Self-organization of bacterial mixtures using motility regulation

J. Tailleur

Laboratoire MSC
CNRS - Université Paris Diderot

active20@KITP

Active matter

Drive at the microscopic level \(\rightarrow\) Strongly out of equilibrium \(\rightarrow\) Fundamentally new physics

- Biological relevance
- Explore new dynamical phenomenology
Active matter

Drive at the microscopic level ➔ Strongly out of equilibrium ➔ Fundamentally new physics

Clusters without attractive interactions
[van der Linden, PRL 2019]

Solitonic waves
[Bricard, Nature 2013]

Filaments
[Thutupalli, PNAS 2018]

- Biological relevance
- Active Soft Materials
- Explore new dynamical phenomenology
- Build generic framework for Active Matter
Active vs Passive particles

\[ m\dot{v} = -V'_{ext}(x) - \gamma v + \sqrt{2\gamma kT} \eta \]

- Colloid in a fluid at equilibrium:
Active vs Passive particles

$$m\dot{v} = -V'_{\text{ext}}(x) - \gamma v + \sqrt{2\gamma kT}\eta$$

- Colloid in a fluid at equilibrium:

  - **Dissipation**: mean (drag) force from the fluid $\propto \gamma$
Active vs Passive particles

\[ m \dot{v} = -V'_{\text{ext}}(x) - \gamma v + \sqrt{2 \gamma kT} \eta \]

- Colloid in a fluid at equilibrium: Fluctuation-Dissipation theorem \( D = kT/\gamma \)
  - Dissipation: mean (drag) force from the fluid \( \propto \gamma \)
  - Injection of energy: fluctuating force from the fluid \( \propto \gamma kT \)
Active vs Passive particles

\[ \dot{mv} = -V'_\text{ext}(x) - \gamma v + \sqrt{2\gamma kT} \eta \]

- Active matter:
  - **Dissipation**: mean (drag) force from the fluid $\propto \gamma$
  - **Injection of energy**: fluctuating force from the fluid $\propto \gamma kT$
Active vs Passive particles

\[ m \dot{v} = -V'_{\text{ext}}(x) - \gamma v + \sqrt{2\gamma kT} \eta + f_P u(\theta) \]

- **Active matter:**
  - **Dissipation:** mean (drag) force from the fluid \( \propto \gamma \)
  - **Injection of energy:** fluctuating force from the fluid \( \propto \gamma kT \)
  - **Injection of energy:** self-propulsion force \( f_P u(\theta) \)
Active vs Passive particles

\[ m \dot{\mathbf{v}} = -V'_{\text{ext}}(x) - \gamma \mathbf{v} + \sqrt{2 \gamma kT \eta} + f_P \mathbf{u}(\theta) \]

- **Active matter:**  → **No FDT:** system driven out of equilibrium
  - **Dissipation:** mean (drag) force from the fluid \( \propto \gamma \)
  - **Injection of energy:** fluctuating force from the fluid \( \propto \gamma kT \)
  - **Injection of energy:** self-propulsion force \( f_P \mathbf{u}(\theta) \)
Active vs Passive particles

\[ 0 = m \dot{v} = -V'_{\text{ext}}(x) - \gamma v + \tilde{\eta} \]

- Active matter: \( \rightarrow \) No FDT: system driven out of equilibrium
  - Dissipation: mean (drag) force from the fluid \( \propto \gamma \)
  - Injection of energy: fluctuating force from the fluid \( \propto \gamma kT \)
  - Injection of energy: self-propulsion force \( f_p u(\theta) \)
Active vs Passive particles

\[ 0 = m \dot{v} = -V'_{\text{ext}}(x) - \gamma v + \tilde{\eta} \]

- Active matter: \(\rightarrow\) No FDT: system driven out of equilibrium
  - \(\rightarrow\) Dissipation: mean (drag) force from the fluid \(\propto \gamma\)
  - \(\rightarrow\) Injection of energy: fluctuating force from the fluid \(\propto \gamma kT\)
  - \(\rightarrow\) Injection of energy: self-propulsion force \(f_p u(\theta)\)
- Breakdown of detailed-balance \(\rightarrow\) Steady-state not easily inferred from dynamics
Passive vs active dynamics

\[ \dot{\mathbf{r}} = -\nabla V(\mathbf{r}) + \sqrt{2D} \eta \]

Gaussian white noise $\eta$


\[ \dot{\mathbf{r}} = -\nabla V(\mathbf{r}) + \mathbf{v}_p \]

Non-Gaussian persistent noise $\mathbf{v}_p$

No working theory
Passive vs active dynamics

\[ \dot{r} = -\nabla V(r) + \sqrt{2D}\eta \]

Gaussian white noise $\eta$


\[ \dot{r} = -\nabla V(r) + v_p \]

Non-Gaussian persistent noise $v_p$

No working theory

Rather frustrating situation: what can be saved from (near-) equilibrium methods?
Passive vs active dynamics

\[ \dot{r} = -\nabla V(r) + \sqrt{2D}\eta \]
Gaussian white noise \( \eta \)

\[ \dot{r} = -\nabla V(r) + v_p \]
Non-Gaussian persistent noise \( v_p \)
No working theory

Rather frustrating situation: what can be saved from (near-) equilibrium methods?

Outside the limit in which \( v_p \) amounts to a Gaussian white noise
• Thermal Equilibrium
  ➔ Time-reversal symmetry in steady-state
  ➔ Boltzman weight: guides our intuition
Self-organization in & out of equilibrium

- **Thermal Equilibrium**
  - Time-reversal symmetry in steady-state
  - Boltzman weight: guides our intuition

- **Example:** Liquid-gas phase transition
  - Passive Brownian particles with attractive interactions
  - Entropy vs Energy: disorder vs cohesion
  - Lowering $T$: transition from gas to liquid (with coexistence)
Self-organization in & out of equilibrium

• Thermal Equilibrium
  ➔ Time-reversal symmetry in steady-state
  ➔ Boltzman weight: guides our intuition

• Example: Liquid-gas phase transition
  ➔ Passive Brownian particles with attractive interactions
  ➔ Entropy vs Energy : disorder vs cohesion
  ➔ Lowering $T$: transition from gas to liquid (with coexistence)

• Outside equilibrium
  ➔ No generic formula for steady-state distribution
  ➔ Little basis upon which to build intuition
  ➔ Few guiding principles for self-assembly
A statistical-mechanics framework for Active Matter

How to go from micro to macro?
To understand and control (self-)organization?

J. Tailleur (CNRS-Univ Paris Diderot)
A statistical-mechanics framework for Active Matter

- How to go from micro to macro?
A statistical-mechanics framework for Active Matter

- How to go from micro to macro?
- To understand and control (self-)organization?

- **Run**: straight line (velocity $v \simeq 20 \mu m.s^{-1}$)

- **Tumble**: new direction (rate $\alpha \simeq 1 s^{-1}$, duration $\tau \simeq 0.1 s$)

- **Run**: straight line (velocity $v \approx 20 \mu \text{m.s}^{-1}$)
- **Tumble**: new direction (rate $\alpha \approx 1 \text{s}^{-1}$, duration $\tau \approx 0.1 \text{s}$)
Self-propelled colloids

- E.g. Janus colloids with \textit{asymmetric} coating

\[ \dot{r}(t) = v_u(\theta(t)) + \sqrt{2}D_t\eta; \quad \dot{\theta}(t) = \sqrt{2}D_r\xi \]

\[ v_{Pt} \approx 1 \mu s^{-1}; \quad D_t \approx 3 \mu^2 s^{-1}; \quad D_{eff} \approx 1 - 4 \mu^2 s^{-1} \]

- Many other types of self-propelled colloids...
- Light-controlled \cite{Palacci2013}

\[ \text{J. Tailleur (CNRS-Univ Paris Diderot)} \]
Self-propelled colloids

- E.g. Janus colloids with asymmetric coating

- Self [diffusio-] phoresis

\[ \dot{r}(t) = v_u(\theta) + \sqrt{2}Dt \eta; \dot{\theta}(t) = \sqrt{2}D \xi \]

\[ \bar{v} \approx 1 \mu s^{-1}; D_t \approx 3 \mu^2 s^{-1}; D_{\text{eff}} \approx 1 - 4 \mu^2 s^{-1} \]

- Many other types of self-propelled colloids...
Self-propelled colloids

- E.g. Janus colloids with asymmetric coating
- **Self [diffusio-] phoresis**
- Active Brownian Particles: continuous rotational diffusion

\[
\dot{\mathbf{r}}(t) = v \mathbf{u}(\theta) + \sqrt{2D_t} \eta; \quad \dot{\theta}(t) = \sqrt{2D_r} \xi
\]

\[
v \simeq 1 \mu \text{s}^{-1}; \quad D_t \simeq 0.3 \mu^2 \text{s}^{-1}; \quad D_{\text{eff}} \simeq 1 - 4 \mu^2 \text{s}^{-1}
\]
Self-propelled colloids

- E.g. Janus colloids with asymmetric coating

- Self [diffusio-] phoresis

- Active Brownian Particles: continuous rotational diffusion

\[
\begin{align*}
\dot{r}(t) &= v\mathbf{u}(\theta) + \sqrt{2D_t}\eta; & \dot{\theta}(t) &= \sqrt{2D_r}\xi \\
v &\approx 1\mu.s^{-1}; & D_t &\approx 3\mu^2.s^{-1}; & D_{\text{eff}} &\approx 1 - 4\mu^2.s^{-1}
\end{align*}
\]

- Many other types of self-propelled colloids...

Motility-control as a self-organization principle

- Self-propelled particles with propelling speed \( v \)
- Diverse reorientation mechanisms (ABPs, RTPs, AOUPs, etc.)
- Generic: properties of \( v \) → Control steady states
Motility-control as a self-organization principle

- Self-propelled particles with propelling speed $v$
- Diverse reorientation mechanisms (ABPs, RTPs, AOUPs, etc.)
- Generic: properties of $v$ → Control steady states

I. Non-interacting particles with spatially varying speed $v(r)$

II. Quorum-sensing: density-dependent speed $v(\rho)$

III. Application to bacterial pattern formation

IV. Multi-component systems
Position-dependent self-propulsion speed \( v(r) \)

- Master-equation for the probability density \( P(r, \theta) \)
  \[
  \partial_t P(r, \theta; t) = -\nabla \cdot [v(r) u(\theta) P(r, \theta)] + \Theta P
  \]

- \( \Theta P \): Randomization of orientation
  \[
  \Theta_{ABP} P = D_r \Delta_{\theta} P(r, \theta); \quad \Theta_{RTP} P = -\alpha P(r, \theta) + \int d\theta' \frac{\alpha}{2\pi} P(r, \theta')
  \]
Position-dependent self-propulsion speed \( v(r) \)

- Master-equation for the probability density \( P(r, \theta) \)

\[
\partial_t P(r, \theta; t) = -\nabla \cdot [v(r)u(\theta)P(r, \theta)] + \Theta P
\]

- \( \Theta P \): Randomization of orientation

\[
\Theta_{ABP} P = D_r \Delta_\theta P(r, \theta); \quad \Theta_{RT} P = -\alpha P(r, \theta) + \int d\theta' \frac{\alpha}{2\pi} P(r, \theta')
\]

- Any isotropic function: \( \Theta f(r) = 0 \implies P_{stat}(r) \propto \frac{1}{v(r)} \) (up to normalization issues)

- SPPs spend more time where they go slower [Schnitzer 1993 PRE, JT & Cates PRL 2008, EPL 2013]
Position-dependent self-propulsion speed $v(r)$

- Master-equation for the probability density $P(r, \theta)$

$$\partial_t P(r, \theta; t) = -\nabla \cdot [v(r)u(\theta)P(r, \theta)] + \Theta P$$

- $\Theta P$: Randomization of orientation

$$\Theta_{ABP} P = D_r \Delta_\theta P(r, \theta); \quad \Theta_{RTP} P = -\alpha P(r, \theta) + \int d\theta' \frac{\alpha}{2\pi} P(r, \theta')$$

- Any isotropic function: $\Theta f(r) = 0 \rightarrow P_{\text{stat}}(r) \propto \frac{1}{v(r)}$ (up to normalization issues)

- SPPs spend more time where they go slower [Schnitzer 1993 PRE, JT & Cates PRL 2008, EPL 2013]

- (A bit of) translational diffusion only changes this quantitatively

$$P_{\text{stat}} \propto \frac{1}{\sqrt{D + v^2 \tau}}; \quad \tau^{-1} = d(d - 1)D_r + d\alpha$$
Experiments with bacteria

- Flagellar rotor can be controlled using light (proteorhodopsin)

- Quantitative check that $\rho(r) \propto \frac{1}{v(r)}$ [Arlt et al., arxiv:1902.10083]

- Accumulation can be triggered by $v(r), \alpha(r), \beta(r)$

- Many ways of slowing down
Experiments with bacteria

- Flagellar rotor can be controlled using light (proteorhodopsin)

- Quantitative check that $\rho(r) \propto \frac{1}{v(r)}$ [Arlt et al., arxiv:1902.10083]

- Painting with bacteria (and light modulation)

![Mona Lisa](image1.png)  
[Vizsnyiczai et al., Nat. Com. (2017)]

![Smiley](image2.png)  
[Arlt et al., Nat. Com. (2018)]
Experiments with bacteria

• Flagellar rotor can be controlled using light (proteorhodopsin)

• Quantitative check that $\rho(r) \propto \frac{1}{v(r)}$ [Arlt et al., arxiv:1902.10083]

• Painting with bacteria (and light modulation)

• Accumulation can be triggered by $v(r), \alpha(r), \beta(r)$ $\rightarrow$ Many ways of slowing down
Interactions: Quorum-Sensing

- Motility requires energy source  →  Interactions with the environment (food, fuel source, etc.)
Interactions: Quorum-Sensing

- Motility requires energy source → Interactions with the environment (food, fuel source, etc.)
- Local competition between particles
- Mobility depends on local density of active particles
Interactions: Quorum-Sensing

- Motility requires energy source \(\rightarrow\) Interactions with the environment (food, fuel source, etc.)
- Local competition between particles
- Mobility depends on local density of active particles
- Simplest of model: Local in time, quasi-local in space [JT, Cates, PRL 2008]

\[
\dot{\mathbf{r}}_i = v[\tilde{\rho}(\mathbf{r}_i)] \mathbf{u}(\theta_i); \quad \dot{\theta}_i = [\ldots]
\]

- Particles measure an effective density \(\tilde{\rho}(r)\)

\[
\tilde{\rho}(\mathbf{r}) = \int d\mathbf{r}' K(\mathbf{r} - \mathbf{r}') \rho(\mathbf{r}')
\]

\[
\rho(\mathbf{r}') = \sum_i \delta(\mathbf{r}' - \mathbf{r}_i)
\]
Interactions: Quorum-Sensing

- Motility requires energy source → Interactions with the environment (food, fuel source, etc.)
- Local competition between particles
- Mobility depends on local density of active particles
- Simplest of model: Local in time, quasi-local in space [JT, Cates, PRL 2008]

\[
\dot{r}_i = v[\bar{\rho}(r_i)]u(\theta_i); \quad \dot{\theta}_i = [...]
\]

- Particles measure an effective density \( \bar{\rho}(r) \)

\[
\bar{\rho}(r) = \int dr' K(r - r') \rho(r')
\]

\[
\rho(r') = \sum_i \delta(r' - r_i)
\]

- In reality, much more complex (taxis, time-delay, etc.)
• Janus colloids in water-lutidine mixture with $T \leq T_c$
  [Volpe et al, Soft Mat. 2011]

• Light $\rightarrow$ Demixing on one side $\rightarrow$ Phoretic (self)-propulsive force
Engineering quorum-Sensing [Bauerle et al Nat Com 2019]

- Janus colloids in water-lutidine mixture with $T \leq T_c$ [Volpe et al, Soft Mat. 2011]

- Light $\rightarrow$ Demixing on one side $\rightarrow$ Phoretic (self)-propulsive force

- $v(\tilde{\rho})$ through feedback mechanism

$\tilde{\rho} = \tilde{v} \rho$

Can we understand this using our simple model?

J. Tailleur (CNRS-Univ Paris Diderot)
Engineering quorum-Sensing [Bauerle et al Nat Com 2019]

- Janus colloids in water-lutidine mixture with $T \leq T_c$
  [Volpe et al, Soft Mat. 2011]

- Light $\rightarrow$ Demixing on one side $\rightarrow$ Phoretic (self)-propulsive force

- $v(\tilde{\rho})$ through feedback mechanism

- Can we understand this using our simple model?

$$v = v(\rho) \quad \text{and} \quad v = v_0 \in \mathbb{R}$$
Consider RTPs and ABPs with QS interactions: 
\[ \dot{r}_i = v[\tilde{\rho}(r_i)]u(\theta_i); \quad \dot{\theta}_i = [...]. \]

• Consider RTPs and ABPs with QS interactions: \( \dot{\mathbf{r}}_i = v[\bar{\rho}({\mathbf{r}}_i)] \mathbf{u}(\theta_i); \quad \dot{\theta}_i = [...]\)


\( v(\rho) \) decreases as \( \rho \) increases → Generic phase separation

- Tumble

- Rotational diffusion
Hand-waving explanation

- Non-uniform speed
  \[ v(r) \dot{P}(r, \theta) = -\nabla r \cdot \left[ v(r) P(r, \theta) u(\theta) \right] + D r \partial^2_\theta P(r, \theta) \]

- Stationary distribution
  \[ P(r, \theta) = \kappa v(r) \] (Schnitzer PRE 1993, JT & Cates PRL 2008)

- Repulsive Interactions
  \[ v'(\rho) < 0 \]

- Feedback loop
  \[ \rho_0 = \kappa v(\rho_0) v(\rho_0) \]
  \[ \rho_0 + \delta \rho = \kappa v(\rho_0) + \delta \rho v(\rho_0) + v'(\rho_0) \delta \rho \]
  \[ \approx \kappa v(\rho_0) \left( 1 - v'(\rho_0) \frac{\delta \rho v(\rho_0)}{\kappa v(\rho_0)} \right) = \rho_0 - \rho_0 v'(\rho_0) \delta \rho \]

- Linear instab.
  \[ 1 \leq -\frac{\dot{\rho}_0 v'(\rho_0)}{v(\rho_0)} \]


- How can we characterize this phase separation?
Hand-waving explanation

- **Non-uniform speed** $v(r)$

  \[ \dot{P}(r, \theta) = -\nabla_r \cdot [v(r) P(r, \theta) u(\theta)] + D_r \partial^2_{\theta} P(r, \theta) \]

- **Stationary distribution** $P(r, \theta) = \frac{\kappa}{v(r)}$ [Schnitzer PRE 1993, JT & Cates PRL 2008]
Hand-waving explanation

- **Non-uniform speed** \( v(r) \)

\[
\dot{P}(r, \theta) = -\nabla_r \cdot [v(r) P(r, \theta) u(\theta)] + D_r \partial^2_\theta P(r, \theta)
\]

- **Stationary distribution** \( P(r, \theta) = \frac{\kappa}{v(r)} \) [Schnitzer PRE 1993, JT & Cates PRL 2008]

- **Repulsive Interactions** \( v'(\rho) < 0 \)
Hand-waving explanation

- **Non-uniform speed** $v(r)$

$$\dot{P}(r, \theta) = -\nabla_r \cdot [v(r) P(r, \theta) u(\theta)] + D_r \partial^2_\theta P(r, \theta)$$

- **Stationary distribution** $P(r, \theta) = \frac{\kappa}{v(r)}$ [Schnitzer PRE 1993, JT & Cates PRL 2008]

- **Repulsive Interactions** $v'(\rho) < 0 \rightarrow$ Feedback loop

\[ \rho_0 = \frac{\kappa}{v(\rho_0)} \]
Hand-waving explanation

- Non-uniform speed $v(r)$
  \[ \dot{P}(r, \theta) = -\nabla_r \cdot [v(r)P(r, \theta)u(\theta)] + D_r \partial_\theta^2 P(r, \theta) \]

- Stationary distribution $P(r, \theta) = \frac{\kappa}{v(r)}$ [Schnitzer PRE 1993, JT & Cates PRL 2008]

- Repulsive Interactions $v'(\rho) < 0 \rightarrow$ Feedback loop

\[ \rho_0 + \delta \rho = \frac{\kappa}{v(\rho_0)} + \delta \rho \]

\[ v(\rho_0) \]
Hand-waving explanation

- Non-uniform speed $v(r)$
  \[
  \dot{P}(r, \theta) = -\nabla_r \cdot [v(r) P(r, \theta) u(\theta)] + D_r \partial_\theta^2 P(r, \theta)
  \]

- Stationary distribution $P(r, \theta) = \frac{\kappa}{v(r)}$ [Schnitzer PRE 1993, JT & Cates PRL 2008]

- Repulsive Interactions $v'(\rho) < 0 \quad \Rightarrow \quad$ Feedback loop

![Diagram showing the feedback loop](image)
Hand-waving explanation

- Non-uniform speed $v(r)$

$$\dot{P}(r, \theta) = -\nabla_r \cdot [v(r)P(r, \theta)u(\theta)] + D_r \partial^2_\theta P(r, \theta)$$

- Stationary distribution $P(r, \theta) = \frac{\kappa}{v(r)}$ [Schnitzer PRE 1993, JT & Cates PRL 2008]

- Repulsive Interactions $v'(\rho) < 0$ → Feedback loop

$$\rho_0 + \delta \rho = \frac{\kappa}{v(\rho_0)} + \delta \rho$$

$\rho(\rho_0) + v'(\rho_0)\delta \rho$
Hand-waving explanation

- **Non-uniform speed** $v(r)$
  
  $$ \dot{P}(r, \theta) = -\nabla_r \cdot [v(r)P(r, \theta)u(\theta)] + D_r \partial^2_\theta P(r, \theta) $$

- **Stationary distribution** $P(r, \theta) = \frac{\kappa}{v(r)}$ [Schnitzer PRE 1993, JT & Cates PRL 2008]

- **Repulsive Interactions** $v'(\rho) < 0 \quad \rightarrow \text{Feedback loop}$

\[ \rho_0 + \delta \rho = \frac{\kappa}{v(\rho_0)} + \delta \rho \]

\[ v(\rho_0) + v'(\rho_0)\delta \rho \approx \frac{\kappa}{v(\rho_0)} \left( 1 - \frac{v'(\rho_0)\delta \rho}{v(\rho_0)} \right) \]
Hand-waving explanation

- Non-uniform speed $v(r)$

$$
\dot{P}(r, \theta) = -\nabla_r \cdot [v(r)P(r, \theta)u(\theta)] + D_r \partial^2_\theta P(r, \theta)
$$

- Stationary distribution $P(r, \theta) = \frac{\kappa}{v(r)}$ [Schnitzer PRE 1993, JT & Cates PRL 2008]

- Repulsive Interactions $v'(\rho) < 0$ → Feedback loop

$$
\rho_0 + \delta \rho = \frac{\kappa}{v(\rho_0)} + \delta \rho
$$

$$
v(\rho_0) + v'(\rho_0)\delta \rho \approx \frac{\kappa}{v(\rho_0)} \left(1 - \frac{v'(\rho_0)\delta \rho}{v(\rho_0)}\right) = \rho_0 - \frac{\rho_0 v'}{v} \delta \rho
$$
Hand-waving explanation

• Non-uniform speed \( v(\mathbf{r}) \)

\[
\dot{P}(\mathbf{r}, \theta) = -\nabla_{\mathbf{r}} \cdot [v(\mathbf{r}) P(\mathbf{r}, \theta) \mathbf{u}(\theta)] + D_r \partial^2_{\theta} P(\mathbf{r}, \theta)
\]

• Stationary distribution \( P(\mathbf{r}, \theta) = \frac{\kappa}{v(\mathbf{r})} \) [Schnitzer PRE 1993, JT & Cates PRL 2008]

• Repulsive Interactions \( v'(\rho) < 0 \) → Feedback loop

\[
\rho_0 + \delta \rho = \frac{\kappa}{v(\rho_0)} + \delta \rho + v(\rho_0) + v'(\rho_0) \delta \rho \approx \frac{\kappa}{v(\rho_0)} (1 - \frac{v'(\rho_0) \delta \rho}{v(\rho_0)}) = \rho_0 - \frac{\rho_0 v'}{v} \delta \rho
\]
Hand-waving explanation

- Non-uniform speed $v(r)$
  \[
  \dot{P}(r, \theta) = -\nabla_r \cdot [v(r)P(r, \theta)u(\theta)] + D_r \partial^2_\theta P(r, \theta)
  \]

- Stationary distribution $P(r, \theta) = \frac{\kappa}{v(r)}$ [Schnitzer PRE 1993, JT & Cates PRL 2008]

- Repulsive Interactions $v'(\rho) < 0 \rightarrow$ Feedback loop

\[\rho_0 + \delta \rho = \frac{\kappa}{v(\rho_0)} + \delta \rho \quad \Rightarrow \quad v(\rho_0) + v'(\rho_0)\delta \rho \approx \frac{\kappa}{v(\rho_0)} (1 - \frac{v'(\rho_0)\delta \rho}{v(\rho_0)}) = \rho_0 - \rho_0 \frac{v'}{v} \delta \rho\]

- Linear instab. if $1 \leq -\rho_0 \frac{v'(\rho_0)}{v(\rho_0)}$
**Hand-waving explanation**

- **Non-uniform speed** \( v(r) \)
  \[
  \dot{P}(r, \theta) = -\nabla_r \cdot [v(r) P(r, \theta) u(\theta)] + D_r \partial^2_{\theta} P(r, \theta)
  \]

- **Stationary distribution** \( P(r, \theta) = \frac{\kappa}{v(r)} \) [Schnitzer PRE 1993, JT & Cates PRL 2008]

- **Repulsive Interactions** \( v'(\rho) < 0 \rightarrow \text{Feedback loop} \)

  \[
  \rho_0 + \delta \rho = \frac{\kappa}{v(\rho_0)} + \delta \rho
  \]

  \[
  v(\rho_0) + v'(\rho_0) \delta \rho \approx \frac{\kappa}{v(\rho_0)} \left( 1 - \frac{v'(\rho_0) \delta \rho}{v(\rho_0)} \right) = \rho_0 - \rho_0 v' \frac{v}{\rho_0} \delta \rho
  \]

- **Linear instab. if** \( 1 \leq -\rho_0 \frac{v'(\rho_0)}{v(\rho_0)} \rightarrow \text{Motility-induced phase-separation} \) [Cates, JT Ann. Rev. Cond. Mat. Phys. 2015]

- **How can we characterize this phase separation?**

J. Tailleur (CNRS-Univ Paris Diderot)
Hydrodynamics of Equilibrium Phase-Separation

- Large-scale dynamics of phase-separating scalar systems away from criticality

\[ \dot{\rho} = -\nabla \cdot J[\rho] \quad \text{where} \quad J[\rho] = -M[\rho] \nabla \frac{\delta \mathcal{F}}{\delta \rho} \]

- Free energy: \( \mathcal{F} = \int dx [f(\rho(x)) + \frac{\kappa(\rho)}{2} (\nabla \rho)^2] + \ldots \)
Hydrodynamics of Equilibrium Phase-Separation

- Large-scale dynamics of phase-separating scalar systems away from criticality
  \[ \dot{\rho} = -\nabla \cdot J[\rho] \quad \text{where} \quad J[\rho] = -M[\rho] \nabla \frac{\delta \mathcal{F}}{\delta \rho} \]

- Free energy: \( \mathcal{F} = \int dx [f(\rho(x)) + \frac{\kappa(\rho)}{2} (\nabla \rho)^2] + \ldots \)

- Most probable profiles \( \iff \) Minimize \( \mathcal{F}[\rho] \) with \( \int d\mathbf{r} \rho(\mathbf{r}) = V \rho_0 \)
Hydrodynamics of Equilibrium Phase-Separation

- Large-scale dynamics of phase-separating scalar systems away from criticality

\[ \dot{\rho} = -\nabla \cdot J[\rho] \quad \text{where} \quad J[\rho] = -M[\rho] \nabla \frac{\delta F}{\delta \rho} \]

- Free energy: \( F = \int dx [f(\rho(x)) + \frac{\kappa(\rho)}{2} (\nabla \rho)^2] + \ldots \)

- Most probable profiles \( \xrightarrow{\text{Minimize}} \) Minimize \( F[\rho] \) with \( \int d\mathbf{r} \rho(\mathbf{r}) = V \rho_0 \)

- Phase-separated profiles:
Hydrodynamics of Equilibrium Phase-Separation

- Large-scale dynamics of phase-separating scalar systems away from criticality
  \[ \dot{\rho} = -\nabla \cdot J[\rho] \quad \text{where} \quad J[\rho] = -M[\rho] \nabla \frac{\delta F}{\delta \rho} \]

- Free energy: \( F = \int dx [f(\rho(x)) + \frac{\kappa(\rho)}{2} (\nabla \rho)^2] + \ldots \)

- Most probable profiles \( \longleftrightarrow \) Minimize \( F[\rho] \) with \( \int d\mathbf{r} \rho(\mathbf{r}) = V \rho_0 \)

- Phase-separated profiles: Common tangent construction on \( f(\rho_0) \)

\[ f(\rho_0) \]
Hydrodynamics of Equilibrium Phase-Separation

• Large-scale dynamics of phase-separating scalar systems away from criticality

\[ \dot{\rho} = - \nabla \cdot J[\rho] \quad \text{where} \quad J[\rho] = - M[\rho] \nabla \frac{\delta F}{\delta \rho} \]

• Free energy: \( F = \int dx \left[ f(\rho(x)) + \frac{\kappa(\rho)}{2} (\nabla \rho)^2 \right] + \ldots \)

• Most probable profiles \( \leftrightarrow \) Minimize \( F[\rho] \) with \( \int d\mathbf{r} \rho(\mathbf{r}) = V \rho_0 \)

• Phase-separated profiles: Common tangent construction on \( f(\rho_0) \)

\[ f(\rho_0) \]

\[ \begin{array}{c}
\text{GAS} \\
\text{LIQUID}
\end{array} \]

\[ \begin{array}{c}
\rho_g \\
\rho \quad \rho_l
\end{array} \]

\[ \begin{array}{c}
\rho_g \quad \rho_l \quad \rho_0 \quad \rho_0 \quad \rho_l
\end{array} \]

\[ \begin{array}{c}
x_g \\
x_l
\end{array} \]

\[ \begin{array}{c}
0.6 \\
0.8 \\
1.0 \\
1.2 \\
1.4
\end{array} \]

• \( F \approx V \rho_0 \) and \( \rho_0 = \frac{N}{V} \) \( \rightarrow \) Chemical potential \( \mu = \frac{\partial F}{\partial N} = f'(\rho_0) \) and Pressure

\[ p = -\frac{\partial F}{\partial V} = \rho f'(\rho) - f(\rho) \]
Quorum sensing self-propelled particles

- \( \dot{r}_i = v[\tilde{\rho}(r_i)]u(\theta_i); \quad \tilde{\rho}(r_i) = \sum_j K(|r_i - r_j|); \quad \sigma^2 = \int dr K(r)r^2 \)

- Rotational diffusivity \( D_r \), tumbling rate \( \alpha \)
Quorum sensing self-propelled particles

- \( \dot{\mathbf{r}}_i = v[\tilde{\rho}(\mathbf{r}_i)]\mathbf{u}(\theta_i); \quad \tilde{\rho}(\mathbf{r}_i) = \sum_j K(|\mathbf{r}_i - \mathbf{r}_j|); \quad \sigma^2 = \int dr K(r)r^2 \)

- Rotational diffusivity \( D_r \), tumbling rate \( \alpha \)

- Assume \( \tilde{\rho}(\mathbf{r}) \) frozen \quad \rightarrow \quad \text{Non-interacting} \quad v(r_i) \quad \rightarrow \quad \text{Determine} \quad \partial_t \rho(\mathbf{r}, t) \)
Quorum sensing self-propelled particles

- $\dot{\mathbf{r}}_i = v[\tilde{\rho}(\mathbf{r}_i)] \mathbf{u}(\theta_i)$;  $\tilde{\rho}(\mathbf{r}_i) = \sum_j K(|\mathbf{r}_i - \mathbf{r}_j|)$;  $\sigma^2 = \int dr K(r)r^2$

- Rotational diffusivity $D_r$, tumbling rate $\alpha$

- Assume $\tilde{\rho}(\mathbf{r})$ frozen  $\rightarrow$ Non-interacting $v(r_i)$  $\rightarrow$ Determine $\partial_t \rho(\mathbf{r}, t)$

- Fluctuating hydro + Mean-field approximation $\rightarrow$ hydro eq.

$$
\dot{\rho} = \nabla \cdot \left\{ \right\};
$$

[Wittkowski et al. Nat. Com. 5, 4351 (2014)]
Quorum sensing self-propelled particles

- \( \dot{\mathbf{r}}_i = v[\bar{\rho}({\mathbf{r}}_i)] \mathbf{u}(\theta_i); \quad \bar{\rho}(\mathbf{r}_i) = \sum_j K(|\mathbf{r}_i - \mathbf{r}_j|); \quad \sigma^2 = \int d\mathbf{r} K(r) r^2 \)

- Rotational diffusivity \( D_r \), tumbling rate \( \alpha \)

- Assume \( \bar{\rho}(\mathbf{r}) \) frozen \quad \rightarrow \quad Non-interacting \( v(r_i) \) \quad \rightarrow \quad Determine \( \partial_t \rho(\mathbf{r}, t) \)

- Fluctuating hydro + Mean-field approximation \quad \rightarrow \quad hydro eq.

\[
\dot{\rho} = \nabla \cdot \left\{ M \nabla \left[ \frac{\delta \mathcal{F}}{\delta \rho} \right] \right\}; \quad M = \rho \frac{v^2}{D_r d(d - 1) + \alpha d}
\]

- \( \mathcal{F}[\rho(x)] = \int d^d r \left[ \rho (\log \rho - 1) + \int \rho \, ds \log[v(s)] \right] \equiv \int d^d r \, f(\rho(r)) \)
Quorum sensing self-propelled particles

- \( \dot{r}_i = v[\tilde{\rho}(r_i)]u(\theta_i) \); \( \tilde{\rho}(r_i) = \sum_j K(|r_i - r_j|) \); \( \sigma^2 = \int dr K(r)r^2 \)

- Rotational diffusivity \( D_r \), tumbling rate \( \alpha \)

- Assume \( \tilde{\rho}(r) \) frozen \( \rightarrow \) Non-interacting \( v(r_i) \) \( \rightarrow \) Determine \( \partial_t \rho(r, t) \)

- Fluctuating hydro + Mean-field approximation \( \rightarrow \) hydro eq.

\[
\dot{\rho} = \nabla \cdot \left\{ M \nabla \left[ \frac{\delta F}{\delta \rho} + \sigma^2 \frac{v'}{v} \Delta \rho \right] \right\}; \quad M = \rho \frac{v^2}{D_r d(d - 1) + \alpha d}
\]

- \( F[\rho(x)] = \int d^d r \left[ \rho(\log \rho - 1) + \int^\rho ds \log[v(s)] \right] \equiv \int d^d r f(\rho(r)) \)

- \( \sigma^2 \frac{v'}{v} \Delta \rho \) does not derive from a free energy
Quorum sensing self-propelled particles

- \( \dot{r}_i = v[\tilde{\rho}(r_i)]u(\theta_i); \quad \tilde{\rho}(r_i) = \sum_j K(|r_i - r_j|); \quad \sigma^2 = \int dr K(r)r^2 \)

- Rotational diffusivity \( D_r \), tumbling rate \( \alpha \)

- Assume \( \tilde{\rho}(r) \) frozen \( \Rightarrow \) Non-interacting \( v(r_i) \) \( \Rightarrow \) Determine \( \partial_t \rho(r, t) \)

- Fluctuating hydro + Mean-field approximation \( \Rightarrow \) hydro eq.

\[
\dot{\rho} = \nabla \cdot \left\{ M \nabla \left[ \frac{\delta F}{\delta \rho} + \sigma^2 \frac{v'}{v} \Delta \rho \right] \right\}; \quad M = \rho \frac{v^2}{D_r d(d - 1) + \alpha d}
\]

- \( F[\rho(x)] = \int d^d r \left[ \rho(\log \rho - 1) + \int_0^\rho ds \log[v(s)] \right] \equiv \int d^d r f(\rho(r)) \)

- \( \sigma^2 \frac{v'}{v} \Delta \rho \) does not derive from a free energy

\[ \Rightarrow \] Common-tangent on \( f(\rho) \) leads to a wrong phase diagram

[Wittkowski et al. Nat. Com. 5, 4351 (2014)]
\[ \dot{\rho} = \nabla \cdot [M \nabla g(\rho)]; \quad g = g_0(\rho) - \kappa(\rho) \Delta \rho \]

\[ g_0 = \log[\rho v(\rho)], \quad \kappa(\rho) = -\sigma^2 \frac{v'(\rho)}{v(\rho)} \]
\[
\dot{\rho} = \nabla \cdot [M \nabla g(\rho)]; \quad g = g_0(\rho) - \kappa(\rho) \Delta \rho
\]

\[
g_0 = \log[\rho v(\rho)], \quad \kappa(\rho) = -\sigma^2 \frac{v'(\rho)}{v(\rho)}
\]

Unfortunately \( g(\rho) \neq \frac{\delta F[\rho]}{\delta \rho} \) 😞
Hydrodynamics of Quorum-sensing active particles

\[ \dot{\rho} = \nabla \cdot [M \nabla g(\rho)]; \quad g = g_0(\rho) - \kappa(\rho) \Delta \rho \]

\[ g_0 = \log[\rho v(\rho)], \quad \kappa(\rho) = -\sigma^2 \frac{v'(\rho)}{v(\rho)} \]

Unfortunately \( g(\rho) \neq \frac{\delta F[\rho]}{\delta \rho} \)

A bit of magic: define \( R'(\rho) \equiv \frac{1}{\kappa(\rho)} \) and \( \phi'(R) = g_0(\rho) \)
Hydrodynamics of Quorum-sensing active particles

\[ \dot{\rho} = \nabla \cdot [M \nabla g(\rho)]; \quad g = g_0(\rho) - \kappa(\rho) \Delta \rho \]

\[ g_0 = \log[\rho v(\rho)], \quad \kappa(\rho) = -\sigma^2 \frac{v'(\rho)}{v(\rho)} \]

Unfortunately \( g(\rho) \neq \frac{\delta F[\rho]}{\delta \rho} \)

A bit of magic: define \( R'(\rho) \equiv \frac{1}{\kappa(\rho)} \) and \( \phi'(R) = g_0(\rho) \)

Then \[ \dot{\rho} = \nabla \left[ M \nabla \frac{\delta \mathcal{H}}{\delta R(\rho)} \right] \quad \text{with} \quad \mathcal{H} = \int dr [\phi(R) + \frac{\kappa}{2R'} (\nabla R)^2] \]
Hydrodynamics of Quorum-sensing active particles

\[ \dot{\rho} = \nabla \cdot [M \nabla g(\rho)]; \quad g = g_0(\rho) - \kappa(\rho) \Delta \rho \]

\[ g_0 = \log[\rho v(\rho)], \quad \kappa(\rho) = -\sigma^2 \frac{v'(\rho)}{v(\rho)} \]

Unfortunately \( g(\rho) \neq \frac{\delta F[\rho]}{\delta \rho} \)

A bit of magic: define \( R'(\rho) \equiv \frac{1}{\kappa(\rho)} \) and \( \phi'(R) = g_0(\rho) \)

Then \( \dot{\rho} = \nabla \left[ M \nabla \frac{\delta H}{\delta R(\rho)} \right] \) with \( H = \int \delta x \left[ \phi(R) + \frac{\kappa}{2R'} (\nabla R)^2 \right] \)

Common-tangent construction on the effective free energy density \( \phi(R) \)
Hydrodynamics of Quorum-sensing active particles

\[ \dot{\rho} = \nabla \cdot [M \nabla g(\rho)]; \quad g = g_0(\rho) - \kappa(\rho) \Delta \rho \]

\[ g_0 = \log[\rho v(\rho)], \quad \kappa(\rho) = -\sigma^2 \frac{v'(\rho)}{v(\rho)} \]

Unfortunately \( g(\rho) \neq \frac{\delta F[\rho]}{\delta \rho} \)

A bit of magic: define \( R'(\rho) \equiv \frac{1}{\kappa(\rho)} \) and \( \phi'(R) = g_0(\rho) \)

Then \[ \dot{\rho} = \nabla \left[ M \nabla \frac{\delta H}{\delta R(\rho)} \right] \text{ with } H = \int dr [\phi(R) + \frac{\kappa}{2R'} (\nabla R)^2] \]

Common-tangent construction on the effective free energy density \( \phi(R) \)

(Almost) quantitative agreement
• **Lattice-gas model of run & tumble particles (RTP)**
  
  [Thompson et al. JSTAT 2011; Soto & Golestanian PRE 2014; Whitelam JCP 2018]

```
+ \frac{\alpha}{2} \quad \bigcirc \quad \frac{\alpha}{2}
```

```
\begin{align*}
0 & \quad d_2^+ & \quad d_4^- & \quad d_6^- & \quad d_6^+ & \quad d_8^+ & \quad 1 \\
1 & \quad 2 & \quad 3 & \quad 4 & \quad 5 & \quad 6 & \quad 7 & \quad 8 & \quad 9 & \quad 10
\end{align*}
```
• **Lattice-gas model** of run & tumble particles (RTP)
  [Thompson et al. JSTAT 2011; Soto & Golestanian PRE 2014; Whitelam JCP 2018]

\[ d_{2}^{+} + d_{4}^{-} + d_{6}^{-} + d_{6}^{+} + d_{8}^{+} + \frac{\alpha}{2} \]

\[ 1 \quad 2 \quad 3 \quad 4 \quad 5 \quad 6 \quad 7 \quad 8 \quad 9 \quad 10 \]

• **Exclusion:**
  \[ d_{i}^{\pm} = v_{0} \left( 1 - \frac{n_{i}}{n_{M}} \right) \]
An exactly solvable case

- Lattice of $\alpha L$ sites with at most one particle per site
An exactly solvable case

- Lattice of $\alpha L$ sites with at most one particle per site

- Symmetric diffusion/exchange at rate $D$

- Asymmetric hopping on empty sites at rate $\lambda/L$

- Particles switch hopping direction at rate $\Gamma/L^2$

- Undergoes MIPS if $\rho_0 = N/L^d$ and $\lambda$ are large enough
An exactly solvable case

- Lattice of $\alpha L$ sites with at most one particle per site
  
  - Symmetric diffusion/exchange at rate $D$
  
  - Asymmetric hopping on empty sites at rate $\lambda / L$
  
  - Particles switch hopping direction at rate $\Gamma / L^2$

  Undergoes MIPS if $\rho_0 = N / L^d$ and $\lambda$ are large enough.
An exactly solvable case

- Lattice of $\alpha L$ sites with at most one particle per site

- Symmetric diffusion/exchange at rate $D$

- Asymmetric hopping on empty sites at rate $\lambda/L$

- Particles switch hopping direction at rate $\Gamma/L^2$

Undergoes MIPS if $\rho_0 = N/L^d$ and $\lambda$ are large enough.
An exactly solvable case

- Lattice of $\alpha L$ sites with at most one particle per site
  
  $\uparrow \frac{\Gamma}{L^2}$ \quad $\lambda/L$ \quad $D$ \quad $D$ \quad $\lambda/L$ \quad $\uparrow \frac{\Gamma}{L^2}$

- Symmetric diffusion/exchange at rate $D$

- Asymmetric hopping on empty sites at rate $\lambda/L$

- Particles switch hopping direction at rate $\Gamma/L^2$

- Undergoes MIPS if $\rho_0 = N/L^d$ and $\lambda$ are large enough
Phase equilibrium

- **Exact hydrodynamic equations** for density and magnetisation

\[
x = \frac{i}{L}, \quad t = t_{\text{micro}} \frac{L^2}{i}
\]


\[
\begin{align*}
\partial_t \rho(x, t) &= D \Delta \rho + \lambda \nabla [m(1 - \rho)] \\
\partial_t m(x, t) &= D \Delta m + \lambda \nabla [\rho(1 - \rho)] - 2\Gamma m
\end{align*}
\]
Phase equilibrium

- **Exact hydrodynamic equations** for density and magnetisation

\[ x = \frac{i}{L}, \ t = \frac{t \text{micro}}{L^2} \]


\[
\begin{align*}
\partial_t \rho(x, t) &= D \Delta \rho + \lambda \nabla [m(1 - \rho)] \\
\partial_t m(x, t) &= D \Delta m + \lambda \nabla [\rho(1 - \rho)] - 2\Gamma m
\end{align*}
\]

- More complicated but can **still be solved using the same transform**

- Exact, parameter-free result
MIPS from repulsive forces

- Self-propelled particles with pairwise forces (PFAPs)
  [Fily & Marchetti PRL 2012, Redner et al. PRL 2013, Stenhammar et al. PRL 2013, Bialké et al. PRL 2013, ...]

\[
\dot{r}_i = v u(\theta_i) - \mu \sum_j F_{ij}(r_i - r_j) + \sqrt{2D_t} \eta_i; \quad \dot{\theta}_i = \sqrt{2D_r} \xi_i
\]

- Interactions yields decreasing \( v(\rho) \equiv \sum_i \dot{r}_i \cdot u(\theta_i) \) [Fily et al PRL (2012)]
MIPS from repulsive forces

- **Self-propelled particles with pairwise forces (PFAPs)**
  
  [Fily & Marchetti PRL 2012, Redner et al. PRL 2013, Stenhammar et al. PRL 2013, Bialké et al. PRL 2013, ...]

\[
\dot{\mathbf{r}}_i = v \mathbf{u}(\theta_i) - \mu \sum_j F_{ij}(\mathbf{r}_i - \mathbf{r}_j) + \sqrt{2D_t} \eta_i; \quad \dot{\theta}_i = \sqrt{2D_r} \xi_i
\]

- Interactions yields decreasing \( v(\rho) \equiv \sum_i \dot{\mathbf{r}}_i \cdot \mathbf{u}(\theta_i) \) [Fily et al PRL (2012)]

  \[\rightarrow\] Same phenomenology as QSAPs

- **Interesting qualitative & quantitative differences** [Tjhung et al, PRX 2018; Caporusso et al, arxiv:2005.06893]
Pressure-driven instability

- Hydrodynamic description [Solon et al., PRE 2016, NJP 2018]

\[
\dot{\rho}(r) = -\nabla \cdot J \quad \text{where} \quad J = \mu \nabla \cdot \sigma; \quad \sigma = \text{[Bunch of bulk correlators]}
\]
Pressure-driven instability

- **Hydrodynamic description** [Solon et al., PRE 2016, NJP 2018]
  \[ \dot{\rho}(\mathbf{r}) = -\nabla \cdot \mathbf{J} \text{ where } \mathbf{J} = \mu \nabla \cdot \mathbf{\sigma}; \quad \mathbf{\sigma} = \text{[Bunch of bulk correlators]} \]

- \( P_{\text{tot}} = -\sigma_{xx} \) is the equation of state of the mechanical pressure
Pressure-driven instability

- **Hydrodynamic description** [Solon et al., PRE 2016, NJP 2018]

  \[ \dot{\rho}(\mathbf{r}) = -\nabla \cdot \mathbf{J} \quad \text{where} \quad \mathbf{J} = \mu \nabla \cdot \sigma; \quad \sigma = \text{[Bunch of bulk correlators]} \]

- \( P_{\text{tot}} = -\sigma_{xx} \) is the equation of state of the mechanical pressure

  \[ P(\rho) = P_D + P_A \quad \text{where} \quad P_A = \rho \frac{v_0 v(\rho)}{2\mu D_r}; \quad v(\rho) = \langle \sum_i \dot{\mathbf{r}}_i \cdot \mathbf{u}(\theta_i) \rangle \]

- \( P_D \) passive pressure: mean force exerted through a plane

- \( P_a \) flux of active impulse & momentum through a plane [Fily et al. JPA (2018)]
Pressure-driven instability

- **Hydrodynamic description** [Solon et al., PRE 2016, NJP 2018]
  \[
  \dot{\rho}(r) = -\nabla \cdot J \quad \text{where} \quad J = \mu \nabla \cdot \sigma; \quad \sigma = \text{[Bunch of bulk correlators]}
  \]

- \( P_{\text{tot}} = -\sigma_{xx} \) is the equation of state of the mechanical pressure

\[
P(\rho) = P_D + P_A \quad \text{where} \quad P_A = \rho \frac{v_0 v(\rho)}{2\mu D_r}; \quad v(\rho) = \langle \sum_i \dot{r}_i \cdot u(\theta_i) \rangle
\]

- \( P_D \) passive pressure: mean force exerted through a plane

- \( P_A \) flux of active impulse & momentum through a plane [Fily et al. JPA (2018)]

- \( P'(\rho) < 0 \) predicts linear instability
Pairwise forces—Summary

- Phase diagram in quantitative agreement with generalized thermodynamical construction
- Equal mechanical pressure in coexisting phases
- Can do isobaric ensemble
- Failure of Maxwell construction
- Quite rich physics still to be explored (surface tension, bubbles, etc.)
Back to bacteria: Motility-Induced Pattern Formation (MIPF)

Patterns instead of MIPS

[Liu et al., Science (2011)]

Nice, but why?

J. Tailleur (CNRS-Univ Paris Diderot)
Back to bacteria: Motility-Induced Pattern Formation (MIPF)

Patterns instead of MIPS

[Liu et al., Science (2011)]

J. Tailleur (CNRS-Univ Paris Diderot)
Back to bacteria: Motility-Induced Pattern Formation (MIPF)

Patterns instead of MIPS [Liu et al., Science (2011)]. Nice, but why?
Interplay between density and mobility: Quorum-sensing interactions

- Particle slow down at high density (slower, more tumbles, longer tumbles . . .)

- Instability mechanism: feedback loop [Cates, Tailleur, Ann. Rev. of Cond. Mat. Phys. 2015]
  
  → Bacteria accumulate where they are less motile
  
  → Bacteria lose motility at high density
Interplay between density and mobility: Quorum-sensing interactions

- Particle slow down at high density (slower, more tumbles, longer tumbles . . . )

- Instability mechanism: feedback loop [Cates, Tailleur, Ann. Rev. of Cond. Mat. Phys. 2015]

  - Bacteria accumulate where they are less motile
  - Bacteria lose motility at high density
  - Microscopic simulations starting from homogeneous systems

\[ v'(\rho) < 0 \]

\[ t = 10^3 \tau \]
\[ t = 10^4 \tau \]
\[ t = 10^5 \tau \]
Interplay between density and mobility: Quorum-sensing interactions

- Particle slow down at high density (slower, more tumbles, longer tumbles ...)

- Instability mechanism: feedback loop [Cates, Tailleur, Ann. Rev. of Cond. Mat. Phys. 2015]
  
  → Bacteria accumulate where they are less motile
  
  → Bacteria lose motility at high density
  
  → Microscopic simulations starting from homogeneous systems

\[ t = 10^3 \tau \quad t = 10^4 \tau \quad t = 10^5 \tau \]

\[ \beta'(\rho) < 0 \]

100 \( v_0 \tau \)
Interplay between density and mobility: Quorum-sensing interactions

- **Particle slow down at high density** (slower, more tumbles, longer tumbles . . .)

- **Instability mechanism: feedback loop** [Cates, Tailleur, Ann. Rev. of Cond. Mat. Phys. 2015]

  - Bacteria accumulate where they are less motile
  - Bacteria lose motility at high density
  - Microscopic simulations starting from homogeneous systems

\[
\alpha'(\rho) > 0
\]

![Simulation images at different times](image_url)
Interplay between density and mobility: Quorum-sensing interactions

- Particle slow down at high density (slower, more tumbles, longer tumbles . . . )

- Instability mechanism: feedback loop [Cates, Tailleur, Ann. Rev. of Cond. Mat. Phys. 2015]
  
  → Bacteria accumulate where they are less motile
  → Bacteria lose motility at high density
  → Microscopic simulations starting from homogeneous systems

\[ t = 10^3 \tau \quad t = 10^4 \tau \quad t = 10^5 \tau \]

\[ \alpha'(\rho) > 0 \]

- Slow coarsening leads to complete motility-induced phase separation

- No finite-size patterns: What is the missing ingredient?
Pattern formation in bacterial colonies: a simple mechanism

• Coarsening is slow → Long-time dynamics (24 hours)

• Large-scale description of run & tumble dynamics:

\[
\dot{\rho} = \nabla \left[ \frac{v^2 \beta}{d\alpha (\beta + \alpha)} \nabla \rho + \frac{\nu \rho}{d\alpha} \nabla \frac{v \beta}{\alpha + \beta} \right]
\]
Pattern formation in bacterial colonies: a simple mechanism

• Coarsening is slow → Long-time dynamics (24 hours)

• Large-scale description of run & tumble dynamics:

\[
\dot{\rho} = \nabla \left[ \frac{v^2 \beta}{d\alpha (\beta + \alpha)} \nabla \rho + \frac{v \rho}{d\alpha} \nabla \frac{v \beta}{\alpha + \beta} \right]
\]

• Missing ingredient: population dynamics

\[
\dot{\rho} = -\nabla \cdot J[\rho] + \mu \rho \left(1 - \frac{\rho}{\rho_0}\right)
\]
Pattern formation in bacterial colonies: a simple mechanism

- Coarsening is slow $\rightarrow$ Long-time dynamics (24 hours)

- Large-scale description of run & tumble dynamics:
  \[
  \dot{\rho} = \nabla \left[ \frac{v^2 \beta}{d\alpha(\beta+\alpha)} \nabla \rho + \frac{v\rho}{d\alpha} \nabla \frac{v\beta}{\alpha+\beta} \right]
  \]

- Missing ingredient: population dynamics
  \[
  \dot{\rho} = -\nabla \cdot J[\rho] + \mu \rho \left( 1 - \frac{\rho}{\rho_0} \right)
  \]

$\rightarrow$ Qualitatively accounts for the experiments

- What happened to the phase-separation?
Birth & death vs phase separation

- **Quorum-sensing** → Motility-Induced Phase separation → \((\rho_{\text{low}}, \rho_{\text{high}})\)
Birth & death vs phase separation

- **Quorum-sensing** → Motility-Induced Phase separation → $(\rho_{\text{low}}, \rho_{\text{high}})$

- **Logistic growth:** $\rho_{\text{low}} \leq \rho_0$ → division; $\rho_{\text{high}} \geq \rho_0$ → death
Birth & death vs phase separation

- **Quorum-sensing** → Motility-Induced Phase separation → \((\rho_{\text{low}}, \rho_{\text{high}})\)

- **Logistic growth:**
  \[ \rho_{\text{low}} \leq \rho_0 \rightarrow \text{division}; \quad \rho_{\text{high}} \geq \rho_0 \rightarrow \text{death} \]

- **Competition** → Micro-phase separation

- **Motility-induced phase separation + population dynamics** → Finite-size patterns

[Cates *et al.* PNAS 2010; Liu *et al.* Science 2011]
Mathematically: linear stability analysis

- Simplified model:
  \[ \partial_t \rho = \nabla \cdot [D_c(\rho) \nabla \rho + \rho \nabla D_c(\rho)] - \kappa \Delta^2 \rho + \alpha \rho \left( 1 - \frac{\rho}{\rho_0} \right) \]
Mathematically: linear stability analysis

- Simplified model:
  \[ \partial_t \rho = \nabla \cdot [D_c(\rho)\nabla \rho + \rho \nabla D_c(\rho)] - \kappa \Delta^2 \rho + \alpha \rho \left(1 - \frac{\rho}{\rho_0}\right) \]

- Linear stability analysis:
  \[ \rho(\mathbf{r}, t) = \rho_0 + \sum_q \delta \rho_q(t)e^{iq \cdot \mathbf{r}} \rightarrow \delta \rho_q(t) = \delta \rho_q(0)e^{\lambda_q t} \]
  \[ \lambda_q = -[D_c(\rho_0) + \rho_0 D'_c(\rho_0)]q^2 - \kappa q^4 - \alpha \]
Mathematically: linear stability analysis

- **Simplified model:**
  \[ \partial_t \rho = \nabla \cdot [D_c(\rho) \nabla \rho + \rho \nabla D_c(\rho)] - \kappa \Delta^2 \rho + \alpha \rho \left(1 - \frac{\rho}{\rho_0}\right) \]

- **Linear stability analysis:**
  \[ \rho(\mathbf{r}, t) = \rho_0 + \sum_q \delta \rho_q(t) e^{i\mathbf{q} \cdot \mathbf{r}} \rightarrow \delta \rho_q(t) = \delta \rho_q(0) e^{\lambda_q t} \]

  \[ \lambda_q = -[D_c(\rho_0) + \rho_0 D'_c(\rho_0)] q^2 - \kappa q^4 - \alpha \]

- **Transition at finite** \( q_c \) **when** \( D_c(\rho_0) + \rho_0 D'_c(\rho_0) \) **strongly negative**

<table>
<thead>
<tr>
<th>( \lambda_q/\alpha )</th>
<th>2</th>
<th>1</th>
<th>0</th>
<th>-1</th>
<th>-2</th>
<th>-3</th>
<th>-4</th>
</tr>
</thead>
<tbody>
<tr>
<td>( q/q_c )</td>
<td>0.0</td>
<td>0.5</td>
<td>1.0</td>
<td>1.5</td>
<td>2.0</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Patterns
Selection of a lengthscale

- Droplet of radius $R$

\[ \delta \text{Flux through boundary } \phi > 0 \]

Local birth/death rate $\alpha > 0$

\[
\frac{d}{dt} \text{(Mass in the droplet)} = -2\pi R \phi + \alpha \pi R^2
\]

Steady-state radius $R \sim \frac{2}{\phi / \alpha}$
Selection of a lengthscale

- Droplet of radius $R$
- MIPS $\phi > 0$ Flux through boundary

\[
\frac{d}{dt} \text{(Mass in the droplet)} = -2\pi R\phi
\]
Selection of a lengthscale

- Droplet of radius $R$
- MIPS $\rightarrow$ Flux through boundary $\phi > 0$
- Local birth/death rate $\alpha > 0$

$$\frac{d}{dt} \text{(Mass in the droplet)} = -2\pi R \phi + \alpha \pi R^2$$
Selection of a lengthscale

- Droplet of radius $R$
- MIPS $\phi > 0$
- Local birth/death rate $\alpha > 0$

\[
\frac{d}{dt} \text{(Mass in the droplet)} = -2\pi R \phi + \alpha \pi R^2
\]

→ Steady-state radius $R \sim 2\phi/\alpha$
Multi-component bacterial colonies (with J. Huang, HKU)

- Idea: two strains $A$ and $B$

- Reciprocal motility control
Multi-component bacterial colonies (with J. Huang, HKU)

- Idea: two strains $A$ and $B$

- Reciprocal motility control

Activator_A

- Constant production of 3OC12HSL
- Enhance expression of CheZ in B

Activator_B

- Constant production of 3OC6HSL
- Reciprocal enhancement or inhibition of motility can be implemented
Multi-component bacterial colonies (with J. Huang, HKU)

- Idea: two strains $A$ and $B$

- Reciprocal motility control

\[ \text{Activator}_A \]

- Constant production of 3OC12HSL $\rightarrow$ Enhance expression of CheZ in $B$

- Enhance expression of CheZ in $A$ $\leftarrow$ Constant production of 3OC6HSL
Multi-component bacterial colonies (with J. Huang, HKU)

- **Idea:** two strains \( A \) and \( B \)

- **Reciprocal motility control**

  - **Activator** _A_
    - Constant production of 3OC12HSL → Enhance expression of CheZ in \( B \)
    - Enhance expression of CheZ in \( A \) ← Constant production of 3OC6HSL
    - Reciprocal enhancement or inhibition of motility can be implemented
Experimental results [N. Zhou, Y. Zhao, A. Daerr]

Mutual activation of motility

Mutual inhibition of motility
Macroscopic dynamics (Agnese Curatolo)

Time evolution of the density fields

- $\rho_A(r, t) = \sum_{\ell=1}^{N_A} \delta(r - r_{\ell}^A(t))$
- $\rho_B(r, t) = \sum_{\ell=1}^{N_B} \delta(r - r_{\ell}^B(t))$

Run-and-tumble dynamics + density-dependent swimming rate $\beta_A(\rho_B)$, $\beta_B(\rho_A)$

$$\dot{\rho}_A(r, t) = \nabla \cdot \left( D_A(\rho_B) \nabla \rho_A - F_A(\rho_B) \rho_A + \sqrt{2D_A(\rho_B)\rho_A} \Lambda_A \right)$$

$$\dot{\rho}_B(r, t) = \nabla \cdot \left( D_B(\rho_A) \nabla \rho_B - F_B(\rho_A) \rho_B + \sqrt{2D_B(\rho_A)\rho_B} \Lambda_B \right)$$

$$D_x(\rho_y) = \frac{v^2}{2\alpha \left( 1 + \frac{\alpha}{\beta_x(\rho_y)} \right)}; \quad F_x(\rho_y) = -\frac{v^2}{2\alpha} \nabla \frac{1}{1 + \frac{\alpha}{\beta_x(\rho_y)}}$$
The origin of the patterns

Linear analysis of the hydrodynamic equations around homogeneous profiles \( \rho_A^0 \) and \( \rho_B^0 \):

\[
\rho_A = \rho_A^0 + \delta \rho_A \quad \rho_B = \rho_B^0 + \delta \rho_B
\]

Mutual activation of the motility

\( \beta_A' > 0 \quad \beta_B' > 0 \)

Segregation

\( \delta \rho_A \delta \rho_B < 0 \)

Mutual inhibition of the motility

\( \beta_A' < 0 \quad \beta_B' < 0 \)

Colocalization

\( \rho_A \rho_B (\rho_A^0, \rho_B^0) \neq 0 \)
The origin of the patterns

Linear analysis of the hydrodynamic equations around homogeneous profiles $\rho_A^0$ and $\rho_B^0$:

$$\rho_A = \rho_A^0 + \delta \rho_A \quad \rho_B = \rho_B^0 + \delta \rho_B$$

$$\frac{\alpha^2}{(\alpha + \beta_A)(\alpha + \beta_B)} \frac{\beta'_A(\rho_B^0)\beta'_B(\rho_A^0)}{\beta_A\beta_B} > \frac{1}{\rho_A\rho_B}$$
The origin of the patterns

Linear analysis of the hydrodynamic equations around homogeneous profiles $\rho_A^0$ and $\rho_B^0$:

$$\rho_A = \rho_A^0 + \delta \rho_A \quad \rho_B = \rho_B^0 + \delta \rho_B$$

$$\frac{\alpha^2}{(\alpha + \beta_A)(\alpha + \beta_B)} \frac{\beta'_A(\rho_B^0)\beta'_B(\rho_A^0)}{\beta_A \beta_B} > \frac{1}{\rho_A \rho_B} > 0$$
The origin of the patterns

Linear analysis of the hydrodynamic equations around homogeneous profiles $\rho_A^0$ and $\rho_B^0$:

$$\rho_A = \rho_A^0 + \delta \rho_A \quad \rho_B = \rho_B^0 + \delta \rho_B$$

$$\frac{\alpha^2}{(\alpha + \beta_A)(\alpha + \beta_B)} \frac{\beta'_A(\rho_B^0)\beta'_B(\rho_A^0)}{\beta_A\beta_B} > \frac{1}{\rho_A\rho_B} > 0$$

**Mutual activation of the motility**

$\beta'_A > 0 \quad \beta'_B > 0$

**Mutual inhibition of the motility**

$\beta'_A < 0 \quad \beta'_B < 0$
The origin of the patterns

Linear analysis of the hydrodynamic equations around homogeneous profiles $\rho_A^0$ and $\rho_B^0$:

$$\rho_A = \rho_A^0 + \delta \rho_A \quad \rho_B = \rho_B^0 + \delta \rho_B$$

$$\frac{\alpha^2}{(\alpha + \beta_A)(\alpha + \beta_B)} \frac{\beta'_A(\rho_B^0)\beta'_B(\rho_A^0)}{\beta_A \beta_B} > \frac{1}{\rho_A \rho_B} > 0$$

Mutual activation of the motility

$\beta'_A > 0 \quad \beta'_B > 0$

Mutual inhibition of the motility

$\beta'_A < 0 \quad \beta'_B < 0$

$\delta \rho_A \delta \rho_B < 0$
The origin of the patterns

Linear analysis of the hydrodynamic equations around homogeneous profiles $\rho_A^0$ and $\rho_B^0$:

\[
\rho_A = \rho_A^0 + \delta \rho_A \quad \rho_B = \rho_B^0 + \delta \rho_B
\]

\[
\frac{\alpha^2}{(\alpha + \beta_A)(\alpha + \beta_B)} \cdot \frac{\beta'_A(\rho_B^0)\beta'_B(\rho_A^0)}{\beta_A\beta_B} > \frac{1}{\rho_A\rho_B} > 0
\]

Mutual activation of the motility

\[
\beta'_A > 0 \quad \beta'_B > 0
\]

Mutual inhibition of the motility

\[
\beta'_A < 0 \quad \beta'_B < 0
\]

Segregation

\[
\delta \rho_A \delta \rho_B < 0
\]

J. Tailleur (CNRS-Univ Paris Diderot)
The origin of the patterns

Linear analysis of the hydrodynamic equations around homogeneous profiles $\rho_A^0$ and $\rho_B^0$:

$$\rho_A = \rho_A^0 + \delta \rho_A \quad \rho_B = \rho_B^0 + \delta \rho_B$$

$$\frac{\alpha^2}{(\alpha + \beta_A)(\alpha + \beta_B)} \frac{\beta'_A(\rho_B^0)\beta'_B(\rho_A^0)}{\beta_A\beta_B} > \frac{1}{\rho_A\rho_B} > 0$$

Mutual activation of the motility
$$\beta'_A > 0 \quad \beta'_B > 0$$

Mutual inhibition of the motility
$$\beta'_A < 0 \quad \beta'_B < 0$$

Segregation
$$\delta \rho_A \delta \rho_B < 0$$

Colocalization
$$\delta \rho_A \delta \rho_B > 0$$
The origin of the patterns

Linear analysis of the hydrodynamic equations around homogeneous profiles $\rho^0_A$ and $\rho^0_B$:

$$\rho_A = \rho^0_A + \delta \rho_A \quad \rho_B = \rho^0_B + \delta \rho_B$$

$$\frac{\alpha^2}{(\alpha + \beta_A)(\alpha + \beta_B)} \frac{\beta'_A(\rho^0_B)\beta'_B(\rho^0_A)}{\beta_A\beta_B} > \frac{1}{\rho_A\rho_B} > 0$$

Mutual activation of the motility

$\beta'_A > 0 \quad \beta'_B > 0$

Mutual inhibition of the motility

$\beta'_A < 0 \quad \beta'_B < 0$

Segregation

$\delta \rho_A \delta \rho_B < 0$

Colocalization

$\delta \rho_A \delta \rho_B > 0$
Overall dynamics

At longer time-scales: population growth

\[ \dot{\rho}_A(r, t) = \nabla \cdot \left[ D_A(\rho_B) \nabla \rho_A - F_A(\rho_B) \rho_A \right] - \kappa \Delta^2 \rho_A + \mu \rho_A \left( 1 - \frac{\rho_A + \rho_B}{\rho_0} \right) \]

\[ \dot{\rho}_B(r, t) = \nabla \cdot \left[ D_B(\rho_A) \nabla \rho_B - F_B(\rho_A) \rho_B \right] - \kappa \Delta^2 \rho_B + \mu \rho_B \left( 1 - \frac{\rho_A + \rho_B}{\rho_0} \right) \]

Quorum-sensing interactions

Population dynamics

Mutual activation of motility

Mutual inhibition of motility
$N$-species MIPF

- $N$ populations of interacting active particles
- Mutual inhibition $\rightarrow$ Phase separation with colocalization
- Mutual activation $\rightarrow$ Phase separation with demixing
- Population dynamics arrest growth: MIPS $\rightarrow$ MIPF

Simulations: spreading of the bacterial mixture
Summary

- A LOT can be achieved using motility-control to self-organize SPPs

- *In silico* & In experiments

- Theory starts to be well established
Summary

- A LOT can be achieved using motility-control to self-organize SPPs

- *In silico* & In experiments

- Theory starts to be well established

A biased, unfair, restricted and incomplete view on MIPS & bacteria

- MIPS
  - Quorum sensing: [Tailleur Cates PRL 100, 218103 (2008); Cates Tailleur EPL 101, 20010 (2013); Solon Cates Tailleur, EPSJT 224, 1231 (2015); ...]
  - Pairwise forces: [Fily Marchetti PRL 108, 235702 (2012); Redner, Baskaran, Hagan PRL 110, 055701 (2013); Solon et al, PRL 114, 198301 (2015); ...]
  - On lattice: [Thompson et al, JSM P02029 (2011); Soto & Golestanian, PRE 89, 012706 (2014); Manacorda & Puglisi, PRL 119, 208003 (2017); Whitelam at al, JCP 148, 154902 (2018); ...]
  - Generalized thermodynamics: [Solon et al., NJP 2018]

- Pattern formation in single-strain bacterial colonies
  - Theory: [Cates et al, PNAS 2010]
  - Experiments: [Liu et al, Science 2011]

- Pattern formation in two-strain bacterial colonies: [Curatolo et al, bioarxiv:2019]