EGT Qual Paper Reading **Winter 2018**

Note 1: Mutation-selection equilibrium in games with multiple strategies

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1.1 Introduction

1.1.1 Basic settings

Let us consider a population of N individuals where game with n strategies is played.

- The payoff values are given by the $n \times n$ payoff matrix $A = [a_{ij}]_{n\times n}$.
- The state of the system is described the the n-dimensional column vector X, where X_i is the number of players using strategy i. The frequencies of strategies are $x = X/N$.
- Approaches
  - traditional (well-mixed populations of infinite size): the deterministic selection dynamics can be described by the replicator equation.
  - recent (populations of finite size): a stochastic description is necessary.

1.1.2 More detailed settings

For simplicity, we focus on stochastic evolutionary dynamics in the population of a large (but still finite) size.

- Evolutionary updating occurs according to the frequency dependent **birth-death** Moran process, where an individual is chosen to reproduce and its offspring will replace an individual (W-F process and P-C process are also discussed). It is worth pointing out that these two individuals can be identical.
- Individuals reproduce proportional to their payoffs but subject to mutation with probability $u > 0$: with probability $1-u$, the child adopts the strategy of the parent; with probability u one of the n strategies is chosen at random.
- In the case of weak selection where $\delta \ll 1/N$, the payoff of strategy i is given by $f_i = 1 + \delta\pi_i$ and the column vector f is given by $f = 1 + \delta Ax$. Further, the total payoff the whole population is $F = X^T f = N(1 + \delta x^T Ax)$.

In the stationary state of the Moran process, we find the system in state X with probability $P_\delta(X)$, the distribution of which is the eigenvector with the largest eigenvalue of the stochastic transition matrix of the system. The stationary probabilities are continuous at $\delta = 0$ and for any state X we can write them as

$$P_\delta(X) = P_{\delta=0}(X)[1 + O(\delta)]. \tag{1.1}$$

1.1.3 Kernel assumptions

We now propose a more general way of identifying the strategy most favored by selection: **the strategy with the highest average frequency (i.e. abundance) in the long time average**. Moreover, we consider that selection favors a strategy if its abundance exceeds $1/n$ and vise versa.

- Although the frequencies of the strategies can widely fluctuate in time, all strategies have approximately the same abundance $1/n$ in the stationary distribution of the mutation-selection process.
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  - For low mutation rates, all players use the same strategy until another strategy takes over most of the time. There are only two strategies involved in a take over.
  - For high mutation rates, the frequencies of all strategies are close to $1/n$ all the time.
- In the stationary state, the average total change of the frequency of any strategy is zero (selection and mutation are in balance).
- Since in the **neutral** stationary state all players are equivalent, exchanging indices does not affect the averages $\langle x_i \rangle$, $\langle x_i x_j \rangle$ and $\langle x_i x_j x_k \rangle$. In particular, we have

$$\langle x_1 x_2 \rangle = \langle (1 - \sum_{2 \le i \le n} x_i) x_2 \rangle = \langle x_1 \rangle - \langle x_1 x_1 \rangle - (n-2)\langle x_1 x_2 \rangle. \tag{1.2}$$

$$\langle x_1 x_2 x_2 \rangle = \langle (1 - \sum_{2 \le i \le n} x_i) x_2 x_2 \rangle = \langle x_1 x_1 \rangle - \langle x_1 x_1 x_1 \rangle - (n-2)\langle x_1 x_2 x_2 \rangle. \tag{1.3}$$

$$\langle x_1 x_2 x_3 \rangle = \langle (1 - \sum_{2 \le i \le n} x_i) x_2 x_3 \rangle = \langle x_1 x_2 \rangle - 2\langle x_1 x_2 x_2 \rangle - (n-3)\langle x_1 x_2 x_3 \rangle. \tag{1.4}$$

1.1.4 Methods

To calculate the deviation from the uniform distribution of the mutation-selection process, we use the perturbation theory given the selection strength δ.

1.1.5 Major results

- For low mutation probability $u \ll 1/N$, selection favors strategy k if

$$L_k = \frac{1}{n} \sum_{i=1}^{n} (a_{kk} + a_{ki} - a_{ik} - a_{ii}) > 0. \tag{1.5}$$

- For high mutation probability $u \gg 1/N$, selection favors strategy k if

$$H_k = \frac{1}{n^2} \sum_{i=1}^{n} \sum_{j=1}^{n} (a_{kj} - a_{ij}) > 0. \tag{1.6}$$

- For arbitrary mutation probability the general expression for selection to favor strategy k is

$$L_k + NuH_k > 0. \tag{1.7}$$

  And Strategy k is more abundant than strategy j if

$$L_k + NuH_k > L_j + NuH_j. \tag{1.8}$$

1.2 Perturbation method

We look into the dynamics of the system in the stationary state.

1.2.1 Abundance of type k

During a single update step, the average number of offspring (fitness) of a k-player due to selection is

$$\omega_k = \underbrace{\boxed{1}}_{\text{the parent itself}} + \underbrace{\boxed{(-1/N)}}_{\text{its random death}} + \underbrace{\boxed{f_k/F}}_{\text{the proliferation proportional to its payoff}} . \tag{1.9}$$

For $\delta \to 0$, we have

$$\frac{f_k}{F} = \frac{1+\delta(Ax)_k}{N(1+\delta x^T Ax)} = \frac{1}{N}[1+\delta(Ax)_k][1-\delta x^T Ax + O(\delta^2)] = \frac{1}{N}[1+\delta((Ax)_k - x^T Ax) + O(\delta^2)].$$

Hence,

$$\omega_k = 1 + \frac{\delta}{N}[(Ax)_k - x^T Ax] + O(\frac{\delta^2}{N}). \tag{1.10}$$

The frequency of k-players changes on average due to selection by

$$\Delta x_k^{\text{sel}} = x_k\omega_k - x_k = \frac{\delta}{N}x_k[(Ax)_k - x^T Ax] + O(\frac{\delta^2}{N}). \tag{1.11}$$

The average change due to selection in the leading order can be written as

$$\begin{aligned} \langle \Delta x_k^{\text{sel}} \rangle_\delta &= \sum_X \Delta x_k^{\text{sel}} P_\delta(X) \\ &\approx \frac{\delta}{N}\sum_X x_k[(Ax)_k - x^T Ax]P_{\delta=0}(X) \times [1+O(\delta)] \\ &\approx \frac{\delta}{N}(\sum_j a_{kj}\langle x_k x_j\rangle - \sum_{i,j} a_{ij}\langle x_k x_i x_j\rangle). \end{aligned} \tag{1.12}$$

Therefore, the expect total change of frequency in state X is

$$\begin{aligned} \Delta x_k^{\text{tot}} = & \underbrace{\boxed{\Delta x_k^{\text{sel}}(1-u)}}_{\text{change in the absence of mutation}} \\ & + \underbrace{\boxed{u \times 1/N \times 1/n}}_{\text{introduction of a random type under mutation}} + \underbrace{\boxed{(-u \times x_k/N)}}_{\text{random death under mutation}} . \end{aligned} \tag{1.13}$$

Given that $\langle \Delta x_k^{\text{tot}} \rangle = 0$, after averaging (1.13) we obtain the abundance in the stationary state expressed by the average change due to selection as

$$\langle x_k \rangle_\delta = \frac{1}{n} + \frac{N(1-u)}{u}\langle \Delta x_k^{\text{sel}} \rangle_\delta. \tag{1.14}$$

1.2.2 Average change of type k

During a single update step, it is obvious that

$$\overset{\text{strategy } k \text{ is more abundant than the average}}{\boxed{\langle x_k\rangle_\delta > 1/n}} \iff \overset{\text{change due to selection is positive}}{\boxed{\langle \Delta x_k^{\text{sel}}\rangle_\delta > 0}} \quad . \tag{1.15}$$

By taking into account the symmetries, we get the following expression for $\langle \Delta x_k^{\text{sel}}\rangle_\delta$

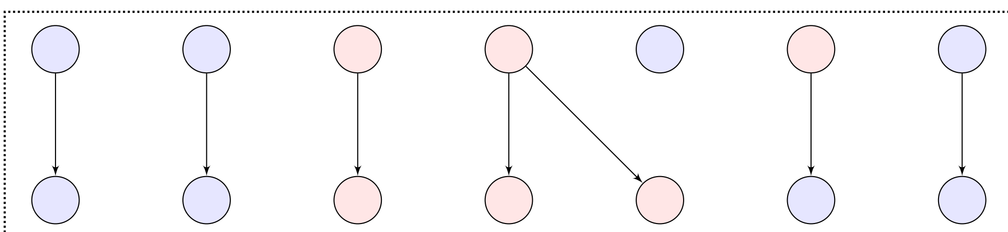
$$\frac{1}{N}\delta[\langle x_1x_1\rangle a_{kk} + \langle x_1x_2\rangle \sum_{i\neq k} a_{ki} - \langle x_1x_1x_1\rangle a_{kk} - \langle x_1x_2x_2\rangle \sum_{i\neq k}(a_{ki}+a_{ii}+a_{ik}) - \langle x_1x_2x_3\rangle \sum_{k\neq i\neq j\neq k} a_{ij}]. \tag{1.16}$$

At last, our main task is to figure out $\langle x_1x_1\rangle$, $\langle x_1x_2\rangle$, $\langle x_1x_1x_1\rangle$, $\langle x_1x_2x_2\rangle$, and $\langle x_1x_2x_3\rangle$, which boils down to the calculation of $\langle x_1x_1\rangle$ and $\langle x_1x_1x_1\rangle$.

1.3 Calculation of correlations

We draw m players at random from the population in the **neutral** stationary state, and define s_m as the probability that both or all of them share the same strategy. To calculate these probabilities, we shall use the birth-death Moran model and apply **coalescent** ideas.

- Two lineages coalesce in an elementary step of update (i.e. two players share the same parent, but not necessarily the same strategy) with probability $2/N^2$.



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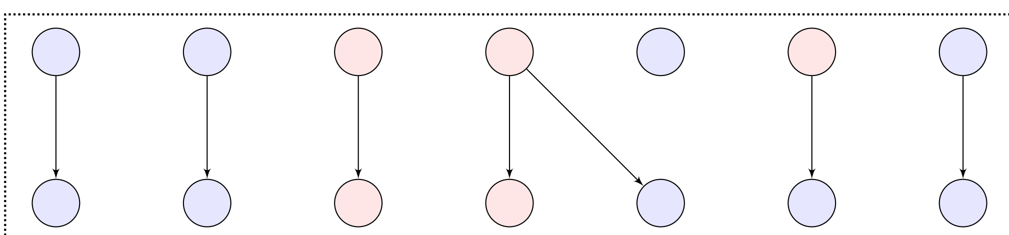


$$\overset{\text{two lineages coalesce}}{\boxed{2/N^2}} = \overset{\text{the parent is not chosen to die}}{\boxed{(1-1/N)}} \times \overset{\text{the parent and the child are selected}}{\boxed{1/\binom{N}{2}}} \quad . \tag{1.17}$$

Thus, the number of time steps for two lineages to coalesce follows a geometric distribution with expectation $N^2/2$. We assume that the population size is large, hence a continuous time description can be used, where the rescaled time is $\tau = t/(N^2/2)$. In the rescaled time, the trajectories of two players coalesce at rate 1.

$$\overbrace{\boxed{N^2/2}}^{\text{average time steps for two lineages to coalesce}} \Longleftrightarrow \overbrace{\boxed{1}}^{\text{average time units for two lineages to coalesce}} .$$
$$\overbrace{\boxed{t}}^{\text{discrete time steps}} \Longleftrightarrow \overbrace{\boxed{\tau}}^{\text{continuous time units}} . \tag{1.18}$$

- Tracking the historical footprint of an individual, we see that mutations happen at rate $\mu/2 = Nu/2$ to each trajectory, where $\mu = Nu$ is the rescaled mutation rate.

$$\overbrace{\boxed{\mu/2}}^{\text{mutation rate of a trajectory}} = \overbrace{\boxed{N^2/2}}^{\text{rescale of time}} \times \overbrace{\boxed{1/N}}^{\text{the individual is chosen to mutate}} \times \overbrace{\boxed{u}}^{\text{mutation probability}} . \tag{1.19}$$

1.3.1 Correlation s_2 of two individuals

The coalescence time τ_2 of two different individuals is described by the probability density function (PDF) $f_2(\tau_2) = e^{-\tau_2}$.

$$\overbrace{\boxed{P(T > t) = (1 - 2/N^2)^t}}^{\text{probability at discrete time}} \Rightarrow \overbrace{\boxed{P(T > t) = e^{-t/(N^2/2)} = e^{-\tau}}}^{N \text{ is large enough}} \Rightarrow \overbrace{\boxed{e^{-\tau_2} = d(1 - e^{-\tau_2})/d\tau_2}}^{\text{PDF at continuous time}} . \tag{1.20}$$

Once the two players coalesce, we immediately get two players of the same strategy. The probability $s_2(\tau)$ that after a fixed time τ they again have the same strategy is[1]

$$\underbrace{\overbrace{\boxed{e^{-\mu\tau}}}^{\text{neither of them mutates}}}_{P(T_2 > \tau) = 1 - \int_0^\tau \mu e^{-\mu s}\, ds} + \underbrace{\overbrace{\boxed{1/n}}^{\text{probability that they have the same strategy}}}_{1/n = n \times 1/n^2} \times \overbrace{\boxed{(1 - e^{-\mu\tau})}}^{\text{at least one mutates}} . \tag{1.22}$$

[1]light bulb problem: There are two light bulbs having independent and identical exponential life with parameter λ. Their lifespan is a random variable t with probability distribution function $f(t) = \lambda e^{-\lambda t}$. The time until the first failure of these two light bulbs will also follow an exponential distribution with parameter 2λ. The proof is straightforward as

$$P(T > t) = e^{-\lambda t} \times e^{-\lambda t} = e^{-2\lambda t}. \tag{1.21}$$

We then obtain the stationary probability s_2 by integrating this expression with the coalescent time density as

$$s_2 = \int_0^{+\infty} s_2(\tau) f_2(\tau)\, d\tau = \int_0^{+\infty} (e^{-\mu\tau} + \frac{1-e^{-\mu\tau}}{n}) e^{-\tau}\, d\tau = \frac{n+\mu}{n(1+\mu)}. \tag{1.23}$$

1.3.2 Correlation s_3 of three individuals

Any two trajectories of three players coalesce at rate 1, hence there is a coalescence at rate 3. The coalescence of two out of the three trajectories then happens at time τ_3, described by the density function $f_3(\tau_3) = 3e^{-3\tau_3}$.

Before the first coalescence at time τ_3 backward, it is possible that

$$\overset{\text{the two players have the same strategy}}{\underset{\text{three identical players}}{\boxed{s_2}}} \tag{1.24}$$

or

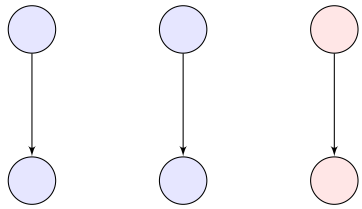
$$\overset{\text{the two players have different strategies}}{\underset{\text{two identical players and one different player}}{\boxed{1-s_2}}} \qquad . \tag{1.25}$$

If we have three identical players, then they are again identical after time τ with probability

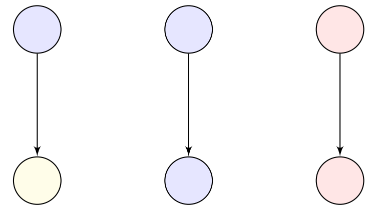
$$\begin{aligned} s_3^*(\tau) = {} & \overset{\text{none of the players have mutated thus they are still the same}}{\underset{P(T_3>\tau) = 1 - \int_0^\tau 3\mu/2 e^{-3\mu s/2}\, ds}{\boxed{e^{-3\mu\tau/2}}}} \\ & + \overset{\text{one of them has mutated but they are the same after mutation}}{\underset{\binom{3}{1}=3,\, P(T_1\le\tau) = \int_0^\tau \mu/2 e^{-\mu s/2}\, ds,\, P(T_2>\tau) = 1-\int_0^\tau \mu e^{-\mu s}\, ds}{\boxed{1/n \times [3(1-e^{-\mu\tau/2})e^{-\mu\tau}]}}} \\ & + \overset{\text{at least two of them have mutated but they are the same after mutation}}{\boxed{1/n^2 \times [1 - e^{-3\mu\tau/2} - 3(1-e^{-\mu\tau/2})e^{-\mu\tau}]}} \\ = {} & \frac{1}{n^2}[1 + 3(n-1)e^{-\mu\tau} + (n-1)(n-2)e^{-3/2\mu\tau}]. \end{aligned} \tag{1.26}$$

If we have two identical players and one different player, then

- the probability that they have the same strategy is 0 under the circumstances below:

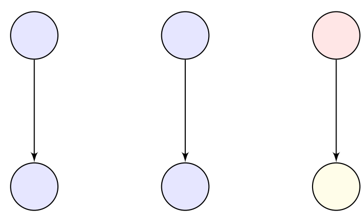


none of the players have mutated with probability $e^{-3\mu\tau/2}$



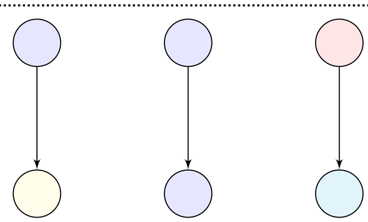
the first or the second one have mutated with probability $2(1 - e^{-\mu\tau/2})e^{-\mu\tau}$

- the probability that they have the same strategy is $1/n$ under the circumstance below:

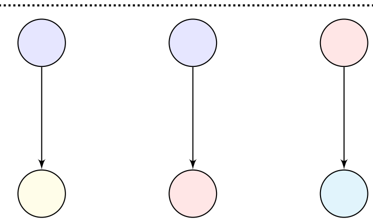


the third one of the players have mutated with probability $(1 - e^{-\mu\tau/2})e^{-\mu\tau}$

- the probability that they have the same strategy is $1/n^2$ under the circumstances below:



two of the players have mutated



all three of the players have mutated

Hence, the probability of all three players having the same strategy after time τ is

$$\begin{aligned} s_3^{**}(\tau) &= \frac{1}{n} \times (1 - e^{-\mu\tau/2})e^{-\mu\tau} + \frac{1}{n^2} \times [1 - e^{-3\mu\tau/2} - 3(1 - e^{-\mu\tau/2})e^{-\mu\tau}] \\ &= \frac{1}{n^2}[1 + (n-3)e^{-\mu\tau} - (n-2)e^{-3/2\mu\tau}]. \end{aligned} \tag{1.27}$$

Moreover, we can simply obtain s_3 as

$$s_3 = \overset{\text{three identical players}}{\boxed{s_2 \times \int_0^{+\infty} s_3^*(\tau) f_3(\tau)\, d\tau}} + \overset{\text{two identical players and one different player}}{\boxed{(1-s_2) \times \int_0^{+\infty} s_3^{**}(\tau) f_3(\tau)\, d\tau}} = \frac{(n+\mu)(2n+\mu)}{n^2(1+\mu)(2+\mu)}. \quad (1.28)$$

1.4 Back to major results :)

Under neutrality, we have

- $$\overset{\text{chance of having strategy one out of } n \text{ possibilities}}{\boxed{\langle x_1 \rangle = 1/n}} \quad (1.29)$$

- $$\underset{\text{the second player uses the same strategy with probability } s_2}{\overset{\text{the first player has strategy one with probability } 1/n}{\boxed{\langle x_1 x_1 \rangle = 1/n \times s_2}}} \quad (1.30)$$

- $$\underset{\text{the second and third players uses the same strategy with probability } s_3}{\overset{\text{the first player has strategy one with probability } 1/n}{\boxed{\langle x_1 x_1 x_1 \rangle = 1/n \times s_3}}} \quad . \quad (1.31)$$

Combined with previous assumptions, we further get

$$\langle x_1 x_2 \rangle = \frac{1-s_2}{n(n-1)}, \qquad \langle x_1 x_2 x_2 \rangle = \frac{s_2 - s_3}{n(n-1)}, \qquad \langle x_1 x_2 x_3 \rangle = \frac{1 - 3s_2 + 2s_3}{n(n-1)(n-2)}. \quad (1.32)$$

By defining

$$L_k = \frac{1}{n} \sum_{i=1}^{n} (a_{kk} + a_{ki} - a_{ik} - a_{ii}), \qquad H_k = \frac{1}{n^2} \sum_{i=1}^{n} \sum_{j=1}^{n} (a_{kj} - a_{ij}), \quad (1.33)$$

we finally arrive at the major results

$$\langle \Delta x_k^{\text{sel}} \rangle_\delta = \frac{\delta \mu (L_k + \mu H_k)}{nN(1+\mu)(2+\mu)}, \qquad \langle x_k \rangle_\delta = \frac{1}{n} \left[1 + \delta N(1-u) \frac{L_k + NuH_k}{(1+Nu)(2+Nu)} \right]. \quad (1.34)$$

- The expression becomes exact in the $N \to \infty$, $N\delta \to 0$ limit, if $Nu = \mu$ is kept constant.