Chaotic Interactions of Selfreplicating RNA

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Abstract

A general system of high-order differential equations describing complex dynamics of replicating biomolecules is given. Symmetry relations and coordinate transformations of general replication systems leading to topologically equivalent systems are derived. Three chaotic attractors observed in Lotka-Volterra equations of dimension $n = 3$ are shown to represent three cross-sections of one and the same chaotic regime. Also a fractal torus in a generalized three-dimensional Lotka-Volterra Model has been *linked* to one of the chaotic attractors. The strange attractors are studied in the equivalent four-dimensional catalytic replicator network. The fractal torus has been examined in adapted Lotka-Volterra equations.
Analytic expressions are derived for the Lyapunov exponents of the flow in the replicator system. Lyapunov spectra for different pathways into chaos has been calculated. In the generalized Lotka-Volterra system a second inner rest point — coexisting with (quasi)-periodic orbits — can be observed; with an abundance of different bifurcations. Pathways from chaotic tori, via quasi-periodic tori, via limit cycles, via multi-periodic orbits — emerging out of periodic doubling bifurcations — to "simple" chaotic attractors can be found.

1. Introduction

1.1. Historic background

In history of Theoretical Biology two apparently different approaches for modeling the dynamical behavior of self-replicating macromolecules have been discussed in literature:

• Self-replicating species which are not catalytically active. This concept of Replication of RNA populations is well known as Eigens *Quasispecies* model (Eigen *et al.*, 1989; Nowak & Schuster, 1989). Due to the simple dynamic the model can easily extended to describe replication dynamics of biological systems on an admittedly complex fitness-landscape. Replication in the $Q\beta$ system is the experimental background of Eigens Quasispecies approach. Although replication of polynucleotides in this system involves a large number of "elementary" reactions as a first simplification it is justifiable to approximate them by first order replication kinetics.

• Self-replication of catalytically active species is usually modeled by higher order replicator equation. The famous classical approach of dynamical system is the *hypercycle* (Eigen & Schuster, 1979). Motivation is a more natural model where various species do interact not only by competition for a given external resource, but also by predator-prey relations or symbiosis. The analogous to an ecosystem on a molecular level is an *autocatalytic network* consisting of self-replicating macromolecules which acts as catalysts in replication reactions of other species or even catalyses their own replication. Although no *in vitro* system exhibiting this type of dynamic is know at present, the discovery of the catalytic potential of RNA, and especially the demonstration that RNA catalyzed template-induced synthesis of RNA is possible (Doudna & Szostak, 1989), suggests that an ecosystem of catalytically active RNAs which catalyses RNA replication might be feasible. In such a model, the fitness of a certain species will depend on the composition of the entire system, i.e. we have to replace the constant fitness value by a function of the population numbers of – in general – all species in the system.

Catalytic interaction between reacting species has been discussed recently in literature: Nuño *et al.* (Andrade *et al.*, 1993; Nuño *et al.*, 1993a; Nuño *et al.*, 1993b; Stadler & Nuño, 1994) suggested a catalytic network introduced through faulty self-replication into a mutant molecular species. Stadler *et al.* (1995) investigated reaction-mutation networks and observed error-thresholds as first order phase transitions. Examples of low dimensional dynamical systems ($n = 2, 3$ and 4) are discussed and complete qualitative analysis is presented. Bagley *et al.* (1992a; 1992b) observed spontaneous emergence of autocatalytic metabolism in a polymer chemistry with catalyzed cleavage and condensation reactions. Fontana *et al.* (Fontana & Buss, 1994; Stadler *et al.*, 1993) studied networks that are a generalization of replicator (or Lotka-Volterra[1]) equations. They model the dynamics of a population of object types whose binary interactions determine the specific type of interaction product.

1.2. Overview of Models

Observing complex and chaotic behavior in these autocatalytic networks is generic and has been predicted by Smale (1976). Studies of chaotic behavior in various population-ecological and prebiotic evolution models can be found in literature[2]:

Gilpin (1979) and Vance (1978) discovered a "quasi-cyclic" trajectory in an one-predator two-prey model:

$$\frac{1}{N_i}\frac{dN_i}{dt} = r_i - \sum_{j=1}^{3} \alpha_{ij} N_j, \quad i,j = 1,\ldots,3,$$

with parameters $r_1 = r_2 = -r_3 = 1$, $a_{11} = a_{12} = a_{22} = 0.001$, $a_{21} = 0.0015$, $a_{13} = 0.01$, $a_{23} = 0.001$, $a_{31} = -0.005$, $a_{32} = -0.0005$, $a_{33} = 0$.

Arneodo, Coullet and Tresser (1980) found a one-parameter family of strange attractors:

$$\frac{dN_i}{dt} = N_i \sum_{j=1}^{3} \alpha_{ij}\left[1 - N_j\right],$$

with

$$\alpha(\mu) = \begin{pmatrix} 0.5 & 0.5 & 0.1 \\ -0.5 & -0.1 & 0.1 \\ \mu & 0.1 & 0.1 \end{pmatrix}$$

Gardini, Lupini and Messia (1989) studied Hopf-Bifurcations and observed a chaotic attractor:

$$\dot{x}_i = x_i \sum_{k=1}^{3} J_{ik}\left[x_k - 1\right]$$

and

$$J(\alpha, g_1, g_2) = \begin{pmatrix} -0.152+\alpha & -0.92082 g_1 & -0.336728 g_2 \\ 0.46482 g_1 & -0.342+\alpha & \frac{0.794908 g_2}{g_1} \\ 0.863272 g_2 & \frac{-0.00509242 g_2}{g_1} & -0.456+\alpha \end{pmatrix}$$

[1]According to Hofbauer (1981) Replicator-equations with $n+1$ species are – apart from a transformation of the time scale – equivalent to a n-species Lotka-Volterra equation

[2]An overview of the four models and a short description of the motivation for introducing these systems is given in the appendix.

An *Explosive Route to Chaos through a Fractal Torus* in a higher order Lotka-Volterra equation has been studied by Samardzija and Greller (1988):

$$\begin{aligned}\dot{X} &= X - XY + CX^2 - AZX^2\\ \dot{Y} &= -Y + XY\\ \dot{Z} &= -BZ + AZX^2\end{aligned}$$

with $A, B, C \geq 0$.

Similar to the intention of Schnabl *et al.* (1991) our aim is to "unify"[3] these four models into one system. For the first three systems we follow the approach in (Schnabl *et al.*, 1991): we first transform Lotka-Volterra Equations into Replicator-Equations and then apply a barycentric transformation yielding to an interior fixed point at $\frac{1}{4}(1,1,1,1)$. The system of Samardzija and Greller we have to treat in a special way. Due to cubic terms the transformation to Replicator-Equation form would introduce very complicated expressions so we omit this step. We will also relate this special case to the other systems. Extensive comparative study of the phase portraits of these systems and the associated plots in three-dimensional parameter spaces will be given. Chaotic pathways between the different attractors found in literature can be found in our unified system. We will discuss various routes to chaos. For a distinct parameter-interval the sequence of periodic orbits of the attractor follows very closely the period doubling scenario of a quadratic map. Also Lyapunov-exponents for these parameter-values are calculated.

2. Autocatalytic Networks

Let us now consider a system $\mathcal{S}$ of n types of objects, where objects $I_{i_1 \dots i_M}$ do interact to produce one or more types of objects I_k. The reaction product is assumed to be again in $\mathcal{S}$ and the interaction partners $I_{i_1 \dots i_M}$ are retained. Hence these $I_{i_1 \dots i_M}$ play the role of substrate and catalyst. Any material needed to build the products is buffered and therefore does not explicitly enter the kinetic equations. Furthermore we have constant organization in mind – i.e. we introduce an unspecific dilution flux $\Phi(t)$ that keeps the total number of objects constant. This setup of a general replication mechanism can be sketched with the following reaction-pathways:

$$(F) + I_{i_1} + \ldots + I_{i_M} \xrightarrow{\mathcal{A}^{(k)}} I_i + \ldots + I_{i_M} + I_k + (W) \qquad (1)$$

$$I_k \xrightarrow{\Phi} \emptyset \qquad (2)$$

In the following we switch to relative concentrations, $0 \leq x_i(t) \leq 1$, $i = 1, \ldots, n$. Here, $\mathcal{A}^{(k)}(\mathbf{x})$ denote general rate constants for the reaction (1) including the effect of the reaction medium on the replication process. (F) is the food out of which new replicators are built up, (W) denotes the waste produced by the reaction. Applying mass action kinetics yields:

$$\dot{x}_k(t) = \mathcal{A}^{(k)}(\mathbf{x}) - x_k \Phi(t), \qquad k = 1, \ldots, n$$

with $\Phi(t)$ such that $\sum_k x_k(t) = 1$ $(\Phi(t) = \sum_k \mathcal{A}^{(k)}(\mathbf{x}))$.

This general replication mechanism describes the complex replication of biopolymers (RNA or DNA) with the necessary large number of interacting molecules and elementary steps. Although it is a reasonable approximation to subsume all these "auxiliary-reactions" in over-all reaction rates

[3]What we mean by *unify* will be defined in chapter 2.1

depending only on the concentrations x_i of the self-replicating species (Eigen *et al.*, 1980). As a first approach we can expand $\mathcal{A}$ as power series in terms of concentrations:

$$\mathcal{A}^{(k)}(\mathbf{x}) = A^{(k)} + \sum_{i=1}^{n} A_i^{(k)} x_i + \sum_{i=1}^{n}\sum_{j=1}^{n} A_{ij}^{(k)} x_i x_j + \dots \qquad k = 1, \dots, n. \tag{3}$$

By truncating of this series expansion one obtains well known models for reaction-networks (i.e. Eigens Quasispecies-model, reaction-mutation models, ...). A detailed study about general reaction networks can be found in (Forst *et al.*, 1995).

Following the approach of Stadler *et al.* (1993) we can rewrite the general rate constants $A^{(k)}_{i_1 \dots i_M}$ into rate constants $A_{i_1 \dots i_M}$ and transmission coefficients $t^{(k)}_{i_1 \dots i_M}$ by defining

$$A_{i_1 \dots i_M} = \sum_{k=1}^{n} A^{(k)}_{i_1 \dots i_M} \text{ and } A^{(k)}_{i_1 \dots i_M} = A_{i_1 \dots i_M} \cdot t^{(k)}_{i_1 \dots i_M}.$$

The $A_{i_1 \dots i_M}$ denote the fraction of reactive collisions between the objects $I_{i_1}, \dots, I_{i_M}$, and $t^{(k)}_{i_1 \dots i_M}$ indicate the relative frequency of the reaction product I_k. The $\sum t^{(k)}_{i_1 \dots i_M} = 1$ for any reactive set $I_{i_1}, \dots, I_{i_M}$ and is equal to 0 for non-reactive ensembles.

In this paper we restrict ourselves to systems with $t^{(k)}_{i_1 \dots i_M} = 0$ iff there exists an $j = 1, \dots, n$ for which $i_j \neq k$. This constraint omits mutation into a new object and is manifested in the well-known replicator-equations. As a second constraint we use polynoms $\wp_k(\mathbf{x})$ with degree two or higher for the rate constant ($\deg(\wp_k) < \infty$). This "simplification" induces formulations of some useful transformations and invariants. The ODE we are dealing with is now as follows:

$$\dot{x}_k = x_k \left[\wp_k(\mathbf{x}) - \sum_{j=1}^{n} \wp_j(\mathbf{x}) x_j\right] \qquad \text{for } k = 1, \dots n \tag{4}$$

2.1. The Models

We will show that all three "simple" systems found in literature (GV, ACT, and GLM) lie in the same chaotic regime, and in changing parameters the strange attractors can be distorted into each other continuously. We can also show that the ACT-model arise as a particular case of the higher order SG-equations. So actually we deal with two representations of the same system nevertheless we have to treat them separately.

First of all we have do define what we mean by *connected* chaotic attractors:

Definition 1. *Two chaotic attractors are called* connected *if there exists a path from the initial to the terminal attractor in parameter-space which consists of chaotic attractors only.*

In the following we will "unify" all four models found in literature into two representations (i.e. the Replicator- and the Lotka-Volterra-model). This means by changing parameters we can change from one chaotic attractor to another.

Table 1: Reaction Matrices

(a) Reaction matrix of Gardini *et al*(1989):

$$A = \begin{pmatrix} 0 & 0.152-\alpha & 0.456-\alpha & 0.342-\alpha \\ 0.152-\alpha+0.92082g_1+0.336728g_2 & 0 & 0.6+0.4\gamma+0.564\nu & 0.342-\alpha-0.92082g_1 \\ 0.456-\alpha-0.863272g_2+0.00509242\frac{g_2}{g_1} & 0.152-\alpha+0.863272g_2 & 0 & 0.342-\alpha-0.00509242\frac{g_2}{g_1} \\ 0.342-\alpha-0.46482g_1-0.794908\frac{g_2}{g_1} & 0.152-\alpha+0.46482g_1 & 0.456-\alpha+0.794908\frac{g_2}{g_1} & 0 \end{pmatrix}$$

(b) Adapted reaction matrix of our system:

$$A = \begin{pmatrix} 0 & 0.5-0.437\nu-0.498\gamma & -0.1+0.100\nu+0.406\gamma & 0.1+0.337\nu+0.092\gamma \\ 1.1-0.563\nu-0.132\gamma & 0 & -0.6+0.564\nu+0.400\gamma & -0.001\nu-0.268\gamma \\ -0.5-0.035\nu-0.474\gamma & 1.0-0.620\nu+0.297\gamma & 0 & 0.655\nu+0.177\gamma \\ 1.7-1.164\nu+\mu-4.125\gamma & -1.0+0.968\nu-\mu+1.234\gamma & -0.2+0.196\nu+2.891\gamma & 0 \end{pmatrix}$$

2.1.1. *Replicator Model*

We used the three-dimensional Lotka-Volterra equation of (Gardini *et al.*, 1989), transformed it to a second-order replicator-equation, applied the barycentric transformation and fitted it in the SSFS-system. This yields a second-order replicator-equation of the form

$$f_{\mathcal{R}}(\mathrm{x}) \stackrel{\mathrm{def}}{=} \dot{x}_k \;=\; x_k \Big(\sum_{i=1}^{n} A_{ki}\, x_i - \sum_{i=1}^{n} \sum_{j=1}^{n} A_{ij}\, x_i x_j \Big), \quad k = 1 \ldots n \tag{5}$$

The reaction-matrix (A_{kj}) used in our studies introduces three parameter γ, μ, and ν. Vance's attractor can be found at $(\gamma, \mu, \nu) = (0, 0, 1)$, the ACT-system lies at $(0, \mu, 0)$, and GLM's model is at $(1, 0, 0)$. As a consequence of the barycentric transformation $\sum_{j=1}^{4} A_{ij} = 0.5$ for all $i = 1, \ldots, 4$ holds. The reaction matrices are shown in table 1.

2.1.2. *Lotka-Volterra Model*

The classical Lotka-Volterra system represents a basic mathematical model which finds application in various fields like biology, physics and economy. A system we study here can be associated with a more general predator-prey interaction:
Samardzija & Greller (1988) presented a three-dimensional generalization of the Lotka-Volterra model. The system proposed by them is

$$\begin{aligned} \dot{X} &= X[1 + CX - Y - AXZ] \\ \dot{Y} &= Y[-1 + X] \\ \dot{Z} &= Z[-B + AX^2] \end{aligned} \tag{6}$$

This set of ODEs describes a *two-predator one-prey* interaction with reaction-pathways shown in Fig. 1:

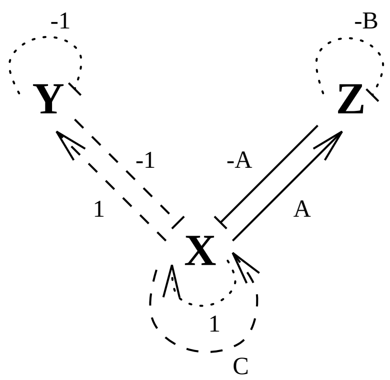


Fig. 1: Reaction-pathway for the SG-system. Arrows and bars resp. denote positive and negative interactions. Dotted lines indicate "self-catalysis", dashed lines determine "simple" Lotka-Volterra type dependencies and solid lines stand for higher-order relationships. Numbers and letters denote corresponding "reaction constants"

The relations between X and Y form the well-known Lotka-Volterra equation in two dimensions, while the interaction between X and Z generalize the latter in three dimensions (c.f. Samardzija and Greller A, B and $C \geq 0$). So $A = 0$ yields the classical predator-prey dynamics whereas for $A > 0$ equ. (6) leads to a competing two predator – one prey system with different dependencies of the growth-rate of the two different predators on the number of prey.

What we have done is as follows: We fitted the SSFS-system transformed into the corresponding Lotka-Volterra equation into the system of Samardzija and Greller. We scaled the y_2 axis and due to the barycentric transformation we moved one equilibrium of equ. (6) to $(1, 1, 1)$ which always exists as we will see in chapter 3.1.2. So we deal with a three-dimensional Lotka-Volterra System with simple polynomials $\wp_k(y)$ of degree two:

$$\begin{aligned} \dot{y}_1 &= y_1[1 + cy_1 - 0.4y_2 + (a - c - 0.6)y_3 - ay_1y_3] \\ \dot{y}_2 &= y_2[-0.5 + 0.5y_1 + 0.1y_2 - 0.1y_3] \\ \dot{y}_3 &= y_3[-b + (0.2 + b)y_1 - 0.1y_2 - (0.1 + a)y_3 + ay_1^2] \end{aligned} \tag{7}$$

In contrast with Samardzija and Greller we allow parameter a, b and c as follows:

$$a \in \mathbb{R}_0^+ \quad b, c \in \mathbb{R}$$

For $a = 0$, and $b = -1.7 - \mu$, and $c = -0.5$ we are "close" to the ACT-system: Comparing the resulting ODEs yields

$$\dot{y}_1 = y_1[1 - 0.5y_1 - 0.4y_2 - 0.1y_3]$$

for our system and

$$\dot{y}_1 = y_1[1.1 - 0.5y_1 - 0.5y_2 - 0.1y_3]$$

for the ACT-model. The equations for $\dot{y}_2$ and $\dot{y}_3$ resp. are identical for both systems[4].

3. Chaotic Interactions

3.1. Rest Points, Stability, and Attractors

3.1.1. Replicator Model

For the three-dimensional system Bomze (1983) found four lemmas to characterize the phase portraits of the various attractors. Stadler & Schuster (1990) did a full characterization of this system. They reduced the nine-dimensional parameter space to three relevant angular coordinates which determine completely the phase portraits and the bifurcation patterns.

Lemma 1. *For a second order replication equation (6) (and the corresponding Lotka-Volterra Equation) holds:*

$$\exists \hat{x} \in intS_n: \quad f_{\mathcal{R}}(\hat{x}) = 0 \Rightarrow \hat{x} \quad unique$$

[4]Note that we use a parameter μ which corresponds to $\mu - 1.5$ in ref. (Arneodo *et al*, 1980).

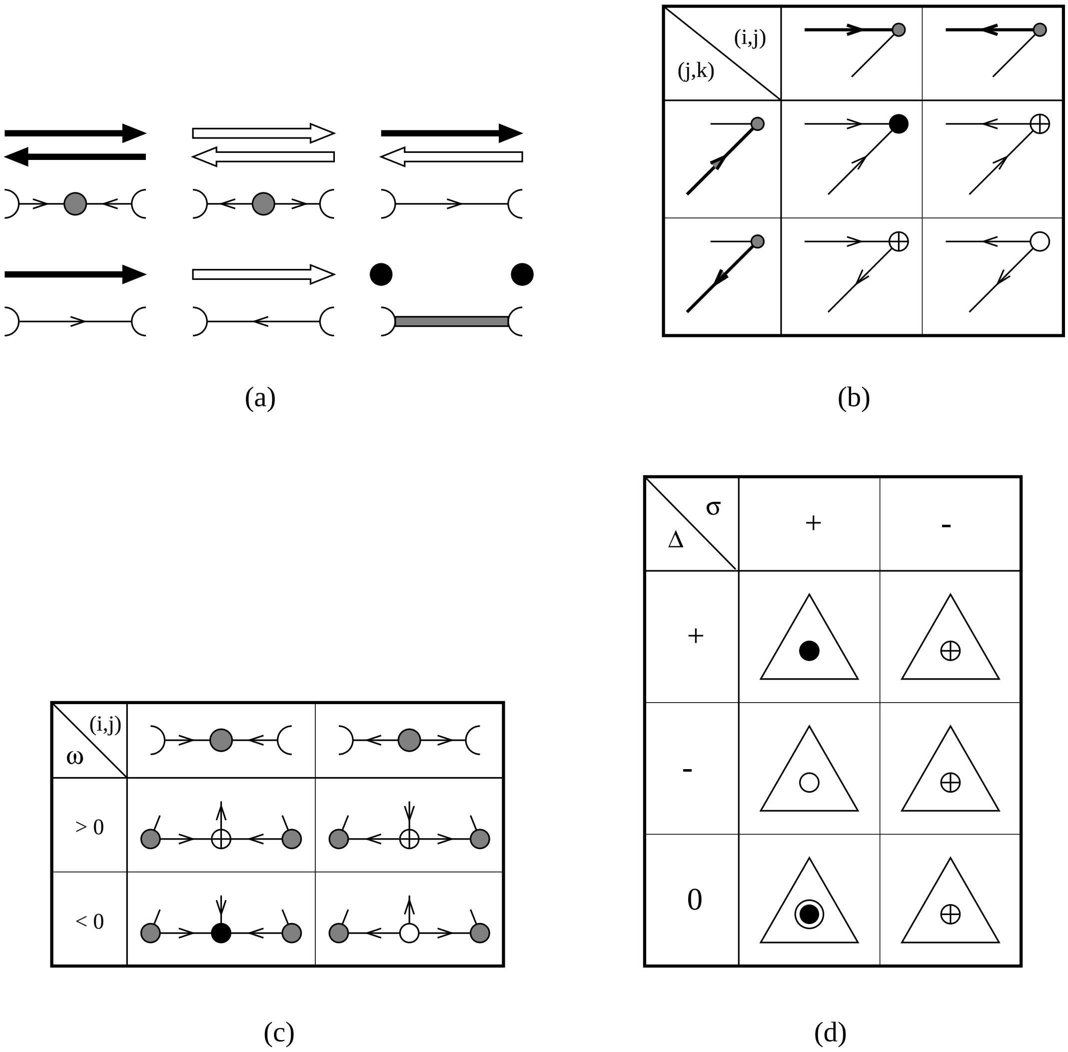


Fig. 2: C.f. (Stadler & Schuster, 1990): Phase portraits of the replicator equation with $n = 3$ according to four lemmas derived by Bomze (Bomze, 1983). (a): flows along edges corresponding to different graphs, (b): flows around corners joining two edges $[i, j]$ and $[j, k]$, (c): flows on edges containing fixed points of different stability and (d): stability of the single fixed point in $\mathrm{int} S_3$ depending on $\mathrm{sgn}\sigma$ and $\mathrm{sgn}\Delta$. Following notation denotes fixed points of different stability: $\circ$ ... source, $\oplus$ ... saddle, $\odot$ ... center, $\bullet$ ... sink and $\circ$ ... "wild card", i.e. not yet determined.

Proof. trivial. For an explicit deduction see (Hofbauer & Sigmund, 1988). ∎

Corollary 1. *Regarding fixed points there can only be three cases:*
(i) no interior fixed point

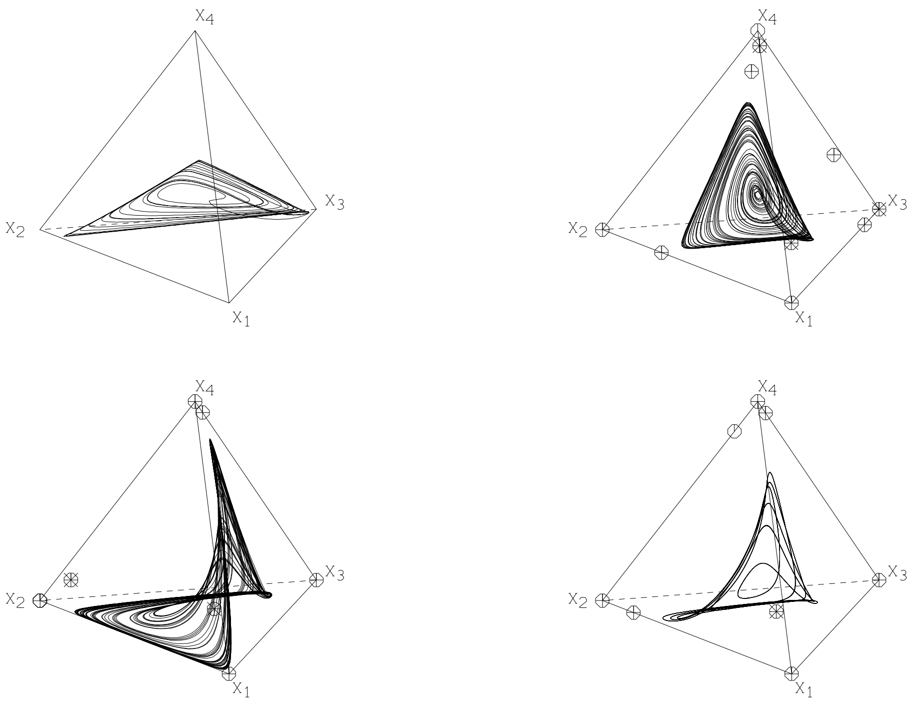


Fig. 3: Different phase portraits refer to different points in the parameter space. By varying the parameters γ, μ, and ν we can get to attractors of the GV-, ACT-, and GLM-systems. Here $\circ$ denotes sources, $\oplus$ indicates saddles and $\circledast$ determines sinks. The parameters (γ, μ, ν) are: $(0, 1, 0)$ for Vance's attractor, $(1, 0, 0)$ for one characteristic attractor of the ACT-model, and $(1, 0.02, 0)$ for one chaotic phase portrait of the GLM-system. The fourth attractor lies at $(0.6, 0.65, 0)$.

(ii) *exactly one interior fixed point*
(iii) *fixed points hyper-planes*

We have chosen the reaction matrix A such that $\frac{1}{4}\mathbf{1}$ is always fixed point. This is a significant simplification for classifying the system in such a way that fixed point analysis is restricted to ∂S_4. Due to Theorem 3 the dynamics on ∂S_4 also obeys the replicator equation. So it is sufficient to analyze fixed points of the reduced replicator equation for $n = 3$ (c.f. Bomze (1983) and Stadler & Schuster (1990)):

The replicator equation with $n = 3$ in normal form has six entries:

$$\begin{pmatrix} 0 & \delta & \gamma \\ \alpha & 0 & \epsilon \\ \zeta & \beta & 0 \end{pmatrix}$$

with determinant $\Delta \stackrel{\text{def}}{=} \det A = \alpha\beta\gamma - \delta\epsilon\zeta$. For simplification we introduce following expressions:

$$\begin{aligned} \omega_1 &\stackrel{\text{def}}{=} \delta\epsilon + \beta\gamma - \beta\epsilon \\ \omega_2 &\stackrel{\text{def}}{=} \alpha\gamma + \zeta\epsilon - \zeta\gamma \\ \omega_3 &\stackrel{\text{def}}{=} \zeta\delta + \alpha\beta - \alpha\delta \end{aligned}$$

To visualize the occurrence of rest points graphically (Fig. 2) we have to define two notations:

- A generalized directed graph can be assigned to every autocatalytic network by means of three rules:
  - (i) a vertex $[k]$ is assigned to every replicator $\mathbf{I}_k$,
  - (ii) an arrow is drawn along the edge $[j,k]$ from $[j]$ to $[k]$ for each nonzero entry of matrix A in normal form, $A_{kj} \neq 0$ and
  - (iii) the *color* of the arrow is *black* if $A_{kj} > 0$ and *white* if $A_{kj} < 0$.
- A fixed point in the interior of the simplex $\mathrm{int}S_3$ exists iff:

$$\mathrm{sgn}\omega_1 = \mathrm{sgn}\omega_2 = \mathrm{sgn}\omega_3 \stackrel{\text{def}}{=} \sigma.$$

Figure 3 shows four attractors of selected parameter-values with the corresponding fixed-points of ∂S_4.

3.1.2. Lotka-Volterra Model

Due to the asymmetric equations (7) we have to analyze the system explicitly. This yields to the results shown in table 2.

Some phase portraits exhibit the complex behavior of the system due to the possible second inner fixed point. Again we can find attractors of our reference systems (ACT, SG) embedded in the same parameter space (Fig. 4). Visualizing the stability is complicated due to the three-dimensionality of this space. In detail the parameter-values for existence and the stabilities of the different fixed points $\hat{\mathbf{y}}$ are as follows ("existence" is understood as $\hat{\mathbf{y}} \in \mathbb{R}^3_+$):

- Corner: $(0,0,0)$ is always existent and always a saddle. For $b < 0$ it is a $(++-)$- and for $b > 0$ it is a $(+--)$-saddle.
- Edges: $(-\frac{1}{c}, 0, 0)$ exists iff $c < 0$. It is a sink for $c \in (-1, 0)$ and $a < bc^2 + bc + \frac{c}{5}$. Else it is a saddle.
  - $(0, 5, 0)$ exists for all parameter-values and is a $(++-)$-saddle for $b < -\frac{1}{2}$. Else it is a $(+--)$-saddle.
  - $(0, 0, -\frac{10b}{1+10a})$ is in $\mathbb{R}^3_+$ iff $b \leq 0$. It is a source for $b > 0$, $0 < a < \frac{1}{10}(2b-1)$ and $c > \frac{1}{10}(-10a + 10ab - 6b - 1)$. It is a sink for the reversed inequalities and a saddle in all other cases.
- Surfaces: $\frac{1}{2+c}(1, 5(1+c), 0) \in \mathbb{R}^3_+ \Leftrightarrow c \geq -1$: λ is positive if $a > bc^2 + 3bc + 2b + \frac{1}{2}c^2 + \frac{13}{10}c + \frac{3}{5}$. λ_{23} is complex if $c \in [9 - \sqrt{96}, 9 + \sqrt{96}] =: I$. The denominator of λ_{23} is positive if $c \in I$. If $c \in I \wedge c > -\frac{1}{3}$ then the rest point is a source if the upper inequality for a is fulfilled. If $c \notin I$ then we have to observe two cases:

$$\begin{array}{lll} c < 9 - \sqrt{96}: \text{ for} & c > -2 & \lambda_2 < 0 \\ & & \lambda_3 > 0 \\ & c < -2 & \lambda_{23} > 0 \\ c > 9 + \sqrt{96}: & & \lambda_{23} > 0 \end{array}$$

Table 2: Rest Points and Eigenvalues

type	coordinates	eigenvalues
corner	$(0,0,0)$	$(-\frac{1}{2}, 1, -b)$
edges	$(-\frac{1}{c}, 0, 0)$ $(0,5,0)$ $(0,0,-\frac{10b}{1+10a})$	$(-1, -\frac{1}{2}(1+\frac{1}{c}), \frac{1}{c^2}(a - bc(1+c) - \frac{c}{5}))$ $(-1, \frac{1}{2}, -\frac{1}{2} - b)$ $(b, \frac{1+10a+2b(3-5a+5c)}{1+10a}, -\frac{1}{2}\frac{1+10a-2b}{1+10a})$
surfaces	$\frac{1}{2+c}(1, 5(1+c), 0)$ $(y_1, 0, y_3)$ $\frac{5}{2(1+5a)}(0, 1+10a-2b, -1-2b)$	$\lambda_1 = \frac{10a-10bc^2-30bc-20b-5c^2-13c-6}{10(2+c)^2}$ $\lambda_{23} = \frac{1}{4(2+c)}[1+3c \pm \omega_1^*]$ very complicated° $\lambda_1 = \frac{3-15a-10ab+10b+10bc+5c}{2(1+5a)}$ $\lambda_{23} = \frac{1}{4(1+5a)}[1+10a+10ab \pm \omega_2^\dagger]$
interior	$(1,1,1)$ (y_1, y_2, y_3) $y_1 = \frac{1}{20a}[-17 - 10(b+c) \pm \omega_3^\ddagger]$ $y_2 = \frac{1}{4a(1+5a)}[100a^2 + 50a(b+c) + 125a$ $-10c(b-c) + 27c + 28 \mp (2+5a+c)w_3]$ $y_3 = \frac{1}{4a(1+5a)}[20a - 10b - 10c(b-c)$ $+17c + 11 \mp (1+c)w_3]$	$100\lambda^3 + 100(2a-c)\lambda^2 + 10(10a^2 + 10ac + 11a$ $+10bc + 6b + 2c + 3)\lambda - 10a^2 - 10ac - 2a - 10bc$ $-10b - 5c - 3 = 0$ $(\lambda_1, \lambda_2, \lambda_3)$ λ very complicated°

* $\omega_1 := \sqrt{c^2 - 18c - 15}$
† $\omega_2 := \sqrt{100a^2b^2 + 40ab^2 - 20ab - 10a + 8b^2 - 1}$
‡ $\omega_3 := \sqrt{400ab + 600a - 60b + 140c + 169 - 100(b-c)^2}$
° High order polynomials which roots are not solvable analytically

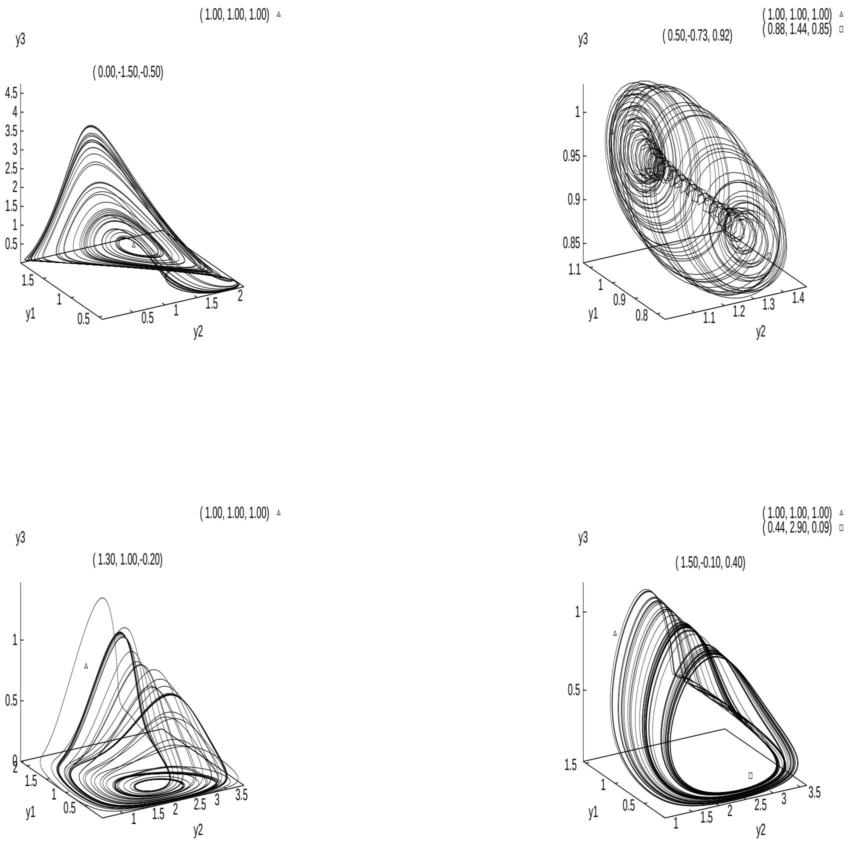


Fig. 4: Phase portraits of selected parameter values for the Lotka-Volterra model. The numbers in the figure title refer to the corresponding parameters a, b, and c resp. In addition the positions and the coordinates of the inner rest points are drawn (from top left to bottom right): ACT-attractor, SG-torus, two more phase portraits of show the richness of this system.

- ∘ $(y_1, 0, y_3)$: This fixed point is too complicated to be analyzed analytically.
- ∘ $\frac{5}{2(1+5a)}(0, 1+10a-2b, -1-2b)$ exists for $b \leq -\frac{1}{2}$. Here $\lambda_1 > 0$ if $a > \frac{10b+10bc+5c+3}{5(3+2b)}$ (if $b = -\frac{3}{2}$ then $\lambda_1 > 0$ if $c < -\frac{6}{5}$). For λ_{23} the following expression is characteristic:

$$b_{\pm} = \frac{5a\sqrt{2} \pm (2+10a)\sqrt{1+5a}}{2\sqrt{2}(25a^2+10a+2)}$$

If $b_- < b < b_+$ then λ_{23} is complex. In this case the sign of these eigenvalues depend on $\mathrm{sgn}(10ab + 10a + 1)$. So $\Re(\lambda_{23}) < 0$ if $b_- < b < -1 - \frac{1}{10a}$.

- Interior: $(1, 1, 1)$ is always existent. Again the determination of the stability of this fixed point is very complicated. Bifurcations occur if $10a^2 + 10ac + 2a + 10bc + 10b + 5c + 3 = 0$. This is the case if

$$a_{\pm} = \frac{1}{10}[-1 - 5c \pm \sqrt{25c^2 - 100bc - 100b - 40c - 29}]$$

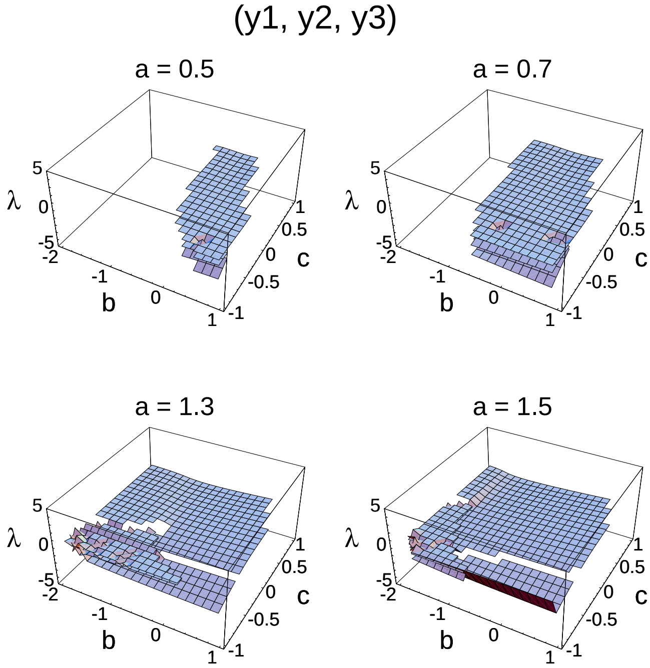


Fig. 5: Eigenvalues of the rest-point (y_1, y_2, y_3) for some chosen parameters a. No surface means $\hat{\mathbf{y}} \notin \mathbb{R}^3_+$ or $\hat{\mathbf{y}}$ nonexistent at all.

For typical parameter sets the eigenvalues of this equilibrium are one real eigenvalue and two conjugate complex eigenvalues. The real parts of these complex eigenvalues have reversed sign to the third real eigenvalue.

- (y_1, y_2, y_3) For this rest point there is nothing known at all so we have to determine the stability of this guy by numerical calculations. Fig. 5 shows eigenvalues for some parameter-values of $\hat{\mathbf{y}} \in \mathbb{R}^3_+$.

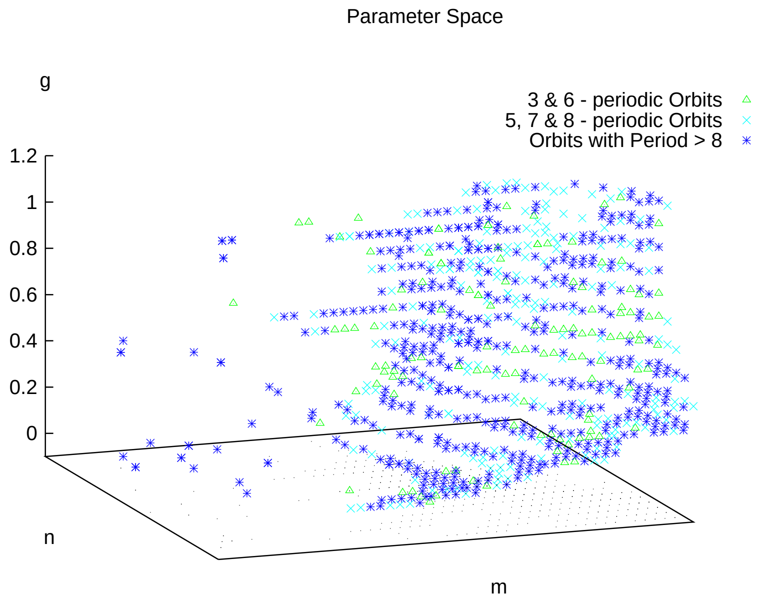
3.2. Parameter Space

To get a close overview of the observed system, we did a systematic survey in the three-dimensional parameter spaces.

3.2.1. Replicator Model

For the Replicator model we start at the well known region of the SSFS attractors (the μ-ν-plane) and slowly alter the third parameter γ. Figure 6 shows an overview of attractors with complex and chaotic behavior embedded in the three-dimensional parameter-space.

Doing a coarse overview on the parameter space we notice a quite similar behavior of the system



(b)

Fig. 6: Three dimensional parameter space of the Replicator model. The different symbols denote different "periodic" attractors. Here we show attractors associated with chaos (three-, five-, and higher-periodic orbits).

for large γ as it was observed for the SSFS-system ($\gamma = 0$; see Figure 7). The main features are (increasing μ):

- Hopf-bifurcation from a fixed point to a limit cycle
- subsequent cascade of period-doubling bifurcation to chaos
- behavior of the bifurcations to chaos starting as an unimodal map up to a map of fourth order (Michielin & Phillipson, 1994; Phillipson & Schuster, 1994)
- collision of the chaotic attractor with the stable manifold of a saddle

Analogous to Schnabl *etal.* (1991) we can relate the periodic doubling scenario and the subsequent period 3 of the system with the dynamic behavior of a quadratic map.

3.2.2. Lotka-Volterra Model

For the Lotka-Volterra equation this survey is a bit more complicated due to the richness of the observed dynamics. The three dimensional parameter space is divided into some regions where periodic, quasi-periodic and chaotic attractors can be observed (Fig. 8). No path of chaotic attractors from the ω-limit of the ACT-system to the sets of tori or to the different shaped attractors has been found. But a connection through periodic orbits can be detected.

Starting from $a = 0$ a second inner rest point emerges and is responsible for the complexity of the system. This very point evolves from a saddle-node in the b, c-plane. for small values of a we can detect similarities in the observed attractors with the ACT-attractor (Fig. 3). Increasing a

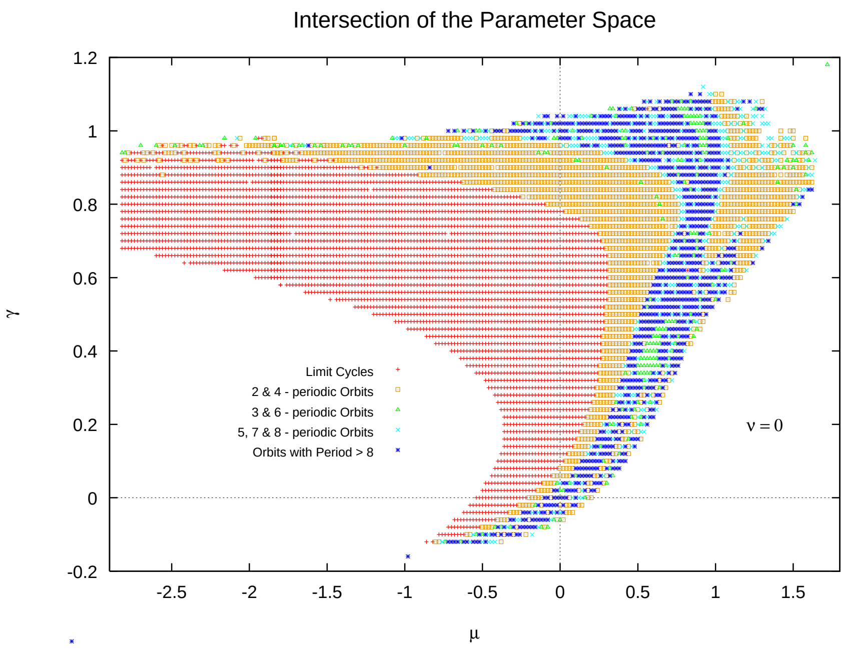


Fig. 7: Two dimensional cut through the three dimensional parameter space at $\nu = 0.0$.

the ω-limit is getting distorted in quite peculiar ways. We can detect shoe-shaped attractors being distorted to tori (Fig. 4).

3.3. Lyapunov Exponents and Route to Chaos

3.3.1. Replicator Model

Following the calculation in (Schnabl *et al.*, 1991) we can give analytic expressions of all of the Lyapunov exponents λ_2-λ_4 but the most positive one λ_1:

$$\begin{aligned}
&\lambda_1 \ldots \text{numerical calculation (c.f. Wolf } et\ al.\text{(1985))} \\
&\lambda_2 = 0 \\
&\lambda_3 = -\frac{1}{8} - \lambda_1 \\
&\lambda_4 = -\frac{1}{8}
\end{aligned}$$

λ_1 has to be calculated numerically. Here are appropriate numerical algorithms (Bennetin *et al.*, 1980) and well tested FORTRAN programs (Wolf *et al.*, 1985) available in literature. λ_2 is always 0 because we only have studied (quasi)-periodic attractors. And for those types of attractors at least one exponent in direction of the trajectory is equals 0. λ_4 is predetermined by the system of

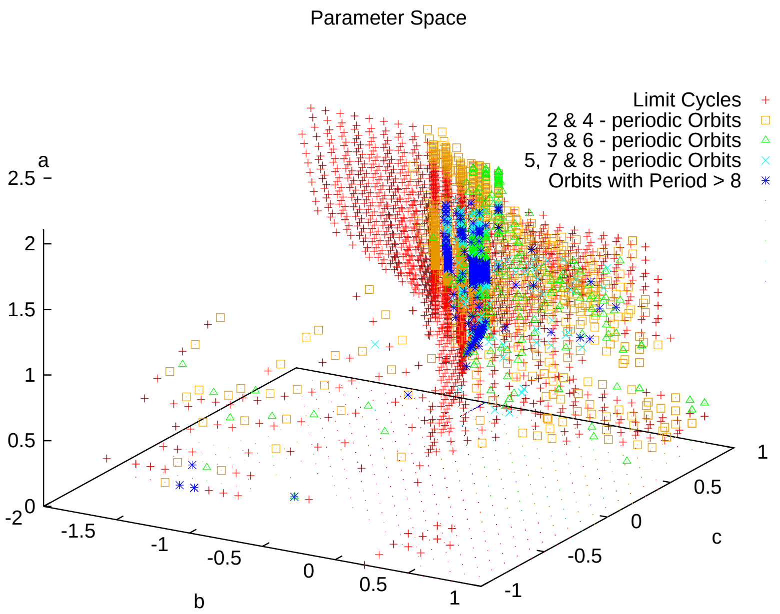


Fig. 8: Three-dimensional parameter space of the Lotka-Volterra model. Again different symbols indicate orbits with different periodicity. Comparing this plot with Fig. 6 we note the disordered region of high-periodic attractors

a second-order replication-equation and by applying the barycentric transformation. So

$$\lambda_4 = -\bar{\Phi} \text{ and } \bar{\Phi} = \frac{1}{n^2}\sum_{i,j=1}^{n} A_{ij}$$

For our system with $n = 4$ and $\sum_{j=1}^{4} A_{ij} = 0.5$ yields $\lambda_4 = -\frac{1}{8}$. We have chosen the $\nu = 0$-plane and we have tracked the *Feigenbaum*-type cascade of bifurcations and calculated the Lyapunov spectrum in dependency of the parameter μ (Forst, 1993). The typical pattern of the Lyapunov exponents can be detected making evident periodic-doubling bifurcations.

Comparing the results with Schnabl *et al.*(1991) by analyzing Fig. 7 ($\nu = 0$) reveals an amount of similarities concerning *routes to chaos* by using μ as bifurcation-parameter. For parameter-values $-0.1 \leq \gamma \geq 0.9$ the global behavior is similar:

- for small μ the inner fixed point is stable
- the chaotic regime is reached via a Hopf bifurcation and a subsequent cascade of period-doubling bifurcations
- beyond the end of the Feigenbaum sequence the chaotic regime ends (interrupted by the period-3 and other periodic windows) in an sharp *interior crisis* resulting in a period two tangent bifurcation.
- the existence of (quasi-) periodic orbits end abruptly at a limit crisis where the attractor collides with the stable manifold of a saddle of ∂S_4

For different values of γ the only difference lie in the length (and of course the starting and final point) of the interval for each attractor with a distinct periodicity and the dynamic behavior of the system between the interior and the limit crisis. Depending on γ different numbers of period two tangent bifurcations occur.

3.3.2. Lotka-Volterra Model

We calculated the Lyapunov-spectra (λ_{min}, λ_{med}, λ_{max}) in dependence of parameter a and c (whereas a is our bifurcation-parameter, c is another variable and $b = -0.70$ is held constant for this study). In most of the observed Lyapunov spectra we can distinguish three major sections:

(i) a section with linear dependency of two of the Lyapunov exponents with the control parameter (one exponent is always zero in our case, cause we only observe 'periodic' solution of our system). It is possible to linearize the system to calculate the slope of this linear section (Forst *et al.*, 1995).

(ii) a section with nonlinear dependency of the exponents from the control parameter — either connected to the linear section or interrupted with a region of fixed points.

(iii) the section with the occurrence of quasi-periodic and chaotic tori which emerge out of a limit cycle due to a second Hopf-Bifurcation.

Table 3: Selected Lyapunov-Exponents ($b = -0.7$)

Position	Bifurcation-parameter: a				
Parameter c	0.70	0.80	0.90	0.95	1.00
at plateau[a]	0.043		0.055	0.062	0.051
max.	0.043	0.037	0.055	0.062	0.054

[a] Here the Lyapunov-exponent is only weakly dependent on a

Fig. 9 shows a Lyapunov spectrum at $b = -0.7$ and $c = 0.95$ depending on parameter a. A comparative table of positive Lyapunov-exponents for different parameter values a and c ($b = -0.70$ fixed) is shown in table 3.

Comparing the bifurcation-behavior of this system with the behavior observed for the replicator representation concerning route to chaos yields following results (table 4):

- Similar to the observation of Schnabl *et al.*(1991) for a distinct parameter-interval the sequence of periodic orbits for the attractor follows very closely the period doubling scenario and subsequent period 3 of a simple quadratic map for both representations (Figure 10).
- Differences occur in the emergence of the initial limit-cycle: For the Replicator representation the limit-cycle originates from a stable fixed point by a Hopf-bifurcation. For the high-order Lotka-Volterra system we can observe a cascade of bifurcations beginning from a chaotic torus via a quasiperiodic torus to a limit-cycle by a Hopf-bifurcation.
- After the occurrence of the period 3 window for the attractors in the Lotka-Volterra representation we can observe another period 3 window in the chaotic regime.

Table 4: Critical Values of Bifurcations ($b = -0.7$)

Period	Bifurcation-parameter: a				
Parameter c	0.70	0.80	0.90	0.95	1.00
$1 \to 2$[a]	1.080	0.955	0.890	0.874	0.870
$2 \to 4$	1.154	1.017	0.939	0.920	0.886
$4 \to 8$	1.170	1.031	0.951	0.930	0.890
$\to \infty$	1.174	1.036	0.955	0.933	0.893
5[b]	1.198			0.944	0.898
3				0.965	0.908
another 3[c]	1.266 – 1.279		1.095 – 1.105	1.065 – 1.075	0.935
$2 \to 8$	1.34 – 1.48	1.072 – 1.38	1.43 – 1.50	1.390 – 1.452	
1 – 3	1.62–	1.59–	1.51–	1.48–	1.47–

[a] Bifurcation-value for period-doubling bifurcation
[b] Start of period-5 window resp.
[c] Boundaries of periodic windows

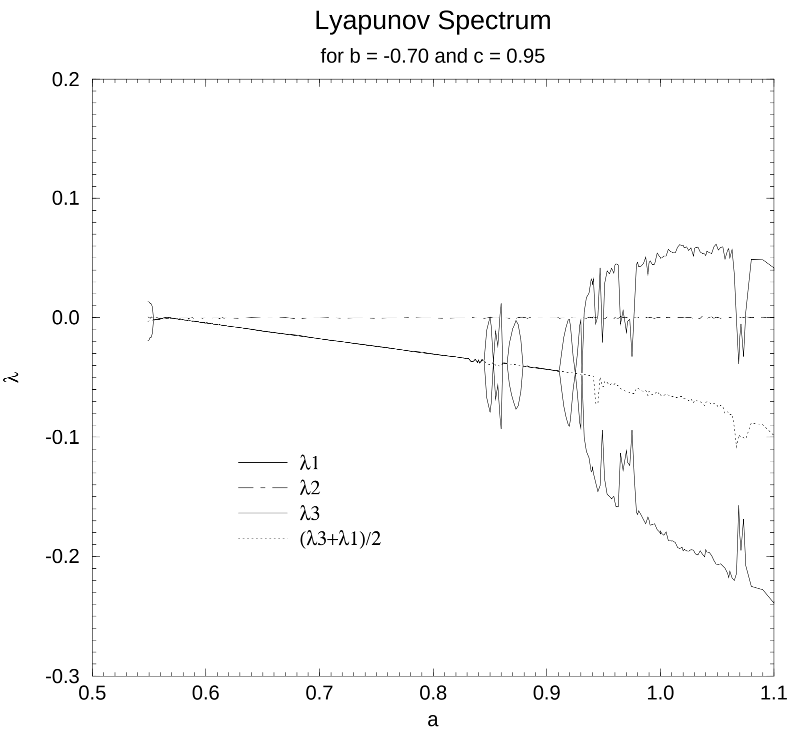


Fig. 9: Lyapunov Spectrum for selected attractors along a path from chaotic tori via quasi-periodic tori, limit cycles to different chaotic attractors through a subsequent cascade of periodic-doubling bifurcations is shown.

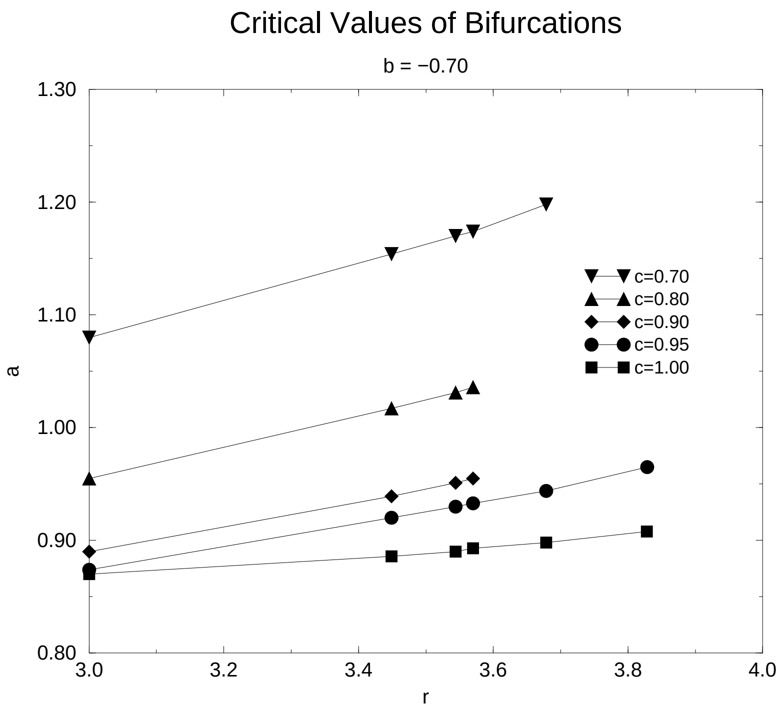


Fig. 10: Relation between the critical values of the parameter r for bifurcations and periodic windows of a quadratic map and the values of the parameter a at which the analogous events occur in the dynamics of our model.

4. Discussion

As long as there is no interaction between replicating species, a population of independently erroneously replicators will eventually converge to a stationary distribution. This description of evolution as optimization-process on an complex combinatory landscapes breaks down if the replicating species are coupled strongly. The resulting system is then properly described by non-linear equations with their richness of complex dynamics.

Different chaotic attractors for different "reaction"-networks have been found in literature with distinct physical or biological motivation. Nevertheless we show equivalence on different levels of these different systems:

Level 1: All chaotic attractors can be "linked" and "live" in a connected region of chaotic attractors. This implies that any two distinct (chaotic) attractors can be transformed continuously into each other without losing their chaotic nature. Regarding *route to chaos*, *bifurcations*, *Lyapunov spectra* all these systems display similar behavior: along selected paths through the parameter-space chaos develops in an almost perfect *Feigenbaum scenario* and breaks down in several crisis and ends in a final limit crisis. Deviation from this behavior occur differently for different pathways. For routes to chaos beginning from chaotic tori another large period 3 window can be observed. For chaotic paths omitting tori period 2 tangent bifurcation are noticed. Lyapunov-spectra with large periodic windows and exponents of ≈ 0.05 have been calculated.

Level 2: Chaotic behavior of interacting biological species (i.e. animals, host$\leftrightarrow$parasite-dynamics, replicating RNA in models of prebiotic evolution, ...) has been observed in different systems independently. Complex dynamics is not only a common feature of interaction-networks but also reveals strong similarities. What we have shown here are explanations of this similar behavior. Experimental verification of complex dynamics in a definite setup has been already discussed in a hypercyclic coupling of RNA (Eigen *et al.*, 1991). Given present day *in vitro* techniques, these issues of rich dynamics are within reach of experimental investigation. We are already able to embed these behavior in a higher context of systems of interacting species.

5. Acknowledgments

The analysis of the chaotic interactions presented here is joint work with Peter Schuster. It will be described in detail elsewhere. Fruitful discussions with Andrea Gaunersdorfer, Juan-Carlos Nuño, Christian Reidys, Bärbel M. Stadler and Peter F. Stadler are gratefully acknowledged. We thank Stephan Kopp and Jacqueline Weber for careful reading of the manuscript. Special thanks to Peter F. Stadler who supplied material for Fig. 2.

6. Appendix

6.1. Models found in Literature

Here we give an overview of models which can be found in literature. These models has been used as an starting point for our studies. In general models of Replicator- or Lotka-Volterra-type have been successfully used in prebiotic evolution, ecology, immunology, medicine, game theory, laser physics, applied mathematics, etc.

GV Vance discovered a "quasi-cyclic" trajectory by studying the rôle of predation on prey coexistence (Vance, 1978). He modeled this system of inter-by using an ordinary Lotka-Volterra equation. Gilpin emphasized the complexity of this ecological model (Gilpin, 1979) and discussed this chaotic behavior with Otto Rössler who refers to it as "spiral chaos".

ACT The aim of Arneode, Coullet, and Tresser was to construct one-parameter families of Lotka-Volterra equations displaying strange attractors (Arneodo *et al.*, 1980). This led them "automatically" to one-predator two-prey systems.

GLM Gardini, Lupini, and Messia characterized the center-critical case of the Hopf-bifurcation of the multi-population equilibrium for a suitable class of Lotka-Volterra systems (Gardini *et al.*, 1989). They reported numerical evidence of transitions to chaotic dynamics, via period-doubling cascades, from the limit cycle.

SG For a two-predator one-prey system Samardzija and Greller studied the behavior of an high order Lotka-Volterra model (Samardzija & Greller, 1988). They observed a explosive route to chaos via a fractal torus. Their model offers a generalization that allows higher-order biological or chemical terms. This is of interest for cases where biological systems experience cataclysmic changes.

SSFS Schnabl, Stadler, Forst, and Schuster observed that the chaotic attractors of the ACT and GV system represent two different cross-sections of one and the same chaotic regime (Schnabl *et al.*, 1991). They used a replicator representation which is based on the simplest possible molecular mechanism of catalyzed replication and mutation. With increasing mutation rates the most relevant result they observed is a substantial reduction in the dynamical *complexity*.

6.2. Transformations and Invariants

In this chapter some symmetry relations and coordinate transformations leading to topologically equivalent systems or systems with the same integrability properties are derived. Let us use the notation

$$\tilde{\wp}_k(x) = a_k^0 + \sum_{j_1=1}^{n} a_{k;j_1}^1 x_{j_1} + \ldots + \sum_{j_1,j_2,\ldots,j_M} a_{k;j_1\ldots j_M}^M x_{j_1} x_{j_2} \ldots x_{j_M} \tag{8}$$

and assume that at least one of the coefficients a^M is non-zero, i.e. $\deg(\wp) = M$. Recalling that $\sum_j x_j = 1$, the following theorem is obvious:

Theorem 1. (*Homogenization.*) Any polynomial replicator equation (4) can be written as homogeneous system

$$\begin{aligned} \dot{x}_k &= x_k \{\wp_k(x) - \sum_{j=1}^{n} \wp_j(x)\} \\ \wp_k(x) &= \sum_{j_1,j_2,\ldots,j_M} A_{j_1 j_2 \ldots j_M} x_{j_1} x_{j_2} \cdot \ldots \cdot x_{j_M} \end{aligned} \tag{9}$$

The coefficients A are given by

$$A_{j_1 j_2 \ldots j_M} = a_k^0 + a_{k;j_1}^1 + a_{k;j_1 j_2}^2 + \ldots + a_{k;j_1 j_2 \ldots j_M}^M \tag{10}$$

Theorem 2. (*Flow Identity on S_n.*) The flow on S_n is identical for two coefficients A and A' if and only if there is a set of constants c such that

$$A_{k;j_1\ldots j_M} - A'_{k;j_1\ldots j_M} = c_{j_1\ldots j_M} \tag{11}$$

for all indices k and j_α.

Proof. Clearly $c_{j_1\ldots j_M} = \sum_k x_k c_{j_1\ldots j_M}$. The sum over all j_α of the first term thus cancels exactly with the second term arising in the flux function Φ. It is obvious that any further manipulation in coefficients does not cancel for all $x \in S_n$. ∎

Theorem 3. (*Reduction Lemma.*) The restriction of (4) to some face of the simplex S_n is again a polynomial replicator equation of at most degree M. The restriction to $\bar{F}_K$ for any index set K is given by omitting all coefficients containing at least one index $j_\alpha \in K$.

For a **proof** see Stadler & Schuster (1992). We remark that the transformations derived thus far apply also to a more general system of ordinary differential equations termed *distributed replicator equations* by Voigt (1989) and recently used as a model for coevolution (Schuster *et al.*, 1993).

Theorem 5. *Barycentric Transformation.* Let $c \in \operatorname{int} R^n_+$ and $A \in (\mathbb{R}^n)^M$. Suppose

$$B_{k;j_1\ldots j_M} = \frac{A_{k;j_1\ldots j_M}}{c_{j_1} c_{j_2} \cdot \ldots \cdot c_{j_M}} \tag{12}$$

Then the polynomial replicator equations with coefficients A and B resp. are topologically equivalent by means of the barycentric transformation

$$y_k = c_k x_k \Big/ \sum_{j=1}^{n} c_j x_j \tag{13}$$

For a **proof** see Forst *et al.*(1995). It is straightforward to compute by calculating $\dot{y}_k$ and using the ODE.

Corollary. Let $\hat{\xi} \in \operatorname{int} S_n$ be a rest point of (4). Then there is positive vector c such that $\hat{\xi}$ is projected onto the barycenter $\frac{1}{n}\mathbf{1}$ of the simplex.

Proof. Choose $c_j = \frac{1}{\hat{\xi}_j}$. Applying theorem 5 immediately completes the proof. ∎

Definition. *Poincaré Transformation.* Let $1 \leq m \leq n$ and define the diffeomorphism $\mathcal{P}$ by

$$\mathcal{P}_m : P_m \to P_m : y_k \to y_k / y_m \quad \forall k \neq m, \text{ and } y_m \to 1/y_m \tag{14}$$

where P_m is the nonnegative orthant without the point for which y_m vanishes, i.e.

$$P_m = \mathbb{R}^n_{+0} \setminus \{x | x_m = 0\}.$$

Theorem 9. For any polynomial Lotka-Volterra equation with polynomials $\wp_k(y)$ of degree $\leq M$ and any $1 \leq m \leq n$ the Poincaré transformed system is topologically equivalent due to a change in velocity to a generalized Lotka-Volterra equation with polynomial $\tilde{\wp}_k(z)$ of degree $\leq M$ on the interior of the positive orthant.

Again we refer for a **proof** to Forst *et al.*(1995).

On the special properties of the Poincaré transformation for quadratic systems we refer to Andronov *et al.* (1973). Its use for the classical Lotka-Volterra Model is discussed in (Hsu, 1978).

Remark. It is possible to obtain sort of a standard form for Lotka-Volterra models with an interior rest point using the barycentric transformation (Theorem 6). The Poincaré transformation then yields a topologically equivalent system which again has this property. Let $G^{(d)}_{k;j_1,\ldots,j_d}(m)$ denote the coefficients of the polynomials of the Poincaré transformed polynomials (0 refers to the initial problem). Then we have

$$\sum_{d=1}^{M} \sum_{j_1,\ldots,j_d=1}^{M} G^{(d)}_{k;j_1,\ldots,j_d}(m) = 0 \tag{15}$$

independent of the considered coordinate (k) or transformation (m). Note that the above coefficients are obtained formally be applying the composite diffeomorphism on $\operatorname{int} \mathbb{R}^n_+$

$$\mathcal{T}_{jm} = \tau_4 \mathcal{P}_m \cdot \tau_3 \mathcal{H}_j \cdot \tau_2 \mathcal{B} \cdot \tau_1 \mathcal{H}_j^{-1}$$

where τ_ℓ denote changes in velocity, $\mathcal{H}_j$ is Hofbauer's transform (1981) projecting $\mathbf{e}_j$ onto the origin and $\mathcal{B}$ denotes the barycentric transformation for the replicator equation.

References

M. A. Andrade, J. C. Nuño, F. Morán, F. Montero, and G. J. Mpitsos. Complex dynamics of a catalytic network having faulty replication into error-species. *Physica D*, 63:21–40, 1993.

A. A. Andronov, E. A. Leontovich, I. I. Gordon, and A. G. Maier. *Qualitative Theory of Second Order Dynamical Systems.* J. Wiley and Sons, New York, 1973.

A. Arneodo, P. Coullet, and C. Tresser. Occurance of strange attractors in three- dimensional volterra equations. *Phys. Lett.*, 79A:259–263, 1980.

R. J. Bagley and J. D. Farmer. Spontaneous emergence of a metabolism. In C. G. Langton, C. Taylor, J. D. Farmer, and S. Rasmussen, editors, *Artificial Life II*, volume X of *Santa Fe Institute Studies in the Science of Complexity*, chapter Origin/Self-Organization, pages 93–141. Addison Wesley, Redwood City, 1992.

R. J. Bagley, J. D. Farmer, and W. Fontana. Evolution of a metabolism. In C. G. Langton, C. Taylor, J. D. Farmer, and S. Rasmussen, editors, *Artificial Life II*, volume X of *Santa Fe Institute Studies in the Science of Complexity*, chapter Origin/Self-Organization, pages 141–158. Addison Wesley, Redwood City, 1992.

G. Bennetin, L. Galgani, A. Giorgilli, and J.-M. Strelcyn. Lyapunow characteristic exponents for smooth dynamical systems and for hamiltonian systems ; a method for computing all of them. *Meccania*, 15:9–21, 1980.

I. M. Bomze. Lotka-Volterra Equation and replicator dynamics: A two-dimensional classification. *Biol. Cybern.*, 48:201–211, 1983.

J. A. Doudna and J. W. Szostak. RNA catalysed synthesis of complementary-strand RNA. *Nature*, 339:519–522, 1989.

M. Eigen. Selforganization of matter and the evolution of biological macromolecules. *Die Naturwissenschaften*, 10:465–523, 1971.

M. Eigen, M. Gebinoga, C. K. Biebricher, and W. C. Gardiner. The hypercycle. coupling of RNA and protein biosynthesis in the infection cycle of an RNA bacteriophage. *Biochemistry*, 30:11005 – 11018, 1991.

M. Eigen, J. McCaskill, and P. Schuster. The molecular Quasispecies. volume 75, pages 149 – 263. J. Wiley & Sons, 1989.

M. Eigen and P. Schuster. *The Hypercycle: a principle of natural self-organization.* Springer, Berlin, 1979 (ZBP:23493).

M. Eigen, P. Schuster, K. Sigmund, and R. Wolff. Elementary step dynamics of catalytic hypercycles. *BioSystems*, 13(1-22), 1980.

W. Fontana and L. W. Buss. "The Arrival of the Fittest": Towards a theory of biological organization. *Bull. Math. Biol.*, 1994. in press.

C. V. Forst. *Chaotic Behavior of Reaction-Networks.* PhD thesis, Inst. Theor. Ch., Univ. Vienna, January 1993.

C. V. Forst, P. F. Stadler, and P. Schuster. Chaotic behavior of general reaction networks. in preparation.

L. Gardini, R. Lupini, and M. G. Messia. Hopf bifurcation and transition to chaos in Lotka-Volterra Equation. *J. Math. Biol.*, 27:259–272, 1989.

M. E. Gilpin. Spiral chaos in a predator-prey system. *Amer. Nat.*, 113:301–306, 1979.

J. Hofbauer. On the occurance of limit cycles in the Lotka- Volterra equation. *Nonlinear Analysis*, 5:1003–1007, 1981.

J. Hofbauer and K. Sigmund. *The Theory of Evolution and Dynamical Systems*. Cambridge University Press (Cambridge), 1988.

B. S. Hsu. The application of the Poincaré transformation to the Lotka-Volterra Model. *J. Math. Biol.*, 6:67–73, 1978.

O. Michielin and P. E. Phillipson. Construction of poincare maps for multiply periodic and chaotic flows. *Phys. Lett.*, A 188(4/6):309, 1994.

M. Nowak and P. Schuster. Error tresholds of replication in finite populations, mutation frequencies and the onset of Muller's ratchet. *Journal of theoretical Biology*, 137:375–395, 1989.

J. C. Nuño, M. A. Andrade, and F. Montero. Non-uniformities and superimposed competition in model of an autocatalytic network formed by error-prone selfreplicative species. *Bull. Math.Biol.*, 55:417–449, 1993.

J. C. Nuño, M. A. Andrade, F. Morán, and F. Montero. A model of an autocatalytic network formetd by error-rone self-replicative species. *Bull. Math. Biol.*, 55:385–415, 1993.

P. E. Phillipson and P. Schuster. Map dynamics of autocatalytic networks and the replicator equations. *J. Math. Biol.*, 32(6):545, 1994.

N. Samardzija and L. D. Greller. Explosive route to chaos through a fractal torus in a generalized Lotka-Volterra Model. *Bull. Math. Biol.*, 50:465–491, 1988.

W. Schnabl, P. F. Stadler, C. Forst, and P. Schuster. Full characterization of a strange attractor: Chaotic dynamics in low dimensional replicator systems. *Physica D*, 48:65 – 90, 1991.

P. Schuster, S. A. Kauffman, P. F. Stadler, and R. Hecht. A two species model for coevolution. *in prep.*, 1993.

S. Smale. On the differential equations of species competition. *J. math. Biol.*, 3:5–7, 1976.

P. F. Stadler, W. Fontana, and J. H. Miller. Random catalytic reaction networks. *Physica D*, 63:378, 1993.

P. F. Stadler and J. C. Nuño. The influence of mutation on autocatalytic reaction networks. *Mathematical Bioscience*, 1994. in press.

P. F. Stadler, W. Schnabl, C. V. Forst, and P. Schuster. Dynamic of small autocatalytic reaction networks – II. Replication, mutation and catalysis. *Bull. Math. Biol.*, 57(1):21–61, 1995.

P. F. Stadler and P. Schuster. Dynamics of small autocatalytic reaction networks. I: Bifurcations, permanence and exclusion. *Bull. Math. Biol.*, 52, no.4:485–508, 1990.

P. F. Stadler and P. Schuster. Mutation in autocatalytic networks - an analysis based on perturbation theory. *J. Math. Biol.*, 30:597–631, 1992.

R. R. Vance. Predation and resource partitioning in one predator - two pray model communities. *Amer. Nat.*, 112:987–813, 1978.

H. M. Voigt. *Evolution and Optimization*. Akademie-Verlag, Berlin, 1989.

A. Wolf, J. B. Swift, H. L. Swine, and J. A. Vastano. Determining Lyapunow exponents from a time series. *Physica D*, pages 285–317, 1985.

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