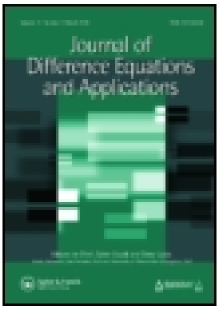

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A dynamic dichotomy for a system of hierarchical difference equations

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A dynamic dichotomy for a system of hierarchical difference equations

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A system of difference equations that arises in population dynamics is studied. Criteria are given for the existence of equilibria lying in the positive cone and for the existence of periodic cycles lying on the boundary of the cone. These equilibria and cycles arise from a bifurcation that occurs as a fundamental parameter R_0 increases through the value 1. Under monotone conditions on the nonlinearities and for R_0 near 1, we derive criteria for the stability of the equilibria and we determine the global dynamics on the boundary of the cone. We show that boundary orbits tend to periodic cycles (all of which we classify into four types). A dynamic dichotomy is established between the equilibria and the cycles, which asserts that one is stable and the other is unstable. We also establish a dynamic dichotomy between the equilibria and the boundary of the cone.

Keywords: hierarchical difference equations; nonlinear matrix models; equilibria; synchronous cycles; bifurcation; stability

AMS Subject Classification: 39A30; 39A28; 39A60

1. Introduction

Systems of difference equations of the form

$$\begin{aligned} x_1(t+1) &= \tau_m(x_1(t), \ldots, x_m(t))x_m(t) \\ x_{i+1}(t+1) &= \tau_i(x_1(t), \ldots, x_m(t))x_i(t), \quad i = 1, 2, \ldots, m-1 \end{aligned}$$

for $t \in Z^+ \triangleq \{0, 1, 2, \ldots\}$, arise in age-structured population dynamics. In that context each component $x_i(t)$ denotes the density of individuals of age i (specifically $i-1$ to i) and the equations describe the dynamics of a semelparous life history in which individuals of age i survive a unit of time with probability $\tau_i > 0$ until they reach the age m at which point they reproduce (at a per capita rate of $\tau_m > 0$ per unit time) and die. These equations define a discrete time semi-dynamical system by means of the map

$$\hat{x} \longrightarrow L(\hat{x})\hat{x} \tag{1}$$

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where $\hat{x} = \text{col}(x_i) \in R_+^m$ (the *positive cone* in R^m) and L is the projection matrix

$$L(\hat{x}) = \begin{pmatrix} 0 & 0 & \cdots & 0 & 0 & \tau_m(\hat{x}) \\ \tau_1(\hat{x}) & 0 & \cdots & 0 & 0 & 0 \\ 0 & \tau_2(\hat{x}) & \cdots & 0 & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots & \vdots \\ 0 & 0 & \cdots & \tau_{m-2}(\hat{x}) & 0 & 0 \\ 0 & 0 & \cdots & 0 & \tau_{m-1}(\hat{x}) & 0 \end{pmatrix}. \quad (2)$$

This has the form of a Leslie matrix model [1,2,4,13,14].

In general, nonlinear matrix models $\hat{x} \to P(\hat{x})\hat{x}$ with non-negative, irreducible projection matrices $P(\hat{x})$ exhibit a fundamental bifurcation when the (extinction) equilibrium $\hat{x} = \hat{0}$ loses stability as the dominant eigenvalue r of $P(\hat{0})$ increases through 1, resulting in the bifurcation of a continuum of positive equilibria (from $\hat{0}$) whose stability depends on the direction of bifurcation. The positive equilibria are stable if the direction of bifurcation is to the right ($r \gtrapprox 1$) and unstable if it is to the left ($r \lessapprox 1$). The latter occurs only if there is sufficient positive feedback, i.e. positive partial derivatives of τ_i at $\hat{x} = \hat{0}$ of sufficiently large magnitude. Such positive derivatives are called Allee effects. If all such derivatives are non-negative (but not all equal to zero), then the bifurcation is to the right. This negative feedback case is the most common assumption in population models. For details about the fundamental bifurcation theorem, see [2,4].

The fundamental bifurcation scenario described above requires that the projection matrix be primitive (i.e. the dominant eigenvalue is strictly dominant). The semelparous Leslie projection matrix (2) is not, however, primitive. Its eigenvalues

$$\left(\prod_{i=1}^{m} \tau_i(\hat{x}) \right)^{1/m} u_k, \quad k = 1, 2, \ldots, m$$

where $u_k = \exp(2\pi(k-1)i/m)$ are the mth roots of unity, all have the same magnitude. As a result, the fundamental bifurcation theorem is inapplicable to the semelparous Leslie matrix model. It turns out that some parts of the theorem are still valid and some are not. The extinction equilibrium $\hat{x} = \hat{0}$ does lose stability as

$$r \circeq \left(\prod_{i=1}^{m} \tau_i(\hat{0}) \right)^{1/m}$$

(the spectral radius of the Jacobian $L(\hat{0})$) increases through 1, or equivalently as the quantity

$$R_0 \circeq \prod_{i=1}^{m} \tau_i(\hat{0})$$

increases through 1. R_0 is known as the inherent net reproductive number (and equals the expected lifetime number of offspring per individual). In fact, the semelparous Leslie matrix model is permanent (dissipative and uniformly persistent) with respect to $\hat{x} = \hat{0}$ for $R_0 > 1$ [2,10,12]. Moreover, a (global, unbounded) continuum of positive equilibria $\hat{x}$

bifurcates (from $\hat{0}$) at $R_0 = 1$ [3]. However, it is not true that the stability of these bifurcating positive equilibria, near the bifurcation point $R_0 = 1$, depend on the direction of bifurcation (as in the general exchange of stability principle for a transcritical bifurcation). This is related to the fact that both the positive cone R^m_+ and its boundary ∂R^m_+ are invariant under maps (1) and (2).

Specifically, by definition a point $\hat{x} \in \partial R^m_+$ has at least one zero component. A zero component advances one position in one time step, ultimately returning to its original position after m time steps. (Positive components in $\hat{x}$ behave in the same way.) Therefore, orbits on the boundary of the cone sequentially visit coordinate hyperplanes and for this reason they are called synchronous orbits. In the population dynamic context, they represent population trajectories that oscillate with synchronized age cohorts and with missing age classes at every point in time. This dynamic is of course quite different from that of the positive equilibria, which represent stationary dynamics with all age classes present. A synchronous (boundary) orbit can be a periodic cycle (of period m or less), in which case it is called a synchronous cycle. Since such cycles always have the same number of missing age classes at any point in time, they can be classified according to the number of age classes present at any point in time. For example, an extreme case is that of a single-class synchronous cycle in which only one age class is present at any point in time.

It is proved in [3] that in addition to a branch of positive equilibria, there also bifurcates (from $\hat{0}$) a continuum of single-class m-cycles at $R_0 = 1$.

In [3], it is shown for the $m = 2$ dimensional case that a dynamic dichotomy occurs between the bifurcating positive equilibria and the single-class 2-cycles when a bifurcation to the right occurs (also see [6,11]). Specifically, it is shown (for $R_0 \gtrapprox 1$) that either the positive equilibrium is stable and the single-class 2-cycle unstable or vice versa. It cannot happen that both are stable or both are unstable. Moreover, the criteria that determines which of the two is (locally asymptotically) stable is related to a ratio c of between-class to within-class competition intensities as measured by weighted averages of the partial derivatives

$$\partial_j \tau_i \,\hat{=}\, \frac{\partial \tau_i}{\partial x_j} \quad \text{and} \quad \partial^0_j \tau_i \,\hat{=}\, \left. \frac{\partial \tau_i}{\partial x_j} \right|_{\hat{x}=\hat{0}}$$

with $j \neq i$ and $j = i$, respectively.

A natural conjecture is that the dynamic dichotomy also holds between the bifurcating positive equilibria and single-class m-cycles in the m-dimensional case. This turns out to be false, however, as is shown in [5] for the $m = 3$ dimensional case. Under certain monotonicity conditions (including the negative feedback assumption that $\partial^0_j \tau_i \leq 0$), a dynamic dichotomy does occur, however, between the bifurcating positive equilibria and the boundary ∂R^3_+ of the cone. This modification of the dichotomy is necessary because, as it turns out, the bifurcation at $R_0 = 1$ involves invariant loops that lie on ∂R^3_+ and which have the geometry of heteroclinic synchronous orbits that connect the phases of the single-class 3-cycle. This includes a case in which both the positive equilibrium and the single-class 3-cycle are simultaneously unstable. Moreover, two-class 3-cycles can also lie on the invariant loop, in which case the boundary dynamics are more complicated.

Whether or not the dynamic dichotomy between the bifurcating positive equilibria and the boundary ∂R^m_+ occurs for the semelparous Leslie models (1) and (2) in dimensions $m \geq 4$ remains an open problem. It is clear, from the case $m = 3$ for example, that the boundary dynamics play an important role with regard to this conjecture and that these dynamics can get considerably more complicated in higher dimensions (as the possibility of more types of multi-class m-cycles and more elaborate invariant loops on ∂R_+^m arises). Numerical simulations of an example with dimension $m = 4$ suggest that this dichotomy in fact does not hold in general (although this has not been proved rigorously); see [7]. Thus, it appears likely that the dichotomy does not in general hold for dimensions $m \geq 4$, although it might hold, of course, for models with special features and properties. In this paper, we will prove that a dynamic dichotomy does hold in dimension $m = 4$ for a certain class of semelparous Leslie models called 'hierarchical of degree one '.

This paper is organized as follows. We describe the model equations and the hypotheses that we require in Section 2, where we also give some preliminary results. In Section 3, we derive a thorough account of the global dynamics on the boundary ∂R_+^4. In Section 4, we establish criteria for the occurrence of a dynamic dichotomy, near the bifurcation point $R_0 = 1$, between the bifurcating positive equilibria and a certain type of synchronous 4-cycle on ∂R_+^4. In Section 5, we give criteria under which the dichotomy occurs between the positive equilibria and the boundary ∂R_+^4. These criteria are in terms of the age-class competition ratio c. The details of mathematical proofs appear in appendices.

2. Preliminaries

We consider the $m = 4$ dimensional semelparous Leslie models (1) and (2) with matrix entries of the form

$$\tau_i = \tau_i(x_i, x_{i+1}), \quad i = 1, 2, 3, \quad \text{and} \quad \tau_4 = \tau_4(x_4, x_1).$$

Biologically speaking, these entries for $i = 1, 2, 3$ describe the situation when the probability an individual in a juvenile class survives one time unit depends, in addition to its own age-class density, only on the density of the next older class. For this reason the model is called 'hierarchical of degree one'. The assumption on τ_4 means that adult fecundity depends only on adult and newborn densities.

We make the following smoothness and normalization assumptions on these entries, in which Ω is an open set in R^4 that contains the *closure* $\bar{R}_+^4$ of the positive cone R_+^4.

A1: $\tau_4 = s_4\sigma_4(x_4, x_1)$ and $\tau_i = s_i\sigma_i(x_i, x_{i+1})$, where $\sigma_i \in C^2(\Omega, (0, 1])$, $\sigma_4(0, 0) = \sigma_i(0, 0) = 1$ and $s_4 > 0$, $0 < s_i < 1$.

We also make the following monotonicity and boundedness assumptions. We assume that the subscript notation is mod(4), so that $x_5 = x_1$.

A2: On Ω we have

(a) $\partial_j\sigma_i \leq 0$ for $1 \leq i, j \leq 4$ and at least one $\partial_i^0\sigma_i < 0$ and one $\partial_{i+1}^0\sigma_i < 0$;
(b) $\partial_i[\sigma_i(x_i, x_{i+1})x_i] \geq 0$ and $\sigma_i(x_i, x_{i+1})x_i$ is bounded for all $i = 1, 2, 3, 4$.

Because of the normalizations on σ_i in A1, the real numbers s_i are the inherent (low density) juvenile survival probabilities and s_4 is the inherent (low density) adult fecundity. The Leslie projection matrix takes the form

$$L(\hat{x}) = \begin{pmatrix} 0 & 0 & 0 & s_4\sigma_4(x_4, x_1) \\ s_1\sigma_1(x_1, x_2) & 0 & 0 & 0 \\ 0 & s_2\sigma_2(x_2, x_3) & 0 & 0 \\ 0 & 0 & s_3\sigma_3(x_3, x_4) & 0 \end{pmatrix}. \quad (3)$$

The eigenvalues of the matrix $L(0)$, which is the Jacobian of the map evaluated at the origin, are

$$\lambda_k = R_0^{1/4} u_k \ \text{ where } \ R_0 \circeq s_1 s_2 s_3 s_4,$$

where we denote the 4th roots of unity by

$$u_k = \exp\left(\frac{\pi(k-1)}{2} i\right), \quad k = 1, 2, 3, 4.$$

The difference equations that define the dynamics of $\hat{x} = \text{col}(x_1 \ \ x_2 \ \ x_3 \ \ x_4)$ are

$$x_1(t+1) = s_4 \sigma_4(x_4(t), x_1(t)) x_4(t) \tag{4a}$$

$$x_2(t+1) = s_1 \sigma_1(x_1(t), x_2(t)) x_1(t) \tag{4b}$$

$$x_3(t+1) = s_2 \sigma_2(x_2(t), x_3(t)) x_2(t) \tag{4c}$$

$$x_4(t+1) = s_3 \sigma_3(x_3(t), x_4(t)) x_3(t). \tag{4d}$$

The prototypical nonlinearities that satisfy assumptions A1 and A2 are the discrete Leslie–Gower (or Lotka–Volterra) type rational functions

$$\sigma_4(x_4, x_1) = \frac{1}{1 + \beta_{44} x_4 + \beta_{41} x_1}, \quad \sigma_i(x_i, x_{i+1}) = \frac{1}{1 + \beta_{ii} x_i + \beta_{i,i+1} x_{i+1}}$$

with non-negative competition coefficients $\beta_{ij} \geq 0$.

The following theorem is a corollary of Theorems 2.1 and 3.1 in [3].

THEOREM 1. *For hierarchical semelparous Leslie model* (4) *of order one satisfying* A1 *and* A2, *the following fundamental bifurcation events occur at* $R_0 = 1$.

(a) *For* $R_0 < 1$ *the extinction equilibrium* $\hat{x} = \hat{0}$ *is globally asymptotically stable on* R_+^4. *For* $R_0 > 1$ *the equilibrium* $\hat{x} = \hat{0}$ *is unstable and the matrix model is dissipative and uniformly persistent* (*permanent*) *with respect to* $\hat{x} = \hat{0}$.

(b) *There exists a continuum of positive equilibria and a continuum of single-class* 4-*cycles that bifurcate* (*to the right*) *from* $\hat{x} = \hat{0}$ *at* $R_0 = 1$.

3. Dynamics on the boundary of the positive cone

The boundary ∂R_+^4 of the positive cone is held invariant by semelparous Leslie models. In this section, we will account for the global dynamics of (4) on ∂R_+^4. This includes proving the existence and global stability properties of boundary 4-cycles of types other than the single-class 4-cycles guaranteed by Theorem 1. The main result is Theorem 2 below.

To account for the global dynamics on the boundary ∂R_+^4, we need to consider the subsets H_1, H_{2a}, H_{2s}, H_3 of the punctured boundary $\partial R_+^4 \backslash \{\hat{0}\}$ defined as follows: H_1 is the set of those $\hat{x} \in \partial R_+^4$ with one positive and three zero entries (in other words, the coordinate axes); H_{2a} and H_{2s} consist of those $\hat{x} \in \partial R_+^4$ with two zero and two positive entries that are, respectively, adjacent and separated; and H_3 consists of those $\hat{x} \in \partial R_+^4$

with one zero and three positive entries. Note that

$$\partial R_+^4 \backslash \{\hat{0}\} = H_1 \cup H_{2a} \cup H_{2s} \cup H_3.$$

A point $\hat{x} \in \partial R_+^4 \backslash \{\hat{0}\}$ necessarily contains a pair of adjacent (mod(4)) zero and positive components. Because, as observed in Section 1, zero and positive entries advance one position (modulo(4)) with each iteration of the map, it follows that within $m = 4$ steps the orbit associated with $\hat{x}$ will have components $x_1 = 0$ and $x_4 > 0$. Therefore, to study the dynamics on $\partial R_+^4 \backslash \{\hat{0}\}$ it is sufficient to consider initial conditions of the form

$$\hat{x} = \begin{pmatrix} 0 \\ y_2 \\ y_3 \\ y_4 \end{pmatrix}, \quad y_4 > 0$$

and to study the orbit generated by the composite map obtained from the four applications of the map defined by (4), which returns this initial point to an image point of the same type. Careful consideration of equation (4) shows that this composite is defined by the three equations

$$y_2(t+1) = R_0 g_2(y_2(t), y_3(t), y_4(t)) y_2(t) \tag{5a}$$

$$y_3(t+1) = R_0 g_3(y_3(t), y_4(t)) y_3(t) \tag{5b}$$

$$y_4(t+1) = R_0 g_4(y_4(t)) y_4(t) \tag{5c}$$

for y_2, y_3, y_4, where the factors g_i equal 1 when all $y_i = 0$. Moreover, the smoothness, monotone and boundedness assumptions on the σ_i in A1 and A2 imply that the g_i have the following properties.

A3: $g_i \in C^2(\Omega_i, (0,1])$, $g_i(0, \ldots, 0) = 1$, where Ω_i is an open set that contains $\bar{R}_+^{5-i}$.

A4: On Ω_i we have

(a) $\partial_j g_i \leq 0$ for $2 \leq i \leq j \leq 4$
(b) $\partial_i[g_i(y_i, \ldots, y_4)y_i] \geq 0$ and $g_i(y_i, \ldots, y_4)y_i$ is bounded for $i = 2, 3, 4$.

Note that this system (5) of difference equations is triangular and that we are interested in initial conditions with $y_4 > 0$. A fixed point of (5) corresponds to a boundary 4-cycle of (4), and if we can account for the fixed points of (5) with $y_4 > 0$ then we can account for the boundary 4-cycles of (4). We do this by starting with the uncoupled scalar (monotone) map (5c) and then by successively treating equations (5b) and (5a) as asymptotically autonomous maps. Relevant theorems about scalar, asymptotically autonomous maps appear in Appendix A.

By Theorem 7 in Appendix A, when $R_0 > 1$ equation (5c) has a positive, hyperbolic, asymptotically stable fixed point $y_4^* > 0$ that globally attracts all orbits with initial conditions $y_4 > 0$. Clearly $\mathrm{col}(y_2 \quad y_3 \quad y_4) = \mathrm{col}(0 \quad 0 \quad y_4^*)$ is a fixed point of (5). Other fixed points with $y_4 > 0$ of the equation (5) are also possible when $R_0 > 1$. Specifically, it is possible to have fixed points with $y_4 > 0$ that lie in H_{2a}, H_{2s}, or H_3, as shown in Table 1.

Criteria for the existence and stability of the fixed points of the composite map (5) in Table 1 appear in the following lemma. The globally attracting assertions all mean globally attracting with respect to initial points in the indicated sets (with $y_4 > 0$).

Table 1. The four possible types of fixed points, with positive component y_4, of the composite equation (5). All y_i^* are positive.

Fixed point of (5)	Type 1	Type 2a	Type 2s	Type 3
$\begin{pmatrix} y_2 \\ y_3 \\ y_4 \end{pmatrix} =$	$\begin{pmatrix} 0 \\ 0 \\ y_4^* \end{pmatrix}$	$\begin{pmatrix} 0 \\ y_3^* \\ y_4^* \end{pmatrix}$	$\begin{pmatrix} y_2^* \\ 0 \\ y_4^* \end{pmatrix}$	$\begin{pmatrix} y_2^* \\ y_3^* \\ y_4^* \end{pmatrix}$

LEMMA 1. *Assume A3, A4 and* $R_0 > 1$. *The following hold for the composite equation* (5).

(1) *There exists a fixed point of Type* 1 *in* H_1 *that is globally attracting in* H_1.
(2) *Suppose* $R_0 g_3(0, y_4^*) < 1$.
  (a) *If* $R_0 g_2(0, 0, y_4^*) < 1$, *then the fixed point of Type* 1 *is globally attracting on* $\partial R_+^4 \backslash \{\hat{0}\}$.
  (b) *If* $R_0 g_2(0, 0, y_4^*) > 1$, *then there exists a fixed point of Type* 2*s in* H_{2s}. *The fixed points of Type* 1 *and Type* 2*s are globally attracting on* $H_1 \cup H_{2a}$ *and* $H_{2s} \cup H_3$, *respectively.*
(3) *Suppose* $R_0 g_3(0, y_4^*) > 1$. *Then there exists a fixed point of Type* 2*a in* H_{2a}.
  (a) *If* $R_0 g_2(0, 0, y_4^*) < 1$, *then the fixed points of Type* 1 *and Type* 2*a are globally attracting on* $H_1 \cup H_{2s}$ *and* $H_{2a} \cup H_3$, *respectively.*
  (b) *Suppose* $R_0 g_2(0, 0, y_4^*) > 1$.
    (i) *If* $R_0 g_2(0, y_3^*, y_4^*) < 1$, *then the fixed points of Type* 1 *and Type* 2*s are globally attracting on* $H_1 \cup H_{2a}$ *and* $H_{2s} \cup H_3$, *respectively.*
    (ii) *If* $R_0 g_2(0, y_3^*, y_4^*) > 1$, *then there is a fixed point of Type* 3 *in* H_3. *The fixed points of Type* 1, *Type* 2*a, Type* 2*s and Type* 3 *are globally attracting on* H_1, H_{2a}, H_{2s} *and* H_3, *respectively.*

The proof of this Lemma appears in Appendix B.

The different types of fixed points of the composite equation (5) appearing in Table 1 and Lemma 1 give, respectively, the following types of 4-cycles (based on the location of their zero and positive components) of the Leslie model (4):

Single-class 4-cycle

$$\hat{x}_1 = \begin{pmatrix} 0 \\ 0 \\ 0 \\ + \end{pmatrix}, \quad \hat{x}_2 = \begin{pmatrix} + \\ 0 \\ 0 \\ 0 \end{pmatrix}, \quad \hat{x}_3 = \begin{pmatrix} 0 \\ + \\ 0 \\ 0 \end{pmatrix}, \quad \hat{x}_4 = \begin{pmatrix} 0 \\ 0 \\ + \\ 0 \end{pmatrix} \tag{6}$$

2-class 4-cycle of Type 2a

$$\hat{x}_1 = \begin{pmatrix} 0 \\ 0 \\ + \\ + \end{pmatrix}, \quad \hat{x}_2 = \begin{pmatrix} + \\ 0 \\ 0 \\ + \end{pmatrix}, \quad \hat{x}_3 = \begin{pmatrix} + \\ + \\ 0 \\ 0 \end{pmatrix}, \quad \hat{x}_4 = \begin{pmatrix} 0 \\ + \\ + \\ 0 \end{pmatrix}$$

2-class 4-cycle of Type 2s

$$\hat{x}_1 = \begin{pmatrix} 0 \\ + \\ 0 \\ + \end{pmatrix}, \quad \hat{x}_2 = \begin{pmatrix} + \\ 0 \\ + \\ 0 \end{pmatrix}, \quad \hat{x}_3 = \begin{pmatrix} 0 \\ + \\ 0 \\ + \end{pmatrix}, \quad \hat{x}_4 = \begin{pmatrix} + \\ 0 \\ + \\ 0 \end{pmatrix}$$

3-class 4-cycle

$$\hat{x}_1 = \begin{pmatrix} 0 \\ + \\ + \\ + \end{pmatrix}, \quad \hat{x}_2 = \begin{pmatrix} + \\ 0 \\ + \\ + \end{pmatrix}, \quad \hat{x}_3 = \begin{pmatrix} + \\ + \\ 0 \\ + \end{pmatrix}, \quad \hat{x}_4 = \begin{pmatrix} + \\ + \\ + \\ 0 \end{pmatrix}$$

The criteria given in Lemma 1 for the existence and attractivity of these various 4-cycles are not transparently related to the original model parameters s_i and σ_i in the semelparous Leslie model (4). We can make these relationships clear, at least near the bifurcation point $R_0 = 1$, by calculating the lower order terms in the ε expansions ($\varepsilon = R_0 - 1$) of each cycle and using them to calculate the lower order terms in expansions for the criteria quantities $R_0 g_3(0, y_4^*)$, $R_0 g_2(0, 0, y_4^*)$, etc. appearing in Lemma 1.

Consider first the single-class 4-cycle (6). For the first point $\hat{x}_1 = \mathrm{col}\begin{pmatrix} 0 & 0 & 0 & y_4^* \end{pmatrix}$ in that 4-cycle, we have from (5c) that $y_4^* = g_4^{-1}\left(R_0^{-1}\right)$ and thus $y_4^*(\varepsilon) = -\varepsilon / \partial_4^0 g_4 + O(\varepsilon^2)$. In order to express the leading coefficient in terms of the original model parameters σ_i, both in this and latter expansions, we need to calculate the partial derivatives $\partial_j^0 g_i$ of the factors g_i in the composite equation (5) with respect to their arguments y_j and evaluate the results at $y_i = 0$. This application of the chain rule, while tedious, is straightforward. The results appear in Table 2. In this table

$$p_j \triangleq \begin{cases} 1 & \text{for} \quad j = 1 \\ \prod_{q=1}^{j-1} s_q & \text{for} \quad j = 2, 3, 4 \end{cases}$$

$$c_w \triangleq \sum_{i=1}^{4} p_i \partial_i \sigma_i^0, \quad c_b \triangleq \sum_{i=1}^{4} p_{i+1} \partial_{i+1}^0 \sigma_i, \quad c \triangleq \frac{c_b}{c_w}.$$

where $\partial_5 \triangleq \partial_1$ and $p_5 \triangleq p_1$. Note that under assumptions A1 and A2 we have $c_w, c_b < 0$ and $0 < p_j \leq 1$. Quantities c_w and c_b measure the intensity of within-in class and between-class competition, respectively. p_j is the inherent probability that a newborn will live to age j.

Table 2. The partial derivatives $\partial_i g_i$ of g_i with respect to y_j evaluated at all $y_i = 0$.

$\partial_2^0 g_2 = p_2^{-1} c_w$	$\partial_3^0 g_2 = p_3^{-1} c_b$	$\partial_4^0 g_2 = 0$
$\partial_3^0 g_3 = p_3^{-1} c_w$	$\partial_4^0 g_3 = p_4^{-1} c_b$	
$\partial_4^0 g_4 = p_4^{-1} c_w$		

From Table 2 we have

$$y_4^*(\varepsilon) = -\frac{s_1 s_2 s_3}{c_w}\varepsilon + O(\varepsilon^2). \tag{7}$$

We can calculate expansions for the other components of the single-class 4-cycle (6) by repeatedly applying the map (4). For example, using $s_4 = p_4^{-1}R_0$ we have

$$p_4^{-1}(1+\varepsilon)\sigma_4(y_4^*(\varepsilon),0)y_4^*(\varepsilon) = -\frac{1}{c_w}\varepsilon + O(\varepsilon^2)$$

for the first component of the second point in the 4-cycle. Similar calculations for the remaining positive components in the points of the single-class 4-cycle (6) yield, for $\varepsilon = R_0 - 1 \gtrapprox 0$, the expansions (recall $c_w < 0$):

Single-class 4-cycle

$$\begin{aligned}
\hat{x}_1(\varepsilon) &= -\frac{1}{c_w}\begin{pmatrix}0\\0\\0\\p_1\end{pmatrix}\varepsilon + O(\varepsilon^2), \quad \hat{x}_2(\varepsilon) = -\frac{1}{c_w}\begin{pmatrix}p_2\\0\\0\\0\end{pmatrix}\varepsilon + O(\varepsilon^2),\\
\hat{x}_3(\varepsilon) &= -\frac{1}{c_w}\begin{pmatrix}0\\p_3\\0\\0\end{pmatrix}\varepsilon + O(\varepsilon^2), \quad \hat{x}_4(\varepsilon) = -\frac{1}{c_w}\begin{pmatrix}0\\0\\p_4\\0\end{pmatrix}\varepsilon + O(\varepsilon^2).
\end{aligned} \tag{8}$$

Next, consider the first point in the Type 2*a* 4-cycle whose two positive entries are

$$y_3^* = y_3^*(\varepsilon), \quad y_4^* = y_4^*(\varepsilon)$$

where the expansion of $y_4^*(\varepsilon)$ is (7). We can calculate the expansion of $y_3^*(\varepsilon)$ from the equation $1 = R_0 g_3\left(y_3^*(\varepsilon), y_4^*(\varepsilon)\right)$, which results from (5b) after a cancellation of the factor $y_3^*(\varepsilon)$, by implicit differentiation with respect to ε followed by an evaluation at $\varepsilon = 0$. The result is

$$y_3^*(\varepsilon) = \left(-p_3\frac{1-c}{c_w}\right)\varepsilon + O(\varepsilon^2).$$

Expansions for the subsequent points in the 4-cycle can be calculated by repeatedly applying the map (4) to these expansions.

2-class 4-cycle of Type 2a

$$\hat{x}_1 = -\frac{1}{c_w}\begin{pmatrix}0\\0\\p_3(1-c)\\p_4\end{pmatrix}\varepsilon + O(\varepsilon^2), \quad \hat{x}_2 = -\frac{1}{c_w}\begin{pmatrix}1\\0\\0\\p_4(1-c)\end{pmatrix}\varepsilon + O(\varepsilon^2), \tag{9}$$

$$\hat{x}_3 = -\frac{1}{c_w}\begin{pmatrix} 1-c \\ p_2 \\ 0 \\ 0 \end{pmatrix}\varepsilon + O(\varepsilon^2), \quad \hat{x}_4 = -\frac{1}{c_w}\begin{pmatrix} 0 \\ p_2(1-c) \\ p_3 \\ 0 \end{pmatrix}\varepsilon + O(\varepsilon^2).$$

Note that for this cycle to lie on ∂R^4_+ it is required that $c < 1$.

Similar calculations yield the following expansions for the 3-class 4-cycle and the 4-cycles of Type 2s:

2-class 4-cycle of Type 2s

$$\hat{x}_1 = -\frac{1}{c_w}\begin{pmatrix} 0 \\ p_2 \\ 0 \\ p_4 \end{pmatrix}\varepsilon + O(\varepsilon^2), \quad \hat{x}_2 = -\frac{1}{c_w}\begin{pmatrix} 1 \\ 0 \\ p_3 \\ 0 \end{pmatrix}\varepsilon + O(\varepsilon^2), \tag{10}$$

$$\hat{x}_3 = -\frac{1}{c_w}\begin{pmatrix} 0 \\ p_2 \\ 0 \\ p_4 \end{pmatrix}\varepsilon + O(\varepsilon^2), \quad \hat{x}_4 = -\frac{1}{c_w}\begin{pmatrix} 1 \\ 0 \\ p_3 \\ 0 \end{pmatrix}\varepsilon + O(\varepsilon^2).$$

3-class 4-cycle

$$\hat{x}_1 = -\frac{1}{c_w}\begin{pmatrix} 0 \\ p_2(c^2-c+1) \\ p_3(1-c) \\ p_4 \end{pmatrix}\varepsilon + O(\varepsilon^2), \quad \hat{x}_2 = -\frac{1}{c_w}\begin{pmatrix} 1 \\ 0 \\ p_3(c^2-c+1) \\ p_4(1-c) \end{pmatrix}\varepsilon + O(\varepsilon^2), \tag{11}$$

$$\hat{x}_3 = -\frac{1}{c_w}\begin{pmatrix} 1-c \\ p_2 \\ 0 \\ p_4(c^2-c+1) \end{pmatrix}\varepsilon + O(\varepsilon^2), \quad \hat{x}_4 = -\frac{1}{c_w}\begin{pmatrix} (c^2-c+1) \\ p_2(1-c) \\ p_3 \\ 0 \end{pmatrix}\varepsilon + O(\varepsilon^2).$$

With these expansions (of the components $y_i^*(\varepsilon)$) in hand, and the derivatives in Table 2, we are in a position to calculate the lowest order terms in the quantities in Lemma 1 which determine the existence and global stability of the four types of boundary

4-cycles:

$$R_0 g_3\left(0, y_4^*\right) = (1+\varepsilon) g_3\left(0, y_4^*(\varepsilon)\right) = 1 + \left[1 + \partial_4^0 g_3 y_4^{*\prime}(0)\right]\varepsilon + O(\varepsilon^2)$$
$$= 1 + [1 - c]\varepsilon + O(\varepsilon^2)$$

$$R_0 g_2\left(0, 0, y_4^*\right) = (1+\varepsilon) g_2\left(0, 0, y_4^*(\varepsilon)\right) = 1 + \left[1 + \partial_4^0 g_2 y_4^{*\prime}(0)\right]\varepsilon + O(\varepsilon^2)$$
$$= 1 + \varepsilon + O(\varepsilon^2).$$

$$\begin{aligned} R_0 g_2\left(0, y_3^*, y_4^*\right) &= (1+\varepsilon) g_2\left(0, y_3^*(\varepsilon), y_4^*(\varepsilon)\right) \\ &= 1 + \left[1 + \partial_3^0 g_2 y_3^{*\prime}(0) + \partial_4^0 g_2 y_4^{*\prime}(0)\right]\varepsilon + O(\varepsilon^2) \\ &= 1 + [1 + c(c-1)]\varepsilon + O(\varepsilon^2). \end{aligned}$$

All three quantities equal 1 to lowest order. Whether or not these quantities are, for $\varepsilon \gtrapprox 0$, greater or less than 1 depends on the sign of the first-order coefficients in their expansions. From Lemma 1, we have the following theorem that describes the boundary dynamics of the model (4). (Note that for $\varepsilon \gtrapprox 0$ we have $R_0 g_2\left(0, 0, y_4^*\right) > 1$ and consequently (2a) and (3a) in Lemma 1 cannot occur.)

THEOREM 2. *Assume A1, A2, and $c \neq 1$. For $R_0 \gtrapprox 1$ all boundary orbits of the hierarchical semelparous Leslie model* (4) (*other than the origin*) *tend to one of the four boundary 4-cycles* (8)–(11). *Specifically, we have the following two alternatives:*

If $c > 1$ then boundary initial conditions $\hat{x} \in H_1 \cup H_{2a}$ or $H_{2s} \cup H_3$ yield orbits that tend, respectively, to the synchronous 4-cycle (8) *or* (10).
If $c < 1$ then boundary initial conditions $\hat{x} \in H_1$ or H_{2a} or H_{2s} or H_3 yield orbits that tend, respectively, to the synchronous 4-cycle (8) *or* (9) *or* (10) *or* (11).

4. A dynamic dichotomy

Our goal in this section is to establish a dynamic dichotomy, for $R_0 \gtrapprox 1$, between the positive equilibria and the 4-cycles (10) of type 2s (which we show below are actually 2-cycles).

Our first goal is to determine criteria for the stability and instability of the positive equilibria near the bifurcation point $R_0 = 1$ that guaranteed by Theorem 1(a). For this purpose, the lowest order terms in the Lyapunov–Schmidt parameterization $\hat{x} = \hat{x}(\varepsilon)$ for $\varepsilon = R_0 - 1$ of the bifurcating branch of positive equilibria will be useful. This calculation is standard (e.g. see [2] or, specifically for semelparous Leslie models, see [3]). The result is

$$\hat{x}(\varepsilon) = \begin{pmatrix} x_1(\varepsilon) \\ x_2(\varepsilon) \\ x_3(\varepsilon) \\ x_4(\varepsilon) \end{pmatrix} = -\frac{1}{c_w + c_b}\begin{pmatrix} p_1 \\ p_2 \\ p_3 \\ p_4 \end{pmatrix}\varepsilon + O(\varepsilon^2). \tag{12}$$

We can investigate the stability of the positive equilibrium (12), using the linearization principle, by investigating the four eigenvalues of the Jacobian of the map (4) evaluated at the equilibrium. Because the Jacobian is a function of ε, its eigenvalues are also functions of ε. When $\varepsilon = 0$, the eigenvalues equal the fourth roots of unity and hence all have magnitude equal to 1. As a result, the magnitude of all four eigenvalues must be investigated (to see if they are less than or greater than 1), unlike the generic bifurcation case in which the projection matrix is primitive and only the dominant eigenvalue needs to be considered. For $\varepsilon \gtrapprox 0$ we need only to calculate the first-order terms in the expansions for the eigenvalues. The details of this calculation appear in Appendix C, with the following result.

THEOREM 3. *Assume A1 and A2 hold. For* $R_0 = s_1s_2s_3s_4 \gtrapprox 1$ *the bifurcating positive equilibria of the hierarchical semelparous Leslie model* (4) *guaranteed by Theorem* 1(*b*) *are locally asymptotically stable if* $c < 1$ *and are unstable if* $c > 1$.

When the projection matrix of a matrix map is primitive, then a right (or supercritical) bifurcation at $R_0 = 1$ always results in stable positive equilibria [2,4]. This is, in fact, a result of the general exchange of stability principle for transcritical bifurcations in nonlinear functional analysis [9]. From Theorem 3, we see that this principle does not hold for the imprimitive semelparous Leslie model (4), for which a right bifurcation does not necessarily result in stable equilibria (also see [3,5] for m dimensional models). Instead, equilibrium stability is determined by the ratio c. The biological interpretation of the stability/instability criteria in Theorem 3 is straightforward: between-class competition of low intensity (relative to within-class competition) results in the bifurcation of stable positive equilibria, whereas between-class competition of high intensity results in the bifurcation of unstable positive equilibria. A natural question is, in the latter case when both the extinction and the positive equilibria are unstable, what are the asymptotic dynamics?

We turn our attention to the 4-cycle (10) of type 2s. Notice that the lowest order ε terms in this cycle suggest that it is actually a 2-cycle. This is in fact true. The two step, two dimensional map

$$\begin{pmatrix} 0 \\ y_2 \\ 0 \\ y_4 \end{pmatrix} \to \begin{pmatrix} s_4\sigma_4(y_4)y_4 \\ 0 \\ s_2\sigma_2(y_2,0)y_2 \\ 0 \end{pmatrix}$$

$$\to \begin{pmatrix} 0 \\ s_1\sigma_1\left(s_4g_1^{(1)}(y_4)y_4, 0\right)s_4g_1^{(1)}(y_4)y_4 \\ 0 \\ s_3\sigma_3\left(s_2g_3^{(1)}(y_2,0)y_2\right)s_2g_3^{(1)}(y_2,0)y_2 \end{pmatrix} \triangleq \begin{pmatrix} 0 \\ s_1s_4g_2^{(2)}(y_4)y_4 \\ 0 \\ s_2s_3g_4^{(2)}(y_2,0)y_2 \end{pmatrix}$$

leads to the fixed point problem

$$y_2 = s_1s_4g_2^{(2)}(y_4)y_4$$
$$y_4 = s_2s_3g_4^{(2)}(y_2,0)y_2$$

which has a branch of positive solutions, as a function of R_0, that bifurcates from the origin at $R_0 = 1$ [2,4]. These fixed points correspond to a branch of 2-cycles of (4). These fixed points are, of course, also fixed points of the fourfold composite and therefore *the 4-cycles of type 2s are actually 2-cycles*. This observation makes a tractable linearization stability analysis of these 2-cycles by a calculation of the eigenvalues of the product $J(\hat{x}_2)J(\hat{x}_1)$ of the Jacobian $J(\hat{x})$ evaluated at the two points $\hat{x}_2$ and $\hat{x}_1$ of the cycles for $\varepsilon \gtrapprox 0$:

$$J(\hat{x}_2(\varepsilon))J(\hat{x}_1(\varepsilon)) = J_0 + J_1\varepsilon + O(\varepsilon^2)$$

where

$$J_0 = \begin{pmatrix} 0 & 0 & p_3^{-1} & 0 \\ 0 & 0 & 0 & s_1p_4^{-1} \\ p_3 & 0 & 0 & 0 \\ 0 & s_1^{-1}p_4 & 0 & 0 \end{pmatrix}$$

$$J_1 = \frac{1}{c_w}\begin{pmatrix} 0 & 0 & \begin{matrix} c_wp_3^{-1} - s_3\partial_4^0\sigma_3 \\ -p_3^{-1}\partial_1^0\sigma_4 \end{matrix} & 0 \\ \begin{matrix} -s_1\partial_1^0\sigma_4 \\ -s_1^2\partial_2^0\sigma_1 \end{matrix} & 0 & 0 & \begin{matrix} c_ws_1p_4^{-1} - 2s_1\partial_4^0\sigma_4 \\ -2s_1p_4^{-1}\partial_1^0\sigma_1 \end{matrix} \\ \begin{matrix} -s_1p_3\partial_2^0\sigma_1 \\ -p_3^2\partial_3^0\sigma_2 \end{matrix} & 0 & 0 & 0 \\ 0 & \begin{matrix} -2s_2p_4\partial_3^0\sigma_3 \\ -2p_4\partial_2^0\sigma_2 \end{matrix} & \begin{matrix} -s_3p_4\partial_4^0\sigma_3 \\ -p_4\partial_3^0\sigma_2 \end{matrix} & 0 \end{pmatrix}$$

The eigenvalues of this product are

$$\lambda_1 = 1 - \frac{1}{2}\varepsilon + O(\varepsilon^2), \quad \lambda_2 = -1 + \frac{1}{2}\varepsilon + O(\varepsilon^2)$$
$$\lambda_3 = 1 + \frac{1}{2}(1-c)\varepsilon + O(\varepsilon^2), \quad \lambda_4 = -1 - \frac{1}{2}(1-c)\varepsilon + O(\varepsilon^2).$$

Since for $\varepsilon \gtrapprox 0$ we see that $0 < \lambda_1 < 1$ and $-1 < \lambda_2 < 0$, it follows from the expansions for λ_3 and λ_4 that stability and instability by the linearization principle depends on the sign of $1 - c$. Specifically, the 2-cycle (10) is unstable if $c > 1$ and locally asymptotically stable if $c < 1$.

THEOREM 4. *Assume A1, A2 and* $c \neq 1$. *For* $R_0 \gtrapprox 1$ *the hierarchical semelparous Leslie model* (4) *of order* 1 *exhibits the following dynamic dichotomy:*

$c < 1$ *implies the positive equilibrium is locally asymptotically stable and the* 2*-cycle* (10) *of type* 2*s is unstable;*

$c > 1$ *implies the positive equilibrium is unstable and the* 4*-cycle* (10) *of type* 2*s is locally asymptotically stable.*

5. Attractor & repeller criteria for the boundary of the non-negative cone

Theorem 4 is analogous to the dynamic dichotomy that occurs at bifurcation in the $m = 2$ dimensional case between the positive equilibrium and a synchronous 2-cycle [6]. In the $m = 3$ case, and indeed in the $m = 2$ case as well, a stronger dynamic dichotomy occurs, namely, one between the positive equilibrium and the boundary of the positive cone. In this section, we consider a dichotomy between the positive equilibrium and the boundary ∂R^4_+ for the $m = 4$ hierarchical case (4). We will use the average Lyapunov function Theorem 9 in Appendix D with function $p(\hat{x}) = \prod_{i=1}^4 x_i$. The method requires a consideration of the ratio $p(L(\hat{x})\hat{x})/p(\hat{x}) = R_0 \prod_{i=1}^4 \sigma_i(\hat{x})$ along boundary orbits.

If $\hat{x}(t)$ is a boundary 4-cycle, then $\ln\left(R_0 \prod_{i=1}^4 \sigma_i(\hat{x}(t))\right)$ is a 4-periodic sequence. Let L_1, L_{2s}, L_{2a} and L_3 denote the averages of this sequence for the four possible boundary 4-cycles in Theorem 2. Near the bifurcation point, these limits are functions of $\varepsilon = R_0 - 1 \gtrapprox 0$:

$$L_1(\varepsilon), \quad L_{2s}(\varepsilon), \quad L_{2a}(\varepsilon), \quad L_3(\varepsilon).$$

If $c \neq 1$, Theorem 2 implies all boundary orbits asymptotically approach one of these 4-cycles. Since the asymptotic average of an asymptotically periodic sequence equals the average of the periodic limit, we have

$$\lim_{t\to+\infty} \frac{1}{t} \sum_{j=0}^{t-1} \ln\left(R_0 \prod_{i=1}^4 \sigma_i(\hat{x}(t))\right) = L_1(\varepsilon), L_{2s}(\varepsilon), L_{2a}(\varepsilon) \text{ or } L_3(\varepsilon)$$

for all boundary orbits. Specifically, we have the following lemma.

Lemma 2. *Assume A1, A2 and $c \neq 1$. For $\varepsilon = R_0 - 1 \gtrapprox 0$ we have for any boundary orbit $\hat{x}(t)$ that*

$$c > 1 \Rightarrow \lim_{t\to+\infty} \frac{1}{t} \sum_{j=0}^{t-1} \ln\left(R_0 \prod_{i=1}^4 \sigma_i(\hat{x}(t))\right) = L_1(\varepsilon) \text{ or } L_{2s}(\varepsilon)$$

$$c < 1 \Rightarrow \lim_{t\to+\infty} \frac{1}{t} \sum_{j=0}^{t-1} \ln\left(R_0 \prod_{i=1}^4 \sigma_i(\hat{x}(t))\right) = L_1(\varepsilon), L_{2s}(\varepsilon), L_{2a}(\varepsilon) \text{ or } L_3(\varepsilon).$$

It is straightforward to calculate expansions of the averages $\sum_{j=1}^4 \ln\left(R_0 \prod_{i=1}^4 \sigma_i(\hat{x}_j(\varepsilon))\right)/4$ with $\hat{x}_j(\varepsilon)$ given by (8)–(11). The results are contained in the next lemma.

Lemma 3. *Assume A1, A2 and $c \neq 1$. For $\varepsilon = R_0 - 1 \gtrapprox 0$ we have*

$$L_1(\varepsilon) = \frac{1}{4}(3-c)\varepsilon + O(\varepsilon^2), \quad L_{2s}(\varepsilon) = \frac{1}{2}(1-c)\varepsilon + O(\varepsilon^2)$$

$$L_{2a}(\varepsilon) = \frac{1}{4}(c^2 - c + 2)\varepsilon + O(\varepsilon^2), \quad L_3(\varepsilon) = \frac{1}{4}(1-c)(c^2+1)\varepsilon + O(\varepsilon^2).$$

We apply the average Lyapunov function Theorem 9 as follows. By assumption A2(b), after at most one step, all orbits lie in a (compact) box $B = [0, b_1] \times [0, b_2] \times [0, b_3] \times$

$[0, b_4] \subset \bar{R}^4_+$ for $t \in Z^+$, where b_i is an upper bound for $\sigma_i(x_i, x_{i+1})x_i$ on Ω. For $R_0 > 1$ the origin is a repeller and therefore there is an open neighbourhood N of the origin for which the punctured box $B \backslash N$ is forward invariant and which all orbits enter in finite time. Thus, all asymptotic dynamics and attractors occur in the compact set $B \backslash N \subset \bar{R}^4_+$. Because ∂R^4_+ is invariant, it follows that $\partial(B \backslash N) = B \backslash N \cap \partial R^4_+$ is also invariant. We apply Theorem 9 with $p(\hat{x}) = \prod_{i=1}^4 x_i$ and $\psi(\hat{x}) = p(L(\hat{x})\hat{x})/p(\hat{x})$ and with $X = B \backslash N$ and $S = \partial(B \backslash N)$.

THEOREM 5. *Assume A1, A2 and $c \neq 1$. For $R_0 \gtrapprox 1$*

$$c > 3 \Rightarrow \partial(B \backslash N) \subset \partial R^4_+ \ \textit{is an attractor}, \quad c < 1 \Rightarrow \partial(B \backslash N) \subset \partial R^4_+ \ \textit{is a repeller}.$$

Proof.

(a) If $c > 3$ then by Lemmas 2 and 3 all boundary orbits in X satisfy, for $\varepsilon \gtrapprox 0$,

$$\lim_{t \to +\infty} \frac{1}{t} \sum_{j=0}^{t-1} \ln\left(R_0 \prod_{i=1}^{4} \sigma_i(\hat{x}(t)) \right) < 0.$$

This in turn implies

$$\inf_{t \geq 1} \prod_{j=0}^{t-1} \psi(\hat{x}(j)) = \inf_{t \geq 1} \prod_{j=0}^{t-1} \left(R_0 \prod_{i=1}^{4} \sigma_i(\hat{x}(j)) \right) < 1,$$

which is the criterion in Theorem 9 that implies X is an attractor.

(b) If $c < 1$ then by Lemmas 2 and 3 all boundary orbits in X satisfy, for $\varepsilon \gtrapprox 0$,

$$\lim_{t \to +\infty} \frac{1}{t} \sum_{j=0}^{t-1} \ln\left(R_0 \prod_{i=1}^{4} \sigma_i(\hat{x}(t)) \right) > 0.$$

This in turn implies

$$\inf_{t \geq 1} \prod_{j=0}^{t-1} \psi(\hat{x}(j)) = \inf_{t \geq 1} \prod_{j=0}^{t-1} \left(R_0 \prod_{i=1}^{4} \sigma_i(\hat{x}(j)) \right) > 1,$$

which is the criterion in Theorem 9 that implies X is a repeller. □

Note that when $c > 3$ the positive equilibrium is unstable (Theorem 3) and when $c < 1$ the positive equilibrium is stable. Consequently, Theorem 5 provides a dynamic dichotomy between the positive equilibrium and the boundary of the cone when c does not lie between 1 and 3.

6. Concluding remarks

We have investigated the dynamics of the $m = 4$ dimensional hierarchical Leslie model (4) near the bifurcation point $R_0 = 1$ under the boundedness and monotone assumptions A1 and A2. From the general bifurcation theory for Leslie matrix models [3], there exists a bifurcating continuum of positive equilibria and of single class 4-cycles as R_0 increases through 1. We have shown that there is a dynamic dichotomy between the positive equilibria and a bifurcating continuum of 2-class 2-cycle (Theorem 4) (not the single-class cycles, perhaps unexpectedly). This is reminiscent of the dichotomy for $m = 2$ Leslie models, except it does not involve the bifurcating single-class cycles. Moreover, as part of our characterization of the global dynamics on the boundary of the positive cone, we have shown that there can be other types of bifurcating 4-cycles on the boundary (Theorem 2). The fact that all boundary orbits asymptotically approach a boundary cycle allows us to prove a limited dichotomy between the positive equilibria and the boundary of the positive cone, limited in that c must not lie between 1 and 3. This result is reminiscent of the dichotomy in the $m = 3$ dimensional case [5]. Our results also show that the ratio c of between-class and within-class effects on survivorship is the crucial parameter in determining the nature of these dichotomies (as in both the $m = 2$ and 3 cases). Even though our results are not for the general $m = 4$ dimensional case, they illustrate the complexity of the bifurcation phenomenon that can occur at $R_0 = 1$ for semelparous Leslie matrix models as the dimension m increases. This increased complexity as n increases arises because of the increased dimension of the boundary dynamics and because of the possibility of more types of boundary cycles.

Many open questions remain. Is the boundary of the cone an attractor or a repeller when $1 < c < 3$? When the boundary is an attractor, what are the omega limit sets of orbits? When $m = 3$ orbits can approach complicated cycle-chains lying on the boundary, consisting of heteroclinic boundary orbits that connect phases of single-class and/or 2-class 3-cycles [5]. Are there such bifurcating cycle-chains (invariant loops) in the $m = 4$ case considered here? What becomes of the dynamic dichotomies for $m = 4$ models that are not hierarchical of order 1? Can the monotone assumptions in A2 be relaxed? (The answer to this question is probably yes, since the investigation is carried out only near the bifurcation point and hence the monotone assumptions are only needed locally near the origin.) And, of course, in higher dimensions $m > 4$ the question remains as to whether or not there is a dynamic dichotomy at bifurcation $R_0 = 1$ and, if so, what is its nature? It would also be of interest to investigate what becomes of the dynamic dichotomy when R_0 is increased far beyond 1? Given the propensity of nonlinear maps to exhibit sequences of bifurcations, routes-to-chaos and so on, what role would the dynamic dichotomy at $R_0 = 1$ play? For example, it is known that multiple positive attractors (i.e. with several classes present) can exist in semelparous Leslie models when R_0 is not close to 1 [8].

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Appendix

A Asymptotically Autonomous 1D Maps

Let R_+^m denote the positive cone in R^m and $Z^+ \triangleq \{0, 1, 2, 3, \ldots\}$. Let $\bar{R}_+^m$ denote the closure of R_+^m.

THEOREM 6. *Suppose* $h \in C^1\left(\bar{R}_+^1 \times Z^+, \bar{R}_+^1\right)$ *and that*

$$\text{(a)} \quad h = h(x,t) \text{ is nonincresing in } x \in \bar{R}_+^1 \text{ for each } t \in Z^+,$$

$$\text{(b)} \quad \limsup_{t\to+\infty} h(0,t) \triangleq h_0 < 1. \tag{13}$$

Then any solution of the non-autonomous difference equation

$$x(t+1) = h(x(t), t)x(t), \quad t \in Z^+$$

with $x(0) \geq 0$ *satisfies* $\lim_{t\to+\infty} x(t) = 0$.

Proof. $x(0) \geq 0$ implies $x(t) \geq 0$ for $t \in Z^+$. By (a) we have $0 \leq x(t+1) \leq h(0,t)x(t)$ for $t \in Z^+$. Since $(1 + h_0)/2 > h_0$ we can find a $T > 0$ so that $h(0,t) \leq (1 + h_0)/2 \triangleq \omega$ for $t \geq T$. It follows that $0 \leq x(t+1) \leq \omega 2x(t)$ for $t \geq T$ and by induction

$$0 \leq x(t) \leq \omega^t x(T) \text{ for } t \geq T.$$

Since $\omega < 1$, it follows that $\lim_{t\to+\infty} x(t) = 0$. □

In what follows Ω_1 denotes an open interval containing $\bar{R}_+^1$ in its interior.

DEFINITION 1. *A function h has Property M on* Ω_1 *if* $h \in C^1\left(\Omega_1, \bar{R}_+^1\right)$ *and*

(a) $\partial_x h(x) < 0$,

(b) $\partial_x(h(x)x) < 0$,
(c) $h(x)x$ *is bounded.*

The limit $h_\infty \triangleq \lim_{x\to+\infty} xh(x)$ exists and is positive. It follows that

$$\lim_{x\to+\infty} h(x) = 0, 0 \le h(x)x \le h_\infty \text{ for } x \in \bar{R}^1_+ \tag{14}$$

Theorem 7. *Suppose* $h(x)$ *has Property M. Consider the difference equation*

$$x(t+1) = h(x(t))x(t), \quad t \in Z^+. \tag{15}$$

(a) *If* $h(0) > 1$ *then there exists a positive, hyperbolic fixed point* $x^* > 0$ *that is globally asymptotically stable on* R^1_+.
(b) *If* $h(0) < 1$ *then* $x^* = 0$ *is globally asymptotically stable on* R^1_+.

Proof. Note by (14) that all solutions of (15) with $x(0) \ge 0$ are non-negative and bounded by h_∞.

(a) For $h(0) > 1$ it follows from the intermediate value theorem that there exists an $x^* > 0$ such that $h(x^*) = 1$. This fixed point of (15) is unique since $h(x)$ is strictly decreasing. Since $0 < \partial_x(h(x)x)|_{x^*} = 1 + x^*\partial_x(h(x))|_{x^*} < 1$, it follows by the linearization principle that x^* is locally asymptotically stable. The inequality $h(0) > 1$ also implies the fixed point is a repeller, since $\partial_x(h(x)x)|_0 = h(0)$. Since (15) defines a monotone maps it follows that all orbits on R^1_+ tend to x^*.
(b) Since $0 < \partial_x(h(x)x)|_0 = h(0) < 1$, it follows by the linearization principle that x^* is locally asymptotically stable. For $x(0) \ge 0$ it follows by Definition 1(a) that $0 \le x(t+1) = h(x(t))x(t) \le h(0)x(t)$ and, by induction, that $0 \le x(t+1) \le [h(0)]^t x(0)$. Hence $\lim_{t\to+\infty} x(t) = 0$. □

Theorem 8. *Suppose* $h \in C^1\left(\Omega_1 \times Z^+, \bar{R}^1_+\right)$ *satisfies the following properties:*

(a) $h(x,t)$ *has Property M as a function of x for each* $t \in Z^+$,
(b) $\lim_{t\to+\infty} h(x,t) \triangleq h_\infty(x)$ *uniformly on compact subsets of* $\bar{R}^1_+$,
(c) $h_\infty(x)$ *satisfies Property M and* $h_\infty(0) > 1$.
Then any bounded solution of the non-autonomous difference equation

$$x(t+1) = h(x(t),t)x(t) \tag{16}$$

with $x(0) > 0$ *satisfies* $\lim_{t\to+\infty} x(t) \triangleq x^* > 0$, *where* x^* *is the globally asymptotically stable fixed point of* $x(t+1) = h_\infty(x(t))x(t)$.

Proof. If $x(0) > 0$ then the solution of (16) satisfies $x(t) > 0$ for $t \in Z^+$. Let ω denote the forward limit set of bounded solution $x(t)$, which is non-empty and lies in $\bar{R}^1_+$.

Step 1: We show that ω contains a positive real. For purposes of contradiction, assume that there exists no positive limit point. Then $\lim_{t\to+\infty} x(t) = 0$ and for any $\varepsilon > 0$ there exists a $T_1(\varepsilon)$ such that $t \ge T_1(\varepsilon)$ implies $0 < x(t) < \varepsilon$. Since $h_\infty(0) > 1$ we can choose a real number r such that $h_\infty(0) > r > 1$. By continuity there exists an $\varepsilon > 0$ such that

$h_\infty(x) > r$ for $0 \leq x \leq \varepsilon$. By (b) there exists a $T_2(\varepsilon)$ such that

$$|h(x,t) - h_\infty(x)| \leq \frac{r+1}{2} \quad \text{for} \quad t \geq T_2(\varepsilon) \quad \text{and} \quad \text{for} \quad 0 \leq x \leq \varepsilon.$$

For $t \geq T(\varepsilon) \triangleq \max\{T_1(\varepsilon), T_2(\varepsilon)\}$ we have $0 < x(t) < \varepsilon$ and

$$x(t+1) = h(x(t),t)x(t) \geq \left[h_\infty(x(t)) - \frac{r+1}{2}\right]x(t) \geq \left[r - \frac{r+1}{2}\right]x(t) = \frac{r-1}{2}x(t)$$

This implies

$$\Rightarrow x(t) \geq \left(\frac{r-1}{2}\right)^{t-T(\varepsilon)} x(T(\varepsilon)) \quad \text{for} \quad t \geq T(\varepsilon)$$

and since $(r-1)/2 > 1$ we find that $x(t)$ grows exponentially as $t \to +\infty$, which contradicts $0 < x(t) < \varepsilon$ for $t \geq T(\varepsilon)$.

Step 3. We prove that for any interval $a \leq x \leq b$ with $a > 0$ and containing $x*$ in its interior there exists a $T(a,b)$ such that $a \leq h(x,t)x \leq b$ for $t \geq T(a,b)$ and all $x \in [a,b]$.

Since $h_\infty(x)$ is decreasing, $h_\infty(0) > 1$, and $h_\infty(x^*) = 1$, it follows that $h_\infty(a) > 1$ and $h_\infty(b) < 1$ and $a < h_\infty(a)a < x^* < h_\infty(b)b < b$. Consequently, $h_\infty(x)x$ maps $[a,b]$ into itself, specifically

$$h_\infty(x)x : [a,b] \to [h_\infty(a)a, h_\infty(b)b] \subset [a,b].$$

Define

$$\delta \triangleq \min\left\{\frac{h_\infty(a)a - a}{2}, \frac{b - h_\infty(b)b}{2}\right\} > 0.$$

Since $\lim_{t\to+\infty} h(x,t)x \triangleq h_\infty(x)x$ uniformly on bounded x intervals, there exists a $T = T(a,b)$ such that

$$|h(x,t)x - h_\infty(x)x| \leq \delta \quad \text{for} \quad t \geq T(a,b) \quad \text{and} \quad \text{for} \quad x \in [a,b].$$

Then for $t \geq T(a,b)$ and all $x \in [a,b]$ we have

$$\begin{aligned}
h_\infty(x)x - \frac{h_\infty(a)a - a}{2} &\leq h(x,t)x \leq \frac{b - h_\infty(b)b}{2} + h_\infty(x)x \\
h_\infty(a)a - \frac{h_\infty(a)a - a}{2} &\leq h(x,t)x \leq \frac{b - h_\infty(b)b}{2} + h_\infty(b)b \\
\frac{h_\infty(a)a + a}{2} &\leq h(x,t)x \leq \frac{b + h_\infty(b)b}{2} \\
\frac{a+a}{2} &\leq h(x,t)x \leq \frac{b+b}{2}.
\end{aligned}$$

Step 4: Next we prove $x^* \in \Omega$. Let l_1 be a positive limit point (Step 2). Then there exists a subsequence $t_i \to +\infty$ such that $x(t_i) \to l_1$. Since

$$x(t_i + 1) = [h(x(t_i), t_i) - h_\infty(x(t_i))]x(t_i) + h_\infty(x(t_i))x(t_i)$$

and since the first term tends to 0 (by (b), because $x(t)$ is bounded) it follows that $x(t_i + 1) \to h_\infty(l_1)l_1$. Thus $l_2 \triangleq h_\infty(l_1)l_1 > 0$ is a limit point. Similarly from

$$x(t_i + 2) = h(x(t_i + 1), t_i + 1)x(t_i + 1)$$

an analogous argument shows

$$x(t_i + 2) \to h_\infty(l_2)l_2 \triangleq l_3 > 0$$

and hence $l_3 \triangleq h_\infty(l_2)l_2 > 0$ is a limit point. Inductively we obtain $x(t_i + j) \to h_\infty(l_j)l_j$ and hence a sequence of positive limit points l_j that satisfies $l_{j+1} = h_\infty(l_j)l_j > 0$, i.e. l_j satisfies (16). Property M and (c) implies $l_j \to x^*$. By the usual diagonalization argument used in analysis we have that $x(t_i + i) \to x^*$ and hence $x^* \in \Omega$.

Step 5: Finally, we prove $\lim_{t\to+\infty} x(t) = x^*$ for any positive orbit. Let $\varepsilon > 0$ be arbitrary. By Step 3 (using $a = x^* - \varepsilon$ and $b = x^* + \varepsilon$), there exists a $T_1 = T(\varepsilon)$ such that $h(x, t)x \in [x^* - \varepsilon, x^* + \varepsilon]$ for $t \geq T(\varepsilon)$ and all $x \in [x^* - \varepsilon, x^* + \varepsilon]$. Since $x^* \in \Omega$ (Step 4) there exists a time $T(\varepsilon) \geq T_1(\varepsilon)$ such that $x(T(\varepsilon)) \in [x^* - \varepsilon, x^* + \varepsilon]$. Since $x(t)$ satisfies (16) it follows that $x(t) \in [x^* - \varepsilon, x^* + \varepsilon]$ for $t \geq T(\varepsilon)$. This is the definition of $\lim_{t\to+\infty} x(t) = x^*$. □

B *Proof of Lemma 1*

We begin by pointing out that all non-negative orbits of the composite equation (5) are (forward) bounded, which follows from assumption A2(b). Uniform convergence, which is required in the applications of Theorem 8 below, follows from the continuity, and hence boundedness, of partial derivatives on compact sets.

(1) This is a consequence of Theorem 7(a), since $h(0) = R_0$.

(2) $R_0 g_3(0, y_4^*) < 1$ and Theorem 8 imply $y_3 \to 0$ as $t \to +\infty$ for positive initial conditions.

  (a) $R_0 g_2(0, 0, y_4^*) < 1$ and Theorem 8 imply $y_2 \to 0$ as $t \to +\infty$ for positive initial conditions.

  (b) If $R_0 g_2(0, 0, y_4^*) > 1$, then Theorem 8 implies that there exists a positive fixed point of the limiting equation

$$y_2(t + 1) = R_0 g_2\left(y_2(t), 0, y_4^*\right)y_2(t)$$

  that attracts all positive solutions y_2 of the asymptotically autonomous equation (5a).

(3) $R_0 g_3(0, y_4^*) > 1$ and Theorem 8 imply that there exists a positive fixed point of the limit equation

$$y_3(t + 1) = R_0 g_3\left(y_3(t), y_4^*\right)y_3(t)$$

that attracts all positive solutions of the asymptotically autonomous equation (5b). Thus, for positive initial conditions, we have $y_3 \to y_3^*$ and $y_4 \to y_4^*$ as $t \to +\infty$.

  (a) If in addition $R_0 g_2(0, 0, y_4^*) < 1$, then Theorem 8 implies $y_2 \to 0$ as $t \to +\infty$.

  (b) $R_0 g_2(0, 0, y_4^*) > 1$ and Theorem 8 imply that there exists a fixed point of the limiting equation

$$y_2(t+1) = R_0 g_2\left(y_2(t), 0, y_4^*\right) y_2(t)$$

that attracts all positive solutions y_2 of the asymptotically autonomous equation (5a). Thus, with initial condition $y_3 = 0$ and with positive initial conditions for y_2 and y_4 we have $y_2 \rightarrow y_2^*$ and $y_4 \rightarrow y_4^*$ as $t \rightarrow +\infty$.

(i) $R_0 g_2\left(0, y_3^*, y_4^*\right) < 1$ and Theorem 8 imply that $y_3 \rightarrow 0$ as $t \rightarrow +\infty$ for positive initial conditions.

(ii) $R_0 g_2\left(0, y_3^*, y_4^*\right) > 1$ and Theorem 8 imply that the limiting equation

$$y_2(t+1) = R_0 g_2\left(y_2(t), y_3^*, y_4^*\right) y_2(t)$$

as a positive fixed point $y_2^* > 0$ that attracts all positive solutions y_2 of the asymptotically autonomous equation (5a). Thus, for positive initial conditions we have $y_2 \rightarrow y_2^*$, $y_3 \rightarrow y_3^*$ and $y_4 \rightarrow y_4^*$ as $t \rightarrow +\infty$.

C Proof of Theorem 3

The goal is to use the Lyapunov–Schmidt expansion (12) of the positive equilibrium to obtain expansions of the Jacobian and its eigenvalues to lowest order in $\varepsilon = R_0 - 1$. These eigenvalues equal the fourth roots of unity at $\varepsilon = 0$ and the lowest order terms in their ε expansions will allow use to determine when the magnitude of each is less than or greater than 1 when $\varepsilon \gtrapprox 0$.

For notational convenience, we define $d \triangleq -(c_w + c_b)$. Then, from (12), the components of the positive equilibria are

$$x_i(\varepsilon) = \frac{p_i}{d}\varepsilon + O(\varepsilon^2), \quad R_0(\varepsilon) = 1 + \varepsilon. \tag{17}$$

The Jacobian of the $m = 4$ dimensional Leslie model (1)–(3) is $J = L + M$ where

$$L = \begin{pmatrix} 0 & 0 & 0 & R_0 p_4^{-1}\sigma_4(x_4, x_1) \\ s_1\sigma_1(x_1, x_2) & 0 & 0 & 0 \\ 0 & s_2\sigma_2(x_2, x_3) & 0 & 0 \\ 0 & 0 & s_3\sigma_3(x_3, x_4) & 0 \end{pmatrix} \tag{18}$$

and

$$M = \begin{pmatrix} R_0 p_4^{-1}\partial_1\sigma_4(x_4, x_1)x_4 & 0 & 0 & R_0 p_4^{-1}\partial_4\sigma_4(x_4, x_1)x_4 \\ s_1\partial_1\sigma_1(x_1, x_2)x_1 & s_1\partial_2\sigma_1(x_1, x_2)x_1 & 0 & 0 \\ 0 & s_2\partial_2\sigma_2(x_2, x_3)x_2 & s_2\partial_3\sigma_2(x_2, x_3)x_2 & 0 \\ 0 & 0 & s_3\partial_3\sigma_3(x_3, x_4)x_3 & s_3\partial_4\sigma_3(x_3, x_4)x_3 \end{pmatrix} \tag{19}$$

When evaluated at the positive equilibrium (17) $M = M(\varepsilon)$, $L = L(\varepsilon)$ and hence $J = J(\varepsilon)$ are functions of ε. The eigenvalues and the right and left eigenvectors of $J(\varepsilon)$ are also functions of ε, which we denote by $\lambda(\varepsilon)$, $\hat{v}(\varepsilon)$ and $\hat{w}(\varepsilon)$, respectively. Thus, $\hat{v}(\varepsilon)$ is the right eigenvector associated with $\lambda(\varepsilon)$ and $\hat{w}(\varepsilon)$ is the left eigenvector associated with the complex conjugate eigenvalue $\bar{\lambda}(\varepsilon)$. Our goal is to calculate the first-order term in the ε. expansions of each of the four eigenvalues of $M(\varepsilon)$. This will require calculating the first-order terms in the expansions

$$J(\varepsilon) = J(0) + J'(0)\varepsilon + O(\varepsilon^2), \quad L(\varepsilon) = L(0) + L'(0)\varepsilon + O(\varepsilon^2)$$
$$M(\varepsilon) = M(0) + M'(0)\varepsilon + O(\varepsilon^2)$$
$$\hat{v}(\varepsilon) = \hat{v}(0) + \hat{v}'(0)\varepsilon + O(\varepsilon^2), \quad \hat{w}(\varepsilon) = \hat{w}(0) + \hat{w}'(0)\varepsilon + O(\varepsilon^2).$$

By definition

$$J(\varepsilon)\hat{v}(\varepsilon) = \lambda(\varepsilon)\hat{v}(\varepsilon) \tag{20}$$

$$\hat{w}(\varepsilon)J(\varepsilon) = \bar{\lambda}(\varepsilon)\hat{w}(\varepsilon). \tag{21}$$

A formula for $\lambda'(0)$ can be obtained as follows. From (20), to zeroth and first orders in ε, we have

$$J(0)\hat{v}(0) = \lambda(0)\hat{v}(0) \tag{22}$$

$$J(0)\hat{v}'(0) + J'(0)\hat{v}(0) = \lambda(0)\hat{v}'(0) + \lambda'(0)\hat{v}'(0) \tag{23}$$

Similarly, from (21) we have

$$\hat{w}(0)J(0) = \hat{w}(0)\bar{\lambda}(0) \tag{24}$$

$$\hat{w}'(0)J(0) + \hat{w}(0)J'(0) = \hat{w}'(0)\bar{\lambda}(0) + \bar{\lambda}'(0)\hat{w}(0) \tag{25}$$

Let $\langle \hat{x}, \hat{y} \rangle$ denote the dot product of the conjugate of $\hat{x}$ with $\hat{y}$: $\langle \hat{x}, \hat{y} \rangle \triangleq \sum_{i=1}^{4} \bar{x}_i y_i$. From (24) we have

$$\lambda(0)\langle \hat{w}(0), \hat{v}'(0) \rangle = \langle \hat{w}(0)\bar{\lambda}(0), \hat{v}'(0) \rangle = \langle \hat{w}(0)J(0), \hat{v}'(0) \rangle = \langle \hat{w}(0), J(0)\hat{v}'(0) \rangle$$

and from (23)

$$\begin{aligned}\lambda(0)\langle \hat{w}(0), \hat{v}'(0) \rangle &= \langle \hat{w}(0), \lambda(0)\hat{v}'(0) \rangle + \langle \hat{w}(0), \lambda'(0)\hat{v}(0) \rangle - \langle \hat{w}(0), J'(0)\hat{v}(0) \rangle \\ &= \lambda(0)\langle \hat{w}(0), \hat{v}'(0) \rangle + \lambda'(0)\langle \hat{w}(0), \hat{v}(0) \rangle - \langle \hat{w}(0), J'(0)\hat{v}(0) \rangle.\end{aligned}$$

Thus, $0 = \lambda'(0)\langle \hat{w}(0), \hat{v}(0) \rangle - \langle \hat{w}(0), J'(0)\hat{v}(0) \rangle$ and

$$\lambda'(0) = \frac{\langle \hat{w}(0), J'(0)\hat{v}(0) \rangle}{\langle \hat{w}(0), \hat{v}(0) \rangle}. \tag{26}$$

We apply this formula to each of the four eigenvalues $\lambda_k(\varepsilon)$, $k = 1, 2, 3, 4$, of the Jacobian $J(\varepsilon)$, whose lowest order terms $\lambda_k(0)$ are the fourth roots of unity, namely, $1, i, -1$ and $-i$. These eigenvalues have the form

$$\begin{aligned}&\lambda_1(\varepsilon) = 1 + \lambda_1'(0)\varepsilon + O(\varepsilon^2), \quad \lambda_2(\varepsilon) = i + \lambda_2'(0)\varepsilon + O(\varepsilon^2) \\ &\lambda_3(\varepsilon) = -1 + \lambda_3'(0)\varepsilon + O(\varepsilon^2), \quad \lambda_4(\varepsilon) = -i + \lambda_4'(0)\varepsilon + O(\varepsilon^2).\end{aligned} \tag{27}$$

To apply the formula (26) for each coefficient $\lambda_k'(0)$, we need two lowest order terms $\hat{v}_k(0), \hat{w}_k(0)$ of the $J(0)$ associated with $\lambda_k(0)$. Since $M(0) = 0_{4\times 4}$, we have

$$J(0) = L(0) = \begin{pmatrix} 0 & 0 & 0 & p_4^{-1} \\ s_1 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 \\ 0 & 0 & s_3 & 0 \end{pmatrix}. \tag{28}$$

By (24) and (27),

$$\begin{aligned} \hat{w}_1(0)J(0) &= \hat{w}_1(0), \quad \hat{w}_2(0)J(0) = -i\hat{w}_2(0) \\ \hat{w}_3(0)J(0) &= -\hat{w}_3(0), \quad \hat{w}_4(0)J(0) = i\hat{w}_4(0). \end{aligned} \tag{29}$$

Without the loss of generality, we take the first component of $\hat{w}_k(0)$ to be 1 and write $\hat{w}_k(0) \triangleq (1 \quad w_{k2} \quad w_{k3} \quad w_{k4})$. By (28), we have

$$\hat{w}_k(0)J(0) = \begin{pmatrix} s_1 w_{k2} & s_2 w_{k3} & s_3 w_{k4} & p_4^{-1} \end{pmatrix} \tag{30}$$

Solving (29) and (30) for the $w_{k1}, w_{k2}, \ldots, w_{km}$, we obtain the four left eigenvectors

$$\begin{aligned} \hat{w}_1(0) &= \begin{pmatrix} 1 & \frac{1}{s_1} & \frac{1}{s_2 s_1} & \frac{1}{s_3 s_2 s_1} \end{pmatrix} = \begin{pmatrix} p_1^{-1} & p_2^{-1} & p_3^{-1} & p_4^{-1} \end{pmatrix} \\ \hat{w}_2(0) &= \begin{pmatrix} 1 & -\frac{1}{s_1} i & -\frac{1}{s_2 s_1} & \frac{1}{s_3 s_2 s_1} i \end{pmatrix} = \begin{pmatrix} p_1^{-1} & -p_2^{-1} i & -p_3^{-1} & p_4^{-1} i \end{pmatrix} \\ \hat{w}_3(0) &= \begin{pmatrix} 1 & -\frac{1}{s_1} & \frac{1}{s_2 s_1} & -\frac{1}{s_3 s_2 s_1} \end{pmatrix} = \begin{pmatrix} p_1^{-1} & -p_2^{-1} & p_3^{-1} & -p_4^{-1} \end{pmatrix} \\ \hat{w}_4(0) &= \begin{pmatrix} 1 & \frac{1}{s_1} i & -\frac{1}{s_2 s_1} & -\frac{1}{s_3 s_2 s_1} i \end{pmatrix} = \begin{pmatrix} p_1^{-1} & p_2^{-1} i & -p_3^{-1} & -p_4^{-1} i \end{pmatrix}. \end{aligned} \tag{31}$$

From similar calculations, we obtain the four right eigenvectors

$$\hat{v}_1(0) = \begin{pmatrix} p_1 \\ p_2 \\ p_3 \\ p_4 \end{pmatrix}, \quad \hat{v}_2(0) = \begin{pmatrix} p_1 \\ -p_2 i \\ -p_3 \\ p_4 i \end{pmatrix}, \quad \hat{v}_3(0) = \begin{pmatrix} p_1 \\ -p_2 \\ p_3 \\ -p_4 \end{pmatrix}, \quad \hat{v}_4(0) = \begin{pmatrix} p_1 \\ p_2 i \\ -p_3 \\ -p_4 i \end{pmatrix}. \tag{32}$$

Thus, $\langle \hat{w}_k(0), \hat{v}_k(0) \rangle = 4$ for $k = 1, 2, 3, 4$ and, by (26) and $J'(0) = L'(0) + M'(0)$,

$$\lambda_k'(0) = \frac{1}{4}\left\langle \hat{w}_k(0), L'(0)\hat{v}_k(0) \right\rangle + \frac{1}{4}\left\langle \hat{w}_k(0), M'(0)\hat{v}_k(0) \right\rangle. \tag{33}$$

It remains for us to calculate $L'(0)$ and $M'(0)$. From (18) and (17), we have

$$L'(0) = \begin{pmatrix} 0 & 0 & 0 & \frac{1}{p_4} + \frac{p_4\partial_4^0\sigma_4 + p_1\partial_1^0\sigma_4}{p_4 d} \\ s_1\frac{p_1\partial_1^0\sigma_1 + p_2\partial_2^0\sigma_1}{d} & 0 & 0 & 0 \\ 0 & s_2\frac{p_2\partial_2^0\sigma_2 + p_3\partial_3^0\sigma_2}{d} & 0 & 0 \\ 0 & 0 & s_3\frac{p_3\partial_3^0\sigma_3 + p_4\partial_4^0\sigma_3}{d} & 0 \end{pmatrix}. \quad (34)$$

From (34), (32) and (31), it is straightforward to compute

$$\begin{aligned} \left\langle \hat{w}_1(0), L'(0)\hat{v}_1(0)\right\rangle &= 1 + \frac{1}{d}\left(p_4\partial_4^0\sigma_4 + p_1\partial_1^0\sigma_4 + p_1\partial_1^0\sigma_1 + p_2\partial_2^0\sigma_1\right. \\ &= \left. + p_2\partial_2^0\sigma_2 + p_3\partial_3^0\sigma_2 + p_3\partial_3^0\sigma_3 + p_4\partial_4^0\sigma_3\right) \\ &= 1 + \frac{1}{d}(-d) = 0. \end{aligned}$$

Similarly, calculations establish that $\langle \hat{w}_k(0), L'(0)\hat{v}_k(0)\rangle = 0$ for $k = 1, 2, 3, 4$ and hence, by (33), that

$$\lambda_k'(0) = \frac{1}{4}\left\langle \hat{w}_k(0), M'(0)\hat{v}_k(0)\right\rangle. \quad (35)$$

Now, from (19) and (17) we have

$$M'(0) = \begin{pmatrix} d^{-1}p_1\partial_1^0\sigma_4^0 & d^{-1}p_1\partial_2^0\sigma_4 & d^{-1}p_1\partial_3^0\sigma_4 & d^{-1}p_1\partial_4^0\sigma_4 \\ d^{-1}p_2\partial_1^0\sigma_1 & d^{-1}p_2\partial_2^0\sigma_1 & d^{-1}p_2\partial_3^0\sigma_1 & d^{-1}p_2\partial_4^0\sigma_1 \\ d^{-1}p_3\partial_1^0\sigma_2 & d^{-1}p_3\partial_2^0\sigma_2 & d^{-1}p_3\partial_3^0\sigma_2 & d^{-1}p_3\partial_4^0\sigma_2 \\ d^{-1}p_4\partial_1^0\sigma_3 & d^{-1}p_4\partial_2^0\sigma_3 & d^{-1}p_4\partial_3^0\sigma_3 & d^{-1}p_4\partial_4^0\sigma_3 \end{pmatrix} \quad (36)$$

and from (34), (32) and (31) it is straightforward to compute the dot products

$$\begin{aligned} \left\langle \hat{w}_1(0), M'(0)\hat{v}_1(0)\right\rangle &= d^{-1}\left(\sum_{i=1}^{4} p_{i+1}\partial_{i+1}^0\sigma_i + \sum_{i=1}^{4} p_i\partial_i^0\sigma_i\right) \\ \langle \hat{w}_2(0), M'(0)\hat{v}_2(0)\rangle &= d^{-1}\left(\sum_{i=1}^{4} p_{i+1}\partial_{i+1}^0\sigma_i + i\sum_{i=1}^{4} p_i\partial_i^0\sigma_i\right) \\ \langle \hat{w}_3(0), M'(0)\hat{v}_3(0)\rangle &= d^{-1}\left(\sum_{i=1}^{4} p_{i+1}\partial_{i+1}^0\sigma_i - \sum_{i=1}^{4} p_i\partial_i^0\sigma_i\right) \\ \langle \hat{w}_4(0), M'(0)\hat{v}_4(0)\rangle &= d^{-1}\left(\sum_{i=1}^{4} p_{i+1}\partial_{i+1}^0\sigma_i - i\sum_{i=1}^{4} p_i\partial_i^0\sigma_i\right). \end{aligned}$$

which, from the definitions of d, c_w and c_b, reduce to

$$\begin{aligned}\langle \hat{w}_1(0), M'(0)\hat{v}_1(0)\rangle &= -1\\ \langle \hat{w}_2(0), M'(0)\hat{v}_2(0)\rangle &= d^{-1}(c_b + ic_w)\\ \langle \hat{w}_3(0), M'(0)\hat{v}_3(0)\rangle &= d^{-1}(c_b - c_w)\\ \langle \hat{w}_4(0), M'(0)\hat{v}_4(0)\rangle &= d^{-1}(c_b - ic_w).\end{aligned}$$

These formulae, together with (35), yield formulae for $\lambda_k'(0)$ and hence approximations (27) to $\lambda_k(\varepsilon)$ to order 1.

Stability is determined by the magnitudes of the eigenvalues $\lambda_k(\varepsilon)$. It is straightforward to show that

$$\begin{aligned}Re(\bar{u}_k\lambda_k'(0)) < 0 &\Rightarrow |\lambda_k(\varepsilon)| < 1 \text{ for } \varepsilon \gtrapprox 0\\ Re(\bar{u}_k\lambda_k'(0)) > 0 &\Rightarrow |\lambda_k(\varepsilon)| > 1 \text{ for } \varepsilon \gtrapprox 0.\end{aligned}$$

Thus, the local stability of the positive equilibrium is determined by the signs of

$$\begin{aligned}Re\big(\lambda_1'(0)\big) &= \frac{1}{4}Re\big(\langle \hat{w}_1(0), M'(0)\hat{v}_1(0)\rangle\big) = -\frac{1}{4}\\ Re\big(i\lambda_2'(0)\big) &= \frac{1}{4}Re\big(-i\langle \hat{w}_2(0), M'(0)\hat{v}_2(0)\rangle\big) = \frac{1}{4}d^{-1}c_w\\ Re\big(-\lambda_3'(0)\big) &= \frac{1}{4}Re\big(-\langle \hat{w}_3(0), M'(0)\hat{v}_3(0)\rangle\big) = -\frac{1}{4}d^{-1}(c_b - c_w)\\ Re\big(-i\lambda_4'(0)\big) &= \frac{1}{4}Re\big(i\langle \hat{w}_4(0), M'(0)\hat{v}_4(0)\rangle\big) = \frac{1}{4}d^{-1}c_w.\end{aligned}$$

Since $d > 0$, $c_w < 0$ and $c_b < 0$ by assumptions A2(a) we see that the first, second and fourth real parts are negative. Thus, stability is determined by the sign of the third real part, i.e. by the sign of $c_b - c_w$. We conclude that the positive equilibrium is stable if $c_w < c_b$ (equivalently $c < 1$) and unstable if $c_w > c_b$ (equivalently $c > 1$).

D Average Lyapunov functions

See Theorems A.1 and A.2 in [12] (and relevant earlier references) for the following theorem concerning a continuous map $T : X \to X$ on a metric space X.

THEOREM 9. *Suppose $S \subset X$ is a compact subset of a compact set X such that S and X/S are forward invariant under a mapping T. Then S is a repeller if there exists a continuous function $P : X \to \bar{R}_+$ such that*

(a) $p(\hat{x}) = 0 \Longleftrightarrow \hat{x} \in S$
(b) *for all* $\hat{x} \in S$

$$\sup_{t\geq 1}\prod_{i=0}^{t-1}\psi(T^i(\hat{x})) > 1 \tag{37}$$

where $\psi : X \to \bar{R}_+$ is a continuous function satisfying

$$p(T(\hat{x})) \geq \psi(\hat{x})p(\hat{x}). \tag{38}$$

On the other hand, S is a attractor if

$$\inf_{t\geq 1}\prod_{i=0}^{t-1}\psi(T^{i}(\hat{x}))<1 \tag{39}$$

where $\psi : X \longrightarrow \bar{R}_{+}$ *is a continuous function satisfying*

$$p(T(\hat{x}))\leq\psi(\hat{x})p(\hat{x}). \tag{40}$$