



The role of intrinsic noise in biological systems: from animal groups to populations to evolution

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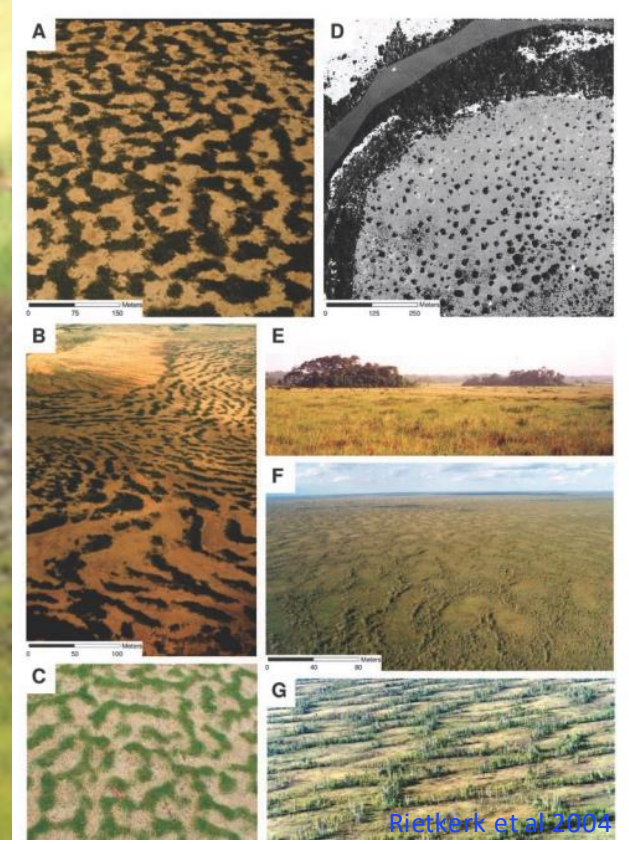
Collaborators (most recent): Guy Theraulaz, Clement Sire, Ramon Escubedo, Tim Rogers, Richard Morris, Danny Raj.

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**Theoretical
Ecology and
Evolution Lab**



Self-Organisation in
Ecology

- Predictive ecology; Nonequilibrium Physics Approaches
- Mechanisms and Functions
- Theory, Simulations, Experiments, and Field Data



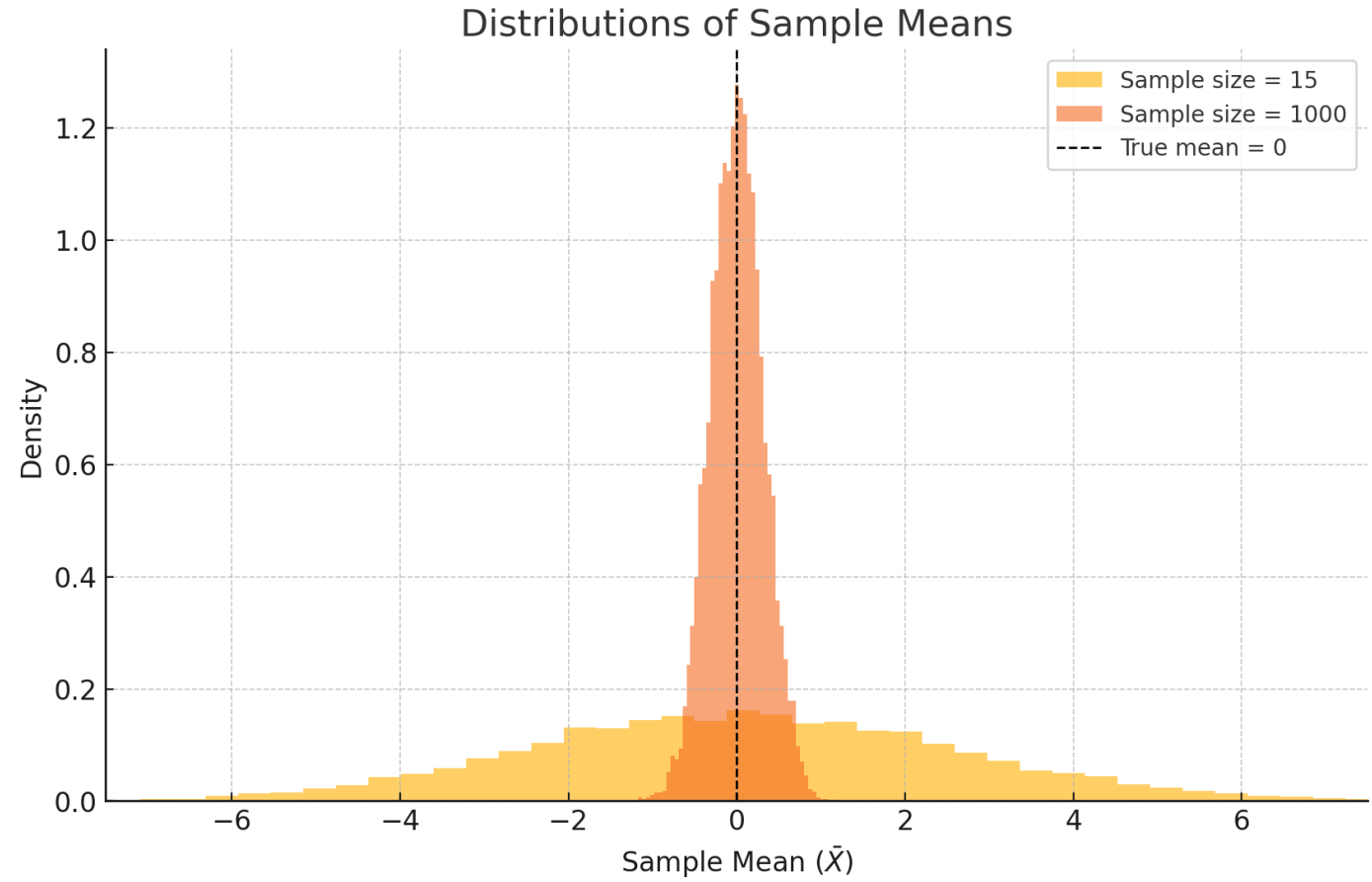
Outline for today's talk: Noise to Order!

- Theme 1: Deciphering dynamics of fish schools
 - Noise helps characterize the nature of synchrony.
 - Experiments of fish schools
- A novel method: Data-driven equation discovery
- Theme 2: Evolution and Noise



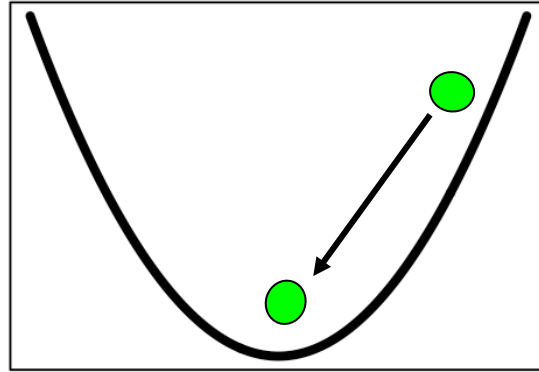
Noise and sample mean

- Take N random numbers:
 X_1 to X_N
- Estimate the sample mean!

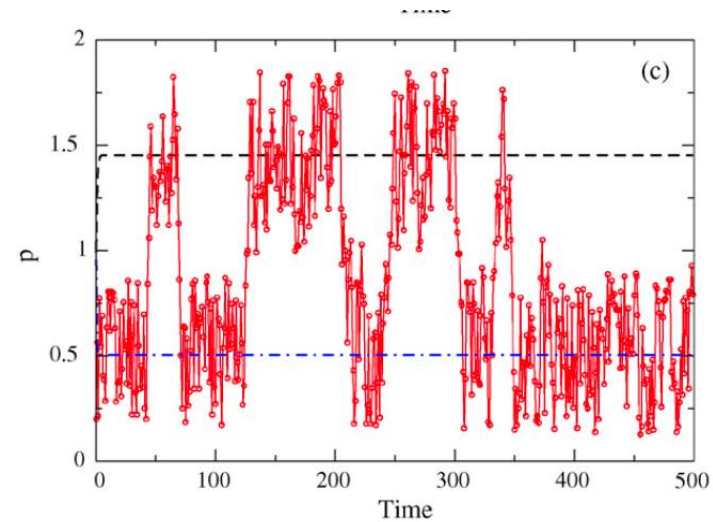
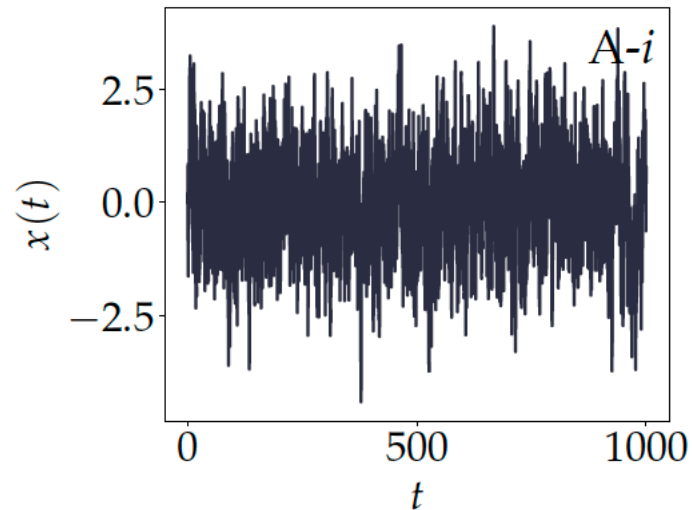
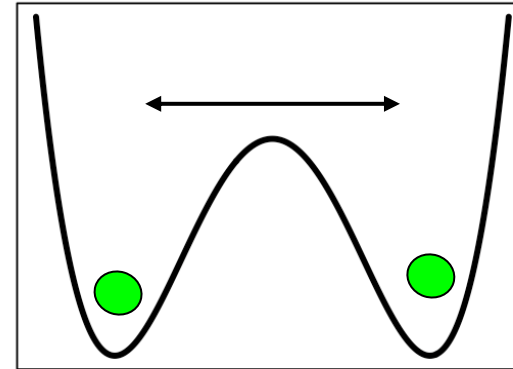


Some cartoon diagrams: potential landscapes

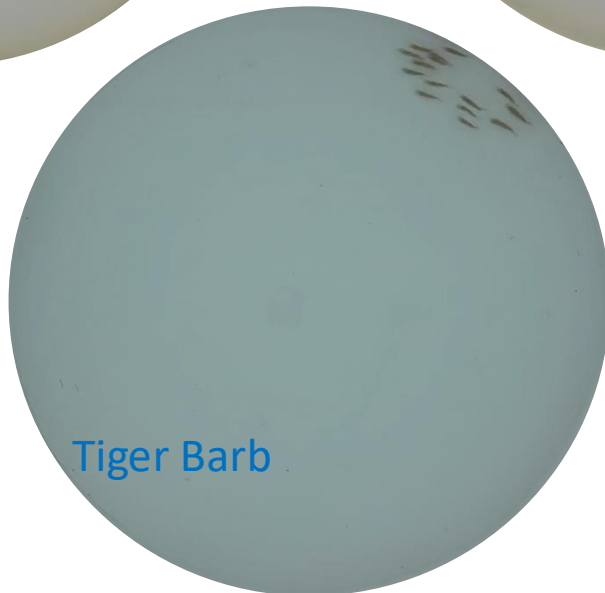
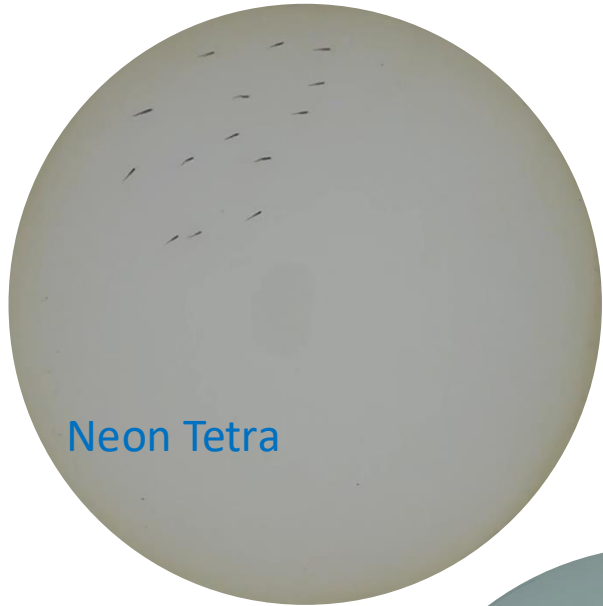
Unistable System + noise



Bistable System + noise



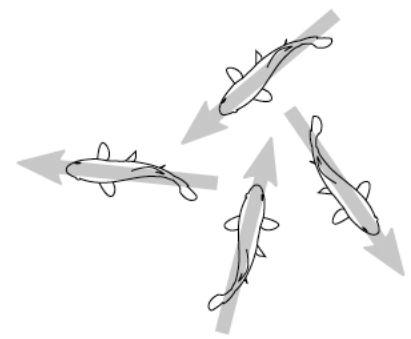
Theme 1: The role of noise in collective synchrony!



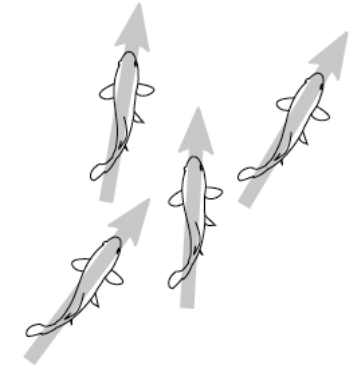
Synchrony Order Parameter

Group Polarisation

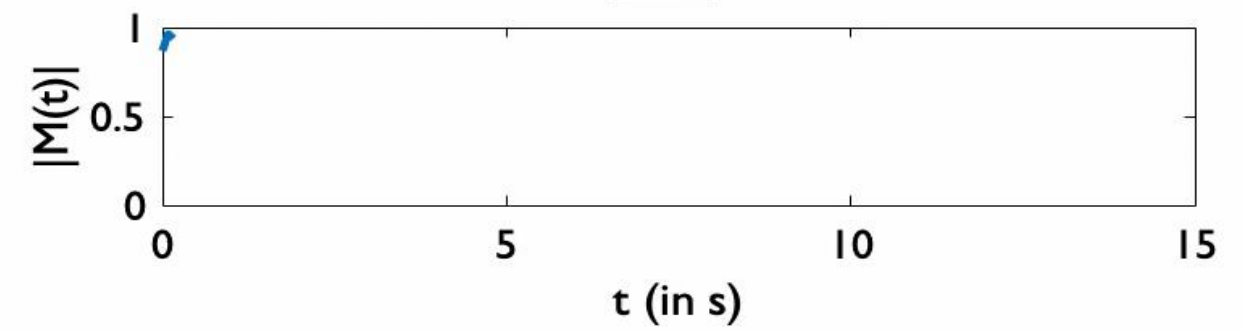
$$\mathbf{M}(t_n) = \frac{1}{N} \sum_{i=1}^N \mathbf{v}_i(t_n).$$



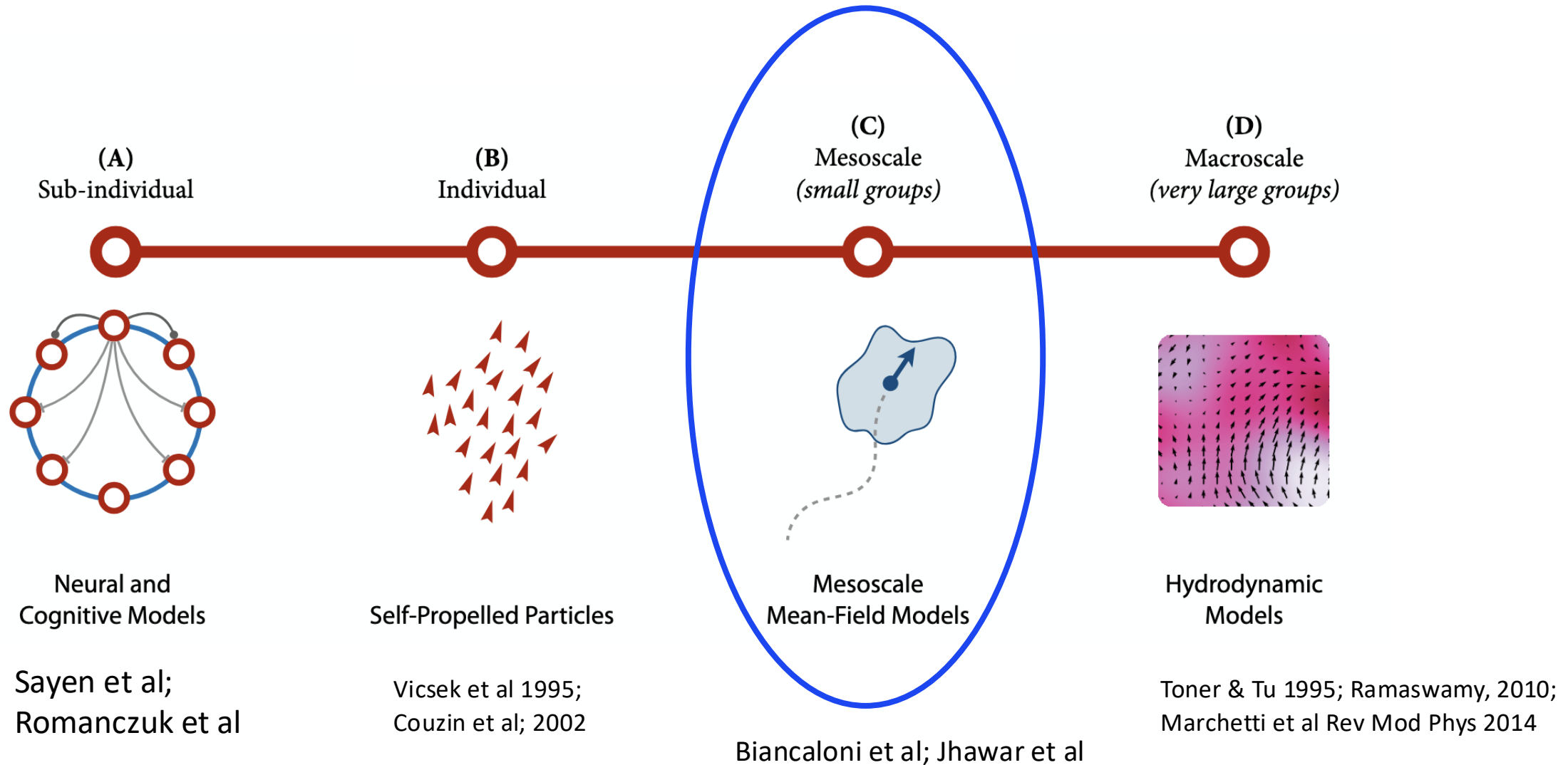
$|\mathbf{M}| \sim 0$ (isotropic)



$|\mathbf{M}| \sim 1$ (polarized)

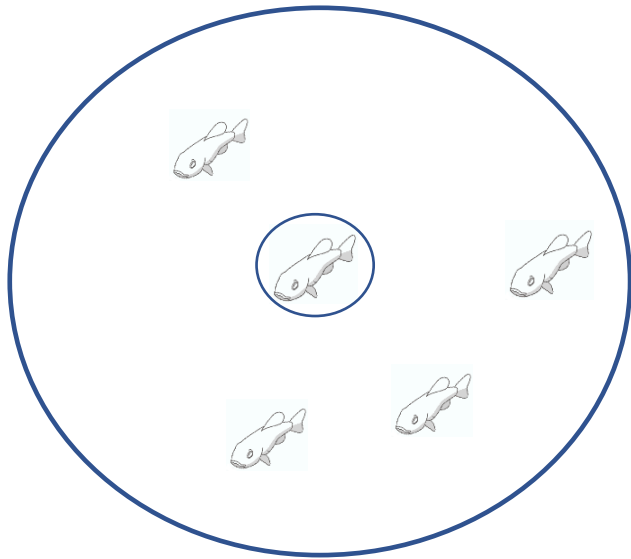


Various approaches to modelling collective dynamics



Agent-based models of flocking systems (Vicsek et al 1995; Couzin et al; 2002)

- A key assumption: Individuals move in an **average direction of neighbours**, with a noise



$$\theta_i(t + 1) = \langle \theta \rangle_r + \overset{\text{noise term}}{\eta(t)}$$

Coarse-grained/hydrodynamic models

- Typically, in the thermodynamic limit (N large):

Flocking order-parameter: $\mathbf{m} = \frac{1}{N} \sum_i \mathbf{v}_i(t)$

$$\frac{\partial \mathbf{m}}{\partial t} = \underbrace{(\alpha - \beta |\mathbf{m}|^2) \mathbf{m}}_{\text{drift term}} + \underbrace{\eta(t)}_{\text{"extrinsic"-noise term}} + \underbrace{\nabla \text{ terms}(c, \mathbf{m})}_{\text{spatial coupling}}$$

Our approach:

1. **Data-driven** characterization of *stochastic and nonlinear dynamics of synchrony* (via Ito-SDEs)

$$\frac{d\mathbf{m}}{dt} = \mathbf{f}(\mathbf{m}) + \mathbf{g}(\mathbf{m}) \cdot \eta(t)$$

The diagram illustrates the components of the Ito-SDE equation. The term $\mathbf{f}(\mathbf{m})$ is labeled as the **Drift** component, which is the **Deterministic part** of the equation. The term $\mathbf{g}(\mathbf{m}) \cdot \eta(t)$ is labeled as the **Diffusion** component, which is the **Stochastic part** of the equation. Arrows point from the labels 'Drift' and 'Diffusion' to their respective terms in the equation.

2. **Theory-Derived SDEs and Compare with Data-Derived SDEs**

Examples of SDE models in Ecology

- **Stochastic Population Models:**

Deterministic term: Could be logistic model term.

Noise term: Demographic noise term or Environmental noise term

- **Evolutionary models:**

Deterministic term: Selection

Noise term: Random genetic drift

$$\frac{d\mathbf{m}}{dt} = \mathbf{f}(\mathbf{m}) + \mathbf{g}(\mathbf{m}) \cdot \eta(t)$$

Drift
Deterministic part

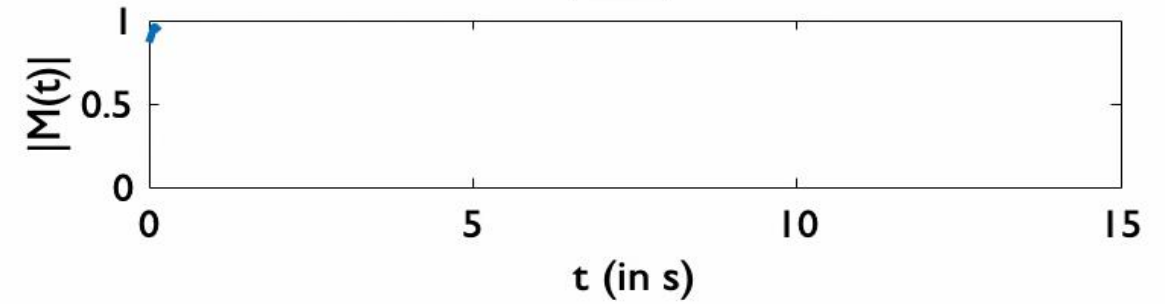
Diffusion
Stochastic part

Synchrony Order Parameter

Group Polarisation

$$\mathbf{M}(t_n) = \frac{1}{N} \sum_{i=1}^N \mathbf{v}_i(t_n).$$

$$\dot{m} = f(m) + g(m)\eta(t),$$




Inverse
problem:

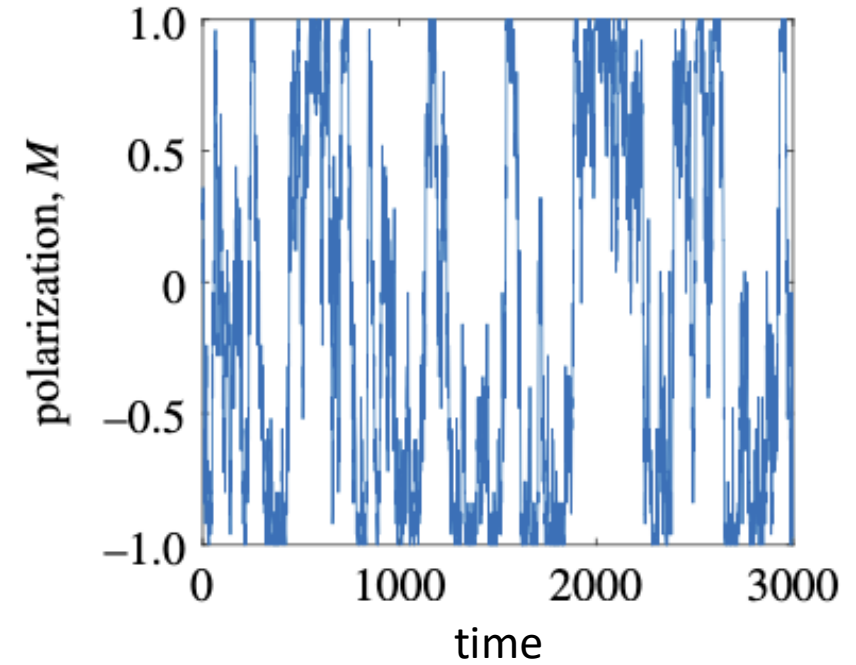
Data to
equations!



Methods: Noise helps characterize the underlying dynamics!

$$\dot{m} = f(m) + g(m)\eta(t),$$


PyDaddy Data
Driven
Dynamics



Jhawar and Guttal, 2020; Nabeel, et al 2025.

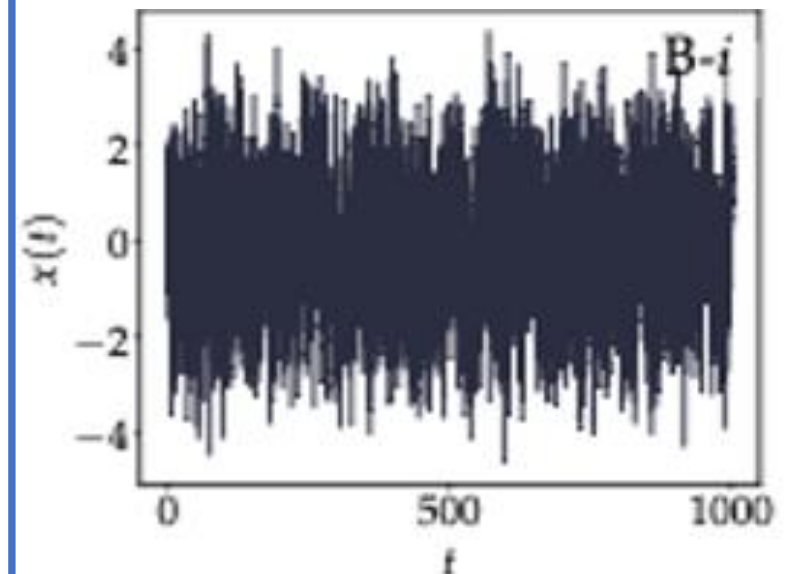
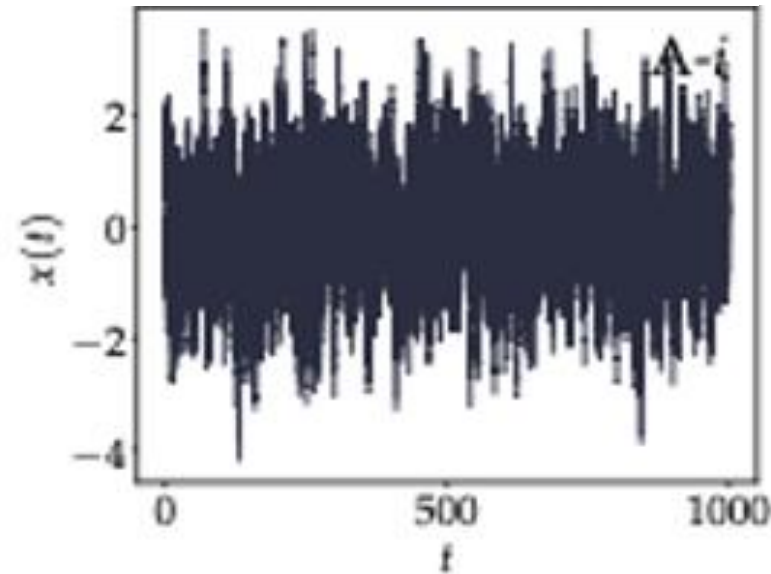
See: **PyDaDDy**: <https://github.com/tee-lab/PyDaddy>



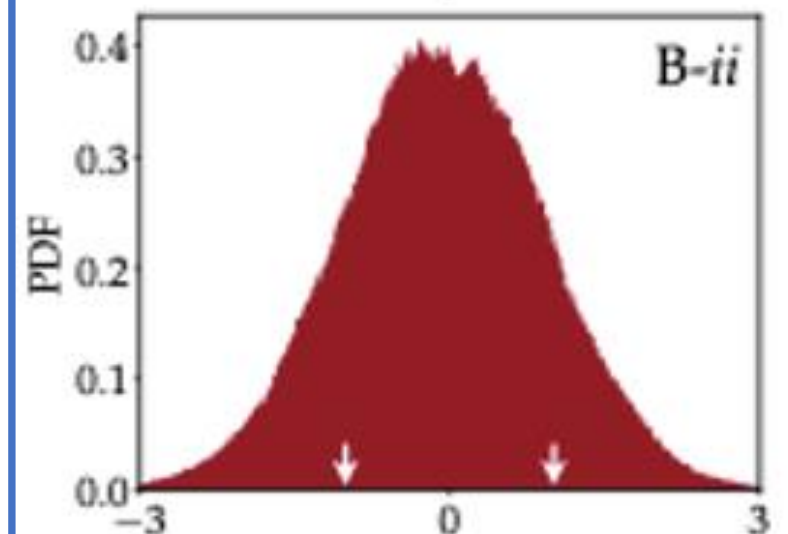
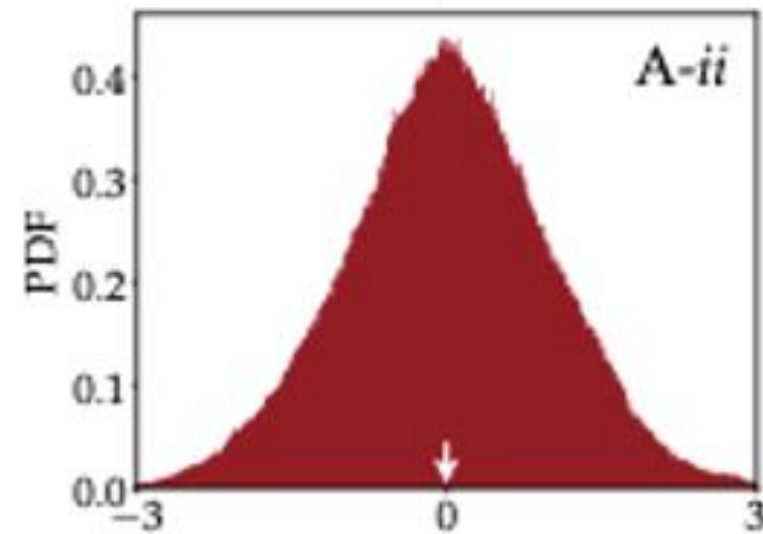
$$\dot{x} = -x + \sqrt{2} \cdot \eta(t),$$

$$\dot{x} = x - x^3 + 2\left(\sqrt{1+x^2}\right) \cdot \eta(t).$$

Time series



Distribution

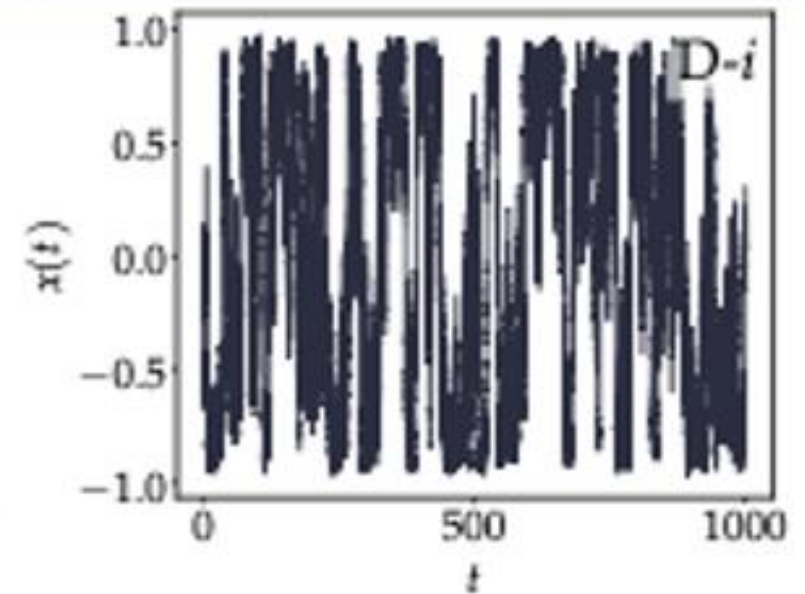
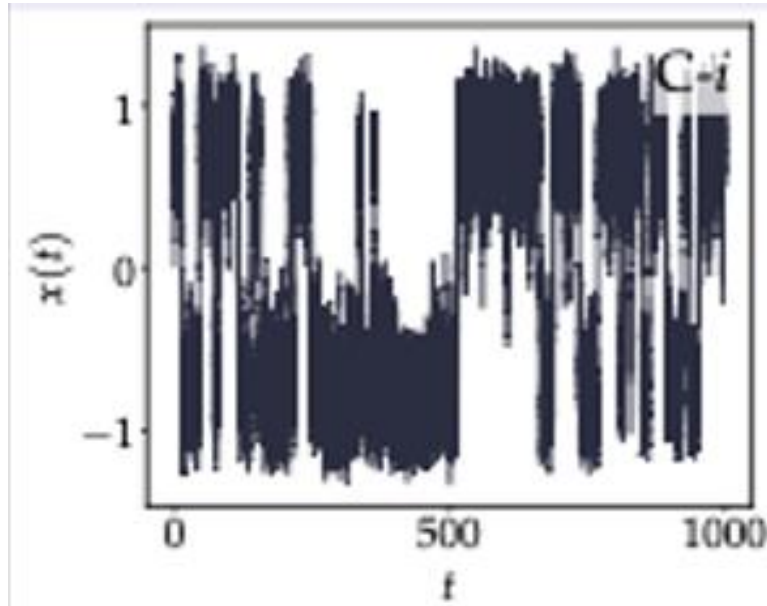


Possible to recover and distinguish above models, even if we had only time series data!

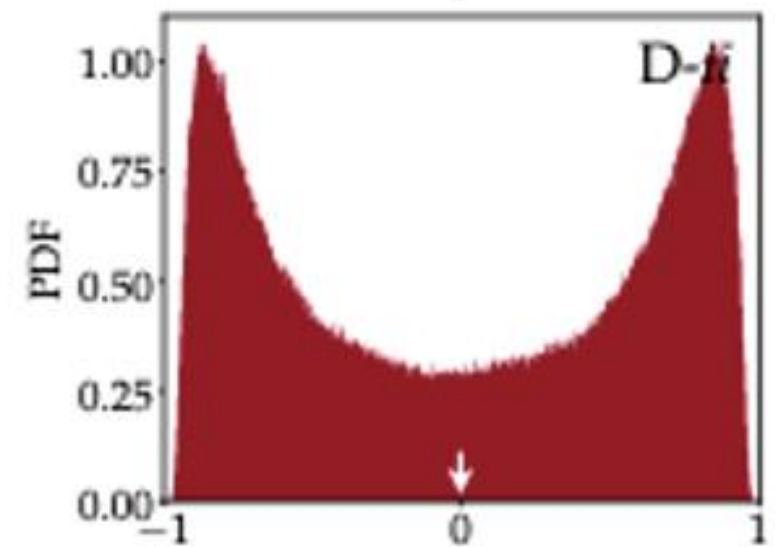
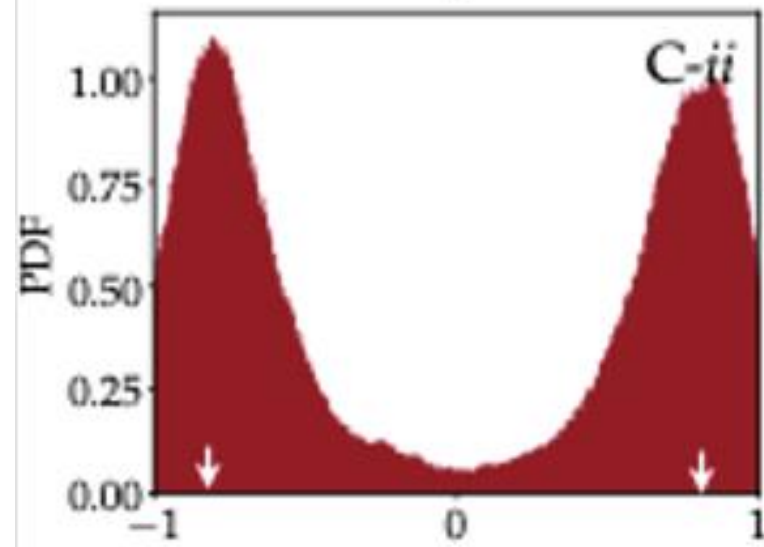
$$\dot{x} = 2x - 3x^3 + \frac{1}{2} \cdot \eta(t),$$

$$\dot{x} = -x + \sqrt{2}(1 - x^2) \cdot \eta(t).$$

Time series



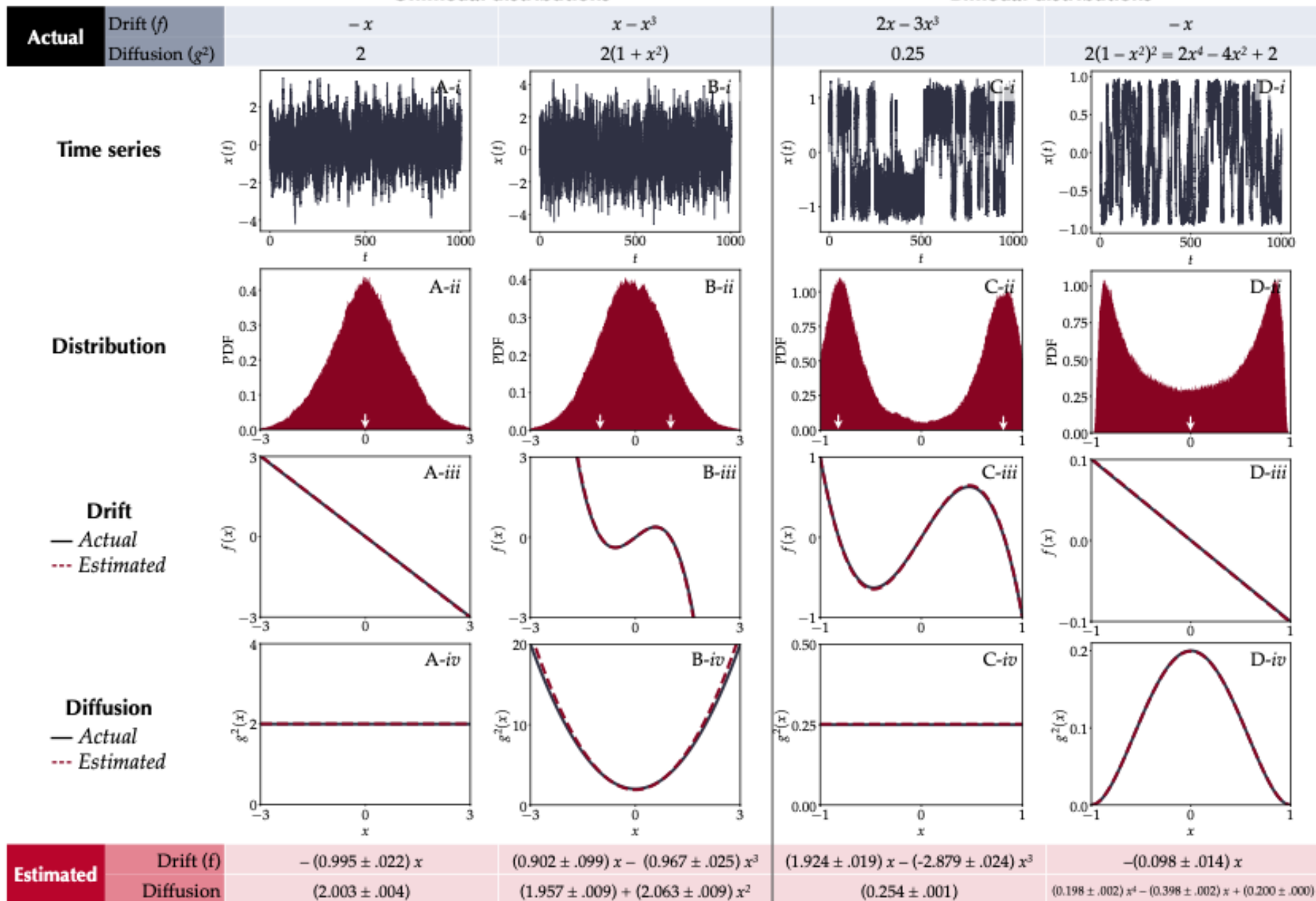
Distribution



Possible to recover and distinguish above models, even if we had only time series data!

Unimodal distributions

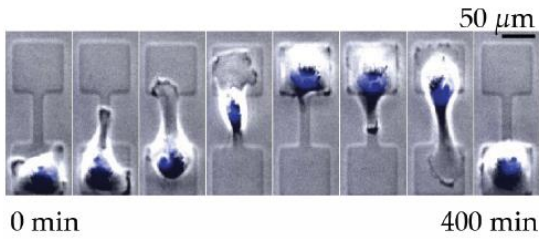
Bimodal distributions



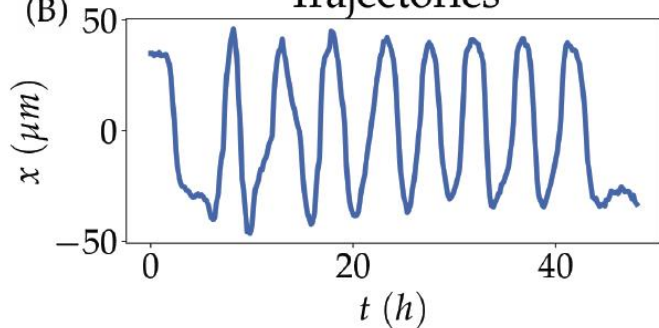
Single cell oscillations => SDEs

- Van-der pol like oscillator + Noise.

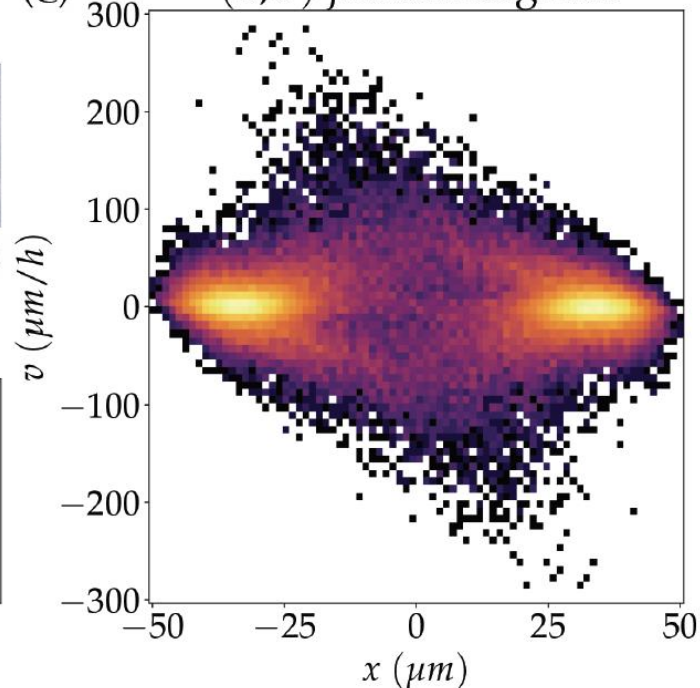
(A) Experimental setup



(B) Trajectories



(C) (x, v) joint histogram



$$\dot{x} = v,$$

$$\dot{v} = f(x, v) + g(x, v) \cdot \eta(t),$$

Nabeel, et al, The American Naturalist, 2025

PyDaddy: <https://github.com/tee-lab/PyDaddy>

Data-derived dynamical equation for fish schooling:

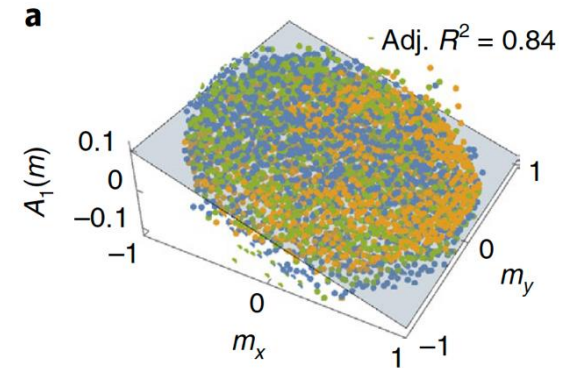
Fish species: *Etroplus suratensis* (Karimeen)



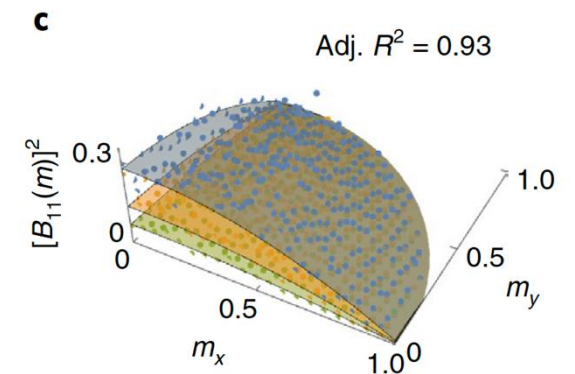
Linear Drift with Quadratic Diffusion

Noise-induced synchrony

$$\frac{d\mathbf{m}}{dt} = -\alpha \mathbf{m} + \left[\frac{\beta(1 - |\mathbf{m}|^2) + \alpha}{N} \right]^{1/2} \mathbb{1} \cdot \boldsymbol{\eta}(t)$$



● $N = 15$ ● $N = 30$ ● $N = 60$



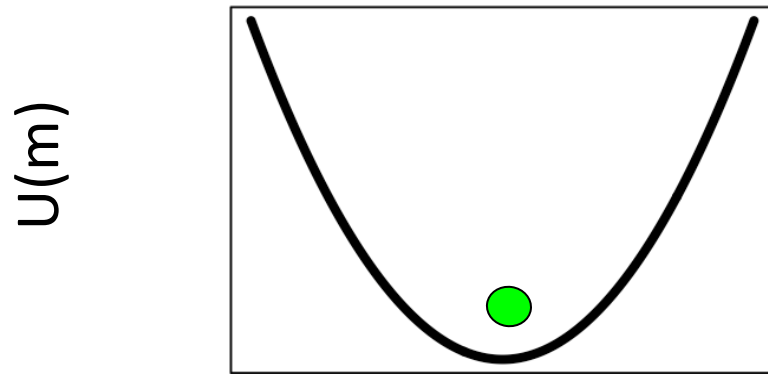
**Noise-induced schooling;
Stochastic Pairwise model**

Jhavar et al, 2020, Nature physics.

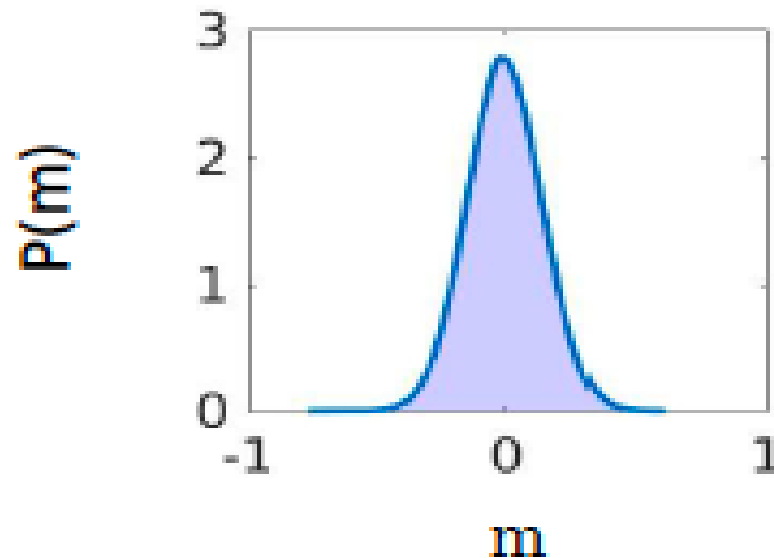
$$\frac{d\mathbf{m}}{dt} = -a\mathbf{m} + \sqrt{\frac{a + c(1 - |\mathbf{m}|^2)}{N}} \mathbb{1} \cdot \boldsymbol{\eta}(t)$$

Our naïve expectation of such an equation

Disorder is the attractor

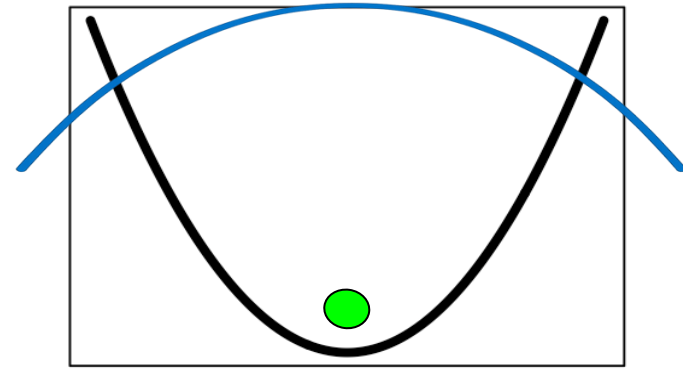


Disorder

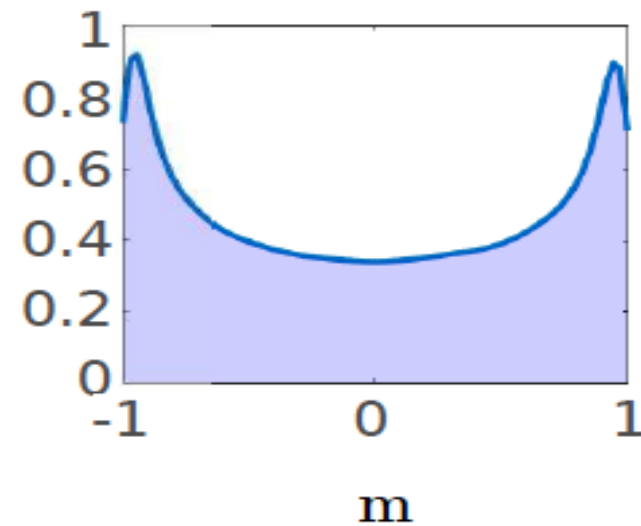


m

***What's actually happening:
Small flocks: High Intrinsic Noise
Ordered state is most likely***



Disorder

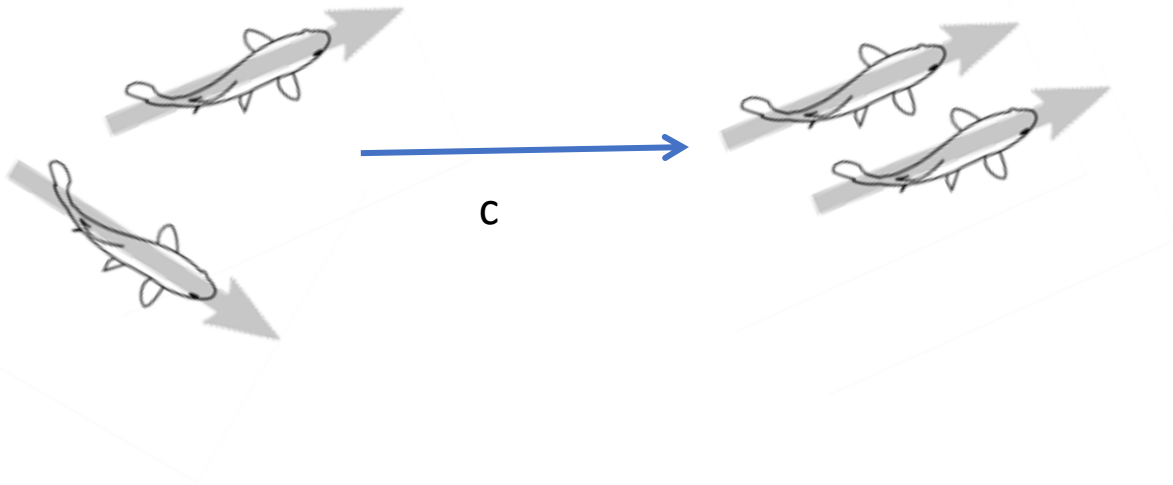


m

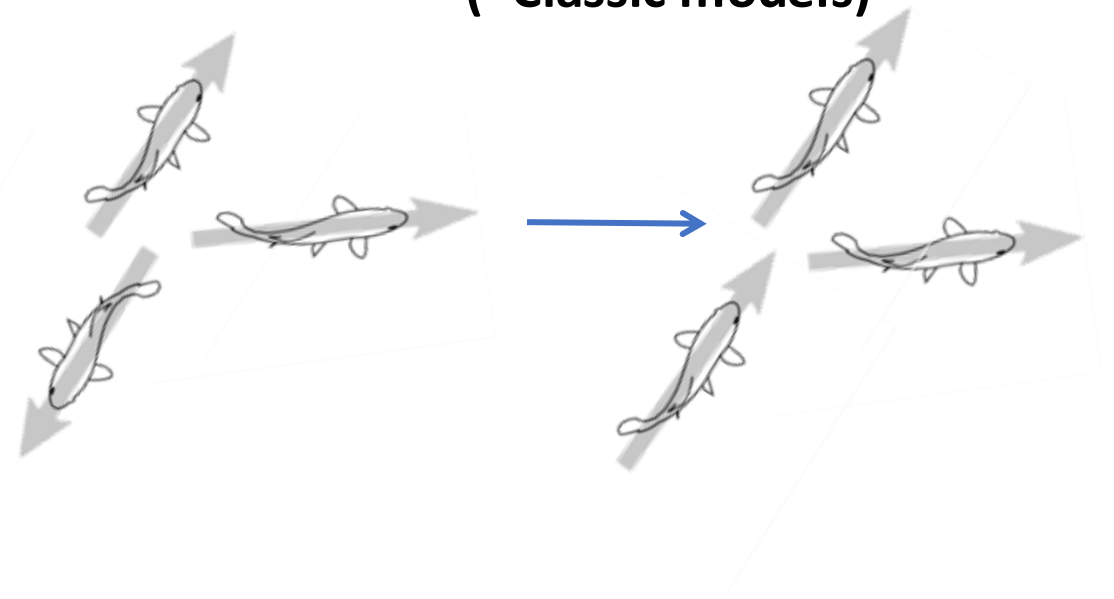
Is there a microscopic model that can explain these results?

A 'spin' model : Stochastic social interaction model

Pairwise copying interaction



**Ternary or average interaction
(~Classic models)**

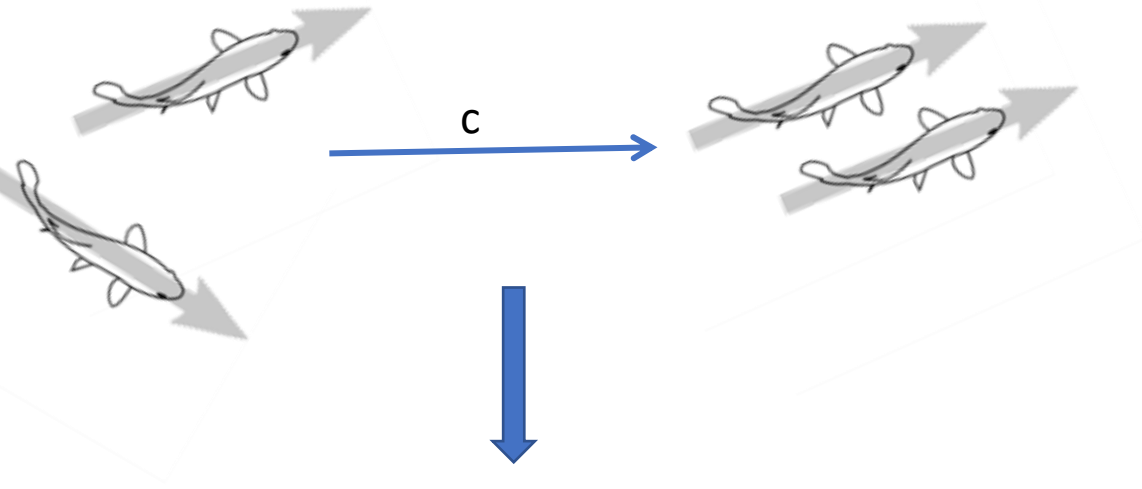


Group polarization:

$$\mathbf{m} = \frac{1}{N} \sum_i \mathbf{v}_i(t)$$

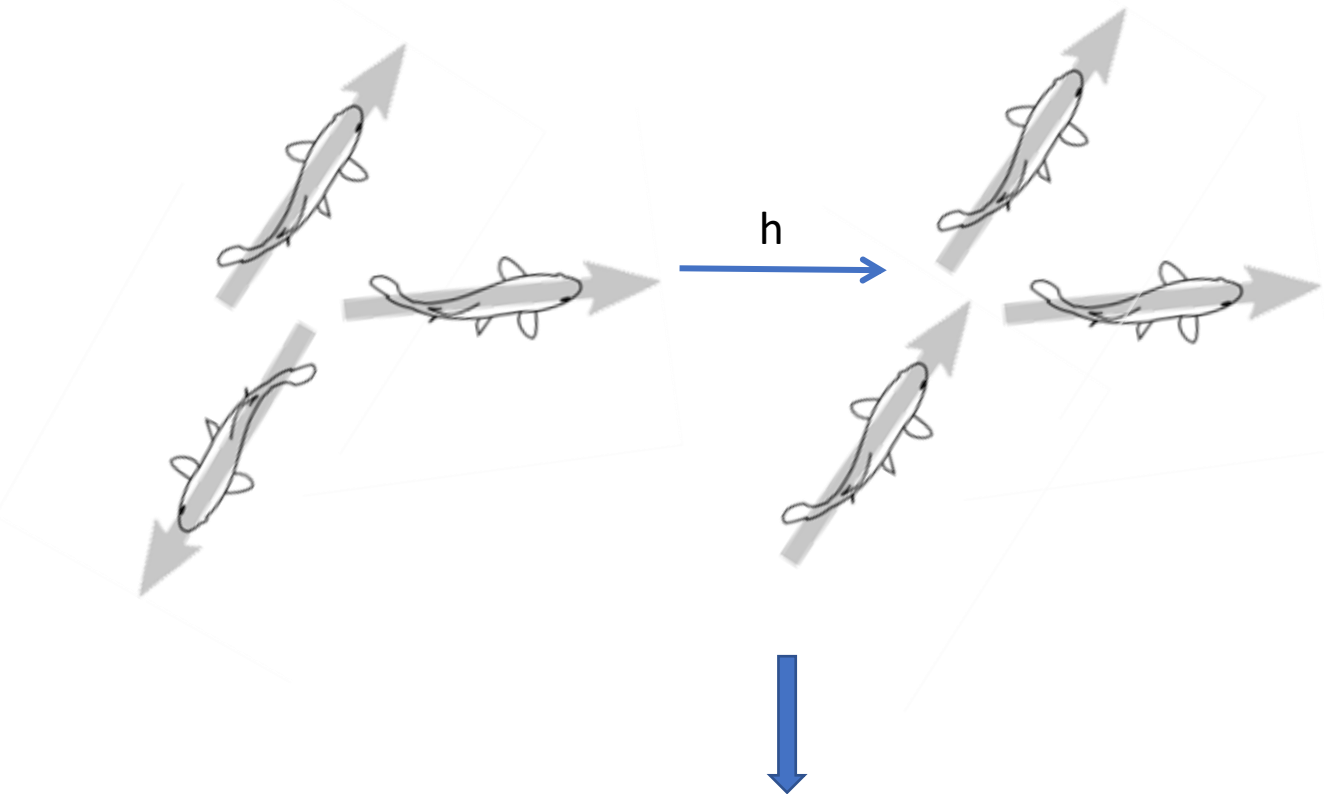
Mesoscopic Theory of Polarisation Dynamics

Only pairwise copying alignment interaction



$$\frac{d\mathbf{m}}{dt} = -a \mathbf{m} + \sqrt{\frac{a + c(1 - |\mathbf{m}|^2)}{N}} \mathbb{1} \cdot \boldsymbol{\eta}(t)$$

Ternary or average alignment interaction
(Classic models)

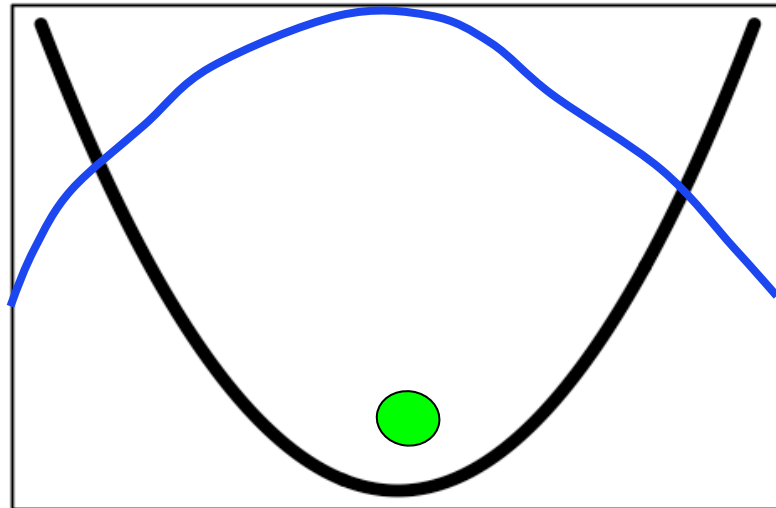


$$\frac{d\mathbf{m}}{dt} = -a \mathbf{m} + h \mathbf{m}(1 - |\mathbf{m}|^2) + \sqrt{\frac{a + (c + h)(1 - |\mathbf{m}|^2)}{N}} \mathbb{1} \cdot \boldsymbol{\eta}(t)$$

Pairwise copying alignment interaction

$$\frac{d\mathbf{m}}{dt} = -a\mathbf{m} + \sqrt{\frac{a + c(1 - |\mathbf{m}|^2)}{N}} \mathbb{1} \cdot \boldsymbol{\eta}(t)$$

Disorder is the attractor



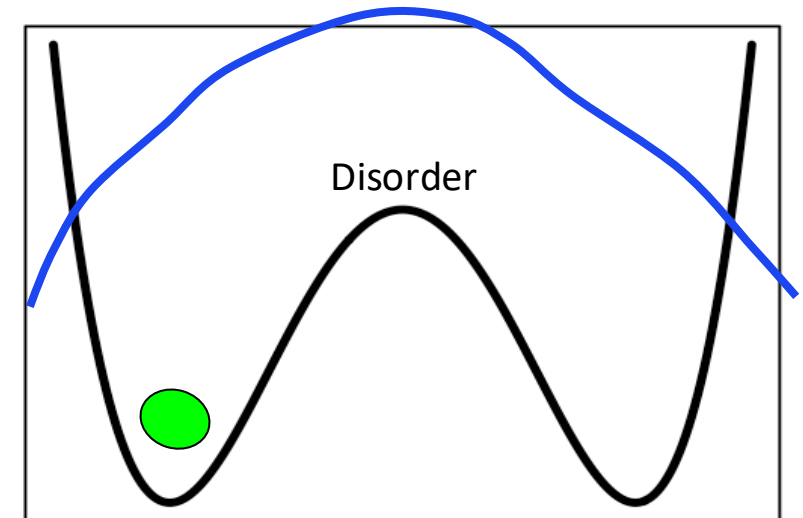
Disorder

Noise-induced synchrony for small flocks

Ternary or average alignment interaction (Classic models)

$$\frac{d\mathbf{m}}{dt} = -a\mathbf{m} + h\mathbf{m}(1 - |\mathbf{m}|^2) + \sqrt{\frac{a + (c + h)(1 - |\mathbf{m}|^2)}{N}} \mathbb{1} \cdot \boldsymbol{\eta}(t)$$

Order is the attractor



Order

Order

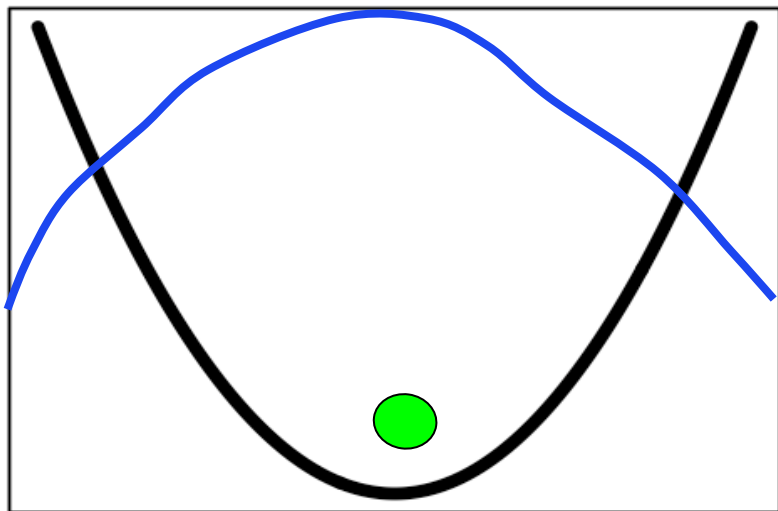
Deterministic order



Pairwise copying alignment interaction

$$\frac{d\mathbf{m}}{dt} = -a\mathbf{m} + \sqrt{\frac{a + c(1 - |\mathbf{m}|^2)}{N}} \uparrow \cdot \boldsymbol{\eta}(t)$$

Disorder is the attractor



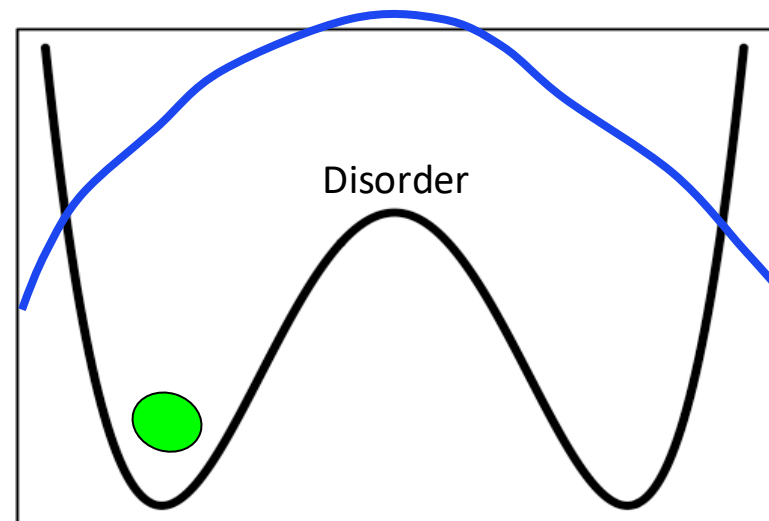
Disorder

*Noise-induced synchrony in *Etropus Suratensis**

Ternary or average alignment interaction (Classic models)

$$\frac{d\mathbf{m}}{dt} = -a\mathbf{m} + h\mathbf{m}(1 - |\mathbf{m}|^2) + \sqrt{\frac{a + (c + h)(1 - |\mathbf{m}|^2)}{N}} \uparrow \cdot \boldsymbol{\eta}(t)$$

Order is the attractor



Order

Order

Disorder

Deterministic order

Do other fish species show similar dynamical structure?



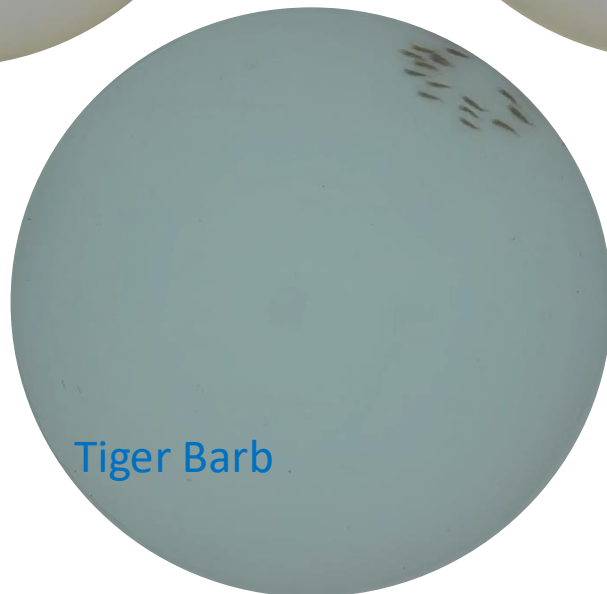
Neon Tetra



Rosy Barb



Serpae Tetra



Tiger Barb



Pearl Spot

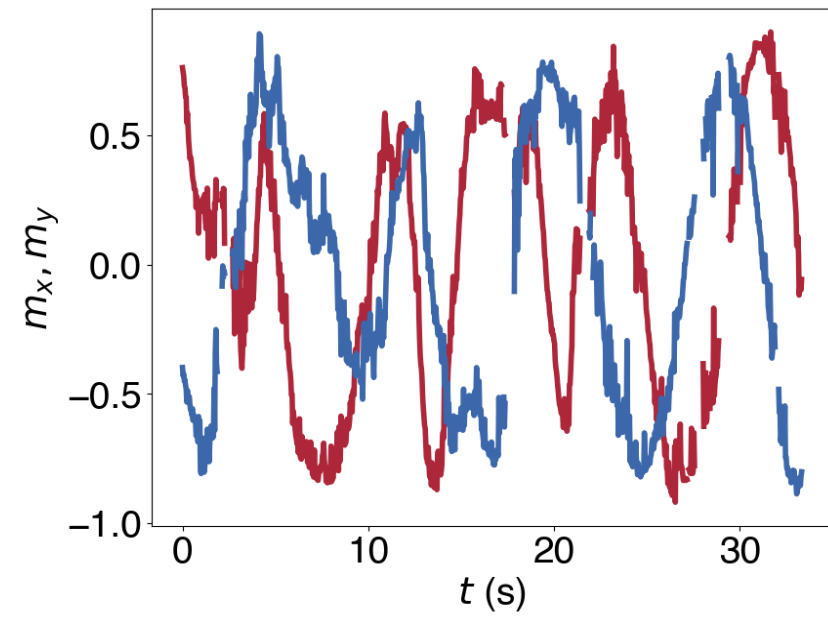
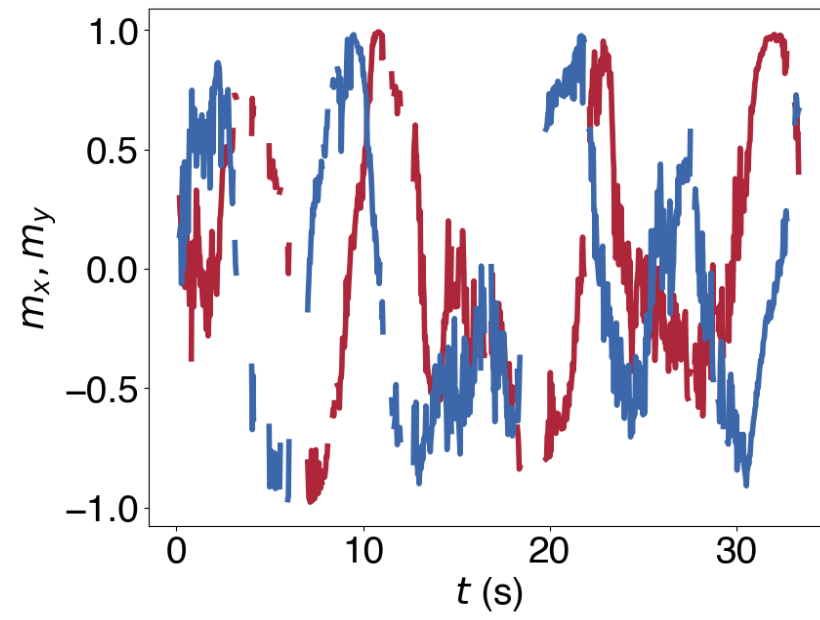
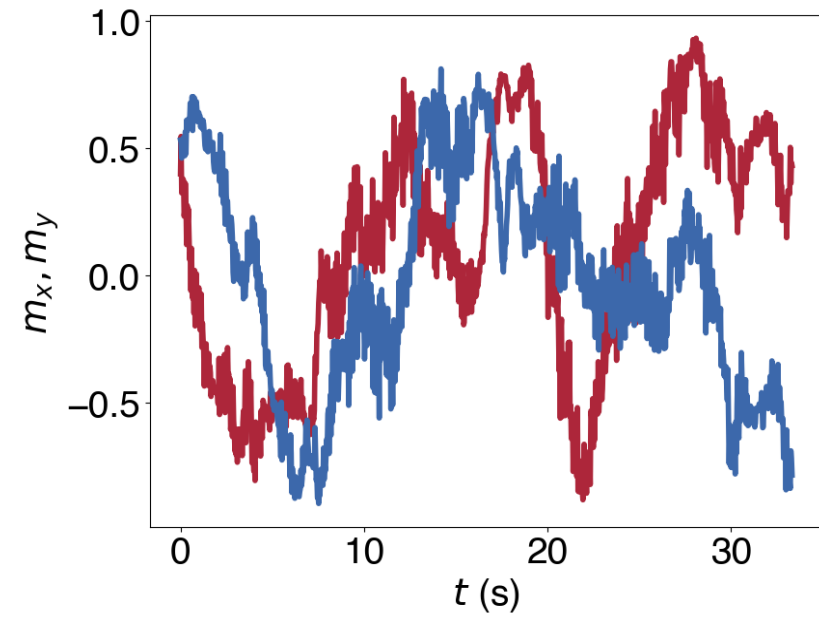


Rummy Nose Tetra

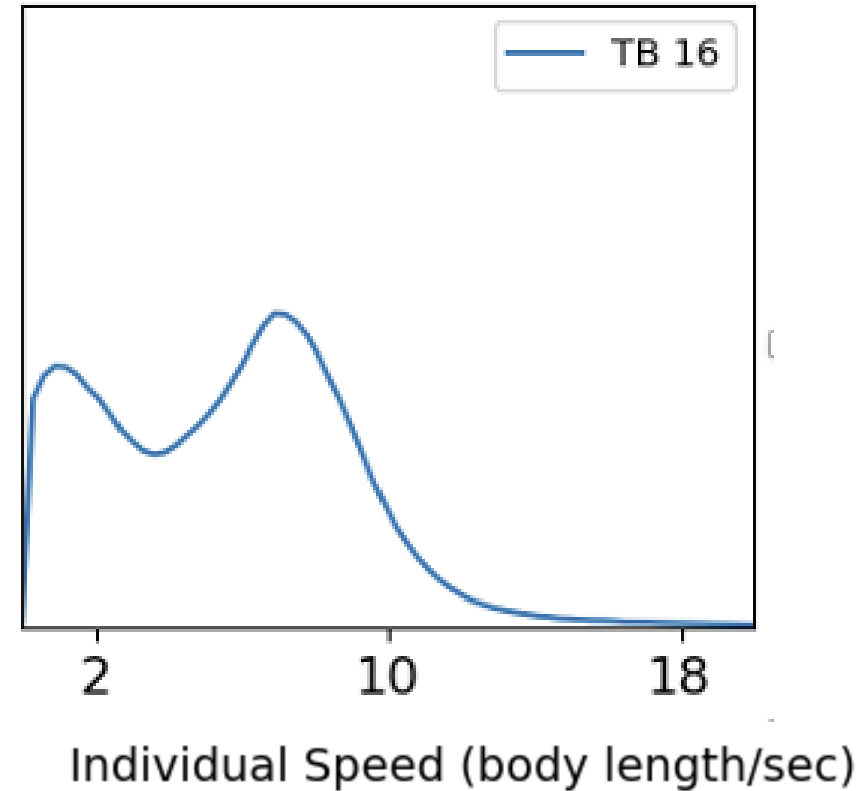
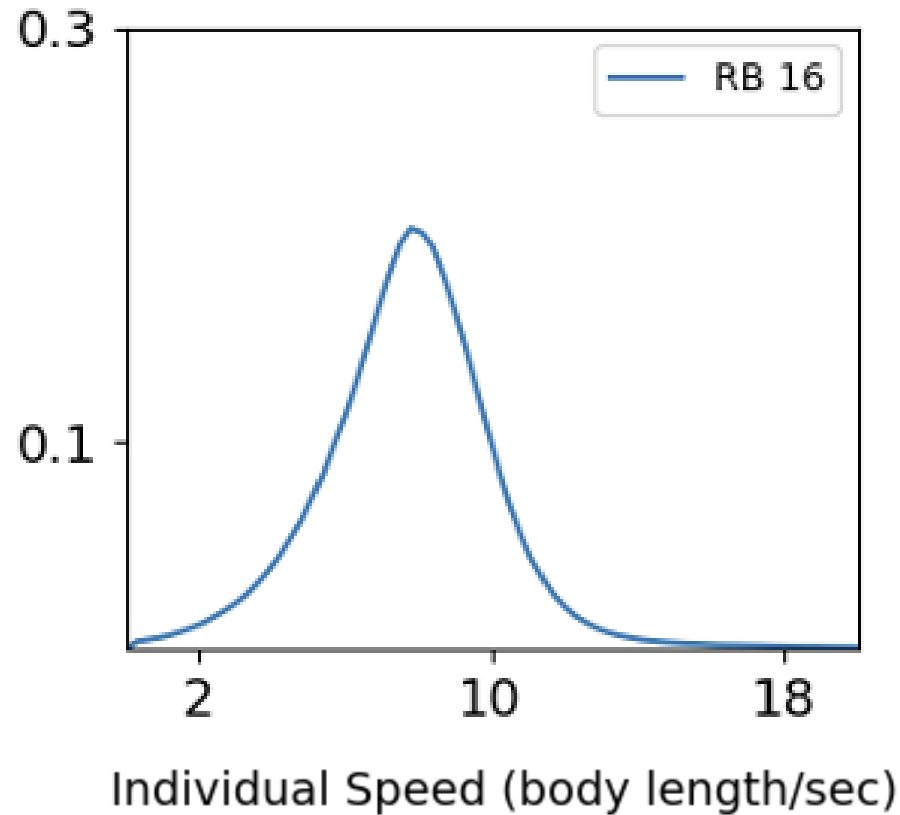
Karimeen

Rosy Barbs

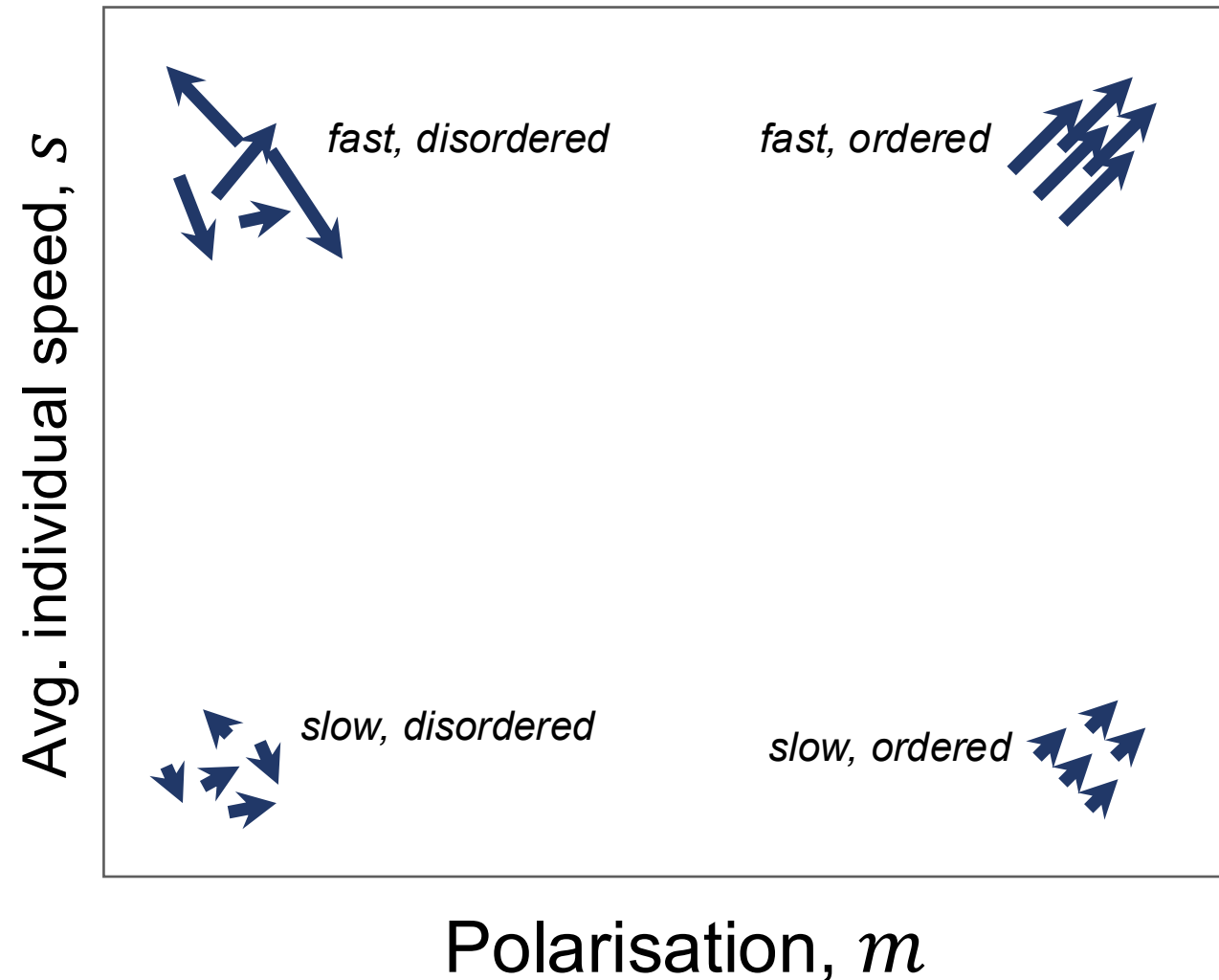
Tiger Barbs



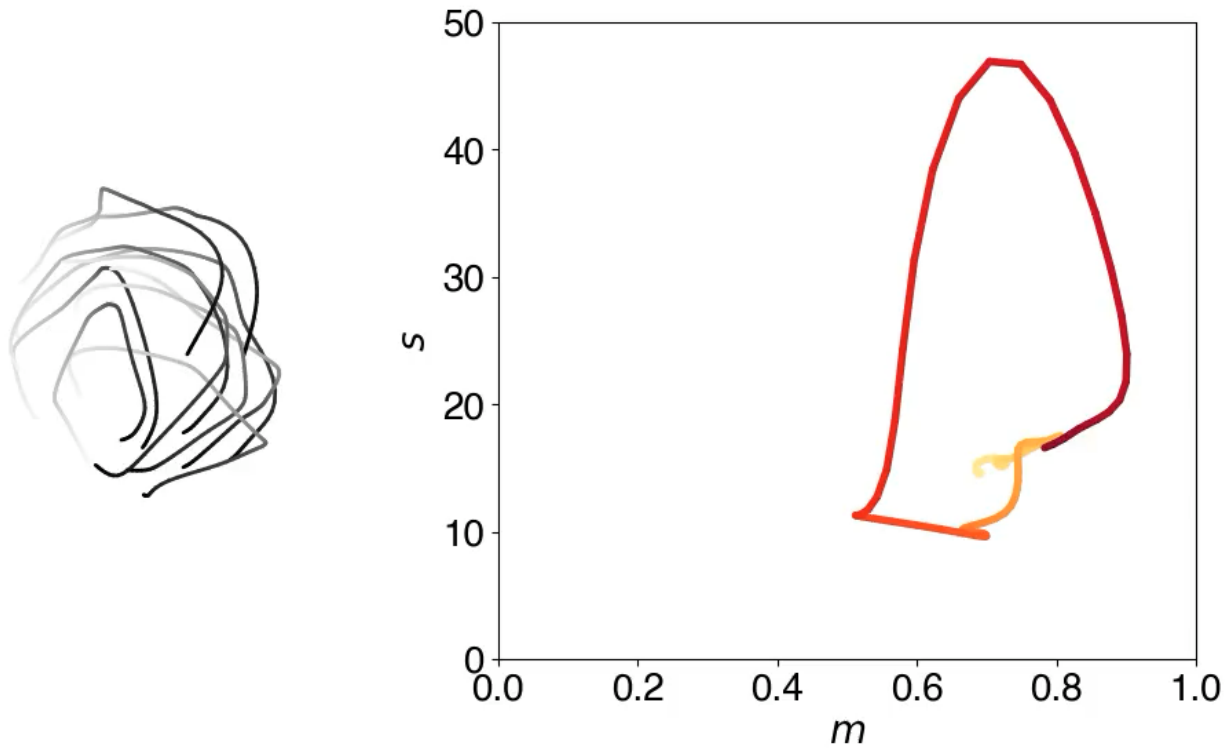
Speed variations can be very different across species



The m - s space (Synchrony – Speed phase-plane)



The m - s space (synchrony – speed phase-plane)



As the school swims in the arena, it is also *swimming* in the $m - s$ space.

How does the school *swim* in the $m - s$ space?



Modelling the dynamics

$$\frac{d}{dt} \begin{bmatrix} \mathbf{m} \\ s \end{bmatrix} = \mathbf{f}(m, s) + G(m, s) \cdot \eta(t)$$

strength of the
fluctuations

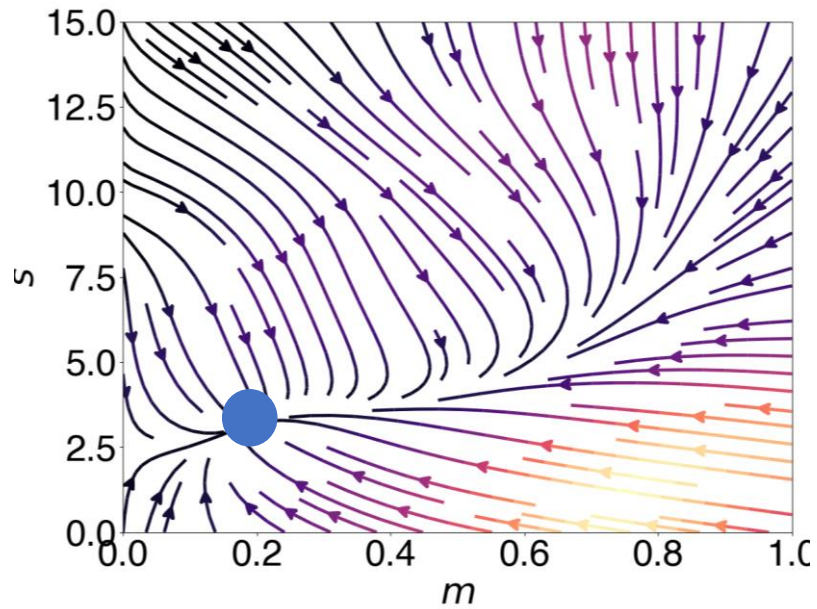
The dynamics of the school
in the m - s space

the average rate of change
of m and s

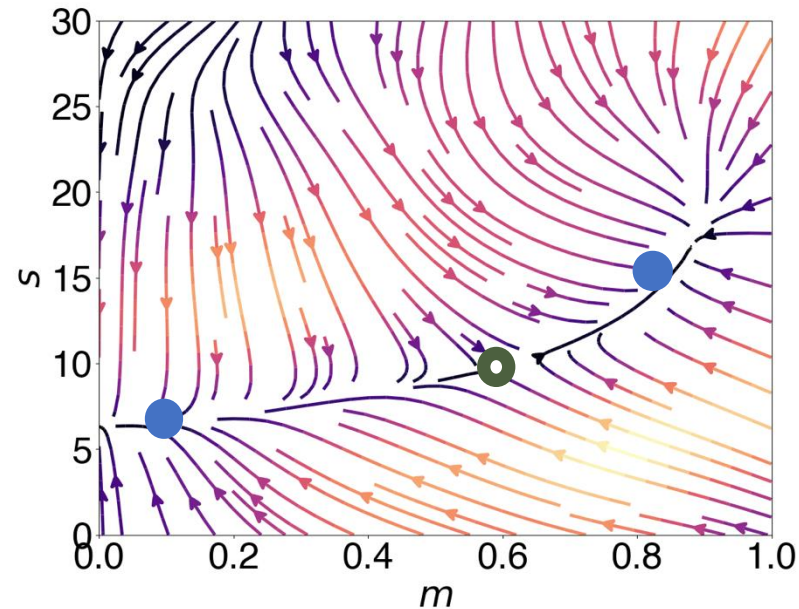
stochastic fluctuations
about the average change

Data-Derived Flow Diagrams/Equations: fixed points, null clines and stability

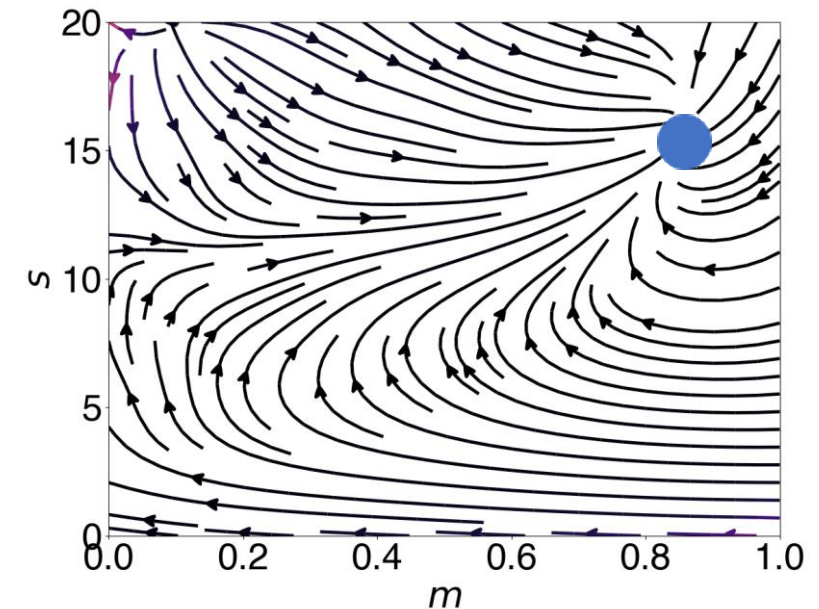
Class I: Intrinsic Noise-induced order!



Class II: Bistable Deterministic Order!



Class III: Deterministic order!



Ongoing work of Arshed Nabeel (with many others)

Summary so far: Noise and synchrony

- Broad classes of dynamics of synchrony:
 - Noise-induced Order
 - Bistable Deterministic Order
 - Unistable Deterministic Order
- Typically: The disordered state exhibits more noise, and pushes system away from the disorder.
- Methodological novelty: Data-driven stochastic differential equations.



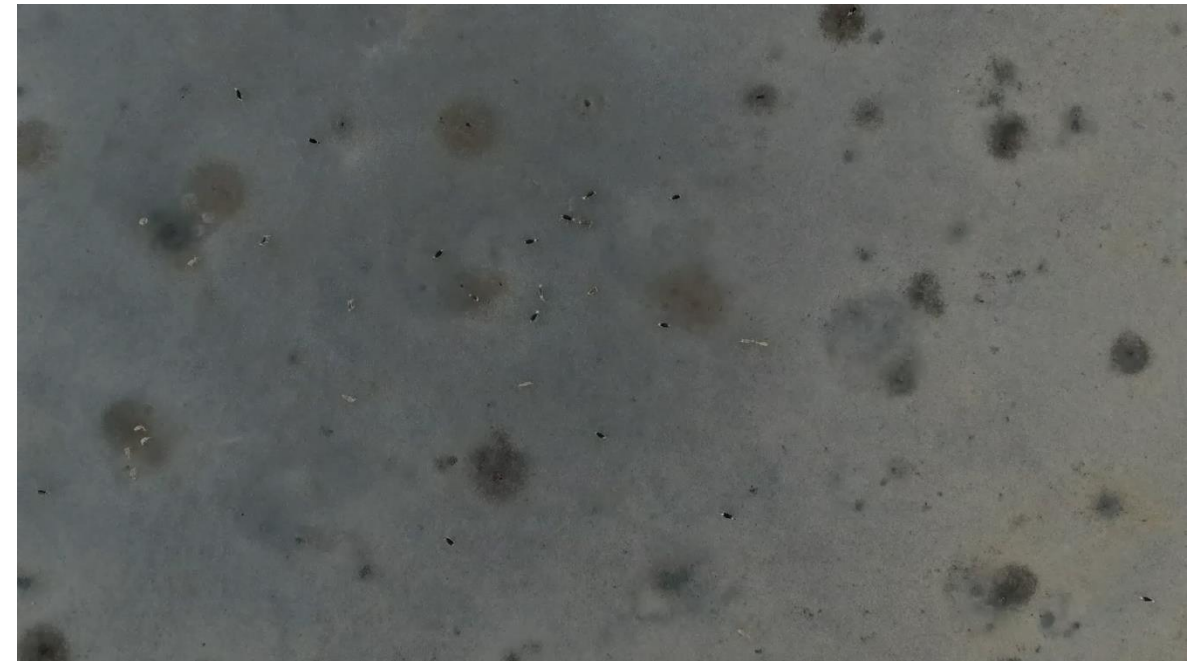
Collective Escape Dynamics: Jadhav et al 2024



Collective Escape Dynamics: Jadhav et al - Ongoing



Rathore et al - Ongoing



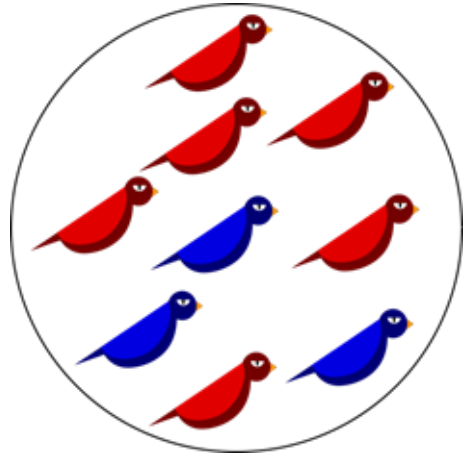
Lekking - a social mating system
Rathore et al, 2023, Phil. Tran. Roy. Soc B

Outline for today's talk: Noise to Order!

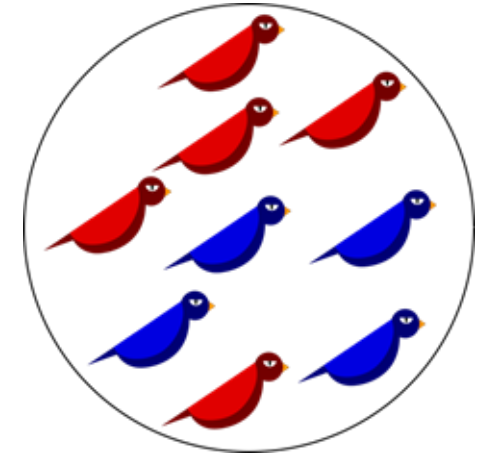
- Theme 1: Deciphering dynamics of fish schools
 - Noise helps characterize the nature of synchrony.
 - Experiments of fish schools
- A novel method: Data-driven equation discovery
- Theme 2: Evolution and Noise



Simplest case of evolutionary dynamics: two types



Birth, death, mutation



p = proportion of type 1

Changes over time, following
the replicator equation!

$$\frac{dp}{dt} = p(1 - p)(w_1 - w_2)$$

w_i : fitness of type i

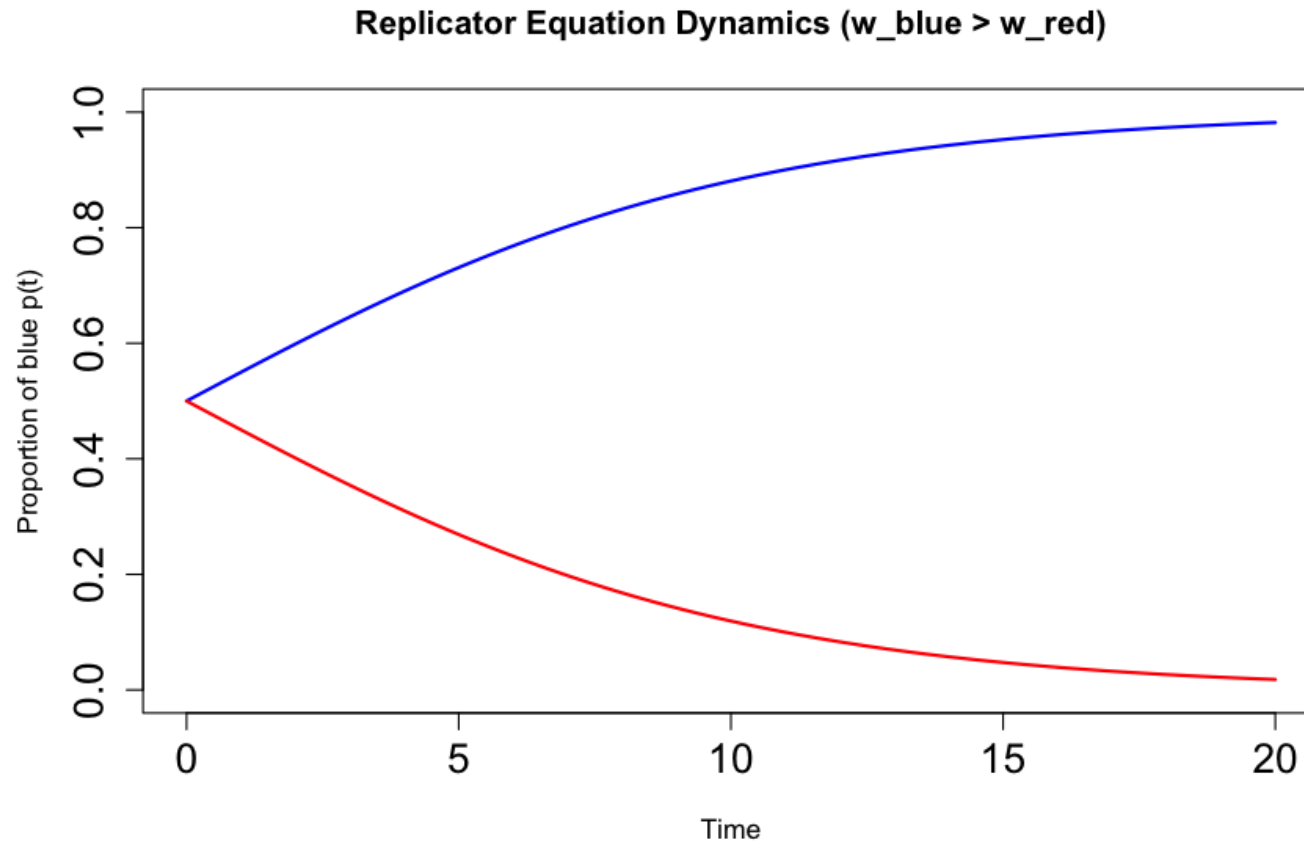
$$w_i = b_i - d_i$$

Natural selection

- ‘Survival of the fittest’:
 - If $w_{blue} > w_{red}$, $p \rightarrow 1$ over time.

Replicator equation

$$\frac{dp}{dt} = p(1-p)(w_1 - w_2)$$

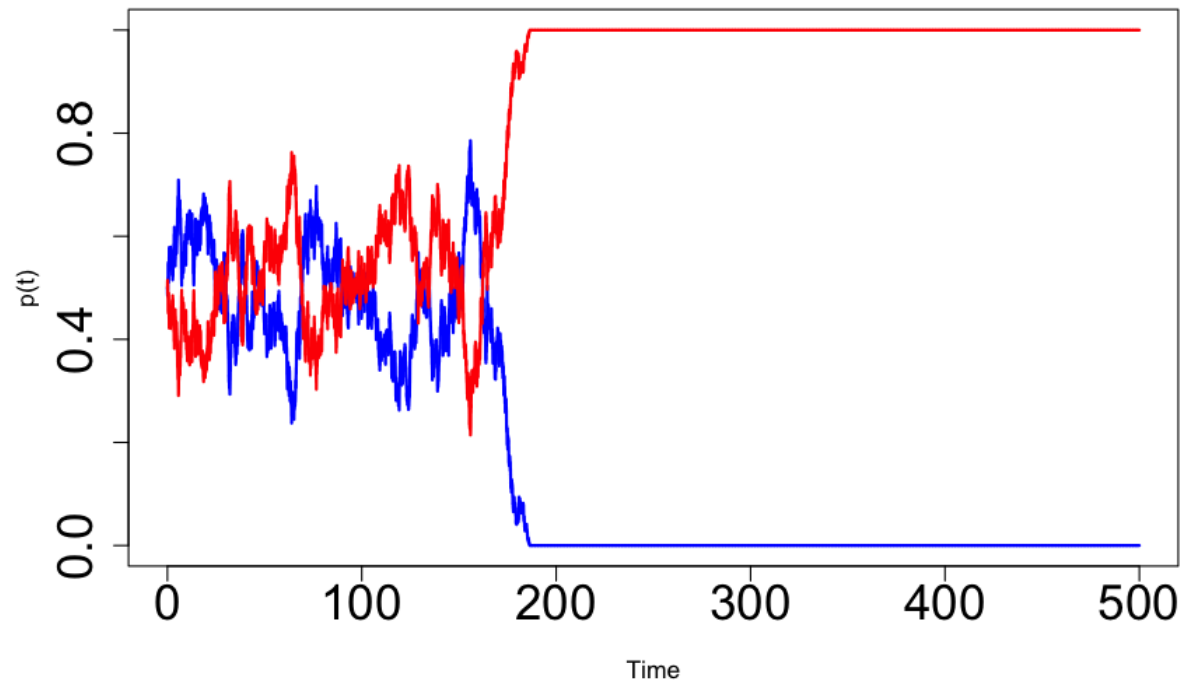


Implicit assumption: Non-structured and Infinitely large population, thus stochasticity can be ignored.

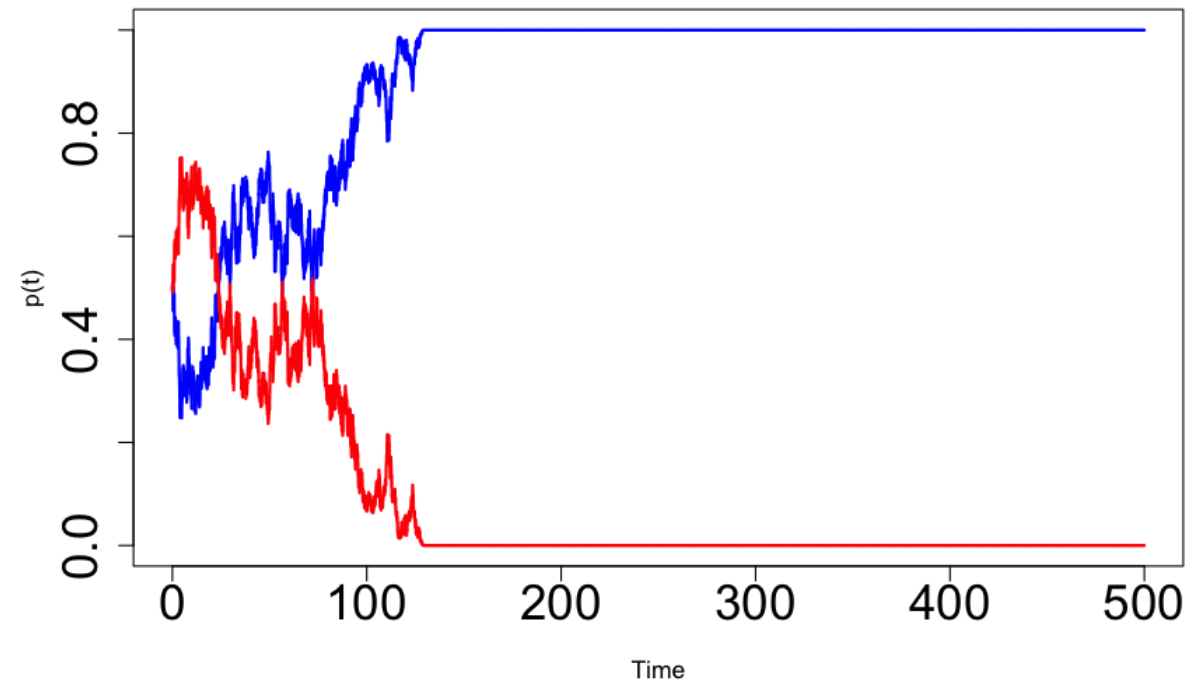
Random genetic drift: finite populations

- Birth and death are stochastic.
 - We can expect stochastic fluctuations even if two traits/alleles are of equal fitness
 $W_{blue} = W_{red}$
 - **Prob of fixation of red (or blue) = Initial frequency of red (or blue)**

Drift ($w_1 = 1.00$, $w_2 = 1.00$, $N = 100$)



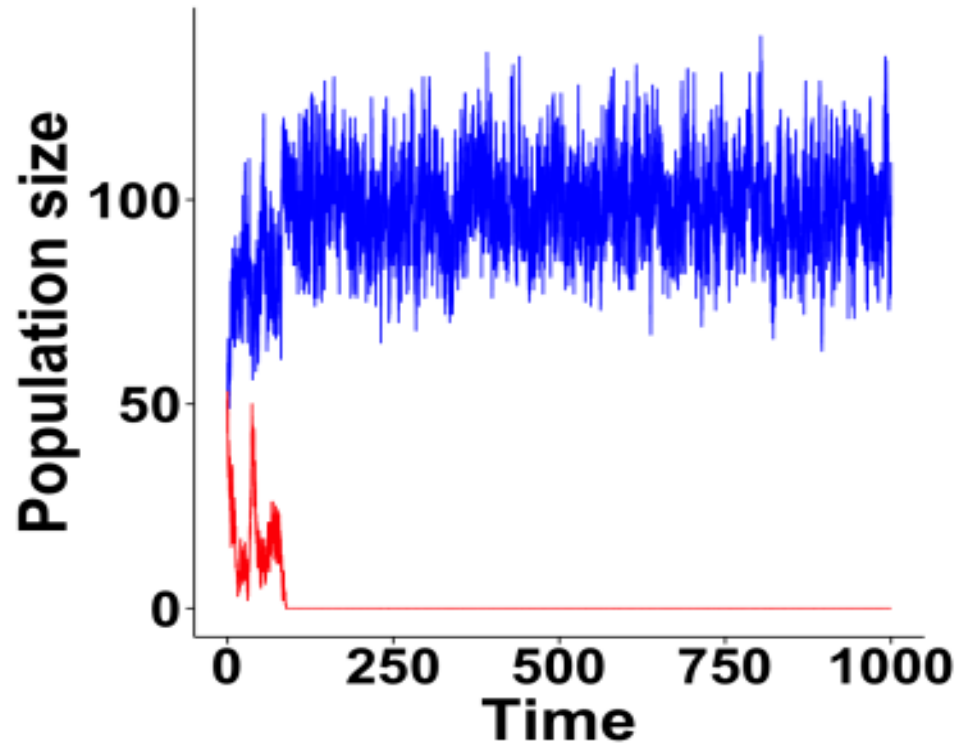
Drift ($w_1 = 1.00$, $w_2 = 1.00$, $N = 100$)



However:

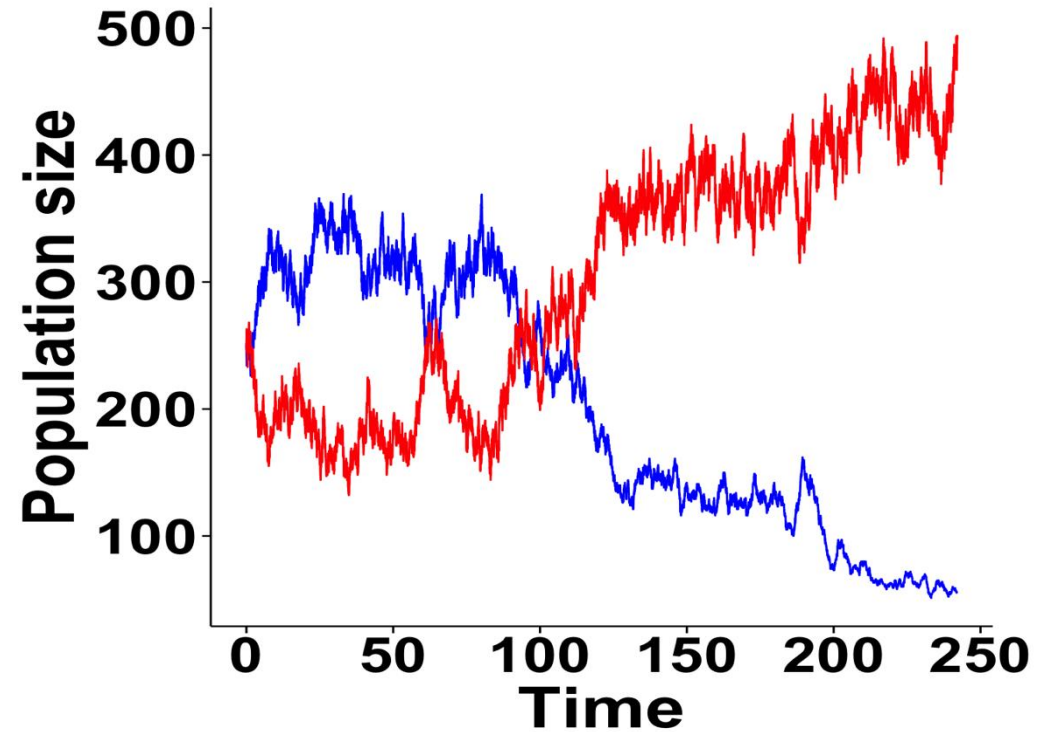
- Much of finite population theory assumes: Population size is fixed.
- Due to stochastic birth and death:
 - p (frequency) fluctuations over time
 - N (population size) also fluctuates over time
- Most classic models ignore that N (population size) also fluctuates over time.

If we allow N to fluctuate: Eco-evolutionary dynamics



K = 100

Small populations: Blue fixation
(Reversal of selection; not merely drift)



K = 1000

Selection: Large populations: Red fixation

An illustration of how noise and ecology may affect evolution

- Assume that Fitness (A) > Fitness (B)
 - Selection prefers A.
- Caveat: This is guaranteed only in infinite populations!
- In finite fluctuating populations:
 - B may be preferred over A: IF trait B has slower turnover rate (i.e. slow birth and slow death rates).
 - *Noise-induced reversal of selection*





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SYNTHESIS

Eco-Evolutionary Dynamics for Finite Populations and the Noise-Induced Reversal of Selection

Ananda Shikhara Bhat^{1,2,*} and Vishweshha Guttal²

Assumption: We can define per-capita birth and death rates



Population density
of type i individuals

Per-capita birth rate of
type i individuals

$$b_i(\mathbf{x}) = x_i \beta_i(\mathbf{x})$$
$$d_i(\mathbf{x}) = x_i \delta_i(\mathbf{x})$$

Per-capita death rate of
type i individuals

Fitness of the i^{th} type $w_i(\mathbf{x}) = \beta_i(\mathbf{x}) - \delta_i(\mathbf{x})$

Turnover rate of the i^{th} type $\tau_i(\mathbf{x}) = \beta_i(\mathbf{x}) + \delta_i(\mathbf{x})$

An equation for population density dynamics



Fitness controls
'deterministic part'



Turnover controls
'stochastic part'

$$dx_i = x_i w_i(\mathbf{x}) dt + \frac{1}{\sqrt{K}} \sqrt{x_i \tau_i(\mathbf{x})} dW_t^{(i)}$$



$\approx N(0, dt)$
random variable

$$\mathbb{E}[dx_i] = w_i x_i$$

$$\text{Var}[dx_i] = \tau_i x_i / K$$



Example: If there are two alleles (red, blue)

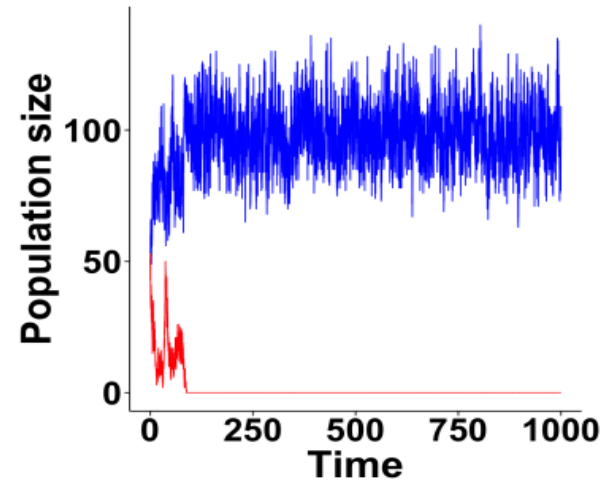
- Assume finite N and no selection ($w_{blue} = w_{red}$)
- **Classic expectation:** $dp = \text{noise}$
 - Random genetic drift: red and blue equally likely to fix (if $p(t=0)=0.5$).
 - TRUE only if $N = \text{fixed}$.
- Our formalism predicts, if N is also fluctuating:

$$dp = - (\tau_{blue} - \tau_{red})/N dt + \text{noise}$$

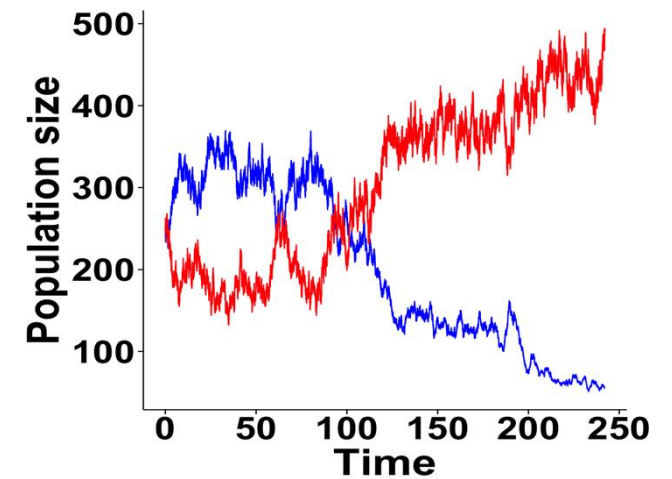
- **The allele with a lower turnover rate has an advantage!**

Recall: Turnover rate of the i^{th} type $\tau_i(\mathbf{x}) = \beta_i(\mathbf{x}) + \delta_i(\mathbf{x})$

- Turnover measures ‘pace of life’
- Key predictions are:
 - Outcomes of larger and smaller populations need not be same, if turnover rates are not same.
 - In smaller populations, slower paced type (those with lower value of τ) has an advantage, even if fitness are equal!
 - A neutral evolution requires traits to equal turnover rates, not just equal fitness.



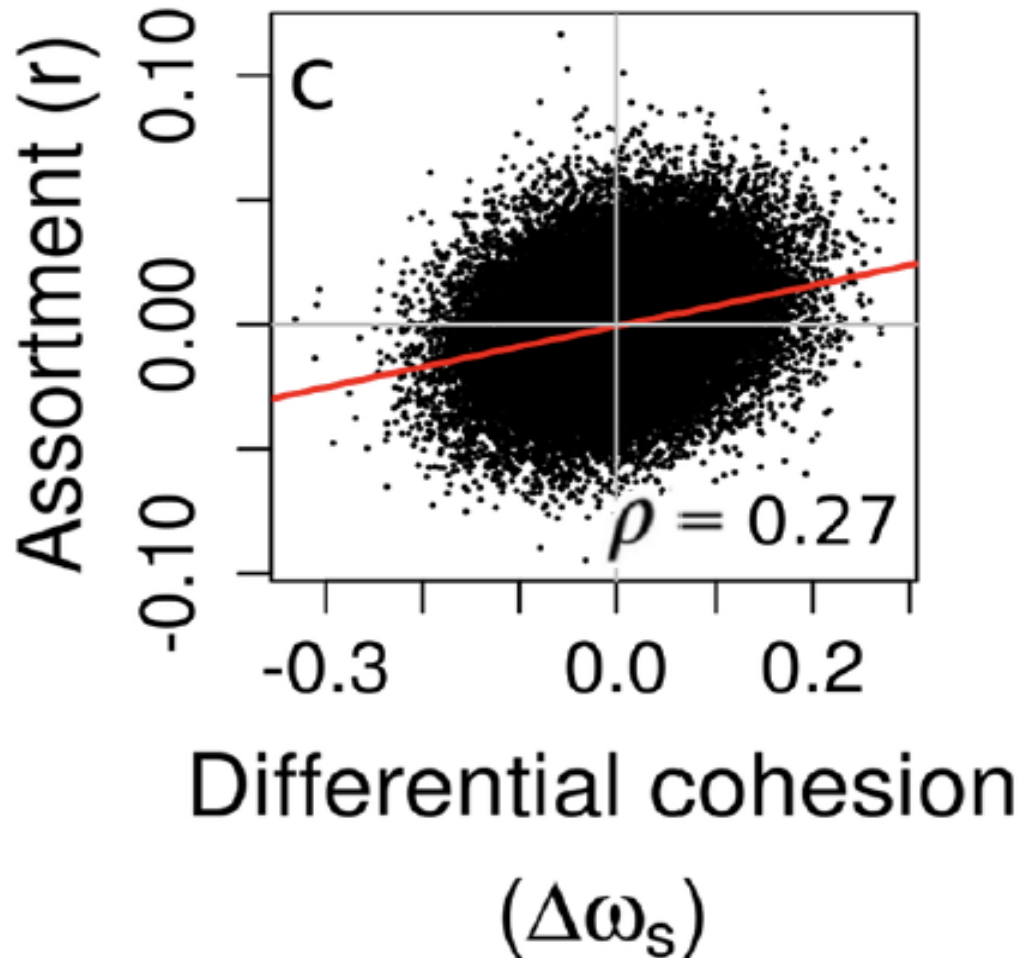
K = 100



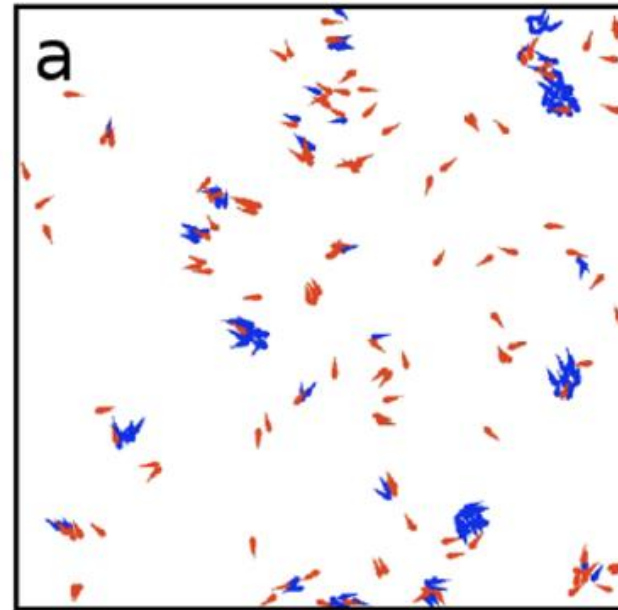
K = 1000

Bhat and Guttal, 2025, Am Nat

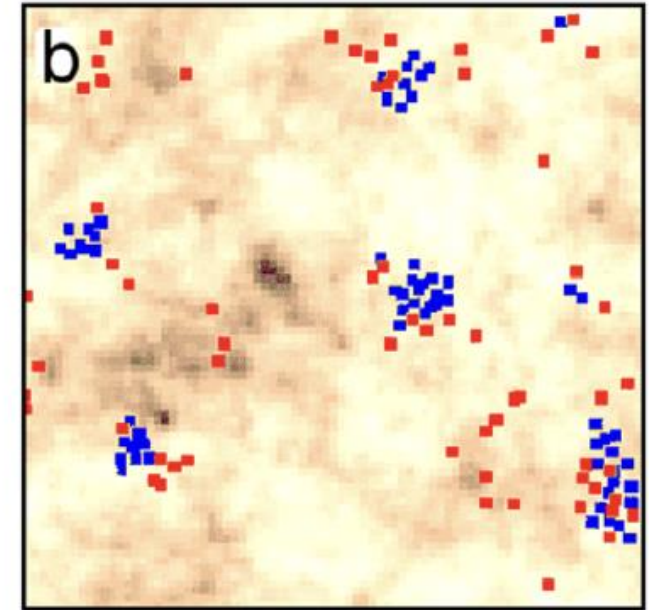
Some older work: Demographic Noise and Evolved differential cohesion leads to assortment of cooperators



Active system



Passive system



Joshi, Couzin, Levin, Guttal 2017 PloS Comp Biology

Joshi and Guttal, 2018, Evolution

Synthesis: Noise – of finite systems -- is intriguing!

- Finite systems => Intrinsic noise.
 - Strength of noise depends on system size and the state of the system!
- Flocking Systems: Three broad classes of collective motion in finite flocks
 - Noise-induced order
 - Bistable disorder and order
 - Deterministic order
 - Typically: The disordered state exhibits more noise, and pushes system away from the disorder.
- Finite-size noise can reverse the direction of selection
 - Can facilitate the evolution of cooperation and flocking; Multi-level selection
 - Turnover rate (birth + death rates) becomes important.

Thank you all – for the invitation and for attending the talk