The effect of competition on the height and length of genealogical trees of large populations

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Population models without competition

Galton–Watson cont. time proc.

- Simple – classical population model in continuous time : Galton–Watson process $\{X_t, \ t \geq 0\}$ with values in $\mathbb{Z}_+$, which can be defined as follows.
  1. X_0 denotes the number of ancestors at time 0.
  2. Each individual lives, independently of the others, an exponential time with parameter $\lambda > 0$.
  3. During his life time, each individual, again independently of the others, gives birth to children at rate μ (i.e. according to a rate μ Poisson process).
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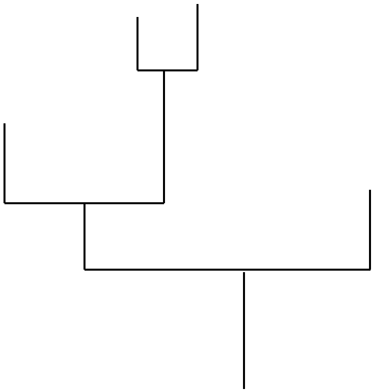
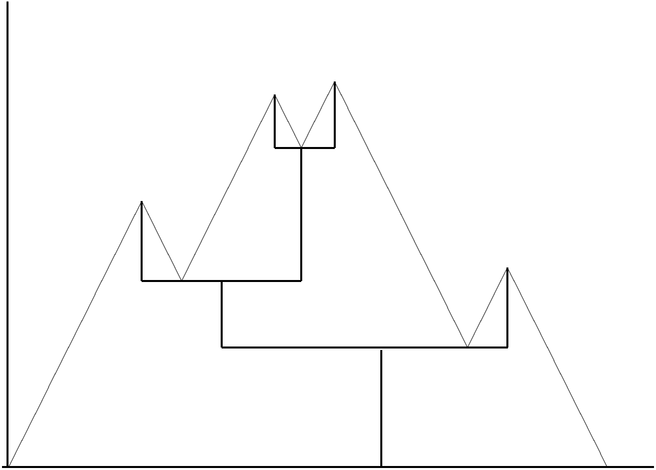
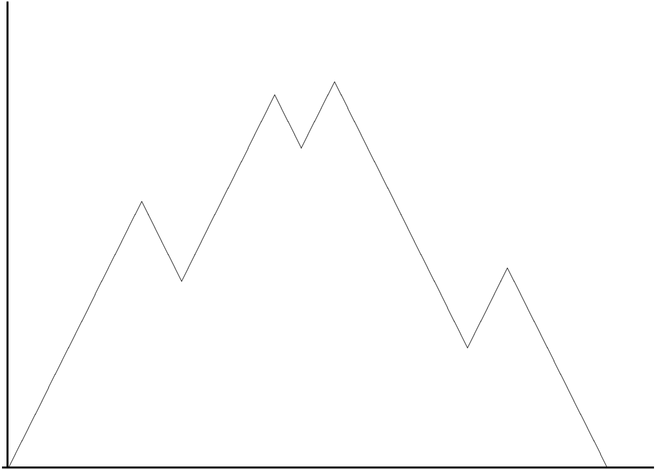
A tree



A tree and its exploration process



The exploration process



Renormalization and convergence

- For each $N \geq 1$, let $X_t^{N,x}$ denote the above population, with $X_0^{N,x} = [Nx]$, $\lambda_N = 2N$, $\mu_N = 2N + \theta$.
- Let $Z_t^{N,x} := N^{-1} X_t^{N,x}$.
- Then $\{Z_t^{N,x},\ t \geq 0\} \Rightarrow \{Z_t^x,\ t \geq 0\}$, where
- $$\begin{cases} dZ_t^x = \theta Z_t^x dt + 2\sqrt{Z_t^x} dB_t,\ t \geq 0, \\ Z_0^x = x, \end{cases}$$

  with $\{B_t,\ t \geq 0\}$ standard Brownian motion.
- One can also take the limit in the genealogical tree (in fact in its "exploration process"), the limit being reflected Brownian motion.

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Population models with competition

Population models with competition

- We want to consider forests of genealogical trees for populations *with competition*.
- A first attempt is to attach to each individual an additional death rate proportional to $(X_t)^{\alpha-1}$, which induces a total additional death rate for the population which is proportional to $(X_t^x)^\alpha$.
- We will assume $\alpha > 0$.

  • $\alpha > 1$ corresponds to competition : the largest the population, the more each individual suffers from competition (the case $\alpha = 2$ is the classical *logistic* model).

  • $\alpha = 1$ is the standard case where individuals are independent.

  • $0 < \alpha < 1$ corresponds to a model where the largest the population, the better off each individual is.

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Population models with competition

- However, we need to improve our description of our population process with interaction.
- Let X_t^m be the number of descendants at time t of m ancestors at time 0. We would like to construct jointly the processes $\{X_t^m,\ t \geq 0\}$ for all $m \geq 1$.
- Order the ancestors from left to right. This order is passed on to theirs descendants. In other words, the forest of genealogical trees is a planar forest, whose branches do not intersect. The descendants of the n "first" ancestors should not feel the effect of the competition with the descendants of the $n+1$th ancestor, while the descendants of this $n+1$th ancestor feel the competition with those of the n first ancestors.

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The case $\alpha = 2$: logistic model

- In the particular case $\alpha = 2$, the effect of the competition is a death rate which is essentially proportional to the number of pairs of individuals in the population. One way to model this is to attach a rate of death to each pair of individuals in the population.
- One may think that at a given rate, each pair is engaged in a pairwise fight, which is concluded by the death of one of the fighters.
- Our pecking order imposes that all fights are won by the individual on the left, and end lethal for the one on the right.
- Each individual is "under attack" from his contemporaries located on his left in the planar tree. The "competition death rate" (superimposed to the "natural death rate" λ) which the individual i suffers at time t is $\gamma\mathcal{L}_i(t)$, where $\mathcal{L}_i(t)$ denotes the number of individuals alive at time t, located on the left of individual i in the planar forest of trees.

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The general case

- In the general case, the "competition death rate" which the individual i suffers at time t is $\gamma[\mathcal{L}_i(t)^\alpha - (\mathcal{L}_i(t) - 1)^\alpha]$, where $\mathcal{L}_i(t)$ denotes the number of individuals alive at time t, located on the left of individual i on the planar tree.
- If again X_t^m denotes the size of the population at time t, descending from m ancestors at time 0, the total "competition death rate" equals

$$\gamma \sum_{k=2}^{X_t^m} [(k-1)^\alpha - (k-2)^\alpha] = \gamma (X_t^m - 1)^\alpha,$$

which is a reasonable approximation of $\gamma (X_t^m)^\alpha$.
- $\{X_t^m,\ t \geq 0\}$ is a continuous time $\mathbb{Z}_+$–valued Markov process, which evolves as follows. If $X_t^m = 0$, then $X_s^m = 0$ for all $s \geq t$. While at state $k \geq 1$, the process

$$X_t^m \text{ jumps to } \begin{cases} k+1, & \text{at rate } \mu k; \\ k-1, & \text{at rate } \lambda k + \gamma (k-1)^\alpha. \end{cases}$$

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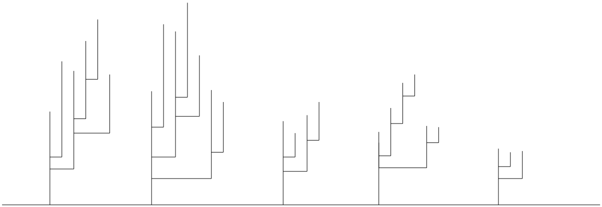
A forest of trees with competition



Reformulation, dependence upon m

- In the case $\alpha = 1$ (no competition), for each fixed $t > 0$, $\{X_t^m,\ m \geq 1\}$ is an independent increments process.
- In the case $\alpha \neq 1$, $\{X_t^m,\ m \geq 1\}$ is not a Markov chain for fixed t. That is to say, the conditional law of X_t^{n+1} given X_t^n differs from its conditional law given $(X_t^1, X_t^2, \ldots, X_t^n)$. The intuitive reason for that is that the additional information carried by $(X_t^1, X_t^2, \ldots, X_t^{n-1})$ gives us a clue as to the level of competition which the progeny of the $n+1$st ancestor had to suffer, between time 0 and time t.
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Description of the Markov chain

- Consequently, in order to describe the law of the whole process, that is of the two–parameter process $\{X_t^m,\ t \geq 0, m \geq 0\}$, it suffices to describe the conditional law of $X_\cdot^n$, given $\{X^{n-1}\}$, for all $n \geq 1$.
- We now describe the conditional law of $X_\cdot^n$, given $X_\cdot^m$ for $0 \leq m < n$. Let $V_t^{m,n} := X_t^n - X_t^m$. Given that $X_t^m = x(t)$, $t \geq 0$, $\{V_t^{m,n},\ t \geq 0\}$ is a $\mathbb{Z}_+$–valued time inhomogeneous Markov process starting from $V_0^{m,n} = n - m$, whose time–dependent infinitesimal generator $\{Q_{k,\ell}(t),\ k, \ell \in \mathbb{Z}_+\}$ is such that its off–diagonal terms are given by
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$$\begin{aligned} Q_{0,\ell}(t) &= 0, \quad \forall \ell \geq 1; \quad \text{and for any } k \geq 1, \\ Q_{k,k+1}(t) &= \mu k, \\ Q_{k,k-1}(t) &= \lambda k + \gamma (x(t) + k - 1)^\alpha, \\ Q_{k,\ell}(t) &= 0, \quad \forall \ell \notin \{k-1, k, k+1\}. \end{aligned}$$

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Renormalized discrete model and convergence

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- For each fixed $x > 0$, $\{Z_t^x, t \geq 0\}$ is a continuous process, solution of the SDE
$$dZ_t^x = [\theta Z_t^x - \gamma(Z_t^x)^\alpha]\, dt + 2\sqrt{Z_t^x} dW_t,\ Z_0^x = x,$$
where $\theta \in \mathbb{R}$, $\gamma > 0$, $\alpha > 0$, and $\{W_t,\ t \geq 0\}$ is a standard Brownian motion. In case $\alpha = 2$, this model has been considered by A. Lambert '05.

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- $\{Z^x_\cdot,\ x \geq 0\}$ is a Markov process with values in $C([0,\infty),\mathbb{R}_+)$, the space of continuous functions from $[0,\infty)$ into $\mathbb{R}_+$, starting from 0 at $x = 0$.
- The transition probabilities of this Markov process are specified as follows. For any $0 < x < y$, $\{V^{x,y}_t := Z^y_t - Z^x_t,\ t \geq 0\}$ solves the SDE

$$dV^{x,y}_t = \left[\theta V^{x,y}_t - \gamma\left\{(Z^x_t + V^{x,y}_t)^\alpha - (Z^x_t)^\alpha\right\}\right]dt + 2\sqrt{V^{x,y}_t}\,dW'_t,$$
$$V^{x,y}_0 = y - x,$$

where the standard Brownian motion $\{W'_t,\ t \geq 0\}$ is independent from $\{Z^x_t,\ t \geq 0\}$.
- In the case $\alpha = 1$, Z^x_t and the increment $V^{x,y}_t = Z^y_t - Z^x_t$ are independent, unlike in the cases $\alpha \neq 1$.

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- $\{Z^x_\cdot,\ x \geq 0\}$ is a Markov process with values in $C([0,\infty),\mathbb{R}_+)$, the space of continuous functions from $[0,\infty)$ into $\mathbb{R}_+$, starting from 0 at $x = 0$.
- The transition probabilities of this Markov process are specified as follows. For any $0 < x < y$, $\{V_t^{x,y} := Z_t^y - Z_t^x,\ t \geq 0\}$ solves the SDE

$$\begin{aligned} dV_t^{x,y} &= \left[\theta V_t^{x,y} - \gamma\left\{(Z_t^x + V_t^{x,y})^\alpha - (Z_t^x)^\alpha\right\}\right] dt + 2\sqrt{V_t^{x,y}}\, dW'_t, \\ V_0^{x,y} &= y - x, \end{aligned}$$

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The genealogical forest of continuous trees

- In the case $\alpha = 2$ (more general case in progress), the exploration process of the forest of discrete genealogical trees converges, as $N \to \infty$, to the unique weak solution of the following reflected SDE
- $$H_s = \frac{\theta}{2}s - \gamma \int_0^s L_r(H_r)dr + B_s + \frac{1}{2}L_s(0),$$

  where $\{B_s,\ s \geq 0\}$ is a standard Brownian motion, $L_s(x)$ denotes the local time accumulated by the process H at level x up to time s. Note that the term $L_s(0)/2$ is responsible for the reflection of H above 0.

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Height and Length of the discrete genealogical tree

Definition

- The height of the forest of genealogical trees of the population $\{X_t^m,\ t \geq 0\}$ is defined as

$$H^m = \inf\{t > 0,\ X_t^m = 0\}$$

- The length L^m of the forest of genealogical trees is defined as

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Results

Theorem

If $0 < \alpha \le 1$, *then*

$$\sup_{m\ge 1} H^m = +\infty \qquad a.\ s.$$

If $\alpha > 1$, *then*

$$\mathbb{E}\left[\sup_{m\ge 1} H^m\right] < +\infty.$$

Theorem

If $0 < \alpha \le 2$, *then*

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Height of the discrete tree

- The case $\alpha \leq 1$ is easy. By monotonocity, it suffices to treat the case $\alpha = 1$, in which case H^m is the maximum of m independent copies of H^1, and $\mathbb{P}(H^1 > t) > 0$, $\forall t > 0$.
- In case $\alpha > 1$, it suffices to consider the case $\lambda = 0$. In the case $\alpha = 2$, formulas for the expectation are very close to a result on the ancestral recombination graph (P., Salamat '09).
- If $\mu = \gamma = 1$,

$$\mathbb{E}\left(H^m\right) = \sum_{k=1}^{m} \frac{1}{k^\alpha} + \sum_{k=1}^{m} (k-1!)^{\alpha-1} \sum_{j=k+1}^{\infty} \frac{1}{(j!)^{\alpha-1}} \frac{1}{j}.$$

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Length of the discrete tree

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$$A_t = \int_0^t X_s^m ds, \quad \eta_t = \inf\{s > 0,\ A_s > t\},$$

  we have that $U_t^m = X_{\eta_t}^m$ follows dynamics very similar to those of X_t^m, but with α replaced by $\alpha - 1$.
- Moreover $L^m = \inf\{t > 0,\ U_t^m = 0\}$.

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Height and Length of the continuous genealogical tree

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- Z_t^x describes the evolution of a population which starts from $Z_0^x = x$.
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Indication for proofs

- The result for the length is reduced to a result for the extinction time of a process with α replaced by $\alpha - 1$, as in the discrete case.
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An auxiliary result

- Let $f : \mathbb{R}_+ \to \mathbb{R}$ be locally Lipschitz and such that

$$\lim_{x\to\infty} \frac{|f(x)|}{x^\alpha} = 0.$$

- Then

Theorem

If $\alpha > 1$, $\gamma > 0$ and f satisfies the above assumption, then there exists a minimal $X \in C((0,+\infty);\mathbb{R})$ which solves

$$\begin{cases} dX_t = [f(X_t) - \gamma(X_t)^\alpha]\mathbf{1}_{\{X_t\ge 0\}}dt + dW_t; \\ X_t \to \infty, \ \text{as } t \to 0. \end{cases} \tag{1}$$

Moreover, if $T_0 := \inf\{t > 0,\ X_t = 0\}$, then $\mathbb{E}[T_0] < \infty$.

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Idea of proof

- Let $V_t = X_t - W_t$. The first part of the result is equivalent to the existence of a minimal solution to the ODE

$$\begin{cases} \frac{dV_t}{dt} = f(V_t + W_t) - \gamma(V_t + W_t)^\alpha; \\ V_t \to \infty, \text{ as } t \to 0. \end{cases}$$

- If f and W would be zero, then this ODE would have the unique solution

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Application to the height of the forest of trees

- Remind that Z_t^x solves the SDE

$$dZ_t^x = [\theta Z_t^x - \gamma (Z_t^x)^\alpha]\, dt + 2\sqrt{Z_t^x} dW_t,\ Z_0^x = x,$$

which is not an equation with additive BM.

- However, $Y_t^x := \sqrt{Z_t^x}$ solves the SDE

$$dY_t^x = \left[\frac{\theta}{2} Y_t^x - \frac{\gamma}{2}(Y_t^x)^{2\alpha-1} - \frac{1}{8Y_t^x}\right] dt + dW_t,\ Y_0^x = \sqrt{x},$$

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References and co–authors

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THANK YOU FOR YOUR ATTENTION !