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BISTABILITY OF A TWO-SPECIES GILPIN-AYALA COMPETITION MODEL WITH STAGE STRUCTURE

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Abstract The dynamic behavior of bistability is considered for a two-species Gilpin-Ayala competition model with stage structure. By the theory of generalized saddle-point behavior for monotone semiflows, it is shown that there admits an invariant and K-unordered C^1-separatrix, which separates the basins of attraction of the two locally stable single-species steady states. This implies that bistability occurs for two species. When two delays vary in their existence regions, we prove that the stability switching of the positive equilibria does not arise. By comparing with classical two-species Gilpin-Ayala competition model, we find that the introduction of stage structure brings negative effect on permanence of one species, but positive effect on its competitor. Finally, some numerical examples are given to illustrate the effectiveness of our theoretical results.

Keywords Gilpin-Ayala, bistability, competition, stage structure, monotone semiflow.

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1. Introduction

In the biological science and population ecology, there are many mathematical competition models in which an increase of the population density of one species does have a negative effect on the per capita growth rate of other species. The most famous one is the Lotka-Volterra competiton model, which has been extensively studied in the literature during the last decades. Later, Gilpin and Ayala [7] pointed out that Lotka-Volterra systems are the linearization of the per capita growth rates $\dot{N}_i/N_i$ about the equilibrium. In order to fit data in their experiments on fruit fly dynamics and to test the validity of competition results, they stated that a slightly more complicated model was needed. Thus, they presented the following

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competition model:

$$\begin{cases} \dot{x}_1(t) = x_1(t)\big(b_1 - a_{11}x_1^{1+\theta_1}(t) - a_{12}x_2(t)\big), \\ \dot{x}_2(t) = x_2(t)\big(b_2 - a_{22}x_2^{1+\theta_2}(t) - a_{21}x_1(t)\big), \\ \big(x_1(0), x_2(0)\big) = x_0 \in \mathbb{R}_+^2, \end{cases} \tag{1.1}$$

where $\theta_i > 0$ $(i = 1, 2)$ stands for a non-linear measure of interspecific interference. There are also many investigations on system (1.1), including deterministic type and random type (see [8, 9, 14, 17, 21, 23]). In these literatures, verifiable sufficient conditions that guarantee the extinction and persistence are provided. However, it is assumed that each species admits the same density-dependent rate and the identical ability to compete with other species. For many animals, whose babies are raised by their parents or are dependent on the nutrition from the eggs, the babies are much weaker than the mature. Their competition with other individuals can be ignored. Based on this, Liu et al. [16] introduced the maturation time delay into the Gilpin-Ayala competition model (1.1) and derived the following model with stage structure,

$$\begin{cases} \dot{y}_1(t) = b_1x_1(t) - d_1y_1(t) - b_1e^{-d_1\tau_1}x_1(t-\tau_1), \\ \dot{x}_1(t) = b_1e^{-d_1\tau_1}x_1(t-\tau_1) - a_{11}x_1^{1+\theta_1}(t) - a_{12}x_1(t)x_2(t), \\ \dot{y}_2(t) = b_2x_2(t) - d_2y_2(t) - b_2e^{-d_2\tau_2}x_2(t-\tau_2), \\ \dot{x}_2(t) = b_2e^{-d_2\tau_2}x_2(t-\tau_2) - a_{22}x_2^{1+\theta_2}(t) - a_{21}x_1(t)x_2(t), \\ x_i(t) = \varphi_i(t), y_i(t) = \xi_i(t), \quad -\tau_i \le t \le 0, \quad i = 1, 2, \end{cases} \tag{1.2}$$

where $x_i(t)$ and $y_i(t)$ $(i = 1, 2)$ denote the density of the mature and that of the immature of the ith species, respectively. τ_i $(i = 1, 2)$ represents the time length of its immature stage. They obtained global asymptotical stability criteria for stable coexistence and competitive exclusion between two species, as well as the effects of the nonlinear intraspecific regulation parameter θ_i $(i = 1, 2)$.

Recall that a biological phenomena is called *Bistability* if a dynamical system possesses three equilibria a, b and c such that a and b are stable attractors, and the state space is divided into three disjoint and invariant parts: the basin of attraction B_1 of a, the basin of attraction B_2 of b and a manifold M containing c with codimension one. Here, M is usually called the separatrix of the domains of attraction B_1 and B_2. Such a system is also said to admit a *saddle-point structure/behavior*. If the equilibrium c is replaced by a set of some equilibria and the same statements as above hold, then such a system is said to admit a *generalized saddle-point structure/behavior* (see Jiang et al. [12]).

Bistability is widely used by theoretical ecologists, chemists and physicists to explain different kinds of biological, chemical and physical phenomena. For example, Murray [18] considered a two-species Lotka-Volterra competition model and observed that the bistability occurs for two competing species under appropriate conditions. More precisely, there admits a separatrix curve connecting the original point to the infinity in the phase space $\mathbb{R}_+^2$ such that species 1 wins whenever the initial value is below the curve, while species 2 wins whenever the initial value is above the curve. By introducing a reaction-diffusion term to two-species competition Lotka-Volterra model, Iida et al. [11] reconsidered its bistability and found an interesting phenomenon. If the two species do not migrate, then the numerically superior species will wipe out the inferior one, however, the numerically superior species may become extinct if the diffusion is taken into consideration. In mathematical epidemilolgy of infectious diseases, a within-host HIV model with immune impairment is presented in Wang et al. [24]. They derived two threshold values for the immune cell proliferation parameter. Moreover, between the two immune thresholds, the model exhibits the dynamic behavior of bistability, which suggests that patients either undergo viral rebound after treatment termination or achieve the post-treatment control. Ferris and Best [6] investigated an evolution equation of host defence to parasitism with seasonality and found that a region of parameter space that allows evolutionary bistability. In delay differential equations, there also exists dynamic behaviors of bistability. In particular, in some models, delay has a destabilizing effect and induces bistability. Recently, Shu et al. [22] proposed an intraguild predation model with delay. They found that the delay in the model can promote very complex dynamics, and further induce three types of bistability: node-node bistability, node-cycle bistability and cycle-cycle bistability. Meanwhile, Chang et al. [4] considered a population model with delayed Allee effect. The basins of attraction of the two locally stable equlibria are characterized in terms of parameter values, which implies that bistability occurs. Furthermore, when the delay is large, the basin of attraction of the persistence equilibrium and limit cycle shrinks to a single point. In view of this, it is interesting for us to consider the bistability of system (1.1) and the effect of the delay on bistability. This is the motivation and the goal of this paper.

Notice that system (1.2) generates a infinite dimensional dynamical system. The state space is a Banach space of continuous functions, not the Euclid space. For abstract two-species competitive systems on ordered Banach spaces, Smith and Thieme [19] first showed that a ”thin” separatrix separates the basins of attraction of the two single-population steady states when a single saddle-point coexistence steady state exists. Besides, sufficient conditions are derived for stable coexistence and competitive exclusion, which implies that a complete classification of all possible competition outcomes is obtained. Based on the above results, Jiang et al. [12] extended and generalized the theory to monotone semiflows and abstract competitive systems with weak bistability structure. They also applied these results to three reaction-diffusion systems: man-environment-man epidemic model, single-loop positive feedback system and two-species competition in a convex spatial domain, and got the dynamic behaviors of bistability of these systems, respectively. Next, we will use the theory of generalized saddle-point behavior for monotone semiflows to investigate the global dynamics of bistability of system (1.2).

The main purpose of this paper is to analyze the bistability of system (1.2) and the effect of the delay on bistability. A sufficient condition is presented to guarantee that there exist two locally stable equilibriums and an unstable coexistence equilibrium in terms of two simple inequalities (see Lemma 3.2). When two delays vary in their existence regions, subsystem (3.1) does not exhibit stability switching (see Corollary 3.1 and 3.2). Theorem 4.1 gives the global dynamics of bistability on the state space C. Finally, with the introduction of stage structure, it is easier for the species to drive itself into extinction (see Corollary 5.1-5.2).

This paper is organized as follows. In Section 2, we introduce some important notations and preliminaries. Section 3 is devoted to study the asymptotical behavior of equilibria of system (1.2) and stability switching of the positive equilibria. The main conclusion of global dynamics of bistability on state space is given in Section 4. The effect of the delay on bistability and some numerical examples to illustrate the theoretical results are provided in Section 5. This paper ends with a discussion in Section 6.

2. Notations and Preliminaries

Let $X_1 = C([-\tau_1, 0], \mathbb{R})$, $X_2 = C([-\tau_2, 0], \mathbb{R})$, $X_1^+ = \{\varphi_1 \in X_1 : \varphi_1(\theta) \geq 0, -\tau_1 \leq \theta \leq 0\}$ and $X_2^+ = \{\varphi_2 \in X_2 : \varphi_2(\theta) \geq 0, -\tau_2 \leq \theta \leq 0\}$. Int$X_i^+$ is the set of all positive functions in X_i, $i = 1, 2$. Define the product space $X = X_1 \times X_2$, then X is a Banach space with the norm $\|\varphi\| = \|\varphi_1\| + \|\varphi_2\|$, where $\|\varphi_1\| = \sup\limits_{-\tau_1 \leq \theta \leq 0} |\varphi_1(\theta)|$ and $\|\varphi_2\| = \sup\limits_{-\tau_2 \leq \theta \leq 0} |\varphi_2(\theta)|$. Let $X^+ = X_1^+ \times X_2^+$ represent the cone of nonnegative functions in X and $\leq$ $(<, \ll)$ be the corresponding (strict, strong) order relations. Obviously, IntX^+ =Int$X_1^+ \times$IntX_2^+. In addition, we write $K = X_1^+ \times (-X_2^+)$, then X is also a Banach space with the positive cone K and the supremum norm, and $\leq_k$ $(<_k, \ll_k)$ is denoted by the (strict, strong) order induced by cone K. Further, IntK^+ =Int$X_1^+ \times$(-IntX_2^+). For a fixed ψ $\in$IntX^+, the order norm is defined by $|\varphi|_\psi = \inf\{\lambda \in \mathbb{R}^+ : -\lambda\psi \leq \varphi \leq \lambda\psi\}$, which induces the order topology in X.

Let $C_0 = \{(\phi_1, \phi_2) \in X^+ : \phi_1 > 0, \phi_2 > 0\}$, $C_1 = \{(\phi_1, 0) \in X^+ : \phi_1 > 0\}$, $C_2 = \{(0, \phi_2) \in X^+ : \phi_2 > 0\}$, then C_0 =IntX^+. Define $C = C_0 \cup C_1 \cup C_2$. Suppose $\Phi : [0, +\infty) \times C \to C$ is a continuous semiflow on C. If $x \in C$, then $O(x) = \{\Phi_t(x) : t \geq 0\}$ is called a positive orbit of Φ. An equilibrium e is a point for which $\Phi_t(e) = e$, $\forall t \geq 0$. An equilibrium e is referred to as locally stable if for any neighborhood U of e, there exists another neighborhood V of e such that $\Phi_t(V) \subset U$, $\forall t \geq 0$; asymptotically stable if it is stable and there is a neighborhood U of e such that $\omega(y) = \{e\}$, $\forall y \in U$. Φ_t is defined as monotone if $\Phi_t(x) \leq \Phi_t(y)$ whenever $x, y \in C$ with $x \leq y$ and $t > 0$; strongly monotone if $\Phi_t(x) \ll \Phi_t(y)$ whenever $x, y \in C$ with $x < y$ and $t > 0$. If Φ_t is monotone and whenever $x < y$ there is some $t_0 > 0$ and open subsets U, V of C with $x \in U$, $y \in V$ such that $\Phi_{t_0}(U) < \Phi_{t_0}(V)$, we say Φ_t is strongly order preserving, known as SOP for short. Next, we give some important hypotheses about Φ_t presented by Jiang et al. [12]:

(A1) There is a positive number τ such that the mapping Φ_τ is a strict α-contraction, that is, there is a positive number $k < 1$ such that $\alpha(\Phi_\tau(B)) \leq k\alpha(B)$ for any bounded subset $B \subset C$.

(A2) The semiflow Φ_t is uniformly bounded in the sense that $O(B) = \cup_{t \geq 0} \Phi_t(B)$

is bounded whenever B is a bounded subset of C.

(A3) $\Phi_t(C) \subset C$ and $\Phi_t(C_j) \subset C_j$, $\forall t > 0$, $j = 1, 2$. The semiflow Φ_t is strictly K-monotone on C, strongly K-order preserving on C_0, and SOP on C_i with respect to the order induced by X_i^+, $i = 1, 2$.

(A4) The set ζ of all equilibria of Φ_t in C is the union of $\bar{E}_0 = (0, 0)$, $\bar{E}_1 = (\overline{x}_1, 0)$ with $\overline{x}_1 \in \mathrm{Int}X_1$, $\bar{E}_2 = (0, \overline{x}_2)$ with $\overline{x}_2 \in \mathrm{Int}X_2$, and a nonempty set ζ^0 of coexistence equilibria in C_0. Moreover, $\bar{E}_0$ does not attract any point in $C \setminus \{\bar{E}_0\}$, and $\bar{E}_i$ is locally stable in C, $i = 1, 2$; For each $e \in \zeta^0$, $D_x\Phi_\tau(e)$ is strongly K-positive and $\rho(e) = r(D_x\Phi_\tau(e)) > 1$ if ζ^0 is not a singleton.

Lemma 2.1 (Theorem 2.4, [12])**.** *Assume that the C^1-semiflow Φ_t satisfies (A1)-(A4), and Φ_τ is strongly K-monotone in C_0. Then $\Gamma = C \setminus (B_1 \cup B_2)$ is a K-unordered and positively invariant Lipschiz manifold with codimension one in the type-K order norm $|\cdot|_\psi$, where B_i is the basin of attraction of $\bar{E}_i$, $i = 1, 2$. Furthermore, Γ is C^1 if Φ_τ is compact.*

3. Equilibria and asymptotic behaviors

For system (1.2), we assume $y_i(0) = \int_{-\tau_i}^0 \xi_i(s) \cdot e^{d_i s} ds$, $i = 1, 2$ to guarantee the continuity of initial conditions. Considering the biological significance, we need to take positive initial values $y_i(0) > 0$ and $\varphi_i(t) > 0$ $(-\tau_i \le t \le 0, i = 1, 2)$. Throughout this paper, we are only concerned with two cases: $\theta_i \ge 1$ $(i = 1, 2)$ and $\theta_i < 1$ $(i = 1, 2)$. From system (1.2), it is easy to see that $y_i(t)$ is completely and linearly determined by $x_i(t), i = 1, 2$, respectively. Therefore, we are devoted to investigate the following subsystem:

$$\begin{cases} \dot{x}_1(t) = b_1 e^{-d_1\tau_1} x_1(t - \tau_1) - a_{11} x_1^{1+\theta_1}(t) - a_{12} x_1(t) x_2(t), \\ \dot{x}_2(t) = b_2 e^{-d_2\tau_2} x_2(t - \tau_2) - a_{22} x_2^{1+\theta_2}(t) - a_{21} x_1(t) x_2(t), \\ x_i(t) = \varphi_i(t) > 0, \quad -\tau_i \le t \le 0; i = 1, 2. \end{cases} \tag{3.1}$$

By a simple calculation or [16], one can get that system (3.1) has three equilibriums,

$$E_0 = (0, 0), \quad E_1 = ((\frac{b_1}{a_{11}} e^{-d_1\tau_1})^{\frac{1}{\theta_1}}, 0), \quad E_2 = (0, (\frac{b_2}{a_{22}} e^{-d_2\tau_2})^{\frac{1}{\theta_2}}).$$

Besides, if

$$\frac{b_1}{a_{12}} e^{-d_1\tau_1} > (\frac{b_2}{a_{22}} e^{-d_2\tau_2})^{\frac{1}{\theta_2}}, \quad \frac{b_2}{a_{21}} e^{-d_2\tau_2} > (\frac{b_1}{a_{11}} e^{-d_1\tau_1})^{\frac{1}{\theta_1}},$$

or

$$\frac{b_1}{a_{12}} e^{-d_1\tau_1} < (\frac{b_2}{a_{22}} e^{-d_2\tau_2})^{\frac{1}{\theta_2}}, \quad \frac{b_2}{a_{21}} e^{-d_2\tau_2} < (\frac{b_1}{a_{11}} e^{-d_1\tau_1})^{\frac{1}{\theta_1}},$$

then there exists a unique positive equilibrium $E = (x_1^*, x_2^*)$, where x_1^* and x_2^* satisfy

$$\begin{cases} b_1 e^{-d_1\tau_1} - a_{11}(x_1^*)^{\theta_1} - a_{12} x_2^* = 0, \\ b_2 e^{-d_2\tau_2} - a_{22}(x_2^*)^{\theta_2} - a_{21} x_1^* = 0. \end{cases} \tag{3.2}$$

By the right-hand side expressions of system (3.1), it follows from the existence and uniqueness theory of delay differential equations in Kuang [13] that the solution of system (3.1) with the positive initial value exists and is unique. The following Lemma tells us that the solution is not only positive, but also ultimately bounded.

Lemma 3.1 (Lemma 4.1, [16]). *Given system (3.1), then:*

(i) System (3.1) with positive initial conditions $\varphi_i(t)$ $(i = 1, 2)$ has strictly positive solutions for all $t > 0$.

(ii) Solutions of system (3.1) are bounded, that is, there exist positive constants $\tilde{M}$ and T $(T > \tau)$ such that $x_i(t) < \tilde{M}$, $i = 1, 2$ for all $t \geq T - \tau$.

By the stability and attraction analysis of equilibria, Liu et al. [16] presented the criteria of competitive exclusion and competitive coexistence as below.

Proposition 3.1. (Proposition 3.1 and Theorem 4.4-4.6, [16])

(1) E_0 is unstable.

(2) If $\frac{b_1}{a_{12}}e^{-d_1\tau_1} < (\frac{b_2}{a_{22}}e^{-d_2\tau_2})^{\frac{1}{\theta_2}}$ and $\frac{b_2}{a_{21}}e^{-d_2\tau_2} > (\frac{b_1}{a_{11}}e^{-d_1\tau_1})^{\frac{1}{\theta_1}}$, then E_1 is globally asymptotically stable.

(3) If $\frac{b_1}{a_{12}}e^{-d_1\tau_1} > (\frac{b_2}{a_{22}}e^{-d_2\tau_2})^{\frac{1}{\theta_2}}$ and $\frac{b_2}{a_{21}}e^{-d_2\tau_2} < (\frac{b_1}{a_{11}}e^{-d_1\tau_1})^{\frac{1}{\theta_1}}$, then E_2 is globally asymptotically stable.

(4) If $\frac{b_1}{a_{12}}e^{-d_1\tau_1} > (\frac{b_2}{a_{22}}e^{-d_2\tau_2})^{\frac{1}{\theta_2}}$ and $\frac{b_2}{a_{21}}e^{-d_2\tau_2} > (\frac{b_1}{a_{11}}e^{-d_1\tau_1})^{\frac{1}{\theta_1}}$, then E is globally asymptotically stable.

For simplicity of presentation, we introduce the following notation:

$$\frac{b_2}{a_{21}}e^{-d_2\tau_2} < (\frac{b_1}{a_{11}}e^{-d_1\tau_1})^{\frac{1}{\theta_1}}, \quad \frac{b_1}{a_{12}}e^{-d_1\tau_1} < (\frac{b_2}{a_{22}}e^{-d_2\tau_2})^{\frac{1}{\theta_2}}. \tag{H}$$

Note that under the condition (H), system (3.1) admits a unique positive equilibria E. By the stability analysis of equilibria E_1, E_2 and E, we have

Lemma 3.2. *Suppose that (H) holds, then E_1 and E_2 are asymptotically stable, while E is unstable for system (3.1).*

Proof. The characteristic equation about E_1 is

$$[\lambda + (1 + \theta_1)b_1e^{-d_1\tau_1} - b_1e^{-d_1\tau_1-\lambda\tau_1}] \times [\lambda + a_{21} \cdot (\frac{b_1}{a_{11}}e^{-d_1\tau_1})^{\frac{1}{\theta_1}} - b_2e^{-d_2\tau_2-\lambda\tau_2}] = 0.$$

The eigenvalues about E_1 are the roots λ of the equation

$$\lambda + (1 + \theta_1)b_1e^{-d_1\tau_1} - b_1e^{-d_1\tau_1-\lambda\tau_1} = 0, \tag{3.3}$$

and the equation

$$\lambda + a_{21} \cdot (\frac{b_1}{a_{11}}e^{-d_1\tau_1})^{\frac{1}{\theta_1}} - b_2e^{-d_2\tau_2-\lambda\tau_2} = 0. \tag{3.4}$$

Firstly, we consider all the roots of (3.3). Let $\lambda = u + iv$, where u, v are real numbers. Substituting λ by $u + iv$ into (3.3), we have

$$F(\lambda) = u + iv + (1 + \theta_1)b_1e^{-d_1\tau_1} - b_1e^{-d_1\tau_1}e^{-(u+iv)\tau_1} = 0.$$

Then

$$ReF(\lambda) = u + (1+\theta_1)b_1e^{-d_1\tau_1} - b_1e^{-d_1\tau_1}e^{-u\tau_1}\cos(v\tau_1) = 0.$$

If $u \geq 0$, then $ReF(\lambda) > 0$, which is a contradiction. Hence, $Re\lambda = u < 0$.

Next, we focus on all roots of (3.4). Assume that there exists a root λ^* of (3.4) such that $Re\lambda^* \geq 0$. Then

$$|\lambda^* + a_{21}\cdot(\frac{b_1}{a_{11}}e^{-d_1\tau_1})^{\frac{1}{\theta_1}}| = |b_2e^{-d_2\tau_2}e^{-\lambda^*\tau_2}| = b_2e^{-d_2\tau_2}|e^{-\lambda^*\tau_2}|.$$

Taking $\lambda^* = u + iv$ into the above equation, we get

$$|u + a_{21}\cdot(\frac{b_1}{a_{11}}e^{-d_1\tau_1})^{\frac{1}{\theta_1}} + iv| = b_2e^{-d_2\tau_2}e^{-u\tau_2}.$$

If $Re\lambda^* = u \geq 0$, then $e^{-u\tau_2} \leq 1$, and hence,

$$|u + a_{21}\cdot(\frac{b_1}{a_{11}}e^{-d_1\tau_1})^{\frac{1}{\theta_1}} + iv| \leq b_2e^{-d_2\tau_2}.$$

Consequently,

$$\Big(u + a_{21}\cdot(\frac{b_1}{a_{11}}e^{-d_1\tau_1})^{\frac{1}{\theta_1}}\Big)^2 + v^2 \leq (b_2e^{-d_2\tau_2})^2.$$

Since $u \geq 0$, it follows that $a_{21}\cdot(\frac{b_1}{a_{11}}e^{-d_1\tau_1})^{\frac{1}{\theta_1}} \leq b_2e^{-d_2\tau_2}$, that is,

$$(\frac{b_1}{a_{11}}e^{-d_1\tau_1})^{\frac{1}{\theta_1}} \leq \frac{b_2}{a_{21}}e^{-d_2\tau_2},$$

which is contrary to the first part of the hypothesis (H). Hence, λ must have negative real part.

By symmetric arguments, one can obtain E_2 that is asymptotically stable provided $\frac{b_1}{a_{12}}e^{-d_1\tau_1} < (\frac{b_2}{a_{22}}e^{-d_2\tau_2})^{\frac{1}{\theta_2}}$.

For the positive equilibria E, its characteristic equation is

$$F(\lambda) = (\lambda + b_1e^{-d_1\tau_1}(1-e^{-\lambda\tau_1}) + a_{11}\theta_1(x_1^*)^{\theta_1}) \times (\lambda + b_2e^{-d_2\tau_2}(1-e^{-\lambda\tau_2}) + a_{22}\theta_2(x_2^*)^{\theta_2}) - a_{12}a_{21}x_1^*x_2^* = 0. \tag{3.5}$$

Clearly,

$$F(0) = a_{11}a_{22}\theta_1\theta_2(x_1^*)^{\theta_1}(x_2^*)^{\theta_2} - a_{12}a_{21}x_1^*x_2^*. \tag{3.6}$$

By the proof of Proposition 3.4 in [16] and the assumption (H), it follows that $F(0) < 0$. On the other hand, by the expression of $F(\lambda)$, it is evident that $F(\lambda) > 0$ for sufficiently large $\lambda > 0$. Therefore, the equation $F(\lambda) = 0$ has at least a positive root, which implies that E is unstable. This Lemma is completed. □

For system (1.2), time delays appear in the survive rate $e^{-d_i\tau_i}, i = 1, 2$ of the delayed populations. Such model is also called model with delay dependent parameters or delay-dependent coefficients. In most types of models, time delay can be both stabilizing and destabilizing, depending on the delay lengths, and hence the corresponding systems will exhibit complex dynamics, see [2,3,10,15]. In particular, An et al. [2] proposed a practical geometric method to study the stability switching properties for delay differential equations with two delays, and delay dependent parameters that dependent only on one of two delays. They also applied this method to a two discrete delay SIR model and obtained the sufficient conditions of stability switch. However, this method does not seem to be applicable for our system (3.1). By the expression of the equations (3.5) and (3.6), we can see that the positive equilibria E always has a positive eigenvalue for any $\tau_i \geq 0$ $(i = 1, 2)$ under the condition (H). This implies that E is always unstable, and hence, the stability switch of E does not occur.

When $\theta_1 \geq 1$ and $\theta_2 \geq 1$, by (H), it follows that $\tau_1 > \tau_1^*$ and $\tau_2 > \tau_2^*$, where

$$\tau_1^* = \frac{1}{d_1(\theta_1\theta_2 - 1)}(\theta_1\theta_2 \ln\frac{b_1}{a_{12}} + \theta_1 \ln\frac{a_{22}}{a_{21}} + \ln\frac{a_{11}}{b_1})$$

and

$$\tau_2^* = \frac{1}{d_2(\theta_1\theta_2 - 1)}(\theta_1\theta_2 \ln\frac{b_2}{a_{21}} + \theta_2 \ln\frac{a_{11}}{a_{12}} + \ln\frac{a_{22}}{b_2}).$$

Let $\tau_1^{**} = \max\{\tau_1^*, 0\}$ and $\tau_2^{**} = \max\{\tau_2^*, 0\}$. Then $I_1 = (\tau_1^{**}, +\infty)$ and $I_2 = (\tau_2^{**}, +\infty)$ are existing regions of two delays τ_1 and τ_2, respectively. For each $(\tau_1, \tau_2) \in I_1 \times I_2$, by the proof of Lemma 3.2, the real parts of eigenvalues of E_1 and E_2 are negative, which implies that E_1 and E_2 are asymptotically stable. For the positive equilibria E, since the expression of $F(0)$ has no relation with τ_1 and τ_2, we have $F(0) < 0$ under the condition H. Again, $F(+\infty) = +\infty$, then there always exists a positive eigenvalue, and hence, E is unstable. This implies that the stabilities of E_1, E_2 and E do not switch as τ_1 and τ_2 vary in $I_1 \times I_2$. Thus, we have

Corollary 3.1. *Suppose that $\theta_1 \geq 1, \theta_2 \geq 1$ and (H) holds. Then, for each $(\tau_1, \tau_2) \in I_1 \times I_2$, the positive equilibria E is always unstable, while E_1 and E_2 are asymptotically stable. This implies that stability switching does not arise.*

When $\theta_1 < 1$ and $\theta_2 < 1$, it follows from (H) that $\tau_1^* > 0, \tau_2^* > 0$, and hence $0 \leq \tau_1 < \tau_1^*$ and $0 \leq \tau_2 < \tau_2^*$. Let $\tilde{I_1} = (0, \tau_1^*)$ and $\tilde{I_2} = (0, \tau_2^*)$. Using similar analysis, we also have

Corollary 3.2. *Suppose that $\theta_1 < 1, \theta_2 < 1$ and (H) holds. Then, for each $(\tau_1, \tau_2) \in \tilde{I_1} \times \tilde{I_2}$, the positive equilibria E is always unstable, while E_1 and E_2 are asymptotically stable. This implies that stability switching does not arise.*

4. Bistability

From the above section, we have known that for any $\phi \in C$, system (3.1) has a unique negative global solution $x(t, \phi)$ on $[0, +\infty)$, which can generates a semiflow on C defined by $\Phi_t(\phi) = x(t, \phi)$. By the linear variational equation of $x(t, \phi)$, $\Phi_t(\phi)$ is continuously differentiable in ϕ for fixed $t \geq 0$. By the generalized saddle-point structure for two-species competitive systems on ordered Banach spaces, the global dynamic behavior of bistability on the state space C is given below.

Theorem 4.1. *Suppose that the condition (H) holds. For system (3.1), there exists a K-unordered, invariant and one-codimensional C^1-separatix $\Gamma = C \setminus B_1 \cup B_2$ on* *the state space C, which separates B_1 and B_2, where B_i is the basin of attraction of $E_i, i = 1, 2$. More precisely, all solutions of system (3.1) with initial positive functions below Γ asymptotically converge to E_1, while all solutions of the system with initial positive functions above Γ asymptotically converge to E_2.*

Proof. By Lemma 3.1(ii), it is easy to see that there exists a large positive constant $\bar{M}$ such that for each $\varphi \in B$, $\|\Phi_t(\varphi)\| \le \bar{M}$, whenever B is a bounded subset of C. This implies that Φ_t is uniformly bounded, that is, the condition (A_2) is satisfied. For convenience, we rewrite system (3.1) as $\dot{x}(t) = f(x(t), x(t-\tau_1), x(t-\tau_2))$, where $x(t) = (x_1(t), x_2(t))$ and $f = (f_1, f_2)$ with

$$\begin{cases} f_1 = b_1 e^{-d_1\tau_1} x_1(t-\tau_1) - a_{11} x_1^{1+\theta_1}(t) - a_{12} x_1(t) x_2(t), \\ f_2 = b_2 e^{-d_2\tau_2} x_2(t-\tau_2) - a_{22} x_2^{1+\theta_2}(t) - a_{21} x_1(t) x_2(t). \end{cases}$$

Then, f maps bounded subsets of C into bounded subsets of $\mathbb{R}^2$, and hence, $\Phi_t'(\varphi)$ is uniformly bounded on $t \ge 0$. By Ascoli-Arzela Theorem, the orbit $\{\Phi_t(\varphi) = x(t, \phi) : t \ge 0\}$ has compact closure in C and $\Phi_t : C \to C$ is a compact mapping for each $t > 0$. From Proposition 7.2(a) in [5], for any $B \subset C$, we have $\alpha(\Phi_t(B)) = 0$, and then Φ_t $(t > 0)$ is also a strict *α-contraction* mapping. Thus, for the semiflow Φ_t $(t > 0)$, the condition (A1) is also satisfied.

For any $(\phi_1, 0) \in C_1$, it follows from the second equation of system (3.1) that $\dot{x}_2(t)|_{(\phi_1,0)\in C_1} \equiv 0$, and then $x_2(t)|_{(\phi_1,0)\in C_1} \equiv 0$ for any $t \ge 0$. Moreover, $\dot{x}_1(t)|_{(\phi_1,0)\in C_1} = b_1 e^{-d_1\tau_1} x_1(t-\tau_1) - a_{11} x_1^{1+\theta_1}(t)$. By Lemma 4.2 and 4.3 in [16], we get that $x_1(t)|_{(\phi_1,0)\in C_1} > 0$ for any $t \ge 0$ and $\lim\limits_{t\to+\infty} x_1(t) = \big(\frac{b_1 e^{-d_1\tau_1}}{a_{11}}\big)^{\frac{1}{\theta_1}}$. This implies that $\Phi_t(C_1) \subset C_1$ for any $t \ge 0$. Since $E_1 = \big((\frac{b_1 e^{-d_1\tau_1}}{a_{11}})^{\frac{1}{\theta_1}}, 0\big)$, we have $W^s(E_1) \cap C_1 = C_1 \setminus \{E_0\}$. By symmetric arguments, we also have $\Phi_t(C_2) \subset C_2$ for any $t \ge 0$, and $W^s(E_2) \cap C_2 = C_2 \setminus \{E_0\}$. By Lemma 3.1, system (3.1) with positive initial functions has strictly positive solutions for all $t > 0$, then $\Phi_t(C_0) \subset C_0$, for any $t \ge 0$. Thus, $\Phi_t(C) \subset C$, for any $t \ge 0$.

Let $Px = u$, where $x = (x_1, x_2)^T, u = (u_1, u_2)^T$ and $P = \begin{pmatrix} 1 & 0 \\ 0 & -1 \end{pmatrix}$. Observe that $P = P^{-1}$, it follows that $x \le_k y$ if and only if $Px \le Py$. Then, system (3.1) can be converted into the following cooperative system:

$$\begin{cases} \dot{u}_1(t) = b_1 e^{-d_1\tau_1} u_1(t-\tau_1) - a_{11} u_1^{1+\theta_1}(t) + a_{12} u_1(t) u_2(t), \\ \dot{u}_2(t) = b_2 e^{-d_2\tau_2} u_2(t-\tau_2) + a_{22}(-1)^{1+\theta_2} u_2^{1+\theta_2}(t) - a_{21} u_1(t) u_2(t). \end{cases} \tag{4.1}$$

Thus system (4.1) generates a semiflow Ψ_t defined by $\Psi_t(u) = P\Phi_t(x) = P\Phi_t(Pu)$. One can easily check that system (4.1) is cooperative and irreducible (see Chapter 5 in [20]). By Corollary 5.3.5 in [20], we can obtain that Ψ_t is eventually strongly monotone. That is, if $\varphi := (\varphi_1, \varphi_2)^T \le_k (\psi_1, \psi_2)^T := \psi$, then $P\varphi \le P\psi$, and hence, $\Psi_t(P\varphi) \ll \Psi_t(P\psi)$, $t > 3T_0$, where $T_0 = \max\{\tau_1, \tau_2\}$. Since $\Psi_t(u) = P\Phi_t(Pu)$, we get $P\Phi_t(P^2\varphi) \ll P\Phi_t(P^2\psi)$, $t > 3T_0$, which implies that $P\Phi_t(\varphi) \ll P\Phi_t(\psi)$, $t > 3T_0$. Consequently, $\Phi_t(\varphi) \ll_k \Phi_t(\psi)$, $t > 3T_0$. By Proposition 1.1.1 in [20], Φ_t

is strongly K-order preserving on C_0. By Lemma 5.3.3 and Theorem 5.1.1 in [20], Φ_t is strictly K-monotone on C.

Since $x_2(t)|_{(\phi_1,0)\in C_1} \equiv 0$ for any $t \geq 0$ and the first equation of system (3.1), we can get $\dot{x}_1(t) = b_1 e^{-d_1\tau_1} x_1(t-\tau_1) - a_{11}x_1^{1+\theta_1}(t)$. In view of $b_1 e^{-d_1\tau_1} > 0$, by Corollary 5.3.5 in [20], we obtain that the semiflow Φ_t on C_1 is eventually strongly monotone with respect to the order relation " $\leq$ ". Therefore, Φ_t is SOP on C_1. Analogously, Φ_t is also SOP on C_2.

Now, we show that E_0 does not attract any point in $C \setminus \{E_0\}$. Since $W^s(E_1) \cap C_1 = C_1 \setminus \{E_0\}$ and $W^s(E_2) \cap C_2 = C_2 \setminus \{E_0\}$, we only need to verify $W^s(E_0) \cap C_0 = \varnothing$. By contradiction, suppose that there exists a positive solution $(x_1(t), x_2(t))$ such that $\lim\limits_{t\to+\infty}(x_1(t), x_2(t)) = (0,0)$. For any sufficient small $\epsilon > 0$, there exists a $T = T(\epsilon) > 0$ such that $0 < x_2(t) < \epsilon$. From the first equation of system (3.1), it follows that

$$\begin{aligned}\dot{x}_1(t) &= b_1 e^{-d_1\tau_1} x_1(t-\tau_1) - a_{11}x_1^{1+\theta_1}(t) - a_{12}x_1(t)x_2(t)\\ &> b_1 e^{-d_1\tau_1} x_1(t-\tau_1) - a_{11}x_1^{1+\theta_1}(t) - a_{12}\epsilon x_1(t).\end{aligned}$$

We can choose $\epsilon > 0$ so small that $b_1 e^{-d_1\tau_1} > a_{12}\epsilon$. By Lemma 4.3 in [16], we can obtain $\lim\limits_{t\to+\infty} x_1(t) = \left(\frac{b_1 e^{-d_1\tau_1} - a_{12}\epsilon}{a_{11}}\right)^{\frac{1}{\theta_1}} > 0$, contradicting $\lim\limits_{t\to+\infty} x_1(t) = 0$. By Lemma 3.2, both E_1 and E_2 are locally stable in C, while the unique positive equilibria E is unstable. Then $\rho(E) := r(D_\phi\Phi_t(E)) > 1$.

Since $x(t,\phi) = \Phi_t(\phi)$ is continuously differentiable in ϕ, we denote $D_\phi x(t,\phi)\beta := y(t,\beta)$ for any $\beta \in K \setminus \{O\}$. Then, $y(t,\beta)$ satisfies the linear variational equation $y'(t) = Df(x_t(\phi))y_t,\ y_0 = \beta$, which generates a strongly K-monotone semiflow from the analysis of system (4.1). Since $\beta >_k 0$, it follows that $y(t,\beta) \gg_k 0$, that is, $D_\phi x(t,\phi)\beta \gg_k 0$. Thus, $D_\phi\Phi_t(E)\beta \gg_k 0$. This implies that $D_\phi\Phi_t(E)$ is strongly K-positive. So far, the conditions (A3) and (A4) are satisfied.

Let B_i be the basin of attraction of E_i, $i = 1,2$. Define $\Gamma = C \setminus (B_1 \cup B_2)$. By Lemma 2.1, Γ is an invariant and K-unordered separatrix with codimension one, which separates the basins of attractions of E_1 and E_2. Since Φ_t is compact for each $t > 0$, Γ is a C^1-manifold. Since $C = B_2 \cup \Gamma \cup B_1$ and $E_2 \ll_k E_1$, all solutions of the system with initial positive functions below Γ asymptotically converge to E_1, while all solutions of the system with initial positive functions above Γ asymptotically converge to E_2. The proof is completed. □

Remark 4.1. By Theorem 4.1, one can see that under the condition (H), the state space C is divided into three invariant parts: B_1, B_2 and the separatrix Γ. Here, B_i is the basin of attraction of E_i $(i = 1,2)$ and Γ connects unstable equilibria E_0 and E to the infinity in C. Since Γ is codimension one, it is said to be a "thin" separatrix bounding the basins of attraction of E_1 and E_2 in Smith and Thieme [19]. In other words, all orbits starting in $C \setminus \Gamma$ converge to E_1 or E_2. E_2 attracts all orbits whenever the initial positive function is above Γ, while E_1 attracts all orbits whenever the initial positive function is below Γ. In the biological context, this implies that in the initial state one species is numerically superior to the other species at their habitat, then the superior species will wipe out the inferior one.

5. Numerical simulation and the effect of the delays

Firstly, we provide some numerical simulations to illustrate our theoretical results. When the difference of the strength of two species is not so large, which species will become extinct crucially depends on the initial data. Two cases are given as below.

Case 1: $\theta_1 = 4 > 1$ and $\theta_2 = 5 > 1$.

By taking parameters $b_1 = 0.22$, $b_2 = 0.2$, $d_1 = 0.1$, $d_2 = 0.15$, $a_{11} = 0.1$, $a_{21} = 0.18$, $a_{12} = 0.14$, $a_{22} = 0.2$, it follows that $\tau_1^* = \tau_1^{**} = 4.5646$ and $\tau_2^* = \tau_2^{**} = 0.1491$. Now we arbitrarily select $\tau_1 = 9$, $\tau_2 = 2$, and different positive initial functions $x_1(t)$, $t \in [-\tau_1, 0]$ and $x_2(t)$, $t \in [-\tau_2, 0]$ in the following two subcases.

Subcase (i): When taking $x_1(t) \equiv 8$, $t \in [-9, 0]$ and $x_2(t) \equiv 3$, $t \in [-2, 0]$, it is obvious that species 1 is numerically superior to species 2. One can see that Species 1 wins the competition as shown in Fig 1.

Subcase (ii): When taking $x_1(t) \equiv 5$, $t \in [-9, 0]$ and $x_2(t) \equiv 7$, $t \in [-2, 0]$, it is obvious that species 2 is numerically superior to species 1. One can see that Species 2 wins the competition as shown in Fig 2.

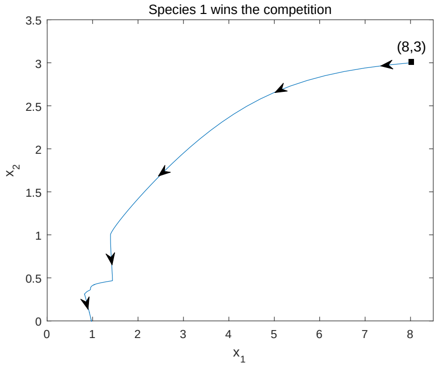

Figure 1.

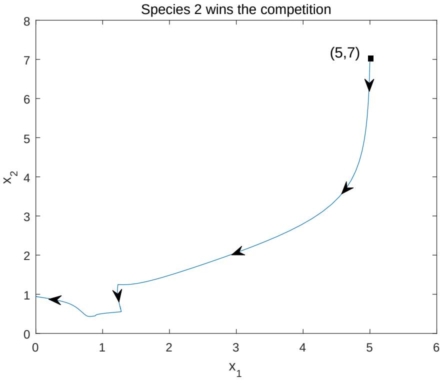

Figure 2.

Case 2: $\theta_1 = \frac{1}{2} < 1$ and $\theta_2 = \frac{1}{4} < 1$.

By taking parameters $b_1 = 0.22$, $b_2 = 0.2$, $d_1 = 0.1$, $d_2 = 0.15$, $a_{11} = 0.1$, $a_{21} = 0.18$, $a_{12} = 0.14$, $a_{22} = 0.1$, it follows that $\tau_1^* = 11.724$ and $\tau_2^* = 5.8217$. Now, we arbitrarily select $\tau_1 = 5$, $\tau_2 = 3$, and different positive initial functions $x_1(t)$, $t \in [-5, 0]$ and $x_2(t)$, $t \in [-3, 0]$ in the following two subcases.

Subcase (i): When taking $x_1(t) \equiv 6$, $t \in [-5, 0]$ and $x_2(t) \equiv 4$, $t \in [-3, 0]$, it is obvious that species 1 is numerically superior to species 2. One can see that Species 1 wins the competition as shown in Fig 3.

Subcase (ii): When taking $x_1(t) \equiv 3$, $t \in [-5, 0]$ and $x_2(t) \equiv 6$, $t \in [-3, 0]$, it is obvious that species 2 is numerically superior to species 1. One can see that Species 2 wins the competition as shown in Fig 4.

In order to consider the effect of the stage structure, we let $\tau_1 = \tau_2 = 0$ and obtain four situations of the competition outcome in model (1.1) by Lemma 3.2 and Theorem 4.1 , namely:

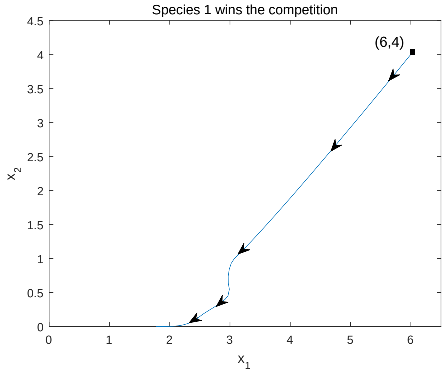

Figure 3.

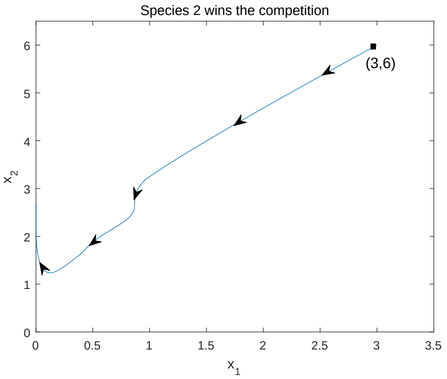

Figure 4.

(A) If $\frac{b_1}{a_{12}} < (\frac{b_2}{a_{22}})^{\frac{1}{\theta_2}}$ and $\frac{b_2}{a_{21}} > (\frac{b_1}{a_{11}})^{\frac{1}{\theta_1}}$, then species 1 wins the competition.

(B) If $\frac{b_1}{a_{12}} > (\frac{b_2}{a_{22}})^{\frac{1}{\theta_2}}$ and $\frac{b_2}{a_{21}} < (\frac{b_1}{a_{11}})^{\frac{1}{\theta_1}}$, then species 2 wins the competition.

(C) If $\frac{b_1}{a_{12}} > (\frac{b_2}{a_{22}})^{\frac{1}{\theta_2}}$ and $\frac{b_2}{a_{21}} > (\frac{b_1}{a_{11}})^{\frac{1}{\theta_1}}$, then two species coexist at a stable equilibrium.

(D) If $\frac{b_2}{a_{21}} < (\frac{b_1}{a_{11}})^{\frac{1}{\theta_1}}$ and $\frac{b_1}{a_{12}} < (\frac{b_2}{a_{22}})^{\frac{1}{\theta_2}}$, then the bistability occurs for two species.

On the other hand, without loss of generality, if species 2 does not have the stage structure, that is, $\tau_2 = 0$, then system (3.1) is converted into the following system

$$\begin{cases} \dot{x}_1(t) = b_1 e^{-d_1\tau_1} x_1(t-\tau_1) - a_{11}x_1^{1+\theta_1}(t) - a_{12}x_1(t)x_2(t), \\ \dot{x}_2(t) = b_2 x_2(t) - a_{22}x_2^{1+\theta_2}(t) - a_{21}x_1(t)x_2(t), \\ x_1(t) = \varphi_1(t) > 0, \quad -\tau_1 \le t \le 0; x_2(0) > 0. \end{cases} \tag{5.1}$$

By Lemma 3.2 and Theorem 4.1, for system (5.1), we have

Corollary 5.1. *Given system (5.1), then:*

(i) *If* $\frac{b_1}{a_{12}}e^{-d_1\tau_1} < (\frac{b_2}{a_{22}})^{\frac{1}{\theta_2}}$ *and* $\frac{b_2}{a_{21}} > (\frac{b_1}{a_{11}}e^{-d_1\tau_1})^{\frac{1}{\theta_1}}$, *then species 1 wins the competition.*

(ii) *If* $\frac{b_1}{a_{12}}e^{-d_1\tau_1} > (\frac{b_2}{a_{22}})^{\frac{1}{\theta_2}}$ *and* $\frac{b_2}{a_{21}} < (\frac{b_1}{a_{11}}e^{-d_1\tau_1})^{\frac{1}{\theta_1}}$, *then species 2 wins the competition.*

(iii) *If* $\frac{b_1}{a_{12}}e^{-d_1\tau_1} > (\frac{b_2}{a_{22}})^{\frac{1}{\theta_2}}$ *and* $\frac{b_2}{a_{21}} > (\frac{b_1}{a_{11}}e^{-d_1\tau_1})^{\frac{1}{\theta_1}}$, *then two species coexist at a stable equilibrium.*

(iv) *If* $\frac{b_1}{a_{12}}e^{-d_1\tau_1} < (\frac{b_2}{a_{22}})^{\frac{1}{\theta_2}}$ *and* $\frac{b_2}{a_{21}} < (\frac{b_1}{a_{11}}e^{-d_1\tau_1})^{\frac{1}{\theta_1}}$, *then the bistability occurs for two species.*

Let

$$\frac{b_2}{a_{21}} < (\frac{b_1}{a_{11}}e^{-d_1\tau_1})^{\frac{1}{\theta_1}}, \quad \frac{b_1}{a_{12}}e^{-d_1\tau_1} < (\frac{b_2}{a_{22}})^{\frac{1}{\theta_2}}. \tag{H$'$}$$

Comparing the conditions of (D) to (H'), since $e^{-d_1\tau_1} < 1$, it follows that $\frac{b_1}{a_{12}} < (\frac{b_2}{a_{22}})^{\frac{1}{\theta_2}}$ implies that $\frac{b_1}{a_{12}}e^{-d_1\tau_1} < (\frac{b_2}{a_{22}})^{\frac{1}{\theta_2}}$ holds. In view of $(\frac{b_1}{a_{11}}e^{-d_1\tau_1})^{\frac{1}{\theta_1}} < (\frac{b_1}{a_{11}})^{\frac{1}{\theta_1}}$, there are two possible cases: $\frac{b_2}{a_{21}} < (\frac{b_1}{a_{11}}e^{-d_1\tau_1})^{\frac{1}{\theta_1}}$ and $\frac{b_2}{a_{21}} > (\frac{b_1}{a_{11}}e^{-d_1\tau_1})^{\frac{1}{\theta_1}}$. Therefore, under the conditions of (D) and the introduction of stage structure of species 1, the dynamical behaviors of system (5.1) will exhibit competitive exclusion or bistability, which depends on the value of $d_1\tau_1$. Consequently, we have

Corollary 5.2. *Assume that* $\frac{b_2}{a_{21}} < (\frac{b_1}{a_{11}})^{\frac{1}{\theta_1}}$ *and* $\frac{b_1}{a_{12}} < (\frac{b_2}{a_{22}})^{\frac{1}{\theta_2}}$ *holds. Define* $\tilde{\tau}_1 = \frac{1}{d_1}(\theta_1 \ln \frac{a_{21}}{b_2} + \ln \frac{b_1}{a_{11}})$. *Then, for system (5.1), the following statements are valid:*

(i) *If* $\tau_1 \in (0, \tilde{\tau}_1)$, *then the bistability occurs for two species.*

(ii) *If* $\tau_1 \in (\tilde{\tau}_1, +\infty)$ *, then species 2 wins the competition.*

Proof. Since $\frac{b_2}{a_{21}} < (\frac{b_1}{a_{11}})^{\frac{1}{\theta_1}}$, it follows that $\tilde{\tau}_1 > 0$. If $0 < \tau_1 < \tilde{\tau}_1$, then $\frac{b_2}{a_{21}} < (\frac{b_1}{a_{11}}e^{-d_1\tau_1})^{\frac{1}{\theta_1}}$. On the other hand, $\frac{b_1}{a_{12}} < (\frac{b_2}{a_{22}})^{\frac{1}{\theta_2}}$ implies that $\frac{b_1}{a_{12}}e^{-d_1\tau_1} < (\frac{b_2}{a_{22}})^{\frac{1}{\theta_2}}$ holds. By Corollary 5.1(iv), the bistability occurs for two species. If $\tau_1 > \tilde{\tau}_1$, then $\frac{b_2}{a_{21}} > (\frac{b_1}{a_{11}}e^{-d_1\tau_1})^{\frac{1}{\theta_1}}$. Together with $\frac{b_1}{a_{12}}e^{-d_1\tau_1} < (\frac{b_2}{a_{22}})^{\frac{1}{\theta_2}}$, by Corollary 5.1(ii), the species 2 wins the competition. $\square$

In the biological context, traditionally the birth rate b_1 of species 1 is replaced by $b_1 e^{-d_1\tau_1}$. Obviously, $b_1 e^{-d_1\tau_1} < b_1$. Notice that $\frac{b_1}{a_{12}}e^{-d_1\tau_1} < (\frac{b_2}{a_{22}})^{\frac{1}{\theta_2}}$, the small birth rate of species 1 is required than that in (D) in the sense that with the introduction of stage structure, it is advantageous for the permanence of species 2. From $\frac{b_2}{a_{21}} < (\frac{b_1}{a_{11}}e^{-d_1\tau_1})^{\frac{1}{\theta_1}}$, we can see that the small birth rate is disadvantageous for the permanence of species 1 in the competition. Further, species 1 may loss the competition and go extinction. This implies that it is easier for species 2 to drive species 1 into extinction by introducing the stage structure of species 1. So, stage structure brings negative effect on the permanence of one species, and positive effect on its competitor in two-species competitive models with stage structure.

In the following, we give some numerical examples to illustrate the effectiveness of above analysis. First, we take $\theta_1 = \frac{1}{2}$, $\theta_2 = \frac{1}{4}$, $b_1 = 0.22$, $b_2 = 0.2$, $a_{11} = 0.16$, $a_{12} = 0.14$, $a_{21} = 0.18$, $a_{22} = 0.1$ in the model (1.1), which satisfies the conditions of (D). When taking initial values $x_1(0) = 8$ and $x_2(0) = 2$, species 1 wins the competition as shown in Fig 5. By taking initial values $x_1(0) = 2$ and $x_2(0) = 19$, species 2 wins the competition as shown in Fig 6. Clearly, the numerically superior species will wipe out the inferior one, and the superior species will win the competition. This implies that the bistability occurs for two species in model (1.1).

For the same parameters $\theta_1 = \frac{1}{2}$, $\theta_2 = \frac{1}{4}$, $b_1 = 0.22$, $b_2 = 0.2$, $a_{11} = 0.16$, $a_{12} = 0.14$, $a_{21} = 0.18$, $a_{22} = 0.1$, then $\tilde{\tau}_1 = 2.6577$. We add the parameters of the stage structure $\tau_1 = 4 > \tilde{\tau}_1$ and $d_1 = 0.1$. By selecting the initial values, $x_1(t) \equiv 8$, $t \in [-4, 0]$ and $x_2(0) = 2$, species 2 wins the competition in system (5.1) as shown in Fig 7.

For the above parameters $\theta_1 = \frac{1}{2}$, $\theta_2 = \frac{1}{4}$, $b_1 = 0.22$, $b_2 = 0.2$, $a_{11} = 0.16$, $a_{12} = 0.14$, $a_{21} = 0.18$, $a_{22} = 0.1$, we take $\tau_1 = 1$ such that $\tau_1 < \tilde{\tau}_1 = 2.6577$. By selecting different initial values, one can see that the bistability of system (5.1) will occur.

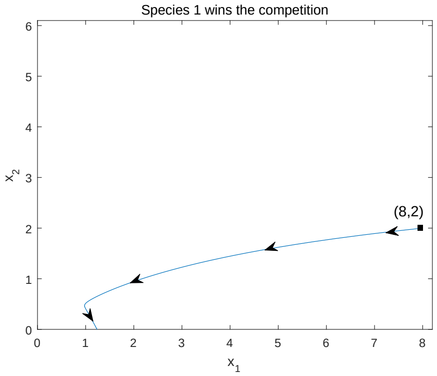

Figure 5.

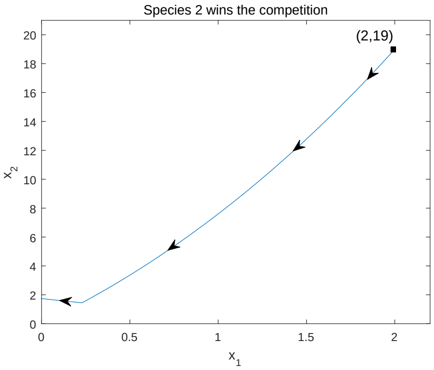

Figure 6.

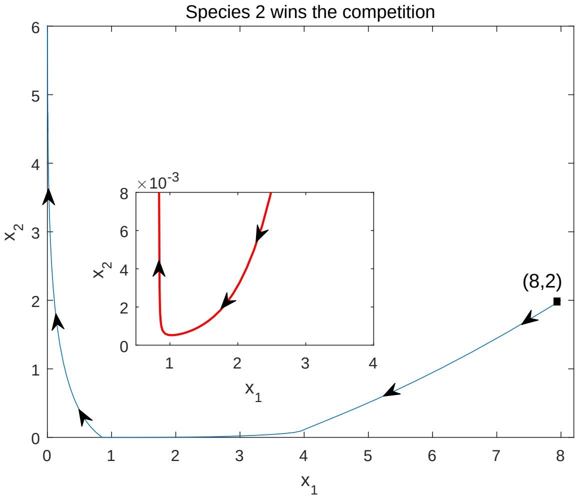

Figure 7. The small graph is a detail view when $x_1 \in [0.5, 4]$.

When taking initial values $x_1(t) \equiv 8, t \in [-1, 0]$ and $x_2(0) = 2$, species 1 wins the competition as shown in Fig 8. Observe that the initial values are the same as those of Fig 7, however, the different delay τ_1 results in different competition outcomes. When taking initial values $x_1(t) \equiv 8, t \in [-1, 0]$ and $x_2(0) = 12$, species 2 wins the competition as shown in Fig 9.

For other cases (A) − (C), one can also make the same analysis to obtain the similar results of stability change.

6. Discussion

In this paper, we focus on the dynamic behavior of bistability of a two-species Gilpin-Ayala competitive model with two delays. By the generalized saddle-point behavior for monotone semiflows, Theorem 4.1 gives a sufficient condition (H), which guarantees the existence of bistability of system (3.1). Together with Proposition 3.1, we

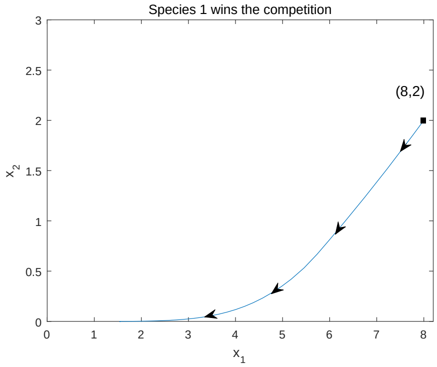

Figure 8.

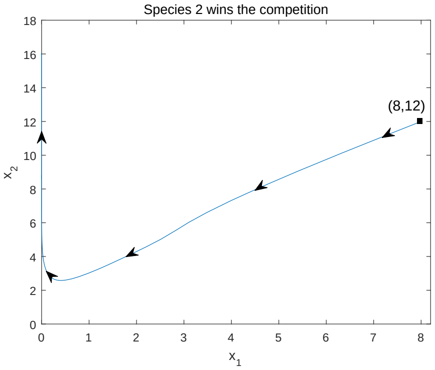

Figure 9.

present a complete classification for global dynamics of system (3.1): competitive exclusion, competitive coexistence and bistability. In addition, there does not exist stability switching for the positive equilibria E as the delay $\tau_i, i = 1, 2$ varies in its existence region. By comparing the classical Gilpin-Ayala competitive model, the species may drive itself into extinction and contribute positively its competitor with the introduction of stage structure. Taking the bistability in (D) as an example, there exists a critical value $\tilde{\tau}_1$. When $\tau_1 \in (0, \tilde{\tau}_1)$, then the bistability occurs for two species in system (5.1) and which species will become extinct crucially depends on the initial data. When $\tau_1 \in (\tilde{\tau}_1, +\infty)$, then species 2 wins the competition and species 1 goes extinction.

However, for higher dimensional case, it does not generate a monotone dynamical system. What are the complete classification for global dynamics? Can the delay deduce the stability switches? Another question is to consider time-periodic environments, or more general dependence on time case. We leave them for future research.

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