Probabilistic approach to a cell growth model

Gregory Derfel
Department of Mathematics
Ben-Gurion University of the Negev Beersheba, Israel

Yaqin Feng
Department of Mathematics
Ohio University, Athens, Ohio 45701, USA

Stanislav Molchanov *
Department of Mathematics and Statistics
University of North Carolina at Charlotte, Charlotte, NC 28223, USA
National Research University, Higher School of Economics, Russian Federation

Abstract: We consider the time evolution of the supercritical Galton-Watson model of branching particles with extra parameter (mass). In the moment of the division the mass of the particle (which is growing linearly after the birth) is divided in random proportion between two offsprings (mitosis). Using the technique of moment equations we study asymptotics of the mass-space distribution of the particles. Mass distribution of the particles is the solution of the equation with linearly transformed argument: functional, functional-differential or integral. We derive several limit theorems describing the fluctuations of the density of the particles, first two moments of the total masses etc. Also, we consider the branching process in the presence of a random spatial motion (say, diffusion). Here we discuss the classical Fisher, Kolmogorov, Petrovski, Piskunov model and distribution of mass inside the propagation front.

1 Introduction

A model for the simultaneous growth and division of a cell population, structured by size, was introduced and studied by Hall and Wake [18] (cf. [23]). The original model deals with symmetrical cell-division, where each cell divides into \( \kappa \) equally sized daughter cells. Under this assumption Hall and Wake proved that the steady-size mass distribution exists and satisfies the celebrated panto-
graph functional-differential equation

\[ y'(x) = ay(\kappa x) + by(x) \]  

(1)

where \( \kappa > 1 \). Since then, different variations and extensions of the original model have been studied and used to describe plant cells, diatoms [2, 4, 11, 8] and also tumor growth [3].

In the present paper, in order to describe cell growth model we use the supercritical Galton-Watson model of branching particles with extra parameter (mass). Similar approach was applied earlier in [11].

Namely, we assume that the mass of the particle is growing linearly between the exponentially distributed splitting moments and that in the moment of the division the mass of the particle is divided in a random proportion between two offspring (see Figure 1 below). Notice that under these assumptions splitting moments depend on mass.

The model described above gives only rather schematic description of the cell growth process, but it is interesting from the mathematical point of view, and hopefully in some cases may reflect an important qualitative features of real biological systems [2, 4, 11, 8, 3].

We start from the study of the total number of the particles \( N(t) \), their distribution with respect to the mass, and first two moments of the total mass distribution. We study the asymptotic of the mass distribution of the particles and prove several limit theorems.

Let \( N(t) \) be the supercritical Galton-Watson process [16] with mortality rate \( \mu \) and splitting rate \( \beta > \mu \geq 0 \). Assume that at initial time \( 0, N(0) = 1 \). For the generating function \( u_z(t) = E_z^N(t) \), we have the well known equation [19]:

\[
\frac{\partial u_z(t)}{\partial t} = \beta u_z(t)^2 - (\beta + \mu)u_z(t) + \mu
\]

(2)

Let \( \delta = \beta - \mu \) and \( \gamma = \frac{\mu}{\beta} \), elementary calculations give for \( N(t) \) the geometric distribution

\[ P(N(t) = k) = \frac{(1 - \gamma)^2 (1 - e^{\delta t})^{k-1} e^{\delta t}}{(\gamma - e^{\delta t})^{k+1}}, k \geq 1, \]

(3)

\[ P(N(t) = 0) = \frac{1 - e^{\delta t}}{1 - \frac{1}{\gamma} e^{\delta t}}, \]

(4)

\[ EN(t) = e^{\delta t}, \]

and for any \( a \geq 0 \), as \( t \to \infty \),

\[ P \left\{ \frac{N(t)}{e^{\delta t}} \in (a, a + da) \right\} = (1 - \gamma) e^{-a} + \gamma \delta_0(a). \]
Assume now that the initial particles have mass \( m > 0 \). The evolution of the mass \( m(t) \) includes two features. First of all we assume the linear growth:

\[
m(t) = m + vt,
\]

where \( v > 0 \) until the splitting. Probability of the splitting in each time interval \([t, t + dt]\) equals \( \beta dt \), i.e. the moment \( \tau_1 \) of splitting of the initial particle has exponential law with parameter \( \beta \) and \( P \{ \tau > t \} = e^{-\beta t} \). At the moment \( \tau_1 \), the particle with mass \( m + v\tau_1 \) is divided into two particles with the random masses:\( m' = \theta (m + v\tau_1) \), \( m'' = (1 - \theta) (m + v\tau_1) \). Here \( \theta \in [0, 1] \) is symmetrically distributed (with respect to the center 0.5 \( \in [0, 1] \)) random variable which has the density \( q(x) = q(1 - x) \), \( x \in [0, 1] \). As usually we assume that the random variable \( \theta_i \), \( i = 1, 2, \ldots \) for different splittings are independent. The dynamics of the sub-populations generated by different offspring are also independent.

Let us introduce the main object of our study: the moment gene rating function of the two random variables:

\[
N(t) := \text{total numbers of particles at the moment } t > 0, \\
M(t) := \text{total mass of the particles at the moment } t.
\]

We introduce the generating function of the form:

\[
u(t, m; z, k) = \mathcal{E} m z N(t) e^{-kM(t)}, |z| \leq 1, k \geq 0.
\]

The following results are the basis for the further analysis:

**Theorem 1.** Let \( u(t, m; z, k) = E z^{N(t)} e^{-kM(t)} \), then \( u(t, m; z, k) \) satisfy the following functional-differential equation:

\[
\frac{\partial u(t, m; z, k)}{\partial t} = \frac{\partial u(t, m; z, k)}{\partial m} v + \beta \int_0^1 u(t, \theta m; z, k) \cdot u(t, (1 - \theta)m; z, k) q(\theta) d\theta \\
- (\beta + \mu) u(t, m; z, k) + \mu \\
u(0, m; z, k) = ze^{-km}.
\]

**Proof.** The formal derivation of this equation is based on the standard technique: balance of the probabilities in the infinitesimal initial time interval \([0, dt]\). Namely, let’s consider

\[
u(t + dt, m; z, k) = E m z^{N(t+dt)} e^{-kM(t+dt)}
\]

and then let’s split the interval \([0, t + dt]\) into two parts \([0, dt] \cup [dt, t + dt] \). At the moment \( t = 0 \), we have one particle in the point \( x \) with mass \( m \) and during \([0, dt]\), we observe one of the following:

- splitting of the initial particle into two particles with probability \( \beta dt \);
- annihilation of the initial particle with probability \( \mu dt \);
- nothing happen, no annihilation and no splitting with probability \( 1 - \beta dt - \mu dt \).
Now one can apply the full expectation formula:
\[
u(t + dt, m; z, k) = \nu(t, m + vdt; z, k)(1 - \beta dt - \mu dt) + \\
\beta dt \int_0^1 \nu(t, \theta m; z, k) \cdot \nu(t, (1 - \theta)m; z, k) q(\theta) d\theta + \mu dt
\]

Theorem 1 is obtained by letting \(dt \to 0\). \(\square\)

For \(k = 0\) in equation (5), it will lead to the equation for \(Ez^N(t)\), which we already discussed. Let’s put \(z = 1\) and study the equation \(6\) as a function of \(k\). Denote \(L_1(t, m) := E_m(M(t)) = \frac{\partial \nu}{\partial k}|_{z=1,k=0}\), then from equation (6), we have
\[
\left\{
\begin{aligned}
\frac{\partial L_1(t,m)}{\partial t} &= v + 2\beta \int_0^1 (L_1(t, \theta m) - L_1(t, m)) q(\theta) d\theta + (\beta - \mu)L_1(t, m) \\
L_1(0, m) &= m.
\end{aligned}
\right.
\]

Differentiate the equation (6) twice over \(k\) and substituting \(z = 1\) and \(k = 0\), we will get the equation for the second moment \(L_2(t, m) := E_m(M^2(t)) = \frac{\partial^2 \nu}{\partial^2 k}|_{z=1,k=0}\)
\[
\left\{
\begin{aligned}
\frac{\partial L_2(t,m)}{\partial t} &= v + 2\beta \int_0^1 (L_2(t, \theta m) - L_2(t, m)) q(\theta) d\theta + (\beta - \mu)L_2(t, m) \\
+ 2\beta \int_0^1 (L_1(t, \theta m) L_1(t, (1 - \theta)m)) q(\theta) d\theta \\
L_2(0, m) &= m^2.
\end{aligned}
\right.
\]

The rest of the paper is organized as follows. In section 2, we discuss the mass process. In section 3, we study the analytic properties of the limiting mass distribution density. Following this, we discuss the moment of total mass of the population in section 4.

## 2 KPP model and distribution of mass inside the propogation front of particles

One can derive now the equation for the distribution of mass in the case of random motion of particles (migration).

The classical KPP model describes the evolution of the new particles in the presence of the branching and random spatial dynamics, say, diffusion[21].

We extended the KPP model by considering an extra parameter mass. We start from the single particle of the mass \(m\) located at the moment \(t = 0\) in the point \(x \in \mathbb{R}^d\), i.e \((x, m) \in \mathbb{R}^d \times \mathbb{R}_+\). Evolution of the particle and its mass until the first reaction is given by the Brownian Motion with the diffusion coefficient \(\kappa\) for the space position
\[
x(t) = x + \kappa b(t)
\]
where $b(t) \in \mathbb{R}^d$ is a standard Brownian Motion. The generator of $x(t)$ is the usual Laplacian $L = \frac{\sigma^2}{2} \Delta$. For the mass $m(t)$, we assume the linear growth:

$$m(t) = m + vt,$$

where $v > 0$, though one can study more general processes containing diffusion.

It starts from the single particle at the point $x \in \mathbb{R}^d$ with mass $m$. The particles perform Brownian motion with the generator $\kappa \Delta$, $\kappa > 0$ is the diffusion coefficient. During time $[t, t + dt]$ each particle in the population can split into two particles (offsprings) with probability $\beta dt$, $\beta > 0$ is the birth rate. After splitting, this mass is randomly distributed between offsprings and starts to grow linearly before the next splitting. During time interval $[t, t + dt]$, any particles of the mass $m$ is divided into two particles of the random mass $m' = \theta m$, $m'' = (1 - \theta)m$, see section 2. Here $\theta \in [0, 1]$ is symmetrically distributed (with respect to the center $0.5 \in [0, 1]$) random variable with the density $q(x) = q(1-x)$, $x \in [0,1]$. The offspring perform the same but independent dynamics like the initial particle.

Like in the standard theory of the reaction-diffusion equations, we can present the evolution of the particles field as a Markov Process in the Fock space

$$X = \emptyset \cup (\mathbb{R}^d \times \mathbb{R}^1_+) \cup \ldots (\mathbb{R}^d \times \mathbb{R}^1_+) \cup \ldots ,$$

see [14].

![Figure 1: Evolution of the particles](image)

For each open set $\Gamma \subset \mathbb{R}^d \times \mathbb{R}^1_+$, let’s define the following notations: $N(t, \Gamma) :=$ total numbers of particles at the moment $t$ in the set $\Gamma$, $M(t, \Gamma) :=$ total mass of the particles at the moment $t$ in the set $\Gamma$. We introduce the generating function of the form:

$$u(t, x, m, \Gamma; z, k) = E_{x,m} z^{N(t,\Gamma)} e^{-k M(t,\Gamma)}, |z| \leq 1, k \geq 0,$$

then we have the following equation for $u(t, x, m, \Gamma; z, k)$. 

5
Theorem 2. Let \( u(t, m; z, k) = E_x z^{N(t, \Gamma)} e^{-kM(t, \Gamma)} \), then \( u(t, m; z, k) \) satisfy the following functional-differential equation:

\[
\frac{\partial u(t, m; z, k)}{\partial t} = \kappa \Delta u(t, m; z, k) - \beta u(t, m; z, k) + \frac{\partial u(t, m; z, k)}{\partial m} v + \beta \int_0^1 u(t, \theta m; z, k) \cdot u(t, (1 - \theta)m; z, k) q(\theta) d\theta \tag{9}
\]

\[
u = \beta \hat{1}_0 u(t, \theta m; z, k) \cdot u(t, (1 - \theta)m; z, k) q(\theta) d\theta + \mu dt
\]

\[u(0, m; z, k) = z e^{-km} I_x(\Gamma)\]

Proof. The formal derivation of this equation is based on the standard technique: balance of the probabilities in the infinitesimal initial time interval \([0, dt]\).

Namely, let’s consider

\[
u = E_x z^{N(t+dt)} e^{-kM(t+dt)}
\]

and then let’s split the interval \([0, t + dt]\) into two parts \([0, dt] \cup [dt, t + dt]\). At the moment \( t = 0 \), we have one particle in the point \( x \) with mass \( m \) and during \([0, dt]\), we observe one of the following:

- Brownian motion;
- splitting of the initial particle into two particles with probability \( \beta dt \);
- annihilation of the initial particle with probability \( \mu dt \);
- nothing happen, no annihilation and no splitting with probability \( 1 - \beta dt - \mu dt \).

Now one can apply the full expectation formula:

\[
u(t + dt, x + \kappa b(t), m; z, k) = u(t, x + \kappa b(t), m + vdt; z, k)(1 - \beta dt - \mu dt) + \beta dt \int_0^1 u(t, \theta m; z, k) \cdot u(t, (1 - \theta)m; z, k) q(\theta) d\theta + \mu dt
\]

Theorem 1 is obtained by letting \( dt \to 0 \).

The proof of Theorem 2 are practically identical to the proof of Theorem 1. We will omit the proof here.

Due to the non-linearity, moment generating function is not the best source of the information about the particle field, it is better to work with the statistical moments. The factorial moments of \( N(t, \Gamma) \) can be calculated by partial derivative of moment generating function with respect to \( z \) at \( z = 1 \). The moments of mass \( M(t, \Gamma) \) can be obtained by differentiated with respect to \( k \) at \( k = 0 \).

Since \( N(t, \Gamma) \) is the number of the particles on the set \( \Gamma \), assume \( u_z(t, x, \Gamma) = E_x z^{N(t, \Gamma)} \) is the generating function and \( x \) is the location of the initial particle, then

\[
\frac{\partial u_z}{\partial t} = \kappa \Delta u + \beta(u_z^2 - u) \tag{10}
\]

\[u_z(0, x, \Gamma) = z \Gamma\]
Each path along the genealogical tree of the population on the time interval $[0, t]$ is a Brownian trajectory with the typical range $O(\sqrt{t})$. The number of the particles is growing exponentially like $\text{Exp}(\beta)$ and due to small deviation probabilities the “radius” of the population has order $O(t)$. Kolmogorov described “the boundary or the front” of the population in terms of the special solution of the corresponding combustion equation

$$\frac{\partial v}{\partial t} = \kappa \Delta v + \beta v(1 - v)$$  \hspace{1cm} (11)

It is equation (10) after substitution $v = 1 - u$. In one dimension case, see [21], the particle soliton like solution of equation (11) is given by

$$v(t, x) = \phi(x - ct)$$

As $z \to -\infty$, $\phi(z) \to 1$ and $z \to \infty$, $\phi(z) \to 0$. The function $\phi(z)$ presents the parameterization of the separatrix connecting two critical points of the ODE

$$\kappa \phi'' + c \phi' + \beta \phi(1 - \phi) = 0.$$  

Such definition of the “front” is not the only interesting one. From the point of view of the population dynamics, another definitions are also possible. Let $l_1(t, x, \Gamma) := E_x N(t, \Gamma)$, and $l_1(t, x, y) = \int_{\Gamma} l_1(t, x, y) dy$, function $l_1(t, x, y)$ is density of the population at moment $t$ starting from the single particle at $x \in \mathbb{R}^d$.

As easy to see,

$$\frac{\partial l_1(t, x, y)}{\partial t} = \kappa \Delta l_1(t, x, y) + \beta l_1(t, x, y)$$

$$l_1(0, x, y) = \delta_x(y)$$

i.e.

$$l_1(t, 0, y) = \exp \frac{-y^2}{4\kappa t} + \beta t \frac{1}{(4\kappa \pi t)^{\frac{d}{2}}}$$

Define the “density front” by the relation $l_1(t, 0, y) = 1$ will give $|y| \approx 2\sqrt{\kappa\beta t}$. This is not a Kolmogorov’s definition of the front, however, it also propagates linearly in time-space. It is convenient for the moments calculations.

Now let us consider the first moment of $M(t, \Gamma)$, let $L_1(t, x, m; \Gamma) := E_{x,m} M(t, \Gamma)$

$$= -\frac{\partial u(t,x,m;\Gamma;z,k)}{\partial k}|_{z=1,k=0},$$

then

$$\frac{\partial L_1(t, x, m; \Gamma)}{\partial t} = \kappa \Delta L_1(t, x, m; \Gamma) + \beta L_1(t, x, m; \Gamma) + \frac{\partial L_1(t, x, m; \Gamma)}{\partial m} v$$

$$+ 2\beta \int_0^1 (L_1(t, x, \theta m, \Gamma) - L_1(t, x, m, \Gamma)) q(\theta) d\theta \quad (12)$$

$$L_1(0, x, m; \Gamma) = m I_x(\Gamma).$$

From equation (12), we can see that the operator in the right part without potential term $\beta L_1(t, x, m; \Gamma)$ describes two independent Markov processes with the generators:

$$L_x f = \kappa \Delta f$$  \hspace{1cm} (13)
and
\[ \mathcal{L}_m f = v \frac{\partial f}{\partial m} + 2 \beta \int_0^1 [f(\theta m) - f(m)] q(\theta) d\theta. \] (14)

\( \mathcal{L}_x \) is the usual Laplacian operator corresponding to Brownian motion, \( \mathcal{L}_m \) is the generator of mass process on half axis \( m > 0 \). As a result, one can find the solution of the first moment
\[ L_1(t, x, m; \Gamma) = \hat{\Gamma} \exp\left(-\frac{(x-y)^2}{4\kappa t} + \beta t\right) \frac{(4\kappa \pi t)^{d/2}}{d!} \rho(t, m, m') m' dm' dy. \] (15)

Consider any bounded open set, say the ball \( B_r(x) = \{ y : |x - y| \leq r \} \). We have that for any \( B_r(x) \) inside the front, \( E^2 N(t, B_r(x)) \ll \text{Variance } N(t, B_r(x)) \).

More precisely, one can prove that
\[ P\left\{ \frac{N(t, B_r(x))}{EN(t, B_r(x))} > a \right\} \xrightarrow{t \to \infty} e^{-a} \quad \text{if } \frac{|x|}{t} \to 0 \]

The limiting distribution is exactly the same like for \( \frac{N(t)}{EN(t)} \). If \( t \to \infty, \frac{|x|}{t} \to \gamma < 2\sqrt{\kappa \beta} \), the limiting distribution for \( \frac{N(t, B_r(x))}{EN(t, B_r(x))} \) depends on \( \gamma \)! This indicates that particles field in the region \( |x| = O(t) \) is more intermittent than in the central zone. It has a structure of relatively large but sparse clusters. The intermittent structure of the population inside the propagating front was studied in detail in the paper [22].

3 Mass process

The equation (7) contains the constant potential \( \beta - \mu \) and the operator
\[ \mathcal{L}_m f = v \frac{\partial f}{\partial m} + 2 \beta \int_0^1 (f(\theta m) - f(m)) q(\theta) d\theta, \] (16)

which is the generator of the one dimension Markov process \( m(t) \). This mass process \( m(t) \) has the following description: it starts at \( t = 0 \) with the initial mass \( m \) and grows linearly \( m(t) = m + vt, \ t \leq \tau_1 \), where \( \tau_1 \) is exponential distributed random variable with parameter \( 2\beta \). At the moment \( \tau_1 + 0 \), this particle splits into two particles with corresponding masses
\[ m' = (m + v\tau_1)\theta_1, \]
\[ m'' = (m + v\tau_1)(1 - \theta_1), \]
where \( \theta_1 \) and \( 1 - \theta_1 \) has the same density \( q(\theta) \). By definition,
\[ m(\tau_1 + 0) = (m + v\tau_1)\theta_1. \]

The graph of \( m(t) \) is presented in the following Figure.
Remark: Factor $2\beta$ instead of $\beta$ appears due to the fact that after splitting, we have two identical particles.

Let us consider the embedded chain $m_n = (m_{n-1} + v\tau_n)\theta_n$, $n \geq 1$, i.e. the mass process $m(t)$ at the Poisson moments $T_1 = \tau_1$, $T_2 = \tau_1 + \tau_2$, \ldots, $T_n = \tau_1 + \cdots + \tau_n$, we will get recursively

$$m(T_1) = \theta_1(m + v\tau_1)$$

Similarly, at the moment of the second splitting,

$$m(T_2) = \theta_2(m + v\tau_2) = \theta_1 \theta_2 m + v\tau_2 \theta_2 + v\tau_1 \theta_1 \theta_2$$

In general,

$$m(T_n) \xrightarrow{\text{law}} \theta_1 \cdots \theta_n m + v\tau_1 \theta_1 + \cdots + v\tau_n \theta_1 \cdots \theta_n$$

so as $n \to \infty$, the limit will have the the form

$$m(T_n) \xrightarrow{\text{law}} m_\infty = v\tau_1 \theta_1 + \cdots + v\tau_n \theta_1 \cdots \theta_n + \cdots$$

The last random series has all moments since $\tau_i$ is exponential distributed with parameter $2\beta$ and $\theta_i$, $i = 1, 2, \cdots$ are bounded. This chain describes the distribution of the mass of new born particles at the moments of splitting. Unfortunately, the law of $m_\infty$ is the invariant distribution for the chain $m(T_n) = m(\tau_1 + \cdots + \tau_n)$, but not for $m(t)$. Let us find the invariant density $\Pi(m)$ for the process $m(t)$.

Denote $\nu(t)$ the number of the Poisson point $T_i$, $i = 1, 2, \cdots$ on the time interval $[0, t]$, i.e. $\nu(t) \sim \text{Poisson}(2\beta t)$. Then for $\nu(t) = n$,

$$m(t) = m_n + v(t - T_n)$$
The points $T_1, \cdots, T_n$ divide $[0, t]$ onto $n+1$ sub-interval (spacing) $\Delta_1, \cdots, \Delta_{n+1}$ with the same distribution. They are not independent of course since $\Delta_1 + \cdots + \Delta_{n+1} = t$. But the points $T_1, T_2, \cdots, T_n$ are the ordered statistics for the set of $n$ independent and uniformly distributed on $[0, t]$ random variable. It is well known [12] that the spacing can be presented in the form

$$\Delta_i = \frac{Z_i t}{Z_1 + \cdots + Z_{i+1}} \quad i = 1, \cdots, n + 1$$

where $Z_i$ are i.i.d random variable with exponential law $\text{Exp}(1)$, then for $\nu(t) = n$

$$m(t) = (\cdots (((m + \Delta_1 v) \theta_1 + \Delta_2 v) \theta_2 + \Delta_3 v) \theta_3 + \cdots + \Delta_n v) \theta_n + \Delta_{n+1} v$$

$$= \frac{\theta_1 \cdots \theta_n m + \frac{t}{Z_1 + \cdots + Z_{n+1}} (\cdots (((Z_1 v) \theta_1 + Z_2 v) \theta_2 + Z_3 v) \theta_3 + \cdots + \xi_n v \theta_n + \xi_{n+1} v)}{\nu(t) Z_1 + \cdots + Z_{\nu(t)+1}} (\xi_0 v + \xi_1 v \theta_1 + \xi_2 v \theta_2 + \cdots)$$

$$\xrightarrow{\text{law}} \frac{\nu(t)}{2\theta} (\xi_0 + \xi_1 \theta_1 + \xi_2 \theta_1 \theta_2 + \cdots)$$

where $\xi_i$ are standard independent $\text{Exp}(1)$ random variable. Note that in the last step we use the following facts:

1. $Z_i$ are i.i.d $\text{Exp}(1)$ random variable and $\frac{\nu(t)}{Z_1 + \cdots + Z_{\nu(t)+1}} \xrightarrow{\text{law}} \frac{1}{E(Z_i)} = 1$;
2. $\nu(t) \sim \text{Poisson}(2\beta t)$ and $E(\nu(t)) = 2\beta t$;
3. $\theta_i$ are i.i.d random variable.

We proved the following result: Markov mass process $m(t)$ has the limiting distribution $\Pi(m)$ which is the law of the random variable

$$m_\infty = \frac{v}{2\beta} (\xi_0 + \xi_1 \theta_1 + \xi_2 \theta_1 \theta_2 + \cdots)$$

$$= v (\tau_0 + \tau_1 \theta_1 + \tau_2 \theta_1 \theta_2 + \cdots)$$

where $\tau_i \sim \text{Exp}(2\beta)$ and $\xi_i$ are i.i.d $\text{Exp}(1)$ random variable and $\theta_i$ are also i.i.d random variable with the symmetric density $q(x) = q(1-x)$ for $x \in [0, 1]$. We will assume that $q(x) = 0$ if $|x - \frac{1}{2}| \geq \delta$, $0 < \delta < \frac{1}{2}$, i.e. $0 < \delta \leq \theta_i \leq 1 - \delta$, $i = 1, 2, \cdots$.

The transition density of the mass process $\rho(t, m, m')$, i.e. the fundamental solution of

$$\left\{ \begin{array}{l}
\frac{\partial \rho(t, m, m')}{\partial t} = \mathcal{L} \rho(t, m, m') \\
\rho(0, m, m') = \delta_{m'}(m) 
\end{array} \right.$$
have a limit $\Pi(m') = \lim_{t \to \infty} \rho(t, m, m')$.

**Theorem 3.** Process $m(t)$ has the invariant density $\Pi(m)$, this density equals to the distribution density of the random geometric series

$$\xi = v\tau_0 + v\tau_1\theta_1 + \cdots + v\tau_n\theta_1 \cdots \theta_n + \cdots$$

(17)

Where $\tau_i, i \geq 0$ are i.i.d $\text{Exp}(2\beta)$ random variable and $\theta_i, i \geq 0$ are i.i.d random variable with the probability density $q(\theta)$, $\tau_i$ and $\theta_i$ are independent.

**Remark:**

- The operator $L_m$ is the unusual Markov generator. It belongs to the class functional-differential operator with linearly transformed argument which appear in many applications. See Derfel et al. [11]. All such Markov processes are directly or indirectly related to the solvable group $\text{Aff}(R^1)$ of the transformations $x \to ax + b$ of $R^1 \to R^1$. This group has the standard matrix representation $g = \begin{bmatrix} a & b \\ 0 & 1 \end{bmatrix}$, $a > 0$. The simplest symmetric random walks on this group have the form

$$g_n = \begin{bmatrix} e^{X_1 + \cdots + X_n} & \sum Y_i e^{X_1 + \cdots + X_{i-1}} \\ 0 & 1 \end{bmatrix}$$

(18)

{X_i} and {Y_i}, $i \geq 1$ are symmetric i.i.d random vector. The upper of diagonal term has the same structure like $m_\infty$.

- One can check that the law $m_\infty$ is invariant density for the mass process directly. It is not difficult to verify that $\Pi(m)$ is the solution of the conjugate equation

$$L^*g = -v \frac{\partial g}{\partial m} + 2\beta \int_0^{1} [g(m\theta) - g(m)]q(\theta)d\theta = 0$$

(19)

This functional-differential equation with rescaling is similar to the archetypal equation which was studied in [10], [5] and [6].

4 Analytic properties of the limiting mass distribution density

Now we’ll calculate the moment for the invariant limiting distribution $\Pi(m)$, the calculation will be based on the following fact:

$$\xi = v\tau + \theta_1 \tilde{\xi}$$

Here $\tilde{\xi} \overset{\text{law}}{=} \xi$ and $\tau, \theta_1$ are independent on $\tilde{\xi}$. Since $\tau$ is exponential random variable with parameter $2\beta$, so

$$E\tau = \frac{1}{2\beta}, E\tau^2 = \frac{1}{2\beta^2}$$
As a result, 

\[ E\xi = E\nu\tau + E\theta_1\tilde{\xi} \]

so

\[ E\xi = \frac{v}{2\beta} + \frac{1}{2} E\xi \]

thus,

\[ E\xi = \frac{v}{\beta} \]

The second moment

\[ E\xi^2 = v^2 E(\tau^2) + 2v E(\tau_0 \xi) + E(\theta_1^2 \tilde{\xi})^2 \]

from the independence, then

\[ E\xi^2 = \frac{v^2}{\beta^2(1 - E\theta_1^2)} \]

so

\[ \text{var}\xi = \frac{v^2}{\beta^2} \left( 1 - \frac{1}{1 - E\theta_1^2} \right) \]

Similarly, the third moments

\[ E\xi^3 = \frac{3v^3}{2\beta^3(1 - E\theta_1^2)(1 - E\theta_1^3)} \]

In general,

\[ E\xi^k = E(\nu\tau + \theta_1\tilde{\xi})^k \]

i.e.

\[ E\xi^k (1 - E\theta_1^k) = \sum_{i=0}^{k-1} \binom{k}{i} (vE\tau)^i E(\theta^i\tilde{\xi})^{k-i} \]

Let’s find the asymptotic of \( \Pi(m) \) for large \( m \) and small \( m \). Since

\[ \xi = \nu\tau_0 + \nu\tau_1\theta_1 + \ldots + \nu\tau_n\theta_1\cdots\theta_n + \ldots \]

Therefore,

\[ E_{\theta}[e^{-\lambda \xi}] = E_{\theta}[e^{-\lambda(\nu\tau_0 + \nu\tau_1\theta_1 + \nu\tau_2\theta_1\theta_2 + \ldots)}] \]

\[ = E\theta[e^{-\lambda \nu\tau_0}] E\theta[e^{-\lambda \nu\tau_1\theta_1}] \cdots e^{-\lambda \nu\tau_n\theta_1\cdots\theta_n} \]

\[ = \frac{1}{(1 + \frac{\lambda \nu}{2\beta})(1 + \frac{\lambda \nu \theta_1}{2\beta}) \cdots (1 + \frac{\lambda \nu \theta_1\cdots\theta_n}{2\beta})} \]

\[ = \frac{c_0}{1 + \frac{\lambda \nu}{2\beta}} + \frac{c_1}{1 + \frac{\lambda \nu \theta_1}{2\beta}} + \ldots + \frac{c_n}{1 + \frac{\lambda \nu \theta_1\cdots\theta_n}{2\beta}} + \ldots \]

\[ = \frac{c_0}{1 + \frac{\lambda \nu}{\nu\tau_1}} + \frac{c_1}{1 + \frac{\lambda \nu \theta_1}{\nu\tau_1}} + \ldots + \frac{c_n}{1 + \frac{\lambda \nu \theta_1\cdots\theta_n}{\nu\tau_1\cdots\theta_n}} + \ldots \]
Here,

\[ c_0 = \frac{1}{(1-\theta_1)(1-\theta_1\theta_2)} \]
\[ c_1 = \frac{1}{(1-\frac{1}{\theta_1})(1-\theta_2)(1-\theta_2\theta_3)} \]
\[ c_n = \frac{1}{(1-\frac{1}{\theta_1...\theta_n})(1-\frac{1}{\theta_2...\theta_n})(1-\frac{1}{\theta_n})(1-\theta_{n+1})(1-\theta_{n+1}\theta_{n+2})...} \]

Now one can find conditional density \( p_\xi(m) \) of random variable if \( \vec{\theta} = (\theta_1, \theta_2, \ldots) \) are known,

\[
p_\xi(m) = E_{\vec{\theta}}[\frac{2\beta}{v}e^{-\frac{2m}{v}}c_0] + E_{\vec{\theta}}[\frac{2\beta}{v\theta_1}e^{-\frac{2m}{v\theta_1}}c_1] + \cdots
\]
\[
= E_{\vec{\theta}}[\frac{2\beta}{v}e^{-\frac{2m}{v}}(1-\theta_1)(1-\theta_1\theta_2)...]
+ E_{\vec{\theta}}[\frac{2\beta}{v\theta_1}e^{-\frac{2m}{v\theta_1}}(1-\frac{1}{\theta_1})(1-\theta_2)(1-\theta_2\theta_3)...] + \cdots
\]
\[
= \frac{2\alpha\beta}{v}e^{-\frac{2m}{v}} - E_{\vec{\theta}}[\frac{2\alpha\beta}{1-\theta_1}e^{-\frac{2m}{v\theta_1}}] + \cdots \tag{20}
\]

where

\[
\alpha = E_n(1-\theta_1)(1-\theta_1\theta_2)... \tag{21}
\]

Let’s formulate several analytic results about the invariant density.

**Theorem 4.** Assume that \( \text{Supp}\theta = [a, 1-a] \), \( 0 < a \leq \frac{1}{2} \), then for large \( m \),

\[
\Pi(m) \xrightarrow{m \to \infty} \frac{2\alpha\beta}{v}e^{-\frac{2m}{v}} + R(m)
\]

The remainder term with the maximum on the boundary has order

\[
R(m) \sim \frac{2\alpha\beta}{a}e^{-\frac{2m}{v(1-a)}}L(m)
\]

Where \( L(m) \xrightarrow{m \to \infty} 0 \) and \( L(m) \) depends on the structure of the distribution \( q(d\theta) \) near the maximum point \( \theta_{\text{critical}} = 1-a \).

**Proof.** From (20), due to the Laplace method, it is trivial to get the result. □

The behavior of \( p_\xi(m) \) as \( m \to 0 \) is much more interesting. Here we will use the Exponential Chebyshev’s inequality. More detailed analysis in the case when \( q(d\theta) \) is a discrete (atomic) measure, has been done in Derfel [9], Cooke & Derfel [7].

For instance, the following result is true for the pantograph equation (1).

(i) Steady-state solution of (1) satisfies the following estimate
\[ |y(x)| < D \exp \{-b \ln^2 |x| \}; \quad D > 0, \quad b = \frac{1}{2 \ln \alpha} \quad (22) \]

in some neighborhood of zero.

(ii) On the other hand, every solution of (1) which satisfies estimate \( y(x) < D \exp \{-a \ln^2 |x| \} \) for with some \( a > b \) is identically equal zero.

Similar results are valid also for more general equation

\[ y(x) = \sum_{j=0}^{l} \sum_{k=0}^{n} a_{jk} y^{(k)}(\lambda_j x), \quad (23) \]

where \( \lambda_j \neq 0 \) under the assumption that \( \Lambda = \max |\lambda_j| < 1 \). Namely, statements (i) and (ii) are fulfilled with \( b = \frac{1}{2 \ln |\lambda|} \) and \( a > m \frac{\ln |\lambda|}{2 \ln \Lambda} \), where \( \lambda = \min |\lambda_j| \).

We conjecture that similar asymptotic behavior occurs also for our model, but currently can prove the following weaker result, only. The asymptotic approximation is shown in Figure 3.

**Theorem 5.** Assume that \( \text{Supp} \theta = [a, 1-a], \) \( 0 < a \leq \frac{1}{2} \), then if \( m \to 0 \), then

\[ P\{\xi \leq m\} \leq e^{-c_1 \ln^2(\frac{1}{m})} \]

where \( c_1 \) is some constant.

**Proof.** Let’s start from the standard calculations, for \( \lambda > 0 \) and fix \( a \leq \theta_i \leq 1-a, \) \( i = 1, 2, \cdots \)

\[ P\{\xi \leq m|\theta\} = P\{e^{-\lambda \xi} > e^{-\lambda m|\theta|}\} \leq \min_{\lambda>0} \frac{E e^{-\lambda \xi}}{e^{-\lambda m}} \]

\[ = \min_{\lambda>0} e^{\lambda m - \ln(1+\frac{\lambda \xi}{2}) - \ln(1+\frac{\lambda \theta_1}{2 \xi}) - \ln(1+\frac{\lambda \theta_2}{2 \xi}) - \cdots} \quad (24) \]

Equation for the critical point \( \lambda_0 = \lambda_0(m) \) has a form:

\[ m = \frac{2\beta}{\theta_1 + \ldots + \theta_k} + \frac{2\beta}{\theta_1 + \ldots + \theta_k} + \cdots + \frac{2\beta}{\theta_1 + \ldots + \theta_k} + \cdots \]

i.e.

\[ m = \frac{1}{2\beta} + \lambda + \frac{1}{2\beta} + \lambda + \cdots + \frac{1}{2\beta} + \lambda + \cdots \]

Define \( k(\lambda) = \min\{k : \frac{2\beta}{\theta_1 + \ldots + \theta_k} \sim \lambda\} \), then \( m \sim \frac{k(\lambda)}{\lambda} \). From \( \frac{2\beta}{\theta_1 + \ldots + \theta_k} \sim k \), we then have \( k(\lambda) \sim \frac{\ln \lambda}{m E \ln(\frac{1}{\theta})} \). Hence, the critical point

\[ \lambda \sim \frac{\ln \left( \frac{1}{m} \right)}{m E \ln(\frac{1}{\theta})} \quad (25) \]
Substitute (25) into Chebyshev’s inequality (24) gives
\[ P \{ \xi \leq m|\theta \} \leq e^{\frac{\ln(\frac{1}{m})}{\frac{\ln(\frac{1}{\theta})}{2m\beta\ln(\frac{1}{\theta})}}} - \ln \left( 1 + \frac{v \ln(\frac{1}{\theta}) \theta^k}{2m\beta\ln(\frac{1}{\theta})} \right) - \cdots - \ln \left( 1 + \frac{v \ln(\frac{1}{\theta}) \theta^k}{2m\beta\ln(\frac{1}{\theta})} \right) \]
\[ \leq e^{\frac{\ln(\frac{1}{m})}{\frac{\ln(\frac{1}{\theta})}{2m\beta\ln(\frac{1}{\theta})}}} - \ln \left( 1 + \frac{v \ln(\frac{1}{\theta}) \theta^k}{2m\beta\ln(\frac{1}{\theta})} \right) - \cdots - \ln \left( 1 + \frac{v \ln(\frac{1}{\theta}) \theta^k}{2m\beta\ln(\frac{1}{\theta})} \right) \]
\[ \leq e^{\frac{\ln(\frac{1}{m})}{\frac{\ln(\frac{1}{\theta})}{2m\beta\ln(\frac{1}{\theta})}}} - \sum_{i=0}^{k} \ln \left( \frac{v \ln(\frac{1}{\theta}) \theta^k}{2m\beta\ln(\frac{1}{\theta})} \right) \]
\[ \leq e^{-c_1 \ln^2 \left( \frac{1}{\theta} \right) \ln(\frac{1}{m})} \]

Figure 3: Asymptotic behavior of \( \Pi(m) \)

5 Moments of total mass of population \( M(t) \)

In this section, we will study the first moment and second moment of the total mass of population \( M(t) \). As discussed in section 1, the first moment \( L_1(t, m) \) is given by equation
\[
\left\{ \begin{array}{l}
\frac{\partial L_1(t, m)}{\partial t} = \frac{\partial L_1(t, m)}{\partial m} v + 2\beta \int_0^1 (L_1(t, \theta m) - L_1(t, m))q(\theta)d\theta + (\beta - \mu)L_1(t, m) \\
L_1(0, m) = m
\end{array} \right.
\]
\[ (26) \]
Corollary 6. Let $L_1(t, m) = E_m(M(t))$ then for $t \to \infty$,

$$L_1(t, m) \to e^{(\beta - \mu)t} \frac{v}{\beta}$$

Proof. From equation (26), Duhamel’s formula gives us

$$L_1(t, m) = e^{(\beta - \mu)t} \int_0^\infty \rho(t, m, m')m'dm'$$

as $t \to \infty$,

$$L_1(t, m) \to e^{(\beta - \mu)t} \int_0^\infty \Pi(m')m'dm' = e^{(\beta - \mu)t} \frac{v}{\beta}.$$ 

The last equality use both Theorem 2 $\rho(t, m, m') \to \Pi(m')$ and the fact that $E\xi = \frac{v}{\beta}$. □

The second moment $L_2(t, m) = E_m(M(t)^2)$ is given by

$$\begin{cases}
\frac{\partial L_2(t, m)}{\partial t} = \frac{\partial L_2(t, m)}{\partial m} v + 2\beta \int_0^1 (L_2(t, \theta m) - L_2(t, m))q(\theta)d\theta + (\beta - \mu)L_2(t, m) \\
+2\beta \int_0^1 (L_1(t, \theta m)L_1(t, (1 - \theta)m))q(\theta)d\theta \\
L_2(0, m) = m^2
\end{cases} \tag{27}$$

From equation (27), we have $\frac{\partial L_2}{\partial t} = \mathcal{L}_m L_2 + f(t, m)$, here $\mathcal{L}_m$ is the operator of the mass process. By applying Duhamel’s principle and one can find that

$$L_2(t, m) = 2 \left( e^{(\beta - \mu)t} \frac{v}{\beta} \right)^2 + O(e^{(\beta - \mu)t})$$

References

[1] Albeverio, S., Bogachev, L. V., and Yarovsky, E. B. (1998). Asymptotics of branching symmetric random walk on the lattice with a single source. Comptes Rendus de l’Academie des Sciences - Series I - Mathematics, 326, 975-980.

[2] Basse, B., Wake, G. C., Wall, D. J. N., and Van Brunt, B. (2004). On a cell-growth model for plankton. Mathematical Medicine and Biology, 21, 49-61.

[3] Basse B., Baguley B., Marshall E., Joseph W., van Brunt B., Wake G.C and Wall D. J. N. (2003). A mathematical model for analysis of the cell cycle in human tumors, J. Math. Biol., 47, 295–312.
[4] Begg, R. E., Wall, D. J. N., and Wake, G. C. (2008). The steady-states of a multi-compartment, age-size distribution model of cell-growth. *European Journal of Applied Mathematics*, 19, 435-458.

[5] Bogachev, L. V., Derfel, G., and Molchanov, S. A. (2015). On bounded continuous solutions of the archetypal equation with rescaling. *Proc. Royal Soc A*. 471, 1-19.

[6] Bogachev, L. V., Derfel, G., and Molchanov, S. A. (2015). Analysis of the archetypal functional equation in the non-critical case. *Dynamical Systems, Differential Equations, and Applications*, AIMS Proceedings, 132–141.

[7] Cooke, K., Derfel, G. (1996). On the sharpness of a theorem by Cooke and Lunel. *J. Math. Anal. Appl.*, 197, N.1, 227-248.

[8] Daukste, L., Basse, B., Baguley B. C., and Wall, D.J.N. (2012), Mathematical determination of cell population doubling times for multiple cell lines, *Bull. Math. Biol.*, 74, 2510 - 2534.

[9] Derfel, G. (1978). On the asymptotics of the solution of some linear functional-differential equations. *Reports of the I.N. Vekua Institute of Applied Mathematics, Tbilisi*, N12-13, 21-23 (in Russian).

[10] Derfel, G. (1989). Probabilistic methods of investigation for a class of functional-differential equations. *Ukrainian Math. J.*, 41, N.10 , 1322-1327 (in Russian). [English translation: 41, N.10 (1989), 1137-1141]

[11] Derfel, G. A., van Brunt, B. and Wake, G. C. (2012). A Cell Growth Model Revisited, *Functional-Differential Equations*, 19, N.1-2, 71-81, available at [http://eprints.maths.ox.ac.uk/824/1/finalOR27.pdf](http://eprints.maths.ox.ac.uk/824/1/finalOR27.pdf) (2009)

[12] Feller, W. (1971). An Introduction to Probability Theory and Its Applications, Vol 2. John Wiley & Sons, New York.

[13] Feng, Y., Molchanov, S. and Whitmeyer J. (2012). Random walks with heavy tails and limit theorems for branching processes with migration and immigration. *Stochastic and Dynamics*, 12, 1- 23.

[14] Fisher, R. A. (1937) .The wave of advance of advantageous genes, *Ann Eugenics*,7, 355-369.

[15] Galton, F. (1873). Problem 4001: On the extinction of surnames. *Educational Times*, 26, 1-17.

[16] Galton, F. and Watson, H. (1875). On the probability of the extinction of families. *The Journal of the Anthropological Institute of Great Britain and Ireland*, 4, 138-144.

[17] Gikhman, I. I. and Skorokhod, A.V. (2004). The theory of stochastic processes I, II. Springer-Verlag, Berlin.
[18] Hall, A. J. and Wake, G. C. (1989). A functional differential equation modelling of cell growth. *J. Austral. Math. Soc. Ser.*, 30, 424-435.

[19] Harris, T. E. (1963). The theory of branching processes. Springer, Berlin.

[20] Harris, T. E. (1974). Contact interactions on a lattice. *The Annals of Probability*, 2, 969-988.

[21] Kolmogorov, A. N., Petrovskii, I. G. and Piskunov, N. S. (1937). A study of the diffusion equation with increase in the quantity of matter, and its application to a biological problem. *Moscow University Mathematics Bulletin Ser. A*(1), 1-25.

[22] Koralov, L., Molchanov, S. (2013). Structure of population inside propagating front, *Journal of Mathematical Sciences (Problems in Mathematical Analysis)*, 189(4), 637-658.

[23] Round, F. E., Crawford, R. M., and Mann, D.G. (1990). The Diatoms. Cambridge University Press, Cambridge.