Spontaneous pattern formation in spatial populations with cyclic dynamics

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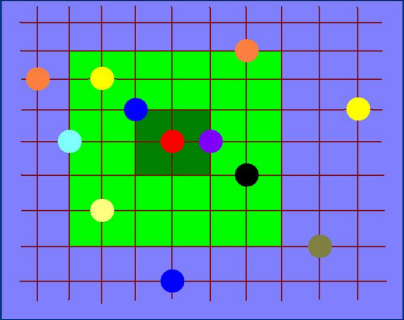
Cyclic spatial models

- Catalytic hypercycles (pre-biotic evolution)
  Greenberg–Hastings model (neuron excitation)
  Rock-Scissors-Paper (colicin)
  Spatial Epidemic

- Spatial structure in microbial communities w/ cyclic dynamics; consumer-driven resource fluctuations

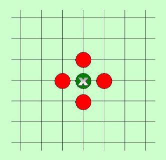
Interacting Particle Systems

- Spatially explicit random dynamics (stochastic, discrete space)
- Specify local interactions – infer global behavior
- Different from behavior in well-mixed liquid (ODE)
- Behavior of related ODE and PDE can provide insight

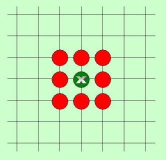


Different types on regular 2-dimensional lattice.

Different neighborhoods



4 nearest neighbors

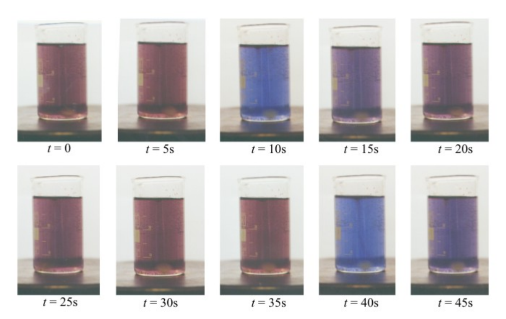


8 nearest neighbors

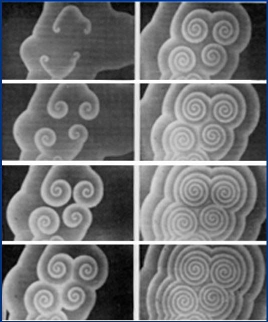
larger neighborhoods possible

Preview: Belousov-Zhabotinsky reaction

chemical oscillator

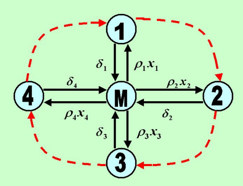


BZ reaction on surface



Spontaneously forming concentric and spiral waves (excitable medium)

Catalytic hypercycles (RNA molecules in pre-biotic evolution)

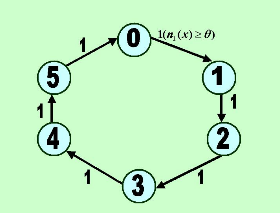


Each species replicates itself. Species $i - 1$ provides catalytic support for i. Spatial models (PDE or IPS) yield spiral waves $\iff n \geq 5$.

$u_i(x,t) =$ density of species i $(i = 1, \ldots, n)$;
$M(x,t) =$ monomer concentration.

$$\begin{aligned} \frac{\partial u_i}{\partial t} &= D_u \Delta u_i + k_i M u_i u_{i-1} + \rho_i M u_i - \delta_i u_i \\ \frac{\partial M}{\partial t} &= D_M \Delta M - \sum_i (k_i M u_i u_{i-1} + \rho_i M u_i) + \delta(1 - M) \end{aligned}$$

Greenberg–Hastings model (neuron excitation)

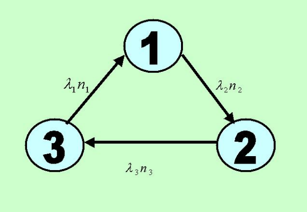


1=excited state; threshold excitation

contact updating for one state; others spontaneous

* Simulations *

Rock-Scissors-Paper (colicin)



Nontransitive competition
all contact updating

* Simulations *

Spatial Epidemic–SIR model

Susceptible $\longrightarrow$ Infective . . . rate βn_1

Infective $\longrightarrow$ Removed . . . rate δ

Removed $\longrightarrow$ Susceptible . . . rate γ

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* Simulations *

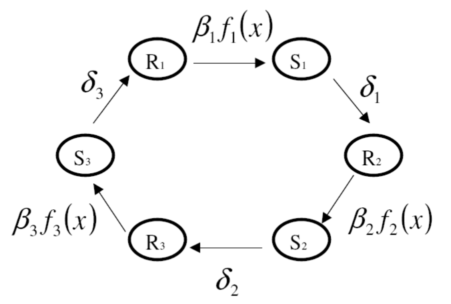
Microbial diversity and a new cyclic model

Cross-section of microbial mat from salt marsh. Bacteria specializing on different nutrients, oxygen levels, etc.

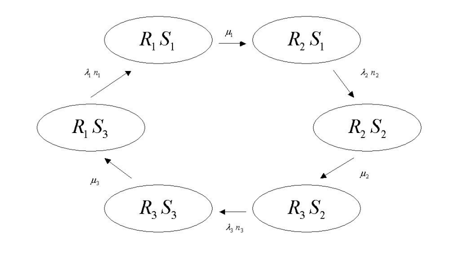
Consumer-driven resource fluctuations

- Resources $R_1, \ldots, R_L$
- Species $S_1, \ldots, S_L$
- species S_i dominates on resource R_i
- consumption of R_i leads to successional growth of R_{i+1} (index reduced modulo n; so $R_{L+1} = R_1$)
- Successive degradation of nutrient (cross-feeding); catalytic support for primary degrader (toxin removal) produces feedback $\rightarrow$ cyclic dynamics

IPS: cyclic resource-species model

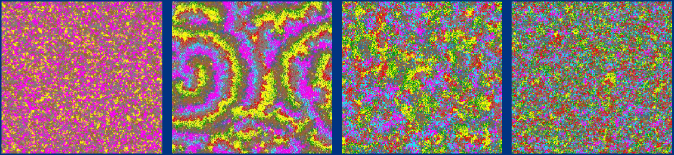


Transition rates for a single patch (L=3 species).



Transition rates for a single patch.

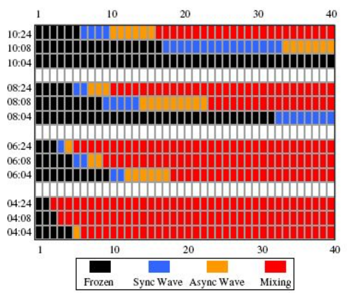
4 patterns



Frozen, synchronous waves, asynchronous waves, mixed

* Stochastic spatial simulator *

IPS simulations: symmetric case



$\delta_1 = \cdots = \delta_L = 1$ and $\beta_1 = \cdots = \beta_L = \beta$

x-axis: β, y-axis: "$2L$: nbhd. size"

Formal classification . . . coefficient of variation, $CV_i = \sigma_i/\mu_i$, for each species i:

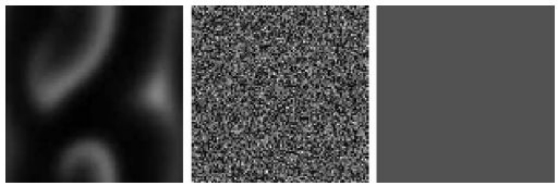
- frozen ($CV = 0$);
- mixing ($0 < CV \leq 0.5$);
- async waves ($0.5 < CV \leq 1$);
- sync waves ($CV > 1$).

CV insensitive to state used (graph based on species 1)

Fast-stirring limit: RDE

$$\begin{cases} \frac{\partial R_1}{\partial t} &= \Delta R_1 + \delta_L S_L - \beta_1 R_1 S_1 \\ \frac{\partial S_1}{\partial t} &= \Delta S_1 - \delta_1 S_1 + \beta_1 R_1 S_1 \\ \frac{\partial R_2}{\partial t} &= \Delta R_2 + \delta_1 S_1 - \beta_2 R_2 S_2 \\ \frac{\partial S_2}{\partial t} &= \Delta S_1 - \delta_2 S_2 + \beta_2 R_2 S_2 \\ &\vdots \\ \frac{\partial R_L}{\partial t} &= \Delta R_L + \delta_L S_L - \beta_L R_L S_L \\ \frac{\partial S_L}{\partial t} &= \Delta S_L - \delta_L S_L + \beta_L R_L S_L \end{cases}$$

Reaction-Diffusion Eqn: L=3



Left: $\beta = 3.8$ (spirals); Middle: random initial configuration; Right: $\beta = 5.8$ (homogeneous)

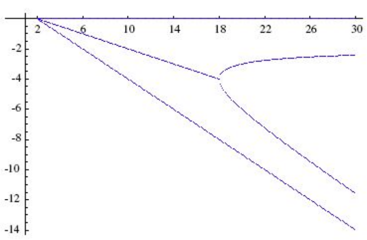
Mean-field ODE

- symmetric case: $\delta_1 = \cdots = \delta_L = 1$ and $\beta_1 = \cdots = \beta_L = \beta$.
- One interior equilibrium point X^* with components $R_1 = \cdots = R_L = \frac{1}{\beta}$ and $S_1 = \cdots = S_L = \frac{1}{L} - \frac{1}{\beta}$.
- Coexistence $\iff \beta > L$.

L=2 Jacobian at interior equilibrium

$$J_f(X^*) = \begin{pmatrix} 1-\frac{\beta}{2} & -1 & 0 & 1 \\ -1+\frac{\beta}{2} & 0 & 0 & 0 \\ 0 & 1 & 1-\frac{\beta}{2} & -1 \\ 0 & 0 & -1+\frac{\beta}{2} & 0 \end{pmatrix}$$

Real part of eigenvalues: L=2



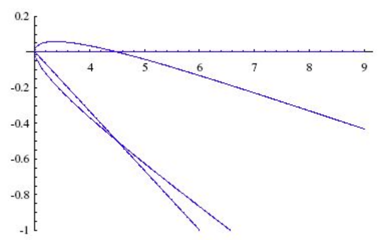
as function of $\beta > 2$.

- Re$(\lambda_i) \leq 0$: perturbations decay $\Longrightarrow$ mixed (or frozen)

L=3 Jacobian at interior equilibrium

$$J_f(X^*) = \begin{pmatrix} 1-\frac{\beta}{3} & -1 & 0 & 0 & 0 & 1 \\ -1+\frac{\beta}{3} & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 1-\frac{\beta}{3} & -1 & 0 & 0 \\ 0 & 0 & -1+\frac{\beta}{3} & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 1-\frac{\beta}{3} & -1 \\ 0 & 0 & 0 & 0 & -1+\frac{\beta}{3} & 0 \end{pmatrix}$$

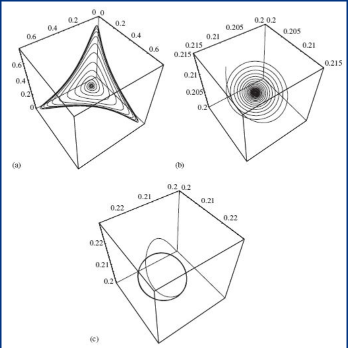
Real part of eigenvalues: L=3



as function of $\beta > 3$.

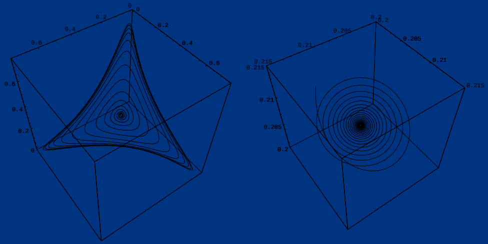
- $\mathrm{Re}(\lambda_1) > 0$ for $3 < \beta < 4.5$: perturbations grow $\Longrightarrow$ spirals (or asynchronous waves)

ODE trajectories of 3 resources, L=3



(a) $\beta = 3.8$ (spiral out, nearly heteroclinic); (b) $\beta = 4.8$ (spiral in, stable equil.); (c) $\beta = 4.5$ (limit cycle)

Coupled map lattice interpretation, L=3

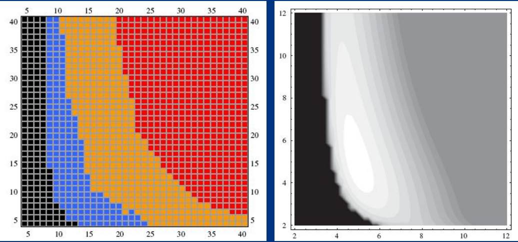


(a) $\beta = 3.8$ (spiral out, nearly heteroclinic); (b) $\beta = 4.8$ (spiral in, stable equil.)

Asymmetric case

- $\delta_1 = \cdots = \delta_L = 1, \quad \beta_2 = \cdots = \beta_L = \beta, \quad$ (majority growth rate), $\quad \beta_1 > \beta$.
- One interior equilibrium point X^* with components $R_1 = \frac{1}{\beta_1}$, $R_2 = \cdots = R_4 = \frac{1}{\beta}$, and $S_1 = \cdots = S_4 = \frac{1}{4} - \frac{1}{4\beta_1} - \frac{3}{4\beta}$.
- Coexistence $\iff \frac{1}{4} - \frac{1}{4\beta_1} - \frac{3}{4\beta} > 0$.

Asymmetric case (L=4): IPS and RDE



x-axis: majority β, y-axis: β_1

RDE: black (extinction) lighter color ... larger real part of dominant eigenvalue

Summary

small number of states $\longrightarrow$ less spatial structure

larger number of states $\longrightarrow$ more spatial structure when coexistence occurs

spatio-temporal mosaic, clustering and spiral formation (necessary for coexistence in some cases)

Number of states $n = 2L \geq 5$ needed to generate spiral waves (as for catalytic hypercycles).

Qualitative behavior of IPS predicted by RDE and mean-field ODE