CSIAM Trans. Life Sci.
doi: 10.4208/csiam-ls.SO-2025-0004

Vol. **x**, No. x, pp. 1-29
xx 2025

Effect of Interspecific Mosquito Competition on Mosquito Suppression with Sterile Mosquitoes

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Received 17 March 2025; Accepted 3 October 2025

In Honor of Professor Zhien Ma's 90th Birthday

Abstract. In the interactive dynamical models, we include two different competing wild mosquito species and sterile mosquitoes which are the same type as one of the competing wild mosquitoes. We study the dynamics of the interspecific competition models in different circumstances. We explore how the interspecific competition affects the wild mosquito control with releases of sterile mosquitoes and establish a new release threshold based on the effect of the competition. Numerical examples are provided in each case to illustrate the impact on the mosquito control.

AMS subject classifications: 34C60, 34D20, 92D25, 92D30, 92D40, 92D45

Key words: Sterile mosquitoes, mosquito population suppression, thresholds, interspecific competition, nullclines.

1 Introduction

In applying the sterile insect technique (SIT) [1–4, 8, 27] to mosquito control, the focus has been on a specific species of mosquitoes such as Aedes aegypti, or Aedes albopictus, and the released engineered sterile mosquitoes are of the same type. As a result, the effect of interspecific interactions between different mosquitoes species have been ignored. Accordingly, while a good number of various mathematical models based on ordinary,

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partial differential equations, or difference equations have been formulated and investigated, modeling studies have basically been focused on only the interactive dynamics of the same type of wild and sterile mosquitoes [2,6,12–14,17–21,26,28–32,34].

There are over 3,500 mosquito species on Earth and over 200 types of mosquitoes live in the continental United States and US territories. Among those, about 12 types spread germs that can make people sick [7,11]. Note that interspecific competitions are ubiquitous in the biological world and occur between two or more different mosquitoes which often have an influence on the dynamics of mosquito populations. For example, both Aedes aegypti and Anopheles stepehensi are container breeding mosquitoes and co-exist which may result in larval competition [10]. When Aedes albopictus develops larvae in the eastern United States, it commonly co-occurs with resident mosquitoes, most notably the eastern tree-hole mosquito, Aedes triseriatus, which results in interspecific competitions [15, 16, 25]. Aedes albopictus and Culex pipiens larvae living in the same breeding site compete for resources [23]. The spatial distributions of Aedes aegypti and Aedes albopictus frequently overlap that creates interspecific competition due to the limitation of food supply [22]. Thus, when we utilize SIT to suppress and eradicate the mosquitoes that spread mosquito-borne diseases and establish strategies of release of sterile mosquitoes, the interspecific competitions cannot be ignored and their effects need to be well understood and investigated.

To have better understanding of such effects, mathematical models have been formulated in [33] where two mosquito species w and z compete for limited resources and the interspecific competition is described by a Lotka-Volterra competition system. Sterile mosquitoes of the same type as w are released to interact with mosquitoes w and, as a result, with z too, even not purposely. How the releases of sterile mosquitoes impact the ecology of the interspecific competition is investigated in [33]. In this study, we focus on how the interspecific competition affects the release threshold and the interactive dynamics of the mosquitoes. We refine the model for interactive wild and sterile mosquitoes and the interspecific competition model in Sections 2 and 3, respectively. We give further mathematical analysis for the model with the interspecific competition and the interactive sterile mosquitoes in Section 4. We provide, for each category, numerical examples to illustrate our findings. We give detailed discussions to show how the inclusion of interspecific competition affects the model dynamics of the interactive wild and sterile mosquitoes mathematically as well as biologically in Section 5.

2 Interactive model with wild and sterile mosquitoes of same type of species

We first consider a species of wild mosquitoes living in the field and assume that the population dynamics of the species are governed by the following logistic-type equation:

$$\frac{dw}{dt}=\alpha_w(1-\xi_w w)w-\mu_w w,$$

where w is the population size of the mosquitoes, α_w is the number of offspring produced per mosquito, ξ_w is the carrying capacity parameter such that $1-\xi_w w$ represents the density-dependent larvae stage progression rate. Let

$$r_w := \frac{\alpha_w - \mu_w}{\alpha_w} \tag{2.1}$$

be the normalized intrinsic growth rates of the population. The model equation can be written as

$$\frac{dw}{dt} = \alpha_w (r_w - \xi_w w) w. \tag{2.2}$$

Assume $\alpha_w > \mu_w$ so that $r_w^0 > 0$. The zero solution of (2.2) is unstable and there exists a unique positive equilibrium

$$w^e = \frac{r_w}{\xi_w},$$

which is globally asymptotically stable.

We assume that sterile mosquitoes of the same type of species are constantly released into the field. Using the same modeling idea as in [28–32], we only include those sexually active sterile mosquitoes such that no separate dynamical equation for the sterile mosquitoes is needed. Let $b>0$ be the number of released sterile mosquitoes at time t. Then, we have the following interactive model for the wild and sterile mosquitoes of the same species ([14, 18]):

$$\frac{dw}{dt} = \frac{\alpha_w w}{w+b}(1-\xi_w w)w - \mu_w w. \tag{2.3}$$

The zero equilibrium of (2.3) is locally asymptotically stable. A positive equilibrium satisfies the equation

$$F_1(w) = -\alpha_w \xi_w w^2 + (\alpha_w - \mu_w) w - \mu_w b = -\alpha_w \xi_w w^2 + r_w \alpha_w w - \mu_w b = 0. \tag{2.4}$$

Define the release threshold of sterile mosquitoes by

$$b_w := \frac{\alpha_w r_w^2}{4\mu_w \xi_w} > 0, \tag{2.5}$$

where r_w is given in (2.1). Then the dynamics of model (2.3) can be described as follows.

Theorem 2.1. *For model* (2.3) *with the interactive wild and sterile mosquitoes of the same type species w, define the release threshold b_w of the sterile mosquitoes in* (2.5). *Then*

(1) If the release rate $b > b_w$, no positive equilibrium exists and the zero solution $w=0$ is globally asymptotically stable which implies that the wild mosquitoes of species w are completely eradicated.

(2) If the release rate $b=b_w$, there exists a unique positive equilibrium

$$w_e^* := \frac{r_w}{2\xi_w}, \tag{2.6}$$

which is unstable or semi-stable. Solutions with initial values less than w_e^* approach zero and solutions with initial values greater than w_e^* approach w_e^*.

(3) If the release rate $b<b_w$, there exist the following two positive equilibria, which are the positive roots of $F_1(w)$ given in (2.4)*:*

$$w_e^{\mp} := \frac{r_w\alpha_w \mp \sqrt{r_w^2\alpha_w^2 - 4\alpha_w\xi_w\mu_w b}}{2\alpha_w\xi_w} = \frac{\sqrt{\alpha_w}r_w \mp 2\sqrt{\xi_w\mu_w}\sqrt{b_w-b}}{2\sqrt{\alpha_w}\xi_w}. \tag{2.7}$$

Equilibrium w_e^- is unstable and w_e^+ is locally asymptotically stable. In this case, the zero solution $w=0$ is locally asymptotically stable. Solutions approach either the zero solution or w_e^+ depending on their initial values. Wild mosquitoes w can either be eradicated or survive.

The proof of Theorem 2.1 is similar to that in [14,18] and thus is omitted.

3 Competition model without sterile mosquitoes

We then assume that another mosquito species living in the same area compete with species w. We denote their population size by z.

Note that mosquitoes undergo complete metamorphosis going through four distinct stages of development during a lifetime [5]. Since the food resource limitation mainly happens in water, the interspecific competition basically occurs in the aquatic stages. We thus only assume density dependence in the larvae progression process and ignore the competition between the adults. Then the interaction between the two mosquito species is described by the following system:

$$\begin{aligned} \frac{dw}{dt} &= \alpha_w(1-\xi_w w - k_1 z)w - \mu_w w, \\ \frac{dz}{dt} &= \alpha_z(1-\xi_z z - k_2 w)z - \mu_z z, \end{aligned} \tag{3.1}$$

where, similarly to (2.3), α_z is the number of offspring produced per mosquito, ξ_z is the carrying capacity parameter such that $1-\xi_z z$ represents the density-dependent larvae stage progression, and μ_z is the death rate for mosquito species z. Moreover, parameters $k_i, i=1,2$, characterize the competition between species w and z.

Similarly to (2.1), we let

$$r_z = \frac{\alpha_z - \mu_z}{\alpha_z}$$

be the normalized intrinsic growth rate of species z. System (3.1) then becomes

$$\begin{aligned} \frac{dw}{dt} &= \alpha_w (r_w - \xi_w w - k_1 z) w, \\ \frac{dz}{dt} &= \alpha_z (r_z - \xi_z z - k_2 w) z. \end{aligned} \tag{3.2}$$

We assume $r_w > 0$ and $r_z > 0$ such that the trivial equilibrium $(0,0)$ of (3.2) is an unstable node.

System (3.2) is a standard Lotka-Volterra competition model which has four ecologically feasible outcomes [9,24]. They can be summarized in Fig. 1 and in Theorem 3.1.

Theorem 3.1. *(1) If*

$$\frac{r_w}{\xi_w} < \frac{r_z}{k_2} \quad \text{and} \quad \frac{r_w}{k_1} < \frac{r_z}{\xi_z},$$

system (3.2) *has no positive equilibrium. Boundary equilibrium $E_1 := (0, r_z/\xi_z)$ is globally asymptotically stable. All solutions approach E_1 regardless of their initial values. Thus, the competitive exclusion occurs and species z is the winner of the competition, as shown in Fig.* 1(a).

(2) If

$$\frac{r_w}{\xi_w} > \frac{r_z}{k_2} \quad \text{and} \quad \frac{r_w}{k_1} > \frac{r_z}{\xi_z},$$

system (3.2) *has no positive equilibrium and boundary equilibrium $E_2 := (r_w/\xi_w, 0)$ is globally asymptotically stable. All solutions approach E_2 regardless their initial values. Thus, again the competitive exclusion occurs and species w wins the competition, as shown in Fig.* 1(b).

(3) If

$$\frac{r_z}{k_2} < \frac{r_w}{\xi_w} \quad \text{and} \quad \frac{r_z}{\xi_z} > \frac{r_w}{k_1},$$

there exists a unique positive equilibrium E_3 which is an unstable saddle. Equilibria E_1 and E_2 are both locally asymptotically stable. Solutions approach either E_1 or E_2 depending on their initial values such that either species w or z wins the competition, depending on their initial population sizes. The two species cannot coexist, as shown in Fig. 1(c).

(4) If

$$\frac{r_w}{\xi_w} < \frac{r_z}{k_2} \quad \text{and} \quad \frac{r_w}{k_1} > \frac{r_z}{\xi_z},$$

the positive equilibrium E_3 exists and is globally asymptotically stable. All solutions approach E_3 regardless of their initial values. That is, the two species coexist no matter what their initial population sizes are, as shown in Fig. 1(d).

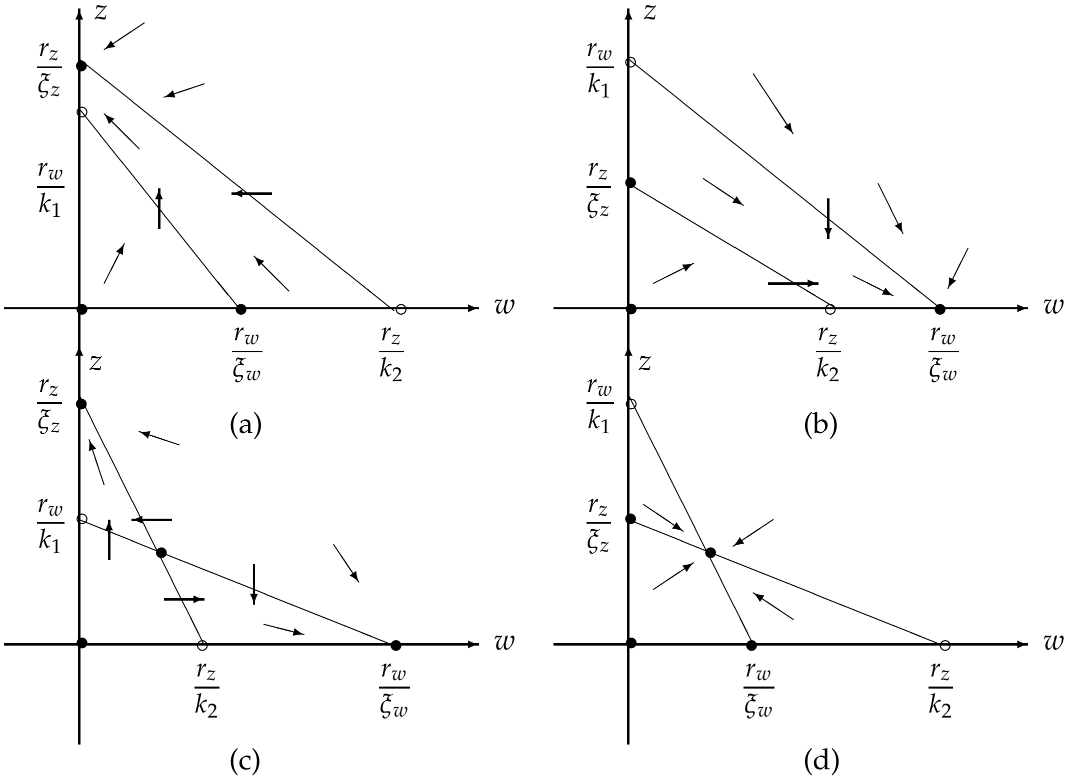

Figure 1: Schematic diagram of the phase plane for system (3.2).

4 Model with competing wild mosquitoes and sterile mosquitoes

We now assume that a constant number b of sterile mosquitoes of the same type of w are released into the field. They basically only mate with wild mosquitoes w directly, but in reality, they interact with species z as well. We assume there is no interspecific mating. Then the interactive dynamics of wild and sterile mosquitoes are governed by the following system:

$$\begin{aligned} &\frac{dw}{dt}=\frac{\alpha_w w}{w+b}(1-\xi_w w-k_1 z)w-\mu_w w=-\frac{w}{w+b}\big(\alpha_w\xi_w w^2-r_w\alpha_w w+\mu_w b+k_1\alpha_w wz\big),\\ &\frac{dz}{dt}=\alpha_z(r_z-\xi_z z-k_2 w)z. \end{aligned} \tag{4.1}$$

It is clear that the first quadrant of the wz-plane is a positively invariant for (4.1), and the trivial equilibrium $(0,0)$ is an unstable saddle point. Thus, it is impossible to have the two wild mosquito species both go extinct.

Before proceeding to investigate the dynamics of system (4.1), we establish the following lemma for the existence and stability of interior positive equilibria.

Lemma 4.1. *(1) If* $\xi_w\xi_z<k_1k_2$ *and*

$$w^u=\frac{\alpha_w(r_w\xi_z-k_1r_z)-\sqrt{\Delta}}{2\alpha_w(\xi_w\xi_z-k_1k_2)}<\frac{r_z}{k_2}, \tag{4.2}$$

where

$$\Delta:=\alpha_w^2(r_w\xi_z-k_1r_z)^2-4\alpha_w\mu_w\xi_z(\xi_w\xi_z-k_1k_2)b>0, \tag{4.3}$$

then system (4.1) *has a unique interior positive equilibrium* $\bar{E}^u=(w^u,z^u)$ *with* $z^u=(r_z-k_2w^u)/\xi_z$*. It is an unstable saddle point.*

(2) If $\xi_w\xi_z>k_1k_2$ *and* $r_w\xi_z\le k_1r_z$*, system* (4.1) *has no interior positive equilibrium.*

(3) Suppose $\xi_w\xi_z>k_1k_2$ *and* $r_w\xi_z>k_1r_z$*. We define another release threshold*

$$b_p:=\frac{\alpha_w(r_w\xi_z-k_1r_z)^2}{4\mu_w\xi_z(\xi_w\xi_z-k_1k_2)}. \tag{4.4}$$

Then

(A) If $b>b_p$*, there exists no interior positive equilibrium.*

(B) If $b=b_p$ *and*

$$w^*=\frac{r_w\xi_z-k_1r_z}{2(\xi_w\xi_z-k_1k_2)}<\frac{r_z}{k_2}, \tag{4.5}$$

there exists a unique interior positive equilibrium $\bar{E}^*=(w^*,z^*)$ *of system* (4.1)*, where* $z^*=(r_z-k_2w^*)/\xi_z$*. It is semi-stable.*

(C) If $b<b_p$*, then*

(C1) There exist two interior positive equilibria $\bar{E}_3^-=(w_1^-,z_1^-)$ *and* $\bar{E}_3^+=(w_1^+,z_1^+)$ *of system* (4.1)*, where*

$$w_1^{\mp}=\frac{\alpha_w(r_w\xi_z-k_1r_z)\mp\sqrt{\Delta}}{2\alpha_w(\xi_w\xi_z-k_1k_2)},\quad z_1^{\mp}=\frac{r_z-k_2w_1^{\mp}}{\xi_z}, \tag{4.6}$$

provided

$$w_1^+<\frac{r_z}{k_2}.$$

Equilibrium $\bar{E}_3^-$ *is an unstable saddle point, and* $\bar{E}_3^+$ *is a locally asymptotically stable node.*

(C2) Equilibrium $\bar{E}_3^-=(w_1^-,z_1^-)$ *is a unique interior equilibrium of system* (4.1) *provided*

$$w_1^-<\frac{r_z}{k_2}<w_1^+.$$

This unique interior positive equilibrium is an unstable saddle point.

Proof. Define the right-hand sides of system (4.1) as the following two functions:

$$\begin{aligned}&G_1(w,z):=-\frac{w}{w+b}\left(\alpha_w\xi_w w^2-r_w\alpha_w w+\mu_w b+k_1\alpha_w wz\right),\\&G_2(w,z):=\alpha_z z(r_z-\xi_z z-k_2 w).\end{aligned}$$

The positive component w of an interior equilibrium of system (4.1) satisfies

$$G_1\left(w,\frac{r_z-k_2w}{\xi_z}\right)=-\frac{w}{w+b}\left(\alpha_w\xi_w w^2-r_w\alpha_w w+\mu_w b+k_1\alpha_w w\frac{r_z-k_2w}{\xi_z}\right)=0,$$

that is,

$$\Phi(w):=\alpha_w(\xi_w\xi_z-k_1k_2)w^2-\alpha_w(r_w\xi_z-k_1r_z)w+\mu_w\xi_z b=0 \tag{4.7}$$

for $w>0$.

(1) If $\xi_w\xi_z<k_1k_2$, there exists a unique positive solution w^u of (4.7) given in (4.2). If $w^u<r_z/k_2$, there exists a unique interior positive equilibrium of system (4.1). In the meantime, there exists another negative solution of (4.7), denoted by $-\tilde{w}$ such that

$$\Phi(w)=\alpha_w(\xi_w\xi_z-k_1k_2)(w-w^u)(w+\tilde{w})=0. \tag{4.8}$$

To determine the local stability of an interior positive equilibrium of system (4.1), we use linearization as follows.

At an equilibrium of (4.1), its Jacobian matrix is

$$J=\begin{pmatrix}J_{11} & J_{12}\\ J_{21} & J_{22}\end{pmatrix},$$

where

$$\begin{aligned}&J_{11}=-\frac{w}{w+b}(2\alpha_w\xi_w w-r_w\alpha_w+k_1\alpha_w z), && J_{12}=-\frac{w}{w+b}k_1\alpha_w w,\\&J_{21}=-\alpha_z k_2 z, && J_{22}=-\alpha_z\xi_z z.\end{aligned}$$

Then

$$\begin{aligned}\frac{w+b}{\alpha_z wz}\det J&=\xi_z\left(2\alpha_w\xi_w w-r_w\alpha_w+k_1\alpha_w\frac{r_z-k_2w}{\xi_z}\right)-k_1k_2\alpha_w w\\&=2\alpha_w\xi_w\xi_z w-r_w\alpha_w\xi_z+k_1\alpha_w r_z-k_1k_2\alpha_w w-k_1k_2\alpha_w w\\&=2\alpha_w(\xi_w\xi_z-k_1k_2)w-\alpha_w(r_w\xi_z-k_1r_z)\\&=\Phi'(w).\end{aligned} \tag{4.9}$$

For the stability of the interior positive equilibrium $\bar{E}^u=(w^u,z^u)$, it follows from (4.8) and (4.9) that

$$\det J|_{\bar{E}^u}=\frac{\alpha_z w^u z^u}{w^u+b}\Phi'(w^u)=\frac{\alpha_z w^u z^u\alpha_w(\xi_w\xi_z-k_1k_2)}{w^u+b}(w^u+\tilde{w})<0.$$

Thus, $\bar{E}^u=(w^u,z^u)$ is an unstable saddle point.

(2) It is clear that the nonexistence of a positive equilibrium for the case of $\xi_w\xi_z > k_1k_2$ and $r_w\xi_z \le k_1r_z$ follows directly.

(3) Suppose $\xi_w\xi_z > k_1k_2$ and $r_w\xi_z > k_1r_z$. Cases (A) and (B) are easy to verify and their proofs are omitted. We focus on the case (C) and assume $b < b_p$. Then $\Delta > 0$ and clearly there are two positive roots of $\Phi(w) = 0$, given in (4.6).

For case (C1), we have $w_1^{\mp} < r_z/k_2$ and thus $z_1^{\mp} > 0$, which verifies the existence of two interior positive equilibria. We then show their stability.

It follows from

$$\Phi(w) := \alpha_w(\xi_w\xi_z - k_1k_2)(w - w_1^-)(w - w_1^+) \tag{4.10}$$

that

$$\Phi'(w_1^-) < 0, \quad \Phi'(w_1^+) > 0,$$

and then, from (4.9),

$$\det J|_{\bar{E}_3^-} < 0, \quad \det J|_{\bar{E}_3^+} > 0.$$

Hence, $\bar{E}_3^-$ is an unstable saddle point.

It follows from (4.9) that $\det J|_{\bar{E}_3^+} > 0$ which implies

$$2\alpha_w\xi_w w - r_w\alpha_w + k_1\alpha_w\frac{r_z - k_2w}{\xi_z} > 0.$$

Hence, $J_{11} < 0$ and then the trace of the Jacobian matrix at $\bar{E}_3^+$ is negative. Thus, equilibrium $\bar{E}_3^+$ is a locally asymptotically stable node.

For case (C2), since $w_1^- < r_z/k_2 < w_1^+$, then $z_1^- > 0$ and $z_1^+ < 0$. Thus, $\bar{E}_3^- = (w_1^-, z_1^-)$ is the only interior positive equilibrium for system (4.1). It follows from (4.10) again that

$$\det J|_{\bar{E}_3^-} = \frac{\alpha_z w_1^- z^u \alpha_w(\xi_w\xi_z - k_1k_2)}{w_1^- + b}(w_1^- - w^+) < 0.$$

Hence, $\bar{E}_1^- = (w_1^-, z_1^-)$ is an unstable saddle point.

The proofs for all cases are complete. □

4.1 Model dynamics

We explore the model dynamics of (4.1) via phase-plane analysis in this section. The following two functions determine the nullclines of system (4.1):

$$-\left(\alpha_w\xi_w w^2 - r_w\alpha_w w + \mu_w b + k_1\alpha_w wz\right) = 0, \tag{L1}$$

$$r_z - \xi_z z - k_2 w = 0. \tag{L2}$$

Solving (L1) for z in terms of w, we obtain

$$z := H_1(w) = -\frac{1}{k_1\alpha_w w}\left(\alpha_w\xi_w w^2 - r_w\alpha_w w + \mu_w b\right) = \frac{F_1(w)}{k_1\alpha_w w},$$

where $F_1(w)$ is given in (2.4). Function $H_1(w)$ is concave downward and its graph is similar to that of $F_1(w)$. In fact, it is easy to check that $H_1''(w)<0$ with a unique positive hump. Thus, with the same threshold b_w defined in (2.5), equation $H_1(w)=0$ has no positive root if $b>b_w$, a unique positive root $w=w_e^*$, given in (2.6), if $b=b_w$, and two positive roots $w_e^{\mp}$, given in (2.7), if $b<b_w$. We further investigate their dynamics, respectively, as follows.

4.1.1 $b>b_w$

We first assume $b>b_w$. Then the only nontrivial equilibrium of system (4.1) is the boundary equilibrium

$$\bar{E}_1=\left(0,\frac{r_z}{\xi_z}\right). \tag{4.11}$$

Its Jacobian matrix is

$$\begin{pmatrix} -\mu_w & 0 \\ \cdot & -\alpha_z r_z \end{pmatrix},$$

and thus $\bar{E}_1$ is a locally asymptotically node. The schematic diagram is given in Fig. 2. There is no interior positive equilibrium with both coordinates positive. Then $\bar{E}_1$ is globally asymptotically stable.

The results can be summarized as follows.

Theorem 4.1. *If the release amount $b>b_w$, boundary equilibrium $\bar{E}_1$, given in* (4.11)*, is the only nontrivial equilibrium and is globally asymptotically stable. All solutions of* (4.1) *approach $\bar{E}_1$, regardless of their initial conditions. The wild mosquitoes of type w are eradicated eventually and their competing species z survive, staying at their steady state.*

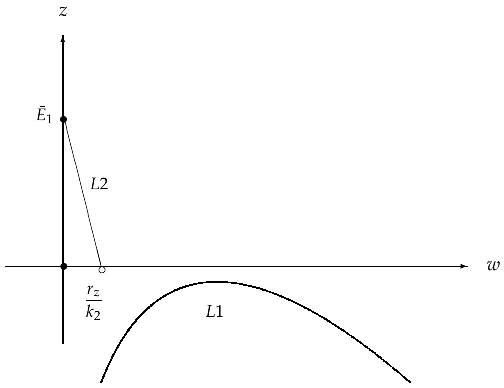

Figure 2: Schematic diagram of the phase plane for system (4.1) in the case where boundary equilibrium $\bar{E}_1$ is the only nontrivial equilibrium.

4.2 $b=b_w$

If $b=b_w$, it is clear that system (4.1) has a unique boundary equilibrium $\bar{E}^*=(w_e^*,0)$ on the w-axis. This boundary equilibrium is unstable. Since the curve of $H_1(w)$ is below the w-axis except the point where the curve is tangent to the w-axis, as shown in Fig. 3, there is no interior positive equilibrium. Boundary equilibrium $\bar{E}_1$ is globally asymptotically stable for all $w\geq 0$ and $z>0$.

We have the results summarized in Theorem 4.2.

Theorem 4.2. *If the release amount $b=b_w$, there is a unique boundary equilibrium $\bar{E}^*=(w_e^*,0)$ on the w-axis, in addition to boundary equilibrium $\bar{E}_1$. Boundary equilibrium $\bar{E}^*$ is unstable and $\bar{E}_1$ is globally asymptotically stable for all $w\geq 0$ and $z>0$. All solutions of* (4.1) *approach $\bar{E}_1$, except those with initial conditions $(w\geq w^*,z=0)$. Thus, as long as sterile mosquitoes are released, the wild mosquitoes w are eventually eradicated when their competing species z presents. Species z survives, staying eventually at their positive steady state.*

4.3 $0<b<b_w$

We now let $0<b<b_w$. Then $G_1(w,0)=0$ has two positive roots $w_e^{\mp}$, given in (2.7), and thus, there are two boundary equilibria on the w-axis

$$\bar{E}_2^-=(w_e^-,0),\quad \bar{E}_2^+=(w_e^+,0).$$

The Jacobian matrices at $\bar{E}_2^{\mp}$ are

$$\begin{pmatrix} \lambda_1^{\mp} & \cdot \\ 0 & -\lambda_2^{\mp} \end{pmatrix},$$

where

$$\lambda_1^{\mp}=\frac{\partial G_1}{\partial w}\bigg|_{w_e^{\mp}},\quad \lambda_2^{\mp}=\alpha_z\left(r_z-k_2w_e^{\mp}\right)=\alpha_z k_2\left(\frac{r_z}{k_2}-w_e^{\mp}\right). \tag{4.12}$$

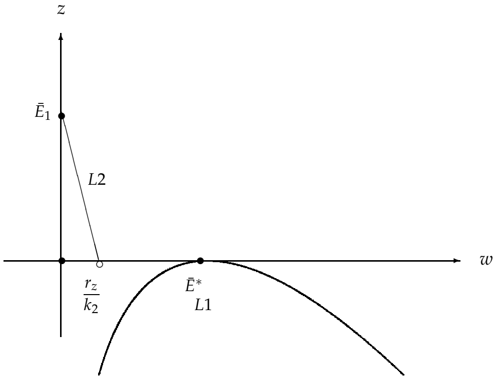

Figure 3: Schematic diagram of the phase plane for system (4.1) in the case where there exists a unique boundary equilibrium $\bar{E}^*$ on the w-axis in addition to boundary equilibrium $\bar{E}_1$.

It follows from

$$\begin{aligned} G_1(w,z) &= -\frac{w}{w+b}\left(\alpha_w\xi_w w^2 - r_w\xi_w w + \mu_w b + k_1\alpha_w wz\right) \\ &= -\frac{\alpha_w\xi_w w}{w+b}(w-w_e^-)(w-w_e^+) - \frac{k_1\alpha_w w^2 z}{w+b} \end{aligned}$$

that

$$\begin{aligned} \left.\frac{\partial G_1}{\partial w}\right|_{\bar{E}_2^-} &= -\frac{\alpha_w\xi_w w_e^-}{w_e^-+b}(w_e^- - w_e^+) > 0, \\ \left.\frac{\partial G_1}{\partial w}\right|_{\bar{E}_2^+} &= -\frac{\alpha_w\xi_w w_e^+}{w_e^++b}(w_e^+ - w_e^-) < 0. \end{aligned}$$

Thus,

$$\lambda_1^- > 0, \quad \lambda_1^+ < 0.$$

The signs of $\lambda_2^\mp$ clearly depend on the positions of $w_e^\mp$ relative to r_z/k_2. Moreover, the existence of interior positive equilibria is also related to the relative positions of the two nullclines, and more specifically, to the positions between the w-intercept of line (L2) and $w_e^\mp$. We describe it in the following lemma.

Lemma 4.2. *Let $0<b<b_w$, and define*

$$b_c := b_w - \frac{\alpha_w(r_w k_2 - 2r_z\xi_w)^2}{4\xi_w\mu_w k_2^2} = \frac{r_z\alpha_w(r_w k_2 - r_z\xi_w)}{k_2^2\mu_w}.$$

Then we have

(A) $r_z/k_2 < w_e^-$ *if and only if*

$$\begin{cases} \dfrac{r_w}{\xi_w} > 2\dfrac{r_z}{k_2}, \\ b > b_c. \end{cases} \tag{4.13}$$

(B) $w_e^+ < r_z/k_2$ *if and only if*

$$\begin{cases} \dfrac{r_w}{\xi_w} < 2\dfrac{r_z}{k_2}, \\ b > b_c. \end{cases} \tag{4.14}$$

(C) $w_e^- < r_z/k_2 < w_e^+$ *if and only if*

$$b < b_c. \tag{4.15}$$

Proof. Since $0<b<b_w$, $w_e^\mp$, given in (2.7), exist. It follows from

$$2\sqrt{\alpha_w}\xi_w k_2\left(w_e^- - \frac{r_z}{k_2}\right) = \sqrt{\alpha_w}r_w k_2 - 2k_2\sqrt{\xi_w\mu_w}\sqrt{b_w-b} - 2\sqrt{\alpha_w}\xi_w r_z$$

$$\begin{aligned}
&=\sqrt{\alpha_w}(r_wk_2-2r_z\xi_w)-2k_2\sqrt{\xi_w\mu_w}\sqrt{b_w-b}\\
&=\frac{\alpha_w(r_wk_2-2r_z\xi_w)^2-4k^2\xi_w\mu_w(b_w-b)}{\sqrt{\alpha_w}(r_wk_2-2r_z\xi_w)+2k_2\sqrt{\xi_w\mu_w}\sqrt{b_w-b}}\\
&=\frac{4k_2^2\xi_w\mu_w\left(\alpha_w(r_wk_2-2r_z\xi_w)^2/(4k^2\xi_w\mu_w)-(b_w-b)\right)}{\sqrt{\alpha_w}\left(r_wk_2-2r_z\xi_w\right)+2k_2\sqrt{\xi_w\mu_w}\sqrt{b_w-b}}\\
&=\frac{4k_2^2\xi_w\mu_w(b-b_c)}{\sqrt{\alpha_w}(r_wk_2-2r_z\xi_w)+2k_2\sqrt{\xi_w\mu_w}\sqrt{b_w-b}};
\end{aligned}$$

that, if

$$\begin{cases} r_wk_2>2r_z\xi_w,\\ b>b_c,\end{cases}$$

then $w_e^->r_z/k_2$, and if

$$r_wk_2<2r_z\xi_w,$$

or

$$\begin{cases} r_wk_2>2r_z\xi_w,\\ b<b_c,\end{cases}$$

then $w_e^-<r_z/k_2$. Hence, (A) is proved.

Similarly, it follows from

$$\begin{aligned}
2\sqrt{\alpha_w}\xi_wk_2\left(w_e^+-\frac{r_z}{k_2}\right)&=\sqrt{\alpha_w}r_wk_2+2k_2\sqrt{\xi_w\mu_w}\sqrt{b_w-b}-2\sqrt{\alpha_w}\xi_wr_z\\
&=\sqrt{\alpha_w}(r_wk_2-2r_z\xi_w)+2k_2\sqrt{\xi_w\mu_w}\sqrt{b_w-b}\\
&=\frac{\alpha_w(r_wk_2-2r_z\xi_w)^2-4k^2\xi_w\mu_w(b_w-b)}{\sqrt{\alpha_w}(r_wk_2-2r_z\xi_w)-2k_2\sqrt{\xi_w\mu_w}\sqrt{b_w-b}}\\
&=\frac{4k_2^2\xi_w\mu_w(b-b_c)}{\alpha_w\left(r_wk_2-2r_z\xi_w\right)-2k_2\sqrt{\xi_w\mu_w}\sqrt{b_w-b}};
\end{aligned}$$

that, if

$$r_wk_2>2r_z\xi_w,$$

or

$$\begin{cases} r_wk_2<2r_z\xi_w,\\ b<b_c,\end{cases}$$

then $w_e^+>r_z/k_2$, and if

$$\begin{cases} r_wk_2<2r_z\xi_w,\\ b>b_c,\end{cases}$$

then $w_e^+<r_z/k_2$. The proof of (B) is complete, and the proof of (C) then follows directly. ☐

We next study the model dynamics for the cases based on Lemma 4.2.

4.3.1 $r_z/k_2 < w_e^-$

Assume that condition (4.13) in Lemma 4.2 holds such that $r_z/k_2 < w_e^-$, as schematically shown in Fig. 4. Then there exists no interior positive equilibrium.

It follows from (4.12) that $\lambda_2^\mp < 0$. Hence, boundary equilibrium $\bar{E}_2^-$ is an unstable saddle point and $\bar{E}_2^+$ is a locally asymptotically stable node. The stable manifold of $\bar{E}_2^-$ divides the nonnegative wz-plane into two regions such that solutions approach either $\bar{E}_1$ or $\bar{E}_2^+$, depending on their initial values. The results are summarized in Theorem 4.3.

Theorem 4.3. *Suppose that the release amount $b < b_w$ and condition* (4.13) *in Lemma* 4.2 *holds such that $r_z/k_2 < w_e^-$. There are two boundary equilibria $\bar{E}_2^\mp = (w_e^\mp, 0)$ on the w-axis, where $w_e^\mp$ are given in* (2.7)*, and boundary equilibrium $\bar{E}_1 = (0, r_z/\xi_z)$ on the z-axis exists. There exists no interior positive equilibrium. Boundary $\bar{E}_2^-$ is an unstable saddle point and boundary equilibria $\bar{E}_2^+$ and $\bar{E}_1$ are both locally asymptotically stable nodes. The stable manifold of $\bar{E}_2^-$ divides the nonnegative wz-plane into two regions. Solutions of* (4.1) *approach either $\bar{E}_1$ or $\bar{E}_2^+$, depending on their initial values.*

We give Example 4.1 below to confirm the results in Theorem 4.3.

Example 4.1. For given parameters

$$\begin{aligned} &\alpha_1 = 48, \quad \xi_1 = 0.12, \quad \mu_1 = 0.11, \quad k_1 = 0.16, \\ &\alpha_2 = 23, \quad \xi_2 = 0.33, \quad \mu_2 = 0.6, \quad k_2 = 0.47, \end{aligned} \tag{4.16}$$

we have

$$b_c = 677.30 < b_w = 904.93.$$

Let $b_c < b = 700 < b_w$. Then there are three boundary equilibria

$$\bar{E}_1 = (0, 2.9513), \quad \bar{E}_2^- = (2.1788, 0), \quad \bar{E}_2^+ = (6.1354, 0).$$

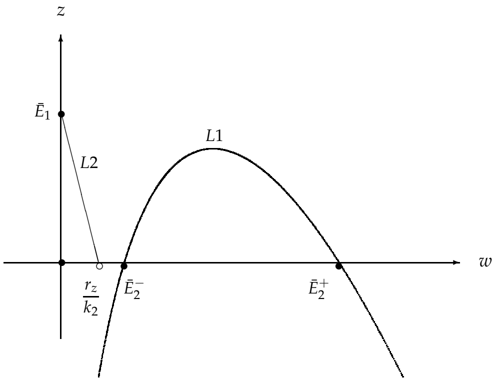

Figure 4: Schematic diagram of the phase plane for system (4.1) when there are two boundary equilibria on the w-axis, with both $w_e^\mp$ greater than r_z/k_2, and there exists no positive interior equilibrium.

Since $b > b_c$ and

$$r_w k_2 - 2 r_z \xi_w = 0.2352 > 0,$$

it follows from Lemma 4.2(A) that $r_z/k_2 = 2.0722 < w_e^- = 2.1788$. Thus, there is no interior positive equilibrium. Boundary equilibrium $\bar{E}_2^-$ is an unstable saddle point, and $\bar{E}_1$ and $\bar{E}_2^+$ are both locally asymptotically stable nodes. The stable manifold of $\bar{E}_2^-$ divides the first quadrant of wz-plane into two regions such that solutions approach either $\bar{E}_1$ or $\bar{E}_2^+$, depending on their initial values, as shown in Fig. 5.

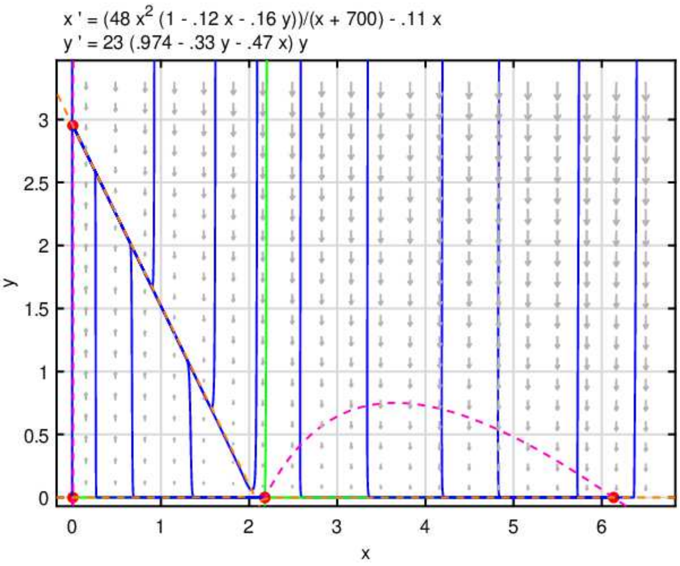

Figure 5: The parameters are given in (4.16). The w-intercept for nullcline (L2) is less than w_e^- so that there is no interior positive equilibrium. Boundary equilibrium $\bar{E}_2^-$ is an unstable saddle point and $\bar{E}_1$ and $\bar{E}_2^+$ are both locally asymptotically stable nodes. The stable manifold of $\bar{E}_2^-$ divides the first quadrant of the wz-plane into two regions such that solutions approach either $\bar{E}_1$ or $\bar{E}_2^+$, depending on their initial values.

4.3.2 $w_e^- < r_z/k_2 < w_e^+$

Suppose that condition (4.15) in Lemma 4.2(C) is satisfied such that $w_e^- < r_z/k_2 < w_e^+$. Then $\lambda_2^- > 0$ and $\lambda_2^+ < 0$, which implies that boundary equilibrium $\bar{E}_2^-$ is an unstable node and $\bar{E}_2^+$ is a locally asymptotically stable node. Since, in this case, the w-intercept of (L2) is in between w_e^- and w_e^+, there is a unique positive equilibrium $\bar{E}^u = (w^u, z^u)$, as shown in the schematic diagram in Fig. 6.

Following from Lemma 4.1, we have $b < b_p$ and either $\xi_w \xi_z < k_1 k_2$ or $\xi_w \xi_z > k_1 k_2$. In either case, the unique interior equilibrium $\bar{E}^u$ is an unstable saddle point, and its stable manifold divides the first quadrant of the wz-plane into two regions. Solutions approach either $\bar{E}_1$ or $\bar{E}_2^+$, depending on their initial values.

In summary, the dynamics of (4.1) are described in Theorem 4.4.

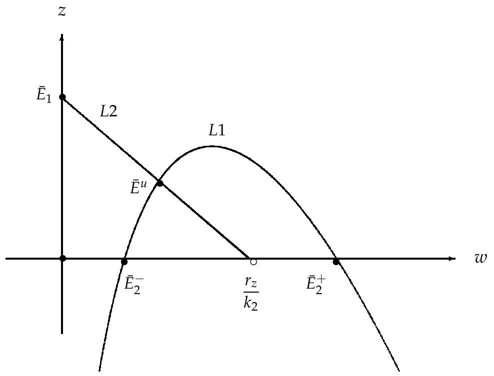

Figure 6: Schematic diagram of the phase plane for system (4.1) when r_z/k_2 is between $w_e^{\mp}$ on the w-axis such that there exists a unique non-degenerate positive interior equilibrium.

Theorem 4.4. *Suppose that the release amount $b < b_w$ and condition* (4.15) *in Lemma* 4.2(C) *is satisfied such that $w_e^- < r_z/k_2 < w_e^+$. Then boundary equilibrium $\bar{E}_2^-$ is an unstable node and $\bar{E}_2^+$ is a locally asymptotically stable node. There exists a unique interior equilibrium $\bar{E}^u = (w^u, z^u)$ with $w^- < w^u < w^+$. It follows from Lemma* 4.1*, we have $\xi_w \xi_z < k_1 k_2$ or $\xi_w \xi_z > k_1 k_2$, and $b < b_p$. In either case, the unique interior equilibrium $\bar{E}^u$ is an unstable saddle point. Its stable manifold divides the first quadrant of the wz-plane into two regions. Solutions of* (4.1) *approach either $\bar{E}_1$ or $\bar{E}_2^+$, depending on their initial values.*

We give an example below to demonstrate the model dynamics described in Theorem 4.4.

Example 4.2. For parameters given by

$$\begin{aligned} &\alpha_w = 41.26, \quad \xi_w = 0.11, \quad \mu_w = 0.45, \quad k_1 = 0.161, \\ &\alpha_z = 14.53, \quad \xi_z = 0.33, \quad \mu_z = 0.73, \quad k_2 = 0.196, \end{aligned} \tag{4.17}$$

the thresholds are $b_c = 202.63 < b_w = 203.86 < b_p = 440.70$. Let $b = 96 < b_c$. Then the boundary equilibria are

$$\bar{E}_1 = (0, 2.9972), \quad \bar{E}_2^- = (1.2256, 0), \quad \bar{E}_2^- = (7.7661, 0).$$

Since $\xi_w \xi_z - k_1 k_2 = 0.0047 > 0, r_w \xi_z - k_1 r_z = 0.1735 > 0$, and $b < b_p$, according to Lemma 4.1(3), there exist two positive solutions $w_1^- = 2.1137 < w_1^+ = 34.4566$ to equation $\Phi(w) = 0$. However, since $b < b_c$, it follows from (4.15) in Lemma 4.2(C) that

$$w_e^- = 1.2256 < \frac{r_z}{k_2} = 4.8457 < w_e^+ = 7.7661.$$

Then $\bar{E}^u = (1.2256, 2.1501)$ is the unique interior positive equilibrium of system (4.1) and is an unstable saddle point. Boundary equilibria $\bar{E}_1$ and $\bar{E}_2^+$ are both locally asymptotically stable nodes and boundary equilibrium $\bar{E}_2^-$ is an unstable node. The stable manifold of $\bar{E}^u$ divides the first quadrat of the wz-plane into two regions such that the solutions approach either $\bar{E}_1$ or $\bar{E}_2^+$, depending on their initial values, as shown in Fig. 7.

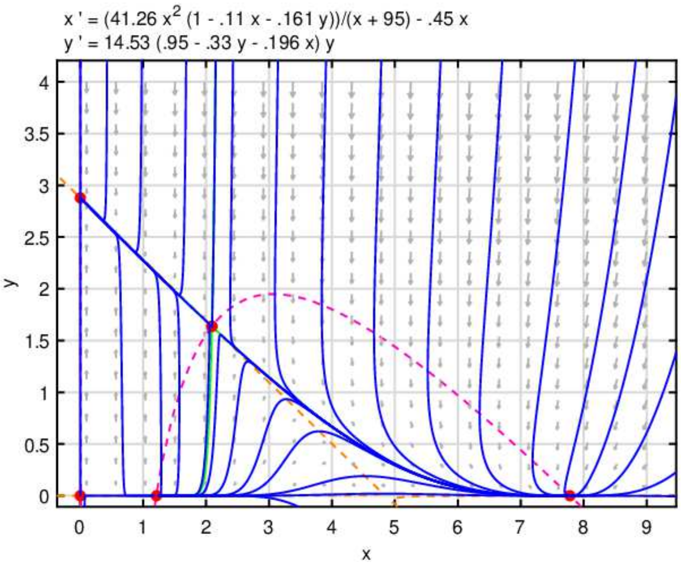

Figure 7: The parameters are given in (4.17) such that $b_c = 202.63 < b_w = 203.86 < b_p = 440.70$. For $b = 96 < b_c$, the boundary equilibria are $\bar{E}_1 = (0,2.9972), \bar{E}_2^- = (1.2256,0)$, and $\bar{E}_2^- = (7.7661,0)$. Since $r_z\xi_w = 0.1045 < k_2 r_w = 0.1939 < 2r_z\xi_w = 0.2090, w_e^- < r_z/k_2 < w_e^+$, there exists a unique positive equilibrium $\bar{E}^u = (1.2256,2.1501)$ which is an unstable saddle point. The stable manifold of $\bar{E}^u$ divides the first quadrat of the wz-plane into two regions such that the solutions approach either $\bar{E}_1$ or $\bar{E}_2^+$, depending on their initial values.

4.3.3 $w_e^+ < r_z/k_2$, $w^* < r_z/k_2$, and $b < b_p$

We assume in this section that condition (4.14) in Lemma 4.2(B) is satisfied such that $w_e^+ < r_z/k_2$. We also assume that the w-component of the point at which the two nullclines $L1$ and $L2$ are tangent satisfies $w^* < r_z/k_2$ so that this tangent point is in the first quadrant of the wz-plane. Hence, b_p in (4.4) in Lemma 4.1 is well defined, and we let $b < b_p$. Then we have the eigenvalues $\lambda_2^{\mp} > 0$ for the two boundary equilibria $\bar{E}_2^{\mp}$, which implies that $\bar{E}_2^-$ is an unstable node and $\bar{E}_2^+$ is an unstable saddle point. In addition, there exist two interior positive equilibria $\bar{E}_3^- = (w_1^-, z_1^-)$ and $\bar{E}_3^+ = (w_1^+, z_1^+)$, as schematically shown in Fig. 8. Their stabilities are determined by Lemma 4.1. We summarize the dynamics of (4.1) in Theorem 4.5.

Theorem 4.5. *Suppose that condition* (4.14) *in Lemma* 4.2(B) *is satisfied such that* $w_e^+ < r_z/k_2$. *We further assume that the w-component of the point, at which the two nullclines are tangent, satisfies* $w^* < r_z/k_2$ *so that this tangent point of the two nullclines is in the first quadrant of the wz-plane. We then let* $b < b_p$. *Thus, boundary equilibrium* $\bar{E}_2^-$ *is an unstable node and* $\bar{E}_2^+$ *is a saddle point. There exist two positive equilibria* $\bar{E}_3^- = (w_1^-, z_1^-)$ *and* $\bar{E}_3^+ = (w_1^+, z_1^+)$. *Equilibrium* $\bar{E}_3^- = (w_1^-, z_1^-)$ *is an unstable saddle point and* $\bar{E}_3^+$ *is a locally asymptotically stable node. The unstable manifold of* $\bar{E}_2^+$ *and the stable manifold of* $\bar{E}_3^-$ *divide the first quadrant of the wz-plane into two regions such that solutions approach* $\bar{E}_1$ *or* $\bar{E}_3^+$, *depending on their initial conditions.*

The following Example 4.3 illustrates the results of Theorem 4.5.

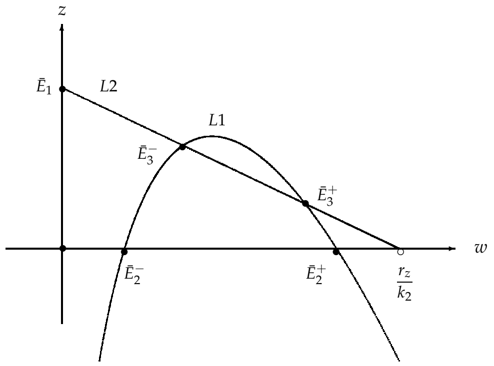

Figure 8: Schematic diagram of the phase plane for system (4.1) in the case where there exist two interior positive equilibria.

Example 4.3. For given parameters

$$\begin{aligned} &\alpha_w=50.26, \quad \xi_w=0.21, \quad \mu_w=0.148, \quad k_1=0.160,\\ &\alpha_z=14.53, \quad \xi_z=0.235, \quad \mu_z=0.112, \quad k_2=0.197, \end{aligned} \tag{4.18}$$

we have

$$b_p=136.81<b_w=401.902.$$

With $b=60<b_p$, there exist three boundary equilibria

$$\bar{E}_1=(0,4.2225), \quad \bar{E}_2^-=(0.1844,0), \quad \bar{E}_2^+=(4.5635,0).$$

Since r_wk_2=0.1964<$r_z\xi_w$=0.2084 such that b_c<0 and then condition (4.14) in Lemma 4.2(B) is satisfied, we have

$$w_e^-=0.6490<w_e^+=3.5879<\frac{r_z}{k_2}=5.0370.$$

Since, in addition, $b<b_p$, there exist two interior positive equilibria

$$\bar{E}_3^-=(0.5428,3.7675), \quad \bar{E}_3^+=(3.7876,1.0474).$$

From Lemma 4.1(3), $\bar{E}_3^-$ is a saddle point and $\bar{E}_3^+$ is a locally asymptotically stable node. Boundary equilibrium $\bar{E}_2^-$ is an unstable node and $\bar{E}_2^+$ is a saddle point. The stable manifold of $\bar{E}_3^-$ and the unstable manifold of $\bar{E}_2^+$ divide the first quadrant of the wz-plane into two regions such that solutions approach $\bar{E}_1$ or $\bar{E}_3^+$, depending on their initial conditions as shown in Fig. 9.

4.3.4 $w_e^+<r_z/k_2$, $w^*<r_z/k_2$, and $b=b_p$

Assume that condition (4.14) in Lemma 4.2(B) holds such that $w_e^+<r_z/k_2$, and that tangent point of the two nullclines is in the first quadrant of the wz-plane such that the

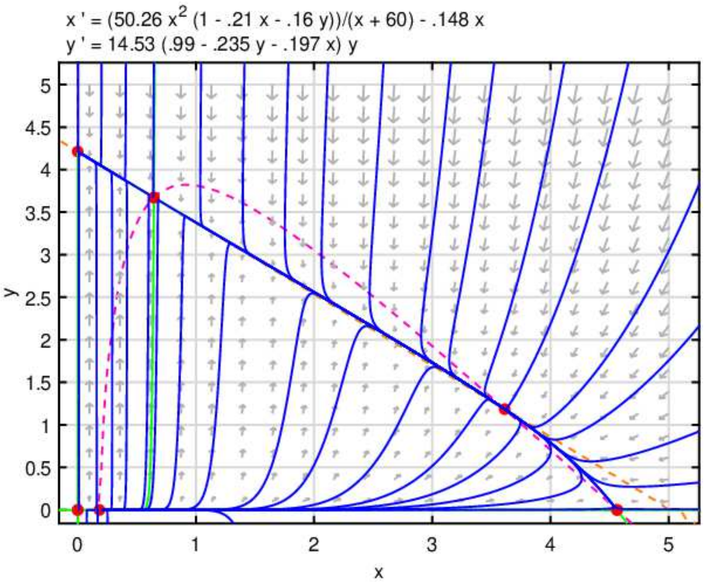

Figure 9: The parameters are given in (4.18) such that $b_p=136.81<b_w=401.902$. For $b=90$, boundary equilibrium $\bar{E}_1=(0,4.2225)$ is a locally asymptotically stable bode, $\bar{E}_2^-=(0.1844,0)$ is an unstable node, and $\bar{E}_2^+=(4.5635,0)$ is a saddle point. Since $b<b_p$ and $r_w k_2=0.1964<r_z\xi_w=0.2084$, there exist two interior positive equilibria $\bar{E}_3^-=(0.5428,3.7675)$ and $\bar{E}_3^+=(3.7876,1.0474)$ where $\bar{E}_3^-$ is a saddle point and $\bar{E}_3^+$ is a locally asymptotically stable node. The stable manifold of $\bar{E}_3^-$ and the unstable manifold of $\bar{E}_2^+$ divide the first quadrant of the wz-plane into two regions such that solutions approach $\bar{E}_1$ or $\bar{E}_3^+$, depending on their initial conditions.

w-component of the tangent point satisfies $w^*<r_z/k_2$. We let $b=b_p$. Then $w_e^+<r_z/k_2$ and the two nullclines (L1) and (L2) are tangent at the unique interior positive equilibrium $\bar{E}^*=(w^*,z^*)$, where w^* is given in (4.5) and $z^*=r_z/\xi_z$, as shown in the schematic diagram in Fig. 10.

According to Lemma 4.1, it is similar to Theorem 4.5 that boundary equilibrium $\bar{E}_2^-$ is an unstable node, and $\bar{E}_2^+$ is a saddle point. The unique interior positive equilibrium $\bar{E}^*$ is semi-stable, and boundary equilibrium $\bar{E}_1$ is asymptotically stable. All solutions approach $\bar{E}_1$ except those with initial values on the stable manifolds of $\bar{E}_2^+$ and $\bar{E}^*$. The model dynamics of (4.1) in this case can be summarized in Theorem 4.6.

Theorem 4.6. *Suppose that condition* (4.14) *in Lemma 4.2(B) is satisfied such that* $w_e^+<r_z/k_2$ *and that the tangent point of the two nullclines is in the first quadrant of the* wz*-plane with its* w*-component satisfying* $w^*<r_z/k_2$*. We let* $b=b_p$*. Then boundary equilibrium* $\bar{E}_2^-$ *is an unstable node and* $\bar{E}_2^+$ *is a saddle point. There exists a unique interior positive equilibrium* $\bar{E}^*=(w^*,z^*)$*, where* w^* *is given in* (4.5) *and* $z^*=r_z/\xi_z$*, is semi-stable. All solutions approach* $\bar{E}_1$ *except those with initial values on the stable manifolds of* $\bar{E}_2^+$ *and* $\bar{E}^*$*.*

We give an example below to demonstrate the model dynamics described in Theorem 4.6.

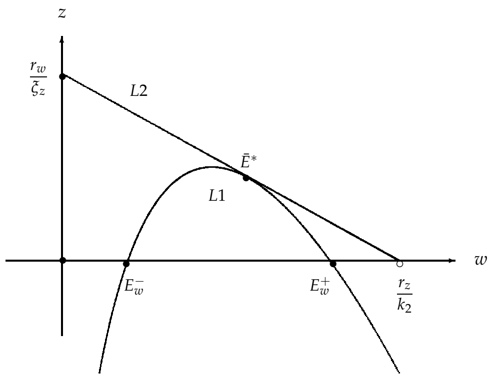

Figure 10: Schematic diagram of the phase plane for system (4.1) when r_z/k_2 is on the right of the two boundary equilibria on the w-axis but $b=b_p$ such that there exists a unique degenerate positive interior equilibrium.

Example 4.4. For parameters given by

$$\begin{aligned} &\alpha_w=38, \quad \xi_w=0.32, \quad \mu_w=0.11, \quad k_1=0.16, \\ &\alpha_z=41, \quad \xi_z=0.33, \quad \mu_z=0.82, \quad k_2=0.078, \end{aligned} \tag{4.19}$$

the thresholds are $b_p=80.38<b_w=268.86$. Let $b=b_p$. The boundary equilibria are

$$\bar{E}_1=(0,3.0215), \quad \bar{E}_2^-=(0.2645,0), \quad \bar{E}_2^+=(2.8514,0).$$

Since $w_e^+=2.8514<r_z/k_2=12.5641$ and $b=b_p$, the two nullclines (L1) and (L2) are tangent at the unique interior positive equilibrium $\bar{E}^*=(0.9248,2.7511)$, which is the unique positive interior equilibrium of system (4.1) and is semi-stable. Boundary equilibrium $\bar{E}_2^-$ is an unstable node, $\bar{E}_2^+$ is a saddle point, and $\bar{E}_1$ is a locally asymptotically stable node. All solutions approach $\bar{E}_1$ except those with initial values on the stable manifolds of $\bar{E}_2^+$ and $\bar{E}^*$, as shown in Fig. 11.

4.3.5 $w_e^+<r_z/k_2$, $w^*<r_z/k_2$, and $b>b_p$

Suppose that condition (4.14) in Lemma 4.2(B) is satisfied such that $w_e^+<r_z/k_2$ and that the tangent point of the two nullclines is in the first quadrant of the wz-plane with its w-component satisfying $w^*<r_z/k_2$, but now we let $b>b_p$, as shown in the schematic diagram in Fig. 12.

There exists no interior positive equilibrium. It follows from (4.12) that $\lambda_2^{\mp}>0$. Thus, boundary equilibrium $\bar{E}_2^-$ is an unstable node and $\bar{E}_2^+$ is a saddle point. All solutions approach $\bar{E}_1$, for $w>0$, $z\geq 0$. We summarize these results in Theorem 4.7.

Theorem 4.7. *Suppose that condition* (4.14) *in Lemma* 4.2(B) *is satisfied such that* $w_e^+<r_z/k_2$ *and that the tangent point of the two nullclines is in the first quadrant of the wz-plane with its w-component satisfying* $w^*<r_z/k_2$*, but* $b>b_p$*. There exists no interior positive equilibrium.*

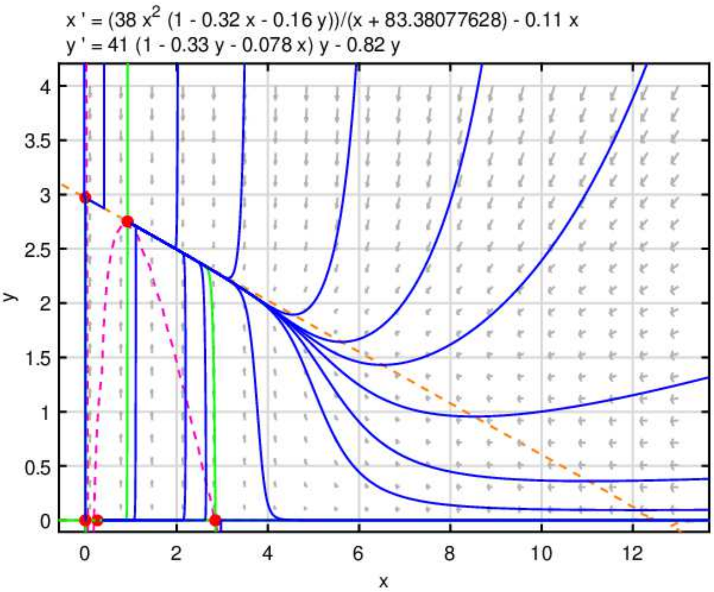

Figure 11: The parameters are given in (4.19) such that b_p=80.38<b_w=268.86. Let b=b_p. Boundary equilibrium $\bar{E}_1=(0,3.0215)$ is a asymptotically stable node, $\bar{E}_2^-=(0.2645,0)$ is an unstable node, and $E_2^+=(2.8514,0)$ is a saddle point.There exists a unique interior positive equilibrium $\bar{E}^*=(0.9248,2.7511)$, which is semi-stable. Solutions approach $\bar{E}_1$ except those with initial values on the stable manifolds of $\bar{E}_2^+$ and $\bar{E}^*$.

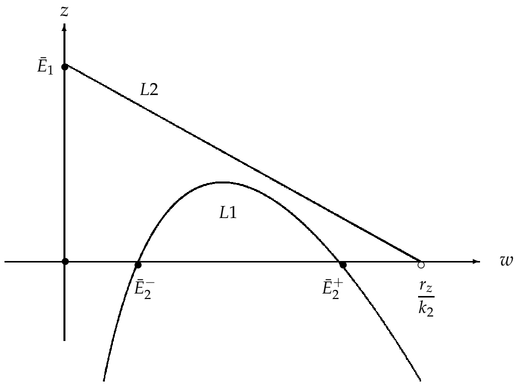

Figure 12: Schematic diagram of the phase plane for system (4.1) when there are two boundary equilibria on the w-axis, both less than r_z/k_2, such that there exists no interior equilibrium.

Boundary equilibrium $\bar{E}_2^-=(w_e^-,0)$ *is an unstable node, and* $\bar{E}_2^+=(w_e^+,0)$ *is a saddle point. Boundary equilibrium* $\bar{E}_1=(0,r_z/\xi_z)$ *is a globally asymptotically stable node for* $w\geq 0$ *and* $z>0$. *Wild mosquitoes of type w are all eradicated as long as their competitors present. Their competing species z stay at their steady state.*

Example 4.5 below demonstrates the results of Theorem 4.7.

Example 4.5. Give parameters

$$\begin{aligned}&\alpha_1=38, \quad \xi_1=0.12, \quad \mu_1=0.11, \quad k_1=0.16,\\ &\alpha_2=41, \quad \xi_2=0.33, \quad \mu_2=0.82, \quad k_2=0.39\end{aligned} \tag{4.20}$$

such that

$$b_c=167.54<b_p=179.73<b_w=268.33.$$

Let $b_p<b=200<b_w$. Then there are three boundary equilibria

$$\bar{E}_1=(0,2.9697), \quad \bar{E}_2^-=(0.7718,0), \quad \bar{E}_2^+=(2.3442,0).$$

Since now

$$r_z\xi_w=0.3136<2r_z\xi_w=0.6272,$$

it follows from (4.14) Lemma 4.2(B) that $w_e^+=2.3442<r_z/k_2=2.5128$. There is no interior positive equilibrium. Boundary equilibrium $\bar{E}_2^-$ is an unstable node, $\bar{E}_2^+$ is a saddle point, and $\bar{E}_1$ is a globally asymptotically stable node for $w\geq 0$ and $z>0$. All solutions with $z>0$ approach $\bar{E}_1$ as shown in the right figure in Fig. 13.

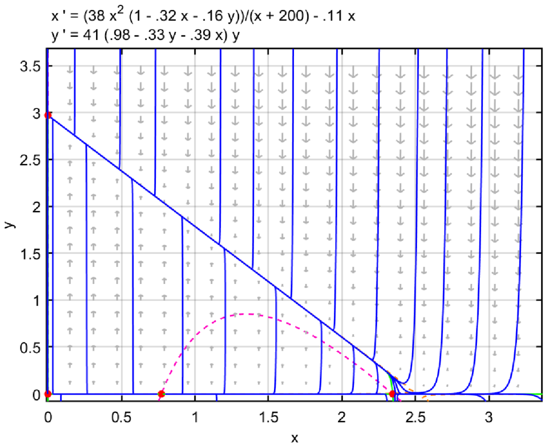

Figure 13: The parameters for the right figure are given in (4.20). The w-intercept for nullcline (L2) is greater than w_e^+, and in addition, $b<b_p$. There is no interior positive equilibrium. Boundary equilibrium $\bar{E}_2^-$ is an unstable node, $\bar{E}_2^+$ is a saddle point, and $\bar{E}_1$ is a globally asymptotically stable node for $w\geq 0$ and $z>0$. All solutions with $z>0$ approach $\bar{E}_1$.

4.3.6 $w_e^+<r_z/k_2\leq w^*$

In this section, we assume that condition (4.14) in Lemma 4.2(B) is satisfied such that $w_e^+<r_z/k_2$ but that the tangent point of the two nullclines is in the fourth quadrant of the wz-plane with its w-component satisfying $r_z/k_2\leq w^*$. When $b=b_p$, the schematic diagram is given in Fig. 14.

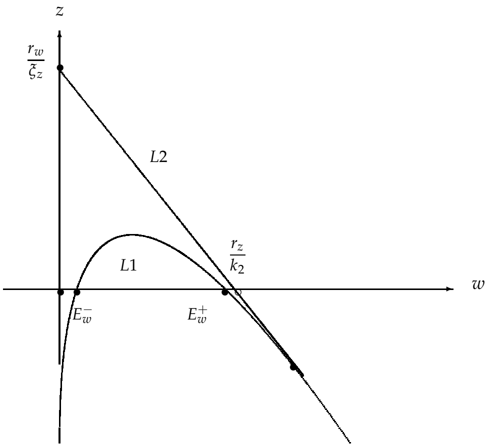

Figure 14: Schematic diagram of the phase plane for system (4.1) when $r_z/k_2 \le w^*$ such that the point where the two nullclines are tangent is in the fourth quadrant.

Since $w_e^+ < r_z/k_2$, boundary equilibrium $\bar{E}_2^+$ is a saddle point and boundary equilibrium $\bar{E}_1$ attracts all positive solutions except those on the stable manifold of $\bar{E}_2^+$.

It follows from $r_z/k_2 \le w^*$ that

$$2r_z(\xi_w\xi_z - k_1k_2) \le (r_w\xi_z - k_1r_z)k_2 < 2r_z(\xi_w\xi_z - k_1k_2),$$

that is,

$$\frac{r_z}{k_2} - \frac{r_zk_1}{\xi_w\xi_z} = \frac{r_z}{k_2}\left(1 - \frac{k_1k_2}{\xi_w\xi_z}\right) \le \frac{r_w}{\xi_w} - \frac{r_z}{k_2}. \tag{4.21}$$

Notice that since we are only concerned with $\xi_w\xi_z > k_1k_2$, it follows from (4.21) that $r_w/\xi_w > r_z/k_2$ and this happens only in the case of (b) or (c) in Theorem 3.1.

5 Discussion and concluding remarks

To have better understanding of the effect of the interspecific competition between two mosquito species w and z on the control of mosquitoes via releasing sterile mosquitoes of type w, we have, in this paper, fully investigated the dynamics of the models formulated and studied in [33].

In the absence of its competing species z, there is release threshold b_w when a constant number b of sterile mosquitoes of type w are released to suppress or eradicate mosquito species w. If $b > b_w$, mosquitoes w are suppressed and eventually eradicated. If $b < b_w$, there exist two positive steady states w_e^-, which is unstable, and w_e^+, which is asymptotically stable. Mosquitoes w die out, or survive and approach w_e^+, depending on their initial values. When species z present, the interspecific competition qualitatively changes the interactive model dynamics and therefore has a significant impact on the release strategies. Since the interspecific competition has inhibitory influences on competing species, and the goal of releasing sterile mosquitoes is to control mosquitoes w, we have basically focused on the case with $b<b_w$.

(A) The effect of the interspecific competition on the control of mosquitoes w depends on how species w resist to z, or how strong species w are in competing with z. Notice that k_2 is the parameter measuring the competitive effectiveness of w on z, and that r_z is the intrinsic growth rate of z. Then r_z/k_2 is the relative competition adjusted growth rate of z, denoted by $\tilde{r}_z$. With larger k_2, mosquitoes w have more competitive effects on z and the interspecific competition leads to smaller $\tilde{r}_z$. Comparing $\tilde{r}_z$ with the components $w_e^{\mp}$ of the two boundary equilibria on the w-axis, we have investigated the dynamics of model (4.1) in Section 4.3 and now summarize the results in Table 1 for the convenience of the reader.

Table 1: Summary table with $w^*<r_z/k_2$. Here $\tilde{r}_z=r_z/k_2$.

		Boundary equilibria		Interior positive equilibria	
		$\bar{E}_2^-$	$\bar{E}_2^+$		
$\tilde{r}_z<w_e^-$		Saddle	ST Node	None	
$w_e^-<\tilde{r}_z<w_e^+$		US node	ST node	Saddle $\bar{E}^u$	
$w_e^+<\tilde{r}_z$	$b<b_p$	US node	Saddle	US Node $\bar{E}_w^-$	Saddle $\bar{E}_w^-$
	$b=b_p$			ST node $\bar{E}^u$	
	$b>b_p$			None	

- If mosquitoes w have very strong competitive effects on mosquitoes z such that mosquitoes z are significantly inhibited with $\tilde{r}_z<w_e^-$, the competition of z on w has negligible impact on the suppression control of w with sterile mosquitoes. That is, there is no interior positive equilibrium and the three boundary equilibria have the same dynamical features as in the absence of z, as shown in Section 4.3.1.
- If the competitiveness of w is weak such that $w_e^- < \tilde{r}_z < w_e^+$, the model dynamics have a relatively small change such that there exists a unique interior positive equilibrium $\bar{E}^u$ which is a saddle point. While boundary equilibrium $\bar{E}_2^-$ becomes an unstable node, $\bar{E}_2^+$ is still locally asymptotically stable node. Solutions approach $\bar{E}_2^+$ in its attracting region. Thus, wild mosquitoes w survive from the interaction with the sterile mosquitoes as long as the number b of the release is less than the threshold b_w, as in Section 4.3.2.
- As the inhibitory influence of mosquitoes w on z becomes even weaker and the competitive effect of z on w is sufficiently large such that $w_e^+ < \tilde{r}_z$, the dynamical structure can change. We focus on the case when the tangent point of the two nullclines is in the first quadrant of the wz-plane such that its w-component satisfying $w^*<r_z/k_2$.

  First, boundary equilibrium $\bar{E}_2^+$ is no longer asymptotically stable which implies that mosquitoes w can be possibly suppressed or eradicated even $b<b_w$. Then,

in this case, there exists another release threshold b_p of the sterile mosquitoes to control mosquitoes w as sterile mosquitoes are released, and the threshold is determined by w^*. This occurs only if the two nullclines are tangentially touched, which clearly leads to $b_p < b_w$.

- If $b<b_p$, there exist two interior positive equilibria $\bar{E}_3^-$, which is a saddle point, and $\bar{E}_3^+$, which is a locally asymptotically stable. Solutions approach either boundary equilibrium $\bar{E}_1$ or $\bar{E}_3^+$, depending on their initial values. While it is possible that some mosquitoes w may be eradicated, most mosquitoes w coexist with z, as shown in Section 4.3.3.
- If $b=b_p$, the unique interior positive equilibrium $\bar{E}^*$ is a saddle point. The solutions with initial values on the stable manifold of $\bar{E}^*$ approach it, but the other solutions approach boundary equilibrium $\bar{E}_1$, which implies that almost all mosquitoes w are eventually eradicated, as shown in Section 4.3.4.
- For $b>b_p$, boundary equilibrium $\bar{E}_1$ is globally asymptotically stable and thus all mosquitoes w are eventually eradicated, as shown in Section 4.3.5.

Therefore, to suppress and eventually eradicate the wild mosquitoes w, the existence of competitive mosquitoes z is beneficial for the strategy of releasing sterile mosquitoes of type w, in particular if the competitive effect of z on w is sufficiently large.

(B) The competitive effect of z on w and the relative competition adjusted growth rate of z are not the only factors to affect the control of mosquitoes w. As discussed above, the most significance appears with $w_e^+ < \tilde{r}_z$. Then, we next focus on this case under the condition $w^* < r_z/k_2$. If follows from Lemma 4.2 that it is equivalent to $r_w/\xi_w < 2r_z/k_2$ and $b_c < b < b_w$.

From Lemma 4.1, to have b_p defined, we assume $\xi_w\xi_z > k_1k_2$ and $r_wk_1 > r_z\xi_z$ which corresponds to the cases in Theorem 3.1(2) and (4). Notice also that, in the case of Theorem 3.1(1), there is no need to release sterile mosquitoes, and in the case of Theorem 3.1(3), the influence of the interspecific competition is relatively small except very locally. Thus, we only consider the cases of Theorem 3.1(2) and (4).

If $r_z/k_2<r_w/\xi_w$ and $r_w/k_1>r_z/\xi_z$ as in Theorem 3.1(2), the releases of sterile mosquitoes can completely change the model dynamics and the fate of the two mosquito species w and z. Without sterile mosquitoes released, mosquitoes z lose the competition and eventually die out. However, after the sterile mosquitoes are released, the second threshold b_p can be defined and if $b>b_p$, the population size of mosquitoes w is reduced and it can even be possibly eradiated, which results in the survival of z.

On the other hand, if $r_w/\xi_w < r_z/k_2$ and $r_w/k_1 > r_z/\xi_z$ as in Theorem 3.1(4), the two mosquito species w and z coexist in the absence of sterile mosquitoes. As the release of the sterile mosquitoes reduces the population size of w, they lose their competitiveness and as a result, mosquitoes w are eventually eradicated and mosquitoes z survive.

(C) We have mostly focused on $w^* < r_z/k_2$. If $w^* \geq r_z/k_2$ as in Section 4.3.6, it happens in the cases of (2) or (3) in Theorem 3.1. Then the releases of sterile mosquitoes can easily change the fate of the two mosquito species and mosquitoes w can be even eradicated with $b < b_p$.

Concluding remarks. In summary, we make the following concluding remarks.

(1) If mosquitoes w are the completely dominating competitor, the interspecific competition may have relatively less effects on the SIT with releases of sterile mosquitoes of the same type as w.

(2) Otherwise, the existence of competing mosquitoes z has inhibitory influences on w which can determine a new release threshold b_p of sterile mosquitoes. This threshold is smaller than the threshold b_w in the absence of z such that the wild mosquitoes w can be possibly eradicated with less amount of released sterile mosquitoes. Therefore, with appropriately monitoring and taking advantages of the presence of its competing species z, we may be able to more effectively and economically efficiently control mosquitoes w.

(3) The suppression of mosquitoes w clearly helps the survival of the competing mosquitoes z. This nevertheless could create side effects if mosquitoes z also spread infectious diseases. This should be taken into consideration when we establish mosquito control strategies. We demonstrate this in Example 5.1.

Example 5.1. Choose parameters

$$\begin{aligned} &\alpha_1 = 87, \quad \xi_1 = 0.32, \quad \mu_1 = 0.13, \quad k_1 = 0.25, \\ &\alpha_2 = 91, \quad \xi_2 = 0.33, \quad \mu_2 = 0.3, \quad\ \ k_2 = 0.39 \end{aligned} \tag{5.1}$$

such that the case Theorem 3.1(2) happens. Boundary equilibrium $\bar{E}_1 = (0,3.0203)$ is unstable and $E_2 = (3.1203,0)$ is globally asymptotically stable, as shown in the Fig. 15(left). That is, mosquito species w wins the interspecific competition and wipes out mosquito species z in the absence of sterile mosquitoes.

With these parameters fixed and assuming sterile mosquitoes are released, we have the thresholds

$$b_p = 403.9095 < b_w = 521.2752.$$

Since, in this case,

$$w^* = 4.9587 > \frac{r_z}{k_1} = 2.5556,$$

even with $b=380<b_p$, boundary equilibrium $\bar{E}_1=(0,3.0203)$ becomes globally asymptotically stable, which implies that mosquitoes w are now eradicated and mosquitoes z take over as shown in the Fig. 15(right).

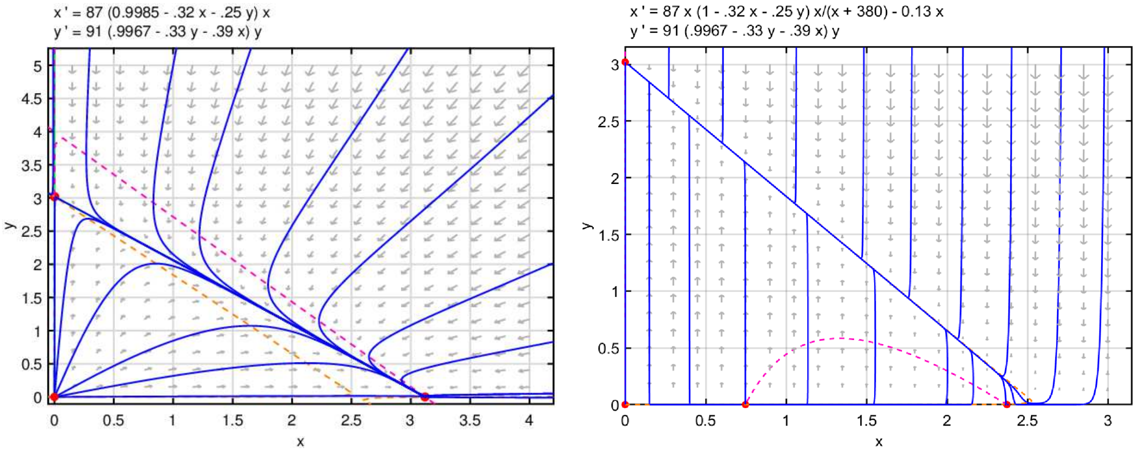

Figure 15: The parameters are given in (5.1). In the absence of sterile mosquitoes, mosquitoes w win the interspecific competition and mosquitoes z go extinct as shown in the left figure. After the sterile mosquitoes are released, mosquitoes w are eventually eradicated and mosquitoes z survive and take over as shown in the right figure.

(4) To focus on the effect of interspecific competition between different mosquito species on mosquito suppression, we have assumed no interspecific matings. However, interspecific mating between mosquito species, such as Aedes albopictus and Aedes aegypti can occur under certain circumstances. Further studies on the effects of interspecific competition together with interspecific mating are to appear in our incoming research.

(5) The work of this study is based on deterministic perspectives and spatially homogeneous populations. Environmental stochasticity and spatial heterogeneity certainly play a role in mosquito populations in the real world. More studies including those factors should be considered.

Acknowledgments

This work was supported by the National Natural Science Foundation of China (Grant Nos. 12171112, 12331017, 12371488).

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