

The Moran Process and the Isothermal Theorem

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Abstract

We formalize the Birth–death Moran process on a finite graph and the “if” direction of the isothermal theorem of Lieberman, Hauert and Nowak (2005): on a connected regular graph, a mutant population of size k with fitness $r \neq 1$ takes over the whole population with probability $(1 - r^{-k})/(1 - r^{-n})$, and with probability k/n when $r = 1$. The complete graph gives Moran’s formula (1958). As in the voter project, eventual probabilities are suprema of increasing finite-time probabilities; no path-space measure is used.

1 The model

Definition 1 (Birth–death Moran kernel). Mutants have fitness $r > 0$ and residents fitness 1. A step chooses a parent u with probability proportional to its fitness and an offspring position w uniformly among the neighbours of u (or $w = u$ if u is isolated); the individual at w is replaced by a copy of the parent.

Lemma 2 (The kernel is well defined). *The weights of (parent, offspring position) pairs are nonnegative and sum to one.*

Proof. Sum over the offspring position first: each parent’s placement weights sum to one. The remaining sum of fitnesses over the total fitness is one. $\square$

2 Invariance on regular graphs

Lemma 3 (Birth mass is r times death mass). *On a d -regular graph, the probability that a step adds a mutant equals r times the probability that it removes one: both are proportional to the number of edges between the two types, counted from either side.*

Proof. For $d > 0$ both masses are the oriented cut divided by Fd , weighted by the parent’s fitness; the cut is symmetric under swapping endpoints. For $d = 0$ both masses vanish. $\square$

Theorem 4 (Invariant potentials). *On a regular graph, $(1/r)^{\#mutants}$ is preserved in expectation by one step; when $r = 1$, so is the number of mutants.*

Proof. A step changes the number of mutants by ± 1 or not at all, so its expectation is affine in the birth and death masses, and these cancel by the previous lemma. $\square$

3 Absorption on connected graphs

Theorem 5 (Fixation or extinction). *On a connected graph, the probability that neither type has taken over tends to zero.*

Proof. Constant configurations are absorbing. From a mixed configuration, a mutant adjacent to a resident (which exists by connectivity) reproduces onto it with positive probability; by induction on the number of residents, fixation is reachable. Apply the shared finite-chain absorption theorem. $\square$

4 Fixation probabilities

Lemma 6 (Fixation from an invariant). *Let an observable be invariant in expectation, equal to 1 on the all-mutant and to 0 on the all-resident configuration. If the all-mutant configuration is absorbing and the probability that neither type has taken over tends to zero, the observable is the fixation probability.*

Proof. This is the finite-horizon optional stopping theorem of the shared `dynamics` package (`Dynamics.Kernel.iSup_event_of_invariant`, roadmap FND-4) with the two constant configurations as targets: the fixation and unfixed indicators are the corresponding events. $\square$

Theorem 7 (Isothermal theorem). *On a connected regular graph with $r \neq 1$, the fixation probability from k mutants is $(1 - r^{-k})/(1 - r^{-n})$.*

Proof. Apply the previous lemma to $\psi = (1 - (1/r)^{\#mutants})/(1 - (1/r)^n)$, invariant by the invariance theorem and equal to 1 and 0 on the two constant configurations; the absorption theorem gives the vanishing survival probability. $\square$

Theorem 8 (Neutral case). *On a connected regular graph with $r = 1$, the fixation probability is k/n .*

Proof. The same argument with $\psi = \#mutants/n$. $\square$

Theorem 9 (Moran's formula). *On the complete graph, the fixation probability from k mutants is $(1 - r^{-k})/(1 - r^{-n})$.*

Proof. The complete graph is connected and $(n - 1)$ -regular. $\square$

The converse of the isothermal theorem is false (Galanis, Göbel, Goldberg, Lapinskas and Richerby, Proposition 12), so only this direction is formalized.

5 Push versus pull on arbitrary graphs

On the complete graph the neutral push and pull voter processes coincide; on an irregular graph they fix a mutant set with different probabilities, weighted by $1/\deg$ and by $\deg$ respectively. In population genetics this is the difference between Birth–death and death–Birth updating.

Definition 10 (Death–Birth kernel). In one pull (death–Birth) step, a uniformly random vertex u adopts the type of a uniformly random neighbour w (an isolated vertex keeps its type), so the pair (u, w) has weight $\frac{1}{n} \cdot \frac{1}{\deg u}$ for $w \sim u$. The neutral push (Birth–death) process is the Moran kernel with $r = 1$.

Definition 11 (Reproductive values). For a configuration with mutant set S , $\Phi_{\text{push}}(S) = \sum_{v \in S} 1/\deg v$ and $\Phi_{\text{pull}}(S) = \sum_{v \in S} \deg v$.

Theorem 12 (Reproductive values are invariant). *On every finite graph, Φ_{push} is invariant in expectation under neutral push and Φ_{pull} is invariant in expectation under pull.*

Proof. Write $x_v \in \{0, 1\}$ for the type of v . Under push, the pair (parent u , target $w \sim u$) has weight $\frac{1}{n} \frac{1}{\deg u}$ and changes Φ_{push} by $(x_u - x_w)/\deg w$, so the expected change is $\frac{1}{n} \sum_{u \sim w} (x_u - x_w)/(\deg u \deg w)$. Under pull, u copies $w \sim u$ with weight $\frac{1}{n} \frac{1}{\deg u}$ and changes Φ_{pull} by $(x_w - x_u) \deg u$, so the expected change is $\frac{1}{n} \sum_{u \sim w} (x_w - x_u)$. Both sums are over ordered adjacent pairs of an antisymmetric function, hence vanish. $\square$

Theorem 13 (Fixation or extinction under pull). *On a connected graph, the probability that the pull process has not reached a constant configuration after t steps tends to 0.*

Proof. As for push: constant configurations are absorbing, and from any other configuration a resident adjacent to a mutant copies it with positive probability, so the number of mutants reaches n with positive probability; the shared absorption theorem concludes. $\square$

Theorem 14 (Push and pull fixation). *On a connected graph with at least two vertices, the fixation probability of a mutant set S is $\sum_{v \in S} \frac{1}{\deg v} / \sum_{v \in V} \frac{1}{\deg v}$ under neutral push and $\sum_{v \in S} \deg v / (2|E|)$ under pull.*

Proof. Apply the fixation-limit lemma to the normalized reproductive values, which are invariant and equal to 1 and 0 on the two constant configurations; the denominators are positive because every degree is at least 1. $\square$

6 Exact fixation on the star

The star with n leaves is Mathlib's `starGraph` c on $n + 1$ vertices: the centre c is adjacent to every leaf and leaves only to c . It is not regular, and it amplifies selection (Lieberman, Hauert and Nowak 2005); its exact fixation probability is due to Broom and Rychtář (2008, §5). Write

$$q = \frac{n + r}{r(nr + 1)}, \quad \kappa = \frac{nr + 1}{r(n + r)} = \frac{1}{r^2 q}.$$

Definition 15 (Star potential). For a configuration with i mutant leaves, $\Phi = q^i$ if the centre is a resident and $\Phi = \kappa q^i$ if it is a mutant.

Theorem 16 (The star potential is invariant). *For every $r > 0$, Φ is invariant in expectation under one Birth-death step on the star.*

Proof. Only the ordered pairs (c, ℓ) and (ℓ, c) for a leaf ℓ carry weight, namely $\text{fit}(c)/(nF)$ and $\text{fit}(\ell)/F$. Along each edge the two contributions cancel: if ℓ is a mutant and c a resident they give $\frac{q^{i-1}}{F} (\frac{1-q}{n} + rq(\kappa - 1)) = 0$, and if c is a mutant and ℓ a resident they give $\frac{q^i}{F} (1 - \kappa + \frac{r\kappa(q-1)}{n}) = 0$; equal types change nothing. $\square$

Theorem 17 (Fixation on the star). *For $r \neq 1$, the fixation probability from s is $(1 - \Phi(s))/(1 - \kappa q^n)$. A single mutant fixes with probability $(1 - q)/(1 - \kappa q^n)$ from a leaf, $(1 - \kappa)/(1 - \kappa q^n)$ from the centre, and $(n(1 - q) + (1 - \kappa))/((n + 1)(1 - \kappa q^n))$ from a uniformly random vertex.*

Proof. For $r > 1$ we have $q \leq 1$ and $\kappa < 1$, so $\kappa q^n \leq \Phi \leq 1$; for $r < 1$ all inequalities reverse. Hence the normalized potential is 1 at fixation, 0 at extinction and in $[0, 1]$ otherwise, and the fixation-limit lemma applies. $\square$

Theorem 18 (The formula of Broom and Rychtář). *For every $r > 0$, a single mutant at a uniformly random vertex fixes with probability*

$$\frac{n \cdot \frac{nr}{nr+1} + \frac{r}{r+n}}{(n+1)(1 + \frac{n}{n+r} \sum_{j=1}^{n-1} q^j)}.$$

Proof. For $r \neq 1$ and $n \geq 1$, sum the geometric series: $1 + \frac{n}{n+r} \sum_{j=1}^{n-1} q^j = r^2(1 - \kappa q^n)/(r^2 - 1)$. For $r = 1$ both sides are $1/(n+1)$, by push-pull fixation; for $n = 0$ both are 1. $\square$

Theorem 19 (The star is an amplifier). *For every $n \geq 2$, the fixation probability from a uniformly random vertex is larger than Moran's $(1 - 1/r)/(1 - r^{-(n+1)})$ for $r > 1$ and smaller for $0 < r < 1$.*

Proof. Put $s = 1/r$ and $t = (1 + ns)/(n + s)$, so that $q = st$ and $\kappa = s/t$. The difference has the sign of $(1 - s)(E(1 - s^{n+1}) - s^{n+1}(1 - t^{n-1}))$ with $E = s^2(n - 1)^2/((n + s)(1 + ns))$. By Bernoulli, $1 - t^{n-1} \leq (n - 1)(1 - t) = (n - 1)^2(1 - s)/(n + s)$, which reduces the claim to $s^{n-1}(1 - s)(1 + ns) < 1 - s^{n+1}$. Its slack is $\sum_{k=0}^{n-2} (1 - s)(s^k - s^n)$, a nonempty sum of positive terms on both sides of $s = 1$. $\square$

Theorem 20 (Large stars amplify r to r^2). *For $r > 1$, the fixation probability from a uniformly random vertex of the star with n leaves tends to $1 - 1/r^2$ as $n \rightarrow \infty$.*

Proof. $n(1 - q)/(n + 1) = \frac{n}{n+1} \cdot \frac{n}{n+1/r} \cdot (1 - r^{-2}) \rightarrow 1 - r^{-2}$, $(1 - \kappa)/(n + 1) \rightarrow 0$, and $0 \leq \kappa q^n \leq r^{-n} \rightarrow 0$ because $q \leq 1/r$ for $n \geq 1$. $\square$