THE MORAN GENEALOGY PROCESS

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ABSTRACT. We give a novel representation of the Moran Genealogy Process, a continuous-time Markov process on the space of size-$n$ genealogies with the demography of the classical Moran process. We derive the generator and unique stationary distribution of the process and establish its uniform ergodicity. In particular, we show that any initial distribution converges exponentially to the probability measure identical to that of the Kingman coalescent. We go on to show that one-time sampling projects this stationary distribution onto a smaller-size version of itself. Next, we extend the Moran genealogy process to include sampling through time. This allows us to define the Sampled Moran Genealogy Process, another Markov process on the space of genealogies. We derive exact conditional and unconditional probability distributions for this process under the assumption of stationarity, and an expression for the likelihood of any sequence of genealogies it generates. This leads to some interesting observations pertinent to existing phylodynamic methods in the literature.

1. Introduction.

The Moran process (Moran, 1958) plays an important role in the theory of population genetics and is intimately related to Kingman’s (1982a; 1982b; 1982c) coalescent process, itself a foundational component of modern population genetics, phylogenetics, and phylodynamics (Hudson, 1991; Donnelly & Tavare, 1995; Stephens & Donnelly, 2000; Rosenberg & Nordborg, 2002; Ewens, 2004; Volz et al., 2009; Rasmussen et al., 2011). Kingman formulated the coalescent as a backward-in-time Markov process whereby genealogical lineages randomly coalesce with one another. He made explicit connections with the classical Wright-Fisher and Moran models, and connections exist with a far broader collection of population genetics models (Ewens, 2004; Etheridge, 2011; Etheridge & Kurtz, 2019).

The literature on coalescent theory is often focused on models whereby frequencies of alleles change within a population according to some idealized stochastic process (Hein, 2005; Durrett, 2008; Wakeley, 2008). Here, we refocus the discussion, onto the evolution of the genealogy that, at any given time, describes the full set of relationships among the members of a population alive at that time. In this respect, our approach bears some resemblance to that of Wirtz & Wiehe (2019), though these authors confine themselves to the discrete topological aspects of genealogies. By contrast, we consider continuous-time stochastic processes that take values in the space of genealogies with real-valued branch lengths. In §2, we give a formal definition of the Moran Genealogy Process and, in our first set of results, show by direct forward-in-time calculation, and without any need for large population-size or sparse sampling assumptions, that this process is uniformly ergodic. In §3, we show that its limiting stationary distribution is identical to that of the Kingman coalescent. Though this first set of results is perhaps unsurprising in itself, especially in light of the very general results of Etheridge & Kurtz (2019), our proofs are novel, constructive, and strictly forward-looking, and therefore shed light on the genealogical process from a different direction.

The representation introduced in §2 provides a platform for our second major set of results, which concern genealogies induced by sequential, asynchronous sampling of the Moran Genealogy Process. In §5, we formally define the Sampled Moran Genealogy Process and derive novel expressions for
its probability distribution. In particular, we derive an expression for the marginal distribution of the
genealogy that relates a sequence of samples of any length. In doing so, we allow for both coalescence
events and events wherein one sample is a direct descendant of an earlier sample. Our results, again,
are exact and hold for all finite population sizes and sampling rates. Curiously, comparison of our
expressions with comparable ones from the phylodynamics literature reveals interesting discrepancies,
with implications for phylodynamic inference methods currently in use. Based on an examination of the
proofs, we anticipate that these results will generalize to a broad class of birth-death processes.

2. The Moran Genealogy Process.

The name of P. A. P. Moran has been associated with a number of related stochastic processes arising in
population genetics. These processes share the common features that they involve a finite population of
asexual individuals who reproduce and die stochastically in continuous time. The population size is kept
deterministically constant by requiring that each reproduction event is coincident with a death event.
Such models are closely related to the coalescent of Kingman (1982a,b,c), which plays a prominent role
in population genetics and phylogenetics. We explore these connections from a new angle by defining the
Moran Genealogy Process (MGP), a stochastic process on the space of genealogies. In common
with other models bearing Moran’s name, we make the assumptions that (a) the process is a continuous-
time Markov process, with a constant event rate, and (b) at each event, one asexual individual gives birth
and another dies, so that the population size remains constant. At any particular time, the state of the
MGP is a genealogy—a tree with branch lengths—that relates the \( n \) living members of the population
via their shared ancestry. This consists of links between living individuals and those past individuals
who are the most recent common ancestors of sets of currently living individuals. As living individuals
reproduce and die, the genealogy grows at its leading edge; it dissolves at its trailing edge, as ancestors
are “forgotten”. Fig. 1 illustrates; see also the animations in the online appendix.

As we shall see, the genealogies of the MGP have two aspects, one discrete, the other continuous. The
discrete aspect, encoding the topological evolution of the genealogies, evolves as a jump process: at
each event, a new branch appears at the leading edge and an internal node is dropped. The continuous
aspect, tracking the quantitative dynamics of branch lengths, evolves as the latter grow continuously at
the leading edge of the tree and jump at event times as internal nodes are dropped. We can study the
discrete process without reference to the continuous one. Accordingly, we will first define a Markov
chain that represents the discrete aspect. We will then examine the full MGP as an extension of the
discrete chain.

Because the MGP is Markov, the waiting times between birth-death events are exponentially distributed
and, as mentioned, the event rate is constant. For convenience in calculations, we take this rate to be
\( \binom{n}{2} \); we will later rescale time to obtain more general expressions.

2A. The Moran genealogy game.

Although genealogies are naturally represented using trees, these representations are not unique, and it
can be challenging to reason about their properties. Accordingly, we map the MGP onto a parlor game
for which intuition is more readily available. In particular, the Moran genealogy process in a population
of size \( n \) is equivalent to the following parlor game for \( n \) players.

**Equipment.** We have \( n \) black balls, numbered 1 . . . , \( n \), and \( n \) green balls, each one of which is inscribed
with the name of one of the players (we assume the names are unique). Each player receives a slate,
the green ball bearing his or her name, and a randomly chosen black ball. We arrange \( n \) seats in a
row and number them 0 through \( n - 1 \). We also have a clock which, when started, runs for a random,
**Setup.** To begin the game, an arbitrarily chosen player takes the first seat. Upon her slate, she writes “$-\infty$”. The remaining players are then seated sequentially, from left to right, in arbitrary order. As each successive player takes a seat, she exchanges her green ball for a randomly selected black ball held by one of the already-seated players. She then writes a real number upon the slate; the only constraint on her choice is that it be at least as large as the number on the slate of the player to her left yet less than zero. Thus, the player taking seat $m$ encounters the following situation. The $m$ players already seated hold among themselves $m$ green balls and $m$ black balls. The player to be seated therefore has $m$ choices as to the black ball she will exchange for her green ball. The leftmost player holds two green balls and the rightmost, two black balls; the other players may have one of each color. Each player’s green ball (other than that of the leftmost player) is held by a player seated to her left.

**Play.** Play proceeds in rounds. Each round begins when the clock is started. When it stops, two black balls are chosen at random (without replacement). The player—call him X—holding the first black ball, stands up. Player X exchanges his second ball for the green ball bearing his name. This will always be held by a player seated to his left. All players to the right of X then shift one seat to the left, leaving the rightmost seat empty. Player X is said to have been “killed”. Next, the player, Y, holding the second randomly-selected black ball, trades it for X’s green ball. Player X now takes the rightmost seat and writes the current time upon his slate. Player Y is said to have “given birth” and player X to have been “reborn”. We sometimes refer to the conjoined birth and death events as a single “Moran event”. Note that, since the player in seat 0 never holds a black ball, she can never be killed and therefore remains in this seat throughout the game. Nor does the number on her slate ever change.
**Figure 2.** The W chain for \( n = 7 \). (A) The \( n - 1 = 6 \) players, named a, . . . , f (green labels), represent the internal nodes. Each player holds two balls, each of which may be green or black. Green balls have names written on them; the named player is an immediate descendant. Black balls have numbers written on them and represent tips. Thus player b holds black ball number 2 and green ball c, while e holds the black balls 3 and 4. (B) In each round of play, an ordered pair of two of the \( n \) black balls is selected at random. In the illustrated case, the first is ball 5, held by player d. Accordingly, player d exchanges green ball f with player c for green ball d and moves to the rightmost position (position 6). Players e and f each shift one position to the left. The second ball selected is ball 2, held by player b, who exchanges ball 2 with player d for ball d. The resulting configuration is shown in panel (C).

**Relation to the Moran genealogy process (MGP).** The correspondence between the MGP and the Moran genealogy game is as follows. The seats numbered 1, \ldots, \( n - 1 \) (that is, all but the leftmost seat) correspond to the time-ordered \( n - 1 \) internal branch points, seat number 1 being the root, i.e., the most recent common ancestor of all extant individuals. The black balls correspond to individuals in the extant population (i.e., the tips of the genealogical tree): if a player holds a black ball, one individual in the extant population has this player as her most recent ancestor shared with someone else in the extant population. The green balls record the topology of the tree: each player holding a green ball is the immediate parent of the player named on that ball. Fig. 1 illustrates.

The MGP is defined to be a continuous-time process on tip-labeled trees with branch lengths and unordered descendants. The topological structure of a tree at time \( t \) is represented by the list \( \mathbf{W}(t) = (W_1(t), \ldots, W_{n-1}(t)) \), where each \( W_m(t) \) is the (unordered) pair of balls held by the player in seat \( m \). Note that \( W_0 \) is left out of \( \mathbf{W} \): the balls held by player 0—who represents the root of the tree in the distant past—convey only redundant information. Let \( \mathbb{W}^n \) be the finite set of all such states. It should be clear that nothing depends on the names of the players or their order.

One can count the number of distinct arrangements to compute the size of \( \mathbb{W}^n \). Accordingly, we ignore the identities of the players entirely in the counting. We see that there are \( \binom{n}{2} \) choices for the two black balls held by the player in seat \( n - 1 \). The player in seat \( n - 2 \) now has \( n - 1 \) balls to choose from: the remaining \( n - 2 \) black balls plus the green ball with the name of the player in seat \( n - 1 \). Continuing to work backward, for each \( m \), the player in seat \( m \) has \( \binom{m+1}{2} \) choices for a pair of balls. Hence, one has

\[
|\mathbb{W}^n| = \prod_{m=1}^{n-1} \binom{m+1}{2} = n! \frac{(n-1)!}{2^{n-1}}.
\]
The number written on a player’s slate is the time at which that player was most recently seated. Let
\( T(t) = (T_1(t), \ldots, T_{n-1}(t)) \) be the vector of numbers on the slates at time \( t \), ordered left to right. Let
\( S(t) = (S_1(t), \ldots, S_{n-1}(t)) \), where for \( m < n - 1 \), \( S_m(t) = T_{m+1}(t) - T_m(t) \) and \( S_{n-1}(t) = t - T_{n-1}(t) \). Then the \( S_m(t) \) are the durations of the coalescent intervals, i.e., the intervals between successive branch points when the latter are ordered in time. The state space of the MGP is defined to be \( \mathbb{X}^n = \mathbb{W}^n \times \mathbb{S}^n \), where \( \mathbb{S}^n := \mathbb{R}_+^{n-1} \) and the MGP itself can be written \( X(t) = (W(t), S(t)) \), for \( t \geq 0 \).

2B. Limiting distribution of \( W \).

With the definitions above, it should be clear that both \( X \) and \( W \) are Markov processes, though \( S \) is not. Here, we show that the unique, limiting distribution of the \( W \) chain is the uniform distribution on \( \mathbb{W}^n \).

It is easy to verify that \( W \) is irreducible, aperiodic, and recurrent, whence it follows that it has a unique, limiting invariant distribution. The proof that this distribution is uniform closely follows the reasoning of Aldous (1999) and is in most respects identical to that found in Harding (1971) and Gernhard (2008).

The key is to retrace the steps of the last-seated player, counting the number of states that can immediately precede a given state. For example, suppose, as in Fig. 2, player \( d \) is in the rightmost seat (position \( n - 1 \)). It is clear that, immediately before sitting down in position \( n - 1 \), player \( d \) received one of the two balls she holds from the player currently holding green ball \( d \) (in Fig. 2C, for example, this is player \( b \)). There are thus two possibilities at this stage. Next, she might have come from any of the \( n - 1 \) seats (including the rightmost one). If she came from seat \( m \), then the \( m \) players seated to the left of \( m \) collectively hold \( m \) green balls bearing their own names. Therefore, there are \( m \) balls (not all of which need be black) held by these \( m \) players that might have been the one player \( d \) exchanged for the ball bearing her name. Thus, there are \( 2 \sum_{m=1}^{n-1} m = n(n-1) \) configurations which might have preceded the current one.

To formalize this reasoning, we first make some definitions. For \( w \in \mathbb{W}^n \), let \( \Upsilon_u(w) \in \mathbb{W}^{n-1} \) be the configuration resulting from the “killing” of the player who holds ball \( u \). For \( w \in \mathbb{W}^{n-1} \), let \( \Phi_u(w) \in \mathbb{W}^n \) be the configuration resulting from the player holding ball \( v \) having “given birth”. Thus, the \( \Phi_u \Upsilon_u \) is the result of the Moran event following the random choice of an ordered pair of black balls \( (u, v) \). Note that if either \( w' = \Phi_u \Upsilon_v(w) \) or \( w' = \Phi_v \Upsilon_u(w) \), then \( w'_{n-1} = \{u, v\} \), i.e., \( u \) and \( v \) are the balls held by the rightmost player immediately after the rearrangement. Let \( \mathcal{M}(w, w') \) be the \( w \) to \( w' \) transition probability. Then, supposing \( w'_{n-1} = \{a, b\} \),

\[
\mathcal{M}(w, w') = \sum_{u,v=1 \atop u \neq v}^n \frac{\mathbb{I}_{\Phi_u \Upsilon_v(w) = w'} - \mathbb{I}_{\Phi_v \Upsilon_u(w) = w'}}{n(n-1)} = \frac{\mathbb{I}_{\Phi_u \Upsilon_v(w) = w'} + \mathbb{I}_{\Phi_v \Upsilon_u(w) = w'}}{n(n-1)},
\]

where \( \mathbb{I}_A \) denotes the indicator function for the condition \( A \). One easily verifies that \( \mathcal{M} \) is stochastic, i.e., \( \sum_{w'} \mathcal{M}(w, w') = 1 \). In fact, \( \mathcal{M} \) is doubly stochastic, i.e., \( \sum_w \mathcal{M}(w, w') = 1 \). To see this, note that, by the reasoning of the last paragraph, for each \( w' \in \mathbb{W}^n \), \( \left| (\Phi_u \Upsilon_v)^{-1}(\{w'\}) \right| = \binom{n}{2} \) when \( w'_{n-1} = \{a, b\} \) and \( |(\Phi_u \Upsilon_v)^{-1}(\{w'\})| = 0 \) otherwise. We summarize with the following propositions.

**Proposition 1.** Let \( q_n \) be the uniform probability distribution on \( \mathbb{W}^n \). That is, for each \( w \in \mathbb{W}^n \),

\[
q_n(w) := \frac{2^{n-1}}{n!(n-1)!}.
\]

Then \( q_n \) is the unique, limiting, stationary distribution of the \( W \) process described above.
Proposition 2. Suppose \( w'_{n-1} = \{a, b\} \). Let
\[
\mathcal{M}_j(w, w') := \frac{\mathbb{I}_{\Phi_b Y_k(w) = w' \land b \in w_j} + \mathbb{I}_{\Phi_a Y_k(w) = w' \land a \in w_j}}{n(n - 1)},
\]
\( \mathcal{M}_j(w, w') \) is the probability that, in the move from \( w \) to \( w' \), the first black ball selected is held by the player in seat \( j \). Clearly, \( \mathcal{M}(w, w') = \sum_{j=1}^{n-1} \mathcal{M}_j(w, w') \). Moreover
\[
\sum_{w \in \mathbb{W}^n} \mathcal{M}_j(w, w') = \frac{j}{\binom{n}{2}} \quad \text{and} \quad \sum_{w' \in \mathbb{W}^n} \mathcal{M}_j(w, w') = \frac{B_j(w)}{n},
\]
where \( B_j(w) = |\{a \in w_j : a \text{ is black}\}| \), i.e., the number of black balls held by the player in seat \( j \).

Proof. Note that, by the counting argument above, \( |\{w : \Phi_b Y_a(w) = w' \land a \in w_j\}| = j \). Furthermore, for each \( w \in \mathbb{W}^n \), the probability that the player in seat \( j \) is killed is just \( B_j(w)/n \). \( \square \)

Corollary 3. Under stationarity,
\[
\mathbb{E} \left[ \frac{B_j(w)}{n} \right] = \frac{j}{\binom{n}{2}}.
\]

2C. Ergodicity.

We establish the stability properties of the Moran genealogy process by studying its resolvent. To this end, let \( R_k \) be the \( k \)-th jump time of a unit-rate Poisson process on \((0, \infty)\). The resolvent of \( X \) is the discrete-time chain \( Y_k = X(R_k), k = 1, 2, \ldots \), resulting from observing \( X \) at times \( R_k \). Let \( ds = \prod_{j=1}^{n-1} ds_j \) and \( dw \) represent Lebesgue measure on \( S^n \) and counting measure on \( \mathbb{W}^n \), respectively. Define the measure \( \eta \) on \( \mathbb{X}^n = \mathbb{W}^n \times S^n \) by
\[
\eta(dw \, ds) := \frac{1}{2^{n-1}} \exp \left[ - \left( \binom{n}{2} \left( s_1 + \cdots + s_{n-1} \right) \right) \right] \, dw \, ds.
\]

To be clear, Eq. 2 defines \( \eta \) as a product measure, where the \( \mathbb{W}^n \)-component is counting measure and the \( S^n \)-component is absolutely continuous with respect to Lebesgue measure.

Now suppose \( x \in \mathbb{X}^n \) is an arbitrary state and \( E \) is a measurable subset of \( \mathbb{X}^n \). Note that for any \( (w, s) \in E \), there is a sample path that leads directly from \( x \) to \( (w, s) \) in precisely \( s_1 + \cdots + s_{n-1} \) units of time and with exactly \( n - 1 \) events transpiring at intervals \( s_1, \ldots, s_{n-1} \). At each event, there is at least one choice of a pair of black balls that can be made. Hence the probability associated with any of these paths is
\[
\frac{1}{2^{n-1}} \exp \left[ - \left( \binom{n}{2} \sum_{m=1}^{n-1} s_m \right) \right] \, ds.
\]
The probability that \( R_{k+1} - R_k = \sum s_m \) is \( \exp(-\sum s_m) \, ds \). Summing over all \( (w, s) \) in \( E \) gives
\[
\mathbb{P} \left[ Y_k \in E \mid Y_{k-1} = x \right] \geq \eta(E)
\]

independent of \( x \) and \( k \). Though we do not use it, in fact the inequality is strict since, although the constructed paths are almost surely those which reach \( (w, s) \) in minimal time, there are many others that arrive by more circuitous routes. Since Eq. 3 holds for all \( x \in \mathbb{X}^n \), the full state space \( \mathbb{X}^n \) is said to be a petite set. It follows from Theorem 16.2.2 of Meyn & Tweedie (2009) that \( Y \) is uniformly ergodic and therefore, a fortiori, that \( Y \) possesses a unique stationary probability distribution, \( \pi_n \). Since the invariant measures of \( Y \) and \( X \) coincide, it follows that \( X \) has the same property. We determine the form of this invariant measure in §3.
For the MGP $X(t)$, we define the probability transition function, $P^t$ in the usual fashion (e.g., Feller, 1957; Meyn & Tweedie, 2009). Specifically, let

$$P^t(x, \mathcal{E}) := \mathbb{P}[X(t) \in \mathcal{E} \mid X(0) = x], \quad (4)$$

for $t \geq 0$, $x \in \mathbb{X}^n$, and measurable $\mathcal{E} \subseteq \mathbb{X}^n$. For each $x$, $P^t(x, \cdot)$ is a measure, while for each $\mathcal{E}$, $P^t(\cdot, \mathcal{E})$ is a measurable function from $\mathbb{X}^n$ to $[0, 1]$.

Define the family of operators, $K_t$, $t \geq 0$, by

$$(K_t f)(x) := \mathbb{E}[f(X(t)) \mid X(0) = x] = \int_{\mathbb{X}^n} P^t(x, dx') f(x') \, dx', \quad (5)$$

for $x \in \mathbb{X}^n$ and $f \in \text{Dom}(K) := \{g : \mathbb{W}^n \times \mathbb{S}^n \to \mathbb{R} \mid \forall w \, g(w, \cdot) \in C^1(\mathbb{S}^n)\}$. With this definition, $K_t$ is a Markov semigroup.

We can now state

**Theorem 4.** The Moran genealogy process is uniformly ergodic. In particular, there are constants $D < \infty$ and $0 \leq \rho < 1$ such that

$$\|P^t(x, \cdot) - \pi_n\|_{TV} < D \rho^t,$$

for all $t \geq 0$ and all $x$. Here, the norm on measures is the total variation norm, defined by

$$\|\mu\|_{TV} := \sup_{|f| \leq 1} |\mu(f)|.$$

Moreover, if $\|\cdot\|_{\infty}$ denotes the $L^\infty$ operator norm, with the same $D$ and $\rho$ as above, we have

$$\|K_t - \pi_n\|_{\infty} < D \rho^t, \quad \text{for } t \geq 0.$$

**Proof.** We verify that $Y$ trivially satisfies a drift condition. Down et al. (1995, Theorem 5.2) show that if, for some petite set $\mathcal{C} \subseteq \mathbb{X}$, some function $V : \mathbb{X} \to [1, \infty)$, some $\lambda < 1$, and some $b < \infty$, one has $\mathbb{E}[V(Y_k) \mid Y_0 = x] \leq \lambda V(x) + b \chi_{x \in \mathcal{C}}$ for every $x$, then one can conclude that $X$ is $V$-uniformly ergodic. We take $V(x) = 1$, $\lambda = b = \frac{1}{2}$, and $\mathcal{C} = \mathbb{X}$. We conclude that $X$ is uniformly ergodic in the sense of Down et al. (1995): this is equivalent to the first statement in the theorem.

Finally, it is easy to see that

$$\|K_t f - \pi_n(f)\|_{\infty} < D \|f\|_{\infty} \rho^t, \quad t \geq 0, \quad f \in \text{Dom}(K).$$

The second statement in the theorem then follows immediately from the definition of the operator norm. \qed 

**2D. Infinitesimal generator.**

With the Markov semigroup $K_t$ defined by Eq. 5, we have

$$(K_t f)(w, s) = \int_{\mathbb{W}^n \times \mathbb{S}^n} \mathcal{P}(t, w; s, w', s') f(w', s') \, dw' \, ds' + o(t),$$
as $t \downarrow 0$, where

$$\mathcal{P}(t, w, s, w', s') := e^{-\binom{n}{2} t} \mathcal{Q}(t, w, s, w', s') + \left(1 - e^{-\binom{n}{2} t}\right) \sum_{j=1}^{n-1} \mathcal{M}_j(w, w') \mathcal{R}_j(s, s'), \quad (6)$$

$$\mathcal{Q}(t, w, s, w', s') := \delta(s_{n-1} + t - s'_{n-1}) \cdot \prod_{j=1}^{n-2} \delta(s_j - s'_j) \cdot \delta(w = \mathbb{w}''), \quad (7)$$

$$\mathcal{R}_j(s, s') := \prod_{k=1}^{j-2} \delta(s_k - s'_k) \cdot \delta(s_{j-1} + s_j - s'_{j-1}) \cdot \prod_{k=j}^{n-2} \delta(s_{k+1} - s_k') \cdot \delta(s'_{n-1}). \quad (8)$$

Here, $\delta$ is the Dirac delta function. The $\mathcal{Q}$ term encodes changes in $\mathbf{X}$ that occur between birth-death events: the $(n-1)$-st coalescent interval grows with time, while the other intervals remain fixed and the topology remains unchanged. The $\mathcal{M}_j\mathcal{R}_j$ terms in the sum of Eq. 6 encode the changes in $\mathbf{X}$ that occur when the selected black ball is held by the player in seat $j$. At such an event, $w$ jumps to $w'$ with probability $\mathcal{M}_j(w, w')$, the $(j-1)$-st coalescent interval subsumes the $j$-th, while the $k$-th interval takes the value of the $(k-1)$-st for $k \geq j$. Moreover, the $(n-1)$-st interval is set to zero.

We compute the infinitesimal generator, $L$, as the linear operator satisfying

$$\lim_{t \downarrow 0} \frac{K_t f - f}{t} = Lf$$

for $f \in \text{Dom}(K)$. This is easily done, and we obtain the following, which we state without proof.

**Proposition 5.** The infinitesimal generator of the MGP is the linear operator $L$ defined by

$$(Lf)(w, s) = \int_{\mathbb{W}^n \times \mathbb{G}^n} \mathcal{L}(w, s, w', s') f(w', s') \, dw' \, ds', \quad (9)$$

whenever $f \in \text{Dom}(L) = \text{Dom}(K)$. The kernel, $\mathcal{L}$, is given by

$$\mathcal{L}(w, s, w', s') := \left(\delta'(s_{n-1} - s'_{n-1}) - \binom{n}{2} \delta(s_{n-1} - s'_{n-1}) \right) \prod_{k=1}^{n-2} \delta(s_k - s_k') \mathbb{I}_{w = \mathbb{w}''}$$

$$+ \binom{n}{2} \sum_{j=1}^{n-1} \mathcal{M}_j(w, w') \mathcal{R}_j(s, s'). \quad (10)$$

Here, the symbol $\delta'$ refers to the derivative of the Dirac delta function.

**2E. Kolmogorov backward equation.**

For $f \in \text{Dom}(K)$, let $u_f(t, w, s) := K_t f(w, s)$. Note that

$$\frac{\partial u_f}{\partial t}(t, w, s) = \lim_{\Delta t \downarrow 0} \frac{K_{t+\Delta t} f(w, s) - K_t f(w, s)}{\Delta t} = \lim_{\Delta t \downarrow 0} \frac{K_{\Delta t} - \text{Id}}{\Delta t} K_t f(w, s)$$

$$= L u_f(t, w, s) = \int_{\mathbb{W}^n \times \mathbb{G}^n} \mathcal{L}(w, s, w', s') u_f(t, w', s').$$
Applying Eq. 10, we obtain the Kolmogorov backward equation

\[ \frac{\partial u_f}{\partial t}(t, w, s) = \frac{\partial u_f}{\partial s_{n-1}}(t, w, s) - \left( \begin{array}{c} n \\ 2 \end{array} \right) u_f(t, w, s) \]

\[ + \left( \begin{array}{c} n \\ 2 \end{array} \right) \sum_{w' \in W^n} \mathcal{M}_1(w, w') u_f(t, w', s_2, \ldots, s_{n-1}, 0) \]

\[ + \left( \begin{array}{c} n \\ 2 \end{array} \right) \sum_{j=2}^{n-1} \sum_{w' \in W^n} \mathcal{M}_j(w, w') u_f(t, w', s_j, \ldots, s_{j-2}, s_{j-1} + s_j, s_{j+1}, \ldots, s_{n-1}, 0). \]

Together with the initial condition, \( u_f(0, w, s) = f(w, s) \), Eq. 11 determines the Markov semigroup \( K_t \).

3. The stationary Moran Genealogy Process.

The invariant measure, \( \pi_n \), of the MGP is characterized by the fact that it is annihilated by the generator, i.e., \( \pi_n L = 0 \). We seek a separable measure \( \pi_n(dw \, ds) = p_0(w) \prod_{k=1}^{n-1} p_k(s_k) \, dw \, ds \). Operating with \( L \) on \( \pi_n \) involves integrating over all possible genealogies \( (w, s) \):

\[ \pi_n L = \int_{W^n \times S^n} \pi_n(dw \, ds) \mathcal{L}(w, s, w', s') \]

\[ = - \left( p'_{n-1}(s'_{n-1}) + \left( \begin{array}{c} n \\ 2 \end{array} \right) p_{n-1}(s'_{n-1}) \right) \prod_{k=1}^{n-2} p_k(s'_k) p_0(w') \]

\[ + \left( \begin{array}{c} n \\ 2 \end{array} \right) \sum_{j=1}^{n-1} \sum_{w} p_0(w) \mathcal{M}_j(w, w') \prod_{k=1}^{j-2} p_k(s'_k) \cdot Q_j(s_{j-1}) \cdot \prod_{k=j}^{n-2} p_{k+1}(s'_k) \cdot \delta(s'_{n-1}) = 0. \]

Here \( p'_{n-1} := \partial p_{n-1}/\partial s_{n-1} \) and \( Q_j \) is defined by

\[ Q_j(s) := \int_{0}^{s} p_j(t) \, p_{j+1}(s - t) \, dt. \]

Integrating out all the \( s_j \) in Eq. 12, we obtain the matrix equation

\[ p_0(w') = \sum_{w} p_0(w) \sum_{j=1}^{n-1} \mathcal{M}_j(w, w') = \sum_{w} p_0(w) \mathcal{M}(w, w'), \]

which is just the expression of the requirement that \( p_0 \) be the stationary distribution of the \( W \) process, which we have already determined: indeed, Proposition 1 states that \( p_0(w) = \text{const} \).

To find the other factors of \( \pi_n \), we divide both sides of Eq. 12 by \( p_0(w) = p_0(w') \) and, after dropping the primes, which are no longer needed, we have

\[ - \left( p'_{n-1}(s_{n-1}) + \left( \begin{array}{c} n \\ 2 \end{array} \right) p_{n-1}(s_{n-1}) \right) \prod_{k=1}^{n-2} p_k(s_k) \]

\[ + \sum_{j=1}^{n-1} \sum_{k=1}^{j-2} p(s_k) \cdot Q_j(s_{j-1}) \cdot \prod_{k=j}^{n-2} p_{k+1}(s_k) \cdot \delta(s_{n-1}) = 0. \]

Note that, in passing from Eq. 12 to Eq. 14, we have applied Proposition 2.
Since Eq. 14 holds for all \( s_{n-1} \), we must have,
\[
p'_{n-1}(s_{n-1}) + \binom{n}{2} p_{n-1}(s_{n-1}) = 0,
\]
for \( s_{n-1} > 0 \), whence
\[
p_{n-1}(s) = \binom{n}{2} e^{-\binom{n}{2} s}.
\]
(15)

Now, we integrate Eq. 12 over \( s_{n-1} \), which yields
\[
-\binom{n}{2} \prod_{k=1}^{n-2} p_k(s_k) + \sum_{j=1}^{n-1} j \prod_{k=1}^{j-2} p_k(s_k) \cdot Q_{j-1}(s_{j-1}) \cdot \prod_{k=j}^{n-2} p_{k+1}(s_k) = 0.
\]
(16)

Notice that each term in the sum of Eq. 16 contains a product of \( n-2 \) factors, each of which is a probability density over a different one of the \( s_1, \ldots, s_{n-2} \) variables. Consequently, by integrating over all \( s_k, k \neq m \), we obtain an expression for the marginal density of \( s_m \):
\[
p_{m+1}(s_m) + \frac{2}{m} Q_m(s_m) - \left(1 + \frac{2}{m} \right)p_m(s_m) = 0,
\]
which holds for \( m = 1, \ldots, n-2 \).

We establish, by reverse induction on \( m \), that \( p_m(s) = \binom{m+1}{2} e^{-\binom{m+1}{2} s} \) for \( m = 1, \ldots, n-1 \). In Eq. 15, we have already shown the result for \( m = n-1 \). Applying the \( \partial/\partial s_m + \binom{m+2}{2} \) operator to both sides of Eq. 17 yields
\[
\left(p'_{m+1} + \binom{m+2}{2} p_{m+1}\right) + \frac{2}{m} \left(Q'_m + \binom{m+2}{2} Q_m\right) - \left(1 + \frac{2}{m} \right) \left(p'_m + \binom{m+2}{2} p_m\right) = 0.
\]
(18)

By the induction hypothesis, the first term of Eq. 18 vanishes and the second term simplifies, and we are left with
\[
p'_m + \frac{m}{m+2} \binom{m+2}{2} p_m = 0.
\]
The result follows. This establishes

**Theorem 6.** The unique invariant probability measure, \( \pi_n \), of the Moran genealogy process of size \( n \) is given by
\[
\pi_n(\text{d}w \text{d}s) = \exp \left(-\sum_{j=1}^{n-1} \binom{j+1}{2} s_j\right) \text{d}w \text{d}s,
\]
where \( \text{d}w \) is the counting measure on \( \mathcal{W}^n \) and \( \text{d}s \) is Lebesgue measure on \( \mathbb{S}^n \).

Up to this point, we have, for convenience, assumed that the base event rate of the MGP is \( \binom{n}{2} \). If instead, it proceeds at an arbitrary constant rate, \( \mu \), a simple rescaling of time gives us the following

**Corollary 7.** If the MGP of size \( n \) proceeds with event rate \( \mu \), then its unique invariant probability measure is given by
\[
\left(\frac{\mu}{\binom{n}{2}}\right)^{n-1} \exp \left(-\sum_{j=1}^{n-1} \binom{j+1}{2} \mu s_j\right) \text{d}w \text{d}s,
\]
where \( \text{d}w \) is the counting measure on \( \mathcal{W}^n \) and \( \text{d}s \) is Lebesgue measure on \( \mathbb{S}^n \).
Thus, the unique limiting stationary measure of the Moran Genealogy Process is identical to the probability measure of the Kingman (1982a) coalescent. Although this result is unsurprising, the proof, which is strictly forward-looking and makes no appeal to exchangeability, sheds some light onto the relationship between the Moran process and the Kingman coalescent.

4. Synchronous sampling.

We now ask about the probability of sampling a given genealogy. Specifically, we imagine that at a given time, we sample \( k \) individuals from the population at random. What is the genealogy linking these individuals?

We can represent the process of sampling a subgenealogy of size \( k \) in terms of the Moran genealogy game as follows. Specifically, we perform the following iterative procedure. (1) The player holding the highest-numbered black ball stands up. (2) He exchanges his second ball for the green ball bearing his name. (3) The standing player is dismissed, all players seated to his right shift one seat to the left, and the rightmost chair is removed. At each iteration of this procedure, we remove the highest-numbered black ball from play and dismiss one player. Thus after \( n - k \) steps, the configuration of the balls held by the remaining \( k \) players, and the numbers written on their slates, together determine the sampled genealogy. Each step in this procedure kills one player, sequentially applying the function \( \Upsilon \) (defined in §2B) for some randomly selected black ball \( u \). For \( w \in W^n \) and \( w' \in W^{n-1} \), let \( \mathcal{H}^n(w, w') \) be the probability that \( \Omega_n(w) = w' \) and denote by \( a \) the unique black ball in \( \bigcup_{j=1}^{n-1} w^j \setminus \bigcup_{j=1}^{n-2} w^j \). Then

\[
\mathcal{H}^n(w, w') = \frac{1}{n} \sum_{u=1}^{n} \mathbb{I}_{\Upsilon_u(w) = w'} = \frac{\mathbb{I}_{\Upsilon_u(w) = w'}}{n}.
\]

A counting argument similar to that employed in §2B shows that

\[
\sum_{w' \in W^{n-1}} \mathcal{H}^n(w, w') = \binom{n}{2}, \text{ for all } w' \in W^{n-1}.
\]  

(19)

As in Proposition 2, we decompose \( \mathcal{H}^n \) into \( n - 1 \) levels, writing \( \mathcal{H}^n(w, w') = \sum_{j=1}^{n-1} \mathcal{H}_j^n(w, w') \), where

\[
\mathcal{H}_j^n(w, w') := \frac{\mathbb{I}_{\Upsilon_a(w) = w' \& a \in w^j}}{n}.
\]  

(20)

Again, simple counting arguments establish that

\[
\sum_{w \in W^n} \mathcal{H}_j^n(w, w') = j \quad \text{and} \quad \sum_{w' \in W^{n-1}} \mathcal{H}_j^n(w, w') = \frac{B_j(w)}{n}.
\]  

(21)

where \( B_j \) is as defined in Proposition 2.
What is the action of the sampling operation $\Omega_n$ on probability measures? Given any probability measure $\nu$ on $\mathbb{X}^n$ and any event $\mathcal{E} \subset \mathbb{X}^{n-1}$, define

$$\Omega_n\nu(\mathcal{E}) := \int_{\mathcal{E}} \nu(\text{d}w \text{d}s) \sum_{j=1}^{n-1} \mathcal{H}_j^n(w, w') \mathcal{R}_j^n(s, s') \text{d}w' \text{d}s'. \tag{22}$$

Here, $\mathcal{R}_j^n$ is defined in a manner similar to Eq. 8, by

$$\mathcal{R}_j^n(s, s') := \prod_{k=1}^{j-2} \delta(s_k - s'_k) \cdot \delta(s_{j-1} + s_j - s'_{j-1}) \cdot \prod_{k=j}^{n-2} \delta(s_{k+1} - s'_{k}),$$

for $s \in \mathbb{S}^n$, $s' \in \mathbb{S}^{n-1}$. Applying Eq. 22 to the stationary measure, $\pi_n$, of the size-$n$ MGP (Theorem 6), we obtain

$$\Omega_n\pi_n(\text{d}w' \text{d}s') = \mathcal{I}(w', s') \text{d}w' \text{d}s',$$

where the density $\mathcal{I}$ satisfies

$$\mathcal{I}(w', s') = \sum_{j=1}^{n-1} \int_{\mathbb{W}^n \times \mathbb{S}^n} q_n(w) \mathcal{H}_j^n(w, w') \mathcal{R}_j^n(s, s') \prod_{m=1}^{n-1} p_m(s_m) \text{d}w \text{d}s$$

$$= \sum_{j=1}^{n-1} \left( \sum_{w \in \mathbb{W}^n} q_n(w) \mathcal{H}_j^n(w, w') \right) \left( \int_{\mathbb{S}^n} \mathcal{R}_j^n(s, s') \prod_{m=1}^{n-1} p_m(s_m) \text{d}s \right)$$

$$= \sum_{j=1}^{n-1} \frac{j^{2n-1}}{n!(n-1)!} \prod_{m=1}^{j-2} p_m(s'_m) \cdot Q_{j-1}(s'_{j-1}) \cdot \prod_{m=j}^{n-2} p_m(s'_m). \tag{23}$$

As before, $p_m(s) := \binom{m+1}{2} \exp\left(-\binom{m+1}{2}s\right)$ and, from Eq. 13,

$$Q_{j-1}(s) = \binom{j}{2} \binom{j+1}{2} \frac{\exp\left(-\binom{j}{2}s\right) - \exp\left(-\binom{j+1}{2}s\right)}{j}.$$

Substituting these expressions into Eq. 23 and doing some routine algebra gives

$$\mathcal{I}(w, s) = \exp\left(-\sum_{j=1}^{n-2} \binom{j+1}{2} s_j\right),$$

which implies that $\Omega_n\pi_n = \pi_{n-1}$. Iterating this result $n - k$ times establishes

**Theorem 8.** Let $X_n$ be the stationary Moran genealogy process of size $n$ and event rate $\mu$. For $k \leq n$, let $Z_k(t) = \Omega_k^n(X_n(t))$ be the corresponding size-$k$ sampled process. Then the marginal probability distribution of $Z_k(t)$ on $\mathbb{X}^k$ is given by the measure

$$\left(\frac{\mu}{\binom{n}{2}}\right)^{k-1} \exp\left(-\sum_{j=1}^{k-1} \binom{j+1}{2} \mu s_j\right) \text{d}w \text{d}s,$$

where, as before, $\text{d}w$ is the counting measure on $\mathbb{W}^n$ and $\text{d}s$ is Lebesgue measure on $\mathbb{S}^n$.

Theorem 8 implies that the genealogy of a synchronous sample contains no information on the population size $n$ unless the event rate $\mu$ is known, and vice versa. To render these parameters independently identifiable, it is necessary to sample asynchronously.
5. The Sampled Moran Genealogy Process.

5A. Moran genealogy game with asynchronous sampling.

We now turn to the situation where sampling occurs asynchronously, resulting in a sequence of genealogies whose probabilistic properties we wish to understand. Accordingly, we add some new rules to our parlor game.

Players and equipment. Before beginning the game, a finite or infinite sequence of times \(0 \leq t_1 < t_2 < \ldots\) is chosen arbitrarily. At each of these times, a single sample will be taken from the population. In addition to the \(n\) players of the Moran genealogy game, we must have two players for each of the samples. The equipment is the same as that used in the Moran genealogy game, but in addition, there is one red and one blue ball for each sample. Each one of the pair of players that will represent a sample receives a slate and a green ball bearing her own (unique) name. One of these players also takes a blue ball while the other takes a red ball. The red-ball holders and blue-ball holders are arranged in parallel queues.

Setup and play. The setup for the game with sampling is identical to that for the original game. Play, too, proceeds as before. However, play stops at each of the pre-selected sampling times. At sampling time \(t_k\), the following maneuvers occur. (1) Two more seats are placed to the right of the rightmost seat. (2) The number of a randomly chosen black ball is called out. (3) The player holding the corresponding black ball exchanges it for the green ball bearing the name, call it A, of the next red-ball holder in the queue. (4) A takes the first of the seats just placed. (5) The next blue-ball holder, call her B, in the queue exchanges her green ball for the red ball held by A. (6) B takes the second of the new seats. (7) Both A and B record the current time \(t_k\) on their slates. Thus, after a sampling event, player B sits in the rightmost seat, holding one blue and one red ball. Player A sits one seat to the left, holding B’s green ball and the randomly selected black ball. An animation depicting a typical simulation of the MGP with sampling can be found in the online appendix.

5B. Sampled Moran Genealogy Process.

Stationarity. While the definition of the Moran genealogy process with sampling, given above, makes sense in the absence of any stationarity assumptions, the results below will depend on the assumption that the underlying MGP is stationary. Accordingly, from this point forward, we assume that, prior to the first sample, the state of the MGP is a random draw from the stationary distribution (Corollary 7).

Pruning. We are naturally interested in the genealogies that express the relationships among only the sampled lineages. Accordingly, we define \(S_k\) to be the genealogy obtained by performing the following pruning procedure. Immediately following sampling time \(t_k\), we take a snapshot of the game tableau. We then sequentially dismiss all players holding black balls, as described in §4. As we noted before, the order in which the players are dismissed does not matter. Next, each player holding a blue ball consults the player to her immediate left. Let X be the name of the player with the blue ball and Y that of the player to her left. If the times recorded on their slates match, it is almost surely the case that Y holds both the green ball inscribed with X’s name. In this case, X trades her red ball for Y’s other ball. Y now trades the green ball bearing X’s name for the green ball bearing his own name, stands up, and is dismissed. All players from X rightward shift one seat to the left. If the slates of X and Y do not match, no action is taken.

Following the pruning, the tableau is reset according to the snapshot and play proceeds to the next sampling time. It is readily checked that one can also obtain \(S_k\) from \(S_{k+1}\) as follows. The rightmost player in \(S_{k+1}\), call him A, always holds both a blue and a red ball. Let B be the player holding the
green ball with A’s name. Let A exchange his red ball for his own green ball, stand up, and be dismissed. Now if B, who has just received this red ball, holds a green ball as well, she exchanges it for her own green ball, stands up, and is dismissed. If she holds a blue ball in addition to the newly received red one, she remains seated. The fact that one can obtain \( G_{k-1} \) from \( G_k \) in this way implies that one can dispense with the snapshots and obtain \( G_1, \ldots, G_k \) by playing the MGP with sampling up to sample \( k \), pruning to obtain \( G_k \), and then successively back-constructing the earlier genealogies as just described.

**Direct descent.** Once pruning has been performed, with probability 1, no two players have slates that match. Moreover, each player holding a blue and a red ball corresponds to a sample with no descendants among the other samples; such a player is called a *live sample*. On the other hand, each player holding both a blue and a green ball (called a *dead sample*) corresponds to a *direct-descent event*, whereby the lineages of two samples coincide exactly up to the time of the earlier sample (Fig. 3A).

**Markov property.** Evidently, when viewed as a discrete-time process, \( \{G_k\} \) is a Markov process; we call it the Sampled Moran Genealogy Process (SMGP). Viewed as a continuous-time jump process, with jump times \( t_k \), the sequence of sample genealogies \( \{G_k\} \) is only semi-Markov, but if the waiting times \( t_{k+1} - t_k \) are independently and identically exponentially distributed, it too is Markov. Animations showing simulations of the SMGP can be found in the online appendix.

**Definitions.** We now define some terms needed in the sequel. A player is represented by an (unordered) pair of colored balls (green, red, or blue) and a time. Given a sequence of sampling times \( \{t_k\} \), the state space \( \mathbb{G} = \mathbb{G}(\{t_k\}) \) consists of a set of finite sequences of players. For \( G \in \mathbb{G} \), \( |G| \) is thus the number of players in that genealogy. For \( j = 0, \ldots, |G| - 1 \), let \( u_j \) be the time on the slate of the player in seat \( j \).

Each player in \( G \) falls into one of three categories: *green* players are those that hold two green balls; *blue* players hold one green ball and one blue ball; *red* players hold one blue and one red ball (cf. Fig. 3). Red players correspond to live samples; blue players, to dead samples. Green players correspond to branch points in the genealogy. Let \( \text{green}(G) \) be the set of numbers of all the green players, excepting the one in seat zero. Similarly, let \( \text{blue}(G) \) and \( \text{red}(G) \) be the set of numbers of the blue and red players, respectively. Then the number of samples in \( G \) is \( k = |\text{blue}(G) \cup \text{red}(G)| \). Moreover, if \( r = |\text{red}(G)| \), then \( |\text{green}(G)| = r - 1 \) and \( |G| = k + r \). Note also that \( u_j = t_i \) for some \( i \) if, and only if, \( j \in \text{blue}(G) \cup \text{red}(G) \).

Now consider a realization of the SMGP, \( \{G_k\}_{k=1}^{\infty} \), with sampling times \( \{t_k\} \). It is clear that \( G_k \) differs from \( G_{k-1} \) just in that the lineage of sample \( k \) coalesces with (i.e., attaches to) \( G_{k-1} \) at some random time \(-\infty < A_k \leq t_{k-1}\). This attachment may happen either in a direct-descent event or else at a branching point (Fig. 3A). If the former, then \( G_k \) differs from \( G_{k-1} \) in that one red player of \( G_{k-1} \) has become blue and one red player has been added. If the latter, then \( G_k \) has added two players (one red and one green) to \( G_{k-1} \).

Given a realization, \( \{G_k\} \), of the SMGP, one can unambiguously define the *attachment times*, \( \{a_k\}_{k=2}^{\infty} \), so that \( a_k \) is the time at which the lineage of sample \( k \) attaches to \( G_{k-1} \). Note that \( a_1 \) is undefined and that \( a_k \leq t_{k-1} < t_k \) for \( k > 1 \). Notice also that every green player corresponds to an attachment: \( j \in \text{green}(G_k) \) when, and only when, \( u_j = a_i \) for some \( i \). Likewise, every blue player corresponds to both a sample and an attachment: \( j \in \text{blue}(G_k) \) if and only if there are \( i_1 \) and \( i_2 \), \( i_1 < i_2 \), such that \( u_j = t_{i_1} = a_{i_2} \).

Define the lineage-count function \( \ell_k : \mathbb{R} \rightarrow \mathbb{N} \) so that, for every \( t \), \( \ell_k(t) \) is the number of live samples in \( G_k \) with seating times greater than \( t \) minus the number of branch points with times greater than \( t \). That is

\[
\ell_k(t) := |\{j \in \text{red}(G_k) : u_j > t\}| - |\{j \in \text{green}(G_k) : u_j > t\}|. \tag{24}
\]
**Figure 3.** The Sampled Moran Genealogy Process (SMGP). (A) The tree representation of $G_{14}$ from a realization of the SMGP with $n = 10$ and $\mu = 10$. Green points correspond to players holding two green balls; red points, to players with one blue and one red ball (live samples); and blue points, to players holding one blue and one green ball (dead samples), which correspond to direct-descent events. The vertical lines indicate the epochs $e_1, \ldots, e_8 \in \text{live}(G_{14})$ as defined in Theorem 9. One can read the attachment times, $a_k$, of each of the samples, from this diagram. For example, the attachment time, $a_{14}$, of the 14th sample is that of the leftmost green ball, while $a_{13}$ is that of the rightmost blue ball, an indication that sample 13 descends directly from sample 10. (B) The lineage count function $\ell_{14}(t)$, as defined in the text. For every $k$, $\ell_k$ is piecewise constant and right continuous. It has a unit increase at every green player and a unit decrease at every red player. It agrees with number of lineages in the tree representation of $G_k$ at all its points of continuity.

We note that $\ell_k$ is right continuous with left limits. In terms of the tree representation of $G_k$, $\ell_k(t)$ is the number of lineages at time $t$ wherever the latter is unambiguous (Fig. 3B). Note too that $\ell_k(t) = 1$ for $t < u_1$ and $\ell_k(t) = 0$ for $t \geq t_k$.

Let $\text{live}(G_k)$ denote the set of sample times of all live samples, i.e., the times written on the slates of all red players and let $\text{dead}(G_k)$ be the set of sample times that are dead (i.e., the times written on the slates of blue players). Note that $e \in \text{live}(G_k)$ implies that $\ell_k$ decreases by one unit at time $e$. By contrast, $\ell_k$ is continuous at $e \in \text{dead}(G_k)$. 

5C. SMGP transition probabilities.

We are interested in the probability measure on genealogies generated by the SMGP. To obtain this, we will begin by deriving an expression for the measure of $G_{k+1}$ conditional on $G_k$. Theorem 9 depends on Lemmas 10 and 11, the statements of which we temporarily postpone.

**Theorem 9.** Let $\text{live}(G_k) = \{e_1, \ldots, e_q\}$, where $e_1 < e_2 < \cdots < e_q$. Then, we have the following

\[ -\log P[A_{k+1} < a \mid G_k] = \int_a^\infty \ell_k(t) \left( \frac{n}{2} \right) \mu(t) dt + \sum_{\{j : a \leq e_j\}} \log \frac{n - \ell_k(e_j)}{n - \ell_k(e_j) - 1}, \]  

\[ \text{(25)} \]

\[ -\log P[A_{k+1} \leq a \mid G_k] = \int_a^\infty \ell_k(t) \left( \frac{n}{2} \right) \mu(t) dt + \sum_{\{j : a < e_j\}} \log \frac{n - \ell_k(e_j)}{n - \ell_k(e_j) - 1}, \]  

\[ \text{(26)} \]

\[ -\log P[A_{k+1} = a \mid G_k] = \begin{cases} \log (n - \ell_k(a)) - \log P[A_{k+1} \leq a], & a \in \text{live}(G_k), \\ 0, & a \notin \text{live}(G_k). \end{cases} \]  

\[ \text{(27)} \]

Moreover, the probability density of $A_{k+1}$, conditional on $G_k$, is given by

\[ f_{A_{k+1}|G_k}(a) \, da = P[A_{k+1} < a \mid G_k] \left( \frac{\ell_k(a)}{\left( \frac{n}{2} \right)} \mu(a) + \sum_{n \in \text{live}(G_k)} \frac{1}{n - \ell_k(a)} \, dn \right), \]  

\[ \text{(28)} \]

where $da$ signifies Lebesgue measure and $dn$, counting measure, both on $\mathbb{R}$.

**Proof.** Let $J(a) := \min\{j : a \leq e_j\}$. It is an identity that

\[ P[A_{k+1} < a] = P[A_{k+1} < a \mid A_{k+1} < e_{J(a)}] \times \prod_{j=J(a)}^q P[A_{k+1} < e_j \mid A_{k+1} \leq e_j] \times \prod_{j=J(a)}^{q-1} P[A_{k+1} \leq e_j \mid A_{k+1} < e_{j+1}] \times P[A_{k+1} \leq e_q]. \]

Now, by Lemma 10,

\[ P[A_{k+1} < a \mid A_{k+1} < e_{J(a)}] = \exp \left( -\int_{a}^{e_{J(a)}} \frac{\ell_k(t)}{\left( \frac{n}{2} \right)} \mu(t) dt \right) \]

and also, for every $j$,

\[ P[A_{k+1} \leq e_j \mid A_{k+1} \leq e_{j+1}] = \exp \left( -\int_{e_j}^{e_{j+1}} \frac{\ell_k(t)}{\left( \frac{n}{2} \right)} \mu(t) dt \right). \]

On the other hand, by Lemma 11, we have

\[ P[A_{k+1} < e_j \mid A_{k+1} \leq e_j] = 1 - P[A_{k+1} = e_j \mid A_{k+1} \leq e_j] = \frac{n - \ell_k(e_j) - 1}{n - \ell_k(e_j)}, \]

for all $j$. Finally, note that $e_q = \ell_k$ and that, therefore, $P[A_{k+1} \leq e_q] = 1$. Putting these all together, we obtain Eq. 25, with Eqs. 26–28 as elementary consequences. \qed

**Lemma 10.** With the definitions as in Theorem 9,

\[ P[A_{k+1} < a \mid A_{k+1} = e_j] = \exp \left( -\int_{a}^{e_j} \frac{\ell_k(t)}{\left( \frac{n}{2} \right)} \mu(t) dt \right), \]

whenever $e_{j-1} < a < e_j$.  


Moreover,
\[ P[A_{k+1} \leq e_j-1 | A_{k+1} < e_j] = \exp \left( - \int_{e_j-1}^{e_j} \frac{\ell_k(t)}{n} \mu \, dt \right). \]

**Proof.** Viewing the lineage attachment as a survival process in backward time, it is sufficient to show that the hazard of attachment is
\[ \lambda(t) = \frac{\ell_k(t)}{n} \mu. \]

To see this, let \( a \) and \( \varepsilon > 0 \) be such that \( e_j-1 \leq a < a + \varepsilon < e_j \). Note that, since the interval \((a, a + \varepsilon)\) lies between adjacent live samples, no direct-descent events can have occurred in this interval. Therefore, conditional on \( A_{k+1} < a + \varepsilon \), coalescence of the lineage of sample \( k + 1 \) with \( S_k \) occurs within this interval if and only if a Moran event occurs in the interval and the pair of players involved in the event include the unique ancestor of sample \( k \) and one of the \( \ell_k(a) = \ell_k(e_j-1) \) players who are ancestors of one or more of the first \( k \) samples. The probability that a Moran event occurred in the interval \((a, a + \varepsilon)\) is \( \mu \varepsilon + o(\varepsilon) \). Conditional on \( A_{k+1} < a + \varepsilon \), the unique ancestor of sample \( k + 1 \) at time \( a + \varepsilon \), by definition, is not among the \( \ell_k(a) = \ell_k(e_j-1) \) lineages of \( S_k \) present at this time. Therefore, if a Moran event has occurred in the interval, of the \( \binom{n}{2} \) pairs that might have been involved in the event, exactly \( \ell_k(a) \) of these involve one of the lineages of \( S_k \) and the unique ancestor of sample \( k + 1 \). Since all of these pairs are equally likely to have been involved, the probability that a coalescence event occurs in the interval is
\[ P[a < A_{k+1} | A_{k+1} < a + \varepsilon] = \frac{\ell_k(a)}{\binom{n}{2}} \mu \varepsilon + o(\varepsilon) = \lambda(a) \varepsilon + o(\varepsilon). \]

The second equation in the statement of the lemma follows from the fact that \( \ell_k \) is right continuous. \( \square \)

**Lemma 11.** With the definitions as in Theorem 9, we have
\[ P[A_{k+1} = e_j | A_{k+1} \leq e_j] = \frac{1}{n - \ell_k(e_j)}. \]

**Proof.** If \( A_{k+1} \leq e_j \), then by definition, the unique ancestor of sample \( k + 1 \) at time \( e_j \) cannot be any one of the \( \ell_k(e_j) \) individuals ancestral at time \( e_j \) to the first \( k \) samples. However, it is equally likely to be any one of the \( n - \ell_k(e_j) \) other members of the population. Of these, exactly one corresponds to the sample at \( e_j \). \( \square \)

Theorem 9 establishes the probability distribution of \( A_k | S_{k-1} \). It is only a short step to that of \( S_k | S_{k-1} \). Let \( f_{S_k|S_{k-1}}(a) \) denote the probability density function of \( S_k \) conditional on \( S_{k-1} \), evaluated at attachment time \( a_k = a \).

**Corollary 12.** The conditional probability density of \( S_k | S_{k-1} \) is
\[ f_{S_k|S_{k-1}}(a_k) \, da_k = P[A_k \leq a_k \mid S_{k-1}] \left( \frac{\mu}{n} \right) da_k + \frac{1}{n - \ell_{k-1}(a_k)} \, dn_k, \]

where \( da_k \) and \( dn_k \) are, respectively, Lebesgue and counting measure on \( \mathbb{R} \), the space of allowable attachment times \( a_k \).

**Proof.** By Theorem 9, we have that
\[ f_{A_k|S_{k-1}}(a_k) \, da_k = P[A_k \leq a_k \mid S_{k-1}] \left( \frac{\ell_{k-1}(a_k)}{n} \right) da_k + \frac{1}{n - \ell_{k-1}(a_k)} \, dn_k, \quad (29) \]
where $d_{nk}$ denotes counting measure on $\mathbb{R}$. The second factor in Eq. 29 has two terms, the first of which accounts for the attachment of the $k$-th sample lineage in one of the intervals between two players of $G_{k-1}$. When such an attachment occurs, there are precisely $\ell_{k-1}(a_k)$ lineages in $G_{k-1}$ to which the new lineage might attach. Equivalently, there are $\ell_{k-1}(a_k)$ green balls bearing the names of players to the right of $a_k$ held by players to the left, one of which is selected at random upon attachment. Under the assumption that the underlying MGP is stationary, each of these is equally likely. On the other hand, when the new lineage attaches via a direct-descent event, there is (almost surely) only one choice as to where the attachment will occur. □

5D. Marginal distribution of SMGP genealogies.

Corollary 12 establishes the probability distribution of each $G_k$, conditional on $G_{k-1}$. We can use this to compute the probability distribution for any sequence of genealogies, $\{G_j\}_{j=1}^k$ generated by the SMGP. In particular, we will derive expressions for probability measures on the set of genealogies $G$. When the underlying MGP is stationary, as we have assumed, these will all be uniform with respect to the genealogies’ discrete aspect (the sequence of pairs of colored balls), but will have nontrivial dependence on the continuous aspect, i.e., the attachment times $\{a_k\}_{k=2}^\infty$ of the second and successive samples. Accordingly, we will focus on the latter. Specifically, we will denote the probability on the space of $k$-sample genealogies by

$$f_{G_k}(a) \, da$$

where $a = (a_2, \ldots, a_k)$ is the vector of attachment times, $da = da_2 \cdots da_k$ denotes Lebesgue measure on $\mathbb{R}^{k-1}$, and $f_{G_k}$ is a probability density function.

We begin by establishing some elementary results regarding the lineage-count functions, $\ell_k$, defined above.

**Lemma 13.** Let $\{G_k\}_{k=1}^\infty$ be an SMGP, with sample times $\{t_k\}$. Let $\{a_k\}_{k=2}^\infty$ be the attachment times of each of the successive samples. Then

$$\sum_{j=2}^k \int_{a_j}^\infty \ell_{j-1}(t) \, dt = \int_{-\infty}^\infty \left( \frac{\ell_k(t)}{2} \right) \, dt.$$

**Proof.** We argue by induction on $k$. First, note that $a_2 \leq t_1 < t_2$. Moreover,

$$\ell_1(t) = \begin{cases} 1, & t < t_1, \\ 0, & \text{otherwise}, \end{cases} \quad \text{and} \quad \ell_2(t) = \begin{cases} 1, & t < a_2, \\ 2, & a_2 \leq t < t_1, \\ 1, & t_1 \leq t < t_2, \\ 0, & \text{otherwise}. \end{cases}$$

It follows that

$$\int_{a_2}^{t_1} \ell_1(t) \, dt = t_1 - a_2 = \int_{a_2}^{t_1} \ell_2(t) \, dt = \int_{-\infty}^{\infty} \left( \frac{\ell_2(t)}{2} \right) \, dt.$$
Now, we suppose that the result holds for $k$ and observe that this implies
\[
\sum_{j=2}^{k+1} \int_{a_j}^{\infty} \ell_{j-1}(t) \, dt = \int_{-\infty}^{\infty} \left( \frac{\ell_k(t)}{2} \right) \, dt + \int_{a_{k+1}}^{\infty} \ell_k(t) \, dt \\
= \int_{-\infty}^{a_{k+1}} \left( \frac{\ell_k(t)}{2} \right) \, dt + \int_{a_{k+1}}^{t_{k+1}} \left( \frac{\ell_k(t) + 1}{2} \right) \, dt + \int_{t_{k+1}}^{\infty} \left( \frac{\ell_k(t) + 1}{2} \right) \, dt \\
= \int_{-\infty}^{\infty} \left( \frac{\ell_{k+1}(t)}{2} \right) \, dt.
\]
Here, we have used the identity $(m/2) + m = (m+1)/2$ and the facts that $\ell_k(t) = 0$ for $t > t_{k+1}$ and
\[
\ell_{k+1}(t) = \begin{cases} 
\ell_k(t) + 1, & a_{k+1} \leq t < t_{k+1}, \\
\ell_k(t), & \text{otherwise.}
\end{cases}
\]
\[
\square
\]

Now observe that sample $j$, taken at time $t_j$, is live in $S_j$. With each subsequent sample, there is a chance that it will die. While it remains alive, however, each subsequent sample may attach to the left or to the right of $t_j$. We define $m(j, k)$ to be the number of samples that attach to the left of $t_j$ up to the point that sample $j$ dies or $k$ is reached. That is, $m(j, k) = \{i : j < i \leq k \text{ and } A_i < t_j \text{ and } A_r \neq t_j \text{ for all } r < i\}$. When $t_j \in \text{ dead}(S_k)$, then $m(j, k)$ is the lineage count at $t_j$ at the time when $t_j$ was killed, i.e., $A_i = t_j$ implies $m(j, k) = \ell_{i-1}(t_j)$. Likewise, $t_j \in \text{ live}(S_k)$ implies $m(j, k) = \ell_k(t_j)$.

**Lemma 14.** Let $\{S_k\}_{k=1}^{\infty}$ be an SMGP, with sample times $\{t_k\}_{k=1}^{\infty}$ and attachment times $\{a_k\}_{k=2}^{\infty}$. Define $m(j, k)$ as above. Then
\[
\sum_{j=1}^{k-1} \sum_{e \in \text{ live}(S_j)} \log \frac{n - \ell_j(e)}{n - \ell_j(e) - 1} \mathbb{I}_{e > a_{j+1}} = \sum_{j=1}^{k-1} \log \frac{n}{n - m(j, k)}.
\]

**Proof.**
\[
S := \sum_{j=1}^{k-1} \sum_{e \in \text{ live}(S_j)} \log \frac{n - \ell_j(e)}{n - \ell_j(e) - 1} \mathbb{I}_{e > a_{j+1}} = \sum_{j=1}^{k-1} \sum_{i=1}^{j} \mathbb{I}_{t_i \in \text{ live}(S_j)} \mathbb{I}_{t_i > a_{j+1}} \log \frac{n - \ell_j(t_i)}{n - \ell_j(t_i) - 1}.
\]
\[
= \sum_{i=1}^{k-1} \sum_{j=i}^{k} \mathbb{I}_{t_i \in \text{ live}(S_j)} \mathbb{I}_{t_i > a_{j+1}} \log \frac{n - \ell_j(t_i)}{n - \ell_j(t_i) - 1}.
\]
Now, note that $t_i \in \text{ live}(S_j)$ and $t_i > a_{j+1}$ if, and only if, $t_i \in \text{ live}(S_{j+1})$ and $t_i > a_{j+1}$. Therefore,
\[
S = \sum_{i=1}^{k-1} \sum_{j=i+1}^{k} \mathbb{I}_{t_i \in \text{ live}(S_j)} \mathbb{I}_{t_i > a_j} \log \frac{n - \ell_{j-1}(t_i)}{n - \ell_{j-1}(t_i) - 1}.
\]

The inner sum contains one term for each sample $j > i$ such that $a_j < t_i$ up to the sample (if any) for which $a_j = t_i$, at which point sample $i$ dies. Because $\ell_j(t_j) = 0$ and, for each such sample $j$, $\ell_j(t_i) = \ell_{j-1}(t_i) + 1$, the sum telescopes, yielding
\[
S = \sum_{i=1}^{k-1} \log \frac{n}{n - m(i, k)}.
\]
\[
\square
We can now state the main result of this section, which gives the joint probability distribution of any sequence of SMGP genealogies and, equivalently, the unconditional probability distribution of each genealogy generated by the SMGP.

**Theorem 15.** Let \( \{S_k\}_{k=1}^\infty \) be the sampled Moran genealogy process, with sampling times \( \{t_k\} \) and attachment times \( \{a_k\} \). Then

\[
f_{S_1,\ldots,S_k}(a) \, da = n^{-k} \left( \frac{\mu}{2} \right)^{r-1} \exp \left( - \int_{-\infty}^\infty \frac{\ell_k(t)}{2} \, dt \right) \prod_{\{i:j>i \, a_j=t_i\}} \left( 1 - \frac{\ell_k(t_i)}{n} \right) \prod_{\{j:j<i \, a_j=t_i\}} da_j \prod_{\{j:j<i \, a_j=t_i\}} dn_j.
\]

where \( r = |\text{live}(S_k)| = \{j : \exists i \, a_j = t_i\} \).

**Proof.** The joint probability density of \( \{S_j\}_{j=1}^k \) is the product of the one-step conditional probability densities:

\[
f_{S_1,\ldots,S_k}(a) \, da = \prod_{j=2}^k f_{S_j|S_{j-1}}(a_j) \, da_j
\]

\[
= \prod_{j=2}^k \mathbb{P}[A_j \leq a_j | S_{j-1}] \prod_{j=2}^k \left( \frac{\mu}{n} \right) da_j + \prod_{j=2}^k \frac{\mu_{a_j \in \text{live}(S_{j-1})}}{\ell_{j-1}(a_j)} dn_j.
\]

Let \( F \) denote the first product in the last expression and \( G \), the second. By Lemmas 13 and 14, we can simplify \( F \):

\[
F = \exp \left( - \int_{-\infty}^\infty \frac{\ell_k(t)}{2} \, dt \right) \prod_{j=1}^k \frac{n-m(j,k)}{n}.
\]

Here we have used the fact that \( m(k,k) = 0 \). Now, \( G \) contains one factor for each sample. We can divide it into two sub-products, according to whether the sample was a direct descendant of an earlier sample or not:

\[
G = \prod_{\{j:a_j \notin \text{live}(S_{j-1})\}} \left( \frac{\mu}{n} \right) da_j \prod_{\{j:a_j \in \text{live}(S_{j-1})\}} \frac{dn_j}{n - \ell_{j-1}(a_j)}.
\]

Here, we have taken the liberty of redefining the continuous portion of the probability density at a finite number of points. We notice that the first product in the above has one term for each green player in \( S_k \), while the second product has one term for each blue player. For \( j \in \text{green}(S_k) \cup \text{blue}(S_k) \), let \( s(j) \) the number of the sample that attaches at \( j \), i.e., \( u_j = a_{s(j)} \). With this definition, we have

\[
G = \prod_{j \in \text{green}(S_k)} \left( \frac{\mu}{n} \right) da_{s(j)} \prod_{j \in \text{blue}(S_k)} \frac{dn_{s(j)}}{n - m(s(j),k)}.
\]

Since every sample is either a red or a blue player, Eq. 31 is equivalent to

\[
G = \left( \frac{\mu}{n} \right)^{r-1} \prod_{j=1}^k \frac{1}{n-m(j,k)} \prod_{e \in \text{live}(S_k)} (n-\ell_k(e)) \prod_{j \in \text{green}(S_k)} da_{s(j)} \prod_{j \in \text{blue}(S_k)} dn_{s(j)}
\]

\[
= \left( \frac{\mu}{n} \right)^{r-1} \prod_{j=1}^k \frac{1}{n-m(j,k)} \prod_{\{i:j>i \, a_j=t_i\}} (n-\ell_k(t_i)) \prod_{\{j:j<i \, a_j=t_i\}} da_j \prod_{\{j:j<i \, a_j=t_i\}} dn_j,
\]
where \( r = |\{ j : \exists i, a_j = t_i \}| \) is the number of red players (live samples) in \( S_k \). Returning to Eq. 30, we obtain the result. □

Observe that the joint density of a sequence \( \{ S_j \}_{j=1}^k \) of SMGP genealogies depends only on the properties of \( S_k \). This is not surprising in view of the following

**Corollary 16.**

\[ f_{S_1, \ldots, S_k} = f_{S_k}. \]

**Proof.** Since, for each \( k \), \( P [ S_{k-1} | S_k ] = 1 \), the result is trivial. □

The log likelihood is of great importance from an inference point of view. It is given explicitly in the following

**Corollary 17.** For \( k > 1 \), if \( S_k \) is a \( k \)-sample genealogy drawn from the Sampled Moran Genealogy Process with sampling times \( t_1, \ldots, t_k \) and attachment times \( a_2, \ldots, a_k \), then the log likelihood is

\[
\log \mathcal{L} = (r - k) \log n + (r - 1) \log \left( \frac{\mu}{(n/2)} \right) - \int_{-\infty}^{\infty} \left( \frac{\ell_k(t)}{2} \right) \mu \, dt + \sum_{e \in \text{live}(S_k)} \log \left( 1 - \frac{\ell_k(e)}{n} \right),
\]

where \( r = |\text{live}(S_k)| \).

In view of the form of the log likelihood given by Corollary 17, it is clear that the population size \( n \) and event rate \( \mu \) are individually identifiable on the basis of sequentially sampled genealogies.

6. Discussion.

The recent paper by Wirtz & Wiehe (2019) defines the Evolving Moran Genealogy Markov chain, which is identical to our \( W \) chain (which encodes the dynamics of the topological structure of the genealogies and ignoring branch lengths) when the latter is stationary. These authors establish a number of results regarding this process, for finite population sizes, including derivations of the evolution of tree balance statistics and the form of the process’ time-reversal.

Etheridge & Kurtz (2019) extend the look-down construction of Donnelly & Kurtz (1996, 1999) to a much richer class of demographies than we consider here: Moran demography is only one of the simpler special cases their elegant abstract approach subsumes. However, Etheridge & Kurtz (2019) are principally concerned with deriving results in the infinite-population limit. Nor do they consider the effects of asynchronous sampling or direct descent, as we do here.

If the sampling time process \( \{ t_k \} \) is a Poisson process with rate \( \nu \), and if \( \nu \ll \mu \), one will have \( r \sim k \) and \( \ell_k \ll n \). In this case, we have the approximation

\[
\log \mathcal{L} \approx (k - 1) \log \left( \frac{\mu}{(n/2)} \right) - \int_{-\infty}^{\infty} \left( \frac{\ell_k(t)}{2} \right) \mu \, dt - \sum_{j=1}^{k} \frac{\ell_k(t_j)}{n}.
\]

One can compare this quantity with that obtained from specializing the phylodynamic methods of Volz et al. (2009) and Rasmussen et al. (2011) to the case of Moran demography. In the same limit \( \nu \ll \mu \) and with \( n \to \infty \), these methods agree and give an expression for the likelihood of a given genealogy that, in our notation, is

\[
\log \mathcal{L}_{\text{VR}} = (k - 1) \log \left( \frac{\mu}{(n/2)} \right) - \int_{-\infty}^{\infty} \left( \frac{\ell_k(t)}{2} \right) \mu \, dt + \sum_{i \in \text{green}(S_k)} \log \left( \frac{\ell_k(a_i)}{2} \right).
\]
Comparing Eqs. 32 and 33, we see that the expressions differ by two terms, one of which depends only on the data and is therefore irrelevant from the perspective of inference. The term that remains is of order \( \frac{\ell_k}{n} \), where \( \langle \ell_k \rangle \) is the mean of \( \ell_k(t) \) across sampling times. Since \( \langle \ell_k \rangle \sim n \sqrt{\nu/\mu} \) as \( n \to \infty \) when \( \nu \ll \mu \), we see that this discrepancy is roughly \( \sqrt{\nu/\mu} \) per sample. Thus the expressions of Volz et al. (2009) and Rasmussen et al. (2011) are good approximations when sampling is relatively sparse and population sizes are large.

More generally, the method of Rasmussen et al. (2011) was derived using layers of approximations which we have shown to be unnecessary. In particular, Volz et al. (2009) derived a coalescent likelihood in a large-population deterministic limit; Rasmussen et al. (2011) then used this as an approximate likelihood for a stochastic model. By contrast, we have derived an exact formula similar to that of Volz et al. (2009) but which applies to a stochastic dynamic model for all population and sample sizes.

A significant achievement of Volz et al. (2009) was to improve on previous attempts to apply coalescent methods for time-varying populations. The present paper does not directly address this extension, but it has not escaped our notice that analogues of Lemmas 10 and 11, and therefore of Theorems 9 and 15, exist for a broad class of birth-death processes, though generalization of these results is beyond the scope of the present paper. In future work, we will develop exact inference methodology that improves upon the heuristic proposal of Rasmussen et al. (2011).

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Online Appendix.

An online appendix is available, containing illustrative animations, simulator code, and numerical verification of some of the statements proved in the text. These materials will be permanently archived upon acceptance of the paper.

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