Stochastic Stability and Disagreements Between Dynamics

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Replicator dynamics

Standard deterministic model. System of differential equations. Captures the short-to-medium run behavior of evolution and isolates the effects of selection.

Frequency-dependent Moran process

Standard stochastic model. Markov process. Can capture long run behavior of evolution and integrate the effects of mutation and drift in finite populations.

Both dynamics capture the idea that types more fit than the population average tend to grow in proportion, while types less fit than average tend to shrink in proportion.

Much work has been done to understand the relationship between the two dynamics.

Replicator dynamics

$$\dot{x} = x[f_i - \bar{f}]$$

Moran process

$$\{X_t^{N,\eta}\}$$

2x2 Game

$$egin{array}{cccc} A & B \ A & \left[egin{array}{cccc} a & b \ c & d \end{array}
ight]$$

Replicator dynamics

$$\dot{x_i} = x_i [f_i - f]$$

Anti-coordination / Polymorphic

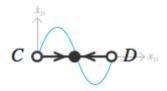
PRISONER'S DELIGHT

A-STABLE

INTERIOR EQUILIBRIUM

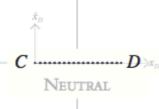
$$b-d$$

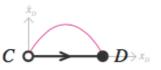
 $b+c-a-d$



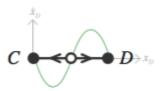


GRAPH OF POSSIBLE DYNAMICS





- > DIRECTION OF FLOW
- A-STABLE FIXED POINT
- O UNSTABLE FIXED POINT
- · · · SET OF FIXED POINTS

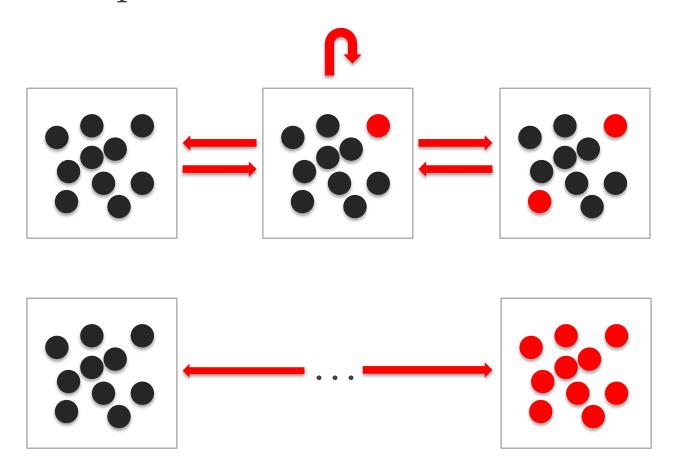


$$\frac{d-b}{d+a-b-c} \quad \begin{array}{c} \text{UNSTABLE} \\ \text{INTERIOR} \\ \text{EQUILIBRIUM} \end{array}$$

Prisoner's dilemma

COORDINATION / BI-STABLE

Moran process



Replacement Probabilities

$$\rho_{AB} > \frac{1}{N}$$

Nowak (2002)

 ESS^N

Traulsen & Hauert (2010)

 $wN \ll 1$

 $wN \gg 1$

 ESS^N

Replicator Dynamics

$$\rho_{AB} < \frac{1}{N} < \rho_{BA}$$

$$\text{Not}(\rho_{AB}, \rho_{BA} > \frac{1}{N})$$

$$\text{BI-STABLE}$$

$$\rho_{AB} < \frac{1}{N}$$

$$\rho_{AB} > \frac{1}{N} > \rho_{BA}$$

$$\rho_{AB} > \frac{1}{N} > \rho_{BA}$$

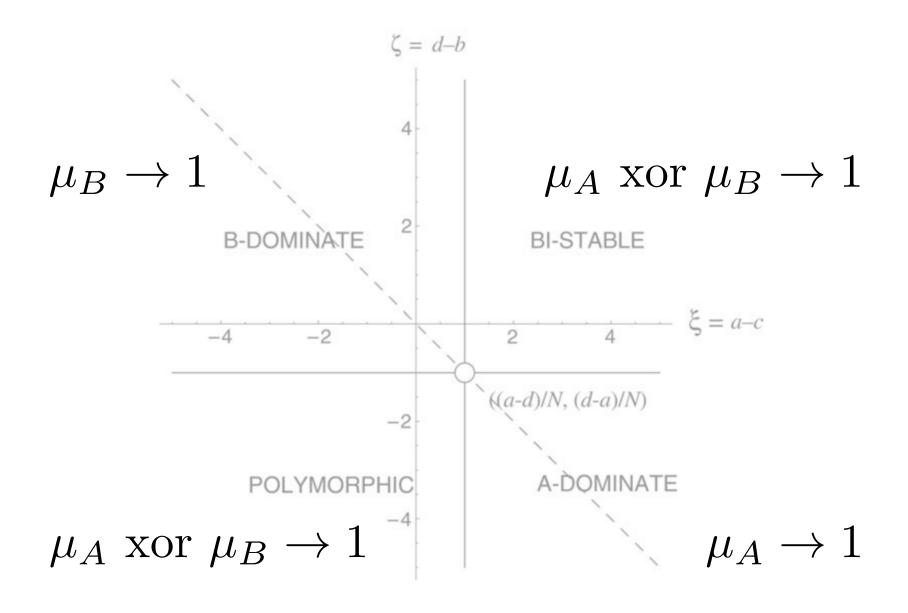
Mutation



$$\mu P = \mu$$

Stochastic Stability (Foster & Young, 1991)

$$\lim_{\eta \to 0} \mu_i^{N,\eta} > 0$$



"When the stochastic shocks are small, the mode of this frequency distribution [the stationary distribution] will tend to be close to the stochastically stable [states] predicted by the theory."

—Young (1998, 20)

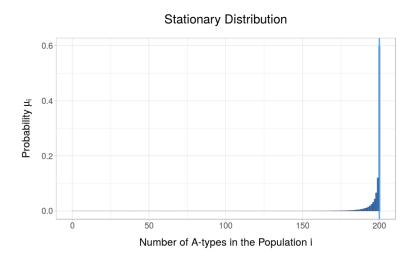
"While [the replicator dynamics] may be a reasonable approximation of the short run (or even medium run) behavior of the process, however, it may be a very poor indicator of the long run behavior of the process"

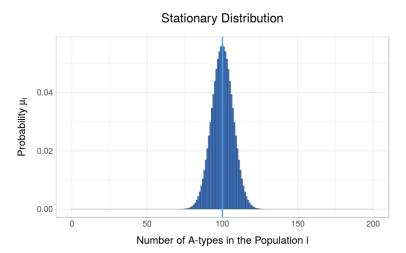
—Young (1998, 47)

Under what conditions is vanishing mutation assumption valid?

Sandholm (2010)

$$a < c \quad \& \quad b > d$$





$$\lim_{\eta \to 0}$$

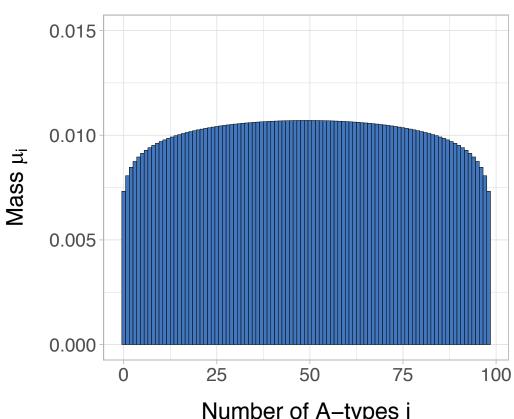
$$\lim_{N\to\infty}$$

Strong Mutation Condition

$$\eta(N+2) > 1$$

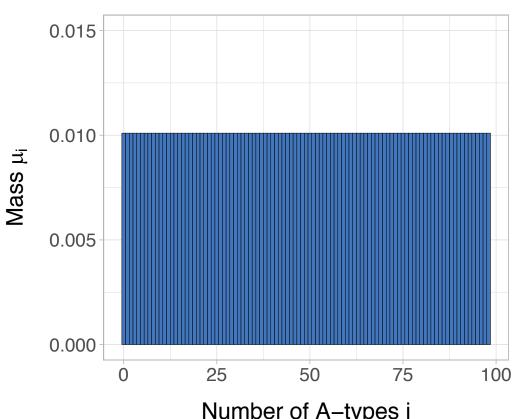
Lemma 1. For any 2×2 game under the Moran process, in the absence of selection w = 0, strong mutation $\eta(N+2) > 1$ is necessary and sufficient for the mode of the stationary distribution to be a polymorphic state.

$$\eta(N+2) > 1$$



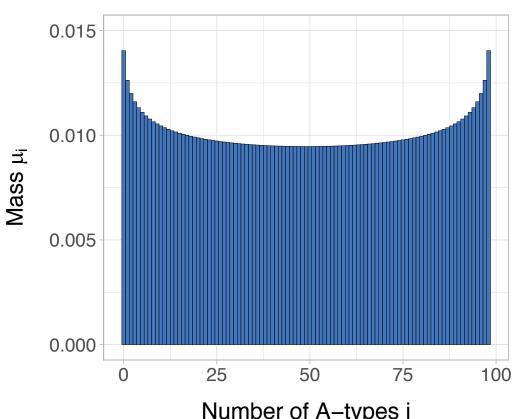
Number of A-types i

$$\eta(N+2) = 1$$



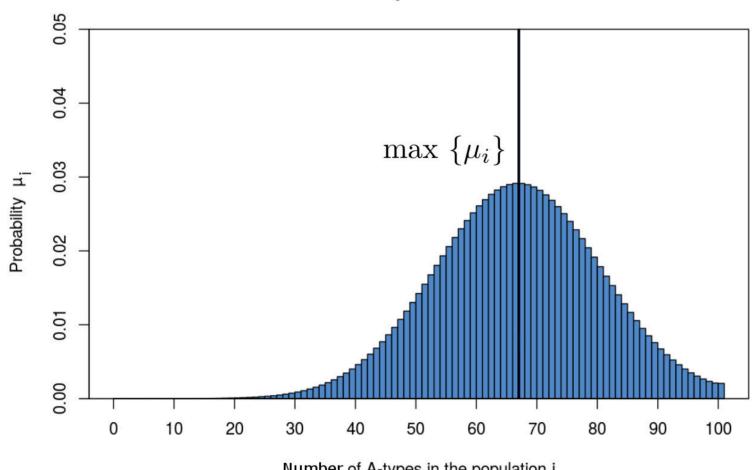
Number of A-types i

$$\eta(N+2) < 1$$



Number of A-types i

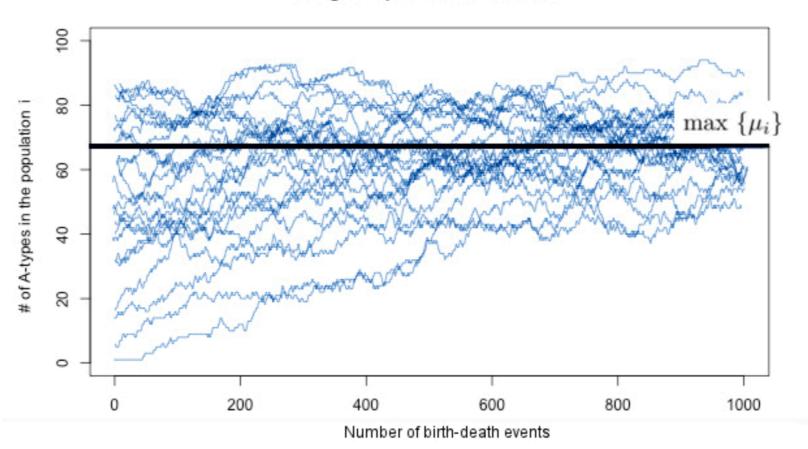
Theorem 1. For any 2×2 symmetric anti-coordination game under the Moran process a < c, b > d, N(b-d) > a-d, for any intensity of selection w > 0 and mutation $\eta < 1/2$, when the strong mutation condition $\eta(N+2) > 1$ is satisfied, the mode of the stationary distribution will be a polymorphism located between the critical point $i^* = \frac{N(b-d)+d-a}{b+c-a-d}$ and the midpoint of the state space $\frac{N+1}{2}$.



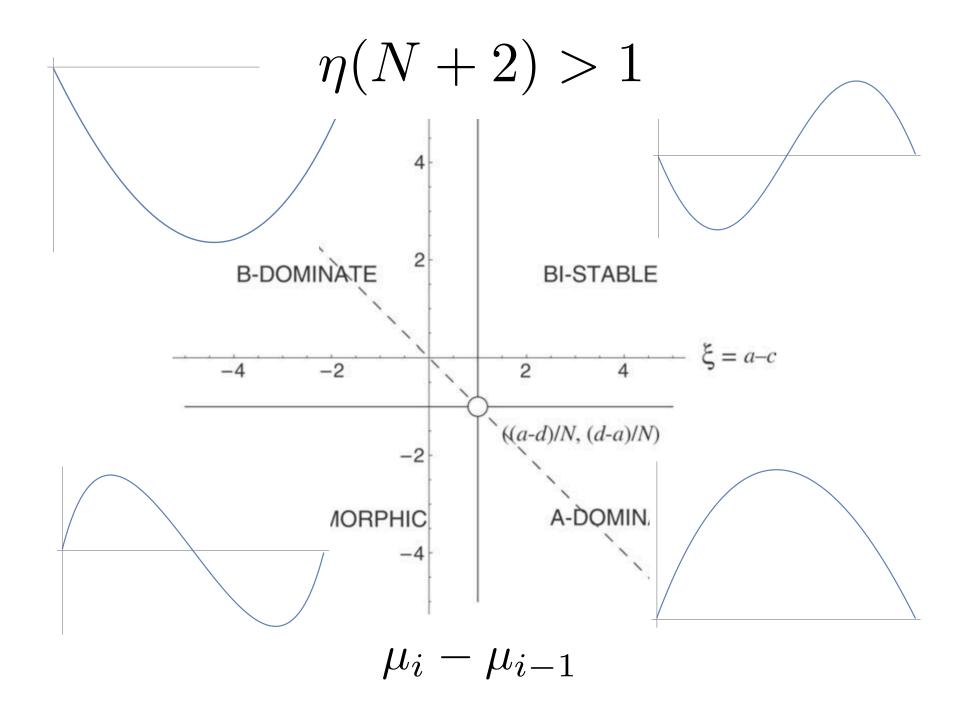
Number of A-types in the population i

Simulation

Single Population Simulation



Corollary 1. For any 2×2 symmetric anti-coordination game under the Moran process a < c, b > d, N(b-d) > a-d, for any intensity of selection w > 0 and mutation $\eta < 1/2$, when the strong mutation condition $\eta(N+2) > 1$ is satisfied, the mass of the states nearest the critical point $i^* = \frac{N(b-d)+d-a}{b+c-a-d}$ monotonically increase with intensity of selection.



When might strong mutation obtain?

Simple organisms e.g., *E. coli*

Per site mutation $\approx 4 \times 10^{-4}$ Clonal colony $\approx 10^6 - 10^8$ (Barrick et al, 2009)

 $\eta N \approx 40k$

Complex organisms e.g., *H. sapiens*

Per site mutation $\approx 10^{-5} - 10^{-10}$ Group size $\approx 50 - 150$ (Drake et al. 1998)

$$\eta N \ll 1$$

Cultural evolution Transmission noise \approx high Group size $\approx 50 - 150$

if $N = 100 \& \eta > 0.1$, then $\eta N > 1$

Upshots

We can characterize the conditions under which the evolutionary systems described by the Moran process:

- (1) will realign with the predictions of the replicator dynamics,
- (2) can sustain long run diversity,
- (3) and should not be analyzed via stochastic stability.

