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EIGEN'S PARADOX AND THE QUASISPECIES MODEL IN A NON-ARCHIMEDEAN FRAMEWORK

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Abstract. In this article we present a new p-adic generalization of the Eigen-Schuster model where the genomes (sequences) are represented by words written in the alphabet $\{0, 1, \ldots, p-1\}$, where p is a prime number, with a time variable length. The time evolution of the concentration of a given sequence is controlled by a p-adic evolution equation. The long term behavior of the concentration of a sequence depends on a fitness function f, a mutation measure Q, and an initial concentration distribution. The new model provides essentially two types of asymptotic scenarios for evolution. If the complexity of sequences grows at the right pace, then in the long term the survival is assured. This agrees with the fact that larger genome size improves the replication fidelity. In other case, the sequences cannot copy themselves with sufficiently fidelity, and in the long term they will not survive. Eigen's paradox is one, among the infinitely many, possible scenarios of the evolution in the long term. The mathematical formulation of this fact requires solving the Cauchy problem for the p-adic Eigen-Schuster model in a rigorous mathematical way. This requires imposing restrictions on the fitness function and on the mutation measure, among other conditions. The study of the mentioned initial value problem requires techniques of p-adic wavelets and p-adic heat kernels developed in the last 35 years.

1. Introduction

A central problem in the origin of life is the reproduction of primitive organisms with sufficient fidelity to maintain the information coded in the primitive genomes. Assuming that genomes have constant length, and the existence of independent point mutations, that is, assuming that during the replication process each nucleotide has a fixed probability of being replaced for another nucleotide, and that this probability is independent of all other nucleotides, Eigen discovered that the mutation process places a limit on the number of nucleotides that a genome may have, see e.g. [9], [10], [23], [29], [33]. This critical size is called the error threshold of replication. The genomes larger than this error threshold will be unable to copy themselves with sufficiently fidelity, and the mutation process will destroy the information in subsequent generations of these genomes. This contradicts the existence of large stable living organisms on earth. To create more complex organisms (that is to have more genetic complexity), it is necessary to encode more information in larger genomes by using a replication mechanism with greater fidelity. But the information for creating error-correcting mechanisms (enzymes) should be encoded in the genomes, which have a limited size. Hence, we arrive to the 'Catch-22' or

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Eigen's paradox of the origin of life: "no large genome without enzymes, and no enzymes without a large genome," see [27, p. 317], [31].

In [26] Scheuring and in [25], Poole, Jeffares, Penny proposed biological hypotheses to explain Eigen's paradox. In both works, the authors pointed out that escaping the Catch-22 (Eigen's paradox) requires that the length of the genomes must growth at the right pace. The standard Eigen-Schuster model is not compatible with the assumption that the length of the sequences growth in time. First, the description of the space of sequences as a metric space of binary sequences endowed with the Hamming distance becomes useless. The Hamming distance make sense only when the length of the sequences is finite and fixed. The classical realization of the Eigen-Schuster model as a system of ODEs in $\mathbb{R}^n$ is useless, because n is the number of sequences (chemical species), if the length of the sequences growth in time, then the number of chemical species grows and consequently n must grow in time. In conclusion, dealing with the assumption that the length of the sequences growth in time requires a new mathematical approach.

In [37], the author introduced a new non-Archimedean model of evolutionary dynamics, where the genomes (sequences) are represented by p-adic numbers. The length of the sequences varies in time, and it is not bounded. The sequences are organized in a tree-like structures resembling the phylogenetic trees. There is a natural distance between two sequences which depends on the first common ancestor of the given sequences. The space of all possible sequences has a fractal nature. The time evolution of the concentration of a sequence is controlled by a p-adic evolution equation, which is a p-adic continuous version of the classical Eigen-Schuster model. This equation depends on a fitness function f and on mutation measure Q. For some families of mutation measures and by using a p-adic version of the Maynard Smith Ansatz, in [37], the author showed the existence of threshold function $M_c(f,Q)$, such that the long term survival of a sequence requires that its length grows faster than $M_c(f,Q)$. This implies that Eigen's paradox does not occur if the complexity of genomes grows at the right pace. In [37] a heuristic approach to the existence of quasispecies was presented, the purpose of this work is to provide a rigorous mathematical analysis of this model, that allows explaining the Eigen paradox. This requires solving, in a rigorous mathematical way, the Cauchy problem attached to our p-adic Eigen-Schuster model under general assumptions on the fitness function, the mutation measure, and the initial datum. Also, it is needed to explain how the old Eigen-Schuster model fits in the new framework.

In the non-Archimedean model a sequence (genome) is specified by a p-adic number:

$$x = x_{-k}p^{-k} + x_{-k+1}p^{-k+1} + \ldots + x_0 + x_1 p + \ldots, \text{ with } x_{-k} \neq 0, \tag{1.1}$$

where p denotes a fixed prime number, and the x_js are p-adic digits, i.e. numbers in the set $\{0, 1, \ldots, p-1\}$. The set of all possible sequences constitutes the field of p-adic numbers $\mathbb{Q}_p$. There are natural field operations, sum and multiplication, on series of form (1.1), see e.g. [19]. There is also a natural norm in $\mathbb{Q}_p$ defined as $|x|_p = p^k$, for a nonzero p-adic number x of the form (1.1). The field of p-adic numbers with the distance induced by $|\cdot|_p$ is a complete ultrametric space. The ultrametric property refers to the fact that $|x-y|_p \leq \max\left\{|x-z|_p, |z-y|_p\right\}$ for any x, y, z in $\mathbb{Q}_p$.

The classical Eigen-Schuster equation describes the concentration $X(I,t)$ of a sequence I at time t. In the non-Archimedean approach the sequence I is codified as a p-adic number of the form

$$I = I_{-M}p^{-M} + I_{-M+1}p^{-M+1} + \cdots + I_0 + \cdots + I_{M-1}p^{M-1},$$

where $M \in \mathbb{N} \smallsetminus \{0\}$ and the set of sequences is $G_M = p^{-M}\mathbb{Z}_p/p^M\mathbb{Z}_p$. In the limit when M tends to infinity G_M becomes $\mathbb{Q}_p$. The p-adic Eigen-Schuster model is given by

$$\frac{d}{dt}X(I,t) = \frac{1}{C}\sum_{J\in G_M} Q(I,J)\, f(J)\, X(J,t) - \Phi_M(t)\, X(J,t)\,,\ I \in G_M,\ \ t > 0, \text{ where}$$

$$\Phi_M(t) = p^{-M}\sum_{I\in G_M} f(I)\, X(I,t),$$

here $[Q(I,J)]_{I,J}$ is the mutation matrix, $f(J)$ is the fitness of the sequence J, and C, p^{-M} are scale constants. In the limit M tends to infinity, I becomes a continuous p-adic variable denoted as x, and the model takes de form

$$\frac{\partial X(x,t)}{\partial t} = \int_{\mathbb{Q}_p} Q(x,y) f(y) X(y,t)\, dy - \Phi(t)\, X(x,t)\,,\ x \in \mathbb{Q}_p,\ t \in \mathbb{R}_+, \text{ where}$$

$$\Phi(t) = \int_{\mathbb{Q}_p} f(y)\, X(y,t)\, dy \ \text{ for } t \geq 0.$$

The integral is with respect to the Haar measure of $\mathbb{Q}_p$. This reasoning is not possible if we use Riemann integrals. This limit can be formulated in a rigorous mathematical way, see e.g. [35]. The above model describes the time evolution of the concentration $X(x,t)$ of the sequence x, which has a length varying in time. A fundamental observation is that the error threshold phenomenon occurs independently of the topology of the space of sequences, see Section 3.3.

In Section 3, we introduce a very general class of models where the mutation measure $Q(x,y,t)dy$ and the fitness function $f(y,t)$ depend on the time t. The study of the Cauchy problems for these equations is an open problem. The case in which the fitness function is supported in the unit ball, and the mutation measure has the form $Q(x-y)dy$ is fully studied in in this article.

We denote by $\mathbb{Z}_p$ the unit ball, which consists of the all the sequences with expansions of the form (1.1) with $-k \geq 0$. The fitness landscape is given by a test function $f : \mathbb{Z}_p \to \mathbb{R}_+$, which means that f is a locally constant function with compact support. With respect to the mutation mechanism, we only assume the existence of a mutation measure $Q_0\left(|x|_p\right) dx$, where $Q_0 : \mathbb{R}_+ \to \mathbb{R}_+$, and dx is the normalized Haar measure of the group $(\mathbb{Z}_p, +)$, with $\int_{\mathbb{Z}_p} Q_0\left(|x|_p\right) dx = 1$, such that the probability that a sequence x mutates into a sequence belonging to the set B is given by $\int_B Q_0\left(|x-y|_p\right) dy$. In our model the concentration $X(x,t) \in [0,1]$

of the sequence x at the time t is controlled by the following evolution equation:

$$\left\{\begin{array}{l}\frac{\partial X(x,t)}{\partial t}=Q_0\left(|x|_p\right)*\left\{f\left(|x|_p\right)X\left(x,t\right)\right\}-\Phi\left(t\right)X\left(x,t\right),\\ \\ X\left(x,0\right)=X_0(x),\ \int\limits_{\mathbb{Z}_p}X_0(x)dx=1,\end{array}\right. \tag{1.2}$$

where $x\in\mathbb{Z}_p, t\geq 0$, and $\Phi\left(t\right)=\int_{\mathbb{Z}_p}f\left(|y|_p\right)X\left(y,t\right)dy$. The term

$$\boldsymbol{W}_0X\left(x,t\right)=Q_0\left(|x|_p\right)*\left\{f\left(|x|_p\right)X\left(x,t\right)\right\}$$

represents the rate at which the sequences are mutating into the sequence x. We assume that the replication reactions occur in a chemostat, see e.g. [33], which is a device that allows the maintenance of a constant population size, this mechanism is implemented by using the term $-\Phi\left(t\right)X\left(x,t\right)$.

We now discuss briefly the main results presented in this article. To study the Cauchy problem (1.2), we first construct an function space invariant under operator $\boldsymbol{W}_0$, and then use p-adic wavelets to construct an explicit solution of the Cauchy problem using the classical method of separation of variables. The construction of the invariant space for $\boldsymbol{W}_0$ was not considered in [37]. We assume that the fitness function is a test function of the form $f(x)=\sum_{J\in G_M}f(J)\Omega\left(p^M\left|x-J\right|_p\right)$, where $f(J)>0$, and $\Omega\left(p^M\left|x-J\right|_p\right)$ is the characteristic function of the ball $J+p^M\mathbb{Z}_p$ and $\mathbb{Z}_p=\bigsqcup_{J\in G_M}\left(J+p^M\mathbb{Z}_p\right)$. The ball $J+p^M\mathbb{Z}_p$ is a cloud of mutants around the master sequence J, any sequence in this cloud reproduces at a rate of $f(J)$ copies per unit of time. We denote by $\mathcal{D}_M$ the $\mathbb{R}$-vector space spanned by the functions $\Omega\left(p^M\left|x-I\right|_p\right)$, $I\in G_M$. The finite dimensional vector space $\mathcal{D}_M$ is invariant under $\boldsymbol{W}_0$, then its restriction to $\mathcal{D}_M$ represented by a matrix $\mathbb{W}^0=\left[\mathbb{W}^0_{I,J}\right]_{I,J\in G_M}$. We denote by $L^2\left(J+p^M\mathbb{Z}_p\right)$ the $\mathbb{C}$-vector space of square-integrable functions defined on the ball $J+p^M\mathbb{Z}_p$. The space $L(\boldsymbol{W}_0)=\mathcal{D}_M\bigoplus\bigoplus_{J\in G_M}L^2\left(J+p^M\mathbb{Z}_p\right)$ is invariant under $\boldsymbol{W}_0$, see Lemma 1.

We solve the Cauchy problem (1.2) in $L(\boldsymbol{W}_0)$:

$$X\left(x,t\right)=\frac{\left(e^{t\mathbb{W}^0}\left[C^0_I(0)\right]_{I\in G_M}\right)\left[\Omega\left(p^M\left|x-I\right|_p\right)\right]^T_{I\in G_M}}{\overline{Y\left(t\right)}}+$$

$$\sum_{I\in G_M}\ \sum_{\operatorname{supp}\Psi_{rnj}\subseteq I+p^M\mathbb{Z}_p}\frac{e^{t\widehat{Q_0}\left(p^{1-r}\right)f(I)}\operatorname{Re}\left(C^I_{rjn}\left(0\right)\Psi_{rnj}\left(x\right)\right)}{\overline{Y\left(t\right)}}, \tag{1.3}$$

where $\Psi_{rnj}\left(x\right)$s are wavelet basis of $L^2\left(\mathbb{Q}_p\right)$, each of these functions has average zero, i.e.

$$\int\limits_{\mathbb{Q}_p}\Psi_{rnj}\left(x\right)dx=0, \tag{1.4}$$

and $\widehat{Q_0}(\xi)$ is the Fourier transform of the radial function $Q_0\left(|x|_p\right)$. Now the initial datum $X(x,0)$ is determined by an element of the set of sequences

$$\mathcal{S} = \bigsqcup_{J\in G_M}\left\{C_J^0(0)\right\}\bigsqcup\bigsqcup_{I\in G_M}\left\{C_{rjn}^I(0)\right\}_{rnj}.$$

If we take the initial datum determined by the conditions $C_{rjn}^I(0)=0$ for any I, rnj and $C_J^0(0)\neq 0$ for some J, i.e. $X(x,0)\in\mathcal{D}_M$, then the condition (1.4) implies that

$$X(x,t)=\frac{\left(e^{t\mathbb{W}^0}\left[C_I^0(0)\right]_{I\in G_M}\right)\left[\Omega\left(p^M|x-I|_p\right)\right]_{I\in G_M}^T}{\overline{Y(t)}},$$

see Theorem 1. A key observation is that given $t\geq 0$, the value of the function $X(x,t)$ depends only on the first M digits of $x=x_0+x_1p+\ldots+x_{M-1}p^{M-1}+\ldots$, since M is fixed, in this model the length of the sequences does not change in time. Since $\mathbb{W}^0$ is a real symmetric matrix, it is diagonalizable and all its eigenvalues are real. In this case $\lim_{t\to\infty}X(x,t)$ exists and it is controlled by the largest eigenvalue of $\mathbb{W}^0$. This situation corresponds to *the survival of the fitter*. This is the typical scenario predicted by the classical Eigen-Schuster model. In this scenario the Eigen paradox may happen. This result says that the classical Eigen-Schuster description of evolution can be obtained using the p-adic Eigen-Schuster model. Our previous publication [37] does not contain a similar result.

To escape to the Eigen paradox the length of the sequences must growth, see Section 3.3, which requires that some of the oscillatory terms (those involving the $\Psi_{rnj}(x)$s) must be preserved in the long term in (1.3). If these oscillatory terms do not vanish in the long term, we have a cloud of sequences in $\mathbb{Z}_p$ (with time variable length, including sequences of infinite length) evolving according to the basic Darwinian principles. Intuitively, one must show that the function $\lim_{t\to\infty}X(x,t)$ depends on infinitely many digits in the p-adic expansion of x. This is a non-trivial mathematical task that requires suitable hypotheses on the mutation measure, and surprisingly non-trivial results on stochastic processes on $\mathbb{Q}_p$. In our previous publication [37] these matters were not considered.

We pick as a mutation measure a family of Gibbs type measures of the form $Q_0\left(|x|_p\right)=\mathcal{N}\Omega\left(|x|_p\right)\exp(-\sigma|x|_p^\alpha)$, where α, σ are positive parameters, $\Omega\left(|x|_p\right)$ is the characteristic function of the unit ball, and $\mathcal{N}$ is a normalization constant. The Fourier transform $Q_0\left(|x|_p\right)$ of satisfies $\mathcal{F}_{x\to\xi}(Q_0\left(|x|_p;\sigma,\alpha\right))=\mathcal{N}Z(\xi;\sigma,\alpha)*\Omega\left(|\xi|_p\right)$, where $Z(\xi;\sigma,\alpha)$ is the classical p-adic heat kernel, which is the transition density of a Markov process in $\mathbb{Q}_p$, see e.g. [5], [18], [34], [36]. We use the extensively the results about the behavior of $Z(\xi;\sigma,\alpha)$ around the origin and at the infinity.

We introduce the following two conditions:

$$\text{Hypothesis A:}\qquad \int_{p^M\mathbb{Z}_p}Q_0\left(|z|_p\right)dz\in\left(\frac{1}{2},1\right).$$

$$\text{Hypothesis B:}\qquad \widehat{Q_0}\left(p^{1-r_0}\right)f(I_0)>\mu_{\max},$$

where $\mu_{\max}$ is the largest eigenvalue of $\mathbb{W}^0$. The hypothesis A says that the probability that a sequence belonging to $I+p^M\mathbb{Z}_p$ mutates into a sequence belonging to

$\bigsqcup_{J\neq I}\left(J+p^{M}\mathbb{Z}_{p}\right)$ is less than $\frac{1}{2}$, for any $I\in G_{M}$. It is important to mention here that Hypothesis A also appears in the Maynard Smith ansatz, see [27], [30], [37].

We denote by $\mathcal{S}_{0}$ the subset of $\mathcal{S}$ consists of the sequences satisfying $C_{rjn}^{I}(0)\neq 0$ for some I, rnj and $C_{J}^{0}(0)\neq 0$ for some J. We show the existence of $\sigma_{\max}$ and $M=M(\sigma,\alpha)$, such that if $X(x,0)\in\mathcal{S}_{0}$, and $Q_{0}\left(|x|_{p};\sigma,\alpha\right)$ satisfies that $\sigma\in(0,\sigma_{\max})$, $\alpha\in(0,\infty)$, and $\int_{p^{M}\mathbb{Z}_{p}}Q_{0}\left(|x|_{p}\right)dx\in\left(\frac{1}{2},1\right)$, then the Cauchy problem (1.2) has a solution with a non-trivial oscillatory behavior at infinity. In this case, we say that (1.2) admits a *quasispecies solution*, see Theorems 2, 3. A quasispecies is a large group of related genotypes that exist in an environment of high mutation rate at stationary state, where a large fraction of offspring are expected to contain one or more mutations relative to the parent, [10]. The p-adic quasispecies correspond to a profile of a solution of the Cauchy problem (4.9) when t tends to infinity.

As a generalization of the classical Eigen-Schuster model, our p-adic model encodes the basic principles of Darwinian evolution. The long term survival of a sequence under the selection pressure depends on the interaction of the fitness function, the mutation measure and the initial concentration of the sequences. Assuming that the mutation measure is a Gibbs measure of type $\Omega\left(|x|_{p}\right)\exp(-\sigma\,|x|_{p}^{\alpha})$, we establish the existence of scenarios where the long-term concentration of sequences with arbitrary length does not vanish. Based on the Maynard Smith ansatz, see Section 3.3, we interpret this situation as that long-term survival requires that the complexity of the genomes grow at the right pace. This agrees with the fact that larger genome size improves the replication fidelity. In other case, the Eigen paradox occurs, which means that the sequences are unable to copy themselves with sufficiently fidelity, and thus in the long term these sequences will not survive. The Eigen paradox is a possible scenario, among infinitely many, in our p-adic evolution model.

It is important to mention here that Avetisov and Zhuravlev pointed out using $1D$ p-adic diffusion equation in biological evolution, see [3]-[4]. This approach does not allow to analyze directly the error catastrophe in the standard sense. On the other hand, the use of p-adic numbers in DNA models and analysis of the genetic code is well-known see e.g. [7], [8], [17], and the references therein.

The article is organized a s follows. In Section 2 we review the essential ideas about p-adic analysis. In Section 3, we review and extend the p-adic version of Eigen-Schuster model introduced in [37]. In the extended models the mutation measure is a transition density function $Q\left(x,y,t\right)\geq 0$ for $x,\ y\in\mathbb{Q}_{p},\ t>0$, of a Markov process. The study of the Cauchy problem for these models is an open problem. In Section 4, we study the existence of a solution for the Cauchy problem considered in the introduction. We use the classical method of separation of variables and p-adic wavelets. In Section 5, we show the existence of p-adic quasispecies and discuss the solution of Eigen's paradox.

2. p-Adic Analysis: Essential Ideas

In this Section, we collect some basic results on p-adic analysis that we use through the article. For a detailed exposition the reader may consult [1], [15], [32], [34].

2.1. **The field of p-adic numbers.** Along this article p will denote a prime number. The field of $p-$adic numbers $\mathbb{Q}_p$ is defined as the completion of the field of rational numbers $\mathbb{Q}$ with respect to the $p-$adic norm $|\cdot|_p$, which is defined as

$$|x|_p = \begin{cases} 0 & \text{if} \quad x = 0 \\ \\ p^{-\gamma} & \text{if} \quad x = p^{\gamma}\frac{a}{b}, \end{cases}$$

where a and b are integers coprime with p. The integer $\gamma := ord(x)$, with $ord(0) := +\infty$, is called the *$p-$adic order of x.*

Any $p-$adic number $x \neq 0$ has a unique expansion of the form

$$x = p^{ord(x)} \sum_{j=0}^{\infty} x_j p^j,$$

where $x_j \in \{0, \ldots, p-1\}$ and $x_0 \neq 0$. By using this expansion, we define *the fractional part of* $x \in \mathbb{Q}_p$, denoted $\{x\}_p$, as the rational number

$$\{x\}_p = \begin{cases} 0 & \text{if} \quad x = 0 \text{ or } ord(x) \geq 0 \\ \\ p^{ord(x)} \sum_{j=0}^{-ord_p(x)-1} x_j p^j & \text{if} \quad ord(x) < 0. \end{cases}$$

For $r \in \mathbb{Z}$, denote by $B_r(a) = \{x \in \mathbb{Q}_p; |x-a|_p \leq p^r\}$ *the ball of radius p^r with center at* $a \in \mathbb{Q}_p$, and take $B_r(0) := B_r$. The ball B_0 equals $\mathbb{Z}_p$, *the ring of $p-$adic integers of* $\mathbb{Q}_p$. We also denote by $S_r(a) = \{x \in \mathbb{Q}_p; |x-a|_p = p^r\}$ *the sphere of radius p^r with center at* $a \in \mathbb{Q}_p$, and take $S_r(0) := S_r$. We notice that $S_0^1 = \mathbb{Z}_p^{\times}$ (the group of units of $\mathbb{Z}_p$). The balls and spheres are both open and closed subsets in $\mathbb{Q}_p$. In addition, two balls in $\mathbb{Q}_p$ are either disjoint or one is contained in the other.

The metric space $\left(\mathbb{Q}_p, |\cdot|_p\right)$ is a complete ultrametric space. As a topological space $(\mathbb{Q}_p, |\cdot|_p)$ is totally disconnected, i.e. the only connected subsets of $\mathbb{Q}_p$ are the empty set and the points. In addition, $\mathbb{Q}_p$ is homeomorphic to a Cantor-like subset of the real line, see e.g. [1], [34]. A subset of $\mathbb{Q}_p$ is compact if and only if it is closed and bounded in $\mathbb{Q}_p$, see e.g. [34, Section 1.3], or [1, Section 1.8]. The balls and spheres are compact subsets. Thus $(\mathbb{Q}_p, |\cdot|_p)$ is a locally compact topological space.

Notation 1. *We will use $\Omega\left(p^{-r}|x-a|_p\right)$ to denote the characteristic function of the ball $B_r(a)$. For more general sets, we denote by 1_A the characteristic function of A.*

2.2. **The Haar measure.** Since $(\mathbb{Q}_p, +)$ is a locally compact topological group, there exists a Borel measure dx, called the Haar measure of $(\mathbb{Q}_p, +)$, unique up to multiplication by a positive constant, such that $\int_U dx > 0$ for every non-empty Borel open set $U \subset \mathbb{Q}_p$, and satisfying $\int_{E+z} dx = \int_E dx$ for every Borel set $E \subset \mathbb{Q}_p$, see e.g. [11, Chapter XI]. If we normalize this measure by the condition $\int_{\mathbb{Z}_p} dx = 1$, then dx is unique. From now on we denote by dx the normalized Haar measure of $(\mathbb{Q}_p, +)$.

2.3. **Some function spaces.** A complex-valued function φ defined on $\mathbb{Q}_p$ is *called locally constant* if for any $x \in \mathbb{Q}_p$ there exist an integer $l(x) \in \mathbb{Z}$ such that

$$\varphi(x + x') = \varphi(x) \text{ for } x' \in B_{l(x)}. \tag{2.1}$$

A function $\varphi : \mathbb{Q}_p \to \mathbb{C}$ is called a *Bruhat-Schwartz function (or a test function)* if it is locally constant with compact support. In this case, we can take $l = l(\varphi)$ in (2.1) independent of x. The largest of such integers is called *the parameter of local constancy* of φ. The $\mathbb{C}$-vector space of Bruhat-Schwartz functions is denoted by $\mathcal{D} := \mathcal{D}(\mathbb{Q}_p, \mathbb{C})$. We will denote by $\mathcal{D}_{\mathbb{R}} := \mathcal{D}(\mathbb{Q}_p, \mathbb{R})$, the $\mathbb{R}$-vector space of test functions.

Given $\rho \in [1, \infty)$, we denote by $L^\rho := L^\rho(\mathbb{Q}_p) := L^\rho(\mathbb{Q}_p, dx)$, the $\mathbb{C}-$vector space of all the complex valued functions g satisfying $\int_{\mathbb{Q}_p} |g(x)|^\rho \, dx < \infty$. The corresponding $\mathbb{R}$-vector spaces are denoted as $L^\rho_{\mathbb{R}} := L^\rho_{\mathbb{R}}(\mathbb{Q}_p) = L^\rho_{\mathbb{R}}(\mathbb{Q}_p, dx)$, $1 \leq \rho < \infty$.

2.4. **Fourier transform.** Set $\chi_p(y) = \exp(2\pi i \{y\}_p)$ for $y \in \mathbb{Q}_p$. The map $\chi_p(\cdot)$ is an additive character on $\mathbb{Q}_p$, i.e. a continuous map from $(\mathbb{Q}_p, +)$ into S (the unit circle considered as multiplicative group) satisfying $\chi_p(x_0 + x_1) = \chi_p(x_0)\chi_p(x_1)$, $x_0, x_1 \in \mathbb{Q}_p$. The additive characters of $\mathbb{Q}_p$ form an Abelian group which is isomorphic to $(\mathbb{Q}_p, +)$, the isomorphism is given by $\xi \to \chi_p(\xi x)$, see e.g. [1, Section 2.3].

If $f \in L^1$ its Fourier transform is defined by

$$(\mathcal{F}f)(\xi) = \int_{\mathbb{Q}_p} \chi_p(\xi x) f(x) dx, \quad \text{for } \xi \in \mathbb{Q}_p.$$

We will also use the notation $\mathcal{F}_{x\to\xi} f$ and $\widehat{f}$ for the Fourier transform of f. The Fourier transform is a linear isomorphism from $\mathcal{D}$ onto itself satisfying

$$(\mathcal{F}(\mathcal{F}f))(\xi) = f(-\xi), \tag{2.2}$$

for every $f \in \mathcal{D}$, see e.g. [1, Section 4.8]. If $f \in L^2$, its Fourier transform is defined as

$$(\mathcal{F}f)(\xi) = \lim_{k\to\infty} \int_{|x|_p \leq p^k} \chi_p(\xi \cdot x) f(x) d^n x, \quad \text{for } \xi \in \mathbb{Q}_p,$$

where the limit is taken in L^2. We recall that the Fourier transform is unitary on L^2, i.e. $||f||_{L^2} = ||\mathcal{F}f||_{L^2}$ for $f \in L^2$ and that (2.2) is also valid in L^2, see e.g. [32, Chapter III, Section 2].

3. p-Adic models of Eigen-Schuster type

In this section we review and extend the p-adic version of Eigen-Schuster model introduced in [37], see e.g. [9], [10], [23], [29], [30], [33] for the classical model. This model describes mutation-selection process of replicating sequences, when the sequences are represented by p-adic numbers.

3.1. **The Model.**

3.1.1. *The space of sequences.* A replicator is a model of an entity with the template property, which means that it serves as a pattern for the generation of another replicator. This copying process is subject to errors (mutations). Along this article we use replicators, genomes and sequences as synonyms. The assumption of the existence of replicators implies that the information stored in the replicators is modified randomly, and that part of it is fixed due to the selection pressure, which in turn is related with the self-replicate capacity of the replicators (their fitness).

In our 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_is run through the set $\{0, 1, \ldots, p-1\}$. Consequently, in our model the sequences are words of arbitrary length written in the alphabet 0, 1,. . ., $p-1$, and the space of sequences is $\left(\mathbb{Q}_p, |\cdot|_p\right)$, which is an infinite ultrametric space.

3.1.2. *Concentrations.* The concentration $X(x,t)$ of sequence $x \in \mathbb{Q}_p$ at the time $t \geq 0$ is a real number between zero and one. In addition, we assume that

$$\int_{\mathbb{Q}_p} X(y,t)\, dy = 1 \text{ for } t > 0. \tag{3.1}$$

This last condition assures that the total concentration remains constant for $t > 0$.

3.1.3. *The mutation measure.* We fix a transition density function $Q(x,y,t) \geq 0$ for x, $y \in \mathbb{Q}_p$, $t > 0$, which means that given a Borel subset $E \subseteq \mathbb{Q}_p$,

$$\int_E Q(x,y,t)\, dy$$

represents the probability that the sequence x will mutate into a sequence belonging to set E at time t. We assume that

$$\int_{\mathbb{Q}_p} Q(x,y,t)\, dy = 1 \text{ for any } x \in \mathbb{Q}_p \text{ and } t > 0.$$

We call $Q(x,y,t)\, dy$ *a mutation measure.* We set $\mathbb{R}_+ = \{y \in \mathbb{R}; y \geq 0\}$. A simple way of constructing time independent mutation measures is as follows. Take $Q : \mathbb{R}_+ \to \mathbb{R}_+$, and set $Q(|x|_p)$ such that

$$\int_{\mathbb{Q}_p} Q\left(|y|_p\right) dy = 1.$$

Then, for a Borel set $E \subseteq \mathbb{Q}_p$ and $x \in \mathbb{Q}_p$, the integral

$$\int_E Q\left(|x-y|_p\right) dy$$

gives the probability that sequence x will mutate into a sequence belonging to E.

3.1.4. *The fitness function.* The *fitness function* $f\ (x,t)$, $x \in \mathbb{Q}_p$, $t > 0$, is a non-negative bounded function. The simplest choice for f is test function independent of the time. This case was considered in [37]. The assumption that function f has compact support means that the evolution process is limited to a certain region of the space of sequences, which is infinite.

3.1.5. *The non-Archimedean replicator equation.* For $t>0$ fixed, and $x\in\mathbb{Q}_p$, we set

$$\left(\boldsymbol{W}\varphi\right)(x)=\int\limits_{\mathbb{Q}_p}Q\left(x,y,t\right)\left\{f\left(y,t\right)\varphi\left(y\right)\right\}dy.$$

Under the hypotheses:

$$f\left(x,t\right)\leq C\text{ for any }x\in\mathbb{Q}_p,$$

where C is a positive constant, and

$$Q\left(x,\cdot,t\right)\in L^2,$$

we have $\boldsymbol{W}:L^2(\mathbb{Q}_p)\to L^2(\mathbb{Q}_p)$ is a well-defined continuous operator.

Our non-Archimedean Eigen-Schuster models have the form:

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

where

$$\Phi\left(t,X\right):=\Phi\left(t\right)=\int\limits_{\mathbb{Q}_p}f\left(y,t\right)X\left(y,t\right)dy\quad\text{for }t\geq0. \tag{3.3}$$

This function $\Phi\left(t\right)$ is used to maintain constant the total concentration in the chemostat.

3.2. **Discretization.** We fix $M\in\mathbb{N}\smallsetminus\{0\}$ and set

$$G_M:=p^{-M}\mathbb{Z}_p/p^M\mathbb{Z}_p.$$

We consider G_M as an additive group and fix the following systems of representatives:

$$I=I_{-M}p^{-M}+I_{-M+1}p^{-M+1}+\cdots+I_0+\cdots+I_{M-1}p^{M-1}, \tag{3.4}$$

where the I_js belong to $\{0,1,\ldots,p-1\}$. Furthermore, the restriction of $\left|\cdot\right|_p$ to G_M induces an absolute value such that $\left|G_M\right|_p=\left\{0,p^{-(M+1)},\cdots,p^{-1},1,\cdots,p^M\right\}$. We endow G_M with the metric induced by $\left|\cdot\right|_p$, and thus G_M becomes a finite ultrametric space. In addition, G_M can be identified with the set of branches (vertices at the top level) of a rooted tree with $2M+1$ levels and p^{2M} branches.

We denote by $\mathcal{D}_M$ the $\mathbb{R}$-vector subspace of $\mathcal{D}_{\mathbb{R}}$ spanned by the functions

$$\Omega\left(p^M\left|x-I\right|_p\right),\ I\in G_M.$$

Notice that $\Omega\left(p^M\left|x-I\right|\right)\Omega\left(p^M\left|x-J\right|\right)=0$ for any x, if $I\neq J$. Thus, any function $\varphi\in\mathcal{D}_M$ has the form

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

where the $\varphi\left(I\right)$s are real numbers. The dimension of $\mathcal{D}_M\left(\mathbb{Q}_p\right)$ is $\#G_M=p^{2M}$.

In order to explain the connection between the non-Archimedean replicator equation (3.2) and the classical one, we assume that $f\left(\cdot,t\right)$ and $X(\cdot,t)$ belong to $\mathcal{D}_M$, and that $Q\left(\cdot,\cdot,t\right)$ belongs to $\mathcal{D}_M\times\mathcal{D}_M$ for any t. This assumption means that the mentioned functions can be very well approximated by functions in $\mathcal{D}_M$, respectively in $\mathcal{D}_M \times \mathcal{D}_M$, see e.g. [35]. Then

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

where $C_M = p^{-M}\sum_{J\in G_M} Q(I,J,t)$, and the $Q(I,J,t)$s are real-valued functions of class C^1 in t,

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

and

$$X(x,t) = \sum_{J\in G_M} X(J,t)\Omega\left(p^M|x-J|_p\right) \text{ for any } t\geq 0,$$

where each $X(I,t)$ is a real-valued function of class C^1 in t. Now

$$\int_{\mathbb{Q}_p} Q(x,y,t)\,f(y,t)\,X(y,t)\,dy =$$
$$\frac{1}{C_M}\sum_{I\in G_M}\left\{\sum_{J\in G_M} Q(I,J,t)\,f(J,t)\,X(J,t)\int_{\mathbb{Q}_p}\Omega\left(p^M|y-J|_p\right)dy\right\}\Omega\left(p^M|x-I|_p\right)$$
$$= \frac{1}{C}\sum_{I\in G_M}\left\{\sum_{J\in G_M} Q(I,J,t)\,f(J,t)\,X(J,t)\right\}\Omega\left(p^M|x-I|_p\right),$$

where $C = p^{-M}\sum_{J\in G_M} Q(I,J,t)$. Finally, using the fact that the $\Omega\left(p^M|x-I|_p\right)$, $I\in G_M$ are $\mathbb{R}$-linearly independent, we get

$$\frac{d}{dt}X(I,t) = \frac{1}{C}\sum_{J\in G_M} Q(I,J,t)\,f(J,t)\,X(J,t) - \Phi_M(t)\,X(J,t)\,, \tag{3.5}$$

for $I\in G_M$, where

$$\Phi_M(t) = p^{-M}\sum_{I\in G_M} f(I,t)\,X(I,t). \tag{3.6}$$

In the case in which the $Q(I,J,t)$s are independent of the time, (3.5)-(3.6) is the classical Eigen-Schuster model on the finite ultrametric space G_M. In [37], see also [35], we argue that the system (3.2)-(3.3) is the limit when M tends to infinity of the system (3.5)-(3.6).

3.3. **The error threshold and the topology of the space of sequences.** In this section we review the Maynard Smith approach to the error threshold problem assuming that the space of sequence is an arbitrary measurable metric space $(\mathbb{Y},\mu)$, see [27], [30] for the classical version. This means that we do not assume a specific topology for the space of sequences, in particular, the length of the sequences is arbitrary. We divide the space of sequences into two disjoint sets:

$$\mathbb{Y}=\mathbb{A}\bigsqcup\mathbb{B}, \tag{3.7}$$

and assume that

$$f\mid_{\mathbb{A}}\equiv a,\quad f\mid_{\mathbb{B}}\equiv b,\ \text{ with } a>b, \tag{3.8}$$

here "$\equiv$" means identically equal. We denote by $X(x,t)$ the concentration of sequences of type $\mathbb{A}$ and by $Y(x,t)$ the concentration of sequences of type $\mathbb{B}$. Notice that the supports of $X(x,t)$ and $Y(x,t)$ are disjoint. We denote by q the probability that a sequence in $\mathbb{A}$ mutates into a sequence belonging to $\mathbb{B}$, and by r the probability of mutation of a sequence from $\mathbb{B}$ into a sequence in $\mathbb{A}$. The system of equations governing the development of these populations is

$$\begin{aligned}\frac{\partial X(x,t)}{\partial t}= &\quad a\left(1-q\right)X(x,t)+brY(x,t)-\Phi\left(t\right)X\left(x,t\right)\\ \frac{\partial Y(x,t)}{\partial t}= &\quad aqX(x,t)+b\left(1-r\right)Y(x,t)-\Phi\left(t\right)Y\left(x,t\right),\end{aligned} \tag{3.9}$$

where

$$\int\limits_{\mathbb{A}}X\left(x,t\right)d\mu\left(x\right)+\int\limits_{\mathbb{B}}Y\left(x,t\right)d\mu\left(x\right)=1,$$

and

$$\begin{aligned}\Phi\left(t\right)&=\int\limits_{\mathbb{A}}f\left(x\right)X\left(x,t\right)d\mu\left(x\right)+\int\limits_{\mathbb{B}}f\left(x\right)Y\left(x,t\right)d\mu\left(x\right)\\ &=a\int\limits_{\mathbb{A}}X\left(x,t\right)d\mu\left(x\right)+b\int\limits_{\mathbb{B}}Y\left(x,t\right)d\mu\left(x\right).\end{aligned}$$

We assume that r is very small, so we can assume that system (3.9) has the form

$$\begin{aligned}\frac{\partial X(x,t)}{\partial t}= &\quad a\left(1-q\right)X(x,t)-\Phi\left(t\right)X\left(x,t\right)\\ \frac{\partial Y(x,t)}{\partial t}= &\quad aqX(x,t)+bY(x,t)-\Phi\left(t\right)Y\left(x,t\right).\end{aligned} \tag{3.10}$$

By taking $Z(x,t)=\frac{X(x,t)}{Y(x,t)}$, system (3.10) becomes

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

Assuming that concentration $Z(x,t)$ achieves a steady concentration $\overline{Z}(x)$ over the time, we get

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

The original population persists, i.e. the sequences in $\mathbb{A}$ survive in a long term, if and only if $\overline{Z}(x)>0$, i.e. if and only if

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

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

$$q<s. \tag{3.11}$$

This is exactly the classical condition determining the error threshold, see e.g. [27], [30]. Then, the error threshold phenomenon occurs independently of the topology of the space of sequences.

3.3.1. *An example.* We take $(\mathbb{Y},\mu)=(\mathbb{Z}_p,dx)$ and consider the mutation measures supported in the unit ball of the form

$$Q_0\left(|x|_p;\sigma,\alpha\right)=Q_0\left(|x|_p\right)=\mathcal{N}\Omega\left(|x|_p\right)\exp(-\sigma\,|x|_p^{\alpha}), \tag{3.12}$$

where for $\sigma,\alpha>0$, and

$$\mathcal{N}\left(\sigma,\alpha\right)=\int\limits_{\mathbb{Z}_p}\exp(-\sigma\,|x|_p^{\alpha})\;dx. \tag{3.13}$$

Then, $Q_0\left(|x|_p\right)dx$ gives rise to a family of mutation measures. We now fix a sequence $0\in\mathbb{Z}_p$, which plays the role of the master sequence, and divide the space of sequences $\mathbb{Z}_p$ into two subsets: $p^M\mathbb{Z}_p$ and $\mathbb{Z}_p\smallsetminus p^M\mathbb{Z}_p$ for some positive integer M. The set $p^M\mathbb{Z}_p$ consists of the sequences in the unit ball that coincide with the sequence 0 up to the digit $M-1$. We also assume that

$$f\mid_{p^M\mathbb{Z}_p}\equiv a,\ f\mid_{\mathbb{Z}_p\smallsetminus p^M\mathbb{Z}_p}\equiv b,\text{ with } a>b.$$

The probability $q\left(\sigma,\alpha\right)$ that a sequence in the set $p^M\mathbb{Z}_p$ mutates into a sequence belonging to the set $\mathbb{Z}_p\smallsetminus p^M\mathbb{Z}_p$ satisfies

$$\begin{aligned}q\left(\sigma,\alpha\right)&=\int\limits_{p^M\mathbb{Z}_p}\;\int\limits_{\mathbb{Z}_p\smallsetminus p^M\mathbb{Z}_p}Q_0\left(|x-y|_p\right)dydx=\int\limits_{p^M\mathbb{Z}_p}\;\int\limits_{\mathbb{Z}_p\smallsetminus p^M\mathbb{Z}_p}Q_0\left(|y|_p\right)dydx\\&=p^{-M}\int\limits_{\mathbb{Z}_p\smallsetminus p^M\mathbb{Z}_p}Q_0\left(|y|_p\right)dy>p^{-M}\int\limits_{|y|_p=p^{-M+1}}Q_0\left(|y|_p\right)dy\\&=\left(1-p^{-1}\right)p^{-2M+1}\mathcal{N}\exp(-\sigma p^{(-M+1)\alpha})\geq\left(p-1\right)p^{-2M}\mathcal{N}\exp\left(-\sigma\right),\end{aligned}$$

where we used that $\exp(-\sigma p^{(-M+1)\alpha})\geq\exp\left(-\sigma\right)$ for $M\geq1$.

We analyze now wether or not the condition (3.11) is satisfied, when M is fixed. The condition M fixed can be relaxed to 'M is upper bounded.' Taking into account that $s>0$ can be arbitrarily close to zero, then there exists $M_c\geq M$ such that

$$q\left(\alpha\right)>\left(p-1\right)p^{-2M_c}\mathcal{N}\exp\left(-\sigma\right)\geq s,$$

which implies the existence of a classical error threshold:

$$M_c\leq-\frac{\ln s}{2\ln p}-\frac{\sigma}{2\ln p}+\frac{\ln\left(p-1\right)\mathcal{N}}{2\ln p}\text{ for } s\in\left(0,1\right). \tag{3.14}$$

If M can grow, the condition (3.11) is satisfied if $\left(p-1\right)p^{-2M_c}\mathcal{N}\exp\left(-\sigma\right)<q\left(\alpha\right)<s$, which implies that

$$M>-\frac{\ln s}{2\ln p}-\frac{\sigma}{2\ln p}+\frac{\ln\left(p-1\right)\mathcal{N}}{2\ln p}\text{ for } s\in\left(0,1\right).$$

Under a 'fierce competition' between the groups $p^M\mathbb{Z}_p$, $\mathbb{Z}_p\smallsetminus p^M\mathbb{Z}_p$, i.e. when rate b approaches from the left to rate a (i.e. $s\rightarrow0^+$), M must grow, which means that the survival of the sequences in the group $p^M\mathbb{Z}_p$ demands that they get closer to master sequence 0, which means, that they must increase their lengths. Then, in this model the 'classical Eigen's paradox does not occur' because the length of the genomes can grow during the evolution process.

4. The p-adic Eigen-Model in the unit ball with a radial mutation measure

In this section we show the existence of a solution for the Cauchy problem associated with (3.2)-(3.3). This goal is achieved by using the classical method of separation of variables and p-adic wavelets, several preliminary results are required.

4.1. p-adic wavelets and pseudo-differential operators.

We take $\mathbb{K}=\mathbb{C}$, $\mathbb{R}$. We denote by $C(\mathbb{Q}_p,\mathbb{K})$ the $\mathbb{K}$-vector space of continuous $\mathbb{K}$-valued functions defined on $\mathbb{Q}_p$.

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

$$\begin{array}{ccc}\mathcal{D} & \rightarrow & C(\mathbb{Q}_p,\mathbb{C})\cap L^2\\ \\ \varphi & \rightarrow & \boldsymbol{A}\varphi,\end{array}$$

where $(\boldsymbol{A}\varphi)(x)=\mathcal{F}_{\xi\rightarrow x}^{-1}\left\{\mathfrak{a}\left(|\xi|_p\right)\mathcal{F}_{x\rightarrow\xi}\varphi\right\}$.

The set of functions $\{\Psi_{rnj}\}$ defined as

$$\Psi_{rnj}(x)=p^{\frac{-r}{2}}\chi_p\left(p^{-1}j\left(p^r x-n\right)\right)\Omega\left(\left|p^r x-n\right|_p\right), \tag{4.1}$$

where $r\in\mathbb{Z}$, $j\in\{1,\cdots,p-1\}$, and n runs through a fixed set of representatives of $\mathbb{Q}_p/\mathbb{Z}_p$, is an orthonormal basis of $L^2(\mathbb{Q}_p)$ consisting of eigenvectors of operator $\boldsymbol{A}$:

$$\boldsymbol{A}\Psi_{rnj}=\mathfrak{a}(p^{1-r})\Psi_{rnj}\text{ for any }r,\,n,\,j, \tag{4.2}$$

see e.g. [18, Theorem 3.29], [1, Theorem 9.4.2]. Notice that

$$\widehat{\Psi}_{rnj}(\xi)=p^{\frac{r}{2}}\chi_p\left(p^{-r}n\xi\right)\Omega\left(\left|p^{-r}\xi+p^{-1}j\right|_p\right),$$

and then

$$\mathfrak{a}\left(|\xi|_p\right)\widehat{\Psi}_{rnj}(\xi)=\mathfrak{a}(p^{1-r})\widehat{\Psi}_{rnj}(\xi).$$

Remark 1. *From now on, we take $Q_0\left(|x|_p\right)$ to be a real-valued, non-negative, radial function supported in $\mathbb{Z}_p$ satisfying $Q_0\in L^1(\mathbb{Z}_p)\cap L^2(\mathbb{Z}_p)$, and $\|Q_0\|_1=1$. By extending Q_0 as zero out of $\mathbb{Z}_p$, we assume that $Q_0\in L^1(\mathbb{Q}_p)\cap L^2(\mathbb{Q}_p)$. The Fourier transform $\widehat{Q_0}$ of Q_0 is a real-valued, continuous function, which is radial in $\mathbb{Q}_p\smallsetminus\{0\}$, satisfying $\widehat{Q_0}(0)=1$, for this reason, we use the notation $\widehat{Q}_0\left(|\xi|_p\right)$.*

We now define

$$\boldsymbol{B}\varphi=Q_0*\varphi\text{ for }\varphi\in\mathcal{D}(\mathbb{Z}_p).$$

Notice that the support of $Q_0*\varphi$ is $\mathbb{Z}_p$ since it is an additive group. Since $\boldsymbol{B}\varphi(x)=\mathcal{F}_{\xi\rightarrow x}^{-1}(\widehat{Q_0}\left(|\xi|_p\right)\mathcal{F}_{x\rightarrow\xi}\varphi)$, we have

$$\boldsymbol{B}\Psi_{rnj}(x)=\widehat{Q_0}\left(p^{1-r}\right)\Psi_{rnj}(x), \tag{4.3}$$

where $\widehat{Q_0}\left(p^{1-r}\right)$ is a real number satisfying $\left|\widehat{Q}_0\left(p^{1-r}\right)\right|\leq 1$, and $\Psi_{rnj}(x)$ is supported in the unit ball.

4.2. **p-adic wavelets supported in balls.** Notice that the restriction of $\Psi_{rnj}(x)$ to the ball $I+p^{R_0}\mathbb{Z}_p$ has the form

$$\Omega\left(p^{R_0}|x-I|_p\right)\Psi_{rnj}(x)= \tag{4.4}$$
$$\begin{cases}\Psi_{rnj}(x) & \text{if } np^{-r}-I\in p^{R_0}\mathbb{Z}_p,\ r\leq -R_0\\ p^{\frac{-r}{2}}\Omega\left(p^{R_0}|x-I|_p\right) & \text{if } np^{-r}-I\in p^{-r}\mathbb{Z}_p,\ r\geq -R_0+1\\ 0 & \text{if } np^{-r}-I\notin p^{-r}\mathbb{Z}_p,\ r\geq -R_0+1.\end{cases}$$

Remark 2. *With the above notation,*

$$\left\{\Psi_{rnj}(x)\,;\textit{supp }\Psi_{rnj}(x)\subseteq I+p^{R_0}\mathbb{Z}_p\right\}=$$
$$\left\{\Psi_{rnj}(x+I)\,;\textit{supp }\Psi_{rnj}(x)\subseteq p^{R_0}\mathbb{Z}_p\right\}.$$

This observation is a very particular case of a general result asserting that the basis (4.1) is the orbit under a group of matrices of a mother wavelet, see [2, Theorem 9].

Proposition 1. *The set of functions*

$$\left\{\Omega\left(p^{R_0}|x|_p\right)\right\}\bigcup\bigcup_{j\in\{1,\dots,p-1\}}\ \bigcup_{r\leq -R_0}\ \bigcup_{\substack{np^{-r}\in p^{R_0}\mathbb{Z}_p\\ n\in\mathbb{Q}_p/\mathbb{Z}_p}}\{\Psi_{rnj}(x)\} \tag{4.5}$$

is an orthonormal basis of $L^2\left(p^{R_0}\mathbb{Z}_p\right)$.

Proof. In the demonstration we use the following results:

Lemma A (see e.g. [1, Lemma 2.3.3]). Consider the compact additive group $\left(p^{R_0}\mathbb{Z}_p,+\right)$. Then any nontrivial continuous additive character $\chi: p^{R_0}\mathbb{Z}_p\to S$ has the form $\chi(x)=\chi_p\left(p^{-l}x\right)$ for some positive integer $l\geq R_0$.

Lemma B (see e.g. [13, Proposition 7.2.2]) Consider the pre-Hilbert space $\left(\mathcal{D}(p^{R_0}\mathbb{Z}_p),\langle\cdot,\cdot\rangle\right)$, where $\langle\cdot,\cdot\rangle$ denotes the standard inner product in $L^2(p^{R_0}\mathbb{Z}_p)$. Let $\Gamma\left(p^{R_0}\mathbb{Z}_p\right)$ be the group of continuous characters of $\left(p^{R_0}\mathbb{Z}_p,+\right)$. Then $\Gamma\left(p^{R_0}\mathbb{Z}_p\right)$ forms an orthonormal basis of $\mathcal{D}(p^{R_0}\mathbb{Z}_p)$. More precisely, every $\varphi\in\mathcal{D}(p^{R_0}\mathbb{Z}_p)$ can be expressed as a finite sum of the form

$$\varphi(x)=\sum_{\chi\in\Gamma\left(p^{R_0}\mathbb{Z}_p\right)}c_\chi\chi(x)\,,\text{ where } c_\chi=\langle\varphi,\chi\rangle\,.$$

We identify a character $\chi\in\Gamma\left(p^{R_0}\mathbb{Z}_p\right)$ with the function $\Omega\left(p^{R_0}|x|_p\right)\chi\in L^2(p^{R_0}\mathbb{Z}_p)$. We denote by $Span\left(\Gamma\left(p^{R_0}\mathbb{Z}_p\right)\right)$ the $\mathbb{C}$-vector space generated by the elements of $\Gamma\left(p^{R_0}\mathbb{Z}_p\right)$. We first show that $\Gamma\left(p^{R_0}\mathbb{Z}_p\right)$ is an orthonormal basis of $L^2(p^{R_0}\mathbb{Z}_p)$, i.e. that

$$\overline{Span\left(\Gamma\left(p^{R_0}\mathbb{Z}_p\right)\right)}=L^2(p^{R_0}\mathbb{Z}_p), \tag{4.6}$$

where the bar means the topological closure with respect to $\|\cdot\|_2$. Given any $f\in L^2(p^{R_0}\mathbb{Z}_p)$ and any $\epsilon>0$, by using the fact that $\mathcal{D}(p^{R_0}\mathbb{Z}_p)$ is dense in $L^2(p^{R_0}\mathbb{Z}_p)$ see e.g. [1, Proposition 4.3.3], there is $\varphi\in\mathcal{D}(p^{R_0}\mathbb{Z}_p)$ such that $\|f-\varphi\|_2<\epsilon$. Now by using Lemma B, $\varphi(x)=\sum_{\chi\in\Gamma\left(p^{R_0}\mathbb{Z}_p\right)} c_\chi\chi(x)$,

$$\left\Vert f-\sum_{\chi\in\Gamma\left(p^{R_0}\mathbb{Z}_p\right)} c_\chi\chi(x)\right\Vert_2<\epsilon \text{ with } \sum_{\chi\in\Gamma\left(p^{R_0}\mathbb{Z}_p\right)} c_\chi\chi(x)\in Span\left(\Gamma\left(p^{R_0}\mathbb{Z}_p\right)\right),$$

which implies (4.6).

Finally, to show that (4.5) is an orthonormal basis of $L^2\left(p^{R_0}\mathbb{Z}_p\right)$, by Lemma A, it is sufficient to show that each $\chi\in\Gamma\left(p^{R_0}\mathbb{Z}_p\right)$ can be represented as a linear combination of elements of the set (4.5). Since the trivial character is exactly $\Omega\left(p^{R_0}\left|x\right|_p\right)$, it is sufficient to show that a character $\Omega\left(p^{R_0}\left|x\right|_p\right)\chi\left(p^{-l}x\right)$, $l\geq R_0+1$, is a linear combinations of wavelets of the form Ψ_{rnj}, with $np^{-r}\in p^{R_0}\mathbb{Z}_p$, $r\leq -R_0$. Since $\Omega\left(p^{R_0}\left|x\right|_p\right)\chi\left(p^{-l}x\right)\in L^2(\mathbb{Q}_p)$, we may compute the Fourier series with respect to the orthonormal basis $\left\{\Psi_{rnj}\right\}_{rnj}$. By using Table 4.4 and the fact that $\int_{p^{R_0}\mathbb{Z}_p}\chi\left(p^{-l}x\right)dx=0$, for $l\geq R_0+1$, we conclude that the non-zero Fourier coefficients C_{rnj} are given by

$$C_{rnj}=$$

$$p^{\frac{-r}{2}}\int\limits_{p^{R_0}\mathbb{Z}_p}\overline{\chi\left(p^{-l}x\right)}\chi_p\left(p^{-1}j\left(p^rx-n\right)\right)\Omega\left(\left|p^rx-n\right|_p\right)dx,$$

for $np^{-r}\in p^{R_0}\mathbb{Z}_p$, $r\leq -R_0$, i.e.

$$\begin{aligned}
C_{rnj} &= \\
& p^{\frac{-r}{2}}\chi_p\left(-p^{-1}jn\right)\int\limits_{p^{-r}n+p^{-r}\mathbb{Z}_p}\chi_p\left(x\left(p^{r-1}j-p^{-l}\right)\right)dx \\
&= p^{\frac{r}{2}}\chi_p\left(-p^{-r-l}n\right)\int\limits_{\mathbb{Z}_p}\chi_p\left(z\left(p^{-1}j-p^{-r-l}\right)\right)dy \quad (\text{taking } x=p^{-r}n+p^{-r}z) \\
&= p^{\frac{r}{2}}\chi_p\left(-p^{-r-l}n\right)\int\limits_{\mathbb{Z}_p}\chi_p\left(z\left(p^{-1}j\right)\right)dy \text{ if } -r\geq l \\
&= 0 \text{ if } -r\geq l.
\end{aligned}$$

Which implies that $\Omega\left(p^{R_0}\left|x\right|_p\right)\chi\left(p^{-l}x\right)$, $l\geq R_0+1$, is a linear combinations of wavelets of the form Ψ_{rnj}, with $np^{-r}\in p^{R_0}\mathbb{Z}_p$, $r\leq -R_0$. □

Remark 3. *Let $I\in\mathbb{Q}_p\smallsetminus p^{R_0}\mathbb{Z}_p$. By using the isometry*

$$\begin{array}{ccc} L^2(I+p^{R_0}\mathbb{Z}_p) & \rightarrow & L^2(p^{R_0}\mathbb{Z}_p) \\ f(x) & \rightarrow & f(x+I), \end{array}$$

we have that any $f\in L^2(I+p^{R_0}\mathbb{Z}_p)$ admits a Fourier expansion of the form

$$f(x)=C_0\Omega\left(p^{R_0}\left|x-I\right|_p\right)+\sum_{rnj}C_{rnj}\Psi_{rnj}\left(x-I\right),$$

where $x \in I + p^{R_0}\mathbb{Z}_p$, $j \in \{1, \ldots, p-1\}$, $n \in \mathbb{Q}_p/\mathbb{Z}_p$, $r \leq -R_0$, $np^{-r} \in p^{R_0}\mathbb{Z}_p$. *By Remark 2,*

$$f(x) = C_0\Omega\left(p^{R_0}|x - I|_p\right) + \sum_{rnj,\ supp\Psi_{rnj}(x)\subseteq I+p^{R_0}\mathbb{Z}_p} C_{rnj}\Psi_{rnj}(x),$$

for $x \in I + p^{R_0}\mathbb{Z}_p$. *We now set*

$$L_0^2(I, R_0) = \left\{ f \in L^2(I + p^{R_0}\mathbb{Z}_p); \int_{I+p^{R_0}\mathbb{Z}_p} f\ dx = 0 \right\}.$$

In conclusion, we have the following result:

Proposition 2. *The space* $L^2(I + p^{R_0}\mathbb{Z}_p)$ *satisfies*

$$L^2(I + p^{R_0}\mathbb{Z}_p) = \mathbb{C}\Omega\left(p^{R_0}|x - I|_p\right) \bigoplus L_0^2(I, R_0)$$

and

$$L^2(I + p^{R_0}\mathbb{Z}_p) = \bigoplus_{j\in\{1,\ldots,p-1\}} \bigoplus_{r\leq -R_0} \bigoplus_{\substack{n\in\mathbb{Q}_p/\mathbb{Z}_p \\ np^{-r}\in p^{R_0}\mathbb{Z}_p}} \overline{Span\left(\Psi_{rnj}(x - I)\right)}$$

$$= \bigoplus_{rnj,\ supp\Psi_{rnj}(x)\subseteq I+p^{R_0}\mathbb{Z}_p} \overline{Span\left(\Psi_{rnj}(x)\right)}. \tag{4.7}$$

The construction of orthonormal basis for $L^2(\mathbb{Z}_p)$ has been widely considered in the literature, see e.g. [6, Theorem 4], [16, Theore 1, Proposition 1, 2] and the references therein. However, we have not specifically found Proposition 2 in the literature.

4.3. The operator $\boldsymbol{W}_0$.

From now on, we assume that the fitness function f is a non-negative test function supported in $\mathbb{Z}_p$, independent of the time, of the form

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

where M is fixed positive integer, $G_M = \mathbb{Z}_p/p^M\mathbb{Z}_p$, and with $f(I) > 0$ for $I \in G_M$. For $\varphi \in L^2(\mathbb{Z}_p)$, we define the operator

$$\boldsymbol{W}_0\varphi(x) = Q_0\left(|x|_p\right) * (f(x)\varphi(x)).$$

Then $\boldsymbol{W}_0 : L^2(\mathbb{Z}_p) \to L^2(\mathbb{Z}_p)$ is a linear bounded operator.

We set $\mathcal{D}_M$ for the $\mathbb{R}$-vector space generated by $\left\{\Omega\left(p^M\left|x-I\right|_p\right)\right\}_{I\in G_M}$ as before. The space $\mathcal{D}_M$ is invariant under $\boldsymbol{W}_0$. Indeed,

$$\begin{aligned}\boldsymbol{W}_0\Omega\left(p^M\left|x-I\right|_p\right) &= f(I)\int\limits_{I+p^M\mathbb{Z}_p} Q_0\left(\left|x-y\right|_p\right)dy = f(I)\int\limits_{x-I+p^M\mathbb{Z}_p} Q_0\left(\left|z\right|_p\right)dz \\ &= \begin{cases} f(I)\int\limits_{p^M\mathbb{Z}_p} Q_0\left(\left|z\right|_p\right)dz & \text{if} \quad x\in I+p^M\mathbb{Z}_p \\ \\ f(I)Q_0\left(\left|J-I\right|_p\right)p^{-M} & \text{if} \quad x\in J+p^M\mathbb{Z}_p,\ I\neq J,\end{cases}\end{aligned}$$

and thus

$$\begin{aligned}\boldsymbol{W}_0\Omega\left(p^M\left|x-I\right|_p\right) = &\sum_{\substack{J\in G_M\\ J\neq I}} Q_0\left(\left|J-I\right|_p\right)p^{-M}\Omega\left(p^M\left|x-J\right|_p\right) \\ &+\left(\int\limits_{p^M\mathbb{Z}_p} Q_0\left(\left|z\right|_p\right)dz\right)\Omega\left(p^M\left|x-I\right|_p\right).\end{aligned}$$

We set $\varphi_I(x) := \Omega\left(p^M\left|x-I\right|_p\right)$, and denote by $\left[\varphi_I\right]_{I\in G_M}$, a column vector, then on $\mathcal{D}_M$ operator $\boldsymbol{W}_0$ is represented by the matrix $\mathbb{W}^0 := \left[\mathbb{W}^0_{I,J}\right]_{I,J\in G_M}$, with

$$\mathbb{W}^0_{I,J} = \begin{cases} f(I)\int\limits_{p^M\mathbb{Z}_p} Q_0\left(\left|z\right|_p\right)dz & \text{if} \quad I=J \\ \\ f(I)Q_0\left(\left|J-I\right|_p\right)p^{-M} & \quad I\neq J,\end{cases} \tag{4.8}$$

Now the space $L^2_0(I,M)$, see (4.7), is invariant under $\boldsymbol{W}_0$ since $\boldsymbol{W}_0\Psi_{rnj}(x) = \widehat{Q_0}\left(p^{1-r}\right)\Psi_{rnj}(x)$ for $\Psi_{rnj}(x)\in L^2_0(I,M)$. We now attach to $\boldsymbol{W}_0$ the real vector space

$$L\left(\boldsymbol{W}_0\right) := \mathcal{D}_M\bigoplus\bigoplus_{I\in G_M}\left\{L^2_0(I,M)\cap L^2_{\mathbb{R}}(I+p^M\mathbb{Z}_p)\right\}.$$

Lemma 1. *The space $L\left(\boldsymbol{W}_0\right)$ is invariant under operator $\boldsymbol{W}_0$, i.e. $\boldsymbol{W}_0\left(L\left(\boldsymbol{W}_0\right)\right)\subset L\left(\boldsymbol{W}_0\right)$, and $\boldsymbol{W}_0\left(L^2_{\mathbb{R}}(\mathbb{Z}_p)\right)\subset L\left(\boldsymbol{W}_0\right)$.*

4.4. **The Cauchy problem for operator $\boldsymbol{W}_0$.** We now consider the following initial value problem:

$$\begin{cases} Y:\mathbb{Q}_p\times\mathbb{R}_+\to\mathbb{R}, & \begin{array}{l}Y(\cdot,t)\in L\left(\boldsymbol{W}_0\right)\cap L^2_{\mathbb{R}}(\mathbb{Z}_p),\\ Y(x,\cdot)\in C^1\left(\mathbb{R}_+,\mathbb{R}\right)\end{array} \\ \\ \frac{dY(x,t)}{dt} = \boldsymbol{W}_0 Y(x,t), & x\in\mathbb{Q}_p, t>0 \\ \\ Y(x,0) = Y_0(x)\in L\left(\boldsymbol{W}_0\right)\cap L^2_{\mathbb{R}}(\mathbb{Z}_p). & \end{cases} \tag{4.9}$$

We solve (4.9) by using the separation of variables method. We first look for a complex-valued solution of (4.9) of the form

$$\widetilde{Y}(x,t)=\sum_{I\in G_M}C_I^0(t)\varphi_I(x)+\sum_{I\in G_M}\sum_{\mathrm{supp}\Psi_{rnj}\subseteq I+p^M\mathbb{Z}_p}C_{rjn}^I(t)\,\Psi_{rnj}(x),$$

where $C_{rjn}^I(t)$ are complex-valued functions, which admit continuous temporal derivatives. By replacing

$$\frac{d}{dt}\widetilde{Y}(x,t)=\sum_{I\in G_M}\left(\frac{d}{dt}C_I^0(t)\right)\varphi_I(x)+\sum_{I\in G_M}\sum_{\mathrm{supp}\Psi_{rnj}\subseteq I+p^M\mathbb{Z}_p}\left(\frac{d}{dt}C_{rjn}^I(t)\right)\Psi_{rnj}(x),$$

and

$$\boldsymbol{W}_0\widetilde{Y}(x,t)=\boldsymbol{W}_0\left(\sum_{I\in G_M}C_I^0(t)\varphi_I(x)\right)+\sum_{I\in G_M}\sum_{\mathrm{supp}\Psi_{rnj}\subseteq I+p^M\mathbb{Z}_p}\widehat{Q_0}\left(p^{1-r}\right)f(I)C_{rjn}^I(t)\,\Psi_{rnj}(x),$$

in (4.9), we get the following systems of differential equations:

$$\frac{d}{dt}C_{rjn}^I(t)=\widehat{Q_0}\left(p^{1-r}\right)f(I)C_{rjn}^I(t)\ \text{ for } I\in G_M,$$

$$\frac{d}{dt}\left[C_I^0(t)\right]_{I\in G_M}=\mathbb{W}^0\left[C_I^0(t)\right]_{I\in G_M}.$$

Therefore

$$\widetilde{Y}(x,t)=\left(e^{t\mathbb{W}^0}\left[C_I^0(0)\right]_{I\in G_M}\right)\left[\varphi_I(x)\right]_{I\in G_M}^T+\sum_{I\in G_M}\sum_{\mathrm{supp}\Psi_{rnj}\subseteq I+p^M\mathbb{Z}_p}e^{t\widehat{Q_0}\left(p^{1-r}\right)f(I)}C_{rjn}^I(0)\,\Psi_{rnj}(x),$$

where $\left[\varphi_I(x)\right]_{I\in G_M}^T$ denotes the transpose of the column vector $\left[\varphi_I(x)\right]_{I\in G_M}$. Notice that

$$\sum_{I\in G_M}\sum_{\mathrm{supp}\Psi_{rnj}\subseteq I+p^M\mathbb{Z}_p}e^{t\widehat{Q_0}\left(p^{1-r}\right)f(I)}C_{rjn}^I(0)\,\Psi_{rnj}(x)\in\bigoplus_{I\in G_M}L_0^2\left(I+p^M\mathbb{Z}_p\right). \tag{4.10}$$

The constants $C_I^0(0)$, $C_{rjn}^I(0)$ are determined by the Fourier expansion of the initial datum $Y_0(x)$, which is a real-valued function. Then $C_I^0(0)\in\mathbb{R}$ for any I, and $C_{rjn}^I(0)\in\mathbb{C}$ for any I, rjn, and

$$Y(x,t)=\mathrm{Re}\left(\widetilde{Y}(x,t)\right)=\left(e^{t\mathbb{W}^0}\left[C_I^0(0)\right]_{I\in G_M}\right)\left[\varphi_I(x)\right]_{I\in G_M}^T+\sum_{I\in G_M}\sum_{\mathrm{supp}\Psi_{rnj}\subseteq I+p^M\mathbb{Z}_p}e^{t\widehat{Q_0}\left(p^{1-r}\right)f(I)}\,\mathrm{Re}\left\{C_{rjn}^I(0)\,\Psi_{rnj}(x)\right\},$$

and due to (4.10),

$$\overline{Y(t)} := \int_{\mathbb{Z}_p} Y(x,t)\,dx = \int_{\mathbb{Z}_p} \left(e^{t\mathbb{W}^0} \left[C_I^0(0) \right]_{I\in G_M} \right) \left[\varphi_I(x) \right]_{I\in G_M}^T dx \tag{4.11}$$
$$= p^{-M} \left(e^{t\mathbb{W}^0} \left[C_I^0(0) \right]_{I\in G_M} \right) \mathbf{1}^T,$$

where $\mathbf{1}^T = [1,1,\ldots,1,1]$.

4.5. **The Cauchy problem for the p-adic Eigen-Schuster equation in the unit ball.** We assume that the fitness function and the mutation measure are supported in the unit ball and that they are time independent. We now consider the p-adic Eigen-Schuster equation in the unit ball:

$$\frac{\partial X(x,t)}{\partial t} = \boldsymbol{W}_0 X(x,t) - \Phi(t)\, X(x,t),\; x\in\mathbb{Z}_p,\; t\in\mathbb{R}_+, \tag{4.12}$$

where

$$\Phi(t,X) := \Phi(t) = \int_{\mathbb{Z}_p} f(y)\, X(y,t)\,dy \quad \text{for } t\geq 0.$$

By changing variables as

$$X(x,t) = Y(x,t)\exp\left(-\int_0^t \Phi(\tau)\,d\tau \right)$$
$$= \frac{Y(x,t)}{\int_{\mathbb{Z}_p} Y(x,t)\,dx} =: \frac{Y(x,t)}{\overline{Y(t)}}$$

(4.12) becomes

$$\frac{\partial Y(x,t)}{\partial t} = \boldsymbol{W}_0 Y(x,t),\;,\; x\in\mathbb{Z}_p,\; t\in\mathbb{R}_+.$$

Therefore

$$X(x,t) = \frac{\left(e^{t\mathbb{W}^0} \left[C_I^0(0) \right]_{I\in G_M} \right) \left[\varphi_I(x) \right]_{I\in G_M}^T}{\overline{Y(t)}} \tag{4.13}$$
$$+ \sum_{I\in G_M} \sum_{\operatorname{supp}\Psi_{rnj}\subseteq I+p^M\mathbb{Z}_p} \frac{e^{t\widehat{Q_0}\left(p^{1-r}\right)f(I)}}{\overline{Y(t)}} \operatorname{Re}\left(C_{rjn}^I(0)\,\Psi_{rnj}(x) \right),$$

where $\overline{Y(t)}$ is given in (4.11) and

$$\operatorname{Re}\left(C_{rjn}^I(0)\,\Psi_{rnj}(x) \right) = p^{\frac{-r}{2}} \operatorname{Re}\left(C_{rjn}^I(0) \right) \cos\left(p^{r-1}jx \right) \Omega\left(\left| p^r x - n \right|_p \right)$$
$$- p^{\frac{-r}{2}} \operatorname{Im}\left(C_{rjn}^I(0) \right) \sin\left(p^{r-1}jx \right) \Omega\left(\left| p^r x - n \right|_p \right).$$

We now assume that $X_0(x) := X(x,0)$ is a real-valued function supported in the unit ball of the form

$$X_0(x) = \sum_{I\in G_M} X_0(I)\Omega\left(p^M \left| x - I \right|_p \right), \tag{4.14}$$

with $G_M = \mathbb{Z}_p / p^M \mathbb{Z}_p$ as before and with $X_0(I) > 0$ for $I \in G_M$. Since

$$\int_{I+p^M\mathbb{Z}_p} \Psi_{rnj}(x) = 0$$

for any $\Psi_{rnj}(x)$ with support contained in $I + p^M\mathbb{Z}_p$, we get that $C^I_{rjn}(0) = 0$ for any I, rnj, in (4.13).

Theorem 1. *The Cauchy problem (4.9) admits a solution $X(x,t)$ of the form (4.13). Furthermore, if the initial datum has the form (4.14), then*

$$X(x,t) = \frac{\left(e^{t\mathbb{W}^0}\left[C^0_I(0)\right]_{I\in G_M}\right)\left[\varphi_I(x)\right]^T_{I\in G_M}}{\overline{Y(t)}}.$$

Which is a classical solution of the Eigen-Schuster model.

Since $\varphi_I(x) = \Omega\left(p^M |x-I|_p\right)$, then the concentration $X(x,t)$ depends only on the M first p-adic digits of x, and thus in this model the length of the sequences do not change in time.

5. The p-adic quasispecies in the unit ball

Since $\mathbb{W}^0$ is a real symmetric matrix, it is diagonalizable and all its eigenvalues are real. Let $\lambda_{\max}$ be the largest eigenvalue of $\mathbb{W}^0$. Then

$$\lim_{t\to\infty} X(x,t) = \lim_{t\to\infty} \frac{\left(e^{t\mathbb{W}^0}\left[C^0_I(0)\right]_{I\in G_M}\right)\left[\varphi_I(x)\right]^T_{I\in G_M}}{\overline{Y(t)}} =$$

$$\lim_{t\to\infty} \frac{e^{t\lambda_{\max}}\sum_I p_I(t)\,\varphi_I(x)}{e^{t\lambda_{\max}}\sum_I p_I(t)} = \sum_{j=1}^{M'} c_j \varphi_{I_j}(x),$$

where the $p_I(t)$s are polynomials in t and the c_js are positive constants. This situation corresponds to *the survival of the fitter*. This is the typical scenario predicted by the classical Eigen-Schuster equation. In this context the Eigen paradox happens naturally. Thus, to get a different asymptotic behavior of solution (4.13), some of the oscillatory terms must be preserved in the long term. If the oscillatory terms in (4.13) do not vanish in the long term, then there are sequences (with arbitrary length) spread out throughout the unit ball. This means that the Eigen paradox does not occur since in the long term there are sequences of infinite length.

Definition 1. *We say that a solution of the Cauchy problem (4.9) admits a quasispecies solution if there exist a solution $X(x,t)$ of the form (4.13) satisfying that $\int_{\mathbb{Q}_p} X(y,t)\,dy = 1$ for $t > 0$, and that the set*

$$\left\{(I, rnj);\ \lim_{t\to\infty} \frac{p^{\frac{-r}{2}}\ e^{t\widehat{Q_0}\left(p^{1-r}\right)f(I)}}{\overline{Y(t)}} \neq 0 \text{ when } C^I_{rjn}(0) \neq 0\right\}$$

is non-empty.

5.1. **Some results about semigroups of matrices.** In order to establish the existence of the p-adic quasispecies we need several preliminary results.

5.1.1. *Diagonally dominant matrices.* A real matrix $B=[B_{ij}]_{i,j\in I}$, $I=\{1,\ldots,n\}$, is said to be *diagonally dominant*, if

$$|B_{ii}|\geq\sum_{j\neq i}|B_{ij}|\quad\text{for any } i\in I.$$

It is *strictly diagonally dominant* if

$$|B_{ii}|>\sum_{j\neq i}|B_{ij}|\quad\text{for any } i\in I.$$

Let $B=[B_{ij}]_{i,j\in I}$ be a strictly diagonally dominant. Then (i) B is non singular; (ii) if $B_{ii}>0$ for all $i\in I$, then every eigenvalue of B has a positive real part; (iii) if B is symmetric and $B_{ii}>0$ for all $i\in I$, then B is positive definite, see [12, Theorem 6.1.10].

We now apply this result to the matrix $\mathbb{W}^0=\left[\mathbb{W}^0_{I,J}\right]_{I,J\in G_M}$, see (4.8). Since

$$\int_{\mathbb{Z}_p}Q_0\left(|z|_p\right)dz=\int_{p^M\mathbb{Z}_p}Q_0\left(|z|_p\right)dz+p^{-M}\sum_{J\neq I}Q_0\left(|J-I|_p\right)=1,$$

we have

$$\mathbb{W}^0_{I,I}+\sum_{J\neq I}\mathbb{W}^0_{I,J}=f(I).$$

We now introduce the hypothesis:

$$\text{(Hypothesis A)}\qquad \int_{p^M\mathbb{Z}_p}Q_0\left(|z|_p\right)dz\in\left(\frac{1}{2},1\right).$$

Under the hypothesis A, $\mathbb{W}^0_{I,I}>\frac{f(I)}{2}$, which implies that $\mathbb{W}^0$ is a strictly diagonally dominant matrix. Then, we have the following result:

Lemma 2. *Under the Hypothesis A, the symmetric matrix* $\mathbb{W}^0$ *is a strictly diagonally dominant, nonsingular, and all its eigenvalues are positive.*

5.1.2. *Semigroups of matrices.* Let $\{\mu_I\}_{I\in G_M}$ be the positive eigenvalues of $\mathbb{W}^0$ repeated according their multiplicity. We set

$$\mu_{\max}:=\max_{I\in G_M}\mu_I>0.$$

Then $\mathbb{W}^0=\mathbb{S}+\mathbb{O}$, where

$$\mathbb{P}^{-1}\mathbb{S}\mathbb{P}=diag\left[\mu_I\right]_{I\in G_M},$$

for some inversible matrix $\mathbb{P}$, and $\mathbb{O}$ a nilpotent matrix of order $k\leq\#G_M$, and

$$\boldsymbol{z}(t)=\mathbb{P}\left(diag\left[\mu_I\right]_{I\in G_M}\right)\mathbb{P}^{-1}\left\{\mathbb{I}+\mathbb{O}t+\cdots+\frac{\mathbb{O}^{k-1}t^{k-1}}{(k-1)!}\right\}\boldsymbol{z}_0$$

is the solution $\frac{d}{dt}\boldsymbol{z}(t)=\mathbb{W}^0\boldsymbol{z}(t)$, $\boldsymbol{z}(0)=\boldsymbol{z}_0$, see e.g. [24, Theorem 1, Corollary 1]. By applying this result to $\overline{Y\left(t\right)}$, see (4.11), we have the following result:

Lemma 3. $\overline{Y\left(t\right)}\leq Ct^{k-1}e^{\mu_{\max}t}$ *for* $t>0$.

5.2. **p-Adic quasispecies.** We now introduce the hypothesis:

(Hypothesis B) $$\widehat{Q_0}\left(p^{1-r_0}\right) f(I_0) > \mu_{\max},$$

for some negative integer r_0 and $I_0 \in G_M$. Which means that operator $\boldsymbol{W}_0$ has a positive eigenvalue greater than $\frac{\mu_{\max}}{f(I_0)}$.

Under the Hypotheses A and B, by Lemma 3, we have

$$\lim_{t\to\infty} \frac{p^{\frac{-r_0}{2}}\ e^{t\widehat{Q_0}\left(p^{1-r_0}\right)f(I_0)}}{\overline{Y(t)}}$$
$$\geq \frac{p^{\frac{-r_0}{2}}}{C} \lim_{t\to\infty} t^{-k+1} e^{t\left\{\widehat{Q_0}\left(p^{1-r_0}\right)f(I_0)-\mu_{\max}\right\}} = \infty,$$

if $C_{r_0jn}^{I_0}(0) \neq 0$ for some $n \in \mathbb{Q}_p/\mathbb{Z}_p$ satisfying $np^{-r_0} \in \mathbb{Z}_p$, see Table 4.4.

By (4.13), the initial condition $X(x,0)$ is completely determined by a sequence from the set

$$\mathcal{S} := \left\{\left[C_I^0(0)\right]_{I\in G_M} \in \mathbb{R}^{\#G_M}; C_I^0(0) \neq 0 \text{ for some } I \in G_M\right\} \bigsqcup$$
$$\bigsqcup_{I\in G_M} \left\{C_{rjn}^{I}(0) \in \mathbb{C}; r \leq 0, j \in \{1,\ldots,p-1\}, n \in \mathbb{Q}_p/\mathbb{Z}_p \text{ with } np^{-r} \in \mathbb{Z}_p\right\}.$$

We use the notation $X(x,0) \in \mathcal{S}$ to mean that $X(x,0)$ is determined by a sequence from $\mathcal{S}$. Notice that condition $C_I^0(0) \neq 0$ for some $I \in G_M$ is needed to guarantee that $\int X(x,0)dx = 1$. Take I_0, r_0 such that Hypothesis B is satisfied, the condition $C_{r_0jn}^{I_0}(0) \neq 0$ defines a a subset $\mathcal{S}_0$ of $\mathcal{S}$.

Theorem 2. *Under the Hypothesis A, B, and assuming that $X(x,0) \in \mathcal{S}_0$, then the Cauchy problem (4.9) admits a quasispecies solution.*

5.3. **A family of Gibbs-type mutation measures.** In this section we present an infinite family of mutation measures supported in the unit ball satisfying the Hypotheses A and B. More precisely,

$$Q_0\left(|x|_p; \sigma, \alpha\right) := Q_0\left(|x|_p\right) = \mathcal{N}\Omega\left(|x|_p\right)\exp(-\sigma|x|_p^{\alpha}), \tag{5.1}$$

where $\sigma, \alpha > 0$, $\mathcal{N} = \int_{\mathbb{Z}_p}\exp(-\sigma|x|_p^{\alpha})dx$, and $\Omega\left(|x|_p\right)$ is the characteristic function of the unit ball. Notice that $Q_0\left(|x|_p\right)$ is integrable. We set

$$Z(\xi;\sigma,\alpha) := \int_{\mathbb{Q}_p} \chi_p(\xi x)\exp(-\sigma|x|_p^{\alpha})dx,$$

for $\sigma, \alpha > 0$. This is the p-adic heat kernel widely studied in connection with the p-adic heat equation, see e.g. [15], [18], [34], [36] The heat kernel $Z(\xi;\sigma,\alpha)$ is non-negative, continuous function in ξ for any $\sigma, \alpha > 0$, see e.g. [36, Theorem 13]. Furthermore, there exist positive constants C_1, C_0 such that

$$\frac{C_1\sigma}{\left(|\xi|_p + \sigma^{\frac{1}{\alpha}}\right)^{1+\alpha}} \leq Z(\xi;\sigma,\alpha) \leq \frac{C_0\sigma}{\left(|\xi|_p + \sigma^{\frac{1}{\alpha}}\right)^{1+\alpha}}, \tag{5.2}$$

for $\sigma, \alpha > 0$, and $\xi \in \mathbb{Q}_p$. The upper bound was established in [15, Lemma 4.1], see also [36, Theorem 32]. The lower bound was established in [5, Theorem 5.17]. In particular, $Z(\cdot;\sigma,\alpha) \in L^1$.

Now,

$$\mathcal{F}_{x\to\xi}(Q_0\left(|x|_p;\sigma,\alpha\right)) = \mathcal{N}\mathcal{F}_{x\to\xi}\left(\exp(-\sigma\,|x|_p^{\alpha})\ \Omega\left(|x|_p\right)\right) = \mathcal{N}Z(\xi;\sigma,\alpha)*\Omega\left(|\xi|_p\right)$$
$$= \mathcal{N}\int_{\mathbb{Q}_p} Z(\xi-y;\sigma,\alpha)\Omega\left(|y|_p\right)dy,$$

and by using the lower bound in (5.2), and the ultrametric property of $|\cdot|$, and assuming that $|\xi|_p > 1$,

$$\mathcal{F}_{x\to\xi}(Q_0\left(|x|_p;\sigma,\alpha\right)) \geq \mathcal{N}C_1\sigma\int_{\mathbb{Q}_p}\frac{\Omega\left(|y|_p\right)dy}{\left(|\xi-y|_p+\sigma^{\frac{1}{\alpha}}\right)^{1+\alpha}}$$
$$\geq \mathcal{N}C_1\sigma\int_{\substack{y\in\mathbb{Z}_p\\ |\xi|_p>|y|_p}}\frac{\Omega\left(|y|_p\right)dy}{\left(|\xi-y|_p+\sigma^{\frac{1}{\alpha}}\right)^{1+\alpha}} = \mathcal{N}C_1\sigma\int_{\substack{y\in\mathbb{Z}_p\\ |\xi|_p>|y|_p}}\frac{\Omega\left(|y|_p\right)dy}{\left(|\xi|_p+\sigma^{\frac{1}{\alpha}}\right)^{1+\alpha}}$$
$$= \frac{\mathcal{N}C_1\sigma}{\left(|\xi|_p+\sigma^{\frac{1}{\alpha}}\right)^{1+\alpha}}\int_{y\in\mathbb{Z}_p}dy = \frac{\mathcal{N}C_1\sigma}{\left(|\xi|_p+\sigma^{\frac{1}{\alpha}}\right)^{1+\alpha}} \text{ for } |\xi|_p > 1.$$

Then, we have the following result:

Lemma 4. *Take $\sigma,\alpha>0$ as before. Then*

$$\mathcal{F}_{x\to\xi}(Q_0\left(|x|_p;\sigma,\alpha\right)) \geq \frac{\mathcal{N}C_1\sigma}{\left(|\xi|_p+\sigma^{\frac{1}{\alpha}}\right)^{1+\alpha}} \textit{ for } |\xi|_p > 1.$$

On the other hand, since $\left(\mathbb{Q}_p, |\cdot|_p\right)$ is a Polish space, a complete, separable metric space, every probability measure is tight, see e.g. [20, Proposition 1.3.24], which implies that given $\epsilon>0$, there exists a compact subset $K_\epsilon\subset\mathbb{Z}_p$ such that $\int_{K_\epsilon}Q_0\left(|x|_p\right)dx > 1-\epsilon$. Now since K_ϵ is bounded, there exists a non-negative integer M such that $K_\epsilon\subset p^M\mathbb{Z}_p$, and consequently,

$$\int_{p^M\mathbb{Z}_p} Q_0\left(|x|_p\right)dx \geq \int_{K_\epsilon}Q_0\left(|x|_p\right)dx > 1-\epsilon. \tag{5.3}$$

By choosing ϵ so that $1-\epsilon\in\left(\frac{1}{2},1\right)$, the Hypothesis A is satisfied. Notice that the integer M depends on ϵ,σ,α.

Now we proceed to analyze Hypothesis B. By using Lemma 4,

$$\widehat{Q_0}\left(p^{1-r_0}\right)f(I_0) \geq \frac{\mathcal{N}C_1\sigma}{\left(p^{1-r_0}+\sigma^{\frac{1}{\alpha}}\right)^{1+\alpha}}, \tag{5.4}$$

since $r_0<0$, $\xi=p^{r_0-1}$satisfies $|\xi|_p>1$. Now, we take $\sigma\geq p^{\frac{1-r_0}{\alpha}}$, from (5.4) we have

$$\frac{\mathcal{N}C_1\sigma}{\left(p^{1-r_0}+\sigma^{\frac{1}{\alpha}}\right)^{1+\alpha}} \geq \frac{\mathcal{N}C_1\sigma}{\left(2\sigma^{\frac{1}{\alpha}}\right)^{1+\alpha}} = \frac{\mathcal{N}C_1}{2^{1+\alpha}\sigma^{\frac{1}{\alpha}}}.$$

Finally, the Hypothesis B is satisfied if by taking $\frac{\mathcal{N}C_1}{2^{1+\alpha}\sigma^{\frac{1}{\alpha}}} > \mu_{\max}$, i.e. if

$$\sigma < \sigma_{\max} =: \left[\frac{\mathcal{N}C_1}{2^{1+\alpha}\mu_{\max}}\right]^{\alpha}. \tag{5.5}$$

Given $\alpha > 0$, we pick $\sigma > 0$ satisfying (5.5), i.e. Hypothesis B is satisfied. Now for α, σ fixed, we pick ϵ so that $1-\epsilon \in \left(\frac{1}{2}, 1\right)$, then there exists an integer M such that (5.3) holds true, i.e. Hypothesis A is satisfied. Then we have the following result.

Theorem 3. *Assume that $X(x,0) \in \mathcal{S}_0$, and that the mutation measure is as in (5.1), with $\sigma \in (0, \sigma_{\max})$, $\alpha \in (0,\infty)$, $\int_{p^M\mathbb{Z}_p} Q_0\left(|x|_p\right)dx \in \left(\frac{1}{2}, 1\right)$, $M = M(\sigma,\alpha)$, then the Cauchy problem (4.9) admits a quasispecies solution.*

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