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Competitive exclusion in age-structured populations

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Abstract

Competitive exclusion principle, which states that two or more species limited by the same resource cannot coexist indefinitely, is a very common phenomenon in population dynamics. It is well-known that competitive exclusion principle occurs in deterministic competition models, diffusive competition models, and evolutionary competition models. In this paper, we consider an age-structured competition model among N species and obtain an interesting result: under suitable scaled birth and death rates, the species with the smallest maximum age always wins the competition to exclude the other species; that is, the competitive exclusion principle occurs in age-structured competition models.

Keywords Age structure · Competition models · Maximum age · Principal eigenvalue

Mathematics Subject Classification 35L04 · 47A10 · 92D25

In memory of Professor Pierre Magal

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1 Introduction

Competition is a very common and dynamic interaction in population dynamics. Volterra (1928) was the first to use a mathematical model to demonstrate that two or more species limited by the same resource cannot coexist indefinitely. This phenomenon has been expanded into the statement that *n species cannot coexist on fewer than n resources or niches* (MacArthur and Levins 1964; Rescigno and Richardson 1965; Armstrong and McGehee 1980) and is now known as the "competitive exclusion principle" (Hardin 1960; Levin 1970). Competitive exclusion principle has been shown to be valid in competitive population models described by ordinary differential equations (Armstrong and McGehee 1980), delay differential equations (Gopalsamy 1992; Kuang 1993), and (spatial or size-structured) partial differential equations (Ackleh et al. 2004; Cantrell and Lam 2021; Dockery et al. 1998). The purpose of this paper is to study if competitive exclusion principle occurs in age-structured competition models.

Consider the following age-structured competition model among N species:

$$\begin{cases} \dfrac{\partial u_i}{\partial t} + \dfrac{\partial u_i}{\partial a} = -\mu(a, a_i)u_i(t, a) - \sigma_i \left(\displaystyle\sum_{j=1}^{N} \int_0^{a_j} u_j(t, a)da \right) u_i(t, a), & t > 0,\ a \in (0, a_i), \\ u_i(t, 0) = \displaystyle\int_0^{a_i} \beta(a, a_i)u_i(t, a)da, & t > 0, \\ u_i(0, a) = u_{0i}(a), & a \in (0, a_i). \end{cases} \tag{1.1}$$

Here $u_i(t, a)$ denotes the density of the i-th species at time t with age a, which admits the maximum age $a_i > 0$. Functions $\mu \in L^\infty_{\text{loc},+}([0, a_i))$ and $\beta \in L^\infty_+(0, a_i)$ with the support supp$\beta \neq \emptyset$ represent the death rate and birth rate of the i-th species, respectively. In addition, $\sigma_i > 0$ describes the competition coefficient of the i-th species affected by all species. We mention that μ and β are dependent on the maximum age a_i for each species, with $a_i \in (0, \infty]$. We assume that

$$\int_0^{a_i} \mu(a)da = +\infty \tag{1.2}$$

to ensure $u_i(t, a_i) = 0$ for any $t > 0$, which is an usual assumption in age-structured models with finite maximum ages. Such a μ can be chosen as a $L^\infty_{\text{loc},+}$ function with blow-up at $a = a_i$, see (Inaba 2017, Fig. 1.2) for an example, which is shown in Figure 1.

In this paper, we investigate the global dynamics of (1.1), with a specific emphasis on the effects of the maximum age on the extinction or persistence of each species. Previous studies on (1.1) or other related age-structured population models mainly focused on the effects of death rates, birth rates, or in particular the nonlinearites, on the global dynamics. More specifically, they studied the existence, uniqueness and stability of positive or semi-trivial equilibria, see (Webb 1984; Cushing 1998; Hastings 1986; Li and Brauer 2008; Iannelli 1995; Magal and Thieme 2004; Magal and Ruan 2018; Li et al. 2020; Martcheva 2015; Thieme 2018 and Iannelli and Milner (2017).

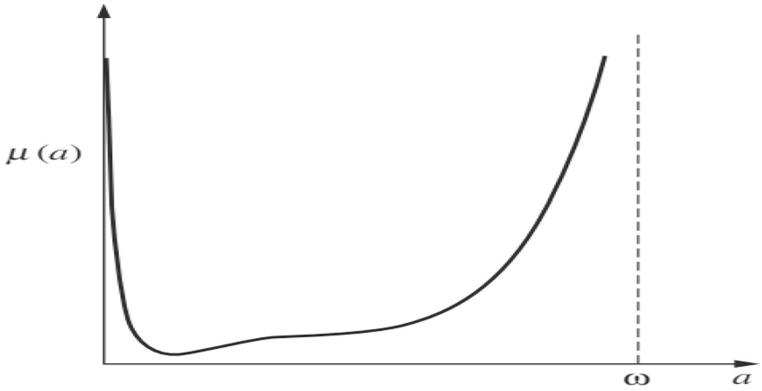


Fig. 1 The graph of the death rate μ (Inaba 2017, Fig. 1.2)

Before proceeding further, we introduce age-structured operators A_i with their domains $D(A_i)$ for $i = 1, \cdots, N$ as follows:

$$\begin{cases} A_i\phi := -\frac{d\phi}{da} - \mu_i\phi, \\ D(A_i) := \{\phi \in W^{1,1}(0, a_i),\, \mu_i\phi \in L^1(0, a_i) \text{ and } \phi(0) = \int_0^{a_i} \beta_i(a)\phi(a)da\}. \end{cases} \tag{1.3}$$

Our main theorem reads as follows.

Theorem 1.1 *Let* $\mu \in L^\infty_{\text{loc},+}([0, a_i))$ *satisfy (1.2) and* $\beta \in L^\infty_+(0, a_i)$. *Then the solution* $(u_1, \cdots, u_N)$ *of (1.1) with initial date* $u_{0i} \geq\not\equiv 0$ *satisfies the following property: if* $u_{0i} \in D(A_i)$ *and* $u_{0i}(a) \neq 0$ *for* $a \in \text{supp}\beta_i$, *and assume* $\lambda_1/\sigma_1 > 0$ *and* $\lambda_1/\sigma_1 > \lambda_j/\sigma_j$, $\forall j \geq 2$, *then*

$$\begin{cases} u_1(t, a) \to \frac{\lambda_1 e^{-\lambda_1 a}\pi(a,0,a_1)}{\sigma_1 \int_0^{a_1} e^{-\lambda_1 a}\pi(a,0,a_1)da} > 0, \\ u_j(t, a) \to 0, \ \forall j \geq 2, \end{cases} \quad \text{in } L^1([0, a_i)) \text{ as } t \to +\infty, \tag{1.4}$$

where $\pi(a, 0, a_1) := e^{-\int_0^a \mu(s,a_1)ds}$ *and* λ_j *for* $j = 1, \cdots, N$ *are the principal eigenvalues of the problems*

$$\partial_a\varphi_j = -\mu(a, a_j)\varphi_j - \lambda\varphi_j, \ \ a \in (0, a_j), \qquad \varphi_j(0) = \int_0^{a_j} \beta(a, a_j)\varphi_j(a)da.$$

Remark 1.2 We would like to mention that the assumption $u_{0i} \in D(A_i)$ is used to ensure the regularity of the solutions $u_i \in C^1([0, \infty), L^1(0, a_i)) \cap C([0, \infty), W^{1,1}(0, a_i))$. One can refer to (Webb 1984, Theorem 2.10) for more details. In addition, the assumption $u_{0i}(a) \neq 0$ for $a \in \text{supp}\beta_i$ is employed to guarantee the existence of persistent solutions, i.e $p_i(t) = \int_0^{a_i} u_i(t, a)da > 0$. The interested readers can refer to (Inaba 2017, Proposition 1.9) for more details.

We mention that the dynamics of (1.1) with more general species' interactions (see (2.1) in the next section) had been studied previously from different aspects, for example, the dynamics of hierarchically age-structured populations by Cushing (1994), non-constant oscillations by Cushing and Saleem (1984), age-structured models with more interactions including the predator-prey type by Busenberg and Iannelli (1985), and optimal control of (1.1) with harvesting by Fister and Lenhart (2004). The interested readers can refer to these studies and references cited therein.

Next we focus on the effects of life span, i.e. the maximum age a_i on the dynamics of system (1.1). Observe that the sign of the principal eigenvalue of species-i (which is used to study the global dynamics of (1.1)) is determined by a nonlocal integral on the whole age interval,

$$\int_0^{a_i} \beta(a, a_i)\pi(a, 0, a_i)da := \int_0^{a_i} \beta(a, a_i)e^{-\int_0^a \mu(s,a_i)ds}da. \tag{1.5}$$

It could be quite complicated: due to the variation of maximum ages a_i, the domains of birth and death rates will also change, in particular the death rate μ will blow up at different points a_i, which results in complicated and subtle behavior of the integral (1.5). Later, one will see this from some concrete examples in Section 3. Thus this motivates us to provide scaled assumptions on β and μ, and consider the following system:

$$\begin{cases} \dfrac{\partial u_i}{\partial t} + \dfrac{\partial u_i}{\partial a} = -\left[(1/a_i)\mu(a/a_i) + \displaystyle\sum_{j=1}^{N}\int_0^{a_j} u_j(t,a)da\right]u_i(t,a), & t > 0,\ a \in (0, a_i), \\ u_i(t,0) = \displaystyle\int_0^{a_i} (1/a_i)\beta(a/a_i)u_i(t,a)da, & t > 0, \\ u_i(0,a) = u_{0i}(a), & a \in (0, a_i). \end{cases} \tag{1.6}$$

With this scaled assumptions on β and μ in hand, we could obtain the monotonicity of the principal eigenvalue with respect to the maximum ages. More precisely, we have the following corollary.

Corollary 1.3 *Let $\mu \in L^\infty_{\text{loc},+}([0, 1))$ satisfy (1.2) and $\beta \in L^\infty_+(0, 1)$. Then the solution $(u_1, \cdots, u_N)$ of (1.6) with initial date $u_{0i} \geq\not\equiv 0$ satisfies the following property: if $u_{0i} \in D(A_i)$ and $u_{0i}(a) \neq 0$ for $a \in \text{supp}\beta_i$, and assume $\lambda_1 > 0$ and $a_1 < a_j$, $\forall j \geq 2$, then*

$$\begin{cases} u_1(t,a) \to \frac{\lambda_1 e^{-\lambda_1 a}\pi(a,0,a_1)}{\int_0^{a_1} e^{-\lambda_1 a}\pi(a,0,a_1)da} > 0, \\ u_j(t,a) \to 0,\ \forall j \geq 2, \end{cases} \quad \text{in } L^1([0, a_i)) \text{ as } t \to +\infty, \tag{1.7}$$

where $\pi(a, 0, a_1) = e^{-(1/a_1)\int_0^a \mu(s/a_1)ds}$ and λ_1 is the principal eigenvalue of the problem

$$\partial_a\varphi = -(1/a_1)\mu(a/a_1)\varphi - \lambda\varphi,\ \ a \in (0, a_1), \qquad \varphi(0) = \int_0^{a_1} (1/a_1)\beta(a/a_1)\varphi(a)da.$$

Regarding the above result, we find that in age-structured competition models with some suitable assumptions on birth and death rates (given as above), the species with the smallest maximum age always wins the competition to exclude the other species. It can be explained mathematically as follows: under the scaled assumptions on β and μ, the characteristic equation of (1.6) linearized at zero reads as follows,

$$\int_0^{a_i} (1/a_i)\beta(a/a_i)e^{-\lambda_i a}e^{-(1/a_i)\int_0^a \mu(s/a_i)ds}da = 1. \tag{1.8}$$

After a change of variables, it can be written as follows

$$\int_0^1 \beta(a)e^{-\lambda_i a a_i}e^{-\int_0^a \mu(s)ds}da = 1. \tag{1.9}$$

Setting $\lambda_i = 0$, this means that the number of newborns that a survived individual produces in its lifespan would be the same and independent of the maximum age. In other words, this scaling leaves the basic reproduction number unaffected. In addition, the life expectation (see (Thieme 2018)) will be proportional to the maximum age. In fact, the life expectation is defined by

$$D(a_i) := \int_0^{a_i} e^{-(1/a_i)\int_0^a \mu(s/a_i)ds}da = a_i\int_0^1 e^{-\int_0^a \mu(s)ds}da.$$

According to (1.9), one can see that $\lambda_i = \lambda_i(a_i)$ is inversely proportional to the maximum age a_i. It follows that the species with smallest maximum age $a_1 = \min\{a_1, \cdots, a_N\}$ has the largest principal eigenvalue λ_1, which thus allows only the first species survive and forces other species to extinction.

As we can see, the competitive exclusion principle occurs in age-structured competition models. Similar results on the optimal age or size in species interaction models were observed before, see (Ackleh et al. 2004; Kozłowski and Wiegert 1987; Argasinski and Broom 2021; John and Müller 2023; Blath and Tóbiás 2020). It is also somehow similar to the conjecture that "the slowest diffuser always wins the competition" in diffusive competition models (see (Dockery et al. 1998)). The latter one says that if a species has the smallest diffusion rate, then it always wins the competition. This conjecture was proved for $N = 2$ in Dockery et al. (1998), while is still open for $N \geq 3$. We refer to Cantrell and Lam (2021); Lam and Lou (2023) for some recent progresses. Here, we prove a similar result which states that "the species with smallest maximum age always wins the competition" for any $N \geq 2$ under appropriate conditions on birth and death rates.

In summary, with the fixed birth and death rates along its lifespan, i.e.

$$\begin{cases} \int_0^{a_i}(1/a_i)\beta(a/a_i)da = \int_0^1 \beta(s)ds, \\ \int_0^{a_i}(1/a_i)\mu(a/a_i)da = \int_0^1 \mu(s)ds, \end{cases} \quad \forall i = 1, \cdots, N,$$

each species will obtain the same $\lambda_i a_i$ determined by (1.9), but the one with smallest maximum age will attain the largest intrinsic growth rate λ_i. One possible biological explanation on this scaling is suggested that the species are in the stage of quiescence, which slow down the metabolism such that the overall mortality and fecundity unaffected. The interested readers can refer to Blath and Tóbiás (2020), where a stochastic individual-based approach employing birth-and-death processes indicates that the slower trait is more likely to go into fixation. In addition, for other age-structured populations and competition exclusion principle, the interested readers can refer to (Ackleh and Allen 2003; Bremermann and Thieme 1989; Duan et al. 2018; Iannelli and Milner 2017; Martcheva 2009, 2015; Martcheva and Li 2013; Smith and Thieme 2013; Smith and Waltman 1995; Thieme 2007, 2018; John and Müller 2023; Kozłowski and Wiegert 1987; Argasinski and Broom 2021; Ackleh et al. 2004) for more results.

The paper is organized as follows. In Section 2, we present the proofs of our main results, Theorem 1.1 and Corollary 1.3. More precisely, we will first find an equivalent system with (1.1), then study the monotonicity of the principal eigenvalue with respect to the maximum age, and finally determine the global dynamics of both (1.1) and (1.6). In Section 3, we provide some examples about more interesting and complicated behavior of the principal eigenvalue with respect to the maximum age.

2 Main proofs

In this section we give the proof of Theorem 1.1 via two steps.

2.1 Equivalent system

First we show that the global dynamics of (1.1) can be determined completely by an N species competition ODE. To include more general interactions, we consider the following age-structured model with N-species,

$$\begin{cases} \dfrac{\partial u_i}{\partial t} + \dfrac{\partial u_i}{\partial a} = -\mu(a, a_i)u_i(t,a) + \left(\displaystyle\sum_{j=1}^{N} \int_0^{a_j} b_{ij}(a)u_j(t,a)da\right) u_i(t,a), & t > 0, \ a \in (0, a_i), \\ u_i(t,0) = \displaystyle\int_0^{a_i} \beta(a, a_i)u_i(t,a)da, & t > 0, \\ u_i(0,a) = u_{0i}(a), & a \in (0, a_i), \end{cases} \tag{2.1}$$

Here $b_{ij} \in L^\infty(0,\infty)$ represents the interaction coefficient between the i-th and j-th species, which is dependent on age a. In Theorem 1.1, $b_{ij} \equiv -\sigma_i$ for all $i = 1, \ldots, N$ describe the competition. In addition, let us recall the principal eigenvalues of corresponding linear age-structured operators A_i defined in (1.3) as follows:

$$\int_0^{a_i} \beta(a, a_i)e^{-\lambda_i a}\pi(a, 0, a_i)da = 1, \quad i = 1, \ldots, N, \tag{2.2}$$

where $\pi(a, b, a_i) := e^{-\int_b^a \mu(s,a_i)ds}$ represents the survival rate from age b to a; see for example (Webb 1984). Then we have the following result.

Theorem 2.1 *Given the following ODE system*

$$\begin{cases} \dfrac{dp_i(t)}{dt} = \lambda_i p_i(t) + \left(\displaystyle\sum_{j=1}^{N} \widetilde{b}_{ij} p_j(t) \right) p_i(t), \quad t > 0, \\ p_i(0) = \displaystyle\int_0^{a_1} u_i(0,a)da, \end{cases} \tag{2.3}$$

where

$$\widetilde{b}_{ij} = \frac{\int_0^{a_j} b_{ij}(a) e^{-\lambda_j a} \pi(a,0,a_j) da}{\int_0^{a_j} e^{-\lambda_j a} \pi(a,0,a_j) da}$$

and λ_i with $i = 1, 2, \ldots, N$ are defined in (2.2). In addition, let the assumptions in Theorem 1.1 hold. Now if (2.3) has uniformly bounded solutions in $\mathbb{R}^N$ and has a globally stable semi-trivial equilibrium $\boldsymbol{p}^* = (\lambda_1/\sigma_1, 0, \ldots, 0)$ with $\lambda_1/\sigma_1 > 0$ and $\lambda_1/\sigma_1 > \lambda_j/\sigma_j$ for any $j \geq 2$, then the solution $u(t,a) = (u_1(t,a), \ldots, u_N(t,a))$ of (2.1) satisfies

$$\begin{cases} \lim\limits_{t\to\infty} u_1(t,a) = \frac{\lambda_1 e^{-\lambda_1 a} \pi(a,0,a_1)}{\sigma_1 \int_0^{a_1} e^{-\lambda_1 a} \pi(a,0,a_1) da}, \\ \lim\limits_{t\to\infty} u_i(t,a) = 0 \, \textit{for} \; i = 2, \ldots, N, \end{cases} \quad \textit{in } L^1([0,a_i]). \tag{2.4}$$

Proof Observe that the interaction term of (2.1) is quadratic type, which is Lipschitz continuous on bounded sets. Thus combining the assumptions on the initial data, there exists a unique solution $u \in C^1([0,\infty), L^1(0,a_1) \times \cdots \times L^1(0,a_N)) \cap C([0,\infty), W^{1,1}(0,a_1) \times \cdots \times W^{1,1}(0,a_N))$, see (Webb 1984, Section 2) or Pazy (1983) for more details. We first transform (2.1) into a decoupled and linear age-structured system. To this end, we define the total density of each species by

$$p_i(t) := \int_0^{a_i} u_i(t,a)da, \quad i = 1, \cdots, N. \tag{2.5}$$

Observe that due to the assumptions imposed on the initial data u_{0i}, we have $p_i(t) > 0$ for all $i = 1, \cdots, N$ and sufficiently large time $t > 0$. By (2.1) and the regularity of u_i, direct calculations yield that p_i satisfies

$$\begin{aligned} \frac{dp_i(t)}{dt} &= \int_0^{a_i} \partial_t u_i(t,a)da \\ &= \int_0^{a_i} \left[-\partial_a u_i(t,a) - \mu(a,a_i)u_i(t,a) + u_i(t,a) \left(\sum_{j=1}^{N} \int_0^{a_j} b_{ij}(a)u_j(t,a)da \right) \right] da \\ &= \int_0^{a_i} (\beta(a,a_i) - \mu(a,a_i)) u_i(t,a)da + \left(\sum_{j=1}^{N} \int_0^{a_j} b_{ij}(a)u_j(t,a)da \right) p_i(t), \end{aligned} \tag{2.6}$$

where we used the fact that $u_i(t, a_i) = 0$ for all $t > 0$ and $i = 1, \cdots, N$ due to (1.2). Next, denote

$$n_i(t, a) := \frac{u_i(t, a)}{p_i(t)}, \quad i = 1, \cdots, N. \tag{2.7}$$

Then it follows from (2.6) that

$$\begin{aligned}
\partial_t n_i + \partial_a n_i =& \frac{1}{p_i(t)} (\partial_t u_i + \partial_a u_i) - \frac{u_i}{p_i^2(t)} \frac{dp_i(t)}{dt} \\
=& \frac{1}{p_i(t)} \left[-\mu(a, a_i) u_i + \left(\sum_{j=1}^N \int_0^{a_j} b_{ij}(a) u_j(t, a) da \right) u_i \right] \\
& - \frac{n_i}{p_i(t)} \left[\int_0^{a_i} (\beta(a, a_i) - \mu(a, a_i))\, u_i(t, a) da \right. \\
& \left. + \left(\sum_{j=1}^N \int_0^{a_j} b_{ij}(a) u_j(t, a) da \right) p_i(t) \right] \\
=& - \mu(a, a_i) n_i - \int_0^{a_i} (\beta(a, a_i) - \mu(a, a_i))\, n_i(t, a) da\, n_i.
\end{aligned} \tag{2.8}$$

For each $i = 1, \ldots, N$, we denote

$$\begin{aligned}
& k(t, a_i) := - \int_0^{a_i} (\beta(a, a_i) - \mu(a, a_i))\, n_i(t, a) da \\
& \text{and} \quad v_i(t, a) := e^{-\int_0^t k(s, a_i) ds} n_i(t, a).
\end{aligned} \tag{2.9}$$

Then we can verify that

$$\begin{cases}
\partial_t v_i + \partial_a v_i = -\mu(a, a_i) v_i, & t > 0,\ a \in (0, a_i), \\
v_i(t, 0) = \displaystyle\int_0^{a_i} \beta(a, a_i) v_i(t, a) da, & t > 0, \\
v_i(0, a) = \frac{u_{0i}(a)}{p_i(0)}, & a \in (0, a_i).
\end{cases} \tag{2.10}$$

Indeed, by (2.8) and (2.9) direct calculations yield

$$\begin{aligned}
\partial_t v_i + \partial_a v_i &= e^{-\int_0^t k(s, a_i) ds} (\partial_t n_i + \partial_a n_i) - k(t, a_i) v_i \\
&= e^{-\int_0^t k(s, a_i) ds} (-\mu(a, a_i) n_i + k(t, a_i) n_i) - k(t, a_i) v_i \\
&= -\mu(a, a_i) v_i,
\end{aligned}$$

and the initial and boundary conditions in (2.10) follow directly from definition (2.9).

Notice that the equation of v_i in (2.10) is linear and admits the existence of the principal eigenvalue, denoted by λ_i, which satisfies (2.2). On the other hand, by (2.6) and (2.9), we observe that for each $i = 1, \ldots, N$, the total population p_i satisfies

$$\begin{cases} \dfrac{dp_i(t)}{dt} = -k(t,a_i)p_i(t) + \left(\displaystyle\sum_{j=1}^{N} \int_0^{a_j} b_{ij}(a)n_j(t,a)da \ p_j(t)\right) p_i(t), \quad t > 0, \\ p_i(0) = \displaystyle\int_0^{a_1} u_i(0,a)da. \end{cases} \tag{2.11}$$

Now we claim that

$$\lim_{t\to\infty} k(t,a_i) = -\lambda_i \quad \text{and} \quad \lim_{t\to\infty} \int_0^{a_j} b_{ij}(a)n_j(t,a)da = \widetilde{b}_{ij}. \tag{2.12}$$

Suppose that the above claim is true. On the other hand, we consider the following autonomous system

$$\begin{cases} \dfrac{dp_i(t)}{dt} = \lambda_i p_i(t) + \left(\displaystyle\sum_{j=1}^{N} \widetilde{b}_{ij} p_j(t)\right) p_i(t), \quad t > 0, \\ p_i(0) = \displaystyle\int_0^{a_1} u_i(0,a)da. \end{cases} \tag{2.13}$$

By assumptions in Theorem 2.1, (2.13) has a uniformly bounded solution $p_i \in \mathbb{R}^N$. In addition, due to (2.12), the solutions of (2.11) are also uniformly bounded in $\mathbb{R}^N$. Then according to (Zhao 2017, Proposition 3.2.2), we see that (2.11) is "asymptotically" equivalent to system (2.13).

Here "asymptotically" means that if the unique equilibrium $\mathbf{p}^*$ of (2.13) is globally stable, then the solutions of (2.11) converges to $\mathbf{p}^*$ as $t \to \infty$. Recalling the definitions of p_i in (2.5) and n_i in (2.7), we can see that the global dynamics of u_i is determined completely by p_i and n_i for all $i = 1, \ldots, N$. Thus the results (2.4) are desired once n_i is determined, see (2.16). □

Proof of the claim (2.12) The proof is motivated by (Webb 1984, Section 5.4) (or see (Busenberg and Iannelli 1985)). For completeness, we include the necessary details. Recall from (Webb 1984, Section 4.3) that

$$\left((\lambda I - A_i)^{-1}\psi\right)(a) = \int_0^a e^{-\lambda(a-s)}\pi(a,s,a_i)\psi(s)ds + e^{-\lambda a}\pi(a,0,a_i)\frac{H_\lambda(\psi)}{\Delta(\lambda)}, \quad \psi \in L^1(0,a_i),$$

where

$$H_\lambda(\psi) := \int_0^{a_i} \beta(a,a_i)e^{-\lambda a}\left(\int_0^a e^{\lambda b}\pi(a,b,a_i)\psi(b)db\right)da,$$

$$\Delta(\lambda) := 1 - \int_0^{a_i} \beta(a,a_i)e^{-\lambda a}\pi(a,0,a_i)da.$$

Next recalling the asynchronous exponential growth of age-structured models (see (Webb 1984, Theorem 4.9)), the solutions v_i with $i = 1, 2, \ldots, N$ of linear age-structured models satisfy

$$\lim_{t\to\infty} v_i(t,a)e^{-\lambda_i t} = \frac{1}{2\pi i}\int_\Gamma (\lambda I - A_i)^{-1} v_{0i}\, d\lambda,$$

where Γ is a positively oriented closed curve in $\mathcal{C}$ enclosing λ_1, but no other point of $\sigma(A_i)$ (the spectrum set of A_i) and $v_{0i} = v_i(0,\cdot)$ denotes the initial data.

Observe that the functions

$$\int_0^a e^{-\lambda(a-s)}\pi(a,s,a_i)v_{0i}(s)ds, \quad i = 1, 2, \ldots, N$$

are holomorphic with respect to λ in the region enclosed by Γ and thus there holds

$$\frac{1}{2\pi i}\int_\Gamma \int_0^a e^{-\lambda(a-s)}\pi(a,s,a_i)v_{0i}(s)ds\, d\lambda = 0.$$

On the other hand, λ_i is a simple zero of $\Delta(\lambda)$ follows from the fact that

$$\Delta'(\lambda_i) = \int_0^{a_i} a\beta(a,a_i)e^{-\lambda_i a}\pi(a,0,a_i)da > 0.$$

Moreover, the residue of $1/\Delta(\lambda)$ at λ_i is

$$\frac{1}{\Delta'(\lambda_i)} = \frac{1}{\int_0^{a_i} a\beta(a,a_i)e^{-\lambda_i a}\pi(a,0,a_i)da}.$$

By using the Residue Theorem we have

$$\begin{aligned}\lim_{t\to\infty} e^{-\int_0^t k(s,a_i)ds}e^{-\lambda_i t} &= \lim_{t\to\infty}\int_0^{a_i} n_i(t,a)e^{-\int_0^t k(s,a_i)ds}e^{-\lambda_i t}da\\ &= \lim_{t\to\infty}\int_0^{a_i} v_i(t,a)e^{-\lambda_i t}da\\ &= \frac{H_{\lambda_i}(v_{0i})}{\int_0^{a_i} a\beta(a,a_i)e^{-\lambda_i a}\pi(a,0,a_i)da}\int_0^{a_i} e^{-\lambda_i a}\pi(a,0,a_i)da.\end{aligned} \tag{2.14}$$

It follows that

$$\lim_{t\to\infty} e^{-\int_0^t k(s,a_i)ds} = \begin{cases}\infty, & \text{if } \lambda_i > 0,\\ 0, & \text{if } \lambda_i < 0.\end{cases} \tag{2.15}$$

Next by (2.14) we have

$$\begin{aligned}\lim_{t\to\infty} n_i(t,a) &= \lim_{t\to\infty}\left(e^{-\lambda_i t} v_i(t,a)\right) e^{\lambda_i t} e^{\int_0^t k(s,a_i)ds} \\ &= \frac{e^{-\lambda_i a}\pi(a,0,a_i)}{\int_0^{a_i} e^{-\lambda_i a}\pi(a,0,a_i)da} \\ &=: w_{i\infty}(a), \quad \text{in } L^1(0,a_i),\end{aligned} \tag{2.16}$$

see (Webb 1984, Theorem 4.9). Next recall the renew theorem of age-structured equations (see (Inaba 2017, Proposition 1.9)), there holds

$$e^{-\lambda_i t} v_i(t,0) \to \frac{H_{\lambda_i}(v_{0i})}{\int_0^{a_i} a\beta(a,a_i)e^{-\lambda_i a}\pi(a,0,a_i)da} \quad \text{as } t\to\infty. \tag{2.17}$$

Moreover, direct computation yields

$$\begin{aligned}&\lim_{t\to\infty}\int_0^{a_i}\mu(a,a_i)n_i(t,a)da \\ &= \lim_{t\to\infty}\int_0^{a_i}\mu(a,a_i)e^{\int_0^t k(s,a_i)ds} v_i(t,a)da \\ &= \lim_{t\to\infty} e^{\int_0^t k(s,a_i)ds} e^{\lambda_i t}\int_0^{a_i}\mu(a,a_i)e^{-\lambda_i t} v_i(t,a)da \\ &= \lim_{t\to\infty} e^{\int_0^t k(s,a_i)ds} e^{\lambda_i t}\int_0^{a_i}\mu(a,a_i)e^{-\lambda_i t} v_i(t-a,0)\pi(a,0,a_i)da \\ &= -\lim_{t\to\infty} e^{\int_0^t k(s,a_i)ds} e^{\lambda_i t}\int_0^{a_i} e^{-\lambda_i(t-a)} v_i(t-a,0)e^{-\lambda_i a}\frac{d}{da}\left(\pi(a,0,a_i)\right)da.\end{aligned}$$

Note from (2.14) that the limit $\lim\limits_{t\to\infty} e^{\int_0^t k(s,a_i)ds} e^{\lambda_i t}$ exists. Combining (2.17) and the fact that $\frac{d}{da}\pi$ is integrable, Lebesgue convergence theorem applies to conclude that

$$\lim_{t\to\infty}\int_0^{a_i}\mu(a,a_i)n_i(t,a)da = \frac{1}{\int_0^{a_i} e^{-\lambda_i a}\pi(a,0,a_i)da} - \lambda_i.$$

On the other hand, due to $\beta(\cdot,a_i) \in L_+^\infty(0,a_i)$, Lebesgue convergence theorem again yields

$$\lim_{t\to\infty}\int_0^{a_i}\beta(a,a_i)n_i(t,a)da = \int_0^{a_i}\beta(a,a_i)w_{i\infty}(a)da = w_{i\infty}(0). \tag{2.18}$$

It follows that

$$\lim_{t\to\infty} k(t,a_i) = -\lim_{t\to\infty}\int_0^{a_i}\left(\beta(a,a_i)-\mu(a,a_i)\right)n_i(t,a)da = -\lambda_i.$$

Finally, recalling (2.16) we have

$$\widetilde{b}_{ij} = \lim_{t\to\infty} \int_0^{a_j} b_{ij}(a) n_j(t,a)da = \int_0^{a_j} b_{ij}(a) w_{j\infty}(a)da. \tag{2.19}$$

Thus the results are desired. □

Now via the transformation in Theorem 2.1, system (1.6) is asymptotically equivalent to

$$\begin{cases} \dfrac{dp_i(t)}{dt} = \left(\lambda_i - \sigma_i \displaystyle\sum_{j=1}^{N} p_j(t)\right) p_i(t), \quad t > 0, \\ p_i(0) = \int_0^{a_1} u_i(0,a)da. \end{cases} \tag{2.20}$$

Let us finish the proof of Theorem 1.1 under the assumption that

$$\lambda_1/\sigma_1 > 0 \quad \text{and} \quad \lambda_1/\sigma_1 > \lambda_j/\sigma_j, \quad \forall j \geq 2. \tag{2.21}$$

We mention that $\lambda_1 > 0$ is used to guarantee the first species to survive, since from the above analysis one can see that $\lambda_i < 0$ implies that $u_i(t,a) \to 0$ as $t \to \infty$. Biologically speaking, $\lambda_i < 0$ means that the birth-death process cannot support the survival of the i-th species before competition happens.

Proof of Theorem 1.1 Let $(p_1(t), \cdots, p_N(t))$ be the solution of (2.20). Then

$$\frac{dp_1}{dt} \leq (\lambda_1 - \sigma_1 p_1)\, p_1 \text{ for all } t > 0,$$

and note that $p_1 > 0$ for all $t > 0$. Define $W_j := p_j^{1/\sigma_j} \big/ p_1^{1/\sigma_1}$ for any $j = 2, \cdots, N$. It follows from (2.20) that

$$\frac{dW_j}{dt} = (\lambda_j/\sigma_j - \lambda_1/\sigma_1)W_j, \quad \forall t > 0, \; j = 2, \cdots, N.$$

Due to $\lambda_1/\sigma_1 > \lambda_j/\sigma_j$ for all $j \geq 2$, we deduce

$$W_j(t) = W_j(0)\exp\{(\lambda_j/\sigma_j - \lambda_1/\sigma_1)t\} \to 0 \quad \text{as} \quad t \to +\infty. \tag{2.22}$$

Since $p_1(t)$ is uniformly bounded, we derive that $p_j(t) \to 0$ for all $j \geq 2$. Recall that the limiting equation of p_1 in (2.20) is the following

$$\frac{dp_1(t)}{dt} \leq (\lambda_1 - \sigma_1 p_1(t))\, p_1(t), \quad t > 0. \tag{2.23}$$

Fix a $t_0 > 0$ and consider the following auxiliary equation:

$$\begin{cases} \frac{dy}{dt} = (\lambda_1 - \sigma_1 y)y, \quad t_0 < t < \infty, \\ y(t_0) = p_1(t_0). \end{cases} \tag{2.24}$$

Clearly, $y \to \lambda_1/\sigma_1$ as $t \to \infty$. Further, by comparison principle, there holds $y(t) \geq p_1(t)$ for all $t \geq t_0$. On the other hand, we have

$$\frac{d}{dt}\ln\left(\frac{p_1}{y}\right) = \frac{p_1'}{p_1} - \frac{y'}{y} = \sigma_1(y - p_1) - \sigma_1\sum_{j=2}^{N} p_j.$$

It follows that

$$y - p_1 = \frac{1}{\sigma_1}\frac{d}{dt}\ln\left(\frac{p_1}{y}\right) + \sum_{j=2}^{N} p_j.$$

Integrating the above equality from t_0 to t, we then obtain

$$\int_{t_0}^{t}(y(\eta) - p_1(\eta))d\eta = \frac{1}{\sigma_1}\ln\left(\frac{p_1(t)}{y(t)}\right) + \sum_{j=2}^{N}\int_{t_0}^{t} p_j(\eta)d\eta \leq M < \infty,$$

where M is independent of t, since $p_1(t)$ and $y(t)$ are both bounded, and $\int_{t_0}^{t} p_j(\eta)d\eta < \infty$ for $j = 2, \ldots, N$ due to (2.22). This implies that $\int_{t_0}^{t}(y(\eta) - p_1(\eta))d\eta < \infty$. Furthermore, it is easily seen that $\frac{d}{dt}(y(t) - p_1(t))$ is bounded in $[t_0, \infty)$. Hence $p_1(t) - y(t) \to 0$ as $t \to \infty$; that is, $p_1(t) \to \lambda_1/\sigma_1$ as $t \to \infty$. Therefore, the desired result (2.4) follows from (2.7) and (2.16). ◻

Remark 2.2 We would like to mention that for system (2.1) with general b_{ij}, one can investigate its dynamics via studying (2.13). In the present paper, to illustrate the effects of the maximum age on the principal eigenvalue, we only focus on the simplest competition case, i.e. $b_{ij} = -\sigma_i$.

2.2 Monotonicity of the principal eigenvalue on the maximal age

We now focus on the effects of the maximum age on the principal eigenvalue, and in particular, show that under the scaled assumptions on β and μ given in (1.6), the principal eigenvalue is increasing with respect to the maximum age. This will imply (2.21) to finish the proof of Theorem 1.1. First from (2.2) observe that λ_i is increasing and decreasing with respect to the birth rate β and death rate μ, respectively. It means that under the same maximum ages, increasing birth rates or decreasing death rates will help the species to win the competition, which is quite reasonable biologically.

As mentioned before, the domains of death and birth rates as functions of a_i are $[0, a_i)$. It follows that once a_i varies, the death rate function $\mu(\cdot, a_i)$ and birth rate function $\beta(\cdot, a_i)$ may change arbitrarily. In particular, the assumption of $\mu(\cdot, a_i)$ in (1.2) will make it change its blow-up points when a_i varies. Based on the above observations, one can imagine that the behavior of $a^+ \to \lambda(a^+)$ could be very complicated, without any monotonicity. This motivates us to provide some suitable assumptions on μ and β to study the monotonicity. Now we present a monotonicity result as follows including more choices on β and μ.

Lemma 2.3 *For each $a^+ > 0$, let $\mu(\cdot, a^+) \in L^\infty_{\mathrm{loc}}([0, a^+))$ be any nonnegative function satisfying $\int_0^{a^+} \mu(a, a^+)da = +\infty$. Let $\lambda(a^+)$ denote the principal eigenvalue of the problem*

$$\begin{cases} \frac{\mathrm{d}\varphi}{\mathrm{d}a} = -\mu(a, a^+)\varphi - \lambda\varphi, & a \in (0, a^+], \\ \varphi(0) = \int_0^{a^+} \beta(a, a^+)\varphi(a)\mathrm{d}a, \end{cases} \tag{2.25}$$

where $\beta(\cdot, a^+) \in L^\infty(0, a^+)$ is any nonnegative function.

- (i) *If $a^+ \mapsto \mu(a, a^+)$ is differentiable and non-increasing and $a^+ \mapsto \beta(a, a^+)$ is differentiable and non-decreasing for any $a > 0$, then $a^+ \mapsto \lambda(a^+)$ is non-decreasing;*
- (ii) *If*

$$\begin{cases} \mu(a, a^+) = (1/a^+)\tilde{\mu}\left(a/a^+\right) & \text{with some } \tilde{\mu} \in L^\infty_{\mathrm{loc},+}([0, 1)), \\ \beta(a, a^+) = (1/a^+)\tilde{\beta}\left(a/a^+\right) & \text{with some } \tilde{\beta} \in L^\infty_+(0, 1), \end{cases}$$

then $\lambda(a^+) = \lambda(1)/a^+$, and in particular, $a^+ \mapsto \lambda(a^+)$ is non-increasing.

Remark 2.4 Observe that Lemma 2.3-(ii) is just our choice of β and μ in (1.6). Thus once Lemma 2.3-(ii) is proved, due to $\sigma_i \equiv 1$, $\lambda_1 > 0$ and $\lambda_1 > \lambda_j$ for all $j = 2, \cdots, N$ hold automatically, thus the proof of Corollary 1.3 is complete.

Proof Similar to (2.2), the principal eigenvalue $\lambda(a^+)$ satisfies

$$\int_0^{a^+} \beta(a, a^+)e^{-\lambda(a^+)a}e^{-\int_0^a \mu(s,a^+)\mathrm{d}s}\mathrm{d}a = 1. \tag{2.26}$$

(i) We first prove the monotonicity of $\lambda(a^+)$ under the assumption (i). To this end, define $H(a^+, \lambda) : (0, \infty) \times \mathbb{R} \mapsto [0, \infty)$ as follows:

$$H(a^+, \lambda) := \int_0^{a^+} \beta(a, a^+)e^{-\lambda a}e^{-\int_0^a \mu(s,a^+)\mathrm{d}s}\mathrm{d}a.$$

Then H is partially differentiable with respect to λ and $\partial_\lambda H(a^+, \lambda) > 0$. Due to the differentiability of μ and β with respect to a^+, by the implicit function theorem, we conclude that $\lambda = \lambda(a^+)$ is differentiable with respect to a^+. Now we can take the derivative of (2.26) and obtain

$$\begin{aligned} &\int_0^{a^+} \frac{\partial\beta(a, a^+)}{\partial a^+}e^{-\lambda(a^+)a}e^{-\int_0^a \mu(s,a^+)\mathrm{d}s}\mathrm{d}a \\ &- \lambda'(a^+)\int_0^{a^+} a\beta(a, a^+)e^{-\lambda(a^+)a}e^{-\int_0^a \mu(s,a^+)\mathrm{d}s}\mathrm{d}a \\ &+ \beta(a^+, a^+)e^{-\lambda(a^+)a^+}e^{-\int_0^{a^+} \mu(s,a^+)\mathrm{d}s} \\ &- \int_0^{a^+} \beta(a, a^+)e^{-\lambda(a^+)a}e^{-\int_0^a \mu(s,a^+)\mathrm{d}s}\left[\int_0^a \frac{\partial\mu(s, a^+)}{\partial a^+}\mathrm{d}s\right]\mathrm{d}a = 0. \end{aligned}$$

Then it follows from (i) that

$$\lambda'(a^+) \geq \frac{\beta(a^+, a^+)e^{-\lambda(a^+)a^+}e^{-\int_0^{a^+}\mu(s,a^+)\mathrm{d}s}}{\int_0^{a^+} a\beta(a, a^+)e^{-\lambda(a^+)a}e^{-\int_0^a \mu(s,a^+)\mathrm{d}s}\mathrm{d}a} \geq 0,$$

which implies that $\lambda(a^+)$ is non-decreasing in a^+.

(ii) Under the assumption in part (ii), by the characteristic equation in (1.9), we calculate that

$$\begin{aligned} 1 &= \int_0^{a^+} \frac{1}{a^+}\tilde{\beta}(a/a^+)\, e^{-\lambda(a^+)\,a}\, e^{-\frac{1}{a^+}\int_0^a \tilde{\mu}(s/a^+)\,ds} da \\ &= \int_0^1 \tilde{\beta}(a)\, e^{-\lambda(a^+)\,a^+\,a}\, e^{-\int_0^a \tilde{\mu}(s)\,ds} da. \end{aligned}$$

This together with the monotonicity of the mapping $\lambda \mapsto \int_0^1 \beta(a)e^{-\lambda a}e^{-\int_0^a \mu(s)ds}da$ implies immediately that $a^+\,\lambda(a^+) = \lambda(1)$. The proof is complete. □

Before ending this subsection, let us mention that there is another situation appeared in previous studies, which also could induce monotonicity. That is individuals can attain ages greater than a_i, but they are no longer tracked in the models. This assumption first appeared in Webb (2008) and is used later by Walker and Zehetbauer (2022). Under this assumption, one can view $\beta(\cdot, a_i) \equiv \beta(\cdot)$ and $\mu(\cdot, a_i) \equiv \mu(\cdot)$ for $i = 1, 2, \ldots, N$ defined directly in $[0, \infty)$, and only let the maximum age a_i vary in $[0, \infty)$.

Then the integral $\int_0^{a_i} \beta(a)\pi(a, 0)da$ is non-decreasing with respect to a_i. This implies that the species with the largest maximum age $\max_i\{a_i\}$ has the largest principal eigenvalue $\lambda_{\max} := \max_i \lambda_i$ for all $i = 1, 2, \ldots$. Then by Theorem 1.1, the species with the largest maximum age will win the competition and drives the others to extinction.

3 Examples and counterexamples

We have investigated the global dynamics of an age-structured competition model (1.6) with equal competition coefficients. In particular, we have studied the effects of maximum ages quantitatively via observing the occurrence of the competitive exclusion phenomenon. Before finishing the paper, we would like to provide some examples which are not included in Lemma 2.3, but with very interesting results.

3.1 Complicated behavior of $\lambda(a^+)$

In this subsection, we provide two examples to show the complicated behavior of the principal eigenvalue $\lambda(a^+)$ with respect to a^+. Observe from (2.2) that the principal eigenvalue $\lambda = \lambda(a^+)$ of problem (2.25) is completely determined by the integral

$$\int_0^{a^+} \beta(a,a^+)\pi(a,0,a^+)da := \int_0^{a^+} \beta(a,a^+)e^{-\int_0^a \mu(s,a^+)ds}da.$$

This explains intuitively why Lemma 2.3-(i) holds. Moreover, we can take an explicit example as follows:

$$\mu(a,a^+) = \frac{1}{a^+ - a}, \quad \beta(a,a^+) \equiv \beta(a) \text{ independent of } a^+ \tag{3.1}$$

which imply that $\pi(a,0,a^+) = 1 - \frac{a}{a^+}$. It follows from the compuation in Lemma 2.3 that

$$\lambda'(a^+) = \frac{\int_0^{a^+} \beta(a)\frac{\partial \pi(a,0,a^+)}{\partial a^+}e^{-\lambda(a^+)a}da}{\int_0^{a^+} \beta(a)\pi(a,0,a^+)ae^{-\lambda(a^+)a}da} > 0, \tag{3.2}$$

which shows that $a^+ \mapsto \lambda(a^+)$ is increasing.

However, if $\beta(a,a^+)$ or $\mu(a,a^+)$ is not monotone with respect to a^+, does it imply that $a^+ \mapsto \lambda(a^+)$ is not monotone? To illustrate this situation, let us consider another example as follows

$$\mu(a,a^+) = \frac{1}{a^+ - a} + a^+, \quad \beta(a,a^+) \equiv 1 \text{ independent of } a^+. \tag{3.3}$$

Direct computation yields

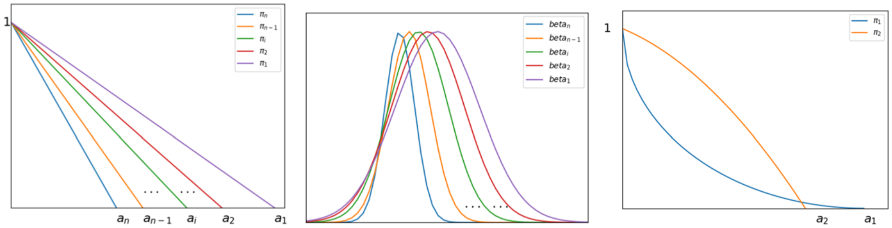
$$\pi(a,0,a^+) = \left(1 - \frac{a}{a^+}\right)e^{-a^+a},$$

and thus for $a^+ > 1$

$$\frac{\partial \pi(a,0,a^+)}{\partial a^+} = \frac{e^{-aa^+}a(1 + aa^+ - (a^+)^2)}{(a^+)^2} \begin{cases} < 0, & a \in (0, a^+ - 1/a^+), \\ > 0, & a \in (a^+ - 1/a^+, a^+). \end{cases}$$

It follows that

$$\begin{aligned} &\int_0^{a^+} \beta(a,a^+)\frac{\partial \pi(a,0,a^+)}{\partial a^+}e^{-\lambda(a^+)a}da \\ &= \frac{1}{(a^+)^2}\int_0^{a^+-1/a^+} e^{-aa^+}a(1 + aa^+ - (a^+)^2)e^{-\lambda(a^+)a}da \\ &\quad + \frac{1}{(a^+)^2}\int_{a^+-1/a^+}^{a^+} e^{-aa^+}a(1 + aa^+ - (a^+)^2)e^{-\lambda(a^+)a}da \\ &\le \left[-\frac{1}{6}(a^+)^2 + \frac{1}{2}\right]e^{-(\lambda(a^+)+a^+)(a^+-1/a^+)} < 0 \quad \text{as } a^+ \gg 1, \end{aligned} \tag{3.4}$$



(a) π_i have the same tendency. (b) β_i have the same tendency. (c) π_i have different shapes.

Fig. 2 different π_i

where we used the fact that $\lambda(a^+)+a^+ > 0$ (otherwise $\int_0^{a^+} e^{-\lambda(a^+)a}\pi(a,0,a^+)da \geq a^+/2 > 1$ for $a^+ \gg 1$). It follows that $a^+ \mapsto \lambda(a^+)$ is decreasing with respect to a^+ for μ and β satisfying (3.3). Hence we have seen that there still could happen that $a^+ \mapsto \lambda(a^+)$ is monotone for $a^+ \gg 1$ under $a^+ \mapsto \beta(a,a^+)$ being monotone but $a^+ \mapsto \mu(a,a^+)$ being not monotone. The behind reason is that the sign of $\lambda'(a^+)$ is determined by the integral

$$\int_0^{a^+} \beta(a)\frac{\partial \pi(a,0,a^+)}{\partial a^+}e^{-\lambda(a^+)a}da,$$

which is the global behavior in the whole interval $[0,a^+)$ rather than the local one.

Next, to illustrate the non-monotone behavior of $a^+ \mapsto \lambda(a^+)$, let us still consider the example (3.3). For $a^+ < 1$, one has

$$\frac{\partial \pi(a,0,a^+)}{\partial a^+} = \frac{e^{-aa^+}a(1+aa^+-(a^+)^2)}{(a^+)^2} > 0, \quad a \in [0,a^+],$$

and thus

$$\begin{aligned}
&\int_0^{a^+} \beta(a,a^+)\frac{\partial \pi(a,0,a^+)}{\partial a^+}e^{-\lambda(a^+)a}da \\
&= \frac{1}{(a^+)^2}\int_0^{a^+} e^{-aa^+}a(1+aa^+-(a^+)^2)e^{-\lambda(a^+)a}da \\
&\geq -\frac{1}{6}(a^+)^2+\frac{1}{2} > 0, \quad \text{for } a^+ < 1,
\end{aligned}$$

where similarly we used the fact that $\lambda(a^+)+a^+ < 0$ (otherwise $\int_0^{a^+} e^{-\lambda(a^+)a}$ $\pi(a,0,a^+)da \leq a^+/2 < 1$ for $a^+ < 1$). In summary, this example (3.3) shows that $a^+ \mapsto \lambda(a^+)$ is increasing first for $a^+ < 1$, and then decreasing when $a^+ \gg 1$, corresponding to the complicated non-monotone behavior of $a^+ \mapsto \lambda(a^+)$. Furthermore, for such non-monotone cases, it would be very interesting to investigate the optimal maximum age to allow the population attain its largest principal eigenvalue in realistic ecology, see (Kozłowski and Wiegert 1987) for more details.

Finally, we illustrate the behavior $a^+ \mapsto \lambda(a^+)$ by three figures, see Figure 2. Note that $\pi(a,0,a^+)$, as the survival rate of the species, is decreasing with respect to a satisfying $\pi(0,0,a^+) = 1$ and $\pi(a^+,0,a^+) = 0$. In Figure 2a, $\mu(a,a^+) = \frac{1}{a^+-a}$, and one can see that $\int_0^{a^+} \pi(a,0,a^+)da$ is increasing with respect to a^+, while in Figure 2c, $\int_0^{a^+} \pi(a,0,a^+)da$ is decreasing with respect to a^+. This shows that if $\beta(a,a^+) \equiv \beta(a)$, then $a^+ \mapsto \lambda(a^+)$ has two completely opposite monotone behaviors, which shows again the very complicated behavior of $a^+ \mapsto \lambda(a^+)$. Finally, Figure 2b is an example that $\int_0^{a^+} \beta(a,a^+)da$ is increasing with respect to a^+, which shows that $a^+ \mapsto \lambda(a^+)$ is increasing provided $\mu(a,a^+) \equiv \mu(a)$ independent on a^+. In summary, the sign of $\lambda'(a^+)$ is determined by the areas and thus the shapes of $\pi(a,0,a^+)$ and $\beta(a,a^+)$ in $[0,a^+)$, which can exhibit complicated behavior.

3.2 Effects of maturation time

In this subsection, we provide a second interesting example again to show the complicated behavior of the principal eigenvalue of problem (2.25) under different choices of $\mu(a,a^+)$ and $\beta(a,a^+)$. We assume $\mu(a,a^+) \equiv \mu(a)$ independent on a^+ and

$$\beta(a,a^+) = \begin{cases} \frac{C}{a^+-\tau}, & a \in [\tau, a^+), \\ 0, & a \in [0,\tau), \end{cases}$$

where $\tau \in (0,a^+)$ represents the maturation time and $C > 1$ is any constant.

With the above choices of μ and β, model (1.6) is corresponding to a two-stage model, including juveniles and adults, whose characteristic equation is given as follows

$$1 = \frac{C}{a^+-\tau} \int_\tau^{a^+} e^{-\lambda(\tau)a} e^{-\int_0^a \mu(s)ds} da. \tag{3.5}$$

The interested readers can refer to Fang et al. (2016) for more details on the derivation of the precise equations of a two-stage model. Here we are interested in the effects of maturation time τ on the principal eigenvalue $\lambda = \lambda(\tau)$. More precisely, we have the following result.

Corollary 3.1 *Let μ, β be defined above and $\lambda(\tau) \geq 0$ hold. Define $\phi : [0,a^+) \times [0,\infty) \mapsto [0,\infty)$ as*

$$\phi(\tau,\lambda) := \frac{C}{a^+-\tau} \int_\tau^{a^+} e^{-\lambda a} e^{-\int_0^a \mu(s)ds} da. \tag{3.6}$$

Then $\tau \mapsto \lambda(\tau)$ is strictly decreasing. Moreover, if $\phi(0,0) > 1$, then there exists a unique $\tau_0 \in (0,a^+)$ such that $\phi(\tau_0,\lambda(\tau_0)) = 1$ with $\lambda(\tau) > 0$ in $[0,\tau_0]$ and $\lambda(\tau) < 0$ in $[\tau_0,a^+]$.

Remark 3.2 The definition of β implies that the total birth rate along the life spans of the population is a constant larger than 1. Furthermore, $\lambda(\tau) \geq 0$ is required to ensure that the species persists, otherwise it will vanish. The conclusion of Corollary 3.1 states that as long as the species survives, the earlier the maturation, the larger the intrinsic growth rate.

Proof of Corollary 3.1 Observe from (3.6) that $\phi(\tau, \lambda) \to 0$ as $\lambda \to \infty$ and $\phi(\tau, \lambda) \to \infty$ as $\lambda \to -\infty$. Due to $\partial_\lambda \phi(\tau, \lambda) < 0$, the implicit function theorem applies to conclude that there exists a unique $\lambda(\tau) \in \mathbb{R}$ such that $\phi(\tau, \lambda(\tau)) = 1$ and $\lambda(\tau)$ has the same sign as $\phi(\tau, 0) - 1$.

On the other hand, the quotient rule yields

$$\partial_\tau \phi(\tau, \lambda) = \frac{C}{(a^+ - \tau)^2} \int_\tau^{a^+} e^{-\lambda a} e^{-\int_0^a \mu(s)ds} da - \frac{C}{a^+ - \tau} e^{-\lambda \tau} e^{-\int_0^\tau \mu(s)ds}.$$

Due to the fact that $\lambda \geq 0$ and $e^{-\lambda a} e^{-\int_0^a \mu(s)ds}$ is strictly decreasing and not constant in $a \in (\tau, a^+)$, we obtain $\partial_\tau \phi(\tau, \lambda) < 0$. Moreover, for any $\tau \in (0, a^+)$, there exists a neighborhood U of τ such that λ is continuously differentiable with respect to τ on U. By the chain rule, there holds

$$\lambda'(\tau) = -\frac{\partial_\tau \phi(\tau, \lambda(\tau))}{\partial_\lambda \phi(\tau, \lambda(\tau))}, \quad \tau \in U.$$

It follows that $\lambda'(\tau)$ has the same sign with $\partial_\tau \phi(\tau, \lambda(\tau))$. Thus $\tau \mapsto \lambda(\tau)$ is strictly decreasing in the region of $\lambda(\tau) \geq 0$. The remaining conclusions are obvious. This completes the proof. □

It makes sense biologically that the species will mature simultaneously after being born, and then will produce new species. In other words, the species with zero maturation period will have the maximal principal eigenvalue and thus the largest intrinsic growth rate.

Finally, we would like to mention that the model presented in this paper is a simplified formulation that only accounts for generic competition effects among species. Such assumptions may imply unrealistic persistence or vanishing of surviving traits under evolutionary forces, which is not observed in natural populations. In reality, several additional ecological features may shape species dynamics. For instance, the intensity of intraspecific competition often depends on external environmental conditions. A relevant example is provided by mosquito species that breed in aquatic habitats. Chemical cues in water bodies can act as selective forces: *Aedes aegypti* tends to oviposit in habitats with lower ammonia concentrations, whereas *Culex quinquefasciatus* is more tolerant of and even prefers higher ammonia levels. Because ammonia levels in natural water resources fluctuate seasonally with rainfall and organic decomposition, the suitability of breeding sites alternates across the year. As a result, different species may thrive during different seasons, leading to temporally varying competitive advantages that are not captured by the current model.

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Data Availability Data sharing is not applicable to this article as no datasets were generated or analyzed during the current study.

Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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