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ORIGINAL PAPER

The asymptotic behavior of a Chemostat model with Crowley–Martin type functional response and time delays

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Abstract In this paper, we introduce an improved Chemostat model with Crowley–Martin type functional response and time delays. By constructing Lyapunov functionals, the global asymptotic stability of the equilibria is shown in the case of a single species. The conditions for the global asymptotical stability of the model with time delays are obtained via monotone dynamical systems in the case of two species. Our results demonstrate that the effects of predator interference may result in coexistence of two species.

Keywords Chemostat · Crowley–Martin type functional response · Lyapunov–LaSalle invariance principle · Stability · Time delay

1 Introduction and statement of improved model

Many kinds of Chemostat models have been studied extensively by the specialists [1,2]. There have been quite a few studies of Chemostat competition models ([1–7], and the references there in). Almost all these papers prove that the principle of competitive exclusion holds. That is to say, at most one species can survive. It is known that there is not only competition between two-species but also mutual interference

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in a species. Considering mutual interference in a species, Yuan and Qiu [8], Qiu et al. [9], Pang and Chen [10] studied Chemostat models with Beddington–DeAngelis functional response. Yuan and Qiu [8] and Qiu et al. [9] demonstrated that mutual interference in a species may result in coexistence of two species. The Beddington–DeAngelis functional response is similar to the well-known Holling type II functional response but has an extra term in the denominator that models mutual interference in a species. In this model, individuals from a population of two or more predators not only allocate time to searching for and processing prey, but also spend some time engaging in encounters with other predators, resulting in a functional response that gives an instantaneous. The models with Beddington–DeAngelis functional response assume that handling and interfering are exclusive activities [11]. Crowley and Martin [12] removed that assumption in what they called their "preemption" model, allowing for interference among predators regardless of whether a particular individual is currently handling prey or searching for prey [13]. The Crowley–Martin type functional response is classified as one of predator-dependent functional response, i.e., that are functions of both prey and predator abundance because of predator interference. It is assumed that predator-feeding rate decreases by higher predator density even when prey density is high, and therefore the effects of predator interference in feeding rate remain important all the time whether an individual predator is handling or searching for a prey at a given instant of time. The per capita feeding rate in this formulation in given by

$$\mu(X, Y) = \frac{\omega X}{1 + aX + bY + abXY},$$

where ω, a, b are positive parameters that describe the effects of capture rate, handling time and the magnitude of interference among predators, respectively, on the feeding rate. Obviously, if $a = 0$, $b = 0$, then Crowley–Martin type functional response reduces to a linear mass-action function response (or Holling type I functional response); if $a > 0$, $b = 0$, then Crowley–Martin type functional response reduces to a Michaelis–Menten (or Holling type II) functional response [14]. The Crowley–Martin functional response is different from the traditional monotone or non-monotone functional response in Chemostat systems. The predator–prey relationship also exists between the nutrient concentration and the microorganism, the Crowley–Martin theory may work in the experiment of the microbial continuous culture. In 2011, Sun considered a class of Chemostat model with Crowley–Martin functional response, by use of qualitative theory of ordinary differential equations, they got the conditions of the micro-organism culture for success and failure [15].

It is well-known that the existence of time delays is inevitable in biology [16]. In recent years, Chemostat models with time delays that account for the time lapsing between the uptakes of nutrient by cells and the incorporation of this nutrient as biomass have been given much attention ([3,17,18], and the references there in). As far as we know, there are almost no literatures to discuss the Chemostat competition model with Crowley–Martin type functional response and time delays. In this paper, we will consider the following Chemostat system:

$$\begin{cases} \dot{S}(t) = Q(S_0 - S(t)) - \frac{\omega_1 S(t) X_1(t)}{\alpha(1+a_1 S(t)+b_1 X_1(t)+a_1 b_1 X_1(t) S(t))} - \frac{\omega_2 S(t) X_2(t)}{\beta(1+a_2 S(t)+b_2 X_2(t)+a_2 b_2 X_2(t) S(t))}, \\ \dot{X}_1(t) = -Q X_1(t) + e^{-Q\tau_1} \frac{\omega_1 S(t-\tau_1) X_1(t-\tau_1)}{1+a_1 S(t-\tau_1)+b_1 X_1(t-\tau_1)+a_1 b_1 X_1(t-\tau_1) S(t-\tau_1)}, \\ \dot{X}_2(t) = -Q X_2(t) + e^{-Q\tau_2} \frac{\omega_2 S(t-\tau_2) X_2(t-\tau_2)}{1+a_2 S(t-\tau_2)+b_2 X(t-\tau_2)+a_2 b_2 X_2(t-\tau_2) S(t-\tau_2)}, \end{cases} \tag{1.1}$$

where $S(t)$, $X_1(t)$ and $X_2(t)$ denote concentrations of the nutrient and the microorganism at time t respectively; S_0 denotes the input concentration of nutrient; Q denotes the volumetric dilution rate (flow rate/volume); constant α, β denote the yield of the nutrient, moreover, $0 < \alpha, \beta < 1$; the function $\mu(S, X_i) = \omega_i X_i/(1 + a_i S + b_i X_i + a_i b_i X_i S)$, $(i = 1, 2)$ denotes the growth rate of the microorganism (i.e., Crowley–Martin type functional response); each constant τ_i, $(i = 1, 2)$ represents the time delays involved in the conversion of the nutrient to viable species. Usually, as discussed in [3–6], the constant $\alpha_i = e^{-Q\tau_i}$ and so $\alpha_i x_i(t - \tau_i)$ represents the biomass of those microorganisms in species x_i that consume nutrient τ_i units of time prior to time t and that survive in the chemostat the τ_i units of time necessary to complete the nutrient conversion process. However, in the proofs of this paper, we need only require that the constant α_i be positive, or even α_i independent of τ_i are permitted.

The paper is organized as follows. In Sect. 2, we state preliminary results. In Sect. 3, we consider the asymptotic behavior of the model with a single species. In Sect. 4, we consider the global asymptotic behavior of two species. We conclude the paper with a discussion in Sect. 5.

2 Preliminary analysis

In this section, we present the basic results on the boundedness of positive solutions and the existence of equilibria. For simplicity, we nondimensionalize the system (1.1) with the following scaling $X_1 = \alpha S_0 x_1$, $X_2 = \beta S_0 x_2$, $S = S_0 y$, $t = T/Q$, $\tau_i = t_i/Q$, and still denotes T with t, t_i with τ_i then the system (1.1) takes the form

$$\begin{cases} \dot{y}(t) = 1 - y(t) - \frac{x_1(t) y(t)}{A_1+B_1 y(t)+C_1 x_1(t)+D_1 x_1(t) y(t)} - \frac{x_2(t) y(t)}{A_2+B_2 y(t)+C_2 x_2(t)+D_2 x_2(t) y(t)}, \\ \dot{x_1}(t) = -x_1(t) + \frac{\alpha_1 x_1(t-\tau_1) y(t-\tau_1)}{A_1+B_1 y(t-\tau_1)+C_1 x_1(t-\tau_1)+D_1 x_1(t-\tau_1) y(t-\tau_1)}, \\ \dot{x_2}(t) = -x_2(t) + \frac{\alpha_2 x_2(t-\tau_2) y(t-\tau_2)}{A_2+B_2 y(t-\tau_2)+C_2 x_2(t-\tau_2)+D_2 x_2(t-\tau_2) y(t-\tau_2)}, \end{cases} \tag{2.1}$$

where $A_1 = Q/(S_0\omega_1)$, $A_2 = Q/(S_0\omega_2)$, $B_1 = Qa_1/\omega_1$, $B_2 = Qa_2/\omega_2$, $C_1 = Qb_1\alpha/\omega_1$, $C_2 = Qb_2\beta/\omega_2$, $D_1 = Qa_1b_1S_0\alpha/\omega_1$, $D_2 = Qa_2b_2S_0\beta/\omega_2$ and the initial conditions of (2.1) are

$$\begin{aligned} &y(t) = \varphi_0(t) \geq 0, \quad x_1(t) = \varphi_1(t) \geq 0, \quad x_2(t) = \varphi_2(t) \geq 0, \\ &\varphi_0^2(t) + \varphi_1^2(t) + \varphi_2^2 \neq 0, \quad t \in [-\tau, 0]. \end{aligned} \tag{2.2}$$

where $\tau = max\{\tau_1, \tau_2\}$.

Theorem 2.1 *The solution* $(y(t), x_1(t), x_2(t))$ *of system* (2.1) *with the initial condition* (2.2) *is existent and non-negative on* $[0, +\infty)$. *Moreover,*

$$y(t) + \frac{x_1(t+\tau_1)}{\alpha_1} + \frac{x_2(t+\tau_2)}{\alpha_2} = 1 + \varepsilon(t).$$

Proof From the theory of local existence of solutions of general functional differential equations [16], it has that $y(t)$, $x_1(t)$ and $x_2(t)$ are existent on $[0, \nu)$ for some positive constant ν. Let us first show that $y(t) > 0$ for $t \in (0, \nu)$. In fact, if not so, by $\varphi(t) \geq 0$ and the continuity of $y(t)$, there must be $t_1 \geq 0$ such that

$$y(t_1) = 0, \quad \dot{y}(t_1) \leq 0, \quad \text{and} \quad y(t) \geq 0\ (-\tau \leq t \leq t_1),$$

where $\dot{y}(t_1)$ denotes the right-hand derivative at $t = t_1$, if $t_1 = 0$. Hence, by the first equation of system (2.1), it has that

$$\dot{y}(t_1) = 1 - y(t_1) - \sum_{i=1}^{2} \frac{\alpha_i x_i(t_1) y(t_1)}{A_i + B_i y(t_1) + C_i x_i(t_1) + D_i x_i(t_1) y(t_1)} = 1 > 0.$$

This is a contradiction to $\dot{y}(t_1) \leq 0$. This shows that $y(t) > 0$ for any $t \in (0, \nu)$.

We further show that $x_i(t) \geq 0$, $(i = 1, 2)$ for any $t \in [0, \nu)$. If not so, from continuity of $x_i(t)$ on $[-\tau_i, \nu)$ and ς being constant, there must exist $t_2 \geq 0$ such that

$$x_i(t_2) < 0, \quad \dot{x_i}(t_2) \leq 0, \quad \text{and} \quad x_i(t_2 - \varsigma) \geq 0,$$

where $\dot{x_i}(t_2)$ denotes the right-hand derivative at $t = t_2$, if $t_2 = 0$. Hence, it follows from the first equation of system (2.1), it has that

$$\dot{x_i}(t_2) = \frac{x_i(t_2-\tau) y(t_2-\tau_i)}{A_i + B_i y(t_2-\tau_i) + C_i x_i(t_2-\tau_i) + D_i x_i(t_2-\tau_i) y(t_2-\tau_i)} - x_i(t_2) \geq -x_i(t_2) > 0.$$

This is a contradiction to $\dot{x_i}(t_2) \leq 0$. Therefore, it has that $x_i(t) \geq 0$, $(i = 1, 2)$ for any $t \in [0, \nu)$.

Next, let us prove that $y(t)$, $x_1(t)$ and $x_2(t)$ are bounded. Let $z(t) = y(t) + \frac{x_1(t+\tau_1)}{\alpha_1} + \frac{x_2(t+\tau_2)}{\alpha_2}$. From (2.1) we obtain $z'(t) = 1 - z(t)$, from which we obtain $z(t) = 1 + \varepsilon(t)$, where $\varepsilon(t) = (z(0) - 1)e^{-t}$ and $\varepsilon(t) \to 0$ exponentially as $t \to +\infty$. Therefore,

$$y(t) + \frac{x_1(t+\tau_1)}{\alpha_1} + \frac{x_2(t+\tau_2)}{\alpha_2} = 1 + \varepsilon(t),$$

which implies that the positive solutions of system (2.1) are bounded. Especially, the solution $(y(t), x_1(t), x_2(t))$ is bounded on finite interval $[0, \nu)$. Therefore, it follows from the theory of continuation of solutions for functional differential equations [16] that the solution $(y(t), x_1(t), x_2(t))$ is existent and non-negative on $[0, +\infty)$. This completes the proof of Theorem 2.1.

Theorem 2.2 *The positive quadrant* $\Omega = \{\phi = (\varphi_0, \varphi_1, \varphi_2) \in C|\ \frac{\gamma_1\gamma_2}{\gamma_1\gamma_2+\gamma_1+\gamma_2} \leq \varphi_0 \leq 1,\ 0 \leq \varphi_1 \leq \frac{\alpha_1}{C_1+D_1},\ 0 \leq \varphi_2 \leq \frac{\alpha_2}{C_2+D_2}\}$ *is positively invariant under* (2.1), *where* $\gamma_i = (A_i(C_i + D_i) + \alpha_i C_i)/\alpha_i$, $i = 1, 2$. *Moreover,*

$$\limsup_{t\to+\infty} y(t) \leq 1, \quad \limsup_{t\to+\infty} x_1(t) \leq \frac{\alpha_1}{C_1 + D_1}, \quad \limsup_{t\to+\infty} x_2(t) \leq \frac{\alpha_2}{C_2 + D_2}.$$

Proof For any $\phi = (\varphi_0, \varphi_1, \varphi_2) \in \Omega$, let $(y(t), x_1(t), x_2(t))$ be the solution of (2.1) with the initial function ϕ. From Theorem 2.1, we have that for any $t \geq 0$, $y(t) \leq 1$, $x_i(t) \geq 0$, $(i = 1, 2)$. Now, we will prove that for any $t \geq 0$, $x_i(t) \leq \frac{\alpha_i}{C_i+D_i}$, $(i = 1, 2)$. If not so, there is a $t_3 \geq 0$, such that $x_i(t) \leq \frac{\alpha_i}{C_i+D_i}$ $(t \leq t_3)$, $x_i(t_3) = \frac{\alpha_i}{C_i+D_i}$ and $\dot{x}_i(t_3) \geq 0$. From the second and the third equations of (2.1), we have

$$\begin{aligned}
\dot{x}_i(t_3) &= -x_i(t_3) + \frac{x_i(t_3 - \tau_i)y(t_3 - \tau_i)}{A_i + B_i y(t_3 - \tau) + C_i x_i(t_3 - \tau_i) + D_i x_i(t_3 - \tau_i)y(t_3 - \tau_i)} \\
&\leq -x_i(t_3) + \frac{x_i(t_3 - \tau_i)}{A_i + B_i + (C_i + D_i)x_i(t_3 - \tau_i)} \\
&\leq -x_i(t_3) + \frac{x_i(t_3)}{A_i + B_i + (C_i + D_i)x_i(t_3)} \\
&= \frac{\alpha_i}{C_i + D_i}\left(-1 + \frac{\alpha_i}{A_i + B_i + \alpha_i}\right) < 0,
\end{aligned}$$

which is a contradiction to $\dot{x}_i(t_3) \geq 0$. Moreover, by simple computation, we can get

$$\limsup_{t\to+\infty} y(t) \leq 1, \quad \limsup_{t\to+\infty} x_1(t) \leq \frac{\alpha_1}{C_1 + D_1}, \quad \limsup_{t\to+\infty} x_2(t) \leq \frac{\alpha_2}{C_2 + D_2}.$$

Next, we show that for any $t \geq 0$, $y(t) \geq \frac{\gamma_1\gamma_2}{\gamma_1\gamma_2+\gamma_1+\gamma_2}$, where $\gamma_i = (A_i(C_i + D_i) + \alpha_i C_i)/\alpha_i$, $i = 1, 2$. From the first equation of (2.1), we have

$$\begin{aligned}
\dot{y}(t) &\geq 1 - y(t) - \frac{\frac{\alpha_1}{C_1+D_1} y(t)}{A_1 + B_1 y(t) + \frac{\alpha_1 C_1}{C_1+D_1} + \frac{\alpha_1 D_1}{C_1+D_1} y(t)} \\
&\quad - \frac{\frac{\alpha_2}{C_2+D_2} y(t)}{A_2 + B_2 y(t) + \frac{\alpha_2 C_2}{C_2+D_2} + \frac{\alpha_2 D_2}{C_2+D_2} y(t)} \\
&\geq 1 - \left(1 + \frac{\alpha_1}{A_1(C_1 + D_1) + \alpha_1 C_1} + \frac{\alpha_2}{A_2(C_2 + D_2) + \alpha_2 C_2}\right) y(t).
\end{aligned}$$

Hence, $y(t) \geq \frac{\gamma_1\gamma_2}{\gamma_1\gamma_2+\gamma_1+\gamma_2}$, $(\gamma_i = (A_i(C_i + D_i) + \alpha_i C_i)/\alpha_i$, $i = 1, 2)$, for any $t \geq 0$. Therefore, Ω is positively invariant with respect to (2.1). This completes the proof of Theorem 2.2.

Let

$$
\begin{array}{ll}
(A1) & A_1 + B_1 < \alpha_1; \\
(A2) & A_2 + B_2 < \alpha_2; \\
(A3) & (\alpha_1 - B_1)y^* - A_1 > 0; \\
(A4) & (\alpha_2 - B_2)y^* - A_2 > 0,
\end{array}
$$

where y^* denotes the unique positive root of $h(y) = 1 - y - \frac{\alpha_1 y - A_1 - B_1 y}{\alpha_1(C_1 + D_1 y)} - \frac{\alpha_2 y - A_2 - B_2 y}{\alpha_2(C_2 + D_2 y)} = 0$ in $(0, 1)$. We have

Theorem 2.3 *(1)* (2.1) *always has a washout equilibrium* $E_0 = (1, 0, 0)$.

(2) The boundary equilibrium $E_{10} = (y_1^*, \alpha_1(1 - y_1^*), 0)$ *exists if (A1) holds; the boundary equilibrium* $E_{20} = (y_2^*, 0, \alpha_2(1 - y_2^*))$ *exists if (A2) holds, where* y_i^* *denotes the unique positive root of* $f(y) = D_i\alpha_i y^2 + (\alpha_i - B_i + C_i\alpha_i - D_i\alpha_i)y - (A_i + C_i\alpha_i) = 0$*, i=1, 2 in* $(0, 1)$.

(3) The unique positive equilibrium $E^+ = (y^*, \frac{(\alpha_1 - B_1)y^* - A_1}{C_1 + D_1 y^*}, \frac{(\alpha_2 - B_2)y^* - A_2}{C_2 + D_2 y^*})$ *exists if conditions (A1)–(A4) hold.*

Proof An equilibrium point must satisfy the following equations:

$$
\begin{cases}
0 = 1 - y - \frac{x_1 y}{A_1 + B_1 y + C_1 x_1 + D_1 x_1 y} - \frac{x_2 y}{A_2 + B_2 y + C_2 x_2 + D_2 x_2 y}, \\
0 = -x_1 + \frac{\alpha_1 x_1 y}{A_1 + B_1 y + C_1 x_1 + D_1 x_1 y}, \\
0 = -x_2 + \frac{\alpha_2 x_2 y}{A_2 + B_2 y + C_2 x_2 + D_2 x_2 y}.
\end{cases}
\tag{2.3}
$$

We can get the washout solution $E_0 = (1, 0, 0)$ easily.

As far as the boundary equilibria are concerned, from (2.3), we have

$$
\begin{cases}
1 - y - \frac{x_1}{\alpha_1} - \frac{x_2}{\alpha_2} = 0, \\
\alpha_1 y = A_1 + B_1 y + C_1 x_1 + D_1 x_1 y, \\
\alpha_2 y = A_2 + B_2 y + C_2 x_2 + D_2 x_2 y.
\end{cases}
\tag{2.4}
$$

Thus, the analysis of the equation $D_i\alpha_i y^2 + (\alpha_i - B_i + C_i\alpha_i - D_i\alpha_i)y - (A_i + C_i\alpha_i) = 0$ $(i = 1, 2)$ is needed. We define

$$
f(y) = D_i\alpha_i y^2 + (\alpha_i - B_i + C_i\alpha_i - D_i\alpha_i)y - (A_i + C_i\alpha_i) = 0 \quad (i = 1, 2).
$$

Because

$$
f(0) = -(A_i + C_i\alpha_i) < 0, \quad f(1) = \alpha_i - (A_i + B_i) \quad (i = 1, 2).
$$

Thus, if $A_i + B_i < \alpha_i (i = 1, 2)$, $f(1) > 0$, there exists a unique positive root in $(0, 1)$. We denote $y_i^* \in (0, 1)$ $(i = 1, 2)$ as the positive root of $f(y)$, and denote $E_{10} = (y_1^*, \alpha_1(1 - y_1^*), 0)$ and $E_{20} = (y_2^*, 0, \alpha_2(1 - y_2^*))$ as the boundary equilibria.

As far as the positive equilibrium, from (2.3), we obtain

$$
x_1 = \frac{\alpha_1 y - A_1 - B_1 y}{C_1 + D_1 y}, \quad x_2 = \frac{\alpha_2 y - A_2 - B_2 y}{C_2 + D_2 y}.
$$

We define

$$h(y) = 1 - y - \frac{\alpha_1 y - A_1 - B_1 y}{\alpha_1(C_1 + D_1 y)} - \frac{\alpha_2 y - A_2 - B_2 y}{\alpha_2(C_2 + D_2 y)}.$$

Because

$$h(0) = 1 + \frac{A_1}{\alpha_1 C_1} + \frac{A_2}{\alpha_2 C_2} > 0, \quad h(1) = -\frac{\alpha_1 - A_1 - B_1}{\alpha_1(C_1 + D_1)} - \frac{\alpha_2 - A_2 - B_2}{\alpha_2(C_2 + D_2)},$$
$$h'(y) = -1 - \frac{\alpha_1 C_1 - B_1 C_1 + A_1 D_1}{\alpha_1(C_1 + D_1 y)^2} - \frac{\alpha_2 C_2 - B_2 C_2 + A_2 D_2}{\alpha_2(C_2 + D_2 y)^2}.$$

If conditions (A1)–(A4) hold, $h(1) < 0$, $h'(y) < 0$. Hence, there exists a unique positive equilibrium, we denote it as $E^+ = (y^*, \frac{(\alpha_1 - B_1)y^* - A_1}{C_1 + D_1 y^*}, \frac{(\alpha_2 - B_2)y^* - A_2}{C_2 + D_2 y^*})$, where, y^* is the unique positive root of $h(y)$ in (0, 1). This completes the proof of Theorem 2.3.

3 The case of a single species

In this section, we analyze the asymptotic behavior of delay models with a single species. Consider the delay models with a single species of the form

$$\begin{cases} \dot{y}(t) = 1 - y(t) - \frac{x_1(t)y(t)}{A_1 + B_1 y(t) + C_1 x_1(t) + D_1 x_1(t) y(t)}, \\ \dot{x_1}(t) = -x_1(t) + \frac{\alpha_1 x_1(t-\tau_1) y(t-\tau_1)}{A_1 + B_1 y(t-\tau_1) + C_1 x_1(t-\tau_1) + D_1 x_1(t-\tau_1) y(t-\tau_1)}, \end{cases} \tag{3.1}$$

From Theorem 2.2, it is enough to consider (3.1) on Ω. For the asymptotical stability of the equilibria, we have the following theorems.

Theorem 3.1 *(1) When $A_1 + B_1 > \alpha_1$, the equilibrium $E_0 = (1, 0)$ is locally asymptotically stable for any time delay $\tau_1 \geq 0$; when $A_1 + B_1 < \alpha_1$, the equilibrium $E_0 = (1, 0)$ is unstable for any time delay $\tau_1 \geq 0$; when $A_1 + B_1 = \alpha_1$, the trivial solution of the linearization system of (3.1) about $E_0 = (1, 0)$ is stable.*
(2) $E_{10} = (y_1^*, \alpha_1(1 - y_1^*))$ is locally asymptotically stable for any time delay $\tau_1 \geq 0$, as long as it exits.

Proof Let $\hat{E} = (\hat{y}, \hat{x}_1)$ be arbitrary equilibrium. Then the characteristic equation about $\hat{E} = (\hat{y}, \hat{x}_1)$ is given by

$$(\lambda + 1 + A)(\lambda + 1 - \alpha_1 C e^{-\lambda\tau_1}) + \alpha_1 A C e^{-\lambda\tau_1} = 0, \tag{3.2}$$

where

$$A = \frac{(A_1 + C_1 \hat{x}_1)\hat{x}_1}{(A_1 + B_1 \hat{y} + C_1 \hat{x}_1 + D_1 \hat{x}_1 \hat{y})^2}, \quad C = \frac{(A_1 + B_1 \hat{y})\hat{y}}{(A_1 + B_1 \hat{y} + C_1 \hat{x}_1 + D_1 \hat{x}_1 \hat{y})^2}.$$

For the washout equilibrium $E_0 = (1, 0)$, then $A = 0$, $C = \frac{1}{A_1+B_1}$ and (3.2) reduces to

$$(\lambda + 1)\left(\lambda + 1 - \frac{\alpha_1}{A_1 + B_1} e^{-\lambda\tau_1}\right) = 0. \tag{3.3}$$

It follows from [16] that

(i) If $A_1 + B_1 > \alpha_1$, all roots of (3.3) have negative real parts for any time delay $\tau_1 \geq 0$, then $E_0 = (1, 0)$ is locally asymptotically stable;
(ii) If $A_1 + B_1 < \alpha_1$, (3.3) has roots which have positive real parts for any time delay $\tau_1 \geq 0$, then $E_0 = (1, 0)$ is unstable;
(iii) If $A_1 + B_1 = \alpha_1$, it has that except $\lambda = 0$, any roots of (3.3) have negative real part for any time delay $\tau_1 \geq 0$. Hence, the trivial solution of the linearization system of (3.1) about $E_0 = (1, 0)$ is stable.

For the equilibrium $E_{10} = (y_1^*, \alpha_1(1 - y_1^*))$, from [15], $E_{10} = (y_1^*, \alpha_1(1 - y_1^*))$ is locally asymptotically stable for $\tau_1 = 0$. By simple computations, it easily has that (3.2) doesn't has imaginary solution, then the stability of (3.1) does not change for any time delay $\tau_1 \geq 0$. Hence, E_{10} is locally asymptotically stable for any time delay $\tau_1 \geq 0$, as long as it exits. This completes the proof of Theorem 3.1.

Theorem 3.2 *For any time delay $\tau_1 \geq 0$, $E_0 = (1, 0)$ is globally asymptotically stable for $A_1 + B_1 > \alpha_1$ and globally attractive for $A_1 + B_1 = \alpha_1$.*

Proof We shall use *Lyapunove–LaSalle* invariance principle [16] to prove Theorem 3.2. Let us define a functional V on Ω as follows,

$$V(\phi) = \alpha_1\varphi_1(0) + \alpha_1 \int_{-\tau_1}^{0} \varphi_1(\theta)d\theta. \tag{3.4}$$

It is clear that $V(\varphi)$ is continuous on the subset Ω and that the derivative of $V(\varphi)$ along the solution of (3.1) satisfies

$$\begin{aligned}
\dot{V}(\varphi)|_{(3.1)} &= \alpha_1\dot{\varphi}_1(0) + \alpha_1\varphi_1(0) - \alpha_1\varphi_1(-\tau_1) \\
&= \frac{\alpha_1^2 x_1(t-\tau_1)y(t-\tau_1)}{A_1 + B_1 y(t-\tau_1) + C_1 x_1(t-\tau_1) + D_1 x_1(t-\tau_1)y(t-\tau_1)} - \alpha_1 x_1(t-\tau_1) \\
&= \frac{\alpha_1\varphi_2(-\tau_1) - A_1 - B_1\varphi_2(-\tau_1) - C_1\varphi_1(-\tau_1) - D_1\varphi_1(-\tau_1)\varphi_2(-\tau_1)}{A_1 + B_1\varphi_2(-\tau_1) + C_1\varphi_1(-\tau_1) + D_1\varphi_1(-\tau_1)\varphi_2(-\tau_1)}\alpha_1\varphi_1(-\tau_1) \\
&\leq \frac{(\alpha_1 - A_1 - B_1)\varphi_2(-\tau_1) - C_1\varphi_1(-\tau_1) - D_1\varphi_1(-\tau_1)\varphi_2(-\tau_1)}{A_1 + B_1\varphi_2(-\tau_1) + C_1\varphi_1(-\tau_1) + D_1\varphi_1(-\tau_1)\varphi_2(-\tau_1)}\alpha_1\varphi_1(-\tau_1)
\end{aligned} \tag{3.5}$$

When $A_1 + B_1 \geq \alpha_1$, $(\alpha_1 - A_1 - B_1)\varphi_2(-\tau_1) - C_1\varphi_1(-\tau_1) - D_1\varphi_1(-\tau_1)\varphi_2(-\tau_1) \leq 0$. Hence, it has that for any time delay $\tau_1 \geq 0$, $V(\varphi)|_{(3.1)} \leq 0$. This shows that $V(\varphi)$ is a Lyapunov functional of (3.1) on the subset Ω. Define the subset G of Ω as

$G = \{\varphi \in \bar{\Omega} | \dot{V}(\varphi)|_{(3.1)} = 0\}$, form (3.5), it has that

$$G = \{\varphi \in \bar{\Omega} | \varphi_1(-\tau_1) = 0 \quad \text{or} \quad (\alpha_1 - A_1 - B_1)\varphi_2(-\tau_1) - C_1\varphi_1(-\tau_1) \\ -D\varphi_1(-\tau_1)\varphi_2(-\tau_1) = 0\}. \tag{3.6}$$

Let M be the largest set in Ω which is invariant with respect to (3.1). Clearly, M is not empty since $E_0 \in M$. We have two cases to be discussed.

(1) If $A_1 + B_1 > \alpha_1$, $(\alpha_1 - A_1 - B_1)\varphi_2(-\tau_1) - C_1\varphi_1(-\tau_1) - D_1\varphi_1(-\tau_1)\varphi_2(-\tau_1) < 0$. Hence, $G = \{\varphi \in \bar{\Omega} | \varphi_1(-\tau_1) = 0\}$. For any $\varphi \in M$, let $(y(t), x_1(t))$ be the solution of (3.1) with the initial function φ. From the invariance of M, it has that $(y_t, x_t) \in M \subset E$ for any $t \in R$. Thus, $x_1(t - \tau_1) = 0$ for any $t \in R$, which implies that $x(t) \equiv 0$ and $\varphi_1 \equiv 0$ for any $t \in R$. From the first equation of system (3.1), it has that $\dot{y}(t) = 1 - y(t)$ for any $t \in R$. Since $y(t) \to 1$ as $t \to +\infty$. Hence, $\varphi_2 \equiv 1$. Therefore, $M = \{(0, 1)\} = \{E_0\}$. The classical *Liapunov–LaSalle* invariance principle [16] shows that E_0 is globally attractive for any time delay $\tau_1 \geq 0$. It follows from Theorem 3.1 that the washout equilibrium E_0 of (3.1) is globally asymptotically stable for any time delay $\tau_1 \geq 0$.

(2) If $A_1 + B_1 = \alpha_1$, it has that $(\alpha_1 - A_1 - B_1)\varphi_2(-\tau_1) - C_1\varphi_1(-\tau_1) - D_1\varphi_1(-\tau_1)\varphi_2(-\tau_1) = -(C_1 + D_1\varphi_2(-\tau_1))\varphi_1(-\tau_1) = 0$ is equivalent to $\varphi_1(-\tau_1) = 0$. By repeating the proof of case (1), it also has that $M = \{E_0\}$. It follows from the *Liapuynov–LaSalle* invariance principle that E_0 is globally attractive for any time delay $\tau_1 \geq 0$. This completes the proof of Theorem 3.2.

Theorem 3.3 *If the function $g(x_1(t), y(t))$ is satisfied with*

$$(g(x_1^*, y^*) - g(x_1(t), y(t)))(g(x_1^*, y(t)) - g(x_1(t), y(t))) \leq 0, \tag{3.7}$$

then, $E_{10} = (y^*, x_1^*)$ is globally asymptotically stable for any time delay $\tau_1 \geq 0$ and $A_1 + B_1 < \alpha_1$, where

$$g(x_1(t), y(t)) = \frac{x_1(t)y(t)}{A_1 + B_1 y(t) + C_1 x_1(t) + D_1 x_1(t) y(t)}.$$

Proof To prove global stability of the positive equilibrium, be inspired by Huang and Takeuchi [19], we define a Lyapunov functional

$$V = V_1 + V_2 + V_3, \tag{3.8}$$

where

$$V_1 = \alpha_1 y(t) - y^* - \alpha_1 \int_{y^*}^{y(t)} \frac{g(x_1^*, y^*)}{g(x_1^*, \xi)} d\xi + x_1(t) - x_1^* - x_1^* \ln \frac{x_1(t)}{x_1^*},$$

$$V_2 = g(x_1^*, y^*) \int_0^{\tau_1} \left(\frac{x_1(t-\theta)}{x_1^*} - 1 - \ln \frac{x_1(t-\theta)}{x_1^*} \right) d\theta,$$

$$V_3 = \alpha_1 g(x_1^*, y^*) \int_0^{\tau_1} \left(\frac{g(x_1(t-\theta), y(t-\theta))}{g(x_1^*, y^*)} - 1 - \ln \frac{g(x_1(t-\theta), y(t-\theta))}{g(x_1^*, y^*)} \right) d\theta.$$

The time derivative of V_1 along solution of (3.1) is given by

$$\begin{aligned} \frac{dV_1}{dt}|_{(3.1)} &= \alpha_1 y^* \left(1 - \frac{y(t)}{y^*}\right)\left(1 - \frac{g(x_1^*, y^*)}{g(x_1^*, y(t))}\right) + \alpha_1 g(x_1^*, y^*) - \frac{\alpha_1 g^2(x_1^*, y^*)}{g(x_1^*, y(t))} \\ &-\alpha_1 g(x_1(t), y(t)) + \frac{\alpha_1 g(x_1^*, y^*) g(x_1(t), y(t))}{g(x_1^*, y(t))} + \alpha_1 g(x_1(t-\tau_1), y(t-\tau_1)) \\ &-x_1(t) - \frac{\alpha_1 x_1^* g(x_1(t-\tau_1), y(t-\tau_1))}{x_1(t)} + x_1^*. \end{aligned}$$

Notice $g(x_1^*, y^*) = \frac{x_1^*}{\alpha_1}$, the derivative of V_2 and V_3 satisfy

$$\begin{aligned} \frac{dV_2}{dt} &= \alpha_1 g(x_1^*, y^*) \frac{d}{dt} \int_0^{\tau_1} \frac{x_1(t-\theta)}{x_1^*} - 1 - \ln \frac{x_1(t-\theta)}{x_1^*} d\theta \\ &= \alpha_1 g(x_1^*, y^*) \int_0^{\tau_1} \frac{d}{dt} \frac{x_1(t-\theta)}{x_1^*} - 1 - \ln \frac{x_1(t-\theta)}{x_1^*} d\theta \\ &= -\alpha_1 g(x_1^*, y^*) \int_0^{\tau_1} \frac{d}{d\theta} \frac{x_1(t-\theta)}{x_1^*} - 1 - \ln \frac{x_1(t-\theta)}{x_1^*} d\theta \\ &= -x_1(t-\tau_1) + x_1(t) + \alpha_1 g(x_1^*, y^*) \ln \frac{x_1(t-\tau_1)}{x_1(t)}, \end{aligned}$$

$$\begin{aligned} \frac{dV_3}{dt} &= -\alpha_1 g(x_1(t-\tau_1), y(t-\tau_1)) + \alpha_1 g(x_1(t), y(t)) + \alpha_1 g(x_1^*, y^*) \\ &\times \ln \frac{g(x_1(t-\tau_1), y(t-\tau_1))}{g(x_1(t), y(t))}). \end{aligned}$$

Hence, the time derivative of V along solution of (3.1) is given by

$$\begin{aligned}\frac{dV}{dt}\Big|_{(3.1)} &= \alpha_1 y^*\left(1-\frac{y(t)}{y^*}\right)\left(1-\frac{g(x_1^*,y^*)}{g(x_1^*,y(t))}\right)+2\alpha_1 g(x_1^*,y^*)-\frac{\alpha_1 g^2(x_1^*,y^*)}{g(x_1^*,y(t))}\\
&\quad+\frac{\alpha_1 g(x_1^*,y^*)g(x_1(t),y(t))}{g(x_1^*,y(t))}-x_1(t-\tau_1)-\frac{\alpha_1 g(x_1^*,y^*)g(x_1(t-\tau_1),y(t-\tau_1))}{x_1(t)}\\
&\quad+\alpha_1 g(x_1^*,y^*)\ln\frac{x_1(t-\tau_1)}{x_1(t)}+\alpha_1 g(x_1^*,y^*)\ln\frac{g(x_1(t-\tau_1),y(t-\tau_1))}{g(x_1(t),y(t))}\\
&=\alpha_1 y^*\left(1-\frac{y(t)}{y^*}\right)\left(1-\frac{g(x_1^*,y^*)}{g(x_1^*,y(t))}\right)+\alpha_1 g(x_1^*,y^*)\ln\left(\frac{x_1(t-\tau_1)}{x_1(t)}\frac{g(x_1(t-\tau_1),y(t-\tau_1))}{g(x_1(t),y(t))}\right)\\
&\quad+\alpha_1 g(x_1^*,y^*)\times\left(2-\frac{g(x_1^*,y^*)}{g(x_1^*,y(t))}-\frac{g(x_1(t-\tau_1),y(t-\tau_1))}{x_1(t)}-\frac{x_1(t-\tau_1)}{x_1^*}+\frac{g(x_1(t),y(t))}{g(x_1^*,y(t))}\right).\end{aligned}$$

Here by using

$$\begin{aligned}&\ln\left(\frac{x_1(t-\tau_1)}{x_1(t)}\cdot\frac{g(x_1(t-\tau_1),y(t-\tau_1))}{g(x_1(t),y(t))}\right)\\
&=\ln\frac{g(x_1(t-\tau_1),y(t-\tau_1))}{x_1(t)}+\ln\frac{x_1(t-\tau_1)}{x_1^*}+\ln\frac{g(x_1^*,y^*)g(x_1^*,y(t))}{g(x_1^*,y(t))g(x_1(t),y(t))},\end{aligned}$$

$$\begin{aligned}\frac{dV}{dt}\Big|_{(3.1)} &= \alpha_1 y^*\left(1-\frac{y(t)}{y^*}\right)\left(1-\frac{g(x_1^*,y^*)}{g(x_1^*,y(t))}\right)\\
&+\alpha_1 g(x_1^*,y^*)\left(1-\frac{g(x_1(t-\tau_1),y(t-\tau_1))}{x_1(t)}+\ln\frac{g(x_1(t-\tau_1),y(t-\tau_1))}{x_1(t)}\right) &(3.9)\\
&+\alpha_1 g(x_1^*,y^*)\left(1-\frac{x_1(t-\tau_1)}{x_1^*}-\ln\frac{x_1(t-\tau_1)}{x_1^*}\right) &(3.10)\\
&+\alpha_1 g(x_1^*,y^*)\left(1-\frac{g(x_1^*,y^*)}{g(x_1^*,y(t))}\cdot\frac{g(x_1^*,y(t))}{g(x_1(t),y(t))}+\ln\left(\frac{g(x_1^*,y^*)}{g(x_1^*,y(t))}\cdot\frac{g(x_1^*,y(t))}{g(x_1(t),y(t))}\right)\right) &(3.11)\\
&+\alpha_1 g(x_1^*,y^*)\left(-1+\frac{g(x_1^*,y^*)}{g(x_1^*,y(t))}\cdot\frac{g(x_1^*,y(t))}{g(x_1(t),y(t))}-\frac{g(x_1^*,y^*)}{g(x_1^*,y(t))}+\frac{g(x_1(t),y(t))}{g(x_1^*,y(t))}\right). &(3.12)\end{aligned}$$

From the monotonicity of the function $g(x, y)$ with respect to y, we have

$$y^*\left(1-\frac{y(t)}{y^*}\right)\left(1-\frac{g(x_1^*,y^*)}{g(x_1^*,y(t))}\right)\le 0,$$

and from the condition (3.8), we have

$$g(x_1^*,y^*)\left(\frac{g(x_1^*,y^*)}{g(x_1^*,y(t))}-\frac{g(x_1(t),y(t))}{g(x_1^*,y(t))}\right)\left(\frac{g(x_1^*,y(t))}{g(x_1(t),y(t))}-1\right)\le 0.$$

Since the function $f(x) = 1 - x - \ln x$ is always non-positive for any $x > 0$, and $f(x) = 0$ if and only if $x = 1$. Therefore, the terms (3.10)–(3.12) are always non-positive.

Hence, the functional V satisfies all the conditions of Kuang [16, Corollary 5.2, p. 30]. This proves that E_{10} is globally asymptotically stable under the conditions $A_1 + B_1 < \alpha_1$ and (3.8). It completes the proof of Theorem 3.3.

4 The case of two species

In this section, we will use the same method as [9] to study the globally asymptotic behavior of system (2.1). In what follows, we state three elementary lemmas, which will prove to be useful.

Lemma 1 [5] *Let $f : R^+ \to R^+$ be a dierentiable function. If $\liminf_{t\to+\infty} f(t) < \limsup_{t\to+\infty} f(t)$, then there are sequences $\{t_m\} \uparrow +\infty$ and $\{s_m\} \uparrow +\infty$ such that for all m*

$$f(t_m) \to \limsup_{t\to+\infty} f(t) \quad as \quad m \to +\infty,\ f'(t_m) = 0,$$
$$f(s_m) \to \liminf_{t\to+\infty} f(t) \quad as \quad m \to +\infty,\ f'(s_m) = 0.$$

Lemma 2 [5] *Let $a \in (-\infty, +\infty)$, and $f : [a, +\infty) \to R$ be a differentiable function. If $\lim_{t\to+\infty} f(t)$ exists (finite) and the derivative function $f'(t)$ is uniformly continuous on $(a, +\infty)$, then, $\lim_{t\to+\infty} f(t) = 0$.*

Let X be a complete metric space. Suppose that $X^0 \subset X$, $X_0 \subset X$, $X^0 \bigcap X_0 = \emptyset$. Assume that $T(t)$ is a C_0 semi-group on X satisfying

$$\begin{cases} T(t) : X^0 \to X^0, \\ T(t) : X_0 \to X_0. \end{cases} \tag{4.1}$$

Let $T_b(t) = T(t)|_{X_0}$ and let A_b be the global attractor for $T_b(t)$. $\tilde{A}_b = \bigcup_{x\in A_b} \omega(x)$ will be called acyclic if there exists some isolated covering $M = \bigcup_{i=1}^{k} M_i$ of $\tilde{A}_b$ such that no subset of the M_i's forms a cycle. An isolated covering satisfying this condition will be called acyclic.

Lemma 3 [21] *Suppose that $T(t)$ satisfies (4.1). If*

(i) There is a $t_0 > 0$ such that $T(t)$ is compact for $t > t_0$.
(ii) $T(t)$ is point dissipative in X.
(iii) A_b is isolated and has an acyclic covering M where

$$M = \{M_1, M_2, \ldots, M_n\}.$$

(iv) $W^s(M_i) \bigcap X^0 = \emptyset$ for $i = 1, 2, \ldots, n$.

Then X_0 is a uniform repellor with respect to X^0, i.e., there is an $\varepsilon > 0$ such that for any $x \in X^0$, $\liminf_{t\to+\infty} d(T(t)x, X_0) \geq \varepsilon$, where d is the distance of $T(t)x$ from X_0.

Theorem 4.1 *If conditions (A1)–(A4) hold, then system* (2.1) *is uniformly persistent, i.e., there exists a constant* $\gamma > 0$*, independent of initial conditions, such that*

$$\liminf_{t\to+\infty} S(t) \ge \gamma, \liminf_{t\to+\infty} x_1(t) \ge \gamma, \liminf_{t\to+\infty} x_2(t) \ge \gamma.$$

Proof We begin by showing that the boundary planes of R^3_+ repel the positive solutions to system (2.1) uniformly. Let us choose

$$W_i = \{(\varphi_0, \varphi_1, \varphi_2) \in C^+([-\tau, 0], R^3_+) : \varphi_i(\theta) \equiv 0, \theta \in [-\tau, 0]\}$$

for $i = 0, 1, 2$. If $X_0 = W_0 \bigcup W_1 \bigcup W_2$ and $X^0 = intC([-\tau, 0], R^3_+)$, it suffices to show that there exists an $\gamma_0 > 0$ such that any solution x_t of system (2.1) initiating from X^0, $\liminf_{t\to+\infty} d(x_t, X_0) \ge \gamma_0$. To this end, we verify below that the conditions of Lemma 3 are satisfied. It is easy to see that X_0 and X^0 are positively invariant. Moreover, conditions (i) and (ii) of Lemma 3 are clearly satisfied. Thus we only need to verify conditions (iii) and (iv). There are three constant solutions E_0, E_{10} and E_{20} in X_0, corresponding, respectively, to $y(t) = 1, x_1(t) = 0, x_2(t) = 0$, $y(t) = y_1^*, x_1(t) = \alpha_1(1 - y_1^*), x_2(t) = 0$, $y(t) = y_2^*, x_1(t) = 0, x_2(t) = \alpha_2(1 - y_2^*)$. From Theorem 3.3, it is easy to see that if invariant sets E_0, E_{10} and E_{20} are isolated, $\{E_0, E_{10}, E_{20}\}$ is isolated and is an acyclic covering. The fact that E_0, E_{10} and E_{20} are isolated will follow from the following proof.

We now show that, $W^s(E_0) \bigcap X^0 = \emptyset$, $W^s(E_{10}) \bigcap X^0 = \emptyset$ and $W^s(E_{20}) \bigcap X^0 = \emptyset$. We restrict our attention to the first and second equations, since the proof for the third is similar to the proof for the second. If it is not true, i.e., $W^s(E_0) \bigcap X^0 = \emptyset$, then there exists a positive solution $(y(t), x_1(t), x_2(t))$ to system (2.1) such that $(y(t), x_1(t), x_2(t)) \to (1, 0, 0)$ as $t \to +\infty$. Let ϵ be sufficiently small. Then we have

$$\begin{cases} \dot{y}(t) \ge 1 - y(t) - \frac{x_1(t)y(t)}{A_1+B_1y(t)+C_1x_1(t)+D_1x_1(t)y(t)} - \epsilon, \\ \dot{x_1}(t) = -x_1(t) + \frac{\alpha_1 x_1(t-\tau_1)y(t-\tau_1)}{A_1+B_1y(t-\tau_1)+C_1x_1(t-\tau_1)+D_1x_1(t-\tau_1)y(t-\tau_1)}. \end{cases} \tag{4.2}$$

Let us consider

$$\begin{cases} \dot{y}(t) = 1 - \epsilon - y(t) - \frac{x_1(t)y(t)}{A_1+B_1y(t)+C_1x_1(t)+D_1x_1(t)y(t)}, \\ \dot{x_1}(t) = -x_1(t) + \frac{\alpha_1 x_1(t-\tau_1)y(t-\tau_1)}{A_1+B_1y(t-\tau_1)+C_1x_1(t-\tau_1)+D_1x_1(t-\tau_1)y(t-\tau_1)}. \end{cases} \tag{4.3}$$

For convenience, we rewrite system (2.1) and (4.3) as

$$\dot{x}(t) = f_1(t, x_t), \quad \text{and} \quad \dot{x}(t) = f_2(t, x_t),$$

respectively. From Theorem 3.3, it can be seen that system (4.3) has unique equilibrium $E'(\bar{y}_1, \bar{x}_1)$, $\bar{x}_1 > 0$ which is globally asymptotically stable. Note that $y(t, t_0, f_1) \ge y(t, t_0, f_2)$, $x_1(t, t_0, f_1) \ge x_1(t, t_0, f_2)$ and $\lim_{t\to+\infty} x_1(t, t_0, f_2) = \bar{x}_1$. This is a contradiction. Hence $W^s(E_0) \bigcap X^0 = \emptyset$.

Suppose that there exists a positive solution $(y(t), x_1(t), x_2(t))$ to system (2.1) such that $(y(t), x_1(t), x_2(t)) \to (y_1^*, \alpha_1(1-y_1^*), 0)$ as $t \to +\infty$. Since $A_2 + B_2 \leq \alpha_2$, we can choose $\kappa > 0$ small enough such that $\frac{\alpha_2(y_1^*-\kappa)}{A_2+B_2(y_1^*-\kappa)} > 1$. Let $t_4 > 0$ such that $y_1^* - \kappa < y(t)$ for $t > t_4$. Then we have

$$\dot{x_2}(t) \geq -x_2(t) + \frac{\alpha_2 x_2(t-\tau_2)(y_1^*-\kappa)}{A_2 + B_2(y_1^*-\kappa) + C_2 x_2(t-\tau_2) + D_2 x_2(t-\tau_2)(y_1^*-\kappa)}$$

for $t > t_4$. Let us consider

$$\dot{x}(t) = -x(t) + \frac{\alpha_2 x(t-\tau_2)(y_1^*-\kappa)}{A_2 + B_2(y_1^*-\kappa) + C_2 x(t-\tau_2) + D_2 x(t-\tau_2)(y_1^*-\kappa)}. \tag{4.4}$$

Let $x_0 > 0$ be small enough such that $x_0 < x_2(t_4)$. Note that $\frac{\alpha_2(y_1^*-\kappa)}{A_2+B_2(y_1^*-\kappa)} > 1$. Hence, if $x(t)$ is a solution to (4.4) satisfying $x(t_4) = x_0$, it follows that $x(t) \to +\infty$. Note that $x_2(t) \geq x(t)$ for $t > t_4$, so that we have $x_2(t) \to +\infty$. This contradicts $x_2(t) \to 0$. At this time, we are able to conclude from Lemma 3 that X_0 repels the positive solutions to (2.1) uniformly. Incorporating this into Theorem 2.2, we can see that system (2.1) is permanent.

Theorem 4.2 *If conditions (A1)–(A4) hold, then the positive equilibrium E^+ is globally asymptotically stable.*

Proof From Theorem 2.3, there exists a unique positive equilibrium. Let us define

$$X_1(t) = \frac{x_1(t+\tau_1)}{\alpha_1}, \quad X_2(t) = \frac{x_2(t+\tau_2)}{\alpha_2}.$$

It follows from Theorem 2.1 that

$$y(t) = 1 + \varepsilon(t) - X_1(t) - X_2(t).$$

Therefore $(X_1(t), X_2(t))$ satisfies the following two-dimensional delay differential equations:

$$\begin{cases} \dot{X}_1(t) = -X_1(t) + \frac{\alpha_1 X_1(t-\tau_1)(1+\varepsilon(t)-X_1(t)-X_2(t))}{A_1+B_1(1+\varepsilon(t)-X_1(t)-X_2(t))+C_1\alpha_1 X_1(t-\tau_1)+D_1\alpha_1 X_1(t-\tau_1)(1+\varepsilon(t)-X_1(t)-X_2(t))}, \\ \dot{X}_2(t) = -X_2(t) + \frac{\alpha_2 X_2(t-\tau_2)(1+\varepsilon(t)-X_1(t)-X_2(t))}{A_2+B_2(1+\varepsilon(t)-X_1(t)-X_2(t))+C_2\alpha_2 X_2(t-\tau_2)+D_2\alpha_2 X_2(t-\tau_2)(1+\varepsilon(t)-X_1(t)-X_2(t))}, \end{cases} \tag{4.5}$$

It is obvious that $E^+ = (X_1^*, X_2^*)$ is the unique positive equilibrium of (4.5), where $X_1^* = \frac{x_1^*}{\alpha_1}$, $X_2^* = \frac{x_2^*}{\alpha_2}$. Now we only need to show that $E^+ = (X_1^*, X_2^*)$ is globally asymptotically stable.

First we will show that $E^+ = (X_1^*, X_2^*)$ is a locally stable point of system (4.5). Let us define the following auxiliary functions:

$$\begin{cases} F(X_1, X_2, Z) = -X_1 + \frac{\alpha_1 X_1(1+Z-X_1-X_2)}{A_1+B_1(1+Z-X_1-X_2)+C_1\alpha_1 X_1+D_1\alpha_1 X_1(1+Z-X_1-X_2)}, \\ G(X_1, X_2, Z) = -X_2 + \frac{\alpha_2 X_2(1-Z-X_1-X_2)}{A_2+B_2(1-Z-X_1-X_2)+C_2\alpha_2 X_2+D_2\alpha_2 X_2(1-Z-X_1-X_2)}, \end{cases} \tag{4.6}$$

After some algebra, we can obtain

$$\begin{vmatrix} \frac{\partial F(X_1,X_2,Z)}{\partial X_1} & \frac{\partial F(X_1,X_2,Z)}{\partial X_2} \\ \frac{\partial G(X_1,X_2,Z)}{\partial X_1} & \frac{\partial G(X_1,X_2,Z)}{\partial X_2} \end{vmatrix}_{(X_1^*,X_2^*,0)} > 0. \tag{4.7}$$

Because of the implicit function theorem, we can conclude that there are two functions

$$X_1 = X_1(Z), X_2 = X_2(Z)$$

defined by (4.6) in the neighborhood of $Z = 0$. However,

$$X_1'(Z)|_{(X_1^*,X_2^*,0)} = -\begin{vmatrix} \frac{\partial F(X_1,X_2,Z)}{\partial Z} & \frac{\partial F(X_1,X_2,Z)}{\partial X_2} \\ \frac{\partial G(X_1,X_2,Z)}{\partial Z} & \frac{\partial G(X_1,X_2,Z)}{\partial X_2} \end{vmatrix} \Bigg/ \begin{vmatrix} \frac{\partial F(X_1,X_2,Z)}{\partial X_1} & \frac{\partial F(X_1,X_2,Z)}{\partial X_2} \\ \frac{\partial G(X_1,X_2,Z)}{\partial X_1} & \frac{\partial G(X_1,X_2,Z)}{\partial X_2} \end{vmatrix} > 0,$$

$$X_2'(Z)|_{(X_1^*,X_2^*,0)} = -\begin{vmatrix} \frac{\partial F(X_1,X_2,Z)}{\partial X_1} & \frac{\partial F(X_1,X_2,Z)}{\partial Z} \\ \frac{\partial G(X_1,X_2,Z)}{\partial X_1} & \frac{\partial G(X_1,X_2,Z)}{\partial Z} \end{vmatrix} \Bigg/ \begin{vmatrix} \frac{\partial F(X_1,X_2,Z)}{\partial X_1} & \frac{\partial F(X_1,X_2,Z)}{\partial X_2} \\ \frac{\partial G(X_1,X_2,Z)}{\partial X_1} & \frac{\partial G(X_1,X_2,Z)}{\partial X_2} \end{vmatrix} < 0.$$

Let $\varepsilon > 0$, and define the following comparison differential equations:

$$\begin{cases} \dot{X}_1(t) = -X_1(t) + \frac{\alpha_1 X_1(t-\tau_1)(1+\varepsilon-X_1(t)-X_2(t))}{A_1+B_1(1+\varepsilon-X_1(t)-X_2(t))+C_1\alpha_1 X_1(t-\tau_1)+D_1\alpha_1 X_1(t-\tau_1)(1+\varepsilon-X_1(t)-X_2(t))}, \\ \dot{X}_2(t) = -X_2(t) + \frac{\alpha_2 X_2(t-\tau_2)(1-\varepsilon-X_1(t)-X_2(t))}{A_2+B_2(1-\varepsilon-X_1(t)-X_2(t))+C_2\alpha_2 X_2(t-\tau_2)+D_2\alpha_2 X_2(t-\tau_2)(1-\varepsilon-X_1(t)-X_2(t))}, \end{cases} \tag{4.8}$$

$$\begin{cases} \dot{X}_1(t) = -X_1(t) + \frac{\alpha_1 X_1(t-\tau_1)(1-\varepsilon-X_1(t)-X_2(t))}{A_1+B_1(1-\varepsilon-X_1(t)-X_2(t))+C_1\alpha_1 X_1(t-\tau_1)+D_1\alpha_1 X_1(t-\tau_1)(1-\varepsilon-X_1(t)-X_2(t))}, \\ \dot{X}_2(t) = -X_2(t) + \frac{\alpha_2 X_2(t-\tau_2)(1+\varepsilon-X_1(t)-X_2(t))}{A_2+B_2(1+\varepsilon-X_1(t)-X_2(t))+C_2\alpha_2 X_2(t-\tau_2)+D_2\alpha_2 X_2(t-\tau_2)(1+\varepsilon-X_1(t)-X_2(t))}, \end{cases} \tag{4.9}$$

When ε is sufficiently small, by the implicit function theorem, (4.8) and (4.9) admits unique positive equilibria $E_+(X_{1+}^*, X_{2-}^*)$ and $E_-(X_{1-}^*, X_{2+}^*)$, respectively. Furthermore, from the sign of $X_1(Z), X_2(Z)$, it follows that $E_- <_k E^+ <_k E_+$ and $E_- \to E^+, E_+ \to E^+$ as $\varepsilon \to 0$, where "$<_k$" ("$\leq_k$") is a notation, which means that if $z = (x, y)$ and $\bar{z} = (\bar{x}, \bar{y})$, we write $z <_k \bar{z}(\leq_k \bar{z})$ if $x < \bar{x}(x \leq \bar{x})$ and

$y > \bar{y}(y \geq \bar{y})$. Obviously, (4.6), (4.8) and (4.9) are competitive systems. For convenience, let us rewrite system (4.6), (4.8), (4.9) as

$$\dot{X} = f_{\varepsilon(t)}(t, X), \quad \dot{X} = f_{+\varepsilon}(t, X), \quad \dot{X} = f_{-\varepsilon}(t, X),$$

respectively. From the comparison theorem, we have

$$X(t, t_0, f_{-\varepsilon}, \varphi) \leq_k X(t, t_0, f_{\varepsilon(t),\varphi}) \leq_k X(t, t_0, f_{+\varepsilon}, \varphi).$$

Thus we have $\hat{E}_- <_k X(t, t_0, f_{\varepsilon(t),\varphi}) <_k \hat{E}_+$ for all φ such that $\hat{E}_- <_k \varphi <_k \hat{E}_+$ and $t > t_0$. This implies that the positive equilibrium $E^+ = (X_1^*, X_2^*)$ is a local stable point.

Second, we will show that the positive equilibrium $E^+ = (X_1^*, X_2^*)$ is global attractor of system (4.5). Considering the following limiting system:

$$\begin{cases} \dot{X}_1(t) = -X_1(t) + \frac{\alpha_1 X_1(t-\tau_1)(1-X_1(t)-X_2(t))}{A_1+B_1(1-X_1(t)-X_2(t))+C_1\alpha_1 X_1(t-\tau_1)+D_1\alpha_1 X_1(t-\tau_1)(1-X_1(t)-X_2(t))}, \\ \dot{X}_2(t) = -X_2(t) + \frac{\alpha_2 X_2(t-\tau_2)(1-X_1(t)-X_2(t))}{A_2+B_2(1-X_1(t)-X_2(t))+C_2\alpha_2 X_2(t-\tau_2)+D_2\alpha_2 X_2(t-\tau_2)(1-X_1(t)-X_2(t))}, \end{cases} \tag{4.10}$$

Let us rewrite system (4.10) as

$$\dot{X} = g(t, x).$$

System (4.10) is a competitive system and has a unique positive equilibrium $E^+ = (X_1^*, X_2^*)$ and two boundary equilibria $E_{10} = (X_1^\partial, 0)$, $E_{20} = (0, X_2^\partial)$, where $X_1^\partial = \frac{x_1^*}{\alpha_1}$, $X_2^\partial = \frac{x_2^*}{\alpha_2}$. From Theorems 2.2 and 4.1 it follows that there exists a $\zeta > 0$ such that

$$\zeta < \liminf_{t\to+\infty} X_1(t) \leq \limsup_{t\to+\infty} X_1(t) < \frac{\alpha_1}{C_1 + D_1} - \zeta,$$
$$\zeta < \liminf_{t\to+\infty} X_2(t) \leq \limsup_{t\to+\infty} X_2(t) < \frac{\alpha_2}{C_2 + D_2} - \zeta.$$

Thus, without loss of generality, we can always assume that the initial data (φ_1, φ_2) for system (4.10) satisfy $(\hat{\zeta}, \hat{X}_2^\partial - \hat{\zeta}) \leq_k (\varphi_1, \varphi_2) \leq_k (\hat{X}_1^\partial - \hat{\zeta}, \hat{\zeta})$. Let $\phi_1 = (\hat{\zeta}, \hat{X}_2^\partial - \hat{\zeta})$ and $\phi_2 = (\hat{X}_1^\partial - \hat{\zeta}, \hat{\zeta})$. Then there exists a $t_1 > 0$ such that $\phi_1 <_k X_{t_1}(t, \phi_1, g)$ and a t_2 such that $X_{t_2}(t, \phi_2, g) <_k \phi_2$. Therefore $X(t, \phi_1, g)$ and $X(t, \phi_2, g)$ both converge to the unique equilibrium $E^+ = (X_1^*, X_2^*)$ as $t \to \infty$. For any initial data φ that satisfies $\phi_1 \leq_k \varphi \leq_k \phi_2$ monotonicity implies that $X(t, \phi_1, g) \leq_k X(t, \varphi, g) \leq_k X(t, \phi_2, g)$ for $t \geq 0$. Since $X(t, \phi_1, g)$ and $X(t, \phi_2, g)$ both converge to the unique equilibrium $E^+ = (X_1^*, X_2^*)$ as $t \to \infty$, it follows that $X(t, \varphi, g)$ converges to $E^+ = (X_1^*, X_2^*)$ as $t \to \infty$, i.e., the positive equilibrium $E^+ = (X_1^*, X_2^*)$ is a global attractor of system (4.10), furthermore, $E^+ = (X_1^*, X_2^*)$ is a global equi-attractor of system (4.10). Let σ_1 be arbitrary, for any initial data φ satisfying $\phi_1 \leq_k \varphi \leq_k \phi_2$, there exists a T_1, which is only dependent on σ_1 such that $(X_1(t), X_2(t)) \in U((X_1^*, X_2^*), \frac{\sigma_1}{2})$. Note that the solution of differential equations depends continuously on the parameters. Hence there exists a $\sigma_2 > 0$ such that

$$|X(t, \varphi, f_{\pm\varepsilon}) - X(t, \varphi, g)| < \frac{\sigma_1}{2}$$

for all $\varepsilon < \sigma_2$ and $t \in [0, T_1]$. Thus there exists a T_2 such that $(X_1(t, \varphi, f_{\varepsilon(t)}), X_2(t, \varphi, f_{\varepsilon(t)})) \in U((X_1^*, X_2^*), \sigma_1)$ for $t > T_2$ and any initial data φ satisfies $\phi_1 \leq_k \varphi \leq_k \phi_2$, i.e., the positive equilibrium $E^+ = (X_1^*, X_2^*)$ is global attractor of system (4.5). This completes the proof.

In a similar way, we can show the following theorems.

Theorem 4.2 *If conditions (A1)–(A3) and the reverse of (A4) hold, then the boundary equilibrium* $E_{10} = (y_1^*, \alpha_1(1 - y_1^*), 0)$ *is globally asymptotically stable.*

Theorem 4.3 *If conditions (A1), (A2), (A4) and the reverse of (A3) hold, then the boundary equilibrium* $E_{20} = (y_2^*, 0, \alpha_2(1 - y_2^*))$ *is globally asymptotically stable.*

5 Discussion

In this paper we analyze a Chemostat model with the Crowley–Martin functional response and delayed response in growth. This model incorporates time delays that allow for cellular components of each competing species to be structured to include unassimilated or stored nutrient. Then, by use of the traditional analysis technique for transcendental equations [16], we give the local asymptotic stability of the equilibria of (3.1). Based on Lyapunov–LaSalle principle for functional differential equations, we completely obtain global asymptotic stability and global attraction of the washout equilibrium of (3.1). Be inspired by Huang and Takeuchi [19], we construct a Lyapunov functional and show that the positive equilibrium of (2.1) is globally asymptotically stable. Our results show that time delay is factually harmless for the local and global asymptotic stability of the equilibria of (2.1). Finally, using the same method as [9], we obtain the global stability of the system (2.1) via monotone dynamical systems. The results in the paper include some known results for Holling type I and II functional response models as special cases. In theory, if $A = 0$, $D = 0$, (2.1) will be the Michaelis–Menten ratio-dependent model [20]; if $D = 0$, (2.1) will be the Beddington–DeAngelis model [9].

References

1. L. Chen, J. Chen, *Nonlinear Biology Dynamics* (Science Press, Beijing, 1993)
2. H.L. Smith, P. Waltman, *The Theory of the Chemostat: Dynamics of Microbial Competition* (Cambridge University Press, Cambridge, UK, 1995)
3. L. Wang, G.S.K. Wolkowicz, A delayed chemostat model with general non-monotone response functions and differential removal rates. J. Math. Anal. Appl. **321**, 452 (2006)
4. G.S.K. Wolkowicz, Z. Lu, Global dynamics of a mathematical model of competition in the chemostat: general response functions and differential death rates. SIAM J. Appl. Math. **52**, 222 (1992)
5. G.S.K. Wolkowicz, H. Xia, Global asymptotic behavior of a chemostat model with discrete delays. SIAM J. Appl. Math. **57**, 1019 (1997)

6. S.F. Ellermeyer, Competition in the chemostat: global asymptotic behavior of a model with delayed response in growth. SIAM J. Appl. Math. **54**, 456 (1994)
7. M. White, X. Zhao, A periodic Droop model for two species competition in a chemostat. Bull. Math. Biol. **71**, 145 (2009)
8. Z. Yuan, Z. Qiu, The asymptotic behavior of chemostat model with the Beddington–DeAngelies functional responses. J. Southwest China Normal Uinv. **28**, 193 (2009)
9. Z. Qiu, J. Yu, Y. Zou, The asymptotic behavior of a chemostat model with the Beddington–DeAngelis functional response. Math. Biosci. **187**, 175 (2004)
10. G. Pang, L. Chen, Analysis of a Beddington–DeAngelis food chain chemostat with periodically varying substrate. J. Math. Chem. **44**, 467 (2008)
11. G.T. Skalski, J.F. Gilliam, Functional response with redator interference: viable alternatives to the Holling type II model. Ecology **82**, 3083 (2001)
12. P.H. Crowley, E.K. Martin, Functional responses and interference within and between year classes of a dragonfly population. J. North Am. Benthol. Soc. **8**, 211 (1989)
13. R.K. Upadhyay, R.K. Naji, Dynamics of a three species food chain model with Crowley–Martin type functional response. Chaos Solitons Fractals **42**, 1337 (2009)
14. X. Shi, X. Zhou, X. Song, Analysis of a stage-structured predator–prey model with Crowley–Martin function. J. Appl. Math. Comput. **36**, 459 (2011)
15. S. Sun, R. Zhang, L. Zeng, Qualitative analysis on a chemostat model with the Crowley–Martain functional response. J. Biomath **26**, 293 (2011)
16. Y. Kuang, *Delay Differential Equations with Applications in Population Dynamics* (Academic Press, San Diego, 1993)
17. S. Ruan, The dynamics of Chemostat models. J. Cent. China Normal Univ. (Nat. Sci.) **31**, 377 (1997)
18. G. Fu, W. Ma, Chemostat dynamics models described by differential equations (I, II). Microbiology, **31**(5), 136 (2004), **31**(6), 128 (2004)
19. G. Huang, Y. Takeuchi, Global analysis on delay epidemiological dynamic models with nonlinear incidence. J. Math. Biol. **63**, 125 (2011)
20. X. Zhang, R. Xu, L. XUE, Global stability for ratio-dependent chemostat model with time delay. J. Ordnance Eng. Coll. **21**, 75 (2009)
21. W. Wang, L. Chen, A predator Cprey system with stage-structure for predator. Comput. Math. Appl. **33**, 83 (1997)