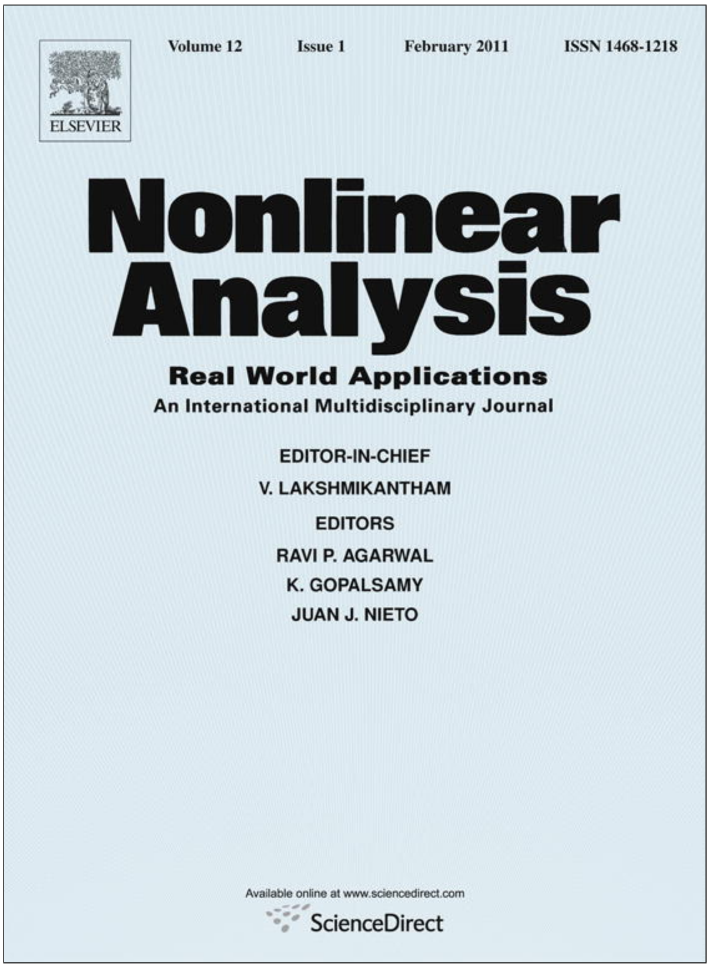
Volume 12 Issue 1 February 2011 ISSN 1468-1218
ELSEVIER
Nonlinear Analysis
Real World Applications
An International Multidisciplinary Journal
EDITOR-IN-CHIEF
V. LAKSHMIKANTHAM
EDITORS
RAVI P. AGARWAL
K. GOPALSAMY
JUAN J. NIETO
Available online at www.sciencedirect.com
ScienceDirect

Nonlinear Analysis: Real World Applications 12 (2011) 658–670

Contents lists available at ScienceDirect

Nonlinear Analysis: Real World Applications

journal homepage: www.elsevier.com/locate/nonrwa

Dynamics of a model of allelopathy and bacteriocin with a single mutation

Lan Zou [a,b], Xingwu Chen [a], Shigui Ruan [b,*], Weinian Zhang [a]

[a] Yangtze Center of Mathematics and Department of Mathematics, Sichuan University, Chengdu, Sichuan 610064, PR China
[b] Department of Mathematics, University of Miami, Coral Gables, FL 33124-4250, USA

ARTICLE INFO

Article history:
Received 20 January 2009
Accepted 12 July 2010

Keywords:
Population dynamics
Saddle–node
Index of equilibrium
Center manifold
Bifurcation

ABSTRACT

In this paper we discuss a model of allelopathy and bacteriocin in the chemostat with a wild-type organism and a single mutant. Dynamical properties of this model show the basic competition between two microorganisms. A qualitative analysis about the boundary equilibrium, a state that both microorganisms vanish, is carried out. The existence and uniqueness of the interior equilibrium are proved by a technical reduction to the singularity of a matrix. Its dynamical properties are given by using the index theory of equilibria. We further discuss its bifurcations. Our results are demonstrated by numerical simulations.

1. Introduction

Antibiotic resistance among bacteria has become a worldwide public health threat [1,2]. One of the limitations of using broad-spectrum antibiotics is that they kill almost any bacterial species not specifically resistant to the drug [3]. Frequent use of these antibiotics result in an intensive selection pressure for the evolution of antibiotic resistance in both pathogen and commensal bacteria [4,3]. Alternative methods of combating infection has been considered [5,3].

Allelopathy is the chemical inhibition of one species by another [6,7]. Bacteriocin, a particular type of allelopathy, is a toxin produced by bacteria that inhibits the growth of closely related species [8]. Bacteriocins provide an alternative solution with their relatively narrow spectrum of killing activity. Special examples of bacteriocin productions involving more than two competing organisms, such as the bacteriocins of *Escherichia coli* and *Klebsiella pneumonia*, are given in [5].

Various mathematical models have been proposed to examine the interaction between bacteriocin-producer and sensitive strains ([9,10,8], etc.). Recently, Abell et al. [8] proposed chemostat-type competition models with mutation and toxin production. Via numerical simulations, they showed how the coexistence of competitors depends upon the growth rates and toxin sensitivity.

A chemostat is a laboratory bio-reactor used to culture microorganisms [11]. Competition for single and multiple resources, the evolution of resource acquisition, and competition among organisms have been investigated in ecology and biology using chemostats [12–17]. Since 1950 [15,16], chemostat models have been studied. We refer to the monograph of Smith and Waltman [11], the surveys of Hsu and Waltman [18] and Ruan [19] and the references cited therein.

In this paper, we study the dynamics of the allelopathy model in the chemostat with a wild-type organism and a single mutation proposed by Abell et al. [8]. Let $S(t)$ be the concentration of the nutrient at time t, $x(t)$ be the density of the wild-type organism X at time t, and $y(t)$ be the density of a mutant Y at time t, respectively. It is assumed that the two

* Corresponding author.
E-mail address: ruan@math.miami.edu (S. Ruan).

1468-1218/$ – see front matter © 2010 Elsevier Ltd. All rights reserved.
doi:10.1016/j.nonrwa.2010.07.008

microorganisms X and Y compete for the nutrient, the wild-type organism X can mutate to the microorganism Y, and the single mutant of a parental species Y can revert to the wild-type X during reproduction. The model takes the following form:

$$\begin{cases} S'(t) = D(S^0 - S(t)) - \dfrac{1}{\gamma} f_1(S)x(t) - \dfrac{1}{\gamma} f_2(S)y(t), \\ x'(t) = x(t)[(1-\alpha)f_1(S) - D] + \beta f_2(S)y(t), \\ y'(t) = y(t)[(1-\beta)f_2(S) - D] + \alpha f_1(S)x(t), \end{cases} \tag{1.1}$$

where D is the dilution rate, γ is the yield constant, $0 \le \alpha \le 1$ is the rate at which X mutates, $0 \le \beta \le 1$ is the rate at which Y reverts to X during reproduction, and $f_i(S) = m_i S/(a_i + S)$ is the Michaelis–Menten–Monod function, in which $m_i > 0$ is the maximum growth rate and $a_i > 0$ is the Michaelis–Menten–Monod constant.

After rescaling the variables and some parameters and using the same notation, the model can be written as follows [8]:

$$\begin{cases} S' = 1 - S - f_1(s)x - f_2(S)y, \\ x' = x[(1-\alpha)f_1(S) - 1] + \beta f_2(S)y, \\ y' = y[(1-\beta)f_2(S) - 1] + \alpha f_1(S)x. \end{cases} \tag{1.2}$$

Let $\Sigma = 1 - S - x - y$. Then, $\Sigma' = -\Sigma$ and system (1.2) can be replaced with

$$\begin{cases} \Sigma' = -\Sigma, \\ x' = x[(1-\alpha)f_1(1-\Sigma-x-y) - 1] + \beta f_2(1-\Sigma-x-y)y, \\ y' = y[(1-\beta)f_2(1-\Sigma-x-y) - 1] + \alpha f_1(1-\Sigma-x-y)x. \end{cases} \tag{1.3}$$

Since solutions of $\Sigma' = -\Sigma$ all tend to 0 as $t \to +\infty$, system (1.2) is asymptotic to the two-dimensional system [20,11]

$$\begin{cases} x' = x\left[(1-\alpha)\dfrac{m_1(1-x-y)}{a_1+1-x-y} - 1\right] + \beta\dfrac{m_2(1-x-y)}{a_2+1-x-y}y := \tilde{f}(x,y), \\ y' = y\left[(1-\beta)\dfrac{m_2(1-x-y)}{a_2+1-x-y} - 1\right] + \alpha\dfrac{m_1(1-x-y)}{a_1+1-x-y}x := \tilde{g}(x,y) \end{cases} \tag{1.4}$$

in the region $\mathcal{G} = \{(x,y) : x \ge 0, y \ge 0, x + y \le 1\}$.

When $\alpha = \beta = 0$, system (1.2) has been discussed in [13]. Later, Hsu et al. [14] presented some results for the case $\beta = 0$ and $0 < \alpha < 1$, which is equivalent to the case $\alpha = 0$ and $0 < \beta < 1$. Therefore, we mainly consider the case $0 < \alpha, \beta \le 1$ in this paper.

Based on the study on system (1.2) in [8], we first discuss the properties of the boundary equilibrium E_0. We then consider the existence and uniqueness of the interior equilibrium E_1 by using a singular matrix. By employing the index of the equilibrium, we study the stability of E_1 by its Jacobian matrix.

The paper is organized as follows. In Section 2 we consider the boundary equilibria. The existence of the interior equilibrium is addressed in Section 3 and the properties of the interior equilibrium are given in Section 4. Section 5 deals with possible bifurcations of the model. Numerical simulations and some remarks are given in Section 6.

2. The boundary equilibria

To find the equalibria of system (1.4), we find zeros of the coupled equations $\tilde{f}(x,y) = 0$, $\tilde{g}(x,y) = 0$, i.e.,

$$\begin{cases} x\left[(1-\alpha)\dfrac{m_1(1-x-y)}{a_1+1-x-y} - 1\right] + \beta\dfrac{m_2(1-x-y)}{a_2+1-x-y}y = 0, \\ y\left[(1-\beta)\dfrac{m_2(1-x-y)}{a_2+1-x-y} - 1\right] + \alpha\dfrac{m_1(1-x-y)}{a_1+1-x-y}x = 0. \end{cases} \tag{2.1}$$

We can see that $E_0 = (0, 0)$ is the unique boundary equilibrium of system (1.4) when $0 < \alpha \le 1$ and $0 < \beta \le 1$. In fact, when $x = 0$, (2.1) is equivalent to that

$$\beta\frac{m_2(1-y)}{a_2+1-y}y = 0 \quad \text{and} \quad y\left[(1-\beta)\frac{m_2(1-y)}{a_2+1-y} - 1\right] = 0,$$

implying that $y = 0$. Similarly, if $y = 0$, (2.1) exists if and only if $x = 0$. Furthermore, on $x + y = 1$, (2.1) is equivalent to that $y = 0$ and $x = 0$, which obviously do not exist on $x + y = 1$. So there is no other boundary equilibrium except E_0.

In order to determine the qualitative properties of E_0, we calculate the Jacobian of system (1.4) at E_0, i.e.,

$$J(E_0) = \begin{bmatrix} \dfrac{(1-\alpha)m_1}{a_1+1} - 1 & \dfrac{\beta m_2}{a_2+1} \\ \dfrac{\alpha m_1}{a_1+1} & \dfrac{(1-\beta)m_2}{a_2+1} - 1 \end{bmatrix}$$

and see that eigenvalues are zeros of the polynomial $P(\lambda) := \lambda^2 - T_0\lambda + D_0$, where

$$T_0 := \mathrm{tr}\, J(E_0) = \frac{(1-\alpha)m_1}{a_1+1} + \frac{(1-\beta)m_2}{a_2+1} - 2,$$

$$D_0 := \det J(E_0) = \frac{(1-\alpha-\beta)m_1m_2}{(a_1+1)(a_2+1)} - \frac{(1-\alpha)m_1}{a_1+1} - \frac{(1-\beta)m_2}{a_2+1} + 1.$$

Since the discriminant

$$\Delta_0 := T_0^2 - 4D_0 = \left(\frac{(1-\alpha)m_1}{a_1+1} - \frac{(1-\beta)m_2}{a_2+1}\right)^2 + 4\frac{\alpha\beta m_1m_2}{(a_1+1)(a_2+1)} > 0. \tag{2.2}$$

It follows that E_0 is neither a focus nor of the center type.

Theorem 1. (i) E_0 *is a saddle if* $D_0 < 0$. *Moreover, the trajectories starting from* $\mathcal{G}$ *all go far away from* E_0, (ii) E_0 *is a stable node if* $D_0 > 0$ *and* $T_0 < 0$. (iii) E_0 *is an unstable node if* $D_0 > 0$ *and* $T_0 > 0$. (iv) *If* $D_0 = 0$, *then the equilibrium* E_0 *is a saddle–node and* E_0 *is stable in* $\mathcal{G}$.

Proof. In order to prove (i), we note that the stable manifold is tangent to the eigenvector (x_s, y_s) at E_0 and the unstable manifold is tangent to the eigenvector (x_u, y_u) at E_0, where x_s, y_s, x_u and y_u satisfy

$$\frac{1}{2}\left[\frac{(1-\alpha)m_1}{a_1+1} - 4 - \frac{(1-\beta)m_2}{a_2+1} - \sqrt{\left(\frac{(1-\alpha)m_1}{a_1+1} - \frac{(1-\beta)m_2}{a_2+1}\right)^2 + 4\frac{\alpha m_1\beta m_2}{(a_1+1)(a_2+1)}}\right]x_u + \frac{\beta m_2}{a_2+1}y_u = 0,$$

$$\frac{1}{2}\left[\frac{(1-\alpha)m_1}{a_1+1} - 4 - \frac{(1-\beta)m_2}{a_2+1} + \sqrt{\left(\frac{(1-\alpha)m_1}{a_1+1} - \frac{(1-\beta)m_2}{a_2+1}\right)^2 + 4\frac{\alpha m_1\beta m_2}{(a_1+1)(a_2+1)}}\right]x_s + \frac{\beta m_2}{a_2+1}y_s = 0,$$

which means that $x_uy_u > 0$ and $x_sy_s < 0$. Therefore, the intersection of the stable manifold and $\mathcal{G}$ is empty, while the intersection of the stable manifold and $\mathcal{G}$ is nonempty. This proves (i).

When $D_0 > 0$, we assure that $T_0 \neq 0$; otherwise, $\Delta_0 = -4D_0 < 0$, a contradiction to (2.2). Thus we only need to discuss the case of $T_0 < 0$ and the case of $T_0 > 0$. In the two cases the assumption $D_0 > 0$ implies results (ii) and (iii), respectively.

In order to discuss the case (iv), we need to determine the qualitative properties in the degenerate case. Applying a time-scaling transformation $t = \tau(a_1 + 1 - x - y)(a_2 + 1 - x - y)$, we can reduce system (1.4) orbital-equivalently to the polynomial differential system

$$\begin{cases} x' = f(x, y), \\ y' = g(x, y), \end{cases} \tag{2.3}$$

where

$$\begin{aligned} f(x,y) &:= [(1-\alpha)m_1 - 1 - a_1](a_2+1)x + \beta m_2(a_1+1)y + \{a_1 + (a_2+2)[1-(1-\alpha)m_1]\}x^2 \\ &\quad + [(a_2+2)(1-(1-\alpha)m_1) + a_1 - \beta m_2(a_1+2)]xy - \beta m_2(a_1+2)y^2 + [(1-\alpha)m_1 - 1]x^3 \\ &\quad + [\beta m_2 - 2 + 2m_1(1-\alpha)]x^2y + [2\beta m_2 - 1 + (1-\alpha)m_1]xy^2 + \beta m_2 y^3, \\ g(x,y) &:= \alpha m_1(a_2+1)x + [(1-\beta)m_2 - a_2 - 1](a_1+1)y - m_1\alpha(a_2+2)x^2 \\ &\quad + [(1-(1-\beta)m_2)(a_1+2) + a_2 - \alpha m_1(a_2+2)]xy + \{a_2 + (a_1+2)[1-(1-\beta)m_2]\}y^2 \\ &\quad + \alpha m_1 x^3 + [2m_1\alpha - 1 + m_2(1-\beta)]x^2y + [\alpha m_1 - 2 + 2(1-\beta)m_2]xy^2 + [(1-\beta)m_2 - 1]y^3. \end{aligned}$$

If $D_0 = 0$, then

$$\{(1-\alpha)m_1 - (a_1+1)\}\{(1-\beta)m_2 - (a_2+1)\} = \alpha\beta m_1m_2. \tag{2.4}$$

Assume that $T_0 \geq 0$. Then,

$$(a_2+1)[(1-\alpha)m_1 - (a_1+1)] \geq -(a_1+1)[(1-\beta)m_2 - (a_2+1)].$$

Substituting (2.4) in it, we get

$$(a_2+1)((1-\alpha)m_1 - (a_1+1))^2 \leq -\alpha\beta m_1m_2(a_1+1),$$

which holds if and only if its both sides vanish. This contradicts to the inequality $\beta m_2\alpha m_1(a_1+1) > 0$. In fact, $\beta > 0$, $\alpha > 0$, $m_1 > 0$, $m_2 > 0$, and $a_1 > 0$. It concludes that $T_0 < 0$. Therefore, only one of eigenvalues of the system vanishes but the other is equal to $T_0 < 0$.

Furthermore, with a transformation

$$\begin{cases} u = -\alpha m_1(a_2+1)x + ((1-\alpha)m_1 - a_1 - 1)(a_2+1)y, \\ v = -\alpha m_1(a_2+1)x - ((1-\beta)m_2 - a_2 - 1)(a_1+1)y, \end{cases}$$

we change system (2.3) into the form

$$\begin{cases}\dot{u} = U(u, v),\\ \dot{v} = \mu v + V(u, v),\end{cases} \tag{2.5}$$

where $\mu = (1-\alpha)m_1(a_2+1) + (1-\beta)m_2(a_1+1) - 2(a_1+1)(a_2+1)$ and U, V are $O(|u|^2 + |v|^2)$ and shown in Appendix A. By the implicit function theorem, there is a unique function $v = \phi(u)$ such that $\phi(0) = 0$ and $V(u, \phi(u)) = 0$. Actually, we can solve from $\mu v + V(u, v) = 0$ that

$$\begin{aligned}\phi(u) = {} & \alpha m_1\{(a_2+1)[(a_2+2)(1-(1-\alpha)m_1) + a_1]\\ & -[(1-\beta)m_2 - (a_2+1)](a_1+1)(a_2+2)\}u^2/[(1-\alpha)m_1(a_2+1)\\ & +(1-\beta)m_2(a_1+1) - 2(a_1+1)(a_2+1)] + O(|u|^3).\end{aligned}$$

Substituting $v = \phi(u)$ in the first equation of (2.5), we get

$$U(u, \phi(u)) = a_1\alpha m_1(a_2+1)^2u^2 + O(|u|^3),$$

which implies that E_0 is a saddle–node of system (2.5). i.e., E_0 is a saddle–node of system (1.4).

Moreover, since $a_1\alpha m_1(a_2+1)^2 > 0$, the two hyperbolic sectors lie on the left but the parabolic sector lies on the right. So E_0 is stable in $\mathcal{G}$. □

3. Existence of interior equilibria

It is much more difficult to determine the interior equilibria because much more complex computation is needed. In this section we consider (1.4) in the interior of the region $\mathcal{G}$, denoted by int$\mathcal{G}$.

Theorem 2. *System (1.4) has at most one interior equilibrium. Furthermore, system (1.4) has exactly one interior equilibrium $E_1 = (x_1, y_1)$ if and only if E_0 is unstable in $\mathcal{G}$, where*

$$x_1 = \frac{\beta m_2 z_1(a_1+z_1)(1-z_1)}{(a_1+z_1)\beta m_2 z_1 - (a_2+z_1)(K_1z_1 - a_1)}, \qquad y_1 = \frac{-(a_2+z_1)(K_1z_1-a_1)(1-z_1)}{(a_1+z_1)\beta m_2 z_1 - (a_2+z_1)(K_1z_1-a_1)},$$

$$z_1 = \begin{cases}\dfrac{-(a_2K_1 + a_1K_2) + \sqrt{\Delta}}{2(\alpha\beta m_1m_2 - K_1K_2)}, & \alpha\beta m_1 m_2 \neq K_1K_2,\\[2ex] \dfrac{a_1a_2}{a_2K_1 + a_1K_2}, & \alpha\beta m_1m_2 = K_1K_2,\end{cases}$$

$$\Delta = (a_2K_1 - a_1K_2)^2 + 4\alpha\beta m_1m_2a_1a_2,$$

$$K_1 = (1-\alpha)m_1 - 1, \qquad K_2 = (1-\beta)m_2 - 1.$$

Proof. The system (2.1) of determining equilibria is equivalent to the system

$$\begin{cases}x[(1-\alpha)m_1(1-x-y) - a_1 - 1 + x + y](a_2+1-x-y) + \beta m_2(1-x-y)(a_1+1-x-y)y = 0,\\ y[(1-\beta)m_2(1-x-y) - a_2 - 1 + x + y](a_1+1-x-y) + \alpha m_1(1-x-y)(a_2+1-x-y)x = 0,\end{cases}$$

which can be rewritten as

$$\begin{bmatrix}(K_1z - a_1)(a_2+z) & \beta m_2 z(a_1+z)\\ \alpha m_1 z(a_2+z) & (K_2z - a_2)(a_1+z)\end{bmatrix}\begin{bmatrix}x\\ y\end{bmatrix} = \begin{bmatrix}0\\ 0\end{bmatrix}, \tag{3.1}$$

where $z := 1 - x - y$. The system has an interior equilibrium if and only if there is a pair of nonzero x and y such that (3.1) holds. It follows that the determinant of coefficient matrix of (3.1) is equal to zero, i.e.,

$$\Upsilon(z) := (\alpha\beta m_1m_2 - K_1K_2)z^2 + (a_2K_1 + a_1K_2)z - a_1a_2 = 0. \tag{3.2}$$

Since the region int$\mathcal{G}$ requires $0 < z < 1$, we need to discuss positive roots of the quadratic equation (3.2).

Case 1. $\alpha\beta m_1m_2 - K_1K_2 > 0$. In this case the quadratic equation (3.2) surely has a positive root, which must be

$$z_1 = \frac{-(a_2K_1 + a_1K_2) + \sqrt{\Delta}}{2(\alpha\beta m_1m_2 - K_1K_2)}, \tag{3.3}$$

because

$$\Delta := (a_2K_1 - a_1K_2)^2 + 4\alpha\beta m_1m_2a_1a_2 > 0 \tag{3.4}$$

and $-a_1a_2 < 0$. Thus, the quadratic equation (3.2) has at most one zero in the interval (0, 1) and system (1.4) has at most one interior equilibrium. Furthermore, with z_1 given by (3.3) we can determine the coordinates x_1, y_1 of the corresponding equilibrium. Actually, from the first equation in (3.1), where z is replaced by z_1, we get

$$\{(a_2 + z_1)(K_1z_1 - a_1)\}x_1 = -\{(a_1 + z_1)\beta m_2 z_1\}y_1.$$

Let

$$\xi = \frac{x_1}{(a_1 + z)\beta m_2 z_1}. \tag{3.5}$$

It implies that

$$y_1 = -(a_2 + z_1)(K_1z_1 - a_1)\xi. \tag{3.6}$$

Noting that $z_1 = 1 - x_1 - y_1$, from (3.5) and (3.6), we obtain

$$1 - z_1 = [(a_1 + z_1)\beta m_2 z_1 - (a_2 + z_1)(K_1z_1 - a_1)]\xi,$$

which implies that

$$\xi = \frac{1 - z_1}{(a_1 + z_1)\beta m_2 z_1 - (a_2 + z_1)(K_1z_1 - a_1)}.$$

Thus, by (3.5) and (3.6), we uniquely obtain

$$\begin{cases} x_1 = \dfrac{\beta m_2 z_1(a_1 + z_1)(1 - z_1)}{(a_1 + z_1)\beta m_2 z_1 - (a_2 + z_1)(K_1z_1 - a_1)}, \\ y_1 = \dfrac{-(a_2 + z_1)(K_1z_1 - a_1)(1 - z_1)}{(a_1 + z_1)\beta m_2 z_1 - (a_2 + z_1)(K_1z_1 - a_1)}. \end{cases} \tag{3.7}$$

Case 2. $\alpha\beta m_1m_2 - K_1K_2 \le 0$. In this case we have $K_1K_2 > 0$, implying that $a_2K_1 + a_1K_2$, the coefficient of the first degree term in $\Upsilon(z)$, does not vanish. Since Eq. (3.2) has no positive roots when $a_2K_1 + a_1K_2 < 0$, we only need to discuss in the case that $a_2K_1 + a_1K_2 > 0$. When $a_2K_1 + a_1K_2 > 0$, we obviously have

$$K_1 > 0, \qquad K_2 > 0. \tag{3.8}$$

In the circumstance that $\alpha\beta m_1m_2 - K_1K_2 = 0$, Eq. (3.2) reduces to a linear equation and has a unique root $z_1 = a_1a_2/(a_2K_1 + a_1K_2)$. It lies in (0, 1) if and only if $a_2K_1 + a_1K_2 - a_1a_2 > 0$. Such a z_1 determines the coordinates x_1, y_1 by the same (3.7) as in the discussion in Case 1. In the other circumstance, i.e., $\alpha\beta m_1m_2 - K_1K_2 < 0$, the quadratic equation (3.2) has two positive roots

$$z_1 = \frac{-(a_2K_1 + a_1K_2) + \sqrt{\Delta}}{2(\alpha\beta m_1m_2 - K_1K_2)}, \qquad z_2 = \frac{-(a_2K_1 + a_1K_2) - \sqrt{\Delta}}{2(\alpha\beta m_1m_2 - K_1K_2)},$$

where Δ is defined in (3.4). Clearly, $z_1 < z_2$. We claim that system (1.4) has at most one interior equilibrium, the same point $E_1 = (x_1, y_1)$ as in Case 1, where x_1 and y_1 are given in (3.7). It suffices to prove that the equilibrium $E_2 = (x_2, y_2)$, determined by z_2, locates outside the region int$\mathcal{G}$. For an indirect proof, assume that $x_2 > 0, y_2 > 0$. It is clear that $0 < z_2 := 1 - (x_2 + y_2) < 1$. Since x_2, y_2 have the same expressions as x_1, y_1 in (3.7) where z_1 is replaced with z_2 and the numerator of x_2, i.e., $\beta m_2 z_2(a_1 + z_2)(1 - z_2)$, is positive, we see that the common denominator $(a_1 + z_2)\beta m_2 z_2 - (a_2 + z_2)(K_1z_2 - a_1)$ is also positive. It follows from the numerator of y_2, i.e., $-(a_2 + z_2)(K_1z_2 - a_1)(1 - z_2)$, that $K_1z_2 - a_1 < 0$. It is equivalent to say

$$-K_1(a_2K_1 + a_1K_2) - 2a_1(\alpha\beta m_1m_2 - K_1K_2) > K_1\sqrt{\Delta}.$$

Taking the square of both sides, we have

$$4a_1\alpha\beta m_1m_2K_1(a_2K_1 - a_1K_2) + 4a_1^2\alpha^2\beta^2m_1^2m_2^2 > 4K_1^2\alpha\beta m_1m_2a_1a_2,$$

which implies that $\alpha\beta m_1m_2 - K_1K_2 > 0$, a contradiction to the assumption that $\alpha\beta m_1m_2 - K_1K_2 < 0$.

In summary, in all cases we considered above, system (1.4) has at most one equilibrium in the region int$\mathcal{G}$. Now we further prove that system (1.4) has at least one equilibrium in this open region when E_0 is unstable. Construct a closed curve Γ with line segments $AB := \{(x, y) : x + y = 1, 0 \le x, y \le 1\}$, $BB_0 := \{(x, y) : y = 0, 0 < \epsilon \le x \le 1\}$, $B_0A_0 := \{(x, y) : x + y = \epsilon, 0 \le x, y \le \epsilon\}$ and $A_0A := \{(x, y) : x = 0, 0 < \epsilon \le y \le 1\}$. Restricted to AB, system (1.4) reduces to the form $\mathrm{d}x/\mathrm{d}t = -x$, $\mathrm{d}y/\mathrm{d}t = -y$, implying that both x and y decrease and trajectories staring from AB all enter $\mathcal{G}$. Restricted to A_0A, system (1.4) implies that $\mathrm{d}x/\mathrm{d}t = \beta m_2(1 - y)y/(a_2 + 1 - y) > 0$, i.e., $x(t)$ increases, and therefore trajectories staring from A_0A all enter $\mathcal{G}$. Similarly, trajectories staring from BB_0 all enter $\mathcal{G}$. Moreover, all trajectories starting from B_0A_0 go away from E_0 as ϵ is chosen sufficiently small when E_0 is unstable. This proves that all trajectories starting from Γ enter the region surrounded by Γ. Therefore, the winding number of the vector field (1.4) along the curve Γ is equal to 1. As indicated in [21, p. 313] and [22, Chpater 3], there is at least one equilibrium in the interior of the region bounded by the curve Γ. As a consequence, system (1.4) has exactly one interior equilibrium E_1 when E_0 is unstable.

Furthermore, we claim that no equilibrium exists in int$\mathcal{G}$ when E_0 is stable. In this case, by Theorem 1, we have $T_0 < 0$ and $D_0 \geq 0$, which respectively implies that $(\frac{(1-\alpha)m_1}{a_1+1}-1)+(\frac{(1-\beta)m_2}{a_2+1}-1) < 0$ and $(\frac{(1-\alpha)m_1}{a_1+1}-1)(\frac{(1-\beta)m_2}{a_2+1}-1) \geq \frac{\alpha\beta m_1 m_2}{(a_1+1)(a_2+1)} > 0$. It means that $\frac{(1-\alpha)m_1}{a_1+1} < 1$ and $\frac{(1-\beta)m_2}{a_2+1} < 1$. Hence,

$$K_1 < a_1, \qquad K_2 < a_2, \tag{3.9}$$

$$\Upsilon(1) = \alpha\beta m_1 m_2 - K_1K_2 + a_1K_2 + a_2K_1 - a_1a_2 \leq 0, \tag{3.10}$$

where Υ is defined in (3.2). In the case that $\alpha\beta m_1m_2 - K_1K_2 > 0$, the quadratic function Υ is convex and has no zeros in $(0, 1)$ by (3.10) and the fact

$$\Upsilon(0) = -a_1a_2 < 0. \tag{3.11}$$

In the case that $\alpha\beta m_1m_2 - K_1K_2 = 0$ the function Υ, linking two non-positive $\Upsilon(0)$ and $\Upsilon(1)$ linearly, also has no zeros in $(0, 1)$. In the case that $\alpha\beta m_1m_2 - K_1K_2 < 0$, the quadratic function Υ is concave. If it has a positive zero then, as discussed in the above Case 2, (3.8) holds, i.e., $K_1 > 0$ and $K_2 > 0$. By (3.9), $0 < K_1K_2 < a_1a_2$. It follows that

$$\sigma := \frac{-a_1a_2}{\alpha\beta m_1m_2 - K_1K_2} > 1. \tag{3.12}$$

If $\Upsilon(1) < 0$ then, by (3.11) and (3.4), the function Υ has either no or two zeros in $(0, 1)$, but (3.12), where we note that σ is equal to the product of two zeros, implies that at least one zero of Υ lies outside $[-1, 1]$. This proves that Υ has no zeros in $(0, 1)$. If $\Upsilon(1) = 0$ then one zero of Υ is $z_1 = 1$ and the other zero is $z_2 = \sigma > 1$ by (3.12). It also implies that Υ has no zeros in $(0, 1)$. Consequently, system (1.4) has no interior equilibria.

Summarizing the above discussion we see that system (1.4) has exactly one interior equilibrium if and only if E_0 is unstable. □

The proof of Theorem 2 also gives a computable condition for the existence of the interior equilibrium, i.e., system (1.4) has exactly one interior equilibrium if and only if

$$0 < z_1 < 1, \qquad K_1z_1 - a_1 < 0, \tag{3.13}$$

where z_1, K_1, K_2 are defined in Theorem 2.

4. Properties of the interior equilibrium

By Theorem 2, we only need to discuss the unique interior equilibrium E_1 in the region int$\mathcal{G}$ when the boundary equilibrium E_0 is unstable.

Theorem 3. *E_1 is asymptotically stable if it exists. Moreover, E_1 is a stable node if*

$$\delta_1 := m_2 z_1^2 (a_1+z_1)^4 (a_2+z_1)^2 \beta^2 + c_1\beta + c_0 \geq 0, \tag{4.1}$$

where

$$\begin{aligned} c_1 &= 2(a_1+z_1)^2(a_2+z_1)m_2z_1[m_1z_1(1+\alpha)(a_1+z_1)(a_2+z_1)^2 - z_1(a_1+z_1)^2(a_2+z_1) \\ &\quad - m_1a_1x_1(a_2+z_1)^2 - 2m_1a_2y_1z_1(a_1+z_1)(a_2+z_1) + m_2a_2y_1(a_1+z_1)^2], \\ c_2 &= (1-\alpha)^2 m_1 z_1^2 (a_1+z_1)^2 (a_2+z_1)^4 - 2(1-\alpha)m_1m_2z_1^2(a_1+z_1)^3(a_2+z_1)^3 + m_2z_1^2(a_1+z_1)^4(a_2+z_1)^2 \\ &\quad - 2(1-\alpha)m_1^2a_1x_1z_1(a_1+z_1)(a_2+z_1)^2 + 2(1-2\alpha)m_1m_2a_1x_1z_1(a_1+z_1)^2(a_2+z_1)^3 \\ &\quad + 2(1-\alpha)m_1m_2a_2y_1z_1(a_1+z_1)^3(a_2+z_1)^2 - 2m_2^2a_2y_1z_1(a_1+z_1)^4(a_2+z_1) + m_1^2a_1^2x_1^2(a_2+z_1)^4 \\ &\quad + 2m_1m_2a_1a_2x_1x_2(a_1+z_1)^2(a_2+z_1)^2 + m_2^2a_2^2y_1^2(a_1+z_1)^4 \end{aligned}$$

and x_1, y_1, z_1 are defined by parameters α, β, a_1, a_2, m_1, m_2 as in (3.7) and (3.3).

Proof. Qualitative properties of E_1 are determined by the signs of the trace T_1, the determinant D_1 and the discriminant Δ_1 of the Jacobian matrix of system (1.4) at E_1. Simple computation shows that

$$\begin{aligned} T_1 &= \frac{(K_1z_1-a_1)(a_1+z_1) - m_1a_1x_1}{(a_1+z_1)^2} + \frac{(K_2z_1-a_2)(a_2+z_1) - m_2a_2y_1}{(a_2+z_1)^2}, \\ D_1 &= 1 - \frac{(1-\alpha)m_1z_1}{a_1+z_1} - \frac{(1-\beta)m_2z_1}{a_2+z_1} + \frac{(1-\alpha-\beta)m_1m_2z_1^2}{(a_1+z_1)(a_2+z_1)} + \frac{m_1a_1x_1}{(a_1+z_1)^2} + \frac{m_2a_2y_1}{(a_2+z_1)^2} \\ &\quad - \frac{(1-\alpha-\beta)m_1m_2a_2z_1y_1}{(a_1+z_1)(a_2+z_1)^2} - \frac{(1-\alpha-\beta)m_1m_2a_1z_1x_1}{(a_1+z_1)^2(a_2+z_1)}, \end{aligned}$$

$$\begin{aligned}\Delta_1 \;=\;& \frac{(1-\alpha)^2 m_1 z_1^2}{(a_1+z_1)^2} + \frac{2m_1m_2z_1^2(\alpha(1+\beta)-(1-\beta))}{(a_1+z_1)(a_2+z_1)} + \frac{(1-\beta)^2 m_2 z_1^2}{(a_2+z_1)^2} - \frac{2(1-\alpha)m_1^2a_1x_1z_1}{(a_1+z_1)^3}\\ &+ \frac{2m_1m_2a_1x_1z_1(1-2\alpha-\beta)}{(a_1+z_1)^2(a_2+z_1)} + \frac{2m_1m_2a_2y_1z_1(1-\alpha-2\beta)}{(a_1+z_1)(a_2+z_1)^2} - \frac{2(1-\beta)m_2^2a_2y_1z_1}{(a_2+z_1)^3}\\ &+ \frac{m_1^2a_1^2x_1^2}{(a_1+z_1)^4} + \frac{2m_1m_2a_1a_2x_1x_2}{(a_1+z_1)^2(a_2+z_1)^2} + \frac{m_2^2a_2^2y_1^2}{(a_2+z_1)^4}.\end{aligned}$$

From the first equation in (3.1) we see that $K_2z_1 - a_2 < -2m_1z_1(a_2+z_1)x_1/\{(a_1+z_1)y_1\} < 0$ since $a_1, a_2, m_1, K_2, x_1, y_1, z_1$ are all positive. Similarly $K_2z_1 - a_2 < 0$ by the second equation in (3.1). It follows that $T_1 < 0$. We further claim that

$$D_1 \geq 0.$$

In fact, if $D_1 < 0$, i.e., E_1 is a saddle, then the index of E_1 is equal to -1. Consider the closed curve Γ composed in the proof of Theorem 2. The fact that all trajectories starting from Γ enter the region surrounded by Γ implies that the winding number of the vector field (1.4) along the curve Γ is equal to 1. This makes a contradiction to the Theorem on the sum of indices ([21, p. 313], [22, Chpater 3]) because of the uniqueness of the interior equilibrium (given in Theorem 2).

In what follows we discuss the case $D_1 > 0$ and the case $D_1 = 0$ separately.

In the case $D_1 > 0$, E_1 is either a stable node or a stable focus because $T_1 < 0$. Furthermore, E_1 is a node if the inequality $\Delta_1 \geq 0$ holds. This inequality can be simplified as the condition (4.1) because $a_1 + z_1 > 0$ and $a_2 + z_1 > 0$.

In the case $D_1 = 0$, the equilibrium E_1 is degenerate. Clearly, $\Delta_1 = T_1^2 > 0$ in this case, i.e., condition (4.1) is satisfied naturally. Since $T_1 < 0$, the two eigenvalues at E_1 are $\lambda_1 = 0$ and $\lambda_2 = T_1 < 0$. This enables us to diagonalize the linear part of the cubic system (2.3) so that the system is transformed into the form

$$\begin{cases}\dfrac{dx}{dt} = G_2(x,y) + G_3(x,y),\\[2mm] \dfrac{dy}{dt} = -y + H_2(x,y) + H_3(x,y),\end{cases} \tag{4.2}$$

where G_j, H_j are homogeneous polynomials of degree j ($j = 2, 3$) and the interior equilibrium E_1 is translated to the origin. By Theorem 7.1 in [22, Chapter 2], the origin of (4.2) is either a stable node or a saddle or a saddle–node. However, by Bendixson's formula (see [23], [22, Chapter 3])

$$J = 1 + \frac{e-h}{2},$$

where J is the index of the equilibrium, h is the number of hyperbolic sectors near the equilibrium and e is the number of elliptic sectors, we get either $J = -1$ when E_1 is a saddle or $J = 0$ when E_1 is a saddle–node, both of which contradict to the Theorem on the sum of indices ([21, p.313], [22, Chapter 3]) because the winding number of the vector field (1.4) along the curve Γ is equal to 1, as proved in the paragraph above (3.10). This implies that E_1 is a stable node. □

5. Bifurcations

It is indicated in Sections 3 and 4 that system (1.4) has either exact one equilibrium in $\mathcal{G}$ when $D_0 > 0$ and $T_0 < 0$ or exact two equilibria in $\mathcal{G}$ in the other case. The following theorem displays the mechanism for the new one to arise. Let $T_{01} := T_0(a_1+1)(a_2+1)$, $D_{01} := D_0(a_1+1)^2(a_2+1)^2$, and

$$\begin{aligned}\mu_0 \;:=\;& \left[3(1-\alpha)m_1(a_2+1) - 4(a_1+1)(a_2+1) + (1-\beta)m_2(a_1+1) - \sqrt{T_{01}^2 - 4D_{01}}\right]\\ &\times\left[2(a_1+a_2+2) - (1-\beta)m_2(3a_1+5) - 3(1-\alpha)m_1(a_2+1) + 4(a_1+1)(a_2+1) + \sqrt{T_{01}^2 - 4D_{01}}\right]\\ &+ 4\alpha\beta m_1m_2(a_1+2)(a_2+1) - 2[a_1 + (a_2+2)(1-(1-\alpha)m_1)]\,[3(1-\alpha)m_1(a_2+1)\\ &+ (1-\beta)m_2(a_2+1) - 4(a_1+1)(a_2+1) + \sqrt{T_{01}^2 - 4D_{01}}\,\Big],\end{aligned}$$

$$\nu_{10} := (3-\alpha)m_1(a_2+1) - 4(1+a_1)(1+a_2) + (1-\beta)m_2(a_1+1) + \sqrt{T_{01}^2 - 4D_{01}}$$

where T_0 and D_0 are defined as in Theorem 1.

Theorem 4. *If $\nu_{10}\mu_0 \neq 0$, system (1.4) experiences a transcritical bifurcation at E_0 when $D_0 = 0$. More concretely, for sufficiently small D_0, a stable equilibrium appears in the first quadrant when $\nu_{10}\mu_0 D_0 > 0$ and an unstable equilibrium appears in the third quadrant when $\nu_{10}\mu_0 D_0 < 0$.*

Proof. As shown in Theorem 1, E_0 is a saddle–node as $D_0 = 0$. Applying the transformation

$$\begin{cases} u = -\alpha m_1(a_2+1)x + \left\{[(1-\alpha)m_1 - a_1 - 1](a_2+1) - \frac{1}{2}\left(T_{01} + \sqrt{T_{01}^2 - 4D_{01}}\right)\right\} y, \\ v = -\alpha m_1(a_2+1)x + \left\{[(1-\alpha)m_1 - a_1 - 1](a_2+1) - \frac{1}{2}\left(T_{01} - \sqrt{T_{01}^2 - 4D_{01}}\right)\right\} y \end{cases} \tag{5.1}$$

to diagonalize the linear part of system of (2.3), we change system (2.3) into the form

$$\begin{bmatrix} u' \\ v' \end{bmatrix} = \begin{bmatrix} \frac{1}{2}\left(T_{01} + \sqrt{T_{01}^2 - 4D_{01}}\right) & 0 \\ 0 & \frac{1}{2}\left(T_{01} - \sqrt{T_{01}^2 - 4D_{01}}\right) \end{bmatrix} \begin{bmatrix} u \\ v \end{bmatrix} + \begin{bmatrix} q_1(u,v) \\ q_2(u,v) \end{bmatrix}, \tag{5.2}$$

where $q_1(u, v)$ and $q_2(u, v)$ are composed of those terms of degree 2 or 3. With a rescaling $d\tau = (T_{01} - \sqrt{T_{01}^2 - 4D_{01}})ds$, the system can be reduced to the following suspended system of (5.2)

$$\begin{cases} u' = 2D_{01}u + \left(T_{01} - \sqrt{T_{01}^2 - 4D_{01}}\right) q_1(u, v), \\ v' = \frac{1}{2}\left(T_{01} - \sqrt{T_{01}^2 - 4D_{01}}\right)^2 v + \left(T_{01} - \sqrt{T_{01}^2 - 4D_{01}}\right) q_2(u, v), \\ D'_{01} = 0. \end{cases} \tag{5.3}$$

By the center manifold theory (see [24]), as $D_0 = 0$ system (5.3) has a two-dimensional center manifold $\mathcal{W}^c : v = W(u, D_{01})$ near E_0. In order to obtain the second-order approximation of function W, let

$$W(u, D_{01}) := \varphi(u, D_{01}) + O(|u, D_{01}|^3), \tag{5.4}$$

where $\varphi(u, D_{01}) := \nu_1 u^2 + \nu_2 uv + \nu_3 v^2$, and let

$$\begin{aligned}(\mathcal{N}\varphi)(u, D_{01}) := {} & \varphi'(u, D_{01}) \left\{2D_{01}u + \left(T_{01} - \sqrt{T_{01}^2 - 4D_{01}}\right) q_1(u, \varphi(u, D_{01}))\right\} \\ & - \frac{1}{2}\left(T_{01} - \sqrt{T_{01}^2 - 4D_{01}}\right)^2 \varphi(u, D_{01}) - \left(T_{01} - \sqrt{T_{01}^2 - 4D_{01}}\right) q_2(u, \varphi(u, D_{01})).\end{aligned}$$

By Theorem 3 in [24, Chapter 1], from the requirement $(\mathcal{N}\varphi)(u, D_{01}) = O(|u, D_{01}|^3)$, we can solve $\nu_2 = \nu_3 = 0$ and

$$\begin{aligned}\nu_1 = {} & \left(\frac{\nu_{10}}{4\alpha m_1(a_2+1)(T_{01}^2 - 4D_{01})}\right) \Bigg\{ \Bigg[3(1-\alpha)m_1(a_2+1) - 4(a_1+1)(a_2+1) + (1-\beta)m_2(a_1+1) \\ & + \sqrt{T_{01}^2 - 4D_{01}} \Bigg] \Bigg[2(a_1+a_2+2) - (1-\beta)m_2(3a_1+5) - 3(1-\alpha)m_1(a_2+1) + 4(a_1+1)(a_2+1) \\ & + \sqrt{T_{01}^2 - 4D_{01}} \Bigg] + 4\alpha\beta m_1 m_2(a_1+2)(a_2+1) - 2[a_1 + (a_2+2)(1-(1-\alpha)m_1)] \Bigg[3(1-\alpha)m_1(a_2+1) \\ & + (1-\beta)m_2(a_2+1) - 4(a_1+1)(a_2+1) + \sqrt{T_{01}^2 - 4D_{01}} \Bigg] \Bigg\}.\end{aligned}$$

Thus, we can substitute (5.4) in (5.3) and obtain the equation

$$u' = 2D_{01}u + \mu u^2 + \mu_1 u^3 + O(|u, D_{01}|)^4, \tag{5.5}$$

the restricted system on $\mathcal{W}^c$, where

$$\mu := \frac{\nu_{10}\mu_0}{4\alpha m_1(a_2+1)(T_{01}^2 - 4D_{01})}, \tag{5.6}$$

μ_0 is defined in the beginning of this section and μ_1 is expressed in Appendix A. Clearly, the expression (5.5) shows that a transcritical bifurcation [25, p. 201] occurs at E_0 as D_{01} varies through the bifurcation value $D_{01} = 0$ when $\mu \neq 0$. Since D_{01} has the same zeros with D_0, the transcritical bifurcation occurs at E_0 as D_0 varies through the bifurcation value $D_0 = 0$. More concretely, when $\nu_{10}\mu_0 D_0 < 0$, the origin O is stable and the other equilibrium A_{-1} appears on the negative u-axis but

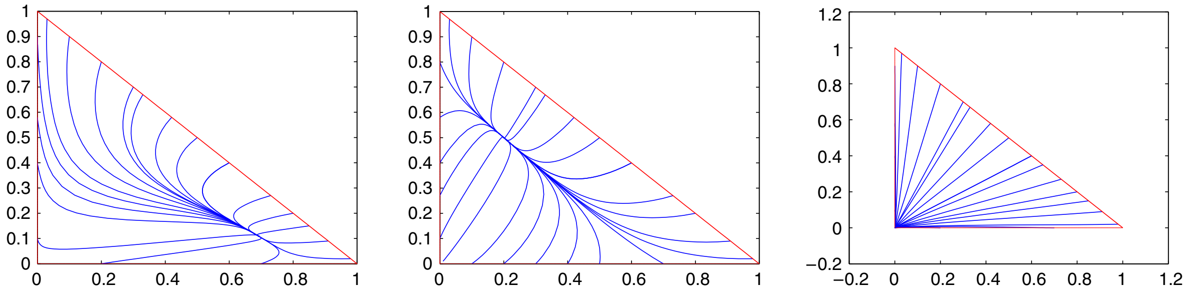

Fig. 1. Phase portraits in cases (S1)–(S3).

is unstable; when $D_0 = 0$, the two equilibria coincide at O; when $\nu_{10}\mu_0 D_0 > 0$, the origin O remains an equilibrium but is unstable while a stable equilibrium A_1 arises on the positive u-axis.

Finally, the transformation (5.1) gives the correspondence between A_1, A_{-1} and the equilibria B_1, B_{-1} of system (2.3), which lie in the first quadrant and the third one, respectively. Note that the third quadrant is of no practical interests. □

This proof shows that equilibrium B_1 (actually the same as the interior equilibrium E_1) arises from a transcritical bifurcation as D_{01} varies through the bifurcation value $D_0 = 0$. This explains how E_1 is produced. We ignore B_{-1} since it does not appear in the first quadrant.

In Theorem 4, the required nondegenerate condition $\nu_{10}\mu_0 \neq 0$ appears in the expression (5.6) of μ. If this condition is violated, i.e., $\nu_{10}\mu_0 = 0$, system (5.5) turns into the form

$$u' = 2D_{01}u + \mu_1 u^3 + O(|u, D_{01}|)^4 \tag{5.7}$$

and the coefficient μ_1 becomes a decisive quantity. Unfortunately, $\mu_1 = 0$. If $\mu_1 \neq 0$, a pitchfork bifurcation [25, p. 201] occurs at E_0 as D_{01} passing through the bifurcation value $D_{01} = 0$. It means that the origin is the unique equilibrium as $D_{01}\mu_1 > 0$, implying as known in Section 3 that the function Υ defined in (3.2) has no real zeros, i.e.,

$$\alpha\beta m_1 m_2 > K_1 K_2, \quad \Delta = (a_2K_1 - a_1K_2)^2 + 4\alpha\beta m_1 m_2 a_1 a_2 < 0. \tag{5.8}$$

This is an obvious contradiction because all parameters are positive. For the same reason we assure that the first nonzero coefficient in the expansion (5.7) appears in an even term. The corresponding bifurcations can be discussed similarly to the proof of Theorem 4.

Note that no bifurcations occur at the interior equilibrium E_1, although its degeneracy for $D_1 = 0$ is shown in the proof of Theorem 3. In fact, when $D_1 = 0$ the asymptotically stable equilibrium E_1 does not coincide with E_0; otherwise, their coincidence gives a saddle–node, which contradicts to the stability of E_1 as shown in Theorem 4. Moreover, ignoring E_0, there also does not occur a bifurcation at E_1, which lies in the interior of $\mathcal{G}$ for $D_1 \geq 0$; otherwise, the only possibility is the pitchfork bifurcation as shown in Theorem 4, which produces three equilibria in the first quadrant as $D_1 > 0$ and makes a contradiction to the uniqueness of interior equilibria (given in Theorem 2).

6. Numerical simulations and remarks

We simulate orbits of the system (1.4) to demonstrate our Theorems 2 and 3. We consider the following cases (S1)–(S3):

	Parameter values (m_1, a_1, α), (m_2, a_2, β)	Equilibrium E_i	Eigenvalues λ_1, λ_2 of $J(E_i)$	Properties
(S1)	(5, 0.7, 0.1), (1, 0.4, 0.1)	$E_0 = (0, 0)$	$\lambda_1 = 1.657$, $\lambda_2 = -0.368$	Saddle
		$E_1 = (0.692, 0.109)$	$\lambda_1 = -3.117$, $\lambda_2 = -0.712$	Stable node
(S2)	(3.1, 0.7, 0.2), (2.4, 0.4, 0.1)	$E_0 = (0, 0)$	$\lambda_1 = 0.754$, $\lambda_2 = 0.247$	Unstable node
		$E_1 = (0.200, 0.499)$	$\lambda_1 = -0.327$, $\lambda_2 = -1.418$	Stable node
(S3)	(0.2, 0.4, 0.2), (0.3, 1, 0.1)	$E_0 = (0, 0)$	$\lambda_1 = -0.852$, $\lambda_2 = -0.899$	Stable node

The phase portraits in the cases (S1)–(S3) are plotted separately in Fig. 1, showing that the wild-type organism X and the mutant Y coexist in both (S1) and (S2), E_0 is a saddle in case (S1) but an unstable node in case (S2), and both X and Y finally go to extinction in case (S3) while E_0 is a stable node.

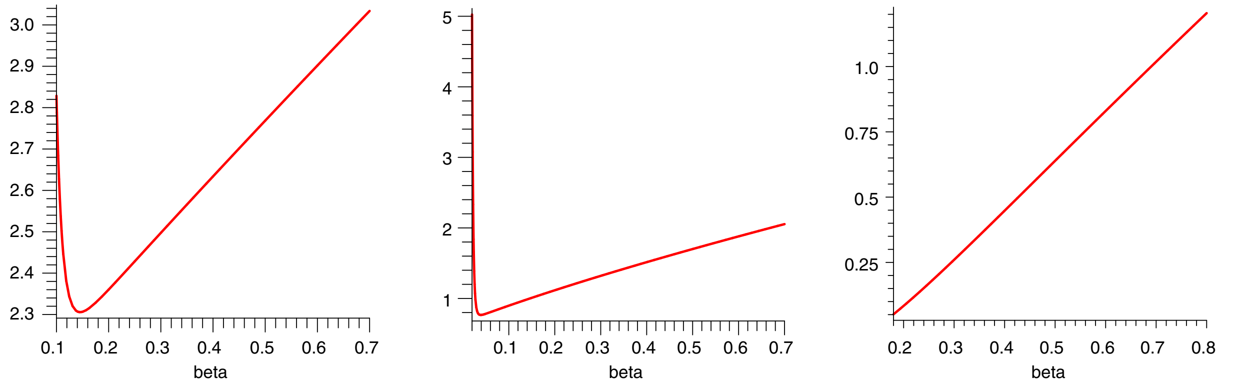

Fig. 2. The graph of $D_1(\beta)$ when $\alpha = 0.1$ (left), 0.4 (middle), and 0.9 (right), separately.

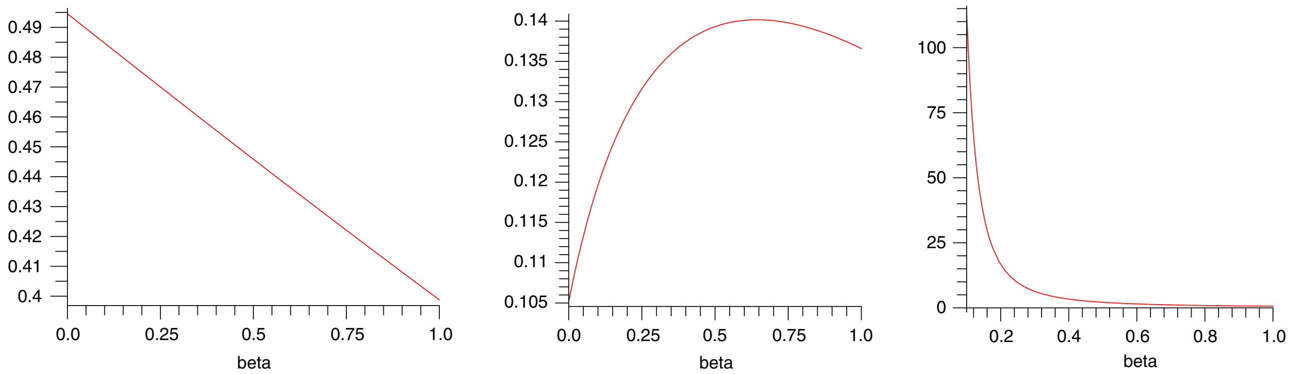

Fig. 3. The graph of $\delta_1(\beta)$ when $\alpha = 0.1$ (left), 0.4 (middle), and 0.9 (right), separately.

When $a_1 > 0, a_2 > 0$ are small enough and $m_1 > 0, m_2 > 0$ are large enough, we see that $D_0 < 0$ as α is small and $D_0 > 0$ as α is large and β is small, implying that the condition $D_0 = 0$ in Theorems 1 and 4 is reasonable. However, it is still difficult to prove either $D_1 \neq 0$ or $D_1 = 0$ for some parameters. Fixing $a_1 = 0.7, a_2 = 0.4, m_1 = 5$ and $m_2 = 1$ for instance, consider the function

$$\begin{aligned} D_1(\beta) := 1 &- \frac{5(1-\alpha)z_1}{0.7+z_1} - \frac{(1-\beta)z_1}{0.4+z_1} + \frac{5(1-\alpha-\beta)z_1^2}{(0.7+z_1)(0.4+z_1)} + \frac{3.5x_1}{(0.7+z_1)^2} + \frac{0.4y_1}{(0.4+z_1)^2} \\ &- \frac{2(1-\alpha-\beta)z_1y_1}{(0.7+z_1)(0.4+z_1)^2} - \frac{3.5(1-\alpha-\beta)z_1x_1}{(0.7+z_1)^2(0.4+z_1)}, \end{aligned}$$

parametrized by α, where x_1, y_1, z_1 are shown in Appendix B. It is shown in Fig. 2 that $D_1(\beta)$ has no zeros when $\alpha = 0.1$, 0.4, 0.9. It seems natural to assert that, in contrast to the statement of Theorem 3, E_1 is a stable *focus* if $\delta_1 < 0$, but it is hard to find a choice of parameters for the simulation of focus at E_1. It suggests a conjecture that E_1 *is a node*.

Furthermore, with the same parameters $a_1 = 0.7, a_2 = 0.4, m_1 = 5$ and $m_2 = 1$, we calculate the function $\delta_1(\beta) = \varsigma_2\beta^2 + \varsigma_1\beta + \varsigma_0$, where $\varsigma_0, \varsigma_1, \varsigma_2$ are shown in Appendix B. Its graphs, plotted in Fig. 3 for the three choices $\alpha = 0.1, 0.4$ and 0.9, show that δ_1 has no zeros in (0, 1). However, it is still difficult to rule out the possibility of the inequality $\delta_1 < 0$.

We have studied the dynamics of an allelopathy model with a single mutant. It was shown that the model has a unique stable interior equilibrium under certain conditions, which differs from the typical dynamics of chemostat models. If x and y denote the populations of the wild-type and resistant bacteria, respectively, the model and results may be used to discuss population dynamics of antibiotic-resistant bacteria [26,27]. It will be interesting to study the dynamics of the general model (11) in [8] with multiple mutants. We leave this for future consideration.

Acknowledgements

The second author was supported by NSFC Tianyuan Fund 10926045 and SRFDP 20090181120082. The third author was partially supported by NIH grant R01GM083607 and NSF grant DMS-0715772. The fourth author was supported by NSFC # 10825104 and China MOE Research Grant.

Appendix A. Expressions of $U(u, v)$, $V(u, v)$

$$\begin{aligned}
U(u, v) \;:=\; & a_1\alpha m_1(a_2+1)^2u^2 + \{-\alpha m_1(a_2+1)[(1-(1-\alpha)m_1)(a_2+2)+a_1-\beta m_2(a_1+2)] \\
& +[(1-\alpha)m_1-1-a_1](a_2+1)[-\alpha m_1(a_2+2)+(1-(1-\beta)m_2)(a_1+2)+a_2]\}uv \\
& +(a_2+1)\{\alpha\beta m_1m_2(a_1+2)+((1-\alpha)m_1-1-a_1)[(1-(1-\beta)m_2)(a_1+2)+a_2]\}v^2 \\
& -\alpha a_1m_1(a_2+1)u^3+(a_2+1)\{-\alpha m_1(-2+2(1-\alpha)m_1+\beta m_2) \\
& +((1-\alpha)m_1-1-a_1)[(1-\beta)m_2-1+2\alpha m_1]\}u^2v+(a_2+1)\{\alpha\beta m_1m_2(a_1+2) \\
& +((1-\alpha)m_1-1-a_1)[(1-(1-\beta)m_2)(a_1+2)+a_2]\}uv^2 \\
& +\{-\alpha m_1(a_2+1)\beta m_2+((1-\alpha)m_1-1-a_1)(a_2+1)((1-\beta)m_2-1)\}v^3,
\end{aligned}$$

$$\begin{aligned}
V(u, v) \;:=\; & \alpha m_1\{-(a_2+1)[(1-(1-\alpha)m_1)(a_2+2)+a_1]+[(1-\beta)m_2-a_2-1](a_1+1)(a_2+2)\}u^2 \\
& +\{-\alpha m_1(a_2+1)[(1-(1-\alpha)m_1)(a_2+2)+a_1-\beta(a_1+2)] \\
& -[(1-\beta)m_2-a_2-1](a_1+1)(-\alpha m_1(a_2+2)+(1-(1-\beta)m_2)(a_1+2)+a_2)\}uv \\
& +\{\alpha\beta m_1m_2(a_2+1)(a_1+2)-[(1-\beta)m_2-a_2-1](a_1+1)[(1-(1-\beta)m_2)(a_1+2)+a_2]\}v^2 \\
& +\{-\alpha m_1(a_2+1)(-1+(1-\alpha)m_1)-[(1-\beta)m_2-a_2-1](a_1+1)\alpha m_1\}u^3 \\
& +\{-\alpha m_1(a_2+1)(-2+2(1-\alpha)m_1+\beta m_2)-[(1-\beta)m_2-a_2-1](a_1+1)[(1-\beta)m_2-1 \\
& +2\alpha m_1]\}u^2v+\{-\alpha m_1(a_2+1)(-1+(1-\alpha)m_1+2\beta m_2) \\
& -[(1-\beta)m_2-a_2-1](a_1+1)(2(1-\beta)m_2-2+\alpha m_1)\}uv^2 \\
& +\{-\alpha m_1(a_2+1)\beta m_2-[(1-\beta)m_2-a_2-1](a_1+1)[(1-\beta)m_2-1]\}v^3
\end{aligned}$$

$$\begin{aligned}
\mu_1 \;=\; & \frac{1}{\alpha m_1(a_2+1)^2[((1-\alpha)m_1(a_2+1)-(1-\beta)m_2(a_1+1))^2+4\alpha\beta m_1m_2(a_1+1)(a_2+1)]} \\
& \times\left\{\frac{((1-\beta)m_2-a_2-1)(a_1+1)}{2((1-\alpha)m_1-a_1-1-\alpha m_1)}\left\{-2\alpha^2\beta m_1^2m_2(a_1+2)(a_2+1)^2\right.\right. \\
& +\frac{1}{2}(a_1+(a_2+2)(1-(1-\alpha)m_1))(3(1-\alpha)m_1(a_2+1) \\
& +(1-\beta)m_2(a_1+1)-4(1+a_1)(1+a_2)-\Theta)(3(1-\alpha)m_1(a_2+1)+(1-\beta)m_2(a_1+1) \\
& -4(1+a_1)(1+a_2)+\Theta)+\alpha m_1(a_2+1)((1-(1-\alpha)m_1)(a_2+2)+a_1 \\
& -\beta m_2(a_1+2))(3(1-\alpha)m_1(a_2+1)+(1-\beta)m_2(a_1+1)+4(a_1+1)(a_2+1)) \\
& -\frac{1}{2}(3(1-\alpha)m_1(a_2+1)+(1-\beta)m_2(a_1+1)-4(1+a_1)(1+a_2)-\Theta) \\
& \times\left[-2(a_2+(1-(1-\beta)m_2)(a_1+2))\alpha m_1(a_2+1)+\frac{1}{2}(3(1-\alpha)m_1(a_2+1)+(1-\beta)m_2(a_1+1)\right. \\
& -4(1+a_1)(1+a_2)-\Theta)(3(1-\alpha)m_1(a_2+1)+(1-\beta)m_2(a_1+1)-4(1+a_1)(1+a_2)+\Theta) \\
& -\frac{1}{2}((1-(1-\beta)m_2)(a_1+2)+a_2-\alpha m_1(a_2+2))(3(1-\alpha)m_1(a_2+1)+(1-\beta)m_2(a_1+1) \\
& \left.\left.+4(a_1+1)(a_2+1))\right]\right\}+\frac{1}{\alpha m_1\Theta}\left[\frac{1}{8}((1-\alpha)m_1-1)(3(1-\alpha)m_1(a_2+1)+(1-\beta)m_2(a_1+1)\right. \\
& -4(1+a_1)(1+a_2)+\Theta)^3+\frac{1}{4}\alpha m_1(a_2+1)(\beta m_2-2+2(1-\alpha)m_1)(3(1-\alpha)m_1(a_2+1) \\
& +(1-\beta)m_2(a_1+1)-4(1+a_1)(1+a_2)+\Theta)^2 \\
& +\frac{1}{2}\alpha^2m_1^2(a_2+1)^2(2\beta m_2-1+(1-\alpha)m_1)(3(1-\alpha)m_1(a_2+1)+(1-\beta)m_2(a_1+1) \\
& -4(1+a_1)(1+a_2)+\Theta)+\alpha^3\beta m_1^3m_2(a_2+1)^3-\frac{1}{2(a_2+1)}(3(1-\alpha)m_1(a_2+1)+(1-\beta)m_2(a_1+1) \\
& -4(1+a_1)(1+a_2)-\Theta)\left(\frac{1}{8}(3(1-\alpha)m_1(a_2+1)+(1-\beta)m_2(a_1+1)-4(1+a_1)(1+a_2)+\Theta)^3\right. \\
& +\frac{1}{4}(2\alpha m_1-1+(1-\beta)m_2)(a_2+1)(3(1-\alpha)m_1(a_2+1)+(1-\beta)m_2(a_1+1)-4(1+a_1)(1+a_2)+\Theta)^2 \\
& +\frac{1}{2}\alpha m_1(\alpha m_1-2+2(1-\beta)m_2)(3(1-\alpha)m_1(a_2+1)+(1-\beta)m_2(a_1+1) \\
& \left.\left.\left.-4(1+a_1)(1+a_2)+\Theta)(a_2+1)^2+((1-\beta)m_2-1)\alpha^2m_1^2(a_2+1)^3\right)\right]\right\},
\end{aligned}$$

where $\Theta := \sqrt{((1-\alpha)m_1(a_2+1)-(1-\beta)m_2(a_1+1))^2+4\alpha\beta m_1m_2(a_1+1)(a_2+1)}$.

Appendix B. Expressions of $x_1, y_1, z_1, \varsigma_0, \varsigma_1, \varsigma_2$

$$z_1 := \frac{1}{\beta}(-0.2 + 0.25\alpha + 0.0875\beta + 0.0125\varpi),$$

$$\begin{aligned} x_1 \; := \; & -0.00625(20\alpha - 73\beta + \varpi - 16)(20\alpha + 63\beta + \varpi - 16)(20\alpha + 7\beta + \varpi - 16)/(64\varpi - 1024 \\ & + 3840\alpha - 160\alpha\varpi + 832\beta - 80\beta\varpi - 4800\alpha^2 + 100\alpha^2\varpi - 3760\alpha\beta + 135\alpha\beta\varpi + 35\beta^2\varpi \\ & + 2000\alpha^3 + 3400\alpha^2\beta + 1645\alpha\beta^2 + 245\beta^3), \end{aligned}$$

$$\begin{aligned} y_1 \; := \; & \frac{1}{\beta}(25.6\varpi - 409.6 + 2048\alpha - 96\alpha\varpi - 793.6\beta + 38.4\beta\varpi - 3840\alpha^2 + 120\alpha^2\varpi + 2080\alpha\beta \\ & - 68\alpha\beta\varpi + 755.2\beta^2 - 64\beta^2\varpi + 3200\alpha^3 - 50\alpha^3\varpi - 1480\alpha^2\beta + 25\alpha^2\beta\varpi - 2798\alpha\beta^2 \\ & + 94.875\alpha\beta^2\varpi + 448\beta^3 - 1000\alpha^4 + 150\alpha^3\beta + 2072.5\alpha^2\beta^2 \\ & + 664.125\alpha\beta^3)/(64\varpi - 1024 + 3840\alpha - 160\alpha\varpi + 832\beta - 80\beta\varpi - 4800\alpha^2 + 100\alpha^2\varpi \\ & - 3760\alpha\beta + 135\alpha\beta\varpi + 35\beta^2\varpi + 2000\alpha^3 + 3400\alpha^2\beta + 1645\alpha\beta^2 + 245\beta^3), \end{aligned}$$

$$\begin{aligned} \varsigma_0 \; = \; & 25z_1^8\alpha^2 - 40z_1^8\alpha + 16z_1^8 + 75z_1^7\alpha^2 - 117z_1^7\alpha + 45.6z_1^7 + 21z_1^6x_1\alpha - 28z_1^6x_1 + 3.2z_1^6y_1 \\ & - 4z_1^6y_1\alpha + 92.25z_1^6\alpha^2 - 139.8z_1^6\alpha + 52.89z_1^6 - 62.3z_1^5x_1 + 44.1z_1^5x_1\alpha + 9.04z_1^5y_1 \\ & - 11.6z_1^5y_1\alpha + 59.6z_1^5\alpha^2 - 87.41z_1^5\alpha + 31.982z_1^5 + 12.25z_1^4x_1^2 + 2.8z_1^4x_1y_1 - 54.25z_1^4x_1 \\ & + 35.7z_1^4x_1\alpha + 0.16z_1^4y_1^2 + 9.992z_1^4y_1 - 13.24z_1^4y_1\alpha + 21.36z_1^4\alpha^2 - 30.204z_1^4\alpha \\ & + 10.6521z_1^4 + 19.6z_1^3x_1^2 - 23.212z_1^3x_1 + 6.16z_1^3x_1y_1 + 13.944z_1^3x_1\alpha + 0.448z_1^3y_1^2 \\ & + 5.3816z_1^3y_1 - 7.42z_1^3y_1\alpha + 4.032z_1^3\alpha^2 - 5.4768z_1^3\alpha + 1.8564z_1^3 + 0.132496z_1^2 + 0.3136z_1^2\alpha^2 \\ & - 4.8944z_1^2x_1 + 11.76z_1^2x_1^2 - 0.40768z_1^2\alpha + 4.956z_1^2x_1y_1 + 2.6208z_1^2x_1\alpha + 0.4704z_1^2y_1^2 + 1.40728z_1^2y_1 \\ & - 2.0384z_1^2y_1\alpha + 3.136z_1x_1^2 + 0.18816z_1x_1\alpha - 0.40768z_1x_1 + 0.142688z_1y_1 \\ & + 1.7248z_1x_1y_1 - 0.21952z_1y_1\alpha + 0.21952z_1y_1^2 + 0.3136x_1^2 + 0.219520x_1y_1 + 0.038416y_1^2, \end{aligned}$$

$$\begin{aligned} \varsigma_1 \; := \; & 10z_1^8\alpha + 8z_1^8 + 33z_1^7\alpha + 25.8z_1^7 + 44.7z_1^6\alpha - 7z_1^6x_1 - 7.2z_1^6y_1 + 34.02z_1^6 - 18.2z_1^5x_1 - 20.64z_1^5y_1 \\ & + 31.79z_1^5\alpha + 23.446z_1^5 + 12.516z_1^4\alpha - 18.55z_1^4x_1 - 23.232z_1^4y_1 + 8.8998z_1^4 + 2.5872z_1^3\alpha \\ & + 1.764z_1^3 - 9.268z_1^3x_1 - 12.8016z_1^3y_1 - 2.2736z_1^2x_1 \\ & + 0.21952z_1^2\alpha - 3.44568z_1^2y_1 + 0.142688z_1^2 - 0.21952x_1z_1 - 0.362208y_1z_1, \end{aligned}$$

$$\varsigma_2 := z_1^8 + 3.6z_1^7 + 5.34z_1^6 + 4.172z_1^5 + 1.8081z_1^4 + 0.41160z_1^3 + 0.038416z_1^2,$$

where $\varpi := \sqrt{256 - 640\alpha + 224\beta + 400\alpha^2 + 280\alpha\beta + 49\beta^2}$.

References

[1] H.C. Neu, The crisis in antibiotic resistance, Science 257 (1992) 1064–1073.
[2] S.B. Levy, B. Marshall, Antibacterial resistance worldwide: causes, challenges and responses, Nat. Med. 10 (2004) S122–S129.
[3] M.A. Riley, J.E. Wertz, Bacteriocins: evolution, ecology, and application, Annu. Rev. Microbiol. 56 (2002) 117–137.
[4] E.S. Walker, F. Levy, Genetic trends in a population evolving antibiotic resistance, Evolution 55 (2001) 1110–1122.
[5] M.A. Riley, Molecular mechanisms of bacteriocin evolution, Annu. Rev. Genet. 32 (1998) 255–278.
[6] R. Durrett, S.A. Levin, Allelopathy in spatially distributed populations, J. Theor. Biol. 185 (1997) 165–171.
[7] Y. Iwasa, M. Nakamaru, S.A. Levin, Allelopathy of bacteria in a lattice population: competition between colicin-sensitive and colicin-producing strains, Evol. Ecol. 12 (1998) 785–802.
[8] M. Abell, J. Braselton, L. Braselton, A model of allelopathy in the context of bacteriocin production, Appl. Math. Comput. 183 (2006) 916–931.
[9] L. Chao, B.R. Levin, Structured habitats and the evolution of anticompetitor in bacteria, Proc. Natl. Acad. Sci. USA 78 (1981) 6324–6328.
[10] S.A. Frank, Spatial polymorphism of bacteriocins and other allelopathic traits, Evolution Ecol. 8 (1994) 369–386.
[11] H.L. Smith, P. Waltman, The Theory of the Chemostat: Dynamics of Microbial Competition, Cambridge University Press, Cambridge, 1992.
[12] D. Herbert, R. Elsworth, R.C. Telling, The continuous culture of bacteria: a theoretical and experimental study, J. Gen. Microbiol. 14 (1956) 601–622.
[13] S.-B. Hsu, S. Hubbell, P. Waltman, A mathematical theory for single-nutrient competition in continuous cultures of micro-organisms, SIAM J. Appl. Math. 32 (1977) 366–383.
[14] S.-B. Hsu, P. Waltman, G.S.K. Wolkowicz, Global analysis of a model of plasmid-bearing, plasmid-free competition in a chemostat, J. Math. Biol. 32 (1994) 731–742.
[15] J. Monod, la technique de la culture continuous: theorie et applications, Ann. Inst. Pasteur 79 (1950) 390–410.
[16] A. Novick, L. Szilard, Description of the chemostat, Science 112 (1950) 215–216.
[17] P.A. Taylor, P.J.L. Williams, Theoretical studies on the coexistence of competing species under continuous-flow conditions, Can. J. Microbiol. 21 (1975) 90–98.
[18] S.-B. Hsu, P. Waltman, A survey of mathematical model of competition with an inhibitor, Math. Biosci. 87 (2004) 53–91.
[19] S. Ruan, The dynamics of chemostat models, J. Central China Normal Univ. Natur. Sci. 31 (1997) 377–397 (in Chinese).
[20] H.R. Thieme, Convergence results and a Poincaré–Bendixon trichotomy for asymptotically autonomous differential equations, J. Math. Biol. 30 (1992) 755–763.
[21] V.I. Arnol'd, Ordinary Differential Equations, Springer-Verlag, Berlin, Heidelberg, 1992, Transl. Roger Cooke.
[22] Z.-F. Zhang, T.-R. Ding, W.-Z. Huang, Z.-X. Dong, Qualitative Theory of Differential Equations, in: Thansl. Math. Monographs, Amer. Math. Soc., Providence, 1992.
[23] I. Bendixson, Sur les courbes définies par des équations différentielles, Acta Math. 24 (1901) 1–88.

[24] J. Carr, Applications of Center Manifold Theory, Springer-Verlag, New-York, 1981.
[25] S.N. Chow, C.Z. Li, D. Wang, Normal Forms and Bifurcation of Planar Vector Fields, Cambridge University Press, 1994.
[26] R.E. Lenski, S.E. Hattingh, Coexistence of two competitors on one resource and one inhibitor: a chemostat model based on bacteria and antibiotics, J. Theor. Biol. 122 (1986) 83–93.
[27] S.L. Peck, Antibiotic and insecticide resistance modeling is it time to start talking? Trends Microbiol. 9 (2001) 286–292.