# Natural Selection as an Inhibitor of Genetic Diversity: Multiplicative Weights Updates Algorithm and a Conjecture of Haploid Genetics

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# Sex or No Sex: Please choose one

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Your goal is for your species to live long and prosper.
Would you equip it with a sexual or asexual method of reproduction?

Is sexual reproduction better than asexual?

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**Easy answer 2:** Sex = Genetic Mixing $\rightarrow$ Genetic Diversity

*Today*: **Sexual reproduction** leads to monomorphic populations (i.e., **societies of clones**) in certain classes of biological species.
*Informal rule of thumb:* In haploid organisms (i.e., organisms with one chromosome per gene) sex does not suffice to protect diversity.

# Outline

# Basic Terms in Biology

- Gene: A unit that determines some characteristic of the organism, and passes traits to offsprings. Controls the expression of traits, e.g., eye color, blood type.
- Locus: The specific location of a gene on a chromosome. (plural loci)
- Allele: One of a number of alternative forms of the same gene, found at the same loci. Different alleles can result in different observable traits, such as different eye color, blood type, e.t.c.
- Genotype: The genetic constitution of an individual organism.
- Diploid: Having two chromosomes.
- Haploid: Having one chromosome.
- Panmictic: Every pair of individuals can produce offspring (no male, female distinction)

# Our Setting: Panmictic, Haploid 2-Loci with Sex

The species has two genes/loci: $X, Y$.
Gene $X$ has $n$ possible alleles: $X_1, X_2, \ldots, X_n$.
Gene $Y$ has $m$ possible alleles: $Y_1, Y_2, \ldots, Y_m$.
Each individual has a genotype of the form $X_i Y_j$.
Let $w_{ij}$ denote the fitness of genotype $X_i Y_j$.
Finally, let $x_i$, $y_j$ the frequencies of allele $X_i$, $Y_j$ respectively.

When two individuals mate: e.g., $X_1 Y_1$ and $X_2 Y_2$ the possible offspring combinations are $X_1 Y_1, X_1 Y_2, X_2 Y_1, X_2 Y_2$ and the number of offsprings reflect their respective $w_{ij}$.

*Chastain, Livnat, Papadimitriou, Vazirani (PNAS '14)* argued that population dynamics reduce to (2-player coordination game):

$$x_i' = x_i \frac{(Wy)_i}{x^T W y} \qquad y_j' = y_j \frac{(x^T W)_j}{x^T W y}$$

where $W$ is a matrix whose $(i, j)$-th entry is $w_{ij}$.

# 2-player coordination games

- $S_1, S_2$ the set of strategies for players 1,2.
- $|S_1| = m, |S_2| = n$ number of strategies for each player.
- $A, B$ $m \times n$ payoff matrices.
- $A_{ij}, B_{ij}$ payoff for players 1,2 if they choose strategies $i, j$ respectively.
- Set of mixed strategies for players 1,2 are
  $\Delta_1 = \{x = (x_1, \ldots, x_m) \mid x \geq 0, \sum_{i=1}^{m} x_i = 1\}$,
  $\Delta_2 = \{y = (y_1, \ldots, y_n) \mid y \geq 0, \sum_{j=1}^{n} y_j = 1\}$.
- The expected payoffs of the first-player and second-player from a mixed-strategy $(x, y) \in \Delta_1 \times \Delta_2$ are respectively

$$\sum_{i,j} A_{ij} x_i y_j = x^T A y \quad \text{and} \quad \sum_{i,j} B_{ij} x_i y_j = x^T B y$$

- In **coordination games**, $A = B$.

# 2-player coordination games (cont.)

## Definition

A strategy profile $(x, y) \in \Delta_1 \times \Delta_2$ is a **Nash equilibrium (NE)** iff $\forall x' \in \Delta_1, x^T Ay \geq x'^T Ay$ and $\forall y' \in \Delta_2,\ x^T By \geq x^T By'$.

## Example

Equilibria where each agent applies a deterministic strategy are called **pure**. Otherwise, they are called **mixed**. Any coordination game has pure Nash equilibria as well (e.g. the state with maximum utility).

| | |
|---|---|
| 1, 1 | 0, 0 |
| 0, 0 | 2, 2 |

# Discrete Replicator Dynamics (or Multiplicative Weights Update Algorithm)

Given a coordination game with payoff matrix $A$, discrete replicator dynamics have the update rule (map) $f : \Delta_1 \times \Delta_2 \rightarrow \Delta_1 \times \Delta_2$:

$$\begin{aligned} \forall i \in S_1, \quad x_i' &= x_i \frac{(Ay)_i}{x^T A y} \\ \forall j \in S_2, \quad y_j' &= y_j \frac{(x^T A)_j}{x^T A y} \end{aligned} \tag{1}$$

- A fixed point $(x^*, y^*)$ satisfies $f(x^*, y^*) = (x^*, y^*)$.
- Set of Nash equilibria is a **subset** of the fixed points.
- $\Delta_1 \times \Delta_2$ is **invariant**.

Discrete replicator dynamics was introduced by *Losert, Akin ('83)* in a game theoretic model about genetic evolution. It was used as a discrete time approximation of replicator dynamics, a classic continuous time model of evolution. *Kleinberg, Piliouras, Tardos ('09)* showed that replicator corresponds to the "fluid limit" of MWUA.

# Does genetic diversity survive?

**Goal:** understand the long term system behavior.
Specifically, does genetic diversity survive?

*Chastain, Livnat, Papadimitriou, Vazirani ('14):* If we choose the entries of $A$ (fitness landscape) randomly then the system has in expectation an exponential number of mixed equilibria.

Mixed equilibria correspond to mixed populations where many different genotypes are present. Any coordination game has pure Nash equilibria as well (e.g. the state with maximum utility). Any such game has trivially at most $n \cdot m$ pure Nash. Typically, there exist at most linearly many pure NE ($\leq \min\{n, m\}$).

# Main theorem

Theorem (*Mehta, P., Piliouras '14*)

*Given a generic two agent coordination game, starting from a generic initial condition, discrete replicator dynamics* ***converges to pure Nash equilibria****.*

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*Given a generic two agent coordination game, starting from a generic initial condition, discrete replicator dynamics **converges to pure Nash equilibria**.*

*Both genericity assumptions are **necessary** and in some sense **minimal**.*
*The game genericity assumption requires that each row/column of the payoff matrix have distinct entries. There exist coordination games with exactly two equal entries on a single column/row that do not satisfy the theorem.*
*There exist coordination games where the (zero measure) set of initial conditions that converge to mixed Nash equilibria has co-dimension 1.*
*Our results carry over even if the game has **uncountably many** of equilibria.*

# High level intuition

Tossing a coin, 3 possible (*e*quilibrium) states:


- Tail Stable

- Head Stable

- Landing on its edge Unstable

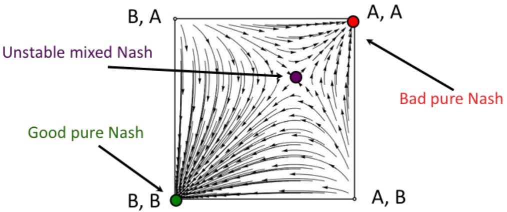
All mixed equilibria correspond to "knife-edge" configurations. No matter how many of them exist, they will never be realized in practice.

# Linguistic confusion around the term (Nash) equilibrium

The term equilbrium has **two, incompatible** interpretations:

- i) the **colloquial** one ("spoken" English)
  *e.g.*, "The financial system was in turmoil, but thankfully it has reached a new equilibrium."
  Google "equilibrium synonyms" $\rightarrow$ stability, ..., composure, calm, tranquility, ...,
- ii) the **technical** one (fixed point of a function $f(x) = x$)
  *e.g.*, Nash equilibrium (stability not included)

| | A | B |
|---|---|---|
| A | 1, 1 | 0, 0 |
| B | 0, 0 | 2, 2 |



# High Level Proof Steps

- 1. Game theoretic characterization of stable equilibria.
- 2. Point-wise convergence to equilibrium and diffeomorphism.
- 3. The set of initial conditions that converge to unstable fixed points is of measure zero.

# 1. Weakly stable Nash Equilibrium

### [Kleinberg, Piliouras, Tardos '09]

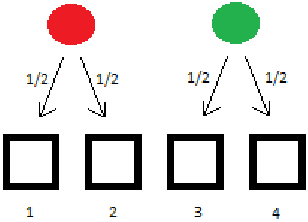
A Nash equilibrium is called **weakly stable** if fixing one of the agents to choosing one of his strategies in his current support with probability one, leaves the other agent indifferent between the strategies in his support.

### Observations

- Trivially any pure Nash Equilibrium is weakly stable.
- Any NE with exactly one randomizing agent is weakly stable.
- The uniformly mixing NE in Rock-Paper-Scissors is **not** weakly stable.
- In a two agent coordination game with distinct elements on each row/column all weakly stable NE are pure.

### Example

Example with balls and bins.




- In this game:

  Red player chooses bin 1,2 with probability half

  Green player chooses bin 3,4 with probability half.

# 1. (Locally) stable fixed point $\rightarrow$ weakly stable Nash

## Definition - Stable fixed point

We call a fixed point $\mathbf{p}$ (linearly) stable, if the eigenvalues of the Jacobian ($J_{ij} = \frac{\partial F_i}{\partial x_j}$) at $\mathbf{p}$ have absolute value less than or equal to 1. Otherwise, it is called (linearly) unstable.

## Lemma

Stable NE $\subset$ weakly stable NE (spectral analysis of the Jacobian).
Under the assumption that every row/column has distinct entries, weakly stable NE $=$ pure NE.

# 2. Coordination games $\subset$ Potential games $\rightarrow$ Convergence to NE

In potential games there exists a single (potential) function $\Phi$, which at each state $s$ captures the deviation incentives for all agents:
$\Phi(s_i, s_{-i}) - \Phi(s'_i, s_{-i}) = u_i(s_i, s_{-i}) - u_i(s'_i, s_{-i}) \;\; \forall s_i, s_{-i} \in S_i$

In potential games, many learning dynamics (including discrete replicator dynamics) act as a gradient-like system whose Lyapunov function is the potential function. I.e. $\Phi(F(x)) \geq \Phi(x)$ where the equality holds if and only if $x$ is an equilibrium.

Hence, the dynamics converge to fixed points. Using Losert and Akin (J. Math. Bio '83) result, we can show point-wise convergence to equilibria and that the rule is a diffeomorphism.
**Do they converge however, for almost all initial conditions, to pure NE?**

# 3. From local to global arguments

### Theorem

The set of initial conditions that converge to unstable fixed points is of measure zero.

### Proof Hints

- Unstable equilibria have zero measure set of attracting initial conditions locally. (Pointwise convergence) + (diffeomorphism) + (Center Stable Manifold theorem)
- Unroll these zero measure sets backwards to argue global zero measure arguments. If $f : A \to A$ is a diffeomorphism, $f$ and $f^{-1}$ map null sets to null sets.
- In the case of continuum of equilibria, chop down the continuum into countable number of pieces and use union bound arguments. (Use Lindelof's lemma: every open cover in $\mathbb{R}^n$ has a countable subcover.)

# Putting everything together

- Discrete replicator dynamics converges point-wise to equilibria in two agent coordination games.
- For all but a zero measure set of initial conditions it converges to weakly stable NE.
- Weakly stable NE coincide with pure NE in any coordination game where each row/column of the payoff matrix has distinct entries.

# Discussion

The result for the $n$-player case is true under hyperbolicity assumptions.

The picture gets completely reversed in **diploid** systems (in terms of diversity):

(Informal) Theorem (Mehta, P., Piliouras, Yazdanbod)

In diploid systems the survival of genetic diversity is likely but computationally hard to predict.

**Open Questions**

- Mutation - change of environment (fitness matrix)
- Quantitative analysis of average performance
- Analyzing other mechanisms that support genetic diversity.

Thank you!

# Can evolution be predicted? To what extent?

- Can we move beyond qualitative analysis of such systems (e.g. mixed vs monomorphic populations)
- Does (sexual) evolution succeed in finding globally optimal configurations w.h.p?

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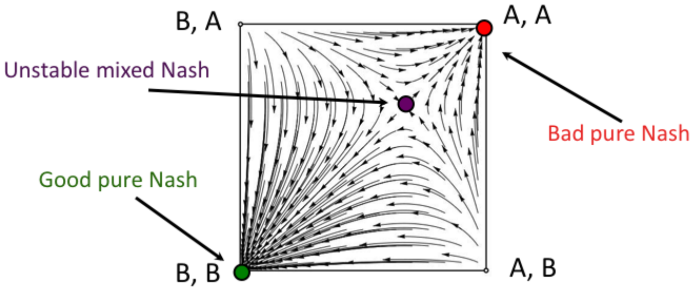

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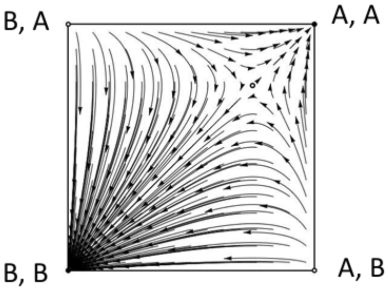

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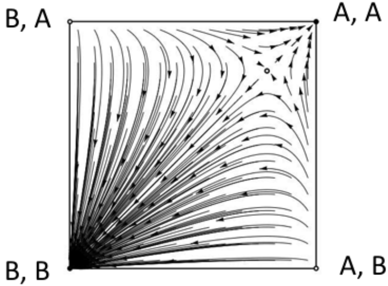
|---|---|---|
| A | 1, 1 | 0, 0 |
| B | 0, 0 | 4, 4 |



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|---|---|---|
| A | 1, 1 | 0, 0 |
| B | 0, 0 | 10, 10 |