Evolutionary dynamics in finite populations: Oscillations, diffusion, and drift reversal

Jens Christian Claussen

1. Lizards, E.coli, Mice, ... and Rock-Paper-Scissors.
2. Evolutionary game theory. Coevolution.
   How to describe coevolutionary dynamics in finite populations?
   Mean-field theory in finite populations:
   Derive replicator equations (and FPEs for internal fluctuations).

Cyclic coevolution: Side-blotched Lizards (*Uta stansburiana*)

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

Orange-throated males establish large territories holding several females. Can be invaded by yellow-striped males (“sneakers”), not contributing to defense.

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- Once sneakers are rare, i.e. **blue-striped** have taken over, it is advantageous to defend a **large territory holding several females**.

This allows for cyclic invasion **O → Y → B → O**

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Cyclic games

<table>
<thead>
<tr>
<th></th>
<th>Scissors</th>
<th>Paper</th>
<th>Rock</th>
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<tbody>
<tr>
<td>Scissors</td>
<td></td>
<td>Paper</td>
<td>Rock</td>
</tr>
<tr>
<td>Paper</td>
<td>beats rock</td>
<td></td>
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<tr>
<td>Rock</td>
<td>beats scissors</td>
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<th>-1</th>
<th>1</th>
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Cyclic coevolution: E.coli “play” RPS in vitro

Cyclic coevolution: E.coli “play” RPS in vitro ... and in mice!


“Chemical warfare between microbes promotes biodiversity”
(Czarán, Hoekstra, Pagie, PNAS 99, 786 (2001))

RSP replicator dynamics - same, but small interaction cost - spatial system
Stability of evolutionary cycles: Possible mechanisms?

What determines the (in)stability of the fixed point (=coexistence)?

- **Payoff** (fitness) values (for non-zero-sum games)
- **Spatial** structure (stabilizes coexistence)
- **Finiteness** of population (usually destabilizes coexistence)
- **Dynamics of the** (microscopic) interaction process
  (and resulting replicator equations)
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What happens in reality?

- E.coli (mixed system): Fixates to border.
- Lizards: damped oscillations → stable fixed point.
- Social strategies: Many strategies do coexist.
- Mating (& parental care) behaviour: Fixates to border (typically).
Main questions:

- How do ("microscopic") evolutionary processes and replicator equations \( \dot{x} = x(1 - x)(\pi^A(x) - \pi^B(x)) \) relate?
- Deterministic limit for \( N \to \infty \). What happens in finite populations?
- Is the discretization stochasticity simply Gaussian noise?

Methods and Approach:

- Use explicitly ("microscopic") dynamics: Moran process and Local update
- Analyze meanfield ("macroscopic") equations of motion
  - Perform \( N \to \infty \) explicitly yielding replicator-type equations
  - What are the dynamical \( 1/N \) corrections?
Microscopic processes: Moran process and local update
The frequency-dependent Moran Process$^{ab}$

- N individuals
- Choose an individual at random proportional to its payoff
- Create identical offspring
- Remove one random individual

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$^b$ M.A. Nowak, A. Sasaki, C. Taylor, and D. Fudenberg, Nature 428, 646 (2004),
Moran evolution dynamics in $2 \times 2$ games

Arbitrary payoff matrix:

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

Frequency-dependent\(^a\) Moran\(^b\) process:

Every agent interacts with a representative sample of the population:

$$\pi^A(i) = \frac{a(i - 1) + b(N - i)}{N - 1},$$

$$\pi^B(i) = \frac{c i + d(N - 1 - i)}{N - 1},$$

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),

Local update: a local microscopic process

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

Pure “2-particle” interaction

- Transition matrix:
  
  $$T^+(i) = \left( \frac{1}{2} + \frac{w}{2} \frac{\pi_i^A - \pi_i^B}{\Delta \pi_{\text{max}}} \right) i \frac{N - i}{N}$$
  $$T^-(i) = \left( \frac{1}{2} + \frac{w}{2} \frac{\pi_i^B - \pi_i^A}{\Delta \pi_{\text{max}}} \right) i \frac{N - i}{N}.$$
Meanfield dynamics
... and finite-size scaling: Fokker-Planck equation
Derivation of the FPE

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 \( \rho(x, t) = N P^\tau(i) \)  
\( x = i/N, t = \tau/N \)

Fokker-Planck equation:

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

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

- Corresponding Langevin equation: \( \dot{x} = a(x) + b(x)\xi \)
- What about the limit \( N \to \infty \)?
For $N \to \infty$, $b(x)$ vanishes with $\frac{1}{\sqrt{N}}$, yielding deterministic equations:

<table>
<thead>
<tr>
<th>Microscopic process</th>
<th>Deterministic equation</th>
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<tbody>
<tr>
<td><strong>Moran process</strong></td>
<td>Adjusted replicator equation</td>
</tr>
<tr>
<td>$p_{B \to A} = \frac{1-w+w \pi_i^A}{1-w+w \langle \pi_i \rangle}$</td>
<td>$\dot{x} = x(1-x) \frac{\pi^A(x) - \pi_i^B}{\Gamma + \langle \pi_i \rangle}$</td>
</tr>
<tr>
<td><strong>Local update</strong></td>
<td>(ordinary) Replicator equation</td>
</tr>
<tr>
<td>$p_{B \to A} = \frac{1}{2} + \frac{w \pi_i^A - \pi_i^B}{2 \Delta \pi_{\text{max}}}$</td>
<td>$\dot{x} = \kappa x (1-x) (\pi^A(x) - \pi^B(x))$</td>
</tr>
<tr>
<td><strong>Fermi process</strong></td>
<td>a nonlinear Replicator equation (TNP)</td>
</tr>
<tr>
<td>$p_{B \to A} = \frac{1}{1+e^{\mp w(\pi_i^A - \pi_i^B)}}$</td>
<td>$\dot{x} = \kappa x (1-x) \tanh(\pi^A(x) - \pi^B(x))$</td>
</tr>
</tbody>
</table>

- Speed of evolution: Moran process fixates faster
- Consequence: Drift reversal in asymmetric conflicts
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Drift reversal in asymmetric conflicts
**Battle of the Sexes** (Richard Dawkins)

- Payoff benefit for a child: \( b = 15 \)
- Total cost of raising an offspring: \(-2c = -20\), covered by both parents (except philanderer males meet fast females)
- Prolonged courtship (coy females insist on) costs both a burden of \(-a = -3\)

<table>
<thead>
<tr>
<th></th>
<th>Female</th>
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<tbody>
<tr>
<td></td>
<td>Coy</td>
<td>Fast</td>
<td></td>
</tr>
<tr>
<td>Faithful Male</td>
<td>2</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>Philanderer</td>
<td>0</td>
<td>15</td>
<td>-5</td>
</tr>
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</table>

The normalized payoff matrix qualitatively preserves the cyclic dominance.
Asymmetric conflicts: BOTS \( P_x = \begin{pmatrix} +1 & -1 \\ -1 & +1 \end{pmatrix} = -P_y \)

Standard replicator equations:

\[
\begin{align*}
\dot{x} &= -2 \, w \, x(1 - x)(2y - 1) \\
\dot{y} &= +2 \, w \, y(1 - y)(2x - 1)
\end{align*}
\]

Constant of motion \( H = -x(1 - x)y(1 - y) \): \( \rightarrow \) Closed trajectories.

Adjusted replicator equations:

\[
\begin{align*}
\dot{x} &= -2 \, \frac{x(1 - x)(2y - 1)}{1 - \frac{w}{w} + (2y - 1)(2x - 1)} \\
\dot{y} &= +2 \, \frac{y(1 - y)(2x - 1)}{1 - \frac{w}{w} - (2y - 1)(2x - 1)}
\end{align*}
\]

\( \dot{H} \leq 0 \). For \( t \to \infty \): Nash eq. \( \left( \frac{1}{2}, \frac{1}{2} \right) \)

Qualitatively different behavior!
Finite-size influence in asymmetric conflicts

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

- 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: when and why?

Claussen (2007), submitted

Again, consider the zero-sum “Battle of the Sexes” with $(+1, -1)$ payoffs. Average drift can be calculated analytically:

Neutral case (payoffs zero): $\langle \Delta H \rangle_{\text{neutral}} = \frac{1}{18N^2}$, drift $\to$ outwards.

Can be overridden by a $o(1/N)$ term $\leftrightarrow \exists N_c$ where sign changes $\leftrightarrow$ “drift reversal”.

Local update (& pairw.comp.), Fermi, ... (quite general class!!!): no drift reversal

Now consider two limits of weak selection!

(Frequency-dependent) Moran process $\Phi_m^A = \frac{1-w+w\pi^A}{1-w+w\langle \pi_m \rangle}$ drift reversal occurs!

(and can be calculated by expanding in $o(w)$ properly, confirming numerics...)

Moran process, linearized at process level, $\Phi_m^A = 1 + w(\pi^A - \langle \pi_m \rangle)$ no drift reversal!

→ For asymmetric conflicts, stability subtly depends on the underlying process.
Drift reversal also in RPS?

- For the zero-sum game with \((+1, -1)\) payoffs drift always goes outwards.
- For \((+1, -s)\) payoffs (and \(s < 1\)) again a drift reversal occurs!

\[
\langle \Delta H \rangle N^2
\]

\(N\) 0 100 200 300 400 500
-0.04 -0.02 0 0.02 0.04

(Claussen & Traulsen 2005/2007)

- Can be calculated **analytically**! – Linear processes (dashed) fit well.
- Drift reversal (due to “cooperative” payoffs) occurs **for all processes** (but \(N_c\) varies)
Coexistence is determined by: Payoffs, spatial structure, dynamics, and population size!
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Systematic approach ("unified theory of coevolutionary processes"): Moran process → adjusted replicator equation
Local update → ordinary replicator equation
Answers an open question asked by John Maynard Smith (1982)!

First-order corrections have the form of a Fokker-Planck equation
Noise is multiplicative and frequency-dependent!
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Different scenarios result! – Finite-size dependent drift reversal.
For finite populations, the Battle of the sexes always comes to rest.

The Raleigh particle: an analogy from physics

Stochastic motion of a large particle \((\text{mass } M)\)

Driven by collisions with small particles \((\text{mass } m)\)\(^a\)

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

\((R = \text{gas constant}, \nu = \text{viscosity}, a = \text{particle radius})\)

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 \(M/m \rightarrow \infty\) again a deterministic trajectory is obtained.

\(^a\) J. B. Perrin, Les Atomes, Paris, Alcan, 1913.
If males (♂) are philanderers (B♂), it pays for females (♀) to be coy (A♀),
If males ($\sigma'$) are philanderers ($B_{\sigma'}$), it pays for females ($\phi$) to be coy ($A_{\phi}$),

Insisting on a long courtship period to make males invest more in the offspring.
If males ($\sigma'$) are philanderers ($B_\sigma'$), it pays for females ($\varphi'$) to be coy ($A_\varphi'$), insisting on a long courtship period to make males invest more in the offspring. However, once most males are faithful ($A_\sigma'$), fast females are favored ($B_\varphi'$) avoiding the costs of courtship.
**Dawkins Battle of the Sexes**

The Battle of the Sexes is a classic example of evolutionary game theory. In this scenario, males and females exhibit different strategies, which can be illustrated in a payoff matrix:

<table>
<thead>
<tr>
<th></th>
<th>Female (Coy)</th>
<th>Female (Fast)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Faithful</td>
<td>1</td>
<td>−1</td>
</tr>
<tr>
<td>Philanderer</td>
<td>−1</td>
<td>1</td>
</tr>
</tbody>
</table>

The payoffs are structured such that if males (\(\sigma\)) are philanderers (\(B_\sigma\)), it pays for females (\(\varphi\)) to be coy (\(A_\varphi\)), insisting on a long courtship period to make males invest more in the offspring. However, once most males are faithful (\(A_\sigma\)), fast females are favored (\(B_\varphi\)) avoiding the costs of courtship. Subsequently, the male investment into the offspring is no longer justified, philanderers are again favored (\(B_\sigma\)), and the cycle continues. Corresponds to ‘Matching pennies’.

Qualitatively different dynamics for adjusted/standard replicator equations!

Corresponding payoff matrix:

<table>
<thead>
<tr>
<th>((\pi_\sigma, \pi_\varphi))</th>
<th>(A_\varphi)</th>
<th>(B_\varphi)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(A_\sigma)</td>
<td>(+1, −1)</td>
<td>(−1, +1)</td>
</tr>
<tr>
<td>(B_\sigma)</td>
<td>(−1, +1)</td>
<td>(+1, −1)</td>
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</table>

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Jens Christian Claussen – p.18/17