# QSS/Mathematics 30.04 - Evolutionary Game Theory

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## Homework 4

### Prompt/Instructions

Recall that in a well-mixed population of finite size $N+1$, the fixation dynamics with death-birth update mechanism can be viewed as a random walk in the state space with integer numbers $i \in [0, N+1]$. Define by $\gamma_i$ the ratio of backward to forward transition probabilities $\gamma_i = \frac{p_{i,i-1}}{p_{i,i+1}}$. Then the fixation probability $\rho_A$ of a single mutant $A$ with relative fitness $r$ to resident population $B$ is given by

$$\rho_A = \frac{1}{1 + \sum_{j=1}^{N} \prod_{i=1}^{j}} \gamma_i = \frac{1 - \frac{1}{r}}{1 - \left(\frac{1}{r}\right)^{N+1}}$$

Let us consider the simplest possible scenario, namely, the neutral drift case with $r = 1$. Then $\rho_A = \frac{1}{N+1}$.

We are now interested in how the heterogeneity of population structure - individuals can have different connectivities (or number of neighbors) – can fundamentally change this conclusion. For this purpose, let us consider neutral evolution on a star graph of $N+1$ nodes with a center node and $N$ periphery nodes. Clearly, the fixation probability of a mutant $A$ will depend on its position in the star graph where it first arises. Intuitively, if the mutant arises in the center node, it will have the most favorable chance to reach fixation, as compared to arise in the periphery nodes (also called as leaves).

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### Question 1

Let $P_i^1$ be the probability of fixation of $A$ given there are $i$ $A$'s in the leaves and an $A$ in the center. Let $P_i^0$ be the probability of fixation of $A$ given there are $i$ $A$'s in the leaves and a $B$ in the center. Show that $P_i^1$ and $P_i^0$ satisfy the following recurrence equations with boundary conditions $P_0^0 = 0$ and $P_N^1 = 1$.

$$\begin{pmatrix} P_{i+1}^1 \\ P_{i+1}^0 \end{pmatrix} = \begin{pmatrix} 1 + 1/N & -1/N \\ 1/N & 1 - 1/N \end{pmatrix} \begin{pmatrix} P_i^1 \\ P_i^0 \end{pmatrix}$$

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Consider first that there are $i$ $A$'s in the leaves and an $A$ in the center. After an update, we may arrive at three states:

- $i$ $A$'s in the leaves and a $B$ in the center.
- $i$ $A$'s in the leaves and an $A$ in the center (stay the same).
- $i+1$ $A$'s in the leaves and an $A$ in the center.

Thus, we get the recurrence relation that

$$P_i^1 = \left(\frac{1}{N+1}\frac{N-i}{N}\right) P_i^0 + \left(\frac{1}{N+1}\frac{i}{N} + \frac{i}{N+1}\right) P_i^1 + \left(\frac{N-i}{N+1}\right) P_{i+1}^1,$$

which simplifies to

$$P_i^1 = \left(\frac{N-i}{N(N+1)}\right) P_i^0 + \left(\frac{i}{N}\right) P_i^1 + \left(\frac{N-i}{N+1}\right) P_{i+1}^1.$$

Solving for $P_{i+1}^1$, we find that

$$\left(\frac{N-i}{N+1}\right) P_{i+1}^1 = \left(1-\frac{i}{N}\right) P_i^1 - \left(\frac{N-i}{N(N+1)}\right) P_i^0,$$

which simplifies to

$$P_{i+1}^1 = \left(1+\frac{1}{N}\right) P_i^1 - \left(\frac{1}{N}\right) P_i^0.$$

Similarly, we consider that there are $i+1$ $A$'s in the leaves and a $B$ in the center. After an update, we may arrive at three states:

- $i$ $A$'s in the leaves and a $B$ in the center.
- $i+1$ $A$'s in the leaves and a $B$ in the center (stay the same).
- $i+1$ $A$'s in the leaves and an $A$ in the center.

Thus, we get the recurrence relation that

$$P_{i+1}^0 = \left(\frac{i+1}{N+1}\right) P_i^0 + \left(\frac{N-(i+1)}{N+1} + \frac{1}{N+1}\frac{N-(i+1)}{N}\right) P_{i+1}^0 + \left(\frac{1}{N+1}\frac{i+1}{N}\right) P_{i+1}^1,$$

which simplifies to

$$P_{i+1}^0 = \left(\frac{i+1}{N+1}\right) P_i^0 + \left(\frac{N-(i+1)}{N}\right) P_{i+1}^0 + \left(\frac{i+1}{N(N+1)}\right) P_{i+1}^1.$$

Solving for $P_{i+1}^0$, we find that

$$\left(\frac{i+1}{N}\right) P_{i+1}^0 = \left(\frac{i+1}{N+1}\right) P_i^0 + \left(\frac{i+1}{N(N+1)}\right) P_{i+1}^1,$$

which simplifies to

$$P_{i+1}^0 = \left(\frac{N}{N+1}\right) P_i^0 + \left(\frac{1}{N+1}\right) P_{i+1}^1.$$

When inputting the expression of $P_{i+1}^1$ into the above equation, we have

$$P_{i+1}^0 = \left(\frac{N}{N+1}\right) P_i^0 + \left(\frac{1}{N+1}\right) \left(\left(1+\frac{1}{N}\right) P_i^1 - \left(\frac{1}{N}\right) P_i^0\right),$$

which simplifies to

$$P_{i+1}^0 = \left(\frac{1}{N}\right) P_i^1 + \left(1-\frac{1}{N}\right) P_i^0.$$

As there is no mutation in the population, the boundary conditions $P_0^0 = 0$ and $P_N^1 = 1$ hold naturally. Thus, we have shown that $P_i^1$ and $P_i^0$ satisfy the recurrence equations as given.

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## Question 2

Using the method of induction, prove that for any integer $n \geq 1$,

$$\begin{pmatrix} 1+\alpha & -\alpha \\ \alpha & 1-\alpha \end{pmatrix}^n = \begin{pmatrix} 1+n\alpha & -n\alpha \\ n\alpha & 1-n\alpha \end{pmatrix}$$

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We define the statement $P(n)$ to be the claim of the equivalence relation above.
Let us start with the base case, in which we prove the statement $P(1)$. This is trivial, as we have

$$\begin{pmatrix} 1+\alpha & -\alpha \\ \alpha & 1-\alpha \end{pmatrix}^1 = \begin{pmatrix} 1+n\alpha & -n\alpha \\ n\alpha & 1-n\alpha \end{pmatrix}$$

For the induction, let $k \in \mathbb{N}$ with $k \geq 1$. We assume $P\left(k\right)$ in an attempt to assert $P\left(k+1\right)$. Under this assumption, we have the following:

$$\begin{pmatrix} 1+\alpha & -\alpha \\ \alpha & 1-\alpha \end{pmatrix}^{k+1} = \begin{pmatrix} 1+\alpha & -\alpha \\ \alpha & 1-\alpha \end{pmatrix}^k \begin{pmatrix} 1+\alpha & -\alpha \\ \alpha & 1-\alpha \end{pmatrix}$$

$$\begin{pmatrix} 1+\alpha & -\alpha \\ \alpha & 1-\alpha \end{pmatrix}^{k+1} = \begin{pmatrix} 1+k\alpha & -k\alpha \\ k\alpha & 1-k\alpha \end{pmatrix} \begin{pmatrix} 1+\alpha & -\alpha \\ \alpha & 1-\alpha \end{pmatrix}$$

When performing the matrix multiplication on the right-hand side of the above expression, we have

$$\begin{pmatrix} \left(1+k\alpha\right)\left(1+\alpha\right)+\left(-k\alpha\right)\left(\alpha\right) & \left(1+k\alpha\right)\left(-\alpha\right)+\left(-k\alpha\right)\left(1-\alpha\right) \\ \left(k\alpha\right)\left(1+\alpha\right)+\left(1-k\alpha\right)\left(\alpha\right) & \left(k\alpha\right)\left(-\alpha\right)+\left(1-k\alpha\right)\left(1-\alpha\right) \end{pmatrix},$$

which simplifies to

$$\begin{pmatrix} 1+\left(k+1\right)\alpha & -\left(k+1\right)\alpha \\ \left(k+1\right)\alpha & 1-\left(k+1\right)\alpha \end{pmatrix},$$

Thus, we verified that $P\left(k+1\right)$ follows. By induction, the statement $P(n)$ is true for all $n \geq 1$.

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## Question 3

Applying Equation (2) to Equation (1), what is the fixation probability given the mutant arises in the center, $P_0^1$? And what is $P_1^0$ (if the mutant arises in the periphery nodes)?

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When applying Equation (2) to Equation (1), we find

$$\begin{pmatrix} P_N^1 \\ P_N^0 \end{pmatrix} = \begin{pmatrix} 1 + N\left(\frac{1}{N}\right) & -N\left(\frac{1}{N}\right) \\ N\left(\frac{1}{N}\right) & 1 - N\left(\frac{1}{N}\right) \end{pmatrix} \begin{pmatrix} P_0^1 \\ P_0^0 \end{pmatrix},$$

which simplifies to

$$\begin{pmatrix} P_N^1 \\ P_N^0 \end{pmatrix} = \begin{pmatrix} 2 & -1 \\ 1 & 0 \end{pmatrix} \begin{pmatrix} P_0^1 \\ P_0^0 \end{pmatrix}.$$

Thus, we may determine $P_0^1$ and $P_0^0$ as follows:

$$P_N^1 = 2P_0^1 - P_0^0 \qquad P_N^0 = P_0^1$$

Given the boundary conditions $P_0^0 = 0$ and $P_N^1 = 1$, we have

$$P_0^1 = P_N^0 = \frac{1}{2}.$$

Thus, the fixation probability given the mutant arises in the center is given by $P_0^1 = \frac{1}{2}$.

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To determine $P_1^0$, we have

$$\begin{pmatrix} P_1^1 \\ P_1^0 \end{pmatrix} = \begin{pmatrix} 1 + \frac{1}{N} & -\frac{1}{N} \\ \frac{1}{N} & 1 - \frac{1}{N} \end{pmatrix} \begin{pmatrix} P_0^1 \\ P_0^0 \end{pmatrix}.$$

Thus, we may determine $P_1^1$ and $P_1^0$ as follows:

$$P_1^1 = \left(1 + \frac{1}{N}\right) P_0^1 - \left(\frac{1}{N}\right) P_0^0 \qquad P_1^0 = \left(\frac{1}{N}\right) P_0^1 + \left(1 - \frac{1}{N}\right) P_0^0.$$

Given the boundary condition $P_0^0 = 0$ and having just found that $P_0^1 = \frac{1}{2}$, we have

$$P_1^1 = \left(1 + \frac{1}{N}\right)\left(\frac{1}{2}\right)$$

$$P_1^0 = \left(\frac{1}{N}\right)\left(\frac{1}{2}\right)$$

Thus, the fixation probability given the mutant arises in the periphery nodes is given by $P_1^0 = \frac{1}{2N}$.