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Permanence of discrete-time Kolmogorov systems for two species and saturated fixed points

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Abstract. This paper considers the dynamics of a discrete-time Kolmogorov system for two-species populations. In particular, permanence of the system is considered. Permanence is one of the concepts to describe the species' coexistence. By using the method of an average Liapunov function, we have found a simple sufficient condition for permanence of the system. That is, nonexistence of saturated boundary fixed points is enough for permanence of the system under some appropriate convexity or concavity properties for the population growth rate functions. Numerical investigations show that for the system with population growth rate functions without such properties, the nonexistence of saturated boundary fixed points is not sufficient for permanence, actually a boundary periodic orbit or a chaotic orbit can be attractive despite the existence of a stable coexistence fixed point. This result implies, in particular, that existence of a stable coexistence fixed point is not sufficient for permanence.

1. Introduction

In this paper, we consider population dynamics given by the following discrete dynamical system:

$$\begin{cases} x_1(t+1) = x_1(t) f_1(x_1(t), x_2(t)) \\ x_2(t+1) = x_2(t) f_2(x_1(t), x_2(t)), \quad t \in \mathbb{Z}_+ = \{0, 1, 2, \dots\}, \end{cases} \tag{1.1}$$

$$x_1(0) \geq 0 \text{ and } x_2(0) \geq 0,$$

which is called a discrete-time Kolmogorov system. The system includes many models for two-species population with non-overlapping generations. For example, we can find several models of Kolmogorov type in Beddington *et al.* [2], Hutson and Moran [11], Hofbauer *et al.* [7], Hadeler and Gerstmann [5], Franke and Yakubu [3], Neubert and Kot [20], Hassell [6], Kot [15], and Kon and Takeuchi [13]. The models have been employed to consider several questions in population ecology.

One of the most important questions in population ecology is to find the coexistence conditions for the species. In order to consider this question, several mathematical concepts of coexistence of species are developed. Permanence is one of such concepts (the definition of permanence is given in the next section). It can

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evaluate possibility of coexistence of species even if the population densities of the species fluctuate in a complicated manner (see Hofbauer *et al.* [7], Anderson *et al.* [1], and Hofbauer and Sigmund [8]). Since discrete dynamical systems such as (1.1) can exhibit very complex behavior (see Beddington *et al.* [2], Hadeler and Gerstmann [5], and Neubert and Kot [20]), permanence is a very useful concept.

Permanence of systems of Kolmogorov type has been investigated in many papers (for example, see Hutson and Moran [11], Hofbauer *et al.* [7], Lu and Wang [16], and Kon and Takeuchi [13]). In these papers, some approaches are used to obtain sufficient conditions for permanence of the systems. One of the methods involves average Liapunov functions (see Hutson [9]). For example, this method was applied to the following discrete-time Lotka-Volterra systems by Hofbauer *et al.* [7]:

$$
\begin{aligned}
x_i(t+1) &= x_i(t) f_i(x_1(t), \dots, x_n(t)) \\
&= x_i(t) \exp\left[r_i + \sum_{j=1}^{n} a_{ij} x_j(t) \right], \quad i = 1, \dots, n.
\end{aligned}
\tag{1.2}
$$

In this application, the averaging property on the convergence of the time average of $x_i(t)$ toward the fixed point was efficiently used. This averaging property relies on the linearity of $\ln f_i$. In this paper, we show that the replacement of the assumption of linearity of $\ln f_i$ by convexity or concavity of $\ln f_i$ results in the average densities being greater than or less than the equilibrium population densities. By using this result, we apply the method of an average Liapunov function to a more general system (1.1) than the Lotka-Volterra system (1.2) with $n = 2$.

It is known that stability of a boundary fixed point plays an important role for permanence of a system in which a time average of the population density tends to a fixed point in the case of Lotka-Volterra systems. If a system does not have such a property for an average population density, not only stability of a boundary periodic orbit but also stability of a boundary fixed point influences permanence of the system. In such a case, we also have to focus on stability of boundary periodic orbits to determine either the system is permanent. Since System (1.1) can have an infinite number of boundary periodic orbits (for example, see May and Oster [18]), a condition for permanence of (1.1) can be very difficult check. Therefore, it is important to clarify the structure of the system whose permanence is determined by stability of boundary fixed points. In this paper, by focusing on convexity and concavity of population growth rate functions, we clarify such a structure and give a simple condition for permanence of (1.1). Furthermore, by considering some particular population models, we discuss the importance of convexity and concavity of population growth rate functions for permanence.

This paper is organized as follows. In Section 2, we introduce some notation and definitions of permanence and a saturated fixed point. In Section 3, we obtain a sufficient condition for permanence of System (1.1). This is the main result of the paper. In Section 4, we apply the result given in Section 3 to systems with predator-prey, competitive, and cooperative interspecific interactions, and obtain sufficient conditions for their permanence. In Section 5, we introduce some particular population models and apply the results given in Section 4 to these models. Moreover, by analyzing the models, we investigate the effect of convexity and concavity of population growth rate functions on permanence of the models. This investigation clarifies the importance of such properties of population growth rates in considering the problems of coexistence of species. In the final section, we discuss future works. A basic theorem and proofs of some mathematical results are given in Appendices.

2. Preliminaries

Let $O = \{(0,0)\}$, $\mathbb{R}^2_+ = \{(x_1, x_2) \in \mathbb{R}^2 : x_1 \geq 0, x_2 \geq 0\}$, $\mathrm{int}\mathbb{R}^2_+ = \{(x_1, x_2) \in \mathbb{R}^2_+ : x_1 x_2 > 0\}$ and $\mathrm{bd}\mathbb{R}^2_+ = \{(x_1, x_2) \in \mathbb{R}^2_+ : x_1 x_2 = 0\}$.

Now, we introduce some notations for a discrete dynamical system $F : X \to X$, where X is a metric space. The orbit starting at $\mathbf{x}$ is the set

$$\gamma_+(\mathbf{x}) = \{\mathbf{y} : \mathbf{y} = F^t(\mathbf{x}) \text{ for } t \in \mathbb{Z}_+\}.$$

The *omega limit set* is defined by

$$\Omega(\mathbf{x}) = \{\mathbf{y} : F^{t_j}(\mathbf{x}) \to \mathbf{y} \text{ for some sequence } t_j \to \infty\}.$$

For a subset $X_0 \subset X$ put

$$\gamma_+(X_0) = \bigcup_{\mathbf{x} \in X_0} \gamma_+(\mathbf{x}), \quad \Omega(X_0) = \bigcup_{\mathbf{x} \in X_0} \Omega(\mathbf{x}).$$

X_0 is said to be *forward invariant* if $F(X_0) \subset X_0$. The set M is *absorbing* for X_0 if it is forward invariant and $\gamma_+(\mathbf{x}) \cap M \neq \emptyset$ for every $\mathbf{x} \in X_0$. Therefore, if M is absorbing for X_0, then every orbit starting in X_0 eventually enters M and remains there.

Definition 2.1. *The system F is said to be dissipative if there exists a compact absorbing set X_0 for X.*

Remark. If F is continuous, the forward invariance of the above X_0 is not necessary for dissipativeness of F since the forward invariance is achieved by considering $\gamma_+(X_0)$ (see Appendix A).

We define permanence of System (1.1) as follows:

Definition 2.2. *System* (1.1) *is said to be permanent if there exists a compact absorbing set $M \subset \mathrm{int}\mathbb{R}^2_+$ for $\mathrm{int}\mathbb{R}^2_+$.*

This definition implies that if System (1.1) is permanent, then there exists a $\delta > 0$ such that

$$\delta \leq \liminf_{t\to\infty} x_i(t) \leq \limsup_{t\to\infty} x_i(t) \leq \frac{1}{\delta}, \quad i = 1, 2,$$

for all $(x_1(0), x_2(0)) \in \mathrm{int}\mathbb{R}^2_+$. Therefore, it ensures that if System (1.1) is permanent, then for sufficiently large t population densities of two species are always greater than a positive constant which is independent of initial conditions.

Finally, we define a saturated fixed point as follows (see Hofbauer and Sigmund [8], p.159):

Definition 2.3. *The fixed point (x_1^*, x_2^*) of* (1.1) *is said to be saturated if $f_i(x_1^*, x_2^*) \leq 1$ for all $i \in \{1, 2\}$.*

3. Permanence

In this section, we obtain a sufficient condition for permanence of System (1.1). The main result of this paper is Theorem 3.2.

We introduce the following basic assumptions for System (1.1):

(H1): f_1 and f_2 are positive continuous functions on $\mathbb{R}^2_+$,
(H2): System (1.1) is dissipative.

By (H2), System (1.1) has a compact absorbing set X_1 for $\mathbb{R}^2_+$. The set of extinction states in X_1 is defined by $\mathrm{bd}\mathbb{R}^2_+ \cap X_1$. We divide the $\mathrm{bd}\mathbb{R}^2_+ \cap X_1$ into two sets as follows:

$$S_1 = \{(x_1, x_2) \in \mathrm{bd}\mathbb{R}^2_+ \cap X_1 : x_2 = 0\},$$
$$S_2 = \{(x_1, x_2) \in \mathrm{bd}\mathbb{R}^2_+ \cap X_1 : x_1 = 0\}.$$

The set S_i $(i \in \{1, 2\})$ implies extinction of the x_j-species $(i \neq j)$. For the application of an average Liapunov function to System (1.1), it is important to know the dynamics in $S_1 \cup S_2$. Hereafter, we obtain some lemmas about the dynamics in S_i $(i \in \{1, 2\})$. Although the following lemma considers the dynamics in S_1, the same result is true for S_2:

Lemma 3.1. *Suppose that* (H1) *and* (H2) *hold. Then,* $\Omega(S_1) = O$ *if System* (1.1) *has no fixed points in* $S_1 \setminus O$.

Proof. Since System (1.1) has no fixed points in $S_1 \setminus O$, then $f_1(x_1, 0) \neq 1$ for all $x_1 > 0$. By the continuity of $f_1(x_1, 0)$, either $f_1(x_1, 0) < 1$ or $f_1(x_1, 0) > 1$ always holds for $x_1 > 0$. Since System (1.1) is dissipative, we see that $f_1(x_1, 0) < 1$ for all $x_1 > 0$, otherwise all orbits with the initial condition in $S_1 \setminus O$ diverge. Therefore, we see that $\lim_{t\to\infty} x_1(t) = 0$ for all $(x_1(0), x_2(0)) \in S_1 \setminus O$, that is, $\Omega(S_1) = O$. □

A time average of the population density plays an important role in application of an average Liapunov function (see Hofbauer *et al.* [7] and Kon and Takeuchi [13, 14]). The average population densities are given by

$$\overline{x}_i(t) = \frac{1}{t} \sum_{n=0}^{t-1} x_i(n), \quad i \in \{1, 2\}. \tag{3.1}$$

For example, the average population density $\overline{x}_1(t)$ can be estimated if the function $\ln f_1(x_1, 0)$ has one of the following properties:

$(\mathrm{A1})_1$: $\ln f_1(x_1, 0)$ is monotonically decreasing and convex,
$(\mathrm{A2})_1$: $\ln f_1(x_1, 0)$ is monotonically decreasing and concave

(note that if the function is monotonically increasing and vanishes at some $x_1^* > 0$, then System (1.1) has an unbounded orbit on S_1). In fact, we have the following lemma (we can also introduce the same assumptions $(\mathrm{A1})_2$ and $(\mathrm{A2})_2$ for the function $\ln f_2(0, x_2)$, and obtain the same result for $\overline{x}_2(t)$ of solutions on S_2):

Lemma 3.2. *Let* $\{(x_1(t), x_2(t))\}_{t\in\mathbb{Z}_+}$ *be a solution of System* (1.1) *with* $(x_1(0), x_2(0)) \in S_1\backslash O$. *Suppose that* (H1) *and* (H2) *hold. Assume that there exists a sequence* $t_k \to \infty$ *and a* $\delta > 0$ *such that* $x_1(t_k) \geq \delta$ *for all* $k \in \mathbb{Z}_+$. *Then, there exists a fixed point* $(x_1^*, 0) \in S_1\backslash O$. *Further, there exists a subsequence, again denoted by* t_k, *such that*

$$x_1^* \leq \lim_{k\to\infty} \overline{x}_1(t_k) \quad \textit{if } \ln f_1(x_1, 0) \textit{ is monotonically decreasing and convex}$$
$$x_1^* \geq \lim_{k\to\infty} \overline{x}_1(t_k) \quad \textit{if } \ln f_1(x_1, 0) \textit{ is monotonically decreasing and concave,}$$

where $\overline{x}_1$ *is the average given by* (3.1).

Proof. First, we show that System (1.1) has a fixed point $(x_1^*, 0) \in S_1\backslash O$. Suppose that System (1.1) does not have such a fixed point. Then, by Lemma 3.1, $\lim_{t\to\infty} x_1(t) = 0$ for all $x_1(0) > 0$. This is a contradiction to the assumption for the existence of a sequence t_k.

By (H2), there exists an interval $[\delta, D]$ such that $x_1(t_k) \in [\delta, D]$ for all $k \in \mathbb{Z}_+$. By the first equation of (1.1), we have

$$\ln \frac{x_1(n+1)}{x_1(n)} = \ln f_1(x_1(n), 0).$$

After summation of both sides from $n = 0$ to $t_k - 1$ and dividing by t_k, we have

$$\frac{\ln x_1(t_k) - \ln x_1(0)}{t_k} = \frac{1}{t_k}\sum_{n=0}^{t_k-1} \ln f_1(x_1(n), 0).$$

Since $\delta \leq x_1(t_k) \leq D$ for all $k \in \mathbb{Z}_+$,

$$0 = \lim_{k\to\infty} \frac{1}{t_k}\sum_{n=0}^{t_k-1} \ln f_1(x_1(n), 0). \tag{3.2}$$

If $\ln f_1(x_1, 0)$ is convex, then Jensen's inequality (e.g., see [17,21]) gives

$$\frac{1}{t_k}\sum_{n=0}^{t_k-1} \ln f_1(x_1(n), 0) \geq \ln f_1\left(\frac{1}{t_k}\sum_{n=0}^{t_k-1} x_1(n), 0\right). \tag{3.3}$$

By Eqs (3.2) and (3.3), we have

$$\operatorname*{Lim}_{k\to\infty} \ln f_1\left(\frac{1}{t_k}\sum_{n=0}^{t_k-1} x_1(n), 0\right) \subset (-\infty, 0], \tag{3.4}$$

where $\operatorname{Lim}_{t\to\infty} x(t) = \{y : \lim_{j\to\infty} x(t_j) = y \text{ for some sequence } t_j \to \infty\}$. Since $\ln f_1(x_1, 0)$ is monotonically decreasing and $\ln f_1(x_1^*, 0) = 0$, Eq. (3.4) implies that there exists a subsequence, again denoted by t_k, such that

$$\lim_{k\to\infty} \frac{1}{t_k}\sum_{n=0}^{t_k-1} x_1(n) \geq x_1^*.$$

Similarly, if $\ln f_1(x_1, 0)$ is concave, we can show that there exists a subsequence, again denoted by t_k, such that

$$\lim_{t\to\infty} \frac{1}{t_k} \sum_{n=0}^{t_k-1} x_1(n) \le x_1^*. \qquad \square$$

We can find a special case of this lemma in Ex 1.6.2 of [8]. Note that the function $\ln f_1(x_1, 0) = r + ax_1$ with $r, a \in \mathbb{R}$ is both convex and concave. By Lemma 3.2, if the function is both convex and concave, $\lim_{k\to\infty} \overline{x}_1(t_k) = x_1^*$ holds. Lotka-Volterra systems have such growth rate functions (see Hofbauer *et al.* [7], Lemma 2.4). It is also worth noting that $S_1\backslash O$ has at most one fixed point if $\ln f_1(x_1, 0)$ is monotone.

Fig. 1 is a set of bifurcation diagrams of one-dimensional maps, which correspond to those of (1.1) on S_1 (or S_2). Fig. 2 shows the average population densities generated by the one-dimensional maps. From Figs 1 and 2, we confirm that the result of Lemma 3.2 holds even if there is a complex solution on S_1 (or S_2).

The convexity or concavity, and monotonicity of $\ln f_2(x_1, 0)$ also influence the dynamics of System (1.1). We introduce the following different sets of assumptions:

$(\mathrm{B1})_1$: $\ln f_2(x_1, 0)$ is monotonically decreasing and convex;
$(\mathrm{B2})_1$: $\ln f_2(x_1, 0)$ is monotonically decreasing and concave;
$(\mathrm{B3})_1$: $\ln f_2(x_1, 0)$ is monotonically increasing and convex;
$(\mathrm{B4})_1$: $\ln f_2(x_1, 0)$ is monotonically increasing and concave.

We can also introduce the same assumptions $(\mathrm{B1})_2$, $(\mathrm{B2})_2$, $(\mathrm{B3})_2$, and $(\mathrm{B4})_2$ for the function $\ln f_1(0, x_2)$. Although the following lemma considers the property of the solution on S_1, the same result also holds for the solution on S_2.

Lemma 3.3. *Let* $\{(x_1(t), x_2(t))\}_{t\in\mathbb{Z}_+}$ *be a solution of System* (1.1) *with* $(x_1(0), x_2(0)) \in S_1\backslash O$*. Suppose that* (H1) *and* (H2) *hold. Assume that one of the following conditions* (I) *or* (II) *holds:*

(I): $\ln f_1(x_1, 0)$ *is monotonically decreasing and convex, and* $\ln f_2(x_1, 0)$ *is monotonically increasing and convex* (*i.e.,* $(\mathrm{A1})_1$ *and* $(\mathrm{B3})_1$);
(II): $\ln f_1(x_1, 0)$ *is monotonically decreasing and concave, and* $\ln f_2(x_1, 0)$ *is monotonically decreasing and convex* (*i.e.,* $(\mathrm{A2})_1$ *and* $(\mathrm{B1})_1$).

Further, assume that there exists a sequence $t_k \to \infty$ *and a* $\delta > 0$ *such that* $x_1(t_k) \ge \delta$ *for all* $k \in \mathbb{Z}_+$*. If the fixed point* $(x_1^*, 0)$ *is not saturated, then there exists a subsequence, again denoted by* t_k*, such that*

$$\lim_{k\to\infty} \frac{1}{t_k} \sum_{n=0}^{t_k-1} \ln f_2(x_1(n), 0) > 0.$$

Proof. By Lemma 3.2, $S_1\backslash O$ has a fixed point $(x_1^*, 0)$. Since $\ln f_2(x_1, 0)$ is convex, there exists ξ and η such that $\ln f_2(x_1, 0) \ge \xi x_1 + \eta$ for all $x_1 > 0$ and $\ln f_2(x_1^*, 0) = \xi x_1^* + \eta$. Then, for every $k \in \mathbb{Z}_+$

$$\frac{1}{t_k} \sum_{n=0}^{t_k-1} \ln f_2(x_1(n), 0) \ge \xi \frac{1}{t_k} \sum_{n=0}^{t_k-1} x_1(n) + \eta.$$

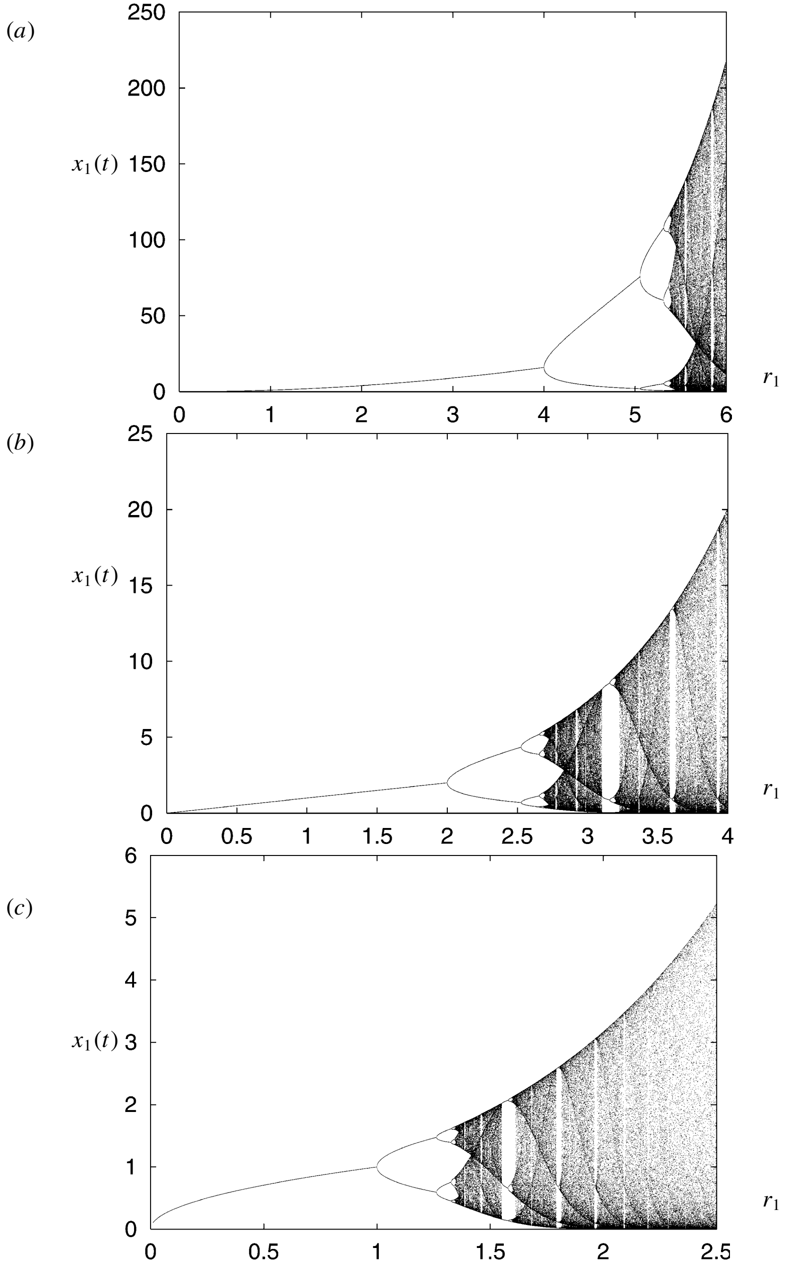

Fig. 1. Bifurcation diagrams of the one-dimensional map $x_1(t+1) = x_1(t)\exp[r_1 - a_{11}x_1(t)^{\nu_{11}}]$ with $a_{11} = 1$. The orbits $\{x_1(t)\}$ with $x_1(0) = 1$ are plotted for $t \in \{10001, \ldots, 10100\}$. The function $r_1 - a_{11}x_1^{\nu_{11}}$ in (a), (b) and (c) are chosen convex ($\nu_{11} = 0.5$), linear ($\nu_{11} = 1$) and concave ($\nu_{11} = 2$), respectively.

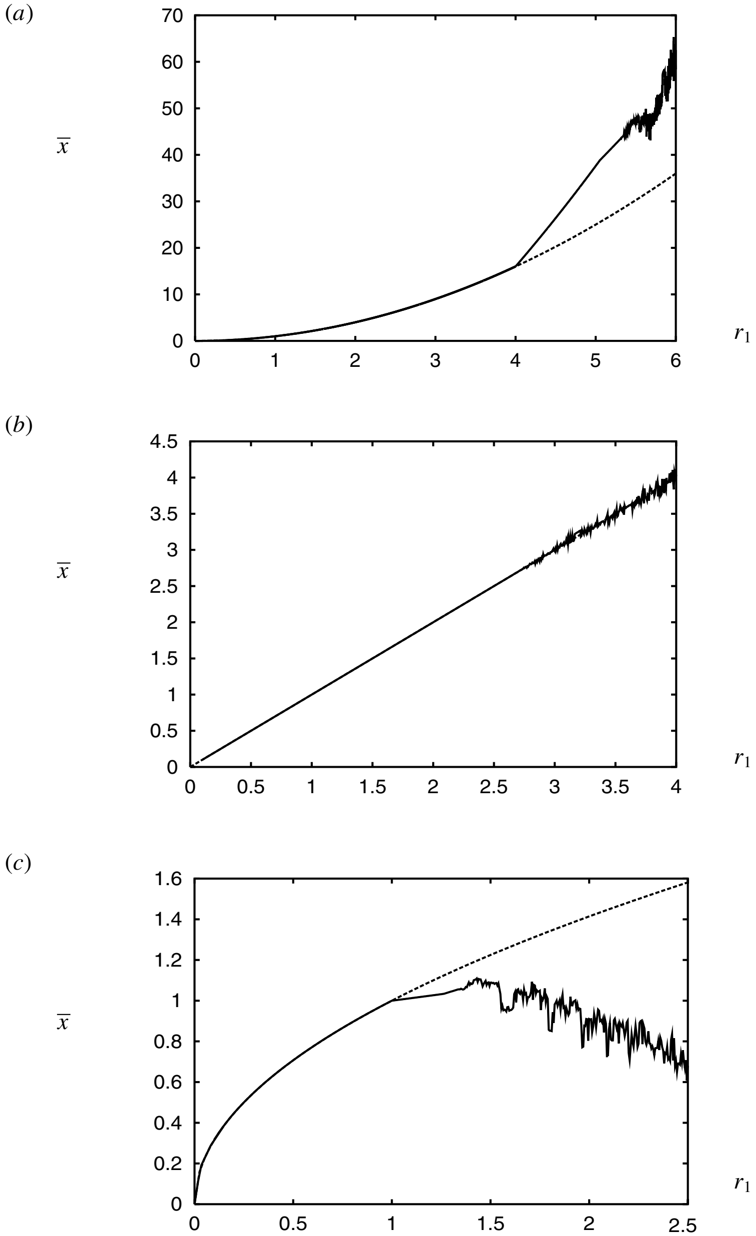

Fig. 2. The average population density $\overline{x}_1$ produced by the one-dimensional map $x_1(t+1) = x_1(t)\exp[r_1 - a_{11}x_1(t)^{\nu_{11}}]$ with $a_{11} = 1$. The $\overline{x}_1$ is given by $\sum_{t=10001}^{10100} x_1(t)/100$ for the orbit $\{x_1(t)\}$ with $x_1(0) = 1$. The $\overline{x}_1$ is represented by the solid line. The dashed line gives a positive fixed point x_1^* of the one-dimensional map. The function $r_1 - a_{11}x_1^{\nu_{11}}$ in (a), (b) and (c) are chosen convex ($\nu_{11} = 0.5$), linear ($\nu_{11} = 1$) and concave ($\nu_{11} = 2$), respectively. (a): $\overline{x}_1 \geq x_1^*$. (b): $\overline{x}_1$ almost coincides with x_1^*. (c): $\overline{x}_1 \leq x_1^*$. See Lemma 3.2.

By (H2), $\sum_{n=0}^{t_k-1} x_1(n)/t_k$ is bounded. By (H1) and (H2), $\sum_{n=0}^{t_k-1} \ln f_2(x_1(n), 0)/t_k$ is also bounded. Hence, there exists a subsequence, again denoted by t_k, such that

$$\lim_{k\to\infty} \frac{1}{t_k} \sum_{n=0}^{t_k-1} \ln f_2(x_1(n), 0) \geq \xi \lim_{k\to\infty} \overline{x}_1(t_k) + \eta.$$

By Lemma 3.2,

$$\xi \lim_{k\to\infty} \overline{x}_1(t_k) + \eta \geq \xi x_1^* + \eta = \ln f_2(x_1^*, 0).$$

Note that if $\ln f_2(x_1, 0)$ is increasing (the case (I)), then $\xi \geq 0$, and if decreasing (the case (II)), then $\xi \leq 0$. Since the fixed point $(x_1^*, 0)$ is not saturated, $\ln f_2(x_1^*, 0) > 0$. This completes the proof. □

To show permanence of (1.1), we need the following theorem:

Theorem 3.1. *Consider System* (1.1) *with* (H1) *and* (H2). *Assume that* $X \subset X_1$ *and* $S \subset X \cap S_i$ *for some* $i \in \{1, 2\}$. *Let* S *and* $X \backslash S$ *be forward invariant. Suppose that the following inequality holds for every* $\mathbf{x}(0) \in \Omega(S)$*:*

$$\sigma_j(\mathbf{x}(0)) = \sup_{t\geq 0} \left(\exp\left[\frac{1}{t} \sum_{n=0}^{t-1} \ln f_j(x_1(n), x_2(n)) \right] \right)^t > 1, \quad (j \in \{1, 2\}, i \neq j). \tag{3.5}$$

Then there is a compact absorbing set $M \subset X \backslash S$ *for* $X \backslash S$.

Remark. This theorem is a special case of Theorem 2.2 and Corollary 2.3 of Hutson [9] with an average Liapunov function $P(x_1, x_2) = x_j$.

Theorem 3.2. *Suppose that* (H1) *and* (H2) *hold. Assume that either there are no fixed points on* $S_1 \backslash O$, *or there is one fixed point on* $S_1 \backslash O$ *and one of the following conditions* (I) *or* (II) *holds:*

- (I): $\ln f_1(x_1, 0)$ *is monotonically decreasing and convex, and* $\ln f_2(x_1, 0)$ *is monotonically increasing and convex* (*i.e.,* $(A1)_1$ *and* $(B3)_1$);
- (II): $\ln f_1(x_1, 0)$ *is monotonically decreasing and concave, and* $\ln f_2(x_1, 0)$ *is monotonically decreasing and convex* (*i.e.,* $(A2)_1$ *and* $(B1)_1$).

Assume that either there are no fixed points on $S_2 \backslash O$, *or there is one fixed point on* $S_2 \backslash O$ *and one of the following conditions* (I)' *or* (II)' *holds:*

- (I)': $\ln f_2(0, x_2)$ *is monotonically decreasing and convex, and* $\ln f_1(0, x_2)$ *is monotonically increasing and convex* (*i.e.,* $(A1)_2$ *and* $(B3)_2$);
- (II)': $\ln f_2(0, x_2)$ *is monotonically decreasing and concave, and* $\ln f_1(0, x_2)$ *is monotonically decreasing and convex* (*i.e.,* $(A2)_2$ *and* $(B1)_2$).

Then, System (1.1) *is permanent if it has no saturated fixed points in* $\mathrm{bd}\mathbb{R}^2_+$.

Proof. Since the fixed point $(0,0)$ is not saturated, then there exists an $i \in \{1,2\}$ such that $f_i(0,0) > 1$. We assume that $i = 1$ without loss of generality.

By (H1), it is clear that S_2 and $X_1 \backslash S_2$ are forward invariant. Let us show that the following inequality holds for every $\mathbf{x}(0) \in \Omega(S_2)$:

$$\sigma_1(\mathbf{x}(0)) = \sup_{t \geq 0} \left(\exp \left[\frac{1}{t} \sum_{n=0}^{t-1} \ln f_1(0, x_2(n)) \right] \right)^t > 1.$$

Since $f_1(0,0) > 1$, then $\sigma_1(\mathbf{x}(0)) > 1$ for $\mathbf{x}(0) \in O$. Therefore, if $\Omega(S_2) = O$, it is clear that $\sigma_1(\mathbf{x}(0)) > 1$ for all $\mathbf{x}(0) \in \Omega(S_2)$. Suppose that $\Omega(\mathbf{x}(0)) \neq O$ for some $\mathbf{x}(0) \in S_2$. Then, there exists a sequence $t_k \to \infty$ and a $\delta > 0$ such that $x_2(t_k) \geq \delta$ for all $k \in \mathbb{Z}_+$. Hence, Lemma 3.2 shows that $S_2 \backslash O$ has a fixed point, and Lemma 3.3 shows that $\sigma_1(\mathbf{x}(0)) > 1$. By Theorem 3.1, we see that there exists a compact absorbing set $X_2 \subset X_1 \backslash S_2$ for $X_1 \backslash S_2$. Therefore, we concentrate on the dynamics in X_2. Similarly to the above, let us show that the following inequality holds for every $\mathbf{x}(0) \in \Omega(S_1 \cap X_2)$:

$$\sigma_2(\mathbf{x}(0)) = \sup_{t \geq 0} \left(\exp \left[\frac{1}{t} \sum_{n=0}^{t-1} \ln f_2(x_1(n), 0) \right] \right)^t > 1.$$

By using Lemmas 3.2 and 3.3, we see that $\sigma_2(\mathbf{x}(0)) > 1$ for all $\mathbf{x}(0) \in S_1 \cap X_2$. This implies that System (1.1) is permanent. □

Note that if $\Omega(S_1 \cup S_2)$ consists only of fixed points, the convexity or concavity of $\ln f_i$ is not important for permanence of (1.1). Indeed, it is well known that under such assumptions non-existence of saturated fixed points on $\mathrm{bd}\mathbb{R}_+^2$ implies permanence of (1.1) irrespective of the convexity or concavity of $\ln f_i$.

4. Applications

In this section, we apply Theorem 3.2 to System (1.1) with specific types of interspecific interactions. First, we consider the predator-prey type with the following assumptions:

(PP1): $0 < f_2(0, x_2) < 1$ for all $x_2 > 0$;
(PP2): $f_1(0,0) > 1$;
(PP3): $f_1(x_1, 0)$ is monotonically decreasing with $x_1^* > 0$ such that $f_1(x_1^*, 0) = 1$;
(PP4): $f_2(x_1, 0)$ is monotonically increasing;

where x_1 and x_2 denote population densities of a prey and a predator, respectively. These assumptions are interpreted biologically as follows: Condition (PP1) implies that the predator cannot survive without the prey. Condition (PP2) means that the prey can survive by itself. Condition (PP3) implies that the population growth rate of the prey decreases as its population density increases (intraspecific competition). Condition (PP4) implies that the invasion rate of the predator increases as the density of its food (prey) increases.

For the predator-prey system, we have the following corollary of Theorem 3.2:

Corollary 4.1. *Suppose that* (H1)*,* (H2)*, and* (PP1)–(PP4) *hold. Assume that* $\ln f_1(x_1, 0)$ *and* $\ln f_2(x_1, 0)$ *are convex. Then, System* (1.1) *is permanent if* $f_2(x_1^*, 0) > 1$.

Proof. By (PP1), $S_2\backslash O$ does not have a fixed point. By (PP3), the system has a fixed point in $S_1\backslash O$. Since $\ln f_1(x_1, 0)$ is monotonically decreasing and convex, the condition $(\mathrm{A1})_1$ holds. Additionally, since $\ln f_2(x_1, 0)$ is monotonically increasing and convex, the condition $(\mathrm{B3})_1$ holds. Therefore, it is enough to check whether or not the fixed points in $\mathrm{bd}\mathbb{R}_+^2$ are saturated. The system has two fixed points, $(0, 0)$ and $(x_1^*, 0)$, in $\mathrm{bd}\mathbb{R}_+^2$. Since $f_1(0, 0) > 1$ and $f_2(x_1^*, 0) > 1$, there are no saturated fixed points in $\mathrm{bd}\mathbb{R}_+^2$. □

The assumption of $\ln f_1(x_1, 0)$ and $\ln f_2(x_1, 0)$ has the following biological meanings. The convexity of $\ln f_1(x_1, 0)$ is achieved if the intensity of the intraspecific competition in the prey population shows a decelerating rise. $\ln f_2(x_1, 0)$ is the number of offspring of the predator when the prey's population density is x_1 and the predator is very rare. In many predator-prey models, this function is given by a saturated function (e.g., type I, II, and III functional responses). Therefore, the assumption that $\ln f_2(x_1, 0)$ is convex is a contradiction to the fact that the function is saturated. However, if $\ln f_2(x_1, 0)$ has type III functional response (i.e., sigmoidal functional response), then the function is convex on some interval $[0, A]$. Hence, if the prey's population density is eventually bounded in this interval, the assumption for $\ln f_2(x_1, 0)$ is satisfied.

Next, consider the competitive type with the following assumptions:

(C1): $f_1(0, 0) > 1$ and $f_2(0, 0) > 1$;
(C2): $f_1(x_1, 0)$ and $f_2(0, x_2)$ are monotonically decreasing with $x_1^* > 0$ and $x_2^* > 0$ such that $f_1(x_1^*, 0) = 1$ and $f_2(0, x_2^*) = 1$;
(CP): $f_1(0, x_2)$ and $f_2(x_1, 0)$ are monotonically decreasing.

These assumptions have the following meanings: Condition (C1) means that both species can survive if they are isolated from each other. Conditions (C2) and (CP) imply that intraspecific and interspecific competition are present, respectively.

For the competitive system, we have the following corollary of Theorem 3.2:

Corollary 4.2. *Suppose that* (H1)*,* (H2)*,* (C1)*,* (C2)*, and* (CP) *hold. Assume that* $\ln f_1(x_1, 0)$ *and* $\ln f_2(0, x_2)$ *are concave, and* $\ln f_1(0, x_2)$ *and* $\ln f_2(x_1, 0)$ *are convex. Then, System* (1.1) *is permanent if* $f_1(0, x_2^*) > 1$ *and* $f_2(x_1^*, 0) > 1$.

Proof. By (C2), the system has fixed points both in $S_1\backslash O$ and $S_2\backslash O$. By the assumptions about the four functions, $\ln f_2(0, x_2)$, $\ln f_1(x_1, 0)$, $\ln f_1(0, x_2)$, and $\ln f_2(x_1, 0)$, we see that the conditions $(\mathrm{A2})_1$, $(\mathrm{A2})_2$, $(\mathrm{B1})_1$, and $(\mathrm{B1})_2$ hold. Finally, $f_1(0, x_2^*) > 1$, $f_2(x_1^*, 0) > 1$ and (C1) ensure that there are no saturated fixed points in $\mathrm{bd}\mathbb{R}_+^2$. □

In this corollary, the function $\ln f_1(x_1, 0)$ (or $\ln f_2(0, x_2)$) is assumed to be concave. This assumption implies that the intensity of the interspecific competition shows an accelerating rise. The assumption that $\ln f_1(0, x_2)$ (or $\ln f_2(x_1, 0)$) is convex means that the intensity of the interspecific competition shows a decelerating rise. Therefore, the assumptions of this corollary imply that the population is more sensitive to the density of the same species than that of the other species.

Finally, we consider the cooperative type with the following (CO) in addition to (C1) and (C2) defined above:

(CO): $f_1(0, x_2)$ and $f_2(x_1, 0)$ are monotonically increasing.

Condition (CO) means that the growth rate of each species is enhanced by an increase of the other species' population density.

The direct application of Theorem 3.2 gives a sufficient condition for permanence of the cooperative system. However, by applying Theorem 3.1 directly to the system, we can easily obtain a better condition than the one given by Theorem 3.2 without assuming the condition (C2).

Theorem 4.1. *Suppose that* (H1)*,* (H2)*,* (C1)*, and* (CO) *hold. Then, System* (1.1) *is permanent.*

Proof. By (H1), it is clear that S_2 and $X_1 \backslash S_2$ are forward invariant. We can easily see that $\sigma_1(\mathbf{x}(0)) > 1$ for all $\mathbf{x}(0) \in S_2$. Indeed, since $f_1(0, x_2)$ is monotonically increasing and $f_1(0, 0) > 1$, then

$$\sigma_1(\mathbf{x}(0)) \geq \sup_{t \geq 0} \left(\exp \left[\frac{1}{t} \sum_{n=0}^{t-1} \ln f_1(0, 0) \right] \right)^t > 1.$$

Hence, Theorem 3.1 shows that there exists a compact absorbing set $X_2 \subset X_1 \backslash S_2$ for $X_1 \backslash S_2$. Consider the dynamics in X_2. The following inequality holds for all $\mathbf{x}(0) \in S_1 \cap X_2$

$$\sigma_2(\mathbf{x}(0)) \geq \sup_{t \geq 0} \left(\exp \left[\frac{1}{t} \sum_{n=0}^{t-1} \ln f_2(0, 0) \right] \right)^t > 1,$$

since $f_2(x_1, 0)$ is monotonically increasing and $f_2(0, 0) > 1$. This implies that the system is permanent. □

Remark. In this theorem, it is assumed that (H2) holds, that is, the system is dissipative. See Appendix B for a dissipative example of cooperative systems.

5. Specific examples

In this section, we consider the dynamics of the following model:

$$\begin{cases} x_1(t+1) = x_1(t) \exp[\beta_1 + \alpha_{11} x_1(t)^{\nu_{11}} + \alpha_{12} x_2(t)^{\nu_{12}}] \\ x_2(t+1) = x_2(t) \exp[\beta_2 + \alpha_{21} x_1(t)^{\nu_{21}} + \alpha_{22} x_2(t)^{\nu_{22}}], \end{cases} \tag{5.1}$$

where α_{ij}, $\beta_i \in \mathbb{R}$ and $\nu_{ij} > 0$, $(i, j \in \{1, 2\})$. The model clearly satisfies the condition (H1). Depending on the sign of the parameters α_{ij} $(i, j \in \{1, 2\})$, System (5.1) can become predator-prey, competitive, and cooperative systems.

5.1. Predator-prey systems

Let

$$\begin{pmatrix} \beta_1 \\ \beta_2 \end{pmatrix} = \begin{pmatrix} r_1 \\ -r_2 \end{pmatrix} \quad \text{and} \quad \begin{pmatrix} \alpha_{11} & \alpha_{12} \\ \alpha_{21} & \alpha_{22} \end{pmatrix} = \begin{pmatrix} -a_{11} & -a_{12} \\ a_{21} & 0 \end{pmatrix},$$

where r_i and a_{ij} $(i, j \in \{1, 2\})$ are positive. Then, System (5.1) expresses the population dynamics of the prey x_1 and the predator x_2. We see that System (5.1) with such parameters satisfies the condition (PP1)–(PP4). With the new parameter notations, System (5.1) is rewritten as follows:

$$\begin{cases} x_1(t+1) = x_1(t) \exp[r_1 - a_{11} x_1(t)^{\nu_{11}} - a_{12} x_2(t)^{\nu_{12}}] \\ x_2(t+1) = x_2(t) \exp[-r_2 + a_{21} x_1(t)^{\nu_{21}}], \end{cases} \tag{5.2}$$

where all parameters are positive constants.

The permanence condition of this system is given as follows:

Corollary 5.1. *Assume that* $0 < \nu_{11} \le 1$ *and* $\nu_{21} \ge 1$*. Then, System* (5.2) *is permanent if*

$$\left(\frac{r_1}{a_{11}}\right)^{\frac{1}{\nu_{11}}} > \left(\frac{r_2}{a_{21}}\right)^{\frac{1}{\nu_{21}}}.$$

Proof. The condition (H2) holds, since System (5.2) is dissipative (see Appendix C). We see that (PP1)–(PP4) hold. The functions $\ln f_1(x_1, 0)$ and $\ln f_2(x_1, 0)$ are convex if $0 < \nu_{11} \le 1$ and $\nu_{12} \ge 1$. Indeed, under such assumptions, the second order derivatives of the functions are positive. Since the fixed point $(x_1^*, 0)$ is not saturated, i.e., $f_2(x_1^*, 0) > 1$, Corollary 4.1 completes the proof. □

Remark. Note that if the inequality is reversed, clearly the system is not permanent, since a boundary fixed point is saturated and attracts an interior orbit.

Since System (5.2) can have not only a fixed point but also a periodic orbit on the x_1-axis (see Fig. 1), there could exist an interior orbit which converges to such a periodic orbit. However, this corollary ensures that under the assumption that $0 < \nu_{11} \le 1$ and $\nu_{21} \ge 1$ there are no interior orbits which converge to the periodic orbit on the x_1-axis as long as the fixed point $(x_1^*, 0)$ is unsaturated.

Hereafter, we consider the case where either $0 < \nu_{11} \le 1$ or $\nu_{21} \ge 1$ does not hold, that is, either $\ln f_1(x_1, 0)$ or $\ln f_2(x_1, 0)$ is not convex. In such a case, we can observe an interesting dynamics in the neighborhood of the x_1-axis (see also Hutson and Moran [11], Hadeler and Gerstmann [5], Neubert and Kot [20], Kon and Takeuchi [12,13], and Kot [15], pp.181–197).

Consider the stability of the periodic orbit $\mathbf{p}^{(m)} = \{(p_1^{(m)}(i), 0)\}_{i=1,\dots,m}$ on the x_1-axis. The stability is determined by the following Jacobian matrix:

$$J^{(m)} = \prod_{i=1}^{m} J(p_1^{(m)}(i), 0),$$

where

$$J(x_1, x_2) = \begin{pmatrix} J_{11}(x_1, x_2) & J_{12}(x_1, x_2) \\ J_{21}(x_1, x_2) & J_{22}(x_1, x_2) \end{pmatrix},$$

$$\begin{aligned} J_{11}(x_1, x_2) &= (1 - a_{11}\nu_{11}x_1^{\nu_{11}}) \exp[r_1 - a_{11}x_1^{\nu_{11}} - a_{12}x_2^{\nu_{12}}] \\ J_{12}(x_1, x_2) &= -a_{12}\nu_{12}x_1x_2^{\nu_{12}-1} \exp[r_1 - a_{11}x_1^{\nu_{11}} - a_{12}x_2^{\nu_{12}}] \\ J_{21}(x_1, x_2) &= a_{21}\nu_{21}x_1^{\nu_{21}-1}x_2 \exp[-r_2 + a_{21}x_1^{\nu_{21}}] \\ J_{22}(x_1, x_2) &= \exp[-r_2 + a_{21}x_1^{\nu_{21}}]. \end{aligned}$$

Since $J_{21}(p_1^{(m)}(i), 0) = 0$ for all $i \in \{1, \dots, m\}$, the periodic orbit $\mathbf{p}^{(m)}$ is stable if

$$\begin{aligned} |\lambda_1^{(m)}| &= \left| \prod_{i=1}^{m} J_{11}(p_1^{(m)}(i), 0) \right| \\ &= \left| \prod_{i=1}^{m} (1 - a_{11}\nu_{11}(p_1^{(m)}(i))^{\nu_{11}}) \exp[r_1 - a_{11}(p_1^{(m)}(i))^{\nu_{11}}] \right| < 1 \end{aligned}$$

and

$$\begin{aligned} |\lambda_2^{(m)}| = \lambda_2^{(m)} &= \prod_{i=1}^{m} J_{22}(p_1^{(m)}(i), 0) \\ &= \exp\left[m \left(-r_2 + a_{21}\frac{1}{m}\sum_{i=1}^{m}(p_1^{(m)}(i))^{\nu_{21}} \right) \right] < 1. \end{aligned}$$

Note that $\mathbf{p}^{(1)}$ corresponds to the fixed point $(x_1^*, 0)$, and $\lambda_2^{(1)} > 1$ implies that the fixed point $(x_1^*, 0)$ is unsaturated. $\lambda_1^{(m)}$ and $\lambda_2^{(m)}$ determine the internal and transversal stability of $\mathbf{p}^{(m)}$, respectively. Hence, we see that if $\lambda_2^{(m)} < 1$ holds, then there exists an interior orbit which converges to $\mathbf{p}^{(m)}$. Additionally, if $|\lambda_1^{(m)}| < 1$ also holds, then $\mathbf{p}^{(m)}$ is stable.

Fig. 3 is the parameter space demarcated with the stability of the boundary periodic orbit $\mathbf{p}^{(m)}$ and the positive fixed point of (5.2). In the hatched region of Fig. 3, the positive fixed point is stable. The internal stability of the boundary periodic orbit $\mathbf{p}^{(m)}$ is estimated by Fig. 1 since the internal stability is identical to the stability of the periodic orbit $\{p_1^{(m)}(i)\}_{i=1,\dots,m}$ of the following one-dimensional map:

$$x_1(t+1) = x_1(t) \exp[r_1 - a_1x_1(t)^{\nu_{11}}].$$

For example, the boundary periodic orbit $\mathbf{p}^{(2)}$ is internally stable ($|\lambda_1^{(2)}| < 1$) if r is approximately in the interval [4, 5] in Fig. 3 (a) and (b), and [1, 1.25] in Fig. 3 (c) and (d). The boundary of the transversal stability of $\mathbf{p}^{(m)}$, which is internally stable, is given by the thin dashed line in Fig. 3. Therefore, with the information on the internal stability estimated by Fig. 1, we confirm that in Fig. 3 (a) and (b), both $|\lambda_1^{(2)}| < 1$ and $|\lambda_2^{(2)}| < 1$ hold if $r_1 \in [4, 5]$, and a_{21} is below the thin dashed line; and in Fig. 3 (c) and (d), $|\lambda_1^{(2)}| < 1$ and $|\lambda_2^{(2)}| < 1$ hold if $r_1 \in [1, 1.25]$, and a_{21} is below the thin dashed line. From Fig. 3 we see that if either $\ln f_1(x_1, 0)$ or $\ln f_2(x_1, 0)$ is not convex (Fig. 3 (a), (c) and (d)), there exists a parameter region (gray region) where $\lambda_2^{(1)} > 1$ and $\lambda_2^{(m)} < 1$ simultaneously hold for some $m \in \mathbb{Z}_+$. These results imply that under the assumption that either $\ln f_1(x_1, 0)$ or $\ln f_2(x_1, 0)$ is not convex, system (5.2) without saturated fixed points in $\mathrm{bd}\mathbb{R}_+^2$ ($\lambda_2^{(1)} > 1$) is not necessarily permanent.

Moreover, in Fig. 3 (a) and (c), there is a parameter region (denoted by A) where both the positive fixed point and the boundary periodic orbits are stable (see also Fig. 4, which is the magnified pictures of Fig. 3 (a) and (c)). The typical solutions of (5.2) with the parameters in such parameter regions are shown in Fig. 5. Fig.5 shows the solution of the bistable system. By this coexistence of multiple attractors, we see that the existence of the stable positive fixed point is not sufficient for permanence.

5.2. *Competitive systems*

Similarly to the predator-prey system, we consider the dynamics of competitive systems. Let

$$\begin{pmatrix}\beta_1\\ \beta_2\end{pmatrix} = \begin{pmatrix} r_1\\ r_2\end{pmatrix} \quad \text{and} \quad \begin{pmatrix}\alpha_{11} & \alpha_{12}\\ \alpha_{21} & \alpha_{22}\end{pmatrix} = \begin{pmatrix}-a_{11} & -a_{12}\\ -a_{21} & -a_{22}\end{pmatrix},$$

where r_i and a_{ij} $(i, j \in \{1, 2\})$ are positive. With the new parameter notations, System (5.1) is rewritten as follows:

$$\begin{cases} x_1(t+1) = x_1(t)\exp[r_1 - a_{11}x_1(t)^{\nu_{11}} - a_{12}x_2(t)^{\nu_{12}}]\\ x_2(t+1) = x_2(t)\exp[r_2 - a_{21}x_1(t)^{\nu_{21}} - a_{22}x_2(t)^{\nu_{22}}],\end{cases} \tag{5.3}$$

where all parameters are positive constants. This system satisfies the condition (C1), (C2), and (CP). Therefore, we can apply Corollary 4.2 to System (5.3).

Corollary 5.2. *Assume that* $\nu_{11} \geq 1$, $\nu_{22} \geq 1$, $0 < \nu_{12} \leq 1$, *and* $0 < \nu_{21} \leq 1$. *Then, System* (5.3) *is permanent if*

$$\left(\frac{r_2}{a_{21}}\right)^{\frac{1}{\nu_{21}}} > \left(\frac{r_1}{a_{11}}\right)^{\frac{1}{\nu_{11}}} \quad \text{and} \quad \left(\frac{r_1}{a_{12}}\right)^{\frac{1}{\nu_{12}}} > \left(\frac{r_2}{a_{22}}\right)^{\frac{1}{\nu_{22}}}.$$

Proof. Obviously the condition (C1), (C2), and (CP) hold. Since System (5.3) is dissipative, (H2) holds (see Appendix C). By considering the second order derivatives of the functions, we see that $\ln f_1(x_1, 0)$ and $\ln f_2(0, x_2)$ are concave, and $\ln f_1(0, x_2)$ and $\ln f_2(x_1, 0)$ are convex. Since both boundary fixed points $(x_1^*, 0)$

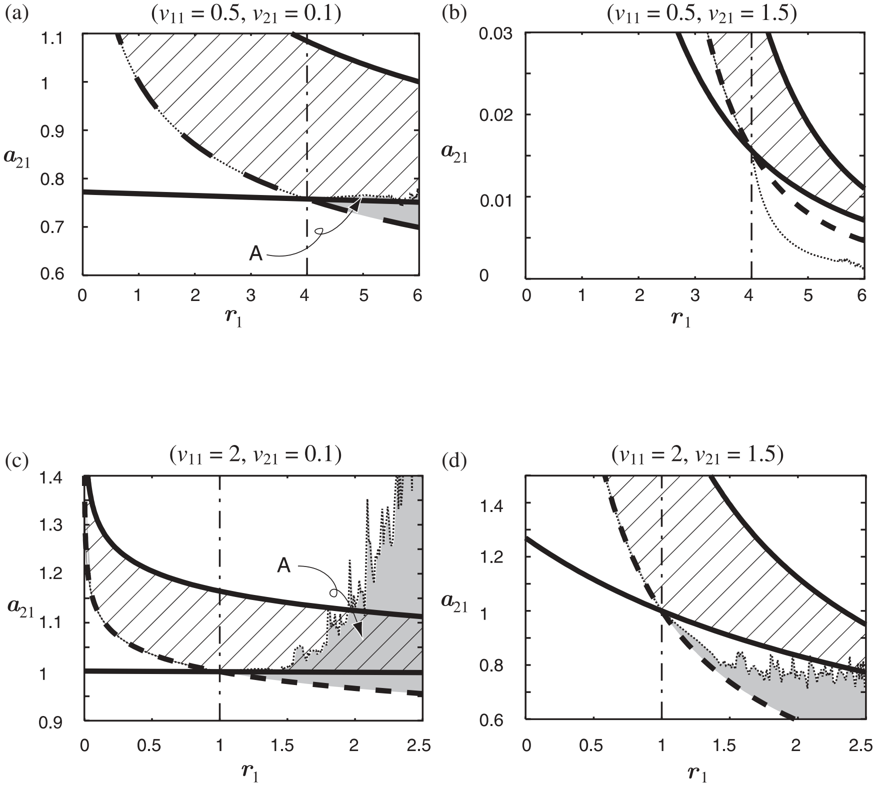

Fig. 3. The r_1-a_{21} parameter space for the predator-prey system (5.2). The thick broken line is the boundary of the transversal stability of the fixed point $(x_1^*, 0)$. Above this line, the fixed point $(x_1^*, 0)$ is unsaturated. The thin dashed line is the boundary of the transversal stability of the periodic orbit, which is internally stable on the x_1-axis. Below the line, the periodic orbit is transversally stable. The dot-dashed line is a boundary for the internal stability of the fixed point $(x_1^*, 0)$ (see also Fig. 1). The thick solid and broken lines give a hatchet region in which the positive fixed point of System (5.2) is stable. The parameters are $a_{11} = 1$, $r_2 = 1$, $a_{12} = 1$, and $\nu_{12} = 1$. In (a), (c), and (d), we can observe that there exists a parameter region (gray region) in which the fixed point $(x_1^*, 0)$ is unsaturated, and a stable periodic orbit exists in $\mathrm{bd}\mathbb{R}_+^2$. The thin dashed line is never above the thick broken line in (b) (see Corollary 5.1). In (a) and (c), we can clearly observe that there is a parameter region (denoted by A) in which both the positive fixed point of (5.2) and the periodic orbit in $\mathrm{bd}\mathbb{R}_+^2$ are stable (see also Fig. 4).

and $(0, x_2^*)$ are unsaturated, i.e., $f_2(x_1^*, 0) > 1$ and $f_1(0, x_2^*) > 1$, Corollary 4.2 completes the proof. □

Remark. Note that if one of the inequalities is reversed, clearly the system is not permanent, since a boundary fixed point is saturated and attracts an interior orbit.

Hereafter, we consider the case where either $\nu_{11} \geq 1$ or $\nu_{21} \leq 1$ does not hold, that is, ln $f_1(x_1, 0)$ is not concave or ln $f_2(x_1, 0)$ is not convex. In this case, we can

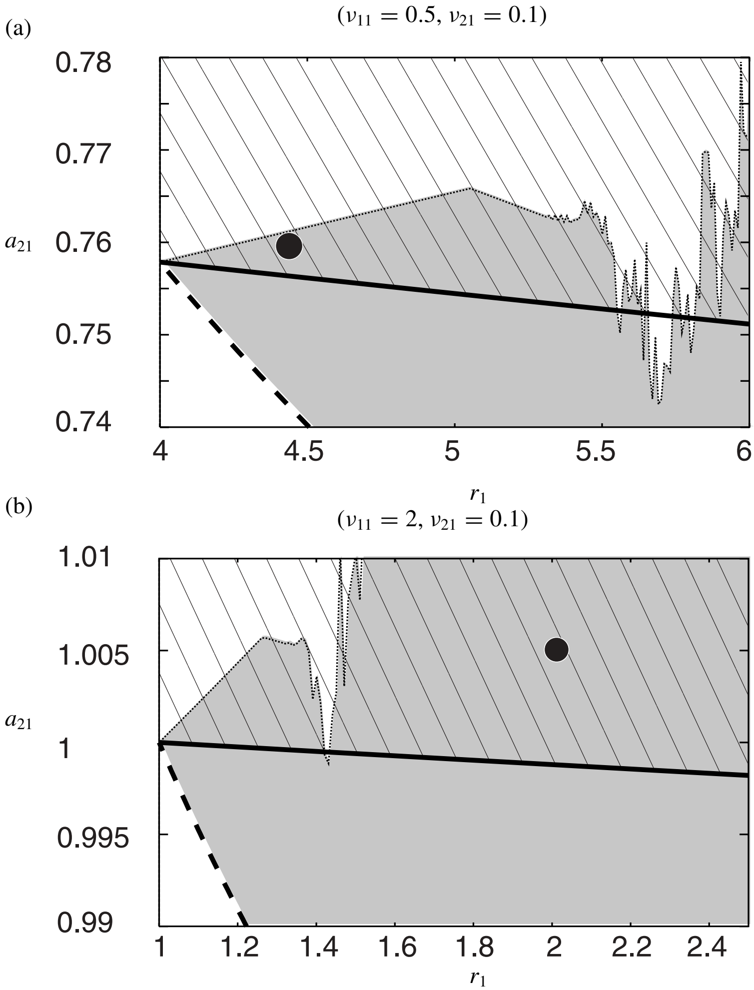

Fig. 4. The enlarged r_1-a_{21} parameter space for the predator-prey system (5.2) given in Fig. 3. Fig. 4 (a) and (b) correspond to Fig. 3 (a) and (c), respectively. The population dynamics with the parameters corresponding to the solid dots in (a) and (b) are given in Fig. 5 (a) and (b), respectively.

find an interesting dynamics in the neighborhood of the x_1-axis similar to the predator-prey systems. Note that if either $\nu_{22} \geq 1$ or $\nu_{12} \leq 1$ does not hold, we can also find similar dynamics in the neighborhood of the x_2-axis. Consider the stability of the periodic orbit $\mathbf{p}^{(m)} = \{(p_1^{(m)}(i), 0)\}_{i=1,\ldots,m}$ on the x_1-axis. The periodic orbit $\mathbf{p}^{(m)}$ is stable if

$$|\lambda_1^{(m)}| = \left| \prod_{i=1}^{m} (1 - a_{11}\nu_{11}(p_1^{(m)}(i))^{\nu_{11}}) \exp[r_1 - a_{11}(p_1^{(m)}(i))^{\nu_{11}}] \right| < 1$$

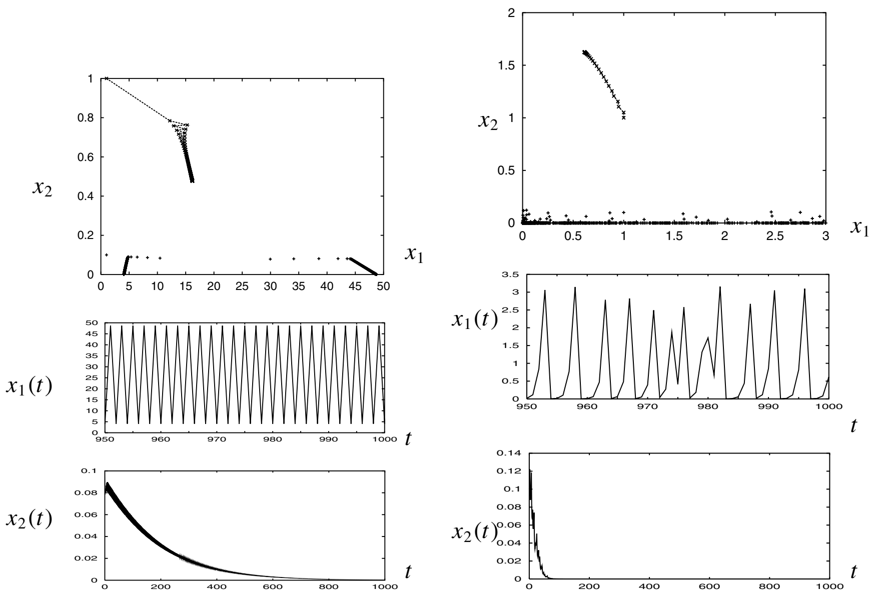

Fig. 5. The population dynamics of System (5.2) with the parameters $a_{11} = 1$, $r_2 = 1$, $a_{12} = 1$, and $\nu_{12} = 1$. The population dynamics with the initial population densities $(x_1(0), x_2(0)) = (1, 1)$ and $(1, 0.1)$ are given in the top figures of (a) and (b). The solution with $(x_1(0), x_2(0)) = (1, 1)$ converges to the positive fixed point, but the solution with $(x_1(0), x_2(0)) = (1, 0.1)$ converges to the boundary fixed point. The lower two figures of (a) and (b) give temporal fluctuations of the prey and the predator with the initial population density $(x_1(0), x_2(0)) = (1, 0.1)$. (a): The parameters are $\nu_{11} = 0.5$, $\nu_{21} = 0.1$, $r_1 = 4.5$, and $a_{21} = 0.76$. In the system with the initial population density $(x_1(0), x_2(0)) = (1, 0.1)$, the predator goes to extinction and the prey fluctuates with period two. (b): The parameters are $\nu_{11} = 2$, $\nu_{21} = 0.1$, $r_1 = 2$, and $a_{21} = 1.005$. In the system with the initial population density $(x_1(0), x_2(0)) = (1, 0.1)$, the predator goes to extinction and the prey fluctuates aperiodically.

and

$$|\lambda_2^{(m)}| = \lambda_2^{(m)} = \exp\left[m \left(r_2 - a_{21} \frac{1}{m} \sum_{i=1}^{m} (p_1^{(m)}(i))^{\nu_{21}} \right) \right] < 1.$$

$\lambda_1^{(m)}$ and $\lambda_2^{(m)}$ determine the internal and transversal stability of $\mathbf{p}^{(m)}$, respectively.

Fig. 6 is the parameter space demarcated with the transversal stability of the fixed point and the periodic orbit on the x_1-axis. The boundary of the transversal stability of the boundary fixed point is given by the thick broken line. The thin dotted line is the boundary of the transversal stability of the boundary periodic orbit, which is internally stable. Above the line there exists a stable boundary periodic orbit on the x_1-axis, i.e., $|\lambda_1^{(m)}| < 1$ and $|\lambda_2^{(m)}| < 1$ hold for some $m \in \mathbb{Z}_+$. In the gray region, we can find a parameter set, which satisfies $\lambda_2^{(1)} > 1$ and $\lambda_2^{(m)} < 1$ for some $m \in \mathbb{Z}_+$. From Fig. 6, we confirm that this region exists if either $\nu_{11} \geq 1$

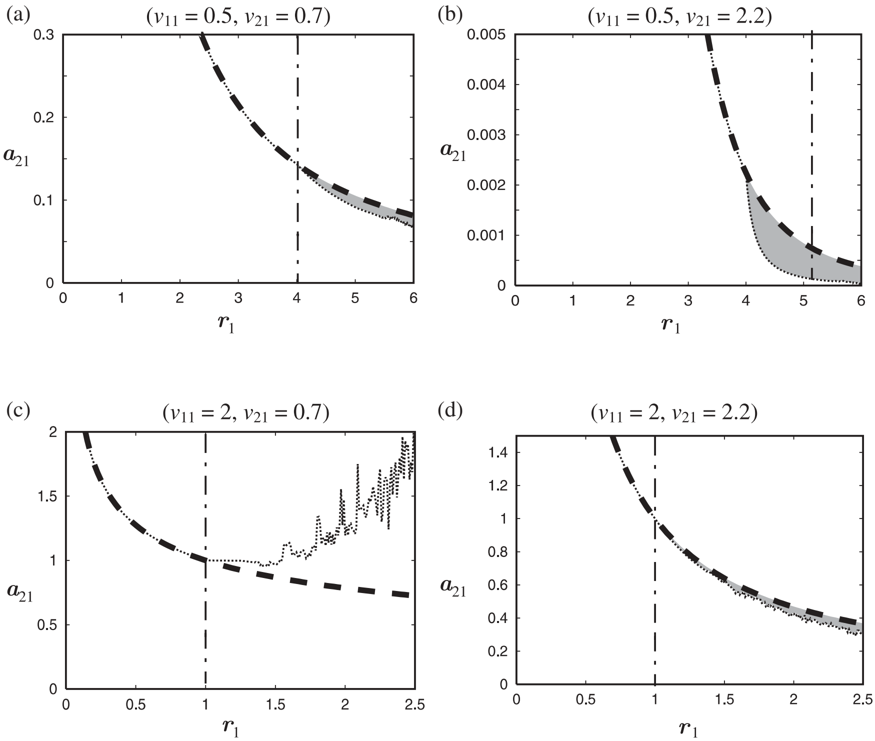

Fig. 6. The r_1-a_{21} parameter space for the competitive system (5.3). The thick broken line is the boundary of transversal stability of the fixed point $(x_1^*, 0)$. Below the line, the fixed point $(x_1^*, 0)$ is unsaturated. The thin dashed line is the boundary of transversal stability of the periodic orbit which is internally stable on the x_1-axis. Above the line, the periodic orbit is transversally stable. The dot-dashed line is a boundary for the internal stability of the positive fixed point $(x_1^*, 0)$ (see also Fig. 1). Similarly to Fig. 3, the parameter region (gray region) which is below the thick broken line and above the thin dashed line implies that there exists a periodic orbit on the x_1-axis that attracts an interior orbit even if the fixed point $(x_1^*, 0)$ is unsaturated. We can find such a parameter region in (a), (b), and (d). The thin dashed line is never below the thick broken line in (c) (see Corollary 5.2). The parameters are $a_{11} = 1$, $r_2 = 1$.

or $\nu_{21} \leq 1$ does not hold. Therefore, we see that under the assumption that either $\ln f_1(x_1, 0)$ is not concave or $\ln f_2(x_1, 0)$ is not convex, unsaturated fixed points do not always imply permanence of System (5.3).

5.3. Cooperative systems

Let

$$\begin{pmatrix} \beta_1 \\ \beta_2 \end{pmatrix} = \begin{pmatrix} r_1 \\ r_2 \end{pmatrix} \quad \text{and} \quad \begin{pmatrix} \alpha_{11} & \alpha_{12} \\ \alpha_{21} & \alpha_{22} \end{pmatrix} = \begin{pmatrix} -a_{11} & a_{12} \\ a_{21} & -a_{22} \end{pmatrix},$$

where r_i and a_{ij} $(i, j \in \{1, 2\})$ are positive. With the new parameter notations, System (5.1) is rewritten as follows:

$$\begin{cases} x_1(t+1) = x_1(t)\exp[r_1 - a_{11}x_1(t)^{\nu_{11}} + a_{12}x_2(t)^{\nu_{12}}] \\ x_2(t+1) = x_2(t)\exp[r_2 + a_{21}x_1(t)^{\nu_{21}} - a_{22}x_2(t)^{\nu_{22}}], \end{cases} \tag{5.4}$$

where all parameters are positive constants. This system satisfies the conditions (C1), (C2) and (CO). Therefore, by Theorem 4.1, if ever System (5.4) is dissipative, then it is permanent. However, it is known that System (5.4) with $\nu_{ij} = 1$ for all $i, j \in \{1, 2\}$ is not dissipative (see Lu and Wang [16]). It is a future work to consider the dissipativeness of (5.4) with $\nu_{ij} \neq 1$ for some $i, j \in \{1, 2\}$. When the terms concerning to the positive effect from the other species, $a_{ij}x_j(t)^{\nu_{ij}}$ $(i \neq j)$, are replaced by saturated functions, the system becomes dissipative (see Appendix B).

6. Discussion

We obtained a sufficient condition for permanence of System (1.1) by using Hutson's theorem (Theorem 3.1). This theorem implies that System (1.1) is permanent if all invariant sets in $\mathrm{bd}\mathbb{R}^2_+$ are unsaturated (see Schreiber [22]). An invariant set in $\mathrm{bd}\mathbb{R}^2_+$ of System (1.1) is determined by an invariant set of a corresponding one-dimensional map. For example, an invariant set on the x_1-axis of System (1.1) is determined by an invariant set of the following map:

$$x_1(t+1) = x_1(t) f_1(x_1(t), 0). \tag{6.1}$$

It is well known that Eq. (6.1) can have rich dynamics (for example, see May and Oster [18]) and complex invariant sets. Therefore, when we directly apply Hutson's theorem to System (1.1), we have to consider such complex invariant sets in $\mathrm{bd}\mathbb{R}^2_+$ mathematically. However, the result of this paper (see Theorem 3.2) gives a simple condition by which we can assure permanence of System (1.1) without knowing the explicit structure of the complex invariant sets in $\mathrm{bd}\mathbb{R}^2_+$.

In Theorem 3.2, one of the following conditions is assumed to be satisfied for every $i \in \{i : S_i \backslash O$ has a fixed point$\}$: (I): $(\mathrm{A1})_i$ and $(\mathrm{B3})_i$, (II): $(\mathrm{A2})_i$ and $(\mathrm{B1})_i$. Under this assumption, nonexistence of boundary saturated fixed points implies permanence of System (1.1) with (H1) and (H2). As described in Corollaries 5.1 and 5.2, the above assumption is reduced to the condition that $\ln f_1(x_1, 0)$ and $\ln f_2(x_1, 0)$ are convex for System (5.2) and that $\ln f_1(x_1, 0)$ and $\ln f_2(0, x_2)$ are concave, and $\ln f_1(0, x_2)$ and $\ln f_2(x_1, 0)$ are convex for System (5.3). In Section 5, by analyzing the specific population models (5.2) and (5.3), we showed that the above assumptions are important. Indeed, we showed that if System (5.2) satisfies one of the following conditions (III), (IV) and (V): (III) $(\mathrm{A1})_1$ and $(\mathrm{B4})_1$; (IV) $(\mathrm{A2})_1$ and $(\mathrm{B3})_1$; and (V) $(\mathrm{A2})_1$ and $(\mathrm{B4})_1$, then it is possible that System (5.2) is not permanent even if all fixed points in $\mathrm{bd}\mathbb{R}^2_+$ are unsaturated (see Fig. 3–5). Similarly, we showed that if System (5.3) satisfies one of the following conditions (VI), (VII) and (VIII): (VI) $(\mathrm{A1})_1$ and $(\mathrm{B1})_1$; (VII) $(\mathrm{A1})_1$ and $(\mathrm{B2})_1$; and (VIII) $(\mathrm{A2})_1$ and $(\mathrm{B2})_1$, then it is possible that System (5.3) is not permanent even if all fixed points in $\mathrm{bd}\mathbb{R}^2_+$ are unsaturated (see Fig. 6). It is a future work to obtain the necessary structure which ensures that nonexistence of boundary saturated fixed points implies permanence of (1.1). Note that in Theorem 4.1, we showed that the cooperative system with (C1) and (CO) is permanent irrespective of the convexity and concavity properties of the growth rate functions if the system is dissipative.

We can find that an attractive positive fixed point and an attractive boundary periodic or chaotic orbits can exist simultaneously in System (5.2), if either $\ln f_1(x_1, 0)$ or $\ln f_2(x_1, 0)$ is not convex (see Figs 4 and 5, and also Hutson and Moran [11], Hadeler and Gerstmann [5], Neubert and Kot [20], and Kot [15], pp.181–189 for the phenomena found in other population models). This phenomenon implies that the predator can go to extinction depending on the initial population densities even if a positive fixed point is stable and a boundary fixed point of the prey is unstable. We see that in this sense the existence of the stable positive fixed point does not imply coexistence of species.

It is well known that the following Kolmogorov system with continuous time can have an invariant set other than fixed points in $\mathrm{bd}\mathbb{R}^n_+$ if $n \geq 3$ (for example, see Hofbauer and Sigmund [8], p.34):

$$\frac{dx_i}{dt} = x_i f_i(x_1, \ldots, x_n) \quad i = 1, \ldots, n. \tag{6.2}$$

In most of the studies that investigate permanence of System (6.2), it is assumed that the omega limit set in $\mathrm{bd}\mathbb{R}^n_+$ consists only of fixed points (for example, see Hutson and Law [10] and Mukherjee *et al.* [19], but see also Gard [4]). To apply our method which focuses on the convexity or concavity of the population growth rate functions to System (6.2) is a future work (but see Mukherjee *et al.* [19]).

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A. Basic theorems

Theorem A.1 (Hutson [9], Lemma 2.1 and Hofbauer *et al.* [7], Lemma 2.1). *Let $F : X \to X$ be continuous, where X is a metric space. Let U be an open set with compact closure, and suppose that V is open and forward invariant, where $\overline{U} \subset V \subset X$. Then if $\gamma_+(\mathbf{x}) \cap U \neq \emptyset$ for every $\mathbf{x} \in V$, $\gamma_+(\overline{U})$ is compact and absorbing for V.*

By this theorem, we see that if there exists a compact set X_0 such that $\gamma_+(\mathbf{x}) \cap (\mathrm{int}X_0) \neq \emptyset$ for every $\mathbf{x} \in X$, then $\gamma_+(X_0)$ is compact and absorbing for X, i.e., F is dissipative.

B. A dissipative example of cooperative systems

Consider the following system:

$$\begin{cases} x_1(t+1) = x_1(t)\exp\left[r_1 - a_{11}x_1(t) + \dfrac{a_{12}x_2(t)}{1+x_2(t)}\right] \\ x_2(t+1) = x_2(t)\exp\left[r_1 + \dfrac{a_{21}x_1(t)}{1+x_1(t)} - a_{22}x_2(t)\right], \end{cases}$$

where the parameters r_i and a_{ij} $(i, j \in \{1, 2\})$ are positive. This system satisfies the conditions (C1), (C2), and (CO). Since the positive effects from the other species are saturated, i.e., $x/(1+x) \le 1$ holds, every solution of the above system satisfies

$$\begin{cases} x_1(t+1) \le x_1(t)\exp\left[r_1 - a_{11}x_1(t) + a_{12}\right] \\ x_2(t+1) \le x_2(t)\exp\left[r_1 + a_{21} - a_{22}x_2(t)\right]. \end{cases}$$

These inequalities imply dissipativeness of the system since $x\exp[r-ax+b]$ has a maximum. Therefore, by Theorem 4.1, the above cooperative system is permanent.

C. Dissipativeness of Systems (5.2) and (5.3)

Lemma C.1. *Systems* (5.2) *and* (5.3) *are dissipative.*

Proof. First, we shall show that System (5.2) is dissipative. By the first equation of (5.2), we have

$$\begin{aligned} x_1(t+1) &\le x_1(t)\exp[r_1 - a_{11}x_1(t)^{\nu_{11}}] \\ &\le \left(\frac{1}{a_{11}\nu_{11}}\right)^{\frac{1}{\nu_{11}}} \exp\left[r_1 - \frac{1}{\nu_{11}}\right] = K_1, \end{aligned} \tag{C.1}$$

since $x_1\exp[r_1 - a_{11}x_1^{\nu_{11}}]$ has a maximum at $x_1 = (1/(a_{11}\nu_{11}))^{1/\nu_{11}}$. Hence, all orbits in $\mathbb{R}^2_+$ eventually enter $M = \{(x_1, x_2) \in \mathbb{R}^2_+ : x_1 \le K_1\}$, where $\mathbf{x} = (x_1, x_2)$, and remain there. If $K_1 < (r_2/a_{21})^{1/\nu_{21}}$, we can easily show that System (5.2) is dissipative, since $x_2(t+1) < x_2(t)$ holds for all $\mathbf{x}(t) \in M$. Therefore, we assume that $K_1 \ge (r_2/a_{21})^{1/\nu_{21}}$.

Let $V(\mathbf{x}) = x_1x_2$. By Eq. (5.2), for all $\mathbf{x}(t) \in M$ we have

$$\begin{aligned} V(\mathbf{x}(t+1)) &= x_1(t)\exp[r_1 - r_2 - a_{11}x_1(t)^{\nu_{11}} + a_{21}x_1(t)^{\nu_{21}}] \\ &\quad \times x_2(t)\exp[-a_{12}x_2(t)^{\nu_{12}}] \\ &\le Lx_2(t)\exp[-a_{12}x_2(t)^{\nu_{12}}], \end{aligned}$$

where $L = \max_{0\le x_1 \le K_1}\{x_1\exp[r_1 - r_2 - a_{11}x_1^{\nu_{11}} + a_{21}x_1^{\nu_{21}}]\}$. Moreover, since $Lx_2\exp[-a_{12}x_2^{\nu_{12}}]$ has a maximum at $x_2 = (1/(a_{12}\nu_{12}))^{1/\nu_{12}}$, we have

$$V(\mathbf{x}(t+1)) \le L\left(\frac{1}{a_{12}\nu_{12}}\right)^{\frac{1}{\nu_{12}}} \exp\left[-\frac{1}{\nu_{12}}\right] = V_M \tag{C.2}$$

for all $\mathbf{x}(t) \in M$. Eqs (C.1) and (C.2) imply that all orbits of System (5.3) eventually enter $M_0 = M \cap \{\mathbf{x} \in \mathbb{R}^2_+ : V(\mathbf{x}) \le V_M\}$ and remain there.

Consider the orbits in M_0. We will show that for every $\mathbf{x}(0) \in M_0$ there exists $T > 0$ such that

$$x_2(t) \le V_M \left(\frac{a_{21}}{r_2}\right)^{\frac{1}{\nu_{21}}} \exp[-r_2 + a_{21} K_1^{\nu_{21}}] = K_2$$

for all $t \ge T$. Let divide M_0 into three regions as follows (see Fig. 7):

$$\begin{aligned} M_1 &= \{\mathbf{x} \in M_0 : x_1 \ge \left(\frac{r_2}{a_{21}}\right)^{\frac{1}{\nu_{21}}}\} \\ M_2 &= \{\mathbf{x} \in M_0 : x_1 < \left(\frac{r_2}{a_{21}}\right)^{\frac{1}{\nu_{21}}}, x_2 \le K_2\} \\ M_3 &= \{\mathbf{x} \in M_0 : x_1 < \left(\frac{r_2}{a_{21}}\right)^{\frac{1}{\nu_{21}}}, x_2 > K_2\}. \end{aligned}$$

By the second equation of (5.2), we have

$$\begin{aligned} x_2(t+1) &= x_2(t) \exp[-r_2 + a_{21} x_1(t)^{\nu_{21}}] \\ &< x_2(t) \end{aligned}$$

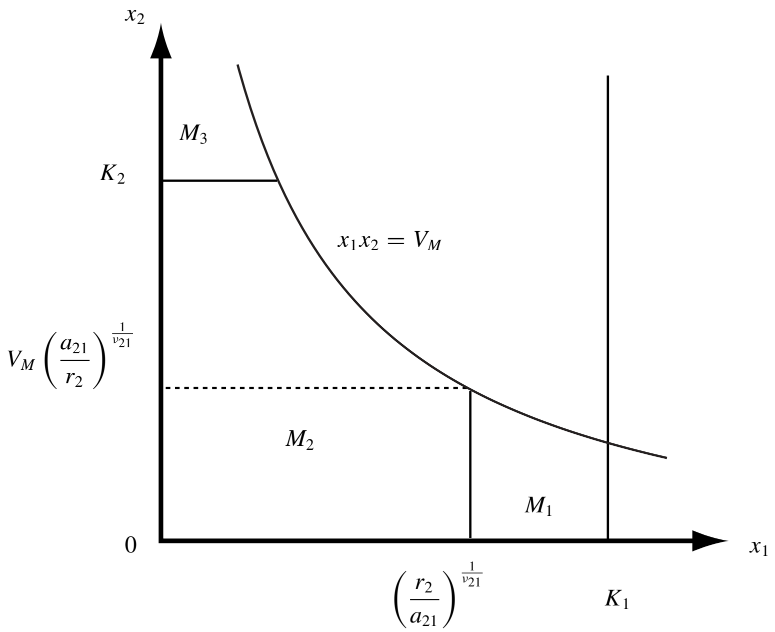

Fig. 7. The phase plane of the predator-prey system (5.2). See the proof of Lemma C.1.

for all $\mathbf{x}(t) \in M_3$. Hence, all orbits in M_3 eventually enter $M_1 \cup M_2$. For $\mathbf{x}(t) \in M_1$, we have

$$\begin{aligned} x_2(t+1) &= x_2(t)\exp[-r_2 + a_{21}x_1(t)^{\nu_{21}}] \\ &\leq V_M \left(\frac{a_{21}}{r_2}\right)^{\frac{1}{\nu_{21}}} \exp[-r_2 + a_{21}K_1^{\nu_{21}}] = K_2. \end{aligned}$$

Hence $\mathbf{x}(t) \in M_1$ implies that $\mathbf{x}(t+1) \in M_1 \cup M_2$. For $\mathbf{x}(t) \in M_2$, we have $x_2(t+1) < x_2(t)$. Therefore, $\mathbf{x}(t) \in M_2$ implies that $\mathbf{x}(t+1) \in M_1 \cup M_2$. It follows that all orbits in M_0 eventually enter $M_1 \cup M_2$ and remain there. This completes the proof for System (5.2).

Consider dissipativeness of System (5.3). By a similar argument used above, we can show that $x_1(t+1) \leq K_1$ for all $\mathbf{x}(t) \in \mathbb{R}^2_+$. Furthermore, by the second equation of (5.2) we have

$$\begin{aligned} x_2(t+1) &\leq x_2(t)\exp[r_2 - a_{22}x_2(t)^{\nu_{22}}] \\ &\leq \left(\frac{1}{a_{22}\nu_{22}}\right)^{\frac{1}{\nu_{22}}} \exp\left[r_2 - \frac{1}{\nu_{22}}\right], \end{aligned}$$

for all $\mathbf{x}(t) \in \mathbb{R}^2_+$. This completes the proof for System (5.3). □

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