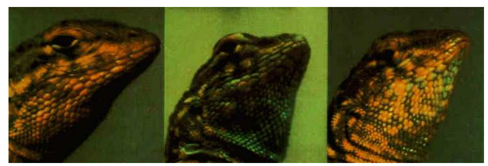
C | A | U
Christian-Albrechts-Universität zu Kiel
Mathematisch-
Naturwissenschaftliche Fakultät

Finite-size Fluctuations and Finite-Size Effects in Coevolutionary Dynamics

Unifying Approches from Evolutionary Game Theory Lay Further Grounds for Quantitative Modelling of Multi-Agent-Systems.

Jens Christian Claussen (Kiel)

Arne Traulsen and Christoph Hauert (Harvard)



1. Evolutionary game theory

   How to describe coevolutionary dynamics in finite populations?

2. Approach: Use microscopic equations of motion directly

   Derive a mean-field theory in finite populations

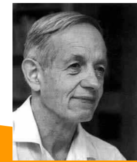
3. Consequences: Drift reversal in asymmetric conflicts

   Extinction, oscillations or coexistence?

Claussen & Traulsen, Phys. Rev. E 71, 025101 (R) (2005)
Traulsen, Claussen & Hauert, Phys. Rev. Lett. 95, 238701 (2005)

Traulsen, Claussen & Hauert, Phys. Rev. E 74, 011901 (July 2006)





Prisoner's dilemma.

Two strategies: Cooperate, Defect.

Payoff matrix elements: remitted years of prison.

	C	D
C	3 ,3	0 ,5
D	5 ,0	1 ,1

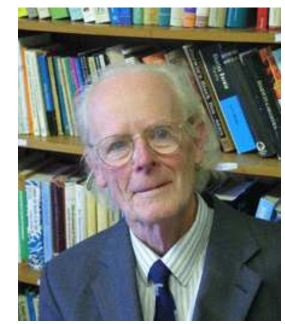
Mutual cooperation pays.

Characterizes many economic and strategic conflict situations.

Nash equilibrium: reached if a single agent's move cannot improve

Evolutionary game theory:

- System of N individuals (agents), defined by
  - a set of strategies 1...k
  - a co-evolutionary fitness ("payoff") matrix $k \times k$



Evolutionary game theory: Maynard Smith 1973

- Agents within a population interact according to the payoff matrix
- Agents reproduce at a rate increasing with the payoff
- Mutation can be included

C | A | U
Christian-Albrechts-Universität zu Kiel
Mathematisch-
Naturwissenschaftliche Fakultät

Main questions:

- Deterministic limit for N$\rightarrow\infty$. What happens in finite populations?
- How do ("microscopic") evolutionary processes and replicator equations relate?
- Is the discretization stochasticity simply Gaussian noise?
- Are there consequences or predictions?

Methods and Approach:

- Use explicitely ("microscopic") dynamics: Moran process and Local update
- Analyze meanfield ("macroscopic") equations of motion
- Perform N$\rightarrow\infty$ explicitely yielding replicator-type equations
- What are the dynamical 1/N corrections?

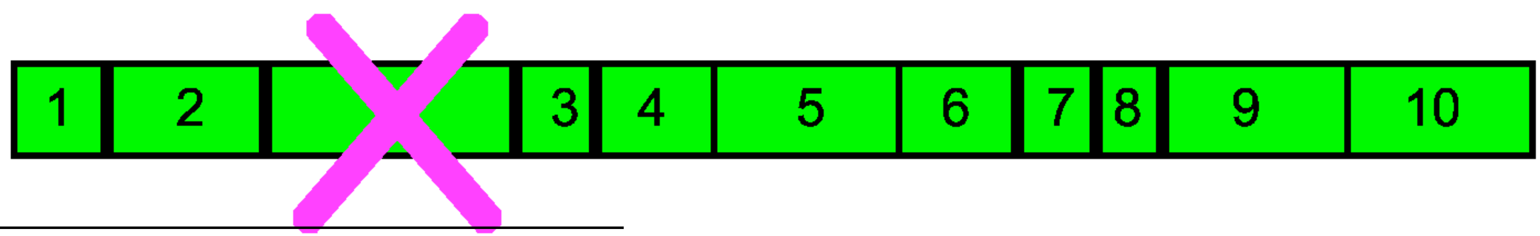
The Moran Process[a,b]

Christian-Albrechts-Universität zu Kiel
Mathematisch-Naturwissenschaftliche Fakultät

- N individuals
- Choose an individual at random proportional to its payoff

- Create identical offspring

- Remove one random individual



[a] Moran, The Statistical Processes of Evolutionary Theory (1962).

[b] M.A. Nowak, A. Sasaki, C. Taylor, and D. Fudenberg, Nature 428, 646 (2004),

Moran evolution dynamics in 2×2 games

C | A | U
Christian-Albrechts-Universität zu Kiel
Mathematisch-Naturwissenschaftliche Fakultät

- Arbitrary payoff matrix:

$P = \begin{pmatrix} a & b \\ c & d \end{pmatrix}$. E.g.: $P_{\rm c} = \begin{pmatrix} a & a \\ c & c \end{pmatrix}$, $P_{\rm CG} = \begin{pmatrix} 0 & 1 \\ 1 & 0 \end{pmatrix}$, $P_{\rm PD} = \begin{pmatrix} 3 & 0 \\ 5 & 1 \end{pmatrix}$

- Frequency-dependent[a] Moran[b] process:

Every agent interacts with a representative sample of the population:

$$\begin{aligned} \pi^A(i) &= \frac{a(i-1)+b(N-i)}{N-1} \\ \pi^B(i) &= \frac{c\,i+d(N-1-i)}{N-1}, \end{aligned}$$

With probability $\pi^A(i)/\langle\pi\rangle$, a copy of an A agent replaces a randomly chosen individual.

[a] M.A. Nowak, A. Sasaki, C. Taylor, and D. Fudenberg, Nature 428, 646 (2004),

[b] P.A.P. Moran, *The Statistical Processes of Evolutionary Theory*, Oxford (1962).

Fluctuations around the average strategy: 4 cases

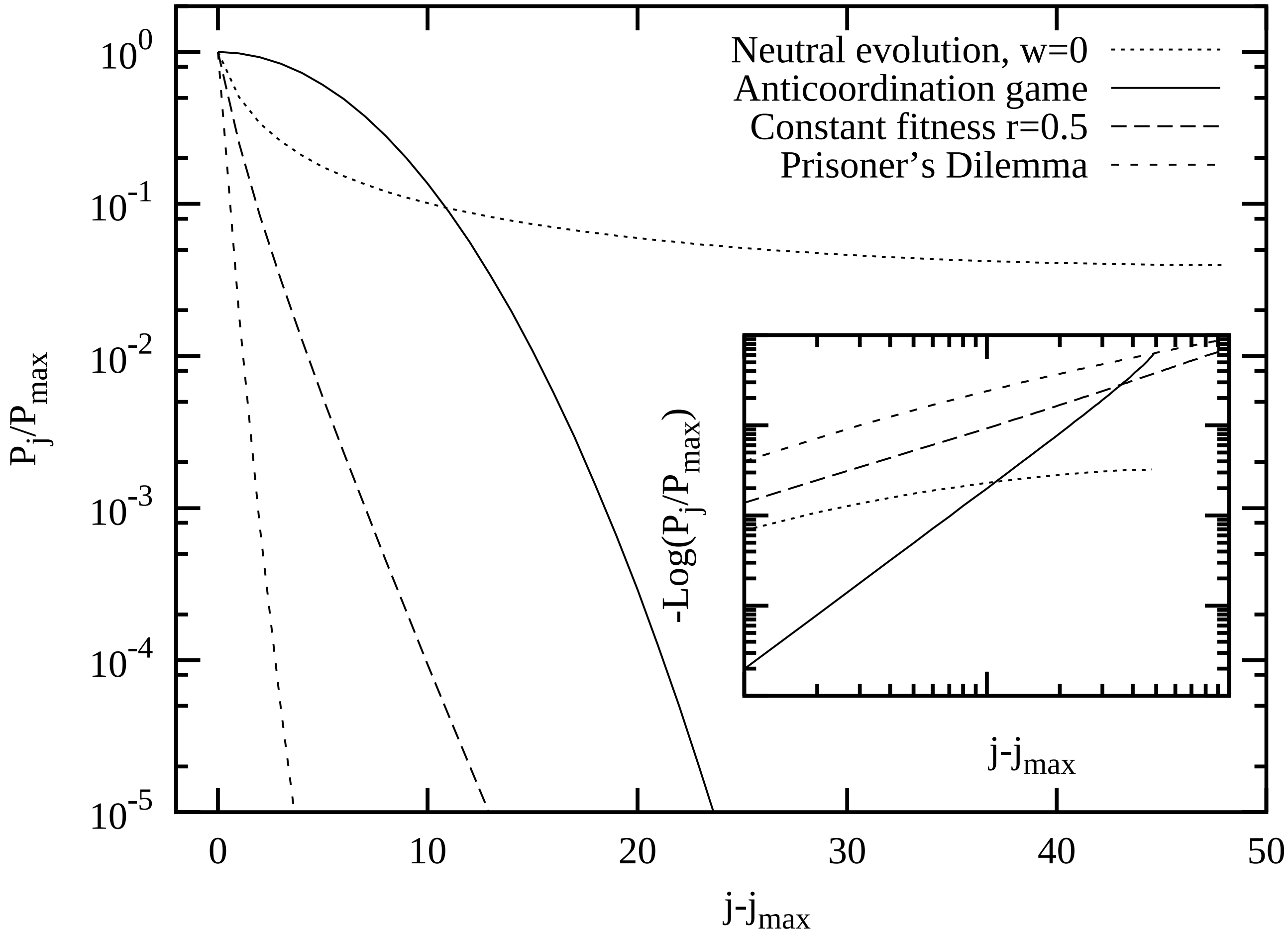
C | A | U
Christian-Albrechts-Universität zu Kiel
Mathematisch-Naturwissenschaftliche Fakultät

For the Moran process, the strategy distribution is generated only by the inherent stochasticity of the finite population. – 4 representative cases:

Payoff matrix	Distribution	$\exp(-bx^\gamma)$	Nash equilibrium
$a = b = c = d$ Neutral evolution	$P_i \sim \frac{1}{i(N-i)}$		(Min. at $i = N/2$)
$a = b < c = d$ constant fitness	$\simeq$ exponential	$\gamma = 0.87$	drift $\rightarrow i = 0$
$P_{AC} = \begin{pmatrix} 0 & 1 \\ 1 & 0 \end{pmatrix}$	$\simeq$ binomial	$\gamma = 2.07$	$i = N/2$ “internal”
$P_{PD} = \begin{pmatrix} 5 & 0 \\ 3 & 1 \end{pmatrix}$		$\gamma = 0.63$	$i = 0$ “external”

Moran process of 2×2 games: Stationary distribution

C | A | U
Christian-Albrechts-Universität zu Kiel
Mathematisch-
Naturwissenschaftliche Fakultät



$P \approx \exp(-bx^\gamma)$, $\gamma_{AC} = 2.06$, $\gamma_{CF} = 0.87$, $\gamma_{PD} = 0.63$.

Corresponds to random motion in an anharmonic potential

Christian-Albrechts-Universität zu Kiel
Mathematisch-
Naturwissenschaftliche Fakultät

Moran process and local update: Meanfield dynamics
. . . and finite-size scaling: Fokker-Planck equation

Local update: a local microscopic process

- Selection mechanism in the Moran process:
  requires perfect global information via $\langle \pi_i \rangle$
- Local update: Microscopic process entirely based on local information
  A randomly chosen individual b compares its payoff to the payoff of a (also randomly chosen).
  It switches with probability

$$p_{b\to a} = \frac{1}{2} + \frac{w}{2}\frac{\pi_a - \pi_b}{\Delta\pi_{\max}},$$

- Transition matrix:

$$T^+(i) = \left(\frac{1}{2} + \frac{w}{2}\frac{\pi_i^A - \pi_i^B}{\Delta\pi_{\max}}\right)\frac{i}{N}\frac{N-i}{N}$$

$$T^-(i) = \left(\frac{1}{2} + \frac{w}{2}\frac{\pi_i^B - \pi_i^A}{\Delta\pi_{\max}}\right)\frac{i}{N}\frac{N-i}{N}.$$

Derivation of the FPE

Christian-Albrechts-Universität zu Kiel
Mathematisch-Naturwissenschaftliche Fakultät

Master equation
$$P^{\tau+1}(i) - P^{\tau}(i) = P^{\tau}(i-1)T^{+}(i-1) - P^{\tau}(i)T^{-}(i) + P^{\tau}(i+1)T^{-}(i+1) - P^{\tau}(i)T^{+}(i)$$

For $N \gg 1$: Taylor expansion of T and $\rho(x,t) = N\,P^{\tau}(i)$ $\quad (x = i/N,\, t = \tau/N)$

Fokker-Planck equation:

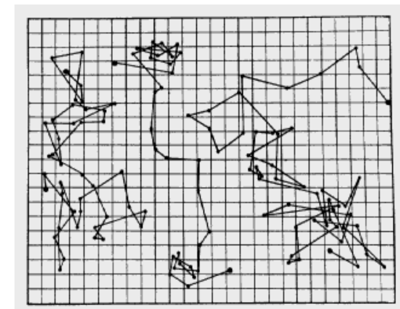
$$\frac{d}{dt}\rho(x,t) = -\frac{d}{dx}\left[a(x)\rho(x,t)\right] + \frac{1}{2}\frac{d^2}{dx^2}\left[b^2(x)\rho(x,t)\right]$$

with $a(x) = T^{+}(x) - T^{-}(x)$ and $b(x) = \sqrt{\frac{1}{N}\left[T^{+}(x) + T^{-}(x)\right]}$.

- Corresponding Langevin equation: $\dot{x} = a(x) + b(x)\xi$
- What about the limit $N \to \infty$?

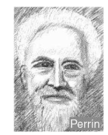
The Raleigh particle: an analogy from physics

- Stochastic motion of a large particle (mass M)



driven by collisions with small particles (mass m)[a]

Einstein/Perrin: $D = \frac{RT}{6\pi\nu a N_A}$



($R =$ gas constant, $\nu =$ viscosity, $a =$ particle radius)

- Motion of the large particle for large (but finite) M/m:

Can be described with a Fokker Planck equation

with a fluctuations term scaling with $\sqrt{m/M}$ (van Kampen)

- For $M/m \to \infty$ again a deterministic trajectory is obtained.

Microscopic processes and replicator equations

Christian-Albrechts-Universität zu Kiel
Mathematisch-Naturwissenschaftliche Fakultät

For $N \to \infty$, $b(x)$ vanishes with $\frac{1}{\sqrt{N}}$, yielding deterministic equations:

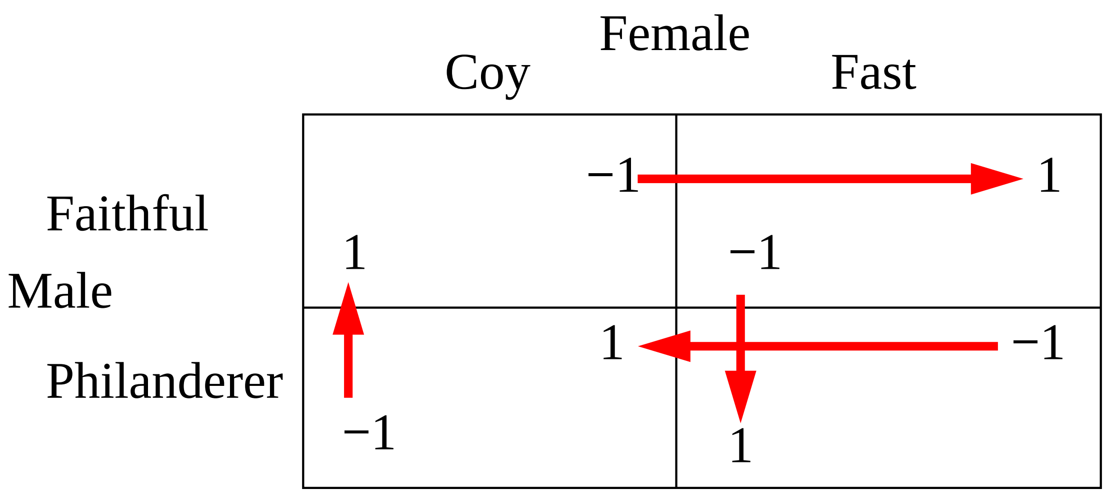
Microscopic process	Deterministic equation
Moran process $p_{B\to A} = \frac{1-w+w\,\pi_i^A}{1-w+w\,\langle\pi_i\rangle}$	Adjusted replicator equation $\dot{x} = x\frac{\pi^A(x)-\langle\pi(x)\rangle}{\Gamma+\langle\pi_i\rangle}$
Local update $p_{B\to A} = \frac{1}{2} + \frac{w}{2}\frac{\pi_i^A-\pi_i^B}{\Delta\pi_{\max}}$	(ordinary) Replicator equation $\dot{x} = \kappa x\left(\pi^A(x) - \langle\pi(x)\rangle\right)$

Consequences:

- Speed of evolution: Moran process fixates faster
- Drift reversal in asymmetric conflicts

Consequences:
Drift reversal in asymmetric conflicts

Dawkins Battle of the Sexes



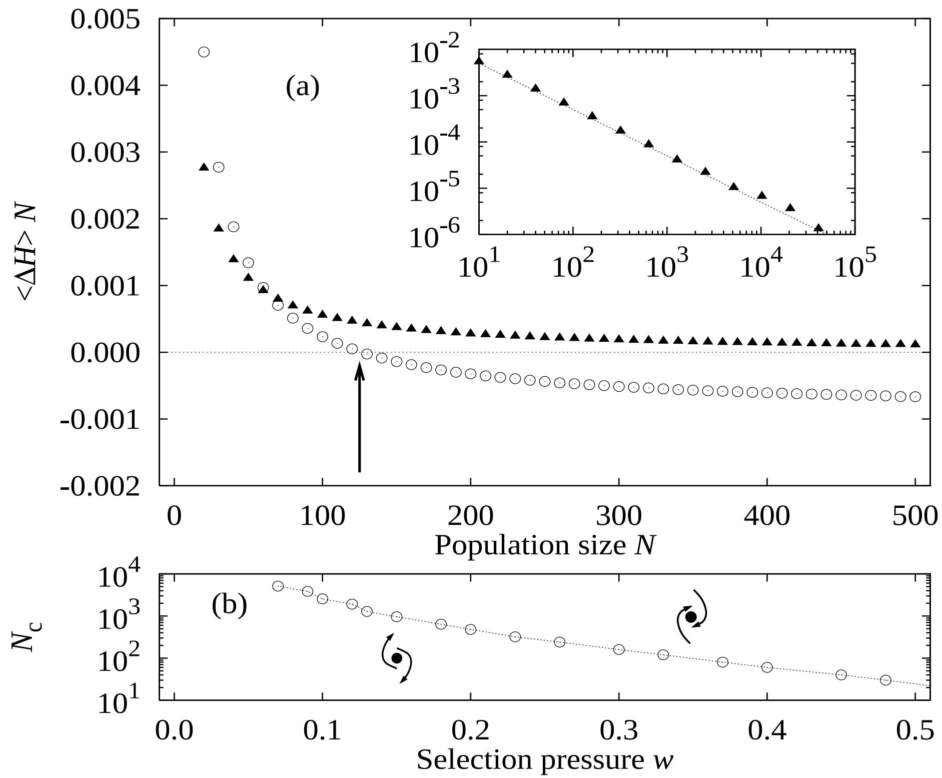
$(\pi_♂, \pi_♀)$	$A_♀$	$B_♀$
$A_♂$	$(+1, -1)$	$(-1, +1)$
$B_♂$	$(-1, +1)$	$(+1, -1)$

- If males (♂) are philanderers ($B_♂$), it pays for females (♀) to be coy ($A_♀$),
- Insisting on a long courtship period to make males invest more in the offspring.
- However, once most males are faithful ($A_♂$), fast females are favored ($B_♀$) avoiding the costs of courtship.
- Subsequently, the male investment into the offspring is no longer justified, philanderers are again favored ($B_♂$), and the cycle continues. Corresponds to ‘Matching pennies”.

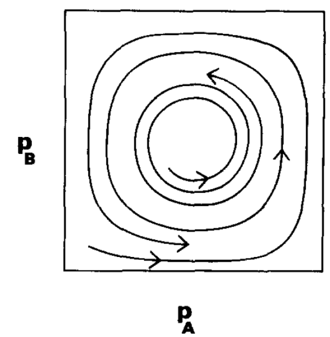
Qualitatively different dynamics for adjusted/standard replicator equations!

Finite-size influence in asymmetric conflicts

C | A | U
Christian-Albrechts-Universität zu Kiel
Mathematisch-Naturwissenschaftliche Fakultät

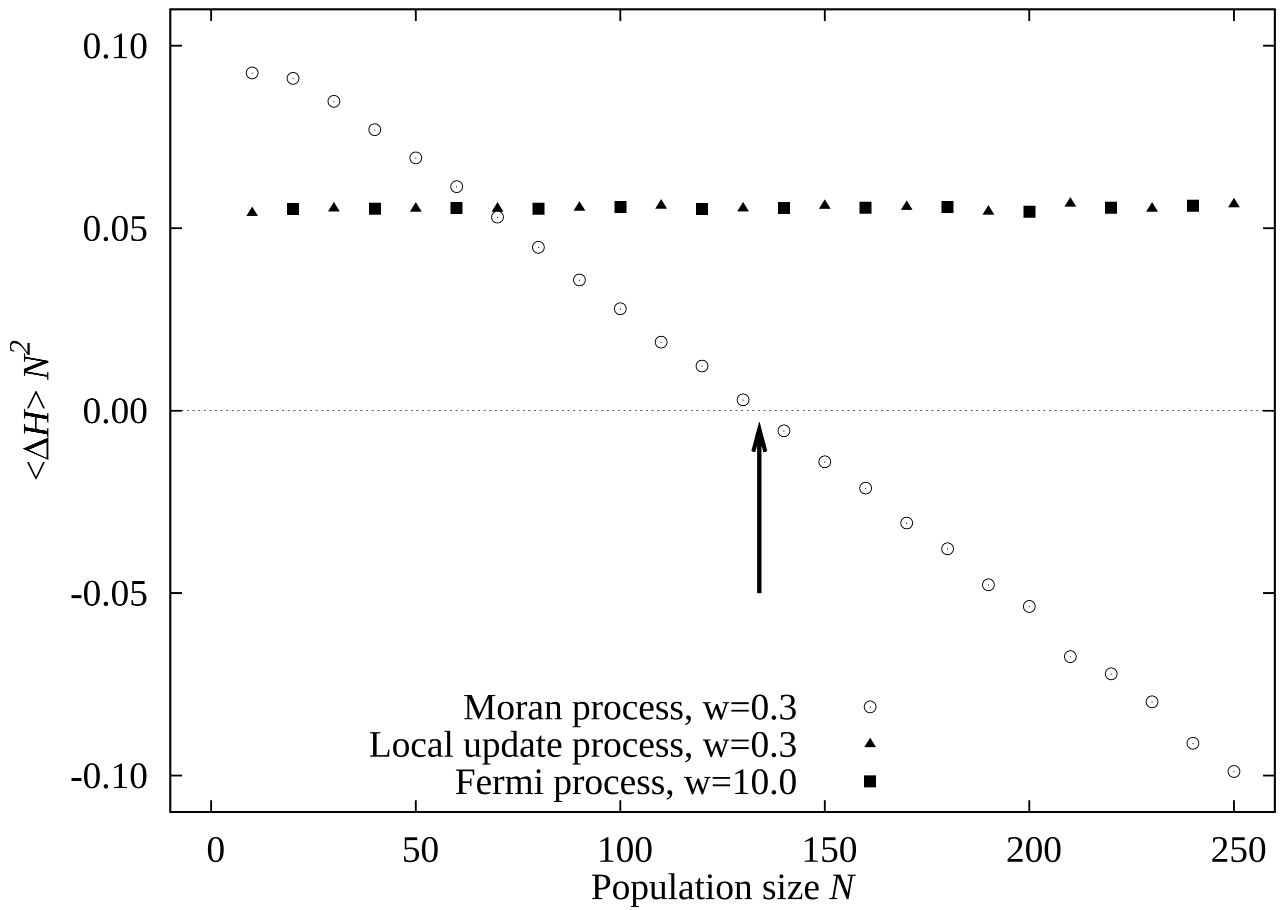


Battle of the sexes for finite population size N. $(1 - w =$ backgr. fitn.)



- Replicator dynamics ($N \to \infty$) predicts eternal oscillations... Spurious result!
- Local update (▲): System spirals to the absorbing boundaries $\langle \Delta H \rangle > 0$.
- Moran process (○): For $N > N_c$ a drift reversal occurs towards the Nash eq. $(\frac{1}{2}, \frac{1}{2})$.
- In finite populations, the Battle of the Sexes always comes to rest.

Drift reversal for Moran, Local, and Fermi process



(Claussen & Traulsen, Proc. “Potentials of Complexity Science”, Budapest 2006)

Microscopic processes and replicator equations

Moran process

$$p^+ = \frac{1-w+w\pi_i^A}{1-w+w\langle\pi_i\rangle}$$
$$p^- = \frac{1-w+w\pi_i^B}{1-w+w\langle\pi_i\rangle}$$

$0 \le w \le 1$

$$T^\pm = p^\pm \frac{i}{N}\frac{N-i}{N}$$

In the $N \to \infty$ limit:

$$\dot{x} = \frac{wx(1-x)(\pi_x^A - \pi_x^B)}{1-w+w\langle\pi(x)\rangle}$$

adjusted replicator equation

Local update

$$p^+ = \frac{1}{2} + \frac{w}{2}\frac{\pi_i^A - \pi_i^B}{\Delta\pi_{\max}}$$
$$p^- = \frac{1}{2} + \frac{w}{2}\frac{\pi_i^B - \pi_i^A}{\Delta\pi_{\max}}$$

$0 \le w \le 1$

$$T^\pm = p^\pm \frac{i}{N}\frac{N-i}{N}$$

$$\dot{x} = \frac{wx(1-x)(\pi_x^A - \pi_x^B)}{\Delta\pi_{\max}}$$

replicator equation

Fermi process

$$p^+ = \frac{1}{1+\mathrm{e}^{-w(\pi_i^A - \pi_i^B)}}$$
$$p^- = \frac{1}{1+\mathrm{e}^{-w(\pi_i^B - \pi_i^A)}}$$

$0 \le w \le \infty$

$$T^\pm = p^\pm \frac{i}{N}\frac{N-i}{N}$$

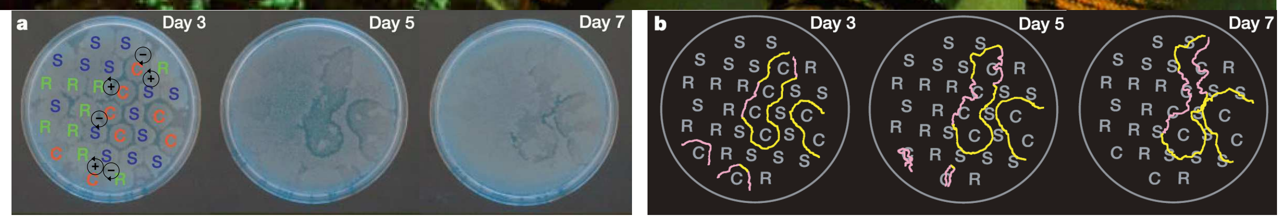
$$\dot{x} = x(1-x)\tanh\left(\frac{w}{2}(\pi_x^A - \pi_x^A)\right)$$

(Traulsen, Nowak, Pacheco PRE 74)

Cyclic coevolution in biology

- Cyclical games: Lizards “playing” a rock-scissors-paper game[c]

- r-p-s in E.coli[d]



in vitro and in vivo (mice)

Cyclic coevolution promotes diversity.

---

[c] Zamudio & Sinervo, PNAS 97, 14427 (2000), Sinervo & Lively, Nature 380, 240 (1996).

[d] Kerr, Riley, Feldman, Bohannan, Nature 418, 171-174 (2002); Kirkup & Riley, Nature 428, 412 (2004)

Summary

- Fluctuations can be nontrivially broadened: $\approx \exp(-bx^{\gamma})$
- Systematic approach:
  Moran process $\longrightarrow$ adjusted replicator equation
  Local update $\longrightarrow$ ordinary replicator equation
- First-order corrections have the form of a Fokker-Planck equation
  Noise is multiplicative and frequency-dependent!
- Different scenarios result! – Finite-size dependent drift reversal.
  For finite populations, the Battle of the sexes always comes to rest.

Claussen & Traulsen PRE 71, 025101(R) (2005), Traulsen & Claussen PRE 70, 046128 (2004)
Traulsen, Claussen & Hauert PRL 95, 238701 (2005) & PRE 74, 011901 (July 2006)