

Gene genealogies in a haploid population evolving according to sweepstakes reproduction – approximating $\mathbb{E}[R_i(n)]$ for the time-changed δ_0 -Beta($\gamma, 2 - \alpha, \alpha$)-coalescent

BJARKI ELDON¹² 

Fix $0 < \alpha < 2$ and $0 < \gamma \leq 1$. Let $\{\xi^n\} \equiv \{\xi^n(t) : t \geq 0\}$ be the continuous-time time-changed δ_0 -Beta($\gamma, 2 - \alpha, \alpha$)-coalescent with time-change function $G(t) = \int_0^t e^{\rho s} ds$. Write $\#A$ for the number of elements in a given finite set A , $L_i(n) \equiv \int_0^{\tau(n)} \#\{\xi \in \xi^n(t) : \#\xi = i\} dt$ and $L(n) \equiv \int_0^{\tau(n)} \#\xi^n(t) dt$ and $\tau(n) \equiv \inf\{t \geq 0 : \#\xi^n(t) = 1\}$ for $i \in \{1, 2, \dots, n-1\}$. We then have $L(n) = L_1(n) + \dots + L_{n-1}(n)$. Define $R_i(n) \equiv L_i(n)/\sum_j L_j(n)$ for $i = 1, 2, \dots, n-1$. Interpreting $\{\xi^n\}$ as ‘trees’ we may view $L_i(n)$ as the random total length of branches supporting $i \in \{1, 2, \dots, n-1\}$ leaves, with the length measured in coalescent time units, and n sample size. With this C++ code we sample the time-changed δ_0 -Beta($\gamma, 2 - \alpha, \alpha$)-coalescent with $0 < \alpha < 2$ and exponential growth parameter $\rho \geq 0$ fixed, and approximate $\mathbb{E}[R_i(n)]$

Contents

1	Copyright	1
2	compilation and output	2
3	intro	3
4	code	4
4.1	includes	5
4.2	random number generators	6
4.3	the merging rate	7
4.4	one experiment	8
4.5	main	10
5	conclusions and bibliography	11

1 Copyright

Copyright © 2026 Bjarki Eldon

This document and any source code it contains is distributed under the terms of the GNU General Public Licence (version ≥ 3). You should have received a copy of the licence along with this file (see file COPYING).

The source codes described in this document are free software: you can redistribute it and/or modify it under the terms of the GNU General Public License as published by the Free Software Foundation, either version 3 of the License, or (at your option) any later version.

¹beldon11@gmail.com

²compiled @ 3:37pm on Tuesday 6th January, 2026; using
kernel 6.18.3+deb14-amd64 GNU/Linux
GNU bash, version 5.3.3(1)-release (x86_64-pc-linux-gnu)
CTANGLE 4.12.1 (TeX Live 2025/Debian)
g++ (Debian 15.2.0-12) 15.2.0
GSL 2.8
CWEAVE 4.12.1 (TeX Live 2025/Debian)
This is LuaHBTeX, Version 1.22.0 (TeX Live 2025/Debian) Development id: 7673
SpiX 1.3.0
GNU Awk 5.3.2, API 4.0, PMA Avon 8-g1, (GNU MPFR 4.2.2, GNU MP 6.3.0)
GNU Emacs 30.2

This document and the code it contains is distributed in the hope that it will be useful, but WITHOUT ANY WARRANTY; without even the implied warranty of MERCHANTABILITY or FITNESS FOR A PARTICULAR PURPOSE. See the GNU General Public License for more details. You should have received a copy of the GNU General Public License along with this file (see COPYING). If not, see <http://www.gnu.org/licenses/>.

2 compilation and output

This CWEB [KL94] document (the `.w` file) can be compiled with `cweave` to generate a `.tex` file, and with `ctangle` to generate a `.c` [KR88] C++ code file.

Use the shell tool `spix` on the script appearing before the preamble (the lines starting with `$$`); simply

```
spix /path/to/the/sourcefile
```

where `sourcefile` is the `.w` file

One may also copy the script into a file and run `parallel` [Tan11] :

```
parallel --gnu -j1 ::: /path/to/scriptfile
```

3 intro

Here we consider the continuous-time δ_0 -Beta($\gamma, 2 - \alpha, \alpha$)-coalescent with the time-change corresponding to exponential population growth where the time-change function $G(t) = \int_0^t e^{\rho s} ds$ for some fixed $\rho \geq 0$.

One samples the δ_0 -Beta($\gamma, 2 - \alpha, \alpha$)-coalescent by sampling group sizes $2 \leq k_1, \dots, k_r \leq n$ with $\sum_i k_i \leq n$, $s = n - \sum_i k_i$, according to

$$\begin{aligned} \lambda_{n;k;s} &= \frac{1}{C_{\kappa,\alpha,\gamma}} \binom{n}{k} \left(\mathbb{1}_{\{r=1, k_1=2\}} C_\kappa + \frac{c\alpha}{\mathfrak{m}^\alpha} B(\gamma, k - \alpha, n - k + \alpha) \right) \\ C_\kappa &= \frac{2}{\mathfrak{m}^2} \left(\mathbb{1}_{\{\kappa=2\}} + \mathbb{1}_{\{\kappa>2\}} \frac{c_\kappa}{2^\kappa(\kappa-2)(\kappa-1)} \right) \\ C_{\kappa,\alpha,\gamma} &= C_\kappa + c\alpha\mathfrak{m}^{-\alpha} B(\gamma, 2 - \alpha, \alpha) \\ \mathfrak{m} &= 1 + \frac{1 + 2^{1-\kappa}}{2(\kappa-1)} \end{aligned} \tag{1}$$

where $2 + \kappa < c_\kappa < \kappa^2$ when $\kappa > 2$, and $B(p, a, b) \equiv \int_0^1 \mathbb{1}_{\{0 < t \leq p\}} t^{a-1} (1-t)^{b-1} dt$ for $a, b > 0$ and $0 < p \leq 1$ fixed.

Let $\#A$ denote the number of elements in a finite set A . For a given coalescent $\{\xi^n\}$ write $L_i(n) \equiv \int_0^{\tau(n)} \# \{\xi \in \xi^n(t) : \#\xi = i\} dt$ and $L(n) \equiv \int_0^{\tau(n)} \#\xi^n(t) dt$ where $\tau(n) \equiv \inf \{t \geq 0 : \#\xi^n(t) = 1\}$. Then $L(n) = L_1(n) + \dots + L_{n-1}(n)$. Write $R_i(n) \equiv L_i(n)/L(n)$ for $i = 1, 2, \dots, n-1$. With this C++ code we use simulations to approximate $\mathbb{E}[R_i(n)]$ when the coalescent is the time-changed continuous-time δ_0 -Beta($\gamma, 2 - \alpha, \alpha$)-coalescent with time-change function $G(t) = \int_0^t e^{\rho s} ds$ for a given fixed $\rho \geq 0$. See Figure 1 in § 5 for an example

The code follows in § 4.1–§ 4.5, we conclude in § 5. Comments within the code in **this font and colour**

4 code

4.1 includes

the included libraries

```
5 <includes 5> ≡  
#include <iostream>  
#include <fstream>  
#include <vector>  
#include <random>  
#include <functional>  
#include <memory>  
#include <utility>  
#include <algorithm>  
#include <ctime>  
#include <cstdlib>  
#include <cmath>  
#include <list>  
#include <string>  
#include <fstream>  
#include <chrono>  
#include <forward_list>  
#include <assert.h>  
#include <math.h>  
#include <unistd.h>  
#include <gsl/gsl_rng.h>  
#include <gsl/gsl_randist.h>  
#include <gsl/gsl_sf.h>  
#include <boost/math/special_functions/beta.hpp>  
#include "deltanull_incbeta_expgrowth.hpp"
```

This code is used in chunk 11.

4.2 random number generators

the random number generators

6 $\langle \text{rngs } 6 \rangle \equiv$

```
std::random_device randomseed;    /*
    Standard Mersenne twister random number engine */
std::mt19937_64 rng(randomseed());
gsl_rng * rngtype;
void setup_rng(const unsigned long int s)
{
    const gsl_rng_type *T;
    gsl_rng_env_setup();
    T = gsl_rng_default;
    rngtype = gsl_rng_alloc(T);
    gsl_rng_set(rngtype, s);
}
```

This code is used in chunk 11.

4.3 the merging rate

7 $\langle \lambda_{n;k;s} \rangle \equiv$

```
double rate(const double m, const double k) {
    assert(k ≤ m);    /*
        the full (non-normalised) incomplete beta function */
    auto incbeta = [] (const double a, const double b, const double x)
    {
        return boost::math::beta(static_cast<long double>(a), static_cast<long
            double>(b), static_cast<long double>(x));
    }
    ;
    const long double lbinom = lgammal(m + 1) - lgammal(k + 1) - lgammal(m - k + 1);
    const long double dnull = (int) k < 3 ? logl((long double)(CKAPPA)) : 0;
    const long double bpart = logl((long double)(CEPS * ALPHA * incbeta(k - ALPHA,
        m + ALPHA - k, GAMMA) / pow(MINF, ALPHA)));
    return (static_cast<double>(expl(lbinom + dnull + bpart)) / CKAG); }
```

This code is used in chunk 11.

¶ totalrate

compute the total rate

8 $\langle \lambda_n \rangle \equiv$

```
void totalrate ( std::vector< double > &v )
{
    for (double m = 2; m ≤ SAMPLE_SIZE; ++m) {
        for (double j = 2; j ≤ m; ++j) {
            assert(j ≤ m);    /*
                § 4.3 */
            v[m] += rate(m, j);
        }
    }
}
```

This code is used in chunk 11.

4.4 one experiment

```

9  ⟨genealogy 9⟩ ≡
    static void genealogy ( const std::vector < double > &vlambdan, std::vector <
        double > &vri ) {
        std::vector < int > t(SAMPLE_SIZE, 1);
        std::size_t ms
        {}
        ;
        double timi
        {}
        ;
        int newb
        {}
        ; std::vector < double > vb(SAMPLE_SIZE);
        std::size_t q
        {}
        ;
        double otimi
        {}
        ; auto newtime = [] (const double lambdab, const double oldtime)
        {
            return (RHO > DBL_EPSILON ? log1p(-(RHO * exp(-RHO * oldtime)/lambdab) *
                log(gsl_rng_uniform_pos(rngtype)))/RHO : gsl_rng_exponential(rngtype, 1./lambdab));
        }
        ;
        auto getmerger = [&vlambdan] (const double m)
        {
            const double u = gsl_rng_uniform(rngtype);
            double j = 2; /*
                § 4.3 */
            double s = rate(m, j);
            while (u > s/vlambdan[static_cast<int>(m)]) {
                ++j;
                assert(j ≤ m);
                s += rate(m, j);
            }
            return static_cast<std::size_t>(j);
        }
        ;
        while (t.size() > 1) {
            timi = newtime(vlambdan[t.size()], otimi);
            assert(timi > DBL_EPSILON);
            otimi += timi;
            std::for_each (t.cbegin(), t.cend(), [&timi, &vb] (const int t)
            {
                assert(t > 0);
                vb[0] += timi;
                vb[t] += timi;
            }
        }
    }

```

```

    }
  );
  ms = getmerger(static_cast<double>(t.size()));
  std::shuffle(t.begin(), t.end(), rng);
  newb = std::accumulate(t.rbegin(), t.rbegin() + ms, 0);
  q = t.size();
  t.resize(q - ms);
  t.push_back(newb); }
  assert(vb[0] > DBL_EPSILON);
  const double d = vb[0];
  std::transform (vb.cbegin(), vb.cend(), vri.begin(), vri.begin(), [&d](const auto &x, const
    auto &y)
  {
    return y + (static_cast<double>(x)/d);
  }
  ); }

```

This code is used in chunk 11.

¶ approximate $\mathbb{E}[R_i(n)]$.

10 $\langle \text{go ahead 10} \rangle \equiv$

```

void approximate() {
  std::vector< double > v_lambdan(static_cast<int>(SAMPLE_SIZE) + 1);
  totalrate(v_lambdan);
  std::vector< double > vri(static_cast<int>(SAMPLE_SIZE));
  int r = EXPERIMENTS + 1;
  while (--r > 0) { /*
    § 4.4 */
    genealogy(v_lambdan, vri);
  }
  std::for_each (vri.begin(), vri.end(), [](const auto &x)
  {
    std::cout << x << '\n';
  }
  ); }

```

This code is used in chunk 11.

4.5 main

the *main* module

```
11      /*
      § 4.1 */
      <includes 5> /*
      § 4.2 */
      <rngs 6> /*
      § 4.3 */
      < $\lambda_{n;k;s}$  7>
      < $\lambda_n$  8> /*
      § 4.4 */
      <genealogy 9>
      <go ahead 10>
      int main(int argc, const char *argv[])
      {
      /*
      § 4.2 */
      setup_rng(static_cast<long unsigned>(atoi(argv[1]))); /*
      § 4.4 */
      approximate();
      gsl_rng_free(rngtype);
      return GSL_SUCCESS;
      }
```

5 conclusions and bibliography

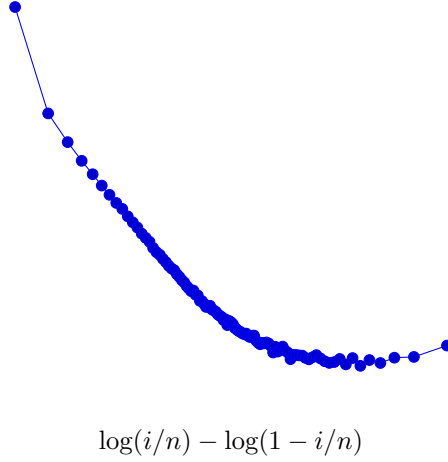


Figure 1: *An example approximation of $\mathbb{E}[R_i(n)]$ for the given parameter values and graphed as logits against $\log(i/n) - \log(1 - i/n)$ for $i = 1, 2, \dots, n - 1$ where n is sample size*

References

- [D2024] Diamantidis, Dimitrios and Fan, Wai-Tong (Louis) and Birkner, Matthias and Wakeley, John. Bursts of coalescence within population pedigrees whenever big families occur. *Genetics* Volume 227, February 2024.
<https://dx.doi.org/10.1093/genetics/iyae030>.
- [CDEH25] JA Chetwyn-Diggle and Bjarki Eldon. Beta-coalescents when sample size is large. 2026 bioRxiv <https://doi.org/10.64898/2025.12.30.697022>
- [DK99] P Donnelly and T G Kurtz. Particle representations for measure-valued population models. *Ann Probab*, 27:166–205, 1999.
<https://dx.doi.org/10.1214/aop/1022677258>
- [KL94] Donald Ervin Knuth and Silvio Levy. *The CWEB system of structured documentation: version 3.0*. Addison-Wesley Longman Publishing Co., Inc., Reading, Massachusetts, 1994.
- [KR88] Brian W Kernighan and Dennis M Ritchie. The C programming language, 1988.
- [Pit99] J Pitman. Coalescents with multiple collisions. *Ann Probab*, 27:1870–1902, 1999.
<https://dx.doi.org/10.1214/aop/1022874819>
- [Sag99] S Sagitov. The general coalescent with asynchronous mergers of ancestral lines. *J Appl Probab*, 36:1116–1125, 1999.
<https://doi.org/10.1239/jap/1032374759>
- [Sch03] J Schweinsberg. Coalescent processes obtained from supercritical Galton-Watson processes. *Stoch Proc Appl*, 106:107–139, 2003.
[https://doi.org/10.1016/S0304-4149\(03\)00028-0](https://doi.org/10.1016/S0304-4149(03)00028-0)
- [S00] J Schweinsberg. Coalescents with simultaneous multiple collisions. *Electronic Journal of Probability*, 5:1–50, 2000.
<https://dx.doi.org/10.1214/EJP.v5-68>
- [Tan11] O Tange. GNU parallel – the command-line power tool. The USENIX Magazine, 2011.

Index

a: 7.
accumulate: 9.
ALPHA: 7.
approximate: 10, 11.
argc: 11.
argv: 11.
assert: 7, 8, 9.
atoi: 11.
b: 7.
begin: 9, 10.
beta: 7.
boost: 7.
bpart: 7.
cbegin: 9.
cend: 9.
CEPS: 7.
CKAG: 7.
CKAPPA: 7.
cout: 10.
d: 9.
DBL_EPSILON: 9.
dnull: 7.
double: 7, 9.
end: 9, 10.
exp: 9.
EXPERIMENTS: 10.
expl: 7.
for_each: 9, 10.
GAMMA: 7.
genealogy: 9, 10.
getmerger: 9.
gsl_ran_exponential: 9.
gsl_rng: 6.
gsl_rng_alloc: 6.
gsl_rng_default: 6.
gsl_rng_env_setup: 6.
gsl_rng_free: 11.
gsl_rng_set: 6.
gsl_rng_type: 6.
gsl_rng_uniform: 9.
gsl_rng_uniform_pos: 9.
GSL_SUCCESS: 11.
incbeta: 7.
j: 8, 9.
k: 7.
lambdab: 9.
lbinom: 7.
lgammal: 7.
log: 9.
logl: 7.
log1p: 9.
m: 7, 8, 9.
main: 11.
math: 7.
MINF: 7.
ms: 9.
mt19937_64: 6.
newb: 9.
newtime: 9.
oldtime: 9.
otimi: 9.
pow: 7.
push_back: 9.
q: 9.
r: 10.
random_device: 6.
randomseed: 6.
rate: 7, 8, 9.
rbegin: 9.
resize: 9.
RHO: 9.
rng: 6, 9.
rngtype: 6, 9, 11.
s: 6, 9.
SAMPLE_SIZE: 8, 9, 10.
setup_rng: 6, 11.
shuffle: 9.
size: 9.
std: 6, 8, 9, 10.
T: 6.
t: 9.
timi: 9.
totalrate: 8, 10.
transform: 9.
u: 9.
v_lambdan: 10.
vb: 9.
vector: 8, 9, 10.
vlambdan: 9.
vri: 9, 10.
x: 7, 9, 10.
y: 9.

List of Refinements

- $\langle \lambda_{n;k;s} \ 7 \rangle$ Used in chunk 11.
- $\langle \lambda_n \ 8 \rangle$ Used in chunk 11.
- $\langle \text{genealogy} \ 9 \rangle$ Used in chunk 11.
- $\langle \text{go ahead} \ 10 \rangle$ Used in chunk 11.
- $\langle \text{includes} \ 5 \rangle$ Used in chunk 11.
- $\langle \text{rngs} \ 6 \rangle$ Used in chunk 11.