Theoretical and computer-aided stability examination of population dynamical systems

Outline of PhD Thesis

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1 Introduction

Population dynamics, which models the time variations of the size and composition of biological populations, has a history of several centuries and its development has extremely accelerated with the appearance of the possibility of computer simulations.

In the thesis we study the stability and bifurcation properties of two population dynamical models, and we delineate an algorithm for calculating attractors of dynamical systems which we created for the study of the two models as well as the computer program realizing the algorithm.

The thesis is based on the following publications of the author:

- Dénes, A., Neimark–Sacker bifurcation in a discrete dynamical model of population genetics, *Electronic Journal of Qualitative Theory of Differential Equations, Proc. 8th Coll. Qualitative Theory of Diff. Equ.*, No. 6. (2008), 1–10.
- Dénes, A., Hatvani, L., Stachó, L. L., Eventual stability properties in a non-autonomous model of population dynamics, *Nonlinear Analysis* **73** (2010) 650–659.
- Dénes, A., Makay, G., Attractors and basins of dynamical systems, *Electronic Journal of Qualitative Theory of Differential Equations*, No. 20. (2011), 1–11.

In this outline we use the same numbering and labeling as in the thesis.

2 The Tusnády model

Biological background

The genetic information of living beings is stored in the *chromosomes*. The segments of the chromosomes that determine the different properties are called *genes*, their different variants are called *alleles*, and their places in the chromosomes are called *loci*. The *genotype* is determined by the two alleles which are really present in the cell. The distribution of genotypes is mainly affected by *selection*, *mutation* and *recombination*. Selection means that different genotypes have different chances to create offspring. When a cell divides, the copying of the chromosomes is not always perfect: certain segments can change. This phenomenon is called mutation. During recombination the genes of the chromosome pairs change.

The model

Gábor Tusnády created a discrete population dynamical model which describes the change of the distribution of gametes from generation to generation taking into account selection, mutation and recombination. Let $x_k(r)$ denote the density of the k^{th} gamete in a given generation. The system of difference equations which describes the model is:

$$x_k(r+1) = \frac{\sum_{i,j=1}^{n} a(i,j,k)x_i(r)x_j(r)}{\sum_{i,j,k=1}^{n} a(i,j,k)x_i(r)x_j(r)},$$

where parameters $a(i,j,k)$ include selection, mutation and recombination.

In Chapter 2 of the dissertetion we investigate this model in the case of one locus and four alleles. Gábor Tusnády studied the accumulation points of the sequences obtained by iterating the mapping, and by computer experiments he found some cases in which the attractor of the system was not one point (i.e. no dynamical equilibrium arises amongst the distributions), but a periodic orbit or even a chaotic set. Gábor Tusnády asked whether this phenomenon could be established mathematically or was just caused by the errors of numerical approximation. In the continuous case the explanation of a similar phenomenon is the presence of a Hopf-bifurcation as it was shown in [6] by László Hatvani, Ferenc Toókos and Gábor Tusnády .

Neimark–Sacker bifurcation

Gábor Tusnády observed the above phenomenon during computer experiments in the following system:

$$x(r+1) = \begin{pmatrix} \frac{2084x_2x_4}{38x_1x_2+414x_2^2+2156x_1x_3+18x_2x_3+2100x_2x_4+226x_3x_4} \\ \frac{16x_2x_4+226x_3x_4}{38x_1x_2+414x_2^2+2156x_1x_3+18x_2x_3+2100x_2x_4+226x_3x_4} \\ \frac{38x_1x_2+18x_2x_3}{38x_1x_2+414x_2^2+2156x_1x_3+18x_2x_3+2100x_2x_4+226x_3x_4} \\ \frac{414x_2^2+2156x_1x_3}{38x_1x_2+414x_2^2+2156x_1x_3+18x_2x_3+2100x_2x_4+226x_3x_4} \end{pmatrix} \tag{3.1}$$

In the thesis we show that the appearance of periodic solutions observed by Gábor Tusnády can be established mathematically: it is caused by a Neimark–Sacker bifurcation. First we investigated the system using the program for calculating attractors delineated in Chapter 4. The figures obtained changing parameter $p = a(2,4,2) = a(4,2,2)$ suggest the presence of Neimark–Sacker-bifurcation: a closed curve arises from the stable fixed point of the system, while the fixed point gets unstable. The phenomenom when the dynamics of a system changes substantially at a small change of a parameter is called bifurcation. The meaning of Neimark–Sacker bifurcation is the following:

Definition 3.4. *Let us consider the paramater-depending discrete dynamical system*

$$x_{r+1} = F(x_r, \alpha), \quad F : \mathbb{R}^n \times \mathbb{R} \to \mathbb{R}^n$$

where F is smooth in x and α. Let $x = x_0$ be the non-hyperbolic fixed point of the system at $\alpha = \alpha_0$. The phenomenon when the eigenvalues of the Jacobian $\partial F/\partial x(x_0, \alpha)$ pass through the unit circle by changing parameter α is called Neimark–Sacker bifurcation.

The main result of Chapter 1 is the following theorem:

Theorem 3.5. *Tusnády's system (3.1) undergoes a supercritical Neimark–Sacker bifurcation at parameter value $p = 139.455$, i.e. a stable invariant curve bifurcates from a stable fixed point, while the fixed point becomes unstable.*

When we change the value of parameter p, a complex pair of eigenvalues of the Jacobian passes through the unit circle. To this complex pair of eigenvalues corresponds a two-dimensional unstable manifold of the fixed point. The invariant closed curve appears on this manifold. To prove that a bifurcation occurs at this parameter value we have to verify that the system satisfies some genericity conditions. Using monograph [9] we delineate the procedure that we can use to prove the nondegenericity of the system. First we formulate the general Neimark-Sacker bifurcation theorem for two-dimensional systems. In the case of systems with dimension higher than 2 essentially the same takes place: there exists a two-dimensional invariant manifold on which the system exhibits the bifurcation, while the behaviour off the manifold is “trivial”, as no bifurcation occurs there. In the thesis we delineate a method with the help of which – using the eigenvalues of the Jacobian and its transpose – we can “project” the system into the critical eigenspace. Finally, following the steps of the procedure we prove Theorem (3.5).

3 Computer-aided examination of attractors of dynamical systems

For the investigation of the model described in Chapter 3 we needed a program that is able to calculate and represent attractors and basins of dynamical systems. However, earlier program packages for the investigation of dynamical systems (e. g. [8], [13]) do not have such an algorithm, or their algorithms can lead to inaccuracies, and the programs were created a long time ago and they are difficult to use on today's computers. That is why we needed a new, more precise algorithm and a program based on the algorithm that is able to represent attractors of dynamical systems of arbitrary dimensions.

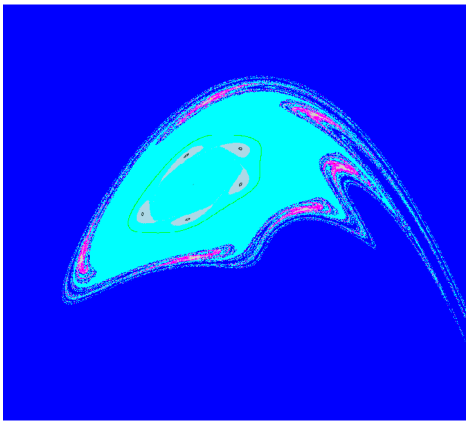
Our new algorithm is a substantial improvement of the procedure *Basins and Attractors* of *Dynamics*.

The algorithm

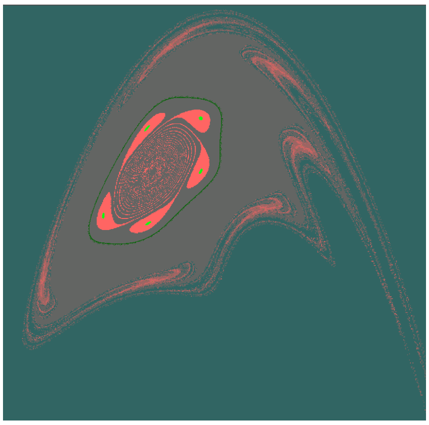
The principle of the algorithm is the following: we divide the n-dimensional domain under examination into equal n-dimensional boxes and from the center of each box we start a trajectory. In each step we examine the points near to our actual point (i.e. the points that fall into the same grid box or neighbouring grid boxes), and if we find a trajectory such that its iterates remain near to the iterates of our actual point for a given number of steps (i.e. the corresponding points fall into the same grid box or neighbouring grid boxes), we give a colour to the trajectory:

1. If the found point is a point of the actual trajectory, we give the trajectory the smallest odd colour not yet used and we also store the point which we first reencountered: from this point on we colour the trajectory with the colour of the attractor. Then we continue iterating long enough in order to find the complete attractor. To avoid identifying different parts of an attractor (lying far from each other) as different attractors, we make a test on this "new" attractor found. We compare the new attractor with all the previously found attractors: if they have enough common points, we verify whether these points remain near to each other after several iterations. If we discover a previously found attractor with this property, we give our actual trajectory the colours of this previously found attractor and basin.
2. If the found point is not a point of the actual trajectory, we give the colour of the found point to our actual trajectory.

At the end of the chapter we demonstrate the use of the program with figures representing the attractors of some well-known discrete dynamical systems and we give an example to show that our algorithm is able to draw precise attractors and basins even in cases where previous algorithms provide an imprecise picture.



1.a. The Bogdanov map (*Dynamics*)



1.b. The Bogdanov map

Djellit and Boukemara [2] have given imprecisely the attractors and basins of the Bogdanov map

$$x_1' = x_1 + 1.0025x_2 + 1.44x_1(x_1 - 1) - 0.1x_1x_2$$
$$x_2' = 1.0025x_2 + 1.44x_1(x_1 - 1) - 0.1x_1x_2,$$

and also *Dynamics* gives an imprecise picture for this system (Figure 1.a.). The figure made by or program (Figure 1.b.) shows the attractors and their basins precisely: according to the figure made by *Dynamics* the basin of the attractor formed by five light green points around the origin consists of five islands around the five points, however – as it is shown on the figure made by our program – this basin is also dense in the area inside the five islands. In the figure of *Dynamics* this area belongs to the basin of the green closed curve around the five points.

4 Eventual stability properties in a non-autonomous model of population dynamics

Description of the model

In Chapter 5 of the thesis we investigate a population dynamical model. The model describes the change of the amount of two fish species (a carnivore and a herbivore) living in Lake Tanganyika and the amount of the plants eaten by the herbivores. In Lake Tanganyika – extraordinarily in the world – carnivore fish have asymmetric faces: some of them have their mouths turned to the left, others to the right [12]. Fish with the mouth turned to the left attack their preys mainly from the left while the other group prefers to attack from the right. It was observed that the prey fish try to adapt to the distribution of left and right attacks against them. Their strategy is rather rigid: a given individual herbivore does not change his preference of paying more attention to attacks from the left or from the right during his life.

Let $\mathcal{I}$ and $\mathcal{K}$ denote two (finite) index sets representing the groups of herbivores and carnivores. Let $n_i = n_i(t)$ denote the number of herbivore fish of type $i \in \mathcal{I}$ at time t. Similarly, $m_k = m_k(t)$ denotes the number of carnivores belonging to group $k \in \mathcal{K}$ at time t.

The whole system of the nutrition chain consisting of plants, herbivores and carnivores is supported by the energy flow provided by the Sun. We assume that the intensity of this flow is constant, and furthermore we assume that the growth of the total mass of the plants due to the constant solar energy flow is C per time unit. Plants will be eaten by herbivores: we assume that an individual with weight w consumes the percentage $\alpha(w)$ from the total mass of plants during a time unit. We assume that each group $i \in \mathcal{I}$ consists of individuals with the same weight $w_i(t)$ at the time t and that each carnivore group $k \in \mathcal{K}$ consists of individuals with weight $u_k = u_k(t)$. By writing $K = K(t)$ for the total mass of plants at time t, our hypothesis concerning plants and herbivores can be formulated as follows:

$$\dot{K} = C - \sum_i n_i \alpha(w_i) K.$$

We assume that carnivores do not die during this time, thus their numbers $m_k(t)$ are constant in time, while the number of herbivores will be decreased by the carnivores. We assume that the various groups are homogeneously located in the lake and the number of attacks is proportional to their density. That is, with some constant ρ, in a time unit we have $\rho n_i m_k$ attacks by carnivores of type k against herbivores of type i. Concerning the outcome of such an attack, we assume that a herbivore from the group i with weight w will be eaten by a carnivore from the group k of weight u with a probability $\beta^{(i,k)}(w, u)$. Thus

$$\dot{n}_i = - \sum_k \rho \beta^{(i,k)}(w_i, u_k) n_i m_k.$$

Let $\gamma(e, w)$ denote the weight that a herbivore of weight w gains by eating e amount of plants. The weight that a carnivore loses without eating during a time unit is denoted by $\tilde{\gamma}(w)$. Thus

$$\dot{w}_i = \gamma(\alpha(w_i)K, w_i) - \tilde{\gamma}(w_i).$$

As we have assumed that during the period of development the carnivores do not die (they just lose weight), we have:

$$\dot{m}_k = 0.$$

Let $\delta(e, u)$ denote the weight that a carnivore of weight u gains by eating e amount of herbivores. The weight that a carnivore loses without eating during a time unit is denoted by $\tilde{\delta}(u)$. Thus

$$\dot{u}_k = \delta\left(\sum_i \rho\beta^{(i,k)}(w_i, u_k) w_i n_i m_k, u_k\right) - \tilde{\delta}(u_k).$$

After a series of simplifications and transformations the system gets the form:

$$\begin{aligned} \dot{L} &= C - LG, \\ \dot{G} &= (L - \lambda(t))G. \end{aligned} \tag{5.4}$$

Here L corresponds to the amount of plants, while G corresponds to the total amount of the herbivores.

This equation does not have an equilbrium, but it has a limit equation:

$$\begin{aligned} \dot{L} &= C - LG, \\ \dot{G} &= (L - \lambda^*)G, \end{aligned}$$

and the limit equation has the equilibrium $(\lambda^*, C/\lambda^*)$ where $\lambda^* = \lim_{t\to\infty} \lambda(t)$. In such cases usually the so-called eventual stability properties (Yoshizawa, [17]) are studied.

Consider a system of differential equations

$$\dot{x} = f(t, x), \tag{5.5}$$

with $f : \mathbb{R}^+ \times \Omega \to \mathbb{R}^n$, where $\mathbb{R}^+ = [0, \infty)$ and Ω is an open subset of $\mathbb{R}^n$; $0 \in \Omega$. Let $\|\cdot\|$ denote any norm in $\mathbb{R}^n$. Suppose that for every $t_0 \geq 0$ and $x_0 \in \Omega$ there exists a unique solution $x(t) = x(t; t_0, x_0)$ of equation (5.5) for $t \geq t_0$ satisfying the initial condition $x(t_0; t_0, x_0) = x_0$.

Definition 5.1. *$x = 0$ is an* eventually stable point *of* (5.5) *if for every $\varepsilon > 0$ and for every $t_0 \geq 0$ there exist $S(\varepsilon) \geq 0$ and $\delta(\varepsilon, t_0) > 0$ such that $t_0 \geq S(\varepsilon)$ and $\|x_0\| < \delta(\varepsilon, t_0)$ imply $\|x(t; t_0, x_0)\| < \varepsilon$ for all $t \geq t_0$. If $\delta = \delta(\varepsilon) > 0$ can be independent of t_0, then the eventual stability is* uniform.

Definition 5.2. $x = 0$ *is an* eventually asymptotically stable point of (5.5) in the large *if it is eventually stable point and every solution tends to zero, as* $t \to \infty$*.*

Definition 5.3. $x = 0$ *is an* eventually quasi-uniform-asymptotically stable point *of* (5.5) *in the large if for every compact set* $\Gamma \subset \Omega$ *and for every* $\gamma > 0$ *there are* $S(\Gamma, \gamma)$ *and* $T(\Gamma, \gamma) > 0$ *such that* $x_0 \in \Gamma$*,* $t_0 \geq S(\Gamma, \gamma)$ *and* $t \geq t_0 + T(\Gamma, \gamma)$ *imply* $\|x(t; t_0, x_0)\| < \gamma$*.*

Definition 5.4. $x = 0$ *is an* eventually uniform-asymptotically stable point of (5.5) in the large *if it is eventually uniform-stable and quasi-uniform-asymptotically stable in the large.*

Main result

Theorem 5.5. $(\lambda^*, C/\lambda^*)$ *is an eventually uniform-asymptotically stable point in the large of* (5.4)*.*

The proof of this theorem uses the theory of limiting equations.

A point $x^* \in \overline{\Omega}$ is said to be a *positive limit point* of a solution x of (5.5) if there exists a sequence $\{t_j\}$ such that $t_j \to \infty$ and $x(t_j) \to x^*$ as $j \to \infty$. The set of all positive limit points of x is called the *positive limit set* of x and is denoted by $\Lambda^+(x)$.

The *translate* of a function $f : \mathbb{R}^+ \times \Omega \to \mathbb{R}^n$ by $a > 0$ is defined as $f_a(t, x) := f(t+a, x)$. The function f is called *asymptotically autonomous* if there exists a function $f^* : \Omega \to \mathbb{R}^n$ such that $f_a(t, x) \to f^*(x)$ as $a \to \infty$ uniformly on every compact subset of $\mathbb{R}^+ \times \Omega$. f^* and $\dot{x} = f^*(x)$ will be called the *limit function* and the *limit equation*, respectively.

Let $f(t, x)$ be asymptotically autonomous. A set $F \subset \Omega$ is said to be *semi-invariant* with respect to equation (5.5) if for every $(t_0, x_0) \in \mathbb{R}^+ \times F$ there is at least one non-continuable solution $x^* : (\alpha, \omega) \to \mathbb{R}^n$ of the limit equation $\dot{x} = f^*(x)$ with $x^*(t_0) = x_0$ such that $x^*(t) \in F$ for every $t \in (\alpha, \omega)$. Suppose that f is asymptotically autonomous. It is known [14] that for every solution x of equation (5.5) the limit set $\Lambda^+(x) \cap \Omega$ is semi-invariant.

The proof of Theorem 5.5 is obtained through the following lemmas:

Lemma 5.7. *The equilibrium point* $(\lambda^*, C/\lambda^*)$ *of the limit equation* (5.6) *is asymptotically stable.*

First we linearize the system to prove (local) asymptotic stability, then we construct the Lyapunov function

$$V(L,G)=\frac{1}{2}(L-\lambda^*)^2-C\ln G+\lambda^* G-C+C\ln\frac{C}{\lambda^*}$$

and using LaSalle's invariance principle we prove that the equilibrium is globally asymptotically stable.

Lemma 5.8. *The equilibrium point* $(\lambda^*, C/\lambda^*)$ *of the limit equation* (5.6) *is asymptotically stable in the large on quadrant* $Q := \{(L,G) : L \geq 0, G > 0\}$.

Lemma 5.10. *There is a constant* M *such that*

$$V(L(t),G(t)) \leq V(L(0),G(0)) + M \qquad (t \geq 0)$$

holds for all solutions of (5.4)*. Moreover, for every* $\varepsilon > 0$ *there exists a* $\tau(\varepsilon) \geq 0$ *such that if* $t_0 \geq \tau(\varepsilon)$ *then every solution of* (5.4) *satisfies the inequality*

$$V(L(t),G(t)) \leq V(L(t_0),G(t_0)) + \varepsilon \qquad (t \geq t_0).$$

Lemma 5.11. $(\lambda^*, C/\lambda^*)$ *is an eventually uniformly stable point of the non-autonomous system* (5.4).

Lemma 5.12. $(\lambda^*, C/\lambda^*)$ *is an eventually asymptotically stable point of the original non-autonomous system* (5.4) *in the large.*

Uniform stability phenomena are the stability properties which can be observed in applications most frequently. E.g. in the case of linear systems uniform asymptotic stability is equivalent to exponential asymptotic stability, which plays a central role in control theory.

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