Nonlinear Dynamics and Systems Theory, **10** (2) (2010) 103–116

On the Dynamics of a Class of Darwinian Matrix Models [†]

J. M. Cushing [*]

Department of Mathematics and the Interdisciplinary Program in Applied Mathematics
University of Arizona, 617 N. Santa Rita, Tucson, AZ 85721 USA

Received: November 15, 2009; Revised: March 24, 2010

Abstract: Using the methodology of evolutionary game theory (EGT), I study a class of Darwinian matrix models which are derived from a class of nonlinear matrix models for structured populations that are known to possess stable (normalized) distributions. Utilizing the limiting equations that result from this ergodic property, I prove extinction and stability results for the limiting equations of the EGT versions of these kinds of structured population models. This is done in a bifurcation theory context. The results provide conditions sufficient for a branch of non-extinction equilibria to bifurcate from the branch of extinction equilibria. When this bifurcation is supercritical (explicit criteria are given), these equilibria are stable and represent stable non-extinction equilibria (which are also candidate ESS equilibria). These kinds of matrix models are motivated by applications to size structured populations, and I give an application of this type. Besides illustrating the formal theory, this application shows the importance of trade-offs among life history parameters that are necessary for the existence of an evolutionarily stable equilibrium.

Keywords: *structured population dynamics; nonlinear matrix model; stable distribution; limiting equation; evolutionary game theory; bifurcation; equilibrium, stability.*

Mathematics Subject Classification (2000): 92D15, 92D25, 39A60.

1 Introduction

Nonlinear matrix models are widely used to describe and study the discrete time dynamics of structured populations. These models take the form

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

[†] Research partially supported by NSF grant DMS 0917435.

[*] Corresponding author: `mailto:cushing@math.arizona.edu`

where $P(x)$ is an $m \times m$ non-negative projection matrix that is assumed primitive (irreducible and possessing a strictly positive dominant eigenvalue) for each (column vector) $x \in \Omega$, where Ω is an open set in R^m containing the origin. Here $x(t)$ is a demographic distribution vector at time $t \in Z_+ = \{0, 1, 2, \cdots\}$ that is based on a classification scheme for individuals in the population (chronological age, weight, size, etc.). For more on matrix models in population dynamics see [1, 9, 10].

In general the projection matrix has the form

$$\begin{gathered} P(x) = F(x) + T(x), \\ F(x) = [f_{ij}(x)], \quad T(x) = [s_{ij}(x)], \end{gathered} \tag{2}$$

where $f_{ij} \geq 0$ is the amount (number, density, etc.) of surviving i-class offspring per j-class individual in a unit of time and where s_{ij}, $0 \leq s_{ij} \leq 1$, is the fraction of j-class individuals that survive and move to the i-class over one unit of time [9, 10]. In one type of model that arises in population dynamics and theoretical ecology, the projection matrix also has the form

$$P(x) = a(x)I + b(x)L, \tag{3}$$

where I is the $m \times m$ identity matrix, L is an $m \times m$ constant matrix, and a, b are scalar valued functions of x. For examples see [2, 7, 6, 9, 15], Chapter 17 in [3], Chapter 3 in [5], and Section 3.

For models of the form (3) there exists an asymptotically stable (normalized) distribution vector. This is a consequence of the following theorem.

Theorem 1.1 [2, 7, 9] *Consider the equation* $x(t+1) = (\alpha(t)I + \beta(t)L)\, x(t)$ *where (a)* α, β *are real valued functions for which there exist constants* α_0, β_0 *such that* $0 \leq \alpha(t) \leq \alpha_0$, $0 < \beta_0 \leq \beta(t)$ *for all* $t \in Z_+$; *(b) the* $m \times m$ *constant matrix* L *has a strictly dominant, simple eigenvalue* $\theta > 0$ *with a positive eigenvector* $v \in int\left(R^m_+\right)$. *Suppose* $x(t)$ *is a solution satisfying* $0 \neq x(t) \geq 0$ *for all* $t \in Z_+$ *and* $p(t)$ *is a weighted total population size:*

$$p(t) \doteq \omega \cdot x(t), \quad 0 \neq \omega \in R^m_+.$$

Then

$$\lim_{t \to +\infty} \frac{x(t)}{p(t)} = \frac{v}{\omega \cdot v}. \tag{4}$$

We can apply Theorem 1.1 to solutions of the nonlinear matrix equation (1)-(3) with $\alpha(t) = a(x(t))$ and $\beta(t) = b(x(t))$. We then use (4) to replace $x(t)$ and $x(t+1)$ in (1) by their asymptotic equivalents $p(t)v/\omega \cdot v$ and $p(t+1)v/\omega \cdot v$ and obtain the scalar limiting equation

$$p(t+1) = \left[a\left(\frac{v}{\omega \cdot v}p(t)\right) + b\left(\frac{v}{\omega \cdot v}p(t)\right)\theta\right]p(t)$$

for the total population size $p(t)$. Thus, for these kinds of matrix models, the high dimensional dynamics of the original model are replaced by those of the scalar limiting equation for total population size (which depend on the dominant eigenvalue θ of L), and the asymptotic distribution (4) (calculated from the eigenvector v associated with θ). For applications see Section 3 and [9] (and papers cited therein).

Under the assumption that $P(x)$ is nonnegative and primitive for $x \in \Omega$, it has a strictly dominant eigenvalue $r = r(x) > 0$. It is easy to see that under the assumption (b) in Theorem 1.1

$$r(x) = a(x) + b(x)\theta$$

and as a result the limiting equation can be written as

$$p(t+1) = r\left(\frac{v}{\omega \cdot v} p(t)\right) p(t). \tag{5}$$

As a special case, if $P = P(p)$ and hence $a = a(p)$ and $b = b(p)$ are functions of a weighted total population size p (as they frequently are in applications), the limiting equation is $p(t+1) = \left[a\left(p(t)\right) + b\left(p(t)\right)\theta\right] p(t)$ or

$$p(t+1) = r\left(p(t)\right) p(t).$$

Theorems relating the (equilibrium and cycle) dynamics of the limiting equation to the dynamics of the original matrix model appear in [7].

In their book Vincent and Brown [17] provide a methodology for extending matrix models for structured populations to an evolutionary setting. Their methodology involves a dynamically evolving phenotypic trait, which affects demographic parameters in the entries of the projection matrix and whose dynamics are in turn affected by the population dynamics. Vincent and Brown refer to this coupling of the evolutionary and population dynamics as Darwinian dynamics. Our goal here is to study Darwinian matrix models with projection matrices of the particular form (3) by making use of the ergodic Theorem 1.1 and the resulting limiting equation (5). In Section 2 we study, in the context of bifurcation theory, the existence and stability of both extinction and non-extinction equilibria. Section 3 contains an application to a Darwinian model based on a class of structured models studied in the literature which has historical roots in a seminal paper of Leslie on matrix models in population dynamics [15].

2 Darwinian Matrix Models

Let u denote the mean of a phenotypic trait (with a heritable component) that is subject to natural selection. The Darwinian dynamics associated with a matrix equation are

$$\begin{aligned} x(t+1) &= P(x(t), u(t)) x(t), \\ u(t+1) &= u(t) + \sigma^2 \frac{\partial \ln r\left(x(t), u(t)\right)}{\partial u}, \end{aligned} \tag{6}$$

where $P = P(x, u)$ is now assumed a function of u as well as x and $r = r(x, u)$ is its dominant eigenvalue. Here the constant σ^2 is the variance of the phenotypic trait each point in time; it is a measure of the speed of evolution. Let $\Upsilon \subseteq R^1$ be an open interval. We make the following assumptions:

$$A: \left\{ \begin{array}{l} \textit{The nonnegative, primitive matrix } P(x,u) \textit{ has the form (3)} \\ \textit{with an } m \times m \textit{ constant matrix } L \textit{ and real valued functions} \\ a, b \in C^2\left(\Omega \times \Upsilon \to R^1_+\right) \textit{ that satisfy the following:} \\ \quad \textit{(a) there exist constants } a_0, b_0 \textit{ such that } 0 \le a(x,u) \le a_0, \\ \qquad \textit{and } 0 < b_0 \le b(x,u) \textit{ for } (x,u) \in \Omega \times \Upsilon; \\ \quad \textit{(b) } L \textit{ has a simple, strictly dominant eigenvalue } \theta > 0 \textit{ with a} \\ \qquad \textit{positive eigenvector } v. \end{array} \right.$$

Under assumption A, Theorem 1.1 applies to (6) with $\alpha(t) = a(x(t), u(t))$ and $\beta(t) = b(x(t), u(t))$ and implies that solutions have a stable normalized distribution (4). From

(6) we derive the two scalar equations

$$p(t+1) = \omega \cdot P\left(x(t), u(t)\right) x(t), \tag{7a}$$

$$u(t+1) = u(t) + \sigma^2 \frac{\partial \ln r\left(x(t), u(t)\right)}{\partial u}, \tag{7b}$$

for the dynamics of the total population size $p(t) = \omega \cdot x(t)$ and the mean trait $u(t)$. Replacing $x(t)$ by $vp(t)/\omega \cdot v$, we obtain the limiting equations [7, 14]

$$p(t+1) = r\left(\frac{p(t)}{\omega \cdot v} v, u(t), \theta\right) p(t), \tag{8a}$$

$$u(t+1) = u(t) + \sigma^2 \left. \frac{\partial \ln r\left(x, u, \theta\right)}{\partial u} \right|_{(x,u)=\left(\frac{p(t)}{\omega \cdot v} v, u(t)\right)}, \tag{8b}$$

for $p(t)$ and $u(t)$, where for convenience we have added θ to the argument list in the dominant eigenvalue

$$r(x, u, \theta) \overset{\circ}{=} a(x, u) + b(x, u)\theta \tag{9}$$

of $P(x, u) = a(x, u)I + b(x, u)L$. This system of limiting equations is two dimensional and therefore more analytically tractable than the original $m + 1$ dimensional matrix model (6). We now turn our attention to an analysis of the equilibrium states of this limiting system. We will relate these dynamics to those of the original matrix model in Section 2.3.

2.1 The limiting system: existence of equilibria

The equilibrium equations for (8) are

$$\begin{aligned} p &= r\left(\frac{p}{\omega \cdot v} v, u, \theta\right) p, \\ 0 &= r_u\left(\frac{p}{\omega \cdot v} v, u, \theta\right), \end{aligned}$$

where the subscript u denotes partial differentiation $\partial/\partial u$. We are interested in the existence of two types of equilibria. An *extinction equilibrium* (p, u) of (8) is one in which $p = 0$ and a *non-extinction equilibrium* is one in which $p > 0$.

We are also interested in the stability of these equilibria, when they exist. We refer to a (locally asymptotically) stable equilibrium as an *evolutionarily stable equilibrium.* (In the language of [17] the associated equilibrium trait has convergent stability.) We say that a population whose orbit tends to a stable extinction equilibrium evolves to extinction, while one whose orbits tend to a non-extinction equilibrium evolutionarily persists and equilibrates.

Definition 2.1 A pair u, θ (with $\theta > 0$) is an **extinction pair** if

$$r_u\left(0, u, \theta\right) = a_u\left(0, u\right) + b_u\left(0, u\right)\theta = 0. \tag{10}$$

An extinction pair u^*, θ^* is a **critical extinction pair** if in addition it satisfies $r\left(0, u^*, \theta^*\right) = 1$. That is to say, a critical extinction pair u^*, θ^* satisfies

$$\begin{aligned} r\left(0, u^*, \theta^*\right) &= a\left(0, u^*\right) + b\left(0, u^*\right)\theta^* = 1, \\ r_u\left(0, u, \theta\right) &= a_u\left(0, u^*\right) + b_u\left(0, u^*\right)\theta^* = 0. \end{aligned} \tag{11}$$

Clearly $(p, u) = (0, u)$ is an extinction equilibrium of (8)-(9) (with parameter value θ) if and only if u, θ is an extinction pair. As we will see, critical extinction pairs serve as bifurcation points for the creation of non-extinction equilibria.

The non-extinction equilibrium equations are

$$\begin{aligned} 1 &= r\left(\frac{p}{\omega \cdot v} v, u, \theta\right), \\ 0 &= r_u\left(\frac{p}{\omega \cdot v} v, u, \theta\right). \end{aligned}$$

If u^*, θ^* is a critical extinction pair, the implicit function theorem implies that these equilibrium equations have a solution $(p, u) = (\pi(\theta), \upsilon(\theta))$ for θ near θ^*, where $\pi(\theta), \upsilon(\theta)$ are twice continuously differentiable functions that satisfy $(\pi(\theta^*), \upsilon(\theta^*)) = (0, u^*)$, provided the Jacobian with respect to p and u

$$\begin{pmatrix} \nabla_x r\left(0, u^*, \theta^*\right) \cdot \frac{v}{\omega \cdot v} & 0 \\ \nabla_x r_u\left(0, u^*, \theta^*\right) \cdot \frac{v}{\omega \cdot v} & r_{uu}\left(0, u^*, \theta^*\right) \end{pmatrix}$$

is non-singular at $(p, u) = (0, u^*), \theta = \theta^*$, i.e. provided

$$\delta \circeq \nabla_x r\left(0, u^*, \theta^*\right) \cdot v \neq 0 \quad \text{and} \quad r_{uu}\left(0, u^*, \theta^*\right) \neq 0.$$

This branch of equilibria $(p, u) = (\pi(\theta), \upsilon(\theta))$ consists of non-extinction equilibria $p = \pi(\theta) > 0$ for $\theta > \theta^*$ if $\pi'(\theta) > 0$ or for $\theta < \theta^*$ if $\pi'(\theta^*) < 0$. An implicit differentiation of $1 = r\left(\pi(\theta) v / \omega \cdot v, \upsilon(\theta), \theta\right)$ shows (recall (11))

$$\pi'(\theta^*) = -\frac{\omega \cdot v}{\delta} r_\theta\left(0, u^*, \theta^*\right).$$

Since $r_\theta\left(0, u^*, \theta^*\right) = b\left(0, u^*, \theta^*\right) > 0$, the sign of $\pi'(\theta^*)$ is the opposite of the sign of δ.

Theorem 2.1 *Assume A and that* u^*, $\theta^* > 0$ *is a critical extinction pair (i.e., a pair that satisfies (11)) for which*

$$\begin{aligned} &\delta \circeq \left[\nabla_x a\left(0, u^*\right) + \nabla_x b\left(0, u^*\right) \theta^*\right] \cdot v \neq 0, \\ &a_{uu}\left(0, u^*\right) + b_{uu}\left(0, u^*\right) \theta^* \neq 0. \end{aligned} \tag{12}$$

Then there exists a (twice continuously differentiable) branch of non-extinction equilibria $(p, u) = (\pi(\theta), \upsilon(\theta))$ *for*

$$\begin{aligned} \theta &\gtrapprox \theta^* \quad \textit{if} \quad \delta < 0, \\ \theta &\lessapprox \theta^* \quad \textit{if} \quad \delta > 0, \end{aligned}$$

such that $(\pi(\theta^*), \upsilon(\theta^*)) = (0, u^*)$.

In many applications, the dependency of the projection matrix, and hence a and b, on x is through a dependency on a weighted population size p, i.e., $a(p, u)$ and $b(p, u)$. In that case, $\delta = r_p\left(0, u^*, \theta^*\right) \omega \cdot v$ and the condition $\delta \neq 0$ is equivalent to

$$a_p\left(0, u^*\right) + b_p(0, u^*)\theta^* \neq 0,$$

where a_p and b_p are the partial derivatives of a and b with respect to p.

We can view the existence result in Theorem 2.1 as a bifurcation phenomenon by using θ as a bifurcation parameter. To clarify this, we distinguish two types of extinction pairs.

Definition 2.2 A **type 1 extinction pair** u, θ is one for which

$$b_u(0,u) = a_u(0,u) = 0 \quad \text{and} \quad \theta \in \Upsilon \text{ is arbitrary.}$$

A **type 2 extinction pair** u, θ is one for which

$$b_u(0,u) \neq 0 \quad \text{and} \quad \theta = -\frac{a_u(0,u)}{b_u(0,u)}.$$

Type 1 extinction pairs produce a branch of extinction equilibria $(p,u) = (0,u^*)$ of the limiting system (8) for all values of $\theta \in \Upsilon$ where u^* satisfies $b_u(0,u^*) = a_u(0,u^*) = 0$. The branch of non-extinction equilibria in Theorem 2.1 intersects this branch of extinction equilibria in a transcritical bifurcation at the critical extinction pair $u, \theta = u^*, \theta^*$ where

$$\theta^* = \frac{1 - a(0,u^*)}{b(0,u^*)}. \tag{13}$$

See Figure 1(a,b).

Type 2 extinction pairs produce a branch of extinction equilibria $(p,u) = (0,u)$ for $\theta = -a_u(0,u)/b_u(0,u)$ and those values of u for which $b_u(0,u) \neq 0$. The branch of non-extinction equilibria in Theorem 2.1 intersects this branch of extinction equilibria in a transcritical bifurcation at the critical extinction pair u^*, θ^* value where u^* satisfies

$$-\frac{a_u(0,u^*)}{b_u(0,u^*)} = \frac{1 - a(0,u^*)}{b(0,u^*)}. \tag{14}$$

and θ^* is given by (13). See Figure 1(c,d).

We say that the bifurcation is *supercritical* (or *to the right*) if $\delta < 0$ and *subcritical* (or *to the left*) if $\delta > 0$.

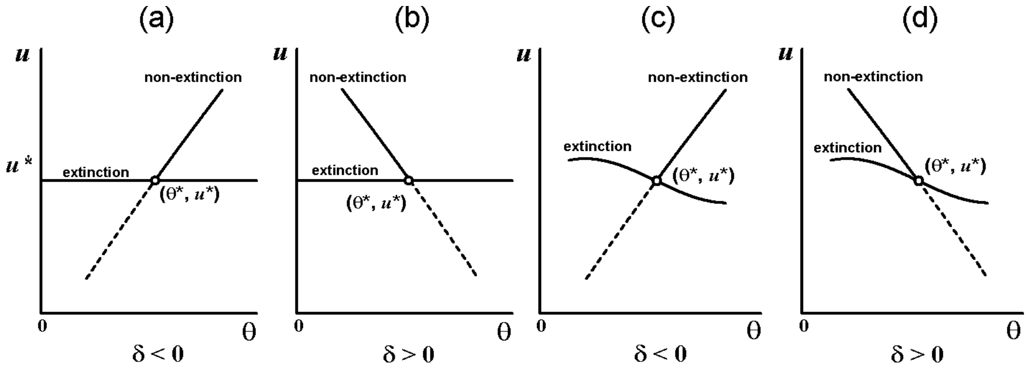

Figure 1. All graphs show intersecting branches of extinction and non-extinction pairs u, θ (which correspond to extinction and non-extinction equilibria of the limiting equations (8) respectively). The dashed lines are pairs that correspond to equilibria with $p < 0$ and therefore are not biologically relevant. The intersection occurs at a critical pair u^*, θ^* with θ^* defined by (13). In graphs (a) and (b) the extinction pairs are of Type 1 and plot as a horizontal straight line where u^* satisfies $b_u(0,u^*) = a_u(0,u^*) = 0$. In graphs (c) and (d) the extinction pairs are of Type 2 and u^* satisfies (14).

2.2 The limiting system: stability of equilibria

The eigenvalues μ_1, μ_2 of the Jacobian of the limiting system (8), which when evaluated at either an extinction or a non-extinction equilibrium has a triangular form (because $r_u\left(\frac{p}{\omega\cdot v}v, u\right)p$ vanishes at either type of equilibrium), are

$$\mu_1 \doteq r\left(\frac{p}{\omega\cdot v}v, u, \theta\right) + p\frac{\nabla_x r\left(\frac{p}{\omega\cdot v}v, u, \theta\right)\cdot v}{\omega\cdot v}, \quad \mu_2 \doteq 1 + \sigma^2 r_{uu}\left(\frac{p}{\omega\cdot v}v, u, \theta\right).$$

For an extinction equilibrium $(p, u) = (0, u)$ these eigenvalues are

$$\mu_1 = r(0, u, \theta), \quad \mu_2 = 1 + \sigma^2 r_{uu}(0, u, \theta).$$

The linearization principle implies the equilibrium is unstable if $r(0, u, \theta) > 1$ or if $r_{uu}(0, u, \theta) > 0$ and is (locally asymptotically) stable if $r(0, u, \theta) < 1$, $r_{uu}(0, u, \theta) < 0$ and $\sigma^2 < -2/r_{uu}(0, u, \theta)$. Note it is necessary for the stability of an extinction equilibrium $(p, u) = (0, u)$ that $r(0, \cdot, \theta)$ have a local maximum at u.

Lemma 2.1 *Assume A and that u, θ is an extinction pair.*
(a) The extinction equilibrium $(0, u)$ of the limiting system (8) is unstable if

$$a(0, u) + b(0, u)\theta > 1 \quad \textit{or} \quad a_{uu}(0, u) + b_{uu}(0, u)\theta > 0.$$

(b) Assume $a_{uu}(0, u) + b_{uu}(0, u)\theta < 0$. Then $(0, u)$ is (locally asymptotically) stable if

$$a(0, u) + b(0, u)\theta < 1 \quad \textit{and} \quad \sigma^2 < -2\left(a_{uu}(0, u) + b_{uu}(0, u)\theta\right)^{-1}.$$

Let u^*, θ^* be a critical extinction pair for which the conditions (12) hold. This point is a bifurcation point for non-extinction equilibria (as in Figure 1) whose stability properties we now consider. If

$$a_{uu}(0, u^*) + b_{uu}(0, u^*)\theta^* > 0,$$

then, because $\mu_2 > 1$, the extinction equilibria for $\theta \approx \theta^*$ are unstable (Lemma 2.1). By continuity, an eigenvalue of the Jacobian evaluated at the bifurcating non-extinction equilibria is also greater than one for $\theta \approx \theta^*$. Thus, in this case equilibria of both types are unstable near the bifurcation point.

If, on the other hand,

$$a_{uu}(0, u^*) + b_{uu}(0, u^*), \theta^* < 0,$$

then by Lemma 2.1 the extinction equilibrium loses stability as the bifurcation parameter θ increases through the critical value θ (assuming $\theta_{cr} > 0$). It follows by the exchange of stability principle for transcritical bifurcations [13] that a supercritical (right) bifurcation results in the stability of the non-extinction equilibria and a subcritical (left) bifurcation results in the instability of the non-extinction equilibria.

We have arrived at our main result concerning the limiting system (8) for the Darwinian matrix model (6).

Theorem 2.2 *Assume A and that u^*, $\theta^* > 0$ is a critical extinction pair for which (12) and $a(0, u^*) < 1$ hold. Then for the limiting system (8) there exist branches of extinction and non-extinction equilibria, parameterized by θ, that transcritically bifurcate (intersect) at $\theta = \theta^*$ given by (13). (a) Assume $a_{uu}(0, u^*) + b_{uu}(0, u^*)\theta^* < 0$. Then* *the extinction equilibria lose stability as θ increases through θ^*. Moreover, near the bifurcation point (i.e. for $\theta \approx \theta^*$), and for σ^2 sufficiently small, i.e., for*

$$\sigma^2 < -2\left(a_{uu}\left(0,u^*\right)+b_{uu}\left(0,u^*\right)\theta^*\right)^{-1},$$

the bifurcating non-extinction equilibria are (evolutionarily) stable if the bifurcation is supercritical ($\delta < 0$) and are unstable if the bifurcation is subcritical ($\delta > 0$). (b) If $a_{uu}\left(0,u^*\right)+b_{uu}\left(0,u^*\right)\theta^* > 0$, then both the extinction equilibria and the non-extinction equilibria are unstable near the bifurcation point, i.e. for ($\theta \approx \theta^*$).

2.3 The Darwinian matrix model

In Sections 2.1 and 2.2, we obtained existence and stability results for the limiting equations (8) of the dynamic equations (7) for $p(t)$ and $u(t)$ associated with the Darwinian matrix equation (6). Under certain hypotheses the asymptotic dynamics of these two systems are related [7, 14]. (The theorems and the proofs given in [7] are for scalar maps, but remain valid virtually verbatim for systems of scalar maps.) Roughly speaking, if the dynamics of the limiting equations are not too complicated, then no orbit of (7) will approach an unstable equilibrium (or cycle) of the limiting system and if $(p(0),u(0))$ is sufficiently close to a (locally asymptotically) stable equilibrium (or cycle) (p_e,u_e) of the limiting equations and if the initial normalized distribution $x(0)/p(0)$ is sufficiently close to the limiting distribution $v/\omega\cdot v$, then

$$\lim_{t\to+\infty}\frac{x(t)}{p(t)}=\frac{v}{\omega\cdot v}\quad\text{and}\quad\lim_{t\to+\infty}(p(t),u(t))=(p_e,u_e).$$

The hypotheses required are that the limiting equations have at most a finite number of equilibria (or cycles) in any compact subset of R_+^2, all of which are hyperbolic, and the ω-limit sets of bounded orbits are equilibria (or cycles).

We conclude with some remarks concerning the results in Sections 2.1 and 2.2.

Remark 2.1. The inequality $r_{uu}(0,u^*,\theta^*)=a_{uu}\left(0,u^*\right)+b_{uu}\left(0,u^*\right)\theta^*>0$ in Theorem 2.2(b) implies that the inherent growth rate $r(0,u,\theta^*)$ has a local minimum (of 1) as a function of the trait u at $u=u^*$ (assuming the eigenvalue $\theta\approx\theta^*$ remains fixed). Since in this case all equilibria on both bifurcating branches (extinction and non-extinction) are unstable, it follows that no population will evolve to have trait $u\approx u^*$, whether the population goes extinct or not.

Remark 2.2. Evolutionarily stable equilibria occur in the transcritical bifurcation when $r_{uu}(0,u^*,\theta^*)<0$ and hence $r(0,u,\theta^*)$ has a local maximum (of 1) as a function of the trait u. In this case, the extinction equilibria are unstable if the demographic parameters in the matrix L are such that $\theta \lessapprox \theta^*$ and populations evolve to extinction. On the other hand, for $\theta \gtrapprox \theta^*$ the extinction equilibria are unstable and the population will not evolve to extinction. In this case the non-extinction equilibria are stable if $\delta<0$ and populations evolve to an evolutionarily stable non-extinction equilibrium (p_e,u_e), $p_e>0$, with a trait $u=u_e$ at which $r(p_e,u,\theta_e)$ has a local maximum. This is because the equilibrium equation is $r_u(p_e,u,\theta_e)=1$ and, by continuity, $r_{uu}(p_e,u_e,\theta_e)<0$ for $\theta_e \gtrapprox \theta^*$. If $r(p_e,u,\theta_e)$ in fact has a global maximum on the trait interval Υ at $u=u_e$, then the evolutionary stability of the equilibrium plus $r_{uu}(p_e,u_e,\theta_e)<0$ implies the equilibrium is an ESS (see the ESS Maximum Principle in [17]). That is to say, the population evolves to a non-extinction equilibrium state that is resistant to invasion by other mutant species.

Remark 2.3. The condition $\delta \mathrel{\hat{=}} \nabla_x r\left(0, u^*, \theta^*\right) \cdot v < 0$, required for a supercritical bifurcation of evolutionarily stable non-extinction equilibria, is a negative feedback condition. This is because it requires sufficiently large negative derivatives of the inherent population growth rate r with respect to the components in the distribution vector x. This condition is met under the usual assumptions of so-called density effects in ecology. In order to fail, i.e., in order for $\delta > 0$, positive feedback terms (Allee effects) would have to out weigh the negative density effects. As we have seen, this would lead to a subcritical bifurcation of unstable non-extinction equilibria.

Remark 2.4. Since $r(x, u) = a(x, u) + b(x, u)\theta$, we have the relationship $r(0, u^*) = a(0, u^*) + b(0, u^*)\theta$ between the dominant eigenvalue $r(0, u^*)$ (the inherent population growth rate at the critical trait u^*) and θ. The bifurcation described in Theorems 2.1 and 2.2 in terms of θ can therefore be restated in terms of the magnitude of $r(0, u^*)$. Thus, the bifurcation phenomenon in these theorems (and hence the possibility of a bifurcation from an evolutionary state of extinction state to an evolutionary state of non-extinction) occurs when the magnitude of $r(0, u^*)$ increases through 1. See [11]. As is shown in [12], this phenomenon can also be equivalently stated in terms of the inherent net reproductive number $R_0(0, u^*)$ at the critical trait. See [12]. The quantity $R_0(0, u^*)$, which is generally more analytically tractable than $r(0, u^*)$, is the dominant eigenvalue of $F(0, u^*)(I - T(0, u^*))^{-1}$ [8, 9, 10].

Remark 2.5. The definition of a type 2 extinction pair u^*, θ^*clearly requires that $a(0, u)$ and $b(0, u)$ have opposite monotonicities at $u = u^*$. In specific applications the biological implication of this fact is usually that some kind of trade-off between two demographic parameters occurs as the the trait u is changed. We will see an example of this in Section 3.

3 An Application

Consider a projection matrix (2) in which the matrix of class transitions are

$$s_{jj} = \pi_j \left(1 - \gamma_j\right), \quad s_{ij} = \pi_i \tau_{ij} \gamma_j.$$

Here γ_j is the fraction that leaves the j^{th} size class per unit time, τ_{ij} is the fraction of those who leave that moves to class i, and π_j is the survival rates per unit time. We can put this general model into the form (3) under the following two assumptions: *the fraction of j-class individuals leaving the j-class, γ_j, and the class specific fertility rates, f_{ij}, are proportional to a function of a resource consumption rate $u \geq 0$ and the survival rates π_j are class independent.* Specifically

$$\gamma_j = \tau_j \phi(u), \quad f_{ij} = \pi_i(u) \varphi_{ij} \phi(u), \quad \pi_i = \pi(u),$$

where $0 \leq \phi(u) \leq 1$ for $u \in \Upsilon = [0, u_{\max})$, $u_{\max} \leq +\infty$. For a reproductively obligate resource, we have $\phi(0) = 0$. For this model, the fertility and transition matrices are

$$F = \pi(u)\phi(u)\left[\varphi_{ij}\right], \qquad T = \pi(u) \begin{bmatrix} 1 - \tau_1\phi(u) & \tau_{12}\tau_2\phi(u) & \cdots & \tau_{1m}\tau_m\phi(u) \\ \tau_{21}\tau_1\phi(u) & 1 - \tau_2\phi(u) & \cdots & \tau_{2m}\tau_m\phi(u) \\ \vdots & \vdots & & \vdots \\ \tau_{m1}\tau_1\phi(u) & \tau_{m2}\tau_2\phi(u) & \cdots & 1 - \tau_m\phi(u) \end{bmatrix}.$$

Let $\tau_k = \max\{\tau_i\}$ and re-write T as

$$T = \pi\left(1 - \tau_k \phi(u)\right) I + \pi\phi(u) \begin{bmatrix} \tau_k - \tau_1 & \tau_{12}\tau_2 & \cdots & \tau_{1m}\tau_m \\ \tau_{21}\tau_1 & \tau_k - \tau_2 & \cdots & \tau_{2m}\tau_m \\ \vdots & \vdots & & \vdots \\ \tau_{m1}\tau_1 & \tau_{m2}\tau_2 & \cdots & \tau_k - \tau_m \end{bmatrix}.$$

Then we can write the projection matrix as

$$P = \pi(u)\left(1 - \tau_k \phi(u)\right) I + \pi(u)\phi(u) L, \tag{15}$$

where

$$L = \begin{bmatrix} \tau_k - \tau_1 + \varphi_{11} & \tau_{12}\tau_2 + \varphi_{12} & \cdots & \tau_{1m}\tau_m + \varphi_{1m} \\ \tau_{21}\tau_1 + \varphi_{21} & \tau_k - \tau_2 + \varphi_{22} & \cdots & \tau_{2m}\tau_m + \varphi_{2m} \\ \vdots & \vdots & & \vdots \\ \tau_{m1}\tau_1 + \varphi_{m1} & \tau_{m2}\tau_2 + \varphi_{m2} & \cdots & \tau_k - \tau_m + \varphi_{mm} \end{bmatrix} \tag{16}$$

is a non-negative matrix. This matrix model is motivated by applications in which the classes are based on physiological size of individuals; see [9] and the references cited therein for examples. It has the form (3) with $a = \pi(u)\left(1 - \tau_k \phi(u)\right)$ and $b = \pi\phi(u)$. We assume L has a positive dominant eigenvalue θ which has an associated positive eigenvector.

For density dependence in the fertility and survivorship rates $\pi = \pi(x, u)$, $\phi = \phi(x, u)$, then

$$a\left(x, u\right) = \pi(x, u)\left[1 - \tau_k \phi(x, u)\right], \quad b(x, u) = \pi(x, u)\phi(x, u).$$

In this application we assume density dependence is through a dependency on a weighted total population size p. Then

$$\gamma_j = \tau_j \phi(p, u), \quad f_{ij} = \varphi_{ij}\phi(p, u), \quad \pi_i = \pi(p, u) \tag{17}$$

in the fertility and transition matrices F and T. Theorems 1.1, 2.1 and 2.2 apply to this population model with

$$a(p, u) = \pi(p, u)\left(1 - \tau_k \phi(p, u)\right), \quad b(p, u) = \pi(p, u)\phi(p, u) \tag{18}$$

in the projection matrix (3). Thus, there is a stable normalized distribution and the asymptotic population dynamics are described by the limiting equations (8). We illustrate the application of Theorems 2.1 and 2.2 with a specific example.

Important in the evolution and adaptation of biological species are trade-offs among life history characteristics and strategies [16]. In the model above, *we assume a trade-off between fertility and survivorship as a function of the resource consumption rate* u. Thus, an increase in u results in an increase in fertility but also a decrease in survivorship. A decrease in survivorship can be the result of many causes: the stress and metabolic costs associated with finding and consuming prey, a resulting exposure to predators, etc.

We take

$$\phi(p, u) = \frac{1}{1 + cp} f(u), \quad \pi(p, u) = \frac{1}{1 + cp}\pi_0\left(1 - f(u)\right), \quad c > 0, \quad 0 < \pi_0 < 1, \tag{19}$$

where $f(u)$ is a twice continuously differentiable, real value function of u on an interval $0 \leq u \leq u_m \leq +\infty$ that satisfies

$$f(0) = 0, \quad f\,'(u) > 0, \quad \lim_{u \to u_m} f(u) = 1.$$

Specific examples include $f(u) = 1 - e^{-\alpha u}$ on $0 \leq u < +\infty$ and $f(u) = u^p$ on $0 \leq u \leq 1$. Here we have taken the dependence of fertility and survivorship on weighted population size p to have the discrete time, logistic form $1/(1 + cp)$ as first consider by Leslie [15]. Note that fertility is 0 at consumption rate $u = 0$ and that survivorship $\pi(p, u)$ is 0 as the consumption rate u approaches u_m. Neither of these two extremes is therefore favorable for the persistence of the population.

Straightforward calculations solving equations (11) show that there exists a (unique) critical extinction pair given by the formulas

$$u^* = f^{\,-1}\left(\frac{-(1-\pi_0) + \sqrt{1-\pi_0}}{\pi_0}\right), \qquad \theta^* = \tau_k + \frac{\pi_0}{2 - \pi_0 - 2\sqrt{1-\pi_0}}. \tag{20}$$

Note that $0 < u^* < u_m$. Moreover, further calculations show

$$\delta = -c\left(1 + \sqrt{1-\pi_0}\right)\omega \cdot v < 0,$$
$$a_{uu}(0, u^*) + b_{uu}(0, u^*)\,\theta^* = -2\left(2 - \pi_0 + 2\sqrt{1-\pi_0}\right)\left(f\,'(u^*)\right)^2 < 0,$$

and, as a result, there is a supercritical bifurcation of evolutionarily stable, non-extinction equilibria as θ increases through θ^* (Theorems 2.1 and 2.2). Since

$$b_u(0, u) = \left(2 - \pi_0 - 2\sqrt{1-\pi_0}\right) f\,'(u^*) > 0,$$

the critical extinction pair is of Type 2 and the bifurcation has the form in Figure 1(c).

As a consequence of these results, the Darwinian model (6) with (15) and (17)-(19) predicts evolution to extinction for $\theta < \theta^*$ and evolution to a non-extinction equilibrium for $\theta \gtrapprox \theta^*$. Note that the bifurcating, evolutionarily stable non-extinction equilibria have traits near u^* and therefore lie between the two unfavorable traits of 0 and u_m.

This bifurcation result is stated in terms of the dominant eigenvalue θ of L the matrix given by (16). Often of interest is how the bifurcation to evolutionarily stable states depends on the class-specific parameters appearing as entries in L. In general, of course, there is no formula that explicitly relates θ to the entries in L (when the number of classes m is large). However, as pointed out in Remark 4, this bifurcation result can be equivalently re-stated in terms of $r(0, u^*) = a(0, u^*) + b(0, u^*)\theta$, namely, that the bifurcation occurs as $r(0, u^*)$ increases through 1 or equivalently as the inherent net reproductive number $R_0(0, u^*)$ (at the critical trait u^*) increases through 1. The quantity $R_0(0, u^*)$ is the dominant eigenvalue of $F(0, u^*)\left(I - T(0, u^*)\right)^{-1}$ and explicit formulas for it in terms of the entries in the projection matrix are often available [8, 9, 10]. This is particularly true, for example, when there is only one newborn class, i.e., when only the first row in F is nonzero.

As an example, suppose the population model is based on an Usher matrix or, as it is called in [1], the standard size-structured model. In this model, individuals either remain in a size class or advance (grow into) the next size class in a unit of time. This means that the transition matrix T is bidiagonal with nonzero entries along the main diagonal and its subdiagonal only. All newborns are assumed to lie in the smallest size class and hence only the first row of the fertility matrix F is nonzero. This Usher model takes the form

$$F=\pi(p,u)\phi(p,u)\begin{bmatrix}\varphi_{11} & \varphi_{12} & \cdots & \varphi_{1m}\\ 0 & 0 & \cdots & 0\\ \vdots & \vdots & & \vdots\\ 0 & 0 & \cdots & 0\end{bmatrix}$$

$$+\,\pi(p,u)\begin{bmatrix}1-\tau_1\phi(p,u) & 0 & \cdots & 0 & 0\\ \tau_1\phi(p,u) & 1-\tau_2\phi(p,u) & \cdots & 0 & 0\\ 0 & \tau_2\phi(p,u) & \cdots & 0 & 0\\ \vdots & \vdots & & \vdots & \vdots\\ 0 & 0 & \cdots & 1-\tau_{m-1}\phi(p,u) & 0\\ 0 & 0 & \cdots & \tau_{m-1}\phi(p,u) & 1\end{bmatrix}.$$

The formula for the inherent net reproductive number of an Usher matrix gives (see [8, 9, 10])

$$R_0(p,u)=\pi(p,u)\phi(p,u)\sum_{i=1}^{m}\varphi_{1i}\prod_{j=1}^{i}\frac{\pi(p,u)\phi(p,u)\tau_{j-1}}{1-\pi(p,u)\left(1-\tau_j\phi(p,u)\right)},$$

where for notational convenience $\tau_0=1$ and $\tau_m=0$. Thus, from (19) and (20) we obtain

$$R_0(0,u^*)=\pi_0\left(1-f(u^*)\right)f(u^*)\sum_{i=1}^{m}\varphi_{1i}\prod_{j=1}^{i}\frac{\pi_0\left(1-f(u^*)\right)f(u^*)\tau_{j-1}}{1-\pi_0\left(1-f(u^*)\right)\left(1-\tau_j f(u^*)\right)},$$

where

$$f(u^*)=\frac{-\left(1-\pi_0\right)+\sqrt{1-\pi_0}}{\pi_0}.$$

The bifurcation to evolutionary non-extinction equilibria occurs for $R_0(0,u^*)\gtrapprox 1$ [12]. In this interpretation, the bifurcation phenomenon can now be determined in terms of the any of the size-specific fertilities φ_{1i} or the growth rates τ_i or the survivorship π_0.

For example, if all size classes but the largest consist of juveniles, so that all $\varphi_{1i}=0$ except $\varphi_{1m}>0$, then we have the formula

$$R_0(0,u^*)=\left[\pi_0\left(1-f(u^*)\right)f(u^*)\right]^{m+1}\varphi_{1m}\prod_{j=1}^{m}\frac{\tau_{j-1}}{1-\pi_0\left(1-f(u^*)\right)\left(1-\tau_j f(u^*)\right)}$$

and the bifurcation requirement that $R_0(0,u^*)\gtrapprox 1$ can now be re-stated as a threshold for adult fertility $\varphi_{1m}\gtrapprox\varphi_{1m}^*$.

4 Concluding Remarks

Theorems 2.1 and 2.2 describe a fundamental bifurcation phenomenon for a class of nonlinear matrix models that describe the evolutionary dynamics of a structured population. The type of matrix models considered in these theorems (which are motivated by certain size-structured models that arise in applications found in the literature) possess a strong ergodic property: solutions, whatever their dynamics, have a stable (normalized) class distribution. This property, when applied to the Darwinian matrix models obtained from these population dynamic models by the methods of evolutionary game theory [17], leads to limiting equations for the evolving phenotypic trait and the total (weighted) population size.

The bifurcation phenomenon in Theorems 2.1 and 2.2 is fundamental in the sense that it concerns the fundamental biological question of extinction versus non-extinction, or in the context of the Darwinian models (6) considered here, evolution to extinction versus evolution to a non-extinction equilibrium state. These theorems show that this transition occurs at (and only at) a critical value θ^* of the bifurcation parameter θ and what we have defined to be a critical extinction trait value $u = u^*$. The bifurcation does not always lead to stable non-extinction equilibria, however, and Theorem 2.2 describes when the bifurcation is stable and when it is not.

The requirements for a stable bifurcation turn out to imply (among other things) that the inherent growth rate r of the population dynamics must attain a (local) maximum at the critical value of the trait (a fact that also implies the evolutionarily stable non-extinction equilibria are candidates for an ESS [17]). Although we do not pursue the issue here, the biological interpretation of these requirements is that some kind of a trade-off must occur among vital life history traits as a function of the phenotypic trait u. This is illustrated by the example in Section 3.

There remain several interesting open problems. Theorem 2.1 provides the existence of a local bifurcating branch of non-extinction equilibria. Similar theorems for population dynamic models without evolution assert the global existence of this branch. A global bifurcation theorem for the Darwinian model is lacking. The instability results in 2.2(b), in which the equilibria on both the extinction equilibrium and non-extinction equilibrium branches are unstable, leave open the question of the asymptotic dynamics in this case. The same question arises in 2.2(a) when the bifurcation is subcritical. Also, the methodology of evolutionary game theory is applicable when more than one phenotypic trait evolves. The ergodic Theorem 1.1 would still apply to the Darwinian matrix models for multiple traits and hence permit an analysis by means of lower dimensional limiting equations. Bifurcation theorems for these multi-trait Darwinian models would be of interest.

In this paper the focus is on the special class of Darwinian matrix models with projection matrices of the form (3). A bifurcation theorem for matrix models with more general projection matrices is given in [11].

References

[1] Caswell, H. *Matrix Population Models: Construction, Analysis and Interpretation*, Second Edition. Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts, 2001.

[2] Crowe, K. M. A nonlinear ergodic theorem for discrete systems. *Journal of Mathematical Biology* **32** (1994) 179–191.

[3] Crowe, K. M. Nonlinear ergodic theorems and symmetric versus asymmetric competition. In: *Structured-Population Models in Marine, Terrestrial, and Freshwater Systems* (S. Tuljapurkar & H. Caswell, eds.), Chapman & Hall, New York, 1997.

[4] Cushing, J. M. Some competition models for size-structured populations. *Rocky Mountain Journal of Mathematics* **20** (4) (1990) 879–897.

[5] Cushing, J. M. Competing size-structured species. *Mathematical Population Dynamics* (O. Arino, D. E. Axelrod, and M. Kimmel, eds.). Marcel Dekker, Inc., New York, 1991.

[6] Cushing, J. M. A discrete model of competing size-structured species. *Theoretical Population Biology* **41** (2) (1992) 372–387.

[7] Cushing, J. M. A strong ergodic theorem for some nonlinear matrix models for the dynamics of structured populations. *Natural Resource Modeling* **3**(3) (1989) 331–375.

[8] Cushing, J. M. and Yicang, Z. The net reproductive value and stability in structured population models, *Natural Resource Modeling* **8** (4) (1994) 1–37.

[9] Cushing, J. M. *An Introduction to Structured Population Dynamics*. CBMS-NSF Regional Conference Series in Applied Mathematics, Vol. 71, SIAM, Philadelphia, 1998.

[10] Cushing, J. M. Matrix models and population dynamics. In: *Mathematical Biology* (Mark Lewis, A. J. Chaplain, James P. Keener, Philip K. Maini, eds.). IAS/Park City Mathematics Series, Vol. 14, American Mathematical Society, Providence, RI, 2009, 47–150.

[11] Cushing, J. M. A bifurcation theorem for Darwinian matrix models. *Nonlinear Studies* **17**(1) (2010) 1–13.

[12] Cushing, J. M. On the relationship between r and R_0 and its role in the bifurcation of stable equilibria of Darwinian matrix models. *Journal of Biological Dynamics* (to appear).

[13] Kielhöfer, H. *Bifurcation Theory: An Introduction with Applications to PDEs*. Applied Mathematical Sciences 156. Springer, New York, 2004.

[14] LaSalle, J. P. *The Stability of Dynamical Systems*. Regional Conference Series in Applied Mathematics, SIAM, Philadelphia, 1976.

[15] Leslie, P. H. Some further notes on the use of matrices in population mathematics. *Biometrika* **35** (1948) 213–245.

[16] Roff, D. A. *Life History Evolution*. Sinauer Associates Inc., Massachusetts, 2002.

[17] Vincent, T. L. and Brown, J. S. *Evolutionary Game Theory, Natural Selection, and Darwinian Dynamics*. Cambridge University Press, Cambridge, 2005.