

Characterizations of Stationary Extrema with Applications to Finite Population Models

Marc Harper, Dashiell Fryer

Jan. 13th, 2015

Motivation: Stationary Stability Theorem

Theorem (Harper and Fryer 2013)

For the Moran process with mutation and sufficiently large population size N , the local maxima and minima of the stationary distribution satisfy an evolutionary stability criterion (ESS Candidate).

Two questions:

- ▶ Can we actually find the stationary extrema?

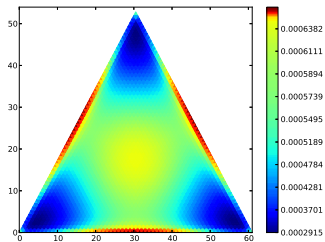
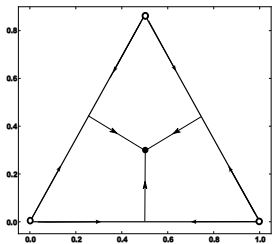
Motivation: Stationary Stability Theorem

Theorem (Harper and Fryer 2013)

For the Moran process with mutation and sufficiently large population size N , the local maxima and minima of the stationary distribution satisfy an evolutionary stability criterion (ESS Candidate).

Two questions:

- ▶ Can we actually find the stationary extrema?
- ▶ Is the converse true?



Motivation

- ▶ In Dashiell Fryer's talk we saw that stationary extrema can be characterized by an entropic measure of paths that start and end in the same state
- ▶ Using recent work from statistical mechanics, we can give a useful characterization by a different measure on more arbitrary paths

Markov Processes

- ▶ Let a finite reversible Markov process X have states $v_0, v_1, \dots \in V$

Markov Processes

- ▶ Let a finite reversible Markov process X have states $v_0, v_1, \dots \in V$
- ▶ Let the transition probabilities be given by a function $T : V \times V \rightarrow [0, 1]$

Markov Processes

- ▶ Let a finite reversible Markov process X have states $v_0, v_1, \dots \in V$
- ▶ Let the transition probabilities be given by a function $T : V \times V \rightarrow [0, 1]$
- ▶ and the stationary distribution by a function $s : V \rightarrow [0, 1]$

Markov Processes

- ▶ Let a finite reversible Markov process X have states $v_0, v_1, \dots \in V$
- ▶ Let the transition probabilities be given by a function $T : V \times V \rightarrow [0, 1]$
- ▶ and the stationary distribution by a function $s : V \rightarrow [0, 1]$
- ▶ Choose a base state v_0 . Then for any trajectory (or path) $v_0 \rightarrow v_1 \rightarrow \dots \rightarrow v_k$

$$s(v_k) = s(v_0) \prod_{j=1}^{k-1} \frac{T(v_j, v_{j+1})}{T(v_{j+1}, v_j)}. \quad (1)$$

Cumulative Skewness

- ▶ There is a close relationship between the extrema of the stationary distribution and the *cumulative skewness* of trajectories of the process.

Cumulative Skewness

- ▶ There is a close relationship between the extrema of the stationary distribution and the *cumulative skewness* of trajectories of the process.
- ▶ For a transition $a \rightarrow b$ the skewness measures the irreversibility of the transition and is defined as

$$\sigma = \log \frac{T(b, a)}{T(a, b)}$$

Cumulative Skewness

- ▶ There is a close relationship between the extrema of the stationary distribution and the *cumulative skewness* of trajectories of the process.
- ▶ For a transition $a \rightarrow b$ the skewness measures the irreversibility of the transition and is defined as

$$\sigma = \log \frac{T(b, a)}{T(a, b)}$$

- ▶ For a trajectory $p : v_0 \rightarrow v_1 \rightarrow \dots \rightarrow v_k$ the cumulative skewness is given by the summation of the skewness along the trajectory

$$\Sigma(p) = \sum_{j=0}^{k-1} \log \frac{T(v_{j+1}, v_j)}{T(v_j, v_{j+1})}.$$

Cumulative Skewness

Proposition

For a reversible Markov process the cumulative skewness Σ of trajectory $p : v_0 \rightarrow \dots \rightarrow v_k$ is given in terms of the stationary distribution by

$$\Sigma = -\log \frac{s(v_k)}{s(v_0)}.$$

Cumulative Skewness

Proposition

For a reversible Markov process the cumulative skewness Σ of trajectory $p : v_0 \rightarrow \cdots \rightarrow v_k$ is given in terms of the stationary distribution by

$$\Sigma = -\log \frac{s(v_k)}{s(v_0)}.$$

This proposition allows us to characterize the local and global extrema of the stationary distribution. Let $V' \subset V$ and define a stationary maximum of V' to be a state $v \in V'$ such that $s(v') < s(v)$ for all $v' \in V' \setminus v$. Then we have a local maximum v if the set V' is the set of neighboring states of v and a global maximum if $V' = V$; similarly for minima. We characterize these states in the following theorem, which follows immediately from Proposition 1 and the relation $\Sigma(p) = -\Sigma(p^{-1})$.

Cumulative Skewness

Theorem

For a reversible Markov process on states V and a subset of states set $V' \subset V$, we have the following for a state $v \in V'$:

- 1. v is a stationary maximum of V' iff $\Sigma(p) < 0$ for every path starting at $v' \in V$ and ending at v , for all $v' \in V'$*
- 2. v is a stationary minimum of V' iff $\Sigma(p) > 0$ for every path starting at v and ending at $v' \in V$, for all $v' \in V'$*

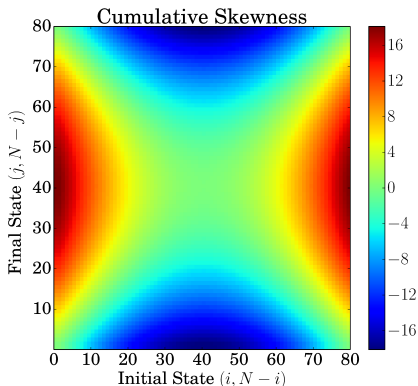
(and similarly for minima).

Cumulative Skewness

The theorem has a number of immediate and obvious consequences for local and global extrema, such as the following.

Corollary

For a reversible Markov process, a state v is a unique global stationary maximum if and only if $\Sigma(p) < 0$ for all paths ending at v and starting at $v' \neq v$.



Irreversible Processes

For more than two types, the Moran process is not reversible and the proposition is no longer valid. We can however extend the theorem to irreversible processes with the following result.

Theorem (Hordijk and Ridder, 1998)

Suppose every path of the Markov process has the property that $p \in P(v_1, v_n)$ implies that $p^{-1} \in P(v_n, v_1)$. Then we have that

$$\frac{s(v_n)}{s(v_1)} \leq \max\{h(v_1, v_n, p) : p \in P(v_1, v_n)\},$$

where

$$\prod_{j=1}^{k-1} \frac{T(v_j, v_{j+1})}{T(v_{j+1}, v_j)}.$$

Establishing Stationary Extrema

Consider the Moran process with mutation for landscapes formed by the following matrices:

$$G = \begin{pmatrix} 1 & 1+c \\ 1+c & 1 \end{pmatrix}$$

For $c > 1$, the landscape is of Hawk-Dove class, for $c = 0$ neutral, and for $c < 0$ the landscape is of Coordination class. Though we know that as $\mu \rightarrow 0$ that the stationary distribution tends to zero except on the two boundary states, for a critical value of μ the central state may flip from local min to local max.

$$\mu = \frac{1}{N+2} - \frac{N-2}{4N}c \quad (2)$$

Converse of Stationary Stability

Theorem (Sandholm)

Let s_N be the stationary distribution of an $n = 2$ Moran process and $x = a/N$. Define $T^+(x) = T((a, N - a), (a + 1, N - a - 1))$ and similarly for T^- . Then we have that

$$\lim_{N \rightarrow \infty} \frac{1}{N} \log \frac{s_N(x)}{s_N(0)} = m(x) := \int_0^x \log \frac{T^+(y)}{T^-(y)} dy$$

Converse of Stationary Stability

Theorem (Sandholm)

Let s_N be the stationary distribution of an $n = 2$ Moran process and $x = a/N$. Define $T^+(x) = T((a, N - a), (a + 1, N - a - 1))$ and similarly for T^- . Then we have that

$$\lim_{N \rightarrow \infty} \frac{1}{N} \log \frac{s_N(x)}{s_N(0)} = m(x) := \int_0^x \log \frac{T^+(y)}{T^-(y)} dy$$

Note that m can also be written as

$$m(x) = \int_0^x -\sigma(y) dy,$$

i.e. as the continuous cumulative skewness.

Converse of Stationary Stability

As a consequence, we have that if m has a critical point at x^* then so does s_N for sufficiently large N . Critical points of m occur when $T^+(x^*) = T^-(x^*)$, which is equivalent to our criterion for ESS candidates.

Corollary

For the $n = 2$ Moran process and sufficiently large N , an ESS candidate is a critical point of the stationary distribution. If the ESS candidate x^ is a maximum or minimum of m , so too is x^* a local maximum or minimum (respectively) of the stationary distribution.*

Converse of Stationary Stability

The general case for $n > 2$ population types is more difficult, but the result of Hordijk and Ridder is again helpful. Choose a base state a of the process. Combining with Sandholm's approach, we have that

$$\lim_{N \rightarrow \infty} \frac{1}{N} \log \frac{s^N(b)}{s^N(a)} \leq m(b) := \max_{p:a \rightarrow b} m_p,$$

with

$$m_p := \oint_p \log \frac{T^{\rightarrow}(y)}{T^{\leftarrow}(y)} dp = \oint_p -\sigma(y) dp,$$

where the functions T^{\rightarrow} and T^{\leftarrow} indicate the transitions along the piecewise path p and along the path p^{-1} respectively, and the maximum is taken over all such paths (again without cycles).

Converse of Stationary Stability

Now if we assume that we have a local maximum of m and that Σ is continuous, then we must have that $\Sigma(p) < 0$ for all “nearby incoming paths”, i.e. a local maximum of the stationary distribution. So we have an analog of Sandholm's theorem for $n > 2$ that yields information about the local maxima of the stationary distribution.

Theorem

Let m and m_p be defined as above. For sufficiently large N , if m has a local maximum or minimum at x^ then so does the stationary distribution.*

Corollary

For the Moran process with mutation and sufficiently large N , ESS candidates are local extrema of the stationary distribution.

Thanks!

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

Marc Harper: marc.harper@gmail.com

Dashiell Fryer: dash.fryer@gmail.com