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Research article

Dynamic behaviors of a non-autonomous allelopathic phytoplankton model with threshold inter-inhibition and feedback controls

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Abstract: This paper investigated a non-autonomous allelopathic phytoplankton model with threshold inhibition and feedback controls. We applied the comparison theorem of differential equations and constructed some suitable Lyapunov functions to obtain sufficient conditions for the permanence and global attractivity of the system. By constructing some suitable Lyapunov-type extinction functions, we further derived sufficient conditions for the extinction of one of the species. The analysis reveals that inter-specific inhibition and toxic substances critically influence the permanence, extinction, and global stability of the two-species system. Some known results are extended.

Keywords: permanence; extinction; global attractivity; phytoplankton; feedback controls

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1. Introduction

Phytoplankton, as primary producers in marine ecosystems, play an important role in carbon dioxide absorption, nutrient cycling, and climate regulation. Their population dynamics—particularly driven by allelopathic interactions—have profound ecological implications. Understanding their population dynamics and mechanisms of species coexistence remains an important topic in the field of ecology.

Traditional competition models often rely on linear inhibition terms. Recently, many scholars contend that competition models incorporating nonlinear saturation inter-inhibition terms which provide a more ecologically realistic representation of species interactions [1–5]. For instance, Wang et al. [1]

proposed the following two-species competition model with saturation inter-inhibition:

$$\begin{aligned} x_1'(t) &= x_1(t)(r_1(t) - a_1(t)x_1(t) - \frac{b_1(t)x_2(t)}{1 + x_2(t)}), \\ x_2'(t) &= x_2(t)(r_2(t) - \frac{b_2(t)x_1(t)}{1 + x_1(t)} - a_2(t)x_2(t)), \end{aligned} \tag{1.1}$$

where $x_1(t), x_2(t)$ are the population density of species x_1 and x_2 at time t, respectively; $r_i(t), i = 1, 2$, are the intrinsic growth rates of the two species; $a_i(t), i = 1, 2$, are the rates of intraspecific competition of the first and second species, respectively; $b_i(t), i = 1, 2$, represent the interspecific competing rates, and $r_i(t), a_i(t), b_i(t), i = 1, 2$, are positive, continuous and bounded. Wang et al. [1] gave the sufficient conditions that ensure the existence and global asymptotic stability of positive, almost-periodic solutions.

During the last decade, the study of the dynamic behaviors of the allelopathic phytoplankton model have become one of the most important topics in biology [4–10]. Based on the work of Yue [4], recently, Xie et al. [5] proposed the following two-species non-autonomous competitive phytoplankton system with saturation inter-inhibition and one toxin producing phytoplankton:

$$\begin{aligned} x_1'(t) &= x_1(t)(r_1(t) - a_1(t)x_1(t) - \frac{b_1(t)x_2(t)}{1 + x_2(t)} - c_1(t)x_1(t)x_2(t)), \\ x_2'(t) &= x_2(t)(r_2(t) - \frac{b_2(t)x_1(t)}{1 + x_1(t)} - a_2(t)x_2(t)), \end{aligned} \tag{1.2}$$

where $c_1(t)$ denotes the rate of toxic inhibition for the species x_1 released by the second species. On the other hand, through experimental data of a recent experimental study on two phytoplankton species, namely *C. polylepis* and *H. triquetra*, Solé et al. [7] found that the allelopathic interaction using $rx_1(t)^2 x_2{}^2(t)$ is more suitable.

$\frac{b_1(t)x_2(t)}{1 + x_2(t)}$ and $\frac{b_2(t)x_1(t)}{1 + x_1(t)}$ reflect the saturation of interspecific competition rates with increasing population density, providing a more realistic representation of ecological interactions. But they fail to capture the threshold-driven competitive behavior observed in many phytoplankton species. In such scenarios, when population densities of competing species are low, space and resources are relatively abundant and interspecific competition is negligible. As the density increases, the competition between phytoplankton species increases slowly. However, once a critical threshold density is surpassed, competitive pressure escalates rapidly toward its maximum, driven by the combined stresses of intra- and interspecific interactions. This S-shaped or switch-like response is not fully captured by standard saturation inter-inhibition terms.

Furthermore, in the real world, ecosystems are continuously influenced by unpredictable environmental fluctuations, such as variations in nutrient inputs, changes in light, and predation pressure. These disturbances can result in some changes of the biological parameters such as survival rates. To describe these ecosystems more accurately, scholars added feedback controls into ecosystems. Extensive studies have been conducted on dynamical systems incorporating feedback controls [3,11–15].

It is worth noting that the analysis process of complex nonlinear dynamic systems proposed in this paper usually relies on the comparison theorem of differential equations and Lyapunov functions. Several authors have resorted to other analytical techniques in addition to these methods to analyze the problems. These include a three-layer FDM for the Neumann initial-boundary value problem of 2D

Kuramoto-Tsuzuki complex equation with strong nonlinear effects [16], and the compact difference method for the 2D Kuramoto-Tsuzuki complex equations with Neumann boundary characterized by strong nonlinear effects [17].

Motivated by the above work, in this paper, we consider the following non-autonomous allelopathic phytoplankton system with threshold inter-inhibition terms and feedback controls:

$$\begin{aligned}
x_1'(t) &= x_1(t)(r_1(t) - a_1(t)x_1(t) - \frac{b_1(t)x_2{}^2(t)}{\alpha_2(t) + x_2{}^2(t)} - \gamma(t)x_1(t)x_2^2(t) - c_1(t)u_1(t)),\\
x_2'(t) &= x_2(t)(r_2(t) - \frac{b_2(t)x_1{}^2(t)}{\alpha_1(t) + x_1{}^2(t)} - a_2(t)x_2(t) - c_2(t)u_2(t)),\\
u_1'(t) &= -e_1(t)u_1(t) + d_1(t)x_1(t),\\
u_2'(t) &= -e_2(t)u_2(t) + d_2(t)x_2(t),
\end{aligned} \tag{1.3}$$

where the parameters $r_i(t), a_i(t), b_i(t), \alpha_i(t), \gamma(t), c_i(t), d_i(t), e_i(t), i = 1, 2$, in system (1.3) are positive, continuous, and bounded on $\mathbb{R}^+ = [0, +\infty)$. In this paper, the saturation inter-inhibition terms $\frac{b_1(t)x_2(t)}{1 + x_2(t)}$ and $\frac{b_2(t)x_1(t)}{1 + x_1(t)}$ are replaced by threshold inter-inhibition terms $\frac{b_1(t)x_2{}^2(t)}{\alpha_2(t) + x_2{}^2(t)}$ and $\frac{b_2(t)x_1{}^2(t)}{\alpha_1(t) + x_1{}^2(t)}$. This function provides a more realistic description of the ecological scenario where competition is weak below a threshold density $\sqrt{\alpha_j(t)}$ and intensifies rapidly near and above this threshold.

The primary objectives of this study are to theoretically investigate how key ecological parameters—including the interspecific competition strengths, the allelopathic toxin production rate, and the intensities of the feedback controls—jointly determine the dynamic behaviors of the two competing phytoplankton populations. We focus on deriving sufficient conditions for permanence, extinction, and global attractivity of the system. These results extend the work of Xie et al. [5] by incorporating threshold inter-inhibition terms and feedback controls, which were not considered in their model.

The organization of this paper is as follows. In Section 2, we will introduce several useful lemmas and prove the permanence of system (1.3). In Section 3, we will discuss the extinction of one species. In Section 4, global attractivity of equilibrium points is studied. Four examples together with their numeric simulations are presented in Section 5 to show the feasibility of the main results. We end this paper with a brief discussion.

2. Permanence

Given a continuous and bounded function $f(t)$, let f^u and f^l denote $\sup_{t\in R} f(t)$ and $\inf_{t\in R} f(t)$, respectively. From the point of view of biology, we assume that $x_i(0) > 0, u_i(0) > 0, i = 1, 2$. Let $\mathbf{Y}(t) = (x_1(t), x_2(t), u_1(t), u_2(t))^{\mathrm{T}}$ and rewrite system (1.3) in vector form, $\mathbf{Y}'(t) = \mathbf{F}(t, \mathbf{Y}(t))$, where $\mathbf{F} = (F_1, F_2, F_3, F_4)^{\mathrm{T}}$ is defined by the right-hand sides of (1.3). Obviously, F_i is continuously differentiable and satisfies the local Lipschitz condition. According to the *Picard–Lindelöf* theorem, for any initial value $X(0) = (x_1(0), x_2(0), u_1(0), u_2(0))$ in $\mathbb{R}_+^4$, there exists a unique solution.

Lemma 2.1. *If $a > 0, b > 0$, and $\dot{x} \geq b - ax$, when $t \geq 0$ and $x(0) > 0$, we have*

$$\liminf_{t\to+\infty} x(t) \geq \frac{b}{a}.$$

If $a > 0, b > 0$, and $\dot{x} \le b - ax$, when $t \ge 0$ and $x(0) > 0$, we have

$$\limsup_{t\to+\infty} x(t) \le \frac{b}{a}.$$

Lemma 2.2. *If $a > 0, b > 0$, and $\dot{x} \ge x(b - ax)$, when $t \ge 0$ and $x(0) > 0$, we have*

$$\liminf_{t\to+\infty} x(t) \ge \frac{b}{a}.$$

If $a > 0, b > 0$, and $\dot{x} \le x(b - ax)$, when $t \ge 0$ and $x(0) > 0$, we have

$$\limsup_{t\to+\infty} x(t) \le \frac{b}{a}.$$

Lemma 2.3. *Every positive solution $(x_1(t), x_2(t), u_1(t), u_2(t))^T$ of system (1.3) is always positive and bounded:*

$$(x_1(t), x_2(t), u_1(t), u_2(t))^T \in R_+^4,$$

$$\limsup_{t\to+\infty} x_i(t) \le \frac{r_i^u}{a_i^l} \overset{\text{def}}{=} M_i, \quad \limsup_{t\to+\infty} u_i(t) \le \frac{d_i^u r_i^u}{e_i^l a_i^l} \overset{\text{def}}{=} N_i, \quad i = 1, 2. \tag{2.1}$$

Proof. For $x_1(t)$ and $x_2(t)$, consider the equation for $x_1(t)$, which can be written as

$$\frac{dx_1}{dt} = x_1\Phi_1(t, x_1, x_2, u_1), \quad \text{where} \quad \Phi_1 = r_1(t) - a_1(t)x_1 - \frac{b_1(t)x_2^2}{\alpha_2(t) + x_2^2} - \gamma(t)x_1x_2^2 - c_1(t)u_1.$$

This is equivalent to

$$\frac{d}{dt}\ln x_1(t) = \Phi_1(t, x_1(t), x_2(t), u_1(t)).$$

Integrating both sides from 0 to t yields

$$\ln\frac{x_1(t)}{x_1(0)} = \int_0^t \Phi_1(s, x_1(s), x_2(s), u_1(s))\,ds.$$

Hence,

$$x_1(t) = x_1(0)\exp\left(\int_0^t \Phi_1(s, x_1(s), x_2(s), u_1(s))\,ds\right).$$

Based on biological considerations, the initial condition of system (1.3) satisfies $x_1(0) > 0$ and the exponential function is always positive, so we have $x_1(t) > 0$.
Similarly, for $x_2(t)$,

$$x_2(t) = x_2(0)\exp\left(\int_0^t \Phi_2(s, x_1(s), x_2(s), u_2(s))\,ds\right) > 0,$$

where $\Phi_2 = r_2(t) - \dfrac{b_2(t)x_1^2}{\alpha_1(t) + x_1^2} - a_2(t)x_2 - c_2(t)u_2$.
For $u_1(t)$ and $u_2(t)$, the equation for $u_1(t)$ is a first-order linear non-homogeneous equation:

$$\frac{du_1}{dt} = -e_1(t)u_1 + d_1(t)x_1(t).$$

Its solution can be expressed using the variation of constants formula:

$$u_1(t) = \exp\left(-\int_0^t e_1(s)\,ds\right)\left[u_1(0) + \int_0^t d_1(\tau)x_1(\tau)\exp\left(\int_0^\tau e_1(s)\,ds\right)d\tau\right].$$

Since $u_1(0) > 0$, $e_1(t) > 0$, $d_1(t) > 0$, and $x_1(\tau) > 0$ (as shown above), the first term and the integrand in the second term are strictly positive. Therefore, $u_1(t) > 0$. The proof for $u_2(t)$ is identical, yielding $u_2(t) > 0$.

So all solutions of system (1.3) with the initial condition are positive. From the first and second equation of system (1.3), it follows that

$$x_i'(t) \le x_i(t)\Big(r_i(t) - a_i(t)x_i(t)\Big) \le x_i(t)\Big(r_i^u - a_i^l x_i(t)\Big), \quad i = 1, 2. \tag{2.2}$$

By applying Lemma 2.2 to differential inequality (2.2), we have

$$\limsup_{t\to+\infty} x_i(t) \le \frac{r_i^u}{a_i^l} \overset{\text{def}}{=} M_i, \quad i = 1, 2. \tag{2.3}$$

For any small positive constant $\varepsilon > 0$, from (2.3), it follows that there exists a $T_1 > 0$, such that for $t > T_1$,

$$x_i(t) \le M_i + \varepsilon. \tag{2.4}$$

From the third and fourth equation of system (1.3), it follows that

$$u_i'(t) = -e_i^l u_i(t) + d_i^u(M_i + \varepsilon). \tag{2.5}$$

By applying Lemma 2.1 to differential inequality (2.5), we have

$$\limsup_{t\to+\infty} u_i(t) \le \frac{d_i^u}{e_i^l}(M_i + \varepsilon), \quad i = 1, 2.$$

Setting $\varepsilon \to 0$ in the above inequalities leads to

$$\limsup_{t\to+\infty} u_i(t) \le \frac{d_i^u}{e_i^l}M_i = \frac{d_i^u r_i^u}{e_i^l a_i^l} \overset{\text{def}}{=} N_i, \quad i = 1, 2.$$

Theorem 2.4. *Assume that*

$$b_1^u < \frac{r_1^l \alpha_2^l}{M_2^2}, \quad b_2^u < \frac{r_2^l \alpha_1^l}{M_1^2} \tag{2.6}$$

hold, and then, for any positive solution $\big(x_1(t), x_2(t), u_1(t), u_2(t)\big)^T$ *of system (1.3), we have*

$$\begin{aligned} m_i &\le \liminf_{t\to+\infty} x_i(t) \le \limsup_{t\to+\infty} x_i(t) \le M_i, \\ n_i &\le \liminf_{t\to+\infty} u_i(t) \le \limsup_{t\to+\infty} u_i(t) \le N_i, \end{aligned} \quad i = 1, 2,$$

i.e., system (1.3) is permanent.

Proof. For any small positive constant $\varepsilon > 0$, from (1.3), without loss of generality, we may choose ε small enough such that

$$b_1^u < \frac{r_1^l \alpha_2^l}{\left(\frac{r_2^u}{a_2^l} + \varepsilon\right)^2} = \frac{r_1^l \alpha_2^l}{(M_2 + \varepsilon)^2}, \quad b_2^u < \frac{r_2^l \alpha_1^l}{\left(\frac{r_1^u}{a_1^l} + \varepsilon\right)^2} = \frac{r_2^l \alpha_1^l}{(M_1 + \varepsilon)^2}. \tag{2.7}$$

For $\varepsilon > 0$, from Lemma (2.3), it follows that there exists $T_2 > 0$ such that for $t > T_2$,

$$x_i(t) \leq M_i + \varepsilon, \quad u_i(t) \leq N_i + \varepsilon, \ i = 1,\ 2. \tag{2.8}$$

From the first equation of system (1.3), it follows that

$$\begin{aligned}
x_1'(t) &= x_1(t)\big(r_1(t) - a_1(t)x_1(t) - \frac{b_1(t){x_2}^2(t)}{\alpha_2(t) + {x_2}^2(t)} - \gamma(t)x_1(t)x_2^2(t) - c_1(t)u_1(t)\big) \\
&\geq x_1(t)\big(r_1(t) - a_1(t)x_1(t) - \frac{b_1(t)}{\alpha_2(t)}{x_2}^2(t) - \gamma(t)x_1(t)x_2^2(t) - c_1(t)u_1(t)\big) \\
&\geq x_1(t)(r_1^l - a_1^u(M_1 + \varepsilon) - \frac{b_1^u}{\alpha_2^l}(M_2 + \varepsilon)^2 - \gamma^u(M_1 + \varepsilon)(M_2 + \varepsilon)^2 - c_1^u(N_1 + \varepsilon)) \\
&\overset{\text{def}}{=} I_1^\varepsilon x_1(t).
\end{aligned} \tag{2.9}$$

Integrating the above differential inequality from s to t, we have

$$x_1(s) \leq x_1(t) \exp\big[- I_1^\varepsilon(t - s)\big]. \tag{2.10}$$

By the third equation of system (1.3), it follows that

$${u_1}'(t) \leq -{e_1}^l u_1(t) + {d_1}^u x_1(t).$$

According to Lemma 2.2 of [13] and inequality (2.10), integrating the above differential inequality from $t_1 (t_1 > T_2)$ to t, we have

$$\begin{aligned}
u_1(t) \ &\leq \ u_1(t_1) \exp\big[- e_1^l(t - t_1)\big] + \int_{t_1}^t {d_1}^u x_1(s) \exp\big[e_1^l(s - t)\big]ds \\
&\leq \ u_1(t_1) \exp\big[- e_1^l(t - t_1)\big] + \int_{t_1}^t d_1^u x_1(t) \exp\big[- I_1^\varepsilon(t - s)\big]ds \\
&= \ u_1(t_1) \exp\big[- e_1^l(t - t_1)\big] + d_1^u x_1(t)\frac{1}{I_1^\varepsilon}\Big(1 - \exp\big\{ - {I_1}^\varepsilon(t - t_1)\big\}\Big) \\
&\leq \ (N_1 + \varepsilon) \exp\big[- e_1^l(t - t_1)\big] + d_1^u x_1(t)\frac{1}{I_1^\varepsilon}\Big(1 - \exp\big\{ - {I_1}^\varepsilon(t - t_1)\big\}\Big).
\end{aligned} \tag{2.11}$$

There exists a T_1^* such that $t - t_1 = {T_1}' \geq {T_1}^*$, and we have

$${c_1}^u(N_1 + \varepsilon) \exp(-e_1^l {T_1}^*) < \frac{1}{2}(r_1^l - \frac{b_1^u}{\alpha_2^l}(M_2 + \varepsilon)^2), \tag{2.12}$$

$$\begin{aligned}
u_1(t) \ &\leq \ (N_1 + \varepsilon) \exp(-e_1^1 {T_1}^*) + d_1^u x_1(t)\frac{1}{I_1^\varepsilon}(1 - \exp(-I_1^\varepsilon {T_1}^*)) \\
&= \ (N_1 + \varepsilon) \exp(-e_1^1 {T_1}^*) + D_1^\varepsilon x_1(t),
\end{aligned} \tag{2.13}$$

where $D_1^\varepsilon = d_1^u \frac{1}{I_1^\varepsilon}(1 - \exp(-I_1^\varepsilon {T_1}^*))$.

By the first equation of system (1.3), we have

$$\begin{aligned} x_1'(t) \quad &\geq \quad x_1(t)\Big[r_1^l - a_1^u x_1(t) - \frac{b_1^u}{\alpha_2^l}(M_2+\varepsilon)^2 - \gamma^u x_1(t)(M_2+\varepsilon)^2 \\ &\qquad - c_1^u(N_1+\varepsilon)\exp(-e_1{}^l T_1{}^*) - c_1^u D_1^\varepsilon x_1(t)\Big] \\ &= \quad x_1(t)\Big[r_1^l - \frac{b_1^u}{\alpha_2^l}(M_2+\varepsilon)^2 - c_1^u(N_1+\varepsilon)\exp(-e_1{}^l T_1{}^*) \\ &\qquad - (a_1^u + \gamma^u(M_2+\varepsilon)^2 + c_1^u D_1^\varepsilon)x_1(t)\Big]. \end{aligned} \tag{2.14}$$

By applying Lemma 2.2 of [13] to the above differential inequality, it follows that

$$\liminf_{t\to+\infty} x_1(t) \geq \frac{r_1^l - \dfrac{b_1^u}{\alpha_2^l}(M_2+\varepsilon)^2 - c_1^u(N_1+\varepsilon)\exp(-e_1{}^l T_1{}^*)}{a_1^u + \gamma^u(M_2+\varepsilon)^2 + c_1^u D_1^\varepsilon}.$$

Setting $\varepsilon \to 0$ in this inequality leads to

$$\liminf_{t\to+\infty} x_1(t) \geq \frac{r_1^l - \dfrac{b_1^u}{\alpha_2^l}M_2^2 - c_1^u N_1 \exp(-e_1{}^l T_1{}^*)}{a_1^u + \gamma^u M_2^2 + c_1^u D_1^\varepsilon} \overset{\text{def}}{=} m_1, \tag{2.15}$$

where

$$D_1^\varepsilon = d_1^u \frac{1}{I_1^\varepsilon}(1 - \exp(-I_1^\varepsilon T_1{}^*)),$$

$$I_1^\varepsilon = r_1^l - a_1^u M_1 - \frac{b_1^u}{\alpha_2^l}M_2^2 - \gamma^u M_1 M_2^2 - c_1^u N_1.$$

From the second equation of system (1.3), it follows that

$$x_2'(t) \geq x_2(t)\Big(r_2^l - a_2^u(M_2+\varepsilon) - \frac{b_2^u}{\alpha_1^l}(M_1+\varepsilon)^2 - c_2^u(N_2+\varepsilon)\Big) \overset{\text{def}}{=} I_2^\varepsilon x_2(t). \tag{2.16}$$

Integrating this inequality from s to t, it follows that

$$x_2(s) \leq x_2(t)\exp\Big\{-I_2^\varepsilon(t-s)\Big\}. \tag{2.17}$$

By the fourth equation of system (1.3), since for all t, it holds that $e_2(t) \geq e_2^l > 0$ and $0 < d_2(t) \leq d_2^u$, and given $x_2(t) > 0$, we obtain

$$u_2{}'(t) \leq -e_2{}^l u_2(t) + d_2{}^u x_2(t). \tag{2.18}$$

Integrating this inequality from t_2 to t, it follows that

$$\begin{aligned} u_2(t) \quad &\leq \quad u_2(t_2)\exp\Big[-e_2^l(t-t_2)\Big] + \int_{t_2}^t d_2{}^u x_2(s)\exp\Big[e_2^l(s-t)\Big]ds, \\ &\leq \quad u_2(t_2)\exp\Big[-e_2^l(t-t_2)\Big] + d_2^u x_2(t)\frac{1}{I_2^\varepsilon}(1 - \exp\{-I_2{}^\varepsilon(t-t_2)\}). \end{aligned} \tag{2.19}$$

From Lemma 2.3, we have

$$u_2(t_2) \leq N_2 + \varepsilon, \quad t_2 > T_2.$$

There exists a T_2^* such that $t - t_2 = T_2{}' \geq T_2{}^*$, and we have

$$c_2{}^u(N_2 + \varepsilon)\exp(-e_2^l T_2{}^*) < \frac{1}{2}(r_2^l - \frac{b_2^u}{\alpha_1^l}(M_1 + \varepsilon)^2),$$

$$u_2(t) \leq (N_2 + \varepsilon)\exp(-e_2^1 T_2{}^*) + D_2^\varepsilon x_2(t), \tag{2.20}$$

where $D_2^\varepsilon = d_2^u \frac{1}{I_2^\varepsilon}(1 - \exp(-I_2^\varepsilon T_2{}^*))$.
From the second equation of system (1.3), we have

$$\begin{aligned} x_2'(t) \quad \geq \quad & x_2(t)\Big[r_2^l - \frac{b_2^u}{\alpha_1^l}(M_1 + \varepsilon)^2 - c_2^u(N_2 + \varepsilon)\exp(-e_2{}^l T_2{}^*) \\ & -(a_2^u + c_2^u D_2^\varepsilon)x_2(t)\Big]. \end{aligned}$$

Similarly to the analysis of (2.14), we can obtain

$$\liminf_{t\to+\infty} x_2(t) \geq \frac{r_2^l - \frac{b_2^u}{\alpha_1^l}M_1^2 - c_2^u N_2 \exp(-e_2{}^l T_2{}^*)}{a_2^u + c_2^u D_2^\varepsilon} \overset{\text{def}}{=} m_2, \tag{2.21}$$

where

$$D_2^\varepsilon = d_2^u \frac{1}{I_2^\varepsilon}(1 - \exp(-I_2 T_2{}^*)),$$

$$I_2^\varepsilon = r_2^l - a_2^u M_2 - \frac{b_2^u}{\alpha_1^l}M_1^2 - c_2^u N_2.$$

For any small positive constant $\varepsilon < \frac{1}{2}min\{m_1, m_2\}$, from (2.15) and (2.21), it follows that there exists a $T_3 > T_i',\ \ i = 1, 2$, such that for $t > T_3$, we have

$$x_i(t) \geq m_i - \varepsilon, \quad i = 1, 2. \tag{2.22}$$

From the third and fourth equation of system (1.3), it follows that

$$u_i'(t) \geq -e_i^u u_i(t) + d_i^l(m_i - \varepsilon), \quad i = 1, 2. \tag{2.23}$$

From Lemma 2.1, we obtain

$$\liminf_{t\to+\infty} u_i(t) \geq \frac{d_i^l(m_i - \varepsilon)}{e_i^u}. \tag{2.24}$$

Setting $\varepsilon \to 0$ in this inequality leads to

$$\liminf_{t\to+\infty} u_i(t) \geq \frac{d_i^l m_i}{e_i^u} \overset{\text{def}}{=} n_i, \quad i = 1, 2. \tag{2.25}$$

3. Extinction

Theorem 3.1. *Assume that*

$$b_1^u < \frac{r_1^l}{r_2^u}\frac{(a_2^l e_2^u + c_2^l d_2^l)}{e_2^u M_2}, \quad b_2^l > (\alpha_1^u + M_1^2)\frac{r_2^u}{r_1^l}\frac{a_1^u e_1^l + c_1^u d_1^u}{e_1^l m_1}, \tag{H_1}$$

and

$$\gamma^u < \min \frac{1}{M_1 M_2^2}\left\{ r_1^l - (\alpha_1^u + M_1^2) r_2^u \frac{a_1^u e_1^l + c_1^u d_1^u}{b_2^l e_1^l m_1}, \quad r_1^l - r_2^u \frac{b_1^u e_2^u M_2}{a_2^l e_2^u + c_2^l d_2^l} \right\} \tag{H_2}$$

hold. Then the species x_1 is permanent and the species x_2 will be driven to extinction, that is, for any positive solution $(x_1(t), x_2(t), u_1(t), u_2(t))^T$ of system (1.3),

$$\lim_{t\to+\infty} x_2(t) = 0, \quad \lim_{t\to+\infty} u_2(t) = 0.$$

Proof. Condition (H_1) is equivalent to

$$\frac{c_1^u}{e_1^l} < \frac{r_1^l}{r_2^u}\frac{b_2^l m_1}{(\alpha_1^u + M_1^2) d_1^u} - \frac{a_1^u}{d_1^u}, \quad \frac{c_2^l}{e_2^u} > \frac{r_2^u}{r_1^l}\frac{b_1^u M_2}{d_2^l} - \frac{a_2^l}{d_2^l}. \tag{3.1}$$

From (H_2) and (3.1), we can select positive constants $\alpha, \beta, \delta_1, \delta_2$ and small-enough positive ε such that the following inequalities hold:

$$\frac{r_1^l}{r_2^u} > \frac{\beta}{\alpha}, \quad \frac{c_1^u}{e_1^l} < \frac{\delta_1}{\alpha} < \frac{\beta b_2^l(m_1+\varepsilon) - (\alpha_1^u + (M_1+\varepsilon)^2)\alpha a_1^u}{(\alpha_1^u + (M_1+\varepsilon)^2)\alpha d_1^u} < \frac{r_1^l b_2^l (m_1+\varepsilon)}{(\alpha_1^u + (M_1+\varepsilon)^2) r_2^u d_1^u} - \frac{a_1^u}{d_1^u},$$

$$\frac{c_2^l}{e_2^u} > \frac{\delta_2}{\beta} > \frac{\alpha b_1^u (M_2+\varepsilon) - \beta a_2^l}{\beta d_2^l} > \frac{r_2^u}{r_1^l}\frac{b_1^u(M_2+\varepsilon)}{d_2^l} - \frac{a_2^l}{d_2^l},$$

$$\frac{(\alpha_1^u + (M_1+\varepsilon)^2)(a_1^u e_1^l + c_1^u d_1^u)}{b_2^l e_1^l (m_1+\varepsilon)} < \frac{\beta}{\alpha} < \frac{r_1^l - \gamma^u (M_1+\varepsilon)(M_2+\varepsilon)^2}{r_2^u},$$

$$\frac{b_1^u e_2^u (M_2+\varepsilon)}{a_2^l e_2^u + c_2^l d_2^l} < \frac{\beta}{\alpha} < \frac{r_1^l - \gamma^u (M_1+\varepsilon)(M_2+\varepsilon)^2}{r_2^u}.$$

That is,

$$\begin{aligned}
&\alpha c_1^u - \delta_1 e_1^l < 0, \;\; \delta_2 e_2^u - \beta c_2^l < 0, \\
&\alpha a_1^u - \frac{\beta b_2^l (m_1+\varepsilon)}{\alpha_1^u + (M_1+\varepsilon)^2} + \delta_1 d_1^u < 0, \;\; \alpha b_1^u (M_2+\varepsilon) - \beta a_2^l - \delta_2 d_2^l < 0, \\
&-\alpha r_1^l + \beta r_2^u + \alpha\gamma^u (M_1+\varepsilon)(M_2+\varepsilon)^2 = -\xi_1 < 0.
\end{aligned} \tag{3.2}$$

Let $(x_1(t), x_2(t), u_1(t), u_2(t))^T$ be a positive solution of system (1.3). For the above ε, from Lemma 2.3, there exists a large-enough T_4, such that

$$x_i(t) < M_i + \varepsilon, \quad u_i(t) < N_i + \varepsilon, \quad t \ge T_4, \quad i = 1, 2. \tag{3.3}$$

Let

$$V_1(t) = x_1^{-\alpha}(t) x_2^{\beta}(t) \exp\Big(\delta_1 u_1(t) - \delta_2 u_2(t)\Big). \tag{3.4}$$

Calculating the derivative of $V_1(t)$, from (3.3), for $t \geq T_4$, we can otain

$$\begin{aligned}
D^+V_1(t) &= V_1(t)\Big[-\alpha\Big(r_1(t) - a_1(t)x_1(t) - \frac{b_1(t){x_2}^2(t)}{\alpha_2(t) + {x_2}^2(t)} - \gamma(t)x_1(t)x_2^2(t) - c_1(t)u_1(t)\Big) \\
&\quad + \beta\Big(r_2(t) - \frac{b_2(t){x_1}^2(t)}{\alpha_1(t) + {x_1}^2(t)} - a_2(t)x_2(t) - c_2(t)u_2(t)\Big) \\
&\quad + \delta_1\Big(-e_1(t)u_1(t) + d_1(t)x_1(t)\Big) - \delta_2\Big(-e_2(t)u_2(t) + d_2(t)x_2(t)\Big)\Big] \\
&= V_1(t)\Big[(-\alpha r_1(t) + \beta r_2(t)) + \Big(\alpha a_1(t) - \frac{\beta b_2(t)x_1(t)}{\alpha_1(t) + {x_1}^2(t)} + \delta_1 d_1(t)\Big)x_1(t) \\
&\quad + \Big(\frac{\alpha b_1(t)x_2(t)}{\alpha_2(t) + x_2^2(t)} - \beta a_2(t) - \delta_2 d_2(t)\Big)x_2(t) + (\alpha c_1(t) - \delta_1 e_1(t))u_1(t) \\
&\quad + (-\beta c_2(t) + \delta_2 e_2(t))u_2(t) + \alpha\gamma(t)x_1(t)x_2^2(t)\Big] \\
&\leq V_1(t)\Big[(-\alpha r_1^l + \beta r_2^u) + (\alpha a_1^u - \frac{\beta b_2^l(m_1 + \varepsilon)}{\alpha_1^u + (M_1 + \varepsilon)^2} + \delta_1 d_1^u)x_1(t) \\
&\quad + (\alpha b_1^u(M_2 + \varepsilon) - \beta a_2^l - \delta_2 d_2^l)x_2(t) + (\alpha c_1^u - \delta_1 e_1^l)u_1(t) \\
&\quad + (-\beta c_2^l + \delta_2 e_2^u)u_2(t) + \alpha\gamma^u(M_1 + \varepsilon)(M_1 + \varepsilon)^2\Big].
\end{aligned}$$

From inequalities (3.2), we obtain

$$V_1'(t) \leq -\xi_1 V_1(t). \tag{3.5}$$

Integrating the above inequality from T_4 to $t(\geq T_4)$, we have

$$V_1(t) \leq V_1(T_4)\exp\Big(-\xi_1(t - T_4)\Big). \tag{3.6}$$

It follows from (3.3) that

$$\begin{aligned}
V_1(T_1) &= x_1^{-\alpha}(T_4)x_2^{\beta}(T_4)\exp\Big(\delta_1 u_1(T_4) - \delta_2 u_2(T_4)\Big) < +\infty, \\
V_1(t) &= x_1^{-\alpha}(t)x_2^{\beta}(t)\exp\Big(\delta_1 u_1(t) - \delta_2 u_2(t)\Big) \\
&> (M_1 + \varepsilon)^{-\alpha}x_2^{\beta}(t)\exp\Big(-\delta_2(N_2 + \varepsilon)\Big).
\end{aligned} \tag{3.7}$$

Combining inequalities (3.6) and (3.7), we have

$$x_2(t) \leq C\exp\Big(-\frac{\xi_1}{\beta}(t - T_4)\Big),$$

where

$$C = (M_1 + \varepsilon)^{\frac{\alpha}{\beta}}\exp\Big(\frac{\delta_2}{\beta}(N_2 + \varepsilon)\Big)V_1(T_4)^{\frac{1}{\beta}}.$$

Hence we obtain that

$$\lim_{t\to+\infty} x_2(t) = 0. \tag{3.8}$$

So, $\forall\varepsilon > 0$, $\exists T_5 > T_4$, such that $x_2(t) < \varepsilon$ for all $t > T_5$. From the fourth equation of system (1.6), we have

$$u_2'(t) \leq -e_2^l u_2(t) + d_2^u\varepsilon. \tag{3.9}$$

From Lemma 2.1, we obtain

$$\lim_{t\to+\infty} u_2(t) \le \limsup_{t\to+\infty} u_2(t) \le \frac{d_2^u\varepsilon}{e_2^l}.$$

Setting $\varepsilon \to 0$ leads to

$$\lim_{t\to+\infty} u_2(t) \le \limsup_{t\to+\infty} u_2(t) \le\ 0,$$

thus

$$\lim_{t\to+\infty} u_2(t) = 0. \tag{3.10}$$

By using the analysis technique of [13], one could show that under the conditions of Theorem 3.1, the first species of system (1.3) is permanent. We omit the detail here. This ends the proof of Theorem 3.1.

Theorem 3.2. *Assume that*

$$b_2^u < \frac{r_2^l}{r_1^u}\frac{a_1^l e_1^u + c_1^l d_1^l}{e_1^u M_1}, \quad b_1^l > \frac{r_1^u}{r_2^l}\frac{\alpha_2^u + M_2^2}{m_2}\frac{a_2^u e_2^l + c_2^u d_2^u}{e_2^l} \tag{H_3}$$

hold, and then species x_1 will be driven to extinction and species x_2 is permanent, that is, for any positve solution $(x_1(t), x_2(t), u_1(t), u_2(t))^T$ of system (1.3),

$$\lim_{t\to+\infty} x_1(t) = 0, \quad \lim_{t\to+\infty} u_1(t) = 0.$$

Proof. Condition (H_3) is equivalent to

$$\frac{c_1^l}{e_1^u} > \frac{r_1^u}{r_2^l}\frac{b_2^u M_1}{d_1^l} - \frac{a_1^l}{d_1^l}, \qquad \frac{c_2^u}{e_2^l} < \frac{r_2^l b_1^l m_2}{(\alpha_2^u + M_2^2) r_1^u d_2^u} - \frac{a_2^u}{d_2^u}. \tag{3.11}$$

From (3.11), we could choose positive constants α,β , δ_1, δ_2 and small-enough positive ε such that

$$\frac{r_1^u}{r_2^l} < \frac{\beta}{\alpha}, \quad \frac{c_1^l}{e_1^u} > \frac{\delta_1}{\alpha} > \frac{\beta b_2^u(M_1+\varepsilon) - \alpha a_1^l}{\alpha d_1^l} > \frac{r_1^u}{r_2^l}\frac{b_2^u(M_1+\varepsilon)}{d_1^l} - \frac{a_1^l}{d_1^l},$$

$$\frac{c_2^u}{e_2^l} < \frac{\delta_2}{\beta} < \frac{\alpha b_1^l(m_2+\varepsilon) - (\alpha_2^u + (M_2+\varepsilon)^2)\beta a_2^u}{(\alpha_2^u + (M_2+\varepsilon)^2)\beta d_2^u} < \frac{r_2^l b_1^l(m_2+\varepsilon)}{(\alpha_2^u + (M_2+\varepsilon)^2) r_1^u d_2^u} - \frac{a_2^u}{d_2^u}.$$

That is,

$$\begin{aligned} &\alpha r_1^u - \beta r_2^l = -\xi_2 < 0, \ \ \delta_1 e_1^u - \alpha c_1^l < 0, \ \ \beta c_2^u - \delta_2 e_2^l < 0, \\ &\beta b_2^u(M_1+\varepsilon) - \alpha a_1^l - \delta_1 d_1^l < 0, \ \ \delta_2 d_2^u + \beta a_2^u - \frac{\alpha b_1^l(m_2+\varepsilon)}{\alpha_2^u + (M_2+\varepsilon)^2} < 0. \end{aligned} \tag{3.12}$$

Let $(x_1(t), x_2(t), u_1(t), u_2(t))^T$ be a positive solution of system (1.3). For the above ε, from Lemma 2.1, there exists a large-enough T_6, such that

$$x_i(t) < M_i + \varepsilon, \quad u_i(t) < N_i + \varepsilon, \quad t \ge T_6, \quad i = 1, 2. \tag{3.13}$$

Let

$$V_2(t) = x_1^{\alpha}(t) x_2^{-\beta}(t) \exp\Big(\delta_2 u_2(t) - \delta_1 u_1(t)\Big). \tag{3.14}$$

Calculating the derivative of $V_2(t)$, we otain

$$\begin{aligned} D^+V_2(t) &= V_2(t)\Big[(\alpha r_1(t)-\beta r_2(t))+\Big(\frac{\beta b_2(t)x_1(t)}{\alpha_1(t)+x_1^2(t)}-\alpha a_1(t)-\delta_1 d_1(t)\Big)x_1(t)\\ &\quad +\Big(\beta a_2(t)+\delta_2 d_2(t)-\frac{\alpha b_1(t)x_2(t)}{\alpha_2(t)+x_2^2(t)}\Big)x_2(t)+(\delta_1 e_1(t)-\alpha c_1(t))u_1(t)\\ &\quad +(\beta c_2(t)-\delta_2 e_2(t))u_2(t)\Big]\\ &\le V_2(t)\Big[(\alpha r_1^u-\beta r_2^l)+(\beta b_2^u(M_2+\varepsilon)-\alpha a_1^l-\delta_1 d_1^l)x_1(t)\\ &\quad +\Big(\delta_2 d_2^u+\beta a_2^u-\frac{\alpha b_1^l(m_2+\varepsilon)}{\alpha_2^u+(M_2+\varepsilon)^2)}\Big)x_2(t)+(\delta_1 e_1^u-\alpha c_1^l)u_1(t)+(\beta c_2^u-\delta_2 e_2^l)u_2(t)\Big],\\ &\le -\xi_2 V_2(t). \end{aligned}$$

Integrating the above inequalities from T_6 to t $(\geq T_6)$, we obtain

$$V_2(t)\le V_2(T_6)\exp\Big(-\xi_2(t-T_6)\Big). \tag{3.15}$$

Similarly to the analysis of (3.7)–(3.10), we have

$$\lim_{t\to+\infty} x_1(t)=0,\ \lim_{t\to+\infty} u_1(t)=0.$$

By using the analysis technique of [13], we can also demonstrate that under the conditions of Theorem 3.2, the second species of system (1.3) is permanent. This ends the proof of Theorem 3.2.

4. Global attractivity

Theorem 4.1 *In addition to (2.6), further assume that*

$$\begin{gathered} b_2^u<\frac{a_1^l-d_1^u}{2(M_1^3+M_1)},\quad b_1^u<\frac{a_2^l-d_2^u}{2(M_2^3+M_2)},\\ \gamma^u<\min\left\{\frac{a_1^l-2(M_1^3+M_1)b_2^u-d_1^u}{M_2^2},\quad \frac{a_2^l-2(M_2^3+M_2)b_1^u-d_2^u}{2M_1M_2}\right\},\\ c_1^u<e_1^l,\quad c_2^u<e_2^l \end{gathered} \tag{H_4}$$

hold. Then, for any positive solution $\big(x_1(t),x_2(t),u_1(t),u_2(t)\big)^T$ *of system (1.3), we have*

$$\lim_{t\to+\infty}|x_i(t)-x_i^*(t)|=0,\qquad \lim_{t\to+\infty}|u_i(t)-u_i^*(t)|=0,\quad i=1,2,$$

where $\big(x_1^*(t),x_2^*(t),u_1^*(t),u_2^*(t)\big)^T$ *is the unique positive equilibrium of system (1.3), i.e., system (1.3) is globally attractive.*

Proof. Condition (H_4) implies that there exists a small-enough positive constant ε, such that

$$a_1^l-2((M_1+\varepsilon)^3+M_1+\varepsilon)b_2^u-d_1^u-\gamma^u(M_2+\varepsilon)^2>\varepsilon,$$

$$\begin{aligned}&a_2^l - 2((M_2+\varepsilon)^3 + M_2+\varepsilon)b_1^u - d_2^u - 2\gamma^u(M_1+\varepsilon)(M_2+\varepsilon) > \varepsilon,\\ &e_1^l - c_1^u > \varepsilon, \quad e_2^l - c_2^u > \varepsilon.\end{aligned} \tag{4.1}$$

For two arbitrary positive solutions $(x_1(t), x_2(t), u_1(t), u_2(t))^T$ and $(x_1^*(t), x_2^*(t), u_1^*(t), u_2^*(t))^T$ of system (1.3), for the above $\varepsilon > 0$, it then follows from Theorem 2.4 that there exists a large-enough T_7, such that for all $t \geq T_7$,

$$x_i(t), x_i^*(t) < M_i + \varepsilon, \ \ u_i(t), u_i^*(t) < N_i + \varepsilon. \tag{4.2}$$

Let

$$\begin{aligned}V_1(t) &= |\ln x_1(t) - \ln x_1^*(t)| + |u_1(t) - u_1^*(t)|,\\ V_2(t) &= |\ln x_2(t) - \ln x_2^*(t)| + |u_2(t) - u_2^*(t)|.\end{aligned} \tag{4.3}$$

Then, by using (4.1), for $t > T_7$, we have

$$\begin{aligned}
& D^+V_1(t)\\
= \ & \operatorname{sgn}(x_1(t) - x_1^*(t))\Bigg[r_1(t) - a_1(t)x_1(t) - \frac{b_1(t)x_2^2(t)}{\alpha_2(t) + x_2^2(t)} - \gamma(t)x_1(t)x_2^2(t) - c_1(t)u_1(t)\\
& -\Big(r_1(t) - a_1(t)x_1^*(t) - \frac{b_1(t)(x_2^*(t))^2}{\alpha_2(t) + (x_2^*(t))^2} - \gamma(t)x_1^*(t)(x_2^*(t))^2 - c_1(t)u_1^*(t)\Big)\Bigg]\\
& - e_1(t)|u_1(t) - u_1^*(t)| + d_1(t)|x_1(t) - x_1^*(t)|\\
\leq \ & -a_1^l|x_1(t) - x_1^*(t)| + \operatorname{sgn}(x_1(t) - x_1^*(t))b_1(t)\Big(- \frac{x_2^2(t)}{\alpha_2(t) + x_2^2(t)} + \frac{(x_2^*(t))^2}{\alpha_2(t) + (x_2^*(t))^2}\Big)\\
& + \operatorname{sgn}(x_1(t) - x_1^*(t))(-\gamma(t)x_1(t)x_2^2(t) + \gamma(t)x_1^*(t)(x_2^*(t))^2)\\
& + c_1^u|u_1(t) - u_1^*(t)| - e_1^l|u_1(t) - u_1^*(t)| + d_1^u|x_1(t) - x_1^*(t)|\\
\leq \ & -a_1^l|x_1(t) - x_1^*(t)| + \operatorname{sgn}(x_1(t) - x_1^*(t))b_1(t)\Big(- \frac{x_2^2(t)}{\alpha_2(t) + x_2^2(t)} + \frac{(x_2^*(t))^2}{\alpha_2(t) + x_2^2(t)}\\
& -\frac{(x_2^*(t))^2}{\alpha_2(t) + x_2^2(t)} + \frac{(x_2^*(t))^2}{\alpha_2(t) + (x_2^*(t))^2}\Big) + \operatorname{sgn}(x_1(t) - x_1^*(t))\gamma(t)\Big(- x_1(t)x_2^2(t) + x_1(t)(x_2^*(t))^2\\
& - x_1(t)(x_2^*(t))^2 + x_1^*(t)(x_2^*(t))^2\Big) + c_1^u|u_1(t) - u_1^*(t)| - e_1^l|u_1(t) - u_1^*(t)| + d_1^u|x_1(t) - x_1^*(t)|\\
\leq \ & -a_1^l|x_1(t) - x_1^*(t)| + \frac{b_1(t)(x_2(t) + x_2^*(t))}{\alpha_2(t) + x_2^2(t)}|x_2(t) - x_2^*(t)| + \frac{b_1(t)(x_2^*(t))^2(x_2(t) + x_2^*(t))}{(\alpha_2(t) + x_2^2(t))(\alpha_2(t) + (x_2^*(t))^2)}\\
& \times |x_2(t) - x_2^*(t)| + \gamma(t)x_1(t)(x_2(t) + x_2^*(t))|x_2(t) - x_2^*(t)| + \gamma(t)(x_2^*(t))^2|x_1(t) - x_1^*(t)|\\
& + c_1^u|u_1(t) - u_1^*(t)| - e_1^l|u_1(t) - u_1^*(t)| + d_1^u|x_1(t) - x_1^*(t)|\\
\leq \ & -a_1^l|x_1(t) - x_1^*(t)| + 2b_1^u(M_2+\varepsilon)|x_2(t) - x_2^*(t)| + 2b_1^u(M_2+\varepsilon)^3|x_2(t) - x_2^*(t)|\\
& + 2\gamma^u(M_1+\varepsilon)(M_2+\varepsilon)|x_2(t) - x_2^*(t)| + \gamma^u(M_2+\varepsilon)^2|x_1(t) - x_1^*(t)|\\
& + c_1^u|u_1(t) - u_1^*(t)| - e_1^l|u_1(t) - u_1^*(t)| + d_1^u|x_1(t) - x_1^*(t)|\\
= \ & [-a_1^l + \gamma^u(M_2+\varepsilon)^2 + d_1^u]|x_1(t) - x_1^*(t)| + [2b_1^u(M_2+\varepsilon)(1 + (M_2+\varepsilon)^2)\\
& + 2\gamma^u(M_1+\varepsilon)(M_2+\varepsilon)]|x_2(t) - x_2^*(t)| + [c_1^u - e_1^l]|u_1(t) - u_1^*(t)|.
\end{aligned}$$

Here $\operatorname{sgn}(x)$ denotes the sign function: when $x > 0$, then $\operatorname{sgn}(x) = 1$, when $x = 0$, then $\operatorname{sgn}(x) = 0$, and when $x < 0$, then $\operatorname{sgn}(x) = -1$.

$$\begin{aligned}
& D^+V_2(t) \\
= \;& \operatorname{sgn}(x_2(t) - x_2^*(t))\Big[r_2(t) - \frac{b_2(t)x_1^2(t)}{\alpha_1(t) + x_1^2(t)} - a_2(t)x_2(t) - c_2(t)u_2(t) \\
& - (r_2(t) - \frac{b_2(t)(x_1^*(t))^2}{\alpha_1(t) + (x_1^*(t))^2} - a_2(t)x_2^*(t) - c_2(t)u_2^*(t))\Big] \\
& - e_2(t)|u_2(t) - u_2^*(t)| + d_2(t)|x_2(t) - x_2^*(t)| \\
\leq \;& \operatorname{sgn}(x_2(t) - x_2^*(t))b_2(t)\Big(- \frac{x_1^2(t)}{\alpha_1(t) + x_1^2(t)} + \frac{(x_1^*(t))^2}{\alpha_1(t) + (x_1^*(t))^2}\Big) \\
& - a_2^l|x_2(t) - x_2^*(t)| + c_2^u|u_2^(t) - u_2^*(t)| - e_2^l|u_2(t) - u_2^*(t)| + d_2^u|x_2(t) - x_2^*(t)| \\
= \;& \operatorname{sgn}(x_2(t) - x_2^*(t))b_2(t)\Big(- \frac{x_1^2(t)}{\alpha_1(t) + x_1^2(t)} + \frac{(x_1^*(t))^2}{\alpha_1(t) + x_1^2(t)} \\
& - \frac{(x_1^*(t))^2}{\alpha_1(t) + x_1^2(t)} + \frac{(x_1^*(t))^2}{\alpha_1(t) + (x_1^*(t))^2}\Big) \\
& - a_2^l|x_2(t) - x_2^*(t)| + c_2^u|u_2^(t) - u_2^*(t)| - e_2^l|u_2(t) - u_2^*(t)| + d_2^u|x_2(t) - x_2^*(t)| \\
\leq \;& 2b_2^u(M_1 + \varepsilon)((M_1 + \varepsilon)^2 + 1)|x_1(t) - x_1^*(t)| + (-a_2^l + d_2^u)|x_2(t) - x_2^*(t)| + (c_2^u - e_2^l)|u_2(t) - u_2^*(t)|.
\end{aligned}$$

Now, let us define a Lyapunov functional

$$V(t) = V_1(t) + V_2(t).$$

So we have

$$\begin{aligned}
D^+V(t) \;\leq\; & [-a_1^l + 2(M_1 + \varepsilon)((M_1 + \varepsilon)^2 + 1)b_2^u + d_1^u + \gamma^u(M_2 + \varepsilon)]|x_1(t) - x_1^*(t)| \\
& + [-a_2^l + 2(M_2 + \varepsilon)(1 + (M_2 + \varepsilon)^2)b_1^u + d_2^u - 2\gamma^u(M_1 + \varepsilon)(M_2 + \varepsilon)|x_2(t) - x_2^*(t)| \\
& + (c_1^u - e_1^l)|u_1(t) - u_1^*(t)| + (c_2^u - e_2^l)|u_2(t) - u_2^*(t)|.
\end{aligned}$$

It follows from (4.1) that

$$D^+V(t) \;\leq\; -\varepsilon \sum_{i=1}^{2} |x_i(t) - x_i^*(t)| - \varepsilon \sum_{i=1}^{2} |u_i(t) - u_i^*(t)|. \tag{4.4}$$

Integrating both sides of the above inequality from T_7 to t, we have

$$V(t) + \varepsilon \int_{T_7}^{t} \Big[\sum_{i=1}^{2} |x_i(t) - x_i^*(t)| + \sum_{i=1}^{2} |u_i(t) - u_i^*(t)|\Big] ds \leq V(T_7) \;\text{ for }\; t \geq T_7. \tag{4.5}$$

Therefore, $V(t)$ is bounded on $[T_7, +\infty)$ and also

$$\int_{T_7}^{t} \Big[\sum_{i=1}^{2} |x_i(t) - x_i^*(t)| + \sum_{i=1}^{2} |u_i(t) - u_i^*(t)\Big] ds < +\infty. \tag{4.6}$$

By Theorem 2.4, $|x_i(t)-x_i^*(t)|$, $|u_i(t)-u_i^*(t)|$, $i=1,2$, are bounded on $[T_7,+\infty)$. On the other hand, it is easy to see that $\dot{x}_1(t)$, $\dot{x}_2(t)$, $\dot{u}_1(t)$ and $\dot{u}_2(t)$ are bounded for $t \geq T_7$. Therefore, $|x_i(t)-x_i^*(t)|$, $|u_i(t)-u_i^*(t)|$, $i=1,2$, are uniformly continuous on $[T_7,+\infty)$. By the Barbălat lemma, one can conclude that

$$\lim_{t\to+\infty}\Big[\sum_{i=1}^{2}|x_i(t)-x_i^*(t)|+\sum_{i=1}^{2}|u_i(t)-u_i^*(t)|\Big]=0.$$

Consequently,

$$\lim_{t\to+\infty}|x_i(x)-x_i^*(x)|=0,\quad \lim_{t\to+\infty}|u_i(x)-u_i^*(x)|=0,\quad i=1,2.$$

This completes the proof of Theorem 4.1.

5. Examples

In this section, we shall give four examples to illustrate the feasibility of our main results.

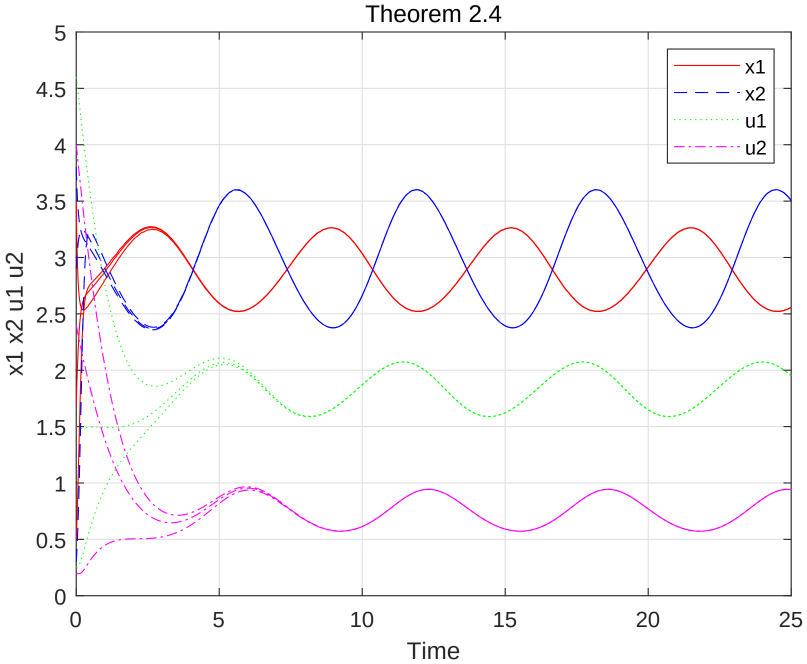

Figure 1. Dynamic behaviors of the solution $(x_1(t),x_2(t),u_1(t),u_2(t))^T$ of system (5.1) with the initial conditions $(x_1(0),x_2(0),u_1(0),u_2(0))=(0.5,0.3,0.25,0.2)^T$, $(1.7,2.9,1.5,2.4)^T$, and $(3.5,3.8,4.6,4)^T$, respectively.

Example 5.1. Consider the following equations:

$$\begin{aligned}
x_1'(t)&=x_1\Big(15+\sin t-(5+0.5\sin t)x_1-\frac{0.01x_2^2}{0.5+0.2\sin t+x_2^2}-0.005x_1{x_2}^2-0.3u_1\Big),\\
x_2'(t)&=x_2\Big(12+2\cos t-\frac{0.005x_1^2}{0.6+0.3\sin t+x_1^2}-(4+0.5\sin t)x_2-0.3u_2\Big),\\
u_1'(t)&=-(0.8+0.2\sin t)u_1+0.5x_1,\\
u_2'(t)&=-(0.8+0.2\sin t)u_2+0.2x_2.
\end{aligned}\tag{5.1}$$

Corresponding to system (5.1), one has

$$b_1^u = 0.01 < \frac{r_1^l \alpha_2^l}{M_2^2} \approx 0.2625, \quad b_2^u = 0.005 < \frac{r_2^l \alpha_1^l}{M_1^2} \approx 0.237.$$

Clearly, condition (2.6) is satisfied, and from Theorem 2.4, we know that system (5.1) is permanent. Figure 1 shows the dynamic behaviors of system (5.1), which are consistent with the conclusion obtained above.

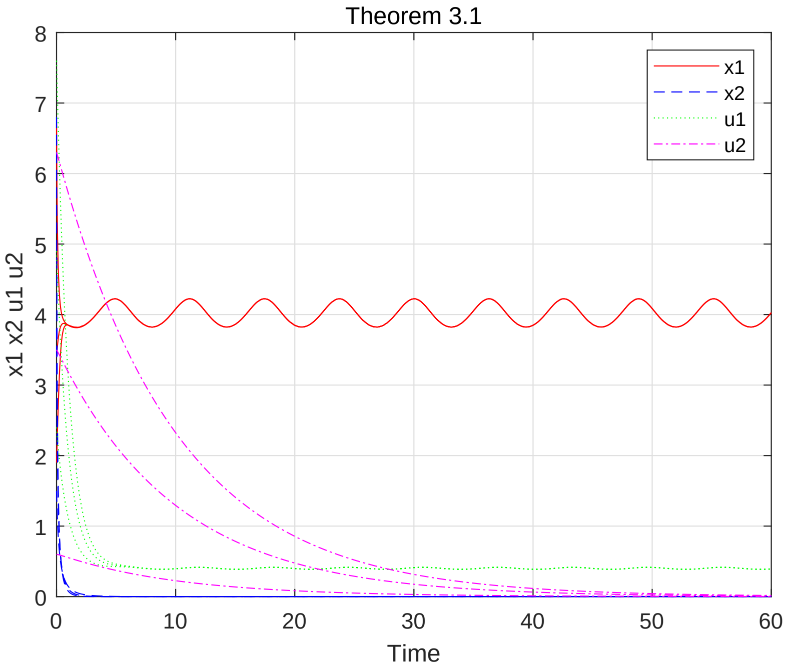

Figure 2. Dynamic behaviors of the solution $(x_1(t), x_2(t), u_1(t), u_2(t))^T$ of system (5.2) with the initial conditions $(x_1(0), x_2(0), u_1(0), u_2(0)) = (1.9, 1.5, 2.4, 0.6)^T$, $(3.4, 3.8, 4.9, 3.5)^T$ and $(6.7, 6.8, 7.6, 6.3)^T$, respectively.

Example 5.2. Consider the following equations:

$$\begin{aligned}
x_1'(t) &= x_1\Big(6 + 0.5\sin t - (1.5 + 0.2\sin t)x_1 - \frac{0.03x_2^2}{0.6 + 0.3\sin t + x_2^2} - 0.005x_1{x_2}^2 - 0.01u_1\Big),\\
x_2'(t) &= x_2\Big(0.25 + 0.05\cos t - \frac{(1.2 + 0.2\cos t)x_1}{0.8 + 0.2\sin t + x_1^2} - (2.5 + 0.5\sin t)x_2 - 0.25u_2\Big),\\
u_1'(t) &= -u_1 + 0.0001x_1,\\
u_2'(t) &= -0.1u_2 + 0.02x_2.
\end{aligned} \tag{5.2}$$

By calculation, one has

$$M_1 = \frac{r_1^u}{a_1^l} = 5, \quad M_2 = \frac{r_2^u}{a_2^l} = 0.15, \quad m_1 \approx 3.23,$$

$$\frac{r_1^l}{r_2^u}\frac{(a_2^l e_2^u + c_2^l d_2^l)}{e_2^u M_2} \approx 7.52, \quad (\alpha_1^u + M_1^2)\frac{r_2^u}{r_1^l}\frac{a_1^u e_1^l + c_1^u d_1^u}{e_1^l m_1} \approx 0.747,$$

$$\frac{1}{M_1M_2^2}\Big(r_1^l-(\alpha_1^u+M_1^2)r_2^u\frac{a_1^ue_1^l+c_1^ud_1^u}{b_2^le_1^lm_1}\Big)\approx 12.38,$$
$$\frac{1}{M_1M_2^2}\Big(r_1^l-r_2^u\frac{b_1^ue_2^uM_2}{a_2^le_2^u+c_2^ld_2^l}\Big)\approx 48.89.$$

We assume that $\gamma^u = 0.00005$, and clearly, conditions (H_1) and (H_2) are satisfied. From Theorem 3.1, we know that the first species is permanent and the rest of the species are driven to extinction. Figure 2 shows the dynamic behaviors of system (5.2), which are consistent with the conclusion obtained above.

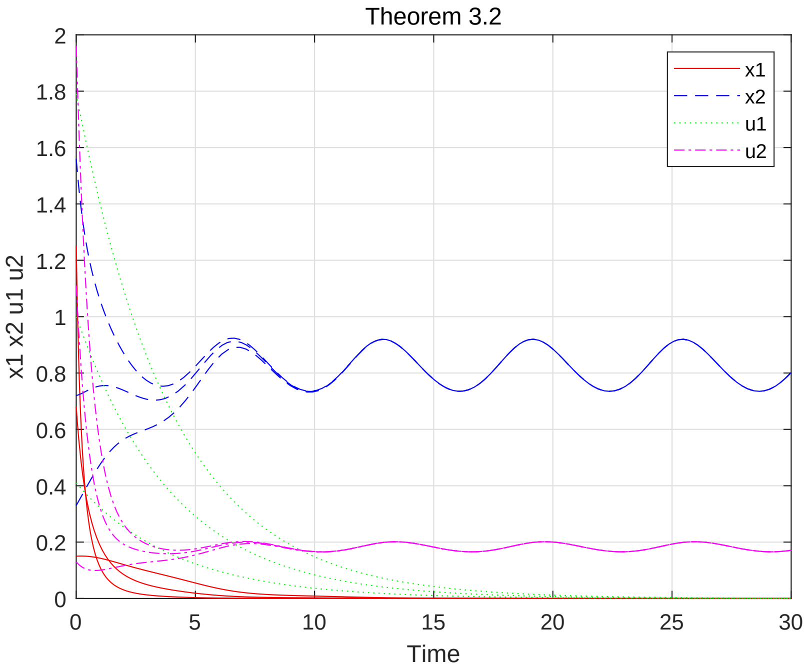

Figure 3. Dynamic behaviors of the solution $(x_1(t),x_2(t),u_1(t),u_2(t))^T$ of system (5.3) with the initial conditions $(x_1(0),x_2(0),u_1(0),u_2(0)) = (0.15,0.33,0.41,0.13)^T$, $(0.68,0.72,1,1.11)^T$, and $(1.25,1.56,1.79,1.96)^T$, respectively.

Example 5.3. Consider the following equations:

$$\begin{aligned}
x_1'(t) &= x_1\Big(0.8+0.05\sin t-(1.6+0.2\sin t)x_1-\frac{2.6x_2^2}{0.9+x_2^2}-0.005x_1{x_2}^2-0.6u_1\Big),\\
x_2'(t) &= x_2\Big(0.6+0.1\cos t-\frac{0.06x_1^2}{0.8+0.2\sin t+x_1^2}-(0.7+0.1\sin t)x_2-0.12u_2\Big),\\
u_1'(t) &= -0.25u_1+0.02x_1,\\
u_2'(t) &= -1.8u_2+0.4x_2.
\end{aligned}\tag{5.3}$$

By calculation, one has

$$M_1=\frac{r_1^u}{a_1^l}\approx 0.607,\quad M_2=\frac{r_2^u}{a_2^l}=1.17,\quad m_1\approx 0.63,$$

$$\frac{r_2^l}{r_1^u}\frac{a_1^l e_1^u + c_1^l d_1^l}{e_1^u M_1} \approx 1.403, \qquad \frac{r_1^u}{r_2^l}\frac{\alpha_2^u + M_2^2}{m_2}\frac{a_2^u e_2^l + c_2^u d_2^u}{e_2^l} \approx 2.53.$$

Clearly, $b_2^u < 1.403, b_1^l > 2.53$, and condition (H_3) is satisfied. From Theorem 3.2, we know that the second species is permanent and the rest of the species are driven to extinction. Figure 3 shows the dynamic behaviors of system (5.3), which are consistent with the conclusion obtained above.

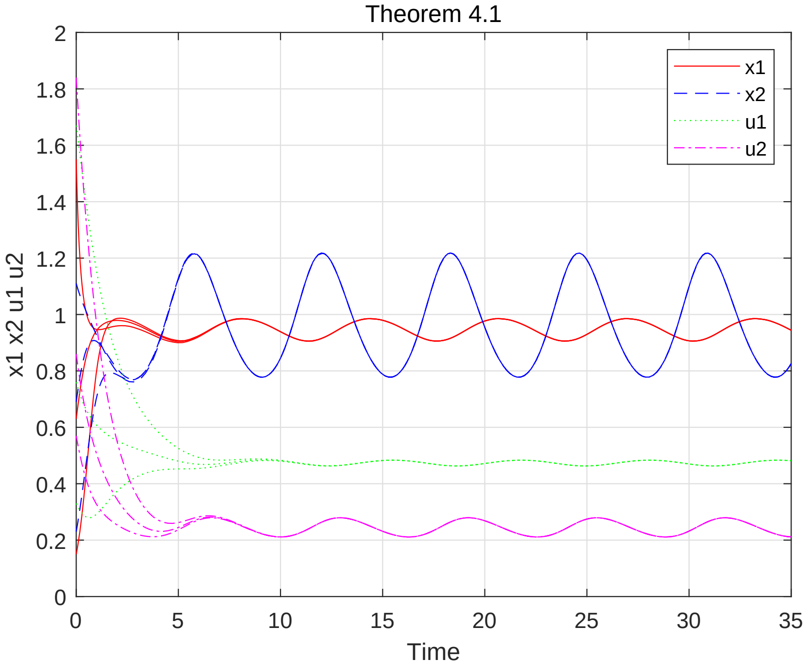

Figure 4. Dynamic behaviors of the solution $(x_1(t), x_2(t), u_1(t), u_2(t))^T$ of system (5.4) with the initial conditions $(x_1(0), x_2(0), u_1(0), u_2(0)) = (0.15, 0.23, 0.33, 0.57)^T$, $(0.63, 0.69, 0.76, 0.86)^T$ and $(1.55, 1.11, 1.67, 1.84)^T$, respectively.

Example 5.4. Consider the following equations:

$$\begin{aligned} x_1'(t) &= x_1\Big(3 + 0.5\sin t - (3 + 0.4\sin t)x_1 - \frac{0.1x_2^2}{0.7 + 0.3\sin t + x_2} - 0.005x_1x_2{}^2 - 0.2u_1\Big), \\ x_2'(t) &= x_2\Big(2 + 0.3\cos t - \frac{0.05x_1^2}{0.9 + 0.4\sin t + x_1^2} - (2 + 0.4\sin t)x_2 - 0.15u_2\Big), \\ u_1'(t) &= -0.6u_1 + 0.3x_1, \\ u_2'(t) &= -0.8u_2 + 0.2x_2. \end{aligned} \tag{5.4}$$

Corresponding to system (5.4), one has

$$M_1 = \frac{r_1^u}{a_1^l} \approx 1.35, \quad M_2 = \frac{r_2^u}{a_2^l} \approx 1.44,$$

$$b_2^u = 0.05 < \frac{a_1^l - d_1^u}{2(M_1^3 + M_1)} \approx 0.302, \quad b_1^u = 0.1 < \frac{a_2^l - d_2^u}{2(M_2^3 + M_2)} \approx 0.158,$$

$$\frac{a_1^l - 2(M_1^3 + M_1)b_2^u - d_1^u}{M_2^2} \approx 0.93, \quad \frac{a_2^l - 2(M_2^3 + M_2)b_1^u - d_2^u}{2M_1M_2} \approx 0.13,$$

$$\gamma^u = 0.005 < \min\left\{ 0.93,\ 0.13 \right\},$$

$$c_1^u = 0.2 < e_1^l = 0.6, \quad c_2^u = 0.15 < e_2^l = 0.8.$$

Clearly, condition (H_4) is satisfied, and from Theorem 4.1, we know that system (5.4) is globally attractive. Figure 4 shows the dynamic behaviors of system (5.4), which are consistent with the conclusion obtained above.

6. Discussion

In this paper, we consider a non-autonomous allelopathic phytoplankton model with threshold inhibition and feedback controls, i.e., Eq (1.3), different from the model in [5], where the inhibition terms are replaced by $\frac{b_1(t)x_2{}^2(t)}{\alpha_2(t) + x_2{}^2(t)}$ and $\frac{b_2(t)x_1{}^2(t)}{\alpha_1(t) + x_1{}^2(t)}$. We further investigate the influence of inhibition terms and toxic substances on the dynamic behaviors of system (1.3).

From the conditions of Theorem 2.4, we find that when the competition coefficient is less than a certain level, it can ensure the permanence of the system, and the feedback controls and toxic substances have no influence on the permanence of the system. This is consistent with the classical phenomenon of weak competition promoting coexistence in ecosystems. But from Theorem 4.1, one interesting finding is that for system (1.3), the feedback controls and toxic substances play an important role on the stability property of the system; only the rate of toxic production and feedback controls are small enough such that inequality (H_4) holds. The toxic substances and feedback controls have no effect on the stability of the system. This finding ties into the ecosystem resilience theory, demonstrating that strong or sustained feedbacks may disrupt this global stability.

From the conditions of Theorems 3.1 and 3.2, we can easily find that the feedback controls and toxic substances play a crucial role on the extinction of system (1.3). Theorem 3.1 shows that, when the environmental adaptability and resource utilization efficiency of the first species surpasses that of the second species, even if the second species releases toxins to elevate its competitiveness, but the toxic rate is very low such that inequality (H_2) holds, it still cannot prevent its extinction. In other words, that lower rate of toxic production could not avoid the extinction of the second species. Theorem 3.2 shows that, when the competitiveness of the first population is weaker than that of the second population, coupled with the inhibitory effect of toxins released by the second population, it will inevitably lead to extinction. The extinction thresholds (Theorems 3.1 and 3.2) explicitly quantify how the competitive exclusion principle can be realized in the allelopathic phytoplankton system.

While this study provides a theoretical foundation for understanding non-autonomous allelopathic phytoplankton systems with threshold inhibition and feedback controls, several avenues remain open for further exploration. For instance, the model could be extended to incorporate time delays, reflecting the lag between toxin production, release, and its effect on competitors, which is ecologically relevant for many phytoplankton species.

Use of AI tools declaration

We have not used Artificial Intelligence (AI) tools in the creation of this article.

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Conflict of interest

The authors declare there are no conflicts of interest.

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