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Periodic solutions in a model of competition between plasmid-bearing and plasmid-free organisms in a chemostat with an inhibitor

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Abstract. We obtain necessary and sufficient conditions on the existence of a unique positive equilibrium point and a set of sufficient conditions on the existence of periodic solutions for a 3-dimensional system which arises from a model of competition between plasmid-bearing and plasmid-free organisms in a chemostat with an inhibitor. Our results improve the corresponding results obtained by Hsu, Luo, and Waltman [1].

1. Introduction

In this paper, we consider the existence of positive equilibriums and positive periodic solutions for a 3-dimensional dynamical system established by Hsu, Luo and Waltman [1] in studying a model of competition between plasmid-bearing and plasmid-free organisms in a chemostat with an inhibitor. The physical setting is well described in that paper, where the chemostat is studied

> "as a model for the manufacture of products by genetically altered organisms. The new product is coded by the insertion of a plasmid, a piece of genetic material, into the cell. This genetic material is reproduced when the cell divides. The organism carrying the plasmid, the plasmid-bearing organism, is likely to be a lesser competitor than one without, the plasmid-free organism, because of the added load on its metabolic machinery. The survival of the organism without the plasmid, reduces the efficiency of the production process, and, if it is a sufficiently better competitor, eliminates the altered organisms from the chemostat, halting the production. Unfortunately, a small fraction of the plasmids are lost during reproduction, introducing the plasmid-free organisms into the chemostat. To compensate for this, an additional piece of genetic material is added to the plasmid, one that codes for resistance to an inhibitor (an antibiotic) and the inhibitor is added to the feed bottle of the chemostat".

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Based on the above principle and the earlier work of Stephanopoulis and Lapidus [7] and Lenski and Hattingh [8], Hsu, Luo, and Waltman constructed the following mathematical model:

$$\begin{aligned}
S' &= (S^{(0)} - S)D - f_1(S)\frac{x_1}{\gamma} - f(p)\, f_2(S)\frac{x_2}{\gamma}\\
x_1' &= x_1[(1-q)f_1(S) - D]\\
x_2' &= x_2[f(p)\, f_2(S) - D] + qf_1(S)x_1\\
p' &= (p^{(0)} - p)D - f_3(p)x_1\\
&\quad S(0) \geq 0,\, p(0) \geq 0,\, x_i(0) > 0, \quad i = 1, 2,
\end{aligned} \tag{1.1}$$

with $f_i(S) = \frac{m_i S}{a_i + S}, i = 1, 2, f_3(p) = \frac{\delta p}{K+p}$, and $f(p) = e^{-\mu p}$. Here S is the limiting nutrient concentration, x_1 is the plasmid-bearing organism, x_2 is the plasmid-free organism, p is the inhibitor. γ is called a yield constant and q is a parameter which reflects the loss of the plasmid, $S^{(0)}$ is the input concentration of the nutrient, D is the washout rate of the chemostat, and $p^{(0)}$ is the input concentration of the inhibitor, all of which are assumed to be constant and are under the control of the experimenter. m_i, a_i, $i = 1$, 2, are the maximal growth rates of the competitors (without an inhibitor) and are Michaels-Menten constants, respectively; δ and K play similar roles for the inhibitor, δ being uptaken by x_1, and K being a Michaels-Menten parameter; all those parameters are measurable in the laboratory. The formulations of f_i, $i = 1, 2, 3$, based on experimental evidences, going back to Monod [14], are most often used as the uptake functions. The function $f(p)$ represents the degree of inhibition of p on the growth rate (or uptake rate) of x_2. However, in this paper, we do not restrict f, and f_i, $i = 1, 2, 3$, to those special forms.

When $p \equiv 0$ in (1.1), the above model reduces to the one studied by Stephanopoulis and Lapidus [7], which concerns the competition of plasmid-bearing and plasmid-free organisms; while when $q = 0$ in (1.1), the model reduces to the one proposed by Lenski and Hattingh [8], which concerns the competition of two organisms in the presence of an inhibitor affecting one of the organisms. If both sets of conditions hold, then (1.1) was studied by Smith and Waltman [6]. Plasmid models are also discussed in [7], [8], [10], [11] and [12].

To reduce the number of parameters in System (1.1), the following scales are used in [1]:

$$\bar{S} = \frac{S}{S^{(0)}}, \qquad \bar{p} = \frac{p}{p^{(0)}}, \quad \bar{x}_i = \frac{x_i}{\gamma S^{(0)}}, \quad \tau = Dt,$$
$$\bar{m}_i = \frac{m_i}{D}, \quad \bar{a}_i = \frac{a_i}{S^{(0)}}, \quad \bar{\delta} = \frac{\gamma\delta S^{(0)}}{D}, \quad \bar{K} = \frac{K}{p^{(0)}}.$$

Then (1.1) becomes, after dropping the bars, the following non-dimensional differential equations:

$$\begin{aligned}
S' &= 1 - S - f_1(S)x_1 - f(p)f_2(S)x_2,\\
x_1' &= x_1[(1-q)f_1(S) - 1],\\
x_2' &= x_2(f(p)f_2(S) - 1) + qf_1(S)x_1,
\end{aligned} \tag{1.2}$$

$$p' = 1 - p - f_3(p)x_1,$$
$$S(0) \geq 0, \ x_i(0) > 0, \ p(0) \geq 0, \quad i = 1, 2.$$

Let $\Sigma(t) = 1 - x_1(t) - x_2(t) - S(t)$. From (1.2) it follows that $\Sigma' = -\Sigma$ and hence $\Sigma(t) = \Sigma(0)e^{-t}$ goes to zero exponentially as $t \to \infty$. Notice also that the equation for p implies that p eventually satisfy $0 \leq p \leq 1$. Therefore, the omega limit set of (1.2) must lie in the set

$$\Delta := \{(S, x_1, x_2, p) : S + x_1 + x_2 = 1, S \geq 0, x_1 \geq 0, x_2 \geq 0, 0 \leq p \leq 1\},$$

and trajectories (x_1, x_2, p) on the omega limit set must satisfy

$$\begin{aligned} x_1' &= x_1[(1-q)\, f_1(1 - x_1 - x_2) - 1] \\ x_2' &= x_2[f(p)\, f_2(1 - x_1 - x_2) - 1] + q\, x_1\, f_1(1 - x_1 - x_2) \\ p' &= 1 - p - f_3(p)\, x_1 \end{aligned} \tag{1.3}$$

with $(x_1(t), x_2(t), p(t)) \in B$ for all $t \in [0, \infty)$, where the set B is defined by

$$B := \{(x_1, x_2, p) : 0 \leq x_1 + x_2 \leq 1, x_1 \geq 0, x_2 \geq 0, 0 \leq p \leq 1\}$$

which is positively invariant set of (1.3) (see Proposition 2.1 in Section 2). Therefore, as in [1], we restrict ourself to study (1.3) in B in the rest of the paper.

When $q = 0$, (1.3) is a competitive system, and so by applying a Poincare–Bendixson-like Theorem [4] for 3-dimensional competitive systems, Hsu and Waltman [3] proved the existence of periodic solutions for (1.3). But when $q \neq 0$, (1.3) is no longer competitive, and so no such a general theorem can be applied. However, by using a perturbation result of Smith [5], Hsu, Luo and Waltman also obtained the existence of periodic solutions of (1.3) for sufficiently small q. Unfortunately the perturbation theorem [5] could not tell that how small q has to be to ensure the existence of such periodic solutions.

In this paper, we will present a set of verifiable conditions on q to ensure the existence of periodic solutions in B for (1.3) with f and f_i, $i = 1, 2, 3$ satisfying certain conditions (see below) which are satisfied by the above specific forms of them. If (1.3) has periodic solutions when $q = 0$, then our conditions on q are automatically satisfied for sufficiently small $q > 0$, which implies by our main result that (1.3) has periodic solutions for sufficiently small $q > 0$. Those periodic solutions can be regarded as bifurcating from the periodic solutions of (1.3) with $q = 0$. This is exactly the existence result of [1]. However, if (1.3) has no periodic solution when $q = 0$, our conditions on q can be still satisfied for some $q > 0$ and the resulting periodic solutions from our result are not found in [1].

We will also give necessary and sufficient conditions on the existence of a unique positive equilibrium point in B for (1.3), which has to be in the interior set $\overset{\circ}{B}$ of B. Such equilibrium points of (1.3) with $q > 0$ sufficiently small bifurcate from the positive equilibrium point of (1.3) with $q = 0$ if it has, or else they bifurcate from the one of equilibrium points of (1.3) with $q = 0$ on the boundary of B. The latter case is not found in [1] either. The existence of positive equilibrium points is necessary to our proof of the existence result on periodic solutions for (1.3).

The plan of this paper is as follows. In Section 2 we will state and prove the results on the existence of a unique positive equilibrium point in B for (1.3). We will present them for $q = 0$ and $q \neq 0$ separately, since the limit, as $q \to 0$, of the necessary and sufficient conditions for the existence of positive equilibrium points of (1.3) with $q > 0$ yields only sufficient conditions for that of (1.3) with $q = 0$. We will also state such existence results obtained in [1] as corollaries of our results. The main result on the existence of periodic solutions of (1.3) is stated and proved in Section 3. Since we do not restrict f and f_i, $i = 1, 2, 3$, to the specific forms as stated above, we will also apply in this section, as an example, our main result to the case of f and f_i, $i = 1, 2, 3$, with those special forms. A brief discussion of our results is given in the last section.

Throughout the paper, we assume that f, f_i, $i = 1, 2, 3$, and q satisfy the following **assumptions:**

(A) f is positive and f' is negative in $[0, 1]$;

(B) f_i and f_i', $i = 1, 2, 3$, are positive, f_2'' is negative in $[0, 1]$, and $f_i(0) = 0$ for $i = 1, 2, 3$;

(C) $q \geq 0$.

We will also use the following definition:

Definition. (i) $\lambda_1^*(q)$ for $q \in [0, 1 - \frac{1}{f_1(1)})$ is defined by

$$f_1(\lambda_1^*(q)) = \frac{1}{1-q} \tag{1.4}$$

whenever $f_1(1) > 1$;

(ii) $g(x_1)$ is the inverse function of $h(p) := (1-p)/f_3(p)$ for $p \in (0, 1]$.

(iii) A positive equilibrium point of (1.3) means that all its components are positive and it lies in B.

Remark 1.1. *(i) Since* $f_1(x)$ *is strictly increasing in* $[0, \infty)$, *it follows that* $\lambda_1^*(q)$ *is well-defined and increasing for* $q \in [0, 1 - 1/f_1(1))$, $\lambda_1^*(0) = f_1^{-1}(1)$, *and* $\lim_{q \to 1 - 1/f_1(1)} \lambda_1^*(q) = 1$. *Hence* $f_1^{-1}(1) \leq \lambda_1^*(q) < 1$ *for* $q \in [0, 1 - 1/f_1(1))$.

(ii) Since $h(p)$ *is positive and decreasing in* $(0, 1]$, $\lim_{p \to 0^-} h(p) = \infty$ *and* $h(1) = 0$, *it follows that* $g(x_1)$ *is positive and decreasing for all* $x_1 \in [0, \infty)$, $g(0) = 1$, *and* $g(\infty) = 0$.

(iii) Since we are only interested in (1.3) in B, *it is natural to consider its equilibrium points only in* B.

2. Existence of positive equilibrium

In this section, we give necessary and sufficient conditions on the existence of a unique positive equilibrium of (1.3). Those conditions will be assumed in our theorem on the existence of periodic solutions of (1.3) in the next section. The main result of this section also improves Theorems 4.2 and 4.3 of [1], where two sets of sufficient conditions were given on the existence of positive equilibrium of (1.3).

Proposition 2.1. *(i) Every positive equilibrium of (1.3) lies in* $\overset{\circ}{B}$*, the interior set of* B*, i.e.*

$$\overset{\circ}{B} = \{(x_1, x_2, p) : x_1 > 0, x_2 > 0, 0 < x_1 + x_2 < 1,\ 0 < p < 1\}.$$

(ii) The plane $x_1 = 0$ *and* p*-axis are both positively invariant for (1.3).*

(iii) B *and* $\overset{\circ}{B}$ *are both positively invariant for (1.3).*

Proof. (i) Assume that $(x_{1c}(q), x_{2c}(q), p_c(q))$ is positive equilibrium of (1.3). It suffices to show that $p_c(q) < 1$ and $x_{1c}(q) + x_{2c}(q) < 1$. The former inequality is derived at once from the third equation of (1.3). Assume that $x_{1c}(q) + x_{2c}(q) = 1$. Then it follows that $f_1(1 - x_{1c}(q) - x_{2c}(q)) = 0$ and then the first equation of (1.3) yields $x_{1c} = 0$, contradicting $x_{1c}(q) > 0$. Therefore $x_{1c}(q) + x_{2c}(q) < 1$.

(ii) Suppose that $x_1(0) = 0$. Then from the first equation of (1.3), it follows that

$$x(t) = x(0)\exp\Big(\int_0^t [(1-q)\, f_1(1 - x_1 - x_2) - 1]\, dt\Big) = 0 \text{ for all } t > 0,$$

and so the plane $x_1 = 0$ is positively invariant.

Suppose that $x_1(0) = x_2(0) = 0$. Then from above $x_1(t) \equiv 0$, and then substituting it into the second equation of (1.3) yields $x_2(t) \equiv 0$ in the same way as that of showing $x_1 \equiv 0$. Therefore, p-axis is also positively invariant.

(iii) Suppose that $(x_1(0), x_2(0), p(0)) \in \overset{\circ}{B}$. Then $x_1(0) + x_2(0) < 1$ yields $x_1(t) + x_2(t) < 1$ for all $t > 0$, for else let t_0 be the first time such that $x_1(t_0) + x_2(t_0) = 1$. Then adding the first two equations of (1.3) together yields

$$(x_1(t_0) + x_2(t_0))' = -(x_1(t_0) + x_2(t_0)) = -1 < 0$$

which contradicts $(x_1(t_0) + x_2(t_0))' \geq 0$. The positive invariance of the plane $x_1 = 0$ from (ii) implies that if $x_1(0) > 0$, then $x_1(t) > 0$ for all $t > 0$.

Assume that there is a $t_1 > 0$ such that $x_2(t_1) = 0$ and $x_2(t) > 0$ in $[0, t_1)$. Then from the second equation of (1.3) we get $x_2'(t_1) = q x_1(t_1)\, f_1(1 - x(t_1)) > 0$ which contradicts $x_2'(t_1) \leq 0$. Hence $x_2(t) > 0$ for all $t \geq 0$.

Assume that there is a $t_2 > 0$ such that $p(t_2) = 0$ and $p(t) > 0$ for $t \in [0, t_2)$. Then the third equation of (1.3) yields $p'(t_2) = 1 > 0$, which contradicts the definition of t_2. Hence $p(t) > 0$ for all $t \geq 0$.

Finally, assume that there is a $t_3 > 0$ such that $p(t_3) = 1$ and $p(t) < 1$ for $t \in [0, t_3)$. Then the third equation of (1.3) yields $p'(t_2) = -x_1(t_3) f_3(1) < 0$, which contradicts the definition of t_3. Hence $p(t) < 1$ for all $t \geq 0$.

Therefore, $\overset{\circ}{B}$ is positively invariant.

By the continuity of solutions with respect to initial data and the invariance of $\overset{\circ}{B}$, it follows that B is positively invariant for (1.3). □

Theorem 2.1. *(1.3) with $q = 0$ has a positive equilibrium point $(x_{1c}(0), x_{2c}(0), p_c(0))$ if and only if*

$$0 < 1 - \frac{1}{f_1(1)}, \quad (i.e.\ f_1(1) > 1), \tag{2.1}$$

and

$$1/f(g(1 - \lambda_1^*(0))) < f_2(\lambda_1^*(0)) < 1/f(1) \tag{2.2}$$

hold. Moreover, this equilibrium point is unique and given by

$$x_{1c}(0) = g^{-1}(p_c(0)),\ \ x_{2c}(0) = 1 - \lambda_1^*(0) - x_{1c}(0),\ \ p_c(0) = f^{-1}(1/f_2(\lambda_1^*(0))). \tag{2.3}$$

Proof. Suppose that (1.3) with $q = 0$ has a positive equilibrium point $(x_{1c}(0), x_{2c}(0), p_c(0))$. Then from the first equation of (1.3) and the definition of $\lambda_1^*(0)$, we get $1 - x_{1c}(0) - x_{2c}(0) = f_1^{-1}(1) = \lambda_1^*(0)$, which yields $0 < \lambda_1^*(0) < 1$ and hence (2.1) holds. From the third equation of (1.3), we get $p_c(0) = g(x_{1c}(0))$. Notice that $1 - \lambda_1^*(0) > x_{1c}(0) > 0$, and g is decreasing and positive in $(0, \infty)$. It follows that $p_c(0) = g(x_{1c}(0)) > g(1 - \lambda_1^*(0)) > 0$. Also note that the third and second equations of (1.3) with $q = 0$ yield $p_c(0) < 1$ and $1/f(p_c) = f_2(\lambda_1^*(0))$. Then (2.2) follows.

Conversely, suppose that (2.1) and (2.2) hold. Then (2.1) and (2.2) yield $0 < \lambda_1(0) < 1$ and $f(1) < 1/f_2(\lambda_1^*(0)) < f(g(1 - \lambda_1^*(0)))$. We therefore can solve $p_c(0)$ uniquely from the second equation of (1.3) and the decrease of f and get $p_c(0) = f^{-1}(1/f_2(\lambda_1^*(0))) \in (g(1 - \lambda_1^*(0)), 1)$. Thus from the third equation of (1.3) and the fact that g^{-1} is decreasing

$$0 < x_{1c}(0) := g^{-1}(p_c(0)) < g^{-1}(g(1 - \lambda_1^*(0))) = 1 - \lambda_1^*(0).$$

Finally, from the first equation of (1.3) we get $x_{2c}(0) = 1 - \lambda_1^*(0) - x_{1c}(0)$. Therefore, (1.3) has a unique positive equilibrium point $(x_{1c}(0), x_{2c}(0), p_c(0))$ satisfying (2.3).

If (1.3) has a positive equilibrium, then the first part of the proof yields (2.1) and (2.2), and the second part of the proof implies that this equilibrium must satisfy (2.3). Therefore, (1.3) has a unique positive equilibrium provided that (2.1) and (2.2) hold. □

Theorem 2.2. *(i) (1.3) with $q > 0$ has a positive equilibrium point if and only if*

$$q < 1 - \frac{1}{f_1(1)}, \quad (i.e. \quad \lambda_1^*(q) < 1) \tag{2.4}$$

and

$$f_2(\lambda_1^*(q)) < 1/f(1) \tag{2.5}$$

hold. This equilibrium point is the unique positive equilibrium of (1.3), is denoted by $(x_{1c}(q), x_{2c}(q), p_c(q))$, and satisfies

$$x_{2c}(q) = 1 - \lambda_1^*(q) - x_{1c}(q), \quad p_c(q) = g(x_{1c}(q)), \tag{2.6}$$

where x_{1c} *is the unique root of the equation*

$$F(x_1) := [f(g(x_1))\, f_2(\lambda_1^*(q)) - 1]\,[1 - \lambda_1^*(q) - x_1] + \frac{q}{1-q}\, x_1 = 0, \tag{2.7}$$

in $(0, 1 - \lambda_1^*(q))$.

Furthermore, if

$$1/f(g(1 - \lambda_1^*(q))) < f_2(\lambda_1^*(q)), \tag{2.8}$$

then,

$$x_{1c}(q) < \tilde{x}_1(q) < 1 - \lambda_1^*(q), \qquad 0 < \nu(q) < x_{2c}(q) < 1 - \lambda_1^*(q) \tag{2.9}$$

where

$$\nu(q) = 1 - \lambda_1^*(q) - \tilde{x}_1(q),\ \ \tilde{x}_1(q) = g^{-1}(\tilde{p}(q)),\ \ \tilde{p}(q) = f^{-1}(1/f_2(\lambda_1^*(q))). \tag{2.10}$$

(ii) The following holds:

$$\lim_{q\to 0}(x_{1c}(q), x_{2c}(q), p_c(q)) = \begin{cases} (x_{1c}(0), x_{2c}(0), p_c(0)) & \text{if } 1/f(g(1-\lambda_1^*(0))) < f_2(\lambda_1^*(0)), \\ (1-\lambda_1^*(0), 0, g(1-\lambda_1^*(0))) & \text{if } 1/f(g(1-\lambda_1^*(0))) \geq f_2(\lambda_1^*(0)). \end{cases} \tag{2.11}$$

Proof. (i) Suppose that $(x_{1c}(q), x_{2c}(q), p_c(q))$ is a positive equilibrium point of (1.3) for given $q \in (0, 1)$. Then the definition of $\lambda_1^*(q)$ and the first equation of (1.3) implies that the first equality in (2.6) holds, and hence $0 < \lambda_1^*(q) = f_1^{-1}(1/(1-q)) < 1$, i.e., (2.4) holds. From the third equations of (1.3), we get the second equality in (2.6). Then substituting the equalities in (2.6) into the second equation of (1.3) it follows that $x_{1c}(q)$ is a positive root of (2.7) in $(0, 1 - \lambda_1^*(q))$. It is easy to see that the equation (2.7) is equivalent to the equation

$$F_1(x_1) = F_2(x_1) \tag{2.12}$$

in $(0, 1 - \lambda_1^*(q))$, where

$$F_1(x_1) = f(g(x_1))\, f_2(\lambda_1^*(q)) - 1, \quad \text{and} \quad F_2(x_1) = -\frac{q x_1}{(1-q)(1-\lambda_1^*(q) - x_1)},$$

and hence $x_{1c}(q)$ is the root of (2.12) in $(0, 1-\lambda_1^*(q))$. Notice that $F_1(x_1)$ is continuous and is strictly increasing on $[0, \infty)$ (since $g(x_1)$ is decreasing and positive in $[0, \infty)$), $F_1(0) = f(1) f_2(\lambda_1^*(q)) - 1$ and $\lim_{x_1\to\infty} F_1(x_1) = f(0)\, f_2(\lambda_1^*(q)) - 1$; Clearly, $F_2(x_1)$ is continuous and is strictly decreasing on $[0, 1 - \lambda_1^*(q))$ for $x \in [0, 1 - \lambda_1^*(q))$, $F_2(0) = 0$ and $\lim_{x_1\to 1-\lambda_1^*(q)} F_2(x_1) = -\infty$. See Figure 1. Therefore $x_{1c}(q)$ is the unique root of (2.12) in $(0, 1 - \lambda_1^*(q))$, and $F_1(0) < F_1(x_{1c}) = F_2(x_{2c}) < 0$, which yields (2.5).

Assume that (2.4) and (2.5) hold. Then $0 < \lambda_1^*(q) < 1$ and $F_1(0) = f(1)\, f_2(\lambda_1^*(q)) - 1 < 0$. Therefore, $F_1(0) - F_2(0) < 0$ and $F_1(x_1) - F_2(x_1) \to$

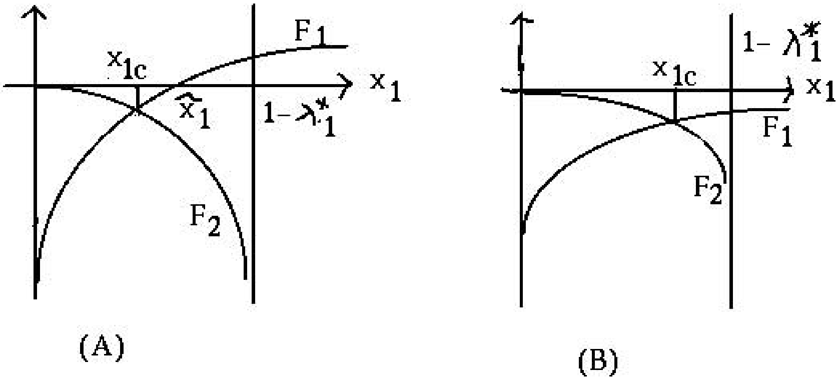

Fig. 1. In (A), $1/f(g(1-\lambda_1^*(q))) < f_2(\lambda_1^*(q)) < 1/f(1)$, while in (B), $f_2(\lambda_1^*(q)) < 1/f(g(1-\lambda_1^*(q)))$.

∞ as $x_1 \to 1-\lambda_1^*(q)$. Hence by mean value theorem and the monotonicity of $F_1(x_1)-F_2(x_1)$ on $[0, 1-\lambda_1^*(q))$, there exists a unique $x_{1c}(q) \in (0, 1-\lambda_1^*(q))$ such that $F_1(x_{1c}(q)) - F_2(x_{1c}(q)) = 0$, and hence $F(x_{1c}(q)) = 0$. Define $x_{2c}(q)$ and $p_c(q)$ by (2.6). Then it follows that $(x_{1c}(q), x_{2c}(q), p_c(q))$ is a positive equilibrium of (1.3).

If (2.8) also holds, then $F_1(1-\lambda_1^*(q)) > 0$ and then $F_1(x_1) = 0$ has a unique root $\tilde{x}_1(q) \in (0, 1-\lambda_1^*(q))$ satisfying (2.10). Notice that $F_1(x_{1c}(q)) < 0$. It follows that $x_{1c}(q) < \tilde{x}_1(q) < 1-\lambda_1^*(q)$, and hence from (2.6) the second inequality in (2.9) also follows.

(ii) Since $\lambda_1^*(q)$ is continuous for $q \in [0, 1-1/f_1(1))$, it follows that the functions F_1 and F_2 are continuous with respect to q. Hence, if $1/f(g(1-\lambda_1^*(0))) < f_2(\lambda_1^*(0))$ holds, then (2.4), (2.5) and (2.8) hold for $q > 0$ sufficiently small, and hence $(x_{1c}(q), x_{2c}(q), p_c(q))$ exists for $q \geq 0$ sufficiently small and $\lim_{q\to 0}(x_{1c}(q), x_{2c}(q), p_c(q)) = (x_{1c}(0), x_{2c}(0), p_c(0))$. However, if $1/f(g(1-\lambda_1^*(0))) > f_2(\lambda_1^*(0))$, then $f_2(\lambda_1^*(0)) < 1/f(1)$ holds and hence (2.4), (2.5) hold for $q > 0$ sufficiently small. Therefore, $(x_{1c}(q), x_{2c}(q), p_c(q))$ exists for $q > 0$ sufficiently small. Notice that $F_1(1-\lambda_1^*(q)) \to F_1(1-\lambda_1^*(0)) \leq 0$ as $q \to 0$ and $\lim_{q\to 0} F_2(x_1) = 0$ for any $x_1 \in [0, 1-\lambda_1^*(q))$ and $\lim_{q\to 0}\lambda_1^*(q) = \lambda_1^*(0)$. It follows that $\lim_{q\to 0} x_{1c}(q) = 1-\lambda_1^*(0)$, and then (2.6) yields $\lim_{q\to 0} x_{2c}(q) = 0$ and $\lim_{q\to 0} p_c(q) = p_c(0)$. If $1/f(g(1-\lambda_1^*(0))) = f_2(\lambda_1^*(0))$, then either $1/f(g(1-\lambda_1^*(q))) < f_2(\lambda_1^*(q))$ or $1/f(g(1-\lambda_1^*(q))) \geq f_2(\lambda_1^*(q))$ for sufficiently small $q > 0$. Either case yields the existence of $(x_{1c}(q), x_{2c}(q), p_c(q))$ for $q > 0$ small. The combination of the above arguments also yields $\lim_{q\to 0}(x_{1c}(q), x_{2c}(q), p_c(q)) = (1-\lambda_1^*(q), 0, g(1-\lambda_1^*(q)))$. This completes the proof of (ii) and therefore the proof of Theorem 2.2. □

Remark 2.1. *1. If $q = 0$, then $F_2 \equiv 0$ and $F(x_1) = F_1(x_1)(1-\lambda_1^*(0)-x_1)$. Hence that $F_1(x_1) = 0$ has a root in $(0, 1-\lambda_1^*(0))$ if and only if $F_1(x_1) = 0$ has a root in $(0, 1-\lambda_1^*(0))$, which is equivalent to $F_1(0) < 0$ and $F_1(1-\lambda_1^*(0)) > 0$, i.e. (2.2). This gives an alternative way to see why (2.2) is necessary for the existence of $(x_{1c}(0), x_{2c}(0), p_c(0))$.*

2. From (2.11) it follows that if $f_2(\lambda_1^*(0)) > 1/f(g(1-\lambda_1^*(0)))$, then $(x_{1c}(q), x_{2c}(q), p_c(q))$ bifurcates from $(x_{1c}(0), x_{2c}(0), p_c(0))$, and else $(x_{1c}(q), x_{2c}(q), p_c(q))$ bifurcates from $(1-\lambda_1^*(0), 0, g(1-\lambda_1^*(0)))$ which is also an equilibrium of (1.3) with $q = 0$. This is exactly implied in the following two corollaries.

Corollary 2.1. *(1.3) has a unique positive equilibrium point for sufficiently small $q \geq 0$ if and only if (2.1) and (2.2) hold. Moreover,* $\lim_{q\to 0}(x_{1c}(q), x_{2c}(q), p_c(q)) = (x_{1c}(0), x_{2c}(0), p_c(0))$.

Corollary 2.2. *Assume that (2.1) and $f_2(\lambda_1^*(0)) \leq 1/f(g(1-\lambda_1^*(0)))$. Then (1.3) has a unique positive equilibrium for sufficiently small $q > 0$, but has no positive equilibrium for $q = 0$. Moreover,* $\lim_{q\to 0}(x_{1c}(q), x_{2c}(q), p_c(q)) = (1-\lambda_1^*(0), 0, g(1-\lambda_1^*(0)))$.

The following two corollaries are generalizations of Theorems 4.2 and 4.3 of [1] respectively.

Corollary 2.3. *Assume that $q > 0$ and that (2.4) holds. Also assume that $f_2(1) < 1/f(1)$. Then (1.3) has a unique positive equilibrium.*

Corollary 2.4. *Assume that $q \in (0, 1)$ and (2.4) hold. Also assume that $\lambda_1^*(q) < \lambda_2^* < 1$, where $f_2(\lambda_2^*) = 1/f(1)$. Then (1.3) has a unique positive equilibrium.*

In the rest of paper, we will drop q in $x_{1c}(q), x_{2c}(q), p_c(q)$ and $\lambda_1^*(q)$ whenever no confusion can be made. Also, we use $\Gamma(t) := (x_1(t), x_2(t), p(t))$ and $E_c = (x_{1c}, x_{2c}, p_c)$ to denote the solutions and the positive equilibrium of (1.3) respectively for any given q as long as they exist. As in [1], the Jacobian of (1.3) at E_c is given by

$$\mathbf{J} = \begin{pmatrix} m_{11} & m_{12} & 0 \\ m_{21} & m_{22} & m_{23} \\ m_{31} & 0 & m_{33} \end{pmatrix},$$

where

$$\begin{aligned}
m_{11} &= m_{12} = -(1-q)x_{1c}\, f_1'(\lambda_1^*), \\
m_{21} &= -x_{2c} f(p_c)\, f_2'(\lambda_1^*) + q\, f_1(\lambda_1^*) - q x_{1c}\, f_1'(\lambda_1^*), \\
m_{22} &= -\frac{x_{1c}}{x_{2c}}\, q f_1(\lambda_1^*) - x_{2c} f(p_c)\, f_2'(\lambda_1^*) - q x_{1c}\, f_1'(\lambda_1^*), \\
m_{23} &= x_{2c} f'(p_c)\, f_2(\lambda_1^*), \\
m_{31} &= = -f_3(p_c), \\
m_{33} &= -1 - f_3'(p_c) x_{1c}.
\end{aligned}$$

We note that x_{2c} in the denominator of the first term of m_{22} was missing in [1]. By the properties of f_1 and f_2, it follows that $m_{11} = m_{12} < 0$, $m_{22} < 0$, $m_{23} < 0$, $m_{31} < 0$, and $m_{33} < 0$. The characteristic equation of $\mathbf{J}$ is given

$$\lambda^3 + B_1\lambda^2 + B_2\lambda + B_3 = 0,$$

where

$$\begin{aligned} B_1 &= -m_{11} - m_{22} - m_{33}, \\ B_2 &= m_{11}(m_{22} - m_{21}) + m_{33}(m_{11} + m_{22}), \\ B_3 &= -m_{11}m_{33}(m_{22} - m_{21}) - m_{12}m_{23}m_{31}. \end{aligned} \tag{2.13}$$

Clearly, $B_1 > 0$. Since $m_{22} - m_{21} = -q\left(1 + \frac{x_{1c}}{x_{2c}}\right) f_1(\lambda_1^*) < 0$ and $m_{11} = m_{12}$, we can easily derive $B_2 > 0$ and $B_3 > 0$. Then by a simple argument or by directly applying Routh Hurwitz criterion we obtain

Proposition 2.2. *If $B_1B_2 > B_3$, then E_c is asymptotically stable. If $B_1B_2 < B_3$, E_c is unstable with a one dimensional stable manifold, and* **J** *has a negative eigenvalue ρ.*

3. Existence of periodic solutions

We first state our main result:

Theorem 3.1. *Assume that $q > 0$ and that (2.4), (2.5), and*

$$B_1B_2 < B_3, \tag{3.1}$$

hold. Assume also that

$$q < \frac{f(p_c(q))f_2'(1 - x_{2c}(q))}{f_1(1 - x_{2c}(q))} x_{2c}(q) =: \nu_1(q) \tag{3.2}$$

holds, where $B_i, i = 1, 2, 3$ are given in (2.13). Then there exists a nontrivial periodic solution of (1.3) lying in the interior of the box B. Moreover, all solutions of (1.3) starting in $\overset{\circ}{B}$, except those in the stable manifold of E_c, oscillates eventually in $\overset{\circ}{B}$ with non-decaying amplitudes.

Remark 3.1. *Assumptions (2.4), (2.5) and (3.1) are just used to guarantee the existence and instability of positive equilibrium. Since system (1.3) with $q > 0$ is not competitive, the existence and instability of positive equilibrium is not, generally speaking, sufficient to ensure the existence of periodic solutions for (1.3) and some extra conditions are needed. Assumption (3.2) is just such a condition. Numerical results shows that it is not the best possible conditions.*

Corollary 3.1. *Assume that $q > 0$ and that (2.4), (2.5), (2.8) and (3.1) hold. Assume also that*

$$q \leq \frac{f(1)f_2'(1 - \nu(q))}{f_1(1 - \nu(q))} \nu(q) =: \nu_2(q), \tag{3.3}$$

where $\nu(q)$ is defined in Theorem 2.2. Then the conclusions of the Theorem 3.1 hold.

Proof. By Theorem 3.1 it suffices to show that $\nu_2(q) < \nu_1(q)$. This follows from the facts that f_1 is increasing and positive on $(0, \infty)$, f_2' is decreasing and positive on $(0, \infty)$, $0 < \nu(q) < x_{2c}(q)$ from Theorem 2.2, and $0 < p_c(q) < 1$. □

Corollary 3.2. *Assume that* $q \geq 0$ *and (2.1), (2.2) and (3.1) hold. Then for sufficiently small* $q > 0$*, the conclusions of Theorem 3.1 hold.*

Proof. Since $\nu(0) = x_{2c}(0)$ from Theorems 2.1 and 2.2, it follows that $0 < \nu(0) < 1$. Hence from the definition of $\nu_2(0)$ in (3.3) we have $\nu_2(0) > 0$, and hence from the continuity of $\nu_2(q)$ with respect to q, (3.3) holds for sufficiently small $q > 0$. Since (2.1), (2.2) and (3.1) implies that (2.4), (2.5), (2.8) and (3.1) also hold for sufficiently small $q > 0$, Corollary 3.2 follows immediately from Corollary 3.1. □

Corollary 3.3. *In addition to the assumptions of Theorem 3.1, we assume that* $f_2(\lambda_1^*(0)) \leq 1/f(g(1-\lambda_1^*(0)))$*. Then the distance between any periodic solution obtained in Theorem 3.1 and the point* $(1-\lambda_1^*(0), 0, g(1-\lambda_1^*(0)))$ *goes to* 0 *as* $q \to 0$.

Remark 3.2. *Corollary 3.2 implies the existence part of Theorem 5.1 [1]. In this case, the periodic solutions of (1.3) with* $q > 0$ *sufficiently small are bifurcated from the periodic solutions of (1.3) with* $q = 0$*. Corollaries 3.3 and 2.2 imply that the periodic solutions and the positive equilibriums of (1.3) with* $q > 0$ *sufficiently small are bifurcated simultaneously from the equilibrium* $(1-\lambda_1^*(0), 0, g(1-\lambda_1^*(0)))$ *of (1.3) with* $q = 0$.

Before proving Theorem 3.1, we address how to check the conditions of Theorem 3.1. For given f_i, $i = 1, 2, 3$, f and q, most of the conditions in Theorem 3.1 are in term of $\lambda_1^*(q)$ and $(x_{1c}(q), x_{2c}(q), p_c(q))$, and therefore we have to compute them in order to check those conditions. To compute $(x_{1c}(q), x_{2c}(q), p_c(q))$, we need to compute $\lambda_1^*(q)$ first. Since, for most functions, the inverses of them (if they have) cannot be calculated analytically, $\lambda_1^*(q) = f_1^{-1}(1/(1-q))$, $g(1-\lambda_1^*(q)) = h^{-1}(1-\lambda_1^*(q))$ and $g(x_{1c}(q)) = h^{-1}(x_{1c}(q))$ would most likely have to be done numerically. Once $\lambda_1^*(q)$ is known, it follows from Theorem 2.2 that we have to solve the equation (2.7) for x_1. This would also most likely have to be done numerically. Next, by means of Mathematica we apply Theorem 3.1 to a concrete case.

Example. Assume that $f(p) = e^{-\mu p}$, $f_i(s) = m_i s/(a_i + s)$ for $i = 1, 2$, and $f_3(s) = \delta s/(K + s)$ with $a_1 = 3.5$, $a_2 = 0.5$, $m_1 = 6.0$, $m_2 = 5.0$, $K = 0.1$, $\delta = 50.0$, and $\mu = 5.0$ as in [3]. In this case, $g(x_1)$ can be calculated explicitly, given by

$$g(x_1) = \frac{1}{2}[\sqrt{(K-1+\delta x_1)^2 + 4K} - (K-1+\delta x_1)]. \tag{3.4}$$

In order for q to satisfy the condition (2.4), it has to be $0 \leq q \leq 0.25$. Set $q = 0.08$. Using Mathematica, we get $\lambda_1^* = 0.774336$, $f_2(\lambda_1^*) = 3.03819$, and $1/f(1) = e^{\mu} = 148.413$. So the condition (2.5) holds. Again by Mathematica we can calculate $x_{1c} = 0.0224377$ from (2.7), $x_{2c} = 0.203226$ and $p_c = 0.224182$ from (2.6), and then $B_1B_2 - B_3 = -0.291389 < 0$ and $\nu_1 = 0.0885201$ by their definitions. Therefore, conditions (3.1) and (3.2) are also satisfied, and hence Theorem 3.1 yields that there is a periodic solution for (1.3) with $q = 0.08$. By using a numerical integration, we indeed can see the periodic solutions (see Figure 2).

It is not surprising that Figure 2 is very similar to Figure 6.6 [3] since we take the same set of parameters as those in [3] except now that q is not equal to 0 but small. We have checked several other values of q smaller than 0.08, and all the conditions of Theorem 3.1 are satisfied. However, we can not tell if that is true for all $q \in [0, 0.08]$. Condition (3.2) fails at $q = 0.1$, though numerically periodic solutions are found there. So apparently the condition (3.2) is not the best possible condition.

Now we outline the proof of Theorem 3.1. From Theorem 2.2, the assumptions (2.4) and (2.5) in Theorem 3.1 imply the existence of the unique positive equilibrium E_c, and from Proposition 2.2 the assumption (3.2) yields that E_c is unstable with a 1-dimensional stable manifold. Let w be the eigenvector of $\mathbf{J}$ associated with its negative eigenvalue ρ. Then it is easy to show that w has the form

$$w = \begin{pmatrix} \frac{m_{12}}{\rho - m_{11}} \\ 1 \\ \frac{m_{31}}{\rho - m_{33}} \cdot \frac{m_{12}}{\rho - m_{11}} \end{pmatrix} c, \quad c \in (-\infty, \infty). \tag{3.5}$$

We claim that $\frac{m_{12}}{\rho - m_{11}} > 0$ and $\frac{m_{31}}{\rho - m_{33}} \cdot \frac{m_{12}}{\rho - m_{11}} > 0$. It suffices to show that $\rho - m_{11} < 0$ and $\rho - m_{33} < 0$. Let ρ_2 and ρ_3 be the other two eigenvalues of $\mathbf{J}$. Then $\rho_2 + \rho_3 \geq 0$. Since $\rho + \rho_2 + \rho_3 = m_{11} + m_{22} + m_{33}$, it follows that $\rho - m_{11} = m_{22} + m_{33} - (\rho_2 + \rho_3) \leq m_{22} + m_{33} < 0$ and, similarly, $\rho - m_{33} < 0$. This confirms our claim. Therefore, it follows from this claim that w points into the positive octant if $c > 0$ and the negative octant if $c < 0$, where the octant is in the

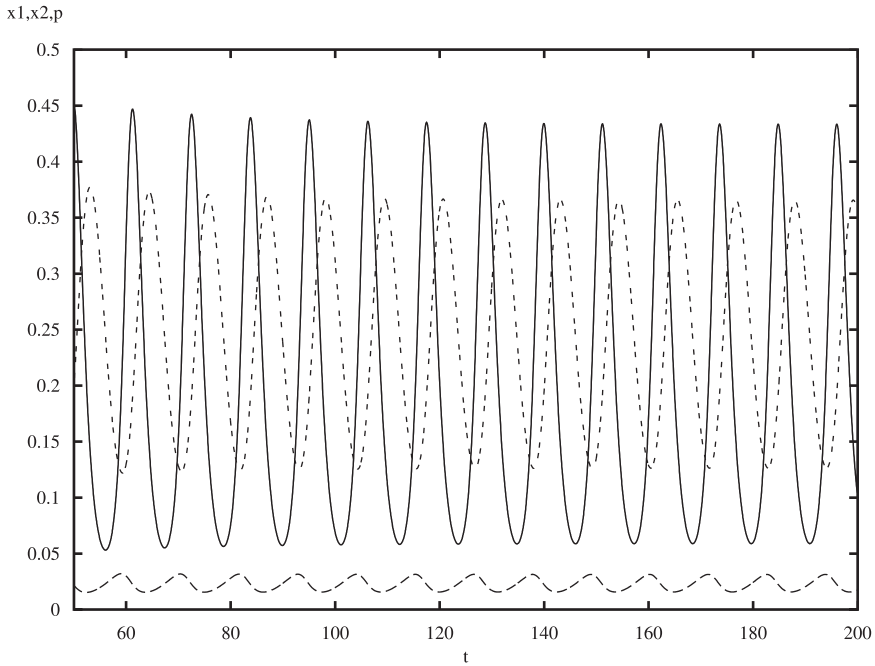

Fig. 2. The graphs of solution $(x1, x2, p)$.

coordinates with the origin translated to E_c. Using the planes $x_1 = x_{1c}$, $x_2 = x_{2c}$ and $p = p_c$ we divide B into eight subsets B_{ijk}, $i, j, k = 0, 1$ (see Figure 3), given by

$$\begin{aligned}
B_{100} &= \{(x_1, x_2, p) \in B: x_{1c} \le x_1 \le 1, 0 \le x_2 \le x_{2c}, 0 \le p \le p_c\},\\
B_{110} &= \{(x_1, x_2, p) \in B: x_{1c} \le x_1 \le 1, x_{2c} \le x_2 \le 1, 0 \le p \le p_c\},\\
B_{010} &= \{(x_1, x_2, p) \in B: 0 \le x_1 \le x_{1c}, x_{2c} \le x_2 \le 1, 0 \le p \le p_c\},\\
B_{011} &= \{(x_1, x_2, p) \in B: 0 \le x_1 \le x_{1c}, x_{2c} \le x_2 \le 1, p_c \le p \le 1\},\\
B_{001} &= \{(x_1, x_2, p) \in B: 0 \le x_1 \le x_{1c}, 0 \le x_2 \le x_{2c}, p_c \le p \le 1\},\\
B_{101} &= \{(x_1, x_2, p) \in B: x_{1c} \le x_1 \le 1, 0 \le x_2 \le x_{2c}, p_c \le p \le 1\},\\
B_{000} &= \{(x_1, x_2, p) \in B: 0 \le x_1 \le x_{1c}, 0 \le x_2 \le x_{2c}, 0 \le p \le p_c\},\\
B_{111} &= \{(x_1, x_2, p) \in B: x_{1c} \le x_1 \le 1, x_{2c} \le x_2 \le 1, p_c \le p \le 1\}.
\end{aligned}$$

To define the Poincâre map, we first define the surface H by

$$H = B_{110} \cap B_{010}.$$

Then, using the assumptions of Theorem 3.1 we can show by a series of lemmas that any solution $\Gamma(t)$ of (1.3) with $\Gamma(0) \in H \setminus \{0\}$ will eventually come back to

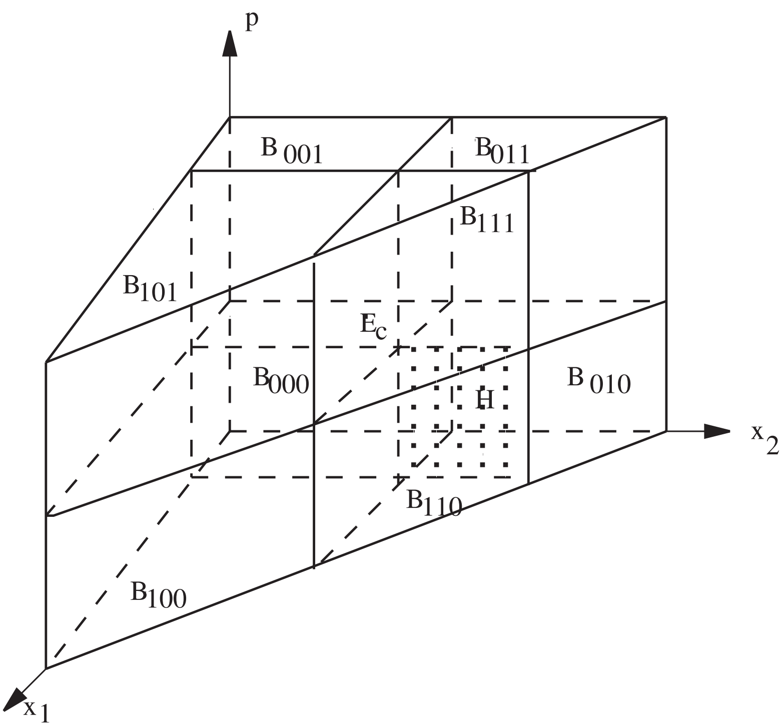

Fig. 3. The sets H and B_{ijk} $(i, j, k = 0, 1)$.

$\overset{\circ}{H}$, the interior set of H, in the following way

$$H \setminus \{0\} \to \begin{cases} \overset{\circ}{B}_{010} \\ \overset{\circ}{B}_{011} \end{cases} \to \overset{\circ}{B}_{011} \leftrightarrow \overset{\circ}{B}_{001} \to \overset{\circ}{B}_{101} \to \overset{\circ}{B}_{100} \leftrightarrow \overset{\circ}{B}_{110} \to \overset{\circ}{H}. \quad (3.6)$$

Therefore, we can define the Poincare map P on $H \setminus \{0\}$ by the first return point of $\Gamma(t)$ in $\overset{\circ}{H}$. We also define $P(E_c) = E_c$. The continuity of P on $\overset{\circ}{H}$ follows from the continuous dependence of solutions with respect to the initial data, while the continuous of P at E_c can be shown from the facts that in a neighborhood of E_c, system (1.3) is topologically equivalent to its linearized system since E_c is a saddle point, and outside this neighborhood, solutions of (1.3) is continuous with respect to the initial data. Therefore by Brouwer fixed point theorem P has at least one fixed point on H. However, notice that E_c is a fixed point for P. Hence we don't know if there is another fixed point for P on H, and if it has, the solution of (1.3) through this point is a nontrivial periodic solution since there is no any other equilibrium point on H for (1.3). To show that P indeed has another fixed point, we will use a similar idea to that used by Hastings and Murray [2], i.e. we will find a simply connected closed subset G of $H \setminus \{E_c\}$ such that P maps G to itself, and hence P has a fixed point on G by applying the Brouwer fixed point to $P|_G$ on G. The construction of G is similar to that employed in [2], and for reader's convenience, we will give its detail in the proof of Theorem 3.1.

The proof of (3.6) is accomplished by Lemmas 3.1-3.7. Lemma 3.1 shows that the solution $\Gamma(t)$ starting from the edge $\{p = p_c\} \cap (H \setminus \{E_c\})$ goes to $\overset{\circ}{B}_{011}$ immediately and $\Gamma(t)$ goes to $\overset{\circ}{B}_{010}$ immediately if it starts from anywhere else in $H \setminus \{E_c\}$. Lemma 3.2 shows that the solution starting from $\overset{\circ}{B}_{010}$ leaves $\overset{\circ}{B}_{010}$ at some time t through the face $\overset{\circ}{B}_{010} \cap \overset{\circ}{B}_{011}$ and then goes into $\overset{\circ}{B}_{011}$ immediately. Lemma 3.3 shows that if the solution escapes from $\overset{\circ}{B}_{011}$, it has to leave from the face $\overset{\circ}{B}_{011} \cap \overset{\circ}{B}_{001}$. Then Lemma 3.4 shows that if the solution leaves from $\overset{\circ}{B}_{001}$, it will leave either through the face $\overset{\circ}{B}_{011} \cap \overset{\circ}{B}_{001}$ and then go to $\overset{\circ}{B}_{011}$ immediately or through the face $\overset{\circ}{B}_{001} \cap \overset{\circ}{B}_{101}$ and then go to $\overset{\circ}{B}_{101}$ immediately. Therefore, it may happen that the solution will move from $\overset{\circ}{B}_{011}$ through the face $\overset{\circ}{B}_{011} \cap \overset{\circ}{B}_{001}$ to $\overset{\circ}{B}_{001}$ forward and backward forever without leaving them, which is not desired. We exclude this possibility in Lemma 3.5 and therefore the solution will eventually go to $\overset{\circ}{B}_{101}$ in a way of (3.6). The rest of (3.6) can be similarly proved and so we just state the corresponding results in Lemmas 3.6 and 3.7 without their proofs. We remark that the condition (3.2) is only used in the proof of Lemma 3.2 and Lemma 3.7 to prevent orbits from $\overset{\circ}{B}_{010}$ going to B_{000} and from $\overset{\circ}{B}_{101}$ going to B_{111} respectively (note that the stable manifold of E_c of (1.3) lies in B_{000} and B_{111}).

Lemma 3.1. *Let* $\Gamma(0) \in H \setminus \{E_c\}$. *Then for* $t >$ *sufficiently small* $\epsilon > 0$, *if* $p(0) = p_c$, *then* $\Gamma(t) \in \overset{\circ}{B}_{011}$, *and else,* $\Gamma(t) \in \overset{\circ}{B}_{010}$.

Proof. According to the possible position of $\Gamma(0)$ on $H \setminus \{E_c\}$, we have to consider the following 8 cases.

Case 1. *Assume that*

$$\Gamma(0) \in \{x = x_{1c}, x_2 = x_{2c}, p = 0\}.$$

Then

$$\begin{aligned} x_1'(0) &= x_{1c}[(1-q)f_1(1-x_{1c}-x_{2c})-1] = 0, \\ x_2'(0) &= x_{2c}[f(0)f_2(\lambda_1^*)-1] + qf_1(\lambda_1^*)x_{1c} \\ &> x_{2c}[f(p_c)f_2(\lambda_1^*)-1] + qx_{1c}f_1(\lambda_1^*) \\ &= 0, \\ p'(0) &= 1, \end{aligned}$$

and

$$x_1''(0) = -(1-q)x_{1c}f_1'(\lambda_1^*)x_2'(0) < 0.$$

So $\Gamma(t) \in \overset{\circ}{B}_{010}$ *for all* $t > 0$ *but small.*

Case 2. *Assume that*

$$\Gamma(0) \in \{x_1 = x_{1c}, x_2 = x_{2c}, 0 < p < p_c\}.$$

Then, by a similar way to that in Case 1 *we can show that*

$$x_1'(0) = 0,\ x_2'(0) > 0,\ x_1'' < 0.$$

Therefore $\Gamma(t) \in \overset{\circ}{B}_{010}$ *for all* $t > 0$ *small.*

Case 3. *Assume that*

$$\Gamma(0) \in \{x_1 = x_{1c}, x_{2c} < x_2 < 1 - x_{1c}, p = 0\}.$$

Then

$$\begin{aligned} x_1'(0) &= x_{1c}[(1-q)f_1(1-x_{1c}-x_2(0))-1] \\ &< x_{1c}[(1-q)f_1(1-x_{1c}-x_{2c})-1] \\ &= 0, \\ p'(0) &= 1 > 0. \end{aligned}$$

Hence, $\Gamma(t) \in \overset{\circ}{B}_{010}$ *for* $t > 0$ *small.*

Case 4. *Assume that*

$$\Gamma(0) \in \{x_1 = x_{1c}, x_{2c} < x_2 < 1 - x_{1c}, 0 < p < p_c\}.$$

Then the same way as that in the proof of Case 3 yields $x_1'(0) < 0$*, and hence* $\Gamma(t) \in \overset{\circ}{B}_{010}$ *for small* $t > 0$.

Case 5. *Assume that*

$$\Gamma(0) \in \{x_1 = x_{1c}, x_{2c} < x_2 < 1 - x_{1c}, p = p_c\}.$$

Then the same way as that in the proof of Case 3 yields $x_1'(0) < 0$*. From the third equation of (1.3) one gets* $p'(0) = 0$ *and* $p''(0) = -f_3(p_c)x_1'(0) > 0$*. Hence* $\Gamma(t) \in \overset{\circ}{B}_{011}$ *for* $t > 0$ *small.*

Case 6. *Assume that*

$$\Gamma(0) \in \{x_1 = x_{1c}, x_2 = 1 - x_{1c}, p = 0\}.$$

Then from (1.3) and the fact that $f_1(0) = f_2(0) = 0$*, we get*

$$\begin{gathered} x_1'(0) = x_{1c}[(1-q)f_1(0) - 1] = -x_{1c} < 0, \\ x_1'(0) + x_2'(0) = -x_{1c} - x_{2c} < 0, \\ p'(0) = 1 > 0, \end{gathered}$$

and then, noting that $x_2(0) = 1 - x_{1c} > 1 - \lambda_1^* - x_{1c} = x_{2c}$*, we have* $\Gamma(t) \in \overset{\circ}{B}_{010}$ *for* $t > 0$ *small.*

Case 7. *Assume that*

$$\Gamma(0) \in \{x_1 = x_{1c}, x_2 = 1 - x_{1c}, 0 < p < p_c\}.$$

Then the same way as that in the proof of Case 6, we get

$$x_1'(0) < 0, \quad x_1'(0) + x_2'(0) < 0, \quad x_2(0) > x_{2c}.$$

Hence $\Gamma(t) \in \overset{\circ}{B}_{010}$ *for* $t > 0$ *small.*

Case 8.

$$\Gamma(0) \in \{x_1 = x_{1c}, x_2 = 1 - x_{1c}, p = p_c\}.$$

Then from the proof of Case 6, $x_1'(0) < 0$*, and* $x_1'(0) + x_2'(0) < 0$*. From the third equation of (1.3), it follows that* $p'(0) = 0$ *and* $p''(0) = -f_3(p_c)x_1'(0) > 0$*. Therefore* $\Gamma(t) \in \overset{\circ}{B}_{011}$ *for* $t > 0$ *small.*

Checking the above cases, we see that $p(0) = p_c$ occurs only in Cases 5 and 8, both of which yield $\Gamma(t) \in \overset{\circ}{B}_{011}$, while all other cases yield $\Gamma(t) \in \overset{\circ}{B}_{010}$ for all small $t > 0$. This completes the proof of Lemma 3.1. □

Lemma 3.2. *Let* $\Gamma(0) \in \overset{\circ}{B}_{010}$*. Then there is* $t_0 > 0$ *such that* $\Gamma(t) \in \overset{\circ}{B}_{010}$ *for* $t \in [0, t_0)$*,* $\Gamma(t_0) \in \partial B_{010}$ *with* $0 < x_1(t_0) < x_{1c}$*,* $x_2(t_0) > x_{2c}$ *and* $p(t_0) = p_c$*,* $p'(t_0) > 0$*, and* $\Gamma(t) \in \overset{\circ}{B}_{011}$ *for* $t \in (t_0, t_0 + \epsilon)$ *and sufficiently small* $\epsilon > 0$*.*

Proof. First, we show that $\Gamma(t)$ cannot stay in $\overset{\circ}{B}_{010}$ for all $t > 0$. Suppose that the claim is not true. Then for all $t \geq 0$

$$p' = 1 - p - f_3(p)x_1 > 1 - p - f_3(p)x_{1c} > 1 - p_c - f_3(p_c)x_{1c} = 0,$$

and hence $p(t) \to \overline{p} \in (0, p_c]$. We show that $\overline{p} = p_c$. Since $0 < \int_0^\infty p'(t)\,dt = \bar{p} - p(0) < \infty$ and $p'' = -p' - f_3(p)p'x_1 - f_3(p)x_1'$ is bounded on $[0, \infty)$, it follows by a simple argument that $p'(t) \to 0$ as $t \to \infty$, and hence from the third equation of (1.3) we get $x_1(t) \to \frac{1-\bar{p}}{f_3(\bar{p})} =: \bar{x}$ as $t \to \infty$. Then, using the function $\frac{1-p}{f_3(p)}$ is decreasing in $(0, 1]$ and $0 < \bar{p} \leq p_c < 1$, we have $\bar{x} \geq x_{1c}$. However, $x_1(t) \leq x_{1c}$ for all $t > 0$ yields $\bar{x} \leq x_{1c}$. Therefore, it must be $\bar{x} = x_{1c}$, which, in turn, yields from the definition of $\bar{x}$ that $\bar{p} = p_c$. Then from the first equation of (1.3), we get $x_2(t) \to x_{2c}$ as $t \to \infty$. So $\Gamma(t) \to E_c$ as $t \to \infty$ and so $\Gamma(t)$ lies on the stable manifold of E_c, which contradicts that the stable manifold of E_c does not lie in B_{010}. Therefore there exists a first time $t_0 > 0$ such that $\Gamma(t_0) \in \partial B_{010}$.

Next, we show that $0 < x_1(t_0) < x_{1c}$, $x_{2c} < x_2(t_0)$ and so, from Proposition 2.1, it must be $p(t_0) = p_c$. Suppose that $x_1(t_0) = x_{1c}$. Then $x_1'(t_0) \geq 0$. However, if $x_2(t_0) > x_{2c}$,

$$\begin{aligned} x_1'(t_0) &= x_{1c}[(1-q)f_1(1 - x_{1c} - x_2(t_0)) - 1] \\ &< x_{1c}[(1-q)f_1(1 - x_{1c} - x_{2c}) - 1] = 0, \end{aligned}$$

which yields a contradiction; if $x_2(t_0) = x_{2c}$, then $p(t_0) < p_c$, and from (1.3)

$$\begin{aligned} x_1'(t_0) &= 0, \\ x_2'(t_0) &= x_{2c}[f(p(t_0))\, f_2(\lambda_1^*) - 1] + x_{1c}qf_1(\lambda_1^*) \\ &> x_{2c}[f(p_c)\, f_2(\lambda_1^*) - 1] + x_{1c}qf_1(\lambda_1^*) = 0, \end{aligned}$$

which again contradicts $x_2'(t_0) \leq 0$. Since $x_2(t_0) \geq x_{2c}$, it follows that $0 < x_1(t_0) < x_{1c}$.

To show $x_2(t_0) \neq x_{2c}$, we again use contradiction. Suppose that $x_2(t_0) = x_{2c}$. Then

$$\begin{aligned} x_2'(t_0) \geq\ & x_{2c}[f(p_c)\, f_2(1 - x_1(t_0) - x_{2c}) - 1] + qx_1(t_0)f_1(1 - x_1(t_0) - x_{2c}) \\ &:= F_3(x_1(t_0)). \end{aligned}$$

We show that $F_3'(x_1) < 0$ for $x_1 \in [0, 1 - x_{2c})$ by (3.2). In fact, since $f_2'(x) > 0$ and $f_2''(x_1) < 0$ for all $x_1 > 0$, it follows that $f_2'(1 - x_1 - x_{2c}) > f_2'(1 - x_{2c})$ and $f_1(1 - x_1 - x_{2c}) < f_1(1 - x_{2c})$ for $x_1 \in [0, 1 - x_{2c})$. Therefore, by (3.2) we have for $x_1 \in [0, 1 - x_{2c})$,

$$\begin{aligned} F_3'(x_1) &= -x_{2c}f(p_c)\, f_2'(1 - x_1 - x_{2c}) + qf_1(1 - x_1 - x_{2c}) - qx_1 f_1'(1 - x_1 - x_{2c}) \\ &\leq -x_{2c}f(p_c)f_2'(1 - x_{2c}) + qf_1(1 - x_{2c}) < 0. \end{aligned}$$

Therefore $F_3(x_1(t_0)) > F_3(x_{1c}) = 0$ and so $x_2'(t_0) > 0$, which contradicts $x_2'(t_0) \leq 0$. Thus, $x_2(t_0) > x_{2c}$.

Finally, from the third equation of (1.3) we get

$$p'(t_0) = 1 - p_c - f_3(p_c)x_1(t_0) > 1 - p_c - f_3(p_c)x_{1c} = 0,$$

which together with the position of $\Gamma(t_0)$ yields $\Gamma(t) \in \overset{\circ}{B}_{011}$ for $t \in (t_0, t_0 + \epsilon)$ and small $\epsilon > 0$. This completes the proof of Lemma 3.2. □

Lemma 3.3. *Let* $\Gamma(0) \in \overset{\circ}{B}_{011}$. *Assume that there is* $t_0 > 0$ *such that* $\Gamma(t_0) \in \partial B_{011}$ *and* $\Gamma(t) \in \overset{\circ}{B}_{011}$ *for* $t \in [0, t_0)$. *Then*

$$0 < x_1(t_0) < x_{1c}, \quad x_2(t_0) = x_{2c}, \quad p_c < p(t_0) < 1,$$

and, either $\Gamma(t) \in \overset{\circ}{B}_{001}$ *or* $\Gamma(t) \in \overset{\circ}{B}_{011}$ *for* $t \in (t_0, t_0 + \epsilon)$ *and sufficiently small* $\epsilon > 0$.

Proof. First, suppose $p(t_0) = p_c$. Then if $x_1(t_0) < x_{1c}$,

$$p'(t_0) = 1 - p_c - f_3(p_c)x_1(t_0) > 1 - p_c - f_3(p_c)x_{1c} = 0.$$

which contradicts $p'(t_0) \le 0$; else if $x_1(t_0) = x_{1c}$, then $x_2(t_0) > x_{2c}$ and then

$$\begin{aligned} x_1'(t_0) &= x_{1c}[(1-q)f_1(1 - x_{1c} - x_2(t_0)) - 1] \\ &< x_{1c}[(1-q)f_1(1 - x_{1c} - x_{2c}) - 1] = 0, \end{aligned} \tag{3.7}$$

which contradicts $x_1'(t_0) \ge 0$. So $p(t_0) > p_c$.

Next, assume that $x_1(t_0) = x_{1c}$. Then if $x_2(t_0) > x_{2c}$, then (3.7) holds, which contradicts $x_1'(t_0) \ge 0$. Therefore if $x_1(t_0) = x_{1c}$, it must be $x_2(t_0) = x_{2c}$. Then from (1.3) we get $x_1'(t_0) = 0$, $x_2'(t_0) < 0$ (since $p(t_0) > p_c$), and $x_1''(t_0) = -(1-q)x_{1c}f_1'(1 - \lambda_1^*)x_2'(t_0) > 0$, which implies that $x_1(t) > x_{1c}$ for $t < t_0$, contradicting $\Gamma(t) \in \overset{\circ}{B}_{011}$ for $t < t_0$. Therefore, $x_1(t_0) < x_{1c}$.

Hence, it follows from $\Gamma(t_0) \in \partial B_{011}$ that $x_2(t_0) = x_{2c}$. Since the sign of $x_2'(t_0)$ cannot be determined from (1.3) and the solution cannot stay in the face $x_2 = x_{2c}$, the lemma 3.3 follows. □

Lemma 3.4. *Let* $\Gamma(0) \in \overset{\circ}{B}_{001}$. *Assume that there is a* $t_0 > 0$ *such that* $\Gamma(t_0) \in \partial B_{001}$. *Then* $p(t_0) > p_c$, *and, for* $t \in (t_0, t_0 + \epsilon)$ *with* $\epsilon > 0$ *small,*

$$\text{either} \quad \Gamma(t) \in \overset{\circ}{B}_{001}, \quad \text{or} \quad \Gamma(t) \in \overset{\circ}{B}_{011}, \quad \text{or} \quad \Gamma(t) \in \overset{\circ}{B}_{101}.$$

Moreover, if the last case occurs, then $x_1(t_0) = x_{1c}$, $x_2(t_0) < x_{2c}$ *and* $x_1'(t_0) > 0$, *and* $\Gamma(t)$ *passes through the face* $\overset{\circ}{B}_{001} \cap \overset{\circ}{B}_{101}$ *transversally from* $\overset{\circ}{B}_{001}$ *into* $\overset{\circ}{B}_{101}$.

Proof. Suppose $p(t_0) = p_c$. Then, if $x_1(t_0) < x_{1c}$,

$$p'(t_0) = 1 - p_c - f_3(p_c)x_1(t_0) > 1 - p_c - f_3(p_c)x_{1c} = 0,$$

which contradicts $p'(t_0) \le 0$. Assume that $x_1(t_0) = x_{1c}$. Then from (1.3), $p'(t_0) = 0$, and

$$\begin{aligned} x_1'(t_0) &= x_{1c}[(1-q)f_1(1-x_{1c}-x_2(t_0))-1] \\ &> x_{1c}[(1-q)f_1(1-x_{1c}-x_{2c})-1] \\ &= 0 \quad \text{(since now } x_2(t_0) < x_{2c}), \end{aligned}$$

and so $p''(t_0) = -f_3(p_c)x'(t_0) < 0$, which combining with $p'(t_0) = 0$ implies $p(t_0) = p_c$ is a local maximum of $p(t)$, contradicting $p(t) > p_c$ for $t < t_0$. Therefore $p(t_0) > p_c$.

Suppose $x_1(t_0) = x_{1c}$. If $x_2(t_0) = x_{2c}$, then

$$\begin{aligned} x_2'(t_0) &= x_{2c}[f(p(t_0))f_2(\lambda_1^*)-1] + qx_{1c}f_1(\lambda_1^*) \\ &< x_{2c}[f(p_c)f_2(\lambda_1^*)-1] + qx_{1c}f_1(\lambda_1^*) = 0, \end{aligned} \tag{3.8}$$

contradicting $x_2'(t_0) \ge 0$. Hence $x_2(t_0) < x_{2c}$, and then

$$\begin{aligned} x_1'(t_0) &= x_{1c}[(1-q)f_1(1-x_{1c}-x_2(t_0))-1] \\ &> x_{1c}[(1-q)f_1(1-x_{1c}-x_{2c})-1] = 0, \end{aligned}$$

which together with $p(t_0) < p_c$, as we just proved, implies $\Gamma(t) \in \overset{\circ}{B}_{101}$ for $t \in (t_0, t_0+\epsilon)$ and small $\epsilon > 0$.

Suppose now that $x_2(t_0) = x_{2c}$. From (3.8) it follows that $x_1(t_0) < x_{1c}$. Since also $p(t_0) > p_c$, the sign of $x_2'(t_0)$ cannot be determined from (1.3): either $x_2'(t_0) \le 0$ or $x_2'(t_0) > 0$. Therefore we have $\Gamma(t) \in (\overset{\circ}{B}_{011} \cup \overset{\circ}{B}_{001})$ for $t \in (t_0, t_0+\epsilon)$ and small $\epsilon > 0$.

Combining above results and Proposition 2.1, Lemma 3.4 follows. $\square$

Lemma 3.5. *Let* $\Gamma(0) \in \tilde{B} := \overset{\circ}{B}_{011} \cup \overset{\circ}{B}_{001} \cup (\{0 < x_1 < x_{1c}, x_2 = x_{2c}, p_c < p < 1\} \cap B)$*, and* $t_0 = \sup\{t > 0 :\ \Gamma(s) \in \tilde{B}$ *for* $s \in ([0,t)\}$*. Then* $t_0 < \infty$*,* $\Gamma(t_0) \in \overset{\circ}{B}_{001} \cap \overset{\circ}{B}_{101}$*,* $x_1'(t_0) > 0$*, and* $\Gamma(t) \in \overset{\circ}{B}_{101}$ *for* $t \in (t_0, t_0+\epsilon)$ *and small* $\epsilon > 0$.

Proof. Write $\tilde{B} = D_1 \cup D_2$, where $D_1 = \{x_1 + x_2 \ge 1 - \lambda_1^*\} \cap \tilde{B}$ and $D_2 = \{x_1 + x_2 < 1 - \lambda_1^*\} \cap \tilde{B}$ (see Figure 4).

Then in D_1, $x_1' \le x_1[(1-q)f_1(\lambda_1^*) - 1] = 0$ and, similarly, $x_1' > 0$ in D_2. We claim that once $\Gamma(t)$ enters into D_2, then $\Gamma(t)$ will not enter D_1 without leaving $\tilde{B}$. Suppose that the claim is not true. Then there is the smallest $t_1 > 0$ such that $x_1(t_1) + x_2(t_1) = 1 - \lambda_1^*$ and $p(t_1) > p_c$, and hence the first equation of (1.3) yields $x_1'(t_1) = 0$. Notice that from the second equation of (1.3) we have $f(p_c)f_2(\lambda_1^*) - 1 = -\frac{qx_{1c}f_1(\lambda_1^*)}{1-x_{1c}-\lambda_1^*}$. Then

$$\begin{aligned} x_2'(t_1) &= x_2(t_1)[f(p(t_1))f_2(\lambda_1^*)-1] + qx_1(t_1)f_1(\lambda_1^*) \\ &< (1-x_1(t_1)-\lambda_1^*)[f(p_c)f_2(\lambda_1^*)-1] + qx_1(t_1)f_1(\lambda_1^*) \end{aligned}$$

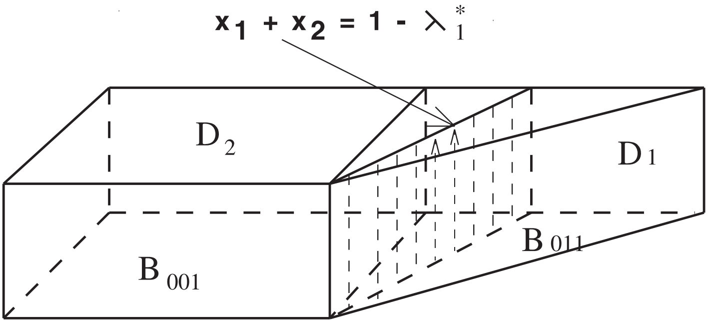

Fig. 4. The sets D_1 and D_2.

$$= \frac{1 - x_1(t_1) - \lambda_1^*}{1 - x_{1c} - \lambda_1^*}(-qx_{1c}f_1(\lambda_1^*)) + qx_1(t_1)f_1(\lambda_1^*)$$

$$= qf_1(\lambda_1^*)\frac{(x_1(t_1) - x_{1c})(1 - \lambda_1^*)}{1 - x_{1c} - \lambda_1^*} \leq 0, \tag{3.9}$$

and hence $(x_1 + x_2)'(t_1) < 0$, contradicting $(x_1 + x_2)'(t_1) \geq 0$. This affirms our claim.

Suppose that Lemma 3.5 is not true. Then $\Gamma(t)$ either stays in D_1 forever, or stays in D_2 after some time $\tilde{t} \geq 0$. In both cases, we have that $x_1(t)$ is monotone after $\tilde{t}$ and so $x_1(t) \to \overline{x}_1 \in [0, x_{1c}]$ as $t \to \infty$. Hence

$$|\int_{\tilde{t}}^{\infty} |x_1'(t)|\,dt| = |\int_{\tilde{t}}^{\infty} x_1'(t)\,dt| = |x_1(\infty) - x_1(\tilde{t})| < \infty.$$

Since $|x_1''(t)|$ is bounded on $[0, \infty)$ it follows that $x_1'(t) \to 0$ as $t \to \infty$ and so $\lim_{t\to\infty}[(1-q)f_1(1-x_1(t)-x_2(t))-1] = 0$ and so $\lim_{t\to\infty}(1-x_1(t)-x_2(t)) = \lambda_1^*$, and so $\lim_{t\to\infty} x_2(t) = 1 - \lambda_1^* - \bar{x}_1 := \bar{x}_2$. Then from the third equation of (1.3) we can get $\lim_{t\to\infty} p(t) = \bar{p} \in [p_c, 1]$. $(\bar{x}_1, \bar{x}_2, \bar{p})$ cannot be E_c because of the directions of stable manifold of E_c. So $(\bar{x}_1, \bar{x}_2, \bar{p}) = (0, 0, 1)$, or $(0, \tilde{x}_2, 1)$ where $\tilde{x}_2 = 1 - f_2^{-1}(1/f(1)) < 1 - \lambda_1^*$, which are another two equilibrium points of (1.3) in $\bar{D}_2$. But then from (2.4) we have in both cases that

$$x_1' = x_1[(1-q)f_1(1-x_1-x_2) - 1] > \frac{(1-q)f_1(\lambda_1^*(q))}{2}x_1 = \frac{1}{2}x_1$$

for sufficiently large $t > 0$, and then $x_1(t) > const \cdot e^{\frac{1}{2}t} \to \infty$ as $t \to \infty$, contradicting $\bar{x}_1 = 0$ in both cases. Therefore, $\Gamma(t)$ will leave $\tilde{B}$ eventually. Lemma 3.3 and Lemma 3.4 yield Lemma 3.5. $\square$

By the similar ways to the proofs of the above lemmas, we can get the following two lemmas, thereby completing the proof of (3.6).

Lemma 3.6. *Let* $\Gamma(0) \in \overset{\circ}{B}_{101}$. *Then, there is a* $t_0 > 0$ *such that* $\Gamma(t) \in \overset{\circ}{B}_{101}$ *for* $t \in [0, t_0)$, $\Gamma(t_0) \in \overset{\circ}{B}_{101} \cap \overset{\circ}{B}_{100}$ *with* $p'(t_0) < 0$, *and* $\Gamma(t) \in \overset{\circ}{B}_{100}$ *for* $t \in (t_0, t_0+\epsilon)$ *and small* $\epsilon > 0$.

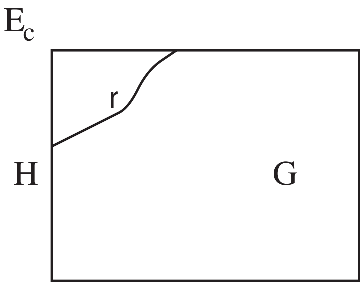

Fig. 5. The sets H and G, the curve r.

Lemma 3.7. *Let* $\Gamma(0) \in \tilde{B}' = \overset{\circ}{B}_{100} \cup \overset{\circ}{B}_{110} \cup (\{x_2 = x_{2c}, x_{1c} < x_1 < 1 - x_{2c}, 0 < p < p_c\} \cap B)$*. Then, there exists* $t_0 > 0$ *such that* $\Gamma(t) \in \tilde{B}'$ *for* $t \in [0, t_0)$*,* $\Gamma(t_0) \in \overset{\circ}{H}$*,* $x_1'(t_0) < 0$*, and* $\Gamma(t) \in \overset{\circ}{B}_{010}$ *for* $t \in (t_0, t_0 + \epsilon)$ *and small* $\epsilon > 0$.

Now we are in the position to prove Theorem 3.1.

Proof of Theorem 3.1. From the above lemmas and (3.6), it follows that for $\Gamma(0) \in H \setminus E_c$, there is a smallest $T = T(\Gamma(0) > 0$ with $\Gamma(T) \in H$. We then define the Poincare mapping P on H by

$$P(\Gamma(0)) = \Gamma(T) \quad \text{if } \Gamma(0) \neq E_c, \qquad P(E_c) = E_c.$$

The continuity of P on $H \setminus E_c$ follows from $x_1'(T) < 0$ and the implicit function theorem.

We next show by construction that there is a simply connected closed set $G \subset H \setminus \{E_c\}$ such that P maps G into itself. Once this is done, Brouwer fixed point theorem yields that $P|_G$ has a fixed point in G and the solution of (1.3) through such a fixed point is a nontrivial periodic solution of (1.3). The following construction of G follows essentially from Hastings and Murray [2]. The idea is to show that there is a simple continuous curve γ in H with the following properties (see Figure 5):

(a) γ does not contain E_c;

(b) γ lies in the interior of H except for its endpoints, which lies in the faces $x = x_{2c}$ and $p = p_c$ respectively;

(c) Define the region G to be the one of the two subregions of H divided by γ which does not contain E_c.

Therefore, it remains to show the existence of the curve γ. In order to to do that, we rewrite the system (1.3) around E_c. Let $\mathbf{J}$ denote, as before, the matrix for the linearized system of (1.3) at E_c. Since $\mathbf{J}$ has one negative eigenvalue and either two positive eigenvalues, which are possibly equal, or two complex conjugate eigenvalues with positive real part, it follows from linear algebra that there is a real nonsingular matrix $\mathbf{S} = \{s_{ij}\}_{3\times 3}$ with $(s_{11}, s_{21}, s_{31})^T = w$ such that

$$\mathbf{S}^{-1}\mathbf{J}\mathbf{S} = \mathbf{K},$$

where w is given in (3.5) with $c = 1$ and $\mathbf{K}$ has the form

$$\mathbf{K} = \begin{pmatrix} \rho & 0 & 0 \\ 0 & r_1 & \sigma_1 \\ 0 & -\sigma_2 & r_2 \end{pmatrix},$$

where $\rho < 0$ is the negative eigenvalue of $\mathbf{J}$ and r_1, r_2, σ_1 and σ_2 are determined by the following three cases:

case (i) $r_1 = r_2 = r > 0$, $\sigma_1 = \sigma_2 = \sigma > 0$, where $r \pm i\sigma$ are the complex conjugate eigenvalues of $\mathbf{J}$ with positive real part;

case (ii) $r_1 > 0$, $r_2 > 0$, where r_1 and r_2 are two positive eigenvalues of $\mathbf{J}$;

case (iii) $r_1 = r_2 = r > 0$, $\sigma_1 = \epsilon > 0$, $\sigma_2 = 0$, where r is the positive eigenvalue of $\mathbf{J}$ with multiplicity of 2 and $\epsilon > 0$ can be arbitrarily small.

If we let $u = (x_1, x_2, p)$ and set $v = S^{-1}(u - E_c)$, then the system (1.3) can be written in the form

$$v' = \mathbf{K}v + h(v) \tag{3.10}$$

where

$$\lim_{\|v\| \to 0} \frac{h(v)}{\|v\|} = 0.$$

Let L denote the line in R^3 through E_c and parallel to the eigenvector w of $\mathbf{J}$ corresponding to ρ. Consider the cylinder C_α, for any $\alpha > 0$, whose axis is v_1-axis and whose equation in the v coordinate system is

$$v_2^2 + v_3^2 = \alpha.$$

Since $S \cdot (v_1, 0, 0)^T = v_1(s_{11}, s_{21}, s_{31})^T = v_1 w^T$, it follows that each $C'_\alpha = S^{-1} \cdot C_\alpha + E_c$, is a cylinder in (x_1, x_2, p)-space with elliptical cross section and axis L (see Figure 6). Along solution curves of (3.10), as $\|v\| \to 0$,

$$(v_2^2 + v_3^2)' = 2r(v_2^2 + v_3^2) + o(\|v\|^2)$$

provided that case (i) occurs,

$$(v_2^2 + v_3^2)' = 2r_1 v_2^2 + 2r_2 v_3^2 + o(\|v\|^2)$$

provided that case (ii) occurs, and

$$(v_2^2 + v_3^2)' = 2r(v_2^2 + v_3^2) + 2\epsilon v_2 v_3 + o(\|v\|^2)$$

provided that case (iii) happens.

From our choice that $c = 1$ in (3.5), the eigenvector w has positive components, and hence $(L \cap \overset{\circ}{B}) \setminus \{E_c\} \subset \overset{\circ}{B}_{000} \cup \overset{\circ}{B}_{111}$. Therefore, C'_α intersects each u_i-axis for $i = 1, 2, 3$, and hence the boundary $\partial A_\alpha \subset C'_\alpha$ provided that $\alpha > 0$ is so small that $A_\alpha \cap \partial B = \emptyset$, where $A_\alpha := [B \setminus (\overset{\circ}{B}_{000} \cup \overset{\circ}{B}_{111} \cup \{E_c\})] \cap C'_\alpha$. Hence, we have $v_2^2 + v_3^2 = \alpha$ for $u \in \partial A_\alpha$. And hence for $u \in \partial A_\alpha$, we have $v_1^2 \le K_1 - (v_2^2 + v_3^2) = K_1 - \alpha$, where $K_1 > 0$ is the constant such that $|v| \le K_1$ for v satisfying $v(u) \in B$, and then

$$v_2^2 + v_3^2 = \alpha = \frac{\alpha}{K_1 - \alpha}(K_1 - \alpha) \ge \frac{\alpha}{K_1 - \alpha} v_1^2 =: \delta v_1^2,$$

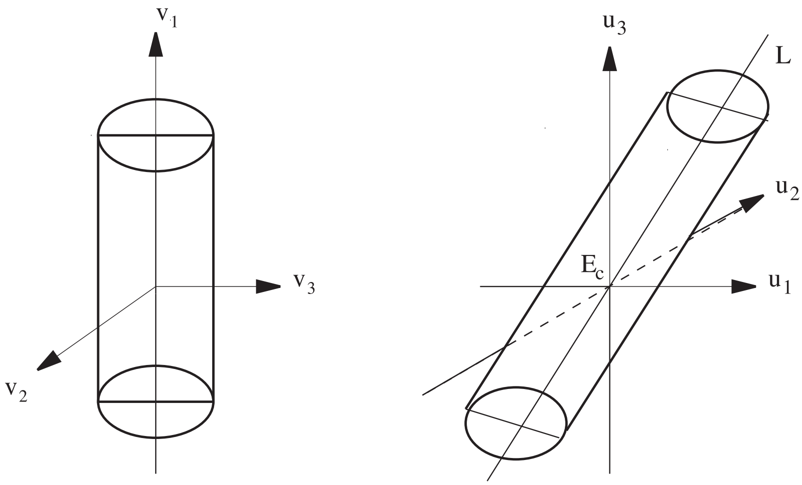

Fig. 6. The cylinders C_α and C'_α.

and then

$$(v_2^2 + v_3^2)' \geq (2\tilde{r} - \epsilon)(v_2^2 + v_3^2) + o(v_2^2 + v_3^2),$$

where $\tilde{r} = r$ if the case (i) or (iii) occurs, and $\tilde{r} = \min\{r_1, r_2\}$ if case (ii) occurs. Therefore, by setting $\epsilon < 2\tilde{r}$, we have that the solution of (1.3) starting in $B \setminus (\overset{\circ}{A}_\alpha \cup \overset{\circ}{B}_{000} \cup \overset{\circ}{B}_{111} \cup \{E_c\})$ will remain inside itself. Now, we fix a sufficiently small $\alpha > 0$ and then define $\gamma = C'_\alpha \cap H = \partial A_\alpha \cap H$. Since C'_α and H are both simply connected sets, it follows that γ is a continuous curve. From our construction, γ also satisfies all other requirements (a), (b) and (c) as mentioned above. This completes the proof of Theorem 3.1. □

4. Discussion

The main result of the paper provides a set of sufficient conditions for the existence of periodic solutions of System (1.3). Though those conditions are not easily checked analytically, they are verifiable, at least numerically as demonstrated. Our result does not provide any information about the stability of the periodic solutions. However, it does show that most solutions starting in $\overset{\circ}{B}$ oscillate eventually in the way as described in (3.6) with finite non-zero amplitudes. This implies that the plasmid-bearing population survives and the host cells do not loose the plasmid and revert to their unaltered phenotype, the plasmid-free cells, which is the interesting part to the model considered. We hope that the parameters satisfying our main result fall within the realistic range of interest to biologists.

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