Some mathematical models from population genetics

1: Some classical models

Alison Etheridge

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Neutral (haploid) population of constant size N

Wright-Fisher model: new generation determined by multinomial sampling with equal weights

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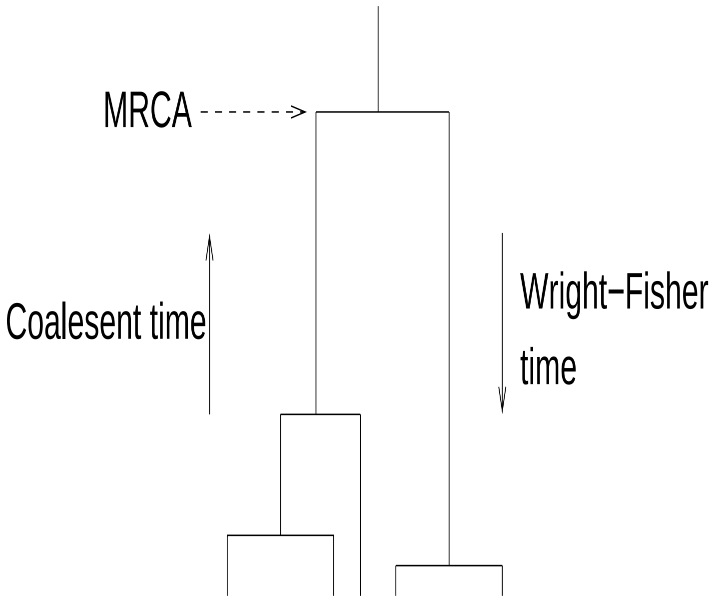

Coalescence rate $\binom{k}{2}$

Some simple extensions

Variable population size $N\rho_t$.

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Genetic structure:

e.g. 2 populations of sizes $N\rho_1$, $N\rho_2$ with migration between. Add mutation step to Wright-Fisher: after reproduction a (small) fixed proportion $\overline{\mu}_i$ of individuals migrates from population i to population j. $\overline{\mu}_1\rho_1 = \overline{\mu}_2\rho_2$.

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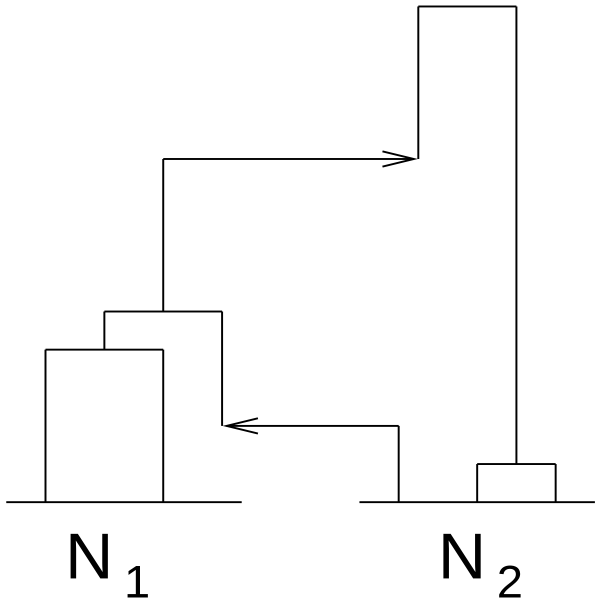

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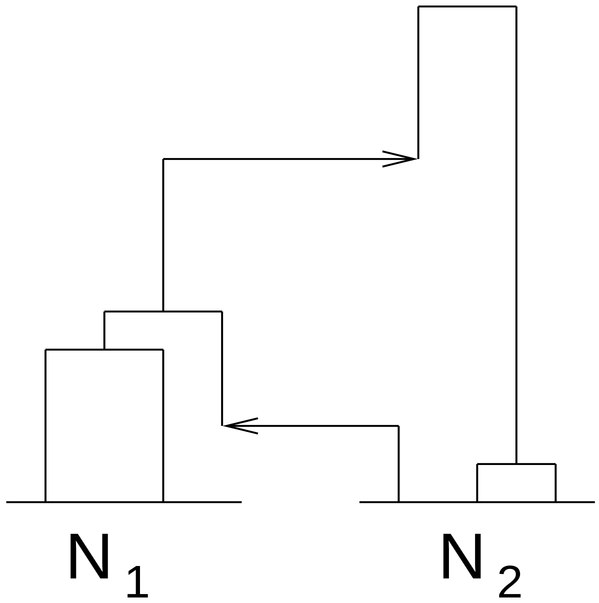

The structured coalescent: within populations coalescence at rate $\frac{1}{\rho_i}\binom{n_i}{2}$. Each lineage *migrates* $1 \mapsto 2$ at rate $\mu_2 \frac{\rho_2}{\rho_1}$ and $2 \mapsto 1$ at rate $\mu_1 \frac{\rho_1}{\rho_2}$.

The Moran model

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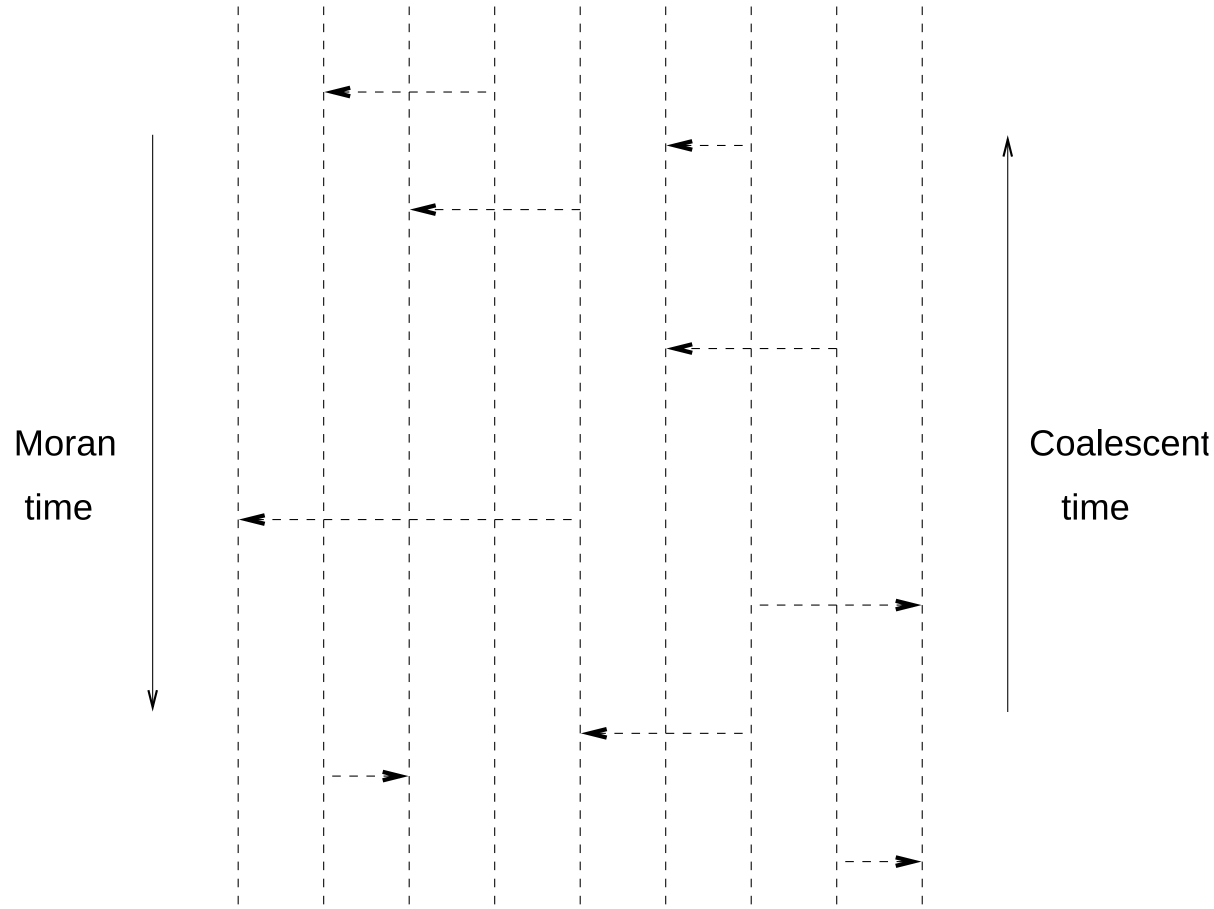
- In the Moran model each individual has zero or two offspring.
- The Moran model is already in 'diffusion' timescale.

Graphical representation



For each pair of indices (i, j) Poiss(1) process of arrows pointing left or right with equal probability.

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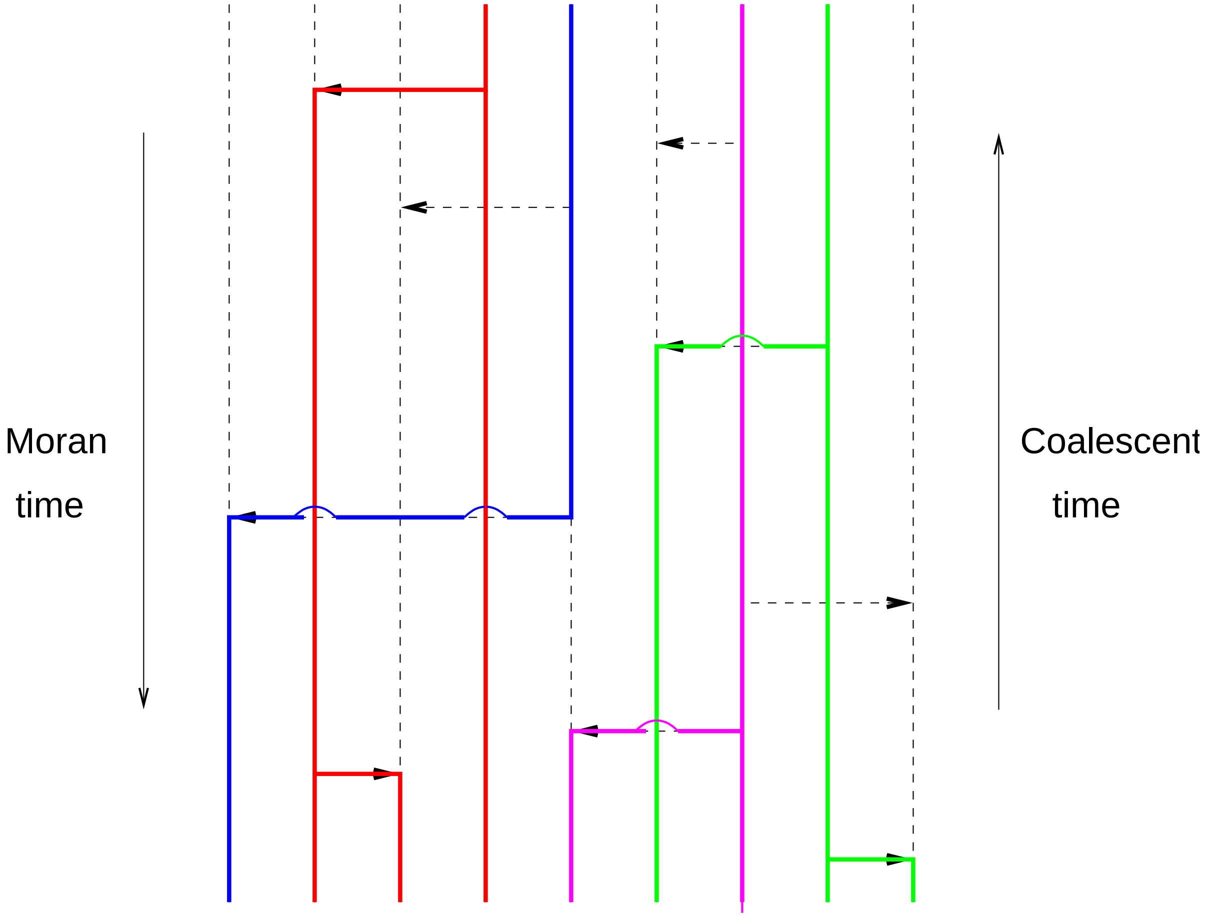

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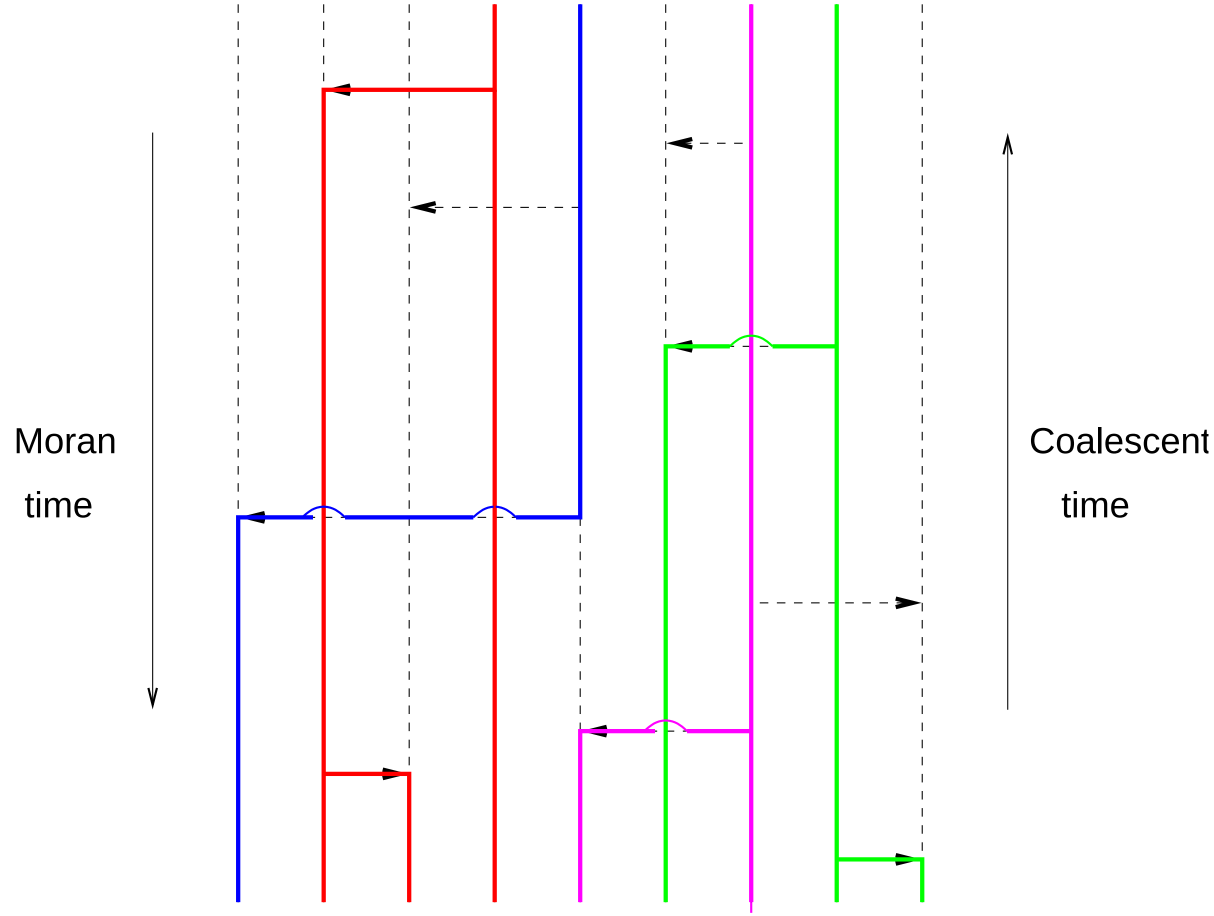

Genealogy given by Kingman's coalescent (independent of N).

The infinite population limit

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Write p_t for the proportion of a-alleles at time t.

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For a 'nice' function f on $[0,1]$, the infinitesimal generator of p is

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\begin{aligned}
\mathcal{L}f(p) &\equiv \frac{d}{dt}\mathbb{E}[f(p_t)|p_0=p]\Big|_{t=0} \\
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To see what happens as $N \to \infty$, perform a Taylor expansion ...

. . . a Taylor expansion

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\mathcal{L}f(p) &= \binom{N}{2}p(1-p)\left(f(p+\frac{1}{N})-f(p)\right) \\
&\quad+\binom{N}{2}p(1-p)\left(f(p-\frac{1}{N})-f(p)\right) \\
&= \binom{N}{2}p(1-p)\Big(f(p)+\frac{1}{N}f'(p)+\frac{1}{2N^2}f''(p)+\mathcal{O}(\frac{1}{N^3})-f(p) \\
&\quad+f(p)-\frac{1}{N}f'(p)+\frac{1}{2N^2}f''(p)+\mathcal{O}(\frac{1}{N^3})-f(p)\Big) \\
&= \frac{1}{2}p(1-p)f''(p)+\mathcal{O}(\frac{1}{N}).
\end{aligned}
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The diffusion limit

It is reasonable to guess then that for the infinite population limit,

$$\frac{d}{dt}\mathbb{E}[f(p_t)|p_0 = p]\Big|_{t=0} = \frac{1}{2}p(1-p)f''(p).$$

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$$dp_t = \sqrt{p_t(1-p_t)}dW_t,$$

where W_t is Brownian motion.

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Diffusion limit:
For $N\sigma \to s$, let $N \to \infty$ (and in WF model measure time in units of size N) to obtain

$$dp_t = sp_t(1-p_t)dt + \sqrt{p_t(1-p_t)}dW_t.$$

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... just as for the Wright-Fisher model.

Feller's diffusion approximation

Offspring $\sim$ Poiss$\left(1+\frac{a}{N}\right)$, generation times $\frac{k}{N}$ and $X_t^{(N)}=\frac{1}{N}Z_t^{(N)}$.

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$$\begin{aligned}
\frac{d}{dt}\mathbb{E}_x\left[s^{X_t}\right]\bigg|_{t=0} &\approx N\left\{\mathbb{E}_x\left[s^{X^{(N)}_{1/N}}\right] - s^x\right\} \\
&= N\left\{e^{Nx\left(1+\frac{a}{N}\right)\left(s^{1/N}-1\right)} - s^x\right\} \\
&\approx \frac{1}{2}x\left(\log s\right)^2 s^x + ax\left(\log s\right)s^x \\
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$N_i(t) = X_i(t) + Y_i(t)$,

$$p_i(t) = \frac{X_i(t)}{X_i(t) + Y_i(t)}.$$

The proportion of type a

$$dp_i(t) = (a_1 - a_2)\, p_i(t)\,(1 - p_i(t))\, dt + \sum_j \frac{N_j}{N_i} m_{ij}\,(p_j(t) - p_i(t))\, dt$$
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The stepping stone model

$$dp_i(t) = s p_i(t)\,(1 - p_i(t))\, dt + \sum_j m_{ij}\,(p_j(t) - p_i(t))\, dt$$

$$s = (a_1 - a_2), \quad \gamma = \frac{\sigma}{N} \qquad + \sqrt{\gamma p_i(t)\,(1 - p_i(t))} dW_i(t).$$

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Strategy: Calculate $d\left(\underline{p}^{\underline{n}}\right)$ for $\underline{n}$ fixed. Choose the process $\underline{n}$ in such a way that equation (*) is satisfied.

Itô's formula gives

$$d\left(\underline{p}^{\underline{n}}\right) = \sum_i n_i \underline{p}^{\underline{n}-\underline{e}_i} \left[s p_i \left(1 - p_i\right) + \sum_j m_{ij} \left(p_j - p_i\right) \right] dt$$

$$+ \sum_i \gamma \frac{1}{2} n_i \left(n_i - 1\right) \underline{p}^{\underline{n}-2\underline{e}_i} p_i \left(1 - p_i\right) dt + \sum_i \left(\ldots\right) dB_i$$

Rearranging,

$$d\left(\underline{p}^{\underline{n}}\right) = \sum_i n_i s \left(\underline{p}^{\underline{n}} - \underline{p}^{\underline{n}+\underline{e}_i}\right) dt$$

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$\underline{n} \mapsto \underline{n} - \underline{e}_i$ at rate $\frac{\gamma}{2} n_i (n_i - 1)$

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The ‘coalescent’ dual

The dual process $\underline{n}$ evolves as follows:

- $n_i \mapsto n_i + 1$ at rate $-sn_i$
- $\left\{ \begin{array}{l} n_i \mapsto n_i - 1 \\ n_j \mapsto n_j + 1 \end{array} \right.$ at rate $n_i m_{ij}$
- $n_i \mapsto n_i - 1$ at rate $\frac{1}{2}\gamma n_i (n_i - 1)$

$$\mathbb{E}\left[\underline{p}_t^{\underline{n}_0}\right] = \mathbb{E}\left[\underline{p}_0^{\underline{n}_t}\right].$$

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$$\mathbb{E}\left[\underline{p}_t^{\underline{n}_0}\right] = \mathbb{E}\left[\underline{p}_0^{\underline{n}_t}\right] \to \overline{p} \quad \text{as } t \to \infty.$$

$$\underline{p}_t \to \begin{cases} \underline{1} & \text{probability } \overline{p} \\ \underline{0} & \text{probability } 1 - \overline{p}. \end{cases}$$

Long-time behaviour

Suppose that $I = \mathbb{Z}^d$ and m_{ij} simple random walk.

- $s < 0$ (selective advantage for A)

$$\mathbb{E}\left[\underline{p}_t^{\underline{n}_0}\right] = \mathbb{E}\left[\underline{p}_0^{\underline{n}_t}\right] \to 0 \quad \text{as } t \to \infty.$$

$\underline{p}_t \to \underline{0}$. The whole population is type A.

- $s = 0$ In $d \leq 2$, $\underline{n} \to$ 'single random walker'.

$$\mathbb{E}\left[\underline{p}_t^{\underline{n}_0}\right] = \mathbb{E}\left[\underline{p}_0^{\underline{n}_t}\right] \to \overline{p} \quad \text{as } t \to \infty.$$

$$\underline{p}_t \to \begin{cases} \underline{1} & \text{probability } \overline{p} \\ \underline{0} & \text{probability } 1 - \overline{p}. \end{cases}$$

Neutral evolution.