A STOCHASTIC MODEL FOR EVOLUTION WITH MASS EXTINCTION ON $\mathbb{T}_d^+$

CAROLINA GREJO, FÁBIO LOPES, FÁBIO MACHADO, AND ALEJANDRO ROLDÁN-CORREA

Abstract. We propose a stochastic model for evolution through mutation and natural selection that evolves on a $\mathbb{T}_d^+$ tree. We obtain sharp and distinct conditions on the set of parameters for extinction and survival both on the whole $\mathbb{T}_d^+$ and on a fixed branch of it.

1. Introduction

We propose a stochastic model for evolution through mutation and natural selection whose dynamic combines features presented in a set of papers as it assumes that (i) the immune system is able to get rid, after a random time, of all the pathogens of a given type at once as in Schinazi and Schweinsberg [9], (ii) the clock which counts down the random time until a type of pathogen is removed from the organism does not start ticking until the pathogen’s progenitor dies, as in Aldous and Krebs [1] and (iii) while we only consider mutations that bring some kind of improvement to the pathogens, we still kill the least fit as in Guiol et al [3].

Our model is an interacting particle system evolving on $\mathbb{T}_d^+$ (a rooted tree whose vertices - except for the root - have $d+1$ nearest neighbours) and whose state space is $\{0, 1\}^{\mathbb{T}_d^+}$. At time $t = 0$ there is only one particle (representing a pathogen) in the system, located at the root of $\mathbb{T}_d^+$, whose type (or fitness) is 0. This particle will have an exponential
lifetime of rate 1. During its lifetime, following a Poisson process of rate $\lambda$, it generates mutations, particles of type 1 which will be placed randomly, one by one, on its $d$ nearest neighbours up to the time it dies or up to the event that all its nearest neighbours are occupied.

In general, each particle of type $i$ generates particles (mutations) of type $i + 1$ which will be placed randomly, one by one, at one of the $d$ nearest neighbours which are farther from the root than its position, up to the time it dies or up to the event that all these $d$ nearest neighbours are occupied. Like the process studied in Aldous and Krebs [1], the ‘clock’ which counts down time until a particle’s death (exponential lifetime of rate 1) does not start ticking until that particle’s parent dies. Unlike that process, there is only one clock for all mutation of same type. As a consequence, (i) a mutation is not at risk while its progenitor is alive and (ii) a death event at a given time, kills all the least fit mutations (types whose numbers are lower) present in the process. In this sense, our model is also related to spatial catastrophic models where large sets of individuals are simultaneously removed, see for example Lanchier [6] and Machado et al. [7]. We can imagine the particles in this process as pathogens in such way that if the process dies out, the disease is defeated.

The aim of this paper is to find conditions under which (i) particles are eventually removed from $T^+_{d}$, (ii) particles are eventually removed from any fixed infinite branch of $T^+_{d}$ and (iii) compare these two conditions.

**Definition 1.1.** If all particles are eventually removed from $T^+_{d}$ with probability 1, we say that the process **dies out**. Otherwise, we say that the process **survives**.

Let us introduce the notation $\eta_t \in \{0, 1\}^{T^+_{d}}$ for the status of the vertices in terms of occupation at time $t$ and $|\eta_t|$ for the amount of particles present at time $t$. Observe now that $\eta_t$ is a Markovian process and that by coupling arguments, one can see that the probability of
survival is a non-decreasing function of $\lambda$. This is so because more births (greater $\lambda$) can only help survival. So we define

$$\lambda_c(d) := \inf \{ \lambda : \mathbb{P}(|\eta_t| \geq 1 \text{ for all } t \geq 0) > 0 \}$$

2. Results

We prove phase transition (meaning that $0 < \lambda_c(d) < \infty$) for this process. An analogous result also holds when we consider only what happens in a fixed branch of $T_d^+$. From these results we point out that there is a region in the space parameter in which we have the extinction of each fixed branch with probability 1, but the process survives on the whole tree with positive probability.

**Theorem 2.1.** For $d$ fixed

$$\lambda_c(d) = \inf \left\{ \lambda : \inf_{0<u<1} \frac{\lambda}{u(1-u)} \left[ 1 - \left( \frac{\lambda}{\lambda+u} \right)^d \right] > 1 \right\}.$$ 

If $\lambda < \lambda_c(d)$ then the process $\eta_t$ gets extinct with probability 1. If $\lambda > \lambda_c(d)$ then the process $\eta_t$ survives with positive probability.

**Theorem 2.2.** For $d$ fixed, let $B$ be a fixed infinite branch of $T_d^+$ and $\lambda_s(d)$ defined by

$$\lambda_s(d) := \inf \left\{ \lambda : d - 2\lambda \left[ 1 - \left( \frac{\lambda}{\lambda+1} \right)^d \right] < 0 \right\}.$$ 

If $\lambda \leq \lambda_s(d)$ then the process gets extinct along $B$ with probability 1. If $\lambda > \lambda_s(d)$ then the process survives along $B$ with positive probability.

**Remark 2.3.** Let us define

$$f_d(\lambda) := \inf_{0<u<1} \frac{\lambda}{u(1-u)} \left[ 1 - \left( \frac{\lambda}{\lambda+u} \right)^d \right],$$

$$h_d(\lambda) := d - 2\lambda \left[ 1 - \left( \frac{\lambda}{\lambda+1} \right)^d \right].$$

The function $f_d(\lambda)$ is continuous and strictly monotone in $(0,1)$, $f_d(0) = 0$ and $f_d(1) > 1$. Thus, by Theorem 2.1, we have that $\lambda_c(d)$
is the unique solution for $f_d(\lambda) = 1$. Analogously, by Theorem 2.2 we have that $\lambda_s(d)$ is the unique solution for $h_d(\lambda) = 0$.

The following table shows some numerical approximations for $\lambda_c(d)$ and $\lambda_s(d)$.

| $d$ | 2   | 3   | 4   | 5   | 6   | 7   |
|-----|-----|-----|-----|-----|-----|-----|
| $\lambda_c(d)$ | 0.29335 | 0.26103 | 0.25333 | 0.25107 | 0.2504 | 0.2501 |
| $\lambda_s(d)$ | 1.6180 | 2.2406 | 2.8650 | 3.4904 | 4.1165 | 4.7429 |

Thus, for any $\lambda \in (\lambda_c(d), \lambda_s(d)]$ the process gets extinct along any fixed infinite branch with probability 1 while it survives on $T_d^+$ with positive probability. From the fact that $\lim_{d \to \infty} f_d(\lambda) = 4\lambda$ and adapting the proof of Proposition 3.1 in Junior et al. [4] one can see that

$$
\lambda_c(d) \to 1/4.
$$

A peripheral curiosity: two positive quantities are in the golden ratio if their ratio is the same as the ratio of their sum to the larger of the two quantities. Algebraically, for quantities $a$ and $b$ with $0 < b < a$

$$
\varphi := \frac{a + b}{a} = \frac{a}{b}
$$

$\varphi$ represents the golden ratio and its value is

$$
\varphi = \frac{1 + \sqrt{5}}{2}
$$

which, by its turn equals $\lambda_s(2)$.

3. Proofs

We first introduce some notation necessary for the proof of Theorem 2.1. For fixed $d \geq 1$, let $N = \{1, \ldots, d\}$ and $\mathcal{N} = \bigcup_{n=0}^{\infty} N^n$ be the set of finite $n$-tuples with entries in $N$ (with $N^0 = \emptyset$). Clearly, there is an one to one mapping between $\mathcal{N}$ and the set of vertices of $T_d^+$. The Figure 3.1 shows a representation of all vertices of $T_2^+$ with vertex depth up to 3.

**Remark 3.1.** The proof below follows the same strategy of the one presented for the survival and extinction of the birth-and-assassination
(BA) process by Aldous & Krebs [1]. Interestingly, for the BA process this strategy works with any clock distribution whose moment generating function is finite in some neighborhood of 0, while in our case there are distributions for which the strategy does not work. The reason for this is that in our model all particles (mutations) of the same type share the same clock, while in the BA process each particle has its own clock. This additional dependence among the particles in our model poses a problem for the comparison with a branching process, which is applied to prove the survival of the BA process in [1]. Nevertheless, when the clocks are exponentially distributed, the lack of memory of these random variables still allow us to make such comparison.

Proof Theorem 2.1. First, we show that, the process goes extinct with probability 1, if \( \inf_{0<u<1} \left\{ \frac{\lambda u}{u(1-u)} \left[ 1 - \left( \frac{\lambda}{\lambda+u} \right)^d \right] \right\} < 1. \)

Let \( X_i, i = 1, \ldots, d, \) denote independent Gamma random variables with parameters \( i \) and \( \lambda, \) respectively, and consider a random variable \( W \) with probability distribution given by

\[
\mathbb{P}(W \leq w) = \frac{1}{d} \left[ \sum_{i=1}^{d} \mathbb{P}(X_i \leq w) \right], \quad w \geq 0.
\]
Note that, for \( u > 0 \),
\[
\mathbb{E} [e^{-uW}] = \frac{1}{d} \left[ \frac{\lambda}{\lambda + u} + \left( \frac{\lambda}{\lambda + u} \right)^2 + \cdots + \left( \frac{\lambda}{\lambda + u} \right)^d \right] = \frac{\lambda}{ud} \left[ 1 - \left( \frac{\lambda}{\lambda + u} \right)^d \right].
\]

In our model, each time a particle occupying a vertex at the \( k \)-th level of \( \mathbb{T}_d^+ \) has an offspring, it chooses uniformly at random a position to place its offspring among its empty neighboring vertices at the \( k + 1 \)-th level of \( \mathbb{T}_d^+ \); once no empty vertex is left all incoming children are ignored. In the absence of any information on these births and the ordering of the occupancy of the neighboring vertices at the \( k + 1 \)-th level, the time which is necessary for a fixed vertex at the \( k + 1 \)-th level to receive a child of a particle on its neighboring vertex at the \( k \)-th level has the same distribution of a random variable \( W \). Of course, such ‘virtual’ births only become ‘real’ ones, if the particle at the \( k \)-th level has these births before the killing event that removes all particles at the \( k \)-th level.

Let \( \{K_i\} \) be independent exponential random variables with parameter 1, and let \( \{W_i\} \) be independent copies of the random variable \( W \). Suppose that no information is known on the genealogy of a vertex at the \( k \)-th level in a given branch of \( \mathbb{T}_d^+ \). Then, the probability that a particle is born at a given vertex at the \( k \)-th level of \( \mathbb{T}_d^+ \) is equal to

\[
\mathbb{P} \left( \sum_{i=1}^{j} W_i < \sum_{i=1}^{j} K_i, \ j = 1, \ldots, k \right),
\]

Note that, this probability is the same for every vertex at the \( k \)-th level and that, there are \( d^k \) such vertices. Thus,
\( \mathbb{E} \) (total number of particles born in the process) =

\[
= \sum_{n \in \mathcal{N}} \mathbb{E}[\mathbb{I}\{ \text{a particle is born at } \bar{n} \}]
\]

\[
= \sum_{k \geq 1} d^k \mathbb{P} \left( \sum_{i=1}^{j} W_i < \sum_{i=1}^{j} K_i, \; j = 1, \ldots, k \right)
\]

\[
\leq \sum_{k \geq 1} d^k \mathbb{P} \left( \sum_{i=1}^{k} W_i < \sum_{i=1}^{k} K_i \right)
\]

\[
\leq \sum_{k \geq 1} d^k \mathbb{E} \left[ e^{u(\sum_{i=1}^{k} K_i - \sum_{i=1}^{k} W_i)} \right],
\]

where the second inequality is obtained by using Markov’s inequality for \( u > 0 \), and the last expression follows from independence and the properties of the moment generating functions of the random variables \( \{ K_i \} \) and \( \{ W_i \} \).

Clearly, if \( \inf_{0 < u < 1} \left\{ \frac{\lambda u}{u(1-u)} \left[ 1 - \left( \frac{\lambda}{\lambda + u} \right)^d \right] \right\} < 1 \), then

\( \mathbb{E} \) (total number of particles born in the process) < +\( \infty \).

In this case, the process goes extinct since with probability 1 only a finite number of particles enters the system.

Next, we show that, when \( \inf_{0 < u < 1} \left\{ \frac{\lambda u}{u(1-u)} \left[ 1 - \left( \frac{\lambda}{\lambda + u} \right)^d \right] \right\} > 1 \), the process survives with positive probability. For this, we need the following lemma of Aldous & Krebs [1], which gives a large deviation estimate for the probability that a particle is born at the \( k \)-th level of \( \mathbb{T}_d^+ \).

**Lemma 3.2.** [1 Lemma 1] Let \( X_1, X_2, \ldots \) be i.i.d. random variables with \( \mathbb{E}[X] < 0 \) and \( \mathbb{P}[X > 0] > 0 \). Let \( \mathbb{E}[e^{uX}] = \psi(u) \) be finite in some neighborhood of 0, and let \( \rho = \inf_{u > 0} \psi(u) \). Then,

\[
\lim_{n \to \infty} \log \mathbb{P} \left[ \sum_{j=1}^{k} X_j > 0, k = 1, \ldots, n. \right] = \log \rho.
\]
Let \( Z_i = K_i - W_i, \ i = 1, \ldots, n \). The probability that a particle is born at a fixed vertex at the \( k \)-th level can be rewritten as

\[
\mathbb{P} \left( \sum_{i=1}^{j} Z_i > 0, \ j = 1, \ldots, k \right).
\]

It is easy to check that, \( \mathbb{E}[Z] < 0 \) if \( \lambda < (d+1)/2 \). So, by Lemma 3.2

\[
\lim_{k \to \infty} \frac{1}{k} \log \mathbb{P} \left( \sum_{i=1}^{j} Z_i > 0, \ j = 1, \ldots, k \right) =
\]

\[
= \log \left[ \inf_{0 < u < 1} \left\{ \frac{\lambda}{u(1-u)} \left[ 1 - \left( \frac{\lambda}{\lambda+u} \right)^d \right] \right\} \right].
\]

Moreover, by assumption, for some \( \delta > 0 \),

\[
\inf_{0 < u < 1} \left\{ \frac{\lambda}{u(1-u)} \left[ 1 - \left( \frac{\lambda}{\lambda+u} \right)^d \right] \right\} = 1 + \delta.
\]

Suppose for now that \( \lambda < (d+1)/2 \) and take \( \epsilon = \delta/2 \). Then, there exists \( K \in \mathbb{N} \) such that for all \( k \geq K \),

\[
\mathbb{E}[\text{number of particles type } k]
\]

\[
= d^k \mathbb{P} \left( \sum_{i=1}^{j} Z_i > 0, \ j = 1, \ldots, k \right)
\]

\[
> d^k \left[ \inf_{0 < u < 1} \left\{ \frac{\lambda}{d u(1-u)} \left[ 1 - \left( \frac{\lambda}{\lambda+u} \right)^d \right] \right\} - \epsilon \right]^k
\]

\[
= \left[ \inf_{0 < u < 1} \left\{ \frac{\lambda}{u(1-u)} \left[ 1 - \left( \frac{\lambda}{\lambda+u} \right)^d \right] \right\} - \epsilon \right]^k
\]

\[
= (1 + \delta/2)^k > 1.
\]

Note that each particle whose type is \((n - 1)k\), may have at most \( d^{nk} \) mutations of type \( nk \). Moreover, the probability that a certain particle of type \((n - 1)k\) has a mutation of type \( nk \) is greater than the probability that the particle originally located at the root has mutation of type \( k \). This follows since by the time a particle of type \((n - 1)k\) is born, it may not be at risk because some killing events corresponding
to the previous types may still be pending. Therefore, the expected number of particles of type \( nk \), mutations of a given particle of type \((n - 1)k\), is also greater than 1.

Now we define \( \{Y_n\}_{n \geq 1} \) as an auxiliary process such that \( Y_n \) is the number of particles of type \( nk \) born in the process \( \eta_t \). Note that, from the definition of \( \eta_t \), \( Y_0 = 1 \) and from the previous paragraph, \( \{Y_n\}_{n \geq 1} \) dominates a Galton-Watson process with mean offspring \( \mathbb{E}[Y_1] \). Since \( \mathbb{E}[Y_1] > 1 \), the process \( \{Y_n\}_{n \geq 1} \) survives with positive probability and, consequently, \( \eta_t \) also does.

To conclude, a simple coupling argument can show that the survival probability is non-decreasing in \( \lambda \). Hence, this result also holds for \( \lambda \geq (d + 1)/2 \) provided \( \inf_{0 < u < 1} \left\{ \frac{\lambda}{u(1-u)} \left[ 1 - \left( \frac{\lambda}{\lambda + u} \right)^d \right] \right\} > 1. \)

\[ \square \]

**Remark 3.3.** Bordenave [2] showed that the BA process dies out at criticality for exponential clocks, Kortchemski [5] extended this result for general clock distributions as in [1]. We could not extend the analytical approach of Bordenave to our model, and believe that the branching random walk approach of Kortchemski cannot be easily extended either due to the extra dependencies in our dynamics mentioned before.

**Proof Theorem 2.2.** Let \( \{B_i\}_{i \geq 1} \) and \( \{K_i\}_{i \geq 1} \) be families of independent and exponentially distributed random variables with rates \( \lambda \) and 1, respectively. Consider a fixed branch \( B \) of \( \mathbb{T}_d^+ \) and \( X(t) \) the amount of types of particles on \( B \) at time \( t \geq 0 \), in particular \( X(0) = 1 \).

Observe that if at time \( t \) there is group of \( k \geq 1 \) particles along \( B \) (a clan), then \((i)\) they are located contiguously and \((ii)\) this amount may increase or decrease by one. It will increase whenever the next event is a birth of a new mutation along that branch. That new mutation can be the \( j \)-th mutation, \( j = 1, \ldots, d \), of the particle which is at the edge of this group, the one with the highest type. It will decrease whenever the head of the clan, the one with the lowest type, dies. The state 0 is absorbing. Therefore \( X_n \), denoting the discrete imbedded process for \( X(t) \), is a Markov chain whose transition probabilities are
\[ pk := \mathbb{P}(X_{n+1} = k + 1 | X_n = k) \]
\[ = \frac{1}{d} \left[ \mathbb{P}(B_1 < K_1) + \mathbb{P}(B_1 + B_2 < K_1) + \cdots + \mathbb{P}(\sum_{i=1}^{d} B_i < K_1) \right] \]
\[ = \frac{1}{d} \left[ \frac{\lambda}{1 + \lambda} + \left( \frac{\lambda}{1 + \lambda} \right)^2 + \cdots + \left( \frac{\lambda}{1 + \lambda} \right)^d \right] \]
\[ = \frac{\lambda}{d} \left[ 1 - \left( \frac{\lambda}{1 + \lambda} \right)^d \right] \]

and
\[ q_k := \mathbb{P}(X_{n+1} = k - 1 | X_n = k) = 1 - p_k. \]

We can take advantage from results to birth and dead Markov chains as those presented in details in Schinazi [8, Proposition 2.2, Chapter 5]. From there we know that \( X_n \) dies out if and only if
\[ \sum_{k=1}^{\infty} \prod_{i=1}^{k} \left( \frac{q_i}{p_i} \right) = \sum_{k=1}^{\infty} \left( \frac{q_1}{p_1} \right)^k = +\infty. \]
This implies \( X(t) \) dies out with probability one if and only if
\[ \frac{q_1}{p_1} \geq 1. \]

\[ \square \]

4. Acknowledgments

F. Lopes and A. Roldán (C. Grejo) wish to thank the Instituto de Matemática e Estatística of Universidade de São Paulo for the warm hospitality during their scientific visits to (her postdoc experience at) that institute. F. Lopes is also grateful for the support of the Centro de Modelamiento Matemático (CMM). The authors are thankful to Daniel Valesin and Iddo Ben Ari for helpful discussions about the model.
REFERENCES

[1] D. Aldous and W. B. Krebs. The Birth-and-Assassination process. *Statistics and Probability Letters*, 10, 427-430, (1990).
[2] C. Bordenave. On the birth-and-assassination process, with an application to scotching a rumor in a network. *Elect. J. Probab.*, 13, 2014-2030, (2008).
[3] H. Guiol, F. Machado and R. Schinazi. A Stochastic model of evolution. *Markov Process. Related Fields*, 17, (2), 253-258, (2011).
[4] V.V. Junior, F.P. Machado and A. Roldán-Correa. Dispersion as a Survival Strategy. *Journal of Statistical Physics*, 159, (4), 937-951, (2016).
[5] I. Kortchemski. Predator-prey dynamics on infinite trees: a branching random walk approach. *J. Theor. Probab.*, 29, 1027-1046 (2016).
[6] N. Lanchier. Contact process with destruction of cubes and hyperplanes: forest fires versus tornadoes. *J. Appl. Probab.* 48, (2), 352-365 (2011)
[7] F.P. Machado, A. Roldán-Correa and R. B. Schinazi. Colonization and Collapse. *ALEA, Lat. Am. J. Probab. Math. Stat.* 14, 719-731 (2017)
[8] R. Schinazi. Classical and spatial stochastic process with applications to biology. Second Edition. *Birkhäuser*. (2014).
[9] R. Schinazi and J. Schweinsberg. Spatial and Non-spatial Stochastic Models for Immune Response. *Markov Process. Related Fields*, 14, (2), 255-276, (2008).

(C. Grejo and F. Machado) INSTITUTE OF MATHEMATICS AND STATISTICS, UNIVERSIDADE DE SÃO PAULO, BRAZIL.

E-mail address: carolina@ime.usp.br
E-mail address: fmachado@ime.usp.br

(F. Lopes) CENTER FOR MATHEMATICAL MODELING, UNIVERSIDAD DE CHILE, CHILE

E-mail address: flopes@dim.uchile.cl

(A. Roldan) INSTITUTO DE MATEMÁTICAS, UNIVERSIDAD DE ANTIOQUIA, COLOMBIA

E-mail address: alejandro.roldan@udea.edu.co