Nonequilibrium Phase Transitions and Spatial Population Genetics

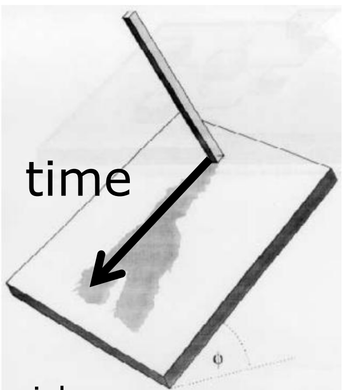
Maxim Lavrentovich
Cooperation and Evolution of Multicellularity
KITP Workshop
February 15, 2013

Outline

- Nonequilibrium phase transitions and connection to evolutionary dynamics
- Directed percolation with inflation and radial range expansions
- Scaling at the phase transition
- Spherical range expansions
- Models of range expansions with mutualism
- Mutualism with rough fronts

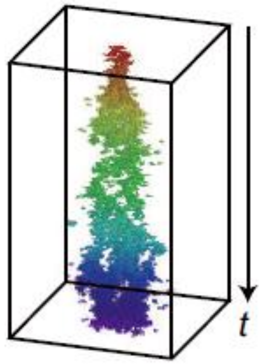
Directed Percolation (DP)

Avalanche Flows



H. Hinrichsen
Braz. J. Phys. **30**(1) (2000)

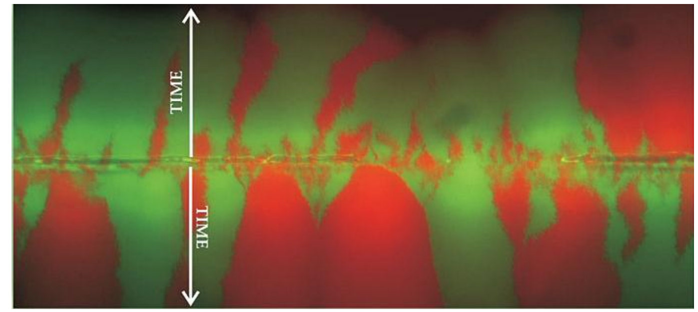
Phase Nucleation



time (different colors)

K. A. Takeuchi et al.
PRE **80** 051116 (2009)

Range Expansions

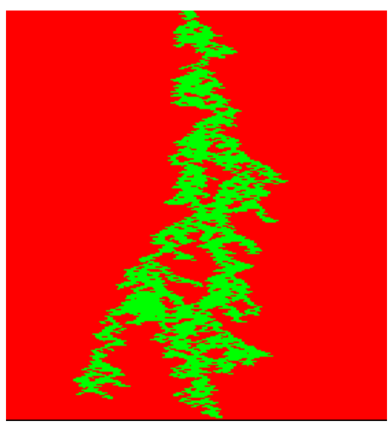


O. Hallatschek and D. R. Nelson
Physics Today **62** (7) (2009)

Typical Initial Conditions

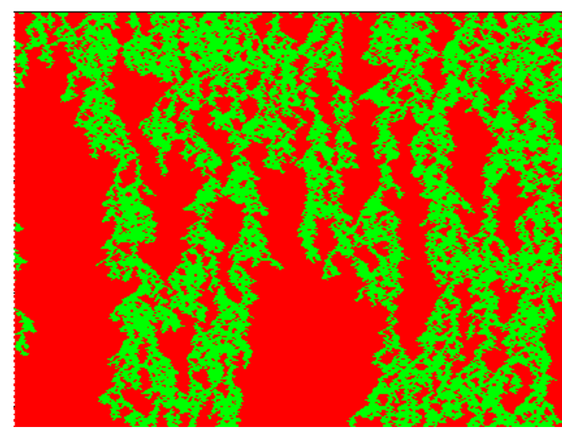
single seed:

time



uniform:

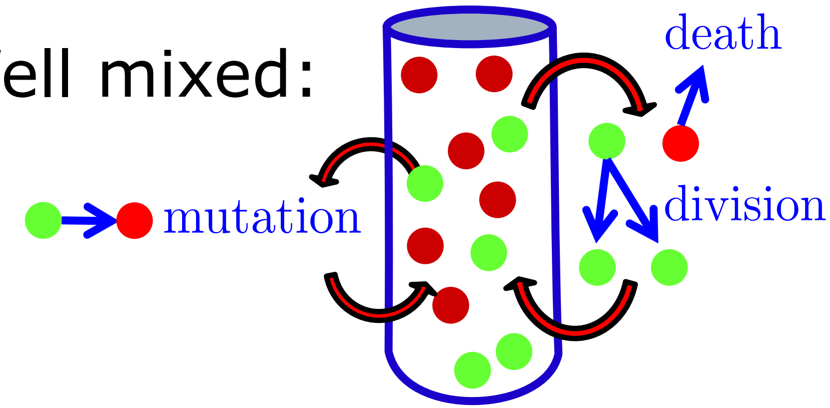
time



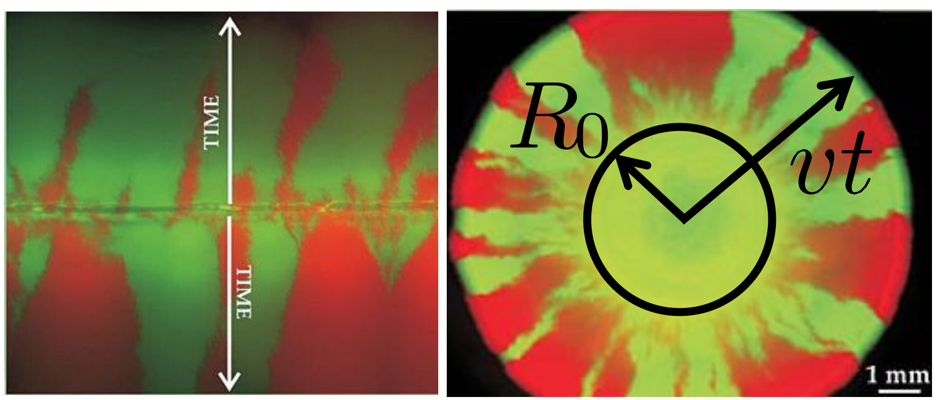
Range expansions and evolution

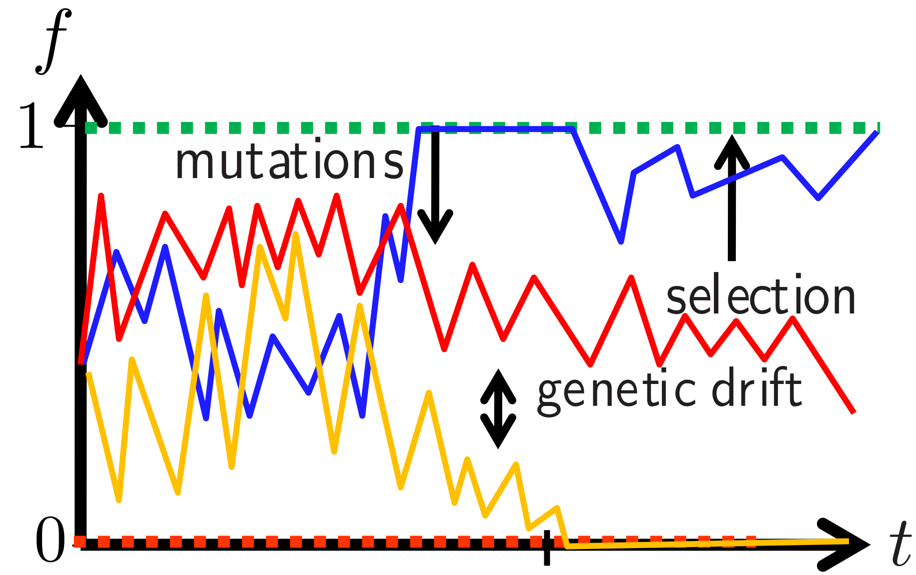
There is an interplay between (spatial) population dynamics and evolutionary dynamics:

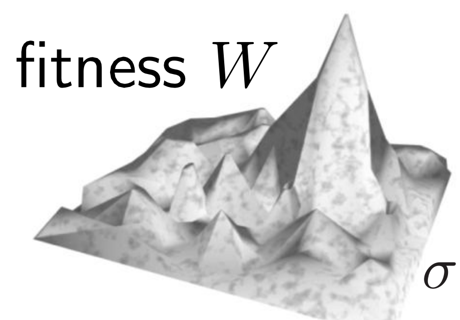
Well mixed:



Spatially distributed:





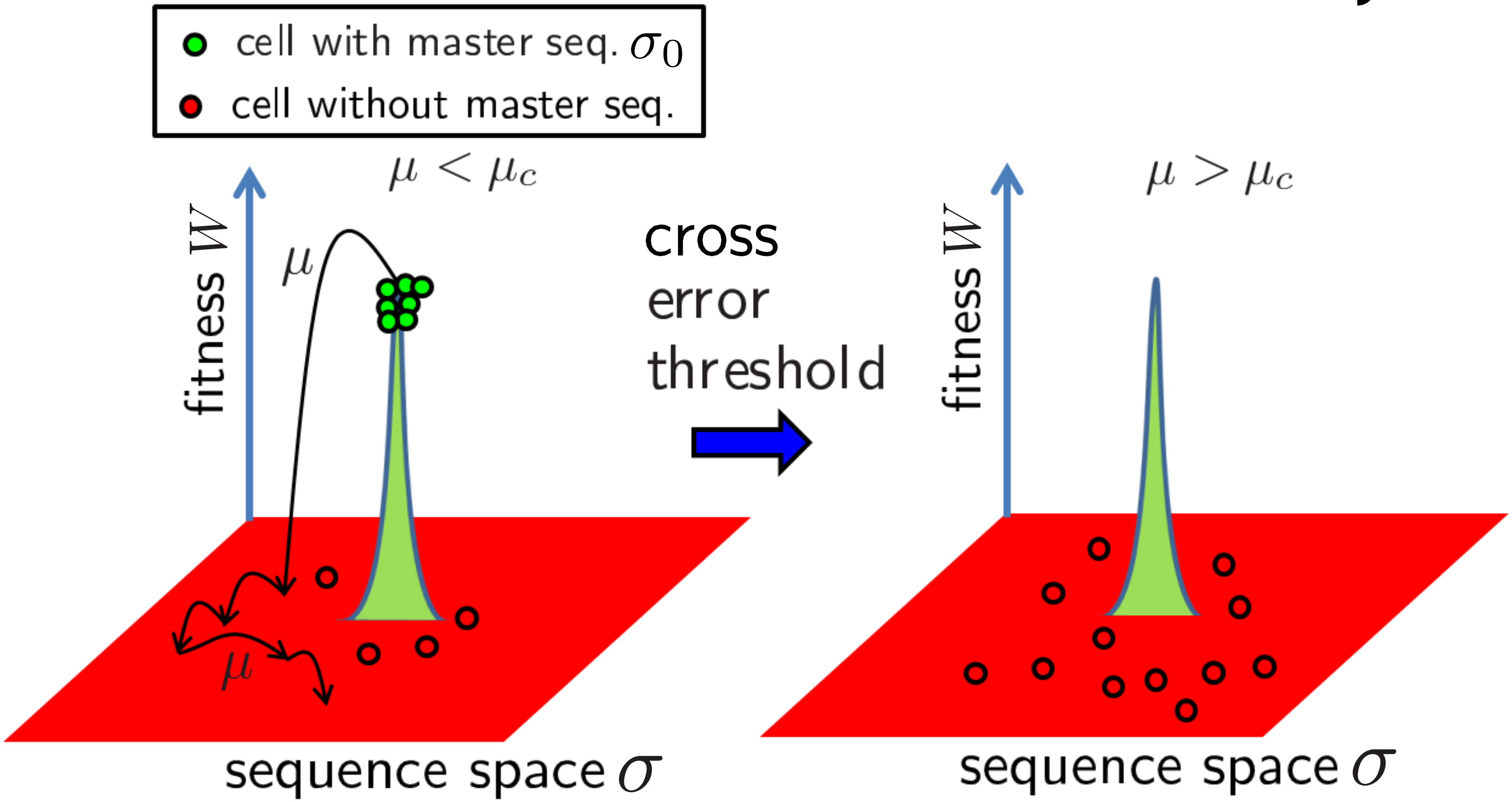


experiment photos from: O Hallatshek and DR Nelson, Physics Today July 2009 p. 44
fitness landscape: I. P. McCarthy **24**(2) 124 (2004)

Quasispecies theory

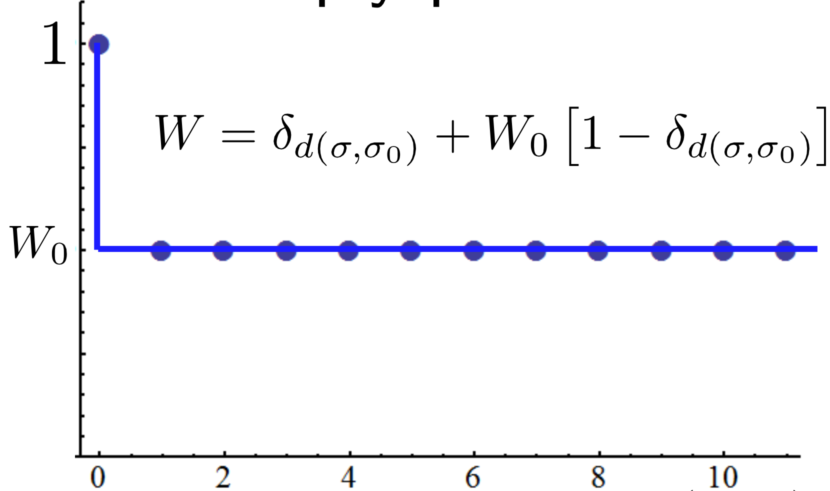
Set of sequences $\{\sigma\}$ with $\sigma = (s_1,\, s_2,\, \ldots, s_N)$ where $s_i = 1, 2, \ldots, \ell$

DNA sequences: ATCGATCGTACGTAACTGCATGCATGACTGTACTGTACGTGACCTT $\}\ \ell = 4$



Quasispecies theory: fitness functions

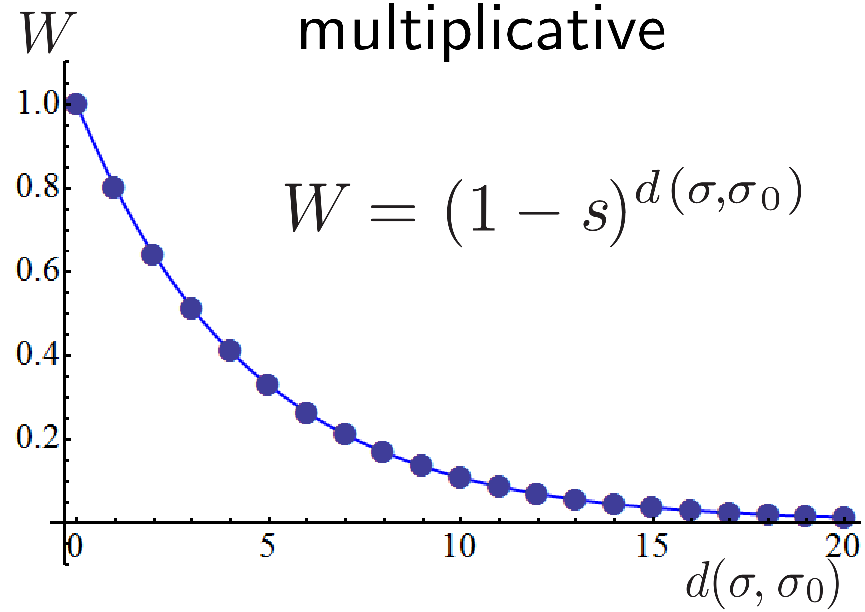
sharply peaked



$$W = \delta_{d(\sigma,\sigma_0)} + W_0 \left[1 - \delta_{d(\sigma,\sigma_0)}\right]$$

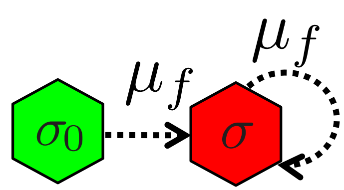
distance from master sequence: $d(\sigma, \sigma_0)$

multiplicative



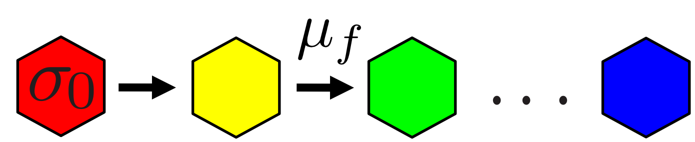
$$W = (1 - s)^{d(\sigma,\sigma_0)}$$

directed percolation



$d(\sigma, \sigma_0)$: 0 $d > 0$

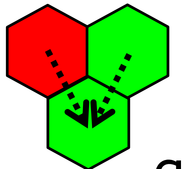
unidirectionally coupled directed percolation



$d(\sigma, \sigma_0)$: 0 1 $2 \ldots K-1$

The Domany-Kinzel model

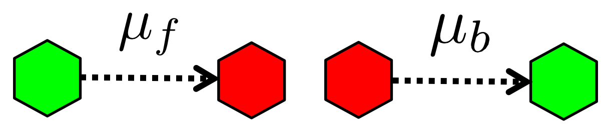
(1) selection with parameter $s \in [0,1]$



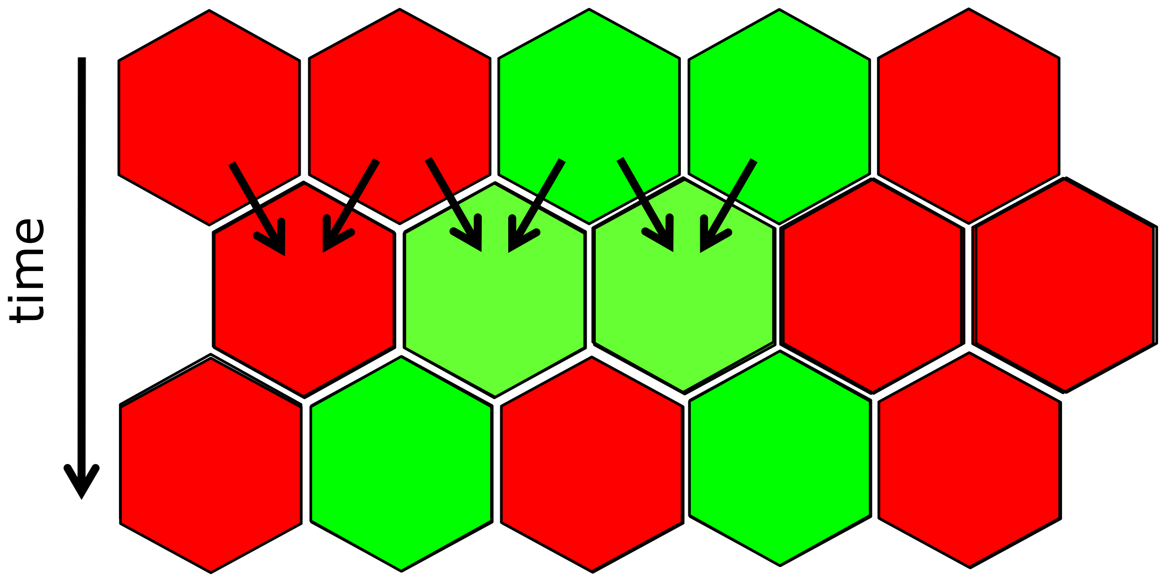
$$p_{\mathrm{G}} = \frac{1}{1+(1-s)}$$

green outcompetes red

(2) mutations



Evolution of a population with 5 individuals:



$t = 0$

$t = 1$

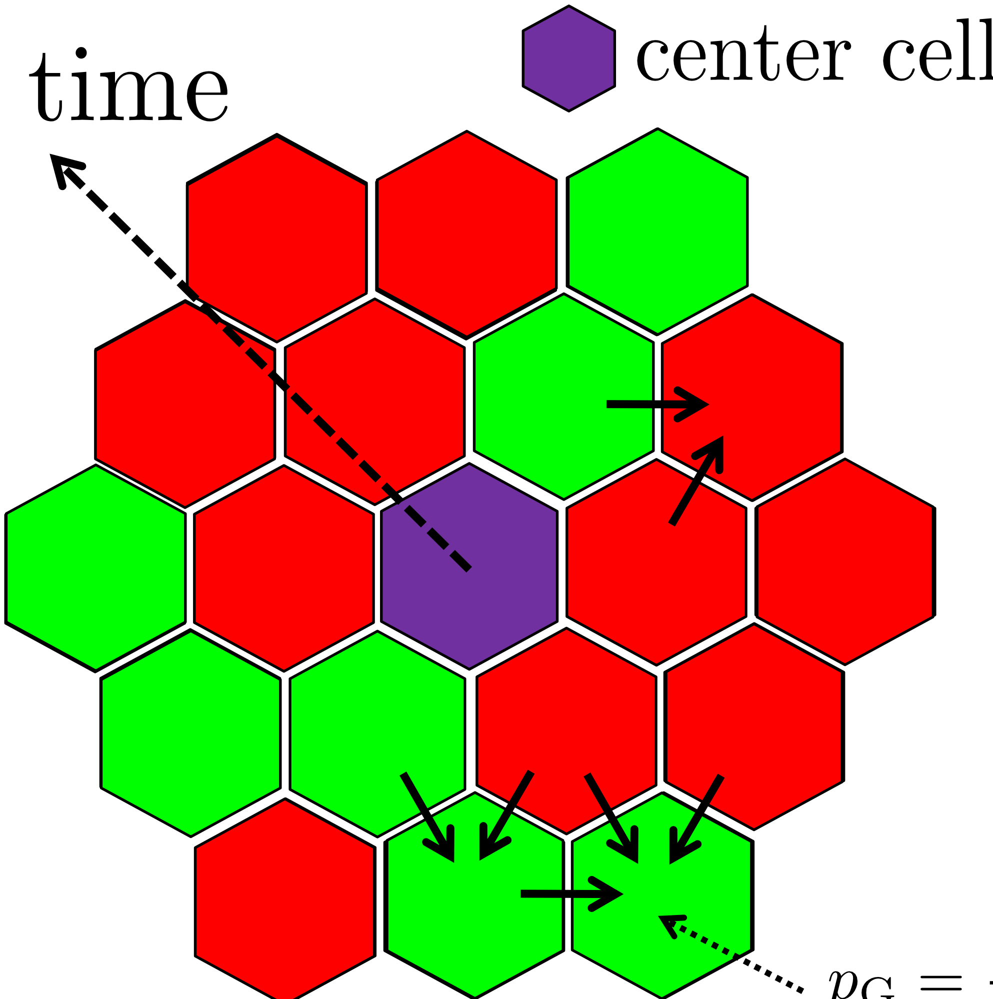
$t = 2$

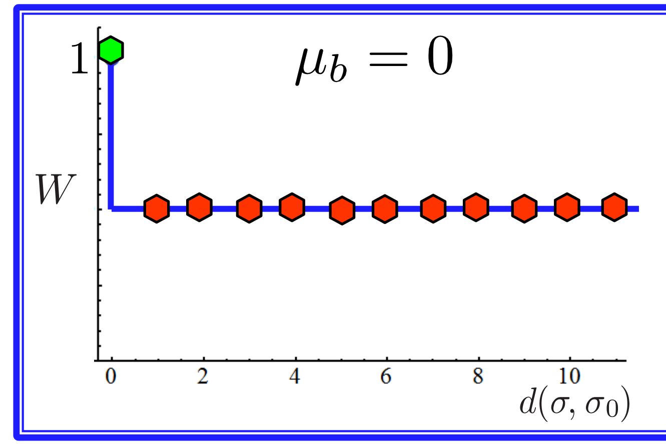
Time is measured in units of the generation time τ_g

periodic boundary conditions

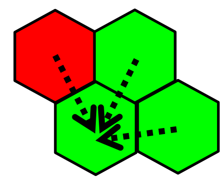
Model described in: H Hinrichsen, Adv. in Phys. 49(7), 815 (2000); E Domany and W Kinzel, PRL 53, 311 (1984)

Radial Domany-Kinzel model



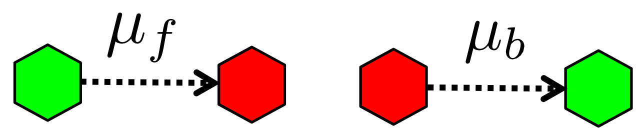


(1) selection



$$p_G = \frac{2}{2 + (1 - s)}$$

(2) mutations:

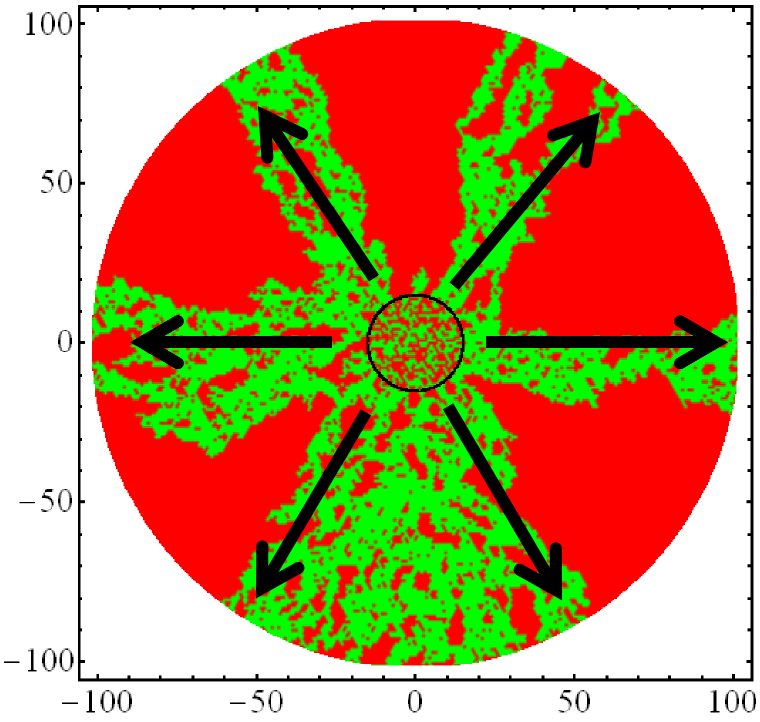


$$p_G = \frac{n_G}{n_G + n_R(1 - s)}$$

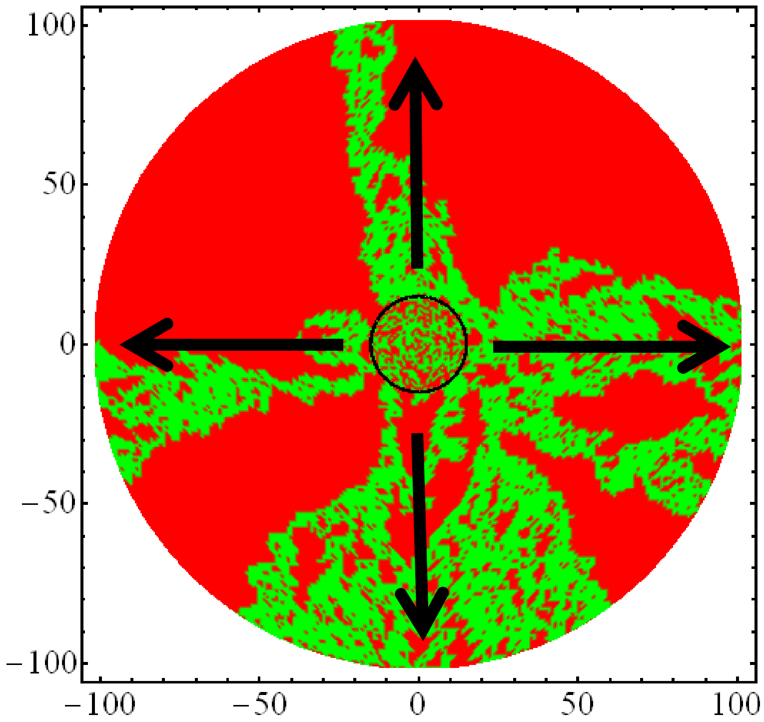
Radial models exhibit lattice artifacts

Simulations with well-mixed initial conditions

hexagonal lattice:



square lattice:



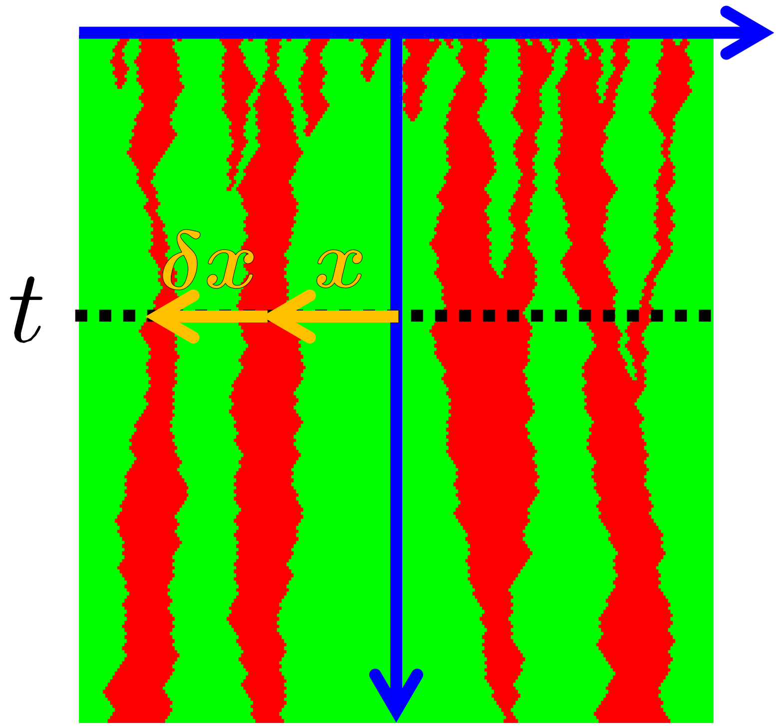
The Heterozygosity

The heterozygosity is the probability two cells are different:

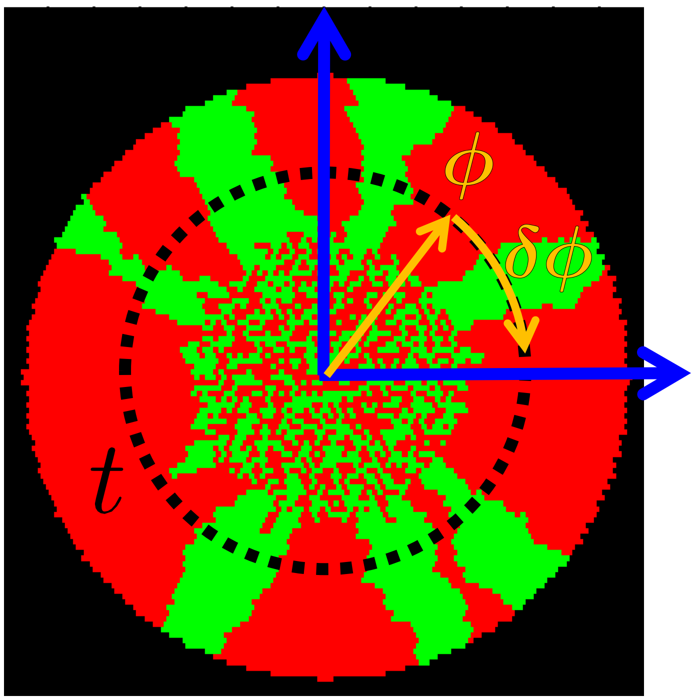
$$H(\delta\mathbf{r},t) \equiv \langle f(\mathbf{r},t)[1-f(\mathbf{r}+\delta\mathbf{r},t)] + f(\mathbf{r}+\delta\mathbf{r},t)[1-f(\mathbf{r},t)]\rangle_{\text{ensemble, }\mathbf{r}}$$

fraction of green cells

linear



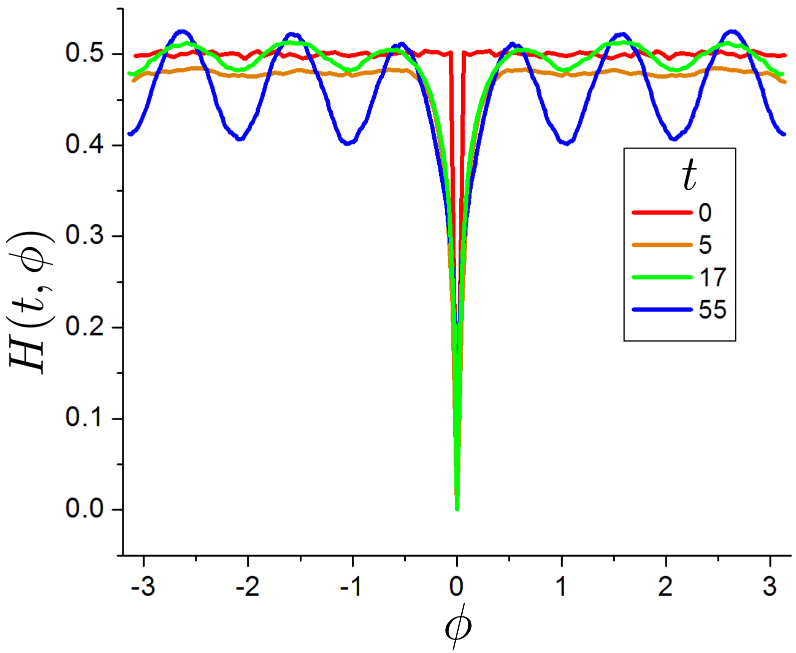
radial

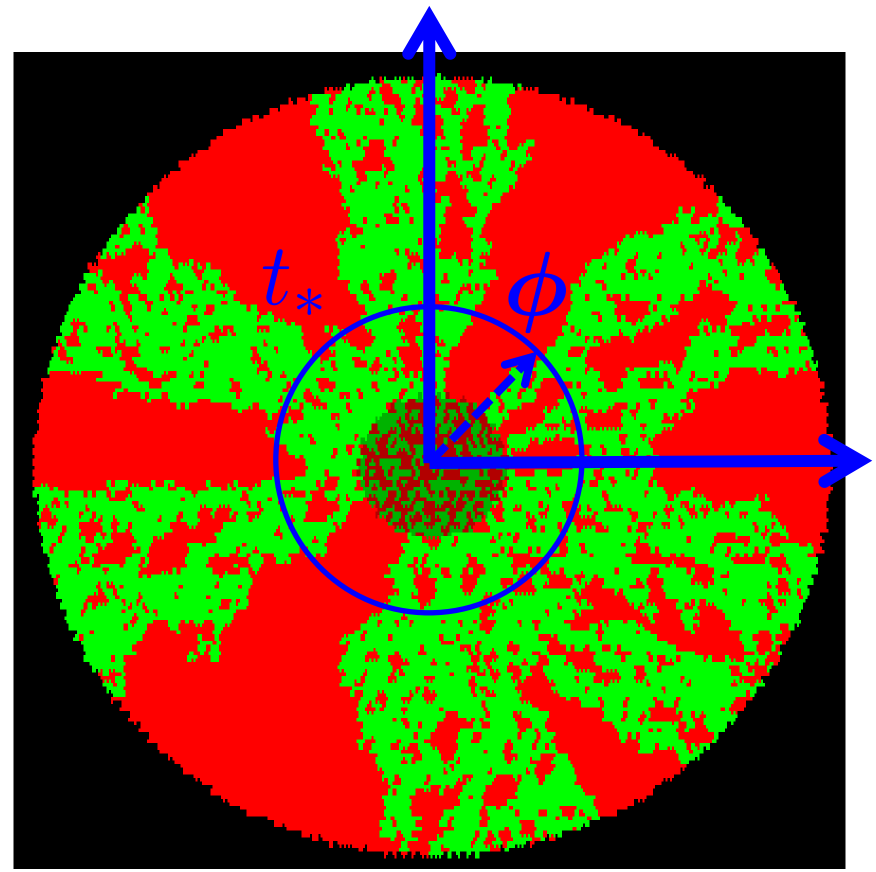


Lattice artifacts (with mutations)

The heterozygosity can capture important spatial features of the dynamics

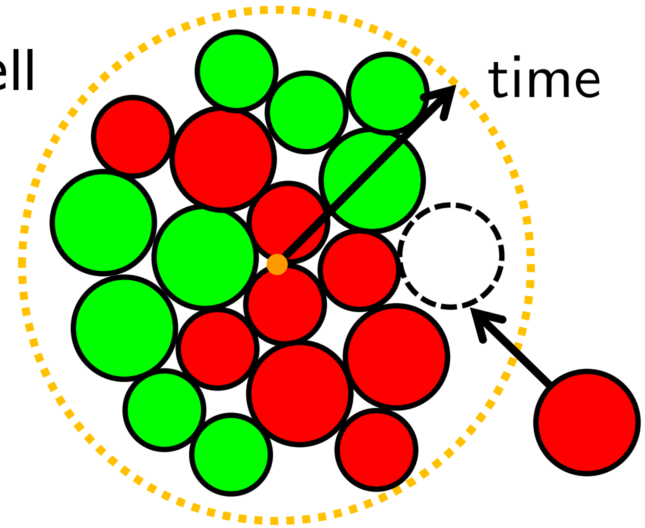
$$\begin{cases} s = 0.57 \\ \mu_f = 0.1 \\ \mu_b = 0 \\ R_0 = 15 \text{ cells} \end{cases}$$



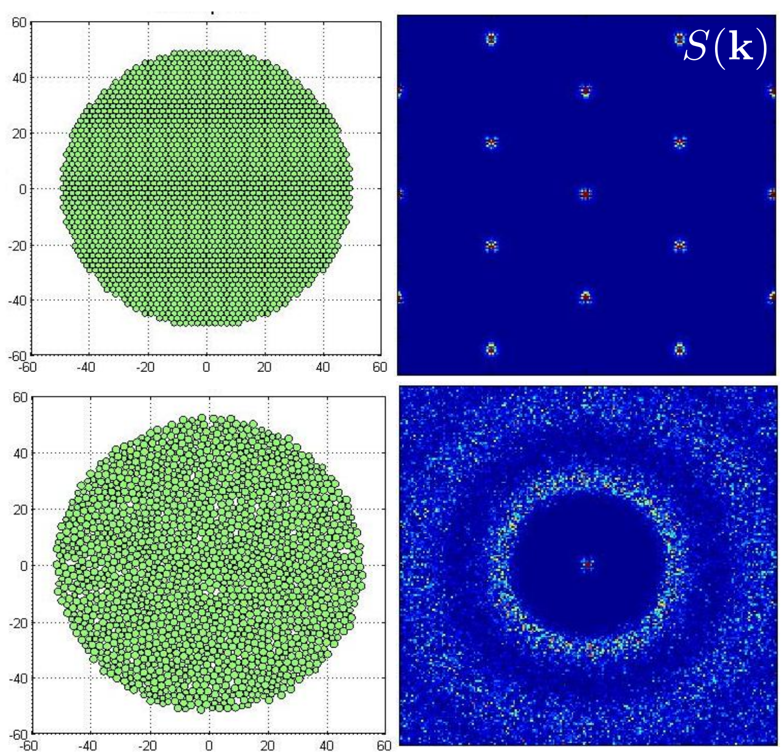


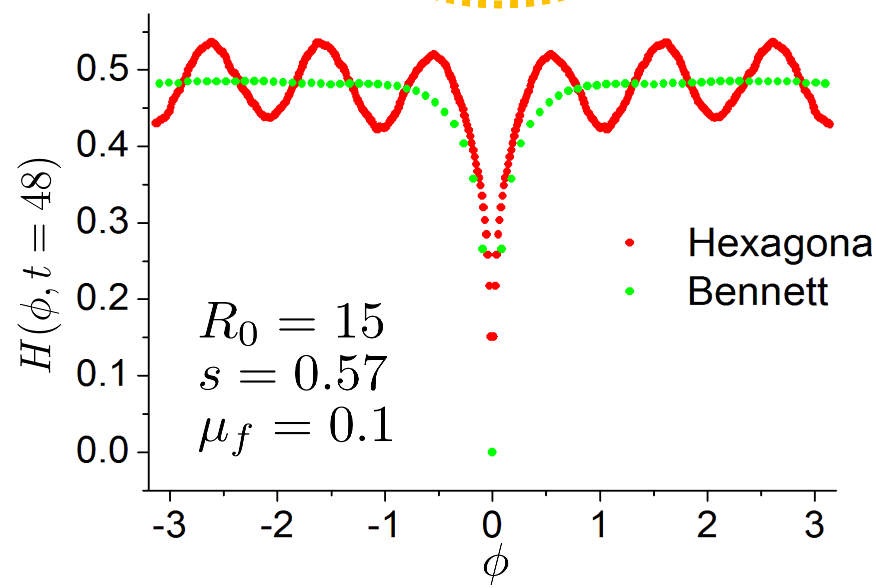
An amorphous lattice fixes the artifacts

We employ a Bennett model using two cell sizes to construct an isotropic lattice:



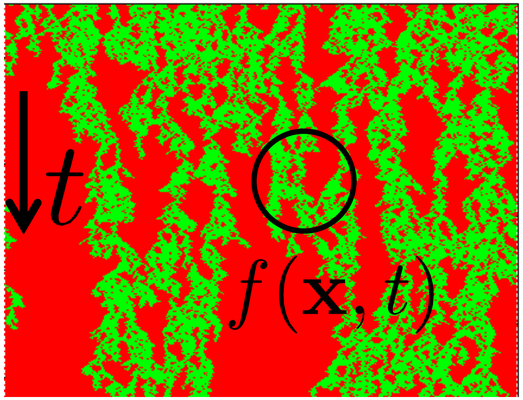
structure factor: $S(\mathbf{k}) \equiv \frac{1}{N} \left| \sum_{i=1}^{N} e^{i\mathbf{k}\cdot\mathbf{r}_i} \right|^2$



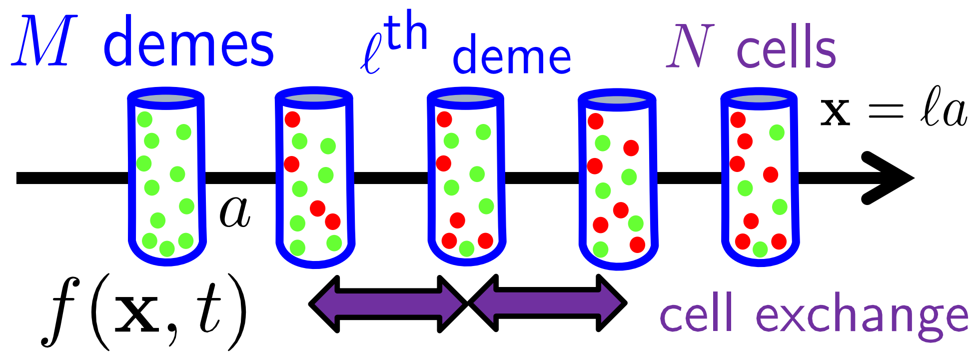


Model described in: MOL, K. Korolev, D. R. Nelson PRE **87**, 012103 (2013);
M Rubenstein and DR Nelson, PRB 26, 6254 (1982)

Stepping stone models and Langevin dynamics



same dynamics as $N \to 1$



The stepping-stone Langevin equation for the green cell density $f(\mathbf{x},t)$ in the limit $N \to 1$ is the same as coarse-grained DK model (at small $s,\ \mu_b,\ \mu_f$):

$$\partial_t f(\mathbf{x},t) = \underbrace{\frac{a^2}{z\tau_g}\nabla^2_{\mathbf{x}} f}_{\text{cell exchange}} + \underbrace{sf(1-f)}_{\text{selection}} + \underbrace{\frac{\mu_b}{\tau_g}(1-f) - \frac{\mu_f}{\tau_g} f}_{\text{mutation}}$$

$$+ \sqrt{2a\tau_g^{-1} f(1-f)}\,\eta(\mathbf{x},t) \quad \text{\} genetic drift}$$

Gaussian noise: $\langle \eta \rangle = 0 \qquad \langle \eta(\mathbf{x},t)\eta(\mathbf{x}',t')\rangle = \delta(t-t')\delta(\mathbf{x}'-\mathbf{x})$

The neutral case $(s = \mu_f = \mu_b = 0)$

From the Langevin equation:

$$\begin{cases} \partial_t H(\mathbf{r}, t) = 2D\nabla^2 H(\mathbf{r}, t) \\ H(\mathbf{r} = 0, t) = 0 \end{cases}$$

Linear: $\partial_t H(r, t) = 2D_l \dfrac{\partial H}{\partial r^2} + \dfrac{2D_l(d-1)}{r} \dfrac{\partial H}{\partial r}$

Radial: $\partial_\eta H(\phi, \eta) = \dfrac{2D_r}{R_0^2} \dfrac{\partial^2 H}{\partial \phi^2} + \dfrac{2D_r(d-1)}{R_0^2 \tan\phi} \dfrac{\partial H}{\partial \phi}$

Absorbing BC: $H(0, \eta) = H(0, t) = 0$

$$0 < t < \infty$$

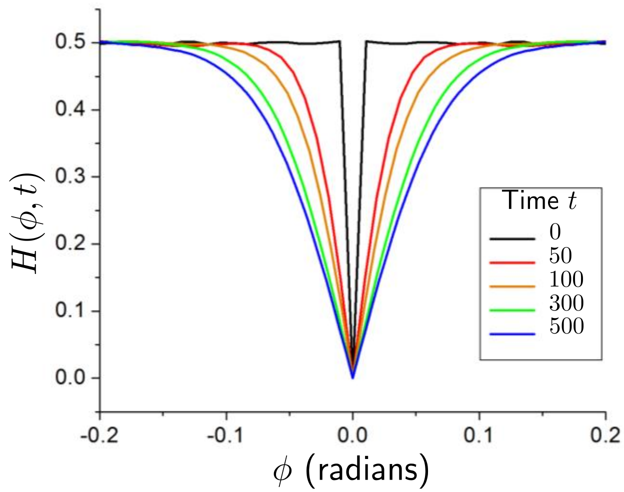
$$\eta = \frac{R_0 t}{R_0 + vt}$$

$$0 < \eta < \frac{R_0}{v}$$

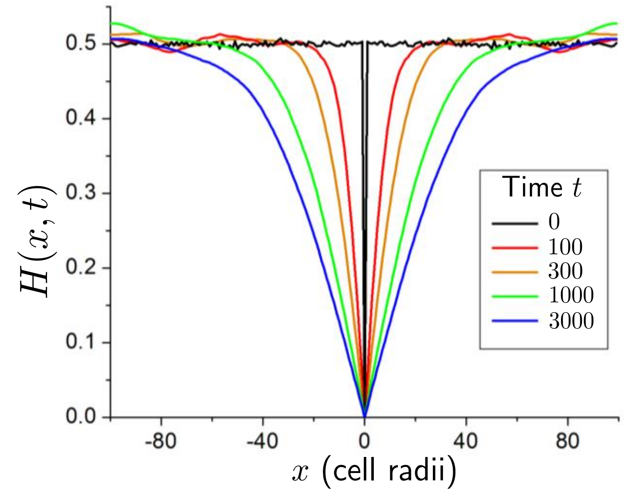
We identify a conformal time coordinate: $\tau = \eta / t^* = \dfrac{t/t^*}{1 + t/t^*}$ with $t^* = \dfrac{R_0}{v}$

The neutral case $(s = \mu_f = \mu_b = 0)$

Radial:

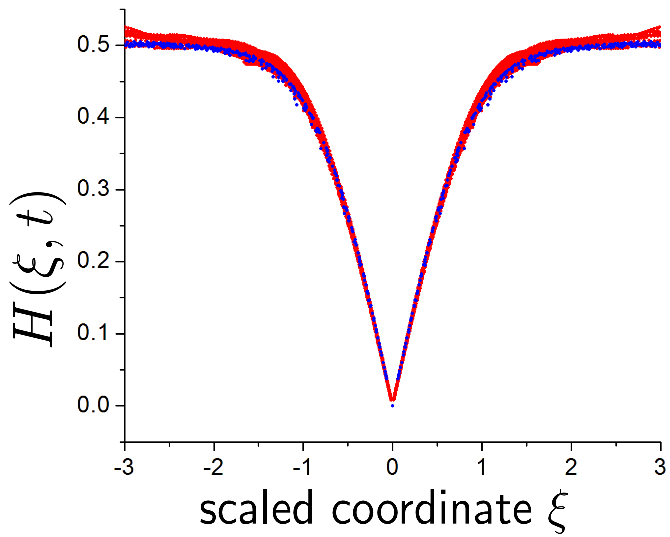


Linear:



Collapsed:

$$\xi = \sqrt{\frac{R_0 + vt}{D_r R_0 t}}\,\phi$$



$$\xi = \sqrt{\frac{1}{D_l t}}\,x$$

Exact solution:

$$H(\xi) = H_0 \,\mathrm{erf}\left|\frac{\xi}{2\sqrt{2}}\right|$$

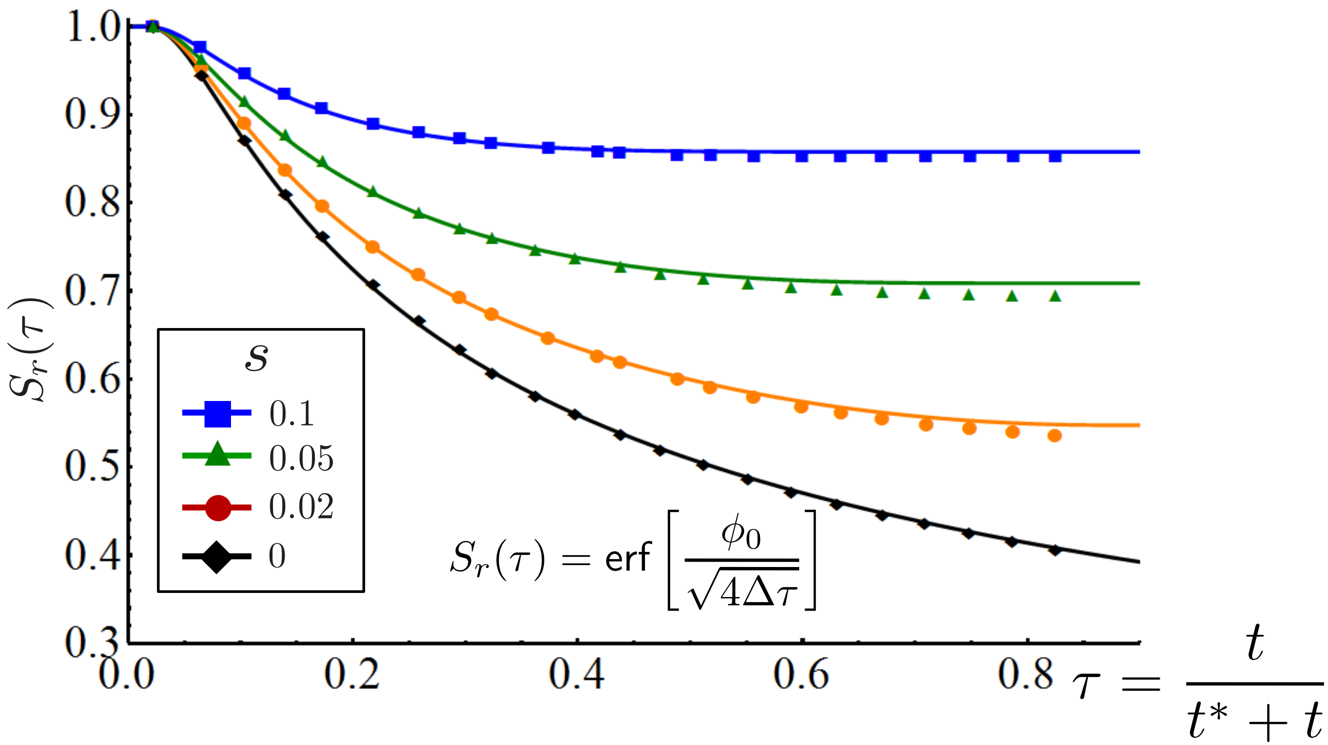
Effective lattice spacing:

$$D_r \approx (2.6)^2 D_l \propto a^2$$

Survival probability without mutations

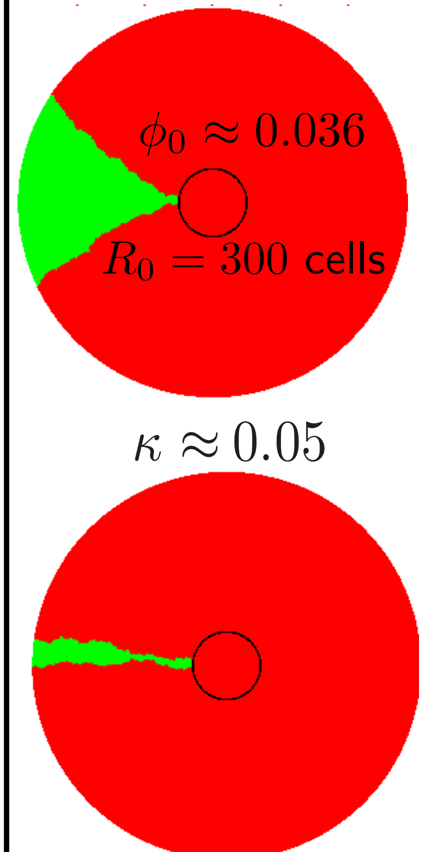
Treating sector boundaries as random walks, we can find the probability $p(\phi,\tau)$ of observing a sector size ϕ:

$$\begin{cases} \partial_\tau p(\phi,\tau) = \left[\Delta \partial_\phi^2 - \frac{w}{1-\tau}\,\partial_\phi\right] p(\phi,\tau) \\ S_r(\tau) = 1 - \Delta \int_0^\tau \mathrm{d}\tau' \, \left[\partial_\phi p(\phi,\tau')\right]\big|_{\phi=0} \end{cases} \qquad \begin{cases} w \approx \gamma\,\frac{as}{v\tau_g} \\ \Delta \approx \frac{a^2}{R_0 v \tau_g} \end{cases}$$



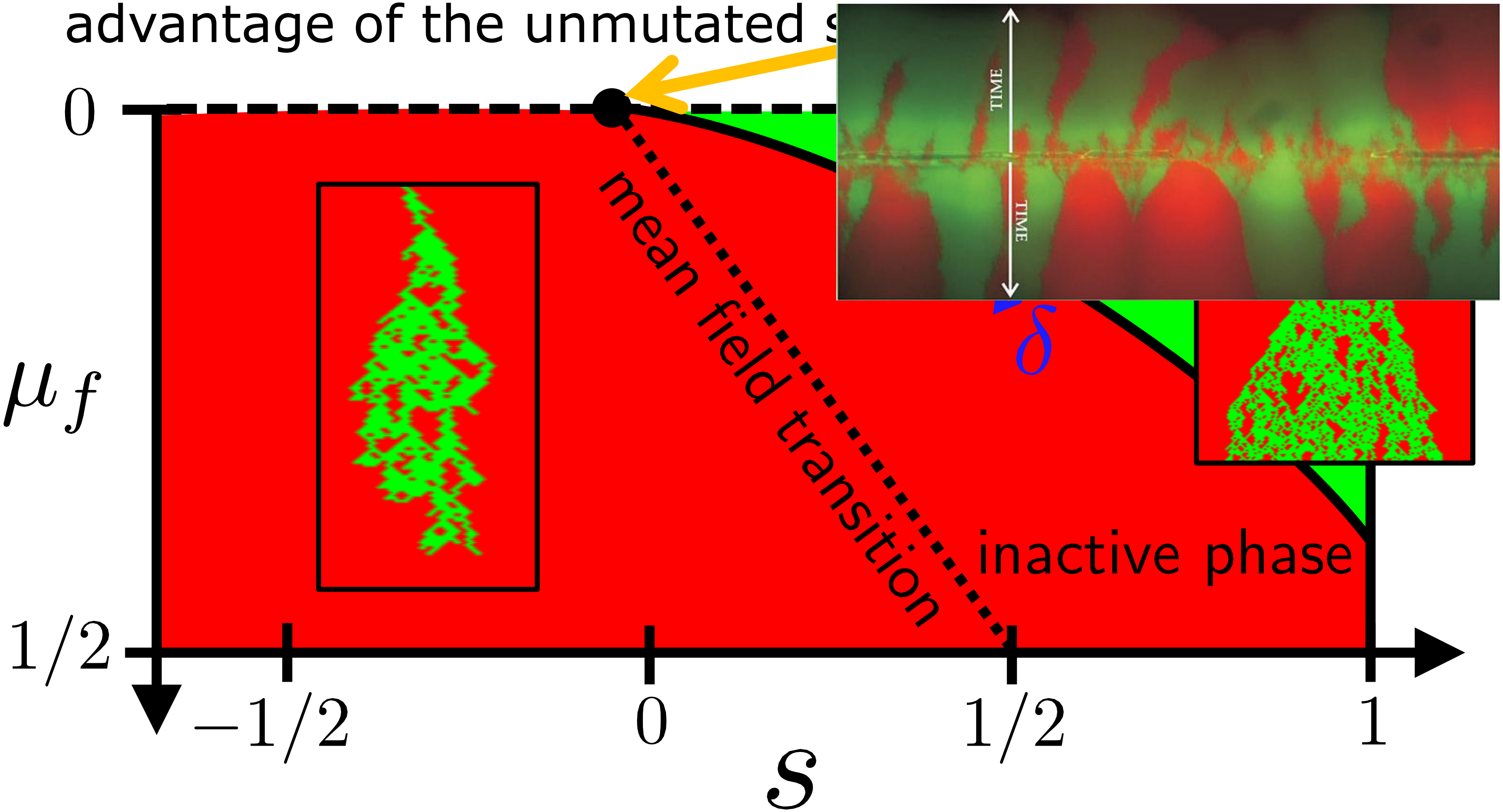
key parameter:

$$\kappa = \frac{w}{\sqrt{2\Delta}} \approx 2.4$$



Directed percolation phase transition

The deleterious mutation rate balances the selective advantage of the unmutated s



Experiment photos from: O Hallatshek and DR Nelson, Physics Today July 2009 p. 44

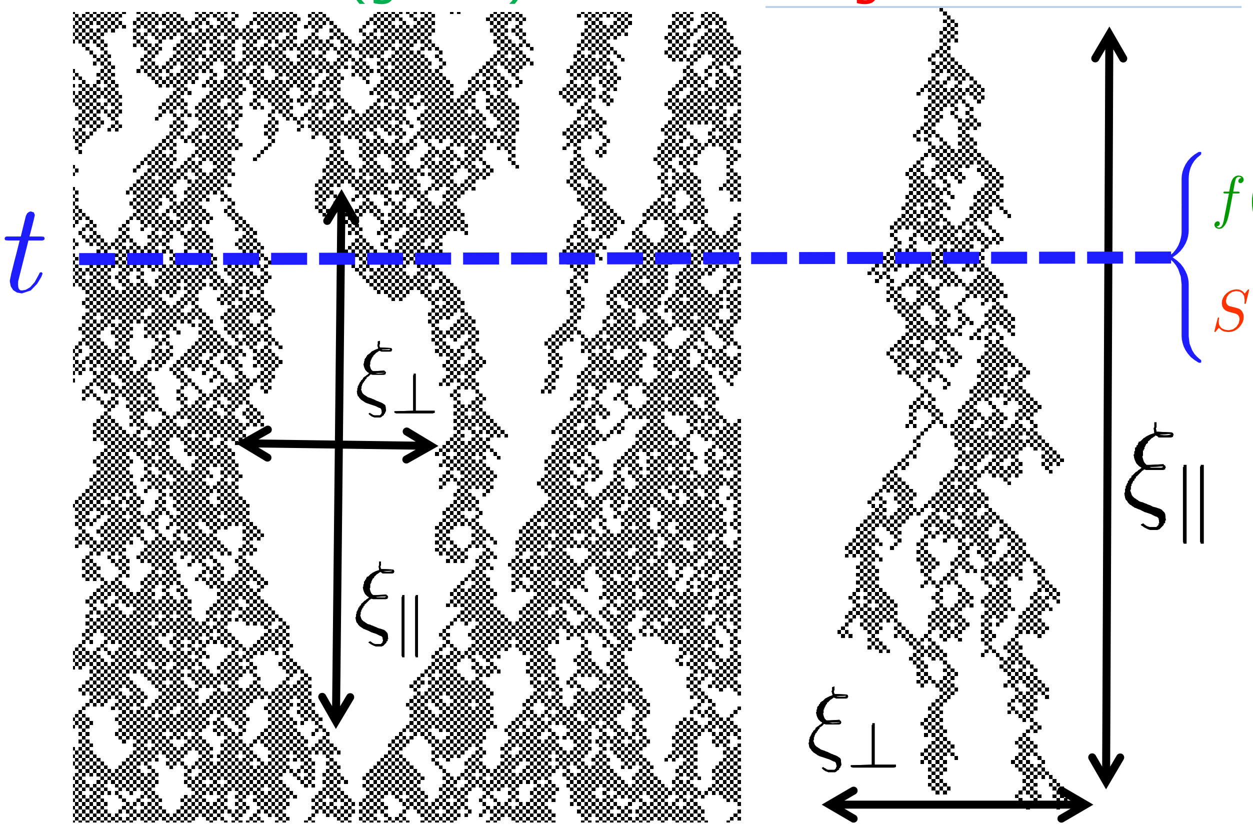
Critical exponents

Absorbing phase transitions generally have four independent critical exponents

Two typical initial conditions:
all active (green)   single seed

$$\xi_\perp \sim |\delta|^{-\nu_\perp}$$

$$\xi_\parallel \sim |\delta|^{-\nu_\parallel}$$



$f(t)$ fraction of active cells

$S(t)$ survival probability

$t \to \infty$:

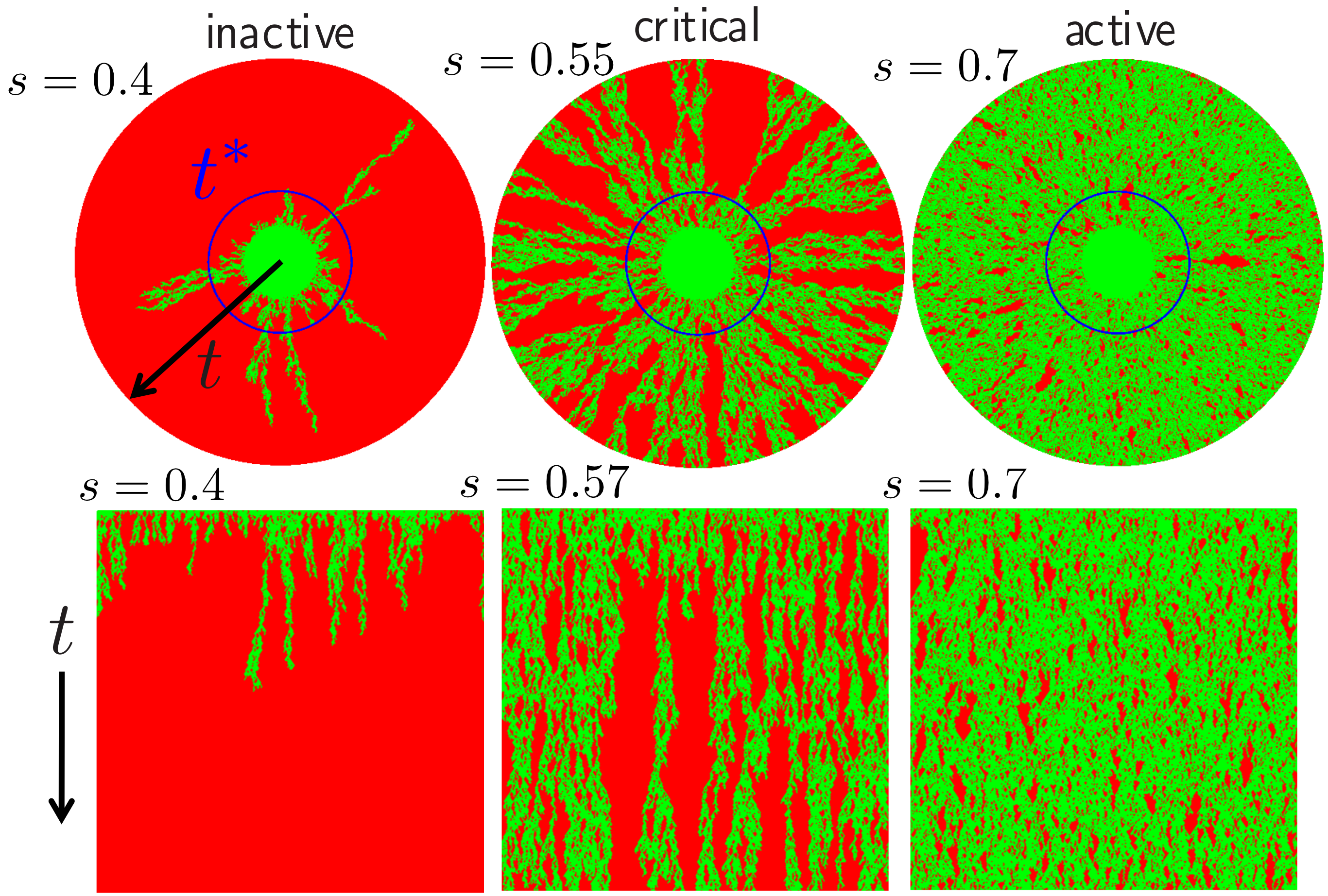
$$f_\infty \sim \delta^{-\beta}$$

$$S_\infty \sim \delta^{-\beta'}$$

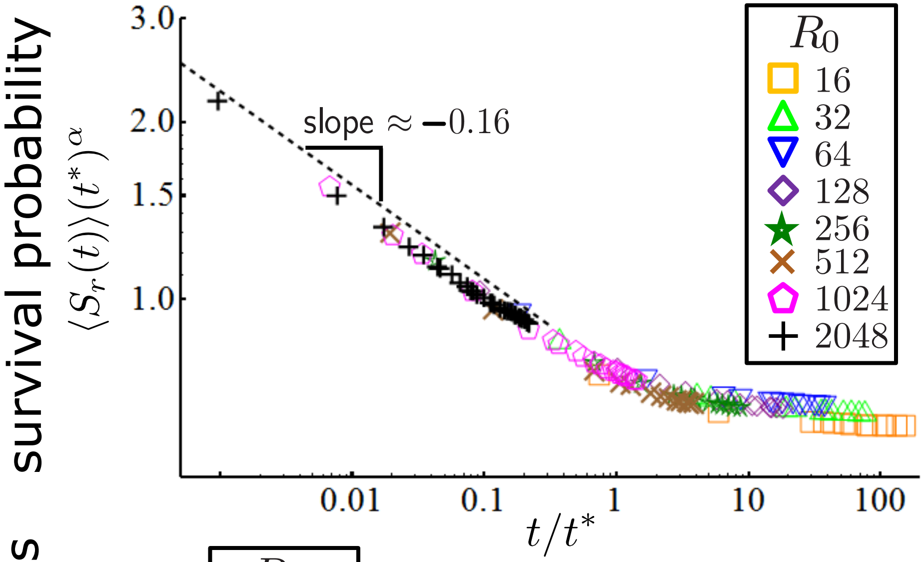
Regular versus inflationary DP

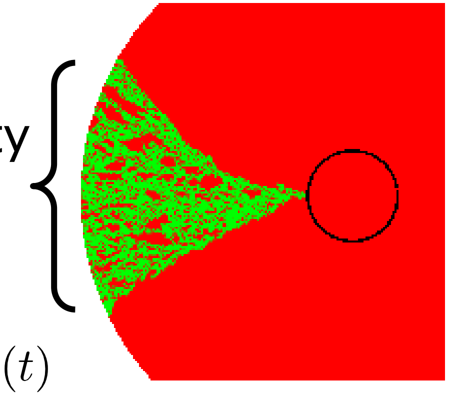
Inflation takes over after a crossover time: $t^* = R_0/v$

For a fixed $\mu_f = 0.1$:



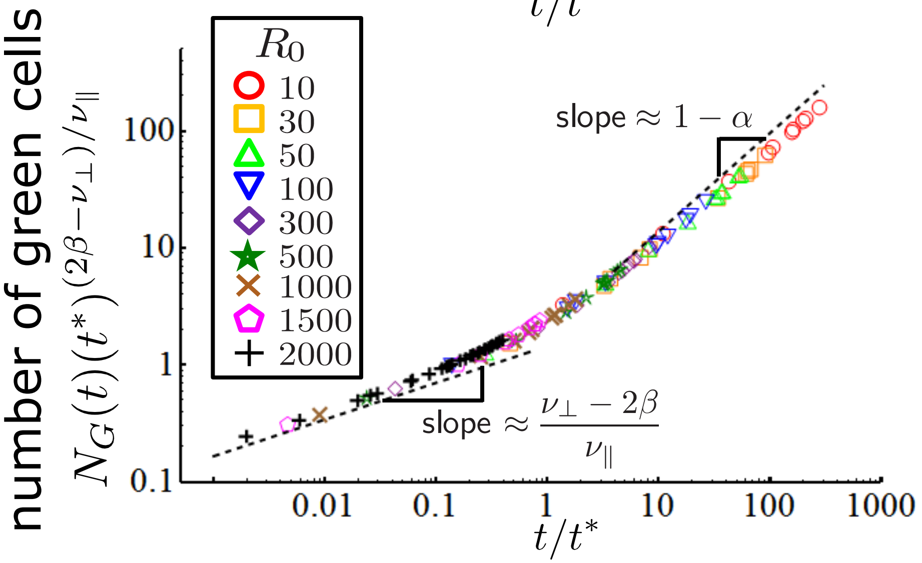
Inflationary single seed scaling





survival probability of a sector: $\langle S_r(t)\rangle$

number of green cells in sector: $N_G(t)$

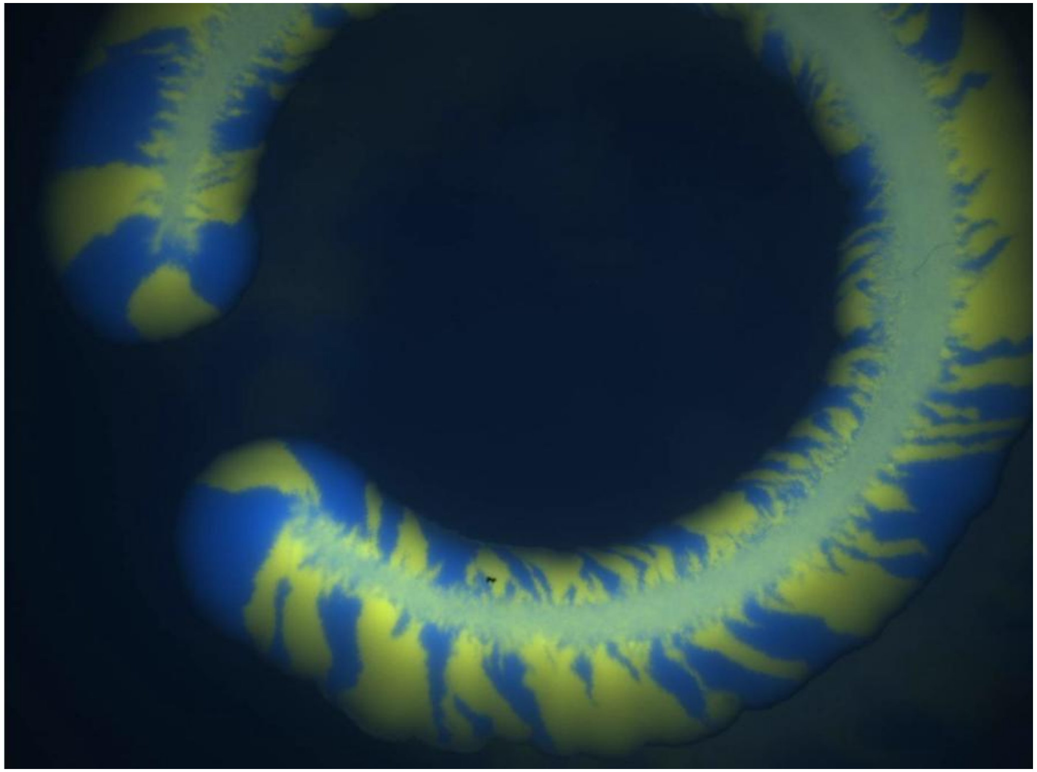


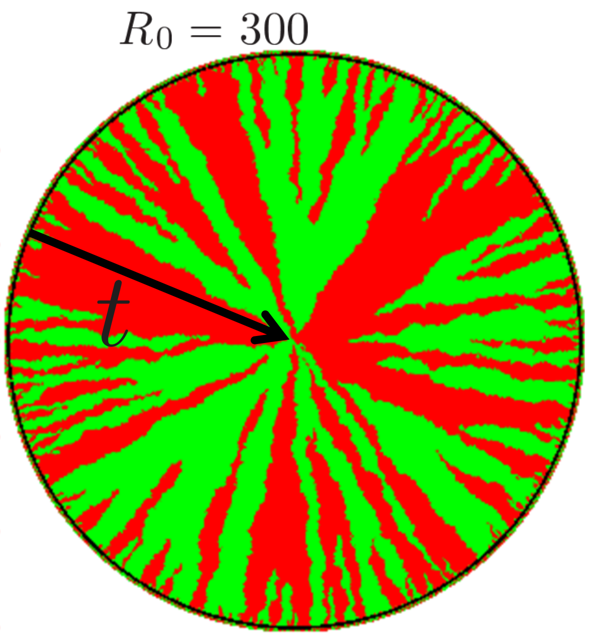
After inflation takes over, surviving sectors will have fixed angular sizes $\Delta\phi$ so that

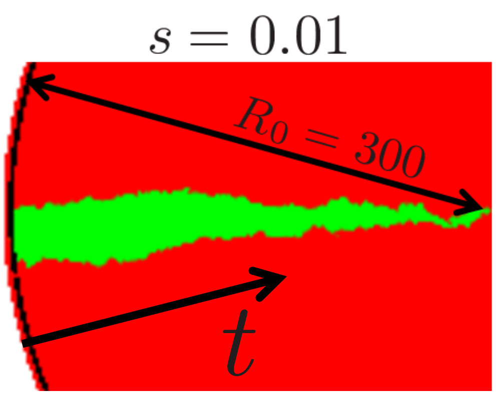
$$N_G(t \gg t_*) \sim (\Delta\phi) R(t)\rho(t)$$
$$\sim \Delta\phi (vt) t^{-\alpha}$$

Range expansions with deflation

Bacterial inoculation on Petri dish
using the rim of a test tube:

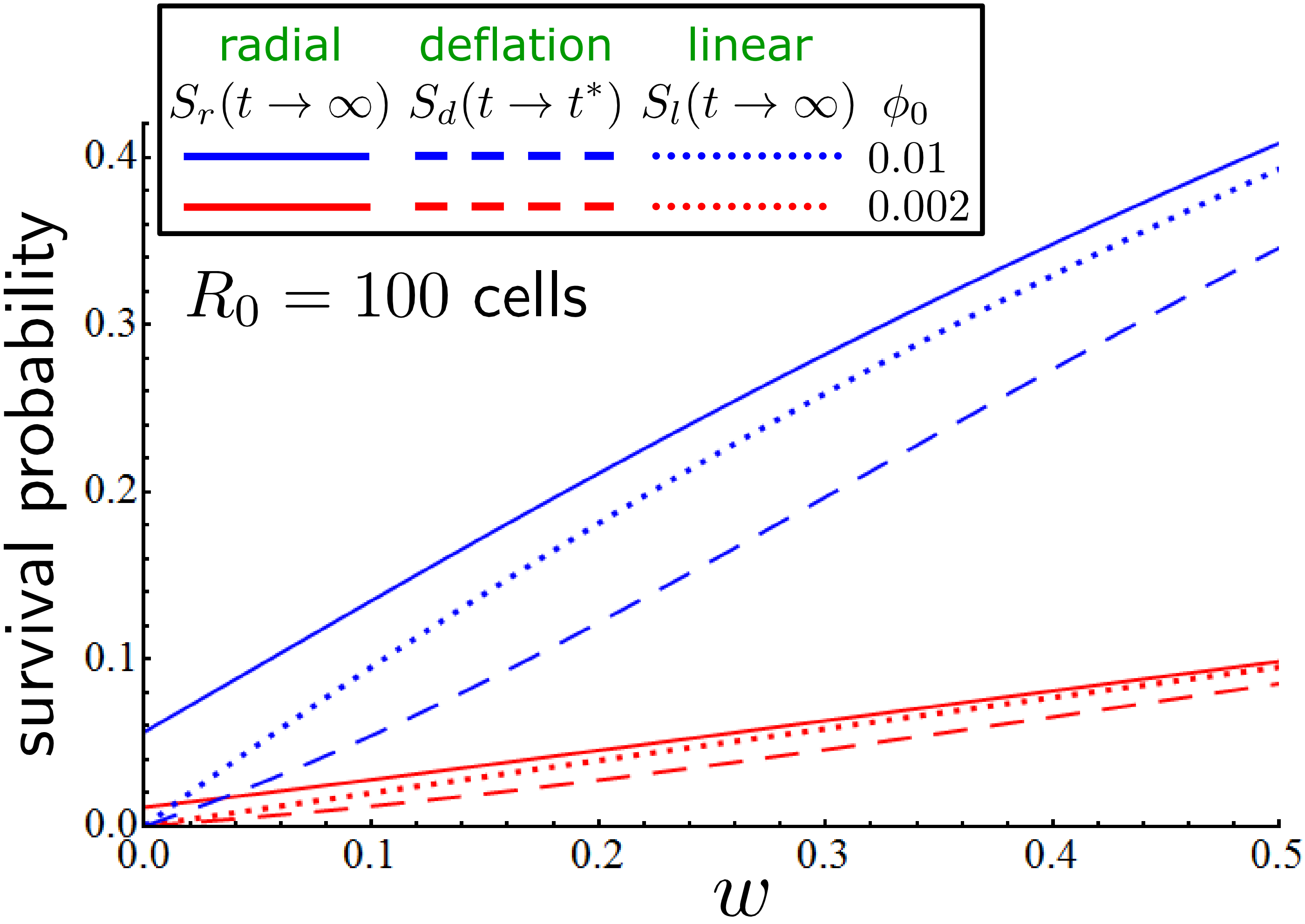


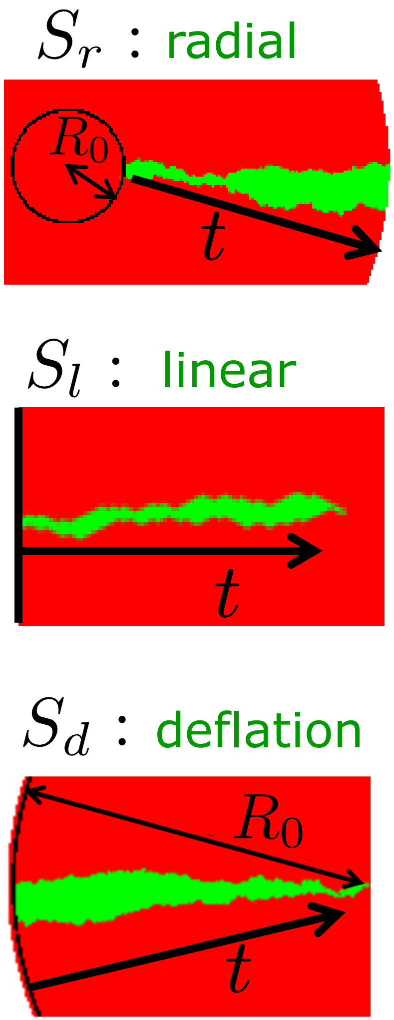




(see MOL, K. Korolev, D. R. Nelson PRE **87**, 012103 (2013))

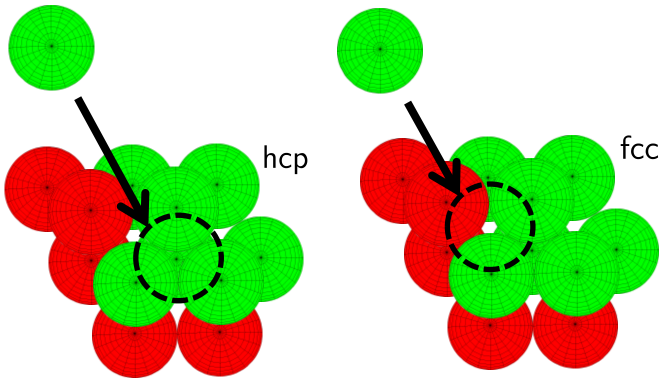
Comparison of survival probabilities





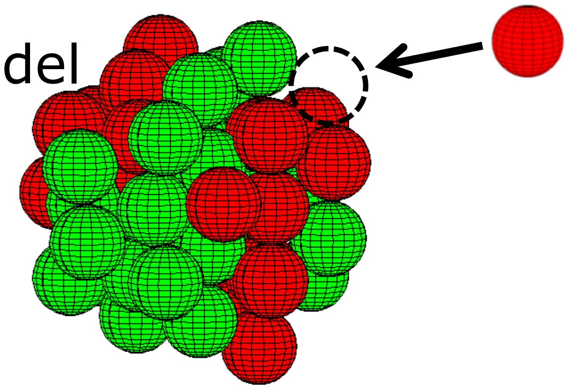
Population genetics in three dimensions

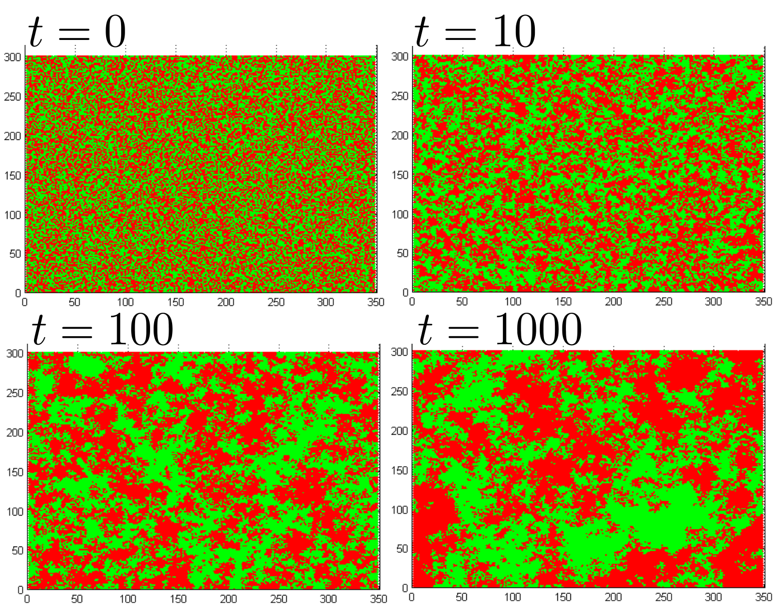
Linear:



Radial:

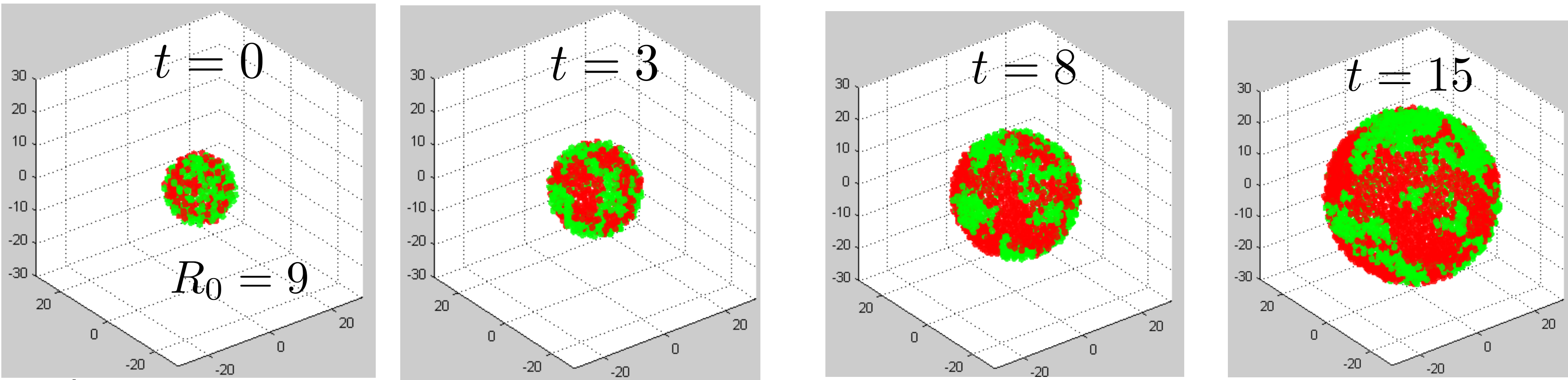
Bennett model cluster

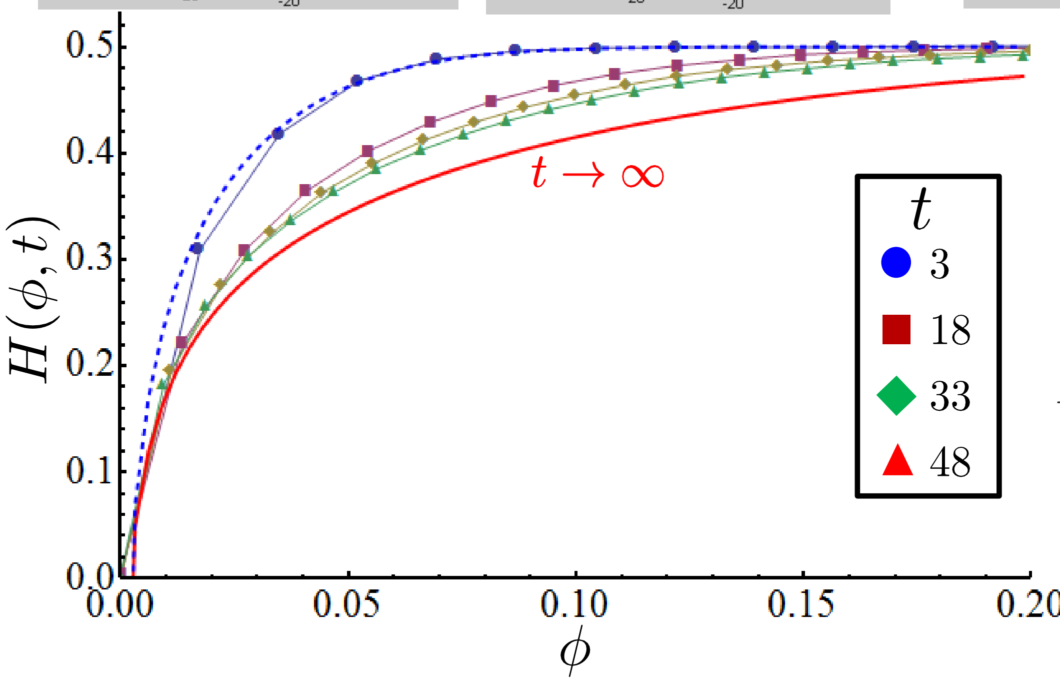




- Logarithmic coarsening of domains $\xi(t) \sim \log t$
- Domains have no line tension ("cluster dilution")
- Boundaries are no longer simple random walks

Spherical range expansions (neutral case)





$$\begin{cases} \partial_t H(\mathbf{r}, t) = 2D\nabla^2 H(\mathbf{r}, t) \\ H(|\mathbf{r}| = a \to 0, t) = 0 \end{cases}$$

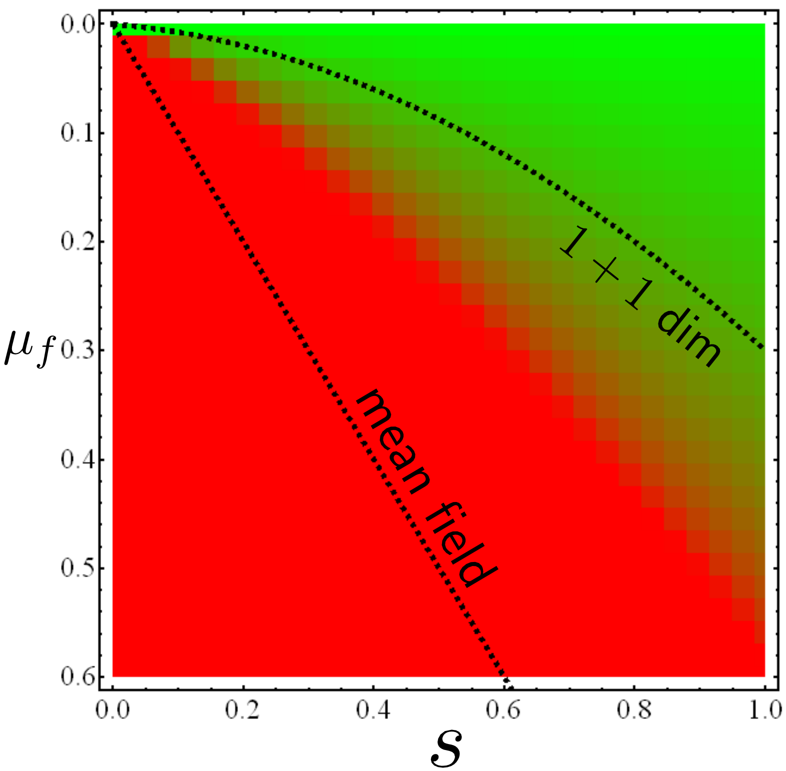
cell size a

$$H(\phi, t) \approx \frac{\ln(R_0 \phi / a)}{2 \ln\left(2\sqrt{2Dt^*\tau}\, e^{-\gamma_E} / a\right)}$$

conformal time: $\tau = \dfrac{t/t^*}{1 + t/t^*}$

Inflationary DP in 2+1 dimensions

$d = 2 + 1$ Phase Diagram



$(R_0 = 10)$ active — $s = 0.6,\ \mu_f = 0.1$

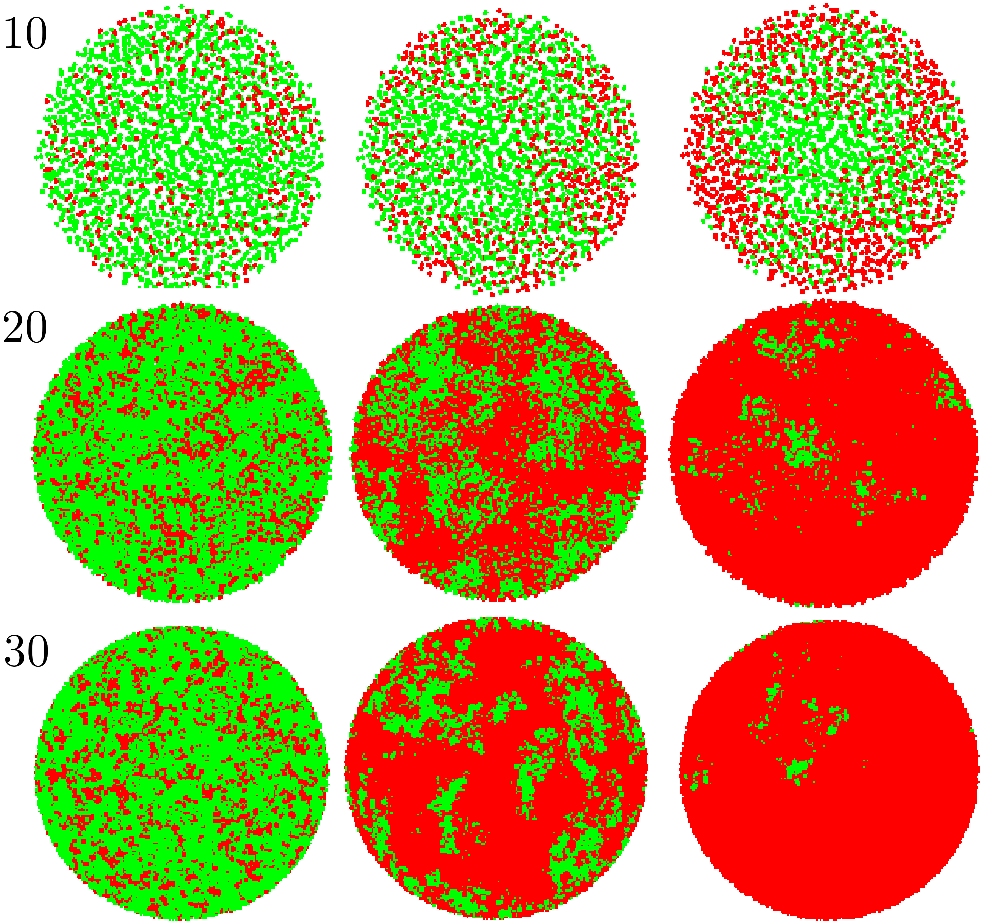
critical — $s = 0.26,\ \mu_f = 0.1$

inactive — $s = 0.3,\ \mu_f = 0.2$

$t = 10$

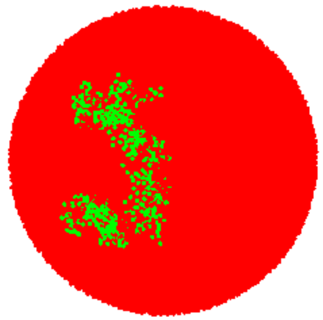
$t = 20$

$t = 30$

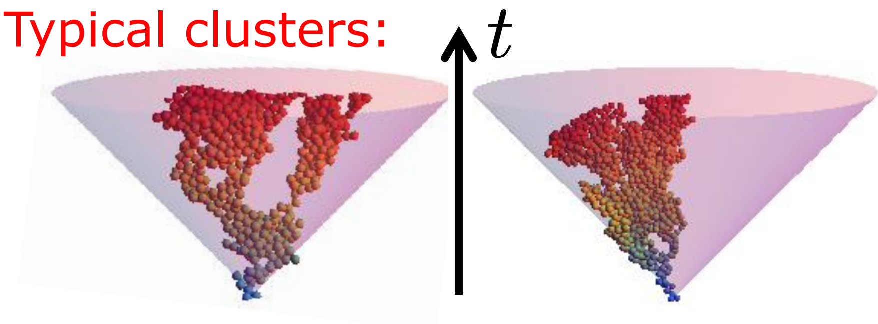


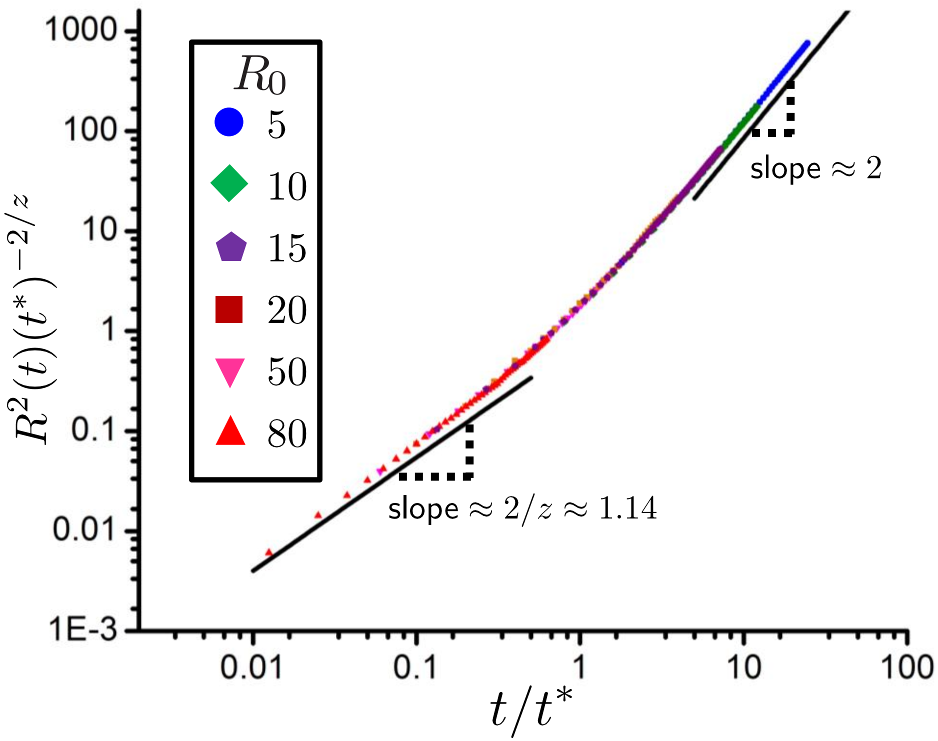
Single seed scaling at criticality

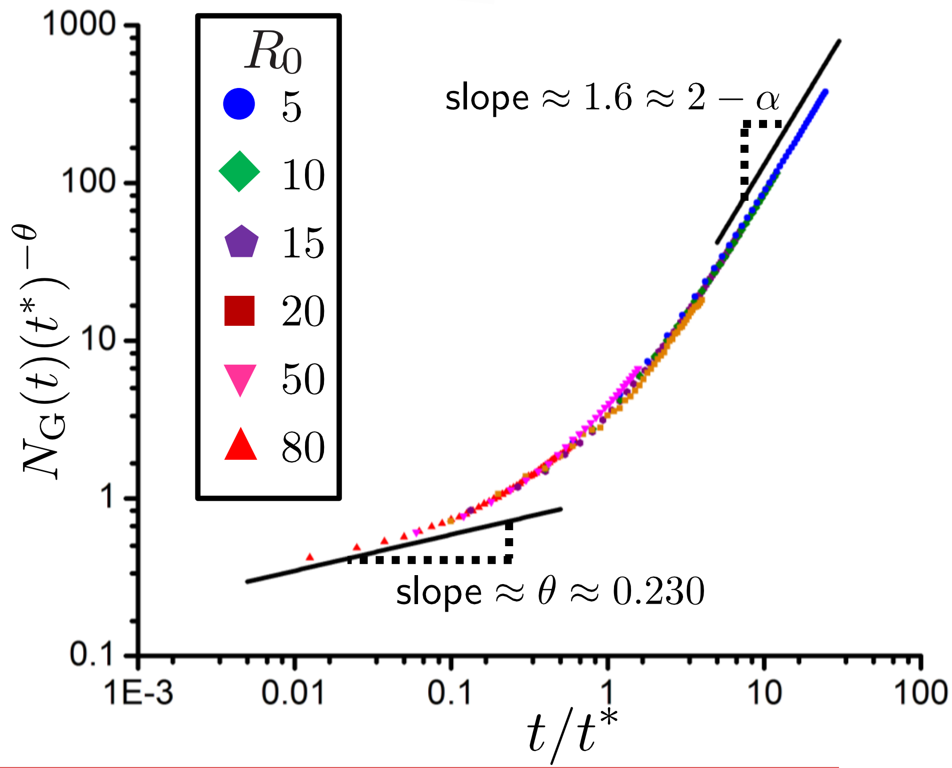
$$\begin{cases} R_0 = 10 \text{ cells} \\ t = 20 \text{ gen.} \end{cases}$$



Typical clusters:

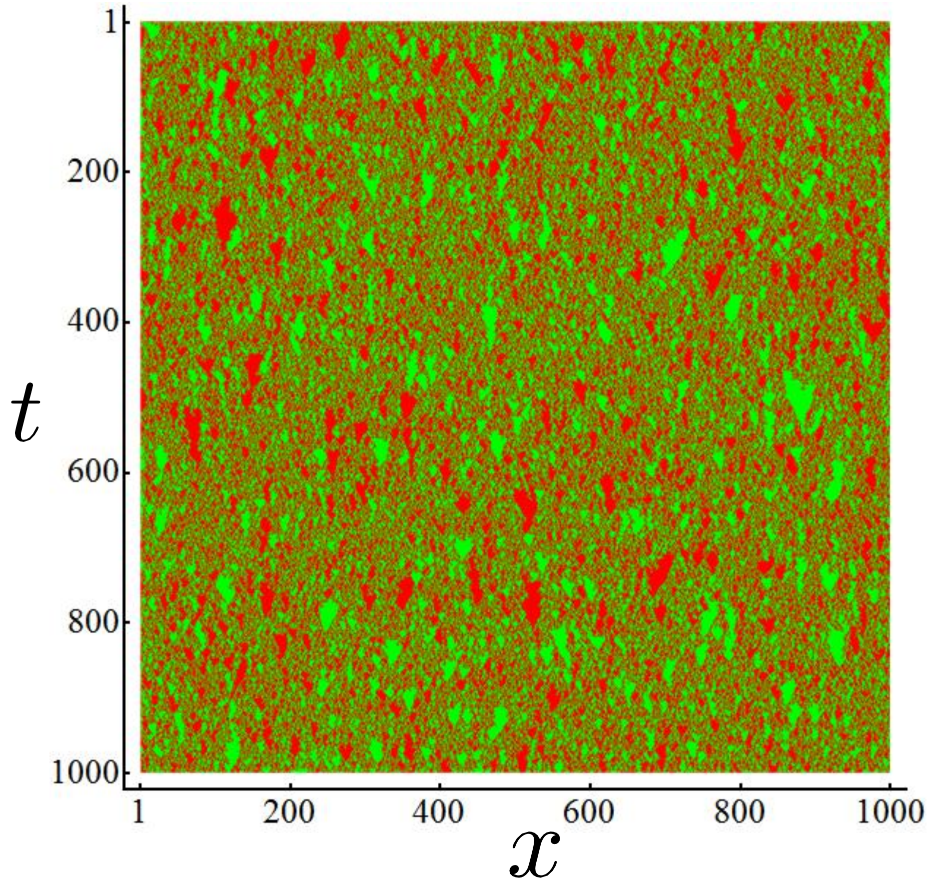






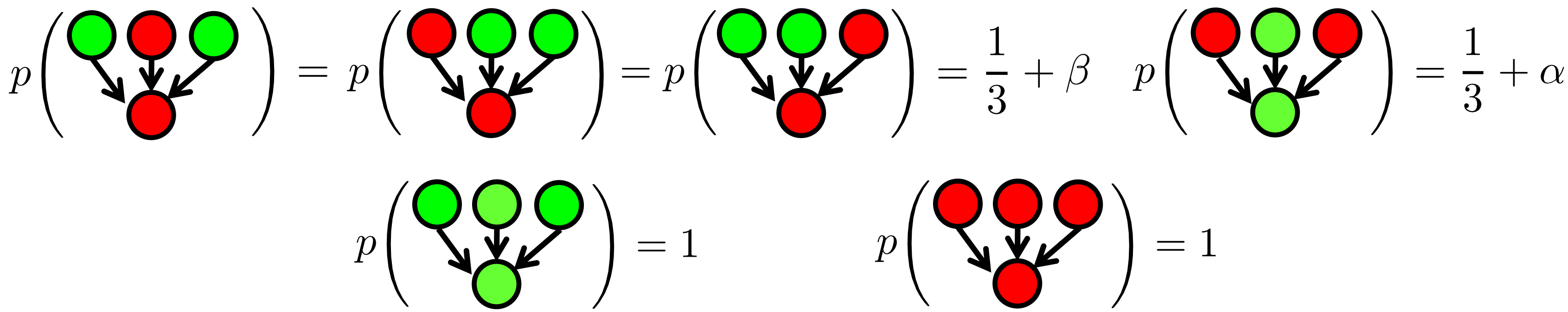
Range Expansions With Mutualism

We are interested in range expansions of two species that grow faster when they are next to each other:



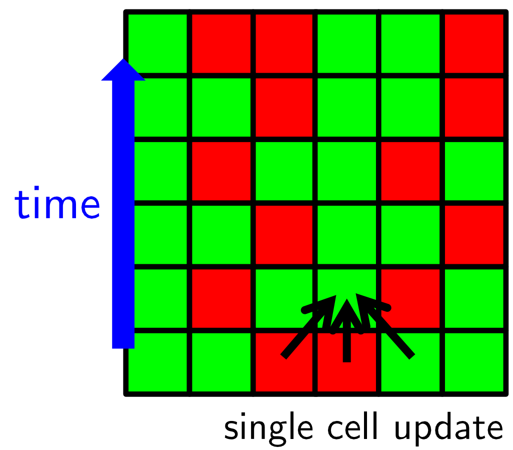
Mutualism with Flat Fronts: Update Rules

Each cell is updated based on its and its neighbor's states:

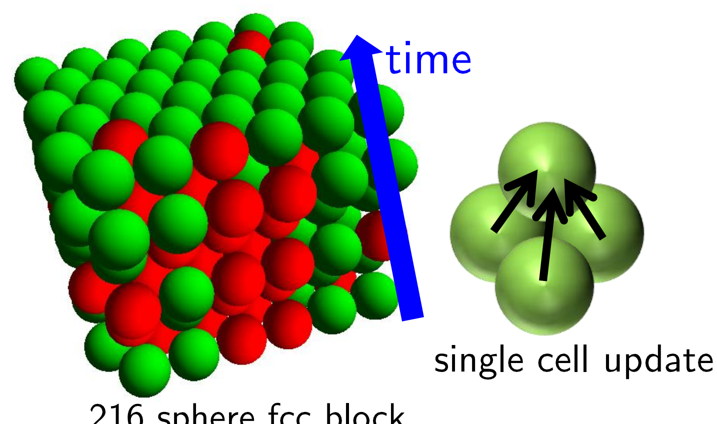


Update rules can be implemented in two or three dimensions:

$d = 1 + 1:$

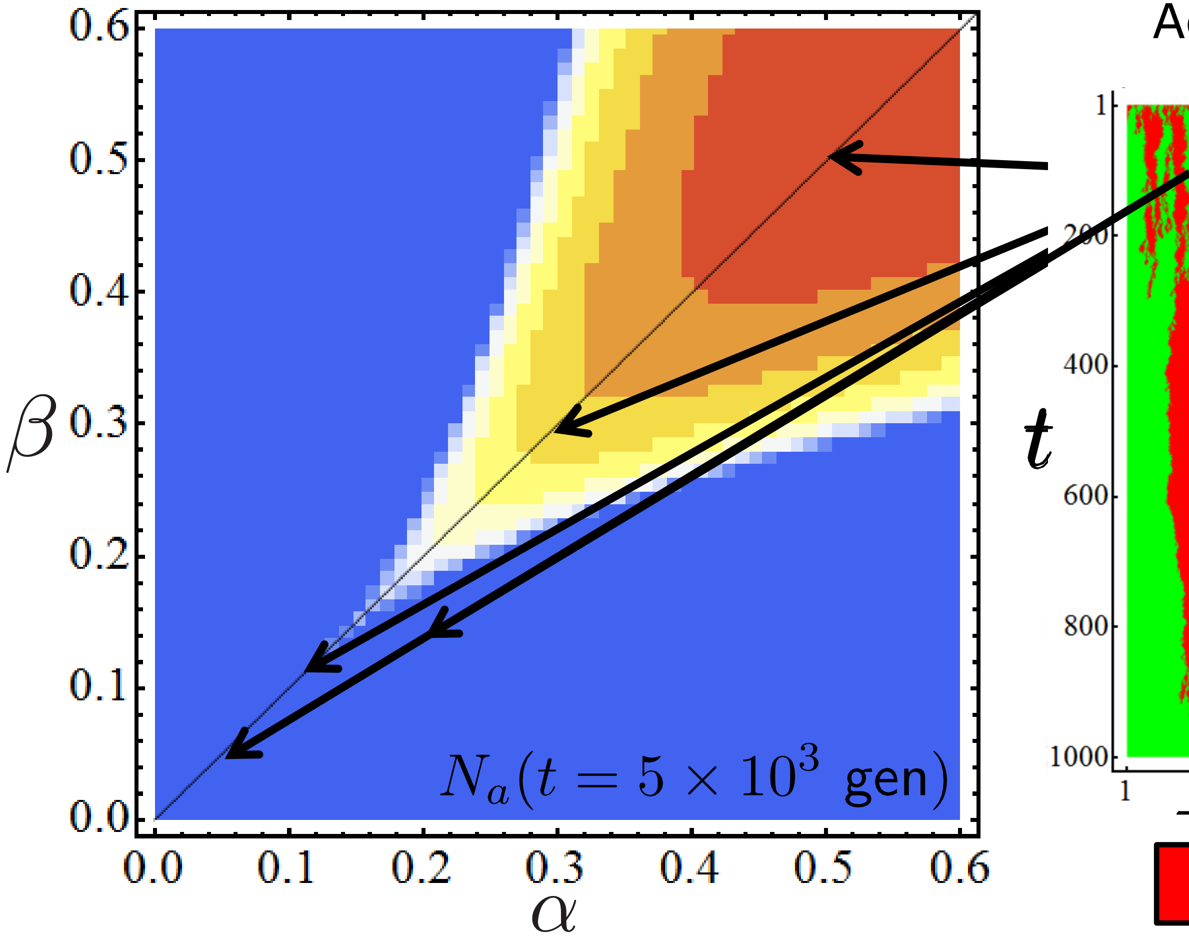


$d = 2 + 1:$

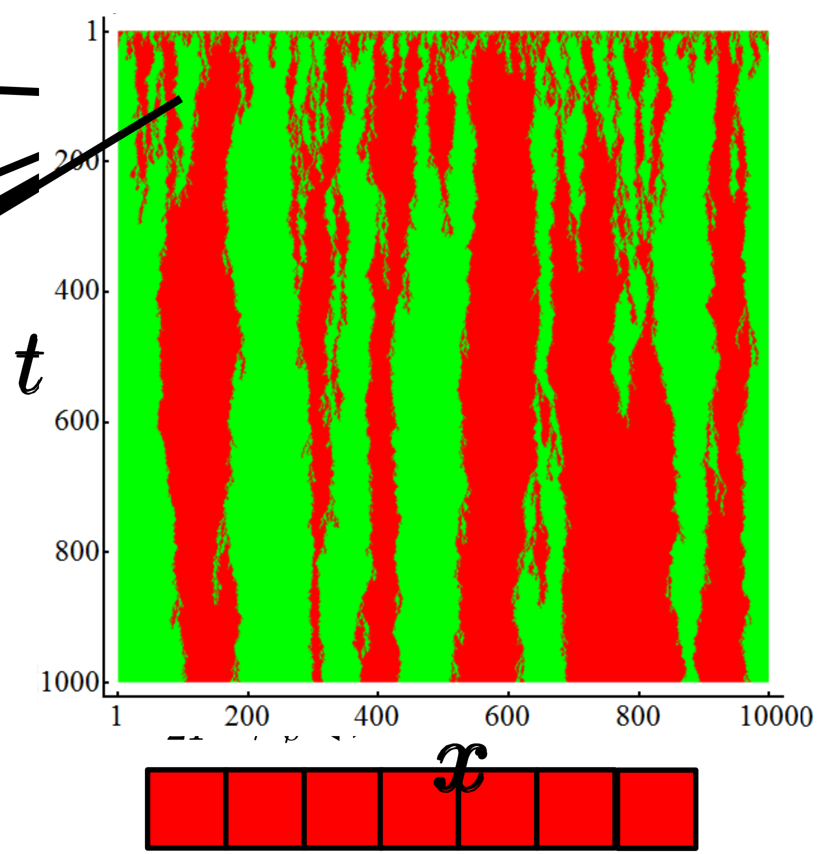


Flat Fronts: Phase Diagram for $d = 1 + 1$

Fluctuations locally fix red and green domains, preventing mixing even for certain $\alpha = \beta > 0$



Active sites marked with ★

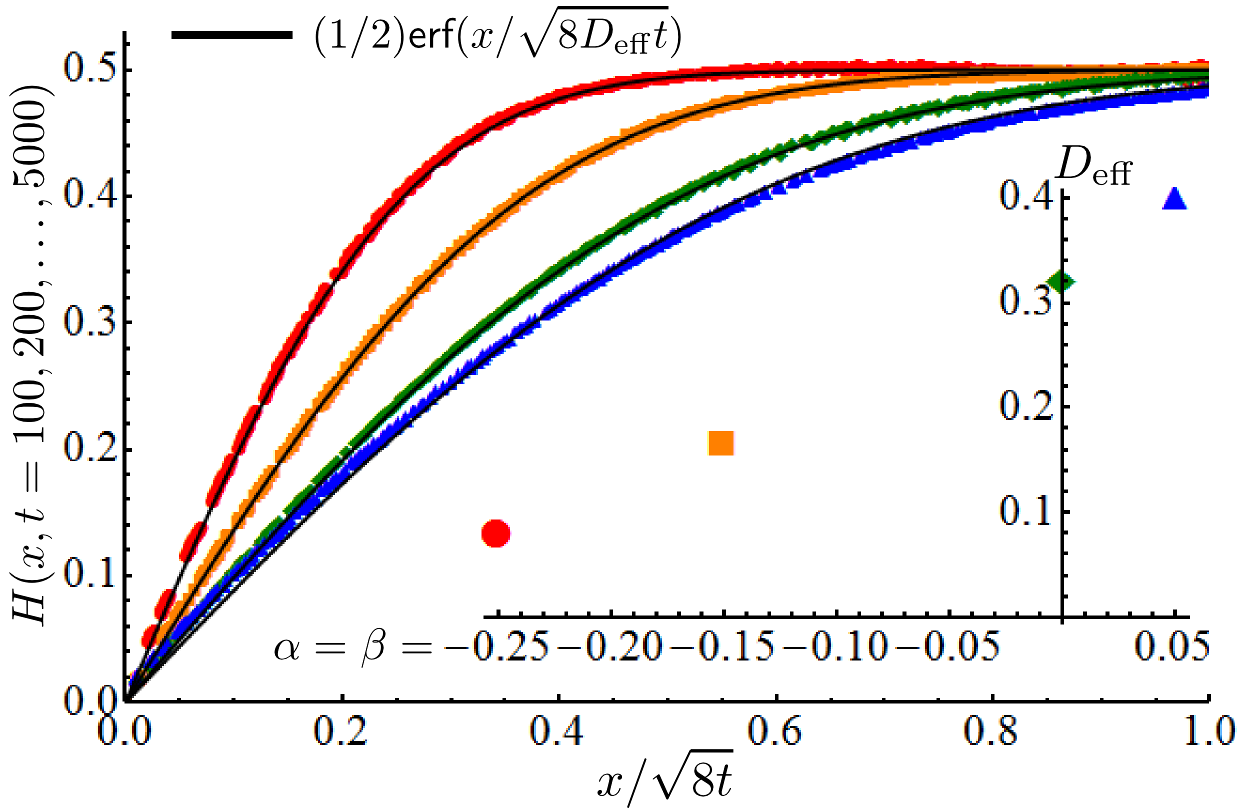


Mutualism with Flat Fronts: Heterozygosity

For compact directed percolation, we expect:

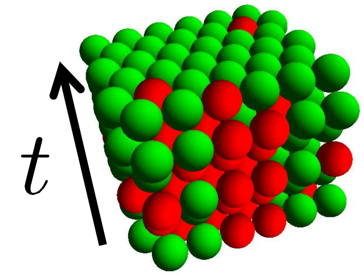
$$\partial_t H(x,t) = 2D_{\text{eff}}\, \partial_x^2 H(x,t) \quad \Rightarrow \quad H(x,t) = H_0\, \text{erf}\left(\frac{x}{\sqrt{8D_{\text{eff}}t}}\right)$$

We test this for various $\alpha = \beta < \alpha_{\text{crit}}$:

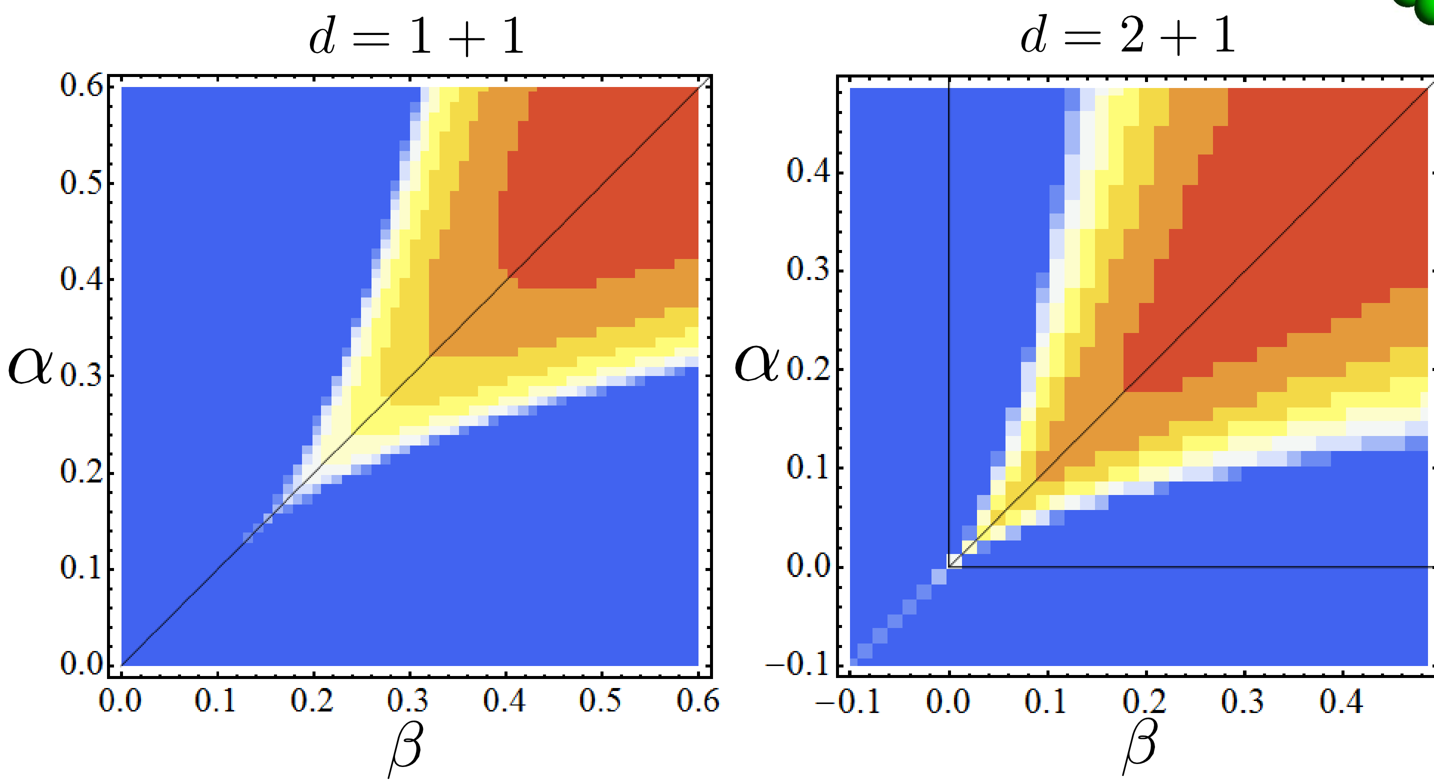


Mutualism in three dimensions

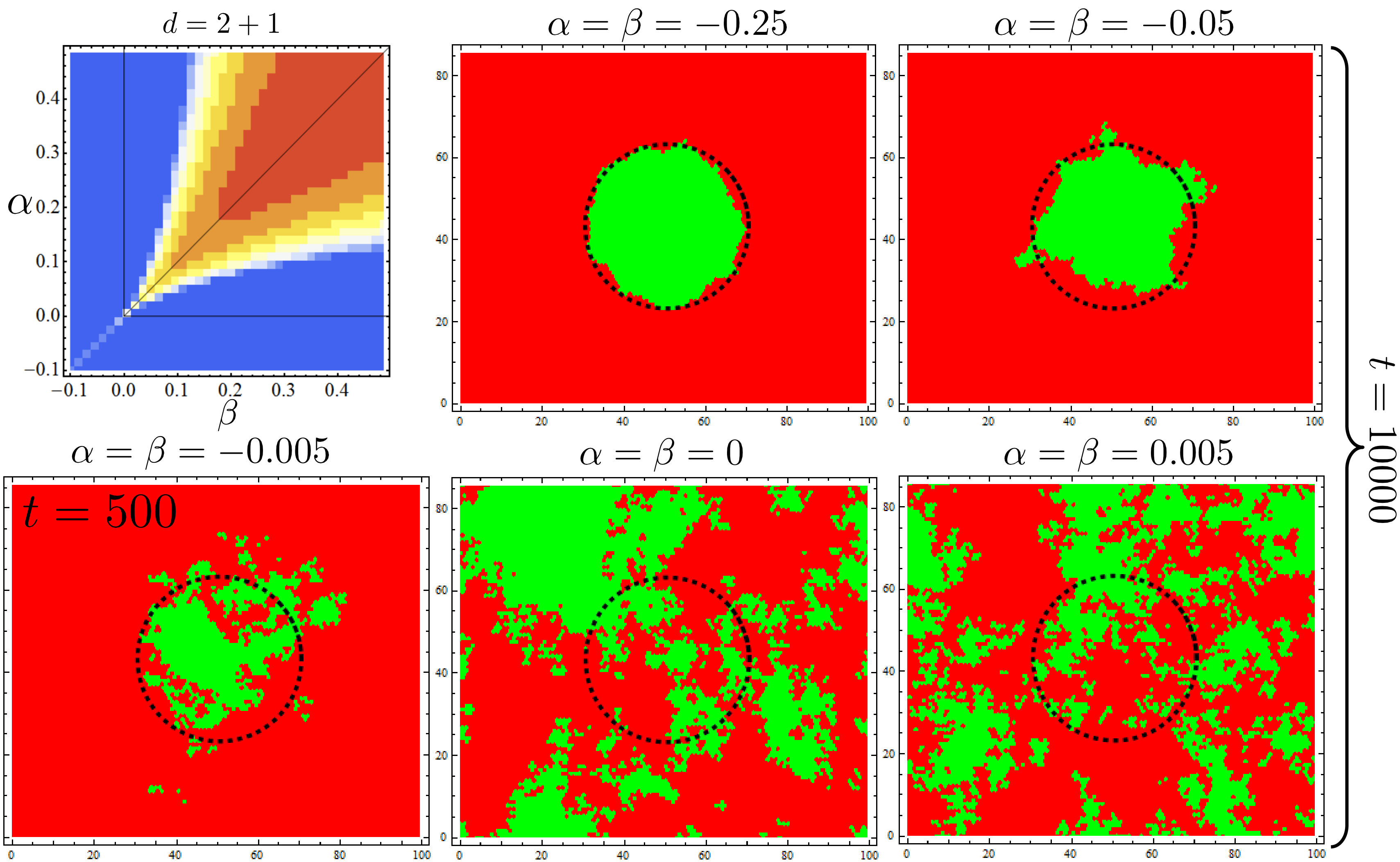
$d = 2 + 1$ simulation



In three dimensions, a mutualistic phase exists for all $\alpha = \beta > 0$



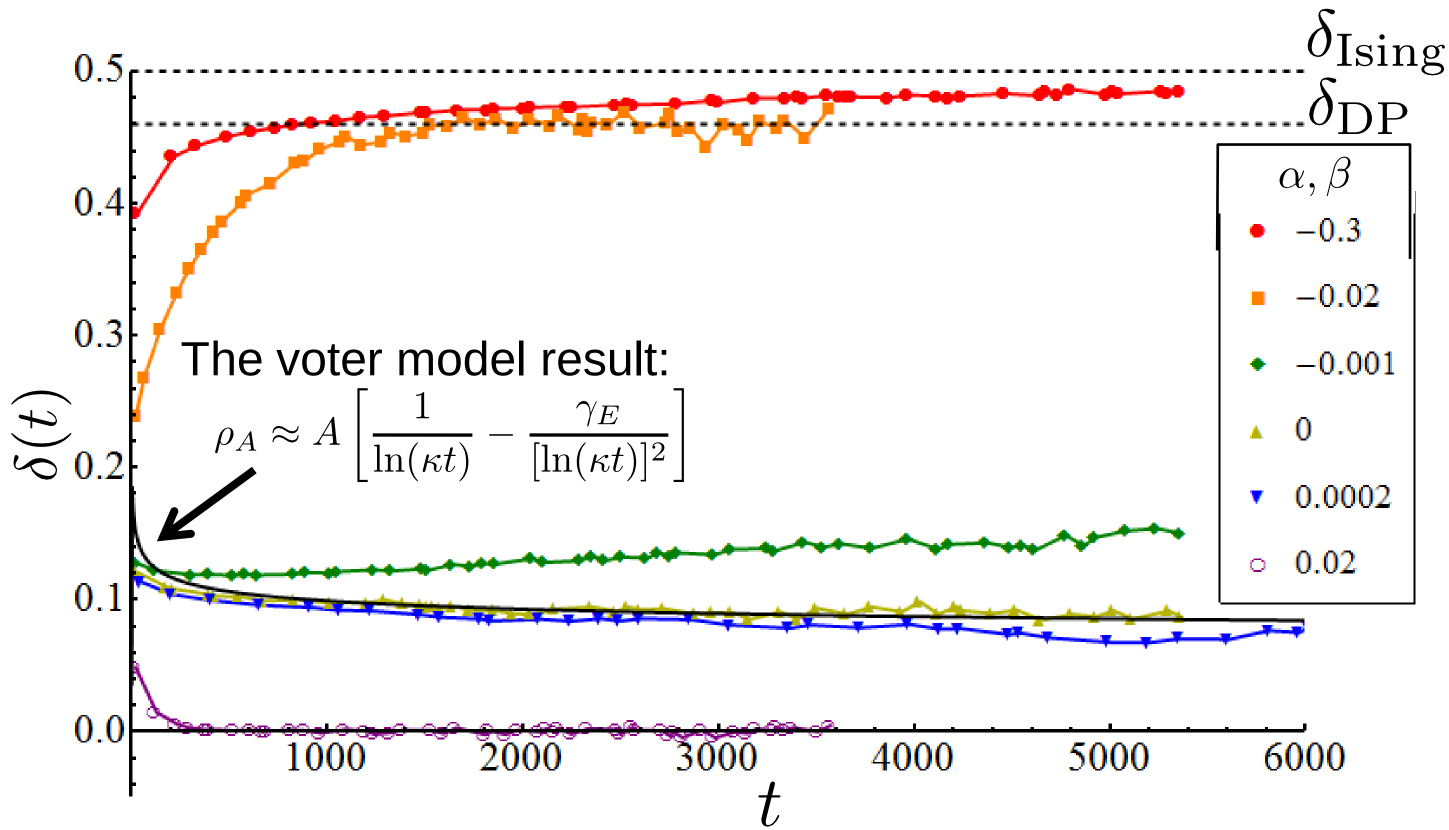
A Droplet Simulation



Interface density decay for $d = 2+1$

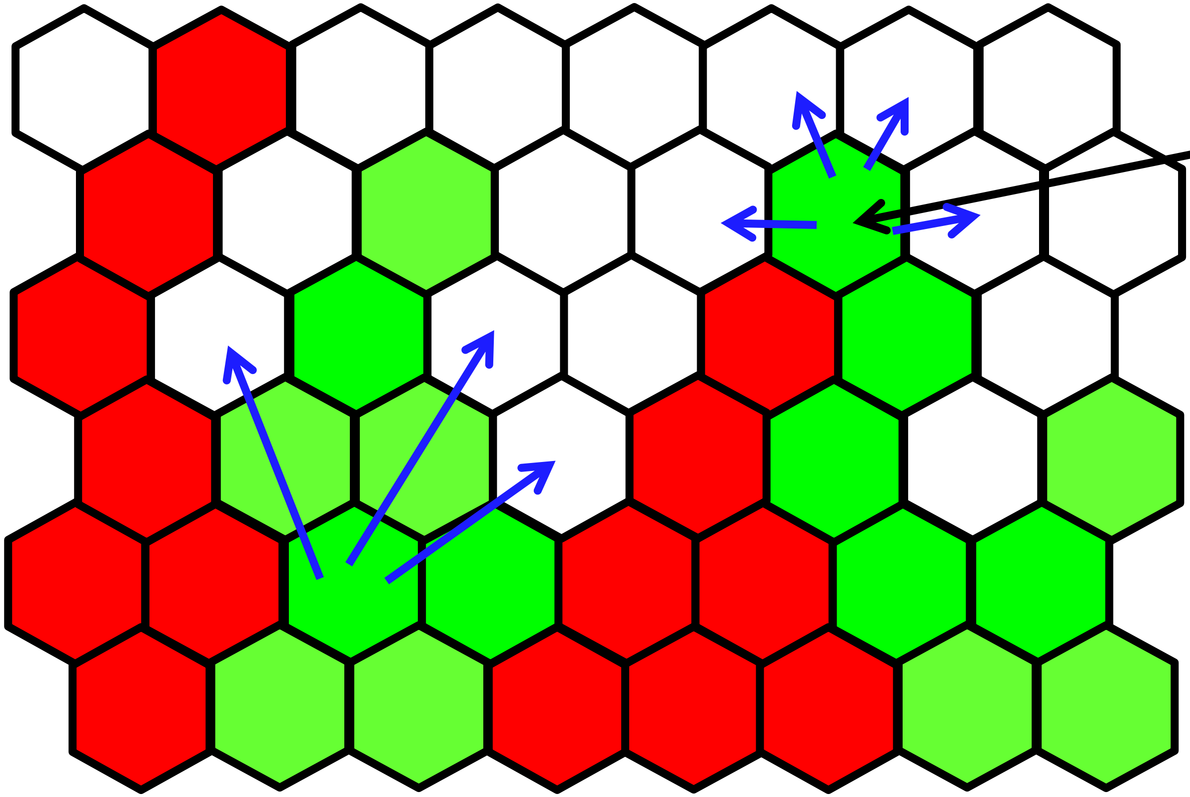
The interface density for an initially well-mixed population decays:

$$\rho(t) \sim t^{-\delta(t)} \text{ with effective exponent } \delta(t) \equiv -\ln\left[\frac{\rho(t+\Delta t)/\rho(t)}{(t+\Delta t)/t}\right]$$



Mutualism with Rough Fronts: Model

Each cell with an empty nearest or next nearest neighbor can reproduce with a certain rate. We pick one cell to reproduce at each time step.



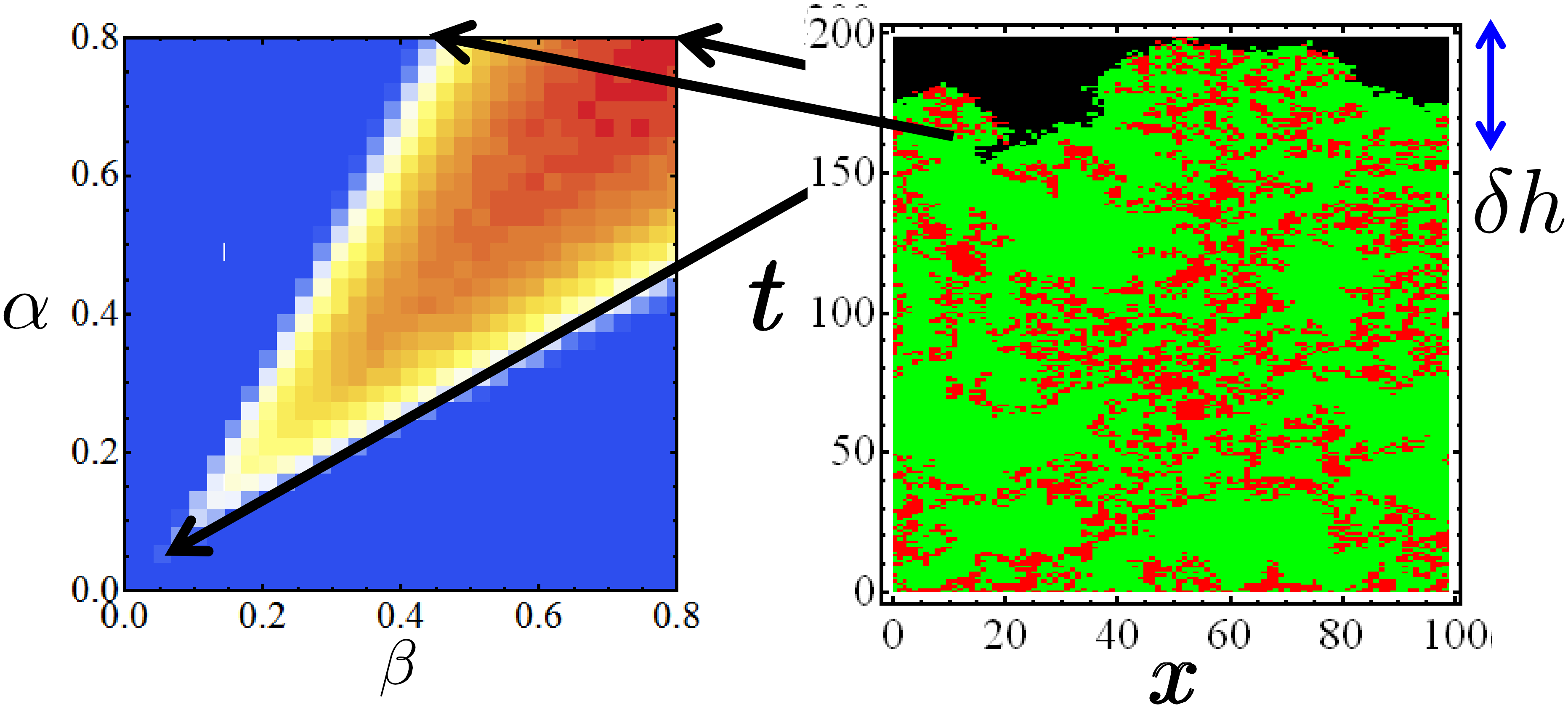
A cell has a reproduction rate:

$$b(i) = \Gamma_g + \alpha N_r(i)$$

Γ_g	base growth rate
α	mutualistic advantage
$N_r(i)$	number of neighbors of opposite color

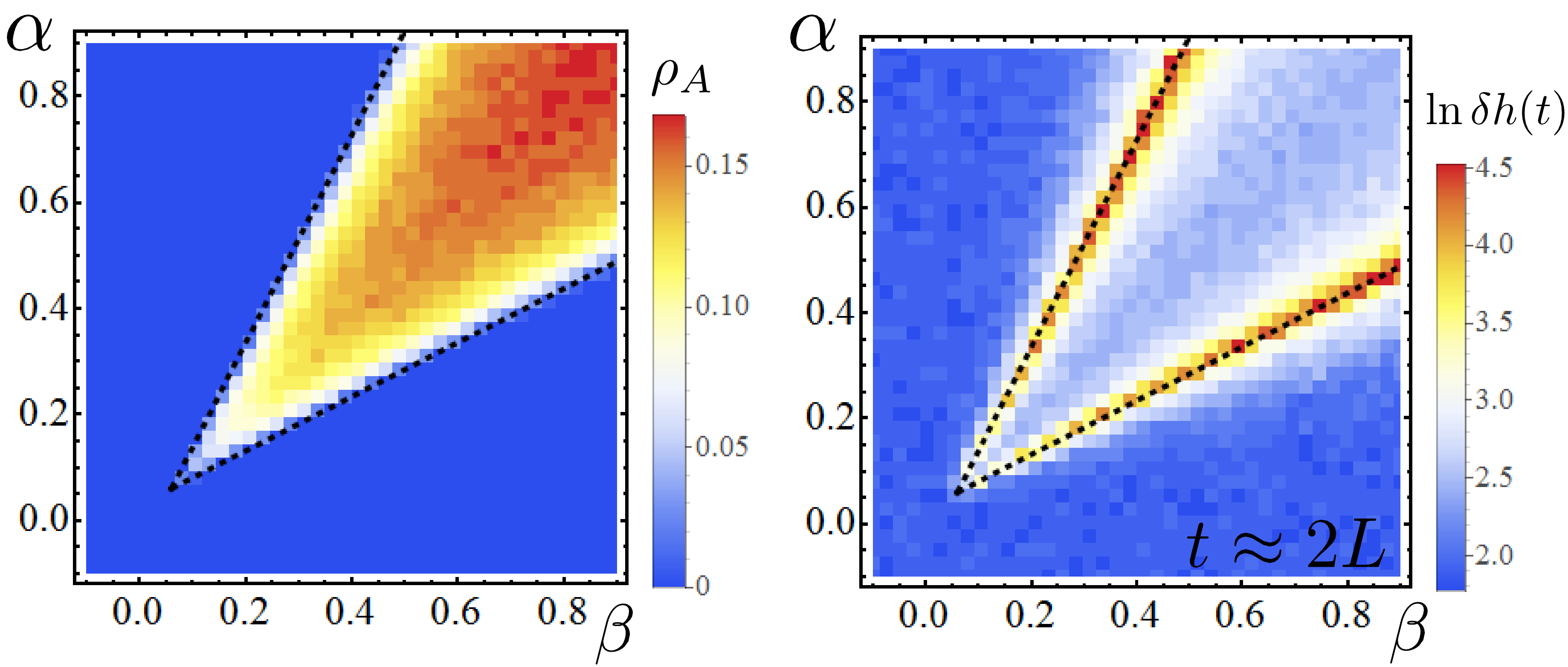
Mutualism with Rough Fronts

Rough fronts preserve the mutualistic phase. However, the dynamics and shape of the phase boundary are different.



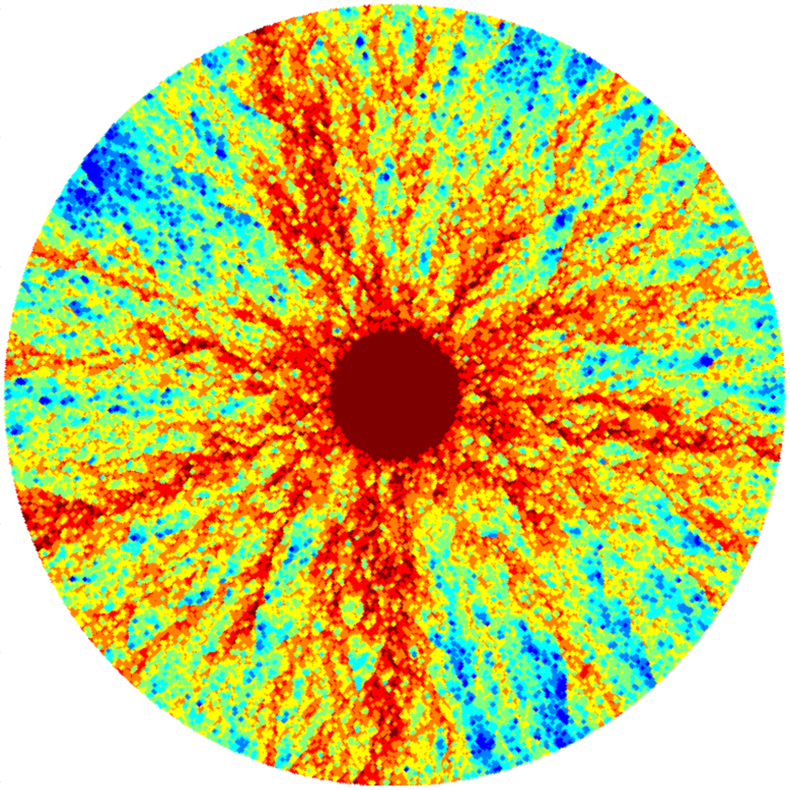
Rough Fronts: Phase Diagrams

We can track the average size of the interface fluctuations. They peak at the phase boundaries and are larger in the mutualistic regime.



Thank you!

- This is work with K. S. Korolev and D. R. Nelson
- MOL, K. Korolev, D. R. Nelson PRE **87**, 012103 (2013)

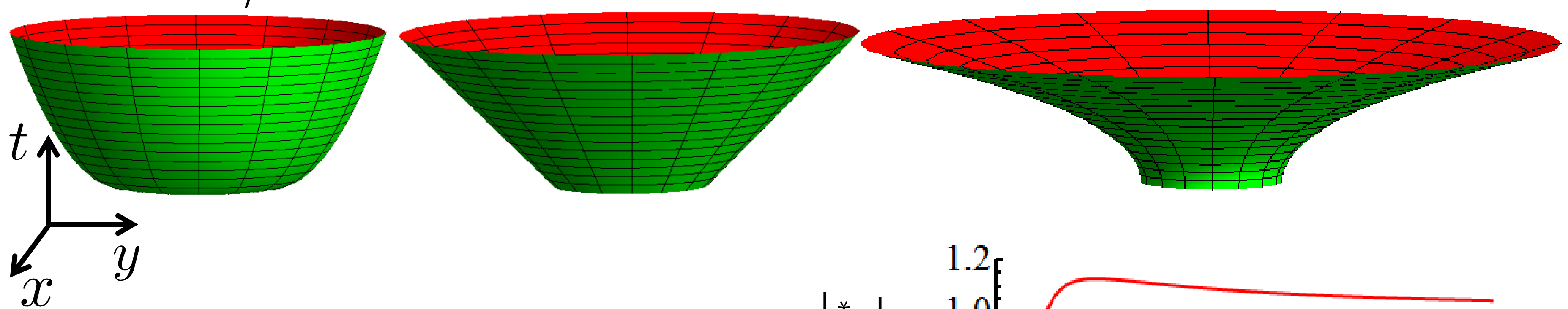


Power law range expansions (neutral case)

Range expansions can inflate with an arbitrary power law:

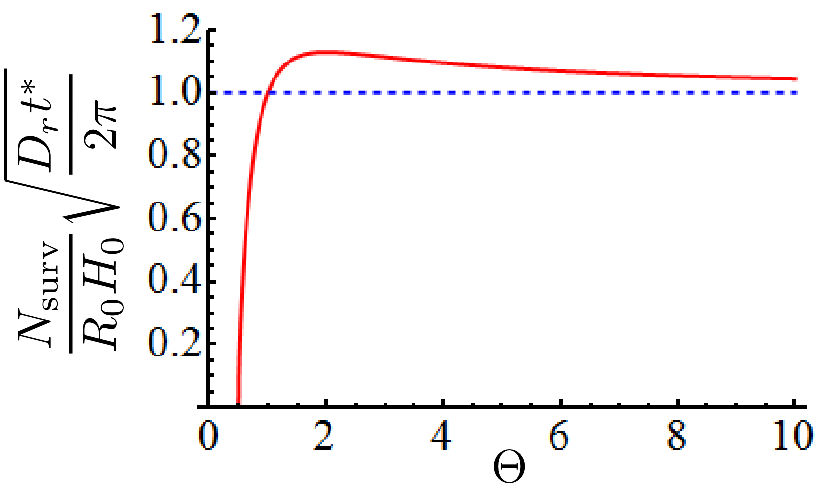
$$R(t) = R_0 \left[1 + \left(\frac{t}{t^*} \right)^{\Theta} \right]$$

$\Theta = 1/2$ $\Theta = 1$ $\Theta = 2$



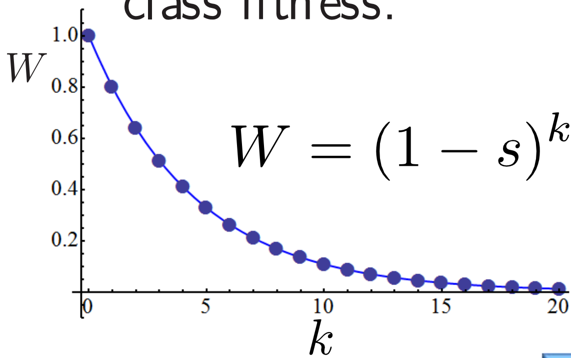
Results for neutral evolution:

$$N_{\text{surv}} = \begin{cases} 0 & \Theta \leq 1/2 \\ R_0 H_0 \sqrt{\frac{2\Theta^2 \sin(\pi/\Theta)}{D_r(\Theta-1)t^*}} & \Theta > 1/2 \end{cases}$$



Multiplicative Fitness (Well-mixed)

class fitness:



$$W = (1-s)^k$$

evolution of classes:

$$\frac{df_k}{dt} = s(\bar{k}-k)f_k - \mu f_k + \mu f_{k-1}$$

steady state:

$$f_k = \frac{(\mu/s)^k e^{-\mu/s}}{k!}$$

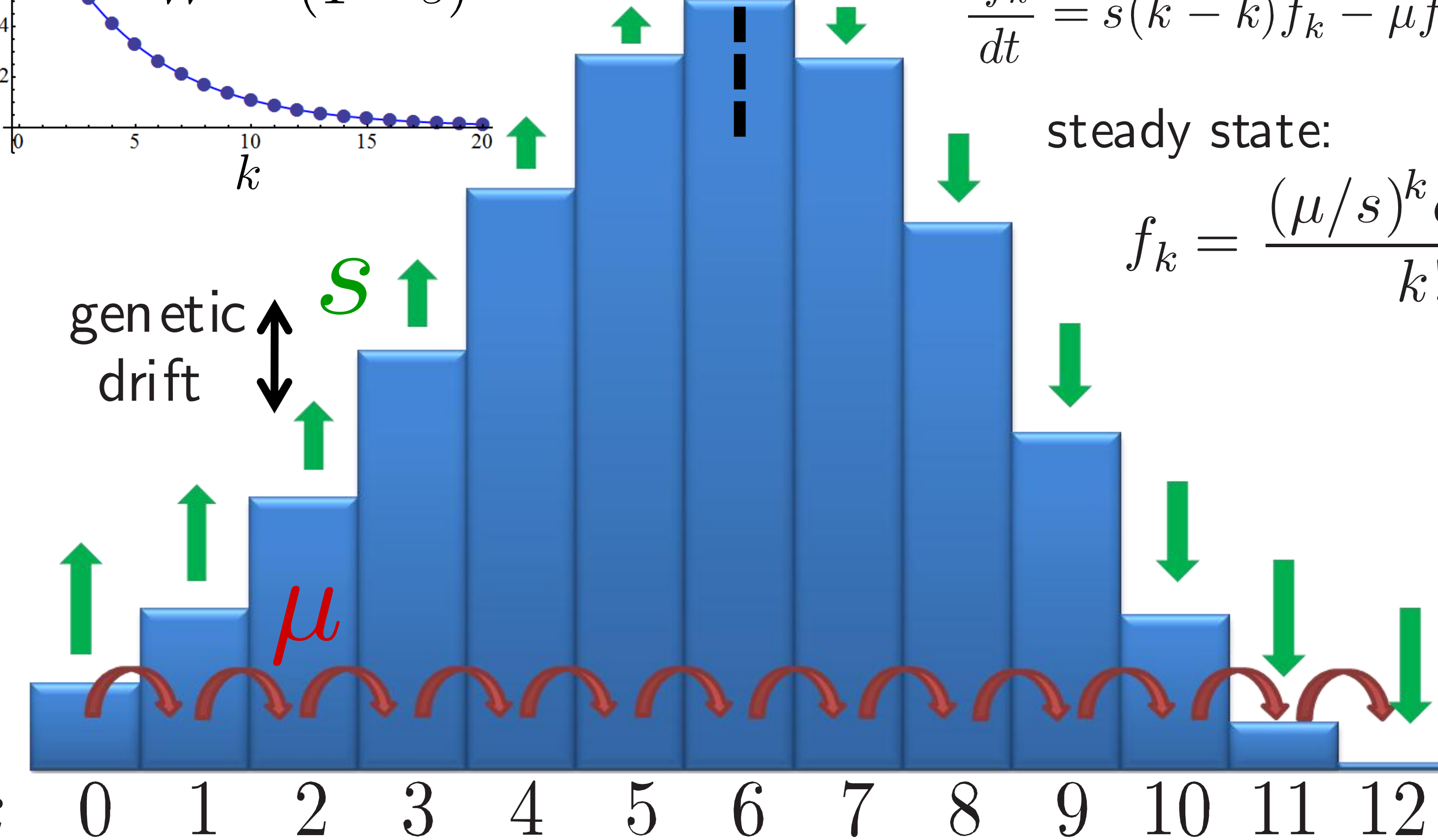
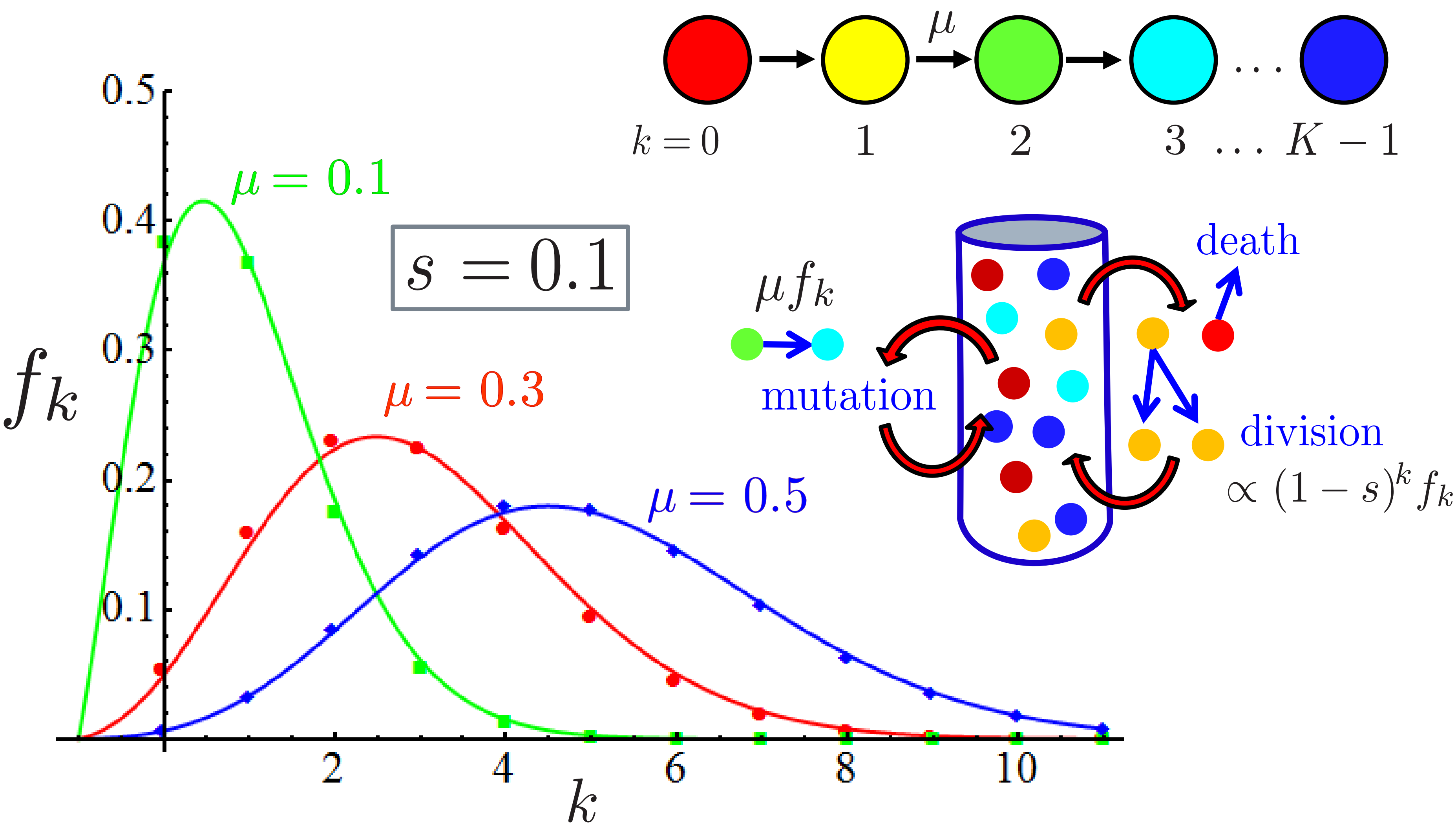


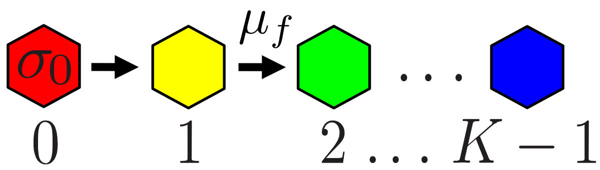
figure from LE Nicolaisen (LEN and M. Desai Mol Biol Evol (2012))

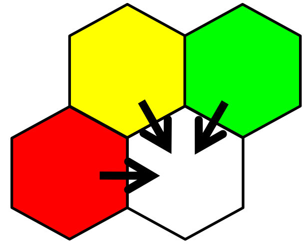
Mutation-Selection Balance



Spatial Mutation-Selection Balance

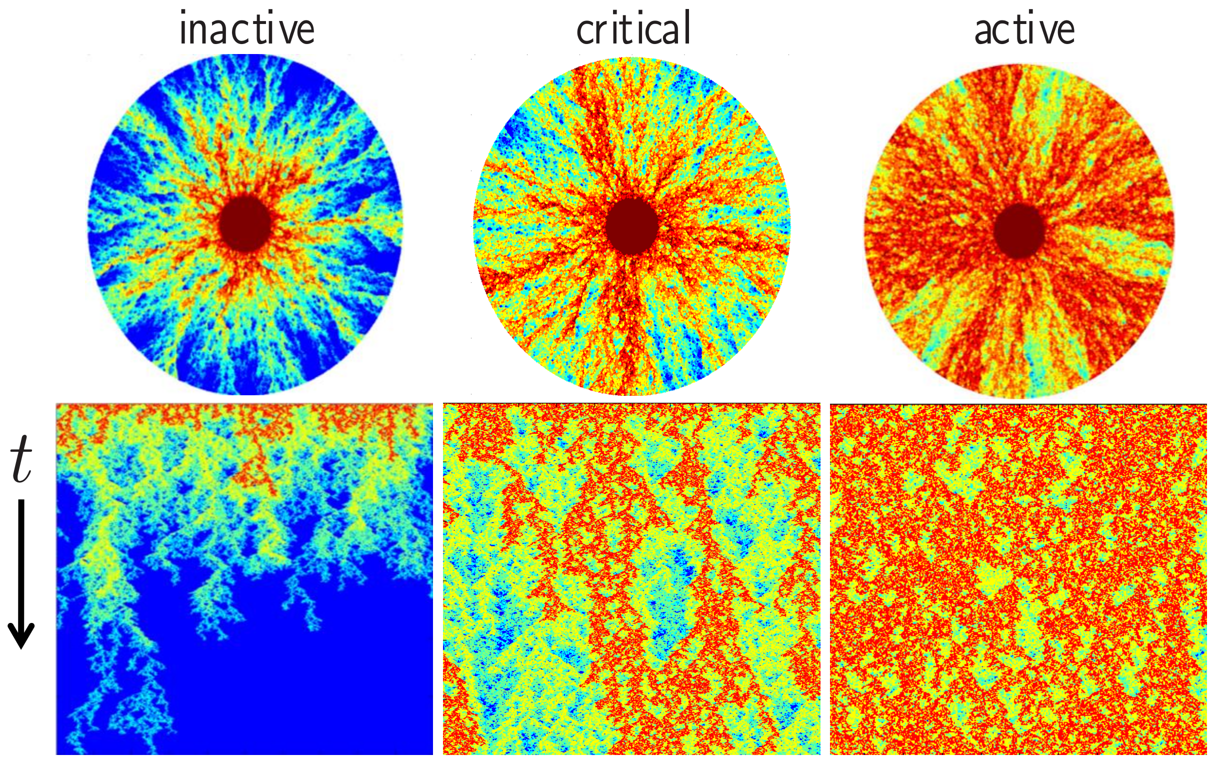
unidirectionally coupled directed percolation

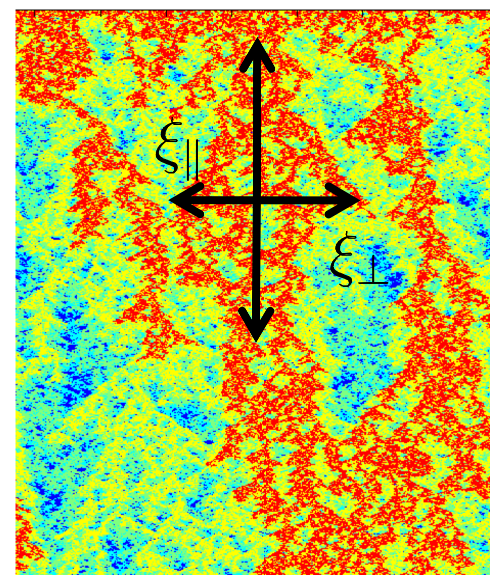




$$p_k = \frac{N_k g_k}{\sum_{k'} N_{k'} g_{k'}}$$

$$g_k = (1-s)^k$$





Muller's Ratchet vs Inactive Phase

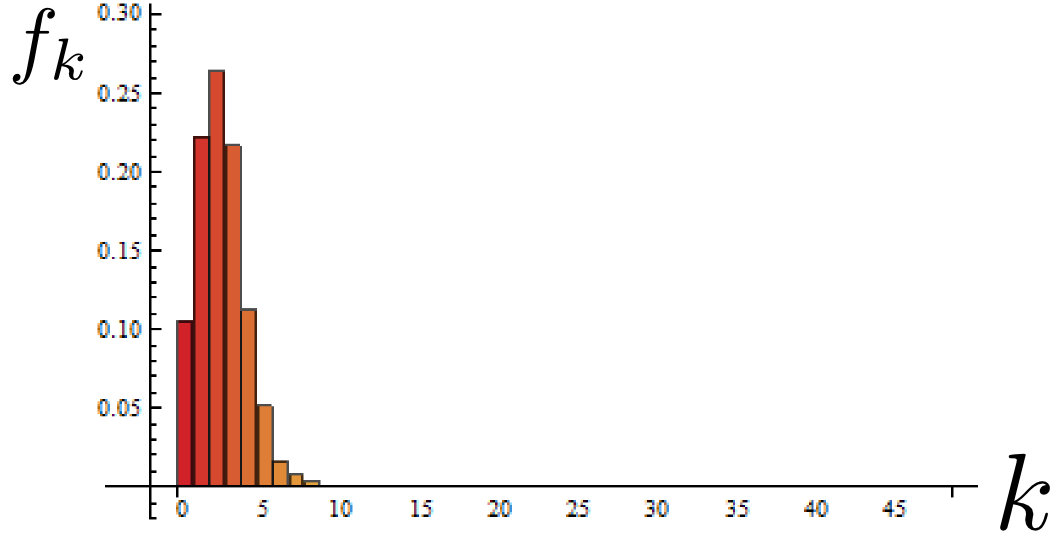
Muller's ratchet

velocity

$$v \sim (1 - f_0)^N \quad f_0 \approx e^{-\mu/s}$$

width

$$W \sim \sqrt{\frac{\mu}{s}}$$



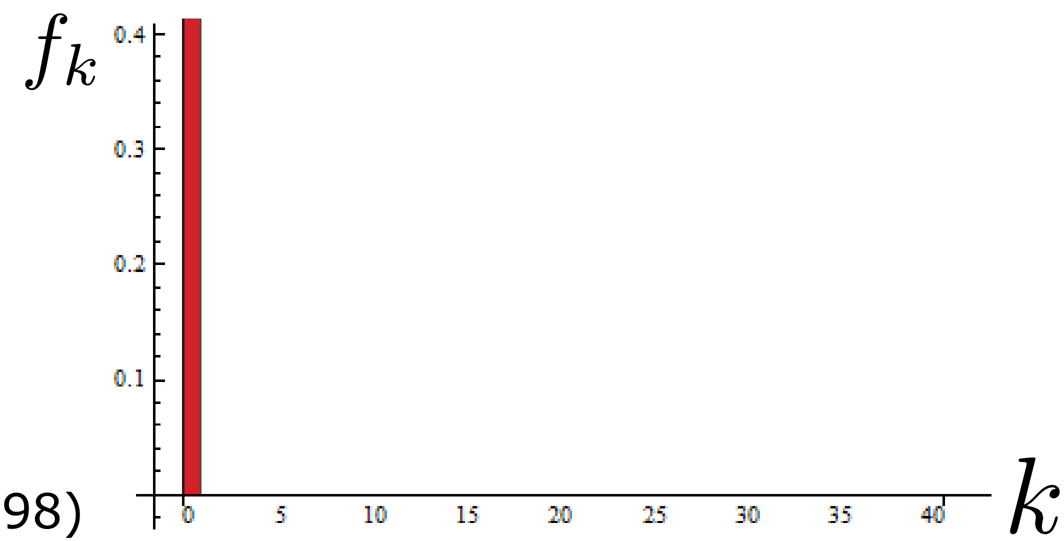
UCDP ratchet

velocity

$$v \sim (\mu - \mu_c)^{\nu_\parallel} \quad \nu_\parallel \approx 1.7$$

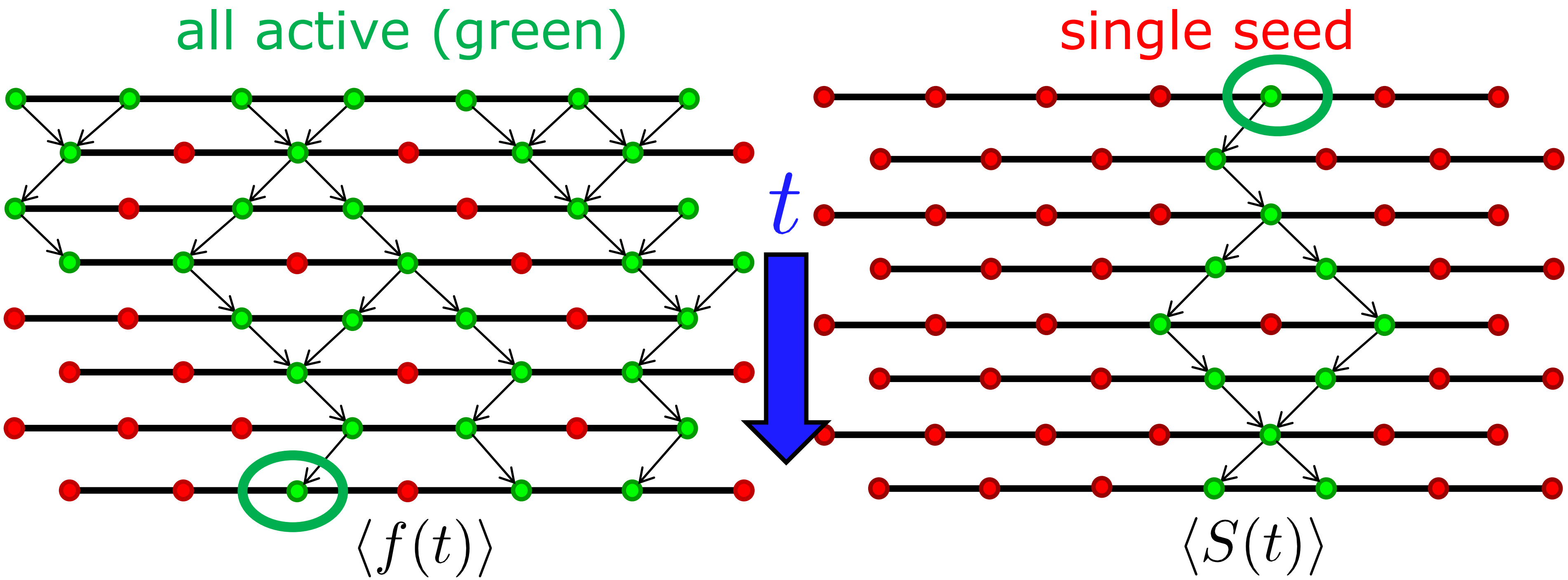
width

$$W \sim (\ln t)^{\gamma} \quad \gamma \approx 0.24$$



U. Alon *et al* PRE **57**(5) (1998)

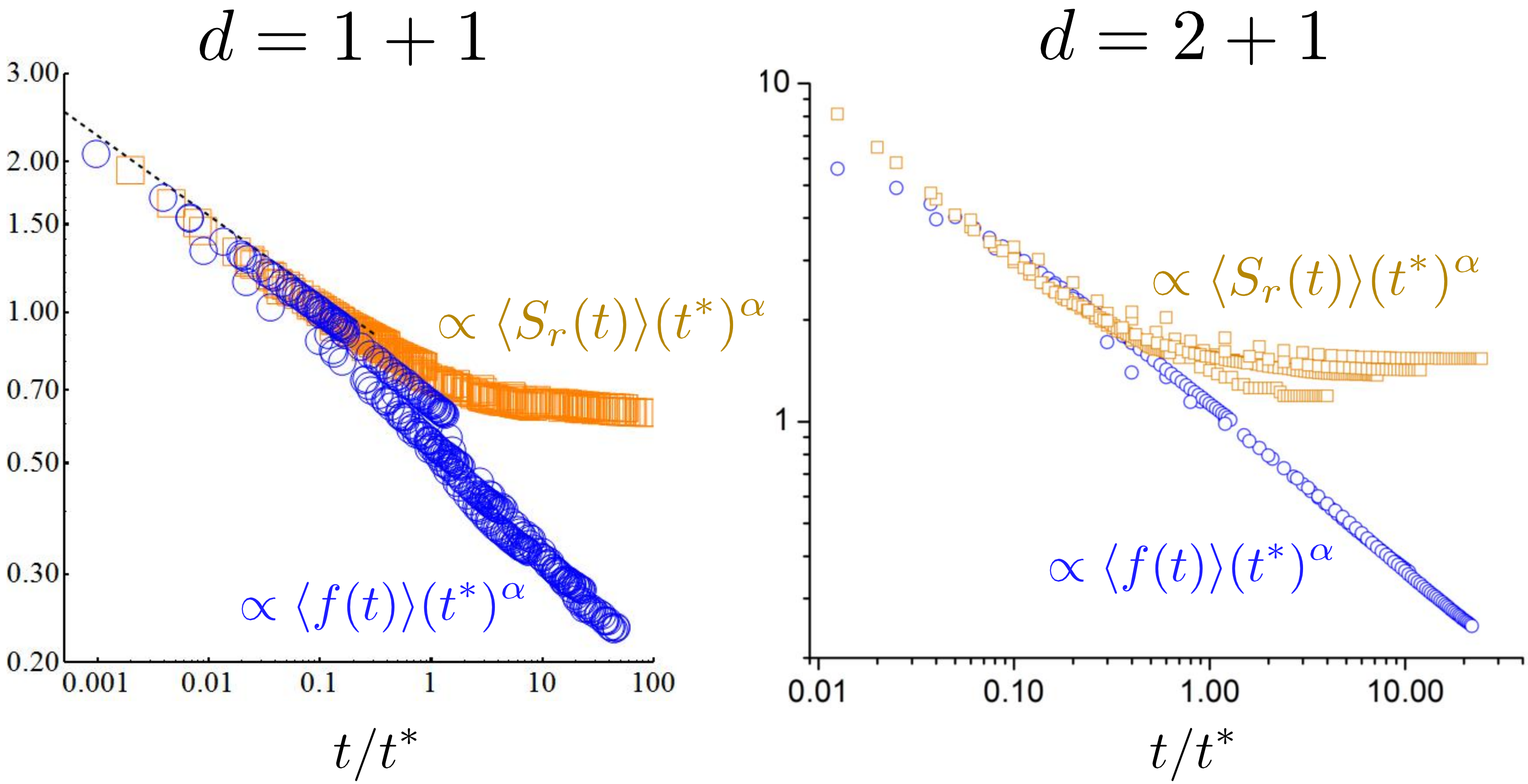
Rapidity reversal symmetry



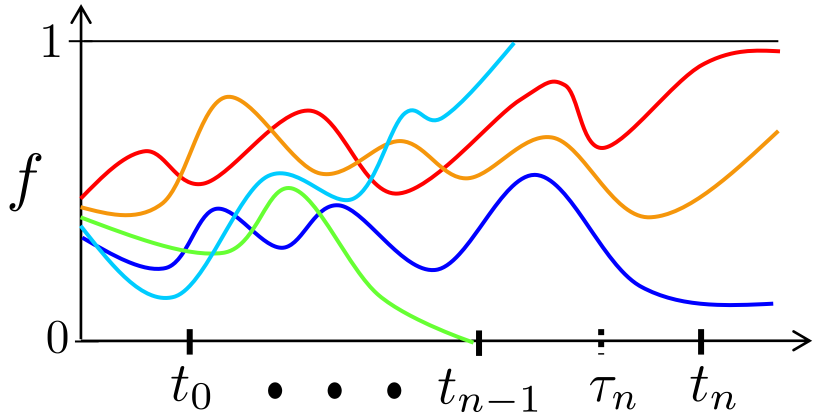
- For bond percolation: $\langle f(t)\rangle = \langle S(t)\rangle$
- In general for DP: $\langle f(t \gg t_{\rm tr})\rangle \simeq \langle S(t \gg t_{\rm tr})\rangle$
- Three exponents characterize DP: $\boxed{\beta = \beta'}\;\; \nu_\perp ,\;\; \nu_\parallel$

Rapidity reversal violation

Inflation breaks rapidity reversal in both dimensions:



Stochastic Differential Equations



$$\partial_t p(f,t) = -\partial_f \left[v(f) p \right] + \partial_f^2 \left[D(f) p \right]$$

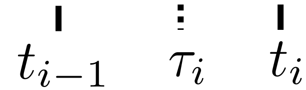
Fokker-Planck Equation

Stochastic Differential Equation

$$\partial_t f = v(f) + \sqrt{2D(f)}\,\eta(t)$$

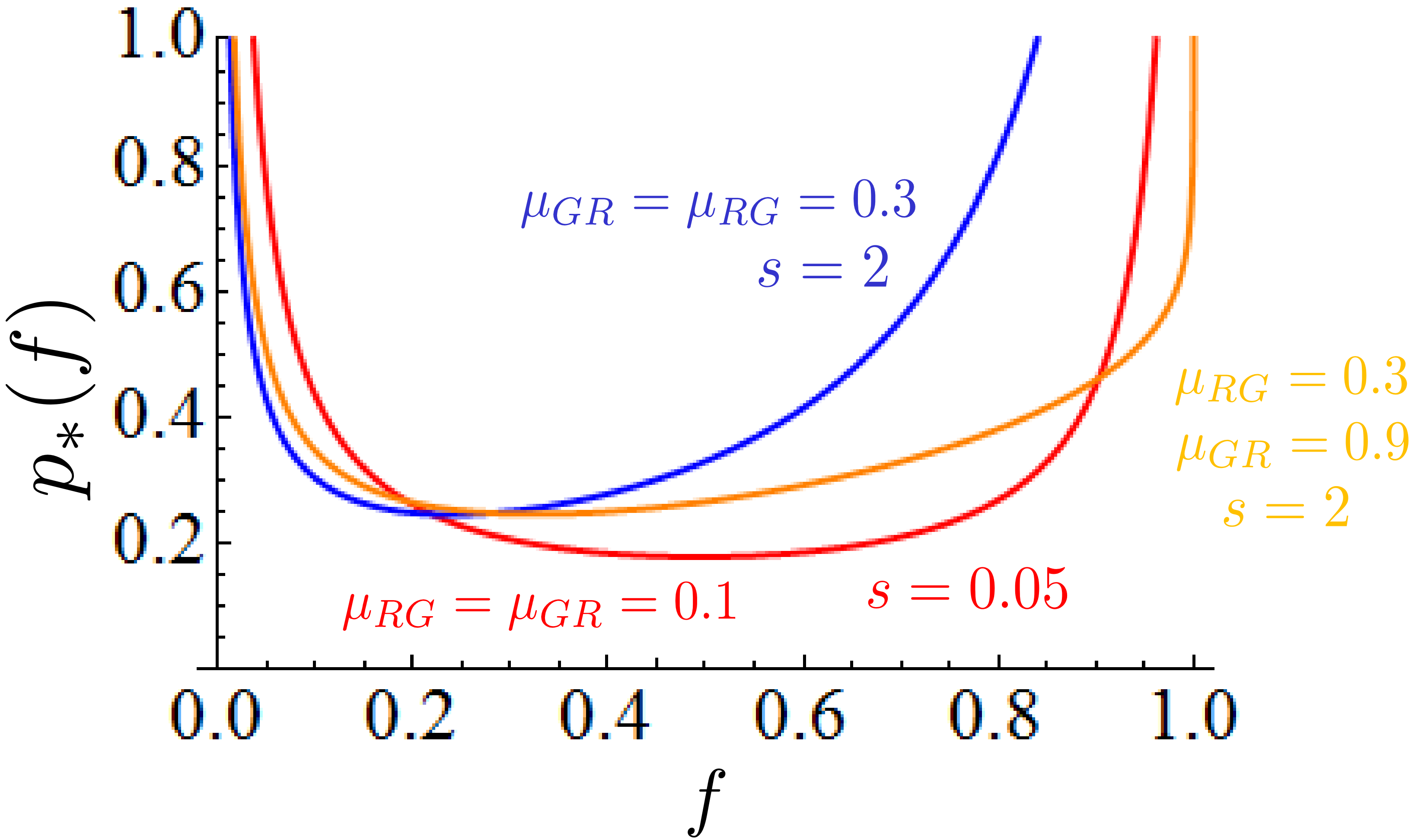
$$\langle \eta(t)\eta(t')\rangle = \delta(t-t') \quad \langle \eta(t)\rangle = 0$$

$$\tau_i = \begin{cases} t_{i-1} & \text{Îto} \checkmark \\ (t_i + t_{i-1})/2 & \text{Stratonovich} \end{cases}$$



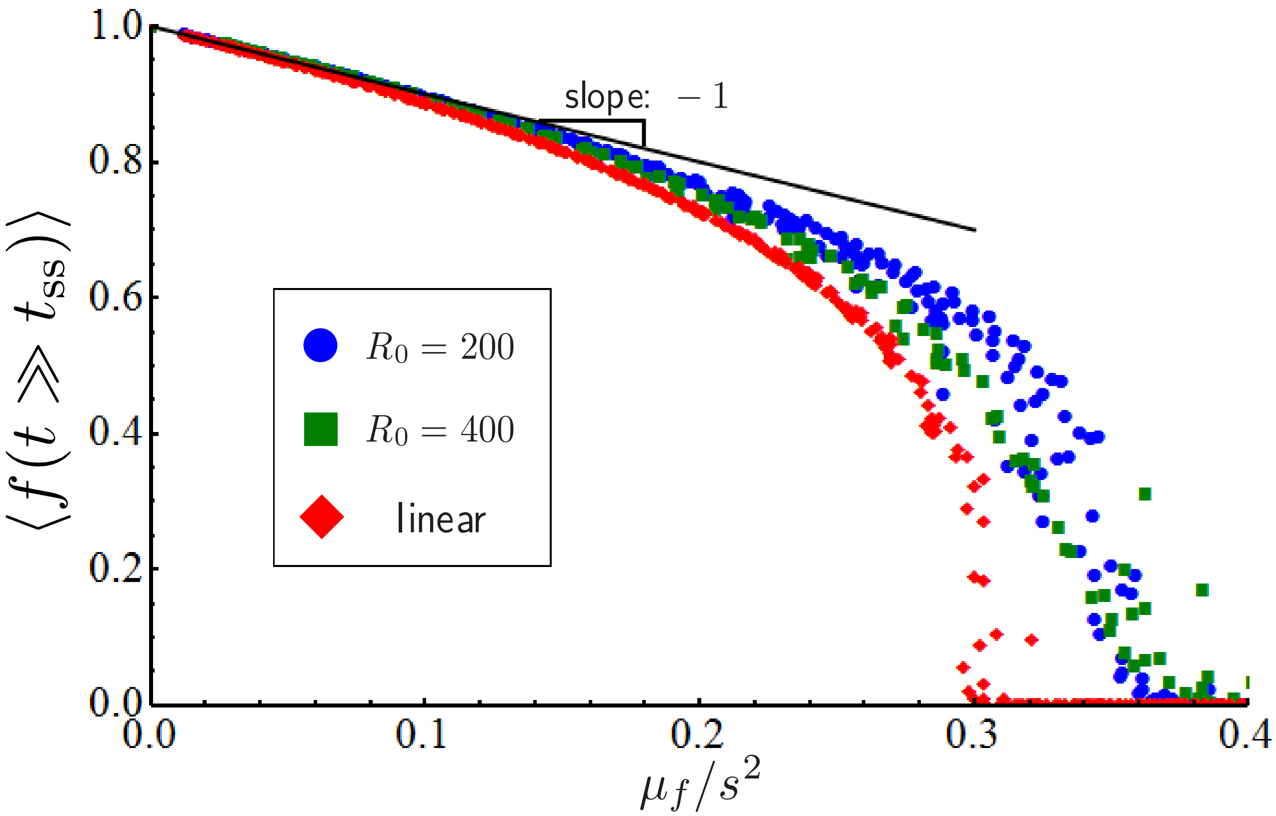
Stationary Distributions

$$p_*(f) = Ce^{sf\tau_{\text{gen}}N} f^{\mu_{RG}\tau_{\text{gen}}N-1}(1-f)^{\mu_{GR}\tau_{\text{gen}}N-1}$$

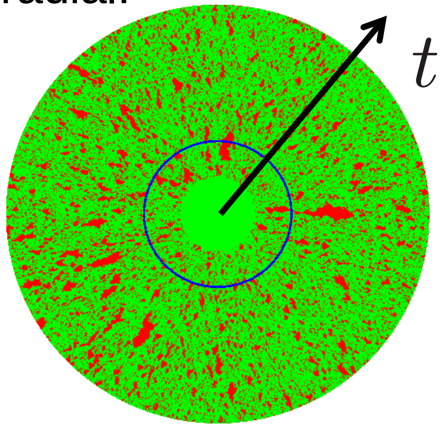


Active state scaling

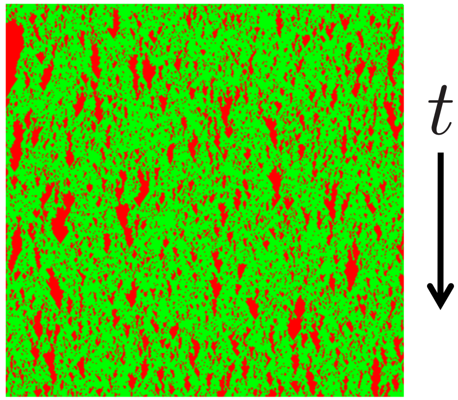
In the active state, linear and radial range expansions have the same steady state.



radial:

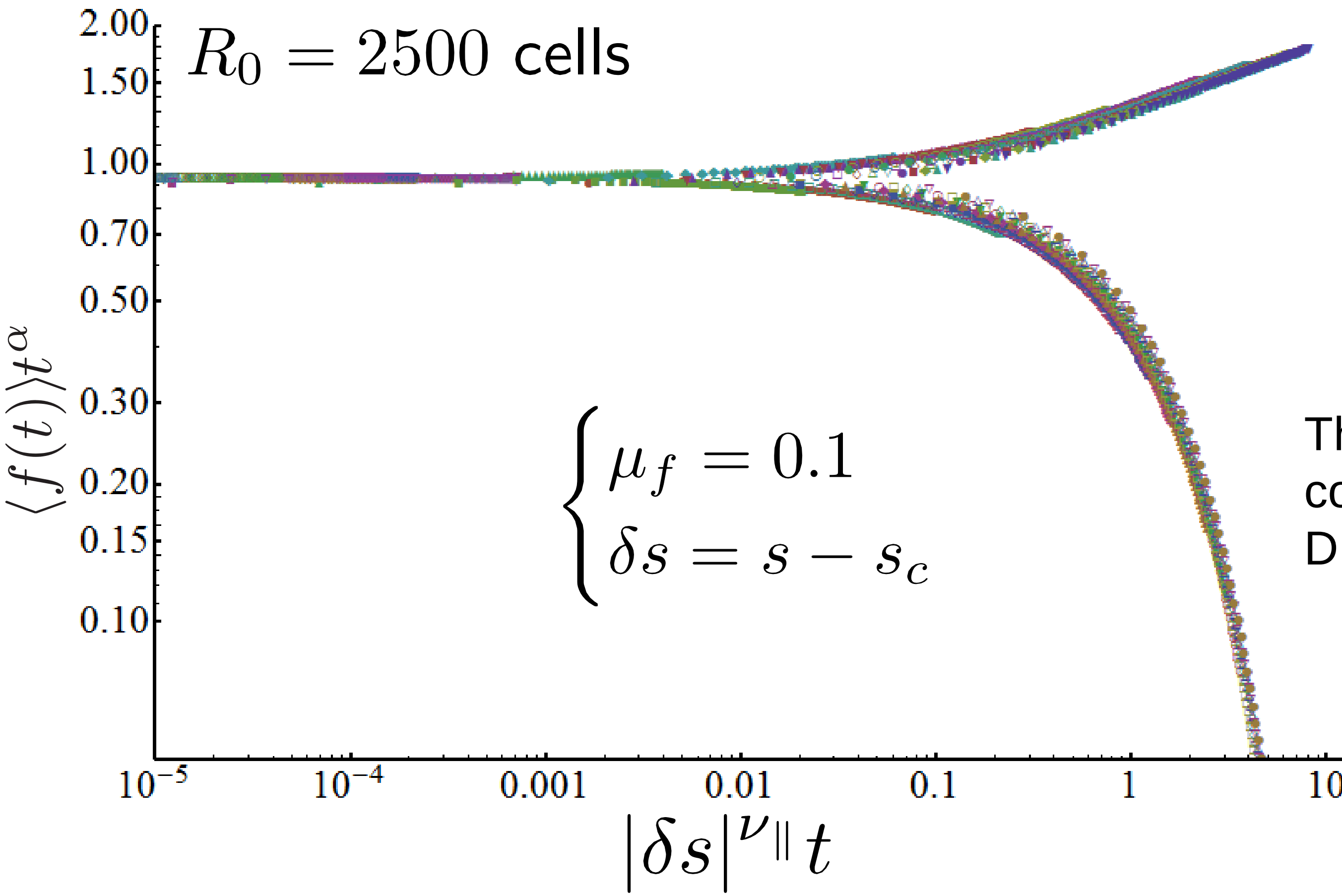


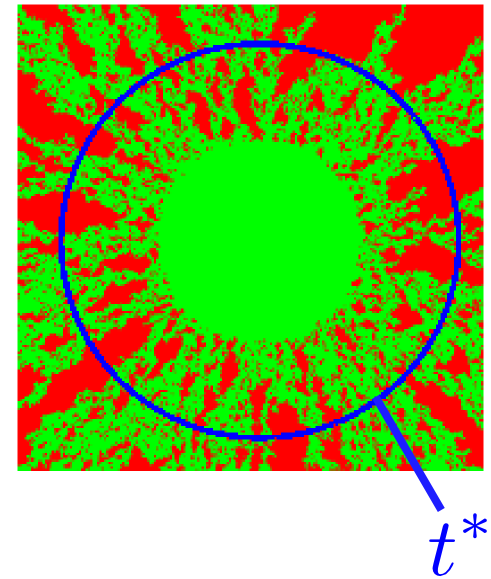
linear:



Regular DP occurs at short times

The early time dynamics are the same in linear and radial range expansions:



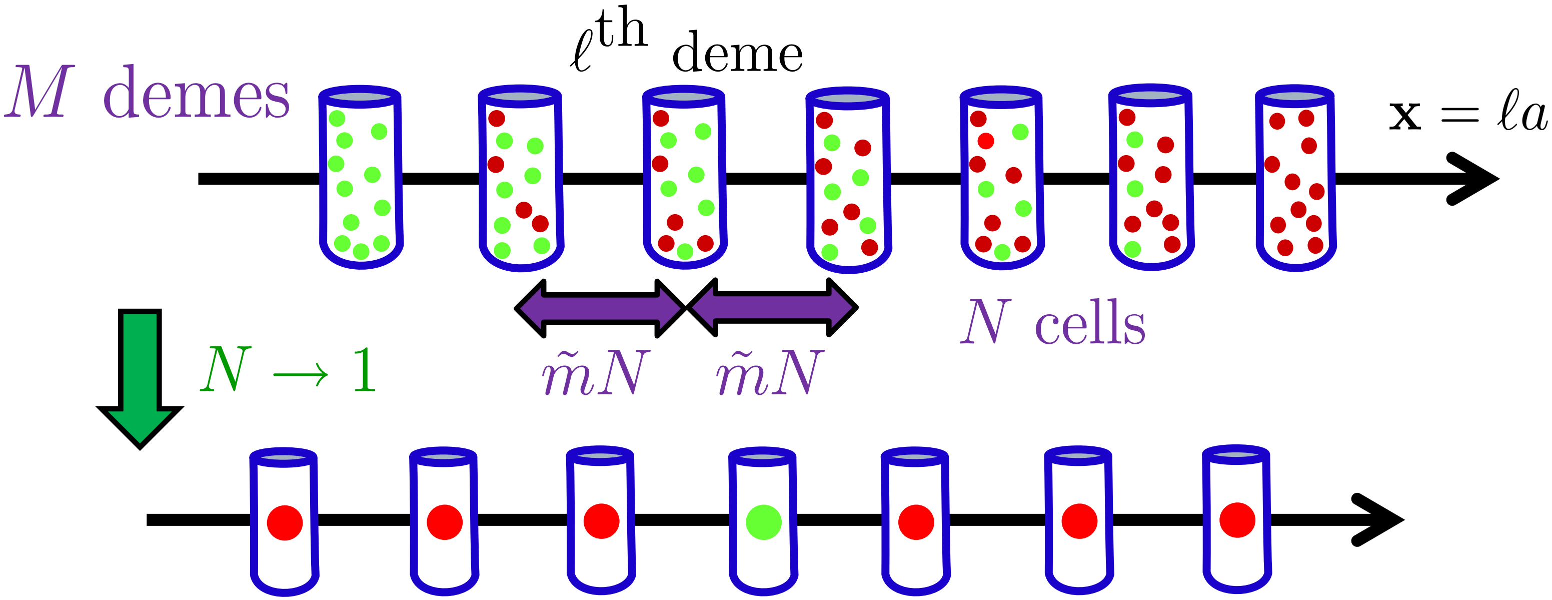


The collapse is consistent with the DP critical exponents:

$$\begin{cases} \alpha = \frac{\beta}{\nu_\parallel} \approx 0.159 \\ \nu_\parallel \approx 1.73 \end{cases}$$

Stepping-Stone Model

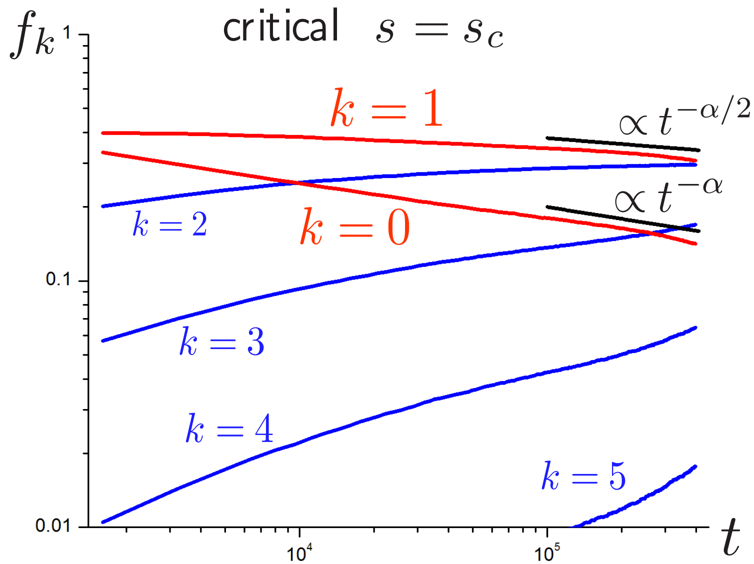
- Spatially Distributed Populations (Demes)
- Exchange of Individuals

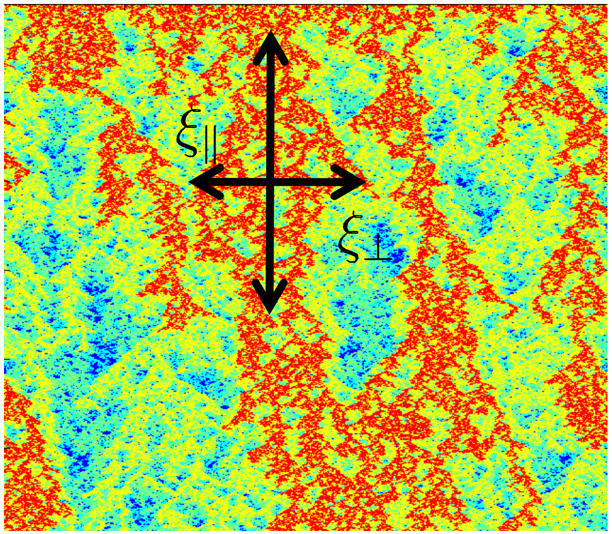


$$\partial_t f(\mathbf{x},t) = \overbrace{m a^2 \nabla^2_{\mathbf{x}} f}^{\text{exchange}} + \overbrace{s f(1-f)}^{\text{selection}} + \overbrace{\mu_{RG}(1-f) - \mu_{GR} f}^{\text{mutations}} + \overbrace{\sqrt{2(N\tau_{\text{gen}})^{-1} f(1-f)}\,\eta(\mathbf{x},t)}^{\text{genetic drift}}$$

Noise correlations: $\langle \eta(\mathbf{x},t)\eta(\mathbf{x}',t')\rangle = \delta(\mathbf{x}-\mathbf{x}')\delta(t-t')$

The Critical Phase





UCDP ratchet

velocity

$$v \sim (\mu - \mu_c)^{\nu_\parallel} \quad \nu_\parallel \approx 1.7$$

width

$$W \to K^{1/2} \quad W_c \sim (\ln t)^\gamma$$
$$\gamma \approx 0.24$$

Muller's ratchet

velocity

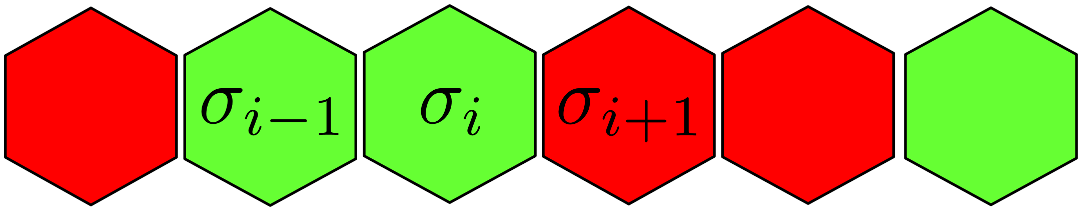
$$v \sim (1 - f_0)^N \quad f_0 \approx e^{-\mu/s}$$

width

$$W \sim \sqrt{\frac{\mu}{s}}$$

The Voter Model (no selection)

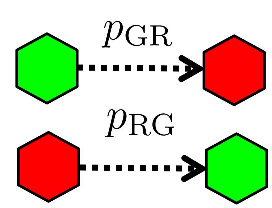
- Consider a lattice of "voters"



$$\sigma_i = \begin{cases} 1 & \text{green} \\ -1 & \text{red} \end{cases}$$

- Flip spin i with rate

$$\omega(\{\sigma\} \to \{\sigma\}_i) = \overbrace{\frac{1}{2}\left[1 - \frac{\sigma_i}{z} \sum_{k \text{ n.n. of } i} \sigma_k\right]}^{\text{drift and exchange}} + \overbrace{\frac{\mu_{\mathrm{GR}}(1+\sigma_i)}{2} + \frac{\mu_{\mathrm{RG}}(1-\sigma_i)}{2}}^{\text{mutations}}$$



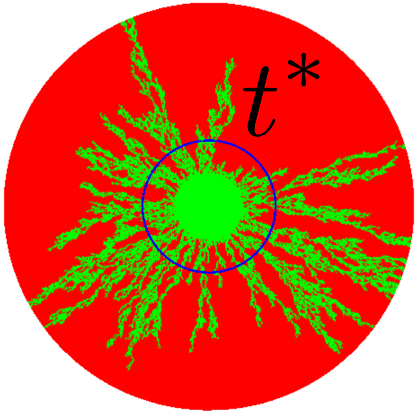
$$\begin{cases} p_{\mathrm{GR}} = \mu_{\mathrm{GR}} \\ p_{\mathrm{RG}} = \mu_{\mathrm{RG}} \end{cases}$$

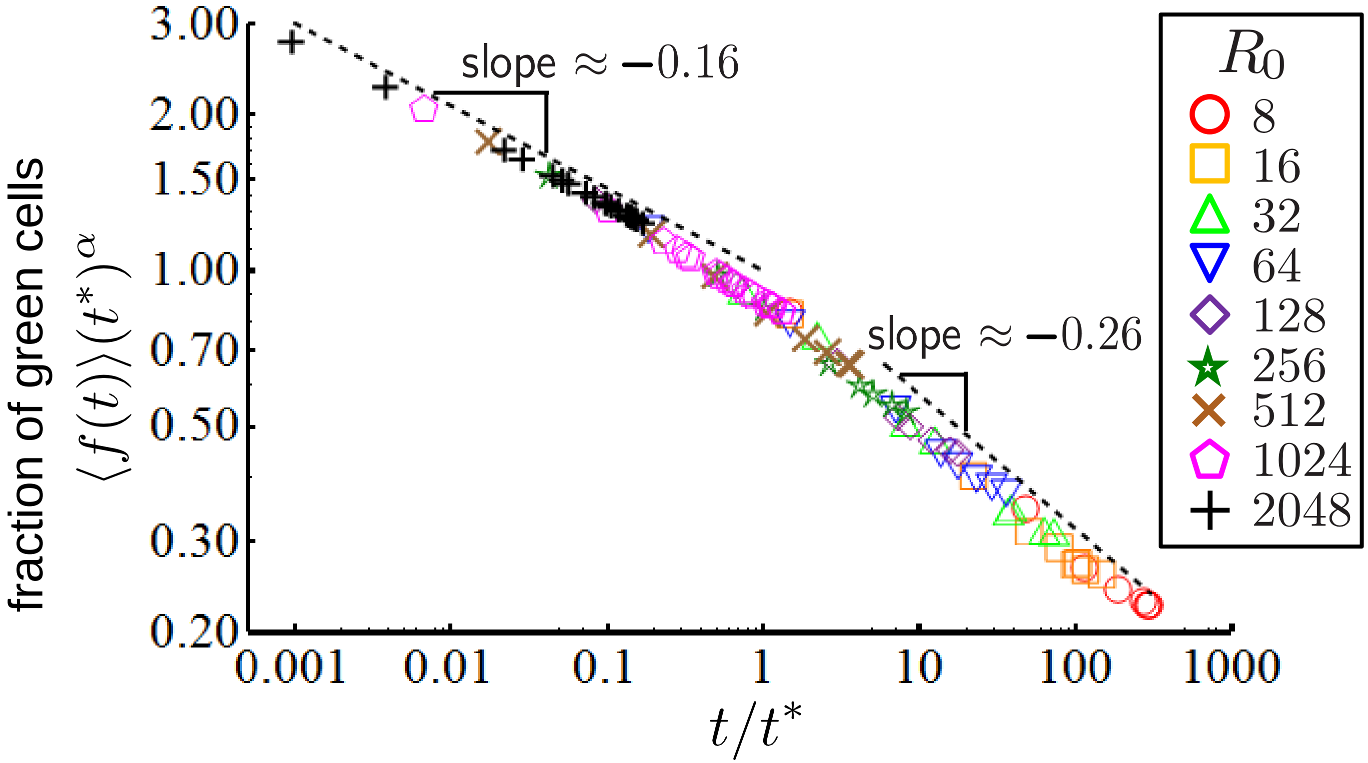
- Continuous time Master Equation

$$\partial_t P(\{\sigma\}, t) = \sum_{\{\sigma'\}} \left[\omega\left(\{\sigma'\} \to \{\sigma\}\right) P(\{\sigma'\}, t) - \omega(\{\sigma\} \to \{\sigma'\}) P(\{\sigma\}, t)\right]$$

Inflationary scaling (all green homeland)

- We treat crossover time t^* as a new variable in all scaling functions
- We find that t^* scales the same way as a finite time variable

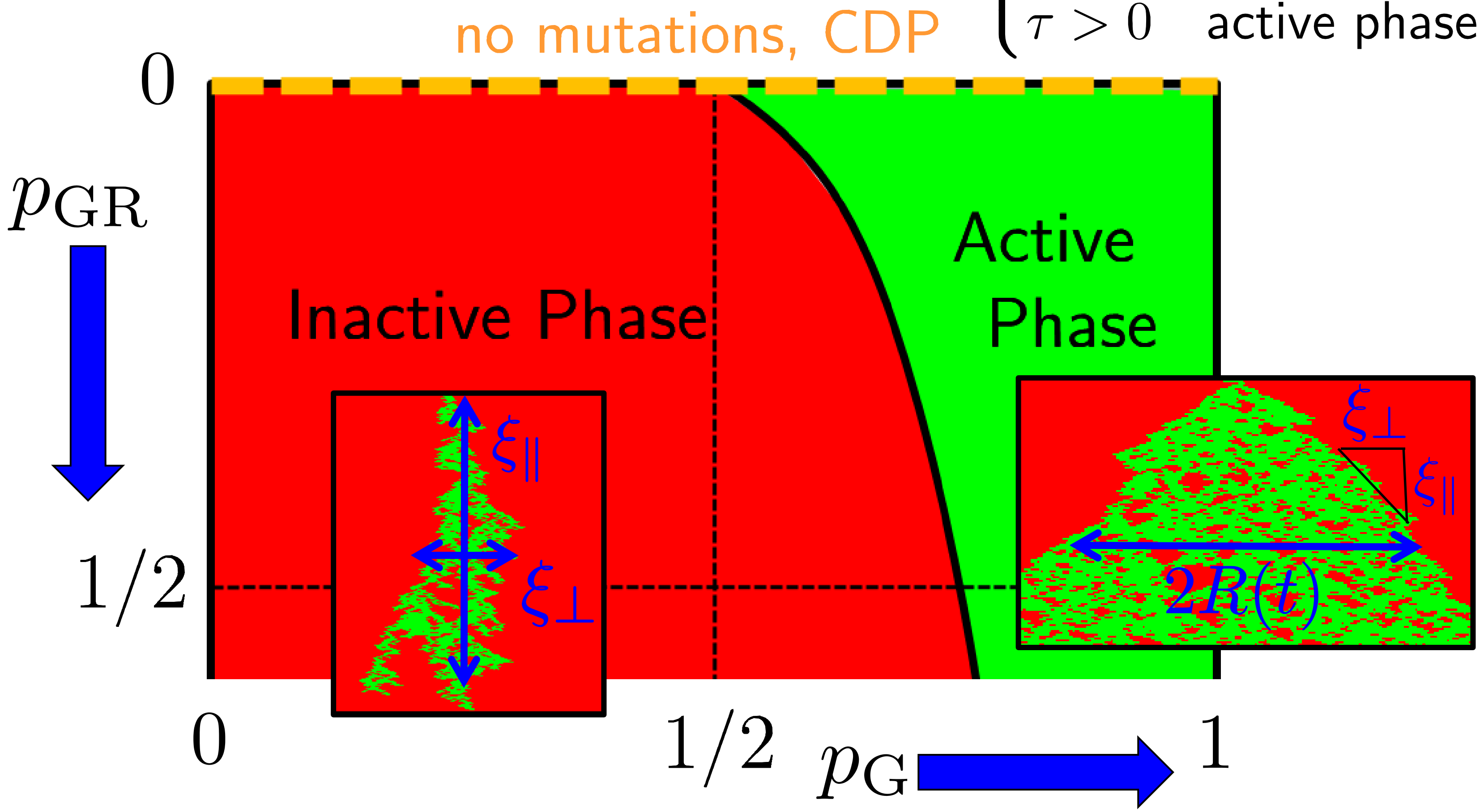




Directed Percolation Phase Transition

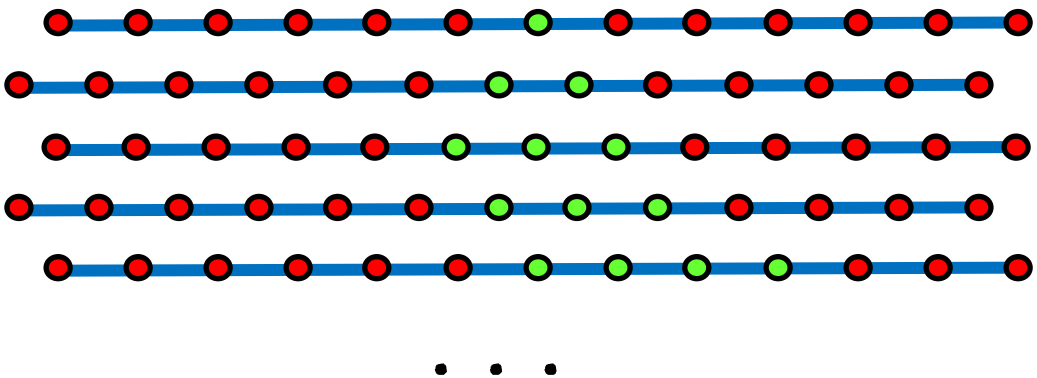
The control parameter: $\tau = p_{\mathrm{G}} - p^*_{\mathrm{G}}$

$$\begin{cases} \tau < 0 & \text{absorbing phase} \\ \tau = 0 & \text{phase transition} \\ \tau > 0 & \text{active phase} \end{cases}$$



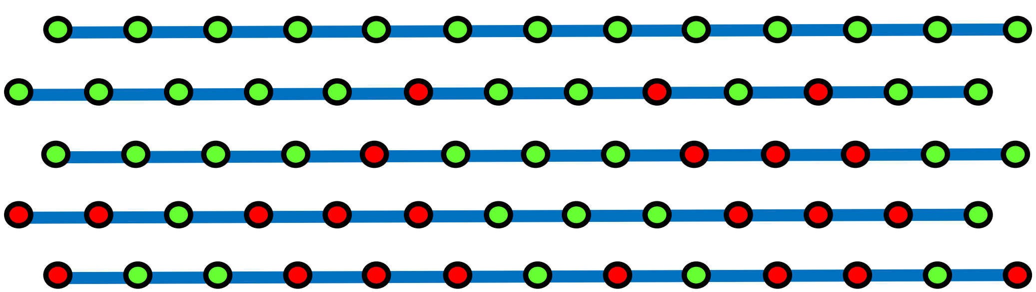
Initial Conditions are Important

1) Isolated seed initial condition:



$$\begin{cases} N_G \sim t^{\Theta} \\ P_{\text{surv}} \sim t^{-\delta} \\ R \sim t^{1/z} \end{cases}$$

2) Fully occupied initial condition:



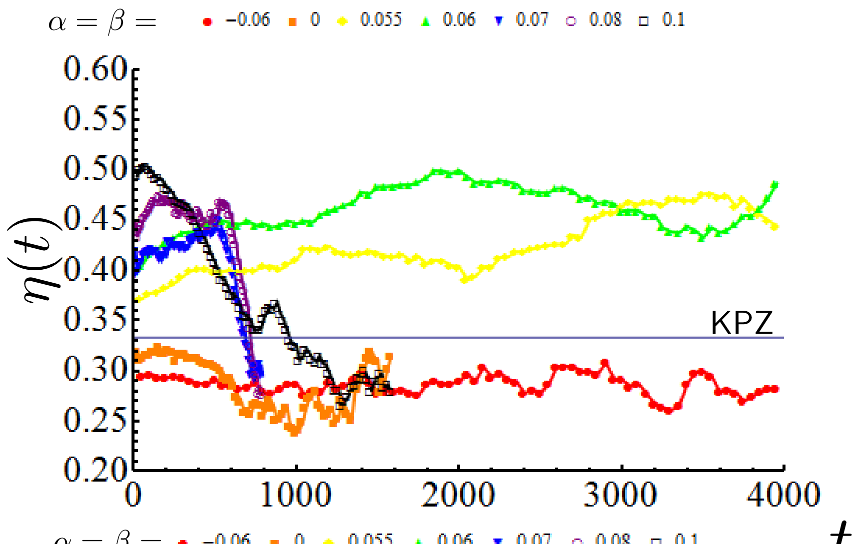
$\rho_G \sim t^{-\alpha}$ . . .

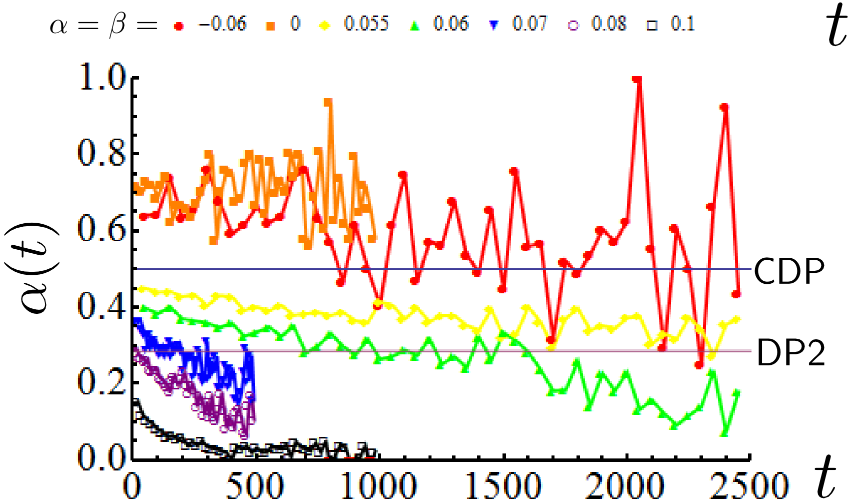
1) $P_{\text{perc}} = \lim_{t\to\infty} P_t(\text{active})$

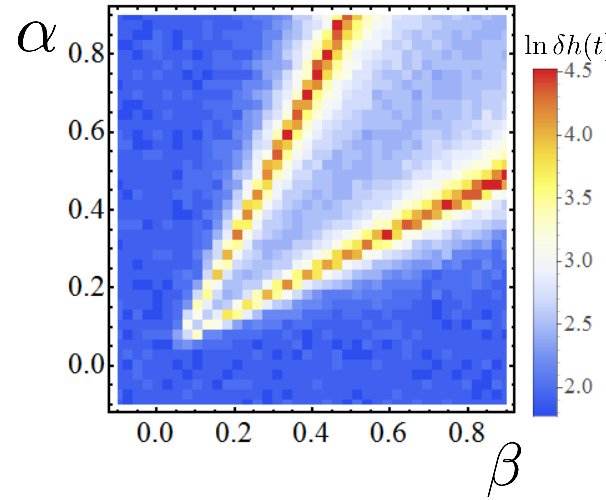
2) $\varrho = \lim_{t\to\infty} P_t(\text{occupied})$

Near critical point:

$P_{\text{perc}} \sim \tau^{\beta'}$ $\qquad \varrho \sim \tau^{\beta}$







Interface width scaling:

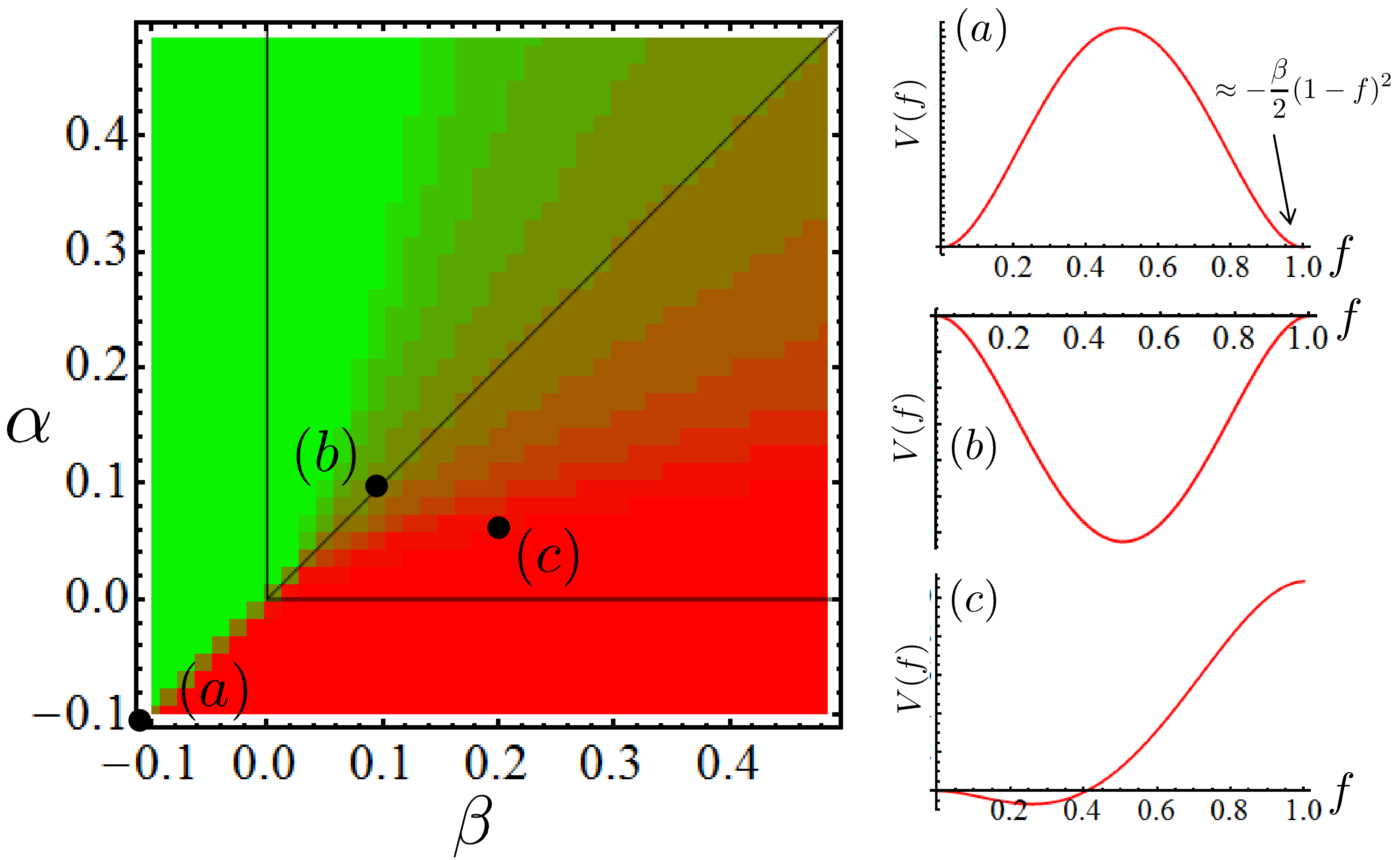
$$\delta h \sim t^{\eta} F_h(L t^{-1/z})$$

$$\sim \begin{cases} L^{\gamma} & L \ll t^{1/z} \\ t^{\eta} & L \gg t^{1/z} \end{cases}$$

Mixed phase density scaling:

$$\rho_A \sim t^{-\alpha}$$

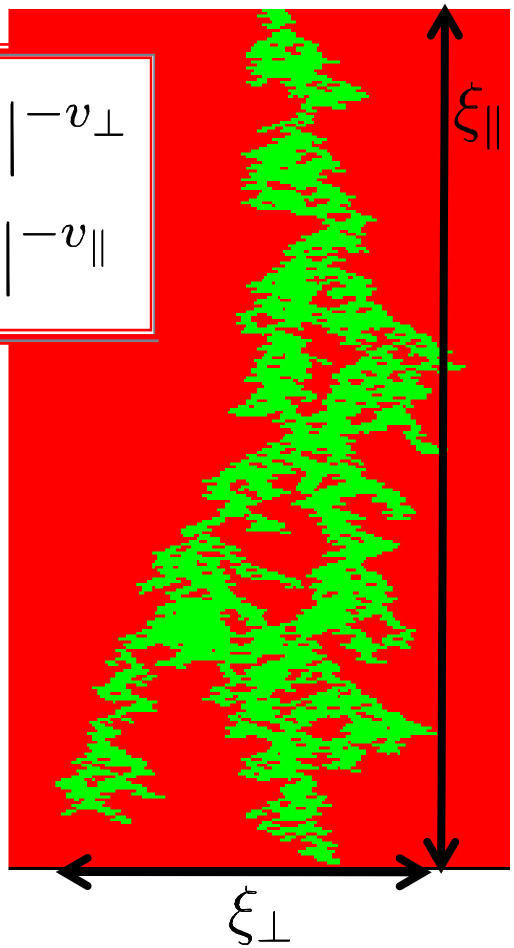
Effective Potentials

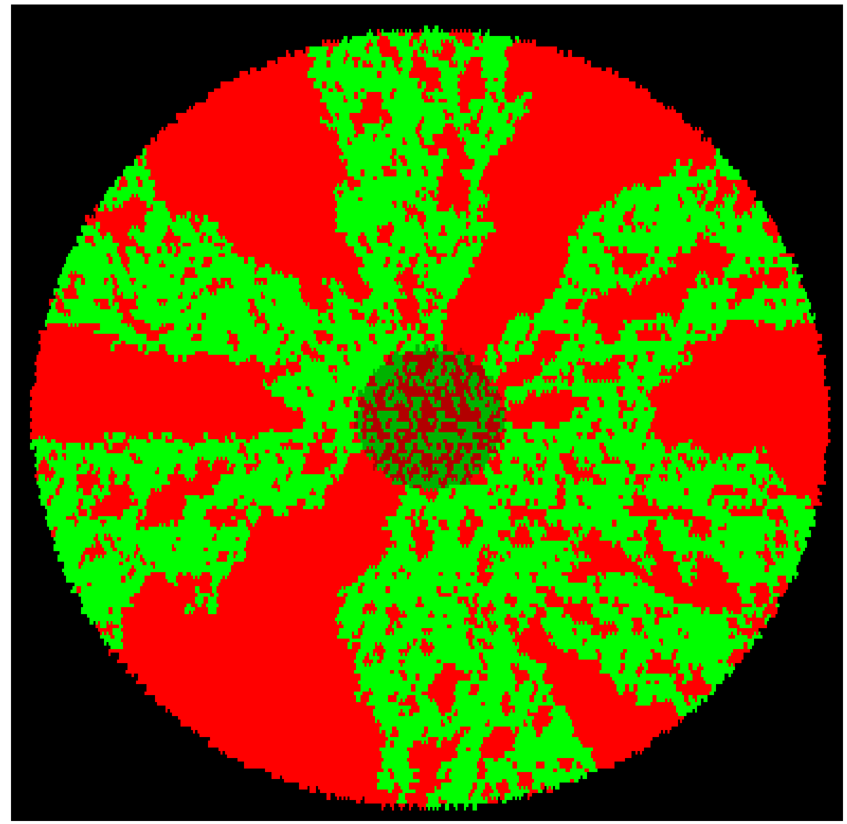


Correlation Lengths

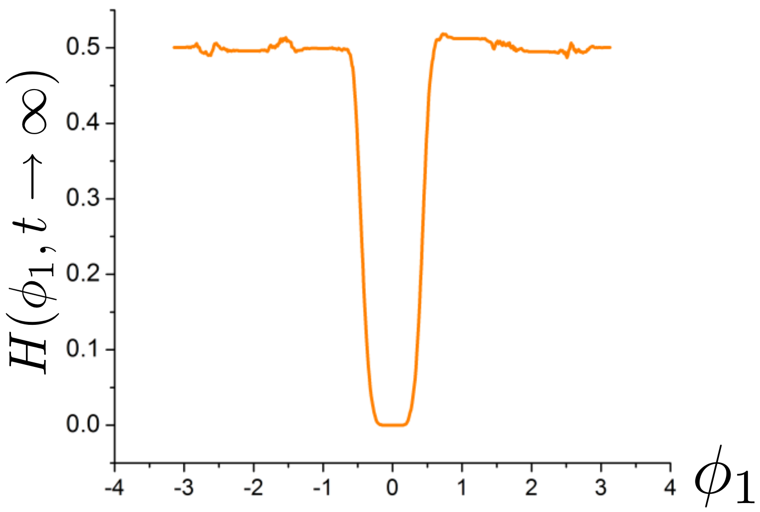
$$\xi_\perp \sim |\tau|^{-v_\perp}$$

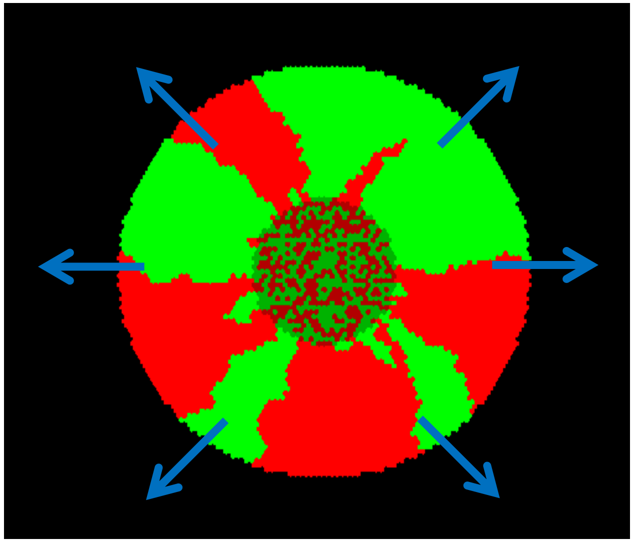
$$\xi_\parallel \sim |\tau|^{-v_\parallel}$$

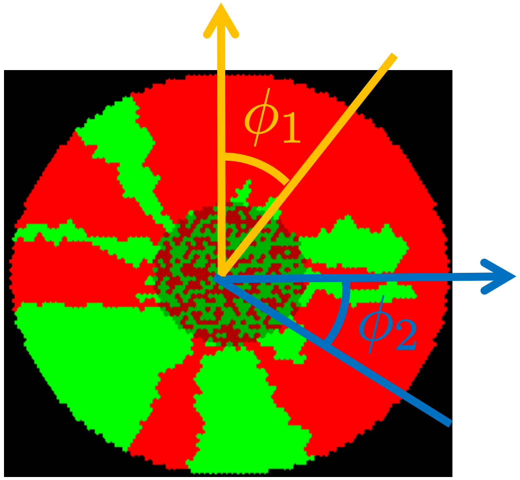


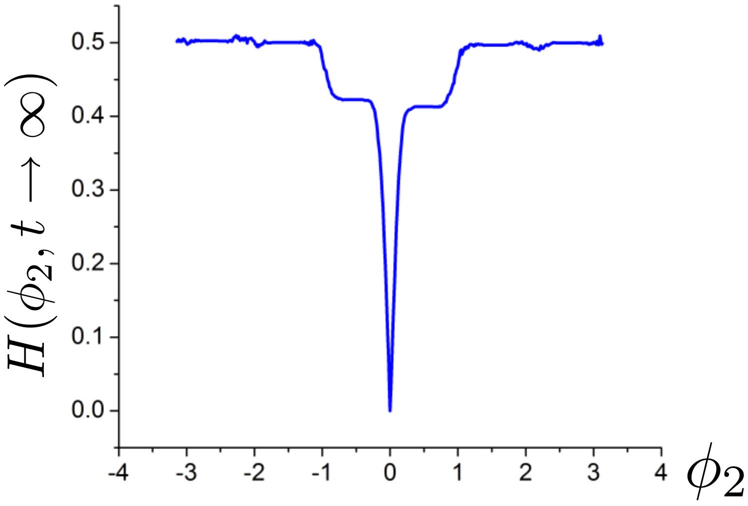


Lattice Effects (no mutations)





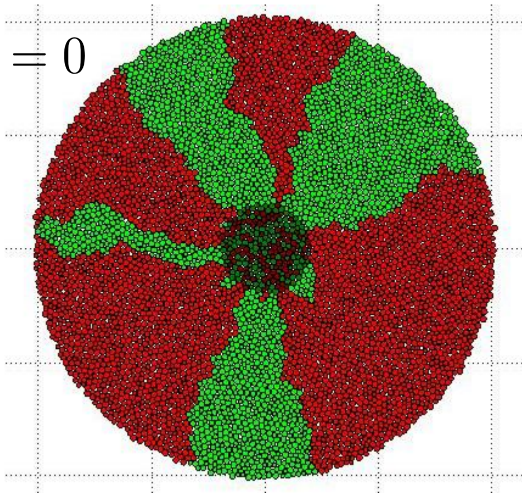




Bennett Model Simulations

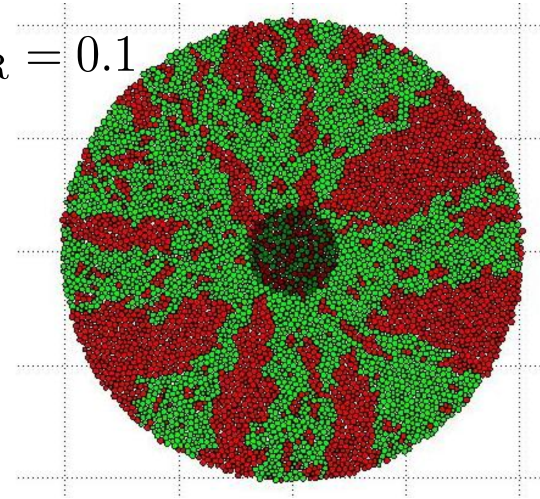
$p_{\mathrm{G}} = 0.5 \quad p_{\mathrm{GR}} = 0$

Compact Directed Percolation:



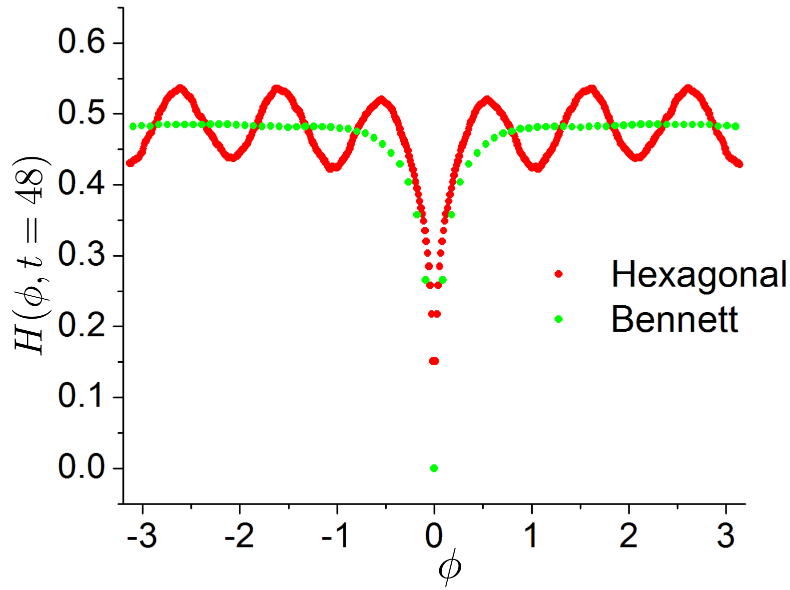
$p_{\mathrm{G}} = 0.7 \quad p_{\mathrm{GR}} = 0.1$

Directed Percolation:



Corrected heterozygosity:

$R_0 = 15 \quad p_{\mathrm{G}} = 0.7 \quad p_{\mathrm{GR}} = 0.1$



Neutral with Mutations

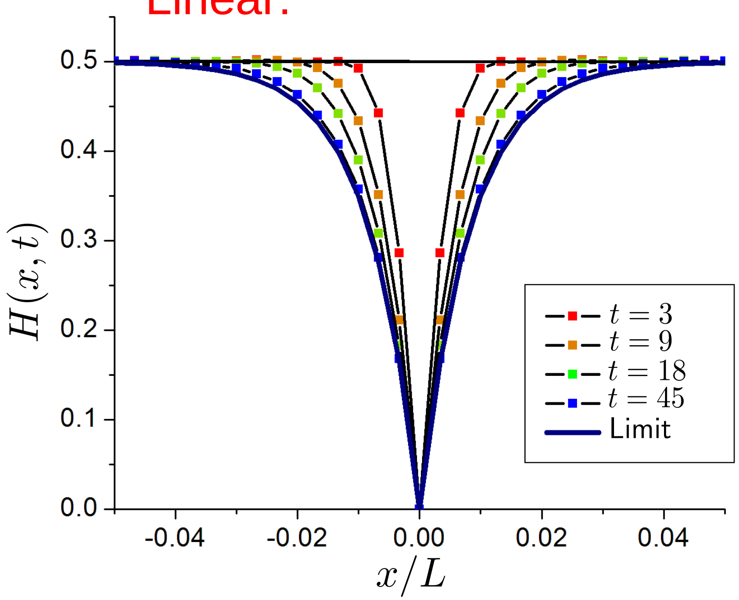
Linear:

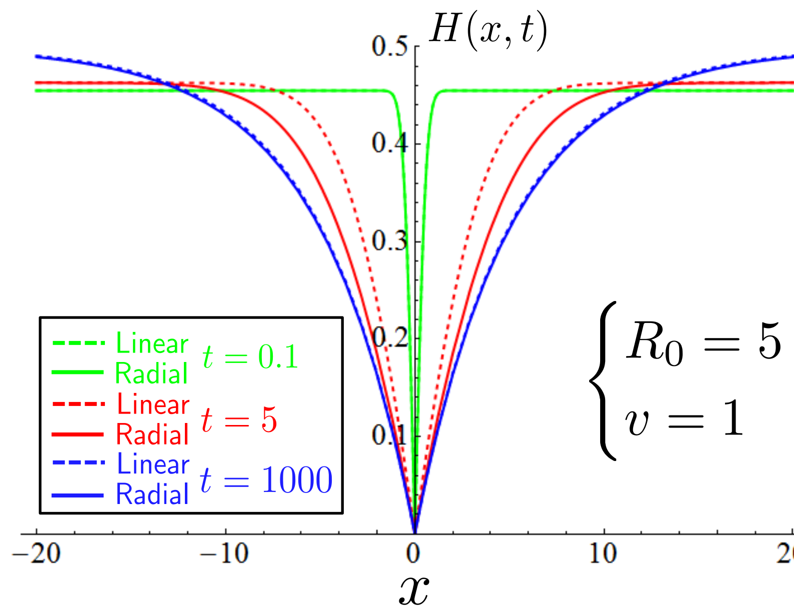
$$H(x,t) = \frac{2\mu_{\mathrm{RG}}\mu_{\mathrm{GR}}}{(\mu_{\mathrm{GR}}+\mu_{\mathrm{RG}})^2}\left[1 - e^{-|x|\sqrt{\frac{2(\mu_{\mathrm{GR}}+\mu_{\mathrm{RG}})}{D}}}\right] + e^{-2t(\mu_{\mathrm{GR}}+\mu_{\mathrm{RG}})} f(x,t)$$

Radial: Approaches the same stationary distribution and exhibits a cross-over time: $t_* = R_0/v$

$$\mu_{\mathrm{GR}} = \mu_{\mathrm{RG}} = 0.01$$

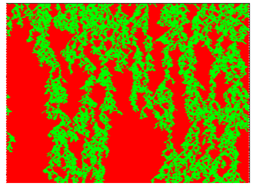
Linear:



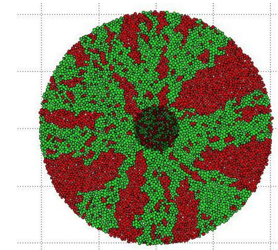


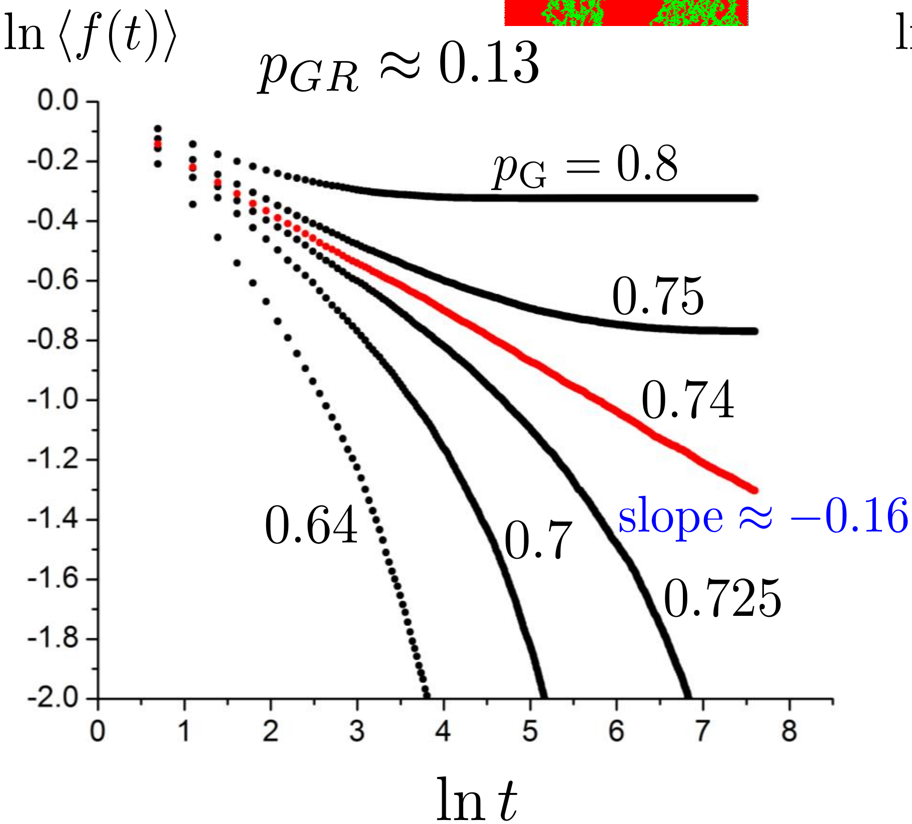
One-way Mutations and Selection

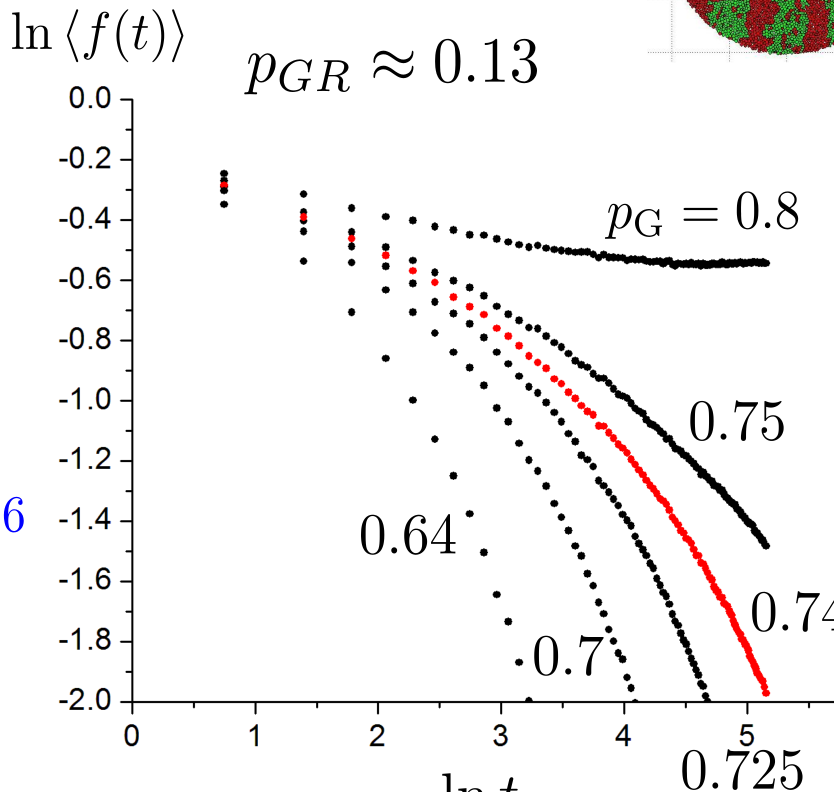
Linear:



Radial: $R_0 = 50$



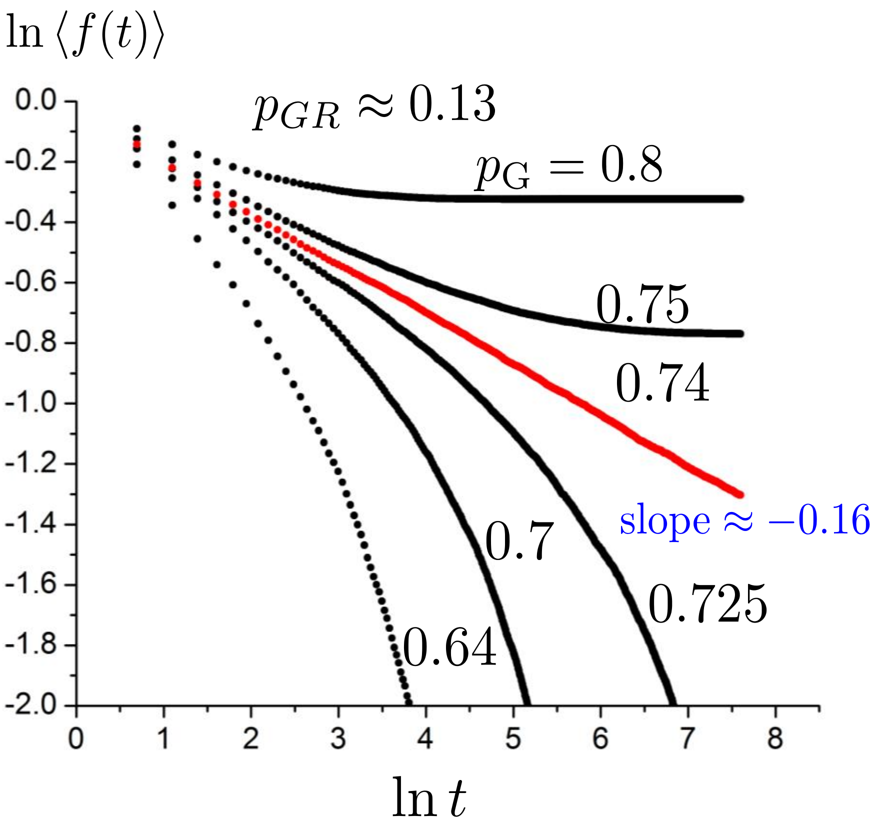




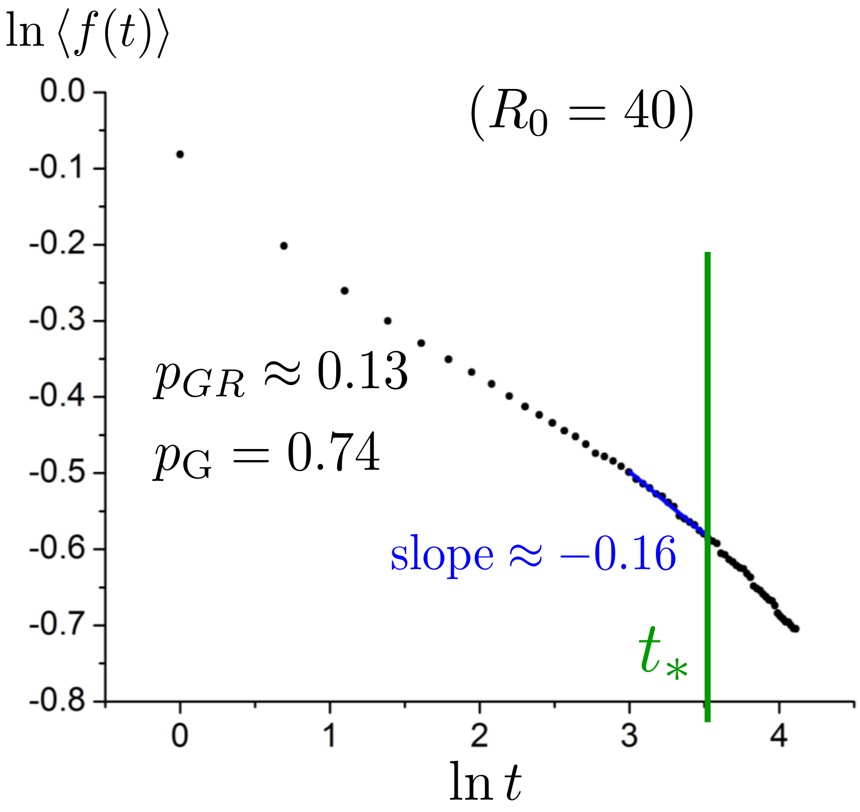
One-way Mutations and Selection

It is easier to connect the linear and radial model on the same lattice:

Linear:



Radial (hexagonal lattice):



References

- M. Henkel, H. Hinrichsen, and S. Lübeck, *Non-Equilibrium Phase Transitions* (Springer, Dordrecht, 2009)
- S. Redner *A Guide to First-Passage Processes* (Cambridge University Press 2001)
- K. Korolev et al. *Genetic demixing and evolution in linear stepping stone models,* Reviews of Modern Physics, **82** (2), 2010, pp. 1691-1718
- N. G. Van Kampen *Stochastic Processes in Physics and Chemistry* (Elsevier 2007)