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THE EFFECT OF INHIBITOR ON THE PLASMID-BEARING AND PLASMID-FREE MODEL IN THE UNSTIRRED CHEMOSTAT*

JIANHUA WU†, HUA NIE†, AND GAIL S. K. WOLKOWICZ‡

Abstract. This paper deals with a chemostat model with an inhibitor in the context of competition between plasmid-bearing and plasmid-free organisms. First, sufficient conditions for coexistence of the steady-state are determined. Second, the effects of the inhibitor are considered. It turns out that the parameter μ, which represents the effect of the inhibitor, plays a very important role in deciding the number of the coexistence solutions. The results show that if μ is sufficiently large this model has at least two coexistence solutions provided that the maximal growth rate a of u lies in a certain range and has only one unique asymptotically stable coexistence solution when a belongs to another range. Finally, extensive simulations are done to complement the analytic results. The main tools used here include degree theory in cones, bifurcation theory, and perturbation technique.

Key words. chemostat, coexistence solution, perturbation theory, stability

AMS subject classifications. 35K55, 35K57,35J65, 92A17

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1. Introduction. The chemostat is a common model in microbial ecology. It is used as an ecological model of a simple lake, as a model of waste treatment, and as a model for commercial production of fermentation processes. It is important in ecology because the parameters are readily measurable and, thus, the mathematical results are readily testable. For a general discussion of competitive systems see [29], while a detailed mathematical description of competition in the chemostat can be found in [30].

Our study focuses on a chemostat model in the context of competition between plasmid-bearing and plasmid-free organisms. This issue has recently received considerable attention. The theoretical literature on this model includes Ryder and DiBiaso [25], Stephanopoulos and Lapidus [28], Hsu, Waltman, and Wolkowicz [17], Lu and Hadeler [22], Levin [20], Luo and Hsu [18], and Macken, Levin, and Waldstätter [23]. In industry, genetically altered organisms are frequently used to manufacture a desired product, for instance, a pharmaceutical. The alteration is accomplished by introducing a piece of DNA into the cell in the form of a plasmid. The burden imposed on the cell by the task of production can result in the genetically altered (the plasmid-bearing) organism being a less able competitor than the plasmid-free organism. Unfortunately, the plasmid can be lost in the reproductive process. Thus, it is possible for the plasmid-free organism to take over the culture. To avoid "capture" of the process by the plasmid-free organism, the obvious choice is to alter the medium in such a way as to favor the plasmid-bearing organism. An example of this would be to introduce an antibiotic into the feed bottle. See [10, 15, 16] for a detailed biological and chemical background. Models in this direction have been studied in Lenski and Hattingh [21], Hsu and Waltman [13, 15, 16], Hsu, Luo, and Waltman [12], Nie and Wu [24], and the references therein.

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†College of Mathematics and Information Science, Shaanxi Normal University, Xi'an, Shaanxi 710062, People's Republic of China (wjhua@snnu.edu.cn).

‡Department of Mathematics and Statistics, McMaster University, Hamilton L8S 4K1, ON, Canada (wolkowic@mcmaster.ca).

This paper is concerned with the competition model between plasmid-bearing and plasmid-free organisms in the unstirred chemostat in the presence of an inhibitor. Here the plasmid-bearing organism devotes a partition of its resource to produce an inhibitor, which diminishes the growth rate of the plasmid-free organism but does not reduce that of the plasmid-bearing organism. The pioneering work on this model is that of Hsu and Waltman in [15]. They proposed an ODE model (see [15]) based on the study of Chao and Levin [1] and Levin [20]. Moreover, they obtained some results on the global asymptotic behavior. In our current paper, we allow a heterogeneous environment and so we remove the well-stirred hypothesis and consider the corresponding PDE system. Let $s(x,t)$ be the nutrient concentration at time t; let $u(x,t)$ and $v(x,t)$ be the concentrations of the plasmid-bearing and plasmid-free organisms in the culture vessel, respectively, and let $p(x,t)$ be the concentration of the inhibitor. Then using similar arguments as in [6, 14, 34, 32, 24] the model in the unstirred case takes the form

$$\begin{array}{ll} s_t = ds_{xx} - \frac{1}{r}auf_1(s) - \frac{1}{r}bvf_2(s)e^{-\mu p}, & x \in (0,1), t > 0, \\ u_t = du_{xx} + a(1-q-k)uf_1(s), & x \in (0,1), t > 0, \\ v_t = dv_{xx} + bvf_2(s)e^{-\mu p} + aquf_1(s), & x \in (0,1), t > 0, \\ p_t = dp_{xx} + akuf_1(s), & x \in (0,1), t > 0 \end{array}$$

with boundary conditions and initial conditions

$$\begin{array}{ll} s_x(0,t) = -s^0, s_x(1,t) + \gamma s(1,t) = 0, & t > 0, \\ u_x(0,t) = u_x(1,t) + \gamma u(1,t) = 0, & t > 0, \\ v_x(0,t) = v_x(1,t) + \gamma v(1,t) = 0, & t > 0, \\ p_x(0,t) = p_x(1,t) + \gamma p(1,t) = 0, & t > 0 \end{array}$$

$$\begin{array}{ll} s(x,0) = s_0(x) \geq 0, & p(x,0) = p_0(x) \geq 0, \not\equiv 0, \\ u(x,0) = u_0(x) \geq 0, \not\equiv 0, & v(x,0) = v_0(x) \geq 0, \not\equiv 0, \end{array}$$

where $s^0 > 0$ is the input concentration of the nutrient, which is assumed to be constant; d is the diffusion rate of the chemostat; r is the growth yield constant and a, b are the maximal growth rates of the plasmid-bearing and plasmid-free organisms (without an inhibitor), respectively. The response functions are denoted by $f_i(s) = s/(k_i + s), i = 1, 2$, where k_i are the Michaelis–Menten constants. The term $e^{-\mu p}$ used by Lenski and Hattingh in [21] represents the degree of inhibition of p on the growth rate of v, where $\mu > 0$ is a constant and represents the effect of the inhibitor on v. The constant q is the fraction of plasmid lost, and k is the fraction of consumption devoted to the production of the inhibitor. Hence, $0 < q, k < 1$, and $1 - q - k > 0$. γ is a positive constant. In this model, the corresponding yield constants are assumed to be equal, just as in [17, 15, 20].

For the sake of convenience, by nondimensionalizing the parameters, which are indicated below with bars, $\bar{s} = s/s^0, \bar{u} = u/rs^0, \bar{v} = v/rs^0, \bar{p} = p/rs^0, \bar{k}_i = k_i/s^0, \bar{\mu} = rs^0\mu, f_i(\bar{s}) = f_i(s^0\bar{s})$, we can rewrite this model in the form

$$\begin{array}{ll} s_t = ds_{xx} - auf_1(s) - bvf_2(s)e^{-\mu p}, & x \in (0,1), t > 0, \\ u_t = du_{xx} + a(1-q-k)uf_1(s), & x \in (0,1), t > 0, \\ v_t = dv_{xx} + bvf_2(s)e^{-\mu p} + aquf_1(s), & x \in (0,1), t > 0, \\ p_t = dp_{xx} + akuf_1(s), & x \in (0,1), t > 0, \\ s_x(0,t) = -1, s_x(1,t) + \gamma s(1,t) = 0, & t > 0, \\ u_x(0,t) = u_x(1,t) + \gamma u(1,t) = 0, & t > 0, \\ v_x(0,t) = v_x(1,t) + \gamma v(1,t) = 0, & t > 0, \\ p_x(0,t) = p_x(1,t) + \gamma p(1,t) = 0, & t > 0, \\ s(x,0) = s_0(x) \geq 0, & p(x,0) = p_0(x) \geq 0, \not\equiv 0, \\ u(x,0) = u_0(x) \geq 0, \not\equiv 0, & v(x,0) = v_0(x) \geq 0, \not\equiv 0. \end{array} \tag{1.1}$$

For simplicity, we drop the bars over the nondimensional quantities.

Introduce the new variables $\Phi(x,t) = s + u + v + p$ and $\Psi(x,t) = p - cu$ into (1.1), where $c = k/(1-q-k)$. Then one can argue in exactly the same way as in [24, 33, 34, 36] to conclude that the limiting system of (1.1) may be written as

$$\text{(PP)} \qquad \begin{array}{ll} u_t = du_{xx} + a(1-q-k)uf_1(z-(1+c)u-v), & x \in (0,1), t > 0, \\ v_t = dv_{xx} + bvf_2(z-(1+c)u-v)e^{-\mu cu} & \\ \qquad +aquf_1(z-(1+c)u-v), & x \in (0,1), t > 0, \\ u_x(0,t) = u_x(1,t) + \gamma u(1,t) = 0, & t > 0, \\ v_x(0,t) = v_x(1,t) + \gamma v(1,t) = 0, & t > 0, \\ u(x,0) = u_0(x) \geq 0, \not\equiv 0, \ v(x,0) = v_0(x) \geq 0, \not\equiv 0, & x \in [0,1], \end{array}$$

where $z(x) = (1+\gamma)/\gamma - x, (1+c)u_0(x) + v_0(x) \leq z(x), \not\equiv z(x)$.

The purpose of the present paper is to investigate nonnegative steady-state solutions of system (1.1) and the effect of the inhibitor on coexistence states of this system. Thus we will concentrate on the simplified elliptic system:

$$\text{(EP)} \qquad \begin{array}{l} du'' + a(1-q-k)uf_1(z-(1+c)u-v) = 0, \qquad x \in (0,1), \\ dv'' + bvf_2(z-(1+c)u-v)e^{-\mu cu} + aquf_1(z-(1+c)u-v) = 0, \\ u'(0) = u'(1) + \gamma u(1) = 0, \qquad v'(0) = v'(1) + \gamma v(1) = 0, \end{array}$$

which is obtained from the steady-state system of (1.1) by introducing the variables $\Phi(x) = s + u + v + p$ and $\Psi(x) = p - cu$. Since the proof is standard, we omit it here. Interested readers can refer to [14, 24, 32, 33, 34] for details.

We are mainly interested in coexistence states of (EP), that is, the positive solutions of (EP). Hence, we redefine the response functions as follows:

$$\bar{f}_i(s) = \begin{cases} f_i(s), & s \geq 0, \\ \tan^{-1}(2s/k_i + 1) - \pi/4, & s < 0. \end{cases}$$

It is easily seen that $\bar{f}_i \in C^1(-\infty, +\infty)$. We will denote $\bar{f}_i(s)$ by $f_i(s)$ for the sake of simplicity.

This work is motivated by numerical simulations that seem to indicate that, when the parameters sit in a certain range, there exists a coexistence solution of (EP). More interestingly, it is possible that (EP) has exactly two coexistence solutions if v is a better competitor than u and the parameter μ is suitably large. From the biological standpoint, the numerical results mean that the inhibitor plays an important role in determining the number of coexistence solutions of (EP). As mentioned before, the main purpose of this paper is to determine when the numerical results hold and confirm them rigorously.

Turning now to a description of the main results, we start by introducing some notation and recalling some well-known facts. Let λ_1, σ_1 be, respectively, the principal eigenvalues of the problems

$$\begin{array}{l} d\varphi_1'' + \lambda_1 f_1(z)\varphi_1 = 0 \ \text{ in } \ (0,1), \ \ \varphi_1'(0) = \varphi_1'(1) + \gamma\varphi_1(1) = 0; \\ d\psi_1'' + \sigma_1 f_2(z)\psi_1 = 0 \ \text{ in } \ (0,1), \ \ \psi_1'(0) = \psi_1'(1) + \gamma\psi_1(1) = 0, \end{array}$$

with the corresponding positive eigenfunctions uniquely determined by the normalization $\max_{[0,1]} \varphi_1 = \max_{[0,1]} \psi_1 = 1$. It is well known (see [14, 33]) that, if $a \leq \lambda_1/(1-q-k)$, the boundary value problem

$$du'' + a(1-q-k)uf_1(z-u) = 0, \qquad x \in (0,1), \qquad u'(0) = u'(1) + \gamma u(1) = 0 \tag{1.2}$$

has zero as its unique nonnegative solution, and if $a > \lambda_1/(1-q-k)$, then it has a unique positive solution, which is denoted by ϑ and satisfies the following properties.

(A) $0 < \vartheta < z$.

(B) ϑ is continuously differentiable for $a \in (\lambda_1/(1-q-k), +\infty)$ and is pointwise increasing when a increases.

(C) $\lim_{a\to\lambda_1/(1-q-k)} \vartheta = 0$ uniformly for $x \in (0,1)$, and $\lim_{a\to\infty} \vartheta = z(x)$ for almost every $x \in (0,1)$.

(D) Let $L_a = d\frac{d^2}{dx^2} + a(1-q-k)(f_1(z-\vartheta) - \vartheta f_1'(z-\vartheta))$ be the linear operator of the above equation at ϑ. Then L_a is a differential operator in $C_B^2([0,1]) = \{u \in C^2([0,1]) : u'(0) = u'(1) + \gamma u(1) = 0\}$, and all eigenvalues of L_a are strictly negative.

Remark 1. For the other steady-state one-species problem

$$dv'' + bvf_2(z-v) = 0, \qquad x \in (0,1), \qquad v'(0) = v'(1) + \gamma v(1) = 0,$$

we have the same outcomes. Since we will need this later, we denote the unique positive solution by θ and the linear operator by $L_b = d\frac{d^2}{dx^2} + b(f_2(z-\theta) - \theta f_2'(z-\theta))$.

Next, we introduce $\hat{\lambda}_1$ as the principal eigenvalue of

$$d\hat{\varphi}_1'' + \hat{\lambda}_1 f_1(z-\theta)\hat{\varphi}_1 = 0 \ \text{ in } \ (0,1), \ \ \hat{\varphi}_1'(0) = \hat{\varphi}_1'(1) + \gamma\hat{\varphi}_1(1) = 0,$$

with the corresponding eigenfunction $\hat{\varphi}_1$ normalized by $\max_{[0,1]} \hat{\varphi}_1 = 1$.

Now we are ready to state the main results of this paper, which give analytic confirmation of some of the numerical results.

THEOREM 1.1. (EP) *has a coexistence solution if either* (i) $a > \lambda_1/(1-q-k)$, $b < \sigma_1$ *or* (ii) $a > \hat{\lambda}_1/(1-q-k)$, $b > \sigma_1$.

THEOREM 1.2. *Suppose* $b > \sigma_1$. *Then for any* $\epsilon > 0$ *small and any* $A \geq \frac{\hat{\lambda}_1}{1-q-k}$, *there exists* $M = M(\epsilon, A)$ *large such that for* $\mu \geq M$,

(i) *if* $a \in [\lambda_1/(1-q-k) + \epsilon, \hat{\lambda}_1/(1-q-k))$, *there exist at least two coexistence solutions of* (EP);

(ii) *if* $a \in [\hat{\lambda}_1/(1-q-k), A]$, *there exists a unique coexistence solution of* (EP), *and it is asymptotically stable.*

THEOREM 1.3. *Suppose* $b > \sigma_1$. *Then there exist* $\epsilon_0 > 0$ *small and* $M_0 > 0$ *large, both independent of* a, *such that if* $a \in [\hat{\lambda}_1/(1-q-k) - \epsilon_0, \hat{\lambda}_1/(1-q-k))$ *and* $\mu \geq M_0$, *then* (EP) *has exactly two coexistence solutions, one asymptotically stable and the other unstable.*

The main tools in proving Theorems 1.1–1.3 include degree theory and bifurcation theory. A crucial point of the proof for Theorems 1.2 and 1.3 is to make use of the limiting equations of (EP) which are obtained by letting $\mu \to \infty$ formally in (EP). It turns out that one of the limiting problems can be understood fully. For the other limiting problem, we can also attain some properties. Finally, perturbation theory leads to the main results of this paper.

The contents of the present paper are as follows: In section 2, some preliminary results are given which are needed in the later sections. In section 3, we consider the general case and prove Theorem 1.1. For the case μ large, the uniqueness and non-uniqueness of the coexistence solutions to (EP) are obtained in section 4. The stability is also obtained for some cases. Finally, in section 5, some numerical simulations are given complementing the analytical results.

2. Preliminaries.

We begin by providing the following well-known lemmas as preliminaries without proofs. They are useful for obtaining the results in this paper.

LEMMA 2.1 (see [9, 19]). *Suppose $q(x) \in C(\overline{\Omega})$ and $q(x) > 0$ on $\overline{\Omega}$ in the eigenvalue problem*

$$\triangle\phi + \lambda q(x)\phi = 0, \qquad x \in \Omega, \qquad \tfrac{\partial\phi}{\partial n} + \gamma(x)\phi = 0, \qquad x \in \partial\Omega, \tag{2.1}$$

where $\gamma(x) \in C(\partial\Omega)$ and $\gamma(x) \geq 0$. Then all eigenvalues of (2.1) can be listed in order

$$0 < \lambda_1(q(x)) < \lambda_2(q(x)) \leq \cdots \to \infty$$

with the corresponding eigenfunctions $\phi_1, \phi_2, \ldots$, where $\phi_1 > 0$ on $\overline{\Omega}$, and the principal eigenvalue

$$\lambda_1(q) = \inf_{\phi} \frac{\int_\Omega |\nabla\phi|^2 dx + \int_{\partial\Omega} \gamma(x)\phi^2 ds}{\int_\Omega q(x)\phi^2 dx}$$

is simple. Moreover, the comparison principle holds: $\lambda_j(q_1) \leq \lambda_j(q_2)$ for $j \geq 1$ if $q_1 \geq q_2$ on $\overline{\Omega}$, and strict inequality holds if $q_1(x) \not\equiv q_2(x)$.

LEMMA 2.2 (see [27]). *Suppose $q \in C(\overline{\Omega})$, $\gamma(x) \in C(\partial\Omega)$, and $\gamma(x) \geq 0$. Let $\sigma_1(q)$ be the first eigenvalue of the problem $-\triangle\omega + q\omega = \lambda\omega, x \in \Omega, \frac{\partial\omega}{\partial n} + \gamma(x)\omega = 0, x \in \partial\Omega$. Then $\sigma_1(q)$ depends continuously on q, and $q_1 \leq q_2, q_1 \not\equiv q_2$ imply $\sigma_1(q_1) < \sigma_1(q_2)$.*

LEMMA 2.3 (see [31]). *Let $q(x) \in C(\overline{\Omega})$ and $q(x) + p > 0$ on $\overline{\Omega}$ with $p > 0$, and let η_1 be the first eigenvalue of the eigenvalue problem*

$$-\triangle\varphi - q(x)\varphi = \eta\varphi, \qquad x \in \Omega, \qquad \frac{\partial\varphi}{\partial n} + \gamma(x)\varphi = 0, \qquad x \in \partial\Omega,$$

where $\gamma(x) \in C(\partial\Omega)$ and $\gamma(x) \geq 0$. If $\eta_1 > 0$ (or $\eta_1 < 0$), then the eigenvalue problem

$$-\triangle\varphi + p\varphi = t(q(x) + p)\varphi, \qquad x \in \Omega, \qquad \frac{\partial\varphi}{\partial n} + \gamma(x)\varphi = 0, \qquad x \in \partial\Omega$$

has no eigenvalue less than or equal to 1 (or has eigenvalues less than 1).

Now, we introduce some more notation that will be used throughout this paper. Let X be a real Banach space, and let $W \subset X$ be a closed convex set. W is called a wedge provided that $\alpha W \subset W$ for all $\alpha \geq 0$. A wedge W is said to be a cone if $W \cap \{-W\} = 0$. Let $y \in W$, and define a wedge

$$W_y := \mathrm{cl}\{x \in X | y + \nu x \in W \ \text{ for some } \ \nu > 0\},$$

where "cl" means the closure of the set. Let S_y be the maximal linear subspace of X contained in W_y. Assume that T is a compact and Fréchet differentiable operator on X such that $y \in W$ is a fixed point of T and $T(W) \subseteq W$. Then the Fréchet derivative $T'(y)$ of T at y leaves W_y and S_y invariant (see [4, 26]). If there exists a closed linear subspace X_y of X such that $X = S_y \oplus X_y$ and W_y is generating, then the index of T at y can be found by analyzing certain eigenvalue problems in X_y and S_y as follows. Let $Q : X \to X_y$ be the projection operator of X_y along S_y. In view of Theorems 2.1 and 2.2 of [26], $\mathrm{index}_W(T, y)$ exists if the Fréchet derivative $T'(y)$ of T at y has no nonzero fixed point in W_y. Furthermore,

(1) $\mathrm{index}_W(T, y) = 0$ if $Q \circ T'(y)$ has an eigenvalue $\lambda > 1$;

(2) $\mathrm{index}_W(T, y) = \mathrm{index}_{S_y}(T'(y), 0)$ if $Q \circ T'(y)$ has no such eigenvalues.

Here $\mathrm{index}_{S_y}(T'(y), 0)$ is the index of the linear operator $T'(y)$ at 0 in the space S_y.

Next, we derive some a priori estimates for positive solutions of (EP). For an accurate estimate for positive solutions of (EP), we first consider the boundary value problem

$$\begin{array}{l} dv'' + bvf_2(z-v) + \frac{aq\vartheta}{1+c}f_1(z-v) = 0,\ x \in (0,1), \\ v'(0) = v'(1) + \gamma v(1) = 0. \end{array} \tag{2.2}$$

LEMMA 2.4. *There exists a unique positive solution of* (2.2)*, denoted by* $\bar{v}(x)$*, which satisfies* $0 < \bar{v}(x) < z$*. In particular,* $\theta < \bar{v}(x) < z$ *if* $b > \sigma_1$*.*

Proof. First, we claim that if $v(x)$ is a positive solution of (2.2), then $0 < v(x) < z$ and that, in addition, if $b > \sigma_1$, then $\theta < v(x) < z$. Indeed, let $\omega = z - v$. Then

$$d\omega'' - bvf_2(\omega) - \frac{aq\vartheta}{1+c}f_1(\omega) = 0, \qquad x \in (0,1), \qquad \omega'(0) = -1, \qquad \omega'(1) + \gamma\omega(1) = 0.$$

Suppose $\inf_{x\in[0,1]} \omega(x) = \omega(x_0) < 0$. Then $x_0 \notin (0,1)$. Otherwise, $\omega''(x_0) \geq 0$. By the previous equation for ω, we have $d\omega''(x_0) = bv(x_0)f_2(\omega(x_0)) + \frac{aq\vartheta(x_0)}{1+c}f_1(\omega(x_0)) < 0$, a contradiction. If $x_0 = 0$, then $\omega'(x_0) \geq 0$, contradicting the boundary condition $\omega'(0) = -1$. Similarly, we can see that $x_0 = 1$ is also impossible. Hence, one must have $\omega \geq 0, \not\equiv 0$ on [0, 1].

Assume $\omega(x_0) = 0$ for some point $x_0 \in [0,1]$. Then $x_0 = 0$ or 1 by the strong maximum principle. On the other hand, from the Hopf boundary lemma, it is easy to see that both $x = 0$ and 1 are impossible, which implies $\omega > 0$ on [0, 1]. That is, $v < z$ on [0, 1]. Moreover, since

$$dv'' + bvf_2(z-v) + \frac{aq\vartheta}{1+c}f_1(z-v) > dv'' + bvf_2(z-v),$$

it is easy to see that $v > \theta$ if $b > \sigma_1$. Hence, our assertion holds.

On the other hand, for sufficiently small $\delta > 0$, $\delta\varphi_1, z$ are the sub- and super-solutions of (2.2), respectively. It follows from the existence-comparison theorem for elliptic systems that the minimal and maximal solutions v_1, v_2 to (2.2) exist and satisfy the relation $\delta\varphi_1 < v_1 \leq v_2 < z$. Next, we show that $v_1 \equiv v_2$, to obtain the uniqueness. Since v_1, v_2 are the solutions of (2.2),

$$\begin{array}{l} dv_1'' + bv_1f_2(z-v_1) + \frac{aq\vartheta}{1+c}f_1(z-v_1) = 0, \\ dv_2'' + bv_2f_2(z-v_2) + \frac{aq\vartheta}{1+c}f_1(z-v_2) = 0. \end{array}$$

Multiplying the first equation by v_2 and the second equation by v_1 and considering the integral $I = \int_0^1 d(v_1''v_2 - v_2''v_1)dx$, we have

$$\int_0^1 bv_1v_2(f_2(z-v_1) - f_2(z-v_2))dx + \frac{aq}{1+c}\int_0^1 \vartheta[v_2f_1(z-v_1) - v_1f_1(z-v_2)]dx = 0.$$

By the monotonity of $f_i (i = 1,2)$ and since $v_1 \leq v_2$, we have $v_1 \equiv v_2$. ∎

The next lemma gives a priori estimates for positive solutions of (EP).

LEMMA 2.5. *Assume* (u,v) *is a nonnegative solution of* (EP) *with* $u \not\equiv 0$ *and* $v \not\equiv 0$*. Then*

1) $0 < u < \frac{\vartheta}{1+c} < \frac{z}{1+c}, 0 < v \leq \bar{v} < z$ *on* $[0,1]$*, where* $\bar{v}$ *defined by Lemma* 2.4*;*
2) $(1+c)u + v < z$ *on* [0, 1]*;*
3) $a > \frac{\lambda_1}{1-q-k}$.

Proof. Clearly, $u > 0$ on $[0, 1]$ by the strong maximum principle and Hopf boundary lemma. Since $0 = du'' + a(1-q-k)uf_1(z-(1+c)u-v) \le du'' + a(1-q-k)uf_1(z-(1+c)u)$, it is easy to check that $u \le \frac{\vartheta}{1+c}$ and $a > \frac{\lambda_1}{1-q-k}$. Moreover, one can find that $u < \frac{\vartheta}{1+c}$ because $v \not\equiv 0$.

For v, we have

$$\begin{aligned} 0 &= dv'' + bvf_2(z-(1+c)u-v)e^{-\mu cu} + aquf_1(z-(1+c)u-v) \\ &\le dv'' + bvf_2(z-v) + \tfrac{aq\vartheta}{1+c}f_1(z-v). \end{aligned}$$

By Lemma 2.4 and the strong maximum principle, it follows that $0 < v \le \bar{v} < z$. It remains to show that $(1+c)u + v < z$ on $[0, 1]$. This proof is similar to the proof of Lemma 4.2 in [33] and so is omitted here. □

3. Existence of coexistence solutions. The goal of this section is to discuss the existence of coexistence solutions of (EP) in the general case and to establish Theorem 1.1.

In order to use the functional analytic framework of degree theory we introduce the spaces

$$\begin{aligned} &X = C([0,1]) \times C([0,1]), \\ &D = \{(u,v) \in X | u \le \tfrac{\vartheta}{1+c}, v \le \max_{[0,1]} \bar{v} + 1\}, \\ &W = \{(u,v) \in X | u \ge 0, v \ge 0 \ \text{ for } \ x \in [0,1]\}, \\ &D' = (\text{int} D) \cap W. \end{aligned}$$

Then W is a cone of X and D' is a bounded open set in W.

We consider the system

$$\begin{aligned} &du'' + \tau a(1-q-k)uf_1(z-(1+c)u-v) = 0, \\ &dv'' + \tau bvf_2(z-(1+c)u-v)e^{-\mu cu} + \tau aquf_1(z-(1+c)u-v) = 0, \\ &u'(0) = u'(1) + \gamma u(1) = 0, \quad v'(0) = v'(1) + \gamma v(1) = 0, \end{aligned} \tag{3.1}$$

where $\tau \in [0,1]$. Assume (u_τ, v_τ) is a nonnegative solution of (3.1). Then it is not hard to show that $u_\tau < \frac{\vartheta}{1+c}, v_\tau \le \bar{v}$ for all $\tau \in [0,1]$.

Since $f_1(z-(1+c)u-v) \ge f_1(z-(1+c)u) - K_1 v$ for some positive constant $K_1 > 0$, we can define $\mathcal{A}_\tau : X \to X, \tau \in [0,1]$ as

$$\begin{aligned} \mathcal{A}_\tau(u,v) = \quad &(-d\tfrac{d^2}{dx^2} + M)^{-1}(\tau a(1-q-k)ug_1(u,v) + Mu, \\ &\tau bvg_2(u,v) + \tau aqug_1(u,v) + Mv) \end{aligned}$$

where $(-d\frac{d^2}{dx^2} + M)^{-1}$ is the inverse operator of $-d\frac{d^2}{dx^2} + M$ subject to the boundary conditions $u'(0) = u'(1) + \gamma u(1) = 0$, $g_1(u,v) = f_1(z-(1+c)u-v)$, $g_2(u,v) = f_2(z-(1+c)u-v)e^{-\mu cu}$, and M is large enough such that $M + \tau a(1-q-k)g_1(u,v) > 0$ and $M + \tau bg_2(u,v) - \tau aquK_1 > 0$ for all $(u,v) \in D'$ and $\tau \in [0,1]$. Clearly, $\mathcal{A}_\tau$ is compact. Let $\mathcal{A} = \mathcal{A}_1$. Then $\mathcal{A} : D' \to W$ is continuously differentiable. It follows from Lemma 2.5 that (EP) has nonnegative solutions if and only if the operator $\mathcal{A}$ has a fixed point in D'. Moreover, $\mathcal{A}_\tau$ has no fixed point on $\partial D'$. By the homotopic invariance of the degree, we obtain

$$\text{index}(\mathcal{A}, D', W) = \text{index}(\mathcal{A}_\tau, D', W) = \text{index}(\mathcal{A}_0, D', W) = \text{index}_W(\mathcal{A}_0, (0,0)).$$

By some standard calculations, we can obtain $\text{index}_W(\mathcal{A}_0, (0,0)) = 1$. Hence, we have the following.

LEMMA 3.1. $\mathrm{index}(\mathcal{A}, D', W) = 1$.

LEMMA 3.2. (i) *Suppose* $a \neq \frac{\lambda_1}{1-q-k}$ *and* $b \neq \sigma_1$. *Then* $\mathrm{index}_W(\mathcal{A}, (0,0)) = 1$ *if* $a < \frac{\lambda_1}{1-q-k}$ *and* $b < \sigma_1$, *and* $\mathrm{index}_W(\mathcal{A}, (0,0)) = 0$ *if* $a > \frac{\lambda_1}{1-q-k}$ *or* $b > \sigma_1$.

(ii) $\mathrm{index}_W(\mathcal{A}, (0,\theta)) = 1$ *if* $a < \frac{\hat{\lambda}_1}{1-q-k}$, *and* $\mathrm{index}_W(\mathcal{A}, (0,\theta)) = 0$ *if* $a > \frac{\hat{\lambda}_1}{1-q-k}$.

Since the proof of this Lemma is very lengthy and quite standard, we include the proof in Appendix A. Now, we turn to prove Theorem 1.1.

Proof of Theorem 1.1. (i) If $a > \lambda_1/(1-q-k)$ and $b < \sigma_1$, then (EP) has no semitrivial nonnegative solution. In view of Lemmas 3.1 and 3.2, $\mathrm{index}_W(\mathcal{A}, D') = 1$ and $\mathrm{index}_W(\mathcal{A}, (0,0)) = 0$, which implies that $\mathcal{A}$ must have a positive fixed point in D'. That is, (EP) has a positive solution in D'.

(ii) If $a > \hat{\lambda}_1/(1-q-k), b > \sigma_1$, then (EP) has a semitrivial nonnegative solution $(0,\theta)$. Suppose $\mathcal{A}$ has no positive fixed point in D'. Then by Lemma 3.1 and the additivity of index,

$$\mathrm{index}_W(\mathcal{A}, (0,0)) + \mathrm{index}_W(\mathcal{A}, (0,\theta)) = \mathrm{index}_W(\mathcal{A}, D') = 1.$$

However, by Lemma 3.2, $\mathrm{index}_W(\mathcal{A}, (0,0)) = 0$, and $\mathrm{index}_W(\mathcal{A}, (0,\theta)) = 0$ in this case, a contradiction. Hence there must exist a positive solution of (EP) in D'. This completes the proof. $\square$

4. The effect of inhibitor. The purpose of this section is to examine the effect of the inhibitor on the multiple coexistence states. In view of the model, the effect of the inhibitor increases as the parameter μ increases. Motivated by the numerical simulations, we consider only the case of $b > \sigma_1$ and μ large enough. Using a perturbation technique, we show that the system has two positive solutions if μ is sufficiently large and the other parameters sit in some suitable range.

First of all, we observe that if a is bounded away from $\lambda_1/(1-q-k)$ and μ is large, positive solutions to (EP) are of two types. More precisely, let (u, v) be any positive solution of (EP); then either (u, v) is close to a positive solution of the problem

$$\begin{aligned} &du'' + a(1-q-k)uf_1(z-(1+c)u-v) = 0, \qquad x \in (0,1),\\ &dv'' + aquf_1(z-(1+c)u-v) = 0, \qquad x \in (0,1),\\ &u'(0) = u'(1) + \gamma u(1) = 0, \qquad v'(0) = v'(1) + \gamma v(1) = 0, \end{aligned} \tag{4.1}$$

or $(\mu u, v)$ is close to a positive solution of the problem

$$\begin{aligned} &d\omega'' + a(1-q-k)\omega f_1(z-v) = 0, \qquad x \in (0,1),\\ &dv'' + bvf_2(z-v)e^{-c\omega} = 0, \qquad x \in (0,1),\\ &\omega'(0) = \omega'(1) + \gamma\omega(1) = 0, \qquad v'(0) = v'(1) + \gamma v(1) = 0. \end{aligned} \tag{4.2}$$

Since the above two equations play an important role in determining the coexistence solutions of (EP), we first study positive solutions of (4.1) and (4.2).

LEMMA 4.1. *Assume* $a > \lambda_1/(1-q-k)$. *Then there exists a unique positive solution* $((1-q-k)\vartheta, q\vartheta)$ *of* (4.1)*, and it is linearly asymptotically stable.*

Proof. Suppose that $(u, v) > 0$ solves (4.1). Let $\omega = qu - (1-q-k)v$. Then we have

$$d\omega'' = 0, \qquad \omega'(0) = \omega'(1) + \gamma\omega(1) = 0,$$

which implies $\omega \equiv 0$. That is, $v = \frac{q}{1-q-k}u$. Substituting $v = \frac{q}{1-q-k}u$ into the first equation of (4.1), we obtain that

$$\begin{aligned} &du'' + a(1-q-k)uf_1\left(z - \frac{u}{1-q-k}\right) = 0, \qquad x \in (0,1),\\ &u'(0) = u'(1) + \gamma u(1) = 0. \end{aligned}$$

Then $u = (1-q-k)\vartheta$ due to $a > \lambda_1/(1-q-k)$, and $v = q\vartheta$. That is, (4.1) has a unique positive solution $((1-q-k)\vartheta, q\vartheta)$. It remains to establish the stability. For this purpose, noting that $c = k/(1-q-k)$, we consider the linearized eigenvalue problem

$$\begin{aligned} &d\phi'' + a(1-q-k)[f_1(z-\vartheta) - (1-q)\vartheta f_1'(z-\vartheta)]\phi\\ &\quad -a(1-q-k)^2\vartheta f_1'(z-\vartheta)\psi = -\eta\phi,\\ &d\psi'' + aq[f_1(z-\vartheta) - (1-q)\vartheta f_1'(z-\vartheta)]\phi - aq(1-q-k)\vartheta f_1'(z-\vartheta)\psi = -\eta\psi,\\ &\phi'(0) = \phi'(1) + \gamma\phi(1) = 0, \qquad \psi'(0) = \psi'(1) + \gamma\psi(1) = 0. \end{aligned} \tag{4.3}$$

Let $\omega = q\phi - (1-q-k)\psi$. Then

$$d\omega'' = -\eta\omega, \qquad \omega'(0) = \omega'(1) + \gamma\omega(1) = 0.$$

If $\omega \not\equiv 0$, then $\eta > 0$. If $\omega \equiv 0$, then $\psi = \frac{q\phi}{1-q-k}$, which leads to

$$\begin{aligned} &d\phi'' + a(1-q-k)(f_1(z-\vartheta) - \vartheta f_1'(z-\vartheta))\phi = -\eta\phi,\\ &\phi'(0) = \phi'(1) + \gamma\phi(1) = 0. \end{aligned}$$

From Lemma 2.2, $\sigma_1(a(1-q-k)(f_1(z-\vartheta) - \vartheta f_1'(z-\vartheta))) < \sigma_1(a(1-q-k)f_1(z-\vartheta)) = 0$. Hence, we can claim that $\eta > 0$. Therefore, (4.3) has no eigenvalue η with $Re\eta \le 0$ and so the stability follows. ∎

Lemma 4.2. *Suppose $b > \sigma_1$ fixed. Then* (4.2) *has a positive solution if and only if $\frac{\lambda_1}{1-q-k} < a < \frac{\hat{\lambda}_1}{1-q-k}$. Moreover, all positive solutions of* (4.2) *are unstable.*

Proof. Suppose (ω, v) is a positive solution of (4.2). Then $a(1-q-k) = \lambda_1(f_1(z-v)) > \lambda_1(f(z)) = \lambda_1$. On the other hand,

$$0 = dv'' + bvf_2(z-v)e^{-c\omega} < dv'' + bvf_2(z-v),$$

which means $v < \theta$. Thus, $a(1-q-k) = \lambda_1(f_1(z-v)) < \lambda_1(f_1(z-\theta)) = \hat{\lambda}_1$. Hence, if (4.2) has a positive solution, then $\frac{\lambda_1}{1-q-k} < a < \frac{\hat{\lambda}_1}{1-q-k}$.

Next, we show that (4.2) has a positive solution if $\lambda_1/(1-q-k) < a < \hat{\lambda}_1/(1-q-k)$. To this end, we first prove that for any given $A > \hat{\lambda}_1/(1-q-k)$, there exists a constant $C > 0$ such that $\|\omega\|_\infty < C$ for any nonnegative solution of (4.2) with $a \in (\lambda_1/(1-q-k), A]$. At first, one can find that (4.2) has only two nonnegative solutions $(0,0)$ and $(0,\theta)$ if $a \ge \hat{\lambda}_1/(1-q-k)$. It remains to show that any positive solution (ω, v) of (4.2) with $\frac{\lambda_1}{1-q-k} < a < \frac{\hat{\lambda}_1}{1-q-k}$ satisfies $\|\omega\|_\infty < C$. Suppose this is not true. Then we may assume that there exists $a_i \to a \in [\lambda_1/(1-q-k), \hat{\lambda}_1/(1-q-k)]$, (ω_i, v_i) positive solutions of (4.2) with $a = a_i$ and $\|\omega_i\|_\infty \to \infty$. Set $\tilde{v}_i = v_i/\|v_i\|_\infty, \tilde{\omega}_i = \omega_i/\|\omega_i\|_\infty$. Then

$$\begin{aligned} &d\tilde{\omega}_i'' + a_i(1-q-k)\tilde{\omega}_i f_1(z - \|v_i\|_\infty \tilde{v}_i) = 0,\\ &d\tilde{v}_i'' + b\tilde{v}_i f_2(z-v_i)e^{-c\|\omega_i\|_\infty \tilde{\omega}_i} = 0,\\ &\tilde{\omega}_i'(0) = \tilde{\omega}_i'(1) + \gamma\tilde{\omega}_i(1) = 0, \qquad \tilde{v}_i'(0) = \tilde{v}_i'(1) + \gamma\tilde{v}_i(1) = 0. \end{aligned}$$

By L^p estimates and the Sobolev embedding theorem, we may assume $\tilde{\omega}_i \to \tilde{\omega} \geq 0, \not\equiv 0$, $\tilde{v}_i \to \tilde{v} \geq 0, \not\equiv 0$ in $C^1([0,1])$, and $\tilde{\omega}$ satisfies

$$d\tilde{\omega}^{''} + a(1-q-k)\tilde{\omega} f_1(z - B\tilde{v}) = 0, \quad \tilde{\omega}'(0) = \tilde{\omega}'(1) + \gamma\tilde{\omega}(1) = 0,$$

where $B = \lim_{i\to\infty} \|v_i\|_\infty < \infty$. (In view of the equation for v_i and $0 < v_i < \theta$, this limit exists by passing to a subsequence.) Thus $\tilde{\omega} > 0$ on $[0, 1]$ by the strong maximum principle and Hopf boundary lemma. Hence $e^{-c\omega_i} = e^{-c\|\omega_i\|_\infty \tilde{\omega}_i} \to 0$ as $i \to \infty$, which implies $v_i \to 0$, and $\tilde{v}$ satisfies

$$d\tilde{v}^{''} = 0, \quad \tilde{v}'(0) = \tilde{v}'(1) + \gamma\tilde{v}(1) = 0.$$

Thus $\tilde{v} \equiv 0$. This is a contradiction to $\tilde{v} \not\equiv 0$ and $\|\tilde{v}\|_\infty = 1$.

Let $\tilde{D} = \{(\omega, v) \in W : \|\omega\|_\infty \leq C+1, \|v\|_\infty \leq \sup_{[0,1]} z + 1\}$,

$$B_\tau(\omega, v) = \left(-d\frac{d^2}{dx^2} + M\right)^{-1} \left(\tau(1-q-k)\omega f_1(z-v) + M\omega,\ bvf_2(z-v)e^{-c\omega} + Mv\right),$$

where W defined in section 3 is the positive cone of X and M is sufficiently large such that $M + \tau(1-q-k)f_1(z-v) > 0$ and $M + bf_2(z-v)e^{-c\omega} > 0$ for all $(\omega, v) \in \tilde{D}$ and $\tau \in (\lambda_1/(1-q-k), A]$.

By virtue of our a priori estimates and the homotopic invariance property of the fixed point index, we obtain $\mathrm{index}_W(B_\tau, \tilde{D}) \equiv \mathrm{const}$ for $\tau > \lambda_1/(1-q-k)$. On the other hand, if $a > \hat{\lambda}_1/(1-q-k)$, then (4.2) has only two nonnegative solutions $(0, 0)$ and $(0, \theta)$. Hence for $\tau \in (\hat{\lambda}_1/(1-q-k), A]$, $\mathrm{index}_W(B_\tau, \tilde{D}) = \mathrm{index}_W(B_\tau, (0,0)) + \mathrm{index}_W(B_\tau, (0, \theta))$. Next, we calculate the index of the two nonnegative solutions.

Let $B'_\tau(0, 0)$ be the Fréchet derivative of B_τ at $(0, 0)$. Then

$$B'_\tau(0,0)(\omega, v) = \left(-d\frac{d^2}{dx^2} + M\right)^{-1} (\tau(1-q-k)\omega f_1(z) + M\omega,\ bvf_2(z) + Mv)$$

for each $(\omega, v) \in X$. Therefore, an eigenvector (ω, v) of $B'_\tau(0, 0)$ satisfies

$$\begin{aligned}
&-d\omega^{''} + M\omega = \tfrac{1}{\lambda}(\tau(1-q-k)f_1(z) + M)\omega,\\
&-dv^{''} + Mv = \tfrac{1}{\lambda}(bf_2(z) + M)v,\\
&\omega'(0) = \omega'(1) + \gamma\omega(1) = 0, \qquad v'(0) = v'(1) + \gamma v(1) = 0.
\end{aligned}$$

Since $b > \sigma_1, \tau > \lambda_1/(1-q-k)$, it is easy to check that $I - B'_\tau(0, 0)$ is invertible in $W_{(0,0)} = \{(\omega, v) \in X : \omega \geq 0, v \geq 0\}$. Moreover, a similar argument as in the proof of Lemma 3.2 (see Appendix A) shows that $B'_\tau(0, 0)$ has eigenvalues larger than 1. It follows from Theorem 2.2 of [26] that $\mathrm{index}_W(B_\tau, (0, 0)) = 0$ for $\tau > \lambda_1/(1-q-k)$.

Let $B'_\tau(0, \theta)$ denote the Fréchet derivative of B_τ at $(0, \theta)$. Then $B'_\tau(0, \theta)(\omega, v) = (-d\frac{d^2}{dx^2} + M)^{-1}(\tau(1-q-k)\omega f_1(z-\theta) + M\omega, b(f_2(z-\theta) - \theta f'_2(z-\theta))v - bc\theta f_2(z-\theta)\omega + Mv)$ for each $(\omega, v) \in X$. In order to apply Theorem 2.2 of [26], we introduce the notation $y = (0, \theta), W_y = \{(\omega, v) \in X : \omega \geq 0\}, S_y = \{(0, v) : v \in C_B([0, 1])\}$, and $X_y = \{(\omega, 0) \in X : \omega \in C_B([0, 1])\}$. Then $X = S_y \oplus X_y$ with projection Q given by $(\omega, v) \to (\omega, 0)$.

Suppose $(\omega, v) \in W_y$ is a fixed point of $B'_\tau(0, \theta)$. Then (ω, v) satisfies

$$\begin{aligned}
&d\omega^{''} + \tau(1-q-k)\omega f_1(z-\theta) = 0,\\
&dv^{''} + b(f_2(z-\theta) - \theta f'_2(z-\theta))v - bc\theta f_2(z-\theta)\omega = 0,\\
&\omega'(0) = \omega'(1) + \gamma\omega(1) = 0, \qquad v'(0) = v'(1) + \gamma v(1) = 0.
\end{aligned}$$

It is easy to check that $I - B'_\tau(0,\theta)$ is invertible in W_y as long as $\tau \neq \hat{\lambda}_1/(1-q-k)$. Hence, $\text{index}_W(B_\tau,(0,\theta))$ is well defined if $\tau \neq \hat{\lambda}_1/(1-q-k)$. Next, we determine the index of B_τ at $(0,\theta)$. In view of the definition $Q(\omega,v)=(\omega,0)$, every eigenfunction of $Q \circ B'_\tau(0,\theta)$ has the form $(\omega,0)$, where ω is a nonzero solution of the equation

$$-d\omega'' + M\omega = \frac{1}{\lambda}(\tau(1-q-k)f_1(z-\theta)+M)\omega,\ \omega'(0)=\omega'(1)+\gamma\omega(1)=0.$$

We can proceed further as in the proof of Lemma 3.2 (see Appendix A) to show that $\text{index}_W(B_\tau,(0,\theta))=0$ if $\tau > \hat{\lambda}_1/(1-q-k)$ and $\text{index}_W(B_\tau,(0,\theta))=1$ if $\tau < \hat{\lambda}_1/(1-q-k)$. Hence, for any $\tau \in (\hat{\lambda}_1/(1-q-k), A]$, $\text{index}_W(B_\tau,\tilde{D}) = \text{index}_W(B_\tau,(0,0)) + \text{index}_W(B_\tau,(0,\theta)) = 0$. Meanwhile, by the homotopic invariance property of the fixed point index, we can claim that $\text{index}_W(B_\tau,\tilde{D}) \equiv 0$ for any $\tau \in (\lambda_1/(1-q-k), A]$. However, for $\lambda_1/(1-q-k) < \tau < \hat{\lambda}_1/(1-q-k)$, $\text{index}_W(B_\tau,(0,0)) + \text{index}_W(B_\tau,(0,\theta)) = 1 \neq \text{index}_W(B_\tau,\tilde{D})$, which implies B_τ has at least a positive fixed point in $\tilde{D}$ for $\lambda_1/(1-q-k) < \tau < \hat{\lambda}_1/(1-q-k)$. Namely, (4.2) has a positive solution when $a \in (\lambda_1/(1-q-k), \hat{\lambda}_1/(1-q-k))$.

It remains to prove the instability of any positive solution (ω_0, v_0) of (4.2). To this end, let us consider the eigenvalue problem

$$\begin{aligned}
&d\varphi'' + a(1-q-k)f_1(z-v_0)\varphi - a(1-q-k)\omega_0 f_1'(z-v_0)\psi + \eta\varphi = 0,\\
&d\psi'' + b[f_2(z-v_0) - v_0 f_2'(z-v_0)]e^{-c\omega_0}\psi - cbv_0 f_2(z-v_0)e^{-c\omega_0}\varphi + \eta\psi = 0,\\
&\varphi'(0)=\varphi'(1)+\gamma\varphi(1)=0, \qquad \psi'(0)=\psi'(1)+\gamma\psi(1)=0.
\end{aligned} \tag{4.4}$$

It is well known (see, e.g., [11]) that one can put this eigenvalue problem in the context of spectral theory of compact strongly positive operators with respect to the order cone $P = \{(\varphi,\psi) \in X : \varphi \geq 0, \psi \leq 0\}$. In particular, by the Krein–Rutman theorem [5, 11], one can show (4.4) has an eigenvalue η_1, which has the following properties: it is real, algebraically simple, and all other eigenvalues have their real part greater than η_1. Moreover, η_1 corresponds to an eigenfunction (φ,ψ) in the interior of P, and it is the only eigenvalue with an eigenfunction in P. Thus it is called the principal eigenvalue of (4.4). The linearized stability criterion for (ω_0,v_0) can be expressed in terms of the principal eigenvalue: (ω_0,v_0) is asymptotically stable if $\eta_1 > 0$; it is unstable if $\eta_1 < 0$. On the other hand, multiplying the first equation of (4.4) by ω_0 and integrating, we obtain

$$\eta_1 \int_0^1 \varphi\omega_0 dx = a(1-q-k)\int_0^1 \omega_0^2 f_1'(z-v_0)\psi dx.$$

Noting that (φ,ψ) belongs to the interior of P, we must have $\eta_1 < 0$, which implies the instability. $\square$

The rest of this section is devoted to the proof of Theorems 1.2 and 1.3, which are important in understanding the effect of the inhibitor on the number of the coexistence solutions. In order to establish Theorem 1.2, we need the following technical results.

LEMMA 4.3. *For any $\epsilon > 0$ small, there exists $M = M(\epsilon)$ large such that if $a \geq \lambda_1/(1-q-k)+\epsilon$, $\mu \geq M$,* (EP) *has a positive solution $(\tilde{u},\tilde{v})$ which satisfies*

$$(1-\delta)(1-q-k)\vartheta \leq \tilde{u} \leq (1-q-k)\vartheta, \quad (1-\delta)q\vartheta \leq \tilde{v} \leq (q+\delta)\vartheta, \tag{4.5}$$

where ϑ are the unique positive solutions of (1.2), *and $0 < \delta \leq \delta_0$, where $\delta_0 > 0$ is small such that $(1+\delta_0)\vartheta < z$ on* $[0,1]$.

Proof. Suppose that (u, v) solves (EP). Let $\chi = (1-q-k)v - qu$. Then (u, χ) satisfies

$$
\begin{aligned}
&du'' + a(1-q-k)uf_1(z - \tfrac{u+\chi}{1-q-k}) = 0,\\
&d\chi'' + b(\chi+qu)f_2(z - \tfrac{u+\chi}{1-q-k})e^{-\mu cu} = 0,
\end{aligned}
\tag{4.6}
$$

with the usual boundary conditions. Since $0 < \vartheta < z$ on [0, 1], we can claim that there exists $\delta_0 > 0$ small such that $(1+\delta_0)\vartheta < z$ on [0, 1]. Set

$$\Sigma = \{(u,\chi) \in X : (1-\delta_0)(1-q-k)\vartheta \le u \le (1-q-k)\vartheta,\ 0 \le \chi \le \delta_0(1-q-k)\vartheta\}.$$

Next, we show (4.6) is quasi-monotone decreasing [35] on Σ provided that μ is large enough. Clearly, $h_1(u,\chi) = a(1-q-k)uf_1(z - \frac{u+\chi}{1-q-k})$ is quasi-monotone decreasing on Σ. On the other hand, let $h_2(u,\chi) = b(\chi+qu)f_2(z-\frac{u+\chi}{1-q-k})e^{-\mu cu}$. Then

$$\frac{\partial h_2(u,\chi)}{\partial u} = be^{-\mu cu}[qf_2(z-\tfrac{u+\chi}{1-q-k}) - \tfrac{\chi+qu}{1-q-k}f_2'(z-\tfrac{u+\chi}{1-q-k}) - \mu c(\chi+qu)f_2(z-\tfrac{u+\chi}{1-q-k})].$$

Recalling that $(1+\delta_0)\vartheta < z$ on [0, 1], it is easy to see that $\frac{\partial h_2(u,\chi)}{\partial u} < 0$ on Σ provided that μ is large enough. That is, $h_2(u,\chi)$ is quasi-monotone decreasing on Σ provided that μ is large enough.

Let $(\bar{u},\ \underline{\chi}) = ((1-q-k)\vartheta(a),\ 0)$ and $(\underline{u},\ \bar{\chi}) = ((1-\delta)(1-q-k)\vartheta,\ \delta(1-q-k)\vartheta)$. By the super- and subsolution method, it suffices to show that $(\bar{u}, \underline{\chi})$ and $(\underline{u}, \bar{\chi})$ are pairs of super-sub solutions of (4.6) for large μ. That is, we need to show that the inequalities

$$
\begin{aligned}
&d\bar{u}'' + a(1-q-k)\bar{u}f_1(z - \tfrac{\bar{u}+\underline{\chi}}{1-q-k}) \le 0,\\
&d\underline{\chi}'' + b(\underline{\chi}+q\bar{u})f_2(z - \tfrac{\bar{u}+\underline{\chi}}{1-q-k})e^{-\mu c\bar{u}} \ge 0
\end{aligned}
$$

and

$$
\begin{aligned}
&d\underline{u}'' + a(1-q-k)\underline{u}f_1(z - \tfrac{\underline{u}+\bar{\chi}}{1-q-k}) \ge 0,\\
&d\bar{\chi}'' + b(\bar{\chi}+q\underline{u})f_2(z - \tfrac{\underline{u}+\bar{\chi}}{1-q-k})e^{-\mu c\underline{u}} \le 0
\end{aligned}
$$

hold. It is trivial to check the inequalities for $\bar{u}, \underline{\chi}$, and $\underline{u}$. For $\bar{\chi}$ to satisfy the above inequality, it suffices to have

$$e^{-\mu c(1-\delta)(1-q-k)\vartheta} \le \frac{\delta a(1-q-k)(k_2+z-\theta)}{b((1-q)\delta+q)(k_1+z-\theta)}.$$

It is well known that there exists $B > 1$ large enough such that $Bk_1 > k_2$. Hence, $\frac{k_2+z-\theta}{k_1+z-\theta} > \frac{k_2}{Bk_1}$. Since $a \ge \lambda_1/(1-q-k)+\epsilon$ and $\vartheta = \vartheta(a) \ge \vartheta(\frac{\lambda_1}{1-q-k}+\epsilon)$, we need to have only

$$e^{-\mu c(1-\delta)(1-q-k)\vartheta(\frac{\lambda_1}{1-q-k}+\epsilon)} \le \frac{\delta[\lambda_1+\epsilon(1-q-k)]k_2}{b((1-q)\delta+q)Bk_1},$$

where $\vartheta(\frac{\lambda_1}{1-q-k}+\epsilon)$ is the unique positive solution of (1.2) with $a = \frac{\lambda_1}{1-q-k}+\epsilon$. Clearly, this inequality holds as long as μ is sufficiently large. Namely, as long as μ is large enough, we have

$$d\bar{\chi}'' + b(\bar{\chi}+q\underline{u})f_2\left(z - \frac{\underline{u}+\bar{\chi}}{1-q-k}\right)e^{-\mu c\underline{u}} \le 0.$$

Thus $(\bar{u}, \underline{\chi})$ and $(\underline{u}, \bar{\chi})$ are the order upper and lower solutions of (4.6). It follows the existence-comparison theorem for elliptic systems that (4.6) has a solution $(\tilde{u}, \tilde{\chi})$, which satisfies

$$(1-\delta)(1-q-k)\vartheta \le \tilde{u} \le (1-q-k)\vartheta, \quad 0 \le \tilde{\chi} \le \delta(1-q-k)\vartheta.$$

Noting that $v = \frac{\chi+qu}{1-q-k}$, we know that (EP) has a positive solution $(\tilde{u}, \tilde{v})$, which satisfies (4.5). ◻

LEMMA 4.4. *For any $\epsilon > 0$ small and any $A > \lambda_1/(1-q-k)$, there exists $M = M(\epsilon, A) > 0$ large such that if $a \in (\lambda_1/(1-q-k)+\epsilon, A]$ and $\mu \ge M$, then any positive solution of* (EP) *that satisfies* (4.5) *is nondegenerate and linearly stable.*

Proof. If $a \in (\lambda_1/(1-q-k)+\epsilon, A]$ and (u, v) satisfies (4.5), then it is easy to see that (EP) is a regular perturbation of (4.1) when μ is large. Since (4.1) has a unique positive solution $((1-q-k)\vartheta, q\vartheta)$ which is linearly stable, this lemma follows from a standard regular perturbation argument. ◻

As noted before, the next lemma shows rigorously that the positive solutions to (EP) are of two types.

LEMMA 4.5. *Suppose $a_i \to a \in (\frac{\lambda_1}{1-q-k}, +\infty), \mu_i \to \infty$, and (u_i, v_i) is a positive solution of* (EP) *with $(a, \mu) = (a_i, \mu_i)$. Then for large i, either (u_i, v_i) is close to $((1-q-k)\vartheta, q\vartheta)$ or $(\mu_i u_i, v_i)$ is close to (ω, v) in $C^1([0,1]) \times C^1([0,1])$, where (ω, v) is a positive solution of* (4.2). *Moreover, if $a_i \ge \frac{\hat{\lambda}_1}{1-q-k}$ for all large i and $a_i \to a$, then (u_i, v_i) converges to $((1-q-k)\vartheta, q\vartheta)$ in the C^1 norm.*

Proof. We argue by contradiction. Suppose we can find $a_i \to a \in (\frac{\lambda_1}{1-q-k}, +\infty)$, $\mu_i \to \infty$, and positive solution (u_i, v_i) bounded away from $((1-q-k)\vartheta, q\vartheta)$ and any positive solution of (4.2). First, by Lemma 2.5, $0 \le (1+c)u_i + v_i < z(x)$. Hence, by elliptic regularity and the Sobolev embedding theorems, we may assume the existence of a subsequence (if necessary), such that $u_i \to u$ and $v_i \to v$ in $C^1([0,1])$ for some $u, v \in C^1_B([0,1])$. Set $\omega_i = \mu_i u_i$ and $\chi_i = (1-q-k)v_i - qu_i$. Then (ω_i, χ_i) satisfies

$$\begin{aligned} &d\omega_i'' + a_i(1-q-k)\omega_i f_1(z-(1+c)u_i - v_i) = 0, \\ &d\chi_i'' + b(1-q-k)v_i f_2(z-(1+c)u_i - v_i)e^{-c\omega_i} = 0, \end{aligned} \tag{4.7}$$

with the usual boundary conditions. By passing to a subsequence, we have two possibilities.

Case a: $\mu_i \|u_i\|_\infty \to \infty$. In this case, one must have $\chi_i \to 0$. Indeed, it suffices to show $e^{-c\omega_i} \to 0$ almost everywhere in (0, 1) as $i \to \infty$. Let $\tilde{\omega}_i = \omega_i/\|\omega_i\|_\infty$. Then $\tilde{\omega}_i$ satisfies

$$-d\tilde{\omega}_i'' = a_i(1-q-k)\tilde{\omega}_i f_1(z-(1+c)u_i - v_i), \quad \tilde{\omega}_i'(0) = \tilde{\omega}_i'(1) + \gamma\tilde{\omega}_i(1) = 0.$$

By L^p estimates and the Sobolev embedding theorem, we may assume $\tilde{\omega}_i \to \tilde{\omega} \ge 0, \not\equiv 0$ in $C^1([0,1])$, and $\tilde{\omega}$ satisfies

$$-d\tilde{\omega}'' = a(1-q-k)\tilde{\omega} f_1(z-(1+c)u - v), \quad \tilde{\omega}'(0) = \tilde{\omega}'(1) + \gamma\tilde{\omega}(1) = 0.$$

Here $0 \le (1+c)u + v \le z$ because $0 < (1+c)u_i + v_i < z$. Therefore, $\tilde{\omega} > 0$ on [0, 1] by the strong maximum principle and Hopf boundary lemma. Thus $e^{-c\omega_i} = e^{-c\|\omega_i\|_\infty \tilde{\omega}_i} \to 0$ as $i \to \infty$, which implies $\chi_i \to 0$. Hence, $(1-q-k)v = qu$, and

$$du'' + a(1-q-k)uf_1\left(z - \frac{u}{1-q-k}\right) = 0, \qquad u'(0) = u'(1) + \gamma u(1) = 0.$$

This implies $u \equiv 0$ or $u = (1-q-k)\vartheta$. If $u \equiv 0$, then $v = \frac{q}{1-q-k}u \equiv 0$. That is, $(u_i, v_i) \to (0,0)$ as $i \to \infty$. Hence, $\tilde{u}_i = u_i/\|u_i\|_\infty$ satisfies

$$d\tilde{u}_i'' + a_i(1-q-k)\tilde{u}_i f_1(z-(1+c)u_i - v_i) = 0, \quad \tilde{u}_i'(0) = \tilde{u}_i'(1) + \gamma\tilde{u}_i(1) = 0.$$

Similarly, by L^p estimates and the Sobolev embedding theorem, we may assume that $\tilde{u}_i \to \tilde{u} \geq 0, \not\equiv 0$ in C^1, and in view of the strong maximum principle, $\tilde{u} > 0$ and satisfies

$$d\tilde{u}'' + a(1-q-k)\tilde{u}f_1(z) = 0, \quad \tilde{u}'(0) = \tilde{u}'(1) + \gamma\tilde{u}(1) = 0,$$

which means $a = \lambda_1/(1-q-k)$, a contradiction. Hence $u = (1-q-k)\vartheta$ and $v = q\vartheta$, which contradicts our assumption.

Case b: $\mu_i\|u_i\|_\infty$ is uniformly bounded, which implies $u_i \to 0$ as $i \to \infty$. Hence, $\chi_i = (1-q-k)v_i - qu_i \to (1-q-k)v$. Since ω_i is uniformly bounded, by the equation for ω_i, we may assume that $\omega_i \to \omega$ in $C^1([0,1])$. It follows from (4.7) that (ω, v) satisfies (4.2). If $\omega \geq 0, \not\equiv 0$, then the strong maximum principle tells us that $\omega > 0$. On the other hand, we claim that $v > 0$ on [0, 1]. Otherwise,

$$d\omega'' + a(1-q-k)\omega f_1(z) = 0, \qquad x \in (0,1), \qquad \omega'(0) = \omega'(1) + \gamma\omega(1) = 0,$$

which implies $a = \lambda_1/(1-q-k)$, a contradiction. Hence, (a, ω, v) is a positive solution of (4.2), which contradicts our assumption that (a_i, ω_i, v_i) is bounded away from any positive solution of (4.2). Therefore, we must have $\omega \equiv 0$. It follows that $v \equiv 0$ or $v = \theta$. Suppose $v \equiv 0$. Then $v_i \to 0$ and $\tilde{\omega}_i = \omega_i/\|\omega_i\|_\infty$ satisfies

$$d\tilde{\omega}_i'' + a_i(1-q-k)\tilde{\omega}_i f_1(z-(1+c)u_i - v_i) = 0, \quad \tilde{\omega}_i'(0) = \tilde{\omega}_i'(1) + \gamma\tilde{\omega}_i(1) = 0.$$

By L^p estimates and the Sobolev embedding theorem, we may assume $\tilde{\omega}_i \to \tilde{\omega} \geq 0, \not\equiv 0$ in $C^1([0,1])$, and by virtue of the strong maximum principle, $\tilde{\omega} > 0$ satisfies

$$d\tilde{\omega}'' + a(1-q-k)\tilde{\omega}f_1(z) = 0, \quad \tilde{\omega}'(0) = \tilde{\omega}'(1) + \gamma\tilde{\omega}(1) = 0,$$

which means $a = \lambda_1/(1-q-k)$, a contradiction. Thus $(\omega_i, v_i) \to (0, \theta)$, and hence $a_i(1-q-k) = \lambda_1(f_1(z-(1+c)u_i - v_i)) \to \lambda_1(f_1(z-\theta)) = \hat{\lambda}_1$. That is, $a_i \to \hat{\lambda}_1/(1-q-k)$. On the other hand, we can show that (4.2) has a positive solution branch bifurcating from $(a, \omega, v) = (\hat{\lambda}_1/(1-q-k), 0, \theta)$ (see Lemma 4.7). Hence, we can find $a = \tilde{a}_i \to \hat{\lambda}_1/(1-q-k)$ such that (4.2) with $a = \tilde{a}_i$ has a positive solution $(\tilde{\omega}_i, \tilde{v}_i)$ converging in L^∞ to $(0, \theta)$. Thus $(a_i, \mu_i u_i, v_i)$ is close to $(\tilde{a}_i, \tilde{\omega}_i, \tilde{v}_i)$ for i large. This again contradicts our assumption. This finishes the proof of the first part of this lemma.

Now, we prove that if $a_i \geq \hat{\lambda}_1/(1-q-k)$ for all large i and $a_i \to a$ as $i \to \infty$, then $(u_i, v_i) \to ((1-q-k)\vartheta, q\vartheta)$. Again we use an indirect argument. We suppose that this is not true. Then by the first part of this lemma and by choosing a subsequence if necessary, we may assume that $(\mu_i u_i, v_i)$ is close to a positive solution of (4.2). This implies $u_i \to 0$ as $i \to \infty$. We divide the arguments into two cases: (i) $a > \hat{\lambda}_1/(1-q-k)$ and (ii) $a = \hat{\lambda}_1/(1-q-k)$.

In case (i), suppose for any $\epsilon > 0$, there exists $a_i \to a \geq \hat{\lambda}_1/(1-q-k)+\epsilon$ such that $u_i \to 0$ as $\mu_i \to \infty$. Then $\omega_i = \mu_i u_i, \chi_i = (1-q-k)v_i - qu_i$ satisfy (4.7). Passing to a subsequence, we have two possibilities.

Case a: $\|\omega_i\|_\infty = \mu_i\|u_i\|_\infty \to \infty$. Noting Lemma 2.5, we claim that $\chi_i \to 0$ as before, which means $v_i = \frac{\chi_i+qu_i}{1-q-k} \to 0$. Let $\tilde{u}_i = u_i/\|u_i\|_\infty$. Then by L^p estimates and the Sobolev embedding theorem, we may assume $\tilde{u}_i \to \tilde{u}$ in $C^1([0,1])$, and by the strong maximum principle, $\tilde{u} > 0$. Moreover, $\tilde{u}$ satisfies

$$d\tilde{u}^{''} + a(1-q-k)\tilde{u}f_1(z) = 0, \qquad \tilde{u}'(0) = \tilde{u}'(1) + \gamma\tilde{u}(1) = 0,$$

which implies $a = \lambda_1/(1-q-k)$, a contradiction.

Case b: $\|\omega_i\|_\infty = \mu_i\|u_i\|_\infty \leq C$. Then by using a priori estimates for v_i (see Lemma 2.5), we may assume that $(\omega_i, v_i) \to (\omega, v)$ in $C^1([0,1])$, where $\omega, v \geq 0$ on [0, 1]. Noting that $\chi_i = (1-q-k)v_i - qu_i$ and $u_i \to 0$, one has $\chi_i \to (1-q-k)v$. It follows from the equations in (4.7) that (ω, v) satisfies (4.2). Namely, (ω, v) is exactly the nonnegative solution of (4.2). If $\omega \geq 0, \not\equiv 0$, then by the strong maximum principle, $\omega > 0$. Hence, $(\hat{\lambda}_1 <)a(1-q-k) = \lambda_1(f_1(z-v))$, which implies $v \not\equiv 0$. It follows from the strong maximum principle that $v > 0$. This contradicts Lemma 4.2; that is, (4.2) has no positive solution provided that $a > \hat{\lambda}_1/(1-q-k)$. Therefore, $\omega \equiv 0$ and $v = \theta$ (the possibility $v \equiv 0$ can be ruled out by similar arguments as in the proof of the first part of this lemma). Set $\tilde{u}_i = u_i/\|u_i\|_\infty$. A similar argument shows that $a = \hat{\lambda}_1/(1-q-k)$, a contradiction. Therefore, our assertion holds.

In case (ii), since $a_i \to \hat{\lambda}_1/(1-q-k)$ and $u_i \to 0$, one can assert that $v_i \to \theta$ and $\mu_i u_i \to 0$ in C^1 norm. Indeed, let $\tilde{u}_i = u_i/\|u_i\|_\infty$. Then $\tilde{u}_i$ satisfies

$$d\tilde{u}_i^{''} + a_i(1-q-k)\tilde{u}_i f_1(z-(1+c)u_i - v_i) = 0, \quad \tilde{u}_i'(0) = \tilde{u}_i'(1) + \gamma\tilde{u}_i(1) = 0.$$

Similarly, we may suppose $\tilde{u}_i \to \tilde{u}$ in $C^1([0,1])$ and $\tilde{u} > 0$ satisfies

$$d\tilde{u}^{''} + \hat{\lambda}_1\tilde{u}f_1(z-v) = 0, \quad \tilde{u}'(0) = \tilde{u}'(1) + \gamma\tilde{u}(1) = 0, \tag{4.8}$$

which implies $v \not\equiv 0$; otherwise, $\hat{\lambda}_1 = \lambda_1$, a contradiction. Noting that $a_i \to \hat{\lambda}_1/(1-q-k), u_i \to 0, v_i \to v \not\equiv 0$, and

$$dv_i^{''} + bv_i f_2(z-(1+c)u_i - v_i)e^{-c\mu_i\|u_i\|_\infty\tilde{u}_i} + a_i q u_i f_1(z-(1+c)u_i - v_i) = 0,$$

we can show that $\mu_i\|u_i\|_\infty$ is uniformly bounded. Hence we may assume that $\mu_i u_i \to \omega$ in $C^1([0,1])$ for some $\omega \geq 0$. Letting $i \to \infty$, we must have $dv^{''} + bvf_2(z-v) \geq 0$, which means $v \leq \theta$. Multiplying (4.8) by $\hat{\varphi}_1$, integrating over [0, 1], and applying Green's formula, we obtain

$$\hat{\lambda}_1 \int_0^1 \tilde{u}\hat{\varphi}_1(f_1(z-v) - f_1(z-\theta))dx = 0,$$

which implies $v = \theta$ since $v \leq \theta$. Moreover, $\tilde{u} = \hat{\varphi}_1$. That is, $v_i \to \theta$. Next, we show $\omega \equiv 0$. If $\omega \geq 0, \not\equiv 0$, then $\omega > 0$ by the strong maximum principle. Noting that $a_i \to \hat{\lambda}_1/(1-q-k), u_i \to 0, v_i \to \theta, \mu_i u_i \to \omega$, we have

$$d\theta^{''} + b\theta f_2(z-\theta)e^{-c\omega} = 0, \quad \theta'(0) = \theta'(1) + \gamma\theta(1) = 0.$$

This means $b = \lambda_1(f_2(z-\theta)e^{-c\omega}) > \lambda_1(f_2(z-\theta)) = b$, a contradiction. Hence our assertion holds. Next, we show $(1+c)u_i + v_i < \theta$ for large i. Let $Q_i = (1+c)u_i + v_i$.

Clearly, $Q_i \to \theta$, and

$$dQ_i^{''} + a_i u_i f_1(z - Q_i) + b v_i f_2(z - Q_i) e^{-c\mu_i u_i} = 0, \quad Q_i'(0) = Q_i'(1) + \gamma Q_i(1) = 0.$$

Hence

$$\begin{aligned} & dQ_i^{''} + bQ_i f_2(z - Q_i) \\ & = u_i[b(1+c) f_2(z - Q_i) - a_i f_1(z - Q_i)] + b v_i f_2(z - Q_i)[1 - e^{-c\mu_i u_i}] \\ & = u_i[b(1+c) f_2(z - Q_i) - a_i f_1(z - Q_i) + b v_i f_2(z - Q_i) c\mu_i + O(\mu_i^2 u_i)] \\ & = u_i[b(1+c) f_2(z - Q_i) - a_i f_1(z - Q_i) + (bcv_i f_2(z - Q_i) + O(\mu_i u_i))\mu_i]. \end{aligned}$$

Since $\mu_i u_i \to 0$ and $\mu_i \to \infty$, we have $dQ_i^{''} + bQ_i f_2(z - Q_i) > 0$ for large i, which implies $Q_i < \theta$ for large i.

Now multiplying the equation for u_i by $\hat{\varphi}_1$ and integrating over [0, 1], we obtain

$$\int_0^1 [a_i(1 - q - k) f_1(z - Q_i) - \hat{\lambda}_1 f_1(z - \theta)]\hat{\varphi}_1 u_i dx = 0.$$

Since $a_i(1 - q - k) \geq \hat{\lambda}_1$ and $f_1(z - Q_i) > f_1(z - \theta)$ for large i, $\int_0^1 [a_i(1 - q - k) f_1(z - Q_i) - \hat{\lambda}_1 f_1(z - \theta)]\hat{\varphi}_1 u_i dx > 0$ for all large i, a contradiction. Hence $(u_i, v_i) \to ((1 - q - k)\vartheta, q\vartheta)$ in the C^1 norm when $a_i \geq \frac{\hat{\lambda}_1}{1-q-k}$ for all large i, $a_i \to a$, and $\mu_i \to \infty$. □

Lemma 4.6. (i) *For any $A \geq \frac{\hat{\lambda}_1}{1-q-k}$, there exists $M > 0$ large such that if $\mu > M$ and $a \in [\frac{\hat{\lambda}_1}{1-q-k}, A]$, then any positive solution (u, v) of* (EP) *is nondegenerate and linearly asymptotically stable, and* $\text{index}_W(\mathcal{A}, (u, v)) = 1$.

(ii) *For any $\epsilon, \delta > 0$ small, there exists $M_{\epsilon,\delta} > 0$ large such that if $a \in [\frac{\lambda_1}{1-q-k} + \epsilon, \frac{\hat{\lambda}_1}{1-q-k})$ and $\mu \geq M_{\epsilon,\delta}$ and if (u, v) is a positive solution of* (EP), *then either* (a) $\|u - (1 - q - k)\vartheta\|_{C^1} + \|v - q\vartheta\|_{C^1} < \delta$ *or* (b) $\|\mu u - \tilde{\omega}\|_{C^1} + \|v - \tilde{v}\|_{C^1} + \|a - \tilde{a}\|_{C^1} < \delta$, *where $(\tilde{\omega}, \tilde{v})$ is a positive solution of* (4.2) *with $a = \tilde{a}$. Moreover, if* (a) *occurs, then (u, v) is nondegenerate linearly asymptotically stable and* $\text{index}_W(\mathcal{A}, (u, v)) = 1$.

Proof. (i) We prove the nondegeneracy and linear stability first. For this purpose, we consider the linearized eigenvalue problem

$$\begin{aligned} & d\phi^{''} + a(1 - q - k)[f_1(z - (1 + c)u - v) - (1 + c)uf_1'(z - (1 + c)u - v)]\phi \\ & \quad -a(1 - q - k)uf_1'(z - (1 + c)u - v)\psi = -\eta\phi, \\ & d\psi^{''} + [b(f_2(z - (1 + c)u - v) - vf_2'(z - (1 + c)u - v))e^{-\mu cu} \\ & \quad -aquf_1'(z - (1 + c)u - v)]\psi \\ & \quad -bv[f_2'(z - (1 + c)u - v)(1 + c) + \mu cf_2(z - (1 + c)u - v)]e^{-\mu cu}\phi \\ & \quad +aq[f_1(z - (1 + c)u - v) - (1 + c)uf_1'(z - (1 + c)u - v)]\phi = -\eta\psi, \\ & \phi'(0) = \phi'(1) + \gamma\phi(1) = 0, \qquad \psi'(0) = \psi'(1) + \gamma\psi(1) = 0. \end{aligned}$$

By Lemma 4.5, (EP) has no positive solution with a small u component when $a \in [\frac{\hat{\lambda}_1}{1-q-k}, A]$ and μ is large. Therefore, we can establish this assertion by a simple variant of the proof of Lemma 4.4.

Next, we prove the statement concerning the fixed point index. Since any positive solution (u, v) to (EP) is nondegenerate, we have

$$\text{index}_W(\mathcal{A}, (u, v)) = \text{index}_X(\mathcal{A}, (u, v)) = \text{index}_X(\mathcal{A}'(u, v), (0, 0)).$$

Let $Q_t(\phi,\psi) = (-d\frac{d^2}{dx^2}+M)^{-1}(f,g)$, where $0 \le t \le 1$ and

$$\begin{aligned} f = \;& a(1-q-k)[f_1(z-(1+c)u-v)-(1+c)uf_1'(z-(1+c)u-v)]\phi + M\phi \\ & -ta(1-q-k)uf_1'(z-(1+c)u-v)\psi, \\ g = \;& [b(f_2(z-(1+c)u-v)-vf_2'(z-(1+c)u-v))e^{-\mu cu} \\ & -taquf_1'(z-(1+c)u-v)]\psi + M\psi \\ & -bv[(1+c)f_2'(z-(1+c)u-v)+\mu c f_2(z-(1+c)u-v)]e^{-\mu cu}\phi \\ & +aq[f_1(z-(1+c)u-v)-(1+c)uf_1'(z-(1+c)u-v)]\phi. \end{aligned}$$

Then there exists a neighborhood $U_\delta \subset X$ of $(0,0)$ such that Q_t has no fixed point on ∂U_δ provided μ is large enough. Moreover, we can choose U_δ such that $\mathcal{A}'(u,v)(\phi,\psi) = (\phi,\psi)$ has only the solution $(\phi,\psi) = (0,0)$ in U_δ. By similar arguments as in Lemma 2.5 in [7] and Theorem 3.1 in [8], we can show $\mathrm{index}_X(\mathcal{A}'(u,v),(0,0)) = \mathrm{index}_X(\mathcal{A}'(u,v),U_\delta) = \mathrm{index}_X(Q_1,U_\delta) = \mathrm{index}_X(Q_0,U_\delta) = \mathrm{index}_X(Q_0,(0,0)) = 1$. Hence $\mathrm{index}_W(\mathcal{A},(u,v)) = 1$.

(ii) The statement on the location of the positive solutions follows directly from Lemma 4.5. The other statements are proved in the same way as in (i) above. $\square$

Proof of Theorem 1.2. (i) For any $\epsilon > 0$ small, let $M = \max\{M(\epsilon), M(\epsilon, \hat\lambda_1/(1-q-k))\}$, where $M(\epsilon), M(\epsilon,\hat\lambda_1/(1-q-k))$ are given by Lemmas 4.3 and 4.4, respectively. Assume that for $\mu \ge M$ and $a \in [\lambda_1/(1-q-k)+\epsilon, \hat\lambda_1/(1-q-k))$, (EP) has only a unique positive solution $(\tilde u,\tilde v)$ as shown in Lemma 4.3. In view of Lemma 4.4, $I - \mathcal{A}'(\tilde u,\tilde v)$ is invertible in X and $\mathcal{A}'(\tilde u,\tilde v)$ has no real eigenvalue greater than one, where $\mathcal{A}'(\tilde u,\tilde v)$ is the Fréchet derivative of $\mathcal{A}$ at $(\tilde u,\tilde v)$. We can argue in the same way as in the proof of Theorem 3.1 in [8] to draw a conclusion that $\mathrm{index}_W(\mathcal{A},(\tilde u,\tilde v)) = 1$. By virtue of Lemmas 3.1 and 3.2, it follows that

$$1 = \mathrm{index}_W(\mathcal{A},D') = \mathrm{index}_W(\mathcal{A},(0,0)) + \mathrm{index}_W(\mathcal{A},(0,\theta)) + \mathrm{index}_W(\mathcal{A},(\tilde u,\tilde v)) = 2.$$

This contradiction completes the proof.

(ii) It follows from Lemma 4.6 that for any $A \ge \frac{\hat\lambda_1}{1-q-k}$, there exists $M > 0$ large such that any positive solution (u,v) of (EP) is nondegenerate and linearly asymptotically stable for $a \in [\frac{\hat\lambda_1}{1-q-k}, A]$ and $\mu \ge M$. Hence, it suffices to show the uniqueness. Set $D_1 = \{(u,v) \in X : \frac{(1-q-k)}{2}\vartheta < u < \frac{\vartheta}{1+c}, \frac{q}{2}\vartheta < v < \max_{[0,1]} \bar v + 1\}$, and define $F_\tau : D_1 \to W$ by

$$F_\tau(u,v) = \left(-d\frac{d^2}{dx^2}+K\right)^{-1}(a(1-q-k)ug_1(u,v)+Ku,\ \tau bvg_2(u,v)+aqug_1(u,v)+Kv),$$

where $\tau \in [0,1]$, $g_1(u,v) = f_1(z-(1+c)u-v)$, $g_2(u,v) = f_2(z-(1+c)u-v)e^{-\mu cu}$, and K is large enough such that $K + a(1-q-k)g_1(u,v) > 0$ and $K + \tau bg_2(u,v) - aquK_1 > 0$ (K_1 is given in section 3) for all $(u,v) \in D_1$ and $\tau \in [0,1]$. Clearly, F_τ is a compact and continuously differentiable operator. Moreover, it follows from Lemma 4.5 that there exists $M > 0$ large such that if $\mu \ge M$ and $a \in [\hat\lambda_1/(1-q-k), A]$, then any positive solution (u,v) of (EP) is close to $((1-q-k)\vartheta, q\vartheta)$. Hence, $(u,v) \in D_1$ for $a \in [\hat\lambda_1/(1-q-k), A]$ and $\mu \ge M$. Namely, if $a \in [\hat\lambda_1/(1-q-k), A]$ and $\mu \ge M$, then (u,v) is a positive solution of (EP) if and only if it is a fixed point of F_1 in D_1. Again by Lemma 4.5, F_τ has no fixed point on ∂D_1 for $a \in [\hat\lambda_1/(1-q-k), A]$ and $\mu \ge M$. Therefore, $\mathrm{index}_W(F_\tau, D_1) \equiv \text{const}$. In particular, $\mathrm{index}_W(F_1,D_1) = \mathrm{index}_W(F_0,D_1)$. It is easy to show that F_0 has a unique fixed point $((1-q-k)\vartheta, q\vartheta)$ in D_1 and $\mathrm{index}_W(F_0,D_1) = \mathrm{index}_W(F_0,((1-q-k)\vartheta,q\vartheta)) = 1$. Hence, $\mathrm{index}_W(F_1,D_1) = 1$.

As mentioned before, from Lemma 4.6, we know that, for $\mu > M$ and $a \in [\hat{\lambda}_1/(1-q-k), A]$, all fixed points of F_1 in D_1 are nondegenerate and linearly stable. Hence by a compactness argument it is easy to show that there are at most finitely many fixed points of F_1, which are denoted by $\{(u_i, v_i)\}_{i=1}^n$. By Lemma 4.6 again, $\text{index}_W(\mathcal{A}, (u_i, v_i)) = 1$. In view of the additivity property of the fixed point index, we have for $a \in [\hat{\lambda}_1/(1-q-k), A]$

$$n = \sum_{i=1}^{n} \text{index}_W(F_1, (u_i, v_i)) = \text{index}_W(F_1, D_1) = 1.$$

Hence for $\mu \geq M$ and $a \in [\hat{\lambda}_1/(1-q-k), A]$, (EP) has only a unique positive solution and it is stable. The proof of Theorem 1.2 is completed. $\square$

Next we wish to establish Theorem 1.3, but first we give the following lemma, which is crucial in proving Theorem 1.3.

LEMMA 4.7. *There exists $\epsilon > 0$ small such that if $\hat{\lambda}_1/(1-q-k) - \epsilon \leq a < \hat{\lambda}_1/(1-q-k)$, then (4.2) has a unique positive solution.*

Proof. Here, we prove this lemma by the local bifurcation theorem of Crandall and Rabinowitz [3]. We regard a as the bifurcation parameter and try to construct a positive solution branch from the semitrivial nonnegative solution branch $\{(a, 0, \theta) : a \in R^+\}$.

After some standard calculations, we obtain that $(\hat{\lambda}_1/(1-q-k), 0, \theta)$ is a bifurcation point. Close to this bifurcation point, (4.2) has a positive solution $(a(s), s(\hat{\varphi}_1 + \Phi(s)), \theta + s(\chi_1 + \Psi(s)))$ $(0 < s \ll 1)$, where $a(0) = \hat{\lambda}_1/(1-q-k), \chi_1 = bcL_b^{-1}(\theta f_2(z-\theta)\hat{\varphi}_1) < 0, \Phi(0) = \Psi(0) = 0$. Putting this positive solution into the first equation of (4.2), dividing by s, and differentiating with respect to s, it follows that the derivative of $a(s)$ with respect to s at $s = 0$ is less than 0. That is, $a'(0) < 0$, which implies the positive solution bifurcation branch is to the left. Namely, there exists $\epsilon > 0$ sufficiently small such that if $\hat{\lambda}_1/(1-q-k) - \epsilon \leq a < \hat{\lambda}_1/(1-q-k)$, then (4.2) has a positive solution with the form of $(a(s), s(\hat{\varphi}_1 + \Phi(s)), \theta + s(\chi_1 + \Psi(s)))$ $(0 < s \ll 1)$. Furthermore, it is unique as long as ϵ is sufficiently small. In fact, it is also unstable. We leave the proof of this assertion to the reader. $\square$

Proof of Theorem 1.3. First we show that for large μ (EP) has a unique asymptotically stable positive solution which is close to $((1-q-k)\vartheta, q\vartheta)$. In fact, if we choose $\delta > 0$ small enough in Lemma 4.6, then by Lemma 4.6 any positive solution of (EP) close to $((1-q-k)\vartheta, q\vartheta)$ is nondegenerate and linearly stable. Next, by a simple variant of the proof of part (ii) of Theorem 1.2, we can find that (EP) has only one positive solution of type (a), and it is asymptotically stable.

On the other hand, we can show that (EP) has a unique unstable positive solution of type (b). If this assertion holds, then by Lemma 4.6 our proof is completed. Hence, our main task is to establish this assertion.

Suppose (u, v) is a positive solution of type (b) of (EP). It follows from Lemmas 4.6 and 4.7; $(\mu u, v)$ is close to (ω, v), where (ω, v) is the unique positive solution of (4.2). Hence to prove the uniqueness, it suffices to show that, for $a \in [\hat{\lambda}_1/(1-q-k) - \epsilon_0, \hat{\lambda}_1/(1-q-k))$ and $\mu \geq M_0$, there is a unique pair $(\mu u, v)$ close to (ω, v) for certain ϵ_0 and M_0.

Set $\hat{u} = \mu u, \epsilon = \frac{1}{\mu}$, and consider the following problem with the usual boundary conditions

$$(4.9) \qquad \begin{aligned} &d\hat{u}'' + a(1-q-k)\hat{u} f_1(z-(1+c)\epsilon\hat{u} - v) = 0, \qquad x \in (0,1), \\ &dv'' + bvf_2(z-(1+c)\epsilon\hat{u} - v)e^{-c\hat{u}} + aq\epsilon\hat{u} f_1(z-(1+c)\epsilon\hat{u} - v) = 0. \end{aligned}$$

Clearly, (u,v) is a solution of (EP) if and only if $(\mu u, v)$ is a solution of (4.9) with $\epsilon = 1/\mu$. Thus it suffices to prove the uniqueness of (4.9). For fixed $\epsilon \geq 0$, regarding a as a bifurcation parameter, we see that $(\hat{\lambda}_1/(1-q-k), 0, \theta)$ is a simple bifurcation point of (4.9). By virtue of a variant of Theorem 1 in Crandall and Rabinowitz [2], there exists $\delta_1 > 0$ and C^1 curves

$$\Gamma_\epsilon = \{(a(\epsilon,s), \hat{u}(\epsilon,s), v(\epsilon,s)) : 0 < s < \delta_1\}, \qquad 0 \leq \epsilon \leq \delta_1,$$

such that if $0 \leq \epsilon \leq \delta_1$, then all positive solutions of (4.9) close to $(\hat{\lambda}_1/(1-q-k), 0, \theta) = (a(0,0), \hat{u}(0,0), v(0,0))$ lie on the curve Γ_ϵ. Hence, we need show only that for fixed ϵ, Γ_ϵ uniformly cover an a-range: $a \in [\hat{\lambda}_1/(1-q-k) - \epsilon_0, \hat{\lambda}_1/(1-q-k))$ only once for suitably chosen ϵ_0. It is easy to obtain

$$\frac{\partial a}{\partial s}(0,0) = \frac{\hat{\lambda}_1 \int_0^1 \hat{\varphi}_1 f_1'(z-\theta)\chi_1}{(1-q-k)\int_0^1 \hat{\varphi}_1^2 f_1(z-\theta)} < 0$$

based on $\chi_1 = L_b^{-1}(bc\theta f_2(z-\theta)\hat{\varphi}_1) < 0$. By taking δ_1 small, we may assume that $\frac{\partial a}{\partial s}(\epsilon, s) < 0$ for $0 \leq \epsilon, s \leq \delta_1$. Hence $\hat{\lambda}_1/(1-q-k) - a(0,\delta_1) = a(0,0) - a(0,\delta_1) > 0$. Since $a(\epsilon,s)$ is continuous, there exists $\delta \in (0,\delta_1]$ such that $\epsilon_0 = \min_{0 \leq \epsilon \leq \delta}(\hat{\lambda}_1/(1-q-k) - a(\epsilon,\delta_1)) > 0$. Therefore, if $a \geq \hat{\lambda}_1/(1-q-k) - \epsilon_0$, then $a(\epsilon,\delta_1) \leq a$ for any $\epsilon \in [0,\delta]$. This shows that for each $\epsilon \in [0,\delta]$, Γ_ϵ covers the a-range $[\hat{\lambda}_1/(1-q-k) - \epsilon_0, \hat{\lambda}_1/(1-q-k))$. Moreover, since $\frac{\partial a}{\partial s}(\epsilon,s) < 0$ for $0 \leq \epsilon, s \leq \delta_1$, each curve covers the range only once. By taking $M_0 = 1/\delta$, we see that, for $\mu \geq M_0$ and $\hat{\lambda}_1/(1-q-k) - \epsilon_0 \leq a < \hat{\lambda}_1/(1-q-k)$, (EP) has exactly one positive solution of type (b).

It remains to show the instability. A simple computation shows that η is an eigenvalue of the linearization of (EP) at (u,v) with eigenfunction (ϕ,ψ) if and only if it is an eigenvalue of that of (4.9) with $\epsilon = 1/\mu$ at $(\mu u, v)$ with eigenfunction $(\mu\phi, \psi)$. Hence it suffices to show that the linearization of (4.9) has a negative eigenvalue at any point on the bifurcation curves Γ_ϵ. This follows from a simple application of a variant of Theorem 1.16 in Crandall and Rabinowitz [3]. More precisely, by Lemma 1.3 in [3], we can obtain a variant of Corollary 1.13 there. That is, there exist $\tau > 0$ and C^1 functions $\gamma : (\hat{\lambda}_1/(1-q-k) - \tau, \hat{\lambda}_1/(1-q-k) + \tau) \times (-\tau,\tau) \to R^1$ and $\beta : (-\tau,\tau) \times (-\tau,\tau) \to R^1$ such that $\gamma(a,\epsilon)$ is a simple eigenvalue of the linearization of (4.9) at $(a,0,\theta)$ and $\beta(s,\epsilon)$ is a simple eigenvalue of the linearization of (4.9) at $(a,u,v) = (a(\epsilon,s), \hat{u}(\epsilon,s), v(\epsilon,s))$ with $0 \leq \epsilon, s \leq \tau$. Moreover, $\gamma(\hat{\lambda}_1/(1-q-k), \epsilon) = \beta(0,\epsilon) = 0$. It is easy to check that, in fact, $\gamma(a,\epsilon)$ is a simple eigenvalue of

$$d\phi'' + a(1-q-k)\phi f_1(z-\theta) = -\gamma(a,\epsilon)\phi$$

with the usual boundary conditions. Hence, $\frac{\partial \gamma}{\partial a}(\hat{\lambda}_1/(1-q-k), \epsilon) < 0$ because of the monotone property. Then it follows from Theorem 1.16 in [3] that $\beta(s,0) \sim -s\frac{\partial a}{\partial s}(0,s)\frac{\partial \gamma}{\partial a}(\hat{\lambda}_1/(1-q-k), 0)$ for $0 < s \ll 1$, which implies $\beta(s,0) < 0$ and the positive solution of type (b) of (EP) is unstable. This completes the proof of Theorem 1.3. ∎

5. Numerical simulation. In this section, we present some results of our numerical simulations that complement the analytic results of the previous sections. All computations in this section are performed with Matlab.

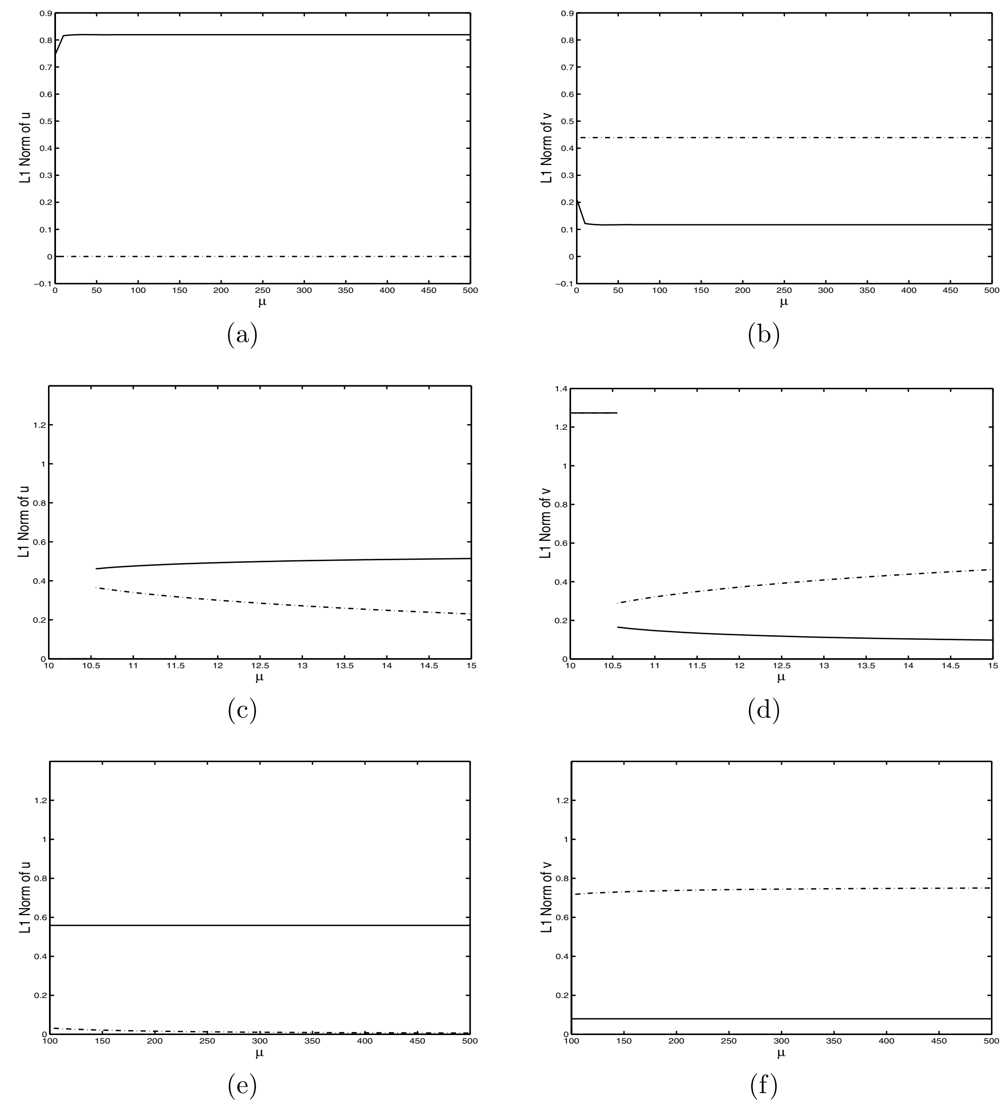

FIG. 1. *Effect of μ:* (a) *and* (b) *are the bifurcation diagrams of u and v, respectively, with respect to μ with the parameters $a = 4, b = 1.5$. Here the two solid lines in* (a) *and* (b) *represent the L^1 norm of components u and v of the stable coexistence solution (u, v), respectively. The two dashed lines in* (a) *and* (b) *represent the L^1 norm of components 0 and θ of the unstable semitrivial nonnegative solution $(0, \theta)$, respectively. Similarly, the pair of* (c) *and* (d) *and the pair of* (e) *and* (f) *are the bifurcation diagrams of u and v, respectively, with respect to μ all with $a = 2.5, b = 5$. Here solid lines denote the stable solutions and dashed lines represent the unstable solutions. Note that $\mu \in [10, 15]$ in* (c) *and* (d) *and that $\mu \in [100, 500]$ in* (e) *and* (f). *The aim of plotting in the above domain is to explicitly show the change tendency of u and v.*

Several parameters are common for all simulations: the diffusion rate $d = 1.0$ and parameters $k_1 = 1, k_2 = 1.1, \gamma = 1, q = 0.1$, and $k = 0.2$. The other parameters are varied in order to illustrate different outcomes. In Figures 1 and 2, the vertical axis is the L_1 norm of u or v. In Figures 3 and 4, the coexistence solutions to (PP) are plotted.

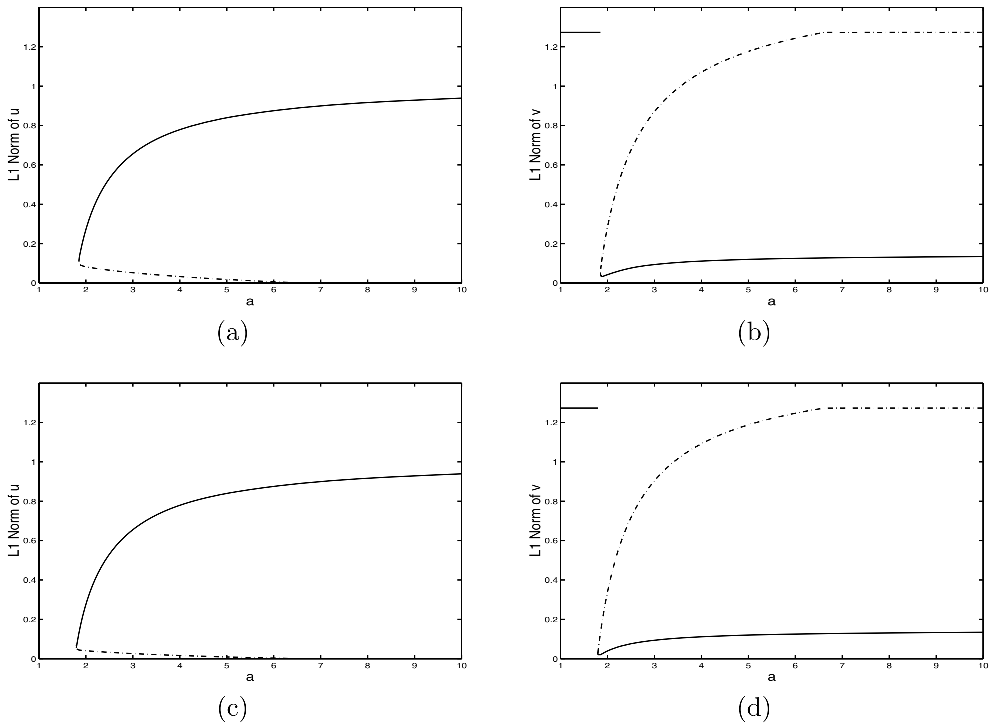

Fig. 2. *Bifurcation diagrams with respect to a:* (a) *and* (b) *with* $\mu = 50, b = 5$ *and* (c) *and* (d) *with* $\mu = 100, b = 5$ *also represent the bifurcation graphs of* u *and* v *with respect to* a*, respectively. Here solid lines denote the stable solutions and dashed lines represent the unstable solutions.*

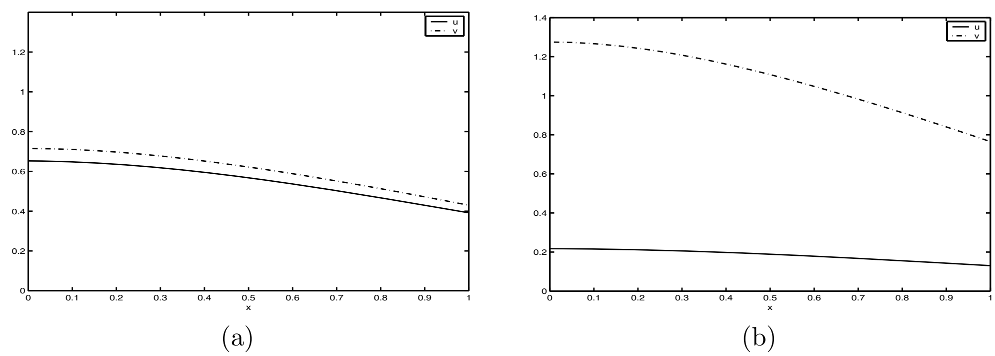

Fig. 3. *Two coexistence solutions of* (PP) *with* $\mu = 1, a = 6.4, b = 5$. *This indicates* (PP) *also has two coexistence solutions when* μ *is not large.*

The simulations presented below illustrate the following major outcomes of the plasmid-bearing and plasmid-free competition in the unstirred chemostat with an internal inhibitor.

(1) If u is a better competitor than v, there exists only a unique globally stable coexistence state of (PP) for any $\mu > 0$ (see Figures 1(a) and 1(b)). That is, if u is a better competitor, then it cannot eliminate its competitor but forces the existence of a coexistence state. This reflects the difference between the plasmid model and the standard competition model in the chemostat.

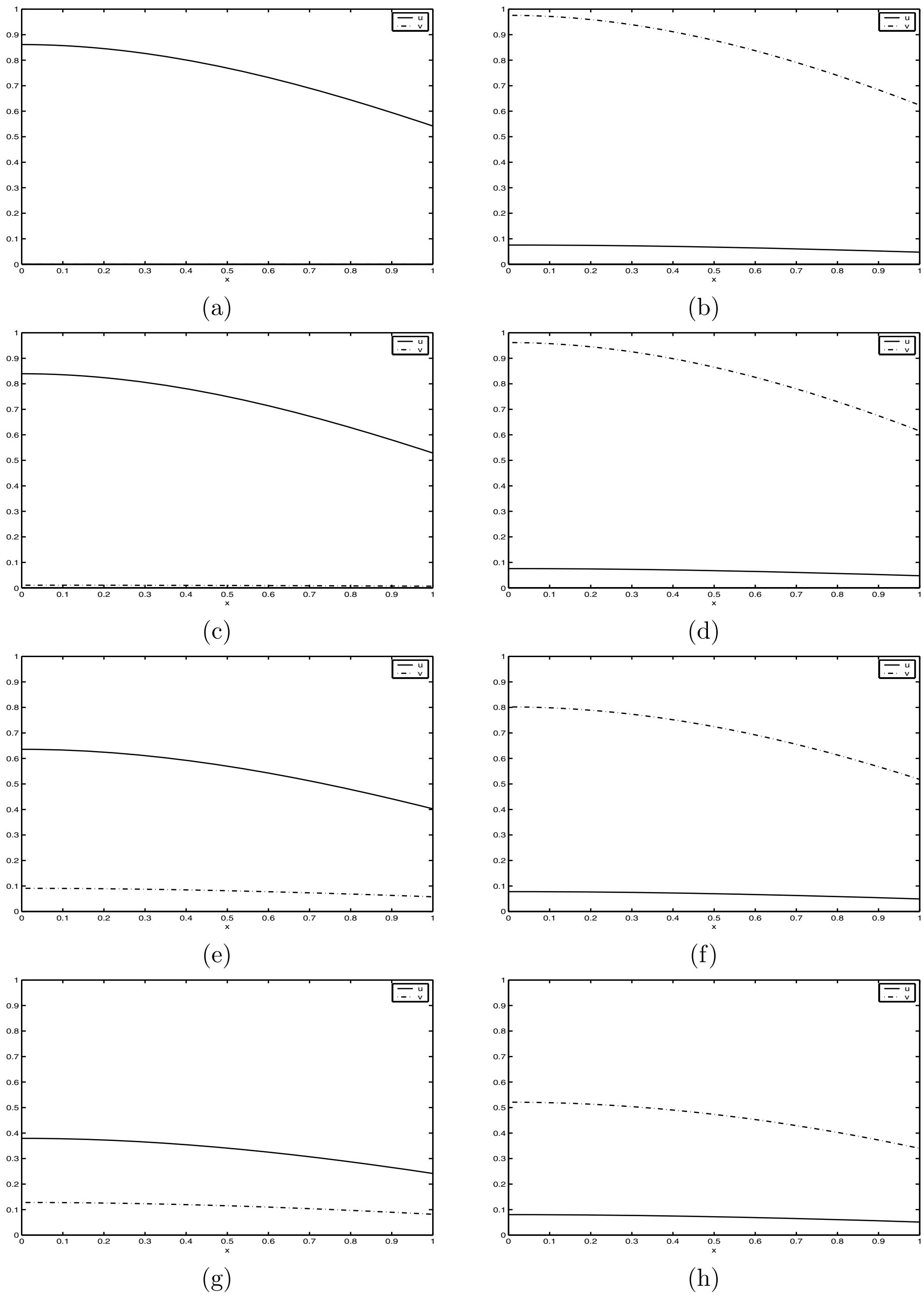

FIG. 4. *The difference between the plasmid model and the standard chemostat competition model in the presence of inhibitor:* (a) *and* (b) *with* $q = 0$, (c) *and* (d) *with* $q = 0.01$, (e) *and* (f) *with* $q = 0.1$, *and* (g) *and* (h) *with* $q = 0.2$. *Here* $a = 2.5, b = 5, \mu = 50$. *The simulations suggest that for large* μ *the plasmid model* ($q > 0$) *has two coexistence solutions; one asymptotically stable,* (c), (e), *and* (g) *with* $q = 0.01, 0.1, 0.2$, *respectively, and the others unstable,* (d), (f) *and* (h) *with* $q = 0.01, 0.1, 0.2$, *respectively. However, the basic chemostat model* ($q = 0$) *seems to have only one unstable coexistence solution,* (b). *Moreover, when* $q \to 0+$, *the stable coexistence solution of* (PP) *goes to the semitrivial nonnegative solution* $(\vartheta, 0)$, (a).

(2) If u is a weaker competitor than v, then there exists a unique number $\mu^* > 0$ such that if $\mu < \mu^*$ there is no coexistence state of (PP) and the semitrivial nonnegative solution $(0, \theta)$ is globally stable; if $\mu > \mu^*$ there are exactly two coexistence states of (PP) (see Figures 1(c)–(f)). One is asymptotically stable, and the theoretical results and plenty of numerical analysis strongly suggest the other coexistence state is the most possibly unstable. Namely, if v is the better competitor, then it will eliminate u unless the effect of the inhibitor is sufficiently large, reflected by the condition $\mu > \mu^*$. This result exactly indicates that the inhibitor can help the genetically altered (plasmid-bearing) organism to avoid capture of the process by the plasmid-free organism.

(3) If μ is sufficiently large and b suitably large, then there exists a unique constant $a_\mu > \frac{\lambda_1}{1-q-k}$ such that (PP) has exactly two coexistence states for $a_\mu < a < \frac{\hat{\lambda}_1}{(1-q-k)}$: one asymptotically stable and the other (most possibly) unstable. Meanwhile, the semitrivial nonnegative solution $(0, \theta)$ is stable as well. But for $a \geq \frac{\hat{\lambda}_1}{(1-q-k)}$, (PP) has only a unique coexistence state, and it is asymptotically stable (see Figure 2). The simulations indicate that it is also globally stable, but we cannot give a rigorous proof. Furthermore, a_μ goes to $\frac{\lambda_1}{1-q-k}$ when $\mu \to \infty$, which is just consistent with our analytic outcomes.

(4) In fact, (PP) may also have two coexistence states in the case that μ is not large enough. For example, taking the parameters $\mu = 1, a = 6.4$, and $b = 5$ and the same parameters as above, (PP) has two positive solutions; see Figure 3. Moreover, the simulations also suggest that the coexistence solution in Figure 3(a) is asymptotically stable and the coexistence solution in Figure 3(b) is (most possibly) unstable.

(5) We discuss the difference between the plasmid model and the standard chemostat competition model in the presence of inhibitor. In (1), we mention the difference between the above two kinds of chemostat models when the plasmid-bearing organism is a better competitor. Here, we mainly concentrate on the case that the plasmid-bearing organism is a weaker competitor than the plasmid-free organism. It is easy to see that the introduction of the plasmid-free organism destroys the competitive property of the system. However, it is this property of the plasmid model that leads to the complex dynamical behavior. Now, numerical simulations help us understand this; see Figure 4. Take the parameters $a = 2.5, b = 5$, and $\mu = 50$ and the same parameters as before except that $q = 0, 0.01, 0.1, 0.2$ for Figures 4(a)–(h). Simulations convince us that when the effect of the inhibitor is very large, represented by large μ, if $q = 0$, that is, for the standard chemostat model with inhibitor, there is only one positive coexistence solution (see Figure 4(b)). Moreover, both the analytic results and many numerical simulations convince us that it is unstable. But once $q > 0$, the plasmid model has one asymptotically stable coexistence solution (see Figures 4(c), 4(e), 4(g)) and one (most likely) unstable coexistence solution (see Figures 4(d), 4(f), 4(h)).

Appendix A. In this section, we give the proof of Lemma 3.2.

Proof. (i) Let $y = (0, 0)$. By computation $W_y = \{(u, v) \in X : u \geq 0, v \geq 0\}$, $S_y = (0, 0)$. Hence $X_y = X$, and $Q = I$ (I is the identity operator in X). We first examine the eigenvalues of $\mathcal{A}'(0, 0)$, where $\mathcal{A}'(0, 0)$ is the Fréchet derivative of $\mathcal{A}$ with respect to (u, v) at $(0, 0)$. By direct computation,

$$\begin{aligned}\mathcal{A}'(0,0)(u,v) = &\left(-d\frac{d^2}{dx^2} + M\right)^{-1} \\ &\times (a(1-q-k)uf_1(z) + Mu,\ bvf_2(z) + Mv + aquf_1(z))\end{aligned}$$

for each $(u,v) \in X$. Hence an eigenvector (u,v) of $\mathcal{A}'(0,0)$ satisfies

$$\begin{aligned}&-du'' + Mu = \tfrac{1}{\lambda}(a(1-q-k)f_1(z) + M)u,\\ &-dv'' + Mv = \tfrac{1}{\lambda}((bf_2(z) + M)v + aquf_1(z)),\\ &u'(0) = u'(1) + \gamma u(1) = 0, \qquad v'(0) = v'(1) + \gamma v(1) = 0.\end{aligned}$$

It is easy to see that $I - \mathcal{A}'(0,0)$ is invertible in W_y since $a \neq \lambda_1/(1-q-k)$ and $b \neq \sigma_1$.

If $u \equiv 0$, then λ is an eigenvalue of

$$-dv'' + Mv = \frac{1}{\lambda}(bf_2(z) + M)v, \; v'(0) = v'(1) + \gamma v(1) = 0. \tag{A.1}$$

Let η_1 be the principal eigenvalue of

$$-d\omega'' - bf_2(z)\omega = \eta_1\omega, \;\; \omega'(0) = \omega'(1) + \gamma\omega(1) = 0.$$

Then $\eta_1 > 0$ if $b < \sigma_1$, and $\eta_1 < 0$ if $b > \sigma_1$. It follows from Lemma 2.3 that if $b < \sigma_1$, then (A.1) has no eigenvalue larger than or equal to 1; if $b > \sigma_1$, then (A.1) has eigenvalues larger than 1. Namely, $\mathcal{A}'(0,0)$ has no eigenvalue larger than or equal to 1 with the corresponding eigenvector of the form $(0,v)$ if $b < \sigma_1$; $\mathcal{A}'(0,0)$ has eigenvalues larger than 1 with the corresponding eigenvector of the form $(0,v)$ if $b > \sigma_1$.

If $u \not\equiv 0$, then λ is an eigenvalue of

$$-du'' + Mu = \frac{1}{\lambda}(a(1-q-k)f_1(z) + M)u, \qquad u'(0) = u'(1) + \gamma u(1) = 0.$$

By Lemma 2.3, we know that if $a < \lambda_1/(1-q-k)$, then $\mathcal{A}'(0,0)$ has no eigenvalue larger than or equal to 1 with the associated eigenfunction (u,v), where $u \not\equiv 0$; if $a > \lambda_1/(1-q-k)$, then $\mathcal{A}'(0,0)$ has eigenvalues larger than 1 with the associated eigenfunction $(u,v)(u \not\equiv 0)$. Hence, by Theorem 2.2 in [26], $\mathrm{index}_W(\mathcal{A},(0,0)) = 1$ if $a < \lambda_1/(1-q-k)$ and $b < \sigma_1$, and $\mathrm{index}_W(\mathcal{A},(0,0)) = 0$ if $a > \lambda_1/(1-q-k)$ or $b > \sigma_1$.

(ii) Let $y = (0,\theta)$. By computation,

$$W_y = \{(u,v) \in X : u \geq 0\}, \; S_y = \{(0,v) : v \in C_B([0,1])\}.$$

Define $X_y = \{(u,0) : u \in C_B([0,1])\}$. Then $X = S_y \oplus X_y$ with projection Q given by $(u,v) \to (u,0)$. We first determine the existence of $\mathrm{index}_W(\mathcal{A},(0,\theta))$. Let $\mathcal{A}'(0,\theta)$ denote the Fréchet derivative of $\mathcal{A}$ with respect to (u,v) at $(0,\theta)$. Then

$$\mathcal{A}'(0,\theta)(u,v) = \left(\left(-d\frac{d^2}{dx^2} + M\right)^{-1} g(u,v), \; \left(-d\frac{d^2}{dx^2} + M\right)^{-1} (h_1(u,v) + h_2(u,v))\right)$$

for $(u,v) \in X$, where

$$\begin{aligned}&g(u,v) = (a(1-q-k)f_1(z-\theta) + M)u,\\ &h_1(u,v) = (-b(1+c)\theta f_2'(z-\theta) - b\mu c\theta f_2(z-\theta) + aqf_1(z-\theta))u,\\ &h_2(u,v) = (b(f_2(z-\theta) - \theta f_2'(z-\theta)) + M)v.\end{aligned}$$

Let $(u,v) \in W_y$ be a fixed point of $\mathcal{A}'(0,\theta)$. Then (u,v) satisfies

$$\begin{aligned}&du'' + a(1-q-k)uf_1(z-\theta) = 0,\\ &dv'' + b(f_2(z-\theta) - \theta f_2'(z-\theta))v\\ &\quad = (b(1+c)\theta f_2'(z-\theta) + b\mu c\theta f_2(z-\theta) - aqf_1(z-\theta))u.\end{aligned}$$

Clearly, if $a \neq \hat{\lambda}_1/(1-q-k)$, then $u \equiv v \equiv 0$. That is, $I - \mathcal{A}'(0,\theta)$ is invertible in W_y, and $\text{index}_W(\mathcal{A},(0,\theta))$ is well defined. Next, we consider the eigenvalues of $Q \circ \mathcal{A}'(0,\theta)$. By virtue of definition $Q(u,v) = (u,0)$, every eigenvector of $Q \circ \mathcal{A}'(0,\theta)$ has the form $(u,0)$, where u is a nonzero solution of the equation

$$-du'' + Mu = \frac{1}{\lambda}(a(1-q-k)f_1(z-\theta) + M)u, \qquad u'(0) = u'(1) + \gamma u(1) = 0.$$

Let η_1 be the first eigenvalue of

$$-d\omega'' - a(1-q-k)\omega f_1(z-\theta) = \eta_1 \omega, \qquad \omega'(0) = \omega'(1) + \gamma\omega(1) = 0.$$

Then $\eta_1 > 0$ if $a < \hat{\lambda}_1/(1-q-k)$; $\eta_1 < 0$ if $a > \hat{\lambda}_1/(1-q-k)$. It follows from Lemma 2.3 that $Q \circ \mathcal{A}'(0,\theta)$ has no eigenvalue larger than or equal to 1 if $a < \hat{\lambda}_1/(1-q-k)$; $Q \circ \mathcal{A}'(0,\theta)$ has an eigenvalue larger than 1 if $a > \hat{\lambda}_1/(1-q-k)$. In view of Theorem 2.2 in [26], $\text{index}_W(\mathcal{A},(0,\theta)) = 0$ if $a > \hat{\lambda}_1/(1-q-k)$; $\text{index}_W(\mathcal{A},(0,\theta)) = \text{index}_{S_y}(\mathcal{A}'(0,\theta),(0,0)) = (-1)^\sigma$ if $a < \hat{\lambda}_1/(1-q-k)$. Here σ is the sum of multiplicities of the eigenvalues λ of $\mathcal{A}'(0,\theta)$ restricted in S_y such that $\lambda > 1$.

It remains to prove that $\text{index}_W(\mathcal{A},(0,\theta)) = 1$ for $a < \hat{\lambda}_1/(1-q-k)$. It suffices to show $\sigma = 0$. Suppose λ is an eigenvalue of $\mathcal{A}'(0,\theta)$ in S_y with the corresponding eigenvector (u,v). Then $u = 0$ and v is a nonzero solution of the equation

$$\text{(A.2)} \qquad -dv'' + Mv = \frac{1}{\lambda}(b(f_2(z-\theta) - \theta f_2'(z-\theta)) + M)v, \qquad v'(0) = v'(1) + \gamma v(1) = 0.$$

It follows from Lemma 2.3 that (A.2) has no eigenvalue larger than or equal to 1, which implies $\sigma = 0$ and $\text{index}_W(\mathcal{A},(0,\theta)) = \text{index}_{S_y}(\mathcal{A}'(0,\theta),(0,0)) = 1$. The proof of this lemma is completed. ∎

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