Age of an allele and gene genealogies of nested subsamples for populations admitting large offspring numbers

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May 5, 2014

Keywords: age of allele, multiple merger coalescent processes, infinite alleles mutation model, Moran model, nested subsamples, weak convergence

Summary Coalescent processes, including mutation, are derived from Moran type population models admitting large offspring numbers. Including mutation in the coalescent process allows for quantifying the turnover of alleles by computing the distribution of the number of original alleles still segregating in the population at a given time in the past. The turnover of alleles is considered for specific classes of the Moran model admitting large offspring numbers. Versions of the Kingman coalescent are also derived whose rates are functions of the mean and variance of the offspring distribution. High variance in the offspring distribution results in higher turnover and younger age of alleles than predicted by the usual Kingman coalescent.

1 Introduction

The age of an allele is central to understanding the nature of extant variation. The first mathematical treatment of the age of alleles were done by [Kimura and Ohta (1973), Maruyama (1974), and Maruyama and Kimura (1975)]. In particular, [Kimura and Ohta (1973)] find, using [Kimura (1964)]’s diffusion model, that alleles in low frequency in the population have surprisingly old expected ages.
More recently, coalescent techniques have been applied to the study of the age of an allele (Donnelly and Tavare, 1986; Griffiths and Tavare, 1998; Saunders et al., 1984; Stephens, 2000; Tavare, 1984; Watterson, 1984). Two main extensions to the coalescent were obtained by Saunders et al. (1984). One is the analysis of the ancestry of nested subsamples, which, for example, yields the probability that a sample shares its’ most recent common ancestor with the whole population. The other extension is the inclusion of neutral mutation in the ancestral process, which, in turn, yields the probability that the oldest allele in a population is included in a sample. These extensions are reviewed by Tavare (1984). Donnelly and Tavare (1986) consider age ordering of alleles in a sample, and obtain, for example, the distribution of the number of representatives of the oldest allele in a sample, a result originally due to Kelly (1977). The ancestral processes derived by Watterson (1984), Saunders et al. (1984), Tavare (1984), and Donnelly and Tavare (1986) were all based on the usual Moran (1958, 1962) model of reproduction. The Moran model belongs to a large class of exchangeable population models, originally introduced by Cannings (1974). The Moran, and indeed the celebrated Wright-Fisher (Fisher, 1930; Wright, 1931) model can be characterized as low offspring number models by allowing individuals to have very many offspring with only negligible probability.

Population models admitting large offspring numbers with non-negligible probability (Eldon and Wakeley, 2006; Huillet and Möhle, 2011; Sargsyan and Wakeley, 2008; Schweinsberg, 2003) have recently been proposed as appropriate for organisms with high fecundity and high initial mortality, characteristics of many marine taxa (Árnason, 2004; Beckenbach, 1994; Hedgecock, 1994; Hedgecock et al., 1982), and possibly forest trees (Ingvarsson, 2010). The gene genealogies of samples drawn from populations admitting large offspring numbers are characterised by multiple mergers of ancestral lineages (Donnelly and Kurtz, 1999; Möhle and Sagitov, 2001; Pitman, 1999; Sagitov, 1999; Schweinsberg, 2000), or in which any number of active ancestral lineages may coalesce to the same common ancestor. In comparison, the Kingman coalescent (Kingman, 1982a,b) allows at most two lineages to coalesce each time. One consequence of the multiple merger property is that exact computations of many quantities of our interest can only be done
The age and rate of turnover of alleles in a population admitting large offspring numbers is our focus. In the spirit of Saunders et al. (1984) and Tavaré (1984), we consider the coancestry of nested subsamples drawn from a modified Moran model population, in which the number of offspring contributed each timestep to the population is random. The rate of turnover of alleles associated with the Kingman coalescent derived from populations with different offspring distributions is considered, as well as probabilities of a subsample carrying the oldest allele of a sample drawn from populations admitting large offspring numbers.

2 A population model of overlapping generations

Consider a simple haploid population models of overlapping generations, in which at each timestep a single individual (the parent) chosen uniformly at random from the population contributes offspring to replace those who perished in that timestep, so the population size stays constant at $N$. The coalescent processes obtained from these population models will then be used to study the coancestry process of nested subsamples. Let $U$ denote the random number of offspring produced by the parent, who always persists. In the usual Moran model, the parent always has one offspring ($U = 1$ a.s.). Eldon and Wakeley (2006) consider a simple mixture distribution, in which $U = 1$ with probability $1 - \varepsilon_N$, and $U$ takes value $\lfloor \psi N \rfloor$ with probability $\varepsilon_N$, in which $\psi \in (0, 1)$ is a constant. Eldon and Wakeley (2006) use this simple model to illustrate the idea that population models admitting large offspring numbers may be more appropriate for high fecundity organisms than the usual Wright-Fisher and Moran models. A clear drawback of the model of Eldon and Wakeley (2006) is that $\psi$ is a constant, which means that the parent always has exactly the same number of parents, even when a large offspring number event occurs. Two simple extensions of the usual Moran model will now be considered. Our aim is to incorporate, in a natural way, the randomness inherent in the number of offspring contributed each timestep.

We will work with two models. First, let us set notation. Let $X$ be a random variable with
probability distribution $P_X$, in which $P[X \geq 1] = 1$, and finite moments, $\sup_N \mathbb{E}[X^k] < \infty$ for all $k \geq 1$. Let $Y$ be a random variable taking values on the unit interval. Finally, let $B$ be a Bernoulli random variable with $P[B = 1] = \varepsilon_N$. In model 1, we take $U$ to be a simple mixture of $X$ and $Y$ (assuming $YN \in \mathbb{N}$):

$$U = X(1 - B) + (NY)B$$

(1)

In model 2, we let $U$ be a Poisson random variable with random mean $M$, in which $M$ is a mixture of $X$ and $Y$, $M = X(1 - B) + (NY)B$.

The idea behind the mixture distribution is the assumption that most of the time the parent contributes only few offspring to the population due to restrictions on resources such as space. Occasionally, however, there is disturbance in the environment, such as a storm or a forest fire. The disturbance wipes away a fraction $Y$ of the population, allowing $NY$ offspring to take foothold in the population. For simplicity, we assume that the difference between the number of individuals that perish, and the number of offspring replacing them, is negligible. These ideas are similar to the ones proposed by Schweinsberg (2003), who models the distribution of ‘potential’ offspring, rather than the ones that actually take foothold in the population. However, Lemma 6 in Schweinsberg (2003) establishes a link between the transition probability of the ancestral process and the distribution of the potential offspring. The timescale in Schweinsberg (2003)’s model depends on a parameter of the distribution of the potential offspring. The timescale in our model will be independent of the distribution on $U$. A similar idea of extending the usual Moran model is also raised by Birkner and Blath (2009). One can also view the mixture distribution as a simple model of a bottleneck followed by a rapid growth, or recolonization. Indeed, Grant and Bowen (1998) suggest populations of sardines and anchovies may have been subject to periodic bottlenecks and recolonizations.

Convergence of the coalescent process $(R_m; m \in \mathbb{N}_0)$ arising from both models is given in Appendix, as proof of convergence relies on standard theory. The coalescent process $(R_m; m \in \mathbb{N})$ without mutation describes the random ancestral relation among a set of $n$ individuals drawn at random from the population at time $m = 0$. A state of the coalescent process $R_m$ is, by
definition, the random equivalence relation containing individuals \((i, j)\) only if \(i\) and \(j\) share a common ancestor at timestep \(r\) in the past. One can think of the coalescent process as following labelled (or enumerated) ancestral lines back in time.

Time in our model will be in units of \(T_N \equiv N^2 \land \varepsilon^{-1}_N\), and will therefore be independent of any parameters associated with the offspring distribution on \(X\) and \(Y\). Thus, if \(N^2 \varepsilon_N \to 0\) then large offspring number events occur with negligible probability in a large population, and the coalescent process admits only mergers of two active ancestral lineages. Otherwise the ancestral process admits multiple mergers of active ancestral lineages.

For our purposes it suffices to consider the gene genealogical process \(\left(A^{(\ell)}(t) ; t \geq 0\right)\) that counts the number of ancestors, in which \(A^{(\ell)}\) is associated with model \(\ell \in \{1, 2\}\). To describe the rate matrix of \(A^{(\ell)}\), write

\[
\beta_1 = \mathbb{E}[X(X + 1)]
\]

\[
\beta_2 = 2\mathbb{E}[X] + \mathbb{E}[X^2]
\]

(2)

If \(N^2 \varepsilon_N \to 0\) large offspring number events are negligible and the rate matrix \(Q^{(\ell)} = \left(q^{(\ell)}_{i,j}\right)_{i,j \in [n]}\) associated with model \(\ell\) is given by

\[
q^{(\ell)}_{i,j} = \begin{cases} 
\binom{i}{2} \beta_{\ell} & \text{if } j = i - 1 \\
-\binom{i}{2} \beta_{\ell} & \text{if } j = i \\
0 & \text{otherwise.}
\end{cases}
\]

(3)

If \(N^2 \varepsilon_N\) tends to a constant \(\phi\) one obtains rate matrix \(Q^{(\ell)}\) given by

\[
q^{(\ell)}_{i,j} = \begin{cases} 
\binom{i}{2} \left(\beta_{\ell} + \phi \mathbb{E}[Y^2(1 - Y)^{i-2}]\right) & \text{if } j = i - 1 \\
\phi \binom{i}{2} \mathbb{E}[Y^k(1 - Y)^{i-k}] & \text{if } j = i - k + 1 \\
-\binom{i}{2} \beta_{\ell} - \phi \mathbb{E}[1 - (1 - Y)^i - iY(1 - Y)^{i-1}] & \text{if } j = i \\
0 & \text{otherwise.}
\end{cases}
\]

(4)

Finally, if \(N^2 \varepsilon_N \to \infty\) large offspring number events are dominating and the rate matrix \(Q\) has entries

\[
q_{i,j} = \begin{cases} 
\binom{i}{k} \mathbb{E}[Y^k(1 - Y)^{i-k}] & \text{if } j = i - k + 1 \\
- (1 - \mathbb{E}[(1 - Y)^i + iY(1 - Y)^{i-1}]) & \text{if } j = i \\
0 & \text{otherwise.}
\end{cases}
\]

(5)

In the present work we will primarily be concerned with three examples of a \(\Lambda\) coalescent. One is the process derived by [Schweinsberg (2003)](Schweinsberg2003), in which \(\Lambda\) is the probability measure associated
with the beta distribution, for $1 < \alpha < 2,$

$$
\Lambda(dx) = \frac{1}{\Gamma(2-\alpha)\Gamma(\alpha)} x^{1-\alpha}(1-x)^{\alpha-1} dx.
$$

In theory one can include the case $\alpha = 1$. When $\alpha = 1$, however, the $\Lambda$ measure is simply the uniform distribution on $[0, 1]$, which may not be biologically realistic. For comparison, $\alpha$ is estimated to be around 1.5 \cite{Eldon2011} for data on Atlantic cod \cite{Arnason2004}. Another example of a $\Lambda$ coalescent we will consider is when $\Lambda$ is a scaled point mass at some point $\psi \in (0, 1)$, $\Lambda(dx) = x^2 \delta_\psi dx$. The point mass process is the process derived by \cite{EldonWakeley2006}. The third example we consider is when $Y$ takes the beta distribution with parameters $\alpha$ and $\beta$, in which case the rate $q_{i,j}$ for $j < i$ of the generator $Q$ in Equation (5) takes the form, with $2 \leq k \leq i$,

$$
q_{i,j} = B(k + \alpha, b - k + \alpha) / B(\alpha, \beta)
$$

in which $B(\cdot, \cdot)$ is the beta function. There is no particular biological reasoning behind the choice of the beta distribution, other than $Y$ takes values between zero and one. Allowing $Y$ to be random seems a more realistic assumption than requiring $Y$ to be fixed at some point between zero and one.

Turning to the rate matrix (3), it differs from the one associated with the usual Kingman coalescent by the factor $\beta_\ell$. To compare our process to the Kingman coalescent, let $\mathbb{E}[T]$ denote the expected value of the time to the most recent common ancestor associated with the Kingman coalescent, and with $\mathbb{E}[T(\ell)]$ we denote the same quantity associated with model $\ell$. Similarly, let $\mathbb{E}[S]$ denote the expected value of the total size of the gene genealogy associated with the Kingman coalescent, and $\mathbb{E}[S(\ell)]$ the same quantity associated with model $\ell$. One immediately obtains

$$
\begin{align*}
\mathbb{E}[T(\ell)] &= \frac{1}{\beta_\ell} \mathbb{E}[T] = \frac{2}{\beta_\ell} (1 - 1/n), \\
\mathbb{E}[S(\ell)] &= \frac{1}{\beta_\ell} \mathbb{E}[S] = \frac{2}{\beta_\ell} \sum_{i=1}^{n-1} \frac{1}{i}, \quad \ell = 1, 2.
\end{align*}
$$

\begin{equation}
(6)
\end{equation}

Hence, populations with offspring distributions whose mean and variance are large are predicted to have lower genetic diversity, as measured in number of segregating sites, than populations with
smaller mean and variance, if they have equal rates of mutation. The unit of time of a standard Moran model population, or of populations associated with either model 1 or 2 is the same when \(N^2\varepsilon_N \to 0\), or \(N^2\) timesteps. Thus, the results in Equation (6) are directly comparable for populations with different offspring distribution. To further compare the different population models, let \(F_S(\ell), F_T(\ell), F_S, \text{ and } F_T\) denote the cumulative density functions of the random variables \(S^{(\ell)}, T^{(\ell)}, S, \text{ and } T\), respectively. Elementary calculations now give \(F_S(\ell)(s) = F_S(\beta_\ell s)\), and \(F_T(\ell)(t) = F_T(\beta_\ell t) (s, t \geq 0)\). In words, the probability that \(S^{(\ell)}\) and \(T^{(\ell)}\) are no larger than some given values \(s\) and \(t\), respectively, equals the probability that \(S\) and \(T\) are no larger than \(\beta_\ell s\) and \(\beta_\ell t\), respectively.

A further comparison between the usual Moran model, and models 1 and 2, can be made by considering the expected age \(E[\zeta_x]\) of a mutation with frequency \(x \in (0, 1)\). In a Moran population,

\[
E[\zeta_x] = \frac{-2x}{1-x} \log(x),
\]

(Griffiths and Tavaré 1998; Kimura and Ohta 1973). The argument of Griffiths and Tavaré (1998) can be adapted to obtain an expression of \(E[\zeta_x]\) in a population with reproduction following models 1 or 2, to give

\[
E[\zeta^{(\ell)}_x] = \frac{1}{\beta_\ell} E[\zeta_x]
\]

(8)

Indeed, let \(\zeta_{n,b}\) denote the age of a mutation in \(b\) copies in a sample of \(n\) individuals drawn from a usual Moran population, and \(\zeta^{(\ell)}_{n,b}\) the corresponding quantity when drawn from a population with reproduction following model 1 or 2. Now,

\[
E[\zeta^{(\ell)}_{n,b}] = \frac{1}{\beta_\ell} E[\zeta_{n,b}],
\]

in which \(E[\zeta_{n,b}]\) is given by Equation (5.4) in Griffiths and Tavaré (1998). Hence, by taking appropriate limits as in Griffiths and Tavaré (1998), one arrives at Equation (8). Hence, the age of mutations will tend to be overestimated if Equation (7) is applied to estimate mutation age in a population with high mean and/or variance in the offspring distribution.
3 Turnover of ancestral lineages

The question on the age of extant genetic variation can be addressed using coalescent methods. Tavaré (1984) and Donnelly and Tavaré (1986) consider the coalescent process including mutation, in which the underlying reproduction mechanism is the usual Moran model. Each time a mutation event occurs, one lineage mutates into a ‘new’ class, and is hence no longer considered ancestral to the sample. This is equivalent of a lineage starting a new line of descent going forward in time.

To study the turnover of ancestral lineages, we will work with the lineage counting process \( \tilde{A}_r; r \in \mathbb{N}_0 \) including mutation. Since we allow mutation, the process \( \tilde{A}_r \) takes values in \( \{n\} \equiv \{0, 1, \ldots, n\} \) if the initial number of lineages is \( n \). When a mutation occurs on the last of the original \( n \) lineages, the process \( \tilde{A}_r \) reaches the absorbing state zero. The way mutation is included in the coalescent process is explained in Appendix. Weak convergence of \( \tilde{A}_{\lfloor rT_N \rfloor} \) to a continuous-time process \( \tilde{A}_t \) follows from convergence of the coalescent process \( \tilde{R} \) including mutation (see Appendix). If \( N^2 \varepsilon_N \rightarrow 0 \) the rate matrix \( \tilde{Q} \equiv (\tilde{q}_{i,j})_{i,j \in \{n\}} \) associated with process \( \tilde{A}_r \) has entries

\[
\tilde{q}_{i,j} = \begin{cases} 
   i(\theta + (i-1)\beta_\ell)/2 & \text{if } j = i-1, 1 \leq i \leq n \\
   -i(\theta + (i-1)\beta_\ell)/2 & \text{if } j = i, 0 \leq i \leq n 
\end{cases}
\]  

in which \( \beta_\ell \) was defined in Equation (2). If \( N^2 \varepsilon_N \rightarrow \phi \) for some constant \( \phi > 0 \), the rate matrix \( \tilde{Q} \) has entries

\[
\tilde{q}_{i,j} = \begin{cases} 
   i((i-1)\beta_\ell + \theta)/2 + \phi \left( \frac{\lambda}{n} \right) \mathbb{E}[Y^2(1-Y)^{i-2}] & \text{if } j = i-1, 1 \leq i \leq n \\
   \phi \left( \frac{\lambda}{n} \right) \mathbb{E}[Y^k(1-Y)^{i-k}] & \text{if } j = i - k + 1, 3 \leq k \leq n \\
   -i((i-1)\beta_\ell + \theta)/2 - \phi \mathbb{E}[1 - (1-Y)^i - iY(1-Y)^{i-1}] & \text{if } j = i \\
   0 & \text{otherwise}
\end{cases}
\]  

Finally, if \( N^2 \varepsilon_N \rightarrow \infty \) the entries of the rate matrix are

\[
\tilde{q}_{i,j} = \begin{cases} 
   i\theta/2 + \left( \frac{\lambda}{n} \right) \mathbb{E}[Y^2(1-Y)^{i-2}] & \text{if } j = i-1, 1 \leq i \leq n \\
   \left( \frac{\lambda}{n} \right) \mathbb{E}[Y^k(1-Y)^{k-2}] & \text{if } j = i - k + 1, 3 \leq k \leq n \\
   -i\theta/2 - \mathbb{E}[1 - (1-Y)^i - iY(1-Y)^{i-1}] & \text{if } j = i \\
   0 & \text{otherwise}
\end{cases}
\]  

The rate of turnover of alleles is quantified with the probability \( h_{i,j}(t) \equiv \mathbb{P}[\tilde{A}_t = j|\tilde{A}_0 = i] \)
given by

\[ h_{i,j}(t) = \sum_{k=j}^{i} e^{t\tilde{q}_{k,k}} r^{(k)} \ell^{(k)}_j, \quad 1 \leq j < i \]

\[ = e^{t\tilde{q}_{i,i}}, \quad j = i \]

\[ = 1 - \sum_{1 \leq j \leq i} h_{i,j}(t), \quad j = 0 \]  

(12)

in which \( r^{(k)} \) and \( \ell^{(k)} \) are the right and left eigenvectors, respectively, of the rate matrix associated with \( \tilde{A} \). Only when the rate matrix of \( \tilde{A} \) is of the form (9), a closed form expression for the eigenvectors can be obtained as follows. Define, for some constant \( c > 0 \), the factorials

\[ a_{(c,k)} \equiv \frac{a(a + c)(a + 2c) \cdots (a + (k-1)c)}{k!}, \]

\[ a_{(c,k)} \equiv \frac{a(a - c)(a - 2c) \cdots (a - (k-1)c)}{(k-1)!}. \]  

(13)

The results of Tavaré (1984) can be adapted to obtain the left \( \ell^{(k)} \) and right \( r^{(k)} \) eigenvectors of the transition matrix given by Equation (9). One obtains

\[ \ell^{(0)}_j = \delta_{j,0}, \quad \ell^{(k)}_j = \begin{cases} 0, & j > k \geq 1; \\ \binom{k}{j} (-1)^{k-j} \frac{(cj + \theta)_{(c,k-1)}}{(ck + \theta)_{(c,k-1)}}, & j \leq k \end{cases} \]  

(14)

in which \( c = B\ell \). In the same way, \( r^{(0)}_j = 1 \) for all \( j \), and

\[ r^{(k)}_j = \begin{cases} 0, & j < k; \\ \left( \frac{k}{j} \right) \frac{(ck + \theta)_{(c,k)}}{(cj + \theta)_{(c,k)}}, & j \geq k. \end{cases} \]  

(15)

Equations (12,15) now give, with \( i_{[k]} \equiv i(i-1) \cdots (i-k+1) \),

\[ h_{i,j}(t) = \sum_{k=j}^{i} e^{t\tilde{q}_{k,k}} (-1)^{k-j} \frac{i_{[k]}}{j!(k-j)!} ((2k-1)c + \theta) \frac{(cj + \theta)_{(c,k-1)}}{(ci + \theta)_{(c,k)}}, \quad 1 \leq j < i. \]  

(16)

One can also view the constant \( c \) as a population size scaling constant. The probability \( h_j(t) \) that \( j \) of original lines of descent from the whole population are still present at time \( t \) is given by

\[ h_j(t) = \sum_{k=j}^{\infty} e^{t\tilde{q}_{k,k}} (-1)^{k-j} ((2k-1)c + \theta) \frac{(cj + \theta)_{(c,k-1)}}{ck! (k-j)!}, \quad 1 \leq j; \]

\[ h_0(t) = 1 + \sum_{k=1}^{\infty} e^{t\tilde{q}_{k,k}} (-1)^{(2k-1)c + \theta} \frac{\theta_{(c,k-1)}}{ck!}, \]  

(17)
obtained by taking \( i \to \infty \). The formulas for \( h_{i,j}(t) \) and \( h_j(t) \) associated with the usual Kingman coalescent with mutation are recovered by taking \( c = 1 \). Even though the sum in Equation 17 is infinite, the terms quickly become small. Even moderate values of \( \theta \) and \( c = \beta \ell \) lead to quick turnover of alleles in the population (Table 1).

The distribution of the number of ancestral lineages of either a finite sample, or, of the whole population, at any given time, is straightforward to obtain using the results of Littler (1975), Griffiths (1979), Griffiths (1980), Watterson (1982), Kingman (1982b), and Tavaré (1984). The form of the eigenvectors associated with the usual Kingman coalescent is the same as when associated with the modified coalescent derived from models 1 or 2; only the eigenvalues of the corresponding rate matrices differ in an obvious way.

An explicit form of \( h_j(t) \) is hard to obtain when associated with a \( \Lambda \) coalescent since the rate matrix is triagonal, and closed form expressions for the eigenvectors are not easy to obtain. The eigenvectors can, however, be computed recursively, as shown in Appendix. The probability \( h_{i,0}(t) \) that all of \( i \) initial ancestral lineages have vanished by time \( t \) is graphed as a function of time \( t \) in Figure 1 for two examples of a \( \Lambda \) coalescent. In Figure 1a is the point mass process \( \Lambda(d\psi) = \psi^2 \delta_{\psi \psi} d\psi \) studied by Eldon and Wakeley (2006), and in Figure 1b is the beta coalescent derived by Schweinsberg (2003). In the beta coalescent, time is in units proportional to \( N^{\alpha^{-1}} \).

Hence, the results in Figure 1b must be interpreted with the timescale property of \( \alpha \) in mind. The \( \psi \) parameter of the point mass process is not a timescale parameter; the values of \( h_{i,0}(t) \) for different values of \( \psi \) can therefore be directly compared. The quantity \( h_{i,0}(t) \) can also be interpreted as the probability that the oldest mutation in a sample of \( i \) sequences is not older than \( t \) time units. Figure 1c reports values of \( h_{i,0}(t) \) when the random variable \( Y \) has the beta distribution with parameters \((\alpha, \beta)\). The values of \( h_{i,0}(t) \) in Figure 1c are directly comparable for different values of the parameters \( \alpha \) and \( \beta \) since they are not timescale parameters. If \( \theta \) is large, ancestral lineages will vanish quickly from a population admitting large offspring numbers, one concludes from Figure 1. In addition, the effects of \( \theta \) seem stronger than those of the coalescence parameters, for the range of parameter values considered in Figure 1.
4 The subsample process

Two alleles drawn at random from a standard Moran population have probability $1/3$ of sharing their most recent common ancestor with the whole population present at the time the two alleles were sampled. This result follows from the probability $(j - 1)(i + 1)/[(j + 1)(i - 1)]$ that $j$ of $i$ lineages share a most recent common ancestor with the $i$ lineages (Saunders et al., 1984). This result indicates that even samples of even moderate size will yield a good estimate of the time to the most recent common ancestor of the whole population. To further study the rate of turnover of alleles in populations admitting large offspring numbers, we consider simple properties of the gene genealogical process of nested subsamples.

One can recursively compute the conditional distribution of the number of ancestors of the subsample, given the number of ancestors of the sample, as shown in section 7.5. Closed-form expressions can be obtained for a population with the Kingman coalescent (Griffiths, 1980; Kingman, 1982b; Littler, 1975; Tavaré, 1984). The presence of multiple mergers makes closed-form expressions hard to obtain for a general $\Lambda$ coalescent. In this section we will be concerned with the probability that a subsample shares it’s most recent common ancestor with the sample. Denote by $A^*_1(u)$ the number of ancestors of the sample when the the number of ancestors of the subsample first reaches a given value $u$. Similary, denote by $A^*_2(v)$ the number of ancestors of the subsample when the number $A_1$ of ancestors of the sample first reaches some value $v$. Closed-form expressions for the distributions of $A^*_1$ and $A^*_2$ have been obtained for a usual Moran population (Saunders et al., 1984). The conditional distributions of $A^*_1$ and $A^*_2$ when associated with a $\Lambda$ coalescent may be computed recursively, as shown in Appendix.

To compute our quantity of interest, let $\psi_{i,j}(u,v) \equiv \mathbb{P}[A^*_1(v) = u | A_1(0) = i, A_2(0) = j]$. The probability $\psi_{i,j}(1,1)$ that the subsample shares its’ most recent common ancestor with the whole sample is straightforward to compute recursively as follows. Writing $i' = i - k + 1$, $j' = (j - \ell + 1)1_{(\ell>0)} + j1_{(\ell=0)}$, one obtains

$$\psi_{i,j}(1,1) = \sum_{k=2}^{i} \beta(i,i') \sum_{\ell=0}^{j\wedge k} \binom{i-j}{k-\ell} \binom{j}{\ell} \psi_{i',j'}(1,1)$$

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with the boundary conditions $\psi_{j,j}(1,1) = 1$ and $\psi_{i,1}(1,1) = 0$ for $i > 1$. The result obtained from the usual Moran model, $\psi_{i,j}(1,1) = (j-1)(i+1)/[(j+1)(i-1)]$, can be recovered from Equation (18). The recursion (18) simplifies considerably when $j = 2$. Writing $\psi(i) = \psi_{i,2}(1,1)$, one obtains

$$
\psi(i) = \sum_{k=2}^{i-2} \beta(i,i-k+1)(i-k)(i+k-1)\psi(i-k+1) + \beta(i,2)\frac{2}{i} + \beta(i,1). \quad (19)
$$

When associated with a Λ coalescent, $\psi(i)$ can be quite small (Table 2). For comparison, the corresponding values when associated with the Kingman coalescent are $\psi(500) = 0.335$, and $\psi(1000) = 0.334$. An indicator of how well a sample represents the population it is drawn from may be taken as the probability $\psi_{\infty,j}(1,1)$. A sample of moderate size drawn from a standard Moran population represents the population quite well, since then $\psi_{\infty,j}(1,1) = (j-1)/(j+1)$.

The results in Table 2 indicate that only a large sample drawn from a population admitting large offspring numbers has a good chance of sharing its’ most recent common ancestor with the whole population, if we interpret the sample as the whole population.

The conditional distributions of $A_1^\ast$ and $A_2^\ast$ will be the same for models 1 and 2 as for the usual Moran model. Hence, samples of size $j$ drawn from populations following a large class of reproduction law, or from populations differing in their population size, will all have probability $(j-1)/(j+1)$ of sharing their most recent common ancestor with the population present at the time of sampling.

5 The subsample process including mutation

The age of an allele is fundamental to population genetics. A sample of size $j$ has probability $j/(j+\theta)$ of including the oldest allele in the population, if drawn from a usual Moran population (Saunders et al. 1984; Tavaré 1984; Watterson and Guess 1977). Slatkin (2000) bases a test for selection on allele age. Results concerning age of alleles can be obtained by considering the ancestral process of nested subsamples when the ancestral process includes mutation.

One might wish to know how the expected number of ancestors of a sample changes given the number of ancestors of a subsample. Define $\tilde{A}_1^\ast$ and $\tilde{A}_2^\ast$ in the same way as $A_1^\ast(a)$ and $A_2^\ast(a)$,
respectively. The quantity $\tilde{A}_1^*(u)$ denotes the number of ancestors of the sample, including mutation, when the number of ancestors of the subsample first takes value $u$. The conditional distributions of $\tilde{A}_1^*$ and $\tilde{A}_2^*$ can be computed recursively (see Appendix) when associated with a population admitting large offspring numbers. The conditional expected value $E[\tilde{A}_2^*(a_1)]$ is graphed as a function of the number $a_1$ of ancestors of the sample for three examples of a $\Lambda$ coalescent. The idea behind calculating $E[\tilde{A}_2^*(a_1)]$ is to infer how the number of ancestors of a sample changes relative to the whole population, by treating the sample as the population. The number of ancestors of a sample drawn from a population admitting large offspring numbers would then, on average, be expected to be smaller than if drawn from a usual Moran population, for a given number of ancestors for the whole population. Furthermore, mutation rate appears to matter little for the Kingman coalescent, while being a more important player for the $\Lambda$ coalescent examples we are considering (Figure 2). The results in Figure 2 suggest that the expected number $E[\Lambda]$, $\tilde{A}_2^*$ of ancestors of the subsample when associated with a $\Lambda$ coalescent would tend to be smaller than the corresponding value $E[K]$, $\tilde{A}_2^*$ associated with the Kingman coalescent. In addition, $E[\Lambda]$, $\tilde{A}_2^*$ may be convex in some cases, while $E[K]$, $\tilde{A}_2^*$ is a concave function of the number of ancestors of the sample. In Figure 3, values of the number $E[\Lambda]$, $\tilde{A}_1^*$ of ancestors of the sample when associated with a $\Lambda$ coalescent are graphed as a function of the number of ancestors of the subsample. The results in Figure 3 show that $E[\Lambda]$, $\tilde{A}_1^*$ may be either smaller or larger than the corresponding value $E[K]$, $\tilde{A}_1^*$ associated with the Kingman coalescent. In addition, while $E[K]$, $\tilde{A}_1^*$ is a convex function of the number of ancestors of the subsample, $E[\Lambda]$, $\tilde{A}_1^*$ seems to range from being convex to appearing an almost linear function of the number of ancestors of the subsample.

An expression for the probability that a subsample of a sample drawn from a usual Moran model population carries the oldest allele of the sample yields a remarkably simple expression for the probability that the sample carries the oldest allele of the population. The probability $\tilde{u}(i, j) \equiv \tilde{\psi}_{i, j}(0, 0)$ that a subsample includes the oldest allele of a sample drawn from a population
admitting large offspring numbers is straightforward to compute recursively, namely
\[
\tilde{u}(i, j) = \frac{j\theta/2}{\lambda(i)} \tilde{u}(i, j - 1) \quad + \quad \frac{(i - j)\theta/2}{\lambda(i)} \tilde{u}(i - 1, j)
\]
\begin{equation}
\quad + \sum_{k=1}^{i-1} \beta(i, i - k) \sum_{\ell=0}^{\frac{(i-j)\theta}{2}} \tilde{u}(i - k, j - \ell 1_{\ell > 1})
\end{equation}

(20)

with boundary probabilities \( \tilde{u}(j, j) = 1 \), and \( \tilde{u}(i, 0) = 0 \) if \( i > 0 \). Table 3 shows values of \( \tilde{u}(1000, 2) \) varying over \( \theta \) and \( \pi \). The corresponding values for the Kingman coalescent are \( \tilde{u}(1000, 2) = 0.667 \) when \( \theta = 1 \), and \( \tilde{u}(1000, 2) = 0.287 \) when \( \theta = 5 \) \cite{Kelly1977, Saunders1984}. The results in Table 3 indicate that two lineages drawn from a population admitting large offspring numbers will, in some cases, have quite a low probability of being the oldest allele of the population, if we interpret the sample as the population. One might also be interested in how quickly the probability of the subsample carrying the oldest allele of the sample increases with the subsample size. Figure 4 reports values of \( \tilde{u}(150, j) \) as a function of \( j \) for the three example \( \Lambda \) coalescents. While \( \tilde{u}(i, j) \) is a concave function of \( j \), and thus increases quickly with \( j \) when associated with the Kingman coalescent, \( \tilde{u}(i, j) \) increases slower, or almost linearly in some cases, when associated with a \( \Lambda \) coalescent. Thus, a subsample of a sample drawn from a population admitting large offspring numbers has smaller probability of carrying the oldest allele of the sample than if the sample was drawn from a usual Moran population.

The conditional distributions of \( \tilde{A}_1^* \) and \( \tilde{A}_2^* \) derived from models 1 or 2 will be different from the distributions derived from the usual Moran model. Denote the conditional distribution of \( \tilde{A}_2^* \) by \( \phi(\ell_1, \ell_2) \),
\[
\phi(\ell_1, \ell_2) \equiv P(\tilde{A}_1^*(\ell_1) = \ell_2 | \tilde{A}_1(0) = i, \tilde{A}_2(0) = j).
\]

Saunders et al. \cite{Saunders1984} obtain \( \phi(\ell_1, \ell_2) \) by solving the recursion (Theorem 6 in Saunders et al. \cite{Saunders1984})
\[
\phi(\ell_1, \ell_2) = \phi(\ell_1 + 1, \ell_2) \frac{(\ell_1 - \ell_2 + 1)(\ell_1 + \ell_2 + \theta)}{\ell_1 + 1} + \phi(\ell_1 + 1, \ell_2 + 1) \frac{(\ell_2 + 1)(\ell_2 + \theta)}{\ell_1 + 1}(\ell_1 + \theta)
\]

(21)

with \( \phi(\ell, \ell) = 1 \) if \( \ell = j \), and \( \phi(\ell, \ell) = 0 \) otherwise. In a population following model 1 or 2,
one obtains
\[
\phi(\ell_1, \ell_2) = \phi(\ell_1 + 1, \ell_2) \frac{(\ell_1 - \ell_2 + 1)((\ell_1 + \ell_2)\beta + \theta)}{(\ell_1 + 1)(\ell_1 \beta + \theta)} + \phi(\ell_1 + 1, \ell_2 + 1) \frac{(\ell_2 + 1)(\ell_2 \beta + \theta)}{(\ell_1 + 1)(\ell_1 \beta + \theta)},
\]
(22)
where we suppress the subscript \( \ell \) on \( \beta (= \beta_\ell) \), and \( \theta^* = \theta / \beta \). Hence, the conditional distribution of \( \tilde{A}^*_2 \) is given by Theorem 6 in [Saunders et al. (1984)], with \( \theta \) replaced by \( \theta / \beta \). The same applies to the conditional distribution of \( \tilde{A}^*_1 \) (see Theorem 7 in [Saunders et al. (1984)]). In this context we must mention the scaling of mutation. We insist that mutation scale in units of \( N^2 \) timesteps exactly, in order for the models to be comparable. Hence, the mutation rate \( \theta \) is the same quantity for all models that yield a Kingman-like coalescent. Thus, the probability that the oldest allele of \( i \) lineages is among a subset of \( j \) lineages is \( j(i\beta + \theta) / [i(j\beta + \theta)] \), when associated with model 1 or 2. The oldest allele of a population associated with model 1 or 2 will therefore be among \( j \) lineages with probability \( j\beta / (j\beta + \theta) \). The constant \( \beta \) can also be interpreted as a population size scaling constant, if we assume that time is scaled in units of \( N^2 \) timesteps. If the size of a Moran population is scaled by factor \( c \), then \( \beta = 1 / c^2 \).

Kelly (1977) and Saunders et al. (1984) obtain the distribution of the number of representatives \( F_i \) of the oldest allele in the sample of size \( i \) drawn from a population with the usual Moran reproduction. Using the same argument as in [Saunders et al. (1984)], one can recursively compute the distribution of \( F_i \), using Equation (20). The expected value \( \mathbb{E}[F_i] \) of \( F_i \) when associated with a \( \Lambda \) coalescent tends to be smaller than when associated with the Kingman coalescent (Table 4). The magnitude of the difference also varies with the type of the \( \Lambda \) coalescent, with values of \( \mathbb{E}[F_i] \) associated with the beta coalescent being quite similar to the ones associated with the Kingman coalescent. In contrast, \( \mathbb{E}[F_i] \) seems to converge to one as \( \psi \) decreases. The expected value of \( F_i \) also tends to one when \( \theta \) increases, when associated with the usual Kingman coalescent. When associated with model 1 or 2, and large offspring number events are negligible, the results of Kelly (1977) and Saunders et al. (1984) yield
\[
\mathbb{E}[F_i] = \frac{i\beta + \theta}{\beta + \theta}, \quad \text{Var}[F_i] = \frac{\beta(\theta + \beta)\theta(i - 1)}{(\beta + \theta)^2(2\beta + \theta)}.
\]
6 Discussion and Conclusion

The Wright-Fisher and Moran models have been the basis of the majority of work in theoretical population genetics. However, they make strong assumptions about the offspring distribution of individuals, that are not fulfilled by most natural populations. The simple generalized versions of the Moran model developed in the present work allow one, in a natural way, to account for at least some of the stochasticity inherent in natural populations. A further benefit is that the modified population models run on the same timescale, and are thus directly comparable.

Population models admitting large offspring numbers are natural candidates for populations with highly fecund individuals, including a diverse group of marine taxa. In this work we consider a model in which a single individual contributes a random number of offspring at each timestep. An important open question is the distribution of the number of offspring, which will require insight into the biology and ecology of natural populations. Accurately modeling offspring distribution may be particularly important in conservation genetics (Amos and Balmford, 2001).

By incorporating the mean and variance of the offspring distribution into the coalescence rates, we show that populations with high variation in their offspring distribution will have lower genetic diversity than predicted by the usual Moran model, as is often observed in particular among marine populations. Admitting large offspring numbers leads to multiple merger coalescent processes, which can predict the starlike pattern of haplotypes often observed among marine fishes (Grant and Bowen, 1998).

The multiple merger coalescent processes derived from population models admitting large offspring numbers are more difficult to handle mathematically than any version of a Kingman coalescent. Closed-form analytic expressions are hard to obtain. Exact computations of many quantities can therefore only be done recursively when associated with multiple merger processes. Recursive computations limit us in some cases to small sample sizes. Important insights can still be obtained, and which can give clues to results for large sample sizes.

In this work we consider the rate of turnover of alleles in populations while paying attention to the offspring distribution. Our main conclusion is that the rate of turnover of alleles increases
with the variance in the offspring distribution. This means that alleles will tend to be younger than in the usual Wright-Fisher or Moran populations. In addition, our results suggest that one may need large sample sizes to accurately predict the age of the most recent common ancestor of a population in populations with large offspring variance. In addition, one may need to draw a large sample from some populations admitting large offspring numbers before having a good chance of having caught the oldest allele of the population.

The author was supported in part by EPSRC grant EP/G052026/1, in part by DFG grant BL 1105/3-1, and by a Junior Research Fellowship at Lady Margaret Hall, University of Oxford.

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7 Appendix
7.1 Weak convergence of the coalescent process including mutation

In this section we establish weak convergence in the function space $D(\mathbb{R}_+)$ of the coalescent process including mutation and derived from a general Cannings model admitting large offspring numbers. In a Cannings model of a population of constant size $N$, the offspring variables $\nu_i$ are exchangeable, and $\nu_1 + \cdots + \nu_N = N$. By convention, let $D(\mathbb{R}_+)$ denote the space of right continuous functions with left limits on $[0, \infty)$ with values in $E$, the set of all equivalence relations on $\{1, \ldots, n\}$. The coalescent process $(R_m)_{m \in \mathbb{N}_0}$ without mutation describes the random ancestral relation among a set of $n$ individuals drawn at random from the population at time $m = 0$. A state $\xi$ of the process $(R_m)_{m \in \mathbb{N}_0}$ is, by definition, the random equivalence relation containing individuals $(i, j)$ only if $i$ and $j$ share a common ancestor at timestep $r$ in the past. The coalescent process starts in state $\{(i, i) : 1 \leq i \leq n\}$. The absorbing state is $\{(i, j) : 1 \leq i, j \leq n\}$. Let $b = b_1 + \cdots + b_a$, in which $b_1, \ldots, b_a$ denote the number of classes of $\xi$ that merge into each of $a$ classes of $\eta$. Write $(m)_a \equiv m(m-1)\cdots(m-a+1)$, $(m)_0 \equiv 1$. Under an exchangeable reproduction model and fixed population size $N$, the transition probability $P_{\xi, \eta}(N) = \mathbb{P}[R_{m+1} = \eta | R_m = \xi]$ from state $\xi$ to $\eta$ is given by

$$
P_{\xi, \eta}(N) = \frac{(N)_a}{(N)_a} \mathbb{E}[(\nu_1)_b \cdots (\nu_a)_b]$$

Time is scaled in units of $1/c_N$, in which $c_N \equiv \mathbb{E}[\nu_1 - 1]/(N-1)$. To pass to a continuous-time process, we require that $\lim_{N \to \infty} c_N = 0$.

We will now list the conditions on the population model under which the scaled process $(R^{(N)}_{t/c_N})_{t \geq 0}$ converges weakly to $(R_t)_{t \geq 0}$ (Sagitov, 1999). Denote by $\Lambda$ a finite measure on the Borel subsets of the unit interval. The three conditions are

$$
\mathbb{E}[(\nu_1 - 1)^2] = o(N); \\
\lim_{N \to \infty} \frac{N}{c_N} \mathbb{P}[\nu_1 > Nx] = \int_x^1 y^{-2} \Lambda(dy), \quad 0 < x < 1; \\
\lim_{N \to \infty} \frac{\mathbb{E}[(\nu_1 - 1)^2 \cdots (\nu_a - 1)^2]}{c_N N^a} = 0, \quad a \geq 2;
$$

(24)
Now define
\[ p_{\xi,\eta}(N) = \frac{(N)_b}{(N)_b} \mathbb{E} \left[ (\nu_1)_{b_1} \cdots (\nu_a)_{b_a} \right], \quad b_1 \geq 2, \quad b_2 = \cdots = b_a = 1. \] (25)

The conditions in Equation (24) yield
\[ \frac{1}{c_N} p_{\xi,\eta}(N) \to \int_0^1 x^{k-2}(1-x)^{b-k-2} \Lambda(dx), \quad k \geq 2, \quad a \geq 1 \] (26)

The coalescent process \((\tilde{R}_m)_{m \in \mathbb{N}}\) with mutation separates each relation into mutant (‘new’) and non-mutant (‘old’) equivalence classes. The terminology ‘old’ and ‘new’ is to remind that mutations are always to new types (alleles), and hence start new lines of descent \([\text{Donnelly and Tavaré, 1986; Tavaré, 1984}]\).

Only non-mutant equivalence classes either coalesce or mutate. Let \(E\) denote the set of all equivalence classes on \(\{1, \ldots, n\}\) in which each class is partitioned into old and new classes (see \([\text{Möhle, 1999}]\)). The total number of old classes of the current state \(\xi\) is \(b + m\). The transition probability for the transition from \(\xi\) to \(\eta\) is
\[ P_{\xi,\eta}(N) = \mu_N^m (1 - \mu_N)^b \frac{(N)_b}{(N)_b} \mathbb{E} \left[ (\nu_1)_{b_1} \cdots (\nu_a)_{b_a} \right] \] (27)

To retain mutations in the limit process, we require that the mutation probability \(\mu_N\) scales according to \(c_N\), namely
\[ \lim_{N \to \infty} \frac{\mu_N}{c_N} = \frac{\theta}{2}, \quad 0 < \theta < \infty. \] (28)

in which \(\theta\) is a constant. By \(\xi \leadsto \eta\) denote a transition due to mutation, in which one old class of \(\xi\) becomes a new class of \(\eta\). By \(\xi \prec \eta\) denote a transition from \(\xi\) to \(\eta\) in which \(\xi \subset \eta\) and \(\eta\) denotes a merger of at least two of the equivalence classes of \(\xi\). Define a sequence \(\tilde{Q}_N = (\tilde{q}_N(\xi,\eta))_{\eta,\xi \in E}\) of generators with entries
\[ \tilde{q}_N(\xi, \eta) = \begin{cases} 
\frac{p_{\xi,\eta}(N)}{c_N} & \text{if } \xi < \eta \\
\frac{\mu_N}{c_N} \mathbb{E} [\nu_1 \cdots \nu_a] & \text{if } \xi \leadsto \eta \\
- \sum_{\xi \to \eta} q_{\xi,\eta}^{(N)} & \text{if } \xi = \eta \\
0 & \text{otherwise.} \end{cases} \] (29)
Equations (26–29) now imply that the sequence \( \tilde{Q}_N \) of generators converges entry-wise to a generator \( \tilde{Q} = (\tilde{q}(\xi, \eta))_{\eta, \xi \in \tilde{E}} \) with entries

\[
\tilde{q}(\xi, \eta) = \begin{cases} 
\int_0^1 x^{k-2}(1-x)^{\vert\xi\vert-k}\Lambda(dx) & \text{if } \xi \prec \eta \\
\theta/2 & \text{if } \xi \sim \eta \\
-\frac{\vert\xi\vert^{\beta}}{2} - \int_0^{1/2} (1-(1-x)^{\vert\xi\vert}) - |\xi|x(1-x)^{\vert\xi\vert-1})x^{-2}\Lambda(dx) & \text{if } \eta = \xi \\
0 & \text{otherwise.}
\end{cases}
\]

Since the state space \( \tilde{E} \) is finite, the entry-wise convergence \( \tilde{Q}_N \to \tilde{Q} \) implies weak convergence in \( D_{\tilde{E}}([0, \infty)) \) of \( \tilde{R}_{\lfloor t/c_N \rfloor} \) to \( (\tilde{R}_t; t \geq 0) \) with generator \( \tilde{Q} \), by Theorem 17.25(i) in Kallenberg (1997).

7.2 Generators of the coalescent processes

In this section we describe the generators of the coalescent processes obtained from models 1 and 2.

By \( E \) denote the set of all equivalence relations on \( \{1, \ldots, n\} \). One readily obtains convergence of the finite-dimensional distributions of \( R_m \). To prove convergence of the time-scaled process \( R_{\{t/T_N\}} \) in the space \( D_E[0, \infty) \) of all functions on \( [0, \infty) \) with values in \( E \) that are right continuous and with left limits, we apply the convergence result of the previous section and obtain that the ancestral process \( (R_{\lfloor t/T_N \rfloor}; t \geq 0) \) when associated with population model 1 or 2 converges weakly in \( D_E[0, \infty) \) to a continuous-time process \( (R_t; t \geq 0) \) whose rate matrix \( Q \) depends on the limit \( N^2 \varepsilon_N \). To describe the transition matrices, define \( \alpha_\ell \) associated with model \( \ell \in \{1, 2\} \),

\[
\alpha_\ell \equiv E[X^2]
\]

\[
\alpha_x \equiv E[X(X+1)]
\]

The constants \( \alpha_\ell \) play similar role as the constants \( \beta_\ell \) associated with the gene genealogical processes. Let \( |\xi| \) denote the number of classes (lineages) in relation \( \xi \). If \( N^2 \varepsilon_N \to 0 \) the rate matrix \( Q_\ell = (q_{\ell, \eta}^{(\xi)})_{\xi, \eta \in E} \) associated with model \( \ell \in \{1, 2\} \) is given by

\[
q_{\ell, \eta}^{(\xi)} = \begin{cases} 
\alpha_\ell & \text{if } \xi \prec \eta \\
-\frac{1}{2} |\xi| \alpha_\ell & \text{if } \xi = \eta \\
0 & \text{otherwise.}
\end{cases}
\]
in which \( \xi < \eta \) now denotes a merger of at most two equivalence classes of \( \xi \). The usual Kingman coalescent is obtained from (32) by taking \( X \) in \( \Pi \) to be a constant with value 1. If large offspring number events are moderately frequent, i.e., if \( N^2 \varepsilon_N \to \phi \) in which \( \phi \) is a constant, the entries \( q_{\xi,\eta}^{(t)} \) of the \( Q_t \) matrix are

\[
q_{\xi,\eta}^{(t)} = \begin{cases} 
\alpha_t + \phi \mathbb{E}[Y^2(1 - Y)^{|\xi| - 2}] & \text{if } \xi < \eta \\
\phi \mathbb{E}[Y^k(1 - Y)^{|\xi| - k}] & \text{if } \xi < \eta, 3 \leq k \leq |\xi| \\
-\alpha_t \left( \frac{|\xi|}{k} \right) - \phi \mathbb{E}[1 - (1 - Y)^{|\xi|} - |\xi|Y(1 - Y)^{|\xi| - 1}] & \text{if } \xi = \eta \\
0 & \text{otherwise.}
\end{cases}
\]  

(33)

in which \( \xi < \eta \) denotes a merger of at least three equivalence classes of \( \xi \). Finally, if \( N^2 \varepsilon_N \to \infty \) then large offspring number events occur quite frequently, and only one \( Q \) matrix is obtained, whose entries are

\[
q_{\xi,\eta} = \begin{cases} 
\mathbb{E}[Y^k(1 - Y)^{|\xi| - k}] & \text{if } \xi < \eta, 2 \leq k \leq |\xi| \\
-\mathbb{E}[1 - (1 - Y)^{|\xi|} - |\xi|Y(1 - Y)^{|\xi| - 1}] & \text{if } \xi = \eta \\
0 & \text{otherwise.}
\end{cases}
\]  

(34)

7.3 Eigenvectors of the rate matrix associated with \( A_t \)

The eigenvectors of the rate matrix associated with either \( A_t \) or \( \tilde{A}_t \) under the Kingman coalescent can be obtained in closed form (Tavaré, 1984). The rate matrix associated with \( A_t \) when associated with a \( \Lambda \) coalescent is triangular. The eigenvectors can be computed recursively as follows. Let \( \ell^{(k)} = \left( \ell_1^{(k)}, \ldots, \ell_n^{(k)} \right) \) and \( r^{(k)} = \left( r_1^{(k)}, \ldots, r_n^{(k)} \right) \) denote the left and right eigenvectors, respectively, corresponding to eigenvalue \( \lambda_k = q_{h,k} \). Then \( \ell_1^{(1)} = \delta_{1i}, \ell_j^{(k)} = 0 \) if \( j > k, \ell_k^{(k)} = 1 \) and, writing \( q_k = q_{h,k} \),

\[
\ell_j^{(k)} = \frac{q_{j+1,j} \ell_{j+1}^{(k)} + \cdots + q_{h,j} \ell_h^{(k)}}{q_h - q_j}, \quad 1 \leq j < k.
\]  

(35)

Considering the right eigenvectors \( r^{(k)} \), we have \( r^{(1)} = (1, \ldots, 1), r_k^{(k)} = 1, r_j^{(k)} = 0 \) if \( j < k \), and

\[
r_j^{(k)} = \frac{q_{j+1,j} r_{j+1}^{(k)} + \cdots + q_{h,j} r_h^{(k)}}{q_h - q_j}, \quad 1 < k < j \leq n
\]  

(36)

One confirms that, for sample size two, \( \ell^{(1)} = (1, 0), \ell^{(2)} = (-1, 1), r^{(1)} = (1, 1), r^{(2)} = (0, 1) \), yielding \( \mathbb{P}[A_t = 1|A_0 = 2] = 1 - \mathbb{P}[A_t = 2|A_0 = 2] = 1 - e^{\phi_2} \).

The eigenvectors of the rate matrix associated with \( \tilde{A}_t \) when associated with a \( \Lambda \) coalescent can similarly be obtained recursively (Equations 35–36), with \( \ell^{(0)} = \delta_{0j} \), and \( r^{(0)} = (1, \ldots, 1) \).
7.4 The subsample coalescent process

In this section we give the generators associated with the coancestry coalescent process, when the ancestry of a subsample is considered jointly with the ancestry of the sample. The convergence follows from the convergence result obtained in the first section of the Appendix. The generators will have similar form, though not quite the same, as the one associated with the gene genealogical coancestry process discussed in the main text.

Let $R_1$ and $R_2$ denote the sample and the subsample process, respectively, on $E$. To specify the joint process $(R_1(t), R_2(t); t \geq 0)$, denote by $\xi \equiv (\xi_1, \xi_2)$ and $\eta \equiv (\eta_1, \eta_2) \in E^2$ the states of the joint process; with $\xi_i$ and $\eta_i$ denoting the states of $R_i$ for $i \in \{1, 2\}$. By $\xi \preceq \eta$ we denote the transition $\xi \preceq \eta \equiv \begin{cases} \xi_1 \preceq \eta_1, & \xi_2 = \eta_2. \end{cases}$ where $\xi_1 \preceq \eta_1$ denotes a merger of two classes of $\xi_1$. By $\xi \prec \eta$ we denote the transition $\begin{cases} \xi_1 < \eta_1, & \xi_2 < \eta_2, \\ \xi_1 < \eta_1, & \xi_2 \prec \eta_2, \\ \xi_1 < \eta_1, & \xi_2 = \eta_2 \end{cases}$ in which $\xi_1 < \eta_1$ denotes a merger of three or more classes of $\eta_1$, which then can involve more than two classes ($\xi_2 < \eta_2$), exactly two ($\xi_2 \prec \eta_2$), or at most one ($\xi_2 = \eta_2$) class of the subsample process.

In discrete time, the joint process $(R_1(r), R_2(m))_{m \in \mathbb{N}}$ is a Markov chain with transition probabilities $P_{\xi, \eta}(N)$ determined by

$$P_{\xi, \eta}(N) = \frac{\mathbb{E}[U^k(N - U - 1, \ldots, \ell)]}{(N)_k} \frac{(|\xi_1| - |\xi_2|)_{\ell}}{(\ell)!}$$

in which $U^k \equiv (U)_k + (U)_{k-1}$. The results of previous sections now give convergence of finite-dimensional distributions of $(R_1([tN]), R_2([tN]))$ to $(R_1(t), R_2(t))$. If $N^2 \varepsilon_N \to 0$ large offspring number events are negligible and the rate matrix $Q_\ell$ of $(R_1(t), R_2(t))$ associated with model $\ell \in \{1, 2\}$ has entries

$$q_{\xi, \eta}^{(\ell)} = \begin{cases} \alpha_\ell \left( \frac{(|\xi_1| - |\xi_2|)_{2-j}}{(\ell)!} \right), & \xi \preceq \eta, \quad 0 \leq j \leq 2 \land |\xi_2| \\ -\alpha_\ell \left( \frac{|\xi_1|}{2} \right), & \xi = \eta. \end{cases}$$

(38)
in which \(\alpha_i\) are given in Equation (31). If \(N^2\xi \rightarrow \phi\) where \(\phi > 0\) is a constant, the rate matrix associated with model \(\ell\) has entries

\[
q_{\ell,\eta}^{(\ell)} = \begin{cases} 
(\xi_1 - |\xi_2|)_2 - (|\xi_2|)_2 & \xi \leq \eta, \quad 0 \leq j \leq k \land |\xi_2| \\
\phi \mathbb{E}[Y^2(1 - Y)^{|\xi_1| - 2}] & 3 \leq k \leq |\xi_1|, \quad 0 \leq j \leq k \land |\xi_2| \\
-\alpha_i(|\xi_2|) - \phi \mathbb{E}[1 - (1 - Y)^{|\xi_1| - |\xi_2|}Y(1 - Y)^{|\xi_1| - 1}] & \xi = \eta.
\end{cases}
\]

If \(N^2\xi \rightarrow 0\) large offspring number events are dominating and only one rate matrix is possible, whose entries are

\[
q_{\ell,\eta} = \begin{cases} 
\mathbb{E}[Y^k(1 - Y)^{|\xi_1| - k}] (|\xi_1| - |\xi_2|)_k & \xi \leq \eta, \quad 2 \leq k \leq |\xi_1|, \\
0 \leq j \leq k \land |\xi_2|; \\
-\mathbb{E}[1 - (1 - Y)^{|\xi_1| - |\xi_2|}Y(1 - Y)^{|\xi_1| - 1}] & \xi = \eta.
\end{cases}
\]

7.5 The conditional distributions of \(A_1\) and \(A_2\)

In this section we obtain the conditional distribution of the number of ancestors \(A_2\) of the subsample, given the number of ancestors \(A_1\) of the sample. The conditional distribution of \(A_2\), and the results of section (7.3) then yield the joint distribution of \(A_1\) and \(A_2\). The results for the subsample process are straightforward extensions of those obtained for the Kingman coalescent (Saunders et al. [1984]). To keep notation in line with Saunders et al. [1984], let \(A_1(t)\) denote the Markov chain counting the number of distinct ancestral lineages at time \(t \geq 0\) before the present of a set of lineages drawn from the population at time zero. Let \(A_2(t)\) denote the corresponding number for a subset of the lineages drawn at time zero. Define \(T_1(a) \equiv \inf \{t : A_1(t) = a\}\), \(T_2(a) \equiv \inf \{t : A_2(t) = a\}\), \(A_1^*(a) \equiv A_1(T_2(a))\), and \(A_2^*(a) \equiv A_2(T_1(a))\). Given \(A_1(t) = a\), denote by \(\beta(a, a - k)\) the probability that the next merger involves \(k + 1\) active ancestral lineages of the sample. The process \((A_2^*(a - \ell_1), \ell_1 = 0, \ldots, a - 1)\) is a Markov chain with transition probabilities

\[
P[A_2^*(a_i - k) = a_j - j | A_2^*(a_i) = a_{i-1}] = \frac{(a_j - a_k) \binom{a_i}{k-j}}{a_j \binom{a_i}{k+1}} \quad (41)
\]

for \(1 \leq j \leq \min(k, a_2 - 1)\), and \(1 \leq k \leq a_i - 1\), and marginal probabilities

\[
P[A_2^*(a_i) = a_2| A_2^*(a_i) = a_{i-1}] = 1, \quad 1 \leq a_2 \leq a_i. \quad (42)
\]
The transition probability (41) is not a function of the coalescence rates, since we condition on a merger of $k+1$ lineages. However, the conditional distribution

$$\phi_{ij}(a_1, a_2) \equiv \mathbb{P}[A_2^*(a_1) = a_2|A_2(0) = j, A_1(0) = i]$$

of $A_2$, given $A_1$, will be, due to the presence of multiple mergers. Write $\phi(\cdot, \cdot) = \phi_{ij}(\cdot, \cdot)$ for ease of presentation. The conditional distribution of $A_2^*$, given $A_1$, can be obtained as a recursion,

$$\phi(a_1, a_2) = \sum_{k=1}^{i-a} \beta(a_1 + k, a_1) \sum_{\ell=1}^{k \wedge j} \left( \phi(a_1 + k, a_2 + \ell) \frac{a_2 + \ell}{a_2 + k} \frac{a_1 + k - a_2 - \ell}{a_1 + k + 1} \right)$$

$$+ \phi(a_1 + k, a_2) \frac{a_2 (a_1 + k - a_2) + (a_1 + k - a_2)}{a_2 + k + 1}$$

with the boundary conditions $\phi_{i,j}(i,j) = 1$ and $\phi_{i,1}(i,1) = 1$ for all $i \geq 1$. By way of example, $\phi_{1,1}(1,1) = \phi_{2,1}(2,1) = \phi_{2,1}(1,1) = 1$ and $\phi_{3,2}(2,1) = \beta(3,2)/3$. The joint distribution of $(A_1(t), A_2(t))$ is

$$\mathbb{P}[A_1(t) = a_1, A_2(t) = a_2|A_1(0) = i, A_2(0) = j] = g_{i,a_1}(t) \phi_{i,j}(a_1, a_2)$$

in which $\phi_{i,j}(a_1, a_2)$ is given in Equation (43).

The distribution of $A_1^*(\cdot)$ can be given via a simple recursion,

$$\mathbb{P}[A_1^*(a_2) = a_1|A_1(0) = i, A_2(0) = j] = \sum_{k=1}^{i-a_1} \beta(a_1 + k, a_1) \sum_{\ell=1}^{k \wedge (j-a_2)} \phi_{i,j}(a_1 + k, a_2 + \ell) \frac{a_2 + \ell}{a_2 + k} \frac{a_1 + k - a_2 - \ell}{a_1 + k + 1}.$$ (45)

### 7.6 The subsample coalescent process including mutation

In this section we give the generators associated with the coancestry coalescent process including neutral mutation. Let $\tilde{R}_1$ and $\tilde{R}_2$ denote the coalescent processes for the sample and the subsample, respectively, including mutation. As we are assuming an infinite allele/sites mutation model, mutation results in ‘new’ alleles, and the probability of recurrent mutation is ignored. The joint process takes values in \( \tilde{E}^2 \), in which the transition $\xi \rightsquigarrow \eta$, as previously, denotes a transition due to mutation:

$$\xi \rightsquigarrow \eta = \begin{cases} \xi_1 \rightsquigarrow \eta_1, & \xi_2 = \eta_2; \\ \xi_1 \rightsquigarrow \eta_1, & \xi_2 \rightsquigarrow \eta_2. \end{cases}$$ (46)
The first line in (46) denotes the transition in which the mutated lineage does not belong to the subsample, while the second line means that the mutated lineage does belong to the subsample. The set \( \tilde{E} \) denotes the space of all equivalence relations on \( \{1, \ldots, n\} \) in which each relation \( \xi \) is partitioned into a set of new and old equivalence classes (Möhle, 1999).

The joint ancestral process \((\tilde{R}(k); k \in \mathbb{N}) \equiv (\tilde{R}_1(k), \tilde{R}_2(k))_{k \in \mathbb{N}}\) is a Markov chain on \( \tilde{E}^2 \) with transition probability \( \tilde{P}_{\ell, \eta}(N) \) given by, in which \( m \) denotes the number of classes that mutate and \( m + b \) is the number of old classes of \( \xi \),

\[
P_{\ell, \eta}(N) = \mu_N^m (1 - \mu_N)^b \mathbb{E}[U^{(k)}(N - 1 - U)_{k-1}] (|\xi_1| - |\xi_2|)_{k-j} (|\xi_2|_j),
\]

in which \( 2 \leq k \leq |\xi_1| \), and \( 0 \leq j \leq k \wedge |\xi_2| \). The joint process \( \tilde{R}([tT_N]) \) associated with model \( \ell \in \{1, 2\} \) converges weakly to \( \tilde{R}(t) \) with generator \( \tilde{Q}_\ell \equiv \left( \tilde{q}_{\ell, \eta}^{(\ell)} \right)_{\xi, \eta \in \tilde{E}^2} \). If \( N^2 \varepsilon_N \rightarrow 0 \) large offspring number events are negligible and the generator associated with model \( \ell \in \{1, 2\} \) has entries

\[
\tilde{q}_{\ell, \eta}^{(\ell)}(\xi, \eta) = \begin{cases}
\theta/2 & \xi \sim \eta \\
\alpha_\ell \frac{(|\xi_1| - |\xi_2|)_{2-j} (|\xi_2|_j)}{|\xi_1|_j} & 0 \leq j \leq 2 \wedge |\xi_2| \\\n-|\xi_1| \frac{\theta}{2} - (|\xi_1|_2) \alpha_\ell & \xi = \eta.
\end{cases}
\]

in which the constants \( \alpha_\ell \) are given in Equation (31). If \( N^2 \varepsilon_N \rightarrow \phi \) where \( \phi > 0 \) is a constant, the generator associated with model \( \ell \) has entries

\[
\tilde{q}_{\ell, \eta}^{(\ell)}(\xi, \eta) = \begin{cases}
\theta/2 & \xi \sim \eta \\
(\alpha_\ell + \phi \mathbb{E}[Y^2 - 1 - Y]^{(|\xi_1| - 2)]} \frac{(|\xi_1| - |\xi_2|)_{2-j} (|\xi_2|_j)}{|\xi_1|_j} & 0 \leq j \leq 2 \wedge |\xi_2| \\
\phi \mathbb{E}[Y|k(1 - Y)|^{(|\xi_1| - k)}] \frac{(|\xi_1| - |\xi_2|)_{k-j} (|\xi_2|_j)}{|\xi_1|_j} & 3 \leq k \leq |\xi_1| \\
-|\xi_1| \frac{\theta}{2} - (|\xi_1|_2) \alpha_\ell - \phi \mathbb{E}[1 - (1 - Y)^{|\xi_1| - |\xi_1|} - |\xi_1|] Y (1 - Y) \xi_1 - 1] & \xi = \eta.
\end{cases}
\]

If \( N^2 \varepsilon_N \rightarrow \infty \) large offspring number events are dominating and the single resulting generator
has entries
\[
\tilde{q}_{\xi,\eta} = \begin{cases} 
\frac{\theta}{2} & \xi \sim \eta \\
\mathbb{E}[Y^2(1 - Y)\xi_{i-2}^j \frac{(\xi_{i-2} - \xi_{i-2-j})_2}{(\xi_{i-2})_2}] & 0 \leq j \leq 2 \& |\xi_2| \\
\mathbb{E}[Y^k(1 - Y)\xi_{i-2}^j \frac{(\xi_{i-2} - \xi_{i-2-j})_k}{(\xi_{i-2})_k}] & 3 \leq k \leq |\xi_1| \\
-|\xi_1|^\theta - \mathbb{E}[(1 - Y)\xi_1^2 | Y(1 - Y)\xi_{i-2}^j] & \xi = \eta.
\end{cases}
\] (50)

7.7 The conditional distributions of \( \tilde{A}_1^* \) and \( \tilde{A}_2^* \)

The conditional distribution of \( \tilde{A}_1^*(\cdot) \), given initial subsample size \( j \) from initial sample size \( i \), is obtained similarly as the conditional distribution of \( A_2^*(\cdot) \). Define
\[
\tilde{\phi}_{i,j}(a_1, a_2) \equiv \mathbb{P}\left[ \tilde{A}_2^*(a_1) = a_2 | \tilde{A}_2(0) = j, \tilde{A}_1(0) = i \right],
\]
let \( \lambda(a) \) denote the transition rate of the sample process \( \tilde{A}_1 \) given a active ancestral lineages, and let \( \beta(a + k, a) \) denote the probability of coalescence of \( k + 1 \) out of \( a + k \) active ancestral lineages. The forward equations of \( \tilde{\phi}(\cdot, \cdot) = \tilde{\phi}_{i,j}(\cdot, \cdot) \) are given by
\[
\tilde{\phi}(a_1, a_2) = \tilde{\phi}(a_1 + 1, a_2) \left( \tilde{\beta}(a_1 + 1, a_1) \frac{(a_1 - a_2 + 1)(a_1 + a_2)}{(a_1 + 1)a_1} + \frac{(a_1 + 1)\theta/2 a_1 - a_2 + 1}{\lambda(a_1 + 1)} \right)
\]
\[
+ \tilde{\phi}(a_1 + 1, a_2 + 1) \left( \tilde{\beta}(a_1 + 1, a_1) \frac{(a_2 + 1)a_2}{(a_1 + 1)a_1} + \frac{(a_1 + 1)\theta/2 a_2 + 1}{\lambda(a_1 + 1)} \right)
\]
\[
+ \sum_{k=2}^{i-a_1} \tilde{\phi}(a_1 + k, a_2) \tilde{\beta}(a_1 + k, a_1) \frac{(a_1 + k - a_2)}{(a_1 + k)}
\]
\[
+ \sum_{k=2}^{i-a_1} \tilde{\phi}(a_1 + k, a_2) \tilde{\beta}(a_1 + k, a_1) \frac{a_2(a_1 + k - a_2)}{(a_1 + k)}
\]
\[
+ \sum_{k=2}^{i-a_1} \sum_{\ell=2}^{k-(j-a_2)} \tilde{\phi}(a_1 + k, a_2 + \ell) \tilde{\beta}(a_1 + k, a_1) \frac{(a_2 + \ell - 1)(a_1 + k - a_2 - \ell)}{(a_1 + k)}
\] (51)

with boundary condition \( \tilde{\phi}_{i,k}(i, k) = \delta_{k,j} \).
The conditional distribution of $\tilde{A}_1^*$ can be obtained similarly. Define,

$$\tilde{\psi}_{i,j}(a_1, a_2) \equiv \mathbb{P} \left[ \tilde{A}_1^*(a_2) = a_1 | \tilde{A}_1(0) = i, \tilde{A}_2(0) = j \right]. \quad (52)$$

The forward equations for $\tilde{\psi}(\cdot, \cdot) = \tilde{\psi}_{i,j}(\cdot, \cdot)$ are given by

$$\tilde{\psi}(a_1, a_2) = \tilde{\psi}(a_1 + 1, a_2 + 1) \left( \beta(a_1 + 1, a_1) \frac{(a_2 + 1)a_2}{(a_1 + 1)a_1} + \frac{(a_1 + 1)\theta/2 a_2 + 1}{\lambda(a_1 + 1) a_1} \right)$$

$$+ \sum_{k=2}^{a_1 - a_1} \beta(a_1 + k, a_1) \sum_{\ell=2}^{k \wedge (j - a_2)} \tilde{\psi}(a_1 + k, a_2 + \ell) \frac{(a_2 + \ell)}{(a_1 + k)} \frac{(a_1 + k - a_2 - \ell)}{(k + 1)} \quad (53)$$

with boundary conditions $\tilde{\psi}_{i,j}(i, j) = \tilde{\psi}_{i,i}(\cdot, \cdot) = 1$. By way of example,

$$\tilde{\psi}_{2,1}(0, 0) = \beta(2, 1) + \frac{\theta}{4 \lambda(2)} \quad (54)$$
Table 1: An approximation of the probability \( h_j(t) \) \(^\text{[17]}\) that \( j \) of the original lines in the population are still segregating at time \( t = 1 \) for different values of \( \theta \) and \( \beta_\ell \). Results for the usual Kingman coalescent are obtained when \( \beta_\ell = 1 \).

| \( \theta \) | \( \beta_\ell \) | \( j \) | \( \geq 2 \) |
|---|---|---|---|
| 1  | 1   | 0.036 | 0.320 | 0.644 |
| 2  | 1   | 0.133 | 0.654 | 0.213 |
| 5  | 1   | 0.273 | 0.718 | 0.009 |
| 5  | 1   | 0.556 | 0.379 | 0.065 |
| 2  | 1   | 0.719 | 0.270 | 0.011 |
| 5  | 1   | 0.836 | 0.164 | 0.000 |
Table 2: The probability $\psi_{i,2}(1,1)$ (Equation 18) of two lineages sharing a most recent common ancestor with the $i$ lineages, varying over $i$ and $\pi$. When $0 < \pi < 1$, $\pi$ denotes $\psi$ of the point mass process; $\pi$ denotes $\alpha$ of the beta coalescent when $1 < \pi < 2$, and finally the vector $(\alpha, \beta)$ of the two-parameter beta coalescent.

| $i$  | $\pi$  | $\psi_{i,2}(1,1)$ |
|------|--------|-------------------|
| 500  | 0.005  | 0.330             |
|      | 0.5    | 0.065             |
| 1000 | 0.005  | 0.328             |
|      | 0.5    | 0.048             |
| 500  | 1.05   | 0.178             |
|      | 1.5    | 0.266             |
| 1000 | 1.05   | 0.163             |
|      | 1.5    | 0.261             |
| 500  | (1.0, 1.0) | 0.061          |
|      | (1.0, 5.0) | 0.122          |
| 1000 | (1.0, 1.0) | 0.041          |
|      | (1.0, 5.0) | 0.105          |
Table 3: The probability $\tilde{u}(1000, 2)$ that the oldest allele of a sample is among two lineages drawn from a sample of size 1000. Cases of $\pi < 1$ refer to the point mass process, of $1 < \pi < 2$ to the beta coalescent, and $\pi = (\alpha, \beta)$ refers to the two-parameter beta coalescent.

| $\theta$ | $\pi$ | $\tilde{u}(1000, 2)$ |
|----------|-------|---------------------|
| 1        | 1.05  | 0.506               |
|          | 1.5   | 0.598               |
| 5        | 1.05  | 0.111               |
|          | 1.5   | 0.189               |
| 1        | 0.05  | 0.063               |
|          | 0.5   | 0.071               |
| 5        | 0.05  | 0.002               |
|          | 0.5   | 0.008               |
| 1        | (1,1) | 0.148               |
|          | (1,5) | 0.010               |
| 5        | (1,1) | 0.022               |
|          | (1,5) | 0.003               |
| 1        | (5,1) | 0.354               |
| 5        | (5,1) | 0.071               |
| 1        | (5,5) | 0.084               |
| 5        | (5,5) | 0.010               |
Table 4: The mean $\mathbb{E}[F_i]$ and variance $\mathbb{V}[F_i]$ of the number $F_i$ of the oldest allele in a sample of size $i = 30$ varying over $\theta$ and $\pi$. The corresponding values for the Kingman coalescent are $\mathbb{E}[F_i] = 15.500$ and $\mathbb{V}[F_i] = 74.917$ for $\theta = 1$, and $\mathbb{E}[F_i] = 5.833$ and $\mathbb{V}[F_i] = 20.139$ for $\theta = 5$.

| $\theta$ | $\pi$ | $\mathbb{E}[F_i]$ | $\mathbb{V}[F_i]$ |
|---------|------|----------------|-----------------|
| 1       | 1.05 | 14.834         | 93.625          |
|         | 1.5  | 15.026         | 84.975          |
| 5       | 1.05 | 5.112          | 34.612          |
|         | 1.5  | 5.269          | 26.698          |
| 1       | 0.05 | 1.061          | 0.096           |
|         | 0.5  | 5.182          | 38.028          |
| 5       | 0.05 | 1.012          | 0.018           |
|         | 0.5  | 1.824          | 5.995           |
| 1       | (1, 1) | 7.792 | 67.565 |
|         | (5, 1) | 13.570 | 96.908 |
|         | (1, 5) | 1.845 | 5.027  |
|         | (5, 5) | 5.752 | 45.621 |
| 5       | (1, 1) | 2.630 | 18.001 |
|         | (5, 1) | 4.923 | 44.402 |
|         | (1, 5) | 1.163 | 0.826 |
|         | (5, 5) | 1.978 | 8.200 |
Figure 1: The probability $h_{i0}(t)$ that $i$ lineages have vanished from the population by time $t$ as a function of time for $i = 20$ and varying over $\theta$ and the coalescence parameters $\psi$ (a), $\alpha$ (b), and $(\alpha, \beta)$ (c) as shown in the legends.
Figure 2: Expected number $E[\tilde{A}_2^*(a_1) = a_2 | \tilde{A}_1 = 150, \tilde{A}_2 = 50]$ of lineages ancestral to the subsample as a function of $a_1$ when the population has the $\alpha$-coalescent with $\alpha$ and the mutation rate $\theta$ varying as shown in the legend. Right panels are for the two parameter beta coalescent.
Figure 3: Expected value $\mathbb{E}[A^*_1(a_2) = a_1|A_1(0) = 150, A_2(0) = 50]$ as a function of the number $a_2$ of ancestral lineages belonging to the subsample varying over $\pi$ and $\theta$ as shown in the legends. By $K$ we denote the Kingman coalescent.

- **Beta coalescent**

  - $(\alpha, \theta)$
    - $(K,1)$
    - $(K,5)$
    - $(1.005,5)$
    - $(1.5,5)$
    - $(1.5,1)$
    - $(1.005,1)$

  - **Point mass coalescent**

  - $(\psi, \theta)$
    - $(K,1)$
    - $(K,5)$
    - $(0.25,5)$
    - $(0.25,1)$

- **Beta $(\alpha, \beta)$ coalescent**

  - $(\alpha, \beta, \theta)$
    - $(K,1)$
    - $(K,5)$
    - $(1.5,5)$
    - $(1.5,1)$
    - $(5.5,1)$
    - $(1.1,1)$

  - **Beta $(\alpha, \beta)$ coalescent**

  - $(\alpha, \beta, \theta)$
    - $(K,1)$
    - $(K,5)$
    - $(1.5,5)$
    - $(5.5,1)$
    - $(1.1,1)$
Figure 4: The probability $\tilde{u}(150, j)$ that the oldest allele of a sample is among $j$ lineages as a function of $j$ from 1 to 50 and varying over $(\pi, \theta)$ as shown in the legends (in the same form as in Figure 3). By $K$ we denote the usual Kingman coalescent.