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A bifurcation theorem for Darwinian matrix models

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Abstract. Matrix models are widely used to describe the discrete time dynamics of structured populations (i.e., biological populations in which individuals are classified into discrete categories such as age, size, etc.). A fundamental biological question concerns population extinction and persistence, i.e., the stability or instability of the extinction state versus the existence of stable positive equilibria. A fundamental bifurcation theorem provides one general answer to this question, using the inherent population growth rate r as a bifurcation parameter, by asserting the existence a continuum of positive equilibria that bifurcates from the extinction state at $r = 1$. Moreover, stability of the bifurcating non-extinction equilibria is determined by the direction of bifurcation (at least near the bifurcation point). Evolutionary game theoretic methods generalize structured population dynamic models so as to include the dynamics of (mean) phenotypic traits subject to natural selection. The resulting Darwinian matrix model describes both the structured population dynamics and the evolutionary trait dynamics and the way in which they interplay. Here we generalize the fundamental bifurcation theorem for structured population dynamics to Darwinian matrix models. We give two applications.

1 Introduction

A matrix model for the discrete time dynamics of a structured population has the form [1], [3]

$$\hat{x}(t+1) = P(\hat{x}(t))\hat{x}(t) \tag{1.1}$$

where the $m \times m$ projection matrix P is nonnegative and $t \in Z_+ = \{0, 1, 2, \cdots\}$, $\hat{x} : Z_+ \to R^m$. Here R^m is m-dimensional Euclidean space . (More will be assumed about P below.) The column vector $\hat{x}$ is a vector of population numbers or densities of individuals lying in m disjoint classes or categories and to be of

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biological interest must, therefore, lie in the closure $\bar{R}_{+}^{m}$ of the positive cone R_{+}^{m}. Equilibrium states are vectors $\hat{x}$ satisfying $\hat{x} = P(\hat{x})\hat{x}$ and include the trivial or *extinction equilibrium* $\hat{x} = \hat{0}$.

A non-negative matrix is primitive if it is irreducible and has a strictly dominant eigenvalue. We make the following assumptions concerning the projection matrix $P(\hat{x}) = (p_{ij}(\hat{x}))$. Here, as throughout, Ω denotes an open neighborhood of the origin $\hat{0} \in R^{m}$.

$$\text{H1:} \quad \begin{cases} p_{ij} \in C^{2}\left(\Omega \to \bar{R}_{+}^{1}\right) \\ \hat{x} \in \bar{R}_{+}^{m} \text{ and } P(\hat{x})\hat{x} = \hat{0} \text{ imply } \hat{x} = \hat{0} \\ P(\hat{x}) \text{ is primitive for all } \hat{x} \in \Omega. \end{cases}$$

Let $r = r(\hat{x})$ denote the strictly dominant, simple and positive eigenvalue of $P(\hat{x})$ (whose existence follows from Perron-Frobenius theory). Then $r \in C^{2}\left(\Omega \to \bar{R}_{+}^{1}\right)$. The number $\lambda = r(\hat{0})$ is called the inherent growth rate. Normalizing the entries of P with respect to $r(\hat{0})$, we write the matrix (1.1) equation as

$$\hat{x}(t+1) = \lambda Q(\hat{x}(t))\hat{x}(t) \tag{1.2}$$

where the normalized projection matrix $Q(\hat{x}) = (q_{ij}(\hat{x}))$ also satisfies H1. Note that 1 is the dominant eigenvalue of $Q(\hat{0})$.

A pair $(\lambda, \hat{x}) \in R^{1} \times \Omega$ is called an *equilibrium pair* of the matrix model (1.2) if

$$\hat{x} = \lambda Q(\hat{x})\hat{x}. \tag{1.3}$$

The *extinction equilibrium pair* $(\lambda, \hat{0})$ is an equilibrium pair for all $\lambda \in R^{1}$. If $(\lambda, \hat{x})$ is an equilibrium pair and if $\hat{x}$ is a locally asymptotically stable equilibrium of the matrix equation (1.2) (or equivalently of (1.1) with $P = \lambda Q$), then we say that the pair $(\lambda, \hat{x})$ is *stable*. Since the Jacobian associated with (1.2) evaluated at an extinction equilibrium pair is $\lambda Q(\hat{0})$, which has dominant eigenvalue λ, the linearization principle [6] establishes part (a) of the following theorem. Parts (b) and (c) follow from Theorems 1.2.4 and 1.2.5 in [3].

Theorem 1. [3] Assume the matrix $Q(\hat{x})$ in the matrix equation (1.2) satisfies H1 and that 1 is the dominant eigenvalue of $Q(\hat{0})$.

(a) The extinction equilibrium pair $(\lambda, \hat{0})$ is stable for $\lambda < 1$ and is unstable for $\lambda > 1$.

(b) There exists a continuum $\mathcal{C}$ of (positive) equilibrium pairs $(\lambda, \hat{x}) \in R_{+}^{1} \times R_{+}^{m}$ of the matrix model (1.2) that contains the extinction pair $(1, \hat{0})$ in its closure.

(c) If $\mathcal{C}$ bifurcates to the right from $(1, \hat{0})$, then the equilibrium pairs on $\mathcal{C}$ near $(1, \hat{0})$ are stable. If $\mathcal{C}$ bifurcates to the left from $(1, \hat{0})$, then the equilibrium pairs on $\mathcal{C}$ near $(1, \hat{0})$ are unstable.

In part (c), bifurcation to the right (left) means that in a neighborhood of $(1, \hat{0})$ the equilibrium pairs $(\hat{x}, \lambda)$ from $\mathcal{C}$ satisfy $\lambda > 1$ $(\lambda < 1)$. This is the familiar exchange of stability principle that occurs for transcritical bifurcations [7].

Theorem 1 applies to the matrix equation (1.1) with $P(\hat{x}) = \lambda Q(\hat{x})$ where $\lambda = r(\hat{0})$ is the dominant eigenvalue of the inherent projection matrix $P(\hat{0})$.

The direction of bifurcation in (c), and hence the stability of the continuum near bifurcation, is determined by the sign of the quantity

$$\kappa \triangleq -\hat{w}^T \left[\nabla_{\hat{x}}\, p_{ij}(\hat{0})\hat{v}\right] \hat{v} \tag{1.4}$$

([3], Theorem 1.2.5). Here the superscript "T" denotes transpose and the gradient $\nabla_{\hat{x}}$ of $p_{ij}(\hat{x})$ with respect to $\hat{x}$ is a row m-vector. The vectors $\hat{w}^T$ and $\hat{v}$ are the (positive) left and right eigenvectors of $P(\hat{0})$ associated with the dominant eigenvalue 1, normalized so that $\hat{w}^T\hat{v} = 1$. If κ is negative, the bifurcation is to the right and, by Theorem 1, is therefore stable. If κ is negative, then the bifurcation is to the left and unstable.

The most common assumption made in population models is that density effects are negative feedback effects, i.e., the derivatives appearing in the gradients $\nabla_{\hat{x}}\, p_{ij}$ are negative (or zero). Clearly this implies $\kappa > 0$ and a stable bifurcation to the right. Only if sufficiently large positive feedbacks occur (i.e., there is at least one positive derivative of sufficient magnitude from one of the gradients $\nabla_{\hat{x}}\, p_{ij}(\hat{0})$) will an unstable bifurcation to the left occur. A positive feedback term is called an Allee effect in population biology. In other words, Allee effects of sufficient magnitude lead to unstable bifurcations to the left. In the absence of Allee effects, the bifurcation is to the right and hence stable.

The continuum C in Theorem 1 in known to exist globally in the sense that it connects to the boundary on which the matrix model is defined, i.e., it connects to the set $\{+\infty\} \times \left(\partial\Omega \cap R_+^m\right)$, where $\partial\Omega$ denotes the boundary of Ω (Theorem 1.2.4 in [3]). In most applications, the nonlinearities in (1.2) are defined on the closure of the positive cone, i.e., $\bar{R}_+^m \subset \Omega$ in H1. In this case, along the continuum of equilibrium pairs $(\lambda, \hat{x})$ either the component λ is unbounded or the magnitude $|\hat{x}|$ is unbounded in R_+^1 (or both). In the former case, there exists at least one non-extinction equilibrium from each $\lambda > 1$. In specific applications, one can often determine which of these properties the equilibrium pairs possess by a careful consideration of the equilibrium equations.

2 Darwinian Matrix Models

In [10] Vincent and Brown develop a theory that extends population dynamic models, and in particular matrix models, to include the dynamics of an evolving (mean) phenotypic trait (that possesses a heritable component) under the influence of natural selection. Under the assumption that the entries in the projection matrix P depend on such a trait, as quantified by a scalar u, we write $P = P(\hat{x}, u)$ and $r = r(\hat{x}, u)$. The so-called Darwinian dynamics of $\hat{x}$ and u are described by the equations [10]

$$\hat{x}(t+1) = P(\hat{x}(t), u(t))\hat{x}(t) \tag{2.1a}$$

$$u(t+1) = u(t) + \sigma^2 \left.\frac{r_u(\hat{x}, u)}{r(\hat{x}, u)}\right|_{(\hat{x},u)=(\hat{x}(t),u(t))} . \tag{2.1b}$$

Here r_u denotes the partial derivative of r with respect to u. The quantity σ^2 is the variance of the trait (from its mean u) that occurs in the population at each time. It is therefore a measure of the speed of evolution.

When there is no evolution $\sigma^2 = 0$, the Darwinian model (2.1) reduces to the population dynamic model (1.1) in which the trait is fixed, say $u(t) \equiv u^*$. In this case, Theorem 1 applies with $P(\hat{x}) = \lambda Q(\hat{x}, u^*)$ and $\lambda = r\left(\hat{0}, u^*\right)$. In this section we extend Theorem 1 to the Darwinian model (2.1) when evolution does occur ($\sigma^2 > 0$).

We make the following assumptions concerning the projection matrix $P(\hat{x}, u) = \left(p_{ij}(\hat{x}, u)\right)$. Here U denotes an open interval in R^1.

$$\text{H2:}\quad \begin{cases} p_{ij} \in C^2\left(\Omega \times U \to \bar{R}^1_+\right) \\ \text{For } u \in U \text{ the only } \hat{x} \in \bar{R}^m_+ \text{ satisfying } P(\hat{x},u)\hat{x} = \hat{0} \text{ is } \hat{x} = \hat{0} \\ P(\hat{x},u) \text{ is primitive for } (\hat{x},u) \in \bar{R}^m_+ \times R^1. \end{cases}$$

We define a *critical trait value* $u = u^* \in U$ to be one for which $r_u(\hat{0},u^*) = 0$ and let $\lambda \triangleq r(\hat{0},u^*)$ denote the dominant eigenvalue of $P(\hat{0},u^*)$. The quantity λ is the inherent growth rate of the population dynamic equation (2.1a) when the trait u is held fixed at u^*. We normalize the entries in the projection matrix P to λ so that $P = \lambda Q$ and re-write the Darwinian equations (2.1) as

$$\hat{x}(t+1) = \lambda Q(\hat{x}(t),u(t))\hat{x}(t) \tag{2.2a}$$

$$u(t+1) = u(t) + \sigma^2 \frac{r_u(\hat{x}(t),u(t))}{r(\hat{x}(t),u(t))}. \tag{2.2b}$$

The matrix $Q(\hat{x},u)$ satisfies H2. The dominant eigenvalue of $Q(\hat{0},u^*)$ is 1.

When $\sigma^2 > 0$, we call $(\lambda,(\hat{x},u)) \in R^1 \times (\Omega \times U)$ an *equilibrium pair* of the Darwinian matrix model (2.2) if

$$\hat{x} = \lambda Q(\hat{x},u)\hat{x} \tag{2.3a}$$

$$0 = r_u(\hat{x},u). \tag{2.3b}$$

Note that if $u^* \in U$ is a critical trait value, then $\left(\lambda,(\hat{0},u^*)\right)$ is an *extinction equilibrium pair* of (2.2) for all values of λ.

We say an equilibrium pair $(\lambda,(\hat{x},u))$ is *positive* if $\hat{x} \in R^m_+$, and we say it is *stable* if $(\hat{x},u)$ is (locally asymptotically) stable as an equilibrium of the Darwinian equations (2.1). To investigate the stability of an equilibrium we calculate the eigenvalues of the Jacobian

$$\mathcal{J}(\lambda,\hat{x},u) = \begin{pmatrix} J(\hat{x},u) & \lambda Q_u(\hat{x},u)\hat{x} \\ \sigma^2 \nabla_{\hat{x}} \frac{r_u(\hat{x},u)}{r(\hat{x},u)} & 1 + \sigma^2 \frac{\partial}{\partial u}\frac{r_u(\hat{x},u)}{r(\hat{x},u)} \end{pmatrix} \tag{2.4}$$

where $J(\hat{x},u)$ is the Jacobian of $\lambda Q(\hat{x},u)$ with respect to $\hat{x}$. For the extinction equilibrium pair $(\lambda,(\hat{x},u)) = \left(\lambda,(\hat{0},u^*)\right)$ we have

$$\mathcal{J}\left(\lambda,\hat{0},u^*\right) = \begin{pmatrix} J(\hat{0},u^*) & \hat{0} \\ \sigma^2 \nabla_{\hat{x}} \frac{r_u(\hat{x},u)}{r(\hat{x},u)}\Big|_{(\hat{x},u)=(\hat{0},u^*)} & 1 + \sigma^2 \frac{\partial}{\partial u}\frac{r_u(\hat{x},u)}{r(\hat{x},u)}\Big|_{(\hat{x},u)=(\hat{0},u^*)} \end{pmatrix}. \tag{2.5}$$

Note that $J(\hat{0},u^*)$ is the Jacobian, with respect to $\hat{x}$, of the population dynamic component (2.2a) of the Darwinian model when the trait u is held fixed at u^* (in other words, when $u = u^*$ and no evolution occurs). The $m+1$ eigenvalues of $\mathcal{J}\left(\lambda,\hat{0},u^*\right)$ are the m eigenvalues of $J(\hat{0},u^*)$ and

$$1 + \sigma^2 \frac{\partial}{\partial u}\frac{r_u(\hat{x},u)}{r(\hat{x},u)}\Big|_{(\hat{x},u)=(\hat{0},u^*)} = 1 + \sigma^2 r_{uu}(\hat{0},u^*).$$

By definition λ is the (strictly) dominant eigenvalue of $J(\hat{0},u^*)$. This leads to the following result.

Theorem 2. Assume H2 and that $u^* \in U$ is a critical trait. For $\lambda \in R^1_+$ the extinction equilibrium pair $(\lambda, (\hat{0}, u^*))$ is unstable if $r_{\mathrm{uu}}(\hat{0}, u^*) > 0$. If $r_{\mathrm{uu}}(\hat{0}, u^*) < 0$, then the extinction equilibrium pair $(\lambda, (\hat{0}, u^*))$ is

(a) unstable if $\lambda > 1$

(b) stable if $\lambda < 1$ provided the speed of evolution σ^2 is sufficiently small, specifically if

$$\sigma^2 < -\frac{2}{r_{\mathrm{uu}}(\hat{0}, u^*)}. \tag{2.6}$$

We point out that the derivation of the Darwinian equation (2.1b) (or (2.2b)) requires that σ^2 is small [10], so that this requirement in part (b) is not restrictive.

3 A Bifurcation Theorem

In Theorem 2, the extinction equilibrium loses stability as λ increases through 1 provided $r_{uu}(\hat{0}, u^*) < 0$, i.e., provided $r(\hat{0}, u)$ has a local maximum as a function of the trait u at the critical trait value $u = u^*$. Since this destabilization occurs because an eigenvalue of the Jacobian leaves the unit circle at 1, we expect that there is an equilibrium bifurcation at $\lambda = 1$. We investigate this possibility by making use of Theorem 1.

We assume that the equilibrium equation (2.3b) can be solved for u as a function of $\hat{x}$.

$$\text{H3a:} \quad \begin{cases} \text{Let } u^* \in U \text{ be a critical trait. Assume there exists a function} \\ \upsilon \in C^2(N, U) \text{ such that } r_u(\hat{x}, \upsilon(\hat{x})) = 0, \ \upsilon(\hat{0}) = u^*, \text{ where} \\ N \subset R^m \text{ is an open neighborhood of } \hat{0}. \end{cases}$$

The following assumption is (by the implicit function theorem) sufficient to guarantee that H3a holds:

H3b: Let $u^* \in U$ be a critical trait such that $r_{uu}(\hat{0}, u^*) \neq 0$.

Under H3a the equilibrium equations (2.3) reduce to

$$\hat{x} = \lambda Q(\hat{x}, \upsilon(\hat{x}))\hat{x} \tag{3.1}$$

to which Theorem 1 applies with $Q(\hat{x})$ and Ω replaced by $Q(\hat{x}, \upsilon(\hat{x}))$ and N respectively. The bifurcating continuum C of positive equilibrium pairs $(\lambda, \hat{x})$ of this equilibrium equation guaranteed by Theorem 1(b) produces a continuum $\mathfrak{C} = \{(\lambda, (\hat{x}, u)) \mid (\lambda, \hat{x}) \in C, u = \upsilon(\hat{x})\}$ of positive equilibrium pairs of the Darwinian model (2.1). This proves part (a) of the following result.

Theorem 3. Assume $u^* \in U$ is a critical trait. Assume H2 and H3a.

(a) There exists a continuum $\mathfrak{C}$ of (positive) equilibrium pairs $(\lambda, (\hat{x}, u)) \in R^1_+ \times \left(R^m_+ \times U\right)$ of (2.1) that contains the extinction pair $(1, (\hat{0}, u^*))$ in its closure.

Suppose the stronger assumption H3b holds.

(b) If $r_{uu}(\hat{0}, u^*) > 0$, then near the bifurcation point the positive equilibrium pairs are unstable.

(c) Suppose $r_{uu}(\hat{0},u^*) < 0$ and σ^2 is small (i.e., (2.6) holds). Near the bifurcation point the positive equilibrium pairs are stable if the bifurcation is to the right, i.e., if

$$\kappa^* \triangleq -\hat{w}^T \left[\nabla_{\hat{x}}\, p_{ij}(\hat{0},u^*)\hat{v}\right] \hat{v} > 0 \tag{3.2}$$

and are unstable if the bifurcation is to the left, i.e., if $\kappa^* < 0$.

Proof. We have only parts (b) and (c) left to prove. Near the bifurcation point $(\lambda,(\hat{x},u)) = \left(1,\left(\hat{0},u^*\right)\right)$ the smoothness assumption H2 guarantees that we can parameterize the bifurcating equilibria :

$$\begin{aligned} \hat{x}(\varepsilon) &= \hat{v}\varepsilon + O(\varepsilon^2) \\ u(\varepsilon) &= \upsilon(\hat{x}(\varepsilon)) = u^* + u_1\varepsilon + O(\varepsilon^2) \\ \lambda(\varepsilon) &= 1 + \kappa^*\varepsilon + O(\varepsilon^2) \end{aligned} \tag{3.3}$$

for small positive $\varepsilon \gtrapprox 0$ [3]. Here $\hat{v}$ is a positive right eigenvector of $P(\hat{0},u^*)$ associated with the dominant eigenvalue 1. We obtain the formula

$$u_1 = -\frac{\nabla_{\hat{x}} r_u(\hat{0},u^*)\hat{v}}{r_{uu}(\hat{0},u^*)} \tag{3.4}$$

from a differentiation of $r_u(\hat{x}(\varepsilon),u(\varepsilon)) = 0$ with respect to ε followed by an evaluation at $\varepsilon = 0$. The parameterization (3.3) allows us, in turn, to parameterize the Jacobian $\mathcal{J}(\lambda(\varepsilon),\hat{x}(\varepsilon),u(\varepsilon))$ and its eigenvalues. At $\varepsilon = 0$ the spectrum of the Jacobian (2.5) are the eigenvalues of $J(\hat{0},u^*)$ and $1+\sigma^2 r_{uu}(\hat{0},u^*)$. By continuity, as $\varepsilon \to 0$ the spectrum of $\mathcal{J}(\lambda(\varepsilon),\hat{x}(\varepsilon),u(\varepsilon))$ approaches that of $\mathcal{J}\left(1,\hat{0},u^*\right)$. Thus, if $r_{uu}(\hat{0},u^*) > 0$, the Jacobian $\mathcal{J}(\lambda(\varepsilon),\hat{x}(\varepsilon),u(\varepsilon))$ has an eigenvalue greater than 1 for $\varepsilon \gtrapprox 0$ and, as a result, the positive equilibria are unstable. This proves part (b).

If, on the other hand $r_{uu}(\hat{0},u^*) < 0$ and (2.6) holds, then 1 is the dominant eigenvalue of $\mathcal{J}\left(1,\hat{0},u^*\right)$, since by construction 1 is the dominant eigenvalue of $J(\hat{0},u^*)$. It is thus unclear whether the eigenvalue $\mathcal{J}(\lambda(\varepsilon),\hat{x}(\varepsilon),u(\varepsilon))$ that approaches 1 does so from above or below. To answer this question we calculate the sign of the coefficient μ_1 in the expansion

$$\mu(\varepsilon) = 1 + \mu_1\varepsilon + O(\varepsilon^2)$$

of the dominant eigenvalue of $\mathcal{J}(\lambda(\varepsilon),\hat{x}(\varepsilon),u(\varepsilon))$. Near the bifurcation point the positive equilibrium pairs are stable if $\mu_1 < 0$ and unstable if $\mu_1 > 0$.

We can use a standard perturbation (Lyapunov-Schmidt) approach to calculate a formula for μ_1. We make use of the expansions (3.3) and of the $(m+1)$-column eigenvector

$$\hat{V}(\varepsilon) = \hat{V}_0 + \hat{V}_1\varepsilon + O(\varepsilon^2)$$

associated with $\mu(\varepsilon)$ in the equation

$$\mathcal{J}(\lambda(\varepsilon),\hat{x}(\varepsilon),u(\varepsilon))\,\hat{V}(\varepsilon) = \mu(\varepsilon)\hat{V}(\varepsilon). \tag{3.5}$$

First, setting $\varepsilon = 0$ in (3.5) we obtain

$$\begin{pmatrix} J(\hat{0},u^*) & \hat{0} \\ \sigma^2 \nabla_{\hat{x}} \frac{r_u(\hat{x},u)}{r(\hat{x},u)}\Big|_{(\hat{x},u)=(\hat{0},u^*)} & 1+\sigma^2 r_{uu}(\hat{0},u^*) \end{pmatrix} \hat{V}_0 = \hat{V}_0$$

and hence

$$\hat{V}_0 = \begin{pmatrix} \hat{v} \\ -\frac{1}{r_{uu}(\hat{0},u^*)} \nabla_{\hat{x}} \frac{r_u(\hat{x},u)}{r(\hat{x},u)}\Big|_{(\hat{x},u)=(\hat{0},u^*)} \hat{v} \end{pmatrix}.$$

We note in passing that the left eigenvector

$$\hat{W}_0 = \begin{pmatrix} \hat{w} \\ 0 \end{pmatrix}$$

satisfies

$$\hat{W}_0^T \hat{V}_0 = \hat{w}^T \hat{v} = 1. \tag{3.6}$$

Differentiating (3.5) with respect to ε and setting $\varepsilon = 0$, we obtain (after some algebraic re-arrangement)

$$\left(\mathcal{J}\left(1,\hat{0},u^*\right) - I\right) \hat{V}_1 = \mu_1 \hat{V}_0 - \frac{d}{d\varepsilon} \mathcal{J}\left(\lambda(\varepsilon),\hat{x}(\varepsilon),u(\varepsilon)\right)\Big|_{\varepsilon=0} \hat{V}_0$$

where I is the $(m+1)\times(m+1)$ identity matrix. This equation is solvable for $\hat{V}_1$ if and only if the right hand side is orthogonal to $\hat{W}_0$, a fact that together with the orthogonality condition (3.6), implies

$$\mu_1 = \hat{W}_0^T \frac{d}{d\varepsilon} \mathcal{J}\left(\lambda(\varepsilon),\hat{x}(\varepsilon),u(\varepsilon)\right)_{\varepsilon=0} \hat{V}_0.$$

What remains is a calculation of the matrix $\frac{d}{d\varepsilon}\mathcal{J}\left(\lambda(\varepsilon),\hat{x}(\varepsilon),u(\varepsilon)\right)\big|_{\varepsilon=0}$ from (2.4) and (3.3). While tedious, this is a straightforward calculation and we omit the details. Since it is only the sign of μ_1 that we wish to know, it is enough to say that the result of the calculation is

$$\mu_1 = -k^2 \kappa^*$$

where k^2 is a positive quantity and, as a result, μ_1 and κ^* have opposite signs. Thus, if $\kappa^* > 0$ we conclude the bifurcation is to the right and the positive equilibria are stable. If, on the other hand, $\kappa^* < 0$ then the bifurcation is to the left and the positive equilibria are unstable. □

In the remarks following Theorem 1, we noted that the bifurcating continuum C connects to the boundary on which the matrix model was defined. Similarly, the continuum of equilibrium pairs of the Darwinian matrix model (2.3) connects to the set of $\{\infty\} \times \left(\left(\partial N \cap R_+^m\right) \times \partial U\right)$. If $r = \upsilon(\hat{x})$ in H3a is defined on the closure of the positive cone, i.e., if $\bar{R}_+^m \subset N$, then along the continuum $\mathfrak{C}$ the component λ or the equilibrium magnitudes $|\hat{x}|$ are unbounded or the trait u approaches the boundary of U (or both). A careful consideration of the equilibrium equations in specific applications can often determine which of these alternatives occurs. It can be of interest to know that the component λ is unbounded along the continuum because this implies the existence of at least one non-extinction equilibrium for each $\lambda > 1$.

Suppose $(\lambda_e, (\hat{x}_e, u_e))$ is an equilibrium pair from the continuum $\mathfrak{C}$ with to $\lambda_e \approx 1$. From the equilibrium equations and assumption H2 follow $r(\hat{x}_e, u_e) = 1$ and $r_u(\hat{x}_e, u_e) = 0$. If $r_{uu}(\hat{0}, u^*) < 0$ (so that an exchange of stability bifurcation occurs by Theorem 3), then $r_{uu}(\hat{x}_e, u_e) < 0$ near the bifurcation point. If follows that in this case the trait component $u = u_e$ from a bifurcating non-extinction equilibrium maximizes the growth rate $r(\hat{x}_e, u)$ (at 1) as a function of u while holding $\hat{x} = \hat{x}_e$ fixed.

As a final comment, we point out that in the event of a bifurcation right bifurcation at $\lambda = 1$, the stability of the bifurcating non-extinction equilibria is guaranteed by Theorem 3 only near the bifurcation point, i.e., for $\lambda \gtrapprox 1$ and equilibria $(\hat{x}, u)$ near $(\hat{0}, u^*)$. Away from the bifurcating point, these equilibria might not be stable. Indeed, the non-extinction equilibria might, depending on the nature of the nonlinearities in the Darwinian model, destabilize and result in periodic or chaotic oscillations. In the second application in the following section, we illustrate this point.

4 Applications

4.1 A Juvenile-Adult Model

The matrix equation (1.1) with the 2×2 projection matrix

$$P(\hat{x}) = \begin{pmatrix} 0 & bf(\hat{x}) \\ s_1 & s_2 \end{pmatrix} \tag{4.1}$$

models the dynamics of a population vector $\hat{x} = \mathrm{col}(x_1, x_2)$ consisting of juveniles x_1 and adults x_2 in which the unit of time equals the length of the juvenile maturation period. The number s_1 is the juvenile survival probability (per unit time) and s_2 is the adult survival probability (per unit time). The term $bf(\hat{x})$ is the recruitment rate (the number of surviving offspring per adult per unit time) when the population vector is $\hat{x}$. Here we normalize the population density dependent factor f so that $f(\hat{0}) = 1$. In this way, the constant $b > 0$ is the inherent recruitment rate, i.e., the recruitment rate when population numbers are low (technically, $\hat{x} = \hat{0}$).

In this example we consider the case when recruitment processes bf depend on the trait u, but the survivorships s_i do not:

$$P(x, u) = \begin{pmatrix} 0 & b(u)f(\hat{x}, u) \\ s_1 & s_2 \end{pmatrix}. \tag{4.2}$$

The assumption H2 holds if

$$\text{H4:} \quad \begin{cases} f \in C^2(\Omega \times U \to (0, 1]), & b \in C^2\left(U \to R^1_+\right) \\ 0 < s_i \leq 1, & 0 < s_2 < 1. \end{cases}$$

From

$$r(\hat{x}, u) = \frac{1}{2}s_2 + \frac{1}{2}\sqrt{4s_1 b(u) f(\hat{x}, u) + s_2^2}$$

we calculate

$$r_u(\hat{0},u) = \frac{s_1 b'(u)}{\sqrt{4s_1 b(u) + s_2^2}}.$$

Thus, critical traits $u = u^*$ are the critical points of $b(u)$, the inherent birth rate, i.e., u^* must satisfy $b'(u^*) = 0$. At such a critical trait, another differentiation yields

$$r_{uu}(0,u^*) = \frac{s_1 b''(u^*)}{\sqrt{4s_1 b(u^*)) + s_2^2}}.$$

Finally, we assume

$$f_{x_i}(\hat{0},u) < 0 \text{ for } u \in U \text{ and either } i = 1 \text{ or } 2 \text{ (or both).}$$

Note that this implies $\kappa^* > 0$.

From Theorem 3 we obtain the following results for the Darwinian juvenile-adult matrix model (2.1) with projection matrix (4.2) under assumption H4. Here

$$\lambda = \frac{1}{2}s_2 + \frac{1}{2}\sqrt{4s_1 b(u^*) + s_2^2}.$$

(1) Critical traits u^* are critical points of the inherent birth rate $b(u)$.
If $b''(u^*) \neq 0$, then a continuum of positive equilibrium pairs
$(\lambda, (\hat{x},u)) \in R_+^1 \times (R_+^2 \times U)$ bifurcates from $(1,(\hat{0},u^*))$.
(2) If $b''(u^*) < 0$, then the extinction equilibrium $(\hat{0},u^*)$ loses stability
as λ increases through 1 the positive equilibria $(\hat{x},u)$ as stable for $\lambda \gtrapprox 1$.
(3) If $b''(u^*) > 0$, then both the extinction equilibria and the bifurcating
positive equilibria are unstable for $\lambda \approx 1$.

Note that the fundamental exchange of stability from extinction to a stable non-extinction (positive) equilibrium occurs in an evolutionary context for the Darwinian model (4.2) at critical trait values u^* that maximize the inherent birth rate $b(u)$. At a minimum of the birth rate, both equilibria are unstable and the nature of the long term asymptotic dynamics remains an open question.

As an illustration consider an inherent birth rate that is normally distributed as a function of the trait u and density factor f that has a Ricker form:

$$b(u) = b_m \exp(-u^2/2b_v)$$

$$f(\hat{x},u) = \exp(-c_1(u)x_1 - c_2(u)x_2), \quad c_i(u) \geq 0, \quad c_1^2(0) + c_2^2(0) \neq 0.$$

Then the only critical point is $u^* = 0$ and the results above imply that non-extinction equilibria bifurcate from the extinction equilibrium pair $((x_1,x_2),u) = ((0,0),0)$ at $\lambda = 1$ where

$$\lambda = \frac{1}{2}s_2 + \frac{1}{2}\sqrt{4s_1 b_m + s_2^2}.$$

The bifurcation is to the right and these equilibria are stable at least for $\lambda \gtrapprox 1$.

Note that the inter-class competition coefficients $c_i(u)$ play no role in these conclusions. This is because they occur in higher order terms near the bifurcation point. They do, however, determine interesting properties of the bifurcating non-extinction equilibria.

For example, a calculation using (3.4) shows

$$u_1 = -\frac{\sqrt{4s_1 b_m + s_2^2}}{s_2 b_v}\left(c_1'(0)v_1 + c_2'(0)v_2\right)$$

where $\hat{v} = \mathrm{col}(v_1, v_2)$ is a right, positive eigenvector of $P(\hat{0}, 0)$, say $\hat{v} = \mathrm{col}(1, s_1/(1-s_2))$. Thus, along the bifurcating continuum, near the bifurcation point, the trait components of the equilibria satisfy

$$\begin{aligned} u < 0 \quad &\text{if} \quad c_1'(0) + c_2'(0)\frac{s_1}{1-s_2} > 0 \\ u > 0 \quad &\text{if} \quad c_1'(0) + c_2'(0)\frac{s_1}{1-s_2} < 0. \end{aligned}$$

This has the following interpretation. The quantity

$$\psi(u) \triangleq c_1(u) + c_2(u)\frac{s_1}{1-s_2}$$

is a measure of the total competitive intensity within the population, weighted according to the expected amount of time a juvenile is expected to spend in each age class during its life. Then the trait components of the equilibria satisfy

$$\begin{aligned} u < 0 \quad &\text{if} \quad \psi'(0) > 0 \\ u > 0 \quad &\text{if} \quad \psi'(0) < 0. \end{aligned}$$

Since the normally distributed inherent rate $b(u)$ is increasing for $u < 0$ and decreasing for $u > 0$, we see that the trait component u near bifurcation will be negative if $\psi'(0) > 0$, which implies at this trait that $\psi(u)$ is increasing. That is to say, both $b(u)$ and $\psi(u)$ have the same monotonicity at the equilibrium trait component. This represents a trade-off in that an increase of the trait from this equilibrium value will increase the birth rate $b(u)$ but decrease the density factor $f(\hat{x}, u)$. (This is in contrast to what happens for $u > 0$ were both $b(u)$ and $f(\hat{x}, u)$ to decrease.) A similar analysis of the case $\psi'(0) < 0$ leads to the same conclusion, namely, that the non-extinction equilibria occur with trait components at which *a trade-off occurs* between the inherent birth rate and the effect of density on recruitment.

4.2 The LPA Model and the Evolution of a Polymorphism

In [9] a Darwinian version of the three life-cycle stage matrix model is used to describe the observed population dynamics and evolution of a polymorphism in a controlled, laboratory experiment involving the beetle *Tribolium castaneum* [5]. In that experiment cultures of *T. castaneum* homozygous for corn oil sensitivity were perturbed by adding homozygous wild type individuals. The observed data included population densities of larvae, pupae, and adults as well as allele frequencies obtained from genetically perturbed cultures.

Rael et al. [9] use a Darwinian version of the LPA model [4]. The LPA model (which has been widely successful in describing and predicting the population dynamics of *Tribolium* [2]) is a $m = 3$ dimensional matrix model with projection matrix

$$P(\hat{x}) = \begin{pmatrix} 0 & 0 & b\exp(-c_{el}x_1 - c_{pa}x_3) \\ 1-\mu_l & 0 & 0 \\ 0 & \exp(-c_{pa}x_3) & 1-\mu_a \end{pmatrix}$$

in which the components of $\hat{x} = \mathrm{col}(x_1, x_2, x_3)$ are the numbers of larval, pupal, and adult individuals.

Sensitivity to corn oil in *T. castaneum* is determined genetically by a single locus with two alleles, a wild and a corn oil sensitivity allele. This sensitivity, it turns out, affects the demographic parameters b, μ_l and μ_a (larva recruitment, larval death, and adult death rates respectively), but not the (cannibalism) coefficients c_{el}, c_{pa} and c_{pa}. Taking the mean frequency of the wild type allele as the trait u in a Darwinian model, Rael et al. use data to determine the following relationships:

$$\begin{aligned} b(u) &= -18v^2 + 21v + 11 \\ \mu_l(u) &= 0.10v^2 - 0.13v + 0.51 \\ \mu_a(u) &= 0.10v^2 - 0.13v + 0.11. \end{aligned} \tag{4.3}$$

Using a computer algebra program, we can calculate the dominant eigenvalue $r(\hat{x}, u)$ of

$$P(\hat{0}, u) = \begin{pmatrix} 0 & 0 & b(u) \\ 1-\mu_l(u) & 0 & 0 \\ 0 & 1 & 1-\mu_a(u) \end{pmatrix}$$

and use the result, together with (4.3) to show that $u^* = 0.62415$ is a critical trait at which $r_{uu}(\hat{0}, u^*) = -1.7745 < 0$. According to Theorem 3 a continuum of non-extinction equilibria of the Darwinian LPA model bifurcates from the equilibrium $(\hat{0}, u^*)$ at $\lambda = 1$. Because the exponential nonlinearities in the LPA model are decreasing functions of population densities x_i (i.e., the density effects are negative feedback effects and there are no Allee effects), the bifurcation is to the right and stable. It follows that the bifurcating non-extinction equilibria are stable for at least $\lambda \gtrapprox 1$ and equilibria $(\hat{x}, u)$ near $(\hat{0}, u^*)$.

Note that near bifurcation, the non-extinction equilibrium pairs have traits $u \approx u^* = 0.62415$. This means that at equilibrium the population is polymorphic with a wild type gene frequency of approximately 62%.

Simulations of the Darwinian LPA model verify the existence and stability of these non-extinction equilibria for $\lambda > 1$ close to 1. For the specific parameterization (4.3), a calculation shows that $\lambda = r(\hat{0}, u^*) = 2.4490$. However, simulations also show that the non-extinction equilibrium is unstable [9] for this value of λ because a period doubling bifurcation occurs along the equilibrium continuum. In fact, 2-periodic oscillations, that are well approximated by the model simulation, are observed in the population data x_i. On the other hand, the model predicted 2-periodic oscillations in the trait u have an amplitude around a mean near $u^* = 0.62415$ that is too small to be observed in the genetic data, which in fact are well approximated by u^* [9].

5 Concluding Remarks

Theorem 1 is a basic theorem in the theory of structured population dynamics in the sense that it deals with the fundamental question of extinction versus survival as a function of the population's inherent growth rate $\lambda = r(\hat{0})$. The theorem treats this basic biological problem as a bifurcation question concerning the general matrix model (1.1) for the dynamics of a structured population. The destabilization of the extinction equilibrium as λ increases through 1 results in the bifurcation of a (global) continuum of positive equilibria whose stability near the bifurcation point depends on the direction of bifurcation.

Theorems 2 and 3 provide an extension of this bifurcation theory to an evolutionary context. Evolutionary game theory methods provide the Darwinian matrix model (2.1) when the population dynamic projection matrix P now depends on a (mean) phenotypic trait that is subject to evolution by natural selection [10]. The loss of stability of the extinction equilibrium and possibility of the bifurcation of positive equilibria can occur only at critical values $u = u^*$ of the phenotypic trait, i.e., at trait values where the inherent growth rate $r(\hat{0}, u)$ has a critical value. Theorems 2 and 3 assert, among other things, that a bifurcation of positive equilibria will occur, and their stability will depend on the direction of bifurcation, provided $r_{uu}(\hat{0}, u) < 0$. In this case, which implies that the inherent growth rate $r(\hat{0}, u)$ has a local maximum at the critical trait $u = u^*$, the bifurcation result is exactly analogous to the non-evolutionary case in Theorem 1.

Evolutionary game theory was developed in the context of the concept of an evolutionary stable strategy (ESS). This concept involves the issue of additional species interacting and possibly invading a resident species. We do not consider this question here, except to say that the condition $r_{uu}(\hat{x}_e, u_e) < 0$ which holds positive equilibria near the bifurcation point is a necessary condition of an ESS (a fact known as the ESS Maximum Principle [10]). See [11].

When $r_{uu}(\hat{0}, u) > 0$ we see from Theorems 2 and 3 that both the extinction equilibrium and the positive equilibria near the bifurcation point are unstable. What the attractor is, in this case, remains an open question. In any case, our results show that it is not an ESS (since the ESS Maximum Principle fails to hold).

We emphasize that the stability and direction of bifurcation result in Theorem 3 is only valid in general near the bifurcation point. One expects (as illustrated in section 4.2), from the well known propensity for difference equations to exhibit non-equilibrium and even chaotic dynamics, that depending on the properties of the nonlinearities in the projection matrix P secondary bifurcations can occur as the result of the destabilization of the positive equilibria as one moves along the continuum away from the bifurcation point.

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The formula for κ^* on page 6 should be

$$\kappa^* = -w^T \left[\nabla_x^0 q_{ij} v\right] v + \frac{\nabla_x^0 r_u v}{r_{uu}^0} w^T \left[\partial_u^0 q_{ij}\right] v > 0 \tag{3.2}$$