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Global asymptotic stability of evolutionary periodic Ricker competition models

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ABSTRACT

This paper is dedicated to Jim Cushing on the occasion of his 80th birthday. It is inspired by his work on evolutionary theory. We investigate the global dynamics of discrete-time phenotypic evolutionary models, both autonomous and periodic. We developed the theory of mixed monotone maps and applied it to show that the positive equilibrium of the autonomous evolutionary Ricker model of single and multi-species is globally asymptotically stable. Then we extend this result to the corresponding evolutionary Ricker model with periodic parameters.

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1. Introduction

The study of evolution and seasonality is crucial for understanding the dynamics of ecological systems, particularly in the context of interactions between competing species [8,19,34]. Both biological observations and mathematical models have provided valuable insights into the impact of these factors on species coexistence, population dynamics, and community structure [18,27]. In this paper, we will explore how evolution, and seasonality reflected by periodicity, are shaping the dynamics of two competing species through evolutionary periodic Ricker competition models.

Evolution, the process by which heritable characteristics of a population change over successive generations, plays a fundamental role in determining the outcomes of species interactions [34]. In the context of competition, evolutionary processes can drive the adaptation of species to exploit different resources or occupy distinct ecological niches, leading to the coexistence or exclusion of competing species [4]. Classic studies such as Darwin's finches in the Galapagos Islands have demonstrated the role of evolutionary divergence in allowing closely related species to coexist by occupying different feeding niches [20]. Additionally, the presence of seasonality in the environment introduces significant challenges and opportunities for competing species. Seasonal variations in temperature, resource

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availability, and other environmental factors impose strong selective pressures on organisms, leading to adaptations and life history strategies optimized for specific seasonal conditions. For instance, the migration patterns of birds and the hibernation behaviours of mammals are adaptations that allow them to cope with seasonal variations in resource availability and environmental conditions.

Mathematical models have provided a powerful framework for studying the dynamics of competing species under the influence of evolution and seasonality. These models integrate ecological and evolutionary principles with mathematical equations to simulate and analyse species interactions over time. By incorporating parameters such as competition coefficients, reproductive rates, and phenotypic plasticity, these models can capture the complex dynamics arising from evolutionary processes and seasonal fluctuations. Several influential studies have explored the interplay between evolution, seasonality, and species competition. For example, classical ecological models, such as Lotka–Volterra models, have been extended to incorporate evolutionary dynamics, yielding insights into the conditions under which coexistence or exclusion occurs. Furthermore, seasonally varying models, such as the Nicholson–Bailey model, have been used to investigate the impact of seasonal fluctuations on predator–prey dynamics [18].

The study of evolution and seasonality is vital for understanding the dynamics of competing species. Both biological observations and mathematical models have provided valuable insights into the mechanisms underlying species coexistence, population dynamics, and community structure.

Mathematical models of Darwinian evolution were introduced in the book of Vincent and Brown [33]. Adaptive dynamics of trait models may be found in the book of Dercole and Rinaldi [15] and the paper of Abrams [1]. Most models in the literature are continuous and autonomous. It was Cushing [2,9–13,28] who established the foundation of discrete phenotype evolutionary models. Several recent papers on discrete evolutionary competition models by Mokni et al. [25,26] and Elaydi et al. [17] were based on the ideas and the methodology established by Cushing. Moreover, Cushing's methodology was also applied to predator–prey models by Ackleh et al. [3]. In this paper, we use the discrete-time modelling framework of Darwinian evolution developed by Jim Cushing to study the global dynamics of evolutionary periodic Ricker Competition models.

Up to this point, all the published papers and books have focused on local stability questions. Global stability was only obtained in a very special case when the trait equations were uncoupled from the populations' dynamic equations. In this paper, using the novelty of mixed monotone maps, we extend the global stability theory of non-evolutionary models in two directions:

(i) First, the global stability results are extended to autonomous evolutionary models in which the trait equations are coupled with the population dynamics equations. This will be presented in Section 2.
(ii) Second, the results obtained in (i) are extended to non-autonomous periodic evolutionary models and asymptotically autonomous evolution models. This will be presented in Section 3.

In the final Section 4, we provide conclusions about our study, the related conjectures, and propose important and interesting open problems for future study.

2. Autonomous evolutionary systems of Ricker type

In this section, we investigate the global stability of the interior equilibrium point of the autonomous evolutionary Ricker model. We start with a single-species and then we extend the obtained results to multi-species models.

2.1. Single-species evolutionary models

The autonomous evolutionary Ricker model [11] of single-species x with a single mean trait u and individual trait v is given as follows:

$$\begin{cases} x(t+1) = x(t)e^{\alpha - \frac{v^2}{2} - c(v,u(t))x(t)}|_{v=u(t)} \\ u(t+1) = u(t) + \sigma^2 \left(-u(t) - \frac{\partial c(v,u(t))}{\partial v}|_{v=u(t)}\right) x(t) \end{cases},$$

where we assume that $c(v, u(t)) = c(v - u(t)) = c(z)$ by setting $z = v - u$ and the function $c(z)$ is continuously differentiable for all values of its argument z. Thus, we have $c(v - u)|_{v=u} = c(0) = c_0$. Therefore, we have the following model (1)

$$\begin{cases} x(t+1) = x(t)e^{\alpha - \frac{u^2}{2} - c_0 x(t)} \\ u(t+1) = (1-\sigma^2)u(t) - c_1\sigma^2 x(t) \end{cases}, \tag{1}$$

where $c_1 := \frac{d}{dz}c(z)|_{z=0}$, and $c_0 = c(0) = c(v - u(t))|_{v=u(t)}$. The details of the model derivations of Model (1) can be found in Cushing [11].

Model (1) can be represented by the map $F(x, u) = (xe^{\alpha - u^2/2 - c_0 x}, (1-\sigma^2)u - c_1\sigma^2 x)$ which has the origin as a fixed point, and another fixed point E^* of the form

$$E^* = \begin{cases} (\alpha/c_0, 0) & \text{if } c_1 = 0 \\ (x^*, -c_1 x^*) & \text{if } c_1 \neq 0 \end{cases},$$

where $x^* = \frac{-c_0 + \sqrt{c_0^2 + 2\alpha c_1^2}}{c_1^2}$.

By using the linearization principle for maps and the well-known results in [16, Theorem 4.4, p. 200], sufficient conditions for a fixed point $\mathbf{x}^*$ of a planar system to be locally asymptotically stable are given by

$$\det(JF(\mathbf{x}^*)) > \operatorname{tr}(JF(\mathbf{x}^*)) - 1, \quad \det(JF(\mathbf{x}^*)) > -\operatorname{tr}(JF(\mathbf{x}^*)) - 1, \quad \det(JF(\mathbf{x}^*)) < 1, \tag{2}$$

where $\det(JF(\mathbf{x}^*))$ and $\operatorname{tr}(JF(\mathbf{x}^*))$ are, respectively, the determinant and the trace of the Jacobian matrix of the mapping F evaluated at the fixed point $\mathbf{x}^*$. The Jacobian matrix of the mapping F of the system (1) is given by

$$JF(x, u) = \begin{pmatrix} (1 - c_0 x)e^{\alpha - \frac{u^2}{2} - c_0 x} & -xue^{\alpha - \frac{u^2}{2} - c_0 x} \\ -c_1\sigma^2 & 1 - \sigma^2 \end{pmatrix}.$$

Thus, we have $JF(0,0) = \begin{pmatrix} e^{\alpha} & 0 \\ -c_1\sigma^2 & 1-\sigma^2 \end{pmatrix}$ which leads to the conclusion that the origin is a saddle fixed point if $\alpha > 0$ and $\sigma^2 < 2$ (and unstable fixed point if $\alpha > 0$ and $\sigma^2 > 2$).

For the non-trivial fixed point E^* we need to consider two cases as follows:

(1) In the case $c_1 = 0$, the fixed point $(\alpha/c_0, 0)$ is locally asymptotically stable when $0 < \alpha \leq 2$ since $JF(\alpha/c_0, 0) = \begin{pmatrix} 1-\alpha & 0 \\ 0 & 1-\sigma^2 \end{pmatrix}$ and $\sigma^2 < 2$. At $\alpha = 2$, a period-doubling bifurcation occurs. Notice that from the equation $u(t+1) = (1-\sigma^2)u(t)$ we get $u(t) = (1-\sigma^2)^t u(0)$. Hence, we have $u(t) \to 0$ as $t \to \infty$. From this, one can conclude that the dynamics of the equation $x(t+1) = x(t)e^{\alpha - u(t)^2/2 - c_0 x(t)}$ is eventually converging to the limiting equation $x(t+1) = x(t)e^{\alpha - c_0 x(t)}$. It is well known that the local stability of the fixed point $x^* = \alpha/c_0$ of the equation $x(t+1) = x(t)e^{\alpha - c_0 x(t)}$ implies its global stability. This statement was first established by May and Oster [24] by using a graphical analysis, and an analytic proof can be derived from Singer [31]. Therefore, the fixed point $(\alpha/c_0, 0)$ is globally asymptotically stable when $0 < \alpha \leq 2$.

(2) In the case $c_1 \neq 0$, the Jacobian $JF(E^*)$ is given by

$$JF(E^*) = \begin{pmatrix} \frac{c_0^2 - \sqrt{c_0^2 + 2\alpha c_1^2}\, c_0 + c_1^2}{c_1^2} & \frac{\left(c_0 - \sqrt{c_0^2 + 2\alpha c_1^2}\right)^2}{c_1^3} \\ -\sigma^2 c_1 & 1 - \sigma^2 \end{pmatrix} = \begin{pmatrix} 1 - c_0 x^* & c_1 (x^*)^2 \\ -\sigma^2 c_1 & 1 - \sigma^2 \end{pmatrix}$$

which gives

$$\det(JF(E^*)) = \frac{-c_0\left(\sigma^2+1\right)\sqrt{2\alpha c_1^2 + c_0^2} + c_1^2\left((2\alpha-1)\sigma^2+1\right) + c_0^2\left(\sigma^2+1\right)}{c_1^2}$$
$$= 1 - \sigma^2 + 2\alpha\sigma^2 - c_0(1+\sigma^2)x^*$$

and

$$\operatorname{tr}(JF(E^*)) = \frac{c_0\left(c_0 - \sqrt{2\alpha c_1^2 + c_0^2}\right)}{c_1^2} - \sigma^2 + 2 = 2 - c_0 x^* - \sigma^2.$$

We observe that $\det(JF(E^*)) > \operatorname{tr}(JF(E^*)) - 1$ is always true. Now, simplifying the two remaining relations in (2), it follows that the fixed point E^* is locally asymptotically stable whenever the following relations are satisfied

$$c_0(2+\sigma^2)x^* < 2((\alpha-1)\sigma^2+2), \tag{3}$$
$$c_0(1+\sigma^2)x^* > (2\alpha-1)\sigma^2. \tag{4}$$

Notice that Relation (3) is equivalent to $\det(JF(E^*)) > -\operatorname{tr}(JF(E^*)) - 1$ and Relation (4) is equivalent to $\det(JF(E^*)) < 1$. The region, in the parameter space bifurcation diagram, where Conditions (3) and (4) are satisfied, is depicted in Figure 1. There are two cases, in the left graph we consider the parameter space $\alpha O c_1$ while in the right graph, we consider $\alpha O \sigma$. We should mention that similar figures may be obtained for the other cases of the fixing parameter. A complete study of local stability properties of the Darwinian Ricker Model (1) may be found in [11].

If the inequality (3) becomes equality, i.e. when

$$\sigma^2 = \frac{2(2 - c_0 x^*)}{c_0 x^* + 2(1-\alpha)},$$

then the Jacobian has -1 as one of its eigenvalues where a period-doubling bifurcation takes place. This phenomenon occurs when the parameters cross the dashed curve in

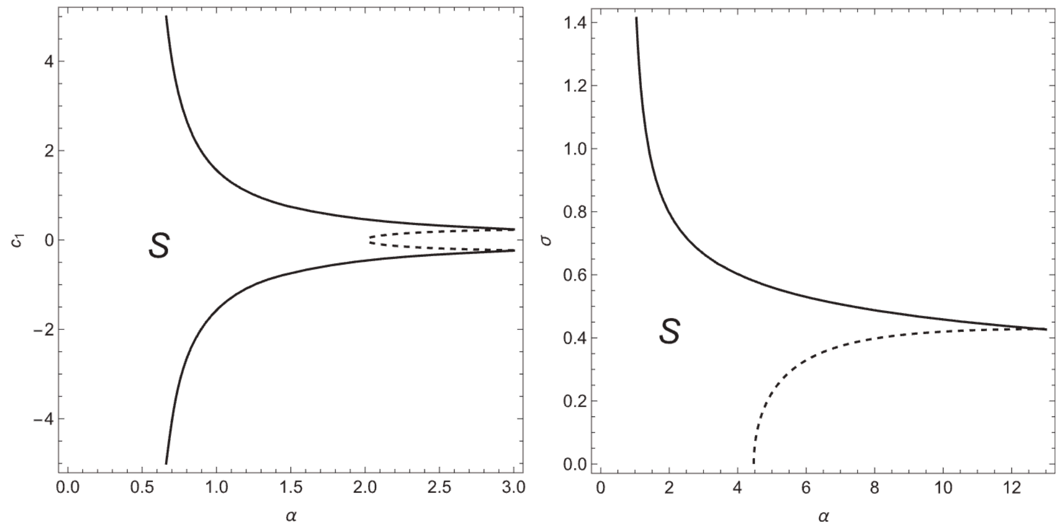

Figure 1. Region, in the parameter space bifurcation diagram, of local stability of the non-trivial fixed point of Model (1). In the region **S**, Conditions (3) and (4) are satisfied for $c_0 = 0.9$. In the left graph we consider $\sigma = 1.1$ while in the right graph we take $c_1 = -1$.

Figure 1. Similarly, if the inequality (4) becomes an equality, i.e.

$$\sigma^2 = \frac{c_0 x^*}{2\alpha - 1 - c_0 x^*},$$

then the Jacobian has a pair of complex eigenvalues whose absolute value equals 1, where Neimark–Sacker bifurcation takes place. This occurs when the parameters cross the solid curve in Figure 1. In Ref. [25], the author presented a detailed analysis of these two types of bifurcation for Model (1).

Based on the analysis above, we have the local stability result as follows:

Theorem 2.1 (Local asymptotically stable): *Let $\alpha > 0, \sigma^2 < 2$ and $c_1 \neq 0$. Then, the fixed point $(x^*, -c_1x^*)$ of the evolutionary Ricker system given by (1) is locally asymptotically stable if $c_0(2+\sigma^2)x^* < 2((\alpha-1)\sigma^2+2)$ and $c_0(1+\sigma^2)x^* > (2\alpha-1)\sigma^2$.*

Notes: Theorem 2.1 requires $\sigma^2 < 2$. Note that one may obtain the following formula of $u(t)$ from Model (1):

$$u(t) = (1-\sigma^2)^t u(0) - c_1\sigma^2 \sum_{j=0}^{t-1} (1-\sigma^2)^j x(t-j-1).$$

Now if $\sigma^2 > 2$, this expression indicates that $u(t)$ would approach infinity with $x(t)$ approaching zero, which has been confirmed in the simulations as well. Thus, for the boundedness of $u(t)$, we require $\sigma^2 < 2$ for the remainder of this paper. Note that $x^* =$

$\frac{-c_0+\sqrt{c_0^2+2\alpha c_1^2}}{c_1^2}$, thus the local stability conditions in Theorem 2.1 becomes

$$\frac{(2\alpha-1)\sigma^2}{c_0(1+\sigma^2)} < x^* = \frac{-c_0+\sqrt{c_0^2+2\alpha c_1^2}}{c_1^2} < \frac{2((\alpha-1)\sigma^2+2)}{c_0(2+\sigma^2)}.$$

From now on we assume that $c_1 \neq 0$. Our goal is to study the global stability of the fixed point E^*. To accomplish this task we use the notion of mixed monotone mappings introduced by Hal Smith [32]. First we deal with an absorbing region in Model (1).

Definition 2.2: A region D in the domain of a map F is called an absorbing region if all the orbits of the points in the domain of F are eventually in D after a number of iterations.

Remark 2.3: It should be noted that an absorbing region is a subset of the basin of attraction and for most systems is not equal to.

Lemma 2.4 (Absorbing region): *Let $0 < \alpha < 1$, $1 < \sigma^2 < 2$ and $c_1 \neq 0$. Then the map F in Model (1) has a compact invariant absorbing region D. Moreover, D is a subset of the fourth quadrant when $c_1 > 0$ and it is a subset of the first quadrant when $c_1 < 0$.*

Proof: Assume that $c_1 > 0$. Now on the x-axis, the absorbing region is bounded above by $e^{\alpha-1}/c_0$ since $x(t)e^{\alpha-c_0t} \le e^{\alpha-1}/c_0$ for all t. However, for $u \neq 0$ we have $x(t)e^{\alpha-u^2(t)/2-c_0x(t)} \le x(t)e^{\alpha-c_0x(t)}$ for all t. Hence, the x component of all orbits is bounded by $e^{\alpha-1}/c_0$.

Since $u(t+1) \ge (1-\sigma^2)u(t) - M$, $M = \sigma^2 c_1 e^{\alpha-1}/c_0 > 0$, we have

$$\liminf_{t\to\infty} u(t) \ge \lim_{t\to\infty}\left((1-\sigma^2)^t u(0) - M\frac{1-(1-\sigma^2)^t}{\sigma^2}\right) \ge -\frac{M}{\sigma^2}.$$

On the other hand the relation $u(t+1) \le (1-\sigma^2)u(t)$ implies that

$$\limsup_{t\to\infty} u(t) \le \lim_{t\to\infty} (1-\sigma^2)^t u(0) = 0.$$

Thus, $\liminf_{t\to\infty} u(t) \le u(t) \le \limsup_{t\to\infty} u(t)$, i.e. $-M\sigma^{-2} \le u(t) \le 0$. Consequently, D is a subset of the fourth quadrant.

Then the set $D = \{(x,u) : 0 \le x \le e^{\alpha-1}/c_0, -M\sigma^{-2} \le u \le 0\}$ is an invariant absorbing region of the map F. Analogously, there is an invariant absorbing region $D = \{(x,u) : 0 \le x \le e^{\alpha-1}/c_0, 0 \le u \le M\sigma^{-2}$ in the first quadrant when $c_1 < 0$. ■

Definition 2.5: Let X be an ordered metric space. A continuous map $F : X \to X$ is mixed monotone if there exists a map (not necessarily continuous) $f : X \times X \to X$ satisfying

(i) $F(\mathbf{x}) = f(\mathbf{x},\mathbf{x})$ for all $\mathbf{x} \in X$;
(ii) for $\mathbf{y} \in X$ and $\mathbf{x}_1 \le \mathbf{x}_2$ we have $f(\mathbf{x}_1,\mathbf{y}) \le f(\mathbf{x}_2,\mathbf{y})$;
(iii) for $\mathbf{x} \in X$ and $\mathbf{y}_1 \le \mathbf{y}_2$ we have $f(\mathbf{x},\mathbf{y}_2) \le f(\mathbf{x},\mathbf{y}_1)$.

The first main result now follows

Lemma 2.6 (Mixed monotonocity): *Let* $0 < \alpha < 1$, $\sigma^2 \in (1, 2)$ *and* $c_1 > 0$. *Then the mapping F of Model* (1) *is mixed monotone.*

Proof: Consider $\leq_{se}$ to denote the southeast partial order, i.e. $(x_1, u_1) \leq_{se} (x_2, u_2)$ if and only if $x_1 \leq x_2$ and $u_2 \leq u_1$ and let $F(x, u) = (xe^{\alpha - u^2/2 - c_0 x}, (1 - \sigma^2)u - \sigma^2 c_1 x)$. From Lemma 2.4, one can consider that all the dynamics of the mapping take place in the fourth quadrant.

Define $f((x_1, u_1), (x_2, u_2)) = F(x_1, u_2)$. Then:

(i) $f((x, u), (x, u)) = F(x, u)$;

(ii) Since $x_1 e^{\alpha - c_0 x_1} \leq x_2 e^{\alpha - c_0 x_2}$ for all $x_1 \leq x_2 \leq 1/c_0$ (notice that the function $g(x) = xe^{\alpha - c_0 x}$, $0 < \alpha < 1$, is increasing in the interval $[0, 1/c_0]$ and we have $g([0, 1/c_0]) = g([1/c_0, +\infty))$, so we can always assume x_1 and x_2 after one iteration, i.e. values on the range), we will have

$$x_1 e^{\alpha - u^2/2 - c_0 x_1} \leq x_2 e^{\alpha - u^2/2 - c_0 x_2},$$

or equivalently, $F(x_1, u) \leq_{se} F(x_2, u)$. So, writing $f((x_i, u_i), (x, u)) = F(x_i, u)$, $i = 1, 2$, for $\mathbf{y} = (x, u)$ and $(x_1, u_1) \leq_{se} (x_2, u_2)$ we have $f(\mathbf{x}_1, \mathbf{y}) \leq_{se} f(\mathbf{x}_2, \mathbf{y})$ with $\mathbf{x}_i = (x_i, u_i)$, $i = 1, 2$.

(iii) For $u_2 \leq u_1 < 0$ we have $e^{-u_2^2/2} \leq e^{-u_1^2/2}$. Hence, for $\mathbf{x} = (x, u)$ and $(x_1, u_1) \leq_{se} (x_2, u_2)$ we have $f(\mathbf{x}, \mathbf{y}_2) \leq_{se} f(\mathbf{x}, \mathbf{y}_1)$ provide that

$$\begin{aligned} f(\mathbf{x}, \mathbf{y}_i) &= f((x, u), (x_i, u_i)) = F(x, u_i) \\ &= (xe^{\alpha - u_i^2/2 - c_0 x}, (1 - \sigma^2)u_i - \sigma^2 c_1 x), \quad i = 1, 2. \end{aligned}$$

Consequently, F is a mixed monotone mapping.

■

To extend this result to the case $c_1 < 0$, we introduce the notion of topological conjugacy.

Definition 2.7 (Topological conjugacy): Two maps F and G are topologically conjugate if there exists a homeomorphism h such that $h \circ G = F \circ h$, or, equivalently, $G = h^{-1} \circ F \circ h$ (Figure 2).

Consider now the map $F(x, u) = (xe^{\alpha - u^2/2 - c_0 x}, (1 - \sigma^2)u - c_1\sigma^2 x)$, where $1 < \sigma^2 < 2$, $0 < \alpha < 1$ and $c_1 < 0$ and let $G(x, u) = (xe^{\alpha - u^2/2 - c_0 x}, (1 - \sigma^2)u - \hat{c}_1\sigma^2 x)$ where $\hat{c}_1 = -c_1 > 0$. For the maps F and G we have the following lemma:

Lemma 2.8: *The maps F and G are topologically conjugate.*

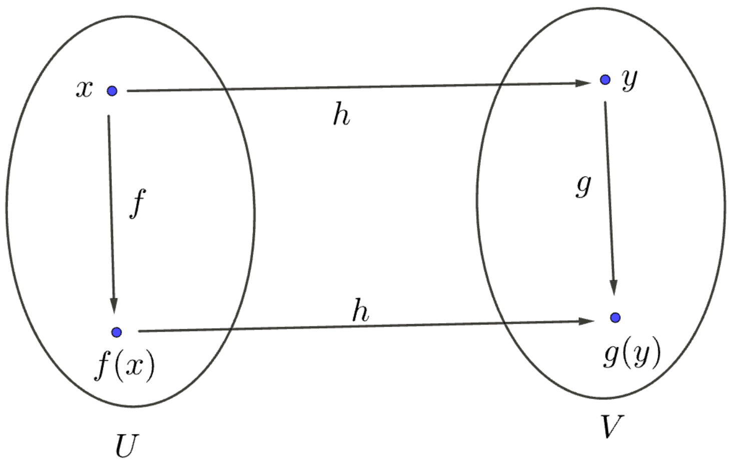

Figure 2. Topological conjugacy of two maps.

Proof: Define $h(x,u) = (x, -u)$. Then clearly h is a homeomorphism. Now for $u > 0$

$$\begin{aligned} h^{-1}(G(h(x,u)) &= h^{-1}(G(x,-u)) \\ &= h^{-1}((xe^{\alpha-u^2/2-c_0x}, (1-\sigma^2)(-u) - \hat{c}_1\sigma^2 x) \\ &= h^{-1}((xe^{\alpha-u^2/2-c_0x}, -((1-\sigma^2)u + \hat{c}_1\sigma^2 x)) \\ &= (xe^{\alpha-u^2/2-c_0x}, (1-\sigma^2)u - c_1\sigma^2 x) \\ &= F(x,u). \end{aligned}$$

Hence the maps F and G are topologically conjugate. ■

Using Lemma 2.8, we get the following result.

Lemma 2.9 (Mixed monotonocity): *Let* $0 < \alpha < 1$, $\sigma^2 \in (1,2)$ *and* $c_1 < 0$. *Then the mapping F of Model* (1) *is mixed monotone.*

As a consequence of the previous results, we have the following important theorem.

Theorem 2.10 (Global Stability): *The equilibrium point* (x^*, u^*) *of the Model* (1) *is globally asymptotically stable if it is locally asymptotically stable and* $0 < \alpha < 1$, $1 < \sigma^2 < 2$, *and* $c_1 < 0$.

Proof: Let D be the absorbing region as defined in Lemma 2.4, and let $B = D - \{(x,u) : x = 0\}$ Let $\mathbf{a} = (x_1, u_1), \mathbf{b} = (x_2, u_2) \in B$. Claim that if $\mathbf{a} \leq_{se} \mathbf{b}, f(\mathbf{a}, \mathbf{b}) \leq_{se} \mathbf{a}$, and $f(\mathbf{b}, \mathbf{a}) \geq_{se} \mathbf{b}$, then $\mathbf{a} = \mathbf{b}$. There are three cases to consider:

(i) $\mathbf{a} <_{se} \mathbf{b}$;
(ii) $x_1 = x_2$ and $u_1 > u_2$;
(iii) $x_1 < x_2$ and $u_1 = u_2$.

Note that $f(\mathbf{a},\mathbf{b}) \leq_{se} \mathbf{a}$ and $f(\mathbf{b},\mathbf{a}) \geq_{se} \mathbf{b}$ imply that $F(x_1,u_2) \leq_{se} (x_1,u_1)$ and $F(x_2,u_1) \geq_{se} (x_2,u_2)$, respectively. Consequently, $\alpha - u_2^2/2 - c_0x_1 \leq 0$ and $\alpha - u_1^2/2 - c_0x_2 \geq 0$. Hence $u_2^2/2 - u_1^2/2 + c_0(x_1 - x_2) \geq 0$ which is false in the three cases. Therefore, $\mathbf{a} = \mathbf{b}$.

Now let $(x,u) \in B$. Then its orbit closure $\overline{O(x,u)} \subset D$ and thus compact. Now $\mathbf{c} = \inf \omega(x,u) \in D$ (the infimum) and $\mathbf{d} = \sup \omega(x,u) \in D$ (the supremum), where $\omega(x,u)$ is the omega limit set of (x,u). Note that $\omega(x,u)$ is invariant and compact. This implies that both $\mathbf{c}$ and $\mathbf{d}$ are in $\omega(x,u)$. If $(y_1,v_1) \in \omega(x,u)$, then there exists $(y_2,v_2) \in \omega(x,u)$ such that $F(y_2,v_2) = (y_1,v_1)$. Hence, $\mathbf{c} \leq_{se} (y_2,v_2) \leq_{se} \mathbf{d}$.

Let $\mathbf{c} = (z,w)$ and $\mathbf{d} = (k,s)$. Then $f(\mathbf{c},\mathbf{d}) = f((z,w),(k,s)) = F(z,s)$ and $f((y_2,v_2)(k,s)) = F(y_2,s) = (y_2e^{\alpha - s^2/2 - c_0y_2}(1-\sigma^2)s - c_1\sigma^2y_2) \leq_{se} (y_2e^{\alpha - v_2^2/2 - c_0y_2}(1-\sigma^2)v_2 - c_1\sigma^2y_2) = (y_1,v_1)$ By the mixed monotonicity of the map, it follows that $f(\mathbf{c},\mathbf{d}) \leq_{se} (y_1,v_1)$. Similarly, $f(\mathbf{d},\mathbf{c}) = f((k,s),(z,w)) = F(k,w)$, and $f((k,s)),(y_2,v_2)) = F(k,v_2) = (ke^{\alpha - v_2^2/2 - c_0k}, (1-\sigma^2)v_2 - c_1\sigma^2k) \geq_{se} (y_2e^{\alpha - v_2^2/2 - c_0y_2}, (1-\sigma^2)v_2 - c_1\sigma^2y_2) = (y_1,v_1)$. By the mixed monotonicity of the map, it follows that $f(\mathbf{d},\mathbf{c}) \geq_{se} (y_1,v_1)$.

Since (y_1,v_1) was arbitrary chosen from $\omega(x,u)$, it follows that $f(\mathbf{c},\mathbf{d}) \leq_{se} \mathbf{c}$ and $f(\mathbf{d},\mathbf{c}) \geq_{se} \mathbf{d}$, which implies that $\mathbf{c} = \mathbf{d}$. Therefore the omega limit set of the point (x,u) is a fixed point in D. Since the origin is a saddle, it can't be the attracting fixed point. Moreover, since the interior fixed point (x^*,u^*) is locally asymptotically stable, then it must be the unique attracting fixed point. Hence, for all points $(x,u) \in D$, we have $\omega(x,u) = (x^*,u^*)$. Therefore (x^*,u^*) is globally asymptotically stable. ■

By topological conjugacy, we obtain the following corollary.

Corollary 2.11 (Global Stability): *If the equilibrium point* (x^*,u^*) *of the model* (1) *is locally asymptotically stable, then it is globally asymptotically stable if* $0 < \alpha < 1$, $1 < \sigma^2 < 2$, *and* $c_1 > 0$.

Combining Theorems 2.1, 2.10 and Corollary 2.11 we have the following result:

Corollary 2.12 (Globally asymptotically stable): *Let* $0 < \alpha < 1$, $1 < \sigma^2 < 2$, *and* $c_1 \neq 0$. *Then the interior equilibrium point of Model* (1) *is globally asymptotically stable if it is locally asymptotically stable.*

Example 2.13: Let $c_0 = 1, \sigma^2 = 1.5, c_1 = 2$ and $\alpha = 0.3$. Then $(0.210977, -0.421954)$ is a fixed point of the map F, where $F(x,u) = (xe^{0.3-u^2/2-x}, -0.5u - 2\sigma^2x)$.

Now, the Jacobian matrix of F evaluated at the fixed point $(0.210977, -0.421954)$ is given by

$$JF = JF(0.210977, -0.421954) = \begin{pmatrix} 0.789023 & 0.0890228 \\ -3. & -0.5 \end{pmatrix}.$$

Hence, $\det JF = -0.127443$ and $\operatorname{tr} JF = 0.289023$. Clearly, the conditions (2) of local stability are satisfied and we have local asymptotic stability by Theorem 2.1. Thus, by Corollary 2.12, the fixed point $(0.210977, -0.421954)$ is a globally asymptotically stable fixed point of F. In Figure 3 it is represented a phase-space diagram in this case.

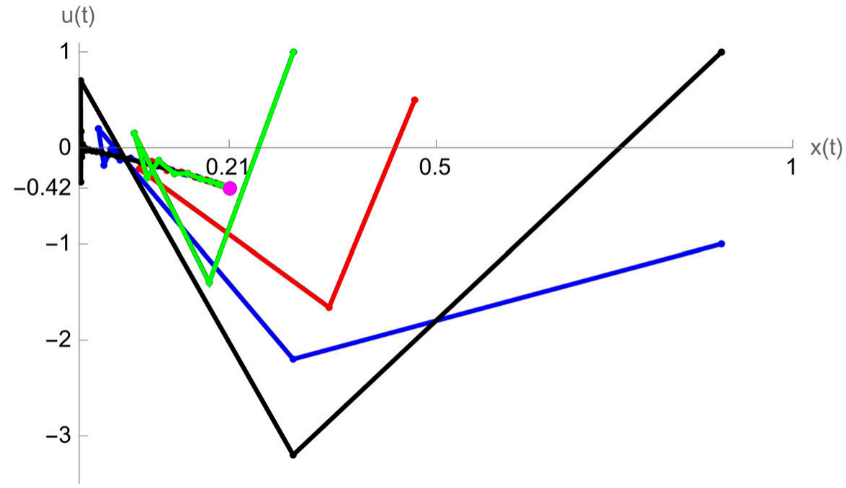

Figure 3. Phase-space diagram for Example 2.13.

2.2. Two-species evolutionary models

In this subsection, we will extend our global analysis to the following two-species evolutionary Ricker competition model

$$\begin{cases} x(t+1) = x(t)e^{\alpha - u_1^2(t)/2 - c_{11}(0)x(t) - c_{12}y(t)} \\ y(t+1) = y(t)e^{\beta - u_2^2(t)/2 - c_{21}x(t) - c_{22}(0)y(t)} \\ u_1(t+1) = (1-\sigma_1^2)u_1(t) - \sigma_1^2 c_1 x(t) \\ u_2(t+1) = (1-\sigma_2^2)u_2(t) - \sigma_2^2 c_2 y(t) \end{cases}, \tag{5}$$

where $\alpha,\ \beta > 0$, $\sigma_i^2 < 2$, $c_i \in \mathbb{R}$, and $c_{12}, c_{21}, c_{11}(0), c_{22}(0) > 0$. Specific details about the local properties of this model may be found in Ref. [17] namely the effects of evolution on the stability of competing species, i.e. the effects of evolution on the stability of the three non-negative fixed points. Here, by non-negative we mean $x \geq 0$ and $y \geq 0$.

System (5) may be represented by the map $F : \mathbb{R}^4 \to \mathbb{R}^4$ given by

$$F(x, y, u_1, u_2) = \Big(xe^{\alpha - u_1^2/2 - c_{11}(0)x - c_{12}y}, ye^{\beta - u_2^2/2 - c_{21}x - c_{22}(0)y}, \\ (1-\sigma_1^2)u_1 - \sigma_1^2 c_1 x, (1-\sigma_2^2)u_2 - \sigma_2^2 c_2 y\Big). \tag{6}$$

Theorem 2.14: *Assume that* $0 < \alpha, \beta < 1$, $\sigma_i^2 \in (1, 2)$ *and* $c_i < 0$, $i = 1, 2$. *Then the map* F *given in (6) is mixed monotone.*

Proof: Defining the map $f : \mathbb{R}^4 \times \mathbb{R}^4 \to \mathbb{R}^4$ as

$$f\left((x_1, y_1, u_1^1, u_2^1), (x_2, y_2, u_1^2, u_2^2)\right) = F(x_1, y_1, u_1^2, u_2^2),$$

it is a straightforward computation to show that the map f satisfies the three conditions of mixed monotonicity. ■

Theorem 2.15: *Suppose that the assumptions of Theorem 2.14 hold. Then the interior fixed point* $\mathbf{x}^* = (x^*, y^*, u_1^*, u_2^*)$ *of System (5) is globally asymptotically stable if it is locally asymptotically stable (Conditions (A1) stated in Appendix).*

Proof: The proof is similar to the proof of Theorem 2.10 considering

$$X = \{(x, y, u_1, u_2) \in \mathbb{R}^4 : \ x, \ y > 0, \ u_1, \ u_2 > 0\},$$

and the conditions of local stability of (x^*, y^*, u_1^*, u_2^*) are in Appendix. ■

Now, following the ideas presented in the preceding subsection, for values of $\sigma_i^2 \in (1, 2)$, $i = 1, 2$, one can show that the maps

$$F(x, y, u_1, u_2) = \Big(xe^{\alpha - u_1^2/2 - c_{11}(0)x - c_{12}y}, ye^{\beta - u_2^2/2 - c_{21}x - c_{22}(0)y},$$
$$(1 - \sigma_1^2)u_1 - \sigma_1^2 c_1 x, (1 - \sigma_2^2)u_2 - \sigma_2^2 c_2 y\Big),$$

and

$$G(x, y, u_1, u_2) = \Big(xe^{\alpha - u_1^2/2 - c_{11}(0)x - c_{12}y}, ye^{\beta - u_2^2/2 - c_{21}x - c_{22}(0)y},$$
$$(1 - \sigma_1^2)u_1 - \sigma_1^2 \hat{c}_1 x, (1 - \sigma_2^2)u_2 - \sigma_2^2 \hat{c}_2 y\Big)$$

are topologically conjugate by using the homeomorphism $h(x, y, u_1, u_2) = (x, y, -u_1, -u_2)$ and setting $c_i > 0$ and $\hat{c}_i = -c_i$, $i = 1, 2$. Therefore, we have the following result.

Theorem 2.16: *Assume that* $0 < \alpha, \beta < 1$, $\sigma_i^2 \in (1, 2)$ *and* $c_i > 0$, $i = 1, 2$. *Then the map* F *given in* (6) *is mixed monotone.*

Theorem 2.17: *The equilibrium point* $\mathbf{x}^* = (x^*, y^*, (u_1)_F^*, (u_2)_F^*)$ *of the Model (5) is globally asymptotically stable if it is locally asymptotically stable (Conditions A1) and* $0 < \alpha, \beta < 1$, $1 < \sigma_i^2 < 2$ *and* $c_i > 0$, $i = 1, 2$.

By applying Theorems 2.15–2.17, we have the following example.

Example 2.18: Let us consider the following values for the parameters

$$\alpha = 0.5, \quad \beta = 0.7, \quad \sigma_1^2 = 1.5, \quad \sigma_2^2 = 1.3, \quad c_1 = 2, \quad c_2 = 3;$$
$$c_{11} = c_{22} = 0.1, \quad c_{12} = c_{21} = 0.5.$$

Then the mapping is mixed monotone by Theorem 2.16 and the interior fixed point is

$$\mathbf{x}^* \approx (0.386667, 0.324621, -0.773334, -0.973863).$$

The coefficients of the characteristic polynomial of the Jacobian matrix of the mapping evaluated at $\mathbf{x}^*$ are

$$p_1 \approx 0.0111288, \ p_2 \approx 0.96765, \ p_3 \approx 0.169139 \text{ and } p_4 \approx 0.107545.$$

It is straightforward to verify that all the conditions (A1) of local stability are satisfied. Since all the conditions of Theorem 2.17 are satisfied, we have global stability of $\mathbf{x}^*$.

3. Periodic systems of Ricker type

In this section, we study the global behaviour of the periodic evolutionary Ricker system that is extended from the previous Section 2 by setting parameters being periodic. We start with the single-species and later on, we study the multi-species. First, we recall a general result of the asymptotic behaviour which is needed in this field.

3.1. Asymptotically periodic systems

Let $\mathbb{R}^n_+$ denote the cone of non-negative vectors in $\mathbb{R}^n$ and let $int(\mathbb{R}^n_+)$ and $\partial(\mathbb{R}^n_+)$ denote the interior and the boundary of $\mathbb{R}^n_+$, respectively. Let $G_t,\ F_t : \mathbb{R}^n_+ \longrightarrow \mathbb{R}^n_+$ to be continuous functions for all $t \in \mathbb{Z}_+$ and $t = 0, 1, \ldots, p$, such that $G_{t+p} = G_t$, for some $p \geq 1$. Assume that

$\boldsymbol{A_1}$ **:** F_t converges uniformly to G_t as $t \to \infty$.

Then $\mathbf{x}(0) \in \mathbb{R}^n_+$ implies that the solutions of the non-autonomous difference equation

$$\mathbf{x}(t+1) = F_t(\mathbf{x}(t)), \tag{7}$$

satisfies $\mathbf{x}(t) \in \mathbb{R}^n_+$, for all $t \in \mathbb{Z}_+$ where $\mathbf{x} = (x_1, x_2, \ldots, x_n) \in \mathbb{R}^n_+$.

The same is true for solutions of the limiting non-autonomous periodic equation

$$\mathbf{x}(t+1) = G_t(\mathbf{x}(t)), \tag{8}$$

where we assume

$\boldsymbol{A_2}$: $F_t : int(\mathbb{R}^n_+) \longrightarrow int(\mathbb{R}^n_+)$. The same is true for the maps G_t.

Theorem 3.1 ([14]): *Assume $\boldsymbol{A_1}$ and $\boldsymbol{A_2}$ and the limiting periodic Equation* (8) *has periodic cycle C_p of period p or a divisor of p in $\mathbb{R}^n_+$. If $C_p \in \mathbb{R}^n_+$ and if it is globally asymptotically stable on $int(\mathbb{R}^n_+)$, then all solutions of the non-autonomous difference equation with* $\mathbf{x}(0) \in$ *$int(\mathbb{R}^n_+)$ tend to C_p.*

3.2. Single-species periodic evolutionary models

In this section, we study the dynamical properties of the evolutionary periodic single-species model as follows:

$$\begin{cases} x(t+1) = x(t)e^{\alpha_t - u^2(t)/2 - c_0 x(t)} \\ u(t+1) = (1-\sigma^2)u(t) - \sigma^2 c_1 x(t) \end{cases}, \tag{9}$$

where $\sigma^2 < 2$, $c_0 > 0$, $c_1 \in \mathbb{R}$ and the sequence of parameter α_t is p-periodic , i.e. $\alpha_{t+p} = \alpha_t$ for all $t = 0, 1, 2, \ldots$, and some positive integer p greater than 1. This model may be represented by the non-autonomous periodic system $\{F_0, F_1, \ldots, F_{p-1}\}$, where

$$F_i(x,u) = \left(xe^{\alpha_i - u^2/2 - c_0 x}, (1-\sigma^2)u - c_1\sigma^2 x\right), \quad i = 0, 1, \ldots, p-1. \tag{10}$$

Notice that from the fact that $\alpha_{t+p} = \alpha_t$ we have $F_{i+p} = F_i$ for all i. This means that the minimum period of the system is p.

We will study first the properties of trivial cycles and later the interior cycle.

3.2.1. Global stability of trivial cycles

The origin is a fixed point of the p-periodic System (9) since it is a fixed point of each individual map F_i. Since the Jacobian of the composition map $\Phi_p = F_{p-1} \circ \ldots \circ F_1 \circ F_0$ is the product of the individual Jacobians, it follows that

$$J\Phi_p(0,0) = \prod_{i=0}^{p} \begin{pmatrix} e^{\alpha_t} & 0 \\ -c_1\sigma^2 & 1-\sigma^2 \end{pmatrix} = \begin{pmatrix} e^{\sum_{i=0}^{p-1}\alpha_t} & 0 \\ --- & (1-\sigma^2)^p \end{pmatrix}.$$

Consequently, the origin is a saddle fixed point of System (9). Thus we have the following result:

Theorem 3.2: *Let $\sigma^2 \in (0,2)$, $p > 1$ is a positive integer, and $\alpha_t > 0$, $t = 0,1,2,\ldots$, with $\alpha_{t+p} = \alpha_t$. Then the origin is a saddle fixed point of the p-periodic System (9).*

Similar to the autonomous case, under the scenario of $c_1 = 0$, from the equation $u(t+1) = (1-\sigma^2)u(t)$ we get $u(t) = (1-\sigma^2)^t u(0)$ and thus $u(t) \to 0$ as $t \to \infty$. Hence, the dynamics of the non-autonomous equation $x(t+1) = x(t)e^{\alpha_t - u_t^2/2 - c_0x(t)}$ converge to the dynamics of the periodic equation $x(t+1) = x(t)e^{\alpha_t - c_0x(t)}$, $\alpha_{t+p} = \alpha_t$. It has been proven by R. Sacker in [29] that the one-dimensional p-periodic Ricker equation $x(t+1) = x(t)e^{\alpha_t - c_0x(t)}$, $\alpha_{t+p} = \alpha_t$, has a globally asymptotically stable p-periodic cycle of the form $\{\bar{x}_0, \bar{x}_1, \ldots, \bar{x}_{p-1}\}$ whenever $\alpha_t \in (0,2)$. Notice that the condition of local stability is $\prod_{i=0}^{p-1}(1-\bar{x}_i) < 1$.

It is clear that if $c_1 = 0$ then p-periodic System (9) has a non-trivial p-periodic cycle of the form

$$C_p = \{(\bar{x}_0, 0), (\bar{x}_1, 0), \ldots, (\bar{x}_{p-1}, 0)\}.$$

It follows that

$$J\Phi_p(C_p) = \prod_{i=0}^{p} \begin{pmatrix} (1-\bar{x}_i)e^{\alpha_t - \bar{x}_i} & 0 \\ 0 & 1-\sigma^2 \end{pmatrix} = \begin{pmatrix} \prod_{i=0}^{p-1}(1-\bar{x}_i) & 0 \\ 0 & (1-\sigma^2)^p \end{pmatrix}$$

provided that $\sum_{t=0}^{p-1}\alpha_t = \sum_{t=0}^{p-1}\bar{x}_t$. Thus, by Theorem 3.1 we have the following result.

Theorem 3.3: *Let $\sigma^2 \in (0,2)$, $p > 1$ is a positive integer, and $0 < \alpha_t < 2$, $t = 0,1,2,\ldots$, such that $\alpha_{t+p} = \alpha_t$. Then the p-periodic evolutionary Ricker system*

$$\begin{cases} x(t+1) = x(t)e^{\alpha_t - u^2(t)/2 - c_0x(t)} \\ u(t+1) = (1-\sigma^2)u(t) \end{cases},$$

has a globally asymptotically stable p-periodic cycle of the form $\{(\bar{x}_0, 0), (\bar{x}_1, 0), \ldots, (\bar{x}_{p-1}, 0)\}$.

It should be noted that Sacker and Bremen conjectured in [30] that the global stability of the one-dimensional p-periodic Ricker model without evolution may occur if

$$\sum_{t=0}^{p-1}\alpha_t < 2p, \quad 0 < \alpha_t < 2 + \epsilon_p,$$

where ϵ_p is a positive number depending on p, $0 \le t \le p-1$. This conjecture was proven for $p = 2$. However, E. Liz showed in [22] that the region of the parameters may be

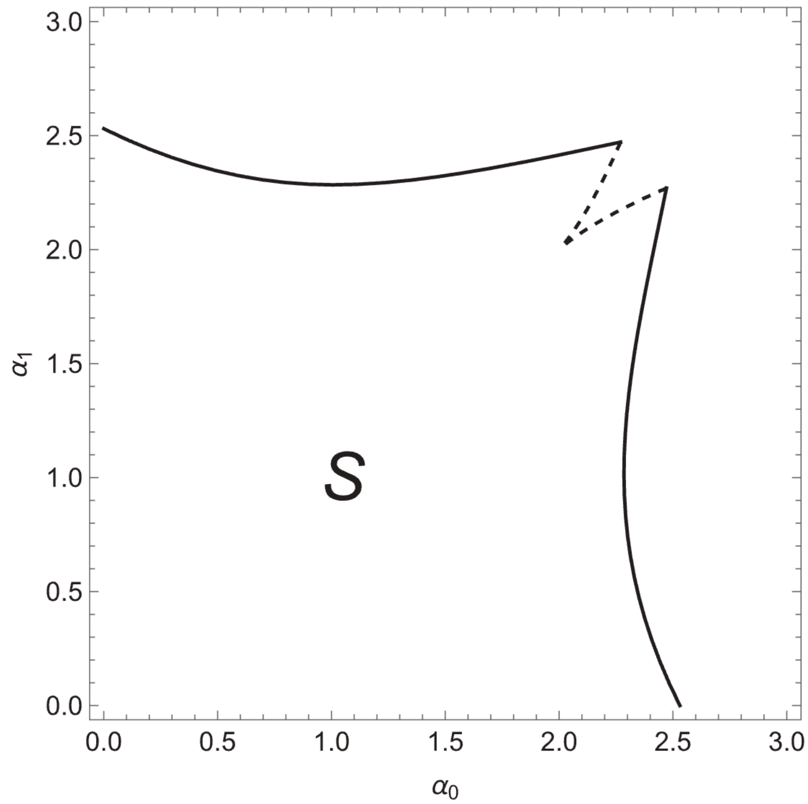

Figure 4. Region **S**, in the parameter space bifurcation diagram, where the one-dimensional 2-periodic Ricker equation $x_{t+1} = x_t e^{\alpha_t - c_0 x_t}$, $c_0 = 1$ and $\alpha_{t+2} = \alpha_t$, for all t, has a non-trivial globally asymptotically stable 2-periodic cycle. As the parameters cross the solid curves a period-doubling bifurcation takes place while when it crosses the dashed curves a saddle-node bifurcation takes place.

extended beyond $\alpha_0 + \alpha_1 < 4$. This fact may be observed in Region **S** in Figure 4. It remains an open problem to show this observation for a general value of $p > 2$.

3.2.2. Mixed monotonicity of systems

In the sequel, we assume that $c_1 \neq 0$ in order to study the properties of a non-trivial p-periodic cycle. We will split our study in two cases: (i) $c_1 > 0$ and (ii) $c_1 < 0$. We start with the case of $p = 2$. If one assumes that $0 < \alpha_t \leq 1$, $i = 0, 1$, $\sigma^2 \in (1, 2)$ and $c_1 > 0$, then from Section 2.1 it follows that each one of the individual maps $F_i : X \to X$, $i = 0, 1$ is a mixed monotone map on a metric space X with associated maps $f_i : X \times X \to X$, $i = 0, 1$. Define the map $\hat{f}_0 : X \times X \to X \times X$, by letting

$$\hat{f}_0((x_1, u_1), (x_2, u_2)) = (F_0(x_1, u_2), F_0(x_1, u_2)).$$

Then

$$\begin{aligned} g_2((x_1, u_1), (x_2, u_2)) &= f_1 \circ \hat{f}_0((x_1, u_1), (x_2, u_2)) = f_1(F_0(x_1, u_2), F_0(x_1, u_2)) \\ &= f_1\left(\left(x_1 e^{\alpha_0 - u_2^2/2 - x_1}, (1 - \sigma^2) u_2 - c_1 \sigma^2 x_1\right), \text{the same}\right) \end{aligned}$$

$$= F_1\left(x_1e^{\alpha_0-u_2^2/2-x_1}, (1-\sigma^2)u_2 - c_1\sigma^2x_1\right)$$
$$= F_1 \circ F_0(x_1, u_2).$$

Next, we are going to show that the composition map $g_2(\mathbf{x}_1, \mathbf{x}_2)$ is a mixed monotone map.

(i) Note that $g_2(\mathbf{x}, \mathbf{x}) = F_1 \circ F_0(\mathbf{x}), \mathbf{x} = (x, u)$;

(ii) Let $\mathbf{y} = (x, u)$ and $\mathbf{x}_i = (x_i, u_i), i = 1, 2$, such that $\mathbf{x}_1 \leq_{se} \mathbf{x}_2$. It is clear that

$$x_1e^{\alpha_0-u^2/2-c_0x_1} \leq x_2e^{\alpha_0-u^2/2-c_0x_2} \quad \text{and}$$
$$(1-\sigma^2)u - c_1\sigma^2x_2 \leq (1-\sigma^2)u - c_1\sigma^2x_1,$$

i.e.

$$\left(x_1e^{\alpha_0-u^2/2-c_0x_1}, (1-\sigma^2)u - c_1\sigma^2x_1\right) \leq_{se} \left(x_2e^{\alpha_0-u^2/2-c_0x_2}, (1-\sigma^2)u - c_1\sigma^2x_2\right).$$

Since $g_2(\mathbf{x}_i, \mathbf{y}) = f_1(F_0(x_i, u), F_0(x_i, u)) = F_1(x_ie^{\alpha_0-u^2/2-c_0x_i}, (1-\sigma^2)u - c_1\sigma^2x_i)$, $i = 1, 2$, it follows from the fact that F_1 is a mixed monotone map that

$$x_1e^{\alpha_0-u^2/2-c_0x_1}e^{\alpha_1-((1-\sigma^2)u-c_1\sigma^2x_1)^2/2-c_1\sigma^2x_1e^{\alpha_0-u^2/2-c_0x_1}}$$
$$\leq x_2e^{\alpha_0-u^2/2-c_0x_2}e^{\alpha_1-((1-\sigma^2)u-c_1\sigma^2x_2)^2/2-c_1\sigma^2x_2e^{\alpha_0-u^2/2-c_0x_2}}$$

and

$$(1-\sigma^2)\left((1-\sigma^2)u - c_1\sigma^2x_2\right) - c_1\sigma^2x_2e^{\alpha_0-u^2/2-c_0x_2}$$
$$\leq (1-\sigma^2)\left((1-\sigma^2)u - c_1\sigma^2x_1\right) - c_1\sigma^2x_1e^{\alpha_0-u^2/2-c_0x_1}.$$

Hence, we have

$$g_2(\mathbf{x}_1, \mathbf{y}) \leq_{se} g_2(\mathbf{x}_2, \mathbf{y}).$$

(iii) Let $\mathbf{x} = (x, u)$ and $\mathbf{y}_i = (x_i, u_i), i = 1, 2$, such that $\mathbf{y}_1 \leq_{se} \mathbf{y}_2$. In this case, we have

$$xe^{\alpha_0-u_2^2/2-c_0x} \leq xe^{\alpha_0-u_1^2/2-c_0x} \quad \text{and} \quad (1-\sigma^2)u_1 - c_1\sigma^2x \leq (1-\sigma^2)u_2 - c_1\sigma^2x$$

provide that $u_2 \leq u_1 < 0$ and $1 < \sigma^2 < 2$. Or equivalently,

$$\left(xe^{\alpha_0-u_2^2/2-c_0x}, (1-\sigma^2)u_2 - c_1\sigma^2x\right) \leq_{se} \left(xe^{\alpha_0-u_1^2/2-c_0x}, (1-\sigma^2)u_1 - c_1\sigma^2x\right).$$

Since $g(\mathbf{x}, \mathbf{y}_i) = F_1(xe^{\alpha_0-u_i^2/2-c_0x}, (1-\sigma^2)u_i - c_1\sigma^2x)$, $i = 1, 2$, it follows from the fact that F_1 is a mixed monotone map that

$$xe^{\alpha_0-u_2^2/2-c_0x}e^{\alpha_1-((1-\sigma^2)u_2-c_1\sigma^2x)^2/2-xe^{\alpha_0-u_2^2/2-c_0x}}$$
$$\leq xe^{\alpha_0-u_1^2/2-c_0x}e^{\alpha_1-((1-\sigma^2)u_1-c_1\sigma^2x)^2/2-xe^{\alpha_0-u_1^2/2-c_0x}}$$

and

$$(1-\sigma^2)\left((1-\sigma^2)u_1 - c_1\sigma^2 x\right) - c_1\sigma^2 x e^{\alpha_0 - u_1^2/2 - c_0 x}$$
$$\leq (1-\sigma^2)\left((1-\sigma^2)u_2 - c_1\sigma^2 x\right) - c_1\sigma^2 x e^{\alpha_0 - u_2^2/2 - c_0 x}.$$

Thus, we have that $g_2(\mathbf{x}, \mathbf{y}_2) \leq_{se} g_2(\mathbf{x}, \mathbf{y}_1)$.

Consequently, the composition of two mixed monotone maps of an evolutionary Ricker type is a mixed monotone map.

Generalizing the preceding ideas, one can define the composition operator Φ_i as

$$\Phi_i(x_1, u_2) = F_{i-1} \circ \ldots \circ F_1 \circ F_0(x_1, u_2), \quad i = 1, 2 \ldots, p,$$

and let the associated map $\hat{f}_i(\mathbf{x}_1, \mathbf{x}_2) = (\Phi_i(x_1, u_2), \Phi_i(x_1, u_2))$, one can use mathematical induction and show that

$$g_i(\mathbf{x}_1, \mathbf{x}_2) = f_{i-1} \circ \hat{f}_{i-1}(\mathbf{x}_1, \mathbf{x}_2) = \Phi_i(x_1, u_2), \quad i = 1, 2, \ldots, p,$$

is a mixed monotone map of evolutionary Ricker type.

We now summarize the preceding discussion in the following result:

Theorem 3.4: *Let $\sigma^2 \in (1, 2)$, $p > 1$ is a positive integer, $c_1 > 0$ and $0 < \alpha_t < 1$, $t = 0, 1, 2, \ldots$ with $\alpha_{t+p} = \alpha_t$. Then, the composition of p mixed monotone maps* (10) *of evolutionary Ricker type is a mixed monotone map.*

Using Lemma 2.8 of topological conjugacy one can prove the following result.

Theorem 3.5: *Let $\sigma^2 \in (1, 2)$, $p > 1$ is a positive integer, $c_1 < 0$ and $0 < \alpha_t < 1$, $t = 0, 1, 2, \ldots$ with $\alpha_{t+p} = \alpha_t$. Then, the composition of p mixed monotone maps* (10) *of evolutionary Ricker type is a mixed monotone map.*

3.2.3. Global stability of periodic cycles

In the sequel, we are going to focus on the stability analysis of the 2-periodic cycle of the periodic System (9) when $p = 2$.

Consider the difference equation

$$\mathbf{x}(t+1) = F(\mathbf{x}(t), \alpha_j) = F_j(\mathbf{x}(t)), \tag{11}$$

where $F : U \times G \to U$ is continuous, $U \subset \mathbb{R}^2_+$, $G \subset \mathbb{R}_+$ and $JF_j(\mathbf{x}) = JF(\mathbf{x}, \alpha_j)$ (the Jacobian matrix) is continuous on $\mathbb{R}^2_+ \times G$. We start our analysis with a perturbation result that is crucial in our investigation of the global stability of the periodic 2-cycle of a 2-periodic system.

In the sequel, we are going to use the notation of an open ball in a metric space X as $B(z, \delta) = \{x \in X : d(x, z) < \delta\}$ where d is the metric defined on X.

Theorem 3.6: *Let $\mathbf{x}_0^* = (x_0^*, u_0^*)$ be the interior equilibrium point of $F_0(\mathbf{x})$, i.e. $F(\mathbf{x}_0^*, \alpha_0) = \mathbf{x}_0^*$. Assume that $(\mathbf{x}_0^*, \alpha_0) \in U \times G$ and the spectral radius $\rho(JF(\mathbf{x}_0^*, \alpha_0)) < 1$ and $\mathbf{x}_0^*$ is globally asymptotically stable hyperbolic interior equilibrium point of* (11). *Then there exists*

$\delta > 0$ and a unique $\mathbf{x}^*(\alpha) \in U$ for $\alpha \in B(\alpha_0, \delta)$ such that $F(\mathbf{x}^*(\alpha), \alpha) = \mathbf{x}^*(\alpha)$ and $F^t(\mathbf{z}) \to \mathbf{x}^*(\alpha)$ as $t \to \infty$ for all $\mathbf{z} \in U$.

Proof: Since $\|JF(\mathbf{x}_0^*, \alpha_0^*))\| < \rho < 1$, and $JF(x, u)$ is continuous, there exists $\delta_1 > 0$ and $\eta > 0$ such that $\|JF(\mathbf{x}, \alpha))\| < \rho < 1$ for all $\mathbf{x} \in B(\mathbf{x}_0^*, \eta)$ and $\alpha \in B(\alpha_0, \delta_1)$. Choose $\delta_0 < \delta_1$ such that $\|F(\mathbf{x}_0^*, \alpha_0) - F(\mathbf{x}_0^*, \alpha)\| < (1-\rho)\eta$, for $\alpha \in B(\alpha_0, \delta_0)$. Thus for $\mathbf{x}_1, \mathbf{x}_2 \in \overline{B(\mathbf{x}_0^*, \eta)}$, $\alpha \in B(\alpha_0, \delta_0)$. Hence by the mean value theorem [21]

$$\|F(\mathbf{x}_1, \alpha) - F(\mathbf{x}_2, \alpha)\| \le \int_0^1 \|JF(s\mathbf{x}_1 + (1-s)\mathbf{x}_2, \alpha)ds\|\mathbf{x}_1 - \mathbf{x}_2\| \le \rho|\mathbf{x}_1 - \mathbf{x}_2\|,$$

and

$\|F(\mathbf{x}_1, \alpha) - F(\mathbf{x}_0^*, \alpha_0)\| \le \|F(\mathbf{x}_1, \alpha) - F(\mathbf{x}_0^*, \alpha)\| + \|F(\mathbf{x}_0^*, \alpha) - F(\mathbf{x}_0^*, \alpha_0)\| \le \rho\|\mathbf{x}_1 - \mathbf{x}_0\| + (1-\rho)\eta$. Thus the map $F(\mathbf{x}, \alpha)$ is a uniform contraction self-map. By the contraction mapping principle [21] there is a continuous function $h : B(\alpha_0, \delta_0) \to \overline{B(\mathbf{x}_0^*, \eta)}$ such that $F(h(\alpha), \alpha) = h(\alpha) = \mathbf{x}^*(\alpha)$ and $h(\alpha_0) = \mathbf{x}_0^*$, and $\lim_{t\to\infty} F_\alpha^t(\mathbf{x}) = h(\alpha) = \mathbf{x}^*(\alpha)$ for all $\mathbf{x} \in \overline{B(\mathbf{x}_0^*, \eta)}$ and $\alpha \in B(\alpha_0, \delta_0)$.

We claim that for sufficiently small δ_0, for all $\alpha \in B(\alpha_0, \delta_0)$ and $\mathbf{x} \in \overline{B(\mathbf{x}_0^*, \eta)}$, $F_\alpha^m(\mathbf{x}) \in B(\mathbf{x}_0^*, \eta)$, for some positive integer m. If not, then there exist sequence $\{\alpha_n\}$ converging to α_0, and $\{\mathbf{x}_n\}$ converging to $\mathbf{x}$, such that $\|F_{\alpha_n}^t(\mathbf{x}) - \mathbf{x}_0^*\| \ge \eta$ for all $t \ge 0$. Since $\mathbf{x}^*(\alpha_0)$ is globally asymptotically stable under the map F_{α_0}, it follows that $\|F_{\alpha_0}^m(\mathbf{x}) - \mathbf{x}_0^*\| < \eta/2$, $h(\mathbf{x}, \alpha) = F_\alpha^m(\mathbf{x})$. By the continuity of the map F, we have $\lim_{n\to\infty} F^m(\mathbf{x}_n, \alpha_n) = F^m(\mathbf{x}, \alpha_0)$. Hence $\|F_{\alpha_n}^m(\mathbf{x}_n) - \mathbf{x}_0^*\| \le \|F_{\alpha_n}^m(\mathbf{x}_n) - F_{\alpha_0}^m(\mathbf{x})\| + \|F_{\alpha_0}^m(\mathbf{x}) - \mathbf{x}_0^*\| < \eta$, for large n, a contradiction. Thus given $\mathbf{x} \in D$, where D is the absorbing region of $\mathbf{x}^*(\alpha_0)$, and $\alpha \in B(\alpha_0, \delta_0)$, there exists large N such that $F_\alpha^t(\mathbf{x}) \in B(\mathbf{x}_0^*, \eta)$ for all $t \ge N$. Hence $\lim_{t\to\infty} F_\alpha^t(\mathbf{x}) = h(\alpha) = \mathbf{x}^*(\alpha)$. ■

Theorem 3.7 (Global stability of the 2-periodic system): *Assume the conditions given in Corollary 2.12, in which $\alpha = \alpha_0$. Then for sufficiently small $\delta > 0$ and letting $\alpha_1 = \alpha_0 \pm \delta$, there is a 2-periodic cycle which is globally asymptotically stable in the interior of the first quadrant if $c_1 < 0$ and in the interior of the fourth quadrant if $c_1 > 0$.*

Proof: We apply the preceding perturbation theorem to the system (1), where we fix all the parameters except α. Then by Theorems 3.4 and 3.5, F^2 is a mixed monotone map. Assuming the conditions given in Corollary 2.12, where $\alpha = \alpha_0$, the interior equilibrium point $\mathbf{x}^*(\alpha_0) = (x^*(\alpha_0), u^*(\alpha_0))$ is globally asymptotically stable with respect to the interior of either the first quadrant (if $c_1 < 0$) or the interior of the fourth quadrant (if $c_1 > 0$).

Let us now consider the second iteration $F^2 = F \circ F$ of the map F of the system (1). We perturb F^2 and write it as the composition of two maps $G = F_1 \circ F_0$, where $F_0 = F$, in which $\alpha = \alpha_0$, and $F_1(x, u) = (xe^{\alpha_1 - u^2/2 - c_0 x}, (1-\sigma^2)u - c_1\sigma^2 x)$ where $\alpha_1 = \alpha_0 \pm \delta$. Using Theorem 3.6, there is an interior 2-periodic cycle that is globally asymptotically stable. ■

Example 3.8: Let $c_0 = 1$, $\sigma^2 = 1.5$, $c_1 = 2$ and $\alpha_0 = 0.3$. Then, from Example 2.13, the fixed point $(0.210977, -0.421954)$ is a globally asymptotically stable fixed point of the

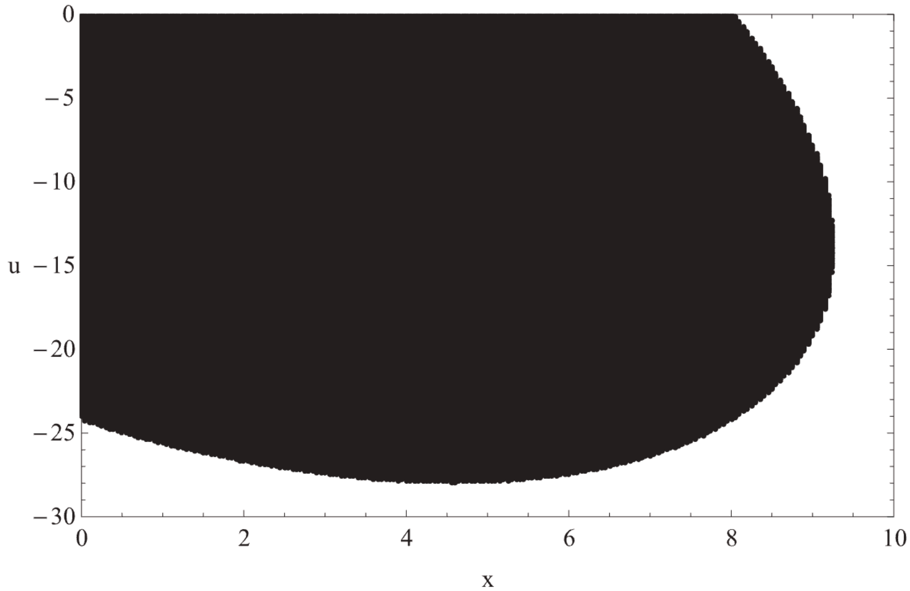

Figure 5. An absorbing region of the 2-periodic cycle in Example 3.8.

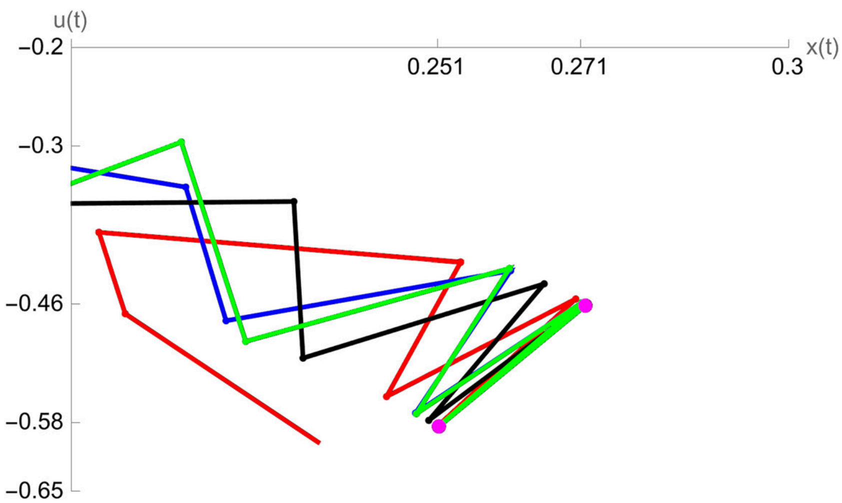

Figure 6. Phase-space diagram for the 2-periodic cycle in Example 3.8.

map F_0, where $F_0(x,u) = (xe^{0.3-u^2/2-x}, -0.5u - 2\sigma^2 x)$. By Theorem 3.4 the mapping F_0^2 is mixed monotone. Now, letting $\alpha_1 = \alpha_0 + 0.2 = 0.5$, we have that

$$C_2 = \{(\bar{x}(0), \bar{u}(0)), (\bar{x}(1), \bar{u}(1))\} \approx \{(0.271644, -0.461582), (0.251217, -0.58414)\}$$

is a (locally stable) 2-periodic cycle of System (9), where the composition map is $G = F_1 \circ F_0$ with $F_1(x,u) = (xe^{0.5-u^2/2-x}, -0.5u - 2\sigma^2 x)$.

Figure 5 shows the absorbing region of the 2-periodic cycle C_2 with given α_0 and α_1. Moreover, Figure 6 illustrates Theorem 3.7 showing that, for sufficiently small $\delta > 0$, the cycle C_2 is globally asymptotically stable in the interior of the fourth quadrant.

Theorem 3.9 (global stability of the p-periodic system): *Assume the conditions given in Corollary 2.12, in which $\alpha = \alpha_0$. Then for sufficiently small $\delta_i > 0$ and letting $\alpha_{i+1} = \alpha_i \pm \delta_i$, $i = 0, 1, \dots, p-2$ such that $0 < \alpha_0 \pm \sum_{i=0}^{p-2} \delta_i < 1$, there is a p-periodic cycle which is globally asymptotically stable in the interior of the first quadrant if $c_1 < 0$ and in the interior of the fourth quadrant if $c_1 > 0$.*

Proof: Similarly to the case $p = 2$, we use the preceding perturbation theorem to the system (1), where we fix all the parameters except α.

By Theorems 3.4 and 3.5, the composition map F^p is mixed monotone. Assuming the conditions given in Corollary 2.11, where $\alpha = \alpha_0$, the interior equilibrium point $\mathbf{x}^*(\alpha_0) = (x^*(\alpha_0), u^*(\alpha_0))$ is globally asymptotically stable with respect to the interior of either the first quadrant (if $c_1 < 0$) or the interior of the fourth quadrant (if $c_1 > 0$).

Now, we perturb F^p and write it as the composition of p maps $G = F_{p-1} \circ \dots \circ F_1 \circ F_0$, where $F_0 = F$, in which $\alpha_0 = \alpha$, and $F_i(x, u) = (xe^{\alpha_i - u^2/2 - c_0 x}, (1-\sigma^2)u - c_1\sigma^2 x)$ where $\alpha_{i+1} = \alpha_i \pm \delta$, $i = 0, 1, \dots, p-2$, such that $0 < \alpha_0 \pm \sum_{i=0}^{p-2} \delta_i < 1$. Using Theorem 3.6, there exists an interior p-periodic cycle that is globally asymptotically stable. ■

Proposition 3.10: *Let and $c_1 \neq 0$ and assume that $p > 1$ is a positive integer and $\alpha_{t+p} = \alpha_t$, for $t = 0, 1, 2, \dots$. If*

$$C_p = \{(\bar{x}(0), \bar{u}(0)), (\bar{x}(1), \bar{u}(1)), \dots, (\bar{x}(p-1), \bar{u}(p-1))\}$$

is a p-periodic cycle of System (9), then

$$\sum_{i=0}^{p-1} \bar{u}(i) = -c_1 \sum_{i=0}^{p-1} \bar{x}(i).$$

Proof: From the second equation in (9) we get

$$\bar{u}(i+1) = (1-\sigma^2)\bar{u}(i) - \sigma^2 c_1 \bar{x}(i), \quad i = 0, 1, 2 \dots.$$

Taking sums in both sides we obtain

$$\sum_{i=0}^{p-1} \bar{u}(i+1) = (1-\sigma^2) \sum_{i=0}^{p-1} \bar{u}(i) - \sigma^2 c_1 \sum_{i=0}^{p-1} \bar{x}(i).$$

Now, since $\bar{u}(p) = \bar{u}(0)$ we have $\sum_{i=0}^{p-1} \bar{u}(i+1) = \sum_{i=0}^{p-1} \bar{u}(i)$. Thus, by simplifying the precedent equality we obtain the result. ■

3.3. Two-species periodic evolutionary models

Consider now the two-species non-autonomous periodic evolutionary Ricker model given by

$$\begin{cases} x(t+1) = x(t)e^{\alpha_t - u_1^2(t)/2 - c_{11}(0)x(t) - c_{12}y(t)} \\ y(t+1) = y(t)e^{\beta_t - u_2^2(t)/2 - c_{21}x(t) - c_{22}(0)y(t)} \\ u_1(t+1) = (1-\sigma_1^2)u_1(t) - \sigma_1^2 c_1 x(t) \\ u_2(t+1) = (1-\sigma_2^2)u_2(t) - \sigma_2^2 c_2 y(t) \end{cases}, \tag{12}$$

where we assume that $\alpha_{t+p} = \alpha$ and $\beta_{t+p} = \beta_t$ for all $t = 0, 1, 2, \dots$ and for some $p > 1$.

The p-periodic system (12) may be represented by the sequence of maps $F_i : \mathbb{R}^4 \to \mathbb{R}^4$ given by

$$F_i(x, y, u_1, u_2) = \Big(xe^{\alpha_i - u_1^2/2 - c_{11}(0)x - c_{12}y}, ye^{\beta_i - u_2^2/2 - c_{21}x - c_{22}(0)y}, \\ (1-\sigma_1^2)u_1 - \sigma_1^2 c_1 x, (1-\sigma_2^2)u_2 - \sigma_2^2 c_2 y\Big). \quad (13)$$

Notice that the dynamics of the system (12) is completely determined by the composition operator

$$\Phi_p(x, y, u_1, u_2) = F_{p-1} \circ \ldots \circ F_1 \circ F_0(x, y, u_1, u_2).$$

3.3.1. Global stability of the trivial cycles

The Jacobian of Φ_p is given by

$$J\Phi_p(x, y, u_1, u_2) = \prod_{i=0}^{p-1} \begin{pmatrix} (1-c_{11}x)A & -c_{12}xA & -u_1xA & 0 \\ -c_{21}yB & (1-c_{22}y)B & 0 & -u_2yB \\ -c_1\sigma_1^2 & 0 & 1-\sigma_1^2 & 0 \\ 0 & -c_2\sigma_2^2 & 0 & 1-\sigma_2^2 \end{pmatrix},$$

where $A = e^{\alpha_i - u_1^2/2 - c_{11}x - c_{12}y}$ and $B = e^{\beta_i - u_2^2/2 - c_{21}x - c_{22}y}$.

Theorem 3.11: *Let $\sigma_i \in (0, 2)$, $i = 1, 2$, $p > 1$ is a positive integer, and α_t, $\beta_t > 0$, $t = 0, 1, 2, \ldots$, with $\alpha_{t+p} = \alpha_t$ and $\beta_{t+p} = \beta_t$. Then origin is a saddle fixed point of the p-periodic System (12).*

Proof: The origin $\mathbf{O}$ is a fixed point of Φ_p since it is a fixed point of the sequence of maps F_i. Now, the eigenvalues of $J\Phi_p(\mathbf{O})$ are $\lambda_1 = \sum_{i=0}^{p-1} e^{\alpha_i}$, $\lambda_2 = \sum_{i=0}^{p-1} e^{\beta_i}$, $\lambda_3 = (1-\sigma_1^2)^p$ and $\lambda_4 = (1-\sigma_2^2)^p$. Clearly λ_1, $\lambda_2 > 1$ and $-1 < \lambda_3$, $\lambda_4 < 1$. Hence the origin is a saddle fixed point. ∎

Now, if $c_i = 0$, $i = 1, 2$, from the equations $u_i(t+1) = (1-\sigma^2)u_i(t)$, $i = 1, 2$ we get $u_i(t) = (1-\sigma^2)^t u_i(0)$ and thus $u_i(t) \to 0$ as $t \to \infty$. Hence, from Theorem 3.1 the dynamics of the non-autonomous subsystem

$$\begin{cases} x(t+1) = x(t)e^{\alpha_t - u_1^2(t)/2 - c_{11}(0)x(t) - c_{12}y(t)} \\ y(t+1) = y(t)e^{\beta_t - u_2^2(t)/2 - c_{21}x(t) - c_{22}(0)y(t)} \end{cases}, \quad (14)$$

converge to the dynamics of the periodic system

$$\begin{cases} x(t+1) = x(t)e^{\alpha_t - c_{11}(0)x(t) - c_{12}y(t)} \\ y(t+1) = y(t)e^{\beta_t - c_{21}x(t) - c_{22}(0)y(t)} \end{cases}. \quad (15)$$

It has been proven by Balreira and Luís in [6] that the two-dimensional p-periodic Ricker system (15) has a globally asymptotically stable p-periodic cycle of the form $\{(\bar{x}_0, \bar{y}_0), (\bar{x}_1, \bar{y}_1), \ldots, (\bar{x}_{p-1}, \bar{y}_{p-1})\}$ whenever $\alpha_t, \beta_t \in (0, 1)$.

It is clear that if $c_i = 0$, $i = 1, 2$, then p-periodic System (12) has a p-periodic cycle of the form

$$C_p = \{(\overline{x}_0, \overline{y}_0, 0, 0), (\overline{x}_1, \overline{y}_0, 0, 0), \dots, (\overline{x}_{p-1}, \overline{y}_0, 0, 0)\}.$$

The Jacobian matrix $J\Phi_p$ evaluated along the cycle C_p has four eigenvalues, two of which are the same as the Jacobian matrix of the globally asymptotically stable p-periodic cycle of the system (15) and the other two are $(1-\sigma_1^2)^p$ and $(1-\sigma_2^2)^p$. Hence, using Theorem 3.1 we have the following result:

Theorem 3.12: *Let $c_i = 0$, $\sigma_i \in (0, 2)$, $i = 1, 2$ and $0 < \alpha_t$, $\beta_t < 1$ such that $\alpha_{t+p} = \alpha_t$ and $\beta_{t+p} = \beta_t$, for all $t = 0, 1, 2, \dots$ and $p > 1$. Then, C_p is a globally asymptotically stable p-periodic cycle of the p-periodic System (12).*

3.3.2. Mixed monotonicity of systems

We assume that $c_i \neq 0$, $i = 1, 2$. Our goal is to study the properties of a non-trivial interior p-periodic cycle of System (12). Similarly to the case of the previous subsection, we are going to prove that the composition of mixed monotone maps (13) is a mixed monotone map.

We start with the case of $p = 2$. If one assume that $0 < \alpha_i$, $\beta_i < 1$, $i = 0, 1$, $\sigma^2 \in (1, 2)$ and $c_i < 0$, from Section 2.2 it follows that each one of the individual maps $F_i : \mathbb{R}^4 \to \mathbb{R}^4$, $i = 0, 1$ is mixed monotone map on a metric space $\mathbb{R}^4$ with associated maps $f_i : \mathbb{R}^4 \times \mathbb{R}^4 \to \mathbb{R}^4$, $i = 0, 1$. Define the map $\hat{f}_0 : \mathbb{R}^4 \times \mathbb{R}^4 \to \mathbb{R}^4 \times \mathbb{R}^4$, by letting

$$\hat{f}_0((x_1, y_1, u_1^1, u_2^1), (x_2, y_2, u_1^2, u_2^2)) = (F_0(x_1, y_1, u_1^2, u_2^2), F_0(x_1, y_1, u_1^2, u_2^2)).$$

Then setting $\mathbf{x}_1 = ((x_1, y_1, u_1^1, u_2^1))$ and $\mathbf{x}_2 = (x_2, y_2, u_1^2, u_2^2)$ we have

$$\begin{aligned} g_2(\mathbf{x}_1, \mathbf{x}_2) &= f_1 \circ \hat{f}_0(\mathbf{x}_1, \mathbf{x}_2) = f_1(F_0(x_1, y_1, u_1^2, u_2^2)), F_0(x_1, y_1, u_1^2, u_2^2))) \\ &= f_1\left(\left(x_1\tilde{A}, y_1\tilde{B}, (1-\sigma_1^2)u_1^2 - \sigma_1^2 c_1 x_1, (1-\sigma_2^2)u_2^2 - \sigma_2^2 c_2 y_1\right), \text{the same}\right) \\ &= F_1\left(x_1\tilde{A}, y_1\tilde{B}, (1-\sigma_1^2)u_1^2 - \sigma_1^2 c_1 x_1, (1-\sigma_2^2)u_2^2 - \sigma_2^2 c_2 y_1\right) \\ &= F_1 \circ F_0(x_1, u_2), \end{aligned}$$

where $\tilde{A} = e^{\alpha_0 - (u_1^2)^2/2 - c_{11}(0)x_1 - c_{12}y_1}$ and $\tilde{B} = e^{\beta_0 - (u_2^2)^2/2 - c_{21}x_1 - c_{22}(0)y_1}$.

It is a straightforward computation to show that $g_2(\mathbf{x}_1, \mathbf{x}_2)$ is a mixed monotone map.

Now, generalizing this process, one can define the composition operator Φ_i as

$$\Phi_i(x_1, y_1, u_1^2, u_2^2) = F_{i-1} \circ \dots \circ F_1 \circ F_0(x_1, y_1, u_1^2, u_2^2), \quad i = 1, 2 \dots, p,$$

and letting the associated map $\hat{f}_i(\mathbf{x}_1, \mathbf{x}_2) = (\Phi_i(x_1, y_1, u_1^2, u_2^2), \Phi_i(x_1, y_1, u_1^2, u_2^2))$, one can use mathematical induction and show that

$$g_i(\mathbf{x}_1, \mathbf{x}_2) = f_{i-1} \circ \hat{f}_{i-1}(\mathbf{x}_1, \mathbf{x}_2) = \Phi_i(x_1, y_1, u_1^2, u_2^2), \quad i = 1, 2, \dots, p,$$

is a mixed monotone map of evolutionary Ricker type.

Theorem 3.13: *Let $c_i < 0, \sigma_i \in (1, 2), i = 1, 2, p > 1$ is a positive integer, and $0 < \alpha_t, \beta_t < 1$ such that $\alpha_{t+p} = \alpha_t$ and $\beta_{t+p} = \beta_t$, for all $t = 0, 1, 2, \ldots$. The composition of p mixed monotone maps (13) of evolutionary Ricker type is a mixed monotone map.*

Now, using Lemma 2.8 of topological conjugacy one can also prove that the composition of p mixed monotone maps (13) of evolutionary Ricker type is a mixed monotone map of evolutionary Ricker type when $c_i > 0, i = 1, 2$.

Theorem 3.14: *Let $c_i > 0, \sigma_i \in (1, 2), i = 1, 2, p > 1$ is a positive integer, and $0 < \alpha_t, \beta_t < 1$ such that $\alpha_{t+p} = \alpha_t$ and $\beta_{t+p} = \beta_t$, for all $t = 0, 1, 2, \ldots$. The composition of p mixed monotone maps (13) of evolutionary Ricker type is a mixed monotone map.*

3.3.3. Global stability of periodic cycles

In this subsection, we study the global stability of a p-periodic cycle of System (12) via perturbation theory. We will follow the techniques introduced in Section 3.2.3.

Now, let us consider the difference equation

$$\mathbf{x}(t+1) = F(\mathbf{x}(t), \gamma_j) = F_j(\mathbf{x}(t)), \quad \mathbf{x}(t+1) = F(\mathbf{x}(t), \alpha) = F_\alpha(\mathbf{x}_\alpha), \tag{16}$$

where $F : U \times G \to U$ is continuous, $U \subset \mathbb{R}^4_+$, $\gamma_j = (\alpha_j, \beta_j) \in G \subset \mathbb{R}^2_+$ and $JF_j(\mathbf{x}) = JF(\mathbf{x}, \gamma_j)$ (the Jacobian matrix) is continuous on $\mathbb{R}^4_+ \times G$. The perturbation result is as follows:

Theorem 3.15: *Let $\mathbf{x}^*_0 = (x^*(0), y^*(0), u^*_1(0), u^*_2(0))$ be the interior equilibrium point of $F_0(\mathbf{x})$, i.e. $F(\mathbf{x}^*_0, \gamma_0) = \mathbf{x}^*_0$. Assume that $(\mathbf{x}^*_0, \gamma_0) \in U \times G$ and the spectral radius $\rho(JF_0(\mathbf{x}^*_0)) < 1$ and $\mathbf{x}^*_0$ is globally asymptotically stable hyperbolic interior equilibrium point of (16). Then there exists $\delta > 0$ and a unique $\mathbf{x}^*(\gamma) \in U$ for $\gamma \in B(\gamma_0, \delta)$ such that $F(\mathbf{x}^*(\gamma), \gamma) = \mathbf{x}^*(\gamma)$ and $F^t(\mathbf{z}) \to \mathbf{x}^*(\gamma)$ as $t \to \infty$ for all $\mathbf{z} \in U$.*

Proof: The proof is similar to the proof of Theorem 3.6 and will be omitted. ■

Theorem 3.16: *Assume the conditions given in Theorems 2.15 and 2.17 and set $\gamma_i = (\alpha_i, \beta_i)$. Then for sufficiently small $\delta_i > 0$ and letting $\gamma_{i+1} = \gamma_i \pm \delta_i$, $i = 0, 1, \ldots, p-2$ such that $0 < \alpha_0 \pm \sum_{i=0}^{p-2} \delta_i < 1$ and $0 < \beta_0 \pm \sum_{i=0}^{p-2} \delta_i < 1$, there is a p-periodic cycle of (12) which is globally asymptotically stable in the interior of $\mathbb{R}^2_+ \times \mathbb{R}^2_+$ if $(c_1, c_2) \in \mathbb{R}^2_-$ and in the interior of of $\mathbb{R}^2_+ \times \mathbb{R}^2_-$ if $(c_1, c_2) \in \mathbb{R}^2_+$.*

Proof: The proof is similar to the proof of Theorems 3.7 and 3.9 and will be omitted. ■

Example 3.17: Let us consider the following values $\alpha_0 = 0.5$, $\beta_0 = 0.7$, $\delta_0 = 0.02$, $\delta_1 = 0.015$, $\sigma_1^2 = 1.5$, $\sigma_2^2 = 1.3$, $c_1 = 2$, $c_2 = 3$; $c_{11} = c_{22} = 0.1$ and $c_{12} = c_{21} = 0.5$. Setting $\alpha_{i+1} = \alpha_i - \delta_i$ and $\beta_{i+1} = \beta_i + \delta_i$, we have $\alpha_1 = 0.48$, $\alpha_2 = 0.465$, $\beta_1 = 0.72$ and $\beta_2 = 0.735$. Let $\alpha_{j+3} = \alpha_j$ and $\beta_{j+3} = \beta_j$ for all $j = 0, 1, 2, \ldots$.

From Example 2.18, we know that $\mathbf{x}^* \approx (0.386667, 0.324621, -0.773334, -0.973863)$ is a globally asymptotically stable fixed point of the map F_0. By Theorem 3.14, F_0^3 is mixed monotone map. It follows that

$$C_3 \approx \{(0.374371, 0.335204, -0.722071, -1.01674), (0.379751, 0.329361, -0.782082, -0.997936), (0.363593, 0.334088, -0.731276, -0.981284)\}$$

is a (locally stable) 3-periodic cycle of the System (12), where the composition map is $G = F_2 \circ F_1 \circ F_0$. Using a specific software, such as Mathematica or Maple, we are able to verify the conditions of Theorem 3.17, i.e. for sufficiently small $\delta_i > 0$, all orbits are attracted to c_3, meaning that the cycle C_3 is globally asymptotically stable in the interior of $\mathbb{R}^2_+ \times \mathbb{R}^2_-$.

Proposition 3.18: *Let $c_i \neq 0$, $\sigma_i \in (1, 2)$, $i = 1, 2$ and $0 < \alpha_t,\ \beta_t < 1$ such that $\alpha_{t+p} = \alpha_t$ and $\beta_{t+p} = \beta_t$, for all $t = 0, 1, 2, \dots$ and $p > 1$. Assume that*

$$C_p = \{(\bar{x}(0), \bar{y}(0), \bar{u}_1(0), \bar{u}_2(0)), \dots, (\bar{x}(p-1), \bar{y}(p-1), \bar{u}_1(p-1), \bar{u}_2(p-1))\}$$

is a p-periodic cycle of System (12). Then

$$\sum_{i=0}^{p-1} \bar{u}_1(i) = -c_1 \sum_{i=0}^{p-1} \bar{x}(i) \text{ and } \sum_{i=0}^{p-1} \bar{u}_2(i) = -c_2 \sum_{i=0}^{p-1} \bar{y}(i).$$

Proof: The proof is similar to the proof of Proposition 3.10 and will be omitted. ∎

4. Conclusion, open problems and conjectures

This paper investigated the global dynamics of evolutionary Ricker competition models. We developed the theory of mixed monotone maps and used it to show that the positive equilibrium of the autonomous evolutionary Ricker model of single and multi-species is globally asymptotically stable. Then we extend this result to the periodic evolutionary Ricker model. We also showed that small perturbations, that lead to periodic systems, will not change the dynamics of the species. There are still many open problems that we will state here and make conjectures regarding them.

Problem 4.1: We have shown that the evolutionary models do not exhibit saddle-node bifurcation just as evolutionary models. Moreover, evolutionary models and non-evolutionary models may exhibit period-doubling bifurcation. However, in contrast to non-evolutionary models, evolutionary models may exhibit a Neimark–Sacker bifurcation. A thorough investigation of the bifurcation theory of evolutionary models is still an open problem. However, for the special case of the evolutionary Leslie–Gower model, Ch-Chaoui and Mokni [7] did study the Neimark–Sacker bifurcation.

Problem 4.2: The global stability of autonomous and periodic evolutionary models with multiple traits is still an open problem.

Problem 4.3: In this paper, we restricted our investigation to the case when the growth rates of the populations α and β is between 0 and 1. For non-evolutionary models,

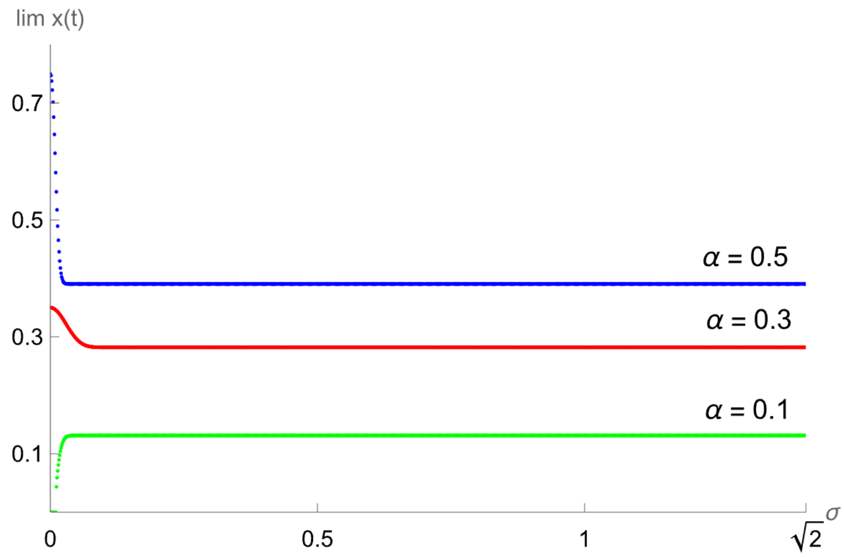

Figure 7. Values of the first component of the family of fixed points (x^*, u^*) for model (1) depending on σ. In this case we use $c_0 = 0.5$ and $c_1 = 2$.

it has been shown by Baigent et al. [5] that the interior equilibrium point is globally asymptotically stable if $0 < \alpha,\ \beta < 2$. Are our results extendable to this general case?

Problem 4.4: In the case of two evolutionary species, we have shown global stability when either $c_i > 0$ or $c_i < 0$, $i = 1, 2$. What happens if $c_1 \times c_2 < 0$?

Conjecture 4.5: Our study was restricted for the case when the speed of evolution σ^2 is restricted to $1 < \sigma^2 < 2$. Based in several simulations (see Figure 7 for three cases), we conjecture that our global stability results for both autonomous and periodic are valid for the case $\sigma^2 < 1$.

Conjecture 4.6: We conjecture that our results may be extended to predator–prey models and host-parasitoid models.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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Appendix. Local stability conditions in 4-dimensional system

Let $JF(\mathbf{x}^*)$ be the Jacobian matrix of the map (6) evaluated at the interior fixed point $\mathbf{x}^* = (x^*, y^*, u_1^*, u_2^*)$ where $x^* > 0$ and $y^* > 0$ with $u_1^* = -c_1 x^*$ and $u_2^* = -c_2 y^*$. The characteristic equation of $JF(\mathbf{x}^*)$ can be written in the form

$$\lambda^4 + p_1\lambda^3 + p_2\lambda^2 + p_3\lambda + p_4 = 0,$$

where

$$p_1 = -\mathrm{tr}\left(JF(\mathbf{x}^*)\right), \quad p_2 = \sum_{1\le i\le j}^{4} JF_{ij}(\mathbf{x}^*), \quad p_3 = -\sum_{i=1}^{4} JF_i(\mathbf{x}^*), \quad p_4 = \det(JF(\mathbf{x}^*)),$$

and det is the determinant of the Jacobian matrix, $JF_i(\mathbf{x}^*)$ is the 3×3 determinant of the 3 sub-matrices JF_i obtained from JF by deleting the i row and the i column, $\sum_{1\le i\le j}^{4} JF_{ij}(\mathbf{x}^*)$ is the 2×2 determinant of the 6 sub-matrix JF_{ij} obtained from JF by deleting the i and j rows and the i and j columns and tr is the trace of the Jacobian matrix. (For more details, see [23] .)

It is well known that all the roots of the characteristic equation lie inside the unit disk [23] if

$$\begin{aligned} \text{Necessary Conditions} : &|p_1 + p_3| < 1 + p_2 + p_4, \\ \text{SufficientConditions} : &|p_4| < 1, \quad |p_1p_4 - p_3| < 1 - p_4^2 \\ &|(p_4^2 - 1)^2 - (p_4p_1 - p_3)^2| \\ &\quad > |(p_4^2 - 1)p_2(p_4 - 1) - (p_3p_4 - p_1)(p_1p_4 - p_3)|. \end{aligned} \tag{A1}$$