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A Darwinian Ricker Equation

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Abstract The classic Ricker equation $x_{t+1} = bx_t \exp\left(-cx_t\right)$ has positive equilibria for $b > 1$ that destabilize when $b > e^2$ after which its asymptotic dynamics are oscillatory and complex. We study an evolutionary version of the Ricker equation in which coefficients depend on a phenotypic trait subject to Darwinian evolution. We are interested in the question of whether evolution will select against or will promote complex dynamics. Toward this end, we study the existence and stability of its positive equilibria and focus on equilibrium destabilization as an indicator of the onset of complex dynamics. We find that the answer relies crucially on the speed of evolution and on how the intra-specific competition coefficient c depends on the evolving trait. In the case of a hierarchical dependence, equilibrium destabilization generally occurs after e^2 when the speed of evolution is sufficiently slow (in which case we say evolution selects against complex dynamics). When evolution proceeds at a faster pace, destabilization can occur before e^2 (in which case we say evolution promotes complex dynamics) provided the competition coefficient is highly sensitive to changes in the trait v. We also show that destabilization does not always result in a period doubling bifurcation, as in the non-evolutionary Ricker equation, but under certain circumstances can result in a Neimark-Sacker bifurcation.

Keywords Ricker equation · Darwinian Ricker equation · Chaos · Evolutionary game theory

1 Introduction

It is well known that difference equations can predict complex asymptotic dynamics in the form of non-equilibrium attractors. The exponential or Ricker equation

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$$x_{(t+1)} = bx_{(t)} \exp(-cx_{(t)}) \tag{1}$$

is the iconic example of a period doubling route to chaos which, as $b > 1$ increases, initiates after $b = e^2$ where the positive equilibrium $x = c^{-1} \ln b$ destabilizes. Despite the ubiquity of this phenomenon in difference equations used as population dynamic models, unequivocal evidence of its occurrence in biological populations is sparse and is, for the most part, limited to populations manipulated in laboratory settings [10]. Several explanations for this can be found in the literature. One is that population time series data tends to be too short to be able to identify complex dynamics and data is usually "noisy" and, as a result, it is difficult to tell the difference between stochastic fluctuations and deterministic fluctuations (such as chaos) [5, 8]. Another explanation is that most populations in the natural world are subject to interactions with other species that can serve to dampen complex dynamics [7]. Yet another explanation is that biological populations are subject to evolutionary change by Darwinian principles and that evolution might select to reduce dynamic complexity, i.e. non-equilibrium dynamics such as periodic oscillations or chaos [4]. In this paper we briefly consider the latter possibility by subjecting the parameters in the Ricker equation (1) to evolutionary changes according to a methodology called evolutionary game theory (or Darwinian dynamics) [9]. This derivation results in a system of difference equations that we refer to as a Darwinian Ricker model. In this short note, we do not strive to carry out a study of the non-equilibrium dynamics that are possible in Darwinian Ricker equations, but instead focus simply on whether or not positive equilibria destabilize for b greater than some critical value and, if they do, whether the critical value is greater or less than e^2. If it is greater than e^2, then we say that evolution selects against non-equilibrium and complex dynamics in the sense that the de-stabilization of the equilibrium occurs for larger values of b than it does when evolution is absent. If the critical value of b occurs before e^2, then we say that evolution promotes non-equilibrium and complex dynamics.

Darwinian Ricker model equations are derived by evolutionary game theoretic methods in Sect. 2. The existence and stability (by linearization) of equilibria of this system of two nonlinear difference equations are studied in Sect. 3. Conclusions obtained from this analysis with regard to the effect of evolution on non-equilibrium dynamics are discussed in Sect. 4.

2 A Darwinian Ricker Equation

In the Ricker equation (1) x represents the total size or density of a population consisting of individual biological organisms. We interpret b as the inherent (i.e. density free) per capita fertility rate. The coefficient c is a measure of the effect that increased population density has on the per capita fertility rate, as might be due to competition with con-specifics for resources (food, space, mates, etc.). We refer to c as the competition coefficient. We assume that both b and c, as coefficients relating to an individual's inherent fertility and susceptibility to intra-specific competition

respectively, are functions of a phenotypic trait of the individual, denoted by v, that is subject to evolutionary change over time. Under the axioms of Darwinian evolution (trait variability, heritability, and differential trait dependent fitness), the method of evolutionary game theory [9] provides a dynamic model for the population density and the population's mean phenotypic trait, under the assumption that the trait has a Gaussian distribution with fixed variance throughout the population at all times. Thus, the distribution of the trait v in the population at any point in time is determined by the population mean trait, which we denote by u.

In the Ricker equation we assume the fertility rate b is a function of v alone, since it is the density free fertility rate of an individual with trait v (i.e. not subject to the presence of other individuals and hence to the population mean u). The competition coefficient c, on the other hand, we assume is dependent on the individual's trait v and that of other individuals with whom it competes, as represented by the mean trait u. Thus we assume

$$b = b(v), \quad c = c(v, u).$$

The density dependent fertility rate is then

$$r(x, v, u) = b(v) \exp(-c(v, u) x). \tag{2}$$

The Darwinian equations governing both population and mean trait dynamics are

$$x_{t+1} = r(x_t, v, u_t)|_{v=u_t} x_t \tag{3}$$

$$u_{t+1} = u_t + \sigma^2 \left. \frac{\partial \ln r(x_t, v, u_t)}{\partial v} \right|_{v=u_t} \tag{4}$$

where $\sigma^2 \geq 0$ is called the speed of evolution (it is proportional to the constant variance of v) [2, 9]. The trait equation (4) says that the change in mean trait is proportional to the fitness gradient, with fitness taken to be $\ln r$ (the equation is often called Lande's or Fisher's equation or the canonical equation of evolution).

To further specify the model, we will place assumptions on $b(v)$ and $c(v, u)$. In this paper we assume that there is a trait at which inherent fertility has a maximum, denoted by b_0, and we choose that trait to be the reference point for v. We also assume that fertility $b(v)$ is distributed in a Gaussian fashion around its maximum b_0 $v = 0$ and, without loss in generality, we scale the trait v so that the variance of $b(v)$ equals 1:

$$b(v) = b_0 \exp\left(-\frac{v^2}{2}\right). \tag{5}$$

With (2) and this choice for $b(v)$, the Darwinian equations (3)–(4) become

$$x_{t+1} = b_0 \left(\exp\left(-\frac{v}{2}\right) \exp\left(-c\left(v, u_t\right) x_t\right) \right) \Big|_{v=u_t} x_t \tag{6}$$

$$u_{t+1} = u_t + \sigma^2 \left(-u_t - \frac{\partial c\left(v, u_t\right)}{\partial v} \Big|_{v=u_t} x_t \right). \tag{7}$$

A common assumption that is made concerning trait dependency of competition coefficients in Darwinian models is that they are functions of the difference $v - u$. In other words, the competition that an individual experiences depends on how different its trait v is from the typical individual in the population, as represented by the mean trait u. We make this assumption here and write $c = c\left(v - u\right)$ where the function $c\left(z\right)$ is continuously differentiable for all values of its argument z. Under this assumption equations (6)–(7) become

$$x_{t+1} = b_0 \left(\exp\left(-\frac{u_t^2}{2}\right) \exp\left(-c\left(0\right) x_t\right) \right) x_t$$

$$u_{t+1} = u_t + \sigma^2 \left(-u_t - \frac{dc\left(z\right)}{dz} \Big|_{z=0} x_t \right).$$

As a final scaling, we assume population units for x are chosen so that $c\left(0\right) = 1$ and obtain the model equations

$$x_{t+1} = b_0 \exp\left(-\frac{u_t^2}{2}\right) \exp\left(-x_t\right) x_t \tag{8}$$

$$u_{t+1} = -c_1 \sigma^2 x_t + \left(1 - \sigma^2\right) u_t \tag{9}$$

where

$$c_1 := \frac{dc\left(z\right)}{dz} \Big|_{z=0}.$$

There are three coefficients in the Eqs. (8)–(9). The coefficient b_0 is the *maximal possible fertility rate*, as a function of the trait v, and the coefficient σ^2 is the *speed of evolution*. The coefficient c_1 is the sensitivity of the competition competition $c\left(z\right)$ to changes in the difference $z = v - u$ at when $v = u$. If $c_1 \neq 0$ then c_1 measures the difference between the competition intensities experienced by individuals that have the population mean trait and those whose traits are slightly different from the mean. For example, if $c_1 > 0$ then an individual that inherits a trait slightly larger (smaller) than the mean u will experience increased (decreased) intraspecific competition. These interpretations can also hold, of course, if $c_1 = 0$ unless $c\left(z\right)$ has an extrema at $z = 0$. In fact, a common modeling assumption is that maximum competition is experience by individuals with the population mean trait, in which case $c\left(z\right)$ has a maximum at $z = 0$ and $c_1 = 0$. A commonly used model for $c\left(z\right)$ assumes it has a Gaussian type distribution

$$c(z) = \exp\left(-\frac{z^2}{2\omega^2}\right) \tag{10}$$

(with variance ω^2). In contrast, if for example

$$c(z) = \exp(c_1 z) \tag{11}$$

then competition intensity either decreases as v decreases or increases from the mean u, depending on the sign of c_1. We refer to this type of competition coefficient $c(z)$, i.e. one for which $c_1 \neq 0$ as heirarchical.

3 Equilibria of the Darwinian Ricker

Our goal is the study the existence and stability properties of equilibria of the Darwinian Ricker equations (8)–(9) using b_0 as a bifurcation parameter. We are interested in equilibria (x, u) with a positive x-component, which we define to be a *positive equilibrium* pair. The equations for a positive equilibrium pair are

$$1 = b_0 \exp\left(-\frac{u^2}{2}\right) \exp(-x)$$
$$0 = -c_1 x - u.$$

If $b_0 < 1$, then one sees from the first equation that there is no positive equilibrium (x, u). However, if $b_0 > 1$ then there exists a unique positive equilibrium obtained from the equations

$$1 = b_0 \exp\left(-\frac{c_1^2 x^2}{2}\right) \exp(-x), \qquad u = -c_1 x \tag{12}$$

The positive root of

$$\frac{c_1^2 x^2}{2} + x = \ln b_0 \tag{13}$$

yields the formulas for positive equilibria:

$$(x(b_0), u(b_0)) = \begin{cases} (\ln b_0, 0) & \text{if } c_1 = 0 \\ \left(\frac{-1+\sqrt{1+2c_1^2 \ln b_0}}{c_1^2}, \frac{1-\sqrt{1+2c_1^2 \ln b_0}}{c_1}\right) & \text{if } c_1 \neq 0 \end{cases}. \tag{14}$$

The Jacobian of Eqs. (8)–(9)

$$J(x, u) = \begin{pmatrix} b_0 e^{-\frac{1}{2}u^2} e^{-x}(1-x) & -u x b_0 e^{-\frac{1}{2}u^2} e^{-x} \\ -c_1 \sigma^2 & 1 - \sigma^2 \end{pmatrix}$$

evaluated at the positive equilibrium becomes, when Eq. (12) are utilized, is

$$J\left(x\left(b_0\right), u\left(b_0\right)\right) = \begin{pmatrix} 1 - x\left(b_0\right) & c_1 x^2\left(b_0\right) \\ -c_1\sigma^2 & 1 - \sigma^2 \end{pmatrix}$$

which by (13), further simplifies to

$$J\left(x\left(b_0\right), u\left(b_0\right)\right) = \begin{pmatrix} 1 - x\left(b_0\right) & \frac{2}{c_1}\left(\ln b_0 - x\left(b_0\right)\right) \\ -c_1\sigma^2 & 1 - \sigma^2 \end{pmatrix} \tag{15}$$

Motivated by the question posed in Sect. 1 we are interested in the case when the positive equilibria are stable for $b_0 > 1$, but near 1 and destabilize at some value of $b_0 > 1$. For b_0 near 1 the eigenvalues of the Jacobian $J\left(x\left(b_0\right), u\left(b_0\right)\right)$ are

$$\lambda_1\left(b_0\right) = 1 - \left(b_0 - 1\right) + O\left(\left(b_0 - 1\right)^2\right)$$
$$\lambda_2\left(b_0\right) = \sigma^2 - 1 + O\left(\left(b_0 - 1\right)^2\right).$$

It follows by the Linearization Principle that for b_0 greater than, but near 1, the equilibria $\left(x\left(b_0\right), u\left(b_0\right)\right)$ are stable if $\sigma^2 < 2$ and unstable if $\sigma^2 > 2$. Therefore, *we will assume that* $\sigma^2 < 2$.

For the case $c_1 = 0$ the eigenvalues of this Jacobian are

$$\lambda_1 = 1 - \ln b_0 \quad \text{and} \quad \lambda_2 = 1 - \sigma^2$$

and the destabilization of the positive equilibrium occurs at the same critical value as does the classic Ricker equation (1).

Theorem 1 *Assume $c_1 = 0$ and $\sigma^2 < 2$ in the Darwinian Ricker equations (8)–(9). There exists positive equilibrium for and only for $b_0 > 1$. They are locally asymptotically stable if $1 < b_0 < e^2$ and unstable if $b_0 > e^2$. When $b_0 = e^2$ the Jacobian has eigenvalue value -1.*

In general when $c_1 = 0$, the trait equation (9) decouples from the population equation (8) and $\lim_{t\to+\infty} u_t = 0$ under the assumption $\sigma^2 < 2$. In this case, the population equation (8) is asymptotically autonomous and the classic Ricker (1) is its limiting equation. This fact allows for further analysis of the dynamics of the Darwinian Ricker model [1, 6], but we will not pursue further analysis here. Note that Theorem 1 applies when the competition coefficient has the Gaussian form (10).

Consider now the case $c_1 \neq 0$. To study the eigenvalues of the Jacobian we employ the trace and determinant criteria which imply both eigenvalues have magnitude < 1 if and only if the three inequalities

$$tr J\left(x, u\right) < 1 + \det J\left(x, u\right) \tag{16}$$

$$-1 - \det J\left(x, u\right) < tr J\left(x, u\right) \tag{17}$$

$$\det J\left(x,u\right) < 1 \tag{18}$$

all hold [3]. If inequality (16) or (17) become equalities, then the Jacobian has an eigenvalue equal to $+1$ or -1 respectively. If inequality (18) becomes an equality, then the Jacobian has a complex eigenvalue whose absolute value equals 1.

For (15) we have

$$\operatorname{tr} J\left(x\left(b_0\right),u\left(b_0\right)\right) = 2 - x\left(b_0\right) - \sigma^2 \tag{19}$$

$$\det\ J\left(x\left(b_0\right),u\left(b_0\right)\right) = \left(1 - x\left(b_0\right)\right)\left(1 - \sigma^2\right) + 2\sigma^2\left(\ln b_0 - x\left(b_0\right)\right). \tag{20}$$

Lemma 1 *Assume $c_1 \neq 0$ in the Darwinian Ricker equations (8)–(9). Inequality (16) holds for all σ^2 and $b_0 > 1$.*

Proof Using (19) and (20), it is easy to show that inequality (16) reduces to $x\left(b_0\right) < 2\ln b_0$. From the Formula (14) and $c_1 \neq 0$, this inequality is

$$\frac{-1 + \sqrt{1 + 2c_1^2 \ln b_0}}{c_1^2} < 2\ln b_0$$

or $\sqrt{1 + 2c_1^2 \ln b_0} < 1 + 2c_1^2 \ln b_0$, which is clearly true and completes the proof.

Next we turn attention to inequality (17).

Lemma 2 *Assume $c_1 \neq 0$ and $\sigma^2 < 2$ in the Darwinian Ricker equations (8)–(9).*

(a) If

$$\sigma^2 < \frac{2}{1 + 8c_1^2} \tag{21}$$

then there exist a real $b_2 > e^2$ such that inequality (17) holds for b_0 satisfying $1 < b_0 < b_2$. Inequality (17) is reversed if b_0 is greater than but near b_2. The Jacobian $J\left(x\left(b_n\right),u\left(b_n\right)\right)$ has eigenvalue -1.

(b) If

$$\sigma^2 > \frac{2}{1 + 8c_1^2} \tag{22}$$

then inequality (17) holds for all $b_0 > 1$.

Proof Using (19) and (20) together with the equilibrium formulas (14), one can re-arrange inequality (17) to the inequality

$$\left(2 + \sigma^2\right)\sqrt{2c_1^2 z + 1} < 2 + \sigma^2 + 2c_1^2\left(2 - \sigma^2\right) + 2\sigma^2 c_1^2 z$$

where we have defined

$$z = \ln b_0 > 0.$$

Since both sides are positive, we can retain the inequality by squaring both sides, after which we re-arrange the result into an equivalent inequality $0 < q_1(z)$ where $q_1(z)$ is the quadratic polynomial

$$q_1(z) := 2c_1^2 \left(2 - \sigma^2\right) \left(\sigma^2 + 2 + \left(2 - \sigma^2\right) c_1^2\right)$$
$$- c_1^2 \left(2 - \sigma^2\right) \left(2 + \left(1 - 4c_1^2\right) \sigma^2\right) z + 2\sigma^4 c_1^4 z^2.$$

The quadratic $q_1(z)$ has a global minimum

$$q_1(z_c) = \frac{1}{8\sigma^4} \left(2 - \sigma^2\right) \left(\sigma^2 + 2\right)^2 \left(1 + 8c_1^2\right) \left(\sigma^2 - \frac{2}{1 + 8c_1^2}\right)$$

attained at the critical point

$$z_c = \frac{2 - \sigma^2}{4\sigma^4 c_1^2} \left(2 + \sigma^2 \left(1 - 4c_1^2\right)\right).$$

(a) Inequality (21) implies $q_1(z_c) < 0$ and hence the existence of two real roots of $q_1(z)$. Since $q_1(0) = 2c_1^2 \left(2 - \sigma^2\right) \left(2 + \sigma^2 + \left(2 - \sigma^2\right) c_1^2\right) > 0$, it follows that the two roots are both negative or both positive, depending on whether $z_c < 0$ or $z_c > 0$ respectively. Clearly $z_c > 0$ if $1 - 4c_1^2 \geq 0$. Suppose, on the other hand, that $1 - 4c_1^2 < 0$. Then $z_c > 0$ if and only if $\sigma^2 < 2 \left(4c_1^2 - 1\right)^{-1}$ which holds by (21) since $\left(4c_1^2 - 1\right)^{-1} > \left(1 + 8c_1^2\right)^{-1}$. Thus, in this case, $q_1(z)$ has two positive roots. If we denote the smaller by z_2 then $0 < q_1(z)$ for $0 < z < z_2$ and $q_1(z)$ changes sign as z increases through z_2. Since $q_1(z_2) = 0$ inequality (17) becomes an equality which means the Jacobian has an eigenvalue of -1. Finally we need to show that $z_2 > 2$. One way to do this is to show $q_1(2) > 0$ and $q_1'(2) < 0$. Calculations in fact show $q_1(2) = 2c_1^4 \left(\sigma^2 + 2\right)^2 > 0$ and, using (21),

$$q_1'(2) = c_1^2 \left(\sigma^2 + 2\right) \left(\sigma^2 + 4\sigma^2 c_1^2 - 2\right) < -\frac{1}{2} c_1^2 \left(\sigma^2 + 2\right) \left(2 - \sigma^2\right) < 0.$$

(b) Inequality (22) implies $q_1(z_c) > 0$ and hence $q_1(z) > 0$ for all z. This completes the proof.

Finally we consider inequality (18).

Lemma 3 *Assume $c_1 \neq 0$ and $\sigma^2 < 2$ in the Darwinian Ricker equations (8)–(9). There exists a real $b_n > \exp(1/2)$ such that inequality (18) holds for $1 < b_0 < b_n$. The Jacobian $J(x(b_n), u(b_n))$ has a complex eigenvalue of absolute value 1. The inequality (18) is reversed for $b_0 > b_n$.*

Proof Inequality (18) can be re-arranged as

$$\sigma^2 \left(2 \ln b_0 - 1\right) < x(b_0) \left(\sigma^2 + 1\right)$$

which is true for $1 < b_0 < \exp(1/2)$. For $b_0 > \exp(1/2)$ we use the Formula (14) for $x(b_0)$ and re-arrange the inequality as

$$1 + (2z - 1)\frac{\sigma^2}{(\sigma^2 + 1)}c_1^2 < \sqrt{1 + 2c_1^2 z}$$

where $z = \ln b_0 > 1/2$. Since both sides are positive, we can square them and re-arrange the inequality to obtain an equivalent inequality

$$0 < q_2(z) := \sigma^2\left(2\sigma^2 - \sigma^2 c_1^2 + 2\right) + 2\left(-\sigma^4 + 2\sigma^4 c_1^2 + 1\right)z - 4\sigma^4 c_1^2 z^2$$

Since $q_2(1/2) = \left(\sigma^2 + 1\right)^2 > 0$, this quadratic polynomial has a unique positive root $z_n > 1/2$ and $q_2(z) > 0$ for $1/2 < z < z_n$. Since $q_2(z_n) = 0$, inequality (18) becomes an equality, which implies the Jacobian has a complex eigenvalue of absolute value 1. This completes the proof.

In Lemma 2(a), the real b_2 is equal to $\exp(z_2)$ where z_2 is the smaller of the positive roots of $q_1(z)$. When (21) holds.a formula for $z_2 > 2$ is

$$z_2 = \frac{\left(2 - \sigma^2\right)\left(2 + \sigma^2 - 4\sigma^2 c_1^2\right) - \left(\sigma^2 + 2\right)\sqrt{\left(2 - \sigma^2\right)\left(2 - \sigma^2 - 8\sigma^2 c_1^2\right)}}{4\sigma^4 c_1^2} \quad (23)$$

When (21) holds define
$$b_2 := \exp(z_2) > e^2. \quad (24)$$

In Lemma 2, the real b_n is equal to $\exp(z_n)$ where z_n is the unique positive root $> 1/2$ of $q_2(z)$. A formula for z_n is

$$z_n = \frac{1 - \sigma^4 + 2\sigma^4 c_1^2 + \left(\sigma^2 + 1\right)\sqrt{\left(\sigma^2 - 1\right)^2 + 4\sigma^4 c_1^2}}{4\sigma^4 c_1^2} > \frac{1}{2}. \quad (25)$$

Define
$$b_n := \exp(z_n) > e^{1/2}. \quad (26)$$

The three Trace-Determinant stability inequalities (16)–(18) for local stability, together with the three Lemmas 1, 2, and 3, yield the following theorem.

Theorem 2 *Assume $c_1 \neq 0$ and $\sigma^2 < 2$ in the Darwinian Ricker equations (8)–(9) and let b_2 and b_n be defined by (24) and (26).*

(a) Assume
$$\sigma^2 < \frac{2}{1 + 8c_1^2}$$

and define $b_m = \min\{b_2, b_n\}$. The positive equilibrium (14) is locally asymptotically stable for $1 < b_0 < b_m$ and is unstable for b_0 greater than but near b_m. If $b_m = b_2$ then the Jacobian has an eigenvalue -1 when $b_0 = b_m$. If $b_m = b_n$ then the Jacobian has a complex eigenvalue of absolute value 1 when $b_0 = b_m$.

(b) If

$$\sigma^2 > \frac{2}{1 + 8c_1^2}$$

then the positive equilibrium (14) is locally asymptotically stable for $1 < b_0 < b_n$. and unstable for b_0 greater than, but near b_n. The Jacobian has a complex eigenvalue of absolute value 1 when $b_0 = b_n$.

Note that the denominators in the Formulas (23) and (25) for z_2 and z_n are identical and the numerator of z_2 vanishes while that of z_n equals 2 when $\sigma^2 = 0$. Thus, for σ^2 small it follows that $b_2 < b_n$. Theorem 2(a) implies the following corollary.

Corollary 1 *Assume $c_1 \neq 0$ in the Darwinian Ricker equations (8)–(9). For σ^2 sufficiently small, the destabilization of the positive equilibria occurs at $b_2 > e^2$.*

For a fixed value of $c_1 \neq 0$, sufficiently large values of σ^2 (but less than 2) can result in destabilization at b_n, which can be either greater than or less than e^2. Examples are provided in the next section.

4 Concluding Remarks

It is not our purpose in this paper to rigorously study the nature of the bifurcations in the Darwinian Ricker equations that occur when the positive equilibrium destabilizes (i.e. to formally prove that they do result in new invariant sets, what the direction of bifurcation is, their stability properties, etc.). We focus only on the occurrence of the destabilization an indicator of the onset of non-equilibrium and complex dynamics. At the point of bifurcation, the equilibrium is nonhyperbolic and, as a result, the linearization principle does not hold. This is irrelevant for our purposes here because it is no concern to us what the stability properties of the equilibrium are at the point of bifurcation; we are interested only in the fact that there is a change from equilibrium stability to instability before and after the bifurcation occurs. With regard to the type of bifurcation that occurs, i.e. what kind of stable invariant sets replace the destabilized equilibrium, we do point out in Theorems 1 and 2 what the Jacobian eigenvalues are at the bifurcation point, specifically where on the complex unit circle an eigenvalue lies. The reason for this is that this information tells us what kind of bifurcation we expect to occur. If at destabilization -1 is an eigenvalue of the Jacobian, then one expects a period doubling bifurcation. If the Jacobian has a complex eigenvalue of absolute value 1, then one expects a Neimark-Sacker bifurcation to an invariant loop [3].

Theorem 1 implies that when $c_1 = 0$ in the Darwinian Ricker equations (8)–(9) the positive equilibria destabilize at $b_0 = e^2$, which is no different from the non-
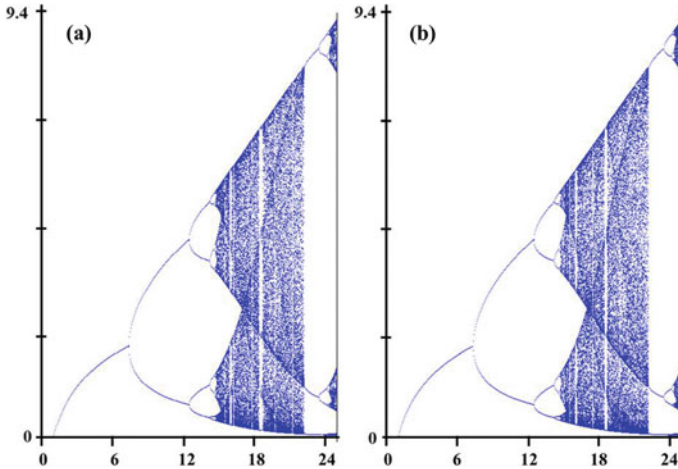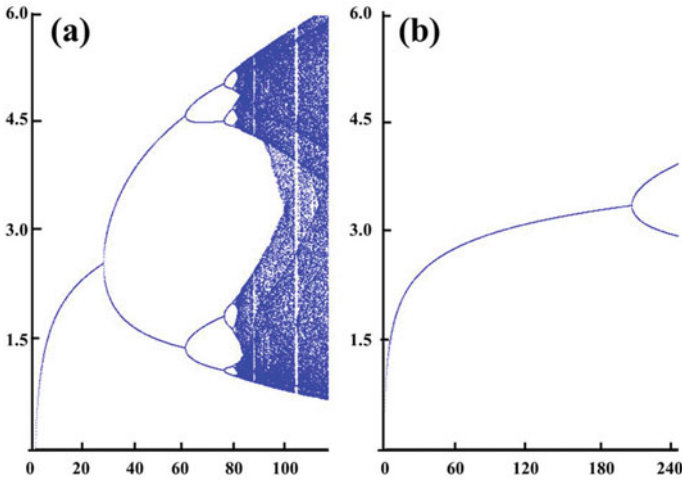
Fig. 1 **a** The familiar bifurcation diagram for the Ricker equation (1) with $c = 1$. **b** The bifurcation diagram showing the x component of the Darwinian Ricker equations (8)–(9) with $c_1 = 0$ and $\sigma^2 = 1$

evolutionary Ricker equation (1). The destabilization occurs because an eigenvalue of the Jacobian increases through -1 as b_0 increases through e^2, which is indicative of a period doubling bifurcation. This is also no different from the non-evolutionary Ricker equation. A sample bifurcation diagram appears in Fig. 1b that illustrates this bifurcation and what is apparently a period doubling route to chaos for the Darwinian Ricker equations that is identical with the non-evolutionary Ricker equation (Fig. 1a).

On the other hand, if $c_1 \neq 0$ then Theorem 2 shows that while destabilization does indeed occur at a critical value of b_0 in Darwinian Ricker equations, it does not necessarily indicate a period doubling bifurcation nor that it occurs at e^2, as in the non-evolutionary Ricker equation. The critical bifurcation point is either $b_2 > e^2$ (which is indicative of a period doubling bifurcation) or $b_n > e^{1/2}$ (which is indicative of a Neimark-Sacker bifurcation [3]). As stated in Corollary 1 equilibrium destabilization occurs at b_2 when the speed of evolution is not too fast. In fact, b_2 can be significantly larger than e^2 and the onset of complexity significantly delayed. Example bifurcation diagrams appear in Fig. 2.

Another difference between the evolutionary and non-evolutionary Ricker models is that destabilization does not necessarily result in period doubling. This occurs (for larger values of σ^2 and c_1^2) when $b_m = b_n$, which is indicative of a Neimark-Sacker bifurcation. Sample bifurcation diagrams appear in Fig. 3. One example (Fig. 3a) is when non-equilibrium dynamics are delayed, i.e. $b_n > e^2$ and the other (Fig. 3(b)) is when they are advanced, i.e. $b_n < e^2$. In the latter case, one could say evolution has promoted non-equilibrium and complexity dynamics.

For the Darwinian versions of the Ricker equation considered here, we arrive at several general conclusions. If $c_1 = 0$ in the trait dependent density coefficient $c(v - u)$, then there is no change in the destabilization point for the fertility rate b_0.

Fig. 2 The bifurcation diagram showing the x component of the Darwinian Ricker equations (8)–(9) with **a** $c_1 = 0.5$ and $\sigma^2 = 0.5$ and **b** $c_1 = 0.6$ and $\sigma^2 = 0.5$. The Formulas (24) and (26) for b_2 and b_n in these two cases yield **a** $b_2 \approx 28.121 < b_n \approx 2304.5$ and **b** $b_2 \approx 207.13 < b_n \approx 342.96$
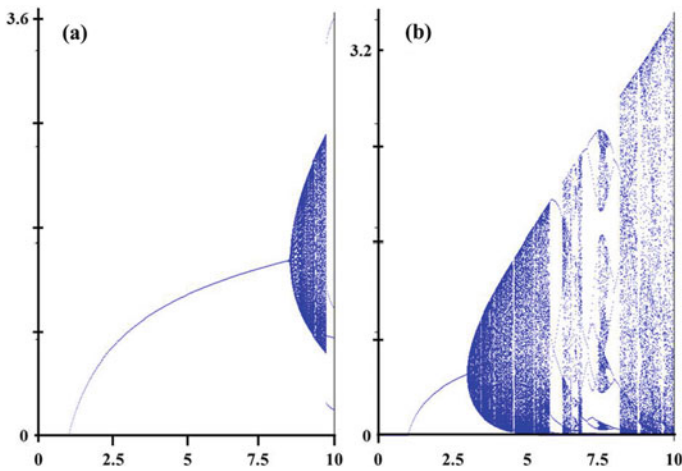
Fig. 3 The bifurcation diagram showing the x component of the Darwinian Ricker equations (8)–(9) with **a** $c_1 = 0.8$ and $\sigma^2 = 0.8$ and **b** $c_1 = 2$ and $\sigma^2 = 0.8$. For these cases, b_2 does not exist and **a** $b_n \approx 8.5253 > e^2 \approx 7.3891$ and **b** $b_n \approx 3.0004 < e^2$

Both models destabilize in period doubling bifurcations at the same critical value e^2. In this sense, we conclude that evolution has no effect on the onset of non-equilibrium and complex dynamics. The opposite is true in the case of hierarchical trait dependent competition coefficients, i.e. when $c_1 \neq 0$. In this case the onset of non-equilibrium and complex dynamics is delayed to a larger critical value of b_0 when evolution procedes slowly (i.e. σ^2 is small). In this case, we say that slow evolution selects against non-equilibrium and complex dynamics. If, on the other hand, evolution procedes at a faster speed, then there are two differences with the non-evolutionary Ricker equation, depending the magitude of the density effects, i.e. the size of c_1. First, the onset of non-equilibrium and complex dynamics can lead not to a period doubling bifurcation, but to a Neimark-Sacker bifurcation. Secondly, in the latter case, the bifurcation point can be either later or earlier than e^2. In the latter case (and only in this case), which occurs for larger σ^2 and c_1 values, we can conclude that evolution promotes non-equilibrium and complex dynamics.

These conclusions are drawn, of course, on the basis of the specific Darwinian Ricker equation considered here. To what extent they remain valid for other Darwinian equations with complex dynamics awaits further study.

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