

Evolutionary Dynamics and Pattern Formation in Communities Exhibiting Cyclic Dominance

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**Workshop on "Non-equilibrium dynamics of spatially
extended interacting particle systems"**

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Most of the work done in collaboration with T. Reichenbach (Rockefeller) and E. Frey (LMU Munich)

- Biological motivation: Experiments on microbial populations
- The rock-paper-scissors games in well-mixed populations
 - The zero-sum case
 - General case
 - The effect of mutations
- Spatial stochastic effects in the May-Leonard model
 - Co-evolution, mobility & pattern formation
 - Mathematical modelling & the impact of noise
 - Spiral waves and phase diagram



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Role of fluctuations & spatial degrees of freedom?

How do they affect the co-evolution?

Microbial laboratory communities

Colicinogenic Bacteria & Rock-paper-scissors Game

Central question in biology & ecology:

Mechanisms allowing the maintenance of biodiversity?

Colicinogenic Bacteria & Rock-paper-scissors Game

Mechanisms allowing the maintenance of biodiversity?

Example of cyclic competition in microbial communities:

- **C**: Toxin producing (colicinogenic) E.coli carry a 'col' plasmid: genes encoding the colicin (toxin), a colicin-specific immunity protein (no 'suicide') and a lysis protein (→ release of the colicin)
- **S**: Colicin-sensitive bacteria (no cost for poison & antidote)
- **R**: Resistant bacteria are mutations of **S** with alterate membrane proteins that bind & translocate colicin (cost for antidote)

Colicinogenic Bacteria & Rock-paper-scissors Game

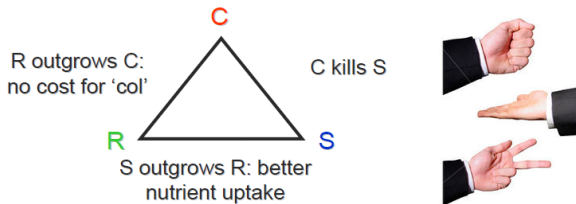
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C-S-R community satisfies a “rock-paper-scissors” relationship:

rock crushes scissors, scissors cut paper and paper wraps rock



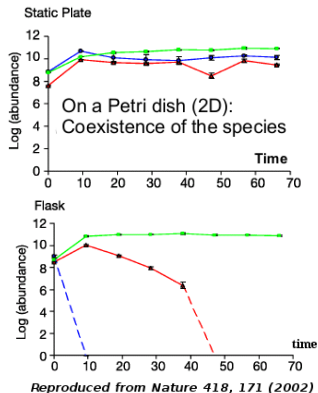
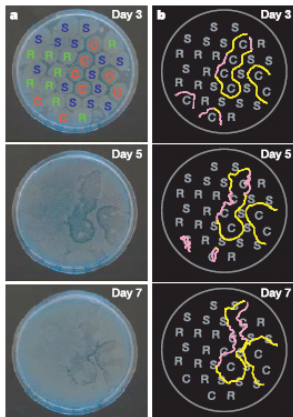
Experimental observations

Co-evolution vs extinction in communities of colicinogenic bacteria

The role of the spatial environment:

Dynamics on Petri dishes (spatial structure) and in flasks (well-mixed)

B. Kerr et al., Nature **418**, 171 (2002)



Spatial structure & local interactions matter !

“... ecologists have increasingly turned, since G. F. Gause’s work in the 1930s, to manipulating mini-worlds inhabited by microbial species. The paper by Kerr et al. gives a new impetus to such investigations, by stressing the importance of the geometry of neighbourhoods. Many habitats resemble the surface of a pizza more than a well-stirred bowl of soup”

M. A. Nowak and K. Sigmund, ‘news and views’ in *Nature* **418**, 138 (2002)

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Central questions:

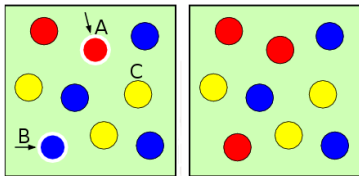
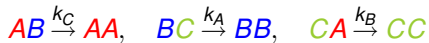
- Is there a transition between population’s uniformity and biodiversity?
- What is the role of mobility and “intrinsic noise”?
- Can we understand the spatio-temporal patterns?

Deterministic well-mixed rock-paper-scissors

Rock-paper-scissors (RPS):

metaphor for co-evolutionary dynamics with cyclic dominance

N individuals of 3 species in an “urn”



Rate (replicator) equations for the densities a , b and c :

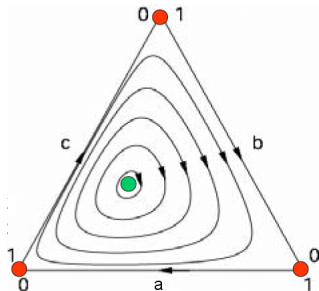
$$\dot{a} = a[k_C b - k_B c] \equiv \alpha_1$$

$$\dot{b} = b[k_A c - k_C a] \equiv \alpha_2$$

$$\dot{c} = c[k_B a - k_A b] \equiv \alpha_3$$

● absorbing fixed point

● reactive (center) fixed point



Well-mixed rock-paper-scissors: stochastic evolution

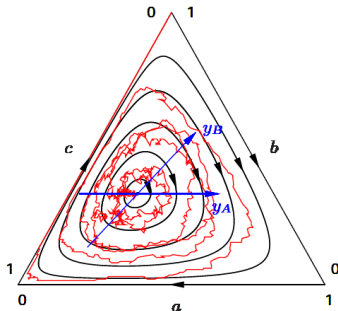
Yet, in experiments there is always extinction in finite time

$N < \infty \Rightarrow$ **finite-size fluctuations are important !**

Description in terms of probability distribution: $P(a, b, c; t) = P(\mathbf{x}, t)$

- Intrinsic fluctuations of the densities (noise strength $\propto N^{-1/2}$)
- $K = a^{k_A} b^{k_B} c^{k_C}$ no longer a constant of motion
- “Random walk” in the phase portrait
- \rightarrow boundary is always reached: extinction

Stochasticity causes loss of coexistence



Extinction probability

Probability $P_{\text{ext}}(t)$ of having 2 species extinct at time t ?

- Rate equations say: $P_{\text{ext}}(t) = 0$ (*always coexistence*)
- Microbial populations in flasks: $P_{\text{ext}} \rightarrow 1$ quickly (*loss of biodiversity*)

Finite-size fluctuations are responsible for $P_{\text{ext}} \rightarrow 1$ in finite time

Fokker-Planck equation ($k_A = k_B = k_C = 1$) in polar coordinates for RPS:

$$\partial_t P = -\omega_0 \partial_\phi P + \frac{1}{12N} \left[\frac{1}{r^2} \partial_\phi^2 + \frac{1}{r} \partial_r + \partial_r^2 \right] P, \text{ with absorbing boundary}$$

(starting from the fixed point)

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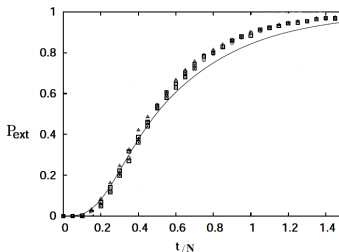
1st-passage problem \rightarrow

$$P_{\text{ext}}(u) \approx 1 - (1 + u)e^{-u},$$

which is scaling function of

$$u = \frac{24}{(1 + \sqrt{3})^2} \frac{t}{N}$$

**Average extinction time T_{ex}
scales linearly with N : $T_{\text{ex}} \propto N$**



Phys. Rev. E **74**, 051907 (2006)

Well-mixed RPS dynamics: the general case

General game-theoretic formulation: interactions specified by the payoff matrix \mathcal{P}

$$\mathcal{P} = \begin{matrix} & \begin{matrix} A & C & B \end{matrix} \\ \begin{matrix} A \\ C \\ B \end{matrix} & \begin{pmatrix} 0 & -\varepsilon & 1 \\ 1 & 0 & -\varepsilon \\ -\varepsilon & 1 & 0 \end{pmatrix} \end{matrix}$$

When A plays against B , payoffs are 1 and $-\varepsilon < 0$ (resp.)

Mean-field description (replicator equations): $\dot{s}_i = s_i[(\mathcal{P}\mathbf{s})_i - \mathbf{s} \cdot \mathcal{P}\mathbf{s}]$, where $\mathbf{s} = (a, b, c)$ and $(\mathcal{P}\mathbf{s})_i$ is the fitness (reproductive potential) of species i , while $\mathbf{s} \cdot \mathcal{P}\mathbf{s}$ is the population's average payoff.

Interior fixed point $\mathbf{s}^* = (1/3, 1/3, 1/3)$ is (i) an attractor if $\varepsilon < 1$; (ii) unstable if $\varepsilon > 1 \Rightarrow$ emergence of heteroclinic cycles; (iii) a center if $\varepsilon = 1$ (corresponds to the *zero-sum game* case just discussed)

When $N < \infty$ finite-size fluctuations cause the extinction of two species after average time T_{ex} (starting from \mathbf{s}^*), where

- $T_{\text{ex}} \propto \exp(\text{constant} \times N)$, when $\varepsilon < 1$
- $T_{\text{ex}} \propto \log(N)$, when $\varepsilon > 1$
- $T_{\text{ex}} \propto N$, if $\varepsilon = 1$

RPS with mutations in a well-mixed population

In addition to cyclic dominance, individuals can now switch from one strategy (species) to another with some small rate μ . (arXiv:0912.5179)

$$A \xrightarrow{\mu} \begin{cases} B \\ C \end{cases}, \quad B \xrightarrow{\mu} \begin{cases} A \\ C \end{cases}, \quad C \xrightarrow{\mu} \begin{cases} A \\ B \end{cases}$$

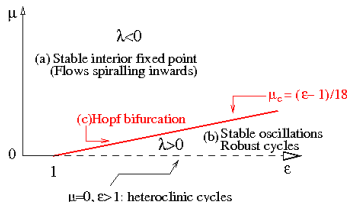
$$\dot{a} = a[b - \varepsilon c - (1 - \varepsilon)\{ab + bc + ac\}] + \mu(1 - 3a)$$

$$\dot{b} = b[c - \varepsilon a - (1 - \varepsilon)\{ab + bc + ac\}] + \mu(1 - 3b),$$

with $c = 1 - a - b$ and $\mathbf{s}^* = (1/3, 1/3, 1/3)$ is interior fixed point.

Bifurcation diagram: 3 scenarios depending on whether

$\lambda = (\varepsilon - 1 - 18\mu)/6$ and μ are > 0 or < 0



Limit cycle in the RPS game with mutations

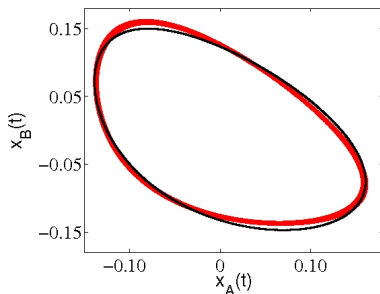
Normal form (supercrit. Hopf bifurcation) in polar coordinates:

$$\begin{aligned}\dot{r} &= r(\lambda + \beta r^2) \\ \dot{\omega} &= \omega_0 - \alpha r^2,\end{aligned}$$

with $\omega_0 = (1 + \varepsilon)/(2\sqrt{3})$, $\alpha = \frac{18\omega_0(1+2\sqrt{3}\omega_0)}{7(1+\varepsilon^2)+\varepsilon(13-9\mu)+9\mu(1+9\mu)}$,

$\beta = 1 - \varepsilon - \left(\frac{6\lambda(1+2\varepsilon\sqrt{3}\omega_0)}{7(1+\varepsilon^2)+\varepsilon(13-9\mu)+9\mu(1+9\mu)} \right) < 0$ (small μ)

\Rightarrow when $\lambda > 0$, limit cycle of radius $r_\infty = \sqrt{\frac{\lambda}{|\beta|}}$



Stochastic dynamics of the RPS game with mutations

Moran Process with rates

$T^{i \rightarrow j} = (1 + \{f_j - \bar{f}\}) s_i s_j + \mu s_i$, with
 $i, j \in (A, B, C)$, $f_A = c - \varepsilon b$,
 $f_B = a - \varepsilon c$, $f_C = b - \varepsilon a$ and
 $\bar{f} = (1 - \varepsilon)(ab + bc + ac)$

Van Kampen expansion in

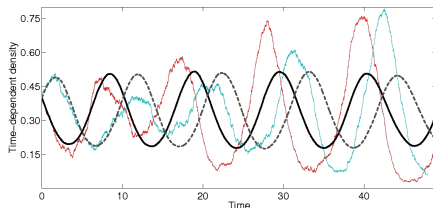
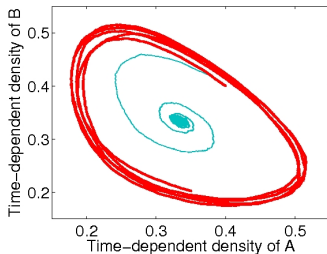
$x_i = s_i - 1/3$:

$\partial_t P(x, t) = -\partial_{x_i} [x_j \mathcal{A}_{ij}(s^*) P(x, t)] +$
 $\frac{1}{2} \mathcal{B}_{ij}(s^*) \partial_{x_i} \partial_{x_j} P(x, t)$,

where

$$\mathcal{A} = \begin{pmatrix} -\frac{1}{3} - 3\mu & -\frac{1}{3}(1 + \varepsilon) \\ \frac{1+\varepsilon}{3} & \frac{\varepsilon}{3} - 3\mu \end{pmatrix}$$

$$\mathcal{B} = \frac{2(1+3\mu)}{9N} \begin{pmatrix} 2 & -1 \\ -1 & 2 \end{pmatrix}$$



Quasi-cycles in the RPS game with mutations

When $\lambda < 0$, fluctuations $\propto N^{-1/2}$
 with large amplitude:
resonance amplification (McKane and
 Newman PRL94, 218102 (2005)) &
 “Phase-forgetting” quasi-cycles

Fourier transform $\tilde{\mathbf{x}}(\Omega)$ & power
 spectrum (VK expansion):

$$P(\Omega) = \langle |\tilde{\mathbf{x}}(\Omega)|^2 \rangle = \frac{8(1+3\mu)}{9N} \frac{\Omega_0^2 + \Omega^2}{(\Omega^2 - \Omega_0^2)^2 + (2\lambda\Omega)^2}, \text{ with}$$

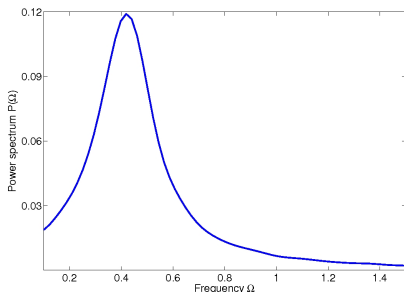
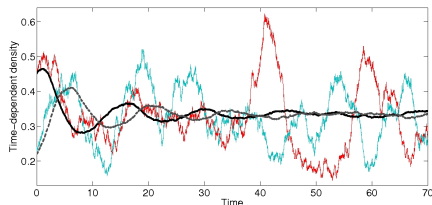
$$9\Omega_0^2 = 1 + 2\sqrt{3}\varepsilon\omega_0 + 9\mu(9\mu + 1 - \varepsilon)$$

Amplification at frequency

$$\Omega^* = \Omega_0 \left(2\sqrt{1 - \left(\frac{\lambda}{\Omega_0}\right)^2} - 1 \right)^{1/2}$$

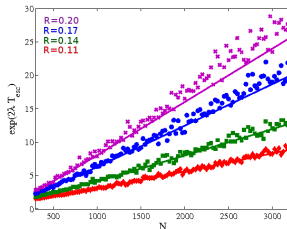
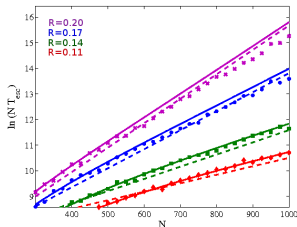
Autocorrelations ($\tau \rightarrow \infty$):

$$\langle x_A(\tau + t)x_A(\tau) \rangle = \frac{4(1+3\mu)}{3N} \frac{e^{-|\lambda|t}}{|\lambda|} \cos(\omega_0 t)$$



Average Escape time from the interior fixed point

From the fixed point $\mathbf{s}^* = (1/3, 1/3, 1/3)$, what is the time T_{esc} to reach a cycle on which oscillations are of amplitude R ?



Backward Kolmogorov equation & van Kampen expansion about \mathbf{s}^* :

$$\left[\lambda \rho + \left(\frac{1+3\mu}{6N} \right) \frac{1}{\rho} \right] T'_{esc}(\rho) + \left(\frac{1+3\mu}{6N} \right) T''_{esc}(\rho) = -1$$

+ absorbing/reflecting boundaries at $\rho = R$ and $\rho = 0 \Rightarrow$

$$T_{esc}(R) = \frac{1}{2\lambda} \int_0^{-\frac{3NR^2\lambda}{1+3\mu}} \frac{du}{u} (1 - e^u) \Rightarrow \text{Asymptotics (large } |\lambda|NR^2):$$

- $\lambda < 0$: $T_{esc} \simeq \left(\frac{1+3\mu}{6(\lambda R)^2 N} \right) \exp \left(\frac{3|\lambda|R^2 N}{1+3\mu} \right)$
- $\lambda > 0$: $T_{esc} \simeq \frac{1}{2\lambda} \left[\ln \left(\frac{3\lambda R^2 N}{1+3\mu} \right) + 0.57721... \right]$

Spatial May-Leonard model

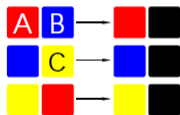
- Warm-up: well-mixed system
- Interacting-particle (individual-based) approach
- Spatio-temporal properties & pattern formation

May-Leonard model: dynamic rules

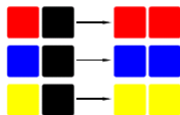
Cyclic competition of 3 species A, B, C and empty sites \emptyset

- Selection: cyclic dominance, rate σ
- Reproduction, rate μ
- *Bacteria swim and tumble* \Rightarrow
Mobility: exchange among nearest neighbours, rate ε
- Finite carrying capacity: at most occupied 1 individual per site

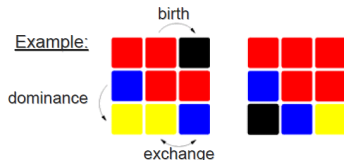
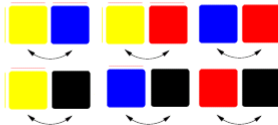
Selection processes



Reproduction processes



Individuals can move



Well-mixed May-Leonard model (warm-up)

Cyclic co-evolutionary dynamics

Selection: Reproduction:

$$AB \xrightarrow{\sigma} \circ A$$

$$BC \xrightarrow{\sigma} \circ B$$

$$CA \xrightarrow{\sigma} \circ C$$

$$A\circ \xrightarrow{\mu} AA$$

$$B\circ \xrightarrow{\mu} BB$$

$$C\circ \xrightarrow{\mu} CC$$

R. May & W. Leonard, SIAM J. Appl. Math. **29**,
243 (1975)

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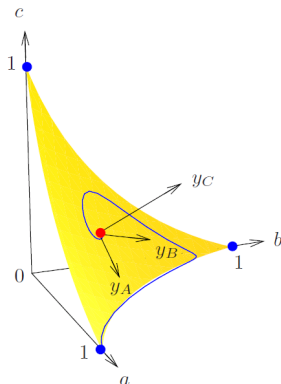
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- Reactive fixed point is unstable
- Heteroclinic cycles around the boundary of the phase portrait
- **Finite-size fluctuations: again, extinction in finite time**
($T_{ex}/N < \infty$)

Dynamics restricted on an invariant manifold:



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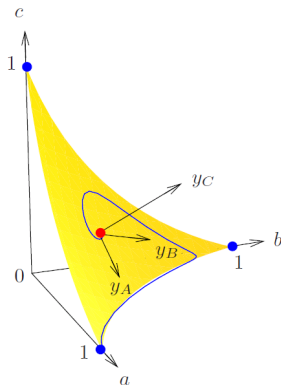
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($T_{ex}/N < \infty$)

**Without spatial structure,
coexistence is unstable**
→ *loss of biodiversity !*

Dynamics restricted on an invariant manifold:



R. May & W. Leonard, SIAM J. Appl. Math. **29**,
243 (1975)

Cyclic Competition on Square Lattices ($N = L^2$)

Known:

- Well-mixed: loss of biodiversity in *finite time* [May & Leonard, 1975]
- *Immobile individuals* on lattices: noisy patches [Durrett & Levin, 1998]

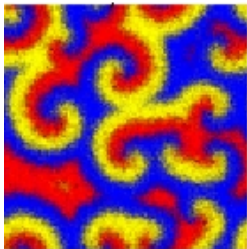
Here: stochastic co-evolution of N mobile individuals in cyclic competition

Mobility: nearest-neighbour pair exchanges

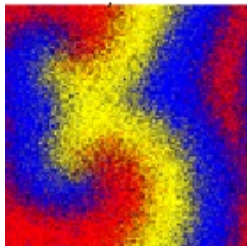
Diffusion constant: $D = \varepsilon/2L^2$

How does the system's behaviour depend on D ?

Snapshot for $D = 3 \times 10^{-5}$, $L = 500$, $\sigma = \mu = 1$



Snapshot for $D = 3 \times 10^{-4}$, $L = 300$, $\sigma = \mu = 1$



Cyclic Competition on Square Lattices ($N = L^2$)

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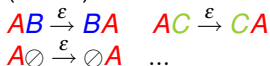
- Size of the emerging spirals increases with the mobility
- **Existence of a mobility threshold** \Rightarrow Below: coexistence. Above: giant spirals outgrow the lattice, *loss of biodiversity*

Nature **448**, 1046 (2007)

Cyclic Competition on Square Lattices

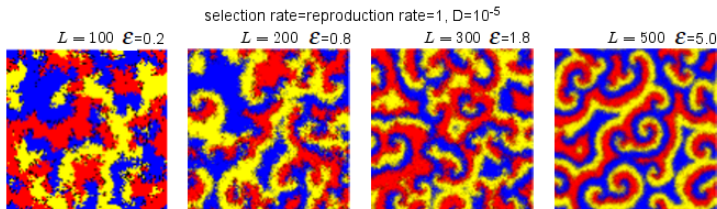
Stochastic co-dominant dynamics of N mobile individuals

Mobility included:
nearest-neighbour exchanges
(rate ε)



Keep diffusion rate $D = \varepsilon/2L^2$
fixed and vary ε and L

- Small systems with low mobility \rightarrow irregular & noisy patches
- Larger L and ε (D finite) \rightarrow *entanglement of regular spiral waves*
- Transition: noisy patches \rightarrow regular spirals already for *finite* ε



When is biodiversity stable and how is it preserved?

- Systems with well-mixed population: biodiversity is lost in finite time!
- For high mixing rate D : again the well-mixed scenario
- Is there a critical value of the diffusivity D below which biodiversity is maintained ?
- If so, what are the spatio-temporal properties of the patterns formed by the individuals?

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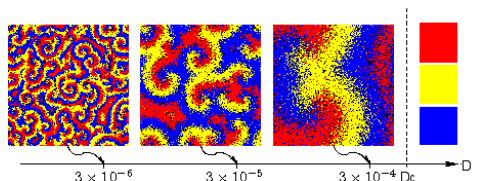
How to discriminate between stable/unstable reactive steady states?

Let T_{ex} be the average extinction time and N the size of the system

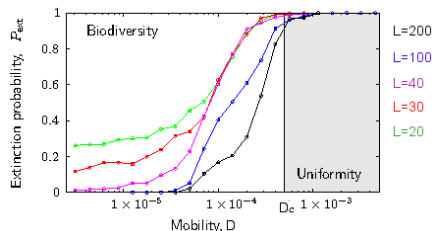
- If $T_{ex}/N \rightarrow O(1)$: neutral / marginal stability
- If $T_{ex}/N \rightarrow \infty$: super-extensive / stable
- If $T_{ex}/N \rightarrow 0$: sub-extensive / unstable

Existence of a critical mobility threshold

Biodiversity is lost above a critical mobility threshold D_c
Below D_c : spiral waves emerge



With $P_{ext} = Prob\{\text{only one species after time } t = N\}$



For $\sigma = \mu = 1$, $D_c = (4.5 \pm 0.5) \times 10^{-4}$

- For large systems, there is a well-defined critical/threshold value $D_c(\sigma, \mu)$ for the mobility above which coexistence is (quickly) lost
- Loss of biodiversity seems related to the size of the emerging patterns (spiral waves)

How can we rationalise and understand these findings?

Description accounting for *internal noise* in terms of local densities $\mathbf{s}(\mathbf{r}, t) = (a(\mathbf{r}, t), b(\mathbf{r}, t), c(\mathbf{r}, t))$ in the continuum limit ($N, \varepsilon \gg 1$ and D is finite)

Dominating noise contribution arises from reactions \rightarrow

$$\partial_t s_i(\mathbf{r}, t) = D \Delta s_i(\mathbf{r}, t) + \alpha_i(\mathbf{s}) + \mathcal{C}_i(\mathbf{s}) \xi_i$$

- Stochastic partial differential equations (Ito)
- With white noise: $\langle \xi_i(\mathbf{r}, t) \xi_j(\mathbf{r}', t') \rangle = \delta_{ij} \delta(\mathbf{r} - \mathbf{r}') \delta(t - t')$
- Exchange of pairs \rightarrow diffusive terms + noise $\propto N^{-1}$
- Reactions \rightarrow **deterministic drift** & **multiplicative noise with strength $N^{-1/2}$**

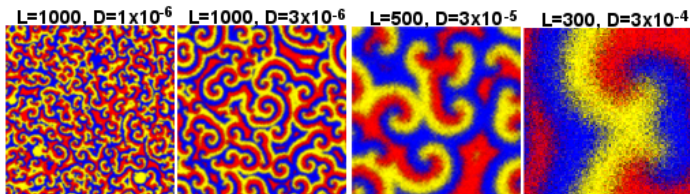
2 sources of noise but, for large systems, noise arising from reactions dominates over noise due to mobility

Phys. Rev. Lett. **99**, 238105 (2007) + J. Theor. Biol. **254**, 368 (2008)

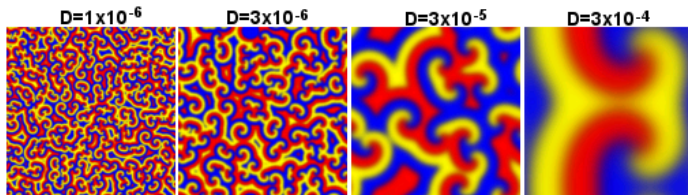
Is such a description accurate?

Here $\sigma = \mu = 1$ and $\varepsilon = 2 - 54$

Stochastic Lattice Simulations



Stochastic Partial Differential Equations



Is such a description accurate?

Description in terms of SPDE :

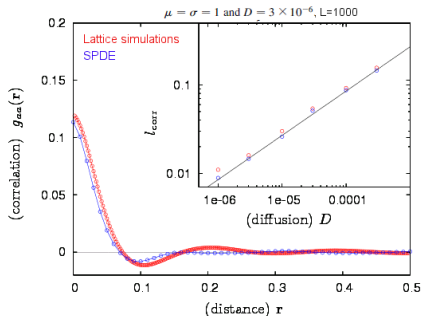
*Expected to be valid for large system sizes and exchange rates
($L, \varepsilon \gg 1$) with finite $D = \varepsilon/2L^2$*

... But turns out to be valid also for finite ε

- Remarkable correspondence between predictions of the SPDE and results of lattice simulations
- SPDE predict scaling:
 $D \rightarrow \lambda D$ implies a rescaling of the spatial coordinates:
 $x \rightarrow x/\sqrt{\lambda} \Rightarrow$ Magnification, or 'zoom in' effect, by factor $\sqrt{\lambda}$
- In the lattice simulations: found the same scaling
- **Both descriptions seem to be statistically equivalent**

Comparison of the spatial correlation functions $g_{ij}(r)$ obtained from lattice simulations and predicted by the SPDE

$$g_{ij}(r) = \lim_{t \rightarrow \infty} \langle s_i(\mathbf{r}, t) s_j(\mathbf{0}, t) \rangle - \langle s_i(\mathbf{r}, t) \rangle \langle s_j(\mathbf{0}, t) \rangle$$



- Excellent agreement between **SPDE** and **lattice simulations**
- Correlation length $\ell_{\text{corr}} \propto \sqrt{D}$
- \Leftrightarrow Raising D the size of the spirals is increased

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About the stochastic spatial May-Leonard model, we have learnt:

- Coexistence is stable or unstable, depending on the diffusion constant D
- In the coexistence phase (continuum limit), emergence of an entanglement *spiral waves*
- Stochastic dynamics: described by SPDE with (white) noise (from the *reactions*) of strength $\propto N^{-1/2}$
- Remarkable agreement between lattice simulations & SPDE ...
Even for finite values of the exchange rate ε

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Remaining questions:

- Role and influence of internal noise ?
- Characterisation of the spatio-temporal patterns ?
- State diagram: when do we have biodiversity/uniformity ?

Role and influence of internal noise

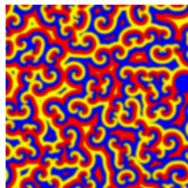
- The SPDE provide a faithful description of the stochastic dynamics in the continuum limit
- In the SPDE, the noise strength is $\propto N^{-1/2}$ with $N \rightarrow \infty$

What happens if noise is ignored: $\partial_t \mathbf{s}_i(\mathbf{r}, t) = D\Delta \mathbf{s}_i(\mathbf{r}, t) + \alpha_i(\mathbf{s})$?

$$D = 3 \times 10^{-6} \text{ and } \sigma = \mu = 1.$$

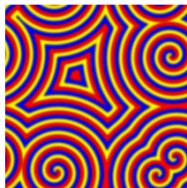
Homogeneous initial condition

SPDE



Slightly inhomogeneous initial condition

PDE



Noise acts as a random source of local inhomogeneities

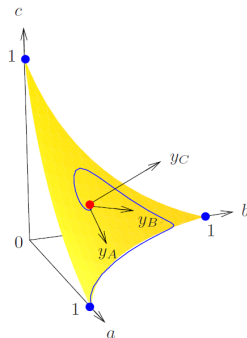
- Spiral waves in both cases:
share the same velocity and wavelength
- SPDE: entanglement of spirals \rightarrow *robust features*
- PDE: geometrically ordered, *dependence on the initial condition*

Characterisation of spatio-temporal patterns

- The spiral waves resulting from the SPDE and the PDE share the same velocity & frequency
- The dynamics of the PDE, restricted on the **invariant manifold**, can be recast in the form of a *Complex Ginzburg Landau Equation* (CGLE):

$$\partial_t z(\mathbf{r}, t) = D\Delta z(\mathbf{r}, t) + (c_1 - i\omega)z(\mathbf{r}, t) - c_2(1 - ic_3) |z(\mathbf{r}, t)|^2 z(\mathbf{r}, t)$$

- Give rise to coherent structures, like *spiral waves*
- Travelling-wave ansatz:
 $z = Ze^{-i\Omega t - i\mathbf{q}\cdot\mathbf{r}}$
- Dispersion relation \rightarrow velocity, selected wavevector, frequency
- Here, spiral waves are the stable solutions



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With $c_1 = \frac{\mu\sigma}{2(3\mu+\sigma)}$, $\omega = \frac{\sqrt{3}\mu\sigma}{2(3\mu+\sigma)}$, $c_2 = \frac{\sigma(3\mu+\sigma)(48\mu+11\sigma)}{56\mu(3\mu+2\sigma)}$ and $c_3 = \frac{\sqrt{3}(18\mu+5\sigma)}{48\mu+11\sigma}$

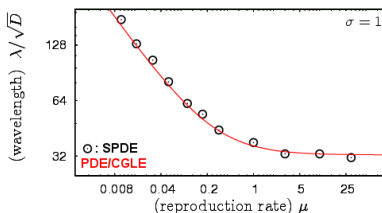
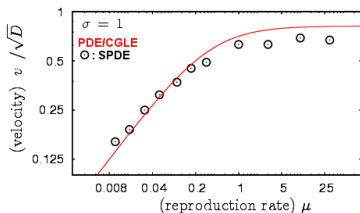
- Velocity: $v = 2\sqrt{c_1 D}$
- Wavelength: $\lambda = \frac{2\pi c_3 \sqrt{D}}{\sqrt{c_1} (1 - \sqrt{1 + c_3^2})}$
- Frequency: $\Omega = \omega + 2\pi v / \lambda$,

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Spiral waves' spreading velocity

Deterministic predictions: $v = 2\sqrt{c_1 D}$ and $\lambda = \frac{2\pi c_3 \sqrt{D}}{\sqrt{c_1}(1 - \sqrt{1 + c_3^2})}$

Expected to be valid for the stochastic model in the continuum limit

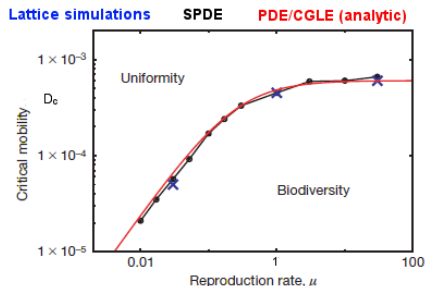


- Agreement between Lattice simulations, SPDE and PDE/CGLE
- Velocity v scales as \sqrt{D}
- Wavelength λ scales as \sqrt{D}

State diagram

- Spiral waves in the coexistence phase: $\lambda \propto \sqrt{D}$
- Size of the spiral increases with $\propto \sqrt{D}$...
- ... for D up to $D_c(\mu, \sigma)$, where $\lambda = \lambda_c$
- **When $D > D_c$: the spirals outgrow the system, biodiversity is lost**

To obtain the state diagram for $\sigma = 1$ (unit of time), one exploits the scaling relation $\lambda(D, \mu) \propto \sqrt{D}$: $D_c(\mu) = \left(\frac{\lambda_c}{\lambda(D, \mu)} \right)^2 D$



- D_c monotonic function
- Small μ : $D_c \propto \mu$

Mathematical descriptions in terms of **interacting particles**, SPDE, **PDE (analytic)** all lead to the **same state diagram**

Nature **448**, 1046 (2007)

Combining various mathematical and theoretical approaches:

- Well-mixed population: fluctuations (finite size effect) → extinction and uniformity
- Oscillatory dynamics of the RPS game: limit cycle in the presence of mutations and quasi-cycles in the presence of demographic noise
- Local interactions: biodiversity and pattern formation
- Mobility mediates between these scenarios: above a threshold D_c biodiversity is lost
- Continuum limit: stochastic dynamics aptly described by SPDE
- Internal noise: random source of inhomogeneities → robustness
- Spirals: characterisation inferred from a proper CGLE

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- Spiral waves observed in other microbial communities: Myxobacteria and Dystostelium

Conclusion

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- Spiral waves observed in other microbial communities: Myxobacteria and Dystostelium
- Methods and approach can be applied to epidemiology, behavioural sciences , chemistry ...

This presentation is based on the following papers:

- arXiv:0912.5179v1 (to appear in the Journal of Theoretical Biology)
- J. Theor. Biol. **254**, 368-383 (2008)
- Banach Center Publications **80**, 259-264 (2008)
- Phys. Rev. Lett. **99**, 238105 (2007)
- Nature **448**, 1046-1049 (2007)
- Phys. Rev. E **74**, 051907 (2006)

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