

EVOLUTIONARY DYNAMICS OF A MULTI-TRAIT SEMELPAROUS MODEL

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ABSTRACT. We consider a multi-trait evolutionary (game theoretic) version of a two class (juvenile-adult) semelparous Leslie model. We prove the existence of both a continuum of positive equilibria and a continuum of synchronous 2-cycles as the result of a bifurcation that occurs from the extinction equilibrium when the net reproductive number R_0 increases through 1. We give criteria for the direction of bifurcation and for the stability or instability of each bifurcating branch. Semelparous Leslie models have imprimitive projection matrices. As a result (unlike matrix models with primitive projection matrices) the direction of bifurcation does not solely determine the stability of a bifurcating continuum. Only forward bifurcating branches can be stable and which of the two is stable depends on the intensity of between-class competitive interactions. These results generalize earlier results for single trait models. We give an example that illustrates how the dynamic alternative can change when the number of evolving traits changes from one to two.

1. Introduction. Biological semelparity is a life history adaptation in which an individual organism reproduces once and then, or shortly thereafter, dies. This reproductive strategy is widespread throughout the plant and animal kingdoms and it is often contrasted with the alternative of iteroparity in the study of life history strategies [40, 43]. Semelparity is found, for example, in many species of insects; annual and monocarpic perennial plants; marine species including Pacific salmon, squid and octopi; many species of bamboo and tropic trees; and even a few mammals. Numerous theoretical studies utilize Leslie matrix models to describe the (discrete time) dynamics of semelparous populations with the goal of understanding the dynamic consequences of semelparity as a life history strategy [3], [4], [5], [9], [10], [11], [14], [16], [17], [19], [20], [21], [20], [21], [22], [23], [29], [30], [31], [32], [33], [37], [46]. These studies have shown that there are two broad and contrasting categories of dynamics fundamentally implied by semelparous Leslie models, namely, equilibration in which generations overlap and synchronized periodic cycles in which they do not. These alternatives trace mathematically to the fact that both

2010 *Mathematics Subject Classification.* Primary: 92D15, 92D25; Secondary: 39A28, 39A30.

Key words and phrases. Juvenile-adult dynamics, evolutionary dynamics, bifurcation, stability, synchronous cycles.

The authors were supported by NSF grant DMS-140756 (program in Mathematical Biology).

the positive cone and its boundary are invariant, a consequence of the imprimitivity of a semelparous Leslie matrix. This dynamic dichotomy is most sharply on display in two dimensional, semelparous Leslie models (with two age classes) [10], [17], which biologically corresponds roughly to a short juvenile maturation period. In this case it is known, under general circumstances, that when the extinction equation is destabilized one of the dynamic alternatives is stable and the other is unstable (which is stable depends on the intensity of between-class competitive interactions). In higher dimensions, the dynamics, and in particular the nature of the dynamic dichotomy between positive equilibria and synchronous cycles, are not fully understood, primarily because the possible dynamics on the boundary of the positive cone (i.e. the possible types and periods of synchronous cycles) can become increasingly complex as the dimension increases [9], [10], [11], [16], [19], [20], [21], [22]. Higher dimensional semelparous Leslie models pose challenging open problems which are of considerable interest since historically many of the motivating applications involved organisms with long maturation periods (the famous periodical cicadas being the prime example [4], [5]).

In this paper we will restrict attention to two dimensional semelparous Leslie models and turn to a study of the dynamics that result when model parameters are subject to change by means of Darwinian evolution. Is there still a dynamic dichotomy and, if so, under what circumstances is each of the alternatives stable?

These questions were thoroughly analyzed for the two dimensional semelparous Leslie model in [18]. In that study the manner in which evolution changes model coefficients is determined by the fitness of individuals, as defined by their survival and reproductive rates which are assumed dependent on a single phenotypic trait subject to evolutionary change. The widely used evolutionary game theory methodology (see for example [1], [36], [47]) is applied to the Leslie model (see [47]) to obtain what are called the Darwinian equations that couple population and evolutionary dynamics. Population and evolutionary times scales are not (necessarily) asymptotically separated, which is relevant when evolution acts on contemporary time scales, as has been observed in an increasing number of studies (for example, see [2], [45]). Such evolutionary changes, often called microevolution or rapid evolution, can occur in as little as a few generations. Species in which this contemporary evolution has been observed include Galapagos finches [27], Trinidad guppies [25], [26] Hawaiian mosquito fish [41], and species of salmon [39], [28]. These rapid evolutionary events have important consequences for conservation as they are often in response to environmental changes such as habitat fragmentation, translocation, harvesting, and invasive species.

Our goal in this paper is to extend the results in [18] to the case when model coefficients are dependent on more than one phenotypic trait subject to evolution. This is a more realistic scenario given that the fitness of organisms generally depends on a suite of phenotypic traits. For example, survival in Chinook salmon depends on many traits including predator avoidance, foraging behavior, and migratory behavior [39]. In Trinidad guppies, predation is a major selective pressure on numerous traits including color patterns, body shape and size, life history patterns, and behavior [24]. In addition, evolution is complicated by the fact that most traits are correlated with a suite of other traits [36]. Therefore, any given phenotype is a result of a number of constraints and trade-offs between various traits. For example, in live-bearing fish species such as guppies, increased predation results in fast-start swimming performance as a means of predator avoidance. However, predation also

increases resource allocation to reproduction, causing large body size and decreased velocity of gravid females. The resulting observed phenotypes are a trade-off between these two traits along with various other traits such as a change in habitat use while pregnant [38].

In section 2 we describe a multi-trait, evolutionary game theoretic version of the two dimensional semelparous Leslie model. We analyze the extinction equilibria in Section 3 and the two dynamic alternatives of positive equilibria and synchronous cycles in Sections 4 and 5 respectively. In Section 6 we illustrate the theoretical results with an example. This example also serves to illustrate that the evolutionary attractor can be different when two traits evolve from what it is when only one trait evolves.

2. The evolutionary model. In this paper, we examine the evolutionary dynamics of a semelparous population by considering a juvenile-adult staged, discrete time model

$$x'_1 = f\phi(x_1, x_2)x_2 \tag{1a}$$

$$x'_2 = s\sigma(x_1, x_2)x_1 \tag{1b}$$

where x_1 and x_2 are the population densities of juveniles and adults respectively and where prime denotes that the density variable is evaluated at the next value of the time variable, which is taken as the maturation period (assumed fixed and not subject to evolution in this model). The probability a juvenile individual survives and becomes an adult, in a unit of time, is $s\sigma(x_1, x_2)$. Under the assumption $\sigma(0, 0) = 1$, s is the inherent (density free) juvenile survival rate. The number of surviving juveniles produced by an adult is $f\phi(x_1, x_2)$ where $\phi(0, 0) = 1$ implies f is the inherent number of surviving juveniles. The density-dependent effects on survival and reproduction are described by the factors $\sigma(x_1, x_2)$ and $\phi(x_1, x_2)$, which allow for competition both between and within age classes. The model describes a semelparous population since equation (1b) implies no adults survive a time unit. Its dynamics have been studied in several papers [10], [17].

The net reproductive number $R_0(x_1, x_2)$ is defined to be the expected number of juveniles a juvenile will produce over its lifetime. For the model equations (1), we have

$$R_0(x_1, x_2) \triangleq f s \phi(x_1, x_2)\sigma(x_1, x_2) \tag{2}$$

under the assumption that the population densities x_1 and x_2 remain fixed. The *inherent* net reproductive number $R_0 \triangleq R_0(0, 0) = fs$ is the expected number of juveniles produced by a juvenile over its life time in the absence of density effects. The linearization principle implies the extinction equilibrium $(x_1, x_2) = (0, 0)$ is (locally asymptotically) stable if $R_0 < 1$ and unstable if $R_0 > 1$. The former case implies the extinction (of at least low density populations). The latter case can be strengthened by the fact that if $R_0 > 1$ then the model is uniformly persistent with respect to the extinction state $(x_1, x_2) = (0, 0)$ [8], [12], [32]. The model can exhibit complex non-extinction dynamics, the nature of which depends on the properties of the density effects and the nonlinearities they introduce into the model. In general, however, the destabilization of $(x_1, x_2) = (0, 0)$ at $R_0 = 1$ leads to a bifurcation resulting in two types of steady states. One of these is an equilibrium with positive entries x_i , which implies a population with overlapping generations. The other alternative is a synchronous 2-cycle in which the two generations do not overlap and temporally alternate in appearance. It has been shown, when only negative

density effects are present, that for $R_0 \gtrsim 1$, a dynamic dichotomy exists between these two steady states, that is to say, one is (locally asymptotically) stable and the other is unstable [10], [17]. Which of these is stable depends on the relative level of competition between and within age classes. Specifically, the positive equilibria are stable when competition within age classes is stronger, relative to that between age classes, and the synchronous 2-cycles are stable when the opposite is true.

However, these results assume that the birth and survival rates in the model change only as functions of population densities. These vital rates could, however, change for other reasons as well, such as stochasticity, periodic or seasonal forcing, etc. They can also change under the influence of evolution by Darwinian selection. An evolutionary version of the juvenile-adult, semelparous model (1) and its dynamic dichotomy was studied in [18] under the assumption that model parameters depend on one adaptive trait. We generalize that study so as to allow for several traits to be subject to evolution.

Following evolutionary game theory methodology [2], [36], [47], we let $\mathbf{v} = (v_1, \dots, v_n)^T$ denote a vector of n phenotypic traits of a focal (or mutant) individual which have a heritable component and are subject to Darwinian selection. Let $\mathbf{u} = (u_1, \dots, u_n)^T$ denote the vector of total population means of these phenotypic traits. Survival and fertility rates of a focal individual, in addition to being density dependent, are assumed dependent on its suite of traits \mathbf{v} and those of other individuals as represented by the mean \mathbf{u} (frequency dependence). In this modeling methodology, the dynamics of the mean trait vector are modeled using what is usually called Lande's equation [34], [35] (or sometimes Fisher's equation for additive genetic variance or the breeder's equation), which assumes that the change in mean is proportional to the fitness gradient (with respect to the focal individual's trait). For general models of discretely structured population models, the mean trait dynamics are derived in [47] using $\ln r$ as fitness, where r is the inherent population growth rate. For the special case of the juvenile-adult, semelparous model (1) these equations take the form

$$x'_1 = f(\mathbf{v})\phi(x_1, x_2, \mathbf{u}, \mathbf{v})|_{\mathbf{v}=\mathbf{u}} x_2 \quad (3a)$$

$$x'_2 = s(\mathbf{v})\sigma(x_1, x_2, \mathbf{u}, \mathbf{v})|_{\mathbf{v}=\mathbf{u}} x_1 \quad (3b)$$

$$\mathbf{u}' = \mathbf{u} + \mathcal{C}\nabla_{\mathbf{v}} \ln r(x_1, x_2, \mathbf{u}, \mathbf{v})|_{\mathbf{v}=\mathbf{u}} \quad (3c)$$

where

$$\mathcal{C} = \begin{pmatrix} \nu_1 & \delta_{12} & \cdots & \delta_{1n} \\ \delta_{12} & \nu_2 & \cdots & \delta_{2n} \\ \vdots & \vdots & \vdots & \vdots \\ \delta_{1n} & \delta_{2n} & \cdots & \nu_n \end{pmatrix}$$

is the (constant) variance-covariance matrix for the variability of the phenotypic traits. The equation for a particular trait u_i is

$$u'_i = u_i + \nu_i \partial_{v_i} \ln r(x_1, x_2, \mathbf{u}, \mathbf{v})|_{\mathbf{v}=\mathbf{u}} + \sum_{j \neq i} \delta_{ij} \partial_{v_j} \ln r(x_1, x_2, \mathbf{u}, \mathbf{v})|_{\mathbf{v}=\mathbf{u}}.$$

In this model fitness is $\ln r(x_1, x_2, \mathbf{u}, \mathbf{v})$ where r defined by

$$r(x_1, x_2, \mathbf{u}, \mathbf{v}) \triangleq \sqrt{R_0(x_1, x_2, \mathbf{u}, \mathbf{v})}$$

$$R_0(x_1, x_2, \mathbf{u}, \mathbf{v}) \triangleq f(\mathbf{v})s(\mathbf{v})\sigma(x_1, x_2, \mathbf{u}, \mathbf{v})\phi(x_1, x_2, \mathbf{u}, \mathbf{v})$$

is the dominant eigenvalue of the projection matrix associated with population dynamics (3a)-(3b), namely

$$\begin{pmatrix} 0 & f(\mathbf{v})\phi(x_1, x_2, \mathbf{u}, \mathbf{v}) \\ s(\mathbf{v})\sigma(x_1, x_2, \mathbf{u}, \mathbf{v}) & 0 \end{pmatrix}.$$

The quantity R_0 is the net reproductive number (expected number of juveniles produced per juvenile per lifetime, if $x_1, x_2, \mathbf{u}, \mathbf{v}$ were held fixed) [7]. When $n = 1$ this is the model considered in [18].

Given the relationship between r and R_0 one can reformulate the trait equation (3c) equivalently in terms of the net reproductive number R_0 . For notational convenience define

$$d_i(x_1, x_2, \mathbf{u}) \triangleq \frac{1}{2} \frac{\partial_{v_i} R_0(x_1, x_2, \mathbf{u}, \mathbf{v})}{R_0(x_1, x_2, \mathbf{u}, \mathbf{v})} \Big|_{\mathbf{v}=\mathbf{u}} \tag{4}$$

and

$$\mathbf{d}(x_1, x_2, \mathbf{u}) \triangleq (d_1(x_1, x_2, \mathbf{u}), \dots, d_n(x_1, x_2, \mathbf{u}))^T.$$

The Darwinian equations (3) become

$$x'_1 = f(\mathbf{u})\phi(x_1, x_2, \mathbf{u}, \mathbf{u})x_2 \tag{5a}$$

$$x'_2 = s(\mathbf{u})\sigma(x_1, x_2, \mathbf{u}, \mathbf{u})x_1 \tag{5b}$$

$$\mathbf{u}' = \mathbf{u} + \mathcal{C}\mathbf{d}(x_1, x_2, \mathbf{u}). \tag{5c}$$

We make the following mathematical assumptions on the coefficients in this evolutionary model.

A1. For open sets $V \subset \mathbb{R}^n$ and $\Omega \subset \mathbb{R}^2$ with $\bar{R}_+^2 \subset \Omega$, assume $\phi \in C^2(\Omega \times V \times V \rightarrow \mathbb{R}_+^1)$ and $s\sigma \in C^2(\Omega \times V \times V \rightarrow [0, 1])$ with $\phi(0, \mathbf{u}, \mathbf{v}) \equiv \sigma(0, \mathbf{u}, \mathbf{v}) \equiv 1$ for $(\mathbf{u}, \mathbf{v}) \in V \times V$. Assume $f \in C^2(V \rightarrow \mathbb{R}_+^1)$ and $s \in C^2(V \rightarrow (0, 1])$.

Note 1. The identities $\phi(0, 0, \mathbf{u}, \mathbf{v}) \equiv \sigma(0, 0, \mathbf{u}, \mathbf{v}) \equiv 1$ imply $f(\mathbf{v})$ and $s(\mathbf{v})$ are the inherent birth and survival rates of the focal individual, i.e. birth and survival rates in a low density environment. We have assumed that in a low density environment an individual’s vital rates are negligibly influenced by other individuals (and their traits) and hence that these vital rates are not dependent on the population mean trait \mathbf{u} .

Note 2. The range restrictions on ϕ and σ allow for the model to exhibit positive density effects at low population densities, i.e. allow for ϕ and/or σ to be larger than 1 and, consequently, for the birth and/or the survival rate to increase with increased densities. That is to say, the model allows for component Allee effects [6].

3. Stability of extinction equilibria. An equilibrium (x_1, x_2, \mathbf{u}) of the Darwinian model (5) is an *extinction equilibrium* if $x_1 = x_2 = 0$. A triple $(x_1, x_2, \mathbf{u}) = (0, 0, \mathbf{u}^*)$ is an extinction equilibrium if and only if the trait component $\mathbf{u}^* = (u_1^*, \dots, u_n^*)$ satisfies the trait equilibrium equation

$$\mathcal{C}\mathbf{d}(0, 0, \mathbf{u}^*) = 0.$$

We refer to such a trait \mathbf{u}^* as a *critical trait* value. We assume

A2: there exists a critical trait \mathbf{u}^* .

Let superscript zero denote evaluation at the extinction equilibrium $(0, 0, \mathbf{u}^*)$. For example,

$$R_0^0 \triangleq R_0(x_1, x_2, \mathbf{u}, \mathbf{v})|_{(0,0,\mathbf{u}^*,\mathbf{u}^*)}, \quad \mathbf{d}^0 \triangleq \mathbf{d}(0, 0, \mathbf{u}^*), \quad s^0 \triangleq s(\mathbf{u}^*)$$

$$\partial_{v_i}^0 f \triangleq \partial_{v_i} f(\mathbf{v})|_{\mathbf{v}=\mathbf{u}^*}, \quad d_i^0 \triangleq \frac{1}{2} \frac{\partial_{v_i} R_0(x_1, x_2, \mathbf{u}, \mathbf{v})}{R_0(x_1, x_2, \mathbf{u}, \mathbf{v})} \Big|_{(0,0,\mathbf{u}^*,\mathbf{u}^*)}.$$

Note that $R_0^0 = f(\mathbf{u}^*) s(\mathbf{u}^*)$ is the inherent net reproductive number of a focal individual with trait $\mathbf{v} = \mathbf{u}^*$. We use this quantity R_0^0 as a bifurcation parameter. For that purpose, we introduce R_0^0 explicitly into the model equations as follows. Assume A2 and write the adult fertility rate as

$$f(\mathbf{v}) = b\beta(\mathbf{v}) \text{ where } \beta(\mathbf{u}^*) = 1. \tag{6}$$

We assume of course that $\beta(\mathbf{v})$ is such that, with f defined by (6), A1 holds. We also assume

A3: \mathcal{C} is non-singular and diagonally dominant, $\nu_i \geq \sum_j |\sigma_{ij}|$ for all $1 \leq i \leq n$.

Often it is assumed in these evolutionary models that the covariance terms are equal to zero [47], in which case the inequalities in A3 are satisfied. We make the less restrictive assumption A3.

By (6) $b = f(\mathbf{u}^*)$ is the inherent (density free) adult fertility rate and the inherent net reproductive number is

$$R_0^0 = bs(\mathbf{u}^*)$$

when a focal individual has trait $\mathbf{v} = \mathbf{u}^*$. We re-write the model equations (5) with $b = R_0^0/s(\mathbf{u}^*)$ to obtain

$$x_1' = R_0^0 \frac{1}{s^0} \beta(\mathbf{u}) \phi(x_1, x_2, \mathbf{u}, \mathbf{u}) x_2 \tag{7a}$$

$$x_2' = s(\mathbf{u}) \sigma(x_1, x_2, \mathbf{u}, \mathbf{u}) x_1 \tag{7b}$$

$$\mathbf{u}' = \mathbf{u} + \mathcal{C}\mathbf{d}(x_1, x_2, \mathbf{u}). \tag{7c}$$

Since covariance matrices are positive semi-definite, A3 implies \mathcal{C} is positive definite. Under this assumption, the extinction trait values \mathbf{u}^* satisfy the equation $\mathbf{d}^0 = \mathbf{0}$, which is equivalent to $\partial_{v_i} R_0(0, 0, \mathbf{u}^*, \mathbf{v})|_{\mathbf{v}=\mathbf{u}^*}$ or

$$s^0 \partial_{v_i}^0 \beta + \partial_{v_i}^0 s = 0 \text{ for all } 1 \leq i \leq n. \tag{8}$$

To examine the local stability of the extinction equilibrium, we apply the linearization principle. We write the Jacobian of (7) as

$$\mathcal{J} = \begin{pmatrix} P & \psi \\ \rho & T \end{pmatrix} \tag{9}$$

where P is the 2×2 matrix

$$P \triangleq \begin{pmatrix} R_0^0 \frac{1}{s^0} \beta(\mathbf{u}) x_2 \partial_{x_1} \phi(x_1, x_2, \mathbf{u}, \mathbf{u}) & R_0^0 \frac{1}{s^0} \beta(\mathbf{u}) \phi(x_1, x_2, \mathbf{u}, \mathbf{u}) + R_0^0 \frac{1}{s^0} \beta(\mathbf{u}) x_2 \partial_{x_2} \phi(x_1, x_2, \mathbf{u}, \mathbf{u}) \\ s(\mathbf{u}) \sigma(x_1, x_2, \mathbf{u}, \mathbf{u}) + s(\mathbf{u}) x_1 \partial_{x_1} \sigma(x_1, x_2, \mathbf{u}, \mathbf{u}) & s(\mathbf{u}) x_1 \partial_{x_2} \sigma(x_1, x_2, \mathbf{u}, \mathbf{u}) \end{pmatrix},$$

ψ and ρ are the $2 \times n$ and $n \times 2$ matrices

$$\psi \triangleq \begin{pmatrix} R_0^0 \frac{1}{s^0} \partial_{u_1} (\beta(\mathbf{u})\phi(x_1, x_2, \mathbf{u}, \mathbf{u})) x_2 & \cdots & R_0^0 \frac{1}{s^0} \partial_{u_n} (\beta(\mathbf{u})\phi(x_1, x_2, \mathbf{u}, \mathbf{u})) x_2 \\ \partial_{u_1} (s(\mathbf{u})\sigma(x_1, x_2, \mathbf{u}, \mathbf{u})) x_1 & \cdots & \partial_{u_n} (s(\mathbf{u})\sigma(x_1, x_2, \mathbf{u}, \mathbf{u})) x_1 \end{pmatrix}$$

$$\rho \triangleq \begin{pmatrix} \nu_1 \partial_{x_1} d_1(x_1, x_2, \mathbf{u}) + \Sigma_{j=2}^n \delta_{1j} \partial_{x_1} d_j(x_1, x_2, \mathbf{u}) & \nu_1 \partial_{x_2} d_1(x_1, x_2, \mathbf{u}) + \Sigma_{j=2}^n \delta_{1j} \partial_{x_2} d_j(x_1, x_2, \mathbf{u}) \\ \vdots & \vdots \\ \Sigma_{j=1}^{n-1} \delta_{1j} \partial_{x_1} d_j(x_1, x_2, \mathbf{u}) + \nu_n \partial_{x_1} d_n(x_1, x_2, \mathbf{u}) & \Sigma_{j=1}^{n-1} \delta_{1j} \partial_{x_2} d_j(x_1, x_2, \mathbf{u}) + \nu_n \partial_{x_2} d_n(x_1, x_2, \mathbf{u}) \end{pmatrix},$$

and T is the $n \times n$ matrix

$$T \triangleq I + CH$$

$$H \triangleq \begin{pmatrix} \partial_{u_1} d_1(x_1, x_2, \mathbf{u}) & \partial_{u_2} d_1(x_1, x_2, \mathbf{u}) & \cdots & \partial_{u_n} d_1(x_1, x_2, \mathbf{u}) \\ \partial_{u_1} d_2(x_1, x_2, \mathbf{u}) & \partial_{u_2} d_2(x_1, x_2, \mathbf{u}) & \cdots & \partial_{u_n} d_2(x_1, x_2, \mathbf{u}) \\ \vdots & \vdots & \ddots & \vdots \\ \partial_{u_1} d_n(x_1, x_2, \mathbf{u}) & \partial_{u_2} d_n(x_1, x_2, \mathbf{u}) & \cdots & \partial_{u_n} d_n(x_1, x_2, \mathbf{u}) \end{pmatrix}$$

(I is the $n \times n$ identity matrix). Evaluated at an extinction equilibrium, the Jacobian (9) becomes the block triangular matrix

$$\mathcal{J}^0 = \begin{pmatrix} P^0 & \mathbf{0}_{2 \times n} \\ \rho^0 & T^0 \end{pmatrix} \tag{10}$$

where $\mathbf{0}_{2 \times n}$ is the $2 \times n$ matrix of zeros

$$P^0 = \begin{pmatrix} 0 & R_0^0 \frac{1}{s^0} \\ s^0 & 0 \end{pmatrix}$$

$$\rho^0 = \begin{pmatrix} \nu_1 \partial_{x_1}^0 d_1 + \Sigma_{j=2}^n \delta_{1j} \partial_{x_1}^0 d_j & \nu_1 \partial_{x_2}^0 d_1 + \Sigma_{j=2}^n \delta_{1j} \partial_{x_2}^0 d_j \\ \vdots & \vdots \\ \Sigma_{j=1}^{n-1} \delta_{1j} \partial_{x_1}^0 d_j + \nu_n \partial_{x_1}^0 d_n & \Sigma_{j=1}^{n-1} \delta_{1j} \partial_{x_2}^0 d_j + \nu_n \partial_{x_2}^0 d_n \end{pmatrix}$$

$$T^0 = I + CH^0, \quad H^0 = \begin{pmatrix} \partial_{u_1}^0 d_1 & \partial_{u_2}^0 d_1 & \cdots & \partial_{u_n}^0 d_1 \\ \partial_{u_1}^0 d_2 & \partial_{u_2}^0 d_2 & \cdots & \partial_{u_n}^0 d_2 \\ \vdots & \vdots & \ddots & \vdots \\ \partial_{u_1}^0 d_n & \partial_{u_2}^0 d_n & \cdots & \partial_{u_n}^0 d_n \end{pmatrix}.$$

From

$$\partial_{u_i} (\partial_{v_j} R_0(x_1, x_2, \mathbf{u}, \mathbf{v})|_{\mathbf{v}=\mathbf{u}}) = \frac{\partial^2 R_0(x_1, x_2, \mathbf{u}, \mathbf{v})}{\partial u_i \partial v_j} \Big|_{\mathbf{v}=\mathbf{u}} + \frac{\partial^2 R_0(x_1, x_2, \mathbf{u}, \mathbf{v})}{\partial v_i \partial v_j} \Big|_{\mathbf{v}=\mathbf{u}}$$

and assumption A1 (which implies that the first term vanishes when evaluated at an extinction equilibrium) we obtain

$$\partial_{u_i}^0 (\partial_{v_j} R_0(x_1, x_2, \mathbf{u}, \mathbf{v})|_{\mathbf{v}=\mathbf{u}}) = \frac{\partial^2 R_0(0, 0, \mathbf{u}^*, \mathbf{v})}{\partial v_i \partial v_j} \Big|_{\mathbf{v}=\mathbf{u}^*}.$$

By the definition of critical trait \mathbf{u}^* we know that $\partial_{v_j}^0 R_0 = 0$ and therefore $\mathbf{v} = \mathbf{u}^*$ is a critical point of $R_0(0, 0, \mathbf{u}^*, \mathbf{v})$. From the definition (4) of $d_i(x_1, x_2, \mathbf{u})$ we have

$$H^0 = \frac{1}{2R_0^0} \begin{pmatrix} \partial_{v_1 v_1}^0 R_0 & \partial_{v_1 v_2}^0 R_0 & \cdots & \partial_{v_1 v_n}^0 R_0 \\ \partial_{v_2 v_1}^0 R_0 & \partial_{v_2 v_2}^0 R_0 & \cdots & \partial_{v_2 v_n}^0 R_0 \\ \vdots & \vdots & \ddots & \vdots \\ \partial_{v_n v_1}^0 R_0 & \partial_{v_n v_2}^0 R_0 & \cdots & \partial_{v_n v_n}^0 R_0 \end{pmatrix},$$

which is a multiple of the Hessian of $R_0(x_1, x_2, \mathbf{u}, \mathbf{v})$ with respect to \mathbf{v} evaluated at the extinction equilibrium. Since $R_0(x_1, x_2, \mathbf{u}, \mathbf{v})$ has continuous partial derivatives, H^0 is symmetric. We make the assumption that

A4: H^0 is non-singular.

In addition to the n eigenvalues of T^0 , the Jacobian \mathcal{J}^0 has eigenvalues $\lambda_{1,2} = \pm\sqrt{R_0^0}$. Therefore, the extinction equilibrium is stable if $R_0^0 < 1$ and the n eigenvalues of T^0 have magnitude less than one.

Recall that a real, symmetric matrix M is positive (semi-) definite if, given a non-zero column vector z , $z^T M z$ is real and positive (non-negative). A matrix M is negative (semi-) definite if $z^T M z$ is real and negative (non-positive). Finally, a matrix M is indefinite if it is neither positive semi-definite nor negative semi-definite. A positive (semi-) definite matrix has all positive (non-negative) eigenvalues, a negative (semi-) definite matrix has all negative (non-positive) eigenvalues and an indefinite matrix has both positive and negative eigenvalues. The stability of the extinction equilibrium depends on the definiteness of H^0 , as seen in the following theorem.

Theorem 3.1. *Assume A1, A2, A3, and A4 hold. If the variances ν_i are small, then the extinction equilibrium $(x_1, x_2, \mathbf{u}) = (0, 0, \mathbf{u}^*)$ of (7) is*

- (a) *locally asymptotically stable if $R_0^0 < 1$ and H^0 is negative definite;*
- (b) *unstable if $R_0^0 > 1$ or H^0 is positive semi-definite or indefinite.*

Proof. Let λ be an eigenvalue of H^0 . In the Appendix, we show that the eigenvalues of $\mathcal{C}H^0$ have the same sign as the eigenvalues of H^0 . Therefore, we can write an eigenvalue of $T^0 = I + \mathcal{C}H^0$ as $\lambda_T = 1 + \alpha\lambda$, where α is some positive constant. If $\lambda > 0$, then $\lambda_T > 1$ and the extinction equilibrium is unstable. Therefore, the extinction equilibrium is unstable if H^0 is positive semi-definite or indefinite.

If H^0 is negative definite, then $\lambda < 0$ and $\lambda_T < 1$. Let $\rho(M)$ denote the spectral radius of matrix M . Since we assumed in A3 that \mathcal{C} is diagonally dominant, $\nu_i \geq \sum_{k \neq i} |\delta_{ik}|$, we have

$$\rho(\mathcal{C}) \leq \|\mathcal{C}\|_1 = \max_i \left(\nu_i + \sum_j |\delta_{ij}| \right) \leq 2 \max_i \nu_i.$$

Since the spectral radius is always less than or equal to a matrix norm and is equal to the 2-norm for symmetric matrices, if $\max_i \nu_i < 1/\rho(H^0)$, then

$$\rho(\mathcal{C}H^0) \leq \|\mathcal{C}H^0\|_2 \leq \|\mathcal{C}\|_2 \|H^0\|_2 \leq \rho(\mathcal{C})\rho(H^0) < 2$$

and $|\lambda_T| < 1$. Since this holds for each eigenvalue of T^0 , the stability of the extinction equilibrium will depend on the value of R_0^0 when H^0 is negative definite. If H^0 is negative definite, the extinction equilibrium is stable for $R_0^0 < 1$ and unstable for $R_0^0 > 1$. \square

In the proof of Theorem 3.1, we pointed out that any eigenvalue of T^0 is of the form $1 + \alpha\lambda$ where λ is an eigenvalue of H^0 and α is a positive constant. Therefore, a necessary condition for the stability of the extinction equilibrium is that all the eigenvalues of H^0 are negative. Notice that Theorem 3.1 does not cover the case when H^0 is negative semi-definite. For this case, at least one of the eigenvalues of T^0 is equal to 1 and the linearization principle does not apply.

When H^0 is negative definite, the extinction equilibrium $(x_1, x_2, \mathbf{u}) = (0, 0, \mathbf{u}^*)$ destabilizes as R_0^0 increases through 1. In general, such an occurrence in a dynamic

model signals the transcritical bifurcation of positive equilibria from the extinction equilibrium. Specifically for general non-evolutionary matrix models see [8], [12]. For imprimitive projection matrices, periodic cycles also bifurcate from the extinction equilibrium as R_0^0 increases through 1. For non-evolutionary matrix models see [10], [16]. That these bifurcations occur in the evolutionary model (7) was shown in [18] for (7) when $n = 1$. Our goal in Sections 4 and 5 is to establish the occurrence of these bifurcations for (7) when $n \geq 1$. We also determine stability criteria of the bifurcating equilibria and cycles.

Note that the assumption that H^0 is negative definite implies that both the inherent net reproductive number

$$R_0(0, 0, \mathbf{u}^*, \mathbf{v}) = b\beta(\mathbf{v})s(\mathbf{v})$$

and the inherent fitness $\ln r(0, 0, \mathbf{u}^*, \mathbf{v}) = \ln b\beta(\mathbf{v})s(\mathbf{v})$ of a focal individual have local maxima at $\mathbf{v} = \mathbf{u}^*$ as functions of \mathbf{v} . (If the Hessian is positive definite or indefinite, \mathbf{u}^* corresponds to a minimum or saddle.)

4. Existence and stability of positive equilibria. An equilibrium $(x_1, x_2, \mathbf{u}) \in R^2 \times V$ of (3) is a *positive* equilibrium if $(x_1, x_2) \in R_+^2$. A positive equilibrium (x_1, x_2, \mathbf{u}) of (3) must satisfy the equilibrium equations

$$x_1 = R_0^0 \frac{1}{s_0} \beta(\mathbf{u}) \phi(x_1, x_2, \mathbf{u}, \mathbf{u}) x_2 \tag{11a}$$

$$x_2 = s(\mathbf{u}) \sigma(x_1, x_2, \mathbf{u}, \mathbf{u}) x_1 \tag{11b}$$

$$0 = C\mathbf{d}(x_1, x_2, \mathbf{u}) \tag{11c}$$

with $(x_1, x_2) \in R_+^2$. In what follows we establish, using the value of R_0^0 as a bifurcation parameter, the existence of a branch of equilibria that bifurcates from the extinction equilibrium $(0, 0, \mathbf{u}^*)$ at $R_0^0 = 1$.

We also establish that connections between the direction of bifurcation and stability of these equilibria. We say that the bifurcation of *positive* equilibria (x_1, x_2, \mathbf{u}) is forward (super-critical or to the right) if in a neighborhood of $(0, 0, \mathbf{u}^*)$ and $R_0^0 = 1$ the bifurcating positive equilibria correspond to $R_0^0 \gtrsim 1$. The bifurcation of *positive* equilibria is backward (sub-critical or to the left) if the bifurcating positive equilibria correspond to $R_0^0 \lesssim 1$.

The following quantities will be important

$$c_w(\mathbf{u}) \triangleq \partial_{x_1} \sigma(0, 0, \mathbf{u}, \mathbf{u}) + s(\mathbf{u}) \partial_{x_2} \phi(0, 0, \mathbf{u}, \mathbf{u}) \tag{12a}$$

$$c_b(\mathbf{u}) \triangleq \partial_{x_1} \phi(0, 0, \mathbf{u}, \mathbf{u}) + s(\mathbf{u}) \partial_{x_2} \sigma(0, 0, \mathbf{u}, \mathbf{u}) \tag{12b}$$

$$a_{\pm}(\mathbf{u}) \triangleq c_w(\mathbf{u}) \pm c_b(\mathbf{u}). \tag{12c}$$

Since σ accounts for the effects of density on juvenile survival and ϕ accounts for the effects of density on adult reproduction, one can interpret the quantities $c_w(\mathbf{u})$ and $c_b(\mathbf{u})$ as measures of the within-class and between-class competition in a population with mean trait vector \mathbf{u} in the absence of density effects. Consequently, $a_+(\mathbf{u})$ is a measure of the total competition within the population and $a_-(\mathbf{u})$ is the difference between within and between class competition.

Theorem 4.1. *Assume A1, A2, A3, A4 and that the variances ν_i are small.*

(a) *If $a_+^0 \neq 0$, then a continuum of positive equilibria (x_1, x_2, \mathbf{u}) of (5), as a function of R_0^0 , bifurcates from the extinction equilibrium $(0, 0, \mathbf{u}^*)$ at $R_0^0 = 1$.*

(b) *The bifurcation is backward if $a_+^0 > 0$. In this case the bifurcating equilibria are unstable.*

(c) The bifurcation is forward if $a_+^0 < 0$. In this case, the bifurcating equilibria are locally asymptotically stable if $a_-^0 < 0$ and H^0 is negative definite. They are unstable if $a_-^0 > 0$, H^0 is positive semi-definite, or H^0 is indefinite.

Proof. (a) To establish the existence of equilibria bifurcating from the extinction equilibrium at $R_0^0 = 1$ we make use of the Implicit Function Theorem. The extinction equilibrium $(0, 0, \mathbf{u}^*)$ satisfies the equilibrium equations (11) for all values of R_0^0 . For positive equilibria ($x_i > 0$), we can re-write the equilibrium equations (11) equivalently as

$$h_1(x_1, x_2, \mathbf{u}, R_0^0) = h_2(x_1, x_2, \mathbf{u}, R_0^0) = g_i(x_1, x_2, \mathbf{u}, R_0^0) = 0$$

where

$$h_1(x_1, x_2, \mathbf{u}, R_0^0) \triangleq R_0^0 \frac{1}{s^0} \beta(\mathbf{u}) s(\mathbf{u}) \phi(x_1, x_2, \mathbf{u}, \mathbf{u}) \sigma(x_1, x_2, \mathbf{u}, \mathbf{u}) - 1 \quad (13a)$$

$$h_2(x_1, x_2, \mathbf{u}, R_0^0) \triangleq s(\mathbf{u}) \sigma(x_1, x_2, \mathbf{u}, \mathbf{u}) x_1 - x_2 \quad (13b)$$

$$g_i(x_1, x_2, \mathbf{u}, R_0^0) \triangleq \nu_i d_i(x_1, x_2, \mathbf{u}) + \sum_{k \neq i} \delta_{ik} d_k(x_1, x_2, \mathbf{u}) \quad \text{for } i = 1, \dots, n. \quad (13c)$$

The extinction equilibrium $(0, 0, \mathbf{u}^*)$ satisfies these three equations if $R_0^0 = 1$. By the Implicit Function Theorem, we can (uniquely) solve equations (13) for

$$(x_1, x_2, \mathbf{u}) = (x_1(R_0^0), x_2(R_0^0), \mathbf{u}(R_0^0))$$

where $x_1(R_0^0)$, $x_2(R_0^0)$, and $\mathbf{u}(R_0^0)$ are twice continuously differentiable functions of $R_0^0 \approx 1$ for which

$$(x_1(1), x_2(1), \mathbf{u}(1)) = (0, 0, \mathbf{u}^*)$$

if the Jacobian of (13) with respect to (x_1, x_2, \mathbf{u}) is nonsingular when evaluated at $(x_1, x_2, \mathbf{u}) = (0, 0, \mathbf{u}^*)$ and $R_0^0 = 1$. This evaluation gives

$$\begin{pmatrix} A & \mathbf{0}_{2 \times n} \\ B & CH^0 \end{pmatrix}.$$

where A is the 2×2 matrix

$$A = \begin{pmatrix} \partial_{x_1}^0 \phi + \partial_{x_1}^0 \sigma & \partial_{x_2}^0 \phi + \partial_{x_2}^0 \sigma \\ s^0 & -1 \end{pmatrix},$$

$\mathbf{0}_{2 \times n}$ is the $2 \times n$ matrix of zeros, and B is a $n \times 2$ matrix we have no need to specify. The determinant of this Jacobian matrix is $-a_+^0 \det(CH^0)$. Since CH^0 is non-singular, the determinant of the Jacobian is non-zero if $a_+^0 \neq 0$. The solutions $(x_1, x_2, \mathbf{u}) = (x_1(R_0^0), x_2(R_0^0), \mathbf{u}(R_0^0))$ resulting from an application of the Implicit Function Theorem constitute equilibria of (5) for $R_0^0 \approx 1$.

(b) Defining $\varepsilon = R_0^0 - 1$ we can consider the equilibria as parameterized by ε and describe the bifurcating branch of equilibria as $(x_1(\varepsilon), x_2(\varepsilon), \mathbf{u}(\varepsilon), R_0^0(\varepsilon))$ where $(x_1(0), x_2(0), \mathbf{u}(0), R_0^0(0)) = (0, 0, \mathbf{u}^*, 1)$. To determine the direction of bifurcation, we calculate Taylor expansions of $(x_1(\varepsilon), x_2(\varepsilon), \mathbf{u}(\varepsilon), R_0^0(\varepsilon))$ to order 1 in ε at $\varepsilon = 0$. These calculations are no different from those carried out for the case of $n = 1$ trait in [18]. The result is

$$x_1(\varepsilon) = \frac{-1}{a_+^0} \varepsilon + \mathcal{O}(\varepsilon^2), \quad x_2(\varepsilon) = \frac{-s^0}{a_+^0} \varepsilon + \mathcal{O}(\varepsilon^2), \quad R_0^0(\varepsilon) = 1 + \varepsilon. \quad (14)$$

If $a_+^0 < 0$ ($a_+^0 > 0$) then the equilibria are positive for $\varepsilon \gtrsim 0$ ($\varepsilon \lesssim 0$) and the bifurcation is forward (backward).

We analyze the local stability of the bifurcating positive equilibria by considering the Jacobian (9) of the model equations (7) evaluated at the positive equilibria $(x_1(\varepsilon), x_2(\varepsilon), \mathbf{u}(\varepsilon), R_0^0(\varepsilon))$ for $\varepsilon \approx 0$.

At $\varepsilon = 0$ the Jacobian (9) reduces to (10) whose eigenvalues are the eigenvalues $\lambda_1 = 1$ and $\lambda_2 = -1$ of P^0 and the n eigenvalues of T^0 . We need to determine whether these eigenvalues have absolute value less than or greater than 1 when $\varepsilon \approx 0$. Taylor expansions of first two eigenvalues $\lambda_1(\varepsilon)$ and $\lambda_2(\varepsilon)$ are calculated exactly as they are in [18] for the case of $n = 1$ trait. The result is

$$\lambda_1(\varepsilon) = 1 - \frac{1}{2}\varepsilon + \mathcal{O}(\varepsilon^2), \quad \lambda_2(\varepsilon) = -1 + \frac{1}{2} \frac{a_-^0}{a_+^0} \varepsilon + \mathcal{O}(\varepsilon^2). \tag{15}$$

The expansion for $\lambda_1(\varepsilon)$ shows that a backward bifurcation (when positive equilibria correspond to $\varepsilon < 0$) is unstable. As we have seen, this occurs when $a_+^0 > 0$.

(c) Suppose $a_+^0 < 0$. Then the bifurcating equilibria (14) are given by $\varepsilon > 0$, which means the bifurcation is forward. From (15) we see that $0 < \lambda_1(\varepsilon) < 1$ for $\varepsilon \gtrsim 0$. The expansion for $\lambda_2(\varepsilon)$ shows $\lambda_2(\varepsilon) < -1$ or $-1 < \lambda_2(\varepsilon) < 0$ for $\varepsilon \gtrsim 0$ if $a_-^0 > 0$ or $a_-^0 < 0$ respectively. Thus the positive equilibria are unstable if $a_-^0 > 0$. If, on the other hand, $a_-^0 < 0$ stability of the positive equilibria is determined by the n eigenvalues of T .

In the proof of Theorem 3.1, we showed that if H^0 has a positive eigenvalue, then the corresponding eigenvalue of T^0 has magnitude greater than 1. By continuity, this eigenvalue has magnitude greater than 1 for $\varepsilon \approx 0$. Hence, the positive equilibria are unstable when H^0 is positive semi-definite or indefinite. On the other hand, when H^0 is negative definite we showed that each eigenvalue of T^0 has magnitude less than one provided $\nu_i \approx 0$ for all i . By continuity, the eigenvalues of T have magnitude less than one for $\varepsilon \approx 0$. Thus, when H^0 is negative definite the positive equilibria are stable. This proves (c). □

Theorem 4.1 establishes the bifurcation of a branch of positive equilibria from the extinction equilibrium at $R_0^0 = 1$. Unlike matrix models whose projection matrices are primitive, the stability of the bifurcating positive equilibria for the semelparous model (7) is not fully determined by the direction of bifurcation. While a backward bifurcation does yield unstable equilibria (Theorem 4.1(b)), a forward bifurcation does not necessarily yield stable equilibria. The criteria for the bifurcation of stable positive equilibria given in Theorem 4.1(c) are the inequalities $a_{\pm}(\mathbf{u}^*) < 0$ and that H^0 be negative definite. How are these criteria to be interpreted ecologically?

The inequalities $a_{\pm}(\mathbf{u}^*) = c_w(\mathbf{u}^*) \pm c_b(\mathbf{u}^*) < 0$ are equivalent to $c_w(\mathbf{u}^*) < 0$ and $|c_b(\mathbf{u}^*)| < |c_w(\mathbf{u}^*)|$. These inequalities mean that the within-class competition intensity must have net negative feedback effect and must be of larger magnitude than the between-class competition intensity (near the bifurcation point, i.e. at low population densities and trait vectors \mathbf{u} and \mathbf{v} near \mathbf{u}^*). These requirements are in keeping with non-evolutionary, semelparous Leslie models [10], [11], [16]. At the end of Section 3 we noted that the interpretation of H^0 being negative definite is that the inherent fitness of a focal individual is at a local maximum when its multi-trait vector \mathbf{v} equals the critical trait vector \mathbf{u}^* . This result is in keeping with the case of only $n = 1$ evolving trait [18].

In the next section we turn attention to the bifurcation of period 2 cycles that accompanies the bifurcation of positive equilibria in Theorem 4.1.

5. Existence and stability of synchronous 2-cycles. Under the map (3), a point (x_1, x_2, \mathbf{u}) with component $x_1 = 0$ maps to a point with component $x_2 = 0$ which in turn maps to a point with component $x_1 = 0$ and so on. Thus, the set $\partial R_+^2 \setminus \{(0, 0)\} \times U$ is invariant. We refer to orbits on $\partial R_+^2 \setminus \{(0, 0)\} \times U$ as *synchronous orbits*. Biologically, juvenile and adult populations do not temporally overlap along synchronous orbits. A periodic orbit on $\partial R_+^2 \setminus \{(0, 0)\} \times U$ is called a *synchronous cycle*. A synchronous 2-cycle temporally alternates between two points of the form $(x_1, 0, \mathbf{u}_1)$ and $(0, x_2, \mathbf{u}_2)$ and is a fixed point of the composite map obtained by applying (3) twice. Thus, a synchronous 2-cycle must satisfy the composite equations

$$x_1 = R_0^0 \frac{1}{s_0} \beta(\mathbf{u}_2) s(\mathbf{u}_1) \phi(0, s(\mathbf{u}_1) \sigma(x_1, 0, \mathbf{u}_1, \mathbf{u}_1) x_1, \mathbf{u}_2, \mathbf{u}_2) \sigma(x_1, 0, \mathbf{u}_1, \mathbf{u}_1) x_1 \tag{16a}$$

$$0 = \mathcal{C}d(x_1, 0, \mathbf{u}_1) + \mathcal{C}d(0, s(\mathbf{u}_1) \sigma(x_1, 0, \mathbf{u}_1, \mathbf{u}_1) x_1, \mathbf{u}_2) \tag{16b}$$

for x_1 and u_1 where

$$\mathbf{u}_2 = \mathbf{u}_1 + \mathcal{C}d(x_1, 0, \mathbf{u}_1).$$

Using these equations, we can establish the existence of a branch of synchronous 2-cycles bifurcating from the extinction equilibrium as a function of R_0^0 .

Theorem 5.1. *Assume A1, A3, A2, A4 and that the variances ν_i are small.*

(a) *If $c_w^0 \neq 0$ then a continuum of positive 2-cycles bifurcates, as a function of R_0^0 , from the extinction equilibrium $(0, 0, \mathbf{u}^*)$ at $R_0^0 = 1$.*

(b) *The bifurcation is backward if $c_w^0 > 0$. The bifurcating 2-cycles are unstable.*

(c) *The bifurcation is forward if $c_w^0 < 0$. The bifurcating 2-cycles are unstable if $a_-^0 < 0$, H^0 is positive semi-definite, or H^0 is indefinite. The bifurcating 2-cycles are locally asymptotically stable if $a_-^0 > 0$ and H^0 is negative definite.*

Proof. (a) To establish the existence of synchronous 2-cycles, we solve the composite equations (16) for $x_1 > 0$ and $\mathbf{u} = \mathbf{u}_1$ as functions of R_0^0 . We do this by applying the Implicit Function Theorem to the equations

$$h(x_1, \mathbf{u}, R_0^0) = 0 \tag{17a}$$

$$g_i(x_1, \mathbf{u}, R_0^0) = 0 \tag{17b}$$

where

$$h(x_1, \mathbf{u}, R_0^0) \triangleq R_0^0 \frac{1}{s_0} \beta(\mathbf{u}_2) s(\mathbf{u}) \phi[0, s(\mathbf{u}) \sigma(x_1, 0, \mathbf{u}, \mathbf{u}) x_1, \mathbf{u}_2, \mathbf{u}_2] \sigma[x_1, 0, \mathbf{u}, \mathbf{u}] - 1$$

$$g_i(x_1, \mathbf{u}, R_0^0) \triangleq d_i(x_1, 0, \mathbf{u}) + d_i[0, s_1(\mathbf{u}) \sigma(x_1, 0, \mathbf{u}, \mathbf{u}) x_1, \mathbf{u}_2(x_1, \mathbf{u})]$$

and $\mathbf{u}_2(x_1, \mathbf{u}) = (u_{2,1}(x_1, \mathbf{u}), \dots, u_{2,n}(x_1, \mathbf{u}))^T$ has components

$$u_{2,j}(x_1, \mathbf{u}) = u_j + \nu_j d_j(x_1, 0, \mathbf{u}) + \sum_{k \neq j} \delta_{jk} d_k(x_1, 0, \mathbf{u}) \text{ for } j = 1, \dots, n.$$

Straightforward calculations verify that the $n \times n$ Jacobian of the equations (17b) with respect to \mathbf{u} , when evaluated at the extinction equilibrium, is the matrix

$$H^0 [2I + CH^0]$$

where I is the $n \times n$ identity matrix. To arrive at this result, note that

$$\partial_{u_i}^0 u_{2,j} = \begin{cases} \nu_j d_{jl}^0 + \sum_{k \neq j} \delta_{jk} d_{kl}^0 & \text{for } j \neq l \\ 1 + \nu_l d_{ll}^0 + \sum_{k \neq l} \delta_{lk} d_{kl}^0 & \text{for } j = l \end{cases} = \begin{cases} a_{jl} & \text{for } j \neq l \\ 1 + a_{ll} & \text{for } j = l \end{cases}$$

where we have defined $d_{ij} \triangleq \partial_{u_j} d_i$ and a_{nm} as the entry of $\mathcal{C}H^0$ located in the n th row and m th column. Therefore,

$$\partial_{u_l}^0 g_i = d_{il}^0 + \sum_j d_{ij}^0 \partial_{u_l}^0 u_{2,j} = 2d_{il}^0 + \sum_j d_{ij}^0 a_{jl}$$

where the last sum is the i th row of H^0 multiplied by the l th column of $\mathcal{C}H^0$.

In the proof of Theorem 3.1, we showed that $\rho(\mathcal{C}H^0) \leq 2 \max_i \nu_i \rho(H^0)$. For sufficiently small variances ν_i , this means that the eigenvalues of $2I + \mathcal{C}H^0$ are positive. Since H^0 is non-singular,

$$\det(H^0 [2I + \mathcal{C}H^0]) = \det(H^0) \det(2I + \mathcal{C}H^0) \neq 0.$$

The nonsingularity of this Jacobian with respect to \mathbf{u} permits an application of the Implicit Function Theorem to the equations (17b), which implies the existence of a (smooth and unique) solution $\mathbf{u} = \eta(x_1) = (\eta_1(x_1), \dots, \eta_n(x_1))^T$ such that $\eta(0) = \mathbf{u}^*$.

To solve the equations (17), and hence obtain a synchronous 2-cycle, we substitute the solution $\mathbf{u} = \eta(x_1)$ of (17b) into equation (17a) and solve the resulting equation for x_1 . This substitution gives

$$\begin{aligned} h(x_1, \eta(x_1), R_0^0) &\triangleq R_0^0 \frac{1}{s_0} \beta(\mathbf{u}_2(x_1)) s(\eta(x_1)) \\ &\quad \times \phi[0, s(\eta(x_1)) \sigma(x_1, 0, \eta(x_1), \eta(x_1)) x_1, \mathbf{u}_2(x_1), \mathbf{u}_2(x_1)] \\ &\quad \times \sigma[x_1, 0, \eta(x_1), \eta(x_1)] - 1 \end{aligned}$$

where $\mathbf{u}_2(x_1, \eta(x_1))$ is now a function of x_1 which we denote simply by $\mathbf{u}_2(x_1)$. The components of $\mathbf{u}_2(x_1) = (u_{2,1}(x_1), \dots, u_{2,n}(x_1))^T$ are

$$u_{2,j}(x_1) = \eta_j(x_1) + \nu_j d_j(x_1, 0, \eta(x_1)) + \sum_{k \neq j} \delta_{jk} d_k(x_1, 0, \eta(x_1)) \text{ for } j = 1, \dots, n.$$

Our goal is to solve the resulting equation

$$h(x_1, \eta(x_1), R_0^0) = 0 \tag{20}$$

for $x_1 = x_1(R_0^0)$, $x_1(1) = 0$, by means of another application of the Implicit Function Theorem. Since $h(0, \mathbf{u}^*, 1) = 0$ this requires showing the derivative of $h(x_1, \eta(x_1), R_0^0)$ with respect to x_1 is nonzero when evaluated at $x_1 = 0$ and $R_0^0 = 1$.

The factors involving ϕ and σ in the triple product defining $f(x_1, \eta(x_1), R_0^0)$ equal 1 when evaluated at $x_1 = 0$ and $R_0^0 = 1$ and their derivatives with respect to \mathbf{u} and \mathbf{v} equal 0 when evaluated at $x_1 = 0$ and $R_0^0 = 1$. These facts follow from assumption A1. As a result we have

$$\left. \frac{dh(x_1, \eta(x_1), R_0^0)}{dx_1} \right|_{x_1=0, R_0^0=1} = c_w^0 + \frac{1}{s_0} \left. \frac{d\beta(\mathbf{u}_2(x_1)) s(\eta(x_1))}{dx_1} \right|_{x_1=0, R_0^0=1}.$$

To complete this calculation we use $\partial_{v_i}^0 \beta s^0 + \partial_{v_i} s^0 = 0$ (equation (8)) and $\partial_{x_1}^0 d_i = \sum_j d_{ij}^0 \partial_{x_1}^0 \eta_j$ together with the calculation

$$\begin{aligned} \partial_{x_1}^0 u_{2,i} &= \partial_{x_1}^0 \eta_i + \nu_i \partial_{x_1}^0 d_i + \sum_{k \neq i} \delta_{ik} \partial_{x_1}^0 d_k + \nu_i \sum_{j=1}^n d_{ij}^0 \partial_{x_1}^0 \eta_j + \sum_{k \neq i} \delta_{ik} \sum_{j=1}^n d_{kj}^0 \partial_{x_1}^0 \eta_j \\ &= \partial_{x_1}^0 \eta_i + 2\nu_i \sum_{j=1}^n d_{ij}^0 \partial_{x_1}^0 \eta_j + 2 \sum_{k \neq i} \delta_{ik} \sum_{j=1}^n d_{kj}^0 \partial_{x_1}^0 \eta_j \\ &= \partial_{x_1}^0 \eta_i + 2\mathcal{C}H^0 \partial_{x_1} \eta. \end{aligned}$$

We obtain

$$\begin{aligned} \frac{dh(x_1, \eta(x_1), R_0^0)}{dx_1} \Big|_{x_1=0, R_0^0=1} &= c_w^0 + \sum_{i=1}^n \partial_{v_i}^0 \beta \partial_{x_1}^0 u_{2,i} + \frac{1}{s^0} \sum_{i=1}^n \partial_{v_i}^0 s \partial_{x_1}^0 \eta_i \\ &= c_w^0 + \frac{1}{s^0} \sum_{i=1}^n (\partial_{v_i}^0 \beta s^0 + \partial_{v_i}^0 s) \partial_{x_1}^0 \eta_i + 2\nabla_{\mathbf{v}} \beta^T \mathcal{C} H^0 \partial_{x_1} \eta \\ &= c_w^0 + 2\nabla_{\mathbf{v}} \beta^T \mathcal{C} H^0 \partial_{x_1} \eta, \end{aligned}$$

where

$$\nabla_{\mathbf{v}} \beta \triangleq (\partial_{u_1}^0 \beta, \dots, \partial_{u_n}^0 \beta)^T \quad \text{and} \quad \partial_{x_1} \eta \triangleq (\partial_{x_1}^0 \eta_1, \dots, \partial_{x_1}^0 \eta_n)^T.$$

Since

$$|\nabla_{\mathbf{v}} \beta^T \mathcal{C} H^0 \partial_{x_1} \eta| \leq 2 \max_i \nu_i \|\nabla_{\mathbf{v}} \beta\| \cdot \|H^0\| \cdot \|\partial_{x_1} \eta\|$$

and $\nu_i \approx 0$, we have $\partial_{x_1}^0 h \neq 0$ provided $c_w^0 \neq 0$. The Implicit Function Theorem implies the existence of a (smooth and unique) function $x_1 = x_1(R_0^0)$ of the equation (20). The pair $(x_1, \mathbf{u}) = (x_1(R_0^0), \eta(x_1(R_0^0)))$ then solves the equations (17) for $R_0^0 \approx 1$ such that $(x_1, \mathbf{u}) = (0, \mathbf{u}^*)$ when $R_0^0 = 1$.

We construct a synchronous 2-cycle for $R_0^0 \approx 1$ by means of the two points

$$(x_1, 0, \mathbf{u}_1) = (x_1(R_0^0), 0, \mathbf{u}_1(R_0^0)) \quad \text{and} \quad (0, x_2, \mathbf{u}_2) = (0, x_2(R_0^0), \mathbf{u}_2(R_0^0))$$

where

$$\begin{aligned} \mathbf{u}_1(R_0^0) &= \mathbf{u}(R_0^0), \quad \mathbf{u}_2(R_0^0) = \mathbf{u}_1(R_0^0) + \mathcal{C} \mathbf{d}(x_1(R_0^0), 0, \mathbf{u}_1(R_0^0)) \\ x_2(R_0^0) &= s(\mathbf{u}_1(R_0^0)) \sigma(x_1(R_0^0), 0, \mathbf{u}_1(R_0^0), \mathbf{u}_1(R_0^0)) x_1(R_0^0). \end{aligned}$$

When $R_0^0 = 1$ both points equal $(0, 0, \mathbf{u}^*)$.

Instead of R_0^0 we can consider the two cycle points to be parameterized by small $\varepsilon \triangleq R_0^0 - 1$ and write

$$(x_1(\varepsilon), 0, \mathbf{u}(\varepsilon)) \quad \text{and} \quad (0, x_2(\varepsilon), \mathbf{u}_2(\varepsilon))$$

where both equal the extinction equilibrium $(0, 0, \mathbf{u}^*)$ when $\varepsilon = 0$.

To determine the direction of bifurcation, we calculate Taylor expansions of $x_1(\varepsilon)$ and $x_2(\varepsilon)$ to order 1 in ε at $\varepsilon = 0$. An implicit differentiation of the equation

$$h(x_1(\varepsilon), \eta(x_1(\varepsilon)), 1 + \varepsilon) = 0,$$

which arises from (20), with respect to ε followed by evaluation at $\varepsilon = 0$ yields

$$\partial_{\varepsilon}^0 x_1 = -\frac{\partial_{\varepsilon}^0 h}{\partial_{x_1}^0 h} = \frac{1}{-c_w^0 - 2\nabla_{\mathbf{v}} \beta^T \mathcal{C} H^0 \partial_{x_1}^0 \eta}$$

whose sign, when $\nu_i \approx 0$, is the same as the sign of $-c_w^0$. From the expansions

$$\begin{aligned} \begin{pmatrix} x_1(\varepsilon) \\ 0 \\ \mathbf{u}(\varepsilon) \end{pmatrix} &= \begin{pmatrix} 0 \\ 0 \\ \mathbf{u}^* \end{pmatrix} + \begin{pmatrix} (-c_w^0 - 2\nabla_{\mathbf{v}} \beta^T \mathcal{C} H^0 \partial_{x_1}^0 \eta)^{-1} \\ 0 \\ \mathbf{u}'_1(0) \end{pmatrix} \varepsilon + O(\varepsilon^2) \\ \begin{pmatrix} 0 \\ x_2(\varepsilon) \\ \mathbf{u}_2(\varepsilon) \end{pmatrix} &= \begin{pmatrix} 0 \\ 0 \\ \mathbf{u}^* \end{pmatrix} + \begin{pmatrix} 0 \\ s^0 (-c_w^0 - 2\nabla_{\mathbf{v}} \beta^T \mathcal{C} H^0 \partial_{x_1}^0 \eta)^{-1} \\ \mathbf{u}'_2(0) \end{pmatrix} \varepsilon + O(\varepsilon^2) \end{aligned}$$

for small ε we see that the synchronous 2-cycles are positive for $\varepsilon \gtrsim 0$ ($\varepsilon \lesssim 0$) if $c_w^0 < 0$ ($c_w^0 > 0$ respectively). This proves part (a).

To complete the proof of Theorem 3 we need to establish the stability assertions in parts (b) and (c). To do this we examine the eigenvalues of the Jacobian of the composite map. The Jacobian of the composite is the product of the Jacobians of the map evaluated at the two points on the 2-cycle. At $\varepsilon = 0$ this reduces to squaring the matrix (10). Therefore, when $\varepsilon = 0$ the eigenvalues of the composite map are the two eigenvalues of $(P^0)^2$, namely, $\lambda_1 = 1$ and $\lambda_2 = 1$ and the n eigenvalues of $(T^0)^2$. We need to determine whether these eigenvalues have absolute value less than or greater than 1 when $\varepsilon \approx 0$.

(b) For the non-evolutionary model, i.e. when $\nu_i = 0$, the parameterizations for the eigenvalues of $(P^0)^2$ are the same as they are in [18] for the case of $n = 1$ trait, namely

$$\lambda_1(\varepsilon) = 1 - \varepsilon + \mathcal{O}(\varepsilon^2), \quad \lambda_2(\varepsilon) = 1 + \frac{a_-^0}{c_w^0} \varepsilon + \mathcal{O}(\varepsilon^2).$$

The expansion for $\lambda_1(\varepsilon)$ shows that the backward bifurcation (when non-negative 2-cycles correspond to $\varepsilon < 0$) is unstable. By continuity, $\lambda_1(\varepsilon) > 1$ for $\varepsilon \lesssim 0$ and $\nu_i \approx 0$. This implies the backward bifurcation of 2-cycles (which occurs when $c_w^0 > 0$) is unstable for $\nu_i \approx 0$.

(c) Consider the case when the bifurcation is forward, i.e. when $c_w^0 < 0$. When $\nu_i = 0$, $a_-^0 < 0$ implies $\lambda_2(\varepsilon) > 1$ for $\varepsilon \gtrsim 0$ and the bifurcating 2-cycles are unstable. However, if $a_-^0 > 0$ then both $\lambda_1(\varepsilon)$ and $\lambda_2(\varepsilon)$ have absolute value less than 1 for $\varepsilon \gtrsim 0$. By continuity, the same is true for $\nu_i \approx 0$ and the stability of the 2-cycles is determined by the n eigenvalues of $(T^0)^2$. In Theorem 3.1, we showed that if H^0 has a positive eigenvalue, then the corresponding eigenvalue of T^0 has magnitude greater than 1. By continuity, this eigenvalue is greater than one for $\varepsilon \approx 0$. Therefore, the 2-cycles are unstable when H^0 is positive semi-definite or indefinite. When H^0 is negative definite, we showed that the eigenvalues of T^0 have magnitude less than 1 provided $\nu_i \approx 0$. By continuity, the eigenvalues have magnitude less than 1 for $\varepsilon \approx 0$ and $\nu_i \approx 0$. Thus when H^0 is negative definite, the bifurcating synchronous 2-cycles are stable. This proves (c). \square

In comparing Theorem 5.1 to Theorem 4.1 we note that the quantity $c_w(\mathbf{u}^*)$ determines the direction of bifurcation of the synchronous 2-cycles in place of the quantity $a_+(\mathbf{u}^*) = c_w(\mathbf{u}^*) + c_b(\mathbf{u}^*)$ for the positive equilibria. This means it is possible that the directions of bifurcation of the two branches are different. Also note that the stability requirements for a forward bifurcation are opposite: $a_-(\mathbf{u}^*) < 0$ for positive equilibria and $a_-(\mathbf{u}^*) > 0$ for synchronous 2-cycles.

6. An example. We give an example to show that the asymptotic outcome of a Darwinian model with one evolving trait can be different from that of the model with more than one evolving trait, all else being the same. In (3) with $n = 2$ we take

$$s(\mathbf{v}) = \bar{s} \exp\left(-\frac{(v_1 - m_1)^2}{2w_1}\right) \exp\left(-\frac{(v_2 - m_2)^2}{2w_2}\right)$$

$$f(\mathbf{v}) = \bar{f} \exp\left(-\frac{(v_1 - m_3)^2}{2w_3}\right) \exp\left(-\frac{(v_2 - m_4)^2}{2w_4}\right).$$

where \bar{s} and \bar{f} are positive constants and density factors are Leslie-Gower type functionals of the form

$$\sigma(x_1, x_2, \mathbf{u}, \mathbf{v}) = \frac{1}{1 + c_{11}(u_1, v_1)x_1 + c_{12}(u_2, v_1)x_2}$$

$$\phi(x_1, x_2, \mathbf{u}, \mathbf{v}) = \frac{1}{1 + c_{21}(u_1, v_2)x_1 + c_{22}(u_2, v_2)x_2}$$

where the competition coefficients c_{ij} depend on the difference between an individual's trait v_i and the population mean trait u_i (frequency dependence):

$$c_{11}(u_1, v_1) = \bar{c}_{11} \exp\left(-\frac{(u_1 - v_1)^2}{w_{11}^2}\right), \quad c_{12}(u_2, v_1) = \bar{c}_{12} \exp\left(-\frac{(u_2 - v_1)^2}{w_{12}^2}\right),$$

$$c_{21}(u_1, v_2) = \bar{c}_{21} \exp\left(-\frac{(u_1 - v_2)^2}{w_{21}^2}\right), \quad c_{22}(u_2, v_2) = \bar{c}_{22} \exp\left(-\frac{(u_2 - v_2)^2}{w_{22}^2}\right).$$

for nonnegative constants \bar{c}_{ij} [47]. Under assumption A3 this model has only one critical trait pair

$$u_1^* = \frac{m_1 w_3 + m_3 w_1}{w_1 + w_3}, \quad u_2^* = \frac{m_2 w_4 + m_4 w_2}{w_2 + w_4}$$

and, at the associated extinction equilibrium, the net productive rate is

$$R_0^0 = \bar{f} \bar{s} \exp\left(-\frac{(u_1^* - m_1)^2}{2\bar{w}_1}\right) \exp\left(-\frac{(u_2^* - m_2)^2}{2\bar{w}_2}\right)$$

$$\bar{w}_1 \triangleq \frac{w_1 + w_3}{w_1 w_3}, \quad \bar{w}_2 \triangleq \frac{w_2 + w_4}{w_2 w_4}.$$

For the specific parameter values

$$\begin{aligned} \bar{s} &= 0.9, \quad \bar{f} = 3 \\ \bar{c}_{11} &= 0.05, \quad \bar{c}_{12} = 0.2, \quad \bar{c}_{21} = 0.02, \quad \bar{c}_{22} = 0.1 \\ w_i &= 2, \quad w_{ij} = 2 \\ m_1 &= 1, \quad m_2 = 2, \quad m_3 = 0, \quad m_4 = 1 \end{aligned} \tag{23}$$

and (nonsingular) variance-covariance matrix

$$\mathcal{C} = \begin{pmatrix} 0.1 & 0.01 \\ 0.01 & 0.1 \end{pmatrix} \tag{24}$$

the extinction equilibrium is $(x_1, x_2, \mathbf{u}) = (0, 0, \mathbf{u}^*)$ where $\mathbf{u}^* = (\frac{1}{2}, \frac{3}{2})$. A calculation shows $c_w^0 = -0.043 < 0$ and $a_+^0 = -0.178 < 0$ and, as a result, Theorems 3.1, 4.1 and 5.1 imply the forward bifurcation of both the branch of positive equilibria and that of the synchronous 2-cycles. It turns out that $a_- = -0.010 < 0$ and, as a result, it is the branch of forward bifurcating positive equilibria that is stable (and the branch of bifurcating 2-cycles is unstable). Since the value of $R_0^0 = 2.103$ is larger than 1, the model prediction is that solutions of (3) will equilibrate with both classes present. Figure 1 corroborates this prediction for three initial conditions:

$$(x_1, x_2, u_1, u_2) = (1, 2, 2, 0.2), (1, 2, 2, 1), (1, 2, 2, 2). \tag{25}$$

By way of comparison, we consider the case when only u_1 evolves, so that $n = 1$ in (3) and u_2 is instead held fixed, in turn, at the three initial conditions in Figure 1, namely, $u_2 = 0.2, 1$ and 2 . (In this case the variance-covariance matrix $\mathcal{C} = (0.1)$ is 1×1 .) Theorems 3.1, 4.1 and 5.1 (or equivalently the theorems in [18]) predict three different outcomes, as given in Figure 2. In all three cases the branches of positive equilibria and synchronous 2-cycles are forward bifurcating. When u_2 is fixed at $u_2 = 0.2$, it turns out that $R_0^0 < 1$ and extinction results, as illustrated in Figure 2(a). When $u_2 = 1$, it turns out that $R_0^0 > 1$ and the branch of bifurcating

2-cycles is stable, as illustrated in Figure 2(b). Finally, when $u_2 = 2$, it turns out that $R_0^0 > 1$ and the branch of bifurcating positive equilibria is stable, as illustrated in Figure 2(c).

When both traits evolve the three different dynamic outcomes in Figure 2 are all changed to the single outcome in Figure 1.

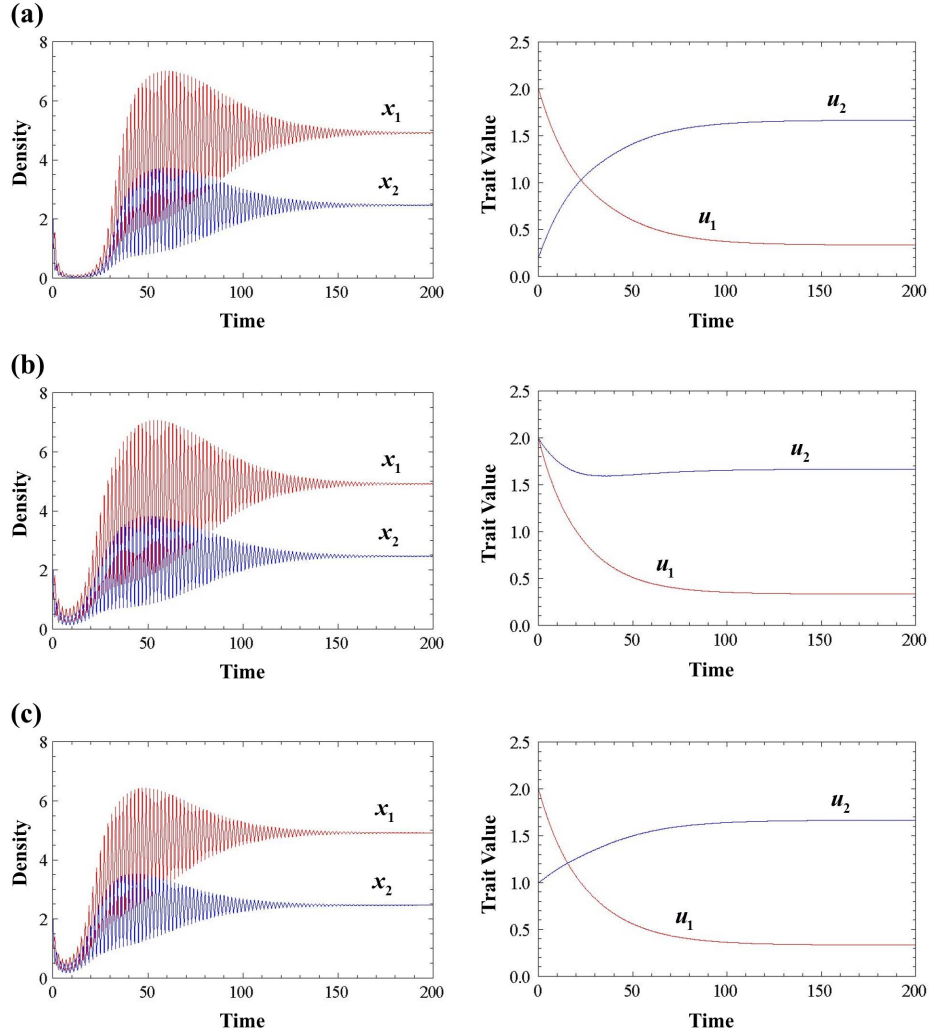


FIGURE 1. Shown are the time series of solutions of the Darwinian equations (3) with parameter values (23), variance-covariance matrix (24), and three initial conditions (25) in rows (a), (b) and (c) respectively. Calculations show $c_w^0 = -0.043 < 0$, $a_+^0 = -0.178 < 0$, $a_- = -0.010 < 0$ and $R_0^0 = 2.103 > 1$.

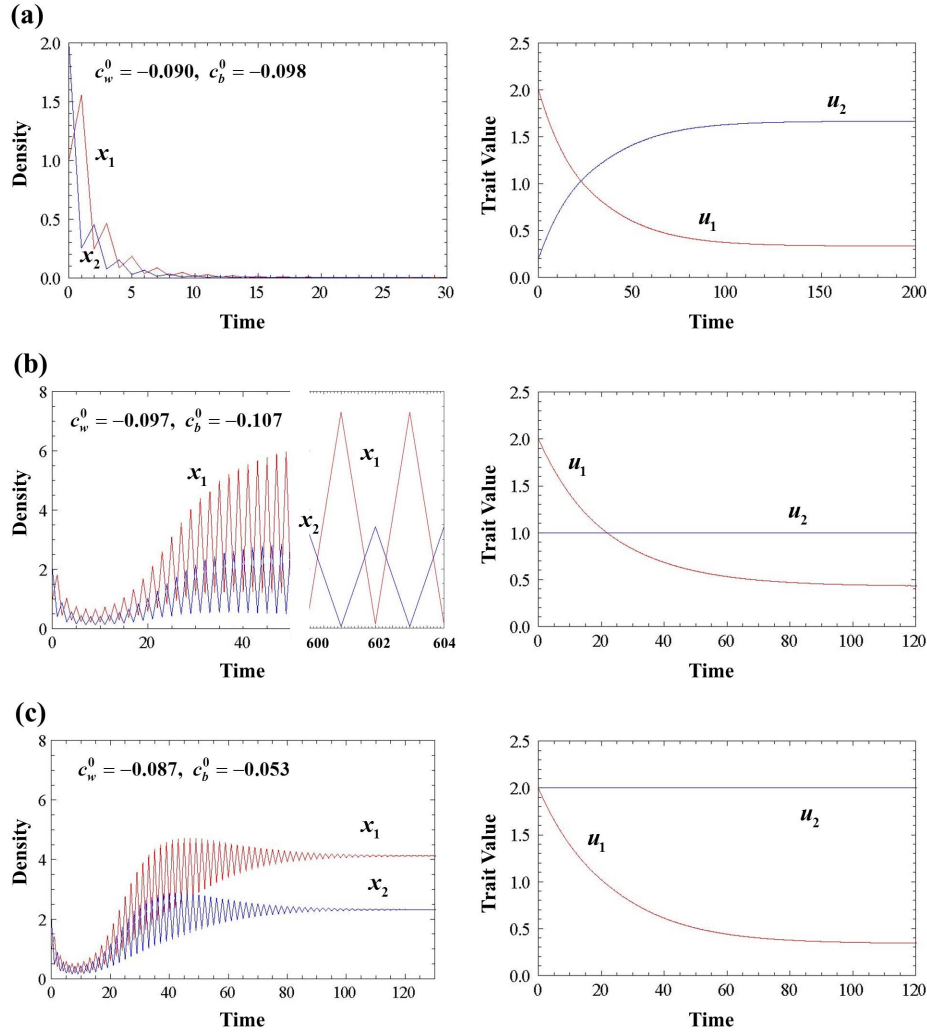


FIGURE 2. The time series of a solution of the Darwinian equations (3) when $n = 1$ with parameter values (23) and variance-covariance matrix $\mathcal{C} = (0.1)$. The trait u_2 does not evolve and is fixed at the three initial conditions used in Figure 1. In all three cases, the bifurcations of both positive equilibria and synchronous 2-cycles are forward since $c_w^0 < 0$ and $a_+^0 < 0$.

(a) $u_2 = 0.2$. Since $R_0^0 = 0.903 < 1$, the population goes extinct.

(b) $u_2 = 1$. In this case $a_-^0 = 0.010 > 0$ and the forward bifurcating 2-cycles are stable. Since $R_0^0 = 1.856 > 1$ the population approaches a synchronous 2-cycle with non-overlapping generations. Although it is not visible in the scale of this plot, the trait u_1 also oscillates with period 2.

(c) $u_2 = 2$. In this case $a_-^0 = -0.034 < 0$ and the forward bifurcating positive equilibria are stable. Since $R_0^0 = 1.856 > 1$ the population equilibrates with overlapping generations.

7. Concluding remarks. Theorems 4.1 and 5.1 describe the dual bifurcation of a continuum of positive equilibria and a continuum of synchronous 2-cycles from an extinction state that occurs in the evolutionary semelparous model (3) as the parameter R_0^0 increases through 1. The signs of the quantities c_w^0 , c_b^0 and a_{\pm}^0 given in (12) determine the nature of these bifurcations near the bifurcation point (namely, their direction and their stability properties). These three quantities are defined in terms of the sensitivities of juvenile survival and adult fertility to changes in (low level) juvenile and adult densities as measured by the partial derivatives $\partial_{x_i}^0 \sigma = \partial_{x_i} \sigma(0, 0, \mathbf{u}^*, \mathbf{u}^*)$ and $\partial_{x_i}^0 \phi = \partial_{x_i} \phi(0, 0, \mathbf{u}^*, \mathbf{u}^*)$. In most ecological models, such density effects are usually assumed to be negative feedback effects, by which is meant that each derivative is negative (if it isn't equal to 0) and therefore an increase in the density of class x_i results in a deleterious effect on survival or fertility. If only negative density effects appear in a model, then clearly c_w^0 and c_b^0 , and hence a_+^0 , are negative and, consequently, the bifurcation of both branches is forward. In that case, Theorems 4.1 and 5.1 show that there occurs a *dynamic dichotomy* at bifurcation in the sense that one branch is stable and the other is unstable. The bifurcating synchronous 2-cycles are stable if the between-class competition intensity $|c_w^0|$ is higher than the within-class competition intensity $|c_b^0|$ (i.e. $a_-^0 = c_w^0 - c_b^0 < 0$). The bifurcating positive equilibria are stable in the opposite case. This kind of competitive exclusion principle involving the two classes has been long observed as a feature of non-evolutionary semelparous Leslie models [17], [19], [22], [30], [31], [33]. Here we have shown that this dynamic dichotomy also occurs in a multi-trait evolutionary version of the two class semelparous Leslie model provided there exists a critical trait vector \mathbf{u}^* at which the fitness function and therefore $R_0(0, 0, \mathbf{u}^*, \mathbf{v})$ are (locally) maximized as functions of \mathbf{v} . This is implied by the negative definiteness of the Hessian H^0 . If this criterion does not hold, then 4.1 and 5.1 provide no attractors in a neighborhood of the bifurcation at $R_0^0 = 1$. These results constitute generalizations of those obtained for the single trait model ($n = 1$) in [18] to the multi-trait case when $n > 1$. The example in Section 6 shows that the dynamic outcome (positive equilibria or synchronous 2-cycles) when one trait is allowed to evolve can be opposite from that when two are allowed to evolve.

Theorems 4.1 and 5.1 are local bifurcation theorems and describe the existence and stability of bifurcation equilibria and synchronous 2-cycles in a neighborhood of the bifurcation point $(x_1, x_2, \mathbf{u}) = (0, 0, \mathbf{u}^*)$ for R_0^0 near 1. These theorems provide no information about equilibria and cycles outside of a neighborhood of the bifurcation point. For non-evolutionary models, the bifurcating branches are known to exist globally (i.e., are unbounded in $R_+^m \times R_+$) [8], [12]. The global extent of the bifurcating branches of equilibria and synchronous 2-cycles for the evolutionary model (3) remains an open question. Nonetheless, the stability/instability assertions in the local bifurcation theorems 4.1 and 5.1 might not persist outside the neighborhood of the bifurcation point. For example, as $R_0^0 > 1$ is increased, the propensity for difference equations to have secondary bifurcations (as the positive equilibrium or the synchronous 2-cycles destabilize), even repeated bifurcating cascades to chaos, is well known. As another example, when H^0 is not negative definite and both bifurcating branches are unstable, the existence and characteristics of attractors, which necessarily lie outside a neighborhood of the bifurcation point, are not described by Theorems 4.1 and 5.1. The nature of the attractors in these cases are, in general, model specific, so it is unlikely that conclusions can be drawn without further conditions placed on the model.

When one of the derivatives $\partial_{x_i}^0 \sigma = \partial_{x_i} \sigma(0, 0, \mathbf{u}^*, \mathbf{u}^*)$ and $\partial_{x_i}^0 \phi = \partial_{x_i} \phi(0, 0, \mathbf{u}^*, \mathbf{u}^*)$ is positive, then an increase in density of class x_i results in beneficial effect on survival or fertility. Such a phenomenon is called component Allee effect [6]. Theorems 4.1 and 5.1 show that for a backward bifurcation to occur it is necessary for one or more component Allee effect to occur and for their combined effects to be of sufficient magnitude so that either $a_+^0 > 0$ or $c_w^0 > 0$. Backward bifurcations are of interest in studying the presence of strong Allee effects, i.e. multiple attractor circumstances when the extinction equilibrium and a non-extinction state (such as a positive equilibrium or synchronous 2-cycles) are both attractors. See [15].

Acknowledgments. In 1979 Paul Waltman gave a stimulating lecture at the University of Arizona on the incorporation of population genetics into ecological models. J. M. Cushing would like to thank Paul for the inspiration provided by that lecture to include evolutionary processes into population dynamic models.

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Appendix. Proof of Theorem 3.1 relies on the following lemma.

Lemma. *The eigenvalues of CH^0 are real and CH^0 has the same number of positive, negative and zero eigenvalues as H^0 .*

Proof. Since \mathcal{C} is symmetric, \mathcal{C} has eigenvalue decomposition $\mathcal{C} = PDP^T$ where P is orthogonal and D is a diagonal matrix containing the eigenvalues of \mathcal{C} . Further, since \mathcal{C} is positive-definite, the eigenvalues of D are positive and $\mathcal{C}^{1/2} = PD^{1/2}P^T$ is a real positive-definite matrix. If λ is an eigenvalue of CH^0 , then λ is also an eigenvalue of $\mathcal{C}^{1/2}H^0\mathcal{C}^{1/2}$. To see this, let \mathbf{x} denote the eigenvector corresponding to λ , $CH^0\mathbf{x} = \lambda\mathbf{x}$. Then

$$CH^0\mathcal{C}^{1/2}\mathcal{C}^{-1/2}\mathbf{x} = \lambda\mathcal{C}^{1/2}\mathcal{C}^{-1/2}\mathbf{x}$$

where we have used $\mathcal{C}^{1/2}\mathcal{C}^{-1/2} = I$. Multiplying on the left by $\mathcal{C}^{-1/2}$ gives

$$\mathcal{C}^{1/2}H^0\mathcal{C}^{1/2}(\mathcal{C}^{-1/2}\mathbf{x}) = \lambda(\mathcal{C}^{-1/2}\mathbf{x}).$$

Since $\mathcal{C}^{-1/2}$ is non-singular, $\mathcal{C}^{-1/2}\mathbf{x} \neq \mathbf{0}$. Therefore, λ is an eigenvalue of $\mathcal{C}^{1/2}H^0\mathcal{C}^{1/2}$ with eigenvector $\mathcal{C}^{-1/2}\mathbf{x}$. Further, since $\mathcal{C}^{1/2}H^0\mathcal{C}^{1/2} = (\mathcal{C}^{1/2})^T H^0 \mathcal{C}^{1/2}$ is symmetric, the eigenvalues are real.

Next, we follow the proof of Strang to show that $(\mathcal{C}^{1/2})^T H^0 \mathcal{C}^{1/2}$ has the same number of positive, negative and zero eigenvalues as H^0 [44]. Suppose the Gram-Schmidt decomposition of $\mathcal{C}^{1/2}$ is given by $\mathcal{C}^{1/2} = QR$ where Q is an orthogonal matrix and R is upper triangular. Define $\mathcal{C}^{1/2}(t) = tQ + (1-t)QR$, $t \in [0, 1]$ so that $\mathcal{C}^{1/2}(0) = \mathcal{C}^{1/2}$ and $\mathcal{C}^{1/2}(1) = Q$. Since $\mathcal{C}^{1/2}$ is non-singular, the diagonal entries of R are positive. Consequently, $\mathcal{C}^{1/2}(t) = Q[tI + (1-t)R]$ is non-singular for all t since $tI + (1-t)R$ is upper triangular with positive diagonal entries. Since $\mathcal{C}^{1/2}(t)$ is non-singular for all t , the eigenvalues of $(\mathcal{C}^{1/2})^T(t)H^0\mathcal{C}^{1/2}(t)$ never touch or cross zero. Therefore, $(\mathcal{C}^{1/2})^T H^0 \mathcal{C}^{1/2}$ has the same number of positive, negative, and zero eigenvalues as $Q^T H^0 Q$. Since Q is orthogonal, the eigenvalues of $Q^T H^0 Q$ are the eigenvalues H^0 . We showed above that the eigenvalues of $(\mathcal{C}^{1/2})^T H^0 \mathcal{C}^{1/2}$ are the eigenvalues of CH^0 . Therefore, CH^0 has the same number of positive, negative, and zero eigenvalues as H^0 . \square

Received December 2014; revised April 2015.

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