# Stochastic predator-prey models: Population oscillations, spatial correlations, and the effect of randomized rates

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# Outline

- Introductory remarks
- Lotka-Volterra predator-prey interaction
- Locally limited resources; predator extinction threshold
- Predator-prey coexistence and oscillations
- Correlations and fluctuation effects; field theory
- Variants: one dimension, triplet model, cyclic predation
- Spatially varying rates and fitness enhancement
- Environmental vs. demographic variability; inheritance
- Summary and conclusions

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# Fluctuations and correlations in biological systems: fertile ground for statistical physics

- finite number of degrees of freedom: $N^{1/2} / N \sim 1$

  ⇒ thermodynamic limit need not apply

- complex cooperative, non-equilibrium phenomena:
  - non-random structures: functionally optimized
  - correlations crucial for dynamical processes,
    e.g., diffusion-limited reactions
  - history dependence, evolving systems with feedback
  - spatial fluctuations non-negligible; prominent both in non-equilibrium steady states and transient features

Physics approach: study simplified models

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# Lotka-Volterra predator-prey interaction

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

mean-field factorization → rate equations for uniform densities:

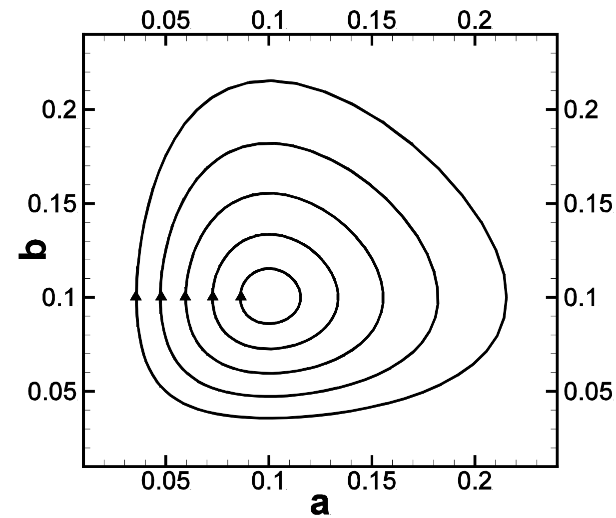
$$da(t) / dt = - \mu\, a(t) + \lambda\, a(t)\, b(t)$$

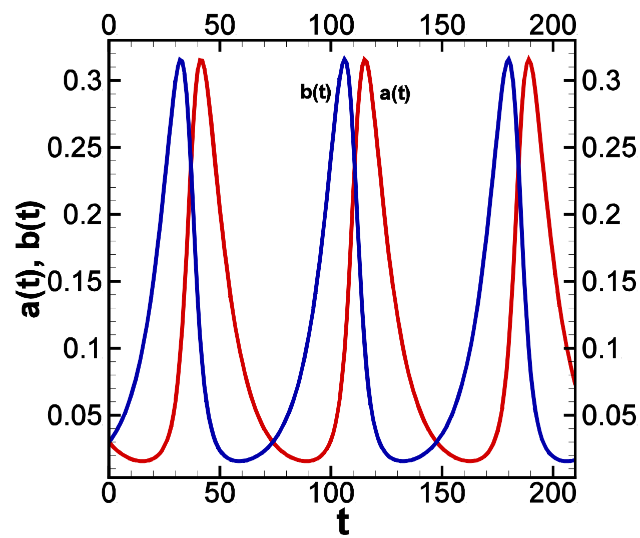
$$db(t) / dt = \sigma\, b(t) - \lambda\, a(t)\, b(t)$$

$$\Rightarrow \quad a^* = \sigma / \lambda\,, \quad b^* = \mu / \lambda$$

$$K = \lambda\,(a + b) - \sigma \ln a - \mu \ln b$$

conserved → neutral cycles, population oscillations with (linear) frequency $\omega = \sqrt{\sigma\mu}$




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

# Model with site restrictions (limited resources)

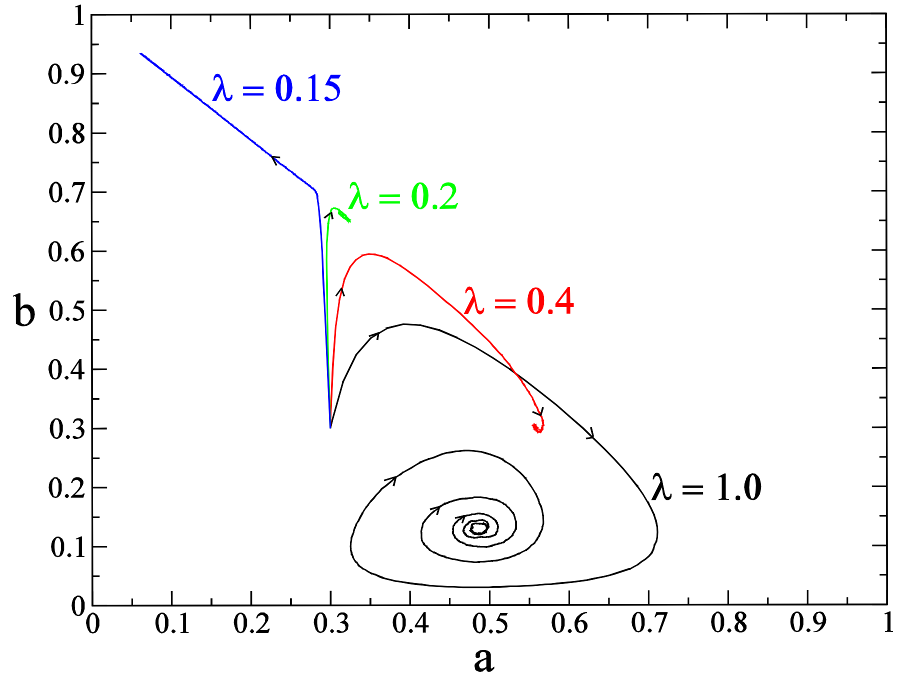
→ modified rate equations for total carrying capacity ρ = 1

$$da / dt = - \mu\, a(t) + \lambda\, a(t)\, b(t)$$
$$db / dt = \sigma\, [1 - a(t) - b(t)]\, b(t) - \lambda\, a(t)\, b(t)$$

- λ < μ: a → 0, b → 1; inactive, absorbing state
- active phase: A / B coexist, fixed point node or focus → transient erratic oscillations
- active to absorbing transition: prey extinction threshold expect directed percolation (DP) universality class

"individual-based" lattice Monte Carlo simulations:

at most single particle per site;
σ = 4.0, μ = 0.1, 200 x 200 sites




Note: finite system always reaches absorbing state, but survival times ~ exp(c N) huge for large N
*(see A. Dobrinevski, E. Frey, 2012)*

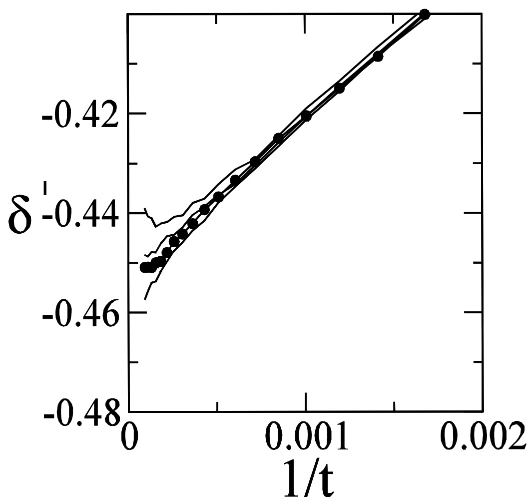
# Predator extinction threshold: critical properties

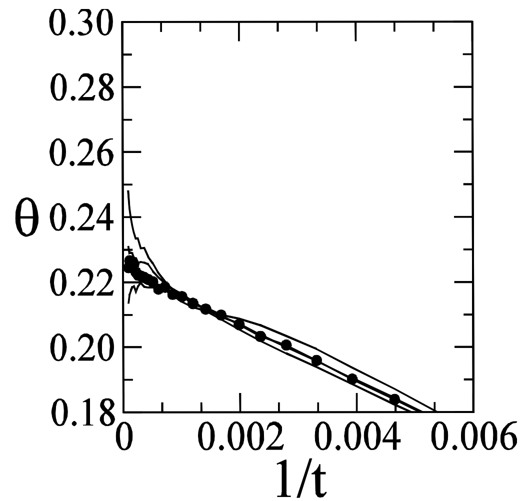
Effective processes for small λ (b ~ 1): A → 0, A ↔ A+A

⟹ expect DP *(A. Lipowski 1999; T. Antal, M. Droz 2001)*

- field theory representation *(M. Doi 1976; L. Peliti 1985)* of master equation for Lotka-Volterra reactions with site restrictions *(F. van Wijland 2001)* → Reggeon effective action
- measure critical exponents in Monte Carlo simulations:

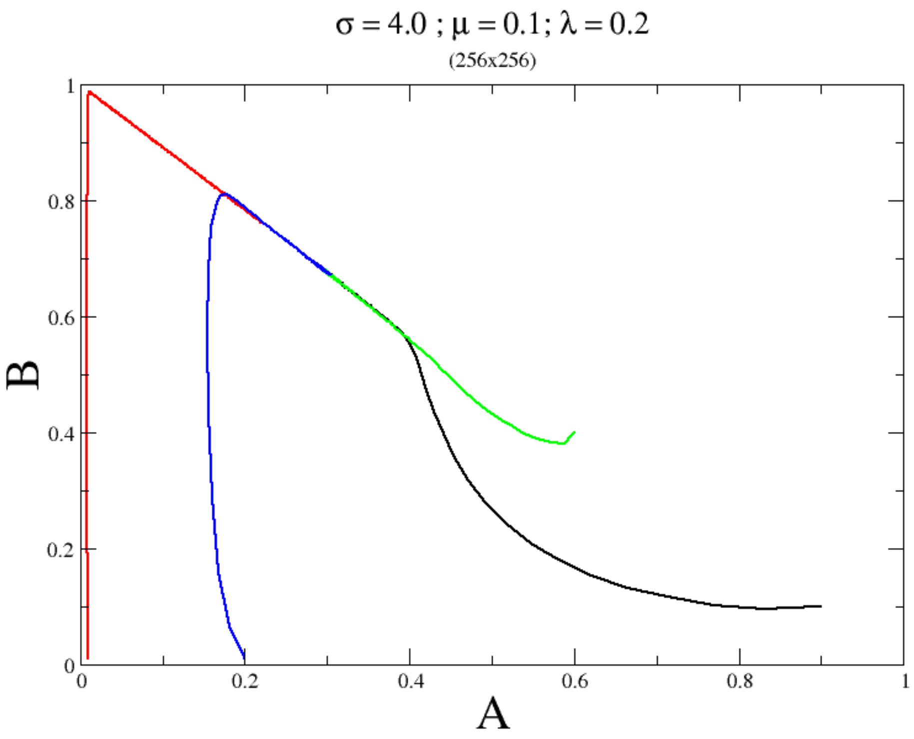
survival probability $P(t) \sim t^{-\delta'}$, $\delta' \approx 0.451$
number of active sites $N(t) \sim t^{\theta}$, $\theta \approx 0.230$
} 2d DP values

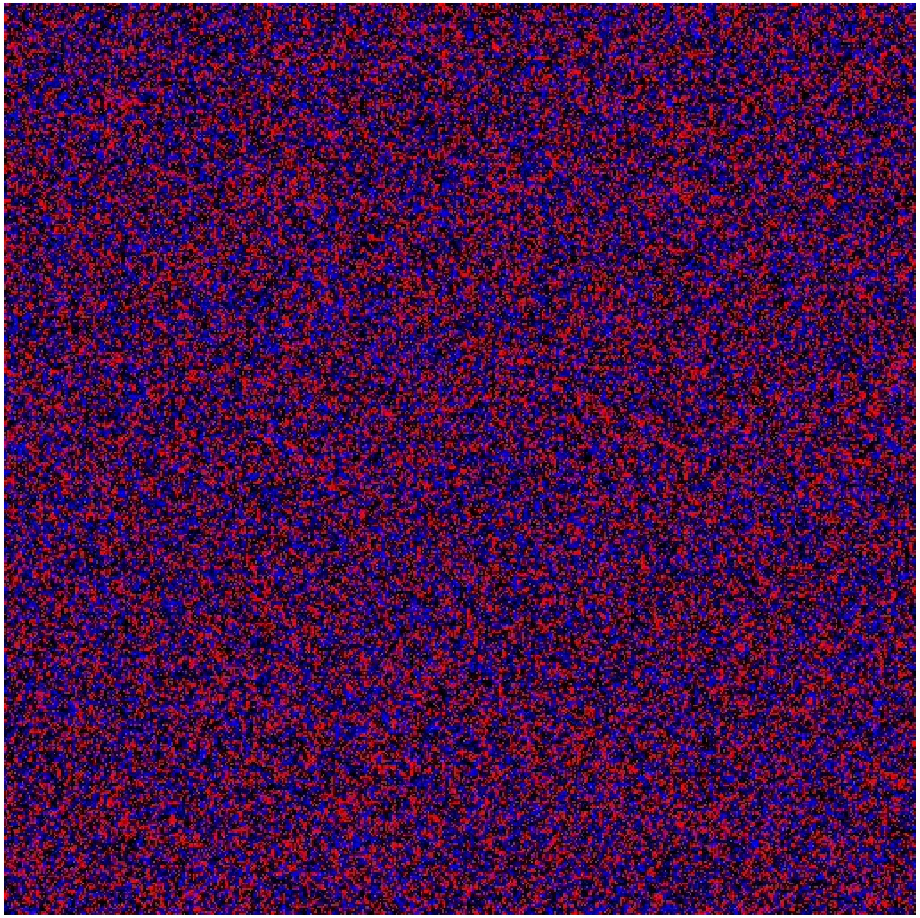



*M. Mobilia, I.T. Georgiev, U.C.T.,* J. Stat. Phys. **128** (2007) 447

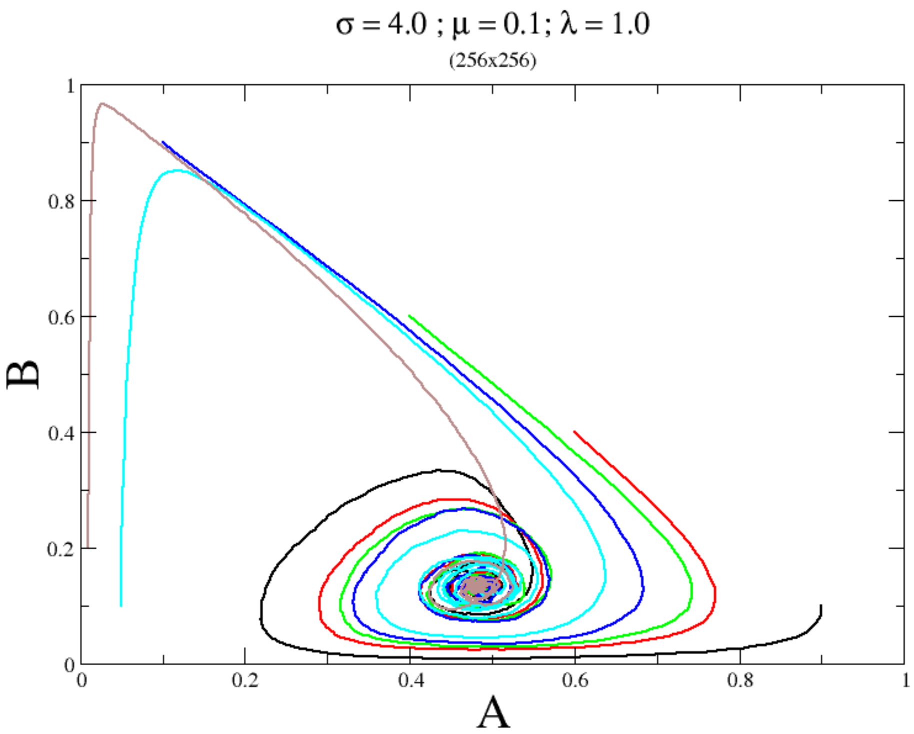
# Predator / prey coexistence:
# Near extinction threshold: stable fixed point is a node

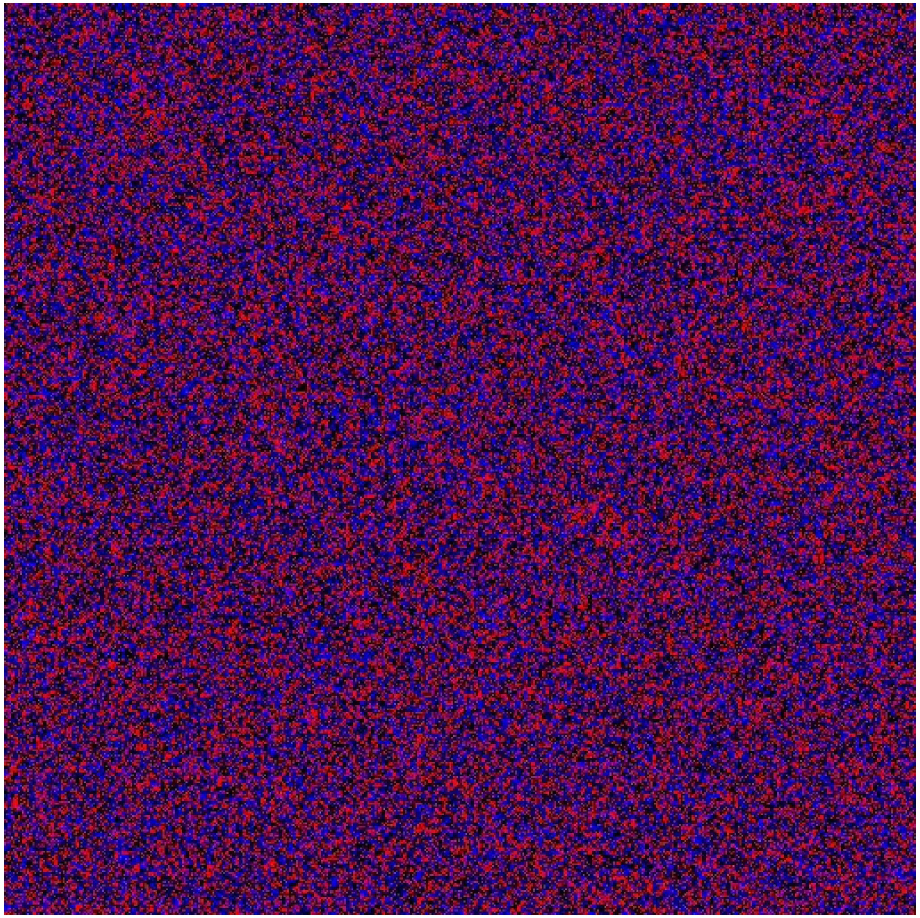


observe local predator clusters
(DP clusters in space-time)

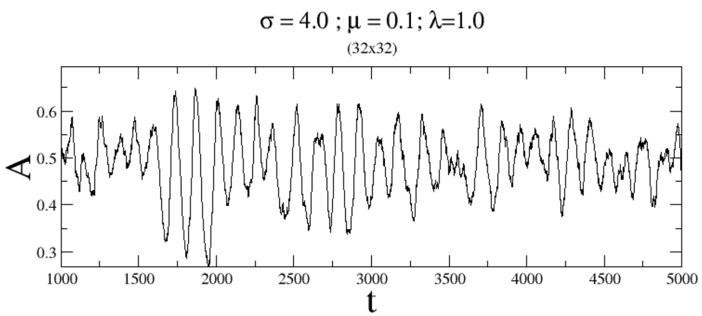
# Predator / prey coexistence:
# Deep in coexistence phase: stable fixed point is a focus

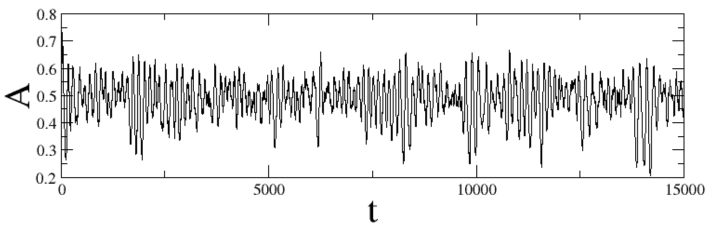


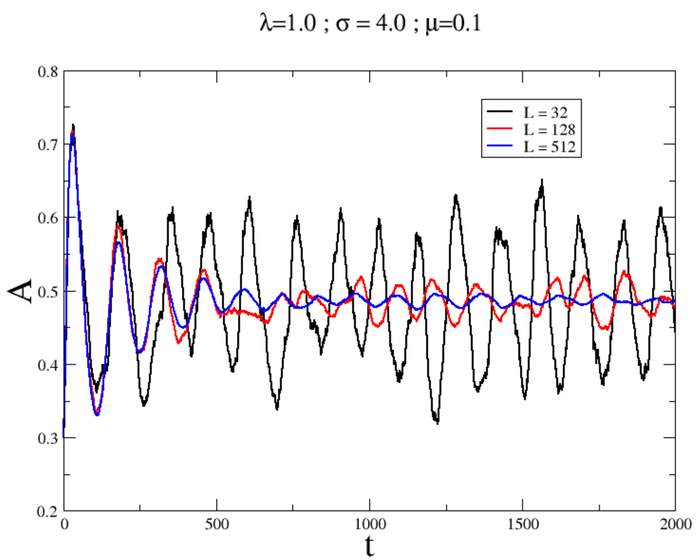
Oscillations near focus:
resonant amplification of
stochastic fluctuations
*(A.J. McKane, T.J. Newman, 2005)*

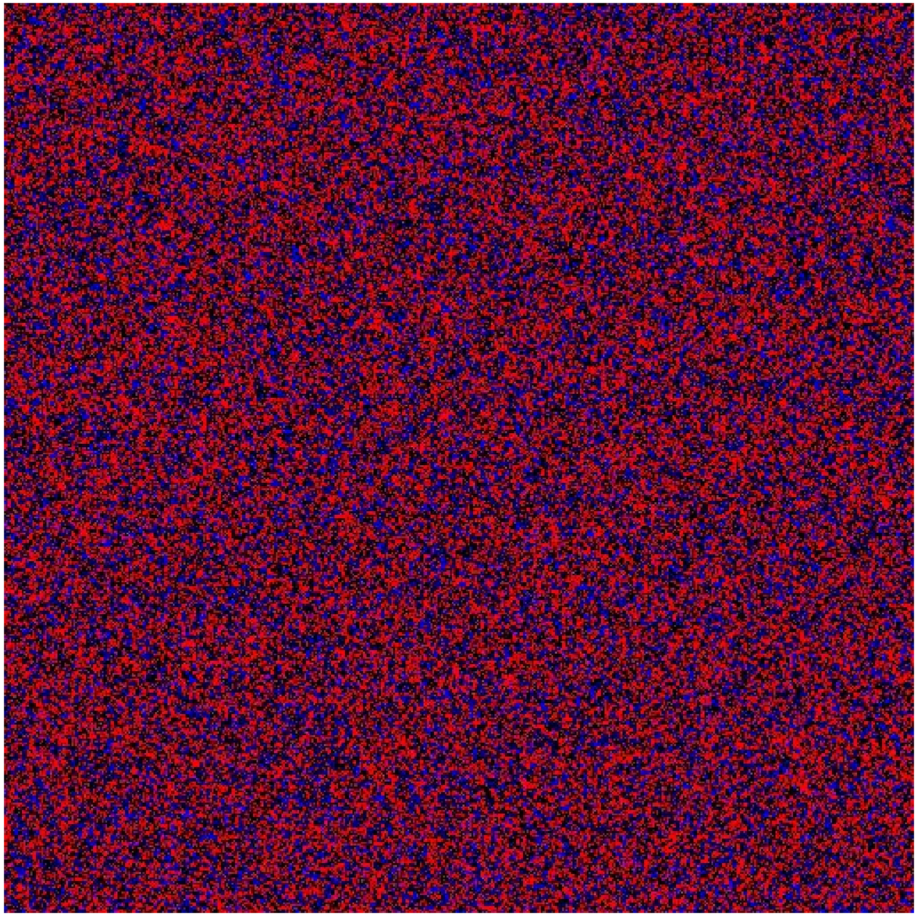
# Population oscillations in finite systems



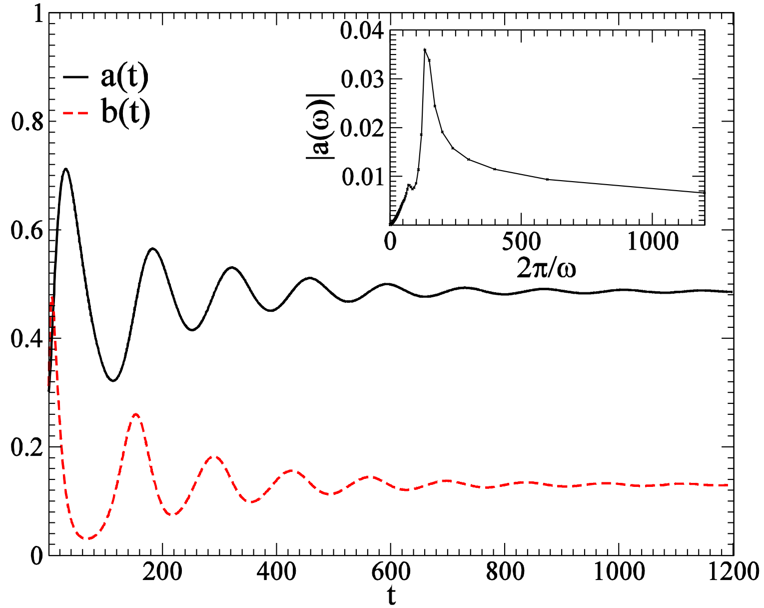




*(A. Provata, G. Nicolis, F. Baras, 1999)*

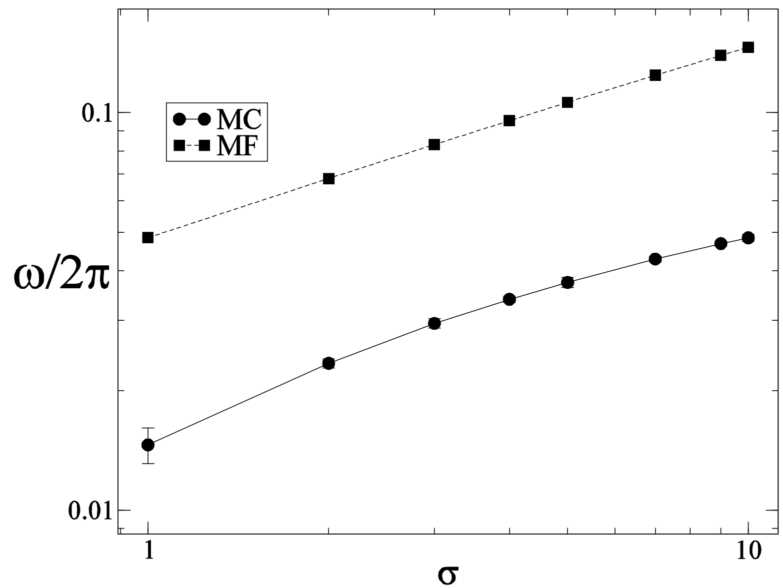


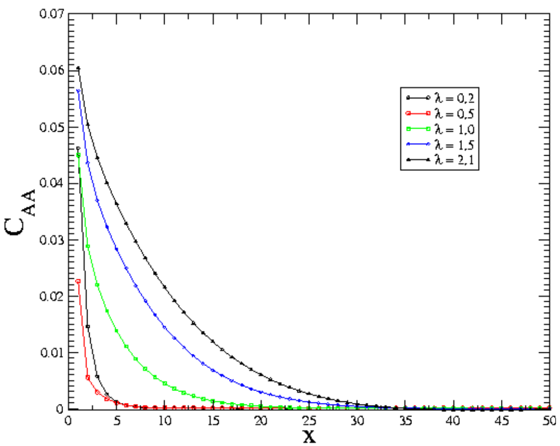
## oscillations for large system:

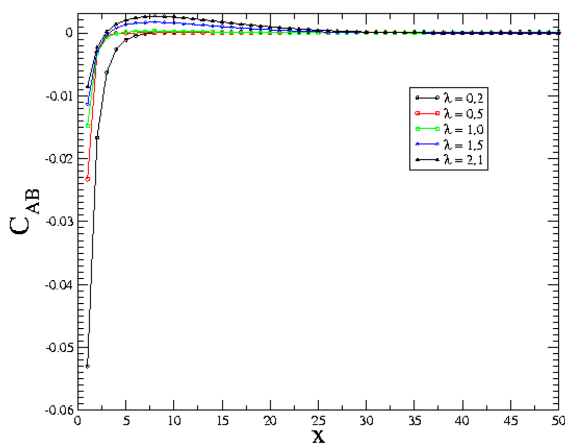


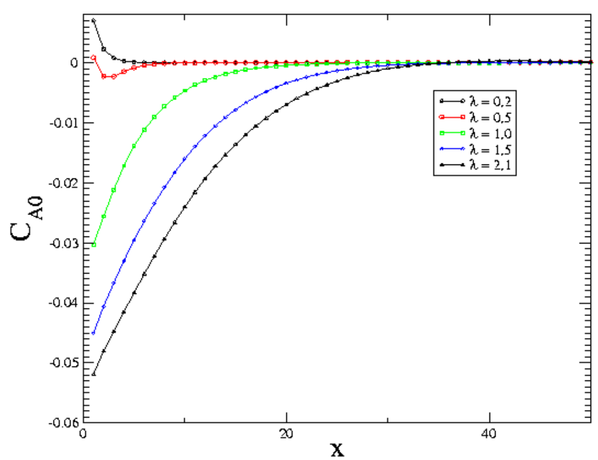

## compare with mean-field prediction:




## Correlations in the active coexistence phase

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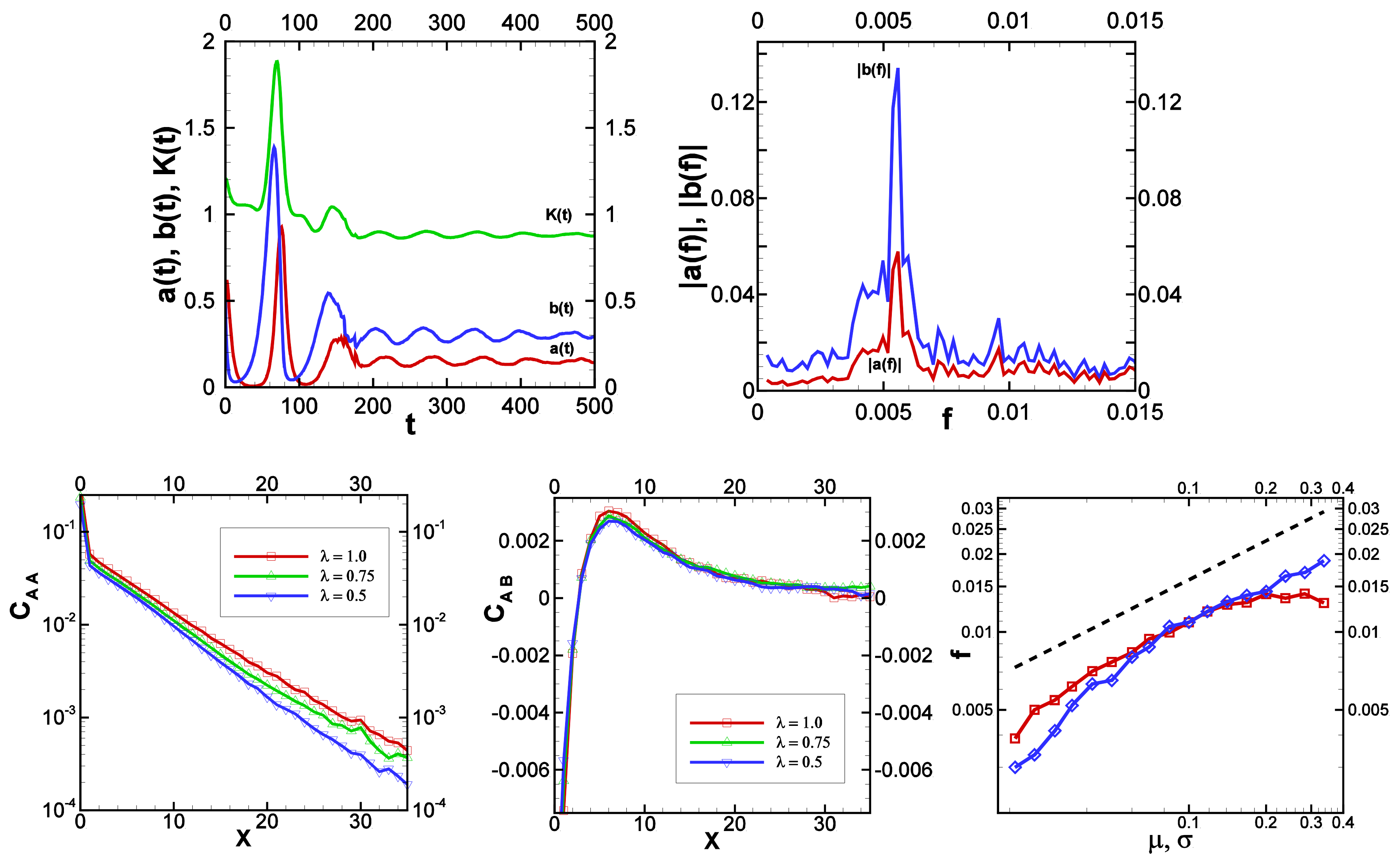
# abandon site occupation restrictions :




*M.J. Washenberger, M. Mobilia, U.C.T.*, J. Phys. Cond. Mat.**19** (2007) 065139

# Doi-Peliti field theory: renormalized parameters

Master equation, contribution from predation reaction:

$$\frac{\partial P(n_i, m_i; t)}{\partial t} = \lambda' \Big[ (n_i - 1)\,(m_i + 1)\, P(n_i - 1, m_i + 1; t) - n_i\, m_i\, P(n_i, m_i t) \Big]$$

Poisson initial distribution: $P(n_i, m_i; 0) = \frac{\overline{n}_0^{n_i}\, \overline{m}_0^{m_i}}{n_i!\, m_i!}\, e^{-\overline{n}_0 - \overline{m}_0}$.

Bosonic ladder operators: $[a_i, a_j] = 0$, $[a_i, a_j^\dagger] = \delta_{ij}$

$\Longrightarrow |n_i\rangle = a_i^{\dagger\, n_i} |0\rangle$, $a_i |n_i\rangle = n_i |n_i - 1\rangle$, $a_i^\dagger |n_i\rangle = |n_i + 1\rangle$.

Similarly for prey, with $[a_i, b_j] = 0 = [a_i, b_j^\dagger]$.

Time-dependent formal state vector:

$$|\Phi(t)\rangle = \sum_{\{n_i\},\{m_i\}} P(\{n_i\}, \{m_i\}; t)\, |\{n_i\}, \{m_i\}\rangle$$

$$\Longrightarrow \frac{\partial |\Phi(t)\rangle}{\partial t} = -H\, |\Phi(t)\rangle \quad \text{or} \quad |\Phi(t)\rangle = e^{-H\,t}\, |\Phi(0)\rangle\ ,$$

with $H_{\text{pred}} = -\lambda' \sum_i (a_i^\dagger - b_i^\dagger)\, a_i^\dagger\, a_i\, b_i$.

Expectation values: use projection state $\langle \mathcal{P}| = \langle 0|\, \Pi_i\, e^{a_i} e^{b_i}$:

$$\begin{aligned} \langle \mathcal{O}(t) \rangle &= \sum_{\{n_i\},\{m_i\}} \mathcal{O}(\{n_i\}, \{m_i\})\, P(\{n_i\}, \{m_i\}; t) \\ &= \langle \mathcal{P}|\, \mathcal{O}(\{a_i^\dagger\, a_i\}, \{b_i^\dagger\, b_i\})\, |\Phi(t)\rangle\ . \end{aligned}$$

Construct path integral representation with coherent states: continuum action ($\lambda = a_0^d\, \lambda'$) gives exponential weight:

$$\begin{aligned} S[\hat{a}, a; \hat{b}, b] = \int d^d x \int dt \Big[ & \hat{a}(\partial_t - D_A \nabla^2) a + \hat{b}(\partial_t - D_B \nabla^2) b \\ & + \mu\, (\hat{a} - 1) a + \sigma\, (1 - \hat{b})\, \hat{b}\, b\, e^{-\rho^{-1} \hat{b} b} + \lambda\, (\hat{b} - \hat{a})\, \hat{a}\, a\, b \Big] \end{aligned}$$

*U.C.T., M.J. Howard, B. Vollmayr-Lee,* J. Phys. A **38** (2005) R79 (review)

Shift $\hat{a} = 1 + \tilde{a}$, $\hat{b} = 1 + \tilde{b}$, and subsequently introduce fluctuating fields $c = a - \langle a \rangle$ and $d = b - \langle b \rangle$:

$$a = \frac{\sigma}{\lambda} \left( 1 - \frac{\mu\, \rho^{-1}}{\lambda} + A_c \right) + c\ , \quad b = \frac{\mu}{\lambda}\, (1 + B_c) + d$$

conditions $\langle c \rangle = 0 = \langle d \rangle$ determine counterterms $A_c, B_c$.

Diagonalize harmonic part of action (assume $D_A = D_B$):

$$c = \frac{1}{\sqrt{2\mu}} \left[ \varphi_+ + \varphi_- - \frac{\gamma_0}{i\omega_0}\, (\varphi_+ - \varphi_-) \right],\ d = \sqrt{\frac{\mu}{2}}\, \frac{\varphi_+ - \varphi_-}{i\omega_0}$$

$$\text{where} \quad \omega_0^2 = \sigma\, \mu \left( 1 - \frac{\mu\, \rho^{-1}}{\lambda} \right) - \gamma_0^2\ , \ \ \gamma_0 = \frac{\sigma\, \mu\, \rho^{-1}}{\lambda}$$

determine renormalized oscillation frequency, damping, diffusivity in perturbation expansion to one-loop order:

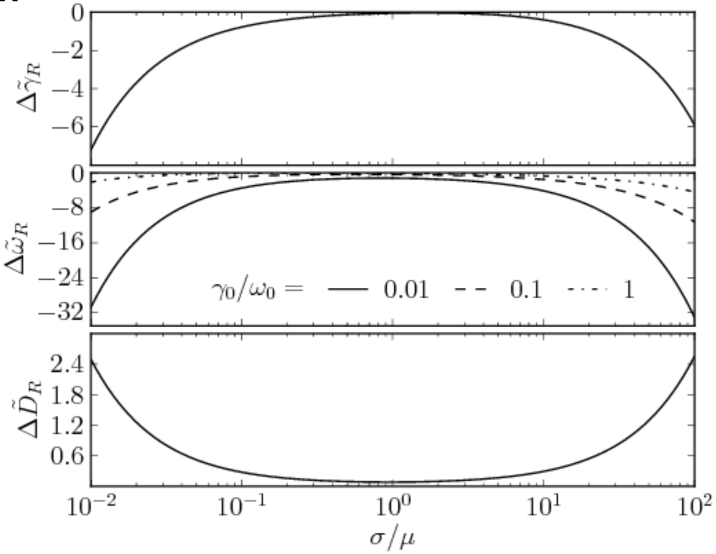
$$d = 2: \quad D_R = D_0 + \frac{\lambda}{96\pi} \left[ 1 + 2 \left( \frac{\sigma}{\mu} + \frac{\mu}{\sigma} \right) \right] + \mathcal{O}(\lambda^2)$$

$$\gamma_R = \lambda\, \frac{\omega_0}{D_0}\, \frac{1}{64} \left[ \frac{6}{\pi} \left( \sqrt{\frac{\sigma}{\mu}} - \sqrt{\frac{\mu}{\sigma}} \right) - \left( \frac{\sigma}{\mu} + \frac{\mu}{\sigma} \right) \right] + \mathcal{O}(\lambda^2)$$

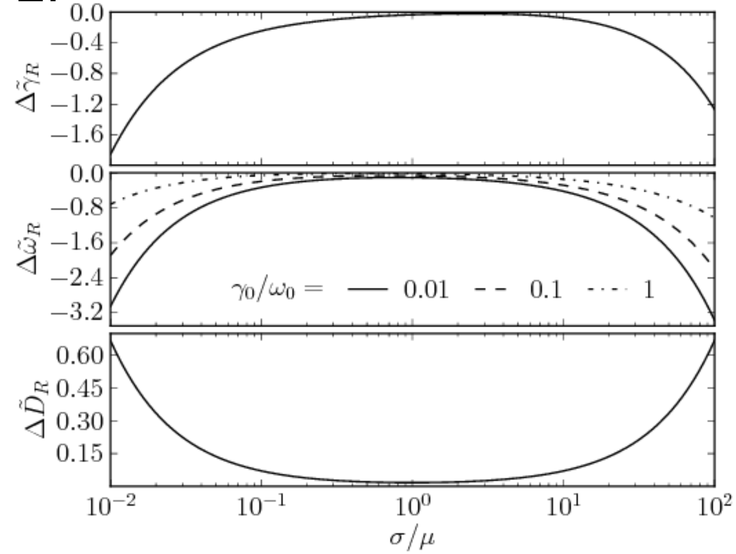
$$\begin{aligned} \omega_R = \omega_0 - \lambda\, \frac{\omega_0}{D_0}\, \frac{1}{32\pi}\, \ln \frac{\omega_0}{\gamma_0} & \left[ 1 + \frac{1}{2} \left( \frac{\sigma}{\mu} + \frac{\mu}{\sigma} \right) \right] \\ + \lambda\, \frac{\omega_0}{D_0}\, \frac{3}{32\pi} & \left[ 1 - \frac{\pi}{3} \sqrt{\frac{\sigma}{\mu}} - \frac{1}{4} \left( \frac{\sigma}{\mu} + \frac{\mu}{\sigma} \right) \right] + \mathcal{O}(\lambda^2) \end{aligned}$$

notice symmetry μ ↔ σ in leading term

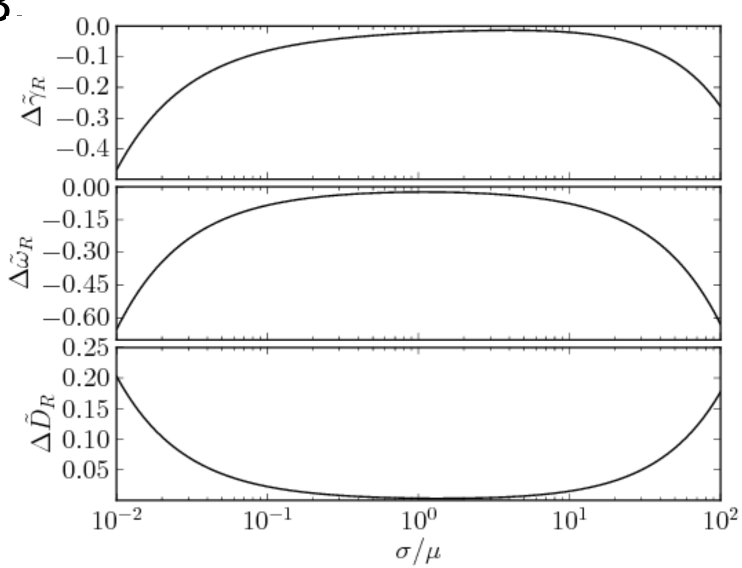
*U.C.T.,* J. Phys. Conf. Ser. **319** (2011) 012019; J. Phys. A **45** (2012) 405002 d = 1:



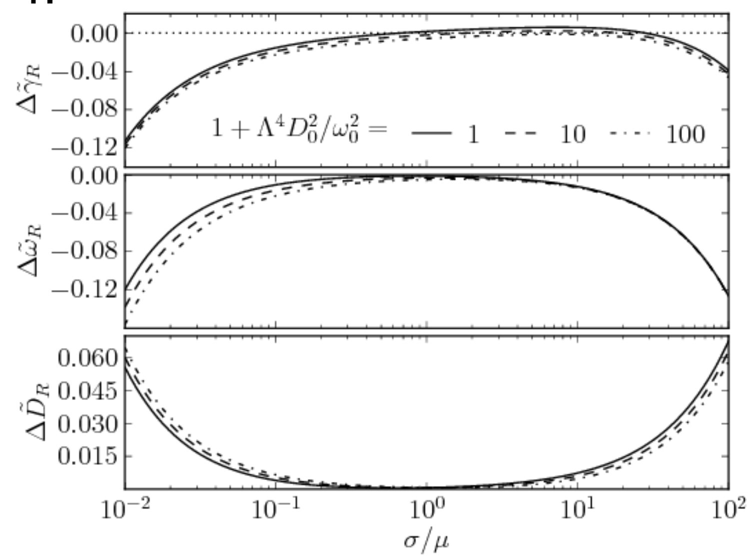

d = 2:




d = 3:




d = 4:



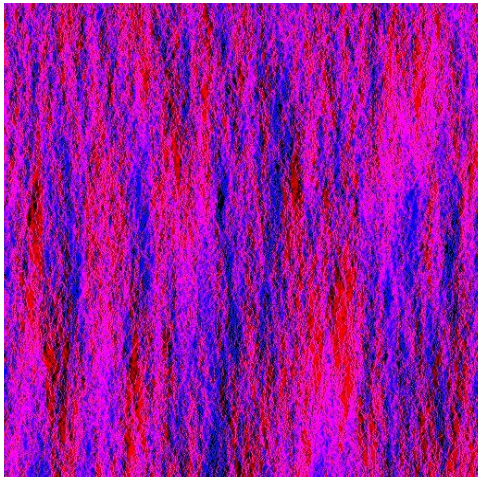

- $\Delta\gamma_R < 0$ → instability against spatial structures
- $\Delta\omega_R < 0$ → drastic frequency reduction; symmetric in $\mu \leftrightarrow \sigma$
- $\Delta D_R > 0$ → (diffusive) spreading accelerated, fronts faster

# Stochastic Lotka-Volterra model in one dimension

- no site restriction:

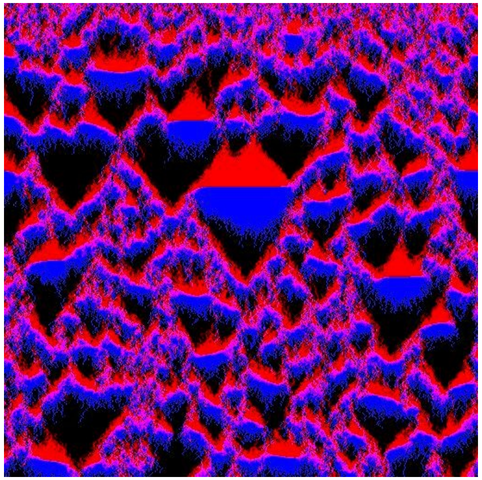
$\sigma = \mu = \lambda = 0.01$: diffusion-dominated

↓t



$\sigma = \mu = \lambda = 0.1$: reaction-dominated

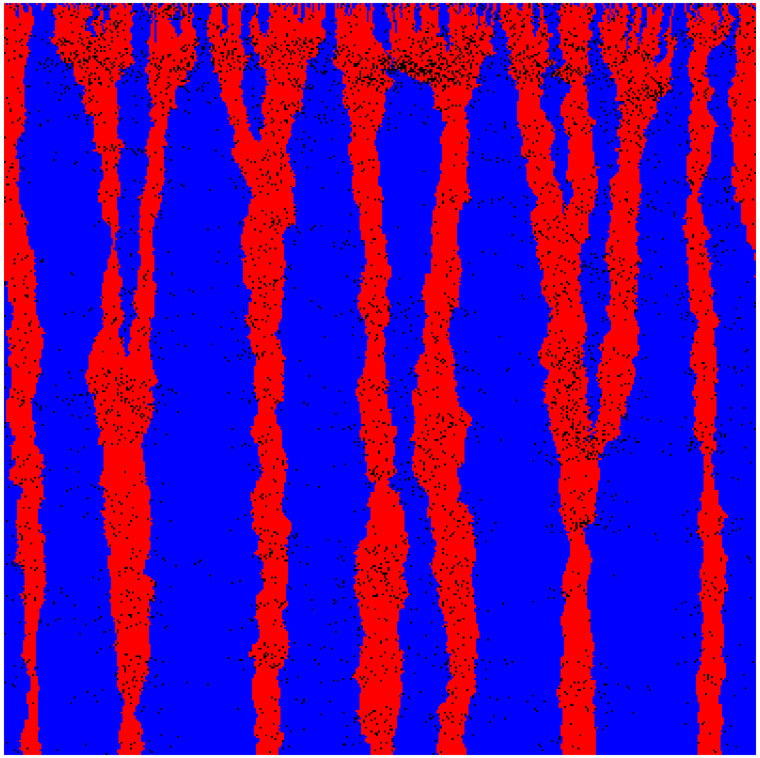
↓
t



- site occupation restriction:
species segregation;
effectively A+A → A

$$a(t) \sim t^{-1/2} \to 0$$

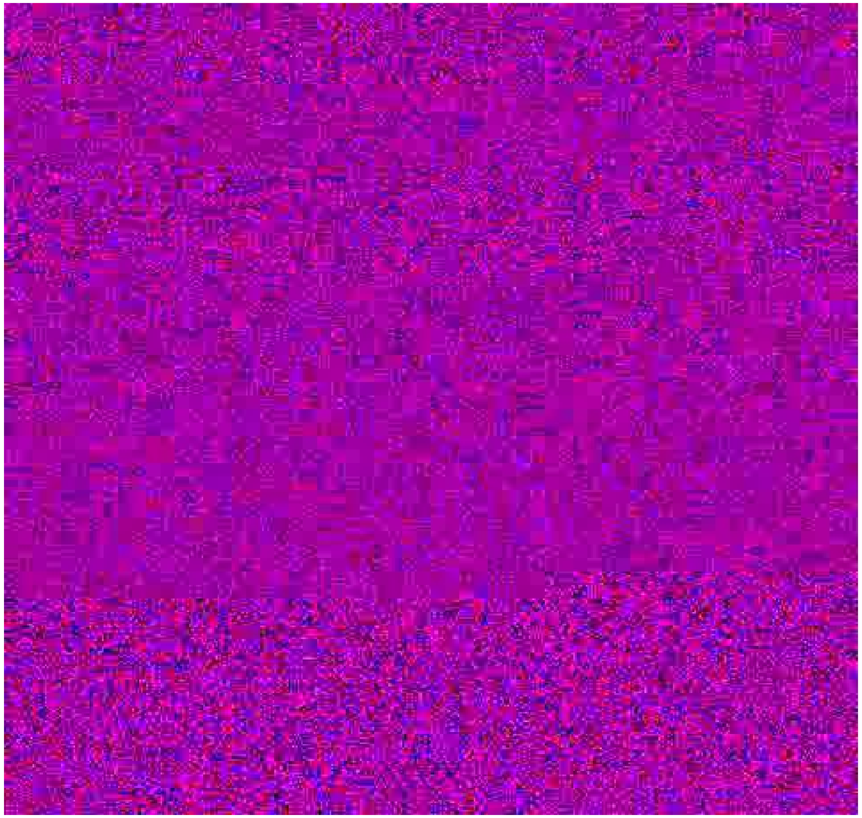
↓
t



# Stochastic lattice Lotka-Volterra model with spatially varying reaction rates

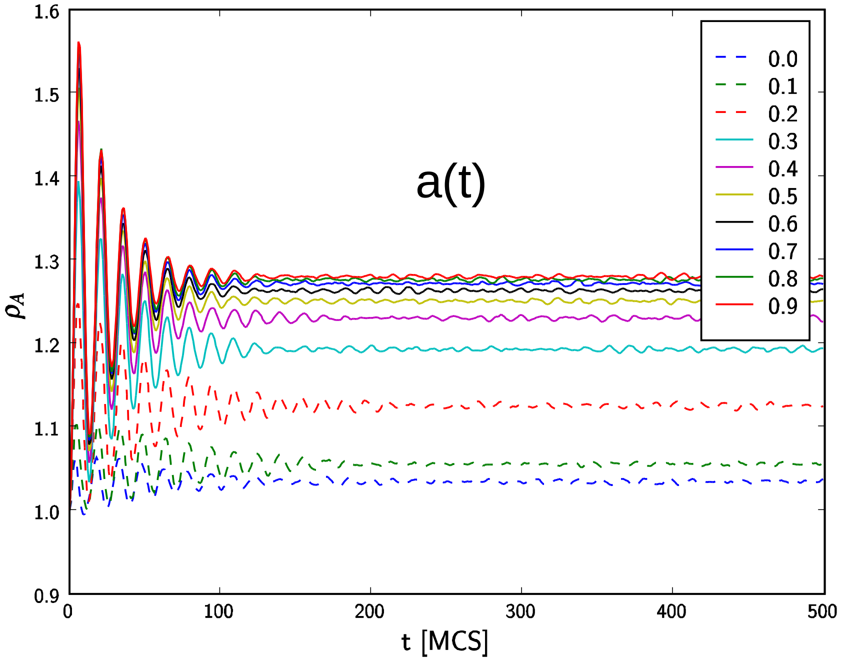
- 512 x 512 square lattice, up to 1000 particles per site
- reaction probabilities drawn from Gaussian distribution, truncated to interval [0,1], fixed mean, different variances; fixed during simulation runs (quenched random variables)

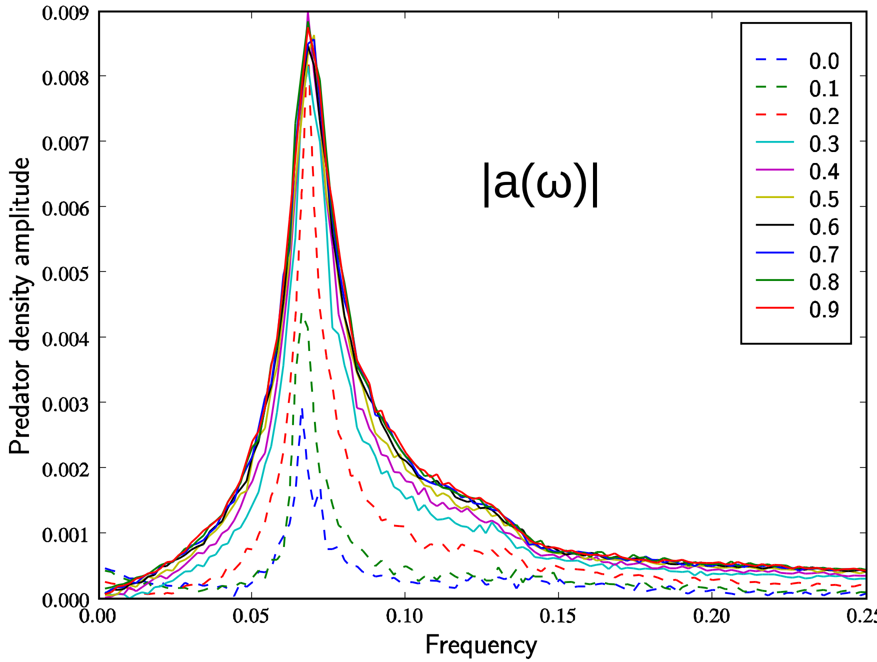
Example:
$\sigma = 0.5$,
$\mu = 0.2$,
$\lambda = 0.5$,
$\Delta\lambda = 0.5$
initially
$a(0) = 1$,
$b(0) = 1$



# Predator density variation with variance Δλ

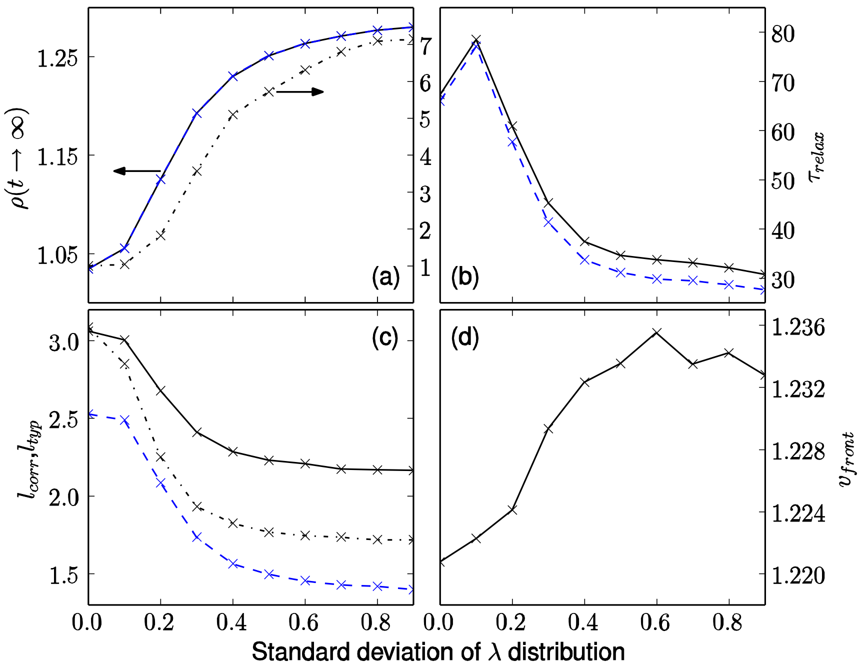
(averaged over 50 simulation runs)



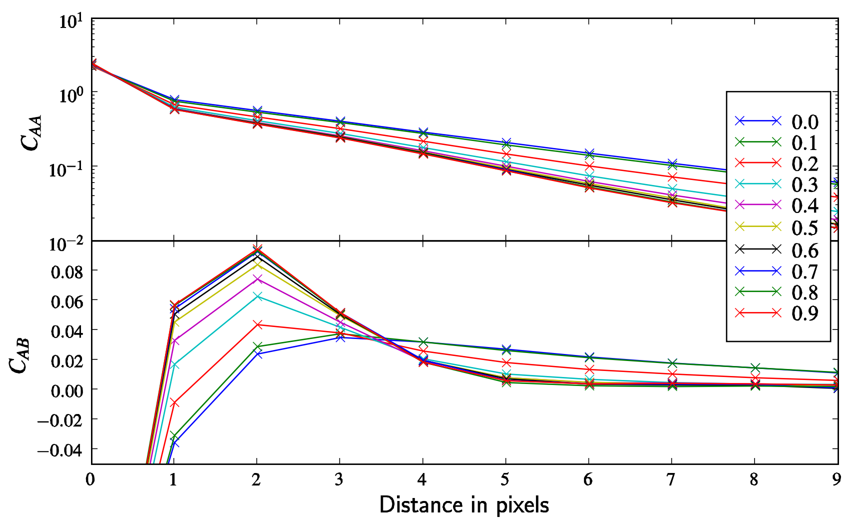




- stationary predator and prey densities increase with Δλ
- amplitude of initial oscillations becomes larger
- Fourier peak associated with transient oscillations broadens
- relaxation to stationary state faster

# Spatial correlations and fitness enhancement




- asymptotic population density
- relaxation time, obtained from Fourier peak width
- A/B correlation lengths, from $C_{AA/BB}(r) \sim \exp(-r / l_{corr})$
- A-B typical separation, from zero of $C_{AB}(r)$
- front speed of spreading activity rings into empty region from initially circular prey patch, with predators located in the center

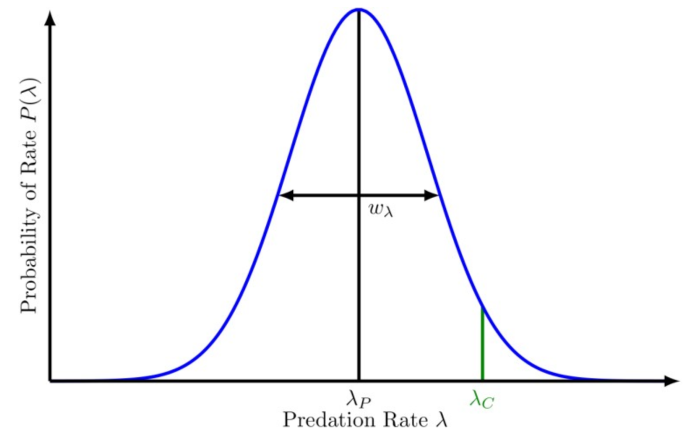



⇨ increasing $\Delta\lambda$ leads to more localized activity patches, which causes enhanced local population fluctuations

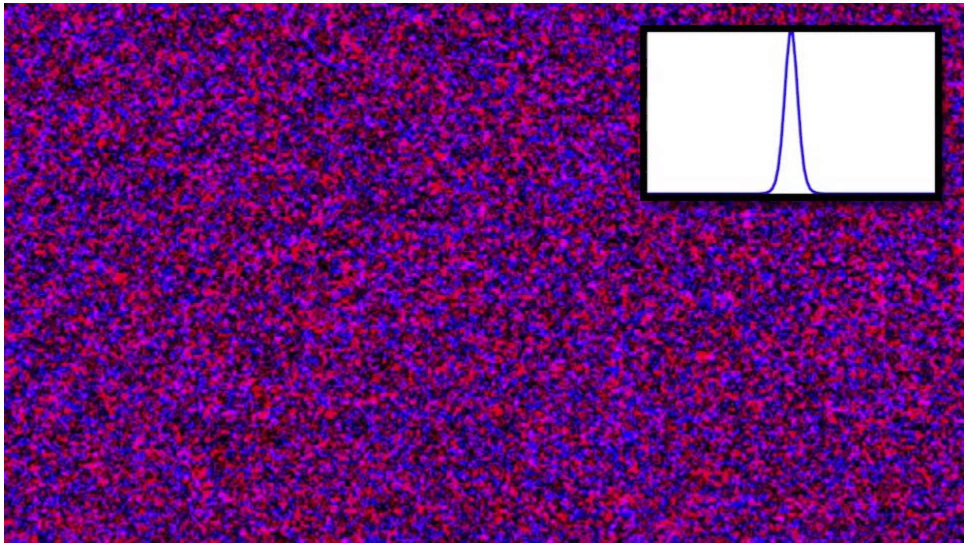
*U. Dobramysl, U.C.T.,*
Phys. Rev. Lett. **101** (2008) 258102

# Environmental vs. demographic variability

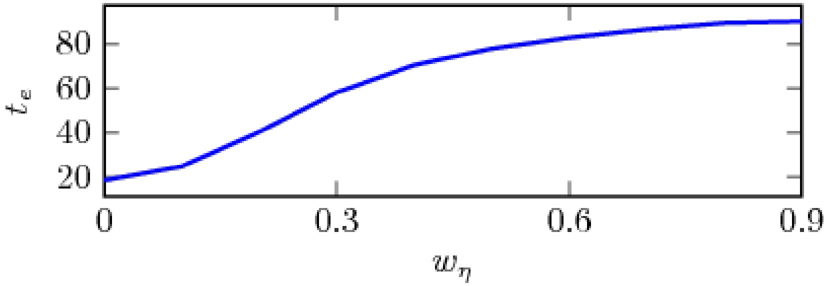
- attach random predation / evasion rates η to lattice sites and *individual* predators / prey; leave σ = 0.5 = μ fixed
- effective predation rate: $\eta' = \frac{1}{2}(\eta_A + \eta_B)$
- offspring rates drawn from Gaussian:
  - centered at parent rate (truncated)
  - width $w_\eta$ → *mutation* probability



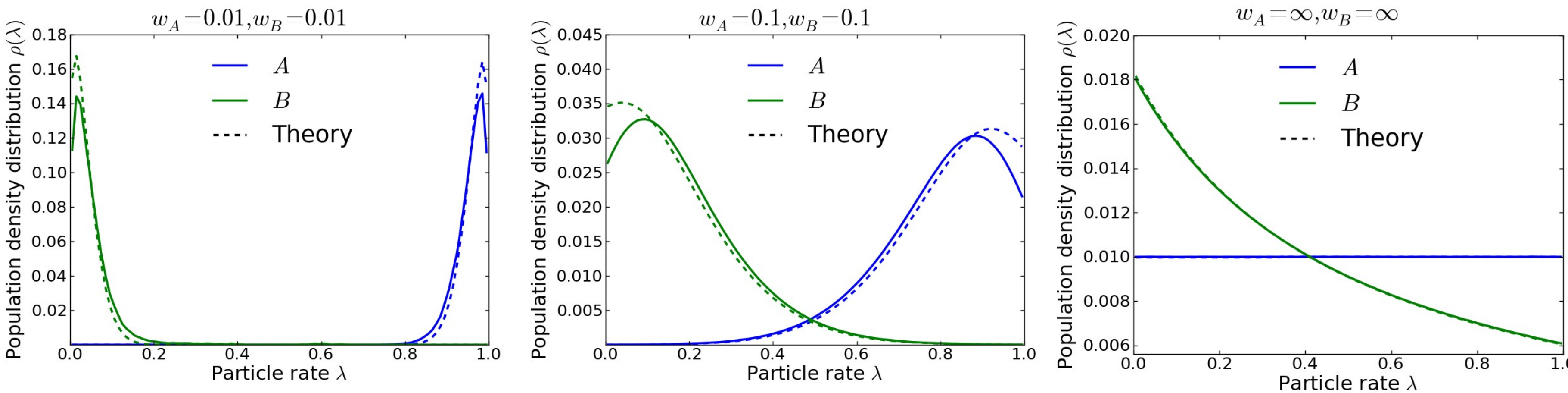

- sharp initial distribution, centered at λ = 0.5
- lattice: *environmental variability* η with $0 \leq \varsigma \leq 1$: $\lambda = \varsigma\,\eta + (1 - \varsigma)\,\eta'$



- extract mean extinction time in small systems (L = 10 x 10): variability enhances robustness

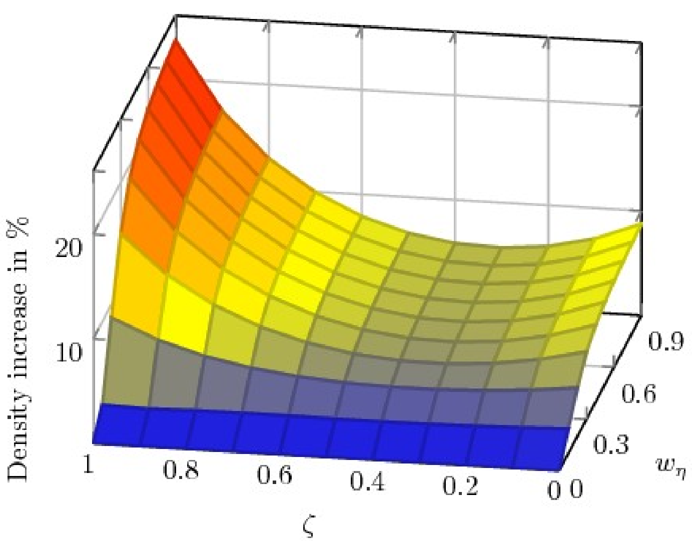


# Variable rates attached to individuals; inheritance




w narrow: predators/prey evolve to large/small λ;
no fixation at extremes 1/0 (nonlinear dynamics)
mean-field theory: (semi-)quantitative analysis

w broad (uniform):
predator rate distribution
stays flat; only prey evolve




Combined spatial environmental and demographic variability:

- characteristic minimum in steady-state population increase at ς ≈ 0.3
- ς ≈ 0 → A, B optimize, overall neutral

*U. Dobramysl, U.C.T.* (2012), arXiv:1206.0973

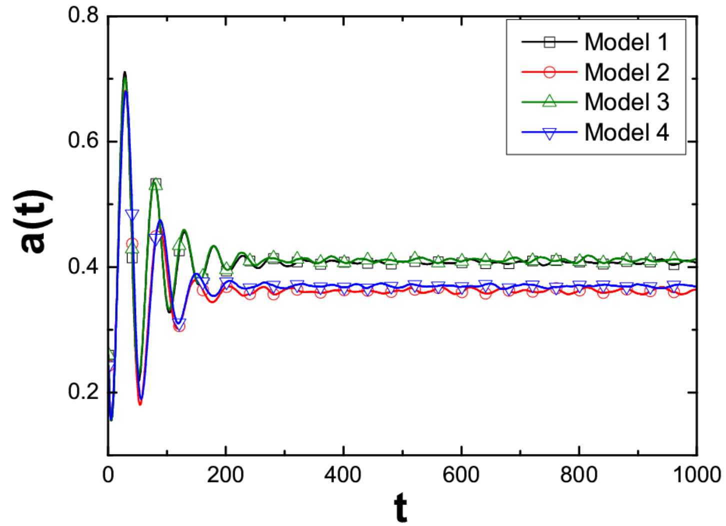
# Cyclic predation: spatial rock-paper-scissors game

A+B → A+A, rate λ
B+C → B+B, rate σ
C+A → C+C, rate μ

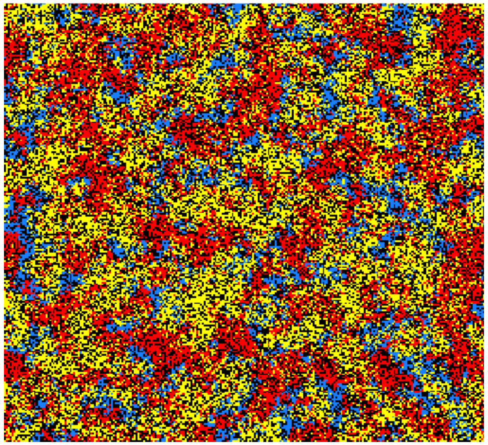
→ total particle density ρ conserved

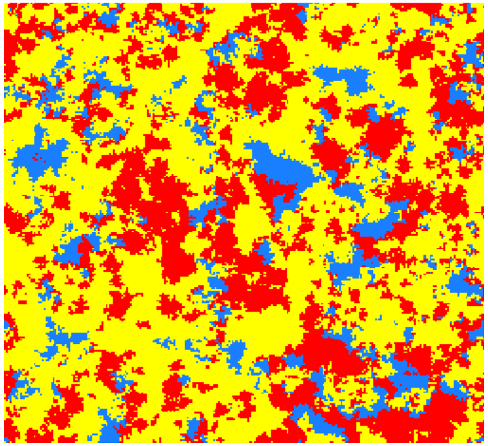
$(a^*, b^*, c^*) = (\sigma, \mu, \lambda)\, \rho \,/\, (\lambda+\sigma+\mu)$

$\lambda = 0.2,\ \sigma = 0.5,\ \mu = 0.8$
256 x 256 lattice sites, 500 MCS
without and with site occupation restrictions: system well-mixed




1: λ homogeneous, no restrictions
2: λ homogeneous, one particle/site
3: $0 \le \lambda \le 0.4$, no site restrictions
4: $0 \le \lambda \le 0.4$, one particle/site





→ negligible disorder effect;
except: extreme asymmetry
$\lambda \gg \sigma, \mu$: → $c^* \approx \rho$,
→ two-species LV system

*Q. He, M. Mobilia, U.C.T.,* Phys. Rev. E **82** (2010) 051909;
Eur. Phys. J. B **82** (2011) 97; *Q. He, U.C.T., R.K.P. Zia,* ibid. **85** (2012) 141

# Summary and conclusions

- predator-prey models with spatial structure and stochastic noise: invalidates Lotka-Volterra mean-field neutral population cycles
- stochastic models yield long-lived erratic population oscillations; resonant amplification mechanism for density fluctuations
- lattice site occupation restrictions / limited resources induce predator extinction; absorbing transition: directed percolation universality class
- spatial stochastic predator-prey systems: complex spatio-temporal structures; spreading activity fronts induce persistent correlations; stochastic spatial scenario robust with respect to model modifications
- fluctuations strongly renormalize oscillation properties; fluctuation corrections captured perturbatively through Doi-Peliti field theory
- spatial variability in the predation rate results in more localized activity patches; population fluctuations in rare favorable regions cause marked increase in the population densities / fitness of both predators and prey
- variable rates attached to individuals with inheritance and mutation: intriguing dynamical evolution of rate distributions, no fixation
- cyclic rock-paper-scissors model: minute effects of disorder, except for extreme asymmetry in reaction rates (recovers two-species LV system).

## Mapping the Lotka-Volterra reaction kinetics near the predator extinction threshold to directed percolation

Construct Doi–Peliti field theory action, with site occupation restrictions, for the reactions $A \to \emptyset$ (rate $\mu$), $B \to B+B$ (rate $\sigma$), and $A+B \to A+A$ (rate $\lambda$):

$$S[\hat{a}, a; \hat{b}, b] = \int d^d x \int dt \Big[\hat{a} \left(\partial_t - D_A \nabla^2\right) a + \mu \left(\hat{a} - 1\right) a + \hat{b} \left(\partial_t - D_B \nabla^2\right) b + \sigma \left(1 - \hat{b}\right) \hat{b}\, b\, e^{-\rho^{-1} \hat{b}\, b} + \lambda \left(\hat{b} - \hat{a}\right) \hat{a}\, a\, b\Big]$$

shift fields $\hat{a} = 1 + \tilde{a}$, $\hat{b} = 1 + \tilde{b}$, expand in $\rho^{-1}$ ($[\rho] = \kappa^d$):

$$S[\tilde{a}, a; \tilde{b}, b] = \int d^d x \int dt \Big[\tilde{a} \left(\partial_t - D_A \nabla^2 + \mu\right) a + \tilde{b} \left(\partial_t - D_B \nabla^2 - \sigma\right) b - \sigma\, \tilde{b}^2\, b + \sigma\, \rho^{-1} \left(1 + \tilde{b}\right)^2 \tilde{b}\, b^2 - \lambda \left(1 + \tilde{a}\right) \left(\tilde{a} - \tilde{b}\right) a\, b\Big]$$

fluctuating fields $c = b_s - b$, $b_s \approx \rho$, $\langle c \rangle = 0$, $\tilde{c} = -\tilde{b}$:

$$S[\tilde{a}, a; \tilde{c}, c] = \int d^d x \int dt \Big[\tilde{a} \left(\partial_t - D_A \nabla^2 + \mu - \lambda\, b_s\right) a + \tilde{c} \left(\partial_t - D_B \nabla^2 + (2 b_s/\rho - 1)\, \sigma\right) c + \sigma\, b_s (2 b_s/\rho - 1)\, \tilde{c}^2 - \sigma\, \rho^{-1}\, b_s^2\, \tilde{c}^3 - \sigma \left(4 b_s/\rho - 1\right) \tilde{c}^2\, c - \sigma\, \rho^{-1} \left(1 + \tilde{c}^2\right) \tilde{c}\, c^2 + 2\sigma\, \rho^{-1}\, \tilde{c}^2 \left(c + b_s\, \tilde{c}\right) c - \lambda\, b_s \left(\tilde{a}^2 + (1 + \tilde{a})\, \tilde{c}\right) a + \lambda \left(1 + \tilde{a}\right) \left(\tilde{a} + \tilde{c}\right) a\, c\Big]$$

rescale fields $\phi = \sqrt{\sigma}\, c$, $\tilde{\phi} = \sqrt{\sigma}\, \tilde{c}$, $\sigma \to \infty$ ($[\sigma] = \kappa^2$):

$$S_\infty[\tilde{a}, a; \tilde{\phi}, \phi] = \int d^d x \int dt \Big[\tilde{a} \left(\partial_t - D_A \nabla^2 + \mu - \lambda\, b_s\right) a - \lambda\, b_s\, \tilde{a}^2\, a + \tilde{\phi}\, \phi + b_s\, \tilde{\phi}^2\Big]$$

add growth-limiting reaction $A + A \to A$ (rate $\tau$), integrate out fields $\phi$ and $\tilde{\phi}$, $u = \sqrt{\tau\, \lambda\, b_s}$:

$$S_\infty[\tilde{\mathcal{S}}, \mathcal{S}] = \int d^d x \int dt \Big[\tilde{\mathcal{S}} \left(\partial_t + D_A \left(r_A - \nabla^2\right)\right) \mathcal{S} - u\, \tilde{\mathcal{S}} \left(\tilde{\mathcal{S}} - \mathcal{S}\right) \mathcal{S} + \tau\, \tilde{\mathcal{S}}^2\, \mathcal{S}^2\Big]$$

$\Longrightarrow$ Reggeon field theory for directed percolation.

*M. Mobilia, I.T. Georgiev, U.C.T.*, J. Stat. Phys. **128** (2007) 447

# Quasi-species mean-field approach

Introduce quasi-species for each rate value: $\lambda_{ij} = \frac{\lambda_i + \lambda_j}{2}$:

$$\begin{aligned} A_i &\to \emptyset && \text{rate } \mu \ , \\ B_i &\to B_i + B_j && \text{rate } f_{ij}\,\sigma \ , \\ A_i + B_j &\to A_i + A_k && \text{rate } f_{ik}\,\lambda_{ij} \ ; \end{aligned}$$

$f_{ij}$ denotes the probability for a particle with predation rate $\lambda_i$ to produce offspring with an assigned rate of $\lambda_j$.
Associated mean-field rate equations:

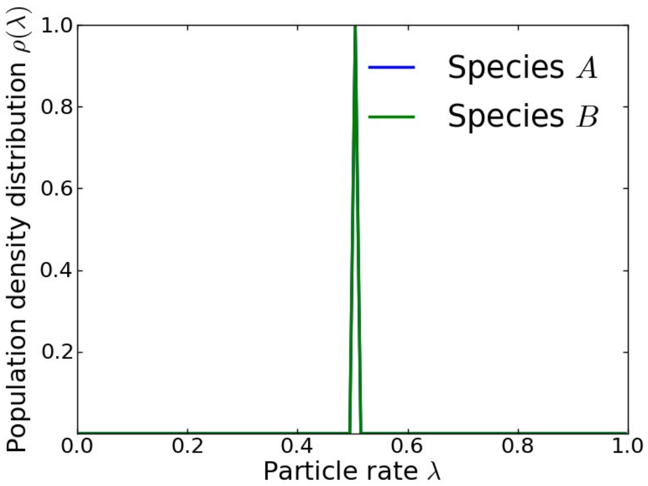
$$\begin{aligned} \dot{a}_i &= -\mu\, a_i + \sum_{j,k} \lambda_{jk}\, f_{ki}\, a_k\, b_j \ , \\ \dot{b}_i &= \sigma \sum_k f_{ki}\, b_k - \sum_j \lambda_{ij}\, a_j\, b_i \ . \end{aligned}$$

General case requires numerical solution; special cases:

- $f_{ij} = \delta_{ij}$, $\lambda_{ij} = \lambda \implies$ standard LV rate equations;
- uniform inheritance distribution $f_{ij} = 1/N \implies$ steady-state solution:

$$a_i = \frac{2\sigma}{N} \sum_j \frac{1}{\lambda_j + \sum_k \lambda_k / N} \ , \quad b_i = \frac{2\mu}{\lambda_i + \sum_k \lambda_k / N}$$

$\implies$ predator rate distribution uniform,
prey rate distribution inverse linear function.

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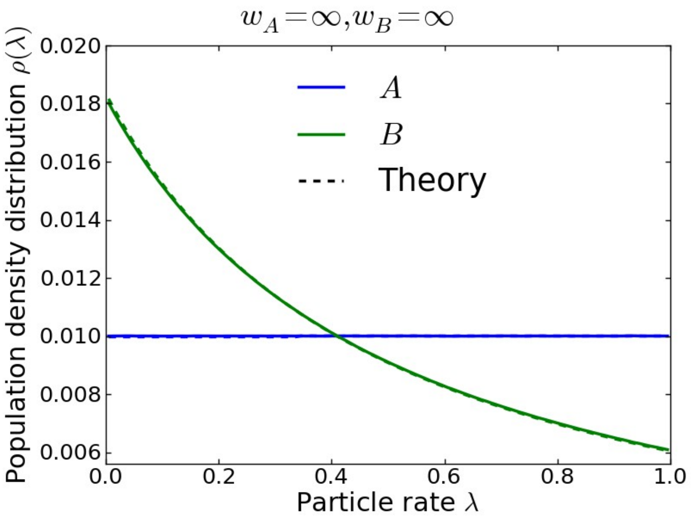

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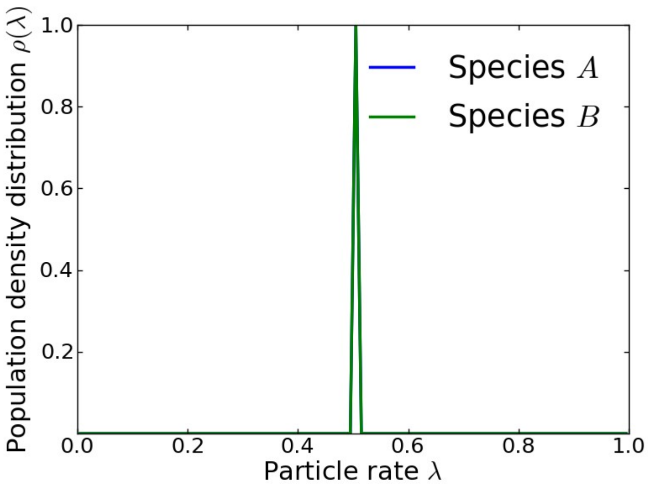


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