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DYNAMICS OF NON-AUTONOMOUS DISCRETE SYSTEMS WITH APPLICATIONS TO EVOLUTIONARY DYNAMICS

Susan Trolle
University of Rhode Island, susan_trolle@uri.edu

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DYNAMICS OF NON-AUTONOMOUS DISCRETE SYSTEMS WITH
APPLICATIONS TO EVOLUTIONARY DYNAMICS

BY
SUSAN TROLLE

A DISSERTATION SUBMITTED IN PARTIAL FULFILLMENT OF THE
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DOCTOR OF PHILOSOPHY DISSERTATION
OF
SUSAN TROLLE

APPROVED:

Dissertation Committee:

Major Professor Mustafa Kulenović

Michael Barrus

Peter Nightingale

Brenton DeBoef

DEAN OF THE GRADUATE SCHOOL

UNIVERSITY OF RHODE ISLAND

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ABSTRACT

This dissertation focuses on difference equations that are of a certain type, non-autonomous competitive and cooperative systems. Previously, systems of this nature were investigated for the single species model. Here, this investigation extends to the case of two species or more, corresponding to a two dimensional system all the way to an n dimensional system. The purpose is to establish global attractivity results for these systems through a method using difference inequalities along with Northeast and Southeast partial ordering for competitive and cooperative systems, respectively. The non-autonomous case of some systems, established and well-known, are discussed for purpose of comparing the process in which global results are achieved. Finally, these systems will be applied to evolutionary dynamics by creating an evolutionary model of the system using an original process.

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DEDICATION

*To My Professor:
Dr. Benjamin Fine
1948 - 2023*

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CHAPTER 1

Introduction

Dynamical systems are systems in which the state variables change according to time. Biological systems are one type of dynamical system. Dynamical systems are typically modeled using difference equations or differential equations and there is an important distinction between the two. A system that changes continuously is modeled by differential equations and is called a continuous dynamical system. An example of this would be the flight of a bird. Difference equations are discrete dynamical systems that are used to model changes in a species' population density with each generation disjoint from the other. For this thesis, the focus will be on difference equations, particularly a special class of equations, called non-autonomous, for both competitive and cooperative systems. These systems will then be applied to evolutionary dynamics. This introduction will first discuss the background of difference equations, following with local stability analysis as well as a short overview of global dynamics and monotone systems, and concluding with a discussion on evolutionary game theory.

1.1 Background on Difference Equations

A difference equation is thought of as a map that charts the current state to a future state, describing the movement of a given quantity or population over discrete time intervals [1]. Difference equations are often used to model changes in population density using the state variable x . Defined recursively, where x_n represents the n^{th} generation of a quantity or population size and x_{n+1}^{st} represents the next generation, we have the following first order difference equation [2]:

$$x_{n+1} = f(x_n) \quad n = 0, 1, 2, 3, 4, \dots \quad (1)$$

where f is a function such that $f : \mathbb{R} \rightarrow \mathbb{R}$. An equation can be either autonomous or non-autonomous; the above equation is autonomous since x_{n+1} does not rely explicitly on n . It is also true that the coefficients for such an equation are constant. When the equation is non-autonomous, the coefficients are no longer constant, but rather sequences. The distinction between these two types of equations will play an important role in this thesis.

Notice that difference equations can be larger in both order and dimension than the one given above. The population of the $n + 1^{st}$ generation can depend on more than the size of the n^{th} generation. For example, for a second order equation x_{n+1} depends on both x_n and x_{n-1} , for a third order equation x_{n+1} depends on x_n , x_{n-1} , and x_{n-2} , and so on. We can also consider more than one population or quantity. As such, a two-dimensional system is when we consider two populations, a three-dimensional system is when we consider three populations, and so on. For the purposes of this thesis alone, we will focus on first order two dimensional systems. This type of system has the form

$$x_{n+1} = f(x_n, y_n), \quad y_{n+1} = g(x_n, y_n), \quad n = 0, 1, 2, 3, \dots \quad (2)$$

where $f, g : \mathbf{D} \rightarrow \mathbb{R}$ are continuous functions and $\mathbf{D} \in \mathbb{R}^2$ is a planar region [2]. The system (2) mapped from a planar region to a planar region has the following form

$$T(x, y) = \begin{pmatrix} f(x, y) \\ g(x, y) \end{pmatrix} \quad (3)$$

where T is a continuous map such that $T : \mathbf{D} \rightarrow \mathbf{D}$ with initial conditions $(x_0, y_0) \in \mathbf{D}$ [2].

As with any recursive equation, if initial value is known then we are able to trace the progression of the quantity or population. Taking iterations of an initial value, x_0 for example, for (1) produces dynamics for the state variable x and gives a sequence $\{x_0, f(x_0), f(f(x_0)), f(f(f(x_0))), \dots\}$ that is a solution to

(1). Further note that the same steps can be taken for (3) where taking iterations of the ordered pair (x_0, y_0) yields the solution $\{(x_0, y_0), T(x_0, y_0), T(T(x_0, y_0)), \dots\}$ for that system. Some equations or systems will have equilibrium points, which are values whose solutions do not change with time. Suppose the initial value x_0 is an equilibrium point. Then for each successive iteration, the numerical value will remain the same and the sequence will contain only the equilibrium point. To find the equilibrium points, the equation is set equal to the identity and this form can change based the dimension of the system. For a one-dimensional system such as (1), it will satisfy the equation $f(\bar{x}) = \bar{x}$. For a two dimensional system, the equilibrium point (\bar{x}, \bar{y}) is found through the system $f(\bar{x}, \bar{y}) = \bar{x}$ and $g(\bar{x}, \bar{y}) = \bar{y}$. It will be clear how important the equilibrium solutions are to the study of difference equations when local stability analysis is discussed in the next section.

1.2 Local Stability Analysis

Once the solution is obtained, the behavior of that particular solution is established. Since a solution can be found for any initial value, multiple solutions can be found, such as in a particular interval, and global behavior can be developed. Before this can be done, local behavior needs to be understood first and is referred to as local stability analysis. For a one dimensional system, it is only necessary to take the derivative of the function and evaluate it at its equilibrium points. For a two dimensional system, such as (3), the system must be linearized and then evaluated at each equilibrium solution to understand local behavior. This is accomplished by finding the Jacobian matrix of the system (3) at the equilibrium (\bar{x}, \bar{y}) which is

$$\begin{pmatrix} \frac{\partial f}{\partial x}(\bar{x}, \bar{y}) & \frac{\partial f}{\partial y}(\bar{x}, \bar{y}) \\ \frac{\partial g}{\partial x}(\bar{x}, \bar{y}) & \frac{\partial g}{\partial y}(\bar{x}, \bar{y}) \end{pmatrix} \quad (4)$$

The linearization of the map T at (\bar{x}, \bar{y}) is given as

$$J_T(\bar{x}, \bar{y}) = \begin{pmatrix} \frac{\partial f}{\partial x}(\bar{x}, \bar{y})x + \frac{\partial f}{\partial y}(\bar{x}, \bar{y})y \\ \frac{\partial g}{\partial x}(\bar{x}, \bar{y})x + \frac{\partial g}{\partial y}(\bar{x}, \bar{y})y \end{pmatrix} \quad (5)$$

The corresponding characteristic equation of the Jacobian matrix given in (4) will be

$$\lambda^2 - \text{tr}(J_T(\bar{x}, \bar{y}))\lambda + \det(J_T(\bar{x}, \bar{y})) = 0 \quad (6)$$

where λ represents the eigenvalues of (4) [2]. These values will be of significance when determining the type of equilibrium solutions.

To classify the equilibrium solutions, we will need the following definition: the Euclidean norm in \mathbb{R}^2 , denoted as $\|\cdot\|$, has the form $\|(x, y)\| = \sqrt{x^2 + y^2}$ and is the Euclidean distance in Euclidean space. The following states definitions on the foundational concept of stability. All these definitions can be found in [2]

Definition 1 Consider an equilibrium point (\bar{x}, \bar{y}) of system (3). Then

(i) (\bar{x}, \bar{y}) is locally stable if for any $\epsilon > 0$ there exists $\delta > 0$ such that for every initial point (x_0, y_0) with $\|(x_0, y_0) - (\bar{x}, \bar{y})\| < \delta$, the iterates (x_n, y_n) satisfy $\|(x_n, y_n) - (\bar{x}, \bar{y})\| < \epsilon$ for all $n > 0$.

(ii) (\bar{x}, \bar{y}) is locally asymptotically stable if, in addition to being stable, $(x_n, y_n) \rightarrow (\bar{x}, \bar{y})$ as $n \rightarrow \infty$ for all (x_0, y_0) that satisfy $\|(x_0, y_0) - (\bar{x}, \bar{y})\| < \delta$

(iii) (\bar{x}, \bar{y}) is said to be unstable if it is not stable.

Now applying the tools we introduced in the previous paragraph, we can determine whether the equilibrium solutions are stable or not. From the Linearized Stability Theorem, where (3) is a continuously differentiable function defined on an open set V in \mathbb{R}^2 and (\bar{x}, \bar{y}) is an equilibrium point of (3), we have two cases. The first case considers the eigenvalues of (4) that have modulus less than one. In this instance, the equilibrium point (\bar{x}, \bar{y}) is asymptotically stable. The second case consists of at least one of the eigenvalues of (4) having modulus greater than

one. When this happens, the equilibrium point (\bar{x}, \bar{y}) is unstable. The following definition goes into greater detail of these classifications: [2]

Definition 2 Consider an equilibrium point (\bar{x}, \bar{y}) of system (3),

(i) If (\bar{x}, \bar{y}) is locally asymptotically stable then the eigenvalues of $J_T(\bar{x}, \bar{y})$ are such that $|\lambda_1|, |\lambda_2| < 1$. In this case, there is an open neighborhood U of (\bar{x}, \bar{y}) in which all points converge to the equilibrium under forward iterations of the map T . That is,

$$T^n(x, y) \rightarrow (\bar{x}, \bar{y}) \text{ for every } (x, y) \in U$$

Such an equilibrium point is referred to as a sink. There are two cases when there is an unstable equilibrium point.

(ii) If the eigenvalues of $J(T)(\bar{x}, \bar{y})$ are such that $|\lambda_1|, |\lambda_2| > 1$, then there is an open neighborhood U of (\bar{x}, \bar{y}) in which all points converge to the equilibrium point under backward iterations of the map T . That is,

$$T^{-n}(x, y) \rightarrow (\bar{x}, \bar{y}) \text{ for every } (x, y) \in U$$

Such an equilibrium point is referred to as a source or repeller.

(iii) If the eigenvalues of $J_T(\bar{x}, \bar{y})$ are such that $|\lambda_1| < 1$ and $|\lambda_2| > 1$, then in any neighborhood U of (\bar{x}, \bar{y}) , the forward iterates under T of some points in U converge to (\bar{x}, \bar{y}) and the backward iterates under T of some points in U converge to (\bar{x}, \bar{y}) . Such a point is referred to as a saddle point.

Note that these are all hyperbolic points since the eigenvalues do not lie on the unit circle. Now if at least one eigenvalue lies on the unit circle, that is, if it has an eigenvalue λ such that $|\lambda| = 1$, then the equilibrium point must be non-hyperbolic. In this case, local stability analysis can be quite complicated and we are not able to classify so definitively as we did with the above definition. In these circumstances,

stability of the equilibrium point is determined by a higher order term in Taylor's expansion of the map T [2].

There is a general method, called the Schur-Cohn or Jury criterion, that can also be used to find the stability of the equilibrium points. The conditions listed in this theorem are inequalities that make use of the trace and determinant of the Jacobian matrix of the map T [2].

Theorem 3 *The following conditions hold for equilibrium points (\bar{x}, \bar{y}) of system (3):*

(i) *An equilibrium point (\bar{x}, \bar{y}) is locally asymptotically stable if*

$$|\operatorname{tr} J_T(\bar{x}, \bar{y})| < 1 + \det J_T(\bar{x}, \bar{y}) < 2$$

(ii) *An equilibrium point (\bar{x}, \bar{y}) is locally a repeller if*

$$|\operatorname{tr} J_T(\bar{x}, \bar{y})| < |1 + \det J_T(\bar{x}, \bar{y})| \text{ and } |\det J_T(\bar{x}, \bar{y})| > 1$$

(iii) *An equilibrium point (\bar{x}, \bar{y}) is locally a saddle point if*

$$|\operatorname{tr} J_T(\bar{x}, \bar{y})| > |1 + \det J_T(\bar{x}, \bar{y})|$$

(iv) *An equilibrium point (\bar{x}, \bar{y}) is nonhyperbolic if*

$$|\operatorname{tr} J_T(\bar{x}, \bar{y})| = |1 + \det J_T(\bar{x}, \bar{y})| \text{ or } |\operatorname{tr} J_T(\bar{x}, \bar{y})| \leq 2 \text{ and } \det J_T(\bar{x}, \bar{y}) = 1$$

There are a few other parts of local stability analysis that should be addressed. If the equilibrium point is asymptotically stable of a map, then there exists an immediate basin of attraction for this point. The immediate basin of attraction for one dimension, denoted as $\mathcal{B}(\bar{x})$, is the maximal set U that contains the equilibrium point such that $f^m(x) \rightarrow \bar{x}$ as $m \rightarrow \infty$ for every $x \in U$. It is very similar for two dimensions, denoted as $\mathcal{B}(\bar{x}, \bar{y})$, where the maximal set U is defined as for every

$(x, y) \in U$, $T^m(x, y) \rightarrow (\bar{x}, \bar{y})$ as $m \rightarrow \infty$. This set U also includes the equilibrium point (\bar{x}, \bar{y}) [2].

Periodic points are fixed points of the m -th iterate of the map, commonly denoted as a periodic point of period m . For a one dimensional system such as (1), this would be the equilibrium point p satisfying the equation $f(p)^m = p$. For a two dimensional system (3), it would be the equation $T(x_p, y_p)^m = (x_p, y_p)$, where (x_p, y_p) is an equilibrium point. Note that this process can be applied to higher dimensions. Notice that a periodic point (x_p, y_p) of period m is stable if (x_p, y_p) is a stable fixed point of T^m for the map T . Likewise, this also holds true for a periodic point (x_p, y_p) of period m that is unstable or asymptotically stable [2].

Another important aspect to local stability analysis are bifurcations. A bifurcation is a change in either the number of equilibrium points, their stability, or periodic points of a system. In bifurcation theory, the changes that occur to a map by changes in the parameters is studied. Often times, periodic points are effected. One type of bifurcation is known as the period-doubling bifurcation. For this bifurcation to occur, there must be [3]

- i) an attracting equilibrium point turning into a repelling one.
- ii) a new period two solution being created

Hence, when the equilibrium solution loses it's stability, the period two solution gains it. As the period two solution loses stability, the period four solution acquires it. This pattern could continue infinitely where, for period k , the prime period- 2^k solution is stable, but the prior periodic solutions $2, \dots, 2^{k-1}$ have become unstable. This is known as period-doubling bifurcation route to chaos [3].

The last note of this section will be about Schwarzian derivatives. Schwarzian derivatives provide a valuable tool used in difference equations as well as other areas of mathematics, such as dynamical systems. The particular use for them in

this thesis occurs when the non-autonomous competitive and cooperative systems are applied to evolutionary dynamics. In order to have global attractivity results for the evolutionary models, Singer's Theorem, stated in the beginning of chapter 3, is needed. One of the conditions in this theorem is that the Schwarzian derivative of an equation must be negative. Here is the following definition [2]

Definition 4 *Let $f(x)$ be a three times continuously differentiable function at a point x such that $f'(x) \neq 0$. The Schwarzian derivative of f at the point x is defined as*

$$\mathcal{S}f(x) = \frac{f'''(x)}{f'(x)} - \frac{3}{2} \left(\frac{f''(x)}{f'(x)} \right)^2 \quad (7)$$

There is then the following corollary on how local stability can be determined through the Schwarzian derivative [2]

Corollary 5 *Let $f(x)$ be a three times continuously differentiable function in a neighborhood of an equilibrium point \bar{x} . Suppose also that either $f'(\bar{x}) = 1$ and $f''(\bar{x}) = 0$, or $f'(\bar{x}) = -1$. Then the following statements hold*

- i) If $\mathcal{S}f(\bar{x}) < 0$, then \bar{x} is a sink of (1)*
- ii) If $\mathcal{S}f(\bar{x}) > 0$, then \bar{x} is a source of (1)*

1.3 Global Dynamics

This section expands upon the ideas of local stability to give more general results. A few different ideas covered in this section will be important to this thesis. The first to be discussed are invariants. An invariant can play a pivotal role in many areas of mathematics. For difference equations specifically, they are used as a tool to investigate stability of systems. Invariants can be quite powerful since if one is known for a system then the system could be solved in exact form. Further, they can be used to find equilibrium points in the case where the equilibrium points depend on the initial conditions. Below is a formal definition [2]

Definition 6 A nonconstant continuous function $I : \mathbb{R}^2 \rightarrow \mathbb{R}$ is an invariant for the system (3) if

$$I(x_{n+1}, y_{n+1}) = I(x_n, y_n) \quad (8)$$

The following is the definition for an invariant interval for (3) [2]

Definition 7 An invariant interval for (3) is an interval I where if two consecutive terms of a solution are in I , then all subsequent terms of the solution are in I as well.

Furthermore, an absorbing or attracting interval for (3) is an invariant interval such that all solutions of the system (3) eventually enter the interval.

Invariants can also be used to construct Lyapunov functions. Lyapunov functions are an important method to obtain global attractivity results. Lyapunov functions are used in both chapter 2 and 3 to show global attraction of an equilibrium point for the autonomous systems as a comparative study with its non-autonomous counterpart. Consider (3) with $\mathbf{D} \subset \mathbb{R}^2$ and $T : \mathbf{D} \rightarrow \mathbb{R}^2$ is continuous. Then

Definition 8 The function $V : \mathbb{R}^2 \rightarrow \mathbb{R}$ is said to be a Lyapunov function on a subset \mathbf{D} of \mathbb{R}^2 if

- i) V is continuous on \mathbf{D}
- ii) $\Delta V(x) = V(T(x)) - V(x) \leq 0$ when x and $T(x) \in \mathbf{D}$

For the next definition, an open ball in \mathbb{R}^2 needs to be defined

$$B(a, r) = \{x \in \mathbb{R}^2 : \|x - a\| < r\}$$

where the open ball has center a and radius r [2].

Definition 9 *The function V is positive definite at the equilibrium \bar{x} if [2]*

i) $V(\bar{x}) = 0$

ii) $V(x) > 0$ for all $x \in B(\bar{x}, r)$ for some $r > 0$.

The first condition states that zero should be the answer when the equilibrium solution, written as a vector, is substituted in to the Lyapunov function. The second condition ensures that the Lyapunov function is positive for all values substituted into it that belong to the open ball or radius r and centered at the equilibrium solution. The following theorem is the most important result in regards to Lyapunov function [2]

Theorem 10 *Let V be a Lyapunov function for (3) on a neighborhood \mathbf{D} of the equilibrium point \bar{x} . Further, define V to be positive definite at \bar{x} . Then*

i) \bar{x} is stable

ii) If $\Delta V(x) < 0$ for all $x, f(x) \in \mathbf{D}$ and $x \neq \bar{x}$, then \bar{x} is asymptotically stable.

iii) If $\mathbf{D} = \mathbb{R}^2$ and

$$V(x) \rightarrow \infty \text{ as } \|x\| \rightarrow \infty$$

then \bar{x} is globally asymptotically stable.

The remaining part of this section will be dedicated to structural stability. Throughout this thesis, global attractivity results for non-autonomous competitive and cooperative systems are obtained, in part, by having the systems be structurally stable. The notion is that when small changes of parameters are applied to the system, the dynamics of it remain unaltered, or that small perturbations do not affect the system. This can occur for systems in which the dynamics change drastically, such as having two fixed points to having none, when the value of the parameter changes. Often when a map is not structurally stable it is discovered that the fixed points are usually non-hyperbolic [3].

1.4 Monotone Systems

In this section, monotonicity is discussed as it plays an important role in both competitive and cooperative systems. An order cone \mathcal{P} is defined as a set that is closed and convex such that $\mathcal{P} \subset \mathbb{R}^m$, $\lambda\mathcal{P} \subset \mathcal{P}$ for all $\lambda \geq 0$, and $\mathcal{P} \cap (-\mathcal{P}) = \{0\}$ where $\mathcal{P} \neq \{0\}$. There exists a partial ordering, denoted \preceq or \prec , for an order cone on \mathbb{R}^m . Now let x, y be any arbitrary points in \mathcal{P} . [4] The partial ordering can be defined as follows:

$$x \preceq y \text{ if and only if } y - x \in \mathcal{P}.$$

$$x \prec y \text{ if and only if } y - x \in \mathcal{P} \setminus \{0\}.$$

$$x \ll y \text{ if and only if } y - x \in \text{int}(\mathcal{P}).$$

The ordered set for partial ordering is

$$\llbracket x, y \rrbracket := \{u \in \mathbb{R}^m : x \preceq u \preceq y\} \quad (9)$$

Consider $\mathbf{D} \subset \mathbb{R}^2$ for the map $T : \mathbf{D} \rightarrow \mathbf{D}$. The classifications on the types of monotonicity can be given as

- The map T is monotone when $x \preceq y$ implies $T(x) \preceq T(y)$.
- The map T is strictly monotone when $x \prec y$ implies $T(x) \prec T(y)$.
- The map T is strongly monotone when $x \prec y$ implies $T(x) \ll T(y)$.

The next theorem gives significant results for monotone systems in relation to difference equations and stability analysis [5].

Theorem 11 *For a nonempty set $\mathbf{D} \in \mathbb{R}^m$ and a partial order \preceq on \mathbb{R}^m , let $T : \mathbf{D} \rightarrow \mathbf{D}$ be an order-preserving map and let $u, v \in \mathbf{D}$ be such that $u \prec v$ and $\llbracket u, v \rrbracket \subset \mathbf{D}$. If $u \preceq T(u)$ and $T(v) \preceq v$, then $\llbracket u, v \rrbracket$ is an invariant set and*

- i) There exists a fixed point of T in $\llbracket u, v \rrbracket$.*

ii) If T is strongly order-preserving then there exists a fixed point of T in $\llbracket u, v \rrbracket$ that is stable relative to $\llbracket u, v \rrbracket$.

iii) If there is only one fixed point in $\llbracket u, v \rrbracket$ then it is a global attractor in $\llbracket u, v \rrbracket$ and therefore asymptotically stable relative to $\llbracket u, v \rrbracket$

The following corollary is a consequence of this theorem

Corollary 12 *If the nonnegative cone of a partial ordering \preceq is a generalized orthant in \mathbb{R}^m , and if T has no fixed points in $\llbracket u, v \rrbracket$ other than u and v , then the interior of $\llbracket u, v \rrbracket$ is either a subset of the basin of attraction of u or the basin of attraction of v*

Note that in one dimension an orthant is a ray and in two dimensions an orthant is a quadrant. In three dimensions, it is an octant. The nonnegative orthant is the generalization of the first quadrant. Now restricting the focus to \mathbb{R}^2 , there are two partial orderings described in these definitions below

Definition 13 *The North-East partial ordering \preceq_{ne} on \mathbb{R}^2 is defined as follows:*

$$\begin{pmatrix} x_1 \\ y_1 \end{pmatrix} \preceq_{ne} \begin{pmatrix} x_2 \\ y_2 \end{pmatrix} \leftrightarrow \begin{cases} x_1 \leq x_2 \\ y_1 \leq y_2 \end{cases} \quad (10)$$

where the positive cone is taken to be the first quadrant. The South-East partial ordering \preceq_{se} on \mathbb{R}^2 is defined as follows:

$$\begin{pmatrix} x_1 \\ y_1 \end{pmatrix} \preceq_{se} \begin{pmatrix} x_2 \\ y_2 \end{pmatrix} \leftrightarrow \begin{cases} x_1 \leq x_2 \\ y_1 \geq y_2 \end{cases} \quad (11)$$

where the positive cone is taken to be the fourth quadrant.

Since competitive and cooperative maps are monotone, these definitions are associated with these maps on \mathbb{R}^2 . If the map T is a competitive system, then it has South-East partial ordering in terms of nondecreasing. The map is considered strongly competitive if it is strictly increasing in regards to South-East partial ordering. [4] A way to determine if the map is strongly competitive is by taking the Jacobian of the system. If the Jacobian matrix has the following sign configuration

$$\begin{pmatrix} + & - \\ - & + \end{pmatrix}$$

then the map will be strongly competitive. If the map T is cooperative, then it has North-East partial ordering. Likewise, the map is strongly cooperative if it is strictly increasing with respect to North-East partial ordering. In this case, the Jacobian matrix has the sign configuration

$$\begin{pmatrix} + & + \\ + & + \end{pmatrix}$$

The subsequent definition and theorems relate specifically to competitive maps.

Definition 14 Suppose $\mathbf{D} \subset \mathbb{R}^2$ is nonempty. A competitive map $T : \mathbf{D} \rightarrow \mathbf{D}$ satisfies the following [4]

- i) the (\mathcal{O}^+) condition if for all $x, y \in \mathbf{D}, T(x) \preceq_{ne} T(y) \leftrightarrow x \preceq_{ne} y$*
- ii) the (\mathcal{O}^-) condition if for all $x, y \in \mathbf{D}, T(x) \preceq_{ne} T(y) \leftrightarrow y \preceq_{ne} x$*

The following theorem provides greater detail on the conditions a competitive map must meet to satisfy \mathcal{O}^+ and \mathcal{O}^- .

Theorem 15 Consider $\mathcal{D} \subset \mathbb{R}^2$, where \mathcal{D} is a Cartesian product of two intervals in \mathbb{R} . Let $T : \mathcal{D} \rightarrow \mathcal{D}$ be a competitive, C^1 map.

1. If T is injective and $\det J_T(x) > 0$ for all $x \in \mathcal{D}$ then T satisfies \mathcal{O}^+ on \mathcal{D} .

2. If T is injective and $\det J_T(x) < 0$ for all $x \in \mathcal{D}$ then T satisfies \mathcal{O}^- on \mathcal{D}

This next theorem demonstrates this as outcome of the preceding theorem and definition [6].

Theorem 16 *Suppose $\mathcal{D} \subset \mathbb{R}^2$. If T is a competitive map that satisfies \mathcal{O}^+ , then for all $x \in \mathcal{D}$, $\{T^m(x)\}$ is eventually component-wise monotone, where m represents the iteration. If the orbit of x has compact closure, then it converges to a fixed point of T . If instead \mathcal{O}^- is satisfied, then for all $x \in \mathcal{D}$, $\{T^m(x)\}$ is eventually component-wise monotone. If the orbit of x has compact closure in \mathcal{D} , then its ω -limit set is either a period-two orbit or a fixed point*

Note that the ω -limit set is the set that all non-equilibrium solutions approach.

1.5 Population Models

In consideration of the competitive and cooperative models studied in this thesis as well as the focus on population dynamics, it is necessary to introduce a few population models. In order to model discrete time deterministic dynamics of biological populations, the difference equation of the form

$$x_{n+1} = f(x_n)x_n, n = 0, 1, \dots \quad (12)$$

is used where x_n measures the population density at discrete census times and $f(x)$ is the per capita growth rate for the population. Since f is the population growth rate, we need the solution x_n to be non-negative so that the function only assumes non-negative values. Understanding the limiting behavior of (12) is important to the study of population dynamics and this depends on the properties of f .

Here are three population growth rates that will be discussed in short detail. The first growth rate is

$$f(x) = \frac{b}{1 + cx} \quad (13)$$

where $b, c > 0$. This model gives the discrete logistic model or Beverton-Holt model. The dynamics for this model will be the same as those for the Beverton-Holt. However, when $b > 1$, a positive equilibrium solution is created, $x_+ = \frac{(b-1)}{c}$. The positive equilibrium x_+ becomes an attractor whereas x_0 destabilizes. Notice that the bifurcation at $b = 1$, x_0 is non-hyperbolic and therefore, the model is not structurally stable at this point.

A second population growth rate is

$$f(x) = be^{-cx} \quad (14)$$

where $b, c > 0$. This model induces the Ricker model. For this model, the extinction equilibrium, $x_0 = 0$ has similar dynamics to the first model (13) where it destabilizes at $b = 1$. When $b > 1$, the positive equilibrium $x_+ = \ln \frac{b}{c}$ is born and is an attractor. This equilibrium solution remains an attractor when $b \in (1, e^2)$. When $b > e^2$, the positive equilibrium x_+ destabilizes. This model exhibits a period doubling route to chaos as the value of b increases.

The final population model to cover is

$$f(x) = \frac{bx}{1+x^2} \quad (15)$$

where $b > 0$. This model yields the Sigmoid Beverton-Holt model or Thomson model. The extinction equilibrium $x_0 = 0$ is globally asymptotically stable for $b < 2$. Another bifurcation occurs, this time at $b = 2$, but the extinction equilibrium remains stable. Instead, there are two equilibrium solutions at this point, as a non-hyperbolic one is added. When $b > 2$, two equilibrium solutions are created, $x_1 = \frac{b-\sqrt{b^2-4}}{2}$ and $x_2 = \frac{b+\sqrt{b^2-4}}{2}$. The equilibrium x_1 , between x_0 and x_2 position-wise, is a repeller and x_2 is globally asymptotically stable. Therefore, the basin of attraction is (x_0, x_1) for x_0 and (x_1, ∞) for x_2 . The existence of a large basin attraction of zero equilibrium is called Allee's effect.

It is important to note that if f only depends on the state variable x , then it is only the current population density that determines the population density at the next time census which makes the model time autonomous. For a model that is non-autonomous and, instead relies on time n , there could be an asymptotically constant environment model where the coefficients are variable with constant limits.

Since competitive and cooperative systems are discussed in detail for this thesis, it is necessary to address a few dynamic scenarios. As will be shown in chapter 3, a two-dimensional competitive system has the form

$$x_{n+1} = f(x_n, y_n), \quad y_{n+1} = g(x_n, y_n), \quad n = 0, 1, \dots \quad (16)$$

where f is nondecreasing in the first variable, nonincreasing in the second and g is nonincreasing in the first variable, nondecreasing in the second.[4] Two species competing for the same resources could be modeled by this type of system. The different types of dynamics that exists for these types of systems are:

- i) Competitive exclusion
- ii) Competitive coexistence
- iii) Allee's effect

Note that Allee's effect was discussed in the preceding paragraph when describing basins of attraction. In this case, Allee's effect occurs when two species with populations not equal to zero are both driven to extinction. Competitive exclusion happens when one species is driven to extinction. Competitive coexistence is when two competing species reach an equilibrium state and are able to coexist. These same dynamics occur for cooperative systems as well [5].

Competitive exclusion models were many of the original competition models that were based on two species and the Lotka-Volterra competitive system of dif-

ferential equations. One of the first models that defined competitive coexistence was the Leslie Gower model of the form

$$\begin{aligned} N_1(t+1) &= \frac{\lambda_1 N_1(t)}{1 + \alpha_1 N_1(t) + \beta_1 N_2(t)} \\ N_2(t+1) &= \frac{\lambda_2 N_2(t)}{1 + \alpha_2 N_2(t) + \beta_2 N_1(t)} \end{aligned} \tag{17}$$

where $t = 0, 1, \dots$ and $\lambda_1, \lambda_2, \alpha_1, \alpha_2, \beta_1, \beta_2$ are positive constants. The model was formulated by J.C. Gower and P.H. Leslie in 1958. This system will be extensively covered throughout chapters 2 and 3 both in the non-autonomous case, where the proofs make use of South-East and North-East partial ordering, as well as in applications to evolutionary dynamics.

1.6 Evolutionary Game Theory

The definition of evolutionary biology rests in the concept that an organism's genes determine its observable characteristics. This impacts the organism's fitness in a given environment. For classic game theory, reasoning and decision making play an integral role when players take part in a given game. As it turns out, the basic ideas of game theory can be applied without the necessity of conscious choices. In evolutionary game theory, the basic ideas of game theory are applied to evolutionary biology. The following analogy can be made: the strategies in a game are an organism's biological characteristics and behaviors and the payoff is its fitness, where that payoff depends on the strategies, or, in this case, characteristics and behaviors, of the players, or organisms, with which it interacts. Here, fitness is defined as the per capita change in population density from one generation to the next. It is important to note that fitness cannot be measured alone. This means that behaviors are largely dependent on one another and an organism's behavior can be impacted by the behaviors of others [7]. The success of any organism depends on this. The rest of this section is based largely on the work from Vincent and Brown's book [1].

Evolutionary game theory is built using Darwinian dynamics. Darwinian dynamics is a combination of strategy dynamics and population dynamics fused together to model the evolutionary process. Before developing the mathematical framework for Darwinian dynamics, a few foundational definitions and notations need to be addressed. The term "strategies" is defined as the adaptive parameters in population dynamic models. They can also be thought of as heritable phenotypes that have consequences. The traits can be either fixed or variable. Note that individuals can have more than one distinct strategy and since these strategies can evolve over time, a strategy dynamic can be determined. The other term defined in the beginning is species. In this context, individuals are of the same species if they have similar strategies that can be grouped together. Now to introduce some notation. Since there are multiple variables to consider for any population, vector and matrix notation is necessary. The number of different species in a population is denoted n_s . The scalar x_i is indicative of the density of species i where the vector \mathbf{x} represents the population densities of multiple species and is given as

$$\mathbf{x} = [x_1, \dots, x_{n_s}]$$

The scalar u_i represents the heritable phenotypes or strategies belonging to a species i . The strategy vector for an individual from species i is as follows

$$u_i = [u_{i1}, \dots, u_{in_i}]$$

The vector for all strategies used by all species in the population is given as

$$\mathbf{u} = [u_1, \dots, u_{n_s}]$$

Resources, as quickly noted in the prior section on population dynamics, can also play a role in evolutionary dynamics. By adding resource dynamics to the model, we simply add another variable. Denoting n_y to be the number of resources, the

vector of all resources is written as

$$\mathbf{y} = [y_1, \dots, y_{n_y}]$$

While this particular thesis does not explore the resource dynamic, it can certainly be applied.

There are three postulates Darwin theorized to explain evolution. They serve as the foundation to the study of ecology and further provide the necessary tools to create fitness functions. The three postulates are as follows

- i) Individuals within species are variable so there exists an heritable variation in traits with each organism.
- ii) There is struggle for existence among organisms.
- iii) Heritable traits influence the struggle for existence.

The first postulate is well known. The second was extended by Darwin to consider resources where individuals of the same species, or even different species, compete for the same limited resources. The remaining postulate plays a pivotal role in understanding evolution and the consequences of it. Each of these postulates can be applied to the development of an evolutionary game. The heritable variation referred to in the first postulate could translate to u_i , an heritable strategy, with each individual possessing a set of strategies. The second postulate could translate to the per capita growth rate determined by the fitness function that relies on the densities and strategies of other individuals. The last postulate means the variation of the fitness function for an individual depending on the choice of the mean strategy u_i .

According to Vincent and Brown[1], there are two discrete forms used to model population dynamics. The second equation should appear familiar as it

first appeared in discussions on population dynamics. In this case, however, specific variables used in evolutionary game theory are applied

$$x_i(t + 1) = x_i F_i(\mathbf{u}, \mathbf{x}) \quad (18)$$

Here F_i is the per capita growth rate, similarly to how it was defined in the population dynamics section. For here, F_i depends on \mathbf{u} , the strategies, and population density, \mathbf{x} . Note that for difference equations, the choice of F_i is important and must be a realistic function to have $x_i \geq 0$ for all positive i . Two types of difference equation are considered in Vincent and Brown[1], but for the purposes of this thesis, only second type, exponential, will be used.

In order to build the equations for an evolutionary game, the fitness function needs to be discussed in greater detail. The corresponding fitness function to the second type of equation is given as

$$F_i(\mathbf{u}, \mathbf{x}, \mathbf{y}) = \exp H_i(\mathbf{u}, \mathbf{x}, \mathbf{y}) \quad (19)$$

Fitness functions carry symmetry property that allows individuals to be grouped together based on similar strategies. These individuals that are grouped based on similar strategies possess the same fitness generating function, commonly denoted as a G-function. This allows the modeler to have one function rather than many individual fitness functions with each with a different strategy. The following notation applies

$$G(v, \mathbf{u}, \mathbf{x})|_{v=u_i} = H_i(\mathbf{u}, \mathbf{x}) \quad (20)$$

where the scalar v is a place holder. It works by replacing v with any strategy to find the fitness function of an individual. To create a G-function, a few steps must be taken. This begins by selecting an appropriate model, such as whether that would be for a single species or multiple species. This is also where the modeler determines if they are modeling a difference equation or differential equation. The

next step is to pick strategies based on what is being modeled. For instance, the strategy sets can be either discrete or continuous. Further, there could be a single set with a single G-function for a model where all individuals are evolutionarily the same. In the last step, the modeler attempts to predict how the strategies, including all individuals in a population, influences the values of the parameters in the population dynamic models. There are many types of G-functions, but we will focus on single scalar G-functions for this thesis. The reader can find other types in Vincent and Brown's book.[1]

An adaptive landscape shows graphically the relationship between fitness and one or more traits. Thus, strategy dynamics can be visualized as occurring on an adaptive landscape. Consider existing traits for a species, \mathbf{u} , coupled with the population size of each species, \mathbf{x} . The adaptive landscape graphs the G-Function as a function of one individual's strategy, v . Note that it is true to its name being that it is adaptive and will change shape depending on population strategies and densities.

The mean strategies can change over time. As stated previously, strategies are distributed throughout a population. Now if the population density changes, then these strategies, or heritable phenotypes, will change as well. This can be represented by the function

$$u_{i+1} - u_i = \sigma_i^2 \frac{\partial G(v, \mathbf{u}, \mathbf{x})}{\partial v} \Big|_{v=u_i} \quad (21)$$

Note that σ_i^2 , denoted as the variance, is often thought of as the speed of the equation. Furthermore, the variance of the distribution strategies, σ_i^2 , is proportional to the rate of strategy change. Applying Fisher's Fundamental Theorem, which states that the rate of increase in fitness is equal to its additive genetic variance in fitness at that time, to this equation, this means that as the value of σ_i^2 becomes larger, the pace of evolution speeds up. Then the system for Darwinian dynamics

is the following

$$\begin{aligned} x_i &= x_i G(v, \mathbf{u}, \mathbf{x}) \Big|_{v=u_i} \\ u_{i+1} - u_i &= \sigma_i^2 \frac{\partial G(v, \mathbf{u}, \mathbf{x})}{\partial v} \Big|_{v=u_i} \end{aligned} \tag{22}$$

When population dynamics is blended with strategic dynamics a new time scale, other than the ecological time scale, is introduced, called the evolutionary time scale. This is due to the fact that sometimes population dynamics occurs on a faster time scale than strategic dynamics. The ecological time scale is associated with population dynamics and the evolutionary time scale is associated with strategy dynamics. Both time scales measure the time it takes for a system to return to an equilibrium solution after begin displaced from a solution. Hence, the importance of having two time scales. There are two cases here: Either there will be a large difference in the time scales or small difference. When there is a large difference, the biological system will stay close to a slowly changing ecological equilibrium solution. Consequently, the population dynamics are given as a fixed point and Darwinian dynamics is reduced to strategy dynamics. When the difference is small, both population and strategy dynamics are needed and we use the system above. Oftentimes, there will be solutions that give non-equilibrium dynamics.

In regards to the stable equilibrium solutions in difference equations as well as differential equations, an evolutionary stable strategy, denoted as ESS, is its equivalent in evolutionary dynamics. An ESS has two conditions for the solution to be so: it must be resistant to invasion and it must have convergence stability. These are both considered forms of evolutionary stability. Resistant to invasion is defined as natural selection favoring strategies that cannot be invaded by other strategies not as common or different. Stability, similar to the ideas of structural stability in dynamics, is where natural selection favors strategies where the equilibrium

remains even through perturbations of \mathbf{x} and \mathbf{u} . It is important to note that one does not imply the other. For instance, a mean strategy having convergence stability does not mean it is resistant to invasion. In this case, the mean strategy would not be ESS. For a strategy to be ESS, it must satisfy the ESS Maximum Principle. The ESS Maximum Principle characterizes the property of resistance to invasion and is defined as a global maximum point of the adaptive landscape. Solutions found this way are considered ESS candidate until it is proven that the solution satisfies convergence stability as well. Thus, the solution cannot satisfy one condition without the other to be ESS, and, further, one condition does not imply the other.

Through these methods illustrated by Vincent and Brown, applying certain systems in difference equations to evolutionary dynamics brings results that can appear parallel to the local and global stability analysis of difference equations. As a final note, it is important to acknowledge that not every system in difference equations can be applied to evolutionary dynamics. Notice that not every non-autonomous system proven in the main results of chapter 2 and 3 appeared in the application to evolutionary dynamics and so the modeler should use discretion when choosing a system.

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CHAPTER 2

Stability of Certain Non-autonomous Competitive Systems of Difference Equations with Application to Evolutionary Dynamics

M. R. S. Kulenović¹¹, M. Nurkanović², Z. Nurkanović², and S. Trolle¹

¹ Department of Mathematics,
University of Rhode Island,
Kingston, RI 02881, USA

² Department of Mathematics,
University of Tuzla,
75000 Tuzla,
Bosnia and Herzegovina

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2.1 Introduction

In this paper, we give some global attractivity results for a non-autonomous competitive systems of difference equations

$$\begin{aligned}x_{n+1} &= a_n f(x_n, y_n) \\ y_{n+1} &= b_n g(x_n, y_n), \quad n = 0, 1, \dots\end{aligned}\tag{23}$$

where f is non-decreasing in the first variable and is non-increasing in the second variable, and g is non-increasing in the first variable and is non-decreasing in the second variable. Here a_n and b_n are sequences which are assumed to be asymptotically constant. Our results are motivated with results for global attractivity for non-autonomous systems of difference equation via linearization in [1] that has significant applications in mathematical biology of single species [2]. Our techniques are based on difference inequalities, which was major method used in [2]. Now we extend the applications from single species models in [2] to the case of two species competition models. Then we apply our results to evolutionary population competition models, which have been considered lately by Cushing, Elaydi and others, see [3, 4, 5, 6, 7, 8]. A typical result in [2], which will be extended to competitive planar systems is Theorem 13:

Theorem 17 *Consider the difference equation*

$$x_{n+1} = a_n f(x_n), \quad n = 0, 1, \dots,\tag{24}$$

where f is nondecreasing function, $\lim_{n \rightarrow \infty} a_n = a$, and the limiting difference equation

$$y_{n+1} = a f(y_n), \quad n = 0, 1, \dots\tag{25}$$

Assume that there exists $\epsilon_0 > 0$ such that every solution of difference equation

$$y_{n+1} = A f(y_n), \quad n = 0, 1, \dots$$

converges to a constant solution \bar{y}_A for every $A \in (a - \epsilon_0, a + \epsilon_0)$. If

$$\lim_{A \rightarrow a} \bar{y}_A = \bar{y},$$

then every solution of the difference equation (24) satisfies

$$\lim_{n \rightarrow \infty} x_n = \bar{y}.$$

The global attractivity results for first order autonomous difference equation that will be used in simulations in this paper were proved by Elaydi and Sacker [9] and Singer [10].

Theorem 18 [9] *Let $f : [a, b] \rightarrow [a, b]$ be a continuous function in equation*

$$x_{n+1} = f(x_n), \quad n = 0, 1, \dots \quad (26)$$

Then the following statements are equivalent:

- (a) *Equation (70) has no minimal period-two solutions in (a, b) .*
- (b) *Every solution of equation (70) that starts in (a, b) converges.*

As an immediate consequence of the Theorem 40, we have the following important result on global asymptotic stability.

Corollary 19 [9] *Let \bar{x} be a fixed point of a continuous map f on the closed and bounded interval $I = [a, b]$. Then \bar{x} is globally asymptotically stable relative to (a, b) if and only if*

$$f^2(x) = f(f(x)) > x, \quad x < \bar{x} \quad \text{and} \quad f(f(x)) < x, \quad x > \bar{x}, \quad (27)$$

for all $x \in (a, b) \setminus \{\bar{x}\}$, and a, b are not periodic points.

The next result known as Singer theorem, see [10] is very useful and efficient tool for establishing global dynamics of first order difference equations.

Theorem 20 Assume that f is C^3 with an equilibrium point $\bar{x} \in [\alpha, \beta]$ such that f satisfies negative feedback condition, that is $f(x) > x$ if $x < \bar{x}$ and $f(x) < x$ if $x > \bar{x}$. Assuming that the Schwarzian derivative

$$Sf(x) = \frac{f'''(x)}{f'(x)} - \frac{3}{2} \left(\frac{f''(x)}{f'(x)} \right)^2 < 0$$

for all $x \in [\alpha, \beta]$, then if $|f'(\bar{x})| \leq 1$, then \bar{x} is globally asymptotically stable. Now condition $|f'(\bar{x})| \leq 1$ is equivalent to local stability or non-hyperbolicity of the equilibrium \bar{x} .

Another result which we use is the following result from [11]:

Theorem 21 Let $f : [a, b] \rightarrow [a, b]$ be a continuous, non-decreasing function in equation (70). Then every solution is monoonic and so it converges to an equilibrium

In this paper, we will use the so-called "north-east" partial ordering of the space \mathbb{R}_+^2 defined it in the following way:

$$X_n = \begin{bmatrix} x_n^{(1)} \\ x_n^{(2)} \end{bmatrix} \preceq_{ne} Y_n = \begin{bmatrix} y_n^{(1)} \\ y_n^{(2)} \end{bmatrix} \iff (x_n^{(1)} \leq y_n^{(1)} \text{ and } x_n^{(2)} \leq y_n^{(2)}),$$

and the so-called "south-east" partial ordering of the space \mathbb{R}_+^2 defined by

$$X_n = \begin{bmatrix} x_n^{(1)} \\ x_n^{(2)} \end{bmatrix} \preceq_{se} Y_n = \begin{bmatrix} y_n^{(1)} \\ y_n^{(2)} \end{bmatrix} \iff (x_n^{(1)} \leq y_n^{(1)} \text{ and } x_n^{(2)} \geq y_n^{(2)}).$$

The paper is organized as follows. The next section contains main results on asymptotic dynamics of non-autonomous systems of difference equations of competitive type in state variables in the plane. The final section presents the application of main results to the evolutionary (Darwinian) systems of difference equations when in addition to state variables we introduce equations or systems of equations that describe dynamics of the traits, that effects the coefficients of state variables.

2.2 Main results

Lemma 22 *Assume that*

a) $F : \mathbb{R}_+^2 \rightarrow \mathbb{R}_+^2$, $F = \begin{bmatrix} f \\ g \end{bmatrix}$ is a competitive map, i.e., $f, g : \mathbb{R}_+^2 \rightarrow \mathbb{R}$ are the functions with the following properties:

i) f is non-decreasing in the first variable and is non-increasing in the second variable,

ii) g is non-increasing in the first variable and is non-decreasing in the second variable;

b) $\{X_n\}$, $\{Y_n\}$, $\{Z_n\}$ are sequences of the real components in \mathbb{R}_+^2 such that $X_0 \preceq_{se} Y_0 \preceq_{se} Z_0$ and

$$\left. \begin{array}{l} X_{n+1} \preceq_{se} F(X_n) \\ Y_{n+1} = F(Y_n) \\ Z_{n+1} \succeq_{se} F(Z_n) \end{array} \right\}, \quad n = 0, 1, 2, \dots .$$

Then,

$$X_n \preceq_{se} Y_n \preceq_{se} Z_n, \quad n = 0, 1, 2, \dots . \quad (28)$$

Proof. The proof follows by induction. Since

$$X_0 \preceq_{se} Y_0 \preceq_{se} Z_0 \iff \left\{ x_0^{(1)} \leq y_0^{(1)} \leq z_0^{(1)} \quad \text{and} \quad x_0^{(2)} \geq y_0^{(2)} \geq z_0^{(2)} \right\},$$

by using properties of monotonicity of the functions f and g , we obtain

$$\begin{aligned} x_1^{(1)} &\leq f(x_0^{(1)}, x_0^{(2)}) \leq f(y_0^{(1)}, y_0^{(2)}) = y_1^{(1)} \leq f(z_0^{(1)}, z_0^{(2)}) = z_1^{(1)} \\ x_1^{(2)} &\geq g(x_0^{(1)}, x_0^{(2)}) \geq g(y_0^{(1)}, y_0^{(2)}) = y_1^{(2)} \geq g(z_0^{(1)}, z_0^{(2)}) = z_1^{(2)}, \end{aligned}$$

i.e.,

$$X_1 \preceq_{se} Y_1 \preceq_{se} Z_1.$$

Analogously, the proof that $X_2 \preceq_{se} Y_2 \preceq_{se} Z_2$ follows in same fashion, and so the proof of (28). ■

Theorem 23 Consider the following non-autonomous system of difference equations

$$X_{n+1} = \begin{bmatrix} a_n f(x_n, y_n) \\ b_n g(x_n, y_n) \end{bmatrix}, \quad n = 0, 1, \dots, \quad (29)$$

where $A_n = \begin{bmatrix} a_n \\ b_n \end{bmatrix}$ and $F = \begin{bmatrix} f \\ g \end{bmatrix} : \mathbb{R}_+^2 \rightarrow \mathbb{R}_+^2$ is a competitive map. Assume that

$$\lim_{n \rightarrow \infty} A_n = \lim_{n \rightarrow \infty} \begin{bmatrix} a_n \\ b_n \end{bmatrix} = \begin{bmatrix} \lim_{n \rightarrow \infty} a_n \\ \lim_{n \rightarrow \infty} b_n \end{bmatrix} = \begin{bmatrix} a \\ b \end{bmatrix} = A,$$

and let

$$Y_{n+1} = \begin{bmatrix} a f(u_n, v_n) \\ b g(u_n, v_n) \end{bmatrix}, \quad n = 0, 1, \dots,$$

be the limiting system of difference equations of (29). Also, assume that there exists $\varepsilon_0 = \begin{bmatrix} \varepsilon_0^{(1)} \\ \varepsilon_0^{(2)} \end{bmatrix} \succ_{ne} \begin{bmatrix} 0 \\ 0 \end{bmatrix}$ such that every solution of the system

$$Y_{n+1} = \begin{bmatrix} \alpha f(u_n, v_n) \\ \beta g(u_n, v_n) \end{bmatrix}, \quad n = 0, 1, \dots$$

converges to a constant $\bar{Y}_{A_\varepsilon} = \begin{bmatrix} \bar{x}_{A_\varepsilon} \\ \bar{y}_{A_\varepsilon} \end{bmatrix}$ for every $A_\varepsilon = \begin{bmatrix} \alpha \\ \beta \end{bmatrix}$, $\alpha \in (a - \varepsilon_0^{(1)}, a + \varepsilon_0^{(1)})$, $\beta \in (b - \varepsilon_0^{(2)}, b + \varepsilon_0^{(2)})$.

If

$$\lim_{A_\varepsilon \rightarrow A} \bar{Y}_{A_\varepsilon} = \bar{Y},$$

then every solution of the system (29) satisfies

$$\lim_{n \rightarrow \infty} X_n = \bar{Y}.$$

Proof. For arbitrary $\varepsilon_1 > 0$ and $\varepsilon_2 > 0$ there exists $N = N(\varepsilon_1, \varepsilon_2)$ such that for $n \geq N$ the following

$$a - \varepsilon_1 < a_n < a + \varepsilon_1,$$

$$b - \varepsilon_2 < b_n < b + \varepsilon_2,$$

holds. So we have

$$\begin{bmatrix} (a - \varepsilon_1) f(x_n, y_n) \\ (b + \varepsilon_2) g(x_n, y_n) \end{bmatrix} \preceq_{se} X_{n+1} = \begin{bmatrix} a_n f(x_n, y_n) \\ b_n g(x_n, y_n) \end{bmatrix} \preceq_{se} \begin{bmatrix} (a + \varepsilon_1) f(x_n, y_n) \\ (b - \varepsilon_2) g(x_n, y_n) \end{bmatrix},$$

$n \geq N$.

By Lemma 22 we obtain

$$L_n \preceq_{se} X_n \preceq_{se} U_n, \quad n \geq N, \quad (30)$$

where $L_n = \left\{ \begin{bmatrix} l_n^{(1)} \\ l_n^{(2)} \end{bmatrix} \right\}$ satisfies

$$L_{n+1} = \begin{bmatrix} (a - \varepsilon_1) f(l_n^{(1)}, l_n^{(2)}) \\ (b + \varepsilon_2) g(l_n^{(1)}, l_n^{(2)}) \end{bmatrix},$$

and $U_n = \left\{ \begin{bmatrix} u_n^{(1)} \\ u_n^{(2)} \end{bmatrix} \right\}$ satisfies

$$U_{n+1} = \begin{bmatrix} (a + \varepsilon_1) f(u_n^{(1)}, u_n^{(2)}) \\ (b - \varepsilon_2) g(u_n^{(1)}, u_n^{(2)}) \end{bmatrix}.$$

Inequalities (30) imply

$$\lim_{n \rightarrow \infty} L_n \preceq_{se} \liminf_{n \rightarrow \infty} X_n \preceq_{se} \limsup_{n \rightarrow \infty} X_n \preceq_{se} \lim_{n \rightarrow \infty} U_n,$$

i.e.,

$$\bar{Y}_{\alpha_\varepsilon} \preceq_{se} \liminf_{n \rightarrow \infty} X_n \preceq_{se} \limsup_{n \rightarrow \infty} X_n \preceq_{se} \bar{Y}_{\beta_\varepsilon}, \quad (31)$$

where $\alpha_\varepsilon = \begin{bmatrix} a - \varepsilon_1 \\ b + \varepsilon_2 \end{bmatrix}$, $\beta_\varepsilon = \begin{bmatrix} a + \varepsilon_1 \\ b - \varepsilon_2 \end{bmatrix}$, and $\varepsilon = \begin{bmatrix} \varepsilon_1 \\ \varepsilon_2 \end{bmatrix}$.

Since $\lim_{\varepsilon \rightarrow \mathbf{0}} \bar{Y}_{\alpha_\varepsilon} = \lim_{\varepsilon \rightarrow \mathbf{0}} \bar{Y}_{\beta_\varepsilon} = \bar{Y}$, where $\mathbf{0} = \begin{bmatrix} 0 \\ 0 \end{bmatrix}$, (31) implies that

$$\liminf_{n \rightarrow \infty} X_n = \limsup_{n \rightarrow \infty} X_n = \lim_{n \rightarrow \infty} X_n = \bar{Y}.$$

■

Example 24 Consider the following system of difference equations modelling competition, [12, 13, 14, 15]

$$\left. \begin{aligned} x_{n+1} &= a \frac{1}{1+y_n} x_n \\ y_{n+1} &= b \frac{1}{1+x_n} y_n \end{aligned} \right\}, \quad n = 0, 1, 2, \dots \quad (32)$$

This system has the following equilibrium points:

a) $E_0 = \begin{bmatrix} 0 \\ 0 \end{bmatrix}$, which is locally asymptotically stable if $0 < a < 1$ and $0 < b < 1$;

b) $E_1 = \begin{bmatrix} b-1 \\ a-1 \end{bmatrix}$ for $a > 1$ and $b > 1$, which is a saddle point;

c) every point $E_x = \begin{bmatrix} x \\ 0 \end{bmatrix}$, $x \in \mathbb{R}_+$ if $a = 1$, which is a non-hyperbolic point;

d) every point $E_y = \begin{bmatrix} 0 \\ y \end{bmatrix}$, $y \in \mathbb{R}_+$ if $b = 1$, which is a non-hyperbolic point,

and

e) every point on the x -axis and every point on the y -axis if $a = b = 1$, which is a non-hyperbolic point.

It implies from Jacobi matrix of the map $F = \begin{bmatrix} ax \frac{1}{1+y} \\ by \frac{1}{1+x} \end{bmatrix}$, which has the form

$$J_F \left(\begin{bmatrix} x \\ y \end{bmatrix} \right) = \begin{bmatrix} \frac{a}{1+y} & -\frac{ax}{(1+y)^2} \\ -\frac{by}{(1+x)^2} & \frac{b}{1+x} \end{bmatrix},$$

so that, for example,

$$J_F(E_0) = \begin{bmatrix} a & 0 \\ 0 & b \end{bmatrix}$$

has eigenvalues $\lambda_1 = a$ and $\lambda_2 = b$, while

$$J_F(E_+) = \begin{bmatrix} 1 & \frac{1-b}{a} \\ \frac{1-a}{b} & b \end{bmatrix}$$

has eigenvalues $\lambda_{\pm} = 1 \pm \sqrt{\frac{(a-1)(b-1)}{ab}}$.

The fact that $E_0 = (0, 0)$ is globally asymptotically stable if $0 < a < 1$ and $0 < b < 1$ follows by using the Lyapunov function $V : \mathbb{R}_+^2 \rightarrow \mathbb{R}$ of the form

$V\left(\begin{bmatrix} x \\ y \end{bmatrix}\right) = x^2 + y^2$ of the map F . Namely, if $x \geq 0$, $y \geq 0$, $(x, y) \neq (0, 0)$, $0 < a < 1$, and $0 < b < 1$, we have that

$$\begin{aligned} \Delta V &= V\left(F\left(\begin{bmatrix} x \\ y \end{bmatrix}\right)\right) - V\left(\begin{bmatrix} x \\ y \end{bmatrix}\right) = \left(ax\frac{1}{1+y}\right)^2 + \left(by\frac{1}{1+x}\right)^2 - x^2 - y^2 \\ &= x^2\left(\left(\frac{a}{1+y}\right)^2 - 1\right) + y^2\left(\left(\frac{b}{1+x}\right)^2 - 1\right) \\ &\leq x^2(a^2 - 1) + y^2(b^2 - 1) < 0. \end{aligned}$$

Since $V\left(\begin{bmatrix} x \\ y \end{bmatrix}\right) = x^2 + y^2 \rightarrow \infty$, as $\left\|\begin{bmatrix} x \\ y \end{bmatrix}\right\| \rightarrow \infty$, then equilibrium point $E_0 = (0, 0)$ is globally asymptotically stable when $0 < a < 1$ and $0 < b < 1$.

This result was proven in a different way in [12]. If we consider now the following system

$$\left. \begin{aligned} x_{n+1} &= a_n \frac{1}{1+y_n} x_n \\ y_{n+1} &= b_n \frac{1}{1+x_n} y_n \end{aligned} \right\}, \quad n = 0, 1, 2, \dots, \quad (33)$$

where $\lim_{n \rightarrow \infty} a_n = a$ and $\lim_{n \rightarrow \infty} b_n = b$, then by using Theorem 23 taking $f(x_n, y_n) = \frac{1}{1+y_n} x_n$ and $g(x_n, y_n) = \frac{1}{1+x_n} y_n$, all solutions of System (33) globally asymptotically converge to $E_0 = (0, 0)$ for $0 < a < 1$ and $0 < b < 1$, and for all $x_0 \geq 0$ and $y_0 \geq 0$.

Theorem 25 *Consider the following non-autonomous competitive system*

$$X_{n+1} = \begin{bmatrix} \frac{x_n}{a_n + y_n} \\ \frac{y_n}{b_n + x_n} \end{bmatrix}, \quad n = 0, 1, 2, \dots \quad (34)$$

Assume that $A_n = \begin{bmatrix} a_n \\ b_n \end{bmatrix}$ and

$$\lim_{n \rightarrow \infty} A_n = \lim_{n \rightarrow \infty} \begin{bmatrix} a_n \\ b_n \end{bmatrix} = \begin{bmatrix} \lim_{n \rightarrow \infty} a_n \\ \lim_{n \rightarrow \infty} b_n \end{bmatrix} = \begin{bmatrix} a \\ b \end{bmatrix} = A,$$

and let

$$Y_{n+1} = \begin{bmatrix} \frac{x_n}{a + y_n} \\ \frac{y_n}{b + x_n} \end{bmatrix}, \quad n = 0, 1, 2, \dots, \quad (35)$$

be the limiting system of System (34). Also, assume that there exists $\varepsilon_0 = \begin{bmatrix} \varepsilon_0^{(1)} \\ \varepsilon_0^{(2)} \end{bmatrix}$
 $\succ_{ne} \begin{bmatrix} 0 \\ 0 \end{bmatrix}$ such that every solution of the system

$$Y_{n+1} = \begin{bmatrix} \frac{x_n}{\alpha + y_n} \\ \frac{y_n}{\beta + x_n} \end{bmatrix}, \quad n = 0, 1, \dots$$

converges to a constant $\bar{Y}_{A_\varepsilon} = \begin{bmatrix} \bar{x}_{A_\varepsilon} \\ \bar{y}_{A_\varepsilon} \end{bmatrix}$ for every $A_\varepsilon = \begin{bmatrix} \alpha \\ \beta \end{bmatrix}$, $\alpha \in (a - \varepsilon_0^{(1)}, a + \varepsilon_0^{(1)})$, $\beta \in (b - \varepsilon_0^{(2)}, b + \varepsilon_0^{(2)})$.

If

$$\lim_{A_\varepsilon \rightarrow A} \bar{Y}_{A_\varepsilon} = \bar{Y},$$

then every solution of the system (34) satisfies

$$\lim_{n \rightarrow \infty} X_n = \bar{Y}.$$

Proof. For arbitrary $\varepsilon_1 > 0$ and $\varepsilon_2 > 0$, there exists $N = N(\varepsilon_1, \varepsilon_2)$ such that for $n \geq N$, the following

$$a - \varepsilon_1 < a_n < a + \varepsilon_1,$$

$$b - \varepsilon_2 < b_n < b + \varepsilon_2,$$

holds. This implies that

$$\begin{bmatrix} \frac{x_n}{a + \varepsilon_1 + y_n} \\ \frac{y_n}{b - \varepsilon_2 + x_n} \end{bmatrix} \preceq_{se} X_{n+1} = \begin{bmatrix} \frac{x_n}{a_n + y_n} \\ \frac{y_n}{b_n + x_n} \end{bmatrix} \preceq_{se} \begin{bmatrix} \frac{x_n}{a - \varepsilon_1 + y_n} \\ \frac{y_n}{b + \varepsilon_2 + x_n} \end{bmatrix}, \quad n \geq N.$$

By Lemma 22 we obtain

$$L_n \preceq_{se} X_n \preceq_{se} U_n, \quad n \geq N, \quad (36)$$

where $\{L_n\} = \left\{ \begin{bmatrix} l_n^{(1)} \\ l_n^{(2)} \end{bmatrix} \right\}$ satisfies

$$L_{n+1} = \begin{bmatrix} \frac{l_n^{(1)}}{a + \varepsilon_1 + l_n^{(2)}} \\ \frac{l_n^{(2)}}{b - \varepsilon_2 + l_n^{(1)}} \end{bmatrix},$$

and $\{U_n\} = \left\{ \begin{bmatrix} u_n^{(1)} \\ u_n^{(2)} \end{bmatrix} \right\}$ satisfies

$$U_{n+1} = \begin{bmatrix} \frac{u_n^{(1)}}{a - \varepsilon_1 + u_n^{(2)}} \\ \frac{u_n^{(2)}}{b + \varepsilon_2 + u_n^{(1)}} \end{bmatrix}.$$

Inequalities (36) imply

$$\lim_{n \rightarrow \infty} L_n \preceq_{se} \liminf_{n \rightarrow \infty} X_n \preceq_{se} \limsup_{n \rightarrow \infty} X_n \preceq_{se} \lim_{n \rightarrow \infty} U_n,$$

i.e.,

$$\bar{Y}_{\alpha_\varepsilon} \preceq_{se} \liminf_{n \rightarrow \infty} X_n \preceq_{se} \limsup_{n \rightarrow \infty} X_n \preceq_{se} \bar{Y}_{\beta_\varepsilon}, \quad (37)$$

where $\alpha_\varepsilon = \begin{bmatrix} a + \varepsilon_1 \\ b - \varepsilon_2 \end{bmatrix}$, $\beta_\varepsilon = \begin{bmatrix} a - \varepsilon_1 \\ b + \varepsilon_2 \end{bmatrix}$, and $\varepsilon = \begin{bmatrix} \varepsilon_1 \\ \varepsilon_2 \end{bmatrix}$. Since $\lim_{\varepsilon \rightarrow \mathbf{0}} \bar{Y}_{\alpha_\varepsilon} = \lim_{\varepsilon \rightarrow \mathbf{0}} \bar{Y}_{\beta_\varepsilon} = \bar{Y}$, where $\mathbf{0} = \begin{bmatrix} 0 \\ 0 \end{bmatrix}$, (37) implies that

$$\liminf_{n \rightarrow \infty} X_n = \limsup_{n \rightarrow \infty} X_n = \lim_{n \rightarrow \infty} X_n = \bar{Y}.$$

■

Theorem 26 Consider the following non-autonomous competitive system

$$X_{n+1} = \begin{bmatrix} \frac{\alpha_n x_n}{a_n + y_n} \\ \frac{\beta_n y_n}{b_n + x_n} \end{bmatrix}, \quad n = 0, 1, \dots \quad (38)$$

Assume that $A_n = \begin{bmatrix} \alpha_n \\ a_n \\ \beta_n \\ b_n \end{bmatrix}$ and

$$\lim_{n \rightarrow \infty} A_n = \lim_{n \rightarrow \infty} \begin{bmatrix} \alpha_n \\ a_n \\ \beta_n \\ b_n \end{bmatrix} = \begin{bmatrix} \lim_{n \rightarrow \infty} \alpha \\ \lim_{n \rightarrow \infty} a_n \\ \lim_{n \rightarrow \infty} \beta_n \\ \lim_{n \rightarrow \infty} b_n \end{bmatrix} = \begin{bmatrix} \alpha \\ a \\ \beta \\ b \end{bmatrix} = A,$$

and let

$$Y_{n+1} = \begin{bmatrix} \frac{\alpha x_n}{a + y_n} \\ \frac{\beta y_n}{b + x_n} \end{bmatrix}, \quad n = 0, 1, 2, \dots, \quad (39)$$

be the limiting system of System (38). Also, assume that there exists $\varepsilon_0 =$

$$\begin{bmatrix} \varepsilon_0^{(1)} \\ \varepsilon_0^{(2)} \\ \varepsilon_0^{(3)} \\ \varepsilon_0^{(4)} \\ \varepsilon_0 \end{bmatrix} \gamma_{ne} \begin{bmatrix} 0 \\ 0 \\ 0 \\ 0 \end{bmatrix} \text{ such that every solution of the system}$$

$$Y_{n+1} = \begin{bmatrix} \frac{\lambda x_n}{\mu + y_n} \\ \frac{\nu y_n}{\xi + x_n} \end{bmatrix}, \quad n = 0, 1, 2, \dots$$

converges to a constant $\bar{Y}_{A_\varepsilon} = \begin{bmatrix} \bar{x}_{A_\varepsilon} \\ \bar{y}_{A_\varepsilon} \end{bmatrix}$ for every $A_\varepsilon = \begin{bmatrix} \lambda \\ \mu \\ \nu \\ \xi \end{bmatrix}$, $\lambda \in$

$(\alpha - \varepsilon_0^{(1)}, \alpha + \varepsilon_0^{(1)})$, $\mu \in (a - \varepsilon_0^{(2)}, a + \varepsilon_0^{(2)})$, $\nu \in (\beta - \varepsilon_0^{(2)}, \beta + \varepsilon_0^{(2)})$, and $\xi \in (b - \varepsilon_0^{(2)}, b + \varepsilon_0^{(2)})$.

If

$$\lim_{A_\varepsilon \rightarrow A} \bar{Y}_{A_\varepsilon} = \bar{Y},$$

then every solution of the system (38) satisfies

$$\lim_{n \rightarrow \infty} X_n = \bar{Y}.$$

Proof. For arbitrary $\varepsilon = \begin{bmatrix} \varepsilon_1 \\ \varepsilon_2 \\ \varepsilon_3 \\ \varepsilon_4 \end{bmatrix} \succ_{ne} \begin{bmatrix} 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}$, there exists $N = N(\varepsilon)$ such that for $n \geq N$, the following

$$\alpha - \varepsilon_1 < \alpha_n < \alpha + \varepsilon_1,$$

$$a - \varepsilon_2 < a_n < a + \varepsilon_2,$$

$$\beta - \varepsilon_3 < \beta_n < \beta + \varepsilon_3,$$

$$b - \varepsilon_4 < b_n < b + \varepsilon_4,$$

holds. This implies that

$$\begin{bmatrix} \frac{(\alpha - \varepsilon_1) x_n}{a + \varepsilon_2 + y_n} \\ \frac{(\beta + \varepsilon_3) y_n}{b - \varepsilon_4 + x_n} \end{bmatrix} \preceq_{se} X_{n+1} = \begin{bmatrix} \frac{x_n}{a_n + y_n} \\ \frac{y_n}{b_n + x_n} \end{bmatrix} \preceq_{se} \begin{bmatrix} \frac{(\alpha + \varepsilon_1) x_n}{a - \varepsilon_2 + y_n} \\ \frac{(\beta - \varepsilon_3) y_n}{b + \varepsilon_4 + x_n} \end{bmatrix}, \quad n \geq N(\varepsilon).$$

Since F is competitive map, Lemma 22 implies

$$L_n \preceq_{se} X_n \preceq_{se} U_n, \quad n \geq N(\varepsilon), \quad (40)$$

where $\{L_n\} = \left\{ \begin{bmatrix} l_n^{(1)} \\ l_n^{(2)} \end{bmatrix} \right\}$ satisfies

$$L_{n+1} = \begin{bmatrix} \frac{(\alpha - \varepsilon_1) l_n^{(1)}}{a + \varepsilon_2 + l_n^{(2)}} \\ \frac{(\beta + \varepsilon_3) l_n^{(2)}}{b - \varepsilon_4 + l_n^{(1)}} \end{bmatrix},$$

and $\{U_n\} = \left\{ \begin{bmatrix} u_n^{(1)} \\ u_n^{(2)} \end{bmatrix} \right\}$ satisfies

$$U_{n+1} = \begin{bmatrix} \frac{(\alpha + \varepsilon_1) u_n^{(1)}}{a - \varepsilon_2 + u_n^{(2)}} \\ \frac{(\beta - \varepsilon_3) u_n^{(2)}}{b + \varepsilon_4 + u_n^{(1)}} \end{bmatrix}.$$

Inequalities (40) imply

$$\lim_{n \rightarrow \infty} L_n \preceq_{se} \liminf_{n \rightarrow \infty} X_n \preceq_{se} \limsup_{n \rightarrow \infty} X_n \preceq_{se} \lim_{n \rightarrow \infty} U_n,$$

i.e., (37)

$$\text{where } \alpha_\varepsilon = \begin{bmatrix} \alpha - \varepsilon_1 \\ a + \varepsilon_2 \\ \beta + \varepsilon_3 \\ b - \varepsilon_4 \end{bmatrix}, \beta_\varepsilon = \begin{bmatrix} \alpha + \varepsilon_1 \\ a - \varepsilon_2 \\ \beta - \varepsilon_3 \\ b + \varepsilon_4 \end{bmatrix}, \text{ and } \varepsilon = \begin{bmatrix} \varepsilon_1 \\ \varepsilon_2 \\ \varepsilon_3 \\ \varepsilon_4 \end{bmatrix}.$$

$$\text{Since } \lim_{\varepsilon \rightarrow \mathbf{0}} \bar{Y}_{\alpha_\varepsilon} = \lim_{\varepsilon \rightarrow \mathbf{0}} \bar{Y}_{\beta_\varepsilon} = \bar{Y}, \text{ where } \mathbf{0} = \begin{bmatrix} 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}, \text{ (37) implies that}$$

$$\lim_{n \rightarrow \infty} X_n = \bar{Y}.$$

■

Theorem 27 Consider the following non-autonomous Leslie-Gower model

$$X_{n+1} = \begin{bmatrix} \frac{a_n x_n}{1 + c_n^{(11)} x_n + c^{(12)} y_n} \\ \frac{b_n y_n}{1 + c^{(21)} x_n + c_n^{(22)} y_n} \end{bmatrix}, \quad n = 0, 1, 2, \dots \quad (41)$$

$$\text{Assume that } A_n = \begin{bmatrix} a_n \\ c_n^{(11)} \\ b_n \\ c_n^{(22)} \end{bmatrix} \text{ and}$$

$$\lim_{n \rightarrow \infty} A_n = \lim_{n \rightarrow \infty} \begin{bmatrix} a_n \\ c_n^{(11)} \\ b_n \\ c_n^{(22)} \end{bmatrix} = \begin{bmatrix} \lim_{n \rightarrow \infty} a_n \\ \lim_{n \rightarrow \infty} c_n^{(11)} \\ \lim_{n \rightarrow \infty} b_n \\ \lim_{n \rightarrow \infty} c_n^{(22)} \end{bmatrix} = \begin{bmatrix} a \\ c^{(11)} \\ b \\ c^{(22)} \end{bmatrix} = A,$$

and let

$$Y_{n+1} = \begin{bmatrix} \frac{ax_n}{1 + c^{(11)} x_n + c^{(12)} y_n} \\ \frac{by_n}{1 + c^{(21)} x_n + c^{(22)} y_n} \end{bmatrix}, \quad n = 0, 1, 2, \dots \quad (42)$$

be the limiting system of System (42). Also, assume that there exists $\varepsilon_0 =$

$$\begin{bmatrix} \varepsilon_0^{(1)} \\ \varepsilon_0^{(2)} \\ \varepsilon_0^{(3)} \\ \varepsilon_0^{(4)} \end{bmatrix} \succ_{ne} \begin{bmatrix} 0 \\ 0 \\ 0 \\ 0 \end{bmatrix} \text{ such that every solution of the system}$$

$$Y_{n+1} = \begin{bmatrix} \frac{\lambda x_n}{1 + \mu x_n + c^{(12)} y_n} \\ \frac{\nu y_n}{1 + c^{(21)} x_n + \xi y_n} \end{bmatrix}, \quad n = 0, 1, 2, \dots .$$

converges to a constant $\bar{Y}_{A_\varepsilon} = \begin{bmatrix} \bar{x}_{A_\varepsilon} \\ \bar{y}_{A_\varepsilon} \end{bmatrix}$ for every $A_\varepsilon = \begin{bmatrix} \lambda \\ \mu \\ \nu \\ \xi \end{bmatrix}$, $\lambda \in (a - \varepsilon_0^{(1)}, a + \varepsilon_0^{(1)})$, $\mu \in (c^{(11)} - \varepsilon_0^{(2)}, c^{(11)} + \varepsilon_0^{(2)})$, $\nu \in (b - \varepsilon_0^{(2)}, b + \varepsilon_0^{(2)})$, and $\xi \in (c^{(22)} - \varepsilon_0^{(2)}, c^{(22)} + \varepsilon_0^{(2)})$.

If

$$\lim_{A_\varepsilon \rightarrow A} \bar{Y}_{A_\varepsilon} = \bar{Y},$$

then every solution of the system (42) satisfies

$$\lim_{n \rightarrow \infty} X_n = \bar{Y}.$$

Proof. For arbitrary $\varepsilon = \begin{bmatrix} \varepsilon_1 \\ \varepsilon_2 \\ \varepsilon_3 \\ \varepsilon_4 \end{bmatrix} \succ_{ne} \begin{bmatrix} 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}$, there exists $N = N(\varepsilon)$ such that for $n \geq N$, the following

$$\begin{aligned} a - \varepsilon_1 &< a_n < a + \varepsilon_1, \\ c^{(11)} - \varepsilon_2 &< c_n^{(11)} < c^{(11)} + \varepsilon_2, \\ b - \varepsilon_3 &< b_n < b + \varepsilon_3, \\ c^{(22)} - \varepsilon_4 &< c_n^{(22)} < c^{(22)} + \varepsilon_4, \end{aligned}$$

holds. This implies that the following inequalities are satisfied for $n \geq N(\varepsilon)$

$$\begin{aligned} \begin{bmatrix} \frac{(a - \varepsilon_1) x_n}{1 + (c^{(11)} + \varepsilon_2) x_n + c^{(12)} y_n} \\ \frac{(b + \varepsilon_3) y_n}{1 + c^{(21)} x_n + (c^{(22)} - \varepsilon_4) y_n} \end{bmatrix} &\preceq_{se} X_{n+1} = \begin{bmatrix} \frac{a_n x_n}{1 + c_n^{(11)} x_n + c^{(12)} y_n} \\ \frac{b_n y_n}{1 + c^{(21)} x_n + c_n^{(22)} y_n} \end{bmatrix} \\ &\preceq_{se} \begin{bmatrix} \frac{(a + \varepsilon_1) x_n}{1 + (c^{(11)} - \varepsilon_2) x_n + c^{(12)} y_n} \\ \frac{(b - \varepsilon_3) y_n}{1 + c^{(21)} x_n + (c^{(22)} + \varepsilon_4) y_n} \end{bmatrix}. \end{aligned} \quad (43)$$

Since $F = \begin{bmatrix} \frac{a_n x}{1 + c_n^{(11)} x + c^{(12)} y} \\ \frac{b_n y}{1 + c^{(21)} x + c_n^{(22)} y} \end{bmatrix}$ is a competitive map, Lemma 22 implies

$$L_n \preceq_{se} X_n \preceq_{se} U_n, \quad n \geq N(\varepsilon), \quad (44)$$

where $\{L_n\} = \left\{ \begin{bmatrix} l_n^{(1)} \\ l_n^{(2)} \end{bmatrix} \right\}$ satisfies

$$L_{n+1} = \begin{bmatrix} \frac{(a - \varepsilon_1) l_n^{(1)}}{1 + (c^{(11)} + \varepsilon_2) l_n^{(1)} + c^{(12)} l_n^{(2)}} \\ \frac{(b + \varepsilon_3) l_n^{(2)}}{1 + c^{(21)} l_n^{(1)} + (c^{(22)} - \varepsilon_4) l_n^{(2)}} \end{bmatrix},$$

and $\{U_n\} = \left\{ \begin{bmatrix} u_n^{(1)} \\ u_n^{(2)} \end{bmatrix} \right\}$ satisfies

$$U_{n+1} = \begin{bmatrix} \frac{(a + \varepsilon_1) u_n^{(1)}}{1 + (c^{(11)} - \varepsilon_2) u_n^{(1)} + c^{(12)} u_n^{(2)}} \\ \frac{(b - \varepsilon_3) u_n^{(2)}}{1 + c^{(21)} u_n^{(1)} + (c^{(22)} + \varepsilon_4) u_n^{(2)}} \end{bmatrix}.$$

Inequalities (44) imply

$$\lim_{n \rightarrow \infty} L_n \preceq_{se} \liminf_{n \rightarrow \infty} X_n \preceq_{se} \limsup_{n \rightarrow \infty} X_n \preceq_{se} \lim_{n \rightarrow \infty} U_n,$$

i.e.,

$$\bar{Y}_{\alpha\varepsilon} \preceq_{se} \liminf_{n \rightarrow \infty} X_n \preceq_{se} \limsup_{n \rightarrow \infty} X_n \preceq_{se} \bar{Y}_{\beta\varepsilon}, \quad (45)$$

where $\alpha_\varepsilon = \begin{bmatrix} a - \varepsilon_1 \\ c^{(11)} + \varepsilon_2 \\ b + \varepsilon_3 \\ c^{(22)} - \varepsilon_4 \end{bmatrix}$, $\beta_\varepsilon = \begin{bmatrix} a + \varepsilon_1 \\ c^{(11)} - \varepsilon_2 \\ b - \varepsilon_3 \\ c^{(22)} + \varepsilon_4 \end{bmatrix}$, and $\varepsilon = \begin{bmatrix} \varepsilon_1 \\ \varepsilon_2 \\ \varepsilon_3 \\ \varepsilon_4 \end{bmatrix}$.

Since $\lim_{\varepsilon \rightarrow \mathbf{0}} \bar{Y}_{\alpha_\varepsilon} = \lim_{\varepsilon \rightarrow \mathbf{0}} \bar{Y}_{\beta_\varepsilon} = \bar{Y}$, where $\mathbf{0} = \begin{bmatrix} 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}$, (45) implies that

$$\liminf_{n \rightarrow \infty} X_n = \limsup_{n \rightarrow \infty} X_n = \lim_{n \rightarrow \infty} X_n = \bar{Y}.$$

■

Remark 28 Note that System (42) has a unique equilibrium point $E_0 = \begin{bmatrix} 0 \\ 0 \end{bmatrix}$, for $0 < a < 1$, $0 < b < 1$, which is locally asymptotically stable. By using Lyapunov function $V : \mathbb{R}_+^2 \rightarrow \mathbb{R}$ of the form $V \left(\begin{bmatrix} x \\ y \end{bmatrix} \right) = x^2 + y^2$ of the map

$$F = \begin{bmatrix} \frac{ax}{1 + c^{(11)}x + c^{(12)}y} \\ \frac{by}{1 + c^{(21)}x + c^{(22)}y} \end{bmatrix},$$

we can conclude that the equilibrium point E_0 is

globally asymptotically stable for $0 < a < 1$ and $0 < b < 1$. Namely, if $x \geq 0$, $y \geq 0$, $(x, y) \neq (0, 0)$ and $0 < a < 1$, $0 < b < 1$, we have that

$$\begin{aligned} \Delta V &= V \left(F \left(\begin{bmatrix} x \\ y \end{bmatrix} \right) \right) - V \left(\begin{bmatrix} x \\ y \end{bmatrix} \right) \\ &= \left(\frac{ax}{1 + c^{(11)}x + c^{(12)}y} \right)^2 + \left(\frac{by}{1 + c^{(21)}x + c^{(22)}y} \right)^2 - x^2 - y^2 \\ &= x^2 \left(\left(\frac{a}{1 + c^{(11)}x + c^{(12)}y} \right)^2 - 1 \right) + y^2 \left(\left(\frac{b}{1 + c^{(21)}x + c^{(22)}y} \right)^2 - 1 \right) \\ &< x^2 (a^2 - 1) + y^2 (b^2 - 1) < 0. \end{aligned}$$

Since $V \left(\begin{bmatrix} x \\ y \end{bmatrix} \right) = x^2 + y^2 \rightarrow \infty$, as $\left\| \begin{bmatrix} x \\ y \end{bmatrix} \right\| \rightarrow \infty$, then equilibrium point $E_0 = (0, 0)$ is globally asymptotically stable.

Example 29 Competitive system considered in [16] was System

$$\left. \begin{aligned} x_{n+1} &= \frac{a + x_n}{b + y_n} \\ y_{n+1} &= \frac{d + y_n}{e + x_n} \end{aligned} \right\} \quad (46)$$

$n = 0, 1, \dots$, for all positive values of parameters a, b, d, e , and non-negative initial conditions x_0, y_0 , where global dynamics was described. We found all values of parameters for which the unique equilibrium solution (\bar{x}, \bar{y}) of (46) was globally asymptotically stable. Consider now the nonautonomous version of System (46):

$$\left. \begin{aligned} x_{n+1} &= \frac{a_n + x_n}{b_n + y_n} \\ y_{n+1} &= \frac{d_n + y_n}{e_n + x_n}, \end{aligned} \right\} \quad (47)$$

$n = 0, 1, \dots$, for non-negative initial conditions x_0, y_0 , where each of positive valued sequences a_n, b_n, d_n, e_n satisfies:

$$\lim_{n \rightarrow \infty} a_n = a, \lim_{n \rightarrow \infty} b_n = b, \lim_{n \rightarrow \infty} d_n = d, \lim_{n \rightarrow \infty} e_n = e.$$

The limiting system for (47) is System (46). So for all values of parameters a, b, d, e for which the unique equilibrium solution (\bar{x}, \bar{y}) of System (46) is globally asymptotically stable we have that

$$\lim_{n \rightarrow \infty} (x_n, y_n) = (\bar{x}, \bar{y}),$$

for every solution (x_n, y_n) of non-autonomous system (47).

Example 30 Competitive system considered in [17] was System

$$\left. \begin{aligned} x_{n+1} &= \frac{ax_n}{1 + x_n + c_1 y_n} + h \\ y_{n+1} &= \frac{by_n}{1 + c_2 x_n + y_n} \end{aligned} \right\} \quad (48)$$

$n = 0, 1, \dots$, for all positive values of parameters a, b, c_1, c_2, h , and non-negative initial conditions x_0, y_0 , where global dynamics was described. We found all values of parameters for which the unique equilibrium solution (\bar{x}, \bar{y}) of (46) was globally asymptotically stable. Consider now the nonautonomous version of System (46):

$$\left. \begin{aligned} x_{n+1} &= \frac{a_n x_n}{1 + x_n + c_1(n) y_n} + h_n \\ y_{n+1} &= \frac{b_n y_n}{1 + c_2(n) x_n + y_n} \end{aligned} \right\} \quad (49)$$

$n = 0, 1, \dots$, for non-negative initial conditions x_0, y_0 , where each of positive valued sequences $a_n, b_n, c_1(n), c_2(n), h_n$ satisfies:

$$\lim_{n \rightarrow \infty} a_n = a, \lim_{n \rightarrow \infty} b_n = b, \lim_{n \rightarrow \infty} c_1(n) = c_1, \lim_{n \rightarrow \infty} c_2(n) = c_2, \lim_{n \rightarrow \infty} h_n = h.$$

The limiting system for (49) is System (48). So for all values of parameters for which the unique equilibrium solution (\bar{x}, \bar{y}) of System (48) is globally asymptotically stable we have that

$$\lim_{n \rightarrow \infty} (x_n, y_n) = (\bar{x}, \bar{y}),$$

for every solution (x_n, y_n) of non-autonomous system (49).

Example 31 Competitive system considered in [18] was System

$$\left. \begin{aligned} x_{n+1} &= \frac{b_1 x_n}{1 + x_n + c_1 y_n} + h_1 \\ y_{n+1} &= \frac{b_2 y_n}{1 + c_2 x_n + y_n} + h_2 \end{aligned} \right\} \quad (50)$$

$n = 0, 1, \dots$, for all positive values of parameters $b_1, b_2, c_1, c_2, h_1, h_2$, and non-negative initial conditions x_0, y_0 , where global dynamics was described for all values of parameters. System (50) has between one and three equilibria, and the number of equilibria determines global behavior of this system. Here h_1 and h_2 are considered as constant stockings of two species which are in competition of Leslie-Gower type. We found in [18] that the unique equilibrium solution (\bar{x}, \bar{y}) of (50) was globally asymptotically stable. We also found sufficient conditions for system (50) to have a unique equilibrium solution.

Consider now the nonautonomous version of System (50):

$$\left. \begin{aligned} x_{n+1} &= \frac{b_1 x_n}{1 + x_n + c_1 y_n} + h_1(n) \\ y_{n+1} &= \frac{b_2 y_n}{1 + c_2 x_n + y_n} + h_2(n) \end{aligned} \right\} \quad (51)$$

$n = 0, 1, \dots$, for non-negative initial conditions x_0, y_0 , where each of the positive valued sequences $h_1(n), h_2(n), h_n$ satisfies:

$$\lim_{n \rightarrow \infty} h_1(n) = h_1, \lim_{n \rightarrow \infty} h_2(n) = h_2.$$

The limiting system for (51) is System (50). So for all values of parameters for which the unique equilibrium solution (\bar{x}, \bar{y}) of System (50) is globally asymptotically stable we have that

$$\lim_{n \rightarrow \infty} (x_n, y_n) = (\bar{x}, \bar{y}),$$

for every solution (x_n, y_n) of non-autonomous system (51). For instance, as a consequence of Theorem 5 in [18] we have the following result:

Corollary 32 *If at least one of the following conditions is satisfied*

$$1 - b_1 + h_1 + c_1 h_2 \geq 0 \quad \text{and} \quad 1 - b_2 + h_2 + c_2 h_1 \geq 0 \quad (52)$$

or

$$c_1 c_2 \leq 1 \quad (53)$$

then system (51) has a unique equilibrium, which is globally asymptotically stable.

Taking $h_1 = h, h_2 = 0$ in Corollary 32 we get the global asymptotic stability result for system (48).

2.3 Examples of competitive evolutionary models

In this section, we consider some competitive evolutionary models using the Beverton-Holt function and its modification.

One of the reasons that model parameters can change in time is Darwinian evolution, which is a case that will be briefly explained here. The detailed explanation is given in [4, 5, 6, 7, 19]. Suppose v is a quantified, phenotypic trait of an individual that is subject to evolution. If we assume the per capita contribution to the population made by an individual depends on its trait v , then $f = f(x, v)$ depends on both x and v . It might happen that this contribution also depends on the traits of other individuals. We can model this situation by assuming that f also depends on the mean trait u in the population so that $f = f(x, v, u)$. A

canonical way to model Darwinian evolution is to model the dynamics of x_n and the mean trait u_n by means of the equations

$$x_{n+1} = f(x_n, v, u_n)|_{v=u_n} x_n \quad (54)$$

$$u_{n+1} = u_n + \sigma^2 \frac{\partial F(x_n, v, u_n)}{\partial v} |_{v=u_n}, \quad (55)$$

see [19].

Equation (72) asserts that the population dynamics can be modeled by assuming the individual trait v is equal to the population mean. Equation (73) (called Lande's or Fisher's or the breeder's equation) prescribes that the change in the mean trait is proportional to the fitness gradient, where fitness in this model is denoted by $F(x, v, u)$. The modeler decides on an appropriate measure of fitness, which is often taken to be f or $\ln f$. The constant of proportionality $\sigma^2 \geq 0$ is called the *speed of evolution*. It is related to the variance of the trait in the population, which is assumed constant in time. Thus, if $\sigma^2 = 0$ no evolution occurs (there is no variability) and one has a one-dimensional difference equation (72) for just population dynamics. If evolution occurs $\sigma^2 > 0$ then the model is a two dimensional system of difference equations with state variable $[x_n, u_n]$. The term x_n in Equation (72) can be vector. Similarly, mean trait u_n can be vector as well. Also x_n can be scalar while u_n can be vector - case when evolution depends on several traits.

Example 33 Now, we investigate the following competitive evolutionary model where the two growth coefficients a and b depend on two independent traits $u_1(n)$

and $u_2(n)$

$$\begin{aligned}
x_{n+1} &= a(u_1(n)) \frac{1}{1+y_n} x_n \\
y_{n+1} &= b(u_2(n)) \frac{1}{1+x_n} y_n \\
u_1(n+1) &= u_1(n) + \sigma_1^2 \frac{a'(u_1(n))}{a(u_1(n))} \\
u_2(n+1) &= u_2(n) + \sigma_2^2 \frac{b'(u_2(n))}{b(u_2(n))},
\end{aligned} \tag{56}$$

where $a(u_1) > 0$ and $b(u_2) > 0$ are twice differentiable functions on their domains. The third and fourth equations of system (56) are called Fisher's or Lande's equations, see [19].

The fixed points of the functions u_1 and u_2 are u_1^* and u_2^* , respectively, where u_1^* and u_2^* are critical points of a and b .

If u_1^* and u_2^* are locally asymptotically stable, that is, if the following inequalities hold

$$\frac{-2}{\sigma_1^2} < \frac{a''(u_1^*)}{a(u_1^*)} < 0 \quad \text{and} \quad \frac{-2}{\sigma_2^2} < \frac{b''(u_2^*)}{b(u_2^*)} < 0, \tag{57}$$

then there exist open neighborhoods \mathcal{U}_1 and \mathcal{U}_2 of u_1^* and u_2^* , respectively, such that

$$\lim_{n \rightarrow \infty} u_1(n) = u_1^* \quad \text{and} \quad \lim_{n \rightarrow \infty} u_2(n) = u_2^*.$$

This implies that the non-autonomous system formed by the first two equations in (56) is asymptotic to the following limiting system

$$\left. \begin{aligned}
x_{n+1} &= a(u_1^*) \frac{1}{1+y_n} x_n \\
y_{n+1} &= b(u_2^*) \frac{1}{1+x_n} y_n
\end{aligned} \right\}. \tag{58}$$

System (58) has a unique equilibrium point $E_0^* = \begin{bmatrix} 0 \\ 0 \end{bmatrix}$ for $0 < a(u_1^*) < 1$ and $0 < b(u_2^*) < 1$, which is locally asymptotically stable.

Based on Theorem 23 and using Example 24 we obtain the following result:

Theorem 34 *If $0 < a(u_1^*) < 1$, $0 < b(u_2^*) < 1$, and the condition (57) holds, then all solutions of non-autonomous system (56) globally asymptotically converge*

$$\text{to } (E_0^*, u_1^*, u_2^*) = \begin{bmatrix} 0 \\ 0 \\ u_1^* \\ u_2^* \end{bmatrix} \in \mathbb{R}_+^2 \times \mathcal{U}_1 \times \mathcal{U}_2, \text{ for all points } x_0 \geq 0 \text{ and } y_0 \geq 0.$$

Example 35 Consider the following model, which is a special case of model (56),

$$\left. \begin{aligned} x_{n+1} &= \left(a + \frac{u_1(n) - 4}{(u_1(n))^2} \right) \frac{1}{1 + y_n} x_n \\ y_{n+1} &= \left(b + \frac{u_2(n)}{(u_2(n))^2 + 4} \right) \frac{1}{1 + x_n} y_n \\ u_1(n+1) &= u_1(n) + \sigma_1^2 \frac{a'(u_1(n))}{a(u_1(n))} \\ u_2(n+1) &= u_2(n) + \sigma_2^2 \frac{b'(u_2(n))}{b(u_2(n))} \end{aligned} \right\} \quad (59)$$

where $a(u_1(n)) = a + \frac{u_1(n) - 4}{(u_1(n))^2}$, $b(u_2(n)) = b + \frac{u_2(n)}{(u_2(n))^2 + 4}$, $0 < a < 1$, and $0 < b < 1$.

From $a'(u_1^*) = \frac{-u_1^* + 8}{(u_1^*)^3} = 0$ and $b'(u_2^*) = \frac{-(u_2^*)^2 + 4}{((u_2^*)^2 + 4)^2} = 0$, we obtain $u_1^* = 8$ and $(u_2^*)_{\pm} = \pm 2$. In the following, we will use $u_2^* = (u_2^*)_+ = 2$. Since $a''(u_1^*) = a''(8) = -\frac{1}{8^3}$, $b''(u_2^*) = b''(2) = -\frac{1}{16}$, $a(u_1^*) = a + \frac{1}{16}$, and $b(u_2^*) = b + \frac{1}{4}$, condition (57) is satisfied if

$$\sigma_1^2 < 64(16a + 1) \quad \text{and} \quad \sigma_2^2 < 8(4b + 1).$$

Then, there exist open neighborhoods \mathcal{U}_1 and \mathcal{U}_2 of u_1^* and u_2^* , respectively, such that

$$\lim_{n \rightarrow \infty} u_1(n) = u_1^* = 8 \quad \text{and} \quad \lim_{n \rightarrow \infty} u_2(n) = u_2^* = 2.$$

Also, the non-autonomous system formed by the first two equations in (59) is asymptotic to the following limiting system

$$\left. \begin{aligned} x_{n+1} &= \left(a + \frac{1}{16} \right) \frac{x_n}{1 + y_n} \\ y_{n+1} &= \left(b + \frac{1}{4} \right) \frac{y_n}{1 + x_n} \end{aligned} \right\}. \quad (60)$$

Based on Theorem 34, we obtain the following two results.

1. If $0 < a < \frac{15}{16}$ and $0 < b < \frac{3}{4}$, then equilibrium point $E_0^* = (0, 0)$ is globally asymptotically stable, i.e., every solution $\{(x_n, y_n)\}$ of (60) satisfies

$$\lim_{n \rightarrow \infty} x_n = \lim_{n \rightarrow \infty} y_n = 0,$$

for all $x_0 \geq 0$ and $y_0 \geq 0$.

2. If $\sigma_1^2 < 64(16a + 1)$, $\sigma_2^2 < 8(4b + 1)$, $0 < a < \frac{15}{16}$, and $0 < b < \frac{3}{4}$, then all solutions of non-autonomous system (59) globally asymptotically converge to $(E_0^*, u_1^*, u_2^*) = (0, 0, u_1^*, u_2^*) \in \mathbb{R}_+^2 \times \mathcal{U}_1 \times \mathcal{U}_2$, for all points $x_0 \geq 0$ and $y_0 \geq 0$.

This shows that σ_1^2 and σ_2^2 are bifurcation parameters in this model.

Example 36 The coefficients of difference equations of state variable may depend on several traits. These traits might be decoupled or coupled. In the case when they are decoupled there will be a single Fisher's equation for each trait.

For instance consider the Leslie-Gower evolutionary model

$$\left. \begin{aligned} x_{n+1} &= \frac{a(u_n)x_n}{1 + x_n + c_1(u_n)y_n} \\ y_{n+1} &= \frac{b(w_n)y_n}{1 + c_2(w_n)x_n + y_n} \end{aligned} \right\} \quad (61)$$

with two Fisher's equations

$$\left. \begin{aligned} u_{n+1} &= p \frac{u_n}{1 + u_n} \\ w_{n+1} &= q \frac{w_n^2}{1 + w_n^2} \end{aligned} \right\} \quad (62)$$

$x_0 > 0, y_0 > 0, p > 0, q > 0, u_0 \geq 0, w_0 \geq 0$, with all positive coefficients for $n = 0, 1, \dots$. The dynamics of two equations in (62) follow from any of Theorems 40, 42 or 43.

The fitness functions for traits u_n and w_n are respectively

$$a(u) = \alpha e^{(1/2 + p + pu - u^2/2)/\sigma_1^2} (1 + u)^{-p/\sigma_1^2}, \quad \alpha > 0 \quad (63)$$

and

$$b(w) = \beta e^{(qw - w^2/2 - q \arctan(w))/\sigma_2^2}, \quad \beta > 0. \quad (64)$$

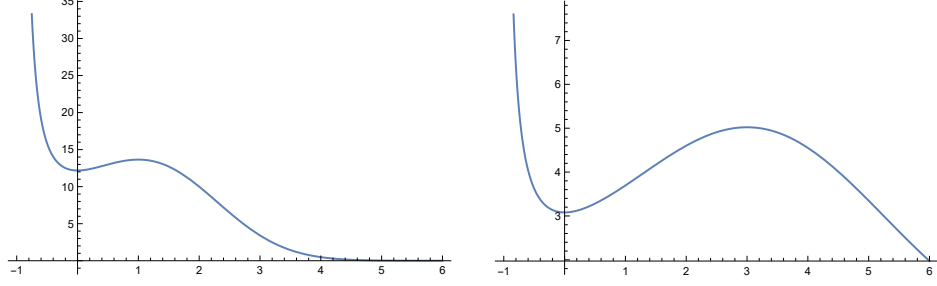


Figure 1: The graphs of fitness functions u_n for Equation (62) for parameter values $\sigma^2 = 1, p = 2$ and $\sigma^2 = 4, p = 4$.

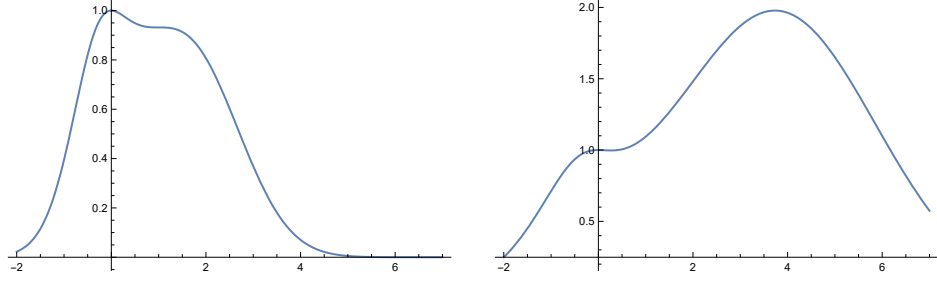


Figure 2: The graphs of fitness functions w_n for Equation (62) for parameter values $\sigma^2 = 1, q = 2$ and $\sigma^2 = 4, q = 4$.

Based on known results for dynamics of Leslie-Gower model and Beverton-Holt's equations we get the following results.

Theorem 37 Consider Equation (61), where two traits u_n and w_n satisfies two Beverton-Holt's equations.

- (i) Assume that $p \leq 1$ and $q \leq 2$. If every solution of (61) converges to the zero equilibrium, which happens if $\alpha < e^{-\frac{1/2+p}{\sigma_1^2}}$ and $\beta < 1$, then every solution of evolutionary model (61), (62) converges to the equilibrium $(0, 0, 0, 0)$.
- (ii) Assume that $p \leq 1$ and $q > 2$. If every solution of (61) converges to the zero equilibrium, which happens if $\alpha < e^{-\frac{1/2+p}{\sigma_1^2}}$ and $\beta < 1$ or $\alpha < e^{-\frac{1/2+p}{\sigma_1^2}}$ and $\beta < e^{-\frac{q\bar{w}_+ - \bar{w}_+/2 - q \arctan(\bar{w}_+)}{\sigma_2^2}}$, then every solution of evolutionary model (61),

(62) converges to the equilibrium $(0, 0, 0, 0)$ or $(0, 0, 0, \bar{w}_+)$, where \bar{w}_+ is larger positive equilibrium of second equation in (62).

(iii) Assume that $p > 1$ and $q \leq 2$. If every solution of (61) converges to the zero equilibrium, which happens if $\alpha < e^{-\frac{p(p+2)}{2\sigma_1^2}} p^{p/\sigma_1^2}$ and $\beta < 1$, then every solution of evolutionary model (61), (62) converges to the equilibrium $(0, 0, p-1, 0)$.

(iv) Assume that $p > 1$ and $q > 2$. If every solution of (61) converges to the zero equilibrium, which happens if $\alpha < e^{-\frac{p(p+2)}{2\sigma_1^2}} p^{p/\sigma_1^2}$, $\beta < e^{-\frac{q\bar{w}_+ - \bar{w}_+ / 2 - q \arctan(\bar{w}_+)}{\sigma_2^2}}$ or $\alpha < e^{-\frac{p(p+2)}{2\sigma_1^2}} p^{p/\sigma_1^2}$, $\beta < 1$, then every solution of evolutionary model (61), (62) converges to the equilibrium $(0, 0, p-1, \bar{w}_+)$ or $(0, 0, p-1, 0)$, where \bar{w}_+ is larger positive equilibrium of second equation in (62).

(v) Assume that $p > 1$ and $q > 2$. If every solution of (61) converges to the interior positive equilibrium, which happens if

$$\alpha > e^{-\frac{p(p+2)}{2\sigma_1^2}} p^{p/\sigma_1^2}, \quad \beta > e^{-\frac{q\bar{w}_+ - \bar{w}_+ / 2 - q \arctan(\bar{w}_+)}{\sigma_2^2}},$$

$$\alpha e^{\frac{p(p+2)}{2\sigma_1^2}} p^{-p/\sigma_1^2} > 1 + c_1(p-1) \left(\beta e^{\frac{q\bar{w}_+ - \bar{w}_+ / 2 - q \arctan(\bar{w}_+)}{\sigma_2^2}} - 1 \right),$$

$$\beta e^{\frac{q\bar{w}_+ - \bar{w}_+ / 2 - q \arctan(\bar{w}_+)}{\sigma_2^2}} > 1 + c_2(\bar{w}_+) \left(\alpha e^{\frac{p(p+2)}{2\sigma_1^2}} p^{-p/\sigma_1^2} - 1 \right)$$

or

$$\alpha > e^{-\frac{p(p+2)}{2\sigma_1^2}} p^{p/\sigma_1^2}, \quad \beta > 1,$$

$$\alpha e^{\frac{p(p+2)}{2\sigma_1^2}} p^{-p/\sigma_1^2} > 1 + c_1(p-1)(\beta - 1),$$

$$\beta > 1 + c_2(0) \left(\alpha e^{\frac{p(p+2)}{2\sigma_1^2}} p^{-p/\sigma_1^2} - 1 \right),$$

then every solution of evolutionary model (61), (62) converges to the equilibrium $(\bar{x}, \bar{y}, p-1, \bar{w}_+)$ or $(\bar{x}, \bar{y}, p-1, 0)$, where \bar{w}_+ is larger positive equilibrium of second equation in (62).

Proof. The proof is a consequence of the global dynamics of first two equations of system (61) in [20, 21] and global dynamics of (62) given in [2, 21]. Notice that global dynamics of (62) follows from Theorem 43. ■

Example 38 Consider system (56) where

$$a(u_1) = b(u_2) = e^{-\frac{u^4}{4} + \frac{2u^3}{3} + \frac{u^2}{2} - 2u}$$

and Fisher's equation has the form

$$u_{n+1} = u_n - \sigma^2(u_n + 1)(u_n - 1)(u_n - 2), \quad n = 0, 1, \dots \quad (65)$$

Equation (65) has three equilibrium solutions $\bar{u}_1 = -1$, $\bar{u}_2 = 1$ and $\bar{u}_3 = 2$. Straightforward local stability analysis implies that $\bar{u}_2 = 1$ is always a repeller, while $\bar{u}_1 = -1$ is locally asymptotically stable when $\sigma^2 < 1/3$ and $\bar{u}_3 = 2$ is locally asymptotically stable when $\sigma^2 < 2/3$. In addition, the function $f(u) = u - \sigma^2(u+1)(u-1)(u-2)$ satisfies negative feedback condition in the neighborhood of the equilibrium solutions \bar{u}_1 and \bar{u}_3 , for the values of σ^2 , which are less than $1/3$ and $2/3$ respectively. Finally the Schwarzian derivative given as

$$-\frac{6\sigma^2(\sigma^2(6x^2 - 8x + 5) + 1)}{(\sigma^2(3x^2 - 4x - 1) - 1)^2}$$

is negative in all points. In view of Theorem 42 both equilibrium solutions are globally asymptotically stable within their immediate basins of attractions (part of basin of attraction which contains the equilibrium) which are given as:

$$B(\bar{u}_1) = \left(\frac{\sigma - \sqrt{9\sigma^2 + 4}}{2}, 1 \right), \quad B(\bar{u}_3) = \left(1, \frac{\sigma + \sqrt{9\sigma^2 + 4}}{2} \right).$$

Since $b(-1) = e^{19/12}$ and $b(2) = e^{-2/3}$, we conclude that the equilibrium $\bar{u}_1 = -1$ is ESS (evolutionary stable), since it is located at a global maximum of the fitness function, see [4, 5, 19]. On the other hand, when the survival equilibrium at $\bar{u}_2 = 1$

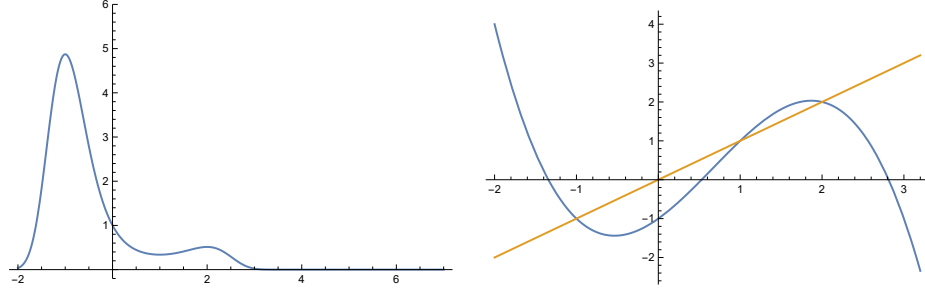


Figure 3: The graph of fitness function for Equation (65) for parameter values $\sigma^2 = 1$ and the graph of right hand side of Fisher's equation for $\sigma^2 = 0.5$. The figure shows the immediate basins of attraction for -1 and 2 .

is stable, the trait \bar{u}_2 is said to be evolutionarily convergent, but not an ESS since it does not yield a global maximum of the fitness function, see [4, 5, 19].

An analysis of second and third iterate of a map f and a bifurcation diagram of trait equation (using the speed of evolution σ^2 as a bifurcation parameter) indicates that period three solutions exist and so period doubling route to chaos is possible. For instance, when $\sigma = 1$ the Fisher's equation has three period-two solutions: $\{-1.48119, 2.67513\}$, $\{-1.21431, 0.311108\}$, $\{1.53919, 2.17009\}$ and six period three solutions such as

$$\{1.64217, 2.24931, 1.23728\}, \quad \{2.22825, 1.32321, 1.83141\}.$$

Assuming that $\sigma^2 < 1/3$ we have that

$$\lim_{n \rightarrow \infty} u_n = \bar{u}_1 \quad \text{for } u_0 \in B(\bar{u}_1)$$

which in turn implies that if $a(\bar{u}_1), b(\bar{u}_1) \in (0, 1)$ every solution of system (58) converges to $(0, 0, \bar{u}_1)$. Similarly, assuming that $\sigma^2 < 2/3$ we have that

$$\lim_{n \rightarrow \infty} u_n = \bar{u}_3 \quad \text{for } u_0 \in B(\bar{u}_3)$$

which in turn implies that if $a(\bar{u}_3), b(\bar{u}_3) \in (0, 1)$ every solution of system (56) converges to $(0, 0, \bar{u}_3)$

Example 39 Consider the Leslie-Gower evolutionary model

$$\left. \begin{aligned} x_{n+1} &= \frac{ax_n}{1 + x_n + c_1(u_n)y_n} \\ y_{n+1} &= \frac{by_n}{1 + c_2(u_n)x_n + y_n} \end{aligned} \right\} \quad (66)$$

with a single Fisher's equation

$$u_{n+1} = p \frac{u_n^3}{1 + u_n^3} \quad (67)$$

$x_0 > 0, y_0 > 0, u_0 \geq 0$, with all positive coefficients $a, b, c_1(u_n), c_2(u_n)$ for $n = 0, 1, \dots$

Fisher's equation (116) has between 2 and 4 equilibrium points given as:

$$E_2 = 0, E_1 = \frac{1}{3} \left(-\sqrt[3]{\frac{3}{2} (\sqrt{81 - 12p^3} + 9)} - p^3 - \frac{p^2}{\sqrt[3]{\frac{3}{2} (\sqrt{81 - 12p^3} + 9)} - p^3} + p \right),$$

$$E_3 = \frac{1}{6} \left(-(-2)^{2/3} \sqrt[3]{3 (\sqrt{81 - 12p^3} + 9)} - 2p^3 + \frac{2\sqrt[3]{-2}p^2}{\sqrt[3]{3 (\sqrt{81 - 12p^3} + 9)} - 2p^3} + 2p \right),$$

$$E_4 = \frac{1}{12}p \left(4 - \frac{4(-1)^{2/3}p}{\sqrt[3]{\frac{3}{2} (\sqrt{81 - 12p^3} + 9)} - p^3} \right) + \frac{1}{3} \sqrt[3]{-\frac{1}{2} \sqrt[3]{3 (\sqrt{81 - 12p^3} + 9)} - 2p^3},$$

where E_3 and E_4 exist if $p < \frac{3}{\sqrt[3]{4}}$. If $p = \frac{3}{\sqrt[3]{4}}$ then there are 3 equilibrium points $E_1 = \frac{-1}{\sqrt[3]{4}}, E_2 = 0, E_3 = \sqrt[3]{2}$. If $p > \frac{3}{\sqrt[3]{4}}$ then there are 2 equilibrium points E_1 and E_2 . The equilibrium points E_2 and E_4 are locally asymptotically stable and the equilibrium points E_1 and E_3 are locally repellers. In addition, E_2 is globally asymptotically stable within its basin of attraction $\mathcal{B}(E_2) = (E_1, E_3)$ while E_4 is globally asymptotically stable within its basin of attraction $\mathcal{B}(E_4) = (E_3, \infty)$.

The fitness function is

$$c_1(x) = c_2(x) = \exp \left(\frac{\frac{1}{6}p \log(x^2 - x + 1) + px - \frac{1}{3}p \log(x + 1) - \frac{p \tan^{-1}\left(\frac{2x-1}{\sqrt{3}}\right)}{\sqrt{3}} - \frac{x^2}{2}}{\sigma^2} \right). \quad (68)$$

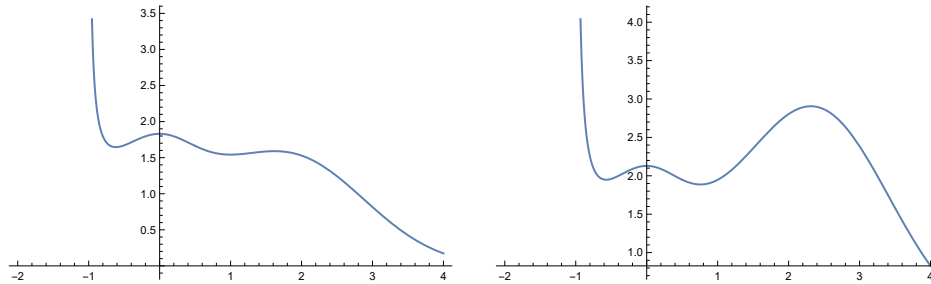


Figure 4: The graphs of fitness function (117) for Equation (116) for parameter values $\sigma^2 = 1$ and $p = 2$ and $p = 2.5$.

In view of Theorem 42 the equilibrium solutions E_2 and E_4 are globally asymptotically stable within their immediate basins of attractions. One of them is ESS (evolutionary stable) and that is the one located at a global maximum of the fitness function, see [4, 5, 19]. The second equilibrium is evolutionarily convergent, but not an ESS since it does not yield a global maximum of the fitness function, see [4, 5, 19]. Figure 4 indicates that the position of the global maximum depends on parameter p .

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CHAPTER 3

Stability and Evolutionary Stability of Certain Non-autonomous Cooperative Systems of Difference Equations

M. R. S. Kulenović¹¹, M. Nurkanović², Z. Nurkanović², and S. Trolle¹

¹ Department of Mathematics,
University of Rhode Island,
Kingston, RI 02881, USA

² Department of Mathematics,
University of Tuzla,
75000 Tuzla,
Bosnia and Herzegovina

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3.1 Introduction and Preliminaries

In this paper, we give some global attractivity results for a non-autonomous cooperative systems of difference equations

$$\begin{aligned}x_{n+1} &= a_n f(x_n, y_n) \\ y_{n+1} &= b_n g(x_n, y_n), \quad n = 0, 1, \dots\end{aligned}\tag{69}$$

where f and g are non-decreasing in the both variables. Here a_n and b_n are sequences which are assumed to be asymptotically constant. Our results are motivated with results for global attractivity for non-autonomous systems of difference equation via linearization in [1] that has significant applications in mathematical biology of single species [2]. Our techniques are based on difference inequalities, which was major tool used in [2]. Here, we extend the applications from single species models in [2] to the case of several (mainly two) species cooperation models. Then we apply our results to evolutionary population cooperation models, which have been considered lately by Cushing, Elaydi and others, see [3, 4, 5, 6, 7, 8]. Some of results presented here will be extended to n -dimensional cooperative systems as it was done in [9] and [10, 11, 12].

The global attractivity results for first order autonomous difference equation that will be used in simulations in this paper, were proved by Elaydi and Sacker [13] and Singer [14].

Theorem 40 [13] *Let $f : [a, b] \rightarrow [a, b]$ be a continuous function in equation*

$$x_{n+1} = f(x_n), \quad n = 0, 1, \dots\tag{70}$$

Then the following statements are equivalent:

- (a) *Equation (70) has no minimal period-two solutions in (a, b) .*
- (b) *Every solution of equation (70) that starts in (a, b) converges.*

As an immediate consequence of the Theorem 40, we have the following important result on global asymptotic stability.

Corollary 41 [13] *Let \bar{x} be a fixed point of a continuous map f on the closed and bounded interval $I = [a, b]$. Then \bar{x} is globally asymptotically stable relative to (a, b) if and only if*

$$f^2(x) = f(f(x)) > x, \quad x < \bar{x} \quad \text{and} \quad f(f(x)) < x, \quad x > \bar{x}, \quad (71)$$

for all $x \in (a, b) \setminus \{\bar{x}\}$, and a, b are not periodic points.

The next result known as Singer theorem, see [14], is very useful and efficient tool for establishing global dynamics of first order difference equations.

Theorem 42 *Assume that f is C^3 with an equilibrium point $\bar{x} \in [\alpha, \beta]$ such that f satisfies negative feedback condition, that is $f(x) > x$ if $x < \bar{x}$ and $f(x) < x$ if $x > \bar{x}$. Assuming that the Schwarzian derivative*

$$Sf(x) = \frac{f'''(x)}{f'(x)} - \frac{3}{2} \left(\frac{f''(x)}{f'(x)} \right)^2 < 0$$

for all $x \in [\alpha, \beta]$, then if $|f'(\bar{x})| \leq 1$, then \bar{x} is globally asymptotically stable. Now condition $|f'(\bar{x})| \leq 1$ is equivalent to local stability or non-hyperbolicity of the equilibrium \bar{x} .

Another result which we use is the following result from [15]:

Theorem 43 *Let $f : [a, b] \rightarrow [a, b]$ be a continuous, non-decreasing function in Equation (70). Then every solution is monotonic and so it converges to an equilibrium*

In this paper, we will use the so-called "north-east" partial ordering of the space \mathbb{R}_+^2 defined in the following way:

$$X_n = \begin{bmatrix} x_n^{(1)} \\ x_n^{(2)} \end{bmatrix} \preceq_{ne} Y_n = \begin{bmatrix} y_n^{(1)} \\ y_n^{(2)} \end{bmatrix} \iff (x_n^{(1)} \leq y_n^{(1)} \quad \text{and} \quad x_n^{(2)} \leq y_n^{(2)}),$$

and the so-called "south-east" partial ordering of the space \mathbb{R}_+^2 defined by

$$X_n = \begin{bmatrix} x_n^{(1)} \\ x_n^{(2)} \end{bmatrix} \preceq_{se} Y_n = \begin{bmatrix} y_n^{(1)} \\ y_n^{(2)} \end{bmatrix} \iff (x_n^{(1)} \leq y_n^{(1)} \quad \text{and} \quad x_n^{(2)} \geq y_n^{(2)}).$$

The extension of north-east ordering to n -dimensional systems is straightforward.

One of the reasons that model parameters can change in time is Darwinian evolution, which is a case that will be briefly explained here. The detailed explanation is given in [4, 5, 6, 7, 16]. Suppose v is a quantified, phenotypic trait of an individual that is subject to evolution. If we assume the per capita contribution to the population made by an individual depends on its trait v , then $f = f(x, v)$ depends on both x and v . It might happen that this contribution also depends on the traits of other individuals. We can model this situation by assuming that f also depends on the mean trait u in the population so that $f = f(x, v, u)$. A canonical way to model Darwinian evolution is to model the dynamics of x_n and the mean trait u_n by means of the equations

$$x_{n+1} = f(x_n, v, u_n)|_{v=u_n} x_n \tag{72}$$

$$u_{n+1} = u_n + \sigma^2 \frac{\partial F(x_n, v, u_n)}{\partial v} \Big|_{v=u_n}, \tag{73}$$

see [16].

Equation (72) asserts that the population dynamics can be modeled by assuming the trait v is equal to the population mean of the trait. Equation (73) (called Lande's or Fisher's or the breeder's equation) prescribes that the change in the mean trait is proportional to the fitness gradient, where fitness in this model is denoted by $F(x, v, u)$. The modeler decides on an appropriate measure of fitness, which is often taken to be f or $\ln f$. The constant of proportionality $\sigma^2 \geq 0$ is called the *speed of evolution*. It is related to the variance of the trait in the population, which is assumed constant in time. Thus, if $\sigma^2 = 0$ no evolution occurs (there is no variability) and one has a one-dimensional difference equation (72) for population

dynamics. If evolution occurs $\sigma^2 > 0$ then the model is a two dimensional system of difference equations with state variable $[x_n, u_n]$. From a mathematical point of view system (72), (73) is a non-autonomous system of difference equations, which is much harder to analyze than the autonomous system. See [10, 17, 1, 2, 18, 9] for some results concerning some special cases of non-autonomous systems. In particular, we use the technique of difference inequalities in [1, 2] to obtain the results for cooperative non-autonomous systems of difference equations. We will apply similar methods here to further our analysis.

3.2 Main results

3.2.1 Certain class of cooperative discrete dynamical systems

The proof of the following lemma is by simple induction and will be omitted. It can be found in [18] and can be extended to a cooperative map in n -dimensional space, where north-east partial ordering is defined in a natural way.

Lemma 44 *Assume that*

a) $F : \mathbb{R}_+^2 \rightarrow \mathbb{R}_+^2$, $F = \begin{bmatrix} f \\ g \end{bmatrix}$ is a cooperative map, i.e., the functions $f, g : \mathbb{R}_+^2 \rightarrow \mathbb{R}$

are non-decreasing functions in both variables,

b) $\{X_n\}, \{Y_n\}, \{Z_n\}$ are sequences of the real components in \mathbb{R}_+^2 such that $X_0 \preceq_{ne} Y_0 \preceq_{ne} Z_0$ and

$$\left. \begin{array}{l} X_{n+1} \preceq_{ne} F(X_n) \\ Y_{n+1} = F(Y_n) \\ Z_{n+1} \succeq_{ne} F(Z_n) \end{array} \right\}, \quad n = 0, 1, \dots .$$

Then,

$$X_n \preceq_{ne} Y_n \preceq_{ne} Z_n, \quad n = 0, 1, \dots .$$

An immediate application of Lemma 44 is the following result:

Theorem 45 Consider the following non-autonomous system of difference equations

$$X_{n+1} = \begin{bmatrix} a_n f(x_n, y_n) \\ b_n g(x_n, y_n) \end{bmatrix}, \quad n = 0, 1, \dots, \quad (74)$$

where $A_n = \begin{bmatrix} a_n \\ b_n \end{bmatrix}$ and $F = \begin{bmatrix} f \\ g \end{bmatrix} : \mathbb{R}_+^2 \rightarrow \mathbb{R}_+^2$ is a cooperative map. Assume that

$$\lim_{n \rightarrow \infty} A_n = \lim_{n \rightarrow \infty} \begin{bmatrix} a_n \\ b_n \end{bmatrix} = \begin{bmatrix} \lim_{n \rightarrow \infty} a_n \\ \lim_{n \rightarrow \infty} b_n \end{bmatrix} = \begin{bmatrix} a \\ b \end{bmatrix} = A, \quad (75)$$

and let, for $A = \begin{bmatrix} a \\ b \end{bmatrix}$,

$$Y_{n+1} = \begin{bmatrix} a f(u_n, v_n) \\ b g(u_n, v_n) \end{bmatrix}, \quad n = 0, 1, \dots, \quad (76)$$

be the limiting system of difference equations. Also, assume that there exists $\varepsilon_0 = \begin{bmatrix} \varepsilon_0^{(1)} \\ \varepsilon_0^{(2)} \end{bmatrix} \succ_{ne} \begin{bmatrix} 0 \\ 0 \end{bmatrix}$ such that every solution of the system

$$Y_{n+1} = \begin{bmatrix} \lambda^{(1)} f(u_n, v_n) \\ \lambda^{(2)} g(u_n, v_n) \end{bmatrix}, \quad n = 0, 1, \dots \quad (77)$$

converges to a constant $\bar{Y}_\Lambda = \begin{bmatrix} \bar{x}_\Lambda \\ \bar{y}_\Lambda \end{bmatrix}$ for every $\Lambda = \begin{bmatrix} \lambda^{(1)} \\ \lambda^{(2)} \end{bmatrix}$, $\lambda^{(1)} \in (a - \varepsilon_0^{(1)}, a + \varepsilon_0^{(1)})$, $\lambda^{(2)} \in (b - \varepsilon_0^{(2)}, b + \varepsilon_0^{(2)})$.

If

$$\lim_{\Lambda \rightarrow A} \bar{Y}_\Lambda = \bar{Y}_A,$$

then every solution of the System (74) is convergent and satisfies

$$\lim_{n \rightarrow \infty} X_n = \bar{Y}_A.$$

Proof. According to (75), for any $\varepsilon = \begin{bmatrix} \varepsilon_1 \\ \varepsilon_2 \end{bmatrix} \succ_{ne} \begin{bmatrix} 0 \\ 0 \end{bmatrix}$, there exists $N = N(\varepsilon)$ such that for $n \geq N$ the following holds

$$a - \varepsilon_1 < a_n < a + \varepsilon_1,$$

$$b - \varepsilon_2 < b_n < b + \varepsilon_2.$$

This implies that

$$\begin{bmatrix} (a - \varepsilon_1) f(x_n, y_n) \\ (b - \varepsilon_2) g(x_n, y_n) \end{bmatrix} \preceq_{ne} X_{n+1} = \begin{bmatrix} a_n f(x_n, y_n) \\ b_n g(x_n, y_n) \end{bmatrix} \preceq_{ne} \begin{bmatrix} (a + \varepsilon_1) f(x_n, y_n) \\ (b + \varepsilon_2) g(x_n, y_n) \end{bmatrix},$$

$n \geq N$.

By Lemma 44 we obtain

$$L_n \preceq_{ne} X_n \preceq_{ne} U_n, \quad n \geq N, \quad (78)$$

where $\{L_n\} = \left\{ \begin{bmatrix} l_n^{(1)} \\ l_n^{(2)} \end{bmatrix} \right\}$ satisfies

$$L_{n+1} = \begin{bmatrix} (a - \varepsilon_1) f(l_n^{(1)}, l_n^{(2)}) \\ (b - \varepsilon_2) g(l_n^{(1)}, l_n^{(2)}) \end{bmatrix},$$

and $\{U_n\} = \left\{ \begin{bmatrix} u_n^{(1)} \\ u_n^{(2)} \end{bmatrix} \right\}$ satisfies

$$U_{n+1} = \begin{bmatrix} (a + \varepsilon_1) f(u_n^{(1)}, u_n^{(2)}) \\ (b + \varepsilon_2) g(u_n^{(1)}, u_n^{(2)}) \end{bmatrix}.$$

By using (78) we have that

$$\lim_{n \rightarrow \infty} L_n \preceq_{ne} \varliminf_{n \rightarrow \infty} X_n \preceq_{ne} \overline{\lim}_{n \rightarrow \infty} X_n \preceq_{ne} \lim_{n \rightarrow \infty} U_n,$$

i.e.,

$$\overline{Y}_{A-\varepsilon} \preceq_{ne} \varliminf_{n \rightarrow \infty} X_n \preceq_{ne} \overline{\lim}_{n \rightarrow \infty} X_n \preceq_{ne} \overline{Y}_{A+\varepsilon}, \quad (79)$$

where $A \pm \varepsilon = \begin{bmatrix} a \pm \varepsilon_1 \\ b \pm \varepsilon_2 \end{bmatrix}$. Since $\lim_{\varepsilon \rightarrow \mathbf{0}} \overline{Y}_{A-\varepsilon} = \lim_{\varepsilon \rightarrow \mathbf{0}} \overline{Y}_{A+\varepsilon} = \overline{Y}_A$, where $\mathbf{0} = \begin{bmatrix} 0 \\ 0 \end{bmatrix}$, (79) implies that the sequence $\{X_n\}$ is convergent and that

$$\lim_{n \rightarrow \infty} X_n = \overline{Y}_A.$$

■

Example 46 The following system of difference equations modelling cooperation was considered in [19]

$$\left. \begin{aligned} x_{n+1} &= Ax_n \frac{y_n}{1+y_n} \\ y_{n+1} &= By_n \frac{x_n}{1+x_n} \end{aligned} \right\}, \quad n = 0, 1, \dots, \quad (80)$$

for all values of parameters A, B except $A \leq 1, B > 1$ and $A > 1, B \leq 1$. When $A \leq 1, B > 1$ then $\{x_n\}$ is a non-increasing sequence and so is convergent to 0, which is the only limiting point. In that case, the second equation implies that there exists M such that $B \frac{x_n}{1+x_n} \leq C < 1$ for $n \geq M$, which implies that $y_{n+1} < Cy_n, n \geq M$ and so $\lim_{n \rightarrow \infty} y_n = 0$. Thus $\lim_{n \rightarrow \infty} (x_n, y_n) = (0, 0)$. The case $A > 1, B \leq 1$ is similar by symmetry and the conclusion is same.

This system has a unique equilibrium point $E_0 = \begin{bmatrix} 0 \\ 0 \end{bmatrix}$ for all values of parameters $A, B \neq 0$. This equilibrium is globally asymptotically stable if $(A, B) \in (0, 1]^2$. Next we consider the following non-autonomous system

$$\left. \begin{aligned} x_{n+1} &= A_n x_n \frac{y_n}{1+y_n} \\ y_{n+1} &= B_n y_n \frac{x_n}{1+x_n} \end{aligned} \right\}, \quad n = 0, 1, 2, \dots, \quad (81)$$

where $\lim_{n \rightarrow \infty} A_n = A$ and $\lim_{n \rightarrow \infty} B_n = B$. By using Theorem 45 taking $f(x_n, y_n) = x_n \frac{y_n}{1+y_n}$ and $g(x_n, y_n) = y_n \frac{x_n}{1+x_n}$, all solutions of System (81) globally asymptotically converge to E_0 for all values of A, B such that $(A(u_1^*), B(u_2^*)) \notin (1, \infty)^2$, and for all $x_0 \geq 0$ and $y_0 \geq 0$.

Remark 47 With the assumptions on A and B in Example 46, it can be shown that the same result as in [19] holds by a different approach. Namely, we will show that using the Lyapunov function. Indeed the global asymptotic stability of the equilibrium point $E_0 = \begin{bmatrix} 0 \\ 0 \end{bmatrix}$ of System (80) under the assumption $0 < A \leq 1, 0 < B \leq 1$, and for all $x_0 \geq 0$ and $y_0 \geq 0$ can be proved as follows. We use the positive definite Lyapunov function $V : \mathbb{R}_+^2 \rightarrow \mathbb{R}$ of the form $V \left(\begin{bmatrix} x \\ y \end{bmatrix} \right) = x^2 + y^2$

of the map

$$F\left(\begin{bmatrix} x \\ y \end{bmatrix}\right) = \begin{bmatrix} Ax\frac{y}{1+y} \\ By\frac{x}{1+x} \end{bmatrix}.$$

Then, for $x \geq 0$, $y \geq 0$, $(x, y) \neq (0, 0)$, we obtain

$$\begin{aligned} \Delta V &= V\left(F\left(\begin{bmatrix} x \\ y \end{bmatrix}\right)\right) - V\left(\begin{bmatrix} x \\ y \end{bmatrix}\right) = \left(Ax\frac{y}{1+y}\right)^2 + \left(By\frac{x}{1+x}\right)^2 - x^2 - y^2 \\ &= x^2\left(A^2\left(\frac{y}{1+y}\right)^2 - 1\right) + y^2\left(B^2\left(\frac{x}{1+x}\right)^2 - 1\right) \\ &\leq x^2(A^2 - 1) + y^2(B^2 - 1). \end{aligned}$$

If $0 < A < 1$, $0 < B < 1$, then $\Delta V < 0$, which implies that $E_0 = \begin{bmatrix} 0 \\ 0 \end{bmatrix}$ is asymptotically stable. Furthermore, since $V\left(\begin{bmatrix} x \\ y \end{bmatrix}\right) = x^2 + y^2 \rightarrow \infty$, as $\left\|\begin{bmatrix} x \\ y \end{bmatrix}\right\| \rightarrow \infty$, the equilibrium point $E_0 = \begin{bmatrix} 0 \\ 0 \end{bmatrix}$ is globally asymptotically stable. In the second case, when $0 < A \leq 1$ and $0 < B \leq 1$, we will use the so-called LaSalle's Invariance Principle [14] to investigate the asymptotic stability of E_0 . Here are two subcases to consider.

i) Assume that $0 < A \leq 1$, $0 < B \leq 1$, and $A + B < 2$. Without loss of generality, we can assume that $0 < A < 1$ and $B = 1$. Then, $\Delta V = x^2(A^2 - 1)$, which is zero if $x = 0$. It means that set

$$\mathfrak{L} = \left\{ \begin{bmatrix} x \\ y \end{bmatrix} \in \mathbb{R}_+^2 : \Delta V\left(\begin{bmatrix} x \\ y \end{bmatrix}\right) = 0 \right\} = \left\{ \begin{bmatrix} 0 \\ y \end{bmatrix} \in \mathbb{R}_+^2 : \Delta V\left(\begin{bmatrix} 0 \\ y \end{bmatrix}\right) = 0 \right\}$$

is the y -axis. Since $F\left(\begin{bmatrix} 0 \\ y \end{bmatrix}\right) = \begin{bmatrix} 0 \\ 0 \end{bmatrix}$ for all $y \in \mathbb{R}_+$, the maximal invariant subset of \mathfrak{L} under mapping F is $M = \left\{ \begin{bmatrix} 0 \\ 0 \end{bmatrix} \right\}$, which is a singleton. Consequently, E_0 is asymptotically stable.

ii) If $A = B = 1$, then $\Delta V = 0$ for $x = 0$ or $y = 0$ and \mathfrak{L} is the union of two coordinate axes. It is clear that $M = \left\{ \begin{bmatrix} 0 \\ 0 \end{bmatrix} \right\}$, which implies that E_0 is asymptotically stable.

It remains to prove the global attractivity of the equilibrium point E_0 in cases i) and ii).

If $0 < A < 1$ and $B = 1$, then we have

$$x_{n+1} = Ax_n \frac{y_n}{1 + y_n} \leq Ax_n \implies x_n \leq A^n x_0, \quad n = 0, 1, \dots,$$

and

$$y_{n+1} = y_n \frac{x_n}{1 + x_n} \leq y_n, \quad n = 0, 1, \dots,$$

which implies that $\lim_{n \rightarrow \infty} x_n = 0$ and so $\lim_{n \rightarrow \infty} y_n = 0$.

Analogously, the proof is performed in the case of $A = 1$ and $0 < B < 1$.

If $A = B = 1$, then the sequences $\{x_n\}$ and $\{y_n\}$ are decreasing and so are convergent. It means that there exist the numbers $r, s \geq 0$ such that

$$\lim_{n \rightarrow \infty} x_n = r, \quad \lim_{n \rightarrow \infty} y_n = s.$$

Clearly $r = s = 0$, since otherwise System (80) would have two equilibrium points in the first quadrant.

It should be mentioned that the method of difference inequalities, that was used, is much more robust than the method of Lyapunov function when extended to the non-autonomous systems.

Remark 48 It is clear that Lemma 44 and Theorem 45 would be valid for a general case of cooperative map $F : \mathbb{R}_+^k \rightarrow \mathbb{R}_+^k$, $F = \begin{bmatrix} f_1 \\ \vdots \\ f_k \end{bmatrix}$, $k \geq 2$, where the functions $f_i : \mathbb{R}_+^k \rightarrow \mathbb{R}$, $i = 1, \dots, k$, are non-decreasing functions in all variables.

Analogous to the proof of Theorem 45, the proof of the following theorem would be derived in the general case.

Theorem 49 Consider the following non-autonomous system of difference equations

$$X_{n+1} = \begin{bmatrix} a_n^{(1)} f_1(x_n^{(1)}, \dots, x_n^{(k)}) \\ \vdots \\ a_n^{(k)} f_k(x_n^{(1)}, \dots, x_n^{(k)}) \end{bmatrix}, \quad n = 0, 1, \dots,$$

where $A_n = \begin{bmatrix} a_n^{(1)} \\ \vdots \\ a_n^{(k)} \end{bmatrix}$ and $F = \begin{bmatrix} f_1 \\ \vdots \\ f_k \end{bmatrix} : \mathbb{R}_+^k \rightarrow \mathbb{R}_+^k$, $k \geq 2$, is a cooperative map, that is all functions $f_i, i = 1, \dots, k$ are non-decreasing. Assume that

$$\lim_{n \rightarrow \infty} A_n = \lim_{n \rightarrow \infty} \begin{bmatrix} a_n^{(1)} \\ \vdots \\ a_n^{(k)} \end{bmatrix} = \begin{bmatrix} \lim_{n \rightarrow \infty} a_n^{(1)} \\ \vdots \\ \lim_{n \rightarrow \infty} a_n^{(k)} \end{bmatrix} = \begin{bmatrix} a^{(1)} \\ \vdots \\ a^{(k)} \end{bmatrix} = A,$$

and let, for $A = \begin{bmatrix} a^{(1)} \\ \vdots \\ a^{(k)} \end{bmatrix}$,

$$Y_{n+1} = \begin{bmatrix} a_n^{(1)} f_1(x_n^{(1)}, \dots, x_n^{(k)}) \\ \vdots \\ a_n^{(k)} f_k(x_n^{(1)}, \dots, x_n^{(k)}) \end{bmatrix}, \quad n = 0, 1, \dots,$$

be the limiting system of difference equations. Also, assume that there exists $\varepsilon_0 =$

$$\begin{bmatrix} \varepsilon_0^{(1)} \\ \vdots \\ \varepsilon_0^{(k)} \end{bmatrix} \succ_{ne} \begin{bmatrix} 0 \\ \vdots \\ 0 \end{bmatrix} \text{ such that every solution of the system}$$

$$Y_{n+1} = \begin{bmatrix} \lambda^{(1)} f_1(x_n^{(1)}, \dots, x_n^{(k)}) \\ \vdots \\ \lambda^{(k)} f_k(x_n^{(1)}, \dots, x_n^{(k)}) \end{bmatrix}, \quad n = 0, 1, 2, \dots$$

converges to a constant $\bar{Y}_\Lambda = \begin{bmatrix} \bar{x}_\Lambda^{(1)} \\ \vdots \\ \bar{x}_\Lambda^{(k)} \end{bmatrix}$ for every $\Lambda = \begin{bmatrix} \lambda^{(1)} \\ \vdots \\ \lambda^{(k)} \end{bmatrix}$, $\lambda^{(i)} \in$

$(a^{(i)} - \varepsilon_0^{(i)}, a^{(i)} + \varepsilon_0^{(i)})$, $i = 1, \dots, k$.

If

$$\lim_{\Lambda \rightarrow A} \bar{Y}_\Lambda = \bar{Y}_A,$$

then every solution of the System (74) is convergent and satisfies

$$\lim_{n \rightarrow \infty} X_n = \bar{Y}_A.$$

Example 50 Consider the following system of difference equations modelling co-operation

$$x_{n+1}^{(i)} = A^{(i)} x_n^{(i)} \frac{\prod_{i \neq j=1}^k x_n^{(j)}}{1 + \prod_{i \neq j=1}^k x_n^{(j)}}, \quad n = 0, 1, \dots; \quad i = 1, 2, \dots, k. \quad (82)$$

System (82), which is n -dimensional version of System (80), has a unique equilibrium point $E_0 = \begin{bmatrix} 0 \\ \vdots \\ 0 \end{bmatrix}$ if $0 < A^{(i)} \leq 1$, $i = 1, 2, \dots, k$. We investigate the

stability of E_0 by using the following Lyapunov function $V : \mathbb{R}_+^k \rightarrow \mathbb{R}$ of the form $V \left(\begin{bmatrix} x^{(1)} \\ \vdots \\ x^{(k)} \end{bmatrix} \right) = \sum_{j=1}^k (x^{(j)})^2$ of the map

$$F \left(\begin{bmatrix} x^{(1)} \\ \vdots \\ x^{(k)} \end{bmatrix} \right) = \begin{bmatrix} A^{(1)} x^{(1)} \frac{\prod_{j=2}^k x^{(j)}}{1 + \prod_{j=2}^k x^{(j)}} & \dots & \dots & A^{(k)} x^{(k)} \frac{\prod_{j=1}^{k-1} x^{(j)}}{1 + \prod_{j=1}^{k-1} x^{(j)}} \end{bmatrix}^T$$

Then,

$$\begin{aligned} \Delta V &= V \left(F \left(\begin{bmatrix} x^{(1)} \\ \vdots \\ x^{(k)} \end{bmatrix} \right) \right) - V \left(\begin{bmatrix} x^{(1)} \\ \vdots \\ x^{(k)} \end{bmatrix} \right) = \sum_{j=1}^k (x^{(j)})^2 \left(\left(A^{(j)} \frac{\prod_{i \neq j=1}^k x^{(i)}}{1 + \prod_{i \neq j=1}^k x^{(i)}} \right)^2 - 1 \right) \\ &\leq \sum_{j=1}^k (x^{(j)})^2 \left((A^{(j)})^2 - 1 \right). \end{aligned}$$

If $0 < A^{(i)} < 1$, $i = 1, 2, \dots, k$, then $\Delta V < 0$, which implies that E_0 is asymptotically stable. Furthermore, since $V \left(\begin{bmatrix} x^{(1)} \\ \vdots \\ x^{(k)} \end{bmatrix} \right) \rightarrow \infty$, as $\left\| \begin{bmatrix} x^{(1)} \\ \vdots \\ x^{(k)} \end{bmatrix} \right\| \rightarrow \infty$, the equilibrium point E_0 is globally asymptotically stable.

In the second case, when $0 < A^{(i)} \leq 1$, $i = 1, 2, \dots, k$, we will use LaSalle's Invariance Principle to investigate the asymptotic stability of E_0 . Then, for the set

$$\mathfrak{L} = \{X \in \mathbb{R}_+^k : \Delta V(X) = 0\}$$

the following holds: X has at least one zero coordinate, and $F(X) = \begin{bmatrix} 0 \\ \vdots \\ 0 \end{bmatrix}$ for all $X \in \mathfrak{L}$. It implies that the maximal invariant subset of \mathfrak{L} under mapping F is $M = \left\{ \begin{bmatrix} 0 \\ \vdots \\ 0 \end{bmatrix} \right\}$. Since M is a singleton, E_0 is asymptotically stable.

It remains to prove the global attractivity of the equilibrium point E_0 when $0 < A^{(i)} \leq 1$, $i = 1, 2, \dots, k$. If for several $i \in \{1, 2, \dots, k\}$, $A_i < 1$, but not for all i , and $A^{(j)} = 1$, for all remaining $l \in \{1, 2, \dots, k\}$, then we have

$$x_{n+1}^{(i)} = A^{(i)} x_n^{(i)} \frac{\prod_{i \neq j=1}^k x_n^{(j)}}{1 + \prod_{i \neq j=1}^k x_n^{(j)}} \leq A^{(i)} x_n^{(i)} \implies x_n^{(i)} \leq (A^{(i)})^n x_0^{(i)}, \quad n = 0, 1, \dots,$$

and

$$x_{n+1}^{(l)} = x_n^{(l)} \frac{\prod_{i \neq j=1}^k x_n^{(j)}}{1 + \prod_{i \neq j=1}^k x_n^{(j)}} \leq x_n^{(l)}, \quad n = 0, 1, \dots,$$

which implies that $\lim_{n \rightarrow \infty} x_n^{(i)} = 0$ and that the sequences $\{x_n^{(l)}\}$ are decreasing and therefore convergent. It is clear that $\lim_{n \rightarrow \infty} x_n^{(l)} = 0$, since otherwise there would exist another equilibrium point in \mathbb{R}_+^k .

If $A^{(i)} = 1$, $i = 1, 2, \dots, k$, then the sequences $\{x_n^{(i)}\}$ are decreasing and so are convergent. It means that there exist the numbers $w^{(i)} \geq 0$ such that

$$\lim_{n \rightarrow \infty} x_n^{(i)} = w^{(i)}.$$

Clearly $w^{(i)} = 0$, since otherwise System (80) would have another equilibrium points in the first quadrant.

Now, we consider the following non-autonomous system

$$x_{n+1}^{(i)} = A_n^{(i)} x_n^{(i)} \frac{\prod_{i \neq j=1}^k x_n^{(j)}}{1 + \prod_{i \neq j=1}^k x_n^{(j)}}, \quad n = 0, 1, \dots; \quad i = 1, 2, \dots, k, \quad (83)$$

where $\lim_{n \rightarrow \infty} A_n^{(i)} = A^{(i)}$, $i = 1, 2, \dots, k$. By using Theorem 49 taking

$$f_i \left(\begin{bmatrix} x^{(1)} \\ \vdots \\ x^{(k)} \end{bmatrix} \right) = x^{(i)} \frac{\prod_{i \neq j=1}^k x^{(j)}}{1 + \prod_{i \neq j=1}^k x^{(j)}},$$

cally converge to E_0 for $0 < A^{(i)} \leq 1$, $i = 1, 2, \dots, k$, and for all $\begin{bmatrix} x_0^{(1)} \\ \vdots \\ x_0^{(k)} \end{bmatrix} \succeq_{ne} \begin{bmatrix} 0 \\ \vdots \\ 0 \end{bmatrix}$.

3.2.2 Global stability of some additive cooperative discrete dynamical systems

Consider the following additive cooperative system

$$\left. \begin{aligned} x_{n+1} &= a_n f_1(x_n) x_n + b_n f_2(y_n) y_n \\ x_{n+1} &= c_n f_3(x_n) x_n + d_n f_4(y_n) y_n \end{aligned} \right\}, \quad n = 0, 1, \dots \quad (84)$$

Note that System (84) can be written in the matrix form as

$$\begin{bmatrix} x_{n+1} \\ y_{n+1} \end{bmatrix} = \begin{bmatrix} a_n f_1(x_n) & b_n f_2(y_n) \\ c_n f_3(x_n) & d_n f_4(y_n) \end{bmatrix} \begin{bmatrix} x_n \\ y_n \end{bmatrix} = g_0 \begin{bmatrix} x_n \\ y_n \end{bmatrix}, \quad n = 0, 1, \dots$$

Theorem 51 *Assume that f_i are non-negative and bounded functions, i.e., $0 \leq f_i(x) \leq M_i$, $i = 1, 2, 3, 4$ for all $x \geq 0$. Also, assume that $\{a_n\}$, $\{b_n\}$, $\{c_n\}$ and $\{d_n\}$ are sequences such that*

$$0 < a_n \leq A, \quad 0 < b_n \leq B, \quad 0 < c_n \leq C, \quad 0 < d_n \leq D, \quad n = 0, 1, \dots \quad (85)$$

Then, every solution of System (84), where initial values x_0, y_0 are non-negative, converges to the zero equilibrium if

$$\max \{AM_1 + CM_3, BM_2 + DM_4\} < 1 \quad \text{or} \quad \max \{AM_1 + BM_2, CM_3 + DM_4\} < 1.$$

Proof. Indeed, when $\|\cdot\|_1$ denotes the L_1 norm, we have that

$$\begin{aligned}\|g_0\|_1 &= \left\| \begin{bmatrix} a_n f_1(x_n) & b_n f_2(y_n) \\ c_n f_3(x_n) & d_n f_4(y_n) \end{bmatrix} \right\|_1 = \max \{a_n f_1(x_n) + c_n f_3(x_n), b_n f_2(y_n) + d_n f_4(y_n)\} \\ &\leq \max \{AM_1 + CM_3, BM_2 + DM_4\} \\ &< 1,\end{aligned}$$

or, when $\|\cdot\|_\infty$ denotes the L_∞ norm, we have that

$$\begin{aligned}\|g_0\|_\infty &= \left\| \begin{bmatrix} a_n f_1(x_n) & b_n f_2(y_n) \\ c_n f_3(x_n) & d_n f_4(y_n) \end{bmatrix} \right\|_2 = \max \{a_n f_1(x_n) + b_n f_2(y_n), c_n f_3(x_n) + d_n f_4(y_n)\} \\ &\leq \max \{AM_1 + BM_2, CM_3 + DM_4\} \\ &< 1.\end{aligned}$$

Now the result follows from Theorem 2 and Corollary 1 in [1]. ■

Consider the following additive cooperative non-autonomous systems

$$\left. \begin{aligned}x_{n+1} &= a_n \frac{x_n}{1+x_n} + b_n \frac{y_n}{1+y_n} \\ y_{n+1} &= c_n \frac{x_n}{1+x_n} + d_n \frac{y_n}{1+y_n}\end{aligned} \right\}, \quad n = 0, 1, \dots, \quad (86)$$

$$\left. \begin{aligned}x_{n+1} &= a_n \frac{x_n}{1+x_n} + b_n \frac{y_n^2}{1+y_n^2} \\ y_{n+1} &= c_n \frac{x_n^2}{1+x_n^2} + d_n \frac{y_n}{1+y_n}\end{aligned} \right\}, \quad n = 0, 1, \dots, \quad (87)$$

$$\left. \begin{aligned}x_{n+1} &= a_n \frac{x_n^2}{1+x_n^2} + b_n \frac{y_n^2}{1+y_n^2} \\ y_{n+1} &= c_n \frac{x_n^2}{1+x_n^2} + d_n \frac{y_n^2}{1+y_n^2}\end{aligned} \right\}, \quad n = 0, 1, \dots. \quad (88)$$

They all are of the form of System (84). Note that in System (86)

$$f_i(u) = \frac{1}{1+u}, \quad M_i = 1 \quad \text{for } i = 1, 2, 3, 4,$$

and in System (87)

$$f_1(u) = f_4(u) = \frac{1}{1+u}, \quad f_2(u) = f_3(u) = \frac{u}{1+u^2}, \quad M_1 = M_4 = 1, \quad M_2 = M_3 = \frac{1}{2},$$

and in System (88)

$$f_i(u) = \frac{u}{1+u^2}, \quad M_i = \frac{1}{2} \quad \text{for } i = 1, 2, 3, 4.$$

Based on Theorem 51, the following three claims are true.

Claim 52 *Assume that for the sequences $\{a_n\}$, $\{b_n\}$, $\{c_n\}$ and $\{d_n\}$ satisfy (85). Then, every solution of System (86), where initial values x_0, y_0 are non-negative, converges to the zero equilibrium if*

$$\max \{A + C, B + D\} < 1 \quad \text{or} \quad \max \{A + B, C + D\} < 1.$$

Claim 53 *Assume that $\{a_n\}$, $\{b_n\}$, $\{c_n\}$ and $\{d_n\}$ satisfy (85). Then, every solution of System (87), where initial values x_0, y_0 are non-negative, converges to the zero equilibrium if*

$$\max \left\{ A + \frac{1}{2}C, \frac{1}{2}B + D \right\} < 1 \quad \text{or} \quad \max \left\{ A + \frac{1}{2}B, \frac{1}{2}C + D \right\} < 1.$$

Claim 54 *Assume that $\{a_n\}$, $\{b_n\}$, $\{c_n\}$ and $\{d_n\}$ satisfy (85). Then, every solution of System (88), where initial values x_0, y_0 are non-negative, converges to the zero equilibrium if*

$$\max \left\{ \frac{1}{2}(A + C), \frac{1}{2}(B + D) \right\} < 1 \quad \text{or} \quad \max \left\{ \frac{1}{2}(A + B), \frac{1}{2}(C + D) \right\} < 1.$$

Remark 55 It is obvious that Theorem 51 is valid for distinct combinations of the functions

$$\frac{u}{1+u}, \quad \frac{u}{1+u^2}, \quad \frac{u^2}{1+u^2}, \quad \frac{u^2}{1+u}.$$

Now, consider the following additive non-autonomous system

$$\left. \begin{aligned} x_{n+1} &= a_n f_1(x_n) + b_n f_2(y_n) \\ y_{n+1} &= c_n f_3(x_n) + d_n f_4(y_n) \end{aligned} \right\}, \quad n = 0, 1, \dots \quad (89)$$

It can be rewritten in the form of System (84) as follows

$$\left. \begin{aligned} x_{n+1} &= a_n \frac{f_1(x_n)}{x_n} x_n + b_n \frac{f_2(y_n)}{y_n} y_n \\ y_{n+1} &= c_n \frac{f_3(x_n)}{x_n} x_n + d_n \frac{f_4(y_n)}{y_n} y_n \end{aligned} \right\}, \quad n = 0, 1, 2, \dots ,$$

or in matrix form

$$\begin{bmatrix} x_{n+1} \\ y_{n+1} \end{bmatrix} = \begin{bmatrix} a_n \frac{f_1(x_n)}{x_n} & b_n \frac{f_2(y_n)}{y_n} \\ c_n \frac{f_3(x_n)}{x_n} & d_n \frac{f_4(y_n)}{y_n} \end{bmatrix} \begin{bmatrix} x_n \\ y_n \end{bmatrix}, \quad n = 0, 1, 2, \dots$$

The proof of the following theorem is the same as the proof of Theorem 51. This system is not cooperative system, but it is sublinear system.

Theorem 56 *Assume that f_i are non-negative and sublinear functions, i.e., $0 \leq \frac{f_i(x)}{x} \leq M_i$, $i = 1, 2, 3, 4$ for all $x > 0$. Also, assume that $\{a_n\}$, $\{b_n\}$, $\{c_n\}$ and $\{d_n\}$ holds (85). Then, every solution of System (89), where initial values x_0, y_0 are positive, converges to the zero equilibrium if*

$$\max \{AM_1 + CM_3, BM_2 + DM_4\} < 1 \quad \text{or} \quad \max \{AM_1 + BM_2, CM_3 + DM_4\} < 1.$$

Remark 57 Let us note that Theorem 56 can be applied in the case when functions are of form $f_i(x) = |\sin(x)|$ $f(x) = \ln(1+x)$ for $x > 0$ because $0 \leq \left| \frac{f_i(x)}{x} \right| \leq 1$ for $x > 0$ and $i = 1, 2, 3, 4$.

The next results holds for cooperative systems.

Theorem 58 *Consider System (89) and assume that $f_i(x)$ are non-decreasing functions, for all $x > 0$. Also, assume that*

$$\lim_{n \rightarrow \infty} (a_n, b_n, c_n, d_n) = (A, B, C, D)$$

and that

$$\left. \begin{aligned} x_{n+1} &= Af_1(x_n) + Bf_2(y_n) \\ y_{n+1} &= Cf_3(x_n) + Df_4(y_n) \end{aligned} \right\}, \quad n = 0, 1, \dots \quad (90)$$

is limiting system.

Also, assume that there exists $\varepsilon_0^{(i)} > 0$, $i = 1, 2, 3, 4$ such that every solution of the system

$$Y_{n+1} = \begin{bmatrix} \lambda_1 f_1(x_n) + \lambda_2 f_2(y_n) \\ \lambda_3 f_3(x_n) + \lambda_4 f_4(y_n) \end{bmatrix}, \quad n = 0, 1, \dots \quad (91)$$

converges to a constant $\bar{Y}_\Lambda = \begin{bmatrix} \bar{x}_\Lambda \\ \bar{y}_\Lambda \end{bmatrix}$ for every

$$\Lambda = \begin{bmatrix} \lambda_1 \\ \lambda_2 \\ \lambda_3 \\ \lambda_4 \end{bmatrix},$$

where $\lambda_1 \in (a - \varepsilon_0^{(1)}, a + \varepsilon_0^{(1)})$, $\lambda_2 \in (b - \varepsilon_0^{(2)}, b + \varepsilon_0^{(2)})$, $\lambda_3 \in (c - \varepsilon_0^{(3)}, c + \varepsilon_0^{(3)})$, $\lambda_4 \in (d - \varepsilon_0^{(4)}, d + \varepsilon_0^{(4)})$.

If

$$\lim_{\Lambda \rightarrow A} \bar{Y}_\Lambda = \bar{Y}_A,$$

then every solution of the System (89) is convergent and satisfies

$$\lim_{n \rightarrow \infty} X_n = \bar{Y}_A.$$

Proof. For arbitrary $\varepsilon = \begin{bmatrix} \varepsilon_1 \\ \varepsilon_2 \\ \varepsilon_3 \\ \varepsilon_4 \end{bmatrix} \succ_{ne} \begin{bmatrix} 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}$, there exists $N = N(\varepsilon)$ such that for $n \geq N$, the following holds:

$$a - \varepsilon_1 < a_n < a + \varepsilon_1,$$

$$b - \varepsilon_2 < b_n < b + \varepsilon_2,$$

$$c - \varepsilon_3 < c_n < c + \varepsilon_3,$$

$$d - \varepsilon_4 < d_n < d + \varepsilon_4,$$

This implies that

$$\begin{aligned} & \begin{bmatrix} (a - \varepsilon_1)f_1(x_n) + (b - \varepsilon_2)f_2(y_n) \\ (c - \varepsilon_3)f_3(x_n) + (d - \varepsilon_4)f_4(y_n) \end{bmatrix} \preceq_{ne} \begin{bmatrix} a_n f_1(x_n) + b_n f_2(y_n) \\ c_n f_3(x_n) + d_n f_4(y_n) \end{bmatrix} \\ & \preceq_{ne} \begin{bmatrix} (a + \varepsilon_1)f_1(x_n) + (b + \varepsilon_2)f_2(y_n) \\ (c + \varepsilon_3)f_3(x_n) + (d + \varepsilon_4)f_4(y_n) \end{bmatrix}, n \geq N(\varepsilon). \end{aligned} \quad (92)$$

Since F is cooperative map, Lemma 5 implies

$$L_n \preceq_{ne} X_n \preceq_{ne} U_n, \quad n \geq N(\varepsilon), \quad (93)$$

where $\{L_n\} = \left\{ \begin{bmatrix} l_n^{(1)} \\ l_n^{(2)} \end{bmatrix} \right\}$ satisfies

$$L_{n+1} = \begin{bmatrix} (a - \varepsilon_1)f_1(l_n^{(1)}) + (b - \varepsilon_2)f_2(l_n^{(2)}) \\ (c - \varepsilon_3)f_3(l_n^{(1)}) + (d - \varepsilon_4)f_4(l_n^{(2)}) \end{bmatrix},$$

and $\{U_n\} = \left\{ \begin{bmatrix} u_n^{(1)} \\ u_n^{(2)} \end{bmatrix} \right\}$ satisfies

$$U_{n+1} = \begin{bmatrix} (a + \varepsilon_1)f_1(l_n^{(1)}) + (b + \varepsilon_2)f_2(l_n^{(2)}) \\ (c + \varepsilon_3)f_3(l_n^{(1)}) + (d + \varepsilon_4)f_4(l_n^{(2)}) \end{bmatrix}.$$

Inequalities (93) imply

$$\lim_{n \rightarrow \infty} L_n \preceq_{ne} \varliminf_{n \rightarrow \infty} X_n \preceq_{ne} \overline{\lim}_{n \rightarrow \infty} X_n \preceq_{ne} \lim_{n \rightarrow \infty} U_n,$$

i.e.,

$$\overline{Y}_{A-\varepsilon} \preceq_{ne} \varliminf_{n \rightarrow \infty} X_n \preceq_{ne} \overline{\lim}_{n \rightarrow \infty} X_n \preceq_{ne} \overline{Y}_{A+\varepsilon} \quad (2)$$

where $A \pm \varepsilon = \begin{bmatrix} a \pm \varepsilon_1 \\ b \pm \varepsilon_2 \\ c \pm \varepsilon_3 \\ d \pm \varepsilon_4 \end{bmatrix}$. Since $\lim_{\varepsilon \rightarrow \mathbf{0}} \overline{Y}_{A-\varepsilon} = \lim_{\varepsilon \rightarrow \mathbf{0}} \overline{Y}_{A+\varepsilon} = \overline{Y}_A$, where $\mathbf{0} = \begin{bmatrix} 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}$, (2)

implies that the sequence $\{X_n\}$ is convergent and, therefore,

$$\lim_{n \rightarrow \infty} X_n = \overline{Y}_A.$$

■

Example 59 Consider the following system of equations:

$$\begin{aligned} x_{n+1} &= \frac{a x_n}{\delta_1 + x_n} + \frac{b y_n}{\delta_2 + y_n} \\ y_{n+1} &= \frac{c x_n}{\delta_2 + x_n} + \frac{d y_n}{\delta_1 + y_n}, n = 0, 1, \dots \end{aligned} \quad (94)$$

where $a, b, c, d, \delta_1, \delta_2 > 0$, $x_0, y_0 \geq 0$. Let $T : \mathbb{R}_+^2 \rightarrow \mathbb{R}_+^2$ be the map associated to (94), that is

$$T(x, y) = \left(\frac{a x}{\delta_1 + x} + \frac{b y}{\delta_2 + y}, \frac{c x}{\delta_2 + x} + \frac{d y}{\delta_1 + y} \right).$$

Theorem 60 *The following statements are true.*

- (a) *T maps the positive quadrant into the invariant set $[0, a + b) \times [0, c + d)$.*
- (b) *For all values of the parameters, the system has the equilibrium point $(0, 0)$.*
- (c) *There is at least one and at most two equilibrium points.*
- (d) *The point $(0, 0)$ is the unique equilibrium if and only if*

$$\delta_1 > \max(a, d) \quad \text{and} \quad \frac{(-a + \delta_1)\delta_2}{b\delta_1} \geq \frac{c\delta_1}{(-d + \delta_1)\delta_2}. \quad (95)$$

In this case, $(0, 0)$ is globally asymptotically stable.

- (e) *A positive interior fixed point (x_+, y_+) exists if and only if condition (95) is not satisfied, that is when*

$$\delta_1 \leq \max(a, d) \quad \text{or} \quad \frac{(a - \delta_1)(d - \delta_1)}{\delta_1^2} < \frac{bc}{\delta_2^2}. \quad (96)$$

In this case, (x_+, y_+) is globally asymptotically stable on $\mathbb{R}_+^2 \setminus (0, 0)$.

Proof. (a): It is clear that T maps the positive quadrant into $[0, a + b) \times [0, c + d)$. For the proof of (b)-(f) we will consider the following equilibrium curves equation of the system

$$\begin{aligned} C_1 : \quad & axy + bxy - x^2y + by\delta_1 - xy\delta_1 + ax\delta_2 - x^2\delta_2 - x\delta_1\delta_2 = 0 \\ C_2 : \quad & cxy + dxy - xy^2 + cx\delta_1 - xy\delta_1 + dy\delta_2 - y^2\delta_2 - y\delta_1\delta_2 = 0. \end{aligned} \quad (97)$$

Now, solving for one variable (y and x respectively) we obtain

$$y = \frac{x(-a + x + \delta_1)\delta_2}{ax + bx - x^2 + b\delta_1 - x\delta_1} \quad \text{and} \quad x = \frac{y(-d + y + \delta_1)\delta_2}{cy + dy - y^2 + c\delta_1 - y\delta_1}.$$

For simplicity, we will set the equilibrium curves as

$$C_1 : \quad y = \frac{x(-a + x + \delta_1)\delta_2}{ax + bx - x^2 + b\delta_1 - x\delta_1} \quad \text{and} \quad C_2 : \quad x = \frac{y(-d + y + \delta_1)\delta_2}{cy + dy - y^2 + c\delta_1 - y\delta_1}.$$

The slopes at the origin of these two curves are as follows

$$\frac{dy}{dx}|_{(C_1)} = \frac{(-a + \delta_1)\delta_2}{b\delta_1} \quad \text{and} \quad \frac{dy}{dx}|_{(C_2)} = \frac{1}{\frac{dx}{dy}}(C_2) = \frac{c\delta_1}{(-d + \delta_1)\delta_2}.$$

(c): Monotonicity and concavity intervals for C_1 and C_2 are obvious. In view of Lemma 5 from [20] if an interior equilibrium exists, it is unique, and also it must belong to the set limited by the asymptotes. The asymptotes of C_1 are

$$x = \frac{1}{2} \left(a + b - \delta_1 + \sqrt{(a + b - \delta_1)^2 + 4b\delta_1} \right), \quad x = \frac{1}{2} \left(a + b - \delta_1 - \sqrt{(a + b - \delta_1)^2 + 4b\delta_1} \right)$$

while the asymptotes of C_2 are

$$y = \frac{1}{2} \left(c + d - \delta_1 + \sqrt{(c + d - \delta_1)^2 + 4c\delta_1} \right), \quad y = \frac{1}{2} \left(c + d - \delta_1 - \sqrt{(c + d - \delta_1)^2 + 4c\delta_1} \right)$$

Since

$$x = \frac{1}{2} \left(a + b - \delta_1 - \sqrt{(a + b - \delta_1)^2 + 4b\delta_1} \right), \quad y = \frac{1}{2} \left(c + d - \delta_1 - \sqrt{(c + d - \delta_1)^2 + 4c\delta_1} \right)$$

are not in \mathbb{R}_+^2 , the interior fixed point, if it exists, must belong to the interior of the set $(0, x_*) \times (0, y_*)$, where

$$x_* = \frac{1}{2} \left(a + b - \delta_1 + \sqrt{(a + b - \delta_1)^2 + 4b\delta_1} \right), \quad y_* = \frac{1}{2} \left(c + d - \delta_1 + \sqrt{(c + d - \delta_1)^2 + 4c\delta_1} \right)$$

Thus the system will have either only $(0, 0)$ as a fixed point or it will also have this unique interior fixed point (x_+, y_+) which belongs to the interior of the set $(0, x_*) \times (0, y_*)$.

(d) and (e): Based on the geometry of the equilibrium curves and their slopes at the origin, we see that there exists an interior equilibrium exactly in the following situations:

(i) at least one slope is negative, 0, or ∞ . (ii) both slopes are positive, and slope of $C_1 <$ slope of C_2 . Thus a necessary and sufficient condition for existence of an interior equilibrium point are that there exists an interior fixed point if and only if one of (i) or (ii) holds,

$$(i) \delta_1 \leq \max(a, d) \quad \text{or} \quad (ii) \delta_1 > \max(a, d) \quad \text{and} \quad \frac{(-a + \delta_1)\delta_2}{b\delta_1} < \frac{c\delta_1}{(-d + \delta_1)\delta_2}.$$

The conditions (i),(ii) can be merged into one as follows,

$$\delta_1 \leq \max(a, d) \quad \text{or} \quad \frac{(a - \delta_1)(d - \delta_1)}{\delta_1^2} < \frac{bc}{\delta_2^2}. \quad (98)$$

Since (98) give conditions for a unique interior fixed point, we also have conditions for $(0, 0)$ to be the unique fixed point. Namely, whenever the interior fixed point does not exist, which is given by the following,

$$\delta_1 > \max(a, d) \quad \text{and} \quad \frac{(-a + \delta_1)\delta_2}{b\delta_1} \geq \frac{c\delta_1}{(-d + \delta_1)\delta_2}. \quad (99)$$

Next it will be shown that when $(0, 0)$ is the unique equilibrium that it is globally asymptotically stable. This is simply the consequence of (a) and Theorem 2.1 of [12].

Now we will show conditions for $(0, 0)$ to be unstable, to show (e). The characteristic polynomial of the Jacobian of the map T at $(0, 0)$ is

$$p(t) = t^2 - \left(\frac{a}{\delta_1} + \frac{d}{\delta_1} \right) t + \frac{bc}{\delta_2^2} + \frac{ad}{\delta_1^2}. \quad (100)$$

From geometric considerations with the function $p(t)$, we can get a sufficient condition for $(0, 0)$ to be unstable as: $(0, 0)$ is unstable if $(p(1) < 0)$ or $(p(1) \geq 0$ and $p'(1) < 0)$, which can be rewritten as follows. The point $(0, 0)$ is unstable if

$$\frac{(a - \delta_1)(d - \delta_1)}{\delta_1^2} < \frac{bc}{\delta_2^2} \quad \text{or} \quad 2\delta_1 < a + d. \quad (101)$$

Now we are working under the assumption

$$\delta_1 \leq \max(a, d) \quad \text{or} \quad \frac{(a - \delta_1)(d - \delta_1)}{\delta_1^2} < \frac{bc}{\delta_2^2}, \quad (102)$$

since these are the conditions for the existence of an interior equilibrium.

Thus if the interior equilibrium exists, then $(0, 0)$ is unstable. Proceeding by contradiction, assume that (101) is false, i.e., assume

$$\frac{(a - \delta_1)(d - \delta_1)}{\delta_1^2} \geq \frac{bc}{\delta_2^2} \quad \text{and} \quad (2\delta_1 \geq a + d).$$

The first inequality in (101) implies $(a - \delta_1)(d - \delta_1) > 0$, so either $\delta_1 > \max(a, d)$ or $\delta_1 \leq \min(a, d)$. But $\delta_1 \leq \min(a, d)$ is ruled out because $2\delta_1 \geq a + d$. Thus $\delta_1 > \max(a, d)$, which contradicts (102).

Next it will be shown that when (x_+, y_+) exists that it is globally asymptotically stable. Note first $T(\mathbb{R}_+^2 \setminus (0, 0)) \subset (0, a + b) \times (0, c + d)$. If the interior equilibrium exists, then $(0, 0)$ is unstable. Given any point (x, y) in $\mathbb{R}_+^2 \setminus (0, 0)$, there is a point $(x_0, y_0) > (0, 0)$ such that $(x_0, y_0) < (x, y) < (a + b, c + d)$. Indeed, (x_0, y_0) may be chosen as a point on the ray with direction vector given by an eigenvector of the jacobian of T at $(0, 0)$ associated with the spectral radius of such jacobian. Then, $T^n(x_0, y_0) < T^n(x, y) < T^n(a + b, c + d)$. Since $\{T^n(x_0, y_0)\}$ and $\{T^n(a + b, c + d)\}$ are monotonic sequences increasing and decreasing respectively, the omega limit of the order interval $[T^n(x_0, y_0), T^n(a + b, c + d)]$ is a singleton set consisting of the interior equilibrium. Thus (x_+, y_+) is globally asymptotically stable completing the proof. ■

Remark 61 System (94) is possible two dimensional version of the Beverton-Holt difference equation

$$x_{n+1} = \frac{ax_n}{1 + x_n}, a > 0, x_0 \geq 0 \quad n = 0, 1, \dots \quad (103)$$

which exhibits the transcritical bifurcation at $a = 1$, in such a way that $\bar{x}_0 = 0$ is globally asymptotically stable for $a \leq 1$ and $\bar{x}_+ = a - 1$ is globally asymptotically stable for $a > 1$ and $x_0 > 0$. In [2], we extended this bifurcation result to the case of the nonautonomous Beverton-Holt difference equation

$$x_{n+1} = \frac{a_n x_n}{1 + x_n}, a_n > 0, x_0 \geq 0 \quad n = 0, 1, \dots \quad (104)$$

Applying Theorem 58 to system

$$\begin{aligned} x_{n+1} &= \frac{a_n x_n}{\delta_1 + x_n} + \frac{b_n y_n}{\delta_2 + y_n} \\ y_{n+1} &= \frac{c_n x_n}{\delta_2 + x_n} + \frac{d_n y_n}{\delta_1 + y_n}, n = 0, 1, \dots \end{aligned} \quad (105)$$

we obtain the following result:

Corollary 62 Consider System (105), where a_n, b_n, c_n, d_n are sequences such that

$$\lim_{n \rightarrow \infty} (a_n, b_n, c_n, d_n) = (a, b, c, d).$$

If (95) holds, then $(0, 0)$ is global attractor of solutions of (105); if (95) is not satisfied, that is when (98) holds, the positive equilibrium (x_+, y_+) is global attractor of solutions of (105) on $\mathbb{R}_+^2 \setminus (0, 0)$.

3.3 Examples of cooperative evolutionary models

In this section, we consider some cooperative evolutionary models where non-linear transition functions are Beverton-Holt functions or Beverton-Holt functions with squares.

Firstly, we investigate the following cooperative evolutionary model

$$\left. \begin{aligned} x_{n+1} &= A(u_1(n)) \frac{y_n}{1+y_n} x_n \\ y_{n+1} &= B(u_2(n)) \frac{x_n}{1+x_n} y_n \\ u_1(n+1) &= u_1(n) + \sigma_1^2 \frac{A'(u_1(n))}{A(u_1(n))} \\ u_2(n+1) &= u_2(n) + \sigma_2^2 \frac{B'(u_2(n))}{B(u_2(n))} \end{aligned} \right\}, \quad n = 0, 1, \dots, \quad (106)$$

where $A(u_1) > 0$ and $B(u_2) > 0$ are twice differentiable functions on their domains. The fixed points of the last two equations in (106) are u_1^* and u_2^* , respectively, where u_1^* and u_2^* are critical points of functions $A(u_1)$ and $B(u_2)$.

Lemma 63 If

$$\frac{-2}{\sigma_1^2} < \frac{A''(u_1^*)}{A(u_1^*)} < 0 \quad \text{and} \quad \frac{-2}{\sigma_2^2} < \frac{B''(u_2^*)}{B(u_2^*)} < 0, \quad (107)$$

then there exist open neighborhoods \mathcal{U}_1 and \mathcal{U}_2 of u_1^* and u_2^* , respectively, such that

$$\lim_{n \rightarrow \infty} u_1(n) = u_1^* \quad \text{and} \quad \lim_{n \rightarrow \infty} u_2(n) = u_2^*. \quad (108)$$

Proof. The proof follows from the fact that (107) is equivalent to $\left| \frac{dG_1}{du_1}(u_1^*) \right| < 1$ and $\left| \frac{dG_2}{du_2}(u_2^*) \right| < 1$ (that is u_1^* and u_2^* are locally asymptotically stable), where

$$\begin{aligned} G_1(u_1(n)) &= u_1(n) + \sigma_1^2 \frac{A'(u_1(n))}{A(u_1(n))}, \\ G_2(u_1(n)) &= u_2(n) + \sigma_2^2 \frac{B'(u_2(n))}{B(u_2(n))}, \end{aligned}$$

since $A'(u_1^*) = 0$ and $B'(u_2^*) = 0$. ■

Lemma 63 implies that the non-autonomous system formed by the first two equations in (106) is asymptotic to the following limiting system

$$\left. \begin{aligned} x_{n+1} &= A(u_1^*) \frac{y_n}{1+y_n} x_n \\ y_{n+1} &= B(u_2^*) \frac{x_n}{1+x_n} y_n \end{aligned} \right\}, \quad n = 0, 1, \dots \quad (109)$$

System (109) has equilibrium point $E_0^* = \begin{bmatrix} 0 \\ 0 \end{bmatrix}$, which is locally asymptotically stable for all values of $A(u_1^*) > 0$ and $B(u_2^*) > 0$, and has one positive equilibrium point $E_+^* = \begin{bmatrix} \frac{1}{B(u_2^*)-1} \\ \frac{1}{A(u_1^*)-1} \end{bmatrix}$, which is a saddle point if $A(u_1^*) > 1$ and $B(u_2^*) > 1$ (see [19]). The following result is a consequence of Example 46.

Theorem 64 *Assume that $(A(u_1^*), B(u_2^*)) \notin (1, \infty)^2$. Then, the equilibrium point $E_0^* = \begin{bmatrix} 0 \\ 0 \end{bmatrix}$ is globally asymptotically stable, i.e., every solution $\{(x_n, y_n)\}$ of (109) satisfies*

$$\lim_{n \rightarrow \infty} x_n = \lim_{n \rightarrow \infty} y_n = 0,$$

for all $x_0 \geq 0$ and $y_0 \geq 0$.

Based on Theorem 45 and using Example 46 we obtain the following result.

Theorem 65 *If $(A(u_1^*), B(u_2^*)) \notin (1, \infty)^2$ and condition (107) holds, then all solutions of non-autonomous system (106) globally asymptotically converge to*

$$(E_0^*, u_1^*, u_2^*) = \begin{bmatrix} 0 \\ 0 \\ u_1^* \\ u_2^* \end{bmatrix} \in \mathbb{R}_+^2 \times \mathcal{U}_1 \times \mathcal{U}_2, \text{ for all points } x_0 \geq 0 \text{ and } y_0 \geq 0.$$

Now, we consider cooperative evolutionary model of the form

$$\left. \begin{aligned} x_{n+1} &= A(u_1(n)) \frac{y_n^2}{1+y_n^2} x_n \\ y_{n+1} &= B(u_2(n)) \frac{x_n^2}{1+x_n^2} y_n \\ u_1(n+1) &= u_1(n) + \sigma_1^2 \frac{A'(u_1(n))}{A(u_1(n))} \\ u_2(n+1) &= u_2(n) + \sigma_2^2 \frac{B'(u_2(n))}{B(u_2(n))} \end{aligned} \right\}, \quad n = 0, 1, \dots, \quad (110)$$

where $A(u_1) > 0$ and $B(u_2) > 0$ are twice differentiable functions on their domains. As in the previous example, fixed points u_1^* and u_2^* , of last two equations in (110) are respectively, critical points of functions $A(u)$ and $B(u)$. Also, under condition (107), there exist open neighborhoods \mathcal{U}_1 and \mathcal{U}_2 of u_1^* and u_2^* , respectively, such that (108) holds. It implies that the non-autonomous system formed by the first two equations in (110) is asymptotic to the following limiting system

$$\left. \begin{aligned} x_{n+1} &= A(u_1^*) \frac{y_n^2}{1+y_n^2} x_n \\ y_{n+1} &= B(u_2^*) \frac{x_n^2}{1+x_n^2} y_n \end{aligned} \right\}, \quad n = 0, 1, \dots \quad (111)$$

By an analogous procedure as in the case of the Example 46, considered in [19], it is obtained that the System (111) has equilibrium point $E_0^* = \begin{bmatrix} 0 \\ 0 \end{bmatrix}$, which is locally asymptotically stable for all values of $A(u_1^*) > 0$ and $B(u_2^*) > 0$, and has one positive equilibrium point $E_+^* = \begin{bmatrix} \frac{1}{\sqrt{B(u_2^*)-1}} \\ \frac{1}{\sqrt{A(u_1^*)-1}} \end{bmatrix}$, which is a saddle point if $A(u_1^*) > 1$ and $B(u_2^*) > 1$. Also, the equilibrium point E_0^* is globally asymptotically stable if $(A(u_1^*), B(u_2^*)) \notin (1, \infty)^2$.

Finally, based on Theorem 45 we obtain the following result.

Theorem 66 *Assume that $(A(u_1^*), B(u_2^*)) \notin (1, \infty)^2$ and condition (107) holds. Then, all solutions of non-autonomous System (110) globally asymptotically converge to $(E_0^*, u_1^*, u_2^*) = (0, 0, u_1^*, u_2^*) \in \mathbb{R}_+^2 \times \mathcal{U}_1 \times \mathcal{U}_2$, for all initial values $x_0 \geq 0$ and $y_0 \geq 0$.*

The following example shows that construction of the model (106) is possible.

Example 67 Consider the following model

$$\left. \begin{aligned} x_{n+1} &= \left(A + \frac{u_1(n) - 1}{(u_1(n))^2} \right) \frac{y_n}{1 + y_n} x_n \\ y_{n+1} &= \left(B + \frac{u_2(n)}{(u_2(n))^2 + 1} \right) \frac{x_n}{1 + x_n} y_n \\ u_1(n+1) &= u_1(n) + \sigma_1^2 \frac{A'(u_1(n))}{A(u_1(n))} \\ u_2(n+1) &= u_2(n) + \sigma_2^2 \frac{B'(u_2(n))}{B(u_2(n))} \end{aligned} \right\}, \quad n = 0, 1, \dots, \quad (112)$$

where $A(u_1(n)) = A + \frac{u_1(n) - 1}{(u_1(n))^2}$, $B(u_2(n)) = B + \frac{u_2(n)}{(u_2(n))^2 + 1}$, and $(A, B) \notin (1, \infty)^2$.

From $A'(u_1^*) = \frac{-u_1^* + 2}{(u_1^*)^3} = 0$ and $B'(u_2^*) = \frac{-(u_2^*)^2 + 1}{((u_2^*)^2 + 1)^2} = 0$, we obtain $u_1^* = 2$ and $(u_2^*)_{\pm} = \pm 1$. In the following presentation, we will use $u_2^* = (u_2^*)_+ = 1$ because for $u_2^* = (u_2^*)_- = -1$ the condition $\frac{B''(u_2^*)}{B(u_2^*)} < 0$ from (107) is not satisfied. Since $A''(u_1^*) = A''(2) = -\frac{1}{8}$, $B''(u_2^*) = B''(1) = -\frac{1}{2}$, $A(u_1^*) = A + \frac{1}{4}$, and $B(u_2^*) = B + \frac{1}{2}$, condition (107) is satisfied if

$$A > \frac{1}{16} (\sigma_1^2 - 4) \quad \text{and} \quad B > \frac{1}{4} (\sigma_2^2 - 2)$$

or

$$\sigma_1^2 < 16A + 4, \quad \sigma_2^2 < 4B + 2. \quad (113)$$

Then, there exist open neighborhoods \mathcal{U}_1 and \mathcal{U}_2 of u_1^* and u_2^* , respectively, such that

$$\lim_{n \rightarrow \infty} u_1(n) = u_1^* = 2 \quad \text{and} \quad \lim_{n \rightarrow \infty} u_2(n) = u_2^* = 1.$$

Also, the non-autonomous system formed by the first two equations in (112) is asymptotic to the following limiting system

$$\left. \begin{aligned} x_{n+1} &= \left(A + \frac{1}{4} \right) \frac{y_n}{1 + y_n} x_n \\ y_{n+1} &= \left(B + \frac{1}{2} \right) \frac{x_n}{1 + x_n} y_n \end{aligned} \right\}, \quad n = 0, 1, \dots \quad (114)$$

Based on Theorems 64 and 65, and assuming that $(A + \frac{1}{4}, B + \frac{1}{2}) \notin (1, \infty)^2$, we obtain the following two results.

1. The equilibrium point $E_0^* = (0, 0)$ is globally asymptotically stable, i.e., every solution $\{(x_n, y_n)\}$ of (114) satisfies

$$\lim_{n \rightarrow \infty} x_n = \lim_{n \rightarrow \infty} y_n = 0,$$

for all $x_0 \geq 0$ and $y_0 \geq 0$.

2. If additionally (113) holds, then all solutions of non-autonomous System (112) globally asymptotically converge to $(E_0^*, u_1^*, u_2^*) = \begin{bmatrix} 0 \\ 0 \\ u_1^* \\ u_2^* \end{bmatrix} \in \mathbb{R}_+^2 \times \mathcal{U}_1 \times \mathcal{U}_2$, for all points $x_0 \geq 0$ and $y_0 \geq 0$.

Example 68 Consider the model

$$\left. \begin{aligned} x_{n+1} &= A(u(n)) \frac{y_n x_n}{1 + y_n} \\ y_{n+1} &= B(u(n)) \frac{x_n y_n}{1 + x_n} \end{aligned} \right\}, \quad n = 0, 1, \dots, \quad (115)$$

where $A(u) > 0$ and $B(u) > 0$ are twice differentiable functions with a single Fisher's equation

$$u_{n+1} = p \frac{u_n^3}{1 + u_n^3} \quad (116)$$

where $x_0 \geq 0, y_0 \geq 0, u_0 \geq 0$, for $n = 0, 1, \dots$

Fisher's equation (116) has between 2 and 4 equilibrium points given as:

$$E_2 = 0, E_1 = \frac{1}{3} \left(-\sqrt[3]{\frac{3}{2} (\sqrt{81 - 12p^3} + 9)} - p^3 - \frac{p^2}{\sqrt[3]{\frac{3}{2} (\sqrt{81 - 12p^3} + 9)} - p^3} + p \right),$$

$$E_3 = \frac{1}{6} \left(-(-2)^{2/3} \sqrt[3]{3 (\sqrt{81 - 12p^3} + 9)} - 2p^3 + \frac{2\sqrt[3]{-2p^2}}{\sqrt[3]{3 (\sqrt{81 - 12p^3} + 9)} - 2p^3} + 2p \right),$$

$$E_4 = \frac{1}{12}p \left(4 - \frac{4(-1)^{2/3}p}{\sqrt[3]{\frac{3}{2}(\sqrt{81-12p^3+9})-p^3}} \right) + \frac{1}{3}\sqrt[3]{-\frac{1}{2}\sqrt[3]{3(\sqrt{81-12p^3+9})-2p^3}},$$

where E_3 and E_4 exist if $p < \frac{3}{\sqrt[3]{4}}$. If $p = \frac{3}{\sqrt[3]{4}}$ then there are 3 equilibrium points $E_1 = \frac{-1}{\sqrt[3]{4}}, E_2 = 0, E_3 = \sqrt[3]{2}$. If $p > \frac{3}{\sqrt[3]{4}}$ then there are 2 equilibrium points E_1 and E_2 . The equilibrium points E_2 and E_4 are locally asymptotically stable and the equilibrium points E_1 and E_3 are locally repellers. In addition, E_2 is globally asymptotically stable within its basin of attraction $\mathcal{B}(E_2) = (E_1, E_3)$ while E_4 is globally asymptotically stable within its basin of attraction $\mathcal{B}(E_4) = (E_3, \infty)$.

The fitness function is

$$A(x) = B(x) = \exp \left(\frac{\frac{1}{6}p \log(x^2 - x + 1) + px - \frac{1}{3}p \log(x + 1) - \frac{p \tan^{-1}\left(\frac{2x-1}{\sqrt{3}}\right)}{\sqrt{3}} - \frac{x^2}{2}}{\sigma^2} \right). \quad (117)$$

Lemma 63 implies that the non-autonomous system (115) is asymptotic to the following limiting autonomous system

$$\left. \begin{aligned} x_{n+1} &= A(u^*) \frac{y_n}{1+y_n} x_n \\ y_{n+1} &= B(u^*) \frac{x_n}{1+x_n} y_n \end{aligned} \right\}, n = 0, 1, \dots \quad (118)$$

Based on Theorem 45 and Example 46 we obtain the following result.

Theorem 69 *If $(A(E_4), B(E_4)) \notin (1, \infty)^2$ and $u_0 \in (E_3, \infty)$ holds, then all solutions of non-autonomous system (115) globally asymptotically converge to*

$$(E_0^*, E_4) = \begin{bmatrix} 0 \\ 0 \\ E_4 \end{bmatrix} \in \mathbb{R}_+^2 \times \mathcal{U}_1, \text{ for all points } x_0 \geq 0 \text{ and } y_0 \geq 0.$$

If $(A(0), B(0)) \notin (1, \infty)^2$ and $u_0 \in (E_1, E_3)$ holds, then all solutions of non-autonomous system (115) globally asymptotically converge to $(E_0^, 0) = \begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix} \in$*

$\mathbb{R}_+^2 \times \mathcal{U}_1$, for all points $x_0 \geq 0$ and $y_0 \geq 0$.

In view of Theorem 42 the equilibrium solutions E_2 and E_4 are globally asymptotically stable within their immediate basins of attractions. One of them is ESS (evolutionary stable) and that is the one located at a global maximum of the fitness function, see [4, 5, 16]. The second equilibrium is evolutionarily convergent, but not an ESS since it does not yield a global maximum of the fitness function, see [4, 5, 16]. Figure 4 indicates that the position of the global maximum depends on parameter p .

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