Invasive Spread of an Advantageous Mutation under Preemptive Competition

Lauren O'Malley, Joseph Yasi, James Basham,
Balázs Kozma, and G. Korniss
(Rensselaer)

Andy Allstadt and Thomas Caraco
(SUNY Albany)

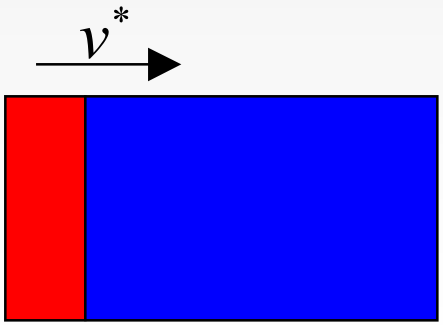
Zoltán Rácz (Eötvös Univ.)

Supported by NSF, Research Corporation

Motivation

- invasive spread of a selectively favored mutation (advantageous allele)
- R.A. Fisher, ‘37, Kolmogorov, Petrovsky & Piscounov, ‘37
- propagating front, initially exists and separates the two spatial regions occupied separately by the two alleles (“domain-wall” motion, propagation into unstable states)

$$\partial_t \rho = \nabla^2 \rho + \rho(1-\rho) \qquad \text{(FKPP)}$$



velocity selection /marginal stability:
Aronson and Weinberger ‘78,
Dee and Langer, ‘83,
van Saarloos ’87)

Model features

Through mutations, an invasive allele appears in a habitat originally dominated by a common resident allele

- mutation is a rare stochastic process
- residents and invaders compete for common limiting resources through clonal propagation (plants)
- competition is pre-emptive (invader allele has an individual-level advantage, but cannot displace residents already present, (Amarasekare, 2003, Shurin et al., 2004)

Lattice Model

0: "empty" lattice site (available resource) □
allele "1": ("resident") ■
allele "2": ("invader") ■

$$n_1(\boldsymbol{x}) = \begin{cases} 1 & \text{if allele 1 is present at site } \boldsymbol{x} \\ 0 & \text{otherwise} \end{cases}$$

$$n_2(\mathbf{x}) = \begin{cases} 1 & \text{if allele 2 is present at site } \mathbf{x} \\ 0 & \text{otherwise} \end{cases}$$

common limiting resources $\rightarrow$ "excluded volume constraint"

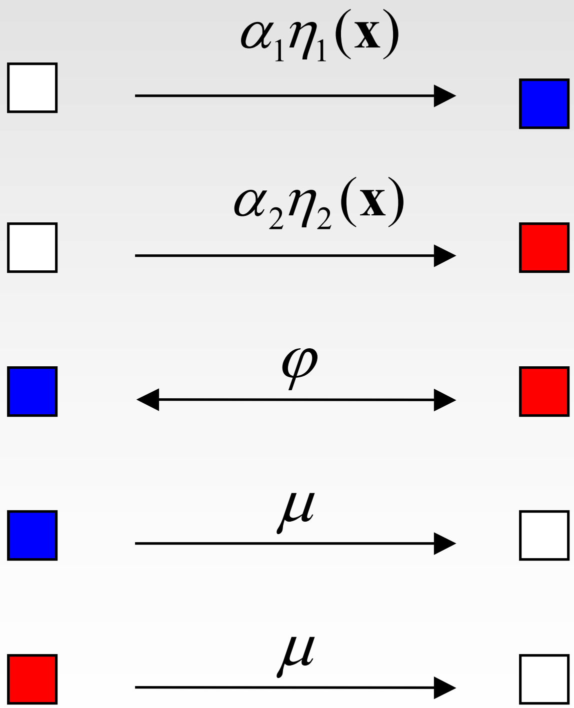
A lattice site represents the minimum level of locally available resources required to sustain an individual organism.

0: "empty" lattice site (available resource) □

1: allele "1" ("resident") ■

2: allele "2" ("invader") ■

local transition rates for an arbitrary site ***x***:



local spread of residents

local spread of invaders

forward-backward recurrent mutation

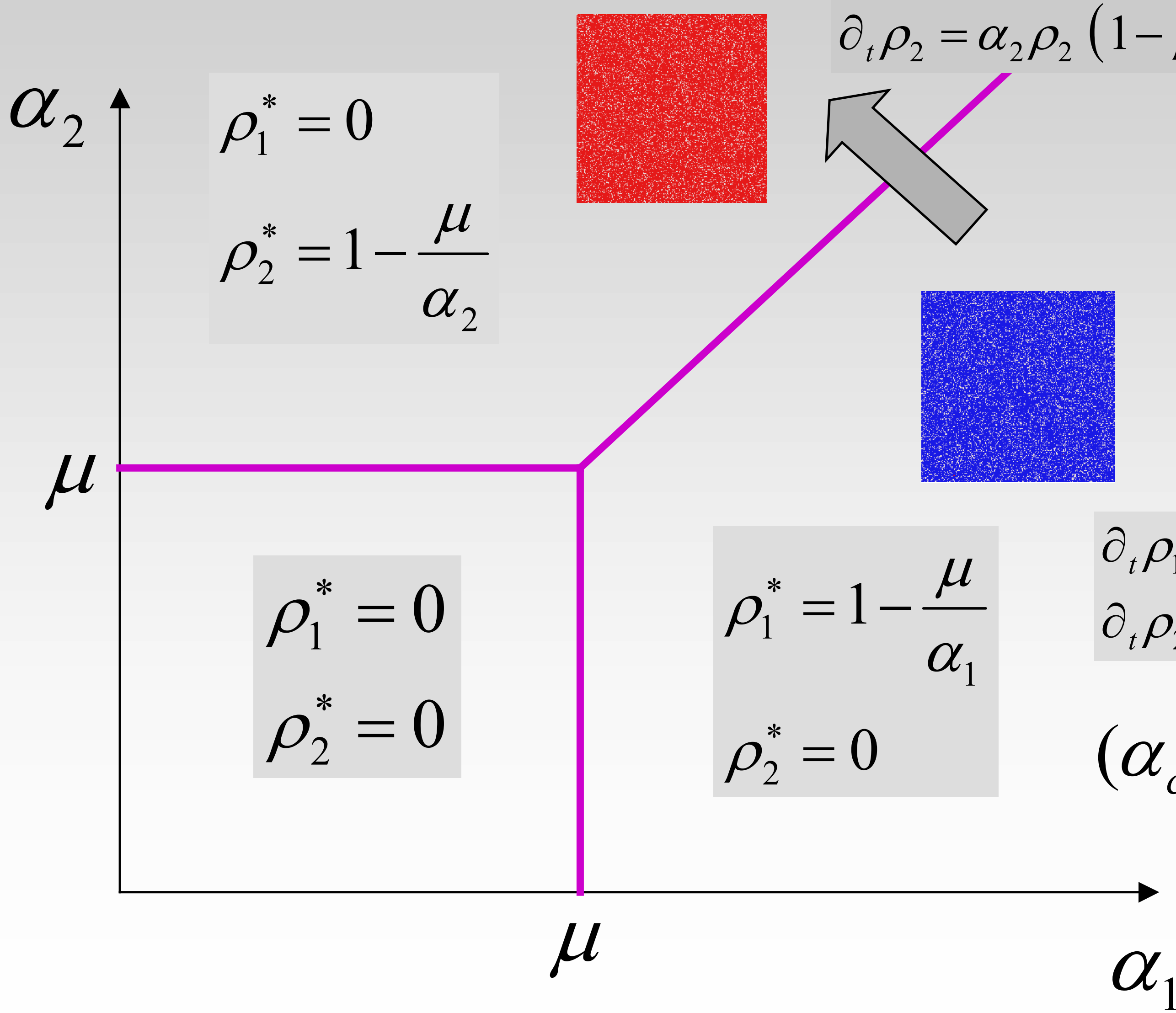
death

$$\eta_i(\mathbf{x}) = \frac{1}{4} \sum_{\mathbf{x}' \in \mathrm{nn}(\mathbf{x})} n_i(\mathbf{x}')$$

$$\varphi << \mu < \alpha_1 < \alpha_2$$

MF Equilibrium (α_1,α_2) phase diagram

$$\partial_t \rho_1 = \alpha_1 \rho_1 \left(1-\rho_1-\rho_2\right) - \mu\,\rho_1 + \phi\left(\rho_2-\rho_1\right)$$
$$\partial_t \rho_2 = \alpha_2 \rho_2 \left(1-\rho_1-\rho_2\right) - \mu\,\rho_2 + \phi\left(\rho_1-\rho_2\right)$$

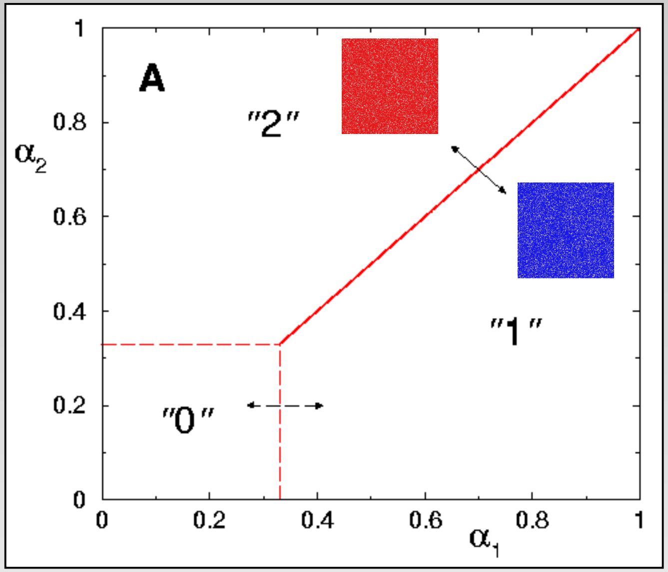


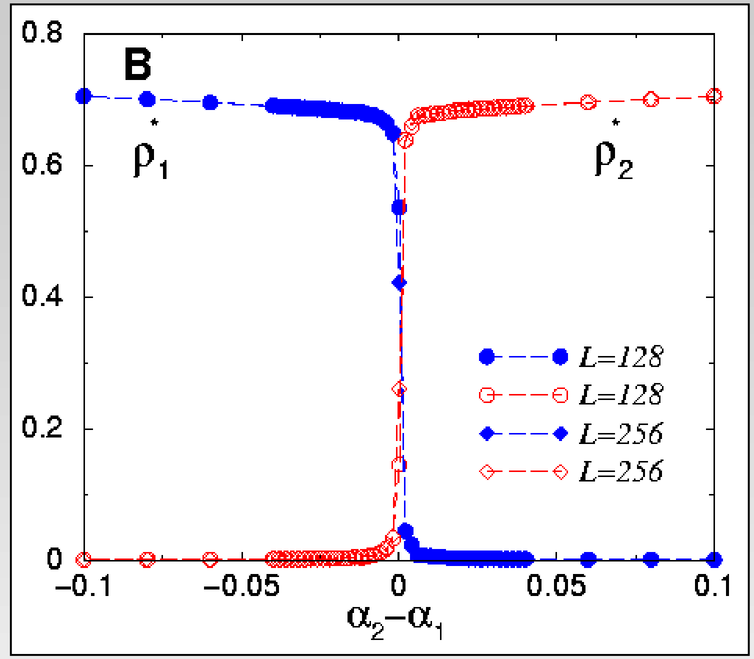
$\varphi \approx 0$

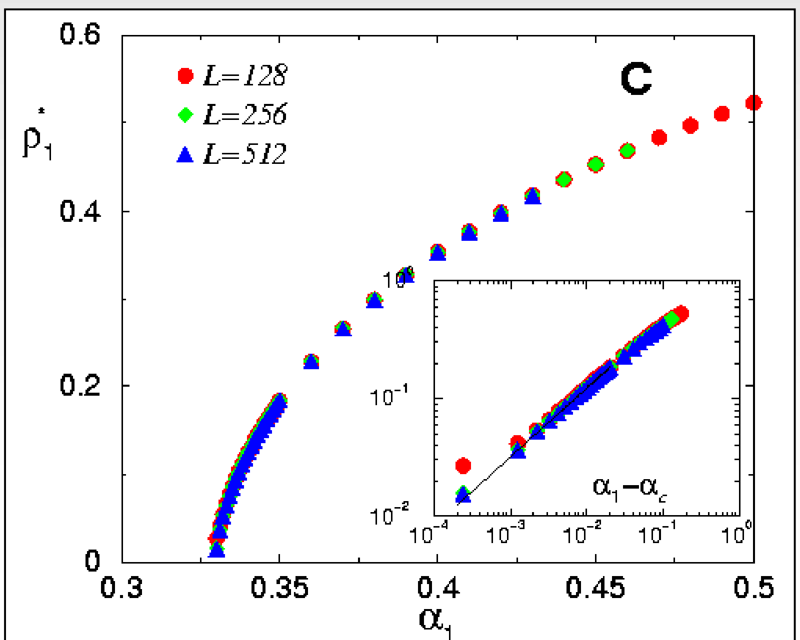
$$\partial_t \rho_1 = \alpha_1 \rho_1 \left(1-\rho_1-\rho_2\right) - \mu\,\rho_1$$
$$\partial_t \rho_2 = \alpha_2 \rho_2 \left(1-\rho_1-\rho_2\right) - \mu\,\rho_2$$

$(\alpha_c = \mu)$

Stationary-State MC Simulations







(single-allele clonal plants:
dispersal-limited extinction,
Oborny et al., 2005)

$$(\alpha_c \approx 1.65\mu)$$

$$\rho_1^* \propto (\alpha_1 - \alpha_c)^\beta \qquad \beta \approx 0.58$$

Invasion time (lifetime)

$$\rho_i(t) = \frac{1}{L^2} \sum_{\mathbf{x}} n_i(\mathbf{x}, t) \quad i = 1,2$$

time-dependent global densities

$$\boxed{\rho_1(t)\Big|_{t=\tau} = \rho_1^* / 2}$$

(first-passage time to a suitably chosen cut-off density)

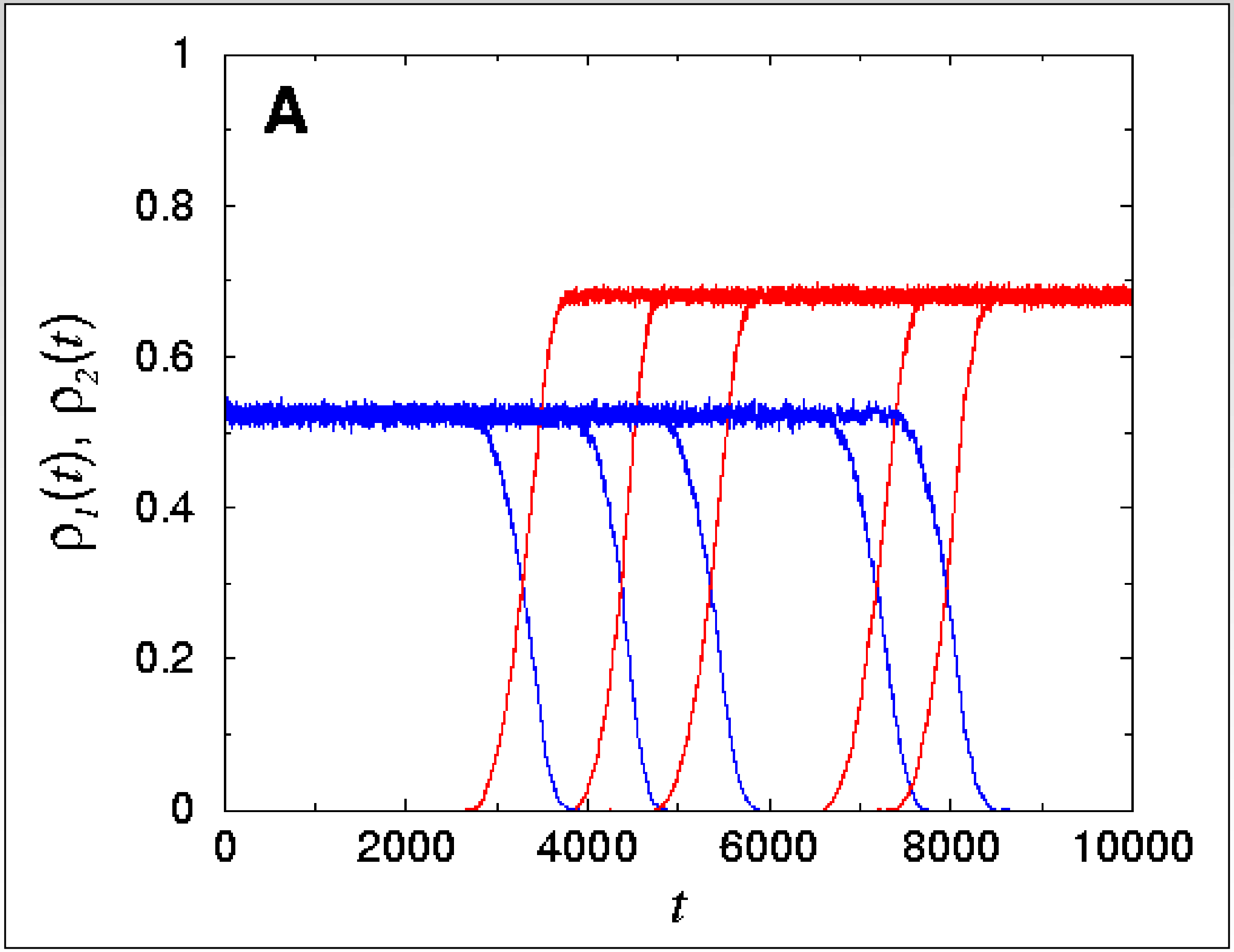
ρ_1^* "metastable" or quasi-equilibrium density of the residents

Single-cluster invasion

$L << R_o$

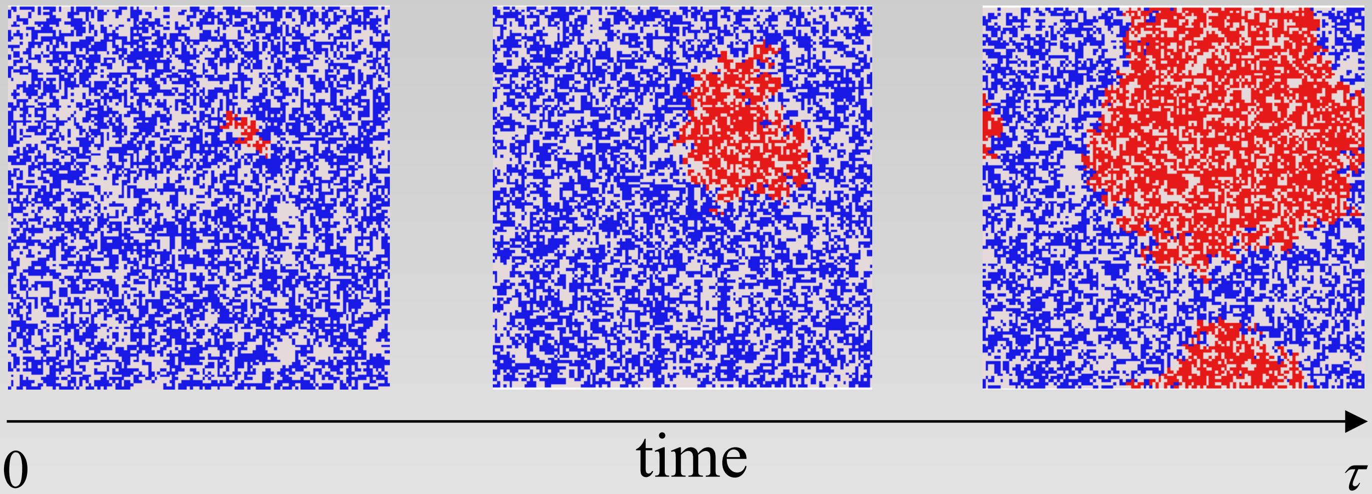
❖ stochastic

$L \times L$ system with p.b.c.



Single-cluster invasion

$L << R_o$



$$P_{not}(t) = \begin{cases} 1 & for\ t \le t_g \\ \exp[-(t - t_g)/\langle t_n \rangle] & for\ t > t_g \end{cases}$$

$\langle t_n \rangle = (L^2 I)^{-1}$ average time between nucleation events

$t_g \sim L / v$ growth time

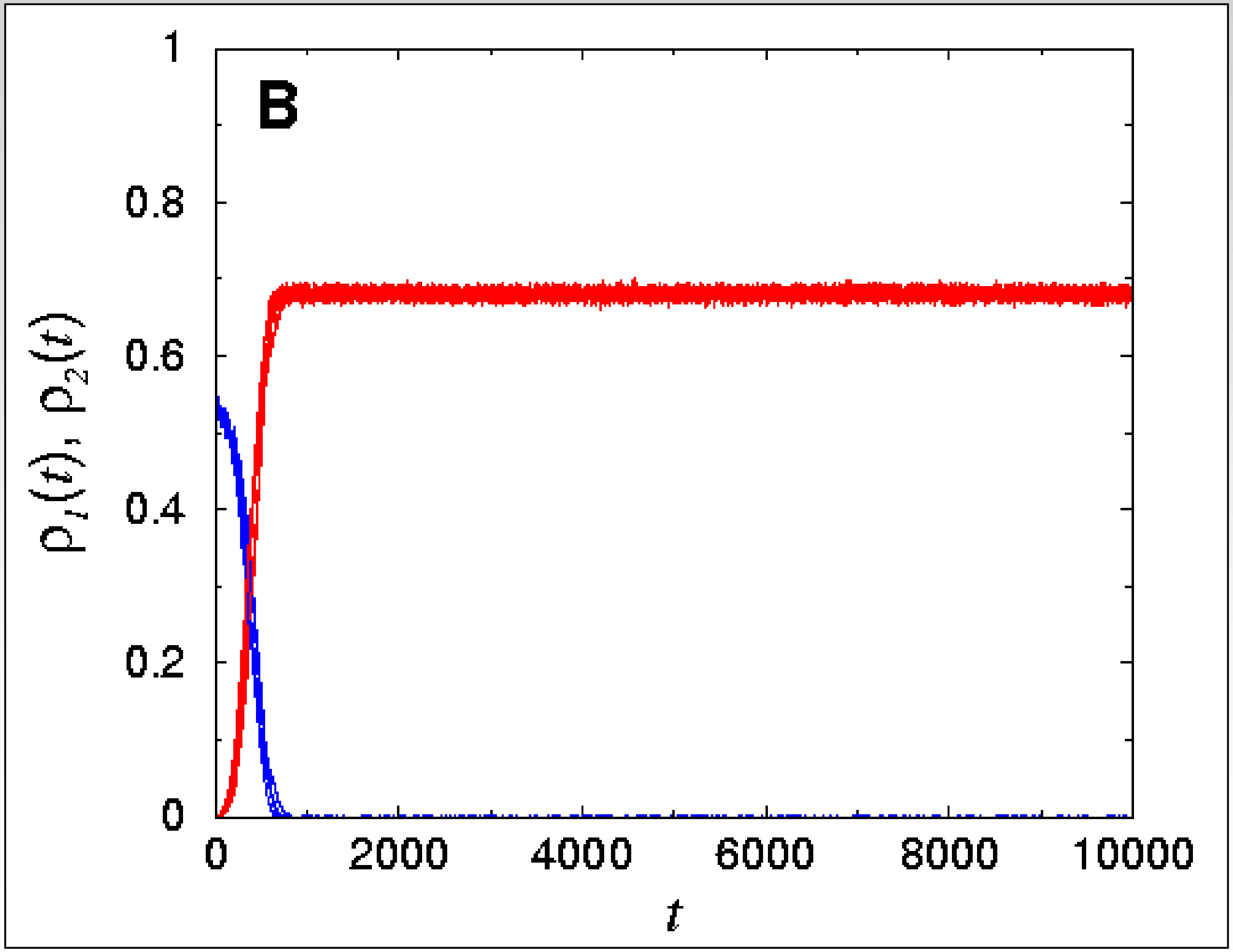
$\langle \tau \rangle = \langle t_n \rangle + t_g \approx \langle t_n \rangle$ average lifetime

Rikvold et al., '94
Richards et al., '95
Ramos et al., '99
Machado et al., '05
GK and Caraco, '05

Multi-cluster invasion

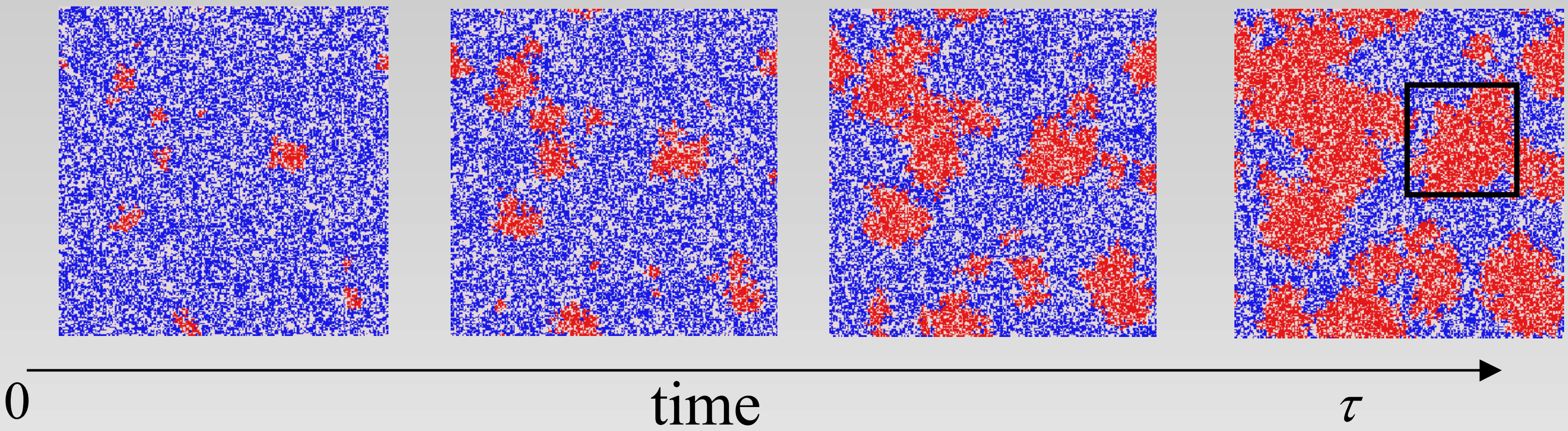
$L >> R_o$

❖ self-averaging (near-deterministic *global densities*)



Multi-cluster invasion

$L >> R_o$



KJMA/Avrami's law (for homogeneous nucleation, *d*=2):

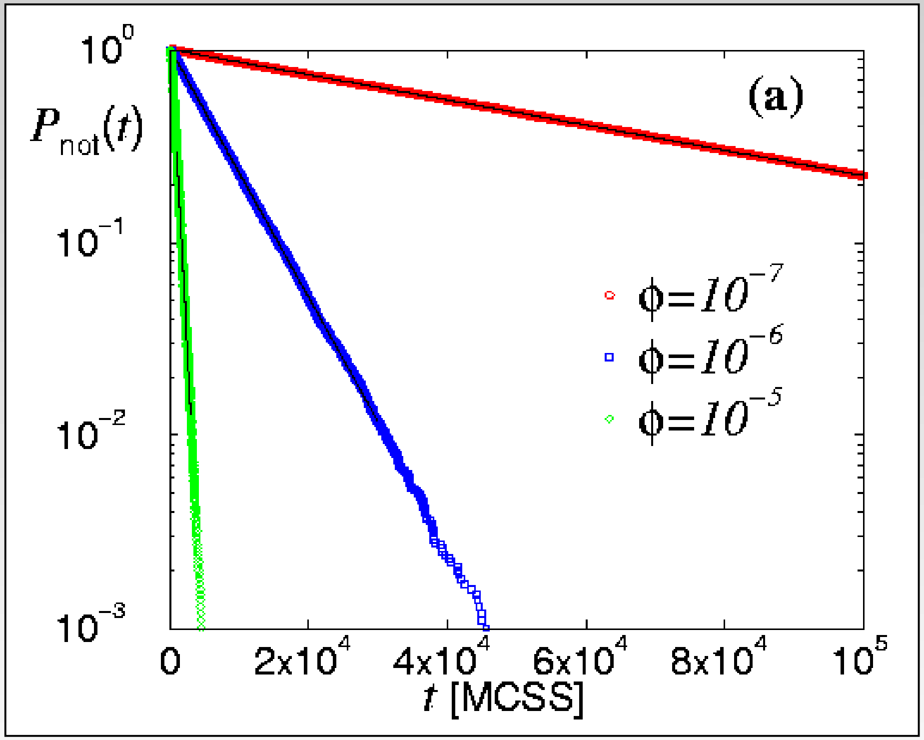
$$\rho_1(t) \approx \rho_1^* e^{-\ln(2)(t/\langle\tau\rangle)^3}$$

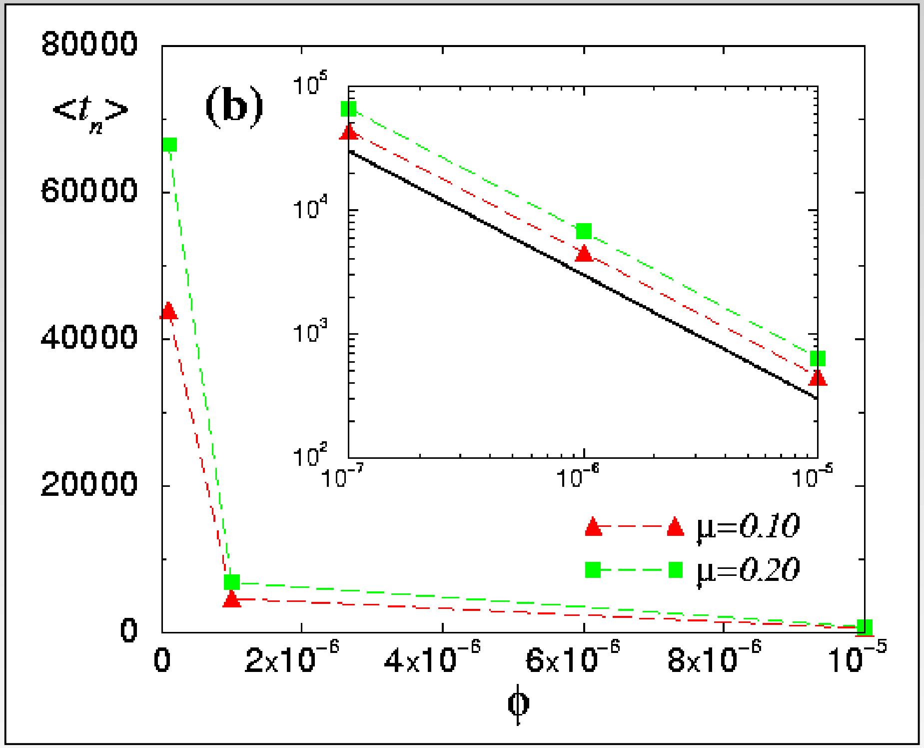
$$I(v\tau)^2\tau \sim 1$$

$\langle\tau\rangle \sim \tau \sim (Iv^2)^{-1/3}$ (average) lifetime

$R_o \sim (v/I)^{1/3}$ average distance between clusters

MC Results - Single-cluster invasion





$L = 32$

$\alpha_1 = 0.50$

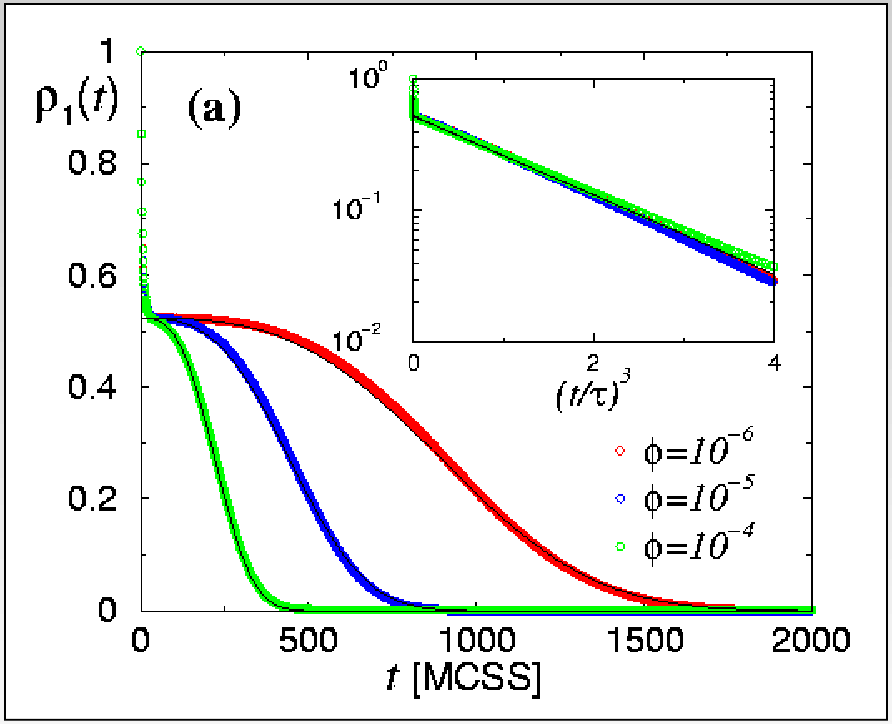
$\alpha_2 = 0.70$

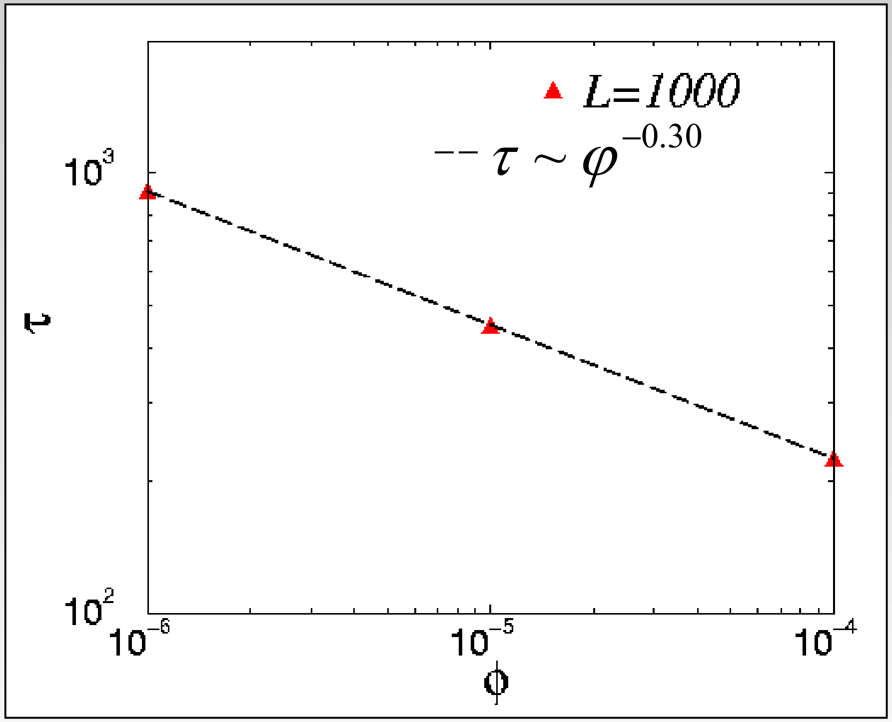
$\mu = 0.20$

$$\langle t_n \rangle \sim \varphi^{-1}$$

$$I \sim \langle t_n \rangle^{-1} \sim \varphi$$

MC Results - Multi-cluster invasion





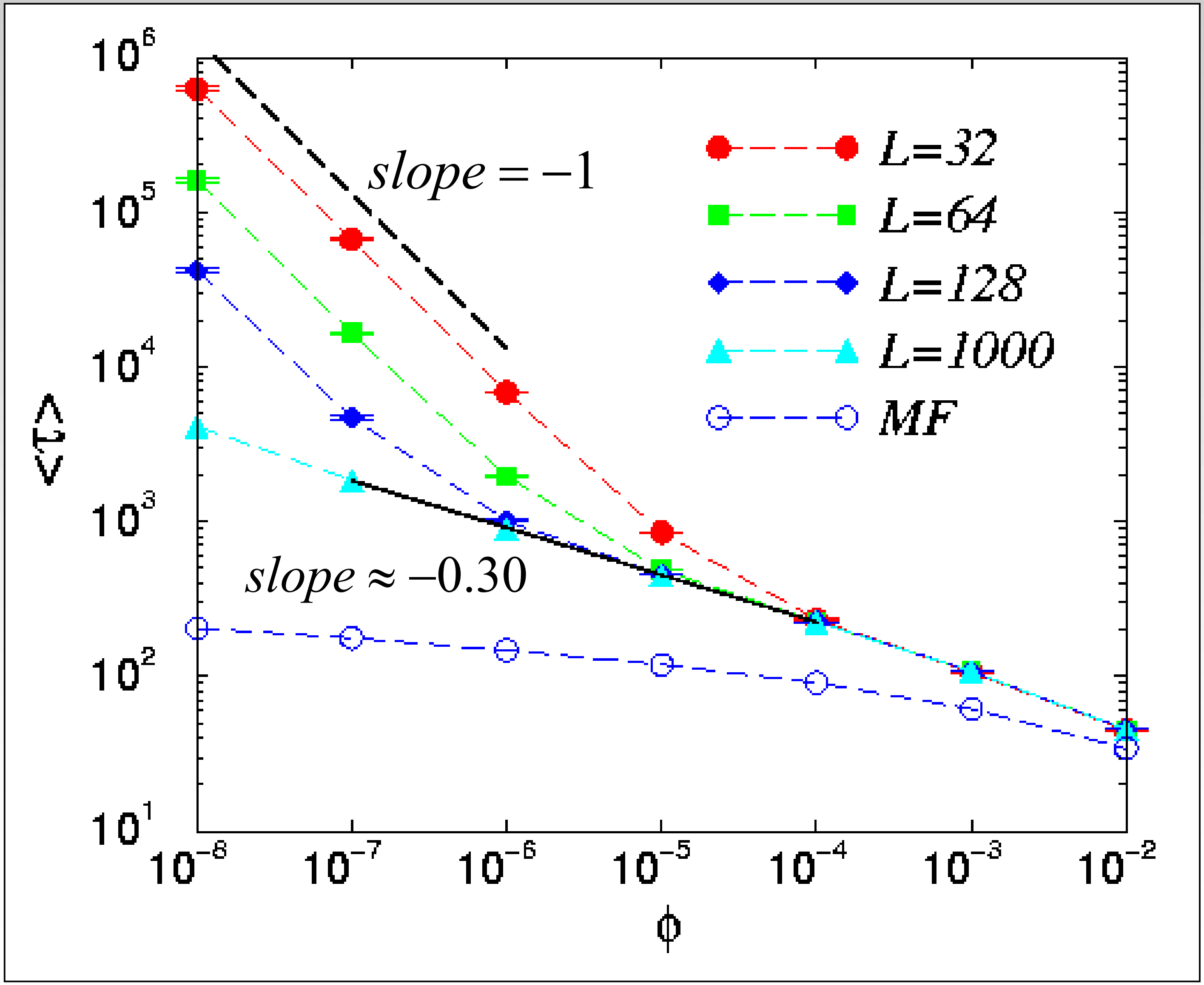
from Avrami's law:

$$\tau \sim I^{-1/3} \sim \varphi^{-1/3}$$

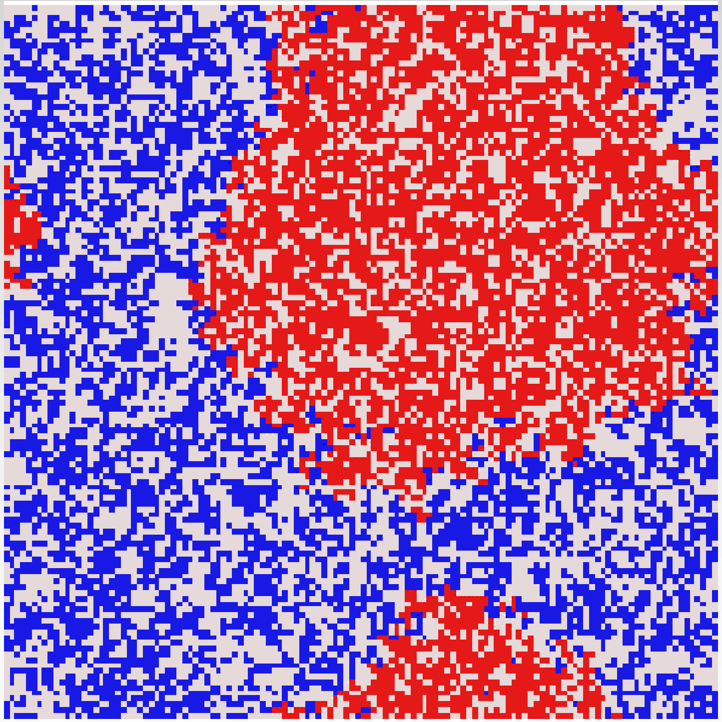
From simulations:

$$\tau \sim \varphi^{-0.30}$$

Summary: Finite-size effects



Surface/interface properties



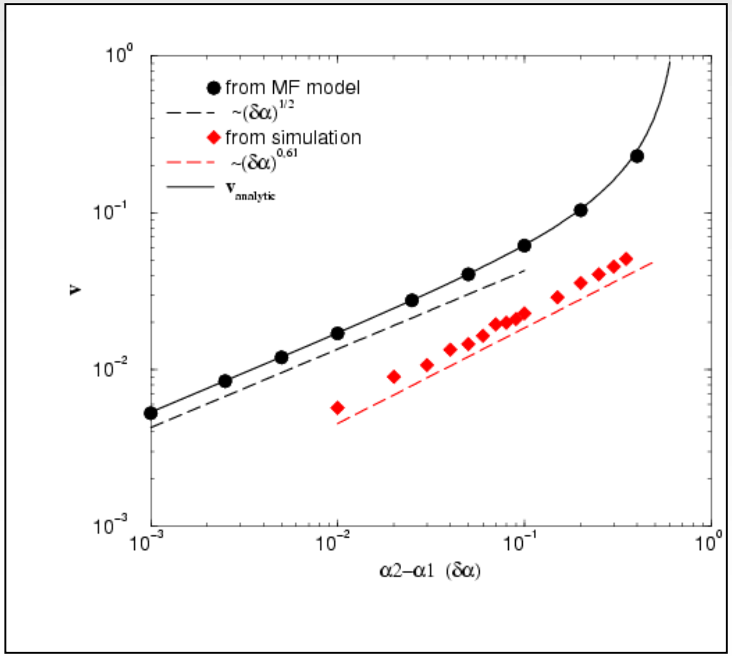
Current work: Wave propagation
PDE approach vs. Monte Carlo

$$\partial_t \rho_1 = \frac{\alpha_1 \delta^2}{4}\left(1-\rho_1-\rho_2\right)\nabla^2 \rho_1 + \alpha_1\left(1-\rho_1-\rho_2\right)\rho_1 - \mu\rho_1$$

$$\partial_t \rho_2 = \frac{\alpha_2 \delta^2}{4}\left(1-\rho_1-\rho_2\right)\nabla^2 \rho_2 + \alpha_2\left(1-\rho_1-\rho_2\right)\rho_2 - \mu\rho_2$$

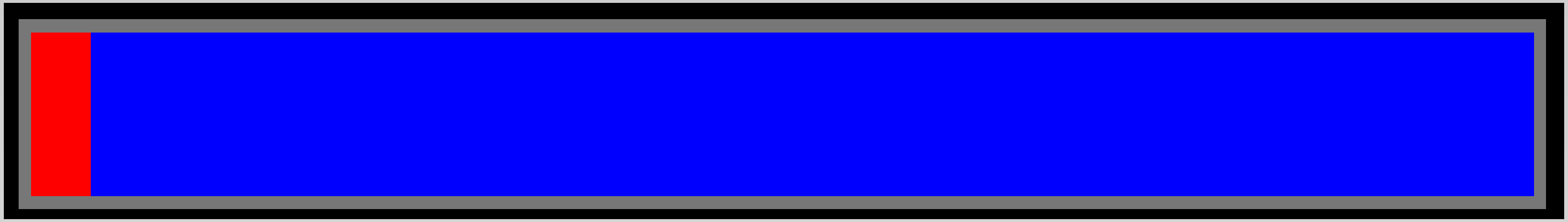
Propagation into unstable states:
Velocity selection /marginal stability
(Aronson and Weinberger '78,
Dee and Langer, '83, van Saarloos '87)

$$v^*(\alpha_1, \alpha_2, \mu) \propto \frac{\mu}{\alpha_1}\sqrt{\alpha_2(\alpha_2-\alpha_1)}$$

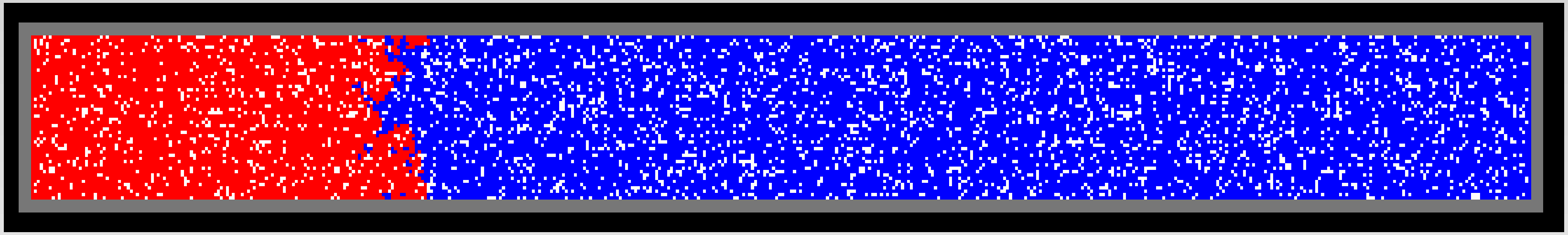


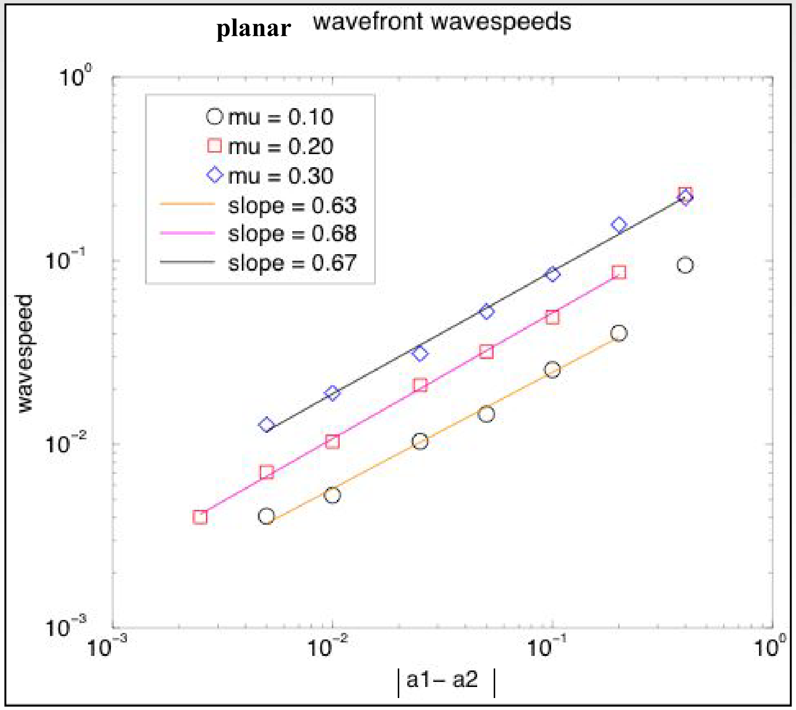
MC simulation for the front velocity

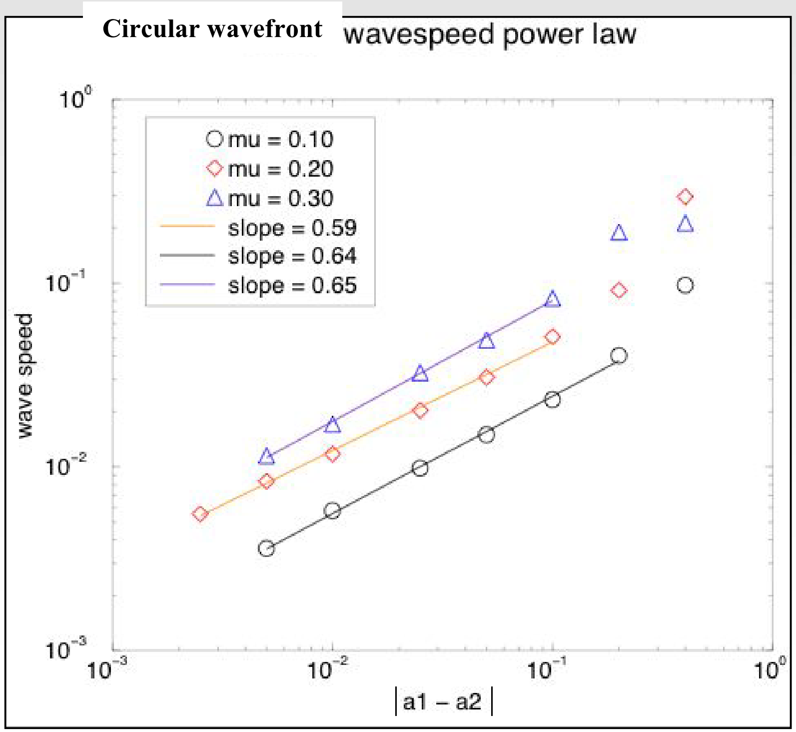
$t = 0$



$t = \infty$

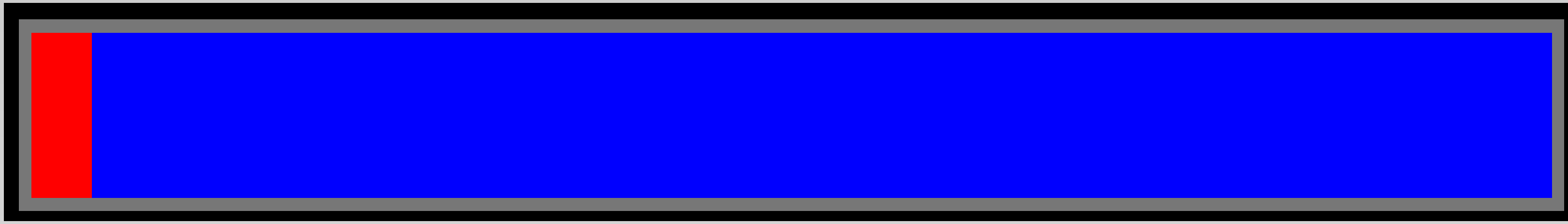




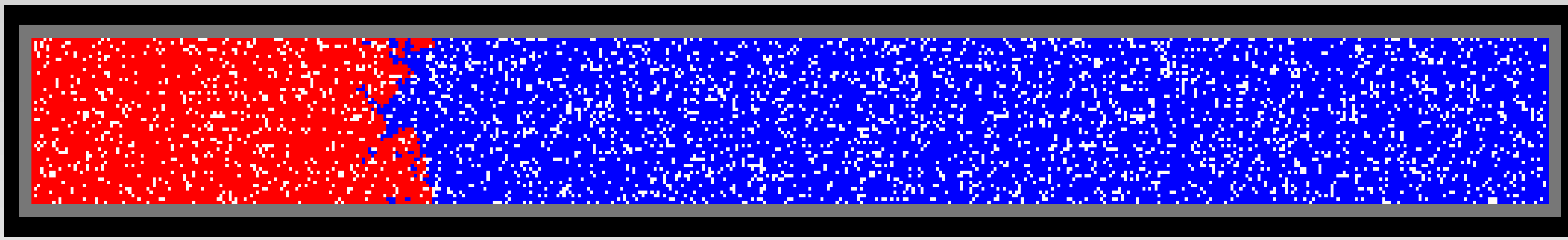


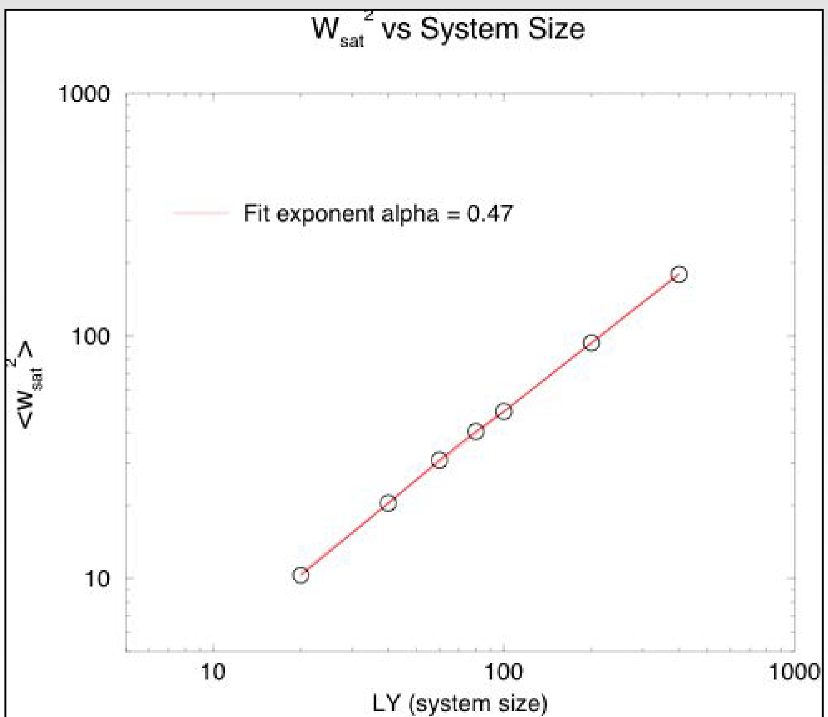
MC simulation for the front roughening

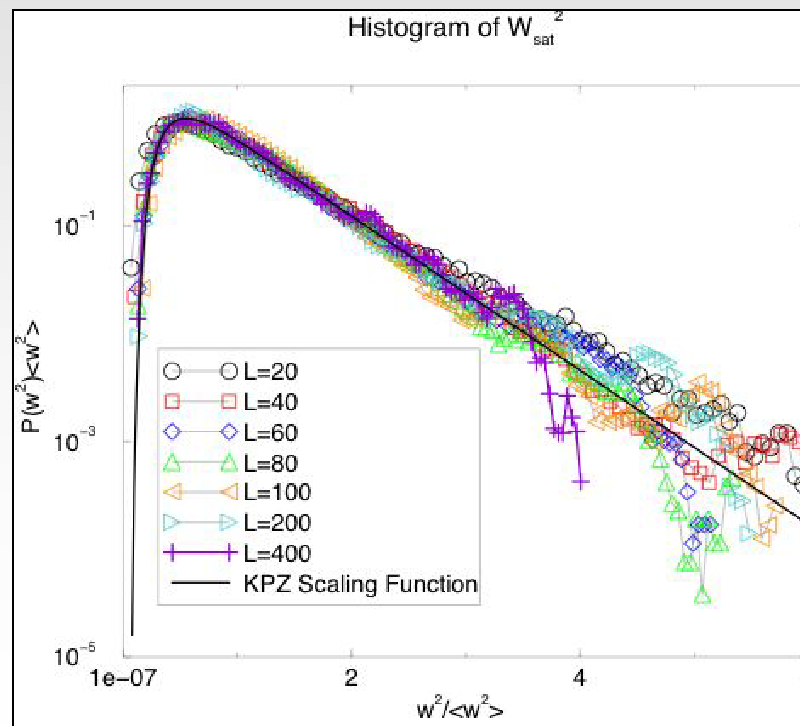
$t = 0$



$t = \infty$







Summary and Outlook

KJMA/Avrami's law applicable to a wide range of systems:

- ferromagnetic (Rikvold et al. '94, Ramos '99) and ferroelectric (Ishibashi & Takagi '71, Duiker & Beale '90) switching
- flame propagation in slow combustion (Karttunen '98)
- chemical reactions (Machado et al. '04)
- invasive allele spread and ecological invasion (GK & Caraco, '04)

- asymptotic linear spreading velocity $v^*(\alpha_1,\alpha_2,\mu)$
- comparison of continuum PDE and discrete Monte Carlo approaches
- properties of critical cluster $R_c(\alpha_1,\alpha_2,\mu)$

G. Korniss and T. Caraco, *J. Theor. Biol.* **233**, 137 (2005).
J.A. Yasi, G. Korniss, and T. Caraco, cond-mat/0505523.

http://www.rpi.edu/~korniss/Research/