Population growth and competition models with decay and competition consistent delay

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Abstract
We derive an alternative expression for a delayed logistic equation in which the rate of change in the population involves a growth rate that depends on the population density during an earlier time period. In our formulation, the delay in the growth term is consistent with the rate of instantaneous decline in the population given by the model. Our formulation is a modification of Arino et al. (J Theor Biol 241(1):109–119, 2006) by taking the intraspecific competition between the adults and juveniles into account. We provide a complete global analysis showing that no sustained oscillations are possible. A threshold giving the interface between extinction and survival is determined in terms of the parameters in the model. The theory of chain transitive sets and the comparison theorem for cooperative delay differential equations are used to determine the global dynamics of the model. We extend our delayed logistic equation to a system modeling the competition between two species. For the competition model, we provide results on local stability, bifurcation diagrams, and adaptive dynamics. Assuming that the species with shorter delay produces fewer offspring at a time than the species with longer delay, we show that there is a critical value, $\tau^*$, such that the evolutionary trend is for the delay to approach $\tau^*$.

Keywords Logistic growth · Extinction threshold · Lotka–Volterra competition · Chain transitive sets · Local and global dynamics · Discrete delay differential equations
**Mathematics Subject Classification** 92D25 Population dynamics · 37N25 Dynamical systems in biology · 92D40 Ecology

## 1 Introduction

The classical logistic equation was introduced by Verhulst (1838) as an ordinary differential equation (ODE) to describe population growth in a limited environment. Hutchinson (1948) noted that the classical logistic equation is not appropriate when there is a lag in some of the population growth processes, so he formulated a model as a delay differential equation (DDE) that is now known as the *delayed logistic equation* or *Hutchinson’s equation*. However, Hutchinson’s model has been criticized by ecological modelers (e.g., Stefan et al. (2012), Nisbet and Gurney (2003), Arino et al. (2006)) because the derivation was not based on clearly defined birth and death processes and some of its predictions are unrealistic, e.g., no matter how long the delay, the population avoids extinction, and the final size of the population is independent of the length of the delay.

Hutchinson’s equation is

\[ x'(t) = rx(t) \left( 1 - \frac{x(t - \tau)}{K} \right), \]  

where \( x(t) \) represents the population density at time \( t \), \( r \) is the intrinsic growth rate, \( K \) as the carrying capacity, and the time lag \( \tau \) is a positive constant. Some authors (Cooke et al. 1999; Bocharov and Hadeler 2000; Hadeler and Bocharov 2003) have argued that a delay should enter the birth term rather than the death term and that the model with delay should take the form

\[ x'(t) = b(x(t - \tau))x(t - \tau)e^{-\mu_0 \tau} - \mu(x(t))x(t), \]

where \( b(x) \), \( \mu_0 \) and \( \mu(x) \) are respectively the birth function, the juvenile death rate, and the adult death function. An equation of the basic form (2) was also derived from age-structured models by Gourley and Liu (2015) and Liu et al. (2016).

For a model where the population is divided into two subpopulations, motile and proliferative, Baker and Röst (2020) proposed the equation

\[ x'(t) = -rx(t) + rx(t - \tau) \left( 2 - r \int_{t - \tau}^{t} x(s) \, ds - x(t) \right), \]

where the integral is related to the population of proliferative agents.

In Arino et al. (2006), an approach in the spirit of Cooke et al. (1999), Bocharov and Hadeler (2000), and Hadeler and Bocharov (2003), was proposed resulting in the delayed logistic growth model

\[ x'(t) = \gamma \frac{\mu e^{-\mu \tau}x(t - \tau)}{\mu + \kappa(1 - e^{-\mu \tau})x(t - \tau)} - \mu x(t) - \kappa x^2(t), \]
in the basic form of (2). They include the delay in the birth rate term. However, they argue further that the delay in the birth or growth rate term should not only involve the natural juvenile death rate, but should be consistent with the overall decline terms given by the model. This approach was also used in Streipert and Wolkowicz (2021) to derive a delayed difference equation model. In the derivation in Arino et al. (2006), it is assumed that the growth of the population at time \( t \) is proportional (with proportionality constant \( \gamma \)) to the number of individuals alive at time \( t - \tau \) that survive until time \( t \) avoiding elimination from the population due to natural death, crowding, or intraspecific competition with other individuals that were alive at time \( t - \tau \)(the rational factor of \( \gamma \) in (4)). They do this in a manner that is consistent with the natural death, crowding, and intraspecific competition given modelled by the equation. However, they ignore decline due to crowding and competition between those born during the time interval \( t - \tau \) to \( t \). This assumption is reasonable when those two age groups are living in very different environments. This is true for example, for insects that undergo metamorphosis such as mosquitoes and butterflies. However, this assumption is not suitable for mammals, since then juveniles and adults share the same environment.

In the new model of delayed logistic growth derived and analyzed in Sect. 2, the competition between the adults and juveniles is also taken into account in a manner consistent with the other terms in the equation. Thus, we assume as in the derivation in (4) in Arino et al. (2006), that growth in the population is proportional to those individuals alive at time \( t - \tau \) that survive until time \( t \). However, in our derivation, the individuals that survive from time \( t - \tau \) to time \( t \), avoid natural death, and crowding and competition with the entire population alive during that time interval. In contrast to the discrete delay model in (4) this new model has both discrete and distributed delay terms as in (3). We determine the global dynamics of the model. In particular, all solutions with positive initial data converge to a globally asymptotically stable equilibrium with value that has a magnitude that depends on the delay. If the delay is too long, this model predicts that the population dies out. A threshold giving the interface between extinction and survival is determined in terms of parameters in the model. The result is consistent with Arino et al. (2006) and does not suffer from the issues raised criticizing Hutchinson’s model.

One advantage of this model over (4), is that it is possible to extend it to cover decline due to competition between two different populations consistent with the decline terms in the model. In Sect. 3, we propose a delay model for two species competition. We analyze the local stability of the equilibria and provide bifurcation diagrams for that model. We also consider adaptive dynamics using the delay as the evolving trait.

Conclusions and a discussion are given in Sect. 4.

### 2 The single species model

In this section we derive a logistic DDE by modifying the classical logistic ODE. The classical logistic ODE can be written as

\[
x'(t) = \gamma x(t) - \mu x(t) - \kappa x(t)^2,
\]

(5)
Fig. 1 The relationship between the populations $x$ and $X$ for $s \in [0, \tau]$. Shown is $x(t - \tau + s)$, the total population alive at time $t - \tau + s$ where $s \in [0, \tau]$ and $X(s; \tau)$, the population of individuals alive at time $t - \tau + s$ that were alive at time $t - \tau$ and survived until time $t - \tau + s$. The two populations are related by (7) with initial condition $X(0; \tau) = x(t - \tau)$ that has explicit solution given by (8)

where $x(t)$ is the population density of the species. The parameters $\gamma$, $\mu$ and $\kappa$ correspond to growth, death, and intraspecific competition, respectively.

We assume that the growth rate depends on the population size some fixed $\tau$ time units in the past. For each fixed time $t \geq 0$, we replace the term $\gamma x(t)$ in (5) by $\gamma X(t; \tau)$ where $X(t; \tau)$ denotes the number of individuals alive at time $t - \tau$ that survive until time $t$ (see Fig. 1).

Denoting by $X'(t; \tau)$ the partial derivative of $X(t; \tau)$ with respect to $t$, the value of $X(t; \tau)$ is determined in Arino et al. (2006) by solving

$$X'(s; \tau) = -\mu X(s; \tau) - \kappa X(s; \tau)^2$$

for $0 \leq s \leq \tau$, with initial condition $X(0; \tau) = x(t - \tau)$. The intraspecific competition term $\kappa X(s; \tau)^2$ is based on the assumption that the population $X(s; \tau)$ only competes with $X(s; \tau)$ itself rather than the entire population $x(t - \tau + s)$. This assumption is reasonable for metamorphosis insects, for which the juveniles and adults have a very different living environment and those two age groups cannot compete with each other. However, this assumption is not suitable for many animals such as mammals, for which juveniles and adults share the same environment. Therefore, we assume that the population $X(s; \tau)$ competes with the entire population $x(t - \tau + s)$. Hence, we modify (6) as follows:

$$X'(s; \tau) = -\mu X(s; \tau) - \kappa X(s; \tau)x(t - \tau + s)$$

for $0 \leq s \leq \tau$. Equation (7) with initial condition $X(0; \tau) = x(t - \tau)$ can be solved explicitly and has solution

$$X(\tau; \tau) = x(t - \tau) \exp \left( -\mu \tau - \kappa \int_{t-\tau}^{t} x(v)dv \right).$$

Replacing the term $\gamma x(t)$ in (5) by $\gamma X(\tau; \tau)$, we arrive at

$$x'(t) = \gamma x(t - \tau) \exp \left( -\mu \tau - \kappa \int_{t-\tau}^{t} x(v)dv \right) - \mu x(t) - \kappa x^2(t)$$
with initial data \( x(t) = \phi(t) \in C([-\tau, 0], \mathbb{R}_+\setminus\{0\}) \).

We call Eq. (9) the mixed alternative logistic DDE. We will discuss basic properties of (9) in Sect. 2.1 and provide global dynamics in Sect. 2.2.

**Remark 1** In Arino et al. (2006), the number of individuals that survive from time \( t - \tau \) to time \( t \) is given by the solution of (6), and the resulting logistic model is given by Eq. (4). The dynamics of (4) is determined by a survival threshold

\[
\tau_H = \frac{1}{\mu} \ln \left( \frac{\gamma}{\mu} \right). \tag{10}
\]

If the time delay is too large, i.e., \( \tau \geq \tau_H \), the population dies out, as one might expect. If the time delay is small enough, i.e., \( \tau < \tau_H \), then the population size approaches a positive equilibrium, interpreted as the delay reduced carrying capacity, since it is a decreasing function of the delay.

### 2.1 Equilibria and local stability

Following the proof of Arino et al. (2006, Proposition 3.1), together with the observation that solutions of (9) satisfy

\[
x'(t) \leq \gamma e^{-\mu \tau} x(t - \tau) - \mu x(t) - \kappa x^2(t), \tag{11}
\]

it can be shown that for any solution of (11) with initial data \( \phi(t) \in C([0, \tau], \mathbb{R}_+\setminus\{0\}) \), a constant \( M \) exists such that

\[
M > \max_{t \in [0, \tau]} \phi(t) \quad \text{and} \quad \gamma e^{-\mu \tau} - \mu - \kappa M < 0,
\]

and the solution \( x(t) \) remains positive and bounded above by \( M \) for all \( t > 0 \). By the standard theory of delay differential equations (see e.g. Hale and Verduyn Lunel 1993), it follows that model (9) is well-posed, i.e., every solution with positive initial data remains positive and is eventually bounded above by \( K = (\gamma e^{-\mu \tau} - \mu)/\kappa \), a decreasing function of the delay, \( \tau \). As in Arino et al. (2006), we also interpret this value as the delay reduced carrying capacity.

The extinction equilibrium \( x = 0 \) always exists. The nontrivial equilibrium of (9) is determined by

\[
\gamma e^{-\tau(\mu + \kappa x)} - (\mu + \kappa x) = 0. \tag{12}
\]

Since the left-hand side of (12) decreases unboundedly as \( x \) increases and equals \( \gamma e^{-\tau \mu} - \mu \) when \( x = 0 \), Eq. (12) has a unique positive root if and only if \( \gamma e^{-\mu \tau} > \mu \). This is equivalent to the condition, \( \tau < \tau_H \), with \( \tau_H \) defined in (10).

We define

\[
\mathcal{R}_0 = \frac{\gamma e^{-\mu \tau}}{\mu}. \tag{13}
\]
Note that \( \mathcal{R}_0 > 1 \) if and only if \( \tau < \tau_H \). Equation (9) always has the trivial equilibrium 0. A positive equilibrium \( x^* \) exists if and only if \( \mathcal{R}_0 > 1 \), where \( \mathcal{R}_0 \) is given in (13).

In this section we show that whenever the positive equilibrium exists, it is locally asymptotically stable.

**Lemma 1** Consider Eq. (9). Let \( \mathcal{R}_0 \) be defined by (13).

(a) If \( \mathcal{R}_0 < 1 \), then the trivial equilibrium \( x = 0 \) is locally asymptotically stable and there is no positive equilibrium.

(b) If \( \mathcal{R}_0 > 1 \), then the trivial equilibrium \( x = 0 \) is unstable and there exists a unique positive equilibrium \( x^* > 0 \). Moreover, \( x^* \) is locally asymptotically stable.

**Proof** Throughout this proof, we scale \( x \mapsto \kappa x \) in Eq. (9), and hence without loss of generality, assume that \( \kappa = 1 \).

First we show that the local stability of an equilibrium \( \bar{x} \) of (9) can be determined by its characteristic equation

\[
\gamma e^{-\tau(\mu + \bar{x})} \left( e^{-\lambda \tau} + \frac{e^{-\lambda \tau} - 1}{\lambda} \bar{x} \right) - \mu - 2\bar{x} - \lambda = 0. \tag{14}
\]

Let \( \mathcal{C} \) be the set of all bounded continuous functions on \([−\tau, \infty)\). For any function \( x \in \mathcal{C} \) and \( t \geq 0 \), we denote \( x_t \) the function in \( \mathcal{C} \) defined by

\[
x_t(s) = x(s + t), \quad s \in [−\tau, \infty).
\]

Let \( F(x_t) \) be the right-hand side of (9) for any \( x \in \mathcal{C} \). Then \( F \) maps \( \mathcal{C} \) into \( \mathcal{C} \). If \( \bar{x} \in \mathcal{C} \) satisfies \( F(\bar{x}) = 0 \), then the linearization \( DF(\bar{x}) \) of \( F \) at \( \bar{x} \) is given by

\[
\begin{align*}
[DF(\bar{x})(\varphi)](t) &= \gamma e^{-\tau(\mu + \bar{x})} \left[ -\left( \int_{t-\tau}^{t} \varphi(s) \, ds \right) \bar{x}(t - \tau) + \varphi(t - \tau) \right] \\
&\quad - \left( \mu + 2\bar{x}(t) \right) \varphi(t) \tag{15}
\end{align*}
\]

for all \( \varphi \in \mathcal{C} \). Taking \( \bar{x} \) to be the constant function \( \bar{x} \), the eigenvalue problem

\[
[DF(\bar{x})(\varphi)](t) = \lambda \varphi(t)
\]

yields

\[
\lambda \varphi(t) = \gamma e^{-\mu t - \bar{x} t} \left[ -\bar{x} \left( \int_{t-\tau}^{t} \varphi(s) \, ds \right) + \varphi(t - \tau) \right] - \left( \mu + 2\bar{x} \right) \varphi(t). \tag{16}
\]

It can be shown by applying the Laplace transform to (16) (see e.g. (Hale and Verduyn Lunel 1993, Section 1.5)) that \( \varphi = e^{\lambda t} \) and that

\[
\lambda e^{\lambda t} = \gamma e^{-\mu t - \bar{x} t} \left[ -\bar{x} \left( \frac{1 - e^{-\tau}}{\lambda} e^{\lambda t} \right) + e^{\lambda(t - \tau)} \right] - \left( \mu + 2\bar{x} \right) e^{\lambda t},
\]

leading to

\[
\left[ \gamma e^{-\tau(\mu + \bar{x})} \left( e^{-\lambda t} + \frac{e^{-\lambda t} - 1}{\lambda} x_0 \right) - \mu - 2\bar{x} - \lambda \right] e^{\lambda t} = 0.
\]
Hence all eigenvalues of $DF(\bar{x})$ are roots of (14). Therefore, if all roots of Eq. (14) have negative real parts, then $\bar{x}$ is locally asymptotically stable and if any root has a positive real part, then $\bar{x}$ is unstable.

At $\bar{x} = 0$, the linearization (15) is

$$\varphi'(t) = \gamma e^{-\tau \mu} \varphi(t) - \mu \varphi(t)$$

(17)

and the characteristic equation (14) at $\bar{x} = 0$ is

$$\gamma e^{-\tau \mu} e^{-\lambda \tau} - \mu - \lambda = 0.$$  

(18)

Note that (17) coincides with the linearization of (4) at $x = 0$ (see Arino et al. 2006, Appendix B). Applying Hayes Theorem (Hayes (1950)), it follows that all roots of Eq. (18) have negative real parts if $\gamma e^{-\mu \tau} < \mu$, and some root of the equation has a positive real part if $\gamma e^{-\mu \tau} > \mu$. This proves (a) and the first part of (b).

To prove the second part of (b), next we assume that $R_0 > 1$. Then a positive equilibrium, $x^* > 0$, for Eq. (9) exists. Using Eq. (12), the characteristic Eq. (14) at $\bar{x} = x^*$ can be written as

$$(\mu + x^*) \left( e^{-\lambda \tau} + \frac{e^{-\lambda \tau} - 1}{\lambda} x^* \right) - \mu - 2x^* - \lambda = 0.$$

Note that $\lambda = 0$ is not a root since the left-hand side of the equation has the nonzero limit, $-[(\mu + x^*) \tau + 1]x^*$, as $\lambda \to 0$. Writing $m = \mu + x^*$, the above equation becomes

$$m(e^{-\lambda \tau} - 1) - \lambda + x^* \left( m \frac{e^{-\lambda \tau} - 1}{\lambda} - 1 \right) = 0,$$

or

$$\left( m \frac{e^{-\lambda \tau} - 1}{\lambda} - 1 \right) (\lambda + x^*) = 0.$$  

(19)

The second factor of the left-hand side of (19) has a single root $\lambda = -x^* < 0$. Let $\lambda = \alpha + i \beta$ be a root of the first factor of the left-hand side of (19). Then

$$m \left[ (e^{-\alpha \tau} \cos \beta \tau - 1) - (e^{-\alpha \tau} \sin \beta \tau)i \right] = \alpha + i \beta.$$

Hence $\alpha < 0$. We conclude that whenever $R_0 > 1$, $x^* > 0$ exists and is local asymptotically stable. \qed
2.2 Global dynamics

In Sect. 2.1 we see that the positive equilibrium $x^*$ of (9) is locally asymptotically stable whenever it exists. In this section we show that in this case $x^*$ attracts all positive solutions and is thus globally asymptotically stable.

The main difficulty in the proof arises from the fact that Eq. (9) does not have a positive delayed feedback, that is, the right hand side of the equation is not an increasing function of the delayed term. In contrast, the alternative logistic DDE (4) has a positive delayed feedback, so the proof in Arino et al. (2006) of the global stability of the positive equilibrium of (4) is not applicable.

**Theorem 1** Consider Eq. (9). Let $\mathcal{R}_0$ be defined by (13).

(a) If $\mathcal{R}_0 \leq 1$, then 0 attracts all nonnegative solutions. Moreover, if $\mathcal{R}_0 < 1$, then 0 is globally asymptotically stable.

(b) If $\mathcal{R}_0 > 1$, then the unique positive equilibrium $x^*$ is globally asymptotically stable.

**Proof** (a) First we assume that $\mathcal{R}_0 \leq 1$. In this case, Eq. (9) has no positive equilibrium. We show that any nonnegative solution $x(t)$ converges to zero as $t \to \infty$. Suppose otherwise. Then

$$\hat{x} := \limsup_{t \to \infty} x(t) > \liminf_{t \to \infty} x(t) \geq 0.$$  

By the fluctuation lemma Hirsch et al. (1985), there exists an increasing sequence of times $\{t_n\}$ such that $\lim_{n \to \infty} x(t_n) = \hat{x}$ and $x'(t_n) = 0$ for all $n$. By (9) it follows that

$$0 = \gamma \exp\left(-\mu \tau - \kappa \int_{t_n - \tau}^{t_n} x(s) \, ds\right) x(t_n - \tau) - \mu \hat{x} - \kappa \hat{x}^2.$$  

Hence

$$0 < \gamma e^{-\mu \tau} x(t_n - \tau) - \mu \hat{x} - \kappa \hat{x}^2.$$  

Taking the lim sup as $n \to \infty$, we obtain

$$0 \leq \gamma e^{-\mu \tau} \hat{x} - \mu \hat{x} - \kappa \hat{x}^2$$  

$$= \hat{x}(\mu(\mathcal{R}_0 - 1) - \kappa \hat{x}) < 0,$$

a contradiction. Hence $\lim_{t \to \infty} x(t)$ exists. By Lemma 1, system (9) has no positive equilibrium when $\mathcal{R}_0 \leq 1$. Hence, all nonnegative solutions converge to 0. By Lemma 1(a) we conclude that 0 is globally asymptotically stable.

(b) Next, we assume that $\mathcal{R}_0 > 1$. For any nonzero nonnegative solution $x(t)$ of (9), we introduce the Lyapunov-type function

$$Y(t) = \gamma \exp\left(-\mu \tau - \kappa \int_{t-\tau}^{t} x(s) \, ds\right) - \mu - \kappa x(t).$$
Then (9) yields

\[
Y'(t) = \gamma \kappa \exp\left(-\mu \tau - \kappa \int_{t-\tau}^{t} x(s)ds\right) \left[-x(t) + x(t-\tau)\right]
- \kappa \left[\gamma \exp\left(-\mu \tau - \kappa \int_{t-\tau}^{t} x(s)ds\right) x(t-\tau) - \mu x(t) - \kappa x^2(t)\right]
= -\kappa x(t)Y(t).
\]

Hence \(Y(t)\) converges monotonically to 0 as \(t\) tends to infinity, that is

\[
\lim_{t \to \infty} \left[\gamma \exp\left(-\mu \tau - \kappa \int_{t-\tau}^{t} x(s)ds\right) - \mu - \kappa x(t)\right] = 0. \tag{20}
\]

By the theory of chain transitive sets (see e.g. Hirsch et al. (2001)), to study the global dynamics of (9), from (20) it is enough to study the restriction of (9) on the set of functions that satisfy the integral equation

\[
\kappa x(t) = \gamma \exp\left(-\mu \tau - \kappa \int_{t-\tau}^{t} x(s)ds\right) - \mu. \tag{21}
\]

The restriction of (9) on the set of functions satisfying (21) can be written as

\[
x'(t) = x(t-\tau)\left[\mu + \kappa x(t)\right] - \mu x(t) - \kappa x^2(t),
\]

or, equivalently,

\[
x'(t) = \left[\mu + \kappa x(t)\right] \left[x(t-\tau) - x(t)\right]. \tag{22}
\]

For any positive solution \(x(t)\) of (22) that satisfies (21), we show that \(x(t)\) converges to \(x^*\). Since the only constant solution satisfying (21) is \(x^*\), it suffices to show that \(x(t)\) converges as \(t \to \infty\).

We set functions

\[
\varphi_n(s) = x(n\tau + s), \quad s \in [0, \tau],
\]

and numbers

\[
A_n = \max_{s \in [0, \tau]} \varphi_n(s),
\]

for \(n = 0, 1, 2, \ldots\). Note that Eq. (22) has a positive delayed feedback. Since each constant function \(A_n\) is a solution of (22), by the comparison theorem for cooperative delay differential equations (Theorem 5.1.1, Smith 1995),

\[
\varphi_{n+1}(s) \leq A_n, \quad s \in [0, \tau],
\]

\[Springer]
Fig. 2 a The function $\varphi_n(s)$ is the restriction of $x(t)$ on the interval $[n\tau, (n+1)\tau]$. The maximum value $A_n$ of $\varphi_n(t)$ is a decreasing sequence. b The function $\psi(t)$ is defined by (25) on $[0, \tau]$ and by (22) for $t \geq \tau$. When $t \geq \tau$, $\psi'(t)$ has the same sign as $\psi(t - \tau) - \psi(t)$. The maximum value of $\psi$ on $[2\tau, 3\tau]$ is strictly less than that on $[0, \tau]$ for $n = 0, 1, 2, \ldots$. It follows that $\{A_n\}$ is a decreasing sequence. Hence,

$$\lim_{n \to \infty} A_n = A,$$

(23)

where $A = \lim \sup_{t \to \infty} x(t)$. To show that $\lim_{t \to \infty} x(t)$ exists, we show that $\{\varphi_n\}_n$ converges to a constant (see Fig. 2a). We claim that every subsequence of $\{\varphi_n\}_n$ has a further subsequence that converges to the constant function $A$ in the $C([0, \tau])$-norm.

Given any subsequence of $\{\varphi_n\}$, since the sequence of functions $\{\varphi_n\}$ is uniformly bounded on the compact set $[0, \tau]$, by the Arzela-Ascoli theorem there is a uniformly convergent further subsequence $\{\varphi_{n_j}\}$. Let $\varphi$ be the limit of $\{\varphi_{n_j}\}$. We extend the domain of $\varphi(s)$ by setting $\varphi(t)$ to be a solution of (22) for $t \geq \tau$. Note that for each $k = 0, 1, 2, \ldots$, the sequence $\{\varphi_{n_j+k}(s)\}_j$ converges uniformly to $\varphi(k\tau + s)$. By (23), it follows that

$$\max_{s \in [0, \tau]} \varphi(k\tau + s) = A$$

(24)

for $k = 0, 1, 2, \ldots$. To prove that $\varphi$ is a constant function, we show that (24) fails to hold for some $k$ if $\varphi$ is non-constant.

Suppose by contradiction that $\varphi$ is non-constant. Then there exists $0 < s_1 < s_2 < \tau$ and $\delta > 0$ such that

$$\varphi(s) < A - \delta, \quad \text{for} \ s \in (s_1, s_2).$$

We define (see Fig. 2b)

$$\psi(s) = \begin{cases} A, & \text{for} \ s \in [0, s_1] \cup [s_2, \tau], \\ A - \delta, & \text{for} \ s \in (s_1, s_2). \end{cases}$$

(25)
Then φ(s) ≤ ψ(s) for s ∈ [0, τ]. We extend the domain of ψ(s) for t ≥ τ by setting ψ(t) to be a solution of (22) for t ≥ τ. With ψ(τ + t) playing the role of x(t) in Eq. (22), the values of ψ′(τ + s) and ψ(s) − ψ(τ + s) have the same sign. By standard ODE theory, it is straightforward to show that

$$\psi(\tau + s) \begin{cases} = A, & \text{for } s \in [0, s_1], \\ < A, & \text{for } s \in (s_1, \tau]. \end{cases} \tag{26}$$

With ψ(2τ + t) playing the role of x(t) in Eq. (22), the values of ψ′(2τ + s) and ψ(s) − ψ(2τ + s) have the same sign. By (26) and the standard ODE theory, it is straightforward to show that

$$\psi(2\tau + s) < A \quad \text{for } s \in [0, \tau]. \tag{27}$$

Since φ(s) ≤ ψ(s) for s ∈ [0, τ], by the comparison theorem we have φ(s) ≤ ψ(s) for s ∈ [0, 3τ]. By (27) it follows that

$$\max_{s \in [0, \tau]} \varphi(2\tau + s) < A,$$

contradicting (24). This implies that φ is a constant function. Hence, x(t) converges to a constant as t → ∞. We conclude that \( \lim_{t \to \infty} x(t) = x^* \). □

### 3 A competition model

In this section, we derive a system modeling the competition between two species, \( x_1 \) and \( x_2 \). For \( i = 1, 2 \), we denote the growth rate of the \( i \)th species by \( \gamma_i \), death rate by \( \mu_i \), decay-consistent delay by \( \tau_i \), the intra-specific competition parameter by \( \kappa_i \), and the inter-specific competition parameter by \( \alpha_i \).

For each fixed time \( t \geq 0 \), we denote by \( X_i(s; \tau_i) \), the number of individuals of species \( x_i \) alive at time \( t - \tau_i \) that survive until time \( t - \tau_i + s \). Assuming decay-consistent delay, the decay rate for species \( x_i \) is a combination of the natural death \( \mu_i X_i(s; \tau_i) \), the intra-specific competition \( \kappa_i X_i(s; \tau_i) x_i(t - \tau_i + s) \), and the inter-specific competition \( \alpha_2 X_1(s; \tau_1) x_2(t - \tau_1 + s) \) rates, \( X_i(s; \tau_i) \) satisfies the following differential equation:

$$X_i'(s; \tau_i) = -\mu_i X_i(s; \tau_i) - \kappa_i X_i(s; \tau_i) x_i(t - \tau_i + s) - \alpha_2 X_1(s; \tau_1) x_2(t - \tau_1 + s),$$

with initial condition, \( X_i(0; \tau_i) = x_i(t - \tau_i) \). This has explicit solution

$$X_i(\tau_1; \tau_1) = x_i(t - \tau_1) \exp\left(-\mu_1 - \int_{t-\tau_1}^{t} \left(\kappa_1 x_1(s) + \alpha_2 x_2(s)\right) ds\right).$$
Similarly, we let $X_2(s; \tau_2)$ be the number of individuals of species $x_2$ that survive from time $t - \tau_2$ to $t - \tau_2 + s$ and assume that

$$X_2(\tau_2; \tau_2) = x_2(t - \tau_2) \exp \left( -\mu \tau_2 - \int_{t-\tau_2}^{t} \left( \kappa_2 x_2(s) + \alpha_1 x_1(s) \right) ds \right).$$

Therefore, we propose the two-species competition model:

\begin{align*}
    x_1'(t) &= \gamma_1 x_1(t - \tau_1) \exp \left( -\mu_1 \tau_1 - \int_{t-\tau_1}^{t} \kappa_1 x_1(s) + \alpha_2 x_2(s) ds \right) \\
    &\quad - \mu_1 x_1(t) - \kappa_1 x_1^2(t) - \alpha_2 x_1(t)x_2(t), \\
    x_2'(t) &= \gamma_2 x_2(t - \tau_2) \exp \left( -\mu_2 \tau_2 - \int_{t-\tau_2}^{t} \kappa_2 x_2(s) + \alpha_1 x_1(s) ds \right) \\
    &\quad - \mu_2 x_2(t) - \kappa_2 x_2^2(t) - \alpha_1 x_1(t)x_2(t). \tag{28}
\end{align*}

Following the proof of Arino et. al. (2006, Proposition 3.1), together with the observation that solutions of (28) satisfy

$$x_i'(t) \leq \gamma_i e^{-\mu_i \tau_i} x_1(t - \tau_i) - \mu_i x_1(t) - \kappa_i x_1^2(t), \quad i = 1, 2, \tag{29}$$

it can be shown that for any solution of (29) with initial data $(\phi_1(t), \phi_2(t))$ where $\phi_1, \phi_2 \in C([0, \tau], \mathbb{R}_+ \setminus \{0\})$, a constant $M$ exists such that

$$M > \max_{t \in [0, \tau]} \phi_i(t) \quad \text{and} \quad \gamma_i e^{-\mu_i \tau_i} - \mu_i - \kappa_i M < 0 \quad \text{for} \quad i = 1, 2,$$

and both components $x_1(t)$ and $x_2(t)$ of the solution remain positive and bounded above by $M$ for all $t > 0$. By the standard theory of delay differential equations, it follows that Eq. (28) is well-posed.

We discuss the existence and stability of equilibria in Sects. 3.1–3.3. Adaptive dynamics for this model is discussed in Sect. 3.4.

**Remark 2** A competition model with state dependent time delays was proposed by Lv et al. (2017), and a diffusive Lotka–Volterra competition model with time delays was proposed by Chen and Shi (2020). Based on the theory of monotone dynamical systems, complete classifications for the global dynamics were derived for both models. However, that method is not applicable for system (28) because even in the absence of $x_2$ (i.e., when setting $x_2 = 0$), the single equation for $x_1$ does not generate a monotone flow due to the negativity of the delayed feedback.

### 3.1 Equilibria

For each species, the survival threshold is defined by

$$R_0^{(i)} = \frac{\gamma_i e^{-\mu_i \tau_i}}{\mu_i}, \quad \text{for} \quad i = 1, 2. \tag{30}$$
There are four possible equilibria: the extinction equilibrium \( E_0 = (0, 0) \); the semi-trivial equilibrium \( E_1 = (x_1^*, 0) \) exists if \( R_0^{(1)} > 1 \); \( E_2 = (0, x_2^*) \) exists if \( R_0^{(2)} > 1 \); and the coexistence equilibrium \( E_c = (x_1^*, x_2^*) \) exists under certain conditions that we will discuss later.

For the semi-trivial equilibrium \( E_i, i = 1, 2, x_i^* \) satisfies

\[
\gamma_i e^{-\tau_i (\mu_i + \kappa_i x_i^*)} = \mu_i + \kappa_i x_i^*.
\]  

The components of \( E_c \) satisfy

\[
\gamma_1 e^{-\tau_1 (\mu_1 + \kappa_1 x_1^* + \alpha_2 x_2^*)} = \mu_1 + \kappa_1 x_1^* + \alpha_2 x_2^*,
\gamma_2 e^{-\tau_2 (\mu_2 + \kappa_2 x_2^* + \alpha_1 x_1^*)} = \mu_2 + \kappa_2 x_2^* + \alpha_1 x_1^*.
\]  

The first equation in (32) implies that the quantity \( \kappa_1 x_1^* + \alpha_2 x_2^* \) satisfies the equation for \( \kappa_1 x_1^* \) in (31). Similarly, the second equation in (32) implies that the quantity \( \kappa_2 x_2^* + \alpha_1 x_1^* \) satisfies the equation for \( \kappa_2 x_2^* \) in (31). Hence,

\[
\kappa_1 x_1^* + \alpha_2 x_2^* = \kappa_1 x_1^*,
\alpha_1 x_1^* + \kappa_2 x_2^* = \kappa_2 x_2^*.
\]  

When \( \kappa_1 \kappa_2 - \alpha_1 \alpha_2 = 0 \), system (33) has a line of solutions in the \( x_1 \)-\( x_2 \) plane. We ignore this marginal case. In the case that \( \kappa_1 \kappa_2 - \alpha_1 \alpha_2 \neq 0 \), system (33) has a unique nonzero solution

\[
x_1^c = \kappa_2 \frac{\kappa_1 x_1^* - \alpha_2 x_2^*}{\kappa_1 \kappa_2 - \alpha_1 \alpha_2}, \quad x_2^c = \kappa_1 \frac{\kappa_2 x_2^* - \alpha_1 x_1^*}{\kappa_1 \kappa_2 - \alpha_1 \alpha_2}.
\]  

Consequently, the coexistence equilibrium \( E_c \) exists when \( R_0^{(1)} > 1, R_0^{(2)} > 1 \) and either the weak interspecific competition condition

\[
\kappa_1 \kappa_2 > \alpha_1 \alpha_2, \quad \kappa_1 x_1^* > \alpha_2 x_2^*, \quad \text{and} \quad \kappa_2 x_2^* > \alpha_1 x_1^* \quad (\text{H}_S)
\]

or the strong interspecific competition condition

\[
\kappa_1 \kappa_2 < \alpha_1 \alpha_2, \quad \kappa_1 x_1^* < \alpha_2 x_2^*, \quad \text{and} \quad \kappa_2 x_2^* < \alpha_1 x_1^* \quad (\text{H}_U)
\]

holds. In Sect. 3.2 we will see that \( E_c \) is locally asymptotically stable if (H_S) holds and is unstable if (H_U) holds.

### 3.2 Local stability

The criteria of local stability of all possible nonnegative equilibria of (28) are listed as follows.
Proof Let $E_0$, $E_1$, $E_2$ and $E_c$ be the possible equilibria given in Sect. 3.1.

(a) $E_0$ is locally asymptotically stable if $R^{(1)}_0 < 1$ and $R^{(2)}_0 < 1$; unstable if either $R^{(1)}_0 > 1$ or $R^{(2)}_0 > 1$.

(b) If $E_1$ exists, it is locally asymptotically stable if $\alpha_1x^*_1 > \kappa_2x^*_2$; unstable if $\alpha_1x^*_1 < \kappa_2x^*_2$.

(c) If $E_2$ exists, it is locally asymptotically stable if $\alpha_2x^*_2 > \kappa_1x^*_1$; unstable if $\alpha_2x^*_2 < \kappa_1x^*_1$.

(d) If a unique $E_c$ exists, it is locally asymptotically stable if $(H_S)$ holds and unstable if $(H_U)$ holds.

The results of this proposition are summarized in Table 1.

Proof Let $E = (\tilde{x}_1, \tilde{x}_2)$ be an equilibrium of (28). Then the corresponding Jacobian matrix at $E$ is

$$
M(E) = \begin{pmatrix}
\gamma_1 e^{-\lambda_1 \tau_1 - \tau_1 m_1} - \mu_1 - 2\kappa_1 \tilde{x}_1 - \alpha_2 \tilde{x}_2 & -\alpha_2 \tilde{x}_1 \\
-\alpha_1 \tilde{x}_2 & \gamma_2 e^{-\lambda_2 \tau_2 - \tau_2 m_2} - \mu_2 - \alpha_1 \tilde{x}_1 - 2\kappa_2 \tilde{x}_2
\end{pmatrix}
$$

where

$$
m_1 = \mu_1 + \kappa_1 \tilde{x}_1 + \alpha_2 \tilde{x}_2, \quad m_2 = \mu_2 + \alpha_1 \tilde{x}_1 + \kappa_2 \tilde{x}_2.
$$

At the equilibrium $E_0 = (0, 0)$,

$$
M(E_0) = \det \begin{pmatrix}
\gamma_1 e^{-\lambda_1 \tau_1 - \tau_1 \mu_1} - \mu_1 - \lambda & 0 \\
0 & \gamma_2 e^{-\lambda_2 \tau_2 - \tau_2 \mu_2} - \mu_2 - \lambda
\end{pmatrix}.
$$

The eigenvalues of $M(E_0)$ are $\mu_1(R^{(1)}_0 - 1)$ and $\mu_2(R^{(2)}_0 - 1)$. Hence $E_0$ is locally asymptotically stable if and only if $R^{(1)}_0 < 1$ and $R^{(2)}_0 < 1$, and is unstable if $R^{(1)}_0 > 1$ or $R^{(2)}_0 > 1$.

Table 1 Criteria of the existence and local stability of all possible nonnegative equilibria of system (28)

| Equilibrium | Existence | Stability conditions |
|-------------|-----------|----------------------|
| $E_0 = (0, 0)$ | Always | $R^{(1)}_0 < 1$ and $R^{(2)}_0 < 1$ |
| $E_1 = (x^*_1, 0)$ | $R^{(1)}_0 > 1$ | $\alpha_1 x^*_1 > \kappa_2 x^*_2$ |
| $E_2 = (0, x^*_2)$ | $R^{(2)}_0 > 1$ | $\alpha_2 x^*_2 > \kappa_1 x^*_1$ |
| $E_c = (x_c, y_c)$ | $R^{(1)}_0 > 1$, $R^{(2)}_0 > 1$ and either $(H_S)$ or $(H_U)$ holds | $(H_S)$ |
When $R_0^{(1)} > 1$, the semi-trivial equilibrium $E_1 = (x_1^*, 0)$ exists. From (31), the number $m_1$ defined in (35) satisfies

$$m_1 = \gamma_1 e^{-\tau_1 m_1}.$$ 

Hence Eq. (34) gives

$$M(E_1) = \begin{pmatrix}
  m_1 e^{-\lambda \tau_1} - \mu_1 - 2\kappa_1 x_1^* & -\alpha_2 x_1^* \\
 0 & -\alpha_1 x_1^*
\end{pmatrix}
+ \begin{pmatrix}
  e^{-\lambda \tau_1 - 1} \kappa_1 x_1^* & \gamma_1 e^{-\tau_1 m_1} e^{-\lambda \tau_1 - 1} \alpha_2 x_1^* \\
 0 & \gamma_2 e^{-\tau_2 m_2}
\end{pmatrix}
- \lambda \begin{pmatrix}1 & 0 \end{pmatrix}.$$

Since $M(E_1)$ is a upper triangular matrix, the roots for $\det(M(E_1)) = 0$ are

$$\lambda_1 = m_1 \left[ e^{-\lambda \tau_1} + \frac{e^{-\lambda \tau_1 - 1}}{\lambda} \kappa_1 x_1^* \right] - \mu_1 - 2\kappa_1 x_1^*$$

and

$$\lambda_2 = \gamma_2 e^{-\lambda \tau_2 = \tau_2 m_2} - \mu_2 - \alpha_1 x_1^*.$$ 

The real part of $\lambda_1$ is negative by the proof of Lemma 1(b). Hence $E_1$ is locally asymptotically stable if and only if the real part of $\lambda_2$ is negative, that is

$$\gamma_2 e^{-\tau_2 (\mu_2 + \alpha_1 x_1^*)} - (\mu_2 + \alpha_1 x_1^*) < 0,$$

or

$$\alpha_1 x_1^* > \kappa_2 x_2^*.$$ 

Similarly, the equilibrium $E_2$ is locally asymptotically stable if and only if

$$\alpha_2 x_2^* > \kappa_1 x_1^*.$$ 

When $R_0^{(1)}$, $R_0^{(2)} > 1$, the coexistence equilibrium, $E_c = (x_1^c, x_2^c)$. From (32), the numbers $m_1$ and $m_2$ defined in (35) satisfy

$$m_1 = \gamma_1 e^{-\tau_1 m_1}, \quad m_2 = \gamma_2 e^{-\tau_2 m_2}.$$ 

Hence Eq. (34) gives

$$M(E_c) = \begin{pmatrix}
  -m_1 - \kappa_1 x_1^* & -\alpha_2 x_1^* \\
  -\alpha_1 x_2^* & -m_2 - \kappa_2 x_2^*
\end{pmatrix}
+ \begin{pmatrix}
  e^{-\lambda \tau_1 m_1} & 0 \\
 0 & e^{-\lambda \tau_2 m_2}
\end{pmatrix}
+ \begin{pmatrix}
  e^{-\lambda \tau_1 - 1} m_1 \kappa_1 x_1^* & e^{-\lambda \tau_1 - 1} m_1 \alpha_2 x_1^* \\
 0 & e^{-\lambda \tau_1 - 1} m_2 \kappa_2 x_2^*
\end{pmatrix}
- \lambda \begin{pmatrix}1 & 0 \end{pmatrix}.$$
By a straightforward computation, the characteristic equation \( \det(M(E^c)) = 0 \) can be written as

\[
\left( m_1 e^{-\lambda \tau_1} - 1 \right) \left( m_2 e^{-\lambda \tau_2} - 1 \right) \left[ (\lambda + \kappa_1 x_1^c)(\lambda + \kappa_2 x_2^c) - \alpha_1 \alpha_2 x_1^c x_2^c \right] = 0.
\]

Note that the terms \( \left( m_i e^{-\lambda \tau_i} - 1 \right), i = 1, 2 \), as shown in the proof of Lemma 1, have no root with non-negative real parts, so all roots of \( \det(M(E^c)) = 0 \) with non-negative real parts are roots of the quadratic equation

\[
\lambda^2 + (\kappa_1 x_1^c + \kappa_2 x_2^c)\lambda + x_1^c x_2^c (\kappa_1 \kappa_2 - \alpha_1 \alpha_2) = 0.
\]

Since \( \kappa_1 x_1^c + \kappa_2 x_2^c > 0 \), this equation has no roots with positive real parts if \( \kappa_1 \kappa_2 > \alpha_1 \alpha_2 \), and has exactly one root with a positive real part if \( \kappa_1 \kappa_2 < \alpha_1 \alpha_2 \). Therefore, we conclude that when \( E_c \) exits, it is locally asymptotically stable when there is weak competition between the competitors, and it is unstable with one dimensional stable manifold under the condition for strong competition. \( \square \)

### 3.3 Some results on global dynamics

In this section we study the global dynamics of system (28). First we show that a necessary condition for the \( i \)th species to survive is \( R_0^{(i)} > 1 \), where \( i \in \{1, 2\} \) and \( R_0^{(i)} \) is defined by (30).

**Theorem 2** If \( R_0^{(i)} \leq 1 \), where \( i \in \{1, 2\} \), then \( \lim_{t \to \infty} x_i(t) = 0 \).

**Proof** We consider only the case \( R_0^{(1)} \leq 1 \) since the case \( R_0^{(2)} \leq 1 \) can be treated similarly. We proceed with proof by contradiction. Suppose that \( x_1(t) \) does not converge to 0. Denote \( \bar{x}_1 = \lim \sup_{t \to \infty} x_1(t) > 0 \). Then either (i) \( x_1(t) \) converges to \( \bar{x}_1 \) or (ii) there exists an increasing sequence of times \( \{t_n\} \) such that \( x_1'(t_n) = 0 \) and \( \lim_{n \to \infty} x_1(t_n) = \bar{x}_1 \).

In case (i), for any \( \varepsilon > 0 \) we have \( \bar{x}_1 - \varepsilon < x_1(t) < \bar{x}_1 + \varepsilon \) for all sufficiently large \( t \). From (28) it follows that

\[
x_1'(t) < \gamma_1 (\bar{x}_1 + \varepsilon) e^{-\mu_1 \tau_1 - (\bar{x}_1 - \varepsilon) \tau_1} - \mu_1 (\bar{x}_1 - \varepsilon).
\]

Note that as \( \varepsilon \to 0 \) the right-hand side of the inequality converges to

\[
\gamma_1 \bar{x}_1 e^{-\mu_1 \tau_1 - \bar{x}_1 \tau_1} - \mu_1 \bar{x}_1 < \gamma_1 \bar{x}_1 e^{-\mu_1 \tau_1} - \mu_1 \bar{x}_1 = \mu_1 \bar{x}_1 (R_0^{(1)} - 1) \leq 0.
\]

This implies that \( \lim \sup x_1'(t) < 0 \), contradicting the assumption that \( x_1(t) \) converges to \( \bar{x}_1 \).

\( \square \) Springer
In case (ii),
\[ 0 = x'_1(t_n) \]
\[ = \gamma_1 x_1(t_n - \tau_1) \exp \left( -\mu_1 \tau_1 - \kappa_1 \int_{t_n - \tau_1}^{t_n} x_1(s) + \alpha_1 x_2(s)ds \right) \]
\[ - \mu_1 x_1(t_n) - \kappa_1 x_1^2(t_n) - \alpha_2 x_1(t_n) x_2(t_n) \]
\[ < \gamma_1 x_1(t_n - \tau_1) \exp (-\mu_1 \tau_1) - \mu_1 x_1(t_n) - \kappa_1 x_1^2(t_n) - \alpha_1 x_1(t_n) x_2(t_n). \]

As \( n \to \infty \),
\[ 0 \leq \gamma_1 e^{-\mu_1 \tau_1} \limsup_{n \to \infty} x_1(t_n - \tau_1) - \mu_1 \bar{x}_1 - \kappa_1 \bar{x}_1^2 - \alpha_1 \bar{x}_1 \inf_{n \to \infty} x_2(t_n) \]
\[ \leq \gamma_1 e^{-\mu_1 \tau_1} \bar{x}_1 - \mu_1 \bar{x}_1 - \kappa_1 \bar{x}_1^2 - \alpha_1 \bar{x}_1 \inf_{n \to \infty} x_2(t_n) \]
\[ = \bar{x}_1 \left[ \gamma_1 e^{-\mu_1 \tau_1} - \mu_1 \right] - \kappa_1 \bar{x}_1^2 - \alpha_1 \bar{x}_1 \liminf_{n \to \infty} x_2(t_n) < 0, \]
a contradiction. Thus \( x_1(t) \) converges to 0. \( \square \)

From this theorem, we conclude that if \( R_0^{(i)} \leq 1 \), then \( x_i \) converges to 0, and system (28) reduces to the single species model (9) studied in Sect. 2. Therefore, when at least one of \( R_0^{(1)} \) and \( R_0^{(2)} \) is less than 1, we have the following results.

**Corollary 1** Consider system (28). Then the following assertions hold for any positive solution \((x_1(t), x_2(t))\).

(a) If \( R_0^{(1)} \leq 1 \) and \( R_0^{(2)} \leq 1 \), then \((x_1(t), x_2(t))\) converges to \( E_0 \).
(b) If \( R_0^{(1)} > 1 \) and \( R_0^{(2)} \leq 1 \), then \((x_1(t), x_2(t))\) converges to \( E_1 \).
(c) If \( R_0^{(1)} \leq 1 \) and \( R_0^{(2)} > 1 \), then \((x_1(t), x_2(t))\) converges to \( E_2 \).

From the local stability analysis in Sect. 3.2 and the simulations shown later in this section, we propose the following conjectures concerning the global dynamics of system (28).

**Conjecture 1** Consider system (28). Assume \( R_0^{(1)} > 1 \) and \( R_0^{(2)} > 1 \). Then, for any solution \((x_1(t), x_2(t))\) with positive initial data, the following assertions hold:

(a) If \( \alpha_1 x_1^* > \kappa_2 x_2^* \) and \( \kappa_1 x_1^* > \alpha_2 x_2^* \), then \((x_1(t), x_2(t))\) converges to \( E_1 \).
(b) If \( \alpha_1 x_1^* < \kappa_2 x_2^* \) and \( \kappa_1 x_1^* < \alpha_2 x_2^* \), then \((x_1(t), x_2(t))\) converges to \( E_2 \).
(c) If \((H_3)\) holds, then \((x_1(t), x_2(t))\) converges to \( E_c \).
(d) If \((H_2)\) holds, then for any initial data that is not on the one-dimensional stable manifold of \( E_c \), the solution \((x_1(t), x_2(t))\) converges to either \( E_1 \) or \( E_2 \).

When time delays are small enough \( (\tau < \tau_H^i) \), then our model of competition between two species has similar outcomes to the corresponding classical Lotka–Volterra competition ODE model. However, when delays are large, i.e., \( \tau > \tau_H^i \), in our delay model, species \( x_i \) dies out. That does not happen in the corresponding ODE model. In Wolkowicz and Xia (1997), the same conclusion was obtained for the two species competition model with delay in a chemostat.
Fig. 3 Bifurcation diagrams for system (28) with strong interspecies competition, i.e., $\alpha_1 \alpha_2 > \kappa_1 \kappa_2$. In region $D$, the conditions $R_0^{(1)} < 1$ and $R_0^{(2)} < 1$ hold, and all solutions converge to $E_0$. Region $C$ is bounded above by the curve $\alpha_1 x_1^* = \kappa_2 x_2^*$ (dashed curve) and bounded below by the curve $\alpha_2 x_2^* = \kappa_1 x_1^*$ (solid curve). Condition (H$_U$) is satisfied in this region, and solutions converge to either $E_1$ or $E_2$. Regions $A$ and $B$ corresponds to cases (a) and (b) in Conjecture 1. For $(\tau_1, \tau_2)$ in region $A$, only $x_1$ survives; for $(\tau_1, \tau_2)$ in region $B$, only $x_2$ survives.

Bifurcation diagrams and numerical simulations that illustrate Conjecture 1 are shown in Figs. 3 and 4. The bifurcations curves are the contours of $R_i^0 = 1$, $i = 1, 2$, $\alpha_1 x_1^* = \kappa_2 x_2^*$ and $\alpha_2 x_2^* = \kappa_1 x_1^*$, which are defined analytically in (30) and (31). The simulations were obtained using dde23 in MATLAB (2021). In the simulations, we introduced variables $\xi_i(t) = \frac{1}{\tau_i} \int_{t-\tau_i}^{t} x(s) \, ds$, $i = 1, 2$ that convert the system of distributed delay equations (28) into the system of discrete delay equations

\[
\begin{align*}
\dot{x}_1(t) &= \gamma_1 x_1(t - \tau_1) e^{-\tau_1[\mu_1 + \kappa_1 x_1(t) + \alpha_2 x_2(t)]} - x_1(t) \left[ \mu_1 + \kappa_1 x_1(t) + \alpha_2 x_2(t) \right] \\
\dot{x}_2(t) &= \gamma_2 x_2(t - \tau_2) e^{-\tau_2[\mu_2 + \alpha_1 x_1(t) + \kappa_2 x_2(t)]} - x_2(t) \left[ \mu_2 + \alpha_1 x_1(t) + \kappa_2 x_2(t) \right] \\
\dot{\xi}_1(t) &= \frac{1}{\tau_1} [x_1(t) - x_1(t - \tau_1)] , \\
\dot{\xi}_2(t) &= \frac{1}{\tau_2} [x_2(t) - x_2(t - \tau_2)].
\end{align*}
\]  

(36)

In both figures, we take $(\gamma_1, \mu_1, \gamma_2, \mu_2) = (2, 0.5, 1.5, 0.5)$ and use the delays $\tau_1$ and $\tau_2$ as bifurcation parameters. In Fig. 3, we take $(\alpha_1, \alpha_2, \kappa_1, \kappa_2) = (1, 1.5, 0.8, 1)$, which satisfies the strong interspecies competition condition $\alpha_1 \alpha_2 > \kappa_1 \kappa_2$. In region
Fig. 4 Bifurcation diagrams for system (28) with weak interspecies competition, i.e., $\alpha_1 \alpha_2 < \kappa_1 \kappa_2$. Regions $A$, $B$ and $D$ are similar to the corresponding regions in Fig. 3. Region $C$ is bounded above by the curve $\alpha_2 x_2^* = \kappa_1 x_1^*$ (solid curve) and bounded below by the curve $\alpha_1 x_1^* = \kappa_2 x_2^*$ (dashed curve). Condition (HS) is satisfied in this region, and all solutions converge to the coexistence equilibrium $E_c$.

$D$, where both $\tau_1$ and $\tau_2$ are greater than certain critical values, the conditions that $R_0^{(1)} < 1$ and $R_0^{(2)} < 1$ hold, so solutions of system (28) converge to $E_0$ according to Theorem 2. Region $C$, bounded above by the curve $\alpha_1 x_1^* = \kappa_2 x_2^*$ and bounded below by the curve $\alpha_2 x_2^* = \kappa_1 x_1^*$ is where condition (H_U) is satisfied. We choose $(\tau_1, \tau_2) = (1, 1.5)$ in region $C$. With the constant initial data $(x_1, x_2) = (0.8, 0.1)$, only $x_1$ survives; with the constant initial data $(x_1, x_2) = (0.1, 0.8)$ only $x_2$ survives. Regions $A$ and $B$ correspond to cases (a) and (b) in Conjecture 1. We chose $(\tau_1, \tau_2) = (1, 2)$ in region $A$ and verified that only $x_1$ survives. We chose $(\tau_1, \tau_2) = (1.5, 1)$ in region $B$ and verified that only $x_2$ survives.

In Fig. 4, we take $(\alpha_1, \alpha_2, \kappa_1, \kappa_2) = (1, 0.5, 1.2, 1)$, which satisfies the weak interspecies competition condition $\alpha_1 \alpha_2 < \kappa_1 \kappa_2$. Regions $A$, $B$, and $D$ are similar to the corresponding regions in Fig. 3. Region $C$, bounded above by the curve $\alpha_2 x_2^* = \kappa_1 x_1^*$ and bounded below by the curve $\alpha_1 x_1^* = \kappa_2 x_2^*$ is where condition (HS) is satisfied. We choose $(\tau_1, \tau_2) = (1, 1)$ in region $C$. With the constant initial data $(x_1, x_2) = (0.8, 0.8)$, we verified that both $x_1$ and $x_2$ survive.
3.4 Adaptive dynamics

Adaptive dynamics is a set of techniques that can be used to predict how traits evolve. In this section, we use adaptive dynamics to consider how the length of the delay, $\tau$, in our model is predicted to evolve.

Assume that the resident species is denoted by $x_1$ and the mutant species is denoted by $x_2$. Assume also that before the arrival of any members of the mutant species, the resident population size has converged to its delay reduced carrying capacity $x_1^*$ given by (31). Then the equation for $x_2'(t)$ at the time of the arrival of the first mutants given by (28) can be assumed to satisfy:

$$x_2' = \gamma_2 \exp \left( -\mu_2 \tau - \kappa_2 \int_{t-\tau_2}^{t} x_2(s) ds - \alpha_1 x_1^* \tau_2 \right) x_2(t - \tau_2) - \mu_2 x_2(t) - \kappa_2 x_2^2(t) - \alpha_1 x_1^* x_2(t).$$

Thus, $x_2$ can invade if

$$0 < \gamma_2 e^{-\tau_2(\mu_2 + \alpha_1 x_1^*)} - \mu_2 - \alpha_1 x_1^*,$$

or, equivalently, using (31),

$$\kappa_2 x_2^* > \alpha_1 x_1^*.$$

Hence, the invasion exponent for mutant $x_2$ (see e.g. Diekmann (2004)) is

$$r_{x_1^*}(x_2^*) = \kappa_2 x_2^* - \alpha_1 x_1^*$$.  \hfill (37)

Notice that $x_2$ can invade if $r_{x_1^*}(x_2^*) < 0$.

We next assume that the resident and mutant populations are identical except for their delay, and thus, $\gamma_1 = \gamma_2 := \gamma$, $\mu_1 = \mu_2 := \mu$ and $\kappa_1 = \kappa_2 = \alpha_1 = \alpha_2 := \kappa$. From (37), it follows that $x_2$ can invade if $x_2^* > x_1^*$. Without loss of generality, we scale $\kappa \mapsto 1$ in this section. We consider the delay reduced carrying capacity as a function of the time delay. Then the positive equilibrium of (9), denoted by $x^*(\tau)$, is given by

$$\gamma e^{-\tau(\mu + x^*(\tau))} = \mu + x^*(\tau).$$

Differentiating this equation implicitly yields

$$\frac{dx^*(\tau)}{d\tau} = -\frac{(\mu + x^*(\tau)) \gamma e^{-\tau(\mu + x^*(\tau))}}{1 + \gamma \tau e^{-\tau(\mu + x^*(\tau))}} < 0.$$  

Hence, the invasion exponent $r_{x_1^*}(x_2^*) = x^*(\tau_2) - x^*(\tau_1)$ is negative if and only if $\tau_2 < \tau_1$. Thus, the following result follows.
**Result 1** If resident and mutant species have identical parameters except for the delay, then if the mutant takes a strategy with shorter delay than the resident it would have a larger delay reduced carrying capacity and would be able to invade successfully. Thus, the evolutionary trend is to make the time delay as short as possible.

The conclusion that the species with shorter maturation time prevails was also derived by Chen and Shi (2020) and Lin et al. (2018) for different models.

Next we discuss the situation where there is a trade-off between the growth rate and time delay. Motivated by the assumption that the species with shorter delay produces fewer newborns than the species with longer delay, we assume that the growth rate is an increasing function of time delay \( \tau \). More specifically, we let \( \gamma(\tau) = \gamma_0(1 + c\tau) \), where \( \gamma_0 \) and \( c \) are positive constants. For simplicity, we assume that \( \mu_1 = \mu_2 := \mu \) and that \( \kappa_i = \alpha_i = 1 \). Then Eq. (12) becomes

\[
\gamma_0(1 + c\tau)e^{-\tau(\mu + c^*x)} - (\mu + x) = 0, \tag{38}
\]

and the threshold value \( \tau_H \) for the existence of \( x^* \) is determined by

\[
\gamma_0(1 + c\tau_H)e^{-\mu\tau_H} = \mu. \tag{39}
\]

We assume that \( \gamma_0 > \mu \) to ensure that the threshold value \( \tau_H \) defined by (39) is positive. Differentiating (38) implicitly yields

\[
\frac{dx^*(\tau)}{d\tau} = \frac{\gamma_0 e^{-\tau(\mu + c^*x(\tau))}}{1 + \gamma_0 \tau e^{-\tau(\mu + c^*x(\tau))}} \left[ c - (1 + c\tau)(\mu + x^*(\tau)) \right]. \tag{40}
\]

Setting \( \tau = 0 \) in (38) gives \( x^*(0) = \gamma_0 - \mu \). By (40) it follows that \( \frac{dx^*}{d\tau}(0) \) has the same sign as \( c - \gamma_0 \). Note also that \( \frac{dx^*}{d\tau}(\tau_H) \leq 0 \) since \( x^*(\tau_H) = 0 \) and \( x^*(\tau) > 0 \) for \( \tau < \tau_H \). Therefore, in the case that \( c > \gamma_0 \), there exists at least one \( \tau^* < \tau_H \) such that \( \tau^* > 0 \) is a critical point of \( x^*(\tau) \). In terms of Evolutionary Game Theory (see e.g. Vincent and Brown (2005)), all members of a population adopting \( \tau = \tau^* \) is an evolutionarily stable strategy (ESS), which means that no mutant strategy could invade the population under the influence of natural selection.

**Result 2** If the growth rate and the delay are linearly positively correlated and the growth rate with no delay is large enough, then there is a critical value \( \tau^* > 0 \) such that taking \( \tau \) to be \( \tau^* \) is an ESS.

Consider for example \( c = 8, \gamma_0 = 3 \) and \( \mu = 2 \). The graph of \( x^*(\tau) \) is shown in Fig. 5. In this case, the function \( x^*(\tau) \) has a global maximum point \( \tau^* \). Thus, for the evolution of trait \( \tau \), the best strategy is to make the delay as close to \( \tau^* \) as possible.

### 4 Conclusion and discussion

Based on the assumption of the decay-consistent delay in growth for model (4) in Arino et al. (2006), we derived the novel single species delayed model (9). The main
**Fig. 5** The graph of $x^*(\tau)$, where $x^*(\tau)$ is the solution of (12) with $\gamma(\tau) = \gamma_0(1 + c\tau)$.

When $c = 8$, $\gamma_0 = 3$ and $\mu = 2$, the threshold delay is $\tau_H \approx 1.48$, and the graph has a unique local maximum $\tau^* \approx 0.14$ in the interval $(0, \tau_H)$.

difference between these two models is whether juveniles and adults compete with each other. In model (4) the mature subgroup only competes within that subgroup. In contrast, in our model (9) the mature subgroup competes with the whole population. These two models fit different types of behavior. Model (4) is suitable for species whose development includes several stages (egg, larva, pupa, and adult) such as holometabolous insects, for which juveniles do not compete with adults because they have different living environments, and there is no intraspecific competition (crowding or direct interference) between juveniles and adults. On the other hand, model (9) is suitable for most mammalian species, for which juveniles and adults share the same environment.

All solutions of our logistic growth DDE (9) converge to an equilibrium with value depending on the delay. If the delay is too long, this model predicts that the population dies out. A threshold giving the interface between extinction and survival is determined in terms of parameters in the model. Our model and model (4) have similar dynamics. While they have different positive equilibria, they have the same survival threshold $R_0$, given by (13). The population approaches the delay reduced carrying capacity if $R_0 > 1$; otherwise it goes to extinction. Thus neither model has sustained oscillations as in Hutchinson’s equation (1), which exhibits stable periodic solutions when $\tau$ is large enough (see e.g. Hale and Verduyn Lunel (1993)).

Using DDE-BIFTOOL Engelborghs et al. (2002); Sieber et al. (2014), we show a comparison of the dynamics of Hutchinson’s equation and models (4) and (9) in Fig. 6. This software can be used to perform the continuation of isolated equilibria on delay differential equations without integrals. The trick of introducing an integral variable $\xi$ as in (36) is not suitable in this situation because the converted system always has lines of equilibria. In the simulations, we approximate the distributed delay equation (9) by the discrete delay equation

$$x'(t) = \gamma x(t - \tau)e^{-\mu \tau - \frac{\tau}{n}} \sum_{i=0}^{n-1} x(t - \frac{i}{n}\tau) - \mu x(t) - \kappa x^2(t)$$  \hspace{1cm} (41)

with positive integer $n$. Using the auxiliary variables $x_i(t) = x(t - \frac{i}{n}\tau)$, $i = 0, 1, 2, \ldots, n - 1$, Eq. (41) can be written as

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Fig. 6 Bifurcation diagrams for (a) Hutchinson’s equation with $r = K = 1$, and (b) the alternative logistic DDE (4), denoted by ADDE, and the mixed alternative logistic DDE (9), denoted by MADDE, with $\gamma = 1.5$, $\mu = 0.5$ and $\kappa = 1$. In each figure, $\text{EP}^-$ indicates asymptotically stable equilibrium point, $\text{EP}^+$ indicates unstable equilibrium point, and $\text{PO}^-$ indicates an orbitally asymptotically stable periodic orbit.

Notice that in (a) the interior equilibrium is a constant function of the delay, but in (b), the interior equilibria are decreasing functions of the delay $\tau$ and on the left of the transcritical bifurcation involving the interior equilibria and the extinction equilibrium, the stable interior equilibrium for the ADDE model is slightly larger than the stable equilibrium for the MADDE model.

Equations (4) and (9) can be written in a unified form

$$x'(t) = \gamma x(t - \tau)e^{-\mu(t-\tau)} - \mu x(t) - \kappa x^2(t)$$

for $i = 0, 1, 2, \ldots, n - 1$, which forms a system of discrete delay equations with a constant delay $\tau$. In Fig. 6b we used system (42) with $n = 6$ to approximate (9) and compared it with the simulation of Eq. (4).

Equations (4) and (9) can be written in a unified form

$$x'(t) = \gamma x(t - \tau)F(x, t)e^{-\mu(t-\tau)} - \mu x(t) - \kappa x^2(t)$$

where, for (4),

$$F(x, t) = \frac{1}{1 + \frac{\kappa}{\mu}(1 - e^{-\mu(t-\tau)})} = 1 - \kappa \tau x(t - \tau) + O(\kappa^2 + \mu^2)$$

as $(\kappa, \mu) \to 0$ and for (9),

$$F(x, t) = \exp\left(-\kappa \int_{t-\tau}^{t} x(s) \, ds\right) = 1 - \kappa \int_{t-\tau}^{t} x(s) \, ds + O(\kappa^2)$$

as $\kappa \to 0$.

Note that the linear parts of (43) and (44) coincide when $x(t)$ is a constant function. This explains why the interior equilibria for both systems are close to each other in Fig. 6b.

Another advantage of our derivation of the logistic DDE is that it can readily involve more than one interacting population. The alternative logistic DDE of Arino...
et al. (2006) can also be extended to a competition model under certain conditions (see Lin et al. (2018)), but it is unclear how to modify that approach in general. Our competitive system (28) was naturally generalized from our logistic DDE (9).

The outcome of (28) parallels that of the two-species Lotka–Volterra competitive ODE system. That is, either one of the three situations holds: competitive exclusion, two species bistability, or the existence of a globally stable coexistence equilibrium. The same conclusion holds for the competition models with time delays studied by Lv et al. (2017) and Chen and Shi (2020).

From the adaptive dynamics analysis, if the resident and mutant species are identical except for their time delay, then the evolutionary trend is to make the delay as short as possible. Thus, after long term evolution, the time delay would approach zero, and the system would reduce to a system of ODEs. However, a time delay for both reproduction and growth does exist in actual species. Therefore, we also consider the case when the mutant has the same parameters except for their time delay and their growth rate, and hence there is a trade-off between the growth rate and the delay. Say the longer delay allows more or larger newborns. Then, there may be a positive delay \( \tau^* \) that maximizes the delay reduced carrying capacity and \( 0 < \tau^* < \tau_H \). In this scenario, the delay trait in natural ecosystems would tend to move toward \( \tau^* > 0 \) according to our model.

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