Lecture 4: Absorbing probability and mean time to absorption in Birth and Death Process. Applications to Moran Model.

Antonina Mitrofanova, NYU, department of Computer Science

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1 Probability of absorption in Birth-and-Death process

1.1 Probabilistic method

Since the growth of the population results exclusively from the existing population, it is clear that when the population size becomes zero, it remains zero thereafter. Let us assume a birth-and-death process with zero as an absorbing state. The probability of ultimate absorbtion into state 0, given that we start in state i, is denoted as u_i. We will perform a first-step analysis and construct a recursion formula for u_i: The first transition will entail the following movements

$$i \longrightarrow i+1 \qquad with\, probability\ \frac{\lambda_i}{\mu_i+\lambda_i}$$
$$i \longrightarrow i-1 \qquad with\, probability\ \frac{\mu_i}{\mu_i+\lambda_i}$$

Invoking the first step analysis, we obtain

$$u_i = \frac{\lambda_i}{\mu_i+\lambda_i}u_{i+1} + \frac{\mu_i}{\mu_i+\lambda_i}u_{i-1}, i \geq 1$$
$$u_i = \frac{1}{\lambda_i+\mu_i}(\lambda_i u_{i+1} + \mu_i u_{i-1})$$
$$\lambda_i u_i + \mu_i u_i = \lambda_i u_{i+1} + \mu_i u_{i-1}$$
$$\lambda_i u_{i+1} - \lambda_i u_i = \mu_i u_i - \mu_i u_{i-1}$$
$$u_{i+1} - u_i = \frac{\mu_i}{\lambda_i}(u_i - u_{i-1})$$

where $u_0 = 1$. If now we let $v_i = u_{i+1} - u_i$, then the above formula becomes

$$v_i = \frac{\mu_i}{\lambda_i}v_{i-1}, i \geq 1$$

Let us iterate on this formula

$$v_i = \frac{\mu_i}{\lambda_i}v_{i-1}$$
$$v_i = \frac{\mu_i}{\lambda_i}\frac{\mu_{i-1}}{\lambda_{i-1}}v_{i-2}$$
$$v_i = \frac{\mu_i}{\lambda_i}\frac{\mu_{i-1}}{\lambda_{i-1}}\frac{\mu_{i-2}}{\lambda_{i-2}}v_{i-3}$$
$$\dots$$
$$v_i = \frac{\mu_i}{\lambda_i}\frac{\mu_{i-1}}{\lambda_{i-1}}\frac{\mu_{i-2}}{\lambda_{i-2}}\frac{\dots}{\dots}\frac{\mu_1}{\lambda_1}v_0$$

If we let

$$\rho_i = \frac{\mu_i \mu_{i-1} \dots \mu_2 \mu_1}{\lambda_i \lambda_{i-1} \dots \lambda_2 \lambda_1}$$

and $\rho_0 = 1$, we can obtain

$$v_i = \rho_i v_0$$

If now we return v_i to $u_{i+1} - u_i$, then

$$u_{i+1} - u_i = \rho_i (u_1 - u_0)$$
$$u_{i+1} - u_i = \rho_i (u_1 - 1)$$

Let us sum both sides from $i = 1$ to $i = m - 1$,

$$\sum_{i=1}^{m-1} (u_{i+1} - u_i) = \sum_{i=1}^{m-1} \rho_i (u_1 - 1)$$

$$(u_2 - u_1) + (u_3 - u_2) + \dots + (u_{m-1} - u_{m-2}) + (u_m - u_{m-1}) = (u_1 - 1) \sum_{i=1}^{m-1} \rho_i$$

$$u_m - u_1 = (u_1 - 1) \sum_{i=1}^{m-1} \rho_i$$

where $u_0 = 1$.

Now, in order to solve for u_1, we let $m \longrightarrow \infty$. In such a case, $u_m \longrightarrow 0$. Thus

$$u_m - u_1 = (u_1 - 1) \sum_{i=1}^{m-1} \rho_i \tag{1}$$

$$0 - u_1 = (u_1 - 1) \sum_{i=1}^{\infty} \rho_i \tag{2}$$

$$0 = u_1 \sum_{i=1}^{\infty} \rho_i - \sum_{i=1}^{\infty} \rho_i + u_1 \tag{3}$$

$$\sum_{i=1}^{\infty} \rho_i = u_1 (\sum_{i=1}^{\infty} \rho_i + 1) \tag{4}$$

$$u_1 = \frac{\sum_{i=1}^{\infty} \rho_i}{1 + \sum_{i=1}^{\infty} \rho_i} \tag{5}$$

We can now plug in u_1 to solve for a general m:

$$u_m - u_1 = (u_1 - 1)\sum_{i=1}^{m-1}\rho_i \tag{6}$$

$$u_m = u_1\sum_{i=1}^{m-1}\rho_i - \sum_{i=1}^{m-1}\rho_i + u_1 \tag{7}$$

$$u_m = \left(\frac{\sum_{i=1}^{\infty}\rho_i}{1+\sum_{i=1}^{\infty}\rho_i}\right)\sum_{i=1}^{m-1}\rho_i - \sum_{i=1}^{m-1}\rho_i + \frac{\sum_{i=1}^{\infty}\rho_i}{1+\sum_{i=1}^{\infty}\rho_i} \tag{8}$$

$$u_m = \frac{\sum_{i=1}^{\infty}\rho_i \times \sum_{i=1}^{m-1}\rho_i - \sum_{i=1}^{m-1}\rho_i(1+\sum_{i=1}^{\infty}\rho_i) + \sum_{i=1}^{\infty}\rho_i}{1+\sum_{i=1}^{\infty}\rho_i} \tag{9}$$

$$u_m = \frac{\sum_{i=1}^{\infty}\rho_i - \sum_{i=1}^{m-1}\rho_i}{1+\sum_{i=1}^{\infty}\rho_i} \tag{10}$$

$$u_m = \frac{\sum_{i=m}^{\infty}\rho_i}{1+\sum_{i=1}^{\infty}\rho_i} \tag{11}$$

$$\tag{12}$$

We can obtain similar results by considering an "embedded random walk" associated with this process.

In Moran model, the absorption in one of the states (either 0 or 2N) is definite. It is of interest to compute a probability of absorbing at 0 and absorbing at 2N (starting at state i) separately. Let us apply a similar analysis to calculating Absorption Probabilities in Moran process (in which X_t is the number of A_1 alleles in a haploid population of 2N genes). In Moran population model, it is possible to make a transition from state i into states $i+1$, i, and $i-1$. Let us denote the probabilities of going to the corresponding states as $p_{i,i+1}$, $p_{i,i}$, and $p_{i,i-1}$. By applying the first step analysis, we are able to obtain the recursive equation for the probability of absorption in 0:

$$u_i = p_{i,i+1}u_{i+1} + p_{i,i}u_i + p_{i,i-1}u_{i-1} \tag{13}$$

$$u_i = p_{i,i+1}u_{i+1} + (1 - p_{i_i+1} - p_{i,i-1})u_i + p_{i,i-1}u_{i-1} \tag{14}$$

$$u_i = p_{i,i+1}u_{i+1} + u_i - p_{i_i+1}u_i - p_{i,i-1}u_i + p_{i,i-1}u_{i-1} \tag{15}$$

$$0 = p_{i,i+1}u_{i+1} - p_{i_i+1}u_i - p_{i,i-1}u_i + p_{i,i-1}u_{i-1} \tag{16}$$

$$p_{i,i+1}u_{i+1} - p_{i_i+1}u_i = p_{i,i-1}u_i - p_{i,i-1}u_{i-1} \tag{17}$$

$$p_{i,i+1}(u_{i+1} - u_i) = p_{i,i-1}(u_i - u_{i-1}) \tag{18}$$

$$u_{i+1} - u_i = \frac{p_{i,i-1}}{p_{i,i+1}}(u_i - u_{i-1}) \tag{19}$$

$$\tag{20}$$

Observe now that this formula corresponds to one derived in section 1:

$$u_{i+1} - u_i = \frac{\mu_i}{\lambda_i}(u_i - u_{i-1}),$$

in which case $p_{i,i-1}$ corresponds to μ_i and $p_{i,i+1}$ corresponds to λ_i.

If apply a similar analysis to a Moran model, then the probability of extinction (absorption at zero) becomes

$$u_m = \frac{2N - m}{2N}$$

Similarly, the probability of fixation (absorption at 2N) is

$$u_m = \frac{m}{2N}$$

since the probability to absorption at 0 and at 2N should sum up to 1.

1.2 Absorption probabilities by Matrix Manipulations (finite states)

Let us consider a finite state space $S = \{0, 1, 2 \dots, M\}$. We assume that $\lambda_0 = \mu_0 = \lambda_M = \mu_M = 0$, and thus 0 and M are absorbing states.

Further we define $\mathbf{W}_1^{'} = (\mu_1, 0, 0, \dots, 0)$, $\mathbf{W}_2^{'} = (0, 0, 0, \dots, \lambda_{M-1})$, and $\mathbf{1}_{M-1} = (1, 1, 1, \dots, 1)$ as vectors of size $(M-1) \times 1$.

Let us consider a matrix $\mathbf{Q}$ (which is an infinitesimal generator of the process) with two absorbing states 0 and M; then we can design a matrix $\hat{\mathbf{Q}}$ with rows and columns ,which correspond two absorbing states, eliminated. In particular, the $\hat{\mathbf{Q}}$ would look like matrix $\mathbf{Q}$ with deleted rows (0 and M) and columns (0 and M):

$$\hat{\mathbf{Q}} = \begin{Vmatrix} -(\lambda_1+\mu_1) & \lambda_1 & 0 & 0 & \dots & 0 \\ \mu_2 & -(\lambda_2+\mu_2) & \lambda_2 & 0 & \dots & 0 \\ 0 & \mu_3 & -(\lambda_3+\mu_3) & \lambda_3 & \dots & 0 \\ \vdots & & \ddots & \ddots & & \vdots \\ \vdots & & & & & \vdots \\ 0 & & & \mu_{M-2} & -(\lambda_{M-2}+\mu_{M-2}) & \lambda_{M-2} \\ 0 & \dots & \dots & 0 & \mu_{M-1} & -(\lambda_{M-1}+\mu_{M-1}) \end{Vmatrix}$$

Observe that a matrix $\mathbf{Q}$ can now be expresses in terms of $\hat{\mathbf{Q}}$ and $\mathbf{W}_1$ and $\mathbf{W}_2$ as

$$\mathbf{Q} = \begin{Vmatrix} 0 & \mathbf{0}' & 0 \\ \mathbf{W}_1 & \hat{\mathbf{Q}} & \mathbf{W}_2 \\ 0 & \mathbf{0}' & 0 \end{Vmatrix}$$

If now we want to calculate $\mathbf{Q}^m$, then

$$\mathbf{Q}^m = \begin{Vmatrix} 0 & \mathbf{0}' & 0 \\ \hat{\mathbf{Q}}^{m-1}\mathbf{W}_1 & \hat{\mathbf{Q}}^m & \hat{\mathbf{Q}}^{m-1}\mathbf{W}_2 \\ 0 & \mathbf{0}' & 0 \end{Vmatrix}$$

Let us now calculate $\mathbf{P}(t) = e^{\mathbf{Q}t}$: considering $\hat{\mathbf{Q}}$ in this formula

$$\sum_{m=0}^{\infty} \frac{t^m}{m!} \hat{\mathbf{Q}}^m = e^{\hat{\mathbf{Q}}t}$$

If we consider $\hat{\mathbf{Q}}^{m-1}\mathbf{W}_1$ in the above calculations:

$$\sum_{m=1}^{\infty} \frac{t^m}{m!} \hat{\mathbf{Q}}^{m-1} \mathbf{W}_1 = \left[\sum_{m=0}^{\infty} \frac{t^m}{m!} \hat{\mathbf{Q}}^{m-1} - \frac{t^0}{0!} \hat{\mathbf{Q}}^{0-1} \right] \mathbf{W}_1 \tag{21}$$

$$= \hat{\mathbf{Q}}^{-1} \left[\sum_{m=0}^{\infty} \frac{t^m}{m!} \hat{\mathbf{Q}}^m - \mathbf{I}_{M-1} \right] \mathbf{W}_1 \tag{22}$$

$$= \hat{\mathbf{Q}}^{-1} \left[\sum_{m=0}^{\infty} \frac{t^m}{m!} \hat{\mathbf{Q}}^m - \mathbf{I}_{M-1} \right] \mathbf{W}_1 = \mathbf{h}_0^{(t)} \tag{23}$$

Similarly, the $\mathbf{h}_M^{(t)}$ can be derived, with respect to $\mathbf{W}_2$. Observe that $\mathbf{h}_0^{(t)}$ is a vector of absorption probabilities of states $\{1, \dots, M-1\}$ into state 0 over time t and $\mathbf{h}_M^{(t)}$ is a vector of absorption probabilities of states $\{1, \dots, M-1\}$ into state M over time t. It follows that

$$\mathbf{P}(t) = e^{\mathbf{Q}t} = \sum_{j=0}^{\infty} \frac{t^j}{j!}\mathbf{Q}^j \tag{24}$$

$$= \left\| \begin{matrix} 1 & \mathbf{0}' & 0 \\ \mathbf{h}_0^{(t)} & e^{\hat{\mathbf{Q}}t} & \mathbf{h}_M^{(t)} \\ 0 & \mathbf{0}' & 1 \end{matrix} \right\| \tag{25}$$

Furthermore, it would follow that $\hat{\mathbf{P}}(t)$, which corresponds to $\hat{\mathbf{Q}}$, is

$$\hat{\mathbf{P}}(t) = e^{\hat{\mathbf{Q}}t}$$

Observe that $e^{\hat{\mathbf{Q}}t} \longrightarrow 0$ as $t \longrightarrow \infty$; therefore $\mathbf{h}_0$ – the vector of ultimate absorption probabilities of the states $\{1, \ldots, M-1\}$ into state 0 is

$$\mathbf{h}_0 = \lim_{t\longrightarrow\infty} \mathbf{h}_0^{(t)} = -\hat{\mathbf{Q}}^{-1}\mathbf{W}_1$$

and the vector of ultimate absorption probabilities of the states $\{1, \ldots, M-1\}$ into state M is

$$\mathbf{h}_M = \lim_{t\longrightarrow\infty} \mathbf{h}_M^{(t)} = -\hat{\mathbf{Q}}^{-1}\mathbf{W}_2$$

Observe that since $\mathbf{W}_1 + \mathbf{W}_2 + \hat{\mathbf{Q}}\mathbf{1}_{M-1} = 0$, then

$$\mathbf{W}_1 + \mathbf{W}_2 = -\hat{\mathbf{Q}}\mathbf{1}_{M-1}$$

If applied to $\mathbf{h}_0 + \mathbf{h}_M$, then

$$\mathbf{h}_0 + \mathbf{h}_M = -\hat{\mathbf{Q}}^{-1}\mathbf{W}_1 + (-\hat{\mathbf{Q}}^{-1}\mathbf{W}_2) \tag{26}$$

$$= -\hat{\mathbf{Q}}^{-1}(\mathbf{W}_1 + \mathbf{W}_2) \tag{27}$$

$$= (-\hat{\mathbf{Q}}^{-1})(-\hat{\mathbf{Q}})\mathbf{1}_{M-1} \tag{28}$$

$$= \mathbf{I}\mathbf{1}_{M-1} = \mathbf{1}_{M-1} \tag{29}$$

This is equivalently to saying that, with probability 1, the states $\{1, \ldots, M-1\}$ will eventually be absorbed into 0 or M.

Let us ease the computation of $-\hat{\mathbf{Q}}^{-1}$ and describe it in terms of birth and death rates λ_j and μ_j. Let us denote the inverse of $-\hat{\mathbf{Q}}$ as $\mathbf{C}$. It turns to be that the entry c_{ts} (where $t = 1, 2, \ldots, M-1$ is the row and $s = 1, 2, \ldots, M-1$ is the column) in the matrix-inverse $\mathbf{C}$ is

$$c_{ts} = \left(\sum_{l=1}^{min(t,s)} \prod_{i=1}^{l-1} \mu_i \prod_{j=l}^{s-1} \lambda_j \right) \left(\sum_{n=1}^{M-s-max(t-s,0)} \prod_{i=s+1}^{M-n} \mu_i \prod_{j=M-n+1}^{M-1} \lambda_j \right) / \left(\sum_{n=1}^{M} \prod_{i=1}^{M-n} \mu_i \prod_{j=M-n+1}^{M-1} \lambda_j \right)$$

Basically, the computation of the probability of absorption into 0 from a state k, h_{0k}, is calculated based on multiplication of $\mathbf{W}_1$ and $\mathbf{C}$. In particular, the element h_{0k} is the product of μ_1 and the element c_{k1}:

$$h_{0k} = \mu_1 c_{k,1} = \mu_1 \left(\sum_{l=1}^{1} 1 \times 1 \right) \left(\sum_{n=1}^{M-1-(k-1)} \prod_{i=s+1}^{M-n} \mu_i \prod_{j=M-n+1}^{M-1} \lambda_j \right) / \left(\sum_{n=1}^{M} \prod_{i=1}^{M-n} \mu_i \prod_{j=M-n+1}^{M-1} \lambda_j \right)$$

$$= \mu_1 \left(\sum_{n=1}^{M-k} \prod_{i=1+1}^{M-n} \mu_i \prod_{j=M-n+1}^{M-1} \lambda_j \right) / \left(\sum_{n=1}^{M} \prod_{i=1}^{M-n} \mu_i \prod_{j=M-n+1}^{M-1} \lambda_j \right)$$

$$= \mu_1 \left(\sum_{n=1}^{M-k} \prod_{i=2}^{M-n} \mu_i \prod_{j=M-n+1}^{M-1} \lambda_j \right) / \left(\sum_{n=1}^{M} \prod_{i=1}^{M-n} \mu_i \prod_{j=M-n+1}^{M-1} \lambda_j \right)$$

$$= \left(\sum_{n=1}^{M-k} \prod_{i=1}^{M-n} \mu_i \prod_{j=M-n+1}^{M-1} \lambda_j \right) / \left(\sum_{n=1}^{M} \prod_{i=1}^{M-n} \mu_i \prod_{j=M-n+1}^{M-1} \lambda_j \right)$$

Similarly, for the probability of absorption into M is

$$h_{Mk} = \lambda_{M-1} c_{k,M-1} = \lambda_{M-1} \left(\sum_{l=1}^{k} \prod_{i=1}^{l-1} \mu_i \prod_{j=l}^{s-1} \lambda_j \right) \left(\sum_{n=1}^{1} 1 \times 1 \right) / \left(\sum_{n=1}^{M} \prod_{i=1}^{M-n} \mu_i \prod_{j=M-n+1}^{M-1} \lambda_j \right)$$

$$= \lambda_{M-1} \left(\sum_{l=1}^{k} \prod_{i=1}^{l-1} \mu_i \prod_{j=l}^{(M-1)-1} \lambda_j \right) / \left(\sum_{n=1}^{M} \prod_{i=1}^{M-n} \mu_i \prod_{j=M-n+1}^{M-1} \lambda_j \right)$$

$$= \lambda_{M-1} \left(\sum_{l=1}^{k} \prod_{i=1}^{l-1} \mu_i \prod_{j=l}^{M-2} \lambda_j \right) / \left(\sum_{n=1}^{M} \prod_{i=1}^{M-n} \mu_i \prod_{j=M-n+1}^{M-1} \lambda_j \right)$$

$$= \left(\sum_{l=1}^{k} \prod_{i=1}^{l-1} \mu_i \prod_{j=l}^{M-1} \lambda_j \right) / \left(\sum_{n=1}^{M} \prod_{i=1}^{M-n} \mu_i \prod_{j=M-n+1}^{M-1} \lambda_j \right)$$

It is easy to check that $h_{0k} + h_{Mk} = 1$, once again satisfying the condition that the ultimate absorption at one of the absorbing states is unescapable.

If we apply the above calculations to the Moran model, in which

$$\mu_i = \lambda_i = \frac{i(M-i)}{M \times M},$$

then the above probabilities become

$$h_{0k} = \frac{M-k}{M}$$

and

$$h_{Mk} = \frac{k}{M}$$

as has been shown before with a probabilistic argument.

2 Mean time to absorption in Birth-and-Death Process

2.1 Probabilistic method

Now, consider a mean time until absorption into state 0 starting from state m (we assume that the absorption is certain) in a birth-and-death process. In this method we would like to consider time spent in each state for the calculation of the mean absorption time. We will use the fact that the mean sojourn time spent in state i is $\frac{1}{\mu_i+\lambda_i}$

Let w_1 be the mean absorption time from state i, then taking into account the waiting (sojourn) time in the state i,

$$w_i = \frac{1}{\mu_i + \lambda_i} + \frac{\lambda_i}{\mu_i + \lambda_i} w_{i+1} + \frac{\mu_i}{\mu_i + \lambda_i} w_{i-1}, i \geq 1$$

where $w_0 = 0$.

Rearranging the above gives

$$w_i = \frac{1}{\mu_i + \lambda_i} + \frac{\lambda_i}{\mu_i + \lambda_i} w_{i+1} + \frac{\mu_i}{\mu_i + \lambda_i} w_{i-1} \tag{30}$$

$$w_i = \frac{1 + \lambda_i w_{i+1} + \mu_i w_{i-1}}{\mu_i + \lambda_i} \tag{31}$$

$$w_i(\mu_i + \lambda_i) = 1 + \lambda_i w_{i+1} + \mu_i w_{i-1} \tag{32}$$

$$\mu_i w_i + \lambda_i w_i = 1 + \lambda_i w_{i+1} + \mu_i w_{i-1} \tag{33}$$

$$\lambda_i w_i - \lambda_i w_{i+1} = 1 + \mu_i w_{i-1} - \mu_i w_i \tag{34}$$

$$\lambda_i(w_i - w_{i+1}) = 1 + \mu_i(w_{i-1} - w_i) \tag{35}$$

$$w_i - w_{i+1} = \frac{1}{\lambda_i} + \frac{\mu_i}{\lambda_i}(w_{i-1} - w_i) \tag{36}$$

$$\tag{37}$$

If now we set $z_i = w_i - w_{i+1}$, then

$$z_i = \frac{1}{\lambda_i} + \frac{\mu_i}{\lambda_i} z_{i-1}$$

Iterating this relation gives

$$z_1 = \frac{1}{\lambda_1} + \frac{\mu_1}{\lambda_1} z_0 \tag{38}$$

$$z_2 = \frac{1}{\lambda_2} + \frac{\mu_2}{\lambda_2} z_1 \tag{39}$$

$$= \frac{1}{\lambda_2} + \frac{\mu_2}{\lambda_2}\left(\frac{1}{\lambda_1} + \frac{\mu_1}{\lambda_1} z_0\right) \tag{40}$$

$$= \frac{1}{\lambda_2} + \frac{\mu_2}{\lambda_2\lambda_1} + \frac{\mu_2\mu_1}{\lambda_2\lambda_1} z_0 \tag{41}$$

$$z_3 = \frac{1}{\lambda_3} + \frac{\mu_3}{\lambda_3\lambda_2} + \frac{\mu_3\mu_2}{\lambda_3\lambda_2\lambda_1} + \frac{\mu_3\mu_2\mu_1}{\lambda_3\lambda_2\lambda_1} z_0 \tag{42}$$

$$\tag{43}$$

It follows that

$$z_m = \left(\sum_{i=1}^{m} \frac{1}{\lambda_i} \prod_{j=i+1}^{m} \frac{\mu_j}{\lambda_j} \right) + z_0 \left(\prod_{j=1}^{m} \frac{\mu_j}{\lambda_j} \right)$$

Again, using the notation $\rho_0 = 1$ and

$$\rho_i = \frac{\mu_1\mu_2 \ldots \mu_i}{\lambda_1\lambda_2 \ldots \lambda_i}$$

we obtain

$$z_m = \sum_{i=1}^{m} \frac{1}{\lambda_i} \frac{\rho_m}{\rho_i} + \rho_m z_0$$

Substituting z_m for $w_m - w_{m+1}$ and noting that $z_0 = w_0 - w_1 = -w_1$ since $w_0 = 0$:

$$w_m - w_{m+1} = \sum_{i=1}^{m} \frac{1}{\lambda_i} \frac{\rho_m}{\rho_i} - w_1 \rho_m \tag{44}$$

$$\frac{1}{\rho_m}(w_m - w_{m+1}) = \frac{1}{\rho_m} \sum_{i=1}^{m} \frac{1}{\lambda_i} \frac{\rho_m}{\rho_i} - w_1 \tag{45}$$

$$\frac{1}{\rho_m}(w_m - w_{m+1}) = \sum_{i=1}^{m} \frac{1}{\lambda_i} \frac{\rho_m}{\rho_i \rho_m} - w_1 \tag{46}$$

$$\frac{1}{\rho_m}(w_m - w_{m+1}) = \sum_{i=1}^{m} \frac{1}{\lambda_i \rho_i} - w_1 \tag{47}$$

$$\tag{48}$$

In order to solve for w_1, we let $m \longrightarrow \infty$:

$$w_1 = \sum_{i=1}^{m} \frac{1}{\lambda_i \rho_i} - \frac{1}{\rho_m}(w_m - w_{m+1}) \tag{49}$$

$$w_1 = \sum_{i=1}^{\infty} \frac{1}{\lambda_i \rho_i} - \lim_{m \longrightarrow \infty} \frac{1}{\rho_m}(w_m - w_{m+1}) \tag{50}$$

$$w_1 = \sum_{i=1}^{\infty} \frac{1}{\lambda_i \rho_i} - 0 \tag{51}$$

$$w_1 = \sum_{i=1}^{\infty} \frac{1}{\lambda_i \rho_i} \tag{52}$$

$$\tag{53}$$

Plugging in the above into the formula for w_m gives

$$w_m - w_{m+1} = \sum_{i=1}^{m} \frac{1}{\lambda_i} \frac{\rho_m}{\rho_i} - \rho_m \sum_{i=1}^{\infty} \frac{1}{\lambda_i \rho_i} \tag{54}$$

$$w_m - w_{m+1} = \sum_{i=1}^{m} \frac{1}{\lambda_i} \frac{\rho_m}{\rho_i} - \sum_{i=1}^{\infty} \frac{1}{\lambda_i} \frac{\rho_m}{\rho_i} \tag{55}$$

$$w_m - w_{m+1} = - \sum_{i=m+1}^{\infty} \frac{1}{\lambda_i} \frac{\rho_m}{\rho_i} \tag{56}$$

$$\tag{57}$$

Summing both sides from $m = 1$ to $m = k - 1$, we obtain

$$\sum_{m=1}^{k-1} w_m - w_{m+1} = - \sum_{m=1}^{k-1} \sum_{i=m+1}^{\infty} \frac{1}{\lambda_i} \frac{\rho_m}{\rho_i} \tag{58}$$

$$w_1 - w_k = - \sum_{m=1}^{k-1} \sum_{i=m+1}^{\infty} \frac{1}{\lambda_i} \frac{\rho_m}{\rho_i} \tag{59}$$

$$w_k = w_1 + \sum_{m=1}^{k-1} \sum_{i=m+1}^{\infty} \frac{1}{\lambda_i} \frac{\rho_m}{\rho_i} \tag{60}$$

$$w_k = \sum_{i=1}^{\infty} \frac{1}{\lambda_i \rho_i} + \sum_{m=1}^{k-1} \rho_m \sum_{i=m+1}^{\infty} \frac{1}{\lambda_i} \frac{1}{\rho_i} \tag{61}$$

$$\tag{62}$$

However, for Moran process we would need to consider a finite state space and two absorption states in order to calculate a mean time to absorption.

2.2 Mean time to Absorption with Matrix method (finite state)

Let us define a vector of mean time to absorption from states $\{1, \ldots, M-1\}$ to either state (0 or M) as $\bar{\mathbf{t}}$. Then, following the calculations above

$$\bar{\mathbf{t}} = -\hat{\mathbf{Q}}^{-1}\mathbf{1}_{M-1}$$

From the previous section we know how to calculate matrix **C**, which is $-\hat{\mathbf{Q}}^{-1}$. Basically, the element $\bar{t}_k$ is equal to the sum of the elements of the k'th row of C :

$$\bar{t}_k = \left[\sum_{s=1}^{M-1} \left(\sum_{l=1}^{min(k,s)} \prod_{i=1}^{l-1} \mu_i \prod_{j=l}^{s-1} \lambda_j \right) \left(\sum_{n=1}^{M-s-max(k-s,0)} \prod_{i=s+1}^{M-n} \mu_i \prod_{j=M-n+1}^{M-1} \lambda_j \right) \right] / \left[\sum_{n=1}^{M} \prod_{i=1}^{M-n} \mu_i \prod_{j=M-n+1}^{M-1} \lambda_j \right]$$

When applied to Moran model (recall that $\lambda_i = \mu_i = \frac{i(M-i)}{M \times M}$), the mean time to absorption becomes

$$\bar{t}_k = (M-k)M \sum_{i=1}^{k} \frac{1}{M-i} + kM \sum_{i=k+1}^{M-1} \frac{1}{i}$$

3 Appendix

3.1 Calculating transition probabilities by Spectral method

Here we are interested in calculating these transition probability matrix by *Spectral Method*. Let **Q** be $(m+1)(m+1)$ matrix with eigenvalues $\alpha_0, \alpha_1, \ldots \alpha_m$ (possibly with repetition) and corresponding eigenvectors

$$\mathbf{x}_0 = \begin{pmatrix} x_{00} \\ \vdots \\ x_{m0} \end{pmatrix}, \ldots, \mathbf{x}_m = \begin{pmatrix} x_{0m} \\ \vdots \\ x_{mm} \end{pmatrix}$$

which are linearly independent.

In general the eigenvalues of the Matrix can be calculated as follows:

x is an eigenvector of **Q** iff there exists an α so that $\mathbf{Qx} = \alpha\mathbf{x}$; then

$$\mathbf{Qx} = \alpha\mathbf{x}$$

$$\mathbf{Qx} = (\alpha\mathbf{I})\mathbf{x}$$

$$(\mathbf{Q} - \alpha\mathbf{I})\mathbf{x} = 0$$

where **I** is the identity matrix (identity matrix has 1's on its main diagonal and 0's elsewhere).

In order for this equation to have non-trivial solution, it is required that the determinant $det(\mathbf{Q} - \alpha\mathbf{I})$ is zero. This determinant is also called the characteristic polynomial of the matrix. The distinct eigenvalues $\alpha_0, \alpha_1, \ldots, \alpha_m$ are given by the zeros of the characteristic polynomial

$$det(\mathbf{Q} - \alpha\mathbf{I})$$

After the eigenvalues $\alpha_0, \alpha_1, \ldots \alpha_m$ are calculated, we can determine eigenvectors (for each eigenvalue) as:

$$\left[\mathbf{Q} - \alpha_i\mathbf{I}\right] \begin{bmatrix} x_{0i} \\ x_{1i} \\ \vdots \\ x_{mi} \end{bmatrix} = 0$$

Let us now have a matrix **B** with columns consisting of eigenvectors of **Q**:

$$\mathbf{B} = (\mathbf{x}_0\mathbf{x}_1\dots\mathbf{x}_m) = \begin{pmatrix} x_{00} & x_{01} & \dots & x_{0m} \\ x_{10} & x_{11} & \dots & x_{1m} \\ \vdots & \vdots & \dots & \vdots \\ x_{m0} & x_{m1} & \dots & x_{mm} \end{pmatrix}$$

Since $\mathbf{Q}\mathbf{x}_i = \alpha_i\mathbf{x}_i$, it follows that

$$\mathbf{Q}\mathbf{B} = (\alpha_0\mathbf{x}_0\ \alpha_1\mathbf{x}_1\dots\alpha_m\mathbf{x}_m) \tag{63}$$

$$\mathbf{Q}^2\mathbf{B} = \mathbf{Q}(\alpha_0\mathbf{x}_0\ \alpha_1\mathbf{x}_1\dots\alpha_m\mathbf{x}_m) = (\alpha_0^2\mathbf{x}_0\ \alpha_1^2\mathbf{x}_1\dots\alpha_m^2\mathbf{x}_m) \tag{64}$$

$$\mathbf{Q}^n\mathbf{B} = (\alpha_0^n\mathbf{x}_0\ \alpha_1^n\mathbf{x}_1\dots\alpha_m^n\mathbf{x}_m) \tag{65}$$

Therefore

$$e^{t\mathbf{Q}}\mathbf{B} = \sum_{n=0}^{\infty}\frac{t^n}{n!}\mathbf{Q}^n\mathbf{B} \tag{66}$$

$$= \sum_{n=0}^{\infty}\frac{t^n}{n!}(\alpha_0^n\mathbf{x}_0\ \alpha_1^n\mathbf{x}_1\ \dots\ \alpha_m^n\mathbf{x}_m) \tag{67}$$

$$= (e^{t\alpha_0}\mathbf{x}_0\ e^{t\alpha_1}\mathbf{x}_1\ \dots\ e^{t\alpha_m}\mathbf{x}_m) \tag{68}$$

$$= \mathbf{B}\ \mathbf{diag}(e^{t\alpha_0},\dots e^{t\alpha_m}) \tag{69}$$

where $\mathbf{diag}(e^{t\alpha_0},\dots e^{t\alpha_m})$ is the $(m+1)(m+1)$ matrix with $e^{t\alpha_i}$s on the main diagonal and zeros elsewhere

$$\mathbf{diag}(e^{t\alpha_0},\dots e^{t\alpha_m}) = \begin{pmatrix} e^{t\alpha_0} & & & \\ & e^{t\alpha_1} & & 0 \\ 0 & & \ddots & \\ & & & e^{t\alpha_m} \end{pmatrix}$$

As a result

$$e^{t\mathbf{Q}} = \mathbf{B}\begin{pmatrix} e^{t\alpha_0} & & & \\ & e^{t\alpha_1} & & 0 \\ 0 & & \ddots & \\ & & & e^{t\alpha_m} \end{pmatrix}\mathbf{B}^{-1}$$

References

[1] W.Y.Tan, *On the Absorption Probabilitied and Absorption Times of Finite Homogeneous Birth-Death Processes*, Biometrics 32, 745-752, 1976.

[2] J.Glaz, *Probabilitied and Moments for Absorption in Finite Homogeneous Birth-Death Processes*, Biometrics 35, 813-816, 1979.

[3] Warren Ewens, ”mathematical Population Genetics”, Second edition, 2004, pp 90-91, 104-109.

[4] Howard Taylor and Samuel Karlin, ”An Introduction to Stochastic Modeling”, Third edition, 1998, pp 380-400.

[5] Sidney Resnick, ”Adventures in Stochastic Processes”, 1992, pp 367-375.

[6] Rabi Bhattacharya, Edward Waymire, ”Stochastic Processes with Applications”, 1990, pp 261-275 ,314-324.

[7] Samuel Karlin, Howard Taylor, ”A second course in Stochastic Processes”, 1981, pp. 138-156.