Competition can rescue endangered species subject to strong Allee effects

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Abstract

In this article, we study population dynamics of a general two-species discrete-time competition model where each species suffers from strong Allee effects and scramble intra-competition. We focus on how combination of intra-specific and inter-specific competition affect the extinction and coexistence of these two competing species that are subject to strong Allee effects. We derive sufficient conditions on the extinction, essential-like extinction and coexistence for such models. One of most interesting findings is that competition can promote coexistence of these two species. This is supported by the outcome of singe species models with strong Allee effects. In addition, we apply theoretical results to a symmetric competition model with strong Allee effects induced by predator saturation where we give a completed study of its possible equilibria and attractors. Numerical simulations are performed to support our results.

Key words: Strong Allee effects, Competition, Essential extinction, Essential-like extinction, Coexistence

1. Introduction

Competition both within and between species is an important topic in ecology, which can be a powerful force affecting the growth, distribution, and abundance of populations in community ecology. This has been supported by evidence from laboratory "bottle" experiments, field observations, and field experiments (Valone and Brown 1995). Competition among members of the same species is known as intra-specific competition, while competition between individuals of different species is known as inter-specific competition. Competition for resources (e.g., food, space and mates) can range between two extreme forms: contest competition where a limited number of individuals obtain a sufficient share of resource while the excess individuals get nothing at all, and scramble competition where all individuals obtain an equal share of the resource which may or may not be sufficient (Calow et al. 1998). The expectation, from classical theory, is that the increasing of overall competitive pressure should generally result in the decline of species coexistence (Vandermeer et al. 2002).

The Allee effect is a phenomenon in biology characterized by a positive interaction between population density and the per capita population growth rate in small populations (Allee et al. 1949). A distinction is made between a strong Allee effect, where a population exhibits a "critical size or density", below which the population declines on average, and above which it may increase, and a weak Allee effect, where a population lacks a "critical density", but where, at lower densities, the population growth rate rises with increasing density (Stephens et al. 1999). A study by Schreiber (2003) indicates that a single species subject to strong Allee effects may exhibit essential extinction (i.e., for a randomly chosen positive initial condition, the population goes to extinction with probability one) even if its initial condition is above the "critical density". Both strong Allee effects and weak Allee effects have important consequences for population dynamics and persistence, which can be induced by difficulties in finding a mate and predator avoidance or defense (McCarthy 1997; Stephens et al. 1999; Schreiber 2003; Courchamp et al. 2009; Kang and Yakubu 2011).

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Many species can experience both Allee effects and competitions with consequences that their populations do not grow optimally at low densities and individuals compete with one another at high densities (Begon et al. 1996; Etiemme et al. 2002). Understanding how interactions between Allee effects and competition affecting population dynamics can advance our understanding of the extinction and establishment of species in ecology communities, with implications for conservation programs (Zhou et al 2004; Courchamp et al. 2009; Kang and Yakubu 2011). Recently, Kang and Yakubu (2011) study how Allee effects affect population dynamics of two competing species in a discrete-time fashion. Their study shows that weak Allee effects induced by predation saturations can promote coexistence of the two competing species, which is supported by the outcome of two-species competition models without Allee effects. In this article we investigate how inter-specific competition affect extinction, essential-like extinction (i.e., one species go extinct and the other one has essential extinction in the limiting system) and coexistence of two competing species, where each species is subject to strong Allee effects and scramble intra-specific competition. One of the most interesting findings is that inter-specific competition can promote coexistence of two competing species at high densities. This result is surprising since inter-specific competition, from classic theory, is expected to have a negative effect on fitness-related characteristics of at least one of the species (Wiens 1989) and may increase local extinction rate in a metapopulation system (Bengtsson 1989). Biological explanation of this finding may have significant implications for conservation programs, and can be considered as a complement to the current studies on populations dynamics in the presence of Allee effects (e.g., Dennis 1989 & 2002; Selgrade and Namkoong 1992; McCarthy 1997; Shigesada and Kawasaki 1997; Greene and Stamps 2001; Keitt et al 2001; Fagan et al 2002; Wang et al 2002; Liebhold and Bascompte 2003; Schreiber 2003; Drake 2004; Zhou et al 2004; Petrovskii et al 2005; Taylor and Hastings 2005; Jang 2006; Aguirre et al 2009; Egami 2009&2010; Thieme et al. 2009; Elaydi and Sacker 2010; Wang et al 2010; Liu et al 2011) as well as various models in patchy environment (e.g., Amarasekare 1998a &1998b; Gyllenberg et al 1999; Ackleh et al 2007; Kang and Lanchier 2010; Kang and Armbruster 2011).

The structure of the remaining article is as follows: In Section 2, we define a general discrete-time two competing species population model and list important conditions that will be used in deriving sufficient conditions on extinction, essential-like extinction and the coexistence of this general model. In Section 3, we show that when these two competing species both suffer from strong Allee effects, a species can not invade the other one at its low densities and both go extinct when their initial conditions are below their Allee thresholds (Theorem 3.1). In Section 4, we give sufficient conditions on the extinction and essential-like extinction for a symmetric two species model with strong Allee effects. Our analytic results combined with simulations suggest that both competing species go to extinction for most initial conditions in one of the following two cases: 1. The sum of inter-specific competition coefficient and intraspecific competition coefficient is too large (Theorem 4.1). 2. Each species has essential extinction and its inter-specific competition coefficient is great than its intra-specific competition coefficient (Theorem 4.2). In Section 5, we give sufficient conditions on the coexistence of a symmetric two species competition model when each species has essential extinction (Theorem 5.1). Our result suggests that competition may save endangered species from extinction. In Section 6, we apply all theoretical results from the previous sections to a concrete symmetric competition model with Allee effects induced by predator saturation. Moreover, we derive the sufficient conditions on all possible interior equilibria and attractors. Our simulations support the fact that competition can promote coexistence when two competing species have essential extinction in their single state. In the last section, we summarize our study and give the potential future study.

2. A general competition model with Allee effects

Consider a discrete-time two competing species population model of the form

$$x_{t+1} = x_t e^{r_1(1-x_t)-a_1 y_t} I^x(x_t) (1)$$

$$y_{t+1} = y_t e^{r_2(1-y_t) - a_2 x_t} I^y(y_t) (2)$$

where x_t and y_t be the population density of two competing species in season t, respectively; r_i , i = 1, 2 represent the intrinsic growth rates which equal to *intra-specific competition* coefficients; a_i , i = 1, 2 be the *inter-specific competition* coefficients defining the equivalences between the two species and I^i , i = x, y represents a positive density-dependent factor of species i that satisfies Condition H1:

Condition **H1**: I^i , i = x, y is smooth in \mathbb{R}_+ and

$$0 \le I^{i}(v) \le 1 \text{ with } (I^{i})' > 0, \left(\frac{(I^{i})'}{I^{i}}\right)' < 0, v \in \mathbb{R}_{+}, i = x, y.$$

where $I^x = I^y = I$ in the symmetric case.

Let $\Omega = \{(x,y) \in \mathbb{R}^2_+ : x > 0, y > 0\}$, $\Omega_x = \{(x,y) \in \mathbb{R}^2_+ : y = 0\}$ and $\Omega_y = \{(x,y) \in \mathbb{R}^2_+ : x = 0\}$, then the basic feature of (1)-(2) can be summarized as follows:

Lemma 2.1. The system (1)-(2) is positively invariant in \mathbb{R}^2_+ , Ω , Ω_x and Ω_y . In addition, it is bounded by $[0, \frac{e^{r_1-1}}{r_1}] \times [0, \frac{e^{r_2-1}}{r_2}]$.

2.1. Dynamics for single species models with strong Alllee effects

If $x_t = 0$ or $y_t = 0$, then system (1)-(2) can be reduced to the following one species population model

$$N_{t+1} = N_t e^{r(1-N_t)} I(N_t) (3)$$

where $I = I^x, r = r_1$ for species x and $I = I^y, r = r_2$ for species y.

Let $u(N) = Ne^{r(1-N/K)}I(N) = Nh(N)$. We say that a species suffers from strong Allee effects if there are two positive values A_i , i = 1, 2 such that $u(A_i) = A_i$ and

$$h(N) < 1 \text{ for } N \in [0, A_1) \cup (A_2, \infty); h(N) > 1 \text{ for } N \in (A_1, A_2),$$

where A_1 is also called the *Allee threshold* of (3). Define the following conditions:

H2: The growth function u(N) has a unique positive value C that leads to the maximum value $M = \max_{N \geq 0} \{u(N)\} = u(C)$. Moreover, species suffers from strong Allee effects with A_1 as its Allee threshold and $A_1 < C < A_2$.

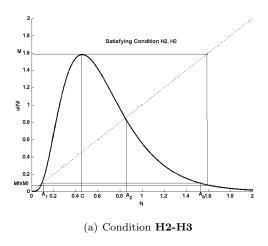
H3: The inequality $M h(M) < A_1$ holds. In addition, the growth function u(N) has a negative Schwartzian derivative (i.e., $\frac{u'''(N)}{u'(N)} - 3/2(\frac{u''(N)}{u'(N)})^2 < 0$) on the interval $[A_1, \infty)$.

H4: The inequality $M h(M) > A_2$ holds.

Assume that (3) satisfies Condition **H2**. Denote $A_b = \max\{u^{-1}(A_1)\}$, then according to the classification of Schreiber (2003), we can have the following two scenarios:

- 1. If u(N) satisfies Condition **H2**, **H3** (see Figure 1(a)), then the dynamics of (3) exhibits essential extinction, i.e., for a randomly chosen initial condition in \mathbb{R}_+ , the population of (3) goes to extinction with probability one.
- 2. If u(N) satisfies Condition **H2**, **H4** (see Figure 1(b)), then the dynamics of (3) exhibits bistability, i.e., the population of (3) persists in $[A_1, A_b]$ and goes to extinction for initial conditions outside this interval.

We define that the dynamics of two species competition model (1)-(2) has essential-like extinction if for any initial condition taken in the interior of \mathbb{R}^2_+ , the population of one species goes extinct and the population of the other one exhibits essential extinction at its single state. Numerical simulations suggest that when eqrefagx-(2) has essential-like extinction, then both species go extinct with probability one for any initial condition taken in the interior of \mathbb{R}^2_+ . In this article, we are interesting in sufficient conditions on the extinction, essential-like extinction and the coexistence of two competing species in (1)-(2) when the population model of each species satisfies Condition H1-H3 or Condition H1, H2, H4 at the absence of the other species.



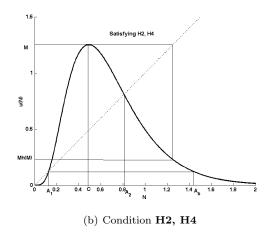


Figure 1: The schematic diagrams when (3) satisfies Condition H2-H3 and Condition H2, H4 respectively.

3. Multiple attractors of competition models with strong Allee effects

In this section, we explore possible attractors of system (1)-(2) and their basins of attractions. If the population model of each species satisfies Condition **H1-H2**, then the boundary equilibria of (1)-(2) are

$$(0,0),(x_1,0),(x_2,0),(0,y_1)$$
 and $(0,y_2)$

where x_i , i = 1, 2 are positive solutions of $e^{r_1(1-x)}I^x(x) = 1$ and $0 < x_1 < x_2 < 1$; and y_i , i = 1, 2 are positive solutions of $e^{r_2(1-y)}I^y(y) = 1$ and $0 < y_1 < y_2 < 1$. Let

$$u^{x}(x) = xe^{r_{1}(1-x)}I^{x}(x)$$
 and $u^{y}(y) = ye^{r_{2}(1-y)}I^{y}(y)$,

then we have the following theorem:

Theorem 3.1. [Attractors of system (1)-(2)]Assume that each single species' population model satisfies Condition H1-H2. Then (0,0) is always a attractor that has

$$B_{(0,0)} = \{(x,y) \in \mathbb{R}^2_+ : 0 < x < x_1, 0 < y < y_1\}$$

contained in its basins of attractions. In addition, if u^i (i = x or i = y) satisfies Condition **H4**, then there is an attractor on x-axis where species x persists if i = x; or there is an attractor on y-axis where species y persists if i = y.

Proof. Since the population model of each species in its single state satisfies Condition H1-H2, then

$$0 < e^{r_1} I^x(0) < 1$$
 and $0 < e^{r_2} I^y(0) < 1$.

The Jacobian matrix of (1)-(2) evaluated at (0,0) is

$$J|_{(0,0)} = \begin{pmatrix} e^{r_1} I^x(0) & 0\\ 0 & e^{r_2} I^y(0) \end{pmatrix}$$
 (4)

whose both eigenvalues are positive and strictly less than 1. Therefore, (0,0) is locally asymptotically stable. Define $B_{(0,0)}$ as follows:

$$B_{(0,0)} = \{(x,y) \in \mathbb{R}^2_+ : 0 < x < x_1, 0 < y < y_1\}.$$

We claim that:

$$\lim_{t \to \infty} \max\{x_t, y_t\} = 0 \text{ if } (x_0, y_0) \in B_{(0,0)}.$$

For any initial condition $(x_0, y_0) \in B_{(0,0)}$, according to Condition **H2**, we have

$$\begin{array}{rcl} x_1 & = & x_0 e^{r_1(1-x_0)-a_1 y_0} I^x(x_0) \le x_0 e^{r_1(1-x_0)} I^x(x_0) < x_0 \\ y_1 & = & y_0 e^{r_2(1-y_0)-a_2 x_0} I^y(y_0) \le y_0 e^{r_2(1-y_0)} I^y(y_0) < y_0. \end{array}$$

Thus, by induction, we can conclude that $\{(x_t, y_t)\}_{t=0}^{\infty}$ is a positively decreasing sequence that converges to (0,0).

Let
$$H^x(x) = r_1(1-x) + \ln(I^x)$$
 and $H^y(y) = r_2(1-y) + \ln(I^y)$, then

$$H^{x}(x) < 0$$
 if $0 < x < x_1$; $H^{x}(x) > 0$ if $x_1 < x < x_2$

and

$$H^{y}(y) < 0 \text{ if } 0 < y < y_1; H^{y}(y) > 0 \text{ if } y_1 < y < y_2.$$

Thus, according to Condition H1-H2, H^x having its unique maximum indicates that

$$\frac{dH^x}{dx}\Big|_{x=x_1} = -r_1 + \frac{(I^x)'}{I^x}\Big|_{x=x_1} > 0.$$

Similarly, we have

$$\frac{dH^y}{dy}\Big|_{y=y_1} = -r_2 + \frac{(I^y)'}{I^y}\Big|_{y=y_1} > 0.$$

If $y_0 = 0$, then (1)-(2) is reduced to (3) with $r = r_1, I^x = I$. Thus, according to the results in Schreiber (2003), we know that if Condition **H1**, **H2**, **H4** holds, species x persists on the interval $[x_1, x_b]$ where

$$u^{x}(x) = xe^{r_{1}(1-x)}I^{x}(x)$$
 and $x_{b} = \max\{(u^{x})^{-1}(x_{1})\}.$

Similarly, if Condition **H4** holds for species y at its single state, species y persists on the interval $[y_1, y_b]$ where

$$u^{y}(y) = ye^{r_{2}(1-y)}I^{y}(y)$$
 and $y_{b} = \max\{(u^{y})^{-1}(y_{1})\}.$

We restrict our dynamics either on $[x_1, x_b]$ or $[y_1, y_b]$. Now we study the external Lyapunov exponent on these two positively invariant intervals by using the extended relative nonlinearity concept in Kang (2011).

Define the following two functions:

$$F(x,y) = r_1(1-x) - a_1y + \ln(I^x(x))$$
 and $G(x,y) = r_2(1-y) - a_2x + \ln(I^y(y))$.

Then we have

$$F(0, y_2) < F(0, y_1) < F(0, 0) < 0, G(x_2, 0) < G(x_1, 0) < G(0, 0) < 0$$

and

$$F_x(x,0) = -r_1 + \frac{(I^x)'}{I^x}, \quad F_{xx}(x,0) = \left(\frac{(I^x)'}{I^x}\right)', \quad F_y(0,y) = -a_1, \qquad F_{yy}(0,y) = 0$$

$$G_x(x,0) = -a_2, \qquad G_{xx}(x,0) = 0, \qquad G_y(0,y) = -r_2 + \frac{(I^y)'}{I^y}, \quad G_{yy}(0,y) = \left(\frac{(I^y)'}{I^y}\right)'.$$

Since

$$F_{yy}(0,y) - \frac{F_y(0,y_1)G_{yy}(0,y)}{G_y(0,y_1)} = a_1 \frac{\left(\frac{(I^y)'}{I^y}\right)'}{-r_2 + \frac{(I^y)'}{I^y}|_{y=y_1}}$$

and

$$G_{xx}(x,0) - \frac{G_x(x_1,0)F_{xx}(x,0)}{F_x(x_1,0)} = a_2 \frac{\left(\frac{(I^x)'}{I^x}\right)'}{-r_1 + \frac{(I^x)'}{I^x}|_{x=x_1}},$$

thus, according to Theorem 3.1 in Kang (2011), the sign of the external Lyapunov exponent of $[y_1, y_b]$ can be determined by the sign of the following expression

$$F(0,y_1) + F_{yy}(0,y) - \frac{F_y(0,y_1)G_{yy}(0,y)}{G_y(0,y_1)} = F(0,y_1) + a_1 \frac{\left(\frac{(I^y)'}{I^y}\right)'}{-r_2 + \frac{(I^y)'}{I^y}|_{y=y_1}}$$

which is negative since $\left(\frac{(I^y)'}{I^y}\right)' < 0$ (Condition **H1**). Then, we can apply Theorem 2.18 in the paper by Hutson and Schmitt (1992) to conclude that $[y_1, y_b]$ is an attractor in the sense that the stable manifold of the omega limit set of $[y_1, y_b]$ is a neighborhood of $[y_1, y_b]$ in Ω . Similarly, we can show that $[x_1, x_b]$ is also an attractor.

Therefore, we have showed the statement.

A direct corollary from Theorem 3.1 can be stated as follows:

Corollary 3.1. [Multiple attractors of (1)-(2)] Assume that each single species' population model satisfies Condition H1-H2. If both u^x and u^y satisfy Condition H4, then system (1)-(2) has at least three attractors: (0,0), boundary attractor contained in $[x_1,x_b]$ on x-axis and boundary attractor contained in $[y_1, y_b]$ on y-axis.

Note: If two competing species both suffer from strong Allee effects, Theorem 3.1 and its corollary 3.1 indicate that a species can not invade the other species at its low densities and both go extinct when their initial conditions are below their Allee thresholds. This implies that competition can not save species with strong Allee effects at their low abundances.

4. Extinction and essential-like extinction of symmetric competition models with strong Allee effects

In this section, we are interesting in studying sufficient conditions that give the extinction and the essential extinction of two competing species system (1)-(2). For convenience, we focus on the symmetric case, i.e., $r_1 = r_2 = r$, $a_1 = a_2 = a$ and $I^x = I^y = I$. Thus (1)-(2) can be rewritten as

$$x_{t+1} = x_t e^{r(1-x_t)-ay_t} I(x_t)$$

$$y_{t+1} = y_t e^{r(1-y_t)-ax_t} I(y_t)$$
(5)

$$y_{t+1} = y_t e^{r(1-y_t) - ax_t} I(y_t) (6)$$

where I satisfies Condition H1. Due to the symmetric property, each single species' population dynamics can be described by (3). If u(x) satisfies Condition **H2**, then it has A_i , i=1,2 as the positive solutions of u(x) = x. Therefore, system (5)-(6) has the following five boundary equilibria: $(0,0), (A_i,0), (0,A_i), i = 1,2$ where $0 < A_1 < A_2 < 1$ and the function h(x) is less than 1 for all $x \in [0, A_1) \cap (A_2, \infty)$ and is greater than 1 for all $x \in (A_1, A_2)$. If the growth function u(x) has a negative Schwartzian derivative on the interval $[A_1, \infty)$ and the inequality $u(M) = M h(M) < A_1$ holds (Condition H3), then each species has essential extinction in its single state. Otherwise, if $u(M) = M h(M) > A_1$ holds (Condition **H4**), then each species persists on $[A_1, A_b]$ in its single state. In the rest of this section, we assume that the growth function u(x) satisfies Condition H1-H2.

Let $u_s(x) = xh_s(x) = xe^{r-(r+a)x}I(x)$ and $M_s = \max_{x\geq 0}\{xh_s(x)\} = u_s(C_s)$ where I(x) satisfies Conditions **H1**. We have the following proposition:

Proposition 4.1. [Dynamics on y = x] Define $\Omega_{y=x}$ as

$$\Omega_{y=x} = \{(x,y) \in \mathbb{R}^2_+ : x = y\},\$$

then $\Omega_{y=x}$ is an invariant set for system (5)-(6). For any initial condition $(x_0, y_0) \in \Omega_{y=x}$, (5)-(6) can be reduced to the following 1-D system

$$u_{t+1} = u_t e^{r(1-u_t) - au_t} I(u_t) = u_t e^{r-(r+a)u_t} I(u_t)$$
(7)

where its basic dynamics can be summarized as follows:

1. If $e^{r-(r+a)x}I(x) < 1$ for all $x \in [0, \frac{e^{r-1}}{r}]$, then

$$\lim_{t \to \infty} \sup u_t = 0, \text{ for all } u_0 > 0.$$

2. If $h_s(C_s) > 1$ for some $0 < C_s < \frac{r}{r+a}$, then (7) has two interior equilibria $u_i^*, i = 1, 2$ such that

$$0 < A_1 < u_1^* < u_2^* < A_2 < 1.$$

If, in addition, u_s has a negative Schwartzian derivative on the interval $[u_1^*, \infty)$ and $u_s(M_s) < u_1^*$, then (7) exhibits essential extinction; otherwise, if $u_s(M_s) > u_1^*$, then (7) persists in $[u_1^*, u_b]$ where $u_b = \max\{u^{-1}(u_1^*)\}$ and goes to extinction in $[0, u_1^*) \cup (u_b, \infty)$.

Proof. If $x_0 = y_0$, then according to (5)-(6), we have

$$\begin{array}{rcl} x_1 & = & x_0 e^{r(1-x_0)-ay_0} I(x_0) = x_0 e^{r(1-x_0)-ax_0} I(x_0) = x_0 e^{r-(r+a)x_0} I(x_0) \\ y_1 & = & y_0 e^{r(1-y_0)-ax_0} I(y_0) = x_0 e^{r(1-x_0)-ax_0} I(x_0) = x_1. \end{array}$$

Thus by induction, we have $x_t = y_t$ for all $t \ge 0$, i.e., $\Omega_{y=x}$ is an invariant set for system (5)-(6). This also implies that (5)-(6) can be reduced to (7) in the invariant manifold $\Omega_{y=x}$.

Since the compact set $[0, \frac{e^{r-1}}{r+a}]$ attracts all initial conditions $u_0 \ge 0$ for system (7) and

$$h_s(x) = e^{r - (r+a)x} I(x) < 1 \text{ for all } x \in [0, \frac{e^{r-1}}{r}],$$

thus, system (7) has no interior equilibrium except the extinction state 0. Let

$$m = \max_{0 \le x \le \frac{e^r - 1}{r}} \{h_s(x)\} < 1,$$

then

$$u_{t+1} = u_t h_s(u_t) \le u_t m \le u_0 m^{t+1} \to 0 \text{ as } t \to \infty.$$

Thus, $\limsup_{t\to\infty} u_t = 0$, for all $u_0 > 0$ if $e^{r-(r+a)x}I(x) < 1$ for all $x \in [0, \frac{e^{r-1}}{r}]$.

Since (3) satisfies Condition **H2**, thus we have $e^r I(0) < 1$ and there exits a unique positive value C such that

$$u'(x) > 0 \text{ for } x \in [0, C) \text{ and } u'(x) < 0 \text{ for } x \in (C, \infty).$$

This indicates that there is only one solution C such that the following equality holds

$$u'(x) = (1 - rx)e^{r(1-x)}I + xe^{r(1-x)}I' = 0 \Rightarrow \frac{I'}{I}\Big|_{x=C} = \frac{C}{rC - 1} > 0.$$

Since

$$(\frac{I'}{I})' < 0$$
 and $(u_s)' = (u(x)e^{-ax})' = (1 - (a+r)x)e^{r-(r+a)x}I + xe^{r-(a+r)x}I'$,

Thus, there is a unique positive value $C_s < C$ such that the following equality holds

$$(u_s(x))' = (1 - (a+r)x)e^{r-(r+a)x}I + xe^{r-(a+r)x}I' = 0 \Rightarrow \frac{I'}{I}\Big|_{x=C_s} = \frac{C_s}{(r+a)C_s - 1} > 0.$$

The interior equilibria of (7) satisfy the following equation:

$$e^{r-(a+r)x}I(x) = 1 \Rightarrow -\ln(I(x)) = r - (a+r)x$$

where

$$(-\ln(I(x)))' = -\frac{I'}{I} < 0 \text{ and } (-\ln(I(x)))'' = -(\frac{I'}{I})' > 0.$$

The inequality $h_s(C_s) > 1$ indicates that

$$e^{r-(r+a)C_s}I(C_s) > 1 \Rightarrow -\ln(I(C_s)) < r - (a+r)C_s.$$

This combined the fact that $h_s(0) = e^r I(0) < 1$, i.e., $-\ln(I(0)) < r$, implies that the positive convex decreasing function $-\ln(I(x))$ has exactly two intercepts with linear decreasing function r-(a+r)x in the first quadrant. Therefore, (7) has two interior equilibria u_i^* , i=1,2 with the following properties:

$$0 < A_1 < u_1^* < u_2^* < A_2 < 1.$$

The rest of Proposition 4.1 holds according to the classification results by Schreiber (2003).

Note: Proposition 4.1 indicates that if (3) satisfies Condition H1-H2, then (7) also satisfies Condition **H1-H2** under the condition that there is some $C_s \in (0, \frac{r}{r+a})$ such that $h_s(C_s) = e^{r-(r+a)C_s}I(C_s) > 1$. The proof of Proposition 4.1 also suggests that if (3) has no strong Allee effects, then (7) has no strong Allee effects either.

Theorem 4.1. [Extinction/Essential-like extinction in (5)-(6)] Let (7) satisfy Condition H1. If (7) has no interior equilibrium, then at least one of two competing species in (5)-(6) goes extinct. If, in addition, (7) satisfies Condition H2-H3, then (5)-(6) has essential extinction in Ω .

Proof. If (7) has no interior equilibrium, then $e^{r-(r+a)x}I(x)=1$ has no positive root. Since (5)-(6) satisfy Condition **H1**, thus

$$e^{r-(r+a)x}I(x) < 1$$
 for all $x > 0$.

According to Lemma 2.1, (5)-(6) is positively invariant in Ω and all initial conditions in Ω are attracted to the compact set $B = [0, \frac{e^{r-1}}{r}] \times [0, \frac{e^{r-1}}{r}]$. Thus, we can restrict the dynamics of (5)-(6) to B. Let $m = \max_{0 \le x \le \frac{e^{r-1}}{r}} \{e^{r-(r+a)x}I(x)\}$, then we have m < 1. According to (5)-(6), we have

$$\begin{array}{rcl} x_{t+1}y_{t+1} & = & x_te^{r(1-x_t)-ay_t}I(x_t)y_te^{r(1-y_t)-ax_t}I(y_t) \\ & = & x_te^{r-(r+a)x_t}I(x_t)y_te^{r-(r+a)y_t}I(y_t) \\ & \leq & m^2x_ty_t \leq m^{2(t+1)}x_0y_0 \end{array}$$

Thus,

$$\lim_{t \to \infty} x_t y_t = 0 \text{ as } t \to \infty.$$

According to Lemma 2.1, (5)-(6) is bounded, thus, we have the following two scenarios:

- 1. Both species go extinct for all initial conditions taken in Ω .
- 2. Only one species goes extinct for all initial conditions taken in Ω .

Without loss of generality, let us assume that species x goes extinct for all initial conditions taken in Ω . Then the limiting dynamics of (5)-(6) can be reduced to (3). Thus, if (3) satisfies Condition **H1-H3**, then it has essential extinction in \mathbb{R}_+ . Therefore, we can conclude that (5)-(6) has essential-like extinction in \mathbb{R}_+^2 .

Note: Theorem 4.1 implies that if the sum of inter-specific competition coefficient and intra-specific competition coefficient is too large (e.g., (7) has no positive equilibrium), then both species of (5)-(6) may go extinct in Ω .

Theorem 4.2. [Essential-like extinction in (5)-(6)] Assume that (3) satisfies Condition **H1-H3**. If r < a, then (5)-(6) has essential-like extinction in $\Omega \setminus \Omega_{y=x}$.

Proof. Take an initial condition in Ω such that $x_0 < y_0$, then according to (5)-(6), we have

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

Since $x_0 < y_0, r < a$ and Condition H1 holds, thus, the following inequality holds

$$\frac{x_1}{y_1} < \frac{x_0}{y_0}.$$

By induction, we can conclude that $\{\frac{x_t}{y_t}\}_{t=0}^{\infty}$ is a strictly decreasing positive sequence bounded by $\frac{x_0}{y_0}$. Therefore, there exists some nonnegative number $0 \le b < 1$ such that

$$\lim_{t \to \infty} \frac{x_t}{y_t} = b \text{ for all } (x_0, y_0) \in \{(x, y) \in \Omega : x < y\}.$$
 (8)

Since (5)-(6) satisfy Condition **H2**, then $e^r I(0) < 1$ and (5)-(6) has nontrivial boundary equilibria $(0, y_1)$ and $(0, y_2)$. The Jacobian matrix of (5)-(6) evaluated at these equilibria can be represented as

$$J|_{(0,y_i)} = \begin{pmatrix} e^{r-ay_i}I(0) & 0\\ -ay_i & 1 + y_i\left(\frac{I'}{I}|_{y=y_i} - r\right) \end{pmatrix}$$
(9)

which indicates that both equilibria $(0, y_1)$ and $(0, y_2)$ have stable manifolds points towards y-axis since $0 < e^{r-ay_i}I(0) < 1, i = 1, 2.$ Thus, there are some initial conditions in Ω such that

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

This implies that b = 0 according to (8). Then according to the property of boundedness by Lemma 2.1, we can conclude that

$$\lim_{t \to \infty} x_t = 0 \text{ for all } (x_0, y_0) \in \{(x, y) \in \Omega : x < y\}.$$

This indicates that the limiting dynamics of (1)-(2) can be reduced to (3). Thus, if (3) satisfies Condition **H1-H3**, then it has essential extinction in \mathbb{R}_+ . Therefore, we can conclude that (5)-(6) has essential-like extinction in $\{(x,y) \in \Omega : x < y\}$ if r < a. Similarly, we can show that (5)-(6) has essential-like extinction in $\{(x,y) \in \Omega : x > y\}$ if r < a. Therefore, the statement of Theorem 4.2 holds.

Notes: Theorem 4.2 indicates that (5)-(6) has no coexistence in $\Omega \setminus \Omega_{y=x}$ if each species has interspecific competition coefficient great than its intra-specific competition coefficient (i.e., r < a). Moreover, essential-like extinction occurs when each species has essential extinction in the absence of the other species. Numerical simulations suggest that when (5)-(6) has essential-like extinction, then both species go extinct with probability one for any initial condition taken in the interior of \mathbb{R}^2_+ .

5. Coexistence of symmetric competition models with strong Allee effects

In this section, we focus on deriving sufficient conditions on the coexistence of two species in (5)-(6) when (3) satisfies Condition **H1-H3**. In particularly, we would like to explore how inter-specific competition can save endangered species subject to *strong Allee effects* from extinction.

Theorem 5.1. [Coexistence of (5)-(6) with strong Allee efects] Assume that (3) satisfies Condition **H1-H3** and (7) satisfies Condition **H1, H2, H4** i.e., (7) persists in $[u_1^*, u_b] \subset \Omega_{y=x}$ and goes to extinction in $([0, u_1^*) \cap (u_b, \infty)) \subset \Omega_{y=x}$. Then the invariant set $[u_1^*, u_b] \subset \Omega_{y=x}$ is locally asymptotically stable if

$$\limsup_{t \to \infty} \sum_{i=0}^{t} \ln \left| 1 + \left(\frac{I'}{I} \right|_{u=u_i} - r + a \right) u_i \right| < 0$$

where $\{u_i\}_{i=0}^{\infty}$ is any orbit of (18) with $u_0 \in [u_1^*, u_b] \subset \Omega_{y=x}$.

Proof. Let $u_t = \frac{x_t + y_t}{2}$, $v_t = \frac{x_t - y_t}{2}$, then (5)-(6) can be rewritten as the following model:

$$u_{t+1} = \frac{1}{2u_t}e^{r-(r+a)u_t} \left(e^{(a-r)v_t}I(u_t+v_t) + e^{(r-a)v_t}I(u_t-v_t)\right) + \frac{1}{2v_t}e^{r-(r+a)u_t} \left(e^{(a-r)v_t}I(u_t+v_t) - e^{(r-a)v_t}I(u_t-v_t)\right) + \frac{1}{2u_t}e^{r-(r+a)u_t} \left(e^{(a-r)v_t}I(u_t+v_t) - e^{(r-a)v_t}I(u_t-v_t)\right) + \frac{1}{2v_t}e^{r-(r+a)u_t} \left(e^{(a-r)v_t}I(u_t+v_t) + e^{(r-a)v_t}I(u_t-v_t)\right)$$

$$(10)$$

Thus, the invariant manifold $\Omega_{y=x}$ of (5)-(6) is transferred to the invariant manifold $\Omega_{v=0}$ of (10) where

$$\Omega_{v=0} = \{(u, v) \in \mathbb{R}^2_+ : v = 0\}.$$

If v_n is very to close to 0, then (10) can be described as

$$u_{t+1} = u_t e^{r - (r+a)u_t} I(u_t) + O(v_t^2)$$

$$v_{t+1} = v_t e^{r - (r+a)u_t} I(u_t) \left(1 + \left(\frac{I'}{I} \Big|_{u=u_t} - r + a \right) u_t \right) + O(v_t^2)$$
(11)

Since (7) persists in $[u_1^*, u_b]$, thus for any initial condition $v_0 = 0$ and u_0 taken in $[u_1^*, u_b]$, we have $v_i = 0$ for all positive integer i and the set defined by

$$\Omega_{v=0}^p = \{(u, v) \in \mathbb{R}^2_+ : v = 0, u \in [u_1^*, u_b]\}$$

is a subset of $\Omega_{v=0}$ which is also positively invariant. Assume that $\{u_i\}_{i=0}^{\infty}$ is an orbit of (18) with $u_0 \in [u_1^*, u_b]$, then due to that fact that (7) persists in $[u_1^*, u_b]$, we have the following equality

$$\sum_{i=0}^{\infty} r - (r+a)u_i + \ln(I(u_i)) = 0$$
(12)

According to (11), the external Lyapunov exponent of the invariant set $\Omega_{v=0}^p$ can be determined by the sign of the following equations:

$$\lim \sup_{t \to \infty} \sum_{i=0}^{t} \ln \left(e^{r - (r+a)u_{i}} I(u_{i}) \middle| 1 + \left(\frac{I'}{I} \middle|_{u=u_{i}} - r + a \right) u_{i} \middle| \right) \\
\leq \lim \sup_{t \to \infty} \sum_{i=0}^{t} r - (r+a)u_{i} + \ln(I(u_{i})) \\
+ \lim \sup_{t \to \infty} \sum_{i=0}^{t} \ln \left| 1 + \left(\frac{I'}{I} \middle|_{u=u_{i}} - r + a \right) u_{i} \middle| \right) \tag{13}$$

Thus, according to (12), we have

$$\lim \sup_{t \to \infty} \sum_{i=0}^{t} \ln \left(e^{r - (r+a)u_i} I(u_i) \left| 1 + \left(\frac{I'}{I} \right|_{u=u_i} - r + a \right) u_i \right| \right)$$

$$\leq \lim \sup_{t \to \infty} \sum_{i=0}^{t} \ln \left| 1 + \left(\frac{I'}{I} \right|_{u=u_i} - r + a \right) u_i \right|$$

$$(14)$$

Therefore, the statement of Theorem 5.1 holds.

Notes: Theorem 5.1 indicates that competition is not always a bad thing, in fact, it may be able to prevent extinction and promote coexistence when their abundances are relative high. Biological explanation for this interesting phenomenon is that single species has *scramble intra-specific competition* (i.e., the high population density this season leads to low population density next season), *inter-specific competition* can bring down the current population density such that it has a larger population density which is above the *Allee threshold* in the next season. The concrete example and simulations for such cases are illustrated in the next season.

6. Application: a symmetric competition model with Allee effects induced by predator saturation

A symmetric competition model with Allee effects induced by predator saturation, i.e., $I(x) = e^{-\frac{m}{1+bx}}$, can be represented as following:

$$x_{n+1} = x_n e^{r(1-x_n) - \frac{m}{1+bx_n} - ay_n} (15)$$

$$y_{n+1} = y_n e^{r(1-y_n) - \frac{m}{1+by_n} - ax_n}$$
(16)

where r and a represent the intrinsic growth rate and the competition coefficient; m represent predation intensities and b represent the product of the proportional to the handling time and the carrying capacities. Then the population of each species at its single state can be described as:

$$N_{t+1} = N_t e^{r(1-N_t) - \frac{m}{1+bN_t}} \tag{17}$$

whose basic dynamics can be summarized as follows:

- 1. The positive density-dependent factor I(N) induced by predator saturation satisfies Condition H1.
- 2. Let $u(N) = Ne^{r(1-N)-\frac{m}{1+bN}}$ has a unique positive value C that leads to the maximum value

$$M=\max_{N\geq 0}\{u(N)\}=u(C).$$

- 3. If r < m and b < 1, then (17) has only extinction equilibrium 0.
- 4. If r < m and $1 < b < \frac{r^2(b+1)^2}{4mr}$, then (17) has two positive equilibria $A_i, i = 1, 2$ where

$$A_1 = \frac{r(b-1) - \sqrt{r^2(b+1)^2 - 4bmr}}{2rb}, \ A_2 = \frac{r(b-1) + \sqrt{r^2(b+1)^2 - 4bmr}}{2rb}.$$

Moreover, this is the case when species suffers from strong Allee effects and u(N) has a negative Schwartzian derivative on $[A_1, \infty)$ based on the study by Schreiber (2003).

The summary above implies that if r < m and $1 < b < \frac{r^2(b+1)^2}{4mr}$, then sing species model (17) satisfies Condition **H1-H2**. According to Proposition 4.1, the dynamics of (15)-(16) on the invariant manifold y = x can be stated as the following corollary:

Corollary 6.1. [Dynamics on y = x] For any initial condition $(x_0, y_0) \in \Omega_{y=x}$, (15)-(16) can be reduced to the following 1-D system

$$u_{t+1} = u_t e^{r(1-u_t) - \frac{m}{1+bu_t} - au_t} = u_t e^{r-(r+a)u_t - \frac{m}{1+bu_t}}$$
(18)

where its basic dynamics can be summarized as follows:

1. If r < m and $b < 1 + \frac{a}{r}$, then the population of (18) goes extinct for any initial condition, i.e.,

$$\limsup_{t\to\infty} u_t = 0, \text{ for all } u_0 > 0.$$

2. If r < m and $1 + \frac{a}{r} < b < \frac{(rb+r+a)^2}{4m(a+r)}$, then (18) has two interior equilibria $u_i^*, i = 1, 2$ where

$$u_1^* = \frac{r(b-1) - a - \sqrt{(rb+r+a)^2 - 4mb(r+a)}}{2b(r+a)}, \ u_2^* = \frac{r(b-1) - a + \sqrt{(rb+r+a)^2 - 4mb(r+a)}}{2b(r+a)}.$$

3. Assume that (18) has two interior equilibria $u_i^*, i = 1, 2$ as defined earlier. Let

$$h_s(x) = e^{r - (r+a)x - \frac{m}{1+bx}}$$
 and $M_s = \max_{0 \le x \le \frac{e^r - 1}{r}} \{xh_s(x)\},$

then we have the following two situations:

- a) if $M_s h_s(M_s) > u_1^*$, then (18) is persist in $[u_1^*, u_b]$ and goes to extinction in $[0, u_1^*)$;
- b) if $M_s h_s(M_s) < u_1^*$, then (18) exhibits essential extinction.

Proof. Let

$$f(u) = r - (r+a)u - \frac{m}{1+bu} = \frac{-b(r+a)x^2 + (rb-a-r)x + r - m}{1+bu},$$

then if $u_i^*, i = 1, 2$ are two roots of f(u), then we have

$$u_1^* + u_2^* = \frac{r(b-1) - a}{b(r+a)}$$
 and $u_1^* u_2^* = \frac{m-r}{b(r+a)}$. (19)

Thus if r < m and $b < 1 + \frac{a}{r}$, then $u_i^* < 0$ according to (19). This implies that f(u) < 0 for all $u \ge 0$, i.e., $e^{f(u)} < 1$ for all $u \ge 0$. Therefore, according to Proposition 4.1, we can conclude that

$$\limsup_{t\to\infty} u_t = 0, \text{ for all } u_0 > 0.$$

Now if r < m and $1 + \frac{a}{r} < b < \frac{(rb+r+a)^2}{4m(a+r)}$, then we have $u_1^* + u_2^* > 0$ and $u_1^*u_2^* > 0$. Thus f(u) has two positive roots which can be represented as:

$$u_1^* = \frac{r(b-1) - a - \sqrt{(rb+r+a)^2 - 4mb(r+a)}}{2b(r+a)}, \ u_2^* = \frac{r(b-1) - a + \sqrt{(rb+r+a)^2 - 4mb(r+a)}}{2b(r+a)}.$$

6.1. Competition promotes coexistence

In this subsection, we apply the coexistence result of Theorem 5.1 to system (15)-(16) to have the following corollary:

Corollary 6.2. [Coexistence in (15)-(16)] If

$$a < r < m, 1 + \frac{a}{r} < b < \min\{\frac{r^2(b+1)^2}{4mr}, \frac{(r-a)^2(a+r+rb)^2}{4mr(r-a)}\}$$

and (18) satisfies Condition $\mathbf{H4}$, i.e., (18) is persist in $[u_1^*, u_b]$, then the invariant set $[u_1^*, u_b]$ is locally asymptotically stable if

$$\limsup_{t \to \infty} \sum_{i=0}^{t} \ln \left| 1 + \left(\frac{mb}{(1 + bu_i)^2} - r + a \right) u_i \right| < 0$$

where $\{u_i\}_{i=0}^{\infty}$ is any orbit of (18) with $u_0 \in [u_1^*, u_b]$.

We give numerical examples to support that competition can promote the coexistence of (15)-(16) when each species has essential extinction at its single state and their initial conditions are large enough (e.g., above their Allee thresholds). From the study by Schreiber (2003), single species model (17) has essential extinction when $r = 4.5, m = 5, b = b^* > 9$ where b^* is the threshold when (17) has essential extinction for r = 4.5, m = 5. For example, when $r = 4.5, m = 5, b = 10 > b^*$, the single species has essential extinctions due to strong Allee effects. However, the competition model (15)-(16) with the same values of r, m, b has an interior attractor living on $[u_1^*, u_b] \subset \Omega_{y=x}$ when the inter-specific competition coefficient is a = 2.5 (Figure 6.1). Moreover, numerical simulations suggest that both species of (15)-(16) go to extinction for almost all initial conditions when $r = 4.5, m = 5, a = 2.5, b > \frac{(r+a)b^*}{r}$ where $\frac{(r+a)b^*}{r}$ is the threshold when (18) has essential extinction for r = 4.5, m = 5 (see Figure 3(h)).

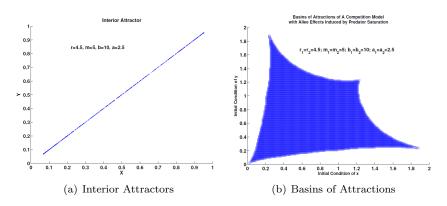


Figure 2: The blue region in the left figure is the interior attractor and its basins of attractions are shown in the blue area of the right figure when r = 4.5, m = 5, b = 10, a = 2.5 for system (15)-(16).

In addition, we would like to point out a result by Kang and Yakubu (2011) (Theorem 4.1) stating that (15)-(16) has bistability if r < a, i.e.,

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

Thus, the introduced *inter-specific competition* should be less than its *intra-specific competition* in order to save endangered species subject to *strong Allee effects* from *essential extinction*.

6.2. Multiple attractors

We denote x^*, y^* as follows:

$$x^* = \frac{(r-a)(a-r+rb) - \sqrt{(r-a)^2(a+r+rb)^2 - 4mbr^2(r-a)}}{2rb(r-a)}, \quad y^* = \frac{(r-a)(a-r+rb) + \sqrt{(r-a)^2(a+r+rb)^2 - 4mbr^2(r-a)}}{2rb(r-a)}$$

Then let i = 1, 2 and we define the following points:

$$E_{0,0} = (0,0), E_{A_i,0} = (A_i,0), E_{0,A_i} = (0,A_i), E_{u_i^*,u_i^*} = (u_i^*, u_i^*), E_{x^*,y^*} = (x^*, y^*), E_{y^*,x^*} = (y^*, x^*). (20)$$

Theorem 6.1. [Equilibria of (15)-(16)] System (15)-(16) can have one, four, five, six, seven and nine equilibria. Their sufficient conditions on having these equilibria are as follows:

One equilibrium: If r < m and b < 1, then (15)-(16) has only extinction equilibrium $E_{0,0}$.

Four equilibria: If r > m, then (15)-(16) has the only following four equilibrium:

$$E_{0,0}, E_{A_2,0}, E_{0,A_2}, E_{u_2^*,u_2^*}.$$

Five equilibria: If r < m and $1 + \frac{a}{r} < b < \frac{r^2(b+1)^2}{4mr}$, then (15)-(16) has the only following five equilibrium:

$$E_{0,0}, E_{A_i,0}, E_{0,A_i}, i = 1, 2.$$

Six equilibria: If $\max\{a,m\} < r < a+m$ and $1+\frac{a}{r} < b < \frac{(r-a)^2(a+r+rb)^2}{4mr(r-a)}$, then (15)-(16) has the only following four equilibrium:

$$E_{0,0}, E_{A_2,0}, E_{0,A_2}, E_{u_2^*,u_2^*}.$$

Seven equilibria: If $r < \min\{a, m\}$ and $1 + \frac{a}{r} < b < \min\{\frac{r^2(b+1)^2}{4mr}, \frac{(r-a)^2(a+r+rb)^2}{4mr(r-a)}\}$, then (15)-(16) has the only following seven equilibrium:

$$E_{0,0}, E_{A_i,0}, E_{0,A_i}, E_{u_i^*,u_i^*}, i = 1, 2.$$

Nine equilibria: If a < r < m and $1 + \frac{a}{r} < b < \min\{\frac{r^2(b+1)^2}{4mr}, \frac{(r-a)^2(a+r+rb)^2}{4mr(r-a)}\}$, then (15)-(16) has all nine equilibria listed in (20).

Proof. According to (15)-(16), all the possible equilibria are (0,0) and the eight nonnegative roots of the following two equations:

$$y = \frac{r(1-x)}{a} - \frac{m}{a(1+bx)} \tag{21}$$

$$x = \frac{r(1-y)}{a} - \frac{m}{a(1+by)} \tag{22}$$

which are listed in (20) and can be classified as follows:

1. $E_{A_i,0}$ and E_{0,A_i} are boundary equilibria where $A_i, i=1,2$ are positive solutions of

$$\frac{r(1-x)}{a} - \frac{m}{1+bx} = 0.$$

The necessary and sufficient conditions for the existence of these four boundary equilibria are

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

If r > m, then we have

$$A_1 + A_2 = \frac{-r + rb}{rb}$$
 and $A_1 A_2 = \frac{m - r}{rb} < 0$.

This implies that the only possible positive boundary equilibria are $E_{A_2,0}$ and E_{0,A_2} .

2. $E_{u_i^*,u_i^*}, i=1,2$ are symmetric equilibria where $u_i^*, i=1,2$ are positive solutions of

$$r - (r+a)x - \frac{m}{1+bx} = 0.$$

The necessary and sufficient conditions for the existence of these two interior symmetric equilibria are

$$r < m \text{ and } 1 + \frac{a}{r} < b < \frac{(r-a)^2(a+rb+b)^2}{4mr(r+a)}.$$

If r > m, then the only positive interior symmetric equilibrium is $E_{u_2^*,u_2^*}$.

3. E_{x^*,y^*} and E_{y^*,x^*} are asymmetric equilibria which satisfy (21) with $x^* \neq y^*$. Since

$$x^*y^* = -\frac{a+rb}{rb^2} + \frac{m}{(r-a)b},$$

thus, the necessary and sufficient conditions of the existence of positive x^*, y^* are

$$a < r < a + m \text{ and } 1 + \frac{a}{r} < b < \frac{(r-a)^2(a+r+rb)^2}{4mr(r-a)}.$$

Based on the discussion above, we can conclude that if r > m, then (15)-(16) has at least the following four equilibria

$$E_{0,0}, E_{A_2,0}, E_{0,A_2}, E_{u_2^*,u_2^*}.$$

If, in addition, the following inequality hold

$$a < r < a + m \text{ and } 1 + \frac{a}{r} < b < \frac{(r-a)^2(a+r+rb)^2}{4mr(r-a)},$$

then (15)-(16) has additional two asymmetric interior equilibria E_{x^*,y^*} and E_{y^*,x^*} .

If r < m and $1 < b < \frac{r^2(b+1)^2}{4mr}$, then (15)-(16) has at least the following five equilibria

$$E_{0,0}, E_{A_{i},0}, E_{0,A_{i}}, i = 1, 2.$$

If, in addition, the inequalities

$$a < r \text{ and } 1 + \frac{a}{r} < b < \frac{(r-a)^2(a+r+rb)^2}{4mr(r+a)},$$

hold, then (15)-(16) has additional two asymmetric interior equilibria E_{x^*,y^*} and E_{y^*,x^*} . Thus, (15)-(16) has exactly seven equilibria

$$E_{0,0}, E_{A_i,0}, E_{0,A_i}, E_{u_i^*,u_i^*}, i = 1, 2.$$

If the following inequality hold

$$a < r < m \text{ and } 1 + \frac{a}{r} < b < \min\{\frac{r^2(b+1)^2}{4mr}, \frac{(r-a)^2(a+r+rb)^2}{4mr(r+a)}\},$$

then (15)-(16) has all nine equilibria listed in (20).

Notes: Theorem 6.1 implies that (15)-(16) cannot have asymmetric interior equilibria if r < a which is a sufficient condition for the extinction of one species of the competition model in $\Omega \setminus \Omega_{y=x}$. Due to the symmetric property of the model, (15)-(16) can not have only three interior equilibria, but it is possible to have two, three or eight equilibria when the model is asymmetric. In addition, combining analysis on the Jacobian matrices with numerical simulations, we can show that that equilibria points $E_{A_1,0}, E_{0,A_1}, E_{u_1^*,u_1^*}, E_{x^*,y^*}, E_{y^*,x^*}$ are always locally unstable.

A direct corollary from Theorem 3.1, Theorem 4.2 and Theorem 4.1 can be stated as follows:

Corollary 6.3. If r < m, then $E_{0,0} = (0,0)$ is always an attractor for (15)-(16) whose basins of attractions contains the region

$$B_{(0,0)} = \{(x,y) \in \mathbb{R}^2_+ : 0 \le x \le A_1, 0 \le y \le A_2\}.$$

If, in addition, (17) satisfies Condition H4 and the inequalities

$$1 < b < \frac{r^2(b+1)^2}{4mr}$$
 and $r < a$

hold, then (15)-(16) has the following three attractors in $\Omega \setminus \Omega_{y=x}$: $E_{0,0}$ and the interval $[A_1, A_b]$ on both x-axis and y-axis.

Proof. Since $I(x) = e^{-\frac{m}{1+bx}}$, then we have

$$\frac{I'}{I} = \frac{mb}{(1+bx)^2} > 0$$
 and $(\frac{I'}{I})' = -\frac{2mb^2}{(1+bx)^3} < 0$ for $x \ge 0$.

Thus, if the inequalities $1 < b < \frac{r^2(b+1)^2}{4mr}$ hold, then the single species model (17) satisfies Condition **H1-H2**. Therefore, if (17) also satisfies Condition **H4**, then according to Theorem 3.1, the statement holds.

Theorem 6.2. [Attractors of (15)-(16)] System (15)-(16) can have one, two, three and four attractors. Their sufficient conditions on having one, three, four attractors are as follows:

Extinction: If r < m and b < 1, then the only attractor of (15)-(16) is $E_{0,0}$.

Essential-like extinction: If $1 < b < \frac{r^2(b+1)^2}{4mr}$ and $r < \min\{a, m\}$ and (17) satisfies Condition **H3**, then (15)-(16) has Essential-like extinction in $\Omega \setminus \Omega_{y=x}$.

Three attractors: If conditions in Corollary 6.3 are satisfied, then (15)-(16) has the following three attractors in $\Omega \setminus \Omega_{u=x}$: $E_{0,0}$ and the interval $[A_1, A_b]$ on both x-axis and y-axis.

Four attractors: If conditions in Corollary 6.2 satisfy, then (15)-(16) has the following four attractors in Ω : $E_{0,0}$, the interval $[A_1, A_b]$ on both x-axis and y-axis and the interval $[u_1^*, u_b]$ in $\Omega_{y=x}$.

Proof. If r < m and b < 1, then according to Theorem 6.1, system (15)-(16) has only extinction equilibrium $E_{0,0}$. This indicates that

$$\frac{r(1-x)}{a} - \frac{m}{a(1+bx)} < y \text{ and } \frac{r(1-y)}{a} - \frac{m}{a(1+by)} < x \text{ for all } (x,y) \in \Omega.$$

Therefore, (15)-(16) has only extinction attractor $E_{0,0}$, i.e.,

$$\lim_{t \to \infty} \max\{x_t, y_t\} = 0.$$

The inequalities

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

indicates that (17) satisfies Condition **H1-H3**. Thus each species has essential extinction in its single state. Since r < a, then two species of (15)-(16) can not coexist in $\Omega \setminus \Omega_{y=x}$ according to Corollary 6.3. Thus, for any initial condition taken in $\Omega \setminus \Omega_{y=x}$, the limiting system is reduced to (17) which has essential extinction. Therefore, (15)-(16) has essential-like extinction in $\Omega \setminus \Omega_{y=x}$ according to Theorem 4.2.

The other two cases are directly followed from Corollary 6.3 and Corollary 6.2.

Note: If conditions in Corollary 6.2 satisfy, and in addition, (17) satisfies Condition **H4**, then (15)-(16) has at least two attractors in $\Omega_{y=x}$: $E_{0,0}$ and an attractor contained in $[u_1^*, u_b] \subset \Omega_{y=x}$. If r < a, then (15)-(16) has at most three attractors: $E_{0,0}$ and $[A_1, A_b]$ on both x, y-axis. Numerical simulations also suggest that (15)-(16) has at most four attractors, i.e., the asymmetric equilibria E_{x^*,y^*} and E_{y^*,x^*} are always unstable.

The numerical simulations on the existence of different attractors are shown in Figure 6.2 when r = 4.5, m = 5, a = 2.5 and b varies from 2 to 13. Notice that there are some strange structures of the basins of attractions of x,y-axis (see Figure 3(c), 3(d) and 3(e)): the basins of attractions of $[A_1, A_b]$ on x-axis consist of two regions in cyan color that are connected by a symmetric equilibrium $E_{u_2^*, u_2^*}$; the basins of attractions of $[A_1, A_b]$ on y-axis consist of two regions in black color that are also connected by $E_{u_2^*, u_2^*}$. This could be caused by the fact that each species suffers from scramble competition. The detailed analysis can be our future study.

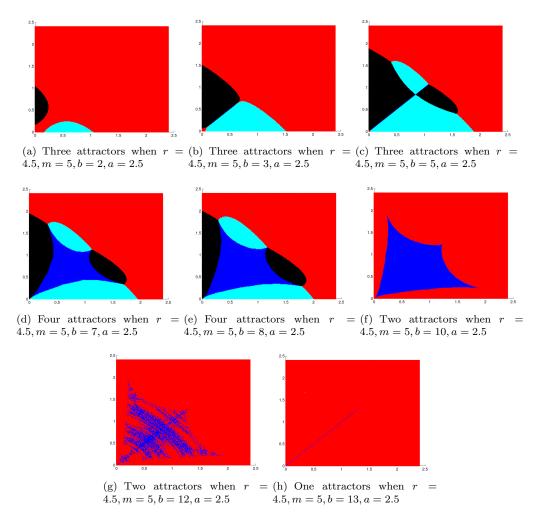


Figure 3: Basins of attractions of different attractors for system (15)-(16) when r = 4.5, m = 5, a = 2.5 and b varying from 2 to 13. The extinction region is in red; the coexistence region is in blue; the persistence of species x is in cyan and the persistence of species y is in black.

7. Discussion

It is common that species suffer from both competition and Allee effects. The interaction between these two ecological processes has great effects on extinction and coexistence of species in ecology communities. Previous study by Kang and Yakubu (2011) implies that weak Allee effects induced by predator saturation may promote the coexistence of two competing species, we explore how competition affects extinction, essential-like extinction and the coexistence of species subject to strong Allee effects in its single state in this article. One of our main finding is that inter-specific competition can save endangered species subject to strong Allee effects from essential extinction at high densities. This result gives a different point of view than the study by Wiens (1989) and Bengtsson (1989) where their results suggest that inter-specific competition may have a negative effect on coexistence. The exact ecological mechanisms as to why this pattern occurs are not transparent, but have to do with proper scramble intra/inter-specific competition that allows population density of each species being above the Allee effect threshold in the next season in the presence of high densities in the current season. We summarize our main findings as follows:

- 1. Theorem 3.1 provides sufficient conditions on multiple attractors of two species competing systems. This result shows that when these two competing species both suffer from *strong Allee effects*, a species can not invade the other species at its low densities and both go extinct when their initial conditions are below their *Allee thresholds*.
- 2. Theorem 4.1 and 4.2 give sufficient conditions on the extinction and essential-like extinction for a symmetric two species model with strong Allee effects. This study indicates that both competing species go to extinction for most initial conditions in one of the following two cases: a. The sum of inter-specific competition coefficient and intra-specific competition coefficient is too large. b. Each species has essential extinction and its inter-specific competition coefficient great than its intra-specific competition coefficient.
- 3. Theorem 5.1 gives sufficient conditions on the coexistence for a symmetric two species competition model when each species has *essential extinction*. Our result suggests that competition may save the endangered species from *essential extinction*.
- 4. We apply previous theoretical results to a symmetric discrete-time two species model where each species suffers from *strong Allee effects* induced by predator saturation. The completed study of all possible equilibria and attractors including coexistence attractor supports our finding that *inter-specific competition* can rescue endangered species subject to *strong Allee effects* at high densities.

Our study in this article and the work by Kang and Yakubu (2011) suggest the following scenarios:

- For a two-species discrete-time competition model, if both species have larger inter-specific competition than their intra-specific competition, then there is no coexistence for both models with or without Allee effects. This is consistent with the classical study of two-species continuous time Lokta-Voltera competition models.
- At low densities, weak Allee effects is able to promote permanence of scramble competition systems. This is due to the fact that weak Allee effects decreases the fitness of resident species such that the other species is able to invade at its low densities.
- At hight densities, scramble inter-specific competition can rescue a species suffering from essential extinction caused by strong Allee effects. This is due to the fact that single species has scramble intra-specific competition, introducing proper inter-specific competition can bring down the current population density such that it can have a larger population density which is above the Allee threshold in the next season.

It is well-known dispersal is a fundamental ecological process that couples the dynamics within and between populations which enables individuals to leave unfavorable habitat, avoid predation or competition, find new food resources, search for mates, evade inbreeding, and (re)colonize areas (Begon et al. 1996; Etiemme et al. 2002). Whether they are successful in doing so can be determined by the interplay between dispersal and other ecological processes such as Allee effects and competition. Gyllenberg et al (1999) study the two-patch metapopulation models subject to Allee effects and competition (both intra/inter-specific competitions) and propose that the Allee effect, migration intensity, and non-local competition should be considered jointly in studies problems like pattern formation in space and invasions of spreading species. Etiemme et al. (2002) study how the interaction between dispersal, the Allee effect and (intra-specific) scramble competition determines the establishment and persistence of a population by using integrodifference models. It will be interesting to explore how different Allee effects combined with intra/inter-specific competition affect extinction and coexistence of species in both patchy models and integrodifference models and compare findings for these two different models. The possible future study may includes the following ecological questions:

- 1. How does fluctuated environment affect population dynamics of competition models with Allee effects?
- 2. How to explain the basins attractions of each species that we observed (see Figure 3(c), 3(d) and 3(e))?
- 3. What are population dynamics when competing species subject to *Allee effects* has different growth functions, e.g., Hassel's model, Beverton-Holt model, Ricker's model?

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