The Evolving Moran Genealogy

Johannes Wirtz*, Thomas Wiehe

Abstract
We study the evolution of the population genealogy in the classic neutral Moran Model of finite size and in discrete time. The stochastic transformations that shape a Moran population can be realized directly on its genealogy and give rise to a process with a state space consisting of the finite set of Yule trees of a certain size. We derive a number of properties of this process, and show that they are in agreement with existing results on the infinite-population limit of the Moran Model. Most importantly, this process admits time reversal, which gives rise to another tree-valued Markov Chain and allows for a thorough investigation of the Most Recent Common Ancestor process.

Keywords: Moran Model, Yule Model, Kingman Coalescent, Time Reversal of Markov Chains

1. Introduction

The Moran Model [1] is a fundamental population model of evolutionary biology. It has been used to study the evolution of a population of fixed size containing individuals of differing allelic types, subject to neutral or selective drift. In the large-population limit, its dual process describing population and sample genealogies is Kingman’s Coalescent [2]. A very intuitive graphical representation of the infinite-population Moran Model is the Lookdown-Construction [3], which has also proven useful in the analysis of genealogical traits of a Moran population; for instance, it can be used to study the underlying process of Most Recent Common Ancestors (MRCA’s), i.e., the speed of evolution, or loss of information on the past [4]. Genealogies of finite samples from such an infinite population can be represented in a discrete setting making use of the Yule Process [5]. This process generates random trees in the graph-theoretical sense and is often interpreted

*Corresponding author

Email addresses: wirtzj0@uni-koeln.de (Johannes Wirtz), twiehe@uni-koeln.de (Thomas Wiehe)
as a model of speciation. The distribution on trees of a given size that it induces, however, is equivalent to Kingman’s Coalescent of finite size with respect to topology [6].

In this work, we observe the evolution of the genealogy of a finite Moran population. We call this process the Evolving Moran Genealogy (EMG). The state space of the EMG can also be represented by the Yule Process of finite iterations. We provide a detailed description of the EMG as a Markov Chain and obtain some finite-population analoga of facts that have been established about the large-population limit. In order to do this, we revisit the Yule Process and the tree structures it generates in detail.

Furthermore, in the discrete setting a time-reversed process of the EMG can be defined (later denoted by $EMG^\flat$), which is in some sense of lower complexity and offers interesting possibilities, such as investigating the "age structure" of coalescent events and the distribution of MRCA jumps during neutral fixations. We also interpret these results in the large-population limit.

2. Material

2.1. Trees generated under the Yule Process

Many variations of the original Yule Process, or Yule Model, as defined by G. U. Yule [7], have been considered throughout the literature of mathematical population genetics. One very basic, discrete version of the process is described in procedure 1 (see also [5]):

Procedure 1: Yule Process

1: Start with a tree consisting of one single leaf node $ι$.
2: while Tree has less than $n$ leaves do
3: Choose one leaf uniformly, label it by the current total number of leaves, turn it into an internal node and append two new leaves to it.
4: end while
5: return Tree with $n$ leaves

Let the output of such a procedure be denoted by $T$. $T$ can be interpreted as a binary tree (connected acyclic graph; see Figure 1) with labeled internal nodes. We assume that the appending of leafs is graphically carried out in downward direction and in such a way that $T$ is a plane graph. $n \in \mathbb{N}$ is the number of iterations of the procedure plus one and also referred to as the size of $T$. After each iteration, the object generated by the process is a tree; we use $ι = T^{(1)}, \ldots , T^{(n)} = T$ to denote the trees at intermediate stages, and
Figure 1: Some possible iterations of the Yule tree-generating procedure

let $\sigma_T(i)$ denote the leaf $\iota$ of $T^{(i)}$ chosen in the $i$'th Yule iteration.

Any such Yule tree $T$ of size $n$ has $n$ leaves (nodes of degree 0 or 1) $\iota_1, \ldots, \iota_n$, and $n - 1$ internal nodes $\nu_1, \ldots, \nu_{n-1}$, which are nodes of degree 2 or 3. We identify the index $k$ of $\nu_k$ with the label of $\nu_k$. If $n \geq 2$, the internal node $\nu_1$ is of degree 2 and is called root of $T$, while all other internal nodes are of degree 3. $T$ furthermore has exactly $2n - 2$ edges (branches).

For any leaf $\iota \in \{\iota_1, \ldots, \iota_n\}$, when moving downward on the unique path from $\nu_1$ toward $\iota$, the sequence of labels of internal nodes on this path is increasing; hence such trees are also called binary increasing trees. Suppose further that all $n$ leaves of $T$ are drawn on the same vertical "height" 0, and all internal nodes $\nu_k$ on height $n - k$. Then, the leaves $\iota_1, \ldots, \iota_n$ are implicitly ordered horizontally, and $T$ divides the plane into $n$ layers $l_1, \ldots, l_n$, where layer $l_k, k = 2, \ldots, n - 1$ is vertically restricted by the heights of $\nu_{k-1}$ and $\nu_k$. Layer 1 extends upwards to infinity from the root’s height, and layer $n$ from height 1 to 0. If $k \geq 2$, the $k$th layer of $T$ is the layer which is crossed by precisely $k$ branches. This notion can be extend to layer 1 by assuming that it contains an imaginary branch extending from the root upwards. We may think of a branch $\beta$ as a composite of branch segments, where a segment only extends over one layer. Then $T$ contains $1 + 2 + \cdots + n = \frac{n(n+1)}{2}$ such segments (counting the imaginary branch as a single segment). We denote them by $b_1, \ldots, b_{\frac{n(n+1)}{2}}$ from top to bottom and left to right and let the function $l(b)$ denote the layer over which a segment $b$ extends (see Figure 2).

After iteration $0 \leq k \leq n - 2$, there exist $k + 1$ leaves and therefore $k + 1$ possibilities in the next iteration. It follows that there are $(n - 1)!$ possibilities of generating a tree $T$ of size $n$, each having probability $\frac{1}{(n-1)!}$. Furthermore, each possibility generates a unique binary increasing tree $T$. It can be shown that this correspondence is bijective; the set $\mathcal{T}_n$ of $n$-sized
Yule trees is therefore of size $|T_n| = (n-1)!$ and the probability of obtaining $T \in \mathcal{T}_n$ from the Yule Process is $\Pr(T) = \frac{1}{(n-1)!}$.

Let $S$ denote a set of leaves of some Yule tree $T$ of size $n$. Connecting all leaves of $S$ according to the branching pattern of $T$ generates another tree $T_S$ on $|S|$ leaves, where $|S| - 1$ internal nodes of $T$ are preserved. If we label the internal nodes of $T_S$ by $1, \ldots, |S| - 1$ such that their relations with respect to height are preserved from $T$, $T_S \in \mathcal{T}_{|S|}$. Each leaf $\iota'$ in $T_S$ equals some leaf $\iota \in \{\iota_1, \ldots, \iota_n\}$ of $T$, and the horizontal order of leaves in $T_S$ is in accordance with that in $T$. Similarly, each internal node $\nu'_k$ in $T_S$ is representative of some internal node $\nu_k$ in $T$; the label $k$ of $\nu'$ in $T_S$ is less than or equal to the label $k'$ of $\nu$ in $T$.

**Definition 1.** For any $n$-sized Yule Tree $T$ and $\emptyset \neq S \subseteq \{\iota_1, \ldots, \iota_n\}$:

- The object $T_S$ is called the ($S$-)induced subtree of $T$.
- For an internal node $\nu' \in \{\nu'_1, \ldots, \nu'_{|S|-1}\}$ of $T_S$, let $\phi(\nu')$ denote the internal node of $T$ that is represented by $\nu'$ in $T_S$.
- For all $j = 1, \ldots, |S| - 1$, let $\tau(j) \in \{1, \ldots, n-1\}$ denote the label of $\phi(\nu'_j)$ in $T$.

See Figure 3 for an example. If $S = \{\iota\}$ for some single leaf $\iota$ of $T$, $T_S$ equals the tree of size 1 consisting just of $\iota$, and $T_{\{\iota_1, \ldots, \iota_n\}} = T$.

In the following Lemma, we state that Yule trees exhibit a form of self-similarity with respect to induced subtrees.
Figure 3: A Yule tree of size 5 and the induced subtree of leaves $\iota_1, \iota_3, \iota_5$.

**Lemma 1** (Sample-Subtree Invariance of Yule trees). Let $T$ be a random tree of size $n$ generated by the Yule Process, and $S \subseteq \{\iota_1, \ldots, \iota_n\}$, $|S| = k$. Then

$$\forall \tilde{T} \in \mathcal{T}_k : \Pr(T_S = \tilde{T}) = \frac{1}{(k-1)!}$$

**Proof.** We show that we can treat $T_S$ as a tree generated by the Yule Process. Since this is obviously true for $|S| = 1$ (or $S = 2$), we apply induction on $k$.

Let $S = \{\iota'_1, \ldots, \iota'_k\}$. Tracing back the iterations $l = n, \ldots, \tau(|S| - 1)$ of the process generating $T$, for each $\iota'_j \in S$ there is a unique leaf $\iota^{(l)}_j$ of $T^{(l)}$ such that either $\iota'_j = \iota^{(l)}_j$ or $\iota'_j$ is appended below $\iota^{(l)}_j$ by one or more Yule iterations. In $T^{(\tau(|S| - 1) - 1)}$, a leaf $\iota^* = \sigma_T(\tau(|S| - 1))$ is turned into $\phi(\nu_{|S|-1})$ in iteration $\tau(|S| - 1)$ and two of the leaves $\iota_m^{(\tau(|S| - 1))}, \iota_{m+1}^{(\tau(|S| - 1))}$ that are the correspondents of $\iota'_m, \iota'_{m+1}$ in $T^{(\tau(|S| - 1))}$ are appended below.

Consider the set $S' = \{\iota'_1^{(\tau(|S| - 1))}, \ldots, \iota'_m^{(\tau(|S| - 1))}, \iota^*, \iota_{m+1}^{(\tau(|S| - 1))}, \ldots, \iota'_k^{(\tau(|S| - 1))}\}$. The induced subtree $T_S^{(\tau(|S| - 1) - 1)}$ is then a random Yule tree of size $k - 1$ by induction hypothesis.

Because of the established correspondence of internal nodes between $T_S$ and $T_S^{(\tau(|S| - 1) - 1)}$, $T_S$ is created out of $T_S^{(\tau(|S| - 1) - 1)}$ by turning $\iota^*$ into an internal node and appending two new leaves. If $\iota^*$ is chosen uniformly from $S'$, then
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this simply corresponds to a \( k - 1 \)'th Yule iteration. We verify this:

\[
\Pr(\sigma_T(S)' = \iota^*) = \Pr(\sigma_T(\tau(|S| - 1)) = \iota^*|\sigma_T(\tau(|S| - 1)) \in S')
\]
\[
= \frac{1/\tau(|S| - 1)}{|S'|/\tau(|S| - 1)}
\]
\[
= \frac{1}{|S'|}
\]

We conclude that the process generating \( T_S \) is a Yule Process of \(|S| - 1 = k - 1\) iterations.

Suppose \( T \in \mathcal{T}_n \) is a Yule tree of size \( n \). Instead of applying an iteration of the Yule process, \( T \) can also be transformed into a tree of size \( n + 1 \) by random grafting\(^2\) a new branch leading to a leaf into \( T \):

Procedure 2: Random Grafting Operation on an \( n \)-sized \( T \)

1: Choose a branch segment \( b \) uniformly from all \( \frac{n(n+1)}{2} \) possible segments and an "orientation" \( \chi \in \{\text{left, right}\} \) uniformly;
2: Split all branch segments \( b', l(b') = l(b) \) into two separate branch segments;
3: Between the two pieces \( b^{(1)}, b^{(2)} \) resulting from splitting \( b \), place a new internal node \( \nu \) with label \( l(b) \).
4: Increase the labels of all internal nodes in layers \( k > l(b) \) by one;
5: At \( \nu \), append a new branch \( \beta \) consisting of \( n - l(b) + 1 \) segments and ending in a new leaf \( \iota \), to the left or right depending on \( \chi \);
6: \textbf{return} Tree \( \hat{T} \) with \( n + 1 \) leaves

Note that \( \chi \) determines the position of \( \iota \) in \( \hat{T} \). A possible realization of procedure\(^2\) is depicted in Figure 4.

Applying procedure\(^2\) we obtain an object \( \hat{T} \in \mathcal{T}_{n+1} \). We write \( T \uparrow \hat{T} \) if \( \hat{T} \) was constructed from \( T \) by random grafting. In total, there are \( k(k + 1) \) possibilities \((b, \chi)\) of performing a grafting in \( T \) of equal probability, and unique with respect to which leaf and internal node of \( \hat{T} \) they generate. However, different grafting operations on \( T \) may generate the same object \( \hat{T} \).

The relation between grafting operation and the original Yule Process is described by the following Lemma:

\textbf{Lemma 2} (Piecewise Recovery by Grafting). \textit{Let \( T \) be a random tree of size \( n \), \( S = \{\iota_1', \ldots, \iota_{k+1}'\} \subseteq \{\iota_1, \ldots, \iota_n\} \) a set of leaves chosen uniformly without replacement, and \( \iota' \in S \) chosen uniformly. Then}

\[
\forall T' \in \mathcal{T}_k, T'' \in \mathcal{T}_{k+1} : \Pr(T_S = T''|T_S \setminus \iota' = T') = \Pr(T' \uparrow T'') \quad (2)
\]
Proof. Let $l \in \mathbb{N}_0$ denote the number of graftings that can be performed on $T'$ to generate $T''$, thus $\Pr(T' \uparrow T'') = \frac{l}{k(k+1)}$. On the other hand,

$$\Pr(T_S = T''|T_{S\setminus \nu'} = T') = \frac{\Pr(T_S = T'', T_{S\setminus \nu'} = T')}{\Pr(T_{S\setminus \nu'} = T')}$$

and by Lemma [1], $\Pr(T_{S\setminus \nu'} = T') = 1/(k-1)!$. Let $m \in \mathbb{N}_0$ denote the number of leaves $\nu' \in S$ such that $T_{S\setminus \nu'} = T'$. Since each tree $\tilde{T} \in T_{k+1}$ is equally likely to be the induced subtree $T_S$ and $\nu' \in S$ is chosen uniformly, we have

$$\Pr(T_S = T'', T_{S\setminus \nu'} = T') = \frac{m}{k!(k+1)}$$

and thus $\Pr(T_S = T''|T_{S\setminus \nu'} = T') = \frac{m}{k(k+1)}$.

Let $\nu' \in S$ such that $T_{S\setminus \nu'} = T'$, and $\nu'$ the internal node $\nu'$ is appended to. There exists exactly one tuple $(b, \chi)$ such that, performing the associated grafting operation in $T'$, we obtain $T''$, the leaf generated by the operation occupies the position of $\nu'$ in $T''$, and the internal node generated by it carries the label of $\nu'$. Conversely, each tuple $(b, \chi)$ such that the associated grafting operation on $T'$ yields $T''$ generates a unique leaf $\nu^*$ with respect to horizontal position and an internal node $\nu^*$. Then, there exists a unique $\nu' \in S$ that occupies the position of $\nu^*$ in $T_S$, and since $T'' = T_S$, the induced subtree $T_{S\setminus \nu'}$ of $T_S$ equals $T'$. Therefore, $m = l$ holds, which ends the proof. \qed
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We immediately conclude

Corollary 1. The distributions of \( n \)-sized Yule trees generated under the Yule Process and generated by random grafting are equal, therefore

\[
\Pr(T|T \text{ generated by random grafting}) = \frac{1}{(n-1)!}
\]

Proof. This follows by induction on \( n \), making use of Lemma 2.

2.2. The Genealogical Process of a Moran Population

The Moran Process of finite size \( n \in \mathbb{N} \) in discrete time is a Markov Chain whose state space consists of ordered multisets \( \mathcal{P}_i = \{x_1, \ldots, x_n\} \) ("populations") of objects ("individuals"), where \( i \in \mathbb{N}_0 \) represents time, and \( \mathcal{P}_0 \) is some initial set. The transition between time steps is determined by the following two stochastic components:

Procedure 3: Iteration of the Moran Process

1: choose one element \( x_k \) of \( \mathcal{P}_i \) with uniform probability;
2: choose another element \( x_l \) of \( \mathcal{P}_i \) with uniform probability;
3: remove \( x_k \) from \( \mathcal{P} \) and replace it by a copy of \( x_k \).

Definition 2. The neutral Moran Process is denoted by \( M = (\mathcal{P}_i)_{i \in \mathbb{N}} \), where \( \mathcal{P}_{i+1} \) is obtained by the application of procedure 3 on \( \mathcal{P}_i \).

One iteration of \( M \) is often interpreted as one individual of \( \mathcal{P}_i \) producing offspring, and one dying. Note that \( k = l \) is not excluded, therefore, there are \( n^2 \) possible transitions of equal probability \( \frac{1}{n^2} \). Several modifications of this process exist \[8\]; for instance, the case of an initial population consisting of two different "types" of individuals \( a, A \) is known as the two-allele Moran Process. Other versions allow mutations between types or let the probabilities of producing offspring and/or dying depend on the type of individuals to model natural selection \[9\]. Here, we only consider the neutral Moran Process with uniform transition probabilities and without mutation. With probability 1, there is a finite time \( i^* \) at which \( M \) will enter a state in which the population consists only of the copies (descendants) of some \( x_k \in \mathcal{P}_0 \), while all other \( x_l \in \mathcal{P}_0, l \neq k \), and their copies have been removed from the population. The individual \( x_k \), or one of its descendants, is thus the Most Recent Common Ancestor (MRCA) dating back to at most time 0, and looking backwards in time, there exists a branching pattern describing how the current population of \( x_k \)-copies has been created, in the form of a binary tree \( T \) with branch lengths given implicitly by the number of time
Figure 5: Iterations of a Moran Process, where the order is maintained according to Procedure 4.

Steps between splits. Considering $n \to \infty$ and rescaling time by $2/n^2$, the (infinitely large) genealogy $T$ after the first time at which there exists a MRCA is a realization of Kingman’s Coalescent [10] and all sample genealogies are Kingman Coalescent trees of sample size $n'$, $n' \in \mathbb{N}$. In this work, we focus on genealogies of finite Moran Processes. We assume that copy and original are indistinguishable after a duplication ($M$ is memoryless), and the copy is placed to the side of the original (instead of replacing the killed individual), and other individuals are shifted to the left or right depending on whether $l < k$ or $l > k$. This is achieved by following procedure 4. Importantly, $T$ can then be treated as a plane graph without having to re-order individuals (see Figure 5).

Procedure 4: Planar order maintenance in $M$

1: if $l < k$ then
2: Lower the position of individuals $x_{l+1}, \ldots, x_{k-1}$ by one;
3: Assign the possible positions $k-1, k$ to individual $x_k$ and its copy with probability $1/2$; \quad $\triangleright$ to ensure memorylessness
4: else if $l > k$ then
5: Increase the position of individuals $x_{k+1}, \ldots, x_{l-1}$ by one;
6: Assign the possible positions $k, k+1$ to individual $x_k$ and its copy with probability $1/2$; \quad $\triangleright$ to ensure memorylessness
7: else
8: No change.
9: end if

Since the time $i^*$ is almost surely finite, we assume in what follows that at $i = 0$ there already exists a genealogy $T_0$. We disregard the branch
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lengths of $T_0$ and instead assume that internal nodes of $T_0$ are labeled by integers $1, \ldots, n - 1$ respecting the order of the past split events which they represent, and obtain an $n$-sized Yule tree, where the leaves $\iota_1, \ldots, \iota_n$ represent the individuals $x_1, \ldots, x_n$ of the population. By [6], $T_0$ can be treated as the result of a Yule process of $n - 1$ iterations. $M$ can then be emulated by observing the genealogy $T_i, i \geq 0$ directly, where $T_i$ is modified according to procedure [5].

Procedure 5: Evolving Moran Genealogy given $T_i$

1: if $k = l$ then
2: $T_{i+1} \leftarrow T_i$
3: else
4: Remove the leaf of the killed individual $x_l$ alongside the branch connecting it to the remainder of $T_i$, and the internal node $\nu_j$ at the position in $T_i$ that branch is attached at;
5: Merge the two branch segments $b, b'$ connected to $\nu_j$ into one;
6: Merge all pairs of branch segments $b, b'$ in layers $j, j + 1$ belonging to the same branch into single branch segments;
7: $> 4-6$ "remove" layer $j + 1$
8: Decrease the labels of $\nu_j', j' > j$ by one in $T_i$;
9: Turn the leaf representing the duplicated individual $x_k$ in $T_i$ into an internal node with two new leaves appended to it and label it by $n - 1$; $T_{i+1} \rightarrow T_i$;
10: end if
11: return $T_{i+1}$

Let $\Phi_{k,l}(T_i)$ denote the output of procedure [5] given $k, l$. Then, we define:

Definition 3.

- The process $(T_i)_{i \in \mathbb{N}}$ with $T_{i+1} = \Phi_{k,l}(T_i)$ for uniform $k, l$ and uniform $T_0$ is called Evolving Moran Genealogy, for short EMG.
- We will identify a leaf $i$ of any $T_i, i \geq 0$ with the individual $x$ representing it and write $x \in T_i$ if an individual $x$ is part of $T_i$.
- For $T, T' \in \mathcal{T}_n$, we define the notation
  $$T \rightarrow T' \iff \exists k, l \in \{1, \ldots, n\} : \Phi_{k,l}(T) = T'$$

The EMG (see Figure [6]) is a Markov Chain on the set $\mathcal{T}_n$. Its transition matrix $E$ has nonzero diagonal entries, since $l = k$ entails $T_{i+1} = T_i$. Secondly, it is recurrent, because at most $n - 1$ transition steps of the above
Figure 6: Two steps in an EMG of size 4. Each step, one individual is killed ("X") and one duplicated ("Λ").

form are needed to transform $T_i$ into some arbitrary $T' \in T_n$. Aperiodicity of the EMG also follows, as $T_{i+1} = T_i$ can occur arbitrarily often.

As a consequence, there exists a stationary distribution $P^*$ of the EMG on $T_n$. Since all Yule trees are equally likely under the coalescent, it follows that $P^*$ is the uniform distribution, i.e. $P^*(T) = \frac{1}{(n-1)!}$ for all $T \in T_n$. We refer to [6] and [11] for details.

The relation $T \rightarrow T'$, indicating that $T$ can be transformed into $T'$ by some duplication/remove combination in $M$, can be used to describe the entries of $E$. Importantly,

$$T = T' \Rightarrow T \rightarrow T'; \quad T \rightarrow T' \nRightarrow T' \rightarrow T$$

Then the $T,T'$-entry of $E$ can be denoted in the following way:

$$\Pr(T_{i+1} = T'|T_i = T) = \begin{cases} 0 & T \nRightarrow T' \\ \frac{1}{n^2} & \text{otherwise} \end{cases}$$

In particular, the diagonal entries of $E$ are nonzero and depend on $T$. Suppose $n = 2^k$ for some $k \geq 2$, and consider the caterpillar $C \in T_n$ obtained under the Yule process by always choosing the leftmost individual to split, and any complete binary search tree $B \in T_n$, i.e. a tree characterized by the fact that there is an equal number of leaves on both subtrees below each internal node. Then $\Pr(T_{i+1} = C'|T_i = C) = \frac{2n}{n^2}$, whereas $\Pr(T_{i+1} = B'|T_i = B) = \frac{n+2}{n^2}$.

3. Results

3.1. The Process of Tree Balance

Since a Yule tree $T$ in the EMG is plane and individuals ordered from left to right, we may consider the left and right subtrees $T^l, T^r$ below the root node $\nu_1$. Essentially, $T^l$ can be thought of as the induced subtree of all leaves on
the left side below $\nu_1$ (the same holds for $T^r$). Suppose we are interested in the dynamics of the number of leaves on the left, i.e. $|T_l|$. 

**Definition 4.** The process $TB := (|T_i^l|)_{i \in \mathbb{N}}$ is called Tree Balance Process of the Evolving Moran genealogy. 

The choice between observing left and right subtree size is arbitrary, since always $|T^r| = n - |T^l|$. Closely related to the process $TB$ is the $\Omega_1$-statistic observed over time, where $\Omega_1(T_i) := \min(|T_i^l|, |T_i^r|)$, and one observes $(\Omega_1)_{i \in \mathbb{N}}$. There is little difference between $TB$ and the process of $\Omega_1$, as paths of $TB$ are essentially mirrored at $n/2$ when considering $\Omega_1$. Determining the dynamics of $TB$ thus suffices to also obtain those of $\Omega_1$.

**Proposition 1.** The transition probabilities of $TB$ are as follows:

If $2 \leq |T_i^l| \leq n - 2$,

$$
\Pr(|T_{i+1}^l| = \omega \mid |T_i^l|) = \begin{cases} 
\frac{|T_i^l|(n-|T_i^l|)}{n^2} & \omega = |T_i^l| + 1 \\
\frac{|T_i^l|^2 + (n-|T_i^l|)^2}{n^2} & \omega = |T_i^l| \\
\frac{|T_i^l|(n-|T_i^l|)}{n^2} & \omega = |T_i^l| - 1 
\end{cases}
$$

If $|T_i^l| = 1$,

$$
\Pr(|T_{i+1}^l| = \omega \mid |T_i^l| = 1) = \begin{cases} 
\frac{1}{n} & \omega = 2 \\
\frac{1}{n^2} & \omega = 1 \\
\frac{1}{n^2} & \text{otherwise}
\end{cases}
$$

And if $|T_i^l| = n - 1$,

$$
\Pr(|T_{i+1}^l| = \omega \mid |T_i^l| = n - 1) = \begin{cases} 
\frac{1}{n} & \omega = n - 2 \\
\frac{(n-1)^2 + 2}{n^2} & \omega = n - 1 \\
\frac{1}{n^2} & \text{otherwise}
\end{cases}
$$

**Proof.** Suppose $2 \leq |T_i^l| \leq n - 2$. $|T_{i+1}^l| = |T_i^l| - 1$ is the case if one individual on the left side is removed and one on the right is duplicated. This happens with probability $\frac{|T_i^l|(n-|T_i^l|)}{n^2}$. We obtain the same probability for the case $|T_{i+1}^l| = |T_i^l| + 1$. Finally, we have $|T_{i+1}^l| = |T_i^l|$ if removal and duplication take place on the same side. The probability of this is $\frac{|T_i^l|^2 + (n-|T_i^l|)^2}{n^2}$. The only difference in the cases $|T_i^l| = 1, n - 1$ is that one has to include the
possibility of a complete removal of $T_l^i$ in the first and $T_r^i$ in the latter case. If this happens, $|T_{i+1}^l|$ and $|T_{i+1}^r|$ are independent of $|T_i^l|$ and $|T_i^r|$. In fact, $|T_{i+1}^l|$ then assumes any value $1, \ldots, n - 1$ with uniform probability $\frac{1}{n^2}$. Therefore, considering $|T_i^l| = 1$, the total probability $\Pr(|T_{i+1}^l| = 2 | |T_i^l| = 1)$ is the sum of the probability that the individual on the left is duplicated and one on the right is removed, which amounts to $\frac{1}{n^2}$, and the probability that it is removed and $|T_{i+1}^l| = 2$ by chance, which happens with probability $\frac{n-1}{n^2} = \frac{1}{n^2}$. This sum equals $\frac{1}{n}$.

For $\Pr(|T_{i+1}^l| = 1 | |T_i^l| = 1)$ and $\Pr(|T_{i+1}^l| = \omega > 2 | |T_i^l| = 1)$ the calculation is similar, and of course the case $|T_i^l| = n - 1$ can be treated analogously.

We may refer to the phases between complete removals of $T_l^i$ or $T_r^i$ as episodes of the process $TB$. We notice that the transition probabilities within an episode are identical to those in a two-allele Moran Model. Thus, in the large-population limit, tree balance can be thought of as a Wright-Fisher Diffusion. Also, if $n$ is large and $|T_i^l| n$ is either close to 0 or 1 (the genealogy is ‘unbalanced’), the strength of diffusion is weakest. Consequently, if the Evolving Moran Genealogy enters an unbalanced state, genealogies in the following generations are expected to be unbalanced as well.

At last, we note that the complete removals of $T_l^i$ or $T_r^i$, i.e. starting and ending times of episodes in $TB$, are precisely the times of MRCA jumps in the EMG, to be discussed in section 3.3.

3.2. Time Reversal of the EMG
We consider a second process on the set $\mathcal{T}_n$ of Yule trees of size $n$. Let $T \in \mathcal{T}_n$ and perform a Merge-Regraft operation:

| Procedure 6: Merge-Regraft on given $T$ |
|------------------------------------------|
| 1: Choose one branch segment $b$ of $T$ from the set $\{b_1, \ldots, b_{\frac{n(n+1)}{2}}\}$ with probability $\Pr(b = b_k) = \begin{cases} \frac{1}{n^2} & b_k$ ends in a leaf \\ \frac{2}{n^2} & otherwise \end{cases}$ and $\chi$ from $\{\text{left, right}\}$ with equal probability; |
| 2: if $b$ ends in a leaf then |
| 3: $T' \leftarrow T$ |
| 4: else |
| 5: Remove the $n$-th layer of $T$; remove $\nu_{n-1}$; place leafs at the tips of the branch segments that extend across layer $n - 1$; |
| 6: $\triangleright$ the position of $\nu_{n-1}$ is then occupied by some leaf |

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7: Regraft a new leaf at branch $b$ with orientation $\chi$ in $T$ according to Procedure 2 (skipping step 1);
8: $T' \leftarrow T$
9: end if
10: return $T'$

One may imagine that in step 5 all leafs are moved up by one layer, such that two of them must "merge". Let the result of this operation be denoted by $\Phi_{b,\chi}'(T)$. $\Phi_{b,\chi}'(T)$ is itself an object of the set $T_n$. The function $\Phi'$ can be thought of as a combinatorial inversion of $\Phi$: The split event facilitated by $\Phi$ is revoked by $\Phi'$, and the leaf that is removed under $\Phi$ can be recovered ("revived") by $\Phi'$ by regrafting; in fact, we have $T \rightarrow T' \iff \exists (b, \chi) : \Phi_{b,\chi}'(T') = T$.

We consider the process $R := (\tilde{T}_i)_{i \in \mathbb{N}}$, where $\tilde{T}_0$ is uniformly chosen and, given $\tilde{T}_i$, $\tilde{T}_{i+1}$ is generated by the mechanism described above, i.e. $\tilde{T}_{i+1} = \Phi_{b,\chi}'(\tilde{T}_i)$ for some random choice of $b$ and $\chi$. (See Figure 7). In what follows, we will show that this process represents a time-reversal of the EMG (where the term time-reversal is used in the sense of e.g. [14]).

**Lemma 3.** For all $T, T' \in T_n$:

$$\Pr_{\text{EMG}}(T_{j+1} = T' | T_j = T) = \Pr_R(\tilde{T}_{i+1} = T | \tilde{T}_i = T')$$

with $\Pr_{\text{EMG}}$ denoting the transition probability of the EMG-process, and $\Pr_R$ that of the process $R$.

**Proof.** Recall that $\Phi$ was dependent on the choice of $k, l$, which were both chosen uniformly. The probability of $k = l$ in one step of the EMG, which for all $T \in T_n$ entails $\Phi_{k,k}(T) = T$, is $\frac{1}{n}$. The probability that the branch segment $b$ chosen in a transition of the process $R$ is inside layer $n$, which always leads to $\Phi_{b,\chi}'(\tilde{T}) = \tilde{T}$, is also $\frac{1}{n}$ in total for any $T$.

We define for arbitrary $T, T' \in T_n, T \rightarrow T'$:

$$S_1 := \{(k, l) \in \{1, \ldots, n\}^2 : \Phi_{k,l}(T) = T', k \neq l\}$$

$$S_2 := \{(b, \chi) \in \{b_1, \ldots, b_{n(n-1)}\} \times \{\text{left}, \text{right}\} : \Phi_{b,\chi}'(T') = T\}$$

If we can show that $|S_1| = |S_2|$, we are done. Let $(k, l) \in S_1$. Let $\nu$ denote the internal node deleted by $\Phi_{k,l}(T)$. Choosing the regrafting site $b$ as the branch segment generated by merging the two segments connected to $\nu$ (compare step 5 in procedure [5]), and $\chi$ according to whether the branch of $x_i$ extends
to the left or right in $T$, we obtain a unique $(b, \chi) \in S_2$, which yields a mapping $\mu : S_1 \to S_2$. Since by definition of the Yule process there cannot be two or more tuples $k, l$ and $k', l$ with $k \neq k'$ such that $\Phi_{k,l}(T) = \Phi_{k',l}(T)$, $\mu$ is injective.

On the other hand, for any $(b, \chi) \in S_2$ such that $\Phi_{b,\chi}(T') = T$, choosing $l$ such that $x_l$ is the leaf regrafted in $T'$ by $\Phi_{b,\chi}(T')$ and $k$ such that $x_k$ is the leaf replacing the highest-labeled internal node in $T'$ by $\Phi_{b,\chi}(T')$ (see step 5 of procedure [5]), we obtain $(k, l) \in S_1$ such that $\mu((k, l)) = (b, \chi)$. Therefore, $\mu$ is a bijection and both sets are equally large.

\[\square\]

**Corollary 2.** The process $R$ represents the time-reversed process of the EMG.

**Proof.** The existence of a time-reversed process $R(EMG)$ on $T_n$ is provided by the fact that it is a recurrent Markov Chain with nonzero stationary distribution. The transition probabilities of this process are

\[
Pr_{R(EMG)}(T_{j+1} = T'|T_j = T) = Pr_{EMG}(T_i = T'|T_{i+1} = T) = \frac{Pr_{EMG}(T_i = T')Pr_{EMG}(T_{i+1} = T)}{Pr_{EMG}(T_i = T')Pr_{EMG}(T_{i+1} = T)}
\]

Since the stationary distribution of the EMG is the uniform distribution, we have $Pr_{EMG}(T_i = T') = Pr_{EMG}(T_{i+1} = T)$. Therefore,

\[
Pr_{R(EMG)}(T_{j+1} = T'|T_j = T) = Pr_{EMG}(T_{i+1} = T|T_i = T')
\]

and these transition probabilities are exactly the ones provided by the process $R$ (compare equation (3)). \[\square\]

**Definition 5.** We call the process $R$ the Evolving Moran Genealogy backwards in time, for short EMG$^\flat$. [15]

We end this section with the remark that the EMG$^\flat$ resembles the Aldous Chain on cladograms [11], of which also an infinite-size limiting process has been described [16]. However, the two processes act on different state-spaces.

### 3.3. MRCA and Age Structure in the EMG$^\flat$

Besides the technical aspects, there are some reasons why the EMG$^\flat$ as a stochastic process can prove useful in theoretical and practical regard. While the transitions in the EMG rely on two random mechanics (duplication and removal), in the EMG$^\flat$ they are unified within the regrafting operation. Because of that, aspects about the genealogy itself may become more tractable.
to analytic investigation. One good example for this is the MRCA-Process. Let $x^*$ denote the MRCA of a genealogy generated by a neutral Moran Process. With probability 1, after some finite time a descendant of $x^*$ will become ancestral to the entire population, establishing a new MRCA. Therefore, defining $\chi_{\text{MRCA}}(i) = 1$ if at time $i$ a new MRCA of the population is established (i.e., the MRCA 'jumps', which in the EMG is represented by the eventual obliteration and repositioning of the root node of $T_i$), and $\chi_{\text{MRCA}}(i) = 0$ otherwise, we call $(\chi_{\text{MRCA}}(i))_{i \geq 0}$ the MRCA-Process.

**Lemma 4.** $(\chi_{\text{MRCA}}(i))_{i \geq 0}$ is a geometric jump process of intensity $\frac{2}{n^2}$.

**Proof.** In the EMG, the root of the genealogy $T_i$ changes if and only if the imaginary branch $b_1$ is chosen for regrafting. This happens with probability $\frac{2}{n^2}$ in each step (see also Figure 8).

This agrees with the results in [4], where the MRCA-Process in the infinite-population limit is identified as a Poisson-Process of intensity 1, which is the limit of the geometric jump process as $n \to \infty$ with time sped up by $\frac{n^2}{2}$. Also by Lemma 4, the number of steps needed to observe any number $r \in \mathbb{N}$ of root jumps follows a negative binomial distribution $\text{NB}(r, \frac{2}{n^2})$.

The discrete structure of the EMG also allows us to derive properties of the MRCA-Process during ongoing fixations in the underlying Moran Process.

**Definition 6.** Suppose a member $\tilde{x}$ in a neutral Moran Process was generated as the result of some duplication at time $i^* \gg 0$, and we observe, by chance, the fixation of descendants of $\tilde{x}$ in the population at time $i^{\text{fix}} \gg 0$.

- $i^{\text{fix}}$ is called fixation time of the individual $\tilde{x}$
- $i^*$ is called birth time of $\tilde{x}$
Lemma 5. In a Moran Population of size $n \geq 2$, we expect to observe $2 - \frac{2}{n}$ MRCA-jumps between (and including) $i^*$ and $i_{\text{fix}}$.

Proof. By our assumptions, we know that one MRCA-jump necessarily happens at the transition of $T_{i_{\text{fix}}-1}$ to $T_{i_{\text{fix}}}$. We claim that we expect another one during the remainder of the fixation time.

Let $l = i_{\text{fix}} - 1 - i^*$. We know $l \geq n - 2$, since the minimal number of steps necessary to fix the descendants of $\tilde{x}$ is $n - 1$. The sequence of genealogies $(T_{i^*}, \ldots, T_{i_{\text{fix}}-1})$ in reverse order is a path $y = (T'_0, \ldots, T'_l)$ of the EMG$^\flat$, where $T'_0 = T_{i_{\text{fix}}-1}, \ldots, T'_l = T'_{i^*}$.

The set of EMG$^\flat$-time steps $\{1, \ldots, l\}$ contains a subset $I = \{i_1, \ldots, i_{n-1}\}$, $i_l \leq i_{l+1}$, where $i \in I$ if and only if $x \in T'_i$ holds for the individual $x$ regrafted at time $i$; i.e., $x$ is also present in the population at the time $l$, which represents the birth time of $\tilde{x}$ in the EMG$^\flat$. $I$ thus consists of exactly the times where individuals of the population at the birth time of $\tilde{x}$ are revived. In particular, $i_1 = 0$ and $i_{n-1} = l$. For $i \in I$, let $S_i := \{x \in T'_i : x \in T'_l\}$ denote the set of individuals that will be members of the population at the birth time of $\tilde{x}$.

Starting from $T'_1$, a root jump can only occur in some step $i$ if $i \in I$. For any $i_j \in I$, we know that regrafting must take place in some layer $k \leq j + 1$. We therefore consider the sequence

$$\hat{T}^{(1)} = (T'_1)_{S_1}, \ldots, \hat{T}^{(n-2)} = (T'_l)_{S_{n-2}}, \hat{T}^{(n-1)} = T'_l$$

of $S_i$-induced subtrees of $T'_i$ for $i \in I$. Since $T'_l$ is a random Yule tree, by Lemma 2 we may assume that each $\hat{T}^{(j)}$, $j = 2, \ldots, n - 1$ is obtained from a random grafting operation performed on $\hat{T}^{(j-1)}$. The probability of a root jump in step $i_j$ is therefore the probability of regrafting at the imaginary branch of $\hat{T}^{(j)}$, which equals $\frac{2}{j(j+1)}$.

The total expected number of root jumps along the EMG$^\flat$-path $y$ is then

$$\sum_{k=2}^{n-1} \frac{2}{k(k+1)} = \frac{n - 2}{n}. $$

This expression equals $1 - \frac{2}{n}$. Adding the root jump that necessarily occurs in step 1, we end up with an expectation of $2 - \frac{2}{n}$.

Considering the infinite-population limit, we conclude that between birth and fixation time of an individual, there are 2 expected MRCA jumps in total.

By similar arguments, we may calculate the exact distribution of root jumps during a neutral fixation for any $n$, and show that these distributions converge
as \( n \to \infty \). For \( n \geq 2 \), let \( Pr_n(k) \) denote the probability of observing \( k \) root jumps during a neutral fixation in an EMG of size \( n \), and \( Pr_\infty(k) \) the same probability in the infinite-population limit. \( Pr_n(k) \) can be written as follows:

\[
Pr_n(k) := \sum_{2 \leq i_1, \ldots, i_{k-1} \leq n-1} \Pi_{i_k}^k \frac{2}{i_k(i_k+1)} \Pi_{j \neq i_1, \ldots, i_{k-1}} \left( 1 - \frac{2}{j(j+1)} \right)
\]

This is obtained by multiplying the probabilities of regrafting at the imaginary branches of \( \hat{T}(i_1), \ldots, \hat{T}(i_{k-1}) \) (in the sense of the notation used in Lemma 5) and not regrafting at the imaginary branches of all other \( \hat{T}(j) \), summed up over all possible choices of \( i_1, \ldots, i_{k-1} \). For \( k = 1 \), in which case the imaginary branch is never chosen for regrafting, we have simply

\[
Pr_n(1) = \Pi_{j=2}^{n-1} \left( 1 - \frac{2}{j(j+1)} \right)
\]

and this expression can be simplified to \( \frac{n+1}{3(n-1)} \). By reordering of the factors, we obtain the following expressions for \( k = 2, 3, \ldots \):

\[
Pr_n(2) = \Pi_{j=2}^{n-1} \left( 1 - \frac{2}{j(j+1)} \right) \left[ \sum_{k=2}^{n-1} \frac{2}{k(k+1) - 2} \right]
\]

\[
Pr_n(3) = \Pi_{j=2}^{n-1} \left( 1 - \frac{2}{j(j+1)} \right) \left[ \sum_{k=2}^{n-2} \frac{2}{k(k+1) - 2} \cdot \left( \sum_{l=k+1}^{n-1} \frac{2}{l(l+1) - 2} \right) \right]
\]

\[\ldots \]

(5)

For \( n = 2 \), \( Pr_n(1) = 1 \), and as \( n \to \infty \), \( Pr_n(1) = \frac{n+1}{3(n-1)} \to \frac{1}{3} = Pr_\infty(1) \), decreasing monotonously. Note that this can be interpreted as an analogon to a result in [4] about the infinite-population limit. In the terminology of this work, the value \( \frac{1}{3} \) corresponds to the probability that the "next fixation curve has not yet started" at the time \( i^* \).
Figure 9: The distributions of $P_n(k)$, $k = 1, \ldots, 8$, $n = 2$ (blue), 5 (turquoise), 10 (green), 25 (red) and $\infty$ (black).

The other probabilities in the infinite-population limit can be calculated numerically by evaluating the infinite-sum expressions on the right-hand sides of (5). By continuity, the probabilities $\sum_{k=1}^{\infty} \Pr_\infty(k)$ sum up to 1. The largest contribution comes from $\Pr_\infty(2) = \frac{11}{27} = \frac{11}{9} \cdot \frac{1}{3}$. As a side note, since $\Pr_n(2)$ increases monotonously with $n$, we can calculate that for $n \leq 9$, the distribution is dominated by $\Pr_n(1)$, whereas for $n \geq 10$, the probability $\Pr_n(2)$ provides the largest value. Figure 9 outlines some of the distributions for different population sizes.

Another implication of the EMG$^\flat$ is that coalescent events are "visible" in the genealogy for a certain average number of steps, such that we can determine their age structure. In general, the time until the internal node labeled $k$ is moved down by one layer is geometrically distributed with parameter $\frac{k(k+1)}{n^2}$, because $\frac{k(k+1)}{2}$ branches exist above this internal node. In the case of the root node, this expectation is $\frac{2}{n^2}$, as stated before.

The expected time until the current root node of $T_i$ vanishes under the EMG$^\flat$ is therefore $\sum_{k=1}^{n-1} \frac{n^2}{k(k+1)} = n^2 \left( 1 - \frac{1}{n} \right)$. In the large-population limit, this corresponds to a rate of $\frac{1}{2}$.

The expected time until an internal node of $T_i$ becomes invisible, averaged
over all nodes, is

\[
\frac{1}{n-1} \sum_{k=1}^{n} n^2 \sum_{j=k}^{n-1} \frac{1}{j(j+1)} = \frac{n^2}{n-1} \sum_{k=1}^{n-1} \left( \frac{1}{k} - \frac{1}{n-1} \right) \\
= \frac{n^2}{n-1} a_{n-1} - \frac{n^2}{(n-1)^2}
\]

\[
\approx n \log(n)
\]

Rescaling time, we obtain \( \frac{2 \log(n)}{n} \to 0 \) as \( n \to \infty \). We conclude that in large populations, most coalescent events only exist for a short time.

4. Discussion

The Evolving Moran Genealogy and time-reversed version reveal interesting properties of the genealogies generated by the neutral Moran Process. We have used them to re-formulate classic diffusion-limit results on the MRCA Process, but also obtain exact expressions for the finite-population setting. Additionally, the distribution of MRCA jumps during fixation periods becomes tractable in the EMG, for both finite and limiting case. Of practical interest may be the fact that the EMG reduces the number of operations from 2 to 1 in contrast to the underlying Moran Model, if we think of the regrafting operation as one single operation.

It will be interesting to extend this to other Moran-type population models, such as ones involving alleles with a selective advantage. In many settings, tree-valued dual processes have been described for the infinite-population limits, e.g. the ancestral selection graph [17], which involves both mutation and selection between and among types, and admits a graphical representation similar to the lookdown-construction under neutrality [18], which gives access to many implicit features of the model [19]. Tree-valued constructions of finite time and population size may help here to bridge the gap between finite and infinite population case likewise.

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