FIXATION TIME FOR AN EVOLUTION MODEL

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ABSTRACT. We study the asymptotic value as $L \to \infty$ of the *time for evolution* τ, understood as the first time to reach a preferred word of length L using an alphabet with N letters. The word is updated at unit time intervals randomly but configurations with letters matching with the preferred word are *sticky*, i.e. the probability to leave the configuration equals $0 \leq \gamma \leq 1$, where γ may depend on the configuration. The model is introduced in [5] in the case $\gamma = 0$, where it was shown that $E[\tau] \sim N \ln(L)$. We first give an alternative proof of the logarithmic scale, by evaluating the mode of τ. We then answer positively a question posed by H. Wilf on whether τ is exponential when$\gamma \neq 0$. The natural scaling $\gamma = O(L^{-1})$ gives rise to several finite order limits, including the *interacting* model when γ depends linearly on the number of matches with the preferred word. The scaling limit of the number of non-matching letters follows a Galton-Watson process with immigration. In a related model, the empirical measure converges to the solution of a discrete logistic equation with possible nonzero steady state.

1. INTRODUCTION

Let N be the size of an alphabet described as $\mathbb{Z}_N = \{0, 1, \ldots, N-1\}$ and L the length of a word formed with letters from the alphabet. On the state space $S = \mathbb{Z}_N^L$ we define a stochastic process $(Z_n)_{n \geq 1}$ whose evolution in time indexed by n is sensitive to reaching one special state. Without loss of generality, this will be equal to the null vector $\mathbf{0} = (0, \ldots, 0) \in S$.

Date: November 7, 2012.

1991 *Mathematics Subject Classification.* Primary: 60J70; Secondary: 60J75, 60J35.

Key words and phrases. evolution, Galton-Watson scaling limit, fixation time, discrete logistic equation.
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1.1. **The uniform model.** Let $Z_n^j \in \mathbb{Z}_N$ denote the components $1 \le j \le L$ of the configuration at time n of the chain $Z_n = (Z_n^1, \ldots, Z_n^L)$. In this first version of the model, the components Z_n^j evolve independently, with Markovian updates of the random vector Z_n to Z_{n+1}. Each component $j \neq 0$ moves by choosing another component with uniform probability N^{-1}. If $j = 0$, the updated character is $j' = 0$ with probability $1 - \gamma$ and any other $j' \neq 0$ with probability $\gamma(N-1)^{-1}$, i.e. conditional on moving away from zero, it is uniformly distributed (explaining the name). Here $0 \le \gamma \le 1$ is constant, but will depend on the current configuration in Section 3 (interacting case).

The hitting time of state $y \in S$, respectively its mean value when starting from $x \in S$ are denoted by

$$\tau(y) = \min\{n > 0 | Z_n = y\}\,, \qquad \rho(x,y) = E_x[\tau(y)]\,, \tag{1.1}$$

where the infimum over the empty set is $+\infty$ (in our discussion the hitting times are finite almost surely). We are interested in asymptotic estimates in L on the first hitting time $\tau = \tau(\mathbf{0})$ of the special state $\mathbf{0}$, more specifically on $\rho(x, \mathbf{0})$, when starting from a generic state $x \in S$.

A simple representation of the problem we are interested in emerges when the alphabet is the set of alleles with N possible types arranged in a chromosome of length L. From an evolutionary point of view, we assume that the state $\mathbf{0}$ is optimal. Random mutations occur at unit time intervals until this state is reached at time τ. If no state is preferred $\gamma = 1 - \frac{1}{N}$. Each update has probability N^{-L} of achieving the state $\mathbf{0}$. By independence, τ is geometric with mean value N^L. The special case $\gamma = 0$ was studied in [5], starting from the observation that an exponential τ may be too long for achieving evolution, since it is stated that in genetical applications N is relatively small ($\sim O(10^2)$), while L is large ($\sim O(10^4)$). Their result is more precise, containing also lower order terms, but we are mostly interested in scaling as $L \to \infty$. It is shown that when x is a state containing no zeros, then $\rho(x, \mathbf{0}) \sim N \ln L$.

The present paper studies the case $\gamma > 0$, seen as a selection parameter. Theorem 1 shows that for any other $\gamma \in (0,1)$ not depending on L, the mean time is again exponential, $E_{\mathbf{x}}[\tau] \ge C^L$, where C depends on the minimum value of the probabilities to reach zero in one step, answering an open question [6] posed by one of the authors of [5].

In some sense this is a negative result, since $\gamma = 0$ is an idealization and τ is too large in all other cases. However, we may refine the setup by allowing dependence on L.

We believe it is important that even under scaling allowing a finite τ, the presence of error γ leads to the possibly more realistic conclusion that genetic dynamics converges to certain steady states not completely fixated at the optimal configuration. In other words, even if there is time for evolution, equilibrium might not be optimal from an evolutionary point of view.

1.2. **The case $\gamma = 0$.** In this setting, τ does not depend on x unless it contains some 0. It has the distribution of the maximum of L independent geometric r.v. with probability of failure $q = 1 - 1/N$. Heuristically, the order of magnitude $\ln L$ can be obtained as follows. First, replace the geometric random variables with their continuous analogue, the exponential random variables of intensity $\lambda = |\ln q|$. We look at the expected value of the maximum of L i.i.d. exponentials.

Starting with L nonzero sites, the mean waiting time for the first to reach fixation (at zero) is equal to the mean value of the minimum of L exponential random variables. This is an exponential r.v. with mean $(|\ln q|L)^{-1}$. Once a site is fixated, we continue from the new configuration, having only $L-1$ nonzero sites. Repeating L times, we obtain

$$\frac{1}{|\ln q|}\left(1 + \frac{1}{2} + \ldots + \frac{1}{L}\right) \sim \frac{1}{|\ln q|}(\ln L + c_e)$$

where $c_e = .5772$ is Euler's constant. This is not rigorous, because the starting configurations at each step are themselves random.

A rigorous and still intuitive explanation of the logarithmic order of magnitude of τ can be obtained by evaluating the mode of the extreme order statistic τ. We recall that the *mode* of a distribution is the value maximizing its probability mass (density) function.

Proposition 1. *The mode T_{max} of the maximum τ of L independent geometric distributions with probability of success $1-q$, $0 < q < 1$ satisfies*

$$T_{max} = \frac{\ln L}{|\ln q|} + \frac{\ln(\frac{1-q}{q|\ln q|})}{|\ln q|} + c(q,L) + O(\frac{1}{L}), \quad |c(q,L)| \le \frac{1}{2}. \tag{1.2}$$

Remark. 1) When $\gamma = 0$, $q = 1 - \frac{1}{N}$ and the leading term is of order $N \ln L$, identical to the one in the asymptotic of $E[\tau]$ in [5].

2) As $q \to 1$ (i.e. $N \to \infty$) the middle term approaches $1/2$, so the term of order one in (1.2) is in $[0,1]$.

Proof. Since $P(\tau > n) = 1 - (1-q^n)^L$, we have to maximize

$$f_\tau(n) = (1-q^n)^L - (1-q^{n-1})^L\,, \quad n \geq 0\,.$$

The function $g(\alpha) = (1-q\alpha)^L - (1-\alpha)^L$ satisfies $g(q^{n-1}) = f_\tau(n)$ and its derivative $g'(\alpha) = L((1-\alpha)^{L-1} - q(1-q\alpha)^{L-1})$ vanishes only once in $[0,1]$. More precisely, $g'(0) > 0$, $g'(1) < 0$ and $g'(\alpha) = 0$ has a unique solution $\alpha = (1-q^{\frac{1}{L-1}})/(1-q^{\frac{L}{L-1}})$. Re-writing $q^{T_{max}-1} \sim \alpha$ and applying the logarithm we have that $T_{max}-1$ is approximated by $\ln\alpha/\ln q$ with error $c(q,L)$ to the nearest integer

$$T_{max} - 1 = |\ln q|^{-1} \ln\left(\frac{1-q^{\frac{L}{L-1}}}{1-q^{\frac{1}{L-1}}}\right) + c(q,L)\,, \quad |c(q,L)| \leq \frac{1}{2}\,.$$

The right hand side can be approximated with a Riemann sum of $\int_0^1 q^s ds = (q-1)/\ln q$

$$\ln\left(\frac{1-q^{\frac{L}{L-1}}}{1-q^{\frac{1}{L-1}}}\right) = \ln L + \ln\left(\frac{1}{L}\sum_{k=1}^{L-1} q^{\frac{k-1}{L-1}}\right) = \ln L + \ln(\frac{1-q}{|\ln q|}) + O(\frac{1}{L})\,,$$

giving (1.2). □

Before proceeding, we give a brief summary of the models under scaling.

In a first stage, $\gamma = c/L$, $c > 0$, independent of the configuration, since estimate (2.13) suggests that the natural scaling for a finite τ as $L \to \infty$ is $\gamma \sim O(L^{-1})$. We note that, asymptotically, τ no longer depends on L, i.e. we have time of evolution of order one.

In a second stage, γ will depend on L and the number of non-zero characters $u = L - e(x)$ of the current configuration, where

$$e(x) = \#\,\text{of components of } x \text{ equal to zero}\,. \tag{1.3}$$

Theorem 2 and its corollary obtain the limit as a Galton-Watson process when γ depends linearly on u of the current configuration.

It is remarkable that according to the criticality of the limiting process, the genome may degenerate moving away from the preferred state with positive probability; may have a quasi-invariant distribution or, for suitable parameters, as in the case of Galton Watson with immigration from Corollary 1, a proper invariant distribution. The same phenomenon occurs in Theorem 3, where the relative frequency (empirical measure) of the non-optimal characters converges to a deterministic sequence with possibly a non-zero steady state.

A third stage would have to consider random updates where the non-preferred characters are no longer chosen uniformly. The uniform model does not differentiate between non-optimal characters: an allele is either 0 or not, for example. This setup allows that $e(Z_n)$ be Markovian. Assume that mutations occur only to a nearest neighbor according to a simple random walk. In order to know $e(Z_n)$, we need to know the number of nearest neighbors of zero, and to know that number, we need, hierarchically, the number of second-order neighbors and so on. On the other hand, the model is closable, i.e. an equation can be written in terms of the empirical measure. In continuous time, under parabolic scaling in N we obtain a family of L diffusions on a torus interacting with *stickiness* about the origin. These directions will be pursued in a different paper.

2. The case $\gamma \neq 0$ independent of configuration

In this case $\gamma > 0$ and constant. The chain Z_n, as well as its independent components, are finite and recurrent.

Proposition 2. *The unique invariant measure $\mu = (\mu_i)_{0\leq i\leq N-1}$ of each component is*

$$\mu_0 = \frac{1}{1+\gamma N}\,, \quad \mu_j = \frac{\gamma N}{N-1}\mu_0\,. \tag{2.1}$$

The dynamics of the Markov chain is reversible with respect to μ.

Proof. The chain is finite irreducible hence positive recurrent and the invariant probability measure is unique and the weights (2.1) satisfy the master equations. Reversibility is easy to check. □

Let $U_n = L - e(Z_n)$, the number of non-zero components of $Z_n \in S$. Under this dynamics, U_n is a Markov chain on $\{0, 1, \ldots, L\}$. Its transition probabilities have generating functions

$$P(s^{U_{n+1}}|U_n = u) = \Big(\frac{1}{N} + (1-\frac{1}{N})s\Big)^u\Big(1-\gamma+\gamma s\Big)^{L-u} = A(s)^u B(s)^L \tag{2.2}$$

with

$$A(s) = \frac{\frac{1}{N} + (1-\frac{1}{N})s}{1-\gamma+\gamma s}\,, \qquad B(s) = 1-\gamma+\gamma s\,. \tag{2.3}$$

In other word, the updated U_{n+1} is the sum of two independent binomials, one with U_n trials and probability of success (to remain non-zero) $1-1/N$ and one with $L-U_n$ trials corresponding to the zero components, with probability of success (i.e. to convert into a non-zero character) equal to γ.

It is easy to guess that $Bin(L,1-\mu_0)$, $\mu_0=(1+\gamma N)^{-1}$ is the invariant measure of U_n. We give a direct proof of this fact.

Since the chain is irreducible with finite state space, the identity

$$\mu_0+(1-\mu_0)s=\Big(\mu_0+(1-\mu_0)A(s)\Big)\Big(1-\gamma+\gamma s\Big)$$

shows that

$$(2.4)\qquad E_{inv}[s^{U_n}]=\sum_{u=0}^{L}s^u\binom{L}{u}(1-\mu_0)^u\mu_0^{L-u}=\Big(\mu_0+(1-\mu_0)s\Big)^L$$

$$=\Big(\mu_0+(1-\mu_0)A(s)\Big)^L\Big(1-\gamma+\gamma s\Big)^L$$

$$=\sum_{u=0}^{L}A(s)^uB(s)^L\binom{L}{u}(1-\mu_0)^u\mu_0^{L-u}$$

$$=\sum_{u=0}^{L}E[s^{U_{n+1}}|U_n=u]P_{inv}(U_n=u)=E_{inv}[s^{U_{n+1}}]\,,$$

where E_{inv} is the expectation under the invariant measure.

Denoting $g_n(s)=E[s^{U_n}]$ the generating and log-generating function of the chain, $\psi_n(s)=\ln g_n(s)$ and $A_n(s)=A\circ A\ldots\circ A(s)$, the n-fold composition of A with itself, $A_0(s)=s$, we verify the relation

$$(2.5)\qquad \psi_{n+1}=\psi_n\circ A+L\ln B(s)\,,$$

derived from

$$(2.6)\qquad g_{n+1}(s)=\sum_{u=0}^{L}E[s^{U_{n+1}}|U_n=u]P(U_n=u)$$

$$=\sum_{u=0}^{L}A(s)^uB(s)^LP(U_n=u)=g_n(A(s))B(s)^L\,,$$

parallel to the generating equation of a Galton-Watson branching processes, where $A(s)$ is replaced by the generating function of the distribution of the offspring of one individual and $B(s) \equiv 1$, a relation explored in more detail in Section 3. Solving the recurrence (2.6) we obtain

$$g_n(s) = g_0(A_n(s))\Pi_{k=1}^{n} B^L(A_{n-k}(s))\,. \tag{2.7}$$

Since $A(s) - s$ has only one zero on $[0,1]$ at $s = 1$ and $A(0) > 0$, the sequence $A_n(s) \to 1$ for all $s \in [0,1]$. Comparing the generating functions of the invariant measure with the limit of the right-hand side of (2.7), we have shown the identity (after simplification by L)

$$1 + (1-\mu_0)(s-1) = \Pi_{k=0}^{\infty}(1 + \gamma(A_k(s) - 1))\,. \tag{2.8}$$

Theorem 1. *Let $\gamma \neq 0$. The time for evolution is exponential in L.*

(i) In the worst case scenario in $x \in S$

$$\max_{x \neq \mathbf{0}} \rho(x, \mathbf{0}) \geq \frac{(1+\gamma N)^L - 1}{1 - (1-\gamma)^L}\,; \tag{2.9}$$

(ii) For any $x \in S$, $x \neq \mathbf{0}$, $\rho(x, \mathbf{0}) \geq \rho_0(N, \gamma, L)$, where

$$\rho_0(N, \gamma, L) = \begin{cases} N(\frac{1}{1-\gamma})^{L-1}\,, & \text{if} \quad 0 \leq \gamma < 1 - \frac{1}{N} \\ N^L\,, & \text{if} \quad 1 - \frac{1}{N} \leq \gamma \leq 1 \end{cases}\,. \tag{2.10}$$

Remark. 1) The two estimates (2.9) and (2.10) are not a consequence of each other. Even though (2.9) is a larger lower bound that (2.10), it applies to maximal values of the expected time while the (2.10) applies to *any* initial configuration, i.e. including minimal expected times.

2)The first case of (2.10) is the most interesting since we expect γ to be small and N a positive integer. The asymptotic value depends linearly of N, but the dependence between L and γ is more relevant.

3) Estimates (2.9) and (2.10) coincide with N^L in the uniform case $N(1-\gamma) = 1$.

4) One can see that (2.10) defines a continuous nondecreasing function of γ with value $(1-\gamma)^{-L} = N^L$ at the critical $\gamma = 1 - \frac{1}{N}$.

5) The estimate of order $\log L$ from [5] cannot be obtained as $\gamma \to 0$.

Proof. Part (i). Since the invariant measure of Z_n is the product measure of the invariant measures over the components, $\mathbf{m}(x) = P_{inv}(Z_n = x) = \Pi_{l=1}^{L}\mu_{x(l)}$, where $x(l)$ is the l - th component of $x \in S$ and μ is defined in (2.1). As is well known in Markov chain theory, the mean time of return to a state y is the reciprocal of the weight at y, implying that

$$\rho(\mathbf{0},\mathbf{0}) = (1+\gamma N)^L \,. \tag{2.11}$$

We note that μ is correctly identified when $\gamma \to 0$ as the delta measure at $\mathbf{0}$, but the following estimates are not available for $\gamma = 0$, since positive recurrence is required.

A lower bound of the worst case scenario can be determined

$$\rho(\mathbf{0},\mathbf{0}) = 1 + \sum_{x\in S, x\neq \mathbf{0}} P_{\mathbf{0}}(Z_1 = x)\rho(x,\mathbf{0}) \leq 1 + P_0(Z_1 \neq \mathbf{0}) \max_{x\neq \mathbf{0}} \rho(x,\mathbf{0})$$

which gives the exponential lower bound in L (2.9).

Part (ii). Estimate (2.9) can now be improved to include any initial state and not just the worst case scenario (i.e. the maximum). The time $\tau(\mathbf{0})$ is equal to the time the chain U_n defined in (2.2) needs to reach the state zero when starting from an arbitrary state $U_0 = L - e(x)$, where $x = Z_0 \neq \mathbf{0}$.

Let q_0 be the upper bound of the probability to reach state $\mathbf{0}$ from an arbitrary state configuration containing at least one non-null character, more precisely

$$P(U_{n+1} = 0 | U_n = u) = (\frac{1}{N})^u (1-\gamma)^{L-u} = \frac{(1-\gamma)^L}{[N(1-\gamma)]^u} \leq q_0 \,, \qquad u \geq 1 \tag{2.12}$$

where the inequality is satisfied in all three cases for $q_0^{-1} = \rho_0(N,\gamma,L)$ from (2.10).

Applying the Markov property, it follows that

$$\rho(x,\mathbf{0}) = \sum_{n=0}^{\infty} P(\tau(\mathbf{0}) > n) \geq \sum_{n=0}^{\infty} (1-q_0)^n = \frac{1}{q_0}$$

which gives the lower bounds (2.10) for the time to reach the null state configuration.

□

Formulas (2.9) and the last line of (2.10) suggest the scaling $\gamma = c/L$, $c > 0$, leading to

$$\liminf_{L\to\infty} \max_{x\neq \mathbf{0}} \rho(x,\mathbf{0}) \geq \frac{e^{cN}-1}{1-e^{-c}} \geq N \tag{2.13}$$

since the lower bound is increasing in c.

3. Case when γ depends on configuration

In this section we look at the dependence of $\rho(x, \mathbf{0})$ on $e(x)$. We consider $\gamma = \gamma(u) = cu/L$, $c \geq 0$, when selection acts by making more stable (γ small) better genomes (with few nonzero entries).

Theorem 2. *As $L \to \infty$ the process U_n converges weakly to a Galton-Watson process where, independently, each individual alive at generation n dies and gives birth to a number X of offsprings where $X \sim Y + Z$ where $Y \sim Bin(1 - \frac{1}{N}, 1)$ (i.e. Bernoulli) and $Z \sim Poisson(c)$, Y, Z independent. The process is subcritical (critical) if $Nc < 1$ ($Nc = 1$) and supercritical when $Nc > 1$.*

Proof. To formalize the convergence in law, we note that the state space of the family of processes $U_N^{(L)}$, indexed by L, is $\mathbb{N}$ and the time is discrete. The only requirement in order to prove tightness of the family of processes is that for any n, $\lim_{M\to\infty} P(U_n^{(L)} > M) = 0$. Since the number of offspring per individual has exponential moments, this is a consequence of Chebyshev's inequality.

By examining (2.2), the limit as $L \to \infty$ of the generating function of U_{n+1}, conditional upon $U_n = u$ coincides with the generating function $\phi(s)^u$ of a sum of u i.i.d. random variables distributed as $Y + Z$ in the theorem.

Once tightness was established, the unique weak limit must solve the martingale problem for the limiting transition probabilities. This is a unique well defined process. Convergence in law follows.

This shows that the limiting process $(U_n)_{N\geq 0}$ is a Galton-Watson branching process with characteristic function

$$\phi(s) = \Big(\frac{1}{N} + (1 - \frac{1}{N})s\Big)e^{-c(1-s)}\,.$$

Let $m_X = E[X] = 1 - \frac{1}{N} + c$ the expected value of the number of individuals in a new generation and $p_0 = P(\tau < \infty)$ the probability of eventual extinction. Criticality depends on the sign of $m_X - 1$, which reduces to the sign of $Nc - 1$ like in the theorem. Since X has finite variance and $P(X < 2) < 1$ (which is always true for $c > 0$ and $N \geq 1$), all standard asymptotic results for Galton-Watson processes are applicable (see [1]). The probability of extinction is the smallest positive solution p_* of $\phi(p) = p$ and is known to be one when $m_X \leq 1$ and $0 < p_* < 1$ when $m_X > 0$. In the super-critical case $\lim_{n\to\infty} U_n/m_X^n = V$

a.s., where V is a mixed r.v. with point mass $P(V=0)=p_*>0$ at zero and continuous otherwise. $\square$

Remark. In the supercritical case with probability $1-p_*>0$ the a.s. limit is infinity - a way of formalizing, under scaling where $U_n << L$ already, the possibility of *devolution.*

It is interesting to consider the limit

$$\lim_{n\to\infty} P(U_n = u \,|\, n<\tau<+\infty) = \nu(u)\,, \qquad u\geq 0\,, \tag{3.1}$$

known to exist in all cases but trivial in the critical case (i.e. $\nu(u)\equiv 0$). Otherwise, both in the sub- and super-critical cases, the limit is a probability measure on $\mathbb{Z}_+$, known as the *quasi-invariant* measure. Its generating function $G_\nu(s)$ satisfies cf. [2]

$$G_\nu(p_0^{-1}\phi(p_0 s)) - 1 = m_X(G_\nu(s)-1)\,.$$

In the critical case, the limit (3.1) in distribution when U_n is replaced by U_n/n is an exponential with mean $\sigma_X^2/2$.

Corollary 1. *If $\gamma(u)=(cu+b)/L$, $c,b>0$, then as $L\to\infty$ the process (U_n) converges in law to the Galton-Watson process from Theorem 2 with immigration at the Poisson rate b. In the subcritical case $Nc<1$, the process has a unique invariant probability measure.*

Proof. Let $H(s)=\exp(b(s-1))$ be the generating function of the immigration variable. Based on [1] p. 264, the necessary and sufficient condition for the existence of the invariant probability measure is

$$\int_0^1 \frac{1-H(s)}{\phi(s)-s}ds<\infty\,.$$

In our setup, the integrand is actually continuous since its limit at $s\to 1$ is equal to $bN/(1-Nc)$. $\square$

3.1. **The empirical measure.** Let $\gamma:[0,1]\to\mathbb{R}$ be a bounded function and $(U_n)_{n\geq 0}$ the process with transition probabilities (2.2), where $\gamma=\gamma(U_n/L)$ is a function of the relative frequency function U_n/L. We note that the case γ constant is just a special case of this setup.

The transition probabilities (2.2) admit a scaling as $L\to\infty$ of the *relative* number of non-zero sites $u_n=u_n^{(L)}=U_n/L$, where the superscript is suppressed to keep notation simple. For $z \in (0,1]$, the generating function $E[z^{u_{n+1}}|u_n]$ of $u_{n+1}^{(L)}$, given $u_n^{(L)}$, can be derived from (2.2) by substituting $z = s^{\frac{1}{L}}$. It is

$$E[z^{u_{n+1}}|u_n] = \Big(\frac{1}{N} + (1-\frac{1}{N})z^{\frac{1}{L}}\Big)^{L(\frac{U_n}{L})}\Big(1-\gamma+\gamma z^{\frac{1}{L}}\Big)^{L(1-\frac{U_n}{L})} \tag{3.2}$$

which reduces to

$$= \Big(1 + (1-\frac{1}{N})(z^{\frac{1}{L}}-1)\Big)^{Lu_n}\Big(1+\gamma(u_n)(z^{\frac{1}{L}}-1)\Big)^{L(1-u_n)}. \tag{3.3}$$

Theorem 3. *Assume that $u_0^{(L)} = U_0/L$ converges in probability as $L \to \infty$, to the deterministic state $u \in [0,1]$ and $\gamma = \gamma(u)$, $0 \le u \le 1$ is continuous. Then, as $L \to \infty$, the Markov process $U_n^{(L)} = U_n/L$, $n \ge 0$, with state space $[0,1]$, converges in distribution to the deterministic process $(u_n)_{n\ge 0}$ on $[0,1]$ satisfying the discrete recurrence*

$$u_{n+1} = (1-\frac{1}{N})u_n + \gamma(u_n)(1-u_n)\,, \qquad u_0 = u\,. \tag{3.4}$$

Proof. The stochastic process $(u_n^{(L)})_{n\ge 0}$ has a compact state space $u_n \in [0,1]$, which implies it is *tight*. Since the time is discrete $n \in \mathbb{Z}_+$, convergence in distribution is equivalent to the convergence of the transition probabilities. For $g \ge 0$ continuous on $[0,1]$, let

$$\Phi_{g,L}(u) = \Big(1 + g(u)(z^{\frac{1}{L}}-1)\Big)^{Lu}, \quad \text{and} \quad \Phi_g(u) = z^{ug(u)}. \tag{3.5}$$

We notice that $0 \le \Phi_g(u) \le 1$ and there exists a constant $C(g,z)$ such that

$$|\Phi_{g,L}(u) - \Phi_g(u)| \le C(g,z)L^{-1}, \quad |\Phi_{g,L}(u)| \le C(g,z) + 1. \tag{3.6}$$

For $g_1(u) = 1 - \frac{1}{N}$, $g_2(u) = \gamma(u)$ we denote $C_i = C(g_i, z)$, $i = 1,2$, $C'(z) = (C_1+1)C_2 + (C_2+1)C_1$ and then we have the estimate

$$|\Phi_{g_1,L}(u)\Phi_{g_1,L}(u) - \Phi_{g_1}(u)\Phi_{g_2}(u)| \le C'(z)L^{-1}. \tag{3.7}$$

Let $n_0 > 0$ arbitrary but fixed and for $0 \le n \le n_0$ let $(u_n)_{n\ge 0}$ be a limit point of the process $(u_n^{(L)})_{n\ge 0}$ on $[0,1]^{\{0,1,\dots,n_0\}}$. For $h \in C_b(\mathbb{R}^{n+1})$, the definition of conditional probability says that (3.2)-(3.4) are equivalent to

$$E[z^{u_{n+1}^{(L)}}h(u_n^{(L)}, u_{n-1}^{(L)}, \dots, u_0^{(L)})] = E[\Phi_{g_1,L}(u_n^{(L)})\Phi_{g_2,L}(u_n^{(L)})h(u_n^{(L)}, u_{n-1}^{(L)}, \dots, u_0^{(L)})]. \tag{3.8}$$

Due to (3.7), the right-hand side is equal to

$$E[\Phi_{g_1}(u_n^{(L)})\Phi_{g_2}(u_n^{(L)})h(u_n^{(L)}, u_{n-1}^{(L)}, \dots, u_0^{(L)})] + O(L^{-1}) \tag{3.9}$$

where the error is uniform in the variables u. Tightness together with the fact that $z^u h(\cdot)$ and $\Phi_{g_1}(u)\Phi_{g_2}(u)h(\cdot)$ are continuous bounded functions implies that the limit as $L \to \infty$ of the left-hand side of (3.8) and the first term of (3.9) are equal, i.e.

$$E[z^{u_{n+1}} h(u_n, u_{n-1}, \dots, u_0)] = E[\Phi_{g_1}(u_n)\Phi_{g_2}(u_n)h(u_n, u_{n-1}, \dots, u_0)]$$

with no superscript (L). This means $E[z^{u_{n+1}}|u_n] = z^{u(g_1(u_n)+g_2(u_n))}$ for the limiting process. Since u_0 is deterministic, the uniqueness of generating functions proves the result. □

Corollary 2. *(i) If $\gamma(u) = \gamma$, then*

$$u_n = (u + 1 - \mu_0)[1 - (\frac{1}{N} + \gamma)]^n + (1 - \mu_0)\,, \tag{3.10}$$

where $\mu_0 = (1 + \gamma N)^{-1}$ is defined in (2.1).

(ii) If $\gamma(u) = cu$, $0 \le c \le 1$, then (u_n) solves the discrete logistic equation

$$u_{n+1} = (1 - \frac{1}{N} + c)u_n - cu_n^2\,. \tag{3.11}$$

For $0 \le c \le \frac{1}{N}$, the solution becomes extinct in finite time, and for $\frac{1}{N} < c \le 1$, the solution converges to the stable stationary state $u_* = 1 - \frac{1}{Nc}$.

Remark. From the point of view of the genetical model, the criticality in (ii) is remarkable. Since $N = O(10^2)$, for about 99% of the spectrum of values c, the empirical measure $u_n = U_n/L$ of *non-optimal* states U_n approaches a positive value. Even though the time scale is finite versus $L \to \infty$, the system does not achieve the evolutionary state $u = 0$. At the same time, since the coefficient $1 - N^{-1} + c < 2$ the behavior is not periodic, nor chaotic.

Proof. Part (i) is immediate. In (ii) we notice that when $c \le \frac{1}{N}$ the sequence is strictly decreasing, unless $u_0 = 0$, in which case $u_n \equiv 0$, $n \ge 0$. Since (u_n) is bounded below, the only possible limit is the steady state $u = 0$. When $c > \frac{1}{N}$, we normalize the sequence by $v_n = \frac{c}{k}u_n$, $k = (1 - N^{-1} + c) \in (0, 1)$ as long as $N > 1$, which is always true since $N = 1$ is trivial. It is well known [3, 4] that the canonical discrete logistic equation $v_{n+1} = kv_n(1-v_n)$, $v_n \in [0, 1]$ has a stable steady state $(k - 1)^{-1}$ when $k \in (1, 3)$.

□

References

[1] Athreya, K. B. and Ney, P. E. (1972). Branching Processes. Springer, New York.

[2] Grimmett, G.; Stirzaker, D. *Probability and Random Processes* Clarendon Press, 2nd ed., Oxford 1992

[3] May, R. M. Simple mathematical models with very complicated dynamics. Nature 1976; 261:459 - 67.

[4] Lopez-Ruiz, R.; Fournier-Prunaret, D. *Periodic and chaotic events in a discrete model of logistic type for the competitive interaction of two species.* Chaos Solitons Fractals 41 (2009), no. 1, 334-347.

[5] Herbert S. Wilf and Warren J. Ewens *There's plenty of time for evolution* PNAS 2010 107: 22454-22456. `www.pnas.org/cgi/doi/10.1073/pnas.1016207107`

[6] Herbert S. Wilf *There's plenty of time for evolution.* University of Miami Colloquium, 2011. `http://www.math.miami.edu/anno/colloquium.htm`