Centro de Investigación y de
Estudios Avanzados del Instituto
Politécnico Nacional
Unidad Zacatenco

Departamento de Matemáticas

Un modelo p-ádico de evolución biológica.

Tesis presentada por

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para obtener el grado de

Maestría en Ciencias en la especialidad de Matemáticas

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Thesis overview

Resumen

En este trabajo, presentamos un modelo de evolución biológica en el espacio de los números p-ádicos, el cual es una versión no arquimediana del modelo clásico de Eigen-Schuster. El modelo de Eigen-Schuster fue introducido originalmente por Manfred Eigen [10], y posteriormente fue desarrollado considerablemente en conjunto con Peter Schuster y otros, [11, 26, 25].

El modelo de Eigen-Schuster describe el comportamiento cualitativo de la evolución de macromoléculas biológicas (secuencias), tales como cadenas de ADN monocatenario y moléculas de ARN. Después de mucha investigación, se encontró que el modelo es útil para describir otros fenómenos, tales como la evolución del lenguaje natural, virus con altas tasas de mutación y la evolución de la reproducción sexual, ver [22].

Al principio, Eigen introdujo el modelo para estudiar la dinámica de evolución de especies químicas dentro de un reactor químico. La dinámica del modelo considera los tres principales ingredientes para la existencia de la evolución: replicación (reproducción), mutación y selección.

Bajo ciertas hipótesis, el mecanismo de mutación-selección impone un límite en la longitud de un genoma para evitar la pérdida de información, y por lo tanto, la existencia de la evolución. Dentro de este modelo, los genomas con una larga longitud son incapaces de replicarse a sí mismos con una tasa de fidelidad lo suficientemente alta. Tal límite es conocido como el umbral de error. Un problema abierto importante de la teoría es dar una explicación satisfactoria a la paradoja de Eigen, es decir, explicar la existencia de sistemas vivos complejos.

Nuestro trabajo está organizado como sigue. En el Capítulo 1, revisamos el modelo clásico de Eigen-Schuster. Consideramos un sistema de n especies moleculares $I_1, I_2, \ldots, I_n$ con la capacidad de autorreplicarse. Sea $x_i(t) \geq 0$ la concentración (población relativa) de la especie I_i al tiempo t en el sistema. Denotamos A_i (respectivamente D_i) la tasa de replicación (respectivamente tasa de degradación) de la especie I_i y definimos $E_i := A_i - D_i$, la *productividad* de la especie I_i. El modelo de Eigen-Schuster está descrito por el siguiente

sistema de ecuaciones diferenciales,

$$\frac{dx_i}{dt} = (A_i Q_{ii} - D_i)x_i + \sum_{j \neq i} A_j Q_{ji} x_j - \Phi(t) x_i \quad i = 1, \ldots, n,$$

donde Q_{ij} es la probabilidad que una molécula de la especie I_i se replique en una molécula de la especie I_j y $\Phi(t) = \sum_{i=1}^{n} E_i x_i(t)$ es un flujo de evacuación que asegura que la población total se mantiene constante.

No solo presentamos las principales ideas matemáticas, sino también simulaciones numéricas que ilustran visualmente conceptos y retos de la teoría. En particular, estudiamos el modelo de Swetina-Schuster [26, 25], que da una descripción explícita de los valores de Q_{ij}, y que es ahora el punto de referencia para el estudio del umbral de error y los fenómenos termodinámicos de transiciones de fase en modelos biológicos.

En el Capítulo 2, introducimos los conceptos principales y los resultados de la teoría del análisis p-ádico. Enunciamos, sin demostración, un conjunto de proposiciones y teoremas que rápidamente introducen al lector no especializado en el tema. Nuestro trabajo es autocontenido, hasta un nivel razonable. Pusimos nuestro mejor esfuerzo en incluir todos los resultados necesarios para el estudio del modelo p-ádico del modelo de Eigen-Schuster, los cuales referenciamos en el capítulo subsecuente cuando sea necesario para hacer la lectura más fácil de seguir. Además, presentamos algunas representaciones gráficas de la bola $\mathbb{Z}_p$ en el plano euclidiano, y mostramos algunos ejemplos de cómo graficar funciones de $\mathbb{Z}_p$ a $\mathbb{R}$ y su visualización en $\mathbb{R}^3$.

En el Capítulo 3, comenzamos revisando el modelo p-ádico de Eigen-Schuster, el cual fue introducido por Zuñiga-Galindo en [31]. En este trabajo, un genoma (secuencia) es representado por un número p-ádico,

$$x = x_{-k} p^{-k} + x_{-k+1} p^{-k+1} + \ldots + x_0 + x_1 p + \ldots, \quad x_j \in \{0, \ldots, p-1\}, j = -k, \ldots.$$

Luego, la longitud del genoma puede crecer arbitrariamente. Asumimos la existencia de una medida de mutación $Q : \mathbb{R}_+ \to \mathbb{R}_+$ tal que $\int_{\mathbb{Q}_p} Q(|x|_p) dx = 1$ donde dx es la medida de Haar normalizada del grupo $(\mathbb{Q}_p, +)$. Adicionalmente, asumimos que el paisaje de aptitud está dado por una función de prueba radial.

En este modelo, la concentración $X(x,t)$ de la secuencia x al tiempo t está controlada por la siguiente ecuación de evolución:

$$\frac{\partial X(x,t)}{\partial t} = Q(|x|_p) * \{f(|x|_p) X(x,t)\} - \Phi(t) X(x,t) \qquad x \in \mathbb{Q}_p, t \in \mathbb{R}_+$$

donde $\Phi(t) = \int_{\mathbb{Q}_p} f(|y|_p) X(y,t) dy$ es un flujo de evacuación. El término

$$Q(|x|_p) * \{f(|x|_p) X(x,t)\} = \int_{\mathbb{Q}_p} Q(|x-y|_p) f(|y|_p) X(y,t) dy$$

representa la tasa a la cual las secuencias mutan a la secuencia x.

Siguiendo el trabajo de [31], mostramos que bajo ciertas hipótesis, podemos recuperar una versión ultramétrica del modelo clásico de Eigen-Schuster, i.e., mostramos un esquema de discretización para el modelo p-ádico que recupera un sistema análogo ultramétrico del caso clásico. Estudiamos la paradoja de Eigen en el contexto p-ádico. En particular, bajo ciertas hipótesis, la paradoja de Eigen no ocurre.

Después de esto, nos restringimos a estudiar la ecuación del replicador p-ádica para una medida de mutación soportada en la bola unitaria $\mathbb{Z}_p$. Usando hipótesis razonables, mostramos la existencia de una solución separable en un subespacio propio cerrado $\mathcal{V}_L \subset L^2(\mathbb{Z}_p, \mathbb{C})$ al problema de Cauchy,

$$\begin{cases} X : \mathbb{Z}_p \times \mathbb{R}_+ \to \mathbb{R}, \qquad X(\cdot, t) \in \mathcal{V}_L \cap L^2(\mathbb{Z}_p, \mathbb{R}), X(x, \cdot) \in C^1(\mathbb{R}_+, \mathbb{R}) \\ \frac{\partial X(x,t)}{\partial t} = \mathbf{W}X(x,t) - \Phi(t)X(x,t), \qquad x \in \mathbb{Z}_p, t \in \mathbb{R}_+ \\ X(x,0) = X_0 \in \mathcal{V}_L \cap L^2(\mathbb{Z}_p, \mathbb{R}). \end{cases}$$

donde $\mathbf{W} : L^2(\mathbb{Z}_p, \mathbb{C}) \to L^2(\mathbb{Z}_p, \mathbb{C})$ está dado por

$$(\mathbf{W}\varphi)(x) = \int_{\mathbb{Z}_p} Q(|x-y|_p) f(|y|_p) \varphi(y) dy,$$

y

$$\Phi(t) = \int_{\mathbb{Z}_p} f(|y|_p) X(y,t) dy.$$

Finalmente, discutimos diferentes técnicas de la teoría del análisis funcional no lineal, y cómo se pueden aplicar al estudio de la existencia de las cuasiespecies, en otras palabras, los estados estacionarios de la ecuación del replicador p-ádica.

En el Apéndice A y el Apéndice B, incluimos el código necesario para realizar las simulaciones numéricas y las gráficas que aparecen a lo largo de este trabajo.

Overview

In this work, we present a model of biological evolution in the space of p-adic numbers, which is a non-Archimedean version of the classical Eigen-Schuster model. The Eigen-Schuster model was originally introduced by Manfred Eigen [10], and then developed considerably together with Peter Schuster and others, [11, 26, 25].

The Eigen-Schuster model describes the qualitative behaviour of evolution of biological macromolecules (sequences), such as single stranded DNA and RNA molecules. After extensive research, the model has found to be useful to describe other phenomena, such as the evolution of natural language, high-mutation-rate viruses and the evolution of sexual reproduction, see [22].

Eigen first introduced the model to study the evolutionary dynamics of chemical species inside a chemical reactor. The model dynamics consider the three main ingredients for the existence of evolution: replication (reproduction), mutation and selection.

Under certain hypothesis, the mutation-selection mechanism places a limit on the length of a genome to avoid the loss of information, and therefore, the existence of evolution. Within this model, genomes with a large length are unable to replicate themselves with high enough fidelity. Such limit is known as the error-threshold. An important open problem of the theory is to provide a suitable explanation to the so called Eigen paradox, that is, to explain the existence of complex living systems.

Our work is organized as follows. In Chapter 1, we review the classical Eigen-Schuster model. Consider a system of n molecular species $I_1, I_2, \ldots, I_n$ with the capacity of self-replication. Let $x_i(t) \geq 0$ be the concentration (relative population) of the species I_i at time t in the system. Denote A_i (respectively D_i) the replication rate (respectively degradation rate) of the species I_i and define $E_i := A_i - D_i$, the *productivity* of the species I_i. The Eigen-Schuster model is described by the following system of differential equations,

$$\frac{dx_i}{dt} = (A_i Q_{ii} - D_i)x_i + \sum_{j \neq i} A_j Q_{ji} x_j - \Phi(t) x_i \quad i = 1, \ldots, n,$$

where Q_{ij} is the probability that a molecule of species I_i replicates to a molecule of species I_j and $\Phi(t) = \sum_{i=1}^{n} E_i x_i(t)$ is an evacuation flux that assures that the total population remains constant.

We not only present the main mathematical ideas but also numerical simulations that visually illustrate concepts and challenges of the theory. In particular, we study the Swetina-Schuster model [26, 25], that gives an explicit description for the values of Q_{ij}, and it is now a point of reference for the study of the error-threshold and the thermodynamic phenomena of phase transitions in biological models.

In Chapter 2, we introduce the main concepts and results of the theory of p-adic analysis. We state, without proof, a set of propositions and theorems that rapidly introduce the

non-specialist reader into the subject. Our work is self-contained, up to a reasonable degree. We tried our best to include all the needed results for the study of the p-adic Eigen-Schuster model, which we reference in the subsequent chapters when needed to make the read easier to follow.

In Chapter 3, we start by reviewing the p-adic Eigen-Schuster model, which was introduced by Zuñiga-Galindo in [31]. In this work, a genome (sequence) is represented by a p-adic number,

$$x = x_{-k}p^{-k} + x_{-k+1}p^{-k+1} + \ldots + x_0 + x_1 p + \ldots, \quad x_j \in \{0, \ldots, p-1\}, j = -k, \ldots.$$

Thus, the genome length can grow arbitrarily. We assume the existence of a mutation measure $Q : \mathbb{R}_+ \to \mathbb{R}_+$ such that $\int_{\mathbb{Q}_p} Q(|x|_p)dx = 1$ where dx is the normalized Haar measure of the group $(\mathbb{Q}_p, +)$. Additionally, we assume that the fitness landscape is given by a radial test function. In this model the concentration $X(x,t)$ of the sequence x at the time t is controlled by the following evolution equation:

$$\frac{\partial X(x,t)}{\partial t} = Q(|x|_p) * \{f(|x|_p)X(x,t)\} - \Phi(t)X(x,t) \qquad x \in \mathbb{Q}_p, t \in \mathbb{R}_+$$

where $\Phi(t) = \int_{\mathbb{Q}_p} f(|y|_p)X(y,t)dy$ is an evacuation flux. The term

$$Q(|x|_p) * \{f(|x|_p)X(x,t)\} = \int_{\mathbb{Q}_p} Q(|x-y|_p)f(|y|_p)X(y,t)dy$$

represents the rate at which the sequences are mutating into sequence x.

Following [31], we show that under certain hypothesis, we can recover an ultrametric version of the classical Eigen-Schuster model, i.e., we show a discretization scheme for the p-adic model that recovers an ultrametric analogous system to the classical case. We study the so called Eigen paradox in the p-adic setting. In particular, under certain hypothesis, we show that the Eigen paradox does not occur.

After that, we restrict ourselves to study the p-adic replicator equation for a mutation measure supported in the unit ball Z_p. Using reasonable hypothesis, we show the existence of a separable solution in a proper closed subspace $\mathcal{V}_L \subset L^2(\mathbb{Z}_p, \mathbb{C})$ to the Cauchy problem,

$$\begin{cases} X : \mathbb{Z}_p \times \mathbb{R}_+ \to \mathbb{R}, \qquad X(\cdot,t) \in \mathcal{V}_L \cap L^2(\mathbb{Z}_p, \mathbb{R}), X(x,\cdot) \in C^1(\mathbb{R}_+, \mathbb{R}) \\ \frac{\partial X(x,t)}{\partial t} = \mathbf{W}X(x,t) - \Phi(t)X(x,t), \qquad x \in \mathbb{Z}_p, t \in \mathbb{R}_+ \\ X(x,0) = X_0 \in \mathcal{V}_L \cap L^2(\mathbb{Z}_p, \mathbb{R}). \end{cases}$$

where $\mathbf{W} : L^2(\mathbb{Z}_p, \mathbb{C}) \to L^2(\mathbb{Z}_p, \mathbb{C})$ is given by

$$(\mathbf{W}\varphi)(x) = \int_{\mathbb{Z}_p} Q(|x-y|_p)f(|y|_p)\varphi(y)dy,$$

and

$$\Phi(t) = \int_{\mathbb{Z}_p} f(|y|_p) X(y,t) dy.$$

We discuss different techniques from the theory of Nonlinear Functional Analysis, and how they can be applied to study the existence of quasispecies, in other words, the steady states of the p-adic replicator equation.

Finally, we present some graphical representations of the ball $\mathbb{Z}_p$ in the Euclidean plane $\mathbb{R}^2$, and we show some examples of how to plot functions from $\mathbb{Z}_p$ to $\mathbb{R}$ and their visualization in $\mathbb{R}^3$.

In Appendix A and Appendix B, we include the code needed to perform the numerical simulations and plots that appear throughout this work.

Chapter 1

Classical molecular evolution models

In this chapter we review the classical ideas and rsults of molecular evolution models following [18].

1.1 Replication and selection

Let us consider a system of n molecular species $I_1, I_2, \ldots, I_n$ with the capacity of self-replication. Let $x_i(t) \geq 0$ be the concentration (relative population) of the species I_i at time t in the system. We denote A_i (respectively D_i) the replication rate (respectively degradation rate) of the species I_i. Molecular degradation is a consequence of interaction between molecules either by radiation or collision, however we will assume that the degradation rates are constant for simplicity. Finally, let us define $E_i := A_i - D_i$ as the *productivity* of the species I_i.

1.1.1 Simple replication

Let us begin studying the simplest model of a kinetic reaction:

$$\begin{aligned} \mu^* + I_i &\xrightarrow{A_i} 2I_i && \text{Replication} \\ I_i &\xrightarrow{D_i} \mu && \text{Degradation} \end{aligned}$$

where μ^* denotes highly energetic monomers (quantity that we will assume constant w.r.t time) and μ denotes the products of molecular degradation. In this model there are no interactions between different species. Thus, we have the following dynamical equation for the concentration of species I_i:

$$\frac{dx_i}{dt} = (A_i - D_i)x_i = E_i x_i \quad i = 1, \ldots, n. \tag{1.1}$$

If we assume that the values E_i are constant then the solutions of this system are as follows:

$$x_i(t) = x_i(0)\exp(E_i t) \quad i = 1, \ldots, n.$$

If $E_i > 0$ the population of the species I_i will grow exponentially. On the contrary, if $E_i < 0$ the corresponding species will disappear. This result does not correspond to the biological concept of selection because there is no selection mechanism.

1.1.2 Replication and selection

We now introduce a term in system (1.1) that plays the role of a selection mechanism, an evacuation flux $\Phi(t)$ that keeps the total population constant:

$$\sum_{i=1}^{n} x_i(t) = 1. \tag{1.2}$$

The evacuation flux is an artificial mechanism that mimics natural selection. We refer to this constraint as the CP (*constant population*) condition. If we assume that the evacuation flux is proportional to the concentration of the species I_i then our system can be described by the following dynamical equations:

$$\frac{dx_i}{dt} = (E_i - \Phi(t))x_i \quad i = 1, \ldots, n. \tag{1.3}$$

If we sum all the equations and we use the CP condition (1.2) we obtain the following:

$$0 = \sum_{i=1}^{n} \frac{dx_i}{dt} = \sum_{i=1}^{n} (E_i - \Phi(t))x_i,$$

i.e.,

$$\Phi(t) = \sum_{i=1}^{n} E_i x_i(t), \tag{1.4}$$

which means that the evacuation flux is the *mean productivity*. We also conclude that the system (1.3) is non-linear because the flux depends on all concentrations. Here we also assume that E_i is constant.

The system (1.3) can be solved using a change of variables. Later on, we solve a more general case, now we only study the steady states. First, if we assume the mean productivity reaches a steady state $\Phi^* = \lim_{t\to\infty} \Phi(t)$, then the steady state of the i-th equation is given by $x_i = 0$ or $E_i = \Phi^*$. Assuming $E_i \neq E_j$ for $i \neq j$ then the asymptotic value of the mean productivity equals the productivity of only one species. Thus, we have the following possibilities for the fixed points

$$u_k^* = \underbrace{(0, 0, \ldots, 1, \ldots, 0)}_{k-\text{th position}}, \text{ with } k = 1, \ldots, n.$$

Clearly $u_0^* = (0, \ldots, 0)$ is also a fixed point, however we have no interest in this point since it does not satisfy (1.2).

If we set $F_i(t,x) := (E_i - \Phi(t))x_i(t)$, where $x := (x_1, \ldots, x_n)$, we have

$$\frac{\partial F_i}{\partial x_j}(t,x) = \begin{cases} E_i - \sum_{k\neq i} E_k x_k - 2E_i x_i & i = j. \\ -E_j x_i & i \neq j. \end{cases}$$

Then, the Jacobian matrix at the point u_k^* is:

$$J(u_k^*) = \begin{pmatrix} E_1 - E_k & 0 & \vdots & 0 & \vdots & 0 \\ 0 & E_2 - E_k & \vdots & 0 & \vdots & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots & 0 \\ -E_1 & -E_2 & \vdots & -E_k & \vdots & -E_n \\ \vdots & \vdots & \vdots & \vdots & \ddots & 0 \\ 0 & 0 & 0 & 0 & 0 & E_n - E_k \end{pmatrix},$$

and its characteristic polynomial is:

$$P(\lambda) = (E_k - \lambda) \prod_{m\neq k} (E_m - E_k - \lambda).$$

Thus, the eigenvalues are $\lambda_m = E_m - E_k$ and $\lambda_k = -E_k$. Here, the eigenvalues are real and the fixed point u_k^* is (locally) stable if the eigenvalues are negative (in general if their real part is), but this occurs if and only if $E_k > E_m$ for all $m \neq k$, i.e. *only the fittest survives.*

1.2 The Eigen-Schuster model

An essential ingredient for evolution is mutation which leads to *diversity*, and which is subjected to a selection process. Let us introduce a matrix $Q = [q_{ij}]$ where q_{ij} is the probability that a molecule of species I_i mutates to a molecule of species I_j as a result of an erroneous replication. Now the kinetic reactions are of the following form:

$$\begin{aligned} \mu^* + I_i &\xrightarrow{A_i Q_{ii}} 2I_i && \text{(Replication without errors)} \\ \mu^* + I_i &\xrightarrow{A_i Q_{ij}} I_i + I_{j\neq i} && \text{(Replication with errors)} \\ I_i &\xrightarrow{D_i} \mu && \text{(Degradation)} \end{aligned}$$

Furthermore,

$$\sum_{j=1}^{n} Q_{ij} = 1,$$

i.e., the matrix Q is a stochastic matrix. Now our system of differential equations becomes

$$\frac{dx_i}{dt} = (A_i Q_{ii} - D_i)x_i + \sum_{j\neq i} A_j Q_{ji} x_j - \Phi(t)x_i \quad i = 1, \ldots, n. \tag{1.5}$$

In this new setting, the evacuation flux still satisfies (1.4), and thus the system (1.5) can be rewritten as:

$$\frac{dx_i}{dt} = \sum_{j=1}^{n} W_{ij}x_j - \Phi(t)x_i \quad i = 1, \ldots, n, \tag{1.6}$$

where $W_{ii} = A_iQ_{ii} - D_i$, are known as *selective values*. The values $W_{ij} = A_jQ_{ji}$ with $j \neq i$ are known as *mutation values*. The system (1.6) is the Eigen-Schuster model. In the particular case where Q is the identity matrix, the system (1.6) reduces to (1.3).

Now, we assume the existence of a *master sequence* I_k, that is $A_k > A_j$ for $k \neq j$. For the next examples we fix $n = 4$, $D_1 = D_2 = D_3 = D_4 = 0$ and $A_1 = A_2 = A_3 = 1, A_4 = 6$. We also fix $\mathbf{x}(0) = (1, 0, 0, 0)^T$. We consider two stochastic matrices, a matrix Q_1 with "small mutation error" and another matrix Q_2 with "large mutation error":

$$Q_1 = \begin{pmatrix} 0.995 & 0.00167 & 0.00167 & 0.00167 \\ 0.001 & 0.997 & 0.001 & 0.001 \\ 0.00267 & 0.00267 & 0.992 & 0.00267 \\ 0.00333 & 0.00333 & 0.00333 & 0.99 \end{pmatrix}, Q_2 = \begin{pmatrix} 0.343 & 0.441 & 0.189 & 0.027 \\ 0.149 & 0.396 & 0.351 & 0.104 \\ 0.0741 & 0.307 & 0.424 & 0.195 \\ 0.0593 & 0.278 & 0.435 & 0.227 \end{pmatrix}. \tag{1.7}$$

As we can see in Figure 1.1, in the case of a high-fidelity replication, a selection process occurs and only the master sequence survives, which is the case of *the survival of the fittest*. If the error in the replication is large, the selective advantage of the master sequence gets lost and the system converges to a steady state where all sequences survive. For more details about this numerical simulation and the simulations below, see Section 1.3.

1.2.1 Solving the Eigen-Schuster system

Now, following [14] we analyse the solutions to the system (1.6). In [28], the authors get the same results using different techniques. The term which corresponds to the sum over $i \neq j$ in (1.5) is known as *backflow*. Originally, Eigen assumed that the *error coefficients* W_{ij} with $j \neq i$ were much smaller than the selective values W_{ii}. Moreover, Eigen also assumed that the *backflow* was also sufficiently small to analyse the behaviour of the system [10]. Here we do not make such assumptions except when we wish to show some asymptotic property of the solution.

We define $\psi(t) := \int_0^t \Phi(s)ds$. Making the following change of variables:

$$x_k(t) = y_k(t)\exp(-\psi(t)), \tag{1.8}$$

the system (1.6) becomes

$$\frac{dy_i}{dt} = \sum_{j=1}^{n} W_{ij}y_j. \tag{1.9}$$

Although we are assuming that the values W_{ij} are constant, even if they were time-dependent, the last equation would be linear. Thus, the change of variables transforms the system (1.6)

which is non-linear to a linear system if the values W_{ij} do not depend on the concentrations.

By the constraint CP (1.2), we have $1 = \sum_i x_i = \exp(-\psi)\sum_i y_i$, and consequently

$$\sum_{i=1}^{n} y_i = \exp(\psi).$$

Then, the solutions of (1.6) can be written as

$$x_k(t) = \frac{y_k(t)}{\sum_i y_i(t)}, \tag{1.10}$$

where y_i is a solution of (1.9). Notice that the equation (1.10) is valid even if the values W_{ij} are not constant. In the case in which all the values W_{ij} are constant, finding solutions to (1.9) becomes a problem of finding eigenvalues. Let us assume that the matrix W is not singular. We also assume that all of its eigenvalues are different, in which case all the eigenvectors are uniquely determined, and the general solution is obtained in the following way.

First, we write (1.9) in matrix form as $\frac{d\mathbf{y}}{dt} = W\mathbf{y}$. Now, using the hypothesis about the eigenvalues of W we can write $W = PDP^{-1}$ where D is a diagonal matrix and P is the matrix which has as columns the eigenvectors of W. Changing variables as $\mathbf{z} = P^{-1}\mathbf{y}$ we get $\frac{d\mathbf{z}}{dt} = D\mathbf{z}$ which is a decoupled system whose solutions are $z_i(t) = c_i \exp(\lambda_i t)$. Now we set $\mathbf{c} := (c_1, c_2, \ldots, c_n)^T$. If we evaluate the solution at zero we get $\mathbf{c} = P^{-1}\mathbf{x}(0)$. Thus, the general solution is

$$x_i(t) = \frac{\sum_{j=1}^{n} P_{ij}\exp(\lambda_j t)\sum_{k=1}^{n} P^{-1}_{jk}x_k(0)}{\sum_{l=1}^{n}\sum_{j=1}^{n} P_{lj}\exp(\lambda_j t)\sum_{k=1}^{n} P^{-1}_{jk}x_k(0)}, \quad i = 1, \ldots, n. \tag{1.11}$$

In the general case, we may have complex eigenvalues, which means that the solutions would oscillate in time.

If W is a symmetric matrix then all of its eigenvalues are real. In particular, if the set of eigenvalues is ordered, say $\lambda_1 > \lambda_2 > \ldots > \lambda_n$ then as $t \to \infty$ the solution of the system converges to a steady state equal to the eigenvector of the largest eigenvalue. Eigen described this situation as *an optimization process*. Moreover, by the Perron-Frobenius theorem [1], the constraints of the system tell us that this is the only steady-state with physical meaning and this state does not depend on the initial conditions.

This steady-state is known as *quasispecies* because in the presence of error in the replication process instead of having *the survival of the fittest*, the selection process gives *a cloud of coupled mutants* as a result. The term *quasispecies* is used instead of the term *species*,

[1] The Perron-Frobenius theorem states that if A is a positive matrix then it has an eigenvalue λ_0 which is positive and $\lambda_0 > |\lambda_r|$ for any other eigenvalue λ_r of A. Moreover this is the only eigenvalue whose associated eigenvector has only positive entries. [3, 21]

which in biology is considered as an organism with a unique genotype and which in general, it reproduces with high-fidelity, giving place to almost-exact copies of its progenitor.

It is of interest to know approximations to the eigenvalues and eigenvectors of W. In [14], assuming $W_{ij} \ll W_{ii}$ and that all of the diagonal values W_{ii} are distinct, the following approximations are obtained by the means of perturbation theory:

$$\lambda_i \approx W_{ii} + \sum_{j \neq i} \frac{W_{ij} W_{ji}}{W_{ii} - W_{jj}}, \tag{1.12}$$

$$P_{ij} \approx \delta_{i,j} + \frac{W_{ij}}{W_{ii} - W_{jj}}, \quad i \neq j. \tag{1.13}$$

In [28], the authors get the solution of (1.6) using integral methods and similar expressions to (1.12) and (1.13). In the appendix of this work a summary of the perturbation theory of matrices is included.

1.2.2 The Swetina-Schuster matrix

We now discuss some ideas originally introduced and developed by Jörg Swetina and Peter Schuster in [26] and later in [25]. After making some considerations based on experimental evidence, they propose to model the replication of chains of polynucleotides only considering mutations of the type purine-purine and pyrimidine-pyrimidine. After making these considerations, we can represent a polynucleotide as a sequence of some fixed length ν, such that each entry has an element of the alphabet of nucleotides (A,G,U,C). Thus, we end up with a set of 4^ν distinct sequences. However, this set can be partitioned in 2^ν subsets with 2^ν elements and these 2^ν elements form a ν-cube. We restrict ourselves to this case, and we consider by simplicity that the sequences are words of length ν written in the binary alphabet $\{0, 1\}$.

During the replication of the DNA or RNA genome, different types of mutations can occur: point mutations, insertions, deletions and recombination. Here, we consider only point mutations, which is the mutational event where one base change for another. In the context of binary sequences, a point mutation means that at some position an entry with a value of 0 (resp. 1) changes its value to 1 (resp. 0) due to an erroneous replication process. Furthermore, we assume that the event of a point mutation in one position is independent of the event of a point mutation in another position. Additionally, we assume that the probability that a mutation occurs in a specific position is the same for all the entries and it is given by $u := 1 - q$ where q is the probability that a specific entry is copied correctly. Under these assumptions we have that the mutation matrix Q is given by:

$$Q_{ij} = q^{\nu - d_{ij}} (1 - q)^{d_{ij}} = u^{d_{ij}} (1 - u)^{\nu - d_{ij}}, \tag{1.14}$$

where $d_{ij} = d_H(I_i, I_j)$ is the Hamming distance between the sequences I_i and I_j. The Hamming distance between two sequences is defined as the number of positions at which

the corresponding entries are different. In the literature, this mutation matrix is known as Swetina-Schuster matrix. In Figure 1.2 we can see different steady-states that the system converges to for different values of u.

On the other hand, we can consider the dependency of the eigenvector corresponding to the largest eigenvalue as a function of u, specially when we have a master sequence that has a large selective advantage. In Figure 1.3 we can see the results of a simulation. For more details about the analysis of the eigenvalues of these type of matrices under more general conditions than those we assumed at the beginning of this section see [24].

Now, suppose $\nu = 7$ and that I_1 is a master sequence. Since $\nu = 7$, we have a system of $n = 2^7 = 128$ equations. Let us assume that all the sequences, except I_1, have the same replication rate. Moreover, suppose that all degradation rates are equal to zero. In Figure 1.4 we can observe how the mutants group themselves in $\nu+1 = 8$ classes. On a first thought, the assumption of the same replication rates for all the sequences I_j, with $j = 2, \ldots, 128$, appears to play a role in this phenomenom. Indeed, in the next section we study a model that allows us to reduce the dimension of our system from 2^ν equations to $\nu + 1$ equations using the assumptions described in this example.

1.2.3 A model for high dimensions $\nu > 3$

For ν relatively large the number of sequences $n = 2^\nu$ restricts strongly the numerical analysis of the system. We group the sequences into classes which will drastically decrease the dimension of the problem. The class Γ_0 contains only the master sequence. The class Γ_1 contains all the $\binom{\nu}{1}$ 1-error mutants. The class Γ_2 contains all the $\binom{\nu}{2}$ 2-error mutants. In general, the class Γ_k contains all the $\binom{\nu}{k}$ k-error mutants. In addition, we assume the following:

- all the degradation rates are equal $D_1 = \ldots = D_{2^\nu} = D$; therefore they do not have any influence on the quasispecies;
- all the replication rates are equal inside a class, i.e. $A_i = A'_k$ for all $I_i \in \Gamma_k$.

With these assumptions, we change variables as

$$y_k(t) = \sum_{I_i \in \Gamma_k} x_i(t). \tag{1.15}$$

We also need an expression for the entries of matrix Q' which describes mutations from one class into another. Using [26], the probability that class Γ_l mutates into class Γ_k is

$$Q'_{lk} = \sum_{j=0}^{m} \binom{\nu-l}{j+\frac{1}{2}(|l-k|-(l-k))} \binom{l}{j+\frac{1}{2}(|l-k|+(l-k))} q^{\nu-2j-|l-k|}(1-q)^{2j+|l-k|}, \tag{1.16}$$

where $m = \lceil \frac{1}{2}(\min l + k, 2\nu - (l+k) - |l-k|) \rceil$. Notice that indices are interchanged, in our work Q' equals Q'^T in [26]. A direct calculation shows that the system of equations becomes

$$\frac{dy_i}{dt} = (A'_i Q'_{ii} - D)y_i + \sum_{i \neq k} A'_k Q'_{ki} y_k - \Phi' y_i, \quad i = 0, \ldots, \nu, \tag{1.17}$$

and $\Phi = \Phi'$. We emphasize that (1.14) is a symmetric matrix, but (1.16) is not.

Let us perform a numerical simulation using the matrix (1.14), assuming there is a master sequence I_1. We use $\nu = 7$, which give a system of $n = 2^7 = 128$ equations. In Figure 1.4, we observe how the mutants group themselves in $\nu + 1 = 8$ classes.

The important thing about having a model that drastically reduces the dimension is that we can test the approximations that are obtained by the means of perturbation methods. Moreover, we can analyse the steady states of the system as a function of the parameter u. For instance, in sequences of length $\nu = 20$ we have a similar behaviour as in the previous cases, see Figure 1.5.

1.2.4 The fitness landscape and the error-threshold

We now consider a function that assigns to each sequence a fitness value (productivity), the *fitness landscape*. In a naive way, one can say that this function is a "mountain range" over the space of sequences, see Figure 1.6 and Figure 1.7. This idea was introduced by Sewall Wright. In this terminology, the quasispecies equation describes the movement of a population of sequences through this mountain range. The quasispecies "feels" gradients in the mountain range, and it tries to reach local or global peaks [22].

Suppose there is a master sequence given by the sequence I_m. The fitness landscape that corresponds to the case where there is a master sequence is called *single-peaked landscape*. We denote the productivity of all the sequences except the master as

$$\Phi_-(t) = \frac{\sum_{j\neq m}^{n} E_j x_j(t)}{\sum_{j\neq m}^{n} x_j(t)} = \frac{\sum_{j=1}^{n} E_j x_j(t) - E_m x_m(t)}{1 - x_m(t)}. \tag{1.18}$$

Then, the concentration of the master sequence is

$$x_m(t) = \frac{\Phi(t) - \Phi_-(t)}{E_m - \Phi_-}. \tag{1.19}$$

In the selective equilibrium, assuming that the selective values of the rest of sequences are really small, we have

$$x_m^* = \frac{W_{mm} - \Phi_-^*}{E_m - \Phi_-^*}. \tag{1.20}$$

This formula implies that Q_{mm} decreases, that the role of the mutant sequences is important, and that Φ_- grows until it reaches the selective value of the master sequence. When this occurs, the population of the master sequences becomes extinct and the information that it carried gets lost. When this *error catastrophe* occurs the value of Q_{mm} is called *error-threshold*, usually denoted as Q_c. By taking $x_m^* = 0$, we get

$$Q_c = \frac{D_m + \Phi_-^*}{A_m} =: \frac{1}{\Theta}, \tag{1.21}$$

where Θ is the *superiority* of the master sequence. Eigen and Schuster disscused the possibility of measuring the value Θ in lab experiments, which can provide information about the error-threshold of some type of chain. For instance, this parameter has been measured in viruses such as the bacteriophage $Q\beta$ and influenza viruses. In fact, it is known that viruses form viral quasispecies that are close to the error-threshold as a survival mechanism to immune systems. Some vaccines have been designed to increase the mutation rate of a virus, causing them an error catastrophe and therefore their infectious capacity gets lost.

In particular, in the Swetina-Schuster matrix-model $Q_{mm} = q^\nu$, in the error-threshold we have

$$\nu_c = -\frac{\log \Theta}{\log q} \approx \frac{\log \Theta}{1-q}, \tag{1.22}$$

where the last approximation is for $q \approx 1$. This condition imposes a constraint to the length of the sequences such that the master sequences does not become extinct. However, to have complex organisms, it is necessary to code more information in long genomic sequences using high-fidelity replication mechanisms. Biologically speaking, this is possible due to enzymes and the necessary information to create them is stored in large length genomes, but as we have seen before, the length of sequences is bounded. Thus, we have reached Eigen's paradox: *there are no large genomes without enzymes, there are no enzymes without large genomes.*

1.2.5 Maynard-Smith's Ansatz

In equation (1.22) in order to calculate the error-threshold we need to have some experimental value for Θ or we need an estimate of Φ^*_-. We now show another way to get an estimate of the $error - threshold$, using Maynard-Smith's *ansatz* .

Let us consider all sequences of length ν. We also assume that we have a unique master sequence I_m with a replication rate a and that the probability that it replicates correctly given by $Q = q^\nu$. Thus, $1-Q$ is the probability that the master sequence replicates into some mutant. We assume that the replication rate for all mutant sequences is 1. Then we make the change of variables $y = \sum_{j \neq m} x_j$, and we denote Q' the probability that y replicates to x_m. For simplicity, $D_m = D_y = 0$. Therefore, we end up with a system of two equations of the following form:

$$\frac{dx_m}{dt} = aQx_m + Q'y - \Phi x_m \tag{1.23}$$

$$\frac{dy}{dt} = a(1-Q)x_m + (1-Q')y - \Phi y, \tag{1.24}$$

where $\Phi = ax_m + y$. Now, assuming that we have a sufficiently large value of ν such that Q' approaches zero and using the constraint $x_m + y = 1$ the system takes the form

$$\frac{dx_m}{dt} = x_m(aQ - 1 - x_m(a-1)). \tag{1.25}$$

By a direct computation, involving a stability analysis, one verifies that if $aQ < 1$, then x_m converges to zero as $t \to \infty$, i.e., the *fittest* sequence cannot survive. On the contrary, if $aQ > 1$, then x_m converges to

$$x_m^* = \frac{aQ - 1}{a - 1}, \tag{1.26}$$

that is, the error-threshold take us to the inequality $aq^\nu > 1$. If $q \approx 1$, we get:

$$\nu < \frac{\log a}{1 - q} = \frac{\log a}{u}. \tag{1.27}$$

If we consider this last inequality as fixing the length ν, then we see that the mutation rate must obey

$$u < \frac{\log a}{\nu}, \tag{1.28}$$

to ensure the survival of the information contained in the master sequence.

Finally, we present some numerical simulations of the error-threshold. Using the inequality in (1.28), taking $a = 10$ and $\nu = 50$, the error-threshold occurs at $u_c = 0.046\ldots$. In Figure 1.8 we observe this phenomenon for $\nu = 50$ and in Figure 1.9 for $\nu = 80$. In the later case, $u_c = 0.028\ldots$.

If we ask ourselves, what happens if there are "two master sequences" (two-peaked landscape)? The answer is quite interesting, see Figures 1.10 and 1.11. The estimation of the error-threshold is far more complicated than in the previous setting, for more details see [25].

Finally, Figure 1.11 shows the distribution of the quasispecies on top of the fitness landscape as a function of the parameter u, for $\nu = 50$. Although there are three sequences with a higher replication rate, the system still behaves as a two-peaked landscape mainly because of the fact that the classes of 49 and 50 error mutants are *close* in the Hamming distance.

1.3 Numerical simulations

During the chapter, we presented several numerical examples to illustrate the behaviour of the Eigen-Schuster system. We use the Runge–Kutta–Fehlberg method, also known as *RKF45*, to compute numerical solutions of the ODE system. The *RKF45* method might not be the most appropriate method to solve this type of systems as they are considered *rigid*, however it is sufficient for our purposes.

We used the implementation of the *RKF45* method for the Maxima CAS [19, 20, 30], written by P. J. Papasotiriou. The code together with its technical documentation can be found in [23] . For information about the *RKF45* method, see Section 5.5 in [4].

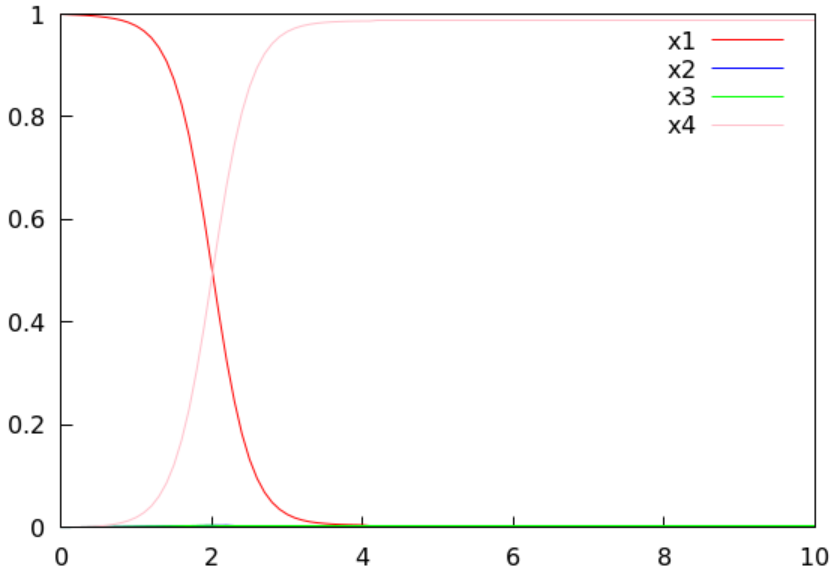
Some of the simulations were performed with the aid of numerical algebra techniques. We used the `dgeev` routine, which is part of the `lapack` library implementation for the Maxima language. Additionally, we utilized the routine `eigs` to compute eigenvalues of matrices in GNU/Octave [9].

We emphazise that as we described in this chapter, there are two approaches to compute the quasispecies. On one hand, we can opt for numerical integration of the ODE system up to a large enough time. This approach is suggested on the Swetina-Schuster work [26, 25]. It is a reasonable approach, as we can analyze the evolution in time.

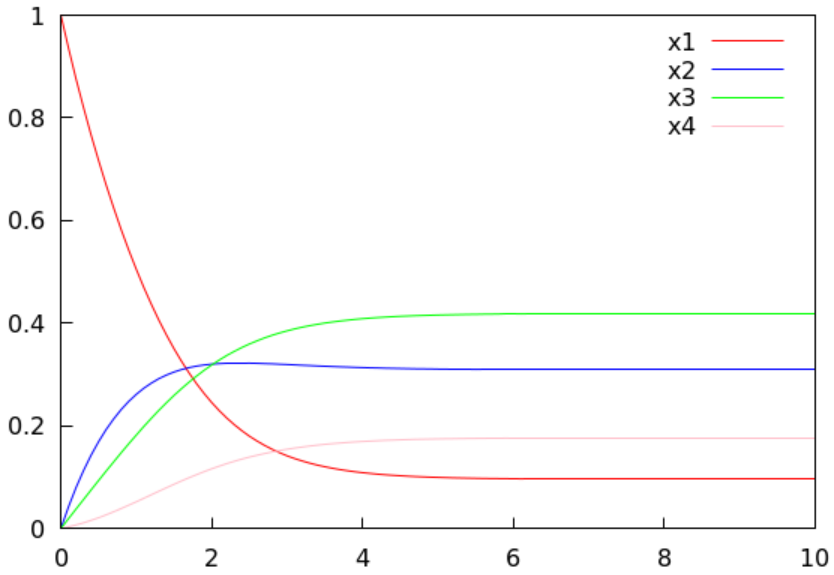
On the other hand, in the more theoretical oriented work by Jones, Enns and Rangnekar [14], it was brought to our attention how the physical meaning of the quasispecies is in agreement with the eigenvector associated to the largest eigenvalue, as a consequence of the Perron-Frobenius theorem. In this setting, our approach is to use numerical linear algebra routines to compute directly the eigenvector associated to the largest eingevalue and normalize it, such that its entries add up to one.

In Figure 1.3 and Figure 1.8 both approaches are compared. We observe that the linear algebra approach seems more accurate. In Figure 1.9 and Figure 1.10 the linear algebra approach was followed, due to the sharpness of the obtained results.

1.3.1 Figures of numerical simulations.



(a)



(b)

Figure 1.1: Graph (a) corresponds to the matrix Q_1, (b) corresponds to matrix Q_2, see Eq. 1.7 .

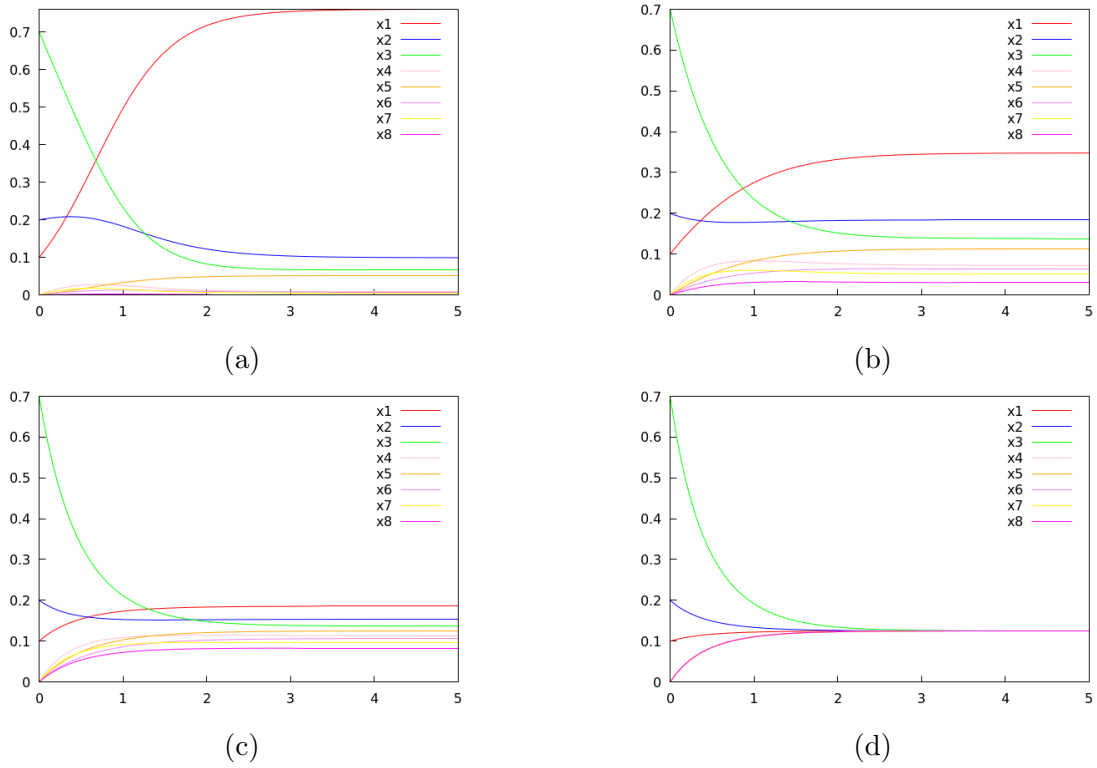
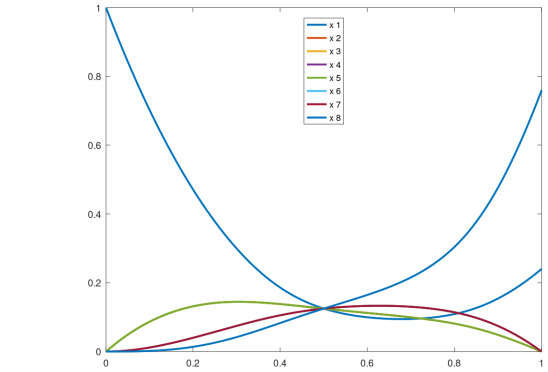
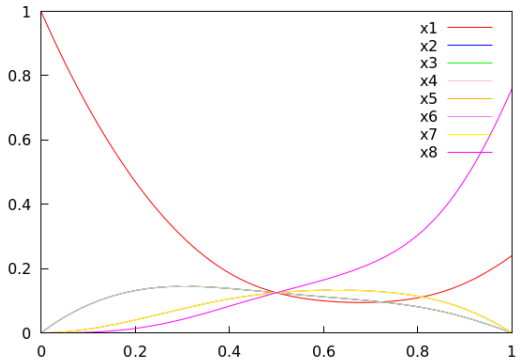


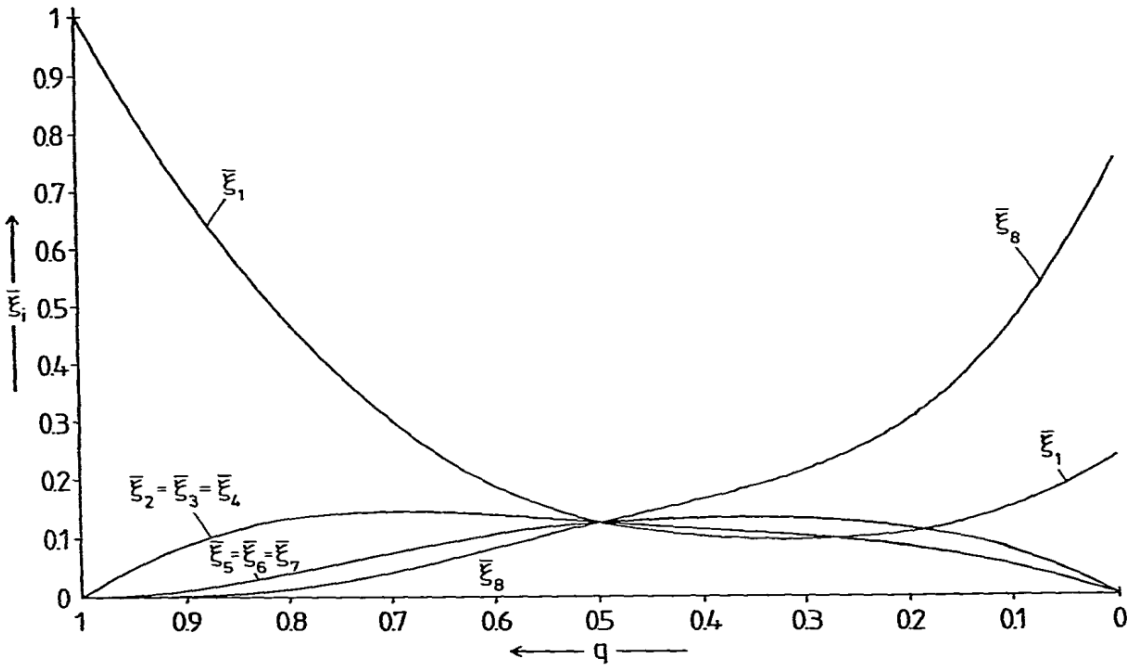
Figure 1.2: Numerical integration of the model with a Swetina-Schuster matrix. The constants are $A_1 = 5, A_2 = 3, A_3 = 2, A_4 = \ldots = A_8 = 1.1$, $D_1 = \ldots = D_8 = 1.0$ and $x_1(0) = 0.1, x_2(0) = 0.2, x_3(0) = 0.7, x_4(0) = \ldots = x_8(0) = 0$. In: (a) $u = 0.05$, (b) $u = 0.2$, (c) $u = 0.35$, (d) $u = 0.50$



(a)



(b)



(c)

Figure 1.3: Steady-states as a function of u. The chosen values are $A_1 = 10, A_2 = \ldots = A_8 = 1$, and every $D_i = 0$. In (a) the simulation was made using the command `eigs` in Octave, in (b) the graph was obtained by numerical integration of the system using the method `rkf45` in Maxima and the *quasispecies* was taken as the state of the system at the time $t = 15$. In (c) we include the graph of the same simulation from [26] for comparison purposes.

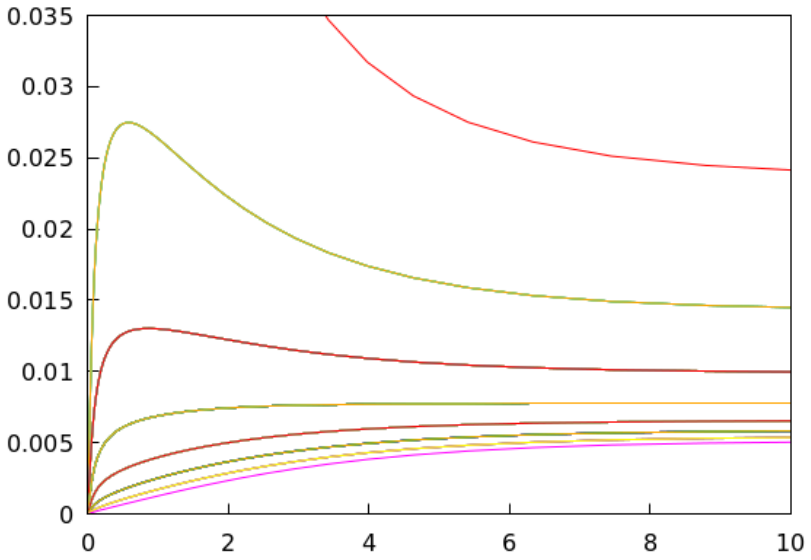


Figure 1.4: Numerical integration of the model with a Swetina-Schuster matrix. The values are $u = 0.3$, $A_1 = 10, A_2 = \ldots = A_{128} = 1$, $D_i = 0$ for all $i = 1, \ldots, 128$.

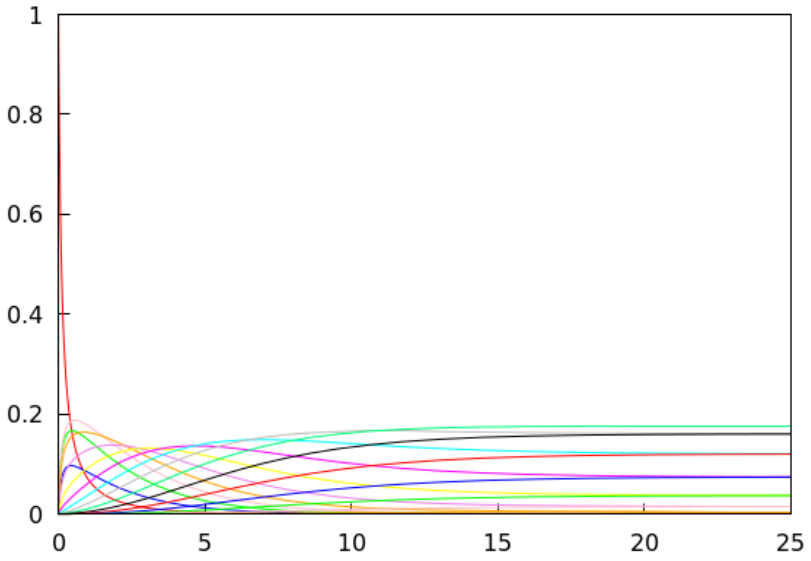


Figure 1.5: Numerical integration of the model with a modified Swetina-Schuster matrix, see 1.16. The values are $u = 0.15$, $A'_0 = 10, A'_2 = \ldots = A'_{20} = 1$, $D'_i = 0$ for all $i = 0, \ldots, 20$.

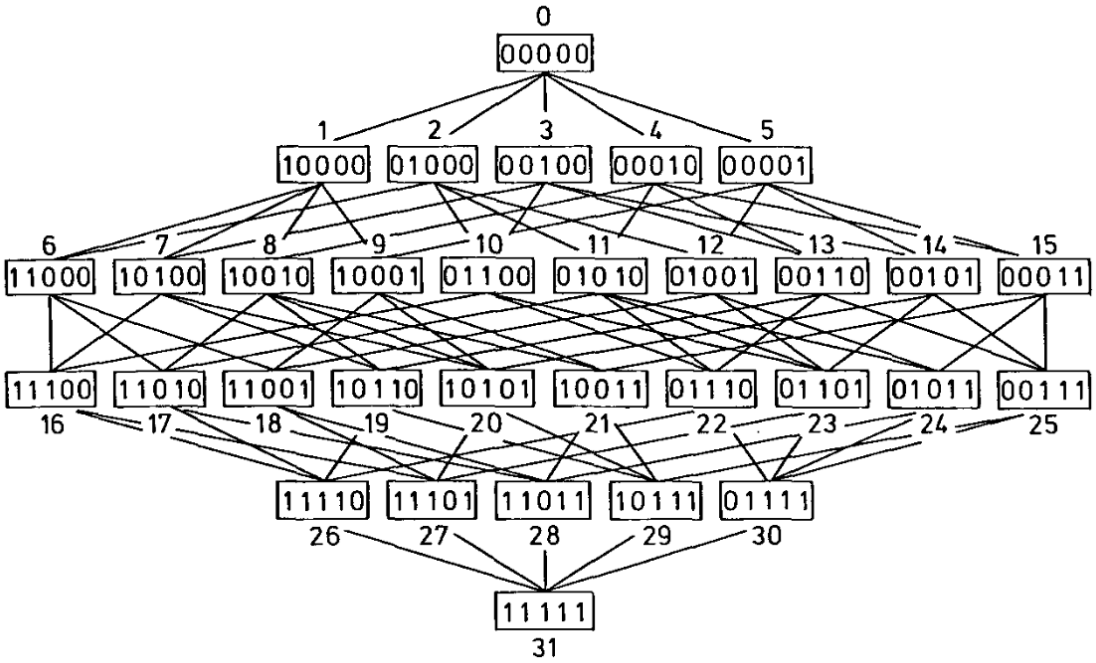
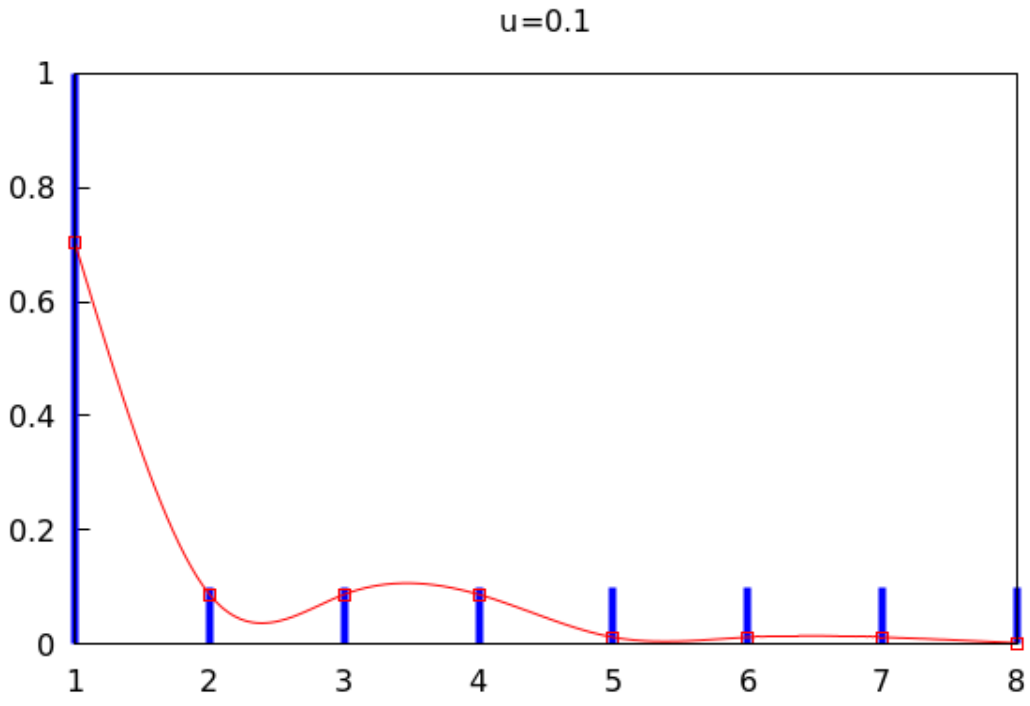
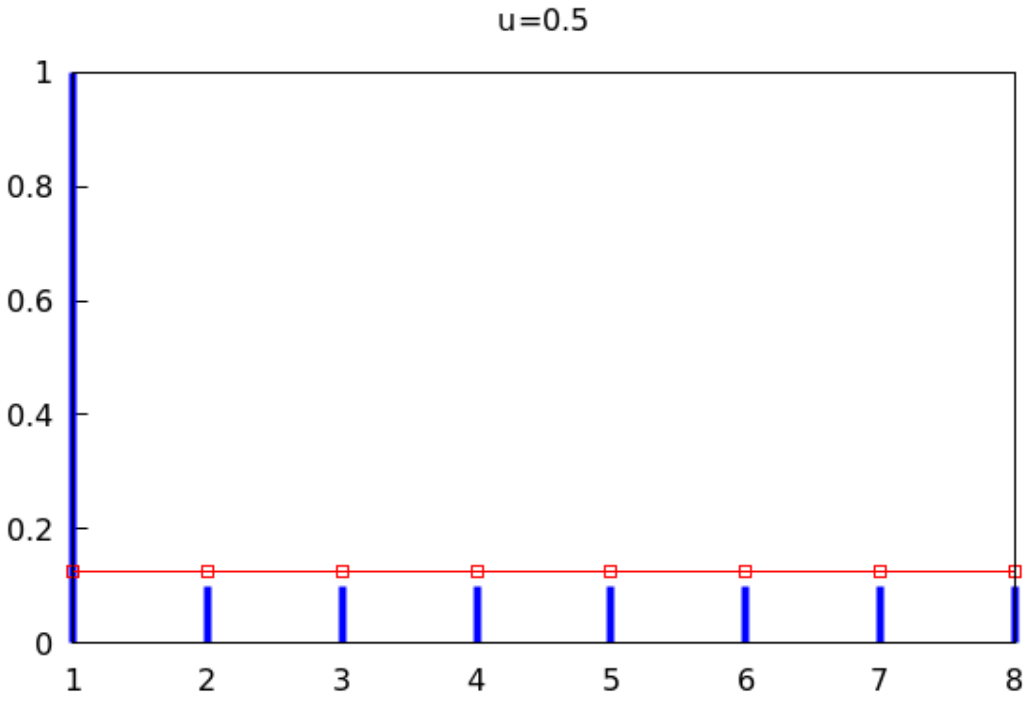


Figure 1.6: Space of binary sequences of length 5 [25].

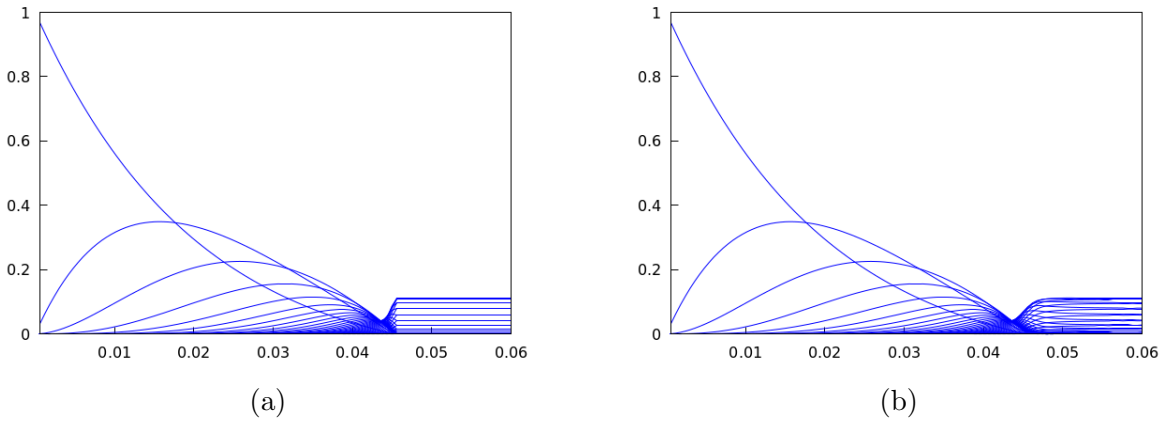


(a)



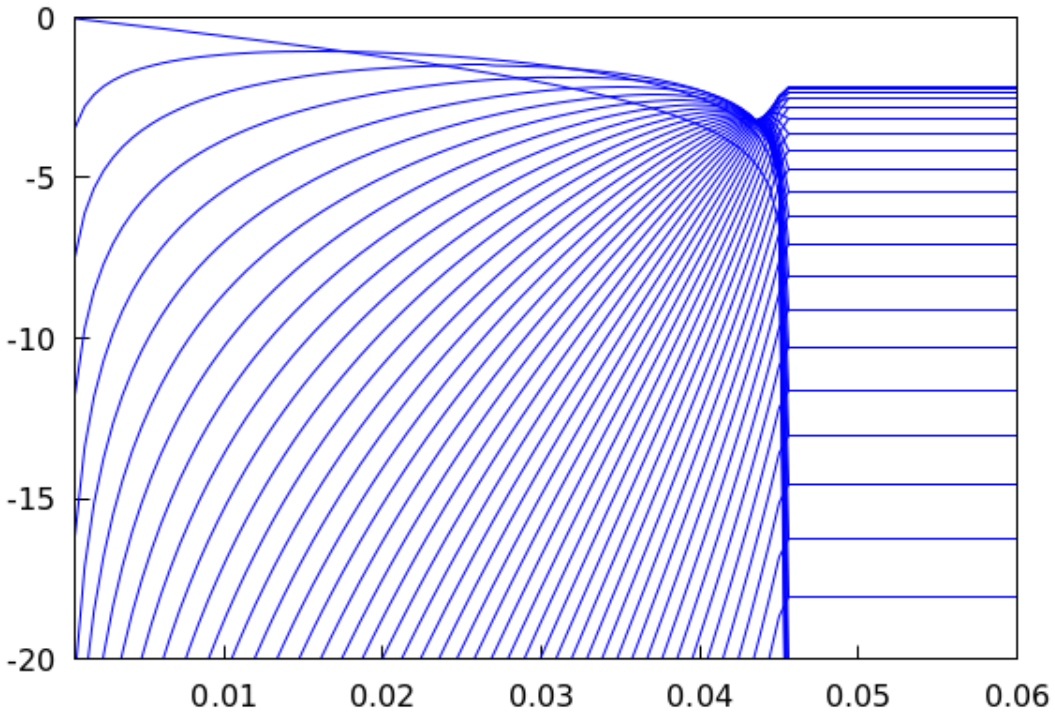
(b)

Figure 1.7: Fitness landscape for the sequences of Figure 1.3 using the enumeration proposed in [25], see Figure 1.6. The fitness values are normalized using the maximum norm. The curve represents the distribution of the quasispecies in the steady-state.



(a)

(b)



(c)

Figure 1.8: Error-threshold for $\nu = 50$. The constant values are $A_0 = 10, A_1 = 1, \ldots, A_{50} = 1, D = 0$. In (a) the simulation was carried on using `dgeev` from the `lapack` library. In (b) the system was solved using `rkf45`. In (c) we show the graph of the simulation in (a) using a logarithmic scale.

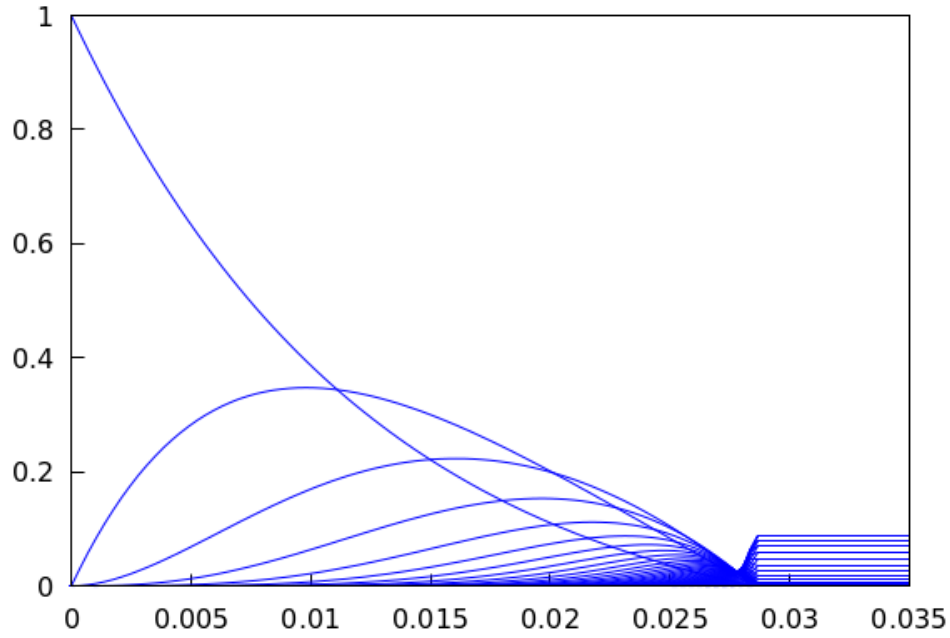


Figure 1.9: Error-threshold for $\nu = 80$. The chosen values for the constants are $A_0 = 10, A_1 = 1, \ldots, A_{80} = 1, D = 0$. Here we have $u_c = .028\ldots$.

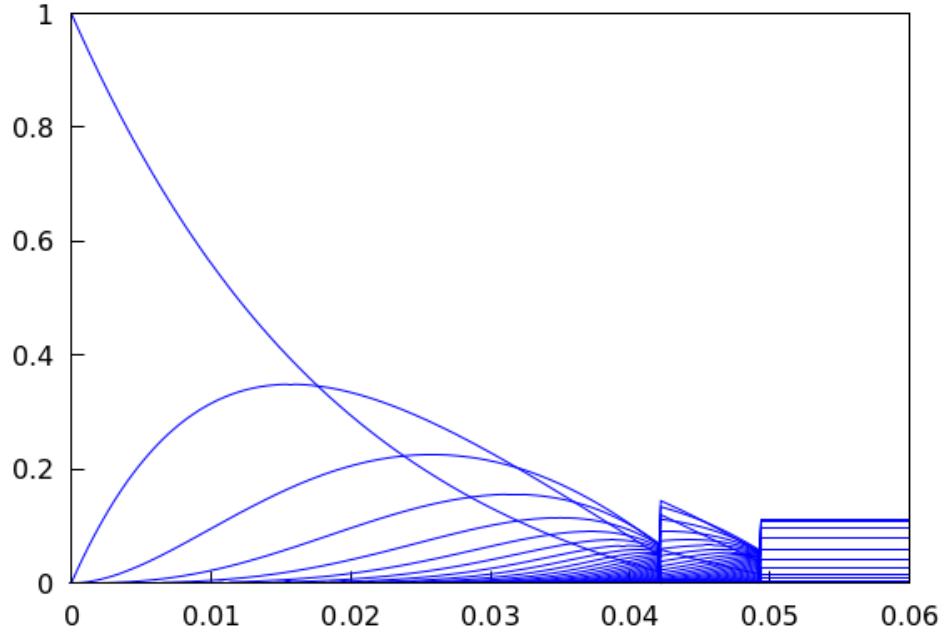


Figure 1.10: Error-threshold for $\nu = 50$. The chosen values for the constants are $A_0 = 10, A_1 = 1, \ldots, A_{48} = 1, A_{49} = 9.9, A_{50} = 10, D = 0$.

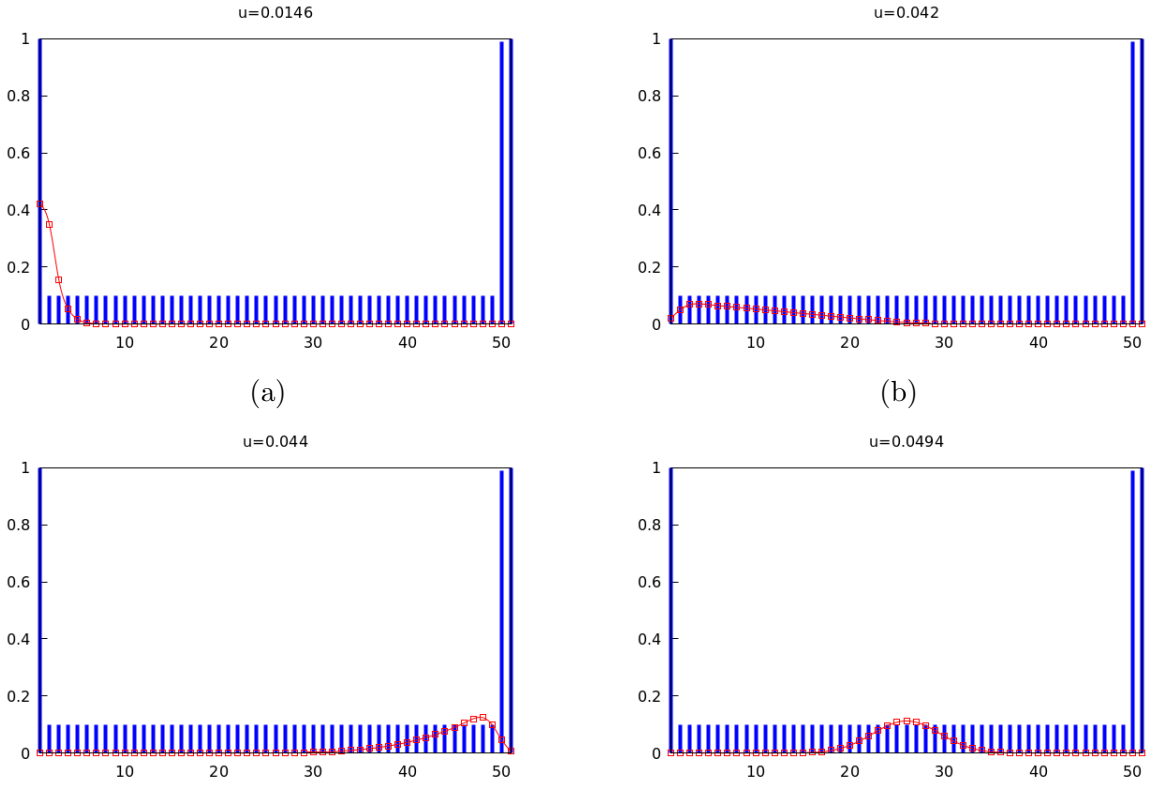


Figure 1.11: Fitness landscape and distribution of the quasispecies for different values of u. Here $\nu = 50$, and the constant values are $A_0 = 10, A_1 = 1, \ldots, A_{48} = 1, A_{49} = 9.9, A_{50} = 10, D = 0$.

Chapter 2

p-adic analysis: Essential ideas

In this chapter we follow closely the references [1, 29].

2.1 The field of p-adic numbers

Let us start by recalling a few basic definitions.

Definition 2.1. Let $\mathbb{F}$ be a field. An absolute value (or norm) on $\mathbb{F}$ is a map $|\cdot| : \mathbb{F} \to \mathbb{R}_+ \cup \{0\}$, which satisfies:

(i) $|x| = 0 \iff x = 0$;

(ii) $(\forall x, y \in \mathbb{F})|xy| = |x||y|$;

(iii) $(\forall x, y \in \mathbb{F})|x + y| \leq |x| + |y|$ (triangle inequality).

The absolute value is called *non-Archimedean* or *ultrametric* if additionally, $|\cdot|$ satisfies

(iii') $(\forall x, y \in \mathbb{F})|x + y| \leq \max\{|x|, |y|\}$ (strong triangle inequality).

Notice that (iii') implies (iii). A field $\mathbb{F}$ together with an absolute value (norm) is called *normed field*. A field $\mathbb{F}$ with a non-Archimedean absolute value is called non-Archimedean field.

Example 2.2. Let $\mathbb{F}$ be a field. Then,

$$|x|_{trivial} = \begin{cases} 1 & x \neq 0 \\ 0 & x = 0. \end{cases}$$

defines an absolute valued which is called *the trivial absolute value*.

Example 2.3. The standard absolute value over the field of rational numbers $\mathbb{Q}$, that is

$$|x| = \begin{cases} x & x \geq 0 \\ -x & x < 0. \end{cases}$$

Using an absolute value $|\cdot|$ we can induce a metric $d(x,y) = |x-y|$. In this case we can regard the field $\mathbb{F}$ as a metric space. It can be shown that a metric induced by a non-Archimedean absolute value is also non-Archimedean, i.e., it satisfies the strong triangle inequality,

$$(\forall x, y, z \in \mathbb{F})\ d(x,z) \leq \max\{d(x,y), d(y,z)\} \quad . \tag{2.1}$$

Such a metric is known as as an *ultrametric*. There are surprising properties of non-Archimedean absolute values.

2.1 Proposition (Prop. 1.2.6, [1]). *Let $\mathbb{F}$ be a non-Archimedean field. Then, for $x, y \in \mathbb{F}$*

$$|x| \neq |y| \implies |x+y| = \max\{|x|, |y|\}.$$

Thus, any triangle in an ultrametric space is isosceles and the length of its base does not exceed the lengths of the sides.

Moreover, remembering that for any field $\mathbb{F}$ we have a map from $\mathbb{Z}$ to $\mathbb{F}$ defined by

$$n \mapsto \begin{cases} \underbrace{1+1+\ldots+1}_{n} & n > 0 \\ 0 & n = 0 \\ -(\underbrace{1+1+\ldots+1}_{-n}) & n < 0 \end{cases}$$

We have the following.

2.2 Theorem (Thm. 2.2.4, [13]). *Let $A \subset \mathbb{F}$ be the image of $\mathbb{Z}$ in $\mathbb{F}$. An absolute vale $|\cdot|$ on $\mathbb{F}$ is non-Archimedean if and only if $|a| \leq 1$ for all $a \in A$. In particular, an absolute value on $\mathbb{Q}$ is non-Archimedean if and only if $|n| \leq 1$ for every $n \in \mathbb{Z}$.*

This last theorem explains the difference between Archimedean and non-Archimedean absolute values.

Definition 2.4. Let p be a prime number. The p-adic order, denoted $\mathrm{ord}_p(x)$, of a rational number $x \in \mathbb{Q}$ is defined as:

(i) If $x \in \mathbb{Z} \setminus \{0\}$, then $\mathrm{ord}_p(x)$ equals the highest power of p which divides x.

(ii) If $x = a/b$ with $a, b \in \mathbb{Z}$, then $\mathrm{ord}_p(x) = \mathrm{ord}_p(a) - \mathrm{ord}_p(b)$.

(iii) We set $\mathrm{ord}_p(0) = +\infty$.

Remark 2.5. Notice that in part (ii), the p-adic order of a rational number x depends solely on x. If we write $x = (ac)/(bc)$ then $\mathrm{ord}_p(a) - \mathrm{ord}_p(b) = \mathrm{ord}_p(ac) - \mathrm{ord}_p(bc)$. This follows from the fact that $\mathrm{ord}_p(xy) = \mathrm{ord}_p(x) + \mathrm{ord}_p(y)$.

Now, we define a map $|\cdot|_p : \mathbb{Q} \to \mathbb{R}$ as follows:

$$|x|_p = p^{-\mathrm{ord}_p(x)} \tag{2.2}$$

We observe that, by definition, $|0|_p = 0$ since $\mathrm{ord}_p(0) = +\infty$. Moreover, the function $|\cdot|_p$ can take only a discrete set of values, namely, $\{p^\gamma : \gamma \in \mathbb{Z}\} \cup \{0\}$.

2.3 Theorem (Thm. 1.3.1, p. 7, [1]). *The map $|\cdot|_p$ is a non-Archimedean absolute value on the field of rational numbers $\mathbb{Q}$.*

Definition 2.6. We say that two absolute values $|\cdot|_1$ and $|\cdot|_2$ on a normed field $\mathbb{F}$ are *equivalent* if they induce equivalent metrics. In this case, we write $|\cdot|_1 \sim |\cdot|_2$

Remark 2.7. If p_1, p_2 are two distinct primer numbers, then $|\cdot|_{p_1}$ and $|\cdot|_{p_2}$ are not equivalent. To see this, consider the sequence $x_n = (p_1/p_2)^n$. Then, $|x_n|_{p_1} = p_1^{-n} \to 0$ as $n \to \infty$. On the contrary, $|x_n|_{p_2} = p_2^n \to \infty$ as $n \to \infty$.

A detailed study of equivalence of absolute values and properties of non-Archimedean norms can be found in [2, 13] and [15]. Now, we state a famous result, proved by Alexander Ostrowski. The proof can be found, for instance, in [16], p. 3.

2.4 Theorem (Ostrowski). *Every non-trivial absolute value on the rational numbers is equivalent to either the standard real absolute value or a p-adic absolute value.*

It can be proven, that the field of rational numbers is not complete with respect to any of its non-trivial norms, see Lemma 3.2.3, p. 63, in [13]. Thus, the next step is knowing how to construct a completion. On this direction, a great reference is [2]. Particularly, section 2.1 develops the theory of the completion of a field with respect to an absolute value and then, it is applied to the construction of the field of p-adic numbers. We summarize the results in the following theorem.

2.5 Theorem (Thm. 1.3, Thm. 1.4, [2]).

(i) Given a field $\mathbb{F}$ and an absolute value $|\cdot|$ on $\mathbb{F}$, there exists a field $\widehat{\mathbb{F}}$ (unique up to a congruence), called the completion of $\mathbb{F}$ with respect to $|\cdot|$, such that $\widehat{\mathbb{F}}$ is a complete field with respect to the metric induced by an absolute value extending $|\cdot|$, and $\mathbb{F}$ is dense in $\widehat{\mathbb{F}}$.

(ii) Denote by $|\mathbb{F}|$ the image of $\mathbb{F}$ in $\mathbb{R}$ under the function $|\cdot|$. If $|\cdot|$ is a non-Archimedean absolute value on $\mathbb{F}$, then $|\mathbb{F}| = |\widehat{\mathbb{F}}|$.

Now, we formally introduce the field of p-adic numbers.

Definition 2.8. The completion of the field $\mathbb{Q}$ of rational numbers with respect to $|\cdot|_p$ is called the field of p-adic numbers and it is denoted by $\mathbb{Q}_p$. We also use $|\cdot|_p$ to denote the extension of $|\cdot|_p$ to $\mathbb{Q}_p$.

Remark 2.9. Notice that the last theorem says that the p-adic absolute value extended to $\mathbb{Q}_p$ takes the same values as $|\cdot|_p$ over $\mathbb{Q}$, namely, $\{p^\gamma : \gamma \in \mathbb{Z}\} \cup \{0\}$.

2.6 Theorem (Thm. 2.1, [2]).

$$\mathbb{Q}_p = \{x = p^\gamma \sum_{k=0}^{\infty} x_k p^k; \gamma \in \mathbb{Z}, x_i \in \{0, 1, \ldots, p-1\}, x_0 \neq 0\} \cup \{0\}.$$

and $|x|_p = p^{-\gamma}$ for $x \in \mathbb{Q}_p \setminus \{0\}$, $|0|_p = 0$. With respect to this representation, the coefficients x_k are unique.

Definition 2.10. The series

$$x = p^{\gamma} \sum_{k=0}^{\infty} x_k p^k. \tag{2.3}$$

is called the *canonical representation* of x. The integer $\gamma = \gamma(x)$ is called *the p-adic order of* x. Finally, we define $\mathrm{ord}_p(0) = +\infty$.

Definition 2.11. By means of (2.3), the *fractional part* $\{x\}_p$ of a p-adic number $x \in \mathbb{Q}_p$ is defined as

$$\{x\}_p := \begin{cases} 0 & \text{if } \gamma(x) \leq 0 \text{ or } x = 0, \\ p^{\gamma} \sum_{k=0}^{|\gamma|-1} x_k p^k & \text{if } \gamma(x) < 0. \end{cases} \tag{2.4}$$

The *integer part* $[x]_p$ of a p-adic number $x \in \mathbb{Q}_p$ is defined as

$$\begin{cases} x & \text{if } \gamma(x) \text{ or } x = 0, \\ p^{\gamma} \sum_{k=|\gamma|}^{\infty} x_k p^k & \text{if } \gamma(x) < 0. \end{cases} \tag{2.5}$$

Definition 2.12. The elements of the set $\mathbb{Z}_p := \{x \in \mathbb{Q}_p^n; |x|_p \leq 1\}$, are called *p-adic integers*. The *group of units* of $\mathbb{Z}_p$ is $\mathbb{Z}_p^{\times} := \{x \in \mathbb{Q}_p^n; |x|_p = 1\}$.

Using canonical representations, $\mathbb{Z}_p$ consists of p-adic numbers of the form:

$$x = \sum_{k=0}^{\infty} x_k p^k. \tag{2.6}$$

Moreover, the following holds.

2.7 Proposition (Prop. 1.7.1, Prop 1.7.2, [1])**.**

(i) $\mathbb{Z}_p$ *is a subring of* $\mathbb{Q}_p$.

(ii) A p-adic integer $x \in \mathbb{Z}_p$ *has a multiplicative inverse element in* $\mathbb{Z}_p$ *if and only if in* (2.6) $x_0 \neq 0$. *Equivalently,* $x \in \mathbb{Z}_p$ *is invertible if and only if* $x \in \mathbb{Z}_p^{\times}$.

(iii) If $x \in \mathbb{Q}_p \setminus \{0\}$, *then* $x = p^m u$, $m \in \mathbb{Z}$ *and* $u \in \mathbb{Z}_p^{\times}$.

2.2 The topology of p-adic numbers

As it was previously mentioned, we can induce a metric using an absolute value over a field. With respect to the metric $\rho_p(x, y) = |x - y|_p$ for $x, y \in \mathbb{Q}_p$, $\mathbb{Q}_p$ is a complete metric space. Since $|\cdot|_p$ is non-Archimedean, the corresponding metric satisfies the strong triangle inequality (2.1), thus, it is an ultrametric.

Since the p-adic norm takes a discrete set of values $\{p^{\gamma}; \gamma \in \mathbb{Z}\} \cup \{0\}$, we only need to consider balls of radius $r = p^{\gamma}$, $\gamma \in \mathbb{Z}$. We denote by $B_{\gamma}(a) = \{x \in \mathbb{Q}_p; |x - a|_p \leq p^{\gamma}\}$

the closed $p-$adic ball centered at $a \in \mathbb{Q}_p$ of radius p^γ. Also, we denote by $S_\gamma(a) = \{x \in \mathbb{Q}_p; |x-a|_p = p^\gamma\}$ the p-adic sphere centered at $a \in \mathbb{Q}_p^n$ of radius p^γ. For the sake of brevity, we just use the power to denote the radius of the balls. Lastly, we set $B_\gamma := B_\gamma(0)$ and $S_\gamma := S_\gamma(0)$.

On a short notice, the fact that the p-adic norm takes a discrete set of values in $\mathbb{R}$, implies that

$$\{x \in \mathbb{Q}_p; |x-a|_p < p^\gamma\} = \{x \in \mathbb{Q}_p; |x-a|_p \leq p^{\gamma-1}\} = B_{\gamma-1}(a).$$

This justifies why we just set the notation for the balls $B_\gamma(a)$ using '$\leq$'. From here, we already see that the topology of $\mathbb{Q}_p$ is quite different from the usual topology of $\mathbb{R}$. We summarize the main topological properties of $\mathbb{Q}_p$ in the following theorem.

2.8 Theorem.

(i) $B_\gamma(a), S_\gamma(a)$ *are open and closed sets in the topology of* $\mathbb{Q}_p$.

(ii) If $b \in B_\gamma(a)$, *then* $B_\gamma(a) = B_\gamma(b)$, *i.e., any point of the ball* $B_\gamma(a)$ *is its center.*

(iii) Any two balls in $\mathbb{Q}_p$ *are either disjoint or one is contained in the other.*

(iv) The boundary of any ball $B_\gamma(a)$ *is the empty set.*

(v) The set of balls of $\mathbb{Q}_p$ *is countable.*

(vi) Every open set in $\mathbb{Q}_p$ *is a union of at most of a countable set of disjoint balls.*

(vii) The Heine-Borel property is valid in $\mathbb{Q}_p$, *i.e., a set* $K \subset \mathbb{Q}_p$ *is compact if and only if it is closed and bounded in* $\mathbb{Q}_p$.

(viii) Every ball $B_\gamma(a)$ *and every sphere is compact. Consequently,* $\mathbb{Q}_p$ *is a locally compact space.*

(ix) The space $\mathbb{Q}_p$ *is totally disconnected.*

(x) $\mathbb{Q}_p$ *is homeomorphic to a Cantor-like set of* $\mathbb{R}$.

Proof. See Sections 1.8 and 1.9 in [1]. □

2.3 Integration in $\mathbb{Q}_p$

A locally compact group is a topological group that is locally compact as a topological space. It is a well-known result that a locally compact group possesses a non-zero left-invariant outer Radon measure, that is, a locally finite Borel measure μ such that

1. $\mu(A) = \inf_{U \supset A} \mu(U)$ holds for every $A \in \mathcal{B}$, where the infimum is taken over all open sets U containing A and $\mathcal{B}$ denotes the σ-algebra of Borel sets.

2. $\mu(A) = \sup_{K \subset A} \mu(K)$ holds for every $A \in \mathcal{B}$ that is open or satisfies $\mu(A) < \infty$, where the supremum is taken over all compact sets K contained in A.

In the case the group is an Abelian group, then the non-zero left-invariant outer Radon measure is also right-invariant. A left-invariant and right-invariant measure is simply called invariant. To be precise, the following holds.

2.9 Theorem (Thm. 1.3.4., [8])**.** *Let $(G,+)$ be a locally compact Abelian group. There exists a non-zero invariant outer Radon measure μ_{Haar} on G, called a Haar measure of G, that is, $\mu_{Haar}(x+E)=\mu_{Haar}(E)$ for every Borel set. It is uniquely determined up to positive multiples. The corresponding integral is called a Haar-integral.*

Since $(\mathbb{Q}_p,+)$ is a locally compact Abelian group, then there exists the additive Haar measure, which is a positive measure μ_{Haar} which is invariant under shifts. We denote the Haar measure by dx, then $\mu_{Haar}(U)=\int_U dx$. The invariance under shifts property can be written as $\int_U dx=\int_{a+U} dx$. Alternatively, we denote this fact as $d(x+a)=dx$, $a\in\mathbb{Q}_p$. If the measure dx is normalized by the condition

$$\int_{\mathbb{Z}_p} dx = 1,$$

then dx is unique. Now, we state an important result of the Haar integral on $(\mathbb{Q}_p,+)$.

2.10 Proposition (Prop. 3.2.1, [1])**.** *For $a\in\mathbb{Q}_p\setminus\{0\}$, we have*

$$d(xa)=|a|_p dx.$$

Alternatively,

$$\int_{aU} dx = |a|_p \int_U dx.$$

Integral	Constraints
$\int_{B_r} dx = p^r$	$r\in\mathbb{Z}$
$\int_{S_r} dx = p^r(1-p^{-1})$	$r\in\mathbb{Z}$
$\int_{\mathbb{Z}_p\setminus\{0\}} \lvert x\rvert_p^s dx = \frac{1-p^{-1}}{1-p^{-1-s}}$	$s\in\mathbb{C}, \mathrm{Re}(s)>-1$

Table 2.1: Some useful p-adic integrals.

2.4 Fourier analysis in $\mathbb{Q}_p$

Definition 2.13. The function

$$\chi_p(x) := \exp 2\pi i\{x\}_p$$

is called the *standard additive character* of $(\mathbb{Q}_p,+)$.

It verifies that

$$\chi_p : (\mathbb{Q}_p,+)\to(S^1,\cdot)$$

is a continuous homomorphism from $(\mathbb{Q}_p,+)$ into the complex unit circle considered as a multiplicative group. The following properties hold true:

1. $|\chi_p(x)| = 1$ for $x \in \mathbb{Q}_p$.
2. $\chi_p(x+y) = \chi_p(x)\chi_p(y)$ for $x, y \in \mathbb{Q}_p$.
3. $\overline{\chi_p(x)} = \chi_p(x)^{-1} = \chi_p(-x)$ for $x \in \mathbb{Q}_p$ and the bar means complex conjugate.
4. $\chi_p(x) \not\equiv 1$ for $x \in \mathbb{Q}_p \setminus \mathbb{Z}_p$.

Now, we can introduce the Fourier transform.

Definition 2.14. For a function $f \in L^1(\mathbb{Q}_p)$, its Fourier transform is the function $\widehat{f}$ defined by

$$\widehat{f}(\xi) = \int_{\mathbb{Q}_p} f(x)\chi_p(x \cdot \xi)dx.$$

We also denote the Fourier transform of f by $\mathcal{F}_{x\to\xi}f, \mathcal{F}(f)$.

Analogously to the classical case, the Fourier transform in the p-adic space also satisfies the following properties.

2.11 Theorem (Thm. 1.1, Thm. 1.6, Thm. 1.8, [27]). *Let $f, g \in L^1(\mathbb{Q}_p)$, then:*

(i) $\|\widehat{f}\|_\infty \leq \|f\|_1$.

(ii) $\widehat{f}$ *is uniformly continuous.*

(iii) (Riemman-Lebesgue Theorem) $\widehat{f}(\xi) \to 0$ *as* $|\xi|_p \to \infty$.

(iv) $\widehat{f * g} = \widehat{f}\widehat{g}$.

The following are some important Fourier transforms.

$$\int_{B_r} \chi_p(\xi \cdot x)dx = \begin{cases} p^r & \text{if } |\xi|_p \leq p^{-r} \\ 0 & \text{if } |\xi|_p \geq p^{-r+1} \end{cases} \tag{2.7}$$

$$\int_{S_r} \chi_p(\xi \cdot x)dx = \begin{cases} p^r(1-p^{-1}) & \text{if } |\xi|_p \leq p^{-r} \\ -p^{r-1} & \text{if } |\xi|_p = p^{-r-1} \\ 0 & \text{if } |\xi|_p \geq p^{-r+2} \end{cases} \tag{2.8}$$

Now, we state the following proposition.

2.12 Proposition (Ex. 8, p. 43, [29]). *Let $f : \mathbb{R}_+ \to \mathbb{C}$ be a function such that $\sum_{r=0}^{\infty} |f(p^{-r})|p^{-r} < \infty$. Then*

$$\int_{\mathbb{Q}_p} f(|x|_p)\chi_p(\xi \cdot x)dx = \frac{1-p^{-1}}{|\xi|_p} \sum_{r=0}^{\infty} f\left(\frac{p^{-r}}{|\xi|_p}\right) p^{-r} - \frac{1}{|\xi|_p} f\left(\frac{p}{|\xi|_p}\right),$$

for $\xi \neq 0$, in the sense of improper integrals.

Remark 2.15. In the above proposition, if $f \in L^1(\mathbb{Q}_p, \mathbb{C})$, then for any fixed $\xi \neq 0$, then $f(|x|_p)\chi_p(\xi \cdot x)$ is integrable with respect to x and so, the above formula holds true. In particular, the above proposition says that the Fourier transform of a radial real-valued and integrable function is real-valued.

Now, we would like to extend the Fourier transform to the space $L^2(\mathbb{Q}_p)$. In order to do this, we need the following result.

2.13 Theorem (Thm. 2.1, [27])**.** *If $f \in L^1(\mathbb{Q}_p) \cap L^2(\mathbb{Q}_p)$ then $\|\widehat{f}\|_2 = \|f\|_2$.*

A consequence of this theorem is that the map $f \to \widehat{f}$ is a linear L^2-isometry from the dense subspace $L^1(\mathbb{Q}_p) \cap L^2(\mathbb{Q}_p)$ to $L^2(\mathbb{Q}_p)$. Therefore, we can extent the Fourier transform to the whole L^2 space and it is an isometry. Moreover, we have the following result, which is analogous to the classical Plancherel's Theorem.

2.14 Theorem (Thm. 2.3, [27])**.** *The Fourier transform is unitary on $L^2(\mathbb{Q}_p)$.*

With this construction, there is a generalization of the convolution theorem (see Thm. 2.11 (iv)).

2.15 Theorem (Thm. 2.7., [27])**.** *Let $f \in L^1(\mathbb{Q}_p)$ and $g \in L^2(\mathbb{Q}_p)$, then*

$$\widehat{f * g} = \widehat{f}\widehat{g} \, a.e.$$

2.5 The space of test functions.

Definition 2.16. A complex-valued function φ defined on an open set $V \subset \mathbb{Q}_p$ is called *locally constant* on V if for any $x \in V$ there exists and integer $l(x) \in \mathbb{Z}$ such that

$$\varphi(x + x') = \varphi(x), \quad x \in B_{l(x)}, \quad x \in V.$$

The characteristic function of the ball $B_r(a)$ constitutes an example of a locally constant function.

Remark 2.17. We denote by Ω the characteristic function of the unit interval $[0, 1] \subset \mathbb{R}$. Considering Ω as a radial function from $\mathbb{Q}_p$ to $\mathbb{R}_+$, we can write characteristic functions of p-adic balls. Indeed,

$$\begin{aligned} \Omega(p^{-r}|x - a|_p) = 1 &\iff |x - a|_p \leq p^r \\ &\iff x \in B_r(a) \end{aligned}$$

In particular, $\Omega(|\cdot|_p)$ is the characteristic function of the unit ball in $\mathbb{Q}_p$.

A direct consequence of the definition is that any locally constant function is continuous. Moreover, the following holds.

2.16 Lemma (Lemma 4.2.1, [1])**.** *Let φ be a locally constant function, and let K be a compact subset of $\mathbb{Q}_p$. Then there exists $l \in \mathbb{Z}$ such that*

$$\varphi(x + x') = \varphi(x), \quad x' \in B_l, x \in K.$$

We denote by $\mathcal{D}(\mathbb{Q}_p)$ the *Bruhat-Schwartz space of test functions* in $\mathbb{Q}_p$ which consists of all locally constant functions with compact support. According to the lemma above, there exists $l \in \mathbb{Z}$ such that

$$\varphi(x + x') = \varphi(x), \quad x' \in B_l, x \in \mathbb{Q}_p.$$

The largest of such numbers $l = l(\varphi)$ is called the parameter of constancy of the function φ.

2.17 Proposition (Prop. 4.3.3, [1])**.** *The space of test functions $\mathcal{D}(\mathbb{Q}_p)$ is dense in $L^p(\mathbb{Q}_p)$, $1 \leq p < \infty$.*

Because of Remark 2.17, if $\varphi(x) = \Omega(p^{-r}|x|_p)$, using equation (2.7) we have the formula $\widehat{\varphi}(\xi) = p^r\Omega(p^r|\xi|_p)$. This, together with the following proposition, facilitates the calculation of Fourier transforms of test functions.

2.18 Proposition (Prop. 4.8.5, [1])**.** *If $\varphi \in \mathcal{D}(\mathbb{Q}_p)$, $a \in \mathbb{Q}_p^{\times}$ and $b \in \mathbb{Q}_p$ then,*

$$\mathcal{F}(\varphi(ax + b))(\xi) = |a|_p^{-1}\chi_p(-\frac{b}{a}\xi)\mathcal{F}(\varphi(x))(\frac{\xi}{a})$$

2.6 p-adic wavelets

We now introduce the Kozyrev wavelet basis of the space $L^2(\mathbb{Q}_p, \mathbb{C})$, which was introduced by Sergei Kozyrev in [17].

$$\Psi_{rjn}(x) = p^{\frac{-r}{2}}\chi_p(p^{r-1}jx)\Omega(|p^r x - n|_p). \tag{2.9}$$

where $r \in \mathbb{Z}, j \in \{1, \ldots, p-1\}$ and n runs trough a system of representatives of $\mathbb{Q}_p/\mathbb{Z}_p$.

2.19 Theorem (Thm. 2, [17])**.** *The Kozyrev wavelet basis $\{\Psi_{rjn}\}$ is an orthonormal basis of the space $L^2(\mathbb{Q}_p, \mathbb{C})$. Here, $r \in \mathbb{Z}, j \in \{1, \ldots, p-1\}$ and the group $\mathbb{Q}_p/\mathbb{Z}_p$ is parametrized by $n = \sum_{k=1}^{m} n_k p^{-k}$ and $n_i \in \{0, \ldots, p-1\}$.*

Using Proposition 2.18, we can compute the Fourier transform of an element of the Kozyrev wavelet basis and we get

$$\widehat{\Psi}_{rjn}(\xi) = p^{\frac{r}{2}}\chi_p(p^r n(\xi + jp^{r-1}))\Omega(|p^{-r}\xi + jp^{-1}|_p). \tag{2.10}$$

On the other hand, an important property of the Kozyrev wavelets, which follows from a direct computation using formula (2.7) is the following:

2.20 Proposition. *Let Ψ_{rjn} be as in formula* (2.9)*. Then,*

$$\int_{\mathbb{Q}_p} \Psi_{rjn}(x)dx = 0.$$

We fix a function $\mathfrak{a} : \mathbb{R}_+ \to \mathbb{R}$ and define the pseudo-differential operator

$$\begin{aligned} \mathbf{A} : \mathcal{D} &\to C(\mathbb{Q}_p, \mathbb{C}) \cap L^2(\mathbb{Q}_p) \\ \varphi &\mapsto \mathcal{A}\varphi, \end{aligned}$$

where $(\mathbf{A}\varphi)(x) := \mathcal{F}^{-1}_{\xi \to x}\{\mathfrak{a}(|\xi|_p)\mathcal{F}_{x \to \xi}\varphi\}$ and $C(\mathbb{Q}_p, \mathbb{C})$ denotes the set of complex-valued continuous functions defined on $\mathbb{Q}_p$. The following theorem holds.

2.21 Theorem. *The set of functions* $\{\Psi_{rjn}\}$ *consists of eigenvectors of the operator* $\mathbf{A}$*:*

$$\mathbf{A}\Psi_{rjn} = \mathfrak{a}(p^{1-r})\Psi_{rnj} \tag{2.11}$$

Proof. Indeed,

$$\begin{aligned}
(\mathbf{A}\varphi)(x) &= \mathcal{F}^{-1}_{\xi\to x}\{\mathfrak{a}(|\xi|_p)\widehat{\Psi}_{rjn}(\xi)\} \\
&= p^{\frac{r}{2}}\int_{\mathbb{Q}_p}\chi_p(-x\cdot\xi)\mathfrak{a}(|\xi|_p)\chi_p(p^r n(\xi+jp^{r-1}))\Omega(|p^{-r}\xi+jp^{-1}|_p)d\xi \\
&= p^{\frac{r}{2}}\chi_p(jp^{-1}n)\int_{\mathbb{Q}_p}\chi_p(p^{-r}n\xi-x\cdot\xi)\mathfrak{a}(|\xi|_p)\Omega(|p^{-r}\xi+jp^{-1}|_p)d\xi \\
&= p^{\frac{-r}{2}}\mathfrak{a}(p^{1-r})\chi_p(jp^{r-1}x)\int_{\mathbb{Z}_p}\chi_p(u(n-p^r x))du \\
&= p^{\frac{-r}{2}}\mathfrak{a}(p^{1-r})\chi_p(jp^{r-1}x)\Omega(|p^r x-n|_p),
\end{aligned}$$

where the forth equality follows changing variables as $u = p^{-r}\xi + jp^{-1}$. Therefore, $\mathbf{A}\Psi_{rjn} = \mathfrak{a}(p^{1-r})\Psi_{rnj}$. □

2.7 Visualization of p-adic numbers.

In this section, we review some ideas aimed at the graphical representation of the p-adic numbers. We follow the work by Chistyakov [5]. We begin by stating a few definitions.

Definition 2.18. Given $n \in \mathbb{Z}$ and $m \in \mathbb{N}\cup\{\infty\}$, we define the complex valued functions $\chi_n^{(m)}(\cdot)$ on $\mathbb{Q}_p$ by the formula,

$$\chi_n^{(m)}(x) = \exp\left(\frac{2\pi i}{p}\sum_{k=0}^{m} x_{n-k}p^{-k}\right) \quad \text{for } x\in\mathbb{Q}_p. \tag{2.12}$$

where x_n is the nth coefficient in the expansion of x into its canonical series 2.3.

Definition 2.19. For every $s \in D \equiv \{z\in\mathbb{Z}; |z|<1\}$ and $\forall m\in\mathbb{N}\cup\{\infty\}$, we define a continuous mapping $\Gamma_s^{(m)} : \mathbb{Q}_p \to \mathbb{C}$ by setting

$$\Gamma_s^{(m)} = \frac{1-s^{\gamma(x)}}{1-s} + \sum_{n=\gamma(x)}^{\infty} s^n\chi_n^{(m)}(x) =: [\Gamma_s^{(m)}](x) + \{\Gamma_s^{(m)}\}(x), \quad \text{for } x\in\mathbb{Q}_p, \tag{2.13}$$

where $\gamma(x)$ is the p-adic order of x. Also, $[\Gamma_s^{(m)}](x) = \sum_{n=0}^{\infty} s^n\chi_n^{(m)}(x)$ is the "integral part" of $\Gamma_s^{(m)}(x)$ and $\{\Gamma_s^{(m)}(x)\} = \Gamma_s^{(m)}(x) - [\Gamma_s^{(m)}](x)$ is the "fractional part" of $\Gamma_s^{(m)}(x)$.

An important fact about the map $\Gamma_s^{(m)}$ is that its image is *self-similar* for $m<\infty$, in the following sense. We set $U_y^n := \Gamma_s^{(m)}\left(\{x\in\mathbb{Q}_p; |x-y|_p \le p^{-n}\}\right)$, that is, U_y^n is the image of the ball $p^n\mathbb{Z}_p$, $n\in\mathbb{Z}$ under $\Gamma_s^{(m)}$. Then, every U_y^n can be obtained as the union of p^m sets $U_{\tilde{y}}^0$

by motions of the plane $\mathbb{C}$ (shifts and rotations) and a scaling transformation. See equations (16), (17) and (18) in [5] .

Next, we define the number:

$$\Delta_s^{(m)} := \inf\{|\Gamma_s^{(m)}(x) - \Gamma_s^{(m)}(y)|; \forall x, y \in \mathbb{Q}_p, |x-y|_p = 1\}.$$

Now, if $|x-y|_p = 1$, then $\{x\}_p = \{y\}_p$. Thus,

$$\begin{aligned}
|\chi_0^{(m)}(x) - \chi_0^{(m)}(y)| &= |\exp\left(\frac{2\pi i}{p}(x_0 + x_{-1}p^{-1} + \ldots + x_{-m}p^{-m})\right) \\
&\quad - \exp\left(\frac{2\pi i}{p}(y_0 + x_{-1}p^{-1} + \ldots + x_{-m}p^{-m})\right)| \\
&= |\exp\left(\frac{2\pi i}{p}x_0\right) - \exp\left(\frac{2\pi i}{p}y_0\right)| \\
&\geq 2\sin\left(\frac{\pi}{p}\right).
\end{aligned}$$

Using the triangle inequality,

$$\frac{\Delta_s^{(m)}}{2} \geq \sin\left(\frac{\pi}{p}\right) - \frac{|s|}{1-|s|}.$$

From here, we have that $\Delta_s^{(m)} > 0$ for $|s| < s_0 = \sin(\pi/p)/(1+\sin(\pi/p)$.

The following theorem gives a sufficient condition to have that $\Gamma_s^{(m)}$ is an embedding.

2.22 Theorem (Thm. 6, [5])**.** *Let s and m be such that $\Delta_s^{(m)} > 0$; then $\Gamma_s^{(m)}$ is a Lipschitz isometry from $\left(\mathbb{Q}_p, |\cdot|_p^{-\log(|s|)}\right)$ into $(\mathbb{C}, |\cdot|)$ and therefore, $\Gamma_s^{(m)}$ is an embedding.*

Remark 2.20.

1. If $|\cdot|_*$ is a non-Archimedean absolute value on a field $\mathbb{F}$, then for any $\alpha > 0$, $|\cdot|_*^\alpha$ defines a non-Archimedean absolute value on $\mathbb{F}$ equivalent to $|\cdot|_*$. For this reason, we can consider the isometry from $\left(\mathbb{Q}_p, |\cdot|_p^{-\log(|s|)}\right)$ into $(\mathbb{C}, |\cdot|)$.

2. A Lipschitz isometry is a Lipschitz map which is a homeomorphism onto its image, and its inverse is also a Lipschitz map.

The map

$$\begin{aligned}
\rho : \mathbb{Q}_p &\to \mathbb{R}_+ \\
\sum_{j=\gamma(x)}^{\infty} x_j p^j &\mapsto \sum_{j=\gamma(x)} x_j p^{-j-1}
\end{aligned}$$

is known as the Monna map. This map satisfies the following properties.

2.23 Lemma (Section 1.9.4, [1])**.** *The map ρ satisfies the following properties.*

1. *The map is surjective but not one-to-one.*
2. *ρ satisfies the Hölder's inequality:*

$$|\rho(x) - \rho(y)| \leq |x - y|_p \quad x, y \in \mathbb{Q}_p.$$

3. *The following identities hold.*

$$\begin{aligned} \rho(p^\gamma x) &= p^{-\gamma}\rho(x), \quad x \in \mathbb{Q}_p \\ \rho(a + x) &= \rho(a) + \rho(x) \quad a \in \mathbb{Q}_p/\mathbb{Z}_p,\, x \in \mathbb{Z}_p \end{aligned}$$

4. *For the map ρ and for $a \in \mathbb{Q}_p/\mathbb{Z}_p$ and $m, k \in \mathbb{Z}$ we have*

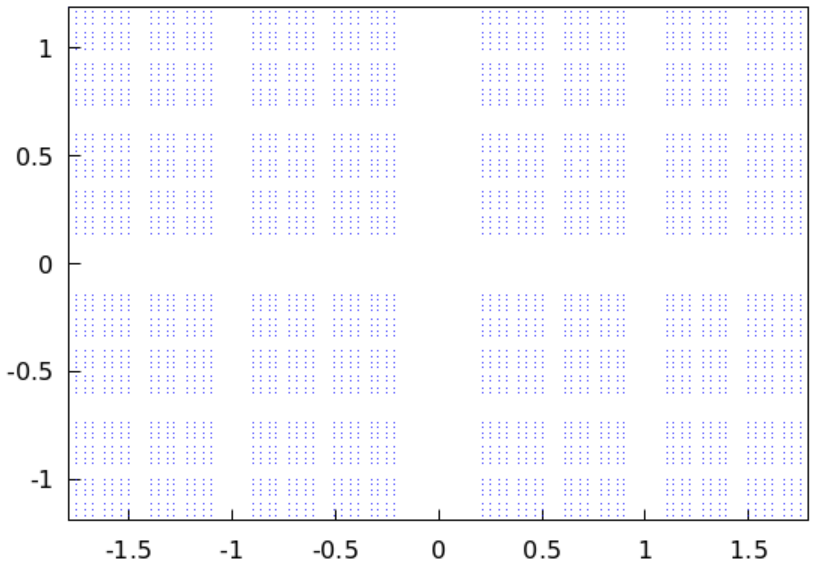
$$\rho : p^m a + p^k\mathbb{Z}_p \to p^{-m}\rho(a) + [0, p^k], \rho : \mathbb{Q}_p \setminus \{p^m a + p^k\mathbb{Z}_p\} \quad \to \mathbb{R}_+ \setminus \{p^{-m}\rho(a) + [0, p^k]\}$$

   up to a finite set of points.

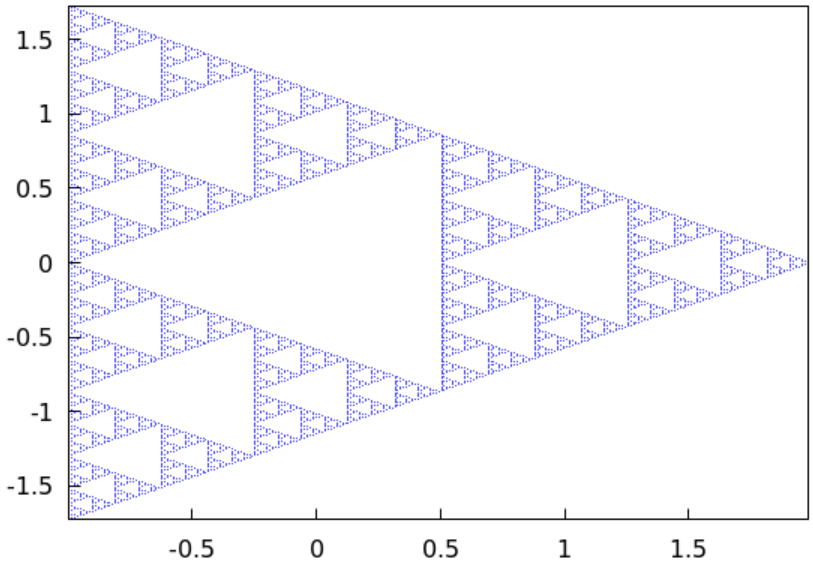
5. *The map ρ transforms the Haar measure on $\mathbb{Q}_p$ to the Lebesgue measure on $\mathbb{R}_+$.*

The Monna map plays a key role in the understanding of the Kozyrev wavelet basis in [17], since for $p = 2$ it relates the Haar wavelet basis to the Kozyrev wavelet basis.

Finally, we present some graphical representations of $\mathbb{Z}_2$ and $\mathbb{Z}_3$ in the complex plane, together with the graph of the Monna map restricted to the unit ball. This map sets a nice example of a function that it is not locally constant, which is important to test as the future goal of our project is to use the graphical routine for representation of the numerical solution of our equation, which might be neither radial or locally constant.

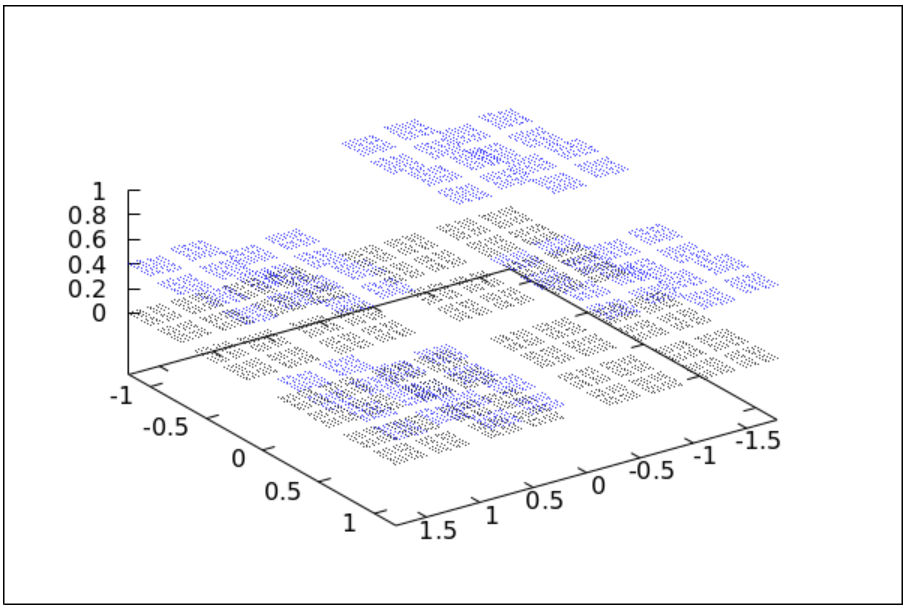


(a)

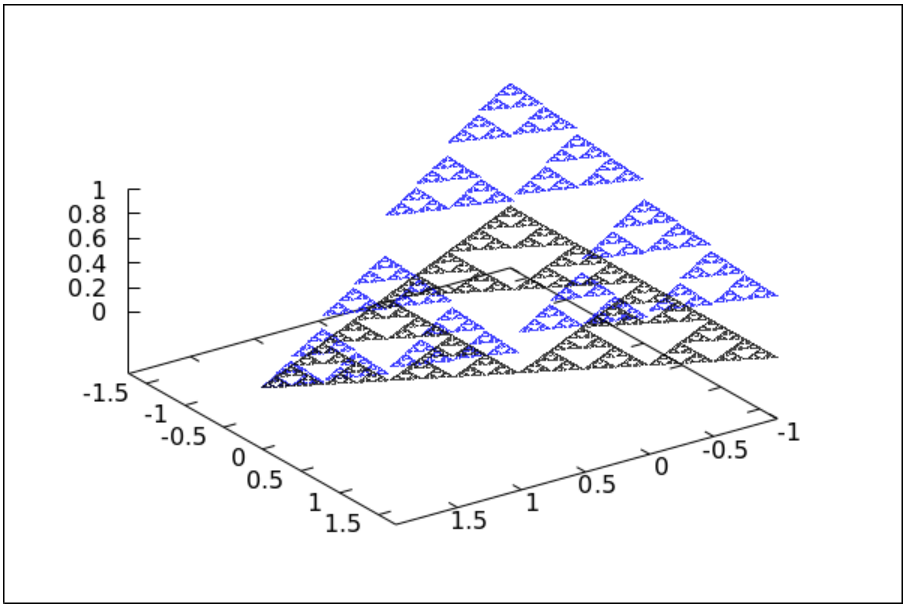


(b)

Figure 2.1: Graph (a) corresponds to an embedding of $\mathbb{Z}_2$ in the plane. The parameters are $m = 0$, $s = (2i)/3$. Graph (b) corresponds to an embedding of $\mathbb{Z}_3$ in the plane. $(m = 0, s = 1/2)$.



(a)



(b)

Figure 2.2: Graph (a) corresponds to the image of $\mathbb{Z}_2$ under the Monna map. Graph (b) corresponds to the image of $\mathbb{Z}_3$ under the Monna map.

Chapter 3

Non-Archimedean models

We now introduce the p-adic version of the Eigen-Schuster model which was developed by Zúñiga-Galindo. We follow closely reference [31]. First of all, we would like to point out that the downside of the classical Eigen-Schuster model is the Eigen paradox which imposes an upper-bound for the length of the sequences (replicators). This is a limitation of the model because it is not able to explain the appearance and evolution of more complex living organisms. We will see that under certain hypothesis and conditions, in the p-adic model the classical Eigen's paradox does not occur.

In this p-adic model, each sequence corresponds to a p-adic number

$$x = x_{-m}p^{-m} + x_{-m+1}p^{-m+1} + \ldots + x_0 + x_1 p + \ldots$$

where the digits x_i belong to the set $\{0, \ldots, p-1\}$. Thus, in this model the sequences are words of arbitrary length written in the alphabet $0, 1, \ldots, p-1$. The space of all sequences is $(\mathbb{Q}_p, |\cdot|_p)$which is an infinite set. The concentration of a sequence $x \in \mathbb{Q}_p$ at the time $t \geq 0$ is denoted $X(x,t)$. This is a real number between zero and one. We assume that the total concentration remains constant for $t \geq 0$, that is,

$$\int_{\mathbb{Q}_p} X(x,t)dx = 1 \qquad \text{for } t \geq 0.$$

We assume the existence of a mutation measure $Q : \mathbb{R}_+ \to \mathbb{R}_+$ such that $\int_{\mathbb{Q}_p} Q(|x|_p)dx = 1$ where dx is the normalized Haar measure of the group $(\mathbb{Q}_p, +)$. Thus, the probability that a sequence x mutates into a sequence belonging to the set B is given by $\int_B Q(|x-y|_p)dy$. Moreover, we assume that the fitness landscape is given by a test function $f : \mathbb{Q}_p \to \mathbb{R}_+$, i.e. f is a locally constant function with compact support. In this model the concentration $X(x,t)$ of the sequence x at the time t is controlled by the following evolution equation:

$$\frac{\partial X(x,t)}{\partial t} = Q(|x|_p) * \{f(|x|_p)X(x,t)\} - \Phi(t)X(x,t) \qquad x \in \mathbb{Q}_p, t \in \mathbb{R}_+, \tag{3.1}$$

where $\Phi(t) = \int_{\mathbb{Q}_p} f(|y|_p)X(y,t)dy$. The term

$$Q(|x|_p) * \{f(|x|_p)X(x,t)\} = \int_{\mathbb{Q}_p} Q(|x-y|_p)f(|y|_p)X(y,t)dy$$

represents the rate at which the sequences are mutating into sequence x.

We set

$$(\mathbf{W}\varphi)(x) := Q(|x|_p) * \{f(|x|_p)\varphi(x)\} = \int_{\mathbb{Q}_p} Q(|x-y|_p) f(|y|_p)\varphi(y)dy.$$

Because of the Young's inequality for the convolution[1], if $1 \leq \rho \leq \infty$ we have that

$$\begin{aligned} \mathbf{W} : \mathcal{L}^\rho(\mathbb{Q}_p, \mathbb{C}) &\longrightarrow \mathcal{L}^\rho(\mathbb{Q}_p, \mathbb{C}) \\ \varphi &\longmapsto \mathbf{W}\varphi \end{aligned}$$

is a well-defined continuous operator. We can rewrite (3.1) as:

$$\frac{\partial X(x,t)}{\partial t} = \mathbf{W}X(x,t) - \Phi(t)X(x,t) \qquad x \in \mathbb{Q}_p, t \in \mathbb{R}_+. \tag{3.2}$$

3.1 An ultrametric version of the classical replicator equation

We now proceed to derive a discretization of equation (3.2) that agrees with the Eigen model in an ultrametric space formed by finite p-adic sequences.

Remark 3.1. In the following, $\mathcal{D} := \mathcal{D}(\mathbb{Q}_p, \mathbb{C})$ denotes the $\mathbb{C}$-vector space of Bruhat-Schwartz (test functions) and $\mathcal{D}_{\mathbb{R}} := \mathcal{D}(\mathbb{Q}_p, \mathbb{R})$ the $\mathbb{R}$-vector space of test functions. Also, we denote by $\Omega(p^{-r}|x-a|_p)$ the characteristic function of the ball $B_r(a)$.

Let us fix $M \in \mathbb{N}$ and consider the additive group $G_M^{-M} := p^{-M}\mathbb{Z}_p/p^M\mathbb{Z}_p$ with the following system of representatives:

$$I = I_{-M}p^{-M} + I_{-M+1} + \ldots + I_0 + \ldots + I_{M-1}p^{M-1} \tag{3.3}$$

where $I_j \in \{0, 1, \ldots, p-1\}$ for all $-M \leq j \leq M-1$. We denote $\mathcal{D}_M^{-M}$ the $\mathbb{R}$-vector subspace of $\mathcal{D}_{\mathbb{R}}$ spanned by the functions $\Omega(p^M|x-I|_p)$ with $I \in G_M^{-M}$. Because of the ultrametric property, the balls $B_{-M}(I), B_{-M}(J)$ are disjoint if $I \neq J$ and thus

$$\Omega(p^M|x-I|_p)\Omega(p^M|x-J|_p) = 0 \quad \text{ if } I \neq J.$$

Consequently, these characteristic functions are linearly independent and therefore any $\varphi \in D_M^{-M}$ can be written as follows:

$$\varphi(x) = \sum_{I \in G_M^{-M}} \varphi(I)\Omega(p^M|x-I|_p) \qquad \varphi(I) \in \mathbb{R}$$

[1]Let $f \in \mathcal{L}^\rho(\mathbb{Q}_p^n)$ and $g \in \mathcal{L}^\mu(\mathbb{Q}_p^n)$ where $1 \leq \rho \leq \infty$ and $\frac{1}{\rho} + \frac{1}{\mu} \geq 1$. Then $f * g \in \mathcal{L}^r(\mathbb{Q}_p^n)$ where $\frac{1}{r} = \frac{1}{\rho} + \frac{1}{\mu} - 1$ and it holds $\|f * g\|_r \leq \|f\|_\rho \|g\|_\mu$. See Theorem 5.2.2 in [1].

Thus, the linear dimension of D_M^{-M} is $\#G_M^{-M}=p^{2M}$. Let us assume that $Q(|x|_p), f(|x|_p), X(x,t)\in D_M^{-M}$ for every $t\geq 0$. Then

$$Q(|x|_p)=\frac{1}{C_M}\sum_{I\in G_M^{-M}}Q(|I|_p)\Omega(p^M|x-I|_p),\quad C_M=p^{-M}\sum_{I\in G_M^{-M}}Q(|I|_p),$$

$$f(|x|_p)=\sum_{I\in G_M^{-M}}f(|I|_p)\Omega(p^M|x-I|_p),$$

$$X(x,t)=\sum_{I\in G_M^{-M}}X(I,t)\Omega(p^M|x-I|_p).$$

The constant C_M is a normalization constant to ensure $\int_{\mathbb{Q}_p}Q(|x|_p)dx=1$. Notice that because of the fact $\Omega(p^M|x-I|_p)\Omega(p^M|x-J|_p)=0$ for $I\neq J$ we have that

$$f(|x|_p)X(x,t)=\sum_{I\in G_M^{-M}}f(|I|_p)X(I,t)\Omega(p^M|x-I|_p)$$

Thus,

$$\begin{aligned}\mathbf{W}X(x,t)&=(\frac{1}{C_M}\sum_{K\in G_M^{-M}}Q(|K|_p)\Omega(p^M|x-K|_p))*(\sum_{I\in G_M^{-M}}f(|I|_p)X(I,t)\Omega(p^M|x-I|_p))\\&=\{\frac{1}{C_M}\sum_{K\in G_M^{-M}}\sum_{I\in G_M^{-M}}Q(|K|_p)f(|I|_p)X(I,t)\}\Omega(p^M|x-K|_p)*\Omega(p^M|x-I|_p)\\&=\{\frac{1}{C_M}\sum_{K\in G_M^{-M}}\sum_{I\in G_M^{-M}}Q(|K|_p)f(|I|_p)X(I,t)\}p^{-M}\Omega(p^M|x-(I+K)|_p)\\&=\frac{1}{C}\sum_{J\in G_M^{-M}}\sum_{I\in G_M^{-M}}Q(|J-I|_p)f(|I|_p)X(I,t)\}\Omega(p^M|x-J|_p)\end{aligned}$$

with $C=\sum_{I\in G_M^{-M}}Q(|I|_p)$. Notice that

$$\int_{\mathbb{Q}_p}f(|x|_p)X(x,t)dx=p^{-M}\sum_{I\in G_M^{-M}}f(|I|_p)X(I,t)$$

Therefore

$$\begin{aligned}\frac{\partial X(x,t)}{\partial t}-\{\mathbf{W}X(x,t)-\Phi(t)X(x,t)\}&=\sum_{J\in G_M^{-M}}\frac{dX(J,t)}{dt}\Omega(p^M|x-J|_p)\\&-\{\frac{1}{C}\sum_{J\in G_M^{-M}}\sum_{I\in G_M^{-M}}Q(|J-I|_p)f(|I|_p)X(I,t)\}\Omega(p^M|x-J|_p)\\&-\left(p^{-M}\sum_{I\in G_M^{-M}}f(|I|_p)X(I,t)\right)\sum_{J\in G_M^{-M}}X(J,t)\Omega(p^M|x-J|_p)\}\\&=0.\end{aligned}$$

Setting $\Phi_M(t) = p^{-M}\sum_{I\in G_M^{-M}} f(|I|_p)X(I,t)$ and using the fact that $\Omega(p^M|x-J|_p)$, $J \in G_M^{-M}$ are $\mathbb{R}$-linearly independent we get

$$\frac{dX(J,t)}{dt} = \frac{1}{C}\sum_{I\in G_M^{-M}} Q(|J-I|_p)f(|I|_p)X(I,t) - \Phi_M(t)X(J,t), \quad J \in G_M^{-M}, \tag{3.4}$$

which is the Eigen model on G_M^{-M}.

3.2 The error-threshold

3.2.1 The Maynard-Smith ansatz

We now proceed to apply the Maynard-Smith ansatz to the p-adic replicator model. First, we fix a sequence I of the form (3.3). Then, we divide the space of sequences into two disjoint sets:

$$\mathbb{Q}_p = [I + p^M\mathbb{Z}_p] \sqcup [\mathbb{Q}_p \setminus I + p^M\mathbb{Z}_p]$$

and we assume that:

$$f|_{I+p^M\mathbb{Z}_p} \equiv a, \quad f|_{\mathbb{Q}_p\setminus I+p^M\mathbb{Z}_p} b, \quad a > b.$$

Notice that instead of having 'a master sequence', $I+p^M\mathbb{Z}_p$ is more like a 'cloud of mutants' that coincide with I up to the digit I_{M-1} and thus this class contains the fittest sequences. Let $X(x,t)$ be the concentration of $I+p^M\mathbb{Z}_p$ and let $Y(x,t)$ be the concentration of $\mathbb{Q}_p\setminus[I+p^M\mathbb{Z}_p]$. If $q := q(M,Q)$ denotes the probability that a sequence in $I+p^M\mathbb{Z}_p$ mutates into a sequence in $\mathbb{Q}_p\setminus[I+p^M\mathbb{Z}_p]$ and $r := r(M,Q)$ denotes the probability that a sequence in $\mathbb{Q}_p\setminus[I+p^M\mathbb{Z}_p]$ mutates into a sequence in $I+p^M\mathbb{Z}_p$ then these populations obey the following system of equations:

$$\begin{aligned}
\frac{\partial X(x,t)}{\partial t} &= a(1-q)X(x,t) + brY(x,t) - \Phi(t)X(x,t)\\
\frac{\partial Y(x,t)}{\partial t} &= aqX(x,t) + b(1-r)Y(x,t) - \Phi(t)Y(x,t)
\end{aligned}$$

In this case, the CP condition translates to:

$$\int_{\mathbb{Q}_p} X(x,t)dx + \int_{\mathbb{Q}_p} Y(x,t)dx = 1 \quad \text{for all } t \geq 0,$$

and

$$\Phi(t) = a\int_{I+p^M\mathbb{Z}_p} X(x,t)dx + b\int_{\mathbb{Q}_p\setminus I+p^M\mathbb{Z}_p} Y(x,t)dx.$$

Let us suppose that for M sufficiently large, $r(M,Q)$ is negligible and therefore the system simplifies to:

$$\begin{aligned}
\frac{\partial X(x,t)}{\partial t} &= a(1-q)X(x,t) - \Phi(t)X(x,t),\\
\frac{\partial Y(x,t)}{\partial t} &= aqX(x,t) + bY(x,t) - \Phi(t)Y(x,t).
\end{aligned}$$

Taking $Z(x,t) = \frac{X(x,t)}{Y(x,t)}$ we get:

$$\frac{\partial Z(x,t)}{\partial t} = Z(x,t)\{a(1-q) - aqZ(x,t) - b.\}$$

If the concentration $Z(x,t)$ achieves a steady concentration $\bar{Z}(x)$ over the time, we must have

$$\bar{Z}(x) = \frac{a(1-q)-b}{aq}.$$

To ensure the survival of the fittest group of sequences, we must have $\bar{Z}(x) > 0$ which implies

$$1 - q > \frac{b}{a}.$$

Setting $s = 1 - \frac{b}{a} \in (0,1)$ the error threshold is given by

$$q < s. \tag{3.5}$$

which is the classical condition determining the error threshold.

3.2.2 Some remarks

If we take $x \in p^M\mathbb{Z}_p$ and $y \in \mathbb{Q}_p \setminus p^M\mathbb{Z}_p$, because of the ultrametric property we must have $|x-y|_p = |y|_p$ and thus,

$$\begin{aligned}
q(M,Q) &= \int_{I+p^M\mathbb{Z}_p} \int_{\mathbb{Q}_p \setminus I+p^M\mathbb{Z}_p} Q(|x-y|_p)dydx \\
&= \int_{p^M} \int_{\mathbb{Q}_p \setminus p^M\mathbb{Z}_p} Q(|x-y|_p)dydx \\
&= \int_{p^M} \int_{\mathbb{Q}_p \setminus p^M\mathbb{Z}_p} Q(|y|_p)dydx \\
&= p^{-M} \int_{\mathbb{Q}_p \setminus p^M\mathbb{Z}_p} Q(|y|_p)dydx \\
&= p^{-M} \int_{\text{supp}Q \cap [\mathbb{Q}_p \setminus p^M\mathbb{Z}_p]} Q(|y|_p)dydx.
\end{aligned}$$

Analogously,

$$\begin{aligned}
r(M,Q) &= \int_{\mathbb{Q}_p \setminus I+p^M\mathbb{Z}_p} \int_{I+p^M\mathbb{Z}_p} Q(|x-y|_p)dxdy \\
&= \int_{\mathbb{Q}_p \setminus p^M\mathbb{Z}_p} \int_{p^M} Q(|x-y|_p)dxdy \\
&= \int_{\mathbb{Q}_p \setminus p^M\mathbb{Z}_p} \int_{p^M} Q(|y|_p)dxdy \\
&= p^{-M} \int_{\mathbb{Q}_p \setminus p^M\mathbb{Z}_p} Q(|y|_p)dy \\
&= p^{-M} \int_{\text{supp}Q \cap [\mathbb{Q}_p \setminus p^M\mathbb{Z}_p]} Q(|y|_p)dy,
\end{aligned}$$

which implies that q is independent of I and moreover $r = r(M, Q) = q$.

3.3 Two families of mutation measures

3.3.1 A class of mutation measures supported in the unit ball

Now we take $\alpha \geq 0$ and consider

$$Q(|x|_p; \alpha) = \frac{|x|_p^\alpha \Omega(|x|_p)}{Z(\alpha)}$$

with

$$Z(\alpha) = \int_{\mathbb{Z}_p} |x|_p^\alpha dx = \frac{1 - p^{-1}}{1 - p^{-1-\alpha}}$$

Notice that the uniform distribution is a particular case of the above family of mutation measures when $\alpha = 0$. Proceeding in a similar way, we fix a sequence $I \in \mathbb{Z}_p$ and divide the space of sequences $\mathbb{Z}_p$ into two subsets: $I + p^M\mathbb{Z}_p$ and $\mathbb{Z}_p \setminus [I + p^M\mathbb{Z}_p]$ for some positive integer M and we compute the probability that a sequence in the set $I + p^M\mathbb{Z}_p$ mutates into a sequence belonging to the set $\mathbb{Z}_p \setminus [I + p^M\mathbb{Z}_p]$:

$$\begin{aligned}
q(\alpha) &= \frac{1}{Z(\alpha)} \int_{I+p^M\mathbb{Z}_p} \int_{\mathbb{Z}_p \setminus I+p^M\mathbb{Z}_p} |x - y|_p^\alpha dy dx \\
&= \frac{1}{Z(\alpha)} \int_{I+p^M\mathbb{Z}_p} \int_{\mathbb{Z}_p \setminus I+p^M\mathbb{Z}_p} |(x - I) - (y - I)|_p^\alpha dy dx \\
&= \frac{1}{Z(\alpha)} \int_{p^M\mathbb{Z}_p} \int_{\mathbb{Z}_p \setminus p^M\mathbb{Z}_p} |x - y|_p^\alpha dy dx \\
&= \frac{1}{Z(\alpha)} \int_{p^M\mathbb{Z}_p} \int_{\mathbb{Z}_p \setminus p^M\mathbb{Z}_p} |y|_p^\alpha dy dx \\
&= \frac{p^{-M}}{Z(\alpha)} \int_{\mathbb{Z}_p \setminus p^M\mathbb{Z}_p} |y|_p^\alpha dy dx
\end{aligned}$$

We now fix H_M a system of representatives of $\mathbb{Z}_p/p^M\mathbb{Z}_p$, thus we can write $\mathbb{Z}_p = \sqcup_{J \in H_M} J + p^M\mathbb{Z}_p$. Then

$$\begin{aligned}
q(\alpha) &= \frac{p^{-M}}{Z(\alpha)} \int_{\mathbb{Z}_p \setminus p^M\mathbb{Z}_p} |y|_p^\alpha dy dx \\
&= \frac{p^{-2M}}{Z(\alpha)} \sum_{J \in H_M} |J|_p^\alpha.
\end{aligned}$$

In addition,

$$q(\alpha) > \frac{p^{-2M}}{Z(\alpha)} |p^{M-1}|_p^\alpha = \frac{p^{-2M-(M-1)\alpha}}{Z(\alpha)} > \frac{p^{-2M-M\alpha}}{Z(\alpha)} > p^{-2M-M\alpha}.$$

If M can grow and α is fixed then the condition (3.5) is satisfied if $p^{-2M-M\alpha} < q(\alpha) < s$ which implies

$$M > \frac{-\ln s}{(2+\alpha)\ln p}, \quad s \in (0,1).$$

3.3.2 Mutation measures of Gibbs type

Let us suppose that we have a mutation measure of the following form

$$\frac{e^{-\beta E(|x|_p)}}{Z(\beta, E)}$$

with $\beta > 0$, $E : \mathbb{R}_+ \to \mathbb{R}_+$ and $Z(\beta, E) = \int_{\mathbb{Q}_p} e^{-\beta E(|x|_p)} dx$. A Gibbs measure is a natural choice when dealing with infinite systems. We now assume that $E(|x|_p) = |x|_p^\alpha$, $\alpha > 0$. Notice that for sufficiently large $\beta > 0$, because of the rapid decay $\exp(-\beta \cdot)$ the most probable mutations are those corresponding to sequences which are close to "the master sequence" I in the p-adic norm, and thus they belong to a ball of type $I + p^M \mathbb{Z}_p$.

With these assumptions, the probability that a sequence $x \in \mathbb{Q}_p$ mutates into a sequence into a Borel subset $B \subset \mathbb{Q}_p$ is given by

$$P(x, B; \alpha, \beta) = \frac{1}{C} \int_B e^{-\beta |x-y|_p^\alpha} dy,$$

where $C(\alpha, \beta) := C$ is a normalization constant such that

$$\frac{1}{C} \int_{\mathbb{Q}_p} e^{-\beta |x-y|_p^\alpha} dy = 1$$

Similarly to the previous cases, the probability that a sequence x mutates into a sequence belonging to $\mathbb{Q}_p \setminus [I + p^M \mathbb{Z}_p]$ is $P(x, \mathbb{Q}_p \setminus [I + p^M \mathbb{Z}_p]; \alpha, \beta)$ and the probability that any sequence from the ball $I + p^M \mathbb{Z}_p$ mutates into a sequence in $\mathbb{Q}_p \setminus [I + p^M \mathbb{Z}_p]$ is

$$q(M, \alpha, \beta) := \frac{1}{C} \int_{I+p^M \mathbb{Z}_p} \int_{\mathbb{Q}_p \setminus I+p^M \mathbb{Z}_p} e^{-\beta |x-y|_p^\alpha} dy$$

Thus,

$$\begin{aligned}
q(M,\alpha,\beta) &= \frac{1}{C}\int_{I+p^M\mathbb{Z}_p}\int_{\mathbb{Q}_p\setminus I+p^M\mathbb{Z}_p} e^{-\beta|(x-I)-(y-I)|_p^\alpha}dy \\
&= \frac{1}{C}\int_{p^M\mathbb{Z}_p}\int_{\mathbb{Q}_p\setminus p^M\mathbb{Z}_p} e^{-\beta|x-y|_p^\alpha}dy \\
&= \frac{1}{C}\int_{p^M\mathbb{Z}_p}\int_{\mathbb{Q}_p\setminus p^M\mathbb{Z}_p} e^{-\beta|y|_p^\alpha}dy \\
&= \frac{p^{-M}}{C}\int_{\mathbb{Q}_p\setminus p^M\mathbb{Z}_p} e^{-\beta|y|_p^\alpha}dy \\
&= \frac{p^{-M}}{C}\int_{\sqcup_{j=-M+1}^{\infty}S_j} e^{-\beta|y|_p^\alpha}dy \\
&= \frac{p^{-M}}{C}\sum_{j=-M+1}^{\infty}\int_{|y|_p=p^j} e^{-\beta|y|_p^\alpha}dy \\
&> \frac{p^{-M}}{C}\int_{|y|_p=p^{-M+1}} e^{-\beta|y|_p^\alpha}dy \\
&= \frac{p^{-2M+1}(1-p^{-1})}{C}e^{-\beta p^{(-M+1)\alpha}} \\
&= \frac{p^{-2M}(p-1)}{C}e^{-\beta p^{(-M+1)\alpha}}.
\end{aligned}$$

Using this inequality, in order to avoid the error threshold we must have

$$\frac{p^{-2M}(p-1)}{C}e^{-\beta p^{(-M+1)\alpha}} < q(M,\alpha,\beta) < s,$$

which implies that

$$M > \frac{-(\beta p^\alpha + \ln s)}{2\ln p} + \frac{\ln\frac{p-1}{C}}{2\ln p}.$$

3.4 The Cauchy problem for the p-adic replicator equation for a mutation measure supported in the unit ball.

We recall that the p-adic replicator equation (3.2) which controls the evolution of the concentration $X(x,t)$ of the sequence x at the time time t is given by

$$\frac{\partial X(x,t)}{\partial t} = (\mathbf{W}\varphi)(x) - \Phi(t)X(x,t), \quad x\in\mathbb{Q}_p, t\in\mathbb{R}_+,$$

where $\Phi(t) = \int_{\mathbb{Q}_p} f(|y|_p)X(y,t)dy$ and the operator $\mathbf{W} := \mathbf{W}(Q,f)$, $\mathbf{W} : L^\rho(\mathbb{Q}_p) \to L^\rho(\mathbb{Q}_p)$ is defined as

$$(\mathbf{W}\varphi)(x) := (Q*(f\varphi))(x) = \int_{\mathbb{Q}_p} Q(|x-y|_p)f(|y|_p)\varphi(y)dy.$$

In this section we study the Cauchy problem for the p-adic replicator equation, assuming that the mutation measure Q is a square-integrable function supported in the unit ball $\mathbb{Z}_p$.

3.4.1 The operator W for a mutation measure supported in the unit ball.

Let us assume that $Q : \mathbb{R}_+ \to \mathbb{R}_+$ is a square-integrable mutation measure supported in the unit ball $\mathbb{Z}_p$, that is, $\operatorname{supp} Q \subseteq \mathbb{Z}_p$, $\int_{\mathbb{Z}_p} Q^2(|x|_p)dx < \infty$ and $\int_{\mathbb{Z}_p} Q(|x|_p)dx = 1$. We also assume that the fitness function f is a test function with $\operatorname{supp} f \subseteq \mathbb{Z}_p$ of the following form. Fix a positive integer L and consider the additive group $G_L := \mathbb{Z}_p/p^L\mathbb{Z}_p$ having the following system of representatives:

$$I = I_0 + I_1 p + \ldots + I_{L-1}p^{L-1}, \quad I_j \in \{0, \ldots, p-1\}, j = 0, \ldots, L-1.$$

We assume that f can be written as

$$f(|x|_p) = \sum_{I \in G_L} f(|I|_p)\Omega(p^L|x - I|_p). \tag{3.6}$$

We set $\mathbf{Q} : L^2(\mathbb{Z}_p, \mathbb{C}) \to L^2(\mathbb{Z}_p, \mathbb{C})$, with

$$(\mathbf{Q}\varphi)(x) := (Q * \varphi)(x) = \int_{\mathbb{Z}_p} Q(|x - y|_p)\varphi(y)dy, \quad \varphi \in L^2(\mathbb{Z}_p, \mathbb{C}), \tag{3.7}$$

i.e., $\mathbf{Q}$ is a convolution operator. Notice that the convolution is well-defined due to the fact that $\mathbb{Z}_p$ is an additive group. For $x \in \mathbb{Q}_p \setminus \mathbb{Z}_p$ let $Q(x) = 0$. Then $Q \in L^1(\mathbb{Q}_p, \mathbb{R}) \cap L^2(\mathbb{Q}_p, \mathbb{R})$. The operator $\mathbf{Q}$ has a natural extension $\mathbf{Q}' : L^2(\mathbb{Q}_p, \mathbb{C}) \to L^2(\mathbb{Q}_p, \mathbb{C})$ given by $(\mathbf{Q}'\varphi)(x) := (Q * \varphi)(x) = \int_{\mathbb{Q}_p} Q(|x - y|_p)\varphi(y)dy$.

Extending a function $\varphi \in L^2(\mathbb{Z}_p, \mathbb{C})$ as zero outside the ball $\mathbb{Z}_p$, we have a natural embedding $L^2(\mathbb{Z}_p, \mathbb{C}) \hookrightarrow L^2(\mathbb{Q}_p, \mathbb{C})$ and the following holds true:

$$\mathbf{Q}'|_{L^2(\mathbb{Z}_p, \mathbb{C})} \equiv \mathbf{Q} \tag{3.8}$$

Indeed, for any $\varphi \in L^2(\mathbb{Z}_p, \mathbb{C})$ and any $x \in \mathbb{Z}_p$,

$$\begin{aligned}
(\mathbf{Q}'\varphi)(x) &= \int_{\mathbb{Q}_p} Q(|x - y|_p)\varphi(y)dy \\
&= \int_{\mathbb{Z}_p} Q(|x - y|_p)\varphi(y)dy + \int_{\mathbb{Q}_p \setminus \mathbb{Z}_p} Q(|x - y|_p)\varphi(y)dy \\
&= \int_{\mathbb{Z}_p} Q(|x - y|_p)\varphi(y)dy \\
&= (\mathbf{Q}\varphi)(x).
\end{aligned}$$

We observe that the first three equalities also hold for $x \in \mathbb{Q}_p \setminus \mathbb{Z}_p$. Moreover, since for any $x \in \mathbb{Q}_p \setminus \mathbb{Z}_p$ and $y \in \mathbb{Z}_p$ we have $|x - y|_p = |x|_p$, then $Q(|x - y|_p) = 0$, see Proposition

2.1. Thus, the ultrametric property of the p-adic norm implies that the support of $\mathbf{Q}'\varphi$ as a function from $\mathbb{Q}_p$ to $\mathbb{C}$ is contained in $\mathbb{Z}_p$.

Now, using Theorem 2.15 and the fact that $Q \in L^1(\mathbb{Q}_p, \mathbb{R}) \cap L^2(\mathbb{Q}_p, \mathbb{R})$ we have that, for any $\varphi \in L^2(\mathbb{Q}_p, \mathbb{C})$

$$(\mathbf{Q}'\varphi)(x) = \int_{\mathbb{Q}_p} Q(|x-y|_p)\varphi(y)dy = \mathcal{F}^{-1}_{\xi\to x}\{\widehat{Q}(|\xi|_p)\mathcal{F}_{x\to\xi}\varphi\},$$

since the Fourier transform of a radial real-valued function is also a radial and real-valued function (see Prop. 2.12). Therefore, the operator $\mathbf{Q}'$ is a pseudodifferential operator with symbol $\widehat{Q}(|\cdot|_p)$.

According to Theorem 2.19 and Theorem 2.21, we know that the Kozyrev wavelet basis $\mathcal{K} := \{\Psi_{rjn}\}$ is an orthonormal basis of $L^2(\mathbb{Q}_p, \mathbb{C})$ consisting of eigenfunctions of the operator $\mathbf{Q}'$. Explicitely, we have that

$$\mathbf{Q}'\Psi_{rjn} = \widehat{Q}(p^{1-r})\Psi_{rjn}.$$

In particular, for each Kozyrev wavelet $\Psi_{rjn} \in \mathcal{K}$ supported in the ball $\mathbb{Z}_p$, because of the equivalence in (3.8) we have

$$\mathbf{Q}\Psi_{rjn} = \widehat{Q}(p^{1-r})\Psi_{rjn}. \tag{3.9}$$

We observe that $\mathbf{W}\varphi = \mathbf{Q}'\mathbf{M}_f\varphi = \mathbf{Q}'(f\varphi)$, where $\mathbf{M}_f$ is the multiplication operator with symbol f. Then, if we restrict the operator $\mathbf{W}$ to the space $L^2(\mathbb{Z}_p, \mathbb{C})$, we have $\mathbf{W} = \mathbf{Q}\mathbf{M}_f$ and therefore $\mathbf{W} : L^2(\mathbb{Z}_p, \mathbb{C}) \to L^2(\mathbb{Z}_p, \mathbb{C})$. Indeed, since $f\varphi \in L^2(\mathbb{Z}_p, \mathbb{C})$, for $\varphi \in L^2(\mathbb{Z}_p, \mathbb{C})$ and $x \in \mathbb{Z}_p$ we have

$$(\mathbf{W}\varphi)(x) = \int_{\mathbb{Z}_p} Q(|x-y|_p)f(|y|_p)\varphi(y)dy \tag{3.10}$$

For the rest of the chapter, we think of $\mathbf{W}$ as its restriction to the space $L^2(\mathbb{Z}_p)$, with its action given by the formula (3.10) above.

The operator $\mathbf{W}$ is a compact operator from $L^2(\mathbb{Z}_p, \mathbb{C})$ to $L^2(\mathbb{Z}_p, \mathbb{C})$. To see this, notice that $\mathbf{W}$ is an integral operator with integral kernel $K_{\mathbf{W}}(x, y) := Q(|x-y|_p)f(|y|_p)$. Since $f \in \mathcal{D}_{\mathbb{R}}$ and $Q \in L^1(\mathbb{Z}_p, \mathbb{R}) \cap L^2(\mathbb{Z}_p, \mathbb{R})$ we have that $K_{\mathbf{W}} \in L^2(\mathbb{Z}_p \times \mathbb{Z}_p)$. Indeed, using Fubini's Theorem and the fact that $\mathbb{Z}_p$ is an additive group we have

$$\begin{aligned}
\int_{\mathbb{Z}_p^2} K^2_{\mathbf{W}}(x, y)d(x, y) &= \int_{\mathbb{Z}_p}\int_{\mathbb{Z}_p} Q^2(|x-y|_p)f^2(|y|_p)dxdy \\
&= \int_{\mathbb{Z}_p} f^2(|y|_p)\left(\int_{\mathbb{Z}_p} Q^2(|x-y|_p)dx\right)dy \\
&= \|f\|_2\|Q\|_2.
\end{aligned}$$

Therefore, using a standard result from functional analysis [2] we conclude that $\mathbf{W}$ is compact. Moreover, using the same argument we see that $\mathbf{W}$ is also compact as an operator from $L^2(\mathbb{Z}_p,\mathbb{R})$ to $L^2(\mathbb{Z}_p,\mathbb{R})$. We will make use of this fact later.

Remark 3.2. The operator $\mathbf{W}$ is not symmetric. Both $\mathbf{Q}$ and $\mathbf{M}_f$ are bounded operators. As we have shown, $\mathbf{Q}$ is unitarily equivalent to a multiplication operator with real-valued symbol, which implies it is self-adjoint. From $\mathbf{W}=\mathbf{Q}\mathbf{M}_f$, we conclude $\mathbf{W}^*=\mathbf{M}_f^*\mathbf{Q}^*=\mathbf{M}_f\mathbf{Q}\neq\mathbf{Q}\mathbf{M}_f$. Thus, the standard spectral theory for compact self-adjoint operators cannot be applied.

We denote $\mathcal{D}_L$ the $\mathbb{C}$-vector subspace of $\mathcal{D}$ spanned by the set of functions

$$\{\Omega(p^L|\cdot-I|_p)\},\quad I\in G_L,$$

which is finite dimensional. On the other hand, we set

$$\begin{aligned}\Lambda_I&:=\{rnj;\operatorname{supp}\Psi_{rnj}\subseteq I+p^L\mathbb{Z}_p\},\\ \mathcal{K}_{L,I}&:=\overline{\operatorname{span}\{\Psi_{rnj}\in\mathcal{K};rnj\in\Lambda_I\}},\\ \mathcal{K}_L&:=\bigoplus_{I\in G_L}\mathcal{K}_{L,I},\\ \mathcal{V}_L&:=\mathcal{D}_L\oplus\mathcal{K}_L,\end{aligned}\tag{3.11}$$

where the closure is taken in the sense of $L^2(\mathbb{Z}_p,\mathbb{C})$. Thus, $\mathcal{K}_{L,I}$, $\mathcal{K}_{\mathcal{I}}$ and $\mathcal{V}_L$ are closed subspaces. For short, by $\Psi_{rjn}^{(I)}$ we mean $\Psi_{rjn}\in\mathcal{K}$ with $rjn\in\Lambda_I$.

Remark 3.3. The *zero mean* property of the elements of the Kozyrev wavelet basis implies that the inner product $\langle\Omega(p^L|\cdot-I|_p),\Psi_{rjn}^{(J)}\rangle=0$ for any $I,J\in G_L$. Therefore, $\mathcal{D}_L\perp\mathcal{K}_L$.

Because of formula (3.6), and the fact that for $I\neq J$ the balls $I+p^L\mathbb{Z}_p$ and $J+p^L\mathbb{Z}_p$ are disjoint, we have that

$$\mathbf{M}_f\Psi_{rnj}^{(I)}=\left(\sum_{J\in G_L}f(|J|_p)\Omega(p^L|\cdot-J|_p)\right)\Psi_{rnj}^{(I)}=f(|I|_p)\Psi_{rnj}^{(I)}.$$

Thus, using (3.9) we have

$$\mathbf{W}\Psi_{rjn}^{(I)}=\widehat{Q}(p^{1-r})f(|I|_p)\Psi_{rjn}^{(I)}.\tag{3.12}$$

[2] **Proposition:** If (X,Ω,μ) is a measure space and $k\in L^2(X\times X,\Omega\times\Omega,\mu\times\mu)$, then $(Kf)(x)=\int k(x,y)f(y)d\mu(y)$, is a compact operator and $\|K\|\leq\|k\|_2$. See Prop. II 4.7, p. 43, [6].

Now, we show that $\mathcal{D}_L$ is a $\mathbf{W}$-invariant subspace. We have that

$$\begin{aligned}\mathbf{W}(\Omega(p^L|\cdot - I|_p))(x) &= \int_{\mathbb{Z}_p} Q(|x-y|_p)\left(\sum_{J\in G_L} f(|J|_p)\Omega(p^L|y-J|_p)\right)\,\Omega(p^L|y-I|_p)dy\\ &= f(|I|_p)\int_{\mathbb{Z}_p} Q(|x-y|_p)\Omega(p^L|y-I|_p)dy\\ &= f(|I|_p)\int_{I+p^L\mathbb{Z}_p} Q(|x-y|_p)dy\\ &= \begin{cases} qf(|I|_p) & \text{if } x\in I+p^L\mathbb{Z}_p\\ p^{-L}f(|I|_p)Q(|I-J|_p) & \text{if } x\in J+p^L\mathbb{Z}_p\end{cases}\end{aligned}$$

where $q := \int_{p^L\mathbb{Z}_p} Q(|z|_p)dz$, which implies that

$$\mathbf{W}(\Omega(p^L|\cdot - I|_p)) = qf(|I|_p)\Omega(p^L|\cdot - I|_p) + \sum_{J\neq I} p^{-L}f(|I|_p)Q(|I-J|_p)\Omega(p^L|\cdot - J|_p) \in \mathcal{D}_L.$$

We observe that $\mathbf{W}$ acts on $\mathcal{D}_L$ as finite linear transformation. Thus, we can represented as a matrix $[\mathbf{W}]$. The above formula imply that

$$[\mathbf{W}]_{JI} = \begin{cases} qf(|I|_p) & J = I\\ p^{-L}f(|I|_p)Q(|I-J|_p) & J\neq I\end{cases} \tag{3.13}$$

In analogy of the classical case, we assume that the "master sequence" is the sequence of zeroes (the p-adic number zero). Then, in the case of high fidelity replication, for large enough L, the mutation measure Q is "concentrated" in the ball $p^L\mathbb{Z}_p$, whereas it takes small values in the spheres $S_0, S_{-1}, \ldots, S_{-L+1}$. In other words, Q as a function from $\mathbb{R}_+$ to $\mathbb{R}_+$ has a "high peak" in the interval $[0, p^{-L}]$.

With this in mind, we argue that $q \approx 1$. Therefore, $[\mathbf{W}]_{II} \approx f(|I|_p) \gg [\mathbf{W}]_{JI} \approx p^{-L}f(|I|_p)$. From now on, we assume that all the eigenvalues of $[\mathbf{W}]$ are distinct and that the matrix $\mathbf{W}$ is non-singular. Therefore, there exists a basis $\{\varphi_I\}_{I\in G_L}$ of $\mathcal{D}_L$ consisting of eigenvectors of the matrix $[\mathbf{W}]$, i.e.,

$$[\mathbf{W}]\varphi_I = \lambda_I\varphi_I, \quad \lambda_I \in \mathbb{C}. \tag{3.14}$$

Notice that the hypothesis that the eigenvalues of $[\mathbf{W}]$ are different is also used in the classical case, see Subsection 1.2.1, and reference [14]. Moreover, the matrix $[\mathbf{W}]$ is positive. Thus, as a consequence of the Perron-Frobenius theorem, we know there is a real and positive eigenvalue, with a unique associated eigenvector that is positive, and it is the eigenvalue with largest absolute value.

According to Remark 3.3, we have that $\mathcal{D}_L \perp \mathcal{K}_L$. After the change of basis of the subspace $\mathcal{D}_L$, we do not necessarily have that $\langle\varphi_I, \Psi^{(J)}_{rjn}\rangle = 0$. However, from $\mathcal{D}_L \perp \mathcal{K}_L$ and

the fact that the set of wavelets $\cup_{I\in G_L}\{\Psi_{rnj}^{(I)}\}$ are an orthonormal basis of $\mathcal{K}_L$ we have that for any $h\in\mathcal{V}_L$ there exist unique coefficients $\{\widetilde{c}_I\}$ and $\{c_{rjn}^{(I)}\}$ such that

$$h=\sum_{I\in G_L}\widetilde{c}_I\varphi_I+\sum_{I\in G_L}\sum_{rnj\in\Lambda_L}c_{rjn}^{(I)}\Psi_{rnj}^{(I)}.$$

3.4.2 The Cauchy problem for a mutation measure supported in the unit ball.

In this subsection, we study a Cauchy problem for a mutation measure supported in the unit ball. We assume a set of hypothesis that introduce in the previous subsection. Summarizing:

1. $Q:\mathbb{R}_+\to\mathbb{R}_+$ is a square-integrable mutation measure supported in the unit ball $\mathbb{Z}_p$, that is, $\operatorname{supp}Q\subseteq\mathbb{Z}_p$, $\int_{\mathbb{Z}_p}Q^2(|x|_p)dx<\infty$ and $\int_{\mathbb{Z}_p}Q(|x|_p)dx=1$.

2. $\mathbf{W}:L^2(\mathbb{Z}_p,\mathbb{C})\to L^2(\mathbb{Z}_p,\mathbb{C})$ is the operator defined by (3.10).

3. $f\in\mathcal{D}_L$ is given by formula (3.6).

4. $\mathcal{V}_L$ be the closed subspace of $L^2(\mathbb{Z}_p,\mathbb{C})$ defined by (3.11).

5. The eigenvalues of the matrix $[\mathbf{W}]$ are distinct. Thus, we assume that Eq. (3.14) holds.

The Cauchy problem for the p-adic replicator equation we solve is as follows.

$$\begin{cases}X:\mathbb{Z}_p\times\mathbb{R}_+\to\mathbb{R}, & X(\cdot,t)\in\mathcal{V}_L\cap L^2(\mathbb{Z}_p,\mathbb{R}),X(x,\cdot)\in C^1(\mathbb{R}_+,\mathbb{R})\\ \frac{\partial X(x,t)}{\partial t}=\mathbf{W}X(x,t)-\Phi(t)X(x,t), & x\in\mathbb{Z}_p,t\in\mathbb{R}_+\\ X(x,0)=X_0\in\mathcal{V}_L\cap L^2(\mathbb{Z}_p,\mathbb{R}),\end{cases}\tag{3.15}$$

where

$$\Phi(t)=\int_{\mathbb{Z}_p}f(|y|_p)X(y,t)dy.\tag{3.16}$$

We recall that we impose some constraints to $X(x,t)$, namely, for every $t\in\mathbb{R}_+$ and $x\in\mathbb{Z}_p$ we have $X(x,t)\in[0,1]$, this is, $X(x,t)$ is the concentration of the sequence x at the time t. Finally, we also assume that the total population remains constant, i.e., $\int_{\mathbb{Z}_p}X(x,t)dx=1$ for every $t\in\mathbb{R}_+$.

After the change of variables $X(x,t)=Y(x,t)\exp(-\int_0^t\Phi(s)ds)$, (3.15) becomes

$$\begin{cases}Y:\mathbb{Z}_p\times\mathbb{R}_+\to\mathbb{R}, & Y(\cdot,t)\in\mathcal{V}_L\cap L^2(\mathbb{Z}_p,\mathbb{R}),Y(x,\cdot)\in C^1(\mathbb{R}_+,\mathbb{R})\\ \frac{\partial Y(x,t)}{\partial t}=\mathbf{W}Y(x,t), & x\in\mathbb{Z}_p,t\in\mathbb{R}_+\\ Y(x,0)=X_0\in\mathcal{V}_L\cap L^2(\mathbb{Z}_p,\mathbb{R}).\end{cases}\tag{3.17}$$

Indeed, using a well-known result [3], since $X(x,t) \leq 1$, $f \in L^1(\mathbb{Z}_p, \mathbb{R})$ and $X(x,\cdot) \in \mathbb{C}^1(\mathbb{R}_+, \mathbb{R})$, we have that Φ is a continuous function on $[0,t]$. Therefore, the Fundamental Theorem of Calculus implies that $\exp(-\int_0^t \Phi(s)ds)$ is differentiable, and consequently

$$\begin{aligned}\frac{\partial X(x,t)}{\partial t} &= \frac{\partial Y}{\partial t}\exp(-\int_0^t \Phi(s)ds) - \Phi(t)Y(x,t)\exp(-\int_0^t \Phi(s)ds) \\ &= \frac{\partial Y}{\partial t}\exp(-\int_0^t \Phi(s)ds) - \Phi(t)X(x,t) \\ &= \frac{\partial Y}{\partial t}\exp(-\int_0^t \Phi(s)ds) - \Phi(t)\exp(-\int_0^t \Phi(s)ds)\mathbf{W}Y(x,t) + \frac{\partial X(x,t)}{\partial t}.\end{aligned}$$

Moreover, if $Y(x,t)$ is a solution of (3.17) then

$$1 = \int_{\mathbb{Z}_p} X(x,t)dx = \exp(-\int_0^t \Phi(s)ds)\int_{\mathbb{Z}_p} Y(x,t)dx,$$

which implies that

$$X(x,t) = \frac{Y(x,t)}{\int_{\mathbb{Z}_p} Y(x,t)dx}. \tag{3.18}$$

Thus, if we have a solution of (3.17), then we have a solution to (3.15).

3.4.3 A separable solution to the Cauchy problem of the p-adic replicator equation

We proceed to solve (3.17) by the method of separation of variables. First, we look for a complex-valued solution $\tilde{Y}(x,t)$ of (3.17). We assume that $\tilde{Y}(x,t) = C(t)U(x)$. Then, after substituting in (3.17) we have

$$\frac{d}{dt}C(t)U(x) = C(t)\mathbf{W}(U(x)).$$

Since we are interested in nontrivial solutions, assuming that $C(t) \neq 0$ and $U(x) \neq 0$, then

$$\frac{\frac{dC}{dt}(t)}{C(t)} = \frac{\mathbf{W}U(x)}{U(x)}.$$

Since the LHS only depends on t and the RHS only depends on x, the above equation implies the existence of constant λ such that

$$\frac{\frac{dC}{dt}(t)}{C(t)} = \lambda = \frac{\mathbf{W}U(x)}{U(x)}. \tag{3.19}$$

[3] **Theorem:** Let $(\Omega, \mathcal{F}, \mu)$ be a measure space. Suppose that $g : \Omega \times [a,b] \to \mathbb{C}(-\infty < a < b < \infty)$ and that $g(\cdot,t) : \Omega \to \mathbb{C}$ is integrable for each $t \in [a,b]$. Let $G(t) = \int_\Omega g(x,t)d\mu(x)$ and suppose that there exists $h \in L^1(\mu)$ such that $|g(x,t)| \leq h(x)$ for all x,t. If $g(x,\cdot)$ is continuous for each x, then G is continuous. See Thm. 2.27, [12] .

The first equality is just an ODE, whereas the second equality implies that $\lambda U = \mathbf{W}U$, therefore, λ must be an eigenvalue of the operator $\mathbf{W}$ with eigenfunction U. Substituting the expression for the eigenvalues (see equations (3.12) and (3.14)) into the left-hand side of (3.19) we get the following equations:

$$\begin{cases} \frac{d}{dt}C_{rjn}^{(I)}(t) = \widehat{Q}(p^{1-r})f(|I|_p)C_{rjn}^{(I)}(t) & \text{corresponding to } \Psi_{rjn}^{(I)}. \\ \frac{d}{dt}\widetilde{C}_I(t) = \lambda_I \widetilde{C}_I(t) & \text{corresponding to } \varphi_I. \end{cases} \tag{3.20}$$

The corresponding solutions are given by

$$\begin{cases} C_{rjn}^{(I)}(t) = C_{rjn}^{(I)}(0)\exp\left(\widehat{Q}(p^{1-r})f(|I|_p)t\right) & \text{corresponding to } \Psi_{rjn}^{(I)}. \\ \widetilde{C}_I(t) = \widetilde{C}_I(0)\exp\left(\lambda_I t\right) & \text{corresponding to } \varphi_I. \end{cases} \tag{3.21}$$

Now, using the linearity of the equation and the superposition principle, we have a solution

$$\widetilde{Y}(x,t) = \sum_{I\in G_L} \widetilde{C}_I(t)\varphi_I + \sum_{I\in G_L}\sum_{rnj\in\Lambda_L} C_{rjn}^{(I)}(t)\Psi_{rnj}^{(I)}.$$

Using the initial condition $Y(0,t) = X_0$ we have that

$$X_0 = \sum_{I\in G_L} \widetilde{C}_I(0)\varphi_I + \sum_{I\in G_L}\sum_{rnj\in\Lambda_L} C_{rjn}^{(I)}(0)\Psi_{rnj}^{(I)}.$$

Taking the inner product with $\Psi_{rnj}^{(I)}$ we obtain,

$$C_{rjn}^{(I)}(0) = \langle X_0, \Psi_{rnj}^{(I)}\rangle.$$

The coefficients of the orthogonal projection of X_0 into $\mathcal{D}_L$ in the basis $\{\Omega(p^L|\cdot - I|_p)\}_{I\in G_L}$ are easy to obtain using the inner product. On the other hand, let P be the of change of basis matrix of $\mathcal{D}_L$ which takes $\{\Omega(p^L|\cdot - I|_p)\}_{I\in G_L}$ to $\{\varphi_I\}_{I\in G_L}$, i.e, the matrix whose columns are the coordinate vectors $\{\varphi_I\}_{I\in G_L}$ in terms of $\{\Omega(p^L|\cdot - I|_p)\}_{I\in G_L}$. Then we get

$$\widetilde{C}_I(0) = \sum_{J\in G_L} P_{IJ}^{-1}\langle X_0, \Omega(p^L|\cdot - J|_p)\rangle,$$

where P_{IJ}^{-1} is the IJ entry of the inverse of P. Since we are looking for real-valued solutions of the equation, the solution $Y(x,t)$ we are looking for is the real part of $\widetilde{Y}(x,t)$.

Finally, we compute the solution to the Cauchy problem (3.15). By using (3.18), the solution of the Cauchy problem (3.15) is given by

$$X(x,t) = \frac{Y(x,t)}{\int_{\mathbb{Z}_p} Y(x,t)dx}.$$

On the other hand, an asymptotic analysis of the solution $X(x,t)$ of the Cauchy problem (3.15) requires considerable analysis of the eigenvalues of the matrix $[\mathbf{W}]$, see (3.13). Roughly

speaking, considering a high fidelity replication rate, we expect its largest eigenvalue to be close to the largest of the values $\{f(|I|_p)\}_{I\in G_L}$, see the approximations (1.12) and compare with (3.13).

Due to the inequality $\|\widehat{Q}\|_\infty \leq \|Q\|_1 = 1$ (see Thm. 2.11) and the expression (3.12) for the eigenvalues corresponding to Kozyrev wavelets , we suspect that the dominant term in time in the expression for $Y(x,t)$ is the one corresponding to the largest eigenvector of $[\mathbf{W}]$, which by the Perron-Frobenius theorem has positive entries with respect to the basis $\{\Omega(p^L|\cdot - I|_p)\}_{I\in G_L}$ of $\mathcal{D}_L$, and this result agrees with the physical interpretation of the model. However, this remains to be studied.

The Cauchy problem for the p-adic replicator equation in the space $L^2(\mathbb{Z}_p,\mathbb{R})$

$$\begin{cases} X:\mathbb{Z}_p\times\mathbb{R}_+\to\mathbb{R}, \qquad X(\cdot,t)\in L^2(\mathbb{Z}_p,\mathbb{R}), X(x,\cdot)\in C^1(\mathbb{R}_+,\mathbb{R}) \\ \frac{\partial X(x,t)}{\partial t} = \mathbf{W}X(x,t) - \Phi(t)X(x,t), \qquad x\in\mathbb{Z}_p, t\in\mathbb{R}_+ \\ X(x,0) = X_0\in L^2(\mathbb{Z}_p,\mathbb{R}), \end{cases} \tag{3.22}$$

is still an open problem.

3.4.4 The existence of the quasispecies

In Section 1.2, the existence of the quasispecies, i.e., the steady state of the system (1.6), was justified using the Perron-Frobenius theorem. Recalling, the Perron-Frobenius theorem states that if A is a positive matrix then it has an eigenvalue λ_0 which is positive and $\lambda_0 > |\lambda_r|$ for any other eigenvalue λ_r of A. Moreover this is the only eigenvalue whose associated eigenvector has only positive entries (see [3, 21]).

We wish to show that this remains true in the p-adic model, in the setting of the Cauchy problem (3.22). Motivated by the classical case, the hope is to use an analogous procedure to conclude that there exist a non-negative function which satisfies suitable hypothesis that is an eigenvector of the operator $\mathbf{W}$. This can be achieved using a generalization of the Perron-Frobenius theorem to Banach spaces that is known as the Krein-Rutman theorem. Before stating this result, we need to write a few definitions.

Definition 3.4. Let X be a Banach space. By a *cone* $K\subset X$, we understand a convex closed set such that $\lambda K\subset K$ for all $\lambda\geq 0$ and $K\cap(-K)=\{0\}$. We say that a cone is *total* if $\overline{K-K}=X$.

Definition 3.5. Let X be a Banach space, $K\subset X$ a cone and $T:X\to X$ a linear bounded operator. We say that T is *positive* if $T\,K\subset K$.

Now, we state the Krein-Rutman theorem, which we use below to argue the existence of the quasispecies.

3.1 Theorem (Thm. 19.2, [7])**.** *Let X be a Banach space, $K\subset X$ a total cone and $T:X\to X$ a linear and compact positive operator with $r(T)>0$. Then $r(T)$ is an eigenvalue with a positive eigenvector.*

As we have showed before, $\mathbf{W}$ is a compact operator on $L^2(\mathbb{Z}_p, \mathbb{R})$. Moreover, notice that Q, f are real valued functions, and the eigenvalues of $\mathbf{W}$ are real (as an operator on $L^2(\mathbb{Z}_p, \mathbb{C})$). Also, its eigenfunctions are elements of the Kozyrev wavelet basis. Taking the real part from both sides of (3.12), we have

$$\mathbf{W}\mathrm{Re}(\Psi^{(I)}_{rjn}) = f(|I|_p)\widehat{Q}(p^{1-r})\mathrm{Re}(\Psi^{(I)}_{rjn}).$$

Therefore, $r(\mathbf{W}) > 0$ on the space $L^2(\mathbb{Z}_p, \mathbb{R})$, since it has non-trivial eigenvalues. Consider $L^2_+ := \{\varphi \in L^2(\mathbb{Z}_p, \mathbb{R}); \varphi \geq 0\, \mu_{Haar}\text{-a.e.}\}$ and set $K := L^2_+$ for short. Then K is a total cone. Indeed, for any positive constants $\alpha, \beta > 0$, and any $\varphi, \psi \in K$ we have that $\alpha\varphi + \beta\psi \in K$.

Moreover, if we take a sequence $\{\varphi_n\} \subset K$ such that $\varphi_n \xrightarrow{L^2(\mathbb{Z}_p,\mathbb{R})} \varphi$, we know that convergence in the space $L^2(\mathbb{Z}_p, \mathbb{R})$ implies the convergence μ_{Haar}-a.e. of a subsequence $\{\varphi_{n_j}\}_j$. Then $\varphi_{n_j}(x) \to \varphi(x)$ μ_{Haar}-a.e., which implies that $\varphi(x) \geq 0$ μ_{Haar}-a.e. Finally, since $\mathcal{D}_{\mathbb{R}} \subset K - K$, we have that $\overline{K - K} = L^2(\mathbb{Z}_p, \mathbb{R})$.

Applying the Krein-Rutman theorem to our operator acting on $L^2(\mathbb{Z}_p, \mathbb{R})$, we conclude there must exist a positive eigenvector associated to $r(\mathbf{W})$, which is the eigenvector we would expect to be the steady-state of the system, because of the physical meaning.

There is a sharper result in the theory of Nonlinear Functional Analysis, that resembles closely the Perron-Frobenius theorem in finite dimensions.

Definition 3.6. Let X be a Banach space and let $K \subset X$ be a cone with non-empty interior. Denote by K^{o} the interior of the cone K. We say that a bounded linear operator $T : X \to X$ is *strongly positive* if $T\,K \subset K^{\mathrm{o}}$.

3.2 Theorem (Thm. 19.3, [7])**.** *Let X be a Banach space, $K \subset X$ a cone with $K^{\mathrm{o}} \neq \emptyset$, $T : X \to X$ a compact linear and strongly positive operator. Then we have*

1. *$r(T) > 0$, $r(T)$ is a simple eigenvalue with an eigenvector $v \in K^{\mathrm{o}}$ and there is no other eigenvalue with a positive eigenvector.*
2. *$|\lambda| < r(T)$ for all eigenvalues $\lambda \neq r(T)$.*

Sadly, our cone L^2_+ has empty interior. We can see how big is the role that the topology plays in infinite dimensions. In Example 19.4 of the book [7], an integral operator $T : C([0,1], \|\cdot\|_\infty) \to C([0,1], \|\cdot\|_\infty)$ with a particular integral kernel is studied. The cone K is given by $C^+([0,1]) := \{x \in C([0,1], \|\cdot\|_\infty); x(t) \geq 0, t \in [0,1]\}$, and it has non-empty interior.

In the mentioned example, the operator T is compact and positive but not strongly positive. However, using the *order topology* (see Section 19.6, [7]), a Banach space X_e together with a cone K_e are constructed, where $e \in C^+([0,1])$ is a suitable element that plays a key role in the construction. It turns out that K_e is a cone with non-empty interior, $T : X_e \to X_e$ is compact, and $T\,K_e \subset {K_e}^{\mathrm{o}}$. Then, the theorem above can be applied.

It is not known to the author if such a construction is possible in the p-adic setting. In different books of functional analysis, the compacity of bounded integral operators on the Banach space $C([0,1],\|\cdot\|_\infty)$ with a continuous integral kernel $k \in C([0,1]\times[0,1])$ is proved using the Arzelà-Ascoli theorem. Motivated by this, it is in our belief that studying the Eigen-Schuster model on $\mathbb{Z}_p$ is of great interest as perhaps, the same method could be applied to get a sharper result with respect to the existence of the quasispecies.

Let $C_{\mathbb{R}}(\mathbb{Z}_p) := C_{\mathbb{R}}(\mathbb{Z}_p,\|\cdot\|_\infty)$ we denote the space of real-valued continuous functions on $\mathbb{Z}_p$ with the uniform norm. We now consider the operator

$$\begin{aligned}\mathbf{W} : C_{\mathbb{R}}(\mathbb{Z}_p) &\longrightarrow C_{\mathbb{R}}(\mathbb{Z}_p)\\ \varphi &\longmapsto (\mathbf{W}\varphi)(x) := \int_{\mathbb{Z}_p} Q(|x-y|_p) f(|y|_p)\varphi(y)dy,\end{aligned}$$

where $Q, f \in C_{\mathbb{R}}(\mathbb{Z}_p)$. Also, we assume that f is a nonnegative function and that Q is a mutation measure on $\mathbb{Z}_p$, that is, $\int_{Z_p} Q(|x|_p)dx = 1$ and $Q(x) \geq 0$ for all $x \in \mathbb{Z}_p$. Notice that as before, $\mathbf{W}\varphi = Q * (f\varphi)$. The convolution is possible since $(\mathbb{Z}_p, +)$ is a group.

As before, our integral kernel is given by $K_{\mathbf{W}}(x,y) = Q(|x-y|_p)f(|y|_p) \in C_{\mathbb{R}}(\mathbb{Z}_p\times\mathbb{Z}_p)$. We claim that $\mathbf{W}$ is a compact operator. Indeed, take a bounded set $A \subset C_{\mathbb{R}}(\mathbb{Z}_p)$, i.e., there exists $M > 0$ such that $\|\varphi\|_\infty \leq M$ for all $\varphi \in A$. Then

$$(\forall \varphi \in A)(\forall x \in \mathbb{Z}_p)|(\mathbf{W}\varphi)(x)| \leq M \max_{x,y\in\mathbb{Z}_p^2} K_{\mathbf{W}}(x,y)$$

This implies that $\mathbf{W}(A)$ is bounded. Moreover, since $K_{\mathbf{W}} \in C_{\mathbb{R}}(\mathbb{Z}_p^2)$ and $\mathbb{Z}_p^2$ is compact, it follows that $K_{\mathbf{W}}$ is uniformly continuous. In particular, for any $y \in \mathbb{Z}_p$ we have

$$(\forall \epsilon > 0)(\exists L \in \mathbb{N})(\forall x_1, x_2 \in \mathbb{Z}_p)\,|x_1 - x_2|_p \leq p^{-L} \implies |K_{\mathbf{W}}(x_1,y) - K_{\mathbf{W}}(x_2,y)| < \frac{\epsilon}{M}.$$

Therefore,

$$(\forall \epsilon > 0)(\exists L \in \mathbb{N})(\forall \varphi \in A)(\forall x_1, x_2 \in \mathbb{Z}_p)\,|x_1 - x_2|_p \leq p^{-L} \implies |(\mathbf{W}\varphi)(x_1) - (\mathbf{W}\varphi)(x_2)| < \epsilon.$$

We conclude that $\mathbf{W}(A)$ is uniformly equicontinuous. Then, the Arzelà-Ascoli theorem [4] implies that $\mathbf{W}(A)$ is relatively compact. This tell us that $\mathbf{W}$ sends bounded sets to relatively compact sets, thus, it is compact.

On the other hand, we set $C^+_{\mathbb{R}}(\mathbb{Z}_p) := \{\varphi \in C_{\mathbb{R}}(\mathbb{Z}_p); \varphi(x) \geq 0, x \in \mathbb{Z}_p\}$. This is a cone with non-empty interior. However, we only have that $\mathbf{W}\,C^+_{\mathbb{R}}(\mathbb{Z}_p) \subset C^+_{\mathbb{R}}(\mathbb{Z}_p)$, so the sharp version of the Krein-Rutman theorem cannot be applied directly. The question about whether is possible to make the described construction or not remains open. Perhaps this construction holds not in the general case, but for a particular family of mutation measures.

[4] **Theorem (Arzelà-Ascoli):** Let X be a compact Hausdorff space. If $\mathcal{F}$ is an equicontinuous, pointwise bounded subset of $C(X)$, then $\mathcal{F}$ is totally bounded in the uniform metric, and the closure of $\mathcal{F}$ in $C(X)$ is compact. See Thm 4.43, [12] .

Chapter 4

Conclusions

In this work, we presented a summary of the classical theory of the Eigen-Schuster model. In particular, we reviewed the so called Eigen paradox. After that, we reviewed some of the ideas concerning the p-adic version of the Eigen-Schuster model, as it was introduced by Zuñiga-Galindo in [31].

Under reasonable hypothesis, we found a real-valued separable solution to the Cauchy problem 3.15 in a closed subspace of $L^2(\mathbb{Z}_p, \mathbb{C})$. However, several questions remain open, namely, the asymptotic behaviour of the solution, and the existence and unicity of a solution in a more general setting. This task seems by no means, easy to accomplish, as most of the known theory for differential equations is not applicable, due to the fact that the operator $\mathbf{W}$ is not self-adjoint and the equation being nonlinear.

The main problems to solve for the future development of the project are:

1. Software with full support for the visualization of functions from $\mathbb{Q}_p$ to $\mathbb{R}$ or $\mathbb{C}$ and its applications to the visualizaton of solutions expressed in terms of the Kozyrev wavelet basis.

2. Numerical methods for the Cauchy problem of the p-adic replicator equation.

Both of these would allow us to understand qualitative properties of the solution and its asymptotic behaviour.

Appendix A

Code for the Eigen-Schuster model simulations.

```
/*
evdynamics

A Maxima package to study evolutionary dynamics

Author: Emmanuel Roque

License: GNU GPLv3, https://www.gnu.org/licenses/gpl-3.0.en.html


*/

load("rkfun.fasl")$
load(interpol)$
load(distrib)$
load(rkf45)$
load(lapack)$
load(operatingsystem)$

make_ode_fun(name_eq,eq,list_vars)::=buildq([name_eq,eq,list_vars],
        name_eq(splice(list_vars)):=block(
            [],
            mode_declare(list_vars,float),
            eq
                )
)$

/*This will be helpful for debugging or comparison purposes
```

```
In the future it might support returning eqs in a specific format, like Octave's

*/

gen_W_matrix(Qmatrix,rep_rate,degr_rate):=block(
    [W%, dim:length(rep_rate)],
    local(W%),
    W%[i,j]:=if is(i=j) then rep_rate[i]*Qmatrix[i][i]-degr_rate[i]
    else rep_rate[j]*Qmatrix[j][i],
    genmatrix(W%,dim,dim)
)$

gen_eqs(Qmatrix,rep_rate,degr_rate,[options]):=block(
    [Wmatrix,W%, dim:length(rep_rate),vars,xx%,xx,E%,stx,x,wrtf,eqs],
    local(W%,x),
    W%[i,j]:=if is(i=j) then rep_rate[i]*Qmatrix[i][i]-degr_rate[i]
    else rep_rate[j]*Qmatrix[j][i],
    Wmatrix:genmatrix(W%,dim,dim),
    stx:assoc('syntax,options,'maxima),
    if is(stx='maxima) then(
    xx%:makelist(concat(x,i),i,1,dim),
    xx:transpose(matrix(xx%)),
    E%:list_matrix_entries(Wmatrix.xx),
    makelist(E%[i]-((rep_rate-degr_rate).xx)*xx%[i],i,1,dim)
    ) elseif is(stx='octave) then(
    xx%:makelist(x(i),i,1,dim),
    xx:transpose(matrix(xx%)),
    E%:list_matrix_entries(Wmatrix.xx),
    eqs:expand(makelist(E%[i]-((rep_rate-degr_rate).xx)*xx%[i],i,1,dim)),
    wrtf:assoc('file_name,options,'eqsf),
    write_data(eqs,sconcat(string(wrtf),".tmp"),semicolon),
    system(sconcat("./eqsformatting.sh ",string(wrtf))),
    delete_file(sconcat(string(wrtf),".tmp")),
    return('done)
    )
    else error("Syntax is not valid")
)$

solve_eigen_model(Qmatrix,rep_rate,degr_rate,x00,t0,tf,[options]):=block(
    [Wmatrix,W%, dim:length(rep_rate),vars,xx%,xx,eqs,E%,
     fun_eq,mthd,stp%,abstol],
    local(W%),
    W%[i,j]:=if is(i=j) then rep_rate[i]*Qmatrix[i][i]-degr_rate[i]
    else rep_rate[j]*Qmatrix[j][i],
    Wmatrix:genmatrix(W%,dim,dim),
```

```
    xx%:makelist(concat(x,i),i,1,dim),
    xx:transpose(matrix(xx%)),
    E%:list_matrix_entries(Wmatrix.xx),
    eqs:makelist(E%[i]-((rep_rate-degr_rate).xx)*xx%[i],i,1,dim),
    vars:append([t],xx%),
    mthd:assoc('method,options,'rkfun),
    abstol:assoc('absolute_tolerance,options,1e-6),
    if is(mthd='rkfun) then (
    fun_eq:makelist(concat(fun,i),i,1,dim),
    stp%:assoc('step_size,options,0.1),
    for i:1 thru dim do apply(make_ode_fun,[concat(fun,i),eqs[i],vars]),
    map(compile,fun_eq),
    rkfun(fun_eq,xx%,x00,[t,t0,tf,stp%])
    ) elseif is(mthd='rkf45) then rkf45(eqs,xx%,x00,[t,t0,tf],
    'absolute_tolerance=abstol)
    else error("The method is not valid")
)$

plot_evolution(sol,[options]):=block(
    [dim:length(first(sol))-1,lbl,yr],
    lbl:assoc('print_labels,options,false),
    yr:assoc('yrange,options,[0,1]),
    if lbl then
    wxdraw2d(
        makelist(
        [
        yrange=yr,
        color=mod(i-1,12),
        key=sconcat("x",i-1),
        points_joined=true,
        point_type=dot,
        points(makelist([p[1],p[i]],p,sol))
        ],
        i,2,dim+1
        )
    )
    else
     wxdraw2d(
        makelist(
        [
        yrange=yr,
        color=mod(i-1,12),
        points_joined=true,
        point_type=dot,
        points(makelist([p[1],p[i]],p,sol))
```

```
        ],
        i,2,dim+1
        )
    )
)$

avg_fitness(sol,rep_rate,deg_rate):=block(
    [space_sol],
    space_sol:map(lambda([e],rest(e,1)),sol),
    list_matrix_entries((rep_rate-deg_rate).transpose(apply('matrix,space_sol)))
)$

/*The weighted concentrations approach does not seem helpful but let's
leave it here for the moment */

weighted_concentrations(fitness,space_sol):=map(lambda([e],e*fitness),space_sol)$



fitness_landscape_evolution(eths,fit,[options]):=block(
    [lngf:length(fit),lngspsol:length(eths),frs,
     weigthedc,wss,plot_fitness,avgfitness,fit_aux,space_sol%,uval],
    space_sol%:map(rest,eths),
    uval:map(first,eths),
    /*How much frames do we want in the animation*/
    frs:assoc('frames,options,lngspsol),
    if is(frs>lngspsol) then error("Number of frames to plot can't be greater
    than the length of the list of solutions"),
    /*Do we want to use weighted concentrations?*/
    weigthedc:assoc('weights,options,false),
    /*Do we want to plot the fitness values? */
    plot_fitness:assoc('plot_fitness_values,options,false),
    /*Do we want to plot the avg fitness?*/
    avgfitness:assoc('avg_fitness,options,makelist(0,j,1,frs)),
    if weigthedc then wss:weighted_concentrations(fit,space_sol%)
    else wss:space_sol%,
    if plot_fitness then(
    ymax:lreduce(max,fit),
    fit_aux:fit/ymax,
    with_slider_draw(
    k, makelist(j,j,1,frs),
    xrange=[1,lngf],
    yrange=[0,1],
    title=sconcat("u=",float(uval[k])),
    points_joined=impulses,line_width=4,color=blue,
```

```
    points(fit_aux),
    line_width=1,
    color=red,
    points_joined=false,
    point_type=square,
    points(wss[k]),
    explicit(cspline(wss[k]),x,1,lngf),
    color=green,
    explicit(avgfitness[k],x,1,lngf)
        )
    )
    else
    with_slider_draw(
    k, makelist(j,j,1,frs),
    xrange=[1,lngf],
    /*ymax=1 if we are not plotting fitness values*/
    yrange=[0,1],
    title=sconcat("u=",float(uval[k])),
    color=red,
    points_joined=false,
    point_type=square,
    points(wss[k]),
    explicit(cspline(wss[k]),x,1,lngf)
    /*explicit(avgfitness[k],x,1,lngf)
    No longer makes sense since it can be larger than 1
    */
    )
)$

 /*Binary sequences of length L, this is an option using recursion
p
 binary_sequences(n):=if is(n>1) then
    apply(append,makelist(map(lambda([e],append([k],e)),
        binary_sequences(n-1)),k,[0,1])) else [[0],[1]]$

 */

 binary_sequences(n)::=buildq([n,%aux:makelist(concat(i,k),k,1,n),
        %aux2:makelist([0,1],k,1,n),
         %aux3:join(makelist(concat(i,k),k,1,n),
        makelist([0,1],k,1,n))],create_list(%aux,splice(%aux3)))$

 hamming(L1,L2):=lsum(i,i,mod(L1+L2,2))$

binary_sequences_ordered(n%):=block(
```

```
    [LL:binary_sequences(n%),hh%:[]],
    for i:0 thru n%+1 do
    hh%:append(hh%,sort(sublist(LL,lambda([x],is(n1s(x)=i))),'ordergreatp)),
    return(hh%)
)$

n1s(ss):=lsum(e,e,ss)$

chop(expr,[options]):=block(
    [abstlr:assoc('absolute_tolerance,options,1.0*10^(-12))],
    scanmap(lambda([x],if is(numberp(x)) then (if is(abs(x)<abstlr)
    then 0.0 else x) else x),expr))$

/*Further details about how to combine mutants into classes according to
their Hamming distance to the
master sequence can be found in [1]
*/

generate_mutation_matrix(u,n%,[options]):=block(
     [seq,cmbd,ord%],local(ham,HH),
    ord%:assoc('order,options,'hamming),
    /*combine mutants by distance?*/
    cmbd:assoc('combine_mutants,options,true),
    if not cmbd then(
    if is(u=0) or is(u=0.0) then return(diagmatrix(2^n%,1))
    elseif is(u=1) or is(u=1.0) then return(genmatrix(lambda([i,j],
    if is(i+j=2^n%+1) then 1.0 else 0.0),2^n%,2^n%))
    else(
    if is(ord%='natural) then seq:binary_sequences(n%) elseif is(ord%='hamming)
    then seq:binary_sequences_ordered(n%)
    else error("Order is not valid"),
    ham[i,j]:=lsum(k,k,mod(seq[i]+seq[j],2)),
    HH[i,j]:=if is(i>j) then float(u^ham[i,j]*(1-u)^(n%-ham[i,j]))
            elseif is(j>i) then HH[j,i] elseif is(i=j) then float((1-u)^n%),
    genmatrix(HH,2^n%,2^n%)
        )
    ) else (
        if is(u=0) or is(u=0.0) then return(diagmatrix(n%+1,1)) else(
        HH[l,k]:=sum((1-u)^(n%-2*j-abs(l-k))*(u)^(2*j+abs(l-k))*
    binomial(n%-(l-1),j+(abs(l-k)-(l-k))/2)*binomial(l-1,j+(abs(l-k)+l-k)/2),
            j,0,ceiling((min(l+k-2,2*n%-(l+k-2))-abs(l-k))/2)),
        genmatrix(HH,n%+1,n%+1)
        )
    )
)$
```

```
steady_state(u,A,D,N,[options]):=block(
    [L,rgt,lft,eq,cmbd],
    /*combine mutants by distance?*/
    cmbd:assoc('combine_mutants,options,true),
    if not cmbd then
    [L,rgt,lft]:dgeev(gen_W_matrix(generate_mutation_matrix(u,N,
    'combine_mutants='false),A,D),true,false)
    else
    [L,rgt,lft]:dgeev(gen_W_matrix(generate_mutation_matrix(u,N),A,D),true,false),
    eq:abs(first(args(transpose(col(rgt,1))))),
    eq/lsum(x,x,eq)
)$

error_threshold(A%,D%,N%,u0,uf,[options]):=block(
    [nop,ert,cmbd],
    ert:uf-u0,
    nop:assoc('number_of_steps,options,100),
    cmbd:assoc('combine_mutants,options,true),
    if not cmbd then
    makelist(cons(u0+ert*j/nop,steady_state(u0+ert*j/nop,A%,D%,N%,
            'combine_mutants='false)),j,0,nop)
    else
    makelist(cons(u0+ert*j/nop,steady_state(u0+ert*j/nop,A%,D%,N%)),j,0,nop)
)$

/*error_threshold(A,D,N,u0,uf,[options]):=block(
    [nos,ert,cmbd,lst],
    ert:uf-u0,
    nos:assoc('number_of_steps,options,ert/100),
    cmbd:assoc('combine_mutants,options,true),
    if not cmbd then
    lst:makelist(cons(ert*j/nos,steady_state(ert*j/nos,A,D,N,
                'combine_mutants='false)),j,1,nos)
    else
    lst:makelist(cons(ert*j/nos,steady_state(ert*j/nos,A,D,N)),j,1,nos),
    lst
)$*/

log__(r):=if is(r<=0) then 0 elseif r>0 then log(r)$

plot_error_threshold(ertshld,[options]):=block(
    [lscl:assoc('log_scale,options,false),n%:length(first(ertshld)),lbl],
    lbl:assoc('print_labels,options,false),
    if is(lscl=false) then if lbl then
```

```
wxdraw2d(
    makelist(
    [yrange=[0,1],
    color=mod(i-1,12),
    key=sconcat("x",i-1),
    points_joined=true,
    point_type=dot,
    points(makelist([p[1],p[i]],p,ertshld))
    ],
    i,makelist(k,k,2,n%)
    )
)
    else(
    wxdraw2d(
    makelist(
    [yrange=[0,1],
    points_joined=true,
    point_type=dot,
    points(makelist([p[1],p[i]],p,ertshld))
    ],
    i,makelist(k,k,2,n%)
        )
    )
)
else(
if lbl then
wxdraw2d(
    makelist(
    [yrange=[-20,0],
    color=mod(i-1,12),
    key=sconcat("x",i-1),
    points_joined=true,
    point_type=dot,
    points(makelist([p[1],log__(p[i])],p,ertshld))
    ],
    i,makelist(k,k,2,n%)
    )

) else
wxdraw2d(
    makelist(
    [yrange=[-20,0],
    points_joined=true,
    point_type=dot,
    points(makelist([p[1],log__(p[i])],p,ertshld))
```

```
        ],
        i,makelist(k,k,2,n%)
        )

        )
    )
)$
```

Appendix B

Code for the graphical representation of p-adic numbers

```
/*
pgraphics

A Maxima package to graph p-adic numbers

Author: Emmanuel Roque

License: GNU GPLv3, https://www.gnu.org/licenses/gpl-3.0.en.html

*/

/* WARNING: Temporary solution. Might break things.

We use tellsimp to simplify

inf+k to inf

for k an integer

*/

matchdeclare(yy,integerp)$
tellsimp(inf+yy,inf)$

/* Since the complex parameter 's' we use have norm
 less than 1, we follow the convention
 s^inf=0

*/
```

```
matchdeclare(aa,numberp)$
tellsimp(aa^inf,0)$


/* This function generates all possible sequences with
entries in 0,...,p-1 of length LL.

pp must be a prime number.

The output can be thought as the canonical representatives of
Z_p/(p^L Z_p), L >0. */

gen_p_seq(LL,pp)::=buildq(
    [LL,%aux:makelist(concat(i,k),k,1,LL),
    %aux2:join(makelist(concat(i,k),k,1,LL),
    makelist(makelist(j,j,0,pp-1),k,1,LL))],
    create_list(%aux,splice(%aux2))
)$

/*

Auxiliar order.

The input xx must be a list of length LL as the lists
 in the output of gen_p_seq. It returns the index of the
first non-zero entry of xx, wich corresponds to
 the first non-zero coefficient  xx.


*/

auxord(xx):=if zeromatrixp(xx) then inf
            else first(sublist_indices(xx,lambda([e],is(e>0))))-1$

/*

We can generate sequences in some ball of radius p^k by a dilatation.

k must be an integer.

*/

add_korder(xx,kk,pp):=cons(auxord(xx)+kk,[xx])$
```

```
/* For practicality, the next function generates,
in some sense,  the canonical representatives of

(p^k Z_p )/(p^k+L Z_p)

*/

genkL_ball(kk,LL%,pp%):=block(
    [auxseq:gen_p_seq(LL%,pp%)],
    map(lambda([e],add_korder(e,kk,pp%)),auxseq)
)$

/*  Just for the sake of completeness
    here is a function to compute the p-adic order
    of a list xx. We won't use it much.
*/

orderp(xx,p):=first(xx)$

/* Now, we implement the homeomorphism Gamma_m described in [2]


with m=0 for simplicity

*/

gamma0p(xxn,s,LL,pp):=block(
    [oo,xx],
    /*
    The p-adic order (oo) can be computed directly, it should
    run faster this way.
    */
        oo:first(xxn),
        xx:second(xxn),
    /*Note: Currently, this throws an error for [inf,[0,...,0]]
    */
        (1-s^oo)/(1-s)+sum(s^n*exp(2*%pi*%i*xx[n+1]/pp),n,oo,LL-1)
)$

/*
Usually we will work with functions with support on Zp.

For practicality, let us have a specific command for this.
*/
```

```
Zp_domain(s,LL,pp):=block(
    /*We first remove the zero element and then we add its image
    under gamma by hand */
    [AA:rest(genkL_ball(0,LL,pp)),dd],
    dd:cons(1/(1-s),map(lambda([e],gamma0p(e,s,LL,pp)),AA)),
    [map(realpart,dd),map(imagpart,dd)]
)$

/*
    For fast evaluation of radial functions,
    let us take as input a list as in the output of genkL_ball
    and return the norms in this order as outputs.

*/

kL_ball_norms(kk,LL,pp):=block(
    [AA:genkL_ball(0,LL,pp)],
    map(lambda([e],(1/pp)^e),map(first,AA))
)$

/*
    Particular case for Zp

*/

Zp_norms(LL,pp):=kL_ball_norms(0,LL,pp)$

/* Visualization of Monna map

See Section 1.9.4 of [1]

*/


Monna_map(xxn,LL,pp):=block(
    [oo,xx],
    /*
    The p-adic order (oo) can be computed directly, it should
    run faster this way.
    */
        oo:first(xxn),
        xx:second(xxn),
    /*Note: Currently, this throws an error for [inf,[0,...,0]]
    */
```

```
        sum(pp^(-n-1)*xx[n+1],n,oo,LL-1)
)$


/*

[1] S. Albeverio, A. Yu. Khrennikov, V.M. Shelkovich -Theory of
    p-adic Distributions: Linear and Nonlinear Models.

[2] D.V. Chistyakov - Fractal Geometry for images of continuous
    embeddings of p-adic numbers and solenoids into Euclidean
    spaces.

*/
```

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