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Single-class orbits in nonlinear Leslie matrix models for semelparous populations

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Abstract The dynamics of a general nonlinear Leslie matrix model for a semelparous population is investigated. We are especially concerned with the attractivity of the single-class state, in which all but one cohort (or year-class) are missing. Our result shows that the single-class state is attractive if inter-class competition is severe. Conversely, if intra-class competition is severe, the single-class state is repelling. Numerical investigations show that all classes do not necessarily coexist even if the single-class state is repelling.

Keywords Permanence · Average Liapunov function · Competitive exclusion · Age-structured model

Mathematics Subject Classification (2000) 37N25 · 92B05

1 Introduction

Synchronous behavior has been recognized as one of the important characteristic behaviors of age-structured population models [1,3,5–8,10,11,20,26,29]. Although many studies have revealed several properties of such synchronous behavior, there are still many open problems to be solved mathematically. In this paper, we focus on discrete-time age-structured population models, namely Leslie matrix models, and provide some mathematical results concerning synchronous behavior.

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Temporal synchronization of the population dynamics can be found in nature (see [1,13]). A typical example is the curious population dynamics of the periodical cicadas inhabiting the Eastern United States. Their life cycles have the fixed length of 17 years (or, in the south, 13 years). Their nymphs spend underground for precisely 17 years before emerging from the ground (see [23,24,27] for the details). The interesting feature of these cicadas is that all individuals in the same population are of the same age and all except one cohort (or year-class) are missing. Thus the adult individuals appear synchronously every 17th year. In addition to the periodical cicadas, several insects such as the May beetle and the oak egger moth are known to be the insects exhibiting the synchronous population dynamics (see [1,13]).

To reveal the ecological mechanism leading to this synchronization is one of the interesting problems in population ecology. Bulmer [1] has tackled this problem by studying nonlinear Leslie matrix models and reached the conclusion that the synchronous behavior occurs if competition is more severe between than within age-classes. This conclusion is based partly on numerical investigations, several studies have been carried out to obtain a further mathematical basis of this conclusion . Davydova et al. [10] concentrated on the Leslie matrix model for a biennial semelparous population, in which individuals are categorized into two age-classes (biennial) and reproduce only once in their life (semelparous). Their model corresponds to the two-dimensional case of Bulmer's model [1]. Davydova et al. [10] showed that the synchronous behavior can occur in the sense that the model can possess a stable cycle corresponding to the synchronous behavior (see also [6,21,22] for the biennial semelparous case). Mjølhus et al. [26] focused on the special case of Leslie matrix models where the density dependence is restricted to the reproduction process (but their model is general in the sense that the number of age-classes is arbitrary fixed). Their result shows that if the reproduction ability is monotonically depressed with increasing the total population density, then the state in which all but one cohort are missing is always attractive. That is, the synchronous behavior involving a single cohort always appears as a stable phenomenon. Our study generalizes these results and provide an additional mathematical basis of Bulmer's conclusion.

In addition to the simple synchronous behavior corresponding to the periodical cicada case, a different type of synchronous behavior is also observed in nonlinear Leslie matrix models. For example, as numerically demonstrated by Bulmer [1], nonlinear Leslie matrix models can exhibit the synchronous behavior in which the dominant single cohorts replace each other successively and the interval of the replacement lengthens monotonically. This dynamics is due to the existence of the heteroclinic orbits connecting the single-cohort behavior with different phases [5,6,11]. Furthermore, Leslie matrix models can exhibit the synchronous behavior involving multiple cohorts [26]. Although we do not address these issues, our results are helpful to understand these synchronous dynamics.

This paper is organized as follows. In Sect. 2, we introduce the Leslie matrix model studied in this paper. In Sect. 3, the rough dynamical properties of the Leslie matrix model are studied. This study provides the condition for the boundedness of the population densities, the persistence of the total population and the global stability of the extinction state. In Sect. 4, we deal with the problem of attractivity of the state in which all but one cohort are missing. Our results are applicable to the case where the density dependence is restricted to a survival process of a single age-class. This generalizes the result by Mjølhus et al. [26]. Our results are also applicable to a general case including the model studied by Bulmer [1]. These results provide a further mathematical basis of Bulmer's conclusion. In Sect. 5, we show some examples illustrating the results obtained in Sect. 4. The final section includes concluding remarks. Some notation and theorems on dynamical systems and matrix population models are given in Appendices.

2 Leslie matrix models

The age-structured population model studied in this paper is the following nonlinear Leslie matrix model for a semelparous population:

$$\mathbf{x}(t+1) = L[\mathbf{x}(t)]\mathbf{x}(t), \tag{2.1}$$

where $\mathbf{x} = (x_0, x_1, \ldots, x_{n-1})^\top$ and

$$L[\mathbf{x}] = \begin{pmatrix} 0 & 0 & \cdots & 0 & s_{n-1}\sigma_{n-1}(\mathbf{x}) \\ s_0\sigma_0(\mathbf{x}) & 0 & \cdots & 0 & 0 \\ 0 & s_1\sigma_1(\mathbf{x}) & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & s_{n-2}\sigma_{n-2}(\mathbf{x}) & 0 \end{pmatrix}.$$

The component $x_i(t)$ of the vector $\mathbf{x}(t)$ denotes the number of individuals of age i at time t. The matrix $L[\mathbf{x}]$ is a special case of the Leslie matrix (see [2,4] for a general case of the Leslie matrix). s_i and $\sigma_i(\mathbf{x})$ are positive constants and functions, respectively. For $i \neq n-1$, $s_i\sigma_i(\mathbf{x})$ denotes the survival probability of the age i individuals. $s_{n-1}\sigma_{n-1}(\mathbf{x})$ includes both survival and reproduction factors. Therefore, $s_{n-1}\sigma_{n-1}(\mathbf{x})$ may exceed one, while $s_i\sigma_i(\mathbf{x}) \leq 1$, $i \neq n-1$, must hold for all nonnegative $\mathbf{x}$. The pattern of the first row of $L[\mathbf{x}]$ implies that only the last age-class can reproduce, and thus (2.1) is a model for a semelparous population. In order that each nonzero entry $s_i\sigma_i(\mathbf{x})$ is reduced to the constant s_i at the *population-free fixed point* $\mathbf{x} = \mathbf{0}$, we assume that $\sigma_i(\mathbf{0}) = 1$.

In this paper, we are concerned with the synchronous dynamics of (2.1) in the nonnegative cone $\mathbb{R}^n_+ = \{\mathbf{x} \in \mathbb{R}^n : x_i \geq 0 \text{ for all } i\}$. An orbit $\mathbf{x}(t)$ is said to be *synchronous* if $\mathbf{x}(t) \in \mathrm{bd}\mathbb{R}^n_+$ for all $t \geq 0$, where $\mathrm{bd}\mathbb{R}^n_+$ denotes the boundary of $\mathbb{R}^n_+$. Along a synchronous orbit there are always missing age-classes. Since every point on $\mathrm{bd}\mathbb{R}^n_+$ is mapped to a point on $\mathrm{bd}\mathbb{R}^n_+$, $\mathrm{bd}\mathbb{R}^n_+$ is forward invariant. This implies that every orbit starting at a boundary point is a synchronous orbit. Among synchronous orbits, we are especially concerned with a synchronous orbit along which all but one cohort (or year-class) are missing, i.e., an orbit remaining in the coordinate axes. Such an orbit is called a *single-class orbit*. We see that every orbit starting at a point on the coordinate axes is a single-class orbit since the union of the coordinate axes is forward invariant. By the sign pattern of $L[\mathbf{x}]$, it is clear that a single-class orbit (except the trivial case $\mathbf{x}(0) = \mathbf{0}$) has the following cyclic sign pattern:

$$(+, 0, 0, \ldots, 0) \to (0, +, 0, \ldots, 0) \to \cdots \to (0, 0, 0, \ldots, +) \to (+, 0, 0, \ldots, 0),$$

in which the plus entry shifts to the right. The union of the coordinate axes is called the *single-class state* since it includes all single-class orbits. Our main concern is to obtain the condition under which the single-class state is attractive.

3 Preliminary results

In this section, we precisely introduce assumptions for system (2.1), and obtain preliminary results concerning the global dynamics of system (2.1)

We assume that our system satisfies the following conditions.

(H1) $s_0, \ldots, s_{n-2} \in (0, 1]$ and $s_{n-1} \in (0, \infty)$; $\sigma_i : \mathbb{R}^n_+ \to (0, \infty)$, $i = 0, 1, \ldots, n-1$, are continuous functions satisfying $\sigma_i(\mathbf{0}) = 1$; $s_i\sigma_i(\mathbf{x}) \leq 1$, $i = 0, 1, \ldots, n-2$, for all $\mathbf{x} \in \mathbb{R}^n_+$ (Note that $s_{n-1}\sigma_{n-1}(\mathbf{x}) \leq 1$ may not hold).

(H2) System (2.1) is dissipative (The definition is given in Appendix A).

Notice that the density dependent effects are not always deleterious. In fact, $\sigma_i(\mathbf{x})$ could increase with increasing some x_j and exceed one under the assumption (H1). By (H1), $\sigma_i(\mathbf{x})$, $i = 1, 2, \ldots, n-2$, are bounded, but $\sigma_{n-1}(\mathbf{x})$ may not be bounded. It is usually assumed that $\sigma_i(\mathbf{x}) \leq 1$ for all $\mathbf{x} \in \mathbb{R}^n_+$, but our relaxed assumption plays an important role when we consider a practical case addressed in the final section.

Under the assumption (H1), the nonnegative cone $\mathbb{R}^n_+$ is forward invariant and the map $f : \mathbb{R}^n_+ \to \mathbb{R}^n_+$ defined by $f(\mathbf{x}) = L[\mathbf{x}]\mathbf{x}$ is continuous. The condition (H2) ensures that there exists a positive constant $D > 0$ such that every solution $\mathbf{x}(t)$ of (2.1) satisfies

$$\limsup_{t\to\infty} |\mathbf{x}(t)| \leq D,$$

where $|\mathbf{x}| = x_0 + x_1 + \cdots + x_{n-1}$. Hence, the population densities are ultimately bounded. The following proposition provides easily verifiable conditions for (H2).

Proposition 3.1 *Suppose that* (H1) *holds and*

(H2)$'$ *the following* (i) *or* (ii) *holds*: (i) *There exist constants* $\lambda \in (0, 1)$ *and* $K > 0$ *such that* $s_{n-1}\sigma_{n-1}(\mathbf{x}) \leq \lambda$ *for all* $\mathbf{x} \in \mathbb{R}^n_+$ *with* $|\mathbf{x}| \geq K$; (ii) *One of* $\sigma_i(\mathbf{x})x_i$, $i = 0, 1, \ldots, n-1$, *is bounded above and* $\sigma_{n-1}(\mathbf{x})$ *is also bounded above.*

Then system (2.1) *is dissipative.*

Proof Suppose that (H1) and (H2)$'$-(i) hold. By using Theorem B.1 of Appendix B, we shall prove this case. Let $c = \lambda^{1/n}$. Then $c \in (0, 1)$. Let $y_0 = x_0, y_1 = cx_1, \ldots, y_{n-1} = c^{n-1}x_{n-1}$. By using these new variables, we can rewrite (2.1) as follows:

$$\mathbf{y}(t+1) = \widetilde{L}[\mathbf{y}(t)]\mathbf{y}(t), \tag{3.1}$$

where $\mathbf{y} = (y_0, y_1, \ldots, y_{n-1})^\top$ and

$$\widetilde{L}[\mathbf{y}] = \begin{pmatrix} 0 & 0 & \cdots & 0 & s_{n-1}\widetilde{\sigma}_{n-1}(\mathbf{y})/c^{n-1} \\ cs_0\widetilde{\sigma}_0(\mathbf{y}) & 0 & \cdots & 0 & 0 \\ 0 & cs_1\widetilde{\sigma}_1(\mathbf{y}) & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & cs_{n-2}\widetilde{\sigma}_{n-2}(\mathbf{y}) & 0 \end{pmatrix}.$$

Note that $\widetilde{\sigma}_i(x_0, cx_1, \ldots, c^{n-1}x_{n-1}) = \sigma_i(x_0, x_1, \ldots, x_{n-1}), i = 0, 1, \ldots, n-1$. It is clear that if (3.1) is dissipative, then (2.1) is also dissipative. By (H1), $cs_i\widetilde{\sigma}_i(\mathbf{y}) \le c < 1, i = 0, 1, \ldots, n-2$, for all $\mathbf{y} \in \mathbb{R}^n_+$ and, by (H2)′-(i), $s_{n-1}\widetilde{\sigma}_{n-1}(\mathbf{y})/c^{n-1} \le c < 1$ for all $\mathbf{y} \in \mathbb{R}^n_+$ with $y_0 + cy_1 + \cdots + c^{n-1}y_{n-1} \ge K$. It follows from Theorem B.1 that (2.1) is dissipative.

Suppose that (H1) and (H2)′-(ii) hold. Let $\sigma_d(\mathbf{x})x_d$ be bounded above. Then there exists a positive constant $K > 0$ such that $\sigma_d(\mathbf{x})x_d \le K$ and $\sigma_0(\mathbf{x}) \le K, \sigma_1(\mathbf{x}) \le K, \ldots, \sigma_{n-1}(\mathbf{x}) \le K$ for all $\mathbf{x} \in \mathbb{R}^n_+$. Consequently, a solution $\mathbf{x}(t)$ of (2.1) satisfies

$$x_{d+1}(t+1) = s_d\sigma_d(\mathbf{x}(t))x_d(t) \le s_dK$$

for all $t \ge 0$. By induction,

$$\begin{aligned} x_{d+j+1}(t+j+1) &= s_{d+j}\sigma_{d+j}(\mathbf{x}(t+j))x_{d+j}(t+j) \\ &\le s_{d+j}Kx_{d+j}(t+j) \\ &\le \prod_{i=0}^{j}(s_{d+i}K) \end{aligned}$$

holds for all $t \ge 0$ and $0 \le j \le n-1$. Here the subscripts of s_i, σ_i and x_i are counted modulo n. This completes the proof. □

We define permanence of system (2.1) as follows.

Definition 3.2 (permanence) System (2.1) is said to be permanent if there exist a positive constant $\delta > 0$ such that

$$\delta \le \liminf_{t\to\infty} |\mathbf{x}(t)| \le \limsup_{t\to\infty} |\mathbf{x}(t)| \le \frac{1}{\delta}$$

for all solutions $\mathbf{x}(t)$ satisfying $\mathbf{x}(0) \in \mathbb{R}^n_+$ and $|\mathbf{x}(0)| > 0$.

It is ensured that if (2.1) is permanent, then the total population density $|\mathbf{x}(t)| = x_0(t) + x_1(t) + \cdots + x_{n-1}(t)$ does not go to zero, i.e., the population survives in total. The following proposition provides a sufficient condition for permanence of (2.1).

Proposition 3.3 *Suppose that* (H1) *and* (H2) *hold. System* (2.1) *is permanent if* $\mathcal{R}_0 := s_0s_1\cdots s_{n-1} > 1$.

Proof By using Theorem B.2 of Appendix B, we shall show that (2.1) is permanent. It is clear that the conditions (A1)–(A4) in Appendix B hold under the assumptions (H1) and (H2). Furthermore, $L[\mathbf{0}]$ is irreducible. Since the characteristic polynomial $\det(L[\mathbf{0}] - \lambda I) = 0$ is reduced to $\lambda^n = \mathcal{R}_0$, the dominant eigenvalue of the non-negative matrix $L[\mathbf{0}]$ is $\mathcal{R}_0^{1/n} > 1$. This shows that (2.1) is permanent. □

The number $\mathcal{R}_0$ is called the *basic reproduction number* of $L[\mathbf{x}]$. This number denotes the expected number of offspring per individual per lifetime when the density dependent effects are ignored. It is clear that (2.1) is not permanent if $\mathcal{R}_0 < 1$. In fact, the population-free fixed point $\mathbf{x} = \mathbf{0}$ is asymptotically stable if $\mathcal{R}_0 < 1$. However, the global asymptotical stability of $\mathbf{x} = \mathbf{0}$ is not clear. The following proposition provides a sufficient condition for the global asymptotical stability of $\mathbf{x} = \mathbf{0}$. This proposition also revels the dynamics of the critical case $\mathcal{R}_0 = 1$.

Proposition 3.4 *Suppose that* (H1) *holds and*

(H3) $\sigma_i(\mathbf{x}) \leq 1$, $i = 0, 1, \dots, n-1$, *for all* $\mathbf{x} \in \mathbb{R}_+^n$ *and there exists an index* $d \in \{0, 1, \dots, n-1\}$ *such that* $\sigma_d(\mathbf{x}) \neq 1$ *for all* $\mathbf{x} \neq \mathbf{0}$.

If $\mathcal{R}_0 \leq 1$, *then the population-free fixed point* $\mathbf{x} = \mathbf{0}$ *is globally asymptotically stable, i.e.,* $\mathbf{x} = \mathbf{0}$ *is stable and* $\lim_{t\to\infty} \mathbf{x}(t) = \mathbf{0}$ *for all* $\mathbf{x}(0) \in \mathbb{R}_+^n$.

Proof By (H3) and $\mathcal{R}_0 \leq 1$, every solution $\mathbf{x}(t)$ of (2.1) satisfies

$$x_i(t+n) \leq \mathcal{R}_0 x_i(t) \leq x_i(t), \quad i = 0, 1, \dots, n-1,$$

for all $t \geq 0$. Therefore, for every $K > 0$ the set $U_K = \{\mathbf{x} \in \mathbb{R}_+^n : |\mathbf{x}| < K\}$ is forward invariant under f^n, where $f(\mathbf{x}) = L[\mathbf{x}]\mathbf{x}$. Consequently, $\mathbf{x} = \mathbf{0}$ is a stable fixed point of f^n. Let $c = \max\{1, s_{n-1}\} \geq 1$. Then $f^i(U_K) \subset U_{c^n K}$ for all $i = 1, 2, n-1$, and $f^n(U_K) \subset U_K$. Hence, $\mathbf{x} = \mathbf{0}$ is also a stable fixed point of f.

Finally, consider the global attractivity of $\mathbf{x} = \mathbf{0}$. Let $\mathbf{x}(0) \in \mathbb{R}_+^n$, and choose a constant $K > 0$ such that $\mathbf{x}(0) \in U_K$. Note that U_K is forward invariant under f^n. Suppose that there exists an $\epsilon > 0$ such that $\mathbf{x}(t) \in U_K \backslash U_\epsilon$ for all $t \geq 0$. Then there exists a $\lambda \in (0, 1)$ such that

$$\sigma_d(\mathbf{x}) \leq \lambda$$

for all $\mathbf{x} \in U_K \backslash U_\epsilon$, and thus $\mathbf{x}(t)$ satisfies

$$x_i(t+n) \leq \mathcal{R}_0 \lambda x_i(t), \quad i = 0, 1, \dots, n-1,$$

for all $t \geq 0$. It follows from $\mathcal{R}_0\lambda < 1$ that $\mathbf{x}(nk) \to \mathbf{0}$ as $k \to \infty$. This is a contradiction, and thus for any $\epsilon > 0$ there exists an integer $T \geq 0$ such that $\mathbf{x}(T) \in U_\epsilon$. Since U_ϵ is forward invariant under f^n, we obtain $\mathbf{x}(nk) \to \mathbf{0}$ as $k \to \infty$. That is, $\mathbf{x} = \mathbf{0}$ is a globally attractive fixed point of f^n. By the same argument as above, we can show that $\mathbf{x} = \mathbf{0}$ is also a globally attractive fixed point of f. □

4 Attractivity of the single-class state

In this section, we consider the attractivity of the single-class state. First, we introduce some notation. Let $N = \{0, 1, \ldots, n-1\}$. Define $F_i = \{\mathbf{x} \in \mathbb{R}^n_+ : x_j = 0$ for all $j \neq i\}$, which denotes the x_i-axis. The union of F_i is denoted by $F = \bigcup_{i \in N} F_i$, which corresponds to the single-class state. Let $O = \{\mathbf{0}\}$ be the set consisting only of the origin. For $\delta \in (0, 1)$, let $X(\delta) = \{\mathbf{x} \in \mathbb{R}^n_+ : \delta \le |\mathbf{x}| \le 1/\delta\}$, $F_i(\delta) = F_i \cap X(\delta)$ and $F(\delta) = F \cap X(\delta)$. Some notation on dynamical systems (e.g., γ_f^+ and ω_f) are defined in Appendix A.

Define the map $f : \mathbb{R}^n_+ \to \mathbb{R}^n_+$ by the right-hand side of (2.1), i.e., $f(\mathbf{x}) = L[\mathbf{x}]\mathbf{x}$. The n-fold composite of the map f is denoted by $G = f^n$. The map G describes how the class distribution changes from one generation to the next. Define $g_i : \mathbb{R}^n_+ \to (0, \infty)$ by

$$g_i(\mathbf{x}) = \mathcal{R}_0 \sigma_{i+n-1}(f^{n-1}(\mathbf{x})) \cdots \sigma_{i+1}(f(\mathbf{x}))\sigma_i(\mathbf{x}),$$

where the subscripts of σ_i are counted modulo n. The function g_i describes how the population of class i is multiplied during one generation. The functions G and g_i satisfy

$$G(\mathbf{x}) = \begin{pmatrix} g_0(\mathbf{x})x_0 \\ g_1(\mathbf{x})x_1 \\ \vdots \\ g_{n-1}(\mathbf{x})x_{n-1} \end{pmatrix}.$$

By definition, if system (2.1) is permanent, then there exists a positive constant $\delta > 0$ such that every solution $\mathbf{x}(t)$ of (2.1) with $\mathbf{x}(0) \in \mathbb{R}^n_+ \backslash O$ eventually enters the interior of $X(\delta)$, $\{\mathbf{x} \in \mathbb{R}^n_+ : \delta < |\mathbf{x}| < 1/\delta\}$, which is an open subset of $\mathbb{R}^n_+$ with the compact closure $X(\delta)$. Furthermore, Theorem A.3 of Appendix A ensures that $\mathcal{X}(\delta) := \gamma_f^+(X(\delta))$ is a compact absorbing set for $\mathbb{R}^n_+ \backslash O$ (Note that $X(\delta) \subset \mathcal{X}(\delta)$). Therefore, if system (2.1) is permanent, the ultimate behavior of (2.1) is determined by the dynamics in $\mathcal{X}(\delta)$. In this section, we apply theorems on average Liapunov functions (Theorems A.1 and A.2) to $G^t|_{\mathcal{X}(\delta)}$ with a certain integer $t \ge 1$ ($G^t|_{\mathcal{X}(\delta)}$ denotes G^t restricted to $\mathcal{X}(\delta)$). By this application, we consider the attractivity of the single-class state F. It is clear that both $\mathcal{F}(\delta) := F \cap \mathcal{X}(\delta)$ and $\mathcal{X}(\delta) \backslash \mathcal{F}(\delta)$ are forward invariant under G^t. The continuous function $P : \mathcal{X}(\delta) \to \mathbb{R}_+$ defined by

$$P(\mathbf{x}) = \prod_{i \in N} \sum_{j \in N \backslash \{i\}} x_j$$

is a candidate for an average Liapunov function. This function satisfies $P(\mathbf{x}) = 0$ if and only if $\mathbf{x} \in \mathcal{F}(\delta)$. Define the continuous functions $\psi_t^- : \mathcal{X}(\delta) \to \mathbb{R}_+$ and

$\psi_t^+ : \mathcal{X}(\delta) \to \mathbb{R}_+$ by

$$\psi_t^-(\mathbf{x}) = \prod_{i\in N} \max_{j\in N\setminus\{i\}} \left\{\prod_{k=0}^{t-1} g_j(G^k(\mathbf{x}))\right\} \quad \text{and} \quad \psi_t^+(\mathbf{x}) = \prod_{i\in N} \min_{j\in N\setminus\{i\}} \left\{\prod_{k=0}^{t-1} g_j(G^k(\mathbf{x}))\right\}.$$

We see that these functions satisfy $P(G^t(\mathbf{x})) \leq \psi_t^-(\mathbf{x})P(\mathbf{x})$ and $P(G^t(\mathbf{x})) \geq \psi_t^+(\mathbf{x}) P(\mathbf{x})$ for all $\mathbf{x} \in \mathcal{X}(\delta)$. By using P as an average Liapunov function, we obtain the following result.

Theorem 4.1 *Suppose that* (H1) *holds and* (2.1) *is permanent.* (i) *If for every* $\delta \in (0, 1)$ *there exists an integer* $t \geq 1$ *such that* $\psi_t^-(\mathbf{x}) < 1$ *for all* $\mathbf{x} \in F(\delta)$*, then for all small* $\delta \in (0, 1)$ *there exists a neighborhood* $U(\delta)$ *of* $F(\delta)$ *in* $\mathbb{R}_+^n$ *such that* $\omega_f(\mathbf{x}) \subset F$ *for all* $\mathbf{x} \in U(\delta)$. (ii) *If for every* $\epsilon \in (0, 1)$ *there exists an integer* $t \geq 1$ *such that* $\psi_t^+(\mathbf{x}) > 1$ *for all* $\mathbf{x} \in F(\epsilon)$*, then* F *is a repeller.*

Proof Let us consider case (i). Since (2.1) is permanent, we can construct a compact set $\mathcal{X}(\delta)$ for $\mathbb{R}_+^n\setminus O$ (see Theorem A.3). Choose $\delta' \in (0, \delta)$ such that $\mathcal{X}(\delta) \subset X(\delta')$. Then, by assumption, there exists an integer $t \geq 1$ such that $\psi_t^-(\mathbf{x}) < 1$ for all $\mathbf{x} \in F(\delta') \supset \mathcal{F}(\delta)$. Let us apply Theorem A.2 to our problem ($\mathcal{X}(\delta)$, $\mathcal{F}(\delta)$ and $G^t|_{\mathcal{X}(\delta)}$ correspond to X, S and f in Theorem A.2, respectively). By Theorem A.2, it follows that there exists a neighborhood $\mathcal{U}(\delta)$ of $\mathcal{F}(\delta)$ in $\mathcal{X}(\delta)$ such that $\omega_{G^t}(\mathbf{x}) \subset \mathcal{F}(\delta)$ for all $\mathbf{x} \in \mathcal{U}(\delta)$. Since f is continuous and $\mathcal{F}(\delta)$ is forward invariant under f, every point close to $\mathcal{F}(\delta)$ is mapped to a point close to $\mathcal{F}(\delta)$ by f. Therefore, $\omega_f(\mathbf{x}) \subset \mathcal{F}(\delta)$ for all $\mathbf{x} \in \mathcal{U}(\delta)$. Since this result holds for all small $\delta \in (0, 1)$, the conclusion of case (i) follows.

Let us consider case (ii). Similarly to the above, we apply Theorem A.1 to $G^t|_{\mathcal{X}(\delta)}$. By this application, the second conclusion immediately follows since $\gamma_f^+(\mathbf{x}) \cap \mathcal{X}(\delta) \neq \emptyset$ for every $\mathbf{x} \in \mathbb{R}_+^n\setminus O$. □

The following lemma is useful when we obtain easily verifiable conditions for the attractivity of F. This lemma shows that the average logarithmic growth of each class during one generation converges to zero when the population density fluctuates along a single-class orbit.

Lemma 4.2 *Suppose that* (H1) *holds and* (2.1) *is permanent. Then for any* $\epsilon > 0$ *and* $\delta \in (0, 1)$ *there exists an integer* $T \geq 1$ *such that*

$$\left| \frac{1}{t} \sum_{k=0}^{t-1} \ln g_i(G^k(\mathbf{x})) \right| \leq \epsilon \tag{4.1}$$

holds for all $\mathbf{x} \in F_i(\delta)$ *and* $t \geq T$.

Proof Let δ be an arbitrary number in the interval $(0, 1)$. Since (2.1) is permanent, we can choose a $\delta' \in (0, \delta)$ such that every solution $\mathbf{x}(t)$ with $\mathbf{x}(0) \in F_i(\delta)$ satisfies $\delta' \leq x_i(tn) \leq 1/\delta'$ for all $t \geq 0$ (see Theorem A.3).

Let $\mathbf{x}(t)$ be a solution of (2.1) with $\mathbf{x}(0) \in F_i(\delta)$. Then, by the definition of g_i,

$$\begin{aligned} x_i(tn) &= g_i(\mathbf{x}((t-1)n))x_i((t-1)n) \\ &= g_i(\mathbf{x}((t-1)n))g_i(\mathbf{x}((t-2)n)) \cdots g_i(\mathbf{x}(0))x_i(0) \end{aligned}$$

holds for all $t \geq 1$, and we obtain

$$\left| \frac{1}{t} \sum_{k=0}^{t-1} \ln g_i(G^k(\mathbf{x}(0))) \right| = \left| \frac{\ln x_i(tn) - \ln x_i(0)}{t} \right| \leq \frac{|2\ln \delta'|}{t}.$$

Hence, (4.1) holds for all $\mathbf{x} \in F_i(\delta)$ and $t \geq |2\ln \delta'|/\epsilon$. □

In the application of Theorem 4.1, we have to find an integer $t \geq 1$ such that either $\psi_t^-(\mathbf{x}) < 1$ for all $\mathbf{x} \in F(\delta)$ or $\psi_t^+(\mathbf{x}) > 1$ for all $\mathbf{x} \in F(\delta)$. These inequalities can be checked by the signs of

$$\Lambda_t^-(\mathbf{x}) = \frac{1}{t} \ln \psi_t^-(\mathbf{x}) \quad \text{and} \quad \Lambda_t^+(\mathbf{x}) = \frac{1}{t} \ln \psi_t^+(\mathbf{x}).$$

It is clear that $\psi_t^-(\mathbf{x}) < 1$ (resp. $\psi_t^+(\mathbf{x}) > 1$) if $\Lambda_t^-(\mathbf{x})$ is negative (resp. $\Lambda_t^+(\mathbf{x})$ is positive). By definition of ψ_t^- and ψ_t^+, the functions Λ_t^- and Λ_t^+ are expressed as follow:

$$\begin{aligned} \Lambda_t^-(\mathbf{x}) &= \sum_{i \in N} \max_{j \in N \setminus \{i\}} \left\{ \frac{1}{t} \sum_{k=0}^{t-1} \ln g_j(G^k(\mathbf{x})) \right\}, \\ \Lambda_t^+(\mathbf{x}) &= \sum_{i \in N} \min_{j \in N \setminus \{i\}} \left\{ \frac{1}{t} \sum_{k=0}^{t-1} \ln g_j(G^k(\mathbf{x})) \right\}. \end{aligned}$$

4.1 Density dependence restricted to a single age-class

In this subsection, we focus on the case where the density dependence is restricted to a single age-class. More precisely, we consider system (2.1) satisfying

(A1) $\sigma_d(\mathbf{x}) = \sigma(\alpha_0 x_0 + \alpha_1 x_1 + \cdots + \alpha_{n-1} x_{n-1})$, $\alpha_i > 0$, and $\sigma_i(\mathbf{x}) = 1$ for all $i \neq d$.

For this special case, we can obtain an easily verifiable condition for the attractivity of F as follows.

Theorem 4.3 *Suppose that* (H1) *and* (A1) *hold and* (2.1) *is permanent. Assume that* σ *is strictly decreasing.* (i) *If the inequalities*

$$\begin{aligned} s_{d-1} &< \alpha_{d-1}/\alpha_d \\ s_{d-1}s_{d-2} &< \alpha_{d-2}/\alpha_d \\ &\vdots \\ s_{d-1}s_{d-2}\cdots s_{d-n+1} &< \alpha_{d-n+1}/\alpha_d \end{aligned} \tag{4.2}$$

hold, then for all small $\delta > 0$ *there exists a neighborhood* $U(\delta)$ *of* $F(\delta)$ *in* $\mathbb{R}^n_+$ *such that* $\omega_f(\mathbf{x}) \subset F$ *for all* $\mathbf{x} \in U(\delta)$. (ii) *If every reversed inequality of* (4.2) *holds, then* F *is a repeller.*

Proof In order to simplify the proof, we consider a rescaled system of (2.1). We use the same rescaling as in [26]. Let $\widetilde{x}_i = \alpha_i x_i$ and

$$\widetilde{s}_0 = s_0\frac{\alpha_1}{\alpha_0}, \quad \widetilde{s}_1 = s_1\frac{\alpha_2}{\alpha_1}, \ldots, \widetilde{s}_{n-1} = s_{n-1}\frac{\alpha_0}{\alpha_{n-1}}.$$

Then we obtain

$$\widetilde{\mathbf{x}}(t+1) = L[\widetilde{\mathbf{x}}(t)]\widetilde{\mathbf{x}}(t)$$

satisfying

(A1)′ $\sigma_d(\widetilde{\mathbf{x}}) = \sigma(|\widetilde{\mathbf{x}}|)$ and $\sigma_i(\widetilde{\mathbf{x}}) = 1$ for all $i \neq d$.

The inequalities (4.2) is reduced to

$$\begin{aligned} \widetilde{s}_{d-1} &< 1 \\ \widetilde{s}_{d-1}\widetilde{s}_{d-2} &< 1 \\ &\vdots \\ \widetilde{s}_{d-1}\widetilde{s}_{d-2}\cdots\widetilde{s}_{d-n+1} &< 1. \end{aligned}$$

Note that each $\widetilde{s}_i$ can be any positive number depending on the distribution of α_i. We investigate the dynamics of the rescaled system satisfying (A1)′ since it has the same qualitative dynamics as (2.1) satisfying (A1). In the remainder of the proof, we omit the tildes.

Consider case (i). Let δ be an arbitrary number in the interval (0, 1). Since (2.1) is permanent, we can choose $\delta' \in (0, \delta)$ such that every solution $\mathbf{x}(t)$ with $\mathbf{x}(0) \in F(\delta)$ satisfies $\mathbf{x}(t) \in F(\delta')$ for all $t \geq 0$ (see Theorem A.3). The condition (4.2) implies that there exists a constant $c \in (0, 1)$ such that each product in (4.2) is less than c. Define $h : [\delta', 1/\delta'] \to \mathbb{R}$ by $h(u) = \ln\sigma(u) - \ln\sigma(cu)$. Then h has the maximum Δ and the monotonicity of σ implies $\Delta < 0$.

Let $\mathbf{x} \in F_i(\delta)$. Then $f^m(\mathbf{x}) \in F_d$ holds for some $m \in N$. Therefore, by (A1)$'$, we have the expression

$$\begin{aligned} g_i(\mathbf{x}) &= \mathcal{R}_0\sigma_{i+n-1}(f^{n-1}(\mathbf{x}))\cdots\sigma_{i+1}(f(\mathbf{x}))\sigma_i(\mathbf{x}) \\ &= \mathcal{R}_0\sigma_d(f^m(\mathbf{x})) \\ &= \mathcal{R}_0\sigma(|f^m(\mathbf{x})|). \end{aligned}$$

Let $j \neq i$. Then $g_j(\mathbf{x}) = \mathcal{R}_0\sigma(|f^{m'}(\mathbf{x})|)$ for some $m' \in N, m' \neq m$. By the definition of c, if $m' > m$,

$$\begin{aligned} |f^{m+n}(\mathbf{x})| &= s_{d-1}s_{d-2}\cdots s_{d-(m+n-m')}|f^{m'}(\mathbf{x})| \\ &< c|f^{m'}(\mathbf{x})|, \end{aligned}$$

and if $m > m'$,

$$\begin{aligned} |f^{m}(\mathbf{x})| &= s_{d-1}s_{d-2}\cdots s_{d-(m-m')}|f^{m'}(\mathbf{x})| \\ &< c|f^{m'}(\mathbf{x})|. \end{aligned}$$

Note that $f^{m+n}(\mathbf{x}), f^m(\mathbf{x}) \in F_d$. Let $\mathbf{x}' = G(\mathbf{x})$ if $m' > m$ and $\mathbf{x}' = \mathbf{x}$ if $m > m'$. Then, by the monotonicity of σ, we obtain

$$\begin{aligned} \ln g_j(\mathbf{x}) - \ln g_i(\mathbf{x}') &= \ln\{\mathcal{R}_0\sigma(|f^{m'}(\mathbf{x})|)\} - \ln\{\mathcal{R}_0\sigma(|f^m(\mathbf{x}')|)\} \\ &= \ln\sigma(|f^{m'}(\mathbf{x})|) - \ln\sigma(|f^m(\mathbf{x}')|) \\ &< \ln\sigma(|f^{m'}(\mathbf{x})|) - \ln\sigma(c|f^{m'}(\mathbf{x})|). \end{aligned}$$

Since $G^k(\mathbf{x}), G^k(\mathbf{x}') \in F_i(\delta')$, the inequality $\ln g_j(G^k(\mathbf{x})) - \ln g_i(G^k(\mathbf{x}')) < \Delta$ holds for all $k \geq 0$.

Let $\epsilon \in (0, -\Delta/n)$. Then, by Lemma 4.2, there exists an integer $T_i \geq 1$ such that (4.1) holds for all $\mathbf{x} \in F_i(\delta') \supset F_i(\delta)$ and $t \geq T_i$. If we choose $T = \max_{i\in N}\{T_i\}$, then

$$\Lambda_T^-(\mathbf{x}) < (n-1)\epsilon + \epsilon + \Delta < 0$$

holds for all $\mathbf{x} \in F(\delta)$. Theorem 4.1 (i) completes the proof for case (i).

Since case (ii) can be proved similarly, we omit its proof. □

Let us interpret condition (4.2). First, assume that $\alpha_0, \alpha_1, \ldots, \alpha_{n-1}$ are identical. Notice that (4.2) does not include the parameter s_d. Hence, under the assumption $s_0, \ldots, s_{n-2} \in (0, 1]$ and $s_{n-1} \in (0, \infty)$, (4.2) holds if $d = n-1$ and $s_{n-2} < 1$. This case corresponds to the case studied by Mjølhus et al.[26]. This result implies that if the density dependence is restricted to the survival process of the matured class, the birth process or both, then the single-class state is attractive. On the other hand, under the assumption $s_0, \ldots, s_{n-2} \in (0, 1]$ and $s_{n-1} \in (0, \infty)$, the condition for case (ii) holds if $d = 0$ and $\mathcal{R}_0 > 1$. This result implies that if only the survival probability of the newborn class is density dependent, then the single-class state does not attract any positive orbits.

Consider the case where $\alpha_0, \alpha_1, \ldots, \alpha_{n-1}$ are not identical. If α_d is sufficiently small in comparison with all other α_i, i.e., the survival provability of class d is insensitive to its own population density x_d, then (4.2) holds. Conversely, the reversed inequalities in (4.2) hold if α_d is sufficiently large in comparison with all other α_i, i.e., the survival provability of class d is sensitive to its own population density x_d.

4.2 Density dependence NOT restricted to a single age-class

In this subsection, we consider a case where all functions σ_i are density dependent. For convenience, we define the functions $\theta_{ij} : \mathbb{R}_+ \to (0, \infty)$, $i, j \in N$, by $\theta_{ij} = \sigma_i|_{F_j}$, which is the function σ_i restricted to F_j. Then an easily verifiable condition for the attractivity of F is given as follows (Theorem 4.4 does not contain Theorem 4.3 as a special case; see below).

Theorem 4.4 *Suppose that* (H1) *holds and* (2.1) *is permanent.* (i) *If the inequalities*

$$\max_{j \in N \setminus \{i\}} \theta_{ji}(u) \le \theta_{ii}(u), \quad i = 0, 1, \ldots, n-1, \tag{4.3}$$

hold for all $u > 0$ and one of the inequalities strictly holds for all $u > 0$, then for all small $\delta > 0$ there exists a neighborhood $U(\delta)$ of $F(\delta)$ in $\mathbb{R}_+^n$ such that $\omega_f(\mathbf{x}) \subset F$ for all $\mathbf{x} \in U(\delta)$. (ii) *If the inequalities*

$$\min_{j \in N \setminus \{i\}} \theta_{ji}(u) \ge \theta_{ii}(u), \quad i = 0, 1, \ldots, n-1, \tag{4.4}$$

hold for all $u > 0$ and one of the inequalities strictly holds for all $u > 0$, then F is a repeller

Proof Consider case (i). Let δ be an arbitrary number in the interval $(0, 1)$. Since (2.1) is permanent, we can choose a $\delta' \in (0, \delta)$ such that every solution $\mathbf{x}(t)$ with $\mathbf{x}(0) \in F(\delta)$ satisfies $\mathbf{x}(t) \in F(\delta')$ for all $t \ge 0$ (see Theorem A.3). Define $h_{ji} : [\delta', 1/\delta'] \to \mathbb{R}$ by $h_{ji}(u) = \ln \theta_{ji}(u) - \ln \theta_{ii}(u)$. Then h_{ji} has the maximum c_{ji} and the assumption on θ_{ji} implies

$$c_{ji} \le 0 \quad \text{and} \quad \min_{i \in N} \max_{j \in N \setminus \{i\}} c_{ji} = \Delta < 0.$$

Let $\mathbf{x} \in F_i(\delta)$. Then, by assumption, we obtain

$$\begin{aligned} \ln g_j(\mathbf{x}) - \ln g_i(\mathbf{x}) &= \sum_{k=0}^{n-1} \Big[\ln\{\theta_{j+k,i+k}(|f^k(\mathbf{x})|)\} - \ln\{\theta_{i+k,i+k}(|f^k(\mathbf{x})|)\} \Big] \\ &\le \sum_{k=0}^{n-1} c_{j+k,i+k} \le \Delta, \end{aligned}$$

where the subscripts of θ_{ij} and c_{ij} are counted modulo n. Since $G^k(\mathbf{x}) \in F_i(\delta')$ for all $k \geq 0$, $\ln g_j(G^k(\mathbf{x})) - \ln g_i(G^k(\mathbf{x})) \leq \Delta$ holds for all $k \geq 0$.

Let $\epsilon \in (0, -\Delta/n)$. Then, by Lemma 4.2, there exists an integer $T_i \geq 1$ such that (4.1) holds for all $\mathbf{x} \in F_i(\delta') \supset F_i(\delta)$. Let $T = \max\{T_i\}$. Then

$$\Lambda_T^-(\mathbf{x}) \leq \epsilon(n-1) + \epsilon + \Delta < 0$$

holds for all $\mathbf{x} \in F(\delta)$. Theorem 4.1 (i) completes the proof for case (i).

Since case (ii) can be proved similarly, we omit its proof. □

Remark As mentioned above, Theorem 4.4 does not contain Theorem 4.3 as a special case. Furthermore, Theorem 4.4 is not applicable to the case where at least one of the functions σ_i is density independent. For instance, assume $\sigma_k(\mathbf{x}) = 1$. Then $\theta_{ll}(u) \neq 1$ must hold for some l (if $\theta_{ii}(u) = 1$ for all i, then all single-class orbits go to infinity or zero, i,e., system (2.1) is not permanent). Hence (4.3) (resp. (4.4)) does not hold for $i = l$ (resp. $i = k$).

Let $\sigma : \mathbb{R}_+ \to (0, \infty)$ be a decreasing function. Suppose that each function θ_{ij} satisfies $\theta_{ij}(u) = \sigma(a_{ij}u)$ with $a_{ij} \geq 0$. Then (4.3) is reduced to

$$\min_{j \in N\setminus\{i\}} a_{ji} \geq a_{ii}, \quad i = 0, 1, \ldots, n-1. \tag{4.5}$$

The parameter a_{ij} denotes the sensitivity of the survival provability of class i to the population density of class j. So, (4.5) implies that the survival provability of each class is sensitive to the population densities of all other classes. That is, competition is more severe between than within age-classes. Similarly, (4.4) is reduced to

$$\max_{j \in N\setminus\{i\}} a_{ji} \leq a_{ii}, \quad i = 0, 1, \ldots, n-1, \tag{4.6}$$

which implies that competition is more severe within than between age-classes.

5 Application

In this section, we apply Theorems 4.3 and 4.4 to specific examples of the Leslie matrix model (2.1).

5.1 Example 1

Consider the application of Theorem 4.3. For simplicity, we assume that $n = 3$ and

$$\sigma_0(\mathbf{x}) = \exp(-\alpha_0 x_0 - \alpha_1 x_1 - \alpha_2 x_2), \quad \sigma_1 = 1, \quad \sigma_2 = 1.$$

Then it follows from Proposition 3.1 that system (2.1) is dissipative [(H2)′–(ii) is satisfied]. Furthermore, by Propositions 3.3 and 3.4, system (2.1) is permanent if and

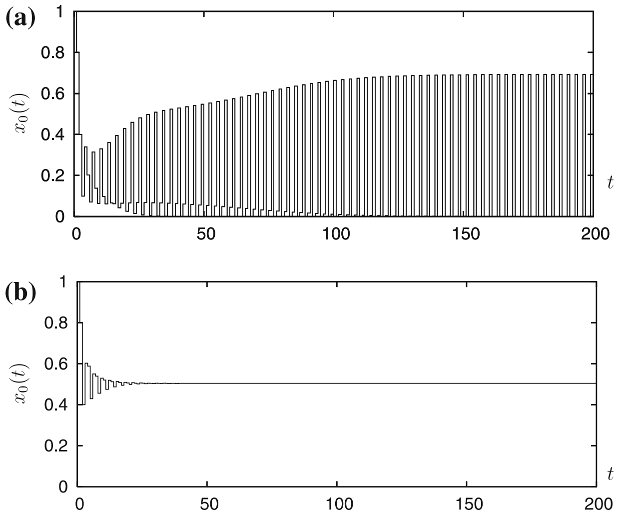

Fig. 1 Temporal variations of system (2.1) with $n = 3$. The functions σ_i are given by $\sigma_0(\mathbf{x}) = \exp(-\alpha_0 x_0 - \alpha_1 x_1 - \alpha_2 x_2)$, $\sigma_1 = \sigma_2 = 1$. The initial condition is $x_0(0) = 1$, $x_1(0) = x_2(0) = 0.1$. The parameters are $s_0 = s_1 = 0.5$, $\mathcal{R}_0 = 2$ (thus $s_2 = \mathcal{R}_0/(s_0 s_1) = 8$), **a** $\alpha_0 = 1$, $\alpha_1 = \alpha_2 = 10$ and **b** $\alpha_0 = \alpha_1 = \alpha_2 = 1$

only if $\mathcal{R}_0 = s_0 s_1 s_2 > 1$. The inequalities in (4.2) are reduced to

$$s_2\alpha_0 < \alpha_2 \quad \text{and} \quad s_1 s_2 \alpha_0 < \alpha_1.$$

These inequalities hold if α_0 is sufficiently small in comparison with α_1 and α_2, i.e., the survival probability of the newborn class is sufficiently insensitive to its own population density. If the above inequalities are satisfied in addition to $\mathcal{R}_0 > 1$, then $F\backslash O$ attracts a positive orbit (see Fig. 1a). Conversely, consider the case

$$s_2\alpha_0 > \alpha_2 \quad \text{and} \quad s_1 s_2 \alpha_0 > \alpha_1.$$

These inequalities hold if α_0 is sufficiently large in comparison with α_1 and α_2, i.e., the survival probability of the newborn class is sufficiently sensitive to its own population density. If the above inequalities are satisfied in addition to $\mathcal{R}_0 > 1$, then F is repelling (see Fig. 1b).

In [28], system (2.1) with $\sigma_1(\mathbf{x}) = \cdots = \sigma_{n-2}(\mathbf{x}) = \sigma(\alpha_0 x_0 + \alpha_1 x_1 + \cdots + \alpha_{n-1} x_{n-1})$ and $\sigma_{n-1}(\mathbf{x}) = 1$ is studied. Although our result (Theorems 4.4 and 4.3) is not applicable to such a system, an attractive single-class orbit is observed in [28].

5.2 Example 2

Let us consider the application of Theorem 4.4. For simplicity, we assume that $n = 3$ and

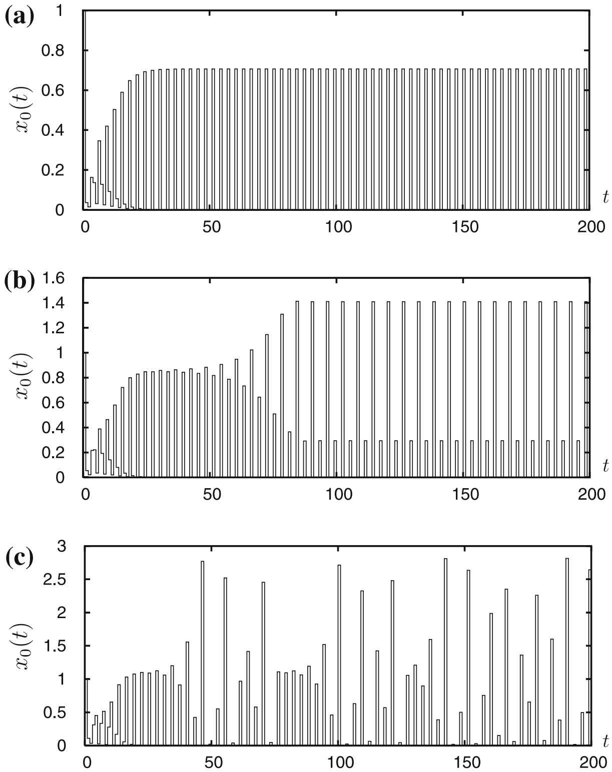

Fig. 2 Temporal variations of system (2.1) with $n = 3$. The functions σ are given by $\sigma_i(\mathbf{x}) = \exp(-\sum_{j=0}^{2} a_{ij}x_j)$ with a_{ij} satisfying (5.1). The initial condition is $x_0(0) = 1$, $x_1(0) = x_2(0) = 0.1$. The parameters are $s_0 = s_1 = 0.5$, **a** $\mathcal{R}_0 = 10$ (thus $s_2 = \mathcal{R}_0/(s_0s_1) = 40$), **b** $\mathcal{R}_0 = 15$ (thus $s_2 = \mathcal{R}_0/(s_0s_1) = 60$) and **c** $\mathcal{R}_0 = 30$ (thus $s_2 = \mathcal{R}_0/(s_0s_1) = 120$)

$$\sigma_i(\mathbf{x}) = \exp\left(-\sum_{j=0}^{2} a_{ij}x_j\right), \quad i = 0, 1, 2,$$

where $a_{ij} > 0$. Then it follows from Proposition 3.1 that system (2.1) is dissipative. Furthermore, by Propositions 3.3 and 3.4, system (2.1) is permanent if and only if $\mathcal{R}_0 = s_0s_1s_2 > 1$. Consider the following matrix $A = (a_{ij})$:

$$A = \begin{pmatrix} 3 & 4 & 4 \\ 4 & 3 & 4 \\ 4 & 4 & 3 \end{pmatrix}. \tag{5.1}$$

In this case, competition is more severe between than within age-classes and the matrix A satisfies (4.3) (see also (4.5)). Thus $F \backslash O$ attracts a positive orbit under $\mathcal{R}_0 > 1$. Three types of population dynamics are shown in Fig. 2. In Fig. 2a, which corresponds to the case where $\mathcal{R}_0$ is slightly larger than one, the orbit converges to a single-class

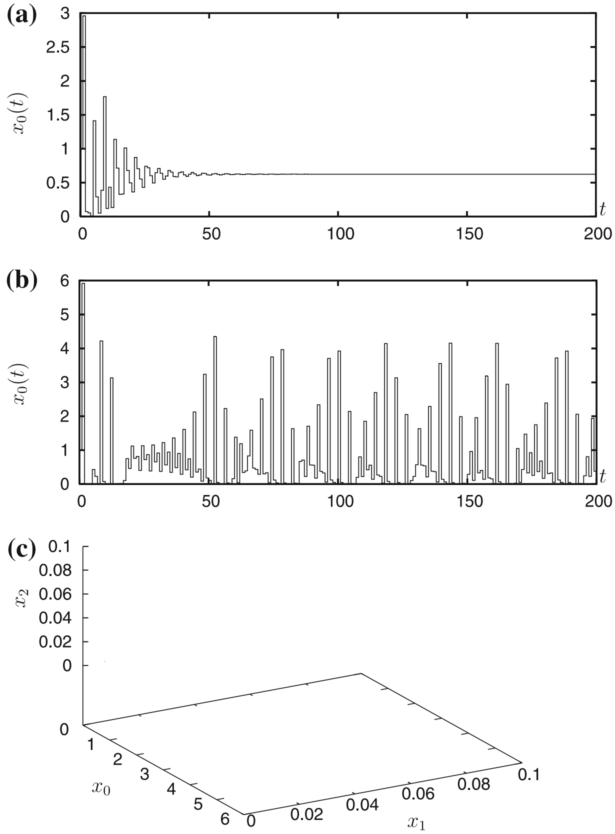

Fig. 3 Temporal variations of system (2.1) with $n = 3$. The functions σ are given by $\sigma_i(\mathbf{x}) = \exp(-\sum_{j=0}^{2} a_{ij}x_j)$ with a_{ij} satisfying (5.2). The initial condition is $x_0(0) = 1$, $x_1(0) = x_2(0) = 0.1$. The parameters are $s_0 = s_1 = 0.5$, **a** $\mathcal{R}_0 = 30$ (thus $s_2 = \mathcal{R}_0/(s_0 s_1) = 120$) and **b** $\mathcal{R}_0 = 60$ (thus $s_2 = \mathcal{R}_0/(s_0 s_1) = 240$). In (**c**), the orbit $\mathbf{x}(t)$ ($t = 0, 1, \ldots, 10^5$) of case (**b**) is depicted in the phase space

3-cycle. Although the population dynamics becomes complex as $\mathcal{R}_0$ increases, the single-class state is still attractive. The population eventually fluctuates periodically with period 6 in Fig. 2b, and aperiodically in Fig. 2c.

On the other hand, F is repelling if competition within age-classes is severe as follows:

$$A = \begin{pmatrix} 3 & 1 & 1 \\ 1 & 3 & 1 \\ 1 & 1 & 3 \end{pmatrix}. \tag{5.2}$$

Figure 3 shows two types of population dynamics. In Fig. 3a, which corresponds to the case where $\mathcal{R}_0$ is slightly larger than one, the orbit converges to an interior fixed point (see Fig. 3a). Although the population dynamics becomes complex as $\mathcal{R}_0$ increases, any positive orbits do not approach the single-class state (see Fig. 3b, c).

6 Concluding remarks

The dynamics of a general nonlinear Leslie matrix model for a semelparous population has been investigated. It was shown that the total population can persist in the sense of permanence if the basic reproduction number $\mathcal{R}_0 > 1$ (see Proposition 3.3). Conversely, under a certain mild condition ($\sigma_i(\mathbf{x}) \leq 1$ for all i, i.e., the density dependence always acts negatively), the population-free fixed point $\mathbf{x} = \mathbf{0}$ is globally asymptotically stable if $\mathcal{R} \leq 1$ (see Proposition 3.4). Therefore, our result provides a condition under which (2.1) is permanent if and only if $\mathcal{R}_0 > 1$.

In Sect. 4, the (local) attractivity of the single-class state F has been considered (note that system (2.1) could have an attractor in the interior of $\mathbb{R}^n_+$ even if F is attractive; see Sect. 9 of [10] for multiple attractors). Theorem 4.3 focuses on the case where the density dependence is restricted to a single age-class, say class d, and σ_d is a strictly decreasing function of the weighted sum $\alpha_0 x_0 + \alpha_1 x_1 + \cdots + \alpha_{n-1} x_{n-1}$. This theorem implies that the single-class state F becomes attractive if the survival probability of individuals in class d is sensitive to the individuals in classes $i \neq d$. If $d = n - 1$, this result is also interpreted as follow: the fecundity is sensitive to the individuals in the lower classes. This is the same result as that in [26]. A more general case is also considered in Sect. 4. For example, Theorem 4.4 is applicable to the case where $\sigma_i(\mathbf{x}) = \exp(-\sum_{i=0}^{n-1} a_{ij} x_i)$. Theorem 4.4 implies that the single-class state F becomes attractive if the survival probability of each class is sensitive to the individuals belonging to the other classes. Therefore, from Theorems 4.3 and 4.4, we can conclude that the single-class state F becomes attractive if competition is more severe between than within age-classes. This conclusion is the same as that in [1]. Our results provide a further mathematical basis of the conclusion by Bulmer [1] (see also [6,10,22]).

Let us focus on the periodical cicada case. As pointed out by May [25], in periodical cicada populations, it is unlikely that inter and intra-class competition are greatly different since there is great variability in size among nymphs of the same age. However, even in such a case, competition can become apparently more severe between than within age-classes by incorporating the effect of predation with a functional response. Let us construct an example. For simplicity, define

$$\sigma(\mathbf{x}) = \exp(-\alpha_0 x_0 - \cdots - \alpha_{n-1} x_{n-1}), \quad \alpha_i > 0,$$

and assume that $\sigma_0(\mathbf{x}) = \cdots = \sigma_{n-2}(\mathbf{x}) = \sigma(\mathbf{x})$. Let $s_0, \ldots, s_{n-2} \in (0, 1]$ and $s_{n-1} \in (0, \infty)$. Then, as usual, $s_i \sigma_i$, $i = 0, 1, \ldots, n-2$, denotes the survival probability of age-class i. To incorporate the effect of predation, we put

$$s_{n-1} \sigma_{n-1}(\mathbf{x}) = \phi p(\mathbf{x}) s \sigma(\mathbf{x}),$$

where $s\sigma(\mathbf{x})$ is the survival probability of the last age-class until emergence, $p(\mathbf{x})$ is the fraction of adult individuals that escape from predation, and ϕ is the reproduction number of an adult individual. Define $p(\mathbf{x})$ by

$$p(\mathbf{x}) = \exp\left(-\frac{aP}{1 + aT_h s\sigma(\mathbf{x})x_{n-1}}\right),$$

where P is the number of predator individuals (P is assumed to be constant), a is the searching constant and T_h is the handling time (see [12, p.12]). Therefore, the Holling type II functional response is assumed. That is, the fraction of the adult individuals that escape from the predation increases as the total number of adults, $s\sigma(\mathbf{x})x_{n-1}$, increases. Let $s_{n-1} = \phi p(\mathbf{0})$ and $\sigma_{n-1}(\mathbf{x}) = p(\mathbf{x})\sigma(\mathbf{x})/p(\mathbf{0})$. Then (H1) and (H2)$'$-(ii) are satisfied. The matrix $\Theta(u) = (\theta_{ij}(u))$ is given by

$$\Theta(u) = \begin{pmatrix} e^{-\alpha_0 u} & e^{-\alpha_1 u} & \cdots & e^{-\alpha_{n-1} u} \\ e^{-\alpha_0 u} & e^{-\alpha_1 u} & \cdots & e^{-\alpha_{n-1} u} \\ \vdots & \vdots & \ddots & \vdots \\ e^{-\alpha_0 u} & e^{-\alpha_1 u} & \cdots & e^{-\alpha_{n-1} u} h(u) \end{pmatrix},$$

where $h(u) = \exp[aP\{1-1/(1+aT_h s e^{-\alpha_{n-1}u} u)\}]$. Hence the inequalities in (4.3) are satisfied, and since $h(u) > 1$ for all $u > 0$, $\max_{j \in N\setminus\{n-1\}} \theta_{j,n-1}(u) < \theta_{n-1,n-1}(u)$ holds for all $u > 0$. That is, with the help of the predation, intra-class competition can be relaxed in comparison with inter-class competition. Therefore, even if inter-class competition is not intense, the effect of predation with a certain functional response can leads to synchronous emergence of the periodical cicadas.

Our results, Theorems 4.3 and 4.4, also provide sufficient conditions under which F is repelling. Since these conditions only ensure that F is repelling, some orbit could converges to $\mathrm{bd}\mathbb{R}^n_+ \setminus F$. In fact, we can construct an example that satisfies (4.4) but some solution converges to a cycle on $\mathrm{bd}\mathbb{R}^n_+ \setminus F$. Consider system (2.1) with $\sigma_i(\mathbf{x}) = \exp(-\sum_{i=0}^{n-1} a_{ij} x_j)$, $n = 5$. We obtain the population dynamics depicted in Fig. 4, if we choose the parameters a_{ij} as follows:

$$\begin{pmatrix} 3 & 0.1 & 2 & 2 & 0.1 \\ 0.1 & 3 & 0.1 & 2 & 2 \\ 2 & 0.1 & 3 & 0.1 & 2 \\ 2 & 2 & 0.1 & 3 & 0.1 \\ 0.1 & 2 & 2 & 0.1 & 3 \end{pmatrix}. \tag{6.1}$$

In Fig. 4, the orbit converges to a 5-cycle, along which two classes are always missing but three classes are always present at any time. It is a future problem to investigate the dynamical behavior in the case where F is repelling or F is neither repelling nor attractive (see [5,6,9,11]).

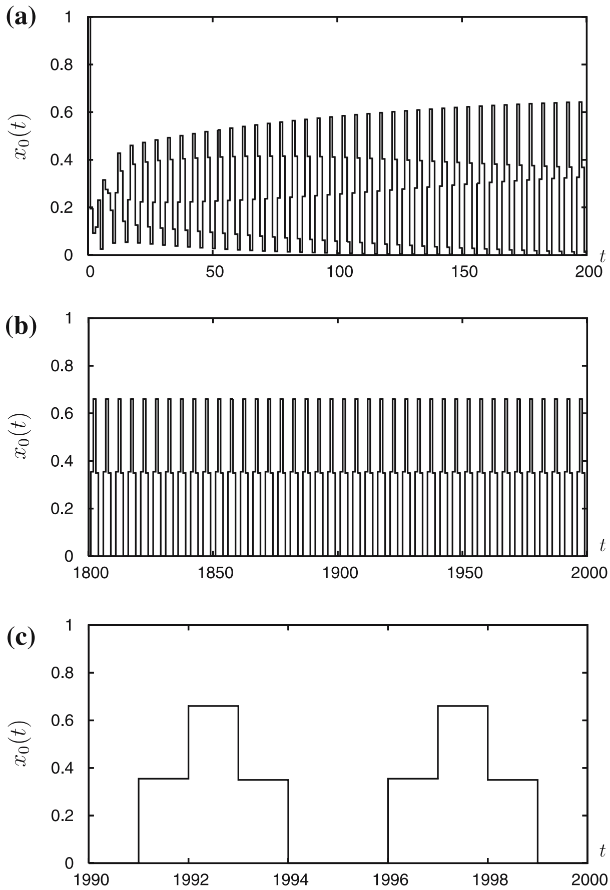

Fig. 4 Temporal variations of system (2.1) with $n = 5$. The functions σ are given by $\sigma_i(\mathbf{x}) = \exp(-\sum_{i=0}^{4} a_{ij}x_j)$, $i = 0, 1, \ldots, 4$, with a_{ij} satisfying (6.1). The initial condition is $x_0(0) = x_1(0) = x_2(0) = 1$, $x_3(0) = x_4(0) = 0.1$. The parameters are $s_0 = s_1 = s_2 = s_3 = 0.5$, $\mathcal{R}_0 = 10$ (thus $s_4 = \mathcal{R}_0/(s_0s_1s_2s_3)$)

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A Appendix A

Consider the semi-dynamical system generated by the continuous map $f : X \to X$, where X is a metric space. The (forward) *orbit* starting at $\mathbf{x}$ is defined by

$$\gamma_f^+(\mathbf{x}) := \{\mathbf{y} \in X : f^t(\mathbf{x}) = \mathbf{y} \quad \text{for some } t = 0, 1, \ldots\}.$$

The *omega-limit set* of $\mathbf{x}$ is defined by

$$\omega_f(\mathbf{x}) := \left\{\mathbf{y} \in X : \lim_{j\to\infty} f^{t_j}(\mathbf{x}) = \mathbf{y} \quad \text{for some sequence } t_j \to \infty\right\}.$$

Let S and V be subsets of X. S is said to be *forward invariant* if $f(S) \subset S$. S is said to be *absorbing for* V if S is forward invariant and $\gamma_f^+(\mathbf{x}) \cap S \neq \emptyset$ for every $\mathbf{x} \in V$. f is said to be *dissipative* if there exists a compact absorbing set S for X. S is said to be a *repeller* if there exists a neighborhood U of S such that for all $\mathbf{x} \notin S$ there exists $T > 0$ satisfying $f^t(\mathbf{x}) \notin U$ for all $t \geq T$. S is said to be an *attractor* if there exists a neighborhood U of S such that $\omega_f(\mathbf{x}) \subset S$ for all $\mathbf{x} \in U$. The following theorem of average Liapunov functions is utilized to show that a compact forward invariant set S is repelling (see also Theorem 2.2 [16] and Theorem 2.17 [18]).

Theorem A.1 (cf. Corollary 2.3 [15]) *Assume that X is compact and that S is a compact subset of X. Let S and $X \backslash S$ be forward invariant. Then S is a repeller if there exists a continuous function $P : X \to \mathbb{R}_+$ such that* (i) $P(\mathbf{x}) = 0$ *if and only if* $\mathbf{x} \in S$, *and* (ii) *for all* $\mathbf{x} \in S$, $\sup_{t \geq 1} \prod_{k=0}^{t-1} \psi(f^k(\mathbf{x})) > 1$, *where $\psi : X \to \mathbb{R}_+$ is a continuous function with $P(f(\mathbf{x})) \geq \psi(\mathbf{x}) P(\mathbf{x})$.*

By using the same technique, we can prove the following theorem, which is used to show that a compact forward invariant set is attractive (see also Theorem 2.7 [14, Corollary 2.3] and Theorem 2.18 [18]).

Theorem A.2 *Assume that X is compact and that S is a compact subset of X. Let S and $X \backslash S$ be forward invariant. Then S is an attractor if there exists a continuous function $P : X \to \mathbb{R}_+$ such that* (i) $P(\mathbf{x}) = 0$ *if and only if* $\mathbf{x} \in S$,*and* (ii) *for all* $\mathbf{x} \in S$, $\inf_{t \geq 1} \prod_{k=0}^{t-1} \psi(f^k(\mathbf{x})) < 1$, *where $\psi : X \to \mathbb{R}_+$ is a continuous function with $P(f(\mathbf{x})) \leq \psi(\mathbf{x}) P(\mathbf{x})$.*

Proof For $p \in (0, 1)$ and $t \geq 1$, define

$$U(p, t) = \left\{ \mathbf{x} \in X : \prod_{k=0}^{t-1} \psi(f^k(\mathbf{x})) < p \right\}.$$

Then $U(p, t)$ is open. Since $\inf_{t \geq 1} \prod_{k=0}^{t-1} \psi(f^k(\mathbf{x})) < 1$ for all $\mathbf{x} \in S$,

$$S \subset \bigcup_{p \in (0,1),\ t \geq 1} U(p, t)$$

holds. By the compactness of S, there exist $\overline{p} \in (0, 1)$ and $\bar{t}_1, \ldots, \bar{t}_m \geq 1$ such that $S \subset \bigcup_{k=1}^m U(\overline{p}, \bar{t}_k) =: W$. Let $\bar{t} = \max\{\bar{t}_1, \ldots, \bar{t}_m\}$.

Let $W_p = \{\mathbf{x} \in X : P(\mathbf{x}) < p\}$. Choose $p \in (0, 1)$ such that $\overline{W}_p \subset W$, where $\overline{W}_p$ is the closure of W_p . Let $\mathbf{x} \in W_p \subset W$. Then there exists $t_0 \in [1, \bar{t}]$ such that $\mathbf{x} \in U(\overline{p}, t_0)$. Furthermore, $P(f^{t_0}(\mathbf{x})) < \overline{p} P(\mathbf{x})$ holds. This implies $f^{t_0}(\mathbf{x}) \in W_p$. Therefore, by iteration, we obtain a sequence $t_j \to \infty$ with $t_{j+1} - t_j \in [1, \bar{t}]$ such that $f^{t_j}(\mathbf{x}) \in W_p$ and $P(f^{t_j}(\mathbf{x})) \to 0$ as $j \to \infty$. Since $P(f^t(\mathbf{x})) \leq \alpha P(f^{t_j}(\mathbf{x}))$ holds for all $t \in [t_j, t_{j+1}]$, where $\alpha = \max\{\prod_{k=0}^{t-1} \psi(f^k(\mathbf{x})) : 1 \leq t \leq \bar{t},\ \mathbf{x} \in X\}$, we conclude that $P(f^t(\mathbf{x})) \to 0$ as $t \to \infty$. This completes the proof. □

The following theorem is utilized to construct a compact absorbing set.

Theorem A.3 (Lemma 2.1 [16]) *Let $Y \subset X$ be open, and let N be open with a compact closure $\overline{N} \subset Y$. Assume that Y is forward invariant and that $\gamma_f^+(\mathbf{x}) \cap N \neq \emptyset$ for every $\mathbf{x} \in Y$. Then $\gamma_f^+(\overline{N})$ is a compact absorbing set for Y.*

B Appendix B

Consider the following difference equation:

$$\mathbf{x}(t+1) = A[\mathbf{x}(t)]\mathbf{x}(t), \tag{B.1}$$

where $A[\mathbf{x}] = (a_{ij}(\mathbf{x}))$ is an $n \times n$ matrix. Suppose that this system satisfies the following conditions:

(A1) Each $a_{ij}(\mathbf{x})$ is continuous;
(A2) $A[\mathbf{x}]\mathbf{x} \geq 0$ for all $\mathbf{x} \geq 0$;
(A3) $A[\mathbf{x}]\mathbf{x} \neq 0$ for all $\mathbf{x} \neq 0$;
(A4) System (B.1) is dissipative.

Here $\mathbf{x} \geq 0$ implies $x_i \geq 0$ for all i. It is clear that system (2.1) with (H1) satisfies (A1)–(A3).

A sufficient condition for dissipativity of (B.1) is given as follows.

Theorem B.1 (Theorem 2.2 [20]) *Assume that* (A1)–(A3) *hold. Suppose that there exist positive constants $K > 0$ and $\lambda_\infty \in (0, 1)$ such that the inequalities $\sum_{i=0}^{n-1} a_{ij}(\mathbf{x}) \leq \lambda_\infty$, $j = 0, 1, \ldots, n-1$, hold for all $\mathbf{x} \geq 0$ with $|\mathbf{x}| \geq K$. Then system* (B.1) *is dissipative.*

The sufficient condition for permanence of (B.1) is given as follows.

Theorem B.2 (Theorem 3 [19]) *Assume that* (A1)–(A4) *hold. Suppose that the matrix $A[\mathbf{0}]$ is irreducible. Then system* (B.1) *is permanent if the dominant eigenvalue λ_0 of $A[\mathbf{0}]$ satisfies $\lambda_0 > 1$.*

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