Non-Archimedean replicator dynamics and Eigen’s paradox

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Received 4 September 2018, revised 4 October 2018
Accepted for publication 26 October 2018
Published 20 November 2018

Abstract

We present a new non-Archimedean model of evolutionary dynamics, in which the genomes are represented by \( p \)-adic numbers. In this model the genomes have a variable length, not necessarily bounded, in contrast with the classical models where the length is fixed. The time evolution of the concentration of a given genome is controlled by a \( p \)-adic evolution equation. This equation depends on a fitness function \( f \) and on mutation measure \( Q \). By choosing a mutation measure of Gibbs type, and by using a \( p \)-adic version of the Maynard Smith ansatz, we show the existence of threshold function \( M^c(f,Q) \), such that the long term survival of a genome 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. About twenty years ago, Scheuring and Poole, Jeffares and Penny proposed a hypothesis to explain Eigen’s paradox. Our mathematical model shows that this biological hypothesis is feasible, but it requires \( p \)-adic analysis instead of real analysis. More exactly, the Darwin–Eigen cycle proposed by Poole et al takes place if the length of the genomes exceeds \( M^c(f,Q) \).

Keywords: Darwinian evolution, Eigen’s paradox, \( p \)-adic analysis, pseudodifferential evolution equations

1. Introduction

In this article we present a new non-Archimedean model of evolutionary dynamics of replicating single-stranded RNA genomes, which constitutes a non-Archimedean generalization of the classical Eigen quasispecies model. Mathematically speaking, the new model is a class of \( p \)-adic pseudodifferential evolution equations, which depends on a fitness function \( f \) and...
on a mutation measure $Qdx$. In the new model a sequence (genome) is specified by a $p$-adic number:

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

(1.1)

where $p$ denotes a fixed prime number, and the $x$s are $p$-adic digits, i.e. numbers in the set $\{0, 1, \ldots, p - 1\}$. Thus, in our model the sequences may have arbitrary length. In the case $p = 2$, we obtain the set of binary sequences of arbitrary length. 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. [29]. 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 $\mathbb{Q}_p$.

We denote by $\mathbb{Z}_p$ the unit ball, which consists of all the sequences with expansions of the form (1.1) with $k \geq 0$, and by $\mathbb{Z}_p^x$, the subset of $\mathbb{Z}_p$ consisting of the $p$-adic numbers with norm $1$. This last set is the disjoint union of sets of the form $j + p\mathbb{Z}_p$, for $j \in \{1, \ldots, p - 1\}$. Each set of the form $j + p\mathbb{Z}_p$ is (in a natural form) an infinite rooted tree. Then, all the sequences contained in the set $j + p\mathbb{Z}_p$ are naturally organized in a ‘phylogenetic tree’, and the set $\mathbb{Z}_p$ is a forest formed by the disjoint union of $p - 1$ infinite rooted trees. On the other hand, $\mathbb{Q}_p \setminus \{0\}$ is a countable disjoint union of scaled versions of the forest $\mathbb{Z}_p^x$, more precisely, $\mathbb{Q}_p \setminus \{0\} = \bigsqcup_{k = -\infty}^{\infty} p^k \mathbb{Z}_p^x$. The field of $p$-adic numbers has a fractal structure, see e.g. [1, 52]. For ‘pictures’ of $p$-adic spaces the reader may consult [17].

Our model of evolutionary dynamics is a $p$-adic continuous model. The fitness landscape is given by a function $f : \mathbb{Q}_p \rightarrow \mathbb{R}_+$. In this article, we assume that $f$ is a test function, 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 $Q\left(|x|^p\right)\,dx$, where $Q : \mathbb{R}_+ \rightarrow \mathbb{R}_+$, $dx$ is the normalized Haar measure of the group $(\mathbb{Q}_p, +)$, and $\int Q\left(|x|^p\right)\,dx = 1$, such that the probability that a sequence $x$ mutates into a sequence belonging to the set $B$ is given by $\int_B Q\left(|x-y|^p\right)\,dy$. In our model the concentration $X(x, t)$ of the sequence $x$ at the time $t$ is controlled by the following evolution equation:

$$\frac{\partial X(x, t)}{\partial t} = Q\left(|x|^p\right) \star \left\{ f\left(|x|^p\right)X(x, t) \right\} - \Phi(t)X(x, t),$$

(1.2)

where $\Phi(t) = \int_{\mathbb{Q}_p} f\left(|y|^p\right)X(y, t)\,dy$.

The term $Q\left(|x|^p\right) \star \left\{ f\left(|x|^p\right)X(x, t) \right\}$ represents the rate at which the sequences are mutating into the sequence $x$. We now assume that the replication reactions occur in a chemostat, see [51] and the references therein, which is a device that allows the maintenance of a constant population size, this corresponds to the term $-\Phi(t)X(x, t)$. From this discussion, we conclude that the instantaneous change of the concentration $X(x, t)$ is given by (1.2).

The mathematical study of the equation (1.2), and in particular of the associated Cauchy problem, is an open problem. The functions $f$ and $Q$ may depend on time, but here we study only the Cauchy problem associated to (1.2) in a particular case, by using $p$-adic wavelets, see section 8.

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. In the case of
sequences (genomes) with constant length, and under the assumption of independent point mutations, that is, assuming that during the replication process each digit (nucleotide) has a fixed probability of being replaced for another digit, and that this probability is independent of all other digits, Eigen discovered that the mutation process places a limit on the number of digits that a genome may have, see e.g. [13, 14, 35, 46, 51]. 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 discussion naturally drives to the following question: how is it possible 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 ‘Cath-22’ or Eigen’s paradox of the origin of life: ‘no large genome without enzymes, and no enzymes without a large genome’, see [42, p 317], [49]. Then main consequence of our \( p \)-adic model of evolution is that it gives a completely ‘new mathematical’ perspective of the Eigen paradox.

We show that there is a finite ultrametric space \( G_M \) consisting of \( p \)-adic sequences of finite length \( 2^M \), which is a rooted tree with \( 2^M + 1 \) levels and \( p^{2^M} \) branches at the top level, and with a distance induced by the restriction of the \( p \)-adic norm to \( G_M \), such that the equation (1.2) admits a discretization (a finite approximation) of the form

\[
\frac{d}{dt}X(J, t) = \frac{1}{C} \sum_{I \in G_M} Q(J - I_p) f \left( |I_p| \right) X(I, t) - \Phi_M (t) X(J, t) \quad \text{for } J \in G_M, 
\]

(1.3)

which is exactly the Eigen model on \( G_M \), see section 4.2. In the classical Eigen model the space of sequences is a finite metric space with a distance induced by the Hamming weight, in our model this space is replaced by \( G_M \). The main restriction of this last model is that the mutation matrix is a function of the \( p \)-adic distance between two sequences.

Heuristically speaking, the limit when \( M \) tends to infinity of the Eigen system (1.3) is the evolution equation (1.2). This heuristics can be justified by using the techniques from [53] and the references therein, more exactly, we have that the solutions of the Cauchy problem associated to (1.2) can be very well approximated by solutions of the Cauchy problem associated to (1.3), in a suitable function space, when \( M \) tends to infinity.

In [42], Maynard Smith introduced a mathematical approximation (the Maynard Smith ansatz) that allows to study the error threshold problem without solving the original Eigen system. This ansatz can be extended to the \( p \)-adic setting, see section 5. In this approximation the space of sequences is divided into two disjoint groups, each of them with a fixed fitness, say \( a \) and \( b \), with \( a > b \). The ansatz provides an inequality which gives a necessary and sufficient condition for the long term survival of the group of sequences with fitness \( a \). It is remarkable that this inequality is the classical one, see section 5. We use this ansatz to study the Eigen paradox for two different families of mutation measures. The measures of the first family are supported in the unit ball, the second is a family of Gibbs measures. In both cases we show that the Eigen paradox does not occur if the length of the sequences grows to the right pace. We propose using a Gibbs type measure:

\[
\frac{1}{C(\alpha, \beta)} e^{-\beta|x|^\alpha} \, dx, \quad \text{where } \alpha, \beta \text{ are positive constants, and } C(\alpha, \beta) \text{ is a normalization constant. The two main reasons for this choice are: first, } |x|^\alpha_p \text{ is the simplest energy function which depends on } \log_p |x|_p, \text{ the } 'p\text{-adic length'} \text{ of the sequence, and second, the discretization of the } p\text{-adic replicator equation (1.2) attached to this mutation }
\]
The \( p \)-adic version of the Maynard Smith ansatz provides a necessary and sufficient condition for the long term survival of a group of sequences of the form \( I + p^M\mathbb{Z}_p \), where \( I \) is an infinite sequence which plays the role of the master sequence, which are in competition with the group of sequences \( Q_{\phi} \setminus \{I + p^M\mathbb{Z}_p\} \). We establish the existence of an error threshold function \( M_c(s, \alpha, \beta) \), which depends on \( \ln s \), with \( 1 - s = \frac{\beta}{\alpha} \), and with \( f |_{s+p^M\mathbb{Z}_p} \equiv a > f |_{Q_{\phi} \setminus I + p^M\mathbb{Z}_p} \equiv b \), such that the long term survival of the sequences in the group \( I + p^M\mathbb{Z}_p \) requires that \( M > M_c(s, \alpha, \beta) \). This means that under a ‘fierce competition’ between the two groups (i.e. when \( s \to 0^+ \)), the long term survival of the first group requires that all the sequences in this group approaches to \( I \), in such way that the logarithm of the \( p \)-adic norm of the difference of any of these sequences and \( I \) is greater than \( M_c(s, \alpha, \beta) \). Notice that the set of sequences of finite length in \( I + p^M\mathbb{Z}_p \) is a dense subset, the mentioned condition implies that the long term survival of these sequences requires that the length of them grow.

On the other hand, if \( M \) is upper bounded, then \( M \leq M_c(s, \alpha, \beta) \) for \( s \) sufficiently small, which is a version of the classical threshold condition. In conclusion, our \( p \)-adic model of evolution predicts that Eigen’s paradox does not occur if the complexity of the genomes grow at the right pace. About twenty years ago, Scheuring [41] and Poole et al [39] proposed a hypothesis to explain Eigen’s paradox. Our mathematical model gives life to this biological hypothesis, more precisely, the Darwin–Eigen cycle [39] takes place under the condition \( M > M_c(s, \alpha, \beta) \): larger genome size improves the replication fidelity, and this in turn increases the Eigen limit on the length of the genome, which allows the evolution of larger genome size. In turn, this allows the evolution of new function, which could further improve the replication fidelity, and so on. See section 7.2 for an in-depth discussion about this matter.

In section 8, we study the Cauchy problem attached to the \( p \)-adic replicator equation, in the case in which the initial concentration and the fitness are test functions. By using \( p \)-adic wavelets and the classical method of separation of variables, we show the existence of a solution \( X(x,t) \) for the mentioned Cauchy problem. Then we show that \( X(x) = \lim_{t \to +\infty} X(x,t) \) exists, and it is a probability density concentrated in the support of the fitness function. This steady state concentration is the \( p \)-adic counterpart of the classical quasi-species. It is controlled by fitness function and by the largest eigenvalue of the operator

\[
W\varphi(x) = Q(|x|_p) * \left\{ f \left( |x|_p \right) \varphi(x) \right\}
\]

for \( \varphi \) supported in a finite union of disjoint balls. The \( p \)-adic quasi-species behave entirely different to the classical ones. An in-depth understanding of the \( p \)-adic quasispecies require developing of numerical methods for \( p \)-adic evolution equations.

An ultrametric space \( (M, d) \) is a metric space \( M \) with a distance satisfying \( d(A, B) \leq \max \{d(A, C), d(B, C)\} \) for any three points \( A, B, C \) in \( M \). In the middle of the 80s the idea of using ultrametric spaces to describe the states of complex biological systems, which naturally possess a hierarchical structure, emerged in the works of Frauenfelder, Parisi, Stein, among others, see e.g. [10, 15, 34, 40]. Mezard, Parisi, Sourlas and Virasoro discovered, in the context of the mean-field theory of spin glasses, that the space of states of such systems has an ultrametric structure, see e.g. [34, 40]. A central paradigm in physics of complex systems (for instance proteins) asserts that the dynamics of such systems can be modeled as a random walk in the energy landscape of the system, see e.g. [15, 28, 30], and the references therein. In this framework, the energy
landscape of a complex system is approximated by a pair consisting of an ultrametric space and a function on this space describing the distribution of the activation barriers, see e.g. [9]. The dynamics of such a system can be described by a system of equations of type

$$\frac{\partial u(i,t)}{\partial t} = \sum_{j \neq i} J(j,i) v(j) u(j,t) - \sum_{j \neq i} J(i,j) v(i) u(i,t), \quad i = 1, \ldots, N, \quad (1.4)$$

where the indices $i, j$ number the states of the system (which correspond to local minima of energy), $u(i,t)$ denotes the concentration of particles at the state $i$ and at time $t$, $J(i,j) \geq 0$ is the probability per unit time (or transition rate) of a transition from $i$ to $j$, and the $v(j) > 0$ are the basin volumes. We now assume that the space of states of the system is a finite ultrametric system (1.3).

Along this article, we 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

$$|x|_p = \left\{ \begin{array}{ll} 0 & \text{if } x = 0, \\ \frac{1}{p^n} & \text{if } x = p^n y, \quad y \in \mathbb{Z}. \end{array} \right.$$
\[ |x|_p = \begin{cases} 
0 & \text{if } x = 0 \\
p^{-\gamma} & \text{if } x = p^\gamma a \end{cases}, \]

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

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

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

where \( x_j \in \{0, \ldots, p-1\} \) and \( x_0 \neq 0 \). By using this expansion, we define the fractional part \( \{x\}_p \), as the rational number

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

In addition, any non-zero \( p \)-adic number can be represented uniquely as \( x = p^{\text{ord}(x)}ac(x) \) where \( ac(x) = \sum_{j=0}^{\infty} x_j p^j \), \( x_0 \neq 0 \), is called the angular component of \( x \). Notice that \( |ac(x)|_p = 1 \).

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 \( B_r \) equals 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 \( S_0 = \mathbb{Z}_p^* \) (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 \((\mathbb{Q}_p, |\cdot|_p)\) 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. \([1, 52]\). A subset of \( \mathbb{Q}_p \) is compact if and only if it is closed and bounded in \( \mathbb{Q}_p \), see e.g. \([52, \text{section 1.3}]\), or \([1, \text{section 1.8}]\). The balls and spheres are compact subsets. Thus \((\mathbb{Q}_p, |\cdot|_p)\) is a locally compact topological space.

**Notation 1.** We will use \( \Omega(\rho^{-1}|x - a|_p) \) to denote the characteristic function of the ball \( B_r(a) \). We will use the notation \( 1_A \) for the characteristic function of a set \( A \).

### 2.2. Some function spaces

A complex-valued function \( \varphi \) 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

\[ \varphi(x + x') = \varphi(x) \quad \text{for} \quad x' \in B_{l(x)}. \]  

(2.1)

A function \( \varphi : \mathbb{Q}_p \rightarrow \mathbb{C} \) 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 \( \varphi \). 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 \( \rho \in [0, \infty) \), 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 \( \int_{\mathbb{Q}_p} |g(x)|^\rho \, dx < \infty \), and \( L^\infty := L^\infty (\mathbb{Q}_p) = L^\infty (\mathbb{Q}_p, dx) \) denotes the \( \mathbb{C} \)-vector space of all the complex valued functions \( g \) such that the essential supremum of \(|g|\) is bounded. The corresponding \( \mathbb{R} \)-vector spaces are denoted as \( L^\rho_\mathbb{R} := L^\rho_\mathbb{R} (\mathbb{Q}_p) = L^\rho_\mathbb{R} (\mathbb{Q}_p, dx) \), \( 1 \leq \rho \leq \infty \).

### 2.3. Integration on \( \mathbb{Q}_p \)

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 \( \int_{E \subset \mathbb{Q}_p} dx = \int_{E} dx \) for every Borel set \( E \subset \mathbb{Q}_p \), see e.g. [16], chapter XI. If we normalize this measure by the condition \( \int_{\mathbb{Q}_p} dx = 1 \), then \( dx \) is unique. From now on we denote by \( dx \) the normalized Haar measure of \((\mathbb{Q}_p, +)\).

A test function \( \varphi : \mathbb{Q}_p \to \mathbb{C} \) can be expressed as a linear combination of characteristic functions of the form \( \varphi(x) = \sum_{i=1}^{l} c_i \Omega(p^{-\gamma} |x-a_i|_p) \), where \( c_i \in \mathbb{C} \) and \( \Omega(p^{-\gamma} |x-a_i|_p) \) is the characteristic function of the ball \( a_i + p^{-\gamma} \mathbb{Z}_p \), for every \( i \). In this case

\[
\int_{\mathbb{Q}_p} \varphi(x) \, dx = \sum_{i=1}^{l} c_i \int_{a_i + p^{-\gamma} \mathbb{Z}_p} \, dx = \sum_{i=1}^{l} c_i \int_{p^{-\gamma} \mathbb{Z}_p} \, dx = \sum_{i=1}^{l} c_i p^n,
\]

where we use the facts that \( dx \) is invariant under translations and that \( \int_{p^{-\gamma} \mathbb{Z}_p} \, dx = p^n \). By using the fact that \( \mathcal{D}(\mathbb{Q}_p) \) is a dense subspace of \( C_0(\mathbb{Q}_p) \), the space of continuous functions with compact support, the functional \( \varphi \to \int_{\mathbb{Q}_p} \varphi(x) \, dx \), \( \varphi \in \mathcal{D}(\mathbb{Q}_p) \) has a unique extension to \( C_0(\mathbb{Q}_p) \). For integrating more general functions, say locally integrable functions, the following notion of improper integral is used.

**Definition 1.** A function \( \varphi \in L^1_{\text{loc}} \) is said to be integrable in \( \mathbb{Q}_p \), if

\[
\lim_{m \to +\infty} \int_{B_m} \varphi(x) \, dx = \lim_{m \to -\infty} \int_{S_m} \varphi(x) \, dx
\]

exists. If the limit exists, it is denoted as \( \int_{\mathbb{Q}_p} \varphi(x) \, dx \), and we say that the (improper) integral exists.

### 2.4. Analytic change of variables

A function \( h : U \to \mathbb{Q}_p \) is said to be analytic on an open subset \( U \subset \mathbb{Q}_p \), if for every \( b \in U \) there exists an open subset \( \bar{U} \subset U \), with \( b \in \bar{U} \), and a convergent power series \( \sum_{i \in \mathbb{N}} a_i (x-b)^i \) for \( x \in \bar{U} \), such that \( h(x) = \sum_{i \in \mathbb{N}} a_i (x-b)^i \) for \( x \in \bar{U} \). In this case, \( \frac{d}{dx} h(x) = \sum_{i \in \mathbb{N}} a_i \frac{d}{dx} (x-b)^i \) is a convergent power series.

Let \( U, V \) be open subsets of \( \mathbb{Q}_p \). Let \( \varphi : V \to \mathbb{C} \) be a continuous function with compact support, and let \( h : U \to V \) be an analytic mapping. Then

\[
\int_{\mathbb{Q}_p} \varphi(y) \, dy = \int_{\mathbb{Q}_p} \varphi(h(x)) \left| \frac{d}{dx} h(x) \right|_p \, dx,
\]

see e.g. [52].
2.5. 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

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

We will also use the notation $F_x \rightarrow \xi f$ for the Fourier transform of $f$. The Fourier transform is a linear isomorphism from $\mathcal{D}$ onto itself satisfying

$$(F(Ff))(\xi) = f(-\xi), \quad \text{for every } f \in \mathcal{D},$$

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

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

where the limit is taken in $L^2$. We recall that the Fourier transform is unitary on $L^2$, i.e. $\|f\|_{L^2} = \|Ff\|_{L^2}$ for $f \in L^2$ and that (2.2) is also valid in $L^2$, see e.g. [50, chapter III, section 2].

3. The model

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 will use replicators, genomes, macromolecules 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 this section we introduce a $p$-adic version of Eigen’s equation, see e.g. [13, 14, 35, 46, 48, 51], which describes mutation-selection process of replicating sequences.

3.1. The space of sequences

In our model each sequence corresponds to a $p$-adic number:

$$x = x_{-n}p^{-m} + x_{-m+1}p^{-m+1} + \ldots + x_0 + x_1p + \ldots$$

where the digits $x_i$ run through the set $\{0, 1, \ldots, p - 1\}$. In the case $p = 2$, the sequences are binary words. 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 $(\mathbb{Q}_p, |)$, which is an infinite set. A key feature of our model is the use of sequences of variable length. It is relevant to mention that Poole et al [39] and Scheuring [41] already proposed solutions for Eigen’s paradox which require the usage of sequences of variable length.

On the other hand, $p$-adic numbers naturally appear in models of the genetic code. For an in-depth discussion the reader may consult [11, 27], [28, chapter 4] and the references therein.
3.2. Concentrations

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

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

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

3.3. The mutation measure

We fix a function $Q : \mathbb{R}_+ \to [0, 1]$, such that

$$0 \leq Q(|x|_p) \leq 1, \quad \int_{\mathbb{Q}_p} Q \left( |y|_p \right) \, dy = 1.$$  

We call $Q(|x|_p) \, dx$ the mutation measure. Given a Borel subset $E \subseteq \mathbb{Q}_p$ 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 $E$. In addition to this hypothesis we do not need additional assumptions about the mutation mechanism. The results presented in this article can be extended to case in which the mutation measure depends on time, more precisely, when $Q(|x|_p, t) \, dx$ is the transition function of a Markov process.

3.4. The fitness function

The fitness function $f$ is a non-negative real-valued test function. Notice that $f$ is a radial function, and by abuse of notation, we will use the notation $f \left( |x|_p \right)$. The assumption that function $f$ has compact support says that the evolution process is limited to a certain region of the space of sequences, which is infinite. This assumption allows very general fitness landscapes, for instance,

$$
\begin{cases}
  c_0 & \text{if } |x|_p \leq p^{L_0} \\
  g \left( |x|_p \right) & \text{if } p^{L_0} < |x|_p \leq p^{L_1} \\
  0 & \text{if } |x|_p > p^{L_1},
\end{cases}
$$

where $c_0$ is a nonnegative constant, $L_0, L_1 \in \mathbb{Z}$, with $L_0 < L_1$, and $g : \mathbb{R}_+ \to \mathbb{R}_+$ is a function.

3.5. The non-Archimedean replicator equation

We set

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

where $Q$ and $f$ are as before. Notice that for $1 \leq \rho \leq \infty$, etc.
\[ L^p(\mathbb{Q}_p, \mathbb{C}) \rightarrow L^p(\mathbb{Q}_p, \mathbb{C}) \]

\[ \varphi \rightarrow W\varphi \]

is a well-defined continuous operator.

Now our non-Archimedean mutation-selection equation has the form

\[ \frac{\partial X(x, t)}{\partial t} = WX(x, t) - \Phi(t)X(x, t), \ x \in \mathbb{Q}_p, \ t \in \mathbb{R}_+, \]  \hspace{1cm} (3.2)

where

\[ \Phi(t, X) := \Phi(t) = \int_{\mathbb{Q}_p} f(|y|_p) X(y, t) \, dy \quad \text{for } t \geq 0. \]

This function \( \Phi(t) \) is used to maintain constant the total concentration in the chemostat. Later on, we will consider the Cauchy problem associated to (3.2) with initial datum

\[ X(x, 0) = X_0 \in \mathcal{D}_\mathbb{R}. \]  \hspace{1cm} (3.3)

By changing variables as

\[ X(x, t) = Y(x, t) \exp\left(-\int_0^t \Phi(\tau) \, d\tau\right), \]  \hspace{1cm} (3.4)

like in the classical case, (3.2) and (3.3) becomes

\[
\begin{cases}
\frac{\partial Y(x)}{\partial t} = WY(x, t), & x \in \mathbb{Q}_p, \ t \in \mathbb{R}_+ \\
Y(x, 0) = X_0 \in \mathcal{D}_\mathbb{R}.
\end{cases}
\]  \hspace{1cm} (3.5)

3.6. Comments

(i) Archimedean evolution equations appear in several models of evolution, see e.g. [38] and [2]. In particular the proposed equation (3.2) makes sense in \( \mathbb{R} \), however, the interpretation of the space variable \( x \) as a sequence of variable length is only natural in the \( p \)-adic setting.

(ii) The equation (3.2) is really a family of models depending on \( f, Q \). We formulated these models in dimension one, that is, just for ‘one type of sequences’. However, the equations introduced here can be extended to dimension \( n \), that is, to the case of \( n \) ‘types of sequences’. In principle, the models introduced here may be extended to include recombination and sexual reproduction.

4. An ultrametric version of the classical replicator equation

Eigen’s evolution model consists of a systems of non-linear ordinary differential equations describing the evolution of the concentrations of sequences, which belong to a finite metric space, where the distance is induced by the Hamming weight. If we use binary sequences, the space of sequences is \( \mathbb{Z}_2/2^M\mathbb{Z}_2 \), for some positive integer \( M \).
In this section by using ideas from [53], we show a discretization of the equation (3.2) that agrees with the Eigen model in an ultrametric space formed by finite $p$-adic sequences, where the mutation probability is a function of the ultrametric distance between sequences. By a suitable normalization the space of sequences is $\mathbb{Z}_p/p^{2M}\mathbb{Z}_p$, and the ultrametric distance is induced by the restriction of the $p$-adic norm to $\mathbb{Z}_p/p^{2M}\mathbb{Z}_p$. This fact shows that our equation (3.2) is a non-Archimedean generalization of the Eigen model.

**Notation 2.** The set of non-negative integers is denoted as $\mathbb{N}$.

4.1. The space of sequences $G_M$

We fix $M \in \mathbb{N}\setminus\{0\}$ 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: any $I \in G_M$ is represented as

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

(4.1)

where the $I_j$s belong to $\{0, 1, \ldots, p - 1\}$. Furthermore, the restriction of $|\cdot|_p$ to $G_M$ induces an absolute value such that $|G_M|_p = \{0, p^{-(M+1)}, \ldots, p^{-1}, 1, \ldots, p^M\}$. We endow $G_M$ with the metric induced by $|\cdot|_p$, 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. Any element $I \in G_M$ can be uniquely written as $p^MI$, where

$$\tilde{I} = I_0 + I_1p + \cdots + I_{2M-1}p^{2M-1} \in \mathbb{Z}_p/p^{2M}\mathbb{Z}_p,$$

with the $I_j$s belonging to $\{0, 1, \ldots, p - 1\}$. The elements of the $\mathbb{Z}_p/p^{2M}\mathbb{Z}_p$ are in bijection with the vertices at the top level of the above mentioned rooted tree. By definition the root of the tree is the only vertex at level 0. There are exactly $p$ vertices at level 1, which correspond with the possible values of the digit $I_0$ in the $p$-adic expansion of $I$. Each of these vertices is connected to the root by a non-directed edge. At level $\ell$, with $1 \leq \ell \leq 2M$, there are exactly $p^{\ell}$ vertices, each vertex corresponds to a truncated expansion of $I$ of the form $I_0 + \cdots + I_{\ell-1}p^{\ell-1}$. The vertex corresponding to $I_0 + \cdots + I_{\ell-1}p^{\ell-1}$ is connected to a vertex $I_0 + \cdots + I_{\ell-2}p^{\ell-2}$ at the level $\ell - 1$ if and only if $(I_0 + \cdots + I_{\ell-1}p^{\ell-1}) - (I_0 + \cdots + I_{\ell-2}p^{\ell-2})$ is divisible by $p^{\ell-1}$. Notice that there are other geometric realizations of $G_M$. For instance, we can chose a forest formed by $p$ rooted trees, each of them with $2M$ levels and $p^{2M-1}$ branches.

4.2. A discretization of equation (3.2)

We denote by $D^{-M}_R$ the R-vector subspace of $D_R$ spanned by the functions

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

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

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

where the $\varphi(I)$s are real numbers. Notice that the dimension of $D^{-M}_R(\mathbb{Q}_p)$ 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 $Q\left(|x|_p\right)$, $f\left(|x|_p\right)$ and $X(x, t)$ belong to $D_{-M}^{-M}$, for any $t$. Then

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

with $C_M = p^{-M} \sum_{I \in G_M} Q\left(|I|_p\right)$.

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

and

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

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

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

= \left\{ \frac{1}{C_M} \sum_{K \in G_M} \sum_{I \in G_M} Q\left(|K|_p\right) f\left(|I|_p\right) X(I, t) \right\} \Omega\left(p^M |x - K|_p\right) * \Omega\left(p^M |x - I|_p\right), \tag{4.2}$$

and by using that $\Omega\left(p^M |x - K|_p\right) * \Omega\left(p^M |x - I|_p\right) = p^M \Omega\left(p^M |x - (I + K)|_p\right)$ and the fact that $G_M$ is an additive group, the right-hand side of (4.2) can be rewritten as

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

with $C = \sum_{I \in G_M} Q\left(|I|_p\right)$. 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

$$\frac{d}{dt} X(J, t) = \frac{1}{C} \sum_{I \in G_M} Q\left(|J - I|_p\right) f\left(|I|_p\right) X(I, t) - \Phi_M(t) X(J, t) \text{ for } J \in G_M, \tag{4.3}$$

where

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

which is exactly the Eigen model on $G_M$, but $G_M$ is an ultrametric space, where the distance comes from the $p$-adic norm.

### 4.3. The limit $M$ tends to infinity

Heuristically speaking, the limit of the system of equation (4.3) when $M$ tends to infinity is the evolution equation (3.2). In [6], Avetisov and Kozyrev et al. established (using physical arguments) that certain non-Archimedean kinetic models, similar to (4.3), have ‘continuous $p$-adic limits’ as reaction-ultradiffusion equations. A mathematical explanation of these constructions
is given in our article [53]. From a mathematical perspective, the Cauchy problem associated with (3.2) can be very well approximated by an initial value problem associated with the system (4.3), in the sense that any solution of (3.2) is arbitrarily close to a suitable solution of (4.3) in a certain function space, when \( M \) tends to infinity, see introduction of [53]. This result follows by applying techniques used in [53] to the system (3.5) with \( X_0 \) a test function, see (3.5).

Now, if consider the system (4.3) as a system of ODEs in \( \mathbb{R}^{2M} \), then it seems not plausible that the ‘limit \( N \rightarrow \infty \)’ can be defined.

5. The Maynard Smith ansatz

In this section we present a \( p \)-adic version of Maynard Smith approach to the error threshold problem, see [42, 48]. We divide the space of sequences into two disjoint sets:

\[
Q_p = \left[ I + p^M \mathbb{Z}_p \right] \bigcup \left[ Q_p \setminus I + p^M \mathbb{Z}_p \right],
\]

where \( I \) is a fixed sequence as in (4.1), with \( M \geq 1 \), and assume that

\[
f \big|_{I+p^M \mathbb{Z}_p} \equiv a, \quad f \big|_{Q_p \setminus I+p^M \mathbb{Z}_p} \equiv b, \quad \text{with } a > b,
\]

here ‘\( \equiv \)’ means identically equal. This means that the group \( I + p^M \mathbb{Z}_p \) contains the fittest sequences and that all these sequences coincide with \( I \) up to digit \( I_{M-1} \). We denote by \( X(x,t) \) and \( Y(x,t) \) the concentration of \( I + p^M \mathbb{Z}_p \) and \( Q_p \setminus \left[ I + p^M \mathbb{Z}_p \right] \), respectively. Notice that the supports of \( X(x,t) \) and \( Y(x,t) \) are disjoint. We denote by \( q := q(M,Q) \) the probability that a sequence in \( I + p^M \mathbb{Z}_p \) mutates into a sequence belonging to \( Q_p \setminus \left[ I + p^M \mathbb{Z}_p \right] \), and we denote by \( r := r(M,Q) \) the probability of mutation of a sequence from \( Q_p \setminus \left[ I + p^M \mathbb{Z}_p \right] \) into a sequence in \( I + p^M \mathbb{Z}_p \). The system of equations governing the development of these populations is

\[
\begin{align*}
\frac{\partial X(x,t)}{\partial t} & = a \left( 1 - q \right) X(x,t) + brY(x,t) - \Phi(t) X(x,t) \\
\frac{\partial Y(x,t)}{\partial t} & = aqX(x,t) + b \left( 1 - r \right) Y(x,t) - \Phi(t) Y(x,t),
\end{align*}
\]

where

\[
\int_{Q_p} X(x,t) \, dx + \int_{Q_p} Y(x,t) \, dx = 1,
\]

and

\[
\Phi(t) = \int_{I+p^M \mathbb{Z}_p} f \left( \left| x \right|_p \right) X(x,t) \, dx + \int_{Q_p \setminus I+p^M \mathbb{Z}_p} f \left( \left| x \right|_p \right) Y(x,t) \, dx
\]

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

We assume that for \( M \) sufficiently large, \( r(M,Q) \) is very small (this condition should be verified for each particular choice of \( Q \)), so we can assume that system (5.3) has the form.
\[
\frac{\partial X(x,t)}{\partial t} = a(1 - q)X(x,t) - \Phi(t)X(x,t)
\]
\[
\frac{\partial Y(x,t)}{\partial t} = aqX(x,t) + bY(x,t) - \Phi(t)Y(x,t).
\]

(5.4) By taking \(Z(x,t) = \frac{X(x,t)}{Y(x,t)}\), system (5.4) becomes
\[
\frac{\partial Z(x,t)}{\partial t} = Z(x,t) \left\{ a(1 - q) - aqZ(x,t) - b \right\}.
\]

Assuming that concentration \(Z(x,t)\) achieves a steady concentration \(\overline{Z}(x)\) over the time, we get
\[
\overline{Z}(x) = \frac{a(1 - q) - b}{aq}.
\]
The original population persists, i.e. the sequences in \(I + p^M Z_p\) 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
\[q < s.
\]
This is exactly the classical condition determining the error threshold, see e.g. [42, 48].

5.1. Comments

Notice that by using the ultrametric property \(|x - y|_p = |y|_p\) for \(x \in p^M Z_p\) and \(y \in Q_p \setminus p^M Z_p\), we have
\[
q = q(M, \alpha) = \int_{I + p^M Z_p} \int_{Q_p \setminus [I + p^M Z_p]} Q \left( |x - y|_p \right) dy dx
\]
\[
= \int_{p^M Z_p} \int_{Q_p \setminus p^M Z_p} Q \left( |x - y|_p \right) dy dx = \int_{p^M Z_p} \int_{Q_p \setminus p^M Z_p} Q \left( |y|_p \right) dy dx
\]
\[
= p^{-M} \int_{Q_p \setminus p^M Z_p} Q \left( |y|_p \right) dy = p^{-M} \int_{\text{supp } Q \setminus [I + p^M Z_p]} Q \left( |y|_p \right) dy,
\]
which implies that \(q\) is independent of \(I, r = r(M, Q) = q\), and that conditions (5.1) and (5.2) can be replaced by
\[
\text{supp } Q = [I + p^M Z_p] \bigcup [\text{supp } Q \setminus [I + p^M Z_p]],
\]
where \(I\) is a fixed sequence as in (4.1), with \(M \geq 1\), and by
\[f |_{I + p^M Z_p} \equiv a, \quad f |_{\text{supp } Q \setminus [I + p^M Z_p]} \equiv b, \quad \text{with } a > b.
\]

6. The error threshold problem using a mutation measure supported in unit ball

In this section we study the error threshold problem using the Maynard Smith ansatz with a mutation measure supported in the unit ball.
6.1. A class of mutation measures supported in the unit ball

Take $\alpha \geq 0$, and consider

$$Q \left( |x|_p : \alpha \right) = \frac{|x|_p^\alpha \Omega \left( |x|_p \right)}{Z(\alpha)}, \tag{6.1}$$

where for $\gamma \in \mathbb{R}$,

$$Z(\gamma) = \int_{\mathbb{Z}_p} |x|_p^\gamma \, dx = \frac{1 - p^{-1}}{1 - p^{-1 - \gamma}} \text{ for } \gamma > -1. \tag{6.2}$$

Then, $Q \left( |x|_p : \alpha \right) \, dx$ gives rise to a family of mutation measures, which include the uniform distribution for $\alpha = 0$.

We now fix a sequence $I \in \mathbb{Z}_p$, which plays the role of the master sequence, and divide the space of sequences $\mathbb{Z}_p$ into two subsets: $I + p^M \mathbb{Z}_p$ and $\mathbb{Z}_p \setminus \left[ I + p^M \mathbb{Z}_p \right]$ for some positive integer $M$. The set $I + p^M \mathbb{Z}_p$ consists of the sequences in the unit ball that coincide with the sequence $I$ up to the digit $M - 1$. We denote by $H_M$ a fixed set of representatives of $\mathbb{Z}_p / p^M \mathbb{Z}_p$. We also assume that

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

Notice that by the remarks made at the end of section 5, we can apply the Maynard Smith ansatz to establish (5.5) under the above mentioned conditions. We now compute the probability that a sequence in the set $I + p^M \mathbb{Z}_p$ mutates into a sequence belonging to the set $\mathbb{Z}_p \setminus \left[ I + p^M \mathbb{Z}_p \right]$ (notice that this probability does not depended on $I$):

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

$$= \frac{1}{Z(\alpha)} \int_{|x - f_j| \leq p^{-M}} \int_{|y - f_j| > p^{-M}} |x - y|_p^\alpha \, dy \, dx$$

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

$$= \frac{p^{-M}}{Z(\alpha)} \int_{\mathbb{Z}_p \setminus p^M \mathbb{Z}_p} |y|_p^\alpha \, dy = \frac{p^{-2M}}{Z(\alpha)} \sum_{j \in H_M, j \neq 0} |J|_p^\alpha,$$

where we use the ultrametric property: $|x - y|_p = |y|_p$ for $|x|_p \leq p^{-M}$ and $|y|_p > p^{-M}$, and that $\mathbb{Z}_p = \bigcup_{j \in H_M} J + p^M \mathbb{Z}_p$, with $H_M = \mathbb{Z}_p / p^M \mathbb{Z}_p$.

Notice that

$$q(\alpha) \geq \frac{p^{-2M}}{Z(\alpha)} \cdot p^{M-1} |J|_p^\alpha = \frac{p^{-2M+M-1} |J|_p^\alpha}{Z(\alpha)} > \frac{p^{-2M-M\alpha}}{Z(\alpha)} > p^{-2M-M\alpha},$$

since $\frac{1}{Z(\alpha)} \in \left[ 1, \frac{1}{1 - p^{-1}} \right]$ for $\alpha \in [0, +\infty)$.

6.1.1. Classical error threshold: $M$ and $\alpha$ fixed. We analyze now weather or not the condition (5.5) is satisfied, when $M$ and $\alpha \in [0, +\infty)$ are 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 $M_0$ such that

$$q(\alpha) > p^{-2M_0-M\alpha} > s,$$

which implies the existence of a classical error threshold:

$$M_c \leq -\frac{\ln s}{(2 + \alpha)\ln p} \text{ for } s \in (0, 1) \text{ and } \alpha \text{ fixed.} \quad (6.3)$$

6.1.2. Overcoming Eigen’s paradox: $M$ variable and $\alpha$ fixed. If $M$ can grow and $\alpha$ is fixed, the condition (5.5) is satisfied if

$$p - 2M - M\alpha < q(\alpha) < s,$$

which implies that

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

Under a ‘fierce competition’ between the groups $I + p^M\mathbb{Z}_p, \mathbb{Z}_p \setminus [I + p^M\mathbb{Z}_p]$, i.e. when rate $\beta$ approaches from the left to rate $a$ (i.e. $s \to 0^+$), $M$ must grow, which means that the survival of the sequences in the group $I + p^M\mathbb{Z}_p$ demands that they get closer to master sequence $I$, 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.

7. The error threshold problem using a mutation measure of Gibbs type

In this section we study the error threshold problem using the Maynard Smith ansatz with a mutation measure of Gibbs type depending only on $|\cdot|_p$.

7.1. A mutation measure of Gibbs type

We propose a mutation measure of type

$$\frac{e^{-\beta E(|I|_p)}}{Z(\beta, E)}, \quad (7.1)$$

where $\beta > 0$, $E : \mathbb{R}_+ \to \mathbb{R}_+$, and $Z(\beta, E) = \int_{\mathbb{Q}_p} e^{-\beta E(|I|_p)}\,dx < \infty$. A Gibbs measure is a natural choice when dealing with infinite systems. On the other hand, matrices of type $Q(I, J) = \frac{e^{-\beta E(I, J)}}{Z(\beta, E)}$ appear naturally in the models of evolution using spin glasses technique, see e.g. [32, equations (6) and (8)]. We pick $E(|I|_p) = |I|_p^\alpha$, with $\alpha > 0$, which corresponds to the simplest energy function. By assuming that $\beta > 0$ is sufficiently large and taking into account the fast decay of the function $\exp(-\beta)$, our hypothesis on the mutation measure implies that the most probable mutations of a given sequence $I$ happen to sequences which are very close to $I$ in the $p$-adic norm, which are sequences belonging to a ball of type $I + p^M\mathbb{Z}_p$, with $M$ sufficiently large. In practical terms, this means that the replicators are not too dispersed on $\mathbb{Q}_p$. It is interesting to quote here that according to [47]: ‘in silico simulations reveal that replicators with limited dispersal evolve towards higher efficiency and fidelity’.

We assume that the probability that a sequence $x \in \mathbb{Q}_p$ mutates into a sequence belonging to set $B$ (a Borel subset of $\mathbb{Q}_p$) is given by
\[ P(x, B; \alpha, \beta) = \frac{1}{C} \int_B e^{-\beta|x-y|^\alpha} \, dy, \]

where \( C(\alpha, \beta) := C \), and \( \alpha, \beta \) are positive constants such that \( \frac{1}{C} \int_{Q_p} e^{-\beta|x-y|^\alpha} \, dy = 1 \). Notice that \( P(x, B; \alpha, \beta) \) is a space homogeneous Markov transition function, the parameter \( \beta \) (which is typically interpreted as proportional to the inverse of the temperature) plays the role of time.

We fix a sequence \( I = \sum_{i=k}^{\infty} I_p^i \), and assume that \( I \) has ‘infinite length’, and consider the ball \( I + p^M \mathbb{Z}_p, M \in \mathbb{N} \), which contains all the sequences that coincide with \( I \) up to the digit \( I_{M-1} \). We can consider \( I \) as the master sequence, and \( M \) is the minimum number of nucleotides that a sequence in the set \( I + p^M \mathbb{Z}_p \) shares with \( I \).

The probability that a sequence \( x \) mutates into a sequence belonging to \( Q_p \setminus (I + p^M \mathbb{Z}_p) \) is \( q(x, Q_p \setminus (I + p^M \mathbb{Z}_p); \alpha, \beta) \), and the probability that any sequence from the ball \( I + p^M \mathbb{Z}_p \) mutates into a sequence in \( Q_p \setminus (I + p^M \mathbb{Z}_p) \) is given by

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

We assert that

\[ q(M, \alpha, \beta) > \frac{(p-1) p^{-2M}}{C} e^{-\beta p^\alpha}. \tag{7.2} \]

Indeed, by using the fact that the measure \( dy \, dx \) is invariant under translations, and the ultrametric property of \( |.|_p \), we have

\[
\begin{align*}
q(M, \alpha, \beta) &= \frac{1}{C} \int_{I + p^M \mathbb{Z}_p} \int_{Q_p \setminus (I + p^M \mathbb{Z}_p)} e^{-\beta|x-y|^\alpha} \, dy \, dx \\
&= \frac{1}{C} \int_{p^M \mathbb{Z}_p} \int_{Q_p \setminus (I + p^M \mathbb{Z}_p)} e^{-\beta|x-y|^\alpha} \, dy \, dx \\
&= \frac{1}{C} \int_{|x| \leq p^{-M}} \int_{|y| > p^{-M}} e^{-\beta|x-y|^\alpha} \, dy \, dx \\
&= \frac{1}{C} \int_{|x| \leq p^{-M}} \int_{|y| > p^{-M}} e^{-\beta|y|^\alpha} \, dy \\
&= \frac{p^{-M}}{C} \int_{|y| > p^{-M}} e^{-\beta|y|^\alpha} \, dy \\
&> \frac{p^{-M}}{C} \int_{|y| > p^{-M-1}} e^{-\beta|y|^\alpha} \, dy \\
&= \frac{(p-1) p^{-2M}}{C} \inf_{M \in \mathbb{N}} e^{-\beta p^\alpha p^{-M}} = \frac{(p-1) p^{-2M}}{C} e^{-\beta p^\alpha}.
\end{align*}
\]

We also notice that

\[
q(M, \alpha, \beta) = \frac{p^{-M}}{C} \int_{|y| > p^{-M}} e^{-\beta|y|^\alpha} \, dy < \frac{p^{-M}}{C} \int_{Q_p} e^{-\beta|y|^\alpha} \, dy = C_0 p^{-M}. \tag{7.3}
\]
where $C_0 = C_0(\alpha, \beta)$ is a positive constant independent of $M$, since $e^{-\beta|y|^p}$ is an integrable function, see e.g. the proof of lemma 4.1 in [19].

On the other hand, we denote by $r := r(M, \alpha, \beta)$ the probability of mutation of a sequence from $\mathbb{Q}_p \backslash [I + p^M\mathbb{Z}_p]$ into $I + p^M\mathbb{Z}_p$. Then

$$r(M, \alpha, \beta) = q(M, \alpha, \beta).$$

(7.4)

7.2. The Eigen paradox

Notice that by (7.3), $r(M, \alpha, \beta) = q(M, \alpha, \beta)$ decays with $M$, so we can use the Maynard Smith ansatz to estimate the error threshold, see section 5. From (5.5), by using that $q(M, \alpha, \beta) > \left(\frac{p-1}{p}\right)^{2M}e^{-\beta p^s}$, with $p, \alpha, \beta, s$ fixed, we have

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

which implies that

$$M > -\frac{(\beta p^s + \ln s)}{2\ln p} + \frac{\ln p}{2\ln p}. \quad (7.5)$$

Under a ‘fierce competition’ between the groups $I + p^M\mathbb{Z}_p, \mathbb{Q}_p \backslash [I + p^M\mathbb{Z}_p]$, i.e. when rate $b$ approaches from the left to rate $a$ (i.e. $s \to 0^+$), $M$ must grow, which means that the survival of the sequences in the group $I + p^M\mathbb{Z}_p$ demands that they get closer to master sequence $I$, which means, that they must increase their lengths. Then in our model the ‘classical Eigen’s paradox does not occur’ because the length of the genomes can grow during the evolution process. Notice that if $M$ does not satisfy (7.5), then the sequences in the set $I + p^M\mathbb{Z}_p$ will not survive in the long term.

For arbitrary $f$ and $Q$, we propose the existence of threshold function for the length of the genomes $M(f, Q)$ such that $M > M(f, Q)$ is a necessary and sufficient condition for the long term survival of the genomes. Formula (7.5) gives an estimate for the function $M(f, Q)$ for the particular case in which $Q$ has the form (7.1). We propose that under the condition $M > M(f, Q)$, the Darwin–Eigen cycle proposed by Poole, Jeffares and Penny takes place, see [39]; the Darwin–Eigen cycle is a positive feedback mechanism. Larger genome size improves the fidelity replication ($q(M, \alpha, \beta)$ decays when $M$ grows see (7.3)), and this increases the Eigen limit (see (7.5)) on the length of the genome, and this allows the evolution of larger genome size. In turn, this allows the evolution of new function, which could further improve the replication fidelity, and so on. See [39, 41] and [18], for a detailed biological discussion.

On the other hand, if $M \leqslant M(f, Q)$ then genomes do not survive in the long term. This is a type of classical error threshold, ‘similar’ to the one provided by the Eigen evolution model with point mutation matrices.

8. The Cauchy problem for the p-adic replicator equation

In this section we show the existence of a solution for the Cauchy problem (3.5), which in turn implies the existence of quasispecies for the $p$-adic replicator equation introduced here. This goal is achieve by using the classical method of separation of variables and $p$-adic wavelets, see [1] and [28]. We assume that the function $Q$ satisfies only the hypotheses given in section 3.3.
8.1. Some remarks on p-adic wavelets

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 $a : \mathbb{R}^+ \to \mathbb{R}^+$ and define the pseudodifferential operator

$$
\mathcal{D} \to C(\mathbb{Q}_p, \mathbb{C}) \cap L^2
$$

$$
\varphi \to A\varphi,
$$

where $(A\varphi)(x) = \mathcal{F}_{x \to \xi}^{-1}\{a(|\xi|_p)\mathcal{F}_{\xi \to x}\varphi\}$.

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

$$
\Psi_{rnj}(x) = p^{-r} \chi_p(p^{-r}jx) \Omega\left(|p^{-r}x - n|_p\right), \quad (8.1)
$$

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

$$
A\Psi_{rnj} = a(p^{1-r})\Psi_{rnj} \text{ for any } r, n, j. \quad (8.2)
$$

This result is due to Kozyrev see e.g. [28, theorem 3.29, [1, theorem 9.4.2]. Notice that

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

and then

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

The Fourier transform $\hat{\varphi}$ of $\varphi$ is a real-valued function, which is radial in $\mathbb{Q}_p \setminus \{0\}$. For this reason, we use the notation $\hat{\varphi}(|\xi|_p)$.

We set

$$
W\varphi = \varphi \ast \varphi \text{ for } \varphi \in \mathcal{D},
$$
as before. Then

$$
W\Psi_{rnj}(x) = \hat{\varphi}(p^{1-r})\Psi_{rnj}(x), \quad (8.3)
$$

where $\hat{\varphi}(p^{1-r})$ is a real number satisfying $|\hat{\varphi}(p^{1-r})| \leq 1$.

8.2. The Cauchy problem for operator $W$

We now consider the following initial value problem:

$$
\begin{cases}
Y : \mathbb{Q}_p \times \mathbb{R}^+ \to \mathbb{R}, & Y(\cdot, t) \in L^2_{\mathbb{R}}, \ Y(\cdot, \cdot) \in C^i(\mathbb{R}_+, \mathbb{R}) \\
\frac{\partial Y(x,t)}{\partial t} = WY(x,t), & x \in \mathbb{Q}_p, t > 0 \\
Y(x,0) = Y_0(x) \in \mathcal{D}_\mathbb{R}.
\end{cases} \quad (8.4)
$$
Notice that the conditions \( Y_0(x) \geq 0 \) and \( \int_{Q_p} Y_0(x) \, dx = 1 \) constitute natural physical restrictions for the function \( Y_0 \), however, here we do not use them.

We solve (8.4) by using the separation of variables method. We first look for a complex-valued solution of (8.4) of the form

\[
\tilde{Y}(x,t) = \sum_{\nu \mu} C_{\nu \mu}(t) \Psi_{\nu \mu}(x)
\]

where \( C_{\nu \mu}(t) \) are complex-valued functions, which admit continuous temporal derivatives. We fix a countable disjoint covering of \( Q_p \) by balls of the form:

\[
B_r\left(p^{-n}n_i\right) = p^{-n}n_i + p^{-r}Z_p,
\]

where \( n_i \in \mathbb{Z} \) and \( n_i = a_{-k}p^{-k} + \cdots + a_{-1}p^{-1} \in Q_p/Z_p \), and the digits \( a_j \) runs through the set \{0, \ldots, p - 1\}, such that

\[
f \mid_{B_r(p^{-n}n) = f(|p^{-n}n|_p)}.
\]

Consequently

\[
f \left(|x|_p\right) = \sum_{i=0}^{l(f)} f\left(|p^{-n}n|_p\right) \Omega\left(|p^r x - n|_p\right), \text{ } l(f) \in \mathbb{N},
\]

due to the fact that the fitness function \( f \) is a locally constant function with compact support.

We now describe the balls contained in \( B_r\left(p^{-n}n_i\right) \). Any such ball has the form:

\[
a_{-k}p^{-n-k} + \cdots + a_{-1}p^{-n-1} + b_1p^{-r} + \cdots + b_{r-1}p^{-1} + p^r Z_p
\]

\[
= p^{-n}n_i + p^r \left(b_1p^{-r-n} + \cdots + b_{r-1}p^{-1}\right) + p^r Z_p =: p^{-n}n_i + p^r n_r + p^r Z_p,
\]

for some integer \( r \geq -n \) and some \( n_r \in Q_p/Z_p \). The amount of such balls is exactly \( p^{r-1} \).

Now, for a fixed \( \Omega\left(|p^r x - n|_p\right) \) and a variable \( \Omega\left(|p^r x - n|_p\right) \), we have

\[
\Omega\left(|p^r x - n|_p\right) \Omega\left(|p^r x - n|_p\right) = \begin{cases} 
\Omega\left(|p^r x - n|_p\right) & \text{if } B_r\left(p^{-n}n\right) \subset B_r\left(p^{-n}n_i\right) \\
0 & \text{if } B_r\left(p^{-n}n\right) \not\subset B_r\left(p^{-n}n_i\right).
\end{cases}
\]

By using (8.8) and (8.9), we have

\[
f \left(|x|_p\right) \tilde{Y}(x,t) = \sum_{i=0}^{l(f)} f\left(|p^{-n}n|_p\right) \sum_{j=1}^{p-1} \sum_{i \geq -n} \sum_{p^{-r}n_i + n} C_{\nu \mu}(t) \left(p^{-r}x - \left(p^{-r}n_i + n\right)\right) \Omega\left(|p^r x - \left(p^{-r}n_i + n\right)|_p\right),
\]

and by using (8.3),
\[
W \left( f \left( |x|_p \right) \tilde{Y}(x, t) \right) \\
= \sum_{i=0}^{l(t)} f \left( |p^{-r}n_i|_p \right) \sum_{j=1}^{p-1} \sum_{r \geq r_i} \sum_{p^{-r}n_i + n_j} C_{(-r)}(p^{-r}n_i + n_j)(t) \\
\times \tilde{Q}(p^{1+r}) p^{2} \chi_p \left( p^{-r-1} jx \right) \Omega \left( |p^{-r}x - (p^{-r}n_i + n_j)|_p \right),
\](8.10)

By replacing (8.5) and (8.10) in (8.4), we obtain
\[
Y(x, t) = \sum_{i=0}^{l(t)} f \left( |p^{-r}n_i|_p \right) \sum_{j=1}^{p-1} \sum_{r \geq r_i} \sum_{p^{-r}n_i + n_j} C_{(-r)}(p^{-r}n_i + n_j)(0) \\
\times \exp \left( f \left( |p^{-r}n_i|_p \right) \tilde{Q}(p^{1+r}) \right) p^{2} \chi_p \left( p^{-r-1} jx \right) \Omega \left( |p^{-r}x - (p^{-r}n_i + n_j)|_p \right),
\](8.11)

where
\[
Y_0(x) = \sum_{i=0}^{l(t)} f \left( |p^{-r}n_i|_p \right) \sum_{j=1}^{p-1} \sum_{r \geq r_i} \sum_{p^{-r}n_i + n_j} C_{(-r)}(p^{-r}n_i + n_j)(0) \\
\times \chi_p \left( p^{-r-1} jx \right) \Omega \left( |p^{-r}x - (p^{-r}n_i + n_j)|_p \right).
\]

Now, we set
\[
\alpha_{r,n_i} := f \left( |p^{-r}n_i|_p \right) \tilde{Q}(p^{1+r}),
\]
then
\[
\exp \left[ f \left( |p^{-r}n_i|_p \right) \tilde{Q}(p^{1+r}) t + 2\pi i \left\{ p^{-r-1} jx \right\}_p \right] \\
= e^{\alpha_{r,n_i}} \left[ \cos \left( 2\pi \left\{ p^{-r-1} jx \right\}_p \right) + \sqrt{-1} \sin \left( 2\pi \left\{ p^{-r-1} jx \right\}_p \right) \right],
\]
and by setting
\[
A_{j,r,n_i} := \text{Re} \ C_{(-r)}(p^{-r}n_i + n_j)(0),
\]
\[
B_{j,r,n_i} := \text{Im} \ C_{(-r)}(p^{-r}n_i + n_j)(0),
\]
the solution \(Y(x, t)\) is the real part of \(\tilde{Y}(x, t)\):
\[
Y(x, t) = \sum_{i=0}^{l(t)} \sum_{j=1}^{p-1} \sum_{r \geq r_i} \sum_{p^{-r}n_i + n_j} p^{2} e^{\alpha_{r,n_i}} \Omega \left( |p^{-r}x - (p^{-r}n_i + n_j)|_p \right) \\
\times \left[ A_{j,r,n_i} \cos \left( 2\pi \left\{ p^{-r-1} jx \right\}_p \right) - B_{j,r,n_i} \sin \left( 2\pi \left\{ p^{-r-1} jx \right\}_p \right) \right].
\](8.12)

In the next section we show that \(Y(x, t)\) is really a finite sum, if \(Y_0 \in D_R\).

### 8.2.1 Some remarks about the Fourier coefficients.
If \(Y_0 \in D_R\), then
\[
C_{(-r)}(p^{-r}n_i + n_j)(0) \neq 0 \iff -r_i \leq r \leq l - 1,
\]
where \( l \) is the index of local constancy of \( Y_0 \). This implies that almost all the \( C_{(−r)}(p^{−r−rni+n}) \) are zero.

Indeed,

\[
f((p^{−r}n_1)p)C_{(−r)}(p^{−r−rni+n})(0) = p^2 \int_{p^{−rni+p'n_i+p'Z_p}} Y_0(x) \chi_p (p^{−r−1}jx) \, dx.
\]

We now use the subdivision

\[
p^{−rni+p'n_i+p'Z_p} = \bigsqcup_{n_i} p^{−rni+p'n_i+p'Z_p}.
\]

Then \( f((p^{−r}n_1)p)C_{(−r)}(p^{−r−rni+n})(0) \) becomes a finite sum of terms of the form

\[
Y_0 \left( p^{−rni+p'n_i+p'ni} \right) \chi_p \left( p^{−r−1}j \right) \left( p^{−rni+p'n_i+p'ni} \right) \left( p^{−rni+p'n_i+p'ni} \right) \times \begin{cases} 1 & \text{if } r \leq l - 1 \\ 0 & \text{if } r > l - 1. \end{cases}
\]

For details about the calculation of the integral involving the additive character, the reader may consult for instance [52, pp 42–43].

8.3. The Cauchy problem for the \( p \)-adic replicator equation

We now consider the following Cauchy problem:

\[
\begin{cases}
X : \mathbb{Q}_p \times \mathbb{R}_+ \to \mathbb{R}, \\
X(x, t) \in L_\mathbb{R} \cap L^2_\mathbb{R}, \ X(x, \cdot) \in C^1(\mathbb{R}_+, \mathbb{R}) \\
\frac{\partial X(x, t)}{\partial t} = WX(x, t) - \Phi(t)X(x, t), \ x \in \mathbb{Q}_p, t > 0 \\
X(x, 0) = Y_0 \in D_\mathbb{R}.
\end{cases}
\] (8.13)

By using (3.1), (3.4) and (8.12), we have

\[
\exp \left( \int_0^t \Phi(\tau) \, d\tau \right) = \int_{\mathbb{Q}_p} Y(x, t) \, dx
\]

\[
= \sum_{i=0}^{l(f)} \sum_{j=1}^{p−1} \sum_{\ell=−l}^{p−rni+n} \sum_{\rho=r−\ell} p^2 \mathcal{D}_{ij\rho,\rho,\rho} \mathcal{D}_{ij\rho,\rho,\rho} =: Y(t),
\]

where the \( D_{ij\rho,\rho,\rho} \) are real constants, which are obtained by integrating (8.12) termwise with respect to \( x \).

Therefore the solution of initial value problem (8.13) is given by
X(x,t) = \frac{1}{Y(t)} \sum_{j=0}^{l(f)} \sum_{p=1}^{p-1} \sum_{r \neq -r_i} \sum_{n_i \neq n_j} p^z e^{\text{Log}_p \Omega \left( \left| p^{-r} x - \left( p^{-r-i} n_i + n_j \right) \right|_p \right)} \times \left[ A_{p,r,n} \cos \left( 2 \pi \left\{ p^{-r-1} j x \right\}_p \right) - B_{p,r,n} \sin \left( 2 \pi \left\{ p^{-r-1} j x \right\}_p \right) \right]. \quad (8.14)

Notice that \( \int_{Q_p} X(x,t) \, dx = 1 \) for \( t > 0 \), and thus the hypothesis (3.1) holds, and consequently \( X(\cdot,t) \in L_\mathbb{R} \) for \( t > 0 \).

8.4. The p-adic quasispecies

In this section we consider the steady state concentration:

\[ \overline{X}(x) := \lim_{t \to +\infty} X(x,t), \quad (8.15) \]

which corresponds, in the classical terminology, to the p-adic quasispecies. We define

\[ \lambda_{\text{max}} = \max_{0 \leq i \leq l(f)} \left\{ f(\left| p^{-r} n_i \right|_p) \hat{Q}(p^{1+r}) \right\}. \]

We recall that the condition \( r \geq -r_i \) involves only a finite number of \( r_i \), since all the sums in (8.14) run through finite sets, this is a consequence of the fact that the Fourier expansion of \( \hat{Y}(x,t) \) is finite. We now define

\[ T = \left\{ rr_i n_f \; f(\left| p^{-r} n_i \right|_p) \hat{Q}(p^{1+r}) = \lambda_{\text{max}} \right\}. \]

Then, we have

\[ \overline{X}(x) = \frac{1}{C} \sum_{rr_i n_f \in T} p^z \Omega \left( \left| p^{-r} x - \left( p^{-r-r_i} n_i + n_j \right) \right|_p \right) \times \left[ A_{p,r,n} \cos \left( 2 \pi \left\{ p^{-r-1} j x \right\}_p \right) - B_{p,r,n} \sin \left( 2 \pi \left\{ p^{-r-1} j x \right\}_p \right) \right], \quad (8.16) \]

where

\[ C = \sum_{rr_i n_f \in T} \sum_{j=0}^{p-1} p^z D_{p,r,n}. \]

**Notation 3.** If \( U \) is an open and compact subset of \( \mathbb{Q}_p \), for instance a finite union of balls, we denote by \( D_\mathbb{R}(U) \), the \( \mathbb{R} \)-vector space of test functions with supports in \( U \).

Consider the following eigenvalue problem:

\[ W \varphi = \lambda \varphi, \quad \text{for} \quad \lambda \in \mathbb{R}, \quad \varphi \in D_\mathbb{R} \left( \prod_{i=0}^{l(f)} B_{p_i} \left( p^{-r_i} n_i \right) \right), \quad (8.17) \]

where \( \prod_{i=0}^{l(f)} B_{p_i} \left( p^{-r_i} n_i \right) \) is the support of \( f \), see (8.7). Then \( \lambda_{\text{max}} \) is the largest eigenvalue associated with (8.17).
On the other hand, from (8.16) we obtain that $X(x)$ is a continuous function with compact support, consequently, this function is integrable. By using the dominated convergence theorem and condition (3.1), we have

$$1 = \lim_{t \to +\infty} \int_{Q_p} X(x, t) \, dx = \int_{Q_p} \lim_{t \to +\infty} X(x, t) \, dx = \int_{Q_p} X(x) \, dx.$$ 

We now use the fact that $X(x, t) \geq 0$ (due to the physical meaning of this function), and thus $X(x) \geq 0$, in this way we reach the conclusion that $X(x)$ is a probability density supported in $\text{supp } f$.

This behavior is completely different from the one presented in the Eigen model. In the classical case, under the hypothesis that the mutation matrix has one largest eigenvalue, the steady state concentration is a constant vector having exactly one non-zero entry.

Acknowledgment

The author wishes to thank the referees for their careful reading of the original manuscript and for their helpful suggestions.

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