One Dimensional Maps as Population and Evolutionary Dynamic Models

Jim M. Cushing

Abstract I discuss one dimensional maps as discrete time models of population dynamics from an extinction-versus-survival point of view by means of bifurcation theory. I extend this approach to a version of these population models that incorporates the dynamics of a single phenotypic trait subject to Darwinian evolution. This is done by proving a fundamental bifurcation theorem for the resulting two dimensional, discrete time model. This theorem describes the bifurcation that occurs when an extinction equilibrium destabilizes. Examples illustrate the application of the theorem. Included is a short summary of generalizations of this bifurcation theorem to the higher dimensional maps that arise when modeling the evolutionary dynamics of a structured population.

Keywords Discrete time dynamics · Difference equations · Population dynamics · Evolutionary dynamics · Bifurcations · Equilibria · Stability · Allee effects

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1 Introduction

Iterative maps of the form

$$x_{t+1} = f(x_t)\,x_t \tag{1}$$

(often called difference equations) are widely used to model the discrete time (deterministic) dynamics of biological populations. Here x_t is some measure of population density at discrete census times $t = 0, 1, 2, \ldots$ and the expression $f(x)$ describes the per capita (or per unit) contribution to the population at the the next census time. We refer to f as the *population growth rate*. In this context the sequence x_t is

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non-negative, and the function f assumes only non-negative values for non-negative values of its argument. An initial condition $x_0 \geq 0$ generates a unique sequence (or trajectory) for $t = 0, 1, 2, \ldots$. The asymptotic properties of the sequence x_t are often of central interest and these depend, of course, on the properties of f. Famous examples include

$$f(x) = b\frac{1}{1+cx}, \quad f(x) = bxe^{-cx} \tag{2}$$

where b, c are positive constants.

The first example in (2) used in (1) gives what historically was called the discrete logistic model (or Pielou's logistic or Beverton-Holt model [23]). For this model, it is well known that the *extinction equilibrium* (fixed point) $x_e = 0$ is globally asymptotically stable for $x_0 \geq 0$ (i.e. it is locally asymptotically stable and attracts all trajectories with $x_0 \geq 0$) if $b < 1$ while the *positive equilibrium* $x_e = c^{-1}(b-1)$ is globally asymptotically stable for $x_0 \geq 0$ when $b > 1$. This is a prototypical example of the fundamental bifurcation that occurs at $b = 1$ where the extinction equilibrium destabilizes and, as a result, a stable positive equilibrium is created. The second example in (2) used in (1) gives the so-called Ricker model. The extinction equilibrium of this model also destabilizes at $b = 1$ with the result that there exists positive equilibrium $x_e = c^{-1}\ln b$ for $b > 1$. The positive equilibrium is (globally) stable for $1 < b < e^2$ but unstable for $b > e^2$. As b increases the Ricker model exhibits a period doubling cascade to chaos, similar to that exhibited by the famous quadratic map given by $f(x) = b(1-cx)$ (which is often called the logistic map, rather inappropriately from a population dynamic point of view). Thus, both of these basic examples illustrate a fundamental bifurcation: when the extinction equilibrium destabilizes, a stable positive equilibria is created (at least for $b \gtrapprox 1$). As we will see, this is a general phenomenon for population models (1).

The function f is often regarded as describing reproductive processes and, as a result, the map (1) assumes all contributions to the population at time $t+1$ are due to reproductive events (and the survival of offspring until the census at $t+1$). This is appropriate, for example, for so-called semelparous (or monocarpic) populations in which individuals die after reproduction and, consequently, no reproductive individuals at time t are alive at time $t+1$. In this case generations do not overlap. It is often stated that one dimensional maps are only applicable to populations with non-overlapping generations, but this is not true. Suppose $s(x)$ is the fraction of the population x at time t that survives a unit of time. Then, if $b(x)$ is the (per capita) number of offspring (that survive until time $t+1$), we have

$$f(x) = b(x) + s(x). \tag{3}$$

The resulting map (1) allows for overlapping generations. We will refer to $b(x)$ as the birth or fertility rate and $s(x)$ as the survival rate.

If f depends only on the state variable x, as indicated above, then it is only the current population density that determines the population density at the next time census and, as a result, the mathematical model (1) is time autonomous. There are, however, many circumstances under which f also depends explicitly on time t. For example, in a seasonally fluctuating environment model coefficients, such as b and c in the discrete logistic or Ricker models, might be assumed periodic functions of time. In this case, the model equation (1) is periodically forced. Or model parameters might fluctuate randomly, due to random fluctuations in the physical environment (environmental stochasticity) or in individual organism characteristics (demographic stochasticity). In this case, the model equation (1) becomes a stochastic dynamical system.

Another reason that model parameters can change in time is Darwinian evolution, which is a case we will consider here. Suppose v is a quantified, phenotypic trait of an individual that is subject to evolution (i.e. it has a heritable component, it has variability among individuals in the population, and it accounts for differential fitness, e.g. individual differences among vital rates such as fertility and survival). If we assume the per capita contribution to the population made by an individual depends on its trait v, then $f = f(x, v)$ depends on both x and v. It might be the case that this contribution also depends on the traits of other individuals (due, for example, to competition for resources or other interactions among individuals). We can model this situation (frequency dependence) by assuming that f also depends on the mean trait u in the population so that $f = f(x, v, u)$. A canonical way to model Darwinian evolution is to model the dynamics of x_t and the mean trait u_t by means of the equations

$$x_{t+1} = f(x_t, v, u_t)|_{v=u_t}\, x_t \tag{4a}$$

$$u_{t+1} = u_t + \sigma^2\, \partial_v F(x_t, v, u_t)|_{v=u_t}\,. \tag{4b}$$

The first equation asserts that the population dynamics can be (reasonably well) modeled by assuming the trait v is set equal to the population mean. The second equation (called Lande's or Fisher's or the breeder's equation) prescribes that the change in the mean trait is proportional to the *fitness gradient*, where fitness in this model is denoted by $F(x, v, u)$ [1, 21, 27, 28, 30, 36]. The modeler decides on an appropriate measure of fitness [32], which is often taken to be f or $\ln f$. The constant of proportionality $\sigma^2 \geq 0$ is called the speed of evolution. It is related to the variance of the trait in the population (exactly how depends on the derivation of the mean trait equation), which is assumed constant in time. Thus, if $\sigma^2 = 0$ no evolution occurs (there is no variability) and one has a one-dimensional map for just population dynamics of the form (1). If evolution occurs $\sigma^2 > 0$ then the model is a two dimensional map with state variable $[x_t, u_t]$.

In Sect. 2 we discuss non-evolutionary models of the form (1)–(3) with a focus on the basic question of extinction versus survival from a bifurcation theory point of view. In Sect. 3 we discuss a general class of evolutionary models from the same point of view.

2 One Dimensional Maps as Population Dynamic Models

The linearization principle applied to the extinction equilibrium $x = 0$ of (1)–(3) implies the extinction equilibrium is (locally asymptotically) stable if the *inherent population growth rate* $r_0 \mathrel{\overset{\circ}{=}} f(0) \geq 0$ satisfies $r_0 < 1$ and unstable if $r_0 > 1$. In order to expose more explicitly the role of the *inherent* birth and death rates (i.e. the birth and death rates in the absence of any density effects) we write

$$f(x) = b_0 \varphi(x) + s_0 \sigma(x), \quad \varphi(0) = \sigma(0) = 1$$

where b_0 and s_0 are inherent birth and survival rates. Let Ω be an open interval of real numbers that contains the half line of nonnegative real numbers $\bar{R}_+$ (the closure of the positive real numbers R_+). We assume the following.

A1. *$b_0, s_0 \in \bar{R}_+$ and the functions φ and σ are twice continuously differentiable as maps from Ω to R_+ and $\bar{R}_+$ respectively that satisfy $\varphi(0) = \sigma(0) = 1$ and*

$$\lim_{x \to +\infty} \varphi(x) = 0 \tag{5}$$

$$0 \leq \sup_{x \in \Omega} s_0 \sigma(x) < 1. \tag{6}$$

Condition (5) insures that the birth rate drops to 0 as population density x increases without bound. Condition (6) (which implies $0 \leq s_0 < 1$) expresses the fact that some mortality occurs during any time step. Specifically, the fraction $1 - s_0 \sigma(x)$ of the population that is lost to mortality is bounded away from 0 uniformly for all $x \geq 0$. We can interpret $s_0 \sigma(x)$ as an individual's probability of survival over one time unit.

An introduction of

$$r_0 \mathrel{\overset{\circ}{=}} b_0 + s_0$$

into

$$f(x) = (r_0 - s_0) \varphi(x) + s_0 \sigma(x) \tag{7}$$

allows easy use of r_0 as a bifurcation parameter in the resulting population model

$$x_{t+1} = ((r_0 - s_0) \varphi(x_t) + s_0 \sigma(x_t)) x_t. \tag{8}$$

Our goal is to study the existence and stability of positive equilibria as they depend on r_0.

The algebraic equation for a positive equilibrium is

$$(r_0 - s_0)\,\varphi(x) + s_0\sigma(x) = 1.$$

Solving this equation for r_0 we obtain

$$r_0 = \gamma(x)$$

where

$$\gamma(x) \mathrel{\mathring{=}} \frac{1 - s_0\sigma(x) + s_0\varphi(x)}{\varphi(x)}.$$

By assumption A1, the function $\gamma(x)$ is a twice continuously differentiable on Ω and satisfies

$$\gamma(0) = 1, \quad \gamma(x) > 0 \text{ for } x \in \Omega, \quad \lim_{x\to+\infty} \gamma(x) = +\infty.$$

The graph C of the positive equilibrium pairs $[r_0, x_e]$, $x_e > 0$, is the set of points $[\gamma(x), x]$ obtained from all values of $x > 0$, which is a continuum that contains the point $[1, 0]$ in its closure. We say that the continuum C of equilibrium pairs *bifurcates from the continuum of extinction equilibrium pairs* $[r_0, 0]$ *at* $r_0 = 1$, i.e. at the point $[1, 0]$.

We define the *spectrum* S of C to be the range of the function $\gamma(x)$ for $x > 0$. The spectrum consists of those values of r_0 for which the population model (1) has a positive equilibrium. Under the assumption A1, the spectrum S is infinite and contains 1 in its closure. It is therefore a half line. If we denote the (positive) infimum of $\gamma(x)$ by r_m, then

$$0 < r_m \mathrel{\mathring{=}} \inf_{x>0} \gamma(x) \le 1$$

and the spectrum is

$$\begin{aligned} S &= \{r_0 : 1 < r_0 < +\infty\} \quad \text{if } r_m = 1 \\ S &= \{r_0 : r_m \le r_0 < +\infty\} \quad \text{if } r_m < 1. \end{aligned} \tag{9}$$

The stability of a positive equilibrium pair $[r_0, x_e] \in C$, as determined by the linearization principle, depends on the quantity

$$\lambda(r_0, x) \mathrel{\mathring{=}} \frac{d\,(f(x)\,x)}{dx} = (r_0 - s_0)\,\varphi(x) + s_0\sigma(x) + \big((r_0 - s_0)\,\varphi'(x) + s_0\sigma'(x)\big)\,x$$

evaluated at the equilibrium pair $[r_0, x_e]$. Here we use a prime "′" to denote the derivative a function of a single variable. A calculation shows

$$\lambda(r_0, x_e) = 1 - \gamma'(x_e)\,\varphi(x_e)\,x_e \tag{10}$$

from which we can conclude that positive equilibrium pairs $[r_0, x_e]$ near the bifurcation point $[1, 0]$ are (locally asymptotically) stable if $\gamma'(0) > 0$ and are unstable if $\gamma'(0) < 0$. (An equilibrium pair is nonhyperbolic if $\gamma'(x_e) = 1$, in which case the linearization principle is unable to determine stability.) The sign of

$$\gamma'(0) = -\left((1 - s_0)\,\varphi'(0) + s_0\sigma'(0)\right)$$

is the opposite of the sign of the weighted average $(1 - s_0)\,\varphi'(0) + s_0\sigma'(0)$. The derivatives $\varphi'(0)$ and $\sigma'(0)$ are the *sensitivities* of fertility and survival to changes low level population density. If one of these sensitivities is positive, it is called a *component Allee effect* [2, 4]. If a derivative is negative, it implies a *negative feedback effect* is caused by (low level) increased density. This is the most commonly made assumption in population models. Thus we see that if, at low population densities, there are no component Allee effects and at least one negative feedback effect is present, then $\gamma'(0) > 0$ and, in a neighborhood of the bifurcation point, small equilibria are locally asymptotically stable. Moreover, in this case, the bifurcating positive equilibria correspond to r_0 values greater than 1 and the bifurcation is said to be *forward*. On the other hand, if least one sensitivity is positive enough so that $\gamma'(0) < 0$ (or if both sensitivities are positive), then in a neighborhood of the bifurcation point small equilibria are unstable. In this case, the bifurcating positive equilibria correspond to values of r_0 less than 1 and the bifurcation is said to be *backward*. Notice that in this case $r_m < 1$ and the spectrum contains 1 in its interior (see (9)).

We arrive at the conclusion: *if* $\gamma'(0) \neq 0$ *then in a neighborhood of the bifurcation point a forward bifurcation is stable (meaning that the equilibria on C are stable) and a backward bifurcation is unstable.* See Fig. 1.

This bifurcation scenario occurring in a neighborhood of the bifurcation point $[r_0, x_e] = [1, 0]$ is quite general for population models. Mathematically it is a transcritical bifurcation exhibiting an exchange of stability principle, which is a phenomenon known to occur in quite general settings from nonlinear functional analysis [24, 31]. It has been established for numerous population models of many mathematical types [6]. For this reason, one can refer to the bifurcation described above as a *fundamental bifurcation theorem* for nonlinear population dynamic models.

However, the stability properties of the positive equilibria near the bifurcation point need not persist entirely along the continuum C of equilibrium pairs. It is well known for one dimensional maps that positive equilibria can destabilize and period doublings and routes-to-chaos can occur. These secondary bifurcations are model dependent, being determined by the properties of the density terms $\varphi(x)$ and $\sigma(x)$. They can occur in models with either forward or backward bifurcations at $[r_0, x_e] = [1, 0]$. One thing we can conclude from (10) is that if $\gamma'(x_e) > 0$ then the equilibrium is unstable. This means that the *equilibria along decreasing segments of the continuum C are unstable*, as illustrated in Fig. 1.

Along increasing segments of C, however, stability is uncertain. One fact we can assert from (10) is that increasing segments in a neighborhood of the isolated critical points of $\gamma(x)$ are (locally asymptotically) stable (because $\gamma'(x_e)$ will be small and positive). Isolated critical points at which a generic extrema occurs $(\gamma''(x_e) \neq 0)$

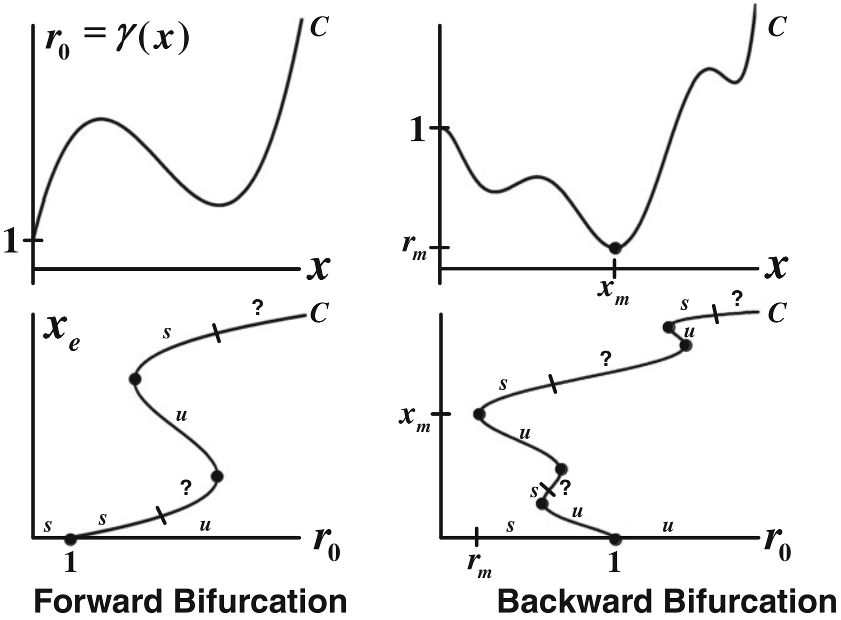

Fig. 1 The graph C of $r_0 = \gamma(x)$ gives the continuum of positive equilibria which bifurcates from the extinction equilibrium $[r_0, x] = [1, 0]$. The second row shows the graphs of equilibria x_e plotted against the inherent population growth rate r_0 obtained by reflecting the graphs above them through the $r_0 = x$ line. On these graphs the letter s indicates a (locally asymptotically) stable positive equilibrium while the letter u indicates an unstable positive equilibrium. The dots in the lower bifurcation diagrams show where blue-sky (*saddle-node*) bifurcations occur. The angled line segments and question marks shown along the curve C indicate that stability is, in general, guaranteed along increasing segments of C in only a neighborhood of a bifurcation point. See Example 1 and Fig. 2

correspond to the “turning or fold points” as seen (and indicated by the solid dots) the lower row of graphs in Fig. 1. These are called *blue-sky bifurcations* (or saddle-node or tangent bifurcations).

Thus, *in the neighborhood of blue-sky bifurcations the lower (decreasing) segment of C will contain unstable equilibria while the upper (increasing) segment of C will have stable equilibria.* See Fig. 1.

We note that a backward bifurcation creates the possibility that positive stable equilibria (or other kinds of attractors) can occur for $r_0 < 1$ when the extinction equilibrium is also stable. Such multiple attractor scenarios, where one attractor is extinction and the other is non-extinction, is called a *strong Allee effect* [4]. A backward bifurcation is not necessary for a strong Allee effect, but it is a common way for them to occur in population models [15].

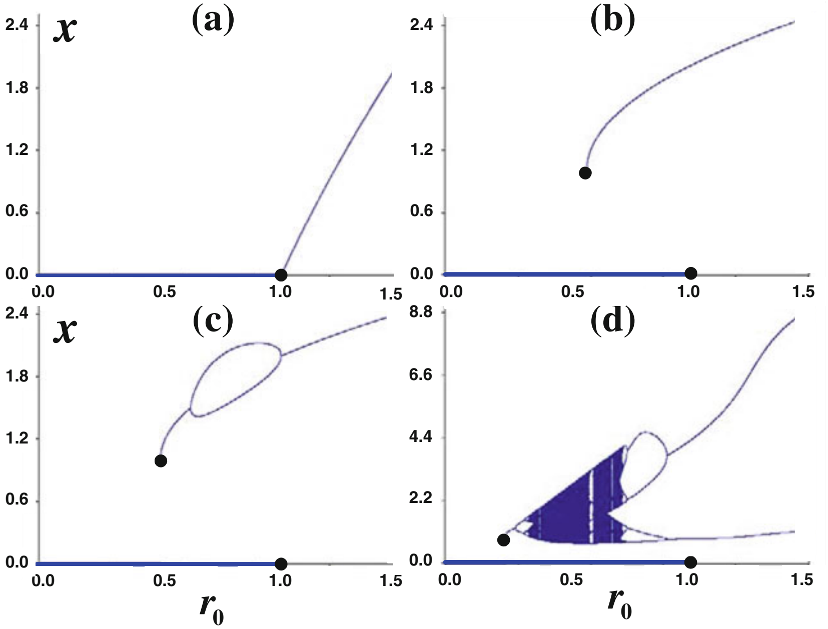

Fig. 2 Shown are bifurcation diagrams for the model Eq. (11) in Example 1. (a) A forward bifurcation of positive equilibria occurs when $a = -5$, $s = 0.5$, and $c = 5$. (b)–(d) Backward bifurcations occur when $a = 1$. The three cases shown in (b)–(d) use $s_0 = 0.5$, 0.4, and 0.1 respectively and all three use $c = 5$. The branches of unstable equilibria that connect the bifurcation point $[r_0, x_e] = [1, 0]$ to the blue-sky bifurcation point (indicated by *solid dots*) are not shown. The blue-sky bifurcation points $[r_m, x_e]$ in Example 1 are $[r_m, a]$ with r_m given by (12), which for these three cases are $r_m = 0.583$, 0.500, and 0.250

Example 1 We consider an example that illustrates both possibilities of forward and backward bifurcations, depending on a parameter value. As seen above, to construct such an example requires a component Allee effect, for at least some parameter values in the model equation. If, in this example, we assume that density dependence is absent in the survival rate and occurs only in fertility rate, then $\sigma(x) \equiv 1$. Thus, to obtain component Allee effects our choice of $\varphi(x)$ must allow for $\varphi'(0) > 0$ for at least some parameter values in addition, of course, to the requirements in A1.

Innumerable functional expressions have been used in the literature to construct difference equation models and, in particular, Allee effects; see for example [4, 20]. For our illustrative purposes here, the specific functional form of $\varphi(x)$ is not so important as that requirements in A1 be satisfied and that it contain a coefficient whose value determines the presence or absence of a component Allee effect. A rationale function that serves these purposes is

$$\varphi(x) = \frac{1 + ca^2}{1 + c(x-a)^2}$$

where $c > 0$ and a is any real number. This expression is that used the discrete Bernoulli equation [33] adapted so as to include the possibility of a component Allee effect. Specifically, since

$$\varphi'(0) = 2a\frac{c}{ca^2 + 1}$$

we see that a component Allee effect is present when $a > 0$ and is absent when $a < 0$. The resulting difference equation is

$$x_{t+1} = \left[(r_0 - s_0)\frac{1 + ca^2}{1 + c(x_t - a)^2} + s_0\right]x_t. \tag{11}$$

To determine the geometry of the bifurcating branch of positive equilibria, we note that

$$\gamma(x) = \frac{1 - s_0}{1 + ca^2}\left(1 + c(x - a)^2\right) + s_0$$

and calculate

$$\gamma'(x) = \frac{2c(1 - s_0)}{1 + ca^2}(x - a), \quad \gamma''(x) = \frac{2c(1 - s_0)}{1 + ca^2} > 0.$$

From

$$\gamma'(0) = -2ac\frac{1 - s_0}{1 + ca^2}$$

we deduce that *a forward bifurcation occurs (i.e.* $\gamma'(0) > 0$*) when* $a < 0$ *and a backward bifurcation occurs (i.e.* $\gamma'(0) < 0$*) if* $a > 0$.

In the case of a backward bifurcation we see from these calculations that $\gamma(x)$ has a minimum at $x_m = a$ and the lower endpoint of the spectrum S is

$$r_m = \frac{1 + s_0 ca^2}{1 + ca^2} \tag{12}$$

at which a blue-sky bifurcation occurs (sometimes called a *tipping point*). There are two positive equilibria for $r_m < r_0 < 1$ and, according to the general principles above (as shown in Fig. 1), the smaller positive equilibria is unstable and the larger equilibrium is stable at least for $r_0 \gtrapprox r_m$. The larger positive equilibrium is not necessarily stable for all values of $r_0 > r_m$ however, a fact demonstrated by the dynamically computed bifurcation diagrams shown in Fig. 2. In those sample diagrams we see the possibility of complicated secondary bifurcations (period doublings, etc.) for $r_0 > r_m$. Specifically, Fig. 2c, d show secondary bifurcations (and apparently chaotic attractors) occurring for values of $r_0 < 1$. In these cases strong Allee effects involving non-equilibrium attractors occur.

3 Evolutionary Dynamics

We begin with a population growth rate in equation (1) given by

$$f(x) = (r_0 - s_0)\,\varphi(x) + s_0\sigma(x), \quad \varphi(0) = \sigma(0) = 1.$$

Concerning model parameter dependence on a heritable trait, we make the following assumptions. First, the inherent individual fertility and survival rates, and hence r_0 and s_0, depend only on the individual's trait v. A rationale for this is that at low population densities the traits (and hence the characteristics and behavior) of other individuals have negligible effect on the individual's vita rates. Thus, it is only the density terms φ and σ that depend on the mean trait u. Moreover, as is commonly done, we assume that these effects are a function of the difference between v and u and that the effects are maximized (or minimized) when $v = u$, i.e. when the individual is most like other individuals (as represented by the mean trait u) [36]. We incorporate these assumptions by writing

$$f(x, v, u) = (r_0(v) - s_0(v))\,\varphi(x, v, v-u) + s_0(v)\,\sigma(x, v, v-u) \tag{13}$$

where, for all values of the arguments v and z in $\varphi(0, v, z)$ and $\sigma(0, v, z)$ we assume

$$\varphi(0, v, z) \equiv \sigma(0, v, z) \equiv 1 \tag{14a}$$

$$\partial_z\varphi(0, v, z)\,|_{z=0} \equiv \partial_z\sigma(0, v, z)\,|_{z=0} \equiv 0 \tag{14b}$$

$$\partial_{zz}\varphi(0, v, z)\,|_{z=0} \neq 0, \quad \partial_{zz}\sigma(0, v, z)\,|_{z=0} \neq 0. \tag{14c}$$

An example is the discrete logistic (Beverton-Holt) or Ricker expressions

$$\varphi = \frac{1}{1+cx}, \quad \varphi = \exp(-cx)$$

in which the coefficient c is under the influence of evolution, that is to say, $c = c(z)$ where the distribution of c values is Gaussian-like (often taken to be the case in evolutionary game theoretic models [36])

$$c(z) = \psi \exp\left(-z^2/w\right)$$

where $\psi > 0$ and $w > 0$ are positive constants. The maximal density effect on fertility is experienced by an individual when its inherited trait v equals the population mean u (i.e. when $z = v - u = 0$). In some models $\psi = \psi(v)$ is assumed a function of the trait v, in which case $c = c(v, z)$. These modeling assumptions on φ satisfy the constraints (14). Similar models can be built using the $c(z) = \psi/\left(1 + wz^2\right)$. In these examples w measures the width of the distribution of c values around $z = 0$.

If, for notational simplicity, we define

$$\varphi(x,v) \mathrel{\mathring{=}} \varphi(x,v,0), \quad \sigma(x,v) \mathrel{\mathring{=}} \sigma(x,v,0)$$
$$f(x,v) \mathrel{\mathring{=}} f(x,v,0)$$

and take fitness to be

$$F(x,v) = \ln f(x,v),$$

then the evolutionary model (15) becomes

$$x_{t+1} = f(x_t,u_t)\,x_t \tag{15a}$$
$$u_{t+1} = u_t + \sigma^2 \frac{\partial_v f(x_t,u_t)}{f(x_t,u_t)}. \tag{15b}$$

Here we have used the notation

$$f(x,u) \mathrel{\mathring{=}} f(x,v)|_{v=u}, \quad \partial_v f(x,u) \mathrel{\mathring{=}} \partial_v f(x,v)|_{v=u}.$$

More explicitly, in (15)

$$f(x,u) = (r_0(u) - s_0(u))\,\varphi(x,u) + s_0(u)\,\sigma(x,u)$$

$$\partial_v f(x,u) = \left(r_0'(u) - s_0'(u)\right)\varphi(x,u) + (r_0(u) - s_0(u))\,\partial_v\varphi(x,u)$$
$$+ s_0'(u)\,\sigma(x,u) + s_0(u)\,\partial_v\sigma(x,u).$$

The assumption we make on the terms in this model are as follows.

A2. *Assume* $r_0(v)$ and $s_0(v)$ *are twice continuously differentiable functions mapping* R *to* R_+ and $\bar{R}_+$. respectively. *Assume* $\varphi(x,v)$ and $\sigma(x,v)$ *are twice continuously differentiable functions mapping* $\Omega \times R$ *to*R_+ and $\bar{R}_+$ *respectively that satisfy*

$$\varphi(0,v) \equiv \sigma(0,v) \equiv 1 \textit{ for all } v \in R \tag{16}$$

and

$$0 \le \sup_{x\in\Omega, v\in R} s_0(v)\,\sigma(x,v) < 1. \tag{17}$$

Conditions (16) and (17) imply $0 \le \sup_{v\in R} s_0(v) < 1$ and

$$\partial_v\varphi(0,v) \equiv \partial_v\sigma(0,v) \equiv 0 \text{ for all } v.$$

The equilibrium equations associated with (15) are

$$x = f(x,u)\,x$$
$$0 = \partial_v f(x,u).$$

Clearly $x = 0$ solves the first equilibrium equation. Thus, a pair $[x, u] = [0, u]$ is an equilibrium if and only if u satisfies

$$\partial_v f\,(0, u) = r_0'\,(u) = 0.$$

Definition 1 An **extinction equilibrium** is an equilibrium $[x, u]$ with $x = 0$. A pair $[0, u^*]$ is an extinction equilibrium if and only if u^* is a **critical trait**, i.e. if and only if $r_0'\,(u^*) = 0$.

We assume throughout that there exists a critical trait u^*. To use

$$r_0^* \mathrel{\overset{\circ}{=}} r_0\left(u^*\right)$$

as a bifurcation parameter we write

$$r_0\,(v) = r_0^*\rho\,(v)\,, \quad \rho\left(u^*\right) = 1, \quad \rho'\left(u^*\right) = 0$$

where $\rho\,(v)$ satisfies the same conditions in A2 as does $r_0\,(v)$. Note that $[0, u^*]$ is an equilibrium for all values of the bifurcation parameter r_0^*.

To investigate the (local asymptotic) stability of the extinction equilibrium $[0, u^*]$ by means of the linearization principle we consider the Jacobian

$$J\,(x, u) = \begin{pmatrix} f\,(x, u) + x\partial_x f\,(x, u) & x\partial_v f\,(x, u) \\ \partial_{xv} \ln f\,(x, u) & 1 + \sigma^2\partial_{vv} \ln f\,(x, u) \end{pmatrix} \tag{18}$$

of (15). Evaluated at an extinction equilibrium $[x, u] = [0, u^*]$ this Jacobian becomes

$$J\,(0, u^*) = \begin{pmatrix} r_0^* & 0 \\ \eta/r_0^* & 1 + \sigma^2\rho''\,(u^*) \end{pmatrix} \tag{19}$$

where

$$\eta \mathrel{\overset{\circ}{=}} \left(-\partial_x\varphi\left(0, u^*\right) + \partial_x\sigma\left(0, u^*\right)\right) s_0'\left(u^*\right) + \left(1 - s^*\right)\partial_{xv}\varphi\left(0, u^*\right) + s_0^*\partial_{xv}\sigma\left(0, u^*\right).$$

The eigenvalues appear along the diagonal.

Theorem 1 *Assume A2 and that u^* is a critical trait.*

(a) Suppose

$$\left|1 + \sigma^2\rho''\left(u^*\right)\right| < 1. \tag{20}$$

Then the extinction equilibrium $[0, u^*]$ of (15) is (locally asymptotically) stable if $r_0^* < 1$ and is unstable if $r_0^* > 1$.

(b) Suppose, on the other hand, that

$$\left|1+\sigma^2\rho''\left(u^*\right)\right|>1. \tag{21}$$

Then the extinction equilibrium is unstable.

Note that (20) holds if $\rho''(u^*)<0$ and σ^2 is small, i.e. ρ has a generic maximum at u^* and evolution is not rapid. Condition (21) holds if $\rho''(u^*)>0$, i.e. ρ has a generic minimum at u^*.

Definition 2 A **positive equilibrium** $[x_e, u_e]$ of (15) is an equilibrium with $x_e>0$.

The equilibrium equations satisfied by positive equilibria are

$$1=f(x,u) \tag{22a}$$
$$0=\partial_v f(x,u) \tag{22b}$$

which we can re-write as

$$g(x,u,r_0^*)=0 \tag{23a}$$
$$h\left(x,u,r_0^*\right)=0 \tag{23b}$$

where

$$\begin{aligned}
g\left(x,u,r_0^*\right) &\mathrel{\hat{=}} \left(r_0^*\rho(u)-s_0(u)\right)\varphi(x,u)+s_0(u)\,\sigma(x,u)-1\\
h\left(x,u,r_0^*\right) &\mathrel{\hat{=}} \left(r_0^*\rho'(u)-s_0'(u)\right)\varphi(x,u)+s_0'(u)\,\sigma(x,u)\\
&\quad+\left(r_0^*\rho(u)-s_0(u)\right)\partial_v\varphi(x,u)+s_0(u)\,\partial_v\sigma(x,u).
\end{aligned}$$

Note that the equations (23) are satisfied by $[x,u]=[0,u^*]$ and $r_0^*=1$. To use the implicit function theorem to solve equations (23) for x and u as functions of r_0^* near this solution, we need $\varDelta(0,u^*,1)\neq 0$ where

$$\varDelta\left(x,u,r_0^*\right)=\det\begin{pmatrix}\partial_x g\left(x,u,r_0^*\right) & \partial_u g\left(x,u,r_0^*\right)\\ \partial_x h\left(x,u,r_0^*\right) & \partial_u h\left(x,u,r_0^*\right)\end{pmatrix}$$

and

$$\begin{aligned}
\partial_x g\left(x,u,r_0^*\right) &= \left(r_0^*\rho(u)-s_0(u)\right)\partial_x\varphi(x,u)+s_0(u)\,\partial_x\sigma(x,u)\\
\partial_u g\left(x,u,r_0^*\right) &= \left(r_0^*\rho'(u)-s_0'(u)\right)\varphi(x,u)+\left(r_0^*\rho(u)-s_0(u)\right)\partial_v\varphi(x,u)\\
&\quad+s_0'(u)\,\sigma(x,u)+s_0(u)\,\partial_v\sigma(x,u)
\end{aligned}$$

$$\begin{aligned}\partial_x h\left(x,u,r_0^*\right) &= \left(r_0^*\rho'(u)-s_0'(u)\right)\partial_x\varphi(x,u)+s_0'(u)\,\partial_x\sigma(x,u)\\ &\quad+\left(r_0^*\rho(u)-s_0(u)\right)\partial_{xv}\varphi(x,u)+s_0(u)\,\partial_{xv}\sigma(x,u)\\ \partial_u h\left(x,u,r_0^*\right) &= \left(r_0^*\rho''(u)-s_0''(u)\right)\varphi(x,u)+\left(r_0^*\rho'(u)-s_0'(u)\right)\partial_v\varphi(x,u)\\ &\quad+s_0''(u)\,\sigma(x,u)+s_0'(u)\,\partial_v\sigma(x,u)\\ &\quad+\left(r_0^*\rho'(u)-s_0'(u)\right)\partial_v\varphi(x,u)+\left(r_0^*\rho(u)-s_0(u)\right)\partial_{vv}\varphi(x,u)\\ &\quad+s_0'(u)\,\partial_v\sigma(x,u)+s_0(u)\,\partial_{vv}\sigma(x,u)\,.\end{aligned}$$

For notational purposes we let an asterisk denote evaluation at $\left([x,u],r_0^*\right)=([0,u^*],1)$, i.e.

$$\partial_x^*\varphi \mathrel{\hat{=}} \partial_x\varphi\left(0,u^*\right),\quad r_0^*=r_0\left(u^*\right),\quad \text{etc.}$$

A calculation shows

$$\Delta\left(0,u^*,1\right)=\det\begin{pmatrix}-\kappa & 0\\ \eta & \rho''(u^*)\end{pmatrix}$$

where

$$\begin{aligned}\kappa &\mathrel{\hat{=}} -\left[\left(1-s_0^*\right)\partial_x^*\varphi+s_0^*\partial_x^*\sigma\right]\\ \eta &\mathrel{\hat{=}} \left(-\partial_x^*\varphi+\partial_x^*\sigma\right)s_0'\left(u^*\right)+\left(1-s_0^*\right)\partial_{xv}^*\varphi+s_0^*\partial_{xv}^*\sigma.\end{aligned}$$

It follows that $\Delta(0,u^*,1)\neq 0$ if and only if $\kappa\neq 0$ and $\rho''(u^*)\neq 0$. Under these conditions the Implicit Function Theorem implies the existence of (unique, smooth) solutions $[x,u]=\left[x_e\left(r_0^*\right),u_e\left(r_0^*\right)\right]$ for r_0^* near 1 with $[x_e(1),u_e(1)]=[0,u^*]$. The latter equality means that this branch of solutions bifurcates from the branch of extinction equilibria at $r_0^*=1$.

To determine whether these solutions are feasible as equilibria of the population model, we need to determine whether $x=x_e(r_0)$ is positive or not. We also want to determine when a positive equilibrium is (locally asymptotically) stable. From the identities

$$\begin{aligned}g\left(x_e\left(r_0^*\right),u_e\left(r_0^*\right),r_0^*\right)&=0\\ g\left(x_e\left(r_0^*\right),u_e\left(r_0^*\right),r_0^*\right)&=0\end{aligned}$$

valid for r_0^* near 1 we find, by differentiation with respect to r_0^* followed by an evaluation at $r_0^*=1$, that

$$\begin{aligned}x_e'(1)\,\partial_x^*g+u_e'(1)\,\partial_u^*g+\partial_{r_0^*}^*g&=0\\ x_e'(1)\,\partial_x^*h+u_e'(1)\,\partial_u^*h+\partial_{r_0^*}^*h&=0\end{aligned}$$

or

$$\begin{aligned}\kappa x_e'(1)+1&=0\\ \eta x_e'(1)+\rho''\left(u^*\right)u_e'(1)&=0\end{aligned}$$

and hence

$$x_e'(1) = \frac{1}{\kappa}, \quad u_e'(1) = \frac{-\kappa}{\eta\rho''(u^*)}.$$

The first equation implies $x_e\left(r_0^*\right)$ is positive for $r_0^* \gtrapprox 1$ if $\kappa > 0$ and for $r_0^* \lessapprox 1$ if $\kappa < 0$. As a result we conclude that a bifurcation of positive equilibrium pairs from the extinction equilibrium $[0, u^*]$ occurs at $r_0^* = 1$ and is forward if $\kappa > 0$ or backward if $\kappa < 0$.

We can determine the stability of the positive equilibria, by the linearization principle, from the eigenvalues of the Jacobian (18) evaluated at $(x, u) = \left(x_e^*\left(r_0^*\right), u_e^*\left(r_0^*\right)\right)$, namely

$$\begin{pmatrix} f\left(x\left(r_0^*\right), u\left(r_0^*\right)\right) + x\left(r_0^*\right)\partial_x f\left(x\left(r_0^*\right), u\left(r_0^*\right)\right) & x\left(r_0^*\right)\partial_v f\left(x\left(r_0^*\right), u\left(r_0^*\right)\right) \\ \partial_{xv}\ln f\left(x\left(r_0^*\right), u\left(r_0^*\right)\right) & 1 + \sigma^2\partial_{vv}\ln f\left(x\left(r_0^*\right), u\left(r_0^*\right)\right) \end{pmatrix}$$

which, because $\left(x\left(r_0^*\right), u\left(r_0^*\right)\right)$ solves the equilibrium equations (22), simplifies to

$$\begin{pmatrix} 1 + x\left(r_0^*\right)\partial_x f\left(x\left(r_0^*\right), u\left(r_0^*\right)\right) & 0 \\ \partial_{xv} f\left(x\left(r_0^*\right), u\left(r_0^*\right)\right) & 1 + \sigma^2\partial_{vv} f\left(x\left(r_0^*\right), u\left(r_0^*\right)\right) \end{pmatrix} \tag{24}$$

The eigenvalues, which appear along the diagonal, are

$$\lambda_1 = 1 - \left(r_0^* - 1\right) + O\left(\left(r_0^* - 1\right)^2\right)$$
$$\lambda_2 = 1 + \sigma^2\rho''\left(u^*\right) + O\left(r_0^* - 1\right).$$

For r_0^* near 1 the positive equilibrium $\left[x_e^*\left(r_0^*\right), u_e^*\left(r_0^*\right)\right]$ is stable if both $|\lambda_i| < 1$ and is unstable if at least one $|\lambda_i| > 1$.

We summarize these results in the theorem below. In that theorem we make use of the following definitions. If $[x_e, u_e]$ is an equilibrium for a value of r_0^*, then we call $\left(r_0^*, [x_e, u_e]\right)$ an *equilibrium pair*. If the equilibrium $[x_e, u_e]$ is positive, stable or unstable, then we say the equilibrium pair $\left(r_0^*, [x_e, u_e]\right)$ is respectively positive, stable or unstable.

Theorem 2 *Assume A2 and that u^* is a critical trait such that $\rho''(u^*) \neq 0$. Assume $\kappa \neq 0$. Then a continuum $\mathcal{C}$ of positive equilibrium pairs $\left(r_0^*, [x_e, u_e]\right)$ of the evolutionary model (15) bifurcates from the extinction equilibrium $[1, (0, u^*)]$. Near the bifurcation point these positive equilibria are approximately*

$$x_e = \frac{1}{\kappa}\left(r_0^* - 1\right) + O\left(\left(r_0^* - 1\right)^2\right) \tag{25a}$$

$$u_e = u^* + \frac{-\kappa}{\eta\rho''(u^*)}\left(r_0^* - 1\right) + O\left(\left(r_0^* - 1\right)^2\right) \tag{25b}$$

The bifurcation is forward if $\kappa > 0$ and backward if $\kappa < 0$.

(a) *If* (20) *holds, then the stability of the bifurcation (meaning the stability of the equilibria* $[x_e, u_e]$ *on the continuum* C *) is determined by the direction of bifurcation. Specifically, a forward bifurcation is stable and a backward bifurcation is unstable.*

(b) *If* (21) *holds, then both forward and backward bifurcations are unstable.*

Note that $\rho''(u^*) > 0$ implies (21) holds. In this case, Theorems 1 and 2 imply that in a neighborhood of the bifurcation point all equilibria – extinction and positive – are unstable. An explanation for this is roughly as follows. The trait dynamic equation (15b) is based on the assumption that the mean trait u_t moves up the fitness gradient, which near the extinction equilibrium is approximately $\ln \rho(v)$. The inequality $\rho''(u^*) > 0$ implies $\ln \rho(v)$ has a local minimum at the critical trait $v = u^*$ and consequently the trait component u_t of orbits in a neighborhood of the extinction equilibrium increases until the orbit leaves the neighborhood. Thus, when $\rho''(u^*) \neq 0$ a necessary condition for stability is $\rho''(u^*) < 0$, which implies $\rho(v)$ has a local maximum at the critical trait $v = u^*$. In this case (20) is equivalent to

$$\sigma^2 < \frac{-2}{\rho''(u^*)}.$$

That is to say, a forward bifurcation will be stable if the speed of evolution σ^2 is not too fast.

Corollary 1 *Assume A2 and that* u^* *is a critical trait such that* $\rho''(u^*) < 0$. *Assume* $\kappa \neq 0$. *If the speed of evolution* σ^2 *is not too fast, then the direction of bifurcation of the positive equilibrium pairs guaranteed by Theorem 2 determines their stability: a forward bifurcation is stable and a backward bifurcation is unstable.*

In A2 we assumed for simplicity that the domain of trait values v is the whole real lie R. Since Theorem 2 and Corollary 1 concern bifurcation phenomena in a neighborhood of an extinction equilibrium $[1, (0, u^*)]$, these results remain valid if R is replaced in A2 by an open set of trait values, so long as the critical trait u^* lies in the set.

Example 2 As mentioned in Sect. 1 the fertility density term

$$\varphi(x) = \frac{1}{1 + c_1 x}, \quad c_1 > 0 \tag{26}$$

is used in the classic discrete logistic (Beverton-Holt) equation for a population with non-overlapping generations ($\sigma(x) \equiv 0$). It expresses a negative feedback of population density on the fertility rate (since $\varphi(x)$ is a *decreasing* function of x). For a population with over-lapping generations the survival rate $\sigma(x)$ would not be identically 0. In our example here, we take $\sigma(x)$ to be an *increasing* function of x, i.e. to have a component Allee effect. The biological rationale for this is that we wish to model a trade-off between density effects on the fertility and survival rates: increased population density suppresses an individual's fertility rate, but enhances an individual's survival probability (through, for example, group defence). Trade-off's of this sort play a fundamental role in the study of life history strategies and usually constitute the driving mechanisms that determine evolutionary dynamics and outcomes [32].

An example mathematical function $\sigma(x)$ that satisfies A1 and that is increasing in x is

$$\sigma(x) = \frac{1 + c_2 s_m x}{1 + c_2 s_0 x}, \quad 0 < s_0 < s_m < 1, \; c_2 > 0 \tag{27}$$

As a function of population density x, the survival rate $s_0 \sigma(x)$ increases monotonically from s_0 to s_m. The coefficients $c_i > 0$ in the density terms (26) and (27) measure the strength of the density effects on these vital rates.

We assume that a heritable trait v, in addition to determining an individual's inherent net reproductive rate $r_0^* \rho(v)$, determines an individual's sensitivities to density increases, i.e. we assume $c_1 = c_1(v) > 0$ and $c_2 = c_2(v) > 0$ are functions of v. In this example, we assume inherent survival s_0 is trait independent. We have then the fitness function

$$f(x, v) = \left(r_0^* \rho(v) - s_0\right) \frac{1}{1 + c_1(v) x} + s_0 \frac{1 + c_2(v) s_m x}{1 + c_2(v) s_0 x} \tag{28}$$

in the model equations (15).

We assume there exists a trait $v = u^*$ at which the inherent growth rate $\rho(v)$ attains a maximum (and does so with $\rho''(u^*) < 0$) and the the numerical scale for the trait is chosen so that $u^* = 0$. On the other hand, we assume the density coefficients c_i are decreasing functions of the trait v. This means that an increase in the trait v results in weaker density effects on fertility and survival.

For the evolutionary model (15)–(28) we calculate the quantity κ, whose sign determines the properties of the bifurcation at $r_0^* = 1$ (according to Theorem 2), to be

$$\kappa = (1 - s_0) c_1(0) - s_0 (s_m - s_0) c_2(0).$$

Suppose the coefficient $c_2(0)$ is small compared to $c_1(0)$ so that $\kappa > 0$. Then by Theorem 2 the bifurcation of positive equilibrium pairs is forward and stable. In other words, *if at the critical trait* $v = 0$ *survival is less sensitive to density effects than is fertility, then the bifurcation of positive equilibrium pairs is forward and there exist (locally asymptotically) stable survival equilibria for* $r_0^* \gtrapprox 1$. On the other hand, if the reverse is true, i.e. *if at the critical trait* $v = 0$ *survival is more sensitive to density effects than is fertility, then the bifurcation of positive equilibrium pairs is backward and unstable*. In this latter case, there is a potential for a strong Allee effect, which is to say, a potential for the existence of a stable positive equilibrium when $r_0^* < 1$ (as discussed in Sect. 2). Evidence that this can indeed occur in this example appears in Fig. 3.

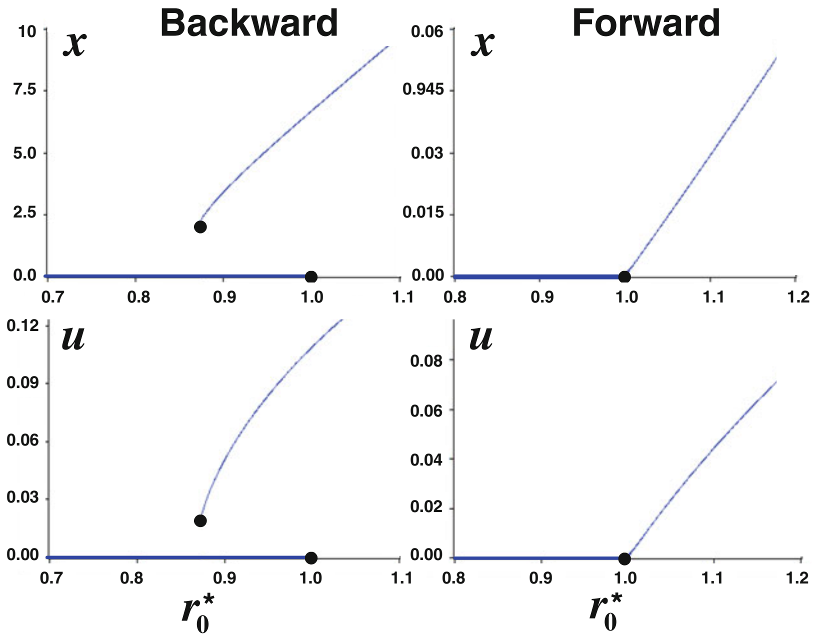

Fig. 3 Bifurcation diagrams plotting the x and u components of (dynamically computed) positive equilibria of the evolutionary model (15) with fitness function (28) and trait dependencies (29). Here $s_0 = 0.3$, $s_m = 0.6$ and $\kappa = 0.7c_1 - 0.09c_2$. The speed of evolution is $\sigma^2 = 0.1$. When $c_1 = 5$, $c_2 = 0.1$ and $\kappa = 3.491 > 0$ a forward, stable bifurcation occurs, as seen in the right column of plots. When $c_1 = 0.1$, $c_2 = 5$ and $\kappa = -0.380 < 0$ a backward, unstable bifurcation occurs, as seen in the left column of plots. In this case a strong Allee effect occurs as can be seen by the existence of positive equilibrium pairs for an interval of r_0^* values less than 1

The bifurcation diagrams shown in Fig. 3 illustrate these results for the evolutionary model (15)–(28) with

$$\rho(v) = e^{-v^2}, \quad c_1(v) = c_1 e^{-v}, \quad c_2(v) = c_2 e^{-v}. \tag{29}$$

In this case, the only critical point of $\rho(v)$ is $v = u^* = 0$ at which inherent fertility has a maximum (note that $\rho''(0) = -2 < 0$). The only extinction equilibrium pairs are $\left(r_0^*, [0, 0]\right)$, which exist for all values of $r_0^* > 0$. The right column of plots in Fig. 1 shows an example when $\kappa > 0$ and the bifurcation from the extinction equilibrium $\left(r_0^*, [0, 0]\right)$ at $r_0^* = 1$ is forward and stable. The left column of plots in Fig. 1 shows an example when $\kappa < 0$ and the bifurcation is backward and unstable. In this case, one can observe the occurrence of a strong Allee effect, i.e. the existence of positive equilibria for an interval of r_0^* values less than 1. Although the intent here is only to illustrate the mathematical results in Theorem 2 by use of the example (15)–(28), we point out some of the resulting biological implications. The biological features implied by (29) are that fertility is optimized at a unique heritable trait $v = 0$ and that an increase in v lessens both the negative density effects on fertility and the positive density effects on survival. The positive equilibrium pairs shown in the bifurcation diagrams of Fig. 3 have a positive mean trait component $u_e > 0$. Thus, evolution does not select to maximize inherent fertility, but selects for a lesser inherent fertility rate and for lower effects of population density on both fertility and survival.

4 Concluding Remarks

We focussed in this paper on one dimensional maps as models of population dynamics. Many of the results given in Sects. 2 and 3 have been extended in several directions. The bifurcation of a global continuum of positive equilibrium as graphically portrayed in Fig. 1 for one dimensional maps has been proved for higher dimensional systems of difference equations of the form

$$x_{t+1} = P(x_t)\, x_t \tag{30}$$

where $x_t \in R_+^m$ and P is an $m \times m$ matrix valued function [6, 8]. This kind of matrix equation arises in structured population dynamics where the vector x_t is the demographic distribution of individuals into specified categories (chronological age, physiological size, weight, etc.) [3]. When the projection matrix P is primitive (non-negative, irreducible and a strictly dominant positive eigenvalue), the direction of bifurcation determines the stability of the bifurcating continuum of positive equilibria (as in Fig. 1). This is a general phenomenon in bifurcation theory [24], as the global extent of the continuum [31].

However, when a non-negative and irreducible projection matrix P is not primitive (its dominant positive eigenvalue is not *strictly* dominant), then it is no longer true in general that the direction of bifurcation determines the stability of the bifurcating positive equilibria. The bifurcation in this case is of higher codimension and is complicated by the possibility of branches of periodic cycles (and even other more complicated invariant sets) that bifurcate simultaneously with positive equilibria [7, 9, 12, 18, 19, 22, 25, 26, 35]. Several lower dimensional species cases have been thoroughly analyzed, but for higher dimensional models a complete theory is lacking. Imprimitive projection matrices do arise in applications [16], and more analysis towards a general theory that determines the properties of the bifurcation at the point where the extinction equilibrium destabilizes would be of interest.

The fundamental bifurcation theorem for matrix equations (30) can be stated using the inherent population growth rate r_0 (the dominant eigenvalue of $P(0)$) as the bifurcation parameter, as is done in Sect. 2 for the $m = 1$ dimensional case. However, it is worth pointing out that for higher dimensional cases it is often mathematically more tractable to use a different bifurcation parameter. As seen in Sect. 2, for the one dimensional case the direction of bifurcation and, consequently, the stability of the bifurcating continuum of positive equilibria is determined by the sign of $r_0 - 1$. Notice that the sign of $r_0 - 1$ is the same as the sign of $R_0 - 1$ where

$$R_0 \mathrel{\overset{\circ}{=}} b_0 \left(1 - s_0\right)^{-1}.$$

This quantity, when written as

$$R_0 = b_0 + b_0 s_0 + b_0 s_0^2 + \cdots = \sum_{i=0}^{\infty} b_0 s_0^i,$$

is seen to be the expected number of newborns per newborn per life time and is referred to as the *inherent net reproduction number*. In higher dimensions, R_0 is defined as follows. The projection matrix is additively decomposed into a fertility matrix F, which accounts for all newborns at the next census, and a transition/survival matrix T, which accounts for survivors at the next census (who might or might not change their classification categories):

$$P\left(x\right) = F\left(x\right) + T\left(x\right)$$

(a direct analog of the decomposition in Sect. 2). Here both F and T are non-negative matrices. The inherent net reproductive number is defined to be the spectral radius of

$$F\left(0\right)\left(I - T\left(0\right)\right)^{-1}.$$

Here an additional constraint on the transition/survival matrix T is that it columns sums are less than or equal to 1 (the number of survivors cannot exceed the original number of individuals) with at least one sum strictly less than 1 (there is some mortality in the population). Or more generally, it is assume that the spectral radius of $T\left(0\right)$ is less than 1, which (as the generalization of $s_0 < 1$) means the expected life span on an individual is finite. It is known that the signs of $R_0 - 1$ and $r_0 - 1$ (here r_0 is the spectral radius of the projection matrix $F + T$) are the same [5, 11, 29]. Thus, either quantity R_0 or r_0 determine the local stability or instability of the extinction equilibrium and, as a result, the bifurcation point $r_0 = R_0 = 1$ in the fundamental bifurcation theorem. One analytic advantage of this result is that frequently a formula (expressed in terms of the entries of the projection matrix) is available for R_0 while, in higher dimensions, this not the case for r_0 [6].

Backward bifurcations and their role in the creation of strong Allee effects for matrix models (30) are investigated in [15] (for an application see [14]). The stability of the "upper" branch of positive equilibria near blue-sky bifurcation bifurcations (cf. Fig. 1) for higher dimensional matrix equations remains an open question, however.

In Sect. 3 the model tracks the dynamics of only one phenotypic trait v. If a vector of phenotypic traits v and their population means are included in the model, then the evolutionary model takes the form

$$\begin{aligned} x_{t+1} &= P\left(x_t, v, u_t\right)\big|_{v=u_t} x_t \\ u_{t+1} &= u_t + C\nabla_v F\left(x_t, v, u_t\right)\big|_{v=u_t} \end{aligned}$$

where F is a measure of fitness and C is a variance-covariance matrix for the variability of the traits [36]. For example, fitness can be taken to be the logarithm of the spectral radius of the dominant eigenvalue of $P(x, v, u)$, as a generalization of $\ln f(x, v, u)$ used in Sect. 3. Some generalizations of Theorem 2 for the evolutionary matrix model have been established. For a single trait v in a structured population model (of arbitrary size m) with primitive projection matrix see [10] and for multiple traits see [17]. For some applications of imprimitive evolutionary models see [13, 34].

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