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Permanence of a single-species model with 2 stages

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1 Introduction

In this paper, we consider permanence of a single-species model with two stages. The model was proposed by Neubert and Caswell[4] to consider the density dependence effect to stage-structured systems. Their model has a complex solution in the wide range of the parameter space. Therefore, we give the conditions for permanence to ensure that the species persists under such complex solutions. This paper is organized as follows. In Section 2, we introduce a single species model with two stages. In Section 3, we give the definition of permanence, and obtain both sufficient and necessary conditions for permanence of the model. The final section includes discussion and future problems.

2 Stage-Structured Model

We consider permanence of the following stage-structured model:

$$\mathbf{x}(t+1) = \mathbf{A}_{\mathbf{x}}\mathbf{x}(t) \tag{1}$$

$$\mathbf{x}(t) = \begin{pmatrix} x_1(t) \\ x_2(t) \end{pmatrix} \in \mathbb{R}^2_+ := \{(x_1, x_2) \in \mathbb{R}^2 : x_i \geq 0, i = 1, 2\}$$

$$t \in \mathbb{Z}_+ := \{0, 1, 2, \dots\}$$

where

$$\mathbf{A_x} = \begin{pmatrix} \sigma_1 f_1(\mathbf{x}(t))\{1 - \gamma f_3(\mathbf{x}(t))\} & \phi f_4(\mathbf{x}(t)) \\ \sigma_1 f_1(\mathbf{x}(t))\gamma f_3(\mathbf{x}(t)) & \sigma_2 f_2(\mathbf{x}(t)) \end{pmatrix}.$$

Each $f_i : \mathbb{R}^2_+ \to (0, 1]$ $(i = 1, \dots, 4)$, which defines the way of density dependence, is a continuous function with $f_i(0, 0) = 1$, and the parameters satisfy $0 \leq \sigma_1 \leq 1$, $0 \leq \sigma_2 \leq 1$, $0 \leq \gamma \leq 1$ and $0 \leq \phi$. System (1) has two stages, namely, juvenile and adult stages (see Fig.1). Population densities in the juvenile and adult stages at generation t are denoted by $x_1(t)$ and $x_2(t)$, respectively.

System (1) is the generalized version of the model introduced by Neubert and Caswell [4]. Putting $f_i(\mathbf{x}(t)) = \exp[-(x_1(t) + x_2(t))]$ one by one, they investigated the dynamics of (1). Fig.2 shows some examples of the complex solutions of System (1).

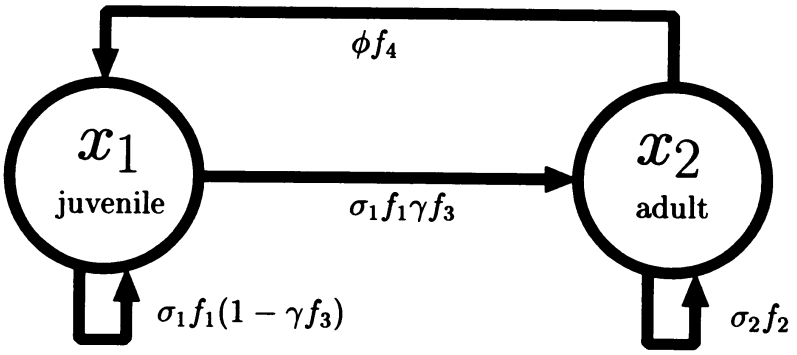

Figure 1: Life cycle of System (1). $\sigma_1 f_1$ and $\sigma_2 f_2$ denote the fraction of juveniles and adults which survive one generation, respectively. γf_3 denotes the fraction of the surviving juveniles that mature to become adult. ϕf_4 is the number of recruited juveniles by one adult individual.

3 Permanence

The definition of permanence is given as follows:

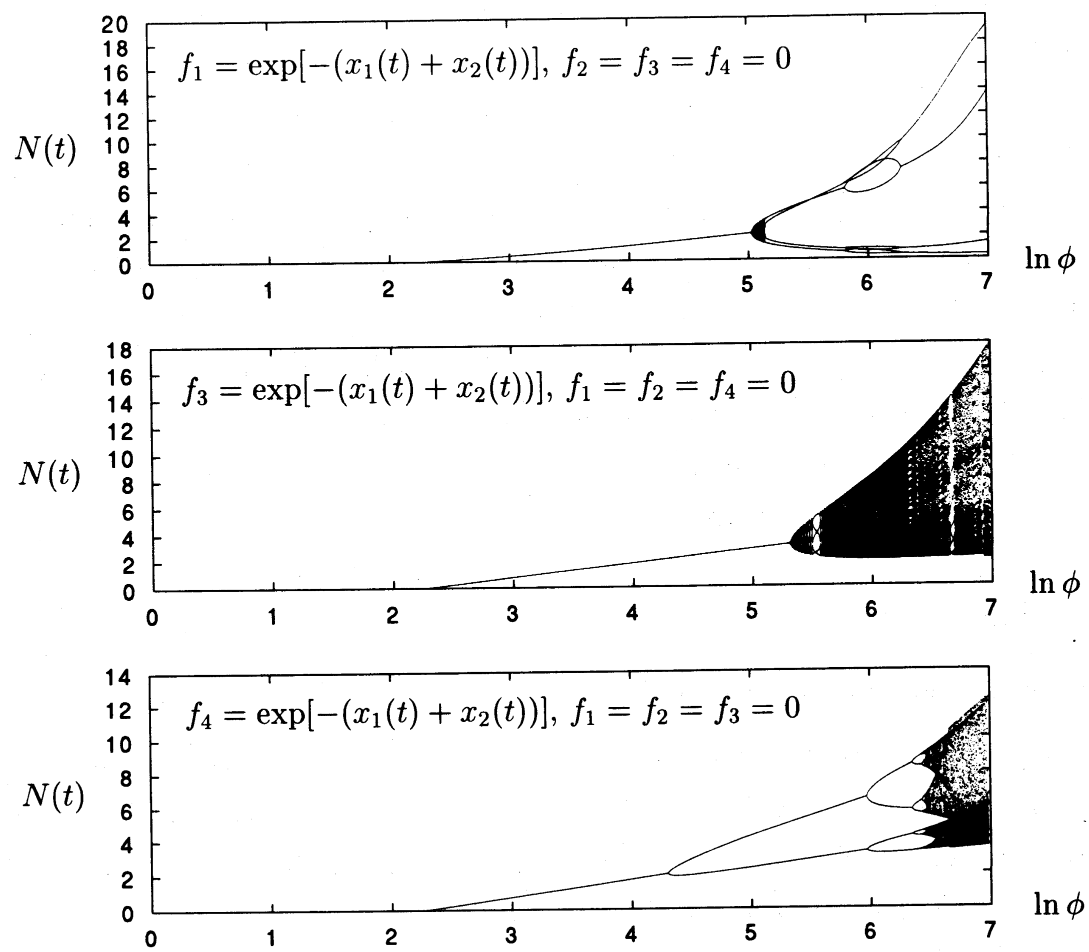

Figure 2: Bifurcation diagrams. The total population density $N(t) = x_1(t) + x_2(t)$ is plotted for the orbit $\{\mathbf{x}(t)\}_{t\in\{1001,\dots,1050\}}$ with $\mathbf{x}(0) = (1,1)$. The parameters are $\sigma_1 = 0.5$, $\sigma_2 = 0.1$ and $\gamma = 0.1$. $\sigma_1\gamma\phi > (1-\sigma_2)\{1-\sigma_1(1-\gamma)\}$ holds for $\ln\phi > \ln 9.9 \approx 2.293$.

Definition 1. *Let* $N(t) = \sum_{i=1}^{2} x_i(t)$*, which is a total population density. Stage-structured system* (1) *is said to be permanent if there exist* $\delta > 0$ *and* $D > 0$ *such that*

$$\delta < \liminf_{t\to\infty} N(t) \le \limsup_{t\to\infty} N(t) \le D$$

for all $\mathbf{x}(0) \in \mathbb{R}_+^2$ *with* $N(0) > 0$.

This definition implies that the following property is enough for permanence of the stage-structured system (1): there exists a compact set $M \subset \mathbb{R}_+^2 \backslash \{(0,0)\}$ such that for all $\mathbf{x}(0) \in \mathbb{R}^2_+ \backslash \{(0,0)\}$ there exists a $T = T(\mathbf{x}(0)) > 0$ satisfying $\mathbf{x}(t) \in M$ for all $t \geq T$.

The definition of permanence seems to be somewhat different from the one used in other literature. That is, in Definition 1 each x_i-axis does not have to be a repellor and only the origin has to be. But this property is appropriate for (1) because if for all generation t there is at least one stage in which population is positive, we can conclude that the species survives. We must note that the variables, x_1 and x_2, of the stage-structured model (1) do not denote the population density of the different species but the population density of the same species.

In order to prove the permanence of System (1), we consider the existence of the δ and D in Definition 1 in turn.

3.1 Repellor

By using the following theorem, we consider the existence of the δ in Definition 1:

Theorem 2. (Hutson [3], Theorem 2.2) *Let (X, d) be a metric space. Consider the system $F : X \to X$, where F is continuous. Assume that X is compact and that S is a compact subset of X with empty interior. Let S and $X \backslash S$ be forward invariant. Suppose that there is a continuous function $P : X \to \mathbb{R}_+$, which is called an average Liapunov function, satisfying the following conditions:*

(a) $P(\mathbf{x}) = 0 \Longleftrightarrow \mathbf{x} \in S$,

(b) $\displaystyle \sup_{t \geq 0} \liminf_{\substack{\mathbf{y} \to \mathbf{x} \\ \mathbf{y} \in X \backslash S}} \frac{P(F^t(\mathbf{y}))}{P(\mathbf{y})} > 1 \quad (\mathbf{x} \in S).$

Then S is a repellor, that is, there is a compact set $M \subset X \backslash S$ such that for all $\mathbf{x} \in X \backslash S$ there exists a $T = T(\mathbf{x}) > 0$ satisfying $F^t(\mathbf{x}) \in M$ for all $t \geq T$.

We need the following lemma for the application of Theorem 2 to the system with uniformly ultimately bounded solutions:

Lemma 3. (Hutson [3], Lemma 2.1, Hofbauer *et al.* [2], Lemma 2.1) *Consider the system $F : X \to X$, where F is continuous. Let U be open with compact closure, and suppose that V is open and forward invariant, where $\overline{U} \subset V \subset X$. If there exists a $T = T(\mathbf{x}) > 0$ such that $F^T(\mathbf{x}) \in U$ for every $\mathbf{x} \in V$, then there exists a forward invariant compact set $X_0 \subset V$ such that there exists a $T_0 = T_0(\mathbf{x}) > 0$ satisfying $F^t(\mathbf{x}) \in X_0$ for all $t \geq T_0$.*

Applying Theorem 2 to System (1) with $S = \{(0,0)\}$ and $P(\mathbf{x}) = x_1 + wx_2$, where w is a positive constant, we obtain the following theorem:

Theorem 4. *Suppose that the solution of System* (1) *is uniformly ultimately bounded. If* $\sigma_1\gamma\phi > (1-\sigma_2)\{1-\sigma_1(1-\gamma)\}$, *then System* (1) *is permanent.*

Proof. Since the solution of System (1) is uniformly ultimately bounded, Lemma 3 guarantees that there exists a forward invariant compact set X such that all orbits in $\mathbb{R}^2_+$ ultimately enter the X. Therefore, it is enough to consider the solutions in X. First, we note that $\sigma_1\gamma\phi > (1-\sigma_2)\{1-\sigma_1(1-\gamma)\}$ implies that $\sigma_1 > 0$, $\gamma > 0$ and $\phi > 0$. Then $X \backslash S$ is clearly forward invariant.

Let w be a positive constant satisfying the following equation:

$$w\sigma_1\{1+\gamma(w-1)\} = \phi + w\sigma_2. \tag{2}$$

Such a positive constant w always exists. Indeed, the quadratic equation

$$g(w) = \sigma_1\gamma w^2 + \{\sigma_1(1-\gamma) - \sigma_2\}w - \phi$$

is negative at $w = 0$, that is, $g(0) = -\phi < 0$.

Let us check the condition (b) in Theorem 2:

$$\begin{aligned}
\sigma &= \sup_{t\geq 0} \liminf_{\substack{\mathbf{y}\to(0,0)\\ \mathbf{y}\in X\backslash S}} \frac{P(F^t(\mathbf{y}))}{P(\mathbf{y})} \\
&= \sup_{t\geq 0} \liminf_{\substack{\mathbf{y}\to(0,0)\\ \mathbf{y}\in X\backslash S}} \frac{P(F^t(\mathbf{y}))}{P(F^{t-1}(\mathbf{y}))} \cdots \frac{P(F^2(\mathbf{y}))}{P(F(\mathbf{y}))}\frac{P(F(\mathbf{y}))}{P(\mathbf{y})} \\
&= \sup_{t\geq 0} \liminf_{\substack{\mathbf{y}\to(0,0)\\ \mathbf{y}\in X\backslash S}} \prod_{i=0}^{t-1} \left[\frac{\sigma_1 f_1(\mathbf{y}(i))\{1+\gamma(w-1)f_3(\mathbf{y}(i))\}y_1(i)}{y_1(i)+wy_2(i)}\right. \\
&\qquad\qquad \left. + \frac{\{\phi f_4(\mathbf{y}(i)) + w\sigma_2 f_2(\mathbf{y}(i))\}y_2(i)}{y_1(i)+wy_2(i)}\right] \\
&= \sup_{t\geq 0} \liminf_{\substack{\mathbf{y}\to(0,0)\\ \mathbf{y}\in X\backslash S}} \prod_{i=0}^{t-1} [\sigma_1 f_1(\mathbf{y}(i))\{1+\gamma(w-1)f_3(\mathbf{y}(i))\} \\
&\qquad + \frac{-w\sigma_1 f_1(\mathbf{y}(i))\{1+\gamma(w-1)f_3(\mathbf{y}(i))\} + \{\phi f_4(\mathbf{y}(i)) + w\sigma_2 f_2(\mathbf{y}(i))\}}{y_1(i)+wy_2(i)} y_2(i)],
\end{aligned}$$

where $\{\mathbf{y}(t)\}_{t\in\mathbb{Z}_+} = \{(y_1(t), y_2(t))\}_{t\in\mathbb{Z}_+}$ is a solution of System (1) with $\mathbf{y} = \mathbf{y}(0)$ and F is defined as a right-hand side of (1). By Eq.(2), we have

$$\lim_{\mathbf{y}(i)\to(0,0)} [-w\sigma_1 f_1(\mathbf{y}(i))\{1+\gamma(w-1)f_3(\mathbf{y}(i))\} + \{\phi f_4(\mathbf{y}(i)) + w\sigma_2 f_2(\mathbf{y}(i))\}] = 0.$$

Furthermore, we have the boundedness of $y_2(i)/(y_1(i)+wy_2(i))$. In fact, the following inequality holds for all $\mathbf{y}(i) \in X\backslash S$:

$$\frac{y_2(i)}{y_1(i)+wy_2(i)} \leq \frac{(y_1(i)+wy_2(i))/w}{y_1(i)+wy_2(i)} = \frac{1}{w}.$$

Therefore, by the continuity of the F, we obtain

$$\sigma = \sup_{t\geq 0}[\sigma_1\{1+\gamma(w-1)\}]^t.$$

After some calculations, we see that $\sigma_1\gamma\phi > (1-\sigma_2)\{1-\sigma_1(1-\gamma)\}$ implies that $\sigma_1\{1+\gamma(w-1)\} > 1$. Hence, the assumptions in Theorem 2 hold. □

3.2 Boundedness

Hereafter, we consider uniform ultimate boundedness of the solution of System (1). Clearly, the boundedness ensures the existence of the D in Definition 1.

Theorem 5. *Suppose that $\sigma_1 \neq 1$ or $\gamma \neq 0$, and $\sigma_2 \neq 1$. If one of $f_1(\mathbf{x})x_1$, $f_3(\mathbf{x})x_1$ or $f_4(\mathbf{x})x_2$ is bounded to the above, then the solution of System (1) is uniformly ultimately bounded.*

Proof. Let $\{\mathbf{x}(t)\}_{t\in\mathbb{Z}_+}$ be a solution of System (1).

First, assume that one of $f_i(\mathbf{x})x_1$ $(i=1,3)$ is bounded to the above, that is, there exists a $K_0 > 0$ such that $x_1 f_i(\mathbf{x}) \leq K_0$ for all $\mathbf{x} \in \mathbb{R}^2_+$ and $i = 1$ or 3. From the second equation of (1), we have

$$\begin{aligned} x_2(t+1) &= \sigma_1 f_1(\mathbf{x}(t))\gamma f_3(\mathbf{x}(t))x_1(t) + \sigma_2 f_2(\mathbf{x}(t))x_2(t) \\ &\leq \sigma_1\gamma f_i(\mathbf{x}(t))x_1(t) + \sigma_2 x_2(t) \\ &\leq \sigma_1\gamma K_0 + \sigma_2 x_2(t). \end{aligned}$$

Since $\sigma_2 \neq 1$ $(0 \leq \sigma_2 < 1)$, there exist $T > 0$ and $K > 0$ such that

$$x_2(t) \leq K$$

for all $t \geq T$. If $\sigma_1 \neq 1$, then from the first equation of (1) we have

$$\begin{aligned} x_1(t+1) &= \sigma_1 f_1(\mathbf{x}(t))\{1-\gamma f_3(\mathbf{x}(t))\}x_1(t) + \phi f_4(\mathbf{x}(t))x_2(t) \\ &\leq \sigma_1 x_1(t) + \phi x_2(t) \leq \sigma_1 x_1(t) + \phi K \end{aligned}$$

for $t \geq T$. If $\gamma \neq 0$, then similarly to the above we have

$$\begin{aligned} x_1(t+1) &= \sigma_1 f_1(\mathbf{x}(t))\{1-\gamma f_3(\mathbf{x}(t))\}x_1(t) + \phi f_4(\mathbf{x}(t))x_2(t) \\ &\leq \{1-\gamma f_3(\mathbf{x}(t))\}x_1(t) + \phi x_2(t) \leq \{1-\gamma f_3(\mathbf{x}(t))\}x_1(t) + \phi K \end{aligned}$$

for $t \geq T$. Note that $\gamma \neq 0$ implies that $0 < 1 - \gamma f_3(\mathbf{x}(t)) < 1$ for all $\mathbf{x}(t) \geq 0$. These inequalities complete the proof of the first case.

Finally, assume that $f_4(\mathbf{x})x_2$ is bounded to the above, that is, there exists a $K_0 > 0$ such that $f_4(\mathbf{x})x_2 \leq K_0$ for all $\mathbf{x} \in \mathbb{R}^2_+$. If $\sigma_1 \neq 1$, then from the first equation of (1) we have

$$\begin{aligned} x_1(t+1) &= \sigma_1 f_1(\mathbf{x}(t))\{1-\gamma f_3(\mathbf{x}(t))\}x_1(t) + \phi f_4(\mathbf{x}(t))x_2(t) \\ &\leq \sigma_1 x_1(t) + \phi f_4(\mathbf{x}(t))x_2(t) \leq \sigma_1 x_1(t) + \phi K_0. \end{aligned}$$

If $\gamma \neq 0$, then similarly to the above we have

$$\begin{aligned} x_1(t+1) &= \sigma_1 f_1(\mathbf{x}(t))\{1-\gamma f_3(\mathbf{x}(t))\}x_1(t) + \phi f_4(\mathbf{x}(t))x_2(t) \\ &\leq \{1-\gamma f_3(\mathbf{x}(t))\}x_1(t) + \phi f_4(\mathbf{x}(t))x_2(t) \leq \{1-\gamma f_3(\mathbf{x}(t))\}x_1(t) + \phi K_0. \end{aligned}$$

Then, there exist $T > 0$ and $K > 0$ such that

$$x_1(t) \leq K$$

for all $t \geq T$. From the second equation of (1), we have

$$\begin{aligned} x_2(t+1) &= \sigma_1 f_1(\mathbf{x}(t))\gamma f_3(\mathbf{x}(t))x_1(t) + \sigma_2 f_2(\mathbf{x}(t))x_2(t) \\ &\leq \sigma_1 \gamma x_1(t) + \sigma_2 x_2(t) \\ &\leq \sigma_1 \gamma K + \sigma_2 x_2(t) \end{aligned}$$

for $t \geq T$. This completes the proof. □

From the following theorem, we see that the boundedness of $f_2(\mathbf{x})x_2$ does not imply uniform ultimate boundedness of the solution of (1).

Theorem 6. *Assume that* $f_1(\mathbf{x}) = f_3(\mathbf{x}) = f_4(\mathbf{x}) = 1$. *If* $\phi > 1$, *then System* (1) *has an unbounded solution.*

Proof. Suppose that all solutions of System (1) are bounded. Then there exist $K > 0$ and $T > 0$ such that

$$x_1(t) \leq K$$

for all $t \geq T$. By (1), we have

$$\begin{aligned} x_1(t+1) + x_2(t+1) &= \sigma_1 x_1(t) + \{\phi + \sigma_2 f_2(\mathbf{x}(t))\} x_2(t) \\ &\geq \phi x_2(t). \end{aligned}$$

Then $x_2(t+1) \geq \phi x_2(t) - x_1(t+1) \geq \phi x_2(t) - K$ for $t \geq T$. Since $\phi > 1$, it is a contradiction to the boundedness of the solution. □

By Theorems 4 and 5, we obtain the following corollary:

Corollary 7. *Assume that* $\sigma_1 \neq 1$ *or* $\gamma \neq 0$, *and* $\sigma_2 < 1$. *Suppose that one of* $f_1(\mathbf{x})x_1$, $f_3(\mathbf{x})x_1$ *or* $f_4(\mathbf{x})x_2$ *is bounded to the above. If* $\sigma_1\gamma\phi > (1-\sigma_2)\{1-\sigma_1(1-\gamma)\}$, *then System* (1) *is permanent.*

The following corollary is an immediate consequence of Theorem 6:

Corollary 8. *Assume that* $f_1(\mathbf{x}) = f_3(\mathbf{x}) = f_4(\mathbf{x}) = 1$. *If* $\phi > 1$, *then System* (1) *is not permanent.*

4 Discussion and Future works

By Corollary 7, it is ensured that the system whose dynamics are shown in Fig.2 is permanent if $\phi > 9.9$ ($\ln \phi > 2.293$).

The condition $\sigma_1\gamma\phi > (1-\sigma_2)\{1-\sigma_1(1-\gamma)\}$ in Theorem 4 has a strong relationship with instability of the origin. In fact, Jacobian matrix at the origin of System (1) is given by

$$A = \begin{pmatrix} \sigma_1(1-\gamma) & \phi \\ \sigma_1\gamma & \sigma_2 \end{pmatrix},$$

and the eigenvalues λ of the matrix satisfy $|\lambda| < 1$ if and only if $\sigma_1\gamma\phi < (1-\sigma_2)\{1-\sigma_1(1-\gamma)\}$ (see Neubert and Caswell[4]). Therefore, it is expected that under the assumption of uniform ultimate boundedness System (1) is permanent if and only if the origin is unstable. It is a future work to show it.

In Theorem 5, we obtained sufficient conditions for uniform ultimate boundedness of the solution of (1). The sufficient conditions require the boundedness of at least one of the functions $f_1(\mathbf{x})x_1$, $f_3(\mathbf{x})x_1$ or $f_4(\mathbf{x})x_2$. However, from the analogy between single-species models with stages and without stages, it is expected that the solution of System (1) can be uniformly ultimately bounded even if all of the $f_1(\mathbf{x})x_1$, $f_3(\mathbf{x})x_1$ and $f_4(\mathbf{x})x_2$ are unbounded. In fact, the solution of the following single-species model with unbounded $f(N)N$ is clearly uniformly ultimately bounded (a positive equilibrium of the system is globally stable, that is, all orbits $\{N(t)\}_{t\in\mathbb{Z}_+}$ with $N(0) > 0$ converge to a positive equilibrium point. This property is proved by Theorem 1 in Cull[1]):

$$N(t+1) = \phi N f(N), \quad \phi > 1$$

$$f(N) = \frac{1}{1+N^{1/2}}.$$

To relax the condition in Theorem 5 is a future work.

System (1) can be easily extended to the system with n-stages. To consider the permanence of the system is also a future work.

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