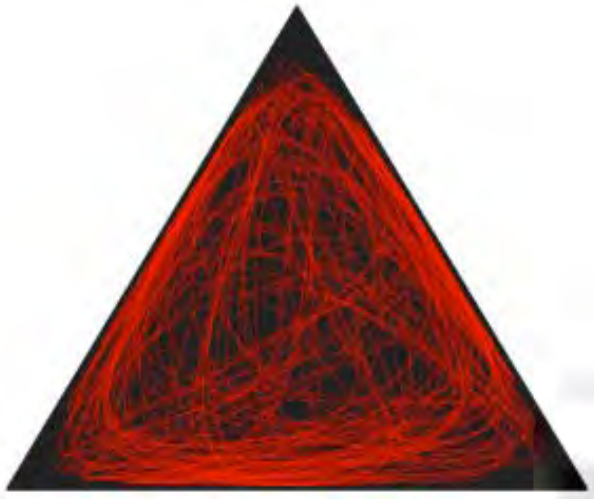


# From finite to infinite populations

Arne Traulsen

Program for Evolutionary Dynamics

Harvard University



1. Replicator dynamics
2. Moran process
3. From finite to infinite populations
4. (Fermi process)

# Games

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Player 2

Player 1

	<i>A</i>	<i>B</i>
<i>A</i>	<i>a</i>	<i>b</i>
<i>B</i>	<i>c</i>	<i>d</i>

# Evolutionary game dynamics

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$$\begin{array}{c} A \\ B \end{array} \begin{pmatrix} a & b \\ c & d \end{pmatrix}$$

Populations

Payoff=Reproductive fitness

Evolutionary dynamics

Fitter individuals produce more offspring

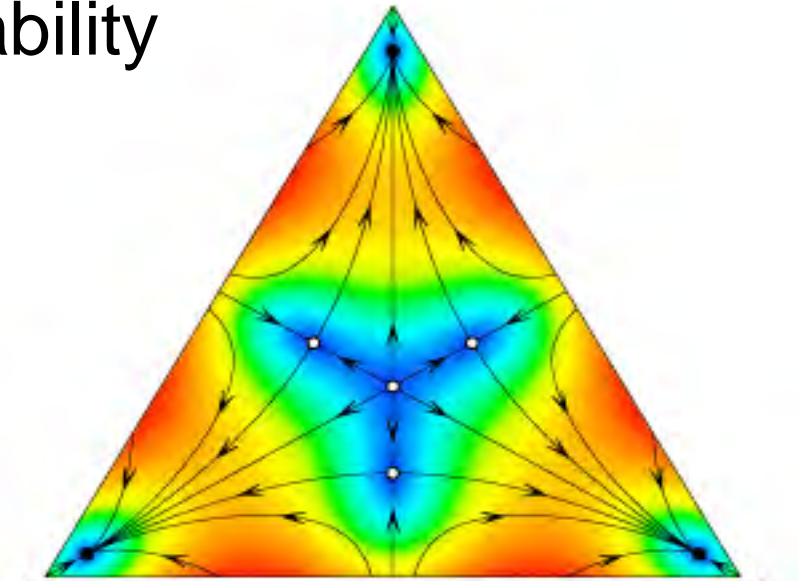




# 1. Replicator dynamics

$$\dot{x}_i = x_i (\pi_i - \langle \pi \rangle)$$

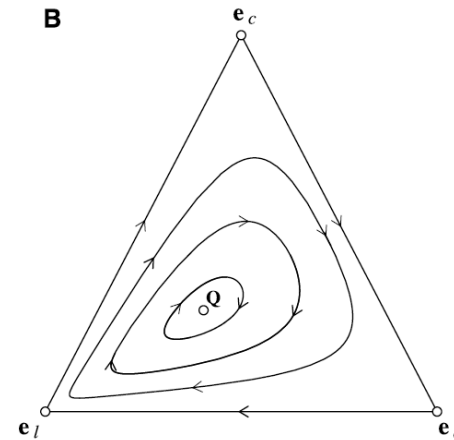
- Fixed points & their stability



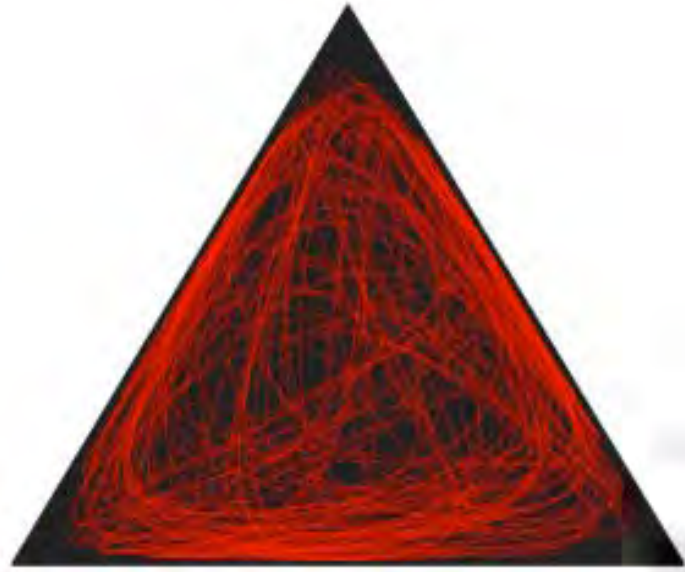
# Replicator dynamics

$$\dot{x}_i = x_i (\pi_i - \langle \pi \rangle)$$

- Constants of motion

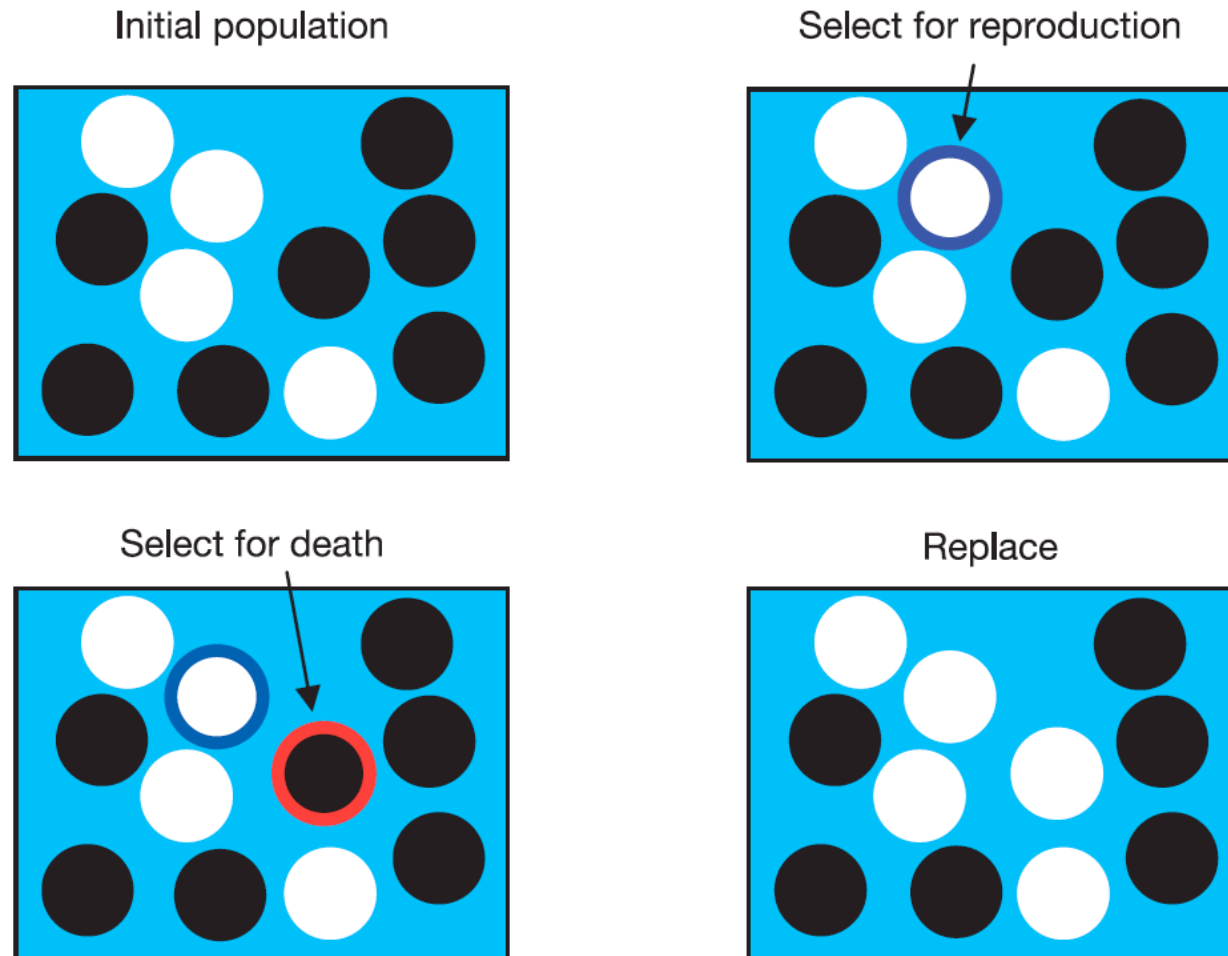


- Deterministic Chaos





## 2. Moran process in finite populations

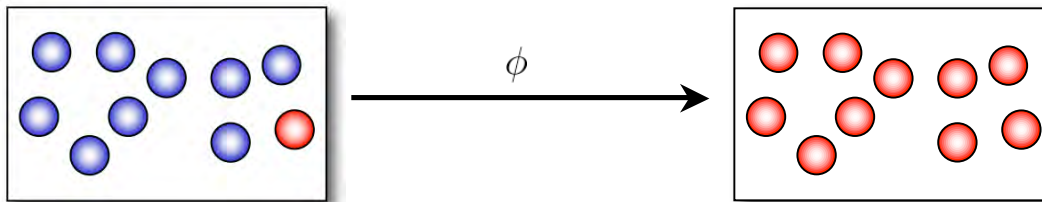


Nowak, Sasaki, Taylor, and Fudenberg, Nature 428, 646 (2004).

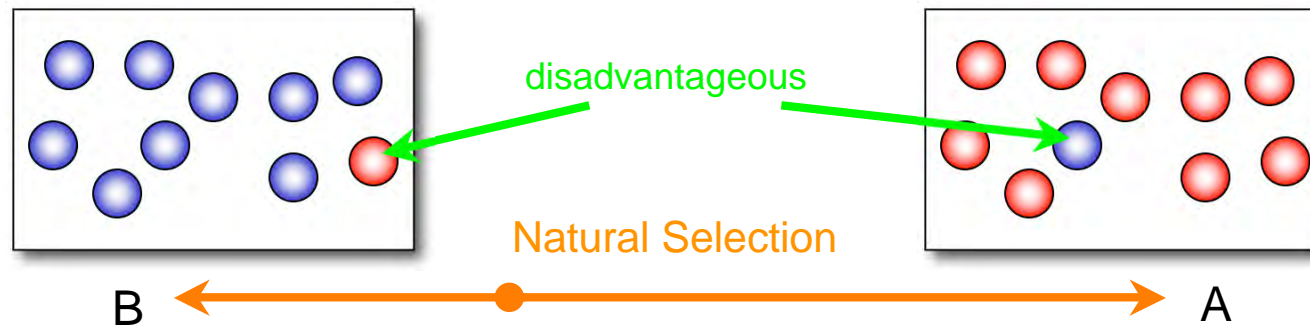
# Results for the Moran process

- Fixation probabilities

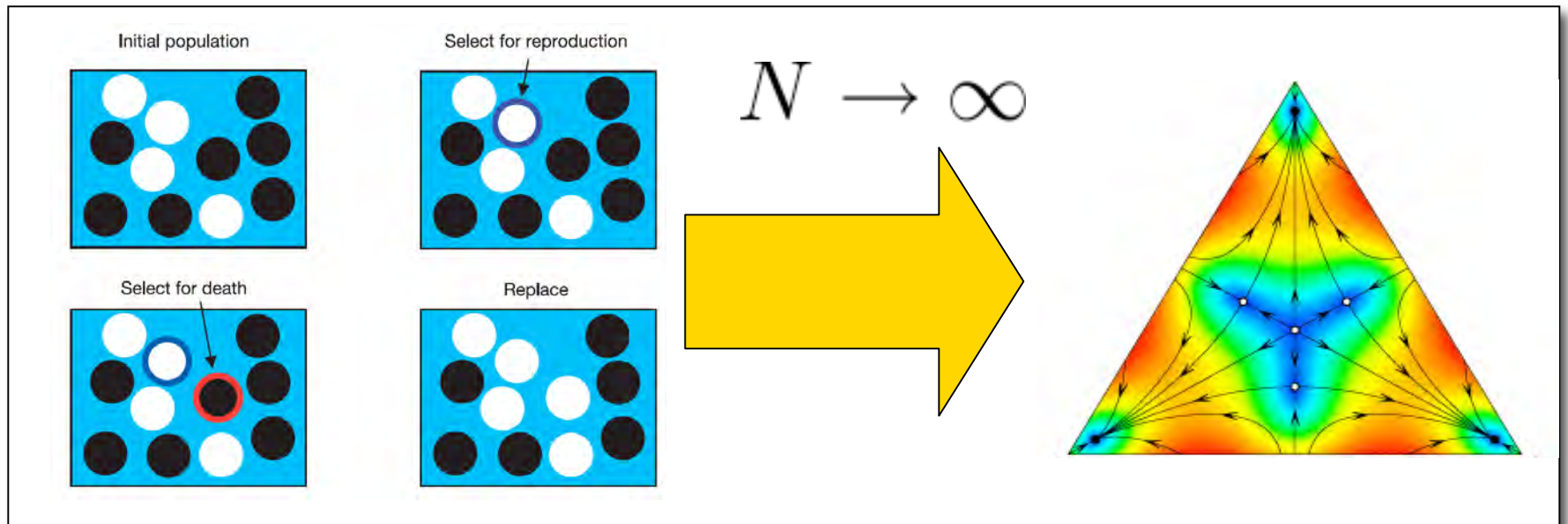
$$\phi = \frac{1}{\sum_{i=0}^{N-1} \prod_{j=1}^i \frac{T_{j \rightarrow j-1}}{T_{j \rightarrow j+1}}}$$



- 1/3 rule for weak selection



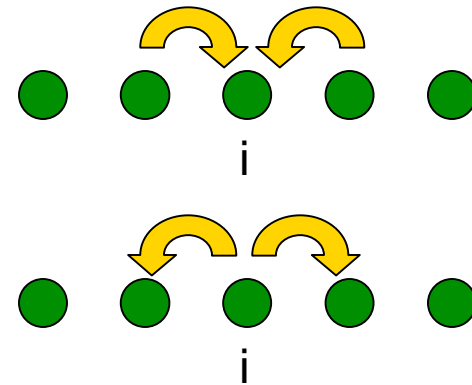
### 3. From finite to infinite populations





# Temporal dynamics of the Moran process

$$\begin{aligned}
 P_i^{\tau+1} &= P_i^{\tau} \\
 &+ P_{i-1}^{\tau} T_{i-1}^{+} + P_{i+1}^{\tau} T_{i+1}^{-} \\
 &- P_i^{\tau} T_i^{+} - P_i^{\tau} T_i^{-}
 \end{aligned}$$



$$x = \frac{i}{N}$$

$$t = \frac{\tau}{N}$$

$$\rho(x, t) = N P_i^{\tau}$$

# Temporal dynamics of the Moran process

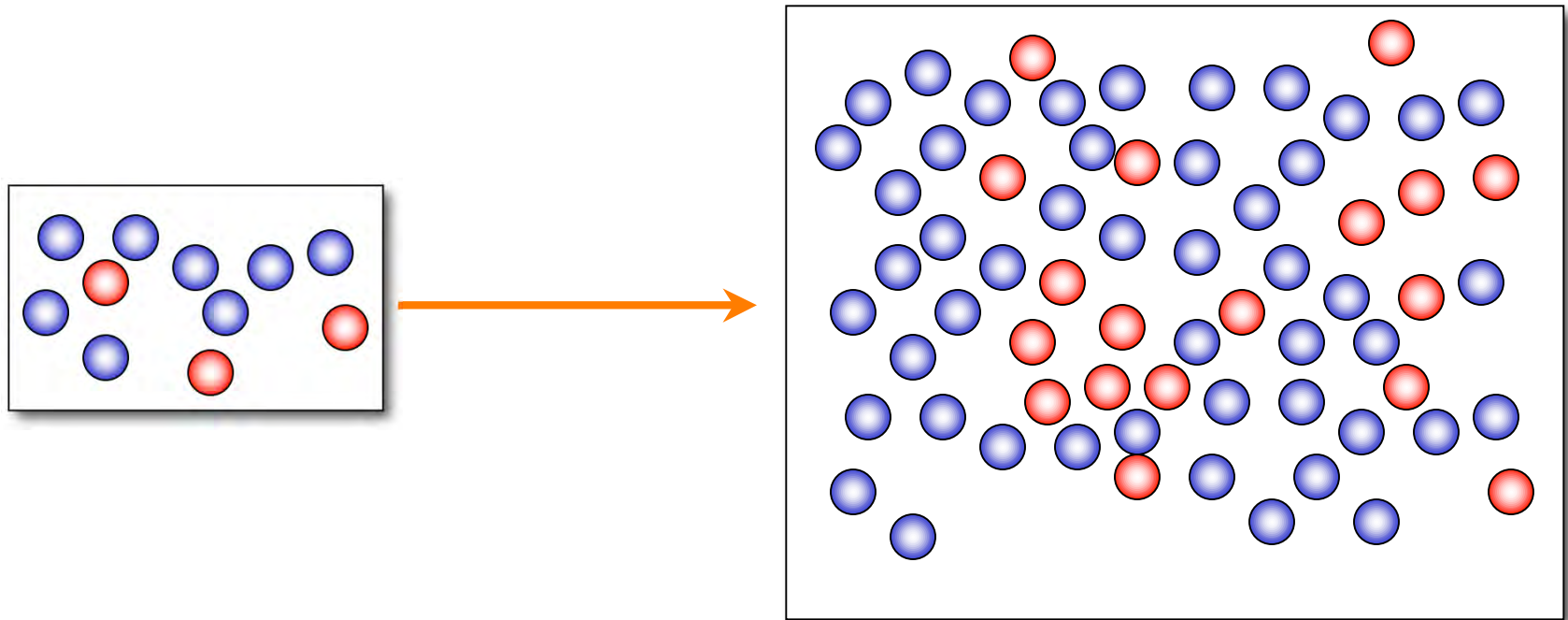
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$$x = \frac{i}{N} \qquad t = \frac{\tau}{N} \qquad \rho(x, t) = NP_i^\tau$$

$$\begin{aligned} \rho(x, t + 1/N) &= \rho(x, t) \\ &+ \rho(x - 1/N, t) T^+(x - 1/N) \\ &+ \rho(x + 1/N, t) T^-(x + 1/N) \\ &- \rho(x, t) T^+(x) \\ &- \rho(x, t) T^-(x) \end{aligned}$$

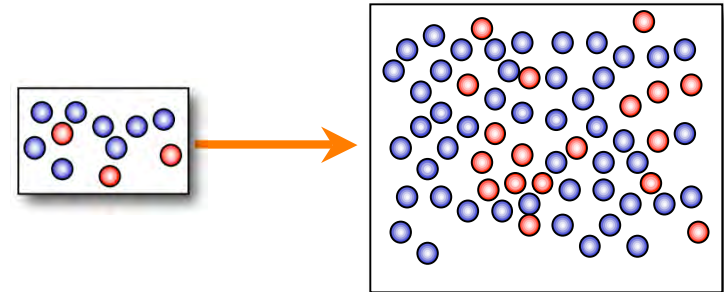
# The limit of large populations

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# Temporal dynamics of the Moran process

$$\begin{aligned}
 \rho(x, t + 1/N) &= \rho(x, t) \\
 &+ \rho(x - 1/N, t) T^+(x - 1/N) \\
 &+ \rho(x + 1/N, t) T^-(x + 1/N) \\
 &- \rho(x, t) T^+(x) \\
 &- \rho(x, t) T^-(x)
 \end{aligned}$$



$$\begin{aligned}
 \rho(x, t + 1/N) &\approx \rho(x, t) + \frac{1}{N} \frac{\partial}{\partial t} \rho(x, t) \\
 \rho(x \pm 1/N, t) &\approx \rho(x, t) \pm \frac{1}{N} \frac{\partial}{\partial x} \rho(x, t) + \frac{1}{2N^2} \frac{\partial^2}{\partial x^2} \rho(x, t) \\
 T^\pm(x \pm 1/N) &\approx T^\pm(x) \pm \frac{1}{N} \frac{\partial}{\partial x} T^\pm(x) + \frac{1}{2N^2} \frac{\partial^2}{\partial x^2} T^\pm(x)
 \end{aligned}$$

# Fokker-Planck equation

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$$\dot{\rho}(x, t) \approx -\frac{\partial}{\partial x} [a(x)\rho(x, t)] + \frac{\partial^2}{\partial x^2} [b^2(x)\rho(x, t)]$$

**Drift**

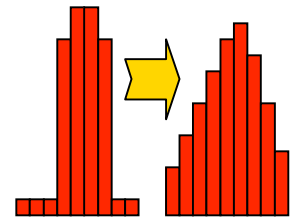
$$a(x) = T^+(x) - T^-(x)$$

**Diffusion**

$$b(x) = \sqrt{\frac{T^+(x) + T^-(x)}{N}}$$

# From Fokker-Planck to Langevin

$$\dot{\rho}(x, t) \approx -\frac{\partial}{\partial x} [a(x)\rho(x, t)] + \frac{\partial^2}{\partial x^2} [b^2(x)\rho(x, t)]$$



Stochastic Calculus

$$\dot{x} = a(x) + b(x)\xi$$



## Back to the replicator equation

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$$\dot{x} = a(x) + \cancel{b(x)\xi}$$

$$b(x) = \sqrt{\frac{T^+(x) + T^-(x)}{N}}$$

$$N \rightarrow \infty$$

$$\dot{x} = a(x)$$

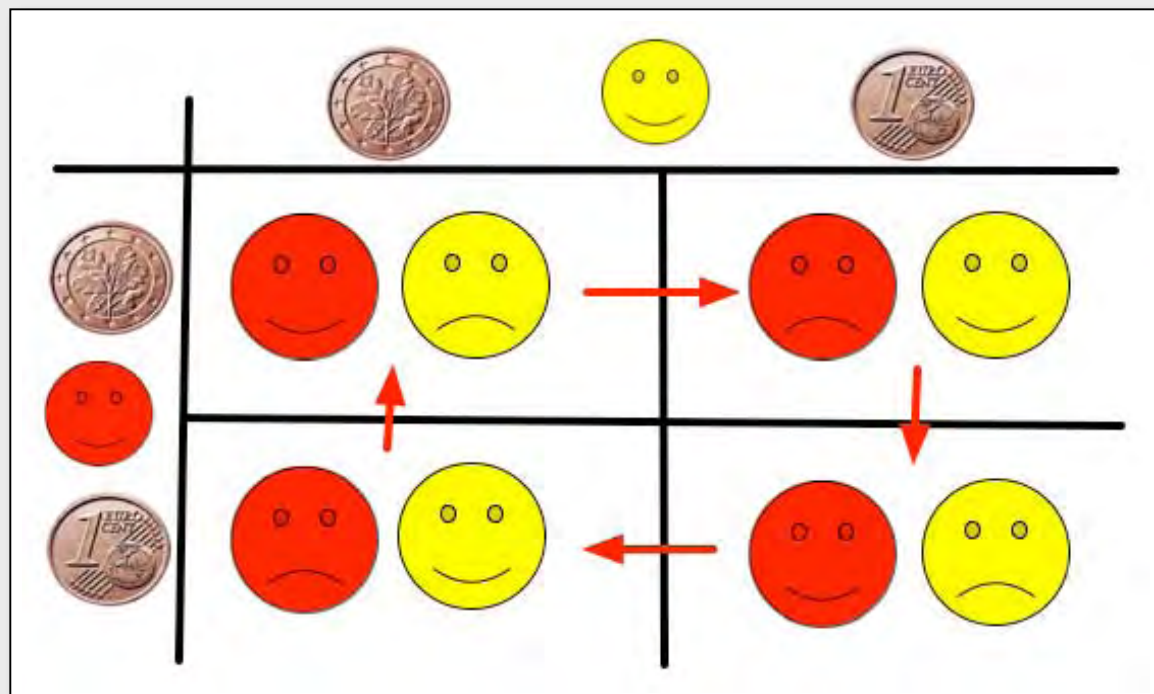
$$= T^+(x) - T^-(x)$$

$$= x \frac{\pi_A}{\langle \pi \rangle} (1 - x) - (1 - x) \frac{\pi_B}{\langle \pi \rangle} x$$

$$= x \frac{\pi_A - \langle \pi \rangle}{\langle \pi \rangle}$$

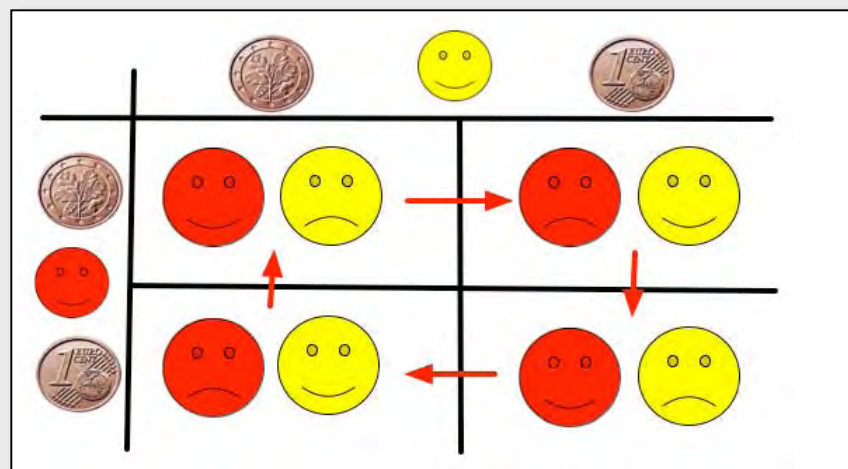
Does this matter?

# Matching pennies

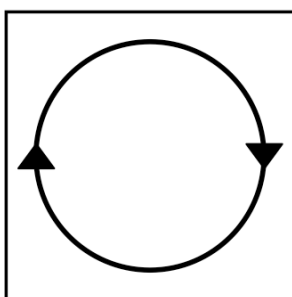




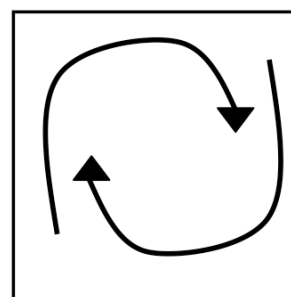
# Matching pennies



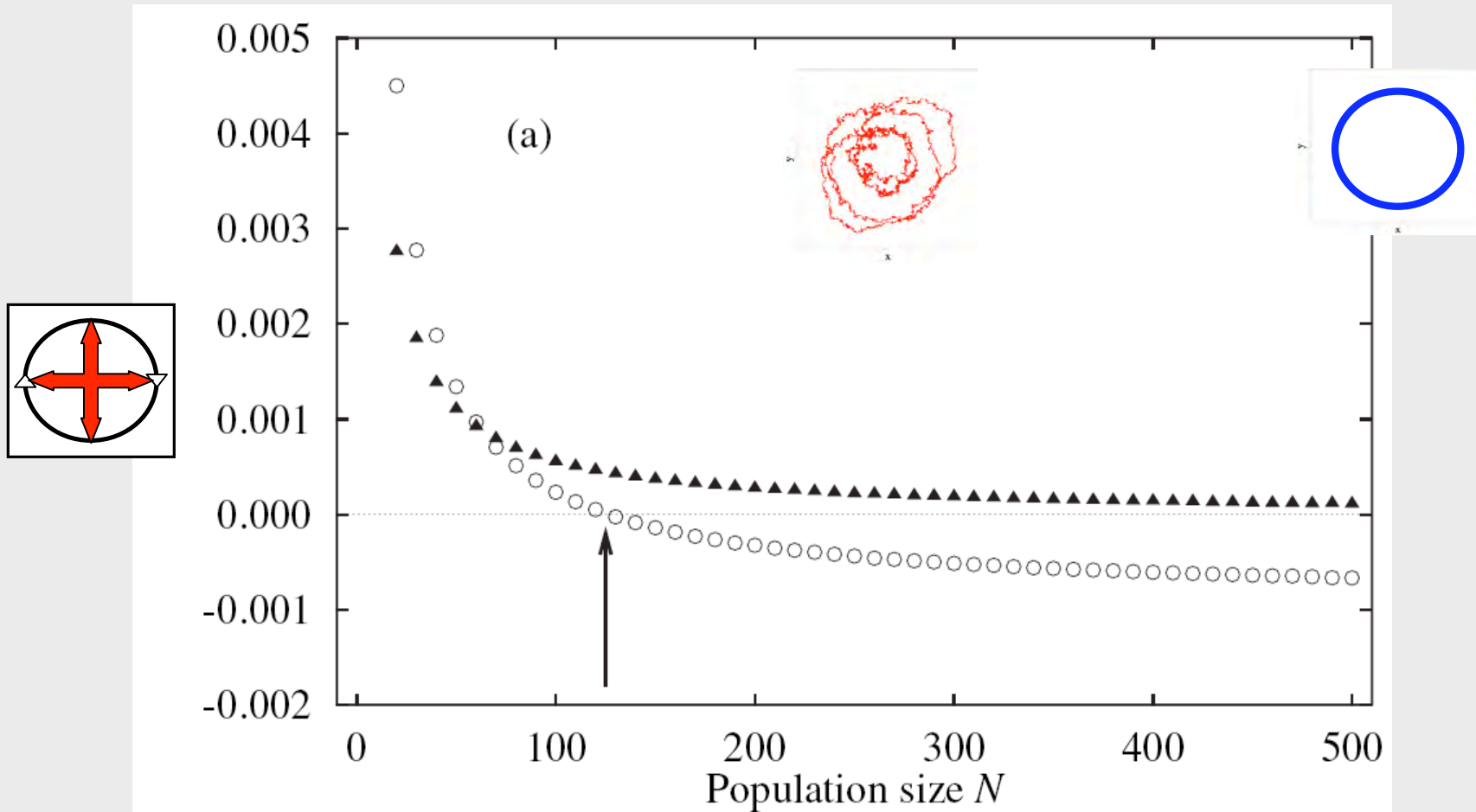
$$\dot{x} = x(\pi_A - \langle \pi \rangle)$$



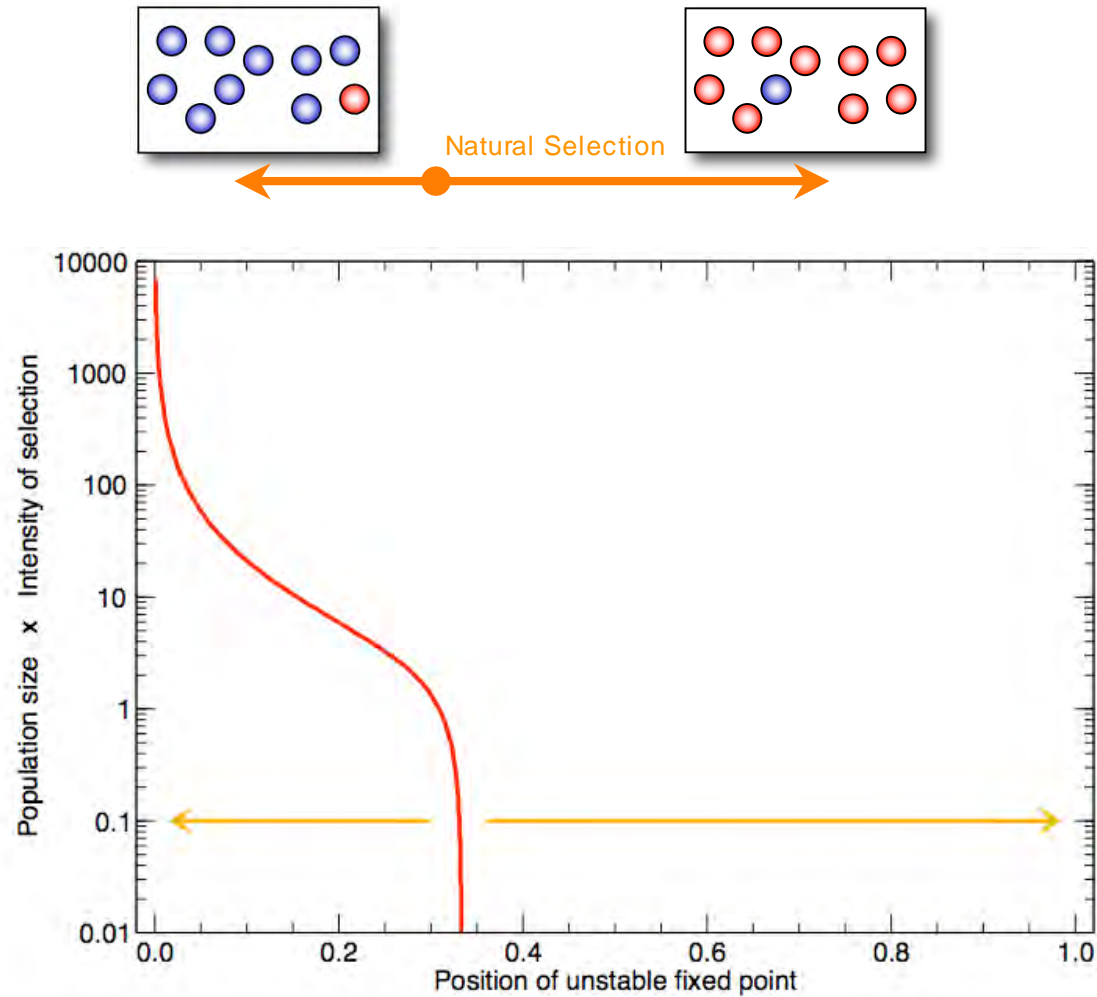
$$\dot{x} = x \frac{\pi_A - \langle \pi \rangle}{\langle \pi \rangle}$$



# Matching pennies in finite populations



# The 1/3 rule for large populations



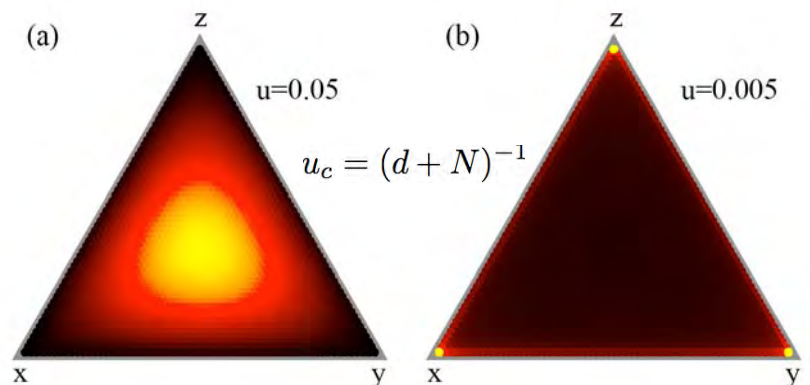
# Generalization to more strategies

- Use  $d$  instead of 2 strategies

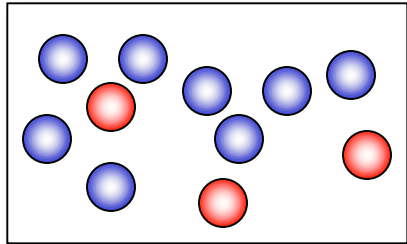
$$\dot{\rho}(\mathbf{x}) = - \sum_{k=1}^{d-1} \frac{\partial}{\partial x_k} \rho(\mathbf{x}) a_k(\mathbf{x}) + \frac{1}{2} \sum_{j,k=1}^{d-1} \frac{\partial^2}{\partial x_k \partial x_j} \rho(\mathbf{x}) b_{jk}(\mathbf{x})$$

$$b_{jk}(\mathbf{x}) = \frac{1}{N} \left[ -T_{jk}(\mathbf{x}) - T_{kj}(\mathbf{x}) + \delta_{jk} \sum_{l=1}^d T_{jl}(\mathbf{x}) + T_{lj}(\mathbf{x}) \right]$$

$$a_k(\mathbf{x}) = \sum_{j=1}^d T_{jk}(\mathbf{x}) - T_{kj}(\mathbf{x})$$



## 4. The Fermi process



A **B** player  
updates its  
strategy

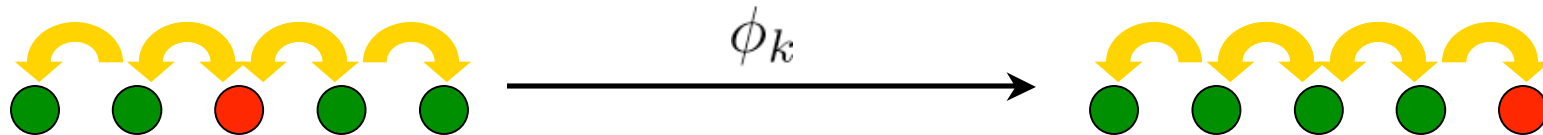
$$T_{i,i+1} = \frac{N-i}{N} \frac{i}{N} \underbrace{\frac{1}{1 + e^{-\beta(\pi_A - \pi_B)}}}_{\text{Probability to switch to A}}$$

The role  
model is **A**

$$T_{i,i-1} = \frac{i}{N} \frac{N-i}{N} \frac{1}{1 + e^{+\beta(\pi_A - \pi_B)}}$$

## Fixation probabilities

---



$$\phi_k = T_{k,k-1}\phi_{k-1} + T_{k,k+1}\phi_{k+1} + T_{k,k}\phi_k$$

$$\phi_k = \frac{\sum_{i=0}^{k-1} \prod_{j=1}^i T_{j,j-1}/T_{j,j+1}}{\sum_{i=0}^{N-1} \prod_{j=1}^i T_{j,j-1}/T_{j,j+1}}$$

## Ratio of transition probabilities

---

$$\phi_k = \frac{\sum_{i=0}^{k-1} \prod_{j=1}^i T_{j,j-1}/T_{j,j+1}}{\sum_{i=0}^{N-1} \prod_{j=1}^i T_{j,j-1}/T_{j,j+1}}$$

## Fixation probability for the Fermi process

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$$\phi_k = \frac{\sum_{i=0}^{k-1} \prod_{j=1}^i \frac{T_{j,j-1}}{T_{j,j+1}}}{\sum_{i=0}^{N-1} \prod_{j=1}^i \frac{T_{j,j-1}}{T_{j,j+1}}}$$

General equation



## Fixation probabilities for arbitrary N and $\beta$

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$$\pi_A - \pi_B = u \cdot i + v$$

 Frequency dependence

### 1. Frequency independent, $u=0$

$$\phi_k = \frac{1 - r^{-k}}{1 - r^{-N}}$$

$$r = e^{2\beta v}$$

### 2. Frequency dependent

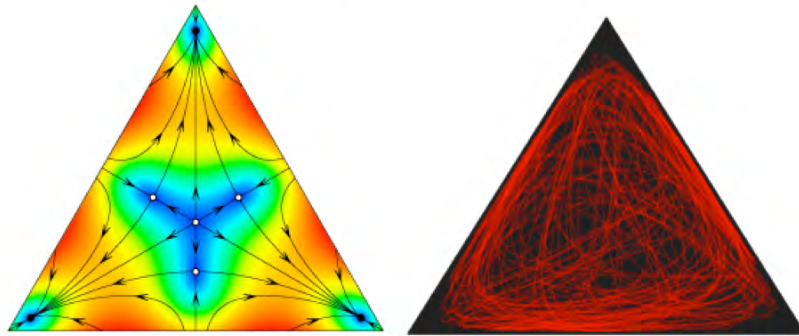
$$\phi_k = \frac{\operatorname{erf} [\xi_k] - \operatorname{erf} [\xi_0]}{\operatorname{erf} [\xi_N] - \operatorname{erf} [\xi_0]}$$

$$\xi_k = \sqrt{\frac{\beta}{u}}(ku + v)$$

# Take home message

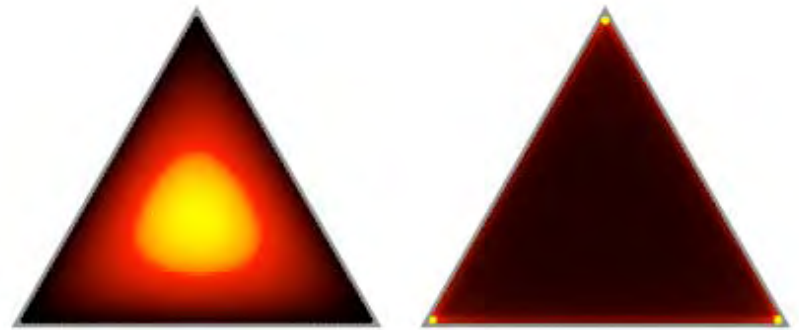
- Large populations  
**deterministic**

$$\dot{x}_i = x_i (\pi_i - \langle \pi \rangle)$$



- Small populations  
**stochastic**

$$P_i^{t+1} = \sum_j P_j^t T_{j \rightarrow i}$$



Unified framework

Convenient process

$$\dot{x}_i = x_i (\pi_i - \langle \pi \rangle) + \frac{b_i(x_j)}{\sqrt{N}} \xi$$

$$T_{i,i+1} = \frac{N-i}{N} \frac{i}{N} \frac{1}{1 + e^{-\beta(\pi_A - \pi_B)}}$$

# Thanks

- Collaborators

J.C. Claussen (Kiel)

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L.A. Imhof (Bonn)

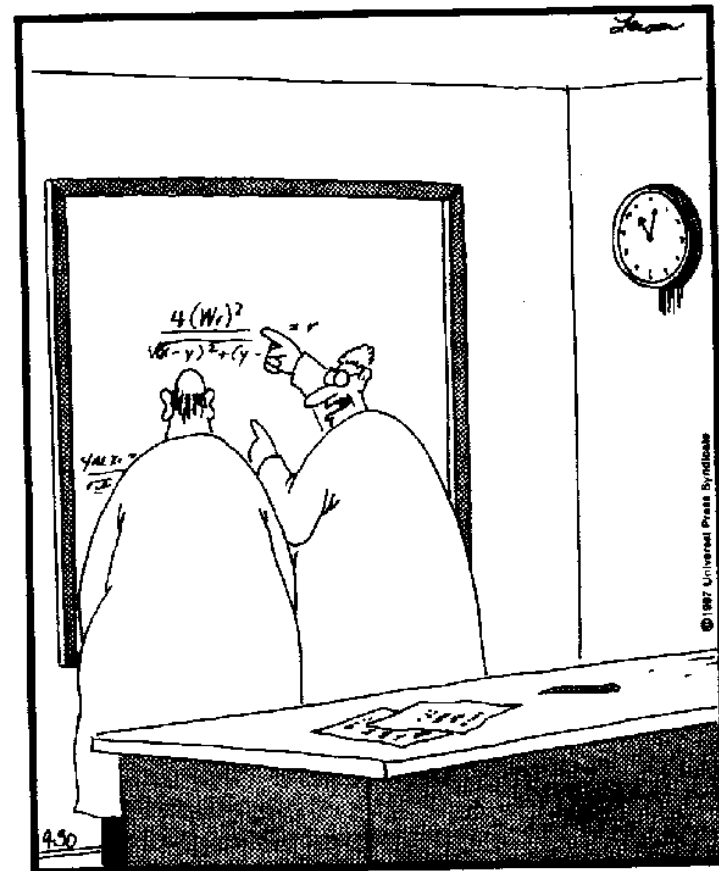
M.A. Nowak (Harvard)

J.M. Pacheco (Lisbon)

- Group at PED

- Funding

Deutsche Akademie der  
Naturforscher Leopoldina  
Halle (Saale)



"Yes, yes, I know that, Sidney . . . everybody knows that!  
. . . But look: Four wrongs squared, minus two wrongs to the  
fourth power, divided by this formula, do make a right."