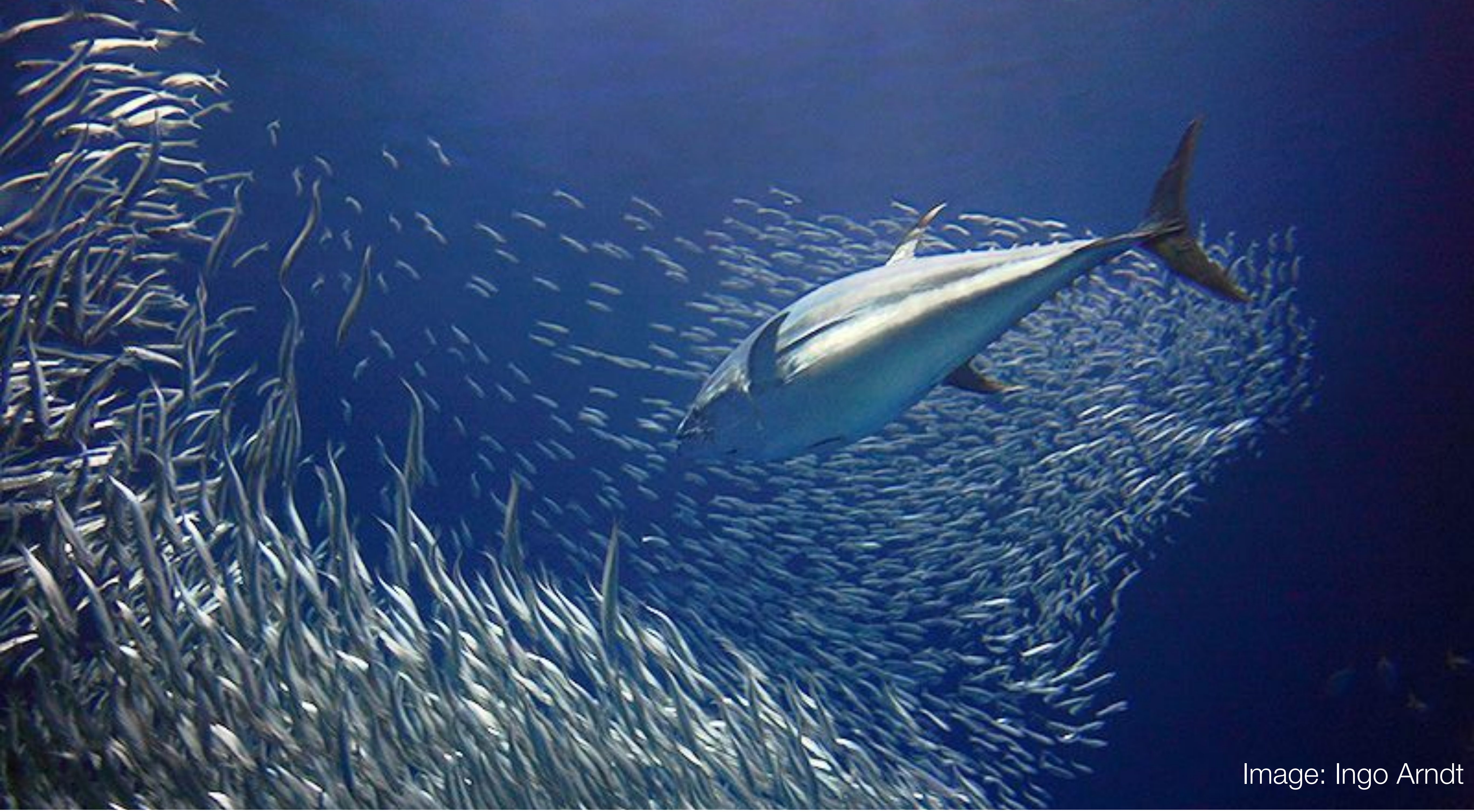
Collective movement and the evolution of cooperation

Vishwesha Guttal
Centre for Ecological Sciences
Indian Institute of Science

Bangalore School on Population Genetics and Evolution

13th March 2018

Amith-Kuma



Self-organization:
Simple math/computational models of collective movement

Inverse problem:
Given real data, can we construct the model?

Evolutionary problem:
Why do organisms show collective movement?

Acknowledgements

- Funding
  - DBT-IISc Partnership Program, CSIR, DBT Ramalingaswamy Fellowship
  - DST-Mathematical Biology Phase II
- **Collaborators**
  - Students: Jaideep Joshi (Phd Student)
  - Simon Levin, Iain Couzin

The dilemma of cooperation

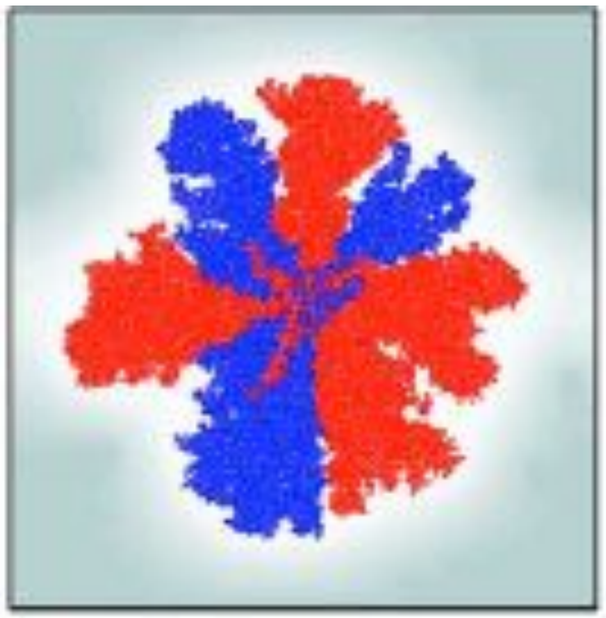
- Cooperation - an action to benefit (b) others at a cost (c) to himself/herself

- Cooperation (C) evolutionarily unstable to invasion by defectors/cheaters (D)

- Pay-offs (w) in a game theoretic framework:
  - D is the Nash-equilibria.
  - C is unstable

	C	D
C	b - c	- c
D	b	0

A solution: spatial assortment



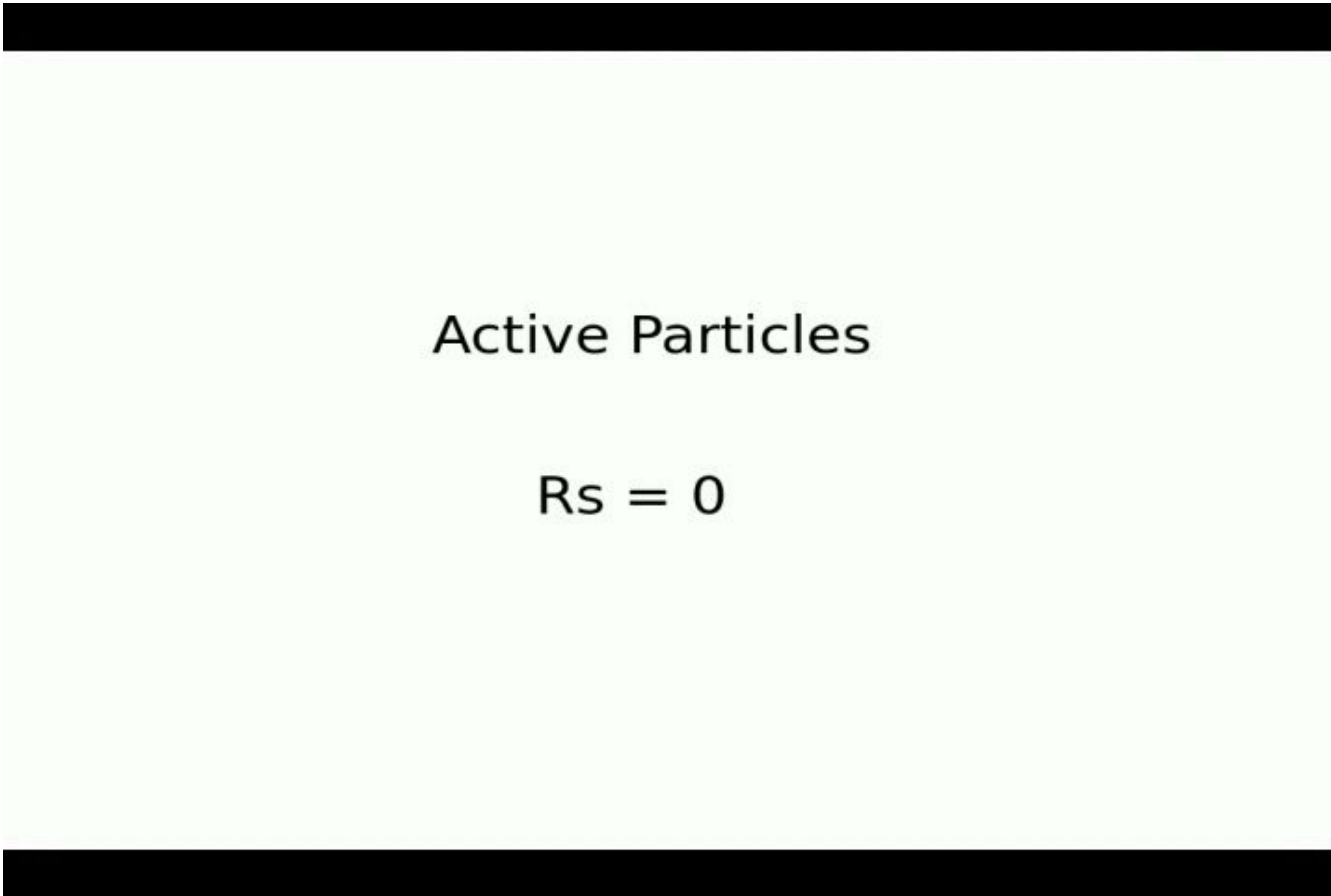
Nadell et al 2010

- If cooperators (red) are spatially assorted, then
  - w(C) > w(D), where w stands for average pay-offs
- Mobility destroys spatial assortment
- We challenge this common assumption
  - Result: Cooperation + Grouping can coevolve in mobile populations, yet maintain assortment

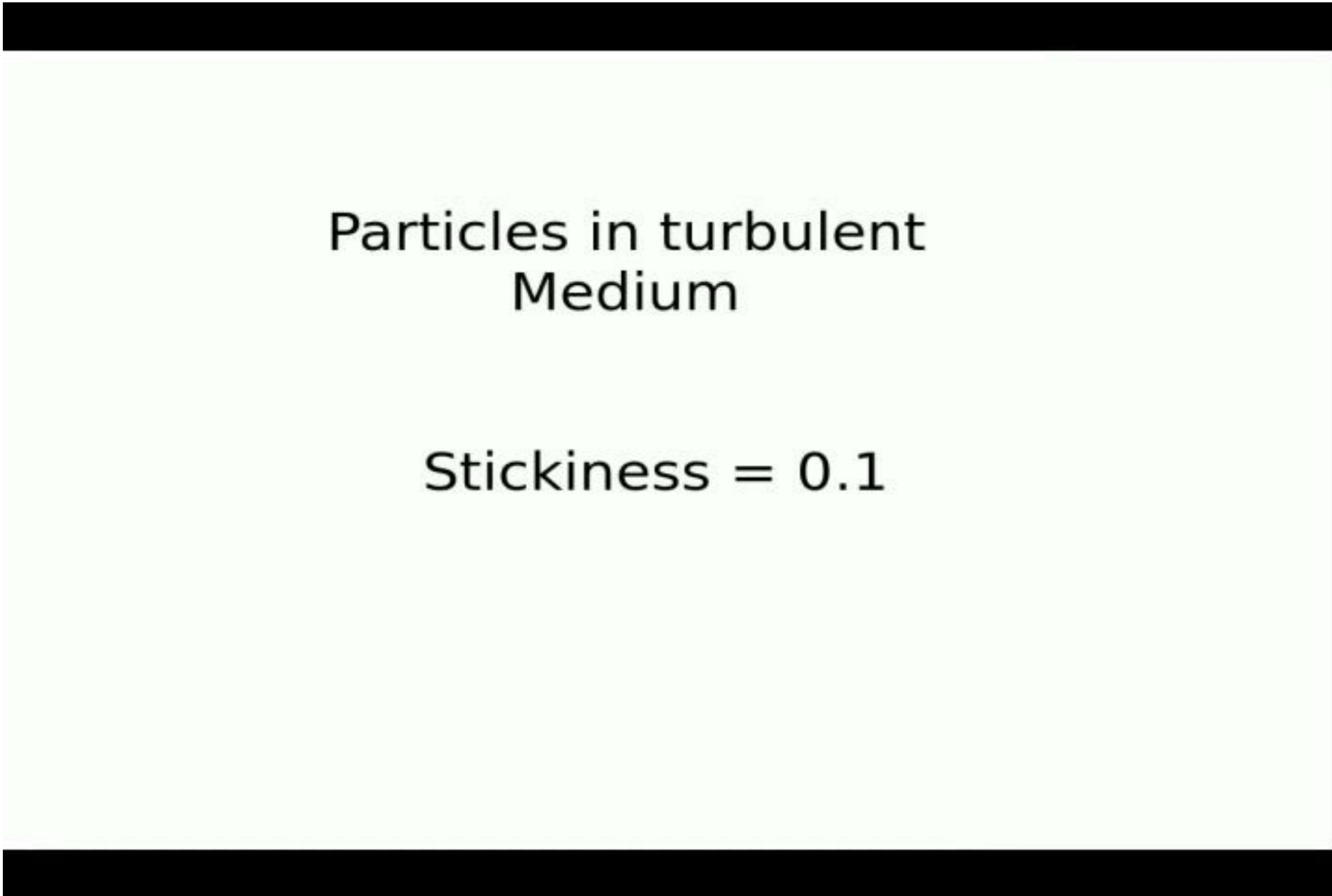
Computational model

- Individual-based (N) & spatially-explicit (two dimensional continuous)
- Each (mobile) individual can have **two costly traits:**Flock (0,1) / Cooperation (0,1)

Simulations of active system



Simulations of passive system

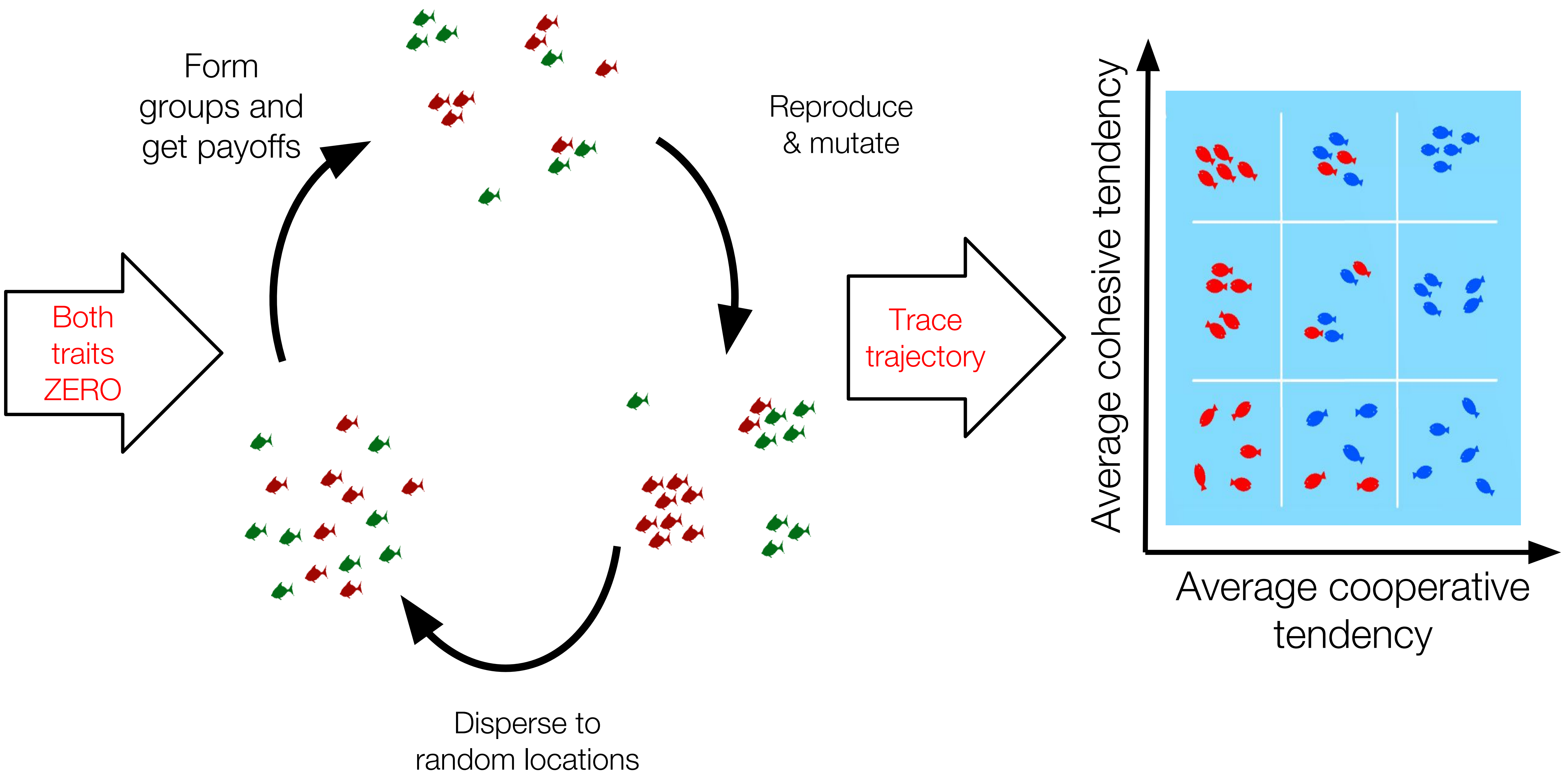


Computational model

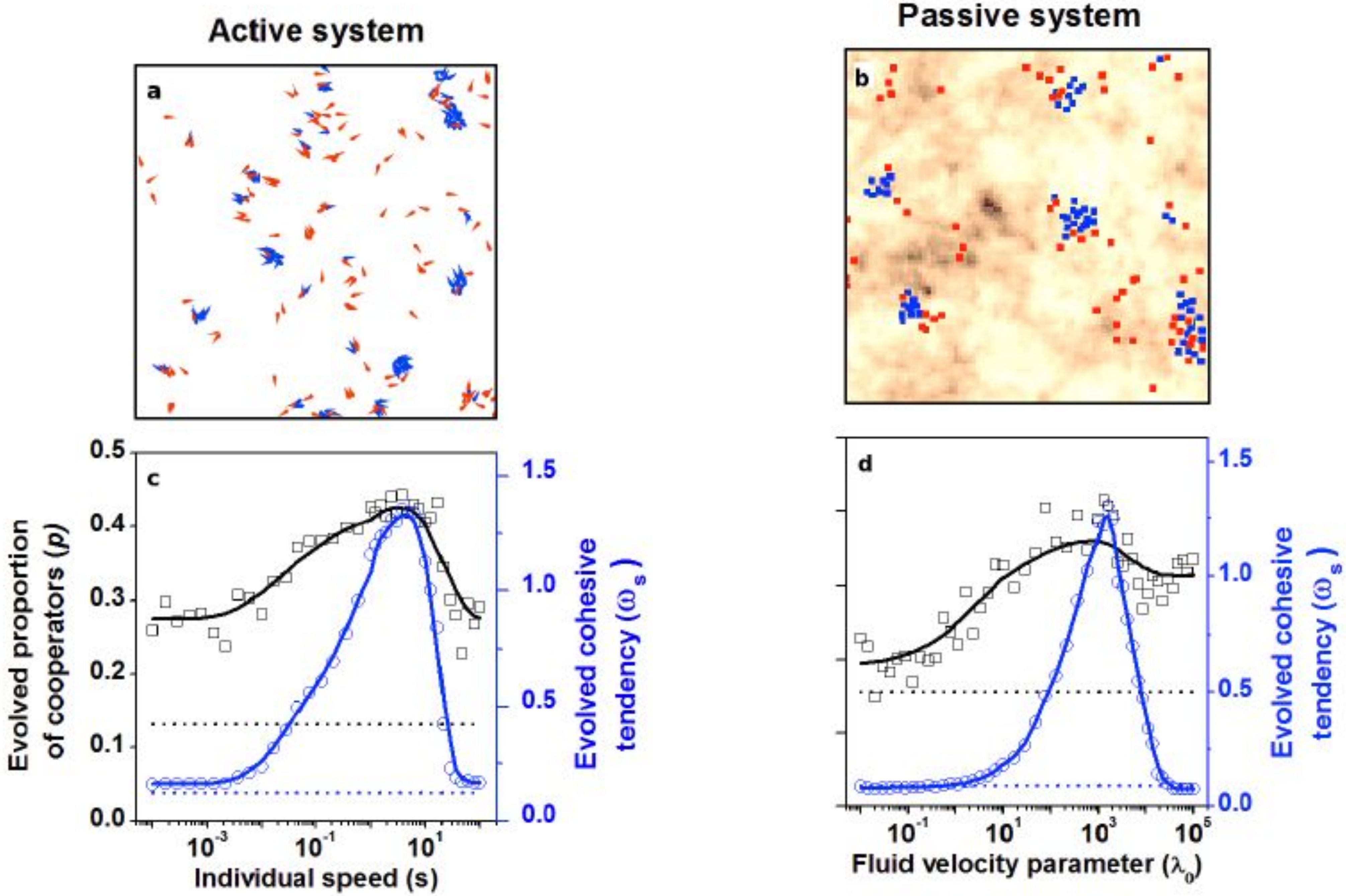
- Individual-based (N) & spatially-explicit (two dimensional continuous)
- Each (mobile) individual can have **two costly traits:**Flock (0,1) / Cooperation (0,1)
- **Four trait combinations** – more complicated pay-off matrix
  - Solitary Defectors (0, 0) [Least costly]
  - Solitary Cooperators (0,1) [Intermediate cost]
  - Flocking Defectors (1,0) [Intermediate cost]
  - Flocking Cooperators (1,1) [Costliest trait combination, but potential for high benefits]
- **In well-mixed populations**: Solitary defector is evolutionarily stable strategy

Trace evolutionary trajectory

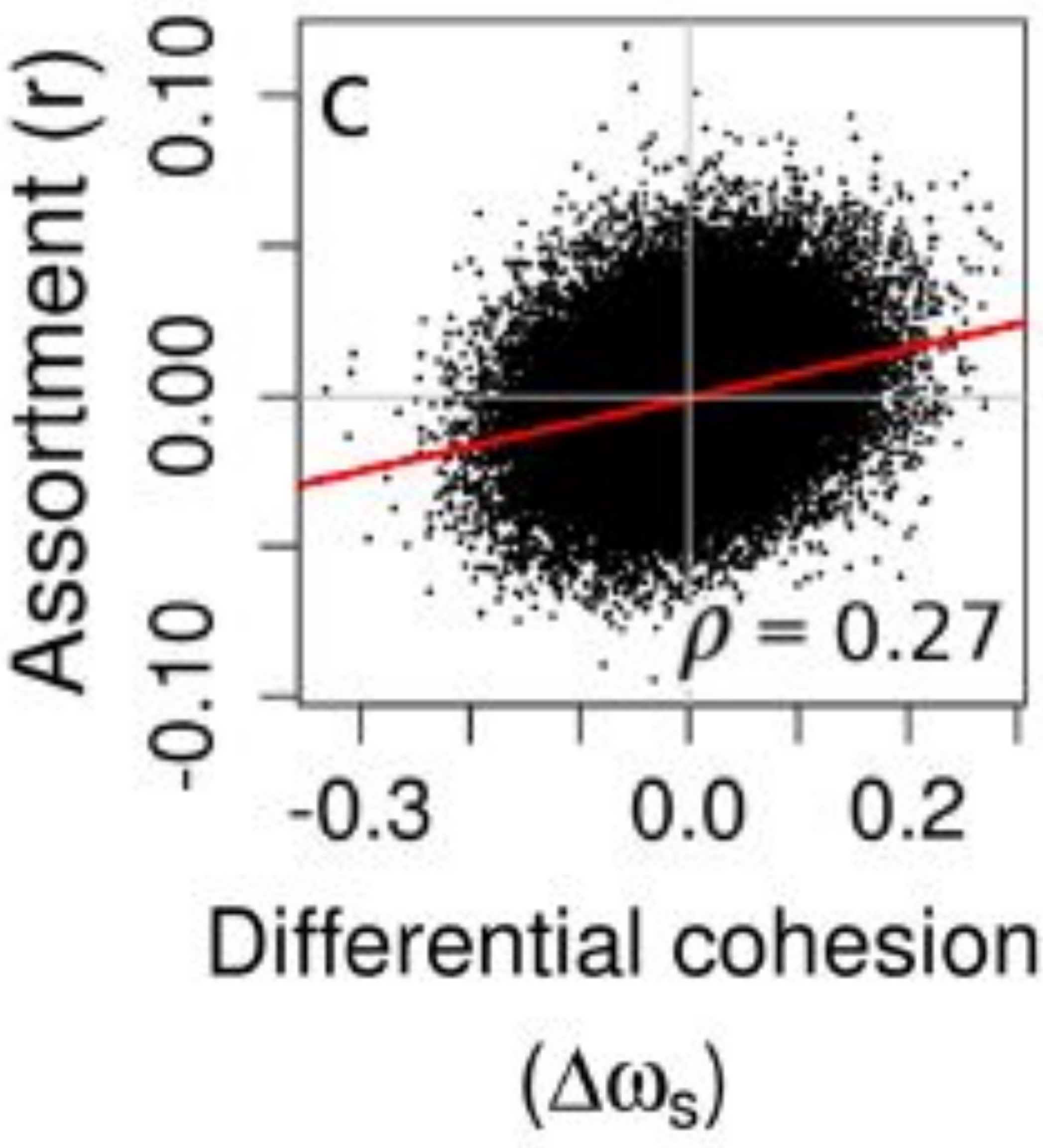
Simulate group formation, reproduction, mutation and dispersal

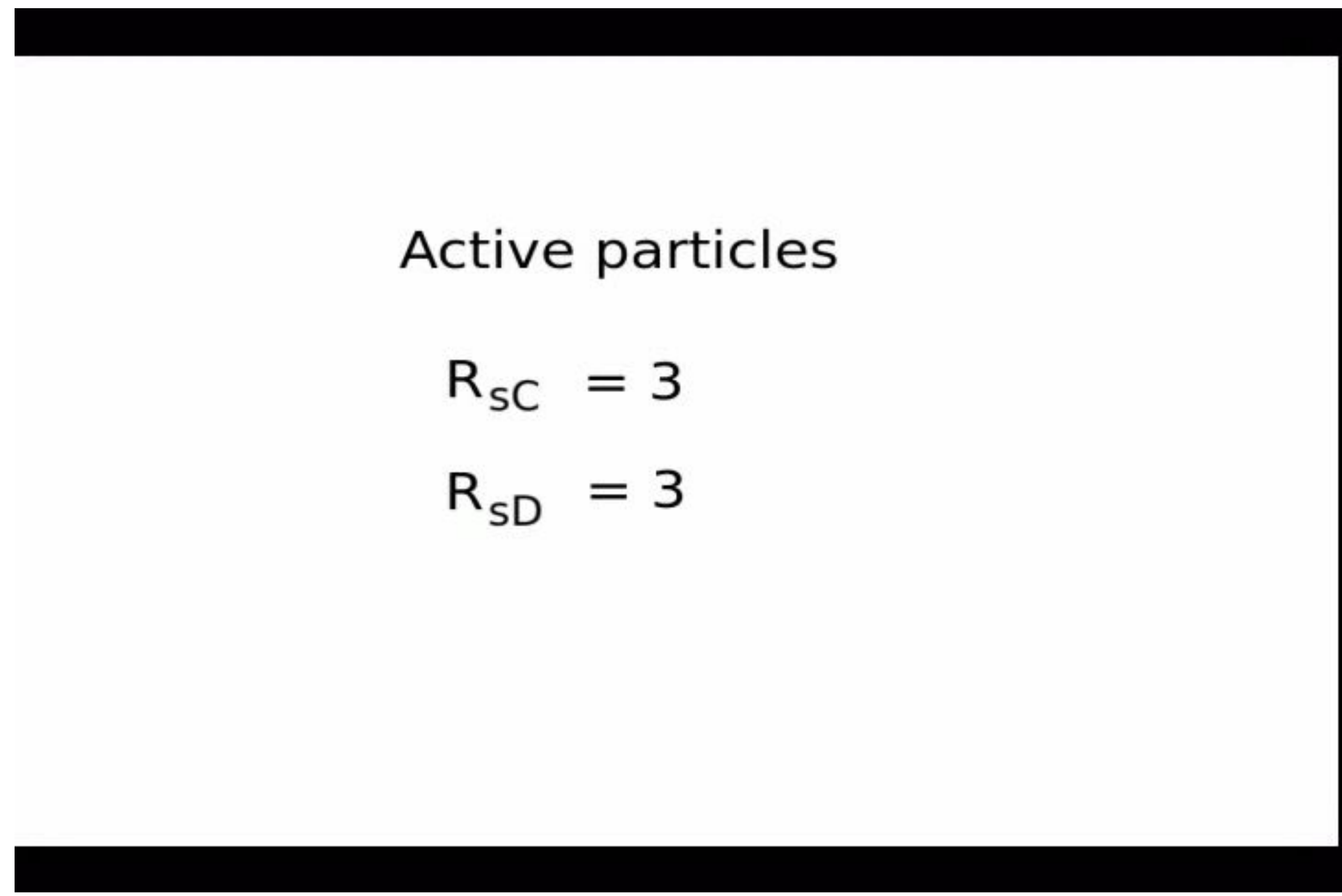


Emergence of flocking and cooperation in mobile populations

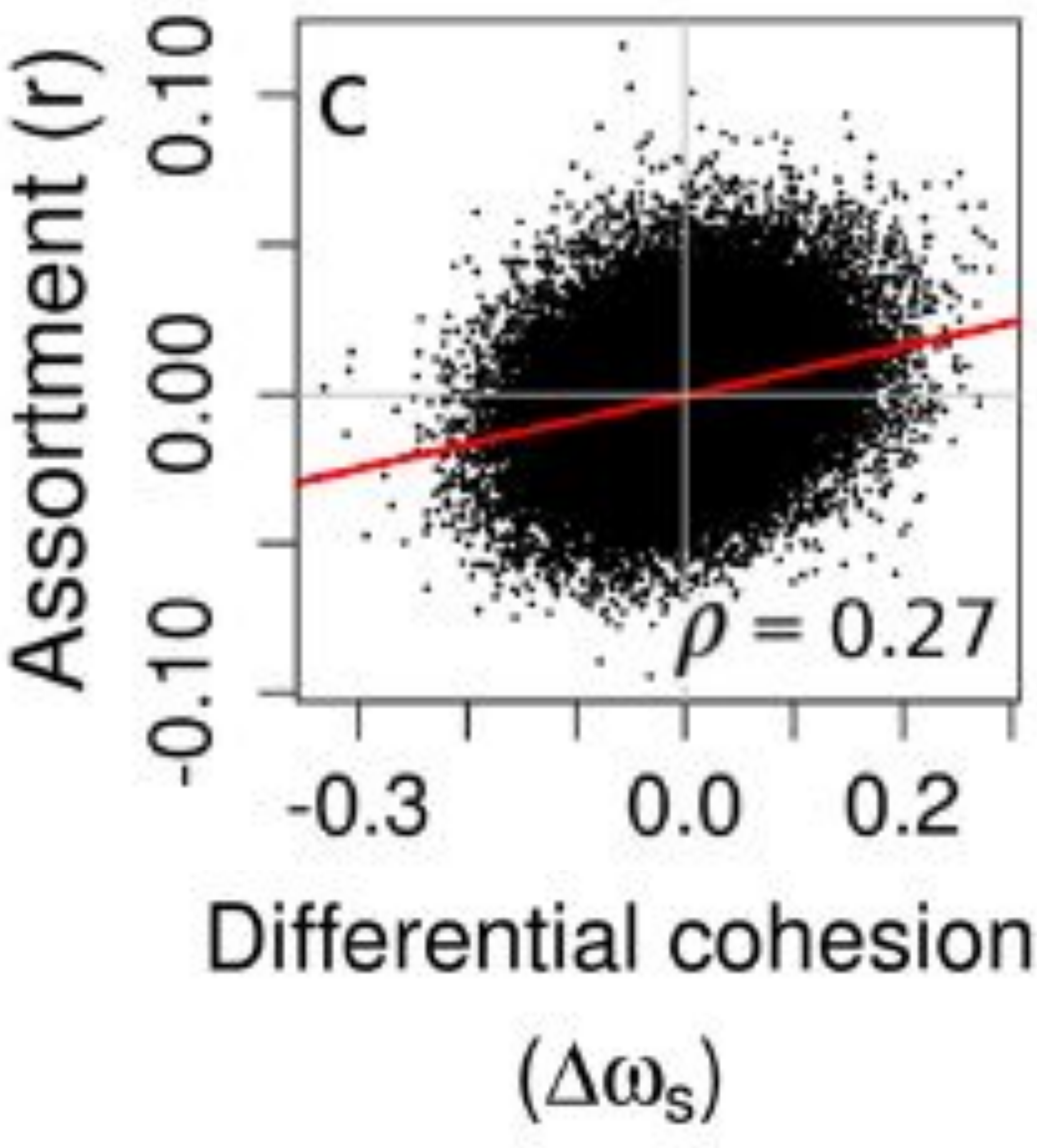


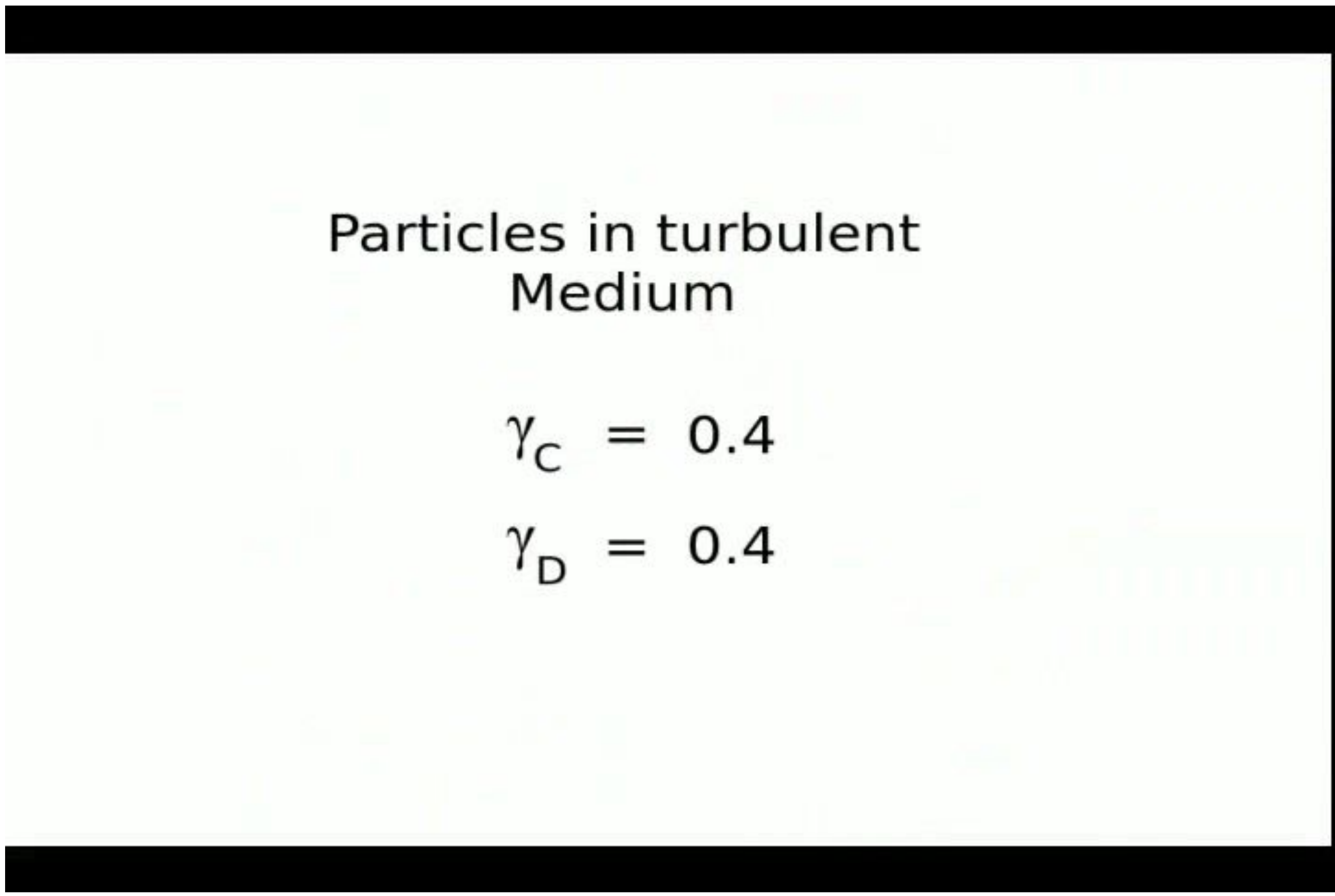
Assortment via differential adhesion





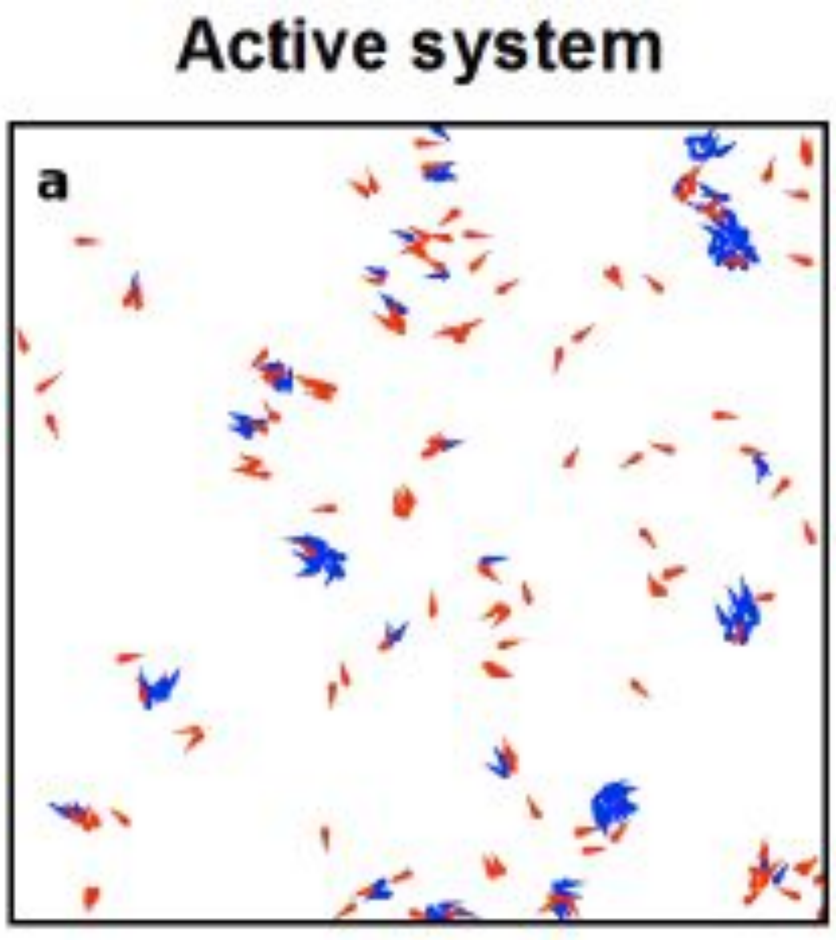
Assortment via differential adhesion





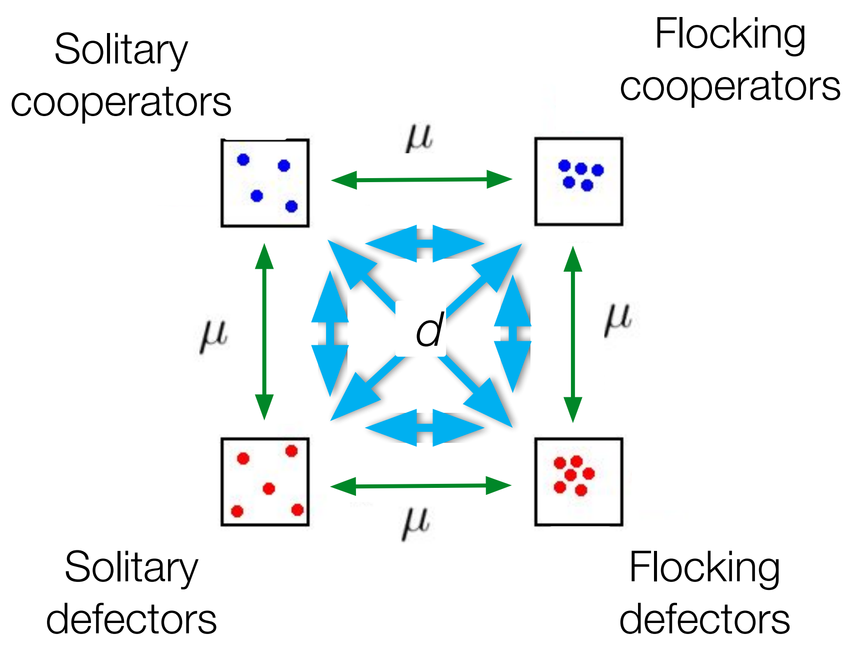
Multi-level selection interpretation

- ‘Within-group’ selection against cooperation.
- Between group selection for cooperations.
- Consistent with inclusive fitness interpretation



Analytical model

- Consider sub-populations and compute their average pay-offs
  - Flocking cooperators (p_f);
  - Solitary cooperators (p_s);
  - Total flocking individuals (q)
  - Total cooperators (p)



- Assume all groups of same size, well mixing within groups, etc.

- **Stochastic coupled replicator equations,** via Master & Fokker-Planck equations, accounting for stochasticity in transitions between states

Analytical mutation-selection-drift model

$$\begin{bmatrix} dp_t \\ dp_s \\ dq \end{bmatrix} = \frac{d}{V_0} \begin{bmatrix} -\left(c + \frac{b}{qN}\right) p_t (1 - p_t) \\ -c p_s (1 - p_s) \\ q(1-q)\left(p_t\left(b - \frac{b}{qN} - c\right) + c p_s - c_s\right) \end{bmatrix} dt$$

Selection

$$+ \mu \begin{bmatrix} 1 - 2p_t + \frac{1-q}{q}(p_s - p_t)\left(1 - \frac{1}{qN}\right) \\ 1 - 2p_s + \frac{q}{1-q}(p_t - p_s)\left(1 - \frac{1}{(1-q)N}\right) \\ 1 - 2q \end{bmatrix} dt$$

$$+ \sqrt{\frac{1}{N}} \begin{bmatrix} 0 & \frac{1-p_t}{q} & 0 & -\frac{p_t}{q} \\ \frac{1-p_s}{1-q} & 0 & -\frac{p_s}{1-q} & 0 \\ 0 & 1 & 0 & 1 \end{bmatrix} \begin{bmatrix} \quad \boldsymbol{G} \quad \end{bmatrix} d\boldsymbol{W}$$

Analytical mutation-selection-drift model

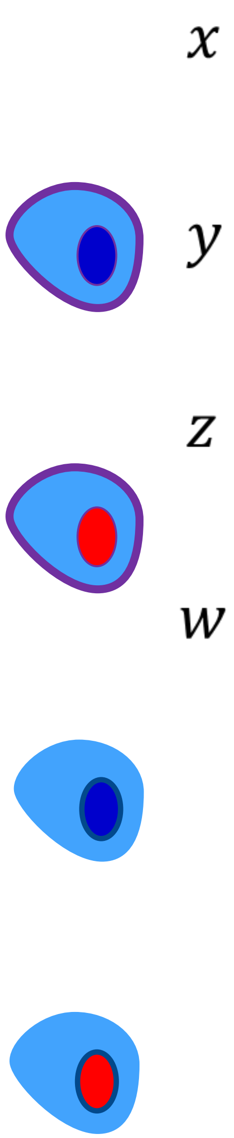
$$\begin{bmatrix} dp_t \\ dp_s \\ dq \end{bmatrix} = \frac{d}{V_0} \begin{bmatrix} -\left(c + \frac{b}{qN}\right) p_t (1-p_t) \\ -c p_s (1-p_s) \\ q(1-q)\left(p_t\left(b - \frac{b}{qN} - c\right) + c p_s - c_s\right) \end{bmatrix} dt$$

$$+ \mu \begin{bmatrix} 1 - 2p_t + \frac{1-q}{q}(p_s - p_t)\left(1 - \frac{1}{qN}\right) \\ 1 - 2p_s + \frac{q}{1-q}(p_t - p_s)\left(1 - \frac{1}{(1-q)N}\right) \\ 1 - 2q \end{bmatrix} dt$$

Mutation

$$+ \sqrt{\frac{1}{N}} \begin{bmatrix} 0 & \frac{1-p_t}{q} & 0 & -\frac{p_t}{q} \\ \frac{1-p_s}{1-q} & 0 & -\frac{p_s}{1-q} & 0 \\ 0 & 1 & 0 & 1 \end{bmatrix} \begin{bmatrix} & \boldsymbol{G} & \end{bmatrix} d\boldsymbol{W}$$

Analytical mutation-selection-drift model



$$\begin{bmatrix} dp_t \\ dp_s \\ dq \end{bmatrix} = \frac{d}{V_0}\begin{bmatrix} -\left(c+\frac{b}{qN}\right)p_t(1-p_t) \\ -cp_s(1-p_s) \\ q(1-q)\left(p_t\left(b-\frac{b}{qN}-c\right)+cp_s-c_s\right) \end{bmatrix} dt$$

$$+\mu\begin{bmatrix} 1-2p_t+\frac{1-q}{q}(p_s-p_t)\left(1-\frac{1}{qN}\right) \\ 1-2p_s+\frac{q}{1-q}(p_t-p_s)\left(1-\frac{1}{(1-q)N}\right) \\ 1-2q \end{bmatrix} dt$$

$$+\sqrt{\frac{1}{N}}\begin{bmatrix} 0 & \frac{1-p_t}{q} & 0 & -\frac{p_t}{q} \\ \frac{1-p_s}{1-q} & 0 & -\frac{p_s}{1-q} & 0 \\ 0 & 1 & 0 & 1 \end{bmatrix}\begin{bmatrix} \quad \boldsymbol{G} \quad \end{bmatrix} d\boldsymbol{W}$$

Drift

Simplified equation for cooperation

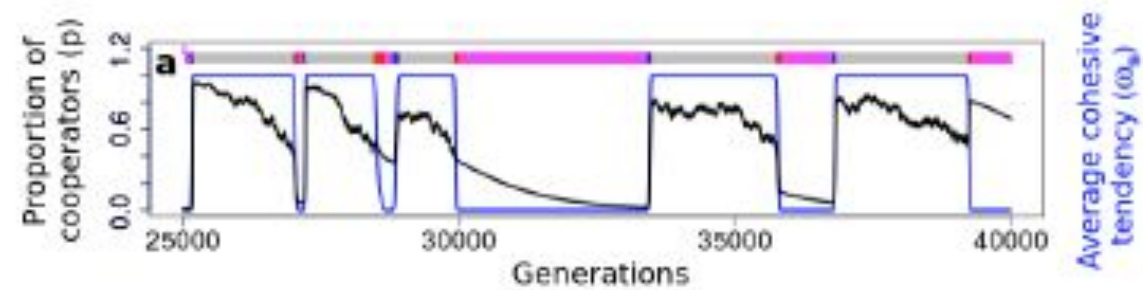
$$\frac{dp}{dt} = p(1-p)(rb_{\text{eff}} - c_{\text{eff}})$$

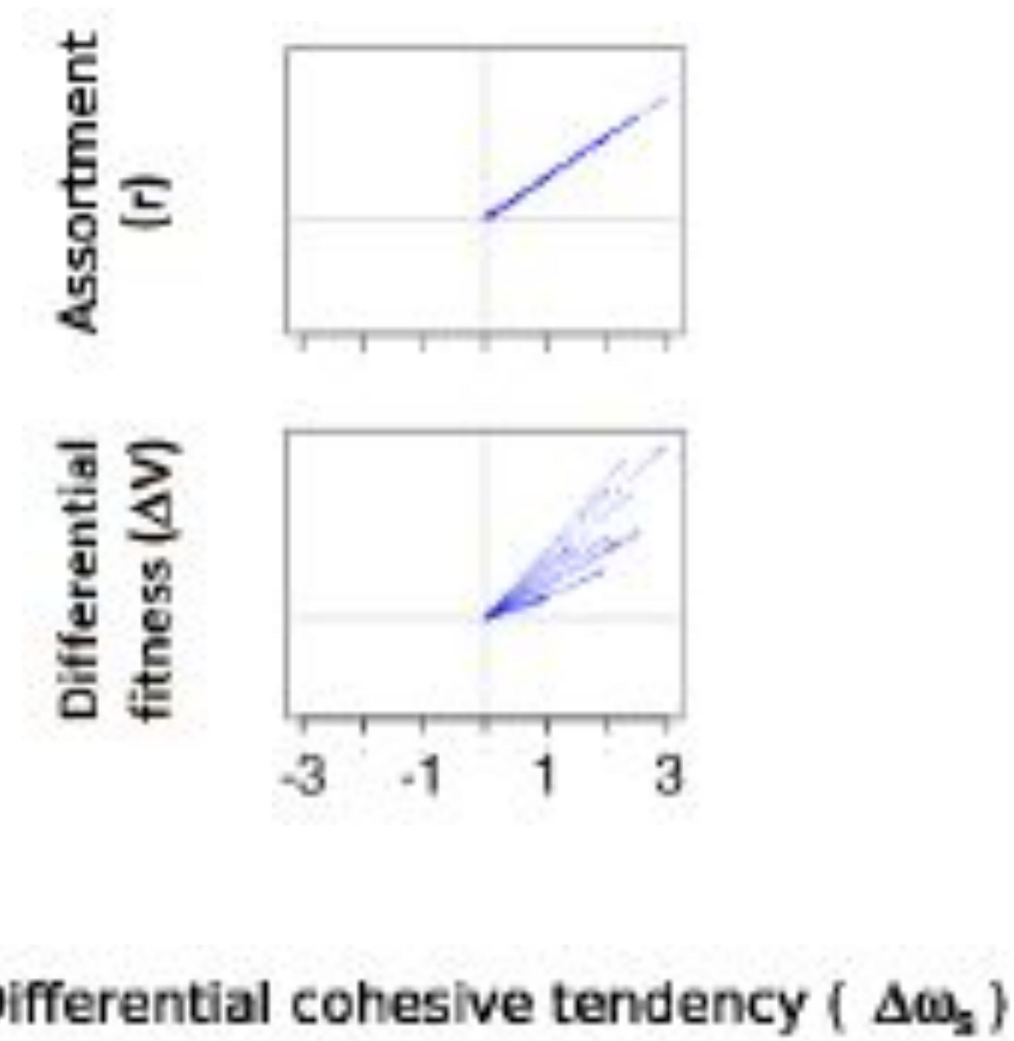
+ noise terms

Condition for cooperation to evolve: $r b_{eff} - c_{eff} > 0$

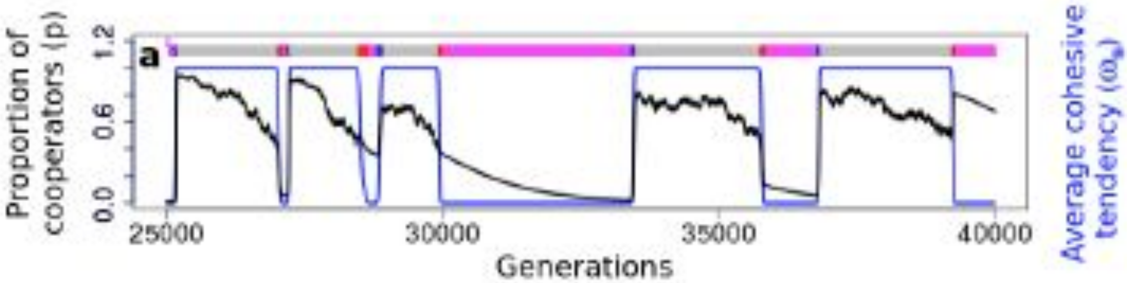
- r is a measure of assortment
- r = Δω = difference in flocking tendency of cooperators and defectors (or differential cohesion, in short)

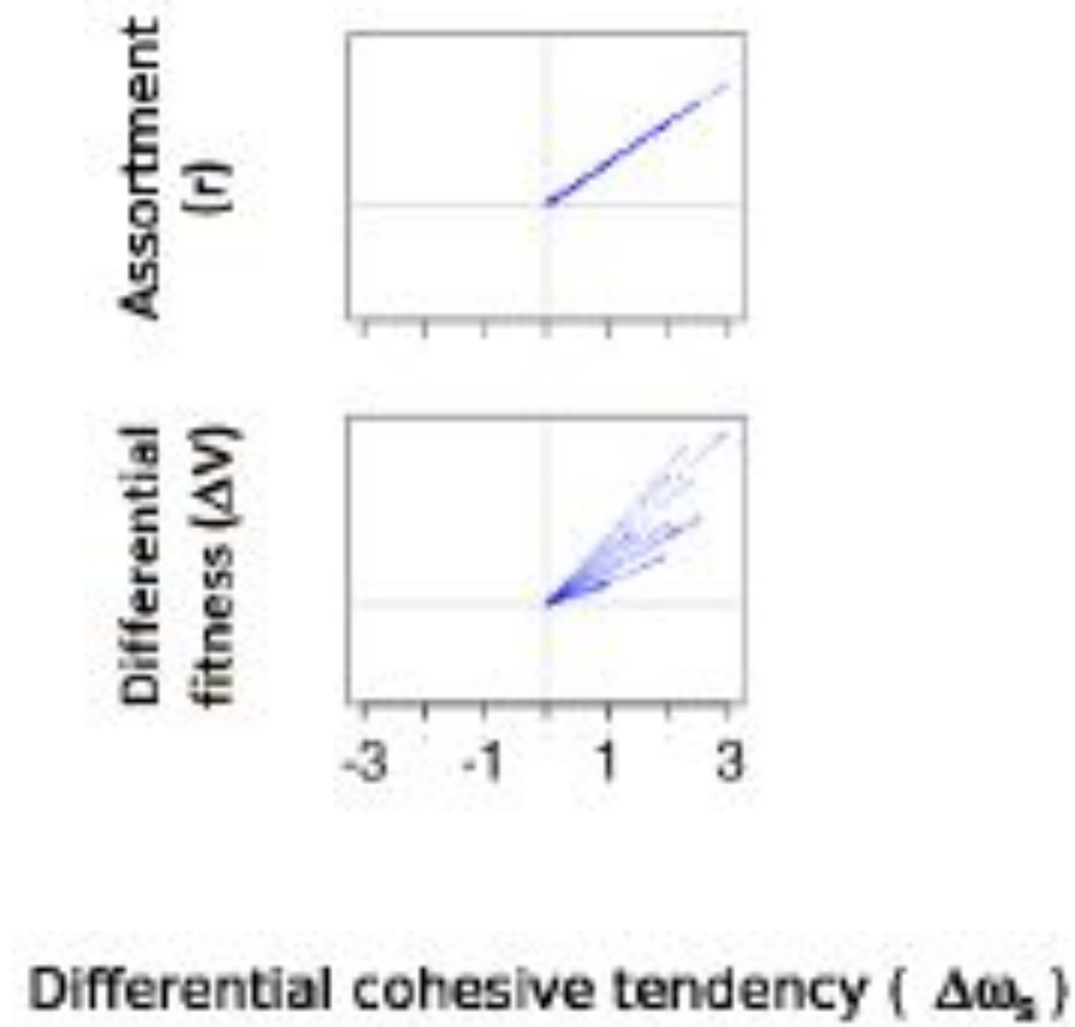
There is no steady-state; but predicts a cycling of various trait combinations





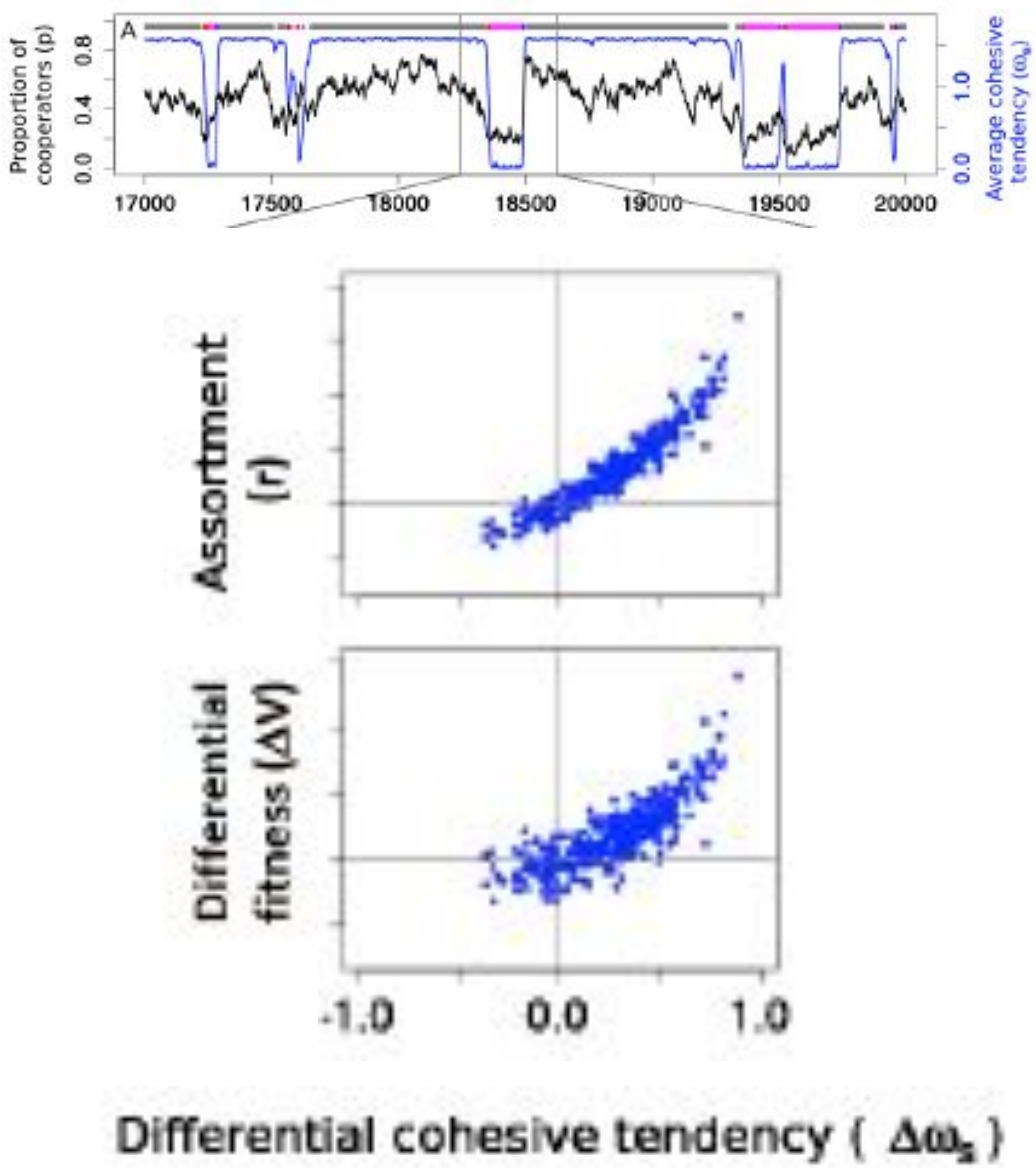
Analytical model predictions

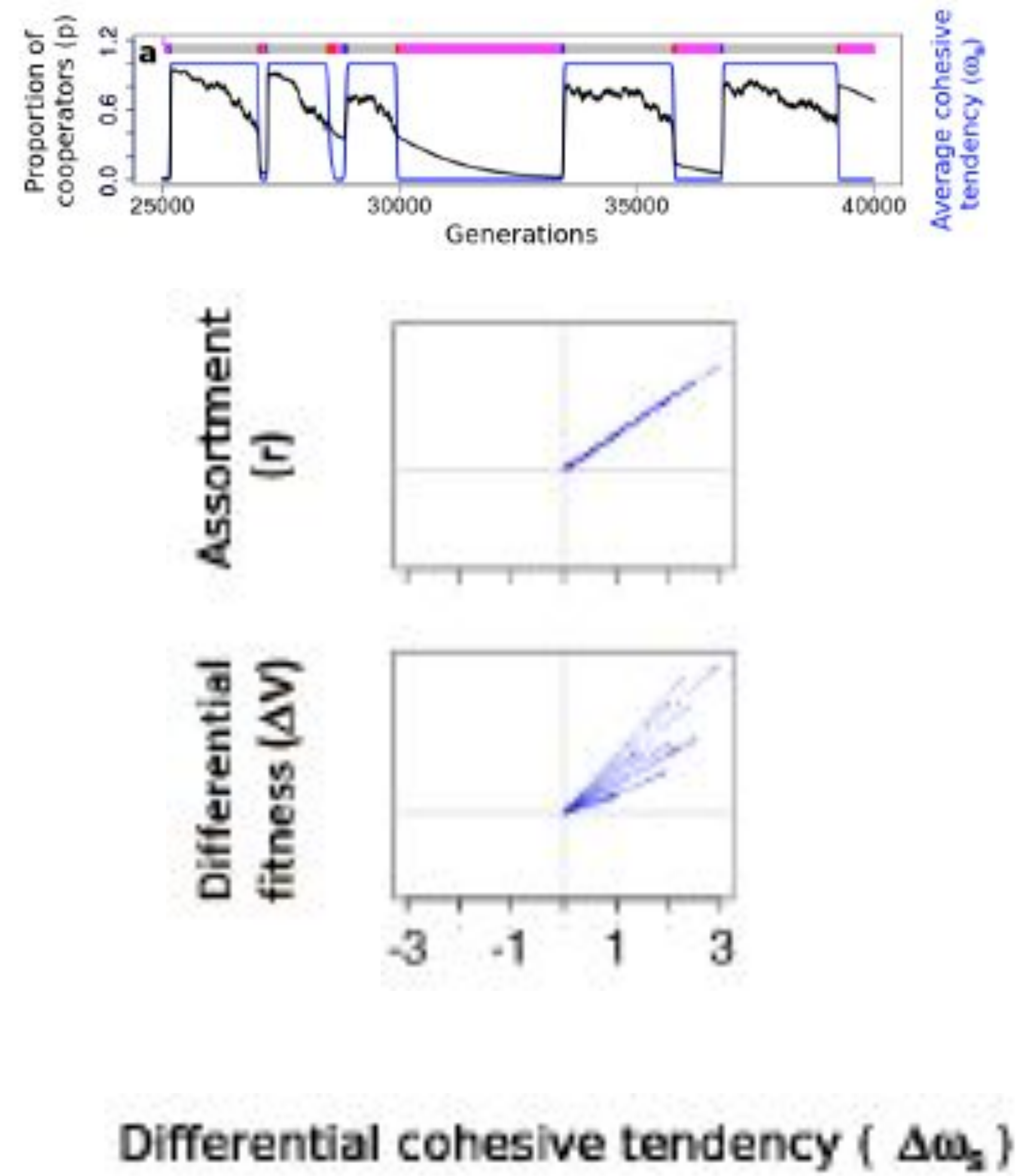




Computational model simulations

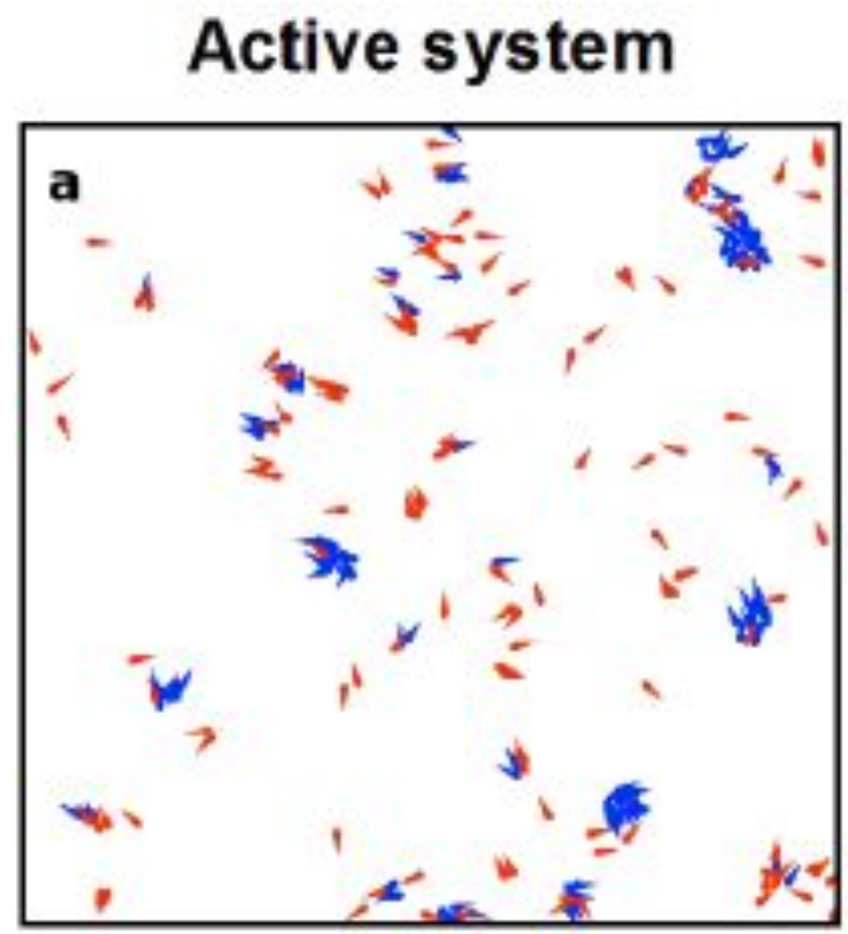
Analytical model predictions





Summary

- Mobility can promote cooperation
- Despite mixing between mobile groups, cooperators assort by evolving relatively stronger flocking tendencies
- Individual based spatial model & analytically derived SDE model results qualitatively agree.



$$r\, b_{eff} - c_{eff} > 0$$

where r = cohesion of cooperators
- cohesion of defectors

PLOS | COMPUTATIONAL BIOLOGY

RESEARCH ARTICLE

Mobility can promote the evolution of cooperation via emergent self-assortment dynamics

Jaideep Joshi[1]*, Iain D Couzin[2,3], Simon A Levin[4], Vishwesha Guttal[1]*

1 Centre for Ecological Sciences, Indian Institute of Science, Bengaluru, India, **2** Department of Collective Behaviour, Max Planck Institute for Ornithology, Konstanz, Germany, **3** Chair of Biodiversity and Collective Behaviour, Department of Biology, University of Konstanz, Konstanz, Germany, **4** Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey, United States of America

Acknowledgements

- Funding
  - DBT-IISc Partnership Program, CSIR, DBT Ramalingaswamy Fellowship
  - DST-Mathematical Biology Phase II
- **Collaborators**
  - Students: Jaideep Joshi (Phd Student)
  - Simon Levin, Iain Couzin