Stochastic predation-prey competition: biodiversity and species extinction

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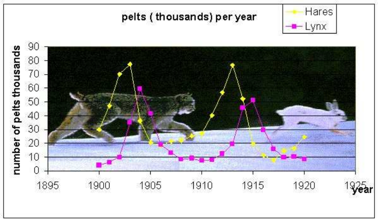
Predator-prey interaction



historic Hudson Bay Company data

Predator-prey interaction

Lotka-Volterra model (A. J. Lotka, 1920; V. Volterra, 1926)

- predators: $A \longrightarrow 0$ death, rate μ
- prey: $B \longrightarrow B + B$ birth, rate σ
- predation: $A + B \longrightarrow A + A$, rate λ

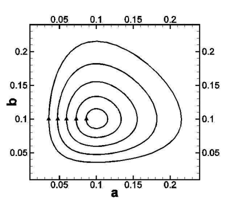
mean-field rate equations for homogeneous densities:

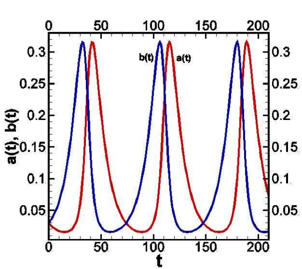
$$\begin{aligned} \frac{da(t)}{dt} &= -\mu\, a(t) + \lambda\, a(t)\, b(t) \\ \frac{db(t)}{dt} &= \sigma\, b(t) - \lambda\, a(t)\, b(t) \end{aligned}$$

conserved quantity: $K = \lambda(a + b) - \sigma \ln a - \mu \ln b$

$\longrightarrow$ limit cycles, population oscillations

Predator-prey interaction





Predator-prey interaction

Generalization: multi-species Lotka-Volterra rate equations

$$\frac{dx_i(t)}{dt} = x_i(t)\left(r_i + \sum_{j=1}^{n} \alpha_{i,j} x_j(t)\right)$$

r_i: intrinsic growth or decay

$\alpha_{i,j}$: represents interaction matrix that encodes competition between species i and j

very general equations that encompass many different cases (food chains)

example: cyclic Lotka-Volterra model

$A_1 + A_2 \longrightarrow 2A_1,\ A_2 + A_3 \longrightarrow 2A_2,\ \cdots,\ A_{n-1} + A_n \longrightarrow 2A_{n-1},$
$A_n + A_1 \longrightarrow 2A_n$

Predator-prey interaction

original (two-species) Lotka-Volterra model

$$\frac{da(t)}{dt} = -\mu\, a(t) + \lambda\, a(t)\, b(t)$$
$$\frac{db(t)}{dt} = \sigma\, b(t) - \lambda\, a(t)\, b(t)$$

stationary states (fixed point)

- $(a^*, b^*) = (0, 0) \longrightarrow$ extinction
- $(a^*, b^*) = (0, \infty) \longrightarrow$ predators extinct, Malthusian prey proliferation
- $(a_c, b_c) = (\sigma/\lambda, \mu/\lambda) \longrightarrow$ species coexistence

linearization about coexistence stationary state

$\Longrightarrow$ purely oscillatory kinetics with characteristic frequency $\omega = \sqrt{\mu\sigma}$

Predator-prey interaction

conservation law for K and related purely oscillatory motion are special features of the deterministic model equations

results unstable with respect to perturbations:

- model modifications
- spatial degrees of freedom
- stochasticity

Stochastic Lotka-Volterra model: no space dependence

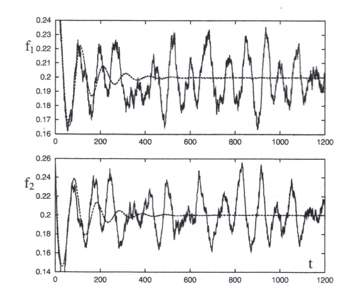
A predators and B preys $\longrightarrow$ discrete degrees of freedom

$$\frac{dP(A,B;t)}{dt} = \lambda(A-1)(B+1)P(A-1,B+1;t) + \mu(A+1)P(A+1,B;t) - (\mu A + \sigma B + \lambda A B)P(A,B;t)$$

only one stable steady state: $P_S(A=0,B=0)=1$ and $P_S(A\neq 0, B\neq 0)=0$

as $t \longrightarrow \infty$, empty (absorbing) state will be reached

at finite times:
erratic population oscillations
(*resonant amplification mechanism*)
McKane/Newman '05



Stochastic Lotka-Volterra model on a lattice

each lattice site either empty or occupied by a predator or a prey

mean-field rate equations for the particle densities

$$\begin{aligned}\frac{da}{dt} &= -\mu a(t) + \lambda a(t) b(t) \\ \frac{db}{dt} &= \sigma[1 - a(t) - b(t)] b(t) - \lambda a(t) b(t)\end{aligned}$$

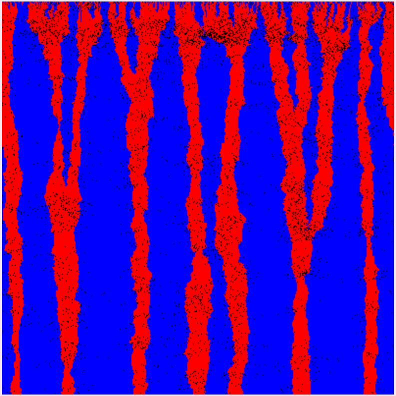
absorbing state: $\lambda < \mu$; $a \longrightarrow 0$, $b \longrightarrow 1$

$\lambda > \mu$: active phase: A and B coexist

active/absorbing phase transition
$\longrightarrow$ nonequilibrium phase transition

Stochastic Lotka-Volterra model on a lattice

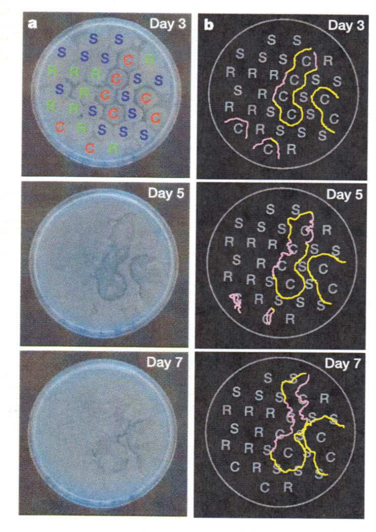
coarsening in one dimension – final state: system full of prey
predator (red) and prey (blue) domains



complicated space-time pattern in two space dimensions
(Mobilia, Georgiev, Täuber '07)

Cyclic dominance of competing species

real-world example: competing bacterial strains (*Escherichia coli*) (Kerr et al. '02)



Rock-Paper-Scissors game

three cyclically competing species: Rock-Paper-Scissors game

$$\begin{aligned} a + b &\xrightarrow{k_a} a + a \\ b + c &\xrightarrow{k_b} b + b \\ c + a &\xrightarrow{k_c} c + c \end{aligned}$$

Rock-Paper-Scissors game

three cyclically competing species: Rock-Paper-Scissors game

$$\begin{array}{ccc} a+b & \xrightarrow{k_a} & a+a \\ b+c & \xrightarrow{k_b} & b+b \\ c+a & \xrightarrow{k_c} & c+c \end{array}$$

three ways of realizing mobility when on a lattice:

- exchange of individuals

$$\begin{array}{ccc} a+b & \overset{s_{ab}}{\rightleftarrows} & b+a \\ b+c & \overset{s_{bc}}{\rightleftarrows} & c+b \\ c+a & \overset{s_{ca}}{\rightleftarrows} & a+c \end{array}$$

  conserved quantity: $N_a + N_b + N_c = N$

- empty sites
- multiple occupancy of sites

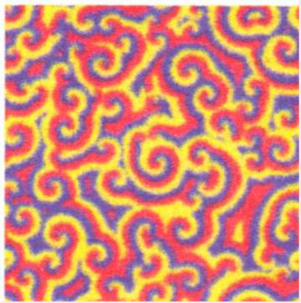
Formation of space-time pattern

May-Leonard model

three species on a two-dimensional lattice

separation of predation and reproduction

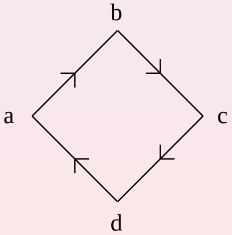
$$A + B \longrightarrow A + 0$$
$$A + 0 \longrightarrow A + A$$



What about more than three species?

Simplest generalization: four species

$$
\begin{aligned}
a + b &\xrightarrow{k_a} a + a \\
b + c &\xrightarrow{k_b} b + b \\
c + d &\xrightarrow{k_c} c + c \\
d + a &\xrightarrow{k_d} d + d
\end{aligned}
$$



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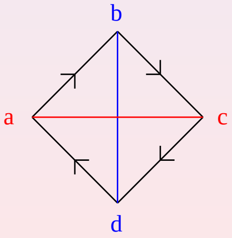
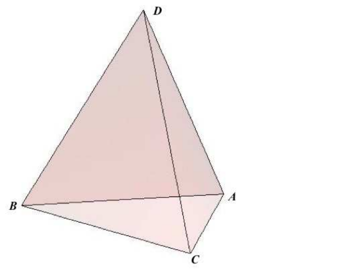


formation of partner-pairs!

Well-mixed system

configuration space for four species



ac and bd pairs do not interact

$\Longrightarrow$ final (absorbing) state displays coexistence of these pairs

every point along $a - c$ and $b - d$ edges represents such a state

$\Longrightarrow 2(N + 1)$ absorbing states

Well-mixed system

mean field approximation for the evolution of the averages of the fractions

$$A(t) \equiv \sum_{\{N_m\}} (N_a/N)\, P\left(\{N_m\}\,;t\right) \quad \text{etc.}$$

neglect all correlations and replace averages of products by the products of averages

MF equations ($k_a + k_b + k_c + k_d = 1$):

$$\begin{aligned}
\partial_t A &= [k_a B - k_d D]\, A \\
\partial_t B &= [k_b C - k_a A]\, B \\
\partial_t C &= [k_c D - k_b B]\, C \\
\partial_t D &= [k_d A - k_c C]\, D
\end{aligned}$$

Well-mixed system

mean field approximation for the evolution of the averages of the fractions

$$A(t) \equiv \sum_{\{N_m\}} (N_a/N)\, P\left(\{N_m\}\,;\, t\right) \quad \text{etc.}$$

neglect all correlations and replace averages of products by the products of averages

MF equations $(k_a + k_b + k_c + k_d = 1)$:

$$\begin{aligned}
\partial_t \ln A &= k_a B - k_d D \\
\partial_t \ln B &= k_b C - k_a A \\
\partial_t \ln C &= k_c D - k_b B \\
\partial_t \ln D &= k_d A - k_c C
\end{aligned}$$

Well-mixed system

contributions from a single species to the growth/decay of two other species:

$$\begin{aligned} \partial_t \left[k_b \ln A + k_a \ln C \right] &= \lambda D \\ \partial_t \left[k_c \ln A + k_d \ln C \right] &= \lambda B \\ \partial_t \left[k_c \ln B + k_b \ln D \right] &= -\lambda A \\ \partial_t \left[k_d \ln B + k_a \ln D \right] &= -\lambda C \end{aligned}$$

key control parameter: $\lambda \equiv k_a k_c - k_b k_d$

quantity

$$Q \equiv \frac{A^{k_b+k_c} C^{k_d+k_a}}{B^{k_c+k_d} D^{k_a+k_b}}$$

evolves in an extremely simple manner:

$$Q(t) = Q(0)\, e^{\lambda t}$$

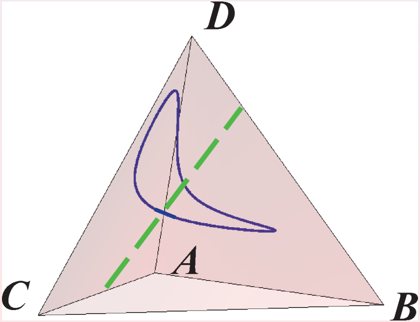
Well-mixed system

$\lambda = 0 \longrightarrow k_a k_c = k_b k_d \longrightarrow Q$ is a constant of motion

numerator/denominator of Q are constant

each defines a (generalized) hyperbolic sheet

intersection is a closed loop ($\sim$ edge of a saddle)



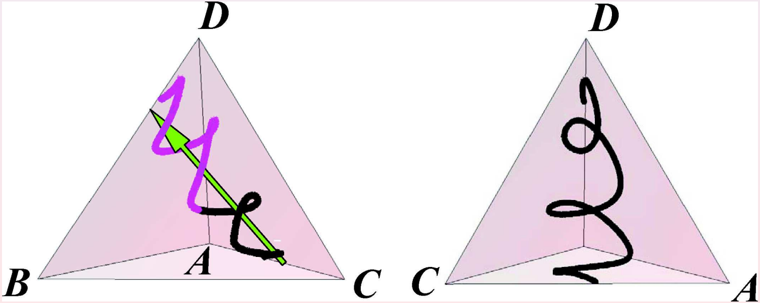
saddle-shaped orbits and fixed points

Well-mixed system

$\lambda \neq 0$

$$Q(t) = Q(0)\, e^{\lambda t} \quad \text{with} \quad Q \equiv \frac{A^{k_b+k_c} C^{k_d+k_a}}{B^{k_c+k_d} D^{k_a+k_b}}$$

spirals and arrows

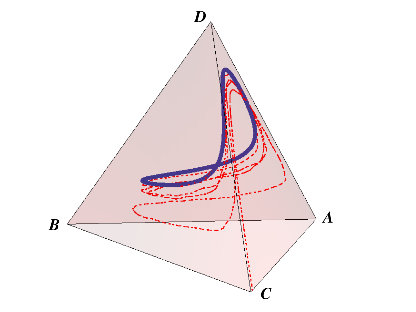


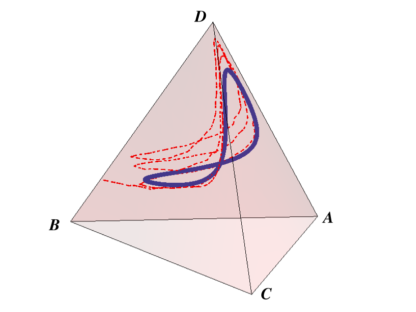
starting from symmetry point with $\lambda = -0.0273$

Well-mixed system

going beyond mean field approximation: numerical simulations

$\lambda = 0$: stochastic effects

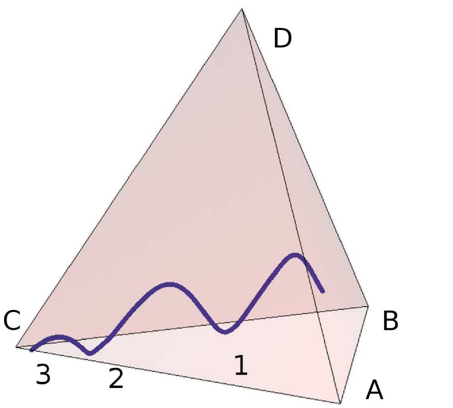




1000 particles, $(k_a, k_b, k_c, k_d) = (0.4, 0.4, 0.1, 0.1)$ and
$(A_0, B_0, C_0, D_0) = (0.02, 0.10, 0.48, 0.40)$

Well-mixed system

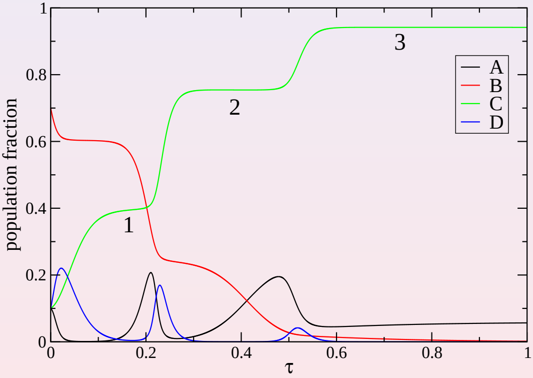
$\lambda \neq 0$: extinction events



$(k_a, k_b, k_c, k_d) = (0.1, 0.0001, 0.1, 0.7999)$ and
$(A_0, B_0, C_0, D_0) = (0.1, 0.7, 0.1, 0.1)$

Well-mixed system

$\lambda \neq 0$: extinction events



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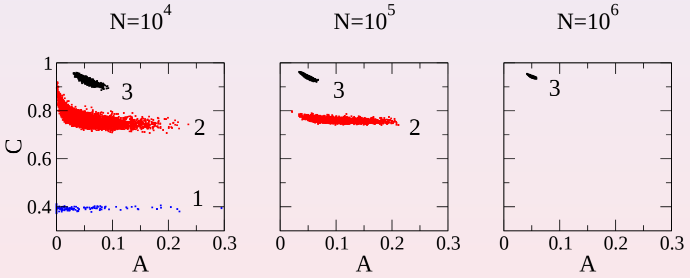
Well-mixed system

going beyond mean field approximation: numerical simulations

$\lambda \neq 0$: extinction events



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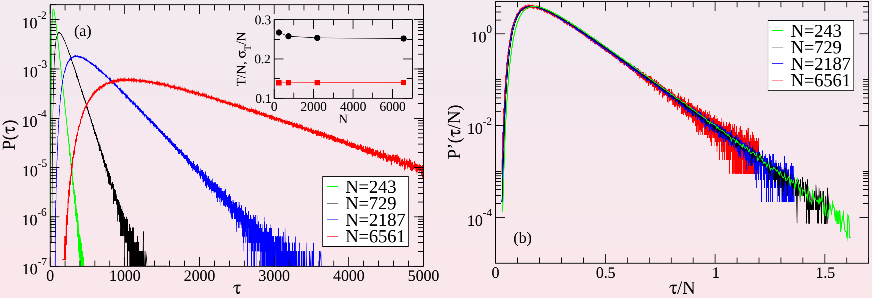
Well-mixed system

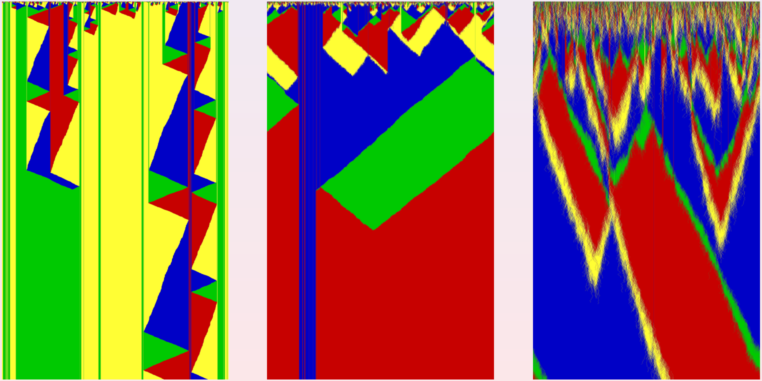
extinction time distributions for small systems



Coarsening and coexistence in one dimension

Symmetric interaction and swapping rates for four species

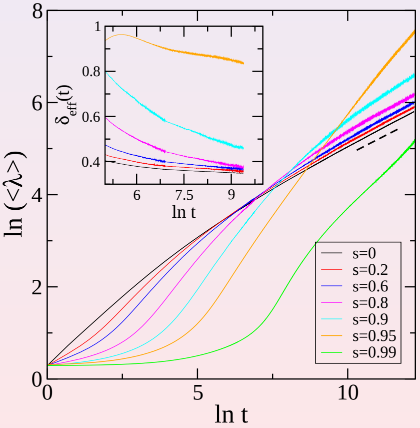
space-time diagrams



$k = 0.8,\ s = 0.2$ $k = 0.1,\ s = 0.9$ $k = 0.01,\ s = 0.99$

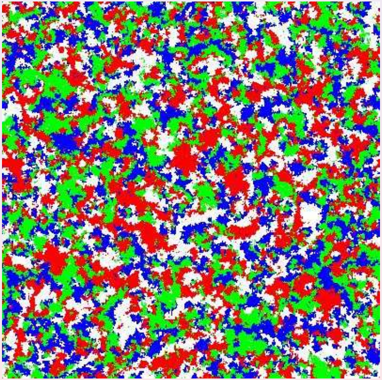
Coarsening and coexistence in one dimension

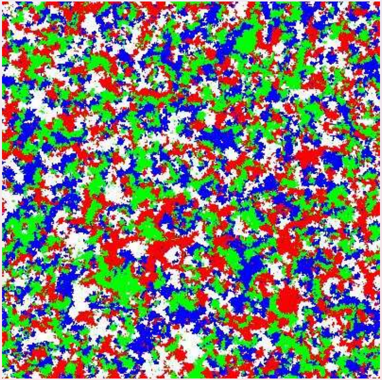
Symmetric interaction and swapping rates for four species
average domain size (for $k + s = 1$)



$\longrightarrow$ exchanges speed up the coarsening process!

four species: coexistence, but no well formed space-time patterns



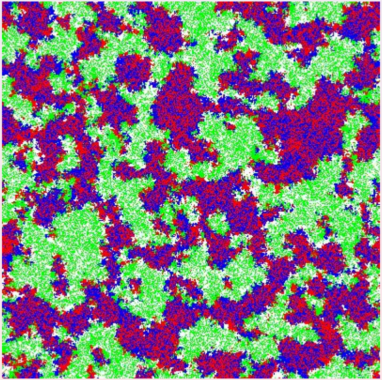


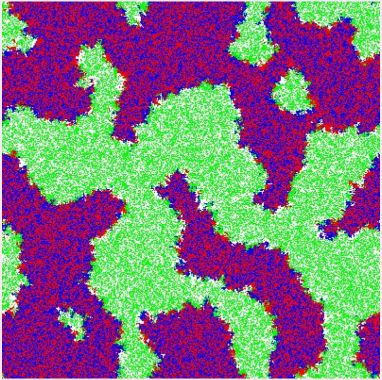
$k = 1$ and $s = 0$

Coarsening in two dimensions

four species with exchanges between individuals belonging to a partner-pair

$\Longrightarrow$ coarsening of partner-pair domains





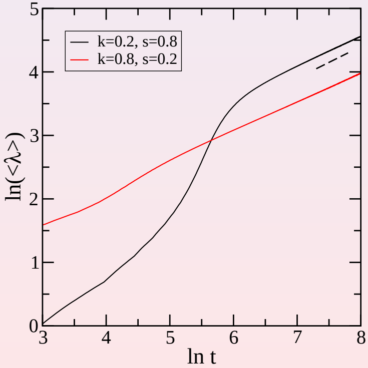
$k = 0.8$ and $s = 0.2$, $s_n = 0.2$

Coarsening in two dimensions

correlation length from the correlation function

$$C(t,\vec{r}) = \sum_i \left[\left\langle n_i(t,\vec{r}) n_i(0,\vec{0}) \right\rangle - \langle n_i(t,\vec{r}) \rangle \left\langle n_i(0,\vec{0}) \right\rangle \right] \ .$$

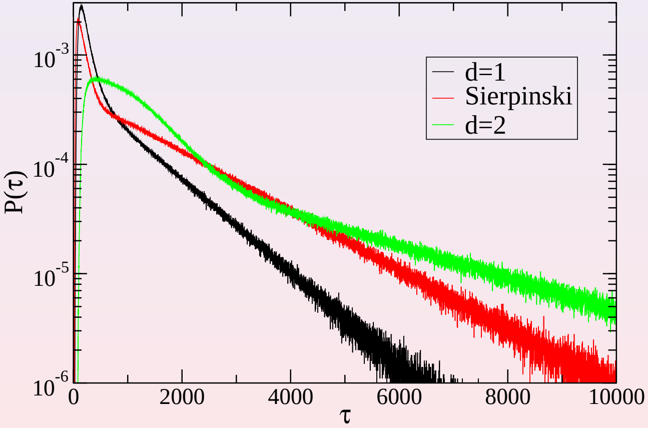
$n_i(t,\vec{r})$: occupation number



dynamical exponent $z = 2$

Extinction times

extinction time distributions for small systems



two different paths to extinction revealed by the distribution function

Generalized May-Leonard games

N different species in two dimensions

X_i: member of species i

reaction scheme:

$$
\begin{aligned}
X_i + X_j &\xrightarrow{\delta_{ij}} \emptyset + X_i && \text{predation} \\
X_i + \emptyset &\xrightarrow{\gamma_i} X_i + X_i && \text{birth} \\
\\
X_i + \emptyset &\xrightarrow{\beta_i} \emptyset + X_i && \text{diffusion} \\
X_i + X_j &\xrightarrow{\alpha_{ij}} X_j + X_i && \text{swapping}
\end{aligned}
$$

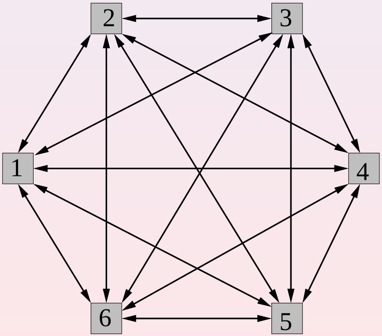
model (N, r): generalized May-Leonard model with N species where each species preys on r other species in a cyclic way

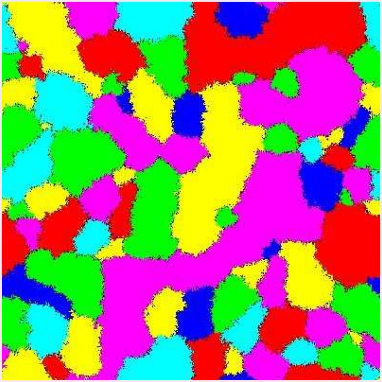
$(N, 1)$: N-species cyclic Lotka-Volterra game discussed until now

Generalized May-Leonard games

space-time pattern and coarsening

model (6,5)

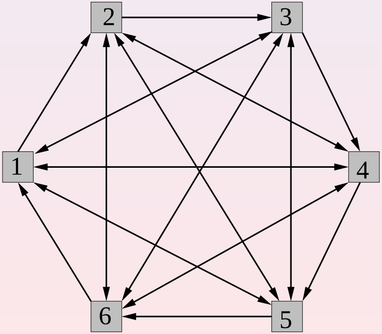


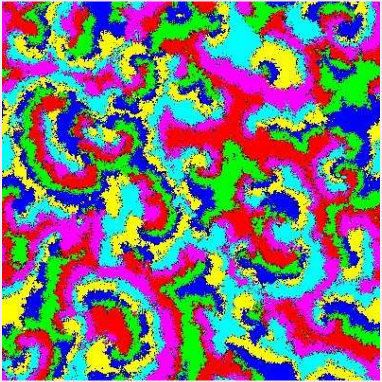


Generalized May-Leonard games

space-time pattern and coarsening

model (6,4)

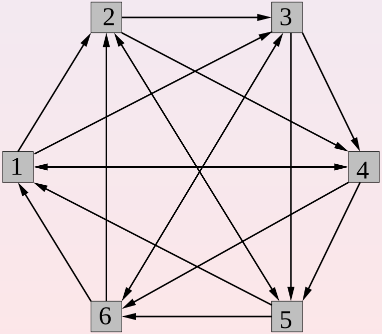


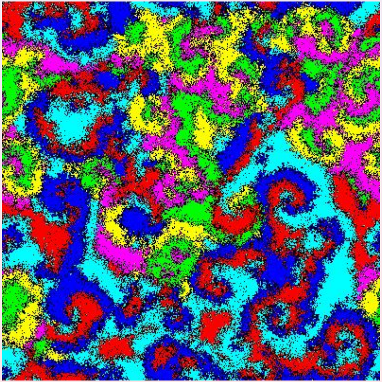


Generalized May-Leonard games

space-time pattern and coarsening

model (6,3)

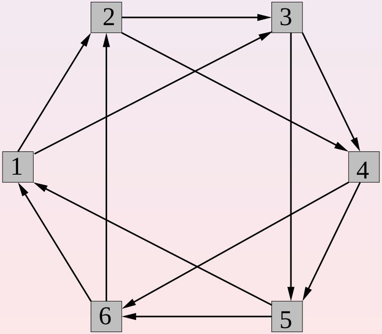


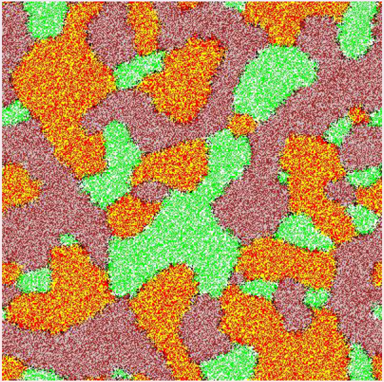


Generalized May-Leonard games

space-time pattern and coarsening

model (6,2)

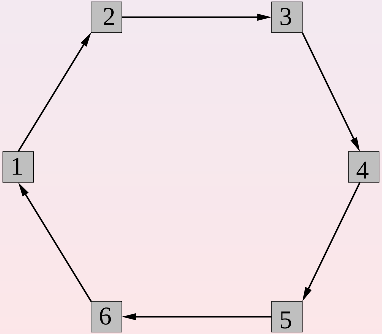


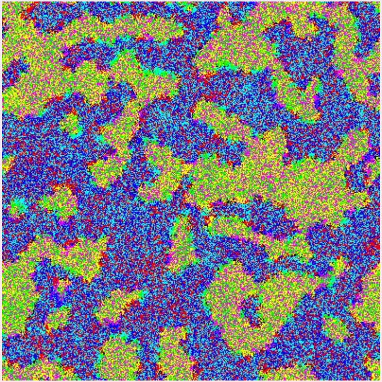


Generalized May-Leonard games

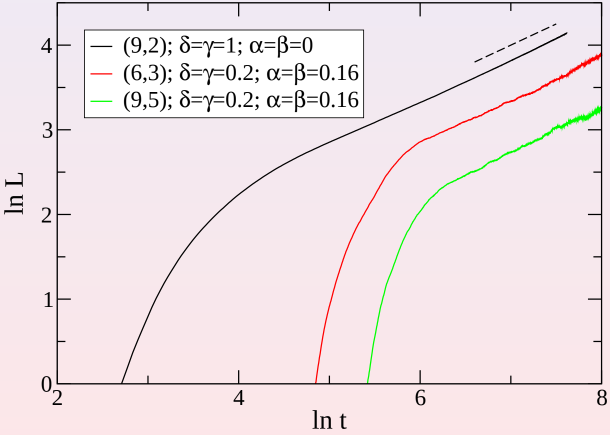
space-time pattern and coarsening

model (6,1)



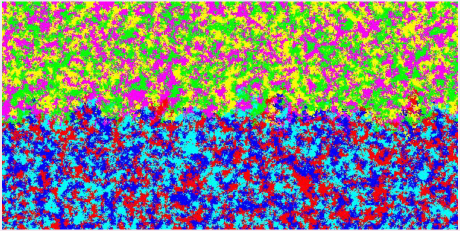


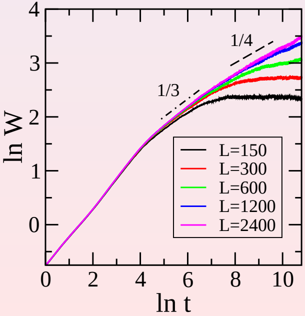
- domains grow as $t^{1/2}$



Generalized May-Leonard games

- interface width: (6,3)

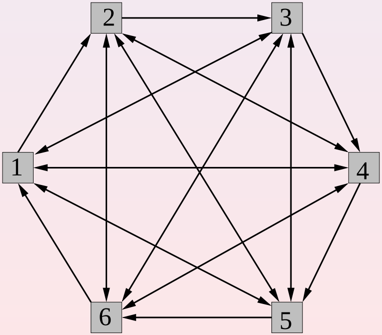


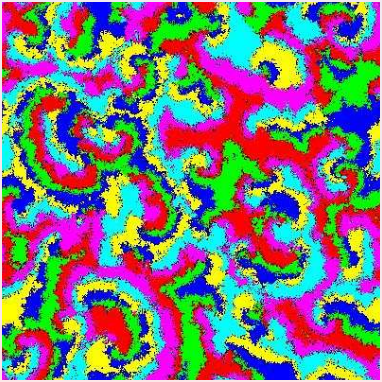


Generalized May-Leonard games

- square of the adjacency matrix contains all information about preferred partnership formations

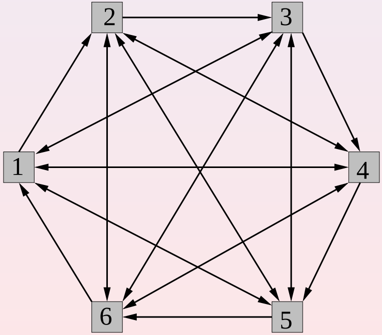
Example: model (6,4)





- square of the adjacency matrix contains all information about preferred partnership formations

Example: model (6,4)



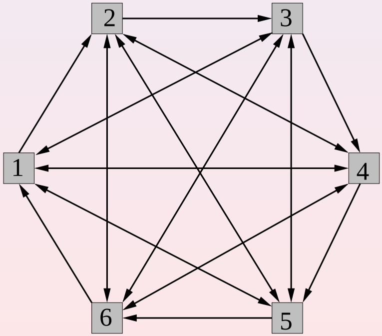
adjacency matrix

$$\mathbf{A} = \begin{pmatrix} 0 & 1 & 1 & 1 & 1 & 0 \\ 0 & 0 & 1 & 1 & 1 & 1 \\ 1 & 0 & 0 & 1 & 1 & 1 \\ 1 & 1 & 0 & 0 & 1 & 1 \\ 1 & 1 & 1 & 0 & 0 & 1 \\ 1 & 1 & 1 & 1 & 0 & 0 \end{pmatrix}$$

Generalized May-Leonard games

- square of the adjacency matrix contains all information about preferred partnership formations

Example: model (6,4)



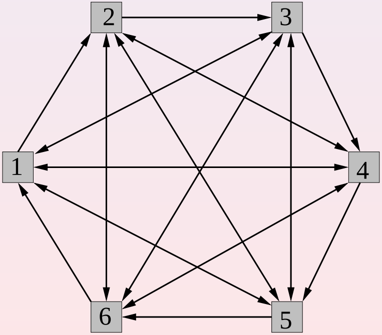
square of the adjacency matrix

$$\mathbf{B} = \begin{pmatrix} 3 & 2 & 2 & 2 & 3 & 4 \\ 4 & 3 & 2 & 2 & 2 & 3 \\ 3 & 4 & 3 & 2 & 2 & 2 \\ 2 & 3 & 4 & 3 & 2 & 2 \\ 2 & 2 & 3 & 4 & 3 & 2 \\ 2 & 2 & 2 & 3 & 4 & 3 \end{pmatrix}$$

Generalized May-Leonard games

- square of the adjacency matrix contains all information about preferred partnership formations

Example: model (6,4)



square of the adjacency matrix

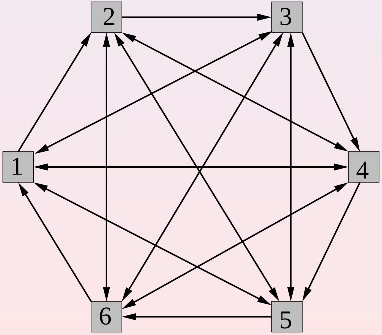
b_{ij}: number of directed paths of length 2 from vertex i to vertex j $(i \longrightarrow k \longrightarrow j)$

the enemy of my enemy is my friend
$\Longrightarrow$ preferred ally of species j:

$$\max_i b_{ij}$$

- square of the adjacency matrix contains all information about preferred partnership formations

Example: model (6,4)



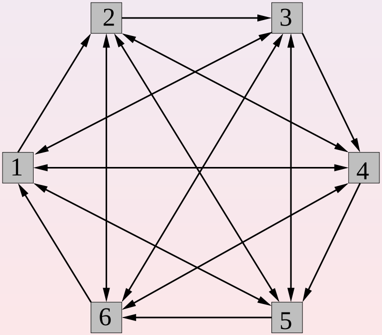
square of the adjacency matrix

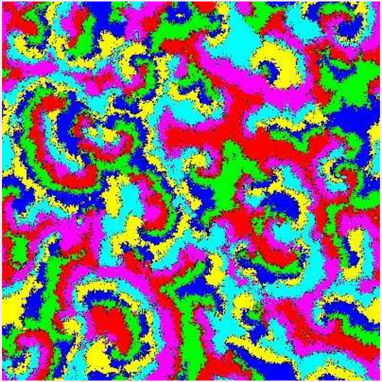
$$\mathbf{B} = \begin{pmatrix} 3 & 2 & 2 & 2 & 3 & 4 \\ 4 & 3 & 2 & 2 & 2 & 3 \\ 3 & 4 & 3 & 2 & 2 & 2 \\ 2 & 3 & 4 & 3 & 2 & 2 \\ 2 & 2 & 3 & 4 & 3 & 2 \\ 2 & 2 & 2 & 3 & 4 & 3 \end{pmatrix}$$

Generalized May-Leonard games

- square of the adjacency matrix contains all information about preferred partnership formations

Example: model (6,4)





Can be generalized to very complicated food networks using additional matrices!

Generalized May-Leonard games

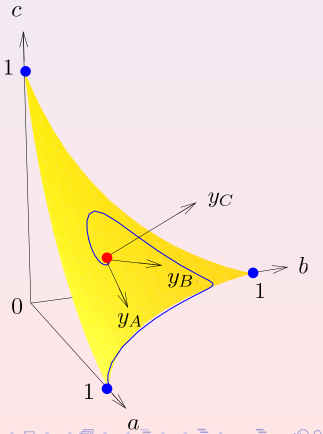
- analytical expressions describing space-time patterns can be obtained through a complex Ginzburg-Landau approach

  starting point: mean-field rate equations

$\longrightarrow$ single coexistence fixed point
$\longrightarrow$ unstable invariant manifold
$\longrightarrow$ rate equations on unstable manifold in vicinity of unstable fixed point
$\longrightarrow$ Stuart-Landau normal form on unstable manifold

$$\dot{z}_s = (c_{1,s} - i\omega_s) z_s - c_{2,s}(1 + i c_{3,s}) z_s \left| z_s \right|^2$$

$\longrightarrow$ expressions for linear spreading velocity, wavelength and frequency of spirals



Conclusion

Stochastic effects very important in population dynamics

- mean-field predictions not valid for small populations
- formation of complicated space-time patterns for three or more species that compete against each other
- generalized May-Leonard systems: coarsening processes with internal dynamics inside the growing domains
- exact method to predict alliance formation and space-time patterns for very general ecological networks

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B. Intoy and M.P., J. Stat. Mech. (2013) P08011

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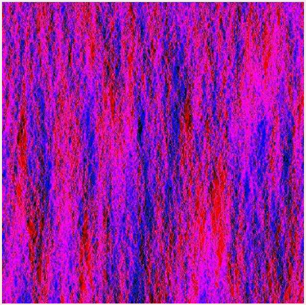
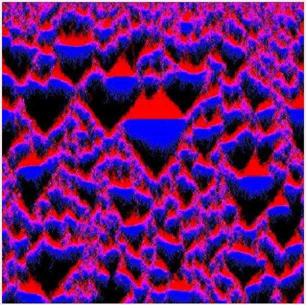
No site restriction

- $d = 2$: always coexistence
  $\Longrightarrow$ absence of active/absorbing phase transition
- $d = 1$: always coexistence

diffusion-dominated



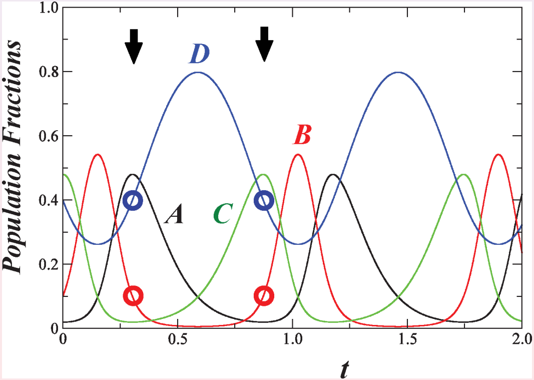
reaction-dominated



Well-mixed system

$\lambda = 0 \longrightarrow k_a k_c = k_b k_d$

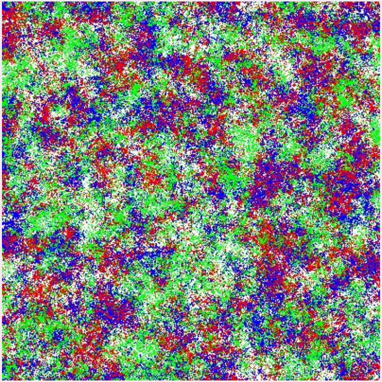
Q is a constant of motion

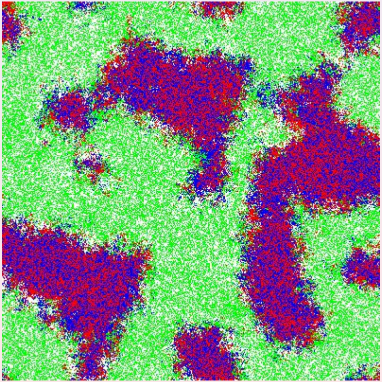


Coarsening in two dimensions

four species with exchanges between individuals belonging to a partner-pair

$\Longrightarrow$ coarsening of partner-pair domains

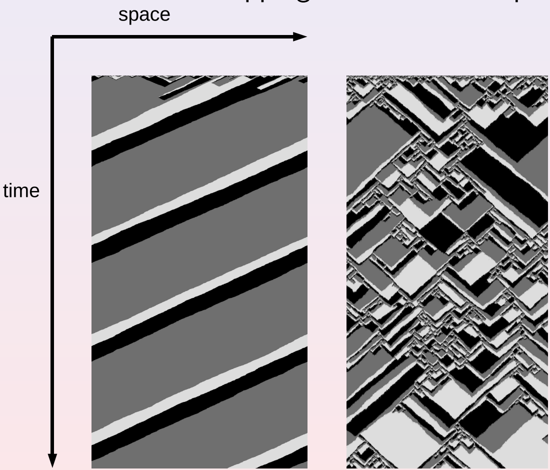




$k = 0.2$ and $s = 0.8$, $s_n = 0.8$

Coarsening and coexistence in one dimension

Symmetric interaction and swapping rates for three species

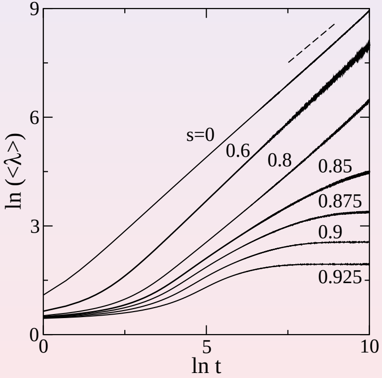


$k = 0.9,\ s = 0.1$ $\quad$ $k = 0.1,\ s = 0.9$

Coarsening and coexistence in one dimension

Symmetric interaction and swapping rates for three species

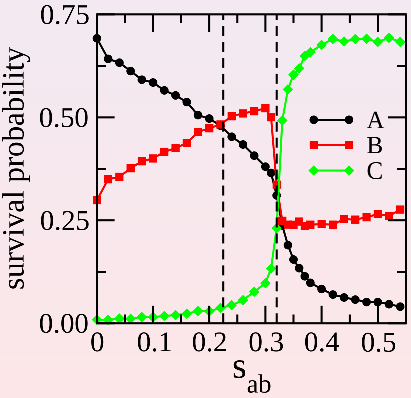
average domain size (for $k + s = 1$)



swapping rates s larger than $s_c \approx 0.84$:
exchange mechanism very effectively mixes different species
$\longrightarrow$ coexistence of species is promoted

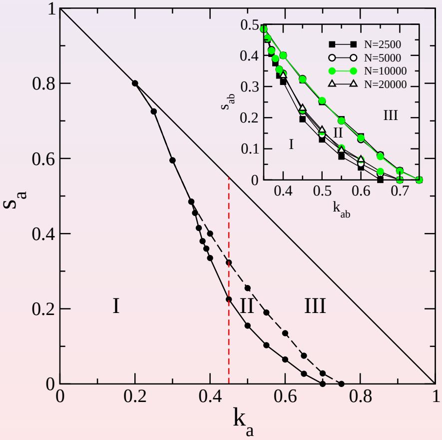
Asymmetric interaction and swapping rates for three species
asymmetry in the rates $\Longrightarrow$ dominance of a single species

Example: $k_a = 0.45,\ k_b = k_c = 0.4,\ s_{bc} = s_{ca} = 0.4$



Coarsening and coexistence in one dimension

Asymmetric interaction and swapping rates for three species dynamical phase diagram for $k_b = k_c = 0.4$, $s_{bc} = s_{ca} = 0.4$



I: A dominates, II: B dominates, III: C dominates

Cyclic dominance of competing species

real-world example: lizard populations in southern California (Sinervo/Lively '96)