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A global bifurcation theorem for Darwinian matrix models

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ABSTRACT
Motivated by models from evolutionary population dynamics, we study a general class of nonlinear difference equations called matrix models. Under the assumption that the projection matrix is non-negative and irreducible, we prove a theorem that establishes the global existence of a continuum with positive equilibria that bifurcates from an extinction equilibrium at a value of a model parameter at which the extinction equilibrium destabilizes. We give criteria for the global shape of the continuum, including local direction of bifurcation and its relationship to the local stability of the bifurcating positive equilibria. We discuss a relationship between backward bifurcations and Allee effects. Illustrative examples are given.

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1. Introduction

A fundamental question concerning the dynamics of a biological population is whether the population is threatened with extinction. With regard to mathematical models of population dynamics, this question concerns the stability or instability of an extinction equilibrium and the answer depends on model parameters, or more specifically on inherent (low density) vital birth and survival rates. Generally, when studied as a function of a parameter (or a combination of parameters) that measures fitness, the extinction equilibrium will lose stability as the parameter increases through a threshold value. This destabilization results in the creation of non-extinction states (positive equilibria). This bifurcation phenomenon, which we refer to as the Fundamental Bifurcation Theorem, has been studied for a variety of model equation types (including ordinary and partial differential equations, integral and integro-differential and difference equations, delay and functional differential equations) and a variety of ecological circumstances (including constant and periodically-fluctuating environments, structured populations, spatial heterogeneous habitats, multi-species interactions) [4–8,10,17].

Recently, the Fundamental Bifurcation Theorem was established for an evolutionary version of matrix models that describe the dynamics of structured populations [12]. Our purpose here is to extend and generalize these results in several directions. We will consider a more general model by allowing flexibility in the choice of bifurcation parameter, a wider class of fitness functions, and frequency dependence in the evolutionary dynamics. We also establish the global existence of a continuum with positive equilibria bifurcating from an

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extinction equilibrium – a fact that is useful, for example, in studying strong Allee effects [13]. The global existence proof extends the work in [12], which provides criteria for only the local existence of a continuum in a neighbourhood of the bifurcation point.

Evolutionary game theory provides a methodology that models the dynamics of a population whose vital rates depend on traits subject to Darwinian evolution. This methodology couples a population dynamics model with Lande's equation (sometimes called Fisher's equation or the breeder's equation) for the dynamics of the population's mean trait [29,34]. At the micro level, the *game* aspect of evolutionary game theory reflects the notion that the fitness of a focal individual is determined by the interplay between his/her own phenotypic trait value (v), the environment (we use the parameter λ as a proxy), and the phenotypic trait values of other individual members of the population. The phenotypic trait values of the other individuals are usually summarized by the population's mean trait value (u) [34].

Consider a stage-structured population with density vector $x \in \mathbb{R}^n$ in which the survival and reproductive rates of individuals are influenced by a phenotypic trait that is subject to Darwinian evolution. We consider a discrete-time, Darwinian matrix model for the dynamics of the population and the population's mean trait described by equations

$$x' = Q(\lambda, x, v, u)x\Big|_{v=u} \tag{1a}$$

$$u' = u + \sigma^2 \partial_v G(\lambda, x, v, u)\Big|_{v=u}. \tag{1b}$$

Here x, v, and u depend on time. We have adopted LaSalle's notation x' and u' for iterates of the map, which provide the population vector x and mean trait u at the next census time. The entries of the projection matrix $Q = (q_{ij})$ are the class-specific birth, survival and transition rates of an individual. Note that we allow these rates to depend on x (density dependence), the phenotypic trait v of an individual, the mean population trait u (frequency dependence), and a designated parameter λ. The parameter λ is chosen at the modeller's discretion to use as a bifurcation parameter. Also at the modeller's discretion is the 'fitness function' G appearing in (1b), where G restricts u to $\mathcal{U}$ and is obtained from the projection matrix Q in some biologically meaningful and feasible way (see Section 5 for examples). A common choice for G is the dominant eigenvalue r of Q, its logarithm, or the net reproduction number R_0 (see Section 5 for a discussion) [2,11,14,27,32].

For a discussion and derivation of the model Equations (1a) and (2b) see [29] and [34]. Equation (2b) is sometimes called the canonical law of Darwinian evolution (or Fisher's or Lande's or the breeder's equation [15,23,28]). It postulates that the change in the population's mean trait is proportional to the fitness gradient with respect to the trait v of a 'focal' or 'mutant' individual. Equation (1a) is a generalization of matrix models introduced by Lewis [26] and Leslie [24,25] for age-structured population dynamics [2]. According to this methodology, the system dynamics are well approximated by evaluating the individual trait at the mean trait value.

That fitness and vital rates of an individual can depend not only on its own trait v, but on other individuals in the population as represented by the mean trait u, allows for frequency dependent evolution. This also accounts for referring to this modelling methodology as evolutionary game theory. When frequency dependence is ignored, i.e. when the restrictive assumption is made that individual fitness and vital rates do not depend on the population's mean fitness u, then for notational simplicity one could replace v and u in System (1) (as in [12]), although this obscures the fact that in Equation (2b) the fitness gradient must be taken with respect to the individual trait rather than the mean trait in order to avoid group selection.

The constant of proportionality, here denoted by σ^2, has different interpretations in different theories and derivations, but is generally proportional to the variance of the trait throughout the population, assumed constant in time, and is often referred to as the speed of evolution.

For notational simplicity, we rewrite System (1) as

$$x' = P(\lambda, x, u)x \tag{2a}$$

$$u' = u + H(\lambda, x, u). \tag{2b}$$

Note that we absorb σ^2 so that H is a rescaled version of the fitness gradient. All calculations and interpretations from hereon are with respect to System (2), but the results can be straightforwardly translated into results for System (1). For a given λ and corresponding equilibrium $(\tilde{x}, \tilde{u})$, we refer to $(\lambda, \tilde{x}, \tilde{u})$ as an *equilibrium pair*. We define an *extinction equilibrium pair* of System (2) as $(\lambda, 0, u^*)$ where u^* satisfies $H(\lambda, 0, u^*) = 0$. We refer to such a u^* as a *critical trait*.

In Section 2, we prove the Fundamental Bifurcation Theorem for System (2) which establishes the global existence of a continuum of equilibrium pairs that bifurcates from a point $(\lambda, x, u) = (\lambda^*, 0, u^*)$ and is unbounded in at least one of its three components. The extinction equilibrium pair $(\lambda, 0, u^*)$ destabilizes at $\lambda = \lambda^*$. In Section 3, we study the direction of bifurcation, relate it to the stability of the bifurcating positive equilibrium pairs, and interpret its biological meaning. Strong Allee effects confound the issue of extinction by allowing attraction basins for extinction and persistence to be initial condition dependent; population density helps determine survival in such cases. In Section 4, we revisit the mathematical linkage between backward bifurcations and strong Allee effects (see [13] for a review) and detail the role mean trait dynamics play in this relationship. In Section 5, we discuss some common choices for λ and G used in the literature. And in Section 6 we present some illustrative examples.

2. Existence of a global bifurcating continuum

Let $\mathbb{R}^n$ denote n-dimensional Euclidean space, define the positive cone as $\mathbb{R}^n_+ = \{x \in \mathbb{R}^n : x_i > 0 \text{ for } i = 1, 2, \cdot, n\}$, and let $\overline{\mathbb{R}^n_+}$ denote the closure of $\mathbb{R}^n_+$. Let Ω denote an open set in $\mathbb{R}^n$ that contains $\overline{\mathbb{R}^n_+}$, and let $\mathcal{U}$ denote an open interval of reals. We refer to an equilibrium pair (λ, x, u) as *positive* if $x \in \mathbb{R}^n_+$. A mean trait $u = u^*$ is called a *critical trait* if $H(\lambda, 0, u^*) = 0$ for all λ. We make the following assumptions.

Assumption A1: *There exists a* λ_{min} *such that if* (λ, x, u) *is a positive equilibrium pair, then* $\lambda > \lambda_{min}$.

Assumption A2: *The matrix* $P(\lambda, x, u) = \big(p_{ij}(\lambda, x, u)\big)$ *is non-negative and irreducible for all* $\lambda \in [\lambda_{min}, \infty)$, $x \in \overline{\mathbb{R}^n_+}$, $u \in \mathcal{U}$ *and* $p_{ij}(\lambda, x, u) \in C^2(\mathbb{R} \times \Omega \times \mathcal{U})$.

Assumption A3: *There exists a critical trait,* u^*, *such that* $\partial_u H(\lambda, 0, u^*) \neq 0$ *for all* $\lambda > \lambda_{min}$.

Assumption A4: *$P(\lambda,0,u^*)=A+\lambda B$ for non-negative matrices $A,B\in\overline{\mathbb{R}_+^{n\times n}}$ and critical trait u^*. Assume $B\neq 0$, $I-A$ is invertible, and $(I-A)^{-1}B$ has an algebraically simple characteristic value, λ^*, which is the only characteristic value corresponding to a positive eigenvector $\xi\in\mathbb{R}_+^n$.*[1] *Let the characteristic value λ be defined as the inverse of the eigenvalue $1/\lambda$.*

Assumption A5: *$H(\lambda,x,u)$ is continuous and differentiable on $(\lambda_{min},\infty)\times\Omega\times\mathcal{U}$. There exist constants $\alpha,\beta\in\mathbb{R}$, $a,b\in\mathbb{R}^n$ and a function $g:(\lambda_{min},\infty)\to\mathbb{R}_+$ such that*

- *(a)* $\nabla_x H(\lambda,0,u^*)=g(\lambda)\left(a+\lambda b\right)$,
- *(b)* $\partial_u H(\lambda,0,u^*)=g(\lambda)\left(\alpha+\lambda\beta\right)$ *where* $\alpha\neq 0$ *and* $-\frac{\beta}{\alpha}\neq\frac{1}{\lambda^*}$.

Usually $\lambda_{\min}=0$ in population models; for example, λ may represent birth rate or another biological quantity describing the reproduction and/or survival of individuals.

Theorem 1: *Under Assumptions A1–A5, System (2) has a continuum $\mathcal{C}$ of equilibrium pairs that bifurcates from $(\lambda,x,u)=(\lambda^*,0,u^*)$.*[2] *The equilibrium pairs on $\mathcal{C}\backslash\left(\lambda^*,0,u^*\right)$ are positive near the bifurcation point.*

Proof: In general, steady states to System (2) must satisfy

$$\begin{aligned} x &= P(\lambda,x,u)x \\ u &= u+H(\lambda,x,u). \end{aligned}\tag{3}$$

Notice the second equation is equivalent to $0=H(\lambda,x,u)$ and hence System (3) is equivalent to

$$\begin{aligned} x &= P(\lambda,x,u)x \\ u &= u+H(\lambda,x,u)/g(\lambda). \end{aligned}\tag{4}$$

We Taylor expand the right-hand side of System (4) around the trivial equilibrium pair $(\lambda,0,u^*)$. Because $H(\lambda,0,u^*)=0$,

$$\begin{aligned} x &= P(\lambda,0,u^*)x+\emptyset_2 \\ u &= u^*+x\nabla_x H(\lambda,0,u^*)/g(\lambda)+(u-u^*)\left(1+\partial_u H(\lambda,0,u^*)/g(\lambda)\right)+\emptyset_2, \end{aligned}\tag{5}$$

where $\emptyset_2$ is shorthand for all second and higher order terms in x and $u-u^*$. Using Assumptions A4 and A5,

$$\begin{aligned} \begin{pmatrix} x \\ u-u^* \end{pmatrix} &= \begin{pmatrix} A+\lambda B & 0_{n\times 1} \\ \nabla_x H(\lambda,0,u^*)/g(\lambda) & 1+\partial_u H(\lambda,0,u^*)/g(\lambda) \end{pmatrix}\begin{pmatrix} x \\ u-u^* \end{pmatrix}+\emptyset_2 \\ &= \begin{pmatrix} A & 0_{n\times 1} \\ a & 1+\alpha \end{pmatrix}\begin{pmatrix} x \\ u-u^* \end{pmatrix}+\lambda\begin{pmatrix} B & 0_{n\times 1} \\ b & \beta \end{pmatrix}\begin{pmatrix} x \\ u-u^* \end{pmatrix}+\emptyset_2 \\ &= \tilde{A}\begin{pmatrix} x \\ u-u^* \end{pmatrix}+\lambda\tilde{B}\begin{pmatrix} x \\ u-u^* \end{pmatrix}+\emptyset_2. \end{aligned}$$

We can then write

$$\begin{pmatrix} x \\ u-u^* \end{pmatrix}=\lambda L\begin{pmatrix} x \\ u-u^* \end{pmatrix}+\emptyset_2 \tag{6}$$

where $L = (I - \tilde{A})^{-1}\tilde{B}$. The existence of L requires the invertibility of $I - A$ (Assumption A4) and $\alpha \neq 0$ (Assumption A5). Using the properties of block matrices, we calculate

$$(I - \tilde{A})^{-1} = \begin{pmatrix} (I - A)^{-1} & 0_{n\times 1} \\ -\frac{a(I-A)^{-1}}{\alpha} & -\frac{1}{\alpha} \end{pmatrix}$$

and

$$L = \begin{pmatrix} (I - A)^{-1}B & 0_{n\times 1} \\ -\frac{a(I-A)^{-1}B}{\alpha} - \frac{b}{\alpha} & -\frac{\beta}{\alpha} \end{pmatrix}. \tag{7}$$

So long as $-\frac{\beta}{\alpha} \neq \frac{1}{\lambda^*}$, λ^* is an algebraically simple characteristic value of L. System (6) is now in a form that allows us to apply the Rabinowitz Alternative (see Theorem 1.40 and Corollary 1.12 in [31]), which states that there exists a continuum $\mathcal{C}$ of equilibrium pairs (λ, x, u) for System (2) bifurcating from $(\lambda, x, u) = (\lambda^*, 0, u^*)$. The continuum initially follows the eigenvector of L corresponding to eigenvalue $1/\lambda^*$. Because this uses the positive eigenvector of $(I - A)^{-1}B$, $\mathcal{C}$ will branch into the positive x-cone. □

Theorem 2: *Under Assumptions A1–A5, $\mathcal{C}\backslash\left(\lambda^*, 0, u^*\right)$ either (i) lies in $\mathbb{R} \times \mathbb{R}^n_+ \times \mathcal{U}$ or (ii) connects to some $(\tilde{\lambda}, 0, \tilde{u})$, where $\tilde{u} \neq u^*$ is another critical trait value of H.*

Proof: Recall $\mathcal{C}$ branches into $\mathbb{R} \times \mathbb{R}^n_+ \times \mathcal{U}$ by Theorem 1. Assume that the x-component of $\mathcal{C}\backslash\left(\lambda^*, 0, u^*\right)$ leaves $\mathbb{R}^n_+$. Then because $\mathcal{C}$ is a continuum there exists some $(\tilde{\lambda}, \tilde{x}, \tilde{u})$ on the continuum where $\tilde{x} \in \partial\mathbb{R}^n_+ = \{x \in \mathbb{R}^n : x_i \geq 0 \text{ for } i = 1, 2, \ldots, n\}\backslash\mathbb{R}^n_+$ is on the boundary of the positive x-cone, as well as a sequence (λ_i, x_i, u_i) on the continuum with positive x-components such that $\lim_{i\to\infty}(\lambda_i, x_i, u_i) = (\tilde{\lambda}, \tilde{x}, \tilde{u})$. We prove that $(\tilde{\lambda}, \tilde{x}, \tilde{u})$ must be of the form $(\tilde{\lambda}, 0, \tilde{u})$ where $\tilde{u} \neq u^*$.

First suppose $\tilde{x} \neq 0$. Then, since $x_i = P(\lambda_i, x_i, u_i)x_i$ is satisfied on $\mathcal{C}$, taking the limit gives $\tilde{x} = P(\tilde{\lambda}, \tilde{x}, \tilde{u})\tilde{x}$, making $\tilde{x}$ an eigenvector of a non-negative irreducible matrix. This contradicts the Perron–Frobenius Theorem since $\tilde{x}$ is non-negative and yet is not strictly positive. Thus, $\mathcal{C}$ must leave $\mathbb{R} \times \mathbb{R}^n_+ \times \mathcal{U}$ through $(\tilde{\lambda}, 0, \tilde{u})$. Let $\xi_i = x_i/|x_i|$ and $\tilde{\xi} = \lim_{i\to\infty} x_i/|x_i|$ so that $\left|\tilde{\xi}\right| = |\xi_i| = 1$. We see

$$\xi_i = P(\lambda_i, x_i, u_i)\xi_i.$$

By taking $i \to \infty$, we have $\tilde{\xi} = P(\tilde{\lambda}, 0, \tilde{u})\tilde{\xi}$. Note $\tilde{\xi}$ is non-negative, being the limit of positive vectors, and is an eigenvector of the non-negative irreducible matrix $P(\tilde{\lambda}, 0, \tilde{u})$, and thus $\tilde{\xi} \in \mathbb{R}^n_+$.

Suppose $\mathcal{C}$ meets $(\tilde{\lambda}, 0, u^*)$. Rabinowitz [31, Theorem 1.40] states that the continuum is either (i) unbounded in one of its three components or (ii) meets $(\tilde{\lambda}, 0, u^*)$ where $\tilde{\lambda} \neq \lambda^*$ is also a characteristic value of L from Equation (7) (see Figure 2(d)). Then $\tilde{\xi} = P(\tilde{\lambda}, 0, u^*)\tilde{\xi}$ gives $\tilde{\xi} = \tilde{\lambda}(I - A)^{-1}B\tilde{\xi}$ by Assumption A4. Also by Assumption A4, $\tilde{\xi} \in \mathbb{R}^n_+$ must correspond to the characteristic value λ^* and hence $\tilde{\lambda} = \lambda^*$. This contradicts Rabinowitz's theorem. Thus $\tilde{u} \neq u^*$, and since $\mathcal{C}$ is a continuum of equilibrium pairs, we know $\tilde{u}$ must satisfy $H(\tilde{\lambda}, 0, \tilde{u}) = 0$, and hence $\tilde{u}$ is a critical trait of H. □

Theorem 3: *Under Assumptions A1–A5, the continuum $\mathcal{C}$ is unbounded in at least one of its three components in $\mathbb{R} \times \mathbb{R}^n \times \mathcal{U}$ (see Figure 2(a)–(c)).*

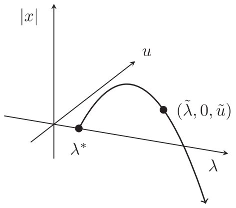
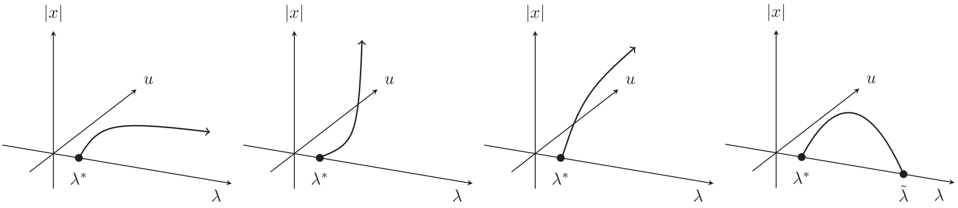


Figure 1. $\mathcal{C}$ may be bounded in the positive x-cone if it connects with another critical trait value.



(a) Unbounded in λ. (b) Unbounded in x. (c) Unbounded in u. (d) Rabinowitz case (ii).

Figure 2. (a)–(c) Different scenarios stemming from Theorem 3, which states that the continuum $\mathcal{C}$ is unbounded in at least one of the three components. (d) An alternate scenario where $(\lambda^*, 0, u^*)$ and $(\tilde{\lambda}, 0, u^*)$ both serve as bifurcation points – this case is ruled out by Theorem 2.

Proof: First, consider case (ii) of Theorem 2, where $\mathcal{C}$ connects to another point $(\tilde{\lambda}, 0, \tilde{u})$ where $\tilde{u}$ is another critical trait value. Then $(\lambda, 0, \tilde{u})$ is a solution for all λ by the definition of a critical trait, and therefore $\mathcal{C}$ is unbounded by connecting to that trivial line of equilibria.

Next, consider case (i) of Theorem 2, where $\mathcal{C}$ is contained in $\mathbb{R} \times \mathbb{R}^n_+ \times \mathcal{U}$. Rabinowitz [31, Theorem 1.40] states that the continuum is either (i) unbounded in one of its three components or (ii) meets $(\tilde{\lambda}, 0, u^*)$ where $\tilde{\lambda} \neq \lambda^*$ is also a characteristic value of L from Equation (7) (see Figure 2(d)). In the proof of Theorem 2, we showed that $\mathcal{C}$ does not meet $(\tilde{\lambda}, 0, u^*)$; thus, the second alternative of Rabinowit'z theorem is ruled out, proving that one of the components of $\mathcal{C}$ must be unbounded. ☐

See Figure 1 for an illustration of Theorem 2(ii) and Section 6.2 for an example. Theorems 1–3 establish the existence of a global continuum $\mathcal{C}$ bifurcating from $(\lambda^*, 0, u^*)$ and outline specifics about the global positioning of the bifurcating branch. Figure 2(a)–(c) show some of the different ways $\mathcal{C}$ may be unbounded in $\mathbb{R} \times \mathbb{R}^n \times \mathcal{U}$; the relevant cases to consider depend on the underlying system of interest. Further examination of the profile of $\mathcal{C}$ involves characterizing the stability of the positive equilibrium pairs as well as determining the initial bifurcation direction.

3. Stability and direction of the bifurcating continuum

In this section, we discuss the local stability of the positive equilibrium pairs along $\mathcal{C}$ in the neighbourhood of $(\lambda^*, 0, u^*)$. As is typical when performing a linear stability analysis for models like System (2), we will calculate the corresponding Jacobian and evaluate it at the steady states of interest. In order to investigate the stability of points along $\mathcal{C}$, we need an analytic representation of the equilibrium pairs. Using the Lyapunov–Schmidt Method, we approximate the positive equilibrium pairs near $(\lambda^*, 0, u^*)$ with the perturbation expansion

$$\begin{aligned}\lambda(\epsilon) &= \lambda^* + \kappa\epsilon + \lambda_2\epsilon^2 + \emptyset(\epsilon^3)\\ x(\epsilon) &= \xi\epsilon + x_2\epsilon^2 + \emptyset(\epsilon^3)\\ u(\epsilon) &= u^* + u_1\epsilon + u_2\epsilon^2 + \emptyset(\epsilon^3)\end{aligned} \tag{8}$$

for small, positive ϵ. It follows that the initial direction of $\mathcal{C}$ is determined by the coefficients κ, ξ, and u_1. Recalling that λ is the bifurcation parameter, we say $\mathcal{C}$ is *forward* bifurcating if $\lambda > \lambda^*$ for equilibrium pairs on $\mathcal{C}$ near $(\lambda^*, 0, u^*)$. Similarly, $\mathcal{C}$ is *backward* bifurcating if $\lambda < \lambda^*$ for equilibrium pairs on $\mathcal{C}$ near $(\lambda^*, 0, u^*)$.

Notice κ specifies the initial λ-direction of $\mathcal{C}$ away from λ^* and thus determines whether the bifurcation is *forward* ($\kappa > 0$) or *backward* ($\kappa < 0$). In the non-evolutionary setting, the sign of κ also dictates the stability of the positive equilibrium pairs near the bifurcation point, known as the *Principle of Exchange of Stability* in [20]. This principle also applies to the specific form of evolutionary models presented in [12]. In the theorem below, we summarize the linkage between bifurcation direction and stability of positive equilibrium pairs. For these results, we require primitivity of $P(\lambda, x, u)$, which implies P is a non-negative and irreducible matrix with a *strictly* dominant eigenvalue. Theorem 4 only holds when u^* is fitness maximizing (i.e. when u^* maximizes the fitness function G) – for the case when u^* is fitness minimizing, the bifurcating equilibria are unstable regardless of the direction of bifurcation (see Appendix 2).

Assumption A6: *The matrix* $P(\lambda, x, u) = \big(p_{ij}(\lambda, x, u)\big)$ *is primitive for all* $\lambda \in [\lambda_{min}, \infty)$, $x \in \overline{\mathbb{R}^n_+}$, $u \in \mathcal{U}$ *and* $p_{ij}(\lambda, x, u) \in C^2(\mathbb{R} \times \Omega \times \mathcal{U})$.

Note that Assumption A6 implies Assumption A2 holds.

Theorem 4: *If Assumptions A1–A6 hold and* $H_u(\lambda^*, 0, u^*) < 0$, *then the trivial equilibrium pairs* $(\lambda, 0, u^*)$ *are stable for* $\lambda < \lambda^*$ *and are unstable for* $\lambda > \lambda^*$. *Furthermore, if* $\kappa \neq 0$, *near* $(\lambda, x, u) = (\lambda^*, 0, u^*)$ *we have the following alternatives:*[3]

(a) $\kappa < 0$. *The bifurcation of* $\mathcal{C}$ *is backward and the equilibrium pairs near* $(\lambda^*, 0, u^*)$ *on* $\mathcal{C}$ *are positive and unstable.*

(b) $\kappa > 0$. *The bifurcation of* $\mathcal{C}$ *is forward and the equilibrium pairs near* $(\lambda^*, 0, u^*)$ *on* $\mathcal{C}$ *are positive and stable.*

See Appendix 2 for proof of (a) and (b) and Figure 3 for illustration. The stability of the trivial equilibrium pairs is detailed in Appendix 3. For notational purposes, let

$$\begin{aligned} P_u^0 &= \left(\frac{\partial p_{ij}}{\partial u}(\lambda^*, 0, u^*)\right),\\ \nabla_x^0 p_{ij} &= \left(\frac{\partial p_{ij}}{\partial x_1}(\lambda^*, 0, u^*), \frac{\partial p_{ij}}{\partial x_2}(\lambda^*, 0, u^*), \cdot, \frac{\partial p_{ij}}{\partial x_n}(\lambda^*, 0, u^*)\right).\end{aligned}$$

To derive ξ and κ, we use the Taylor expansion of $x = P(\lambda, x, u)x$ derived in Appendix 1:

$$x = (A + \lambda B)x + D(x)x + (u - u^*)P_u^0 x + \emptyset_3 \text{ where } d_{ij}(\tilde{x}) = \left(\nabla_x^0 p_{ij}\right)\tilde{x} \tag{9}$$

where $\emptyset_3$ contains all terms of order three and higher in combinations of x, $(u - u^*)$ and $(\lambda - \lambda^*)$.

Expanding Equation (9), at $\emptyset(\epsilon)$ we see $\xi = (A + \lambda^* B)\xi$, which makes ξ the positive right-eigenvector of $P(\lambda^*, 0, u^*)$ corresponding to eigenvalue 1, and also the eigenvector of $(I-A)^{-1}B$ corresponding to eigenvalue $1/\lambda^*$ from Assumption A4. Note the positivity of ξ implies $x \in \mathbb{R}^n_+$ for equilibrium pairs on $\mathcal{C}$ near $(\lambda^*, 0, u^*)$, as mentioned at the end of Theorem 1.

At $\mathcal{O}(\epsilon^2)$, we see

$$x_2 = P(\lambda^*, 0, u^*)x_2 + \kappa B\xi + D(\xi)\xi + u_1 P^0_u \xi,$$

or equivalently

$$\left(I - P(\lambda^*, 0, u^*)\right) x_2 = \kappa B\xi + D(\xi)\xi + u_1 P^0_u \xi.$$

By the Fredholm Alternative, this is solvable if and only if

$$\zeta^T \left(\kappa B\xi + D(\xi)\xi + u_1 P^0_u \xi\right) = 0$$

for every ζ^T such that $\zeta^T \left(I - P(\lambda^*, 0, u^*)\right) = 0$, which occurs at the single left-eigenvector of $P(\lambda^*, 0, u^*)$ corresponding to eigenvalue 1. Solving for κ,

$$\kappa = -\frac{\zeta^T \Big(D(\xi) + u_1 P^0_u\Big)\xi}{\zeta^T B\xi}.$$

To calculate u_1, we differentiate the equilibrium equation $H(\lambda(\epsilon), x(\epsilon), u(\epsilon)) = 0$ with respect to ϵ and then evaluate the expression at $\epsilon = 0$. From this, we get

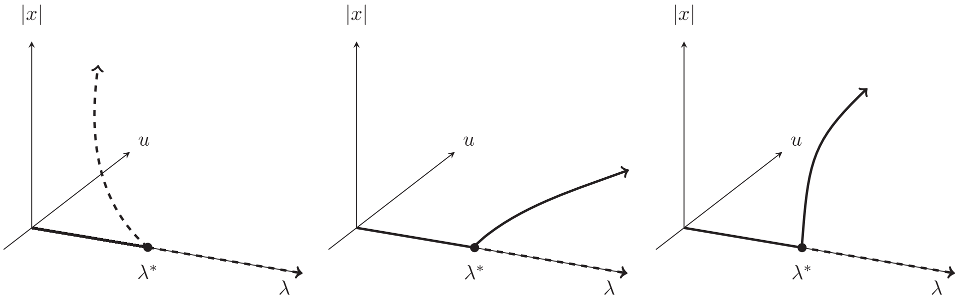
$$u_1 = -\frac{\nabla_x H(\lambda^*, 0, u^*)\xi + \partial_\lambda H(\lambda^*, 0, u^*)\kappa}{\partial_u H(\lambda^*, 0, u^*)}.$$

Because $H(\lambda, 0, u^*) = 0$, given by the critical trait equation, is a level curve in the λ direction, we have $H_\lambda(\lambda, 0, u^*) = 0$. Thus

$$u_1 = -\frac{\nabla_x H(\lambda^*, 0, u^*)\xi}{\partial_u H(\lambda^*, 0, u^*)}.$$

Note ζ and ξ are positive, while B is a nonnegative matrix (Assumption A4). So the sign of κ is determined by $D(\xi) + u_1 P^0_u$. This term is a weighted sum that takes two types of effects into account: (1) the inherent *density* effects each class has on the growth of each other class and (2) the inherent *evolutionary* effects a changing phenotypic trait has on the growth of each class. The weights, ξ and u_1, represent the initial direction of bifurcation in the x components and in u and determine the influence of *density* and *evolutionary* effects on the direction of bifurcation. Unlike ξ, the sign of u_1 is generally unrestricted and may be positive or negative depending on if the relationship between trait dynamics and population growth is one of positive-feedback ($\partial_x H(\lambda^*, 0, u^*) > 0$) or negative-feedback ($\partial_x H(\lambda^*, 0, u^*) < 0$) at low density and whether u^* is a fitness maximizer ($\partial_u H(\lambda^*, 0, u^*) < 0$) or minimizer ($\partial_u H(\lambda^*, 0, u^*) > 0$).

The inherent density effects are described by $\nabla^0_x p_{ij}$. Note p_{ij} gives functional form to the relationship between class j and growth of class i, and $\nabla_x p_{ij}$ reflects how this functional relationship responds to changes in the density of each class. Thus $\nabla^0_x p_{ij}$ quantifies the change in functional response when class densities are small. The evolutionary effects are



(a) $\kappa < 0$, backward bifurcation.

(b) $\kappa > 0$, forward bifurcation.

(c) $\kappa = 0$, $\mathcal{C}$ can bifurcate in either direction.

Figure 3. The bifurcation direction and the stability of positive equilibrium pairs on $\mathcal{C}$ near $(\lambda^*, 0, u^*)$ can be determined by κ when $\kappa \neq 0$. When $\kappa = 0$, direction and stability must be determined independently. The solid lines indicate stable equilibria and the dashed lines indicate unstable equilibria.

described by $\partial_u p_{ij}$, which quantifies how the change in trait value affects the sensitivity of class i to the density of class j.

In the next section, we use the interpretation of the terms comprising κ to comment on a phenomenon of increasing interest, which stems from positive-feedback effects at low density, and discuss the phenomenon's relation to the initial direction and stability of the equilibrium pairs on $\mathcal{C}$.

4. Remarks on strong Allee effects

A component Allee effect is the occurrence of a positive feedback in a component p_{ij} at low population densities. Such a phenomenon is often present in populations that gain some fitness advantage from grouping together (e.g. mate selection [16], predator vigilance [18], and predator confusion [19]) which can assist with survival at low densities. The fitness advantage diminishes as groups get larger and intraspecific competition begins to play a dominating role. As a result, sufficiently large component Allee effects can create a dichotomous population threshold that arises from the occurrence of multiple attractors, one of which is an extinction equilibrium pair and the other a non-extinction attractor. Such a scenario is called a *strong Allee effect*.

A sufficient condition for a strong Allee effect is the existence of an asymptotically stable positive equilibrium pair at a λ-value where the extinction equilibrium pair $(\lambda, 0, u^*)$ is also asymptotically stable. In addition to being the initial bifurcation location, λ^* serves as the stability threshold for the extinction equilibrium pairs when u^* is a fitness maximizer, where $(\lambda, 0, u^*)$ is stable for $\lambda < \lambda^*$ and is unstable for $\lambda > \lambda^*$. This means that strong Allee effects can only occur for λ values below λ^*; we use this fact in Assumption A8 and in the proof of the theorem stated below, which guarantees strong Allee effects in Darwinian matrix models of the form of System (2).

Assumption A7: *There exists a point* $(\lambda^*, x_+, \tilde{u})$ *where* $x_+ \in \mathbb{R}^n_+$ *such that*

(a) $(\lambda^*, x_+, \tilde{u})$ *satisfies the equilibrium equations of System* (3)

(b) $\rho\left[\mathcal{J}(\lambda^*, x_+, \tilde{u})\right] < 1$ *where* $\mathcal{J}$ *is the Jacobian of System* (3) *with respect to x and u evaluated at* $(\lambda^*, x_+, \tilde{u})$.

Assumption A8: *The critical trait u^* is fitness maximizing, such that $\partial_u H(\lambda, 0, u^*) < 0$.*

Theorem 5: *Assumptions A1–A8 provide sufficient conditions for System (2) to have coexistence of a stable positive equilibrium pair and a stable extinction equilibrium pair for each λ in some interval $(\tilde{\lambda}, \lambda^*)$, and hence a strong Allee effect on said interval.*

Proof: Assumption A7 ensures that at $\lambda = \lambda^*$ there exists a locally asymptotically stable equilibrium pair with $x_+ \in \mathbb{R}^n_+$. Because $\rho[\mathcal{J}(\lambda^*, x_+, \tilde{u})] < 1$, the Jacobian of $P(\lambda, x, u)x - x$ and $u + H(\lambda, x, u) - u$ at $(\lambda^*, x_+, \tilde{u})$ is nonsingular. Thus $\mathcal{J}(\lambda^*, x_+, \tilde{u}) - I$ is nonsingular.

We can then invoke the Implicit Function Theorem, which gives a solution $x(\lambda), u(\lambda) \in C^1$ in a neighbourhood of λ^* such that $(x(\lambda^*), u(\lambda^*)) = (x_+, \tilde{u})$. By continuity, $x(\lambda) \in \mathbb{R}^n_+$ and $\rho[\mathcal{J}(\lambda, x(\lambda), u(\lambda))] < 1$ in a neighbourhood of λ^*, which implies local asymptotic stability of $(\lambda^*, x_+, \tilde{u})$. Thus, there exists a basin of attraction within which populations persist and another in which populations go extinct due to the stability of the trivial equilibrium pair (see Theorem 4). □

Assumption A7 is most commonly satisfied when a backward bifurcating $\mathcal{C}$ bends back in the direction of increasing λ at some $\tilde{\lambda} < \lambda^*$ (see Figure 3(a)); this is known as a saddle-node or blue sky bifurcation. In such a case, $\mathcal{C}$ produces unstable equilibrium pairs near $(\lambda^*, 0, u^*)$ but the bend may give rise to a branch of stable equilibrium pairs. Thus, a strong Allee effect is present at each λ between $\tilde{\lambda}$ and λ^*.

For a backward bifucation ($\kappa < 0$) to occur, at least one of the $\partial^0_{x_k} p_{ij}$ or $u_1 \partial^0_u p_{ij}$ terms must be positive (see Table 1). As in the non-evolutionary case, $\partial^0_{x_k} p_{ij} > 0$ indicates a positive-feedback relationship between the growth of class i and the density of class k. The criterion unique to the evolutionary case, $u_1 \partial^0_u p_{ij} > 0$, means that the initial change in u along $\mathcal{C}$, when the population is small, positively influences population growth. When an increasing trait value hurts population growth ($\partial^0_u p_{ij} < 0$), the more advantageous strategy is to reduce that trait ($u_1 < 0$). Similarly, when an increasing trait value enhances population growth ($\partial^0_u p_{ij} > 0$), it is more advantageous to initially increase that trait ($u_1 > 0$). In essence, the extra criterion implies that trait dynamics initially evolve in the direction that benefits fitness, and when that effect is sufficiently strong it may cause a strong Allee effect.

In the setting of a backward bifurcation, $\mathcal{C}$ will bend back if Theorem 2(i) holds and the λ-component of $\mathcal{C}$, $\{\lambda : (\lambda, x, u) \in \mathcal{C}\}$, is unbounded. To prove unboundedness, it is sufficient to bound the x- and u-components in terms of λ:

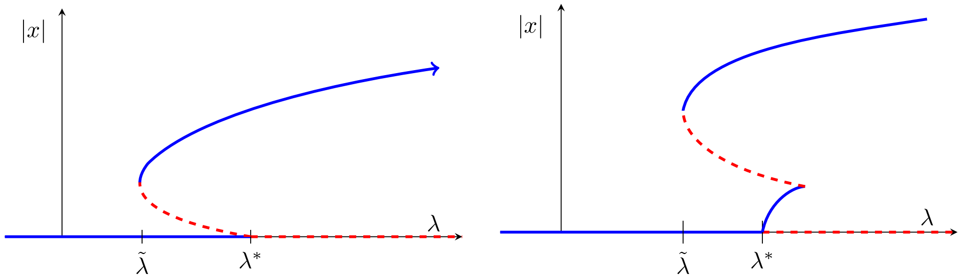
$$|x| \leq m(\lambda) \text{ and } |u| \leq n(\lambda) \text{ for every } (\lambda, x, u) \in \mathcal{C}.$$

In practice, one proves such bounds for all equilibrium pairs (λ, x, u) in the model domain. Then, in order for the continuum to be unbounded as proved in Section 2, the λ-component must be unbounded. Note that the x- and u-components may still be unbounded. In population models, where growth is eventually hampered by limited resources and spatial barriers, we expect $\mathcal{C}$ to be bounded in the x-direction and expect λ, a nonnegative growth parameter, to characterize this bounded growth. Similarly, since u represents a phenotypic trait, it is reasonable to assume the trait space is bounded.

Strong Allee effects can also result from more complicated bifurcation scenarios; for instance, $\mathcal{C}$ may bifurcate forwards (see Figure 4(b) below for an example from [1]). The persistence attractor in strong Allee scenarios can also take a more complex form, such

Table 1. Necessary and sufficient conditions to arrive at a backward bifurcation ($\kappa < 0$) in both the non-evolutionary and evolutionary models.

	Non-evolutionary	Evolutionary
Sufficient	all $\partial^0_{x_k} p_{ij} > 0$	all $\partial^0_{x_k} p_{ij} > 0$ and $u_1 \partial^0_u p_{ij} > 0$
Necessary	one $\partial^0_{x_k} p_{ij} > 0$	one $\partial^0_{x_k} p_{ij} > 0$ or $u_1 \partial^0_u p_{ij} > 0$



(a) A backward bifurcation with a strong Allee effect for $\lambda \in (\tilde{\lambda}, \lambda^*)$.

(b) A forward bifurcation with a strong Allee effect for $\lambda \in (\tilde{\lambda}, \lambda^*)$.

Figure 4. Example illustrations of cases with a strong Allee effect where the solid lines indicate stable equilibria and the dashed lines indicate unstable equilibria.

as a two-cycle, n-cycle, or chaotic attractor [13,33]. In Section 6.1, we use Theorem 5 to illustrate the potential for strong Allee effects in Darwinian matrix models.

5. Commonly used bifurcation parameters and fitness functions

To aid the discussion of common choices for λ and G, we begin with a small change in notation. Starting with the premise that a bifurcation parameter is yet to be chosen let

$$G = G(a, x, v, u),$$

where $a \in \mathbb{R}^j$ is a vector containing the j relevant parameters of the model (such as the vital rates). In some instances, the bifurcation parameter of choice is an explicit rate within the model ($\lambda \in a$). In other cases, the choice of λ is a combination of parameters ($\lambda = \eta(a)$ where $\eta : \mathbb{R}^j \to \mathbb{R}$) that the modeller can make explicit to satisfy Assumption A4. Two such common bifurcation parameters are the *inherent population growth rate* (r) and the *inherent net reproduction number* (R_0).[4] Both quantities describe population growth at low densities and lead to identical conclusions concerning long-term population persistence.[5] In matrix population models, the typical expectation is that populations possessing $r < 1$ ($R_0 < 1$) tend toward extinction while populations with $r > 1$ ($R_0 > 1$) persist; the narrative may become more complex when positive density effects are present (see Section 4). Assumptions A1–A5 do not hold for all possible choices of λ. In most models, however, P satisfies Assumption A4 using $\lambda = R_0$, and $\lambda = \lambda^*$ corresponds to $R_0 = 1$.

Both r and R_0 are derived from more general expressions that serve as candidate fitness functions. We now discuss and present these fitness functions and highlight the derivation of r and R_0. Past modelling studies [2,30,35] use the spectral radius of P to measure population fitness:

$$G(a, x, v, u) = \rho[P(a, x, v, u)] \tag{10}$$

where $\rho[M]$ denotes the spectral radius of a square matrix M, which for primitive M equals the dominant eigenvalue. We calculate r by evaluating Equation (10) at the extinction equilibrium pair $(a, x, v, u) = (a, 0, u^*, u^*)$. In general, Equation (10) uses density- and trait-dependent growth to quantify long-term persistence and serves as one possible measure of population fitness. Other functional transformations of Equation (10) are also present in the literature, such as $\ln\left(\rho[P(a, x, v, u)]\right)$ which is commonly used in discrete-time matrix population models [12,34].

Deriving an explicit algebraic expression for Equation (10) can be complicated or even impossible for models of dimension greater than two. As an alternative, one can rewrite P as the additive result of transition and fecundity components, i.e.

$$P(a, x, v, u) = T(a, x, v, u) + F(a, x, v, u)$$

where T describes the transition and survival rates and F describes the birth rates of each class. Then another possible representation of fitness is given by

$$G(a, x, v, u) = \rho\left[\left(I - T(a, x, v, u)\right)^{-1} F(a, x, v, u)\right]. \tag{11}$$

We derive R_0 by evaluating Equation (11) at the extinction equilibrium pair $(a, x, v, u) = (a, 0, u^*, u^*)$.[6]

When using the fitness functions in Equations (10) and (11) it is natural, though not required, to use $\lambda = r$ and $\lambda = R_0$ respectively as bifurcation parameters. In practice, formulas for R_0 are often available for models of arbitrary dimension [13], but it is worth restating that other, often simple and explicit, bifurcation parameter choices are possible. In the next biological example, we use the maximum birth rate – which shares a one-to-one correlation with R_0 – as the bifurcation parameter and Equation (11) as the fitness function.

6. Examples

6.1. Example 1: juvenile-adult population model

Consider a stage-structured population model with juvenile population x and adult population y, where density-dependent feedback and frequency-independent selection drive individual survival and fitness. We model the population dynamics with

$$P(\lambda, x, y, v, u) = \begin{pmatrix} 0 & b_{\max} b(v) f(y) \\ s_1 \sigma_1(y) & s_2 \end{pmatrix}. \tag{12}$$

The term $b_{\max} b(v) f(y)$ represents the number of surviving offspring per adult with trait v. The density-dependent term $f(y)$ determines the newborn offspring survival rate. The birth rate, $b_{\max} b(v)$, is comprised of the maximum birth rate, $b_{\max}$, and the normalized birth function, $b(v)$, which describes the dependence of birth rate on the individual's trait v and satisfies $\sup_v b(v) = 1$. The juvenile survival probability, $0 < s_1\sigma_1(y) \leq 1$, depends on adult density, while the adult survival probability, $0 < s_2 < 1$, is constant. We assume that $\sigma_1(0) = 1$ so that s_1 is the inherent juvenile survival probability. For the bifurcation parameter, we set $\lambda = b_{\max}$. We use the fitness function G given by Equation (12) to derive the rescaled fitness gradient,

$$H(\lambda, x, y, u) = \sigma^2 \left[G_v(\lambda, x, y, v, u)\right]\Big|_{v=u} = \frac{\sigma^2 \lambda b'(u) f(y) s_1 \sigma_1(y)}{1 - s_2}. \tag{13}$$

To establish the existence of a bifurcating continuum from Theorem 1 for matrix models developed with Equations (12) and (13), we first check when Assumptions A1–A5 hold:

(A1) This assumption is satisfied by the choice of $\lambda = b_{\max} > 0$.

(A2) $P(\lambda, x, y, u)$ is primitive (and therefore non-negative and irreducible) since $f(y)$, $s_1\sigma_1(y), s_2 > 0$ for $y \in \overline{\mathbb{R}_+}$ and $b(u) > 0$ on $\mathcal{U}$. Furthermore, if the aforementioned functions are $\mathcal{C}^2$ then so is P.

(A3) To fulfill this assumption we assume there exists a $u^* \in \mathcal{U}$ such that $b'(u^*) = 0$ and $b''(u^*) \neq 0$.

(A4) We can write the inherent transition and fecundity matrices as

$$A = \begin{pmatrix} 0 & 0 \\ s_1 & s_2 \end{pmatrix} \text{ and } B = \begin{pmatrix} 0 & b(u^*)f(0) \\ 0 & 0 \end{pmatrix}.$$

Assumption A2 guarantees that $B \neq 0$, and $I - A$ is invertible because $s_2 < 1$. So

$$(I - A)^{-1}B = \begin{pmatrix} 0 & b(u^*)f(0) \\ 0 & \frac{b(u^*)f(0)s_1}{1-s_2} \end{pmatrix}$$

which has the algebraically simple characteristic value and corresponding positive eigenvector

$$\lambda^* = \frac{1 - s_2}{b(u^*)f(0)s_1} \text{ and } \xi = \left({}^{(1-s_2)/s_1}_{1} \right).$$

(A5) The functions $b(u), f(y), \sigma_1(y)$ are $\mathcal{C}^2$ and hence $H(\lambda, x, u)$ is continuous and differentiable. Furthermore, the derivatives of the fitness gradient take the appropriate forms

$$\nabla_{x,y} H(\lambda, 0, u^*) = g(\lambda)(a + \lambda b) = (0, 0)$$

$$H_u(\lambda, 0, u^*) = g(\lambda)(\alpha + \lambda\beta) = \frac{\sigma^2 \lambda b''(u^*) f(0) s_1}{1 - s_2}$$

where $g(\lambda) = \lambda$, $\alpha = \sigma^2 b''(u^*)f(0)s_1/(1 - s_2)$, and $\beta = 0$. It follows that $\alpha \neq 0$ and $-\beta/\alpha \neq \lambda^*$.

Assumptions A2 and A5 are generally satisfied with biologically motivated functions. Assumption A3 requires a birth function with a local minimum or maximum; with traits like body size, where fecundity is reduced or absent at the extremes, it is likely that a birth-maximizing trait value exists. To address the boundedness, initial direction, and stability of the equilibrium pairs on the bifurcating continuum, we develop criteria that allow for the application of Theorems 2–5.

If $b(u)$ has only one local minimum or maximum, then Theorem 2(i) holds and the x-component of $\mathcal{C}$ is positive. If Theorem 2(i) holds and $yf(y)$ is bounded for $y > 0$, then the x- and y-components of $\mathcal{C}$ are also bounded, so either the λ- or u-component (or both) will be unbounded along the continuum. Theorem 2(ii) may hold if multiple critical traits exist, with a birth module $b(v)$ having more than one maximum or minimum, but such a case is perhaps less biologically plausible. However, in a model where survival also depends on the individual's trait, the inherent trade-offs between adult fecundity and survival may generate multiple critical traits.

The exchange of stability principle given in Theorem 4 attributes initial direction and stability of the equilibrium pairs on $\mathcal{C}$ near $(\lambda^*, 0, u^*)$ to a single term, κ. Note that Assumption A6 is satisfied by our comment above of Assumption A2. Use of Theorem 4 requires that $H_u(\lambda, 0, u^*) < 0$; equivalently, the critical trait, u^*, must maximize the birth module, $b(v)$. Assuming $b''(u^*) < 0$, we use $\xi^T = \big((1-s_2)/s_1, 1\big)$ and $\zeta^T = \big(s_1, 1\big)$ to calculate

$$\kappa = \frac{-(1-s_2)\left(\sigma_1'(0) + f'(0)/f(0)\right)}{s_1 b(u^*) f(0)}. \tag{14}$$

The sign of κ depends on the inherent sensitivity of offspring and juvenile survivorship to adult density. Considering the form of κ in Equation (14), it is more transparent how the presence and magnitude of component Allee effects affects the initial direction of bifurcation. If there are no component Allee effects and only negative density effects, then $\sigma_1'(0), f'(0) < 0$, so $\kappa > 0$ and $\mathcal{C}$ bifurcates forward. If there are only component Allee effects, then $\sigma_1'(0), f'(0) > 0$, so $\kappa < 0$ and $\mathcal{C}$ bifurcates backward.

The sign of κ is uncertain in cases where, for example, adults bolster juvenile survival through protection and training ($\sigma_1'(0) > 0$) but hamper newborn survival via filial cannibalism ($f'(0) < 0$) [21]. For illustrative purposes, let

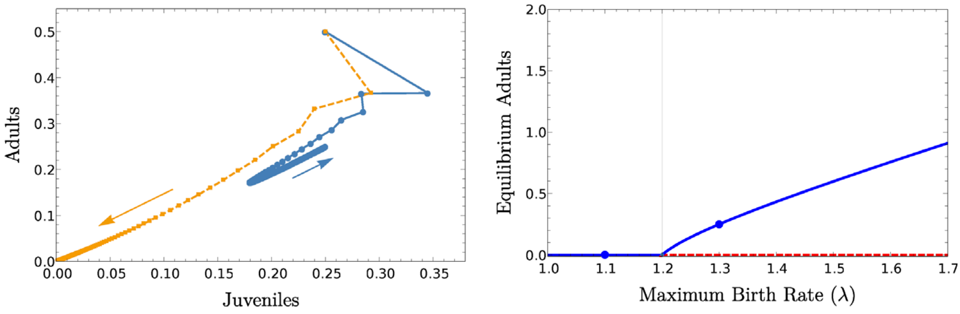
$$\sigma_1(y) = \frac{1 + 2c_1 y}{1 + c_1 y} \tag{15}$$

$$f(y) = \frac{1}{1 + c_2 y}. \tag{16}$$

The positive coefficients c_1 and c_2 determine adult density effects on juvenile and offspring survival respectively. At low population densities, c_1 represents the inherent rate of change in juvenile survival and c_2 is the magnitude component of the inherent rate of change in newborn survival (since $f'(0) = -c_2$). Let the birth term, $b(u)$, be $u^3(a-u)^5$ rescaled to have a maximum of 1:

$$b(u) = \begin{cases} \frac{u^3(a-u)^5}{(3a/8)^3(3a/8)^5} & u \in (0, a) = \mathcal{U} \\ 0 & u \notin \mathcal{U}. \end{cases} \tag{17}$$

Note that the critical trait, $u^* = 3a/8$, is the global maximizer of $b(u)$. Due to the form of Equation (14), change in fitness is proportional to $b'(u)$, so u will tend toward u^* and so remain within $\mathcal{U} = (0, a)$. If we assume $u \in \mathcal{U}$ initially, then $b(u)$ remains strictly positive and Assumption A2 is satisfied. If $u \notin \mathcal{U}$ initially then $b(u) = 0$, ensuring extinction. See Figures 5 and 6 for trajectories and bifurcation diagrams using specific parameters.



(a) Phase diagrams of x and y with $x(0) = 0.25, y(0) = 0.5, u(0) = 1$. The dashed extinction trajectory uses $\lambda = 1.1$, while the solid persistence trajectory uses $\lambda = 1.3$.

(b) Bifurcation diagram showing the forward bifurcation. The dots indicate the equilibrium pairs towards which the trajectories in (a) asymptote.

Figure 5. For parameters $a = 10, c_1 = 1, c_2 = 1.2, s_2 = 0.4$, and $\sigma = 1/\sqrt{10}$, we compute $\kappa = 0.24$ and $\mu_1 = -0.4$, which implies a forward bifurcation. The solid lines indicate stable equilibria and the dashed lines indicate unstable equilibria.

Applying Equations (15) and (17), we can bound the x- and y-components along the continuum:

$$x = \lambda b(u) \frac{y}{1 + c_2 y} \leq \lambda \quad \text{and} \quad y = \frac{s_1}{1 - s_2} \frac{1 + 2c_1 y}{1 + c_1 y} x \leq \frac{2\lambda s_1}{1 - s_2}.$$

Since $\mathcal{U}$ is bounded and $\left|(x, y)\right| \leq \lambda + \frac{2\lambda s_1}{1 - s_2} = m(\lambda)$, we use Theorem 2(ii) and Theorem 3 to conclude that the λ-component of $\mathcal{C}$ is unbounded. Thus, for every $\lambda > \lambda^*$ there is a corresponding equilibrium pair on the continuum.

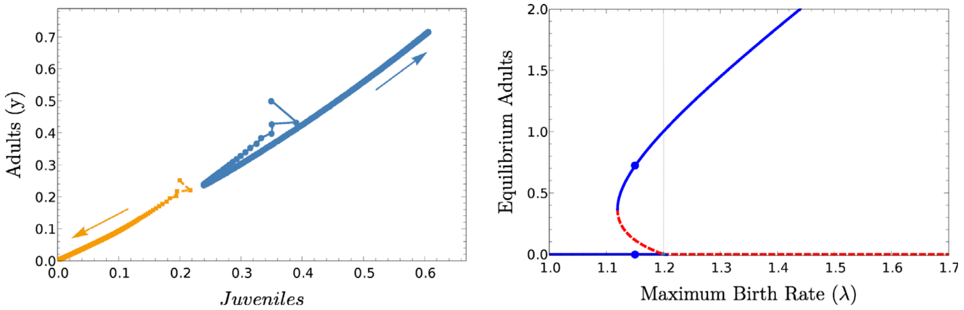
The functional forms in Equations (15) and (17) also simplify criteria for the initial direction of $\mathcal{C}$ with $\kappa = (1 - s_2)(c_2 - c_1)/s_1$. Direction of bifurcation depends solely on the difference in magnitudes between the inherent sensitivities for newborn and juvenile survival. When low-density populations are more sensitive to declines in newborn survival vs. increases in juvenile survival ($c_2 > c_1$), species survival is not possible for $\lambda < \lambda^*$ (Figure 5(b)). When the opposite case holds ($c_1 > c_2$), component Allee effects outweigh negative density effects and, by using Theorem 5, one can show that the population exhibits a Strong Allee effect (Figure 6(b)). The latter case ($c_1 > c_2$) suggests that sufficiently positive interactions between adults and their young can steer populations away from extinction.

6.2. Example 2: connecting to another critical trait

Here we provide a mathematical example that illustrates alternative (ii) of Theorem 2 that is not biologically motivated. Consider system (2) with

$$\begin{aligned} P(\lambda, x, u) &= \lambda(u + 1) \\ H(\lambda, x, u) &= u(u - 1) + x^2/\lambda \end{aligned}$$

where $\lambda > 0$. We begin by verifying the assumptions required for the application of Theorem 2.



(a) Phase diagrams of x and y. Both trajectories use $\lambda = 1.15$. The extinction trajectory uses $x_1(0) = 0.2, x_2(0) = 0.25, u(0) = 1$, while the persistence trajectory uses $x_1(0) = 0.35, x_2(0) = 0.5, u(0) = 1$.

(b) Bifurcation diagram showing the backward bifurcation. The dots indicate the equilibrium pairs towards which the trajectories in (a) asymptote.

Figure 6. For parameters $a = 10, c_1 = 1, c_2 = 0.5, s_1 = 0.5, s_2 = 0.4$, and $\sigma = 1/\sqrt{10}$, we compute $\kappa = -0.6$ and $\mu_1 = 0.3$, which implies a backward bifurcation. The solid lines indicate stable equilibria and the dashed lines indicate unstable equilibria.

(A1) Because $\lambda > 0$, we take $\lambda_{\min} = 0$.
(A2) Because $n = 1$, $P(\lambda, x, u)$ is clearly primitive (and hence non-negative and irreducible) and C^2 on $[0, \infty) \times \overline{\mathbb{R}_+} \times \mathcal{U}$, where $\mathcal{U} = (0, \infty)$.
(A3) There are two critical traits, $u^* = 0$ and $\tilde{u} = 1$.
(A4) Due to the simplicity of P, we see $A = 0, B = 1, \lambda^* = 1$, and $\zeta^T = \xi = 1$.
(A5) Continuity and differentiability of $H(\lambda, x, u)$ is satisfied, and $H_x(\lambda, 0, 0) = 0$ and $H_u(\lambda, 0, 0) = -1$ (so that $\alpha = -1, \beta = 0$).

From the trait equation it follows that,

$$u' = u + H(\lambda, x, u) = u + u(u-1) + x^2/\lambda \geq u^2 \geq 0$$

and so the u-component of orbits that originate in $\mathcal{U}$ never leave.

This system has the trivial solutions of $(\lambda, x, u) = (\lambda, 0, 0)$ and $(\lambda, 0, 1)$. It has nontrivial solutions

$$u_e = (1-\lambda)/\lambda \quad \text{and} \quad x_e^{\pm} = \pm\sqrt{\frac{(1-\lambda)(2\lambda-1)}{\lambda}}$$

when $\lambda \in (\frac{1}{2}, 1)$. The continuum of equilibrium pairs satisfies alternative (ii) of Theorem 2 (see Figure 7).

We find $u_1 = 0$, $\kappa = 0$, and $\mu_1 = 0$; thus Theorem 4 does not apply and the direction of bifurcation of $\mathcal{C}$ cannot be determined without further terms in the Taylor expansions. We directly prove the instability of the positive equilibrium pairs.

The Jacobian of the system is

$$\mathcal{J}(\lambda, x, u) = \begin{pmatrix} \lambda(u+1) & \lambda x \\ \frac{2}{\lambda}x & 2u \end{pmatrix}.$$

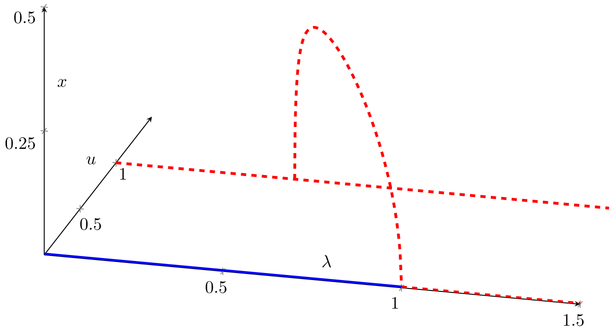


Figure 7. An example of Theorem 2(ii) where the solid lines indicate stable equilibria and the dashed lines indicate unstable equilibria. The continuum of positive equilibrium pairs bifurcates from $(1, 0, 0)$ and connects to the bifurcation point $(0.5, 0, 1)$ which lies on another line of trivial equilibrium pairs. Note that near the first bifurcation point $H_u(\lambda, 0, 0) < 0$ and so we see the backward bifurcation corresponds to unstable positive equilibrium pairs, with the line $(\lambda, 0, 0)$ going from stable to unstable, as proved by Theorem 4. Near the bifurcation point $(0.5, 0, 1)$, $H_u(\lambda, 0, 1) > 0$ and so although the bifurcation is forward, the positive and trivial equilibrium pairs are all unstable (see Appendix 2).

Evaluated at the positive equilibrium pairs,

$$\mathcal{J}\left(\lambda, x_e^+, u_e\right) = \begin{pmatrix} 1 & \lambda\sqrt{\frac{(1-\lambda)(2\lambda-1)}{l}} \\ \frac{2}{\lambda}\sqrt{\frac{(1-\lambda)(2\lambda-1)}{l}} & 2(\frac{1}{\lambda}-1) \end{pmatrix}.$$

The Jury conditions state that the absolute value of the eigenvalues are strictly less than 1 if and only if $\left|\mathrm{tr}\mathcal{J}\left(\lambda, x_e^+, u_e\right)\right| < 1 + \det\mathcal{J}\left(\lambda, x_e^+, u_e\right) < 2$. The first inequality is true if

$$\frac{2-\lambda}{\lambda} < 1 + \frac{4(1-\lambda)^2}{\lambda} \quad \text{which reduces to the inequality} \quad 1 < 2(1-\lambda)$$

which is false for $\lambda \in (\frac{1}{2}, 1)$. Thus the positive equilibrium pairs are unstable.

7. Conclusion

In this paper, we extend the theory in [12,13,31] to prove the global existence of a bifurcating continuum for Darwinian matrix models with a general bifurcation parameter. We provide a checklist of assumptions and formulae so modellers can quickly discern the existence, shape, and initial direction of a bifurcating continuum of positive equilibrium pairs, which is helpful for studying long-term Darwinian dynamics. In addition to assuming the population matrix is non-negative and irreducible, we assume existence of a critical trait of the fitness function, a specific form of the population matrix given a chosen bifurcation parameter, and the existence of an algebraically simple characteristic value λ^* derived from the population matrix. In this context, an unbounded continuum of equilibrium pairs bifurcates from a trivial equilibrium. The unboundedness must occur in at least one of the three components (parameter, population, or trait), so bounding two, such as the population size and phenotypic trait values, implies that the third is unbounded. The continuum may be unbounded such that every equilibrium pair has a positive population value, or it may connect to another trivial equilibrium at another critical trait of the fitness function, truncating the relevant continuum – this is an alternative not present in the non-evolutionary setting. We present examples of both alternatives.

Moving past the issue of existence, we derive an equation for the initial direction of bifurcation and relate it to the stability of the equilibrium pairs on the continuum near the bifurcation point. In this analysis, we require primitivity of the population matrix. As in the non-evolutionary setting, the Principle of Exchange of Stability holds: backward bifurcation corresponds to unstable equilibria and forward bifurcation corresponds to stable equilibria. In the case of a backward bifurcation, we present sufficient conditions for the existence of strong Allee effects in a given parameter region and interpret the quantities that determine such phenomena. Past studies emphasize the role that component Allee effects play in generating strong Allee effects [3,13,22]. Within the context of matrix models, we discuss component Allee effects as well as how trait dynamics can suppress or enhance strong Allee effects. We find that strong Allee effects may occur when trait dynamics heavily influence population growth and shift in a direction that maximizes fitness. Like component Allee effects, the inherent effects of an evolving phenotypic trait must have positive influence on population growth; however, the direction of the evolving trait is unconstrained. Finally, we discuss common fitness functions for use in creating evolutionary models and highlight their common corresponding bifurcation parameter counterparts.

Our stability theory does not apply to evolutionary models with an imprimitive population matrix. This is because there is no longer a dominant eigenvalue associated with a positive eigenvector – a fact which we use throughout Section 3 and in Theorem 4. Also, if the population matrix at extinction and the critical trait is not writable in the form of Assumption A4, then the theory does not apply and we cannot use the theorem from [31] which gives the unbounded continuum. Such contexts are possible avenues for future research and may provide different conclusions.

Notes

1. The positive eigenvector is also the eigenvector of $P(\lambda^*, 0, u^*)$ corresponding to eigenvalue 1.
2. Rabinowitz [31] defines a continuum as a closed connected set. Thus, the point $(\lambda^*, 0, u^*)$ is contained in the continuum.
3. In the case of $\kappa = 0$, the direction of the bifurcation of $\mathcal{C}$ will depend on the next non-zero coefficient in the $\lambda(\epsilon)$ expansion. In this case, the direction may or may not determine the stability.
4. For a Leslie matrix P, R_0 is the average number of offspring produced by a single individual during its lifetime in a low-density population. See [9] for a more general interpretation in the case of a non-Leslie matrix.
5. The two quantities also share the important relationship [14,27]

$$0 < R_0 < r < 1 \text{ or } R_0 = r = 1 \text{ or } 1 < r < R_0$$

under the assumption that the lifetime of an individual is finite.

6. While R_0 is usually derived using $\rho\left[F(I-T)^{-1}\right]$ instead of $\rho\left[(I-T)^{-1}F\right]$ for interpretation purposes, the spectral radii are equivalent. Furthermore, the form derived from Equation (11) corresponds nicely with $(I-A)^{-1}B$.

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Appendix 1.

We Taylor expand $x = P(\lambda, x, u)x$ at $(\lambda^*, 0, u^*)$. Let $\varnothing_3$ denote terms of order 3 in $(\lambda - \lambda^*)$, x, and $(u - u^*)$. Let $D(x)$ be $d_{ij}(\tilde{x}) = \left(\nabla^0_x p_{ij}\right)\tilde{x}$.

Looking at the expansion of the dynamics of a single class,

$$x_i = \underbrace{\sum_j x_j p^0_{ij}}_{\text{order 1}} + \frac{1}{2!} \times \underbrace{\left[\left(2(\lambda - \lambda^*)\sum_j x_j \partial^0_\lambda p_{ij}\right) + \left(2(u - u^*)\sum_j x_j \partial^0_u p_{ij}\right) + \left(2\sum_j\sum_k x_j x_k \partial^0_{x_j} p_{ik}\right)\right]}_{\text{order 2}} + \varnothing_3.$$

Note that because $p_{ij} \in C^2$, we have $P_\lambda(\lambda, x, u)\big|_{(\lambda,x,u)=(\lambda^*,0,u^*)} = B$. Then for the whole system, this equates to

$$\begin{aligned} x &= P(\lambda^*, 0, u^*)x + (\lambda - \lambda^*)Bx + (u - u^*)P_u^0 x + D(x)x + \varnothing_3 \\ &= (A + \lambda^* B)x + (\lambda - \lambda^*)Bx + (u - u^*)P_u^0 x + D(x)x + \varnothing_3 \\ &= (A + \lambda B)x + (u - u^*)P_u^0 x + D(x)x + \varnothing_3. \end{aligned}$$

Appendix 2.

The Jacobian of System (2) is

$$\mathcal{J}(\lambda, x, u) = \begin{pmatrix} P(\lambda, x, u) + \left(\sum_{k=1}^n x_k \partial_{x_j} p_{ik}\right) & P_u(\lambda, x, u)x \\ \nabla_x H(\lambda, x, u) & 1 + H_u(\lambda, x, u) \end{pmatrix}.$$

Along the parametrized continuum, $\mathcal{J}(\lambda(\epsilon), x(\epsilon), u(\epsilon)) = \mathcal{J}_0 + \mathcal{J}_1\epsilon + \varnothing(\epsilon^2)$. At $\epsilon = 0$,

$$\begin{aligned} \mathcal{J}_0 &= \begin{pmatrix} P(\lambda^*, 0, u^*) & 0 \\ \nabla_x H(\lambda^*, 0, u^*) & 1 + H_u(\lambda^*, 0, u^*) \end{pmatrix} \\ &= \begin{pmatrix} P^0 & 0 \\ \nabla_x H^0 & 1 + H_u^0 \end{pmatrix} \end{aligned}$$

which has eigenvalues from $P(\lambda^*, 0, u^*)$ and $1 + H_u(\lambda^*, 0, u^*)$.

Recall that $P(\lambda^*, 0, u^*)$ is a primitive matrix with $\xi = P(\lambda^*, 0, u^*)\xi$ and hence $\rho(P(\lambda^*, 0, u^*)) = 1$. When $H_u(\lambda^*, 0, u^*) > 0$, the positive and trivial equilibrium pairs are unstable due to continuity (Assumption A5b). Because $H_u(\lambda^*, 0, u^*) \neq 0$, the remaining case is when $H_u(\lambda^*, 0, u^*) < 0$, where it is possible for the equilibrium pairs on the two continua to have separate stability. Looking along the parametrized continuum of positive equilibrium pairs, let

$$\mu(\epsilon) = 1 + \mu_1\epsilon + \varnothing(\epsilon^2)$$

be the dominant eigenvalue of $P(\lambda(\epsilon), x(\epsilon), u(\epsilon))$. If $\mu_1 < 0$, the positive equilibrium pairs are stable; if $\mu_1 > 0$, they are unstable. As is the case with $\kappa = 0$, if $\mu_1 = 0$ then the stability is determined by the next non-zero term in the expansion.

Let $\Xi(\epsilon)$ denote the eigenvector of $\mathcal{J}$ corresponding to $\mu(\epsilon)$.

$$\mathcal{J}(\epsilon)\Xi(\epsilon) = \mu(\epsilon)\Xi(\epsilon) \tag{B1}$$

$$\mathcal{J}'(\epsilon)\Xi(\epsilon) + \mathcal{J}(\epsilon)\Xi'(\epsilon) = \mu'(\epsilon)\Xi(\epsilon) + \mu(\epsilon)\Xi'(\epsilon). \tag{B2}$$

Expanding in orders of ϵ, we get

$$\begin{gathered} \mathcal{J}_0\Xi_0 = \mu_0\Xi_0 \\ \mathcal{J}_1\Xi_0 + \mathcal{J}_0\Xi_1 = \mu_1\Xi_0 + \mu_0\Xi_1 \end{gathered}$$

which makes Ξ_0 the positive right eigenvector, and Z_0^T the positive left eigenvector, of $\mathcal{J}_0$. Thus

$$\Xi_0 = \begin{pmatrix} \xi \\ -\frac{\nabla_x^0 H\xi}{H_u^0} \end{pmatrix}, \quad Z_0^T = \begin{pmatrix} \zeta^T & 0 \end{pmatrix}.$$

Combining Equations (B1) and (B2), we get

$$(\mathcal{J}_0 - \mu_0 I)\Xi_1 = \mu_1\Xi_0 - \mathcal{J}_1\Xi_0$$

which is solvable by the Fredholm Alternative if and only if

$$Z_0^T(\mu_1 \Xi_0 - J_1 \Xi_0) = 0,$$

i.e.

$$\mu_1 = \frac{Z_0^T \mathcal{J}_1 \Xi_0}{Z_0^T \Xi_0}.$$

Note $\mathcal{J}_1 = \frac{\mathrm{d}}{\mathrm{d}\epsilon}\mathcal{J}(\lambda(\epsilon), x(\epsilon), u(\epsilon))|_{\epsilon=0}$. Evaluating the derivative of the top row of $\mathcal{J}$,

$$\begin{aligned}\left((\mathcal{J}_1)_{11}\right)_{ij} &= \frac{\mathrm{d}}{\mathrm{d}\epsilon}\left(p_{ij} + \left(\sum_{k=1}^{n} x_k \partial_{x_j} p_{ik}\right)\right)\Bigg|_{\epsilon=0} \\ &= \nabla_x^0 p_{ij}\xi + u_1 \partial_u^0 p_{ij} + \kappa \partial_\lambda^0 p_{ij} + \sum_{m=1}^{n} \xi_m \partial_{x_j}^0 p_{im}\end{aligned}$$

and

$$\begin{aligned}(\mathcal{J}_1)_{12} &= \frac{\mathrm{d}}{\mathrm{d}\epsilon}\Big(P_u\left(\lambda(\epsilon), x(\epsilon), u(\epsilon)\right) x\Big)\Big|_{\epsilon=0} \\ &= P_u^0 \xi.\end{aligned}$$

Then

$$\begin{aligned}\mu_1 \zeta^T \xi &= Z_0^T \mathcal{J}_1 \Xi_0 \\ &= \zeta^T\left((\nabla_x^0 p_{ij})\xi + u_1 \partial_u^0 p_{ij} + \kappa \partial_\lambda^0 p_{ij} + \sum_{m=1}^{n} \xi_m \partial_{x_j}^0 p_{im}\right)\xi + \zeta^T\left(P_u^0 \xi\right)\left(-\frac{\nabla_x^0 H \xi}{H_u^0}\right) \\ &= \zeta^T\Big(D(\xi) + u_1 P_u^0\Big)\xi + \kappa \zeta^T B \xi + \zeta^T\left(\nabla_x^0 p_{ij}\xi\right)\xi - \zeta^T P_u^0 \xi \frac{\nabla_x^0 H \xi}{H_u^0} \\ &= -\kappa \zeta^T B \xi.\end{aligned}$$

Because $\zeta^T, \xi > 0$ and B is non-negative, the Principle of Exchange of Stability, outlined in Kielhöfer [20], holds and the sign of κ also determines the stability of equilibrium pairs on the continuum $\mathcal{C}$ close to the trivial equilibrium pair $(\lambda^*, 0, 0)$.

Appendix 3.

We use the same method as in Appendix 2 to calculate the stability along the line of trivial equilibrium pairs. We start by parametrizing the line as $x(\epsilon) = 0$, $u(\epsilon) = u^*$, $\lambda(\epsilon) = \lambda^* + \lambda_1\epsilon$ with an arbitrary $\lambda_1 > 0$.

We again consider $\mathcal{J}(\lambda(\epsilon), x(\epsilon), u(\epsilon)) = \mathcal{J}_0 + \mathcal{J}_1\epsilon + \mathcal{O}(\epsilon^2)$. This gives the same $\mathcal{J}_0$ as in Appendix 2 and hence the same conclusions for its eigenvalues. When $H_u(\lambda^*, 0, u^*) > 0$, the equilibrium pairs on both sides of λ^* are unstable due to continuity. We again let $\mu(\epsilon) = 1 + \mu_1\epsilon + \mathcal{O}(\epsilon^2)$ denote the dominant eigenvalue of $P(\lambda(\epsilon), x(\epsilon), u(\epsilon))$. Note that Ξ_0 and Z_0^T also remain the same.

We calculate

$$\begin{aligned}\left(\mathcal{J}_1\right)_{11} &= \lambda_1 B, \\ (\mathcal{J}_1)_{12} &= 0.\end{aligned}$$

Then

$$\begin{aligned}\mu_1 \zeta^T \xi &= Z_0^T \mathcal{J}_1 \Xi_0 \\ &= \lambda_1 \zeta^T B \xi\end{aligned}$$

and hence $\mu_1 > 0$. When $\epsilon > 0$, this gives $\lambda(\epsilon) > \lambda^*$ and $\mu(\epsilon) > 1$; and when $\epsilon < 0$, we have $\lambda(\epsilon) < \lambda^*$ and $\mu(\epsilon) < 1$. Thus, when $H_u(\lambda^*, 0, u^*) < 0$, the trivial equilibrium pairs are stable for $\lambda < \lambda^*$ and are unstable for $\lambda > \lambda^*$.