



The coalescent point process of multi-type branching trees

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Abstract

We define a multi-type coalescent point process of a general branching process with countably many types. This multi-type coalescent fully describes the genealogy of the (quasi-stationary) standing population providing types along ancestral lineages of all individuals in the standing population. We show that the coalescent process is a functional of a certain Markov chain defined by the planar embedding of the multi-type branching process.

We use the multi-type coalescent process to determine statistical properties of the ancestral tree, such as the time to the most recent common ancestor (MRCA) of two consecutive individuals in the standing population, as well as of two individuals of the same type. These quantities are particularly simple to calculate for branching processes with a multi-type linear-fractional (LF) offspring distribution. We illustrate how an (a)symmetrical offspring distribution affects features of the ancestral tree in an example of a two-type LF branching processes.

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1. Introduction

Evolutionary biologists use phylogenetic trees of extant species to study the speciation and extinction patterns of different groups of species. Numerous phylogenetic trees have been made

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using sequence data, allowing systematists to investigate the mechanisms of evolutionary dynamics that led to the formation of such a species clade. Most inferences were based on methods that used type independent evolutionary rates of speciation and extinction, and studies of phenotype evolution have not generally accounted for type dependent diversification rates. Currently a number of more type-dependent extensions are being considered (Maddison et al. [17], Magnuson-Ford & Otto [18], Fitzjohn et al. [4], Igic & Goldberg [8,9], and so on) with interesting consequences for validity of previously held beliefs (e.g. Dollo's law).

In the study of macroevolution one uses phylogenetic trees (with or without branch lengths) obtained by genetic sequencing to fit models of speciation and extinction and possibly infer some features of this process, e.g. whether rates are time dependent or trait dependent etc. All (but a small subset) of these methods rely on simulation of branching processes suggested by the model in forward time and calculating the likelihood of obtaining the chosen phylogenetic trees. In population genetics an alternative way of assessing the fit of the ancestral relationship based on the phylogenetic trees uses backward simulations based on a coalescent approach. In macroevolution this poses the problem of pre-specifying the unknown random process of fluctuation species numbers over time. One way of avoiding this problem uses the point process approach based on a standing branching population as developed in [20], further extended by [13].

From a mathematical point of view a phylogenetic tree is a genealogical (or reduced) tree derived from a branching process. The randomness of the branching process implies a distribution on trees that are derived in this manner, and depends on the specifications of the branching process (offspring distributions in discrete time, plus lifetime rates in continuous time). A fair amount is known about the distribution of genealogical trees derived from single type branching processes, both for trees of finite size and for their rescaled limits as the size becomes infinite. Much less is known about the same objects for multi-type branching processes, other than asymptotic results based on the almost sure convergence of types for the supercritical multi-type processes (see [11,6]).

Deriving an exact distribution for the ancestral tree of a standing population of an arbitrary branching process is unsurprisingly challenging. The first problem, addressed in [14], is in handling the branch points in the ancestral tree with multiple surviving offspring. The second problem, arising only for multi-type branching processes, is in handling the fact that branch points require the knowledge of the parental type. The latter requires a modification of the contour process approach which keeps track of full memory of the ancestral types of any individual in the standing population (for example via snake construction of [15,3]). We make the analogous modification in the coalescent point process of the ancestral tree.

In this modification the ancestral tree that is analysed is that of a population in quasi-stationary equilibrium. From the biological point of view this was indeed the most common assumption when reconstructing phylogenies from sequence data, though the logic of making this assumption has recently been questioned in the practice of fitting models of evolution of phenotypes [8,4]. From the mathematical point of view, more often than not, quasi-stationary distributions of branching processes cannot be calculated explicitly [19], and one would have to resort to numerical calculations for its generating function based on a certain partial difference equation. Our approach avoids the need to explicitly calculate the quasi-stationary distribution, relying on a relationship (in sub- and critical cases) between our doubly infinite planar embedding and an embedding of a quasi-stationary tree from its leftmost infinite spine on [12, Theorem 4.2.2].

In order to make comparisons on the effect of different branching distributions on the shape of ancestral trees we focus on a special case of branching processes. These are multi-type processes whose generating function has a linear-fractional form, and for which many of the

point process calculations significantly simplify. A different and complementary set of results on linear fractional multi-type branching processes, on the recurrence on the type space and long term behaviour of such a branching process with countably many types, was recently obtained by [21]. A number of their results rely on calculations from the contour process of the multi-type branching process, which is intimately related to our point process construction as well.

In this work we will provide:

- (1) an explicit and algorithmic way to construct an ancestral tree of the standing population of a (quasi-stationary) multi-type branching process in terms of a Markov chain; and
- (2) explicit formulae for calculating: (a) basic statistical features that describe the ancestral tree (the law of coalescence times together with the types on the ancestral lineages), as well as (b) statistical features that link types in the standing population with the shape of the tree (the law of same-type coalescence times).

As an example of what one can infer from these results, we will consider the special case of a multi-type branching process with linear-fractional offspring distribution, and we will obtain very simple formulae for their statistical features. We will then use these formulae to assess the differences in the ancestral trees of two different linear-fractional offspring distributions: one ‘symmetrical’ and the other completely ‘asymmetrical’ in the treatment of different offspring types. The ‘symmetry’ and ‘asymmetry’ are clearly featured in the statistics of the ancestral trees, and could be used to infer the extremeness of parameters that determine this (a)symmetry in the offspring distribution.

2. Multi-type coalescent model and general results

In this paper we extend the coalescent point process construction of [14] to the case of multi-type branching processes. Our goal is to exploit the Markovian features of the coalescent point process in order to derive features of multi-type phylogenetic trees, and identify the statistics in multi-type phylogenetic trees that are not present in single type trees. We first derive the distribution of the most recent common ancestor of two species from the standing population. We then derive the time of the most recent common ancestor of two species of the same type, and its dependence on the species type.

2.1. Multi-type branching process

We start with notation for multi-type branching processes. Let $\{1, 2, 3, \dots\}$ denote a countable space of *types* of a population. A *multi-type branching process* is a vector-valued Markov process in discrete time $(\mathbf{Z}^{(n)})_{n \geq 0}$, with $\mathbf{Z}^{(n)} = (Z_1^{(n)}, Z_2^{(n)}, \dots)$ an infinite-dimensional random vector whose ℓ th coordinate is the number of individuals of type ℓ at generation n . It is assumed that at any time $n \geq 0$ only a finite number of entries of this vector are non-zero almost surely. Generations will be indexed by $n \in \mathbb{N}_0$ in the superscript, and types will be indexed by $\{1, 2, \dots\}$ in the subscript. All the arguments in this paper are valid as well for a finite number of types.

For any $\mathbf{z} = (z_1, z_2, \dots) \in \mathbb{N}_0^{\mathbb{N}}$ with $|\mathbf{z}| = z_1 + z_2 + \dots < \infty$, the matrix of transition probabilities, and the n th iteration of this matrix, are denoted by

$$P_\ell(\mathbf{z}) = \mathbb{P}(\mathbf{Z}^{(1)} = \mathbf{z} \mid \mathbf{Z}^{(0)} = \mathbf{e}_\ell), \quad P_\ell^{(n)}(\mathbf{z}) = \mathbb{P}(\mathbf{Z}^{(n)} = \mathbf{z} \mid \mathbf{Z}^{(0)} = \mathbf{e}_\ell),$$

where e_ℓ is a unit vector of ℓ th coordinate. For $s = (s_1, s_2, \dots)$, the probability generating function of the offspring distribution ξ is denoted by $f(s) := (f_1, f_2 \dots)(s)$ where

$$f_\ell(s) = \mathbb{E}(s^{Z^{(1)}} \mid Z^{(0)} = e_\ell) = \sum_{z=(z_1, z_2, \dots) \in \mathbb{N}^{\mathbb{N}}: |z| < \infty} P_\ell(z) s_1^{z_1} s_2^{z_2} \dots,$$

for $s_1, s_2, \dots \in [0, 1]$,

and the probability generating function of the n th generation population, the n -fold composition of $f(s)$, is denoted by $f^{(n)}(s)$ where $f_\ell^{(n)}(s) = \mathbb{E}(s^{Z^{(n)}} \mid Z^{(0)} = e_\ell)$. For $n = 0$ let $f^{(0)}(s) = s$, and note that $f^{(1)}(s) = f(s)$.

We let $M = (m_{\ell\ell'})_{1 \leq \ell, \ell' \leq \infty}$ be the matrix of the expected number of offspring of each type from parents of different types:

$$m_{\ell\ell'} = \mathbb{E}(Z_{\ell'}^{(1)} \mid Z^{(0)} = e_\ell) = \left. \frac{\partial f_\ell(s)}{\partial s_{\ell'}} \right|_{s=\mathbf{1}}, \quad \text{for } \ell, \ell' = 1, 2, \dots$$

where $\mathbf{1} = (1, 1, \dots)$ and we assume all $m_{\ell\ell'} < \infty$. A multi-type Galton–Watson process is called *positive regular or irreducible* if for some $n > 0$ the mean matrix of its n th generation population M^n is positive (all of the entries $m_{\ell\ell'}^{(n)} > 0$ are strictly positive entries). A process is called *singular* if each individual has exactly one offspring. We assume that the multi-type G–W process is non-singular and irreducible throughout this paper. Furthermore, we assume the following conditions for M :

- M is *aperiodic*, that is, for all ℓ , the greatest common divisor of all natural numbers n such that $m_{\ell\ell}^n > 0$, is equal to 1.
- M is *R-recurrent*, that is $\sum_{n \geq 0} m_{\ell\ell}^n R^n = \infty$, for all $\ell \geq 1$, where $0 \leq R < \infty$ is the common convergence radius of all entries of the power series $M(s) = \sum_{n \geq 0} M^n s^n$.
- M is *R-positive*, that is $\mathbf{v}u^t < \infty$, where \mathbf{u} and \mathbf{v} are positive vectors such that $RMu^t = u^t$, $RvM = v$.

Refer to Theorems 6.1, 6.2 and 6.5 from [22] for the existence of R , \mathbf{u} and \mathbf{v} . We scale the vectors \mathbf{u} and \mathbf{v} so that $\mathbf{u} \cdot \mathbf{v} = 1$ and $\mathbf{u} \cdot \mathbf{1} = 1$. The role that $\rho = 1/R$ plays in the countably many types setting is similar to the role of μ in the one type case, distinguishing *subcritical, critical or supercritical* processes when $\rho < 1$, $\rho = 1$ or $\rho > 1$, respectively. Equivalently we say that the process is *subcritical, critical or supercritical* if $R > 1$, $R = 1$ or $R < 1$, respectively.

When a multi-type branching process is irreducible, non-singular, aperiodic, R -recurrent and R -positive, then in the sub- and critical cases the process has a quasi-stationary equilibrium [22,21] determined by eigenvector of M corresponding to the eigenvalue $1/R$, and the extinction probability of the process. In the super-critical case the same is true if the process is also conditioned on extinction.

2.2. Single-type coalescent point process

The coalescent point process of a branching tree is a process describing the genealogy of the standing population backwards in time, directly displaying the coalescence times as a sequence running over the current population size. It constructs a set of points, each corresponding to a most recent common ancestor of two individuals in the current population, whose depth (or vertical height) corresponds to the time when the lineages of these two individuals branched off (separated) from each other. The coalescent point process has a bijective correspondence with

the ancestral tree of the current population, and allows the full ancestral tree to be reconstructed from its values. It was introduced in [20] for the ancestral tree of a continuous time single type branching process conditioned on its current population size, and called the *genealogical point process*. Its distribution was obtained from its relationship with the contour (or height) process associated with a unit speed traversal of the branching tree. The convenient property of that particular branching model is that its contour process is Markovian, which implied that the points in this point process are *simple* that is, each branch point has degree two- and that they are independent samples from the same distribution of depths. This allows one to reconstruct the ancestral tree of a population of n current individuals based simply on a sample of size n from this distribution (see Fig. 2 of [20]). This genealogical point process was used in [1] to obtain statistical information for the ancestral trees of a critical branching process, was extended to non-critical binary processes in [7] and to homogeneous binary Crump–Mode–Jagers processes in [13].

The original construction of the genealogical point process had to be extended to accommodate Galton–Watson branching processes with general offspring distribution when the contour process of the branching tree is no longer Markovian. In this case depths of points in the process are no longer sufficient in order to fully reconstruct the ancestral tree, as the most recent common ancestors were no longer distinct for every pair of current individuals. In other words, branch points in the ancestral tree no longer always have degree exactly equal to two, and it was necessary to keep track of the multiplicity of these points as given by their branching degree. In [14] a construction was made which, rather than having all simple points with mass one, has points with (positive) integer valued masses. Each point again corresponds to a most recent common ancestor of two individuals in the current population, and its depth records the time when the two individuals' lineages separated. The mass of this point records the number of current individuals with the same most recent common ancestor as these two which are embedded after (or horizontally to the right) of them. This process was called the *coalescent point process (with multiplicities)*.

Before we present our extension of this construction we first recall the notation from [14]. Consider an arbitrarily large population at the present time from a general quasi-stationary branching process originating at an unspecified arbitrarily large time in the past. In the planar embedding of this process, individuals are located at points of a discrete lattice ($n \in \mathbb{Z}, i \in \mathbb{N}$), where the first coordinate n denotes the generation and the second coordinate i denotes the position of the individual in the planar embedding from left to right. The number of offspring of individual (n, i) is denoted by $\xi(n, i)$. See Fig. 3, while ignoring the types/colours of individuals/vertices for now—the doubly infinite embedding of the tree is shown in the figure on the left. Its coordinates (n, i) represent its location on the two dimensional grid. The *standing population* is the population at the present time (generation $n = 0$), and its *ancestral tree* is the subtree of the branching tree obtained by following only the branches that lead to an individual present in the standing population. The ancestral tree is more easily observed in the right figure in Fig. 3. The ancestry of an individual from generation 0 can be traced backwards in time as follows. Define

$$a_i(n) := \text{index of the ancestor of individual } (0, i) \text{ in generation } -n.$$

The *coalescent time* $C_{i,j}$ of individuals $(0, i)$ and $(0, j)$ is the time of the most recent common ancestor between these two, that is,

$$C_{i,j} := \min\{n \geq 1 : a_i(n) = a_j(n)\}, \quad \text{with } \min(\emptyset) = \infty.$$

In particular, define $A_i := C_{i,i+1}$ which identifies the coalescent time of individuals $(0, i)$ and $(0, i + 1)$. It can be easily shown that $C_{i,j} = \max\{A_i, A_{i+1}, \dots, A_{j-1}\}$. The sequence $(A_i)_{i \geq 1}$ is called the *coalescent point process*. The genealogy back in time of the present population,

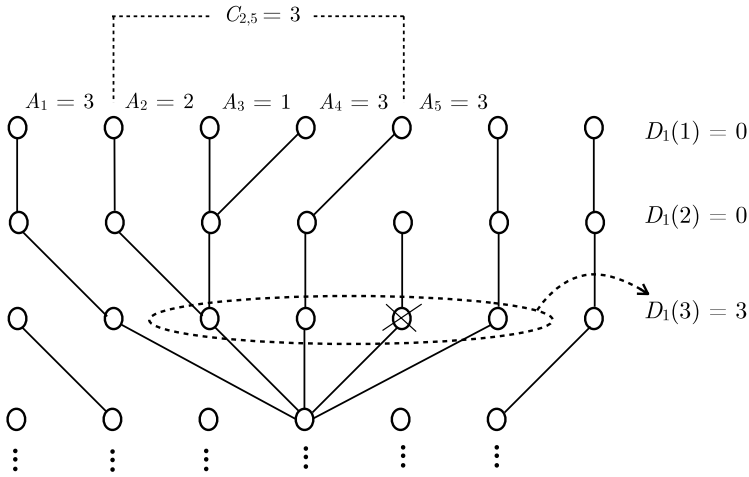


Fig. 1. The coalescent times $\{C_{i,j}\}_{i < j=1,2,\dots}$ of individuals $(0, i)$ and $(0, j)$; the coalescent point process $(A_i)_{i \geq 1}$; and the auxiliary process $(D_i)_{i \geq 1}$ of sequences $\{D_i(n), n \geq 1\}$.

that is its ancestral tree, is then uniquely determined by the process $(A_i)_{i \geq 1}$. (This was sufficient information for the genealogical point process of binary branching processes in [20,1,7,13].) The coalescent point-process (with multiplicities) can be seen in Fig. 1. Define an auxiliary process $(D_i)_{i \geq 1}$ of integer valued sequences $D_i = \{D_i(n), n \geq 1\}$ for each $i \geq 1$, which records future branch degrees along the ancestral lineage of individual $(0, i)$

$D_i(n) :=$ number of *surviving* offspring of individual $(n, a_i(n))$ embedded in the *ancestral tree* to the right of the lineage of $(0, i)$ itself.

The sequences $A_i, C_{i,j}, D_i$ can all be seen in Fig. 1.

It turns out that the process $(D_i)_{i \geq 1}$ has all the nice properties needed to identify the law of the coalescent point-process (Theorem 2.1 of [14]): A_i is a functional of D_i given by

$$A_i = \min\{n \geq 1 : D_i(n) \neq 0\}$$

and the law of the process $(D_i, i \geq 1)$ is determined by the fact that it is a sequence-valued Markov chain, started at the null sequence $D_0 = (0, 0, \dots)$, with transitions given as follows— for any sequence $(d_n; n \geq 0) \in \mathbb{N}^{\mathbb{N}}$

$$(D_{i+1}(n) \mid D_i(\cdot) = d.) \stackrel{d}{=} \begin{cases} d_n & \text{for } n > A_i, \\ d_{A_i} - 1 & \text{for } n = A_i, \\ \zeta'_n & \text{for } 1 \leq n < A_i, \end{cases}$$

where the random variables $\zeta'_1, \zeta'_2, \dots, \zeta'_{A_i-1}$ are independent random variables.

The distributions of variables $\{\zeta'_n\}_{n \geq 1}$ are specified as follows. If ξ is the offspring distribution of this Galton–Watson branching process with probability generating function $f(s)$, the random variables $\xi(n, j)$, representing the number of offspring of individual (n, j) for any indices $n, j \in \mathbb{N}$, are all independent identically distributed as ξ . The survival probability to generation 0 of each offspring of an individual in generation $-n$ is given by $p_{n-1} := 1 - f^{(n-1)}(0)$ where $f^{(n-1)}$ is the $(n - 1)$ -fold composition of f . This, in particular, holds for the offspring of $(n, a_i(n))$, the ancestor of $(0, i)$ in generation $-n$. If we let $\{\epsilon_n^1, \epsilon_n^2, \dots\}$ be an independent

sequence of i.i.d. Bernoulli variables with parameter $\mathbb{P}(\epsilon_n^m = 1) = p_{n-1}$ (we deviate slightly notation from [14] here), and use an independent variable ξ , we can define the random sum

$$\zeta_n := \sum_{m=1}^{\xi} \epsilon_n^m$$

and, for each $n \geq 1$, the law of ζ'_n is defined by

$$\zeta'_n := \stackrel{d}{=} (\zeta_n - 1 | \zeta_n \neq 0).$$

2.3. Multi-type coalescent point process

Our construction of the coalescent point process for a multi-type Galton–Watson branching tree is a natural generalization of the single-type coalescent point process from the previous section. For the sake of completeness, we describe its construction, without relying on previous concepts. Consider a multi-type Galton–Watson process, whose distribution for the offspring (their number and types) of each individual depends on its type, and for an individual of type ℓ is denoted by $\mathbb{P}(\mathbf{Z}^{(1)} | \mathbf{Z}^{(0)} = \mathbf{e}_\ell)$. We consider a particular doubly-infinite embedding of a Galton–Watson branching tree as in Fig. 3 (left), infinite in the number of standing individuals as well as in the number of past generations. In this embedding each vertex in the grid represents an individual of some type, say ℓ , and is connected to its offspring represented by vertices in the level above, distributed according to $\mathbb{P}(\mathbf{Z}^{(1)} | \mathbf{Z}^{(0)} = \mathbf{e}_\ell)$. The embedding of the tree in a two dimensional grid is made in such a way that empty spaces and intersections between lineages are avoided. In the sub- and critical cases this law corresponds to a genealogical tree of a quasi-stationary Galton–Watson process with an infinite branch embedded as the left most spine in the plane (see Chapter 4 of [12]). We also specify a convention for the *order of embedding* an individual’s offspring. We assume that the order in which they are embedded is chosen *uniformly* at random from all possible ways to order them. In a later section we will assume a more *specific ordering* in the case where the offspring distribution is linear-fractional.

Unlike the single-type case, a Markov process from which the multi-type coalescent point process can be reconstructed will have to contain information on the individuals’ types as well. This, unfortunately, also makes notation for the multi-type process lengthier. Throughout the paper we will reserve boldface symbols for vectors and matrices.

Each individual in the genealogical tree is defined by its location coordinates, where (n, i) identifies the i th individual from the left in generation $-n$. Let

$$t(n, i) := \text{type of the individual } (n, i).$$

Let

$$a_i(n) := \text{index of the ancestor of individual } (0, i) \text{ in generation } -n.$$

Coalescence times between individuals $(0, i)$ and $(0, i + 1)$ in generation 0 are defined as $A_i := \min\{n \geq 1 : a_i(n) = a_{i+1}(n)\}$ for $i \geq 1$, and by convention $A_0 = +\infty$. Furthermore, the *ancestral lineage* of individual $(0, i + 1)$ back to its most recent common ancestor with individual $(0, i)$ is, for $i \geq 1$, denoted by $\mathbf{A}_i \in \{1, 2, \dots\}^{\mathbb{N}_0}$, and including a special 0th coordinate is defined as:

$$\mathbf{A}_i := (t(0, a_{i+1}(0)), t(-1, a_{i+1}(1)), \dots, t(-A_i + 1, a_{i+1}(A_i - 1)), t(-A_i, a_{i+1}(A_i))).$$

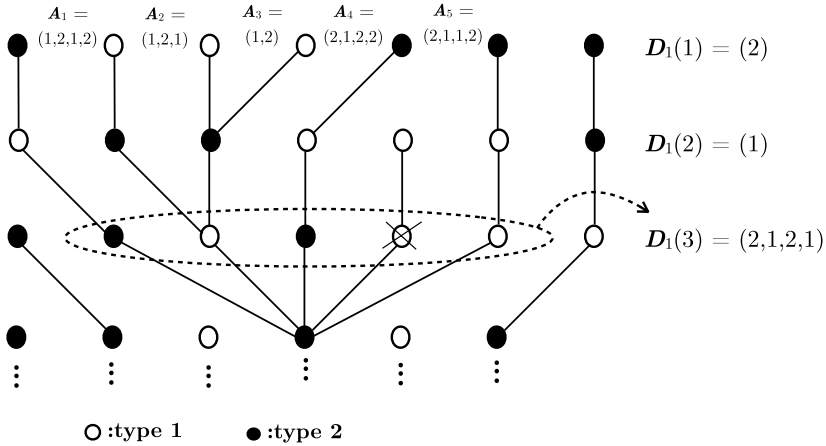


Fig. 2. The coalescent times $\{C_{i,j}\}_{i < j=1,2,\dots}$ of individuals $(0, i)$ and $(0, j)$; the coalescent point process $(A_i)_{i \geq 1}$; and the auxiliary process $(D_i)_{i \geq 1}$ of sequences $\{D_i(n), n \geq 1\}$.

The type enriched ancestral lineages can be seen in Fig. 3 (right), the ancestral lineage of individual $(0, 2)$ until depth $A_1 = 1$ has two types: $A_1 = (2, 1)$; of individual $(0, 3)$ until depth $A_2 = 1$ has two types: $A_2 = (2, 1)$; of individual $(0, 4)$ until depth $A_3 = 2$ has three types: $A_3 = (1, 2, 1)$; of individual $(0, 5)$ until depth $A_4 = 1$ has two types: $A_4 = (2, 2)$, etc.

For a vector $\mathbf{v} \in \{1, 2, \dots\}^{\mathbb{N}_0}$ let $v_{[j]}$ denote its j th coordinate and $\|\mathbf{v}\|$ denote its number of entries, with the convention that $\|\mathbf{v}\| = 0$ if $\mathbf{v} = \emptyset$. Note that $A_i = \|A_i\| - 1$. Since $a_{i+1}(0) = i + 1$, the 0 th coordinate $A_{i[0]}$ of the vector A_i is the type of the individual $(0, i + 1)$. Also, since $A_0 = \infty$ the first ancestral lineage A_0 consists of types of all individuals on the left most infinite (back into the past) spine of the ancestral tree. This special left most lineage in the example in Fig. 3 (right) has the sequence of types: $A_0 = (2, 1, 1, 2, 2, 1, 2, \dots)$. We will call the process $(A_i)_{i \geq 1}$ the *multi-type coalescent point process*. This type enriched coalescent point process can be seen in Fig. 2.

We define the process $(D_i)_{i \geq 1}$ of vector valued sequences $D_i = \{D_i(n), n \geq 1\}$ in such a way that each $D_i(n) \in \{1, 2, \dots\}^{\mathbb{N}}$ is a vector of types of offspring of the ancestor $a_i(n)$ in generation $-n$ embedded to the right of the lineage of $(0, i)$ that are ‘survivors’ (meaning that they have progeny that are alive in generation 0):

$$D_i(n) := \text{vector of types of surviving offspring of individual } (-n, a_i(n)) \text{ embedded in the ancestral tree to the right of and including the lineage of } (0, i).$$

Clearly $\|D_i(n)\| \geq 1$, and note that $D_i(n) := \|D_i(n)\| - 1$ is the number of surviving offspring of individual $(-n, a_i(n))$ embedded to the right of (and excluding) the lineage of $(0, i)$, as in the single type process. This type enriched auxiliary process can be seen in Fig. 2. The values of this process for the tree in Fig. 3 are given in Fig. 4, the ancestor of individual $(0, 1)$ in generation -1 has three surviving offspring all of type 2: $D_1(1) = (2, 2, 2)$, the ancestor of individual $(0, 1)$ in generation -2 has only two offspring with surviving progeny of types 1 and 2: $D_1(2) = (1, 2)$, the ancestor of individual $(0, 1)$ in generation -3 has only one offspring with surviving progeny of type 1: $D_1(3) = (1)$, etc. Note that (because the left most ancestral lineage is extremely ‘special’ and should not be part of the sequence $(A_i, i \geq 1)$) the labelling of the sequences is such that A_{i-1} and D_i are sequences that describe the ancestral lineage of

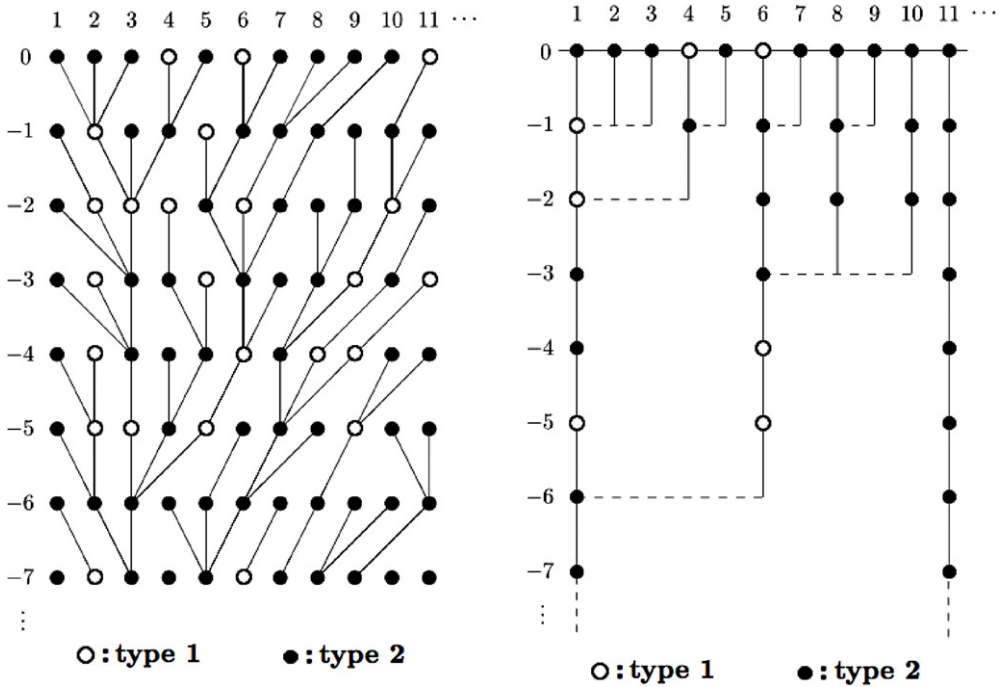


Fig. 3. Planar embedding of a two-type branching process (left), and types along its ancestral lineages A_i (right): the special left most lineage here has types $A_0 = (2, 1, 1, 2, 2, 1, 2, 2, \dots)$, the coalescent times here are $A_1 = 1, A_2 = 1, A_3 = 2, \dots$ with types along ancestral lineages $A_1 = (2, 1), A_2 = (2, 1), A_3 = (1, 2, 1), \dots$

individual $(0, i)$. In particular, for each $i \geq 1$ the value of A_i is equal to the first depth n at which $D_i(n) = \|D_i(n)\| - 1 \neq 0$, and the value of ancestral types $A_{i-1}(n-1)$ for $1 \leq n \leq A_i + 1$ are the same values as the first coordinates of $D_i(n)$ for $1 \leq n \leq A_i + 1$.

In order to describe the law of D we need to provide notation for surviving lineages. Let ξ_ℓ be the offspring distribution of an individual of type ℓ with probability generating function $f_\ell(s)$. For individual (n, i) the law of the number of its offspring, given that its type is $t(n, i) = \ell$, is that of ξ_ℓ . The survival probability of an offspring of some type ℓ' in some generation $-n'$ is given by $p_{n'-1, \ell'} := 1 - f_{\ell'}^{(n'-1)}(0, 0, \dots)$ where $f_{\ell'}^{(n'-1)}$ is the $(n' - 1)$ -fold composition of f .

We consider all the survivor progeny of a generation $-n$ ancestor of some individual from the standing population, and suppose that the type of this generation $-n$ ancestor is ℓ . For different $\ell' \in \{1, 2, \dots\}$ let $\{\epsilon_{n, \ell'}^1, \epsilon_{n, \ell'}^2, \dots\}$ be independent sequences of i.i.d. Bernoulli variables with parameters $\mathbb{P}(\epsilon_{n, \ell'}^m = 1) = p_{n-1, \ell'}$. Start with an independent variable ξ_ℓ , which takes values in $\mathbb{N}_0^{\mathbb{N}}$ and has $\xi_{\ell, \ell'}$ offspring of type ℓ' , and define the vector of random sums:

$$\zeta_{n, \ell} := \left(\sum_{m=1}^{\xi_{\ell, 1}} \epsilon_{n, 1}^m, \sum_{m=1}^{\xi_{\ell, 2}} \epsilon_{n, 2}^m, \dots \right),$$

whose ℓ' coordinate is denoted by $\zeta_{n, \ell, \ell'}$. Then, the law of $\zeta'_{n, \ell}$, which represents the number of surviving offspring of different types in generation $-(n - 1)$ of the initiating generation $-n$

$A_0 = \infty$	$A_1 = 1$	$A_2 = 1$	$A_3 = 2 \dots$
$A_0 = (2,1,1,\dots)$	$A_1 = (2,1)$	$A_2 = (2,1)$	$A_3 = (1,2,1) \dots$
$D_1(1) = (2,2,2)$	$D_2(1) = (2,2)$	$D_3(1) = (2)$	$D_4(1) = (1,2)$
$D_1(2) = (1,2)$	$D_2(2) = (1,2)$	$D_3(2) = (1,2)$	$D_4(2) = (2)$
$D_1(3) = (1)$	$D_2(3) = (1)$	$D_3(3) = (1)$	$D_4(3) = (1)$
$D_1(4) = (2)$	$D_2(4) = (2)$	$D_3(4) = (2)$	$D_4(4) = (2)$
$D_1(5) = (2)$	$D_2(5) = (2)$	$D_3(5) = (2)$	$D_4(5) = (2)$
$D_1(6) = (1,1)$	$D_2(6) = (1,1)$	$D_3(6) = (1,1)$	$D_4(6) = (1,1)$
$D_1(7) = (2)$	$D_2(7) = (2)$	$D_3(7) = (2)$	$D_4(7) = (2)$
\vdots	\vdots	\vdots	\vdots

Fig. 4. Sequences $(A_i, D_i(\cdot))_{i \geq 1}$ of surviving offspring types along the lineages of individuals $((0, i))_{i \geq 1}$ corresponding to the two-type ancestral tree given in Fig. 3: note that for each $i \geq 1$ and $1 \leq n \leq A_i + 1$ we have $A_{i-1}(n-1) = D_i(n)_{[1]}$ (including $i = 1$ when $A_0 = +\infty$).

ancestor, is given by:

$$\zeta'_{n,\ell} := \left(\zeta_{n,\ell} \left| \sum_{\ell'=1}^{\infty} \zeta_{n,\ell,\ell'} \neq 0 \right. \right).$$

Let $d(\zeta'_{n,\ell}) \in \{1, 2, \dots\}^{\mathbb{N}}$ be an ordering of all the offspring counted by $\zeta'_{n,\ell}$ chosen uniformly at random from all possible orderings (or in some specific way, as in the next section).

Recall that $v_{[j]}$ denotes the j th coordinate of a vector $v \in \{1, 2, \dots\}^{\mathbb{N}}$. Then $J := d(\zeta'_{n,\ell})_{[1]}$ is the type of the left most surviving offspring in generation $-(n - 1)$ of the ancestor from generation $-n$. Again, for different $\ell' \in \{1, 2, \dots\}$ let $\{\epsilon_{n-1,\ell'}^1, \epsilon_{n-1,\ell'}^2, \dots\}$ be independent sequences of i.i.d. Bernoulli variables with parameters $\mathbb{P}(\epsilon_{n-1,\ell'}^m = 1) = p_{n-2,\ell'}$ (independent of all earlier sequences of Bernoulli variables). Proceed with an independent variable ξ_J , and define the vector of random sums:

$$\zeta_{n-1,J} := \left(\sum_{m=1}^{\xi_{J,1}} \epsilon_{n-1,1}^m, \sum_{m=1}^{\xi_{J,2}} \epsilon_{n-1,2}^m, \dots \right), \quad \zeta'_{n-1,J} := \left(\zeta_{n-1,J} \left| \sum_{\ell'=1}^{\infty} \zeta_{n-1,J,\ell'} \neq 0 \right. \right),$$

and let $d(\zeta'_{n-1,J}) \in \{1, 2, \dots\}^{\mathbb{N}}$ be the ordering of these surviving offspring. Then $\kappa := d(\zeta'_{n-1,J})_{[1]}$ is the type of the left most surviving progeny in generation $-(n - 2)$ of the initiating individual from generation $-n$. Following the left most surviving progeny of an individual of type 1 can be seen in Fig. 5, where the ancestor in generation -5 of the individual $(0, 6)$ is followed.

We proceed in this way recursively until generation -1 when we obtain the set of offspring $d(\zeta'_{1,i})$. In order to collect all types of the left most surviving progeny (and their siblings) in different generations $0, -1, \dots, -(n - 2)$, and $-(n - 1)$ in one vector, we define an n long sequence of vectors in type space initiated by individual of type ℓ :

$$\eta_{n,\ell} := (d(\zeta'_{1,i}), \dots, d(\zeta'_{n-2,\kappa}), d(\zeta'_{n-1,J}), d(\zeta'_{n,\ell})),$$

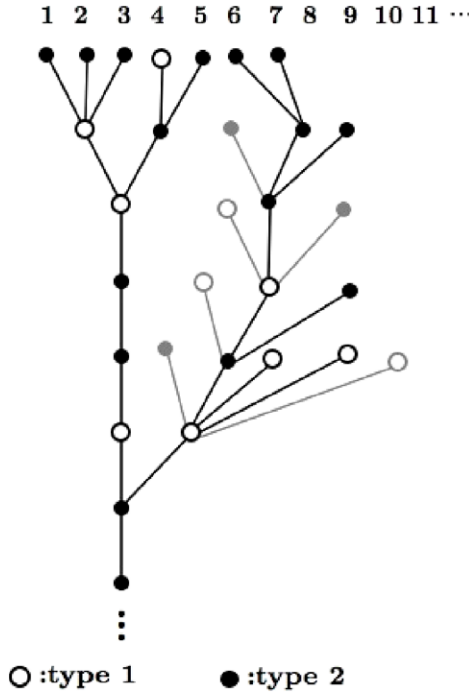


Fig. 5. Sequences $(\eta_{A_i-1, D_i(A_i)_{[2]}}(n))_{1 \leq n \leq A_i}$ of surviving subtrees in $D_{i+1}(n)$, $1 \leq n \leq A_i$ are illustrated for the case $i = 5$ where $A_5 = 6$: the collection of offspring on the ancestral lineage of individual $(0, 6)$ originating from its common ancestor in generation -6 with individual $(0, 5)$ is marked with either dark edges (surviving to generation 0) or light edges (non-surviving).

whose coordinates are then the vectors of surviving offspring types in different generations $\eta_{n,\ell}(1) := d(\xi'_{1,i}), \dots, \eta_{n,\ell}(n-1) := d(\xi'_{n-1,j}), \eta_{n,\ell}(n) := d(\xi'_{n,\ell})$.

We introduce one final piece of notation. For a vector $\mathbf{v} \in \{1, 2, \dots\}^{\mathbb{N}}$, let $(\mathbf{v}_{[2]}, \mathbf{v}_{[3]}, \dots)$ define a vector obtained from \mathbf{v} by eliminating the first coordinate $\mathbf{v}_{[1]}$ and shifting the rest of its coordinates one coordinate to the left. Having defined the random variables $\eta_{n,\ell}$, for arbitrary n and ℓ , the reconstruction of the ancestral tree from the auxiliary process is possible as in the single type case.

Theorem 2.1. *The coalescent times $(A_i)_{i \geq 1}$ and types along the ancestral tree $(A_i)_{i \geq 1}$ are both functionals of $(D_i)_{i \geq 1}$ given by*

$$A_i = \min\{n \geq 1 : \|D_i(n)\| - 1 \neq 0\},$$

$$A_i = (D_{i+1}(1)_{[1]}, \dots, D_{i+1}(A_i)_{[1]}, D_{i+1}(A_i + 1)_{[1]}).$$

The sequence $(D_i)_{i \geq 1}$ is a Markov chain with transition probabilities given by:

$$(D_{i+1}(n) | D_i) \stackrel{d}{=} \begin{cases} D_i(n) & \text{for } n > A_i, \\ (D_i(n)_{[2]}, D_i(n)_{[3]}, \dots) & \text{for } n = A_i, \\ \eta_{A_i-1, D_i(A_i)_{[2]}}(n) & \text{for } 1 \leq n < A_i \end{cases} \quad (1)$$

where the law of the $A_i - 1$ long sequence of type vectors $(D_{i+1}(1), \dots, D_{i+1}(A_i - 1))$ is distributed as the vector $\eta_{n,\ell}$ of types of the left most surviving progeny (and their siblings) in generations $-1, \dots, -(A_i - 1)$ of generation $-n = -(A_i - 1)$ individual whose type is $\ell = D_i(A_i)_{[2]}$.

The Markov chain $(D_i)_{i \geq 1}$ allows us to calculate some statistical features of the ancestral tree. The most relevant are coalescence times $(A_i)_{i \geq 1}$ which indicate the shape of the ancestral tree, and form a non-Markovian process. We have the following result on the law of the coalescent time A_1 .

Corollary 2.2. *For a single type value $\mathbf{a}_{[n]} \in \{1, 2, \dots\}$ and branching process \mathbf{Z} with infinitely many types*

$$\mathbb{P}(A_1 > n | \mathbf{A}_{0[n]} = \mathbf{a}_{[n]}) = \mathbb{P}\left(\sum_{\ell=1}^{\infty} Z_{\ell}^{(n)} = 1 \mid \mathbf{Z}^{(n)} \neq \mathbf{0}, \mathbf{Z}^{(0)} = \mathbf{e}_{\mathbf{a}_{[n]}}\right). \tag{2}$$

We next give a more general formula for the *joint law* of a coalescent time A_1 of individuals $(0, 1)$ and $(0, 2)$ together with the values of types along the whole ancestral lineage $\mathbf{A}_0 = (t(0, a_1(0)), t(-1, a_1(1)), \dots)$ of individual $(0, 1)$. It illustrates the role of ancestral types when determining branching times in the ancestral tree of the standing population. For a sequence $\mathbf{a} \in \{1, 2, \dots\}^{\mathbb{N}_0}$ let $\mathbf{a}_{|n'}$ denote the vector of the first coordinates up to n' th one in this sequence $\mathbf{a}_{|n'} := (\mathbf{a}_{[0]}, \mathbf{a}_{[1]}, \dots, \mathbf{a}_{[n']})$.

Proposition 2.3. *For a sequence of types $\mathbf{a} = (\mathbf{a}_{[0]}, \mathbf{a}_{[1]}, \dots) \in \{1, 2, \dots\}^{\mathbb{N}_0}$*

$$\mathbb{P}(A_1 > n, \mathbf{A}_{0|n-1} = \mathbf{a}_{|n-1} | \mathbf{A}_{0[n]} = \mathbf{a}_{[n]}) = \frac{1}{p_{n, \mathbf{a}_{[n]}}} \prod_{n'=1}^n \left(\frac{\partial f_{\mathbf{a}_{|n'}}(s)}{\partial s_{\mathbf{a}_{|n'-1}}} \Big|_{s=\mathbf{1}-\mathbf{p}_{n'-1}} \right), \tag{3}$$

where $\mathbf{1} - \mathbf{p}_{n'-1} := (1 - p_{n'-1,1}, 1 - p_{n'-1,2}, \dots) = \mathbf{f}^{(n'-1)}(\mathbf{0})$ is the vector of extinction probabilities by generation $n' - 1$.

Remark 2.4. Note that the choice of embedding the offspring of each parent uniformly at random in the tree is not reflected in these formulae at all. This is in particular evident in (2). Moreover, (2) can be obtained from (3) by summing over all the possible values of $\mathbf{A}_{0|n'}$ of types of the $0 \leq n' < n$ generations' ancestors of the individual $(0, 1)$ which start with $\mathbf{A}_{0|n'} = \mathbf{a}_{[n]}$. In the next section we consider a different choice of ordering the offspring for a specific offspring distribution, and show consistency of these two expressions.

A statistical feature which reflects the distribution of types in the ancestral tree is given by coalescence times between individuals in the standing population that are of the same type. Suppose the type of the first individual in generation 0 is $\mathbf{A}_{0[0]} = \ell$, and define the sequence $i_{\ell,0} := 0, i_{\ell,1} := \min\{i' > 0 : \mathbf{A}_{i'[0]} = \ell\}, \dots, i_{\ell,i} := \min\{i' > i_{\ell,i-1} : \mathbf{A}_{i'[0]} = \ell\}, \dots$ representing the indices of consecutive individuals of type ℓ from the standing population. Define the sequence of *same-type coalescence times* for individuals of type ℓ by

$$B_{\ell,1} := \max\{A_{i_{\ell,1}}, \dots, A_{i_{\ell,2}-1}\}, \dots, \quad B_{\ell,i} := \max\{A_{i_{\ell,i}}, \dots, A_{i_{\ell,i+1}-1}\}, \dots$$

As before, we also have the following result on the law of the same-type coalescent time $B_{\ell,1}$.

Corollary 2.5. *For a single type value $\mathbf{a}_{[n]} \in \{1, 2, \dots\}$ and a multi-type branching process \mathbf{Z}*

$$\mathbb{P}(B_{\ell,1} > n | \mathbf{A}_{0[n]} = \mathbf{a}_{[n]}, \mathbf{A}_{0[0]} = \ell) = \mathbb{P}(Z_{\ell}^{(n)} = 1 \mid Z_{\ell}^{(n)} \neq 0, \mathbf{Z}^{(0)} = \mathbf{e}_{\mathbf{a}_{[n]}}). \tag{4}$$

Using the values of types on the left most infinite spine \mathbf{A}_0 we can determine the joint distribution of $B_{\mathbf{A}_{0[0]},1}$ and $\mathbf{A}_{0|n-1}$ as follows.

Proposition 2.6. For a sequence of types $\mathbf{a} = (\mathbf{a}_{[0]}, \mathbf{a}_{[1]}, \dots) \in \{1, 2, \dots\}^{\mathbb{N}}$ with $\mathbf{a}_{[0]} = \ell$

$$\begin{aligned} &\mathbb{P}(B_{\ell,1} > n, \mathbf{A}_{0|n-1} = \mathbf{a}_{|n-1} | \mathbf{A}_{0|n} = \mathbf{a}_{|n}, \mathbf{A}_{0|0} = \ell) \\ &= \frac{1}{p(n, \ell, \mathbf{a}_{|n-1})} \prod_{n'=1}^n \left(\frac{\partial f_{\mathbf{a}_{|n'}}(s)}{\partial s_{\mathbf{a}_{|n'-1}}} \Big|_{s=\mathbf{1}-\mathbf{p}(n'-1, \ell')} \right) \end{aligned} \tag{5}$$

where $\mathbf{1}-\mathbf{p}(n'-1, \ell) := (1 - p(n'-1, \ell), 1, 1 - p(n'-1, \ell), 2, \dots) = \mathbf{f}^{(n'-1)}(\hat{\mathbf{e}}_{\ell'})$ with $\hat{\mathbf{e}}_{\ell'} = \mathbf{1}-\mathbf{e}_{\ell'}$, is the vector of extinction probabilities for lineages with type ℓ descendants after $n' - 1$ generations.

It might be tempting to provide a formula for the distribution of A_2, A_3, \dots and $B_{\ell,2}, B_{\ell,3}, \dots$ in a similar vein using the values of the types on the ancestral lineage of the individuals $(0, 2), (0, 3), \dots$ respectively. The information, analogous to that of types of individuals on the left most (infinite into the past) spine \mathbf{A}_0 used in the formulae for A_1 and $B_{\ell,1}$, which one would need to use for A_{i+2} would be the types along the ancestral lineage of $(0, i + 1)$. That is, for $i \geq 0$ one could define the *infinite ancestral lineage* $\mathbf{A}^{\infty i}$ of individual $(0, i + 1)$ as the infinite sequence:

$$\mathbf{A}^{\infty i} := (t(0, a_{i+1}(0)), t(-1, a_{i+1}(1)), t(-2, a_{i+1}(2)), \dots).$$

Note that the restriction of $\mathbf{A}^{\infty i}$ to its first A_i entries equals the sequence \mathbf{A}_i called the *ancestral lineage* of $(0, i + 1)$, and that $\mathbf{A}_0^{\infty} = \mathbf{A}_0$. It is easy to see, as a consequence of Theorem 2.1, that $(\mathbf{A}_i^{\infty})_{i \geq 1}$ is also a functional of $(\mathbf{D}_i)_{i \geq 1}$ given by:

$$\mathbf{A}_i^{\infty} = (\mathbf{D}_{i+1}(1)_{[1]}, \mathbf{D}_{i+1}(2)_{[1]}, \mathbf{D}_{i+1}(3)_{[1]}, \dots).$$

This follows from the fact that the first $1 \leq n \leq A_i$ entries in this sequence are the same as in \mathbf{A}_i , while for the subsequent $n > A_i$ entries the ancestry of $(0, i + 1)$ is equal to the ancestry of $(0, i)$ (as their ancestors already coalesced) and we have $\mathbf{D}_{i+1}(n) = \mathbf{D}_i(n)$.

Providing a formula for $\mathbb{P}(A_{i+2} > n | \mathbf{A}_{i+1|n} = \mathbf{a}_{|n})$ for any $i \geq 0$ can be done only in case the branching mechanism is such that in the coalescent point-process all points are simple (have multiplicities equal to one). This is because, in case of multiple coalescence points, all ancestral lineages, except for that of $(0, 1)$, in addition to information about the lineage of individual $(0, i)$ also contains information about the ancestral lineages of $(0, i')$, $1 \leq i' < i$. In other words, the calculation (used in the proofs of Propositions 2.3 and 2.6, see Section 4) which exploits the equivalence $\{A_1 > n, \mathbf{A}_{0|n-1} = \mathbf{a}_{|n-1}\}$ iff $\{\text{individuals } \mathbf{a}_{|n'}, 1 \leq n' \leq n \text{ on the ancestral lineage } \mathbf{A}_0 \text{ have a single offspring with descendants surviving to generation } 0\}$ is no longer valid in general. This is a clear consequence of the fact that the process $(\mathbf{A}_i, i \geq 0)$ is in general not itself Markovian. There is a special case for the offspring distribution for which, despite higher multiplicities of points in the coalescent point-process, the sequence $(\mathbf{A}_i, i \geq 0)$ has an exceptional memoryless property. In the next section we explore this special case for the offspring distribution of linear-fractional form, and extend the above results for the coalescent times as well as for the same-type coalescence times.

In case the branching mechanism is such that in the coalescent point-process all points are simple, the results of Proposition 2.3 can be used to simulate ancestral trees with types along their lineages. In this case, the same joint law (3) applies to each A_i and $\mathbf{A}_{i-1|A_i-1}$ for $i \geq 1$. A modification of formula (3) gives $\mathbb{P}(A_i = n, \mathbf{A}_{i-1|n-1} = \mathbf{a}_{|n-1} | \mathbf{A}_{i-1|n} = \mathbf{a}_{|n})$. In order to simulate the types along the ancestral tree, one would start by drawing from this distribution to obtain types along the ancestral lineage of individual $(0, 2)$ until its MRCA with individual $(0, 1)$. Then, one would draw independently from this distribution to obtain types along the ancestral lineage

of individual (0, 3) until its MRCA with individual (0, 2), and so on. Notice that, if the value of MRCA for (0, 2) and (0, 1) drawn is smaller than the MRCA for (0, 3) and (0, 2), then the types on the ancestral lineage of individual (0, 3) continue below its MRCA with individual (0, 2) and are drawn along the left most ancestral spine A_0 (see the example of $i = 3$ or $i = 5$ in Fig. 1 (right)). According to this algorithm one can simulate in a sequential manner the genealogy of an arbitrary number of individuals in the standing population.

Remark 2.7. The construction of the ancestral tree in case of the most general branching process is based on the Markovian property of the auxiliary process $(D_i)_{i \geq 1}$. A simulation algorithm for ancestral trees in general would require the simulation of the whole process $(D_i)_{i \geq 1}$. To initiate this process requires either knowing D_1 *a priori*, or drawing D_1 from $\eta_{\infty, \ell_\infty}$ for some (infinitely old) originating type ℓ_∞ . One way to draw from this distribution would be to start from generation 0 and time reverse the quasi-stationary distribution for the branching process. For the case of a single type branching process a construction like this was discussed in [5]. The multi-type extension is straightforward, with the infinitely old originating individual having, in the sub- and critical cases, the size-biased version of the offspring distribution given by

$$\widehat{\mathbb{P}}(\mathbf{Z}^{(1)} = \mathbf{z} | \mathbf{Z}^{(0)} = \mathbf{e}_\ell) = \frac{\mathbb{P}(\mathbf{Z}^{(1)} = \mathbf{z} | \mathbf{Z}^{(0)} = \mathbf{e}_\ell)}{\rho} \frac{\mathbf{z} \cdot \mathbf{u}}{\mathbf{e}_\ell \cdot \mathbf{u}},$$

where \mathbf{u} is the right eigenvector of the mean matrix \mathbf{M} obtained under the assumptions at the end of Section 2.1 (see [23,2]).

3. Special case: linear-fractional branching processes

Many of the complications which arise in calculating the distribution of ancestral trees in multi-type branching processes simplify a great deal in the special case when the offspring distribution is of the linear-fractional (LF) type. This type of offspring distribution leads to a number of particularly nice features involving the memoryless property of the geometric distribution. We first recall the definition of the multi-type linear-fractional offspring distribution, and then give a series of specific results for the distribution of the ancestral tree of the standing population, which both illustrate and extend our general results from the previous section.

3.1. Multi-type linear-fractional branching process

We use the same notation as [21] for ease of drawing on known results and making comparisons. Let \mathbf{H} be an infinite square sub-stochastic matrix, that is, each row \mathbf{h}_ℓ of \mathbf{H} is a non-negative vector with $\sum_{\ell' \geq 1} h_{\ell \ell'} \leq 1$, and let $h_{\ell 0} = 1 - \sum_{\ell' \geq 1} h_{\ell \ell'}$. Let \mathbf{g} be a non-negative vector such that $\mathbf{g} \mathbf{1}^t = \sum_{\ell' \geq 1} g_{\ell'} = 1$. Let $m > 0$. For any $\mathbf{z} = (z_1, z_2, \dots) \in \mathbb{N}_0^{\mathbb{N}}$, let $|\mathbf{z}| = \sum_{\ell \geq 1} z_\ell$.

A random vector ξ_ℓ taking values in $\mathbb{N}_0^{\mathbb{N}}$ has a *linear-fractional distribution* LF($\mathbf{h}_\ell, \mathbf{g}, m$) if for any non-negative integer vector $\mathbf{z} = (z_1, z_2, \dots)$ with $|\mathbf{z}| < \infty$

$$\mathbb{P}(|\xi_\ell| = 0) = h_{\ell 0}, \quad \mathbb{P}(\xi_\ell = \mathbf{e}_{\ell'} + \mathbf{z}) = h_{\ell \ell'} \frac{m^{|\mathbf{z}|}}{(1+m)^{|\mathbf{z}|+1}} \binom{|\mathbf{z}|}{z_1, z_2, \dots} \mathbf{g}^{\mathbf{z}},$$

where $\mathbf{g}^{\mathbf{z}} = g_1^{z_1} g_2^{z_2} \dots$. The probability generating function of ξ_ℓ has the linear fractional form

$$f_\ell(\mathbf{s}) = h_{\ell 0} + \frac{\sum_{\ell' \geq 1} h_{\ell \ell'} s_{\ell'}}{1 + m - m \sum_{\ell' \geq 1} g_{\ell'} s_{\ell'}}.$$

One can also represent the random vector ξ_ℓ as a sequence of offspring, where the first offspring has type distribution given by \mathbf{h}_ℓ and the children after the first one have geometric distribution with mean m and type distribution given by \mathbf{g} independently for each offspring. Moreover, the probability generating function of $(\xi_\ell | \xi_\ell \neq \mathbf{0})$ is that of a shifted Multivariate-Geometric distribution

$$\mathbb{E}(\mathbf{s}^{\xi_\ell} | \xi_\ell \neq \mathbf{0}) = \frac{(1 - h_{\ell 0})^{-1} \sum_{\ell' \geq 1} h_{\ell \ell'} s_{\ell'}}{1 + m - m \sum_{\ell' \geq 1} g_{\ell'} s_{\ell'}}.$$

A multi-type linear-fractional branching process $\text{LF}(\mathbf{H}, \mathbf{g}, m)$ is a branching process in which each individual of type $\ell \in \{1, 2, \dots\}$ reproduces according to the $\text{LF}(\mathbf{h}_\ell, \mathbf{g}, m)$ offspring distribution ξ_ℓ . In other words, the probability generating function of the offspring distribution is $\mathbf{f}(\mathbf{s}) = (f_1, f_2, \dots)(\mathbf{s})$ with f_ℓ as above. Its mean matrix is given by $\mathbf{M} = \mathbf{H} + m\mathbf{H}\mathbf{1}^t\mathbf{g}$.

The fact that the parameters \mathbf{g} and m do not depend on the parent’s type ensures that the population size in each generation of this process also has a linear fractional distribution. This is given by the following known result.

Theorem 3.1 (Proposition 3 [10], Theorem 3 [21]). *The n th generation population size vector $\mathbf{Z}^{(n)}$ of a multi-type linear-fractional branching process $\text{LF}(\mathbf{H}, \mathbf{g}, m)$ started with one individual $\mathbf{Z}^{(0)} = \mathbf{e}_\ell$ has a linear-fractional distribution $\text{LF}(\mathbf{h}_\ell^{(n)}, \mathbf{g}^{(n)}, m^{(n)})$ whose parameters are determined by:*

$$\begin{aligned} m^{(n)} &= m\mathbf{g}(\mathbf{I} + \mathbf{M} + \dots + \mathbf{M}^{n-1})\mathbf{1}^t, \\ \mathbf{g}^{(n)} &= \frac{m}{m^{(n)}}\mathbf{g}(\mathbf{I} + \mathbf{M} + \dots + \mathbf{M}^{n-1}), \\ \mathbf{H}^{(n)} &= \mathbf{M}^n - \frac{m^{(n)}}{1 + m^{(n)}}\mathbf{M}^n\mathbf{1}^t\mathbf{g}^{(n)}, \end{aligned} \tag{6}$$

where the vector $\mathbf{h}_\ell^{(n)}$ is the ℓ th row of the matrix $\mathbf{H}^{(n)}$, and $\mathbf{1}^t$ is the transpose of $\mathbf{1} = (1, 1, \dots)$.

Note that, as a consequence, $(\mathbf{Z}^{(n)} | \mathbf{Z}^{(n)} \neq \mathbf{0}, \mathbf{Z}^{(0)} = \mathbf{e}_\ell)$ is distributed as a shifted Multivariate-Geometric distribution

$$\mathbb{E}(\mathbf{s}^{\mathbf{Z}^{(n)}} | \mathbf{Z}^{(n)} \neq \mathbf{0}, \mathbf{Z}^{(0)} = \mathbf{e}_\ell) = \frac{(1 - h_{\ell 0}^{(n)})^{-1} \sum_{\ell' \geq 1} h_{\ell \ell'}^{(n)} s_{\ell'}}{1 + m^{(n)} - m^{(n)} \sum_{\ell' \geq 1} g_{\ell'}^{(n)} s_{\ell'}}.$$

This theorem was proved in [10] for the case of finitely many types using an algebraic approach, while [21] provided a different proof using the jumping contour representation of the branching process and its nice Markovian structure.

3.2. Coalescent times in linear-fractional ancestral tree

We use the coalescent point-process construction to get simpler results for the distribution of coalescent times (and same-type coalescent times) for this special class of multi-type branching processes. For this purpose we make one change in our original construction pertaining to the embedding of the multi-type tree in the plane. For a general offspring distribution we made the

assumption that the offspring of any parent are embedded in a left to right order chosen *uniformly* at random from all possible orderings. For the linear-fractional offspring distribution we make a particular assumption that the offspring with distribution given by the vector \mathbf{h} is embedded as the left most individual, followed by the rest of the offspring according to an arbitrary order.

Proposition 3.2. *The coalescence times $(A_i)_{i \geq 0}$ in the ancestral tree of a LF($\mathbf{H}, \mathbf{g}, m$) branching process are independent identically distributed variables with*

$$\mathbb{P}(A_1 > n) = \prod_{n'=1}^n \frac{1}{1 + m - m \sum_{\ell' \geq 1} \mathbf{g}_{\ell'} h_{\ell'}^{(n'-1)}} = \frac{1}{1 + m^{(n)}}, \tag{7}$$

where $h_{\ell'}^{(n'-1)} = 1 - \mathbf{h}_{\ell'}^{(n'-1)} \mathbf{1}^t$, $\mathbf{h}_{\ell'}^{(n'-1)}$ is the ℓ' th row of the matrix $\mathbf{H}^{(n)}$ from (6), $h_{\ell'}^{(0)} = 0 \ \forall \ell'$. The law of the coalescent times also satisfies $\mathbb{P}(A_1 > n | \mathbf{A}_{0[n]} = \mathbf{a}_{[n]}) = \mathbb{P}(A_1 > n)$.

Remark 3.3. The second, simpler expression in (7) can be obtained either using arithmetic properties of parameters (6) from Theorem 3.1, or using the expression in terms of the n th generation of a multi-type LF branching process.

Proposition 3.4. *For any type $\ell \in \{1, 2, \dots\}$, the same-type coalescence times $(B_{\ell,i})_{i \geq 0}$ are independent identically distributed variables with*

$$\mathbb{P}(B_{\ell,1} > n | \mathbf{A}_{0[0]} = \ell) = \prod_{n'=1}^n \frac{1}{1 + m - m \sum_{\ell' \geq 1} \mathbf{g}_{\ell'} \tilde{h}_{\ell'}^{(n'-1)}} = \frac{1}{1 + m^{(n)} g_{\ell}^{(n)}} \tag{8}$$

where, for $n' > 1$, $\tilde{h}_{\ell'}^{(n'-1)}$ is given by

$$\tilde{h}_{\ell'}^{(n'-1)} = h_{\ell'}^{(n'-1)} + \frac{1 - h_{\ell'}^{(n'-1)} - h_{\ell'}^{(n'-1)}}{1 + m^{(n'-1)} g_{\ell}^{(n'-1)}},$$

and $\tilde{h}_{\ell'}^{(0)} = 1 \ \forall \ell' \neq \ell$, while $\tilde{h}_{\ell}^{(0)} = 0$.

Although the multi-type LF offspring distribution has a seemingly small level of dependence between the offspring and parent type, it still affects the distribution of types in the ancestral tree. One can also consider a multi-type branching process where offspring distribution is completely independent of the parent type. In this case the shape of the tree and the types on the tree can be decoupled, and the distribution of types is only governed by the frequency of this type in the population.

Consider a special case of a LF distribution where $\mathbf{H} := \mathbf{1}^t \mathbf{h}$, for $\mathbf{h} \mathbf{1}^t = h_1 + h_2 + \dots \leq 1$, then each parent has the same LF($\mathbf{h}, \mathbf{g}, m$) offspring distribution. Further, if we have no distinction between the first offspring and the rest, then we would have $\mathbf{h} := (1 - h_0) \mathbf{g}$, for $h_0 \in (0, 1)$. In this case all parents have the same offspring laws, where their number of offspring has a single-type LF(h_0, m) distribution with probability generating function $h_0 + (1 - h_0)s / (1 + m - ms)$, and given the number of offspring, the distribution of their types is Multinomial with parameter \mathbf{g} . In this case we get the following formulae for the law of coalescence times and same-type coalescence times.

Corollary 3.5. *If the offspring distribution of each parent is independent of the parent’s type with $LF((1 - h_0)\mathbf{1}^g, \mathbf{g}, m)$ distribution, then*

$$\mathbb{P}(A_1 > n) = \begin{cases} \frac{m - h_0(1 + m)}{m(1 + m)^n(1 - h_0)^n - h_0(1 + m)} & \text{if } (1 - h_0)(1 + m) \neq 1, \\ \frac{1 - h_0}{1 - h_0 + nh_0} & \text{if } (1 - h_0)(1 + m) = 1 \end{cases}$$

and

$$\mathbb{P}(B_{\ell,1} > n | \mathbf{A}_{0[0]} = \ell) = \frac{1 - \mathbb{P}(A_1 \leq n)}{1 - \mathbb{P}(A_1 \leq n)(1 - g_\ell)}. \tag{9}$$

As expected, the distribution of types \mathbf{g} has no effect on the law of $(A_i)_{i \geq 1}$ and the shape of the tree, but appears in the distribution of types in the tree as indicated by the law of $(B_{\ell,i})_{i \geq 1}$.

We can consider the process of coalescent times $(A_i)_{i \geq 0}$ as a simple point-process A on $\{1, 2, \dots\} \times \{-1, -2, \dots\}$ with intensity measure $\nu_A[\{i\} \times \{-(n + 1), \dots\}] = \mathbb{P}(A_1 > n)$, $\forall i \geq 1$. Similarly for each $\ell \in \{1, 2, \dots\}$, $(B_{\ell,i})_{i \geq 0}$ can be regarded as a simple point-process B_ℓ with intensity $\nu_{B_\ell}[\{i\} \times \{-(n + 1), \dots\}] = \mathbb{P}(B_{\ell,1} > n)$ on $\{1, 2, \dots\} \times \{-1, -2, \dots\}$. Note that for any $i \geq 1, n \geq 1$, (9) implies that

$$\nu_{B_\ell}[\{i\} \times \{-1, \dots, -n\}] = \frac{\nu_A[\{i\} \times \{-1, \dots, -n\}]g_\ell}{\nu_A[\{i\} \times \{-(n + 1), \dots\}] + \nu_A[\{i\} \times \{-1, \dots, -n\}]g_\ell}$$

showing that only a fraction of all coalescent times are candidates for same-type coalescence times for type ℓ . One way to understand this formula, is to consider the sequence of coalescent times in the point-process $A_{i_{\ell,0}}, A_{i_{\ell,0}+1}, \dots$ where $i_{\ell,i}$ is the index of the i th individual of type ℓ in the standing population. Such a coalescence time occurs either inside or outside the set $\{-1, \dots, -n\}$. Mark the occurrences of it inside independently with probability g_ℓ that the next individual in the standing population is of type ℓ . The coalescent time $B_{\ell,i}$ inside the set $\{-1, \dots, -n\}$ can only see the marked coalescence times $A_{i_{\ell,0}}, A_{i_{\ell,0}+1}, \dots$, so the fraction of times they occur in this set is the proportion of times a marked version of a general coalescence time occurs inside this set as opposed to a general coalescence time occurring outside the set.

Note that the intensity measures $\{\nu_{B_\ell}\}_{\ell \in \{1,2,\dots\}}$ do not partition in full the measure ν_A . That is $\cup_{\ell=1}^\infty \{B_{\ell,1} \leq n\} \subsetneq \{A_1 \leq n\}$ or equivalently $\{A_1 > n\} \subsetneq \cap_{\ell=1}^\infty \{B_{\ell,1} > n\}$ since the fact that $0 < g_\ell < 1$ implies

$$\prod_{\ell=1}^\infty \mathbb{P}(B_{\ell,1} > n) = \prod_{\ell=1}^\infty \frac{\mathbb{P}(A_1 > n)}{\mathbb{P}(A_1 > n) + \mathbb{P}(A_1 \leq n)g_\ell} > \mathbb{P}(A_1 > n).$$

This is a consequence of the fact that not all coalescence times are in fact same-type coalescence times for some ℓ (for example, in Fig. 3 the coalescence time $A_4 = 1$ of $(0, 4)$ and $(0, 5)$ is neither a same-type $\mathbf{1}$ nor a same-type $\mathbf{2}$ coalescence time).

3.3. Comparison of ancestral trees in two-type models

We next give an example of using the same-type coalescent times to investigate the effect of differences in offspring distribution on the distribution of types in the ancestral trees they produce. One question that motivated our work is the effect of different diversification rates for different types of individuals (phenotypes). We translate these questions into a discrete time defining an asymmetrical offspring distribution law.

Specifically, in a population with only two types of individuals, if the transition rates of one type to the other are relatively high, while the other type never transitions into the first, this will be reflected in the distribution of types along the tree. In a discrete time process this is translated in the probability of a parent of the first type giving birth to individuals of the second type and vice versa. We consider this difference in the context of a two-type LF offspring distribution. In order to investigate only the effect on the distribution of types, we will make the distribution of the shape of the tree the same in both cases.

We consider the following two LF offspring distributions on $k = 2$ types of individuals. Let the parameters $\mathbf{g} = (g, 1 - g)$, $g \in [0, 1/2]$, $m > 0$ and $h_1 = 1 - h_0$, $h_0 \in [0, 1]$ be the same in both distributions, and for $p \in (0, 1)$ let

$$\mathbf{H}_s = h_1 \begin{pmatrix} p & 1 - p \\ 1 - p & p \end{pmatrix}, \quad \mathbf{H}_a = h_1 \begin{pmatrix} p & 1 - p \\ 0 & 1 \end{pmatrix},$$

be, respectively, associated with the symmetrical and the asymmetrical offspring distribution. In the symmetrical case parents of either type produce offspring of their own type and of the other type. In the asymmetrical case only a parent of type **1** will do that, while a parent of type **2** can only produce offspring of its own type. Since the number of offspring of each parent depends only on h_0 and m , the distribution of the ancestral tree with types erased will be the same in both cases. However, the distribution of the two types **1** and **2** is different, as can be seen in the following result.

Remark 3.6. Note that we can assume without loss of generality that $g \in [0, 1/2]$, since in case $g \in [1/2, 1]$ we can simply reverse the notation of the two types. For $p = 1$ there is no asymmetry, nor are there offspring of different type than the parent—individuals in the whole tree are all of the same type. For $(g, p) = (1/2, 1/2)$ the symmetric case is special, and the offspring distribution is independent of the type of the parent, as discussed in Corollary 3.5.

Proposition 3.7. *The distributions of coalescence times $(A_i)_{i \geq 1}$ are the same in both cases. The distribution of same-type coalescence times $(B_{1,i})_{i \geq 1}$ and $(B_{2,i})_{i \geq 1}$ satisfy the following stochastic dominance relations: $\forall p \in [0, 1]$,*

$$\mathbb{P}_a(B_{1,i} > n \mid \mathbf{A}_{0[0]} = \mathbf{1}) \geq \mathbb{P}_s(B_{1,i} > n \mid \mathbf{A}_{0[0]} = \mathbf{1}),$$

and

$$\mathbb{P}_a(B_{2,i} > n \mid \mathbf{A}_{0[0]} = \mathbf{2}) \leq \mathbb{P}_s(B_{2,i} > n \mid \mathbf{A}_{0[0]} = \mathbf{2}).$$

Also $\forall p \geq 1/2$ the two above inequalities are related by:

$$\mathbb{P}_s(B_{1,i} > n \mid \mathbf{A}_{0[0]} = \mathbf{1}) \geq \mathbb{P}_s(B_{2,i} > n \mid \mathbf{A}_{0[0]} = \mathbf{2}).$$

The explicit formulae for all of the above probabilities in terms of the parameters g, h_1, p are complicated and can be found in the proof of the Proposition. We see that the consequence of asymmetry (irrespective of the value of p) is that the same-type coalescence times are typically shorter for type **2** than in the symmetrical case, while they are longer for type **1**. This intuitively makes sense, since subtrees of a type **2** can only contain type **2** individuals, while subtrees of a type **1** individual contain a mixture of types.

We can also see the effect that the ‘strength’ p of not transitioning to a different type plays in the symmetric case. When $p \geq 1/2$ having the same type offspring as parent is more likely. In the symmetric case $g \leq 1/2$ further implies that type **1** is overall less frequent than type **2** in

the tree. Hence, one would expect that the same-type coalescence times are typically going to be longer for type 1 than for type 2.

4. Proofs

4.1. Proof of results for general multi-type coalescent point process

We first state a spine decomposition of a multi-type branching process conditioned on survival to a certain generation, which shows that, if we consider the infinite (back into the past) lineage of a current individual, at every generation back in the past the subtrees of siblings of the ancestor in that generation are independent of the infinite lineage and are distributed as trees of an unconditioned multi-type branching process. Moreover, *knowing the values of their own initial individuals*, these trees are independent from their sibling subtrees, and are independent of their rank in the planar ordering.

For single-type processes this result first appeared in [16,5]. For multi-type processes a decomposition of a tree relative to a spine that is infinite *into the future* is stated in [11], and in [6] for branching in continuous time. We present a statement in the form of Lemma 2.1 from [5] for decomposition of trees conditioned only to survive to a fixed generation, and give its proof. Consider a multi-type branching process \mathbf{Z} which is still non-extinct in generation $n + 1$, let $T^{(i)}, 1 \leq i \leq |\mathbf{Z}^{(1)}|$ denote the subtrees descending from the offspring in the first generation. Let $\mathbf{d}(\mathbf{Z}^{(1)})$ be a uniform ordering of all the offspring types in the first generation, and let R_{n+1} be the rank of the first offspring whose descendants survive to generation $n + 1$.

Lemma 4.1. *The subtrees $T^{(i)}, 1 \leq i \leq |\mathbf{Z}^{(1)}|, d_i \in \{1, 2, \dots\}$, are conditionally independent given $\{\mathbf{Z}^{(0)} = \mathbf{e}_\ell, \mathbf{Z}^{(1)} = \mathbf{z}, \mathbf{d}(\mathbf{Z}^{(1)}) = \mathbf{d}(\mathbf{z}), R_{n+1} = j\}$, for $1 \leq j \leq |\mathbf{z}|$ and $\mathbf{z} = (z_1, z_2, \dots)$ with $\mathbf{d}(\mathbf{z}) = (d_1, \dots, d_{|\mathbf{z}|})$*

$$\begin{aligned} & \mathbb{P}(T^{(i)} \mid \mathbf{Z}^{(0)} = \mathbf{e}_\ell, \mathbf{Z}^{(1)} = \mathbf{z}, \mathbf{d}(\mathbf{z}) = (d_1, \dots, d_{|\mathbf{z}|}), R_{n+1} = j) \\ & \stackrel{d}{=} \begin{cases} \mathbb{P}(T \mid \mathbf{Z}^{(n)}(\mathcal{T}) = \mathbf{0}, \mathbf{Z}^{(0)}(\mathcal{T}) = \mathbf{e}_{d_i}), & 1 \leq i \leq j - 1 \\ \mathbb{P}(T \mid \mathbf{Z}^{(n)}(\mathcal{T}) \neq \mathbf{0}, \mathbf{Z}^{(0)}(\mathcal{T}) = \mathbf{e}_{d_i}), & i = j \\ \mathbb{P}(T \mid \mathbf{Z}^{(0)}(\mathcal{T}) = \mathbf{e}_{d_i}), & j + 1 \leq i \leq |\mathbf{z}|, \end{cases} \end{aligned}$$

where \mathcal{T} denotes the law of a tree of multi-type branching processes with the p.g.f. of \mathbf{Z} . Further, the conditional joint distribution of $R_{n+1}, \mathbf{Z}^{(1)}, \mathbf{d}(\mathbf{Z}^{(1)})$ is given by

$$\begin{aligned} & \mathbb{P}(R_{n+1} = j, \mathbf{Z}^{(1)} = \mathbf{z}, \mathbf{d}(\mathbf{Z}^{(1)}) = \mathbf{d}(\mathbf{z}) \mid \mathbf{Z}^{(n+1)} \neq \mathbf{0}, \mathbf{Z}^{(0)} = \mathbf{e}_\ell) \\ & = \frac{\mathbb{P}(\xi_\ell = \mathbf{z}) \mathbb{P}(\mathbf{d}(\mathbf{z}) = (d_1, \dots, d_{|\mathbf{z}|})) \mathbb{P}(\mathbf{Z}^{(n)} \neq \mathbf{0} \mid \mathbf{Z}^{(0)} = \mathbf{e}_{d_j}) \prod_{\ell'=1}^{j-1} \mathbb{P}(\mathbf{Z}^{(n)} = \mathbf{0} \mid \mathbf{Z}^{(0)} = \mathbf{e}_{d_{\ell'}})}{\mathbb{P}(\mathbf{Z}^{(n+1)} \neq \mathbf{0} \mid \mathbf{Z}^{(0)} = \mathbf{e}_\ell)}. \end{aligned}$$

Proof of Lemma 4.1. Let \mathcal{T} denote the tree of a branching process with the p.g.f. of \mathbf{Z} . Let \mathbf{z} be a sample value of $\mathbf{Z}^{(1)}$, and consider $j \in \{1, \dots, |\mathbf{z}|\}$ fixed. Let $(A_i)_{1 \leq i \leq |\mathbf{z}|}$ be measurable subsets of the space of multi-type rooted planar trees with roots of type d_i , where $\mathbf{d}(\mathbf{z}) = (d_1, \dots, d_{|\mathbf{z}|})$. Assume that for $1 \leq i \leq j - 1$;

$$A_i \subseteq \{T : \mathbf{Z}^{(n)}(\mathcal{T}) = \mathbf{0}, \mathbf{Z}^{(0)}(\mathcal{T}) = \mathbf{e}_{d_i}\}, \quad A_j \subseteq \{T : \mathbf{Z}^{(n)}(\mathcal{T}) \neq \mathbf{0}, \mathbf{Z}^{(0)}(\mathcal{T}) = \mathbf{e}_{d_j}\},$$

and assume no additional condition on A_i for $i > j$. Since $\{T^{(i)} \in A_i\}_{1 \leq i \leq j-1}$ implies that the first $j - 1$ subtrees are extinct by generation n , and $T^{(j)} \in A_j$, which implies that the j th subtree

$T^{(j)}$ has survived to generation n , together imply that $R_{n+1} = j$, we have,

$$\left\{ \bigcap_{i=1}^{|z|} \{T^{(i)} \in A_i\}, \mathbf{Z}^{(1)} = \mathbf{z}, \mathbf{d}(\mathbf{Z}^{(1)}) = \mathbf{d} \right\} \subset \{R_{n+1} = j\},$$

so from the independence of offspring trees without any condition on their shape:

$$\begin{aligned} &\mathbb{P}(\{T^{(i)} \in A_i\}_{1 \leq i \leq |z|}, \mathbf{Z}^{(1)} = \mathbf{z}, \mathbf{d}(\mathbf{Z}^{(1)}) = \mathbf{d}, R_{n+1} = j | \mathbf{Z}^{(0)} = \mathbf{e}_\ell) \\ &= \mathbb{P}(\mathbf{Z}^{(1)} = \mathbf{z} | \mathbf{Z}^{(0)} = \mathbf{e}_\ell) \mathbb{P}(\mathbf{d}(\mathbf{z}) = \mathbf{d}) \prod_{i=1}^{|z|} \mathbb{P}(T^{(i)} \in A_i | \mathbf{Z}^{(0)}(T^{(i)}) = \mathbf{e}_{d_i}). \end{aligned}$$

From this equality we have that the subtrees $T^{(i)}$ are conditionally independent given $\{\mathbf{Z}^{(0)} = \mathbf{e}_\ell, \mathbf{Z}^{(1)} = \mathbf{z}, \mathbf{d}(\mathbf{Z}^{(1)}) = \mathbf{d}(\mathbf{z}), R_{n+1} = j\}$, since the measurable sets A_i are arbitrary under those conditions.

We next prove that for $1 \leq i \leq j - 1$,

$$(T^{(i)} | \mathbf{Z}^{(1)} = \mathbf{z}, \mathbf{d}(\mathbf{Z}^{(1)}) = \mathbf{d}, \mathbf{Z}^{(0)} = \mathbf{e}_\ell, R_{n+1} = j) \stackrel{d}{=} (\mathcal{T} | \mathbf{Z}^{(n)}(\mathcal{T}) = \mathbf{0}, \mathbf{Z}^{(0)}(\mathcal{T}) = \mathbf{e}_{d_i})$$

by showing that for every measurable subset $\hat{A}_i \subset \{\mathcal{T} | \mathbf{Z}^{(n)}(\mathcal{T}) = \mathbf{0}, \mathbf{Z}^{(0)}(\mathcal{T}) = \mathbf{e}_{d_i}\}$, we have

$$\begin{aligned} &\mathbb{P}(T^{(i)} \in \hat{A}_i | \mathbf{Z}^{(1)} = \mathbf{z}, \mathbf{d}(\mathbf{Z}^{(1)}) = \mathbf{d}, \mathbf{Z}^{(0)} = \mathbf{e}_\ell, R_{n+1} = j) \\ &= \mathbb{P}(\mathcal{T} \in \hat{A}_i | \mathbf{Z}^{(n)}(\mathcal{T}) = \mathbf{0}, \mathbf{Z}^{(0)}(\mathcal{T}) = \mathbf{e}_{d_i}). \end{aligned} \tag{10}$$

The left hand side of the above equality can be rewritten as

$$\frac{\mathbb{P}(T^{(i)} \in \hat{A}_i, \mathbf{Z}^{(1)} = \mathbf{z}, \mathbf{d}(\mathbf{Z}^{(1)}) = \mathbf{d}, R_{n+1} = j | \mathbf{Z}^{(0)} = \mathbf{e}_\ell)}{\mathbb{P}(\mathbf{Z}^{(1)} = \mathbf{z}, \mathbf{d}(\mathbf{Z}^{(1)}) = \mathbf{d}, R_{n+1} = j, | \mathbf{Z}^{(0)} = \mathbf{e}_\ell)}. \tag{11}$$

Using shorthand notation for events $E_i := \{\mathcal{T} : \mathbf{Z}^{(n)}(\mathcal{T}) = \mathbf{0}, \mathbf{Z}^{(0)}(\mathcal{T}) = \mathbf{e}_{d_i}\}$, for $1 \leq i \leq j - 1$, $E_j := \{\mathcal{T} : \mathbf{Z}^{(n)}(\mathcal{T}) \neq \mathbf{0}, \mathbf{Z}^{(0)}(\mathcal{T}) = \mathbf{e}_{d_j}\}$, and $E_i := \{\mathcal{T} : \mathbf{Z}^{(0)}(\mathcal{T}) = \mathbf{e}_{d_i}\}$, for $j < i \leq |z|$, the numerator of (11) becomes

$$\begin{aligned} &\mathbb{P}(T^{(i)} \in \hat{A}_i, \{T^{(r)} \in E_r\}_{r \neq i}, \mathbf{Z}^{(1)} = \mathbf{z}, \mathbf{d}(\mathbf{Z}^{(1)}) = \mathbf{d}, R_{n+1} = j | \mathbf{Z}^{(0)} = \mathbf{e}_\ell) \\ &= \mathbb{P}(\mathbf{Z}^{(1)} = \mathbf{z} | \mathbf{Z}^{(0)} = \mathbf{e}_\ell) \mathbb{P}(\mathbf{d}(\mathbf{z}) = \mathbf{d}) \mathbb{P}(\mathcal{T} \in \hat{A}_i | \mathbf{Z}^{(0)}(\mathcal{T}) = \mathbf{e}_{d_i}) \\ &\quad \times \prod_{r \neq i} \mathbb{P}(\mathcal{T} \in E_r | \mathbf{Z}^{(0)}(\mathcal{T}) = \mathbf{e}_{d_r}), \end{aligned}$$

while the denominator is equal to

$$\begin{aligned} &\mathbb{P}(\mathbf{Z}^{(1)} = \mathbf{z}, \mathbf{d}(\mathbf{Z}^{(1)}) = \mathbf{d}, R_{n+1} = j | \mathbf{Z}^{(0)} = \mathbf{e}_\ell) \\ &= \mathbb{P}(\mathbf{Z}^{(1)} = \mathbf{z}, \mathbf{d}(\mathbf{Z}^{(1)}) = \mathbf{d}, \{T^{(r)} \in E_r\}_{r=1, \dots, |z|}, R_{n+1} = j | \mathbf{Z}^{(0)} = \mathbf{e}_\ell) \\ &= \mathbb{P}(\mathbf{Z}^{(1)} = \mathbf{z} | \mathbf{Z}^{(0)} = \mathbf{e}_\ell) \mathbb{P}(\mathbf{d}(\mathbf{z}) = \mathbf{d}) \prod_{r=1}^{|z|} \mathbb{P}(\mathcal{T} \in E_r | \mathbf{Z}^{(0)}(\mathcal{T}) = \mathbf{e}_{d_r}). \end{aligned}$$

Together the last two equalities show that (11) is equal to

$$\mathbb{P}(T^{(i)} \in \hat{A}_i | R_{n+1} = j, \mathbf{Z}^{(1)} = \mathbf{z}, \mathbf{d}(\mathbf{Z}^{(1)}) = \mathbf{d}, \mathbf{Z}^{(0)} = \mathbf{e}_\ell) = \frac{\mathbb{P}(\mathcal{T} \in \hat{A}_i | \mathbf{Z}^{(0)}(\mathcal{T}) = \mathbf{e}_{d_i})}{\mathbb{P}(\mathcal{T} \in E_j | \mathbf{Z}^{(0)}(\mathcal{T}) = \mathbf{e}_{d_j})},$$

which by definition of E_j is then equal to the right hand side of Eq. (10). This proves the statement about the law of different subtrees. To prove the statement about the joint law of the index of the first subtree surviving to generation n and the number and types of the offspring in

generation 1, it is sufficient to condition on $Z_1 = z$ and use independence of the unconditioned offspring trees. \square

Proof of Theorem 2.1. Observe that,

$$\begin{aligned} A_i > n &\Leftrightarrow \forall n' \leq n, \quad a_i(n') \neq a_{i+1}(n') \\ &\Leftrightarrow \forall n' \leq n, \quad (-n', a_i(n')) \text{ has no surviving progeny in} \\ &\quad \{(0, i + 1), (0, i + 2), \dots\} \\ &\Leftrightarrow \forall n' \leq n, \quad \|\mathbf{D}_i(n')\| = 1 \end{aligned}$$

so that A_i is the level of the first term of the sequence \mathbf{D}_i such that $D_i(n) = \|\mathbf{D}_i(n)\| - 1 \neq 0$.

In addition, notice that $\mathbf{D}_{i+1}(n)$ records the types of offspring of the ancestor of $(0, i + 1)$ in generation $-n$ which have surviving progeny embedded to the right of $(0, i + 1)$, including the one that is on the lineage of $(0, i + 1)$. Thus $\mathbf{D}_{i+1}(n)_{[1]}$ is the ancestor's type of $(0, i + 1)$ in generation $-(n - 1)$, and continuing recursively this proves the formula for A_i in terms of \mathbf{D}_{i+1} .

At level A_i we have the most recent common ancestor $a_i(A_i) = a_{i+1}(A_i)$ of individuals $(0, i)$ and $(0, i + 1)$, whose offspring with surviving progeny embedded to the right of $(0, i + 1)$ do not include the ancestor of $(0, i)$, which is recorded in $\mathbf{D}_i(A_i)_{[1]}$, but do include all the others. So,

$$(\mathbf{D}_{i+1}(A_i)_{[1]}, \mathbf{D}_{i+1}(A_i)_{[2]}, \mathbf{D}_{i+1}(A_i)_{[3]}, \dots) = (\mathbf{D}_i(A_i)_{[2]}, \mathbf{D}_i(A_i)_{[3]}, \dots).$$

At any level $n > A_i$ below the most recent, the common ancestors of $(0, i)$ and $(0, i + 1)$ are the same since $a_i(A_i) = a_{i+1}(A_i)$ implies $a_i(n) = a_{i+1}(n)$, so

$$\forall n > A_i, \quad \mathbf{D}_i(n) = \mathbf{D}_{i+1}(n).$$

For levels $n < A_i$ above the most recent common ancestor, note that by Lemma 4.1 the subtrees descending from different surviving offspring of $(-A_i, a_i(A_i))$ are independent copies of multi-type branching processes whose initial individuals are of types $\mathbf{D}_i(A_i)_{[1]}, \mathbf{D}_i(A_i)_{[2]}, \dots$ and which are conditioned to survive for at least $n' := A_i - 1$ generations. In particular, the subtree containing the lineage of $(0, i + 1)$ above $(-A_i, a_i(A_i))$ is independent of the subtree whose lineage is recorded in $\{\mathbf{D}_i(n), n < A_i\}$ and is initiated by an individual of type $\ell := \mathbf{D}_i(A_i)_{[2]}$. By definition $(\mathbf{D}_{i+1}(n), 1 \leq n < A_i)$ records the survivor types (and their siblings) along the left most ancestral lineage of $(0, i + 1)$ above the level A_i . Furthermore, by Lemma 4.1 the distribution of this sequence of type vectors for a multi-type branching process with initial individual of type ℓ conditioned to survive at least n' generations is distributed as the sequence of type vectors $\eta_{n', \ell}$. So,

$$(\mathbf{D}_{i+1}(1), \dots, \mathbf{D}_{i+1}(A_i - 1)) \stackrel{d}{=} \eta_{A_i - 1, \mathbf{D}_i(A_i)_{[2]}} \Leftrightarrow \forall 1 \leq n < A_i,$$

$$\mathbf{D}_{i+1}(n) \stackrel{d}{=} \eta_{A_i - 1, \mathbf{D}_i(A_i)_{[2]}}(n).$$

As in the single type case, the sequence $\mathbf{D}_{i+1} = (\mathbf{D}_{i+1}(n), n \geq 1)$ depends only on \mathbf{D}_i and not on $\mathbf{D}_{i'}$ for $i' < i$; and its transition law is determined by values of $(\mathbf{D}_i(n), n \geq A_i)$ and an independent random variable $\eta_{n', \ell}$ with $n' = A_i - 1$ and $\ell = \mathbf{D}_i(A_i)_{[2]}$. \square

Proof of Corollary 2.2. The fact that $\{A_1 \neq 1, \dots, A_1 \neq n\}$ iff the subtree of the ancestor $(-n, a_1(n))$ of $(0, 1)$ in generation $-n$ has exactly one offspring with surviving progeny, directly implies that

$$\mathbb{P}(A_1 > n | \mathbf{A}_{0[n]} = \mathbf{a}_{[n]}) = \mathbb{P}\left(\sum_{\ell \geq 1} Z_\ell^{(n)} = 1 \mid \mathbf{Z}^{(n)} \neq \mathbf{0}, \mathbf{Z}^{(0)} = \mathbf{e}_{a_{[n]}}\right). \quad \square$$

Proof of Proposition 2.3. Observe that $\{A_1 \neq 1, \dots, A_1 \neq n\}$ iff all the ancestors $(-n', a_1(n'))$ of $(0, 1)$ in generations $-n', 1 \leq n' \leq n$ have exactly one offspring with surviving progeny. Observe also that when types of ancestral individuals are known, by Lemma 4.1 the events of having exactly one offspring surviving progeny are independent across different generations. If $\mathbf{a}_{[n']} = \mathbf{A}_{0[n']}$ denotes the type of the ancestor $(-n', a_1(n'))$ of $(0, 1)$ in generation $-n'$, furthermore by Lemma 4.1 then those events can be expressed in terms of the random variable $\eta_{n, \mathbf{a}_{[n]}}$ and in terms of the random variables $\zeta'_{n', \mathbf{a}_{[n']}}, 1 \leq n' \leq n$ as

$$\begin{aligned} & \mathbb{P}(A_1 > n, \mathbf{A}_{0|n-1} = \mathbf{a}_{|n-1} | \mathbf{A}_{0[n]} = \mathbf{a}_{[n]}) \\ &= \mathbb{P}(\eta_{n, \mathbf{a}_{[n]}} = (\{\mathbf{a}_{[0]}\}, \{\mathbf{a}_{[1]}\}, \dots, \{\mathbf{a}_{[n-1]}\})) \\ &= \mathbb{P}(\forall 1 \leq n' \leq n : \zeta'_{n', \mathbf{a}_{[n']}, \mathbf{a}_{[n'-1]}} = 1, \zeta'_{n', \mathbf{a}_{[n']}, \ell'} = 0 \forall \ell' \neq \mathbf{a}_{[n'-1]}) \\ &= \prod_{n'=1}^n \mathbb{P}(\zeta'_{n', \mathbf{a}_{[n']}, \mathbf{a}_{[n'-1]}} = 1, \zeta'_{n', \mathbf{a}_{[n']}, \ell'} = 0 \forall \ell' \neq \mathbf{a}_{[n'-1]}), \end{aligned}$$

where we can write the above as a product because the subtrees descending from different offspring are independent. For each product term we have

$$\begin{aligned} & \mathbb{P}(\zeta'_{n', \mathbf{a}_{[n']}, \mathbf{a}_{[n'-1]}} = 1, \zeta'_{n', \mathbf{a}_{[n']}, \ell'} = 0 \forall \ell' \neq \mathbf{a}_{[n'-1]}) \\ &= \frac{\mathbb{P}(\zeta_{n', \mathbf{a}_{[n']}, \mathbf{a}_{[n'-1]}} = 1, \zeta_{n', \mathbf{a}_{[n']}, \ell'} = 0 \forall \ell' \neq \mathbf{a}_{[n'-1]})}{\mathbb{P}\left(\sum_{\ell' \geq 1} \zeta_{n', \mathbf{a}_{[n']}, \ell'} \neq 0\right)}. \end{aligned}$$

Conditioning on the value of variable $\xi_{\mathbf{a}_{[n']}}$ which, when Bernoulli sampled by the vector $\mathbf{p}_{n'-1} := \mathbf{1} - \mathbf{f}^{(n'-1)}(0, 0, \dots)$ of survival probabilities of different types by generation $n' - 1$ (i.e., each entry i is kept with probability $p_{n'-1, i}$), gives the distribution of $\zeta_{n', \mathbf{a}_{[n']}}$, we get for the numerator

$$\begin{aligned} & \mathbb{P}(\zeta_{n', \mathbf{a}_{[n']}, \mathbf{a}_{[n'-1]}} = 1, \zeta_{n', \mathbf{a}_{[n']}, \ell'} = 0 \forall \ell' \neq \mathbf{a}_{[n'-1]}) \\ &= \mathbb{E}\left(\mathbb{P}(\zeta_{n', \mathbf{a}_{[n']}, \mathbf{a}_{[n'-1]}} = 1, \zeta_{n', \mathbf{a}_{[n']}, \ell'} = 0 \forall \ell' \neq \mathbf{a}_{[n'-1]} | \xi_{\mathbf{a}_{[n]}})\right) \\ &= \mathbb{E}\left(\xi_{\mathbf{a}_{[n']}, \mathbf{a}_{[n'-1]}} \frac{p_{n'-1, \mathbf{a}_{[n'-1]}}}{(1 - p_{n'-1, \mathbf{a}_{[n'-1]}})} \prod_{\ell' \geq 1} (1 - p_{n'-1, \ell'})^{\xi_{\mathbf{a}_{[n']}, \ell'}}\right), \\ &= p_{n'-1, \mathbf{a}_{[n'-1]}} \frac{\partial f_{\mathbf{a}_{[n']}}(s)}{\partial s_{\mathbf{a}_{[n'-1]}}} \Big|_{s=\mathbf{1}-\mathbf{p}_{n'-1}}, \end{aligned}$$

and for the denominator

$$\mathbb{P}\left(\sum_{\ell' \geq 1} \zeta_{n', \mathbf{a}_{[n']}, \ell'} \geq 1\right) = 1 - f_{\mathbf{a}_{[n']}}^{(n')}(0, 0, \dots) = p_{n', \mathbf{a}_{[n']}}.$$

Since survival probability to generation 0 is $p_{0, \mathbf{a}_{[0]}} = 1$, we have

$$\begin{aligned} \mathbb{P}(A_1 > n, \mathbf{A}_{0|n-1} = \mathbf{a}_{|n-1} | \mathbf{A}_{0[n]} = \mathbf{a}_{[n]}) &= \prod_{n'=1}^n \left(\frac{\partial f_{\mathbf{a}_{[n']}}(s)}{\partial s_{\mathbf{a}_{[n'-1]}}} \Big|_{s=\mathbf{1}-\mathbf{p}_{n'-1}} \frac{p_{n'-1, \mathbf{a}_{[n'-1]}}}{p_{n', \mathbf{a}_{[n']}}} \right) \\ &= \frac{1}{p_{n, \mathbf{a}_{[n]}}} \prod_{n'=1}^n \left(\frac{\partial f_{\mathbf{a}_{[n']}}(s)}{\partial s_{\mathbf{a}_{[n'-1]}}} \Big|_{s=\mathbf{1}-\mathbf{p}_{n'-1}} \right), \end{aligned}$$

and note that for $n' = 1$ the evaluation of the derivative is at $s = \mathbf{1} - \mathbf{p}_0 = \mathbf{0}$. \square

Proof of Corollary 2.5. The fact that $\{B_{\ell,1} > n\}$ iff the subtree of the ancestor $(-n, a_1(n))$ of $(0, 1)$ in generations $-n$ has exactly one descendant of type ℓ after n generations, so

$$\mathbb{P}(B_{\ell,1} > n | \mathbf{A}_{0[n]} = \mathbf{a}_{[n]}, \mathbf{A}_{0[0]} = \ell) = \mathbb{P}(Z_\ell^{(n)} = 1 | Z_\ell^{(n)} \neq 0, \mathbf{Z}^{(0)} = \mathbf{e}_{a_{[n]}}). \quad \square$$

Proof of Proposition 2.6. Observe that $\{B_{\ell,1} \neq 1, \dots, B_{\ell,1} \neq n\}$ iff all the ancestors $(-n', a_1(n'))$ of $(0, 1)$ in generations $-n', 1 \leq n' \leq n$ have exactly one descendant in the standing population that has type ℓ . As before, let $\mathbf{a}_{[n']} = \mathbf{A}_{0[n']}$ denote the type of the ancestor $(-n', a_1(n'))$ of $(0, 1)$ in generation $-n'$, and note that $\mathbf{a}_{[0]} = \ell$.

We need to introduce new random variables which will count the number of offspring with descendants of type ℓ in the standing population. If $\mathbf{f}^{(n'-1)} = (f_1^{(n'-1)}, f_2^{(n'-1)}, \dots)$ is the probability generating function of the $n' - 1$ generation in a multi-type branching process initiated by individuals of type $\{1, 2, \dots\}$, then the probability that a multi-type process after $n' - 1$ generations has no individuals of type ℓ is given by the vector $\mathbf{f}^{(n'-1)}(\hat{\mathbf{e}}_\ell)$, where $\hat{\mathbf{e}}_\ell := \mathbf{1} - \mathbf{e}_\ell$. Let $\mathbf{p}^{(n'-1, \ell)} := \mathbf{1} - \mathbf{f}^{(n'-1)}(\hat{\mathbf{e}}_\ell)$ denote the probability of having at least one descendant of type ℓ after $n' - 1$ generations, that is, for each $j' \in \{1, 2, \dots\}$, we have $p^{(n'-1, \ell), j'} = 1 - f_{j'}^{(n'-1)}(\hat{\mathbf{e}}_\ell)$. For all different offspring types $j' \in \{1, 2, \dots\}$, let $\{\varepsilon_{(n', \ell), j'}^1, \varepsilon_{(n', \ell), j'}^2, \dots\}$ be independent sequences of Bernoulli variables with parameter $\mathbb{P}(\varepsilon_{(n', \ell), j'}^m = 1) = p^{(n'-1, \ell), j'}$. For an independent offspring variable ξ_j with $\xi_{j, j'}$ offspring of type j' define

$$\zeta_{(n', \ell), j} := \left(\sum_{m=1}^{\xi_{j,1}} \varepsilon_{(n', \ell), 1}^m, \sum_{m=1}^{\xi_{j,2}} \varepsilon_{(n', \ell), 2}^m, \dots \right),$$

whose j' coordinate is denoted by $\zeta_{(n', \ell), j, j'}$. Then, $\zeta_{(n', \ell), j}$ records the number of offspring (of different types), in the first generation of a multi-type branching process initiated by an individual of type j , which have at least one descendant of type ℓ after $n' - 1$ generations.

Then the law of $\zeta'_{(n', \ell), j}$ representing the number of offspring (of different types) in generation $-(n' - 1)$ of a type j ancestor from generation $-n'$ whose descendants contain an individual of type ℓ in the standing population, given that there is at least one, is given by:

$$\zeta'_{(n', \ell), j} \stackrel{d}{=} \left(\zeta_{(n', \ell), j} \mid \sum_{j' \geq 1} \zeta_{(n', \ell), j, j'} \geq 1 \right).$$

The event $\{B_{\ell,1} > n\} = \{B_{\ell,1} \neq 1, \dots, B_{\ell,1} \neq n\}$ can now be expressed in terms of the newly defined random variables $\zeta'_{(n', \ell), a_{[n']}}, 1 \leq n' \leq n$ as

$$\begin{aligned} &\mathbb{P}(B_{\ell,1} > n, \mathbf{A}_{0[n-1]} = \mathbf{a}_{[n-1]} | \mathbf{A}_{0[n]} = \mathbf{a}_{[n]}, \mathbf{A}_{0[0]} = \ell) \\ &= \mathbb{P}(\forall 1 \leq n' \leq n : \zeta'_{(n', \ell), a_{[n']}, a_{[n'-1]}} = 1, \zeta'_{(n', \ell), a_{[n']}, j'} = 0 \forall j' \neq a_{[n'-1]}) \\ &= \prod_{n'=1}^n \mathbb{P}(\zeta'_{(n', \ell), a_{[n']}, a_{[n'-1]}} = 1, \zeta'_{(n', \ell), a_{[n']}, j'} = 0 \forall j' \neq a_{[n'-1]}), \end{aligned}$$

where the product form follows since, by Lemma 4.1, subtrees of different offspring are independent. For each product term we have

$$\begin{aligned} &\mathbb{P}(\zeta'_{(n', \ell), a_{[n']}, a_{[n'-1]}} = 1, \zeta'_{(n', \ell), a_{[n']}, j'} = 0 \forall j' \neq a_{[n'-1]}) \\ &= \frac{\mathbb{P}(\zeta_{(n', \ell), a_{[n']}, a_{[n'-1]}} = 1, \zeta_{(n', \ell), a_{[n']}, j'} = 0 \forall j' \neq a_{[n'-1]})}{\mathbb{P}\left(\sum_{j' \geq 1} \zeta_{(n', \ell), j, j'} \geq 1\right)}. \end{aligned}$$

A similar calculation to the one in the proof of Proposition 2.3, conditioning on $\xi_{\mathbf{a}_{[n']}}$, gives the numerator to be

$$\begin{aligned} & \mathbb{P}(\zeta_{(n', \ell), \mathbf{a}_{[n']}, \mathbf{a}_{[n'-1]}} = 1, \zeta_{(n', \ell), \mathbf{a}_{[n']}, J'} = 0 \forall J' \neq \mathbf{a}_{[n'-1]}) \\ &= \mathbb{E}\left(\mathbb{P}\left(\zeta_{(n', \ell), \mathbf{a}_{[n']}, \mathbf{a}_{[n'-1]}} = 1, \zeta_{(n', \ell), \mathbf{a}_{[n']}, J'} = 0 \forall J' \neq \mathbf{a}_{[n'-1]} \mid \xi_{\mathbf{a}_{[n']}}\right)\right) \\ &= \mathbb{E}\left(\xi_{\mathbf{a}_{[n']}, \mathbf{a}_{[n'-1]}} \frac{P_{(n'-1, \ell), \mathbf{a}_{[n'-1]}}}{(1 - P_{(n'-1, \ell), \mathbf{a}_{[n'-1]}})} \prod_{j' \geq 1} (1 - P_{(n'-1, \ell), J'})^{\xi_{\mathbf{a}_{[n']}, j'}}\right) \\ &= P_{(n'-1, \ell), \mathbf{a}_{[n'-1]}} \left. \frac{\partial f_{\mathbf{a}_{[n']}}(\mathbf{s})}{\partial s_{\mathbf{a}_{[n'-1]}}} \right|_{\mathbf{s}=\mathbf{1}-\mathbf{p}_{(n'-1, \ell)}}, \end{aligned}$$

while the denominator is calculated in the same way and equals

$$\begin{aligned} \mathbb{P}\left(\sum_{\ell' \geq 1} \zeta_{(n', \ell), \mathbf{a}_{[n']}, \ell'} \geq 1\right) &= 1 - \mathbb{E}\left(\prod_{\ell' \geq 1} (1 - P_{(n'-1, \ell), \ell'})^{\xi_{\mathbf{a}_{[n']}, \ell'}}\right) \\ &= 1 - f_{\mathbf{a}_{[n']}}(\mathbf{1} - \mathbf{p}_{(n'-1, \ell)}) = 1 - f_{\mathbf{a}_{[n']}}(\hat{\mathbf{e}}_\ell) = P_{(n', \ell), \mathbf{a}_{[n']}} \end{aligned}$$

the cross terms of probabilities of a lineage with descendants of type ℓ cancel, and

$$\begin{aligned} & \mathbb{P}(B_{\ell, 1} > n, \mathbf{A}_{0|n-1} = \mathbf{a}_{[n-1]} \mid \mathbf{A}_{0|n} = \mathbf{a}_{[n]}, \mathbf{A}_{0|0} = \ell) \\ &= \frac{1}{P_{(n, \ell), \mathbf{a}_{[n]}}} \prod_{n'=1}^n \left. \frac{\partial f_{\mathbf{a}_{[n']}}(\mathbf{s})}{\partial s_{\mathbf{a}_{[n'-1]}}} \right|_{\mathbf{s}=\mathbf{1}-\mathbf{p}_{(n'-1, \ell)}}. \quad \square \end{aligned}$$

4.2. Proof of results for the LF multi-type branching process

Proof of Proposition 3.2. The most immediate approach to the proof uses Corollary 2.2 and follows from the fact that in a multi-type LF branching process, all offspring other than the first one (which according to our current convention is the left-most one) are independent of the type of the parent, and have a Multivariate-Geometric distribution with mean $m^{(n)}$ and type distribution given by $\mathbf{g}^{(n)}$ (whose formula is given in (6)). This fact was also used in [21] (see Section 4.1) to establish the formula (6) using the jumping contour representation of the branching process and its nice Markovian structure. Since by Corollary 2.2

$$\mathbb{P}(A_1 > n \mid \mathbf{A}_{0|n} = \mathbf{a}_{[n]}) = \mathbb{P}\left(\sum_{\ell \geq 1} Z_\ell^{(n)} = 1 \mid \mathbf{Z}^{(n)} \neq \mathbf{0}, \mathbf{Z}^{(0)} = \mathbf{e}_{\mathbf{a}_{[n]}}\right),$$

by the result of Theorem 3.1 the right-hand side is simply the probability the Geometric variable with mean $m^{(n)}$ is 0, which is equal to $1/(1 + m^{(n)})$ regardless of the type of the initial individual $\mathbf{Z}^{(0)}$.

In addition to the above approach, we thought it would be instructive to show the agreement with the formula for the joint law of A_1 and $\mathbf{A}_{0|n-1}$ in Proposition 2.3 via a summation approach. We start from a formula based on (3)

$$\mathbb{P}(A_1 > n \mid \mathbf{A}_{0|n} = \mathbf{a}_{[n]}) = \sum_{\mathbf{a}_{[0], \dots, \mathbf{a}_{[n-1]}}} \prod_{n'=1}^n \left(\frac{P_{n'-1, \mathbf{a}_{[n'-1]}}}{P_{n', \mathbf{a}_{[n']}}} \left. \frac{\partial f_{\mathbf{a}_{[n']}}(\mathbf{s})}{\partial s_{\mathbf{a}_{[n'-1]}}} \right|_{\mathbf{s}=\mathbf{1}-\mathbf{p}_{n'-1}} \right),$$

in which we perform the summation in a ‘top-down’ order, from possible values for $\mathbf{a}_{[0]}$ down to $\mathbf{a}_{[n-1]}$, and observe that since the summations are nested we can write this as $\mathbb{P}(A_1 > n | \mathbf{A}_{0[n]} = \mathbf{a}_{[n]}) = c_1 \cdots c_n$, where

$$c_{n'} \equiv c_{n'}(\mathbf{a}_{[n']}) = \frac{1}{P^{n', \mathbf{a}_{[n']}} \sum_{\mathbf{a}_{[n'-1]}=1}^{\infty} P^{n'-1, \mathbf{a}_{[n'-1]}} \left. \frac{\partial f_{\mathbf{a}_{[n']}}(\mathbf{s})}{\partial s_{\mathbf{a}_{[n'-1]}}} \right|_{\mathbf{s}=\mathbf{1}-P^{n'-1}}} \tag{12}$$

It turns out that in the linear fractional case the $c_{n'}$ are constants which do not depend on $\mathbf{a}_{[n']}$. More specifically

$$c_{n'}(\mathbf{a}_{[n']}) = \frac{1}{U_{n'}}$$

where $U_{n'} = 1 + m - m \sum_{\ell' \geq 1} g_{\ell'} h_{\ell'0}^{(n'-1)}$, so

$$\mathbb{P}(A_1 > n) = \prod_{n'=1}^n \frac{1}{1 + m - m \sum_{i \geq 1} g_i h_{i0}^{(n'-1)}}$$

We can rewrite this formula using the parameters defined in (6) from Theorem 3.1 according to which

$$\mathbf{H}^{(n)} = \mathbf{M}^n - \frac{m^{(n)}}{1 + m^{(n)}} \mathbf{M}^n \mathbf{1}^t \mathbf{g}^{(n)},$$

which when multiplied by \mathbf{g} on the left and by $\mathbf{1}^t$ on the right becomes $\mathbf{gH}^{(n)}\mathbf{1}^t = \frac{\mathbf{gM}^n\mathbf{1}^t}{1+m^{(n)}}$ or $\sum_{\ell \geq 1} g_{\ell} h_{\ell 0}^{(n)} = 1 - \frac{\mathbf{gM}^n\mathbf{1}^t}{1+m^{(n)}}$. Using this equality in the formula for $\mathbb{P}(A_1 > n)$ we get

$$\begin{aligned} \mathbb{P}(A_1 > n) &= \prod_{n'=1}^n \frac{1}{1 + m \frac{\mathbf{gM}^{n'-1}\mathbf{1}^t}{1+m^{(n'-1)}}} = \prod_{n'=1}^n \frac{1 + m^{(n'-1)}}{1 + m^{(n'-1)} + m\mathbf{gM}^{n'-1}\mathbf{1}^t} \\ &= \prod_{n'=1}^n \frac{1 + m^{(n'-1)}}{1 + m^{(n')}} = \frac{1}{1 + m^{(n)}}, \end{aligned}$$

because $m^{(n'-1)} + m\mathbf{gM}^{n'-1}\mathbf{1}^t = m\mathbf{g}(\mathbf{I} + \mathbf{M} + \cdots + \mathbf{M}^{n'-2})\mathbf{1}^t + m\mathbf{gM}^{n'-1}\mathbf{1}^t = m^{(n')}$, and $m^{(0)} = 0$. \square

Proof of Proposition 3.4. By Corollary 2.5

$$\mathbb{P}(B_{\ell,1} > n | \mathbf{A}_{0[n]} = \mathbf{a}_{[n]}, \mathbf{A}_{0[0]} = \ell) = \mathbb{P}(Z_{\ell}^{(n)} = 1 | Z_{\ell}^{(n)} \neq \mathbf{0}, \mathbf{Z}^{(0)} = \mathbf{e}_{\mathbf{a}_{[n]}}),$$

which is equal to $\partial_{s_{\ell}} f_{\mathbf{a}_{[n]}}^{(n)}(\hat{\mathbf{e}}_{\ell}) / (1 - f^{(n)}(\hat{\mathbf{e}}_{\ell}))$, and as a result of Theorem 3.1 and some simple arithmetic can be shown to be equal to $1 / (1 + m^{(n)} g_{\ell}^{(n)})$ regardless of the type of the initial individual $\mathbf{Z}^{(0)}$.

As in the proof of Proposition 3.2 we also show a different approach using (5) from Proposition 2.6,

$$\begin{aligned} &\mathbb{P}(B_{\ell,1} > n | \mathbf{A}_{0[n]} = \mathbf{a}_{[n]}, \mathbf{A}_{0[0]} = \ell) \\ &= \sum_{\mathbf{a}_{[0], \dots, \mathbf{a}_{[n-1]}} \prod_{n'=1}^n \left(\frac{P^{(n'-1), \ell, \mathbf{a}_{[n'-1]}}}{P^{(n'), \ell, \mathbf{a}_{[n']}} \left. \frac{\partial f_{\mathbf{a}_{[n']}}(\mathbf{s})}{\partial s_{\mathbf{a}_{[n'-1]}}} \right|_{\mathbf{s}=\mathbf{1}-P^{(n'-1), \ell}}} \right). \end{aligned}$$

For each $1 \leq n' \leq n - 1$ the sums

$$\tilde{c}_{n'} \equiv \tilde{c}_{n'}(\mathbf{a}_{[n']}) = \frac{1}{P^{(n', \ell), \mathbf{a}_{[n']}}} \sum_{\mathbf{a}_{[n'-1]} \geq 1} P^{(n'-1, \ell), \mathbf{a}_{[n'-1]}} \left. \frac{\partial f_{\mathbf{a}_{[n']}}(\mathbf{s})}{\partial s_{\mathbf{a}_{[n'-1]}}} \right|_{\mathbf{s}=\mathbf{1}-\mathbf{p}^{(n'-1, \ell)}} \tag{13}$$

are independent of the value of $\mathbf{a}_{[n']}$ in the linear fractional case, with

$$\tilde{c}_{n'} = \frac{1}{\tilde{U}_{n'}} = \frac{1}{1 + m - m \sum_{\ell' \geq 1} g_{\ell'} \tilde{h}_{\ell'}^{(n'-1)}},$$

and

$$\tilde{h}_{\ell'}^{(n'-1)} = h_{\ell'}^{(n'-1)} + \frac{1 - h_{\ell'}^{(n'-1)} - h_{\ell'}^{(n'-1)}}{1 + m^{(n'-1)} g_{\ell'}^{(n'-1)}}$$

so $\mathbb{P}(B_{\ell,1} > n | \mathbf{A}_{0[0]} = \ell) = \prod_{n'=1}^n \tilde{c}_{n'}$.

We can rewrite this formula in a similar way as before by noting that the first product term in (8) is equal to $1/(1 + mg_{\ell})$, and, using many arithmetic steps established by the relationship of parameters in (6), the rest of the terms for $n' > 1$ can be shown to be equal to

$$\frac{(1 + m^{(n'-1)})(1 + m^{(n'-1)} g_{\ell}^{(n'-1)})}{(1 + m^{(n'-1)})(1 + mg_{\ell} \mathbf{H}^{(n'-1)} \mathbf{e}_{\ell}) + m^{(n'-1)} g_{\ell}^{(n'-1)} (1 + m^{(n')})} = \frac{1 + m^{(n'-1)} g_{\ell}^{(n'-1)}}{1 + m^{(n')} g_{\ell}^{(n')}}.$$

hence

$$\mathbb{P}(B_{\ell,1} > n | \mathbf{A}_{0[0]} = \ell) = \frac{1}{1 + mg_{\ell}} \prod_{n'=2}^n \frac{1 + m^{(n'-1)} g_{\ell}^{(n'-1)}}{1 + m^{(n')} g_{\ell}^{(n')}} = \frac{1}{1 + m^{(n)} g_{\ell}^{(n)}}. \quad \square$$

Proof of Corollary 3.5. One approach is to use equivalence of offspring laws for different parents. Since types do not affect the reproduction law, the ancestral tree shape can be decoupled from the individual types. In other words, we can first construct the branching process using the single-type LG offspring distribution with parameters (h_0, m) , and subsequently assign types to all individuals independently according to probabilities \mathbf{g} . As the only factor affecting the coalescent times of the standing population is the offspring number of each individual, their law is the same as in the case of the associated single-type LF coalescent times.

According to Proposition 5.1 from [14] for the single-type LF case, the coalescent times have distribution (in their notation $a \mapsto h_0, b \mapsto m/(1+m)$ and offspring mean $m \mapsto (1+m)(1-h_0)$)

$$\mathbb{P}(A_1 > n) = \frac{m - h_0(1 + m)}{m(1 + m)^n(1 - h_0)^n - h_0(1 + m)},$$

if $(1 + m)(1 - h_0) \neq 1$, while if $(1 + m)(1 - h_0) = 1$

$$\mathbb{P}(A_1 > n) = \frac{1 - h_0}{1 - h_0 + nh_0}.$$

To see that this agrees with result (7) note $\mathbf{H} = (1 - h_0)\mathbf{1}^t \mathbf{g}, \mathbf{M} = \mathbf{H} + m\mathbf{H}\mathbf{1}^t \mathbf{g}$ implies

$$\begin{aligned} \mathbf{M} &= (1 - h_0)\mathbf{g} + m(1 - h_0)\mathbf{1}^t \mathbf{g}\mathbf{1}^t \mathbf{g} = (1 - h_0)(1 + m)\mathbf{1}^t \mathbf{g}, \\ \mathbf{M}^{n'} &= (1 - h_0)^{n'}(1 + m)^{n'} \mathbf{1}^t \mathbf{g}. \end{aligned}$$

$$\begin{aligned}
 m^{(n)} &= mg(\mathbf{I} + (1 - h_0)(1 + m)\mathbf{1}^t \mathbf{g} + \dots + (1 - h_0)^{n-1}(1 + m)^{n-1}\mathbf{1}^t \mathbf{g})\mathbf{1}^t \\
 &= m \sum_{n'=0}^{n-1} (1 - h_0)^{n'}(1 + m)^{n'} = m \frac{1 - (1 - h_0)^n(1 + m)^n}{1 - (1 - h_0)(1 + m)}, \\
 &\text{if } (1 - h_0)(1 + m) \neq 1
 \end{aligned}$$

while if $(1 - h_0)(1 + m) = 1$ then $\mathbf{M}^{n'} = \mathbf{M}$, $m^{(n)} = mn = nh_0/(1 - h_0)$. Using this in (7) the formula $\mathbb{P}(A_1 > n) = 1/(1 + m^{(n)})$ gives the same result as above.

From the result for A_1 we can obtain the law of $B_{\ell,1}$ using its original definition as the maximum of all coalescence times until the first next individual in the current population whose type is ℓ : $B_{\ell,1} := \max\{A_{i_{\ell,1}}, \dots, A_{i_{\ell,2}-1}\}$. The only reason why this calculation is simple is due to the decoupling of the branching tree and the individual types. Since, given the branching tree, all individuals are assigned types independently according to probabilities \mathbf{g} , the index $i_{\ell,2} := \min\{i' > i_{\ell,1} \equiv 1 : A_{i'[0]} = \ell\}$ is such that $i_{\ell,2} - 1$ is a random variable with a shifted Geometric distribution with parameter g_ℓ . Conditioning on the value of $i_{\ell,2} - 1$, and using the fact that $(A_i)_{i \geq 1}$ is an i.i.d. sequence, we get

$$\begin{aligned}
 \mathbb{P}(B_{\ell,1} \leq n) &= \mathbb{E}\left(\mathbb{P}(\max\{A_1, \dots, A_{i_{\ell,2}-1}\} \leq n \mid i_{\ell,2} - 1)\right) \\
 &= \sum_{i'-1=1}^{\infty} \mathbb{P}(A_1 \leq n)^{i'-1} (1 - g_\ell)^{i'-2} g_\ell = \frac{g_\ell \mathbb{P}(A_1 \leq n)}{1 - \mathbb{P}(A_1 \leq n)(1 - g_\ell)},
 \end{aligned}$$

and

$$\mathbb{P}(B_{\ell,1} > n) = 1 - \mathbb{P}(B_{\ell,1} \leq n) = \frac{1 - \mathbb{P}(A_1 \leq n)}{1 - \mathbb{P}(A_1 \leq n)(1 - g_\ell)}. \quad \square$$

4.3. Calculations for two-type LF branching process

Proof of Proposition 3.7. Formulae (6) imply (after much arithmetic using Maple) that for $\mathbf{x} \in \{\mathbf{a}, \mathbf{s}\}$

$$\begin{aligned}
 m^{(n)} &= m_{\mathbf{x}}^{(n)} = m \sum_{n'=0}^{n-1} h_1^{n'}(m + 1)^{n'} = \frac{m(h_1^n(1 + m)^n - 1)}{h_1(1 + m) - 1}, \\
 \mathbf{g}_{\mathbf{s}}^{(n)} &= \left(\left(g - \frac{1}{2}\right)G(2p - 1) + \frac{1}{2}, -\left(g - \frac{1}{2}\right)G(2p - 1) + \frac{1}{2} \right), \\
 \mathbf{g}_{\mathbf{a}}^{(n)} &= (gG(p), -gG(p) + 1),
 \end{aligned}$$

where G is a rather complicated polynomial

$$G(x) = \frac{h_1^{n-1}(h_1(1 + m) - 1)}{h_1^n(1 + m)^n - 1} \left[\sum_{n'=0}^{n-2} \left(\frac{h_1 m + 1}{h_1^{n-n'-1}} + \sum_{i=1}^{n-n'-2} (1 + m)^i h_1^{i-n+n'+2} \right) x^{n'} + x^{n-1} \right],$$

which satisfies $G(0) = 0$, $G(1) = 1$. From (7) we have the same formulae for the distribution of coalescent times in the two cases for $\mathbf{x} \in \{\mathbf{a}, \mathbf{s}\}$:

$$\mathbb{P}_{\mathbf{x}}(A_1 > n) = (1 + m^{(n)})^{-1},$$

and from (8) we get the following formulae for same-type coalescent times in the two cases:

$$\mathbb{P}_{\mathbf{x}}(B_{\ell,i} > n \mid A_{0[0]} = \ell) = (1 + m^{(n)} g_{\mathbf{x}\ell}^{(n)})^{-1}, \quad \text{for } \ell \in \{\mathbf{1}, \mathbf{2}\}$$

where the two coordinates of vectors $\mathbf{g}_{\mathbf{x}}^{(n)} = (g_{\mathbf{x}1}^{(n)}, g_{\mathbf{x}2}^{(n)})$ for $\mathbf{x} \in \{\mathbf{a}, \mathbf{s}\}$ are given above.

We next prove that for $g \leq 1/2$ we have

$$1 + m^{(n)} g_{a1}^{(n)} \leq 1 + m^{(n)} g_{s1}^{(n)} \Leftrightarrow g_{a1}^{(n)} \leq g_{s1}^{(n)},$$

$$1 + m^{(n)} g_{s2}^{(n)} \leq 1 + m^{(n)} g_{a2}^{(n)} \Leftrightarrow g_{s2}^{(n)} \leq g_{a2}^{(n)}.$$

Both of these inequalities are equivalent to

$$gG(p) + \left(\frac{1}{2} - g\right)G(2p - 1) - \frac{1}{2} \leq 0,$$

which holds since all multiplying coefficients of the polynomial $G(x)$ are nonnegative, so G is increasing and both $G(p)$, $G(2p - 1) \leq G(1) = 1$.

For the last comparison we need to show that for $g \leq 1/2 \leq p$

$$1 + m^{(n)} g_{s1}^{(n)} \leq 1 + m^{(n)} g_{s2}^{(n)} \Leftrightarrow g_{s1}^{(n)} \leq g_{s2}^{(n)},$$

which is equivalent to

$$2\left(\frac{1}{2} - g\right)G(2p - 1) \geq 0,$$

and holds as long as $p \geq 1/2$ so that the polynomial $G(x)$ is evaluated on $x \geq 0$. \square

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