Dynamics of a generalized Beverton-Holt competition model subject to Allee effects

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Abstract

In this article, we propose a generalized Beverton-Holt competition model subject to Allee effects and study its population dynamics to obtain insights on how the interplay of Allee effects and contest competition affects the persistence and the extinction of two competing species. By using the theory of monotone dynamics and the properties of critical curves for non-invertible maps, our analysis indicates that the proposed model has relatively simple dynamics, i.e., almost every trajectory converges to a locally asymptotically stable equilibrium if the intensity of intra-specific competition intensity exceeds that of inter-specific competition. This equilibrium dynamics is also possible when the intensity of intra-specific competition intensity is less than that of inter-specific competition but under conditions that the maximum intrinsic growth rate of one species is not too large. The coexistence of two competing species occurs only if the system has four interior equilibria. We provide an approximation to the basin attractions of the boundary attractors (i.e., the extinction of one or both species) which suggests that contest species are prone to extinction at low densities. Our study suggests the following points of our generalized Beverton-Holt competition model: (i) The model can have only three boundary attractors without coexistence or four attractors among which only one is a persistent attractor; (ii) The model has only equilibrium dynamics; and (iii) The synergy between Allee effects and contest competition make two competing species prone to extinct.

Key words: Allee effects, Scramble competition models, Contest competition models, Basins of attractions, Extinction, Coexistence

1. Introduction

The Allee effect is a phenomenon in biology characterized by a positive correlation between population density and its per capita growth rate at small population densities (Allee et al. 1949). A distinction is made between a strong Allee effect and a weak Allee effect: a strong Allee effect refers to a population that exhibits a “critical size or density”, below which population declines to extinction, and above which it may persist; A population with a weak Allee effect lacks a “critical density” and has, at low densities, a per capita growth rate that increases with increasing densities (Stephens et al. 1999; Lidicker 2010). Allee effects have been detected in natural populations for a wide array of taxa and are believed to be strong regulators of extinction, colonization success of invasive species, and disease dynamics. Mathematical models can help us understand these combined effects on the persistence or extinction of biological species. There is a considerable amount of literature on populations dynamics in the presence of Allee effects (e.g., Dennis 1989 & 2002; Selgrade and Nanokoong 1992; Cantrell et al 1996; 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

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In another direction, Cushing and Hudson (2012) investigated the global dynamics of an evolutionary model for a population subject to strong Allee effects. One of their results suggests that evolution is beneficial in the sense that reduces the possibility of extinction due to an Allee effect.

Contest and scramble-type competition are two extreme forms of competition, which are characterized by resource monopolization and resource sharing, respectively. Contest competition results in a constant number of survivors with enough resource gain against an initial density of competitors, while scramble competition (also called over-compensation) results in an increased number of survivors with decreased resource intake and an increased number of competitors (Calow et al. 1998). A well-known model for contest competition is the Beverton-Holt equation while the well-known model for scramble competition is the Ricker equation. Even though Allee effects are expected commonly in nature, they are often ignored in studies of species coexistence mechanisms. Many species can experience different forms of competition at high densities and Allee effects at low densities with the consequence 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; Kang 2013). The potential effects of combining positive density dependence from Allee effects with negative density dependence coming from different types of competition are expected to generate different and rich dynamics due to the fact that outcomes of different patterns of competition have different consequences for population dynamics and the evolution of individual traits (Godfray 1987; Lomnicki 1988; Ives 1989). For instance, with a species at a low density, in the invader state, it faces both intra-specific and inter-specific competition, but obtains a lesser effect of reduced intra-specific competition due to Allee effects compared with the standard investigations of models of competing species. As comparisons between intra-specific and inter-specific density dependence are critical to competitive coexistence, ignoring the potential that Allee effects can greatly modify intra-specific competition, is a critical oversight. For instance, Chesson and Ellner (1989) point out the potential for major effects (such as interior invariant regions for stochastic models) if low-density growth rates are depressed by Allee effects. Hopf et al (1993) also point out potential major implications for community structure with the introduction of Allee effects into a competition model.

Recently, Kang and Yakubu (2011) and Kang (2013) have explored population dynamics of two competing species when both species suffer from scramble competition (i.e., Ricker-type models) and Allee effects induced by predator saturation. The positive density dependence from weak Allee effects can decrease the fitness of resident species so that the other species is able to invade at its low densities. Thus weak Allee effects can promote the permanence of two competing species at their low densities (Kang and Yakubu 2011). In the presence of strong Allee effects, scramble inter-specific competition can lower population density, although not below the Allee threshold. Thus the synergy effects of strong Allee effects and scramble inter-specific competition can potentially save endangered two competing species from essential extinction at the high densities under certain conditions (Kang 2013). Here essential extinction means that species goes extinction with probability one in the presence of strong Allee effects (Schreiber 2003). Understanding how different forms of competition affect population dynamics in the presence of Allee effects can advance our understanding of the extinction and persistence of species in ecological communities. This in turn has implications for conservation programs (Zhou et al 2004; Courchamp et al. 2009; Kang and Yakubu 2011; Kang 2013).

A recent work by Livadiotis and Elaydi (2012) considered a general framework of population models subject to strong Allee effects. We adopt and extend their mathematical formulation of strong Allee effects in single species models. Our main purpose is to investigate the dynamic outcome in two species contest competition models when both species have Allee effects. The contest competition models in this article refer to a generalized Beverton-Holt competition model while scramble competition models refer to species that have one-hump growth functions (e.g., Ricker’s map). More precisely, we would like to explore answers to the following ecological questions.
1. What are the dynamical outcomes of a two species competition model when both species suffer from both strong Allee effects and contest competition?

2. How do the dynamics of models with a strong Allee effect and contest competition compare to those of models with a strong Allee effect and scramble competition?

3. What are the generic dynamical features of population models subject to strong Allee effects and different forms of competition at low and high densities?

The paper is organized as follows: In Section 2, we mathematically formulate Allee effects in single species contest and scramble competition models. We derive a generalized Beverton-Holt competition model in which each species is subject to strong Allee effects. In addition, we provide the important results of single species models with strong Allee effects and contest competition that can be applied to two species competition models. In Section 3, we apply the theory of monotone dynamics to obtain sufficient conditions when our two species competition model has equilibrium dynamics. This result can establish some generic dynamical features of contest competition models subject to Allee effects. We also approximate the attraction basins of boundary attractors (i.e., initial conditions that lead to the extinction of one or both species). Moreover, we obtain conditions that lead to the coexistence of two competing species. These results help us understand the coexistence and the extinction conditions for two competing species which are subject to contest competition and Allee effects. In Section 4, we apply the theoretical results derived in Section 3 to a specific two competing species model with strong Allee effects and contest competition. Numerical simulations offer more insights into the generic features of two species models with strong Allee effects and contest competition. The results obtained from Section 3 & 4 partially answer the three questions above. In Section 5, we discuss the dynamic outcomes of two competing species population models with different types of competition (i.e., contest and scramble competition) where each species has strong Allee effects. In addition, we summarize our results and mention some potential future studies. In Appendix, we provide detailed proofs of our theoretical results. Do you think that we should keep this paragraph to give readers a general view of the manuscript?

2. Model Derivations

2.1. Single species population models

We begin by describing how we will mathematically account for scramble competition, contest competition, and/or Allee effects in a single species model. Let $u_t$ be a species population density at time $t$. Its density at time $t+1$ is given by the equation:

$$ u_{t+1} = H(u_t) = u_t h(u_t) $$

where $H(u) \geq 0, u \in \mathbb{R}_+$ is the growth function of species $u$ and $h(u)$ is the per capital growth rate. We assume that $\lim_{u \to \infty} h(u) = 0$, which guarantees the boundedness of population (Kang and Chesson 2010; Kang 2012 b). We say that species $u$ has *contest intra-specific competition* if $\lim_{u \to \infty} H(u) = c > 0$. This implies that there is a constant lower bound on the number of individuals that obtain enough resources to survive, for any initial density of competitors. We say species $u$ has *scramble intra-specific competition* if $\lim_{u \to \infty} H(u) = 0$. This implies that a sufficiently high initial density of competitors will lead to a decreased number of survivors because of a decrease in the amount of resources available for each individual. For example, an important ecological example of contest intra-specific competition is the Beverton-Holt model whose $H$ takes the form of $H(u) = \frac{ru}{1+au}$. A well-known ecological example of scramble intra-specific competition is the Ricker’s model whose $H$ takes the form of $H(u) = u e^{r-au}$.

The Beverton-Holt model has relatively simple population dynamics where population goes to 0 if $r < 1$ and population goes to $r-1$ if $r > 1$. The Ricker’s model has very complicated population dynamics (e.g., periodic orbits, chaos) depending on the values of $r$.

We define the following four conditions with respect to Model (1):
A1: There exists some $\epsilon > 0$ such that $\frac{\partial h}{\partial u} > 0$ for $u \in (0, \epsilon)$.

A2: $h(u)$ is continuous and differentiable with $h(u) \geq 0$ and $\lim_{u \to \infty} h(u) = a < 1$.

A3: There exists unique two numbers $0 < A < K$, such that $h(A) = h(K) = 1$ and $h'(A) > 1$. In addition, $h(0) < 1$.

A4: There exists a unique fixed point $K$, i.e., $h(K) = 1$. In addition, $h(0) > 1$.

Condition A1 indicates that the per capita growth rate has a positive correlation with population density for small populations. Condition A2 indicates that the population is positively invariant (i.e., all future populations are nonnegative for any nonnegative initial population) and bounded. Condition A3 indicates that the population has two steady states $A$ and $K$ where $A$, called the Allee threshold, is always unstable and $K$, called the carrying capacity, can be locally stable under certain conditions. Condition A4 indicates that species $u$ is persistent and may be locally stable at its carry capacity $K$. Now we can define the following terms:

- Species $u$ has Allee effects if its population model (1) satisfies Condition A1, A2.
- Species $u$ has strong Allee effects if its population model (1) satisfies Condition A1, A2, A3 (see blue curves in Figure 2.1-1(b)).
- Species $u$ has weak Allee effects if its population model (1) satisfies Condition A1, A2, A4 (see black curves in Figure 2.1-1(b)).

Our definition of Allee effects is more general than Livadiotis and Elaydi (2012) in the sense that we are able to use Condition A1, A2, A3, A4 to define the concept of Allee effects, strong Allee effects and weak Allee effects. Livadiotis and Elaydi (2012) only define strong Allee effects by using the following three conditions: i) $h'(u) > 0$ for $u \in (0, \epsilon)$ for some $\epsilon > 0$; ii) $h(0) < 1$ and iii) There exists a unique $K > 0$, such that $h(K) = 1, h'(K) < 0$. Our definition and the definition introduced by Livadiotis and Elaydi (2012) regarding the concept of strong Allee effects can be considered the same in terms of classifying the models with strong Allee effects. When species $u$ is subject to strong Allee effects, i.e., its population model (1) satisfies Condition A1, A2, A3, its population dynamics can be summarized as follows: When initial population density is below $A$, the population goes extinct; when initial population density is above $A$, the population may be able to sustain itself; when $H(\max_{A \leq u \leq K} \{H(u)\}) < A$, then (1) may have essential extinction (i.e., for any positive initial condition, the population converges to 0 with probability 1) due to strong Allee effects (Schreiber 2003). See Figure 2.1-1(b) for an illustration of strong Allee effects (blue curves in both figures) v.s. weak Allee effects (black curves in both figures).

Outcomes of different patterns of intra-specific competition (e.g., contest competitions or scramble competitions) have different consequences for population dynamics (1) when species suffers from Allee effects. A well-known contest competition model introduced by Thomson (1993) for fisheries is called the Sigmoid Beverton-Holt model. It can be described as

$$u_{t+1} = H(u_t) = u_t h(u_t) = u_t \frac{ru_t^{\delta-1}}{1 + u_t^\delta} \quad (2)$$

where $r, \delta > 0$. Model (2) is a depensatory generalization of the Beverton-Holt stock-recruitment relationship used to develop a set of constraints designed to safeguard against overfishing (Thomson 1993; Myers et al 1995; Myers and Mertz 1998; Stoner and Ray-Culp 2000; Myers 2001; Gascoigne and Lipcius 2004; Harry et al 2012). One important feature of (2) is that it exhibits the Allee effect if $\delta > 1$. The dynamical properties of (2) have been proposed by Harry et al (2012). Here we summarize the important dynamics of (2) that will be used later for our two-species model as the following proposition:
The growth function $H(u) = uh(u)$.

The per capita growth rate $h(u) = \frac{H(u)}{u}$.

Figure 1: An illustration of strong Allee effects v.s. weak Allee effects of their growth functions $H(u) = uh(u)$ and their per capita growth rates $h(u) = \frac{H(u)}{u}$. The red curve is $H = u$ or $h = 1$; the green curve is the case when $(1)$ has no Allee effects; the blue curve is the case when $(1)$ has strong Allee effects and the black curve is the case when $(1)$ has weak Allee effects.

**Proposition 2.1** (Dynamical behavior of $(2)$). Let $r, \delta > 0$ and assume $(2)$ has an initial condition $x_0 > 0$. If $\delta > 1$, we define

$$r_{\text{crit}} = \delta(\delta - 1)^{\frac{1}{\delta} - 1}.$$  

Then the following statements are true:

1. If $\delta \in (0, 1)$, then Model $(2)$ has two non-negative equilibria: an unstable equilibrium $0$ and a stable positive equilibrium $K$.

2. If $\delta > 1$ and $r < r_{\text{crit}}$, then the only equilibrium of Model $(2)$ is $0$ and it is locally stable.

3. If $\delta > 1$ and $r > r_{\text{crit}}$, then Model $(2)$ has three non-negative equilibria: $0$, $A$ and $K$ such that $0 < A < \frac{r(\delta - 1)}{\delta} < K$. The $0$ equilibrium is stable with the basin of attraction $[0, A)$; $A$ is unstable (repeller), while $K$ is stable with the basin of attraction $(A, \infty)$.

Harry et al (2012, Proposition 1) gave similar results to Proposition 2.1 but without rigorous proof. We give a detailed proof in the Appendix. Proposition 2.1 implies that Model $(2)$ has Allee effects for any $r, \delta > 0$. Precisely, Model $(2)$ has weak Allee effects if $\delta \in (0, 1)$ while Model $(2)$ has strong Allee effects if $\delta > 1$ and $r > r_{\text{crit}}$. In addition, we would like to point out that when $\delta = 2$, Elaydi and Sacker (2009) have extended $(2)$ to the following generalized form:

$$u_{t+1} = u_t \frac{du_t + e}{u_t^2 + bu_t + c}$$  

where $b$ is called the shock recovery parameter and $c$ can be considered as a carrying capacity. The dynamics of $(3)$ are similar to $(2)$ when $\delta = 2$. Define a single species population model as follows

$$u_{t+1} = H(u_t) = u_t h(u_t) = u_t \frac{ru_t^{\delta-1}}{a + u_t^\delta}$$  

where $r$ is the maximum intrinsic growth rate and $a$ is a parameter that can measure the carrying capacity of species. $a$ in the model $(4)$ has the same biological meaning as the parameter $c$ defined in Model $(3)$. The following corollary follows from Proposition 2.1. Here we define

$$r_{\text{crit}}^a = a^{1/\delta}(\delta - 1)^{\frac{1}{\delta} - 1}.$$  

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Corollary 2.1. Let \( r, a, \delta > 0 \), and \( x_0 > 0 \). If \( a, \delta > 1 \) and \( r > r_{\text{crit}}^a \), then Model (4) has two interior equilibria \( A^a \) and \( K^a \) such that \( 0 < A < A^a < K^a < K \) where \( A, K \) are as in Proposition 2.1.

A prototypical scramble competition model with an Allee effect can be based on the Ricker model:

\[
    u_{t+1} = u_t h(u_t) = u_t e^{r(1-u_t) - \frac{m}{1+bu_t}}.
\]

Here \( r \) represents the intrinsic growth rate (also the scramble intra-specific competition coefficient); \( m \) represents predation intensities and \( b \) is proportional to the product of the handling time and the carrying capacity. For Model (5), we have

\[
    h(u) = e^{r(1-u) - \frac{m}{1+bu}} \quad \text{and} \quad h'(u) = \frac{[bm - r(1+bu)^2]e^{r(1-u) - \frac{m}{1+bu}}}{(1+bu)^2}.
\]

Thus, according to the definitions above, Model (5) has Allee effects if \( mb > r \); Model (5) has weak Allee effects if \( bm > r > m \); and Model (5) has strong Allee effects if \( r < m < \frac{r(1+b)^2}{4b}, b > 1 \). In addition, Model (5) has more complicated dynamics (e.g., chaos, essential extinctions) than the contest competition model subject to Allee effects (2). The detailed dynamics of (5) has been studied by Schreiber (2003).

Another example of scramble competition with Allee effects is a generalized Maynard Smith-Slatkin model that can be described as follows:

\[
    u_{t+1} = H(u_t) = u_t h(u_t) = u_t \frac{r u_t^{\delta-1}}{1 + u_t^{\delta} + bu_t^d}
\]

where all parameters are positive. \( r, \delta \) have the same biological meanings as in Model (2) and \( b, d \) have the same biological meaning as in Model (3). Model (6) can exhibit similar complicated dynamics as Model (5). This is due to the generic feature of scramble competition. Here we summarize the basic dynamics of (6) that will be used in the later sections in the following theorem.

**Theorem 2.1 (Dynamics of Model (6)).** If \( \delta > 1 \), we define

\[
    r_{\text{crit}} = \left( \frac{\delta}{b(d-\delta)} \right)^{(1-\delta)/d} \left[ \frac{d}{d-\delta} + \left( \frac{\delta}{b(d-\delta)} \right)^{\delta/d} \right].
\]

Depending on the values of \( r, b, \delta, d, \) the basic dynamics of (6) can be classified by the following cases.

1. If \( \delta > d \), then the trajectory of Model (6) with initial condition \( x_0 > 0 \) converges to one of its equilibria. More specifically, we have the following two cases:
   - (a) If \( \delta < 1 \), then Model (6) has two non-negative equilibria 0 and \( K \) where 0 is unstable and \( K \) is globally stable.
   - (b) If \( \delta > 1 \), then \( u = 0 \) is unstable and Model (6) can have 0 or two or even four positive equilibria. Moreover, 0 is globally asymptotically stable when there exists no positive equilibrium.

2. If \( \delta = d \), then Model (6) is reduced to Model (2) and its dynamics are as in Proposition 2.1.

3. If \( \delta < d \), then \( u = 0 \) is locally asymptotically stable. In addition,
   - (a) If \( \delta < 1 \), then Model (6) has two non-negative equilibria 0 and \( K \) and 0 is unstable.
   - (b) If \( \delta > 1 \) and \( r > r_{\text{crit}} \), then Model (6) has at least two distinct positive roots \( A, K \) such that \( 0 < A < u_c < K \) where \( u_c \) is the unique critical point of \( H(u) \), i.e., \( H'(u_c) = 0 \).
4. If both $\delta$ and $d$ are positive integers, then Model (6) has at most two positive equilibria.

Theorem 2.1 implies that Model (6) can exhibit strong Allee effects if $\delta > \max\{1,d\}$ or $1 < \delta < d$, $r > r_{crit}$. Model (2) can exhibit strong Allee effects only if $\delta > 1$ and $r > r_{crit}$. Even though Part 1 (b) and Part 3 (b) of Theorem 2.1 do not state that Model (6) has exactly two interior equilibria, numerical simulations suggest that Model (6) has at most two interior equilibria. In addition, if $1 < \delta < d$ and $r > r_{crit}$, then Model (6) is a unimodal map that can have very complicated dynamics as the Ricker’s map including essential extinction due to strong Allee effects. Numerical simulations suggest that increasing values of $r, b, \delta$ can destabilize the system while increasing value of $d$ can stabilize the system (see Figure 2-2(b) as examples).

![Figure 2: Time series of Model (6). These orbits show that Model (6) can have complicated dynamics such as periodic orbits and chaos.](image)

2.2. A generalized Beverton-Holt competition model with Allee effects

A generalized Beverton-Holt two species competition model with Allee effects derived from single species models (2) is

\[
x_{t+1} = \frac{r_1 x_t^{\delta_1}}{1 + x_t^{\delta_1} + b_1 y_t^{\delta_2}} \tag{7}
\]

\[
y_{t+1} = \frac{r_2 y_t^{\delta_2}}{1 + y_t^{\delta_2} + b_2 x_t^{\delta_4}} \tag{8}
\]

where $r_i, i = 1, 2$ describe the maximum intrinsic growth rate of each species; $b_i, i = 1, 2$ describe the relative inter-specific competition coefficient to its intra-specific competition; $\delta_i, i = 1, 2$ describe the strength of the density dependence in the intensity of the intra-specific competition while $\delta_i, i = 3, 4$ describe the strength of the density dependence in the intensity of the inter-specific competition. This implies that $\delta_i, i = 1, 2, 3, 4$ measure how the intensity of competition changes with density. Increasing one of the $\delta_i$’s has the effect of making competition stronger for large populations but weaker for small ones. Models (2) can be obtained in the special symmetric case of Model (7)-(8) where there are solutions with $x = y$.

**H1**: $\delta_i > 1$, $r_i > r_{crit}^i$, $i = 1, 2$ where $r_{crit}^i = \delta_i(\delta_i - 1)^{\frac{1}{\delta_i - 1}}$, $i = 1, 2$.

According to Proposition 2.1, each species of Model (7)-(8) suffers both contest intra-specific competition and strong Allee effects if **H1** is satisfied. Due to our interests, we mainly focus on the dynamics of (7)-(8) when Condition **H1** is satisfied.
3. Dynamical properties of a generalized Beverton-Holt competition model with Allee effects

In this section, we explore basic dynamical properties of Model (7)-(8) and their implications with respect to the extinction and coexistence of two competing species. If Condition H1 is satisfied, Model (7)-(8) always has the following five boundary equilibria:

\[ E_0 = (0, 0), \; E_{x,0} = (A_1, 0), \; E_{x,0} = (K_1, 0), \; E_{0y_1} = (0, A_2) \; \text{and} \; E_{0y_2} = (0, K_2) \]

where \( A_i, i = 1, 2 \) is the Allee threshold of species \( i \) and \( K_i, i = 1, 2 \) is the carrying capacity of species \( i \). Note that \( 0 < A_i < K_i, i = 1, 2 \) is the carrying capacity of species \( i \). A routine analysis using the linearization principle shows that \( E_0, E_{x,0} \) and \( E_{0y_k} \) are locally asymptotically stable, thus these three boundary equilibria are also attractors for Model (7)-(8). This gives the main results of the following lemma:

**Lemma 3.1.** With respect the map defined by Model (7)-(8) the positive cone \( \mathbb{R}_+^2 \) is forward invariant and the rectangular region \([0, r_1] \times [0, r_2]\) attracts all solutions. If Condition H1 is satisfied, then Model (7)-(8) has five boundary equilibria \( E_0, E_{x,0}, E_{x,0}, E_{0y_1} \) and \( E_{0y_2} \) where \( E_0, E_{x,0} \) and \( E_{0y_k} \) are locally asymptotically stable and \( E_{x,0}, E_{0y_1}, E_{0y_2} \) are unstable. In addition, let \( X_1 = \{(x, 0) \in \mathbb{R}_+^2 \} \) and \( X_2 = \{(0, y) \in \mathbb{R}_+^2 \} \), then both \( X_i, i = 1, 2 \) are forward invariant sets for Model (7)-(8).

We can check that the set \([0, r_1] \times [0, r_2]\) is forward invariant and all orbits in the positive cone \( \mathbb{R}_+^2 \) lie in this set after one time step. The stability of the boundary can be obtained by straight forward calculations, i.e., calculating the eigenvalues of the Jacobian matrix evaluated at the boundary equilibria. Thus, we omit the details here. Also, we would like to point out that \( E_{x,0} \) and \( E_{0y_k} \) are saddle nodes: \( E_{x,0} \) is a saddle node with the unstable manifold lying on the x-axis and the stable manifold tangent to the vertical eigenvector emanating from \( E_{x,0} \); similarly, \( E_{0y_k} \) is a saddle node with the unstable manifold lying on the y-axis and the stable manifold tangent to the horizontal eigenvector emanating from \( E_{0y_k} \).

3.1. Competitive systems

Monotonicity properties have been used successfully to study the dynamical behavior of solutions to differential equations (e.g., see [Smith 1995] for an overview) and difference equations (e.g., Selgrade and Ziehe 1987; Dancer and Hess 1991; Hess and Lazer 1991; Smith 1998; Wang and Jiang 2001; Clark et al 2003). A competitive map is one type of monotone system.

To continue our study, we first define a partial order on \( \mathbb{R}^2 \) so that the positive cone in this new partial order is the fourth quadrant. Specifically, for \( u = (u_1, u_2), v = (v_1, v_2) \in \mathbb{R}_+^2 \), we say that \( u \leq_K v \) if \( u_1 \leq v_1 \) and \( u_2 \leq v_2 \). Two points \( u, v \in \mathbb{R}_+^2 \) are said to be related (or \( K \)-ordered) if \( u \leq_K v \) or \( v \leq_K u \). A strict inequality between points can be defined as \( u <_K v \) if \( u < v \) and \( u \neq v \). A stronger inequality can be defined as \( u <_K v \) if \( u < v \) and \( v <_K u \). A map \( T : \text{Int} \mathbb{R}_+^2 \rightarrow \text{Int} \mathbb{R}_+^2 \) is competitive (or \( K \)-order preserving) if \( u \leq_K v \) implies that \( T(u) \leq_K T(v) \) for all \( u, v \in \text{Int} \mathbb{R}_+^2 \). A map \( T : \text{Int} \mathbb{R}_+^2 \rightarrow \text{Int} \mathbb{R}_+^2 \) is strictly competitive (strongly competitive) if \( u <_K v \) implies that \( T(u) <_K T(v) \) and \( T(u) <_K T(v) \) for all \( u, v \in \text{Int} \mathbb{R}_+^2 \). Clearly, being related is an invariant under iteration of a strongly competitive map. Let \( J \) be the Jacobian matrix of a map \( T \), then \( J \) is \( K \)-positive (\( K \)-strongly positive) if its diagonal entries are nonnegative (positive) and its off-diagonal entries are nonpositive (negative).

**Theorem 3.1** (Competitive systems case 1). If \( \delta_1 \delta_2 \geq \delta_3 \delta_4 \), then Model (7)-(8) is strongly competitive and all orbits in the positive cone \( \mathbb{R}_+^2 \) converge to an equilibrium which can be on the boundary or the interior.

The proof of Theorem 3.1 uses the monotone properties of Model (7)-(8) (see the Appendix). Our result indicates that Model (7)-(8) has equilibrium dynamics (e.g., no nontrivial periodic orbits) whenever \( \delta_1 \delta_2 \geq \delta_3 \delta_4 \). Recall that \( \delta_i, i = 1, 2 \) measure the intensity of the intra-specific competition of species, and \( \delta_i, i = 3, 4 \) represents the inter-specific competition. Then we can define \( \delta_1 \delta_2 \) and \( \delta_3 \delta_4 \) as intensities of
the inter- and intra-specific competition, respectively. Then our result is that the dynamics equilibrate when the intensity of intra-specific competition exceeds that of inter-specific competition.

From the proof of Theorem 3.1, we can see that Model (7)-(8) is strictly competitive in $\mathbb{R}_+^2$ and is strongly competitive in $\text{Int} \mathbb{R}_+^2$ if $\delta_1 \delta_2 > \delta_3 \delta_4$ is satisfied. For the case that $\delta_1 \delta_2 < \delta_3 \delta_4$, we have the following theorem:

**Theorem 3.2** (Competitive systems case 2). Assume that $\delta_1 \delta_2 < \delta_3 \delta_4$. If

$$r_1 < \left( \frac{\delta_1 \delta_2}{b_2[\delta_3 \delta_4 - \delta_1 \delta_2]} \right)^{1/\delta_4} \text{ or } r_2 < \left( \frac{\delta_1 \delta_2}{b_1[\delta_3 \delta_4 - \delta_1 \delta_2]} \right)^{1/\delta_3},$$

then every orbit of Model (7)-(8) converges to an equilibrium which can be on the boundary or the interior.

The proof of Theorem 3.2 uses the monotone properties of Model (7)-(8) as well as the properties of non-invertible maps. A proof appears in the Appendix. In the case that $\delta_1 \delta_2 < \delta_3 \delta_4$, Theorem 3.2 indicates that the dynamics of (7)-(8) can still have equilibrium dynamics, as in the case when $\delta_1 \delta_2 \geq \delta_3 \delta_4$ (Theorem 3.1) , provided the intrinsic growth rates of both species are not too large. However, when one or both growth rates are large, Model (7)-(8) can have non-equilibrium attractors as shown by results of Terescká (1996) and Smith (1998). For example, if we let $\delta_1 = \delta_2 = \delta$, $\delta_3 = \delta_4 = d$, $r_1 = r_2$, $b_1 = b_2$, then the dynamics of (7)-(8) on the invariant manifold $\Omega_{x=y} = \{(x, y) \in \mathbb{R}_+^2 : x = y\}$ can be reduced to Model (6) which can have complicated dynamics. See Figure 2-2(b) as examples for different dynamics on $\Omega_{x=y}$ when $\delta = 2; d = 5; b = 0.1$ and $r = 7.5$ (Figure 2) and $r = 25$ (Figure 2(b)).

3.2. Basins of attraction of no-coexistence equilibria

Assume that Condition **H1** is satisfied for Model (7)-(8). We define the sets:

$$O_0 = [0, A_1] \times [0, A_2], \quad O_{ex} = \{(x, y) \in \mathbb{R}_+^2 : x < A_1\} \text{ and } O_{ey} = \{(x, y) \in \mathbb{R}_+^2 : y < A_2\}$$

and make the following assumptions:

**H2:** $\delta_1 > 1$ and $r_1 > r_{crit}^{a_1}$ where $r_{crit}^{a_1} = (a_1)^{1/\delta_1} \delta_1 (\delta_1 - 1)^{-\frac{1}{\delta_1} - 1}$ and $a_1 = 1 + b_1(A_2)^{\delta_3}$.

**H3:** $\delta_2 > 1$ and $r_2 > r_{crit}^{a_2}$ where $r_{crit}^{a_2} = (a_2)^{1/\delta_2} \delta_2 (\delta_2 - 1)^{-\frac{1}{\delta_2} - 1}$ and $a_2 = 1 + b_2(A_1)^{\delta_3}$.

The conditions that **H2** or **H3** impose on $\delta$ are the same as those in **H1**. **H2** indicates that the first species has a growth rate $r_1$ that is large enough that the single species model for the first species still has two positive equilibria if the density of second species is held fixed at its Allee threshold $A_2$. Condition **H3** indicates something similar with the roles of the species reversed. If the single species Model (6) satisfies Condition **H2** when $r = r_1, a = a_1, b = b_1, \delta = \delta_1, d = \delta_3$, then according to Corollary 2.1, it has two interior equilibria $A_1^{a_1}$ and $K_i^{a_1}$ where $A_1^{a_1}$ is the Allee threshold and $K_i^{a_1}$ is the carrying capacity. Similarly, if Model (6) satisfies Condition **H3** when $r = r_2, a = a_2, b = b_2, \delta = \delta_2, d = \delta_4$ , then it has two interior equilibria $A_2^{a_2}$ and $K_2^{a_2}$ where $A_2^{a_2}$ is the Allee threshold and $K_2^{a_2}$ is the carrying capacity. Define

$$O_x = \{(x, y) \in \mathbb{R}_+^2 : x > A_1^{a_1}, y < A_2\} \text{ and } O_y = \{(x, y) \in \mathbb{R}_+^2 : x < A_2, y > A_2^{a_2}\}.$$

We define a boundary attractor as an attractor that resides on the boundary, i.e., orbits that approach the boundary of the cone. The extinction equilibrium is an example of boundary attractors.

**Theorem 3.3** (Basins of attractions of boundary attractors 1). Assume the competition Model (7)-(8) satisfies Condition **H1**. Then

- For any initial value in $O_{ex}$, we have $\lim_{t \to \infty} x_t = 0$. 

9
\begin{itemize}
  \item For any initial value in $O_{xy}$, we have $\lim_{t \to \infty} y_t = 0$.
  \item For any initial value in $O_0$, we have $\lim_{t \to \infty} (x_t, y_t) = E_0$.
\end{itemize}

If the single species Model (4) satisfies Condition H2, then for any initial value in $O_x$, we have $\lim_{t \to \infty} (x_t, y_t) = E_{xk_1}$.

If the single species Model (4) satisfies Condition H3, then for any initial value in $O_y$, we have $\lim_{t \to \infty} (x_t, y_t) = E_{0y_{k_2}}$.

Theorem 3.3 (see the proof in the Appendix) provides an approximation of the boundary attractor’s basins of attractions for Model (7)-(8) when each species suffers from contest competition and strong Allee effects. In the absence of other species, each species’ extinction region is $[0, A_i]$. In the presence of other species, the extinction region of a species becomes larger due to the inter-specific competition. Thus introducing a competitor into a resident species that is subject to contest competition and strong Allee effects can make the resident species prone to extinction at their low densities. In order to maintain species $x$’s population, species $x$’s initial condition should be larger than $A_1^{q_1} > A_1$ while species $y$’s initial condition should be less than $A_2$. However, excluding species $y$ does not always seem necessary to maintain species $x$ since coexistence of both species $x$ and $y$ are possible at their high densities under proper conditions. This has been explored in Theorem 3.5. In addition, Theorem 3.3 implies that the basins of attractions of the boundary attractors $E_{xk_1}$ and $E_{0y_{k_2}}$ are unbounded (see Figure 5(d), 5(e) and 5(f)).

Define
\[
O^l_{ex} = \bigcup_{k>0} \{ (x, kx) \in \text{Int} \mathbb{R}_+^2 : x > \left( \frac{r_1-A_1}{b_1k+a_1} \right)^{\frac{1}{r_1-r_1}} \},
\]
\[
O^l_{ey} = \bigcup_{k>0} \{ (ky, y) \in \text{Int} \mathbb{R}_+^2 : y > \left( \frac{r_2-A_2}{b_2k+a_1} \right)^{\frac{1}{r_2-r_2}} \},
\]

and let $O^l_0 = O^l_{ex} \cap O^l_{ey}$. Then we have the following theorem:

**Theorem 3.4** (Basins of attractions of boundary attractors II). Assume that Model (7)-(8) satisfies Condition H1.

- If $\delta_3 > \delta_1$, then for any initial value in $O_{ex} \cup O^l_{ex}$, we have $\lim_{t \to \infty} x_t = 0$.
- If $\delta_4 > \delta_2$, then for any initial value in $O_{ey} \cup O^l_{ey}$, we have $\lim_{t \to \infty} y_t = 0$.
- If $\delta_3 > \delta_1$ and $\delta_4 > \delta_2$, then for any initial value in $O_0 \cup O^l_0$, we have $\lim_{t \to \infty} (x_t, y_t) = E_0$.

The detailed proof of Theorem 3.4 is provided in the Appendix. This theorem indicates that if a species’ relative competition degree is less than 1 (i.e., $\delta_3 > \delta_1$ or $\delta_4 > \delta_2$), then its extinction region (i.e., the initial conditions that lead to the extinction of two species) consists of two distinct components, of which one is stated in Theorem 3.3 and the other one is the area where the two competitors’ population densities are large enough. This phenomenon is a typical property of non-invertible maps which is caused by the large degree of the inter-specific competition, i.e., $\delta_3 > \delta_1$ or $\delta_4 > \delta_2$. Theorem 3.4 also indicates that the basins of attractions of $E_0$ may be unbounded. In fact, the basin of attraction of $E_0$ is a connected and unbounded region when there is no interior equilibrium (see Figure 5(a) and 5(d)). The basin of attraction of $E_0$ consists of two parts when there is an interior equilibrium: one part is a bounded region including the neighborhood of $E_0$ while the other part is a connected unbounded region including very large initial values of both species (see Figure 5(e) and 5(f)).
3.3. Persistent equilibria

Assume that Model (7)-(8) satisfies Condition H1, then according to Theorem 3.3, it always has three boundary attractors. This suggests that the coexistence of two species is possible only if there exists an interior equilibrium. We are going to prove the following theorem regarding the number of interior equilibria.

**Theorem 3.5 (Interior equilibria).** Assume that Model (7)-(8) satisfies Condition H1. Let

\[ F_1(x) = \left( \frac{r_1 x^{d_1-1} - x^{d_1} - 1}{b_1} \right)^{1/d_1} \quad \text{and} \quad F_2(y) = \left( \frac{r_2 y^{d_2-1} - y^{d_2} - 1}{b_2} \right)^{1/d_2}, \]

then we have the following statements:

- If \( F_1(x_c) < A_2 \) or \( F_2(y_c) < A_1 \), then Model (7)-(8) has no interior equilibrium.
- If \( A_2 < F_1(x_c) < K_2, K_1 < F_2(y_c) \) or \( A_1 < F_2(y_c) < K_1, K_2 < F_1(x_c) \), then Model (7)-(8) can have zero, one two, three, or four interior equilibria depending on the details of how large \( F_1(x_c) \) is.
- If \( F_1(x_c) > K_2 \), then Model (7)-(8) has four interior equilibria.

where \( x_c = \frac{r_1 (d_1-1)}{d_1} \) and \( y_c = \frac{r_2 (d_2-1)}{d_2} \).

See Figure 3(a)-3(d) regarding the generic nullclines of Model (7)-(8). Theorem 3.5 (its proof stated in the Appendix) gives us two scenarios when Model (7)-(8) has interior equilibria where coexistence occurs only if Model (7)-(8) has four interior equilibria (see Figure 5(c) and Figure 5(f)). Sufficient conditions guaranteeing four interior equilibria is that \( F_1(x_c) > K_2 \) and \( F_2(y_c) > K_1 \), i.e.

\[ x_c < \frac{r_1 x_c^{d_1}}{1 + x_c^{d_1} + b_1 K_2^{d_1}} \quad \text{and} \quad y_c < \frac{r_2 y_c^{d_2}}{1 + y_c^{d_2} + b_2 K_1^{d_2}}, \]

which indicates that any initial condition in \([x_c, K_1] \times [y_c, K_2]\) lead to a locally asymptotically stable interior equilibrium according to the monotonicity of the system. Biologically, this implies that both species are able to persist under proper initial conditions if \( F_1(x_c) > K_2 \) and \( F_2(y_c) > K_1 \) holds. In the next subsection, we explore the local stability of a symmetric system.

3.4. A symmetric competition model with Allee effects

In order to obtain more insights on the coexistence of two competing species, we focus on a symmetric case of (7)-(8) where \( r_1 = r_2 = r, b_1 = b_2 = b, \delta_1 = \delta_2 = \delta, \delta_3 = \delta_4 = d \) which gives the following model

\[ x_{t+1} = \frac{r x_t^\delta}{1 + x_t^\delta + b y_t^\delta}, \]
\[ y_{t+1} = \frac{r y_t^\delta}{1 + y_t^\delta + b x_t^\delta}. \]

Understanding the dynamics of (9)-(10) also can help us obtain a better understanding of the dynamics of asymmetric cases due to the robust property (known from numerical simulations) of our system (7)-(8).

We can verify that (9)-(10) is reduced to the 1-D model described by (6) if \( x_0 = y_0 \), i.e., the manifold defined by \( \Omega_{y=x} = \{(x,y) \in \mathbb{R}^2_+ : x = y\} \) is invariant. According to Theorem 2.1, Model (9)-(10) has at least two symmetric equilibria \((A,A)\) and \((K,K)\) such that 0 < \( A < \left( \frac{r(d-\delta)}{\delta} \right)^{1/d} < K \) if

\[ d > \delta > 1 \quad \text{and} \quad r > r_{crit} = \left( \frac{\delta}{b(d-\delta)} \right)^{(1-\delta)/d} \left[ \frac{d}{d-\delta} + \left( \frac{\delta}{b(d-\delta)} \right)^{\delta/d} \right]. \]

Now we have the following theorem regarding the stability of \((K,K)\).
Figure 3: Schematic nullclines when Model (7)-(8) has zero, two, four interior equilibria. The red curve is $F_1(x) = \left( \frac{r_1 x_1^{\delta_1-1} - x_1^{\delta_1-1}}{\delta_1^{\delta_1}} \right)^{1/\delta_1}$ where its maximum $F_1(x_c)$ occurs at $x_c = \frac{r_1 (\delta_1-1)}{\delta_1}$. The blue curve is $F_2(y) = \left( \frac{r_2 y_2^{\delta_2-1} - y_2^{\delta_2-1}}{\delta_2^{\delta_2}} \right)^{1/\delta_2}$ where its maximum $F_2(y_c)$ occurs at $y_c = \frac{r_2 (\delta_2-1)}{\delta_2}$.

**Theorem 3.6 (Stability of the symmetric equilibrium).** Assume that Model (9)-(10) satisfies the inequalities (11). Then (9)-(10) has at least two symmetric equilibria $(A, A)$ and $(K, K)$ such that $0 < A < \left( \frac{r_1 (\delta_1-1)}{\delta_1} \right)^{1/d} < K$. Moreover, the symmetric interior equilibrium $(x^*, x^*)$ is locally asymptotically stable if

$$\left| \frac{\delta + b(\delta - d) (x^*)^d}{1 + (x^*)^d + b(x^*)^d} \right| < 1 \quad \text{and} \quad \frac{\delta + b(\delta + d) (x^*)^d}{1 + (x^*)^d + b(x^*)^d} < 1. \quad (12)$$

While the symmetric interior equilibrium $(x, x)$ is unstable if

$$\left| \frac{\delta + b(\delta - d) (x^*)^d}{1 + (x^*)^d + b(x^*)^d} \right| > 1 \quad \text{or} \quad \frac{\delta + b(\delta + d) (x^*)^d}{1 + (x^*)^d + b(x^*)^d} > 1. \quad (13)$$

Theorem 3.6 indicates that it is impossible for the interior equilibrium of the symmetric model (9)-(10) to have Neimark-Sacker bifurcation from the invariant set $\Omega_{x=y}$ since the eigenvalue that determines the points moving towards or away from $\Omega_{x=y}$ is always positive (see the detailed proof in the Appendix). This suggests that (9)-(10) may have relatively simple dynamics.
In the absence of species $y$, i.e., $y = 0$, (14)-(15) is reduced to a single species model (2) when $r = r_1$ and $\delta = 2$, i.e.,

$$x_{t+1} = \frac{r_1 x_t^2}{1 + x_t^2 + b_1 y_t^{\delta_t}}, \quad y_{t+1} = \frac{r_2 y_t^2}{1 + y_t^2 + b_2 x_t^{\delta_t}}. \tag{15}$$

Model (16) is a well-known fisheries model when fish is subject to contest intra-specific competition and strong Allee effects. The dynamics of (16) is very simple: 1. If $r_1 < 2$, then (16) converges to 0 for any $x_0 > 0$. 2. If $r_1 > 2$, then (16) has two interior equilibria $A_1$ and $K_1$ where

$$A_1 = \frac{r_1 - \sqrt{r_1^2 - 4}}{2} \quad \text{and} \quad K_1 = \frac{r_1 + \sqrt{r_1^2 - 4}}{2}.$$
such that (16) converges to 0 if \( x_0 < A_1 \) while (16) converges to \( K_1 \) if \( x_0 > A_1 \).

Similarly, in the absence of species \( x \), i.e., \( x_0 = 0 \), (14)-(15) is reduced to a single species model (2) for the case that \( r = r_1 \) and \( \delta = 2 \), i.e.,

\[
y_{t+1} = \frac{r_2 y_t^2}{1 + y_t^2}
\]

where it also has two interior equilibria \( A_2 \) and \( K_2 \) where

\[
A_2 = \frac{r_2 - \sqrt{r_2^2 - 4}}{2} \quad \text{and} \quad K_2 = \frac{r_2 + \sqrt{r_2^2 - 4}}{2}.
\]

Due to our interests, we focus on the case that \( r_i > 2, i = 1, 2 \) for Model (14)-(15). Then apply Theorem 3.1, Theorem 3.3, Theorem 3.2, Theorem 3.4 and Theorem 3.5, we obtain the following corollary regarding the dynamics of (14)-(15):

**Corollary 4.1.** Assume that \( r_i > 2 \). Define

\[
r_{\text{crit}}^{a_1} = \sqrt{2} \sqrt{1 + b_1 \left( \frac{r_2 - \sqrt{r_2^2 - 4}}{2} \right)^{1/\delta_3}} \quad \text{and} \quad r_{\text{crit}}^{a_2} = \sqrt{2} \sqrt{1 + b_2 \left( \frac{r_2 - \sqrt{r_2^2 - 4}}{2} \right)^{1/\delta_4}}.
\]

Then the following statements are true:

1. If \( \delta_3 \delta_4 \leq 4 \), then every orbit of Model (14)-(15) with any initial condition in \( \mathbb{R}_+^2 \) converges to one of its equilibria.

2. If \( \delta_3 \delta_4 > 4 \) and

\[
r_1 \left( \frac{4}{b_2 [\delta_3 \delta_4 - 4]} \right)^{1/\delta_3} \quad \text{or} \quad r_2 \left( \frac{4}{b_2 [\delta_3 \delta_4 - 4]} \right)^{1/\delta_4},
\]

then every orbit of Model (14)-(15) with any initial condition in \( \mathbb{R}_+^2 \) converges to one of its equilibria.

3. Model (14)-(15) always has three boundary attractors \( E_0, E_{x_1,0}, E_{0y_0} \) where

\[
E_0 = (0, 0), \quad E_{x_1,0} = \left( \frac{r_1 + \sqrt{r_1^2 - 4}}{2}, 0 \right) \quad \text{and} \quad E_{0y_0} = \left( 0, \frac{r_2 + \sqrt{r_2^2 - 4}}{2} \right).
\]

Moreover,

- For any initial value in \( O_{xx} \), we have \( \lim_{t \to \infty} x_t = 0 \). If \( \delta_3 > 2 \), then for any initial value in \( O_{xx} \cup O_{xx}^l \), we have \( \lim_{t \to \infty} x_t = 0 \).
- For any initial value taken in \( O_{xy} \), we have \( \lim_{t \to \infty} y_t = 0 \). If \( \delta_4 > 2 \), then for any initial value in \( O_{xy} \cup O_{xy}^b \), we have \( \lim_{t \to \infty} y_t = 0 \).
- For any initial value taken in \( O_0 \), we have \( \lim_{t \to \infty} (x_t, y_t) = E_0 \). If \( \delta_3 > 2 \) and \( \delta_4 > 2 \), then for any initial value in \( O_0 \cup O_0^b \), we have \( \lim_{t \to \infty} (x_t, y_t) = E_0 \).
- If \( r_1 > r_{\text{crit}}^{a_1} \), then for any initial value in \( O_x \), we have

\[
\lim_{t \to \infty} (x_t, y_t) = E_{x_1,0}.
\]

If \( r_2 > r_{\text{crit}}^{a_2} \), then for any initial value in \( O_y \), we have

\[
\lim_{t \to \infty} (x_t, y_t) = E_{0y_0}.
\]
4. Model (14)-(15) has no interior equilibrium if
\[
\left( \frac{r_1^2/4 - 1}{b_1} \right)^{1/\delta_1} < \frac{r_2 - \sqrt{r_2^2 - 4}}{2} \quad \text{or} \quad \left( \frac{r_2^2/4 - 1}{b_2} \right)^{1/\delta_2} < \frac{r_1 - \sqrt{r_1^2 - 4}}{2}.
\]

Model (7)-(8) has four interior equilibria if
\[
\left( \frac{r_2^2/4 - 1}{b_1} \right)^{1/\delta_1} > \frac{r_2 + \sqrt{r_2^2 - 4}}{2} \quad \text{and} \quad \left( \frac{r_2^2/4 - 1}{b_2} \right)^{1/\delta_2} > \frac{r_1 + \sqrt{r_1^2 - 4}}{2}.
\]

The corollary above does not give us information on the dynamic patterns of the system. Due to the complexity of the model, we use numerical simulations to investigate their dynamical patterns. According to simulations, we summarize its dynamical patterns as follows:

- **No interior equilibrium:** When Model (14)-(15) has no interior equilibrium (see Figure 5(a)), it has exactly three boundary attractors, i.e., (0,0), \((x_2,0)\), and \((0,y_2)\), and no interior attractor. The basins of attractions of these three attractors are unbounded (shown in Figure 5(d)) where the extinction area (i.e., basins of attractions of \(E_0 = (0,0)\)) is an open and unbounded region in red. This implies that the inter-specific competition makes both two competing species prone to extinction.

- **Two interior equilibrium:** When Model (14)-(15) has two interior equilibrium (see Figure 5(b)), it has exactly three boundary attractors, i.e., (0,0), \((x_2,0)\), and \((0,y_2)\), and no interior attractor. The basins of attractions of these three boundary attractors are unbounded (shown in Figure 5(e)). The basins of attractions of \((x_2,0)\) and \((0,y_2)\) are connected and unbounded while the basins of attractions of \(E_0\) consists of a bounded-connected and an unbounded-connected region.

- **Four interior equilibrium:** This is the only case when Model (14)-(15) has an interior attractor (i.e., the coexistence of two species). When Model (14)-(15) has four interior equilibria (see Figure 5(c)), it has four attractors of which three are boundary attractors: (0,0), \((x_2,0)\), and \((0,y_2)\), and one is an interior attractor \((x^*, y^*)\) whose basins of attractions is a bounded and connected region. The basins of attractions of these four attractors are shown in Figure 5(f) where the features of basins of attractions of boundary attractors are the same as the two interior equilibria case.

Numerical simulations suggest that the observations above for Model (14)-(15) should be able to apply to a general model (7)-(8). In addition, we would like to point out that Model (7)-(8) can have coexistence of two species only if it has four interior equilibria.

5. Discussion

Competition is an important ecological process which, in the short run, can cause a reduction in the number of species living within an area, by preventing very similar species from co-occurring; while in the long term, is likely to increase species diversity, by acting as a force for specialization and divergence. Competition can vary between two extreme forms: contest v.s. scramble. The Allee effect is another important ecological process that leads to a positive correlation of the per capita growth rate of a species and low population densities. The interplay of the strong strength of Allee effects and negative density dependent ecological factors such as intra-specific competition can result in a critical threshold level of population density, called Allee threshold, below which species goes to extinction; while above which species may persist. This is referred to as a strong Allee effect. When there is no such threshold, such low density positive feedback effects are referred to as weak Allee effects. Many species in nature are subject to both Allee effects and competition. The combinations of Allee effects and different type of competition can generate different dynamical outcomes, especially with regard to the coexistence of
species. Allee effects in competition models can have a significant impact on the predictions of models about the consequent diversity and community structure (Chesson and Ellner 1989; Hopf et al 1993). Allee effects impose a cost of rarity (Mechanism R). When communities of organisms are subject to a cost of rarity imposed by Allee effects, they should be comprised of distinct species with differences in resource use that are greater than expected by chance (Hopf et al 1993).

Kang and Yakubu (2011) and Kang (2013) studied the population dynamics of a two competing species model where each species suffers from Allee effects and scramble competition. They showed that weak Allee effects may promote the permanence of two competing species at their low densities. The biological explanation for this is that weak Allee effects decrease the fitness of resident species so that the other species is able to invade at its low densities. Kang (2013) showed that scramble inter-specific competition, under proper conditions, can save two competing species from essential extinctions due to strong Allee effects at their high population densities. The biological explanation for this is that scramble competition can bring the current high population density to a lower population density but is above the Allee threshold in the next season with the consequence that both competing species are able to persist. To extend the study by Kang and Yakubu (2011) and Kang (2013), this article studies the population dynamics of a generalized Beverton-Holt two species competition model when each species has strong Allee effects, with the goal of exploring the coexistence and the competitive exclusion of two competing species.
5.1. **Two dimensional strong Allee effects of symmetric competition models**

The main purpose of this subsection is to compare dynamics of scramble competition models with Allee effects to dynamics of contest competition models with Allee effects. Should we keep this section? Or maybe we can have a better way to present this part?

Adopting the definition of Allee effects for single species, we are able to define Allee effects of a symmetric two species competition model that can be represented as

\[
\begin{align*}
x_{t+1} &= F(x_t, y_t) = x_t f(x_t, y_t) \\
y_{t+1} &= F(y_t, x_t) = y_t f(y_t, x_t).
\end{align*}
\]  

(18)  

where \( \frac{\partial f(x, y)}{\partial y} < 0 \). Then we say two dimensional system (18)-(19) has **two dimensional strong Allee effects** if both \( f(x, 0) \) and \( f(x, x) \) satisfy Condition A1, A2, A3. Model (9)-(9) subject to inequalities (11) provides an example of two competing species suffering from **contest competition and two dimensional strong Allee effects**. The ecological examples when two competing species suffering from **scramble competition and two dimensional strong Allee effects** are the following two examples:

**Model I:** Scramble competition with strong Allee effects due to mating limitations

\[
\begin{align*}
x_{t+1} &= x_t e^{r(1-x_t) - a y_t - \frac{a y_t}{r + a x_t}} \\
y_{t+1} &= y_t e^{r(1-y_t) - a x_t - \frac{a x_t}{r + a y_t}}
\end{align*}
\]

(20)  

(21)

where \( r \) represent the intrinsic growth rates as well as intra-specific competition coefficient; \( b \) represent the product of an individual’s searching efficiency and the carrying capacities and \( a \) represents the inter-specific competition coefficient. If

\[
\frac{e^{r-1}}{r + a} > \frac{1}{r + a} + \frac{1}{b},
\]

then **Model I** has **two dimensional strong Allee effects**.

**Model II:** Scramble competition with strong Allee effects due to predation saturations

\[
\begin{align*}
x_{t+1} &= x_t e^{r(1-x_t) - a y_t - \frac{m}{r + b x_t}} \\
y_{t+1} &= y_t e^{r(1-y_t) - a x_t - \frac{m}{r + b y_t}}
\end{align*}
\]

(22)  

(23)

where \( r \) represents the intrinsic growth rates as well as intra-specific competition coefficient; \( m \) represents predation intensities; \( b \) represent the product of the proportional to the handling time and the carrying capacities and \( a \) represents the inter-specific competition coefficient. If

\[
r < m < \frac{(br + r + a)^2}{4b(a + r)} \text{ and } b > 1 + a/r,
\]

then **Model I** has **two dimensional strong Allee effects**.

Kang and Yakubu (2011) and Kang (2013) have studied the detailed dynamics of **Model I & II** introduced above. By comparing our results to their study on a two competing species model where each species is subject to scramble competition and strong Allee effects (i.e., **Model I & II**), we are able to obtain some generic dynamical features of a two-species competition model subject to strong Allee effects and the different dynamical outcomes due to different types of competition introduced in the models as follows:

**Generic dynamic features of scramble v.s. contest competition models with strong Allee effects:**
1. Both contest and scramble competition models with strong Allee effects can have either tri-stability (i.e., three boundary attractors $E_0, E_{x,k}, E_{0,y}$) or four attractors (i.e., three boundary attractors plus an interior attractor) depending on certain conditions.

2. The coexistence of two competing species is possible only if the system has at least four interior equilibria.

3. Both models can exhibit two dimensional strong Allee effects in the symmetric case.

4. The basins of attractions of $E_0$ are unbounded, which suggests that two competing species are not able to coexist if their population densities are too low or too high.

**Different dynamical outcomes of scramble v.s. contest competition models with strong Allee effects:**

1. In the absence of strong Allee effects, our generalized Beverton-Holt two species (representing contest competition) model can have only extinction attractor, namely $E_0$, when the growth rates are too small. In the presence of strong Allee effects, the proposed Beverton-Holt contest competition model always has three boundary attractors $E_0, E_{x=k}, E_{0,y}$. The two-species Ricker models (representing scramble competition) subject to strong Allee effects can have either one (i.e., extinction of two species) or three boundary attractors where the extinction is caused by strong Allee effects (i.e., each species has essential extinction at its single state).

2. Scramble competition models with strong Allee effects can promote the coexistence of two competing species at their high densities under certain conditions. This is not the case for contest competition models with strong Allee effects.

3. Scramble competition models can have complicated structures of attractors (e.g., chaos, essential extinctions) while the contest competition model may have relative simple dynamics (e.g., from performed simulations, we only observed locally asymptotically stable equilibria as attractors).

4. The basins of attractions of attractors where a single species persists are bounded and may consist of different distinct parts for scramble competition models (see black and cyan areas in Figure 3&4 in Kang 2013) while the basins of attractions of attractors where a single species persists are unbounded and connected for contest competition models (see black and cyan areas in Figure 5(d), 5(e) and 5(f)).

The discussion above regarding contest v.s. scramble competition models with strong Allee effects are based on our study on the generalized Beverton-Holt competition model (7)-(8) and Ricker-type competition models with Allee effects studied in Kang and Yakubu (2011) and Kang (2013). The comparison may provide us useful insights of general two species competition models where each species has strong Allee effects in its single state. However, in order to obtain more general results, we need to classify the different types of intra- and inter-specific competition rigorously and study how their combinations with Allee effects lead to different dynamical outcomes. For example, the following example can be considered as a combination of contest inter-specific competition and scramble intra-specific competition subject to Allee effects:

\[
\begin{align*}
x_{t+1} &= x_t e^{r_1(1-x_t)} I_t(x_t) \\
y_{t+1} &= y_t e^{r_2(1-y_t)} I_t(y_t)
\end{align*}
\]

where $I_t, i = x, y$ represents positive density dependence that can lead to Allee effects and $c_i, i = 1, 2$ are relatively inter-specific competition coefficients. This could be our future research project.
5.2. Conclusion

In this article, we propose a generalized Beverton-Holt competition model to investigate how the interactions of Allee effects and contest competition affect the species’s establishment and extinction. More precisely, we addressed following questions: 1. What are the population dynamic outcomes of a two species competitive interactions when each species suffers from both strong Allee effects and contest competition? 2. How does contest competition combined with strong Allee effects affect species’ persistence and extinction? 3. What are the generic dynamical features of population models subject to strong Allee effects and competition? Here, we summarize our main results from the study as follows:

1. Theorem 3.1 and Theorem 3.2 reveal that our proposed contest competition model with Allee effects has equilibrium dynamics, provided that the intensity of intra-specific competition intensity either exceeds that of inter-specific competition or is less than that of inter-specific competition but the maximum intrinsic growth rate of one species is not too large. This partially answers the first question.

2. Theorem 3.3 and Theorem 3.4 provide approximations of basins to the attractions of boundary attractors (i.e., the initial conditions that lead to the extinction of one or both species). This indicates that the inter-specific competition can make a species prone to extinction if it suffers from both strong Allee effects and contest competition; moreover, the situation worsens if the relative competition degree is less than 1. In addition, Theorem 3.5, 3.6 combined with numerical simulations suggest that decreasing the values of the inter-specific competition coefficient and degree can promote the coexistence of two species. These results can answer the second question.

3. The third question partially answered by comparing with dynamics of two species scramble competition models subject to strong Allee effects in Kang (2013) to our Theorem 3.5 (combined with numerical simulations). The comparison suggests the following. (i) Both contest and scramble competition models can have either three boundary attractors or four attractors with only one interior attractor. The extinction equilibrium can be a unique attractor for the scramble competition model, an occurrence that is due to strong Allee effects. (ii) Scramble competition models represented by Ricker-type models can have more complicated interior attractors than do contest competition models. (iii) The synergy of scramble competition and strong (weak) Allee effects can promote the coexistence of two species at high (low) densities.

Our study combined with the results from Kang and Yakubo (2011) and Kang (2013) provide useful insights into how Allee effects interact with different forms of competition to have an impact on the persistence and extinction of species. One direct application of these results is that we may be able, under certain conditions, to save species from essential extinction (i.e., extinction occurs for all initial conditions excluding a measure zero set) due to strong Allee effects by introducing another competing species.

It would be interesting to investigate the following questions: 1. What are the population dynamics of two competing species when one or both experience different forms of competition in their different life stages as well as Allee effects? 2. What are necessary conditions for a general two species population model to generate two dimensional strong Allee effects? 3. How can we predict more precise initial conditions that lead to the extinction and the coexistence of two species?

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Appendix

Proof of Proposition 2.1

Proof. First, it is easy to see that Model (2) is positively invariant and bounded in $\mathbb{R}_+$. Notice that

$$H(0) = 0, \quad \frac{dH(u)}{du} = \frac{ru \delta u^{\delta - 1}}{(1 + u^\delta)^2} > 0 \quad \text{and} \quad \lim_{u \to \infty} H(u) = r > 0,$$

we can apply Proposition 2.1 of Kang and Dieter (2011) to obtain the following conclusion: Assume that $u = H(u)$ has $n + 1$ consecutive, distinct and non-degenerate solutions $\bar{u}^i, i = 0, 1, ..., n$ with the following property

$$0 = \bar{u}^0 < \bar{u}^1 < \cdots < \bar{u}^n.$$

then the even $\bar{u}^i, i \geq 2$ is locally asymptotical stable with $(\bar{u}^{i-1}, \bar{u}^{i+1})$ as its basin of attraction when $\bar{u}^0 = 0$ is locally asymptotical stable (i.e., $\frac{dH(u)}{du} |_{u=0} < 1$) and the odd $\bar{u}^i, i \geq 1$ is locally asymptotical stable with $(\bar{u}^{i-1}, \bar{u}^{i+1})$ as its basin of attraction when $\bar{u}^0 = 0$ is unstable (i.e., $\frac{dH(u)}{du} |_{u=0} > 1$).

According $\frac{dH(u)}{du} = \frac{ru \delta u^{\delta - 1}}{(1 + u^\delta)^2}$, we can conclude that $\bar{u}^0 = 0$ is unstable if $\delta < 1$ and $\bar{u}^0 = 0$ is locally asymptotical stable if $\delta > 1$. Therefore, we have the following statements: i) If $\delta \in (0, 1)$ and Model (2) has two non-negative equilibria $0, K$, then $0$ is an unstable and and $K$ is a stable positive equilibrium that attracts all points in $(0, \infty)$. ii) If $\delta > 1$ and the only equilibrium of Model (2) is $0$, then $0$ is globally stable. iii) If $\delta > 1$ and Model (2) has three non-negative distinct equilibria: $0, A$ and $K$ such that $0 < A < K$, then $0$ equilibrium is locally asymptotical stable with the basin of attraction $(0, A); A$ is unstable (repellor), while $K$ is locally asymptotical stable with the basin of attraction $(A, \infty)$.

Now we only need to derive the conditions when (2) has only one, two or three equilibria. As we know, $0$ is always an equilibrium of (2). If $u^*$ is a nontrivial positive equilibrium of (2), then we have $h(u^*) = 1$, i.e., $u^*$ is a positive root of $F(u) = u^\delta - ru^{\delta - 1} + 1$. If $\delta < 1$, then we have

$$\lim_{u \to 0^+} F(u) = -\infty, \quad \lim_{u \to \infty} F(u) = \infty \quad \text{and} \quad \frac{dF}{du} = \delta u^{\delta - 1} - r(\delta - 1)u^{\delta - 2} > 0.$$

This implies that $F(u) = u$ has a unique positive solution $u^*$ and

$$\frac{dH}{du} |_{u=u^*} = \frac{\delta (u^*)^{\delta - 1}}{(1 + (u^*)^\delta)^2} = \frac{\delta}{1 + (u^*)^\delta} < \delta < 1.$$

Therefore, if $\delta \in (0, 1)$, Model (2) has only two non-negative equilibria $0, K$ where $0$ is an unstable and and $K$ is a stable positive equilibrium that attracts all points in $(0, \infty)$.

If $\delta > 1$, then $\frac{dF}{du} = \delta u^{\delta - 1} - r(\delta - 1)u^{\delta - 2} = u^{\delta - 2}[\delta u - r(\delta - 1)] = 0$ when $u = u_c = \frac{r(\delta - 1)}{\delta}$. Notice that

$$F(0) = 1 > 0, \quad \frac{dF}{du} |_{u<u_c} < 0 \quad \text{and} \quad \frac{dF}{du} |_{u>u_c} > 0,$$

thus $F(u) = 0$ (i.e., $h(u) = 1$) have no positive root if

$$F(u_c) > 0 \Rightarrow h(u_c) < 1 \Rightarrow \frac{ru_c^{\delta - 1}}{1 + u_c^\delta} = \frac{r \left(\frac{r(\delta - 1)}{\delta}\right)^{\delta - 1}}{1 + \left(\frac{r(\delta - 1)}{\delta}\right)^\delta} < 1 \Rightarrow r > r_{crit} = \delta(\delta - 1)^{\frac{1}{\delta}}$$

and $F(u) = 0$ have two non-negative distinct equilibria $0 < A < u_c < K$ if

$$F(u_c) < 0 \Rightarrow h(u_c) > 1 \Rightarrow \frac{ru_c^{\delta - 1}}{1 + u_c^\delta} = \frac{r \left(\frac{r(\delta - 1)}{\delta}\right)^{\delta - 1}}{1 + \left(\frac{r(\delta - 1)}{\delta}\right)^\delta} > 1 \Rightarrow r > r_{crit} = \delta(\delta - 1)^{\frac{1}{\delta}}.$$

Therefore the statements of Proposition 2.1 hold.
Proof of Theorem 2.1

Proof. First, we can easily verify that Model (6) is positively invariant and bounded in $\mathbb{R}_+$. If $u^*$ is a positive equilibrium of (6), then it is a positive root of $F(u) = bu^d + u^\delta - r u^{\delta-1} + 1$. Since

$$F'(u) = bd u^{d-1} + \delta u^{\delta-1} - r(\delta - 1) u^{\delta-2} = u^{\delta-2} [bd u^{d-\delta+1} + \delta u - r(\delta - 1)] = u^{\delta-2} G(u)$$

where $G(u) = bd u^{d-\delta+1} + \delta u - r(\delta - 1)$. If $\delta < 1$, then we have $G(u) > 0$ and

$$\lim_{u \to 0^+} F(u) = -\infty, \quad F'(u) > 0, \quad \lim_{u \to 0^+} F'(u) = \infty$$

thus, $F(u)$ has a unique positive root $K > 0$.

Moreover, we have $H(0) = 0$ and $H'(u) = \frac{u^{\delta-1} [\delta + bu^d(\delta-d)]}{(1 + u^d + bu^d r)}$. This indicates the following three cases:

1. If $\delta \geq d$, then $H'(0) > 0$, thus, Model (6) is a monotone system where its dynamics can be classified into the following two cases:
   
   (a) If $\delta < 1$, then Model (6) has two non-negative equilibria 0 and $K$ where 0 is unstable and $K$ is globally stable.

   (b) If $\delta > 1 + d$, then we have $u = 0$ is locally stable and there exists some unique positive $u^c$ such that $G'(u)|_{u < u^c} < 0$ and $G'(u)|_{u > u^c} > 0$. Since $\lim_{u \to 0^+} G(u) = \infty$ and $\lim_{u \to \infty} G(u) = \infty$, therefore, $G(u)$ has exactly two positive roots if $G(u_c) < 0$. Also, we can conclude that $G(u) > 0$ if $G(u_c) > 0$. This implies that if $G(u_c) < 0$, then $F(u)$ has exactly two positive distinct critical points $0 < u_1^c < u^c < u_2^c$. Therefore, we can conclude that 1) $F(u)$ has exactly four distinct positive roots if $F(u_1^c) < 0$ and $F(u_2^c) > 0$; 2) $F(u)$ has exactly two distinct positive roots if $F(u_1^c) = 0$ and $F(u_2^c) < 0$; 3) $F(u)$ has exactly two positive roots if $F(u_1^c) > 0$ and $F(u_2^c) > 0$. In that case $F(u)$ has no positive root, we can conclude that $u = 0$ is globally stable. If $G(u_c) > 0$, then $G(u) > 0$ for all $u > 0$, therefore, we have $F'(u) > 0$. Since $F(0) = 0$, thus $F(u)$ has no interior root. This implies that $u = 0$ is globally stable.

(c) If $1 + d > \delta > 1$, then we have $u = 0$ is locally stable and

$$G(0) = -r(\delta - 1), \quad G'(u) > 0 \quad \lim_{u \to \infty} G(u) = \infty,$$

thus, $G(u)$ has a unique positive root $u_c$ which is the unique critical point of $F(u)$, i.e.,

$$F'(u_c) = 0 \quad \text{and} \quad F'(u)|_{u < u_c} < 0 \quad \text{and} \quad F'(u)|_{u > u_c} > 0.$$ 

Therefore, if $h(u_c) > 1$, then Model (6) has at least two consecutive, distinct and non-degenerate equilibria $A, K$ such that $0 < A < u_c < K$.

2. If $\delta < d$, then there exists a unique critical point $u_c = \left( \frac{r(\delta)}{d} \right)^{1/d}$ such that

$$H'(u)|_{u < u_c} > 0, \quad H'(u_c) = 0 \quad \text{and} \quad H'(u)|_{u > u_c} < 0.$$ 

We consider the following two cases:

(a) If $\delta < 1$, then Model (6) is a unique hump model that is similar to the Ricker’s map, thus, it has two non-negative equilibria 0 and $K$ where 0 is unstable.

(b) If $\delta > 1$, then $H'(0) = 0$, thus $u = 0$ is locally asymptotically stable. If $r > r_{crit}$, then we have $H(u_c) > u_c$. This implies that Model (6) has at least two distinct positive roots $A, K$ such that $0 < A < u_c < K$. 

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If both $\delta$ and $d$ are positive integers, then the number of positive roots of the following polynomial:

$$F(x) = bx^d + x^\delta - r x^{\delta-1} + 1.$$ 

Descartes’ rule of signs (Smith and Latham 1954; Meserve 1982) states that if the terms of a single-variable polynomial with real coefficients are ordered by descending variable exponent, then the number of positive roots of the polynomial is either equal to the number of sign differences between consecutive nonzero coefficients, or is less than it by a multiple of 2. Therefore, the statement of Part 4 holds.

Proof of Theorem 3.1

Proof. Denote by $T : \mathbb{R}^2_+ \rightarrow \mathbb{R}^2_+$ the map defined by the right side of Model (7)-(8), then we have

$$T = (T_1(x, y), T_2(x, y)) = \left( \frac{r_1x^{\delta_1}}{1 + x^{\delta_1} + b_1y^{\delta_3}}, \frac{r_2y^{\delta_2}}{1 + y^{\delta_2} + b_2x^{\delta_4}} \right). \quad (24)$$

Thus, $T$ is $C^1$ and $T_i < r_i, i = 1, 2$. The Jacobian matrix of $T$ can be represented as follows:

$$J = \begin{bmatrix}
\frac{r_1\delta_1 x^{\delta_1-1}(1+b_1y^{\delta_3})}{(1+x^{\delta_1}+b_1y^{\delta_3})^2} & -\frac{r_1b_1\delta_1 x^{\delta_1} y^{\delta_3-1}}{(1+x^{\delta_1}+b_1y^{\delta_3})^2} \\
-\frac{r_2\delta_2 y^{\delta_2-1}(1+b_2x^{\delta_4})}{(1+y^{\delta_2}+b_2x^{\delta_4})^2} & \frac{r_2b_2\delta_2 y^{\delta_2}}{(1+y^{\delta_2}+b_2x^{\delta_4})^2}
\end{bmatrix} \quad (25)$$

which gives

$$\text{det}(J) = r_1 r_2 [\delta_1 \delta_2 (x^{\delta_1-1}y^{\delta_2-1} + b_2 x^{\delta_1+\delta_4-1} y^{\delta_2-1} + b_1 x^{\delta_1-1} y^{\delta_2+\delta_3-1}) + b_1 b_2 x^{\delta_1+\delta_4-1} y^{\delta_2+\delta_3-1} (\delta_1\delta_2 - \delta_3\delta_4)]$$

$$\left(1 + x^{\delta_1} + b_1y^{\delta_3}\right)^2 \left(1 + x^{\delta_1} + b_1y^{\delta_3}\right)^2 \quad (26)$$

Thus, according to Lemma 3.1, we know that the map $T$ is positively invariant in $\text{Int} \mathbb{R}^2_+$, i.e., $T : \text{Int} \mathbb{R}^2_+ \rightarrow \text{Int} \mathbb{R}^2_+$. Thus, if $(x, y) \in \text{Int} \mathbb{R}^2_+$, we have $\text{det}(J) \geq 0$ (where equality occurs when $\delta_1\delta_2 = \delta_3\delta_4$) and $J$ has a constant sign configuration as $J = \left[ \begin{array}{cc} + & - \\ - & + \end{array} \right]$. This indicates that (25) is K-positive in $\text{Int} \mathbb{R}^2_+$ if $\delta_1\delta_2 \geq \delta_3\delta_4$ and it is K-strongly positive if $\delta_1\delta_2 > \delta_3\delta_4$. 

Take $u, v \in \text{Int} \mathbb{R}^2_+$ such that $u <_K v$, then by the mean value theorem and (25), we have

$$T_1(v) - T_1(u) = \frac{\partial T_1}{\partial x}(v_1 - u_1) + \frac{\partial T_1}{\partial y}(v_2 - u_2) > 0$$

$$T_2(v) - T_2(u) = \frac{\partial T_2}{\partial x}(v_1 - u_1) + \frac{\partial T_2}{\partial y}(v_2 - u_2) < 0$$

where the partial derivatives are evaluated at a point on the line segment connecting $u$ and $v$. This implies that $T(u) <_K T(v)$, i.e., the map $T$ is strongly competitive.

Choose any $(x_0, y_0) \in T(\text{Int} \mathbb{R}^2_+)$, we have $x_0 < r_1$ and $y_0 < r_2$. Let $(x, y)$ be a preimage of $(x_0, y_0)$, then it satisfies the following equation:

$$x_0 = \frac{r_1 x^{\delta_1}}{1 + x^{\delta_1} + b_1y^{\delta_3}} \quad (27)$$

$$y_0 = \frac{r_2 y^{\delta_2}}{1 + y^{\delta_2} + b_2x^{\delta_4}} \quad (28)$$

This indicates that

$$x_0 = \frac{r_1 x^{\delta_1}}{1 + x^{\delta_1} + b_1\left(\frac{y_0(1 + b_2x^{\delta_4})}{r_2 - y_0}\right)^{\delta_3/\delta_2}} = f(x) \quad (29)$$

$$y_0 = \frac{r_2 y^{\delta_2}}{1 + y^{\delta_2} + b_2\left(\frac{x_0(1 + b_1y^{\delta_3})}{r_1 - x_0}\right)^{\delta_4/\delta_1}} = g(y). \quad (30)$$
Since $\delta_1 \delta_2 \geq \delta_3 \delta_4$, we have

$$f'(x) = \frac{r_1(\delta_1 \delta_2 x^3 + b_2 x^2 + b_1 x + \delta_3)}{\delta_2 x (1 + b_2 x^2 + b_1) \left(\frac{\delta_3}{\delta_2} x^2 + \delta_3 \right)} > 0$$

$$g'(y) = \frac{r_2(\delta_1 \delta_2 y^2 + b_1 y + \delta_2)}{\delta_1 y \left(1 + b_2 y^2 + b_2 \delta_2 y^2 \right) \left(\frac{\delta_1}{\delta_2} y^2 + \delta_4 \right)} > 0$$  \hspace{1cm} (31)

This implies that both $f^{-1}(x)$ and $g^{-1}(y)$ have only one point, i.e., $(x, y) \in T(Int \mathbb{R}^n_+)$ has only one preimage. Thus, the map $T$ is injective in $Int \mathbb{R}^n_+$.

It is easy to check that $Int \mathbb{R}^n_+$ contains order intervals and is $\leq_K$-convex (i.e., it contains the line segment joining any two of its points that are $K$-ordering). Therefore, we can apply Corollary 4.4 of Smith (1998) to obtain that $\{T^n(x_0, y_0) = (x_n, y_n)\}$ is eventually component-wise monotone for every $(x_0, y_0) \in Int \mathbb{R}^n_+$, i.e., there exists a positive integer $N$ such that either $x_n \leq x_{n+1}$ for all $n > N$ or $x_{n+1} \leq x_n$ for all $n > N$ and similarly for $y_n$. Notice that

$$T(Int \mathbb{R}^n_+) \subset T(\mathbb{R}^n_+) \subset [0, r_1] \times [0, r_2],$$

thus, $\{T^n(x_0, y_0) = (x_n, y_n)\}$ converges to an equilibrium of Model (7)-(8) in $[0, r_1] \times [0, r_2]$. \qed

\textbf{Proof of Theorem 3.2}

\textbf{Proof}. If $\delta_1 \delta_2 < \delta_3 \delta_4$, then (26) vanishes at the following curves:

$$LC_{1,1}^2 : \quad xy = 0$$

$$LC_{2,1}^2 : \quad \delta_1 \delta_2 [1 + b_2 x^3 + b_1 y^3] + b_1 b_2 y^3 x^3 [\delta_2 \delta_1 - \delta_4 \delta_3] = 0.$$  \hspace{1cm} (27)

Thus, we have

$$LC_{2,1}^2 : \quad y = \gamma(x) = \left(\frac{\delta_1 \delta_2 [1 + b_2 x^3]}{b_1 [b_2 x^3 (\delta_4 \delta_3 - \delta_2 \delta_1) - \delta_1 \delta_2]}\right)^{1/\delta_3}, \quad \text{provided that} \quad x > \left(\frac{\delta_1 \delta_2}{b_2 \delta_3 \delta_4 - \delta_1 \delta_2}\right)^{1/\delta_3},$$

or

$$LC_{2,1}^2 : \quad x = \gamma^{-1}(y) = \left(\frac{\delta_1 \delta_2 [1 + b_1 y^3]}{b_2 [b_1 y^3 (\delta_4 \delta_3 - \delta_2 \delta_1) - \delta_1 \delta_2]}\right)^{1/\delta_3}, \quad \text{provided that} \quad y > \left(\frac{\delta_1 \delta_2}{b_1 \delta_4 \delta_1 - b_1 \delta_2}\right)^{1/\delta_3},$$

which gives that

$$\gamma'(x) = -\frac{b_2 b_1 \delta_2 \delta_3^{3/2} x^{\delta_3 - 1}}{b_1 [b_2 x^3 (\delta_4 \delta_3 - \delta_2 \delta_1) - \delta_1 \delta_2]^2} \left(\frac{\delta_1 \delta_2 [1 + b_2 x^3]}{b_1 [b_2 x^3 (\delta_4 \delta_3 - \delta_2 \delta_1) - \delta_1 \delta_2]}\right)^{1/\delta_3 - 1} < 0$$

provided that $x > \left(\frac{\delta_1 \delta_2}{b_2 [b_3 \delta_4 - \delta_2 \delta_1]}\right)^{1/\delta_3}$. In addition, by straightforward calculations, we have

$$\gamma''(x) > 0 \quad \text{if} \quad \delta_3 \geq \delta_4 \geq 1.$$  \hspace{1cm} (28)

The curve $\gamma(x)$ separates $Int \mathbb{R}^n_+$ into two connected unbounded components. The one unbounded component containing $(0, \epsilon) \times (0, \epsilon)$ for very small $\epsilon$ is denoted by $\Omega_+$ and it has $det(J) > 0$. While the other unbounded component is denoted by $\Omega_-$ and it has $det(J) < 0$.

Let $T$ be the map describing Model (7)-(8). The image of $\gamma(x)$ under the map $T$, i.e., $T(\gamma)$, called the critical curves in (Mira et al. 1996; Smith 1998; Kang 2012; Kang and Smith 2012), together with the portions of the coordinate axes which it cuts off, form the boundary of $T(Int \mathbb{R}^n_+)$. Because the curve $\gamma$ is linearly ordered by $< <_K$ (i.e., $\gamma(x) < 0$ indicates that any two points in $\gamma$ are related in the sense of strictly $K$-ordering) and $T$ preserves the strong ordering, $T(\gamma)$ is linearly ordered by $< <_K$ and connects
(0, r_2) to (r_1, 0). Let B denote the bounded component of Int \( \mathbb{R}^2_+ \setminus T(\gamma) \). Then \( T(\Omega_+) = T(\Omega_-) = B \), i.e., the map \( T \) folds \( \text{Int} \mathbb{R}^2_+ \) over at \( \gamma \) and maps both unbounded components onto \( B \).

If
\[
r_1 < \left( \frac{\delta_1 \delta_2}{b_2 [\delta_3 \delta_4 - \delta_1 \delta_2]} \right)^{1/\delta_4}
\]
or
\[
r_2 < \left( \frac{\delta_1 \delta_2}{b_1 [\delta_3 \delta_4 - \delta_1 \delta_2]} \right)^{1/\delta_5},
\]
then \( B \) is disjoint from \( \gamma \) and is totally contained in \( \Omega_+ \). This implies that \( \det(T)_{B} > 0 \). Note that the unbounded component of \( \text{Int} \mathbb{R}^2_+ \setminus T(\gamma) \) contains the points without pre-image (e.g., choosing a point with x-coordinate larger than \( r_1 \) and y-coordinate larger than \( r_2 \)), then all the points in \( \text{Int} \mathbb{R}^2_+ \setminus T(\gamma) \) have no pre-image. This because that the cardinality of \( T^{-1}(w), w \in \text{Int} \mathbb{R}^2_+ \setminus T(\gamma) \) is finite and constant according to Lemma 3.4 of Chow and Hale (1982). Similarly, we can show that the cardinality of \( T^{-1}(w), w \in B \) is two where one is located in \( B \) and the other one is located in \( \text{Int} \mathbb{R}^2_+ \setminus T(\gamma) \). This implies that
\[
T : B \to B \text{ is injective}.
\]

Therefore, we apply Corollary 4.4 of Smith (1998) to obtain that \( \{T^n(x_0, y_0) = (x_n, y_n)\} \) is eventually componentwise monotone for every \((x_0, y_0) \in \text{Int} \mathbb{R}^2_+ \). This indicates that every orbit of Model (7)-(8) with any initial condition in \( \mathbb{R}^2_+ \) converges to one of its equilibria.

Proof of Theorem 3.3

Proof. For any initial value \((x_0, y_0)\) taken in \( O_{ex} \), we have \( x_0 < A_1 \), thus we have
\[
x_1 = T_1(x_0, y_0) = \frac{r_1 x_0^{\delta_1}}{1 + x_0^{\delta_1} + b_1 y_0^{\delta_3}} \leq T_1(x_0, 0).
\]
Since \( \frac{\partial T_1}{\partial x} |_{x>0} > 0 \), thus we have
\[
x_{t+1} = T_t^1(x_0, y_0) \leq T_t^1(x_0, 0).
\]
According to Proposition 2.1, we have \( \lim_{t \to \infty} T_t^1(x_0, 0) = 0 \). Since Model (7)-(8) is positively invariant in \( \mathbb{R}^2_+ \) by Lemma 3.1, thus, \( \lim_{t \to \infty} x_t = 0 \) holds for Model (7)-(8) if Condition H1 is satisfied and its initial condition is taken in \( O_{ex} \).

Similarly, we can use the same argument to show that \( \lim_{t \to \infty} y_t = 0 \) holds for Model (7)-(8) if Condition H1 is satisfied and its initial condition is taken in \( O_{eq} \). Therefore,
\[
\lim_{t \to \infty} (x_t, y_t) = (0, 0) = E_0 \text{ provided } (x_0, y_0) \in O_0.
\]

Based on our arguments above, we can conclude that for any initial value \((x_0, y_0)\) taken in \( O_x \), we have \( \lim_{t \to \infty} y_t = 0 \). In addition, we have
\[
x_1 = T_1(x_0, y_0) = \frac{r_1 x_0^{\delta_1}}{1 + x_0^{\delta_1} + b_1 y_0^{\delta_3}} \geq T_1(x_0, A_2) = \frac{r_1 x_0^{\delta_1}}{1 + x_0^{\delta_1} + b_1 (A_2)^{\delta_3}}.
\]
Then by induction, we have \( x_{t+1} = T_t^1(x_0, y_0) \geq T_t^1(x_0, A_2) \). Since Model (7)-(8) satisfies Condition H2 and \( x_0 > A_1^{a_1} \), then according to Corollary 2.1, we have
\[
\lim_{t \to \infty} T_t^1(x_0, A_2) = K_1^{a_1} > A_1^{a_1} > A_1.
\]
This indicates that for Model (7)-(8), we have
\[
\liminf_{t \to \infty} x_t \geq K_1^{a_1} > A_1^{a_1} > A_1.
\]
Notice that \( \lim_{t \to \infty} y_t = 0 \), thus, for any \( \epsilon > 0 \), there exists a \( N \) large enough, such that for any \( t > N \), we have
\[
x_{t+1} \geq \frac{r_1 x_t^{\delta_1}}{1 + x_t^{\delta_1} + \epsilon} \geq A_1^{a_1} > A_1.
\]
Let $\epsilon \rightarrow 0$, then the limiting system of Model (7)-(8) becomes $T_1(x, 0)$. Since Condition H1 is satisfied and the initial value is larger than $A_1$, thus according to Proposition 2.1, we have $\lim_{t \rightarrow \infty} x_t = K_1$.

Similarly, we can apply the same argument above to show the case when an initial value $(x_0, y_0)$ is taken in $O_x$. Therefore, the statement of Theorem 3.3 holds.

\[ \square \]

Proof of Theorem 3.4
Proof. Assume that Model (7)-(8) satisfies Condition H1. Let $y = kx$, then from (24) any point $(x, kx) \in \text{Int} \mathbb{R}^2_+$ maps to the following point

\[ T(x, kx) = (T_1(x, kx), T_2(x, kx)) = \left( \frac{r_1 x^{\delta_1}}{1 + x^{\delta_1} + b_1(kx)^{\delta_3}}, \frac{r_2(kx)^{\delta_2}}{1 + (kx)^{\delta_2} + b_2x^{\delta_3}} \right). \]

If $\delta_3 > \delta_1$, then we have

\[ \frac{\partial T_1(x, kx)}{\partial x} \bigg|_{x < x_c} > 0 \quad \text{and} \quad \frac{\partial T_1(x, kx)}{\partial x} \bigg|_{x > x_c} < 0, \quad x_c = \left( \frac{\delta_1}{b_1 k^{\delta_3} (\delta_3 - \delta_1)} \right)^{1/\delta_3}. \]

Let $h(x) = \frac{r_1 x^{\delta_1}}{1 + b_1 k^{\delta_3} x^{\delta_1}} = \frac{r_1 x^{\delta_1}}{1 + b_1 k^{\delta_3} x^{\delta_1 - \delta_1}} > T_1(x, kx)$. Since $h(x) > T_1(x, kx)$ and $h'(x) < 0$ provided $\delta_3 > \delta_1$, thus we have

\[ T_1(x, kx) < h(x) < A_1 \iff x > \left( \frac{r_1 - A_1}{b_1 k^{\delta_3}} \right)^{\frac{1}{\delta_3 - \delta_1}}. \]

This gives

\[ T_1(x, kx) < A_1 \quad \text{whenever} \quad x > \left( \frac{r_1 - A_1}{b_1 k^{\delta_3}} \right)^{\frac{1}{\delta_3 - \delta_1}}. \]

Define

\[ O^t_{ex} = \bigcup_{k > 0} \{(x, kx) \in \text{Int} \mathbb{R}^2_+ : x > \left( \frac{r_1 - A_1}{b_1 k^{\delta_3}} \right)^{\frac{1}{\delta_3 - \delta_1}} \}. \]

Then we can conclude that if Model (7)-(8) satisfies Condition H1 and $\delta_3 > \delta_1$, then for any initial value taken in $O^t_{ex}$, we have

\[ \lim_{t \rightarrow \infty} x_t = 0. \]

Similarly, we can conclude that if Model (7)-(8) satisfies Condition H1 and $\delta_4 > \delta_2$, then for any initial value taken in $O^t_{ey}$ where

\[ O^t_{ey} = \bigcup_{k > 0} \{(ky, y) \in \text{Int} \mathbb{R}^2_+ : y > \left( \frac{r_2 - A_2}{b_2 k^{\delta_4}} \right)^{\frac{1}{\delta_4 - \delta_2}} \}, \]

we have

\[ \lim_{t \rightarrow \infty} y_t = 0. \]

Let $O^t_0 = O^t_{ex} \cap O^t_{ey}$. Then based on the arguments above, we can conclude that if Model (7)-(8) satisfies Condition H1 and $\delta_3 > \delta_1, \delta_4 > \delta_2$, then for any initial value taken in $O^t_0$, we have

\[ \lim_{t \rightarrow \infty} (x_t, y_t) = E_0. \]

The argument above combined with the results of Theorem 3.3, we can conclude that the statement is hold. \[ \square \]
Proof of Theorem 3.5

Proof. Since Model (7)-(8) satisfies Condition H1, thus if \((x, y)\) is an interior equilibrium of (7)-(8), we have the the following two equations:

\[
\begin{align*}
1 &= \frac{r_1 x^{\delta_1 - 1}}{1 + x^{\delta_1} + b_1 y^{\gamma_1}} 
\Rightarrow y = \left(\frac{r_1 x^{\delta_1 - 1} - x^{\delta_1 - 1}}{b_1}\right)^{1/\delta_3} = F_1(x), \quad 0 < A_1 < x < K_1 \\
1 &= \frac{r_2 y^{\delta_2 - 1}}{1 + y^{\delta_2} + b_2 x^{\gamma_2}} 
\Rightarrow x = \left(\frac{r_2 y^{\delta_2 - 1} - y^{\delta_2 - 1}}{b_2}\right)^{1/\delta_4} = F_2(y), \quad 0 < A_2 < y < K_2.
\end{align*}
\]

Since

\[
\begin{align*}
F_1'(x) &= x^{\delta_1 - 2} \left(\frac{r_1 x^{\delta_1 - 1} - x^{\delta_1 - 1}}{b_1}\right)^{1/\delta_3 - 1} \left[r_1(\delta_1 - 1) - \delta_1 x\right] \\
F_2'(y) &= y^{\delta_2 - 2} \left(\frac{r_2 y^{\delta_2 - 1} - y^{\delta_2 - 1}}{b_2}\right)^{1/\delta_4 - 1} \left[r_2(\delta_2 - 1) - \delta_2 y\right],
\end{align*}
\]

thus we have,

\[
\frac{dF_1}{dx}_{x=x_c} > 0, \quad \frac{dF_1}{dx}_{x=x_c} = 0 \text{ and } \frac{dF_1}{dx}_{x=x_c} < 0,
\]

and

\[
\frac{dF_2}{dy}_{y=y_c} > 0, \quad \frac{dF_2}{dy}_{y=y_c} = 0 \text{ and } \frac{dF_2}{dy}_{y=y_c} < 0
\]

where

\[
x_c = \frac{r_1(\delta_1 - 1)}{\delta_1} \quad \text{and} \quad y_c = \frac{r_2(\delta_2 - 1)}{\delta_2}.
\]

Therefore, according to the geometry of \(y = F_1(x)\) and \(x = F_2(y)\), we have follows:

- If \(F_1(x_c) < A_2\) or \(F_2(y_c) < A_1\), then Model (7)-(8) has no interior equilibrium (see Figure 3(a)-3(b)).

- If \(F_1(x_c) > K_2\) and \(F_2(y_c) > K_1\), then Model (7)-(8) has four interior equilibria (see Figure 3(d)).

If \(A_2 < F_1(x_c) < K_2\), \(K_1 < F_2(y_c)\) or \(K_2 < F_1(x_c)\), then Model (7)-(8) can have 0, 1, 2, 3, or 4 interior equilibria depending on the details of how large \(F_1(x_c)\) is. WLOG, let us focus on the case of \(A_2 < F_1(x_c) < K_2\), \(K_1 < F_2(y_c)\).

Let \(b_1\) be a bifurcation parameter and fix values of other parameters such that \(F_1(x_c) < A_2\), \(K_1 < F_2(y_c)\) hold. Notice that

\[
\frac{\partial F_1(x)}{\partial b_1} = -\frac{F_1(x)}{\delta_1 b_1} < 0,
\]

thus, decreasing \(b_1\) increases \(F_1(x_c)\). If \(b_1\) is very large, the graph of \(y = F_1(x)\) lies entirely below the graph of \(x = F_2(y)\) (see Figure 3(b)). As \(b_1\) decreases the graph of \(y = F_1(x)\) is stretched upward until \(F(x_c) = A_2\), and the further decreasing value of \(b_1\) leads to the case \(A_2 < F_1(x_c) < K_2\), \(K_1 < F_2(y_c)\) and still there is no interior equilibrium (see Figure 5:no). As \(b_1\) decreases further the graph of the graph of \(y = F_1(x)\) is stretched further upward until it intersects the lower branch of the graph of \(x = F_2(y)\) at some point \((x*, y*)\) with \(y* > A_2\). At that value of \(b_1\) there is a single positive equilibrium, but that value of \(b_1\) is a bifurcation point where a fold bifurcation leading to two positive equilibria occurs (see Figure 4(c)). As \(b_1\) increases still further the graph of \(y = F_1(x)\) is stretched still further upward until it intersects the upper branch of the graph of \(x = F_2(y)\) at some point \((x**, y**)\) with \(y* < y** < K_2\) so that there are three equilibria (see Figure 4(d)), and another fold bifurcation then occurs leading to two new positive equilibria for a total of four (see Figure 3(d)). There remain four positive equilibria as \(b_1\) decreases further, and eventually \(F_1(x_c)\) gets bigger than \(K_2\).
Proof of Theorem 3.6

Proof. Let \((x^*, x^*)\) be a symmetric interior equilibrium of Model (9)-(10), then we have
\[
r(x^*)^{\delta-1} = 1 + (x^*)^{\delta} + b(x^*)^d.
\]
This indicates that the Jacobian matrix of Model (9)-(10) evaluated at the symmetric interior equilibrium \((x^*, x^*)\) can be represented as
\[
J(x^*, x^*) = \begin{bmatrix}
\frac{\delta(1+b(x^*)^d)}{1+(x^*)^d+b(x^*)^d} & -\frac{bd(x^*)^d}{1+(x^*)^d+b(x^*)^d} \\
-\frac{bd(x^*)^d}{1+(x^*)^d+b(x^*)^d} & \frac{\delta(1+b(x^*)^d)}{1+(x^*)^d+b(x^*)^d}
\end{bmatrix}.
\]

The eigenvalues of (32) are
\[
\lambda_1(x^*) = \frac{\delta + b(\delta - d)(x^*)^d}{1 + (x^*)^d + b(x^*)^d} \quad \text{and} \quad \lambda_2(x^*) = \frac{\delta + b(\delta + d)(x^*)^d}{1 + (x^*)^d + b(x^*)^d}
\]
where \(\lambda_1(x^*)\) denotes the stability of \((x^*, x^*)\) on the invariant manifold \(\Omega_{y=x}\) and the sign of \(\lambda_2(x^*) - 1\) denotes whether the eigenvector associated with \(\lambda_2\) is pointing towards or away from \(\Omega_{y=x}\).

Therefore, the statement of Theorem 3.6 holds.

References


