

# Equilibrium Selection for Markov Processes via Random Trajectory Entropy with Applications to Finite Population Biology

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- ▶ Finite population dynamics are not usually deterministic and require different tools (Markov processes, fixation probabilities, etc.)
- ▶ Rather than rest or accumulation points, quantities like stationary distributions and entropy rate are used to characterize long run behavior of a Markov Process
- ▶ Entropy rate also incorporates short run behavior from the entropy of the distribution of transition probabilities

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- ▶ Entropy Rate is an invariant (actually the Kolmogorov-Sinai invariant of a dynamical system)
- ▶ Can be used for equilibrium selection for a process in conjunction with random walk entropy



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Since the process is irreducible, we have that the sum over all possible such trajectories from  $v_0$  to  $v_k$  is one, forming a probability distribution. Let  $\mathcal{T}(v_0, v_k)$  be the set of all such paths and define the *random trajectory entropy* (RTE) from  $v_0$  to  $v_k$  to be the entropy of the probability distribution on  $\mathcal{T}(v_0, v_k)$ , i.e.

$$H_{v_0 v_k} = - \sum_{v \in \mathcal{T}(v_0, v_k)} Pr(v) \log Pr(v).$$

## Random Trajectory Entropy

Let the stationary distribution of the Markov process  $X$  be given by  $s$  and the entropy rate by  $H(X)$ . It was shown Ekroot and Cover (Theorem 1, p.1419, 1993) that when the starting and ending states  $v$  are the same, the entropy of the random trajectory is determined by the entropy rate and the stationary probability at the state:

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# Random Trajectory Entropy

For two states of the same process, we can compare the relative stability by comparing the stationary distribution values:

$$\frac{H_v}{H_w} = \frac{H(X) s(w)}{s(v) H(X)} = \frac{s(w)}{s(v)}$$

## Example: Moran Process

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- ▶  $N = a + b$  is the total population size
- ▶ The entropy rate vanishes  $\lim_{\mu \rightarrow 0} H(X) = 0$
- ▶ The limiting stationary distribution becomes a delta distribution on the two states where one of the population types dominates the population,  $(0, N)$  or  $(N, 0)$

## Example: Moran Process

We can express the limiting stationary distribution in terms of the fixation probabilities of the two types  $\rho_A$  and  $\rho_B$ :

$$\lim_{\mu \rightarrow 0} s(0, N) = \frac{\rho_B}{\rho_A + \rho_B} \quad \text{and} \quad \lim_{\mu \rightarrow 0} s(N, 0) = \frac{\rho_A}{\rho_A + \rho_B}$$

Hence we have that

$$\lim_{\mu \rightarrow 0} \frac{H_{(0, N)}}{H_{(N, 0)}} = \lim_{\mu \rightarrow 0} \frac{s(N, 0)}{s(0, N)} = \frac{\rho_B}{\rho_A}$$

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For the classical Moran process with game matrix  $G = \begin{pmatrix} r & r \\ 1 & 1 \end{pmatrix}$

$$\lim_{\mu \rightarrow 0} \frac{H_{(0, N)}}{H_{(N, 0)}} = \frac{\rho_B}{\rho_A} = \frac{1 - r^{1-N}}{1 - r^{-1}}$$

As expected, whether  $r > 1$  determines which equilibrium is favored. If  $r = 1$ ,  $\rho_A = 1/N = \rho_B$  and the RTEs are equal.

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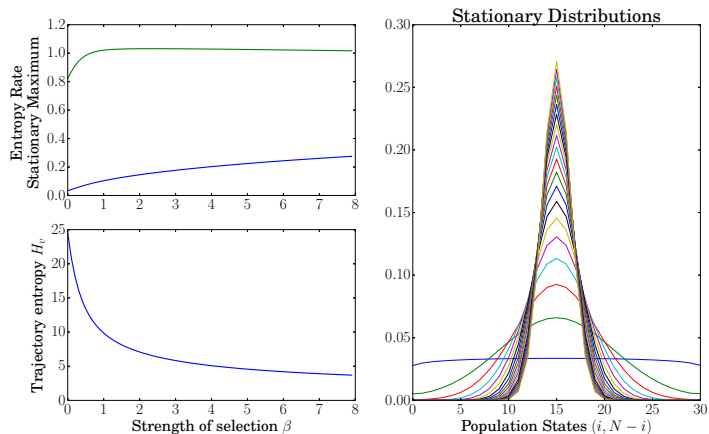
- ▶ (Harper, Fryer, 2013) The stationary local maxima of the Moran process with mutation capture the evolutionarily stable states (e.g. for the replicator equation)
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- ▶ (Harper, Fryer, 2013) The stationary local maxima of the Moran process with mutation capture the evolutionarily stable states (e.g. for the replicator equation)
- ▶ As various parameters (mutation rate  $\mu$ , strength of selection  $\beta$ , and population size  $N$ ) change so does the entropy rate and the stationary distribution
- ▶ The random trajectory entropy allows us to compare stability of equilibria as the parameters vary



## Example: Hawk-Dove Game



**Figure :** Right: Stationary distributions for Hawk-Dove landscapes for varying strength of selection  $\beta \in [0, 10]$ ,  $N = 30$ ,  $\mu = 1/N$ . Upper Left: As  $\beta$  increases, so does the stationary probability (blue, lower curve) of the maxima at (15, 15). The entropy rate (green, upper) is not monotonically increasing in  $\beta$ .

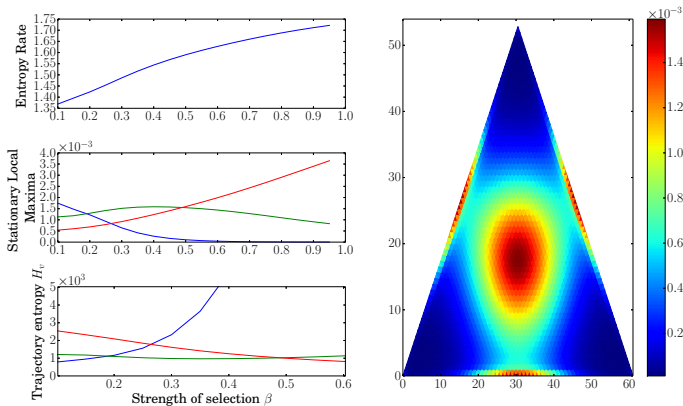
## Varying Parameters

We now consider examples for the landscape derived from the three-type game matrix:

$$G = \begin{pmatrix} 0 & 1 & 1 \\ 1 & 0 & 1 \\ 1 & 1 & 0 \end{pmatrix} \quad (1)$$

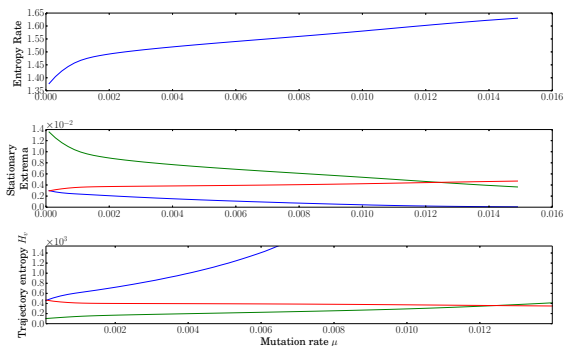
This landscape typically has several local extrema. Let the population size  $N' = 6N$ . Then we have extrema at the simplex corners  $(6N, 0, 0)$ ,  $(0, 6N, 0)$ ,  $(0, 0, 6N)$ , center of the boundary simplices  $(3N, 3N, 0)$ ,  $(3N, 0, 3N)$ ,  $(0, 3N, 3N)$ , and the center  $(2N, 2N, 2N)$ .

# Varying Parameters



**Figure :** This  $n = 3$  player example with  $N = 60$ ,  $\mu = 1/N$  has multiple local stationary extrema, at the center of the simplex, on the centers of the boundary simplices, and on the corners of the simplex. Right: Stationary distribution for  $\beta = 0.5$ . Left: The relative stability of equilibria changes with  $\beta$ .

# Varying Parameters



**Figure :** Same process as before with  $\beta = 1$  and varying rate of mutation  $\mu$ . The value of  $\mu$  can determine which of the equilibria is most stable. As  $\mu \rightarrow 0$  the corner states are favored. As  $\mu$  increases, the interior equilibrium becomes more stable.

Thanks!

*Stationary Stability for Evolutionary Dynamics in Finite Populations*, Marc Harper, Dashiell Fryer, ArXiv:1311.0941

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