FUNDAMENTAL DISAGREEMENTS BETWEEN EVOLUTIONARY DYNAMICS

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ABSTRACT

The replicator dynamics and Moran process represent the main deterministic and stochastic models employed in evolutionary game theory. However, there are conditions under which their predictions disagree. I demonstrate that the disagreement between their predictions is caused by a standard technique used in the analysis of the Moran process—stochastic stability analysis. My investigation reveals problems for stochastic stability analysis in a broad class of games: anti-coordination games, and games containing anti-coordination subgames. I characterize the conditions—in terms of population sizes, mutation rates, and intensities of selection—under which stochastic stability will mispredict the long run behavior of the Moran process, and demonstrate a novel domain of agreement between the two dynamics.

TLDR: *For a brief overview, follow the red text.*

THE PUZZLE

OBSERVATION: Under certain conditions, the canonical replicator dynamics and Moran process models can yield contradictory predictions as to the probable outcomes of evolutionary processes.

Q: Why should this be puzzling?
A: Because the two models are intimately connected—the replicator dynamics provides the average behavior of the Moran process for large populations over long but finite durations[15].

AN EXAMPLE
of DISAGREEMENT BETWEEN THE TWO DYNAMICS

Take the following simple, symmetric *anti-coordination* game:

	A	B
A	0	1
B	1	0

Assume in both models: large populations; the absence of mutation; and infinite horizon play.

The **replicator dynamics predicts**: evolution will deliver the population to the polymorphic state $x{=}1/2$.

Whereas the **Moran process predicts:** evolution will deliver the population, with equal probability, to one of the monomorphic states $x{=}0$ or $x{=}1$.

What is a moral certainty in one model is an impossibility in the other.

THE ANSWER TO THE PUZZLE
& CAUSE OF THE DISAGREEMENT

SPOILER: The problem lies in the standard technique of *stochastic stability analysis*. In particular, it lies in the idealizations of *vanishing mutation* and *weak selection* employed in making the derivation of stochastic stability tractable.

Under conditions I will characterize, these idealizations lead to the misprediction of homogeneity by stochastic stability analysis, when long run diversity is to be expected.

But, to understand the solution, we need to get an understanding of our dynamics and how we derive predictions from them.

MOTIVATION
& CONNECTION TO THE LITERATURE

Q: Why does this matter?
A: Because the use of stochastic stability analysis is ubiquitious.

Those that have employed stochastic stability to analyze the behavior of the Moran process include:

> Darong (2010), Fudenberg et al (2006), Imhof et al (2006), Nowak (2009, 2007, 2006), Ohtsuki et al (2007), Pitchaimani & Rajaji (2016), Sandholm (2010), Taylor et al (2004), Trauelsen et al (2007), Trauelsen & Hauert (2009), and Young (2015, 2001, 1998, 1993).

This list can read like a a who's-who of evolutionary game theory. Extraordinary game theorists have used stochastic stability analysis to explain the processes of cultural and biological evolution. Stochastic stability is an important tool in both theoretical and applied work, and understanding its limitations is important.

THE TWO MODELS

REPLICATOR DYNAMICS

The replicator dynamics is the first and most important model in evolutionary game theory[17]. This is due to the fact that it allows us to consider the qualitative behavior of selection unperturbed by the complicating factors of drift, mutation, recombination, and so on.

The leading idea behind the replicator dynamics is that types that are more fit than the population average fitness grow in proportion, and types that are less fit than average shrink in proportion.

This can be described by a system of differential equations

$$\dot{x}_i = x_i[u(i,x) - u(x,x)], \quad i = 1,2$$

where $\dot{x}_i$ denotes the rate of change of the population proportion of type i, x_i denotes the population proportion of type i, $u(i,x)$ denotes the expected fitness of type i from interacting with the population x, and $u(x,x)$ denotes the population average fitness.

The plausible outcomes of an evolutionary process described by the replicator dynamics are typically taken to be the *asymptotically stable* states of the system[15]. These are the fixed points of the system—where the rate of change of all types is zero—that also have nonempty basins of attraction, and are stable under small perturbations in population proproportions.

MORAN PROCESS

The standard stochastic model in evolutionary game theory, the frequency-dependent Moran process[10], departs from the simplicity of the replicator dynamic to introduce stochasticity, finite population sizes, and drift.

The Moran process is a birth-death process in which, for each time step, two individuals are chosen: one for reproduction and the other for elimination.

The individual chosen for death is selected uniformly at random from the population, while the individual chosen for birth is chosen probabilitically as determined by the relative expected payoffs of the two types.

Formally, we define the Moran process with population size N and mutation rate η as a Markov process $\{X^{N,\eta}\}$ over the finite state space $\chi{=}\{x \,\varepsilon\, X\colon Nx \,\varepsilon\, Z^N\}$ of possible compositions of the population, and with transition probabilities between states given by

$$\hat{P}_{i,j} = \begin{cases} (1-\eta)\dfrac{N-i}{N}\dfrac{if_i}{if_i+(N-i)g_i} + \eta\dfrac{N-i}{N}\dfrac{(N-i)g_i}{if_i+(N-i)g_i} & \text{if } j = i+1 \\ (1-\eta)\dfrac{i}{N}\dfrac{(N-i)g_i}{if_i+(N-i)g_i} + \eta\dfrac{i}{N}\dfrac{if_i}{if_i+(N-i)g_i} & \text{if } j = i-1 \\ 1-\hat{P}_{i,i+1}-\hat{P}_{i,i-1} & \text{if } j = i \\ 0 & \text{otherwise} \end{cases}$$

which composes a tri-diagonal matrix. The fitness of each type, A and B, are given as functions, f_i and g_i, of the number i of A-types in the population.

STOCHASTIC STABILITY ANALYSIS
& LONG RUN BEHAVIOR OF THE MORAN PROCESS

Stochastic stability, introduced to game theory by Foster & Young[22][23], aims to pick out the most probable outcome of a stochastic process.

The stationary distribution captures both the proportion of time the process will spend at each of the states in the state space, and where we may expect to locate the process in the limit of time.

Formally, a probability distribution $\mu \,\varepsilon\, R^{\chi}$ is a *stationary distribution* of the irreducible Markov process $\{X^{N,\eta}\}$ if

$$\sum_{i\in\chi} \mu_i P_{ij} = \mu \text{ for all } j \in \chi$$

That is, taking the product of the stationary distribution and the matrix of transition probabilities simply returns the stationary distribution.

A stochastically stable state then is the (typically unique) state in the stationary distribution that has positive mass after we have taken the limit as the mutation rate approach zero—i.e., upon assuming *vanishing mutation*.

Formally, a state $i \,\varepsilon\, X^N$ is *stochastically stable* in the small mutation limit if $\lim_{\eta\to 0} \mu_i^{N,\eta} > 0$[16].

Typically, questions about stochastic stability can be answered by using particular well-chosen graphs, obviating the need to compute the stationary distribution.[24]

But we can do better. We can investigate the stationary distrbution directly, and relax the idealizing assumptions of stochastic stability to explore a broader range of behaviors.

RESULTS
1 LONG RUN PERSISTENCE OF DIVERSITY IN THE MORAN PROCESS

When we relax the idealizing assumptions of stochastic stability, we can see that—for a significant range of mutation rates, population sizes, and intensities of selection—even the long run behavior of the Moran process will qualitatively diverge from the predictions yielded by stochastic stability analysis.

In particular, in the class of anti-coordination games, polymorphic population states can retain positive mass in the stationary disturbution. This is shown both in derivations of the stationary distribution (Figure 2) for various parameterizations, and in computational simulations of the process (Figure 1).

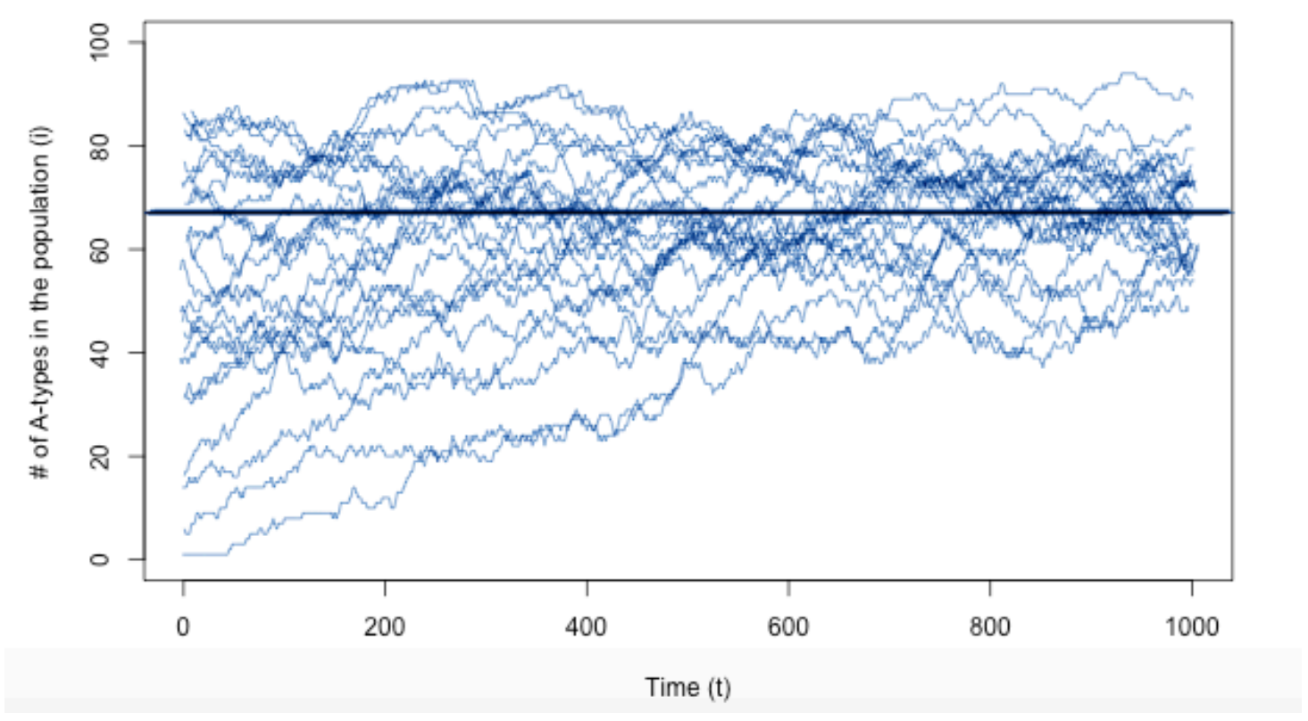
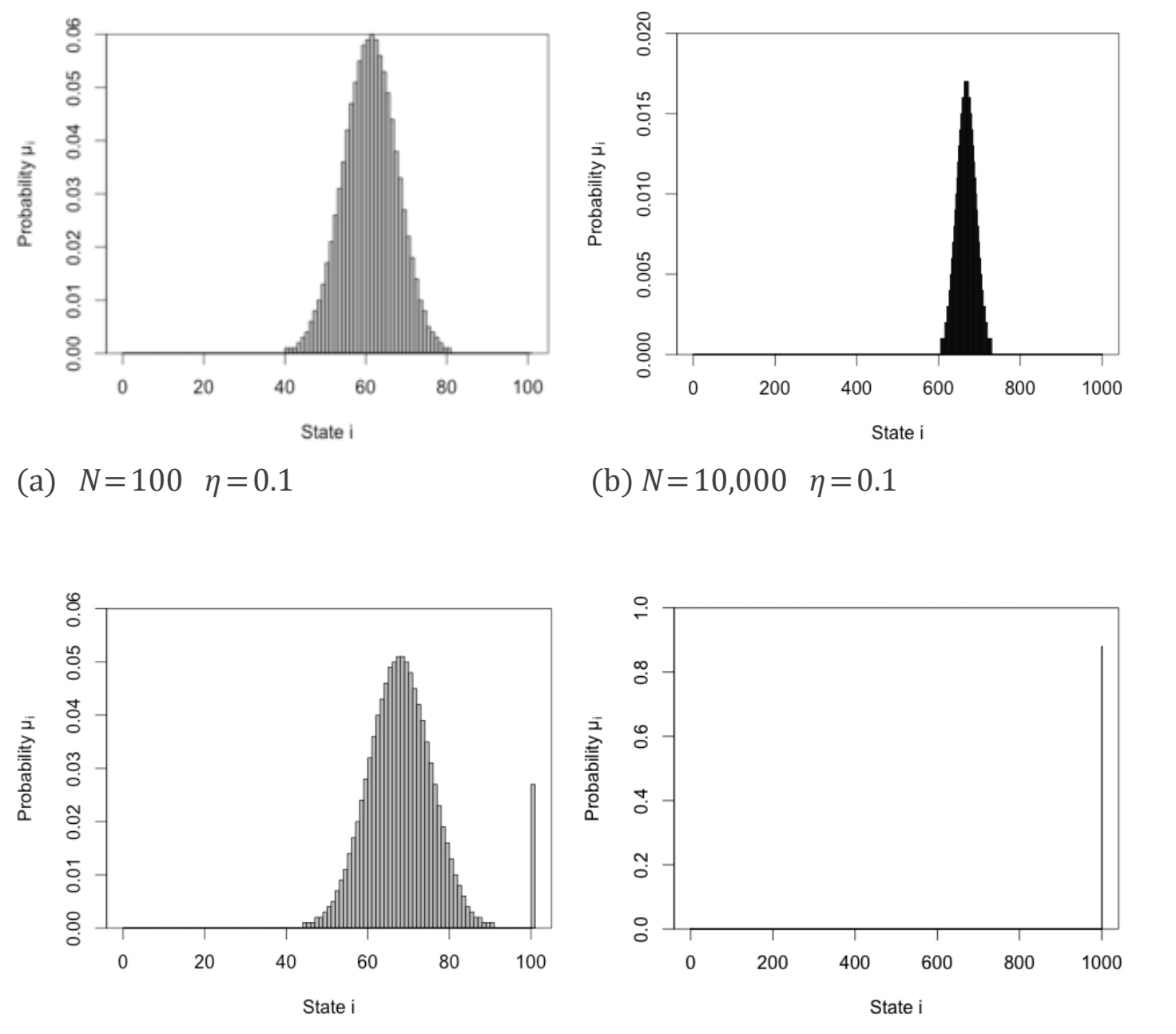


FIGURE 1: Single Population Simulations of the Moran Process

Thus stochastic stability analysis can mispredict homogeneity, when long run diversity is to be expected.

But under what conditions should we expect such misprediction? And should we expect these conditions to obtain in real-world target systems?

The Answer to the former question is given by the result in the next section, and the answer to the latter question is "sometimes, yes". An examination of the literature reveals that many traits of interest in model organisms such as E. coli, C. elegans, and drosophila will exhibit the population sizes, mutation rates, and selection intensities that will make stochastic stability ill-suited to their analysis[7][8][9][13]. In more complex organisms, however, smaller population sizes mean that the conditions will typically not obtain.



(a) $N{=}100 \quad \eta{=}0.1$ (b) $N{=}10{,}000 \quad \eta{=}0.1$

(c) $N{=}100 \quad \eta{=}10^{-5}$ (d) $N{=}10{,}000 \quad \eta{=}10^{-7}$

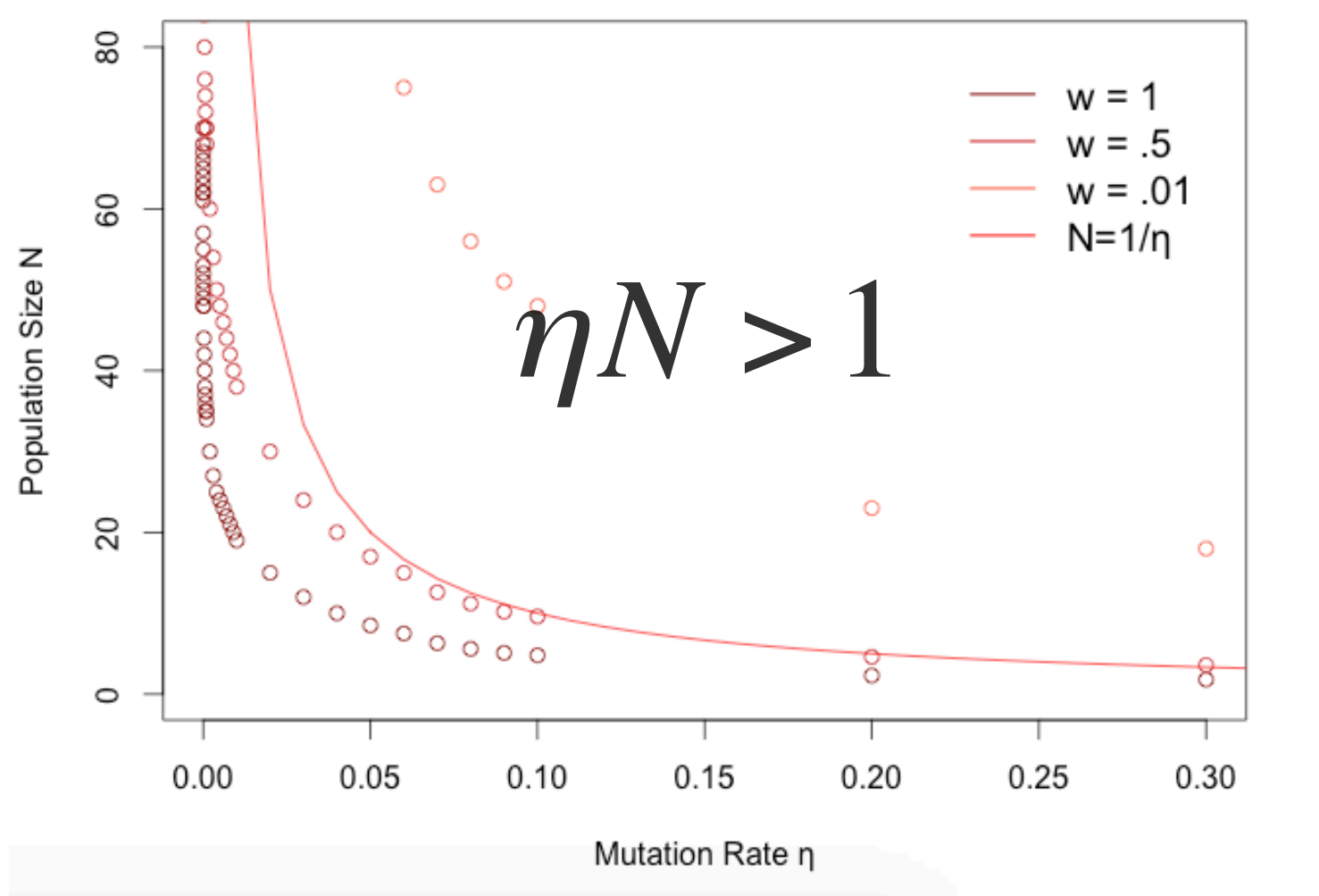
FIGURE 2: Stationary Distributions with Varying Population Sizes and Mutation Rates

2 A NOVEL DOMAIN OF AGREEMENT BETWEEN THE MODELS

Our result is that we can characterize the domain under which stochastic stability mispredicts the behavior of the Moran process. Interestingly, this also provides a novel domain for which the behavior of the Moran process can be shown to realign with the predictions of the replicator dynamics.

(MP-RD harmony for strong mutation) For most 2×2 symmetric normal form anticoordination games, in the presence of strong mutation[20] $\eta N > 1$, and strong selection $w = 1$, if a state i is asymptotically stable under the replicator dynamics, then it is near the peak of the stationary distribution μ of the Moran process.

FIGURE 3: Conditions for the Persistence of Interior Equilibria



CONCLUSION

UPSHOTS: My analysis gives the conditions under which the evolutionary systems described by the Moran process (1) should not be analyzed using stochastic stability analysis, and (2) will sustain diversity and realign with the predictions of the replicator dynamics, even in infinite horizon play. In normal science, we learn to use the correct model and method of analysis when the appropriate conditions obtain.

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