COEXISTENCE FROM INTERSPECIFIC MATINGS FOR MOSQUITOES WITH STAGE STRUCTURE*

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Dedicated to Professor Jibin Li on the occasion of his 80th birthday.

Abstract Stage-structured models, including groups of larvae and adults, for two interacting mosquito species are studied in this paper. When there are no interspecific matings, the model dynamics follows the competitive exclusion principle such that only one of the two species can survive and there is no coexistent positive equilibrium. As interspecific matings take place, the interactive dynamics become complex. One of the two species can still dominate and drive the other species extinct with no existence of positive equilibrium, either species can survive or die out depending on initial sizes of the species where there exists an unstable positive equilibrium, or the two species coexist with a locally asymptotically stable positive equilibrium under certain conditions. Other dynamical features can occur as well. Detailed mathematical analysis and numerical examples are provided. Brief biological discussions are also given.

Keywords Mosquito population, stage structure, interspecific matings, competitive exclusion, coexistence, stability.

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1. Introduction

There are 112 genera of mosquitoes containing approximately 3,500 species among which three genera transmit mosquito-borne diseases [16,17,21]. Anopheles mosquitoes carry human malaria, *Culex* mosquitoes carry encephalitis, filariasis, and the West Nile virus, and *Aedes* mosquitoes carry yellow fever, dengue, chikungunya, and Zika [15, 18, 21]. It is well known that to prevent spread of mosquito-borne diseases, it is essential to control mosquitoes. To make effective strategies in control of mosquitoes, we need to have better understanding of the distributions of the mosquito species and their ecological behavior and characters.

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The mosquito species that transmit diseases are widespread and some of their spatial distributions frequently overlap and change. Many factors contribute to distribution changes among which competition plays an important role [13]. In fact, interspecific or heterospecific competition in which individuals of different species compete for the same resources is common in ecosystems. With no exception, different species of mosquitoes, such as Aedes albopictus and Aedes japonicus, and Aedes *aegypti* and *Aedes albopictus* share larval habitats and interspecific competition for limited resources thus is inevitable [4, 8, 9, 12, 14]. These interspecific competitions have important impacts on structuring communities of mosquitoes which may lead to a species dominant or replaced by a new species through competitive exclusion or invasion [9]. The different structures then certainly affect arbovirus infections or the efficacy of releases of genetically engineered mosquitoes such as Wolbachia-infected mosquitoes [1, 19]. Moreover, it is well documented that two different mosquito species such as Aedes (Stegomyia) albopictus (Skuse) and Aedes (Stegomyia) cretinus can inhabit the same geographic region and share the same ecological niche. Some of them are sympatric.

Note that mosquitoes undergo complete metamorphosis going through four distinct stages of development during a lifetime: egg, pupa, larva, and adult [3]. In addition to the intraspecific competition where the effect of crowding basically takes place in water with the egg, pupa, and larva stages in a mosquito's life cycle presenting, the interspecific competition between different species of mosquitoes also occurs in their aquatic stages. The intraspecific and interspecific competitions in aquatic stages then represent a major density dependent source for the population dynamics of mosquitoes [5, 6, 20].

It is also pointed out in [22] that as one of the critical behaviors characterizing the mosquito life strategy, mating has been much ignored and the least understood and most understudied in mosquito biology. Nevertheless, interspecific or heterospecific matings have been observed. They may have important effects in the mosquitoes ecology and distribution, and also play an important role for different species to coexist [2,7].

To explore the impacts of the interspecific or heterospecific competition and matings on the dynamics of the mosquitoes populations and their ecology, we formulate stage-structured models for two interactive mosquito species in this paper. We include the metamorphic stage structure in our model formulation as in [10,11], and also include interspecific matings between the two species. To make the model analysis more attractable, we group the first three aquatic stages as one class, called larvae, and let the adults be the other class for each species. Due to the fact that the food resource limitation mainly happens in the water, we ignore the competition between the adults and thus only assume density dependence in the larvae. We first present the fundamental dynamics of the two species populations without interaction in Section 2. We then investigate the interactive dynamics between the two populations with interspecific competition but with no interactive matings in Section 3. Including interspecific matings, we study their interactive dynamics and give numerical examples to demonstrate our findings in Section 4. Brief discussions are given in Section 5.

2. Single species population dynamics

We consider two interacting mosquito species sharing same resources. Since the interspecific competition basically occurs at the larva stages, we include stage structure in our models. To simplify the model formulation, similarly to the modeling process in [10,11], we divide each mosquito population into only two groups, called larvae and adults, and denote the larvae and adults for the two species by J_i and A_i , i = 1, 2, respectively.

Before proceeding with the modeling of the interaction between the two mosquitoes species, we assume that the dynamics of each population without interaction are governed by the following system:

$$\frac{dJ_i}{dt} = \beta_i A_i - \alpha_i J_i - (d_i + \xi_i J_i) J_i,
\frac{dA_i}{dt} = \alpha_i J_i - \mu_i A_i,$$
(2.1)

i = 1, 2, where β_i are the birth rates, that is the oviposition rate of adults, α_i are the progression or emergence rate from larvae to adults, d_i and μ_i are the density independent death rates of larvae and adults, respectively, and ξ_i are the factors for density dependent deaths of larvae. We ignore the density dependence in the death of adults.

Assume $\beta_i > \mu_i$ and define the intrinsic growth rate for each mosquito population as

$$n_i^0 := \frac{\beta_i \alpha_i}{\mu_i (\alpha_i + d_i)},\tag{2.2}$$

i = 1, 2. The dynamics of system (2.1) can be summarized as follows.

Theorem 2.1. For i = 1 or 2, if $n_i^0 \leq 1$, where n_i^0 is defined in (2.2), the trivial equilibrium (0,0) of system (2.1) is a globally asymptotically stable node and there exists no positive equilibrium. If $n_i^0 > 1$, the trivial equilibrium (0,0) is unstable and there exists a unique positive equilibrium $E_i^* = (J_i^{(00)}, A_i^{(00)})$ given by

$$J_i^{(00)} = \frac{\alpha_i + d_i}{\xi_i} \left(n_i^0 - 1 \right), \qquad A_i^{(00)} = \frac{\alpha_i (\alpha_i + d_i)}{\xi_i \mu_i} \left(n_i^0 - 1 \right), \tag{2.3}$$

for i = 1, 2, respectively. Each of the positive equilibria is a globally asymptotically stable node.

3. Interactive model formulation without interspecific mating

Assume that the interaction between the two populations takes place. It results in interspecific competition in larvae and the density-dependent death rates become $\xi_i(J_1+J_2)$. We still assume no competition for resources between adults, and arrive

at the following system:

$$\frac{dJ_1}{dt} = \beta_1 A_1 - \alpha_1 J_1 - (d_1 + \xi_1 (J_1 + J_2)) J_1,
\frac{dA_1}{dt} = \alpha_1 J_1 - \mu_1 A_1,
\frac{dJ_2}{dt} = \beta_2 A_2 - \alpha_2 J_2 - (d_2 + \xi_2 (J_1 + J_2)) J_2,
\frac{dA_2}{dt} = \alpha_2 J_2 - \mu_2 A_2.$$
(3.1)

The origin (0, 0, 0, 0) is a trivial equilibrium of system (3.1). It is easy to check that it is locally asymptotically stable if $n_i^0 < 1$, for i = 1, 2, and is unstable if $n_i^0 > 1$, for i = 1 or 2, where n_i^0 are defined in (2.2).

System (3.1) has boundary equilibrium $E_{01} := (J_1^{(00)}, A_1^{(00)}, 0, 0)$ if $n_1^0 > 1$, and boundary equilibrium $E_{02} := (0, 0, J_2^{(00)}, A_2^{(00)})$ if $n_2^0 > 1$, where $J_i^{(00)}$ and $A_i^{(00)}$ are given in (2.3).

The Jacobian matrix of (3.1) at E_{01} has the form

$$\begin{pmatrix} J_{11} & \cdot \\ 0 & J_{22} \end{pmatrix},$$

where

$$J_{11} = \begin{pmatrix} -\alpha_1 - d_1 - 2\xi_1 J_1^{(00)} & \beta_1 \\ \alpha_1 & -\mu_1 \end{pmatrix}, \quad J_{22} = \begin{pmatrix} -\alpha_2 - d_2 - \xi_2 J_1^{(00)} & \beta_2 \\ \alpha_2 & -\mu_2 \end{pmatrix}.$$

It is clear that matrix J_{11} is stable if $n_1^0 > 1$ since $\beta_1 > \mu_1$. The trace of J_{22} is negative and

det
$$J_{22} = \xi_2 \mu_2 J_1^{(00)} + \mu_2 (\alpha_2 + d_2) - \beta_2 \alpha_2 = \xi_2 \mu_2 J_1^{(00)} + \mu_2 (\alpha_2 + d_2)(1 - n_2^0)$$

= $\xi_2 \mu_2 \left(J_1^{(00)} - J_2^{(00)} \right).$

Thus, E_{01} is locally asymptotically stable if $J_1^{(00)} > J_2^{(00)}$ and unstable if $J_1^{(00)} < J_2^{(00)}$. Similarly, we can determine the stability of E_{02} .

In summary, we have the following results for the boundary equilibria of system (3.1).

Theorem 3.1. Boundary equilibria $E_{01} := \left(J_1^{(00)}, A_1^{(00)}, 0, 0\right)$ and $E_{02} := \left(0, 0, J_2^{(00)}, A_2^{(00)}\right)$ exist if $n_1^0 > 1$ and $n_2^0 > 1$, respectively. If $J_1^{(00)} > J_2^{(00)}$, that is $\beta_1 \alpha_1 - \mu_1(\alpha_1 + d_1) = \beta_2 \alpha_2 - \mu_2(\alpha_2 + d_2)$

$$\frac{\beta_1 \alpha_1 - \mu_1(\alpha_1 + d_1)}{\xi_1 \mu_1} > \frac{\beta_2 \alpha_2 - \mu_2(\alpha_2 + d_2)}{\xi_2 \mu_2}$$

 E_{01} is locally asymptotically stable and E_{02} is unstable. If $J_1^{(00)} < J_2^{(00)}$, that is

$$\frac{\beta_1 \alpha_1 - \mu_1(\alpha_1 + d_1)}{\xi_1 \mu_1} < \frac{\beta_2 \alpha_2 - \mu_2(\alpha_2 + d_2)}{\xi_2 \mu_2},$$

 E_{01} is unstable and E_{02} is locally asymptotically stable.

We then explore the existence of a positive equilibrium of (3.1). If it exists, from (3.1), it satisfies

$$\frac{\beta_1 \alpha_1 - \mu_1(\alpha_1 + d_1)}{\mu_1 \xi_1} = \frac{\alpha_1 + d_1}{\xi_1} \left(n_1^0 - 1 \right) = J_1 + J_2$$
$$= \frac{\beta_2 \alpha_2 - \mu_2(\alpha_2 + d_2)}{\mu_2 \xi_2} = \frac{\alpha_2 + d_2}{\xi_2} \left(n_2^0 - 1 \right).$$

Thus there exists a continuum of positive equilibria with

$$\begin{cases} 0 < J_1 < \frac{\alpha_1 + d_1}{\xi_1} \left(n_1^0 - 1 \right), \\ A_1 = \frac{\alpha_1}{\mu_1} J_1, \end{cases} \begin{cases} J_2 = \frac{\alpha_1 + d_1}{\xi_1} \left(n_1^0 - 1 \right) - J_1, \\ A_2 = \frac{\alpha_2}{\mu_2} J_2, \end{cases}$$

if and only if

$$\frac{\alpha_1 + d_1}{\xi_1} \left(n_1^0 - 1 \right) = \frac{\alpha_2 + d_2}{\xi_2} \left(n_2^0 - 1 \right) > 0.$$
(3.2)

It is clear that every point on the continuum is locally stable.

Biologically, condition (3.2) rarely holds in reality. We skip further investigations under (3.2) and conclude that coexistence of two different competing species of mosquitoes is impossible; that is, competitive exclusion holds for system (3.1) if there is no interspecific matings unless the special condition (3.2) holds.

4. Interactive model formulation with interspecific mating

We now assume that there are interspecific matings between the two species. The model dynamics are then described by the following system:

$$\frac{dJ_1}{dt} = \frac{a_1A_1 + a_2A_2}{A_1 + A_2}A_1 - \alpha_1J_1 - (d_1 + \xi_1(J_1 + J_2))J_1,
\frac{dA_1}{dt} = \alpha_1J_1 - \mu_1A_1,
\frac{dJ_2}{dt} = \frac{b_1A_1 + b_2A_2}{A_1 + A_2}A_2 - \alpha_2J_2 - (d_2 + \xi_2(J_1 + J_2))J_2,
\frac{dA_2}{dt} = \alpha_2J_2 - \mu_2A_2,$$
(4.1)

where a_i and b_i , i = 1, 2, are corresponding birth rates.

Write the right-hand side of (4.1) as $F_i(J_1, A_1, J_2, A_2)$, $i = 1, \dots, 4$, respectively. We have $F_1(0, A_1, J_2, A_2) > 0$, for all $A_i \ge 0$ and $A_1 + A_2 > 0$; $F_2(J_1, 0, J_2, A_2) > 0$, for all $J_1 > 0$; $F_3(J_1, A_1, 0, A_2) > 0$, for all $A_i \ge 0$ and $A_1 + A_2 > 0$; and $F_4(J_1, A_1, J_2, 0) > 0$, for all $J_2 > 0$.

Let $J := J_1 + J_2$, $A := A_1 + A_2$, $\bar{c} := \max\{a_i, b_i\}$, $\underline{c} := \min\{a_i, b_i\}$, $\bar{m} = \max\{\mu_i\}$, $\underline{m} := \min\{\mu_i\}$, $\bar{a} := \max\{\alpha_i\}$, $\underline{a} := \min\{\alpha_i\}$, $\bar{s} := \max\{\xi_i\}$, and $\underline{s} := \{\xi_i\}$, i = 1, 2. Then

$$\begin{cases} \frac{dJ}{dt} \ge \underline{c}A - \bar{a}J - (\bar{d} + \bar{s}J)J, \\ \frac{dA}{dt} \ge \underline{a}J - \bar{m}A, \end{cases}$$

and

$$\begin{cases} \frac{dJ}{dt} \leq \bar{c}A - \underline{a}J - (\underline{d} + \underline{s}J)J, \\ \frac{dA}{dt} \leq \bar{a}J - \underline{m}A. \\ \frac{\bar{a}\left(\bar{c} - \underline{m}\right)}{\underline{d}\ \underline{m}} > \frac{\underline{a}\left(\underline{c} - \bar{m}\right)}{\bar{d}\bar{m}} > 1, \end{cases}$$
(4.2)

 \mathbf{If}

then there exists a bounded region in the first octant of the 4-dimensional space
which is a positively invariant and attracting region of system
$$(4.1)$$
. We assume
 (4.2) holds hereafter.

4.1. Boundary equilibria and their stability

Under assumption (4.2), system (4.1) has two boundary equilibria $E_{01} := \left(J_1^{(0)}, A_1^{(0)}, 0, 0\right)$ and $E_{02} := \left(0, 0, J_2^{(0)}, A_2^{(0)}\right)$, with

$$J_{i}^{(0)} = \frac{\alpha_{i} + d_{i}}{\xi_{i}} \left(r_{i}^{0} - 1 \right), \qquad A_{i}^{(0)} = \frac{\alpha_{i}(\alpha_{i} + d_{i})}{\xi_{i}\mu_{i}} \left(r_{i}^{0} - 1 \right),$$

where

$$r_1^{(0)} = \frac{a_1 \alpha_1}{\mu_1(\alpha_1 + d_1)}, \quad r_2^{(0)} = \frac{b_2 \alpha_2}{\mu_2(\alpha_2 + d_2)}.$$

The Jacobian matrix of (3.1) at E_{01} is

$$\begin{pmatrix} J_{11}^{(2)} & \cdot \\ 0 & J_{22}^{(2)} \end{pmatrix},$$

where

$$J_{11}^{(2)} = \begin{pmatrix} -\alpha_1 - d_1 - 2\xi_1 J_1^{(0)} & a_1 \\ \alpha_1 & -\mu_1 \end{pmatrix}, \quad J_{22}^{(2)} = \begin{pmatrix} -\alpha_2 - d_2 - \xi_2 J_1^{(0)} & b_1 \\ \alpha_2 & -\mu_2 \end{pmatrix}.$$

Matrix $J_{11}^{\left(2\right)}$ is stable and the determinant of $J_{22}^{\left(2\right)}$ is

$$\det J_{22}^{(2)} = \xi_2 \mu_2 J_1^{(0)} + \mu_2 (\alpha_2 + d_2) - \alpha_2 b_1$$

= $\xi_2 \mu_2 J_1^{(0)} + \mu_2 (\alpha_2 + d_2) - \alpha_2 b_2 + \alpha_2 (b_2 - b_1)$
= $\xi_2 \mu_2 J_1^{(0)} + \mu_2 (\alpha_2 + d_2) (1 - r_2^0) + \alpha_2 (b_2 - b_1)$
= $\xi_2 \mu_2 \left(J_1^{(0)} - J_2^{(0)} \right) + \alpha_2 (b_2 - b_1).$

Thus, E_{01} is locally asymptotically stable if $J_1^{(0)} > J_2^{(0)} + \frac{\alpha_2}{\xi_2 \mu_2} (b_1 - b_2)$. Similarly, we can obtain the stability of E_{02} . We summarize the results as

follows.

Theorem 4.1. Assume condition (4.2) holds for system (4.1). Boundary equilibrium $E_{01} := (J_1^{(0)}, A_1^{(0)}, 0, 0)$ exists if $r_1^0 > 1$ and is locally asymptotically stable if

$$J_1^{(0)} > J_2^{(0)} + \frac{\alpha_2}{\xi_2 \mu_2} (b_1 - b_2).$$
(4.3)

It is unstable if

$$J_1^{(0)} < J_2^{(0)} + \frac{\alpha_2}{\xi_2 \mu_2} (b_1 - b_2).$$
(4.4)

Boundary equilibrium $E_{02} := (0, 0, J_2^{(0)}, A_2^{(0)})$ exists if $r_2^0 > 1$ and is locally asymptotically stable if

$$J_2^{(0)} > J_1^{(0)} + \frac{\alpha_1}{\xi_1 \mu_1} (a_2 - a_1).$$
(4.5)

It is unstable if

$$J_2^{(0)} < J_1^{(0)} + \frac{\alpha_1}{\xi_1 \mu_1} (a_2 - a_1).$$
(4.6)

4.2. Positive equilibrium

The coexistence of the two species is partly characterized by the existence and dynamics of possible positive equilibria of system (4.1).

4.2.1. Existence of Positive equilibrium

We first explore the existence of a positive equilibrium of system (4.1) as follows.

From system (4.1), we have $J_i = \frac{\mu_i}{\alpha_i} A_i$, i = 1, 2, at a positive equilibrium. Then to solve for a positive equilibrium of (4.1), it is equivalent to solve the following system for $A_i > 0$, i = 1, 2:

$$\frac{\alpha_1 \left(a_1 A_1 + a_2 A_2\right)}{\mu_1 (A_1 + A_2)} - \left(\alpha_1 + d_1 + \xi_1 \left(\frac{\mu_1 A_1}{\alpha_1} + \frac{\mu_2 A_2}{\alpha_2}\right)\right) = 0,$$

$$\frac{\alpha_2 \left(b_1 A_1 + b_2 A_2\right)}{\mu_2 (A_1 + A_2)} - \left(\alpha_2 + d_2 + \xi_2 \left(\frac{\mu_1 A_1}{\alpha_1} + \frac{\mu_2 A_2}{\alpha_2}\right)\right) = 0,$$
(4.7)

which leads to

$$\frac{\alpha_1\xi_2\left(a_1A_1+a_2A_2\right)}{\mu_1(A_1+A_2)} - \xi_2\left(\alpha_1+d_1\right) = \frac{\alpha_2\xi_1\left(b_1A_1+b_2A_2\right)}{\mu_2(A_1+A_2)} - \xi_1\left(\alpha_2+d_2\right). \quad (4.8)$$

The two sides of (4.8), based on assumption (4.2), are positive, and equation (4.8) is equivalent to

$$\xi_{2}\mu_{2}\left(\left(a_{1}\alpha_{1}-\mu_{1}(\alpha_{1}+d_{1})\right)A_{1}+\left(a_{2}\alpha_{1}a_{2}-\mu_{1}(\alpha_{1}+d_{1})\right)A_{2}\right) \\ =\xi_{1}\mu_{1}\left(\left(b_{1}\alpha_{2}-\mu_{2}(\alpha_{2}+d_{2})\right)A_{1}+\left(b_{2}\alpha_{2}-\mu_{2}(\alpha_{2}+d_{2})\right)A_{2}\right).$$

$$(4.9)$$

Solving (4.9) for A_2 in terms of A_1 yields

$$A_{2} = \frac{\xi_{2}\mu_{2}(a_{1}\alpha_{1} - \mu_{1}(\alpha_{1} + d_{1})) - \xi_{1}\mu_{1}(b_{1}\alpha_{2} - \mu_{2}(\alpha_{2} + d_{2}))}{\xi_{1}\mu_{1}(b_{2}\alpha_{2} - \mu_{2}(\alpha_{2} + d_{2})) - \xi_{2}\mu_{2}(a_{2}\alpha_{1} - \mu_{1}(\alpha_{1} + d_{1}))}A_{1} := CA_{1}.$$
 (4.10)

Notice that

$$\begin{split} &\xi_{2}\mu_{2}\big(a_{1}\alpha_{1}-\mu_{1}(\alpha_{1}+d_{1})\big)-\xi_{1}\mu_{1}\big(b_{1}\alpha_{2}-\mu_{2}(\alpha_{2}+d_{2})\big)\\ &=\xi_{2}\mu_{1}\mu_{2}\left(\frac{a_{1}\alpha_{1}}{\mu_{1}}-\alpha_{1}-d_{1}\right)-\xi_{1}\mu_{1}\mu_{2}\left(\frac{b_{2}\alpha_{2}}{\mu_{2}}-\alpha_{2}-d_{2}+\frac{\alpha_{2}(b_{1}-b_{2})}{\mu_{2}}\right)\\ &=\xi_{1}\xi_{2}\mu_{1}\mu_{2}\left(J_{1}^{(0)}-J_{2}^{(0)}-\frac{\alpha_{2}}{\xi_{2}\mu_{2}}(b_{1}-b_{2})\right), \end{split}$$

and similarly,

$$\begin{aligned} \xi_1 \mu_1 \left(b_2 \alpha_2 - \mu_2 (\alpha_2 + d_2) \right) &- \xi_2 \mu_2 \left(a_2 \alpha_1 - \mu_1 (\alpha_1 + d_1) \right) \\ = &\xi_1 \mu_1 \mu_2 \left(\frac{b_2 \alpha_2}{\mu_2} - \alpha_2 - d_2 \right) - \xi_2 \mu_1 \mu_2 \left(\frac{a_1 \alpha_1}{\mu_1} - \alpha_1 - d_1 + \frac{\alpha_1 (a_2 - a_1)}{\mu_1} \right) \\ = &\xi_1 \xi_2 \mu_1 \mu_2 \left(J_2^{(0)} - J_1^{(0)} - \frac{\alpha_1}{\xi_1 \mu_1} (a_2 - a_1) \right). \end{aligned}$$

Then

$$C = \frac{J_1^{(0)} - J_2^{(0)} - \frac{\alpha_2}{\xi_2 \mu_2} (b_1 - b_2)}{J_2^{(0)} - J_1^{(0)} - \frac{\alpha_1}{\xi_1 \mu_1} (a_2 - a_1)} > 0$$
(4.11)

and thus there exists a positive equilibrium only if

$$\frac{\alpha_2}{\xi_2\mu_2}(b_1 - b_2) < J_1^{(0)} - J_2^{(0)} < \frac{\alpha_1}{\xi_1\mu_1}(a_1 - a_2),$$
(4.12)

or

$$\frac{\alpha_1}{\xi_1\mu_1}(a_1 - a_2) < J_1^{(0)} - J_2^{(0)} < \frac{\alpha_2}{\xi_2\mu_2}(b_1 - b_2).$$
(4.13)

Suppose condition (4.12) or (4.13) holds. Substituting $A_2 = CA_1$ into the first equation in (4.7) yields

$$A_1 = \frac{\alpha_1 \alpha_2}{\xi_1(\alpha_2 \mu_1 + \alpha_1 \mu_2 C)} \left(\frac{\alpha_1(a_1 + a_2 C)}{\mu_1(1 + C)} - \alpha_1 - d_1 \right).$$
(4.14)

It follows from (4.2) that

$$A_{1} \geq \frac{\alpha_{1}\alpha_{2}}{\xi_{1}(\alpha_{2}\mu_{1} + \alpha_{1}\mu_{2}C)} \left(\underline{c}\frac{\alpha_{1}}{\mu_{1}} - \alpha_{1} - d_{1}\right)$$

$$\geq \frac{\alpha_{1}\alpha_{2}}{\xi_{1}(\alpha_{2}\mu_{1} + \alpha_{1}\mu_{2}C)} \left(\frac{\alpha_{1}(\underline{c} - \bar{m})}{\mu_{1}d_{1}} - 1\right) d_{1} > 0.$$

Therefore, if (4.12) or (4.13) holds, there exists a unique positive equilibrium. In summary, we have the following existence results.

Theorem 4.2. Assume (4.2) holds. Then system (4.1) has a unique positive equilibrium

$$E^* := (J_1, A_1, J_2, A_2) = \left(\frac{\mu_1}{\alpha_1} A_1, A_1, \frac{\mu_2}{\alpha_2} C A_1, C A_1\right),$$
(4.15)

where C is given in (4.11) and A_1 is given in (4.14), if and only if condition (4.12) or (4.13) is satisfied.

Remark 4.1. Condition (4.12) is equivalent to the case where the two boundary equilibria E_{01} and E_{02} are both locally asymptotically stable, and condition (4.13) is equivalent to that the two boundary equilibria are both unstable. That is, if the two boundary equilibria are both locally asymptotically stable or both unstable, system (4.1) has a unique positive equilibrium. Otherwise if one of the two boundary equilibria is asymptotically stable and the other is unstable, there exists no positive equilibrium. This can be seen in Example 4.1 given below.



Figure 1. With parameters given in (4.16) and (4.17), boundary equilibrium $E_{01} = (16.6923, 15.4083, 0, 0)$ is locally asymptotically stable and $E_{02} = (0, 0, 29.5185, 34.3648)$ is unstable. The solution curves of system (4.1) are shown in the left figure. When parameters are given in (4.16) and (4.18), boundary equilibrium $E_{01} = (12.0769, 11.1479, 0, 0)$ is unstable and $E_{02} = (0, 0, 19.3952, 22.5795)$ is locally asymptotically stable. The solution curves of system (4.1) are shown in the right figure. In either case, there exists no positive equilibrium.

Example 4.1. Given parameters

$$\alpha_1 = 0.6, \, \alpha_2 = 0.78, \, d_1 = 0.5, \, d_2 = 0.58,
\xi_1 = 0.1, \, \xi_2 = 0.23, \, \mu_1 := 0.65, \, \mu_2 = 0.67,$$
(4.16)

we first let

$$a_1 = 3, a_2 = 7, b_1 = 4, b_2 = 7.$$
 (4.17)

Then we have $r_1^0 = 2.5175$ and $r_2^0 = 5.9920$ such that system (4.1) has two boundary equilibria $E_{01} = (16.6923, 15.4083, 0, 0)$ and $E_{02} := (0, 0, 29.5185, 34.3648)$, and $J_1^{(0)} < J_2^{(0)}$. It follows from

$$\frac{\alpha_1}{\xi_1\mu_1}(b_1 - b_2) = -15.1849 < J_1^{(0)} - J_2^{(0)} = -12.8262$$

and

$$\frac{\alpha_2}{\xi_2\mu_2}(a_1 - a_2) = -36.9231 < J_1^{(0)} - J_2^{(0)}$$

that E_{01} is locally asymptotically stable and E_{02} is unstable from Theorem 4.1. Then there exists no positive equilibrium from Theorem 4.2. The solution curves are shown in the left figure in Figure 1. Then we choose

$$a_1 = 2.5, a_2 = 3, b_1 = 8, b_2 = 5.$$
 (4.18)

The two boundary equilibria are $E_{01} = (12.0769, 11.1479, 0, 0)$ and $E_{02} = (0, 0, 19.3952, 22.5795)$. It follows from

$$\frac{\alpha_1}{\xi_1\mu_1}(b_1 - b_2) = 15.18494484 > J_1^{(0)} - J_2^{(0)} = -7.3183$$

and

$$\frac{\alpha_2}{\xi_2\mu_2}(a_1 - a_2) = -4.6154 > J_1^{(0)} - J_2^{(0)}$$

that E_{02} is unstable and E_{01} is locally asymptotically stable, and there exists no positive equilibrium. The solution curves are shown in the right figure in Figure 1.

4.2.2. Stability of Positive equilibrium of system (4.19)

The stability analysis directly for system (4.1) is mathematically untractable. However, it is clear that the equilibria of system (4.1) exist only in the subspace

$$\Omega := \{ (J_1, A_1, J_2, A_2), \ \alpha_1 J_1 = \mu_1 A_1 \text{ and } \alpha_2 J_2 = \mu_2 A_2, \ \forall t \ge 0 \}.$$

We then focus on Ω and consider the following reduced system:

$$\frac{dA_1}{dt} = \frac{\alpha_1 \left(a_1 A_1 + a_2 A_2\right) A_1}{\mu_1 (A_1 + A_2)} - \left(\alpha_1 + d_1 + \xi_1 \left(\frac{\mu_1 A_1}{\alpha_1} + \frac{\mu_2 A_2}{\alpha_2}\right)\right) A_1,
\frac{dA_2}{dt} = \frac{\alpha_2 \left(b_1 A_1 + b_2 A_2\right) A_2}{\mu_2 (A_1 + A_2)} - \left(\alpha_2 + d_2 + \xi_2 \left(\frac{\mu_1 A_1}{\alpha_1} + \frac{\mu_2 A_2}{\alpha_2}\right)\right) A_2.$$
(4.19)

We investigate the local stability of the positive equilibrium of system (4.19) by linearization as follows.

The Jacobian matrix of system (4.19) at a positive equilibrium has the form

$$J := \begin{pmatrix} J_{11} & J_{12} \\ J_{21} & J_{22} \end{pmatrix}, \tag{4.20}$$

where

$$J_{11} = \frac{\alpha_1}{\mu_1} \left(\frac{a_1 A_1 + a_2 A_2}{A_1 + A_2} + \frac{(a_1 - a_2) A_1 A_2}{(A_1 + A_2)^2} \right) - \left(\alpha_1 + d_1 + \xi_1 \frac{\mu_1}{\alpha_1} A_1 + \xi_1 \frac{\mu_2}{\alpha_2} A_2 \right) - \xi_1 \frac{\mu_1}{\alpha_1} A_1 = \frac{\alpha_1}{\mu_1} \left(\frac{a_1 A_1 + a_2 A_2}{A_1 + A_2} + \frac{(a_1 - a_2) A_1 A_2}{(A_1 + A_2)^2} \right) - \frac{\alpha_1}{\mu_1} \frac{a_1 A_1 + a_2 A_2}{A_1 + A_2} - \xi_1 \frac{\mu_1}{\alpha_1} A_1 = \frac{\alpha_1}{\mu_1} \frac{(a_1 - a_2) A_1 A_2}{(A_1 + A_2)^2} - \xi_1 \frac{\mu_1}{\alpha_1} A_1, J_{12} = \frac{\alpha_1}{\mu_1} \frac{(a_2 - a_1) A_1^2}{(A_1 + A_2)^2} - \xi_1 \frac{\mu_2}{\alpha_2} A_1, J_{21} = \frac{\alpha_2}{\mu_2} \frac{(b_1 - b_2) A_2^2}{(A_1 + A_2)^2} - \xi_2 \frac{\mu_1}{\alpha_2} A_2, J_{22} = \frac{\alpha_2}{\mu_2} \frac{(b_2 - b_1) A_1 A_2}{(A_1 + A_2)^2} - \xi_2 \frac{\mu_2}{\alpha_2} A_2.$$

$$(4.21)$$

Based on (4.20) and (4.21), the local stability of the unique positive equilibrium of system (4.19) and thus of system (4.1) can be described in the following theorem.

Theorem 4.3. Suppose that the inequalities in (4.12) or (4.13) hold such that system (4.1) or (4.19) has a unique positive equilibrium. Then

- (A) If the inequalities in (4.12) hold and then the two boundary equilibria are both locally asymptotically stable, the unique positive equilibrium is an unstable saddle point.
- (B) If the inequalities in (4.13) hold and, in addition,(B1)

$$a_1 \le a_2 \quad and \quad b_1 \ge b_2, \tag{4.22}$$

(B2)

$$a_1 \le a_1, \quad b_1 \le b_2, \quad and \quad \xi_1 \ge \xi_2,$$
 (4.23)

(B3) $a_1 \ge a_2, \quad b_1 > b_2, \quad and \quad \xi_1 \le \xi_2,$ (4.24)

$$a_1 < a_2, \ b_1 \le b_2, \ \frac{1}{2}\xi_2 < \xi_1 < \xi_2, \ and \ 2\alpha_1\mu_2 J_1^{(0)} < \alpha_2\mu_1 J_2^{(0)}, \ (4.25)$$

or (**B5**)

$$a_1 \ge a_2, \ b_1 > b_2, \ \frac{1}{2}\xi_1 < \xi_2 < \xi_1, \ and \ 2\alpha_2\mu_1 J_2^{(0)} < \alpha_1\mu_2 J_1^{(0)}, \ (4.26)$$

then the unique positive equilibrium is locally asymptotically stable.

Proof. We give detailed proofs as follows.

The determinant of the Jacobian matrix J in (4.20) can be computed as

$$\det J = \begin{vmatrix} \frac{\alpha_1}{\mu_1} \frac{(a_1 - a_2)A_1A_2}{(A_1 + A_2)^2} - \xi_1 \frac{\mu_1}{\alpha_1}A_1 & \frac{\alpha_1}{\mu_1} \frac{(a_2 - a_1)A_1^2}{(A_1 + A_2)^2} - \xi_1 \frac{\mu_2}{\alpha_2}A_1 \\ \frac{\alpha_2}{\mu_2} \frac{(b_1 - b_2)A_2^2}{(A_1 + A_2)^2} - \xi_2 \frac{\mu_1}{\alpha_1}A_2 & \frac{\alpha_2}{\mu_2} \frac{(b_2 - b_1)A_1A_2}{(A_1 + A_2)^2} - \xi_2 \frac{\mu_2}{\alpha_2}A_2 \end{vmatrix}$$
$$= -\frac{\alpha_1}{\mu_1} \frac{(a_1 - a_2)A_1A_2}{(A_1 + A_2)^2} \xi_2 \frac{\mu_2}{\alpha_2}A_2 - \frac{\alpha_2}{\mu_2} \frac{(b_2 - b_1)A_1A_2}{(A_1 + A_2)^2} \xi_1 \frac{\mu_1}{\alpha_1}A_1 \\ + \frac{\alpha_1}{\mu_1} \frac{(a_2 - a_1)A_1^2}{(A_1 + A_2)^2} \xi_2 \frac{\mu_1}{\alpha_1}A_2 + \frac{\alpha_2}{\mu_2} \frac{(b_1 - b_2)A_2^2}{(A_1 + A_2)^2} \xi_1 \frac{\mu_2}{\alpha_2}A_1 \\ = \frac{\alpha_1\xi_2(a_2 - a_1)A_1A_2}{\mu_1(A_1 + A_2)^2} \left(\frac{\alpha_1}{\mu_1}A_1 + \frac{\alpha_2}{\mu_2}A_2\right) + \frac{\alpha_2\xi_1(b_1 - b_2)A_1A_2}{\mu_2(A_1 + A_2)^2} \left(\frac{\alpha_1}{\mu_1}A_1 + \frac{\alpha_2}{\mu_2}A_2\right) \\ = \frac{\xi_1\xi_2A_1A_2}{\mu_2(A_1 + A_2)^2} \left(\frac{\alpha_1}{\mu_1}A_1 + \frac{\alpha_2}{\mu_2}A_2\right) \left(\frac{\alpha_1(a_2 - a_1)}{\mu_1\xi_1} + \frac{\alpha_2(b_1 - b_2)}{\mu_2\xi_2}\right).$$

(A) Suppose that the inequalities in (4.12) hold. Then both (4.3) and (4.5) are satisfied. Hence the two boundary equilibria are both locally asymptotically stable and

$$\frac{\alpha_1(a_2-a_1)}{\mu_1\xi_1} + \frac{\alpha_2(b_1-b_2)}{\mu_2\xi_2} < 0.$$

Thus, the determinant of the Jacobian matrix J at the unique positive equilibrium is negative which implies that there exists at least one positive eigenvalue of J. Hence the unique positive equilibrium is an unstable saddle point.

(B) Suppose that the inequalities in (4.13) hold, that is,

$$\frac{\alpha_1}{\xi_1\mu_1}(a_1-a_2) < J_1^{(0)} - J_2^{(0)} < \frac{\alpha_2}{\xi_2\mu_2}(b_1-b_2).$$

Then both (4.4) and (4.6) are satisfied, and the two boundary equilibria are unstable and

$$\frac{\alpha_1(a_2-a_1)}{\mu_1\xi_1} + \frac{\alpha_2(b_1-b_2)}{\mu_2\xi_2} > 0.$$

Thus, the determinant of the Jacobian matrix J at the unique positive equilibrium is positive. We then show that the trace of J

$$\operatorname{tr} J = \frac{\alpha_1}{\mu_1} \frac{(a_1 - a_2)A_1A_2}{(A_1 + A_2)^2} - \xi_1 \frac{\mu_1}{\alpha_1} A_1 + \frac{\alpha_2}{\mu_2} \frac{(b_2 - b_1)A_1A_2}{(A_1 + A_2)^2} - \xi_2 \frac{\mu_2}{\alpha_2} A_2$$
$$= -\frac{A_1A_2}{(A_1 + A_2)^2} \left(\frac{\alpha_1}{\mu_1} (a_2 - a_1) + \frac{\alpha_2}{\mu_2} (b_1 - b_2) \right) - \left(\xi_1 \frac{\mu_1}{\alpha_1} A_1 + \xi_2 \frac{\mu_2}{\alpha_2} A_2 \right)$$
(4.27)

at the positive equilibrium is negative so that the unique positive equilibrium is locally asymptotically stable under conditions (4.22)-(4.26), respectively, as follows.

(B1) When condition in (4.22) is satisfied, it is clear that tr J < 0 and thus the unique positive equilibrium is locally asymptotically stable.

(B2) If (4.23) is satisfied, then

$$\begin{aligned} \frac{\alpha_1}{\mu_1}(a_2 - a_1) + \frac{\mu_2}{\alpha_2}(b_1 - b_2) &\geq \frac{\alpha_1(a_2 - a_1)}{\mu_1} + \frac{\xi_1}{\xi_2} \frac{\alpha_2(b_1 - b_2)}{\mu_2} \\ &= \xi_1 \left(\frac{\alpha_1(a_2 - a_1)}{\mu_1\xi_1} + \frac{\alpha_2(b_1 - b_2)}{\mu_2\xi_2} \right) > 0. \end{aligned}$$

Thus tr J < 0 and the unique positive equilibrium is locally asymptotically stable.

(B3) The proof under condition (4.24) is similar to that in (B2) and is omitted. (B4) Suppose (4.25) holds. We rewrite A_1 in (4.14) as

$$A_{1} = \frac{\alpha_{1}\alpha_{2}}{\xi_{1}(\alpha_{2}\mu_{1} + \alpha_{1}\mu_{2}C)} \left(\frac{\alpha_{1}(a_{2} - a_{1})C}{\mu_{1}(1 + C)} + \frac{\alpha_{1}a_{1}}{\mu_{1}} - \alpha_{1} - d_{1}\right)$$

$$= \frac{\alpha_{1}\alpha_{2}}{\alpha_{2}\mu_{1} + \alpha_{1}\mu_{2}C} \left(\frac{\alpha_{1}(a_{2} - a_{1})C}{\xi_{1}\mu_{1}(1 + C)} + J_{1}^{(0)}\right).$$
(4.28)

Similarly to deriving the formula of A_1 in (4.14), substituting $A_1 = \frac{1}{C}A_2$ into the second equation in (4.7) yields

$$A_{2} = \frac{\alpha_{1}\alpha_{2}C}{\xi_{2}(\alpha_{2}\mu_{1} + \alpha_{1}\mu_{2}C)} \left(\frac{\alpha_{2}(b_{1} + b_{2}C)}{\mu_{2}(1 + C)} - \alpha_{2} - d_{2}\right)$$

$$= \frac{\alpha_{1}\alpha_{2}C}{\alpha_{2}\mu_{1} + \alpha_{1}\mu_{2}C} \left(\frac{\alpha_{2}(b_{1} - b_{2})}{\xi_{2}\mu_{2}(1 + C)} + J_{2}^{(0)}\right).$$
(4.29)

Thus,

$$\xi_{1} \frac{\mu_{1}}{\alpha_{1}} A_{1} + \xi_{2} \frac{\mu_{2}}{\alpha_{2}} A_{2} = \left(\xi_{1} \frac{\mu_{1}}{\alpha_{1}} + \xi_{2} \frac{\mu_{2}}{\alpha_{2}} C\right) A_{1} = \frac{\xi_{1} \alpha_{2} \mu_{1} + \xi_{2} \alpha_{1} \mu_{2} C}{\alpha_{1} \alpha_{2}} A_{1}$$

$$= \frac{\xi_{1} \alpha_{2} \mu_{1} + \xi_{2} \alpha_{1} \mu_{2} C}{\alpha_{2} \mu_{1} + \alpha_{1} \mu_{2} C} \left(\frac{\alpha_{1} (a_{2} - a_{1}) C}{\xi_{1} \mu_{1} (1 + C)} + J_{1}^{(0)}\right).$$

$$(4.30)$$

Substituting (4.28) and (4.29) into $A_2 = CA_1$, we obtain

$$\frac{\alpha_1(a_2-a_1)C}{\xi_1\mu_1(1+C)} + \frac{\alpha_2(b_2-b_1)}{\xi_2\mu_2(1+C)} = J_2^{(0)} - J_1^{(0)}.$$

Thus

$$\frac{\alpha_2(b_1-b_2)}{\mu_2} = \frac{\xi_2 \alpha_1(a_2-a_1)C}{\xi_1 \mu_1} + \xi_2(1+C) \left(J_1^{(0)} - J_2^{(0)}\right),$$

and then

$$\frac{\alpha_1(a_2-a_1)}{\mu_1} + \frac{\alpha_2(b_1-b_2)}{\mu_2} = \frac{\alpha_1(a_2-a_1)}{\mu_1} \left(1 + \frac{\xi_2}{\xi_1}C\right) + \xi_2(1+C) \left(J_1^{(0)} - J_2^{(0)}\right).$$
(4.31)

Substituting (4.30) and (4.31) into (4.27), we then have

$$\operatorname{tr} J = -\frac{A_1 A_2}{(A_1 + A_2)^2} \left(\frac{\alpha_1}{\mu_1} (a_2 - a_1) + \frac{\alpha_2}{\mu_2} (b_1 - b_2) \right) - \left(\xi_1 \frac{\mu_1}{\alpha_1} A_1 + \xi_2 \frac{\mu_2}{\alpha_2} A_2 \right)$$

$$= -\frac{C}{(1+C)^2} \left(\frac{\alpha_1 (a_2 - a_1)}{\mu_1} \left(1 + \frac{\xi_2}{\xi_1} C \right) + \xi_2 (1+C) \left(J_1^{(0)} - J_2^{(0)} \right) \right)$$

$$- \frac{\xi_1 \alpha_2 \mu_1 + \xi_2 \alpha_1 \mu_2 C}{\alpha_2 \mu_1 + \alpha_1 \mu_2 C} \left(\frac{\alpha_1 (a_2 - a_1) C}{\xi_1 \mu_1 (1+C)} + J_1^{(0)} \right).$$

It follows from (4.13) that

$$\begin{aligned} \operatorname{tr} J &< -\frac{C}{(1+C)^2} \left(\xi_1 \left(J_2^{(0)} - J_1^{(0)} \right) \left(1 + \frac{\xi_2}{\xi_1} C \right) + \xi_2 (1+C) \left(J_1^{(0)} - J_2^{(0)} \right) \right) \\ &- \frac{\xi_1 \alpha_2 \mu_1 + \xi_2 \alpha_1 \mu_2 C}{\alpha_2 \mu_1 + \alpha_1 \mu_2 C} \left(\frac{\left(J_2^{(0)} - J_1^{(0)} \right) C}{1+C} + J_1^{(0)} \right) \\ &= -\frac{C}{(1+C)^2} \left(\xi_1 \left(J_2^{(0)} - J_1^{(0)} \right) \left(1 + \frac{\xi_2}{\xi_1} C \right) + \xi_2 (1+C) \left(J_1^{(0)} - J_2^{(0)} \right) \right) \\ &- \frac{\xi_1 \alpha_2 \mu_1 + \xi_2 \alpha_1 \mu_2 C}{\alpha_2 \mu_1 + \alpha_1 \mu_2 C} \left(\frac{\left(J_2^{(0)} - J_1^{(0)} \right) C}{1+C} + J_1^{(0)} \right) \\ &= -\frac{\left(\xi_1 - \xi_2 \right) \left(J_2^{(0)} - J_1^{(0)} \right) C}{(1+C)^2} - \frac{\xi_1 \alpha_2 \mu_1 + \xi_2 \alpha_1 \mu_2 C}{\alpha_2 \mu_1 + \alpha_1 \mu_2 C} \frac{J_1^{(0)} + J_2^{(0)} C}{1+C} \\ &= -\frac{\left(\xi_2 \alpha_2 \mu_1 + (2\xi_2 - \xi_1) \alpha_1 \mu_2 C \right) J_1^{(0)} + \left((2\xi_1 - \xi_2) \alpha_2 \mu_1 + \xi_1 \alpha_1 \mu_2 C \right) C J_2^{(0)}}{(\alpha_2 \mu_1 + \alpha_1 \mu_2 C) (1+C)^2} \end{aligned}$$

$$= -\frac{\xi_1 \alpha_1 \mu_2 J_2^{(0)} C^2 + \xi_2 \alpha_2 \mu_1 J_1^{(0)}}{(\alpha_2 \mu_1 + \alpha_1 \mu_2 C)(1 + C)^2} - \frac{\xi_1 \left(2\alpha_2 \mu_1 J_2^{(0)} - \alpha_1 \mu_2 J_1^{(0)} \right) + \xi_2 \left(2\alpha_1 \mu_2 J_1^{(0)} - \alpha_2 \mu_1 J_2^{(0)} \right)}{(\alpha_2 \mu_1 + \alpha_1 \mu_2 C)(1 + C)^2} C.$$

Notice that $2\alpha_2\mu_1 J_2^{(0)} - \alpha_1\mu_2 J_1^{(0)}$ and $2\alpha_1\mu_2 J_1^{(0)} - \alpha_2\mu_1 J_2^{(0)}$ cannot be both negative. If $2\alpha_1\mu_2 J_1^{(0)} - \alpha_2\mu_1 J_2^{(0)} \ge 0$, then

$$\xi_1 \left(2\alpha_2 \mu_1 J_2^{(0)} - \alpha_1 \mu_2 J_1^{(0)} \right) + \xi_2 \left(2\alpha_1 \mu_2 J_1^{(0)} - \alpha_2 \mu_1 J_2^{(0)} \right)$$

$$\geq \xi_1 \left(2\alpha_2 \mu_1 J_2^{(0)} - \alpha_1 \mu_2 J_1^{(0)} + 2\alpha_1 \mu_2 J_1^{(0)} - \alpha_2 \mu_1 J_2^{(0)} \right) > 0,$$

and the trace of J is negative.

Suppose $2\alpha_1\mu_2 J_1^{(0)} - \alpha_2\mu_1 J_2^{(0)} < 0$ and $2\alpha_2\mu_1 J_2^{(0)} - \alpha_1\mu_2 J_1^{(0)} \ge 0$, that is, $2\alpha_1\mu_2 J_1^{(0)} < \alpha_2\mu_1 J_2^{(0)}$. If $\frac{1}{2}\xi_2 < \xi_1 < \xi_2$, then

$$\xi_1 \left(2\alpha_2 \mu_1 J_2^{(0)} - \alpha_1 \mu_2 J_1^{(0)} \right) + \xi_2 \left(2\alpha_1 \mu_2 J_1^{(0)} - \alpha_2 \mu_1 J_2^{(0)} \right)$$

$$\geq \xi_2 \left(\alpha_2 \mu_1 J_2^{(0)} - \frac{1}{2} \alpha_1 \mu_2 J_1^{(0)} + 2\alpha_1 \mu_2 J_1^{(0)} - \alpha_2 \mu_1 J_2^{(0)} \right) > 0,$$

which leads to the trace of J negative. The proof is complete.

(B5) The proof under condition (4.26) is similar to that in (B4) and is omitted.

We provide two examples below to confirm and demonstrate our findings.

Example 4.2. Given parameters

$$a_{1} = 4, \quad a_{2} = 3, \quad b_{1} = 3, \quad b_{2} = 10, \quad \alpha_{1} = 0.9, \quad \alpha_{2} = 0.78, \\ d_{1} = 0.5, \quad d_{2} = 0.58, \quad \xi_{1} = 0.1, \quad \xi_{2} = 0.23, \quad \mu_{1} := 0.55, \quad \mu_{2} = 0.67, \end{cases}$$
(4.32)

we have $r_1^0 = 3.9560$ and $r_2^0 = 8.5601$ such that system (4.1) has two boundary equilibria $E_{01} = (41.3846, 57.3018, 0, 0)$ and $E_{02} = (0, 0, 44.7034, 52.0428)$ with $J_1^{(0)} < J_2^{(0)}$. It follows from

$$\frac{\alpha_1}{\xi_1\mu_1}(b_1 - b_2) = -35.43153796 < J_1^{(0)} - J_2^{(0)} = -3.31882392$$
$$< \frac{\alpha_2}{\xi_2\mu_2}(a_1 - a_2) = 13.84615385$$

that condition (4.12) is satisfied. Therefore, the two boundary equilibria are both locally asymptotically stable and there exists a unique positive equilibrium $E^* =$ $(J_1^*, A_1^*, J_2^*, A_2^*) = (10.0343, 13.8937, 33.3241, 25.9928)$ which is unstable. The phase plane diagram of system (4.19) is shown in the upper figure in Figure 1. The solution curves of system (4.1) are shown in the lower figures where solutions either approach E_{01} as in the left figure or approach E_{02} as in the right figure in Figure 2, depending on their initial values.

Example 4.3. For parameters

$$a_1 = 4, \quad a_2 = 9, \quad b_1 = 12, \quad b_2 = 15, \quad \alpha_1 = 0.9, \quad \alpha_2 = 0.78, \\ d_1 = 0.5, \quad d_2 = 0.58, \quad \xi_1 = 0.1, \quad \xi_2 = 0.23, \quad \mu_1 = 0.65, \quad \mu_2 = 0.67, \end{cases}$$
(4.33)



Figure 2. With parameters given in (4.32), condition (4.12) is satisfied, system (4.1) has a unique positive equilibrium $E^* = (J_1^*, A_1^*, J_2^*, A_2^*) = (10.0343, 13.8937, 33.3241, 25.9928)$. The two boundary equilibria $E_{01} = (41.3846, 57.3018, 0, 0)$ and $E_{02} = (0, 0, 44.7034, 52.0428)$ are both locally asymptotically stable and E^* is unstable. The phase plane diagram of system (4.19) is shown in the upper figure. The solution curves of system (4.1) are shown in the lower figures where solutions either approach E_{01} as in the left figure or approach E_{02} as in the right figure, depending on their initial values.

we have $r_1^0 = 3.9560$ and $r_2^0 = 12.8402$ such that system (4.1) has two boundary equilibria $E_{01} = (41.3846, 57.3018, 0, 0)$ and $E_{02} := (0, 0, 70.0117, 81.5061)$, and $J_1^{(0)} < J_2^{(0)}$. It follows from

$$\frac{\alpha_1}{\xi_1\mu_1}(a_1 - a_2) = -69.2308 < J_1^{(0)} - J_2^{(0)} = -28.6271 < \frac{\alpha_2}{\xi_2\mu_2}(b_1 - b_2) = -15.1849$$

that condition (4.13) is satisfied. Therefore, the two boundary equilibria are both unstable and there exists a unique positive equilibrium $E^*=(42.0476,58.2197,16.5559, 19.2470)$ which is locally asymptotically stable. The phase plane diagram of system (4.19) is shown in the left figure and the solution curves of system (4.1) are shown in the right figure in Figure 3.



Figure 3. With parameters given in (4.33), condition (4.13) is satisfied. System (4.1) has a unique positive equilibrium $E^* = (J_1^*, A_1^*, J_2^*, A_2^*) = (42.0476, 58.2197, 24.7103, 19.2470)$. The two boundary equilibria $E_{01} = (41.3846, 57.3018, 0, 0)$ and $E_{02} = (0, 0, 70.0117, 81.5061)$ are both unstable and E^* is locally asymptotically stable. The phase plane diagram of system (4.19) is shown in the left and the solution curves of system (4.1) are shown in the right.

5. Concluding remarks

We formulated stage-structured models for two mosquito species in this paper. We first showed that when there are no interspecific matings in model (3.1), one of the two boundary equilibria is globally asymptotically stable, the other boundary equilibrium is unstable, and there exists no positive equilibrium. Thus the competitive exclusion principle holds and the two mosquito species cannot coexist. We then included interspecific matings between the two species in model (4.1) and showed that the two boundary equilibria can be both locally asymptotically stable or both unstable if condition (4.12) or (4.13) holds. If the two boundary equilibria are both locally asymptotically stable, there exists a unique positive equilibrium but it is an unstable saddle point. One of the two species survives and the other go extinct depending on their initial sizes. The two mosquito species thus are still unable to coexist. If the two boundary equilibria are both unstable, there exists a unique positive equilibrium and it is locally asymptotically stable for most of the parameter settings given in (4.22), (4.23), (4.24), (4.25), or (4.26).

Notice that, under condition (4.12), system (4.1) has a positive equilibrium, but it is unstable. In such a case, the intraspecific mating is dominant such that $a_1 > a_2$ and $b_2 > b_1$. Either species may go extinct asymptotically depending on the initial sizes of the two species. No coexistence is possible. On the other hand, if the interspecific mating plays a more important role with $a_2 > a_1$ or $b_1 > b_2$, condition (4.13) is satisfied and it is then possible for the two species to coexist as shown in Example 4.3.

Nevertheless, there is also a parameter setting with which the model exhibits more complex dynamical features. For example, if the parameters are given by

$$a_1 = 1.7211, a_2 = 3.4121, b_1 = 1.8862, b_2 = 7.0020, \alpha_1 = 0.1685, \alpha_2 = 0.3605, d_1 = 0.6132, d_2 = 0.6257, \xi_1 = 0.0336, \xi_2 = 0.2215, \mu_1 = 0.3638, \mu_2 = 0.5154, (5.1)$$

condition (4.13) is satisfied and the two boundary equilibria are both unstable. System (4.19) and then (4.1) has a unique positive equilibrium $E^* = (J_1^*, A_1^*, J_2^*, A_2^*) =$ (3.4685, 1.6065, 0.3923, 0.2744). However, this unique positive equilibrium is unstable and there exists a locally asymptotically stable periodic solution as shown in Figure 4. In such a case, the two mosquito species can coexist but they do not approach a steady state asymptotically.



Figure 4. With parameters given in (5.1), condition (4.13) is satisfied. System (4.1) has a unique positive equilibrium $E^* = (J_1^*, A_1^*, J_2^*, A_2^*) = (3.4685, 1.6065, 0.3923, 0.2744)$. The two boundary equilibria $E_{01} = (0.4600, 0.2131, 0, 0)$ and $E_{02} := (0, 0, 17.6587, 12.3515)$ are both unstable, and E^* is also unstable. There exists a locally asymptotically stable periodic solution. The phase plan diagram of system (4.19) is shown in the left and the solution curves of system (4.1) are shown in the right.

Direct analysis on the 4-dimensional stage-structured model (4.1) is more difficult and less attractive. Our main results for the dynamics of the positive equilibrium, when it exists, are derived from the reduced 2-dimensional system (4.19). While we have gained insights into the interactive dynamics of the two mosquito species, our analysis is incomplete. Other dynamical features may occur as shown in Figure 4, and more complexity may exist. It is worth for further investigation both mathematically and biologically.

References

- B. W. Alto, L. P. Lounibos, S. Higgs and S. A. Juliano, Larval competition differentially affects arbovirus infection in aedes mosquitoes, Ecology, 2005, 86(12), 3279–3288.
- [2] I. Bargielowski, E. Blosser and L. P. Lounibos, The effects of interspecific courtship on the mating success of aedes aegypti and aedes albopictus (diptera: culicidae) males, Ecol. Popul. Biol., 2015, 108(4), 513–518.
- [3] N. Becker, Mosquitoes and Their Control, Kluwer Academic/Plenum, New York, 2003.
- [4] M. A. H. Braks, N. A. Honório, L. P. Lounibos, R. Lourenço-De-Oliveira and S. A. Juliano, Interspecific Competition Between Two Invasive Species of Container Mosquitoes, Aedes aegypti and Aedes albopictus (Diptera: Culicidae), in Brazil, Ann. Entomol. Soc. Am., 2004, 97(1), 130–139.

- [5] C. Dye, Intraspecific competition amongst larval aedes aegypti: Food exploitation or chemical interference, Ecol. Entomol., 1982, 7(1), 39–46.
- [6] R. M. Gleiser, J. Urrutia and D. E. Gorla, Effects of crowding on populations of aedes albifasciatus larvae under laboratory conditions, Entomologia Experimentalis et Applicata, 2000, 95(2), 135–140.
- [7] A. Giatropoulos, D. P. Papachristos, G. Koliopoulos, A. Michaelakis and N. Emmanoue, Asymmetric mating interference between two related mosquito species: aedes (stegomyia) albopictus and aedes (stegomyia) cretinus, PLoS One, 2015, 10(5), e0127762. https://doi.org/10.1371/journal.pone.0132862.
- [8] S. Juliano, L. Lounibos and G. O'Meara, A field test for competitive effects of Aedes albopictus on A. aegypti in South Florida: differences between sites of

coexistence and exclusion? Oecologia, 2004, 139(4), 583-593.

[9] B. Kesavaraju, P. T. Leisnham, S. Keane, N. Delisi and Rachel Pozatti, Interspecific Competition between Aedes albopictus and A. sierrensis: Potential for Competitive Displacement in the Western United States, PLoS ONE, 2014, 9(2), e89698.

https://doi.org/10.1371/journal.pone.0089698.

- [10] J. Li, Simple stage-structured models for wild and transgenic mosquito populations, J. Diff. Eqns. Appl., 2009, 15(4), 327–347.
- [11] J. Li, Malaria model with stage-structured mosquitoes, Math. Biol. Eng., 2011, 8(3), 753–768.
- [12] Z. Liu, C. Tian and S. Ruan, On a network model of two competitors with applications to the invasion and competition of aedes albopictus and aedes aegypti mosquitoes in the United States, SIAM J. Appl. Math., 2020, 80(2), 929–950.
- [13] L. P. Lounibos and S. A. Juliano, Where vectors collide: the importance of mechanisms shaping the realized niche for modeling ranges of invasive Aedes mosquitoes, Biol. Invas., 2018, 20(8), 1913–1929.
- [14] G. Marini, G. Guzzetta, F. Baldacchino et al., The effect of interspecific competition on the temporal dynamics of Aedes albopictus and Culex pipiens, Parasites & Vectors, 2017, 10, 102.
- [15] B. McKenzie, A. Wilson and S. Zohdy, Aedes albopictus is a competent vector of Zika virus: A meta-analysis, PLoS ONE, 2019, 14(5), e0216794. https://doi.org/10.1371/journal.pone.0216794.
- [16] Mosquitoes, National Geographic, 2021. https://www.nationalgeographic.com/animals/invertebrates/facts/ mosquitoes.
- [17] Mosquito Squad, How many species of mosquitoes are there? 2022. https://www.mosquitosquad.com/blog/mosquitoes-facts-more/ how-many-species-of-mosquitoes-are-there-.
- [18] Napa County, Encephalitis Mosquitoes, 2022. https://www.napamosquito.org/encephalitis-mosquitoes.
- [19] S. de Oliveira, D. A. M. Villela, F. B. S. Dias, L. A. Moreira and R. M. de Freitas, *How does competition among wild type mosquitoes influence the*

performance of Aedes aegypti and dissemination of Wolbachia pipientis? PLoS Negl. Trop. Dis., 2017, 11(10), e0005947 https://doi.org/10.1371/journal.pntd.0005947.

- [20] M. Otero, H. G. Solari and N. Schweigmann, A stochastic population dynamics model for Aedes aegypti: formulation and application to a city with temperate climate, Bull. Math. Biol., 2006, 68(8), 1945–1974.
- [21] PMI, World Mosquito Day. www.pmi.gov/world-mosquito-day-2021/.
- [22] W. Takken, C. Costantini, G. Dolo, A. Hassanali, N'. Sagnon and E. Osir, *Mosquito mating behaviour*, In: Bridging Laboratory and Field Research for Genetic Control of Disease Vectors, (Knols, B.G.J., Louis, C. (Eds.)), Springer, 2006, 183–188.