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Asymptotic Stability, Bifurcation Analysis and Chaos Control for Some Discrete Evolutionary Population Models

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Prof. Saber Elaydi; https://www.trinity.edu/directory/selaydi

RESUMÉ

Ce travail est dédié à l'analyse dynamique de certains modèles Darwiniens (évolutionnaires), formulés en utilisant la théorie du jeu Darwinienne (évolutionnaire selon la selection naturelle de Darwin [15]). Plus précisément, nous développons une nouvelle approche pour analyser la stabilité asymptotique globale pour une classe de modèles Darwiniens. Ensuite, une analyse de bifurcations est entamée pour certains modèles Darwiniens couplés de types Ricker et Beverton. Le contrôle du chaos constitue une contribution importante dans notre travail afin de retarder ou éliminer certains comportements indésirables en systèmes dynamiques discrets.

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CHAPTER

1

INTRODUCTION AND GENERAL OVERVIEW

In this chapter, we present the motivation and reasons behind our mathematical modeling to investigate the dynamical behavior of single and multi-species populations.

1.1 Preview of Thesis Contributions

The aims of this research are:

- To derive new evolutionary discrete-time population models by using the evolutionary game theory methodology and investigate the dynamical behavior of their fixed points (equilibria).

- To develop a rigourous analysis of bifurcations by using bifurcation theory and center manifold theory.

- To control the chaos produced by bifurcations to avoid unstable orbits.

- To develop detailed numerical simulations to justify the theoretical results and show more rich dynamics.

1.2 Motivation & Literature review

This section is organized as follows: In Subsection (1.2.1), we review briefly some works on discrete-time dynamical systems. In Subsection (1.2.2), we present the mathematical approach used to derive the models studied in this dissertation. In (1.2.4), we discuss some relevant Cushing's works on evolutionary modeling and present our main contribution.

1.2.1 Discrete Dynamical System: A Literature review

Because of their complexity, population models have long piqued the curiosity of researchers. Population dynamics are influenced by size, age distribution, genetics, and a variety of other natural phenomena. Seasonal oscillations and other external environmental factors can result in both chaotic and periodic outcomes [34, 35]. An increase in the inherent growth rate may cause bifurcations and chaos in these models.

There are two types of mathematical models known in population dynamics, the continuous time models represented by differential equations that are used for some populations with overlapping generations due to the frequent interactions between their constituents. For some populations with non-overlapping generations, discrete dynamical systems are better suited because interactions occur during regular breeding seasons. Such models seem to be more realistic than their continuous counterparts, particularly when the population size is small. Furthermore, discrete-time models may provide more efficient computational models for numerical simulations [22, 46].

We first start by briefly reviewing some works on discrete-time models, which have been widely studied in the decades. In [2], Ackleh *et al.* explored a continuous-time model for Alzheimer's disease and investigated two corresponding discrete-time approximations to the model that are dynamically consistent. They proved numerically that the continuous-time model generates sigmoidal growth, while the discrete-time approximations may display oscillatory dynamics. In [4], the authors established conditions for the interior equilibrium's persistence and local asymptotic stability for two discrete-time predator-prey models, one without evolution and another to resist toxicant. The aforementioned prey-predator model was later investigated in [27]. The hybrid control strategy was applied to control the Neimark-Sacker bifurcation in this model. In [42], Li *et al.* explored a discrete-time model of Ricker type. They showed that the model exhibits period-doubling bifurcations and investigated the existence and stability of the cycles. Their main contribution is that the Allee effect has a stabilizing effect on the dynamics of populations. Zhang *et al.* explored a discrete prey-predator model with Holling type-I functional response in [58]. The model takes into consideration the strong Allee effect. The authors established sufficient conditions for stability and employed a feedback control method to stabilize the chaotic behaviors caused by bifurcation. In the excellent survey [23], some latest developments on the global dynamics of difference equations and discrete dynamical systems are presented. Elaydi highlighted some open problems and conjectures to provide new research directions. Some recent works on discrete-time models can be found, among many others, in [26, 30, 48, 50, 51, 57].

1.2.2 The mathematical approach

The fundamental principle of evolution was first pioneered by the naturalist Charles Darwin in his 1859 book *On the origin of species* [15]. Darwinian evolution theory is founded on three axioms known as the *axioms of natural selection* which include variation, inheritance, and competition. Variation is where individuals within a population have different phenotypes, whereas inheritance is where offspring inherit a mixture of both parents' phenotypes. Competition occurs when more offspring are produced than can survive, so offspring with traits better matched to the environment will survive and reproduce more effectively than others [15]. Based on these axioms, evolution theory asserts that a population will select the traits that allow for more successful competition, greater survivability, and better reproduction. In other words, the theory of evolution underlines the key role of selection of traits or behavioral strategies against certain criteria [56]. Since its inception, numerous efforts have been made to quantitatively formalize Darwin's theory of evolution by natural selection as a mathematical game using concepts from the well-established field of game theory.

Model parameters in a difference equation population model may depend on some phenotypic traits that are subject to the axioms of Darwinian evolution [15]. Evolutionary dynamics can be modeled using evolutionary game theory (EGT) by coupling the ecological population dynamics and the evolutionary dynamics equation together. For a thorough description of the evolutionary game theory methodology, see Vincent and Brown [56] and for the mathematical framework for deriving discrete-time evolutionary population models, see Jim Cushing's work [8].

In [56], the concept of the fitness generating function, or G-function (for short), is introduced as a single mathematical expression to describe the fitness function for individuals using strategy u_i when it is substituted for the focal individual's strategy v in $\mathcal{U}$. In other words, $G(\mathbf{x}, v, \mathbf{u})$ gives the expected per capita growth rate of a focal individual using strategy v in $\mathcal{U}$ when the population is in state $(\mathbf{x}, \mathbf{u})$. As a result, when v is replaced by a mean strategy value u_i, the G-function generates the fitness H_i for population i, that is, $G(\mathbf{x}, v, \mathbf{u})|_{v=u_i} = H_i(\mathbf{x}, \mathbf{u})$. The G-function can also be interpreted as an adaptive landscape, which is a plot of a species' fitness with a mean strategy v, given the population vector x and strategy vector u. For a discrete time model, fitness (noted later by $r(x, v, u)$) is given as the logarithm of the per capita population growth rate, i.e., $\ln G(\mathbf{x}, v, \mathbf{u})$ and the fitness gradient is with respect to the trait v, i.e., $\left.\frac{\partial \ln G(\mathbf{x},v,\mathbf{u})}{\partial v}\right|_{v=\mathbf{u}}$. The dynamical equation for the change in the trait equation is described by

$$\mathbf{u}(t+1) = \mathbf{u}(t) + \sigma^2 \left.\frac{\partial \ln G(\mathbf{x}(t), v, \mathbf{u}(t))}{\partial v}\right|_{v=\mathbf{u}(t)},$$

where the constant of proportionality ${\sigma_i}^2$ is the variance of the distribution of strategies (phenotypic traits) in species x_i about the mean phenotypic trait u_i. ${\sigma_i}^2$ also known as the evolutionary speed. The phenotypic trait equation states that the change in the mean trait is proportional to the fitness gradient (with respect to an individual's trait). This means that greater variation in strategies produces more rapid evolution. The fitness gradient moves the strategy uphill, in the direction of the positive gradient on the adaptive landscape, which is in accordance with Fisher's fundamental theorem of natural selection [28]. Evolutionary or Darwinian dynamics is then modeled by coupling the ecological population dynamics in terms of a G-function and the evolutionary dynamics equation together to give the following general system of difference equations:

$$x_i(t+1) = x_i(t) r(\mathbf{x}(t), v, \mathbf{u}(t))\Big|_{v=u_i(t)}, \tag{1.1a}$$

$$u_i(t+1) = u_i(t) + \sigma_i^2 \left.\frac{\partial \ln r(\mathbf{x}(t), v, \mathbf{u}(t))}{\partial v}\right|_{v=u_i(t)}, \tag{1.1b}$$

where $\mathbf{x} = (x_1, x_2, ..., x_n) \in \mathcal{U}$ and $\mathbf{u} = (u_1, u_2, ..., u_n) \in \mathcal{U}$.

The first equation asserts that the population dynamics can modeled by assuming that the trait v is set equal to the population mean trait. The second equation (called Lande's or Fisher's or the canonical equation of evolution) prescribes that the change in the mean trait is proportional to the fitness gradient, where fitness in this model is chosen to be $\ln r$ [8, 56]. It is related to the variance of the trait in the population (exactly how depends on the derivation of the mean trait equation), which is assumed constant in time.

1.2.3 The ecological context

Wee present two ecological effects that are incorporated into this thesis: the Allee effect and the immigration effect.

The Allee effect

The Allee effect is a biological phenomenon characterized by a positive correlation between population density and its *per capita* (individual) growth [12]. It may be widely defined as a decline in individual fitness at low populations sizes or densities [52]. Some authors distinguish between a strong Allee effect and a weak Allee effect: a strong Allee effect refers to a population that exhibits a "critical density," below which populations decline to extinction and above which populations survive, whereas a weak Allee effect refers to a population that lacks a "critical density," but where the population growth rate rises with increasing densities at lower densities [53].

Mathematically speaking, if we consider a population with density $x(t) \in \mathbb{R}^+$ at discrete season or generation t. The growth of the population $x(t)$ can be modeled with the general difference equation,

$$x(t+1) = f(x(t)) = x(t)\, r(x(t)), \tag{1.2}$$

where f is a $\mathcal{C}^3$-map and $r(x(t)) \geq 0$ is the per-capita population growth rate from one season period to the next and is density-dependent. The Allee effect is present if $r \in \mathcal{C}^1$ and $r'(x) > 0$ for x sufficiently small. The Alle effect is called strong is in addition to the previous assumption, there exist a positive equilibrium A such that, if $x < A$ one have r is less than one, and greater than one for some densities higher than A, see Fig. 1.1.

The dynamics of (1.2) in the presence of a strong Allee effect can be divided into two distinct categories based on how the population began at maximum density, whether under A or not. Indeed, if a population is started at the maximal density N with $(Nr(N) > A)$, there is an interval of initial densities for which the population persists. On the other hand, if one has $Nr(N) < A$, then extinction occurs for almost every population density, according to Schreiber [52]. In the case of the strong Allee effect, the function $r(x(t))$ is defined as product of two functions $\mathcal{G}(x(t))$ and $\mathcal{I}(x(t))$, $r(x) = \mathcal{G}(x)\mathcal{I}(x)$ [43, 44], where $\mathcal{G}$ stands for a negative density factor and $\mathcal{I}$ is a positive density factor. Many scholars are interested in discrete-time models with Allee effects in the literature, for instance : [16, 24, 25, 44, 45, 58] and their bibliographies.

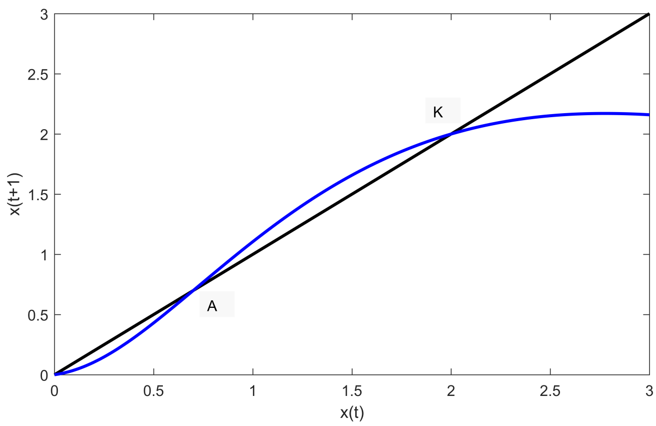


Figure 1.1: The map of the Ricker model with a strong Allee effect induced by predation saturation: $f(x) = x\exp(r - cx - m/(1 + sx))$ with parameter values $r = 1.6$; $c = .5$; $s = 2$; $m = 3$ (the blue curve) and $y = x$ (the black curve). There are three possible fixed points: trivial (extinction), A (threshold Allee point) and K (carrying capacity) .

Immigration effect

Consider a single population whose growth is regulated by simple birth and growth rates. We are interested in exploring what might result if there were a constant (typically small) influx of individuals into the population via the immigration process. Under what parameters's conditions would this influx stabilize or destabilize the population's fixed point in the presence of evolution. Holt [32] was one of the first to recognize that an influx of immigrants from surrounding peripheral island populations could stabilize a chaotic mainland population. Later, Stonne in [54] showed that immigration may alter the well-known period-doubling route to chaos and cause unexpected period-doubling reversals. From a mathematical point of view, the immigration effect can be modeled in Eq. (1.4) as follows [55]:

$$x(t + 1) = f(x(t)) + c, \tag{1.3}$$

where c is a positive constant representing immigration into the population.

Elaydi introduced and investigated the case of a species' population experiencing immigration proportional to its density [45]:

$$x(t + 1) = f(x(t)) + hx(t), \tag{1.4}$$

where h is a positive immigration parameter ($0 \leq h \leq 1$).

As known in a wide class of models without immigration, an increase in some parameters causes period-doubling bifurcations, leading to chaos. A small amount of immigration into the population is often sufficient to eventually reverse this process and reduce the chaos [55], and sufficiently large values of the immigration parameter can lead to dramatically different behavior, as demonstrated by [45].

Chaos

When we say chaos, we don't mean the absence of order or rules. Chaos is sometimes mistaken for instances such as a teenager's disorderly room or the behavior of an elementary school class when the teacher is away for a few minutes. Bounded aperiodic behavior that cannot be expected is the hallmark of mathematical chaos, which is generated by deterministic equations. Aperiodic simply means that no recurrence pattern occurs. Furthermore, a characteristic property of chaotic behavior, which is often oscillatory in nature, is a high sensitivity to initial conditions, i.e., given two arbitrarily close starting points, the distance between the generated trajectories would exponentially diverge in time [22].

Edward Lorenz [47], a meteorologist and mathematician, presented one of the most intriguing instances of chaotic systems. He concluded from his research on weather forecasting that weather is unpredictable despite being deterministic. As a result, long-term weather forecasting will always be a challenge for science. This is due to the fact that weather patterns are sensitive to initial conditions.

Chaos is not a phenomenon unique to weather; it is a quantifiable property [1] and the reference therein. It is a phenomenon that surrounds us and that we must take advantage of. For example, the logistic map:

$$x(t+1) = rx(t)(1 - x(t)), \tag{1.5}$$

which is often referred to as an archetypal example of how complex, chaotic behavior can arise from very simple nonlinear dynamical equations [22,36]. It has been applied to studying the dynamics of population growth. The bifurcation diagram of the logistic map has a form that mimics the silhouette of a dress, see Fig (1.2), according to Kazuyuki Aihara, a professor at the University of Tokyo [29].

Figure 1.2: (a) Bifurcation diagram of the logistic map drawn by taking r as a bifurcation parameter. (b): Dress based on the bifurcation diagram. For the original dress, see [29]

1.2.4 Motivation & Main Contributions

In this subsection, we first briefly review some of Cushing's works related to EGT methodology. In [8], Cushing describe evolutionary game theoretic methodology for extending a difference equation population dynamic model in a way so as to account for the Darwinian evolution of model coefficients. He gave a general theorem that describes the familiar transcritical bifurcation that occurs in non-evolutionary models when the extinction equilibrium destabilizes. Cushing and Stefanko developed a discrete dynamical difference equation in [9] to represent a trade-off between fertility and post-reproduction survival and to allow for density dependency in fertility. The evolutionary corresponding model is being analyzed to determine which conditions favor low post-reproduction survival and which ones favor high post-reproduction survival. In [3], Ackech et *et al.* investigated an evolutionary version of Lotka–Volterra dynamics in order to show the effect of evolutionary adaptation in the competitive outcome. In the reference [10], Cushing derived a coupled evolutionary version of the Beverton-Holt model using the EGT methodology. The model's global asymptotic stability is demonstrated under certain specialized ecological assumptions in which the trait equation is decoupled from the derived system.

The models presented in this manuscript and their related analysis build upon the previously referenced research. Our first key contribution is the development of a new approach established in [37] to investigate the global asymptotic stability of a special class of discrete-time evolutionary models. Furthermore, motivated by the fact that uncoupling is uncommon in evolutionary models, we investigated the dynamical behavior of various coupled evolutionary models: For instance, in [38], the asymptotic stability and Neimark-Sacker bifurcation are studied, and several chaos control strategies are employed to avoid chaotic orbits. Another interesting contribution is to take into account the Allee and immigration effects on the evolutionary dynamics, see [39, 40]. We proved that under some parametric conditions, the chaos caused by Neimark-Sacker bifurcation and period-doubling bifurcation may be delayed or completely eliminated.

1.3 Outlines of the Thesis

This thesis is outlined as follows:

Chapter 2: Discrete dynamical systems and Difference equations.

In this Chapter, we outline the mathematical framework and the theoretical tools that are utilized in the modeling approach in brief. The notions of a difference equation and a discrete dynamical system are presented. We define asymptotic stability for a discrete dynamical system and provide appropriate criteria for one- and two-dimensional system stability [21]. Finally, the center manifold theorem and certain observed bifurcations in planar discrete-time models are presented. Furthermore, in our derived Darwinian models, Neimark-Sacker (discrete Hopf) and period-doubling bifurcation (also known as flip bifurcation) are the most explored.

Chapter 3: Global Stability for a Special class of Discrete Evolutionary Population Models [37].

In this Chapter, we establish some global stability results for a special class of discrete-time Darwinian models, for both single and multi-species populations, that are derived according to the evolutionary game theory methodology. The decoupling of the mean trait dynamics from the population dynamics is the central idea behind the study that we provide in our first contribution. This approach is applied to a variety of Darwinian models. The theory of non-autonomous discrete dynamical systems has been developed by many authors (see for example [19, 23] and references within). The work in [19], which is the foundation of the new approach presented in this chapter, focuses on the topological and dynamical properties of the omega limit sets in non-autonomous discrete dynamical systems that are asymptotic to autonomous systems. The theoretical results were then applied to non-autonomous triangular maps and to some classical population models, such as Ricker's model.

Chapter 4: Dynamical Analysis and Chaos Control of a Discrete Evolutionary Beverton-Holt Model [38,39]

In this Chapter, we formulate two discrete-time evolutionary Beverton-Holt models, stated in terms of difference equations, that describe the size evolution of a single-species population of a biological organism.

These models are motivated by the fact that uncoupling is not as common in evolutionary models due to the specialized and ecological assumptions that are required. We prove analytically that the derived models experience Neimark-Sacker bifurcations under certain parametric conditions. The bifurcation theory is used in the analysis [33]. Furthermore, the chaos control strategies are implemented to avoid chaotic features.

Chapter 5: An Evolutionary Ricker model under Immigration effect [40]

In this Chapter, we expand and explore the Darwinian model derived by Cushing in [11], by including the immigration effect. The novelties in this Chapter are twofold: In contrast to Chapter 4, the fixed point can be identified explicitly, and the dynamics are more complicated. Indeed, the model under consideration has both Neimark-Sacker and period-doubling bifurcations. In this Chapter, we explore how the maximal fertility rate influences the evolutionary dynamics in the presence of the immigration effect.

Chapter 6: An Evolutionary Beverton-Holt model under Immigration effect [41]

A discrete-time evolutionary Beverton-Holt population model is developed in this Chapter. The model accounts for the immigration effect. Bifurcation and center manifold theory are used in the analysis to demonstrate various bifurcations, such as the Neimark-Sacker bifurcation and the period-doubling bifurcation. The difference from Chapter 5, is that we investigate the immigration effect on the stabilization or destabilization of the evolutionary dynamics. Furthermore, immigration has been shown to have a stabilizing effect on the dynamics. We employed various techniques to achieve chaos control influenced by Neimark-Sacker and period-doubling bifurcations for lower values of immigration's effect. Numerical simulations give evidence of the successful implementation of these techniques.

CHAPTER

2

DISCRETE DYNAMICAL SYSTEMS AND DIFFERENCE EQUATIONS

2.1 Introduction

In the first Chapter, we set the notations used in the text and present the main background motivations to study the derived discrete mathematical models [22].
The contents of this Chapter is delivered by three more sections as follows: In Section (2.2), we define a discrete dynamical system. The notion of stability and some useful criteria are presented in Section (2.3). Finally, the center manifold theory and bifurcation in a two-dimensional system are discussed in section (2.4).

2.2 Discrete dynamical systems

A discrete dynamical system, abbreviated DDS, is the formal description of an evolutive phenomena in terms of a map whose image is included in its domain: starting from any admissible initial value, a sequence of values is generated by the iterated computation of the given map.

Definition 2.1. *[19] Let (Y, d) be a metric space, T a topological group, and let $\pi : Y \times T \to Y$. Then the triple (Y, T, π) is called a* dynamical system *if*

(1) *(identity axiom) $\pi(y, 0) = y$ for all $y \in Y$, where 0 is the identity of T;*

(2) *(homomorphism axiom) $\pi(\pi(y, r), s) = \pi(y, r + s)$;*

(3) *(continuity axiom) π is continuous.*

If T is a topological semi group, then (Y, T, π) is called a *semi dynamical system.*
If $T = \mathbb{N}$, then the orbit of a point y with respect to π, is defined as $\mathcal{O}(y, \pi) = \{\pi(y, t), t \in \mathbb{N}\}$ and the ω-limit set of π at $y \in Y$ is

$$\omega(y, \pi) = \{z : \exists\{t_k\} \subseteq \mathbb{N},\ with\ \ \pi(y, t_k) \to z,\ t_k \to \infty\ as\ \ k \to \infty\}. \tag{2.1}$$

In the sequel, we use $\mathcal{O}(y)$ instead of $\mathcal{O}(y, \pi)$ and $\omega(y)$ instead of $\omega(y, \pi)$, when no confusion arises.
A subset B of Y is invariant if $\pi(B, t) = B$ for each $t \geq 0$.
Recall that, if $y \in Y$ and B and E are subsets of Y, then $d(y, B) = \inf\{d(y, y_1), y_1 \in B\}$, $d(B, E) = \inf\{(y, y_1) : y \in B, y_1 \in E\}$.
Let B and E be two (nonempty) subsets of Y. The set B is said to attract E if

$$d(\pi(E, t), B) \to 0,\ \ as\ t \to +\infty.$$

If the orbit closure of y, that is the closure of the orbit of y, $\overline{\mathcal{O}(y)}$, is compact then $\omega(y)$ attracts y, that is

$$\lim_{t \to +\infty} d(w(y), f^t(y)) = 0.$$

A closed invariant subset B of Y is said to be invariantly connected if it cannot be represented as the union of two nonempty, disjoint, closed, invariant sets.

Definition 2.2. *Let $(Y, \mathbb{N}, \pi)$ be a semi dynamical system generated by a continuous map f. Then the ω-limit set of π at $y \in Y$, $\omega(y, \pi)$, or simply $\omega(y)$, is the set*

$$\omega(y, f) = \{z : \exists\{t_k\} \subseteq \mathbb{N}\ \ with\ \ f^{t_k}(y) \to z, t_k \to \infty, k \to +\infty\}.$$

Theorem 2.1. *[19] Let $(Y, \mathbb{N}, \pi)$ be a semi dynamical system, and $y \in Y$ such that its orbit closure $\overline{\mathcal{O}(y)}$ is compact. Then, $w(y, \pi)$ is non-empty, closed, invariant, and invariantly connected.*

Theorem 2.2. *[19] Let $(Y, \mathbb{N}, \pi)$ be a semi dynamical system, with Y compact. Then, for each $y \in Y$, the set $\omega(y, \pi)$ is non-empty, closed, invariant, and invariantly connected.*

If $T = \mathbb{N}$, a semi-dynamical system may be generated by a continuous map f, where $\pi(y, t) = f^t(y)$. Then the (forward) orbit of a point y with respect to π, is the set $\mathcal{O}(y, f) = \{f^t(y) : t \in \mathbb{N}\}$. Then a subset B of Y is invariant if $f(B) = B$.

Let $Y = \mathbb{R}$, we consider the difference equation

$$y(t+1) = f(y(t)). \tag{2.2}$$

Definition 2.3. *A point y^* is said to be a fixed point of the map f or an equilibrium point of Equation (2.2) if $f(y^*) = y^*$.*

Theorem 2.3. *Let $I \subset \mathbb{R}$, $f : I \to I$ be a continuous map, where $I = [a, b]$ is a closed interval in $\mathbb{R}$. Then, f has a fixed point.*

2.3 Concept of Stability

In this section, we present briefly the notion of stability in discrete dynamical systems. In Subsection (2.3.1) some useful definition are given. In Subsection (2.3.2), some powerful criteria for local stability of fixed points are presented.

2.3.1 Definitions

Definition 2.4. *[21] Let $f : I \to I$ be a function and y^* be it's fixed point, where I is an interval in the set of real numbers $\mathbb{R}$. Then*

(1) *y^* is stable if for any $\epsilon > 0$ there exists $\delta > 0$ such that for all $y_0 \in I$ with $\mid y_0 - y^* \mid < \delta$ we have $\mid f^t(y_0) - y^* \mid \leq \epsilon$ for all $t \in \mathbb{N}$. Otherwise, the fixed point y^* is called unstable.*

(2) *y^* is attracting if there exists $\eta > 0$ such that $\mid y_0 - y^* \mid < \eta$ implies $\lim_{t \to +\infty} f^t(y_0) = y^*$.*

(3) *y^* is asymptotically stable if it is stable and attracting. If in (2) $\eta = \infty$, then y^* is globally asymptotically stable.*

2.3.2 Stability criteria

Definition 2.5. *A fixed point y^* is called hyperbolic if $\mid f'(y^*) \mid \neq 1$, and non-hyperbolic if $\mid f'(y^*) \mid = 1$.*

Theorem 2.4. *Let y^* be a hyperbolic fixed point of a map f, where f is continuously differentiable at y^*. The following statements then hold true:*

- *If $\mid f'(y^*) \mid < 1$, then y^* is asymptotically stable.*
- *If $\mid f'(y^*) \mid > 1$, then y^* is unstable.*

The stability criteria for non-hyperbolic fixed points are more involved. We summarize the criteria for stability in the following theorems. The first result concerns the case $f'(y^*) = 1$ and the second one concerns the case $f'(y^*) = -1$.

Theorem 2.5. *If $f : I \to I$ with $\mathcal{C}^3$ function. Let y^* be a fixed point of f such that $f'(y^*) = 1$, then the following statements hold:*

- *If $f''(y^*) = 0$, then y^* is unstable (semi-stable).*
- *If $f''(y^*) = 0$ and $f'''(y^*) > 0$, then y^* is unstable.*
- *If $f''(y^*) = 0$ and $f'''(y^*) < 0$, then y^* is asymptotically stable.*

Example.
Let $f(y) = -y^3 + y$. Then $y^* = 0$ is the only fixed point of f. Note that $f'(0) = 1$, $''(0) = 0$, $f'''(0) < 0$. Hence, by the Theorem (2.5), 0 is asymptotically stable.
Before dealing with the second case $f'(y^*) = -1$, we need to introduce the notion of the **Schwarzian derivative**.

Definition 2.6. *[21] The Schwarzian derivative, Sf, of a function f is defined by*

$$Sf(y) = \frac{f'''(y)}{f'(y)} - \frac{3}{2}\left[\frac{f''(y)}{f'(y)}\right]^2,$$

and if $f'(y^*) = -1$, then

$$Sf(y^*) = -f'''(y^*) - \frac{3}{2}[f''(y^*)]^2.$$

Therefore, the asymptotic stability for the second non-hyperbolic case is given as follows:

Theorem 2.6. *Let $f : I \to I$ with $\mathcal{C}^3$. If $f'(y^*) = -1$, then*

1. *If $Sf(y^*) < 0$, then y^* is asymptotically stable.*
2. *If $Sf(y^*) > 0$, then y^* is unstable.*

Definition 2.7. *[21] Let y be in the domain of a function f. Then y is said to be a* ***periodic point*** *of f with period k if $f^k(y) = y$ for some positive integer k. In this case y may be called k-periodic. If in addition $f^r(y) \neq y$ for $0 < r < k$, then k is called the minimal period of y. Note that y is k-periodic if it is a fixed point of the map f^k.*

The orbit of a k-periodic point or (k-periodic cycle) is the set

$$\mathcal{O}(y) = \{y, f(y), f^2(y), ..., f^{k-1}(y)\}.$$

We extend the previous results on the asymptotic stability for two-dimensional system [21]. Toward this, we consider the difference equation.

$$y(t+1) = My(t), \tag{2.3}$$

where M is a 2×2 matrix. The following results are concerned with the stability of the origin $y^* = (0, 0)$.

Theorem 2.7. *The following statements hold for Equation (2.3):*

- If $\rho(M) < 1$, then the origin is asymptotically stable.
- If $\rho(M) > 1$, then the origin is unstable.

Here ρ is the spectral radius of the matrix M (i.e. the maximum of their all eigenvalues in absolute value).

Theorem 2.8. *Let M be a 2×2 matrix. Then $\rho(M) < 1$ if and only if*

$$|\ trM\ | -1 < \det M < 1, \tag{2.4}$$

where tr and $\det$ are the trace and determinant of the matrix M respectively.

Theorem 2.9. *The following statements hold for any 2×2 matrix M. If $|\ trM\ | -1 = \det M$, then we have*

- *the eigenvalues of M are $\lambda_1 = 1$ and $\lambda_2 = \det M$ if $trM > 0$,*
- *the eigenvalues of M are $\lambda_1 = -1$ and $\lambda_2 = -\det M$ if $trM < 0$.*

Theorem 2.10. *Let $f : I \subset \mathbb{R}^2 \to \mathbb{R}^2$ be a $\mathcal{C}^1$ function where I is an open subset of $\mathbb{R}^2$. y^* is a fixed point of f. Let $M = Df(y^*)$ be the Jacobian matrix evaluated at the fixed point y^*. Then the following statements hold true:*

1. If $\rho(M) < 1$, then y^* is asymptotically stable.

2. If $\rho(M) > 1$, then y^* is unstable.

3. If $\rho(M) = 1$, then y^* may or may not be stable.

Lemma 2.1. *Assume that $P(\lambda) = \lambda^2 - tr(M)\lambda + \det(M)$ where $tr(M)$ and $\det(M)$ are constants. Suppose that $P(1) > 0$, λ_1, λ_2 are two roots of $P(\lambda) = 0$. Then*

(a) *$|\lambda_1| < 1$ and $|\lambda_2| < 1$ if and only if $P(-1) > 0$ and $P(0) < 1$;*

(b) *($|\lambda_1| > 1$ and $|\lambda_2| < 1$) or ($|\lambda_1| < 1$ and $|\lambda_2| > 1$) if and only if $P(-1) < 0$;*

(c) *$|\lambda_1| > 1$ and $|\lambda_2| > 1$ if and only if $P(-1) > 0$ and $P(0) > 1$;*

(d) *$\lambda_1 = -1$ and $|\lambda_2| \neq 1$ if and only if $P(-1) = 0$ and $P(0) \neq 1$;*

(e) *λ_1 and λ_2 are complex and $|\lambda_1| = 1$ and $|\lambda_2| = 1$ if and only if $(tr(M))^2 - 4\det(M) < 0$ and $P(0) = 1$.*

2.4 Bifurcation in a two-dimension system

A bifurcation means a qualitative change in dynamical proprieties of a given dynamical system under infinitesimal variations of a parameter, that is, a cycle may appear/dispaear or change its stability. Theorem (2.10) gives a complete determination of the stability of two-dimensional maps by using linearization, when the fixed points are hyperbolic. However, for the non-hyperbolic case, we need the center manifold theory [22].

2.4.1 Center Manifold

In this part, we define the Center Manifold and its associated theory. A center manifold is a set $\mathcal{W}^c$ in a lower dimensional space, where the original system's dynamics can be obtained by studying the dynamics of $\mathcal{W}^c$. The dynamics in $\mathbb{R}^2$, for example, are related with the center manifold in dimension 1 ($\mathcal{W}^c$). Consider the function $F(\gamma, y)$, $F : \mathbb{R}^s \times \mathbb{R}^k \to \mathbb{R}^k$ with $y \in \mathbb{R}^k$, $\gamma \in \mathbb{R}^s$, with $F \in \mathcal{C}^r$, $r \geq 3$, on some sufficiently large open set in $\mathbb{R}^s \times \mathbb{R}^k$. Let (γ^*, y^*) be a fixed point of F, ie

$$F(\gamma^*, y^*) = y^*.$$

The Jacobian matrix associated to F is

$$J = D_y F(\gamma^*, y^*). \tag{2.5}$$

If one of the eigenvalues λ of (2.5) has a modulus of one, that is $\mid \lambda \mid = 1$, then there are three scenarios in which (γ^*, y^*) is nonhyperbolic.

- J has one real eigenvalue equal to 1 and the other eigenvalues are off the unit circle.
- J has one real eigenvalue equal to -1 and the other eigenvalues are off the unit circle.

J has two complex conjugate eigenvalues with modulus 1 and the other eigenvalues are off the unit circle.

For simplicity, we will assume that F can be expressed in the form

$$y_1 \mapsto M_1 y_1 + f_1(y_1, y_2), \tag{2.6a}$$

$$y_2 \mapsto M_2 y_2 + f_2(y_1, y_2), \tag{2.6b}$$

where J in Equation (2.5) has the form $J = \begin{pmatrix} M_1 & 0 \\ 0 & M_2 \end{pmatrix}$. Furthermore,

$$f_1(0,0), \quad f_2(0,0) = 0, \tag{2.7a}$$

$$Df_1(0,0), \quad Df_2(0,0) = 0. \tag{2.7b}$$

The system (2.6) corresponds to the system of difference equations

$$y_1(t+1) \mapsto M_1 y_1(t) + f_1(y_1(t), y_2(t)), \tag{2.8a}$$

$$y_2(t+1) \mapsto M_2 y_2(t) + f_2(y_1(t), y_2(t)). \tag{2.8b}$$

From now on, we assume that M_1 is a $t \times t$ matrix and M_2 is an $s \times s$ matrix, with $t + s = k$. The following results are taken from

Theorem 2.11. *There is a $\mathcal{C}^r$ center manifold for System (2.6) that can be represented locally as*

$$\mathcal{W}^c = \Bigg\{(y_1, y_2) \in \mathbb{R}^t \times \mathbb{R}^s : \; y_2 = \vartheta(y_1), \;\; | \, y_1 \, |< \epsilon, \;\; D\vartheta(0) = 0, \;\; for \; a \; sufficiently \; small \; \epsilon\Bigg\}. \tag{2.9}$$

Furthermore, the dynamics restricted to $\mathcal{W}^c$ are given locally by the function

$$y_1 \mapsto M_1 y_1 + f_1(y_1, \vartheta(y_1)), \quad y_1 \in \mathbb{R}^t. \tag{2.10}$$

This theorem asserts the existence of a center manifold, i.e. a curve $y_2 = \vartheta(y_1)$ on which the dynamics of System (2.6) is given by Equation (2.10). The next result states that the dynamics on the center manifold $\mathcal{W}^c$ determines completely the dynamics of System (2.6).

Theorem 2.12. *The following statements hold.*

1. *If the fixed point $(0, 0)$ of Equation (2.10) is stable, asymptotically stable, or unstable, then the fixed point $(0, 0)$ of System (2.6) is stable, asymptotically stable, or unstable, respectively.*

2. *If For any solution $(y_1(t), y_2(t))$ of System (2.6) with an initial point $(y_1(0), y_2(0))$ in a small neighborhood around the origin, there exists a solution $z(n)$ of Equation (2.10) and positive constants L, $\beta > 1$, such that*

$$| \, y_1(t) - z(t) \, | \leq L\beta^t \;\; and \;\; | \, y_2(t) - \vartheta(z(t)) \, | \leq L\beta^t, \quad for \; all \;\; t \in \mathbb{Z}^+.$$

The next steps is to compute the curve $y_2 = \vartheta(y_1)$. The first thing is to substitute for y_2 in System (2.6) to obtain the system

$$y_1(t + 1) = M_1 y_1(t) + f_1(y_1(t), \vartheta(y_1(t))), \tag{2.11}$$

$$y_2(t + 1) = \vartheta(y_1(t + 1)) = \vartheta\Bigg(M_1 y_1(t) + f_1(y_1(t), \vartheta(y_1(t)))\Bigg) = M_2 \vartheta(y_1(t)) + f_2(y_1(t), \vartheta(y_1(t))). \tag{2.12}$$

Equating the two equations (2.11)-(2.12), yields the functional equation

$$\mathcal{G}(\vartheta(y_1)) = \vartheta\Bigg(M_1 y_1 + f_1(y_1, \vartheta(y_1))\Bigg) - M_2 \vartheta(y_1) - f_2(y_1, \vartheta(y_1)) = 0. \tag{2.13}$$

Solving Equation (2.13) is a formidable task, so at best one can hope to approximate its solution via power series. The next result provides the theoretical justification for the approximation

Theorem 2.13. *Let* $\psi : \mathbb{R}^t \to \mathbb{R}^s$ *be a* $\mathcal{C}$ *map with* $\psi(0) = \psi'(0) = 0$ *Suppose that* $\mathcal{G}(\vartheta(y_1)) = O(\mid y_1 \mid^r)$ *as* $x_1 \to 0$ *for some* $r > 1$*. Then,*

$$\vartheta(y_1) = \psi(y_1) + O(\mid y_1 \mid^r), \quad y_1 \to 0,$$

Center Manifolds Depending on Parameters

Suppose now that System (2.6) depends on a vector of parameters, say $\gamma \in \mathbb{R}^m$. Then, system (2.6) takes the form

$$y_1(t+1) \mapsto M_1 y_1(t) + f_1(\gamma, y_1(t), y_2(t)), \tag{2.14a}$$

$$y_2(t+1) \mapsto M_2 y_2(t) + f_2(\gamma, y_1(t), y_2(t)), \tag{2.14b}$$

where

$$f_1(0,0,0), \quad f_2(0,0,0) = 0, \tag{2.15a}$$

$$Df_1(0,0,0), \quad Df_2(0,0,0) = 0, \tag{2.15b}$$

where f_1 and f_2 are $\mathcal{C}^r$ functions ($r \geq 3$) in some neighborhood of $(y_1, y_2, \gamma) = (0,0,0)$. The first step in handling Equation (2.14) is to increase the numbers of equations to $k+m$ by writing it in the form

$$y_1(t+1) = M_1 y_1(t) + f_1(\gamma(t), y_1(t), y_2(t)), \tag{2.16a}$$

$$\gamma(t+1) = \gamma(t), \tag{2.16b}$$

$$y_2(t+1) = M_2 y_2(t) + f_2(\gamma(t), y_1(t), y_2(t)). \tag{2.16c}$$

The center manifold $\mathcal{W}^c$ now takes the form

$$\mathcal{W}^c = \Big\{(\gamma, y_1, y_2) : \; y_2 = \vartheta(y_1, \gamma), \;\; \mid y_1 \mid < \epsilon_1, \;\; \mid \gamma \mid < \epsilon_2, \; \vartheta(0,0) = 0, \;\; D\vartheta(0,0) = 0\Big\}. \tag{2.17}$$

Substituting for y_2 into System (2.16) yields

$$y_1(t+1) = M_1 y_1(t) + f_1(\gamma, y_1(t), \vartheta(y_1(t))), \tag{2.18}$$

$$y_2(t+1) = \vartheta\Big(y_1(t+1)\Big) = \vartheta\Big(M_1 y_1(t) + f_1(y_1(t), \vartheta(\gamma, y_1(t)))\Big) = \tag{2.19}$$

$$M_2\vartheta\Big(y_1(t)\Big) + f_2\Big(y_1(t), \vartheta(\gamma, y_1(t))\Big).$$

The latter equations lead to the functional equation

$$\mathcal{G}(\vartheta(\gamma, y_1)) = \vartheta\Big(M_1 y_1 + f_1(y_1, \vartheta(\gamma, y_1))\Big) - M_2\vartheta(\gamma, y_1) - f_2(y_1, \vartheta(\gamma, y_1)) = 0. \tag{2.20}$$

$\vartheta(\gamma, y_1)$ takes the form

$$\vartheta(\gamma, y_1) = c_1 y_1^2 + c_2 y_1 \gamma + ...$$

2.4.2 Bifurcations types

In this subsection, we explore briefly the bifurcation in two-dimensional system, associated to the one parameter family of maps:

$$F(\gamma, y) : \mathbb{R} \times \mathbb{R}^2 \to \mathbb{R}, \tag{2.21}$$

with $y = (y_1, y_2) \in \mathbb{R}^2$, $\gamma \in \mathbb{R}$ and $F = (f_1, f_2) \in \mathcal{C}^r$, $r \geq 5$, if (γ^*, y^*) is a fixed point, then we make a change of variables, so that our fixed point is $(0, 0)$. Let $JF_y(0, 0)$. Then using the center manifold theorem, we find one dimensional map $f_\gamma(y_1)$ defined on the center manifold $\mathcal{W}^c$. By Theorem (4.6), we deduce the following statements [21]:

1. Suppose that J has an eigenvalue equal to 1. Then we have

   (a) a saddle-node bifurcation if $\frac{\partial f_1}{\partial \gamma}(0, 0) \neq 0$ and $\frac{\partial^2 f_1}{\partial^2 y_1}(0, 0) \neq 0$,

   (b) a pitchfork bifurcation, if $\frac{\partial f_1}{\partial \gamma}(0, 0) = 0$ and $\frac{\partial^2 f_1}{\partial^2 y_1}(0, 0) = 0$,

   (c) a transcritical bifurcation, if $\frac{\partial f_1}{\partial \gamma}(0, 0) = 0$ and $\frac{\partial^2 f_1}{\partial^2 y_1}(0, 0) \neq 0$.

2. If J has an eigenvalue equals to -1, then we have a period-doubling bifurcation.

3. If J has a pair of complex conjugate eigenvalues of modulus 1, a closed invariant curve appears which indicate the occurrence of the Neimark-Sacker bifurcation.

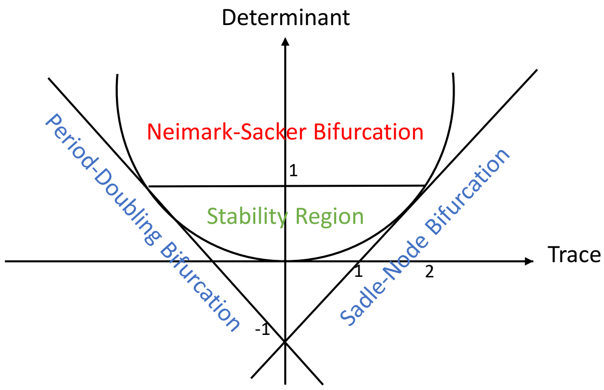


Figure 2.1: The occurrence of bifurcations in a two-dimensional discrete dynamical system.

CHAPTER

3

GLOBAL STABILITY FOR A SPECIAL CLASS OF DISCRETE EVOLUTIONARY POPULATION MODELS

Substantial part of this chapter is published in [37]

3.1 Introduction

In this chapter, we consider discrete time population models that are governed by difference equations. These equations describe typically autonomous, discrete-time dynamics with population vital rates (coefficients) as the only temporal change. These coefficients can change in time through density effects or because of evolutionary processes according to Darwinian principles, resulting in non-autonomous difference equations [8].

This chapter is organized as follows:

- In section 3.2, we formulate a special class of evolutionary competition models for single and multi-species populations. These models build on prior works of [8, 10, 11, 21, 22].

- In section 3.3, we give a brief exposition of the theory of non-autonomous difference equations and the construction of the associated autonomous skew product discrete dynamical systems based on our recently published work [19]. We then use it to develop the mathematical foundation of the results in this paper as described in the new Theorem 3.4.

- In section 3.4, we establish the global stability of the equilibrium points of populations of single and multi-species. Here, we only consider a special type of evolutionary dynamics in which the mean trait equation is decoupled from the ecological dynamic equation(s) of the species.

- In section 3.5, a special attention is carried out to the global asymptotic stability of evolutionary hierarchical competition models of populations of multi-species. An interesting aspect of hierarchical systems is that they are represented by maps (called triangular maps). These maps have a lower triangular Jacobian matrix [5–7, 24]

- In section 3.6, we establish the global stability of the periodic non-autonomous difference equations, the case when the equilibrium points of the trait equation are unstable and either a saddle-node bifurcation or a period-doubling bifurcation occur. The exchange of stability occurs and a new asymptotically stable equilibrium point is born.

3.2 Some evolutionary population models

3.2.1 Single-species evolutionary models

We first start by considering the general difference equation of a single-species population given by

$$x(t+1) = x(t)r(x(t)), \tag{3.1}$$

where $x(t+1)$ and $x(t)$ are the populations size or densities in successive generations and $r(x(t))$ is the density-dependent per capita population growth rate of the population from one time period to the next. The global dynamics of difference equation models have been extensively investigated analytically and their global dynamics are studied using the following fundamental Theorem.

Theorem 3.1 (Allwright-Singer). *Let $f : [a, b] \to [a, b]$, b may be ∞, such that f is a C^3-map with a unique equilibrium point $x^* \in (a, b)$ such that $f(x) > x$ if $x < x^*$ and $f(x) < x$ for $x > x^*$. Assume 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 $x \in [a, b]$. If $|f'(x^*)| \leq 1$, then x^* is globally asymptotically stable.*

To give the model (3.1) an evolutionary dimension, we follow the EGT mathematical framework described in (1) :

$$x(t+1) = x(t)r(x(t), v, u(t))|_{v=u(t)}, \tag{3.2a}$$

$$u(t+1) = u(t) + \sigma^2 \frac{\partial \ln r(x(t), v, u(t))}{\partial v}\bigg|_{v=u(t)}. \tag{3.2b}$$

Throughout this chapter we will assume that the fitness gradient is independent of the population density x, In other words, we will assume that

$$\frac{\partial}{\partial x} \frac{\partial \ln r(x, v, u)}{\partial v}\bigg|_{v=u} = 0, \tag{3.3}$$

for all x, v, u in their domains.

This condition leads to the decoupling of the trait equation from the population equation. Hence equations (3.2) become

$$x(t+1) = x(t)r(x(t), u(t)), \tag{3.4a}$$

$$u(t+1) = u(t) + h(u(t)), \tag{3.4b}$$

where $h(u) = \sigma^2 \frac{\partial \ln r(x,v,u)}{\partial v}\Big|_{v=u}$.

Next, we illustrate this modeling approach using Beverton-Holt and the Ricker evolutionary models.

Example 3.1. *The Beverton-Holt evolutionary model was first studied by Cushing [10] and is given by:*

$$x(t+1) = x(t) \frac{b(v)}{1 + c(v, u(t))x(t)}\bigg|_{v=u(t)},$$

$$u(t+1) = u(t) + \sigma^2 \frac{\partial \ln r(x(t), v, u(t))}{\partial v}\bigg|_{v=u(t)},$$

$$\textit{where} \quad r(x, v, u) = \frac{b(v)}{1 + c(v, u)x},$$

,

with coefficients b (inherent growth rate) and c (intraspecific competition) are assumed to be functions of a phenotypic trait that are subject to Darwinian dynamics. Using the same set of assumptions from [10] which we state here: b depends only on the individual's trait v (and not on the traits of others in the population), and c is a function of the difference between traits v and u which is maximized (or minimized) when $v = u$. In other words, $c = c(v - u) = c(z)$, $c'(0) = 0$. Using assumption (3.3), the Beverton-Holt evolutionary model can now be decoupled as follows:

$$x(t+1) = \frac{b(u(t))}{1 + c_0 x(t)} x(t), \tag{3.5a}$$

$$u(t+1) = u(t) + \sigma^2 \frac{b'(u(t))}{b(u(t))}, \tag{3.5b}$$

where $b'(u(t)) = \frac{\partial b(v)}{\partial v}|_{v=u(t)}$ and $c_0 = c(0)$.

Example 3.2. *The second example is the Ricker Evolutionary model [21, 22] given by:*

$$x(t+1) = x(t) e^{\alpha(v) - c(v,u(t))x(t)}\Big|_{v=u(t)},$$

$$u(t+1) = u(t) + \sigma^2 \frac{\partial \ln r(x(t), v, u(t))}{\partial v}\Bigg|_{v=u(t)},$$

$$\text{where} \quad r(x, v, u) = e^{\alpha(v) - c(v,u)x}.$$

The coefficients α (inherent growth rate) and c (intraspecific competition) are assumed to be functions of a phenotypic trait that are subject to Darwinian dynamics. Under the same assumptions as in Beverton-Holt example, the Ricker evolutionary model can now be decoupled as follows:

$$x(t+1) = x(t) e^{\alpha(u(t)) - c_0\, x(t)}, \tag{3.6a}$$

$$u(t+1) = u(t) + \sigma^2 \alpha'(u(t)), \tag{3.6b}$$

where $\alpha'(u(t)) = \frac{\partial \alpha(v)}{\partial v}|_{v=u(t)}$ and $c_0 = c(0)$.

3.2.2 Multi-species evolutionary models

Let $x_1, x_2, \ldots, x_n$ be n interacting species. Then an evolutionary competition model may be given by

$$x_i(t+1) = x_i(t) r(\mathbf{x}(t), v, \mathbf{u}(t))\big|_{v=u_i(t)}, \tag{3.7a}$$

$$u_i(t+1) = u_i(t) + \sigma_i^2 \frac{\partial \ln r(\mathbf{x}(t), v, \mathbf{u}(t))}{\partial v}\bigg|_{v=u_i(t)}, \tag{3.7b}$$

where $i = 1, 2, \ldots, n$, $\mathbf{x} = (x_1, x_2, \ldots, x_n) \in \mathbb{R}_+^n$, $\mathbf{u} = (u_1, u_2, \ldots, u_n) \in \mathbb{R}_+^n$. As in Section 3.2.1, we will assume throughout this chapter that the fitness gradient of each species is independent of x_i. In other words, we will assume that

$$\frac{\partial}{\partial x_i} \frac{\partial \ln r(\mathbf{x}, v, \mathbf{u})}{\partial v}\bigg|_{v=u_i} = 0, \tag{3.8}$$

for all x_i, v, u_i in their domains. This main assumption leads to the decoupling of the trait equations from the population equations. Hence we have the following system of difference equations

$$x_i(t+1) = x_i(t) r_i(\mathbf{x}(t), \mathbf{u}(t)), \tag{3.9a}$$

$$u_i(t+1) = u_i(t) + h_i(\mathbf{u}(t)), \tag{3.9b}$$

where $i = 1, 2, \ldots, n$, u_i is the mean trait of species x_i, and $h_i(\mathbf{u}) = \sigma_i^2 \frac{\partial \ln r(\mathbf{x}, v, \mathbf{u})}{\partial v}\Big|_{v=u_i}$.

Next, we give two examples to illustrate this modeling procedure: the Leslie-Gower and Ricker evolutionary competition model of two species.

Example 3.3. *Consider the Leslie-Gower competition model of two-species,*

$$x(t+1) = \frac{ax(t)}{1 + c_{11}x(t) + c_{12}y(t)},$$
$$y(t+1) = \frac{by(t)}{1 + c_{21}x(t) + c_{22}y(t)}.$$

Where a and b are the intrinsic population growth rates and c_{ij} intraspecific (for $i = j$) or interspecific ($i \neq j$) competition coefficients. Using the EGT methodology of Vincent and Brown [56], and assuming that a, b and c_{ij} to be functions of a phenotypic trait that are subject to Darwinian dynamics, we define the Leslie-Gower evolutionary competition model by

$$x(t+1) = r(x(t), y(t), v, u_1(t))\Big|_{v=u_1(t)} x(t),$$

$$y(t+1) = r(x(t), y(t), v, u_2(t))\Big|_{v=u_2(t)} y(t),$$

$$u_1(t+1) = u_1(t) + \sigma_1^2 \frac{\partial \ln r(x(t), y(t), v, u_1(t))}{\partial v}\Big|_{v=u_1(t)},$$

$$u_2(t+1) = u_2(t) + \sigma_2^2 \frac{\partial \ln r(x(t), y(t), v, u_2(t))}{\partial v}\Big|_{v=u_2(t),},$$

with

$$r(x, y, v, u_1) = \frac{a(v_1)}{1 + c_{11}(v, u_1)x + c_{12}y},$$

$$r(x, y, v, u_2) = \frac{b(v_2)}{1 + c_{21}x + c_{22}(v, u_2)y}.$$

We will assume that a and b are functions of the corresponding individual traits v, the intraspecific competition parameters c_{11} and c_{22} are functions of the difference in traits $v - u_i$, $i = 1, 2$, respectively, and the interspecific competition parameters c_{12} and c_{21} are constants. We further assume that $c_{ij}(0, 0) \neq 0$, $i, j = 1, 2$. Applying assumption (3.8), the Leslie-Gower evolutionary competition model can be uncoupled as follows:

$$x(t+1) = \frac{a(u_1(t))x(t)}{1 + c_{11}(0)x(t) + c_{12}y(t)}, \tag{3.10a}$$

$$y(t+1) = \frac{b(u_2(t))y(t)}{1 + c_{21}x(t) + c_{22}(0)y(t)}, \tag{3.10b}$$

$$u_1(t+1) = u_1(t) + \sigma_1^2 \frac{a'(u_1(t))}{a(u_1(t))}, \tag{3.10c}$$

$$u_2(t+1) = u_2(t) + \sigma_2^2 \frac{b'(u_2(t))}{b(u_2(t))}, \tag{3.10d}$$

where $a'(u(t)) = \frac{\partial a(v)}{\partial v}|_{v=u(t)}$ and $b'(u(t)) = \frac{\partial b(v)}{\partial v}|_{v=u(t)}$.

Example 3.4. *Consider the Ricker competition model of two species [22],*

$$x(t+1) = x(t)e^{\alpha - c_{11}x(t) - c_{12}y(t)},$$

$$y(t+1) = y(t)e^{\beta - c_{21}x(t) - c_{22}y(t)},$$

where α and β are the intrinsic growth rate for species x and y respectively, and c_{ij} intraspecific (for $i = j$) or interspecific ($i \neq j$) competition coefficients. Using the EGT methodology of Vincent and Brown [56], and assuming that α, β and c_{ij} to be functions of a phenotypic trait that are subject to Darwinian dynamics, we define the evolutionary Ricker competition model by

$$x(t+1) = x(t)e^{\alpha(v)-c_{11}(v-u_1(t))x(t)-c_{12}y(t)}\Big|_{v=u_1(t)},$$

$$y(t+1) = y(t)e^{\beta(v)-c_{21}x(t)-c_{22}(v-u_2(t))y(t)}\Big|_{v=u_2(t)},$$

$$u_1(t+1) = u_1(t) + \sigma_1^2 \frac{\partial \ln r(x(t), y(t), v, u_1(t))}{\partial v}\Big|_{v=u_1(t)},$$

$$u_2(t+1) = u_2(t) + \sigma_2^2 \frac{\partial \ln r(x(t), y(t), v, u_2(t))}{\partial v}\Big|_{v=u_2(t)}.$$

Making the same assumptions as in the Leslie-Gower competition model and applying assumption (3.8), we get the uncoupled system for the Ricker evolutionary competition model

$$x(t+1) = x(t)e^{\alpha(u_1(t))-c_{11}(0)x(t)-c_{12}y(t)}, \tag{3.11a}$$

$$y(t+1) = y(t)e^{\beta(u_2(t))-c_{21}x(t)-c_{22}(0)y(t)}, \tag{3.11b}$$

$$u_1(t+1) = u_1(t) + \sigma_1^2\alpha'(u_1(t)), \tag{3.11c}$$

$$u_2(t+1) = u_2(t) + \sigma_2^2\beta'(u_2(t)). \tag{3.11d}$$

3.3 Nonautonomous difference equations

In this section, we develop the mathematical foundation of the results in this paper and give a brief exposition of the theory of non-autonomous difference equations and the construction of the associated autonomous skew product discrete dynamical systems based on [19].

Definition 3.1. *Skew-product dynamical system*

Let X and Y be two topological spaces. A dynamical system $\pi = (\phi, \sigma)$ on a product space $X \times Y$ is

$$
\begin{array}{ccc}
X \times \mathcal{F} \times \mathbb{Z}^{+} & \xrightarrow{\pi} & X \times \mathcal{F} \\
p \times i_d \big\downarrow & & \big\downarrow p \\
\mathcal{F} \times \mathbb{Z}^{+} & \xrightarrow{\sigma} & \mathcal{F}
\end{array}
$$

Figure 3.1: The construction of a skew-product semi-dynamical system, where p is the projection, id is the identity map and σ is the shift map defined as $\sigma(f_i, t) = f_{i+t}$.

said to be a skew-product dynamical system if there exist continuous mappings $\phi : X \times Y \times \mathbb{Z} \to X$ and $\sigma : Y \times \mathbb{Z} \to Y$ such that

$$\pi(x, y, t) = \Big(\phi(x, y, t), \sigma(y, t)\Big).$$

If $\mathbb{Z}$ is replaced by $\mathbb{Z}^{+}$, then π is called a skew-product semi-dynamical system.

Now let us construct a skew-product semi-dynamical system from the nonautonomous difference equation.

Let (X, d) be a compact metric space and let $\mathcal{F} = \{f_0, f_1, ..., f_i, ..\}$ with $f_i : X \to X$, $i \in \mathbb{Z}^{+}$ is a subset of the space of continuous functions equipped with the compact open topology. We examine the semi-dynamical system

$$\pi : (X \times \mathcal{F}) \times \mathbb{Z}^{+} \to X \times \mathcal{F}$$

with $\pi((x, f_i), 0) = (x, f_i)$ for $x \in X$ and $i \in \mathbb{Z}^{+}$, $\pi((x, f_i), t) = (\Phi_{t,i}, f_{t+i})$, $\Phi_{t,i} = f_{i+t-1} \circ f_{i+t-2} \circ \cdots \circ f_i$. Define for $x \in X$, $x_0 = x$, $x_1 = f_0(x)$, $x_2 = (f_1 o f_0)(x_0)$, and for each $t \in \mathbb{N}$, $x_{t+1} = (f_t o f_{t-1} o .....o f_1 o f_0)(x_0)$ (see Figures 3.2 and 3.1). One obtains

$$x_{t+1} = f_t(x_t). \tag{3.12}$$

Then the sequence of function (3.12) would generate the nonautonomous difference equation

$$\mathbf{x}(t+1) = f_t(\mathbf{x}(t)),\ \mathbf{x} = (x_1, x_2, \ldots, x_n) \in \mathbb{R}^n_{+}. \tag{3.13}$$

We will assume that the map $\{f_t\}_{t=0}^{\infty}$ are continuous and converges uniformly to a continuous function $f : \mathbb{R}^n_{+} \to \mathbb{R}^n_{+}$. The map f generates the autonomous difference equation:

$$\mathbf{x}(t+1) = f(\mathbf{x}(t)),\ \mathbf{x} = (x_1, x_2, \ldots, x_n) \in \mathbb{R}^n_{+}. \tag{3.14}$$

Equation (3.13) models populations $x_1, x_2, \ldots, x_n$, with fluctuating habitats, where habitats are chang-

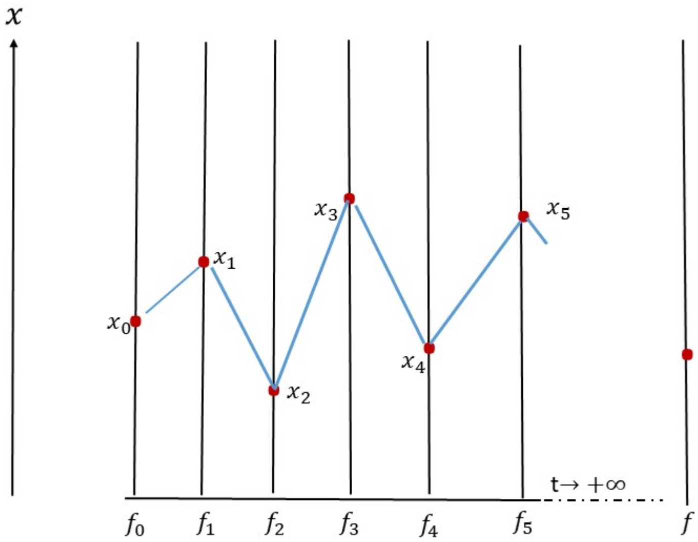


Figure 3.2: A non-autonomous system that is asymptotically autonomous. The graph depicts a sequence of maps $\mathcal{F} = \{f_t : t = 0, 1, 2, \ldots\}$ converging uniformly to a map f, i.e. $\lim_{t\to\infty} f_t = f$.

ing from one time period to another.

Theorem 3.2. *[19] Let (X, d) be a compact metric space and let $f_t : X \to X$, $t = 0, 1, \ldots$ be a sequence of continuous maps uniformly convergent to a function f. Then $\overline{\mathcal{F}} = \mathcal{F} \bigcup \{f\}$ is compact in the compact open topology.*

Then it may be shown [19] that the system $(\mathbb{R}^n_+ \times \mathcal{F}, \mathbb{Z}^+, \pi) \equiv (\mathbb{R}^n_+ \times \mathcal{F}, \pi)$ is a discrete semi dynamical system. Moreover, one may extend this semi dynamical system to the closure of $\mathcal{F}$, $\overline{\mathcal{F}} = \mathcal{F} \bigcup \{f\}$ by letting $\widetilde{\pi}((\mathbf{x}, f), t) = (f^t(\mathbf{x}), f)$.

Theorem 3.3. *The map $\widetilde{\pi} : X \times \overline{\mathcal{F}} \times \mathbb{Z}^+ \to X \times \overline{\mathcal{F}}$ is a semi dynamical system, that is*

(1) $\widetilde{\pi}((x, f_1), 0) = (x, f_1)\ \forall x \in X,\ f_1 \in \overline{\mathcal{F}} = \mathcal{F} \bigcup \{f\}$,

(2) $\widetilde{\pi}(\widetilde{\pi}(x, f_1), s), t) = \widetilde{\pi}((x, f_1), s + t),\ \forall x \in X,\ f_1 \in \overline{\mathcal{F}}, s, t \in \mathbb{Z}^+$,

(3) $\widetilde{\pi}$ *is continuous, that is for each $j \in \mathbb{N}$*

$$\lim_k (x_{t_k}, f_{t_k}) = (x, f) \Rightarrow \lim_k \widetilde{\pi}((x_{t_k}, f_{t_k}), j) = \widetilde{\pi}((x, f), j).$$

Remark 3.1. *Let $(X \times \overline{\mathcal{F}}, \widetilde{\pi})$ be the semi dynamical system discussed above. Note that, if $(x, f_i) \in X \times \overline{\mathcal{F}}$ then the omega-limit set $\omega(x, f_i)$ is*

$$\omega(x, f_i) = \{(x, f) : \exists (t_k) \subseteq \mathbb{Z}^+ \ \ with \ \ \widetilde{\pi}((x, f_i), t_k) \to (x, f), \ t_k \to \infty \ \ as \ \ k \to +\infty\}.$$

In the sequel, we will restrict our study on nonautonomous population models in order to avoid certain pathological examples in which all orbits of the nonautonomous system converge to an unstable fixed point of the limiting equation. The following example from Cushing [13] illustrates this situation.

Example 3.5. *Let $g(x)$ be a map with $g'(0) > 1$ and 0 is a fixed point of g. Let $\{f_i\}$ be a sequence of maps such that $f_0(x) = 0$ for all x, and $f_i(x) = g(x)$ for all $i > 0$. Then all the orbits of the nonautonomous system $\{f_i\}$ converge to the unstable fixed point 0 of the limiting map g. Notice that one of the maps f_0 maps all the points to the unstable equilibrium point 0 of the limiting map g This example may be generalized to higher dimension systems. Let g be a map on $\mathbb{R}^2_+$ such that $(0, 0)$ is an unstable equilibrium point of the map g. Let $\{f_i\}$ be a sequence of maps such that, for some i, $f_i(x, y) = (0, 0)$ for all (x, y) in $\mathbb{R}^2_+$, and $f_j(x, y) = g(x, y)$ for all $j \neq i$. Then all the orbits of the nonautonomous system $\{f_i\}$ converge to the unstable fixed point $(0, 0)$ of the limiting map g.*

In order to avoid the above scenarios, we put conditions on the nonautonomous system as well as on the limiting autonomous system. Let $\mathbb{R}^n_+$ denote the cone of nonnegative vectors in $\mathbb{R}^n$ and let int($\mathbb{R}^n_+$) and $\partial(\mathbb{R}^n_+)$ denote the interior and the boundary of $\mathbb{R}^n_+$, respectively. Assume

A_1: f and $f_t : \mathbb{R}^n_+ \longrightarrow \mathbb{R}^n_+$ are continuous for all $t \in \mathbb{Z}_+$, f_t converges uniformly to f as $t \to \infty$. Then $\mathbf{x(0)} \in \mathbb{R}^n_+$ implies solutions of the nonautonomous difference equation

$$\mathbf{x}(t+1) = f_t(\mathbf{x}(t)), \ \mathbf{x} = (x_1, x_2, \ldots, x_n) \in \mathbb{R}^n_+, \tag{3.15}$$

satisfies $\mathbf{x(t)} \in \mathbb{R}^n_+$, for all $t \in \mathbb{Z}_+$. (That is to say $\mathbb{R}^n_+$ is forward invariant). The same is true for solutions of the limiting equation

$$\mathbf{x}(t+1) = f(\mathbf{x}(t)). \tag{3.16}$$

A key assumption is

$$A_2 : \quad f_t \ : \ int(\mathbb{R}^n_+) \longrightarrow int(\mathbb{R}^n_+).$$

Then it is always true that $\mathbf{x(0)} \in int(\mathbb{R}^n_+)$ implies solutions of the nonautonomous difference equation

(3.15) satisfies $\mathbf{x(t)} \in int(\mathbb{R}^n_+)$, for all $t \in \mathbb{Z}_+$.

The main result that we need here is the following theorem ([19], Theorem 4.1.)

Theorem 3.4. *[19] Assume A_1 and A_2 and the limiting equation has a fixed point $\mathbf{x}^* \in \mathbb{R}^n_+$. Then (i) if $\mathbf{x}^* \in int(\mathbb{R}^n_+)$, and if it is globally asymptotically stable on $int(\mathbb{R}^n_+)$ as a fixed point of limiting equation (3.16), then all solutions of the nonautonomous difference equation (3.15) with $\mathbf{x}(\mathbf{0}) \in int(\mathbb{R}^n_+)$ tend to $\mathbf{x}^*$. (ii) if $\mathbf{x}^* \in \partial(\mathbb{R}^n_+)$, and if it is globally asymptotically stable on $int(\mathbb{R}^n_+)$, then all solutions of the nonautonomous difference equation (3.15) with $\mathbf{x}(\mathbf{0}) \in int(\mathbf{R}^n_+)$ tend to $\mathbf{x}^*$.*

3.4 Applications

In this section, we apply Theorem 3.4 to one and two-species competition models:

Example 3.6. *Beverton-Holt evolutionary model [10]*

$$x(t+1) = \frac{b(u(t))}{1 + c_0 x(t)} x(t) = f_t(u(t), x(t)), \tag{3.17}$$

$$u(t+1) = u(t) + \sigma^2 \frac{b'(u(t))}{b(u(t))} = g(u(t)), \tag{3.18}$$

where $b(u) > 0$ is twice differentiable on its domain.

The survival (positive) equilibrium is given by $(x^*, u^*) = \left(\frac{b(u^*)-1}{c_0}, u^*\right)$, with $b(u^*) > 1$, where u^* is any critical trait that satisfies $b'(u^*) = 0$. Now if $|g'(u^*)| < 1$ or, equivalently, $-2 < \sigma^2 \frac{b''(u^*)}{b(u^*)} < 0$. Hence there exists an open neighborhood W of u^* such that $\lim_{t \to \infty} u(t) = u^*$ if $u(0) \in W$. Hence the maps $\{f_t : t \in \mathbb{Z}^+\}$ converges uniformly to the map $f(x) = \frac{b(u^*)x}{1+c_0\, x}$, which has the equilibrium point (x^*, u^*). It is a well known fact for the autonomous Beverton-Holt model represented by the map, the equilibrium point x^* is globally asymptotically stable. Hence by Theorem 3.4, the equilibrium point (x^*, u^*) is globally asymptotically stable in $\mathbb{R}^+ \times W$. On the other hand, if $b(u^*) \leq 1$, then $(0, u^*)$ is the only equilibrium point of Equations (3.17), and (3.18), which is globally asymptotically stable in $\mathbb{R}^+ \times W$.

Example 3.7. *Ricker evolutionary model*

$$x(t+1) = x(t) e^{\alpha(u(t)) - c_0 x(t)},$$

$$u(t+1) = u(t) + \sigma^2 \alpha'(u(t)),$$

where $\alpha(u) > 0$ is twice differentiable on its domain.

The model has two equilibria, the extinction equilibrium $(0, u^*)$ and the survival equilibrium (x^*, u^*), where $x^* = \frac{\alpha(u^*)}{c_0}$. Note that u^* is any value such that $\alpha'(u^*) = 0$.

The following statements hold true.

(i) If $\alpha(u^*) < 0$ and $|1 + \sigma^2 \alpha''(u^*)| < 1$, then there exists an open neighborhood W of u^* such that the extinction equilibrium $(0, u^*)$ is globally asymptotically stable on the interior of $\mathbb{R}_+ \times W$.

(ii) If $0 < \alpha(u^*) < 2$ and $|1 + \sigma^2 \alpha''(u^*)| < 1$, then the survival equilibrium (x^*, u^*) is globally asymptotically stable on the interior of $\mathbb{R}_+ \times W$.

To prove these two statements, consider the autonomous Ricker model $x(t+1) = x(t)e^{\alpha(u*) - c_0\, x(t)} = f(x(t))$ where $0 < \alpha(u^*) < 2$ ($i.e$: $x^* \in [0, \frac{2}{c_0}]$).

It is well known [21], [22], that $f(x) > x$ when $x < x^*$ and $f(x) < x$ when $x > x^*$. The Schwarzian derivate of f can be written as follows

$$Sf(x) = \frac{c_0^2}{2(1 - c_0 x)^2}\, P(x).$$

Where $P(x) = -c_0^2 x^2 + 4\, c_0 x - 6$ a second degree polynomial, with discriminant $\Delta < 0$. Thus $sign\Big(Sf(x)\Big) = sign(-c_0^2)$, and thus $Sf(x) < 0$ for all $x \in \mathbb{R}^+$. Hence by Theorem 3.1, the equilibrium point x^* of the autonomous Ricker model is globally asymptotically stable.

Now, the maps $\{f_t : t \in \mathbb{Z}^+\}$ converges uniformly to the map $f(x) = e^{\alpha(u*) - c_0\, x}\, x$, which has the equilibrium point (x^*, u^*), and by Theorem 3.4, the equilibrium point (x^*, u^*) is globally asymptotically stable on the interior of $\mathbb{R}^+ \times W$.

Example 3.8. *The Leslie-Gower evolutionary model.*

$$x(t+1) = \frac{a(u_1(t))x(t)}{1 + c_{11}x(t) + c_{12}y(t)}, \tag{3.19}$$

$$y(t+1) = \frac{b(u_2(t))y(t)}{1 + c_{21}x(t) + c_{22}y(t)}, \tag{3.20}$$

$$u_1(t+1) = u_1(t) + \sigma_1^2 \frac{a'(u_1(t))}{a(u_1(t))} = H_1(u_1(t)),$$

$$u_2(t+1) = u_2(t) + \sigma_2^2 \frac{b'(u_2(t))}{b(u_2(t))} = H_2(u_2(t)),$$

where $a(u_1) > 1$ and $b(u_2) > 1$ are twice differentiable on their domains. The equilibrium points of u_1 and u_2 are u_1^* and u_2^*, where u_1^* is any value that satisfies $a'(u_1^*) = 0$ and u_2^* is any value that satisfies $b'(u_2^*) = 0$. Now if $|H_1'(u_1^*)| < 1$ and $|H_2'(u_2^*)| < 1$, then there exists open neighborhoods U_1 and U_2 such that $\lim_{t\to\infty} u_1(t) = u_1^*$ and $\lim_{t\to\infty} u_2(t) = u_2^*$ for all initial values $(u_1(0), u_2(0)) \in U_1 \times U_2$.

Hence the nonautonomous system (3.19) and (3.20) is asymptotic to the limiting system

$$x(t+1) = \frac{a(u_1^*)x(t)}{1 + c_{11}x(t) + c_{12}y(t)}, \tag{3.21}$$

$$y(t+1) = \frac{b(u_2^*)y(t)}{1 + c_{21}x(t) + c_{22}y(t)}. \tag{3.22}$$

The following Theorem may be found in [3, 14]. There are four equilibrium points of (3.21) and (3.22),

$$E_1^* = (0,0), \quad E_2^* = \left(\frac{a(u_1^*) - 1}{c_{11}}, 0\right), \quad E_3^* = \left(0, \frac{b(u_2^*) - 1)}{c_{22}}\right),$$

and

$$E_4^* = \left(\frac{(a(u_1^*) - 1)c_{22} - (b(u_2^*) - 1)c_{12}}{c_{11}c_{22} - c_{21}c_{12}}, \frac{(b(u_2^*) - 1)c_{11} - (a(u_1^*) - 1)c_{21}}{c_{11}c_{22} - c_{21}c_{22}}\right).$$

Theorem 3.5. *The following statements hold true:*

Scenario (i) If $c_{12} - c_{22} < 0$ *and* $c_{21} - c_{11} > 0$, *then* $\lim_{t\to\infty}(x(t), y(t)) = E_2^*$, *for all points* $(x(0), y(0))$ *in the interior of* $\mathbb{R}_+^2$.

Scenario (ii) If $c_{12} - c_{22} < 0$ *and* $c_{21} - c_{11} < 0$, *then* $\lim_{t\to\infty}(x(t), y(t)) = E_4^*$, *for all points* $(x(0), y(0))$ *in the interior of* $\mathbb{R}_+^2$.

Scenario (iii) If $c_{12} - c_{22} > 0$ *and* $c_{21} - c_{11} < 0$, *then* $\lim_{t\to\infty}(x(t), y(t)) = E_3^*$, *for all points* $(x(0), y(0))$ *in the interior of* $\mathbb{R}_+^2$.

This may be illustrated by the phase space diagrams (Figure 3.3), and using Theorem 3.4, we obtain the following result

Theorem 3.6. *(i) Under scenario (i), the orbits of the nonautonomous system* (3.19) *and* (3.20) *converge to* $(E_2^*, u_1^*, u_2^*) \in \mathbb{R}_+^2 \times U_1 \times U_2$, *for all points* $(x(0), y(0))$ *in the interior of* $\mathbb{R}_+^2$.

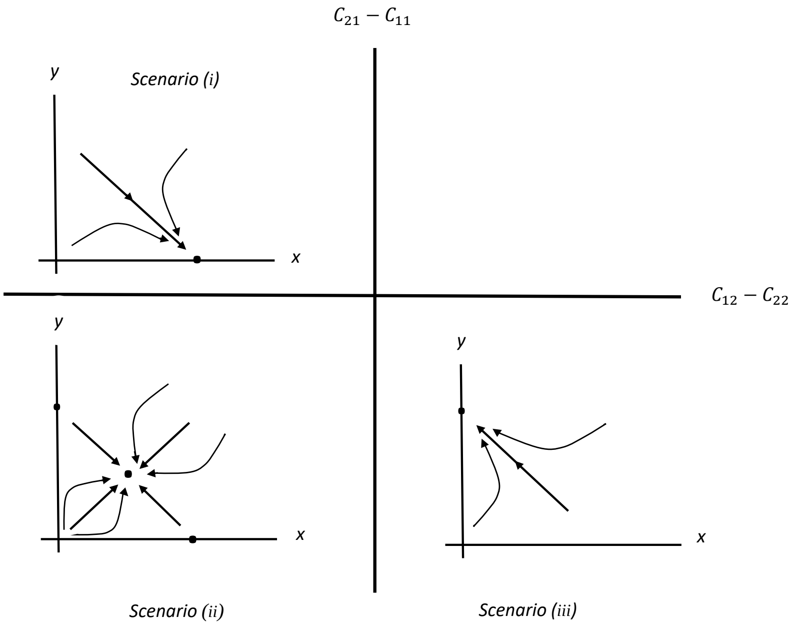


Figure 3.3: Some Competitive Outcomes Plane related to Leslie-Gower competition model

(ii) *Under scenario (ii), the orbits of the nonautonomous system* (3.19) *and* (3.20) *converge to* $(E_4^*, u_1^*, u_2^*) \in \mathbb{R}_+^2 \times U_1 \times U_2$*, for all points* $(x(0), y(0))$ *in the interior of* $\mathbb{R}_+^2$*.*

(iii) *Under scenario (iii), the orbits of the nonautonomous system* (3.19) *and* (3.20) *converge to* $(E_3^*, u_1^*, u_2^*) \in \mathbb{R}_+^2 \times U_1 \times U_2$*, for all points* $(x(0), y(0))$ *in the interior of* $\mathbb{R}_+^2$*.*

Example 3.9. *Consider now the evolutionary Ricker competition model of two-species.*

$$x(t+1) = x(t)e^{\alpha(u_1)-c_{11}(0)x(t)-c_{12}y(t)}, \tag{3.23}$$

$$y(t+1) = y(t)e^{\beta(u_2)-c_{21}x(t)-c_{22}(0)y(t)}, \tag{3.24}$$

$$u_1(t+1) = u_1(t) + \sigma_1^2\alpha'(u_1(t)),$$

$$u_2(t+1) = u_2(t) + \sigma_2^2\beta'(u_2(t)).$$

Now if $|1+\alpha'(u_1^*)| < 1$ *and* $|1+\beta'(u_2^*)| < 1$*, then there exists neighborhoods* G_1 *of* u_1^* *and* G_2 *of* u_2^* *such that* $\lim_{t\to\infty} u_1(t) = u_1^*$ *and* $\lim_{t\to\infty} u_2(t) = u_2^*$ *if* $u_1(0) \in G_1$ *and* $u_2(0) \in G_2$*. Thus the nonautonomous system*

(3.23) *and* (3.24) *is asymptotic to the autonomous system*

$$x(t+1) = x(t)e^{\alpha(u_1^*)-c_{11}(0)x(t)-c_{12}y(t)}, \tag{3.25}$$

$$y(t+1) = y(t)e^{\beta(u_2^*)-c_{21}x(t)-c_{22}(0)y(t)}. \tag{3.26}$$

There are four equilibrium points $E_1^* = (0,0)$, $E_2^* = \left(\frac{\alpha(u_1^*)}{c_{11}(0)}, 0\right)$, $E_3^* = \left(0, \frac{\beta(u_2^*)}{c_{22}(0)}\right)$, and $E_4^* = \left(\frac{\alpha(u_1^*)c_{22}(0)-\beta(u_2^*)c_{12}}{c_{11}(0)c_{22}(0)-c_{21}c_{12}}, \frac{\beta(u_2^*)c_{11}(0)-\alpha(u_1^*)c_{21}}{c_{11}(0)c_{22}(0)-c_{21}c_{22}(0)}\right)$.

The following result on the global stability of E_4^* may be found in [6] which was improved by [49]. But before stating this result, we need to introduce a few definitions.

Definition 3.2. *Let $F : \mathbb{R}_+^2 \to \mathbb{R}_+^2$ be a differentiable map. Then the set of singular points $\mathcal{S}$ is defined as the set of all points $(x, y) \in \mathbb{R}_+^2$, for which the determinant of the Jacobian matrix is equal to zero.*

In the case of system (3.23) and (3.24), we have

$$\mathcal{S} = \left\{ (x,y) : y = \frac{(1-x)}{1 - \left(1 - \frac{c_{12}c_{21}}{c_{22}c_{11}}\right)x}, x \neq \frac{1}{1 - \frac{c_{12}c_{21}}{c_{22}c_{11}}} \right\}.$$

The set $\mathcal{S}$ consists of two curves, which we will call Lc_{-1}^1, Lc_{-1}^2 (see Figure 3.4).

Now equations (3.25) and (3.26) are generated by a map $F : \mathbb{R}_+^2 \to \mathbb{R}_+^2$.

Let us denote $F(Lc_{-1}^i)$ as Lc_0^i and $F^n(Lc_{-1}^i)$ as Lc_{n-1}^i. Then we have the following result.

Theorem 3.7. *[6] Consider the system* (3.25) *and* (3.26)*. We make the following assumptions:*

(i) $1 < \alpha$, $\beta < 2$, $\frac{c_{12}}{c_{22}} < 1$ *and* $\frac{c_{21}}{c_{11}} < 1$.

(ii) The equilibrium E_4^* is locally asymptotically stable.

(iii) $Lc_{-1}^1 < Lc_1^1 < Lc_0^1$ *and* $Lc_0^1 \bigcap Lc_{-1}^2 = \emptyset$ *(see Figure 3.5).*

(iv) $\alpha \in \left(\frac{c_{11}c_{12}+c_{11}c_{22}-2c_{12}c_{11}\sqrt{\frac{c_{21}}{c_{11}}}}{c_{11}c_{22}-c_{12}c_{21}}, \frac{c_{11}c_{12}+c_{11}c_{22}+2c_{12}c_{11}\sqrt{\frac{c_{21}}{c_{11}}}}{c_{11}c_{22}-c_{12}c_{21}} \right)$ *and*

$\beta \in \left(\frac{c_{21}c_{22}+c_{11}c_{22}-2c_{21}c_{22}\sqrt{\frac{c_{12}}{c_{22}}}}{c_{11}c_{22}-c_{12}c_{21}}, \frac{c_{21}c_{22}+c_{11}c_{22}+2c_{21}c_{22}\sqrt{\frac{c_{12}}{c_{22}}}}{c_{11}c_{22}-c_{12}c_{21}} \right)$.

Then the equilibrium point E_4^* is globally asymptotically stable with respect to the interior of the first quadrant.

Corollary 3.1. *Under the conditions of Theorem 3.7 every orbit, in the interior of $\mathbb{R}_+^2$, of the nonautonomous system* (3.23) *and* (3.24) *converges to the equilibrium point (E_4^*, u_1^*, u_2^*).*

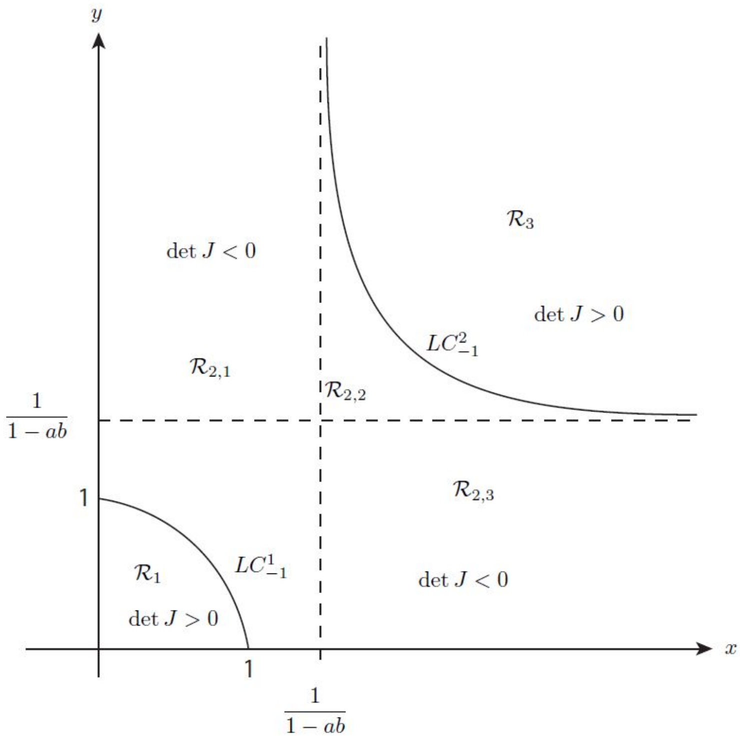


Figure 3.4: The set of singular points consists of two critical curves, a lower one Lc^1_{-1} and an upper one Lc^2_{-1}.

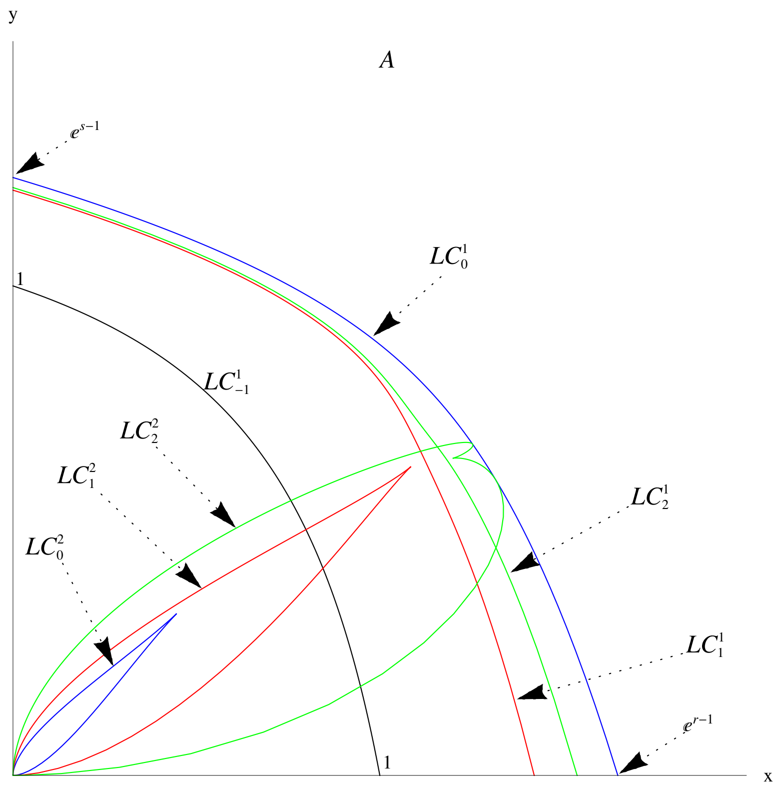


Figure 3.5: The figure shows the requirement $Lc_0^1 \bigcap Lc_{-1}^2 = \emptyset$ and $Lc_{-1}^1 < Lc_1^1 < Lc_0^1$.

3.5 Hierarchical competition models

By hierarchical models of n species $x_1, x_2, \ldots, x_n$, we mean that species x_1 is a "silverback" species that gets first choice of resources and whose growth is limited by its own intraspecific competition, while the last species x_n is an "inferior" species that gets what resources are left after all the other species, and the growth of species x_i depends on all the species $x_{i-1}, x_{i-2}, \ldots, x_1$. These models have been investigated by [7, 24], to mention only a few. Such models may be represented by the difference system

$$\mathbf{x}(t+1) = F(\mathbf{x}(t)), \tag{3.27}$$

where $F : \mathbb{R}_+^n \to \mathbb{R}_+^n$, $F = (f_1, f_2, \ldots, f_n)$, $\mathbf{x} = (x_1, x_2, \ldots, x_n) \in \mathbb{R}_+^n$, and $F(x_1, x_2, \ldots, x_n)$ $= (f_1(x_1), f_2(x_1, x_2), \ldots, f_n(x_1, x_2, \ldots, x_n))$. In dynamical systems, these maps are called triangular maps

[6] since their Jacobian matrix $JF(\mathbf{X})$ is a lower triangular given by

$$JF(\mathbf{x}) = \begin{pmatrix} \frac{\partial f_1}{\partial x_1} & 0 & 0 & \cdots & 0 \\ \frac{\partial f_2}{\partial x_1} & \frac{\partial f_2}{\partial x_2} & 0 & \cdots & 0 \\ \vdots & \vdots & & & \\ \frac{\partial f_n}{\partial x_1} & \frac{\partial f_n}{\partial x_2} & \cdots & \cdots & \frac{\partial f_n}{\partial x_n} \end{pmatrix}.$$

The main result on hierarchical models is the following result that describes their global dynamics. But before stating the theorem, we need to make the following assumptions:

(A_1) All orbits are bounded.

(A_2) There are only finitely many equilibrium points.

(A_3) There are no periodic orbits of prime (minimal) period 2.

Theorem 3.8. *[24] Let $F : \mathbb{R}^n_+ \to \mathbb{R}^n_+$ be a continuous triangular map of Kolmogorov type such that Assumptions (A_1), (A_2), (A_3) hold true. Then every orbit must converge to a equilibrium point in $\mathbb{R}^n_+$.*

Corollary 3.2. *Under the above assumptions, if the map F has a locally asymptotically stable equilibrium point, then it is globally asymptotically stable.*

Recall that by a Kolmogorov map, we mean a map of the form

$$F(x_1, x_2, \ldots, x_n) = (x_1 g(x_1), x_2 g(x_1, x_2), \ldots, x_n g(x_1, x_2, \ldots, x_n)).$$

This is to ensure that the origin is an equilibrium point and, more importantly, these are types of models that are considered here. Let us illustrate these results by the following example.

Example 3.10. *Consider the 3-species Ricker competition model*

$$\left.\begin{aligned} x(t+1) &= x(t)e^{\alpha - c_{11}x(t)}, \\ y(t+1) &= y(t)e^{\beta - c_{21}x(t) - c_{22}y(t)}, \\ z(t+1) &= z(t)e^{\gamma - c_{31}x(t) - c_{32}y(t) - c_{33}z(t)}. \end{aligned}\right\} \tag{3.28}$$

This system has seven equilibrium points, the origin, three equilibria on the three axes, three planar equilibria, and one coexistence (positive) equilibrium point. We will assume here that the coexistence equilibrium $\mathbf{x}^* = (x^*, y^*, z^*)$ is locally asymptotically stable.

Theorem 3.9. *[24] If $\mathbf{x}^*$ is locally asymptotically stable, where $\mathbf{x}^*$ is the coexistence equilibrium point of* (3.28)*, then it is globally asymptotically stable in the interior of $\mathbb{R}^3_+$.*

The corresponding evolutionary hierarchical model is given by

$$\left.\begin{aligned} x(t+1) &= x(t)e^{\alpha(u_1(t))-c_{11}(0)x(t)}, \\ y(t+1) &= y(t)e^{\beta(u_2(t))-c_{21}x(t)-c_{22}(0)y(t)}, \\ z(t+1) &= z(t)e^{\gamma(u_3(t))-c_{31}x(t)-c_{32}y(t)-c_{33}(0)z(t)}, \end{aligned}\right\} \tag{3.29}$$

$$\left.\begin{aligned} u_1(t+1) &= u_1(t) + \sigma_1^2\alpha'(u_1(t)), \\ u_2(t+1) &= u_2(t) + \sigma_2^2\beta'(u_2(t)), \\ u_3(t+1) &= u_3(t) + \sigma_3^2\gamma'(u_3(t)). \end{aligned}\right\} \tag{3.30}$$

Let u_1^*, u_2^*, u_3^* be the equilibrium points of the equations in (3.30)*, respectively, when $\alpha'(u_1^*) = \beta'(u_2^*) = \gamma'(u_3^*) = 0$. If*

$$|1 + \gamma_1^2\alpha''(u_1^*)| < 1, \; |1 + \sigma_2^2\beta''(u_2^*)| < 1, \; |1 + \sigma_3^3\gamma''(u_3^*)| < 1. \tag{3.31}$$

Then there exist open neighborhoods U_1 of u_1^*, U_2 of u_2^*, and U_3 of u_3^* such that $\lim_{t\to\infty} u_i(t) = u_i^*$, $i = 1, 2, 3$, whenever $u_i(0) \in U_i$, $i = 1, 2, 3$. Now under Assumption (3.31)*, and using Theorem 3.9, we conclude that $\lim_{t\to\infty}(x(t), x(t), z(t), u_1(t), u_2(t), u_3(t)) = (x^*, y^*, z^*, u_1^*, u_2^*, u_3^*)$ if $(u_1(0), u_2(0), u_3(0)) \in U_1 \times U_2 \times U_3$ and $(x(0), y(0), z(0)) \in$ Interior $(\mathbb{R}^3_+)$.*

3.6 Asymptotically Periodic Non-autonomous Difference Equations

To this end, we have investigated the case when the trait equation has stable equilibrium points. In this section, we will investigate the cases when the equilibrium points of the trait equation are unstable and either a saddle-node bifurcation or a period-doubling bifurcation occur. In the case of the saddle-node bifurcation and exchange of stability occurs and a new asymptotically stable equilibrium point is born. On the other hand, in the case of periodic-doubling bifurcation, the fixed point loses its stability and a stable new periodic cycle of period 2 is born. This period doubling bifurcation will lead to chaos [22].

3.6.1 Theoretical development

Let us assume that $\{f_t : t \in \mathbb{Z}^+\}$ be a sequence of functions $f_t : \mathbb{R}^n_+ \to \mathbb{R}^n_+$, that converges uniformly to the p-periodic system $\mathcal{G} = \{g = g_{p-1}og_{p-2}o.....g_1og_0\}$, where $g_i : \mathbb{R}^n_+ \to \mathbb{R}^n_+$ for $i = 0, .., p-1$. Then we have two equations, a non-autonomous difference equations and an autonomous periodic difference equation:

$$\mathbf{x}(t+1) = f_t(\mathbf{x}(t)),\ \mathbf{x} = (x_1, x_2, \ldots, x_n) \in \mathbb{R}^n_+, \tag{3.32}$$

and

$$\mathbf{x}(t+1) = g(\mathbf{x}(t)). \tag{3.33}$$

We extend the skew-product semi-dynamical system $(\mathbb{R}^n_+ \times \mathcal{F}, \mathbb{Z}^+, \pi) \equiv (\mathbb{R}^n_+ \times \mathcal{F}, \pi)$ to the closure of $\mathcal{F}$, $\overline{\mathcal{F}} = \mathcal{F} \bigcup \{\mathcal{G}\}$ by letting $\pi((\mathbf{x}, g_i), t) = (\Phi_{t,i}(\mathbf{x}), g_{(i+t) \mod p})\ (\mathbf{x}), \mathcal{G})$. (see Figure 3.2).

In this setting we are going to make two assumptions similar to those we had in Section 4. We assume A_1: g_i and $f_t : \mathbb{R}^n_+ \longrightarrow \mathbb{R}^n_+$ are continuous for all $t \in \mathbb{Z}_+$, f_t converges uniformly to $\mathcal{G}$ as $t \to \infty$. Then $x(0) \in \mathbb{R}^n_+$ implies solutions of the nonautonomous difference equation

$$\mathbf{x}(t+1) = f_t(\mathbf{x}(t)),\ \mathbf{x} = (x_1, x_2, \ldots, x_n) \in \mathbb{R}^n_+. \tag{3.34}$$

satisfies $x(t) \in \mathbb{R}^n_+$, for all $t \in \mathbb{Z}^+$. That is to say $\mathbb{R}^n_+$ is forward invariant. The same is true for solutions of the limiting system

$$\mathbf{x}(t+1) = g(\mathbf{x}(t)), \tag{3.35}$$

and

A_2: $f_t : int(\mathbb{R}^n_+) \longrightarrow int(\mathbb{R}^n_+)$. Then it is always true that $x(0) \in int(\mathbb{R}^n_+)$ implies solutions of the nonautonomous difference equation (3.34) satisfies $x(t) \in int(\mathbb{R}^n_+)$, for all $t \in \mathbb{Z}_+$.

The main result that here is the following theorem ([19], Theorem 4.1.)

Theorem 3.10. *[19] Assume A_1 and A_2 and that the periodic system $\mathcal{G}$ has a globally asymptotically stable cycle c_p of period p or a divisor of p. Then*

(i) if $c_p \in int(\mathbb{R}^n_+)$, and if it is globally asymptotically stable on $int(\mathbb{R}^n_+)$ as a periodic cycle of the limiting equation (3.16), then all solutions of the nonautonomous difference equation (3.15) with $x(0) \in int(\mathbb{R}^n_+)$ tend to c_p.

(ii)if $c_p \in \partial(\mathbb{R}^n_+)$, and if it is globally asymptotically stable on $int(\mathbb{R}^n_+)$, then all solutions of the nonautonomous difference equation (3.15) with $x(0) \in int(\mathbb{R}^n_+)$ tend to c_p.

Proof. Let $\Psi = g_{p-1} \circ g_{p-2} \circ \cdots \circ g_1 \circ g_0$. Then an equilibrium point of the composition map Ψ is a periodic point of period p or of a divisor of p. The dynamics of the periodic system $\mathcal{G} = \{g_i : i = 0, 1, 2, \ldots, p-1\}$ is determined by the single map Ψ. Hence, applying theorem 3.10, the conclusion of the theorem follows.

□

CHAPTER

4

A DISCRETE EVOLUTIONARY BEVERTON-HOLT MODEL

Substantial part of this chapter is published in [38, 39]

4.1 Plan of Chapter

This Chapter is organized as follows:

1. In Section (4.2), we present the mathematical model and discuss the existence of positive fixed point.

2. In Section (4.3), we perform the dynamical analysis of the derived model and discuss the existence of the Neimark-Sacker bifurcation for the positive fixed point.

3. In Section (4.4), we extend the discrete evolutionary system presented in (4.2) to add the Allee effect caused by mating limitation and develop the related qualitative dynamics.

4. In Section (4.5) the OGY method is employed to control the chaos influenced by the Neimark-Sacker bifurcation.

5. The Section (4.6) contains numerical simulations that demonstrate the rich dynamics of the derived models.

4.2 The mathematical model and existence of the positive fixed point

The classical Beverton-Holt model can be written as

$$x(t+1) = x(t)\frac{b}{1+cx(t)} = x(t)r(x(t)), \quad x(0) \geq 0. \tag{4.1}$$

In Eq. (4.1), the *per capita* population rate is

$$r(x(t)) = \frac{b}{1+cx(t)}, \tag{4.2}$$

and x is the size of the population. The two parameters b and c stand for the inherent growth rate for an individual and the inter-competition coefficient, respectively. The dynamics of (4.1) are similar to those of the continuous-time logistic model. If the intrinsic growth rate is less than 1, then the fixed point 0 is globally asymptotically stable (GAS). However, if $b > 1$, the unique fixed point $x^* = \dfrac{b-1}{c}$ is GAS.
To give an evolutionary dimension to the classical model Eq. (4.1). The two model's parameters b and c are considered functions of some phenotypic traits. In particular, b depends on the trait inherited by an individual (labeled v). The parameter c is taken to be assumed dependent on the individual trait v and that of other individuals with whom it competes, described by the main trait labeled u [56].
The density dependent growth rate (4.2) becomes

$$r(x,v,u) = \frac{b(v)}{1+c(v,u)x}. \tag{4.3}$$

We assume that the function b takes Gaussian form around the trait v, and takes maximin value at a trait $v = v_m$:

$$b(v) = b_0 \exp(-\frac{(v-v_m)^2}{2\,w^2}). \tag{4.4}$$

As often made in [56], c is considered to be function of the difference $v-u$, that is $(c=c(y)=c(v-u))$ and $c \in \mathcal{C}(\mathbb{R},\mathbb{R}^{+})$:

$$c(v-u)=c_0\exp(-c_1(v-u)), \quad c_1>0. \tag{4.5}$$

The coefficient c_1 measures how the intensity of competition changes as a function of the trait different $(v-u)$, and we take $c_0=1$ for simplicity.

Based on the assumptions (4.4) and (4.5), the following discrete evolutionary Beverton-Holt model is derived:

$$x(t+1)=b_0x(t)\frac{\exp(-\frac{u^2(t)}{2})}{1+x(t)}, \tag{4.6}$$

$$u(t+1)=(1-\sigma^2)u(t)+\sigma^2\frac{c_1x(t)}{1+x(t)}. \tag{4.7}$$

In this model, b_0 represents the maximal possible inherent growth rate, and σ^2 represents the speed of evolution. The model's parameter c_1 indicates how the competition coefficient changes as a function of $v-u$. Furthermore, if no evolution occurs ($\sigma^2=0$), the trait $u(t)$ remains fixed, and the dynamics of (4.6)-(4.7) are reduced to the dynamics of $x(t+1)=x(t)\dfrac{\widetilde{b_0}}{1+x(t)}$, where $\widetilde{b_0}=b_0\,\exp{(-\frac{u^2(0)}{2})}$.

In the following section, our main concern is to study the dynamical characteristics of the positive fixed point noted (x^*,u^*). The existence and uniqueness are established in [Theorem 1., [38]] and stated as follows:

Theorem 4.1. *Let $\sigma^2>0$, if $b_0>1$, then the evolutionary system (4.6)-(4.7) admits a unique positive fixed point, noted (x^*,u^*).*

4.3 Dynamical behavior of (4.6)-(4.7)

The Jacobian matrix for system (4.6)-(4.7) evaluated at the positive fixed point (x^*,u^*), can be simplified as follows

$$J(x^*,u^*)=\begin{pmatrix} \frac{1}{1+x^*} & -\frac{c_1x^{*2}}{1+x^*} \\ \frac{c_1\sigma^2}{(1+x^*)^2} & 1-\sigma^2 \end{pmatrix}. \tag{4.8}$$

The characteristic polynomial of (4.8) is given by:

$$P(\kappa)=\kappa^2-trJ(x^*,u^*)\kappa+\det J(x^*,u^*)=0, \tag{4.9}$$

where

$$T := trJ(x^*, u^*) = \frac{1}{1+x^*} + 1 - \sigma^2, \tag{4.10}$$

and

$$Q := \det J(x^*, u^*) = \frac{1-\sigma^2}{1+x^*} + \frac{c_1^2\sigma^2 x^{*2}}{(1+x^*)^3}. \tag{4.11}$$

The following Lemma summarizes the results of the local dynamics associated to (4.6)-(4.7):

Lemma 4.1. *The following results hold true for system (4.6)-(4.7):*

- *The positive fixed point (x^*, u^*) is asymptotically stable if and only if $0 < \sigma^2 < 2$ and*

$$1 - \frac{1}{1+x^*} + \frac{c_1^2 x^{*2}}{(1+x^*)^3} > 0, \tag{4.12}$$

$$2 - \sigma^2 + \frac{1}{1+x^*}(2-\sigma^2) + \frac{c_1^2\sigma^2 x^{*2}}{(1+x^*)^3} > 0, \tag{4.13}$$

$$\frac{1-\sigma^2}{1+x^*} + \frac{c_1^2\sigma^2 x^{*2}}{(1+x^*)^3} < 1. \tag{4.14}$$

- *The positive fixed point (x^*, u^*) is saddle if and only if*

$$1 - \frac{1}{1+x^*} + \frac{c_1^2 x^{*2}}{(1+x^*)^3} > 0, \tag{4.15}$$

$$2 - \sigma^2 + \frac{1}{1+x^*}(2-\sigma^2) + \frac{c_1^2\sigma^2 x^{*2}}{(1+x^*)^3} < 0. \tag{4.16}$$

- *The positive fixed point (x^*, u^*) is source if and only if $0 < \sigma^2 < 2$ and*

$$1 - \frac{1}{1+x^*} + \frac{c_1^2 x^{*2}}{(1+x^*)^3} > 0, \tag{4.17}$$

$$2 - \sigma^2 + \frac{1}{1+x^*}(2-\sigma^2) + \frac{c_1^2\sigma^2 x^{*2}}{(1+x^*)^3} > 0, \tag{4.18}$$

$$\frac{1-\sigma^2}{1+x^*} + \frac{c_1^2\sigma^2 x^{*2}}{(1+x^*)^3} > 1. \tag{4.19}$$

- *The positive fixed point (x^*, u^*) is non-hyperbolic if and only if*

$$\left(\frac{1}{1+x^*} + 1 - \sigma^2\right)^2 - 4\left(\frac{1-\sigma^2}{1+x^*} + \frac{c_1^2\sigma^2 x^{*2}}{(1+x^*)^3}\right) < 0, \tag{4.20}$$

and

$$\frac{1-\sigma^2}{1+x^*}+\frac{c_1^2\sigma^2x^{*2}}{(1+x^*)^3}=1. \tag{4.21}$$

Now, if conditions (4.20) and (4.21) are verified, the roots of the characteristic equation (4.9) at (x^*,u^*) is given by

$$\kappa_{1,2}=\frac{trJ(x^*,u^*)\pm i\sqrt{4\det J(x^*,u^*)-(trJ(x^*,u^*))^2}}{2}, \tag{4.22}$$

where κ_1, κ_2 are the pair of complex conjugate eigenvalues, and $trJ(x^*,u^*)$ and $\det J(x^*,u^*)$ are defined in (4.10) and (4.11) respectively.

We construct then the following set related to occurrence of Neimark-Sacker bifurcation

$$\mathcal{N}_s=\Big\{(b_0,\sigma^2,c_1)/,\ b_0=\overline{b_0},\ T^2-4Q<0,\ b_0>1,\ 0\le\sigma^2\le 2,\ c_1>0\Big\}. \tag{4.23}$$

Setting the values of all parameters in (4.23), and if we vary b_0 in a small neighborhood of $b_0=\overline{b_0}$, then the positive fixed point will experiences Neimark-Sacker bifurcation.

Taking a small perturbation b_0^* (where $|\ b_0^*\ |\ll 1$) of the parameter b_0 in the neighborhood of $b_0=\overline{b_0}$ in the system (4.6)-(4.7) we obtain

$$x(t+1)=(b_0+b_0^*)x(t)\frac{\exp(-\frac{u^2(t)}{2})}{1+x(t)}=f(x(t),u(t),b_0^*), \tag{4.24a}$$

$$u(t+1)=(1-\sigma^2)u(t)+\sigma^2\frac{c_1x(t)}{1+x(t)}=g(x(t),u(t),b_0^*). \tag{4.24b}$$

Let $w(t)=x(t)-x^*$, $z(t)=u(t)-u^*$. Then, system (4.24) becomes

$$w(t+1)=(\overline{b_0}+b_0^*)(w(t)+x^*)\frac{\exp(-\frac{(z(t)+u^*)^2(t)}{2})}{1+w(t)+x^*}-x^*, \tag{4.25a}$$

$$z(t+1)=(1-\sigma^2)(z(t)+u^*)+\sigma^2\frac{c_1(w(t)+x^*)}{1+w(t)+x^*}-u^*. \tag{4.25b}$$

The characteristic equation of the system (4.24) has the roots

$$\kappa_{1,2}(b_0^*)=\frac{trJ(b_0^*)\pm i\sqrt{4\det J(b_0^*)-(tr(b_0^*))^2}}{2}, \tag{4.26}$$

where

$$trJ(b_0^*)=\frac{(\overline{b_0}+b_0^*)\exp(-u^{*2}/2)}{(1+x^*)^2}+1-\sigma^2,$$

and

$$\det J(b_0^*) = \left(\frac{(\overline{b_0}+b_0^*)\exp(-u^{*2}/2)}{(1+x^*)^2}\right)\left(1-\sigma^2\right) + \frac{c_1\sigma^2(\overline{b_0}+b_0^*)\exp(-u^{*2}/2)}{(1+x^*)^3},$$

and satisfy

$$\mid \kappa_{1,2}(b_0^*) \mid = \sqrt{\det J(b_0^*)}.$$

Moreover, when b_0^* tends to zero, yields

$$\det(J(0)) = 1 \ \text{, and } \ \frac{d \mid \kappa_{1,2} \mid}{db_0^*}|_{b_0^*=0} \neq 0. \tag{4.27}$$

Furthermore, we demanded that when $b_0^* = 0$, $\kappa_{1,2}^m \neq 1$, $m = 1, 2, 3, 4$. This is equivalent to $trJ(0) \neq -2, -1, 1, 2$.

Expanding (4.25) in Taylor series at $(w(t), z(t)) = (0, 0)$ up to second order, we obtain

$$\begin{aligned} w(t+1) &= \alpha_1 w(t) + \alpha_2 z(t) + \alpha_{12} w(t)z(t) + \alpha_{11} w^2(t) + \\ &\quad \alpha_{22} z^2(t) + O\left((\mid w(t) \mid + \mid z(t) \mid)^2\right), \end{aligned} \tag{4.28}$$

$$z(t+1) = \beta_1 w(t) + \beta_2 z(t) + \beta_{11} w^2(t) + O\left((\mid w(t) \mid + \mid z(t) \mid)^2\right), \tag{4.29}$$

where

$$\begin{aligned} \alpha_1 &= f_x(x^*, u^*, 0) = \frac{1}{1+x^*}, \\ \alpha_2 &= f_u(x^*, u^*, 0) = -\frac{c_1 x^{*2}}{1+x^*}, \\ \alpha_{12} &= f_{xu}(x^*, u^*, 0) = \frac{c_1 x^*(-1+x^*)}{1+x^*}, \\ \alpha_{11} &= f_{xx}(x^*, u^*, 0) = \frac{-1}{1+x^*} + \frac{x^*}{(1+x^*)^2}, \\ \alpha_{22} &= f_{uu}(x^*, u^*, 0) = \frac{-x^*}{2} + \frac{c_1 x^{*2}}{2(1+x^*)}, \\ \beta_1 &= g_x(x^*, u^*, 0) = \frac{\sigma^2 c_1}{(1+x^*)^2}, \\ \beta_2 &= g_u(x^*, u^*, 0) = 1 - \sigma^2, \\ \beta_{11} &= g_{xx}(x^*, u^*, 0) = \frac{-\sigma^2 c_1}{(1+x^*)^3}. \end{aligned}$$

For the normal form of (4.28)-(4.29), we take $\eta = \Re(\kappa_{1,2})$, and $\xi = \Im(\kappa_{1,2})$, and define the invertible matrix $P = \begin{pmatrix} \alpha_2 & 0 \\ \eta-\alpha_1 & -\xi \end{pmatrix}$, and using the transformation $\begin{pmatrix} w(t) \\ z(t) \end{pmatrix} = P \begin{pmatrix} X(t) \\ U(t) \end{pmatrix}$. Then the system (4.28)-(4.29) reduces to the following form

$$\begin{pmatrix} X(t+1) \\ U(t+1) \end{pmatrix} = \begin{pmatrix} \eta & -\xi \\ -\xi & \eta \end{pmatrix} \begin{pmatrix} X(t) \\ U(t) \end{pmatrix} + \begin{pmatrix} F(w(t),z(t)) \\ G(w(t),z(t)) \end{pmatrix}, \tag{4.30}$$

where

$$\begin{aligned} F(w(t),z(t)) &= \alpha_{12}\frac{\eta-\alpha_1}{\xi\alpha_2}w(t)z(t) + (\alpha_{11}\frac{\eta-\alpha_1}{\xi\alpha_2} + \\ & \quad \frac{\alpha_{12}}{\alpha_2}w(t)z(t) + \frac{\alpha_{11}}{\alpha_2}w^2(t) + \frac{\alpha_{22}}{\alpha_2}z^2(t), \\ G(w(t),z(t)) &= -\frac{\beta_{11}}{\xi})w(t)^2 + \alpha_{22}\frac{\eta-\alpha_1}{\xi\alpha_2}z^2(t). \end{aligned}$$

Writing $w(t) = \alpha_2 X(t)$, $z(t) = (\eta-\alpha_1)X(t) - \xi U(t)$, we obtain

$$\begin{aligned} F(X(t),U(t)) &= \left(\frac{\alpha_{12}\alpha_2(\eta-\alpha_1)+\alpha_{11}\alpha_2^2+\alpha_{22}(\eta-\alpha_1)^2}{\alpha_2}\right)X^2(t) - \\ & \left(\frac{(\xi\alpha_{12}\alpha_2 + 2\alpha_{22}\xi(\eta-\alpha_1))}{\alpha_2}\right)X(t)U(t) + \left(\frac{\alpha_{22}\xi^2}{\alpha_2}\right)U^2(t), \end{aligned} \tag{4.31}$$

and

$$\begin{aligned} G(X(t),U(t)) &= \left[\left(\alpha_{12}\alpha_2(\eta-\alpha_1) + \alpha_{11}\alpha_2^2 + \alpha_{22}(\eta-\alpha_1)^2\right)\frac{\eta-\alpha_1}{\xi\alpha_2} - \frac{\beta_{11}\alpha_2^2}{\xi}\right]X^2(t) \\ & -\left[\left(\xi\alpha_{12}\alpha_2 + 2\alpha_{22}\xi(\eta-\alpha_1)\right)\frac{\eta-\alpha_1}{\xi\alpha_2}\right]X(t)U(t) + \\ & \left(\alpha_{22}\xi\frac{\eta-\alpha_1}{\alpha_2}\right)U^2(t). \end{aligned} \tag{4.32}$$

Finally, we proved that the following quantity is nonzero:

$$L = -\Re[\tfrac{(1-2\overline{\kappa})\overline{\kappa}^2}{1-\kappa}\tau_{11}\tau_{20}] - \tfrac{1}{2} \mid \tau_{11} \mid^2 - \mid \tau_{02} \mid^2 + \Re(\overline{\kappa}\tau_{21}), \tag{4.33}$$

where

$$\tau_{11} = \tfrac{1}{4}[F_{X(t)X(t)} + F_{U(t)U(t)} + i(G_{X(t)X(t)} + G_{U(t)U(t)})]_{(0,0)}, \tag{4.34}$$

$$\tau_{02} = \frac{1}{8}[F_{X(t)X(t)} - F_{U(t)U(t)} - 2G_{X(t)U(t)} + i(G_{X(t)X(t)} - G_{U(t)U(t)} + 2F_{X(t)U(t)})]_{(0,0)}, \tag{4.35}$$

$$\tau_{20} = \frac{1}{8}[F_{X(t)X(t)} - F_{U(t)U(t)} + 2G_{X(t)U(t)} + i(G_{X(t)X(t)} - G_{U(t)U(t)} - 2F_{X(t)U(t)})]_{(0,0)}, \tag{4.36}$$

and

$$\begin{aligned} \tau_{21} = {} & \frac{1}{16}[F_{X(t)X(t)X(t)} + F_{X(t)U(t)U(t)} + G_{X(t)X(t)U(t)} + \\ & G_{U(t)U(t)U(t)} + i(G_{X(t)X(t)X(t)} + G_{X(t)U(t)U(t)} - \\ & F_{X(t)X(t)U(t)} - F_{U(t)U(t)U(t)})]_{(0,0)}, \end{aligned} \tag{4.37}$$

where, the functions F and G are defined in (4.31) and (4.32) respectively.

Furthermore, the calculation of (4.34), (4.35), and (4.36), (4.37) yields

$$\begin{aligned} \tau_{02} = {} & \frac{1}{4}\Bigg[\Bigg(\frac{\alpha_{12}\alpha_2(\eta-\alpha_1)+\alpha_{11}\alpha_2^2+\alpha_{22}(\eta-\alpha_1)^2}{\alpha_2} - \frac{\alpha_{22}\xi^2}{\alpha_2} + \frac{(\xi\alpha_{12}\alpha_2+2\alpha_{22}\xi(\eta-\alpha_1))}{\alpha_2}\Bigg) + i\Bigg(\Bigg(\alpha_{12}\alpha_2(\eta-\alpha_1) \\ & +\alpha_{11}\alpha_2^2 + \alpha_{22}(\eta-\alpha_1)^2\Bigg)\frac{\eta-\alpha_1}{\xi\alpha_2} - \frac{\beta_{11}\alpha_2^2}{\xi} - \alpha_{22}\xi^2\frac{\eta-\alpha_1}{\xi\alpha_2} - \Bigg(\xi\alpha_{12}\alpha_2 + 2\alpha_{22}\xi(\eta-\alpha_1)\Bigg)\frac{\eta-\alpha_1}{\xi\alpha_2}\Bigg)\Bigg], \end{aligned}$$

$$\begin{aligned} \tau_{11} = {} & \frac{1}{2}\Bigg[\Bigg(\frac{\alpha_{12}\alpha_2(\eta-\alpha_1)+\alpha_{11}\alpha_2^2+\alpha_{22}(\eta-\alpha_1)^2}{\alpha_2} + \frac{\alpha_{22}\xi^2}{\alpha_2}\Bigg) + i\Bigg(\Bigg(\alpha_{12}\alpha_2(\eta-\alpha_1) + \alpha_{11}\alpha_2^2 + \alpha_{22}(\eta-\alpha_1)^2\Bigg)\frac{\eta-\alpha_1}{\xi\alpha_2} - \\ & \frac{\beta_{11}\alpha_2^2}{\xi} + \alpha_{22}\xi\frac{\eta-\alpha_1}{\alpha_2}\Bigg)\Bigg], \end{aligned}$$

$$\begin{aligned} \tau_{20} = {} & \frac{1}{4}\Bigg[\Bigg(\frac{\alpha_{12}\alpha_2(\eta-\alpha_1)+\alpha_{11}\alpha_2^2+\alpha_{22}(\eta-\alpha_1)^2}{\alpha_2} - \frac{\alpha_{22}\xi^2}{\alpha_2} - \frac{\xi\alpha_{12}\alpha_2}{\alpha_2} + \frac{2\alpha_{22}\xi(\eta-\alpha_1)}{\alpha_2}\Bigg) + i\Bigg(\Bigg(\alpha_{12}\alpha_2(\eta-\alpha_1) + \alpha_{11}\alpha_2^2 + \\ & \alpha_{22}(\eta-\alpha_1)^2\Bigg)\frac{\eta-\alpha_1}{\xi\alpha_2} - \frac{\beta_{11}\alpha_2^2}{\xi} - \alpha_{22}\xi\frac{\eta-\alpha_1}{\alpha_2} + \frac{(\xi\alpha_{12}\alpha_2+2\alpha_{22}\xi(\eta-\alpha_1))}{\alpha_2}\Bigg)\Bigg], \end{aligned}$$

$$\tau_{21} = 0.$$

Based on the above analysis, we state the following main Theorem.

Theorem 4.2. *If the condition (4.27) holds and L defined in (4.33) is nonzero, then the model (4.6)-(4.7) experiences Neimark-Sacker bifurcation around its positive fixed point (x^*, u^*) when b_0^* varies near the origin, and $(b_0, c_1, \sigma^2) \in$ (4.23). Moreover, if $L < 0$ ($L > 0$) then an attracting (respectively repelling)* *invariant closed curve bifurcates from the fixed point* (x^*, u^*) *for* $b_0 > \overline{b_0}$ *(respectively,* $b_0 < \overline{b_0}$ *).*

4.4 Allee Effect and Evolutionary Dynamics

The aim of this section is to extend the discrete Beverton-Holt model investigated in the two previous sections and considered the Allee effect in the evolutionary dynamics. We focus our analysis on the Allee effect caused by mating limitation [20]. Therefore, we consider the following single-species model subject to the Allee effect [31]:

$$x(t+1) = x(t)\frac{b}{1+cx(t)}\underbrace{\frac{x(t)}{m+x(t)}}_{\text{Allee effect}} = x(t)\, r(x(t)), \tag{4.38}$$

where the added term $\dfrac{x}{x+m}$ models the probability of an individual successfully finding a mate to reproduce. The asymptotic dynamics of (4.38) are well established in [Theorem 2.1, [31]].

Based on the EGT methodology, we derive the following evolutionary system [39]:

$$x(t+1) = b_0 x(t)\frac{\exp(-\frac{u^2(t)}{2})}{(1+x(t))}\frac{x(t)}{x(t)+m_0}, \tag{4.39}$$

$$u(t+1) = (1-\sigma^2)u(t) + \sigma^2\frac{c_1 x(t)}{1+x(t)}. \tag{4.40}$$

It is assumed that the initial value of solutions of system (4.39)-(4.40) satisfies $x(0) > 0$, $u(0) > 0$ and all the parameters are positive. Then it is easy to prove that, if $0 < \sigma^2 \leq 1$ and the initial values $(x(0), u(0))$ are positive, then the corresponding solution $(x(t), u(t))$ is positive too.

The existence of the unique positive fixed point is guaranteed by the following result:

Proposition 4.1. *Let* $b_0 > 1 + m_0 + \sqrt{m_0}$*. If* $0 < c_1 < \sqrt{2\ln\frac{b_0\sqrt{m_0}}{(1+\sqrt{m_0})(\sqrt{m_0}+m_0)}}\frac{1+\sqrt{m_0}}{\sqrt{m_0}}$ *, then the system (4.39)-(4.40) admits a unique positive fixed point, noted* (x^*, u^*)*.*

The Jacobian matrix for system (4.39)-(4.40) evaluated at the positive fixed point (x^*, u^*) is

$$J(x^*, u^*) = \begin{pmatrix} \frac{2m_0+x^*m_0+x^*}{(1+x^*)(m_0+x^*)} & -x^*u^* \\ \frac{\sigma^2 c_1}{(1+x^*)^2} & 1-\sigma^2 \end{pmatrix} = \begin{pmatrix} \frac{2m_0+x^*m_0+x^*}{(1+x^*)(m_0+x^*)} & -\frac{c_1 x^{*2}}{1+x^*} \\ \frac{\sigma^2 c_1}{(1+x^*)^2} & 1-\sigma^2 \end{pmatrix}. \tag{4.41}$$

The characteristic equation of (4.41) is

$$\omega^2 - trJ(x^*, u^*)\omega + \det J(x^*, u^*) = 0, \tag{4.42}$$

where

$$trJ(x^*, u^*) = \frac{2m_0 + x^* m_0 + x^*}{(1 + x^*)(m_0 + x^*)} + 1 - \sigma^2, \tag{4.43}$$

and

$$\det J(x^*, u^*) = \frac{2m_0 + x^* m_0 + x^*}{(1 + x^*)(m_0 + x^*)}\left(1 - \sigma^2\right) + \frac{\sigma^2 c_1^2 x^{*2}}{(1 + x^*)^3}. \tag{4.44}$$

Theorem 4.3. *Assume* $0 < \sigma^2 \leq 1$. *Let* $c(m_0) = \sqrt{2 \ln \frac{b_0 \sqrt{m_0}}{(1+\sqrt{m_0})(\sqrt{m_0}+m_0)}} \frac{1+\sqrt{m_0}}{\sqrt{m_0}}$. *If* $0 < c_1 < c(m_0)$, *then*

- *The positive fixed point* (x^*, u^*) *is locally asymptotically stable if*

$$m_0 < \min\left\{\frac{x^{*2}(1 + x^*)^2 + c_1^2 x^{*3}}{(1 + x^*)^2 - c_1^2 x^{*2}}, \frac{x^*[(\sigma^2 + x^*)(1 + x^*)^2 + c_1^2 \sigma^2 x^{*2})]}{c_1^2 \sigma^2 x^{*2} + (1 + x^*)^2 - \sigma^2(x^* + 2)(x^* + 1)^2}\right\}.$$

- *The positive fixed point* (x^*, u^*) *is non-hyperbolic if*

$$m_0 = \frac{x^*[(\sigma^2 + x^*)(1 + x^*)^2 + c_1^2 \sigma^2 x^{*2})]}{c_1^2 \sigma^2 x^{*2} + (1 + x^*)^2 - \sigma^2(x^* + 2)(x^* + 1)^2}. \tag{4.45}$$

If the non-hyperbolic condition (4.45) holds, then the eigenvalues of (4.42) are a pair of complex conjugate numbers with modulus 1.

Let us consider the following set:

$$N_s = \left\{(b_0, m_0, \sigma^2, c_1) \in \mathbb{R}_+^4, \quad tr^2 J(x^*, u^*) < 4 \det J(x^*, u^*), m_0 = \frac{x^*[(\sigma^2 + x^*)(1 + x^*)^2 + c_1^2 \sigma^2 x^{*2})]}{c_1^2 \sigma^2 x^{*2} + (1 + x^*)^2 - \sigma^2(x^* + 2)(x^* + 1)^2}\right\}. \tag{4.46}$$

Let Neimark-Sacker occurs at $\overline{m_0} = \frac{x^*[(\sigma^2+x^*)(1+x^*)^2+c_1^2\sigma^2x^{*2})]}{c_1^2\sigma^2x^{*2}+(1+x^*)^2-\sigma^2(x^*+2)(x^*+1)^2}$. After technical calculations, one gets the quantity below is non zero

$$\mathcal{L} = -\Re[\frac{(1-2\overline{\omega})\overline{\omega}^2}{1-\omega}\rho_{11}\rho_{20}] - \frac{1}{2} \mid \rho_{11} \mid^2 - \mid \rho_{02} \mid^2 + \Re(\overline{\omega}\rho_{21}). \tag{4.47}$$

The existence conditions of the Neimark-Sacker bifurcation are proved in the following theorem, where the detailed proof is reported in [39]:

Theorem 4.4. *There exists a Neimark-Sacker bifurcation near* (x^*, u^*) *whenever* m_0 *deviates in the neighborhood of* $\overline{m_0} = \dfrac{x^*[(\sigma^2 + x^*)(1 + x^*)^2 + c_1^2 \sigma^2 x^{*2})]}{c_1^2 \sigma^2 x^{*2} + (1 + x^*)^2 - \sigma^2(x^* + 2)(x^* + 1)^2}$. *Moreover, if the Lyapunoc coefficient* $\mathcal{L}$ *in (4.47) is negative (respectively positive), then an attracting (respectively repelling) invariant closed curve bifurcates from the fixed point* (x^*, u^*) *for* $m_0 > \overline{m_0}$ *(respectively,* $m_0 < \overline{m_0}$ *).*

4.5 Control of Neimark-Sacker bifurcation

In this section, we apply the OGY method [46] to control the chaos produced by Neimark-Sacker bifurcation. To do this, we write the system (4.39)-(4.40) in the following form

$$x(t+1) = b_0 x(t) \frac{\exp(-\frac{u^2(t)}{2})}{1+x(t)} \frac{x(t)}{x(t)+m_0} = f(x(t), u(t), m_0), \tag{4.48}$$

$$u(t+1) = (1-\sigma^2)u(t) + \sigma^2 \frac{c_1 x(t)}{1+x(t)} = g(x(t), u(t), m_0), \tag{4.49}$$

where m_0 denotes the parameter subject to be controlled. Suppose that m_0 lies in a small interval, that is, $m_0 \in (\widehat{m_0} - \delta, \widehat{m_0} + \delta)$, such that $\delta > 0$, and $\widehat{m_0}$ represents nominal value for m_0 which belongs to a chaotic region. Suppose that (x^*, u^*) denotes an unstable fixed point of (4.48)-(4.49) influenced by Neimark-Sacker bifurcation . In this case (4.48)-(4.49) is approximated in the neighborhood of (x^*, u^*) as follows

$$\begin{pmatrix} x(t+1) - x^* \\ u(t+1) - u^* \end{pmatrix} \simeq J(x^*, u^*, \widehat{m_0}) \begin{pmatrix} x(t) - x^* \\ u(t) - u^* \end{pmatrix} + M \begin{pmatrix} m_0 - \widehat{m_0} \end{pmatrix}, \tag{4.50}$$

where

$$J(x^*, u^*, \widehat{m_0}) = \begin{pmatrix} \frac{\partial f(x^*,u^*,\widehat{m_0})}{\partial x} & \frac{\partial f(x^*,u^*,\widehat{m_0})}{\partial u} \\ \frac{\partial g(x^*,u^*,\widehat{m_0})}{\partial x} & \frac{\partial g(x^*,u^*,\widehat{m_0})}{\partial u} \end{pmatrix}$$

$$= \begin{pmatrix} \frac{b_0 \exp(-\frac{u^{*2}}{2}) x^* (2\widehat{m_0} + x^* \widehat{m_0} + x^*)}{(1+x^*)^2 (\widehat{m_0} + x^*)^2} & -\frac{b_0 x^{*2} u^* \exp(-\frac{u^{*2}}{2})}{(1+x^*)^2 (\widehat{m_0}+x^*)^2} \\ \frac{\sigma^2 c_1}{(1+x^*)^2} & 1-\sigma^2 \end{pmatrix},$$

and

$$M = \begin{pmatrix} \frac{\partial f(x^*,u^*,\widehat{m_0})}{\partial m_0} \\ \frac{\partial g(x^*,u^*,\widehat{m_0})}{\partial m_0} \end{pmatrix} = \begin{pmatrix} -\frac{b_0 x^{*2} \exp(-\frac{u^{*2}}{2})}{(1+x^*)(\widehat{m_0}+x^*)^2} \\ 0 \end{pmatrix}.$$

Moreover, the system (4.48)-(4.49) is controllable since the rank of the following matrix is two:

$$C = (M : JM) = \begin{pmatrix} -\frac{b_0 x^{*2} \exp(-\frac{u^{*2}}{2})}{(1+x^*)(\widehat{m_0}+x^*)^2} & -\frac{b_0^2 \exp(-u^{*2}) x^{*3} (2\widehat{m_0} + x^* \widehat{m_0} + x^*)}{(1+x^*)^3 (\widehat{m_0}+x^*)^4} \\ 0 & -\frac{b_0 \sigma^2 c_1 \exp(-\frac{u^{*2}}{2}) x^{*2}}{(1+x^*)^3 (\widehat{m_0}+x^*)^2} \end{pmatrix}. \tag{4.51}$$

Furthermore, we set $\begin{pmatrix} m_0 - \widehat{m_0} \end{pmatrix} = -Q \begin{pmatrix} x(t) - x^* \\ u(t) - u^* \end{pmatrix}$, where $Q = \begin{pmatrix} q_1 & q_2 \end{pmatrix}^T$. Therefore, the system (4.50) is written as follows

$$\begin{pmatrix} x(t+1)-x^* \\ u(t+1)-u^* \end{pmatrix} \simeq \begin{pmatrix} J-MQ \end{pmatrix} \begin{pmatrix} x(t)-x^* \\ u(t)-u^* \end{pmatrix}. \tag{4.52}$$

In this case, the corresponding control system of (4.48)-(4.49) is given as follows

$$x(t+1) = b_0 x(t) \frac{\exp(-\frac{u^2(t)}{2})}{(1+x(t))} \frac{x(t)}{x(t)+(\widehat{m_0}-q_1(x(t)-x^*)-q_2(u(t)-u^*))}, \tag{4.53}$$

$$u(t+1) = (1-\sigma^2)u(t)+\sigma^2\frac{c_1 x(t)}{1+x(t)}. \tag{4.54}$$

Moreover, the positive fixed point of (4.53)-(4.54) is locally asymptotically stable if and only if the absolute values of both eigenvalues of $J-MQ$ are less than one. Moreover, the matrix $J-MQ$ is given as follows

$$J-MQ = \begin{pmatrix} J_1 & J_2 \\ J_3 & J_4 \end{pmatrix}, \tag{4.55}$$

where

$$\begin{aligned}
J_1 &= \frac{b_0\exp(-\frac{u^{*2}}{2})}{(1+x^*)^2(\widehat{m_0}+x^*)^2)}\Big[(2x^*\widehat{m_0}-x^{*2}+x^{*2}\widehat{m_0})+q_1(1+x^*)x^{*2}\Big],\\
J_2 &= \frac{b_0 x^{*2}\exp(-\frac{u^{*2}}{2})}{(1+x^*)(\widehat{m_0}+x^*)^2)}\Big[-u^*(\widehat{m_0}+x^*)+q_2\Big],\\
J_3 &= \frac{c_1\sigma^2}{(1+x^*)^2},\\
J_4 &= 1-\sigma^2.
\end{aligned}$$

The characteristic equation of (4.55) is given as follows

$$\begin{aligned}
&\kappa^2-\Bigg(\frac{b_0\exp(-\frac{u^{*2}}{2})}{(1+x^*)^2(\widehat{m_0}+x^*)^2}\Big[(2x^*\widehat{m_0}-x^{*2}+x^{*2}\widehat{m_0})+q_1(1+x^*)x^{*2}\Big]+1-\sigma^2\Bigg)\kappa+ \\
&\Bigg(\frac{b_0\exp(-\frac{u^{*2}}{2})}{(1+x^*)^2(\widehat{m_0}+x^*)^2}\Big[(2x^*\widehat{m_0}-x^{*2}+x^{*2}\widehat{m_0})+q_1(1+x^*)x^{*2}\Big]\Bigg)\Big(1-\sigma^2\Big)+ \\
&\frac{c_1\sigma^2}{(1+x^*)^2}\Bigg(\frac{b_0\exp(-\frac{u^{*2}}{2})}{(1+x^*)(\widehat{m_0}+x^*)^2}\Big[-u^*(\widehat{m_0}+x^*)+q_2\Big]\Bigg)=0.
\end{aligned} \tag{4.56}$$

Assume that κ_1 and κ_2 represent the roots of (4.56), then it follows that

$$\kappa_1 + \kappa_2 = \frac{b_0 \exp(-\frac{u^{*2}}{2})}{(1+x^*)^2(\widehat{m_0}+x^*)^2}\Bigg[(2x^*\widehat{m_0} - x^{*2} + x^{*2}\widehat{m_0}) + q_1(1+x^*)x^{*2}\Bigg] + 1 - \sigma^2, \tag{4.57}$$

$$\kappa_1\kappa_2 = \Bigg(\frac{b_0 \exp(-\frac{u^{*2}}{2})}{(1+x^*)^2(\widehat{m_0}+x^*)^2}\Bigg[(2x^*\widehat{m_0} - x^{*2} + x^{*2}\widehat{m_0}) + q_1(1+x^*)x^{*2}\Bigg]\Bigg)\Bigg(1-\sigma^2\Bigg) + \frac{c_1\sigma^2}{(1+x^*)^2}\Bigg(\frac{b_0 \exp(-\frac{u^{*2}}{2})}{(1+x^*)(\widehat{m_0}+x^*)^2)}\Bigg[-u^*(\widehat{m_0}+x^*) + q_2\Bigg]\Bigg). \tag{4.58}$$

Moreover, we take $\kappa_1 = \pm 1$ and $\kappa_1\kappa_2 = 1$. Then, the stability domain of (4.53)-(4.54) is delimited by the following lines:

$$L_1 : \frac{b_0 \exp(-\frac{u^{*2}}{2})}{(1+x^*)^2(\widehat{m_0}+x^*)^2}(2x^*\widehat{m_0} - x^{*2} + x^{*2}\widehat{m_0})(1-\sigma^2) + \frac{b_0 x^{*2} \exp(-\frac{u^{*2}}{2})}{(1+x^*)(\widehat{m_0}+x^*)^2}(1-\sigma^2)q_1 - \frac{b_0 c_1\sigma^2 u^* \exp(-\frac{u^{*2}}{2})}{(1+x^*)^3(\widehat{m_0}+x^*)} + \frac{b_0 c_1\sigma^2 \exp(-\frac{u^{*2}}{2})}{(1+x^*)^3(\widehat{m_0}+x^*)^2}q_2 = 1, \tag{4.59}$$

$$L_2 : \sigma^2\frac{b_0 \exp(-\frac{u^{*2}}{2})}{(1+x^*)^2(\widehat{m_0}+x^*)^2}\Bigg[(2x^*\widehat{m_0} - x^{*2} + x^{*2}\widehat{m_0}) + q_1(1+x^*)x^{*2}\Bigg] - \sigma^2 + \frac{b_0 c_1\sigma^2 u^* \exp(-\frac{u^{*2}}{2})}{(1+x^*)^3(\widehat{m_0}+x^*)} - \frac{b_0 c_1\sigma^2 \exp(-\frac{u^{*2}}{2})}{(1+x^*)^3(\widehat{m_0}+x^*)^2)}q_2 = 0, \tag{4.60}$$

$$L_3 : \Bigg(\frac{b_0 \exp(-\frac{u^{*2}}{2})}{(1+x^*)^2(\widehat{m_0}+x^*)^2}\Bigg[(2x^*\widehat{m_0} - x^{*2} + x^{*2}\widehat{m_0}) + q_1(1+x^*)x^{*2}\Bigg]\Bigg)\Bigg(2-\sigma^2\Bigg) + 2 - \sigma^2 - \frac{b_0 c_1\sigma^2 u^* \exp(-\frac{u^{*2}}{2})}{(1+x^*)^3(\widehat{m_0}+x^*)} + \frac{b_0 c_1\sigma^2 \exp(-\frac{u^{*2}}{2})}{(1+x^*)^3(\widehat{m_0}+x^*)^2}q_2 = 0. \tag{4.61}$$

4.6 Numerical simulations

We set $\sigma^2 = 0.95$ and $c_1 = 3.2$, with initial conditions $(0.5, 0.6)$. We also set $m_0 = 0$, indicating the absence of the Allee effect, and let b_0, the maximal fertility rate, vary. It is expected that increasing b_0 will generate manifestations of complicated dynamics. Panel (a) of Fig. (4.2) depicts the stable dynamics of the population x and its trait, which means that all orbits attract towards the positive fixed point $(0.69, 1.3)$ if b_0 is less than $b_0 = 3.9$. In particular, the system (4.39)-(4.40) starts to lose its stability, and meanwhile, a closed curve appears as reported in Fig. (4.2). As a result, for $b_0 = 4.3$ and $b_0 = 4.8$, the system (4.39)-(4.40) undergoes Neimark-Sacker bifurcation, and a chaotic region appears. Fig. (4.1) depicts the related bifurcation diagram with respect to b_0 for $m_0 = 0$.

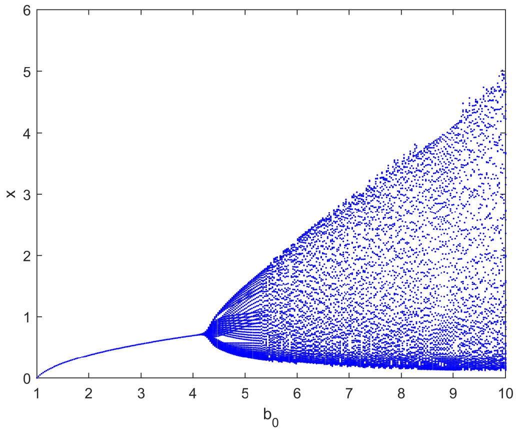
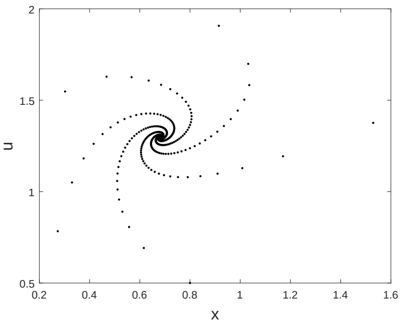
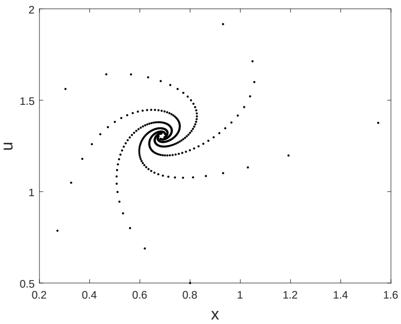


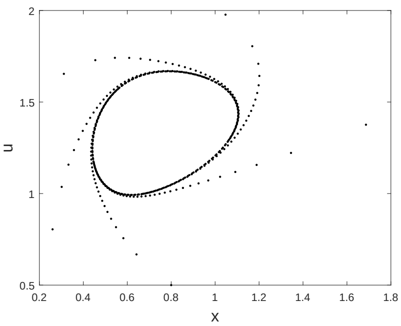
Figure 4.1: Neimark-Sacker bifurcation of (4.39)-(4.40) with respect to b_0 in the case $m_0 = 0$.



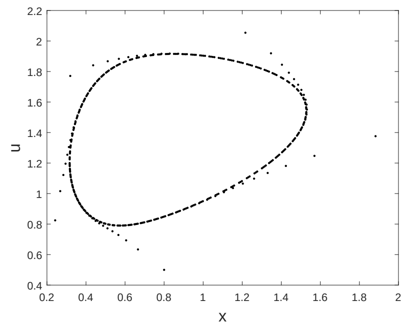
(a): $b_0 = 3.9$



(b): $b_0 = 3.95$



(c): $b_0 = 4.3$



(d): $b_0 = 4.8$

Figure 4.2: Phase portraits of the discrete model (4.39)-(4.40) for different values of b_0 in the case: $m_0 = 0$.

To demonstrate the Allee effect, we chose a chaotic value of $b_0 = 5.5$. The bifurcation diagram with regard to m_0 is reported in Fig.(4.3).

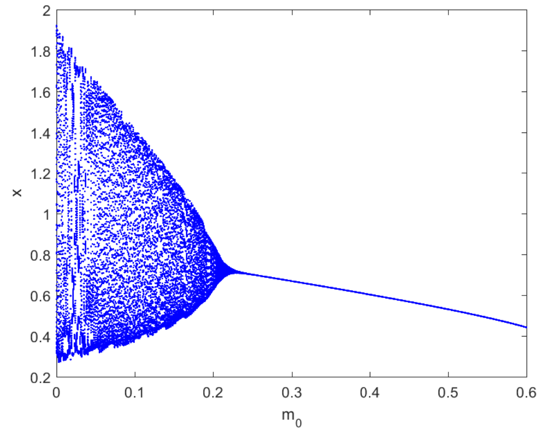


Figure 4.3: Neimark-Sacker bifurcation of (4.39)-(4.40) with respect to m_0 for fixed $b_0 = 5.5$.

The positive fixed point $(0.67, 1.28)$ is asymptotically stable for $m_0 = 0.3$. Decreasing the value of m_0 from $m_0 = 0.3$ until $m_0 = 0$ the asymptotic stability is lost. In particular, the existence of a reppeling closed invariant curve implies that the discrete-time model (4.39)-(4.40)undergoes a Neimark-Sacker bifurcation around $(x^*, u^*) = (0.67, 1.28)$. As a result, increasing the value of m_0 has a stabilizing effect on population dynamics.

Now, we implement the OGY method to achieve asymptotic stability for the chaotic features in which small values of the Allee effect failed to stabilize unstable orbits (e.g. $\widehat{m_0} = 0.2$).

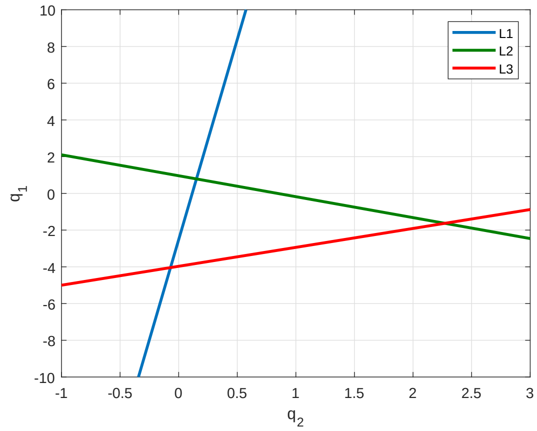


Figure 4.4: Stability region for the discrete model (4.53)-(4.54).

As discussed in Section. 4.5, we consider the control force related to the Allee effect as follows: $m_0 = \widehat{m_0} - q_1(x(t) - x^*) - q_2(u(t) - u^*)$ at the unstable fixed point $(x^*, u^*) = (1.06, 1.63)$ related to $\widehat{m_0} = 0.2$

with $q_1 = -1$, and $q_2 = 0.5$, chosen from the triangular region drawn in Fig. (4.4).

Time series for these values is shown in Fig.(4.6) demonstrating that the system (4.53)-(4.54) tends to the fixed point $(0.67, 1.28)$. The diagram of bifurcation with respect to q_2 for $q_1 = -1$ is reported in Fig. (4.5).

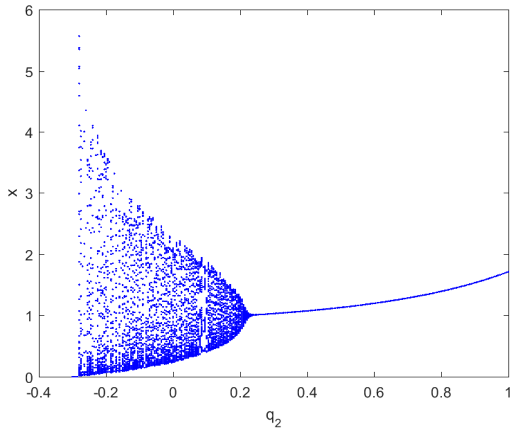
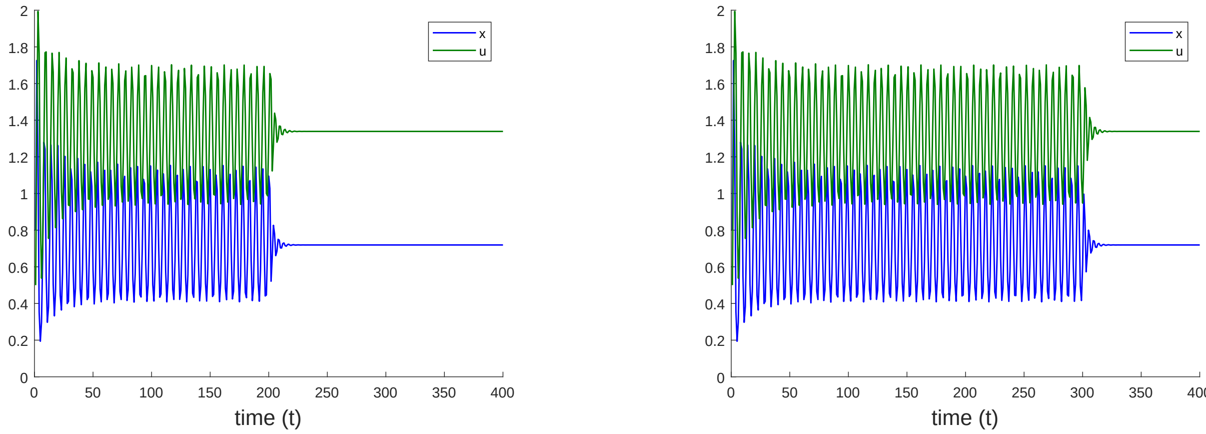


Figure 4.5: Bifurcation diagram of (4.53)-(4.54) with respect to q_2 for $m_0 = 0.2$ and $b_0 = 5.5$.



(a) (b)

Figure 4.6: Time series of x and for u for the model (4.53)-(4.54) for $b_0 = 5.5$ and $\widehat{m_0} = 0.2$. In (a) the chaos is controlled after time t=200, and in (b) the chaos is controlled after time $t = 300$.

CHAPTER

5

AN EVOLUTIONARY RICKER MODEL WITH IMMIGRATION

Substantial part of this chapter is published in [40]

5.1 Introduction

In this chapter, we investigate the evolutionary dynamics of a single-species population of biological organisms. The aforementioned dynamics are described by the following type-Ricker model:

$$x(t+1) = b\exp(-cx(t))x(t) + h\,x(t) = r(x(t))x(t), \tag{5.1}$$

where the nonnegative parameters b and c stand for *per capita* fertility rate, and the competition coefficient respectively.

The coefficient h indicates the effect of immigration $0 \leq h < 1$ [45]. The density dependant fertility rate is

$$r(x) = b\exp(-cx) + h. \tag{5.2}$$

In [40], we derived the following evolutionary model to (5.1):

$$x(t+1) = b_0 \exp(-\frac{u(t)^2}{2}) \exp(-x(t)) x(t) + h\, x(t), \tag{5.3}$$

$$u(t+1) = u(t) + \sigma^2 b_0 \exp(-\frac{u(t)^2}{2}) \exp(-x(t)) \frac{-u(t) + c_1 x(t)}{b_0 \exp(-\frac{u(t)^2}{2}) \exp(-x(t)) + h}, \tag{5.4}$$

where b_0 represents the maximal fertility rate, h represents the immigration coefficient, σ^2 is the speed of evolution and c_1 measure the pressure of traits competition.

The presentation of this chapter is structured as follows: In section (5.2) we discuss the qualitative behavior of the model.

In section (5.3) we give the outlines of the theoretical analysis of the Neimark-Saker bifurcation and Period-doubling bifurcation respectively.

In section (5.4) the chaos influenced by bifurcations is controlled.

In section (5.5) some numerical simulations are given to illustrate our theoretical findings.

5.2 Asymptotic stability

The equations for the fixed point pair are

$$1 = b_0 \exp(-\frac{u^2}{2}) \exp(-x) + h, \tag{5.5}$$

$$0 = -u + c_1 x. \tag{5.6}$$

If $b_0 < 1 - h$, then from Eq. (5.5) there is no positive fixed point. However, if $b_0 > 1 - h$, then there exists a unique positive fixed point given by the explicit formulas

$$\Big(x(b_0), u(b_0)\Big) = \begin{cases} \Big(\ln \frac{b_0}{1-h}, 0\Big), & \text{if } \; c_1 = 0, \\ \Big(\frac{-1+\sqrt{1+2c_1^2 \ln(\frac{b_0}{1-h})}}{c_1^2}, \frac{-1+\sqrt{1+2c_1^2 \ln(\frac{b_0}{1-h})}}{c_1}\Big), & \text{if } \; c_1 \neq 0. \end{cases} \tag{5.7}$$

The Jacobian matrix of (5.3)-(5.4) evaluated at the positive fixed point (5.7) when $c_1 \neq 0$ is

$$J(x(b_0), u(b_0)) = \begin{pmatrix} 1 - x(b_0)(1-h) & -\frac{2}{c_1}(1-h)(\ln(\frac{b_0}{1-h}) - x(b_0)) \\ \sigma^2 c_1 (1-h) & 1 - \sigma^2(1-h) \end{pmatrix}. \tag{5.8}$$

For the case $c_1 = 0$ the eigenvalues are

$$\lambda_1 = 1 - \ln(\frac{b_0}{1-h})(1-h), \quad \lambda_2 = 1 - \sigma^2(1-h). \tag{5.9}$$

Theorem 5.1. *Assume $c_1 = 0$, and $\sigma^2 < \frac{2}{1-h}$, there exists positive fixed points for and only for $b_0 > 1-h$ that are locally asymptotically stable if $1-h < b_0 < (1-h)e^{\frac{2}{1-h}}$, and unstable if $b_0 > (1-h)e^{\frac{2}{1-h}}$. When $b_0 = (1-h)e^{\frac{2}{1-h}}$ the Jacobian has eigenvalue value -1.*

Consider now the case $c_1 \neq 0$. To study the eigenvalues of the Jacobian we employ the trace and determinant criteria which imply both eigenvalues have magnitude less than 1 and the positive fixed point is locally asymptotically stable if and only if the three inequalities [21]

$$tr J(x,u) < 1 + \det J(x,u), \tag{5.10}$$

$$-1 - \det J(x,u) < tr J(x,u), \tag{5.11}$$

$$\det J(x,u) < 1. \tag{5.12}$$

If inequality (5.10) or (5.11) become equalities, then the Jacobian has an eigenvalue equal to $+1$ or -1 respectively. If inequality (5.12) becomes an equality, then the Jacobian has a complex eigenvalue whose absolute value equals 1. The characteristic equation of Jacobian matrix (5.8) can be written as

$$\lambda^2 - tr\Big(J(x(b_0), u(b_0))\Big) + \det\Big(J(x(b_0), u(b_0))\Big) = 0, \tag{5.13}$$

where

$$tr\Big(J(x(b_0), u(b_0))\Big) = 2 - x(b_0)(1-h) - \sigma^2(1-h), \tag{5.14}$$

and

$$\det\Big(J(x(b_0), u(b_0))\Big) = \Big(1 - x(b_0)(1-h)\Big)\Big(1 - \sigma^2(1-h)\Big) + 2\sigma^2(1-h)^2\Big(\ln(\frac{b_0}{1-h}) - x(b_0)\Big), \tag{5.15}$$

and the discriminant of (5.13) is

$$\Delta = tr J(x(b_0), u(b_0))^2 - 4\det J(x(b_0), u(b_0)). \tag{5.16}$$

The following lemmas are required to prove the asymptotic stability of the positive fixed point, and their proofs are given in [40].

Lemma 5.1. *Assume $c_1 \neq 0$ in the evolutionary Ricker model (5.3)-(5.4). The inequality (5.10) is true for all σ^2 and $b_0 > 1-h$.*

Lemma 5.2. *Assume $c_1 \neq 0$ and $\sigma^2 < \frac{2}{1-h}$ in the evolutionary equations (5.3)-(5.4).*

- *If*

$$\sigma^2 < \frac{2}{(1-h)+8c_1^2}, \tag{5.17}$$

then there exist a real $\kappa > (1-h)\exp(\frac{2}{1-h})$ such that inequality (5.11) holds for b_0 satisfying $1 < b_0 < \kappa$ where

$$\kappa = (1-h)\exp\left(\frac{(2-\sigma^2(1-h)(2+\sigma^2(1-h)-4\sigma^2c_1^2)-(\sigma^2(1-h)+2)\sqrt{(2-\sigma^2(1-h))(2-\sigma^2(1-h)-\sigma^2 8c_1^2)}}{4\sigma^4c_1^2(1-h)^2}\right), \tag{5.18}$$

the inequality (5.11) is reversed if b_0 is greater than but near κ.

The Jacobian $J(x(\kappa), u(\kappa))$ has eigenvalue -1.

- *If*

$$\sigma^2 > \frac{2}{(1-h)+8c_1^2}, \tag{5.19}$$

then inequality (5.11) holds for all $b_0 > 1-h$.

Lemma 5.3. *Assume $c_1 \neq 0$ and $\sigma^2 < \frac{2}{1-h}$ in the evolutionary equations (5.3)-(5.4). There exists a real $\gamma > (1-h)\exp(\frac{1}{2(1-h)})$ such that inequality (5.12) holds for $1-h < b_0 < \gamma$ where*

$$\gamma = (1-h)\exp\left(\frac{1-\sigma^4(1-h)^2+2(1-h)c_1^2\sigma^4+(\sigma^2(1-h)+1)\sqrt{(\sigma^2(1-h)+1)^2+4(1-h)c_1^2\sigma^4}}{4c_1^2\sigma^4(1-h)^2}\right), \tag{5.20}$$

the Jacobian $J(x(\gamma), u(\gamma))$ has a complex eigenvalue of absolute value 1.

The three Trace-Determinant stability inequalities (5.10)-(5.11)-(5.12) for local stability, together with the three Lemmas (5.1) (5.2)(5.3), yield the following result.

Theorem 5.2. *[40] Assume $c_1 \neq 0$ and $\sigma^2 < \frac{2}{1-h}$ in the evolutionary discrete model (5.3)-(5.4), and let κ and γ defined by (5.18)-(5.20).*

- *Assume*

$$\sigma^2 < \frac{2}{(1-h)+8c_1^2}, \tag{5.21}$$

and defined $b_1 = \min\{\kappa, \gamma\}$*. The positive fixed point (5.7) is locally asymptotically stable for* $1 - h < b_0 < b_1$ *and is unstable for* b_0 *greater than but near* b_1*. If* $b_1 = \kappa$ *then the Jacobian has an eigenvalue* -1 *when* $b_0 = \kappa$*. If* $b_1 = \gamma$ *then the Jacobian has a complex eigenvalue of absolute value 1 when* $b_0 = \gamma$*.*

- *If*

$$\sigma^2 > \frac{2}{(1-h) + 8c_1^2}, \tag{5.22}$$

then the positive fixed point (5.7) is locally asymptotically stable for $1 - h < b_0 < \gamma$ *and unstable for* b_0 *greater than, but near* γ*. The Jacobian has a complex eigenvalue of absolute value 1 when* $b_0 = \gamma$*.*

5.3 Bifurcations analysis

In this section, we explore the Neimark-Sacker bifurcation and Period-doubling bifurcation respectively. Based on Theorem (5.2), the existence of bifurcations about the positive fixed point $(x(b_0), u(b_0))$ can be summarized as follows:

- From Theorem (5.2), we see that if $b_0 = \kappa$ (κ is defined in (5.18))holds, then one of the eigenvalues is -1 . So a period-doubling bifurcation exists by the variation of parameter in a small neighborhood of $b_0 = \kappa$. More precisely we can also represent the parameters satisfying $b_0 = \kappa$ as

$$P_d(x(b_0), u(b_0)) = \Big\{(b_0, h, c_1, \sigma^2) > 0, \quad 0 \le h < 1, \quad \sigma^2 < \frac{2}{(1-h) + 8c_1^2}, \tag{5.23}$$

$$trJ(x(b_0), u(b_0))^2 > 4 \det J(x(b_0), u(b_0)), \quad b_0 = \kappa\Big\},$$

- If $b_0 = \gamma$ (γ is defined in (5.20) holds, then one of the eigenvalues of J are a pair of complex conjugate with modulus 1. So a Neimark-Sacker bifurcation exists by the variation of parameter in a small neighborhood of $b_0 = \gamma$. More precisely, we can also represent the parameters satisfying $b_0 = \gamma$ as

$$N_s(x(b_0), u(b_0)) = \Big\{(b_0, h, c_1, \sigma^2) > 0, \ 0 \le h < 1, \ \sigma^2 < \frac{2}{(1-h) + 8c_1^2}, \tag{5.24}$$

$$trJ(x(b_0), u(b_0))^2 < 4 \det J(x(b_0), u(b_0)), \quad b_0 = \gamma\Big\}.$$

5.3.1 Neimark-Sacker bifurcation about $(x(b_0), u(b_0))$

The roots of the characteristic equation (5.13) at $(x(b_0), u(b_0))$ are a pair of complex conjugate numbers λ_1, λ_2 given by

$$\lambda_{1,2} = \frac{trJ(x(b_0), u(b_0)) \pm i\sqrt{4\det J(x(b_0), u(b_0)) - (trJ(x(b_0), u(b_0))^2}}{2}, \tag{5.25}$$

with $trJ(x(b_0), u(b_0))$ and $\det J(x(b_0), u(b_0))$ are given in (5.14)and(5.15) respectively. The Neimark-Sacker bifurcation occurs when one of the roots of the above equation are complex conjugates with unit modulus. If we vary b_0 in the neighborhood of $b_0 = \gamma$ and keeping other parameters constant. Then $(x(b_0), u(b_0))$ undergoes Neimark-Sacker bifurcation.

Taking a perturbation b_0^* where $(b_0^* \ll 1)$ of the parameter b_0 in the neighborhood of $b_0 = \gamma$ in the system (5.3)-(5.4), we have

$$x(t+1) = (b_0 + b_0^*)x(t)\exp(-x(t))\exp(-\frac{u(t)^2}{2}) + h\,x(t), \tag{5.26a}$$

$$u(t+1) = u(t) + \sigma^2(b_0 + b_0^*)\exp(-\frac{u(t)^2}{2})\exp(-x(t))\frac{-u(t) + c_1x(t)}{(b_0 + b_0^*)\exp(-\frac{u(t)^2}{2})\exp(-x(t)) + h}. \tag{5.26b}$$

The characteristic equation associated to the model (5.26) is

$$\lambda^2 - trJ(b_0^*)\lambda + \det J(b_0^*) = 0. \tag{5.27}$$

The roots of (5.27) are

$$\lambda_{1,2}(b_0^*) = \frac{trJ(b_0^*) \pm i\sqrt{4\det J(b_0^*) - (trJ(b_0^*))^2}}{2}, \tag{5.28}$$

with

$$|\lambda_{1,2}(b_0^*)| = \sqrt{\det J(b_0^*)}, \quad \frac{d|\lambda_{1,2}|}{db_0^*}\,|_{b_0^*=0} \neq 0, \tag{5.29}$$

we required that when $b_0^* = 0$, $\lambda_{1,2}^m \neq 1$, for $m = 1, 2, 3, 4$ which corresponds to $trJ(0) \neq -2, 0, 1, 2$. After linearizing the system (5.26) one gets

$$v(t+1) = \alpha_1 v(t) + \alpha_2 w(t) + \alpha_{12}v(t)w(t) + \alpha_{11}v^2(t) + \alpha_{22}w^2(t) + O\Big((|\ v(t)\ | + |\ w(t)\ |)^2\Big), \tag{5.30a}$$

$$w(t+1) = \beta_1 v(t) + \beta_2 w(t) + \beta_{12}v(t)w(t) + \beta_{11}v^2(t) + \beta_{22}w^2(t) + O\Big((|\ v(t)\ | + |\ w(t)\ |)^2\Big), \tag{5.30b}$$

where

$$\alpha_1 = f_x(x(b_0), u(b_0), 0) = 1 - (1-h)x(b_0),$$

$$\alpha_2 = f_u(x(b_0), u(b_0), 0) = -c_1(1-h)x^2(b_0),$$

$$\alpha_{12} = f_{xu}(x(b_0), u(b_0), 0) = -(1-h)c_1 x(b_0)(1 + x(b_0)),$$

$$\alpha_{11} = f_{xx}(x(b_0), u(b_0), 0) = (1-h)(-1 + \frac{x(b_0)}{2}),$$

$$\alpha_{22} = f_{uu}(x(b_0), u(b_0), 0) = (-\frac{x(b_0)}{2} + \frac{c_1^2 x^3(b_0)}{2})(1-h),$$

$$\beta_1 = g_x(x(b_0), u(b_0), 0) = \sigma^2(1-h)c_1,$$

$$\beta_2 = g_u(x(b_0), u(b_0), 0) = 1 - \sigma^2(1-h),$$

$$\beta_{12} = g_{xu}(x(b_0), u(b_0), 0) = \sigma^2 h(1-h)(1 - c_1^2 x(b_0)),$$

$$\beta_{11} = g_{xx}(x(b_0), u(b_0), 0) = -\sigma^2 h(1-h)c_1,$$

$$\beta_{22} = g_{uu}(x(b_0), u(b_0), 0) = \sigma^2 h(1-h)c_1 x(b_0).$$

making some technical algebraic translation, the system (5.30) reduces to the following form

$$\begin{pmatrix} X(t+1) \\ U(t+1) \end{pmatrix} = \begin{pmatrix} \eta & -\xi \\ -\xi & \eta \end{pmatrix} \begin{pmatrix} X(t) \\ U(t) \end{pmatrix} + \begin{pmatrix} F(X(t), U(t)) \\ G(X(t), U(t)) \end{pmatrix}, \tag{5.31}$$

where

$$\eta = \Re(\lambda_{1,2}), \qquad \xi = \Im(\lambda_{1,2}),$$

$$F(X(t), U(t)) = \tfrac{\alpha_{12}\alpha_2(\eta-\alpha_1)+\alpha_{11}\alpha_2^2+\alpha_{22}(\eta-\alpha_1)^2}{\alpha_2} X^2(t) + \tfrac{-(\xi\alpha_{12}\alpha_2+2\alpha_{22}\xi(\eta-\alpha_1))}{\alpha_2} X(t)U(t) +$$

$$\tfrac{\alpha_{22}\xi^2}{\alpha_2} U^2(t),$$

$$G(X(t), U(t)) = \left((\alpha_{12}\alpha_2(\eta - \alpha_1) + \alpha_{11}\alpha_2^2 + \alpha_{22}(\eta - \alpha_1)^2) \tfrac{\eta-\alpha_1}{\xi\alpha_2} - \tfrac{\beta_{12}\alpha_2(\eta-\alpha_1)+\beta_{11}\alpha_2^2+\beta_{22}\xi^2}{\xi} \right) X^2(t) -$$

$$\left((\alpha_{12}\alpha_2 + 2\alpha_{22}(\eta - \alpha_1)) \tfrac{\eta-\alpha_1}{\alpha_2} - (\beta_{12}\alpha_2 + 2\beta_{22}(\eta - \alpha_1)) \right) X(t)U(t) + \left(\alpha_{22}\xi \tfrac{\eta-\alpha_1}{\alpha_2} - \beta_{22}\xi \right) U^2(t).$$

In order for (5.3)-(5.4) to undergo a Neimark-Sacker bifurcation, the following discriminatory quantity must be nonzero, (i.e, $L \neq 0$ [33]),

$$L = -\Re\left[\frac{(1-2\overline{\lambda})\overline{\lambda}^2}{1-\lambda}\tau_{11}\tau_{20}\right] - \frac{1}{2} \mid \tau_{11} \mid^2 - \mid \tau_{02} \mid^2 + \Re(\overline{\lambda}\tau_{21}), \tag{5.32}$$

where

$$\tau_{02} = \frac{1}{4}\Bigg[\Bigg(\frac{\alpha_{12}\alpha_2(\eta-\alpha_1)+\alpha_{11}\alpha_2^2+\alpha_{22}(\eta-\alpha_1)^2}{\alpha_2}\Bigg) - \frac{\alpha_{22}\xi^2}{\alpha_2} + \Bigg((\xi\alpha_{12}\alpha_2 + 2\alpha_{22}\xi(\eta-\alpha_1))\frac{\eta-\alpha_1}{\xi\alpha_2} - \frac{(\xi\beta_{12}\alpha_2+2\beta_{22}\xi(\eta-\alpha_1))}{\xi}\Bigg) + i\Bigg(\Bigg((\alpha_{12}\alpha_2(\eta-\alpha_1)+\alpha_{11}\alpha_2^2+\alpha_{22}(\eta-\alpha_1)^2)\frac{\eta-\alpha_1}{\xi\alpha_2} + \frac{\beta_{12}\alpha_2(\eta-\alpha_1)+\beta_{11}\alpha_2^2+\beta_{22}(\eta-\alpha_1)^2}{\xi}\Bigg) - \Bigg(\alpha_{22}\xi\frac{\eta-\alpha_1}{\alpha_2} - \beta_{22}\xi\Bigg) + \Bigg(\frac{(\xi\alpha_{12}\alpha_2+2\alpha_{22}\xi(\eta-\alpha_1))}{\alpha_2}\Bigg)\Bigg)\Bigg],$$

$$\tau_{11} = \frac{1}{2}\Bigg[\Bigg(\frac{\alpha_{12}\alpha_2(\eta-\alpha_1)+\alpha_{11}\alpha_2^2+\alpha_{22}(\eta-\alpha_1)^2}{\alpha_2}\Bigg) + \frac{\alpha_{22}\xi^2}{\alpha_2} + i\Bigg(\Bigg((\alpha_{12}\alpha_2(\eta-\alpha_1)+\alpha_{11}\alpha_2^2 + \alpha_{22}(\eta-\alpha_1)^2)\frac{\eta-\alpha_1}{\xi\alpha_2} + \frac{\beta_{12}\alpha_2(\eta-\alpha_1)+\beta_{11}\alpha_2^2+\beta_{22}(\eta-\alpha_1)^2}{\xi}\Bigg) + \Bigg(\alpha_{22}\xi\frac{\eta-\alpha_1}{\alpha_2} - \beta_{22}\xi\Bigg)\Bigg)\Bigg],$$

$$\tau_{20} = \frac{1}{4}\Bigg[\Bigg(\frac{\alpha_{12}\alpha_2(\eta-\alpha_1)+\alpha_{11}\alpha_2^2+\alpha_{22}(\eta-\alpha_1)^2}{\alpha_2}\Bigg) - \frac{\alpha_{22}\xi^2}{\alpha_2} - \Bigg((\xi\alpha_{12}\alpha_2 + 2\alpha_{22}\xi(\eta-\alpha_1))\frac{\eta-\alpha_1}{\xi\alpha_2} - \frac{(\xi\beta_{12}\alpha_2+2\beta_{22}\xi(\eta-\alpha_1))}{\xi}\Bigg) + i\Bigg(\Bigg((\alpha_{12}\alpha_2(\eta-\alpha_1)+\alpha_{11}\alpha_2^2+\alpha_{22}(\eta-\alpha_1)^2)\frac{\eta-\alpha_1}{\xi\alpha_2} + \frac{\beta_{12}\alpha_2(\eta-\alpha_1)+\beta_{11}\alpha_2^2+\beta_{22}(\eta-\alpha_1)^2}{\xi}\Bigg) - \Bigg(\alpha_{22}\xi^2\frac{\eta-\alpha_1}{\xi\alpha_2} - \frac{\beta_{22}\xi^2}{\xi}\Bigg) + \Bigg(\frac{(\xi\alpha_{12}\alpha_2+2\alpha_{22}\xi(\eta-\alpha_1))}{\alpha_2}\Bigg)\Bigg)\Bigg],$$

$$\tau_{21} = 0.$$

Based on the above analysis, we arrive to the following result on Neimark-Sacker bifurcation.

Theorem 5.3. *If the condition (5.29) holds and L defined in (5.32)is nonzero, then the evolutionary Ricker model (5.3)-(5.4) undergoes a Neimark-Sacker bifurcation at the positive fixed point* $(x(b_0), u(b_0))$ *when* b_0^* *changes in the small neighborhood of* $b_0 = \gamma$ *and* $(b_0, h, c_1, \sigma^2) \in (5.24)$ *Moreover, if* $L < 0$ *(*$L > 0$*) then an attracting (respectively repelling) invariant closed curve bifurcates from the fixed point* $(x(b_0), u(b_0))$ *for* $b_0 > \gamma$ *(respectively,* $b_0 < \gamma$ *).*

5.3.2 Period-doubling bifurcation about $(x(b_0), u(b_0))$

The system (5.3)-(5.4) admits a period-doubling bifurcation at the positive fixed point $(x(b_0), u(b_0))$ if b_0 varies in the small neighborhood of $b_0 = \kappa$ and $(b_0, h, c_1, \sigma^2) \in P_d$. Giving a perturbation b_0^* (where $b_0^* \ll 1$)

of the parameter b_0 in the neighborhood of $b_0 = \kappa$ to the system (5.3)-(5.4) we have

$$x(t+1) = (b_0 + b_0^*)x(t)\exp(-x(t))\exp(-\tfrac{u(t)^2}{2}) + h\,x(t) = f(x(t), u(t), b_0^*), \tag{5.33}$$

$$u(t+1) = u(t) + \sigma^2(b_0 + b_0^*)\exp(-\tfrac{u(t)^2}{2})\exp(-x(t))\frac{-u(t)+c_1x(t)}{(b_0+b_0^*)\exp(-\frac{u(t)^2}{2})\exp(-x(t))+h} = g(x(t), u(t), b_0^*). \tag{5.34}$$

Making the transformation $v(t) = x(t) - x(b_0)$, $w(t) = u(t) - u(b_0)$ to the system (5.33)-(5.34) and expanding it in Taylor series at $(v(t), w(t), b_0^*) = (0, 0, 0)$, then we have

$$v(t+1) = \alpha_1 v(t) + \alpha_2 w(t) + \alpha_{12} v(t)w(t) + \alpha_{11} v^2(t) + \alpha_{22} w^2(t) + \tag{5.35a}$$

$$\alpha_{13} b_0^* v(t) + \alpha_{23} b_0^* w(t) + \alpha_{123} b_0^* v(t)w(t) + \alpha_{113} b_0^* v^2(t) + \alpha_{223} b_0^* w^2(t),$$

$$w(t+1) = \beta_1 v(t) + \beta_2 w(t) + \beta_{12} v(t)w(t) + \beta_{11} v^2(t) + \beta_{22} w^2(t) + \tag{5.35b}$$

$$\beta_{13} b_0^* v(t) + \beta_{23} b_0^* w(t) + \beta_{123} b_0^* v(t)w(t) + \beta_{113} b_0^* v^2(t) + \beta_{223} b_0^* w^2(t),$$

where

$$
\begin{aligned}
\alpha_1 &= f_x(x(b_0), u(b_0), 0) = 1 - x(b_0)(1-h),\\
\alpha_2 &= f_u(x(b_0), u(b_0), 0) = -c_1(1-h)x^2(b_0),\\
\alpha_{12} &= f_{xu}(x(b_0), u(b_0), 0) = -(1-h)c_1 x(b_0)(1 + x(b_0)),\\
\alpha_{11} &= f_{xx}(x(b_0), u(b_0), 0) = (1-h)(-1 + \frac{x(b_0)}{2}),\\
\alpha_{22} &= f_{uu}(x(b_0), u(b_0), 0) = (-\frac{x(b_0)}{2} + \frac{c_1^2 x^3(b_0)}{2})(1-h),\\
\alpha_{13} &= f_{xb_0^*}(x(b_0), u(b_0), 0) = \exp(-\frac{u(b_0)^2}{2})\exp(-x(b_0))(1 - x(b_0)) + h,\\
\alpha_{23} &= f_{ub_0^*}(x(b_0), u(b_0), 0) = -\exp(-\frac{u(b_0)^2}{2})\exp(-x(b_0))c_1 x^2(b_0),\\
\alpha_{123} &= f_{xub_0^*}(x(b_0), u(b_0), 0) = -\exp(-\frac{u(b_0)^2}{2})\exp(-x(b_0))c_1 x(b_0)(1 + x(b_0)),\\
\alpha_{113} &= f_{xxb_0^*}(x(b_0), u(b_0), 0) = \exp(-\frac{u(b_0)^2}{2})\exp(-x(b_0))(-1 + \frac{x(b_0)}{2}),\\
\alpha_{223} &= f_{uub_0^*}(x(b_0), u(b_0), 0) = \exp(-\frac{u(b_0)^2}{2})\exp(-x(b_0))(-\frac{x(b_0)}{2} + \frac{c_1^2 x^3(b_0)}{2}),\\
\beta_1 &= g_x(x(b_0), u(b_0), 0) = \sigma^2(1-h)c_1,\\
\beta_2 &= g_u(x(b_0), u(b_0), 0) = 1 - \sigma^2(1-h),\\
\beta_{12} &= g_{xu}(x(b_0), u(b_0), 0) = \sigma^2 h(1-h)(1 - c_1^2 x(b_0)),\\
\beta_{11} &= g_{xx}(x(b_0), u(b_0), 0) = -\sigma^2 h(1-h)c_1,\\
\beta_{22} &= g_{uu}(x(b_0), u(b_0), 0) = \sigma^2 h(1-h)c_1 x(b_0),\\
\beta_{13} &= g_{xb_0^*}(x(b_0), u(b_0), 0) = \exp(-\frac{u^2(b_0)}{2})\exp(-x(b_0))\sigma^2 c_1 h,\\
\beta_{23} &= g_{ub_0^*}(x(b_0), u(b_0), 0) = -\sigma^2 h\exp(-\frac{u^2(b_0)}{2})\exp(-x(b_0)),\\
\beta_{123} &= g_{xub_0^*}(x(b_0), u(b_0), 0) = \sigma^2\exp(-\frac{u(b_0)^2}{2})\exp(-x(b_0))(2h^2 - h + c_1 x^2(b_0)(2 + h - 2h^2)),\\
\beta_{113} &= g_{xxb_0^*}(x(b_0), u(b_0), 0) = \sigma^2\exp(-\frac{u(b_0)^2}{2})\exp(-x(b_0))c_1 h(1-2h),\\
\beta_{223} &= g_{uub_0^*}(x(b_0), u(b_0), 0) = \sigma^2\exp(-\frac{u(b_0)^2}{2})\exp(-x(b_0))c_1 x(b_0)(3h - 4 + 2c_1 x(b_0)(1-h)).
\end{aligned}
$$

Applying technical algebraic transformation, the system (5.35) is reduced to

$$\begin{pmatrix} X(t+1) \\ U(t+1) \end{pmatrix} = \begin{pmatrix} -1 & 0 \\ 0 & \lambda_2 \end{pmatrix} \begin{pmatrix} X(t) \\ U(t) \end{pmatrix} + \begin{pmatrix} F_1(X(t), U(t), b_0^*) \\ G_1(X(t), U(t), b_0^*) \end{pmatrix}, \tag{5.36}$$

where

$$F_1(X(t),U(t),b_0^*) = \tfrac{1}{1+\lambda_2}\Big(\tfrac{\lambda_2-\alpha_1}{\alpha_2}(-\alpha_{12}\alpha_2(1+\alpha_1)+\alpha_{11}\alpha_2^2+\alpha_{22}(1+\alpha_1)^2)-(-\beta_{12}\alpha_2(1+\alpha_1)+ \tag{5.37}$$

$$\beta_{11}\alpha_2^2+\beta_{22}(1+\alpha_1)^2)\Big)X^2(t)+\tfrac{1}{1+\lambda_2}\Big(\tfrac{\lambda_2-\alpha_1}{\alpha_2}(\alpha_{113}\alpha_2^2+\alpha_{223}(1+\alpha_1)^2-\alpha_{123}\alpha_2(1+\alpha_1))-(\beta_{113}\alpha_2^2+$$

$$\beta_{223}(1+\alpha_1)^2-\beta_{123}\alpha_2(1+\alpha_1))\Big)X^2(t)b_0^*+\tfrac{1}{1+\lambda_2}\Big(\tfrac{\lambda_2-\alpha_1}{\alpha_2}(\alpha_{12}\alpha_2(\lambda_2-\alpha_1)+\alpha_{11}\alpha_2^2+\alpha_{22}(\lambda_2-\alpha_1)^2)-$$

$$(\beta_{12}\alpha_2(\lambda_2-\alpha_1)+\beta_{11}\alpha_2^2+\beta_{22}(\lambda_2-\alpha_1)^2)\Big)U^2(t)+\tfrac{1}{1+\lambda_2}\Big(\tfrac{\lambda_2-\alpha_1}{\alpha_2}(\alpha_{223}\alpha_2^2+\alpha_{223}(\lambda_2-\alpha_1)^2+\alpha_{123}\alpha_2$$

$$(\lambda_2-\alpha_1))-(\beta_{223}\alpha_2^2+\beta_{223}(\lambda_2-\alpha_1)^2+\beta_{123}\alpha_2(\lambda_2-\alpha_1))\Big)U^2(t)b_0^*+\tfrac{1}{1+\lambda_2}\Big(\tfrac{\lambda_2-\alpha_1}{\alpha_2}(\alpha_{12}\alpha_2$$

$$(\lambda_2-\alpha_1)-\alpha_{12}\alpha_2(1+\alpha_1)+2\alpha_{11}\alpha_2^2-2\alpha_{22}(1+\alpha_1)(\lambda_2-\alpha_1))-(\beta_{12}\alpha_2(\lambda_2-\alpha_1)-\beta_{12}\alpha_2(1+\alpha_1)+2\beta_{11}\alpha_2^2-$$

$$2\beta_{22}(1+\alpha_1)(\lambda_2-\alpha_1))\Big)X(t)U(t)+\tfrac{1}{1+\lambda_2}\Big(\tfrac{\lambda_2-\alpha_1}{\alpha_2}(2\alpha_{113}\alpha_2^2+2\alpha_{223}(1+\alpha_1)(\lambda_2-\alpha_1)+\alpha_{123}\alpha_2(\lambda_2-\alpha_1)-$$

$$\alpha_{123}\alpha_2(1+\alpha_1))-(2\beta_{113}\alpha_2^2+2\beta_{223}(1+\alpha_1)(\lambda_2-\alpha_1)+\beta_{123}\alpha_2(\lambda_2-\alpha_1)-\beta_{123}\alpha_2(1+\alpha_1))\Big)X(t)U(t)b_0^*+$$

$$\tfrac{1}{1+\lambda_2}\Big(\tfrac{\lambda_2-\alpha_1}{\alpha_2}(\alpha_{13}\alpha_2-\alpha_{23}(1+\alpha_1))-(\beta_{13}\alpha_2-\beta_{23}(1+\alpha_1))\Big)X(t)b_0^*+\tfrac{1}{1+\lambda_2}\Big(\tfrac{\lambda_2-\alpha_1}{\alpha_2}(\alpha_{13}\alpha_2+$$

$$\alpha_{23}(\lambda_2-\alpha_1))-(\beta_{13}\alpha_2+\beta_{23}(\lambda_2-\alpha_1))\Big)U(t)b_0^*,$$

and

$$G_1(X(t),U(t),b_0^*) = \tfrac{1}{1+\lambda_2}\Big(\tfrac{1+\alpha_1}{\alpha_2}(-\alpha_{12}\alpha_2(1+\alpha_1)+\alpha_{11}\alpha_2^2+\alpha_{22}(1+\alpha_1)^2)+(-\beta_{12}\alpha_2(1+\alpha_1)+ \tag{5.38}$$

$$\beta_{11}\alpha_2^2+\beta_{22}(1+\alpha_1)^2)\Big)X^2(t)+\tfrac{1}{1+\lambda_2}\Big(\tfrac{1+\alpha_1}{\alpha_2}(\alpha_{113}\alpha_2^2+\alpha_{223}(1+\alpha_1)^2-\alpha_{123}\alpha_2(1+\alpha_1))+(\beta_{113}\alpha_2^2+$$

$$\beta_{223}(1+\alpha_1)^2-\beta_{123}\alpha_2(1+\alpha_1))\Big)X^2(t)b_0^*+\tfrac{1}{1+\lambda_2}\Big(\tfrac{1+\alpha_1}{\alpha_2}(\alpha_{12}\alpha_2(\lambda_2-\alpha_1)+\alpha_{11}\alpha_2^2+\alpha_{22}(\lambda_2-\alpha_1)^2)+$$

$$(\beta_{12}\alpha_2(\lambda_2-\alpha_1)+\beta_{11}\alpha_2^2+\beta_{22}(\lambda_2-\alpha_1)^2)\Big)U^2(t)+\tfrac{1}{1+\lambda_2}\Big(\tfrac{1+\alpha_1}{\alpha_2}(\alpha_{223}\alpha_2^2+\alpha_{223}(\lambda_2-\alpha_1)^2+$$

$$\alpha_{123}\alpha_2(\lambda_2-\alpha_1)) + (\beta_{223}\alpha_2^2+\beta_{223}(\lambda_2-\alpha_1)^2+\beta_{123}\alpha_2(\lambda_2-\alpha_1))\Big)U^2(t)b_0^* + \tfrac{1}{1+\lambda_2}\Big(\tfrac{1+\alpha_1}{\alpha_2}(\alpha_{12}\alpha_2(\lambda_2-\alpha_1)-$$

$$\alpha_{12}\alpha_2(1+\alpha_1)+2\alpha_{11}\alpha_2^2-2\alpha_{22}(1+\alpha_1)(\lambda_2-\alpha_1)) + (\beta_{12}\alpha_2(\lambda_2-\alpha_1)-\beta_{12}\alpha_2(1+\alpha_1)+2\beta_{11}\alpha_2^2-$$

$$2\beta_{22}(1+\alpha_1)(\lambda_2-\alpha_1))\Big)X(t)U(t) + \tfrac{1}{1+\lambda_2}\Big(\tfrac{1+\alpha_1}{\alpha_2}(2\alpha_{113}\alpha_2^2+2\alpha_{223}(1+\alpha_1)(\lambda_2-\alpha_1)+\alpha_{123}\alpha_2(\lambda_2-\alpha_1)-$$

$$\alpha_{123}\alpha_2(1+\alpha_1)) + (2\beta_{113}\alpha_2^2+2\beta_{223}(1+\alpha_1)(\lambda_2-\alpha_1)+\beta_{123}\alpha_2(\lambda_2-\alpha_1)-\beta_{123}\alpha_2(1+\alpha_1))\Big)X(t)U(t)b_0^*+$$

$$\tfrac{1}{1+\lambda_2}\Big(\tfrac{1+\alpha_1}{\alpha_2}(\alpha_{13}\alpha_2-\alpha_{23}(1+\alpha_1)) + (\beta_{13}\alpha_2-\beta_{23}(1+\alpha_1))\Big)X(t)b_0^*+$$

$$\frac{1}{1+\lambda_2}\Big(\frac{1+\alpha_1}{\alpha_2}(\alpha_{13}\alpha_2+\alpha_{23}(1+\alpha_1)) + (\beta_{13}\alpha_2+\beta_{23}(1+\alpha_1))\Big)U(t)b_0^*.$$

We determine the center manifold $\mathcal{W}_c(0,0,0)$ of (5.36) about $(0,0,0)$ in a small neighborhood of b_0^*. By center manifold theorem, there exists a center manifold $\mathcal{W}_c(0,0,0)$ that can be represented as follows:

$$\mathcal{W}_c(0,0,0) = \{(X(t),U(t),b_0^*)>0,\ \ U(t)=h(X(t),b_0^*)=h_1X(t)^2+h_2X(t)b_0^*+h_3b_0^{*2}+O((\mid X(t)\mid+\mid b_0^*\mid)^2)\}, \tag{5.39}$$

where $O((\mid X(t)\mid+\mid b_0^*\mid)^2)$ is a function with order at least three in their variables $(X(t),b_0^*)$. Moreover, the center manifold must satisfy

$$h\Big(-X(t)+F_1(X(t),h(X(t),b_0^*)),b_0^*),b_0^*\Big)-\lambda_2h(X(t),b_0^*)-G_1(X(t),h(X(t),b_0^*),b_0^*)=0. \tag{5.40}$$

By equating coefficients of like powers to zero, we obtain

$$h_1=\tfrac{1}{1-\lambda_2^2}\Big(\tfrac{1+\alpha_1}{\alpha_2}(-\alpha_{12}\alpha_2(1+\alpha_1)+\alpha_{11}\alpha_2^2+\alpha_{22}(1+\alpha_1)^2)+(-\beta_{12}\alpha_2(1+\alpha_1)+\beta_{11}\alpha_2^2+\beta_{22}(1+\alpha_1)^2)\Big),$$

$$h_2=-\tfrac{1}{(1+\lambda_2)^2}\Big(\tfrac{1+\alpha_1}{\alpha_2}(\alpha_{13}\alpha_2-\alpha_{23}(1+\alpha_1))+(\beta_{13}\alpha_2-\beta_{23}(1+\alpha_1))\Big),$$

$$h_3=0.$$

Therefore, we consider the map which is the map (5.36) restricted to the center manifold $\mathcal{W}_c(0,0,0)$

$$f=X(t+1)=-X(t)+\varphi_1X(t)b_0^*+\varphi_2X^2(t)+\varphi_3X^2(t)b_0^*+\varphi_4X^3(t), \tag{5.41}$$

where

$$\varphi_1 = \frac{1}{1+\lambda_2}\Bigg(\frac{\lambda_2-\alpha_1}{\alpha_2}(\alpha_{13}\alpha_2-\alpha_{23}(1+\alpha_1))-(\beta_{13}\alpha_2-\beta_{23}(1+\alpha_1))\Bigg),$$

$$\varphi_2 = \frac{1}{1+\lambda_2}\Bigg(\frac{\lambda_2-\alpha_1}{\alpha_2}(-\alpha_{12}\alpha_2(1+\alpha_1)+\alpha_{11}\alpha_2^2+\alpha_{22}(1+\alpha_1)^2)-(-\beta_{12}\alpha_2(1+\alpha_1)+\beta_{11}\alpha_2^2+\beta_{22}(1+\alpha_1)^2)\Bigg),$$

$$\varphi_3 = \frac{1}{1+\lambda_2}\Bigg(\frac{\lambda_2-\alpha_1}{\alpha_2}(\alpha_{113}\alpha_2^2+\alpha_{223}(1+\alpha_1)^2-\alpha_{123}\alpha_2(1+\alpha_1))-(\beta_{113}\alpha_2^2+\beta_{223}(1+\alpha_1)^2-\beta_{123}\alpha_2(1+\alpha_1))\Bigg)+$$

$$h_2\frac{1}{1+\lambda_2}\Bigg(\frac{1+\alpha_1}{\alpha_2}(\alpha_{12}\alpha_2(\lambda_2-\alpha_1)-\alpha_{12}\alpha_2(1+\alpha_1)+2\alpha_{11}\alpha_2^2-2\alpha_{22}(1+\alpha_1)(\lambda_2-\alpha_1))+(\beta_{12}\alpha_2(\lambda_2-\alpha_1)-$$

$$\beta_{12}\alpha_2(1+\alpha_1)+2\beta_{11}\alpha_2^2-2\beta_{22}(1+\alpha_1)(\lambda_2-\alpha_1))\Bigg)+h_1\frac{1}{1+\lambda_2}\Bigg(\frac{\lambda_2-\alpha_1}{\alpha_2}(\alpha_{13}\alpha_2+$$

$$\alpha_{23}(\lambda_2-\alpha_1))-(\beta_{13}\alpha_2+\beta_{23}(\lambda_2-\alpha_1))\Bigg),$$

$$\varphi_4 = h_1\frac{1}{1+\lambda_2}\Bigg(\frac{\lambda_2-\alpha_1}{\alpha_2}(\alpha_{12}\alpha_2(\lambda_2-\alpha_1)-\alpha_{12}\alpha_2(1+\alpha_1)+2\alpha_{11}\alpha_2^2-2\alpha_{22}(1+\alpha_1)(\lambda_2-\alpha_1))-$$

$$(\beta_{12}\alpha_2(\lambda_2-\alpha_1)-\beta_{12}\alpha_2(1+\alpha_1)+2\beta_{11}\alpha_2^2-2\beta_{22}(1+\alpha_1)(\lambda_2-\alpha_1))\Bigg),$$

In order for the map (5.41) to undergo a period-doubling bifurcation, we require that the following discriminatory quantities are non-zero [22, 33]:

$$\pi_1 = \left(\frac{\partial^2 f}{\partial X(t)\partial b_0^*}+\frac{1}{2}\frac{\partial f}{\partial b_0^*}\frac{\partial^2 f}{\partial^2 X(t)}\right)|_{(0,0)}\neq 0,$$

$$\pi_2 = \left(\frac{1}{6}\frac{\partial^3 f}{\partial X(t)^3}+(\frac{1}{2}\frac{\partial^2 f}{\partial X(t)^2})^2\right)|_{(0,0)}\neq 0.$$

After calculating we get

$$\pi_1 = \varphi_1 \neq 0,$$

$$\pi_2 = \varphi_4 + \varphi_2^2 \neq 0.$$

Finally, we have the following theorem

Theorem 5.4. *If $\pi_2 \neq 0$, and $\pi_1 \neq 0$ the map (5.41) undergoes a period-doubling bifurcation about the* *unique positive fixed point $(x(b_0), u(b_0))$ when b_0^* varies in a small neighborhood of b_0. Moreover, if $\pi_2 > 0$ (resp $\pi_2 < 0$), then the period 2 points that bifurcate from $(x(b_0), u(b_0))$ are stable (unstable).*

5.4 Controlling chaos

In this section, we implement the state feedback control method. In this method, the chaotic system is converted into a piecewise linear system to attain an optimal controller that minimizes the upper bound and then solves the optimization problem under certain constraints [17]. To use this technique, we analyze the evolutionary system associated to the system (5.3)-(5.4)

$$x(t+1) = b_0 \exp(-\frac{u(t)^2}{2}) \exp(-x(t))x(t) + hx(t) - P(t), \tag{5.42}$$

$$u(t+1) = u(t) + \sigma^2 b_0 \exp(-\frac{u(t)^2}{2}) \exp(-x(t)) \frac{-u(t) + c_1 x(t)}{b_0 \exp(-\frac{u(t)^2}{2}) \exp(-x(t)) + h}. \tag{5.43}$$

Here, $P(t) = \alpha(x(t) - x(b_0)) + \beta(u(t) - u(b_0))$ is the feedback controlling force at the positive fixed point $(x(b_0), u(b_0))$ where α, β are feedback gains. b_0 belongs to some chaotic regions. The Jacobian matrix at $(x(b_0), u(b_0))$ is

$$J(x(b_0), u(b_0)) =$$

$$\begin{pmatrix} b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2})(1 - x(b_0)) + h - \alpha & -b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2}) c_1 x^2(b_0) - \beta \\ \frac{\sigma^2 b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2}) c_1}{b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2}) + h} & 1 - \sigma^2 \frac{b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2})}{b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2}) + h} \end{pmatrix}.$$

The corresponding characteristic equation is

$$\zeta^2 - \left[b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2})(1 - x(b_0)) + h - \alpha + 1 - \sigma^2 \frac{b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2})}{b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2}) + h} \right] \zeta + \tag{5.44}$$

$$\left[\left(b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2})(1 - x(b_0)) + h - \alpha \right) \left(1 - \sigma^2 \frac{b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2})}{b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2}) + h} \right) + \right.$$

$$\left. \frac{\sigma^2 b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2}) c_1}{b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2}) + h} \left(b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2}) c_1 x^2(b_0) + \beta \right) \right] = 0.$$

Let ζ_1 , ζ_2 are the eigenvalues of the characteristic (5.44) then sum and product of the roots is given by

$$\zeta_1 + \zeta_2 = b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2})(1 - x(b_0)) + h - \alpha + 1 - \sigma^2 \frac{b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2})}{b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2}) + h}, \tag{5.45}$$

$$\zeta_1\zeta_2 = \left(b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2})(1 - x(b_0)) + h - \alpha\right)\left(1 - \sigma^2 \frac{b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2})}{b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2}) + h}\right) + \tag{5.46}$$

$$\frac{\sigma^2 b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2})c_1}{b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2}) + h}\left(b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2})c_1 x^2(b_0) + \beta\right).$$

Lemma 5.4. *The system (5.42)-(5.43) is asymptotically stable if all the eigenvalues of the characteristic (5.44) lie in an open unit disc.*

The lines (5.47), (5.48) and (5.49) give the conditions for the eigenvalues to have absolute value less than 1. The triangular region bounded by these lines accommodates stable eigenvalues.

$$L_1 : -\left(1 - \sigma^2 \frac{b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2})}{b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2}) + h}\right)\alpha + \frac{\sigma^2 b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2})c_1}{b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2}) + h}\beta = \tag{5.47}$$

$$1 - \left(b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2})(1 - x(b_0)) + h\right)\left(1 - \sigma^2 \frac{b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2})}{b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2}) + h}\right) -$$

$$\frac{\sigma^2 b_0^2 \exp(-x(b_0) - \frac{u^2(b_0)}{2})^2 c_1^2 x^2(b_0)}{b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2}) + h},$$

$$L_2 : \sigma^2 \frac{b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2})}{b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2}) + h}\alpha + \frac{\sigma^2 b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2})c_1}{b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2}) + h}\beta = \tag{5.48}$$

$$\sigma^2 \frac{b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2})}{b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2}) + h}\left(b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2})(1 - x(b_0)) + h - 1\right) -$$

$$\frac{\sigma^2 b_0^2 \exp(-x(b_0) - \frac{u^2(b_0)}{2})^2 c_1^2 x^2(b_0)}{b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2}) + h},$$

$$L_3 : \left(\sigma^2 \frac{b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2})}{b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2}) + h} - 2\right)\alpha + \frac{\sigma^2 b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2})c_1}{b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2}) + h}\beta = \tag{5.49}$$

$$\left(\sigma^2 \frac{b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2})}{b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2}) + h} - 2\right)\left(b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2})(1 - x(b_0)) + h + 1\right) -$$

$$\frac{\sigma^2 b_0^2 \exp(-x(b_0) - \frac{u^2(b_0)}{2})^2 c_1^2 x^2(b_0)}{b_0 \exp(-x(b_0) - \frac{u^2(b_0)}{2}) + h}.$$

5.5 Numerical Study

In this section, we present some numerical simulations to verify our theoretical results. Choosing the following set of parameters

$$\sigma^2 = 0.8,\ c_1 = 2,\ h = 0.2.$$

We vary the value of b_0 accordingly. Fig. (5.1) shows the stable dynamics of the population and its trait, which converge to the positive fixed point (0.62, 1.24) for the initial condition $(x(0), u(0)) = (1, 1)$. The system (5.3)-(5.4) starts to lose its stability for $b_0 = 3$. As a result, the existence of an attracting closed invariant curve implies that the discrete-time model (5.3)-(5.4) undergoes a Neimark-Sacker bifurcation about (0.62, 1.24).

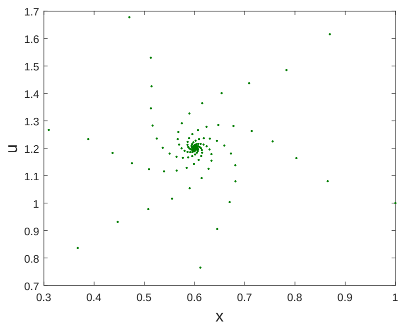


Figure 5.1: Phase portrait of the evolutionary (5.3)-(5.4) for $b_0 = 3$.

To see this if $b_0 > 3.29$, the model (5.3)-(5.4) becomes

$$x(t+1) = (3 + b_0^*)x(t)\frac{\exp(-\frac{u^2(t)}{2})}{1 + x(t)} + 0.2x(t), \tag{5.50}$$

$$u(t+1) = u(t) + 0.8(3 + b_0^*)\exp(-\frac{u(t)^2}{2})\exp(-x(t))\frac{-u(t) + 2x(t)}{(3 + b_0^*)\exp(-\frac{u(t)^2}{2})\exp(-x(t)) + 0.2}. \tag{5.51}$$

The value of L defined in (5.32) is $L = -0.20945448 < 0$. Hence, the model (5.50)-(5.51) undergoes a Neimark-Sacker bifurcation if $b_0 > 3$, and meanwhile, stable curve appears, as depicted in Fig.(5.2).

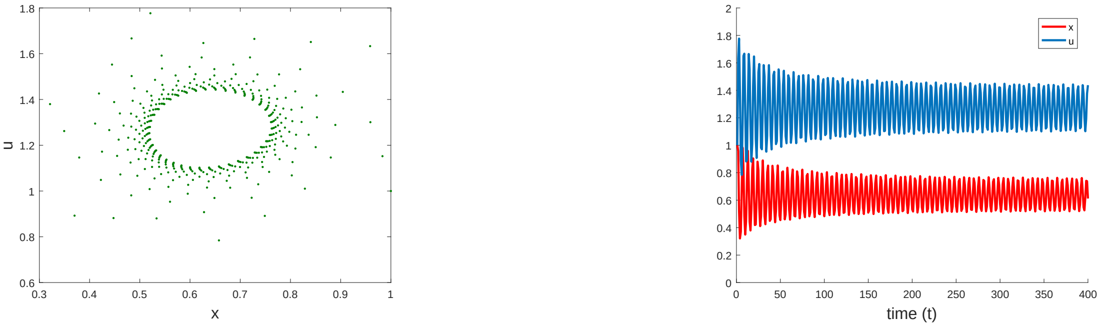
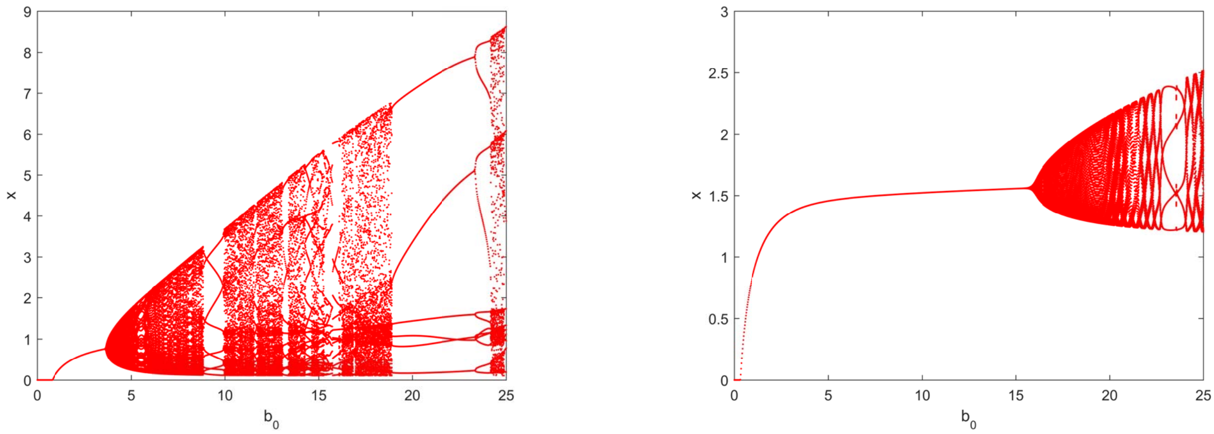


Figure 5.2: Phase portrait and time series of the evolutionary Ricker system (5.50)-(5.51) for $b_0 = 3.8$,

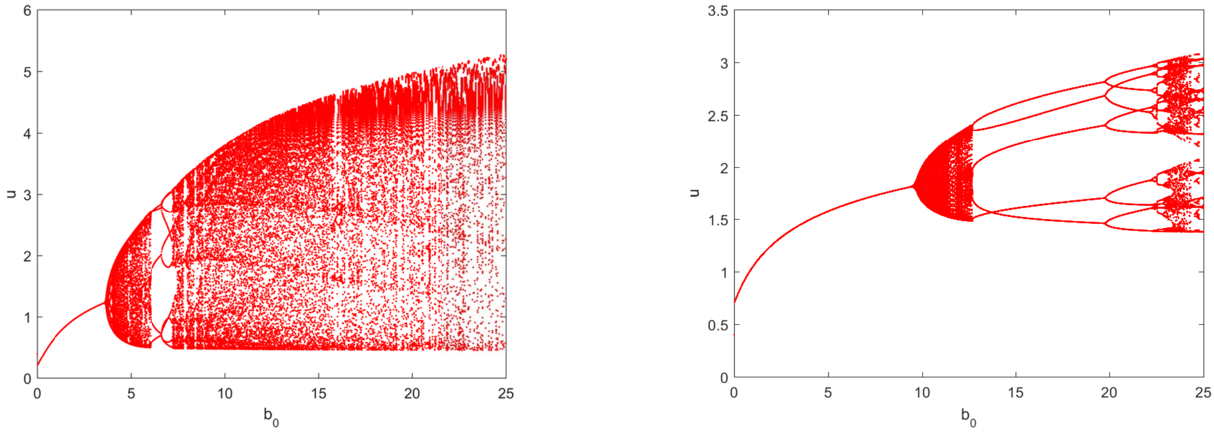
To explore the complexity of the system (5.3)-(5.4), bifurcation diagrams are plotted in Figs. (5.3)-(5.4)with respect to b_0 for two different value of h. The evolutionary system (5.3)-(5.4) exhibits a range of period-doubling route to chaos phenomenon for $b_0 \in (22.5, 25)$.



(a): $h = 0.2$

(d): $h = 0.7$

Figure 5.3: Diagram of bifurcations for system (5.50)-(5.51) of x with respect to b_0.



(a): $h = 0.2$ (d): $h = 0.7$

Figure 5.4: Diagram of bifurcations for system (5.50)-(5.51) of u with respect to b_0.

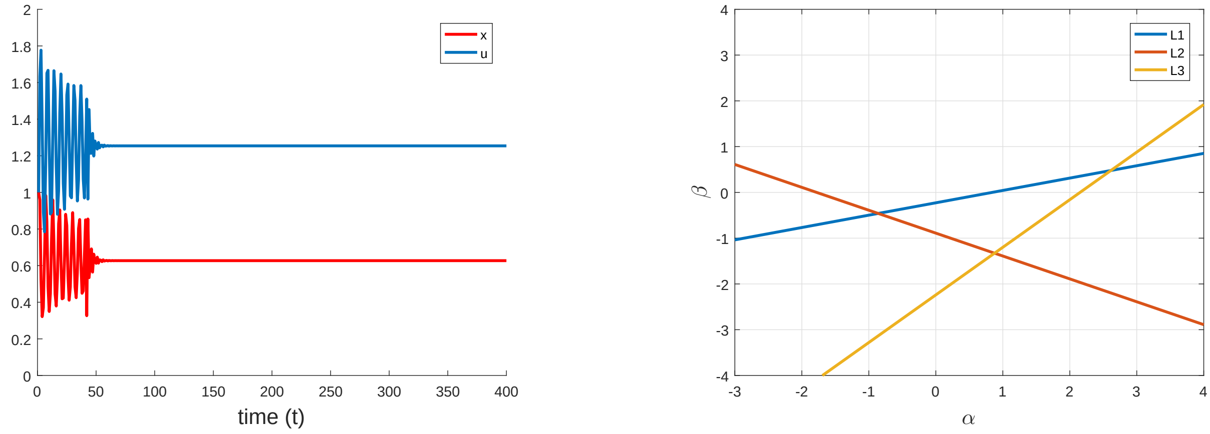
For the controlled method *state feedback control*, It is exhibited for $b_0 = 3.8$. As shown in Fig.(5.2) the system shows closed curve. In order to implement this method, lemma (5.4) gives the following lines of marginal stability of the system (5.42)-(5.43)

$$L_1: \; -0.352690278\alpha + 1.2946194445\beta = -0.294619445,$$

$$L_2: \; -0.647309722\alpha - 1.2946194445\beta = 1.153180741,$$

$$L_3: \; -1.352690278\alpha + 1.2946194445\beta = -2.90294468.$$

The system (5.42)-(5.43) is stable for the triangular region bounded by the marginal lines L_1, L_2 and L_3. Now, in order to make the unstable fixed point $(x(b_0), u(b_0)) = (0.67, 1.33)$ locally asymptotically stable, consider the feedback controlling force $P(t) = \alpha(x(t) - x(b_0)) + \beta(u(t) - u(b_0))$ with feedback gains are $\alpha = 2$, $\beta = 0.3$, chosen from the triangular region from Fig.(5.5)(a). For these values, a time series is drawn in Fig. (5.5)(b) which shows that the system (5.42)-(5.43) achieves stability and converges to the positive fixed point(0.62, 1.24).



(a) (b)

Figure 5.5: (a): stability region of the controlled system (5.42)-(5.43), In (b) the chaos is controlled after time $t = 40$.

CHAPTER

6

AN EVOLUTIONARY BEVERTON-HOLT MODEL UNDER IMMIGRATION EFFECT

6.1 Introduction

Through this Chapter, we consider the following evolutionary Beverton-Holt population model with immigration developed in [41].

$$x(t+1) = b_0 x(t) \frac{\exp(-\frac{u^2(t)}{2})}{1+x(t)} + hx(t), \tag{6.1}$$

$$u(t+1) = u(t) + \sigma^2 b_0 \exp(-\frac{u^2(t)}{2}) \frac{c_1 x(t) - u(t)(1+x(t))}{(1+x(t))^2 (\frac{b_0 \exp(-\frac{u^2(t)}{2})}{1+x(t)} + h)}. \tag{6.2}$$

The system (6.1)-(6.2) is built on the same ecological assumptions as the previous chapter (5). This model is based on the EGT approach and takes the immigration effect into consideration. The scientific question addressed in this chapter is to show how immigration affects on the evolutionary dynamics of the system (6.1)-(6.2).

This Chapter is organized as follows:

- Section 6.2 discusses the existence as well as dynamical behaviors of the positive fixed point of (6.1)-(6.2).

- In Section 6.3, different types of bifurcation are discussed, including period-doubling bifurcation and Neimark–Sacker bifurcation under certain conditions.

- In Section 6.4, two chaos control methods are employed to stabilize unstable orbits.

- In Section 6.5, some numerical simulations are performed to justify the theoretical results.

6.2 Properties of the positive fixed point

6.2.1 Existence of the positive fixed point

The isocline equations for (6.1)-(6.2) are

$$b_0 \exp(-\frac{u^2}{2}) = (1+x)(1-h), \tag{6.3}$$

and

$$0 = c_1 x - u(1+x). \tag{6.4}$$

The equations (6.3) and (6.4) can be written respectively as follows

$$u = \psi_1(x) = \sqrt{2 \ln \frac{b_0}{(1+x)(1-h)}}, \tag{6.5}$$

and

$$u = \psi_2(x) = \frac{c_1 x}{1+x}. \tag{6.6}$$

The map ψ_1 is defined in $[0, \frac{b_0}{1-h} - 1]$, where $b_0 > 1-h$. We have that $\psi_1(0) = \sqrt{2 \ln \frac{b_0}{1-h}} > 0$, and a direct differentiations yields

$$\psi_1'(x) = \frac{-1}{(1+x)\sqrt{2 \ln \frac{b_0}{(1+x)(1-h)}}} < 0.$$

Thus ψ_1 is strictly decreasing in $[0, \frac{b_0}{1-h} - 1]$. The map ψ_2 is defined in $\mathbb{R}^+$, we have $\psi_2(0) = 0$, a direct differentiation yields

$$\psi_2'(x) = \frac{c_1}{(1+x)^2}.$$

Therefore the map ψ_2 is strictly decreasing (increasing) if $c_1 < 0$ ($c_1 > 0$).

Setting $\psi_3(x) = \psi_1(x) - \psi_2(x)$, ψ_3 is defined in $[0, \frac{b_0}{1-h} - 1]$, differentiating ψ_3 with respect to x, one gets

$$\psi_3'(x) = \frac{-1}{(1+x)\sqrt{2\ln\frac{b_0}{(1+x)(1-h)}}} - \frac{c_1}{(1+x)^2} < 0. \tag{6.7}$$

The function ψ_3 is strictly decreasing if $c_1 > 0$, in $[0, \frac{b_0}{1-h} - 1]$. Now

$$\psi_3(0) = \psi_1(0) - \psi_2(0) = \sqrt{2\ln\frac{b_0}{1-h}} > 0, \tag{6.8}$$

and

$$\psi_3(\frac{b_0}{1-h} - 1) = \psi_1(\frac{b_0}{1-h} - 1) - \psi_2(\frac{b_0}{1-h} - 1) = -\frac{c_1(\frac{b_0}{1-h} - 1)}{\frac{b_0}{1-h} - 1} < 0. \tag{6.9}$$

By the theorem of Bolzano and the conditions (6.7)-(6.8) and (6.9), there exists a unique α in $]0, \frac{b_0}{1-h} - 1[$, such that $\psi_3(\alpha) = 0$ ie $\psi_1(\alpha) = \psi_2(\alpha)$. Therefore there exists a unique positive fixed point of the system (6.1)-(6.2), noted $P = (x^*, u^*)$. see Fig.(6.1).

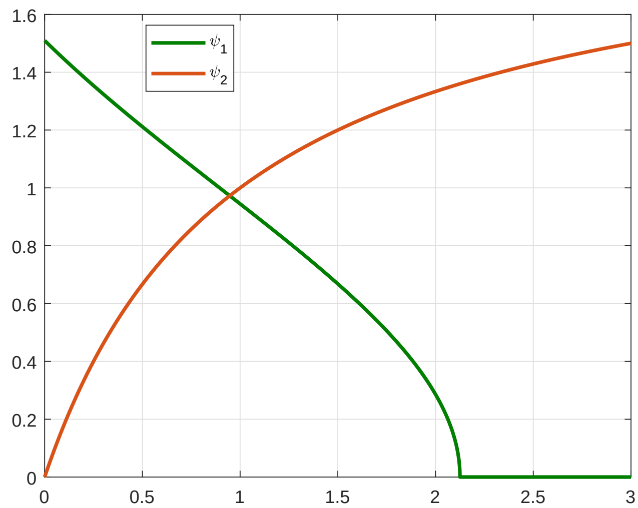


Figure 6.1: Existence of the unique positive fixed point for $b_0 = 2.5$, $h = 0.2$ and $c_1 = 2$.

6.2.2 Stability analysis of the positive fixed point P

The Jacobian matrix for the system (6.1)-(6.2) at any fixed point is

$$J(x,u) = \begin{pmatrix} j_{11} & j_{12} \\ j_{21} & j_{22} \end{pmatrix}, \tag{6.10}$$

where

$$j_{11} = b_0 \frac{\exp(-\frac{u^2}{2})}{(1+x)^2} + h, \quad j_{12} = -b_0 \frac{xu\exp(-\frac{u^2}{2})}{1+x},$$

$$j_{21} = \sigma^2 b_0 \exp(-u^2/2) \frac{(c_1-u)(1+x)^2 \left(b_0 \frac{\exp(-\frac{u^2}{2})}{(1+x)} + h\right) - \left(c_1 x - u(1+x)\right)\left(2(1+x)(b_0 \frac{\exp(-\frac{u^2}{2})}{(1+x)} + h) - b_0 \exp(-\frac{u^2}{2})\right)}{(1+x)^4 (b_0 \frac{\exp(-\frac{u^2}{2})}{(1+x)} + h)^2}$$

and

$$j_{22} = 1 + \sigma^2 b_0 \frac{\exp(-\frac{u^2}{2})}{(1+x)^2} \frac{-\left(u(c_1 x - u(1+x)) + (1+x)\right)\left(b_0 \frac{\exp(-\frac{u^2}{2})}{(1+x)} + h\right) + u b_0 \exp(-u^2)\left(\frac{c_1 x}{1+x} - u\right)}{(b_0 \frac{\exp(-\frac{u^2}{2})}{(1+x)} + h)^2}.$$

The matrix (6.10) evaluated at the positive fixed point P is

$$J(P) = \begin{pmatrix} \frac{1+hx^*}{1+x^*} & -\frac{c_1 x^{*2}}{1+x^*}(1-h) \\ \frac{\sigma^2 c_1 (1-h)}{(1+x^*)^2} & 1 - \sigma^2(1-h) \end{pmatrix}. \tag{6.11}$$

Then, the characteristic equation related to (6.11) is

$$S(\eta) = \eta^2 - A\eta + B, \tag{6.12}$$

where

$$A \doteq trJ(P) = \alpha_1 + h\alpha_2,$$

and

$$B \doteq \det J(P) = \alpha_3 h^2 + \alpha_4 h + \alpha_5,$$

with

$$\alpha_1 = \frac{1}{1+x^*} + 1 - \sigma^2,$$
$$\alpha_2 = \frac{x^*}{1+x^*} + \sigma^2,$$
$$\alpha_3 = \frac{\sigma^2 x^*}{1+x^*} + \frac{c_1^2\sigma^2 x^{*2}}{(1+x^*)^3},$$
$$\alpha_4 = \frac{\sigma^2 + x^* - \sigma^2}{1+x^*} - \frac{2c_1^2\sigma^2 x^{*2}}{(1+x^*)^3},$$
$$\alpha_5 = \frac{1-\sigma^2}{1+x^*} + \frac{c_1^2\sigma^2 x^{*2}}{(1+x^*)^3}.$$

The following proposition shows the local dynamics of the unique positive fixed point P.

Proposition 6.1. *Let P be the unique positive fixed point of system (6.1)-(6.2), and the following propositions hold:*

(a) *P is locally asymptotically stable if and only if*

1. $1 - \alpha_1 + \alpha_5 - h(\alpha_2 - \alpha_4) + \alpha_3 h^2 > 0,$
2. $1 + \alpha_1 + \alpha_5 + h(\alpha_2 + \alpha_4) + \alpha_3 h^2 > 0,$
3. $\alpha_3 h^2 + \alpha_4 h + \alpha_5 < 1.$

(b) *P is source if and only if*

1. $1 - \alpha_1 + \alpha_5 - h(\alpha_2 - \alpha_4) + \alpha_3 h^2 > 0,$
2. $1 + \alpha_1 + \alpha_5 + h(\alpha_2 + \alpha_4) + \alpha_3 h^2 > 0,$
3. $\alpha_3 h^2 + \alpha_4 h + \alpha_5 > 1.$

(c) *P is saddle if and only if*

1. $1 - \alpha_1 + \alpha_5 - h(\alpha_2 - \alpha_4) + \alpha_3 h^2 > 0,$
2. $1 + \alpha_1 + \alpha_5 + h(\alpha_2 + \alpha_4) + \alpha_3 h^2 < 0,$

(d) *P is non-hyperbolic if and only if*

1. $\mid A \mid < 2, \quad h = \frac{-\alpha_4 \pm \sqrt{\alpha_4^2 - 4\alpha_3(\alpha_5 - \alpha_1)}}{2\alpha_3}.$
2. $A < 0, \quad h = \frac{-(\alpha_2+\alpha_4) \pm \sqrt{(\alpha_2+\alpha_4)^2 - 4\alpha_3(1+\alpha_1+\alpha_5)}}{2\alpha_3}.$

If the non hyperbolic condition $(d)(1)$ of Proposition (6.1) holds, then the eigenvalues of P are a pair of complex conjugate numbers with modulus 1. Thus condition $(d)(1)$ of (6.1) can be written as

$$\mathcal{N}=\Big\{(b_0,h,c_1,\sigma^2)>0,\;\; b_0>1-h,\quad 0<h\leq 1,\quad \mid A\mid<2,\quad h=h_1=\frac{-\alpha_4\pm\sqrt{\alpha_4^2-4\alpha_3(\alpha_5-\alpha_1)}}{2\alpha_3}\Big\}. \tag{6.13}$$

Now, if the non hyperbolic condition $(d)(2)$ of Proposition (6.1) holds, then, one of the eigenvalues of P is -1 and the other is neither $\mid\eta_2\mid\neq 1$. Thus, the condition $(d)(2)$ of (6.1) can be written as

$$\mathcal{P}=\Big\{(b_0,h,c_1,\sigma^2)>0,\quad b_0>1-h,\quad 0<h\leq 1,\quad A<0, \tag{6.14}$$

$$h=h_2=\frac{-(\alpha_2+\alpha_4)\pm\sqrt{(\alpha_2+\alpha_4)^2-4\alpha_3(1+\alpha_1+\alpha_5)}}{2\alpha_3}\Big\}.$$

6.3 Bifurcation Analysis

6.3.1 Neimark-Sacker bifurcation at the positive fixed point P

The fixed point P is non hyperbolic at $h=h_1$. A Neimark–Sacker bifurcation occurs when the eigenvalues of the characteristic equation are complex conjugate with unit modulus ie $\mid\eta_1\mid=1$, $\mid\eta_2\mid=1$. Let us choose h as the bifurcation parameter. Giving a perturbation h_1^* of the parameter h in the neighborhood of $h=h_1$. The system can be written as

$$x(t+1)=b_0x(t)\frac{\exp(-\frac{u^2(t)}{2})}{1+x(t)}+(h+h_1^*)x(t), \tag{6.15}$$

$$u(t+1)=u(t)+\sigma^2b_0\exp(-\frac{u^2(t)}{2})\frac{c_1x(t)-u(t)(1+x(t))}{(1+x(t))^2(\frac{b_0\exp(-\frac{u^2(t)}{2})}{1+x(t)}+(h+h_1^*))}. \tag{6.16}$$

The roots of the characteristic equation associated to the jacobian matrix of (6.15)-(6.16) are

$$\mid\eta_{1,2}(h_1^*)\mid=\frac{A(h_1^*)\pm\sqrt{4B(h_1^*)-(A(h_1^*))^2}}{2},\quad \mid\eta_{1,2}\mid=\sqrt{B(h_1^*)},$$

when $h_1^*=0$, we have

$$B(0)=1,\qquad \frac{d\mid\eta_{1,2}\mid}{dh}\mid_{h=h_1^*}\neq 0. \tag{6.17}$$

Additionally, we required that when $h_1^* = 0$, $\eta_{1,2}^m \neq 1$, $m = 1,2,3,4$. This is equivalent to $A(0) \neq -2,-1,1,2$. By using the substitution $X(t) = x(t) - x^*$, $U(t) = u(t) - u^*$, the fixed point P is shifted to the origin by expanding the system (6.1)-(6.2) to the origin, one gets

$$\begin{pmatrix} X(t+1) \\ U(t+1) \end{pmatrix} \to \begin{pmatrix} \theta_{100}X(t) + \theta_{010}U(t) + \theta_{110}X(t)U(t) + \theta_{200}X^2(t) + \theta_{020}U^2(t), \\ \vartheta_{100}X(t) + \vartheta_{010}U(t) + \vartheta_{110}X(t)U(t) + \vartheta_{200}X^2(t) + \vartheta_{020}U^2(t) \end{pmatrix}, \tag{6.18}$$

where

$$\begin{aligned}
\theta_{100} &= \frac{1-h}{1+x^*} + h, \\
\theta_{010} &= -(1-h)u^*x^*, \\
\theta_{110} &= -(1-h)(-u^* + \frac{x^*u^*}{2}), \\
\theta_{200} &= -(1-h)\frac{1}{1+x^*}, \\
\theta_{020} &= (1-h)(-\frac{x^*}{2} + x^*u^{*2} + \frac{x^*}{(1+x^*)^2}), \\
\vartheta_{100} &= \frac{c_1\sigma^2(1-h)}{(1+x^*)^2}, \\
\vartheta_{010} &= 1 - \sigma^2(1-h), \\
\vartheta_{110} &= \frac{\sigma^2(1-h)}{1+x^*}\left(-2 + h + \frac{2x^* + 2 - c_1x^* - c_1^2x^* + (1-h)c_1^2x^*}{1+x^*} - \frac{(1-h)c_1^2x^{*2}}{(1+x^*)^2}\right), \\
\vartheta_{200} &= \frac{\sigma^2(1-h)\left(-2c_1 + 2u^* - (1-h)(u^* - c_1)\right)}{(1+x^*)^2}, \\
\vartheta_{020} &= \frac{\sigma^2(1-h)}{1+x^*}\left(u^* + x^*u^* - (1-h)(1+x^*)u^*\right).
\end{aligned}$$

We construct the invertible matrix

$$I = \begin{pmatrix} \theta_{010} & 0 \\ \mu - \theta_{100} & -\nu \end{pmatrix},$$

where $\mu = \frac{A}{2}$, $\nu = \frac{\sqrt{4B - A^2}}{2}$. By using the transformation

$$\begin{pmatrix} X(t) \\ U(t) \end{pmatrix} = I \begin{pmatrix} Y(t) \\ Z(t) \end{pmatrix},$$

the system (6.18) is reduced to

$$\begin{pmatrix} Y(t+1) \\ Z(t+1) \end{pmatrix} = \begin{pmatrix} \mu & -\nu \\ -\nu & \mu \end{pmatrix} \begin{pmatrix} Y(t) \\ Z(t) \end{pmatrix} + \begin{pmatrix} f(Y(t),Z(t)) \\ g(Y(t),Z(t)) \end{pmatrix},$$

where

$$f(Y(t),Z(t)) = \Big(\frac{\theta_{110}\theta_{010}(\mu-\theta_{100}) + \theta_{200}\theta_{010}^2 + \theta_{020}(\mu-\theta_{100})^2}{\theta_{010}}\Big)Y^2(t) +$$

$$\Big(\frac{-(\nu\theta_{110}\theta_{010} + 2\theta_{020}\nu(\mu-\theta_{100}))}{\theta_{010}}\Big)Y(t)Z(t) + \Big(\frac{\theta_{020}\nu^2}{\theta_{010}}\Big)Z^2(t),$$

and

$$g(Y(t),Z(t)) = \Big(\Big(\theta_{110}\theta_{010}(\mu-\theta_{100}) + \theta_{200}\theta_{010}^2 + \theta_{020}(\mu-\theta_{100})^2\Big)\frac{\mu-\theta_{100}}{\nu\theta_{010}} -$$

$$\frac{\vartheta_{110}\theta_{010}(\mu-\theta_{100}) + \vartheta_{200}\theta_{010}^2 + \vartheta_{020}(\mu-\theta_{100})^2}{\nu}\Big)Y^2(t) + \Big(-\Big(\nu\theta_{110}\theta_{010} + 2\theta_{020}\nu(\mu-\theta_{100})\Big)\frac{\mu-\theta_{100}}{\nu\theta_{010}} -$$

$$\frac{-(\nu\vartheta_{110}\theta_{010} + 2\vartheta_{020}\nu(\mu-\theta_{100}))}{\nu}\Big)Y(t)Z(t) + \Big(\theta_{020}\nu^2\frac{\mu-\theta_{100}}{\nu\theta_{010}} + \frac{\vartheta_{020}\nu^2}{\nu}\Big)Z^2(t),$$

The nondegeneracy condition for the Neimark–Sacker bifurcation is given by

$$\chi = -\Re[\frac{(1-2\overline{\eta})\overline{\eta}^2}{1-\eta}\varphi_{11}\varphi_{20}] - \frac{1}{2} \mid \varphi_{11} \mid^2 - \mid \varphi_{02} \mid^2 + \Re(\overline{\eta}\varphi_{21}), \tag{6.19}$$

where

$$\varphi_{11} = \frac{1}{2}\Big(\chi_1 + i\chi_2\Big),$$

$$\varphi_{02} = \frac{1}{4}\Big(\chi_3 + i\chi_4\Big),$$

$$\varphi_{20} = \frac{1}{4}\Big(\chi_5 + i\chi_6\Big),$$

$$\varphi_{21} = 0,$$

with

$$\chi_1 = \frac{\theta_{110}\theta_{010}(\mu-\theta_{100}) + \theta_{200}\theta_{010}^2 + \theta_{020}(\mu-\theta_{100})^2 + \theta_{020}\nu^2}{\theta_{010}},$$

$$\chi_2 = \Big(\theta_{110}\theta_{010}(\mu-\theta_{100}) + \theta_{200}\theta_{010}^2 + \theta_{020}(\mu-\theta_{100})^2\Big)\frac{\mu-\theta_{100}}{\nu\theta_{010}} + \frac{1}{\nu}\Big(\vartheta_{110}\theta_{010}(\mu-\theta_{100}) + \vartheta_{200}\theta_{010}^2 +$$

$$\vartheta_{020}(\mu-\theta_{100})^2\Big) + \Big(\theta_{020}\nu^2\frac{\mu-\theta_{100}}{\nu\theta_{010}} + \frac{\vartheta_{020}\nu^2}{\nu}\Big),$$

$$\chi_3 = \frac{\theta_{110}\theta_{010}(\mu-\theta_{100}) + \theta_{200}\theta_{010}^2 + \theta_{020}(\mu-\theta_{100})^2}{\theta_{010}-\theta_{020}\nu^2} + \Big(\nu\theta_{110}\theta_{010} + 2\theta_{020}\nu(\mu-\theta_{100})\Big)\frac{\mu-\theta_{100}}{\nu\theta_{010}} +$$

$$\frac{1}{\nu}\Big(\nu\vartheta_{110}\theta_{010} + 2\vartheta_{020}\nu(\mu-\theta_{100})\Big),$$

$$\chi_4 = \Big(\theta_{110}\theta_{010}(\mu-\theta_{100}) + \theta_{200}\theta_{010}^2 + \theta_{020}(\mu-\theta_{100})^2\Big)\frac{\mu-\theta_{100}}{\nu\theta_{010}} - \Big(\theta_{020}\nu^2\frac{\mu-\theta_{100}}{\nu\theta_{010}} + \frac{\vartheta_{020}\nu^2}{\theta_{010}} +$$

$$\Big(\frac{-(\nu\theta_{110}\theta_{010} + 2\theta_{020}\nu(\mu-\theta_{100}))}{\nu}\Big),$$

$$\chi_5 = \frac{\theta_{110}\theta_{010}(\mu-\theta_{100}) + \theta_{200}\theta_{010}^2 + \theta_{020}(\mu-\theta_{100})^2}{\theta_{010}-\theta_{020}\nu^2} + \Big(\nu\theta_{110}\theta_{010} + 2\theta_{020}\nu(\mu-\theta_{100})\Big)\frac{\mu-\theta_{100}}{\nu\theta_{010}} +$$

$$\frac{1}{\nu}\Big(-(\nu\vartheta_{110}\theta_{010} + 2\vartheta_{020}\nu(\mu-\theta_{100}))\Big),$$

and

$$\chi_6 = \Big(\theta_{110}\theta_{010}(\mu-\theta_{100}) + \theta_{200}\theta_{010}^2 + \theta_{020}(\mu-\theta_{100})^2\Big)\frac{\mu-\theta_{100}}{\nu\theta_{010}} + \frac{1}{\nu}\Big(\vartheta_{110}\theta_{010}(\mu-\theta_{100}) +$$

$$\vartheta_{200}\theta_{010}^2 + \vartheta_{020}(\mu-\theta_{100})^2\Big) -$$

$$\Big(\theta_{020}\nu^2\frac{\mu-\theta_{100}}{\nu\theta_{010}} + \frac{\vartheta_{020}\nu^2}{\nu}\Big) - \Big(\frac{-(\nu\theta_{110}\theta_{010} + 2\theta_{020}\nu(\mu-\theta_{100}))}{\theta_{010}}\Big).$$

Now, we substitute the values of φ_{ij} in the above expression (6.19) and solve it for χ, one gets

$$\chi = \tfrac{1}{8((1-\mu)^2+\nu^2))}\Big[((1-2\mu)(\mu^2-\nu^2)+4\mu\nu^2)(\chi_1\chi_5-\chi_2\chi_6)-(2\nu(\mu^2-\nu^2)-2\nu\mu(1-2\mu)(\chi_2\chi_5+\chi_1\chi_6))\Big)\Big(1-\mu\Big)+$$

$$\Big((2\nu(\mu^2-\nu^2) - 2\mu\nu(1-2\mu))(\chi_1\chi_5 - \chi_2\chi_6) + ((1-2\mu)(\mu^2-\nu^2) + 4\nu^2\mu)(\chi_2\chi_5 + \chi_1\chi_4)\Big)\Big] \neq 0.$$

Thus, the aforementioned argument provides the following theorem for the occurrence of Neimark-Sacker bifurcation

Theorem 6.1. *The system (6.1)- (6.2) undergoes a Neimark-Sacker bifurcation if the condition (6.17) holds and $\chi \neq 0$ at P. Moreover an attracting (respectively, repelling) invariant closed curve appears at $h = h_1$ if $\chi < 0$ ($\chi > 0$).*

6.3.2 Period-doubling bifurcation at P

The conditions for occurrence of a period-doubling bifurcation is determined at the positive fixed point $P(x^*, u^*)$, it is non-hyperbolic as h passes through h_2 with eigenvalues as $\eta_1 = -1$ and $\eta_2 = 2-\sigma^2(1-h)+\frac{1+hx^*}{1+x^*}$, with $\mid \eta_2 \mid \neq \pm 1$, to explore the period doubling bifurcation, we choose h as a bifurcation parameter. Let us take $X(t) = x(t) - x^*$, $U(t) = u(t) - u^*$, $h_2^* = h - h_2$, h_2^* is sufficiently small. The positive fixed point P is shifted to the origin, and the right-hand side of the map (6.1)-(6.2) is expanded. We obtain

$$\begin{pmatrix} X(t+1) \\ U(t+1) \end{pmatrix} = \tag{6.20}$$

$$\begin{pmatrix} \theta_{100}X(t) + \theta_{010}U(t) + \theta_{110}X(t)U(t) + \theta_{200}X^2(t) + \theta_{020}U^2(t) + \theta_{101}X(t)h_2^*, \\ \vartheta_{100}X(t) + \vartheta_{010}U(t) + \vartheta_{110}X(t)U(t) + \vartheta_{200}X^2(t) + \vartheta_{020}U^2(t) + \vartheta_{101}X(t)h_2^* + \vartheta_{011}U(t)h_2^* + \\ \vartheta_{111}X(t)U(t)h_2^* + \vartheta_{201}X^2(t)h_2^* + \vartheta_{021}U^2(t)h_2^*. \end{pmatrix},$$

where

$$
\begin{aligned}
\theta_{100} &= \frac{1-h}{1+x^*} + h,\\
\theta_{010} &= -(1-h)u^*x^*,\\
\theta_{110} &= -(1-h)(-u^* + \frac{x^*u^*}{2}),\\
\theta_{200} &= -(1-h)\frac{1}{1+x^*},\\
\theta_{020} &= (1-h)(-\frac{x^*}{2} + x^*u^{*2} + \frac{x^*}{(1+x^*)^2}),\\
\theta_{101} &= 1,\\
\vartheta_{100} &= \frac{c_1\sigma^2(1-h)}{(1+x^*)^2},\\
\vartheta_{010} &= 1-\sigma^2(1-h),\\
\vartheta_{110} &= \frac{\sigma^2(1-h)}{1+x^*}\Bigg(-2+h+\frac{2x^*+2-c_1x^*-c_1^2x^*+(1-h)c_1^2x^*}{1+x^*} - \frac{(1-h)c_1^2x^{*2}}{(1+x^*)^2}\Bigg),\\
\vartheta_{200} &= \frac{\sigma^2(1-h)\Bigg(-2c_1+2u^*-(1-h)(u^*-c_1)\Bigg)}{(1+x^*)^2},\\
\vartheta_{020} &= \frac{\sigma^2(1-h)}{1+x^*}\Bigg(u^*+x^*u^*-(1-h)(1+x^*)u^*\Bigg),\\
\vartheta_{101} &= \frac{\sigma^2(1-h)}{1+x^*}(-c_1+u^*),\\
\vartheta_{011} &= 1+x^*,\\
\vartheta_{111} &= 1+c_1u^* - \frac{2x^*+2}{1+x^*} - u^*,\\
\vartheta_{201} &= \frac{2(c_1-u^*)}{1+x^*},\\
\vartheta_{021} &= -u^*(1+x^*).
\end{aligned}
$$

We take an invertible matrix, say M

$$
M = \begin{pmatrix} \theta_{010} & \theta_{010} \\ -\theta_{100}-1 & \eta-\theta_{100} \end{pmatrix},
$$

By using transformation

$$\begin{pmatrix} x_1(t) \\ u_1(t) \end{pmatrix} = M \begin{pmatrix} X(t) \\ U(t) \end{pmatrix},$$

the system (6.1)-(6.2) is reduced to

$$\begin{pmatrix} x_1(t+1) \\ u_1(t+1) \end{pmatrix} = \begin{pmatrix} -1 & 0 \\ 0 & \eta_2 \end{pmatrix} \begin{pmatrix} x_1(t) \\ u_1(t) \end{pmatrix} + \begin{pmatrix} f_1(x_1(t), u_1(t), h_2^*) \\ g_1(x_1(t), u_1(t), h_2^*) \end{pmatrix}, \tag{6.21}$$

where

$$\begin{aligned}
f_1(x_1(t), u_1(t), h_2^*) = \Bigg(& \frac{\eta_2 - \theta_{100}}{\theta_{010}(1+\eta_2)} \Big(\theta_{020}(\theta_{100}+1)^2 - \theta_{110}\theta_{010}(1+\theta_{100}) + \theta_{200}\theta_{010}^2 \Big) - \\
& \frac{1}{1+\eta_2} \Big(-\vartheta_{110}\theta_{010}(1+\theta_{100}) + \vartheta_{200}\theta_{010}^2 + \vartheta_{020}(1+\theta_{100})^2 \Big) \Bigg) x_1(t)^2 \\
& - \frac{1}{1+\eta_2} \Big(\vartheta_{201}\theta_{010}^2 + \vartheta_{021}(1+\theta_{100})^2 - \vartheta_{111}\theta_{010}(1+\theta_{100}) \Big) x_1^2(t) h_2^* + \\
\Bigg(\frac{\eta_2 - \theta_{100}}{\theta_{010}(1+\eta_2)} & \Big(\theta_{020}(\eta_2 - \theta_{100})^2 + \theta_{110}\theta_{010}(\eta_2 - \theta_{100}) + \theta_{200}\theta_{010}^2 \Big) - \frac{1}{1+\eta_2} \Big(\vartheta_{110}\theta_{010}(\eta_2 - \theta_1) + \vartheta_{200}\theta_{010}^2 + \\
& \vartheta_{020}(\eta_2 - \theta_{100})^2 \Big) \Bigg) u_1(t)^2 - \frac{1}{1+\eta_2} \Big(\vartheta_{021}\theta_{010}^2 + \vartheta_{021}(\eta_2 - \theta_{100})^2 + \vartheta_{111}\theta_{010}(\eta_2 - \theta_{100}) \Big) u(t)^2 h_2^* + \\
\Bigg(\frac{\eta_2 - \theta_{100}}{\theta_{010}(1+\eta_2)} & \Big(-2\theta_{020}(\eta_2 - \theta_{100})(\theta_{100}+1) + \theta_{110}\theta_{010}(\eta_2 - \theta_{100}) - \theta_{110}\theta_{010}(1+\theta_{100}) + 2\theta_{200}\theta_{010}^2 \Big) - \\
\frac{1}{1+\eta_2} & \Big(\vartheta_{110}\theta_{010}(\eta_2 - \theta_{100}) - \vartheta_{110}\theta_{010}(1+\theta_{100}) + 2\vartheta_{200}\theta_{010}^2 - 2\vartheta_{020}(1+\theta_{100})(\eta_2 - \theta_{100}) \Big) \Bigg) x_1(t) u_1(t) - \\
\frac{1}{1+\eta_2} & \Big(2\vartheta_{201}\theta_{010}^2 + 2\vartheta_{021}(1+\theta_{100})(\eta_2 - \theta_{100}) + \vartheta_{111}\theta_{010}(\eta_2 - \theta_{100}) - \vartheta_{111}\theta_{010}(1+\theta_{100}) \Big) x_1(t) u_1(t) h_2^* + \\
& \Bigg(\frac{\theta_{101}\theta_{010}(\eta_2 - \theta_{100})}{\theta_{010}(1+\eta_2)} - \frac{1}{1+\eta_2} \Big(\vartheta_{101}\theta_{010} - \vartheta_{011}(1+\theta_{100} \Big) \Bigg) x_1(t) h_2^* + \\
& \Bigg(\frac{\theta_{101}\theta_{010}(\eta_2 - \theta_{100})}{\theta_{010}(1+\eta_2)} - \frac{1}{1+\eta_2} \Big(\vartheta_{101}\theta_{010} + \vartheta_{011}(\eta_2 - \theta_{100}) \Big) \Bigg) u_1(t) h_2^*,
\end{aligned}$$

and

$$\begin{aligned}
g_1(x_1(t), u_1(t), h_2^*) = \Bigg(& \frac{1+\theta_{100}}{\theta_{010}(1+\eta_2)} \Big(\theta_{020}(\theta_{100}+1)^2 - \theta_{110}\theta_{010}(1+\theta_{100}) + \theta_{200}\theta_{010}^2 \Big) + \\
& \frac{1}{1+\eta_2} \Big(-\vartheta_{110}\theta_{010}(1+\theta_{100}) + \vartheta_{200}\theta_{010}^2 + \vartheta_{020}(1+\theta_{100})^2 \Big) \Bigg) x_1(t)^2 +
\end{aligned}$$

$$\frac{1}{1+\eta_2}\Big(\vartheta_{201}\theta_{010}^2+\vartheta_{021}(1+\theta_{100})^2-\vartheta_{111}\theta_{010}(1+\theta_{100})\Big)x_1^2(t)h_2^*+$$

$$\Big(\frac{1+\theta_{100}}{\theta_{010}(1+\eta_2)}\Big(\theta_{020}(\eta_2-\theta_{100})^2+\theta_{110}\theta_{010}(\eta_2-\theta_{100})+\theta_{200}\theta_{010}^2\Big)+\frac{1}{1+\eta_2}\Big(\vartheta_{110}\theta_{010}(\eta_2-\theta_1)+$$

$$\vartheta_{200}\theta_{010}^2+\vartheta_{020}(\eta_2-\theta_{100})^2\Big)\Big)u_1(t)^2+\frac{1}{1+\eta_2}\Big(\vartheta_{021}\theta_{010}^2+\vartheta_{021}(\eta_2-\theta_{100})^2+\vartheta_{111}\theta_{010}(\eta_2-\theta_{100})\Big)u^2(t)h_2^*+$$

$$\Big(\frac{1+\theta_{100}}{\theta_{010}(1+\eta_2)}\Big(-2\theta_{020}(\eta_2-\theta_{100})(\theta_{100}+1)+\theta_{110}\theta_{010}(\eta_2-\theta_{100})-\theta_{110}\theta_{010}(1+\theta_{100})+2\theta_{200}\theta_{010}^2\Big)+$$

$$\frac{1}{1+\eta_2}\Big(\vartheta_{110}\theta_{010}(\eta_2-\theta_{100})-\vartheta_{110}\theta_{010}(1+\theta_{100})+2\vartheta_{200}\theta_{010}^2-2\vartheta_{020}(1+\theta_{100})(\eta_2-\theta_{100})\Big)\Big)x_1(t)u_1(t)+$$

$$\frac{1}{1+\eta_2}\Big(2\vartheta_{201}\theta_{010}^2+2\vartheta_{021}(1+\theta_{100})(\eta_2-\theta_{100})+\vartheta_{111}\theta_{010}(\eta_2-\theta_{100})-\vartheta_{111}\theta_{010}(1+\theta_{100})\Big)x_1(t)u_1(t)h_2^*+$$

$$\Big(\frac{\theta_{101}\theta_{010}(1+\theta_{100})}{\theta_{010}(1+\eta_2)}+\frac{1}{1+\eta_2}\Big(\vartheta_{101}\theta_{010}-\vartheta_{011}(1+\theta_{100}\Big)\Big)x_1(t)h_2^*+$$

$$\Big(\frac{\theta_{101}\theta_{010}(1+\theta_{100})}{\theta_{010}(1+\eta_2)}+\frac{1}{1+\eta_2}\Big(\vartheta_{101}\theta_{010}+\vartheta_{011}(\eta_2-\theta_{100})\Big)\Big)u_1(t)h_2^*.$$

The center manifold is considered as

$$\mathcal{W}^c(0,0,0)=\Big\{(x_1(t),u_1(t),h_2^*)\in\mathbb{R}^3,\quad u_1(t)=\ell(x_1(t),h_2^*)=a_1x_1^2(t)+a_2x_1(t)h_2^*+a_3h_2^{*2},\tag{6.22}$$

$$\ell(0,0)=D\ell(0,0)=0\Big\}.$$

Then,

$$\ell\Big(-x_1(t)+f_1(x_1(t),\ell(x_1(t),h_2^*),h_2^*)\Big)-\eta_2\ell(x_1(t),h_2^*)-g_1\Big(x_1(t),\ell(x_1(t),h_2^*),h_2^*\Big)=0.\tag{6.23}$$

From (6.23), one gets

$$a_1=\frac{1}{1-\eta_2}\Big(\frac{1+\theta_{100}}{\theta_{010}(1+\eta_2)}\Big(\theta_{020}(\theta_{100}+1)^2-\theta_{110}\theta_{010}(1+\theta_{100})+\theta_{200}\theta_{010}^2\Big)+$$

$$\frac{1}{1+\eta_2}\Big(-\vartheta_{110}\theta_{010}(1+\theta_{100})+\vartheta_{200}\theta_{010}^2+\vartheta_{020}(1+\theta_{100})^2\Big)\Big)$$

,

$$a_2=-\frac{1}{(1+\eta_2)}\Big(\frac{\theta_{101}\theta_{010}(1+\theta_{100})}{\theta_{010}(1+\eta_2)}+\frac{1}{1+\eta_2}\Big(\vartheta_{101}\theta_{010}-\vartheta_{011}(1+\theta_{100}\Big)\Big),$$

$$a_3=0.$$

Therefore, the map (6.21), restricted to the center manifold, is given by

$$f = -x_1(t) + \ell_1 x_1^2(t) + \ell_2 x_1^2(t) h_2^* + \ell_3 x_1(t) h_2^* + \ell_4 x_1^3(t), \tag{6.24}$$

where

$$\ell_1 = \left(\frac{\eta_2 - \theta_{100}}{\theta_{010}(1+\eta_2)}\left(\theta_{020}(\theta_{100}+1)^2 - \theta_{110}\theta_{010}(1+\theta_{100}) + \theta_{200}\theta_{010}^2\right) - \frac{1}{1+\eta_2}\left(-\vartheta_{110}\theta_{010}(1+\theta_{100}) + \vartheta_{200}\theta_{010}^2 + \vartheta_{020}(1+\theta_{100})^2\right)\right),$$

$$\ell_2 = a_2\left(\frac{\eta_2 - \theta_{100}}{\theta_{010}(1+\eta_2)}\left(-2\theta_{020}(\eta_2-\theta_{100})(\theta_{100}+1) + \theta_{110}\theta_{010}(\eta_2-\theta_{100}) - \theta_{110}\theta_{010}(1+\theta_{100}) + 2\theta_{200}\theta_{010}^2\right) - \frac{1}{1+\eta_2}\left(\vartheta_{110}\theta_{010}(\eta_2-\theta_{100}) - \vartheta_{110}\theta_{010}(1+\theta_{100}) + 2\vartheta_{200}\theta_{010}^2 - 2\vartheta_{020}(1+\theta_{100})(\eta_2-\theta_{100})\right)\right) + \left(-\frac{1}{1+\eta_2}\left(\vartheta_{201}\theta_{010}^2 + \vartheta_{021}(1+\theta_{100})^2 - \vartheta_{111}\theta_{010}(1+\theta_{100})\right)\right) + a_1\left(\frac{\theta_{101}\theta_{010}(\eta_2-\theta_{100})}{\theta_{010}(1+\eta_2)} - \frac{1}{1+\eta_2}\left(\vartheta_{101}\theta_{010} + \vartheta_{011}(\eta_2-\theta_{100})\right)\right),$$

$$\ell_3 = \left(\frac{\theta_{101}\theta_{010}(\eta_2-\theta_{100})}{\theta_{010}(1+\eta_2)} - \frac{1}{1+\eta_2}\left(\vartheta_{101}\theta_{010} - \vartheta_{011}(1+\theta_{100}\right)\right),$$

$$\ell_4 = a_1\left(\frac{\eta_2 - \theta_{100}}{\theta_{010}(1+\eta_2)}\left(-2\theta_{020}(\eta_2-\theta_{100})(\theta_{100}+1) + \theta_{110}\theta_{010}(\eta_2-\theta_{100}) - \theta_{110}\theta_{010}(1+\theta_{100}) + 2\theta_{200}\theta_{010}^2\right) - \frac{1}{1+\eta_2}\left(\vartheta_{110}\theta_{010}(\eta_2-\theta_{100}) - \vartheta_{110}\theta_{010}(1+\theta_{100}) + 2\vartheta_{200}\theta_{010}^2 - 2\vartheta_{020}(1+\theta_{100})(\eta_2-\theta_{100})\right)\right).$$

In order to show that the system undergoes a period doubling bifurcation; it is required that the following discriminant β_1, β_2 must be non- zero, i.e.,

$$\beta_1 = \left(\frac{\partial^2 f}{\partial x_1(t)\partial h_2^*} + \frac{1}{2}\frac{\partial f}{\partial h_2^*}\frac{\partial^2 f}{\partial^2 x_1^2(t)}\right)|_{(0,0)} \neq 0,$$

$$\beta_2 = \left(\frac{1}{6}\frac{\partial^3 f}{\partial x_1(t)^3} + (\frac{1}{2}\frac{\partial^2 f}{\partial x_1^2(t)})^2\right)|_{(0,0)} \neq 0.$$

After calculating, we get

$$\beta_1 = \ell_3,$$

$$\beta_2 = \ell_4 + \ell_1^2.$$

From the above analysis we have the following theorem.

Theorem 6.2. *If $\beta_1,\ \beta_2 \neq 0$ and the parameter h_2^* varies in the small neighborhood of the point $(0,0)$, then the system (6.1)-(6.2) undergoes a period doubling bifurcation at the fixed point P. Moreover, the discriminant β_2 determines the stability of period 2 point i.e., if β_2 is positive (negative), then the period 2 points that bifurcates from the fixed point P are stable (unstable)*

6.4 Chaos control

This section is dedicated for implementation of chaos control methods to system (6.1)-(6.2). Two chaos methods are implemented to the system (6.1)-(6.2), hybrid control method based on parameter perturbation has been proposed in [18] to control the chaos influenced by period doubling bifurcation, and the second is new chaos hybrid control strategy of exponential type proposed by Din in [17] to control the chaos produced by Neimark-Sacker bifurcation.

We first apply the hybrid control method to system (6.1)-(6.2) to get the following control system:

$$x(t+1) = \zeta\left(b_0 x(t)\frac{\exp(-\frac{u^2(t)}{2})}{1+x(t)} + hx(t)\right) + (1-\zeta)x(t), \tag{6.25}$$

$$u(t+1) = \zeta\left(u(t) + \sigma^2 b_0 \exp(-\frac{u^2(t)}{2})\frac{c_1 x(t) - u(t)(1+x(t))}{(1+x(t))^2(\frac{b_0\exp(-\frac{u^2(t)}{2})}{1+x(t)} + h)}\right) + (1-\zeta)u(t), \tag{6.26}$$

where $0 < \zeta < 1$ is control parameter for the hybrid control method. The Jacobian matrix $J_\zeta(P(x^*,u^*))$ of system (6.25)-(6.26) at its unique positive fixed point $P(x^*,u^*)$ is given as follows:

$$J_\zeta(P(x^*,u^*)) = \begin{pmatrix} 1+\zeta\left(b_0\frac{\exp(-u^{*2}/2)}{(1+x^*)^2} + h - 1\right) & -\zeta b_0 \frac{x^* u^* \exp(-u^{*2}/2)}{1+x^*} \\ \zeta\frac{\sigma^2 b_0 \exp(-u^{*2}/2)(c_1-u^*)}{(1+x^*)^2(b_0\frac{\exp(-u*^2/2)}{(1+x^*)}+h)} & 1+\zeta\left(1-\sigma^2 b_0\frac{\exp(-u^{*2}/2)}{(1+x^*)(b_0\frac{\exp(-u^{*2}/2)}{(1+x^*)}+h)} - 1\right) \end{pmatrix}. \tag{6.27}$$

The characteristic polynomial for (6.27) is

$$\omega^2 - \left(1+\zeta\left(b_0\frac{\exp(-u^{*2}/2)}{(1+x^*)^2} + h - 1\right) + 1 + \zeta\left(1-\sigma^2 b_0\frac{\exp(-u^{*2}/2)}{(1+x^*)(b_0\frac{\exp(-u^{*2}/2)}{(1+x^*)}+h)} - 1\right)\right)\omega +$$

$$\left(1+\zeta\left(1-\sigma^2 b_0\frac{\exp(-u^{*2}/2)}{(1+x^*)(b_0\frac{\exp(-u^{*2}/2)}{(1+x^*)}+h)} - 1\right)\right)\left(1+\zeta\left(b_0\frac{\exp(-u^{*2}/2)}{(1+x^*)^2} + h - 1\right)\right) +$$

$$\zeta^2 b_0 \frac{xu\exp(-u^{*2}/2)}{1+x^*}\frac{\sigma^2 b_0\exp(-u^{*2}/2)(c_1-u^*)}{(1+x^*)^2(b_0\frac{\exp(-u^{*2}/2)}{(1+x^*)}+h)}.$$

Taking into account the controllability of system (6.25)-(6.26), the following Lemma is presented.

Lemma 6.1. *The positive fixed point P of system (6.25)-(6.26) is locally asymptotically stable if the following condition is satisfied:*

$$\left|2+\zeta\left(b_0\frac{\exp(-u^{*2}/2)}{(1+x^*)^2}+h-1\right)+\zeta\left(1-\sigma^2 b_0\frac{\exp(-u^{*2}/2)}{(1+x^*)(b_0\frac{\exp(-u^{*2}/2)}{(1+x^*)}+h)}-1)\right|<$$

$$1+\left(1+\zeta\left(1-\sigma^2 b_0\frac{\exp(-u^{*2}/2)}{(1+x^*)(b_0\frac{\exp(-u^{*2}/2)}{(1+x^*)}+h)}-1)\right)\left(1+\zeta\left(b_0\frac{\exp(-u^{*2}/2)}{(1+x^*)^2}+h-1\right)\right)+$$

$$\zeta^2 b_0\frac{x^*u^*\exp(-u^{*2}/2)}{1+x^*}\frac{\sigma^2 b_0\exp(-u^{*2}/2)(c_1-u^*)}{(1+x^*)^2(b_0\frac{\exp(-u^{*2}/2)}{(1+x^*)}+h)}<2.$$

Secondly, our goal is to control the chaos by using exponential type chaos control strategy, we obtain the following control system

$$x(t+1)=\exp(-\delta_1(x(t)-x^*))\left(b_0 x(t)\frac{\exp(-\frac{u^2(t)}{2})}{1+x(t)}+hx(t)\right), \tag{6.28}$$

$$u(t+1)=\exp(-\delta_2(u(t)-u^*))\left(u(t)+\sigma^2 b_0\exp(-\frac{u^2(t)}{2})\frac{c_1x(t)-u(t)(1+x(t))}{(1+x(t))^2(\frac{b_0\exp(-\frac{u^2(t)}{2})}{1+x(t)}+h)}\right), \tag{6.29}$$

where δ_1 and δ_2 are the control parameters for exponential control strategy. Controllability of the system (6.28)-(6.29) is related to the stability of the system at its positive fixed point P. The jacobian matrix $J_c(P)$ of the system (6.28)-(6.29) about P is

$$J_c(P(x^*,u^*))=\begin{pmatrix} -\delta_1\left(b_0x^*\frac{\exp(-u^{*2}/2)}{1+x^*}+hx^*\right)+b_0\frac{\exp(-u^{*2}/2)}{(1+x^*)^2}+h & -b_0\exp(-u^{*2}/2)\frac{c_1x^*}{(1+x^*)^2} \\ \frac{\sigma^2b_0(-u^{*2}/2)(c_1-u^*)}{(1+x^*)^2(b_0\frac{\exp(-u^{*2}/2)}{(1+x^*)}+h)} & -\delta_2u^*+1-\sigma^2b_0\frac{\exp(-u^{*2}/2)}{(1+x^*)(b_0\frac{\exp(-u^{*2}/2)}{(1+x^*)}+h)}\end{pmatrix}. \tag{6.30}$$

The characteristic polynomial for (6.30)is

$$\lambda^2-\Bigg(-\delta_1\left(b_0x^*\frac{\exp(-u^{*2}/2)}{1+x^*}+hx^*\right)+b_0\frac{\exp(-u^{*2}/2)}{(1+x^*)^2}+h+-\delta_2u^*+$$

$$1-\sigma^2b_0\frac{\exp(-u^{*2}/2)}{(1+x^*)(b_0\frac{\exp(-u^{*2}/2)}{(1+x^*)}+h)}\Bigg)\lambda+\Bigg(-\delta_1\Bigg(b_0x^*\frac{\exp(-u^{*2}/2)}{1+x^*}+$$

$$hx^*\Big) + b_0\frac{\exp(-u^{*2}/2)}{(1+x^*)^2} + h\Big)\Big(- \delta_2 u^* + 1 - \sigma^2 b_0 \frac{\exp(-u^{*2}/2)}{(1+x^*)(b_0\frac{\exp(-u^{*2}/2)}{(1+x^*)} + h)}\Big) +$$

$$b_0\exp(-u^{*2}/2)\frac{c_1 x^*}{(1+x^*)^2}\Big(\frac{\sigma^2 b_0(-u^{*2}/2)(c_1-u^*)}{(1+x^*)^2(b_0\frac{\exp(-u^{*2}/2)}{(1+x^*)}+h)}\Big).$$

Taking into account the controllability of system (6.28)-(6.29), the following Lemma is presented.

Lemma 6.2. *The Positive fixed point P of system (6.28)-(6.29) is a locally asymptotically stable if the following condition is satisfied:*

$$\Big| - \delta_1\Big(b_0 x^*\frac{\exp(-u^{*2}/2)}{1+x^*} + hx^*\Big) + b_0\frac{\exp(-u^{*2}/2)}{(1+x^*)^2} + h + -\delta_2 u^* + 1 - \sigma^2 b_0\frac{\exp(-u^{*2}/2)}{(1+x^*)(b_0\frac{\exp(-u^{*2}/2)}{(1+x^*)} + h)}\Big| < 1+$$

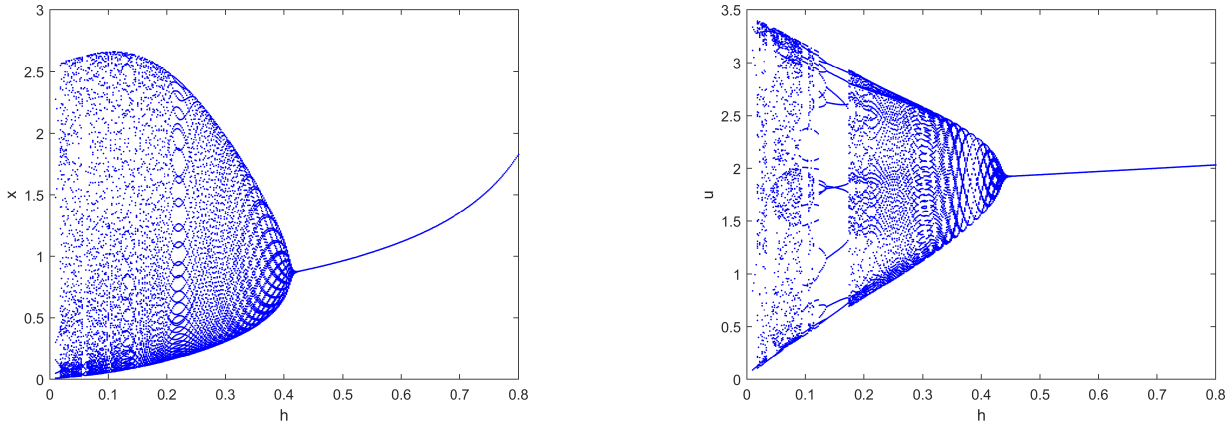
$$\Big(- \delta_1\Big(b_0 x^*\frac{\exp(-u^{*2}/2)}{1+x^*} + hx^*\Big) + b_0\frac{\exp(-u^{*2}/2)}{(1+x^*)^2} + h\Big)\Big(- \delta_2 u^* + 1 - \sigma^2 b_0\frac{\exp(-u^{*2}/2)}{(1+x^*)(b_0\frac{\exp(-u^{*2}/2)}{(1+x^*)} + h)}\Big) +$$

$$b_0\exp(-u^{*2}/2)\frac{c_1 x^*}{(1+x^*)^2}\Big(\frac{\sigma^2 b_0(-u^{*2}/2)(c_1-u^*)}{(1+x^*)^2(b_0\frac{\exp(-u^{*2}/2)}{(1+x^*)}+h)}\Big) < 2.$$

6.5 Numerical Simulations

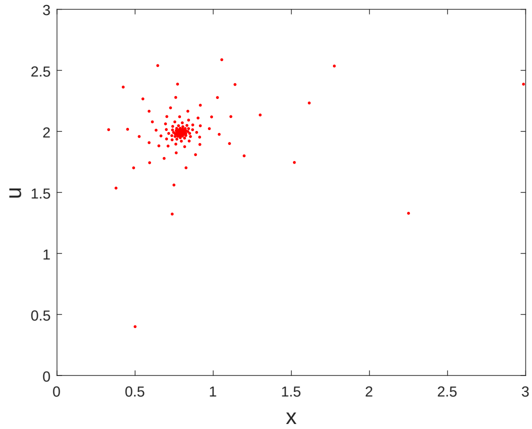
This section is committed to prove the presence of period-doubling bifurcation and Neimark-Sacker bifurcation for system (6.1)-(6.2) for specific numerical values of its parameters (b_1, h, c_1, σ^2) whereas we take h as bifurcation parameter. The verification of period-doubling and Neimark-Sacker bifurcation is demonstrated using bifurcation diagrams and phase portraits. In addition, hybrid control and exponential-type methods for chaos control are illustrate by numerical simulations.

Example 6.1. *First, we take $(b_0, c_1, \sigma^2) = (6.5, 4.5, 0.95)$, and the initial values $(x(0), u(0)) = (0.5, 0.5)$. The system (6.1)-(6.2) admits Neimark-Sacker bifurcation as h a bifurcation parameter $h = 0.43$. From bifurcation diagrams of both x and u see Fig.(6.2), one can observe that the fixed point $P = (0.8, 2)$ is stable for $h > 0.43$, and unstable at $h = 0.43$ and the Neimark-Sacker occurs for $h > 0.43$. This bifurcation diagram confirms the existence of chaotic behavior in system (6.1)-(6.2). Phase portraits are drawn for different value of h in Fig.(6.3). The value $\chi = 2.26560 > 0$ in theorem (6.1). This proves analytically the existence of Neimark-Sacker bifurcation.*

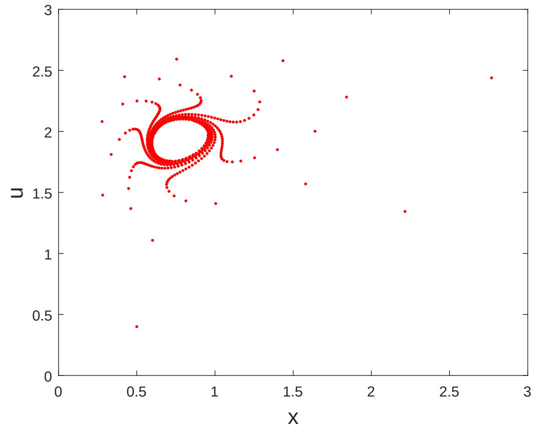


(a) (b)

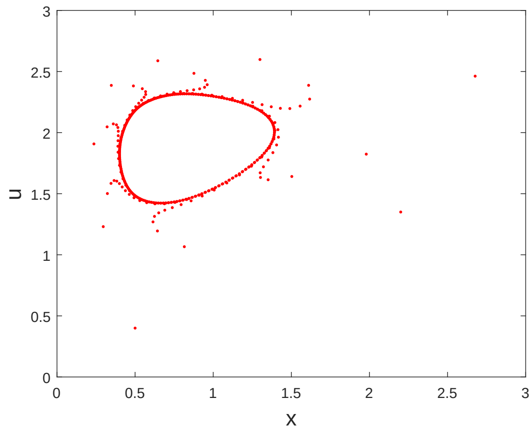
Figure 6.2: Bifurcation diagram for x and u with respect to h.



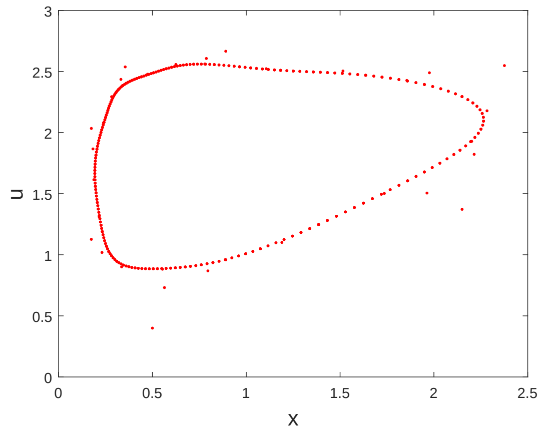
(a): $h = 0.5$



(b): $h = 0.43$



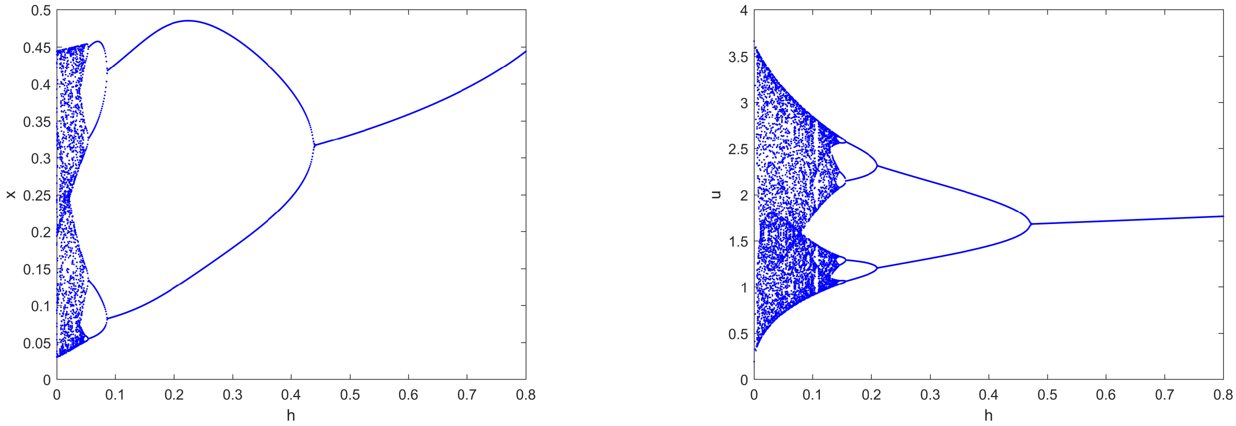
(c): $h = 0.4$



(d): $h = 0.3$

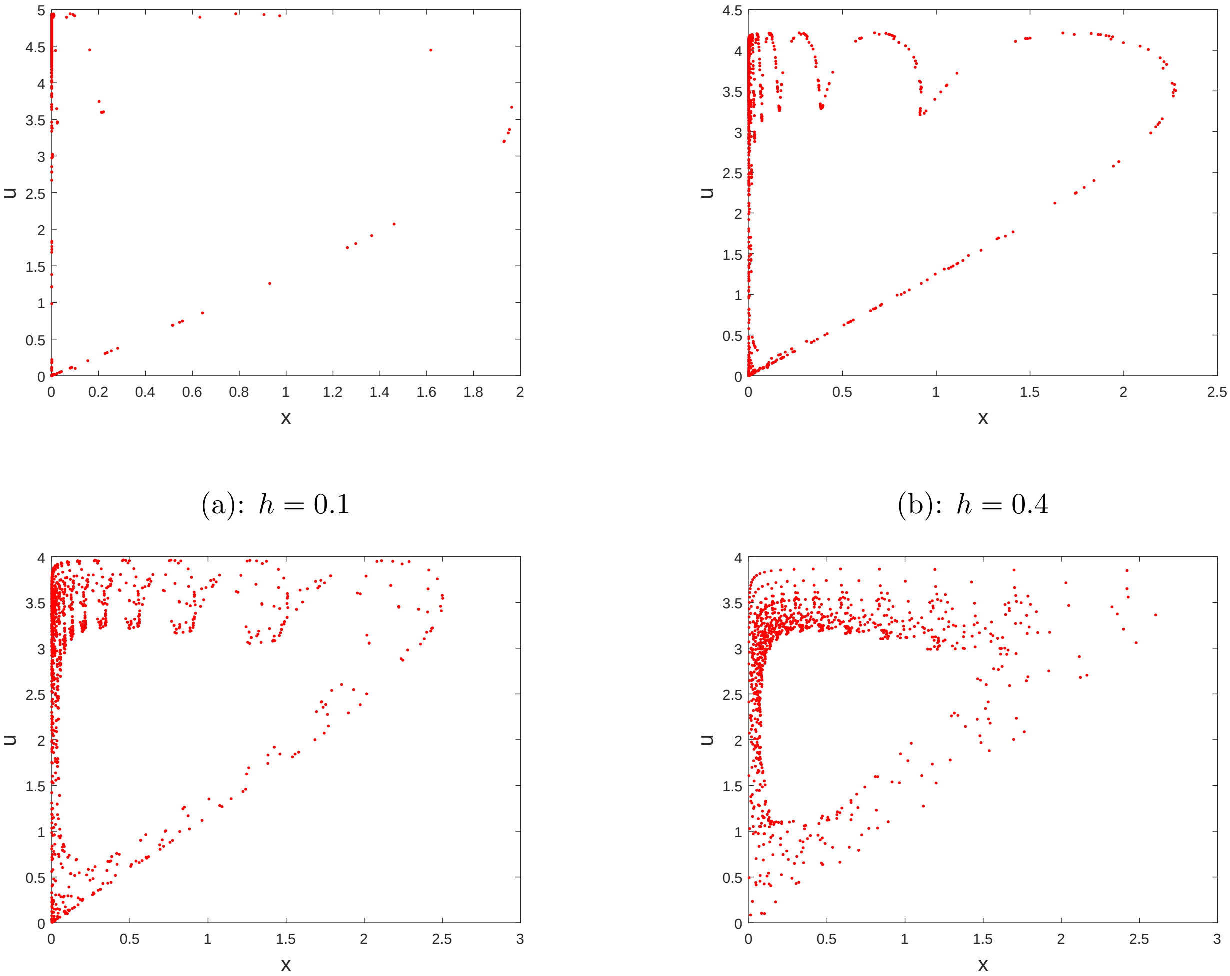
Figure 6.3: Phase portrait of the system (6.1)-(6.2) for $(b_0, c_1, \sigma^2) = (6.5, 4.5, 0.95)$, $(x(0), u(0)) = (0.5, 0.5)$ for different value of h.

Example 6.2. *Next, we choose $(b_0, c_1, \sigma^2) = (7, 10, 0.95)$, and the initial values $(x(0), u(0)) = (0.1, 0.1)$. Then system (6.1)-(6.2) admits period-doubling bifurcation as bifurcation parameter h changes in the small neighborhood of $h_2 = 0.46$. From bifurcation diagrams, drawn in (6.4), for $h_2 > 0.46$ the fixed point P is unstable at $h_2 = 0.46$ and period-doubling bifurcation occurs for $h_2 < 0.46$. This confirms the existence of chaotic behavior in system (6.1)-(6.2). Phase portraits associated to these values are drawn in Fig. (6.5).*



(a) (b)

Figure 6.4: Period doubling bifurcation of the system (6.1)-(6.2) of x and u with respect to h.



(a): $h = 0.1$ (b): $h = 0.4$

(c): $h = 0.6$ (d): $h = 0.8$

Figure 6.5: Phase portrait of the system (6.1)-(6.2) for $(b_0, c_1, \sigma^2) = (10, 7, 0.95)$, $(x(0), u(0)) = (0.1, 0.1)$ for different value of h.

Example 6.3. *For an application of the exponential chaos control technique for Neimark-Sacker bifurcation to the system (6.1)-(6.2), we select a value* $h_1 = 0.4$*, from chaotic region see Fig. (6.2)-(6.3) at* $(b_0, c_1, \sigma^2) = (6.5, 4.5, 0.95)$ *in this case, the fixed point* $P = (0.64, 2.28)$ *is source (unstable), hence the system (6.28)-(6.29) can be written as*

$$x(t+1) = \exp(-\delta_1(x(t) - 0.64))\left(6.5x(t)\frac{\exp(-\frac{u^2(t)}{2})}{1 + x(t)} + 0.4x(t)\right), \tag{6.31}$$

$$u(t+1) = \exp(-\delta_2(u(t) - 2.28))\left(u(t) + 6.175\exp(-\frac{u^2(t)}{2})\frac{4.5x(t) - u(t)(1 + x(t))}{(1 + x(t))^2(\frac{6.5\exp(-\frac{u^2(t)}{2})}{1+x(t)} + 0.4)}\right). \tag{6.32}$$

The fixed point is source because eigenvalue of system (6.1)-(6.2) are $\eta_1 = 0.5816 + 1.1523i$ *and* $\eta_2 = 0.5816 - 1.1523i$ *with* $\mid \eta_1 \mid = \mid \eta_2 \mid = 1.66 > 1$*. For this, we apply the exponential-type method to control chaos produced by Neimark-Sacker bifurcation. In order to see the controllability of system (6.28)-(6.29). The Jacobian matrix associated is*

$$J_c(0.64, 2.28) = \begin{pmatrix} -0.71097\delta_1 + 0.67150 & -0.78193 \\ 0.72557 & -2\delta_2 + 0.47758 \end{pmatrix}.$$

The characteristic polynomial for $J_c(0.64, 2.28)$ *is given by*

$$\lambda^2 - \left(0.71097\delta_1 - 2\delta_2 + 0.47758\right)\lambda + 1.42194\delta_1\delta_2 - 0.33949\delta_1 + 0.56735.$$

An application of Jury condition gives that system (6.28)-(6.29) is controllable if $\mid 0.71097\delta_1 - 2\delta_2 + 0.47758 \mid < 1.56735 + 1.42194\delta_1\delta_2 - 0.33949\delta_1 < 2$*, the controllable region in* δ_1 δ_2 *plane with exponential-type method is shown in* $6.6(a)$*, we choose a point inside this region, for instance (*$\delta_1 = 0.5, \delta_2 = -0.5$*), then the controlled system (6.28)-(6.29) converges to the fixed point after chaotic behavior, see Fig. (6.6)*$(c)-(d)$.

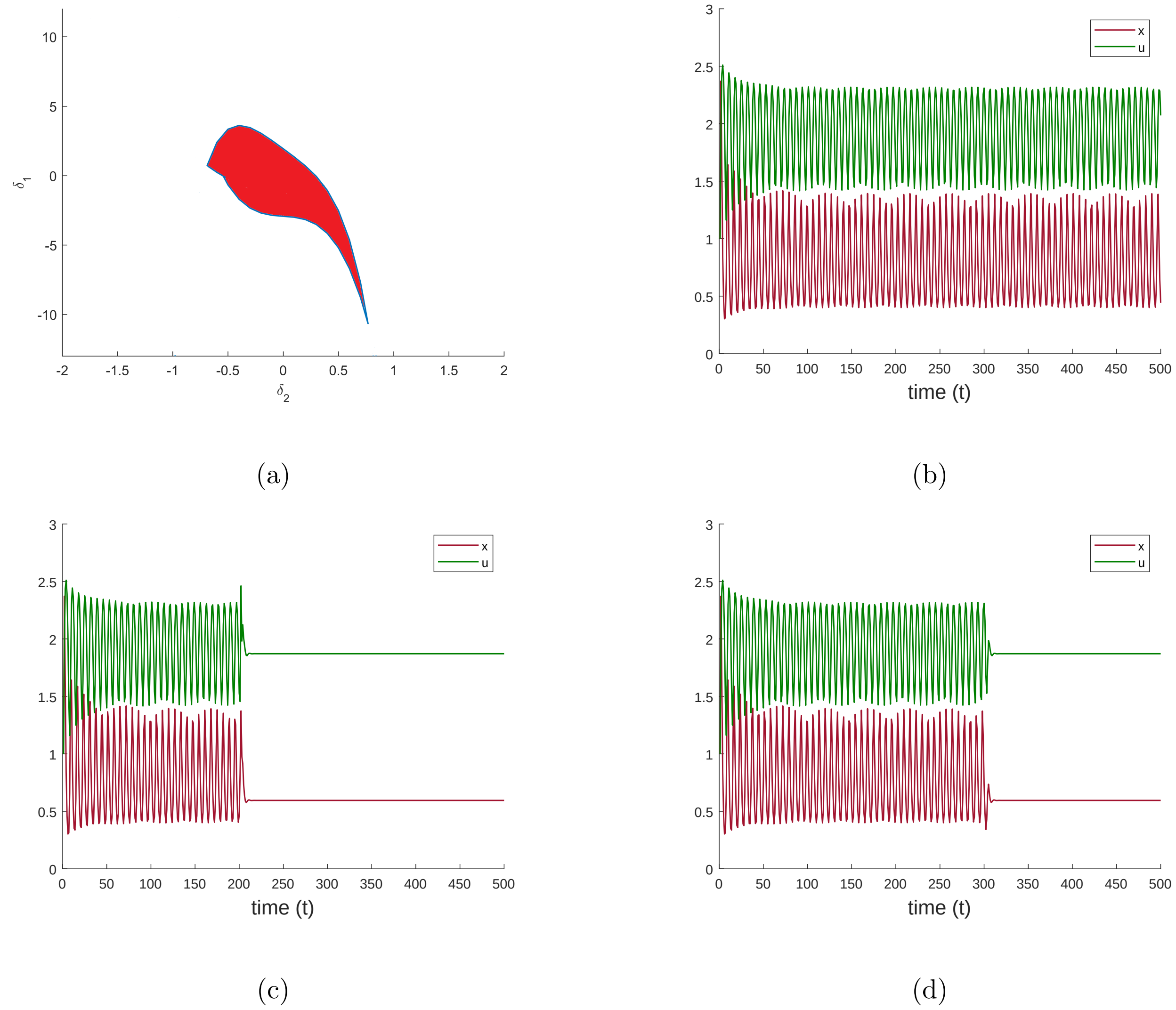


Figure 6.6: (a) Stability regions for system (6.28)-(6.29)with $(b_0, h, c_1, \sigma^2) = (6.5, 0.4, 4.5, 0.95)$; (b) Chaotic behavior; (c) the system (6.28)-(6.29) is controlled after 200 for (δ_1, δ_2) = (0.5,-0.5) taken from stability region 6.3; (d) the system (6.28)-(6.29) is controlled after 300.

Example 6.4. *For an application of the hybrid control technique for period-doubling bifurcation to the system (6.1)-(6.2), we select a value $h = 0.05$, from chaotic region see Fig. (6.4) at $(b_0, c_1, \sigma^2) = (7, 10, 0.95)$ in this case, the fixed point P is source, hence the system (6.25)-(6.26) can be written as*

$$x(t+1) = \zeta\left(7x(t)\frac{\exp(-\frac{u^2(t)}{2})}{1+x(t)} + 0.05x(t)\right) + (1-\zeta)x(t), \tag{6.33}$$

$$u(t+1) = \zeta\left(t) + 6.65\exp(-\frac{u^2(t)}{2})\frac{10x(t) - u(t)(1+x(t))}{(1+x(t))^2(\frac{7\exp(-\frac{u^2(t)}{2})}{1+x(t)} + 0.05)}\right) + (1-\zeta)u(t). \tag{6.34}$$

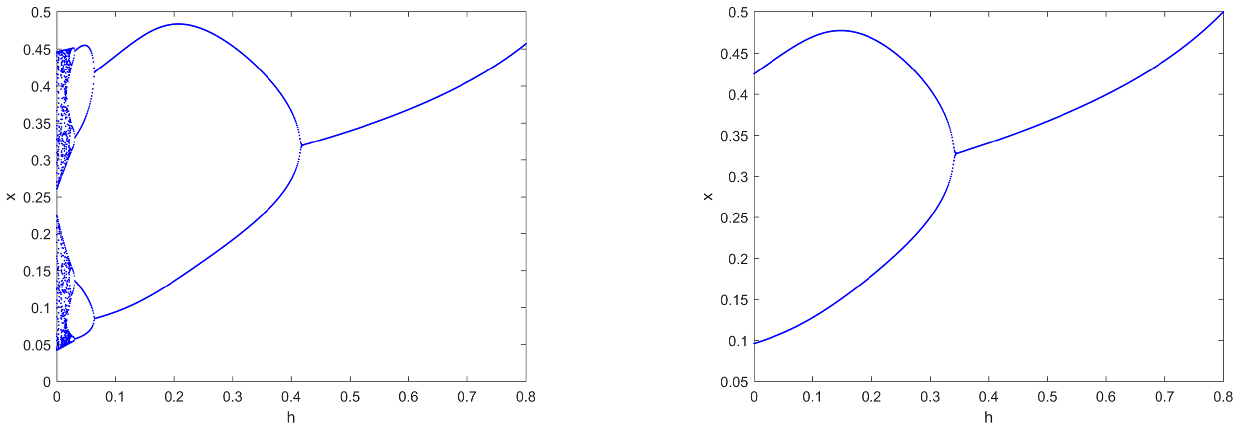
The jacobian matrix associated to (6.33)-(6.34) at $P = (0.34, 2.5)$ *is*

$$J_{\zeta}(P) = \begin{pmatrix} 1 - 0.778715\zeta & -0.1452359751\zeta \\ 4.366047\zeta & 1 - 0.780066\zeta \end{pmatrix}. \tag{6.35}$$

The characteristic equation associated to (6.35) is

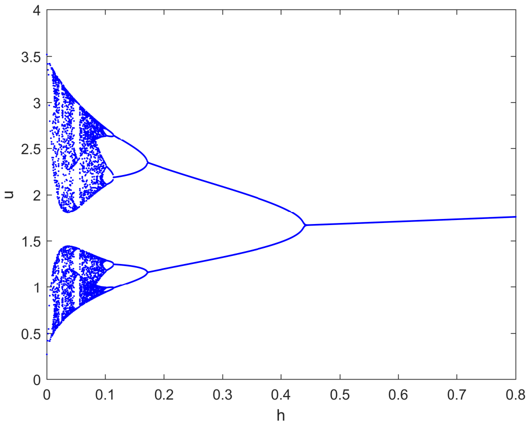
$$\omega^2 - \Big(2 - 1.558781\zeta\Big)\omega + 1 - 1.558781\zeta + 1.241551\zeta^2 = 0.$$

An application of Jury condition gives that system (6.33)-(6.34) is controllable if $\mid 2 - 1.558781\zeta \mid < 2 - 1.558781\zeta + 1.241551\zeta^2 < 2$, *for* $\zeta = 0.92$, *we have* $\mid 0.565921 \mid < 1.616770 < 2$. *Figs. (6.7)-(6.8) show the effect of hybrid control method on invading the chaotic region for* $\zeta = \{0.98, 0.92\}$.

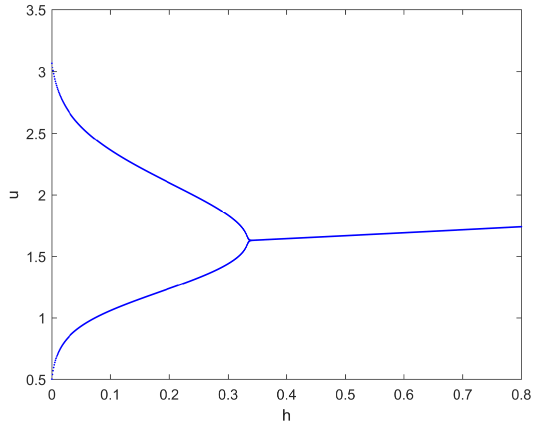


(a): $\zeta = 0.98$ (b): $\zeta = 0.92$

Figure 6.7: Bifurcation diagram for x with respect to h of the controlled system (6.25)-(6.26) for two different value of ζ.



(a): $\zeta = 0.98$



(b): $\zeta = 0.92$

Figure 6.8: Bifurcation diagram for u with respect to h of the controlled system (6.25)-(6.26) for two different value of ζ.

CHAPTER

7

CONCLUSION & PERSPECTIVES

In this thesis, we have investigated the dynamical properties of some discrete evolutionary models that are derived using evolutionary game theory (EGT). The method EGT, which is used in this dissertation, is capable of modeling the interaction between population dynamics and evolutionary dynamics. We focused in Chapter 3 on the global asymptotic stability for a special class of single and multi-species population evolutionary models. The key to the analysis is the decoupling of the mean trait dynamics from the population dynamics. We embedded non-autonomous evolutionary models into autonomous difference systems using skew-product discrete dynamical systems.As a result, we were able to apply the well-developed theory of autonomous dynamical systems.

The third chapter, Chapter 4 investigates the local dynamics and the existence of bifurcation in two single-species evolutionary Beverton-Holt population models. A rigorous analysis of the Neimark-Sacker bifurcation is established, and the Allee effect is added to the modeling. Detailed numerical simulations are developed to validate our theoretical findings and show more complex dynamics. We showed that small values of the strong Allee effect may lead to the stability of the positive fixed point. Another interesting contribution in this chapter is the control of chaos produced by Neimark-Sacker bifurcation. More specifically, we utilized two different chaos strategies to restore asymptotic stability: the OGY method and the hybrid method. The provided numerical examples give evidence of the successful implementation of these methods. The OGY method restores the evolutionary system's asymptotic stability for a certain parameter range, while the hybrid control strategy works effectively.

Chapters 5 and 6 represent our first attempt to investigate the immigration effect on stabilizing and destabilizing evolutionary dynamics. A rigorous analysis of bifurcations is established based on bifurcation and center manifold theories. Several chaos-control strategies are employed to avoid chaotic behaviors.

In conclusion, the following points of emphasis will be considered challenging topics:

• The dynamical behavior of evolutionary models with multiple traits will be an interesting problem to investigate.

• The study of the coupled equation of the mean trait with the equation of the population is very challenging. Establishing global stability in this case will be part of our future research.

• The eradication and control of chaos are critical in discrete dynamical systems. As a result, the main question is to understand the mechanics that control the chaos produced by some emergent bifurcations and give the related biological and ecological explanations.

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