Global dynamics of a special class of nonlinear semelparous Leslie matrix models

Yunshyong Chow & Ryusuke Kon

Published online: 17 Jun 2020.

Submit your article to this journal ⬏

Article views: 321

View related articles ⬏

View Crossmark data ⬏

Taylor & Francis
Taylor & Francis Group

Global dynamics of a special class of nonlinear semelparous Leslie matrix models

Yunshyong Chow[a] and Ryusuke Kon[b]

[a]Academia Sinica and National Central University, Taipei and Tao-yuan, Taiwan; [b]Faculty of Engineering, University of Miyazaki, Miyazaki, Japan

ABSTRACT

This paper considers the dynamics of nonlinear semelparous Leslie matrix models. First, a class of semelparous Leslie matrix models is shown to be dynamically consistent with a certain system of Kolmogorov difference equations with cyclic symmetry. Then, the global dynamics of a special class of the latter is fully determined. Combining together, we obtain a special class of semelparous Leslie matrix models which possesses generically either a globally asymptotically stable positive equilibrium or a globally asymptotically stable cycle. The result shows that the periodic behaviour observed in periodical insects can occur as a globally stable phenomenon.

1. Introduction

A *periodical insect* means an insect whose life cycle has a fixed length of n years ($n > 1$) and where adults only appear every nth year. Periodical cicadas are one of the most famous examples of periodical insects. To understand the mechanism that produces the periodic behaviour in periodical insects, Bulmer [4] studied a special case of the following system of difference equations:

$$u_1(t+1) = s_n\sigma_n(u_1(t), u_2(t), \ldots, u_n(t))u_n(t),$$
$$u_2(t+1) = s_1\sigma_1(u_1(t), u_2(t), \ldots, u_n(t))u_1(t),$$
$$\vdots$$
$$u_n(t+1) = s_{n-1}\sigma_{n-1}(u_1(t), u_2(t), \ldots, u_n(t))u_{n-1}(t), \tag{1}$$

where $t \in \mathbb{Z}_+ = \{0, 1, 2, \ldots\}$. This system is a nonlinear semelparous Leslie matrix model and describes the dynamics of an age-structured population divided into n age-classes. The variable $u_i(t)$, $1 \le i \le n$, denotes the number of age-i individuals at time t. For $1 \le i \le n - 1$, the product of the constant s_i and the function $\sigma_i(\boldsymbol{u})$ represents the probability

that an age-i individual survives a unit of time. The product of the constant s_n and the function $\sigma_n(\boldsymbol{u})$ represents the fertility of an age-n individual. Here, we set all $\sigma_i(\boldsymbol{0}) = 1$. Thus, system (1) assumes that only the last age-class is reproductive. That is only $u_n(t)$ represents the number of adult individuals. In this sense, system (1) describes the population dynamics of *semelparous* species such as cicadas and beetles.

With $\sigma_i(\boldsymbol{u}) = \exp(-\sum_{1 \leq j \leq n} a_{ij}u_j)$ in system (1), Bulmer [4] gave a sufficient condition for such a system to have a locally stable cycle and reached the conclusion that periodic behaviour results if competition is more severe between age-classes than within age-classes. To mathematically verify this claim, system (1) has been studied in many papers. For example, Cushing and Li [11] studied bifurcations that occur around the extinction equilibrium of (1) with $n = 2$ and classified the stability of bifurcating positive equilibria and 2-cycles. This study was extended by Cushing [9] to the case $n = 3$; see also [8, 10, 19]. It was found that a heteroclinic cycle connecting three periodic points of a 3-cycle can also bifurcate from the extinction equilibrium. Besides these bifurcation studies, Davydova *et al.* [13] examined the asymptotic behaviour of (1) mathematically and numerically for the special case $n = 2$ and $\sigma_i(u_1, u_2) = \exp(-a_i(c_1u_1 + c_2u_2))$, $i = 1, 2$. In addition, given that the coordinate axes include every cycle associated with the periodic behaviour in periodical insects, the attractivity of the coordinate axes was studied by Mjølhus *et al.* [25], Kon [18], Kon and Iwasa [20] and Diekmann and Planqué [14]. All these studies only reveal the local behaviour around equilibria, cycles or the coordinate axes (but see [14] for an example of (1) where the coordinate axes attract a large set of initial conditions).

This paper aims at the global behaviour of system (1). We first try to find a certain class of (1) that is dynamically consistent with the following system of difference equations:

$$x_1(t+1) = g(x_1(t), x_2(t), \ldots, x_n(t))x_1(t),$$
$$x_2(t+1) = g(x_2(t), x_3(t), \ldots, x_1(t))x_2(t),$$
$$\vdots$$
$$x_n(t+1) = g(x_n(t), x_1(t), \ldots, x_{n-1}(t))x_n(t). \tag{2}$$

That is $x_i(t+1) = g(P^{-i+1}\boldsymbol{x}(t))x_i(t)$ for $1 \leq i \leq n$ with

$$P = \begin{pmatrix} 0 & 0 & \cdots & 0 & 1 \\ 1 & 0 & \cdots & 0 & 0 \\ 0 & 1 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & 1 & 0 \end{pmatrix} \quad \text{and} \quad \boldsymbol{x}(t) = \begin{pmatrix} x_1(t) \\ x_2(t) \\ \vdots \\ x_n(t) \end{pmatrix}. \tag{3}$$

Here, $x_i(t)$ and $g(P^{-i+1}\boldsymbol{x}(t))$ are, respectively, the population size and the growth rate of species i at time t.

System (2) is a special system of Kolmogorov difference equations which have been used to study the population dynamics of n interacting species. There are many works on systems of Kolmogorov difference equations. See, for instance, [2, 3, 7, 17, 23, 31]. Some specific examples of system (2) with $n = 2$ and 3 are reported in [16, 26–29]. In Theorem 2.2, it is shown that under some conditions on system (1), there exists a sequence

of non-singular matrices A_t with period n such that any solutions $\boldsymbol{u}(t)$ of (1) and $\boldsymbol{x}(t)$ of (2) satisfy

$$\boldsymbol{u}(t) = A_t \boldsymbol{x}(t) \text{ for all } t \in \mathbb{Z}_+ \text{ as long as } \boldsymbol{u}(0) = A_0 \boldsymbol{x}(0). \qquad (4)$$

This means systems (1) and (2) are dynamically consistent.

The next step is to determine the global dynamics of (2). For a general system, this is not an easy task. Inspired by the Leslie–Gower competition model [22], we are led to some simplified versions of (2) like the following

$$x_i(t+1) = x_i(t)h\left(x_i(t) + c\sum_{j\neq i} x_j(t)\right), \quad 1 \leq i \leq n, \qquad (5)$$

where the constant c means all interspecific competition coefficients are the same and the growth rate function h is assumed to be positive, continuous, strictly decreasing on $[0, \infty)$ with $h(0) > 1 > h(\infty)$. Furthermore, $xh(x)$ is assumed to be strictly increasing. Using some elementary comparison methods, we obtain in Sections 3 and 4 that depending on whether $c < 1$ or not, system (5) and its analogues have, generically, either a globally asymptotically stable positive equilibrium or a globally asymptotically stable set of single-species equilibria.

Via the dynamical consistency relation (4), we finally get in Theorem 5.1 the global dynamics of semelparous Leslie matrix models (1) in which

$$\sigma_i(u_1, u_2, \ldots, u_n) = (s_1 s_2 \cdots s_n)^{-(1/n)} h\left(\frac{u_i}{d_i} + c\sum_{j\neq i} \frac{u_j}{d_j}\right). \qquad (6)$$

Because of the periodicity of A_t in (4), we will find that the set of single-species equilibria of (5) corresponds to a single-class n-cycle in system (1). Thus, we obtain that depending on whether $c < 1$ or not, system (1) has, generically, either a globally asymptotically stable positive equilibrium or a globally asymptotically stable single-class n-cycle. In particular, the case $c > 1$ verifies Blumer's claim that periodic behaviour observed in periodical insects can occur as a globally stable cycle. Note that in (6), $(d_1, d_2, \ldots, d_n)$ is a positive eigenvector of the linearized system of (1) at the origin and $(s_1 s_2 \cdots s_n)^{1/n}$ the corresponding eigenvalue which is greater than 1 as $\sigma_i(\boldsymbol{0}) = 1 < h(0)$ by assumption.

This paper is organized as follows. In Section 2, we derive a condition under which (4) holds, thus determining a certain class of semelparous Leslie matrix models (1) which is dynamically consistent with the Kolmogorov difference equations (2). In Sections 3 and 4, we consider a special class of Kolmogorov difference equations that include (5) and completely determine its global dynamics together with the asymptotic stability of the equilibria. Combining together the results in Sections 2–4, we obtain in Section 5 the global dynamics of those semelparous Leslie matrix models whose survival functions are given in (6). Finally, some conclusions are given in Section 6.

2. Dynamical consistency between systems (1) and (2)

In this section, we derive a condition under which the semelparous Leslie matrix model (1) is dynamically consistent with the Kolmogorov difference Equation (2). Note that system (2) has *cyclic symmetry* in the sense that if $x(t)$ is a solution of (2), then so is $Px(t)$. In fact, we have

$$(Px(t+1))_i = x_{i-1}(t+1) = g(x_{i-1}(t), x_i(t), \ldots, x_{i+n-2}(t))x_{i-1}(t)$$
$$= g(P^{-i+1}Px(t))(Px(t))_i,$$

where the subscripts of x_i are counted mod n and $(Px)_i$ denotes the ith component of the vector Px.

Let $\mathbb{R}^n_+ = \{x \in \mathbb{R}^n : x_i \geq 0 \text{ for all } i\}$ and $\text{int}\mathbb{R}^n_+ = \{x \in \mathbb{R}^n : x_i > 0 \text{ for all } i\}$. Assume that

(H1) $s_i > 0$ and $\sigma_i : \mathbb{R}^n_+ \to (0, \infty)$ with $\sigma_i(\mathbf{0}) = 1$ for $1 \leq i \leq n$.

It is clear that both $\mathbb{R}^n_+$ and $\text{int}\mathbb{R}^n_+$ are forward invariant under (1). If each σ_i is differentiable, then the linearization of system (1) at the origin yields the linear difference equation $u(t+1) = Uu(t)$, where

$$U = \begin{pmatrix} 0 & 0 & \cdots & 0 & s_n \\ s_1 & 0 & \cdots & 0 & 0 \\ 0 & s_2 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & s_{n-1} & 0 \end{pmatrix} \quad \text{and} \quad u(t) = \begin{pmatrix} u_1(t) \\ u_2(t) \\ \vdots \\ u_n(t) \end{pmatrix}.$$

Being a non-negative irreducible matrix, Perron–Frobenius Theorem ensures that U has a dominant eigenvalue $\lambda_0 > 0$ and a positive eigenvector, say, $d = (d_1, d_2, \ldots, d_n)^\top$ associated with λ_0. It is straightforward to show that $\lambda_0 = \mathcal{R}_0^{1/n}$, where $\mathcal{R}_0 = s_1 s_2 \cdots s_n$ is called the basic reproduction number and represents the number of offspring reproduced by an individual in its lifetime when the density effects are ignored and $\{d_i\}$ satisfy

$$\frac{d_n}{d_1}s_n = \frac{d_1}{d_2}s_1 = \cdots = \frac{d_{n-1}}{d_n}s_{n-1} = \mathcal{R}_0^{1/n}, \tag{7}$$

which implies that once d_1 is fixed, $d_2, d_2, \ldots, d_n$ are uniquely determined by

$$d_i = \frac{s_{i-1}s_{i-2}\cdots s_1}{\mathcal{R}_0^{(i-1)/n}}d_1, \quad 2 \leq i \leq n.$$

Because U is the Jacobian matrix of system (1) evaluated at the origin, the origin of (1) is asymptotically stable if $\mathcal{R}_0 < 1$ and unstable if $\mathcal{R}_0 > 1$. Moreover, $Ud = \lambda_0 d$ implies that the vector $(1/\sum_{i=1}^n d_i)d$ gives a stationary age-distribution for the linearized system $u(t+1) = Uu(t)$. In fact, if the initial population $u(0)$ is proportional to d, then so is $u(t)$ for each $t \in \mathbb{Z}_+$. This motivates us to consider the following normalized population:

$$y_i(t) = u_i(t)/d_i \text{ for } 1 \leq i \leq n, \text{ i.e., } Dy(t) = u(t), \tag{8}$$

where D is the diagonal matrix whose diagonal entries are $d_1, d_2, \ldots, d_n$. We will see below how the desired dynamical consistency is obtained via $y(t)$. Using (7) and (8), it is easy to

check that (1) becomes

$$y_1(t+1) = \mathcal{R}_0^{1/n}\sigma_n(d_1y_1(t), d_2y_2(t), \ldots, d_ny_n(t))y_n(t),$$

$$y_2(t+1) = \mathcal{R}_0^{1/n}\sigma_1(d_1y_1(t), d_2y_2(t), \ldots, d_ny_n(t))y_1(t),$$

$$\vdots$$

$$y_n(t+1) = \mathcal{R}_0^{1/n}\sigma_{n-1}(d_1y_1(t), d_2y_2(t), \ldots, d_ny_n(t))y_{n-1}(t). \qquad (9)$$

We introduce the following assumption on the survival probabilities above:

(H2) $\quad \mathcal{R}_0^{1/n}\sigma_i(D\boldsymbol{x}) = g(P^{-i+1}\boldsymbol{x})$ for all $\boldsymbol{x} \in \mathbb{R}_+^n$ and $1 \leq i \leq n$.

Here, matrices P and D are given in (3) and (8), respectively. Under this assumption, (9) is equivalent to

$$y_i(t+1) = g(y_{i-1}(t), y_i(t), \ldots, y_{i-2}(t))y_{i-1}(t) \quad \text{for } 1 \leq i \leq n, \qquad (10)$$

which would be the same as system (2) if the subscripts of all y terms on the right-hand side are shifted forward by one.

Denote by $\boldsymbol{F}$ and $\boldsymbol{G}$ the maps defined by (2) and (9), respectively. Similarly, the t-fold compositions of $\boldsymbol{F}$ and $\boldsymbol{G}$ with themselves are denoted by $\boldsymbol{F}^t$ and $\boldsymbol{G}^t$, respectively. By definition, both $\boldsymbol{F}^0$ and $\boldsymbol{G}^0$ mean the identity map.

Lemma 2.1: *Assume that* (H1) *and* (H2) *hold. Then* $\boldsymbol{F}$ *and* $\boldsymbol{G}$ *are maps from* $\mathbb{R}_+^n$ *to itself and*

$$\boldsymbol{G}^t(\boldsymbol{x}) = P^t\boldsymbol{F}^t(\boldsymbol{x}) \text{ for all } \boldsymbol{x} \in \mathbb{R}_+^n \text{ and } t \in \mathbb{Z}_+. \qquad (11)$$

In particular, $\boldsymbol{G}^{nk}(\boldsymbol{x}) = \boldsymbol{F}^{nk}(\boldsymbol{x})$ *for all* $\boldsymbol{x} \in \mathbb{R}_+^n$ *and* $k \in \mathbb{Z}_+$.

Proof: Clearly, $\boldsymbol{F}$ and $\boldsymbol{G}$ are maps from $\mathbb{R}_+^n$ to itself. Since $\boldsymbol{F}^0$ and $\boldsymbol{G}^0$ are the identity map, (11) holds trivially for $t = 0$. We show now that it holds for $t = 1$, so that we may use mathematical induction. The cyclic symmetry of (2) implies that

$$P\boldsymbol{F}(\boldsymbol{x}) = \boldsymbol{F}(P\boldsymbol{x}) \text{ for all } \boldsymbol{x} \in \mathbb{R}_+^n. \qquad (12)$$

Then assumption (H2) ensures that for all $\boldsymbol{x} \in \mathbb{R}_+^n$,

$$\boldsymbol{G}(\boldsymbol{x}) = \begin{pmatrix} \mathcal{R}_0^{1/n}\sigma_n(D\boldsymbol{x})x_n \\ \mathcal{R}_0^{1/n}\sigma_1(D\boldsymbol{x})x_1 \\ \vdots \\ \mathcal{R}_0^{1/n}\sigma_{n-1}(D\boldsymbol{x})x_{n-1} \end{pmatrix} = \begin{pmatrix} g(P^{-n+1}\boldsymbol{x})x_n \\ g(\boldsymbol{x})x_1 \\ \vdots \\ g(P^{-n+2}\boldsymbol{x})x_{n-1} \end{pmatrix} = P\boldsymbol{F}(\boldsymbol{x}). \qquad (13)$$

That verifies (11) for $t = 1$. Suppose $\boldsymbol{G}^t(\boldsymbol{x}) = P^t\boldsymbol{F}^t(\boldsymbol{x})$ holds for some $t \geq 1$. Then

$$\boldsymbol{G}^{t+1}(\boldsymbol{x}) = \boldsymbol{G}(\boldsymbol{G}^t(\boldsymbol{x})) = \boldsymbol{G}(P^t\boldsymbol{F}^t(\boldsymbol{x})) = P\boldsymbol{F}(P^t\boldsymbol{F}^t(\boldsymbol{x})),$$

where (13) was used for the last equality above. Applying (12) repeatedly, we obtain $PF(P^t F^t(x)) = P^{t+1} F^{t+1}(x)$ and thus

$$G^{t+1}(x) = P^{t+1} F^{t+1}(x).$$

This completes the proof of (11) by mathematical induction. The final assertion follows from the fact that P^{nk} is the identity matrix for any $k \in \mathbb{Z}_+$. ∎

The desired dynamical consistency relation (4) with $A_t = DP^t$ follows from Lemma 2.1.

Theorem 2.2: *Assume* (H1) *and* (H2) *hold. Let* $u(t)$ *and* $x(t)$ *be solutions of* (1) *and* (2), *respectively. Then* $u(t) = DP^t x(t)$ *for all* $t \in \mathbb{Z}_+$ *whenever* $u(0) = Dx(0)$. *Here, matrices P and D are given in* (3) *and* (8), *respectively.*

Proof: By (8), the assumption $u(0) = Dx(0)$ implies $y(0) = x(0)$. Thus, by Lemma 2.1, $G^t(y(0)) = P^t F^t(x(0))$ holds for all $t \in \mathbb{Z}_+$. This implies that $y(t) = P^t x(t)$ for all $t \in \mathbb{Z}_+$. By (8), we finally obtain that $u(t) = DP^t x(t)$ for all $t \in \mathbb{Z}_+$. ∎

3. Global dynamics of Kolmogorov difference equations

As shown in [16], system (2) can have a rich dynamics even under the cyclic symmetry restriction. In order to obtain some results on the global dynamics, we will study in this section the following special case of (2): For $1 \leq i \leq n$ and $t \in \mathbb{Z}_+ = \{0, 1, 2, \ldots\}$,

$$x_i(t+1) = x_i(t) \prod_{\ell=1}^{m} h_\ell \left(x_i(t) + c_\ell \sum_{j \neq i} x_j(t) \right), \tag{14}$$

where all $c_\ell \geq 0$. Equation (14) means that the effect of the other species on the growth rate of species i is determined by their total population size $\sum_{j \neq i} x_j(t)$. We study system (14) under the assumptions that for $1 \leq \ell \leq m$,

(A1) $h_\ell(x)$ are positive, continuous and strictly decreasing functions on $[0, \infty)$,
(A2)   there are positive constants α_ℓ with $\sum_{\ell=1}^{m} \alpha_\ell = 1$ such that $x^{\alpha_\ell} h_\ell(x)$ are increasing functions on $[0, \infty)$,
(A3) $\prod_{\ell=1}^{m} h_\ell(0) > 1 > \lim_{x \to \infty} \prod_{\ell=1}^{m} h_\ell(x)$. In particular,

$$\text{there exist } L > 0 \text{ and } \lambda \in (0, 1) \text{ such that } \prod_{\ell=1}^{m} h_\ell(x) < \lambda \text{ for all } x \geq L. \tag{15}$$

When $m = 1$, (14) is reduced to (5). Assumptions (A1)–(A3) above then become

(A1)′ $h(x)$ is positive, continuous and strictly decreasing on $[0, \infty)$,
(A2)′ $xh(x)$ is increasing on $[0, \infty)$,
(A3)′ $h(0) > 1 > \lim_{x \to \infty} h(x)$.

It is straightforward to show that the functions

$$h_\ell(x) = \left(\beta_\ell + \frac{a_\ell}{1+x}\right)^{\alpha_\ell}, \quad 1 \le \ell \le m, \tag{16}$$

satisfy (A1)–(A3) if all β_ℓ, a_ℓ and α_ℓ are positive constants with $\sum_{\ell=1}^m \alpha_\ell = 1$ and $\prod_{\ell=1}^m (\beta_\ell + a_\ell)^{\alpha_\ell} > 1 > \prod_{\ell=1}^m \beta_\ell^{\alpha_\ell}$. Thus, the following system is an example of (14) satisfying (A1)–(A3): For $1 \le i \le n$ and $t \in \mathbb{Z}_+ = \{0, 1, 2, \ldots\}$,

$$x_i(t+1) = x_i(t) \prod_{\ell=1}^m \left(\beta_\ell + \frac{a_\ell}{1 + x_i(t) + c_\ell \sum_{j \ne i} x_j(t)}\right)^{\alpha_\ell}. \tag{17}$$

When $m = 1$, $\beta_1 = 0$, $a_1 = a > 1$, and $c_1 = c \ge 0$, system (17) becomes

$$x_i(t+1) = \frac{ax_i(t)}{1 + x_i(t) + c\sum_{j \ne i} x_j(t)}, \quad 1 \le i \le n, \tag{18}$$

which satisfies $(A1)' – (A3)'$ and is a special case of the Leslie–Gower model [22]:

$$x_i(t+1) = \frac{\lambda_i x_i(t)}{1 + x_i(t) + \sum_{j \ne i} c_{ij} x_j(t)}, \quad 1 \le i \le n. \tag{19}$$

Here, we may assume without loss of generality that the carrying capacities $\lambda_i - 1$ are positive and strictly decreasing in i. For $n = 2$, Cushing *et al.* [7] determined the asymptotic behaviours of all solutions as the theory of planar competitive maps guarantees that every positive solution converges, see, e.g. Liu and Elaydi [23] and Smith [31]. For $n \ge 3$, there are only some partial results. For instance, Ruiz-Herrera [30], Chow and Hsieh [5] and Ackleh *et al.* [1] show that in the competitive Leslie–Gower model, the competitive exclusion principle holds if only one species has the largest carrying capacity. So every solution converges to a boundary equilibrium which is globally stable. Recently, Balreira *et al.* [3] gave a general result on higher dimensional monotone maps that guarantees the global asymptotic stability of an interior equilibrium of system (19) with $n = 3$ and all $c_{ij} = c < (\lambda_3 - 1)/(\lambda_1 + \lambda_2 - \lambda_3 - 1)$. Chow and Palmer [6] showed that when $n = 3$ and $c_{ij} = c \gg 1$, the unique interior equilibrium of system (19), if exists, is a saddle with one dimensional stable manifold. They conjectured that every positive solution converges. We are thus motivated to find some special systems like (14) and (18) such that this conjecture holds.

It is clear that assumption (A1) implies both $\mathbb{R}_+^n$ and $\mathrm{int}\mathbb{R}_+^n$ are forward invariant for system (14). The following lemma shows that any solution of system (14) converges to neither **0** nor infinity under assumption (A3).

Lemma 3.1: *Assume that* (A1) *and* (A3) *hold. Then for any* $x \in \mathbb{R}_+^n \backslash \{\mathbf{0}\}$, *the omega-limit set* $\omega(x)$ *of system* (14) *is a compact subset of* $\mathbb{R}_+^n \backslash \{\mathbf{0}\}$.

Proof: Let $K_i = \{x \in \mathbb{R}^n_+ : x_i \leq L\}$, $1 \leq i \leq n$ and $x(t)$ be a solution of (14). Remember L and $\lambda < 1$ are defined in (15). Suppose that $x(t) \in \mathbb{R}^n_+ \setminus K_i$. Then

$$x_i(t) + c_\ell \sum_{j \neq i} x_j(t) \geq x_i(t) > L$$

holds for all $1 \leq \ell \leq m$. By (15) and (14), we have

$$\prod_{\ell=1}^{m} h_\ell \left(x_i(t) + c_\ell \sum_{j \neq i} x_j(t) \right) < \lambda < 1 \text{ and then } x_i(t+1) \leq \lambda x_i(t).$$

Thus, the solution $x(t)$ eventually enters $\bigcap_{i=1}^{n} K_i$. Since the right-hand side of (14) is a continuous function of $x(t)$ and $\bigcap_{i=1}^{n} K_i$ is compact, the solution $x(t)$ is bounded. Thus, $\omega(x(0))$ is compact. Similarly, the first inequality in (A3) implies $x(t)$ with $x(0) \in \mathbb{R}^n_+ \setminus \{0\}$ eventually enters the compact set $K = \bigcap_{i=1}^{n} K_i \cap \{x \in \mathbb{R}^n_+ : \epsilon \leq \sum_{i=1}^{n} x_i\}$ with sufficiently small $\epsilon > 0$. Since the right-hand side of (14) is a continuous function of $x(t)$ and all $h_\ell > 0$ by (A1), we can conclude that $\omega(x(0)) \subset \mathbb{R}_+ \setminus \{0\}$. ∎

Based on assumptions (A1) and (A2), we first show a preliminary lemma.

Lemma 3.2: *Assume* (A1) *and* (A2) *hold. Then for any $b_\ell > 0$ and $1 \leq \ell \leq m$, both $x \prod_{\ell=1}^{m} h_\ell(x + b_\ell)$ and $x \prod_{\ell=1}^{m} h_\ell(b_\ell x)$ are increasing for $x \in [0, \infty)$.*

Proof: Let $0 < \alpha_\ell < 1$ be given in (A2). Then $(x + b_\ell)^{\alpha_\ell} - x^{\alpha_\ell}$ is positive, decreasing in x as

$$\frac{d}{dx}((x + b_\ell)^{\alpha_\ell} - x^{\alpha_\ell}) = \alpha_\ell((x + b_\ell)^{\alpha_\ell - 1} - x^{\alpha_\ell - 1}) \leq 0.$$

By (A2) and (A1), $(x + b_\ell)^{\alpha_\ell} h_\ell(x + b_\ell)$ increases and $h_\ell(x + b_\ell)$ decreases in x. Hence,

$$0 \leq x^{\alpha_\ell} h_\ell(x + b_\ell) = (x + b_\ell)^{\alpha_\ell} h_\ell(x + b_\ell) - ((x + b_\ell)^{\alpha_\ell} - x^{\alpha_\ell}) h_\ell(x + b_\ell)$$

is increasing in x. Using $\sum_{\ell=1}^{m} \alpha_\ell = 1$, the first claim follows from

$$x \prod_{\ell=1}^{m} h_\ell(x + b_\ell) = \prod_{\ell=1}^{m} \left(x^{\alpha_\ell} h_\ell(x + b_\ell) \right).$$

Similarly, $(b_\ell x)^{\alpha_\ell} h_\ell(b_\ell x)$ increases in x by (A2). The remaining claim follows from multiplying these functions together and using $\sum_{\ell=1}^{m} \alpha_\ell = 1$ again. ∎

Define $c = (c_1, c_2, \ldots, c_m)^\top$ and $\mathbf{1} = (1, 1, \ldots, 1)^\top$. Using Lemmas 3.1 and 3.2, we now show the following result on global dynamics of system (14).

Theorem 3.3: *Assume that* (A1)–(A3) *hold and $x(t)$ is a solution of system* (14) *with $x(0) \in \text{int}\mathbb{R}^n_+$. Let $M = \max_{1 \leq i \leq n} x_i(0)$ and $J = \{i : x_i(0) = M\}$.*

(a) *If all $c_\ell \in [0, 1]$ and $c \neq \mathbf{1}$, then $\lim_{t \to \infty} x(t) = \eta\mathbf{1}$, where η is uniquely determined by $\prod_{\ell=1}^{m} h_\ell((1 + c_\ell(n - 1))\eta) = 1$.*

(b) *If all $c_\ell \geq 1$ and $\boldsymbol{c} \neq \boldsymbol{1}$, then $\lim_{t\to\infty} \boldsymbol{x}(t) = \eta \sum_{j\in J} \boldsymbol{e}_j$, where η is uniquely determined by $\prod_{\ell=1}^m h_\ell((1 + c_\ell(|J| - 1))\eta) = 1$ and $\boldsymbol{e}_j$ is the jth unit vector. In particular, $\lim_{t\to\infty} x_i(t) = 0$ for $i \notin J$.*

(c) *If all $c_\ell = 1$, then $\lim_{t\to\infty} \boldsymbol{x}(t) = \eta \boldsymbol{x}(0)$, where η is uniquely determined by $\prod_{\ell=1}^m h_\ell(\eta \sum_{j=1}^n x_j(0)) = 1$.*

Proof: Note that the existence and uniqueness of η in (a) –(c) is due to assumptions (A1) and (A3). Define $S_i(t) = \sum_{j\neq i} x_j(t)$. By symmetry, we may assume $x_1(0) = M$.

Part (a). We show by induction on $t \in \mathbb{Z}_+ = \{0, 1, 2, \ldots\}$ that for $2 \leq i \leq n$,

$$\frac{x_i(t)}{x_1(t)} \leq 1 \text{ and is increasing in } t. \text{ Thus } \lim_{t\to\infty} \frac{x_i(t)}{x_1(t)} = r_i \in (0, 1] \text{ exists.} \qquad (20)$$

Assume that all $x_i(t) \leq x_1(t)$ hold for some $t \in \mathbb{Z}_+$. Note that all $x_i(0) \leq M = x_1(0)$ by assumption. Then certainly $S_i(t) \geq S_1(t)$. Using (14) and the first claim in Lemma 3.2, we obtain $x_i(t + 1)/x_1(t + 1) \leq 1$ as follows:

$$x_i(t + 1) = x_i(t) \prod_{\ell=1}^m h_\ell(x_i(t) + c_\ell S_i(t)) \leq x_1(t) \prod_{\ell=1}^m h_\ell(x_1(t) + c_\ell S_i(t))$$

$$\leq x_1(t) \prod_{\ell=1}^m h_\ell(x_1(t) + c_\ell S_1(t)) = x_1(t + 1),$$

where in the last inequality (A1) and $S_i(t) \geq S_1(t)$ are used.

Since all $c_\ell \leq 1$, $x_i(t) + c_\ell S_i(t) \leq x_1(t) + c_\ell S_1(t)$ can be verified as follows:

$$(x_i(t) + c_\ell S_i(t)) - (x_1(t) + c_\ell S_1(t)) = (1 - c_\ell)(x_i(t) - x_1(t)) \leq 0. \qquad (21)$$

Using (14), (21) and (A1) again, we obtain

$$\frac{x_i(t + 1)}{x_i(t)} = \prod_{\ell=1}^m h_\ell(x_i(t) + c_\ell S_i(t)) \geq \prod_{\ell=1}^m h_\ell(x_1(t) + c_\ell S_1(t)) = \frac{x_1(t + 1)}{x_1(t)}. \qquad (22)$$

Thus $x_i(t)/x_1(t) \leq x_i(t + 1)/x_1(t + 1)$ and (20) is verified by induction.

Equation (20) and Lemma 3.1 imply that $\omega(\boldsymbol{x}(0)) \subseteq \{\boldsymbol{x} = s(r_1, r_2, r_3, \ldots, r_n)^\top : s \in (0, \infty)\} = Y$, where $r_1 = 1$ so that (20) is valid for $i = 1$ as well. On the half-line Y, system (14) is reduced to n one-dimensional equations:

$$x_i(t + 1) = x_i(t) \prod_{\ell=1}^m h_\ell \left(x_i(t) \left(1 + \frac{c_\ell}{r_i} \sum_{j\neq i} r_j \right) \right). \qquad (23)$$

Note that, by Lemma 3.2 and (A1), every solution on Y converges to the point $(\eta_1, \eta_2, \ldots, \eta_n)^\top$, where $\eta_i > 0$ is uniquely determined by $\prod_{\ell=1}^m h_\ell(\eta_i(1 + (c_\ell/r_i) \sum_{j\neq i} r_j))$ = 1. Since $\omega(\boldsymbol{x}(0)) \subseteq \mathbb{R}_+^n \backslash \{\boldsymbol{0}\}$ is compact by Lemma 3.1, $\boldsymbol{x}(t)$ is bounded for $t \geq 0$. The boundedness ensures that $\omega(\boldsymbol{x}(0))$ is also nonempty and invariantly connected (e.g. see

Theorem 5.2, LaSalle [21]). Since $\{(\eta_1, \eta_2, \ldots, \eta_n)^\top\}$ is a unique nonempty invariantly connected set in Y, we can conclude that $\omega(\boldsymbol{x}(0)) = \{(\eta_1, \eta_2, \ldots, \eta_n)^\top\}$, i.e. for $1 \leq i \leq n$,

$$\lim_{t \to \infty} x_i(t) = \eta_i. \tag{24}$$

We will see below that r_i and thus η_i are independent of the initial condition.

Write $\eta_1 = \eta$. Then $\eta_i = r_i\eta$ by (20). Remember $r_1 = 1$. The defining equations for η_1 and η_i above can be rewritten as

$$\prod_{\ell=1}^{m} h_\ell \left(\eta \left(r_1 + c_\ell \sum_{j \neq 1} r_j \right) \right) = 1 \text{ and } \prod_{\ell=1}^{m} h_\ell \left(\eta \left(r_i + c_\ell \sum_{j \neq i} r_j \right) \right) = 1. \tag{25}$$

Since all $c_\ell \leq 1$ by assumption and $r_i \leq 1 = r_1$ by (20), we find that

$$\left(r_1 + c_\ell \sum_{j \neq 1} r_j \right) - \left(r_i + c_\ell \sum_{j \neq i} r_j \right) = (1 - c_\ell)(r_1 - r_i) \geq 0 \text{ for all } \ell \leq m, i \leq n. \tag{26}$$

Because each h_ℓ is strictly decreasing by (A1), equality in (26) holds by (25). Then all $r_i = r_1 = 1$ and thus, all $\eta_i = \eta$ as some $c_\ell < 1$ by assumption. We conclude from (24) and (25) that $\lim_{t \to \infty} x_i(t) = \eta$ for $1 \leq i \leq n$ and η is uniquely determined by $\prod_{\ell=1}^{m} h_\ell(\eta(1 + c_\ell(n-1))) = 1$. This verifies the assertion in (a).

Part (b). Since $x_1(0) = M$ by assumption, we have $x_i(0) = x_1(0)$ for $i \in J$ and $x_i(0) < x_1(0)$ for $i \notin J$. As was done to show (20), we show by induction on t that for $2 \leq i \leq n$,

$$\frac{x_i(t)}{x_1(t)} \leq 1 \text{ and is decreasing in } t \text{ with } \frac{x_i(t)}{x_1(t)} = 1 \text{ for } i \in J. \tag{27}$$

As a consequence, there exist constants $r_i \in [0, 1]$ with $r_1 = 1$ such that

$$\lim_{t \to \infty} \frac{x_i(t)}{x_1(t)} = r_i \text{ and } r_i = 1 \text{ if and only if } i \in J. \tag{28}$$

Assume that all $x_i(t) \leq x_1(t)$ hold for some $t \in \mathbb{Z}_+$ with equality held for $i \in J$. The inequality $x_i(t+1) \leq x_1(t+1)$ can be verified exactly as in the formula before (21). Since $c_\ell \geq 1$, the inequality in (21) is reversed with equality held for $i \in J$. So is the inequality in (22). Hence, $x_i(t+1)/x_1(t+1) \leq x_i(t)/x_1(t)$ with equality held for $i \in J$. This proves (27) by induction and thus (28) is verified.

Following the same arguments in the proof of Part (a), we have $\omega(\boldsymbol{x}(0)) \subseteq \{\boldsymbol{x} = s(r_1, r_2, r_3, \ldots, r_n)^\top : s \in (0, \infty)\}$. Let $K = \{i \notin J : r_i > 0\}$. On the half-line above, system (14) is reduced to

$$x_i(t+1) = x_i(t) \prod_{\ell=1}^{m} h_\ell \left(x_i(t) \left(1 + \frac{c_\ell}{r_i} \sum_{j \neq i} r_j \right) \right) \quad \text{for } i \in J \cup K,$$

and $\lim x_i(t) = 0$ for $i \notin J \cup K$ as $\boldsymbol{x}(t)$ is bounded by Lemma 3.1 and $r_i = 0$ for $i \notin J \cup K$. Similar to (24), we can get from Lemma 3.2 and (28) that

$$\lim_{t \to \infty} x_i(t) = \eta_i \quad \text{for } 1 \leq i \leq n. \tag{29}$$

Here, $\eta_i = \eta$ for $i \in J$, $\eta_i = r_i\eta < \eta$ for $i \in K$ and $\eta_i = 0$ for $i \notin J \cup K$. Moreover, the defining equations for $\eta_1 = \eta$ and $\eta_i = \eta r_i$, $i \in K$ are given by

$$\prod_{\ell=1}^{m} h_\ell\left(\eta\left(r_1 + c_\ell \sum_{j \neq 1} r_j\right)\right) = 1 \text{ and } \prod_{\ell=1}^{m} h_\ell\left(\eta\left(r_i + c_\ell \sum_{j \neq i} r_j\right)\right) = 1. \tag{30}$$

We claim $K = \emptyset$. Then the conclusion in Part (b) follows from (29) with η uniquely determined by $\prod_{\ell=1}^{m} h_\ell(\eta(1 + c_\ell(|J| - 1))) = 1$ as shown in the first equality in (31).

Suppose the contrary that $K \neq \emptyset$. Using $r_j = r_1 = 1$ for $j \in J$ and $r_j = 0$ for $j \notin J \cup K$, we may rewrite (30) as

$$1 = \prod_{\ell=1}^{m} h_\ell\left(\eta\left(1 + c_\ell\left(|J| - 1 + \sum_{j \in K} r_j\right)\right)\right) = \prod_{\ell=1}^{m} h_\ell\left(\eta\left(r_i + c_\ell\left(|J| + \sum_{\substack{j \neq i \\ j \in K}} r_j\right)\right)\right). \tag{31}$$

Since all $c_\ell \geq 1$ by assumption and $r_i < 1 = r_1$ for $i \in K$ by (28),

$$\left(1 + c_\ell\left(|J| - 1 + \sum_{j \in K} r_j\right)\right) - \left(r_i + c_\ell\left(|J| + \sum_{\substack{j \neq i \\ j \in K}} r_j\right)\right) = (1 - c_\ell)(1 - r_i) \leq 0 \tag{32}$$

for all $1 \leq \ell \leq m$. Because all h_ℓ decreases strictly by (A1), the equality in (32) holds by (31). This leads to a contradiction as $\boldsymbol{c} \neq \boldsymbol{1}$ by assumption and $r_i < 1$ for $i \in K$.

Part (c). When all $c_\ell = 1$, all $x_i(t) + c_\ell S_i(t)$ equal $\sum_{j=1}^{n} x_j(t)$. The inequalities in both (21) and (22) become equalities. So we have

$$\frac{x_i(t+1)}{x_1(t+1)} = \frac{x_i(t)}{x_1(t)} = \frac{x_i(t-1)}{x_1(t-1)} = \cdots = \frac{x_i(0)}{x_1(0)}.$$

That is,

$$x_j(t) = x_1(t)\frac{x_j(0)}{x_1(0)} \text{ for all } 2 \leq j \leq n \text{ and } t \geq 0. \tag{33}$$

Therefore, system (14) for $i = 1$ can be written as

$$x_1(t+1) = x_1(t)\prod_{\ell=1}^{m} h_\ell\left(x_1(t)\frac{\sum_{1 \leq j \leq n} x_j(0)}{x_1(0)}\right). \tag{34}$$

Then $\lim_{t \to \infty} x_1(t) = \eta x_1(0)$ with η uniquely determined by $\prod_{\ell=1}^{m} h_\ell(\eta \sum_{j=1}^{n} x_j(0)) = 1$. By (33), $\lim_{t \to \infty} x_i(t) = \eta x_i(0)$ for $2 \leq i \leq n$ as claimed. The proof is complete. ∎

As a consequence, we have the following result for system (5).

Corollary 3.4: *Assume h satisfies* (A1)′-(A3)′ *and $\boldsymbol{x}(t)$ is a solution of (5) with $\boldsymbol{x}(0) \in$* int$\mathbb{R}_+^n$. *Let $M = \max_{1 \leq i \leq n} x_i(0)$ and $J = \{i : x_i(0) = M\}$.*

(a) *For $0 \leq c < 1$, $\lim_{t \to \infty} \boldsymbol{x}(t) = \eta \boldsymbol{1}$ with η uniquely determined by $h((1 + c(n - 1))\eta) = 1$.*

(b) *For $c > 1$, $\lim_{t \to \infty} \boldsymbol{x}(t) = \eta \sum_{j \in J} \boldsymbol{e}_j$ with η uniquely determined by $h((1 + c(|J| - 1))\eta) = 1$. In particular, $\lim_{t \to \infty} x_i(t) = 0$ for $i \notin J$.*

(c) *For $c = 1$, $\lim_{t \to \infty} \boldsymbol{x}(t) = \eta \boldsymbol{x}(0)$ with η uniquely determined by $h(\eta \sum_{j=1}^{n} x_j(0)) = 1$.*

We remark that since $x_i(0) = 0$ implies $x_i(t) = 0$ for all $t \in \mathbb{Z}_+$, the results above can be easily extended to $\boldsymbol{x}(0) \in \mathbb{R}_+^n$. Depending on $c < 1$, $c = 1$ or $c > 1$, the asymptotic behaviour of system (5) is quite different. Yet, both Theorem 3.3 and Corollary 3.4 show that every positive solution converges to some equilibrium.

4. Asymptotic stability of Kolmogorov difference equations

We discuss in this section the local asymptotic stability of some equilibria in system (14). For this purpose, we have to assume that besides (A1)–(A3), all h_ℓ in system (14) are differentiable. Note that $h'_\ell \leq 0$ by assumption (A1). Theorem 3.3 (a) says that $E^* = \eta^* \boldsymbol{1}$ is the unique interior equilibrium with η^* uniquely determined by

$$\prod_{\ell=1}^{m} h_\ell(N_\ell) = 1, \text{ where } N_\ell = (1 + c_\ell(n - 1))\eta^*. \tag{35}$$

Furthermore, Theorem 3.3(b) says that if $x_i(0) > \max_{i \neq j} x_j(0)$, then $|J| = 1$ and the solution $\boldsymbol{x}(t)$ of (14) converges to the single-species equilibrium $E_i = \eta \boldsymbol{e}_i$, where η is uniquely determined by

$$\prod_{\ell=1}^{m} h_\ell(\eta) = 1. \tag{36}$$

Concerning the local asymptotic stability of these equilibria, we have the following result.

Theorem 4.1: *Besides (A1)–(A3), we assume all $h'_\ell < 0$ on $(0, \infty)$.*

(a) *If all $c_\ell \in [0, 1]$ and $\boldsymbol{c} \neq \boldsymbol{1}$, then $E^* = \eta^* \boldsymbol{1}$ is locally asymptotically stable.*

(b) *If all $c_\ell \geq 1$ and $\boldsymbol{c} \neq \boldsymbol{1}$, then each $E_i = \eta \boldsymbol{e}_i$, $1 \leq i \leq n$, is locally asymptotically stable.*

Proof: Part (a). Let $B(\boldsymbol{x})$ be the Jacobian matrix of system (14) evaluated at $\boldsymbol{x}$. Using (35), $B(E^*)$ is an $n \times n$ matrix whose diagonal and off-diagonal entries are, respectively, given by

$$1 + \eta^* \sum_{k=1}^{m} \prod_{\ell \neq k} h_\ell(N_\ell) h'_k(N_k) \text{ and } \eta^* \sum_{k=1}^{m} \prod_{\ell \neq k} h_\ell(N_\ell) h'_k(N_k) c_k,$$

where N_ℓ are defined in (35). Being a circulant matrix [12], its eigenvalues are

$$\lambda_p = 1 + \eta^* \sum_{k=1}^{m} \prod_{\ell \neq k} h_\ell(N_\ell) h'_k(N_k) + \eta^* \sum_{k=1}^{m} \prod_{\ell \neq k} h_\ell(N_\ell) h'_k(N_k) c_k \sum_{j=1}^{n-1} e^{(2\pi i/n)jp}$$

for $0 \le p \le n-1$. Using $(1 + c_k(n-1))\eta^* = N_k$ and all $h_\ell > 0, h'_\ell < 0$, we get

$$\lambda_0 = 1 + \sum_{k=1}^{m} \prod_{\ell \ne k} h_\ell(N_\ell) h'_k(N_k) N_k < 1. \tag{37}$$

Because all $c_\ell \in [0,1]$ with some $c_\ell < 1$ by assumption and $\sum_{j=1}^{n-1} e^{(2\pi i/n)jp} = -1$ for $p \ge 1$,

$$\lambda_p = 1 + \sum_{k=1}^{m} \prod_{\ell \ne k} h_\ell(N_\ell) h'_k(N_k)(1 - c_k)\eta^* < 1 \text{ for } 1 \le p \le n-1. \tag{38}$$

We claim that for $1 \le p \le n-1$,

$$\lambda_p \ge \lambda_0 \ge 0. \tag{39}$$

Together with (37) and (38), we then have all $\lambda_p \in [0,1)$ and thus E^* is asymptotically stable. Using $N_k = (1 + c_k(n-1))\eta^*$, the first inequality above follows easily as:

$$\lambda_p - \lambda_0 = -\sum_{k=1}^{m} \prod_{\ell \ne k} h_\ell(N_\ell) h'_k(N_k) c_k n\eta^* \ge 0 \text{ for } p \ge 1.$$

It remains to show $\lambda_0 \ge 0$. By assumption (A2),

$$0 \le \frac{\mathrm{d}}{\mathrm{d}x} \left(x^{\alpha_k} h_k(x) \right) \Big|_{x=N_k} = \alpha_k N_k^{\alpha_k - 1} h_k(N_k) + N_k^{\alpha_k} h'_k(N_k),$$

which yields $h'_k(N_k)N_k \ge -\alpha_k h_k(N_k)$. Applying this inequality to (37), we get

$$\lambda_0 \ge 1 + \sum_{k=1}^{m} \prod_{\ell \ne k} h_\ell(N_\ell)(-\alpha_k)h_k(N_k) = 1 + \sum_{k=1}^{m}(-\alpha_k) \prod_{\ell=1}^{m} h_\ell(N_\ell) = 0$$

as $\prod_{\ell=1}^{m} h_\ell(N_\ell) = 1$ by (35) and $\sum_{k=1}^{m} \alpha_k = 1$ by (A3).

Part (b). By symmetry, it suffices to consider $E_1 = \eta e_1$. It is straightforward to show that $B(E_1) = (b_{ij})$ satisfies $b_{ij} = 0$ for $j \ne i \ge 2$. Moreover, (36) implies that

$$b_{11} = 1 + \eta \sum_{k=1}^{m} \prod_{\ell \ne k} h_\ell(\eta) h'_k(\eta) \text{ and } b_{ii} = \prod_{\ell=1}^{m} h_\ell(c_\ell \eta) \text{ for } 2 \le i \le n. \tag{40}$$

Being an upper triangular matrix, $\{b_{ii} : 1 \le i \le n\}$ are eigenvalues of $B(E_1)$. Because all $c_\ell \ge 1$ with some $c_\ell > 1$ and $0 < h_\ell$ decreases strictly by (A1), we get from (36) that

$$0 \le \prod_{\ell=1}^{m} h_\ell(c_\ell \eta) < \prod_{\ell=1}^{m} h_\ell(\eta) = 1. \tag{41}$$

By Lemma 3.2, $x \prod_{\ell=1}^{m} h_\ell(x)$ is increasing. Therefore,

$$0 \le \frac{\mathrm{d}}{\mathrm{d}x} \left(x \prod_{\ell=1}^{m} h_\ell(x) \right) \Big|_{x=\eta} = 1 + \eta \sum_{k=1}^{m} \prod_{\ell \ne k} h_\ell(\eta) h'_k(\eta) < 1, \tag{42}$$

where we have used (36) and the assumption that all $h_\ell > 0$, $h'_\ell < 0$. Combining together (40)–(42), we obtain that all eigenvalues b_{ii} lie in $[0, 1)$. The assertion that $E_1 = \eta e_1$ is asymptotically stable is verified. ∎

Note that functions h_ℓ defined in (16) satisfy all the assumptions in Theorem 4.1. By combining Theorem 4.1 with Theorem 3.3, we can conclude that, under the assumptions (A1)–(A3) and all $h'_\ell < 0$, the interior equilibrium E^* of system (14) is globally asymptotically stable in int$\mathbb{R}^n_+$ if all $c_\ell \in [0, 1]$ and $c \neq 1$. Furthermore, every single-species equilibrium $E_i = \eta e_i$, $1 \leq i \leq n$, is globally asymptotically stable in $\{x \in \text{int}\mathbb{R}^n_+ : x_i > \max_{j \neq i} x_j\}$ if all $c_\ell \geq 1$ and $c \neq 1$.

5. Global dynamics of semelparous Leslie matrix models

While assumptions (H1) and (H2) are sufficient for the dynamical consistency relation shown in Theorem 2.2, they are too weak to get any global results for system (1). We need to impose some extra conditions on the growth rate function g in system (2):

(H3) $g(x) = h(x_1 + c \sum_{j \neq 1} x_j)$ with function h satisfying (A1)'–(A3)'.

Then, Corollary 3.4 can be applied to system (2) and global dynamics of system (1) follows immediately from Theorem 2.2.

Before stating the results, we note that $\sigma_i(\mathbf{0}) = 1$ by (H1) and $h(0) > 1$ by (A3)'. Then (H2) and (H3) imply that

$$\sigma_i(\mathbf{u}) = \mathcal{R}_0^{-(1/n)} h \left(\frac{u_i}{d_i} + c \sum_{j \neq i} \frac{u_j}{d_j} \right), \tag{43}$$

where function h satisfies (A1)'–(A3)' and $h(0) = \mathcal{R}_0^{1/n} = (s_1 s_2 \cdots s_n)^{1/n} > 1$. For $j \neq i$, the constant c above measures the effect that the normalized density u_j/d_j of age-class j has on the survival of age-class i. Thus competition intensities between age-classes are independent of age if the density effect is measured by the normalized population vector $(u_1/d_1, u_2/d_2, \ldots, u_n/d_n)^\top$. For example, if σ_i and g are given by

$$\sigma_i(\mathbf{u}) = \frac{1}{1 + \frac{u_i}{d_i} + c \sum_{j \neq i} \frac{u_j}{d_j}} \quad \text{and} \quad g(x) = \frac{\mathcal{R}_0^{1/n}}{1 + x_1 + c \sum_{j \neq 1} x_j},$$

then (H2) and (H3) are satisfied with $h(x) = \mathcal{R}_0^{1/n}/(1 + x)$. With $\mathcal{R}_0 = s_1 s_2 \cdots s_n$, we may use (43) to rewrite system (1) as

$$u_1(t + 1) = s_n \mathcal{R}_0^{-(1/n)} h \left(\frac{u_n(t)}{d_n} + c \sum_{j \neq n} \frac{u_j(t)}{d_j} \right) u_n(t),$$

$$u_2(t+1) = s_1 \mathcal{R}_0^{-(1/n)} h \left(\frac{u_1(t)}{d_1} + c \sum_{j \neq 1} \frac{u_j(t)}{d_j} \right) u_1(t),$$

$$\vdots$$

$$u_n(t+1) = s_{n-1} \mathcal{R}_0^{-(1/n)} h \left(\frac{u_{n-1}(t)}{d_{n-1}} + c \sum_{j \neq n-1} \frac{u_j(t)}{d_j} \right) u_{n-1}(t). \tag{44}$$

Remember that matrices P and D are defined in (3) and (8), respectively.

Theorem 5.1: *Assume $s_i > 0$ for $1 \leq i \leq n$ and h satisfies* (A1)′ –(A3)′ *with $h(0) = \mathcal{R}_0^{1/n} > 1$. Let $\mathbf{u}(t)$ be a solution of (44) with $\mathbf{u}(0) \in \mathrm{int}\mathbb{R}_+^n$. Define $M = \max_{1 \leq i \leq n} u_i(0)/d_i$ and $J = \{i : u_i(0)/d_i = M\}$.*

(a) *If $0 \leq c < 1$, then $\lim_{t \to \infty} \mathbf{u}(t) = \hat{E}$, where $\hat{E} = \eta D\mathbf{1}$ with η uniquely determined by $h((1 + c(n-1))\eta) = 1$.*

(b) *If $c > 1$, then $\mathbf{u}(t)$ converges to a cycle as $t \to \infty$, i.e. $\omega(\mathbf{u}(0)) = \{\mathbf{p}_1, \mathbf{p}_2, \ldots, \mathbf{p}_n\}$, where $\mathbf{p}_i = \eta \sum_{j \in J} DP^{i-1}\mathbf{e}_j$ for $1 \leq i \leq n$ and η is uniquely determined by $h((1 + c(|J| - 1))\eta) = 1$. In particular, $\mathbf{u}(t)$ converges to the n-cycle*

$$P^* \stackrel{\text{def}}{=} \left\{ \begin{pmatrix} \eta d_1 \\ 0 \\ \vdots \\ 0 \end{pmatrix}, \begin{pmatrix} 0 \\ \eta d_2 \\ \vdots \\ 0 \end{pmatrix}, \ldots, \begin{pmatrix} 0 \\ 0 \\ \vdots \\ \eta d_n \end{pmatrix} \right\}$$

as $t \to \infty$ if $|J| = 1$, i.e. $\mathbf{u}(0) \in \bigcup_{i=1}^n V_i$, where $V_i = \{\mathbf{u} \in \mathrm{int}\mathbb{R}_+^n : u_i/d_i > \max_{j \neq i} u_j/d_j\}$.

(c) *If $c = 1$, then $\mathbf{u}(t)$ converges to a cycle as $t \to \infty$, i.e. $\omega(\mathbf{u}(0)) = \{\mathbf{p}_1, \mathbf{p}_2, \ldots, \mathbf{p}_n\}$, where $\mathbf{p}_i = \eta DP^{i-1}D^{-1}\mathbf{u}(0)$ for $1 \leq i \leq n$ and η is uniquely determined by $h((\sum_{j=1}^n u_j(0)/d_j)\eta) = 1$.*

If h is also differentiable, then $\hat{E}$ is globally asymptotically stable in $\mathrm{int}\mathbb{R}_+^n$ if $0 \leq c < 1$ and P^* is globally asymptotically stable in $\bigcup_{i=1}^n V_i$ if $c > 1$.

Proof: Let $\mathbf{x}(0) = D^{-1}\mathbf{u}(0)$ and $\mathbf{x}(t)$ be the solution of system (5) with the initial vector $\mathbf{x}(0)$. Note that $\mathbf{x}(0)$ is positive.

Part (a). By Corollary 3.4, $\mathbf{x}(t)$ converges to $\eta\mathbf{1}$ as $t \to \infty$. Then, Theorem 2.2 implies that $\mathbf{u}(nk) \to \eta D\mathbf{1}$ as $k \to \infty$. Since it holds for any positive $\mathbf{u}(0)$, we conclude that $\mathbf{u}(t) \to \eta D\mathbf{1}$ as $t \to \infty$.

Part (b). Note that $M = \max\{x_1(0), x_2(0), \ldots, x_n(0)\}$ and $J = \{i : x_i(0) = M\}$. As above, we get from Corollary 3.4 that $\mathbf{x}(t) \to \eta \sum_{j \in J} \mathbf{e}_j$ as $t \to \infty$. By Theorem 2.2, $\mathbf{u}(nk + m) \to \eta \sum_{j \in J} DP^m\mathbf{e}_j$ as $k \to \infty$ for every $0 \leq m \leq n-1$. Thus $\mathbf{u}(t)$ converges to the cycle $\{\eta \sum_{j \in J} D\mathbf{e}_j, \eta \sum_{j \in J} DP\mathbf{e}_j, \ldots, \eta \sum_{j \in J} DP^{n-1}\mathbf{e}_j\}$.

Part (c). By Corollary 3.4, $\mathbf{x}(t)$ converges to $\eta\mathbf{x}(0)$ as $t \to \infty$. Using Theorem 2.2, $\mathbf{u}(nk + m) \to \eta DP^m\mathbf{x}(0) = \eta DP^m D^{-1}\mathbf{u}(0)$ as $k \to \infty$ for every $0 \leq m \leq n-1$. Thus $\mathbf{u}(t)$ converges to the cycle $\{\eta\mathbf{u}(0), \eta DPD^{-1}\mathbf{u}(0), \ldots, \eta DP^{n-1}D^{-1}\mathbf{u}(0)\}$.

The assertion on the asymptotic stability follows from Theorem 4.1.   ■

Note that the set $\mathrm{int}\mathbb{R}_+^n \setminus \bigcup_{i=1}^n V_i$ has measure zero as it is a subset of $\bigcup_{1 \leq i \neq j \leq n} W_{ij}$, where

$$W_{ij} = \left\{ \boldsymbol{u} \in \mathbb{R}_+^n : \frac{u_i}{d_i} = \frac{u_j}{d_j} \right\} \text{ for } 1 \leq i \neq j \leq n.$$

Therefore, we find that generic solutions of (1) converge to the n-cycle P^* if $c > 1$.

6. Concluding remarks

This paper provides a class of semelparous Leslie matrix models that are dynamically consistent with a certain system of Kolmogorov difference equations with cyclic symmetry. For some special class of the latter, we can determine its global dynamics. Then using the dynamical consistency established above, we obtain in Theorem 5.1 a class of semelparous Leslie matrix models that has, generically, either a globally asymptotically stable positive equilibrium or a globally asymptotically stable n-cycle. In Theorem 5.1, a strong assumption is imposed on the survival probabilities of the models. For instance, it is required that the competition intensities between age-classes are independent of age when the density effect is measured by suitably normalized population densities. It is shown that if the competition intensity between-age-class is larger than that of within-age-class, i.e. the case $c > 1$ in Theorem 5.1, then the n-cycle associated with the periodic behaviour in periodical insects are globally asymptotically stable. It is also shown that if the situation is reversed, i.e. the case $c < 1$ in Theorem 5.1, then the positive equilibrium, at which a constant number of adult insects emerge every year, is globally asymptotically stable. These results are consistent with Bulmer's conclusion that periodical behaviour results if competition is more severe between age-classes than within age-classes.

In order to show the dynamical consistency mentioned above, we have assumed in Theorem 2.2 that the competition intensity between age-classes depends only on their unidirectional age-distance. This assumption fails if there are some age-specific density effects. Such could take place when predators attack only adult individuals as observed in periodical cicadas. Therefore, our results seem not applicable directly to the case of periodical cicadas, which are one of the most famous examples of periodical insects ; see, e.g. [14, 15, 24]. However, the assumption might be fulfilled for other periodical insects such as May beetles and the northern oak eggar since the possibility that intraspecific competition is a dominant factor maintaining their periodical behaviour is not denied [4].

As said above, we have imposed some strong assumption on the survival probabilities of our models. However, as far as we know, it is the first result on the global stability of nonlinear semelparous Leslie matrix models. Although a recent study by Diekamann and Planqué [14] shows a class of semelparous Leslie matrix models that periodical behaviour results for a large set of initial conditions, the possibility of bistability is not excluded in their models.

Disclosure statement

No potential conflict of interest was reported by the author(s).

References

[1] A.S. Ackleh, R.J. Sacker, and P. Salceanu, *On a discrete selection-mutation model*, J. Differ. Equ. Appl. 20 (2017), pp. 1383–1403.

[2] S. Baigent and Z. Hou, *Global stability of discrete-time competitive population models*, J. Differ. Equ. Appl. 23 (2017), pp. 1378–1396.

[3] E.C. Balreira, S. Elaydi, and R. Luıs, *Global stability of higher dimensional monotone maps*, J. Differ. Equ. Appl. 23 (2017), pp. 2037–2071.

[4] M.G. Bulmer, *Periodical insects*, Amer. Natur. 111 (1977), pp. 1099–1117.

[5] Y. Chow and J. Hsieh, *On multidimensional discrete-time Beverton–Holt competition models*, J. Differ. Equ. Appl. 19 (2013), pp. 491–506.

[6] Y. Chow and K. Palmer, *On a discrete three-dimensional Leslie–Gower competition model*, Discrete Contin. Dyn. Syst. Ser. B 24 (2019), pp. 4367–4377.

[7] J. Cushing, S. Levarge, N. Chitnis, and S.M. Henson, *Some discrete competition models and the competitive exclusion principle*, J. Differ. Equ. Appl. 10 (2004), pp. 1139–1151.

[8] J.M. Cushing, *Nonlinear semelparous Leslie models*, Math. Biosci. Eng. 3 (2006), pp. 17–36.

[9] J.M. Cushing, *Three stage semelparous Leslie models.*, J. Math. Biol. 59 (2009), pp. 75–104.

[10] J.M. Cushing and S.M. Henson, *Stable bifurcations in semelparous Leslie models*, J. Biol. Dyn. 6 (2012), pp. 80–102.

[11] J.M. Cushing and J. Li, *On Ebenman's model for the dynamics of a population with competing juveniles and adults*, Bull. Math. Biol. 51 (1989), pp. 687–713.

[12] P. Davis, Circulant Matrices, Wiley-Interscience, New York, NY, 1979.

[13] N.V. Davydova, O. Diekmann, and S.A. van Gils, *Year class coexistence or competitive exclusion for strict biennials?*, J. Math. Biol. 46 (2003), pp. 95–131.

[14] O. Diekmann and R. Planqué, *The winner takes it all: how semelparous insects can become periodical*, J. Math. Biol. (2019). Available at https://doi.org/10.1007/s00285-019-01362-3.

[15] F.C. Hoppensteadt and J.B. Keller, *Synchronization of periodical cicada emergences*, Science 194 (1976), pp. 335–337.

[16] H. Jiang and T.D. Rogers, *The discrete dynamics of symmetric competition in the plane*, J. Math. Biol. 25 (1987), pp. 573–596.

[17] J. Jiang and L. Niu, *On the equivalent classification of three-dimensional competitive Leslie/Gower models via the boundary dynamics on the carrying simplex*, J. Math. Biol. 74 (2017), pp. 1223–1261.

[18] R. Kon, *Competitive exclusion between year-classes in a semelparous biennial population*, in *Mathematical Modeling of Biological Systems*, Vol. II, A. Deutsch, R.B. de la Parra, R.J. de Boer, O. Diekmann, P. Jagers, E. Kisdi, M. Kretzschmar, P. Lansky, and H. Metz, eds., Birkhäuser, Boston, MA, 2007, pp. 79–90.

[19] R. Kon, *Stable bifurcations in multi-species semelparous population models*, in *Advances in Difference Equations and Discrete Dynamical Systems*, Springer Proceedings in Mathematics & Statistics, 212, S. Elaydi, Y. Hamaya, H. Matsunaga and C. Pötzsche, eds., Springer, Singapore, 2017, pp. 3–25.

[20] R. Kon and Y. Iwasa, *Single-class orbits in nonlinear Leslie matrix models for semelparous populations*, J. Math. Biol. 55 (2007), pp. 781–802.

[21] J.P. LaSalle, The Stability of Dynamical Systems, SIAM, Philadelphia, PA, 1976.

[22] P.H. Leslie and J.C. Gower, *The properties of a stochastic model for two competing species*, Biometrika 45 (1958), pp. 316–330.

[23] P. Liu and S.N. Elaydi, *Discrete competitive and cooperative models of Lotka–Volterra type*, J. Comput. Anal. Appl. 3 (2001), pp. 53–73.

[24] J. Machta, J.C. Blackwood, A. Noble, A.M. Liebhold, and A. Hastings, *A hybrid model for the population dynamics of periodical cicadas*, Bull. Math. Biol. 81 (2018), pp. 1122–1142.

[25] E. Mjølhus, A. Wikan, and T. Solberg, *On synchronization in semelparous populations*, J. Math. Biol.50 (2005), pp. 1–21.

[26] L.I.W. Roeger, *Hopf bifurcations in discrete May–Leonard competition models*, Can. Appl. Math. Q.11 (2003), pp. 175–194.

[27] L.I.W. Roeger, *Discrete May–Leonard competition models III*, J. Difference Equ. Appl. 10 (2004), pp. 773–790.

[28] L.I.W. Roeger, *Discrete May–Leonard competition models II*, Discrete Contin. Dyn. Syst. Ser. B 5 (2005), pp. 841–860.

[29] L.I.W. Roeger and L.J. Allen, *Discrete May–Leonard competition models I*, J. Differ. Equ. Appl. 10 (2004), pp. 77–98.

[30] A. Ruiz-Herrera, *Exclusion and dominance in discrete population models via the carrying simplex*, J. Differ. Equ. Appl. 19 (2013), pp. 96–113.

[31] H.L. Smith, *Planar competitive and cooperative difference equations*, J. Differ. Equ. Appl. 3 (1998), pp. 335–357.