

ASYMPTOTICS OF POSTERIOR DISTRIBUTIONS FOR BINARY BRANCHING PROCESSES

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Abstract

We compute the posterior distributions of the initial population and parameter of binary branching processes, in the limit of a large number of generations. We compare this Bayesian procedure with a more naïve one, based on hitting times of some random walks. In both cases, central limit theorems are available, with explicit variances.

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1. Introduction

This paper is devoted to some estimation procedures of binary branching processes in a Bayesian setting. To be more specific, let $(X_n)_{n \geq 0}$ denote a Galton-Watson process which starts from the initial population $X_0 \geq 1$ and whose offspring is ruled by the distribution

$$(1 - U) \delta_1 + U \delta_2 \quad \text{with } 0 < U < 1,$$

where δ_x denotes the Dirac mass at x . This means that, at every generation, each individual dies and is replaced by 1 or 2 individuals, with probability $1 - U$ and U respectively, independently of the fate of the other individuals, and that X_n counts generation n .

In a Bayesian framework, the initial population X_0 and the offspring parameter U are both random and unknown. To keep things simple, we also assume that X_0 and U are independent, and we wish to estimate them from the observation of a finite path $x_{1:n} = (x_k)_{1 \leq k \leq n}$ of the process $X_{1:n} = (X_k)_{1 \leq k \leq n}$ up to a given time $n \geq 1$.

Well known motivations for such a study are various biological settings where one observes $X_{1:n}$ but X_0 and U are unknown. One example is the modeling of polymerase chain reaction. Probabilistic models of polymerase chain reactions were proposed and studied by Sun (1995), Weiss and von Haeseler (1995) and (1997), Peccoud and Jacob (1996), Piau (2002), (2004), (2005), and Jagers and Klebaner (2003). Recently, Lalam and Jacob (2007) introduced and studied the Bayesian setting above, see also Lalam (2007). For other Bayesian approaches of branching processes, see Scott (1987), Prakasa Rao (1992), Mendoza and Gutiérrez-Peña (2000), and, for the interesting model of bisexual branching process, Molina, González and Mota (1998) for example. Finally, the idea of studying a branching process backwards, but to estimate its age rather than its initial population, is in Klebaner and Sagitov (2002).

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In models of polymerase chain reactions and in similar contexts, the initial population X_0 is the size of a small sample, extracted at random from a much larger population. This suggests that the initial population X_0 should be Poisson distributed, say with parameter Λ . We assume that Λ is random as well. Jeffreys' principle, see Kass and Wasserman (1996), then indicates that the prior distributions of Λ and U should be proportional to measures which we compute below. To sum up the result of these computations, the prior of Λ is easy to write down but improper and the prior of U is awkward but proper. However, the posterior of (X_0, U) conditionally on $X_{1:n}$ is a proper distribution, which can be computed explicitly. In particular, this posterior distribution depends only on X_1, X_n and $S_n = X_1 + \dots + X_n$. Unfortunately, it is also rather unwieldy.

In such situations, one may rely on numerical algorithms, based on MCMC for example, to simulate the posterior distributions with any prescribed degree of accuracy. Rather, we look for simple asymptotics in realistic regimes. Namely, we assume that n is large and we are interested in the asymptotic posterior distribution of (X_0, U) assuming that X_n is large and that the ratio S_n/X_n converges to a finite limit. This assumption is almost surely fulfilled by the paths of binary branching processes since these are supercritical. In this setting, we show that the posterior distributions indeed converge and we compute explicitly their limit.

2. Results

To describe our results, we introduce some notations. Let $x_{0:\infty} = (x_n)_{n \geq 0}$ denote a sequence of positive integers. We say that such a sequence is admissible if, for every nonnegative n , $x_n \leq x_{n+1} \leq 2x_n$. We say that an admissible sequence is regular if furthermore, x_n/s_n converges to a positive limit when n goes to infinity, where $s_n = x_1 + \dots + x_n$. The binary index $B(x_{0:\infty})$ of a regular admissible sequence $x_{0:\infty}$ is the real number in $]0, 1]$ defined by

$$B(x_{0:\infty}) = \lim_{n \rightarrow \infty} \frac{x_{n+1}}{s_n}.$$

The renormalized index $R(x_{0:\infty})$ of a regular admissible sequence $x_{0:\infty}$ is the real number in $[0, +\infty[$ defined by

$$R(x_{0:\infty}) = \lim_{n \rightarrow \infty} \frac{(s_n - x_{n+1})^2}{4x_{n+1}s_n}.$$

Almost every (sequence which can be realized as a) path of a binary branching process is admissible and regular. The renormalized index is a function of the binary index, namely $R(x_{0:\infty}) = \varrho(B(x_{0:\infty}))$ where, for every u in $]0, 1]$,

$$\varrho(u) = \frac{(1-u)^2}{4u}.$$

The binary index and the normalized index are asymptotic quantities, in the sense that, for every nonnegative integer n , the indexes of a regular admissible sequence $x_{0:\infty}$ do not depend on the first values $x_{0:n}$.

From now on, letters k and n are used to enumerate generations of the process (that is, the time) and symbols x, x_k, x_n and y are used to measure population sizes.

Definition 1. (*Distributions.*) For every positive real number r and every positive integer x , the finite discrete measure $\nu(r, x)$ and the discrete probability measure $\mu(r, x)$, both on the positive integers, are defined by

$$\nu(r, x) = \sum_{y=h(x)}^x \binom{2y}{y} \binom{y}{x-y} r^y \delta_y, \quad \mu(r, x) = \frac{\nu(r, x)}{|\nu(r, x)|}.$$

For every positive integer x , the integer $h(x)$ in the formula above is the upper half of x , that is, the smallest integer such that $2h(x) \geq x$. In other words, $h(2x) = h(2x-1) = x$ for every positive integer x .

Our main result is as follows.

Theorem 1. (Posterior distributions.) (1) *The path $X_{0:\infty}$ of a binary branching process with parameter U is almost surely regular admissible and its binary index is almost surely $B(X_{0:\infty}) = U$.*

(2) *Assume that the prior distribution of (X_0, U) satisfies Jeffreys' principle. Then, for every regular admissible sequence $x_{1:\infty}$ with binary index $u = B(x_{1:\infty})$ in $]0, 1[$, the posterior distribution of (X_0, U) conditionally on $X_{1:n} = x_{1:n}$ converges when n goes to infinity to the distribution $\mu(\varrho(u), x_1) \otimes \delta_u$.*

Theorem 1 shows that the limit posterior distribution of X_0 when n goes to infinity is almost surely $\mu(r, x)$ with $r = \varrho(U)$ and $x = X_1$. Unless $r = 0$, $r = 1$ or $x = 1$, $\mu(r, x)$ is not degenerate, hence the value of X_0 can be determined only with some uncertainty, even from an infinite trajectory $X_{1:\infty}$. On the contrary, U is a function of the infinite trajectory $X_{1:\infty}$.

The limit distribution $\mu(\varrho(u), x_1) \otimes \delta_u$ in theorem 1 converges to the Dirac distribution at $(x_1, 0)$ when u converges to 0 and to the Dirac distribution at $(h(x_1), 1)$ when u converges to 1. Our next result describes the intuitively obvious variations of $\mu(r, x)$ with respect to r and x . First, since $r = \varrho(u)$ is a decreasing function of u and the offspring distribution of the branching process is stochastically increasing with u , one should expect $\mu(r, x)$ to increase stochastically when r increases. Likewise, since x represents the population at time 1, one should expect $\mu(r, x)$, which represents the population at time 0, to increase stochastically when x increases.

We recall that a measure μ_1 is stochastically larger than a measure μ_2 if and only if $\mu_1([z, +\infty)) \geq \mu_2([z, +\infty))$ for every real number z .

Proposition 1. (Ordering of limit posterior distributions.) *For every positive integer x , the family $(\mu(r, x))_{r \geq 0}$ is stochastically increasing. For every positive real number r , the family $(\mu(r, x))_{x \geq 1}$ is stochastically increasing.*

We now characterize the limit of $\mu(r, x)$ for every fixed value of r , when x converges to infinity.

Theorem 2. (Limit posterior distributions of initial populations.) *Fix u in $]0, 1[$. For every positive integer x , let ξ_x denote a random variable with distribution $\mu(\varrho(u), x)$. When x converges to infinity, the expectation and the mode of ξ_x/x both converge to*

$$m_u = 1/(1 + u),$$

and the random variables $(\xi_x - m_u x) / \sqrt{x}$ converge in distribution to a centered Gaussian distribution with variance

$$\sigma_u^2 = u(1 - u)/(1 + u)^3.$$

For the sake of comparison, we turn to another natural way to estimate initial populations of branching processes with known offspring distributions, based on hitting times. To describe this in the setting of binary branching processes, we first introduce some notations.

Definition 2. (*Hitting times.*) Fix a real number u in $]0, 1[$, and let $(\varepsilon_x)_{x \geq 1}$ denote a sequence of independent Bernoulli random variables with distribution $(1 - u)\delta_1 + u\delta_2$. For every positive integer x , let $\sigma_x := \varepsilon_1 + \dots + \varepsilon_x$. Define the distribution of the hitting time η_x by the relation

$$\mathbb{P}(\eta_x = y) = \mathbb{P}(\sigma_y = x \mid H_x), \quad \text{where } H_x = \{\exists z \geq 1; \sigma_z = x\}.$$

When the value of u is known, an estimation procedure of X_0 based on $X_1 = x$ is to propose the value y for X_0 with probability $\mathbb{P}(\eta_x = y)$, thus an estimator of X_0 when $X_1 = x$ is the distribution of η_x .

Recall that $m_u = 1/(1 + u)$ and $\sigma_u^2 = u(1 - u)/(1 + u)^3$.

Theorem 3. (*Initial populations through hitting times.*) Fix a real number u in $]0, 1[$. For every positive integer x ,

$$|\mathbb{E}(\eta_x) - m_u x| \leq 2u/(1 + u)^2 \leq 1/2.$$

Furthermore, when x converges to infinity, $(\eta_x - m_u x) / \sqrt{x}$ converges in distribution to a centered Gaussian variable with variance σ_u^2 .

The rest of the paper is organized as follows. We prove theorem 1 and proposition 1 in section 3 and theorem 2 in section 4. Finally, the proof of theorem 3, sharper bounds on $\mathbb{E}(\eta_x)$ and a brief comparison with another, non Bayesian, estimation procedure are in section 5.

3. Posterior distributions

3.1. Preliminaries

Jeffreys' principle, see Kass and Wasserman (1996), indicates that the prior measure for a parameter θ governing the distribution ν_θ of a random variable Z should have a density proportional to $J(\theta)^{1/2}$, where

$$J(\theta) = -\mathbb{E}_\theta \left(\frac{\partial^2}{\partial \theta^2} \log \nu_\theta(Z) \right).$$

We apply this to the parameter (Λ, U) . Parts of lemma 1 are in Lalam and Jacob (2007).

Lemma 1. For every positive integer n , the prior measure for (Λ, U) according to Jeffreys' principle and based on $X_{0:n}$ is the product of the prior measures for Λ and

U . The prior measures for Λ and for U are respectively proportional to the measures $d\lambda/\sqrt{\lambda}$ on $\lambda > 0$ and $\pi_n(u) du$ on $0 < u < 1$, where

$$\pi_n(u) = \sqrt{\frac{(1+u)^n - 1}{u^2(1-u)}}.$$

In particular, the prior of U is proper.

Proof of lemma 1. Assume that X_0 is Poisson distributed with parameter Λ and that $X_{0:n}$ is a binary branching process with parameter U . Then the distribution $\nu_{\Lambda,U}$ of $X_{0:n}$ is such that

$$\nu_{\Lambda,U}(x_{0:n}) = e^{-\Lambda} \frac{\Lambda^{x_0}}{x_0!} \prod_{k=1}^n \binom{x_{k-1}}{x_k - x_{k-1}} U^{x_k - x_{k-1}} (1-U)^{2x_{k-1} - x_k}.$$

Up to a factor $C(x_{0:n})$ which does not depend on (Λ, U) , $\log \nu_{\Lambda,U}(x_{0:n})$ is

$$-\Lambda + x_0 \log \Lambda + (x_n - x_0) \log U + (s_n - 2x_n + 2x_0) \log(1-U) + C(x_{0:n}).$$

This is the sum of a function of Λ and a function of U , hence the prior measures are product measures. As regards the prior for Λ ,

$$\frac{\partial^2}{\partial \Lambda^2} \log \nu_{\Lambda}(x_{0:n}) = -\frac{x_0}{\Lambda^2}, \quad \text{hence } J(\Lambda) = \frac{\mathbb{E}_{\Lambda}(X_0)}{\Lambda^2} = \frac{1}{\Lambda}.$$

As regards the prior for U ,

$$\frac{\partial^2}{\partial U^2} \log \nu_U(x_{0:n}) = -(x_n - x_0)/U^2 - (s_n - 2x_n + 2x_0)/(1-U)^2,$$

hence

$$J_n(U) = \frac{\mathbb{E}_U(X_n - X_0)}{U^2} + \frac{\mathbb{E}_U(S_n - 2X_n + 2X_0)}{(1-U)^2},$$

where $S_n = X_1 + \dots + X_n$. Since $\mathbb{E}_U(X_k) = (1+U)^k \mathbb{E}(X_0)$ for every nonnegative integer k , one finds that $J_n(U) = \mathbb{E}(X_0) \pi_n(U)^2$ with the notations of the lemma.

Finally, up to multiplicative constants, $\pi_n(u)$ behaves like $1/\sqrt{u}$ when u converges to 0 and like $1/\sqrt{1-u}$ when u converges to 1. Hence, π_n is integrable and there exists a (proper) prior distribution for U . This concludes the proof of lemma 1.

From now on, we fix a positive integer n , we assume that the observations are $X_{1:n} = x_{1:n}$ with $x_{1:n} = (x_k)_{1 \leq k \leq n}$ and we recall that $s_n = x_1 + \dots + x_n$. The posterior distribution in lemma 2 is similar, but not equal, to a posterior distribution computed in Lalam and Jacob (2007).

Lemma 2. *The posterior distribution of (X_0, U) conditionally on $X_{1:n} = x_{1:n}$ depends only on x_1 , x_n and s_n , and is proportional to the measure*

$$\sum_{x=h(x_1)}^{x_1} 2^{-2x} \binom{2x}{x} \binom{x}{x_1 - x} u^{x_n - x} (1-u)^{s_n - 2x_n + 2x} \pi_n(u) \delta_x \otimes du.$$

Proof of lemma 2. Fix $u, x_{1:n}$ and x such that $h(x_1) \leq x \leq x_1$. Then, the conditional probability $\mathbb{P}(U \in du, X_0 = x \mid X_{1:n} = x_{1:n})$ is proportional to

$$\nu_U(du) \int \nu_\Lambda(d\lambda) \mathbb{P}_\lambda(X_0 = x) \mathbb{P}_u(X_{1:n} = x_{1:n} \mid X_0 = x),$$

where $\nu_U(du) = \pi_n(u)du$ and $\nu_\Lambda(d\lambda) = d\lambda/\sqrt{\lambda}$. Hence,

$$\int \nu_\Lambda(d\lambda) \mathbb{P}_\lambda(X_0 = x) = \frac{\Gamma(x + 1/2)}{\Gamma(x + 1)} = \sqrt{\pi} 2^{-2x} \binom{2x}{x}.$$

Likewise, using the computations in the proof of lemma 1, one gets

$$\mathbb{P}_u(X_{1:n} = x_{1:n} \mid X_0 = x) = C(x_{1:n}) \binom{x}{x_1 - x} u^{x_n - x} (1 - u)^{s_n - 2x_n + 2x},$$

where $C(x_{1:n})$ does not depend on (x, u) . This concludes the proof of lemma 2.

3.2. Proof of theorem 1

Part (1) follows from the fact that, when n converges to infinity, $X_n/(1 + U)^n$ converges almost surely to a random positive and finite limit.

A sketch of the proof of part (2) is as follows. Consider the distribution in lemma 2 and assume that x_n converges to infinity and that $x_n/(s_n - x_n)$ converges to v . Then $s_n - x_n$ is equivalent to x_n/v , hence

$$u^{x_n} (1 - u)^{s_n - 2x_n} = (u^v (1 - u)^{1-v})^{s_n - x_n + o(x_n)}.$$

The inner parenthesis is maximal when $u = v$, and the exponent converges to infinity, hence this contribution becomes concentrated around the value $u = v$. The remaining factor involving u in the distribution described in lemma 2 is $\varrho(u)^x$, and the convergence to $\mu(\varrho(v), x_1)$ follows.

For a detailed proof of part (2), we consider a sequence $x_{1:\infty}$ such that x_n converges to infinity and $x_n/(s_n - x_n)$ converges to v . For every positive integer n , we introduce random variables (T_n, U_n) distributed as (X_0, U) conditionally on $X_{1:n} = x_{1:n}$. We first show the convergence in probability of U_n , then the convergence in distribution of (T_n, U_n) .

Lemma 3. *With the notations above, U_n converges to v in probability.*

Proof of lemma 3. Lemma 2 yields

$$\mathbb{P}(T_n = x, U_n \in du) = c_n p_x \varrho(u)^x b_n(u) q_n(u) du,$$

where c_n denotes a normalizing constant which is independent on x and u , p_x depends only on x and x_1 , $b_n(u)$ depends only on u, x_n and s_n , and $q_n(u)$ depends only on u and n . More precisely, for every integer x such that $x_1 \leq 2x \leq 2x_1$ and every real number u in $]0, 1[$,

$$\begin{aligned} p_x &= \binom{2x}{x} \binom{x}{x_1 - x}, \\ b_n(u) &= u^{x_n - 1/2} (1 - u)^{s_n - 2x_n - 1/2}, \\ q_n(u) &= \sqrt{\frac{(1 + u)^n - 1}{u}}. \end{aligned}$$

We aim to show that, for every integer x such that p_x is positive and every positive real number z , when n converges to infinity,

$$\mathbb{P}(T_n = x, |U_n - v| \geq z) \ll \mathbb{P}(T_n = x).$$

Since the function q_n is nondecreasing,

$$\mathbb{P}(T_n = x, |U_n - v| \geq z) \leq c_n p_x q_n(1) \int_{|u-v| \geq z} \varrho(u)^x b_n(u) \mathbf{1}_{[0,1]}(u) du,$$

and

$$\mathbb{P}(T_n = x) \geq c_n p_x q_n(0) \int_0^1 \varrho(u)^x b_n(u) du.$$

The ratio of the two integrals written above is $\mathbb{P}(|B_n - v| \geq z)$, where B_n is a beta random variable of parameters (α_n, β_n) , with

$$\alpha_n = x_n - x + 1/2, \quad \beta_n = s_n - 2x_n + 2x + 1/2.$$

Since α_n and β_n both converge to infinity and $\alpha_n/(\alpha_n + \beta_n)$ converges to v , it is an easy matter to show that B_n converges in probability to v . However, we need a stronger statement, namely the fact that $\mathbb{P}(|B_n - v| \geq z) \ll q_n(0)/q_n(1)$. Note that $q_n(0) = \sqrt{n}$ and $q_n(1) \sim 2^{n/2}$, hence $q_n(0)/q_n(1) \ll 1$.

One can write an elementary proof of this, based on the representation of beta random variables with integer parameters as ratios of sums of i.i.d. exponential random variables and on large deviations properties of these sums. Instead, we rely on approximations of beta distributions by normal distributions provided by Alferts and Dinges (1984). A rephrasing of corollary 1 on page 405 of this paper is as follows. Let $(Y_k)_k$ denote a sequence of beta random variables of parameters $(ka_k, k(1 - a_k))$. Assume that k converges to infinity and that a_k converges to a limit $0 < a < 1$. Then, for every fixed y such that $a < y < 1$, the ratio

$$\frac{\mathbb{P}(Y_k \geq y)}{\mathbb{P}\left(Z \geq \sqrt{2k\ell(a_k, y)}\right)}$$

converges to a finite and positive limit, which depends on a and y only, where Z denotes a standard Gaussian random variable, and ℓ denotes the function defined by

$$\ell(\alpha, y) = \alpha \log\left(\frac{\alpha}{y}\right) + (1 - \alpha) \log\left(\frac{1 - \alpha}{1 - y}\right).$$

Since a_k converges to a and $\ell(\alpha, y)$ is a continuous function of α , standard estimates of Gaussian tails and the result by Alferts and Dinges show that there exists a positive constant $C < 1$, independent on k , such that for every k large enough,

$$\mathbb{P}(Y_k \geq y) \leq C^k.$$

Applying this to our setting, first to the random variables B_n and to $y = v + z$, then to the random variables $1 - B_n$ and to $y = 1 - v + z$, one gets the existence of a constant $C < 1$ such that, for every n large enough,

$$\mathbb{P}(|B_n - v| \geq z) \leq 2C^{\alpha_n + \beta_n}.$$

Since $\alpha_n + \beta_n = s_{n-1} + x + 1 \geq s_{n-1} \gg n$, $2C^{\alpha_n + \beta_n} \ll q_n(0)/q_n(1)$, and the proof of lemma 3 is complete.

We now apply lemma 3 to the proof of part (2). Introduce the finite sums

$$p(u) = \sum_x p_x \varrho(u)^x.$$

For every u in $]0, 1[$, the distribution of T_n conditionally on $U_n = u$ is independent on n and such that

$$\mathbb{P}(T_n = x | U_n = u) = p(u)^{-1} p_x \varrho(u)^x.$$

Hence, for every measurable subset B of $]0, 1[$,

$$\mathbb{P}(T_n = x, U_n \in B) = \mathbb{E} (p(U_n)^{-1} p_x \mathbf{1}_B(U_n) \varrho(U_n)^x).$$

The function $u \mapsto p(u)^{-1} p_x \mathbf{1}_B(u) \varrho(u)^x$ is bounded by 1 on $]0, 1[$ and, as soon as v is not in the boundary of B , continuous at $u = v$. Since U_n converges in distribution to v , this implies that $\mathbb{P}(T_n = x, U_n \in B)$ converges to $p(v)^{-1} p_x \mathbf{1}_B(v) \varrho(v)^x$, for instance for every interval $B = [0, u]$ with $u \neq v$. This is equivalent to the desired convergence in distribution.

3.3. Remarks

For every positive integer n and every admissible sample, $s_n \geq 2x_n(1 - 1/2^n)$ since $x_k \geq x_{k+1}/2$ for every nonnegative integer k , hence $s_n - x_n \geq x_n + o(x_n)$ and $u \leq 1$ in the asymptotics that we consider. Furthermore, the function ϱ decreases from $\varrho(0^+) = +\infty$ to $\varrho(1^-) = 0$.

The measures $\mu(r, x)$ for the first values of x are as follows: $\mu(r, 1) = \delta_1$,

$$\mu(r, 2) = \frac{\delta_1 + 3r\delta_2}{1 + 3r}, \quad \mu(r, 3) = \frac{3\delta_2 + 5r\delta_3}{3 + 5r}, \quad \mu(r, 4) = \frac{3\delta_2 + 30r\delta_3 + 35r^2\delta_4}{3 + 30r + 35r^2},$$

and

$$\mu(r, 5) = \frac{15\delta_3 + 70r\delta_4 + 63r^2\delta_5}{15 + 70r + 63r^2}.$$

3.4. Proof of proposition 1

The monotonicity with respect to r is valid in a wider setting, described in proposition 2 below, but the monotonicity with respect to x is more specific.

Proposition 2. *Let μ denote a nonzero bounded measure on the real line with exponential moments. For every real number a , introduce the measures ν_a and μ_a defined by the relations $\nu_a(dx) = e^{ax}\mu(dx)$ and $\mu_a = \nu_a/|\nu_a|$. Then the family $(\mu_a)_a$ is stochastically nondecreasing.*

Proof of proposition 2. Fix x in the real line. The derivative of $\mu_a([x, +\infty))$ with respect to a has the sign of $D(x)$, with

$$D(x) = \int_{y \geq x} ye^{ay} \mu(dy) \int e^{az} \mu(dz) - \int_{y \geq x} e^{ay} \mu(dy) \int ze^{az} \mu(dz).$$

The variations of $D(x)$ with respect to x are given by

$$dD(x) = e^{ax} \mu(dx) \int (y - x) e^{ay} \mu(dy).$$

The integral in the right hand side is a nonincreasing function of x . Since $D(-\infty) = D(+\infty) = 0$, the function $x \mapsto D(x)$ is nondecreasing for $x \leq x_a$ and nonincreasing for $x \geq x_a$, where x_a solves the equation

$$\int ye^{ay} \mu(dy) = x_a \int e^{ay} \mu(dy).$$

This proves that $D(x) \geq 0$ for every x , hence $\mu_a([x, +\infty)) \leq \mu_b([x, +\infty))$ for every $a \leq b$. This concludes the proof of proposition 2.

We turn to the monotonicity of $\nu(r, x)$ with respect to x . We fix a value of r and write every $\nu(r, x)$ as

$$\nu(r, x) = \sum_y a_y^x \delta_y.$$

We want to prove that for every fixed x , $G(z) \geq 0$ for every z , with

$$G(z) = \sum_y a_y^x \sum_{y \geq z} a_y^{x+1} - \sum_{y \geq z} a_y^x \sum_y a_y^{x+1}.$$

One sees that $G(0) = G(\infty) = 0$, and simple computations show that

$$F(z) = \frac{1}{a_z^x} (G(z+1) - G(z)) = \sum_y a_y^{x+1} - \frac{a_z^{x+1}}{a_z^x} \sum_y a_y^x.$$

At this point, we use the specific form of the coefficients a_z^x , which yields

$$\frac{a_z^{x+1}}{a_z^x} = 2 \frac{(2x+1)(2z-x)}{(x+1)(x+1-z)}.$$

This shows that $(F(z))_z$ is a nonincreasing sequence, hence $G(z+1) - G(z) \geq 0$ if $z < z_*$ and $G(z+1) - G(z) \leq 0$ if $z \geq z_*$, for a given z_* . Hence the sequence $(G(z))_z$ is nondecreasing on $z \leq z_*$ and nonincreasing on $z \geq z_*$. Since $G(0) = G(\infty) = 0$, this implies that $G(z) \geq 0$ for every positive z . This concludes the proof of proposition 1.

4. Limit posterior distributions of initial populations

4.1. Expectations

Let u in $]0, 1[$ and $r = \varrho(u)$. We are interested in the limit as $x \rightarrow \infty$ of the sequence

$$\frac{1}{x} \mathbb{E}(\xi_x) = \frac{A(r, x)}{x B(r, x)},$$

with the notations

$$A(r, x) = \sum_y y \nu(r, x)(y) = \sum_y y \binom{2y}{y} \binom{y}{x-y} r^y,$$

and

$$B(r, x) = |\nu(r, x)| = \sum_y \binom{2y}{y} \binom{y}{x-y} r^y.$$

Definition 3. For every positive λ and r , introduce

$$C_\lambda(r, z) = (1 - 4rz(1 + z))^{-\lambda} = \sum_{x \geq 0} c_\lambda(r, x) z^x.$$

Starting from the expansion

$$(1 - 4z)^{-1/2} = \sum_{x \geq 0} \binom{2x}{x} z^x,$$

one can write $B(r, x)$ as the coefficient of z^x in the expansion of $C_{1/2}(r, x)$ along the powers of z , namely, $B(r, x) = c_{1/2}(r, x)$. Likewise, $A(r, x)$ is r times the derivative of $B(r, x)$ with respect to r , hence $A(r, x)$ is the coefficient of z^x in the expansion of $2rz(1 + z)C_{3/2}(r, x)$ along the powers of z . This yields

$$A(r, x) = 2r (c_{3/2}(r, x - 1) + c_{3/2}(r, x - 2)),$$

and

$$x B(r, x) = 2r (c_{3/2}(r, x - 1) + 2c_{3/2}(r, x - 2)).$$

Definition 4. For every positive r , introduce

$$\gamma(r) = \frac{1}{2} \left(\sqrt{\frac{1+r}{r}} - 1 \right), \quad m(r) = \frac{1 + \gamma(r)}{1 + 2\gamma(r)} = \frac{1}{2} \left(1 + \sqrt{\frac{r}{1+r}} \right).$$

Note that, for every u in $]0, 1[$,

$$\gamma(\varrho(u)) = \frac{u}{1-u}, \quad m(\varrho(u)) = \frac{1}{1+u} = m_u.$$

Lemma 4. For every positive λ and r , when x converges to infinity,

$$c_\lambda(r, x) \sim c_\lambda(r) x^{\lambda-1} \gamma(r)^{-x}, \quad c_\lambda(r) = m(r)^\lambda / \Gamma(\lambda).$$

Proof of lemma 4. This is a consequence of known expansions of powers of $1/(1-z)$. First, recall that

$$(1-z)^{-\lambda} = \sum_{x \geq 0} d_\lambda(x) z^x, \quad d_\lambda(x) = \frac{\Gamma(x+\lambda)}{\Gamma(x+1)\Gamma(\lambda)} \sim \frac{x^{\lambda-1}}{\Gamma(\lambda)}.$$

We use this and the decomposition

$$1 - 4rz(1 + z) = \left(1 - \frac{z}{\gamma(r)} \right) \left(1 + \frac{z}{\gamma(r) + 1} \right),$$

to get the expansion

$$C_\lambda(r, z) = \sum_x d_\lambda(x) \left(\frac{z}{\gamma(r)} \right)^x \sum_x d_\lambda(x) \left(\frac{-z}{1 + \gamma(r)} \right)^x,$$

which implies

$$c_\lambda(r, x) = d_\lambda(x) \gamma(r)^{-x} \sum_{y=0}^x \left(\frac{-\gamma(r)}{\gamma(r)+1} \right)^y d_\lambda(y) \frac{d_\lambda(x-y)}{d_\lambda(x)}.$$

When x converges to infinity, the ratios $d_\lambda(x-y)/d_\lambda(x)$ converge to 1, hence, by dominated convergence,

$$c_\lambda(r, x) \sim d_\lambda(x) \gamma(r)^{-x} \sum_{y \geq 0} \left(\frac{-\gamma(r)}{\gamma(r)+1} \right)^y d_\lambda(y) = d_\lambda(x) \gamma(r)^{-x} \left(1 + \frac{\gamma(r)}{1+\gamma(r)} \right)^{-\lambda},$$

where the equality stems from the definition of the coefficients $d_\lambda(\cdot)$. Plugging the equivalent of $d_\lambda(x)$ into this and using the fact that $1 + \gamma(r)/(1 + \gamma(r)) = 1/m(r)$, one deduces lemma 4.

Lemma 4 for $\lambda = \frac{3}{2}$ yields that, when x converges to infinity, there exists a constant α , whose value is irrelevant, such that

$$A(r, x) \sim 2r\alpha x^{1/2} \gamma(r)^{-x} \gamma(r) (1 + \gamma(r)),$$

and

$$xB(r, x) - A(r, x) \sim 2r\alpha x^{1/2} \gamma(r)^{-x} \gamma(r)^2.$$

Hence $(xB(r, x) - A(r, x))/A(r, x)$ converges to $\gamma(r)/(1 + \gamma(r))$, and

$$\frac{A(r, x)}{xB(r, x)} \text{ converges to } \frac{1 + \gamma(r)}{1 + 2\gamma(r)} = m(r).$$

This is the desired convergence of the expectations because, as mentioned above, the relation $r = \varrho(u)$ means that $m(r) = m_u$.

4.2. Modes

To study the mode of ξ_x , one compares $\nu(r, x)(y+1)$ to $\nu(r, x)(y)$. The ratios

$$\frac{\nu(r, x)(y+1)}{\nu(r, x)(y)} = \frac{(y+1/2)(x-y)r}{(y+1-x/2)(y+1/2-x/2)}$$

are the terms of a nonincreasing sequence indexed by y . Writing y as $y = x(1+s)/(2s)$ with $s \geq 1$, when x is large, one gets

$$\frac{\nu(r, x)(y+1)}{\nu(r, x)(y)} \sim r(s^2 - 1).$$

This implies that the sequence $(\nu(r, x)(y))_y$ is increasing on $y \leq y_*$ and decreasing on $y \geq y_*$, for a value of y_* such that $y_* = x(1+s_*)/(2s_*) + o(x)$ with $s_*^2 = 1 + 1/r$. Finally, this shows that, when $r = \varrho(u)$, the mode of $\mu(r, x)$ is at $x/(1+u) + o(x)$.

4.3. Distributions

Our next computation is based on characteristic functions. Fix u in $]0, 1[$ and let $r = \varrho(u)$. For every positive integer x , introduce

$$F_x(t) = \mathbb{E} \left(\exp \left(t \frac{\xi_x - x m}{\sqrt{x}} \right) \right).$$

Recall that

$$m(r) = \frac{1 + \gamma(r)}{1 + 2\gamma(r)}, \quad \frac{1}{1 + 2\gamma(r)} = \sqrt{\frac{r}{1+r}}, \quad r = \frac{(1-u)^2}{4u}.$$

Since $\mathbb{E}(\exp(t\xi_x)) = B(re^t, x)/B(r, x)$,

$$F_x(t) = e^{-t\sqrt{x}m} B(re^{t/\sqrt{x}}, x)/B(r, x).$$

We turn to the study of the sequence of functions $(B(\cdot, x))_{x \geq 1}$.

Since $B(r, x) = c_{1/2}(r, x)$, a consequence of lemma 4 is that, when x converges to infinity,

$$\frac{B(re^{t/\sqrt{x}}, x)}{B(r, x)} \sim \left(\frac{\gamma(r)}{\gamma(re^{t/\sqrt{x}})} \right)^x \frac{S(x, t/\sqrt{x})}{m(r)^{1/2}},$$

where, for every s ,

$$S(x, s) = \sum_{y=0}^x \left(\frac{-\gamma(re^s)}{\gamma(re^s) + 1} \right)^y d_{1/2}(y) \frac{d_{1/2}(x-y)}{d_{1/2}(x)}.$$

We get rid of the fraction involving $S(x, t/\sqrt{x})$ through lemmas 5 and 6.

Lemma 5. *For every nonnegative x and y , $d_{1/2}(y) d_{1/2}(x) \leq d_{1/2}(x+y)$.*

Proof of lemma 5. A probabilistic proof is as follows. For every nonnegative x , $d_{1/2}(x) = 2^{-2x} \binom{2x}{x}$ is the probability that a simple symmetric random walk on the integer line is at its starting point after $2x$ steps. Hence $d_{1/2}(x+y)$ is the probability that the random walk is at its starting point after $2x+2y$ points and $d_{1/2}(y) d_{1/2}(x)$ is the probability that the random walk is at its starting point after $2x$ steps and also after $2x+2y$ points. The latter event being included in the former, this shows the desired inequality.

Lemma 6. *When x converges to infinity, $S(x, t/\sqrt{x})$ converges to $m(r)^{1/2}$.*

Proof of lemma 6. Since $S(x, 0)$ converges to $S(\infty, 0) = m(r)^{1/2}$ when x converges to infinity, we show that $S(x, t/\sqrt{x}) - S(x, 0)$ converges to 0. By lemma 5, the ratios of coefficients $d_{1/2}$ involved in $S(x, t/\sqrt{x})$ and $S(x, 0)$ are bounded by 1. Adding terms such that $y \geq x+1$, one gets $|S(x, t/\sqrt{x}) - S(x, 0)| \leq T(t/\sqrt{x})$, where

$$T(t/\sqrt{x}) = \sum_{y=0}^{+\infty} \left| \left(\frac{\gamma(re^{t/\sqrt{x}})}{\gamma(re^{t/\sqrt{x}}) + 1} \right)^y - \left(\frac{\gamma(r)}{\gamma(r) + 1} \right)^y \right|.$$

All the terms in the sum have the same sign, hence

$$T(t/\sqrt{x}) = \left| \sum_{y=0}^{+\infty} \left(\frac{\gamma(re^{t/\sqrt{x}})}{\gamma(re^{t/\sqrt{x}}) + 1} \right)^y - \left(\frac{\gamma(r)}{\gamma(r) + 1} \right)^y \right|.$$

One can compute the sum of each geometric series. This yields

$$|S(x, t/\sqrt{x}) - S(x, 0)| \leq T(t/\sqrt{x}) = \left| \gamma(re^{t/\sqrt{x}}) - \gamma(r) \right|,$$

which proves the lemma since $\gamma(\cdot)$ is a continuous function.

Lemma 6 above shows that

$$\frac{B(re^{t/\sqrt{x}}, x)}{B(r, x)} \sim \left(\frac{\gamma(re^{t/\sqrt{x}})}{\gamma(r)} \right)^{-x}.$$

The rest of the proof is standard. A Taylor expansion of $\gamma(\cdot)$ around r yields

$$\gamma(re^{t/\sqrt{x}}) = \gamma(r) + (e^{t/\sqrt{x}} - 1) \gamma'(r) + (e^{t/\sqrt{x}} - 1)^2 \gamma''(r)/2 + o((e^{t/\sqrt{x}} - 1)^2).$$

Using the expansion of $e^{t/\sqrt{x}}$ along powers of $1/\sqrt{x}$ and dividing everything by $\gamma(r)$, one gets

$$\frac{\gamma(re^{t/\sqrt{x}})}{\gamma(r)} = 1 + \left(r \frac{\gamma'(r)}{\gamma(r)} \right) \frac{t}{\sqrt{x}} + \left(r \frac{\gamma'(r)}{\gamma(r)} + r^2 \frac{\gamma''(r)}{\gamma(r)} \right) \frac{t^2}{2x} + o\left(\frac{1}{x}\right).$$

Note that

$$r \frac{\gamma'(r)}{\gamma(r)} = -m(r).$$

Taking logarithms, writing the ratio of functions γ as

$$(\gamma(re^{t/\sqrt{x}})/\gamma(r))^{-x} = \exp(-x \log(\gamma(re^{t/\sqrt{x}})/\gamma(r))),$$

and using the expansion $\log(1+z) = z - z^2/2 + o(z^2)$ when $z = o(1)$, one gets that $F_x(t)$ is equivalent to the exponential of

$$-tm(r)\sqrt{x} - x \left(-m(r) t/\sqrt{x} + (m_2(r) - m(r)) t^2/(2x) - m(r)^2 t^2/(2x) + o(1/x) \right),$$

where

$$m_2(r) = r^2 \frac{\gamma''(r)}{\gamma(r)}.$$

Finally, $F_x(t)$ converges to $e^{\sigma^2(r)t^2/2}$, with

$$\sigma^2(r) = m(r)^2 + m(r) - m_2(r).$$

Using the definitions of $m(r)$ and $m_2(r)$ as functions of $\gamma(r)$ and its derivatives, one gets

$$\sigma^2(r) = r \left(-r \frac{\gamma'(r)}{\gamma(r)} \right)' = r m'(r).$$

Using the formula for $m(r)$ at the beginning of this section, one gets finally

$$\sigma^2(r) = \frac{1}{4} \sqrt{\frac{r}{(1+r)^3}} = \frac{u(1-u)}{(1+u)^3} = \sigma_u^2.$$

The proof is complete.

5. Conditional hitting times

5.1. Proof of theorem 3

We introduce the renewal process $(\zeta_x)_{x \geq 1}$ with increments $(\varepsilon_x)_{x \geq 1}$, that is

$$\zeta_x = \inf\{y \geq 1; \sigma_y \geq x\}.$$

The usual central limit theorem for renewal processes states that $(\zeta_x - mx)/\sqrt{x}$ converges in distribution to a centered Gaussian variable whose variance is the variance $u(1-u)$ of every ε_x divided by the cube of the mean $1+u$ of every ε_x , that is $u(1-u)/(1+u)^3 = \sigma_u^2$.

Our next lemma expresses the distribution of η_x for every positive x in terms of the distributions of the random variables $(\zeta_z)_{1 \leq z \leq x+1}$.

Lemma 7. *For every positive x and y ,*

$$\mathbb{P}(\eta_x = y) = \frac{1+u}{1-(-u)^{x+1}} \sum_{z=0}^{x-1} (-u)^z \mathbb{P}(\zeta_{x+1-z} = y+1).$$

Proof of lemma 7. Let x and y denote positive integers. We begin with the fact that

$$\{\zeta_{x+1} = y+1\} = \{\sigma_y = x\} \cup \{\sigma_y = x-1, \varepsilon_{y+1} = 2\},$$

hence

$$\mathbb{P}(\sigma_y = x) = \mathbb{P}(\zeta_{x+1} = y+1) - u \mathbb{P}(\sigma_y = x-1).$$

Iterating this recursion, one gets

$$\mathbb{P}(H_x) \mathbb{P}(\eta_x = y) = \mathbb{P}(\sigma_y = x) = \sum_{z=0}^{x-1} (-u)^z \mathbb{P}(\zeta_{x+1-z} = y+1).$$

Summing over every positive value of y and using the facts that $\mathbb{P}(\zeta_z = 1) = 0$ if $z \geq 3$ and that $\mathbb{P}(\zeta_2 = 1) = u$, one gets

$$\mathbb{P}(H_x) = (-u)^{x-1}(1-u) + \sum_{z=0}^{x-2} (-u)^z = \frac{1-(-u)^{x+1}}{1+u}.$$

This concludes the proof.

Lemma 7 above, the fact that $|u| < 1$ and the convergence of the distribution of $(\zeta_x - mx)/\sqrt{x}$, imply the same convergence for the distribution of $(\eta_x - mx)/\sqrt{x}$.

Finally, $(\xi_x - mx)/\sqrt{x}$, $(\zeta_x - mx)/\sqrt{x}$ and $(\eta_x - mx)/\sqrt{x}$ all converge in distribution to the same limit, which is the centered Gaussian distribution with variance σ_u^2 .

5.2. Sharp bounds

Lemma 8. *For every positive x ,*

$$\mathbb{E}(\eta_x) = \frac{x+1}{1+u} \frac{1+(-u)^{x+2}}{1-(-u)^{x+1}} - \frac{1+u^2}{(1+u)^2}.$$

For instance,

$$\mathbb{E}(\eta_1) = 1, \quad \mathbb{E}(\eta_2) = 2 - \frac{u}{1 - u(1 - u)}.$$

For every positive integer x , one can deduce from the exact formula above that

$$\frac{x}{1 + u} - \frac{2u^2}{(1 + u)^2} \leq \mathbb{E}(\eta_x) \leq \frac{x}{1 + u} + \frac{2u}{(1 + u)^2}.$$

The width of the interval delimited by the upper and the lower bounds of $\mathbb{E}(\eta_x)$ above is $2u/(1 + u) \leq 1$.

Bounds on $\mathbb{E}(\eta_x)$, depending on the parity of x , are as follows. For every odd x ,

$$\mathbb{E}(\eta_x) \geq x/(1 + u),$$

and for every even x ,

$$\mathbb{E}(\eta_x) \leq x/(1 + u) + u(1 - u)/(1 + u) \leq (x + 1/4)/(1 + u).$$

These refined bounds yield intervals around $\mathbb{E}(\eta_x)$, which depend on the parity of x , and whose width is always at most $2u/(1 + u)^2 \leq 1/2$.

Proof of lemma 8. Fix a positive integer x , a real number u in $]0, 1[$, and let $r = \varrho(u)$. Let $p_x^y = \mathbb{P}(\sigma_y = x)$. Then $\eta_x(\mathbb{P})$ is proportional to the measure $\sum_y p_x^y \delta_y$ and, for every positive y ,

$$\sum_{x=y}^{2y} p_x^y t^x = ((1 - u)t + ut^2)^y.$$

Hence the distribution of η_x is $\mu_\eta(r, x)$, where $\mu_\eta(r, x) = \nu_\eta(r, x)/|\nu_\eta(r, x)|$ and

$$\nu_\eta(r, x) = \sum_{y=h(x)}^x \binom{y}{x-y} 4^y r^y \delta_y.$$

When $u = 0$, $r = \infty$ and $\mu_\eta(\infty, x)$ is the Dirac distribution at x . When $u = 1$, $r = 0$ and $\mu_\eta(0, x)$ is the Dirac distribution at $h(x)$. For the first values of x , the distributions $\mu_\eta(r, x)$ are as follows: $\mu_\eta(r, 1) = \delta_1$,

$$\mu_\eta(r, 2) = \frac{\delta_1 + 4r\delta_2}{1 + 4r}, \quad \mu_\eta(r, 3) = \frac{2\delta_2 + 4r\delta_3}{2 + 4r}, \quad \mu_\eta(r, 4) = \frac{\delta_2 + 12r\delta_3 + 16r^2\delta_4}{1 + 12r + 16r^2}.$$

This implies that, for every positive x ,

$$\mathbb{E}(\eta_x) = r g'_x(r)/g_x(r), \quad g_x(r) = \sum_{y=h(x)}^x \binom{y}{x-y} 4^y r^y.$$

To study the generating functions g_x , we introduce $g_0(r) = 1$ and

$$G(r, z) = \sum_{x \geq 0} g_x(r) z^x.$$

Summing first over $y \leq x \leq 2y$, then over $y \geq 0$, one gets

$$G(r, z) = \sum_{y \geq 0} (4rz)^y (1+z)^y = 1/(1-4rz(1+z)) = C_1(r, z).$$

From the proof of lemma 4, one knows that the poles of $C_1(r, z)$ are $z = \gamma(r)$ and $z = -\gamma_2(r)$ with $\gamma_2(r) = \gamma(r) + 1$, hence,

$$G(r, z) = \frac{1}{\gamma(r) + \gamma_2(r)} \left(\frac{\gamma_2(r)}{1 - z/\gamma(r)} + \frac{\gamma(r)}{1 + z/\gamma_2(r)} \right).$$

This shows that, for every nonnegative x ,

$$g_x(r) = \frac{\gamma(r)\gamma_2(r)}{\gamma(r) + \gamma_2(r)} \left(\gamma(r)^{-(x+1)} - (-\gamma_2(r))^{-(x+1)} \right).$$

From here, the expression of $\gamma(r)$ as a function of r and tedious computations of derivatives yield the result.

5.3. Comparison with a naïve estimator

For a given value u in $]0, 1[$ and for a branching process $X_{0:\infty}$ with offspring distribution $(1-u)\delta_1 + u\delta_2$, when n converges to infinity,

$$S_n \sim X_n(1 + 1/(1+u) + 1/(1+u)^2 + \dots) = X_n(1 + 1/u) \quad \text{almost surely,}$$

hence $B(X_{0:\infty}) = u$ almost surely. The naïve pointwise prediction of the mean initial population conditional on $X_1 = x$, namely $N_u(x) = x/(1+u)$, should be compared to the Bayesian prediction $\mathbb{E}_u(\xi_x)$ for $r = \rho(u)$. For $x = 2$, one gets

$$\frac{\mathbb{E}_u(\xi_2)}{N_u(2)} = \frac{(4u + 6(1-u)^2)(1+u)}{2(4u + 3(1-u)^2)}.$$

This ratio is 1 when $u = 0$ or $u = 1$, greater than 1 for every u in $]0, \frac{1}{3}[$, and smaller than 1 for every u in $]\frac{1}{3}, 1[$. Hence the naïve and Bayesian predictions cannot be easily compared, at least on $X_1 = x$ for a given finite x .

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