COALESCENT RESULTS FOR TWO-SEX POPULATION MODELS

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Abstract

'Convergence-to-the-coalescent' theorems for two-sex neutral population models are presented. For the two-sex Wright–Fisher model the ancestry of n sampled genes behaves like the usual n-coalescent, if the population size N is large and if the time is measured in units of $4N$ generations. Generalisations to a larger class of two-sex models are discussed.

Keywords: Coalescent; two-sex population models; genealogical process; population genetics; robustness; two-sex Wright–Fisher model

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1. Introduction

A special stochastic process, called the coalescent, is of fundamental interest in population genetics. For a large class of haploid population models this process is the appropriate tool to analyse the ancestral structure of a sample of n genes (or individuals), if the total number of genes in the population is sufficiently large. A corresponding convergence theorem for a large class of exchangeable population models was first proved by Kingman [4, 5, 6]. During recent years a variety of publications have appeared in order to extend the coalescent-theory to more general and more complicated models, for example, models with underlying mutation, selection or recombination, models with variable population size or non-exchangeable models. See, for example, Donnelly and Tavaré [1], Griffiths and Majoram [2], Hudson and Kaplan [3], Möhle [9], Tavaré [11] and references therein. One speaks of the robustness of the coalescent, as this process appears in a lot of quite different models as the total population size tends to infinity.

The purpose here is to illustrate how the coalescent-theory can be extended to two-sex neutral population models. The standard two-sex Wright–Fisher model with fixed population size [7] is studied in Theorem 1. For a larger class of two-sex models a convergence result is given in Theorem 2. Both theorems are based on a more general convergence result for sequences of Markov chains with the same finite state space, which can be found in [10, Lemma 1 and Theorem 1].

2. Two-sex population models

Consider a two-sex population model with non-overlapping generations, numbered, as usual, backwards in time by $r \in \mathbb{N}_0 := \{0, 1, 2, \dots\}$. Assume a fixed number of N pairs

of individuals consisting of a male and a female. The N pairs of a generation r produce N daughters and N sons altogether, and these $2N$ children form the N pairs of the next generation $r - 1$ at random. Let $\alpha_i^{(r)}$ and $\beta_i^{(r)}$ respectively denote the number of daughters and sons of the pair i in generation r, $i \in \{1, \dots, N\}$, $r \in \mathbb{N}$. The offspring vectors $(\alpha_1^{(r)}, \beta_1^{(r)}, \dots, \alpha_N^{(r)}, \beta_N^{(r)})$ are required to be independent and identically distributed for different generations and to satisfy

$$\sum_{i=1}^{N} \alpha_i^{(r)} = N = \sum_{i=1}^{N} \beta_i^{(r)}.$$

The total number of children born to the pair i of generation r is given by $\nu_i^{(r)} := \alpha_i^{(r)} + \beta_i^{(r)}$. Write ν_i for $\nu_i^{(0)}$ and call a pair (or individual) alive in generation r an r-pair (or an r-individual) for convenience.

Consider a single diploid gene locus and assume that each individual chooses one gene from its mother and the other one from its father randomly and independently of the rest of the process. Number the four genes of each pair (for example) in such a way that the genes 1 and 2 are the genes of the female and the genes 3 and 4 are the genes of the male.

Let $g_{ij}^{(r)}$, $i \in \{1, \dots, N\}$, $j \in \{1, 2, 3, 4\}$ denote the number of genes in generation $r - 1$ descended from the jth gene of the ith pair alive in generation r. Obviously

$$g_{i1}^{(r)} + g_{i2}^{(r)} = \nu_i^{(r)} = g_{i3}^{(r)} + g_{i4}^{(r)}.$$

Conditional on $\nu_i^{(r)}$ the variable $g_{ij}^{(r)}$ has a binomial distribution with parameters $\nu_i^{(r)}$ and $1/2$. Hence the descending factorial moments are given by $\mathrm{E}((g_{ij}^{(r)})_k) = (1/2)^k \mathrm{E}((\nu_i^{(r)})_k)$ for all $k \in \mathbb{N}_0$, where the notation $(x)_0 := 1$ and $(x)_k := x(x-1)\cdots(x-k+1)$ for all $k \in \mathbb{N}$ is used. The common distribution of the $g_{ij}^{(r)}$, i.e. the probabilities

$$P\left(\bigcap_{i=1}^{N} \bigcap_{j=1}^{4} \{g_{ij}^{(r)} = m_{ij}\}\right), \tag{1}$$

$(0 \leq m_{ij} \leq 2N)$, can be expressed in terms of the $\nu_i^{(r)}$, $i \in \{1, \dots, N\}$, as follows. Each child chooses one gene from its father with probability $1/2$ and one gene from its mother with probability $1/2$. Thus given $\nu_i^{(r)} = m_{i1} + m_{i2} = m_{i3} + m_{i4}$ (for all i) the above probability is

$$\prod_{i=1}^{N} \binom{m_{i1} + m_{i2}}{m_{i1}} \left(\frac{1}{2}\right)^{m_{i1}+m_{i2}} \cdot \binom{m_{i3} + m_{i4}}{m_{i3}} \left(\frac{1}{2}\right)^{m_{i3}+m_{i4}}$$

and hence (1) can be calculated via,

$$P\left(\bigcap_{i=1}^{N} \{\nu_i^{(r)} = m_{i1} + m_{i2} = m_{i3} + m_{i4}\}\right) \left(\frac{1}{2}\right)^{4N} \prod_{i=1}^{N} \binom{m_{i1} + m_{i2}}{m_{i1}} \binom{m_{i3} + m_{i4}}{m_{i3}}. \tag{2}$$

The probability that two randomly chosen genes belonging to different $(r - 1)$-pairs have a common ancestor in generation r is given by $c_r = w_r/4$, where

$$w_r := \sum_{i=1}^{N} \left(\frac{\mathrm{E}((\nu_i^{(r)})_2)}{4(N)_2} - \frac{\mathrm{E}(\alpha_i^{(r)} \beta_i^{(r)})}{2N(N)_2}\right)$$

is the probability that two randomly chosen individuals belonging to different $(r-1)$-pairs are children of the same r-pair (See [8]). Note that $\alpha_i^{(r)}\beta_i^{(r)} \leq (v_i^{(r)})_2$. Hence

$$w_r \sim \frac{1}{4N^2}\sum_{i=1}^{N}E((v_i^{(r)})_2)$$

for large N and

$$c_r \sim \frac{1}{(4N)_2}\sum_{i=1}^{N}E((v_i^{(r)})_2) = \frac{1}{(4N)_2}\sum_{i=1}^{N}\sum_{j=1}^{4}E((g_{ij}^{(r)})_2)$$

which corresponds to the 'coalescence probability' used in haploid population models (See [9]).

Example 1. In the two-sex Wright–Fisher model it is assumed that $\alpha^{(r)} := (\alpha_1^{(r)}, \ldots, \alpha_N^{(r)})$ and $\beta^{(r)} := (\beta_1^{(r)}, \ldots, \beta_N^{(r)})$ are independent and both multinomially distributed according to $Mn(N, 1/N, \ldots, 1/N)$. In this case the joint distribution of the children offspring variables is a multinomial distribution,

$$(v_1^{(r)}, \ldots, v_N^{(r)}) \stackrel{d}{=} Mn(2N, 1/N, \ldots, 1/N)$$

and $g_{ij}^{(r)} \stackrel{d}{=} B(2N, 1/(2N))$. Note that the joint distribution of the gene offspring variables is not a multinomial distribution. Further,

$$w_r = N\left(\frac{(2N)_2(1/N)^2}{4(N)_2} - \frac{1}{2N(N)_2}\right) = \frac{1}{N}$$

and hence $c_r = 1/(4N)$.

3. The ancestral process and the coalescent

Fix $n \leq 4N$ and choose n genes at random (without replacement) from the current generation 0. For $r \in \mathbb{N}_0$, let $\mathcal{R}_r$ denote the equivalence relation which contains (i, j) iff the ith and the jth gene have a common ancestor in the rth generation. In contrast to the well-developed theory for haploid population models, the so-called backward process $(\mathcal{R}_r)_{r \in \mathbb{N}_0}$ is not time-homogeneous, which makes it much more complicated to analyse the ancestral structure for diploid population models. So far the author was able to derive a 'convergence-to-the-coalescent' theorem for the case of the two-sex Wright–Fisher model. For other models, only results for the case $n = 2$ are derived.

Theorem 1. *For the two-sex Wright–Fisher model the finite-dimensional distributions of $(\mathcal{R}_{[4Nt]})_{t\geq0}$ converge to those of the n-coalescent.*

Proof. The basic idea is to apply the convergence theorem given in [10, Lemma 1 and Theorem 1]. Define a finer, more detailed ancestral structure which distinguishes so many states that the corresponding backward process becomes a time-homogeneous Markov chain, which can be analysed more easily than the non-time-homogeneous process $(\mathcal{R}_r)_{r \in \mathbb{N}_0}$. Consider the ancestral genes of the n sampled genes r generations backwards in time. A pair has by

definition the type $k \in \{0, 1, 2, 3, 4\}$, if exactly k genes of the ancestral genes belong to this pair. For a pair of type 2 we distinguish further two sub-types. The first, '21', applies if the two genes belong to different individuals and the second, '22', if both genes belong to the same individual.

Now let $\mathcal{X}_{rk}$ denote the number of pairs in generation r of type $k \in \{0, 1, 21, 22, 3, 4\}$. Define $\mathcal{X}_r := (\mathcal{X}_{rk})_{k \in \{0,1,21,22,3,4\}}$ and consider the time-homogeneous Markov process $(\mathcal{C}_r)_{r \in \mathbb{N}_0} := (\mathcal{R}_r, \mathcal{X}_r)_{r \in \mathbb{N}_0}$. The state space of this process is of the form $S = \bigcup_{\xi \in \mathcal{E}_n} S_\xi$, where

$$S_\xi := \bigcup_{x \in C_\xi} \{(\xi, x)\}$$

and C_ξ is the set of all $x = (x_0, x_1, x_{21}, x_{22}, x_3, x_4)$, with $\sum_{i=0}^4 x_i = N$ and $\sum_{i=0}^4 i x_i = b :=$ $|\xi|$, where $x_2 := x_{21} + x_{22}$ and $|\xi|$ denotes the number of equivalence classes of ξ. Note that for $N \geq b$,

$$|S_\xi| = |C_\xi| = \sum_{\substack{x_0,x_1,x_2,x_3,x_4 \in \mathbb{N}_0 \\ x_0+x_1+x_2+x_3+x_4=N \\ x_1+2x_2+3x_3+4x_4=b}} (x_2 + 1) = \sum_{\substack{X_1,X_2,X_3,X_4 \in \mathbb{N}_0 \\ x_1+x_2+x_3+x_4 \leq N \\ x_1+2x_2+3x_3+4x_4=b}} (x_2 + 1)$$

$$= \sum_{\substack{x_1,x_2,x_3,x_4 \in \mathbb{N}_0 \\ x_1+2x_2+3x_3+4x_4=b}} (x_2 + 1) = \sum_{\substack{x_2,x_3,x_4 \in \mathbb{N}_0 \\ 2x_2+3x_3+4x_4 \leq b}} (x_2 + 1) =: L_b,$$

depends only on b. Thus for $N \geq n$ it follows that

$$|S| = \sum_{\xi \in \mathcal{E}_n} |S_\xi| = \sum_{b=1}^n S(n, b) L_b,$$

where the $S(n, b)$ are the Stirling numbers of the second kind.

b	L_b	b	L_b		n	$|S|$	n	$|S|$
1	1	6	17		1	1	6	1 141
2	3	7	21		2	4	7	5 972
3	4	8	32		3	14	8	33 496
4	8	9	39		4	54	9	200 411
5	10	10	55		5	236	10	1 274 293

It is shown later that there is a high probability that the process stays in states of the form $(\xi, x(b))$ with $x(b) := (N - b, b, 0, 0, 0, 0)$. This means that the b ancestral genes belong to different pairs. For $i = (\xi, x)$, $j = (\eta, y) \in S$ define the transition probability

$$\pi_{ij} := P(\mathcal{C}_r = j \mid \mathcal{C}_{r-1} = i),$$

and analyse the transition matrix $\Pi_N = (\pi_{ij})_{i,j \in S}$. It is convenient to divide the transition matrix Π_N into $|\mathcal{E}_n|^2$ sub-matrices,

$$\Pi_N = (\Pi_{N\xi\eta})_{\xi,\eta \in \mathcal{E}_n},$$

where $\Pi_{N\xi\eta} := (\pi_{(\xi,x),(\eta,y)})_{x\in C_\xi,y\in C_\eta}$ is a $(|S_\xi| \times |S_\eta|)$-sub-matrix. In the Wright–Fisher model, conditional on $C_{r-1} = (\xi, x)$ with probability $1 + O(N^{-1})$, no coalescence will occur while proceeding from generation $r - 1$ to generation r, i.e. one generation backwards in time. Furthermore with probability $1 + O(N^{-1})$,

(1) the ancestral genes of genes belonging to different $(r - 1)$-individuals will belong to different r-pairs and,

(2) the ancestral genes of the two genes of a $(r - 1)$-individual will belong to different r-individuals.

Thus travelling two (or any other fixed number of more) generations backwards in time, with probability $1 + O(N^{-1})$, all ancestral genes will belong to different pairs and no coalescence will occur. Thus the transition matrix Π_N has a decomposition of the form

$$\Pi_N = A + c_N B_N,$$

where $A := \lim_{N\to\infty} \Pi_N$ does not depend on N, $c_N := 1/(4N)$ and $(B_N)_{N\in\mathbb{N}}$ is a bounded matrix sequence. More detailed (in terms of the sub-matrix structure) this decomposition is given by

$$\Pi_N = (A_{\xi\eta})_{\xi,\eta\in\mathcal{E}_n} + c_N (B_{N,\xi\eta})_{\xi,\eta\in\mathcal{E}_n},$$

where $A_{\xi\eta} = 0$ for $\xi \neq \eta$ and

$$\lim_{m\to\infty} A^m_{\xi\xi} = \begin{pmatrix} 0 & \cdots & 0 & 1 \\ \vdots & & \vdots & \vdots \\ 0 & \cdots & 0 & 1 \end{pmatrix} =: P_\xi,$$

which corresponds to the fact that after two (or any other fixed number of more) steps backwards in time the ancestral genes will belong to different pairs with probability $1 + O(N^{-1})$. Hence it follows that

$$P := \lim_{m\to\infty} A^m = (P_{\xi\eta})_{\xi,\eta\in\mathcal{E}_n},$$

with $P_{\xi\eta} := 0$ for $\xi \neq \eta$ and $P_{\xi\xi} := P_\xi$. Now, it is straightforward to verify that

$$G := \lim_{N\to\infty} P B_N P = \lim_{N\to\infty} (P_\xi B_{N,\xi\eta} P_\eta)_{\xi,\eta\in\mathcal{E}_n}$$

$$= \lim_{N\to\infty} \left(\begin{pmatrix} 0 & \cdots & 0 & s_{\xi\eta} \\ \vdots & & \vdots & \vdots \\ 0 & \cdots & 0 & s_{\xi\eta} \end{pmatrix} \right)_{\xi,\eta\in\mathcal{E}_n},$$

where $s_{\xi\eta}$ denotes the sum of all the entries of the last row of the matrix $B_{N,\xi\eta}$. That is,

$$s_{\xi\eta} = \sum_{y\in C_\eta\setminus\{x(a)\}} \frac{\pi_{(\xi,x(b)),(\eta,y)}}{c_N} + \frac{\pi_{(\xi,x(b)),(\eta,x(a))} - \delta_{\xi\eta}}{c_N}$$

$$= c_N^{-1} \left(\sum_{y\in C_\eta} \pi_{(\xi,x(b)),(\eta,y)} - \delta_{\xi\eta} \right)$$

$$= c_N^{-1} \left(\sum_{y\in C_\eta} P(C_r = (\eta, y) \mid C_{r-1} = (\xi, x(b))) - \delta_{\xi\eta} \right)$$

$$= c_N^{-1} (P(\mathcal{R}_r = \eta \mid C_{r-1} = (\xi, x(b))) - \delta_{\xi\eta}),$$

where $a := |\eta|$ and $b := |\xi|$. Note that $\mathcal{X}_{r-1} = x(b)$ means that the b ancestral genes in generation $r-1$ belong to different $(r-1)$-pairs. Now consider the b individuals of generation $r-1$ where these b genes are located. In the Wright–Fisher model, each of these individuals chooses randomly his parent pair. Thus in the Wright–Fisher model the b genes choose their ancestral genes randomly under the $4N$ genes of the previous generation r. As in a haploid Wright–Fisher model with population size $4N$, it follows that

$$P(\mathcal{R}_r = \eta \mid \mathcal{C}_{r-1} = (\xi, x(b))) = \frac{(4N)_a}{(4N)^b} = \delta_{\xi\eta} + c_N q_{\xi\eta} + o(c_N),$$

where

$$q_{\xi\eta} := \begin{cases} -|\xi|(|\xi| - 1)/2 & \text{if } \xi = \eta, \\ 1 & \text{if } \xi \prec \eta, \\ 0 & \text{otherwise,} \end{cases}$$

and $\xi \prec \eta :\Longleftrightarrow \xi \subseteq \eta$ and $|\xi| = |\eta| + 1$. Note that the $q_{\xi\eta}$ are exactly the entries of the infinitesimal generator of the n-coalescent. Hence $\lim_{N\to\infty} s_{\xi\eta} = q_{\xi\eta}$ and

$$G = \left(\begin{pmatrix} 0 & \cdots & 0 & q_{\xi\eta} \\ \vdots & & \vdots & \vdots \\ 0 & \cdots & 0 & q_{\xi\eta} \end{pmatrix} \right)_{\xi,\eta\in\mathcal{E}_n}.$$

Now apply Lemma 1 of [10] to verify that $\lim_{N\to\infty} \Pi_N^{[t/c_N]} = P - I + \mathrm{e}^{tG} = P\mathrm{e}^{tG} =: \Pi(t)$ for all $t > 0$. Thus the finite-dimensional distributions of the process $(\mathcal{C}_{[t/c_N]})_{t\geq 0}$ converge to those of a Markov process $(C_t)_{t\geq 0} = (R_t, X_t)_{t\geq 0}$, with transition matrix $\Pi(t)$ and infinitesimal generator G. Note that

$$P(\mathcal{X}_0 = x(n)) = P(\text{'The } n \text{ chosen genes belong to different pairs'})$$

$$= (4N)_n^{-1} \prod_{i=0}^{n-1} (4N - 4i) = (4N)_n^{-1} 4^n (N)_n,$$

converges to 1 as N tends to infinity and hence $X_0 \equiv x(n)$. All the states (ξ, x) with $x \neq x(|\xi|)$ are instantaneous. By eliminating all these states, it follows that the infinitesimal generator of the 'marginal process' $(R_t)_{t\geq 0}$ is given by $Q = (q_{\xi\eta})_{\xi,\eta\in\mathcal{E}_n}$, which is (by definition) equivalent to the generator of the n-coalescent. Hence the finite-dimensional distributions of the 'marginal process' $(\mathcal{R}_{[4Nt]})_{t\geq 0}$ converge to those of the n-coalescent.

We have been able to prove a 'convergence-to-the-coalescent' theorem for the larger class of two-sex population models defined in Section 2, for the case of $n = 2$ sampled genes.

Theorem 2. *For the case $n = 2$, the finite-dimensional distributions of $(\mathcal{R}_{[t/c_N]})_{t\geq 0}$ converge to those of the 2-coalescent if and only if $\lim_{N\to\infty} c_N = 0$.*

Proof. Consider the set of all ancestral genes r generations backwards in time. Define

$$\mathcal{C}_r := \begin{cases} 1, & \text{if the two ancestor genes are the same (identical by descent),} \\ 2, & \text{if the genes are distinct, but belong to the same individual,} \\ 3, & \text{if the genes belong to different individuals of the same pair,} \\ 4, & \text{if the genes belong to different pairs.} \end{cases}$$

$(\mathcal{C}_r)_{r \in \mathbb{N}_0}$ is a time-homogeneous Markov chain with initial distribution

$$P(\mathcal{C}_0 = i) = \begin{cases} 1/(4N) & \text{if } i \in \{1, 2\}, \\ 1/(2N) & \text{if } i = 3, \\ 1 - 1/N & \text{if } i = 4, \end{cases}$$

and transition matrix

$$\Pi_N = \begin{pmatrix} 1 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ \frac{1}{4}g_N & \frac{1}{4}g_N & \frac{1}{2}g_N & 1 - g_N \\ \frac{1}{4}w_N & \frac{1}{4}w_N & \frac{1}{2}w_N & 1 - w_N \end{pmatrix},$$

where $g_N := N^{-2} \sum_{i=1}^{N} \mathrm{E}(\alpha_i \beta_i)$ is the probability that two individuals of a pair are brother and sister, and

$$w_N := \frac{1}{(N)_2} \sum_{i=1}^{N} \left(\frac{\mathrm{E}((\nu_i)_2)}{4} - \frac{\mathrm{E}(\alpha_i \beta_i)}{2N} \right)$$

is the probability that two randomly chosen individuals of different pairs are children of the same pair ([8], Lemma 4.5). Obviously $\Pi_N = A + c_N B_N$, where $c_N = w_N/4$,

$$A := \begin{pmatrix} 1 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 1 \end{pmatrix} \quad \text{and} \quad B_N := \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ g_N/w_N & g_N/w_N & 2g_N/w_N & -4g_N/w_N \\ 1 & 1 & 2 & -4 \end{pmatrix}.$$

Furthermore

$$P := \lim_{m \to \infty} A^m = \begin{pmatrix} 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 1 \end{pmatrix}.$$

From $\alpha_i \beta_i \leq (\nu_i)_2$ it follows that $g_N \leq N^{-2} \sum_{i=1}^{N} \mathrm{E}((\nu_i)_2) \sim 4 w_N$. Hence $(B_N)_{N \in \mathbb{N}}$ is bounded. Further, it can be easily checked that

$$P B_N P = \begin{pmatrix} 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & -1 \\ 1 & 0 & 0 & -1 \\ 1 & 0 & 0 & -1 \end{pmatrix} =: G$$

does not depend on N. If $\lim_{N \to \infty} c_N = 0$, then by Lemma 1 of [10], it follows that $\Pi_N^{[t/c_N]}$ converges to

$$\Pi(t) := P - I + \mathrm{e}^{tG} = P\mathrm{e}^{tG} = \begin{pmatrix} 1 & 0 & 0 & 0 \\ 1 - \mathrm{e}^{-t} & 0 & 0 & \mathrm{e}^{-t} \\ 1 - \mathrm{e}^{-t} & 0 & 0 & \mathrm{e}^{-t} \\ 1 - \mathrm{e}^{-t} & 0 & 0 & \mathrm{e}^{-t} \end{pmatrix}$$

for all $t > 0$ as N tends to infinity. Hence the finite-dimensional distributions of $(\mathcal{C}_{[t/c_N]})_{t \geq 0}$ converge to those of a process $(C_t)_{t \geq 0}$ with initial value $C_0 \equiv 4$ and transition matrix $\Pi(t)$,

$t > 0$. The states 2 and 3 are instantaneous. Eliminating these states leads to the usual 2-coalescent. Thus the finite-dimensional distributions of $(\mathcal{R}_{[t/c_N]})_{t\geq 0}$ converge to those of the 2-coalescent.

Remark 1. Unfortunately I was not able to extend Theorem 2 to the case of n sampled genes. Some additional, and so far, unknown conditions are necessary in order to prove the existence of the limit $P = \lim_{m\to\infty} A^m$ for the general case. Finding the explicit form of P causes further difficulties. Nevertheless I am convinced that the same theorem is valid for more general models under some additional moment conditions similar to those given in [9].

Acknowledgement

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