

# Permanence of a general discrete-time two-species-interaction model with nonlinear per-capita growth rates

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## Abstract

The per-capita growth rate of a species is influenced by density-independent, positive and negative density-dependent factors. These factors can lead to nonlinearity with a consequence that species may process multiple nontrivial equilibria in its single state (e.g., Allee effects). This makes the study of permanence of discrete-time multi-species population models very challenging due to the complex boundary dynamics. In this paper, we explore the permanence of a general discrete-time two-species-interaction model with nonlinear per-capita growth rates for the first time. We find a simple sufficient condition for guaranteeing the permanence of the system by applying and extending the ecological concept of the relative nonlinearity to estimate systems' external Lyapunov exponents. Our method allows us to fully characterize the effects of nonlinearities in the per-capita growth functions and implies that the fluctuated populations may devastate the permanence of systems and lead to multiple attractors. These results are illustrated with specific two species competition and predator-prey models with generic nonlinear per-capita growth functions. Finally, we discuss the potential biological implications of our results.

*Keywords:* Allee Effects Nonlinear Per-Capita Growth Rates Permanence Relative Nonlinearity Two-Species-Interaction Population Models

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## 1. Introduction

The per-capita growth rate of a population given by the symbol  $\lambda = \frac{N_{t+1}}{N_t}$ , or as  $r = \ln \lambda$ , is a summary parameter that tell us trends in population density or abundance, i.e., it provides us the information on whether density and abundance are increasing or decreasing as well as how fast they are changing (Sibly and Hone 2002). In addition, it can be broken down into density-independent factors, negative and positive density-dependent factors (Shreiber 2003): Negative density-dependent factors include resource depletion due to competition (Tilman 1982), environment modification (Jones *et al.* 1997), mutual interference (Arditi and Akcakaya 1990) and cannibalism (Fox 1975) while positive density-dependent factors include predator saturation, cooperative predation or resource defense, increased availability of mates, and conspecific enhancement of reproduction (Courchamp *et al.* 2009; Stephens and Sutherland 1999; Stephens *et al.* 1999; Kang and Lanchier 2011). The synergy of all these density-dependent factors can result in the nonlinearity of a population's per-capita growth rate with respect to its population density, i.e., it can be below 1 in some range of population density and can be above 1 in some other ranges. As a consequence, the population of a species may process multiple nontrivial equilibria in its single state. The possibility that plant and animal populations have multiple positive equilibria (also refer to alternative states sometimes) has received considerable attentions in the ecological literature. Theory and observation indicate that natural multi-species assemblies of plants and animals are likely to possess several different equilibrium points (May 1973). Ecological examples include fish (e.g., Peterman 1977; Spencer and Collie 1997), insects (e.g., Ludwig *et al.* 1978; Kuussaari *et al.* 1998; Solow *et al.* 2003), and phytoplankton (e.g., Beltrami 1989). Moreover, subtidal marine ecosystems in general, and

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reefs in particular, have several attributes which favor the existence of multiple stable states (Knowlton 1992). Studying how species with multiple stable states in its single state may affect the persistence of other species and the coexistence of all species in a ecological community can provide us important implications for the conservation and management of natural systems (Carpenter 2001).

Mathematical population models have been widely used by many ecologists to explore coexistence mechanisms of species. For discrete time models, single species models with monotonic per-capita growth rate (e.g., Ricker's model) can exhibit complex dynamics, such as chaos, periodic windows (May 1973). This makes the study of discrete-time two-species population models very challenging. Needless to say, the difficulty increases when population models have multiple-species with nonlinear per-capita growth rates in their single state. In this article, we propose a general discrete-time two-species population model with nonlinear per capita growth rates for the first time and study sufficient conditions that give the coexistence of two species (i.e., permanence) for such model.

Permanence, which guarantees convergence on an interior attractor from any strictly positive initial conditions, is regarded as a strong form of coexistence. Permanence of dynamical systems has been studied by many researchers using Lyapunov exponents (Shreiber 2000; Garay and Hofbauer 2003; Salceanu and Smith 2009a&b) and average Lyapunov functions (Garay and Hofbauer 2003; Kon 2004; Kang and Chesson 2010) have used Lyapunov exponents and the notions of unsaturated invariant sets and measures for Kolmogorov-type discrete-time population models. Recent study by Kang and Chesson (2010) make use of the ecological concept of the relative nonlinearity (Chesson 1994) to extend Kon's (2004) results beyond convexity and concavity conditions to arbitrary nonlinearities for two dimensional discrete-time competition and prey-predator models. However, Kang and Chesson (2010) as well as Kon (2004) make assumptions on the monotonicity of the per-capita growth rate of each species. In this article, we will drop this assumption and derive a easy-to-check permanence criterion for a general two-species interaction model with the nonlinear per capita growth rates by using the theory of Lyapunov exponents and extending the ecological concept of the relative nonlinearity. The original concept of the relative nonlinearity is a species-coexistence mechanism that results from different species having different nonlinear responses to competition together with fluctuations in time or space in the intensity of competition (Chesson 1994& 2000; Kang and Chesson 2010). This extended concept allows us to fully characterize the effects of nonlinearities in the per capita growth functions, which are of major significance in the presence of multiple nontrivial boundary fixed points.

The structure of the rest paper is organized as follows: In section 2, we propose a general two-species interaction model and prove the important lemmas that are critical to derive sufficient criterion for the permanence of such model; In section 3, we give a sufficient permanence criterion for *ultimate competition* models; In section 4, we give a simple sufficient condition for permanence of *ultimate prey-predation* models; In section 5, we apply our results to a competition model and prey-predator model with nonlinear per-capita growth rates. In the last section, we conclude our results and discuss the broader implications of our study.

## 2. Models and the preliminary results

We are interested in the dynamics of a general discrete-time two-species interactions model with nonlinear per-capita growth rates that can be described by the following equations:

$$x_{n+1} = x_n f(x_n, y_n) \tag{1}$$

$$y_{n+1} = y_n g(x_n, y_n) \tag{2}$$

where  $x_n$  and  $y_n$  denote population densities of species  $x$  and  $y$  in season  $n$  respectively;  $f(x, y)$  and  $g(x, y)$  are per-capita growth rates of these two species, which are nonnegative and twice differentiable in  $\mathbb{R}_+^2$ . In addition, at least one of  $\frac{\partial f}{\partial x}$ ,  $\frac{\partial f}{\partial y}$ ,  $\frac{\partial g}{\partial x}$ ,  $\frac{\partial g}{\partial y}$  change signs in  $\mathbb{R}_+^2$ , i.e., the per-capita growth rates are nonlinear.

We first define the following important sets:

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

and

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

Let  $H$  be a two dimensional discrete-time system described by (1)-(2), then it maps  $X$  to  $X$  and satisfies  $H^0(x, y) = (x, y)$  and  $H^n(x, y) = (x_n, y_n)$ . Then it is easy to check that  $X, S_x, S_y, M$  and  $S$  are positively invariant. The main goal of this paper is to find sufficient conditions on  $f$  and  $g$  such that System (1)-(2) is permanent in  $X$  when  $f$  and  $g$  are nonlinear in  $X$ .

### 2.1. External Lyapunov exponents

Let  $\{(x_i, y_i)\}_{i=0}^{\infty}$  to be the positive orbit with an initial condition  $(x_0, y_0) \in S$ . Then the average per-capita growth rates of species  $x, y$  with initial condition  $(x_0, 0) \in S_x$  (or  $(0, y_0) \in S_y$ ) after  $n - 1$  generations can be represented as

$$r_n^{xx}(x_0, 0) = \frac{\sum_{i=0}^{n-1} \ln f(x_i, 0)}{n} \quad (3)$$

$$r_n^{yx}(x_0, 0) = \frac{\sum_{i=0}^{n-1} \ln g(x_i, 0)}{n} \quad (4)$$

$$r_n^{yy}(0, y_0) = \frac{\sum_{i=0}^{n-1} \ln g(0, y_i)}{n} \quad (5)$$

$$r_n^{xy}(0, y_0) = \frac{\sum_{i=0}^{n-1} \ln f(0, y_i)}{n} \quad (6)$$

Define  $\check{r}^{xx}(x_0, 0), \check{r}^{yx}(x_0, 0), \check{r}^{yy}(0, y_0), \check{r}^{xy}(0, y_0)$  as the limsup of the sequences

$$\{r_n^{xx}(x_0, 0)\}_{n=1}^{\infty}, \{r_n^{yx}(x_0, 0)\}_{n=1}^{\infty}, \{r_n^{yy}(0, y_0)\}_{n=1}^{\infty}, \{r_n^{xy}(0, y_0)\}_{n=1}^{\infty}$$

respectively. Moreover, we use

$$\bar{r}^{xx}(x_0, y_0), \bar{r}^{yx}(x_0, 0), \bar{r}^{yy}(x_0, y_0), \bar{r}^{xy}(0, y_0)$$

instead if their limits actually exist.

Notice that the quantity  $\check{r}^{yx}(x_0, 0)$  (or  $\check{r}_{xy}(0, y_0)$ ) is the *external Lyapunov exponent* of  $S_x$  (or  $S_y$ ), which gives the average invasion speed of the invader  $y$  (or  $x$ ) (Rand, Wilson and McGlade 1994). If both  $\check{r}^{yx}(x_0, 0)$  and  $\check{r}_{xy}(0, y_0)$  are positive for all  $x_0 \geq 0, y_0 \geq 0$ , then species  $y$  and  $x$  are able to coexist. The key question is that what kind of conditions on  $f(x, y), g(x, y)$  can guarantee this, therefore guarantee System (1)-(2) is permanent in  $X$ . In order to answer this question, we need the following two lemmas first.

**Lemma 2.1.** [Bounded population density] Assume that  $f(x, y)$  in System (1)-(2) is  $f(x, y)$  is positive and twice differentiable in  $X$ . Then if there exists  $0 < a_{\infty} < 1$  such that

$$\limsup_{x \rightarrow \infty} \sup_{y \geq 0} f(x, y) = a_{\infty},$$

then the population density of species  $x$  is bounded by some positive constant. If, in addition,  $f(0, 0) > 1$  and any initial condition  $(x_0, y_0) \in S_x$  with  $x_0 > 0$ , then

$$\bar{r}^{xx}(x_0, 0) = 0, x_0 > 0.$$

*Proof.* Define  $a_1(x) = \sup_{y \geq 0} f(x, y)$ , then the condition  $\limsup_{x \rightarrow \infty} \sup_{y \geq 0} f(x, y) = a_\infty < 1$  indicates that for any  $\epsilon + a_\infty < 1$ , there exists a number  $L_\epsilon$  large enough such that

$$a_1(x) < a_\infty + \epsilon < 1 \text{ for all } x \geq L_\epsilon.$$

Since  $a_1(x) = \sup_{y \geq 0} f(x, y)$ , then we have

$$f(x, y) \leq a_1(x) < a_\infty + \epsilon < 1 \text{ for all } x \geq L_\epsilon, y \geq 0.$$

Now if an initial condition of species  $x$  is greater than  $L_\epsilon$ , i.e.,  $x_0 \geq L_\epsilon$ , then there exists a positive integer  $N$  such that  $x_N < L_\epsilon$ . Assume that this is not true, then for any positive integer  $n$ , we have  $x_n \geq L_\epsilon$ . In particular, we have

$$x_n = x_{n-1} f(x_{n-1}, y_{n-1}) = x_0 \prod_{i=0}^{n-1} f(x_i, y_i) < x_0 (a_\infty + \epsilon)^n \rightarrow 0 \text{ as } n \rightarrow \infty.$$

This is a contradiction to the fact that  $x_n \geq L_\epsilon$  for all  $n \in \mathbb{Z}_+$ . Therefore, there exists a positive integer  $N$ , such that  $x_N < L_\epsilon$ .

Define  $L_m = L_\epsilon \max_{(x,y) \in [0, L_\epsilon]^2} \{f(x, y)\}$ . We claim that if  $x_N < L_\epsilon$ , then  $x_n \leq L_m$  for all  $n > N$ . Suppose that this is not true, then there exists some positive integer  $P$  such that  $x_{N+p} > L_m$ . Let  $p_m = \min\{p + N : x_{N+p} > L_m\}$ , then we have

$$x_{p_m} > L_m \text{ and } x_{p_m-1} \leq L_m.$$

This implies that either

$$x_{p_m-1} \leq L_\epsilon \text{ or } L_\epsilon < x_{p_m-1} \leq L_m.$$

If  $x_{p_m-1} \leq L_\epsilon$ , then

$$x_{p_m} = x_{p_m-1} f(x_{p_m-1}, y) \leq L_\epsilon \max_{(x,y) \in [0, L_\epsilon]^2} \{f(x, y)\} = L_m$$

which is a contradiction to  $x_{p_m} > L_m$ .

If  $L_\epsilon < x_{p_m-1} \leq L_m$ , then due to the fact that

$$f(x, y) < a_\infty + \epsilon < 1 \text{ for all } (x, y) \in [L_\epsilon, \infty) \times [0, \infty),$$

we have

$$x_{p_m} = x_{p_m-1} f(x_{p_m-1}, y) \leq x_{p_m-1} (a_\infty + \epsilon) < L_m$$

which is also a contradiction to  $x_{p_m} > L_m$ . Therefore, we have

$$x_n \leq L_m \text{ for all } n > N.$$

This implies that for any initial condition  $(x_0, y_0) \in X$  with  $x_0 > 0$ , there exists a positive integer  $p_m$ , such that

$$x_n \leq L_m \text{ for all } n > p_m.$$

Therefore, the population density of species  $x$  is bounded in System (1)-(2).

Next, notice that  $S_x$  is positively invariant, then for any initial condition in  $S_x$ , we have  $y_n = 0$  for all future  $n > 0$ , i.e., we have the following boundary dynamics,

$$x_{n+1} = x_n f(x_n, 0) \text{ for all } n \geq 0.$$

Then by applying Lemma B.1 (Kang and Chesson 2010), we can conclude that for any initial condition  $(x_0, 0)$  with  $x_0 > 0$ , the following inequalities hold

$$0 < b < \liminf_{n \rightarrow \infty} x_n \leq \limsup_{n \rightarrow \infty} x_n \leq L_m.$$

Let  $\{(x_i, 0)\}_{i=0}^{\infty}$  to be the positive orbit  $\gamma^+(x_0, 0)$  starting at  $x_0 > 0$ , then we have

$$\lim_{n \rightarrow \infty} \frac{\ln \frac{b}{x_0}}{n} \leq \liminf_{n \rightarrow \infty} \frac{\ln \frac{x_{n-1}}{x_0}}{n} \leq \lim_{n \rightarrow \infty} \frac{\ln \frac{x_{n-1}}{x_0}}{n} \leq \limsup_{n \rightarrow \infty} \frac{\ln \frac{x_{n-1}}{x_0}}{n} \leq \limsup_{n \rightarrow \infty} \frac{\ln \frac{B}{x_0}}{n}$$

This implies that for all  $x_0 > 0$ , we have

$$\bar{r}^{xx}(x_0, 0) = \lim_{n \rightarrow \infty} \frac{\sum_{i=0}^{n-1} \ln f(x_i, 0)}{n} = \lim_{n \rightarrow \infty} \frac{\sum_{i=0}^{n-1} \ln \frac{x_{n-1}}{x_0}}{n} = 0.$$

Therefore, we have proved the statement.  $\square$

**Remark:** Lemma 2.1 gives an easy-to-check sufficient criterion for the population of species  $x$  being bounded. Most species in competition models or prey in prey-predator models can satisfy conditions of the lemma, even for mutualism interaction population models as follows:

$$x_{n+1} = x_n e^{r_1 - a_{11}x_n^{v_{11}} + \frac{a_{12}y_n^{v_{12}}}{1+y_n^{v_{12}}}} \quad (7)$$

$$y_{n+1} = y_n e^{r_2 - a_{22}y_n^{v_{21}} + \frac{a_{21}x_n^{v_{22}}}{1+x_n^{v_{22}}}} \quad (8)$$

where all parameters  $r_i, a_{ij}, v_{ij}, i, j = 1, 2$  are strictly positive. In addition, from Lemma 2.1, we have the following corollary:

**Corollary 2.1.** *If System (1)-(2) is positive invariant in a compact set  $A$  where*

$$A = \{(x, y) \in S : x > 0, y > 0\},$$

then

$$\bar{r}^{xx}(x_0, 0) = 0 \quad \text{and} \quad \bar{r}^{yy}(0, y_0) = 0, \quad x_0 > 0, \quad y_0 > 0.$$

For convenience, define  $F(x, y) = \ln f(x, y), G(x, y) = \ln g(x, y)$  and  $F_i, G_i, i = x, y$  are the first partial derivative respect to  $i$ ;  $F_{ii}, G_{ii}, i = x, y$  are the second partial derivative respect to  $i$ . Let  $\{(x_i, 0)\}_{i=0}^{\infty}$  to be a positive orbit  $\gamma^+(x_0, 0)$  with  $x_0 \geq 0$ . Then we have the following lemma:

**Lemma 2.2.** *[The external Lyapunov exponent] Let  $(x^*, 0) \in S_x$  be a nontrivial boundary fixed point such that  $F(x^*, 0) = 0$  and  $F_x(x^*, 0) \neq 0$ . Then the following two cases hold if both  $f(x, y)$  and  $g(x, y)$  are positive and twice differentiable in  $X$  and  $\lim_{n \rightarrow \infty} f(x, 0) = a_1 < 1$ .*

**Case one:** *If  $f(0, 0) > 1$ , then  $\bar{r}^{xx}(x_0, 0) = 0$ . In addition, the external Lyapunov exponent of  $S_x$  is*

$$\tilde{r}^{yx}(x_0, 0) = G(x^*, 0) + \Delta_y(x_0), \quad x_0 > 0.$$

**Case two:** *If  $f(0, 0) \leq 1$ , then  $\tilde{r}^{xx}(x_0, 0) \leq 0$ . In addition, if  $\frac{G_x(x^*, 0)}{F_x(x^*, 0)} \leq 0$ , then the external Lyapunov exponent of  $S_x$  satisfies follows*

$$\tilde{r}^{yx}(x_0, 0) \geq G(x^*, 0) + \Delta_y(x_0), \quad x_0 > 0$$

where

$$\Delta_y = \limsup \frac{\sum_{i=0}^{n-1} (x_i - x^*)^2 \int_0^1 (1-t) \left[ G_{xx}(x_{it}, 0) - \frac{G_x(x^*, 0)F_{xx}(x_{it}, 0)}{F_x(x^*, 0)} \right] dt}{n}$$

and  $x_{it} = x^* + (x_i - x^*)t$ .

*Proof.* The condition that  $\lim_{n \rightarrow \infty} f(x, 0) = a_1 < 1$ , indicates that the superior of the average growth rate of the species  $x$  without species  $y$  is less than or equal zero by applying Lemma 2.1, i.e., for all initial conditions  $x_0 > 0$ , we have

$$\tilde{r}^{xx}(x_0, 0) = \lim_{n \rightarrow \infty} \frac{\sum_{i=0}^{n-1} F(x_i, 0)}{n} \leq 0.$$

Doing exact  $2^{nd}$  order Taylor expansion on  $F(x_i, 0), G(x_i, 0)$  around  $x = x^*$  gives:

$$\begin{aligned} F(x_i, 0) &= F(x^*, 0) + F_x(x^*, 0)(x_i - x^*) + (x_i - x^*)^2 \int_0^1 (1-t) F_{xx}(x_{it}, 0) dt \\ G(x_i, 0) &= G(x^*, 0) + G_x(x^*, 0)(x_i - x^*) + (x_i - x^*)^2 \int_0^1 (1-t) G_{xx}(x_{it}, 0) dt \end{aligned}$$

where  $x_{it} = x^* + (x_i - x^*)t$ . Since  $F(x^*, 0) = 0$ , then we have

$$\begin{aligned} r_n^{xx}(x_0, 0) &= \frac{\sum_{i=0}^{n-1} F(x_i, 0)}{n} \\ &= F_x(x^*, 0) \frac{\sum_{i=0}^{n-1} (x_i - x^*)}{n} + \frac{\sum_{i=0}^{n-1} (x_i - x^*)^2 \int_0^1 (1-t) F_{xx}(x_{it}, 0) dt}{n} \end{aligned}$$

This implies that we have

$$\frac{\sum_{i=0}^{n-1} (x_i - x^*)}{n} = \frac{r_n^{xx}(x_0, 0)}{F_x(x^*, 0)} - \frac{\sum_{i=0}^{n-1} (x_i - x^*)^2 \int_0^1 (1-t) F_{xx}(x_{it}, 0) dt}{n F_x(x^*, 0)}$$

This implies that we can rewrite  $r_n^{yx}(x_0)$  as follows:

$$\begin{aligned} r_n^{yx}(x_0) &= \frac{\sum_{i=0}^{n-1} G(x_i, 0)}{n} \\ &= G(x^*, 0) + G_x(x^*, 0) \frac{\sum_{i=0}^{n-1} (x_i - x^*)}{n} + \frac{\sum_{i=0}^{n-1} (x_i - x^*)^2 \int_0^1 (1-t) G_{xx}(x_{it}, 0) dt}{n} \\ &= G(x^*, 0) + G_x(x^*, 0) \left[ \frac{r_n^{xx}(x_0, 0)}{F_x(x^*, 0)} - \frac{\sum_{i=0}^{n-1} (x_i - x^*)^2 \int_0^1 (1-t) F_{xx}(x_{it}, 0) dt}{n F_x(x^*, 0)} \right] \\ &\quad + \frac{\sum_{i=0}^{n-1} (x_i - x^*)^2 \int_0^1 (1-t) G_{xx}(x_{it}, 0) dt}{n} \\ &= G(x^*, 0) + \frac{r_n^{xx}(x_0, 0) G_x(x^*, 0)}{F_x(x^*, 0)} \\ &\quad + \frac{\sum_{i=0}^{n-1} (x_i - x^*)^2 \int_0^1 (1-t) \left[ G_{xx}(x_{it}, 0) - \frac{G_x(x^*, 0) F_{xx}(x_{it}, 0)}{F_x(x^*, 0)} \right] dt}{n} \end{aligned}$$

Therefore, we have

**Case one:** If  $f(0, 0) > 1$ , then by applying Lemma 2.1, we have

$$\bar{r}^{xx}(x_0, 0) = \lim_{n \rightarrow \infty} r_n^{xx}(x_0, 0) = 0.$$

This indicates that

$$\tilde{r}^{yx}(x_0, 0) = G(x^*, 0) + \Delta_y(x_0)$$

**Case two:** If  $\frac{G_x(x^*, 0)}{F_x(x^*, 0)} \leq 0$ , then due to the fact that

$$\liminf_{n \rightarrow \infty} r_n^{xx}(x_0, 0) \leq \tilde{r}^{xx}(x_0, 0) \leq 0,$$

we have

$$\begin{aligned} \tilde{r}^{yx}(x_0, 0) &\geq G(x^*, 0) + \liminf_{n \rightarrow \infty} \frac{r_n^{xx}(x_0, 0) G_x(x^*, 0)}{F_x(x^*, 0)} + \Delta_y(x_0) \\ &\geq G(x^*, 0) + \Delta_y(x_0) \end{aligned}$$

□

A directly application of Lemma 2.1-2.2 is the following corollary:

**Corollary 2.2.** [Two positive invariant sets] Assume that all conditions in Lemma 2.2 are hold, i.e.,  $(x^*, 0) \in S_x$  is a nontrivial boundary fixed point such that  $F(x^*, 0) = 0$  and  $F_x(x^*, 0) \neq 0$ ; both  $f(x, y)$  and  $g(x, y)$  are positive and twice differentiable in  $X$  with  $\lim_{n \rightarrow \infty} f(x, 0) = a_1 < 1$ . If, in addition, the following conditions hold

1. The omega limit set of  $S_x$  is contained in a compact set  $[0, A]$ , i.e.,  $\omega(S_x) \subseteq [0, A]$ .
2.  $f(0, 0) \leq 1$  and the population of single species  $x$  converges to 0 for any initial values less than  $x_c$ .
3. The population of single species  $x$  persists in  $[x_c, A]$ , i.e.,

$$\liminf_{n \rightarrow \infty} x_n \geq x_c \text{ for any } x_0 \in [x_c, A].$$

then the external Lyapunov exponent of  $S_x$  satisfies follows

$$\inf_{x_0 \geq 0} \check{r}^{yx}(x_0, 0) \geq \min \left\{ G(0, 0), \inf_{x_0 \in [x_1, A]} [G(x^*, 0) + \Delta_y(x_0)] \right\}.$$

**Remark:** Corollary 2.2 applies to the case when a species suffers from strong Allee effects (see the application in Section 5). Here, we would like to point out that the expression  $G_{xx}(x, 0) - \frac{G_x(x^*, 0)F_{xx}(x, 0)}{F_x(x^*, 0)}$  is the extended ecological concept of the relative nonlinearity from Kang and Chesson (2010). This expression allows us to give an easy-to-check sufficient criterion for permanence applicable to a broad range of situations and avoids checking the detailed information on  $\omega(S_x)$  and calculating the external Lyapunov exponent  $\check{r}^{yx}(x_0, 0)$ . Depending on the signs of  $G(x^*, 0)$  and  $\Delta_y(x_0)$ , there are four situations:

**Permanence:** If both  $G(x^*, 0)$  and  $\Delta_y(x_0)$  are nonnegative and at least one of them is positive for all  $x_0 \in \mathbb{R}$ , then the *external Lyapunov exponent*  $\check{r}^{yx}(x_0, 0)$  of  $S_x$  is positive. Thus we can apply Theorem 2.2 and its corollary 2.3 of Hutson (1984) to show that species  $y$  is permanent. We will focus on this case in this paper.

**Relative Permanence:** Notice that it is possible that  $G(x^*, 0) < 0$  but  $\check{r}^{yx}(x_0, 0)$  is still positive for almost every  $x_0 \in S_x$ . This is the case when permanence fails due to the nontrivial boundary equilibrium point  $(x^*, 0)$  being saturated, which give a proper setting for the *relative permanence* (Kang 2011; Kang and Smith 2011).

**Boundary Attractor:** The case when  $\check{r}^{yx}(x_0, 0) < 0$  for all  $(x_0, 0) \in S_x$  represents the case when fluctuations associated with the non-point attractor undermine permanence because then the invasion rate is lower than that predicted by the point attractor  $(x^*, 0)$ . Thus, the system has no permanence due to existing attractors on the  $S_x$ . There are many models (Kon 2006; Kang *et al* 2008) presenting this scenario under some proper parameter ranges.

**Multiple Attractors:** The case when  $\check{r}^{yx}(x_0, 0) > 0$  for a dense set of  $x_0 \in S_x$  is a mixture of case 2 and 3, which can generate rich dynamics such as riddled basin of attractions (Ashwin *et al* 1996; Ferriere and Gatto 1995; Kon 2006).

### 3. Sufficient conditions for the permanence of a general two-species competition model

Let species  $x$  and  $y$  interact with each other in an ecology community and their population density can be described by System (1)-(2). Then we call a two-species system (1)-(2) an *ultimate competition* model if it satisfies the following conditions:

**C1:** Both  $f(x, y)$  and  $g(x, y)$  are strictly positive and twice differentiable in  $X$  with  $f(0, 0) > 1$  and  $g(0, 0) > 1$ .

**C2:** There exists  $a_1, a_2$  such that

$$\limsup_{x \rightarrow \infty} \sup_{y \geq 0} f(x, y) = a_1 < 1 \text{ and } \limsup_{y \rightarrow \infty} \sup_{x \geq 0} g(x, y) = a_2 < 1.$$

**C3:** Assume that species  $x$  has  $u$  nontrivial boundary equilibria in its single state and species  $y$  has  $v$  nontrivial boundary equilibria in its single state. Let  $(x_i^*, 0), (y_j^*, 0)$  be any nontrivial distinct boundary equilibria, then

$$f(0, y_j^*) > 1 \text{ and } g(x_i^*, 0) > 1, \text{ for all } 1 \leq i \leq u, 1 \leq j \leq v.$$

**C4:** For all  $x > 0, y > 0$ , there exists some boundary equilibrium  $(x_i^*, 0), 1 \leq i \leq u$  and  $(y_j^*, 0), 1 \leq j \leq v$ , such that the following two equalities hold

$$r^y(x) = G_{xx}(x, 0) - \frac{G_x(x_i^*, 0)F_{xx}(x, 0)}{F_x(x_i^*, 0)} \geq 0 \quad (9)$$

$$r^x(y) = F_{yy}(0, y) - \frac{F_y(0, y_j^*)G_{yy}(0, y)}{G_y(0, y_j^*)} \geq 0 \quad (10)$$

Condition **C1** guarantees that the population of species  $x$  and  $y$  will not be too close to the origin  $(0, 0)$ , i.e.,  $(0, 0)$  is a repeller. Condition **C2** implies that both species  $x$  and  $y$  suffer from large intra-competition, which drops their per-capita growth rates below 1 if their population density is too large. Condition **C3** ensures that both species  $x$  and  $y$  are able to invade each other at the nontrivial boundary equilibria. Condition **C4** guarantees both species  $x$  and  $y$  have positive invading speed when their population densities are rare. More importantly, it has a very important biological implications. In fact, (9)-(10) can be associated with relative nonlinearity introduced by Chesson (Chesson 2000&2009). Relative nonlinearity is a species-coexistence mechanism that results from different species having different nonlinear responses to competition together with fluctuations in time or space in the intensity of competition (Chesson 1994). Rewrite (9) as

$$G_{xx}(x, 0) - \frac{G_x(x_i^*, 0)F_{xx}(x, 0)}{F_x(x_i^*, 0)} = G_x(x_i^*, 0) \left( \frac{G_{xx}(x, 0)}{G_x(x_i^*, 0)} - \frac{F_{xx}(x, 0)}{F_x(x_i^*, 0)} \right)$$

Then  $\frac{G_{xx}(x, 0)}{G_x(x_i^*, 0)} - \frac{F_{xx}(x, 0)}{F_x(x_i^*, 0)}$  can be treated as a general form of relative nonlinearity when  $F_x(x, 0), G_x(x, 0)$  are non-invertible (Chesson 2000). More generally, we can consider  $r^y(x)$  (or  $r^x(y)$ ) as a contribution to the invading speed of species  $y$  (or  $x$ ) due to species  $x$  (or  $y$ ) has fluctuated population in its single state, e.g., if species  $x$  (or  $y$ ) has only point attractors  $(x_i^*, 0), i = 1, \dots, u$  (or  $(0, y_j^*), j = 1, \dots, v$ ), then  $r^y(x) = 0$  (or  $r^x(y) = 0$ ). If the species  $x$  has non-point attractors, then the contribution  $r^y(x)$  can be positive or negative (see the classification in the previous section). In this paper, we focus on the case when both  $r^y(x)$  and  $r^x(y)$  are nonnegative. The main goal of this section is to prove the following theorem:

**Theorem 3.1** (Sufficient conditions on permanence of an *ultimate competition model*). *If System (1)-(2) satisfies Condition C1-C4, then it is permanent in  $X$ .*

*Proof.* Since System (1)-(2) satisfies Condition **C1-C2**, then according to Lemma 2.1, there exists a positive number  $L_m$ , such that for any initial condition  $(x_0, y_0) \in X$ , we have

$$\limsup_{n \rightarrow \infty} \max\{x_n, y_n\} \leq L_m.$$

This implies that System (1)-(2) is dissipative in  $X$ , i.e., the set  $M = [0, L_m] \times [0, L_m]$  is a compact global attractor.

According to Lemma 2.1 again, Condition **C1-C2** indicates that the following equalities hold

$$\bar{r}^{xx}(x_0, 0) = 0 \text{ and } \bar{r}^{yy}(0, y_0) = 0 \text{ for all } x_0 > 0, y_0 > 0.$$



Let

$$\{(x_i, 0)\}_{i=0}^{\infty}, \quad \{(0, y_i)\}_{i=0}^{\infty}$$

are positive orbit with initial conditions  $x_0 > 0, y_0 > 0$  respectively, and

$$x_i^* \in \{x_k^*\}_{k=1}^u, \quad x_{it} = x^* + (x_i - x^*)t, \quad y_j^* \in \{y_k^*\}_{k=1}^v, \quad y_{jt} = y^* + (y_j - y^*)t.$$

Then by applying Lemma 2.2, we have

$$\tilde{r}^{yx}(x_0, 0) = G(x_i^*, 0) + \Delta_y(x_0) \quad \text{and} \quad \tilde{r}^{xy}(0, y_0) = F(0, y_j^*) + \Delta_x(y_0)$$

where

$$\Delta_y(x_0) = \limsup \frac{\sum_{k=0}^{n-1} (x_k - x_i^*)^2 \int_0^1 (1-t) \left[ G_{xx}(x_{kt}, 0) - \frac{G_x(x_i^*, 0)F_{xx}(x_{kt}, 0)}{F_x(x_i^*, 0)} \right] dt}{n},$$

and

$$\Delta_x(y_0) = \limsup \frac{\sum_{k=0}^{n-1} (y_k - y_j^*)^2 \int_0^1 (1-t) \left[ F_{yy}(0, y_{kt}) - \frac{F_y(0, y_j^*)G_{yy}(0, y_{kt})}{G_y(0, y_j^*)} \right] dt}{n}.$$

Therefore, according to Condition **C3-C4** and Lemma 2.2, we have

$$\inf_{x_0 \geq 0} \tilde{r}^{yx}(x_0, 0) > 0 \quad \text{and} \quad \inf_{y_0 \geq 0} \tilde{r}^{xy}(0, y_0) > 0.$$

Define  $P(x, y) = xy$ , then we have

$$\begin{aligned} \frac{P(x_n, y_n)}{P(x_0, y_0)} &= \prod_{i=0}^{n-1} f(x_i, y_i)g(x_i, y_i) = \prod_{i=0}^{n-1} e^{(F(x_i, y_i) + G(x_i, y_i))} \\ &= e^{\sum_{i=0}^{n-1} (F(x_i, y_i) + G(x_i, y_i))} = e^{n[r_n^{xx}(x_0, y_0) + r_n^{yy}(x_0, y_0)]} \end{aligned}$$

Therefore, the following inequalities hold

$$\sup_{n \geq 0} \liminf_{(x_0, y_0) \in M \rightarrow (x, 0) \in S_x} \frac{P(x_n, y_n)}{P(x_0, y_0)} \geq e^{(\bar{r}^{xx}(x, 0) + \inf_{x \geq 0} \tilde{r}_{yx}(x, 0))} > 1 \quad (11)$$

$$\sup_{n \geq 0} \liminf_{(x_0, y_0) \in M \rightarrow (0, y) \in S_y} \frac{P(x_n, y_n)}{P(x_0, y_0)} \geq e^{(\bar{r}_{yy}(0, y) + \inf_{y \geq 0} \tilde{r}_{xy}(0, y))} > 1 \quad (12)$$

In addition, for all  $(x, y) \in S$ , we have

$$P(x, y) = 0 \quad (13)$$

Thus, according to Theorem 2.2 of Hutson (1984), we can conclude that System (1)-(2) is permanent in  $X$ .  $\square$

**Remark:** Notice that Condition **C1-C4** does not have restrictions on the number of boundary equilibria and the signs of  $\frac{\partial f}{\partial x}, \frac{\partial f}{\partial y}, \frac{\partial g}{\partial x}, \frac{\partial g}{\partial y}$ . Thus, it allows System (1)-(2) to model more realistic two-species interactions, e.g.,  $f(x, y)$  and  $g(x, y)$  may be above 1 for certain range of population density and be below 1 for other ranges of population density. When we apply Theorem 3.1 to certain ecological model, the permanence condition derived from Condition **C1-C4** may provide us species coexistence mechanism, which give us some insights on how different species with different nonlinear response to different interactions (e.g., competition, predation or mutualism) together with fluctuations in time or space in the intensity of interactions.

In addition, the proof of Theorem 3.1 indicates that Condition **C3-C4** is enough to System (1)-(2) when it is dissipative in  $X$ .

**Corollary 3.1** (Convexity and Concavity). *Assume that System (1)-(2) satisfies Condition C1-C4. Then the following conditions can guarantee that it is permanent in  $X$ :*

1. Both  $F(0, y)$  and  $G(x, 0)$  are convex (or linear); and
2. Let  $(x_i^*, 0)$  be some nontrivial boundary equilibrium.  $F(x, 0)$  is convex (or linear) and  $\frac{G_x(x_i^*, 0)}{F_x(x_i^*, 0)} \leq 0$ ; or  $F(x, 0)$  is concave (or linear) and  $\frac{G_x(x_i^*, 0)}{F_x(x_i^*, 0)} \geq 0$ .
3. Let  $(0, y_j^*)$  be some nontrivial boundary equilibrium.  $G(0, y)$  is convex (or linear) and  $\frac{F_y(0, y_j^*)}{G_y(0, y_j^*)} \leq 0$ ; or  $G(0, y)$  is concave (or linear) and  $\frac{F_y(0, y_j^*)}{G_y(0, y_j^*)} \geq 0$ .

**Remark:** The proof of Corollary 3.1 is straightforward, therefore we omit the details. We would like to point out that when System (1)-(2) is discrete version of Lotka-Volterra model, then  $F(x, 0), G(x, 0)$  and  $F(0, y), G(0, y)$  are linear functions in  $x$  and  $y$  respectively. Therefore, according to Corollary 3.1, if a discrete-time Lotka-Volterra model satisfies Condition C3, then it is permanent. Theorem 3.1 and its Corollary 3.1 have extended our previous study in Kang and Chesson (2010), i.e., the results here can apply to a much broader ecological competition models (or *ultimate competition models* in our definition) with nonlinear per-capita growth rates. We will illustrate this in the application section.

#### 4. Sufficient conditions for the permanence of a general prey-predator model

Let species  $x$  and  $y$  interact with each other in an ecology community and their population density can be described by System (1)-(2). Then we call a two-species system (1)-(2) an *ultimate prey-predator* model if it satisfies the following conditions::

**P1:** Both  $f(x, y)$  and  $g(x, y)$  are strictly positive and smooth in  $X \setminus \{(0, 0)\}$  with  $f(0, 0) > 1$  and  $g(0, 0) \leq 1$ .

**P2:** System (1)-(2) satisfies Condition C2-C3.

**P3:** System (1)-(2) satisfies Condition C4 and the inequality  $\frac{F_y(0, y_j^*)}{G_y(0, y_j^*)} \leq 0$ .

Condition **P1-P3** allows System (1)-(2) to model but not limit to the following non-overlapping two-species interactions:

1. When predator species  $y$  is generalist and suffers strong Allee effects, e.g.,  $g(0, 0) < 1$ , with more than one nontrivial equilibrium in its single state (i.e.,  $S_y$ ). See an example provided in the Application Section for details.
2. A traditional prey-predator models with  $g(0, y) < 1$  for all  $y \geq 0$ . This condition implies that the predator  $y$  goes to extinct without prey  $x$ , thus, System (1)-(2) has no nontrivial boundary equilibrium in  $S_y$ . Condition **P2** indicates that  $\lim_{y \rightarrow \infty} g(x, y) = a_2 < 1$  for any given  $x > 0$ , which implies that for a given population of prey  $x$ , the per-capita growth rate of predator drops below 1 due to its huge population density. Such behavior is normally described as predator interference, i.e., predator individuals interact negatively with one another limiting their ability to hunt prey. Alternatively, this condition might represent intra-specific competition for some other resource, such as nesting sites, rather than for prey (Kang and Chesson 2010).

The main goal of this section is to show the following theorem:

**Theorem 4.1.** *If System (1)-(2) satisfies Condition P1-P3, then it is permanent in  $X$ .*

*Proof.* Since System (1)-(2) satisfies Condition **P1-P2**, then according to the proof in Theorem 3.1, we can conclude that it is dissipative in  $X$  with the set  $M = [0, L_m] \times [0, L_m]$  as its compact global attractor where  $L_m$  is some positive large number.

From Condition **P1**, the fact that  $g(0, 0) \leq 1$ , implies that the trivial boundary equilibrium  $(0, 0)$  is a saddle. Since System (1)-(2) satisfies Condition **P3**, we can apply Lemma 2.2 to get that

$$\inf_{y_0 \geq 0} \tilde{r}^{xy}(0, y_0) > 0.$$

Therefore, according to Theorem 2.2 of Hutson (1984), we have shown that species  $x$  is persistent in  $M$ , i.e., for any  $(x_0, y_0) \in M$ , there exists  $b, L_m$  such that

$$0 < b < \liminf_{n \rightarrow \infty} x_n \leq \limsup_{n \rightarrow \infty} x_n \leq L_m.$$

This implies that we can restrict the system on the compact space  $[b, L_m] \times [0, B]$ . Then we can apply Theorem 2.2 and its corollary of Hutson (1984) to the system again to show that species  $y$  is also persistent in  $M$ . Therefore, System (1)-(2) is permanent in  $X$ .  $\square$

**Remark:** We can get a similar result as stating in Corollary 3.1 when the per capita growth functions  $F, G$  are linear or satisfy some convex and concavity properties. In addition, we have the following corollary from Theorem 4.1:

**Corollary 4.1.** *System (1)-(2) is permanent in  $X$  if it satisfies Condition **P1-P2** and Condition  $\widetilde{P3}$  where*

$\widetilde{P3}$ : *The population dynamics of single species  $y$  satisfies conditions in Corollary 2.2 and System (1)-(2) satisfies Condition **C4**.*

## 5. Applications

In this section, we apply our results to an *ultimate competition* model and an *ultimate prey-predator* model where predator is generalist and suffers from strong Allee effects.

### 5.1. An ultimate competition model

Multiple stable states occur when more than one type of community can stably persist in a single environmental regime. Simple theoretical analyses predict multiple stable states for single species dynamics via the Allee effect. Dynamics for a single population showing an Allee effect, combined with some recruitment from external sources (Yodzis 1989), can be modeled as

$$x_{n+1} = x_n e^{r(x_n - \theta_1)(\theta_2 - x_n)(x_n - 1)} \quad (14)$$

where

$$r > 0 \text{ and } 0 < \theta_1 < \theta_2 < 1.$$

The equation (14) models the reproduction of single species  $x$  has inverse density dependence, i.e., declining per-capita reproduction with declining abundance below a critical density  $\theta_2$ . The result is two stable interior states: high density 1 and very low density  $\theta_1$  maintained by recruitment from elsewhere. These two states are separated by a threshold density  $\theta_2$ ; populations just above the threshold may increase to high abundance attractor, while those just below may decrease to low abundance attractor.

Let  $x_n$  and  $y_n$  represent the population of two competing species at generation  $n$ . Then their population density can be modeled as

$$x_{n+1} = x_n e^{r_1[(x_n - \theta_1)(\theta_2 - x_n)(x_n - 1) - (a_1 y_n)^{v_1}]} \quad (15)$$

$$y_{n+1} = y_n e^{r_2[1 - a_2 x_n^2(x_n - x_c) - (a_3 y_n)^{v_2}]} \quad (16)$$

where

$$r_i > 0, v_i > 0, x_c > 0, a_j > 0, i = 1, 2, j = 1, 2, 3 \text{ and } 0 < \theta_1 < \theta_2 < 1.$$

System (15)-(16) has two features:

1. Species  $x$  has multiple equilibria at its single state.
2. Species  $y$  benefits from species  $x$  when population density of species  $x$  is below a threshold  $x_c$  and competes with species  $x$  while population density of species  $x$  is above  $x_c$ .

First, it is easy to check that System (15)-(16) satisfies Condition **C1- C2**. Then we solve the following two equations,

$$\begin{aligned} r_1(x_n - \theta_1)(\theta_2 - x_n)(x_n - 1) &= 0 \Rightarrow x_1^* = \theta_1, x_2^* = \theta_2, x_3^* = 1 \\ r_2[1 - (a_3y)^{v_2}] &= 0 \Rightarrow y^* = \frac{1}{a_3} \end{aligned}$$

to obtain the following nontrivial boundary equilibria:

$$(\theta_1, 0), (\theta_2, 0), (1, 0) \text{ and } \left(0, \frac{1}{a_3}\right).$$

Let

$$\begin{aligned} F(x, 0) &= r_1(x - \theta_1)(\theta_2 - x)(x - 1), & G(x, 0) &= r_2[1 - a_2x^2(x - x_c)], \\ F(0, y) &= r_1[\theta_1\theta_2 - (a_1y)^{v_1}], & G(0, y) &= r_2[1 - (a_3y)^{v_2}] \end{aligned}$$

Then if

$$\text{Either } x_c \geq 1 \text{ or } \min\{G(\theta_1, 0), G(\theta_2, 0), G(1, 0)\} > 0$$

and

$$F(0, y^*) = r_1\theta_1\theta_2 - \left(\frac{a_1}{a_3}\right)^{v_1} > 0,$$

we can conclude that System (15)-(16) also satisfies Condition **C3**.

Since  $F(0, y)$  and  $G(0, y)$  have inverse functions in  $y > 0$ , then we can apply Theorem 4.1 and Corollary 6.1 in Kang and Chesson (2010) to obtain that species  $x$  is persistent in  $X$  if  $0 < v_1 \leq v_2$

In order to seek an sufficient condition that species  $y$  is able to invade species  $x$ , we should look at the first and second derivatives of  $F(x, 0)$  and  $G(x, 0)$  with respect to  $x$  in  $S_x$ , i.e.,

$$\begin{aligned} F_x(x, 0) &= r_1[(\theta_2 - x)(2x - \theta_1 - 1) - (x - \theta_1)(x - 1)], & G_x(x, 0) &= -r_2a_2x(3x - 2x_c), \\ F_{xx}(x, 0) &= 2r_1(1 + \theta_1 + \theta_2 - 3x), & G_{xx}(x, 0) &= -2r_2a_2(3x - x_c). \end{aligned}$$

Then we have

$$\begin{aligned} r^y(x) &= G_{xx}(x, 0) - \frac{G_x(x_i^*, 0)F_{xx}(x, 0)}{F_x(x_i^*, 0)} \\ &= -2r_2a_2(3x - x_c) - 2r_1(1 + \theta_1 + \theta_2 - 3x) \frac{G_x(x_i^*, 0)}{F_x(x_i^*, 0)} \\ &= 6x \left( r_1 \frac{G_x(x_i^*, 0)}{F_x(x_i^*, 0)} - r_2a_2 \right) + 2 \left[ r_2a_2x_c - r_1(1 + \theta_1 + \theta_2) \frac{G_x(x_i^*, 0)}{F_x(x_i^*, 0)} \right] \end{aligned}$$

where  $x_i^* \in \{\theta_1, \theta_2, 1\}$ . Thus, if there is a  $x_i^* \in \{\theta_1, \theta_2, 1\}$  such that the following inequalities hold

$$\frac{r_2a_2}{r_1} \leq \frac{G_x(x_i^*, 0)}{F_x(x_i^*, 0)} \leq \frac{r_2a_2x_c}{r_1} (1 + \theta_1 + \theta_2). \quad (17)$$

Then System (15)-(16) satisfies Condition C4. Notice that

$$\begin{aligned}\frac{G_x(\theta_1,0)}{F_x(\theta_1,0)} &= \frac{r_2 a_2 \theta_1 (3\theta_1 - 2x_c)}{r_1 (1-\theta_1)(\theta_2 - \theta_1)} \\ \frac{G_x(\theta_2,0)}{F_x(\theta_2,0)} &= \frac{r_2 a_2 \theta_2 (2x_c - 3\theta_2)}{r_1 (1-\theta_2)(\theta_2 - \theta_1)} \\ \frac{G_x(1,0)}{F_x(1,0)} &= \frac{r_2 a_2 \theta_2 (3 - 2x_c)}{r_1 (1-\theta_2)(1-\theta_1)}\end{aligned}$$

Thus, if one of the following inequalities holds,

$$\begin{aligned}\frac{r_2 a_2}{r_1} \leq \frac{G_x(\theta_1,0)}{F_x(\theta_1,0)} \leq \frac{r_2 a_2 x_c}{r_1} (1 + \theta_1 + \theta_2) &\iff 1 \leq \frac{\theta_1 (3\theta_1 - 2x_c)}{(1-\theta_1)(\theta_2 - \theta_1)} \leq x_c (1 + \theta_1 + \theta_2) \\ \frac{r_2 a_2}{r_1} \leq \frac{G_x(\theta_2,0)}{F_x(\theta_2,0)} \leq \frac{r_2 a_2 x_c}{r_1} (1 + \theta_1 + \theta_2) &\iff 1 \leq \frac{\theta_2 (2x_c - 3\theta_2)}{(1-\theta_2)(\theta_2 - \theta_1)} \leq x_c (1 + \theta_1 + \theta_2) \\ \frac{r_2 a_2}{r_1} \leq \frac{G_x(1,0)}{F_x(1,0)} \leq \frac{r_2 a_2 x_c}{r_1} (1 + \theta_1 + \theta_2) &\iff 1 \leq \frac{\theta_2 (3 - 2x_c)}{(1-\theta_2)(1-\theta_1)} \leq x_c (1 + \theta_1 + \theta_2)\end{aligned}\quad (18)$$

then (17) holds. Based on the discussion above, we can apply Theorem 3.1 to obtain the following corollary,

**Corollary 5.1.** *Assume that all the parameters of System (15)-(16) are positive. Then (15)-(16) is permanent, if the following conditions hold*

*Condition 1:*  $r_1 \theta_1 \theta_2 > \left(\frac{a_1}{a_3}\right)^{v_1}$  and  $0 < v_1 \leq v_2$ .

*Condition 2:* Either  $x_c \geq 1$  or  $\min\{G(\theta_1, 0), G(\theta_2, 0), G(1, 0)\} > 0$ .

*Condition 3:* One of the inequalities in (18) holds.

.

**Remark:** For example, if we take  $\theta_1 = 0.4, \theta_2 = 0.6, x_c = 1.2$ , then for any value of  $v_i, a_j, r_i, i = 1, 2, j = 1, 2, 3$  such that

$$0 < v_1 \leq v_2, \quad a_1 = a_3, \quad r_1 > \frac{1}{\theta_1 \theta_2} = 25/6, \quad r_2 > 0, \quad a_2 > 0,$$

we can conclude that System (15)-(16) satisfies Condition 1-3 in Corollary 5.1, thus it is permanent in  $X$ .

### 5.2. An ultimate prey-predator model with a generalist predator subject to strong Allee effects

Let  $x_n$  and  $y_n$  represent the population density of prey  $x$  and predator  $y$  at generation  $n$  respectively. Then a prey-predator model can be defined as

$$x_{n+1} = x_n e^{r_1 [1 - (x_n)^{v_1} - (a_1 y_n)^v]} \quad (19)$$

$$y_{n+1} = y_n e^{r_2 \left[1 - y_n - \frac{m}{1 + b y_n} + \frac{a_2 (x_n)^{v_2}}{1 + a (x_n)^{v_2}}\right]} \quad (20)$$

where  $r_i > 0, m > 1, b > 1, a > 0, a_i > 0, v > 0, v_i > 0, i = 1, 2$  and  $(b + 1)^2 > 4bm$ . We can see that System (19)-(20) has the following features:

1. Species  $x$  was eaten by species  $y$ , thus its population density decreases with respect to the population density of species  $y$ . At the mean time, the per-capita growth rate of species  $x$  decreases with respect to its own population density.
2. Species  $y$  benefits from species  $x$ , or preys on species  $x$ .
3. Species  $y$  suffers from strong Allee effects induced by predator saturation in its single state when  $\min\{b, m\} > 1$  and  $(b + 1)^2 > 4bm$ .

The fact that all the parameters are nonnegative and  $m > 1$  implies that System (19)-(20) satisfies Condition **P1-C2**. There are three nontrivial boundary equilibria if  $\min\{m, b\} > 1$  and  $(b+1)^2 > 4bm$ :

$$(x^*, 0) = (1, 0), (y_1^*, 0) = \left(0, \frac{b-1-\sqrt{(b+1)^2-4bm}}{2b}\right), (y_2^*, 0) = \left(0, \frac{b-1+\sqrt{(b+1)^2-4bm}}{2b}\right).$$

Let

$$\begin{aligned} F(x, 0) &= r_1 [1 - x^{v_1}], & G(x, 0) &= r_2 \left[1 - m + \frac{a_2 x^{v_2}}{1 + a x^{v_2}}\right], \\ F(0, y) &= r_1 [1 - (a_1 y)^v], & G(0, y) &= r_2 \left[1 - y - \frac{m}{1 + by}\right] \end{aligned}$$

Then System (19)-(20) satisfies Condition **C3** if the following inequality holds:

$$\begin{aligned} F(0, y_1^*) &= r_1 [1 - (a_1 y_1^*)^v] > 0 & \iff & y_1^* < \frac{1}{a_1} \\ F(0, y_2^*) &= r_1 [1 - (a_1 y_2^*)^v] > 0 & \iff & y_2^* < \frac{1}{a_1} \\ G(x^*, 0) &= r_2 \left[1 - m + \frac{a_2}{1+a}\right] > 0 & \iff & m < 1 + \frac{a_2}{1+a} \end{aligned} \quad (21)$$

Therefore, if  $y_2^* < \frac{1}{a_1}$  and  $m < 1 + \frac{a_2}{1+a}$ , then System (19)-(20) satisfies Condition **C3**.

Notice that  $y_2^* = \frac{b-1+\sqrt{(b+1)^2-4bm}}{2b}$ , thus, if  $(b+1)^2 > 4mb$  and  $\max\{b, m\} > 1$ , we have

$$\begin{aligned} (1 + by_2^*)^2 - mb &= \left(\frac{b+1+\sqrt{(b+1)^2-4bm}}{2}\right)^2 - mb = \frac{(b+1)^2 + (b+1)\sqrt{(b+1)^2-4bm} - 4mb}{2} \\ &= \frac{\sqrt{(b+1)^2-4bm}}{2} \left[\sqrt{(b+1)^2-4bm} + (b+1)\right] > 0. \end{aligned}$$

Since

$$\begin{aligned} G_x(x, 0) &= \frac{r_2 a_2 v_2 x^{v_2}}{x(1+ax^{v_2})^2} > 0, & F_x(x, 0) &= -v_1 x^{v_1-1} < 0 \\ G_{xx}(x, 0) &= -\frac{r_2 a_2 v_2 x^{v_2} [(1+ax^{v_2})(1+v_2) - 2v_2]}{x^2(1+ax^{v_2})^3}, & F_{xx}(x, 0) &= -v_1(v_1-1)x^{v_1-2} \\ G_y(0, y) &= r_2 y \left[\frac{bm}{(1+by)^2} - 1\right], & F_y(0, y) &= -r_1 a_1 v (a_1 y)^{v-1} < 0 \\ G_{yy}(0, y) &= -\frac{2r_2 mb^2}{(1+by)^3} < 0, & F_{yy}(0, y) &= r_1 v(1-v)(a_1)^v y^{v-2} > 0 \text{ if } 0 < v < 1. \end{aligned}$$

then if  $0 < v < 1$  and  $y > 0$ , we have

$$F_{yy}(0, y) - \frac{F_y(0, y_2^*)}{G_y(0, y_2^*)} G_{yy}(0, y) = r_1 v(1-v) a_1^v y^{v-2} + \frac{r_1 v a_1^v (y_2^*)^{v-2}}{1 - \frac{bm}{(1+by_2^*)^2}} \frac{2mb^2}{(1+by)^3} > 0.$$

Let  $A = \max_{y>0} \{yg(0, y)\} = \max_{y>0} \{ye^{r_2(1-y-\frac{m}{1+by})}\}$ , then the population of single species  $y$  satisfies conditions in Corollary 2.2 if

$$Ag(0, A) \leq y_1^*, (b+1)^2 > 4mb \text{ and } \max\{b, m\} > 1.$$

Therefore, we can conclude that species  $x$  is persistent, i.e.,

$$\tilde{r}^{xy}(y_0, 0) > 0 \text{ for all } y_0 \geq 0$$

if

$$0 < v < 1, y_2^* < \frac{1}{a_1}, Ag(0, A) \leq y_1^*, (b+1)^2 > 4mb \text{ and } \max\{b, m\} > 1.$$

On the other hand, from the fact that both  $F(x, 0)$  and  $G(x, 0)$  have inverse functions in  $x > 0$ , then we can apply Theorem 4.1 and Corollary 6.1 in Kang and Chesson (2010) to obtain that the sign of  $r^y(x)$  is determined by the sign of the following expression,

$$\frac{G_{xx}(x, 0)}{G_x(x, 0)} - \frac{F_{xx}(x, 0)}{F_x(x, 0)} = -\frac{v_1 + v_2}{x} + \frac{2v_2}{x(1 + ax^{v_2})} = \frac{2v_2 - (v_1 + v_2)(1 + ax^{v_2})}{x(1 + ax^{v_2})}.$$

Notice that the population of species  $x$  is bounded by  $(r_1 v_1)^{-v_1^{-1}} e^{r_1 - v_1^{-1}}$  according to System (19)-(20). Thus, we are able to show species  $y$  is persistent if

$$m < 1 + \frac{a_2}{1 + a} \text{ and } 2v_2 - [v_1 + v_2] \left[ 1 + a \left( (r_1 v_1)^{-v_1^{-1}} e^{r_1 - v_1^{-1}} \right)^{v_2} \right] > 0.$$

According to our discussion above, we have the following corollary:

**Corollary 5.2.** *System (19)-(20) is permanent in  $X$ , if the following conditions hold*

*Condition 1:*  $b > 1$ ,  $y_2^* < \frac{1}{a_1}$  and  $1 < m < \min\{1 + \frac{a_2}{1+a}, \frac{(b+1)^2}{4b}\}$  where  $y_2^* = \frac{b-1+\sqrt{(b+1)^2-4bm}}{2b}$ .

*Condition 2:*  $2v_2 - [v_1 + v_2] \left[ 1 + a \left( (r_1 v_1)^{-v_1^{-1}} e^{r_1 - v_1^{-1}} \right)^{v_2} \right] > 0$ .

*Condition 3:*  $0 < v < 1$  and  $Ag(0, A) \leq y_1^*$  where

$$y_1^* = \frac{b-1-\sqrt{(b+1)^2-4bm}}{2b} \text{ and } A = \max_{y \geq 0} \left\{ y e^{r_2(1-y-\frac{m}{1+by})} \right\}.$$

**Remark:** For example, if we take  $r_2 = 6, m = 2, b = 8$ , then single species  $y$  has two interior equilibrium  $y_1^* = 0.18$  and  $y_2^* = 0.695$  with its maximum population  $A = 0.917$  obtained at  $y = 0.490$ . Since  $Ag(0, A) = 0.364 > y_1^*$ , thus the population dynamics of single specie  $y$  satisfies conditions in Corollary 2.2. Let  $0 < v < 1, v_1 = 0.25, v_2 = 1, r_1 = 2.5, a = 0.1, a_1 = 1, a_2 = 2$ , then we have

$$\frac{1}{a_1} = 1 > y_2^*, 1 + \frac{a_2}{1+a} > 2 = m, \text{ and } 2v_2 - [v_1 + v_2] \left[ 1 + a \left( (r_1 v_1)^{-v_1^{-1}} e^{r_1 - v_1^{-1}} \right)^{v_2} \right] = 0.567 > 0.$$

Therefore, we can conclude that System (15)-(16) satisfies Condition 1-3 in Corollary 5.2, thus it is permanent in  $X$ .

## 6. Discussion

Many species in nature have seasonal life cycles. Data has been collected in discrete time intervals. Thus, discrete-time population models have been favored by ecologists to exploit the mechanisms of coexistence which has been an important ecological research question for many decades. Permanence is a strong form of coexistence that ensures populations persist despite large perturbations of the initial conditions, i.e., there exists some positive number such that the population of any species in the system is not less than this number asymptotically for any initial value. Sufficient conditions that lead to permanence of a population model can provide us useful insights on the mechanisms of coexistence. Many mathematicians (e.g., Fonda 1988; Freedman and So 1989; Shreiber 2000; Zhao 2003; Salceanu and Smith 2009a&b) have studied sufficient conditions on permanence of the dynamical systems. However, these conditions in general are difficult to check, especially for discrete-time population models, since discrete-time models tend to exhibit complicated dynamics like chaos even in one dimension (May 1973). Recent paper by Kang and Chesson (2010) has applied the ecological concept of the relative nonlinearity (Chesson 1994) to derive an easy-to-check criterion for the permanence of a traditional discrete-time two dimensional competition and prey-predator models with monotonic per-capital growth rates. In this

article, we focus on deriving a simple sufficient condition on permanence of a general discrete-time two dimensional two-species interaction models with nonlinear per-capital growth rates for the first time.

We first derive an easy-to-check criterion (Lemma 2.1) for a species having a bounded population where its population dynamics can be described by a general discrete-time two species interacting model with nonlinear per-capita growth rates. Then we proceed to estimate the external Lyapunov exponent of boundary systems of two cases (Lemma 2.2 and its corollary 2.2) by extending the work of Kang and Chesson (2010). Based on these preliminary but important steps, we are able to give a simple sufficient condition on the permanence of a general discrete-time two species interacting model with nonlinear per-capita growth rates (Theorem 3.1-4.1 and its corollaries). A traditional competition model assumes that the per-capita growth rate of a species is decreasing with respect to its own density and other species' density while a traditional prey-predator model assumes that the per-capita growth rate of predator is decreasing with respect to its own density and is increasing with respect to the other species' density. However, in reality, this may not be all the cases. For example, the per-capita growth rate of a species is nonlinear when it suffers from Allee effects which is common phenomena in ecology. More naturally, when two species interact with each other, their per capita growth rates tend to be a nonlinear function of two species' population density. Theorem 3.1-4.1 and its corollaries provide us a convenient tool to study the mechanisms of two-species coexistence in the following context:

1. When one species has multiple steady states in its single state. For example, when it suffers from Allee effects.
2. The per-capita growth rate of a species may be above 1 for certain range of population density and be below 1 for other ranges of population density, i.e., these two species can have competing relationship in certain range of population densities, have prey-predation relationship in some range of population densities and have mutualistic relationship in other range of population densities.

We have applied these theoretical results to two typical ecological models with nonlinear per-capita growth rates. These applications implies that our results allow us to explore the coexistence mechanisms of two interacting species in much more realistic situations than traditional ones. Extending our current method to study the permanence of higher dimensional discrete-time systems (i.e., a population model with more than 2 species) can be our future work.

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## Appendix A. Definitions

We call that  $H$  is *dissipative*, if there exists  $B > 0$ , for all initial condition  $(x, y) \in X$  such that

$$\limsup \max\{x_n, y_n\} \leq B.$$

This implies that  $H$  has a compact absorbing set in  $X$ . For convenience, when a system  $H$  is dissipative, we will consider  $X$  is a compact metric space.

We call that  $H$  is *permanent*, if there exists two positive numbers  $0 < b < B$ , for all initial condition  $(x, y) \in M$  such that

$$b \leq \liminf \min\{x_n, y_n\} \leq \limsup \max\{x_n, y_n\} \leq B.$$

This implies that  $H$  has a compact interior attractor  $B \subset M$  that attracts all the points in  $M$ .



The boundary equilibrium  $(x^*, y^*) \in S$  is *unsaturated* if

$$f(x^*, y^*) \geq 1 \text{ and } g(x^*, y^*) \geq 1.$$

The *positive orbit* of  $H$  with initial condition  $(x_0, y_0) \in X$  is defined as

$$\gamma^+(x_0, y_0) = \{(x_i, y_i) : (x_i, y_i) = H^i(x_0, y_0), \text{ for all } i \in \mathbb{Z}^+\}.$$

The *omega limit set* of  $(x, y) \in R_+^2$  is defined as

$$\omega(x, y) = \{(\xi, \eta) : H^{t_j}(x, y) \rightarrow (\xi, \eta) \text{ for some sequences } t_j \rightarrow \infty\}.$$

The *omega limit set* of a subset  $S \subset X$  of  $X$  is defined as

$$\omega(S) = \bigcup_{(x,y) \in S} \omega(x, y).$$

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