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Equilibria, synchronous cycles, and dynamic dichotomies in imprimitive Leslie models

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Abstract

The bifurcation of positive equilibria and synchronous cycles, as well as the determination of their dynamic nature is considered for imprimitive Leslie models.

The system of m nonlinear difference equations

$$x_i(t+1) = s_{i-1}\sigma_{i-1}\left(x_1(t), \cdots, x_m(t)\right) x_{i-1}(t) \tag{1}$$

with $s_0 > 0$ and $0 < s_1, \cdots, s_{m-1} < 1$, and where $\sigma_{i-1} : \mathbb{R}_+^m \longrightarrow (0,1]$ are $C^1(\mathbb{R}_+^m)$ functions such that $\sigma_{i-1}(0, \cdots, 0) = 1$, for $i = 1, 2, \ldots m$, arises from a Leslie age-structured matrix model for the dynamics of semelparous populations (in which only individuals of age m reproduce, after which they die). In matrix form

$$x(t+1) = L(x(t))x(t), \quad x = \mathrm{col}(x_i)$$

where $L(x)$ is a (non-negative) Leslie matrix which is irreducible, but not primitive (its dominant eigenvalue is not *strictly* dominant). From the Linearization Principle, it follows that the (extinction) equilibrium $x = 0$ is LAS (locally asymptotically stable) if $R_0 < 1$ and is unstable if $R_0 > 1$ where

$$R_0 \mathrel{\hat{=}} \Pi_{j=0}^{m-1} s_j,$$

is the inherent net reproductive number (expected number of offspring per individual per life time). The Fundamental Bifurcation Theorem for nonlinear matrix models with *primitive* projection matrices guarantees [2, 4]:

(a) the existence of a bifurcating branch of positive equilibria from $x = 0$ at $R_0 = 1$;

(b) the bifurcating positive equilibria are LAS when the bifurcation is to the right.

Bifurcation to the right means that, near the bifurcation point, the positive equilibria exist for $R_0 \gtrapprox 1$. It occurs, for example, under negative feedback conditions:

$$\partial_i \sigma_j \mathrel{\hat{=}} \frac{\partial \sigma_j}{\partial x_i} \leq 0 \text{ (not all equal to 0).} \tag{2}$$

For the *imprimitive* Leslie model (1) it is known that (a) still holds, but that (b) can fail to hold [3, 5]. Since many biological species, across many taxa, are semelparous, it is of biological as well as mathematical interest to determine what kind of stable attractors are created by the bifurcation at $R_0 = 1$ for the semelparous Leslie model (1).

The interior and the boundary of the positive cone are held (forward) invariant under the map defined by (1). Indeed, k-dimensional coordinate hyperplanes are held invariant (and are visited sequentially by orbits). Orbits lying on k-dimensional coordinate hyperplanes are called k-class synchronous orbits (because exactly k age classes are nonzero at each time t).

For the case $m = 2$ the bifurcation at $R_0 = 1$ is completely understood [1, 3]. A branch of positive equilibria and a branch of single-class synchronous 2-cycles simultaneously bifurcate from $x = 0$. Moreover, there is a dynamic dichotomy between the two branches: one is LAS and the other is not. Indeed, it is known that either the positive equilibria are (locally asymptotically) stable and the boundary of the positive cone is a repeller or the equilibria are unstable and the boundary of the cone is an attractor. This alternative depends on the relative magnitudes of $\partial_i^0 \sigma_i$ versus $\partial_i^0 \sigma_j$, $i \neq j$ (the derivatives (2) evaluated at $x = 0$), i.e., the relative intensity of within-class versus between-class competition.

For the case $m = 3$ the bifurcation is also understood [5]. At $R_0 = 1$ a branch of positive equilibria and a branch of invariant loops lying on the boundary of the positive cone bifurcate from $x = 0$. The invariant loop is a cycle chain consisting of a single-class synchronous 3-cycle, and possibly a two-class synchronous 3-cycle, and heteroclinc synchronous orbits that connect their phases. Moreover, a dynamic dichotomy exists between the positive equilibria and the boundary of the positive cone: one is an attractor and the other is a repeller. Once again, which is alternative holds depends on the relative magnitudes of $\partial_i^0 \sigma_i$ versus $\partial_i^0 \sigma_j$, for $i \neq j$.

For the higher dimensional case $m \geq 4$ it is known that a branch of positive equilibria and a branch of single-class, synchronous m-cycles bifurcate from $x = 0$ at $R_0 = 1$, [3]. However, the full nature of the bifurcation at $R_0 = 1$ remains an open question. In particular, it would be of interest to know if a dynamic dichotomy occurs between the equilibria and the synchronous m-cycles or the boundary of the positive cone.

Part of the answer to this question involves, of course, the stability of the bifurcating positive equilibria. This problem has recently been solved by myself, in collaboration with S. M. Henson.

Theorem 0.1. *For $R_0 \gtrapprox 1$ the bifurcating positive equilibria of (1) are*

(i) Locally asymptotically stable if

$$\sum_{i=1}^{m} \partial_i \sigma_i^0 p_i + \sum_{\substack{i,j=1 \\ i-j \neq 0}}^{m} \partial_j \sigma_i^0 p_j \operatorname{Re} u_k^{i-j} < 0,$$

$$\textit{for all } k = \begin{cases} 2, \cdots, \frac{m+2}{2} & \textit{if } m \geq 2 \textit{ is even, and} \\ 2, \cdots, \frac{m+1}{2} & \textit{if } m \geq 3 \textit{ is odd.} \end{cases}$$

(ii) Unstable if

$$\sum_{i=1}^{m} \partial_i \sigma_i^0 p_i + \sum_{\substack{i,j=1 \\ i-j \neq 0}}^{m} \partial_j \sigma_i^0 p_j \operatorname{Re} u_k^{i-j} > 0,$$

$$\textit{for at least one } k = \begin{cases} 2, \cdots, \frac{m+2}{2} & \textit{if } m \geq 2 \textit{ is even, and} \\ 2, \cdots, \frac{m+1}{2} & \textit{if } m \geq 3 \textit{ is odd,} \end{cases}$$

where u_k are the mth roots of unity.

For $m = 2$ and $m = 3$ the stability and instability criteria reduce to those in [3, 5]:

> *The positive equilibria near bifurcation are locally asymptotically stable if $c < 1$, and unstable if $c > 1$, where*
> $$c \doteq \frac{\Sigma_{i \neq j} \partial_i \sigma_i^0 p_i}{\Sigma_i \partial_i \sigma_i^0 p_i}$$
> *is a competition intensity ratio that measures the intensity of between-class competition relative to that occurring with-in class.*

For $m \geq 4$ a determination of when the boundary is attracting or repelling is open question. Key to this problem is an understanding of the dynamics on the boundary of the cone, whose possibilities become more complex as m increases. A recent paper on the $m = 4$ dimensional case gives a thorough analysis of the boundary dynamics and the dynamic dichotomy at bifurcation for a class of equations called hierarchical. Recent numerical simulation studies of other $m = 4$ dimensional systems suggest, however, that in general a dichotomy between the equilibria and the boundary of the positive cone might not necessarily hold and that other, more complicated, invariant sets might also bifurcate at $R_0 = 1$. The analysis of higher dimensional semelparous Leslie models remains a challenging problem. And it is of more than just mathematical interest, since higher dimensional models are used in the study of semelparous populations with long maturation periods, such as the famous periodical insects (e.g. cicadas).

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