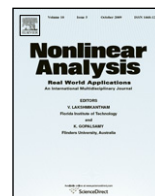




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Weak Allee effects and species coexistence

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ABSTRACT

In this article, we study the population dynamics of a two-species discrete-time competition model where each species suffers from either predator saturation induced Allee effects and/or mate limitation induced Allee effects. We focus on the following two possible outcomes of the competition: 1. one species goes to extinction; 2. the system is permanent. Our results indicate that, even if one species' intra-specific competition is less than its inter-specific competition, weak Allee effects induced by predation saturation can promote coexistence of the two competing species. This is supported by the outcome of two-species competition models without Allee effects. Also, we discuss our results and future work on multiple attractors in competition models with Allee effects.

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1. Introduction

The Allee effect and species competition are two basic ecological mechanisms that set lower and upper bounds on population density of species [1,2]. The Allee effect, defined as a reduced per-capita population growth rate at low densities, has important consequences for population dynamics and persistence. The effect can be caused by difficulties in finding a mate and predator avoidance or defense [3–6]. Competition for resources (e.g., food, space) may lead to lower population growth rate at high local population densities. Thus, small population density can be a result of competition among different species. Understanding the role of competition in populations subject to Allee effects can advance our understanding of extinction and establishment, with implications for conservation programs. However, the potential for synergism between the mechanisms generating the Allee effect and competition is not well understood and largely unconsidered [6,7].

In this article we investigate species extinction and permanence in discrete-time two-species competition models, where each species is subject to predator saturated and/or mate limitation induced Allee effects. One of our main findings is that predator saturated weak Allee effect can promote coexistence of two competing species; which is supported by two-species competition models without Allee effects. This result may have important implications for conservation programs, and can be considered as a complement to the current studies on population dynamics in the presence of Allee effects (e.g., [3,5,7–29]) as well as various models in patchy environment (e.g., [30–35]).

To study the extinction and permanence of discrete-time two-species competition models, we first start with a single-species discrete-time model that has a mechanism for generating Allee effects. There has been a great deal of literature on deriving population models with Allee effects (e.g., [36], [5, Chapter 7], [25,37]). Our two-species competition models are based on single-species population models that were introduced by Schreiber [5].

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Note: Model I has no non-symmetric interior equilibrium point if $r_i = r < m_i = m, a_i = a, b_i = b, i = 1, 2$ and $r < a$. If this is not true, then let $(x^*, y^*), x^* \neq y^*$ be the interior equilibrium of **Model I** which satisfies the following equations:

$$r(1 - x^*) - \frac{m}{1 + bx^*} = ay^* \quad \text{and} \quad r(1 - y^*) - \frac{m}{1 + by^*} = ax^*. \tag{6}$$

Define a map $H : \mathbb{R}_+ \rightarrow \mathbb{R}_+$, where $H(x) = \frac{r(1-x)}{a} - \frac{m}{a(1+bx)}$. Eqs. (6) hold only if there is some x in the interval of

$$\frac{r(b-1) - \sqrt{(br+r)^2 - 4bmr}}{2br} < x < \frac{r(b-1) + \sqrt{(br+r)^2 - 4bmr}}{2br}$$

such that $\frac{dH}{dx} \leq -1$. However,

$$\frac{dH}{dx} = -\frac{r}{a} + \frac{bm}{a(1+bx)^2} > -\frac{r}{a} > -1.$$

Thus, **Model I** has no non-symmetric interior equilibrium point if $r_i = r < m_i = m, a_i = a, b_i = b, i = 1, 2$ and $r < a$. In addition, **Proposition 2.1** suggests that two competing species subject to strong Allee effects need larger b in order to coexist since the sufficient condition for one-species model to have possible locally stable interior equilibrium point is (from **Lemma 1.1**)

$$r < m < \frac{r(b+1)^2}{4b} \quad \text{and} \quad b > 1.$$

2.2. Competition model with mating induced Allee effects

Model II: Competition between two species that both are subject to mate limitation can be modeled as

$$x_{t+1} = x_t e^{r_1(1-x_t)-a_1y_t} \frac{b_1x_t}{1 + b_1x_t} \tag{7}$$

$$y_{t+1} = y_t e^{r_2(1-y_t)-a_2x_t} \frac{b_2y_t}{1 + b_2y_t} \tag{8}$$

where $r_i, i = 1, 2$ represent the intrinsic growth rates as well as intra-specific competition coefficients and $b_i, i = 1, 2$ represent the product of an individual's searching efficiency and the carrying capacities.

The sufficient condition on the existence of interior equilibria of **Model II** when $r_i = r < m_i = m, a_i = a, b_i = b, i = 1, 2$ can be stated as follows:

Proposition 2.2 (Existence of Interior Equilibria). Assume that $r_i = r < m_i = m, a_i = a, b_i = b, i = 1, 2$. Then if $\frac{e^{r-1}}{r+a} > \frac{1}{r+a} + \frac{1}{b}$, then **Model II** has two symmetric interior equilibria (p^*, p^*) such that the following equation holds

$$p^* e^{r(1-p^*)-ap^*} = p^* + \frac{1}{b}.$$

Proof. Since $r_i = r < m_i = m, a_i = a, b_i = b, i = 1, 2$, then the interior equilibrium has the symmetric form (p^*, p^*) which satisfies the following equations:

$$p^* e^{r(1-p^*)-ap^*} = p^* + \frac{1}{b}.$$

Let p_c to be the critical point of $pe^{r(1-p)-ap}$, i.e. $p_c = \frac{1}{r+a}$. Then from **Fig. 1**, we can conclude that **Model II** has two interior equilibria if

$$p_c e^{r(1-p_c)-ap_c} = \frac{e^{r-1}}{r+a} > \frac{1}{r+a} + \frac{1}{b}.$$

Therefore, the statement regarding **Model II** holds. □

Note: Proposition 2.2 suggests that two competing species subject to strong Allee effects may also need larger b in order to coexist since the sufficient condition for one-species model to have possible locally stable interior equilibrium point is (from **Lemma 1.2**)

$$\frac{e^{r-1}}{r} > \frac{1}{r} + \frac{1}{b}.$$

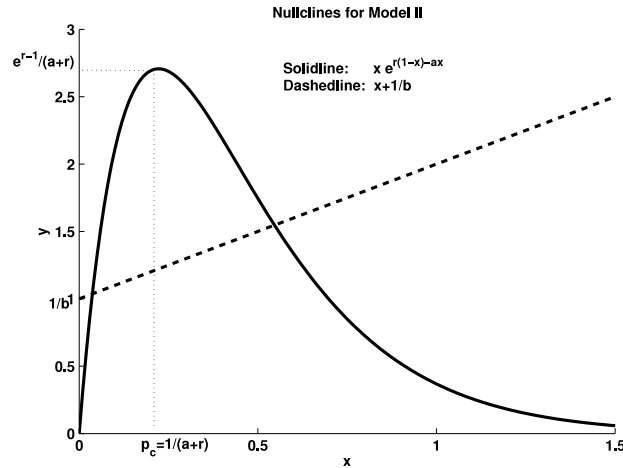
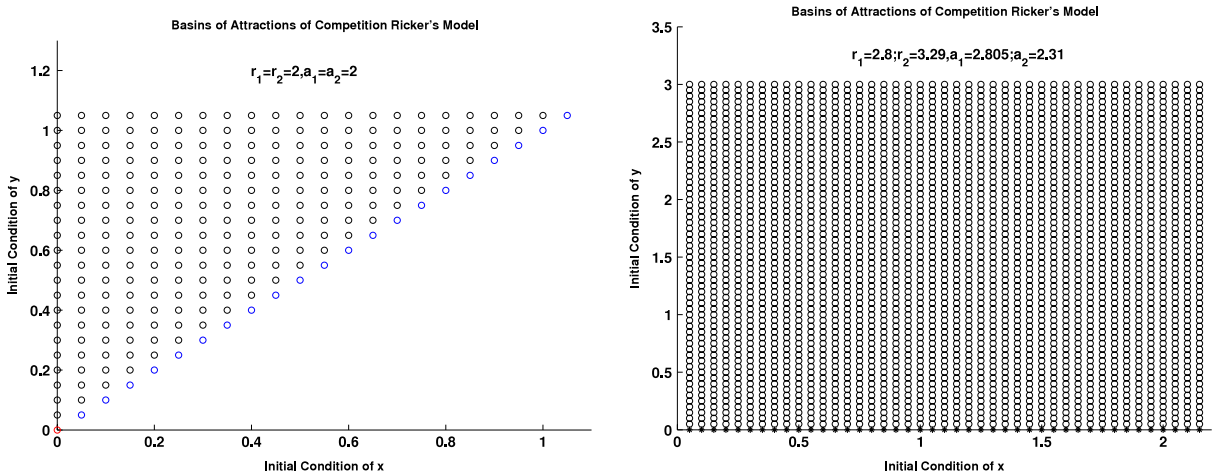


Fig. 1. Nullclines of Model II when $r_i = r < m_i = m, a_i = a, b_i = b, i = 1, 2$ and $\frac{e^{r-1}}{r+a} > \frac{1}{r+a} + \frac{1}{b}$.



(a) Basins of attraction of boundary attractors when $r_1 = r_2 = 1.5, a_1 = a_2 = 2$ for the system (17)–(18).

(b) Basins of attraction of boundary attractors when $r_1 = 2.8, r_2 = 3.29, a_1 = 2.805, a_2 = 2.31$ for the system (17)–(18).

Fig. 2. The basins of attraction of attractors on x -axis are the white region and the basins of attraction of attractors on y -axis are the region with black open circles. The coexistence region is the area with blue open circles. The extinction region is the area with red open circles. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.3. Competition model with mixed Allee effects

Model III: Competition between a species x subject to predation by a generalist predator with a saturating functional response and a species y subject to mate limitation can be modeled as:

$$x_{t+1} = x_t e^{r_1(1-x_t) - \frac{m}{1+b_1x_t} - a_1y_t} \tag{9}$$

$$y_{t+1} = y_t e^{r_2(1-y_t) - a_2x_t} \frac{b_2y_t}{1 + b_2y_t} \tag{10}$$

where $r_i, i = 1, 2$ represent the intrinsic growth rates as well as intra-specific competition coefficients; m represents predation intensity for species x ; b_1 represents the product of the proportional to the handling time and the carrying capacity of species x ; b_2 represents the product of an individual's (species y) searching efficiency and the carrying capacity of species y .

If (x^*, y^*) is an interior equilibrium of **Model III**, then it should satisfy the following equations:

$$e^{r_1(1-x^*) - \frac{m}{1+b_1x^*} - a_1y^*} = 1 \quad \text{and} \quad e^{r_2(1-y^*) - a_2x^*} \frac{b_2y^*}{1 + b_2y^*} = 1. \tag{11}$$

If b_2 is too small, e.g., $\frac{b_2 e^{r_2-1}}{r_2} < 1$, then **Model III** has no interior point since

$$y_{t+1} = y_t e^{r_2(1-y_t)-a_2 x_t} \frac{b_2 y_t}{1 + b_2 y_t} \leq y_t \max_{y>0} \{b_2 y e^{r_2(1-y)}\} \leq y_t \frac{b_2 e^{r_2-1}}{r_2} < y_t.$$

2.4. A general two-species competition model subject to Allee effects

Based on the derivations of two-species competition models with Allee effects induced by the different mechanisms in the previous subsections, we now derive a general two-species competition model with Allee effects.

Let x_t and y_t be the population density of two competing in season t , then their population dynamics without Allee effects can be described by

$$x_{t+1} = x_t f(x_t, y_t) \tag{12}$$

$$y_{t+1} = y_t g(x_t, y_t) \tag{13}$$

where f and g are per-capita growth rates of species x, y respectively that satisfy the following two conditions:

Condition H1: Both $f(x, y)$ and $g(x, y)$ are strictly positive and twice differentiable in \mathbb{R}_+^2 with

$$f(0, 0) > 1 \quad \text{and} \quad g(0, 0) > 1.$$

Condition H2:

$$\lim_{x \rightarrow \infty} f(x, 0) = a_1 < 1, \quad \frac{\partial f(x, y)}{\partial x} < 0, \quad \frac{\partial f(x, y)}{\partial y} < 0$$

$$\lim_{x \rightarrow \infty} g(0, y) = a_1 < 1, \quad \frac{\partial g(x, y)}{\partial x} < 0, \quad \frac{\partial g(x, y)}{\partial y} < 0.$$

Then according to Lemmas 3.1 and 3.2 [39], we have the following properties of the competition model (12)–(13):

1. System (12)–(13) is dissipative, i.e., (12)–(13) has a compact attractor in \mathbb{R}_+^2 that attracts all points in \mathbb{R}_+^2 :

$$\limsup_{t \rightarrow \infty} \max\{x_t, y_t\} < B$$

for any initial condition $(x_0, y_0) \in \mathbb{R}_+^2$ and B is some positive number.

2. Both species x and y are persistent and have only one nontrivial equilibrium point $(x^*, 0), (0, y^*)$ in their single-species state (i.e., other species is absent), i.e., for any initial condition $(x_0, 0)$ and $(0, y_0)$ with $x_0 > 0, y_0 > 0$, there exists positive numbers $0 < b < B$ such that

$$b \leq \liminf_{t \rightarrow \infty} \min\{x_t, y_t\} \leq \limsup_{t \rightarrow \infty} \max\{x_t, y_t\} \leq B.$$

If both species x and y suffer from Allee effects, then their population dynamics can be represented by

$$x_{t+1} = x_t f(x_t, y_t) I^x(x_t) \tag{14}$$

$$y_{t+1} = y_t g(x_t, y_t) I^y(y_t) \tag{15}$$

where $I^i, i = x, y$ represents a positive density-dependent factor of species i which satisfies **Condition H3**:

Condition H3: $I^i, i = x, y$ is differentiable in \mathbb{R}_+ and

$$0 \leq I^i(0) \leq 1 \quad \text{with} \quad \frac{dI^i(u)}{du} > 0, \quad u \in \mathbb{R}_+, \quad i = x, y.$$

For convenience, we define

$$X = \{(x, y) : x \geq 0, y \geq 0\}, \quad S_x = \{(x, 0) : x \geq 0\}, \quad S_y = \{(0, y) : y \geq 0\}$$

and

$$S = S_x \cup S_y, \quad M = X \setminus S = \{(x, y) : x > 0, y > 0\}.$$

One of our main goals of this subsection is to derive a sufficient criterion that can lead to the permanence of (14)–(15) in X , i.e., (14)–(15) has a compact attractor in M that attracts all points in M :

$$b \leq \liminf_{n \rightarrow \infty} \min\{x_n, y_n\} \leq \limsup_{n \rightarrow \infty} \max\{x_n, y_n\} \leq B$$

for any initial condition $(x_0, y_0) \in M$ and b, B are some positive numbers. First, we have the following dissipative results on (14)–(15):

Lemma 2.1 (Dissipative). *If the system (14)–(15) satisfies Condition H1, H2, H3, then it is positively invariant and dissipative in X.*

Proof. The positively invariant property of (14)–(15) is straight forward from the non-negativity and continuity properties of f, g, I^x, I^y . Since the system (14)–(15) satisfies Condition H1–H2, then according to Lemmas 3.1 and 3.2 [39], we have the system (12)–(13) is dissipative in X. Since the system (14)–(15) also satisfies Condition H3, then

$$\begin{aligned} x_{t+1} &= x_t f(x_t, y_t) I^x(x_t) \leq x_t f(x_t, y_t) \\ y_{t+1} &= y_t g(x_t, y_t) I^y(y_t) \leq y_t g(x_t, y_t). \end{aligned} \tag{16}$$

Therefore, the competitive system with Allee effects (14)–(15) is also dissipative in X according to (16). □

Theorem 2.1 (Persistence and Extinction of Species in (14)–(15)). *Assume that the system (14)–(15) satisfies Condition H1–H3. Then we have the following two cases:*

1. *If $f(0, 0) \limsup_{x \rightarrow \infty} I^x(x) < 1$ and $g(0, 0) \limsup_{y \rightarrow \infty} I^y(y) < 1$, then both species of (14)–(15) go to extinct, i.e., for any initial condition $(x_0, y_0) \in X$, we have*

$$\limsup_{t \rightarrow \infty} \max\{x_t, y_t\} = 0.$$

2. *If $f(0, 0) I^x(0) > 1$ and $g(0, 0) I^y(0) > 1$, then both species have nontrivial boundary equilibria, i.e., there exists $x^* > 0$ and $y^* > 0$ such that*

$$f(x^*, 0) I^x(x^*) = 1 \quad \text{and} \quad g(0, y^*) I^y(y^*) = 1$$

and the total population of two species is persistent in X, i.e., there exists some positive number ϵ such that for any initial condition $(x_0, y_0) \in X \setminus \{(0, 0)\}$, we have

$$\liminf_{t \rightarrow \infty} x_t + y_t \geq \epsilon.$$

Proof. Let $I^x = \limsup_{x \rightarrow \infty} I^x(x)$. Since the system (14)–(15) satisfies Condition H1–H3, thus we have

$$x_{t+1} = x_t f(x_t, y_t) I^x(x_t) \leq x_t f(0, 0) \limsup_{x \rightarrow \infty} I^x(x) = f(0, 0) I^x x_t \leq [f(0, 0) I^x]^t x_0.$$

If $f(0, 0) I^x < 1$, then

$$x_{t+1} \leq [f(0, 0) I^x]^t x_0 \Rightarrow 0 \quad \text{as } t \rightarrow \infty.$$

Thus, $\limsup_{t \rightarrow \infty} x_t = 0$. Similarly, we can show that if

$$g(0, 0) \limsup_{y \rightarrow \infty} I^y(y) < 1, \quad \text{then } \limsup_{t \rightarrow \infty} y_t = 0.$$

Therefore, the first part of Theorem 2.1 holds.

Now assume that $f(0, 0) I^x(0) > 1$ and $g(0, 0) I^y(0) > 1$, then we can conclude that $(0, 0)$ is a source. Let $K^\epsilon(0, 0) = \{(x, y) \in X : x + y \leq \epsilon\}$. If $\epsilon > 0$ is small enough, then any point in $K^\epsilon(0, 0)$ will emit from $K^\epsilon(0, 0)$ in some future time. According to Lemma 2.1, the system (14)–(15) is dissipative in X, thus any initial point $(x_0, y_0) \in X \setminus \{(0, 0)\}$ will enter the compact set $A^\epsilon = \{(x, y) \in X : \epsilon \leq x + y \leq B\}$ in some future time.

Now define $C^\epsilon = \{(x, y) \in X : b^\epsilon \leq x + y \leq B\}$ where $b^\epsilon = \epsilon \min\{f(B, B) I^x(0), g(B, B) I^y(0)\}$. Let (x_t, y_t) be a point in C^ϵ , then we have $x_t + y_t \geq \epsilon$ and

$$\begin{aligned} x_{t+1} + y_{t+1} &= x_t f(x_t, y_t) I^x(x_t) + y_t g(x_t, y_t) I^y(y_t) \geq x_t f(B, B) I^x(0) + (\epsilon - x_t) g(B, B) I^y(0) \\ &\geq \epsilon \min\{f(B, B) I^x(0), g(B, B) I^y(0)\} = b^\epsilon. \end{aligned}$$

This indicates that any point in $X \setminus \{(0, 0)\}$ will enter A^ϵ in some future time and then will be trapped in C^ϵ for all future time. Therefore, given some ϵ small enough, then for any initial condition $(x_0, y_0) \in X \setminus \{(0, 0)\}$ we have

$$\liminf_{t \rightarrow \infty} x_t + y_t \geq \epsilon.$$

In addition, Condition H2 implies that there exist some positive number L such that

$$f(L, 0) I^x(L) < 1 \quad \text{and} \quad g(0, L) I^y(L) < 1.$$

Then according to the continuity of (14)–(15), we can conclude that the condition $f(0, 0) I^x(0) > 1$ and $g(0, 0) I^y(0) > 1$ indicates that there exists $x^* > 0$ and $y^* > 0$ such that

$$f(x^*, 0) I^x(x^*) = 1 \quad \text{and} \quad g(0, y^*) I^y(y^*) = 1.$$

Therefore, Theorem 2.1 holds. □

Note: The first part of **Theorem 2.1** indicates that both species go to *extinction* when the max per-capita growth rates (i.e., $f(0, 0) \limsup_{x \rightarrow \infty} I^x(x)$ and $g(0, 0) \limsup_{y \rightarrow \infty} I^y(y)$) are less than one. We want to point out that if a species goes to *essential extinction* without other species presence, then this species may or may not go to *essential extinction* in the competition system (14)–(15). A direct corollary from **Theorem 2.1** can be stated as follows:

Corollary 2.1 (*Persistence of (12)–(13)*). Assume that the system (12)–(13) satisfies Condition **H1–H2**. Then the total population of two species is persistent in X , i.e., there exists a positive number ϵ such that for any initial condition $(x_0, y_0) \in X \setminus \{(0, 0)\}$, we have

$$\liminf_{t \rightarrow \infty} x_t + y_t \geq \epsilon.$$

Proof. This is straightforward from **Theorem 2.2**, thus we omit it. \square

Theorem 2.2 (*Permanence of Two Species in (14)–(15)*). Assume that the system (14)–(15) satisfies Condition **H1–H3**. Then the system (14)–(15) is permanent in M if the following conditions hold

C1: $f(0, 0)I^x(0) > 1$ and $g(0, 0)I^y(0) > 1$;

C2: Let $(x^*, 0)$ and $(0, y^*)$ be any nontrivial boundary equilibria of (14)–(15), then $f(0, y^*)I^x(y^*) > 1$ and $g(x^*, 0)I^y(x^*) > 1$;

C3: Let $F(x, y) = \ln f(x, y) + \ln I^x(x)$ and $G(x, y) = \ln g(x, y) + \ln I^y(y)$ and $(x^*, 0), (0, y^*)$ be some nontrivial boundary equilibria, then

$$G_{xx}(x, 0) - \frac{G_x(x^*, 0)F_{xx}(x, 0)}{F_x(x^*, 0)} \geq 0, \quad \text{for all } x > 0$$

and

$$F_{yy}(0, y) - \frac{F_y(0, y^*)G_{yy}(0, y)}{G_y(0, y^*)} \geq 0, \quad \text{for all } y > 0.$$

Note: **Theorem 2.2** answers the first question listed in the introduction, which is a special case of **Theorem 3.1** of Kang [40]. Condition **H1, H2, H3, C1** in **Theorem 2.2** covers Condition **H, G1** in **Theorem 3.1** of Kang [40]. Condition **C2** covers Condition **G2**; Condition **C3** covers Condition **G3, G4**. We apply **Theorem 2.2** to specific models in Section 6.

3. Two-species competition models without Allee effects

A two-species competition model with Ricker’s recruitments can be modeled by the following equations:

$$x_{t+1} = x_t e^{r_1(1-x_t) - a_1 y_t} \tag{17}$$

$$y_{t+1} = y_t e^{r_2(1-y_t) - a_2 x_t} \tag{18}$$

where $r_i, i = 1, 2$ and $a_i, i = 1, 2$ represent the intrinsic growth rates (also intra-specific competition coefficients) and the inter-specific competition coefficients for each species. The dynamics of the similar competition models as (17)–(18) have been studied by many researchers, e.g., [41–44]. In this section, we will only focus on the dynamics of (17)–(18) where at least one species goes to extinction. First, we have the following results regarding the existence of the interior point of (17)–(18).

Proposition 3.1 (*Local Stability of Interior Point of (17)–(18)*). If $r_i > a_i, i = 1, 2$ or $r_i < a_i, i = 1, 2$, then the system (17)–(18) has a unique interior equilibrium point $(x^*, y^*) = \left(\frac{r_2(r_1 - a_1)}{r_1 r_2 - a_1 a_2}, \frac{r_1(r_2 - a_2)}{r_1 r_2 - a_1 a_2} \right)$ where (x^*, y^*) is locally unstable if $r_i < a_i, i = 1, 2$ and is locally stable if

$$r_i > a_i, i = 1, 2, \quad \text{and} \quad 2 > 2 + \frac{r_1 r_2 (r_1 - a_1)(r_2 - a_2)}{r_1 r_2 - a_1 a_2} - \frac{r_1 r_2 (r_1 + r_2 - a_1 - a_2)}{r_1 r_2 - a_1 a_2} > \left| 2 - \frac{r_1 r_2 (r_1 + r_2 - a_1 - a_2)}{r_1 r_2 - a_1 a_2} \right|.$$

Proof. From the expression of the system (17)–(18), we know that the interior equilibrium (x^*, y^*) should satisfy the following equations:

$$r_1(1 - x^*) - a_1 y^* = 0 \quad \text{and} \quad r_2(1 - y^*) - a_2 x^* = 0.$$

We can solve the equations above to get $(x^*, y^*) = \left(\frac{r_2(r_1 - a_1)}{r_1 r_2 - a_1 a_2}, \frac{r_1(r_2 - a_2)}{r_1 r_2 - a_1 a_2} \right)$. This indicates that (17)–(18) has a unique interior equilibrium (x^*, y^*) if

$$r_i > a_i \quad \text{or} \quad r_i < a_i, i = 1, 2.$$

Local extinction: If $r_1 < a_1$ and $r_2 > a_2$, then there exists some $\epsilon > 0$, for any initial condition such that $\frac{x_0^{1/r_1}}{y_0^{1/r_2}} < 1$, the following holds

$$\limsup_{t \rightarrow \infty} x_t = 0 \quad \text{and} \quad \liminf_{t \rightarrow \infty} y_t \geq \epsilon.$$

Similarly, if $r_1 > a_1$ and $r_2 < a_2$, then for any initial condition $\frac{y_0^{1/r_2}}{x_0^{1/r_1}} < 1$, the following holds

$$\limsup_{t \rightarrow \infty} y_t = 0 \quad \text{and} \quad \liminf_{t \rightarrow \infty} x_t \geq \epsilon.$$

Proof. First notice that the system (17)–(18) is positively invariant and dissipative in X , i.e.,

$$\limsup_{t \rightarrow \infty} \max\{x_t, y_t\} \leq \max\left\{\frac{e^{r_1-1}}{r_1}, \frac{e^{r_2-1}}{r_2}\right\} = B.$$

If $r_i < a_i$, $i = 1, 2$, then apply the relative nonlinearity concept in the paper by Kang and Chesson [39] to obtain that the external Lyapunov exponent of y -axis is $r_1 - a_1 y|_{y=1} = r_1 - a_1 < 0$ and the external Lyapunov exponent of x -axis is $r_2 - a_2 x|_{x=1} = r_2 - a_2 < 0$. We can apply Theorem 2.18 in the paper by Hutson and Schmitt [46] to conclude that both x -axis and y -axis are attractors in the sense that the stable manifold of x and y -axis are neighborhood of both axes in X .

Now if $r_1 = r_2 = r < a_1 = a_2 = a$ and $x_0 < y_0$, then

$$\frac{x_1}{y_1} = \frac{x_0 e^{r(1-x_0)-ay_0}}{y_0 e^{r(1-y_0)-ax_0}} = \frac{x_0}{y_0} e^{(a-r)(x_0-y_0)} < \frac{x_0}{y_0} < 1.$$

By induction, we have

$$\frac{x_t}{y_t} < \frac{x_{t-1}}{y_{t-1}} < \dots < \frac{x_0}{y_0}.$$

Thus, $\{\frac{x_t}{y_t}\}_{t=0}^\infty$ is a strictly decreasing sequence that converges to some point $\alpha \in \mathbb{R}_+$, i.e.,

$$\lim_{t \rightarrow \infty} \frac{x_t}{y_t} = \alpha.$$

We claim that $\alpha = 0$. Suppose that $\alpha > 0$, then

$$\frac{1}{1/\alpha + 1} = \lim_{t \rightarrow \infty} \frac{1}{\frac{y_t}{x_t} + 1} = \lim_{t \rightarrow \infty} \frac{x_t}{y_t + x_t} \leq \lim_{t \rightarrow \infty} \frac{x_t}{y_t} = \alpha.$$

From the dissipativeness of (17)–(18) and Corollary 2.1, we have

$$\liminf_{t \rightarrow \infty} \frac{x_t}{2B} \leq \lim_{t \rightarrow \infty} \frac{x_t}{y_t + x_t} = \frac{\alpha}{1 + \alpha} \leq \limsup_{t \rightarrow \infty} \frac{x_t}{\epsilon}.$$

This implies that species x is weakly persistent in X , i.e.,

$$\limsup_{t \rightarrow \infty} x_t \geq \frac{\alpha \epsilon}{1 + \alpha} > 0.$$

However, this contradicts to the fact that $(0, 1)$ has a stable manifold in M since $r < a$. Therefore $\alpha = 0$. This indicates that

$$\lim_{t \rightarrow \infty} \frac{x_t}{x_t + y_t} = 0.$$

According to Corollary 2.1, we have $\liminf_{t \rightarrow \infty} x_t + y_t \geq \epsilon$, thus,

$$\limsup_{t \rightarrow \infty} x_t = 0 \quad \text{and} \quad \liminf_{t \rightarrow \infty} y_t \geq \epsilon.$$

Apply the above argument to the case when $r_1 = r_2 = r < a_1 = a_2 = a$ and $x_0 > y_0$, then we can also show that

$$\limsup_{t \rightarrow \infty} y_t = 0 \quad \text{and} \quad \liminf_{t \rightarrow \infty} x_t \geq \epsilon.$$

Therefore, the first part of Theorem 3.1 holds.

Now assume that $a_2 \leq r_1 < r_2 \leq a_1$, then for any $(x_0, y_0) \in M$, we have

$$\frac{x_t}{y_t} = \frac{x_{t-1} e^{r_1(1-x_{t-1})-a_1 y_{t-1}}}{y_{t-1} e^{r_2(1-y_{t-1})-a_2 x_{t-1}}} = \frac{x_{t-1}}{y_{t-1}} e^{r_1-r_2+(r_2-a_1)y_{t-1}+(a_2-r_1)x_{t-1}} < \frac{x_{t-1}}{y_{t-1}} e^{r_1-r_2} < \frac{x_0}{y_0} e^{t(r_1-r_2)}.$$

Extinction: If $a_2 \leq r_1 < r_2 \leq a_1$, $m_2 \leq m_1$ and $b_1 m_2 \leq b_2 m_1$, then we have

$$\limsup_{t \rightarrow \infty} x_t = 0 \quad \text{if } x_0 < y_0.$$

If $a_1 \leq r_2 < r_1 \leq a_2$, $m_1 \leq m_2$ and $b_2 m_1 \leq b_1 m_2$, then we have

$$\limsup_{t \rightarrow \infty} y_t = 0 \quad \text{if } y_0 < x_0.$$

For **Model II**,

Bistability: Assume that $r_i = r$, $a_i = a$, $b_i = b$, $i = 1, 2$ and $r < a$, then

$$\limsup_{t \rightarrow \infty} x_t = 0 \quad \text{if } x_0 < y_0; \quad \text{and} \quad \limsup_{t \rightarrow \infty} y_t = 0 \quad \text{if } x_0 > y_0.$$

Extinction: If $a_2 \leq r_1 < r_2 \leq a_1$ and $b_1 \leq b_2$, then we have

$$\limsup_{t \rightarrow \infty} x_t = 0 \quad \text{if } x_0 < y_0.$$

If $a_1 \leq r_2 < r_1 \leq a_2$ and $b_2 \leq b_1$, then we have

$$\limsup_{t \rightarrow \infty} y_t = 0 \quad \text{if } y_0 < x_0.$$

For **Model III**, if $a_1 \leq r_2 < r_1 \leq a_2$ and $r_2 + m \leq r_1$, then for any initial condition $(x_0, y_0) \in M$, we have

$$\limsup_{t \rightarrow \infty} y_t = 0.$$

Proof. For **Model I**, if $r_i = r$, $a_i = a$, $b_i = b$, $m_i = m$, $i = 1, 2$ and $x_0 < y_0$, then

$$\frac{x_1}{y_1} = \frac{x_0}{y_0} e^{(r-a)(y_0-x_0) + \frac{m}{1+by_0} - \frac{m}{1+bx_0}} = \frac{x_0}{y_0} e^{\left(r-a - \frac{bm}{(1+bx_0)(1+by_0)}\right)(y_0-x_0)} < \frac{x_0}{y_0} < 1.$$

By induction, we have

$$\frac{x_t}{y_t} < \frac{x_{t-1}}{y_{t-1}} < \dots < \frac{x_0}{y_0}.$$

Thus, $\{\frac{x_t}{y_t}\}_{t=0}^\infty$ is a strictly decreasing sequence that converges to some point $\alpha \in \mathbb{R}_+$, i.e.,

$$\lim_{t \rightarrow \infty} \frac{x_t}{y_t} = \alpha < 1.$$

This indicates that if $\alpha > 0$, then

$$\left(r - a - \frac{bm}{(1+bx_t)(1+by_t)}\right) (y_t - x_t) = y_t \left(r - a - \frac{bm}{(1+bx_t)(1+by_t)}\right) \left(1 - \frac{x_t}{y_t}\right) \rightarrow 0 \quad \text{as } t \rightarrow \infty.$$

Therefore,

$$\lim_{t \rightarrow \infty} y_t = 0 \quad \text{and} \quad \lim_{t \rightarrow \infty} x_t = 0.$$

If $\alpha = 0$, then for any positive integer N , there exist some $T_N > 0$ such that

$$\frac{x_t}{y_t} < \frac{1}{N} \quad \text{for all } t > T_N.$$

Assume that $\lim_{t \rightarrow \infty} x_t$ is not true, then there exists some $\delta > 0$ and a sequence $\{x_{t_i}\}_{i=1}^\infty$ such that

$$x_{t_i} > \delta \quad \text{and} \quad t_i \rightarrow \infty \quad \text{as } i \rightarrow \infty.$$

Thus, if $t_i > T_N$, we have

$$\frac{\delta}{y_{t_i}} < \frac{x_{t_i}}{y_{t_i}} < \frac{1}{N} \Rightarrow y_{t_i} > N\delta.$$

This indicates that $\limsup_{t \rightarrow \infty} y_t = \infty$ which is a contradiction to the fact that **Model I** is dissipative in X according to **Lemma 2.1**. Thus, $\lim_{t \rightarrow \infty} x_t = 0$. Similarly, we can show that $\lim_{t \rightarrow \infty} y_t = 0$ if

$$r_i = r, \quad a_i = a, \quad b_i = b, \quad m_i = m, \quad i = 1, 2, \quad r < a \quad \text{and} \quad y_0 < x_0.$$

Note: **Theorem 4.1** answers the second question listed in the introduction for certain competition models with Allee effects. In general, if both species' intra-specific competition coefficients are less than the inter-specific competition coefficients, then the extinction of one species is more likely to happen. For **Model II** and **Model III**, if $\frac{b_1 e^{r_1-1}}{r_1} < 1$, then species x goes to extinction. Similarly, for **Model II**, if $\frac{b_2 e^{r_2-1}}{r_2} < 1$, then species y goes to extinction. In addition, **Theorem 4.1** indicates that: 1. For symmetric cases, both **Model I** and **Model II** have neither coexistence of two species nor the locally stable interior equilibrium if the intra-specific competition coefficients are less than the inter-specific competition coefficients, i.e. $r < a$; 2. For asymmetric cases, the sufficient conditions of no coexistence of two species for all models need additional conditions as well as the intra-specific competition coefficients are less than the inter-specific competition coefficients, i.e. $r_i < a_i, i = 1, 2$. The additional conditions suggestion that it may be possible that **Model I**, **Model II** and **Model III** can have coexistence of two species even if $r_i < a_i, i = 1, 2$.

5. Weak Allee effects and permanence of Model I

The first part of **Theorem 3.1** gives sufficient conditions when species x and y cannot coexist in the symmetric form of (17)–(18). In this section, we explore the possibility of the permanence of (4)–(5) when the competition model without Allee effects (17)–(18) does not have coexistence. A direct application of **Theorem 2.2** to the system (4)–(5) can be summarized as the following corollary which is also a Corollary 5.2 in [40]:

Corollary 5.1. *System (4)–(5) is permanent if the following conditions hold*

- Condition 1: $r_i > m_i, i = 1, 2$.
- Condition 2: $f(0, y^*)I^x(y^*) > 1$ and $g(x^*, 0)I^y(x^*) > 1$.
- Condition 3: $r_2 > \frac{b_2 m_2}{(1+b_2 y^*)^2}$ and $r_1 > \frac{b_1 m_1}{(1+b_1 x^*)^2}$

where $x^* = \frac{r_1(b_1-1)+\sqrt{r_1^2(1+b_1)^2-4m_1b_1r_1}}{2r_1b_1}$ and $y^* = \frac{r_2(b_2-1)+\sqrt{r_2^2(1+b_2)^2-4m_2b_2r_2}}{2r_2b_2}$.

Corollary 5.1 suggests that the competition without Allee effects (17)–(18) excludes coexistence but two competing species with weak Allee effects (4)–(5) may coexist. To illustrate this result, let us take a concrete example when $r_1 = 2.8, r_2 = 3.29, a_1 = 2.805, a_2 = 2.31, b_1 = 1.55, b_2 = 1.06, m_1 = 0.4, m_2 = 0.95$.

First notice that the system (4)–(5) satisfies Condition **H1, H2, H3**. If $r_i > m_i, i = 1, 2$, then the boundary fixed points are

$(0, 0), (x^*, 0)$ and $(0, y^*)$

where $x^* = \frac{r_1(b_1-1)+\sqrt{r_1^2(1+b_1)^2-4m_1b_1r_1}}{2r_1b_1} = 0.942$ and $y^* = \frac{r_2(b_2-1)+\sqrt{r_2^2(1+b_2)^2-4m_2b_2r_2}}{2r_2b_2} = 0.848$ when $r_1 = 2.8, r_2 = 3.29, a_1 = 2.805, a_2 = 2.31, b_1 = 1.55, b_2 = 1.06, m_1 = 0.4, m_2 = 0.95$.

Now define $F(x, y)$ and $G(x, y)$ as follows:

$$F(x, y) = r_1(1 - x) - \frac{m_1}{1 + b_1x} - a_1y \quad \text{and} \quad G(x, y) = r_2(1 - y) - \frac{m_2}{1 + b_2y} - a_2x.$$

Then $F(0, 0) = r_1 - m_1 = 2.4 > 0$ and $G(0, 0) = r_2 - m_2 = 2.34 > 0$, thus the system (4)–(5) satisfies Condition **C1**. In addition, we have the following:

$$F_x(x, 0) = -r_1 + \frac{b_1 m_1}{(1 + b_1x)^2}, \quad F_{xx}(x, 0) = -\frac{2b_1^2 m_1}{(1 + b_1x)^3}, \quad F_y(0, y) = -a_1, \quad F_{yy}(0, y) = 0$$

$$G_x(x, 0) = -a_2, \quad G_{xx}(x, 0) = 0, \quad G_y(0, y) = -r_2 + \frac{b_2 m_2}{(1 + b_2y)^2}, \quad G_{yy}(0, y) = -\frac{2b_2^2 m_2}{(1 + b_2y)^3}.$$

Notice that

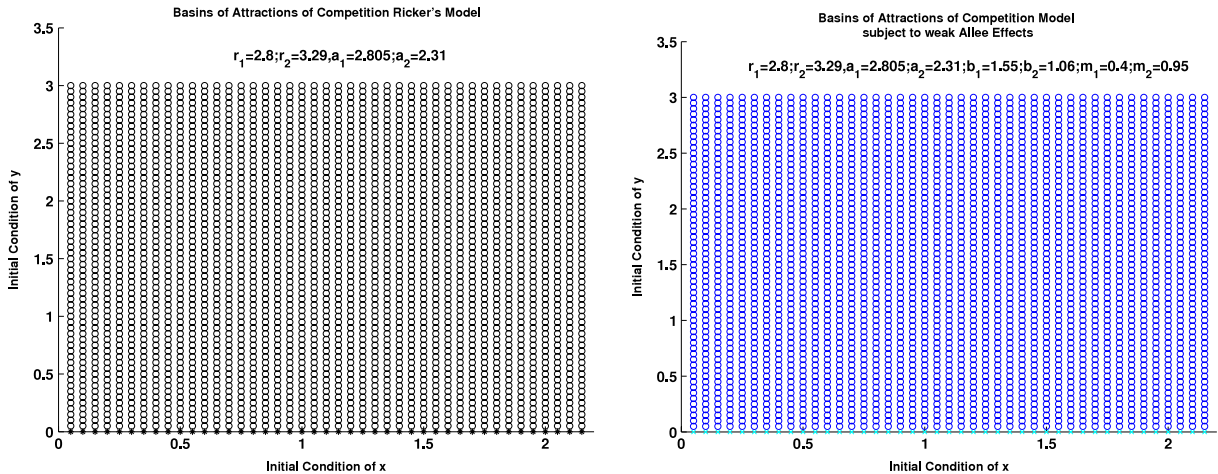
$$F_{yy}(0, y) - \frac{F_y(0, y^*)G_{yy}(0, y)}{G_y(0, y^*)} = \frac{2a_1 b_2^2 m_2}{(r_2 - \frac{b_2 m_2}{(1+b_2 y^*)^2})(1 + b_2 y)^3}$$

and

$$G_{xx}(x, 0) - \frac{G_x(x^*, 0)F_{xx}(x, 0)}{F_x(x^*, 0)} = \frac{2a_2 b_1^2 m_1}{(r_1 - \frac{b_1 m_1}{(1+b_1 x^*)^2})(1 + b_1 x)^3},$$

thus, the signs of the above two equations are determined by the signs of $r_2 - \frac{b_2 m_2}{(1+b_2 y^*)^2}$ and $r_1 - \frac{b_1 m_1}{(1+b_1 x^*)^2}$. When $r_1 = 2.8, r_2 = 3.29, a_1 = 2.805, a_2 = 2.31, b_1 = 1.55, b_2 = 1.06, m_1 = 0.4, m_2 = 0.95$, we have

$$r_2 - \frac{b_2 m_2}{(1 + b_2 y^*)^2} = 3.011 > 0 \quad \text{and} \quad r_1 - \frac{b_1 m_1}{(1 + b_1 x^*)^2} = 2.698 > 0.$$



(a) Basins of attraction of boundary attractors when $r_1 = 2.8, r_2 = 3.29, a_1 = 2.805, a_2 = 2.31$ for the system (17)–(18). (b) Basins of attraction of boundary attractors when $r_1 = 2.8, r_2 = 3.29, a_1 = 2.805, a_2 = 2.31, b_1 = 1.55, b_2 = 1.06, m_1 = 0.4, m_2 = 0.95$ for the system (4)–(5).

Fig. 3. The basins of attraction of attractors on y-axis are the region with black open circles. The coexistence region is the area with blue open circles. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

In addition, we have

$$F(0, y^*) = 0.164 > 0 \quad \text{and} \quad G(x^*, 0) = 0.022 > 0.$$

Therefore, the system (4)–(5) satisfies Condition **C2, C3**. Thus, according to **Theorem 2.2**, we can conclude that the system (4)–(5) is permanent in M in the case that $r_1 = 2.8, r_2 = 3.29, a_1 = 2.805, a_2 = 2.31, b_1 = 1.55, b_2 = 1.06, m_1 = 0.4, m_2 = 0.95$. Numerical simulation **Fig. 3(b)** supports our conclusion. However, according to the third part of **Theorem 3.1** indicates that the competition without Allee effects (17)–(18) cannot coexist when the density of species x is low since $r_1 = 2.8 < a_1 = 2.805$ and its numerical simulation **Fig. 3(a)** suggests that species x goes to extinction for all initial conditions taken in M . Thus, we are able to conclude that weak Allee effects induced by predator saturation can promote the coexistence of two species, which answers the third question listed in the introduction.

The ecological implication of **Corollary 5.1** and the concrete example above is that weak Allee effects decrease the fitness of species x (or species y) such that the other species y (or species x) is able to invade at the low density of species y (or species x).

In addition, we conclude that competition models with Allee effects induced by mate limitations cannot be permanent (e.g., **Model II** and **Model III**). This is due to the fact that the per capita growth rate of species that suffers from Allee effects induced by mate limitation is less than 1 at low densities, e.g.,

$$e^{r_2(1-y_t)-a_2x_t} \frac{b_2y_t}{1+b_2y_t} < b_2y_t e^{r_2-a_2x_t} \rightarrow 0 \quad \text{as } y_t \rightarrow 0.$$

6. Discussion

In this paper, we study the extinction of one species and the permanence of two-species competition models that have Allee effects induced by predator saturation and/or mate limitations. Our analytical results indicate that a species tends to go extinct if its intra-specific competition is less than its inter-specific competition for both competition models with or without Allee effects. We are able to show competition exclusion for Ricker's competition model without Allee effects: species y out compete species x when species y 's intra-specific competition coefficient r_2 is greater than species x 's inter-specific competition coefficient a_2 but less than species x 's intra-specific competition r_1 and its own inter-specific competition coefficient a_1 , i.e., $a_1 \leq r_2 < r_1 \leq a_2$. Moreover, our results show that if the intra-specific competition coefficient of one species is less than its inter-specific competition coefficient, e.g., $a_2 < r_1 < a_1 < r_2$, then a two-species competition model with weak Allee effects induced by predator saturation can still be permanent while its corresponding two-species competition model without Allee effects is not permanent according to **Theorem 4.1** and even does not have coexistence (see **Fig. 3(a)**). This result implies that weak Allee effects can promote coexistence of two competing species. The biological explanation for this phenomenon is that weak Allee effects decrease the fitness of species x (or species y) such that the other species y (or species x) is able to invade at low densities of species y (or species x).

We summarize our findings as follows: In **Theorem 2.2**, we obtain sufficient conditions that guarantee coexistence of the two competing species each of which is subject to an Allee effect. In **Theorems 2.1** and **4.1**, we obtain sufficient conditions

that lead to the extinction of at least one species when the Allee effect occurs in each competitor. In Section 5, we provide a concrete example based on 5.1 to illustrate the occurrence of the Allee effect can promote coexistence where there is extinction of a species in the absence of Allee effects.

The full dynamics of all three models introduced in this article (i.e., **Model I**, **Model II** and **Model III**) can be very complicated due to two factors; model structure and Allee effects. It is well known that population models with Allee effects can have multiple attractors for both continuous and discrete-time cases (e.g., [18,25,30–32,34,35,47–49]). It will be interesting to explore how different Allee effects combined with inter-specific competition affect the number of attractors and their basins of attractions. In addition, the study by Gyllenberg et al. [32] on metapopulation two-patch models subject to Allee effects and competition suggests that Allee effect and the non-local competition can conserve spatial heterogeneity (there exist stable equilibria with unequal population densities in the two patches) as well as create heterogeneity (instability of the equilibrium with equal population densities in two patches). The competition between two species in our models can be analogous to the dispersal between two patches. Thus, we can expect to have similar phenomena in terms of conserving heterogeneity (there exist stable equilibria with unequal population densities for two species) as well as creating heterogeneity (instability of the equilibrium with equal population densities in two species).

In addition, it will also be interesting to explore the following questions:

1. When does strong Allee effects promote species coexistence where there is a species extinction without it?
2. Can competition rescue an endangered species from *essential extinction* due to strong Allee effects?

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