(1+\varepsilon_1)}$. Hence, the characteristic polynomial is

$$\det(B - \lambda I) = \lambda \underbrace{\left(\lambda^2 + \frac{c}{D}\lambda - \frac{\mu_M}{D}\right)}_{P_M(\lambda)} \underbrace{\left[-\lambda^2 + \left(\frac{v_E + \mu_E}{c} - \frac{c}{D}\right)\lambda + \frac{v_E + \mu_E}{c} + \frac{\mu_F}{D}\right]}_{P_F(\lambda)}.$$

It is clear that $\lambda_0 = 0$ is an eigenvalue associated to the eigenvector $U_0 = \begin{pmatrix} E_{\varepsilon_1}^* \\ F_{\varepsilon_1}^* \\ M_{\varepsilon_1}^* \\ 0 \\ 0 \end{pmatrix}$. Denote eigenvalues

$\lambda_M^+ > 0, \lambda_M^- < 0$ which are the roots of $P_M(\lambda)$, $\lambda_F^+ > 0, \lambda_F^- < 0$ which are the roots of $P_F(\lambda)$. We aim at building a solution $U(x)$ that converges to U_0 when $x \rightarrow -\infty$, then we construct U of the following form

$$U(x) = U_0 + e^{\lambda_M^+ x} U_M^+ + e^{\lambda_F^+ x} U_F^+,$$

where U_M^+, U_F^+ the corresponding eigenvectors of λ_M^+, λ_F^+ . We consider the following cases:

Case 1: $\lambda_M^+ \neq \lambda_F^+$: Since λ_M^+ is a root of $P_M(\lambda)$, then $U_M^+ = \begin{pmatrix} 0 \\ 0 \\ a \\ 0 \\ a\lambda_M^+ \end{pmatrix}$ for some $a \in \mathbb{R}$. Denote

$U_F^+ = \begin{pmatrix} b_1 \\ b_2 \\ b_3 \\ b_4 \\ b_5 \end{pmatrix}$ an eigenvector associated to λ_F^+ . We have $BU_F^+ = \lambda_F^+ U_F^+$, and since $\text{rank}(B - \lambda_F^+ I) = 4$ then

all entries b_2, b_3, b_4, b_5 depend explicitly on $b_1 \in \mathbb{R}$. More precisely, using the formula of $E_{\varepsilon_1}^*, F_{\varepsilon_1}^*, M_{\varepsilon_1}^*$, we have

$$b_2 = b_1 \frac{F_{\varepsilon_1}^*}{E_{\varepsilon_1}^*} \left(1 - \frac{c\lambda_F^+}{v_E + \mu_E}\right), \quad b_3 = b_1 \frac{M_{\varepsilon_1}^*}{E_{\varepsilon_1}^*} \frac{\mu_M}{-D[(\lambda_F^+)^2 + \frac{c}{D}\lambda_F^+ - \frac{\mu_M}{D}]}, \quad b_4 = \lambda_F^+ b_2. \quad (37)$$

For any $x < 0$, we have

$$\hat{E}(x) = E_{\varepsilon_1}^* + b_1 e^{\lambda_F^+ x}, \quad \hat{F}(x) = F_{\varepsilon_1}^* + b_2 e^{\lambda_F^+ x}, \quad \hat{M}(x) = M_{\varepsilon_1}^* + a e^{\lambda_M^+ x} + b_3 e^{\lambda_F^+ x}.$$

We choose $b_1 = -E_{\varepsilon_1}^*$, $a = -M_{\varepsilon_1}^* - b_3$. Thus we obtain that $\hat{E}(0) = 0, \hat{M}(0) = 0, \hat{F}(0) = \frac{cF_{\varepsilon_1}^* \lambda_F^+}{v_E + \mu_E} < 0$.

Then, there exists a unique constant $y_F < 0$ such that $\hat{F}(y_F) = 0$.

Claim: For any $x < 0$, one has $\hat{E}(x) < E_{\varepsilon_1}^*, \hat{F}(x) < F_{\varepsilon_1}^*, \hat{M}(x) < M_{\varepsilon_1}^*$.

Indeed, since $b_1 < 0$, we deduce from (37) that $b_2 < 0$, then for any $x < 0$, $\hat{E}(x) < E_{\varepsilon_1}^*, \hat{F}(x) < F_{\varepsilon_1}^*$. It remains to show that $\hat{M}(x) < M_{\varepsilon_1}^*$ for any $x < 0$. One has

$$\hat{M}(x) = M_{\varepsilon_1}^* (1 - e^{\lambda_M^+ x}) + b_3 (e^{\lambda_F^+ x} - e^{\lambda_M^+ x}).$$

We only need to show that $b_3 (e^{\lambda_F^+ x} - e^{\lambda_M^+ x}) < 0$ for any $x < 0$. Indeed,

◦ if $\lambda_F^+ < \lambda_M^+$, then $e^{\lambda_F^+ x} - e^{\lambda_M^+ x} > 0$ for any $x < 0$ and $(\lambda_F^+)^2 + \frac{c}{D} \lambda_F^+ - \frac{\mu_M}{D} < 0$. From (37), we deduce that $b_3 < 0$;

◦ if $\lambda_F^+ > \lambda_M^+$, we have $e^{\lambda_F^+ x} - e^{\lambda_M^+ x} < 0$ for any $x < 0$ and $b_3 > 0$.

Case 2: $\lambda_F^+ = \lambda_M^+ = \lambda^+$: Now λ^+ has one-dimensional eigenspace generated by $U^+ = \begin{pmatrix} 0 \\ 0 \\ a \\ 0 \\ a\lambda^+ \end{pmatrix}$

for some constant a . The solution of $U' = BU$ becomes $U(x) = U_0 + x e^{\lambda^+ x} U^+ + e^{\lambda^+ x} V^+$, with V^+ some vector to be determined. Plugging this $U(x)$ into the equation yields

$$e^{\lambda^+ x} U^+ + \lambda^+ x e^{\lambda^+ x} U^+ + \lambda^+ e^{\lambda^+ x} V^+ = U'(x) = BU = \lambda^+ x e^{\lambda^+ x} U^+ + e^{\lambda^+ x} B V^+.$$

Hence, $(B - \lambda^+ I)V^+ = U^+$. Denote $V^+ = \begin{pmatrix} b_1 \\ b_2 \\ b_3 \\ b_4 \\ b_5 \end{pmatrix}$, one has
$$\begin{cases} b_2 = b_1 \frac{F_{\varepsilon_1}^*}{E_{\varepsilon_1}^*} \left(1 - \frac{c\lambda^+}{v_E + \mu_E}\right), \\ b_4 = \lambda^+ b_2, \\ b_5 = \lambda^+ b_3 + a, \\ a = -\frac{M_{\varepsilon_1}^*}{E_{\varepsilon_1}^*} \frac{1}{1 + \frac{2D\lambda^+}{\mu_M}} b_1. \end{cases}$$

Then, we have

$$\hat{E}(x) = E_{\varepsilon_1}^* + b_1 e^{\lambda^+ x}, \quad \hat{F}(x) = F_{\varepsilon_1}^* + b_2 e^{\lambda^+ x}, \quad \hat{M}(x) = M_{\varepsilon_1}^* + a x e^{\lambda^+ x} + b_3 e^{\lambda^+ x}.$$

We choose $b_1 = -E_{\varepsilon_1}^*, b_3 = -M_{\varepsilon_1}^*$, then $\hat{E}(0) = 0, \hat{M}(0) = 0, \hat{F}(0) = \frac{cF_{\varepsilon_1}^* \lambda^+}{v_E + \mu_E} < 0$. Thus, there exists a unique constant $y_F < 0$ such that $\hat{F}(y_F) = 0$.

Since we have $a = \frac{M_{\varepsilon_1}^*}{1 + \frac{2D\lambda^+}{\mu_M}} > 0$, we obtain that for any $x < 0$, $\hat{E}(x) < E_{\varepsilon_1}^*, \hat{F}(x) < F_{\varepsilon_1}^*, \hat{M}(x) < M_{\varepsilon_1}^*$.

Hence, in both cases, we constructed solution $(\hat{E}(x), \hat{F}(x), \hat{M}(x))$ of (36) such that $\hat{E}(x) < E_{\varepsilon_1}^*, \hat{F}(x) < F_{\varepsilon_1}^*, \hat{M}(x) < M_{\varepsilon_1}^*$. Moreover, $(\hat{E}, \hat{F}, \hat{M})$ converges to $(E_{\varepsilon_1}^*, F_{\varepsilon_1}^*, M_{\varepsilon_1}^*)$ at $-\infty$. Now, we use these functions to construct a sub-solution for (22).

Construction of a sub-solution:

Now, we construct ϕ_E, ϕ_F, ϕ_M a sub-solution of system (15) taking $\phi_s = \phi_s$ defined in (34) with $\varepsilon \in (0, \varepsilon_1)$ that will be fixed later on. Due to a translation of space, without loss of generality, we can

assume here that $x_{\varepsilon_1}^* = 0$. Next, we define

$$\underline{\phi}_E(x) = \begin{cases} \hat{E}(x) & \text{when } x \leq 0, \\ 0 & \text{when } x > 0, \end{cases} \quad \underline{\phi}_F(x) = \begin{cases} \hat{F}(x) & \text{when } x \leq y_F, \\ 0 & \text{when } x > y_F, \end{cases} \quad \underline{\phi}_M(x) = \begin{cases} \hat{M}(x) & \text{when } x \leq 0, \\ 0 & \text{when } x > 0. \end{cases} \quad (38)$$

Note that, by the definitions of $\underline{\phi}_s$, the fraction $\frac{\underline{\phi}_M}{\underline{\phi}_M + \gamma \underline{\phi}_s}$ is well-defined in \mathbb{R} . We now check the sub-solution inequalities for $(\underline{\phi}_E, \underline{\phi}_F, \underline{\phi}_M)$. We can see that for any $x > 0$, the inequalities are trivial.

◦ **Checking for $\underline{\phi}_E(x)$:** For any $x \leq y_F < 0$, since $\underline{\phi}_E \leq E_{\varepsilon_1}^*$, thus

$$-c\underline{\phi}_E' - \beta\underline{\phi}_F \left(1 - \frac{\underline{\phi}_E}{K}\right) + (v_E + \mu_E)\underline{\phi}_E \leq -c\hat{E}' - \beta\hat{F} \left(1 - \frac{E_{\varepsilon_1}^*}{K}\right) - (v_E + \mu_E)\hat{E} = 0,$$

For any x such that $y_F < x \leq 0$, we have

$$-c\underline{\phi}_E' - \beta\underline{\phi}_F \left(1 - \frac{\underline{\phi}_E}{K}\right) + (v_E + \mu_E)\underline{\phi}_E = -c\hat{E}' + (v_E + \mu_E)\hat{E} = \beta\hat{F} \left(1 - \frac{E_{\varepsilon_1}^*}{K}\right) < 0,$$

since $\hat{F} < 0$ on $(y_F, 0]$. At $x = 0$, we also have $\lim_{x \rightarrow 0^-} \underline{\phi}_E'(x) = \hat{E}'(0) = -\lambda^+ E_{\varepsilon_1}^* < 0 = \lim_{x \rightarrow 0^+} \underline{\phi}_E(x)$.

◦ **Checking for $\underline{\phi}_F(x)$:** First, we consider the case where $x \leq y_F$. Taking $\varepsilon < \min\left(\frac{\varepsilon_1}{2}, \frac{1}{\gamma} \varepsilon_1 \min_{x \leq y_F} \phi_M\right)$ it follows, recalling that in this case, $\underline{\phi}_s = \varepsilon$, one has

$$-c\underline{\phi}_F' - D\underline{\phi}_F'' - r v_E \underline{\phi}_E \frac{\underline{\phi}_M}{\underline{\phi}_M + \gamma \underline{\phi}_s} + \mu_F \underline{\phi}_F = r v_E \underline{\phi}_E \left[\frac{1}{1 + \varepsilon_1} - \frac{\hat{M}}{\hat{M} + \gamma \varepsilon} \right] \leq 0,$$

due to the fact that $(\hat{E}, \hat{F}, \hat{M})$ is a solution of (36).

For $y_F < x \leq 0$, we have $\underline{\phi}_F(x) = 0$, $\underline{\phi}_E(x) = \hat{E}(x) \geq 0$, $\phi(x) = A$, $\underline{\phi}_M(x) = \hat{M}(x) > 0$, thus

$$-c\underline{\phi}_F' - D\underline{\phi}_F'' - r v_E \underline{\phi}_E \frac{\underline{\phi}_M}{\underline{\phi}_M + \gamma \phi} + \mu_F \underline{\phi}_F = -r v_E \hat{E} \frac{\hat{M}}{\hat{M} + \gamma A} \leq 0.$$

At $x = y_F$, we have $\lim_{x \rightarrow y_F^-} \underline{\phi}_F'(x) = \hat{F}'(0) = -\lambda^+ F_{\varepsilon_1}^* \left(1 - \frac{c\lambda^+}{v_E + \mu_E}\right) < 0 = \lim_{x \rightarrow y_F^+} \underline{\phi}_F(x)$.

◦ **Checking for $\underline{\phi}_M(x)$:** For any $x \leq 0$, one has

$$-c\underline{\phi}_M' - D\underline{\phi}_M'' - (1-r)v_E \underline{\phi}_E + \mu_M \underline{\phi}_M = -c\hat{M}' - D\hat{M}'' - (1-r)v_E \hat{E} + \mu_M \hat{M} = 0.$$

Similarly, at $x = 0$, in both cases $\lim_{x \rightarrow 0^-} \underline{\phi}_M'(x) = \hat{M}'(0) < 0 = \lim_{x \rightarrow 0^+} \underline{\phi}_M(x)$.

It finishes the establishment of the sub-solution. \square

4.5 Construction of the traveling wave for (9) (Proof of Theorem 4)

As mentioned above, we prove the existence of traveling wave solutions using the sub and the super solutions constructed before. We underline the following

Remark 2. For a certain speed $c < 0$ and function $\phi(x - ct) = \Lambda(t, x)$ defined in (7), there exists a solution ϕ_s of equation

$$-c\phi_s' - D\phi_s'' = \phi - \mu_s \phi_s, \quad \phi_s(\pm\infty) = 0,$$

such that for $A > C_s$ large enough and $\eta > 0$ small enough, one has $\bar{\phi}_s \leq \phi_s \leq \underline{\phi}_s$ in \mathbb{R} .

Thanks to Remark 2, we are able to prove Theorem 4.

Proof of Theorem 4. First, notice that since the equation for ϕ_s is independent from the other equations, we deduce that ϕ_s exists and is provided in the proof of Lemma 2. Next, in section 4.3, we obtained that $(\overline{\phi_E}, \overline{\phi_F}, \overline{\phi_M}, \overline{\phi_s})$ is a super-solution of the original system. In section 4.4, we obtain that $(\underline{\phi_E}, \underline{\phi_F}, \underline{\phi_M}, \underline{\phi_s})$ is a sub-solution of the original system. Moreover, we have by construction that $(\underline{\phi_E}, \underline{\phi_F}, \underline{\phi_M}) \leq (\overline{\phi_E}, \overline{\phi_F}, \overline{\phi_M})$ and according to Remark 13, we have $\overline{\phi_s} \leq \phi_s \leq \underline{\phi_s}$.

By applying the comparison principle for the cooperative system (9), we deduce that there exists a traveling wave solution $(\phi_E, \phi_F, \phi_M, \phi_s)$ for system (9) with

$$(\underline{\phi_E}, \underline{\phi_F}, \underline{\phi_M}) \leq (\phi_E, \phi_F, \phi_M) \leq (\overline{\phi_E}, \overline{\phi_F}, \overline{\phi_M})$$

Thus (ϕ_E, ϕ_F, ϕ_M) converges to 0 at $+\infty$, and at $-\infty$, one has

$$(E_{\varepsilon_1}^*, F_{\varepsilon_1}^*, M_{\varepsilon_1}^*) \leq (\phi_E, \phi_F, \phi_M) < (E^*, F^*, M^*).$$

It only remains to prove by contradiction that $(\phi_E, \phi_F, \phi_M) \xrightarrow{x \rightarrow -\infty} (E^*, F^*, M^*)$.

Assume it is not the case, we denote

$$(E_*, F_*, M_*) = (\liminf_{x \rightarrow -\infty} \phi_E(x), \liminf_{x \rightarrow -\infty} \phi_F(x), \liminf_{x \rightarrow -\infty} \phi_M(x)).$$

It follows

$$\max(E^* - E_*, F^* - F_*, M^* - M_*) > 0.$$

Next, we introduce

$$\varepsilon_2 = \inf\{\varepsilon > 0 : (E_\varepsilon, F_\varepsilon, M_\varepsilon) \leq (E_*, F_*, M_*)\}.$$

Notice that by assumption $\varepsilon_2 > 0$. The end of the proof is split into three claims:

1. Prove by contradiction that $F_* - F_{\varepsilon_2}^* > \delta_F$ (where δ_F is a small positive constant),
2. Prove by contradiction that $E_* - E_{\varepsilon_2}^* > \delta_E$ (where δ_E is a small positive constant),
3. Prove by contradiction that $M_* - M_{\varepsilon_2}^* > \delta_M$ (where δ_M is a small positive constant).

Then the three steps above are in contradiction with the definition of ε_1 . Indeed, if the claims are true since the dependence of $(E_\varepsilon, F_\varepsilon, M_\varepsilon)$ with respect to ε is continuous, we deduce the existence of $\varepsilon_3 < \varepsilon_2$ such that

$$(E_{\varepsilon_2}^*, F_{\varepsilon_2}^*, M_{\varepsilon_2}^*) < (E_{\varepsilon_3}^*, F_{\varepsilon_3}^*, M_{\varepsilon_3}^*) \leq (E_*, F_*, M_*).$$

Therefore, if the claims are true, the contradiction follows and the proof is achieved.

• **Claim 1.** Assume by contradiction that $F_* = F_{\varepsilon_2}^*$. It follows the existence of a decreasing and unbounded sequence x_n such that $\phi_F(x_n) < F_{\varepsilon_2}^* + 1/n$, $\phi_F'(x_n) = 0$ and $-\phi_F''(x_n) \leq 0$. Such sequence exists because if ϕ_F' does not change its sign, it follows that ϕ_F converges and this is absurd since it can only converge to F^* . Notice that we also have by definition of ε_2 that $\phi_E(x_n) > E_{\varepsilon_2}^* + o_1(n)$ and $\phi_M(x_n) > M_{\varepsilon_2}^* + o_n(1)$. Inserting these inequalities in the equation that ϕ_F satisfies, we obtain

$$r\nu_E \phi_E(x_n) \frac{1}{1 + \gamma \phi_s(x_n) / \phi_M(x_n)} - \mu_F \phi_F(x_n) = c \phi_F'(x_n) - \Delta \phi_F(x_n) \leq 0.$$

Since $\phi_M(x_n) \geq M_* + o_n(1)$ and $\phi_s(x_n) = o_n(1)$, we deduce, thanks to (35),

$$\begin{aligned}
r\nu_E \phi_E(x_n) \frac{1}{1 + \gamma \phi_s(x_n) / \phi_M(x_n)} - \mu_F \phi_F(x_n) &> r\nu_E E_{\varepsilon_2}^* \frac{1}{1 + o_n(1)} - \mu_F F_{\varepsilon_2}^* + o_n(1) \\
&> r\nu_E E_{\varepsilon_2}^* \frac{1}{1 + o_n(1)} - r\nu_E E_{\varepsilon_2}^* \frac{1}{1 + \varepsilon_2} + o_n(1) \\
&> r\nu_E E_{\varepsilon_2}^* \frac{\varepsilon_2 - o_n(1)}{(1 + \varepsilon_2)(1 + o_n(1))} + o_n(1) \\
&> 0.
\end{aligned}$$

Taking n large enough, it follows that $F_* - F_{\varepsilon_2}^* > \delta_F$ for some positive constant δ_F .

• **Claim 2.** Assume by contradiction that $E_* = E_{\varepsilon_2}^*$. It follows the existence of a decreasing and unbounded sequence x_n such that $\phi_E(x_n) < E_{\varepsilon_2}^* + 1/n$, $\phi_E'(x_n) = 0$. Inserting this inequality in the equation satisfied by ϕ_E , we obtain as above

$$\begin{aligned}
0 &= -c\phi_E'(x_n) \\
&= r\nu_E \phi_F(x_n) \left(1 - \frac{\phi_E(x_n)}{K}\right) - (\mu_E + \nu_E)\phi_E(x_n) \\
&> r\nu_E \phi_F(x_n) \left(1 - \frac{E_{\varepsilon_2}^*}{K}\right) - r\nu_E F_{\varepsilon_2}^* \left(1 - \frac{E_{\varepsilon_2}^*}{K}\right) + o_n(1) \\
&> r\nu_E \left(1 - \frac{E_{\varepsilon_2}^*}{K}\right) [\phi_F(x_n) - F_{\varepsilon_2}^*] + o_n(1).
\end{aligned}$$

Recalling that $E_{\varepsilon_2}^* < E^* < K$ (since $\mathcal{R}_0 > 1$ and by the definition of E^*) and using claim 1, it follows the following contradiction by taking n large enough such that $o_n(1)$ is small enough

$$r\nu_E \left(1 - \frac{E_{\varepsilon_2}^*}{K}\right) [\phi_F(x_n) - F_{\varepsilon_2}^*] + o_n(1) > r\nu_E \left(1 - \frac{E_{\varepsilon_2}^*}{K}\right) \delta_F + o_n(1) > 0.$$

We conclude to the existence of a positive constant δ_E such that $E_* - E_{\varepsilon_2}^* > \delta_E$.

• **Claim 3.** Assume by contradiction that $M_* = M_{\varepsilon_2}^*$. It follows the existence of a decreasing and unbounded sequence x_n such that $\phi_M(x_n) < M_{\varepsilon_2}^* + 1/n$, $\phi_M'(x_n) = 0$ and $-\phi_M''(x_n) \leq 0$. Inserting these inequalities in the equation satisfied by ϕ_M , we obtain as above

$$\begin{aligned}
0 &\geq -c\phi_M'(x_n) - \phi_M''(x_n) \\
&= (1-r)\nu_E \phi_E(x_n) - \mu_M \phi_M(x_n) \\
&> (1-r)\nu_E \phi_E(x_n) - (1-r)\nu_E E_{\varepsilon_2}^* + o_n(1) \\
&> (1-r)\nu_E (\phi_E(x_n) - E_{\varepsilon_2}^*) + o_n(1).
\end{aligned}$$

Recalling claim 2, it follows the following contradiction by taking n large enough such that $o_n(1)$ is small enough:

$$(1-r)\nu_E (\phi_E(x_n) - E_{\varepsilon_2}^*) + o_n(1) > (1-r)\nu_E \delta_E + o_n(1) > 0.$$

We conclude to the existence of a positive constant $\delta_M > 0$ such that $M_* - M_{\varepsilon_1}^* > \delta_M$.

It concludes the proof. \square

A Proofs of Propositions 1 and 3

We recall [31, Theorem 4.2] which shows the estimate of the spreading speed c^* for the monostable system in discrete setting

$$\mathbf{u}_{n+1} = \mathcal{Q}[\mathbf{u}_n]$$

where the vector-valued function $\mathbf{u}_n(x) = (u_n^1(x), u_n^2(x), \dots, u_n^k(x))$ represents the population densities of the populations of k species at the point x and the time $n\tau$, with τ a fixed generation time. Then in section 4 of this work, the authors showed how to apply the results to a reaction-diffusion system by letting \mathcal{Q} be its time τ map. That is, replacing \mathcal{Q} by \mathcal{Q}_τ where $\mathcal{Q}_\tau[\mathbf{u}_0] := \mathbf{u}(x, \tau)$. Next, we recall the result of this work and apply it to the system (3).

Consider the system of reaction-diffusion equations $\partial_t u_i - d_i \partial_{xx} u_i = f_i(\mathbf{u})$, with $1 \leq i \leq k$ and denote $\mathbf{f} = (f_1, f_2, \dots, f_k)$. The reaction function \mathbf{f} needs to satisfy the following assumptions.

Assumptions 2.

- i. $\mathbf{f}(\mathbf{0}) = \mathbf{0}$ and there is a vector $\bar{\mathbf{u}} \gg \mathbf{0}$ such that $\mathbf{f}(\bar{\mathbf{u}}) = \mathbf{0}$ which is minimal in the sense there are no $\bar{\mathbf{v}}$ other than $\mathbf{0}$ and $\bar{\mathbf{u}}$ such that $\mathbf{f}(\bar{\mathbf{v}}) = \mathbf{0}$ and $\mathbf{0} \ll \bar{\mathbf{v}} \leq \bar{\mathbf{u}}$.
- ii. The system is cooperative, that is, $f_i(\mathbf{u})$ is nondecreasing in all components of \mathbf{u} with the possible exception of the i^{th} one.
- iii. $\mathbf{f}(\mathbf{u})$ is continuous and piecewise continuously differentiable at \mathbf{u} for $\mathbf{0} \leq \mathbf{u} \leq \bar{\mathbf{u}}$ and differentiable at $\mathbf{0}$.
- iv. The Jacobian matrix $\mathbf{f}'(\mathbf{0})$ is in Frobenius form. The principal eigenvalue $\eta_1(\mathbf{0})$ of its upper left diagonal block is positive and strictly larger than the principal eigenvalues $\eta_\sigma(\mathbf{0})$ of its other diagonal blocks, and there is at least one nonzero entry to the left of each diagonal block other than the first one.

For any positive parameter μ , if the initial data are of the form $e^{-\mu x} \mathbf{u}_0$ then the solution of this system has the form $e^{-\mu x} \mathbf{v}$, where the vector-valued function \mathbf{v} is the solution of the system of ordinary differential equations with constant coefficients $\partial_t \mathbf{v} = C_\mu \mathbf{v}$, with $\mathbf{v}(\mathbf{0}) = \mathbf{u}_0$. The coefficient matrix is given by

$$C_\mu = \text{diag}(d_i \mu^2) + \mathbf{f}'(\mathbf{0}), \quad (39)$$

and denote $\gamma_\sigma(\mathbf{0})$ the principal eigenvalue of the σ th diagonal block of the matrix C_μ . We introduce the constant

$$\bar{c} := \inf_{\mu > 0} \frac{\gamma_1(\mu)}{\mu}. \quad (40)$$

Let $\bar{\mu} \in (0, \infty]$ again denote the value of μ at which this minimum is attained, and let $\zeta(\mu)$ be the eigenvector of C_μ which correspond to the eigenvalue $\gamma_1(\mu)$. Then, the following theorem presents the main result

Theorem 18 (Theorem 4.2 in [31]). *Suppose that \mathbf{f} satisfies the Assumptions 2. Assume that either (a) $\bar{\mu}$ is finite,*

$$\gamma_1(\bar{\mu}) > \gamma_\sigma(\bar{\mu}) \text{ for all } \sigma > 1, \quad (41)$$

and

$$\mathbf{f}(\rho \zeta(\bar{\mu})) \leq \rho \mathbf{f}'(\mathbf{0}) \zeta(\bar{\mu}), \quad (42)$$

for all positive ρ ;

or

(b) *There is a sequence $\mu_v \nearrow \bar{\mu}$ such that for each v the inequalities (41) and (42) with $\bar{\mu}$ replaced by μ_v are valid.*

Then the system has a unique speed $c^ = \bar{c}$ with c^* defined in Proposition 1.*

Now we apply this theorem to system (3) with $\mathbf{f}(E, F, M) = \begin{pmatrix} \beta F \left(1 - \frac{E}{K}\right) - (v_E + \mu_E)E \\ rv_E E - \mu_F F \\ (1-r)v_E E - \mu_M M \end{pmatrix}$, and we

provide the proof as follows

Proof of Propositions 1 and 3. First, we need to show that \mathbf{f} satisfies Assumptions 2. With $\beta rv_E > \mu_F(v_E + \mu_E)$, we can deduce that \mathbf{f} has two zeros $(0, 0, 0)$, (E^*, F^*, M^*) , and satisfies (i). When $E \leq K$, one has \mathbf{f} is cooperative, thus \mathbf{f} satisfies (ii). It is easy to see that \mathbf{f} satisfies (iii). Now we only need to check the assumption (iv). The Jacobian of \mathbf{f} at $(0, 0, 0)$

$$\mathbf{f}'(\mathbf{0}) = \begin{pmatrix} -v_E - \mu_E & \beta & 0 \\ rv_E & -\mu_F & 0 \\ (1-r)v_E & 0 & -\mu_M \end{pmatrix} \quad (43)$$

is in Frobenius form with two diagonal blocks $B_1 = \begin{pmatrix} -v_E - \mu_E & \beta \\ rv_E & -\mu_F \end{pmatrix}$ and $B_2 = -\mu_M$. There is a positive entry $(1-r)v_E$ to the left of B_2 .

The block B_1 has two eigenvalues $\eta_{\pm} = \frac{-(v_E + \mu_E + \mu_F) \pm \sqrt{(v_E + \mu_E - \mu_F)^2 + 4\beta rv_E}}{2}$. Denote $\begin{pmatrix} e_{\pm} \\ f_{\pm} \end{pmatrix}$ the eigenvectors corresponding to eigenvalues η_{\pm} of B_1 . Then, one has

$$-(v_E + \mu_E)e_{\pm} + \beta f_{\pm} = \frac{-(v_E + \mu_E + \mu_F) \pm \sqrt{(v_E + \mu_E - \mu_F)^2 + 4\beta rv_E}}{2} e_{\pm}.$$

So

$$\beta f_{\pm} = \frac{v_E + \mu_E - \mu_F \pm \sqrt{(v_E + \mu_E - \mu_F)^2 + 4\beta rv_E}}{2} e_{\pm}.$$

Since $\frac{v_E + \mu_E - \mu_F - \sqrt{(v_E + \mu_E - \mu_F)^2 + 4\beta rv_E}}{2} < 0$, then e_- and f_- always have different signs. Hence, η_+ is the only eigenvalue that has the corresponding positive eigenvector, and it is the principal eigenvalue of B_1 . Moreover, due to the assumption $\beta rv_E > \mu_F(v_E + \mu_E)$, one has $\eta_1(\mathbf{0}) = \eta_+ > 0 > -\mu_M = \eta_2(\mathbf{0})$. This concludes that \mathbf{f} satisfies (iv).

Now, one has the matrix

$$C_{\mu} = \begin{pmatrix} -v_E - \mu_E & \beta & 0 \\ rv_E & D\mu^2 - \mu_F & 0 \\ (1-r)v_E & 0 & D\mu^2 - \mu_M \end{pmatrix}.$$

Similarly to the matrix $\mathbf{f}'(\mathbf{0})$, the principal eigenvalue of the first block of C_{μ} is

$$\gamma_1(\mu) = \frac{D\mu^2 - v_E - \mu_E - \mu_F + \sqrt{(D\mu^2 + v_E + \mu_E - \mu_F)^2 + 4\beta rv_E}}{2}$$

By the assumption $\beta rv_E > \mu_F(v_E + \mu_E)$ and $D > 0$, we have $\gamma_1(\mu) > 0$. It is easy to see that $\frac{\gamma_1(\mu)}{\mu} \sim \frac{1}{\mu}$ when $\mu \rightarrow 0^+$, and $\frac{\gamma_1(\mu)}{\mu} \sim \mu$ when $\mu \rightarrow +\infty$. Hence, one can deduce that there exists a finite constant $\bar{\mu} \in (0, +\infty)$ such that $\frac{\gamma_1(\bar{\mu})}{\bar{\mu}} = \inf_{\mu > 0} \frac{\gamma_1(\mu)}{\mu}$.

Consider $\zeta(\bar{\mu}) = \begin{pmatrix} e \\ f \\ m \end{pmatrix}$ the eigenvector corresponding to the eigenvalue $\gamma_1(\bar{\mu})$ of $C_{\bar{\mu}}$, where $\begin{pmatrix} e \\ f \end{pmatrix}$ is the positive eigenvector associated to the principal eigenvalue $\gamma_1(\bar{\mu})$ of the first diagonal block. So $m > 0$ if and only if $\gamma_1(\bar{\mu}) > \gamma_2(\bar{\mu}) = D\bar{\mu}^2 - \mu_M$, that is

$$2\mu_M - D\bar{\mu}^2 - v_E - \mu_E - \mu_F + \sqrt{(D\bar{\mu}^2 + v_E + \mu_E - \mu_F)^2 + 4\beta r v_E} > 0. \quad (44)$$

Hence, whenever the parameters satisfy condition (44), the inequality (41) holds, the eigenvector $\zeta(\bar{\mu}) = \begin{pmatrix} e \\ f \\ m \end{pmatrix}$ is positive, and for any positive ρ , $\mathbf{f}(\rho\zeta(\bar{\mu})) - \rho\mathbf{f}(\mathbf{0})\zeta(\bar{\mu}) = \rho \begin{pmatrix} -\frac{\beta}{k}ef\rho \\ 0 \\ 0 \end{pmatrix} < 0$, then (42) holds.

Now, applying the result of Theorem 18, we obtain the spreading speed $c^* = \bar{c}$. By applying Theorem 4.1 in [31], the solution of (3) satisfies

$$\lim_{t \rightarrow +\infty} \left[\max_{|x| \geq t(c^* + \varepsilon)} \max(E, F, M)(t, x) \right] = 0,$$

if the initial data (E^0, F^0, M^0) is compactly supported and $0 \leq (E^0, F^0, M^0) \ll (E^*, F^*, M^*)$. Furthermore, for any strictly positive constant ω , there is a positive R_ω with the property that if $\min(E^0, F^0, M^0) \geq \omega$ on an interval of length $2R_\omega$, then

$$\lim_{t \rightarrow +\infty} \left[\max_{|x| \leq t(c^* - \varepsilon)} \max(E^* - E, F^* - F, M^* - M)(t, x) \right] = 0.$$

Moreover, Proposition 3.3 in the work of Lui [23] provides, in a discrete setting, some conditions in which the constant R_ω can be chosen to be arbitrarily small and independent of ω . This result can be transposed to the continuous case like what has been done in section 4 of [31] and it is simple to verify that, when $\min E_0 > 0$ or $\min F_0 > 0$, our system satisfies those conditions so we leave it to the readers. Hence, by applying this result, we deduce that if the initial data E^0 or F^0 are strictly positive on a set with a positive measure, then the result in Proposition 1 holds.

Now, to prove Proposition 3, the paper [15] provides some conditions in which the spreading speed estimated in [31] of the monostable system is the minimum speed of the traveling wave. The authors in [5] have checked all the conditions for the same system as (3), hence we obtain the same result for our system. \square

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