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Permanence of single-species stage-structured models

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Abstract. In this paper, we consider population survival by using single-species stage-structured models. As a criterion of population survival, we employ the mathematical notation of permanence. Permanence of stage-structured models has already been studied by Cushing (1998). We generalize his result of permanence, and obtain a condition which guarantees that population survives. The condition is applicable to a wide class of stage-structured models. In particular, we apply our results to the Neubert-Caswell model, which is a typical stage-structured model, and obtain a condition for population survival of the model.

1. Introduction

In population ecology, it is one of the most important task to predict population dynamics. In particular, it is important to predict whether a given population can survive in the long term. In this paper, by focusing on population dynamics of a single species, we consider this problem and obtain a criterion which ensures that population survives.

By using one-dimensional discrete-time models, conditions that ensure population survival have been considered by several authors (for example, see Freedman and So, 1987 and Cull, 1986). A general class of models is given by:

$$N(t+1) = f(N(t))N(t), \tag{1}$$

where $t \in \mathbb{Z}_+ = \{0, 1, 2, \dots\}$, $N(t)$ is a population density at time t and $f(N)$ is a population growth rate which depends on the population density. The one-dimensional discrete-time model (1) assumes that the vital rates of each individual, such as rates of survival, development and reproduction, are uniform in the population. However, they are different among the individuals and depend on a stage of life cycle. To incorporate such heterogeneity into the model is one of the step to give reality for the model. Such heterogeneity is incorporated in stage-structured models (see Caswell, 2001). This paper considers the population survival of a single species by using stage-structured models.

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There are several mathematical criteria for population survival. Stability of a coexistence equilibrium point is a simple criterion. However, it is well known that the population can survive without stable coexistence equilibrium points (for example, see May and Oster, 1975). Moreover, it is known that even if the model has a stable coexistence equilibrium point, populations can go extinct depending on the initial population densities (see Hadeler and Gerstmann, 1990, Neubert and Kot, 1992, Kon and Takeuchi, 2001, Kot, 2002, Chapter 11). Therefore, we use permanence, which is defined below, as a criterion for population survival. The criterion can evaluate the possibility of population survival irrespective of stability of coexistence equilibrium points (see Hutson and Schmitt, 1992 for review of permanence and Anderson, 1992 for shorter introductions).

Studies of permanence for single-species stage-structured models are found in Cushing (1998). A sufficient condition for permanence is given in his book. We show that our result generalizes his result and is applicable to a wider class of stage-structured models.

This paper is organized as follows. In Section 2, we introduce a general stage-structured model of a single species given by an autonomous difference equation, which has density dependence terms. We also give a specific example of a single-species stage-structured model. In Section 3, we define permanence of a stage-structured model, and obtain a mathematical criterion for permanence. Moreover, we apply our results to a specific example which is introduced in Section 2. The final section includes discussion and future problems. Some proofs are given in the Appendices.

2. Stage-structured models

We consider population dynamics of a single species. The population is assumed to be divided into n classes depending on age, size or developmental stages. Let $\mathbf{x}(t) = (x_1(t), \dots, x_n(t))^T$ be a population density vector. Each $x_i(t)$ $(i \in \{1, \dots, n\})$ indicates population density in the i-th stage at time t. Then a stage-structured model is given by the following:

$$\mathbf{x}(t+1) = A_{\mathbf{x}(t)}\mathbf{x}(t), \quad t \in \mathbb{Z}_+, \tag{2}$$

where $A_\mathbf{x}$ is an $n \times n$ matrix whose elements depend on $\mathbf{x}$. If $\mathbf{x} = \mathbf{0}$, then $A_\mathbf{x}$ is denoted by A_0. The (i, j) elements of the matrix A_0 is denoted by a_{ij} $(i, j \in \{1, \dots, n\})$. By biological restrictions, the matrix $A_\mathbf{x}$ is assumed to be non-negative for all $\mathbf{x} \in \mathbb{R}^n_+ = \{\mathbf{x} \in \mathbb{R}^n : x_1 \geq 0, \dots, x_n \geq 0\}$. Then the solution with $\mathbf{x}(0) \in \mathbb{R}^n_+$ does not leave $\mathbb{R}^n_+$ (i.e., $\mathbb{R}^n_+$ is forward invariant).

Stage-structured models are often characterized by directed graph, which is called a *life cycle graph*. The life cycle graph is constructed by drawing a directed edge from a node j to i whenever $a_{ij} > 0$. A particular example of the life cycle graph is given in Fig. 1.

One of the important properties of the matrix A_0 is irreducibility. A non-negative matrix is said to be reducible if it can be rearranged into the following form by renumbering the indices of the rows and columns:

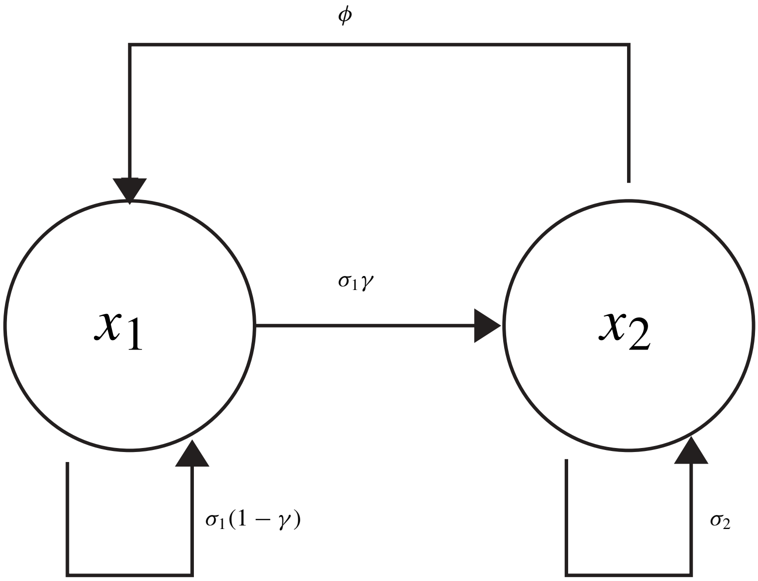

Fig. 1. The life cycle graph of Model (3)

$$\begin{pmatrix} A_{11} & O \\ A_{21} & A_{22} \end{pmatrix},$$

where the matrices A_{ii} are square matrices and O denotes the matrix with only zero elements. The irreducibility can be checked using life cycle graphs (see Caswell, 2001, p.81). A non-negative matrix is irreducible if and only if the corresponding life cycle graph contains a path from every node to every other node along directed edges.

The example of a typical stage structured model is a Neubert-Caswell model (see Neubert and Caswell, 2000), which is given by (2) with

$$A_{\mathbf{x}} = \begin{pmatrix} \sigma_1 f_1(\mathbf{x})(1-\gamma f_3(\mathbf{x})) & \phi f_4(\mathbf{x}) \\ \sigma_1 f_1(\mathbf{x})\gamma f_3(\mathbf{x}) & \sigma_2 f_2(\mathbf{x}) \end{pmatrix}, \tag{3}$$

where $\sigma_1, \sigma_2, \gamma \in [0, 1]$, $\phi > 0$ and $f_i : \mathbb{R}^2_+ \to (0, 1]$ with $f_i(\mathbf{0}) = 1$ for $i \in \{1, \ldots, 4\}$. The population is assumed to be divided into two classes depending on developmental stages, immature and mature stages. The functions f_i $(i = 1, \ldots, 4)$ represent the density dependence part of the parameters σ_1, σ_2, γ and ϕ, respectively. The parameters have the following meanings if $\mathbf{x} = \mathbf{0}$. σ_1 and σ_2 are the fractions of juveniles and adults that survive to the next generation, respectively. γ is the fraction of the surviving juveniles that mature to become adults. ϕ is the number of juveniles produced by an adult. The life cycle graph of the system is given in Fig. 1. By the figure, we see that the matrix A_0 is irreducible if and only if

$$\sigma_1\gamma\phi > 0. \tag{4}$$

We will consider this particular example of stage-structured models in the subsection 3.1 of Section 3.

3. Permanence

We define permanence as follows (see also Fig. 2):

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

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

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

Remark. In the book of Cushing (1998), System (2) is said to be *uniformly persistent* (with respect to $\mathbf{0}$) if there exists a $\delta > 0$ such that $\liminf_{t\to\infty} N(t) > \delta$ for all $\mathbf{x}(0) \in \mathbb{R}_+^n$ with $N(0) > 0$. Therefore, uniformly persistent system is permanent if and only if it has no unbounded solutions in the sense that there exists a $D > 0$

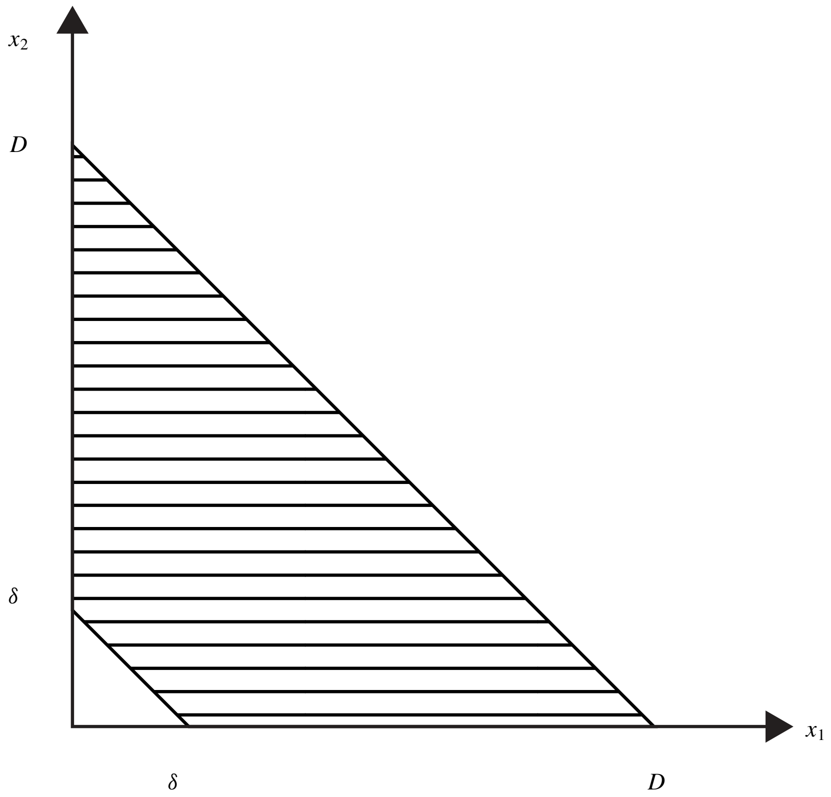

Fig. 2. The definition of permanence in the case of two stages. If the system is permanent, all orbits which do not start at the origin eventually enter and remain in the hatched region

such that $\limsup_{t\to\infty} N(t) < D$ for all $\mathbf{x}(0) \in \mathbb{R}^n_+$ with $N(0) > 0$. In the theorem of uniform persistence given by Cushing (1998), it is assumed that a system has no unbounded solutions. Hence, we can simply compare the results of uniform persistence given by Cushing (1998) and permanence given in the present paper (see below).

The definition of permanence ensures that the total population density neither explodes nor goes to zero if the system is permanent. From this definition, we see that even if the system is permanent, the population density in each of stages does not have to be positive at every time, and we require it only for the total population density. This property is appropriate for the stage-structured system (2) because if for every time t there is at least one stage in which population density is positive, we conclude that the species survives. We must also note that the variables $x_1, \ldots, x_n$ of the stage-structured model (2) do not denote population densities of different species but the population density of the same species.

The property that the population density does not explode is important for permanence. This property is defined mathematically as *dissipativeness*:

Definition 2. *System* (2) *is said to be dissipative if there exists a compact set* $X \subset \mathbb{R}^n_+$ *such that for all* $\mathbf{x}(0) \in \mathbb{R}^n_+$ *there exists a* $T = T(\mathbf{x}(0))$ *satisfying* $\mathbf{x}(t) \in X$ *for all* $t \geq T$.

We obtain the following theorem of permanence (see Appendix A for the proof):

Theorem 3. *Suppose System* (2) *is continuous and dissipative. Assume the matrix* A_0 *is irreducible and* $\mathbb{R}^n_+\backslash\{\mathbf{0}\}$ *is forward invariant* (*i.e.,* $A_{\mathbf{x}}\mathbf{x} \in \mathbb{R}^n_+\backslash\{\mathbf{0}\}$ *for all* $\mathbf{x} \in \mathbb{R}^n_+\backslash\{\mathbf{0}\}$). *System* (2) *is permanent if* A_0 *has an eigenvalue* λ *with* $|\lambda| > 1$ (*i.e., the magnitude of the dominant eigenvalue of* A_0 *is greater than one*).

Remark. Note that if the magnitude of the dominant eigen value of A_0 is less than one, then the system is not permanent since the origin is stable.

Remark. Cushing (1998) shows that System (2) is permanent if the above assumptions hold and, additionally, the matrix A_0 is *primitive* (i.e., there exits a $k > 0$ such that all elements of A_0^k are positive) and *hyperbolic* (i.e., no eigenvalues λ of A_0 satisfy $|\lambda| = 1$) (see Theorem 1.2.1 in Cushing, 1998). Therefore, Theorem 3 generalizes his result. An example which shows that System (2) can be permanent without primitivity of the matrix A_0 is given in Section 4 (see also Fig. 5).

Remark. By this theorem, it is ensured that an irreducible non-negative matrix A_0 with the dominant eigenvalue $\lambda > 1$ cannot have non-negative eigenvectors of eigenvalues with module less than one since stable manifolds of the origin cannot belong to $\mathbb{R}^n_+$ (see also Gantmacher, 1959, p.63)

The condition about eigenvalues of A_0 in Theorem 3 implies that the origin of System (2) is unstable since A_0 is equal to the Jacobian matrix of System (2) at the origin. Note that we have assumed that $A_{\mathbf{x}}$ is non-negative for all $\mathbf{x} \in \mathbb{R}^n_+$, which implies the invariance of $\mathbb{R}^n_+$ for System (2).

3.1. Example (The Neubert-Caswell model)

We consider permanence of the Neubert-Caswell model (that is, System (2) with (3)). Hereafter, we check the conditions in Theorem 3 one by one. The system is clearly continuous if each f_i is a continuous function. Since all f_i are defined as $f_i : \mathbb{R}^2_+ \to (0, 1]$, $A_\mathbf{x}$ is non-negative. Moreover, $\mathbb{R}^2_+ \setminus \{\mathbf{0}\}$ is forward invariant if

$$\sigma_1 > 0 \quad \text{or} \quad \sigma_2 + \phi > 0. \tag{5}$$

The dissipativeness of the system is given by the following theorems (see Appendix B for the proof):

Theorem 4. *Suppose*

$$1 - \sigma_1(1-\gamma) > 0 \quad \textit{and} \quad 1 - \sigma_2 > 0. \tag{6}$$

If one of $f_1(\mathbf{x})x_1$, $f_3(\mathbf{x})x_1$ or $f_4(\mathbf{x})x_2$ is bounded above, then the Neubert-Caswell model is dissipative.

It is worth to note that the system can have an unbounded orbit even if it has a density dependent term. In fact, we have the following theorem (see Appendix C and also Neubert and Caswell, 2000):

Theorem 5. *Assume that $f_1(\mathbf{x}) = f_3(\mathbf{x}) = f_4(\mathbf{x}) = 1$. If $\phi > [1 - \sigma_1(1 - \gamma)]/(\sigma_1\gamma)$, then the Neubert-Caswell model has an unbounded solution.*

Theorem 5 shows that it is possible for the Neubert-Caswell model to be non-dissipative if the assumption of Theorem 4 is not satisfied.

The matrix A_0 of the system is given by

$$A_0 = \begin{pmatrix} \sigma_1(1-\gamma) & \phi \\ \sigma_1\gamma & \sigma_2 \end{pmatrix},$$

which is clearly non-negative under the assumption that $\sigma_1, \sigma_2, \gamma \in [0, 1]$ and $\phi \geq 0$. By the life cycle graph, Fig. 1, we can see that A_0 is irreducible if and only if (4) holds. The matrix A_0 has an eigenvalue λ with $|\lambda| > 1$ if and only if the following inequality holds (see Neubert and Caswell, 2000):

$$\sigma_1\gamma\phi > (1 - \sigma_2)\{1 - \sigma_1(1-\gamma)\}. \tag{7}$$

Define an inherent net reproductive rate R_0 as follows (see Neubert and Caswell, 2000):

$$R_0 = \frac{\sigma_1\gamma\phi}{(1-\sigma_2)\{1 - \sigma_1(1-\gamma)\}}. \tag{8}$$

It is easy to check that (7) implies (4) and (5). Furthermore, (6) implies that the denominator of (8) is positive. Therefore, under the assumption that (6) holds, the inequality $R_0 > 1$ implies that (4), (5) and (7) hold. Then we obtain the following result:

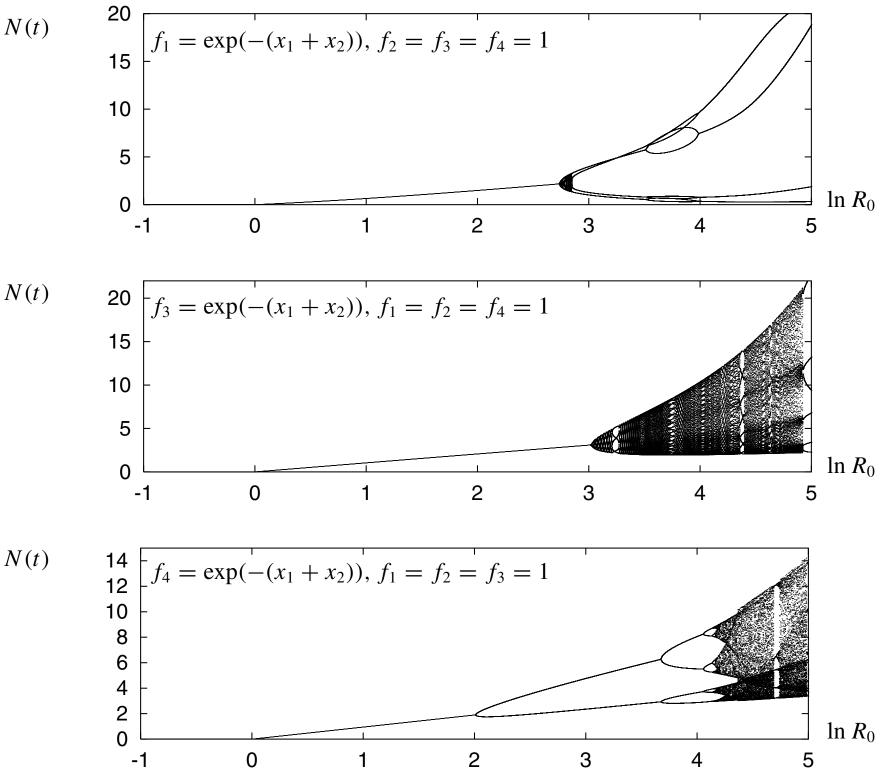

Fig. 3. Bifurcation diagrams of the Neubert-Caswell model. The total population density $N(t) = x_1(t) + x_2(t)$ is plotted for the orbit $\{\mathbf{x}(t)\}_{t\in\{1001,\ldots,1050\}}$ with $\mathbf{x}(0) = (1, 1)$ against $\ln R_0 \approx (\ln \phi) - 2.293$. The parameters are $\sigma_1 = 0.5$, $\sigma_2 = 0.1$ and $\gamma = 0.1$

Theorem 6. *Assume the conditions in Theorem 4 hold. The Neubert-Caswell model is permanent if* $R_0 > 1$.

As an example, consider $f_i(\mathbf{x}) = \exp(-(x_1 + x_2))$ $(i \in \{1, 3, 4\})$ as density dependence functions. The bifurcation diagram of the model is given in Fig. 3. Clearly, if the condition in Theorem 6 holds, the population survives. From Fig. 3, we see that permanence of the Neubert-Caswell model can be estimated by Theorem 6 irrespective of the complexity of the internal orbits (see Neubert and Caswell, 2000, for details of the complex interior orbits of the model).

4. Discussion

In this paper, we considered the survival of populations whose dynamics are described by the stage-structured model (2), and obtain conditions for permanence. We show that the magnitude of the dominant eigenvalue of A_0 is important in the study of permanence (see Theorem 3). Theorem 3 is applicable to a wide class of stage-structured models and the conditions for permanence (except dissipativeness) are usually straightforward to check. As an illustration we applied Theorem 3 to the Neubert-Caswell model and obtained conditions for its permanence (Theorem 6). An interesting problem is to obtain criteria for the dissipativeness of model (2).

Global dynamical properties of stage-structured models with density dependence terms have been investigated in literature (for example, see Cushing, 1998 and Crowe, 1994 and 2001). The studies of Cushing (1998) and Crowe (2001) are related to ours since they investigated the possibility that population survives for stage-structured models with density dependence terms. In the book of Cushing (1998), he assumed that the matrix A_0 is primitive in order to show that the stage-structured model (2) is permanent. However, our result (Theorem 3) shows that this assumption is not necessary for permanence. An example of the model which is permanent but has an imprimitive matrix A_0 is given below. Crowe (2001) studied a class of nonlinear models possessing a stable stage distribution, that is, $\lim_{t\to\infty} \mathbf{x}(t)/\sum_{i=1}^{n} x_i(t)$ exists for all $\mathbf{x}(0) \in \mathbb{R}^n_+\backslash\{\mathbf{0}\}$. Therefore, we see that our results can be applied to a wider class of stage-structured models than the result given by Crowe (2001) (see Fig. 4 for a system which is permanent without a stable stage distribution).

In Section 2, we defined a permanent system with stages by the system whose total population density is bounded both from zero and infinity. Therefore, even if the system has a stable cycle on $\mathrm{bd}\mathbb{R}^n_+$ (the boundary of $\mathbb{R}^n_+$), the system is permanent as long as the total population density is bounded both from zero and infinity. In some stage-structured models, cycles on $\mathrm{bd}\mathbb{R}^n_+$ such as $\{(x_1^*, 0, \ldots, 0), (0, x_2^*, \ldots, 0), \ldots, (0, 0, \ldots, x_n^*)\}$ are found (see Cushing and Li, 1992, Wikan and Mjølhus,

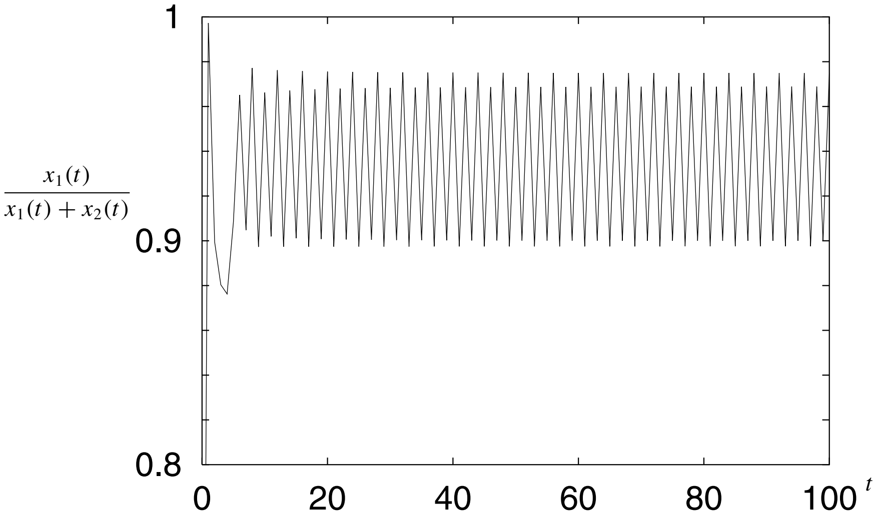

Fig. 4. The fluctuation of $x_1(t)/(x_1(t) + x_2(t))$. The initial condition is $\mathbf{x}(0) = (1, 1)$. The parameters are $\sigma_1 = 0.5$, $\sigma_2 = 0.1$, $\gamma = 0.1$ and $\phi = \exp(6)$. The density dependence terms are set by $f_1 = f_2 = f_3 = 1$ and $f_4 = \exp(-(x_1 + x_2))$. The inherent net reproductive rate $R_0 \approx 40.7$. By Theorem 6, the system is permanent. However, the dynamics of $x_1(t)/(x_1(t) + x_2(t))$ shows that the system does not have a stable stage distribution

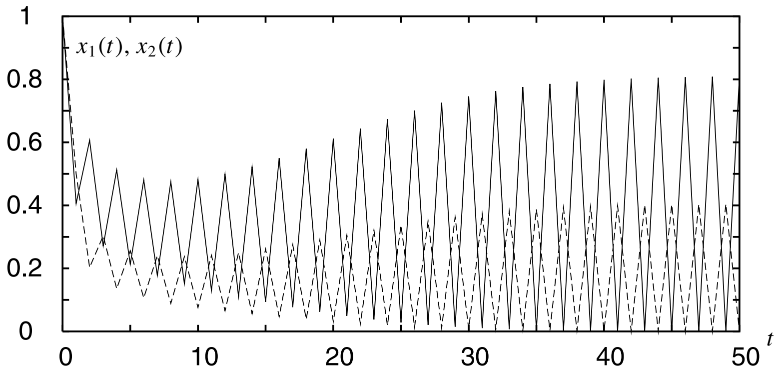

Fig. 5. The fluctuation of population densities in each stage. The solid and dashed lines represent population dynamics of $x_1(t)$ and $x_2(t)$, respectively. The initial condition is $\mathbf{x}(0) = (1, 1)$. The parameters are $\sigma_1 = 0.5$, $\sigma_2 = 0$, $\gamma = 1$ and $\phi = 3$. The density dependence terms are $f_1(\mathbf{x}) = f_2(\mathbf{x}) = f_3(\mathbf{x}) = 1$ and $f_4(\mathbf{x}) = \exp(-(x_1 + x_2))$. In this case, $R_0 = 1.5$

1996, Davydova *et al.*, 2003). For example, consider the Neubert-Caswell model with $\sigma_1 \in (0, 1]$, $\sigma_2 = 1$, $\gamma = 1$, $\phi > 0$ and $f_3(\mathbf{x}) = 1$. Then the system is rewritten as follows:

$$\begin{cases} x_1(t+1) = \phi f_4(x_1(t), x_2(t))x_2(t) \\ x_2(t+1) = \sigma_1 f_1(x_1(t), x_2(t))x_1(t). \end{cases}$$

Note that the matrix A_0 corresponding to this system is imprimitive. The system can have a 2-cycle of the form $\{(x_1^*, 0), (0, x_2^*)\}$, which satisfies

$$\begin{cases} x_1^* = \phi f_4(0, x_2^*)x_2^* \\ x_2^* = \sigma_1 f_1(x_1^*, 0)x_1^*. \end{cases}$$

If $f_1(\mathbf{x}) = 1$ and $f_4(\mathbf{x}) = \exp(-(x_1 + x_2))$, then the system becomes a special case of the system investigated by Wikan and Mjølhus (1996) and Davydova *et al.* (2003). In this case, the 2-cycle exists if and only if $R_0 = \phi\sigma_1 > 1$, and is stable if $0 < \ln \phi\sigma_1 < 2$ (see Fig. 5 for an illustration and Davydova *et al.*, 2003, for the full details of the analysis of the system). Note that the system shown in Fig. 5 is permanent since the conditions in Theorem 6 hold. Hence, we can see that the definition of permanence of stage-structured models evaluates properly the survival of the populations. It is a future work to obtain a criterion of permanence of the stage-structured model (2) with respect to $\mathrm{bd}\mathbb{R}_+^n$, which ensures that there exist $\delta > 0$ and $D > 0$ such that $\delta < \liminf_{t\to\infty} x_i(t) \le \limsup_{t\to\infty} x_i(t) < D$ for all $\mathbf{x}(0) \in \mathrm{int}\mathbb{R}_+^n = \mathbb{R}_+^n \backslash \mathrm{bd}\mathbb{R}_+^n$ and $i \in \{1, 2, \dots, n\}$.

A. The proof of Theorem 3

Before giving the proof of Theorem 3, we introduce some mathematical notation and theorems about the dynamical system $F : X \to X$ and non-negative matrices.

The orbit starting at $\mathbf{x}$ is the set

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

where F^t represents the t-th composition of F. For a subset $X_0 \subset X$ let

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

X_0 is said to be forward invariant if $F(X_0) \subset X_0$. A set M is absorbing for X_0 if it is forward invariant and $\gamma_+(\mathbf{x}) \cap M \neq \emptyset$ for every $\mathbf{x} \in X_0$.

Theorem 7 (Hutson, 1984, Theorem 2.2)**.** *Let (X, d) be a metric space. Consider a continuous function $F : X \to X$. Assume X is compact and S is a compact subset of X with empty interior. Let S and $X \backslash S$ be forward invariant. Suppose there is a continuous function $P : X \to \mathbb{R}_+$, called an average Liapunov function* (Hutson, 1984)*, that satisfies the following conditions:*

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

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

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 use the following theorem in the application of Theorem 7 to dissipative systems:

Theorem 8 (Hutson, 1984, Lemma 2.1, Hofbauer et al., 1987, Lemma 2.1)**.** *Let $F : X \to X$ be continuous, where X is a metric space. Let U be open 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.*

F is said to be dissipative if there exists a compact set $U_0 \subset X$ such that for all $\mathbf{x} \in X$ there exists a $T = T(\mathbf{x})$ satisfying $F^t(\mathbf{x}) \in U_0$ for all $t \geq T$. Even if F is dissipative (let U_0 be the corresponding set) it is not ensured that U_0 is forward invariant since $F^t(\mathbf{x})$ can be allowed to belong to $X \backslash U_0$ for some $t > 0$. However, this theorem ensures that if F is continuous, $\gamma_+(\overline{U})$ becomes forward invariant for some open set $U \supset U_0$ with compact closure. Hence, if System (2) is dissipative, we can construct a compact absorbing set for $\mathbb{R}^n_+$. Therefore, for the consideration of permanence it is enough to investigate the dynamics in the compact absorbing set, which, hereafter is denoted by X.

Theorem 9 (The Perron-Frobenius theorem)**.** *Suppose A is an irreducible $n \times n$ matrix with non-negative elements. Then there exists a positive eigenvalue λ which is dominant in the sense that $|\mu| \leq \lambda$ for all other eigenvalues μ of A. There exist right and left eigenvectors $\mathbf{u} > 0$ and $\mathbf{v} > 0$ such that $A\mathbf{u} = \lambda\mathbf{u}$ and $A^T\mathbf{v} = \lambda\mathbf{v}$.*

Proof of Theorem 3. Since System (2) is dissipative, Theorem 8 guarantees that there exists a forward invariant compact set $X \subset \mathbb{R}^n_+$ such that all orbits in $\mathbb{R}^n_+$ ultimately enter X. Therefore, it is enough to focus on the orbits in X.

Let $S = \{\mathbf{0}\}$. Since the origin is a fixed point and $\mathbb{R}^n_+ \backslash \{\mathbf{0}\}$ is forward invariant, it is clear that S and $X \backslash S$ are forward invariant.

We construct an average Liapunov function as follows. By the Perron-Frobenius theorem, there exists a left eigenvector $\mathbf{v} > 0$ such that $A_0^T \mathbf{v} = \lambda \mathbf{v}$, where λ is a positive eigenvalue of A_0. We employ $P(\mathbf{x}) = \mathbf{v} \cdot \mathbf{x}$ as an average Liapunov function, where "$\cdot$" denotes inner product. The condition (a) in Theorem 7 clearly holds.

Let us check the condition (b) in Theorem 7:

$$
\begin{aligned}
\sigma &= \sup_{t \geq 0} \liminf_{\substack{\mathbf{y} \to \mathbf{0} \\ \mathbf{y} \in X \backslash S}} \frac{P(F^t(\mathbf{y}))}{P(\mathbf{y})} \\
&= \sup_{t \geq 0} \liminf_{\substack{\mathbf{y} \to \mathbf{0} \\ \mathbf{y} \in X \backslash S}} \frac{P(F^t(\mathbf{y}))}{P(F^{t-1}(\mathbf{y}))} \cdots \frac{P(F^2(\mathbf{y}))}{P(F(\mathbf{y}))} \frac{P(F(\mathbf{y}))}{P(\mathbf{y})} \\
&= \sup_{t \geq 0} \liminf_{\substack{\mathbf{y} \to \mathbf{0} \\ \mathbf{y} \in X \backslash S}} \prod_{i=0}^{t-1} \left[\frac{\mathbf{v} \cdot F^{i+1}(\mathbf{y})}{\mathbf{v} \cdot F^i(\mathbf{y})} \right] \\
&= \sup_{t \geq 0} \liminf_{\substack{\mathbf{y} \to \mathbf{0} \\ \mathbf{y} \in X \backslash S}} \prod_{i=0}^{t-1} \left[\lambda + \frac{\mathbf{v} \cdot F^{i+1}(\mathbf{y}) - \lambda \mathbf{v} \cdot F^i(\mathbf{y})}{\mathbf{v} \cdot F^i(\mathbf{y})} \right] \\
&= \sup_{t \geq 0} \liminf_{\substack{\mathbf{y} \to \mathbf{0} \\ \mathbf{y} \in X \backslash S}} \prod_{i=0}^{t-1} \left[\lambda + (A^T_{F^i(\mathbf{y})} \mathbf{v} - \lambda \mathbf{v}) \cdot \left(\frac{F^i(\mathbf{y})}{\mathbf{v} \cdot F^i(\mathbf{y})} \right) \right],
\end{aligned}
$$

where F is defined as a right-hand side of (2). Note that $F^i(\mathbf{y}) \neq 0$ for every $i \geq 0$ by the forward invariance of $\mathbb{R}^n_+ \backslash \{\mathbf{0}\}$. By the definition of $\mathbf{v}$ and λ, we have

$$
\lim_{\mathbf{y} \to \mathbf{0}} A^T_{F^i(\mathbf{y})} \mathbf{v} - \lambda \mathbf{v} = \mathbf{0}.
$$

Furthermore, we have the boundedness of $F^i(\mathbf{y}) / (\mathbf{v} \cdot F^i(\mathbf{y}))$. In fact, the following inequality holds for all $F^i(\mathbf{y}) \in X \backslash S$:

$$
\frac{(F^i(\mathbf{y}))_k}{\mathbf{v} \cdot F^i(\mathbf{y})} \leq \frac{(\mathbf{v} \cdot F^i(\mathbf{y}))/v_k}{\mathbf{v} \cdot F^i(\mathbf{y})} = \frac{1}{v_k},
$$

where $(F^i(\mathbf{y}))_k$ and v_k are a k-th elements of the vector $F^i(\mathbf{y})$ and $\mathbf{v}$, respectively. Therefore, we obtain $\sigma = \sup_{t \geq 0} \lambda^t > 1$. This implies that the system is permanent.

B. The proof of Theorem 4

Let $\{\mathbf{x}(t)\}_{t\in\mathbb{Z}_+}$ be a solution of the Neubert-Caswell model. First, assume that one of $f_i(\mathbf{x})x_1$ $(i = 1, 3)$ is bounded above, that is, there exists a $K_0 > 0$ such that $f_i(\mathbf{x})x_1 \leq K_0$ for all $\mathbf{x} \in \mathbb{R}^2_+$ and $i = 1$ or 3. From the equation for x_2, 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 $0 \leq \sigma_2 < 1$, there exists $T_1 = T_1(\mathbf{x}(0)) > 0$ such that

$$x_2(t) \leq \frac{\sigma_1\gamma K_0}{1-\sigma_2} \times 2 = K_1$$

for all $t \geq T_1(\mathbf{x}(0))$. If $\sigma_1 \neq 1$, then from the equation for x_1 we have

$$\begin{aligned} x_1(t+1) &= \sigma_1 f_1(\mathbf{x}(t))\{1-\gamma f_3(\mathbf{x}(t))\}x_1(t) + \phi f_4(\mathbf{x}(t))x_2(t) \\ &\leq \sigma_1 x_1(t) + \phi x_2(t) \\ &\leq \sigma_1 x_1(t) + \phi K_1 \end{aligned}$$

for $t \geq T_1(\mathbf{x}(0))$. Then by induction there exists $T_2 = T_2(\mathbf{x}(0))$ such that

$$x_1(t) \leq \frac{\phi K_1}{1-\sigma_1} \times 2 = K_2$$

for all $t \geq T_2(\mathbf{x}(0))$. Take $T(\mathbf{x}(0)) = \max\{T_1(\mathbf{x}(0)), T_2(\mathbf{x}(0))\}$ and $K = \max\{K_1, K_2\}$. Then $x_1(t) \leq K$ and $x_2(t) \leq K$ for $t \geq T(\mathbf{x}(0))$. If $\gamma \neq 0$, then similarly we have

$$\begin{aligned} x_1(t+1) &= \sigma_1 f_1(\mathbf{x}(t))\{1-\gamma f_3(\mathbf{x}(t))\}x_1(t) + \phi f_4(\mathbf{x}(t))x_2(t) \\ &\leq \{1-\gamma f_3(\mathbf{x}(t))\}x_1(t) + \phi x_2(t) \\ &\leq \{1-\gamma f_3(\mathbf{x}(t))\}x_1(t) + \phi K_1 \end{aligned}$$

for $t \geq T_1(\mathbf{x}(0))$. Note that $\gamma \neq 0$ implies that $0 < 1-\gamma f_3(\mathbf{x}(t)) < 1$ for all $\mathbf{x}(t) \geq 0$. Then there exists K_2 in the argument above. This completes the proof of the first case.

Next, assume that $f_4(\mathbf{x})x_2$ is bounded 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 $0 \leq \sigma_1 < 1$, then from the equation for x_1 we have

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

Then there exists $T_1 = T_1(\mathbf{x}(0)) > 0$ such that

$$x_1(t) \leq \frac{\phi K_0}{1-\sigma_1} \times 2 = K_1$$

for all $t \geq T_1(\mathbf{x}(0))$. If $\gamma \neq 0$, then similarly we have

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

Since $\gamma \neq 0$ implies that $0 < 1 - \gamma f_3(\mathbf{x}(t)) < 1$ for all $\mathbf{x}(t) \geq 0$, there exists $T_1 = T_1(\mathbf{x}(0)) > 0$ and K_1 such that $x_1(t) \leq K_1$ for all $t \geq T_1(\mathbf{x}(0))$. From the equation for x_2, we have

$$\begin{aligned} x_2(t+1) &= \sigma_1 f_1(\mathbf{x}(t))\gamma f_3(\mathbf{x}(t))x_1(t) + \sigma_2 f_2(\mathbf{x}(t))x_2(t) \\ &\leq \sigma_1\gamma x_1(t) + \sigma_2 x_2(t) \\ &\leq \sigma_1\gamma K_1 + \sigma_2 x_2(t) \end{aligned}$$

for $t \geq T_1(\mathbf{x}(0))$. Then there exists $T_2 = T_2(\mathbf{x}(0))$ such that

$$x_1(t) \leq \frac{\sigma_1\gamma K_1}{1-\sigma_2} \times 2 = K_2$$

for all $t \geq T_2(\mathbf{x}(0))$. Take $T(\mathbf{x}(0)) = \max\{T_1(\mathbf{x}(0)), T_2(\mathbf{x}(0))\}$ and $K = \max\{K_1, K_2\}$. Then $x_1(t) \leq K$ and $x_2(t) \leq K$ for $t \geq T(\mathbf{x}(0))$. This completes the proof. □

C. The proof of Theorem 5

When $f_1(\mathbf{x}) = f_3(\mathbf{x}) = f_4(\mathbf{x}) = 1$, the Neubert-Caswell model is given by $\mathbf{x}(t+1) = A_{\mathbf{x}}\mathbf{x}(t)$, where

$$A_{\mathbf{x}} = \begin{pmatrix} \sigma_1(1-\gamma) & \phi \\ \sigma_1\gamma & \sigma_2 f_2(\mathbf{x}) \end{pmatrix}.$$

Consider

$$\mathbf{y}(t+1) = B\mathbf{y}(t),$$

where

$$B = \begin{pmatrix} \sigma_1(1-\gamma) & \phi \\ \sigma_1\gamma & 0 \end{pmatrix}.$$

By the assumption, the matrix B has an eigenvalue $\lambda > 1$ and from the Perron-Frobenius theory, there exists a right eigenvector $\mathbf{u} > \mathbf{0}$ such that $B\mathbf{u} = \lambda\mathbf{u}$. Choose $\mathbf{y}(0) = \mathbf{u}$. Then the solution $\mathbf{y}(t) = \lambda^t\mathbf{u} \to +\infty$ as $t \to +\infty$. It is trivial that $\mathbf{x}(t) \geq \mathbf{y}(t)$ if $\mathbf{x}(0) \geq \mathbf{y}(0)$. In fact,

$$\mathbf{x}(t+1) - \mathbf{y}(t+1) = \begin{pmatrix} \sigma_1(1-\gamma) & \phi \\ \sigma_1\gamma & 0 \end{pmatrix}(\mathbf{x}(t) - \mathbf{y}(t)) + \begin{pmatrix} 0 \\ \sigma_2 f_2(\mathbf{x}(t))x_2(t) \end{pmatrix} \geq 0$$

for $\mathbf{x}(t) \geq \mathbf{y}(t)$. This shows that $\mathbf{x}(t) \to +\infty$ as $t \to +\infty$ for $\mathbf{x}(0) \geq \mathbf{y}(0) = \mathbf{u}$. This completes the proof. □

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References

Anderson, H.M., Hutson, V., Law, R.: On the conditions for permanence of species in ecological communities. Am. Naturalist. **139**, 663–668 (1992)

Caswell, H.: Matrix Population Models. Sunderland: Sinauer, 2001

Crowe, K.M.: A nonlinear ergodic theorem for discrete systems, J. Math. Bio. **32**, 179–191 (1994)

Crowe, K.M.: Persistence in systems of asymptotically autonomous difference equations. J. Diff. Eqs. Appl. **7**, 143–165 (2001)

Cull, P.: Local and global stability for population models. Biol. Cybernetics **54**, 141–149 (1986)

Cushing, J.M., Li, L.: Intra-specific competition and density dependent juvenile growth. Bulletin of Math. Bio. **54**, 503–519 (1992)

Cushing, J.M.: An Introduction to Structured Population Dynamics. CBMS-NSF Regional Conference Series in Applied Mathematics, 71, SIAM, Philadelphia, 1998

Davydova, N.V., Diekmann, O., van Gils, S.A.: Year class coexistence or competitive exclusion for strict biennials? J. Math. Bio. **46**, 95–131 (2003)

Freedman, H.I., So, J.W.-H.: Persistence in discrete models of a population which may be subjected to harvesting. Natural Resource Modeling **2**, 135–145 (1987)

Gantmacher, F.R.: The theory of matrices. Vol, **2**, AMS Chelsea Publishing, American Mathematical Society, Providence, Rhode Island, 1959

Hadeler, K.P., Gerstmann, I.: The discrete Rosenzweig model. Math. Biosci. **98**, 49–72 (1990)

Hofbauer, J., Hutson, V., Jansen, W.: Coexistence for systems governed by difference equations of Lotka-Volterra type. J. Math. Bio. **25**, 553–570 (1987)

Hutson, V.: A theorem on average Liapunov functions. Monatshefte für Mathematik **98**, 267–275 (1984)

Hutson, V., Schmitt, K.: Permanence and dynamics of biological systems. Math. Biosci. **111**, 1–71 (1992)

Kon, R., Takeuchi, Y.: The effect of evolution on host-parasitoid systems. J. Theor. Bio. **209**, 287–302 (2001)

Kot, M.: Elements of mathematical ecology. Cambridge University Press, Cambridge, 2002

May, R.M., Oster, G.F.: Bifurcations and dynamics complexity in simple ecological models. Am. Naturalist **110**, 573–599 (1975)

Neubert, M.G., Caswell, H.: Density-dependent vital rates and their population dynamic consequences. J. Math. Bio. **41**, 103–121 (2000)

Neubert, M.G., Kot, M.: The subcritical collapse of predator populations in discrete-time predator-prey models. Math. Biosci. **110**, 45–66 (1992)

Wikan, A., Mjølhus, E.: Onvercompensatory recruitment and generation delay in discrete age-structured population models. J. Math. Bio. **35**, 195–239 (1996)