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DYNAMICAL STUDY OF THE HYPERCYCLE

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Contents

1	Introduction	3
2	Basic concepts	6
2.1	Discrete Dynamical Systems	6
2.2	Continuous Dynamical Systems	7
3	Numerical tools	14
3.1	Numerical Integrators	14
3.1.1	Error control using one step method Integrators	14
3.1.2	The Runge-Kutta-Fehlberg 4-5 method	16
3.2	A numerical computation of the Poincaré map	18
3.3	The Euler-Newton Continuation Method	20
4	The Hypercycle with error tail	24
4.1	The general case	24
4.2	The symmetric case	27
4.2.1	Existence and nature of the fixed points	27
4.2.2	Circulant Matrices	29
4.2.3	Stability of the fixed points	31
4.2.4	Symmetry and periodic orbits	33
4.3	The non-symmetric case	37
4.3.1	Existence and nature of the fixed points	37
4.3.2	Stability of the fixed points	41
4.3.3	Breaking the symmetry for periodic orbits	43
5	Conclusions	45

Abstract

The present manuscript consists in a study of the Hypercycle model with error tail based on previous articles and the original work of Eigen and Schuster. We have analyzed the nature of the fixed points and periodic orbits using analytic and numerical methods. A distinction between the symmetric cases and the non-symmetric ones has been made in order to simplify the study.

Motivation and goals

The original idea for this thesis was to use the Hypercycle as an excuse to learn more about numerical methods in Dynamical Systems, specifically concerning the study of periodic orbits. However during the process we have developed an increasing interest for the biological problem that has led us to give an interpretation of the mathematical results.

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Chapter 1

Introduction

What is the Hypercycle model?

Understanding the meaning of the Hypercycle model implies being familiar with many concepts in Biology. It is not our intention to give a detailed explanation of the biological problem but just a simple version of it so the reader can have an idea of the importance of the model in the biological context.

The elementary Hypercycle described by Eigen and Schuster in [4] attempts to describe the evolution of the relative concentrations in a set of self-replicative molecular species $\{I_1, \dots, I_n\}$ such that every one of them catalyzes the synthesis of the next one, where the one going after I_n is I_1 (cyclic structure). The most known example is the one in which I_1, \dots, I_n are strands of RNA (templates). It was initially conceived by Eigen and Schuster to solve the information crisis in prebiotic evolution.

The information crisis in prebiotic evolution must be understood in the context of the quasispecies model (proposed previously also by Eigen and Schuster), which is another model trying to describe the evolution of macromolecular systems under Darwinian conditions. Basically what they were trying to do is a mathematical model for the behavior of certain systems of macromolecules that evolve under the same conditions as living organisms (Darwinian conditions). The first one they came up with was the quasispecies model but it has a few limitations, namely it is unable to describe the coexistence between different molecular species and it also fails to allow them to have the adequate length. Being unable to model coexistence means leading all species to extinction except from one (this is not very accurate because it is not all species but all quasispecies, for a proper version see [4]). The Hypercycle model seems to solve the coexistence problem, but the length issue has been avoided in most of the studies and even proved to remain unsolved under some hypothesis [7]. Although this second problem should not be ignored, in this work our main interest are the tools used for the study of the system and not the biological meaning, so we shall only treat the first problem.

The elementary Hypercycle model

Assume we have n self replicative molecular species $\{I_1, \dots, I_n\}$. As we said before, the i th component catalyzes the next one and the catalytic aid is expressed in the form of a quadratic term. The differential equation describing the templates concentration $x = (x_1, \dots, x_n)$ is of the form

$$\dot{x}_i = A_i x_i + K_i x_i x_{i-1} - \phi(x), \quad i \in \{1, \dots, n\}, \quad (1.0.1)$$

where $x_0 \equiv x_n$, A_i is the self-replicative rate for the i th template, K_{i+1} the catalytic rate (how the presence of the i th template helps to the formation of the next one) and $\phi(x)$ is a dilution term to keep the total concentration constant. It can be proved as we will do further on in this work for our case of interest that $\phi(x) = \sum_{i=1}^n A_i x_i + \sum_{i=1}^n K_i x_i x_{i-1}$ keeps the total concentration equal to one (provided we start at an initial condition which satisfies that the total concentration is equal to one).

This system satisfies having a stable fixed point with non vanishing components for $n \leq 4$ and for greater values of n stable periodic orbits with non vanishing components as well [4]. This means that the model allows the coexistence of molecular species, which is exactly one of the problems that we wanted to solve from the biological point of view.

The maximal size of macromolecules is not treatable in this case because we are assuming perfect replicative accuracy, which brings no condition on the length of the molecules.

In contrast with the elementary Hypercycle, the Hypercycle model with error tail enables us to consider mutations, which in the mathematical model are collected in a new component of the system representing all the mistranslated copies of the other molecular species. This correction might be seen then as a way to allow the consideration of mutations in our system without interfering with the catalytic relation between templates of the elementary Hypercycle.

The equations for this new model are

$$\dot{x}_i = f_i(x) = x_i(A_i Q + K_i x_{i-1} Q - \Phi(x)), \quad i = 1, \dots, n,$$

and

$$\dot{x}_e = f_e(x) = x_e(A_e - \Phi(x)) + (1 - Q) \sum_{i=1}^n x_i(A_i + K_i x_{i-1}),$$

where $x_0 \equiv x_n$, $K_i, A_i > 0 \forall i \in \{1, \dots, n\}$, $Q \in (0, 1)$ and

$$\Phi(x) = \sum_{i=1}^n x_i(A_i + K_i x_{i-1}) + A_e x_e.$$

Here Q is the replicative accuracy (probability of correct replication). Notice that x_e represents the concentration of the mistranslated copies (error tail), whose derivative with respect to time increases for decreasing values of Q . This implies that a good replicative accuracy will make the error tail smaller and vice versa, exactly as it is supposed to be. The other constants represent the same as in the elementary Hypercycle. A detailed study of this model can be found in chapter 4.

Chapter 2

Basic concepts

In this section we introduce some definitions and results on Dynamical Systems that will be used in our study of the Hypercycle model. Most of these concepts are explained in undergraduate courses from the University of Barcelona so many of the proofs will be omitted. Some of the following results are based on [1] and [2].

2.1 Discrete Dynamical Systems

Consider a discrete dynamical system given by a diffeomorphism $F : U \subseteq \mathbb{R}^n \longrightarrow \mathbb{R}^n$, U an open set. Then

Definition 2.1. $x_0 \in U$ is said to be a fixed point if $F(x_0) = x_0$.

Definition 2.2. We say that a fixed point x_0 is stable if $\forall \epsilon > 0$ there exists a $\delta > 0$ such that for any $x \in B(x_0, \delta)$, $F^k(x) \in B(x_0, \epsilon)$, $\forall k \in \mathbb{N}$.

Definition 2.3. A fixed point x_0 is said to be an attractor if it is stable and there exists an $\epsilon > 0$ such that $\forall x \in B(x_0, \epsilon)$, $\lim_{k \rightarrow \infty} F^k(x) = x_0$.

Definition 2.4. A fixed point x_0 is said to be a repelling fixed point if it is an attractor for F^{-1} .

Definition 2.5. We will say a fixed point p is hyperbolic if $|\lambda| \neq 1$, $\forall \lambda \in \text{Spec}\{DF_p\}$.

Theorem 2.1. Given a linear diffeomorphism $A : \mathbb{R}^n \longrightarrow \mathbb{R}^n$ we denote $\text{Spec}\{A\} = \{\lambda_1, \dots, \lambda_n\}$. Then the three following statements hold:

- (i) If $|\lambda_i| < 1 \forall \lambda_i \in \text{Spec}\{A\}$ then $\vec{0}$ is a global attractor.
- (ii) If $|\lambda_i| > 1 \forall \lambda_i \in \text{Spec}\{A\}$ then $\vec{0}$ is a repelling fixed point.
- (iii) If for some $1 \leq m < n$ we have $|\lambda_1| \leq \dots \leq |\lambda_m| < 1 < |\lambda_{m+1}| \leq \dots \leq |\lambda_n|$, then there exist two subspaces $E^s \subseteq \mathbb{R}^n$ of dimension m and $E^u \subseteq \mathbb{R}^n$ of dimension $n - m$ such that $A|_{E^u}$ is an expansion and $A|_{E^s}$ is a contraction, with $E^s \oplus E^u = \mathbb{R}^n$.

Theorem 2.2. Given a diffeomorphism $F : U \subseteq \mathbb{R}^n \longrightarrow \mathbb{R}^n$, p a fixed point, we denote $\text{Spec}\{DF_p\} = \{\lambda_1, \dots, \lambda_n\}$. Then the three following statements hold:

- (i) If $|\lambda_i| < 1 \forall \lambda_i \in \text{Spec}\{DF_p\}$ then p is an attractor.
- (ii) If $|\lambda_i| > 1 \forall \lambda_i \in \text{Spec}\{DF_p\}$ then p is a repelling fixed point.
- (iii) If for some $1 \leq m < n$ we have $|\lambda_1| \leq \dots \leq |\lambda_m| < 1 < |\lambda_{m+1}| \leq \dots \leq |\lambda_n|$, then locally around p there exist two manifolds

$$W_p^s = \left\{ x \in \mathbb{R}^n \mid \lim_{k \rightarrow \infty} F^k(x) = p \right\}, \quad W_p^u = \left\{ x \in \mathbb{R}^n \mid \lim_{k \rightarrow -\infty} F^k(x) = p \right\},$$

of dimension m and $n - m$ respectively such that $T_p W_p^s = E_p^s$, $T_p W_p^u = E_p^u$, where E_p^s , E_p^u are the corresponding subspaces from Theorem 2.1 for the map $DF_p : \mathbb{R}^n \rightarrow \mathbb{R}^n$.

We shall now state a theorem to characterize saddle-node bifurcations in dimension n .

Theorem 2.3. *Given the C^r map, $r \geq 2$,*

$$\begin{aligned} F : \mathbb{R}^n \times \mathbb{R} &\longrightarrow \mathbb{R}^n \\ (x, \mu) &\longmapsto F(x, \mu), \end{aligned}$$

such that for some $(x_0, \mu_0) \in \mathbb{R}^n \times \mathbb{R}$

- (i) $F(x_0, \mu_0) = x_0$.
- (ii) $DF_x(x_0, \mu_0)$ has eigenvalues $\lambda_1 = 1$ and $|\lambda_i| \neq 1, \forall \lambda_i \in \text{Spec}\{DF_x(x_0, \mu_0)\} = \{\lambda_1, \dots, \lambda_n\}$ with $i \geq 2$. We denote by v_1 the corresponding eigenvector to λ_1 .
- (iii) $w^T (D^2 F_x(x_0, \mu_0))(v_1, v_1) \neq 0$, where w is the left eigenvector for λ_1 .
- (iv) $w^T \frac{\partial F_1}{\partial \mu}(x_0, \mu_0) \neq 0$.

Then there exists a parametrized curve γ

$$\begin{aligned} \gamma : I &\longrightarrow \mathbb{R}^n \times \mathbb{R} \\ t &\longmapsto (x(t), m(t)) \end{aligned}$$

satisfying $\gamma(0) = (x_0, \mu_0)$ and $F(x(t), m(t)) = x(t) \forall t \in I$. Then the point (x_0, μ_0) is said to be a saddle node bifurcation point.

2.2 Continuous Dynamical Systems

We will first collect some results on Ordinary Differential Equations.

Definition 2.6. *A function $f : \mathbb{R}^n \rightarrow \mathbb{R}^n$ is said to be locally Lipschitz if for any $x \in \mathbb{R}^n$ there exists a neighborhood U of x and a constant $M_U > 0$ such that for every $y, z \in U$, $\|f(y) - f(z)\| \leq M_U \|y - z\|$.*

Proposition 2.1. *A function $f : \mathbb{R}^n \rightarrow \mathbb{R}^m$ is locally Lipschitz if and only if for every compact set $K \subset \mathbb{R}^n$ there exists a constant $M_K > 0$ such that for every $z, y \in K$, $\|f(y) - f(z)\| \leq M_K \|y - z\|$.*

Proof. Suppose f is locally Lipschitz. For any $K \subset \mathbb{R}^n$ a compact set we can find a cover $\{U_i\}_{i \in I}$ of K such that $f|_{U_i}$ is Lipschitz. Since K is a compact set it accepts a finite cover $\{U_j\}_{j \in J}$, $J \subset I$ a finite set. Take the maximum value among the constants $\{M_{U_j}\}_{j \in J}$ from definition 2.6, $M_K = \max_{j \in J} \{M_{U_j}\}$. Then for any $z, y \in K$ we have $\|f(y) - f(z)\| \leq M_K \|y - z\|$. The other implication is straightforward. For any $x \in \mathbb{R}^n$ we take K a compact set containing an open set U such that $x \in U$. Then the definition of being Locally Lipschitz is satisfied if we choose $M_U = M_K$. \square

Proposition 2.2. *Let $f : \mathbb{R}^n \rightarrow \mathbb{R}^m$ be a map of class C^r , $r \geq 1$. Then f is locally Lipschitz.*

The previous results have been written for a function with domain \mathbb{R}^n but all of them are still true for U an open subset of \mathbb{R}^n .

Theorem 2.4. *Consider a differential equation $\dot{x} = f(t, x)$, where*

$$\begin{aligned} f : \Omega \subseteq \mathbb{R} \times \mathbb{R}^n &\longrightarrow \mathbb{R}^n \\ (t, x) &\longmapsto f(t, x) \end{aligned}$$

is continuous and locally Lipschitz on x . Then the Initial Value Problem

$$\begin{cases} \frac{d\phi(t)}{dt} = f(t, \phi(t)) \\ \phi(t_0) = x_0 \end{cases}$$

has a unique and maximal solution. This means there exists a solution $\phi : I \subseteq \mathbb{R} \rightarrow \mathbb{R}^n$ with I an open interval such that for any other solution of our IVP, $\psi : J \subseteq \mathbb{R} \rightarrow \mathbb{R}^n$, $J \subseteq I$ and $\psi(t) = \phi(t) \forall t \in J$.

Usually when we talk about the solution of an IVP we are implicitly making reference to its maximal solution.

In order to define the flow for an autonomous differential equation it will be useful to introduce another result on the solutions of differential equations in a more general manner than we did previously in Theorem 2.4.

Proposition 2.3. *Given a differential equation $\dot{x} = f(t, x)$, where*

$$\begin{aligned} f : \Omega \subseteq \mathbb{R} \times \mathbb{R}^n &\longrightarrow \mathbb{R}^n \\ (t, x) &\longmapsto f(t, x) \end{aligned}$$

is C^r ($r \geq 0$) and locally Lipschitz on x , there exists a unique maximal C^r function,

$$\begin{aligned} \Phi : D \subseteq \mathbb{R} \times \Omega \subseteq \mathbb{R} \times \mathbb{R} \times \mathbb{R}^n &\longrightarrow \mathbb{R}^n \\ (t, t_0, x_0) &\longmapsto \Phi(t, t_0, x_0), \end{aligned}$$

such that

- (i) D is an open subset of $\mathbb{R} \times \mathbb{R} \times \mathbb{R}^n$.
- (ii) $\Phi(t_0, t_0, x_0) = x_0$.
- (iii) $\Phi(t, t_1, \phi(t_1, t_0, x_0)) = \Phi(t, t_0, x_0)$.
- (iv) $\frac{d\Phi(t, t_0, x_0)}{dt} = f(t, \Phi(t, t_0, x_0)) \quad \forall (t, t_0, x_0) \in D$.

Consider now a dynamical system given by the autonomous differential equation $\dot{x} = f(x)$, where $f : \Omega \subseteq \mathbb{R}^n \longrightarrow \mathbb{R}^n$ is continuous and locally Lipschitz and Ω is an open set. Equivalently we can consider

$$\begin{aligned} f : \mathbb{R} \times \Omega &\longrightarrow \mathbb{R}^n \\ (t, x) &\longmapsto f(x). \end{aligned}$$

We will call the function

$$\begin{aligned} \phi : D_0 \subseteq \mathbb{R} \times \Omega &\longrightarrow \mathbb{R}^n \\ (t, x_0) &\longmapsto \Phi(t, 0, x_0) \end{aligned}$$

the flow associated to f , where Φ is the solution of the differential equation from proposition 2.3 and $D_0 = \{(t, 0, x_0) \in D\}$. Defined in this way ϕ is a continuous function satisfying the fundamental property of the flow,

- (i) $\phi(t + s, x) = \phi(t, \phi(s, x))$.
- (ii) $\phi(0, x) = x, \quad \forall x \in \Omega$.

We denote by $O_{x_0} = \{\phi(t, x_0), t \in I_{x_0}\}$ the orbit of x_0 , where $I_{x_0} = \{t \in \mathbb{R} \mid (t, 0, x_0) \in D\}$.

Notice that $\phi(\cdot, x_0) : I_{x_0} \longrightarrow \mathbb{R}^n$ is the solution for the Initial Value Problem:

$$\begin{cases} \frac{d\phi(t)}{dt} = f(t, \phi(t)) \\ \phi(0) = x_0 \end{cases}$$

In the following results we will consider an autonomous differential equation $\dot{x} = f(x)$, where $f : \Omega \subseteq \mathbb{R}^n \longrightarrow \mathbb{R}^n$ is continuous and locally Lipschitz, and we will denote its flow by ϕ .

Theorem 2.5. *For all $x_0 \in \Omega$, if $\phi(\cdot, x_0) : I_{x_0} \longrightarrow \mathbb{R}^n$ is such that $\mathbb{R}^+ \cap I_{x_0} = [0, t^*)$ with $t^* < \infty$ then $\forall K \subset \Omega$ a compact set there exists a $t_k^+ \in I_{x_0}$ such that $\forall t_k^+ < t < t^*$ we have $\phi(t, x_0) \notin K$.*

Definition 2.7. A point $p \in \Omega$ is a periodic point with (least) period $T > 0$ provided $\phi(T, p) = p$ and $\phi(t, p) \neq p, \forall 0 < t < T$. Then the set $O_p = \{\phi(t, x_0), 0 \leq t < T\}$ is called a periodic orbit.

Proposition 2.4. The solutions $\phi(\cdot, x_0) : I_{x_0} \longrightarrow \mathbb{R}^n$ have one of the three following forms:

- (i) $\phi(t, x_0) = x_0 \forall t \in I_{x_0}$.
- (ii) $\phi(\cdot, x_0)$ is such that its orbit is periodic.
- (iii) $\phi(\cdot, x_0)$ is a one to one function.

Notice that the three possible types of flow from last proposition are clearly mutually exclusive.

Definition 2.8. We say $x_0 \in \Omega$ is a fixed point if $f(x_0) = 0$.

Definition 2.9. A fixed point x_0 is stable in the Lyapunov sense if $[0, \infty) \subseteq I_{x_0}$ and $\forall \epsilon > 0$ there exists some $\delta > 0$ such that if $x \in B(x_0, \delta) \cap \Omega$ then $\phi(t, x) \in B(x_0, \epsilon), \forall t \geq 0$.

Definition 2.10. A fixed point $x_0 \in \Omega$ is an attractor if it is stable and there exists some $\epsilon > 0$ such that if $x \in B(x_0, \epsilon) \cap \Omega$ then $\lim_{t \rightarrow \infty} \phi(t, x) = x_0$.

Definition 2.11. A point $x_0 \in \Omega$ is a repelling fixed point of f if it is an attracting fixed point for the differential equation $\dot{x} = g(x)$ with $g = -f$.

As we did in the discrete case we will now give a sufficient criteria to decide the character of a fixed point.

Definition 2.12. We will say a fixed point p is hyperbolic if $Re \lambda \neq 0, \forall \lambda \in Spec\{Df_p\}$.

Theorem 2.6. Consider a differential equation $\dot{x} = Ax, A \in \mathbb{R}^{n \times n}, Spec\{A\} = \{\lambda_1, \dots, \lambda_n\}$. Then the three following statements hold:

- (i) If $Re \lambda_i < 0 \forall \lambda_i \in Spec\{A\}$ then $\vec{0}$ is a global attractor.
- (ii) If $Re \lambda_i > 0 \forall \lambda_i \in Spec\{A\}$ then $\vec{0}$ is a repelling fixed point.
- (iii) If for some $1 \leq m < n$ we have

$$Re \lambda_1 \leq \dots \leq Re \lambda_m < 0 < Re \lambda_{m+1} \leq \dots \leq Re \lambda_n,$$

then there exist two subspaces $E^s \subseteq \mathbb{R}^n$ of dimension m and $E^u \subseteq \mathbb{R}^n$ of dimension $n - m$ such that $E^s \oplus E^u = \mathbb{R}^n$ and

$$\forall v \in E^s \phi(t, v) \in E^s \forall t \in \mathbb{R}, \lim_{t \rightarrow \infty} \phi(t, v) = \vec{0},$$

$$\forall w \in E^u \phi(t, w) \in E^u \forall t \in \mathbb{R}, \lim_{t \rightarrow -\infty} \phi(t, w) = \vec{0}.$$

Theorem 2.7. Given the differential equation $\dot{x} = f(x), p$ a fixed point, we denote $Spec\{Df_p\} = \{\lambda_1, \dots, \lambda_n\}$. Then the three following statements hold:

- (i) If $\operatorname{Re} \lambda_i < 0 \forall \lambda_i \in \operatorname{Spec} \{Df_p\}$ then p is an attractor.
- (ii) If $\operatorname{Re} \lambda_i > 0 \forall \lambda_i \in \operatorname{Spec} \{Df_p\}$ then p is a repelling fixed point.
- (iii) If for some $1 \leq m < n$ we have

$$\operatorname{Re} \lambda_1 \leq \dots \leq \operatorname{Re} \lambda_m < 0 < \operatorname{Re} \lambda_{m+1} \leq \dots \leq \operatorname{Re} \lambda_n,$$

then there exist two manifolds

$$W_p^s = \left\{ x \in \mathbb{R}^n \mid \lim_{t \rightarrow \infty} \phi(t, x) = p \right\}, \quad W_p^u = \left\{ x \in \mathbb{R}^n \mid \lim_{t \rightarrow -\infty} \phi(t, x) = p \right\},$$

of dimension m and $n - m$ respectively such that $T_p W_p^s = E_p^s$, $T_p W_p^u = E_p^u$, where E_p^s , E_p^u are the corresponding subspaces from Theorem 2.6 for the differential equation $\dot{x} = Df_p x$.

Recall that the autonomous differential equations in our previous hypothesis are usually called vector fields. The following results and their proofs are based on the notes of a master course on Dynamical Systems given by Ernest Fontich.

Definition 2.13. Let $\dot{x} = f(x)$ and $\dot{y} = g(y)$ be vector fields defined on the open sets U and V respectively. If we denote by ϕ and ψ the respective flows, the two vector fields are topologically conjugated if there exists a homeomorphism $h : U \rightarrow V$ such that

$$h(\phi(t, x)) = \psi(t, h(x)), \quad \forall x \in U,$$

for all $t \in \mathbb{R}$ such that this expression makes sense. In this case we say h is a conjugation between the two vector fields. If h is a diffeomorphism of class C^r , $r \geq 1$, the two vector fields are said to be C^r conjugated.

Proposition 2.5. Given two vector fields $\dot{x} = f(x)$ and $\dot{y} = g(y)$ defined respectively on U and V , a homeomorphism $h : U \rightarrow V$ is a conjugation between both vector fields if and only if

$$Dh(x)f(x) = g(h(x)), \quad \forall x \in U.$$

Proof. Suppose first that h is a conjugation between the two vector fields. Then taking the derivative with respect to t in both sides of the equality

$$h(\phi(t, x)) = \psi(t, h(x)),$$

for any $x \in U$ we obtain $Dh(\phi(t, x))f(\phi(t, x))$ on the left hand side and $g(\psi(t, h(x)))$ on the right one. Evaluating both expressions at $t = 0$ leads to the equality

$$Dh(x)f(x) = g(h(x)), \quad \forall x \in U.$$

We will prove the opposite implication by showing that $\forall x \in U$ the functions $\alpha(t) = h(\phi(t, x))$ and $\beta(t) = \psi(t, h(x))$, wherever they are defined, satisfy the same initial value problem. In that case Theorem 2.4 will tell us that $h(\phi(t, x)) = \phi(t, h(x))$ is actually true.

$$\begin{cases} \alpha'(t) = Dh(\phi(t, x))f(\phi(t, x)) = g(h(\phi(t, x))) = g(\alpha(t)) \\ \alpha(0) = h(\phi(0, x)) = h(x), \end{cases}$$

and on the other hand

$$\begin{cases} \beta'(t) = \psi'(t, h(x)) = g(\psi(t, h(x))) = g(\beta(t)) \\ \beta(0) = \psi(0, h(x)) = h(x). \end{cases}$$

□

Next we shall define what the Poincaré map is and prove its existence under certain conditions.

Definition 2.14. A hypersurface $\Sigma \subset \Omega \subseteq \mathbb{R}^n$ is called a transversal section of a vector field $f : \Omega \rightarrow \mathbb{R}^n$ if

$$\langle f(x) \rangle \oplus T_x \Sigma = \mathbb{R}^n, \quad \forall x \in \Sigma.$$

Lemma 2.1. Let $f : \Omega \rightarrow \mathbb{R}^n$ be a vector field of class C^r . Then the flow ϕ of f is also of class C^r .

Proposition 2.6. Let γ be a periodic orbit of period T of the vector field of class C^r ($r > 0$) $f : \Omega \rightarrow \mathbb{R}^n$ and Σ a transversal section of f of class C^r such that there exists a point $x_0 \in \Sigma \cap \gamma$.

Then there exists a neighborhood $U \subseteq \Omega$ of x_0 and a C^r map $\tau : U \rightarrow \mathbb{R}$ satisfying $\tau(x_0) = T$ such that $\phi(\tau(x), x) \in \Sigma \forall x \in U$ and the function

$$\begin{aligned} P : U \cap \Sigma &\longrightarrow \Sigma \\ x &\longmapsto \phi(\tau(x), x) \end{aligned}$$

is of class C^r . P is the so called Poincaré map.

Proof. We know that Σ is a differentiable manifold so we can assume that in a neighborhood V of x_0 it is given by the equation $\psi(x) = 0$, with ψ of class C^r . It is also true that $T_{x_0} \Sigma = \text{Ker} D\psi(x_0)$. The result will come then from applying the Implicit Function Theorem to the composition $\psi \circ \phi$ restricted to an open set $W \ni (T, x_0)$ such that $\phi(W) \subset V$ (such W exists by lemma 2.1). This function is clearly of class C^r , satisfies $\psi \circ \phi(T, x_0) = 0$ and also

$$\frac{d\psi \circ \phi}{dt}(T, x_0) = D\psi(x_0) \cdot f(\phi(T, x_0)) = D\psi(x_0) \cdot f(x_0) \neq 0.$$

The last expression is different from zero because

$$\left. \begin{array}{l} T_{x_0}\Sigma = \text{Ker}D\psi(x_0) \\ f(x_0) \notin T_{x_0}\Sigma \end{array} \right\} \Rightarrow f(x_0) \notin \text{Ker}D\psi(x_0).$$

Therefore we can apply the IFT to prove that there must be a neighborhood U of x_0 and a function $\tau : U \rightarrow \mathbb{R}$ of class C^r such that $\tau(x_0) = T$ and $\psi(\phi(\tau(x), x)) = 0$, $\forall x \in U$. This last equation means, since $\phi(\tau(x), x) \in V$ because of our choice of the initial domain, that $\phi(\tau(x), x)$ is also in Σ . We conclude that P defined as above is a map resulting from the composition of C^r maps (so it is itself of class C^r) and that the image of this map is contained in Σ (so it exists as we had defined it). \square

Finally we are going to give a definition of stability for periodic orbits, the easiest one we can give with our background (there exists at least another definition that we will not use). First notice that given a transversal or Poincaré section Σ and P_Σ the corresponding Poincaré map (where it is defined), if for some $x_0 \in \Sigma$ we have $P_\Sigma(x_0) = x_0$ then O_{x_0} is a periodic orbit. This result can be proved using proposition 2.4.

Definition 2.15. *Given a Poincaré section Σ and $x_0 \in \Sigma$ such that $P_\Sigma(x_0) = x_0$, we will say the periodic orbit O_{x_0} is stable if x_0 is a stable fixed point for P_Σ . In general we say that O_{x_0} has the same character as x_0 as a fixed point.*

Chapter 3

Numerical tools

In this section we will discuss the numerical methods we have used in the study of the Hypercycle model. All the algorithms explained have been programmed in C and used to produce the numerical results given in section 4. In order to simplify the implementation some functions related to linear algebra such as solving systems of linear equations or calculating eigenvalues have been taken from the GSL-GNU Scientific Library (<https://www.gnu.org/software/gsl/>).

3.1 Numerical Integrators

For integrating ODEs we have used the well-known Runge-Kutta Fehlberg Method, which is a particular case of an error-control method using two one-step methods of order one a unit higher than the other. We assume the reader is familiar with basic methods for approximating solutions of differential equations. All these contents can be found in [3], as well as any previous definition on the matter the reader may need to know. The only difference will be that we generalize to the n th dimensional case.

3.1.1 Error control using one step method Integrators

Consider a continuous and locally Lipschitz function $f : \Omega \rightarrow \mathbb{R}^n$, where $\Omega \subseteq \mathbb{R} \times \mathbb{R}^n$. By Theorem 2.4 we know that there exists a unique maximal solution $\phi : (a, b) \rightarrow \mathbb{R}^n$ for the initial value problem:

$$\begin{cases} \frac{d\phi(t)}{dt} = f(t, \phi(t)) \\ \phi(t_0) = x_0 \end{cases}$$

with $(t_0, x_0) \in \Omega$.

Any one-step method $\{\bar{\phi}_i\}_i$ to approximate ϕ is defined by:

$$\bar{\phi}_{i+1} = \bar{\phi}_i + h_i \cdot \psi(t^i, h_i, \bar{\phi}_i),$$

with $h_i = t^{i+1} - t^i$, $t^0 = t_0$ and $\bar{\phi}_0 = x_0$. ψ depends on the specific method. Examples of these methods are the Euler method, Higher-Order Taylor methods and Runge-Kutta methods.

Recall that a one step method $\{\bar{\phi}_i\}_i$ is said to be of order n if:

$$\phi(t^{i+1}) = \bar{\phi}_i + h_i \cdot \psi(t^i, h_i, \bar{\phi}_i) + O(h_i^{n+1}),$$

assuming $\bar{\phi}_i = \phi(t^i)$. This implies

$$\lim_{h \rightarrow 0} \frac{\|\phi(t^{i+1}) - \bar{\phi}_i - h_i \cdot \psi(t^i, h_i, \bar{\phi}_i)\|}{h_i^n} = 0.$$

Then we know that for an n th-order one-step method, given $\epsilon > 0 \exists h_i > 0$ such that

$$error(i) = \|\bar{\phi}_{i+1} - \phi(t^i + h_i)\| \leq \epsilon \cdot h_i^n.$$

The previous formula shows these methods will work fine locally as long as we take h_i (step length of the i th step) small enough, but we don't have a way to know how small h_i must be in order to obtain a specific bound for the local error. To reach a better control of the error and make our numerical study more consistent, we can use a method of integration with error control. We shall explain how they work in general.

Imagine we have two one step methods of order n and $n + 1$, say $\{\bar{\phi}_{n,i}\}_i$ and $\{\bar{\phi}_{n+1,i}\}_i$. Our goal is to obtain an approximation of $\tau_n(h_i) = \frac{\bar{\phi}_{n,i+1} - \phi(t^i + h_i)}{h_i}$. This last expression gives us the idea of how big is the local error for the n -th order method compared to the step size.

$$\tau_n(h_i) = \frac{\bar{\phi}_{n,i+1} - \phi(t^i + h_i)}{h_i} = \frac{\bar{\phi}_{n,i+1} - \bar{\phi}_{n+1,i+1} + O(h_i^{n+2})}{h_i} = \frac{\bar{\phi}_{n,i+1} - \bar{\phi}_{n+1,i+1}}{h_i} + O(h_i^{n+1}).$$

If we denote $\tilde{\tau}(h_i) = \frac{\bar{\phi}_{n,i+1} - \bar{\phi}_{n+1,i+1}}{h_i}$, the last equality implies

$$\lim_{h_i \rightarrow 0} \frac{\|\tau_n(h_i) - \tilde{\tau}(h_i)\|}{h_i^n} = 0 \Rightarrow \lim_{h_i \rightarrow 0} \frac{\tilde{\tau}(h_i)}{h_i^n} = \lim_{h_i \rightarrow 0} \frac{\tau_n(h_i)}{h_i^n} = \vec{l} \neq \vec{0} \quad (3.1.1)$$

for a certain $\vec{l} \in \mathbb{R}^n$. This is the reason why we consider $\|\tilde{\tau}(h_i)\|$ as a good approximation for $\|\tau_n(h_i)\|$ when taking h_i small.

Now that we have the approximation of the error for the n th order one step method depending on the step length, we are able to use it in order to modify h_i whenever $\|\tilde{\tau}(h_i)\|$ is not below a certain tolerance. When this happens, we can calculate the new step size multiplying h_i by a certain $q \in \mathbb{R}$, which is chosen using the following criteria. We know

$$\lim_{h_i \rightarrow 0} \frac{\tau_n(qh_i)}{q^n \cdot h_i^n} = \lim_{qh_i \rightarrow 0} \frac{\tau_n(qh_i)}{(qh_i)^n} = \vec{l} = \lim_{h_i \rightarrow 0} \frac{\tilde{\tau}_n(h_i)}{h_i^n},$$

where in the last equality we use (3.1.1). Therefore

$$\lim_{h_i \rightarrow 0} \frac{\tau_n(qh_i)}{h_i^n} = \lim_{h_i \rightarrow 0} \frac{q^n \cdot \tilde{\tau}_n(h_i)}{h_i^n}.$$

This last equality tells us that $q^n \cdot \|\tilde{\tau}_n(h_i)\|$ is a good approximation for $\|\tau_n(qh_i)\|$ when h_i is small, so if we want to impose $\|\tau_n(qh_i)\| \leq \epsilon$ we can do it by choosing q such that

$$q \leq \sqrt[n]{\frac{\epsilon}{\|\tilde{\tau}_n(h_i)\|}}.$$

Then we recalculate $\bar{\phi}_{n,i+1}$ with our new $h'_i = q \cdot h_i$, and we keep on with the process. Notice that this method will require to recalculate many times the step length during the whole process of integration, namely every time that the inequality $\|\tilde{\tau}(h_i)\| \leq \epsilon$ doesn't hold. In the next section we specify the Algorithm for the method we have used.

3.1.2 The Runge-Kutta-Fehlberg 4-5 method

In this section we present the algorithm for the Runge-Kutta-Fehlberg 4-5 method, which is an error control method using Runge-Kutta of order 4 and 5 as one-step methods.

The notation we have used corresponds to the following IVP:

$$\begin{cases} \frac{d\phi(t)}{dt} = f(t, \phi(t)) \\ \phi(t_0) = x_0 \end{cases}$$

for $a \leq t \leq b$.

In order to avoid the problem of recalculating h too many times Algorithm 1 prevents the possible failure of the next step by changing the value of h every time. We will not justify the specific values for the coefficients K_i , $i \in \{1, \dots, n\}$.

Algorithm 1 RKF 4-5

```
function RKF( $a, b, x_0$ )
  set:  $t = a, flag = 1, tol, h_{max}, h_{min}, h$ 
  while  $flag = 1$  do
    function RKF-STEP( $\tau, t, x_0, x_1, h$ )
      if  $\tau \leq tol$  then
         $t = t + h$ 
        output ( $t, x_1$ )
         $x_0 = x_1$ 
         $\delta = 0.84 \sqrt[4]{\frac{tol}{\tau}}$ 
        if  $\delta \leq 0.1$  then
           $h = 0.1h$ 
        else if  $\delta \geq 4$  then
           $h = 4h$ 
        else
           $h = \delta h$ 
        if  $h > h_{max}$  then
          set  $h = h_{max}$ 
        if  $t \geq b$  then
           $flag = 0$ 
        else if  $t + h > b$  then
           $h = b - t$ 
        else if  $h < h_{min}$  then
           $flag = 0$ , output error message
```

Algorithm 2 One step RKF

```
function RKF-STEP( $\tau, t, x_0, x_1, h$ )
   $K_1 = h \cdot f(x_0)$ 
   $K_2 = h \cdot f(t + \frac{1}{4}h, x_0 + \frac{1}{4}K_1)$ 
   $K_3 = h \cdot f(t + \frac{3}{8}h, x_0 + \frac{3}{32}K_1 - \frac{9}{32}K_2)$ 
   $K_4 = h \cdot f(t + \frac{12}{13}h, x_0 + \frac{1932}{2197}K_1 - \frac{7200}{2197}K_2 + \frac{7296}{2197}K_3)$ 
   $K_5 = h \cdot f(t + h, x_0 + \frac{439}{216}K_1 - 8K_2 + \frac{3680}{513}K_3 - \frac{845}{4104}K_4)$ 
   $K_6 = h \cdot f(t + \frac{1}{2}h, x_0 - \frac{8}{27}K_1 + 2K_2 + \frac{3544}{2565}K_3 + \frac{1859}{4104}K_4 - \frac{11}{40}K_5)$ 
   $x_1 = x_0 + \frac{25}{216}K_1 + \frac{1408}{2565}K_3 + \frac{2197}{4104}K_4 - \frac{1}{5}K_5$ 
   $\tau = \frac{1}{h} \| \frac{1}{360}K_1 - \frac{128}{4275}K_3 - \frac{2197}{75240}K_4 + \frac{1}{50}K_5 + \frac{2}{55}K_6 \|$ 
```

3.2 A numerical computation of the Poincaré map

Consider we are in the same hypothesis as in section 3.1.1, with the only difference that now we have an autonomous differential equation. A theoretical definition and study of the Poincaré map properties can be found in section 2.2.

Suppose the Poincaré section is a hyperplane. We will build the Poincaré map P associated to the vector field $\dot{x} = f(x)$ numerically (whenever it is possible, because it is not even sure it exists) by using the Runge-Kutta Fehlberg Method and Newton's Method. Firstly, we can assume that the Poincaré section is of the form $\Sigma = \{(x^1, \dots, x^n) \in \mathbb{R}^n \mid x^j = c\}$ for some $c \in \mathbb{R}$, $j \in \{1, \dots, n\}$. If that was not the case we could always make a linear change of variables in order to obtain the desired expression for Σ . We can also assume that $f_j(a)$ is either strictly positive or negative because we have assumed that Σ is transversal to ϕ in a .

The idea of the method is to start iterating our numerical integrator at some point x_0 on the Poincaré section Σ and check when does $\{\bar{\phi}_i\}_i$ cross the section again (in the same direction). The point where it does so will not be found precisely in this way, so we will adjust it by applying Newton's method. This means that once we have crossed the section (how to check it is specified in Algorithm 3) we will recalculate the new step length h used by the function RKF-step in Algorithm 2 using the formula

$$h = \frac{c - \phi_i^j}{f_j(\phi_i)}, \quad (3.2.1)$$

where we are supposing that we have crossed the section at the i th step. Next we iterate formula (3.2.1) until convergence to Σ is achieved (or not, then we stop and return an error message) at some k th step, where

$$|\phi_k^j - c| < tol,$$

with tol the maximal distance we allow between our final point and Σ . If the Newton Method converges, the point where it does will then be considered a numerical approximation of $P(x_0)$.

Here $\{\bar{\phi}_i\}_i$ is the Iterative method we are using to solve the Initial Value Problem, which in our case is RK-Fehlberg but in general it could be any method for integrating ODEs.

Notice that in Algorithm 3, b is an upper bound for the integration time, that is, if we have not crossed the hyperplane again before b then we stop the process (it could happen that we never get to cross the section so we must stop at some point), whereas in Algorithm 1 we do the whole integration from a to b . Furthermore in this case the differential equation is autonomous so we could use always $a = 0$.

Algorithm 3 Poincaré map

```
function PMAP( $a, b, x_0$ )
  set:  $t = a, flag = 1, flag2 = 0, flag3 = 0, flag4 = 0, countmax,$ 
   $tol, h_{max}, h_{min}, h$ 
  while  $flag = 1$  do
    function RKF-STEP( $\tau, t, x_0, x_1, h$ )
      if  $\tau \leq tol$  then
         $t = t + h$ 
        if  $flag3 = 1$  or Condition1 or Condition2 then
           $\triangleright$  Condition1 is ( $x_0^j > c$  and  $x_1^j < c$ ) and  $flag2 = 0$ 
           $\triangleright$  Condition2 is ( $x_1^j > c$  and  $x_0^j < c$ ) and  $flag2 = 1$ 
           $h = \frac{c-x_1^j}{f_j(x_1)}$ 
           $flag3 = 1$ 
           $count = count + 1$ 
          if  $|x_1^j - c| < tol$  then
             $flag = 0, flag4 = 1$ 
           $x_0 = x_1$ 
          if  $count > countmax$  then
             $flag = 0$ 
        if  $flag3 = 0$  then
           $\delta = 0.84 \sqrt[4]{\frac{tol}{\tau}}$ 
          if  $\delta \leq 0.1$  then  $h = 0.1h$ 
          else if  $\delta \geq 4$  then  $h = 4h$ 
          else  $h = \delta h$ 
          if  $h > h_{max}$  then
            set  $h = h_{max}$ 
          if  $t \geq b$  then
             $flag = 0$ 
          else if  $t + h > b$  then
             $h = b - t$ 
          else if  $h < h_{min}$  then
             $flag = 0, \text{output error message}$ 
    if  $flag4 = 0$  then
      output error message
```

3.3 The Euler-Newton Continuation Method

Let us give first some previous results on parametric curves and the arc length parametrization.

Definition 3.1. A parametric curve is a differentiable map $\alpha : I \rightarrow \mathbb{R}^n$, with I an open interval of \mathbb{R} .

Definition 3.2. Let $\alpha : I \rightarrow \mathbb{R}^n$ be a parametric curve. The arc length map $s : I \rightarrow \mathbb{R}$ with origin $t_0 \in I$ is defined as:

$$t \mapsto s(t) = \int_{t_0}^t \|\alpha'(t)\| dt$$

Definition 3.3. The parameter t from a parametric curve α is said to be the arc length parameter if $\|\alpha'(t)\| = 1, \forall t \in I$. In this case α is said to be parametrized by the arc length.

Definition 3.4. A parametric curve $\alpha : I \rightarrow \mathbb{R}^n$ is said to be 1-regular if $\|\alpha'(t)\| \neq 0 \forall t \in I$.

Definition 3.5. Let $\alpha : I \rightarrow \mathbb{R}^n$ be a parametric curve. Any diffeomorphism $h : I \rightarrow J$, with J an open interval of \mathbb{R} is said to be a reparametrization of α . We call $\alpha \circ h^{-1} : J \rightarrow \mathbb{R}^n$ the reparametrized curve.

Proposition 3.1. Any 1-regular parametric curve $\alpha : I \rightarrow \mathbb{R}^n$ can be reparametrized by the arc length. In fact for every $t_0 \in I$, the reparametrized curve given by composing α with the inverse of the arc length function s with origin in t_0 is a curve parametrized by the arc length.

Assume we are given some function $f : U \rightarrow \mathbb{R}^n$, $U \subseteq \mathbb{R}^{n+1}$ an open set, f of class C^r , $r \geq 1$. Suppose that we have an initial point $x_0 \in U$ such that $f(x_0) = \vec{0}$ and $\text{rank}(Df(x_0)) = n$.

Our goal is to find a numerical expression for a function

$$\begin{aligned} g : J &\longrightarrow \mathbb{R}^n \\ t &\longmapsto (g_1(t), \dots, g_n(t)) \end{aligned}$$

such that $f(g(t)) = \vec{0} \forall t \in J$ and $g(t_0) = x_0$ for a certain $t_0 \in J$. We will now describe a first attempt to solve the problem.

We know by means of the Implicit Function Theorem (IFT) that our solution does exist near $x_0 = (x_0^0, x_0^1, \dots, x_0^n)$, that is that there exists an open interval $J \subseteq \mathbb{R}$, $x_0^i \in J$ for some $i \in \{0, 1, \dots, n\}$ and a function

$$\begin{aligned} x : J &\longrightarrow \mathbb{R}^n \\ x^i &\longmapsto (x_1(x^i), \dots, x_n(x^i)) \end{aligned}$$

such that $f(x_1(x^i), \dots, x^i, \dots, x_n(x^i)) = \vec{0}, \forall x^i \in J$ and $x(x_0^i) = x_0$.

If we compute the derivative of the last function with respect to x^i we will be able to apply one step of the Euler Method in x_0 and then apply Newton's Method to obtain a new point in $\{x \in \mathbb{R}^{n+1} | f(x) = 0\}$. From this new point we could repeat the process.

This procedure is fine except for two facts. The first is that it is difficult to compute if we do not have a way to know with respect to which variable is the IFT going to work. The second problem is that the function f goes from \mathbb{R}^{n+1} to \mathbb{R}^n , which is not the right setting for applying the Newton method (the two spaces should have the same dimension). In the following we shall give an explanation based on [9] of how Euler-Newton's Continuation method really works, which consists basically in the same process but solving these problems. We know from $f(x(x^i)) \equiv 0$ that $Df(x(x_0^i))x'(x_0^i) = 0$. Developing this last equation :

$$\begin{pmatrix} \frac{\partial f_1(x(x_0^i))}{\partial x^0} & \cdots & \frac{\partial f_1(x(x_0^i))}{\partial x^{n-1}} & \frac{\partial f_1(x(x_0^i))}{\partial x^n} \\ \frac{\partial f_n(x(x_0^i))}{\partial x^0} & \cdots & \frac{\partial f_n(x(x_0^i))}{\partial x^{n-1}} & \frac{\partial f_n(x(x_0^i))}{\partial x^n} \end{pmatrix} \begin{pmatrix} x^{0'}(x_0^i) \\ \vdots \\ x^{n'}(x_0^i) \end{pmatrix} = \begin{pmatrix} 0 \\ \vdots \\ 0 \end{pmatrix} \Rightarrow$$

$$\underbrace{\begin{pmatrix} \frac{\partial f_1(x(x_0^i))}{\partial x^0} & \cdots & \widehat{\frac{\partial f_1(x(x_0^i))}{\partial x^i}} & \frac{\partial f_1(x(x_0^i))}{\partial x^n} \\ \frac{\partial f_n(x(x_0^i))}{\partial x^0} & \cdots & \widehat{\frac{\partial f_n(x(x_0^i))}{\partial x^i}} & \frac{\partial f_n(x(x_0^i))}{\partial x^n} \end{pmatrix}}_{D_i} \begin{pmatrix} x^{0'}(x_0^i) \\ \widehat{x^{i'}(x_0^i)} \\ x^{n'}(x_0^i) \end{pmatrix} = -x^{i'}(x_0^i) \cdot \begin{pmatrix} \frac{\partial f_1(x(x_0^i))}{\partial x^i} \\ \vdots \\ \frac{\partial f_n(x(x_0^i))}{\partial x^i} \end{pmatrix}$$

We also know that $rank(Df(x_0)) = n$, so there exists $i \in \{0, 1, \dots, n\}$ such that $det(D_i) \neq 0$. If this is the i we are considering, we know the previous linear system has a unique solution. Denoting

$$A_j = \begin{vmatrix} \frac{\partial f_1(x(x_0^i))}{\partial x^0} & \cdots & \widehat{\frac{\partial f_1(x(x_0^i))}{\partial x^j}} & \cdots & \frac{\partial f_1(x(x_0^i))}{\partial x^n} \\ \frac{\partial f_n(x(x_0^i))}{\partial x^0} & \cdots & \widehat{\frac{\partial f_n(x(x_0^i))}{\partial x^j}} & \cdots & \frac{\partial f_n(x(x_0^i))}{\partial x^n} \end{vmatrix}$$

and using Cramer's rule we have this solution is given by

$$\frac{x^{j'}(x_0^i)}{x^{i'}(x_0^i)} = (-1)^{j-i} \cdot \frac{A_j}{det(D_i)} = (-1)^{j-i} \cdot \frac{A_j}{A_i}$$

Since $\overline{x^i(x_0^i)} = 1$ this leads us to the equality

$$x^{j'}(x_0^i) = (-1)^{j-i} \cdot \frac{A_j}{A_i} \quad j \in \{1, \dots, n\}. \quad (3.3.1)$$

We would like to find the derivative of our function x parametrized by the arc length if the reparametrization with respect to the arc length is possible. Let's prove this is actually the case. Since $\overline{x^i(x^i)} = 1, \forall x^i \in J \Rightarrow \|x'(x^i)\| \geq 1, \forall x^i \in J$. Then x is a regular curve so using proposition 3.1 we get the desired result.

Now to be able to compute the reparametrized curve we only need to find its derivative. We know by definition of the arc length s that:

$$s'(x_0^i)^2 = \sum_{j=0}^{j=n} (x^{j'}(x_0^i))^2 = \frac{\sum_{j=0}^{j=n} A_j^2}{A_i^2} \Rightarrow s'(x_0^i) = \frac{\sqrt{\sum_{j=0}^{j=n} A_j^2}}{A_i}, \quad (3.3.2)$$

where we are using (3.3.1). Notice that $s'(x_0^i) \neq 0$. We finally find, using equalities (3.3.1) and (3.3.2):

$$\frac{dx^j}{ds}(s(x_0^i)) = \frac{x^{j'}(x_0^i)}{s'(x_0^i)} = (-1)^{j-i} \cdot \frac{A_j}{\sqrt{\sum_{k=0}^{k=n} A_k^2}}, \quad \forall j \in \{1, \dots, n\}. \quad (3.3.3)$$

This last formula gives us a way to compute the derivatives of x^j with respect to the arc length for every j . This turns out to be very helpful in the sense that we don't need to worry at each step about with respect to which variable the IFT is applicable.

Remark. If we want to continue the curve in the opposite direction we just have to change all signs in (3.3.3).

We still need to solve our second problem though. Remember that now what we should do is calculating a first approximation $x_0^{(1)}$ of the next point of the curve applying one step of the Euler method, and after that we should find some way to generate a sequence $\{x_0^{(k)}\}_k$ converging to a point in $\{x \in \mathbb{R}^{n+1} \mid f(x) = 0\}$. A way to find an adequate recurrence for this sequence is through considering the problem of minimizing $\|\Delta x\|^2$ subject to the constraint $f(x) + Df(x)\Delta x = 0$. The idea of the method is to find a point on the curve (imposed by the constraint at first order) as close as possible to the first approximation (minimizing $\|\Delta x\|^2$). The Lagrangian function associated to this conditioned extrema problem is:

$$L(\Delta x, \lambda) = \|\Delta x\|^2 + \lambda^T \cdot (f(x) + Df(x)\Delta x).$$

To find its solution we must solve the system given by the equations:

$$\begin{cases} 0 &= \frac{dL}{d\Delta x_i} = 2\Delta x_i + \sum_{j=1}^{j=n} \lambda_j \frac{df_j}{dx_i}, & i \in \{1, \dots, n\} \\ f(x) &= -Df(x)\Delta x. \end{cases}$$

From the first one we automatically get $\Delta x_i = \frac{1}{2} \sum_{j=1}^{j=n} \lambda_j \frac{df_j}{dx_i}$. By substituting into the second equation we have

$$f(x) = -\frac{-Df(x)(\lambda^T Df(x))^T}{2} \Rightarrow \lambda = (-2Df(x)Df(x)^T)^{-1}f(x),$$

and finally coming back to the former expression of Δx_i we obtain the equality $\Delta x = -Df(x)^T(Df(x)Df(x)^T)^{-1}f(x)$, which gives us the desired recurrence

$$x^{(k+1)} = x^{(k)} - Df(x^{(k)})^T(Df(x^{(k)})Df(x^{(k)})^T)^{-1}f(x^{(k)}).$$

There is a proof of the convergence of this sequence to $\{x \in \mathbb{R}^{n+1} \mid f(x) = 0\}$ in [8].

This ends one step of the procedure. Iterating the process we can continue the curve as long as the required condition on the rank of the differential of f at the following points is satisfied. Let us summarize the whole process by giving the corresponding algorithm.

Algorithm 4 Euler-Newton Continuation method

```

function ENCMETHOD( $x_0$ ,  $maxiter$ ,  $h$ )
  set:  $s = 0$ ,  $countmax$ ,  $count = 0$ ,  $tol$ 
  for  $i = 0$  to  $i = maxiter$  do
     $x_0 = x_1$ 
    Calculate  $Df(x_0)$ 
    Calculate  $A_j$ ,  $j \in \{1, \dots, n\}$ 
    for  $j = 0$  to  $j = n + 1$  do
       $\frac{dx_j}{ds} = (-1)^j \cdot \frac{A_j}{\sqrt{\sum_{k=0}^{k=n} A_k^2}}$ 
     $x_1 = x_0 + h \cdot \frac{dx_j}{ds}$ 
    while  $count < countmax$  or  $|f(x_1)| > tol$  do
       $x_0 = x_1$ 
       $x_1 = x_0 - Df(x_0)^T(Df(x_0)Df(x_0)^T)^{-1}f(x_0)$ 
       $count = count + 1$ 
    if  $count = countmax$  then
      output error message
    output  $x_1$ 
     $count = 0$ ,  $i = i + 1$ 

```

Chapter 4

The Hypercycle with error tail

4.1 The general case

In this section we define the Hypercycle model with error tail and discuss some of its basic properties. For the sake of simplicity and since we only treat this case there is no possible misunderstanding, we will name it also as the Hypercycle model. Many of the ideas in this chapter and the definition of the model have been taken from [6].

Definition 4.1. *We will call a Hypercycle model of dimension n the dynamical system defined by the following differential equation:*

$$\dot{x}_i = f_i(x) = x_i(A_i Q + K_i x_{i-1} Q - \Phi(x)), \quad i = 1, \dots, n \quad (4.1.1)$$

and

$$\dot{x}_e = f_e(x) = x_e(A_e - \Phi(x)) + (1 - Q) \sum_{i=1}^n x_i(A_i + K_i x_{i-1})$$

where $x_0 \equiv x_n$, $K_i, A_i > 0 \quad \forall i \in \{1, \dots, n\}$, $Q \in (0, 1)$ and

$$\Phi(x) = \sum_{i=1}^n x_i(A_i + K_i x_{i-1}) + A_e x_e.$$

Notice that $f = (f_1, \dots, f_n, f_e)$ is a polynomial on $x = (x_1, \dots, x_n, x_e)$ so it is of class C^∞ and therefore locally Lipschitz by proposition 2.2. Thus by Theorem 2.4 for any IVP there exists a unique continuous maximal solution. The component x_e is clearly the one representing the error tail.

Proposition 4.1. *The hyperplane $H = \{x \in \mathbb{R}^{n+1} \mid \sum_{i=1}^n x_i + x_e = 1\}$ is invariant under the action of the hypercycle model.*

Proof. Consider the solution $x(\cdot) = x(\cdot, x_0) : I \longrightarrow \mathbb{R}^{n+1}$ for the hypercycle model with initial condition $x_0 \in H$ and maximal domain $I \subseteq \mathbb{R}$. Then $y(t) = \sum_{i=1}^n x_i(t) + x_e(t)$ satisfies the differential equation $\dot{y} = F(t, y)$, where

$$\begin{aligned} F : I \times \mathbb{R} &\longrightarrow \mathbb{R} \\ (t, y) &\longmapsto \Phi(x(t))(1 - y). \end{aligned}$$

The result comes from the equality

$$\begin{aligned} \frac{dy}{dt} &= \sum_{i=1}^n f_i(x(t)) + f(x_e(t)) = \sum_{i=1}^n x_i(t)(A_i Q + K_i x_{i-1}(t)Q - \Phi(x(t))) + \\ &+ x_e(t)(A_e - \Phi(x(t))) + (1 - Q) \sum_{i=1}^n x_i(t)(A_i + K_i x_{i-1}(t)) = \\ &= x_e(t)(A_e - \Phi(x(t))) + \sum_{i=1}^n x_i(t)(A_i + K_i x_{i-1}(t)) - \sum_{i=1}^n \Phi(x(t))x_i(t) = \\ &= \Phi(x(t)) - \underbrace{\Phi(x(t)) \left(x_e(t) + \sum_{i=1}^n x_i(t) \right)}_{y(t)} = \Phi(x(t)) - \Phi(x(t))y(t). \end{aligned}$$

This allows us to find $y(t)$ as the solution for the initial value problem:

$$\begin{cases} \frac{dy(t)}{dt} = F(t, y(t)) = \Phi(x(t))(1 - y(t)) \\ y(0) = 1. \end{cases} \quad (4.1.2)$$

But it turns out that the solution of this IVP is precisely $\tilde{y}(t) \equiv 1$, because for any $t \in I$ we have

$$F(t, \tilde{y}(t)) = \Phi(x(t)) - \Phi(x(t)) = 0 = \frac{d\tilde{y}(t)}{dt}.$$

Notice that F is continuous and locally Lipschitz on y . Then using Theorem 2.4 we obtain that $\tilde{y}(t) \equiv 1$ is the only solution of (4.1.2), so

$$\sum_{i=1}^n x_i(t) + x_e(t) = 1, \quad \forall t \in I.$$

□

From now on we will restrict our study to the solutions in H , and we will often omit the term x_e because it is given implicitly by $x_e = 1 - \sum_{i=1}^n x_i$. It is clear then that studying the differential equation

$$\dot{x}_i = \hat{f}_i(x) = x_i(A_i Q + K_i x_{i-1} Q - \hat{\Phi}(x)), \quad i = 1, \dots, n,$$

where $\hat{\Phi}(x) = \sum_{i=1}^n x_i(A_i + K_i x_{i-1}) + A_e(1 - \sum_{i=1}^n x_i)$ with $x = (x_1, \dots, x_n) \in H$ is enough to understand the dynamics of our system inside H .

The following proposition can be seen as a consequence of this fact and it will be useful later when we study the existence of fixed points.

Proposition 4.2. *A point $x^* \in H$ is a fixed point of the general Hypercycle model if and only if $f_i(x^*) = 0, \forall i \in \{1, \dots, n\}$.*

Proof. From proposition 4.1 we know any point $x \in H$ satisfies $\sum_{i=1}^n f_i(x) + f_e(x) = 0$. Then we have $f_i(x^*) = 0, \forall i \in \{1, \dots, n\} \Rightarrow f_e(x^*) = -\sum_{i=1}^n f_i(x^*) = 0 \Rightarrow x^*$ is a fixed point. The other implication is true by definition of fixed point. \square

Proposition 4.3. *The set*

$$S = \left\{ (x_1, \dots, x_n, x_e) \in H \mid x_i \in [0, 1] \quad \forall i \in \{1, \dots, n\}, \sum_{i=1}^n x_i \leq 1 \right\}$$

is positively invariant under the action of the Hypercycle model.

Proof. Notice that $S = \{(x_1, \dots, x_n, x_e) \in H \mid x_e, x_i \in [0, 1], \forall i \in \{1, \dots, n\}\}$. Imagine we have a solution $x(t)$ of our IVP with initial condition in S such that for a certain $t^* \in J, t^* \geq 0$, (where J is the maximal domain of our solution) $x(t^*) = (x_1(t^*), \dots, x_n(t^*))$ is such that $x_i(t^*) = 0$ for some $i \in \{1, \dots, n\}$. Consider now the solution of the new differential equation of dimension n given by the equations of the Hypercycle model except from the i th one and taking $x_i \equiv 0$.

$$\begin{cases} \dot{x}_j = f_j(x), & \forall j \in \{1, \dots, \hat{i}, \dots, n\} \\ \dot{x}_e = f_e(x). \end{cases}$$

This is a continuous and locally Lipschitz function so it still has a unique maximal solution $\tilde{x}(t) = (\tilde{x}_1(t), \dots, \widehat{\tilde{x}_i(t)}, \dots, \tilde{x}_n(t), \tilde{x}_e(t))$ for the IVP with initial condition $\tilde{x}_0 = (x_1(t^*), \dots, \widehat{x_i(t^*)}, \dots, x_n(t^*), x_e(t^*))$. Then $x(t) = (\tilde{x}_1(t), \dots, 0, \dots, \tilde{x}_n(t), \tilde{x}_e(t))$ solves the original IVP and by Theorem 2.4 it is the unique solution. This implies we cannot cross the hyperplane $\{x \in \mathbb{R}^{n+1} \mid x_i = 0\}$. Informally any solution on it will stay there, and no solution can reach it from outside.

We must check as well that we cannot cross $\{(x_1, \dots, x_n, x_e) \in \mathbb{R}^{n+1} \mid x_e = 0\}$. So imagine now that we have a solution of our IVP with starting point in S such that for a certain $t^* \in J, t^* \geq 0, x(t^*) = (x_1(t^*), \dots, x_n(t^*), x_e(t^*))$ is such that $x_e(t^*) = 0$. This implies

$$\begin{aligned} f_e(x(t^*)) &= x_e(t^*)(A_e - \Phi(x(t^*))) + (1 - Q) \sum_{j=1}^n x_j(t^*)(A_j + K_j x_{j-1}(t^*)) = \\ &= (1 - Q) \sum_{j=1}^n x_j(t^*)(A_j + K_j x_{j-1}(t^*)) > 0, \end{aligned}$$

so it is clear we cannot cross $\{(x_1, \dots, x_n, x_e) \in \mathbb{R}^{n+1} \mid x_e = 0\}$ from S . Notice that we could cross it from outside S ! This is why S is positively invariant and not invariant.

The cases $x_i(t^*) = 1$ for some $i \in \{1, \dots, n\}$ or $x_e(t^*) = 1$ are included in the previous ones. Notice $\sum_{i=1}^n x_i(t^*) + x_e(t^*) = 1$ holds by proposition 4.1, so if one variable is equal to 1 the rest must be 0. \square

Corollari 4.1. *For any $x_0 \in S$ the Hypercycle solution $x(\cdot, x_0)$ is defined $\forall t \in [0, \infty)$.*

Proof. Suppose the opposite. Since the closure of S is a compact set in \mathbb{R}^{n+1} we know by Theorem 2.5 that if $x(\cdot, x_0)$ is such that $\mathbb{R}^+ \cap I_{x_0} = [0, t^*)$ with $t^* < \infty$ there exists $t_S < t^*$ such that $\forall t > t_S$ $x(t, x_0) \notin S$, in contradiction with S being positively invariant by proposition 4.3. \square

Definition 4.2. *We will say that a fixed point $x^* = (x_1^*, \dots, x_n^*)$ in S is a chain of dimension $m + 1$ with $1 \leq m < n - 1$ and initial component x_i if it satisfies $x_j^* \neq 0$ for $j \in \{i, \dots, i + m\}$ and $x_j^* = 0$ for $j \notin \{i, \dots, i + m\}$.*

In the following sections we will assume $n > 2$, $K = 1$ in order to simplify the model. We also restrict our study of the model to the dynamics of the Hypercycle inside S , where it is physically meaningful. This is the reason why proposition 4.3 turns out to be useful, it tells us that the region in which we are interested is positively invariant. Notice that, as we said before, we will often note the points in S as $x = (x_1, \dots, x_n)$ instead of $x = (x_1, \dots, x_n, x_e)$.

4.2 The symmetric case

In this section we consider the Hypercycle model assuming that $A_i = a = A_e$ $\forall i \in \{1, \dots, n\}$, for some $a > 0$. We call it the symmetric Hypercycle model.

4.2.1 Existence and nature of the fixed points

Lemma 4.1. *The symmetric Hypercycle model has no fixed points $x^* = (x_1^*, \dots, x_n^*)$ in S such that $x_i^* \neq 0$ and $x_{i-1}^* = x_{i+1}^* = 0$ for any $i \in \{1, \dots, n\}$.*

Proof. Suppose x^* is such a fixed point for some $i \in \{1, \dots, n\}$. Inserting $x_{i-1}^* = 0$ in the equation $f_i(x^*) = 0$ gives us $aQ = \Phi(x^*)$. Then looking at $f_e(x^*)$ we obtain

$$f_e(x^*) = x_e^*(a - aQ) + (1 - Q) \sum_{j=1}^n x_j^*(a + x_{j-1}^*) > 0,$$

where we are using that $0 < Q < 1$ implies both terms in the last sum are positive. On the other side x^* is a fixed point so we should have $f_e(x^*) = 0$. Therefore x^* cannot be a fixed point. \square

Lemma 4.2. *The symmetric Hypercycle model has no chains in S .*

Proof. Suppose x^* is a chain with initial component $i \in \{1, \dots, n\}$. We know $x_i^* \neq 0$ and $x_{i-1}^* = 0$ together with $f_i(x^*) = x_i^*(aQ + x_{i-1}^*Q - \Phi(x^*))$ imply $aQ = \Phi(x^*)$. Now using $0 = f_i(x^*) = x_{i+1}^*(aQ + x_i^*Q - aQ)$ we obtain $x_{i+1}^*x_i^*Q = 0$, which implies either x_{i+1}^* or x_i^* must be 0, leading to a contradiction (the dimension of the chain must be at least 2!). \square

Proposition 4.4. *The symmetric Hypercycle model has no fixed points $x^* \neq \vec{0}$ such that $x_i^* = 0$ for some $i \in \{1, \dots, n\}$.*

Proof. If the opposite is true, we can assume x^* has at least two components $x_i^* = 0$ and $x_j^* = 0$ with $i > j$ and $x_k^* \neq 0$ for $j < k < i$. If we had just one component equal to 0 we would be in contradiction with lemma 4.2 (x^* would be a chain). If the condition $x_k^* \neq 0$ for $j < k < i$ did not hold we could always take a bigger j and/or a smaller i . We can also assume $j - i > 2$, because the opposite would be in contradiction with lemma 4.1. Then the proof ends finding a contradiction exactly as in the last lemma. \square

Proposition 4.5. *The symmetric Hypercycle model has no fixed points on ∂S except from $(x_1, \dots, x_n) = \vec{0}$.*

Proof. We know $\partial S = \bigcup_{i=0}^n \{x \in H \mid x_i = 0\} \cup \{x \in H \mid x_e = 0\} \subset S$. Proposition 4.4 tells us there can be no fixed points in $\bigcup_{i=0}^n \{x \in H \mid x_i = 0\}$ different than $(x_1, \dots, x_n) = \vec{0}$.

Suppose we had a fixed point $x^* \in \{x \in H \mid x_e = 0\}$. This would lead to

$$f_e(x^*) = (1 - Q) \sum x_i^*(a + x_{i-1}^*) > 0.$$

We already know by definition of fixed point that this is not possible, so there are no fixed points in $\{x \in H \mid x_e = 0\}$.

The only point left on ∂S is $(x_1, \dots, x_n) = \vec{0}$, which is actually a fixed point. It is easy to check that $x = (x_1, \dots, x_n, x_e) = (0, \dots, 0, 1) \Rightarrow (f_1(x), \dots, f_n(x), f_e(x)) = (0, \dots, 0)$. \square

Now that we have already found where the fixed points cannot be, we would like to give some result on where are the fixed points of the symmetric Hypercycle and for which values of the parameters a and Q these are actually in S .

Proposition 4.6. *For the values of (a, Q) such that $\frac{Q^2}{1-Q} \geq 4na$ there are two fixed points $x^{*,+}$ and $x^{*,-}$ in S given by:*

$$x_i^{*,+} = \frac{Q + \sqrt{Q^2 - 4na(1-Q)}}{2n} \quad (4.2.1)$$

$$x_i^{*,-} = \frac{Q - \sqrt{Q^2 - 4na(1-Q)}}{2n} \quad (4.2.2)$$

$\forall i \in \{1, \dots, n\}$. Furthermore, when they exist these are the only fixed points in S apart from $\vec{0}$.

Proof. Imposing the condition of being a fixed point of the symmetric Hypercycle different from $\vec{0}$ on $x^* = (x_1^*, \dots, x_n^*) \in H$ is the same as imposing $f_i(x^*) = 0$ and $x_i^* \neq 0 \forall i \in \{1, \dots, n\}$. This comes from proposition 4.2 and proposition 4.4.

Therefore we have, imposing that $x^* \neq \vec{0}$ is a fixed point in H ,

$$0 = f_{i+1}(x^*) = x_{i+1}^*(aQ + x_i^*Q - \Phi(x^*)) \Leftrightarrow aQ + x_i^*Q - \Phi(x^*) = 0 \Leftrightarrow x_i^* = \frac{\Phi(x^*) - aQ}{Q},$$

for all $i \in \{1, \dots, n\}$. In particular this implies $x_i^* = x_j^* \forall i, j \in \{1, \dots, n\}$. So using $\Phi(x^*) = \sum_{i=1}^n x_i^*(a + x_{i-1}^*) + ax_e^*$ and $x_e^* = 1 - \sum_{i=1}^n x_i^*$ we obtain

$$\begin{aligned} x_i^* &= \frac{\sum_{i=1}^n x_i^*(a + x_{i-1}^*) + ax_e^* - aQ}{Q} = \dots = \frac{n(x_i^*)^2 + a(1 - Q)}{Q} \Leftrightarrow \\ &\Leftrightarrow n(x_i^*)^2 - Qx_i^* + a(1 - Q) = 0 \Leftrightarrow x_i^* = \frac{Q \pm \sqrt{Q^2 - 4na(1 - Q)}}{2n}. \end{aligned}$$

We will denote these points as $x^{*,+}$ and $x^{*,-}$ respectively. We consider them only if $\frac{Q^2}{1-Q} \geq 4na$. Otherwise the discriminant is negative and they are not real, so not in S .

Suppose $\frac{Q^2}{1-Q} \geq 4na$ holds. Then $x^{*,+}$ and $x^{*,-}$ are fixed points of the symmetric Hypercycle model, but we still shall proof they are in S . As we only have obtained conditions on x_i^* for $i \in \{1, \dots, n\}$ nothing is in contradiction with our assumption $x^{*,+}, x^{*,-} \in H$. At the same time since $0 < Q < 1$ and $Q > \sqrt{Q^2 - 4na(1 - Q)} \geq 0$ we have

$$0 < \frac{Q \pm \sqrt{Q^2 - 4na(1 - Q)}}{2n} < \frac{1}{n} \Rightarrow \left\{ \begin{array}{l} \sum_{i=1}^n x_i^{*,s} \leq 1 \\ x_i^{*,s} \in [0, 1], \quad i \in \{1, \dots, n\} \end{array} \right\} \Rightarrow x^{*,s} \in S$$

$\forall s \in \{+, -\}$. This ends the proof, the only two fixed points in S for the symmetric Hypercycle model are the ones given by (4.2.1) and (4.2.2) when $\frac{Q^2}{1-Q} \geq 4na$. \square

4.2.2 Circulant Matrices

In this section we give the definition of circulant matrix and characterize its eigenvalues. The results given are based on [5].

Definition 4.3. A circulant matrix $(a_{i,j}) = A \in \mathbb{R}^{n \times n}$ is a matrix satisfying

$$a_{i,j} = a_{(i-j) \bmod n},$$

so that it only has n different coefficients and looks like:

$$A = \begin{pmatrix} a_0 & a_1 & \dots & a_{n-2} & a_{n-1} \\ a_{n-1} & a_0 & a_1 & & a_{n-2} \\ \vdots & a_{n-1} & \ddots & \ddots & \vdots \\ a_2 & & \ddots & & a_1 \\ a_1 & a_2 & \dots & a_{n-1} & a_0 \end{pmatrix}.$$

The useful property of the circulant matrices is that there exists a formula giving its eigenvalues and eigenvectors. This will play a crucial role when we study the stability of the fixed points in the next section.

Lemma 4.3. *Given $\rho \neq 1$ a root of unity then $\sum_{k=0}^{n-1} \rho^k = 0$.*

Proof. We just need to use that this sum is a geometric progression so

$$\sum_{k=0}^{n-1} \rho^k = \frac{\rho^n - 1}{\rho - 1} = 0,$$

where in the second equality we are using that ρ is a root of unity different from 1 (otherwise the denominator would be 0). \square

Theorem 4.1. *Every circulant matrix A diagonalizes and has eigenvectors*

$$\vec{v}_j = \frac{1}{\sqrt{n}}(1, e^{2\pi ij/n}, \dots, e^{2\pi ij(n-1)/n})$$

with corresponding eigenvalues $\lambda_j = \sum_{k=0}^{n-1} a_k e^{2\pi ijk/n}$, $j \in \{1, \dots, n\}$.

Proof. Given a circulant matrix $A = (a_{i,j})$ any of its eigenvectors v must satisfy

$$Av = \lambda v$$

for some $\lambda \in \mathbb{C}$. This gives us the following system of equations:

$$\sum_{k=0}^{n-m-1} a_k v_{m+k} + \sum_{k=n-m}^{n-1} a_k v_{k-n+m} = \lambda v_m, \quad m \in \{0, \dots, n-1\}.$$

Now we simply realize that taking ρ an n th root of unity and $v = \frac{1}{\sqrt{n}}(1, \rho, \dots, \rho^{n-1})$ the last equality becomes

$$\sum_{k=0}^{n-m-1} a_k \frac{1}{\sqrt{n}} \rho^{m+k} + \sum_{k=n-m}^{n-1} a_k \frac{1}{\sqrt{n}} \rho^{k-n+m} = \lambda \frac{1}{\sqrt{n}} \rho^m.$$

Here we can simplify the terms $\frac{1}{\sqrt{n}}$ and ρ^m on both sides and we also have $\rho^{-n} = 1$, so we obtain

$$\lambda = \sum_{k=0}^{n-m-1} a_k \rho^k + \sum_{k=n-m}^{n-1} a_k \rho^k = \sum_{k=0}^{n-1} a_k \rho^k. \quad (4.2.3)$$

Since for this λ and v the system of equations is satisfied, $v = \frac{1}{\sqrt{n}}(1, \rho, \dots, \rho^{n-1})$ is an eigenvector of A with eigenvalue the λ from (4.2.3) for any $\rho \in \{e^{2\pi ij/n}\}_{j=0}^{n-1}$.

So for any $j \in \{0, \dots, n-1\}$ we have that $\lambda_j = \sum_{k=0}^{n-1} a_k e^{2\pi ijk/n}$ is an eigenvalue of A with corresponding eigenvector

$$\vec{v}_j = \frac{1}{\sqrt{n}}(1, e^{2\pi ij/n}, \dots, e^{2\pi ij(n-1)/n}).$$

It can be seen using lemma 4.3 that the inverse of $B = (\vec{v}_0 \mid \vec{v}_1 \mid \dots \mid \vec{v}_{n-1})$ is C^T , where $C = (\vec{v}_0 \mid \vec{v}_{n-1} \mid \vec{v}_{n-2} \mid \dots \mid \vec{v}_1)$. Notice that

$$\vec{v}_j^T \vec{v}_l = \frac{1}{n} \sum_{k=0}^{n-1} e^{2\pi ik} = 1, \quad l, j \in \{1, \dots, n-1\}, j+l=n,$$

and

$$\vec{v}_j^T \vec{v}_l = \frac{1}{n} \sum_{k=0}^{n-1} e^{2\pi i \frac{(j+l)}{n} k} = 0, \quad l, j \in \{1, \dots, n-1\}, j+l \neq n.$$

where in the first equation we use Euler's formula and in the second one lemma 4.3. This implies that $\vec{v}_0, \dots, \vec{v}_{n-1}$ are linearly independent vectors, so they form a basis of eigenvectors of the matrix A . Therefore A is diagonalizable. \square

4.2.3 Stability of the fixed points

In this section we will classify the character of the fixed points. Let us first introduce the notation

$$f_i(x) = x_i F_i(x), \quad i \in \{1, \dots, n\},$$

where $F_i(x) = a(Q-1) + Qx_{i-1} - \sum_{j=1}^n x_j x_{j-1}$. We can calculate the derivative of F_i with respect to x_j ,

$$\frac{\partial F_i}{\partial x_j}(x) = \begin{cases} Q - x_{i-2} - x_i, & j = i-1 \\ -x_{j+1} - x_{j-1}, & j \notin \{i-1, i\} \\ -x_{i+1} - x_{i-1}, & j = i \end{cases} \quad (4.2.4)$$

and it is straightforward to see that the Jacobian of f verifies

$$\frac{\partial f_i}{\partial x_j}(x) = \delta_{ij} F_i(x) + x_i \frac{\partial F_i}{\partial x_j}(x),$$

so using (4.2.4) we get

$$\frac{\partial f_i}{\partial x_j}(x) = \begin{cases} x_i(Q - x_{i-2} - x_i), & j = i - 1 \\ x_i(-x_{j+1} - x_{j-1}), & j \notin \{i - 1, i\} \\ F_i(x) + x_i(-x_{i+1} - x_{i-1}), & j = i \end{cases} \quad (4.2.5)$$

We already know that the stability of the fixed points is given by the eigenvalues of $Df(x^*)$. We will start by $x^* = 0$. Substitution into (4.2.5) leads to

$$Df(\vec{0}) = \begin{pmatrix} a(Q - 1) & 0 & \dots & 0 \\ 0 & a(Q - 1) & & \vdots \\ \vdots & & \ddots & 0 \\ 0 & \dots & 0 & a(Q - 1) \end{pmatrix}.$$

Therefore the eigenvalues of $Df(\vec{0})$ are all equal to $a(Q - 1) < 0 \Rightarrow x^* = \vec{0}$ is an attracting fixed point independently of the parameter values (a, Q) , $a > 0$, $Q \in (0, 1)$ by Theorem 2.7.

In the same way we will analyze the stability of the fixed points $x^{*,+}$ and $x^{*,-}$ from Proposition 4.6. We will take advantage of the fact that these points have all components equal.

$$x_1^{*,\pm} = x_i^{*,\pm} = \frac{Q \pm \sqrt{Q^2 - 4na(1 - Q)}}{2n}, \quad \forall i \in \{1, \dots, n\}.$$

Using again equation (4.2.5) together with the fact that all the components are equal we obtain the following expression for the Jacobian matrix:

$$\frac{\partial f_i}{\partial x_j}(x^{*,\pm}) = \begin{cases} x_1^{*,\pm}(Q - 2x_1^{*,\pm}), & j = i - 1 \\ -2(x_1^{*,\pm})^2, & j \notin \{i - 1, i\} \\ F_i(x^{*,\pm}) - 2(x_1^{*,\pm})^2, & j = i \end{cases} \quad (4.2.6)$$

Notice that $F(x^{*,\pm}) = a(Q - 1) + Qx_1^* - n(x_1^*)^2 = 0$ because the components x_1^* are found by proposition 4.6 exactly as the solutions of $n(x_i^*)^2 - Qx_i + a(1 - Q) = 0$. Therefore

$$Df(x^{*,\pm}) = \begin{pmatrix} -2(x_1^{*,\pm})^2 & \dots & -2(x_1^{*,\pm})^2 & x_1^{*,\pm}(Q - 2x_1^{*,\pm}) \\ x_1^{*,\pm}(Q - 2x_1^{*,\pm}) & -2(x_1^{*,\pm})^2 & \dots & -2(x_1^{*,\pm})^2 \\ -2(x_1^{*,\pm})^2 & & & \vdots \\ \vdots & \ddots & & \\ -2(x_1^{*,\pm})^2 & \dots & x_1^{*,\pm}(Q - 2x_1^{*,\pm}) & -2(x_1^{*,\pm})^2 \end{pmatrix},$$

which is clearly a circulant matrix. Then we can use formula (4.2.3) given in Theorem 4.1 to find its eigenvalues

$$\lambda_j^\pm = \sum_{k=0}^{n-2} -2(x_1^{*,\pm})^2 e^{2\pi ijk/n} + x_1^{*,\pm}(Q - 2x_1^{*,\pm}) e^{2\pi ij(n-1)/n}, \quad j \in \{0, \dots, n - 1\}.$$

If $j \neq 0$ we know by lemma 4.3 that $\sum_{k=0}^{n-1} e^{2\pi ijk/n} = 0$ so we can simplify the term $-2(x_1^{*,\pm})^2 \sum_{k=0}^{n-1} e^{2\pi ijk/n}$ to obtain

$$\lambda_j^\pm = x_1^{*,\pm} Q e^{2\pi ij(n-1)/n}, \quad j \in \{1, \dots, n-1\}.$$

For $j = 0$ we get

$$\lambda_0^\pm = x_1^{*,\pm} (Q - 2x_1^{*,\pm}) - 2(n-1)(x_1^{*,\pm})^2 = Qx_1^{*,\pm} - 2n(x_1^{*,\pm})^2.$$

It is easy to see now that $\lambda_0^\pm = 0 \Leftrightarrow x_1^{*,\pm} = 0$ or $x_1^{*,\pm} = \frac{Q}{2n}$, which looking at the expression of $x_1^{*,\pm}$ automatically leads to $\lambda_0^- \geq 0$ and $\lambda_0^+ \leq 0$.

Having an expression for the eigenvalues allows us to analyze the character of the fixed points using Theorem 2.7.

For $n > 4 \exists j \in \{1, \dots, n-1\}$ such that $Re\lambda_j^\pm > 0$ so $x^{*,\pm}$ will be an unstable fixed point.

If $x^{*,+} \neq \frac{Q}{2n}$ for the case $n < 4$, $Df(x^{*,+})$ will always have all eigenvalues with negative real part, so $x^{*,+}$ is in that case an attracting fixed point. On the other hand $Re\lambda_0^- > 0$, so $x^{*,+}$ is an unstable fixed point whenever $x^{*,+} \neq x^{*,+}$.

In the cases $n = 4$ and $x_1^{*,\pm} = \frac{Q}{2n}$ for $n < 4$ the fixed points are hyperbolic so Theorem 2.7 cannot help us, we should know more about central manifolds to discuss these cases.

Remark. If we are in the case (iii) from Theorem 2.7 we know that our fixed point is unstable because there exists a manifold where it behaves as a repelling fixed point, so the condition of stability from definition 2.9 cannot hold.

4.2.4 Symmetry and periodic orbits

The symmetry of our equations in this specific case is transferred to the dynamics of our system in a remarkable way.

Proposition 4.7. *The linear map $R : \mathbb{R}^n \rightarrow \mathbb{R}^n$ defined by the matrix:*

$$R = \begin{pmatrix} 0 & \dots & 0 & 1 \\ 1 & 0 & \dots & 0 \\ 0 & 1 & 0 & \dots & 0 \\ \vdots & \ddots & \ddots & & \vdots \\ 0 & & 0 & 1 & 0 \end{pmatrix}$$

is a conjugation between the Hypercycle symmetric model and itself.

Proof. Using proposition 2.5 we only need to prove $DR(x)f(x) = f(R(x))$, $\forall x \in \mathbb{R}^n$, which using $DR(x) = R$ turns out to be the same condition as

$$R(f(x)) = f(R(x)) \quad \forall x \in \mathbb{R}^n.$$

This last equality holds because of the structure of our equations. \square

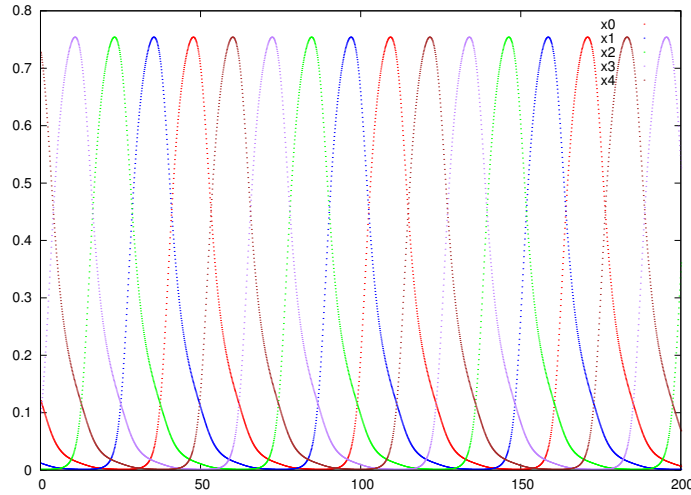


Figure 4.1: Attracting periodic orbit for $a = 0.5$, $Q = 0.99$, $n = 5$. $x_i(t)$ for $i \in \{0, \dots, 4\}$ are represented in different colors.

The last result is important in the sense that conjugations are known to send fixed points to fixed points and periodic orbits to periodic orbits. Since the only fixed points we have for the symmetric case have equal components this is not very helpful, but in the case of periodic orbits it tells us that if there is a periodic orbit going through $\vec{x} = (x_1, \dots, x_n)$ then there is a periodic orbit going through $R^k \vec{x}$, $\forall k \in \{1, \dots, n-1\}$. It would seem a plausible conjecture then that R sends some periodic orbit to itself, because using the numerical computation of the Poincaré map in section 3.2 we have found the attracting periodic orbit shown in Figure 4.1 (in fact we have only found this one).

Remark. To find periodic orbits we have implemented a program that given a Poincaré section takes random values on it and iterates the Newton method for the Poincaré map to see if it converges to a fixed point. All the fixed points we find correspond to periodic points and therefore their orbit is periodic (as we explained in chapter 2), but this program does not necessarily find all the periodic points on the section.

An interesting thing to do now is trying to continue this periodic orbit (represented as a fixed point of the Poincaré map) with respect to Q . This can be done by applying Algorithm 4 to the function $f(x, Q) = P(x, Q) - x$, where P is the Poincaré map with Poincaré section $\Sigma = \{x = (x_0, \dots, x_4) \in \mathbb{R}^5 \mid x_1 = 0.002\}$ with the only difference that we let it depend also on Q . The choice of the section is based on the observation that periodic orbits in this model always get very close to 0 at some time for any component, so we expect the flow to cross this hyperplane. The results of this continuation are shown in Figure 4.2. We observe that a saddle node bifurcation appears, indicating the existence of an unstable periodic orbit in a certain interval of Q .

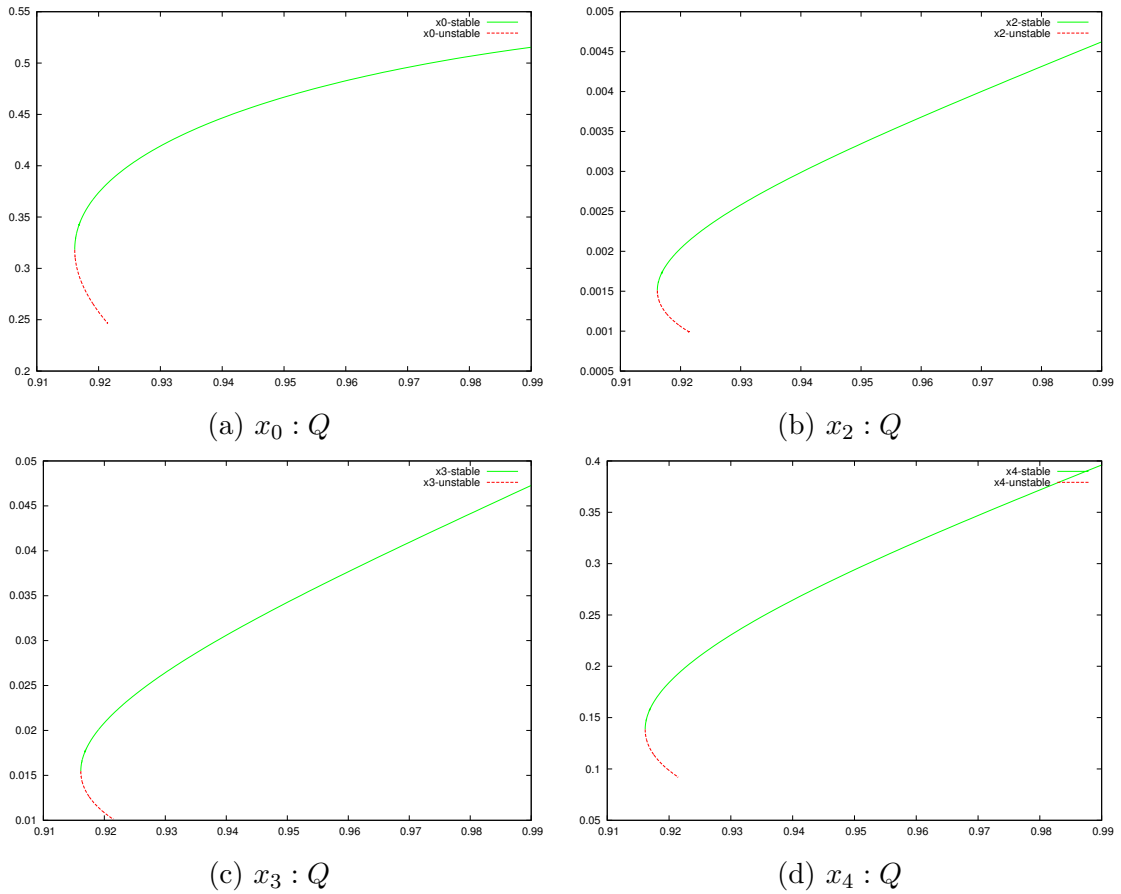


Figure 4.2: Continuation of stable periodic orbit with respect to Q for $a = 0.5$, $n = 5$. On the y axis the components specified and Q on the x axis. The attracting periodic points are in green, the unstable ones in red.

Remark. Although the geometric behavior of the curve around the turning point in Figure 4.2 is exactly the one expected for a saddle node bifurcation, we have only verified (i) and (ii) from Theorem 2.3.

The character of the periodic orbits in the sense of definition 2.15 has been numerically verified by calculating the eigenvalues of DP all along the curve. We have also represented one of the unstable periodic orbits for a specific value of Q in Figure 4.3.

Remark. When we integrate the unstable periodic orbit we see there is a transient state where the approximated solution is close to the orbit because of the flow being continuous with respect to initial conditions but after a while it becomes completely different. Notice that numerical errors are less important when we integrate attracting periodic orbits.

It can also be numerically verified that **for values of Q below 0.916**, which is the approximated value for which the bifurcation occurs, $\vec{0}$ **becomes a global attractor in S** (except in a set of measure zero). This has been checked by integrating the solutions corresponding to several different initial conditions on S

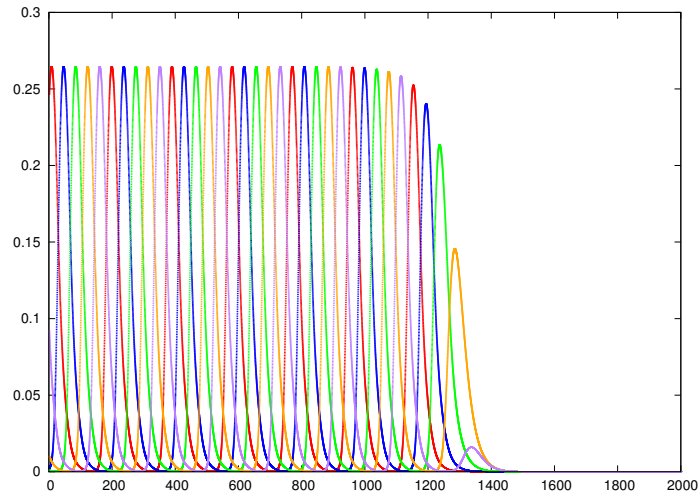


Figure 4.3: Unstable periodic orbit for $a = 0.5$, $Q = 0.92139$, $n = 5$. $x_i(t)$ for $i \in \{0, \dots, 4\}$ are represented in different colors.

and observing that all tend to $\vec{0}$ when $t \rightarrow \infty$, but of course this is far from being a mathematical proof. Nevertheless, it turns the non-existence of stable periodic orbits for $Q < 0.916$ into a very plausible conjecture. In general for any value of a the same behavior is expected for a different Q .

4.3 The non-symmetric case

In this section we consider the case $a = A_1 \neq A_i = A_e = A, \forall i \in \{2, \dots, n\}$. We call it the non-symmetric Hypercycle model.

4.3.1 Existence and nature of the fixed points

Proposition 4.8. *The non-symmetric hypercycle model has no fixed points $x^* = (x_1^*, \dots, x_n^*)$ in S such that $x_i^* \neq 0$ and $x_{i-1}^* = x_{i+1}^* = 0, i \in \{2, \dots, n\}$.*

Proof. Suppose that such a fixed point exists. Then we have:

$$0 = f_i(x^*) = x_i^*(AQ + \overbrace{x_{i-1}^*Q}^0 - \Phi(x^*)) \Rightarrow AQ + \overbrace{x_{i-1}^*Q}^0 - \Phi(x^*) = 0 \Rightarrow AQ = \Phi(x^*),$$

and on the other hand

$$\begin{aligned} f_e(x^*) &= x_e^*(A - \Phi(x^*)) + (1 - Q)\left(\sum_{i=2}^n x_i^*(A + x_{i-1}^*) + x_1^*(a + x_n^*)\right) = \\ &= (A - AQ)x_e^* + (1 - Q)\left(\sum_{i=2}^n x_i^*(A + x_{i-1}^*) + x_1^*(a + x_n^*)\right) > 0. \end{aligned}$$

This leads to a contradiction because a fixed point must satisfy $f_e(x^*) = 0$.

□

Proposition 4.9. *The non-symmetric hypercycle model has no chains in S with initial component different than x_1 . Furthermore, these chains can only exist if $a > A$.*

Proof. Suppose we have a chain x^* with initial component x_i with $i \notin \{1, n\}$. Since $x_i^* \neq 0$ we have

$$0 = f_i(x^*) = x_i^*(AQ - \Phi(x^*)) = 0 \Rightarrow AQ = \Phi(x^*),$$

and at the same time we know

$$0 = f_{i+1}(x^*) = x_{i+1}^*(AQ + x_i^*Q - \Phi(x^*)) = x_{i+1}^*(x_i^*Q).$$

So $x_{i+1}^* = 0$ must hold, which leads to a contradiction because of the definition of chain, specifically concerning the fact that the chain dimension must be at least 2.

Suppose $a > A$, and also that our chain has initial component x_n . In this case we also have $AQ = \Phi(x^*)$ from $f_n(x^*) = 0$. From $x_1^*(aQ + x_n^*Q - \Phi(x^*)) =$

$f_1(x^*) = 0$ and $x_n^* \neq 0$ we deduce $aQ + x_n^*Q - AQ = 0$, which is the same as $x_n^* = A - a < 0 \Rightarrow x^* \notin S$.

If $a < A$ and we have initial component x_1 , we see that $x_1^*(aQ + x_n^*Q - \Phi(x^*)) = f_1(x^*) = 0$ together with $x_n^* = 0$ imply $aQ = \Phi(x^*)$, which inserted into the equation $x_2^*(AQ + x_1^*Q - \Phi(x^*)) = f_2(x^*) = 0$ leads to $x_1^* = \frac{Q(a-A)}{Q} = a - A < 0 \Rightarrow x^* \notin S$.

Suppose then that the initial component is x_n (still in the case $a < A$). Then we have $f_n(x^*) = 0 \Rightarrow AQ = \Phi(x^*)$, and from $x_1^*(aQ + x_n^*Q - AQ) = f_1(x^*) = 0$, $x_1^* \neq 0$, we know $x_n^* = A - a$. But then using $\Phi(x^*) = AQ$ we get $x_2^*(x_1^*Q) = f_2(x^*) = 0 \Rightarrow x_2^* = 0$. So the chain is at most of dimension 2. Also using $\Phi(x^*) = Q$ we find the equality

$$x_1^* = \frac{A(Q - 1 + x_n^*)}{(a - A) + x_n^*},$$

which leads to a contradiction because since $(a - A) + x_n^* = a - A + A - a = 0$ we have either $x_1^* = \infty$ or $x_1^* = 1$. It is clear why the first one is not possible, and the second one would lead to $x_1^* + x_n^* > 1 \Rightarrow x^* \notin S$. We conclude that there are no chains in the case $a < A$. □

We would like to find an expression for the chains and the space of parameters where they exist. As we have already proved this discussion only makes sense in the case $a > A$ and for chains with initial component x_1 .

Proposition 4.10. *There exists an m -dimensional chain x^* of the non-symmetric Hypercycle model in S if and only if $A < a \leq 1 + A$ and $Q \geq Q_m = \frac{(m-1)(a-A)^2 + A}{a}$. It can be expressed as a function of a and Q as*

$$x^* = (x_1^*, \dots, x_m^*, \dots, x_n^*) = \left(a - A, a - A, \dots, \frac{Qa - A - (m-1)(a-A)^2}{a - A}, 0, \dots, 0 \right).$$

Proof. We know that if x^* is an m -dimensional chain in H we have $f_i(x^*) = 0 \forall i \in \{1, \dots, n\}$ and $x_j^* = 0 \forall j \in \{m+1, \dots, n\}$. Obviously we also have the condition that the point must be in H , but as we will only obtain restrictions on (x_1^*, \dots, x_n^*) we will always be able to choose x_e^* such that x^* is in H . Imposing the first conditions we obtain

$$0 = f_{i+1}(x^*) = x_{i+1}^*(AQ + Qx_i^* - \Phi(x^*)) \Leftrightarrow AQ + x_i^*Q - aQ = 0 \Leftrightarrow x_i^* = a - A$$

$\forall i \in \{1, \dots, m-1\}$, where we are using $x_{i+1}^* \neq 0 \forall i \in \{1, \dots, m-1\}$ and also $\Phi(x^*) = aQ$ (deduced as usual from $f_1(x^*) = 0$ and $x_n^* = 0$).

To find the value of x_m^* we use equations $aQ = \Phi(x^*)$ and $x_e^* = 1 - \sum_{i=1}^n x_i^*$, taking into account that $x_j^* = 0 \forall j \in \{m+1, \dots, n\}$ by definition of chain. This is the way we find

$$x_m^* = \frac{Qa - A - (m-1)(a-A)^2}{a - A}.$$

Reciprocally, with these values for the components of x^* (and 0's on the rest) we obtain that x^* satisfies $f_i(x^*) = 0 \forall i \in \{1, \dots, n\}$, so x^* is an m -dimensional chain in H if and only if

$$x^* = \left(a - A, a - A, \dots, \frac{Qa - A - (m-1)(a-A)^2}{a-A}, 0, \dots, 0 \right).$$

But is it in S ? In general this is not true, we need to impose some restrictions on a and Q . In particular we know these conditions are:

$$0 \leq x_i^* \leq 1, \quad \forall i \in \{1, \dots, n\}, \quad (4.3.1)$$

$$\sum_{i=1}^n x_i^* \leq 1. \quad (4.3.2)$$

Condition (4.3.1) for $i \in \{1, \dots, m-1\}$ leads to $0 \leq a - A \leq 1 \Leftrightarrow A \leq a \leq 1 + A$. For m we have

$$x_m^* \geq 0 \Leftrightarrow Q \geq \frac{(m-1)(a-A)^2}{a} + \frac{A}{a} = Q_m,$$

whereas $x_m^* \leq 1$ is always true because $\frac{Qa-A}{a-A} < 1$ and $(m-1)(a-A) > 0$.

The fact that $\sum_{i=1}^m x_i^* = \frac{Qa-A}{a-A} < 1$ implies condition (4.3.2) is always satisfied, so it does not give extra conditions on a and Q . Therefore

$$x^* = \left(a - A, a - A, \dots, \frac{Qa - A - (m-1)(a-A)^2}{a-A}, 0, \dots, 0 \right)$$

is an m -dimensional chain of the non-symmetric Hypercycle model if and only if $A < a \leq 1 + A$ and $Q \geq Q_m$. □

Remark. In the same way it has been done in the previous proposition we can also prove

$$\hat{x} = \left(\frac{aQ - A}{a - A}, 0, \dots, 0 \right)$$

is a fixed point in S of the non-symmetric Hypercycle model when $Q > \frac{A}{a}$ is satisfied.

Letting aside the case $x^* = \vec{0}$, which also in this case turns out to be a fixed point (this can be proved exactly as we did it in the symmetric case), we must study the remaining fixed points.

Proposition 4.11. *Any fixed point in S of the non-symmetric Hypercycle model which is neither $\vec{0}$, \hat{x} or a chain has all components different from 0.*

Proposition 4.12. *Let x^* be a fixed point in S of the non-symmetric Hypercycle which is neither $\vec{0}$, \hat{x} or a chain. Such a point will exist if and only if $P(Q) \geq 0$ and either (i) or (ii) hold, with*

$$(i) \quad a < A \text{ and } Q \geq A - a,$$

$$(ii) \quad A < a \text{ and } Q \geq Q_n,$$

where $Q_n = \frac{A}{a} + \frac{1}{a}(n-1)(a-A)^2$ and $P(Q) = (Q+a-A)^2 - 4n(1-Q)A$.

Then x^* will be either $x^{*,+}$ or $x^{*,-}$, where $x^{*,s} = (x_1^{*,s}, \dots, x_n^{*,s})$ with $s \in \{+, -\}$ is given by the equations

$$x_i^{*,s} = \frac{Q+a-A \pm \sqrt{(Q+a-A)^2 - 4n(1-Q)A}}{2n}, \quad i \in \{1, \dots, n-1\}, \quad (4.3.3)$$

$$x_n^{*,s} = x_1^{*,s} - (a-A). \quad (4.3.4)$$

Proof. Assuming x^* is such a fixed point by proposition 4.11 we have $f_i(x^*) = 0$ and $x_i^* \neq 0 \forall i \in \{1, \dots, n\}$, which implies that x^* satisfies the equations

$$AQ + x_i^*Q - \Phi(x^*) = 0, \quad i \in \{1, \dots, n-1\} \quad (4.3.5)$$

$$aQ + x_n^*Q - \Phi(x^*) = 0 \quad (4.3.6)$$

Then $x_n^* = x_1^* - (a-A)$ is obtained directly from the relation between (4.3.5) and (4.3.6), and using the expression of Φ given in the definition of the Hypercycle together with the fact that the $n-1$ first components are equal (from (4.3.5)) one obtains that equation (4.3.5) is the same as

$$n(x_i^*)^2 - (Q+a-A)x_i^* + A(1-Q) = 0, \quad i \in \{1, \dots, n-1\}. \quad (4.3.7)$$

This proves a fixed point different from $\vec{0}$, \hat{x} or a chain is given by the equations (4.3.3) and (4.3.4).

Now we still have to discuss when are these points in S . We need to impose once more conditions (4.3.1) and (4.3.2).

The first thing we must verify is when $x_1^* \in \mathbb{R}$, and that is exactly when the discriminant $P(Q)$ of (4.3.7) is positive.

Finally we analyze conditions (4.3.1) and (4.3.2) independently for the cases $a < A$ and $a > A$.

- (i) Suppose $a < A$. First of all condition $x_1^{*,s} \geq 0$ in (4.3.1) will hold if and only if $Q \geq A - a$. Suppose this last condition is satisfied. Then we see (4.3.2) holds if and only if

$$\sum_{i=1}^n x_i^{*,s} = nx_1^{*,s} + A - a \leq 1 \Leftrightarrow x_1^{*,s} \leq \frac{1 - (A - a)}{n},$$

which is true because

$$\sqrt{(Q + a - A)^2 - 4n(1 - Q)A} < Q + a - A < 1 + a - A.$$

Notice that here we are using many things implicitly, mainly that for the last inequality to be true we need $Q + a - A > 0$ (we have already assumed this), and also that one has to look at formula (4.3.3) to realize that this last inequality implies the first one. The rest of conditions in (4.3.1) hold automatically because $x_1^{*,s} < \frac{1-(A-a)}{n} \Rightarrow x_1^{*,s} < 1 - (A - a) \Rightarrow x_1^{*,s} \leq 1$ and also $0 < x_1^{*,s} < x_n^{*,s} = x_1^{*,s} + A - a \leq 1$.

- (ii) Suppose $a > A$. From imposing (4.3.2) we get again that $x_1^{*,s} \leq \frac{1+a-A}{n}$ must hold. One can prove this inequality is true exactly as in the last case with the only difference that in this one $Q + a - A > 0$ (so we don't need to impose this condition now).

The inequalities in (4.3.1) contain $x_n^{*,s} \geq 0$, which is the same as $x_1^{*,s} \geq a - A$. Developing this inequality one gets $Q \geq Q_n$. Once we impose this condition $x_n^{*,s} \geq 0$ and we obtain automatically $x_1^{*,s} \geq x_n^{*,s} \geq 0$. The other two inequalities in (4.3.1) ($x_1^{*,s}$ and $x_n^{*,s}$ less or equal than 1) come from $x_1^{*,s}$ and $x_n^{*,s}$ being positive together with (4.3.2). More explicitly:

$$\left. \begin{array}{l} \sum_{i=1}^n x_i^{*,s} \leq 1 \\ x_i^{*,s} \geq 0, \quad \forall i \in \{1, \dots, n\} \end{array} \right\} \Rightarrow x_i^{*,s} \leq 1, \quad \forall i \in \{1, \dots, n\}.$$

This means that the only condition we need to impose for $x^{*,s}$ to be in S for $s \in \{+, s\}$ is $Q \geq Q_n$ (apart from the discriminant to be positive).

□

An important idea of this section is that when we change the self replicative rate for the first template (A_1) new fixed points appear with respect to the symmetric case (all the chains).

4.3.2 Stability of the fixed points

In the non-symmetric case it is not possible to obtain a formula for the eigenvalues of Df as we did in the symmetric one, where we used properties of circulant matrices. Nevertheless for any fixed point x^* one can always approximate the eigenvalues of $Df(x_0)$ numerically. The case $x^* = \vec{0}$ is the only in which this is not needed. In the same way we did it for the symmetric case we find now

$$Df(\vec{0}) = \begin{pmatrix} aQ - A & 0 & \dots & 0 \\ 0 & A(Q - 1) & & \vdots \\ \vdots & & \ddots & 0 \\ 0 & \dots & 0 & A(Q - 1) \end{pmatrix}.$$

Theorem 2.7 implies then that the origin will be an attracting fixed point if $aQ < A$, and unstable for $aQ > A$. Notice that the other eigenvalues have always negative real part, so it is the first one that determines the character of $x^* = \vec{0}$ as a fixed point.

The stability for the rest of the fixed points can be studied numerically. As an example fixing $a = 0.5$, $n = 5$, we have verified that for the values of (A, Q) where they exist the fixed points from proposition 4.12 are always unstable according to Theorem 2.7, because at least one of the eigenvalues of their corresponding Jacobian matrices has real part greater than 0. This seems to agree with the result for the fixed points from proposition 4.6 in the symmetric case.

We have not done it but it could be interesting to see in detail which is the character of the chains.

4.3.3 Breaking the symmetry for periodic orbits

In this section we present a numerical illustration of what happens with periodic orbits when we change the parameter $A_1 = a$ to pass from the symmetric hypercycle model to the non-symmetric one, restricting ourselves to the case $n = 5$. We have applied the Euler-Newton Continuation method to $f(x, a) = P(x, a) - x$ starting at $A = a = 0.5$ for the stable periodic orbit shown in Figure 4.1, section 4.2.4. In this example the Poincaré section we are using is $\Sigma = \{x \in \mathbb{R}^5 \mid x_1 = 0.499\}$. The result is shown in Figure 4.4. Numerical evaluation of the DP eigenvalues shows the stability of the orbit is preserved.

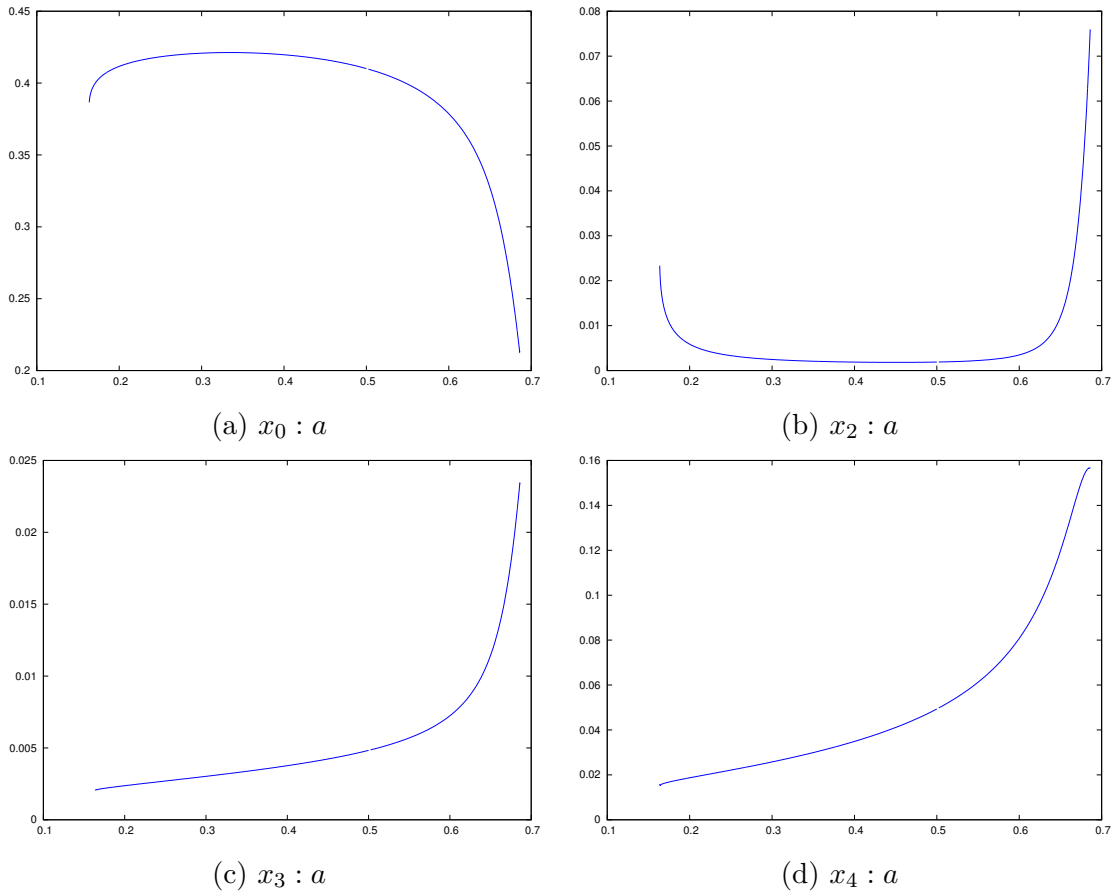


Figure 4.4: Continuation of attracting periodic orbit with respect to a for $Q = 0.99$, $n = 5$. On the y axis the components specified and a on the x axis

Although the ending points of this curve seem to correspond to possible bifurcation points in fact they correspond to points where the periodic orbit becomes tangent to the Poincaré section. This can be seen by integrating the periodic orbits for these periodic points. As an example we can see in Figure 4.5 the corresponding orbit to $x^* = (x_0, x_1, x_2, x_3, x_4) = (0.38192, 0.49900, 0.02761, 0.00204, 0.01504)$. Recall that $x_0 \equiv x_n$.

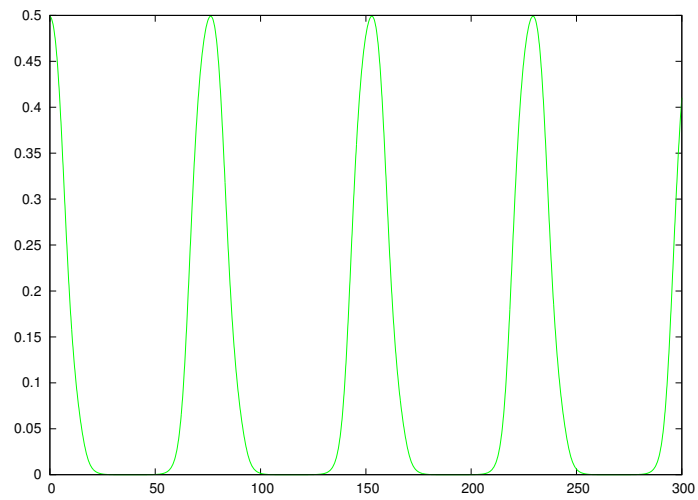


Figure 4.5: Attracting periodic orbit; $x_1(t)$ for $a = 0.16371$, $Q = 0.99$, $n = 5$

In order to continue the curve further we could take a different Poincaré section where maybe this will not occur or it will occur later.

Chapter 5

Conclusions

From all the results found during this thesis we would like to remark that in section 4.2.4 for a specific value of a in the case $n = 5$ we have found a stable coexistence state for all the templates in the form of an attracting periodic orbit. This coexistence state is preserved when we change the self-replicative rate for the first template (at least in a certain interval, as it was shown in section 4.3.3). The fact that when we decrease Q the periodic orbit disappears and $\vec{0}$ becomes a global attractor indicates that when the replicative accuracy decreases the coexistence becomes impossible. This result makes sense in the biological context because if the molecular species mutate easily then this will have a negative effect on the stability of the system.

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