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A Bifurcation Theorem for Nonlinear Matrix Models of Population Dynamics

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Abstract. We prove a general theorem for nonlinear matrix models of the type used in structured population dynamics that describes the bifurcation that occurs when the extinction equilibrium destabilizes as a model parameter is varied. The existence of a bifurcating continuum of positive equilibria is established and their local stability is related to the direction of bifurcation. Our theorem generalizes existing theorems found in the literature in two ways. First, it allows for a general appearance of the bifurcation parameter (existing theorems require the parameter to appear linearly). This significantly widens the applicability of the theorem to population models. Second, our theorem describes circumstances in which a backward bifurcation can produce stable positive equilibria (existing theorems allow for stability only when the bifurcation is forward). The signs of two diagnostic quantities determine the stability of the bifurcating equilibrium and the direction of bifurcation. We give examples that illustrate these features.

Keywords: Nonlinear difference equations, matrix equations, population dynamics, equilibrium, bifurcation, stability

AMS Subject Classification: 39A28, 39A30, 37G35

1 Introduction

Many mathematical models of population dynamics use measures of total population size as their state variables and ignore differences among individuals within the population. However, in all populations there is a diversity among individuals with regard to genetic, physiological, behavioral, and life history stage characteristics, and in many population these differences can be highly variable. Since reproduction, fitness adaptations, and evolutionary selection occur at the level of the individual, the most accurate population models take individual differences into account. With regard to the long term fate of a population, the problem is then to relate individual characteristics to the dynamics of the population as a whole. The earliest modelling of so-called structured populations utilized chronological age as the distinguishing characteristic of individuals. Models treating age as a continuous or a discrete variable were both developed [9]. The well-known seminal work of Lewis [28] and Leslie [26],[27] categorized individuals into a finite number of age classes and utilized the demographic vector of age class numbers or densities as the state variable of the model. Leslie advanced the demographic variable in discrete time by multiplication by a *projection matrix* of fertilities and survival probabilities, matrices which have become known as Leslie matrices (see

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Section 6). It was noticed early on that this modeling methodology for the dynamics of structured populations need not be restricted to age classes [25], [32] and it has been widely utilized into innumerable contexts [2].

If all the vital rates incorporated into the projection matrix remain constant in time, then mathematically the map defined by a matrix model is linear and autonomous. However, these vital rates in general do not remain constant and are subject to changes that can be due to many factors. Ignoring external environmental changes (regular or stochastic), vital rates and hence the projection matrix can depend on the densities in the demographic vector as it changes in time, which then makes the map nonlinear.

A basic question in population dynamics is the extinction or survival of a population. In the absence of immigration or seeding into the population, this question concerns the stability of the zero demographic vector (the *extinction equilibrium*). If the extinction equilibrium is (locally asymptotically) stable, then the population is threatened with extinction. Mathematically, this depends on the values of the coefficients (parameters) in the model. A change in a model parameter that destabilizes the extinction equilibrium signals the possibility of population survival through the creation of stable, positive equilibria by means of bifurcation theory.

Thus, a fundamental question concerning population models concerns the nature of the bifurcation that occurs upon the destabilization of the extinction equilibrium as a model parameter is varied. In this paper we extend theorems dealing with this bifurcation that appear in the literature [6], [9], [15], [18], [30] in a manner that allows and facilitates application to a wider range of population models. Specifically, we allow a general appearance in the model equations of the manipulated parameter – the bifurcation parameter, which we denote by μ – in contrast to existing theorems, which require that the parameter appear in a linear fashion. As a result, our theorem allows for studies of the fundamental, extinction equilibrium destabilization bifurcation as a function of a wider variety of model parameters and circumstances.

The mathematical formulation of the model equation we consider is as follows. Let R^m denote m-dimensional Euclidean space and R_+^m the set of nonnegative (column) vectors $x = \mathrm{col}\,(x_i) \in R^m$, i.e. vectors with nonnegative components $x_i \geq 0$. We use the norm

$$|x| = \textstyle\sum_{i=1}^m |x_i| \,.$$

The interior of R_+^m is the set of positive vectors, i.e. vectors all of whose components $x_i > 0$ are positive. We consider the difference equation

$$x\,(t+1) = P\,(\mu, x\,(t))\, x\,(t) \tag{1}$$

for $t = 0, 1, 2, ...$ where the projection matrix $P\,(\mu, x)$ satisfies the following assumptions.

> A1: $P\,(\mu, x) = [p_{ij}\,(\mu, x)]$ is a nonnegative, irreducible $m \times m$ matrix for all $(\mu, x) \in I_\mu \times \Omega^m$ where I_μ is an open interval in R^1 and Ω^m is an open set in R^m containing R_+^m. Assume the real (non-negative) valued entries $p_{ij}\,(\mu, x)$ are twice continuously differentiable on $I_\mu \times \Omega^m$.

Our focus in this paper is on the study the fixed points, i.e. equilibrium solutions, of equation (1) as they depend on the real parameter μ. Equilibria are solutions $x \in R^m$ of the equilibrium equation

$$x = P\,(\mu, x)\, x. \tag{2}$$

Clearly $x = 0$ is an equilibrium (the *extinction equilibrium*) for any value of μ. Our goal is to find values of the parameter $\mu \in I_\mu$ for which there exist *non-extinction equilibria*, i.e. equilibria $x \neq 0$ whose entries are nonnegative. Non-extinction equilibria are solutions $x \in R_+^m \backslash \{0\}$ of the equilibrium equation (2).

The entries of the matrix $P(\mu, 0)$ are called the *inherent or intrinsic* model parameters in that they describe vital parameters governing population growth in the absence of density effects. For this reason, we call $P(\mu, 0)$ the *inherent (or intrinsic) projection matrix.*

2 Some Preliminaries

We begin by gathering together some basic facts about the algebraic equation

$$x = Lx + f \tag{3}$$

where x, $f \in R^m$ and L is an $m \times m$ real matrix. There exists a unique solution $x = (I - L)^{-1} f$ if and only if $I - L$ is non-singular. Suppose, however, that $I - L$ is singular and that its null space has dimension 1. Let w_L and w_R be left and right eigenvectors of L associated with eigenvalue 1. Equation (3) has a solution if and only if $w_L^T f = 0$ in which case the general solution is $x = \varepsilon w_R + z$ where $\varepsilon \in R^1$ is an arbitrary scalar and z is any particular solution.[2] Out of this general solution we can extract a unique solution that satisfies $w_R^T x = 0$ (by choosing $\varepsilon = -w_R^T z / w_R^T w_R$). Let $V^\perp$ and $W^\perp$ denote the spaces orthogonal to V and W, the spans of w_R and w_L respectively, i.e.

$$\begin{aligned} V^\perp &= \left\{ y \in R^m : w_R^T y = 0 \right\} \\ W^\perp &= \left\{ y \in R^m : w_L^T y = 0 \right\}. \end{aligned}$$

Then $R^m = W \oplus W^\perp = V \oplus V^\perp$. For each $f \in W^\perp$ the equation $x = Lx + f$ has a unique solution $x \in V^\perp$. This correspondence defines a linear transformation of $W^\perp$ into $V^\perp$. Let G be the matrix associated with this transformation so that Gf is the unique solution of (3) lying in $V^\perp$. Then the general solution of $x = Lx + f$ has the form $x = \varepsilon w_R + Gf$ where $\varepsilon \in R^1$ is arbitrary.

Consider the nonlinear algebraic equation

$$x = Lx + f(x) \tag{4}$$

where $I - L$ is singular and its null space is one dimensional. Suppose $x \in R^m$ is a solution. Since $R^m = V \oplus V^\perp$ we can write $x = \varepsilon w_R + z$, $\varepsilon \in R^1$, $z \in V^\perp$. It must be the case that $f(x) \in W^\perp$, i.e. $w_L^T f(x) = 0$, and therefore that $z = Gf(x)$. Thus, ε and $z \in V^\perp$ satisfy the pair of equations

$$\begin{aligned} 0 &= w_L^T f\left(\varepsilon w_R + z\right) \\ z &= Gf\left(\varepsilon w_R + z\right). \end{aligned} \tag{5}$$

Conversely, if $\varepsilon \in R^1$ and $z \in V^\perp$ satisfy these two equations then $x = \varepsilon w_R + z$ satisfies the equation (4). In this sense the nonlinear equation (4) for x is equivalent to the pair of equations (5) for ε and z.

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[2] T denotes vector transpose.

3 A General Bifurcation Theorem

By Perron-Frobenius theory, $A1$ implies $P(\mu, x)$ has a geometrically simple, positive, dominant eigenvalue $\lambda = \lambda(\mu, x)$.[3] We also make the following assumption on the projection matrix in equation (1).

> A2: In addition to A1, assume there exists a $\mu_0 \in I_\mu$ such that $\lambda(\mu_0, 0) = 1$ (i.e. the inherent projection matrix has, when $\mu = \mu_0$, a dominant eigenvalue of 1) and let w_R and w_L denote associated positive right and left eigenvectors w_R and w_L in $R_+^m \setminus \{0\}$:
>
> $$w_R = P(\mu_0, 0) w_R, \quad w_L^T = w_L^T P(\mu_0, 0).$$

Defining

$$L(\mu) := P(\mu, 0), \quad h(\mu, x) := P(\mu, x) x - L(\mu) x \tag{6}$$

we can re-write the equilibrium equation (2) as

$$x = L(\mu) x + h(\mu, x) \tag{7}$$

where by A1 h is twice continuously differentiable in μ and x and

$$h(\mu, x) = O\left(|x|^2\right)$$

near $x = 0$ uniformly on bounded μ intervals in I_μ. Clearly $x = 0$ is a solution of (7) for all $\mu \in I_\mu$. Our goal is to prove the existence of positive equilibria $x \in R_+^m \setminus \{0\}$ for μ near μ_0 as given in A2.

Theorem 1 *Assume A1 and A2 hold and that*

$$w_L^T \frac{\partial P(\mu_0, 0)}{\partial \mu} w_R \neq 0.$$

Then in an open neighborhood of $(\mu, x) = (\mu_0, 0)$ *there exists a branch of equilibria of equation (1) that has, for an* $\varepsilon_0 > 0$*, the parametric form*

$$\mu = \mu_0 + \eta(\varepsilon), \quad x = \varepsilon w_R + z(\varepsilon) \tag{8}$$

where $\eta \in C^2\left((-\varepsilon_0, \varepsilon_0), R^1\right)$, $z \in C^2\left((-\varepsilon_0, \varepsilon_0), V^\perp\right)$ *and* $\eta(0) = z(0) = dz(0)/d\varepsilon = 0$.[4]

For $\varepsilon > 0$ the equilibria (8) are positive equilibria. For $\varepsilon = 0$ these equilibria collapse to $x = 0$ and in this sense the branch is said to bifurcate from the extinction equilibrium $x = 0$ at $\mu = \mu_0$.

Proof. Let $\eta = \mu - \mu_0$ and write

$$L(\mu) = L(\mu_0 + \eta) = L(\mu_0) + \frac{\partial L(\mu_0)}{\partial \mu} \eta + H(\eta, \mu_0)$$

where

$$H(\eta, \mu_0) = O\left(|\eta|^2\right)$$

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[3] In population dynamics the dominant eigenvalue of the projection matrix is called the population growth rate and is traditionally denoted by r.

[4] $(-\varepsilon_0, \varepsilon_0)$ denotes the interval $|\varepsilon| < \varepsilon_0$.

near $\eta = 0$. Re-write equation (7) as

$$x = L(\mu_0)\,x + \left[\eta \frac{\partial L(\mu_0)}{\partial \mu} x + H(\eta, \mu_0)\,x + h(\mu_0 + \eta, x)\right].$$

To solve the equilibrium equation (2) for a nonzero pair (μ, x), $x \neq 0$, is to solve this equation, or its equivalent pair of equations (see (5))

$$\begin{array}{ll} \text{(a)} & 0 = w_L^T f(\eta, \varepsilon w_R + z) \\ \text{(b)} & 0 = z - Gf(\eta, \varepsilon w_R + z), \end{array} \tag{9}$$

for $(\eta, \varepsilon w_R + z) \in R^1 \times V \oplus V^\perp$ where

$$f(\eta, x) = \eta \frac{\partial L(\mu_0)}{\partial \mu} x + H(\eta, \mu_0)\,x + h(\mu_0 + \eta, x).$$

The goal is to solve this pair of equations for $\eta \in R^1$ and $z \in V^\perp$ as functions of ε.

Notice that equation (9b) is satisfied by $z = 0$ when $(\varepsilon, \eta) = (0, 0)$. Also notice that the Jacobian of the right side with respect to z, when evaluated at $z = 0$ and $(\varepsilon, \eta) = (0, 0)$, equals the identity and hence is invertible. By the implicit function theorem, equation 9(b) has a (unique and twice differentiable) solution

$$z = z(\varepsilon, \eta), \quad z(0, 0) = 0 \tag{10}$$

for (ε, η) near $(0, 0)$.

Our final step is to substitute $z(\varepsilon, \eta)$ into equation (9a) and solve the resulting equation for η as a function of ε. Before doing this we observe that $z = 0$ solves both equations (9a) and (9b) when $(\varepsilon, \eta) = (0, 0)$ and therefore $z(0, \eta) = 0$ for all η near 0. Consequently we can write

$$z(\varepsilon, \eta) = \varepsilon \zeta(\varepsilon, \eta)$$

where $\zeta(\varepsilon, \eta)$ is continuously differentiable near $(\varepsilon, \eta) = (0, 0)$. Moreover, that $z(\varepsilon, \eta)$ solves equation (9b) for all (ε, η) near $(0, 0)$ implies, after a cancellation of ε, that $\zeta(\varepsilon, \eta)$ satisfies

$$0 = \zeta - \eta G \frac{\partial L(\mu_0)}{\partial \mu} (w_R + \zeta) - GH(\eta, \mu_0)(v + \zeta) - \varepsilon^{-1} G h(\mu_0 + \eta, \varepsilon v + \varepsilon \zeta)$$

for $\varepsilon \neq 0$ and all η near 0. Placing $\eta = 0$ and $\varepsilon = 0$ in this equation results in $\zeta = 0$ and hence

$$\zeta(0, 0) = 0.$$

The solution of (9) now reduces to solving equation (a) with $z(\varepsilon, \eta) = \varepsilon \zeta(\varepsilon, \eta)$, namely

$$0 = w_L^T f(\eta, \varepsilon w_R + \varepsilon \zeta(\varepsilon, \eta))$$

for $\eta = \eta(\varepsilon)$, which we do by another application of the implicit function theorem. After a cancellation of ε this equation is

$$\begin{aligned} 0 = {} & \eta w_L^T \frac{\partial L(\mu_0)}{\partial \mu} w_R + \eta w_L^T \frac{\partial L(\mu_0)}{\partial \mu} \zeta + w_L^T H(\eta, \mu_0)(w_R + \zeta) \\ & + \varepsilon^{-1} w_L^T h(\mu_0 + \eta, \varepsilon w_R + \varepsilon \zeta). \end{aligned}$$

Note that the last term is continuously differentiable in ε at $\varepsilon = 0$ because $h(\mu, x) = O(|x|^2)$. This equation has solution $\eta = 0$ when $\varepsilon = 0$ and the derivative of the right side with respect to η, when evaluated at $\eta = 0$ and $\varepsilon = 0$, equals

$$w_L^T \frac{\partial L(\mu_0)}{\partial \mu} w_R = w_L^T \frac{\partial P(\mu_0, 0)}{\partial \mu} w_R \neq 0.$$

Thus, the implicit function theorem allows us to solve (9a) for a (unique) continuously differentiable solution $\eta = \eta(\varepsilon)$, $\eta(0) = 0$.

Using $z(\varepsilon) = \varepsilon\zeta(\varepsilon, \eta(\varepsilon))$ we obtain a C^k solution pair $\mu = \mu_0 + \eta(\varepsilon)$, $x = \varepsilon w_R + z(\varepsilon)$ of (1) for ε near 0. ■

Note that since w_R is a positive vector, the equilibria in Theorem 1 are positive for $\varepsilon > 0$ small. We say the bifurcation described in Theorem 1 is *forward* (respectively *backward*) if, in a neighborhood of the bifurcation point $(\mu, x) = (\mu_0, 0)$ the *positive equilibria* correspond to $\mu > \mu_0$ (respectively $\mu < \mu_0$). The direction of bifurcation is determined by the sign of $d\eta(0)/d\varepsilon$, a formula for which appears in the next lemma. Define the quantity

$$\kappa = -w_L^T \left[\nabla_x p_{ij}(\mu_0, 0) w_R\right] w_R. \tag{11}$$

Lemma 1 *Assume A1 and A2 hold and that*

$$w_L^T \frac{\partial P(\mu_0, 0)}{\partial \mu} w_R \neq 0.$$

Then the bifurcation (of positive equilibria) guaranteed by Theorem 1 is forward (respectively backward) if $d\eta(0)/d\varepsilon > 0$ *(respectively* $d\eta(0)/d\varepsilon < 0$*) where*

$$\frac{d\eta(0)}{d\varepsilon} = \frac{\kappa}{w_L^T \frac{\partial P(\mu_0, 0)}{\partial \mu} w_R}. \tag{12}$$

Proof. Our goal is to establish the formula (12). That (12) are solutions of the equilibrium equation (7) for small ε implies

$$\varepsilon w_R + z(\varepsilon) = L(\mu_0 + \eta(\varepsilon))(\varepsilon w_R + z(\varepsilon)) + h(\mu_0 + \eta(\varepsilon), \varepsilon w_R + z(\varepsilon))$$

for small ε. We calculate $d\eta(0)/d\varepsilon$ by differentiating both sides twice with respect to ε and evaluating the result at $\varepsilon = 0$.

This results in

$$\partial_\varepsilon^2 z(0) = L(\mu_0) \frac{\partial^2 z(0)}{\partial \varepsilon^2} + \left[2 \frac{d\eta(0)}{d\varepsilon} \frac{\partial L(\mu_0)}{\partial \mu} w_R + \hat{s}(\mu_0)\right] \tag{13}$$

where

$$\hat{s}(\mu_0) = \operatorname{col}\left(w_R^T H_i(\mu_0, 0) w_R\right)$$

and

$$H_i(\mu, x) = \left[\frac{\partial^2 h_i(\mu, x)}{\partial x_k \partial x_j}\right]$$

is the Hessian of the i^{th} component of $h(\mu, x)$. From (13) follows

$$w_L^T \left[2 \frac{d\eta(0)}{d\varepsilon} \frac{\partial L(\mu_0)}{\partial \mu} w_R + \hat{s}(\mu_0)\right] w_R = 0$$

and

$$\frac{d\eta\left(0\right)}{d\varepsilon}=-\frac{1}{2}\frac{w_L^T\hat{s}(\mu_0)}{w_L^T\frac{\partial L(\mu_0)}{\partial\mu}w_R}. \tag{14}$$

A calculation using the definition (6) of $h\left(\mu,x\right)$ yields

$$H_i\left(\mu_0,0\right)=\left[\frac{\partial p_{ik}\left(\mu_0,0\right)}{\partial x_j}+\frac{\partial p_{ij}\left(\mu_0,0\right)}{\partial x_k}\right]$$

and

$$w_R^TH_i\left(\mu_0,0\right)w_R=\sum_{k=1}^m w_{Rk}\sum_{j=1}^m w_{Rj}\frac{\partial p_{ik}\left(\mu_0,0\right)}{\partial x_j}+\sum_{k=1}^m w_{Rk}\sum_{j=1}^m w_{Rj}\frac{\partial p_{ij}\left(\mu_0,0\right)}{\partial x_k}$$

Interchanging the order of summation in the first term and re-labeling the indices in the second term by interchanging j with k we get

$$w_R^TH_i\left(\mu_0,0\right)w_R=2\sum_{j=1}^m w_{Rj}\sum_{k=1}^m w_{Rk}\frac{\partial p_{ik}\left(\mu_0,0\right)}{\partial x_j}$$

and

$$\begin{aligned}
w_L^T\hat{s}(\mu_0)&=\operatorname{col}\left(w_R^TH_i\left(\mu_0,0\right)w_R\right)\\
&=2w_L^T\operatorname{col}\left(\sum_{j=1}^m w_{Rj}\sum_{k=1}^m w_{R_k}\frac{\partial p_{ik}\left(\mu_0,0\right)}{\partial x_j}\right)\\
&=2\sum_{i=1}^m w_{L_i}\sum_{j=1}^m w_{R_j}\sum_{k=1}^m w_{R_k}\frac{\partial p_{ik}\left(\mu_0,0\right)}{\partial x_j}\\
&=2\sum_{i=1}^m w_{L_i}\sum_{k=1}^m w_{R_k}\sum_{j=1}^m w_{R_j}\frac{\partial p_{ik}\left(\mu_0,0\right)}{\partial x_j}
\end{aligned}$$

or

$$w_L^T\hat{s}(\mu_0)=2w_L^T\left[\nabla_x p_{ij}\left(\mu_0,0\right)w_R\right]w_R. \tag{15}$$

From this and (14) we get

$$\frac{d\eta\left(0\right)}{d\varepsilon}=-\frac{w_L^T\left[\nabla_x p_{ij}\left(\mu_0,0\right)w_R\right]w_R}{w_L^T\frac{\partial L(\mu_0)}{\partial\mu}w_R}$$

and hence (12). ■

4 Equilibrium Stability

We say the transcritical *bifurcation of positive equilibria* described in Theorem 1 is a *stable* (respectively *unstable*) *bifurcation* if, in a neighborhood of the bifurcation point $(\mu,x)=(\mu_0,0)$ the positive equilibria are locally asymptotically stable (respectively unstable).

Lemma 2 *Assume A1 and A2 hold and that*

$$w_L^T \frac{\partial P(\mu_0, 0)}{\partial \mu} w_R \neq 0.$$

(a) If

$$w_L^T \frac{\partial P(\mu_0, 0)}{\partial \mu} w_R > 0$$

then $x = 0$ loses stability as μ increases through μ_0. If

$$w_L^T \frac{\partial P(\mu_0, 0)}{\partial \mu} w_R < 0$$

then $x = 0$ loses stability as μ decreases through μ_0.

(b) In addition assume that μ_0 is a strictly dominant eigenvalue of $P(\mu_0, 0)$ (i.e. $P(\mu_0, 0)$ is primitive). Then the bifurcation (of positive equilibria) guaranteed by Theorem 1 is stable if $\kappa > 0$ and unstable if $\kappa < 0$.

Proof. To perform a linearized stability analysis on equation (1) we calculate the Jacobian of the right hand side evaluated at the equilibrium of interest.

(a) The Jacobian evaluated at $x = 0$ is $P(\mu, 0)$, which by A1 has a real, positive dominant eigenvalue $\lambda(\mu, 0)$. By A2 we have $\lambda(\mu_0, 0) = 1$. By the linearization principle [22], $x = 0$ is unstable if $\lambda(\mu, 0) > 1$ and (locally asymptotically) stable if $\lambda(\mu, 0) < 1$. For μ near μ_0 which is the case can be determined by the sign of $d\lambda(\mu_0, 0)/d\mu$, provided it is nonzero. We can calculate $d\lambda(\mu_0, 0)/d\mu$ by an implicit differentiation of

$$P(\mu, 0) w_R(\mu) = \lambda(\mu, 0) w_R(\mu)$$

where $w_R(\mu)$ is an eigenvector such that $w_R(\mu_0) = w_R$ in A2. From

$$\frac{\partial P(\mu, 0)}{\partial \mu} w_R(\mu) + P(\mu, 0) \frac{dw_R(\mu)}{d\mu} = \frac{d\lambda(\mu, 0)}{d\mu} w_R(\mu) + \lambda(\mu, 0) \frac{dw_R(\mu)}{d\mu}$$

evaluated at $\mu = \mu_0$ we have

$$P(\mu_0, 0) \frac{dw_R(\mu_0)}{d\mu} = \frac{dw_R(\mu_0)}{d\mu} + \left[\frac{d\lambda(\mu_0, 0)}{d\mu} w_R - \frac{\partial P(\mu_0, 0)}{\partial \mu} w_R \right]$$

from which follows

$$w_L^T \left[\frac{d\lambda(\mu_0, 0)}{d\mu} w_R - \frac{\partial P(\mu_0, 0)}{\partial \mu} w_R \right] = 0$$

and

$$\frac{d\lambda(\mu_0, 0)}{d\mu} = \frac{w_L^T \frac{\partial P(\mu_0, 0)}{\partial \mu} w_R}{w_L^T w_R}.$$

Since $w_L^T w_R > 0$ we have

$$sign \frac{d\lambda(\mu_0, 0)}{d\mu} = sign \left(w_L^T \frac{\partial P(\mu_0, 0)}{\partial \mu} w_R \right).$$

(b) To carry out a linearized stability analysis of the positive equilibria guaranteed by Theorem 1 we can make use of the ε-parametrization of $\mu = \mu(\varepsilon)$ and $x = x(\varepsilon)$ given by (8). The Jacobian

$$J(\mu, x) = \left[p_{ij}(\mu_0, 0)(\mu, x) + \sum_{k=1}^{m} x_k \frac{\partial p_{ik}(\mu_0, 0)(\mu, x)}{\partial x_j} \right] \tag{16}$$

of $P(\mu, x)\, x$ evaluated at these equilibria is a function of ε as are its eigenvalues, including its strictly dominant eigenvalue which we denote by $\bar{\lambda}(\varepsilon)$, $\bar{\lambda}(0) = 1$. (The second matrix is row and column indexed by i and j respectively.) The positive equilibria are (locally asymptotically) stable if $\bar{\lambda}(\varepsilon) < 1$ for $\varepsilon > 0$ sufficiently small and unstable if $\bar{\lambda}(\varepsilon) > 1$ for $\varepsilon > 0$ sufficiently small. Which is the case can be determined by the sign of $d\bar{\lambda}(0)/d\varepsilon$, provided it is nonzero. The Jacobian evaluated at $\mu = \mu(\varepsilon)$ and $x = x(\varepsilon)$, to order ε, is

$$J(\mu(\varepsilon), x(\varepsilon)) = J_0 + J_1 \varepsilon + O\left(\varepsilon^2\right).$$

Let

$$q(\varepsilon) = q_0 + q_1 \varepsilon + O\left(\varepsilon^2\right)$$

be an eigenvector associated with $\bar{\lambda}(\varepsilon)$ so that

$$J(\mu(\varepsilon), x(\varepsilon))\, q(\varepsilon) = \bar{\lambda}(\varepsilon)\, q(\varepsilon). \tag{17}$$

Note that $J_0 = P(\mu_0, 0)$ and therefore $q(0) = w_R$.

A differentiation of (17) with respect to ε followed by an evaluation at $\varepsilon = 0$, yields

$$P(\mu_0, 0)\, q_1 = q_1 + \left[\frac{d\bar{\lambda}(0)}{d\varepsilon} w_R - J_1 w_R \right]$$

and hence

$$w_L^T \left[\frac{d\bar{\lambda}(0)}{d\varepsilon} w_R - J_1 w_R \right] = 0$$

or

$$\frac{d\bar{\lambda}(0)}{d\varepsilon} = \frac{w_L^T J_1 w_R}{w_L^T w_R}.$$

From $x_k(0) = 0$ and $dx_k(0)/d\varepsilon = w_{Rk}$ we obtain from (16)

$$\begin{aligned}
w_L^T J_1 w_R &= w_L^T \frac{d}{d\varepsilon} \left[p_{ij}(\mu_0, 0)(\mu(\varepsilon), x(\varepsilon)) + \sum_{k=1}^{m} x_k(\varepsilon) \frac{\partial p_{ik}(\mu_0, 0)(\mu(\varepsilon), x(\varepsilon))}{\partial x_j} \right] \Bigg|_{\varepsilon=0} w_R \\
&= w_L^T \left[\frac{\partial p_{ij}(\mu_0, 0)}{\partial \mu} \frac{d\mu(0)}{d\varepsilon} + \nabla_x p_{ij}(\mu_0, 0)\, w_R + \sum_{k=1}^{m} w_{R_k} \frac{\partial p_{ik}(\mu_0, 0)}{\partial x_j} \right] w_R \\
&= w_L^T \left[\frac{\partial p_{ij}(\mu_0, 0)}{\partial \mu} \frac{d\mu(0)}{d\varepsilon} + \sum_{k=1}^{m} w_{R_k} \frac{\partial p_{ij}(\mu_0, 0)}{\partial x_k} + \sum_{k=1}^{m} w_{R_k} \frac{\partial p_{ik}(\mu_0, 0)}{\partial x_j} \right] w_R \\
&= \frac{d\mu(0)}{d\varepsilon} w_L^T \frac{\partial P(\mu_0, 0)}{\partial \mu} w_R + w_L^T \operatorname{col}\left(w_R^T H_i(\mu_0, 0)\, w_R \right) \\
&= \frac{d\mu(0)}{d\varepsilon} w_L^T \frac{\partial P(\mu_0, 0)}{\partial \mu} w_R + w_L^T \hat{s}(\mu_0)
\end{aligned}$$

Since $d\mu(0)/d\varepsilon = d\eta(0)/d\varepsilon$ we get by (15) that

$$\begin{aligned} w_L^T J_1 w_R &= \frac{d\eta(0)}{d\varepsilon} w_L^T \frac{\partial P(\mu_0, 0)}{\partial \mu} w_R - 2\frac{d\eta(0)}{d\varepsilon} w_L^T \frac{\partial P(\mu_0, 0)}{\partial \mu} w_R \\ &= -\frac{d\eta(0)}{d\varepsilon} w_L^T \frac{\partial P(\mu_0, 0)}{\partial \mu} w_R \end{aligned}$$

from which, together with (12), we obtain

$$\frac{d\bar{\lambda}(0)}{d\varepsilon} = -\frac{\kappa}{w_L^T w_R}.$$

■

From Lemmas 1 and 2 we see that the stability of the bifurcating positive equilibria is determined by the direction of bifurcation, in one of two mirrored situations depending on the sign of $w_L^T \frac{\partial P(\mu_0,0)}{\partial \mu} w_R$. This is summarized in the following theorem.

Theorem 2 *Assume A1 and A2 hold and that*

$$w_L^T \frac{\partial P(\mu_0, 0)}{\partial \mu} w_R \neq 0.$$

Assume $P(\mu_0, 0)$ is primitive. Then the stability or instability of the bifurcating positive equilibria guaranteed by Theorem 1 is determined by the direction of bifurcation in one of two ways.

(a) If

$$w_L^T \frac{\partial P(\mu_0, 0)}{\partial \mu} w_R > 0$$

then the equilibrium $x = 0$ loses stability as μ increases through μ_0. Moreover, the bifurcation of positive equilibria is forward and stable if $\kappa > 0$ and backward and unstable if $\kappa < 0$.

(b) If

$$w_L^T \frac{\partial P(\mu_0, 0)}{\partial \mu} w_R < 0$$

then the equilibrium $x = 0$ loses stability as μ decreases through μ_0. Moreover, the bifurcation is backward and stable if $\kappa > 0$ and forward and unstable if $\kappa < 0$.

Remark 1 *Note that in order to apply Theorem 2 one needs only to determine the signs of the two quantities*

$$w_L^T \frac{\partial P(\mu_0, 0)}{\partial \mu} w_R \quad \text{and} \quad \kappa = -w_L^T \left[\nabla_x p_{ij}(\mu_0, 0) w_R\right] w_R. \tag{18}$$

It is not required to compute these quantities to apply Theorem 2. Of course, one might want to know how the properties of the bifurcation depend on other model parameters, in which case formulas for these quantities in terms of model parameters would be needed.

Remark 2 *The sign of κ determines the direction of bifurcation and the stability of bifurcating positive equilibria. From the formula (11) we see that this diagnostic quantity is a linear combination, with positive coefficients, of the partial derivatives $\partial p_{ij}(\mu_0, 0)/\partial x_k$ of the entries $p_{ij}(\mu, x)$ in the projection matrix $P(\mu, x)$ with respect to the components x_k of x, evaluated at $(\mu, x) = (\mu_0, 0)$. In* *population models, these partial derivatives measure the effects that changes in low level, class specific densities have on the vital rates modeled by* $p_{ij}(\mu, x)$. *A negative partial derivative contributes to the possible negativity of* κ *and hence a forward, stable bifurcation. On the other hand, a positive partial derivative (called a component Allee effect [4]) contributes to the possible positivity of* κ *and hence a backward, unstable bifurcation.*

Notice that if all nonzero derivatives $\partial p_{ij}(\mu_0, 0)/\partial x_k$ *are negative, then* $\kappa > 0$. *In this case, which can often be seen in applications by simple inspection, there is no need to calculate* κ *in order to see that it is positive and the bifurcation is stable. Similarly, if all nonzero derivatives* $\partial p_{ij}(\mu_0, 0)/\partial x_k$ *are positive the bifurcation is unstable. Only if there is a mix of negative and positive derivatives is it necessary to calculate* κ *in order to determine its sign.*

Remark 3 *In a manner similar to the determination of the sign of* κ *in Remark 2, one can often determine the sign of the first quantity in (18) without actually calculating it, but by observing the signs of the derivatives* $\partial p_{ij}(\mu_0, 0)/\partial \mu$. *If all nonzero derivatives are positive (negative), then clearly the quantity is positive (negative).*

Remark 4 *Theorem 2 is no longer valid if the assumption that* $P(\mu_0, 0)$ *is primitive is dropped (nor is Lemma 2(b)). When* $P(\mu_0, 0)$ *is imprimitive, it is well known that the direction of bifurcation does not alone determine the stability of the bifurcating positive equilibria. As pointed out in [2] imprimitive inherent projection matrices rarely arise in population models, and therefore this assumption is not restrictive. On the other hand, there are a few models with imprimitive inherent projection matrices that arise under very specialized biological assumptions (such as Leslie models under strict semelparity). Extensive studies of these specialized models have shown that forward bifurcations are not necessarily stable. The reason is that imprimitivity, in general, creates the simultaneous bifurcation of equilibria and other types of invariant sets (synchronous cycles, cycle chains, and other complicated invariant sets on the boundary of the positive cone). The transcritical bifurcations that occur in the imprimitive case are well understood in dimensions* $m = 2$ *[7], [17] and* $m = 3$ *[14]. For higher dimensions little is known about the stability or instability these simultaneously bifurcating continua [16], except for imprimitive matrices of a highly specialized forms [33], [34]. Some authors have mused about the imprimitive case that, as the dimension* m *increase, the number and complexity of the combinatorial possibilities for the existence and stability of bifurcating invariant sets become so overwhelming that the existence of a general rule for determining which are stable is unlikely. It remains a challenging, open problem to determine the properties of the bifurcation that occurs when the extinction equilibrium destabilizes in the case of an imprimitive projection matrix* $P(\mu_0, 0)$.

5 The Net Reproduction Number

To apply the results in Section 3 one needs to find a value μ_0 of the bifurcation parameter $\mu = \mu_0$ for which the dominant eigenvalue $\lambda(\mu, 0)$ of the (nonnegative and irreducible) inherent projection matrix $P(\mu, 0)$ is equal to 1. Since formulas for $\lambda(\mu, 0)$ are not generally available, the calculation of such a μ_0 is usually intractable analytically. A method that is in general more analytically tractable utilizes the inherent net reproduction number $R_0(\mu, 0)$, which is defined as follows.

The demographic population vector x_{t+1} consists of offspring produced since time t plus survivors from the population x_t. If $f_{ij}(\mu, 0)$ is the number of offspring of class i produced by an adult of class j per unit time, then the demographic population of offspring at time $t+1$ is $F(\mu, 0)\, x$ where

$F(\mu,0) = [f_{ij}(\mu,0)]$ is the fertility matrix. If $\tau_{ij}(\mu,0)$ is the fraction of j class individuals who survive and move to class i per unit time, then the demographic population vector of survivors is $T(\mu,0)\,x$ where $T(\mu,0) = [\tau_{ij}(\mu,0)]$ is the survival-transition matrix. Thus, the projection matrix has the additive decomposition

$$P(\mu,0) = F(\mu,0) + T(\mu,0).$$

Note that both $F(\mu,0)$ and $T(\mu,0)$ are nonnegative matrices whose entries satisfy

$$f_{ij}(\mu,0) \geq 0, \quad 0 \leq \tau_{ij}(\mu,0) \leq 1. \tag{19}$$

Without immigration into the population, the total survivors can be no larger than the original population so that $\Sigma_{i=1}^{m}\tau_{ij}(\mu,0) \leq 1$.

Recall that a nonnegative matrix has a nonnegative, dominant eigenvalue with associated nonnegative right and left eigenvalues [1]. Let $\lambda_T(\mu) \geq 0$ be the (not necessarily strictly) dominant eigenvalue of $T(\mu,0)$. The vector of survivors from $x(0)$ at time t is $T^t(\mu,0)\,x(0)$ and the population of survivors is $|T^t(\mu,0)\,x(0)|$. To rule out immortality, we assume $\lim_{t\to+\infty}|T^t(\mu,0)\,x(0)| = 0$ for all nonnegative initial vectors $x(0)$. This is equivalent to $\lambda_T(\mu,0) < 1$ and implies the matrix $I - T(\mu,0)$ (where I is the $m \times m$ identity matrix) has a nonnegative inverse:

$$(I - T(\mu,0))^{-1} = I + T(\mu,0) + T^2(\mu,0) + \cdots$$

[29], [24]. The nonnegative matrix $F(\mu,0)(I - T(\mu,0))^{-1}$ is called the next generation matrix and its dominant eigenvalue $R_0(\mu,0)$ is the *inherent net reproduction number* [5].

The following theorem follows from results in [5] and [29].

Theorem 3 *Assume $f_{ij}(\mu,0)$ and $\tau_{ij}(\mu,0)$ are continuously differentiable functions on I_μ that satisfy (19). Assume $P(\mu,0) = F(\mu,0) + T(\mu,0)$ is nonnegative and irreducible, $T(\mu,0) \neq 0$, and $\lambda_T(\mu,0) < 1$ for $\mu \in I_\mu$. Then $\lambda(\mu,0)$ and $R_0(\mu,0)$ are on the same side of 1 and $\lambda(\mu,0) = 1$ if and only if $R_0(\mu,0) = 1$.*

Remark 5 *Theorem 3 implies that a value of μ required in assumption A2 can be found by solving $R_0(\mu,0) = 1$ for $\mu = \mu_0$ instead of solving $\lambda(\mu,0) = 1$ for $\mu = \mu_0$.*

The advantage of using $R_0(\mu,0)$ to find μ_0 is that one can often calculate an analytic formula for it. $\subset$The reason for this is that the fertility matrix is usually of low rank (because the number of juvenile classes is usually low), which produces only a small number of nonzero rows in $F(\mu,0)$. For example, the most common case is that all juveniles lie in a single class in the classification scheme, usually class $i = 1$. In this case only the first row in $F(\mu,0)$, and consequently also in the next general matrix, is nonzero and, as a result, $R_0(\mu,0)$ is the first row, first column entry in the next generation matrix. Thus, $R_0(\mu,0)$ is the inner product of the first row of $F(\mu,0)$ and the first column of $(I - T(\mu,0))^{-1}$.

For example, the classic Leslie, age-structured, projection matrix has fertility matrix

$$F(\mu,0) = \begin{bmatrix} f_{11} & f_{12} & \cdots & f_{1,m-1} & f_{1m} \\ 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & 0 & 0 \end{bmatrix}$$

and transition matrix

$$T(\mu,0)=\begin{bmatrix} 0 & \cdots & 0 & 0 & 0 \\ \tau_{21}(\mu,0) & \cdots & 0 & 0 & 0 \\ \vdots & & \vdots & \vdots & \vdots \\ 0 & \cdots & \tau_{m-1,m-1}(\mu,0) & 0 & 0 \\ 0 & \cdots & 0 & \tau_{m,m-1}(\mu,0) & \tau_{mm}(\mu,0) \end{bmatrix}$$

from which one can calculate

$$\begin{aligned} R_0(\mu,0) = {} & f_{11}(\mu,0)+\textstyle\sum_{j=1}^{m-1} f_{1j}(\mu,0)\prod_{i=2}^{j-1}\tau_{i,i-1}(\mu,0) \\ & + f_{1m}(\mu,0)\frac{1}{1-\tau_{mm}(\mu,0)}\textstyle\prod_{i=2}^{m}\tau_{i,i-1}(\mu,0). \end{aligned} \tag{20}$$

For other examples of R_0 formulas for special projection matrices see [9].

6 Examples

We consider two structured population models to illustrate the use of the results in Section 3. The first example involves an $m = 2$ dimensional model that classifies individuals into two classes: juveniles and adults. Adult fertility is assumed to be a function of the amount μ of a food resource available to adults. We use μ as the bifurcation parameter to study the destabilization of the extinction equilibrium and the resulting bifurcation of positive equilibria by applying Theorem 2. Theorems about this bifurcation available in the literature do not apply to this example because μ does not appear linearly. A second example involves the well known LPA model, an $m = 3$ dimensional model in which individuals are classified by the life history stages of larva, pupa, and adults. By using the adult death rate as the bifurcation parameter, we see an example of a backward and stable bifurcation of positive equilibria (which is in contrast to the more familiar forward and stable bifurcation found in most applications and which is found in the LPA model if instead the adult fertility rate is used as the bifurcation parameter).

6.1 A Juvenile-Adult Model

A basic life stage model is the $m = 2$ dimensional matrix model in which the population is classified into juveniles x_1 and adults x_2 and the time unit is taken equal to the juvenile maturation period. This results in a projection matrix of the form [7], [17] [20], [21], [31]

$$\begin{bmatrix} 0 & f \\ s_1 & s_2 \end{bmatrix}.$$

In this matrix $f > 0$ is the per adult fertility rate (the number of juveniles produced by an adult during one time unit), and s_1 and s_2 are the fractions of juveniles and adults that survive one time step.

In this example we consider a nonlinear version of this model with projection matrix

$$P(\mu,x)=\begin{bmatrix} 0 & bh(\mu)\beta(x_2) \\ s_1 & s_2 \end{bmatrix}.$$

Here adult fertility f is assumed proportional to a food resource harvest rate $h(\mu)$ where μ is the amount of food resource available to adults, b is the number of offspring produced per unit resource per adult, and $\beta(x_2)$ is the effect on reproduction of adult population density. For example, a commonly used mathematical expressions for h is the Holling II type harvest rate

$$h(\mu) = h^* \frac{\mu}{c + \mu} \tag{21}$$

where $h^* > 0$ is the maximal possible amount of food resource that can be harvested per unit time per adult and $c > 0$ is the half saturation level. Commonly used density factors are

$$\beta(x_2) = \frac{1}{1 + cx_2} \quad \text{or} \quad \exp(-cx_2) \quad \text{or} \quad \frac{1 + ax_2}{1 + cx_2 + ax_2^2} \tag{22}$$

where $a, c > 0$. Note that the first two examples are monotone decreasing functions of x as is the third if $a < c$. If $a > c$ then the third example initially increases to a maximum at $x = \left(\sqrt{a - c + 1} - 1\right)/a$ after which it is monotone decreasing. (An increase in fertility with increased low level density, such as this, is called a component Allee effect.) All three examples tend to 0 as x increases without bound, that is to say, fertility effectively ceases at extremely large adult densities.

Our goal is to apply Theorem 2 using the resource availability μ as a bifurcation parameter. We'll do this under the following assumptions. The survival rates satisfy

$$0 < s_1 \leq 1, \quad 0 < s_2 < 1$$

(if $s_2 = 0$ the inherent projection matrix is imprimitive) and the harvest and density factors h and β are, on an open interval containing R^1_+, twice continuously differentiable and nonnegative valued functions of their arguments that satisfy

$$\frac{dh(\mu)}{d\mu} > 0$$

(i.e. the harvest rate increases with an increase in resource availability) and

$$\beta(0) = 1, \text{ and } 0 \leq \beta(x)\, x \leq \beta^* < +\infty$$

for all $x > 0$ and some positive constant $\beta^* > 0$. Then the inherent projection matrix

$$P(\mu, 0) = \begin{bmatrix} 0 & bh(\mu) \\ s_1 & s_2 \end{bmatrix} = \begin{bmatrix} 0 & bh(\mu) \\ 0 & 0 \end{bmatrix} + \begin{bmatrix} 0 & 0 \\ s_1 & s_2 \end{bmatrix}$$

is primitive and by (20) the inherent net reproduction number is

$$R_0(\mu, 0) = bh(\mu) \frac{s_1}{1 - s_2}.$$

Assume there exists a resource availability μ_0 for which $R_0(\mu_0, 0) = 1$, i.e.

$$\frac{1 - s_2}{bs_1} \text{ lies in the range of } h(\mu) \tag{23}$$

so that

$$\mu_0 = h^{-1}\left(\frac{1 - s_2}{bs_1}\right). \tag{24}$$

For example, for the Holling II harvest rate

$$\mu_0 = c\frac{1 - s_2}{bh^* s_1 - (1 - s_2)}$$

under the assumption that the maximal harvest rate h^* is sufficiently large:

$$h^* > \frac{1 - s_2}{bs_1}.$$

To apply Theorem 2, according to Remark 1, we only need to determine the signs of the two quantities (18). To do this we can make use of Remarks 3 and 2. The only nonzero entry in $\partial P\left(\mu_0, 0\right)/\partial \mu$ is

$$\frac{\partial p_{12}\left(\mu_0, 0\right)}{\partial \mu} = b\frac{dh\left(\mu_0\right)}{d\mu} > 0.$$

and it follows that

$$w_L^T \frac{\partial P\left(\mu_0, 0\right)}{\partial \mu} w_R > 0.$$

Second, the only nonzero partial derivative $\partial p_{ij}\left(\mu_0, 0\right)/\partial x_k$ is

$$\frac{\partial p_{12}\left(\mu_0, 0\right)}{\partial x_2} = bh\left(\mu_0\right)\frac{d\beta\left(0\right)}{dx_2}$$

whose sign is that of $d\beta\left(0\right)/dx$. It follows by Remark 2 that the sign of κ is that of $-d\beta\left(0\right)/dx$. Applying Theorem 2, we arrive at the following conclusions.

> Assuming (23) holds, the extinction equilibrium destabilizes as the resource availability μ increases through μ_0 given by (24). The resulting bifurcation of positive equilibria is forward and stable if $d\beta\left(0\right)/dx_2 < 0$ and backward and unstable if $d\beta\left(0\right)/dx > 0$.

As specific examples, the bifurcation is forward for the first two density factors $\beta\left(x_2\right)$ in (22). For the third density factor in (22), the bifurcation is forward and stable if $a < c$ and backward and unstable if $a > c$.

6.2 The LPA Model

The well-known LPA for the dynamics of an insect population has projection matrix $P\left(\mu, x\right) = F\left(\mu, x\right) + T\left(\mu, x\right)$ where

$$F\left(\mu, x\right) = \begin{bmatrix} 0 & 0 & b\exp\left(-c_{el}x_2 - c_{ea}x_3\right) \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix}$$

$$T\left(\mu, x\right) = \begin{bmatrix} 0 & 0 & 0 \\ 1 - \mu_l & 0 & 0 \\ 0 & \exp\left(-c_{pa}x_3\right) & 1 - \mu_a \end{bmatrix}$$

where the demographic population vector consists of larva x_1, pupa x_2, and adults x_3. (The bifurcation parameter μ is yet to be chosen.) For a derivation of the model see [19] and for its many application see [3], [8], [11]. The unit of time is that for a larva to become a pupa, which in this model is the same amount of time spent as a pupa. The density-free number of larvae produced per adult per unit time is $b > 0$ and μ_l and μ_a are the larval and pupal death probabilities (per unit time):

$$0 < \mu_l,\ \mu_a < 1.$$

The density coefficients c_{el}, c_{ea}, and c_{pa} are positive (and measure the effects of larva and adult cannibalism of eggs and pupae).

The inherent projection matrix

$$\left[\begin{array}{ccc} 0 & 0 & b \\ 1-\mu_l & 0 & 0 \\ 0 & 1 & 1-\mu_a \end{array}\right]$$

primitive provided $\mu_a \neq 1$ and by (20) the inherent net reproduction number is

$$b\frac{1-\mu_l}{\mu_a}$$

As a first application of the bifurcation results in Section 3, we take the bifurcation parameter to be the adult death rate $\mu = \mu_a$. Then

$$R_0\left(\mu,0\right) = b\frac{1-\mu_l}{\mu}$$

and

$$\mu_0 = b\left(1-\mu_l\right).$$

To be meaningful μ_0 must be less than 1, so we assume

$$b\left(1-\mu_l\right) < 1. \tag{25}$$

Then

$$P\left(\mu_0,0\right) = \left[\begin{array}{ccc} 0 & 0 & b \\ 1-\mu_l & 0 & 0 \\ 0 & 1 & 1-b\left(1-\mu_l\right) \end{array}\right]$$

is primitive.

To apply Theorem 2, according to Remark 1, we only need to determine the signs of the two quantities (18). To do this we can make use of Remarks 3 and 2. First, since the only nonzero entry in $\partial P\left(\mu_0,0\right)/\partial\mu$ is

$$\frac{\partial p_{33}\left(\mu_0,0\right)}{\partial\mu} = -1 < 0$$

it follows that

$$w_L^T\frac{\partial P\left(\mu_0,0\right)}{\partial\mu}w_R < 0.$$

Second, by inspection we see that the only nonzero partial derivatives $\partial p_{ij}\left(\mu_0,0\right)/\partial x_k$ are negative and therefore it follows by Remark 2 that $\kappa > 0$. Applying Theorem 2, we arrive at the following conclusions.

> Assuming $\mu = \mu_a$ and (25) holds, the extinction equilibria of the LPA model destabilizes as μ decreases through μ_0 and the resulting bifurcation of positive equilibria is backward and stable.

If instead we chose the bifurcation parameter to be the inherent adult fertility rate $\mu = b$, then

$$\mu_0 = \frac{\mu_a}{1-\mu_l}$$

and

$$P(\mu_0, 0) = \begin{bmatrix} 0 & 0 & \frac{\mu_a}{1-\mu_l} \\ 1-\mu_l & 0 & 0 \\ 0 & 1 & 1-\mu_a \end{bmatrix}$$

is primitive. In this case, the only nonzero entry in $\partial P(\mu_0, 0) / \partial \mu$ is

$$\frac{\partial p_{13}(\mu_0, 0)}{\partial \mu} = 1 > 0$$

which implies

$$w_L^T \frac{\partial P(\mu_0, 0)}{\partial \mu} w_R > 0.$$

By the same reasoning as above, $\kappa > 0$ and we reach the following conclusion.

> Assuming $\mu = b$, the extinction equilibria of the LPA model destabilizes as μ increases through μ_0 and the resulting bifurcation of positive equilibria is forward and stable.

For more on the LPA model at its bifurcations using $\mu = b$ as the parameter see [12].

7 Concluding Remarks

Theorem 2 generalizes available theorems concerning the bifurcation that occurs when the extinction equilibrium destabilizes in two ways. First, it allows for a general appearance of the bifurcation parameter μ and therefore allows for a wider range of applications. Second, it includes the case when backward bifurcations are stable. The theorem concerns the autonomous nonlinear matrix equation (1) whose projection matrix depends on time only in that it depends on the population demographic vector at time t.

Population vital rates can vary with time in other ways as well. Vital rates varying periodically in time (for example, due to seasonal, monthly or daily fluctuations of environmental conditions) give rise to a projection matrix that is explicitly dependent on time in a periodic fashion. It would be of interest to generalize Theorem 2 to the case of periodically forced matrix equations, so as to generalize existing theorems [10], [23], [13]. Another reason the entries in the projection matrix can vary with time is adaptation by means of evolutionary selection. Available theorems describing the fundamental bifurcation from a destabilizing extinction state for Darwinian (evolutionary game theoretic) matrix models assume a linear appearance of the bifurcation parameter [15], [17], [18], [30] and it would be of interest to extend Theorem 2 to Darwinian matrix models.

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