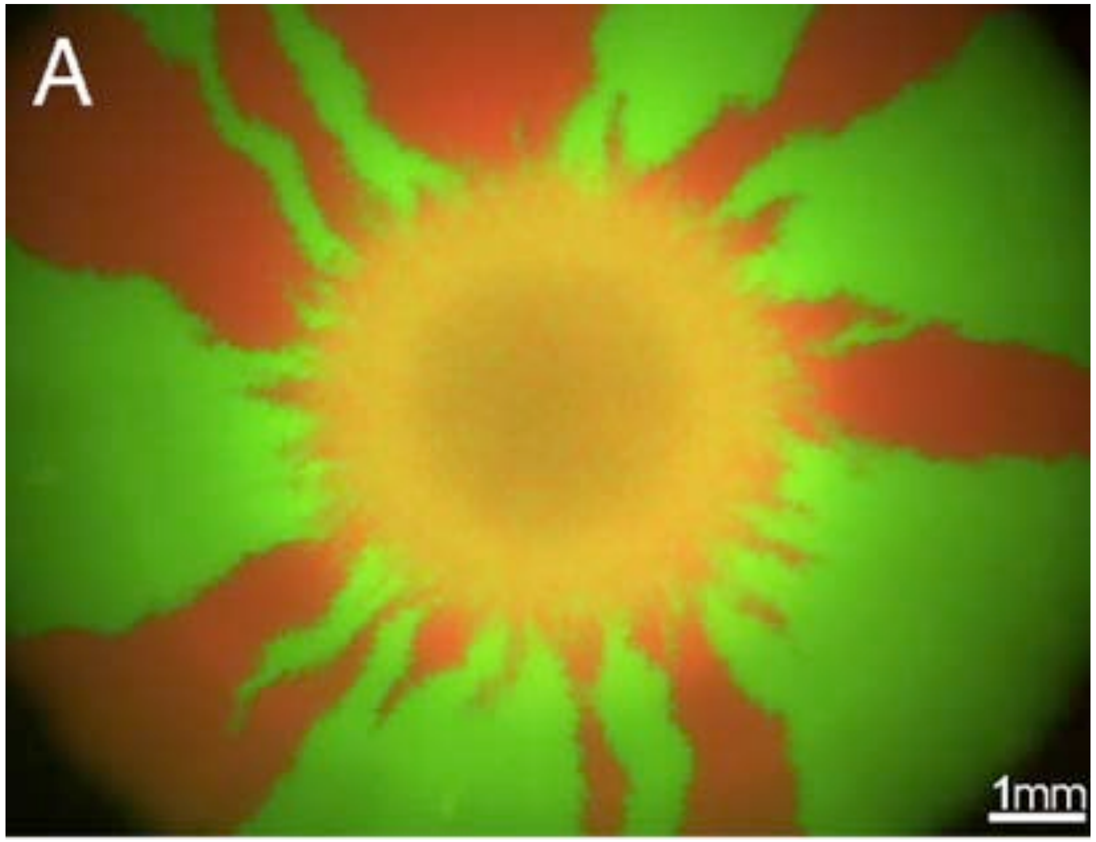
# Growth, competition, and cooperation in spatial population genetics

Simone Pigolotti
KITP, 24/01/2013

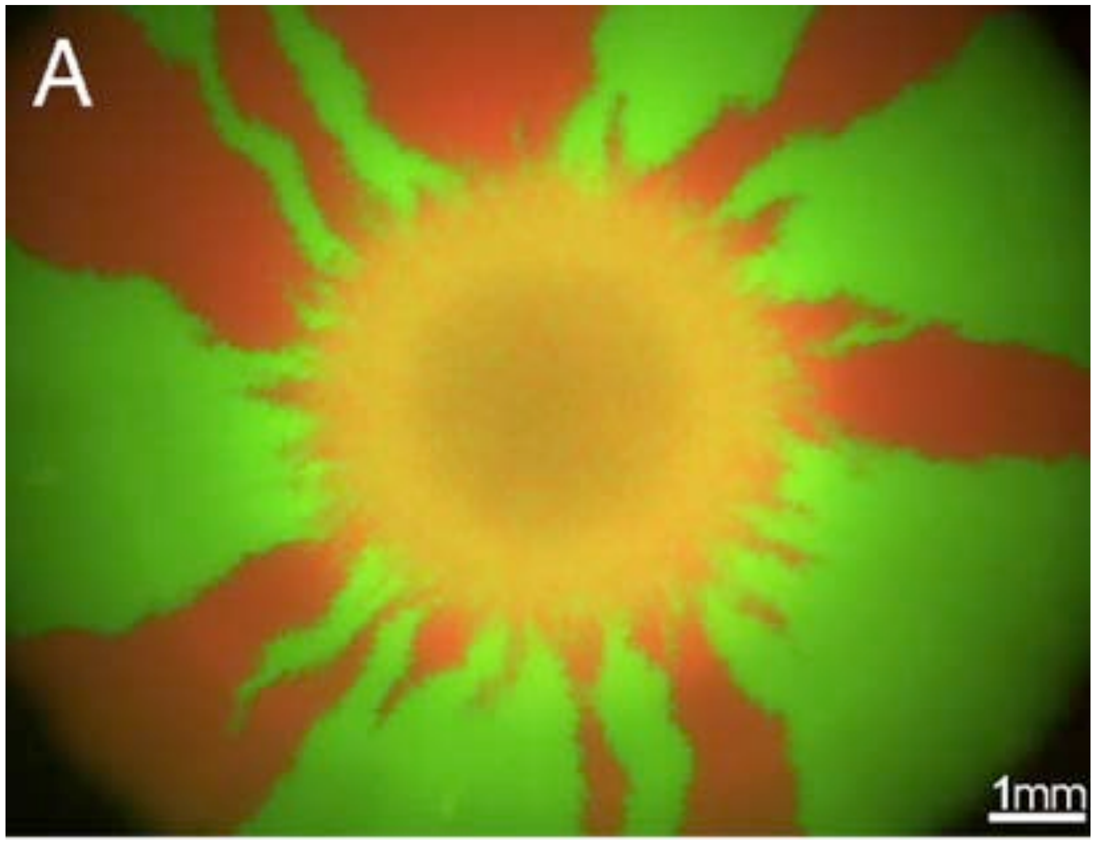
# Competition



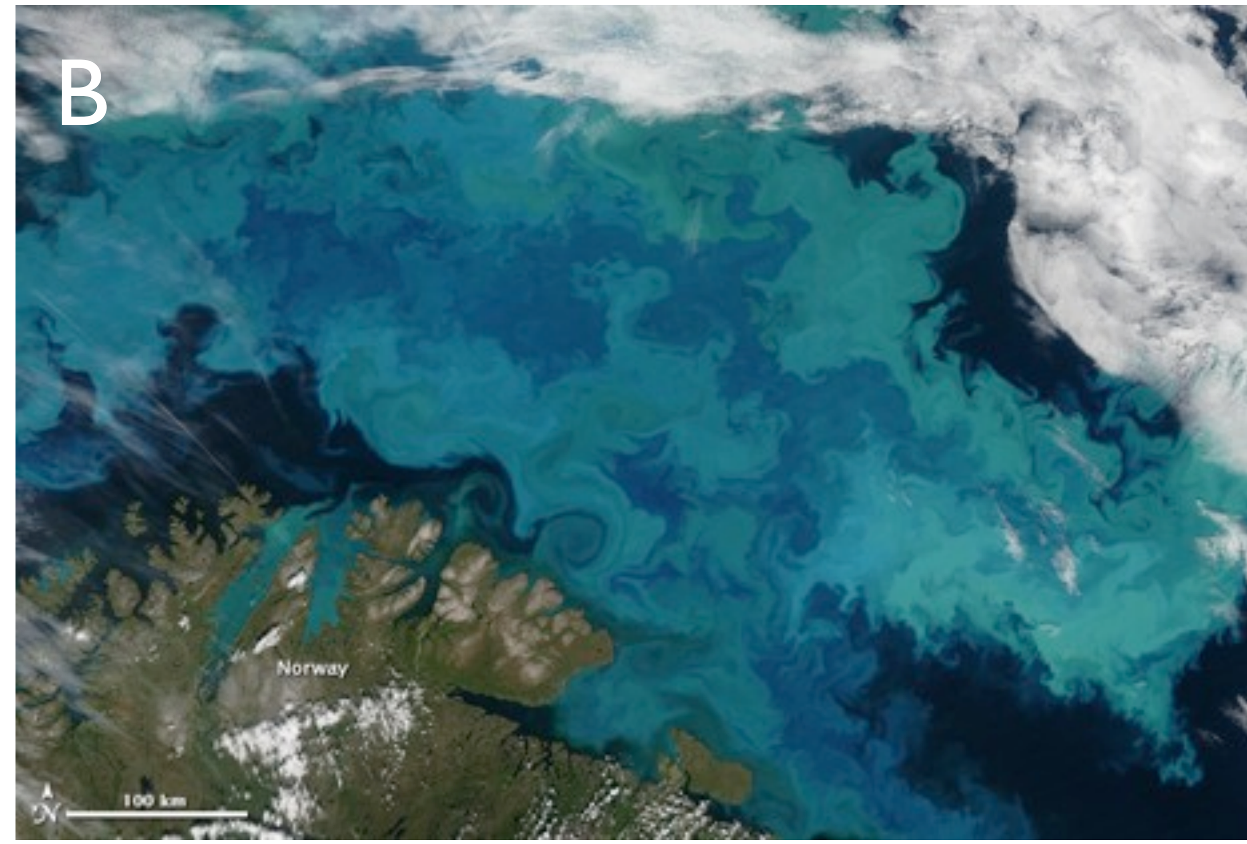

growth of a colony of two neutral E.Coli strains

Hallatscheck and Nelson (2007)

# Competition in the ocean




?

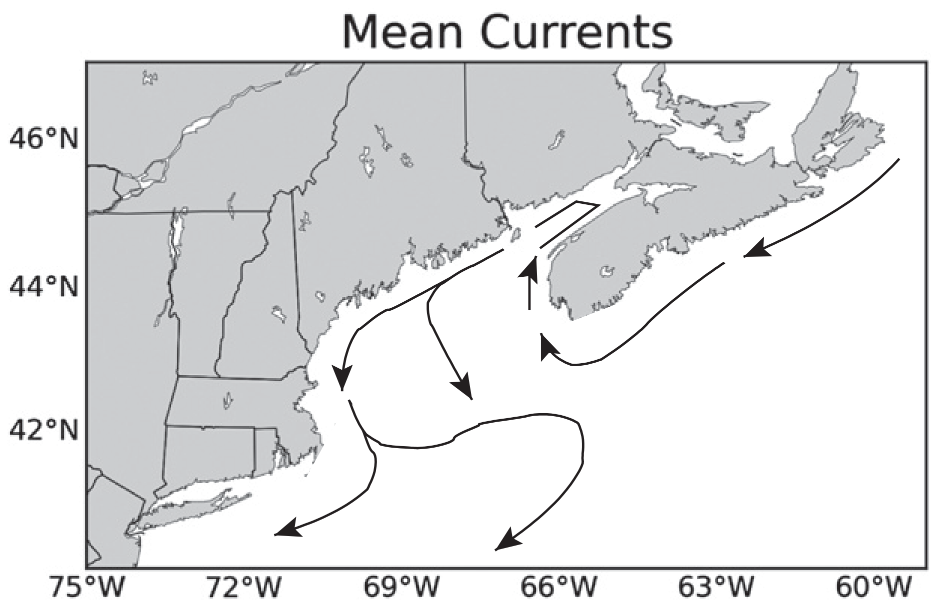


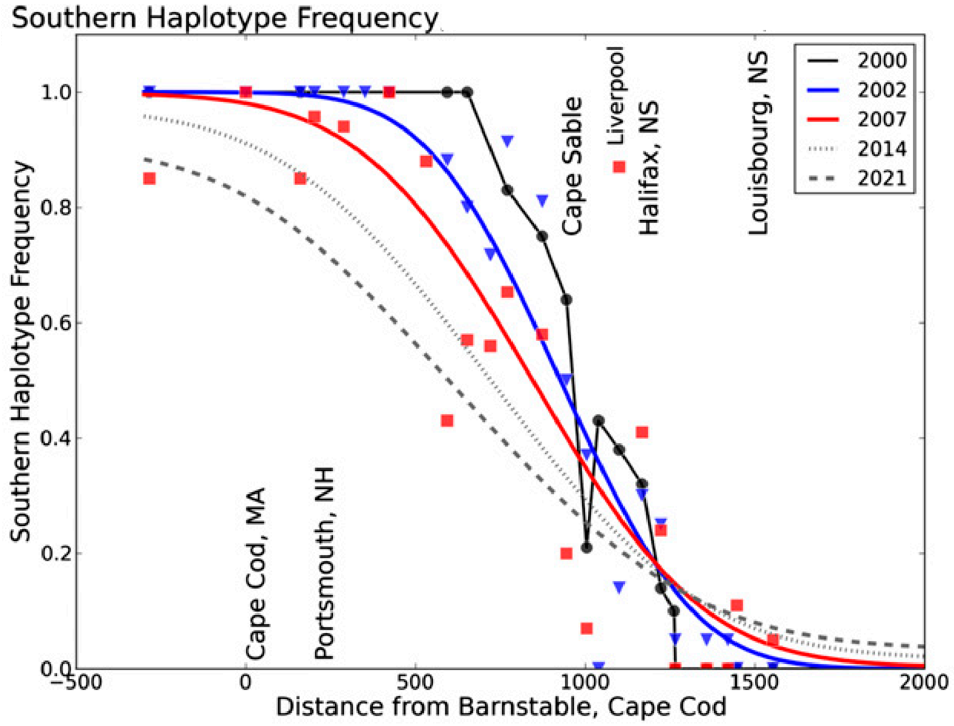

growth of a colony of two neutral
E.Coli strains

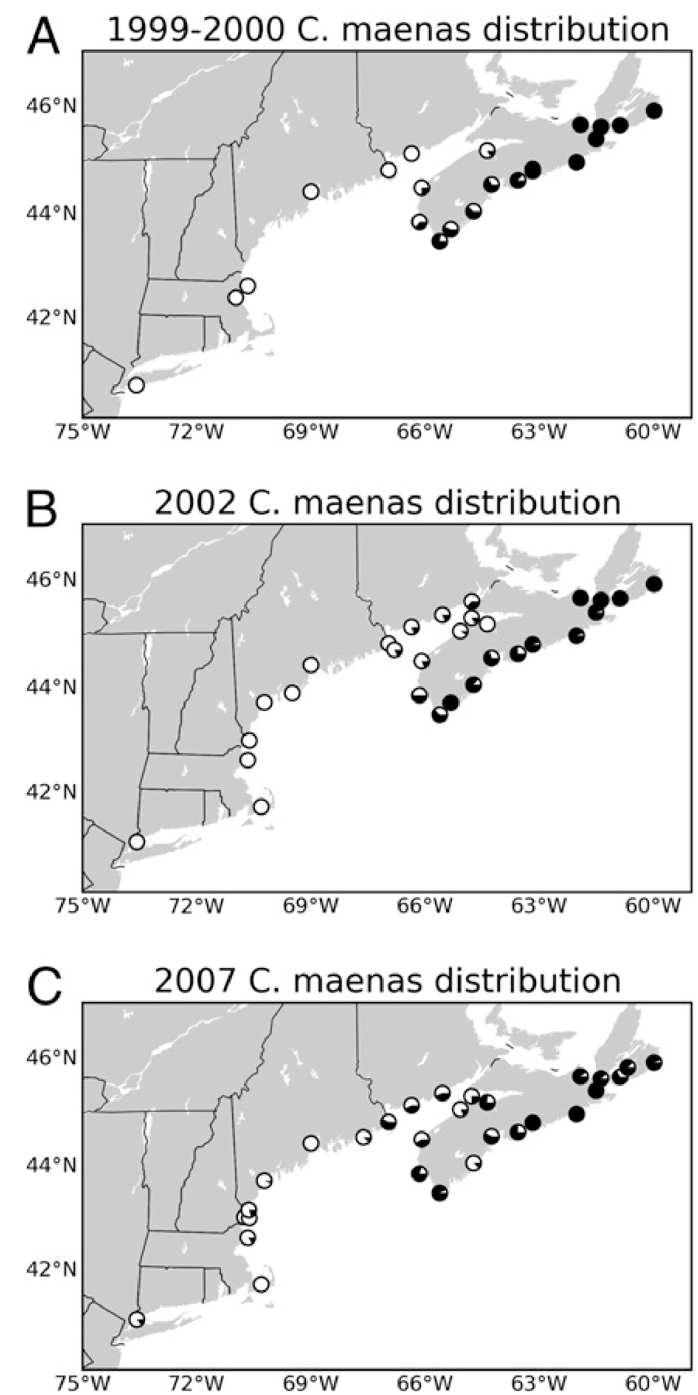
plankton bloom in the Barents sea

Hallatscheck and Nelson (2007)
Tel et al. (2005)

# Coastal competition and transport



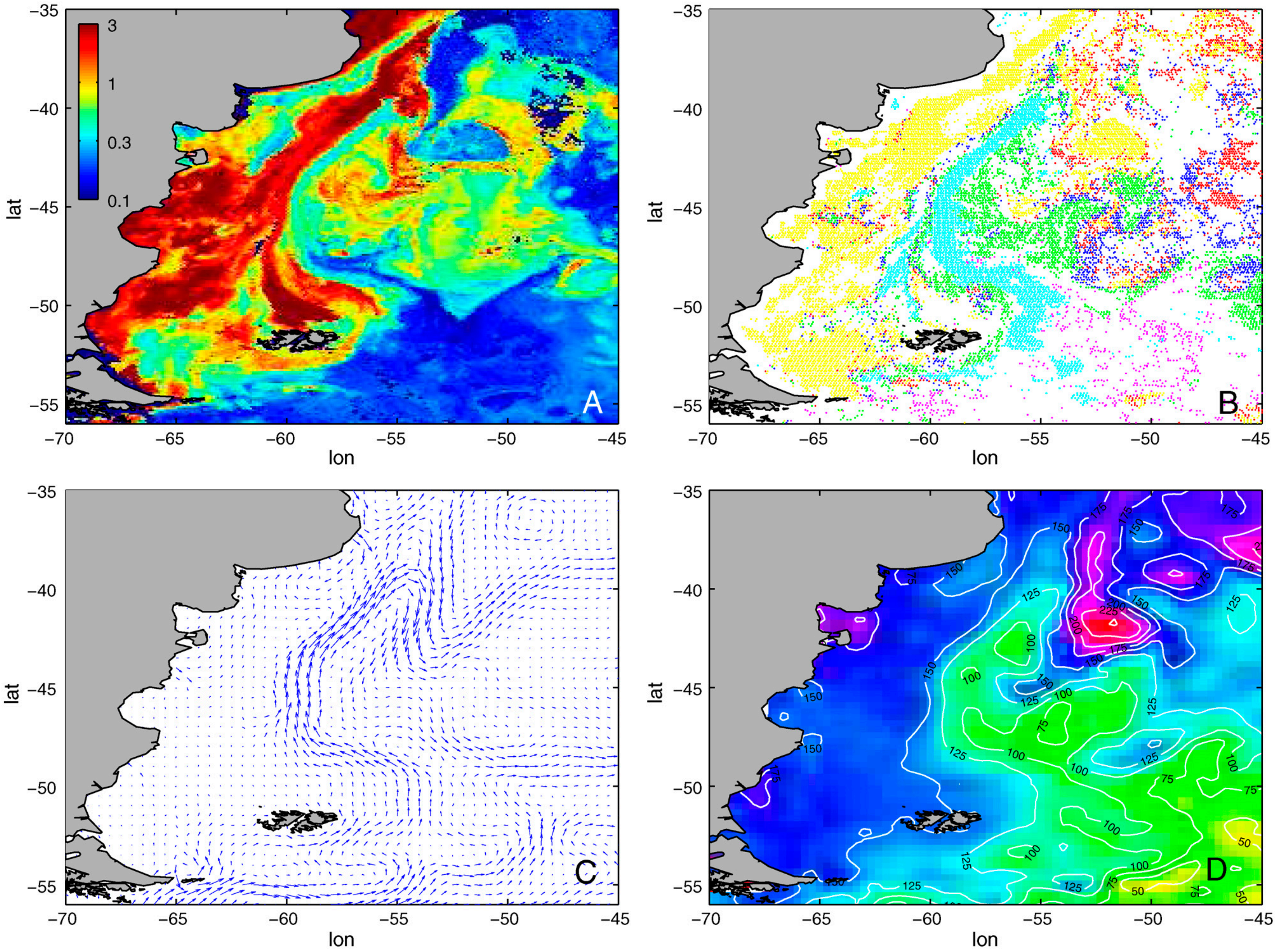




Invasion of a neutral variant of green crab along the eastern north american coast
Transport of larvae from currents (rather than fitness) determines invasion

Pringle et al. (2011)

# Phytoplankton types




A: total clorophyll density
B: phytoplankton types
C: average flow
D: sea surface height

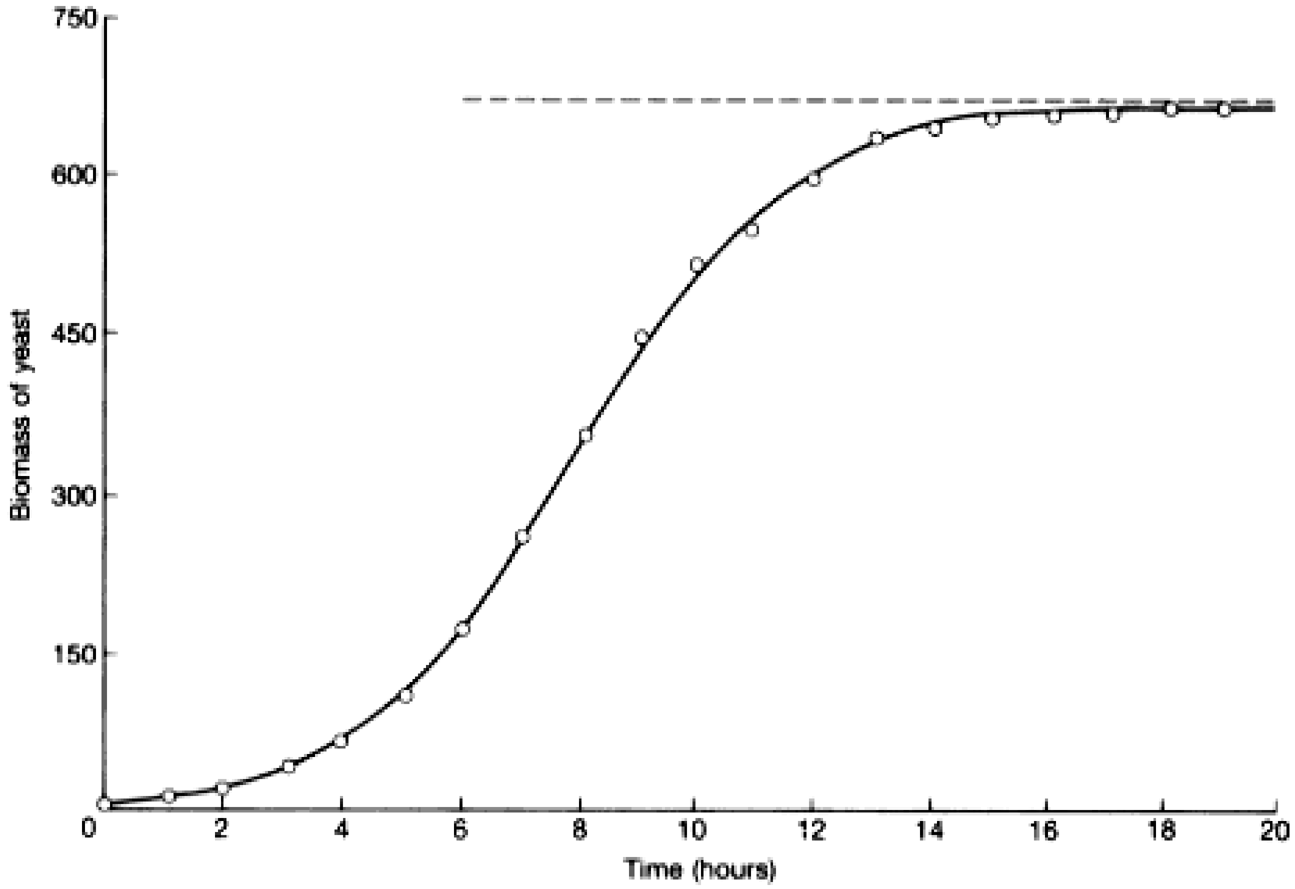
F. D'Ovidio et al. (2010)

# Logistic growth

$$\frac{d}{dt}c = ac - bc^2$$

- exponential growth at small density
- saturation at higher density (finite resources)

interpretation: growth of a population
OR spread in a population of an advantageous mutation




from J. Maynard Smith, “Evolutionary Genetics”, 1998

# Fisher equation

$$\partial_t c = D\partial_x^2 c + sc(1-c)$$

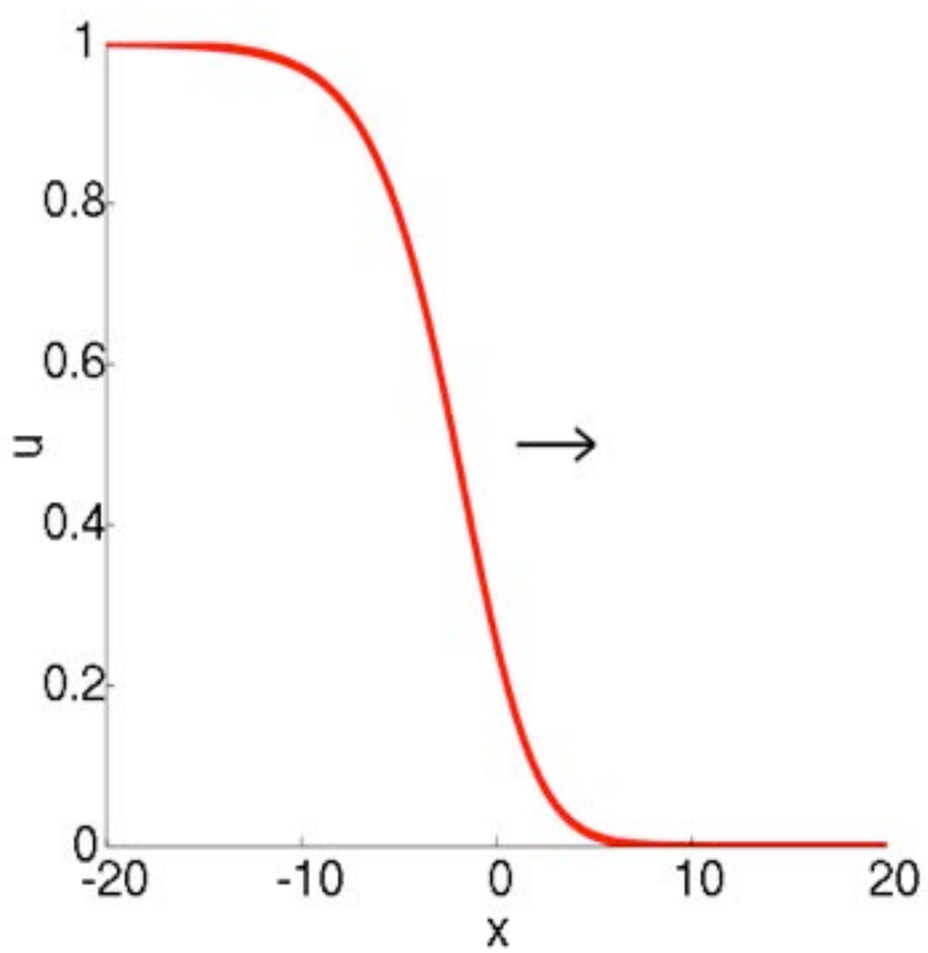
Spread of a population (or advantageous mutation) in space

Fisher (1937)

# Fisher equation

$$\partial_t c = D\partial_x^2 c + sc(1-c)$$

Spread of a population (or advantageous mutation) in space

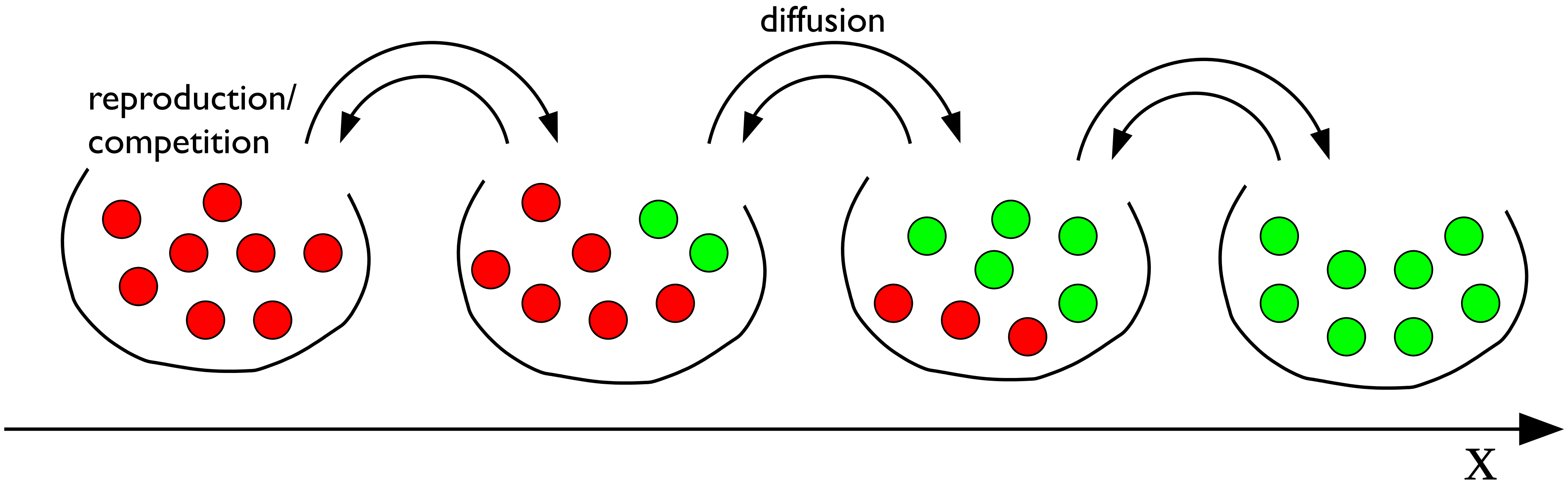



Basic result: propagating front of velocity

$$v = \sqrt{2Ds}$$

Fisher (1937)

# Stochasticity and the stepping stone model




continuum limit: stochastic Fisher equation

$$\partial_t c = D\partial_x^2 c + \mu c(1-c) + \sqrt{2c(1-c)/N}\xi$$

where:

c(x,t) = fraction of one of the two species
$\mu$ = selective advantage
N = local population size
D = diffusion constant

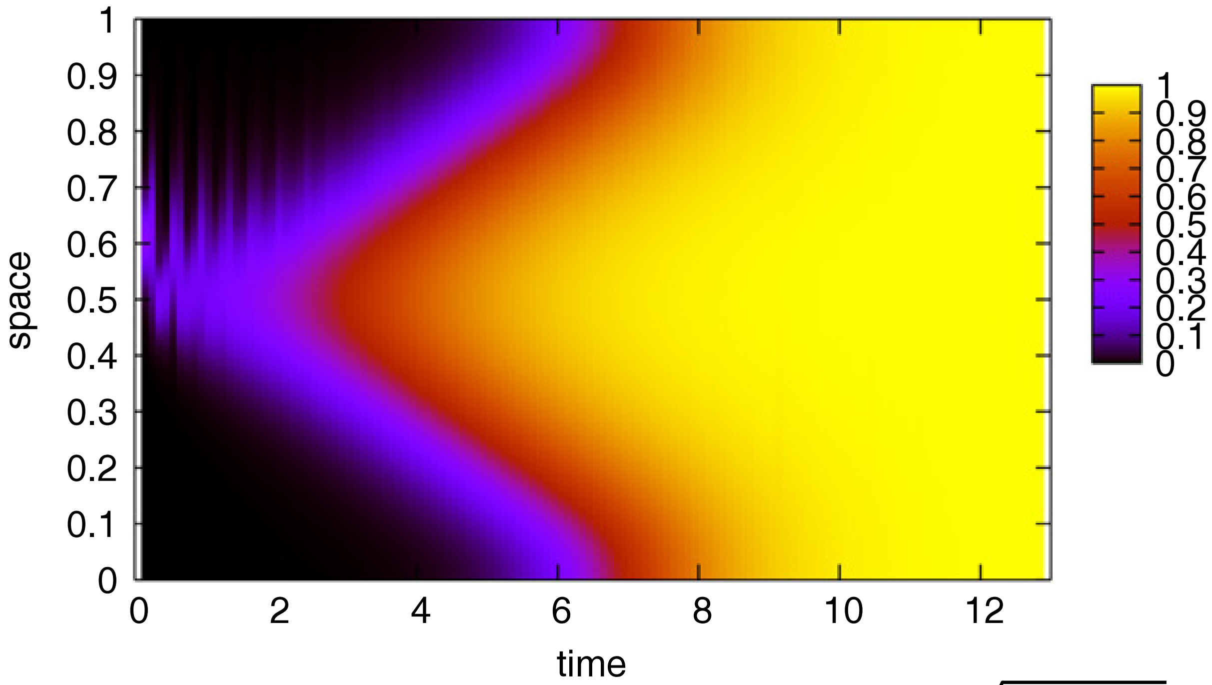
Kimura et al (1964)

# Two different fixation mechanisms

stochastic Fisher equation

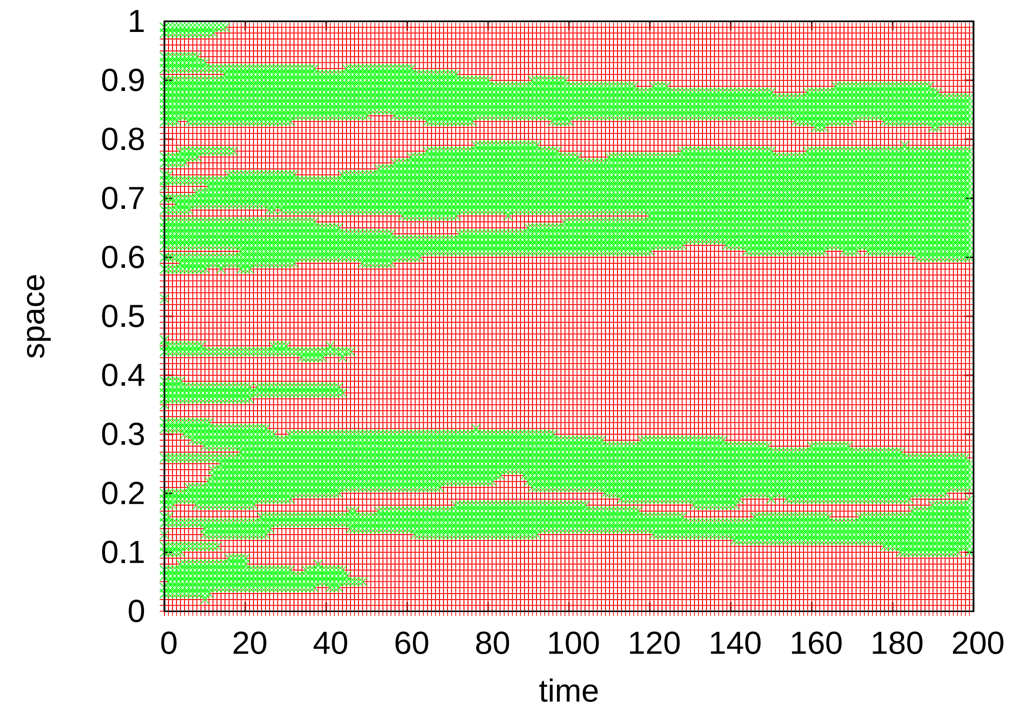
$$\partial_t c = D\partial_x^2 c + \mu c(1-c) + \sqrt{2c(1-c)/N}\xi$$

$\mu \gg 1/N$




Fisher wave, speed = $\sqrt{2D\mu}$

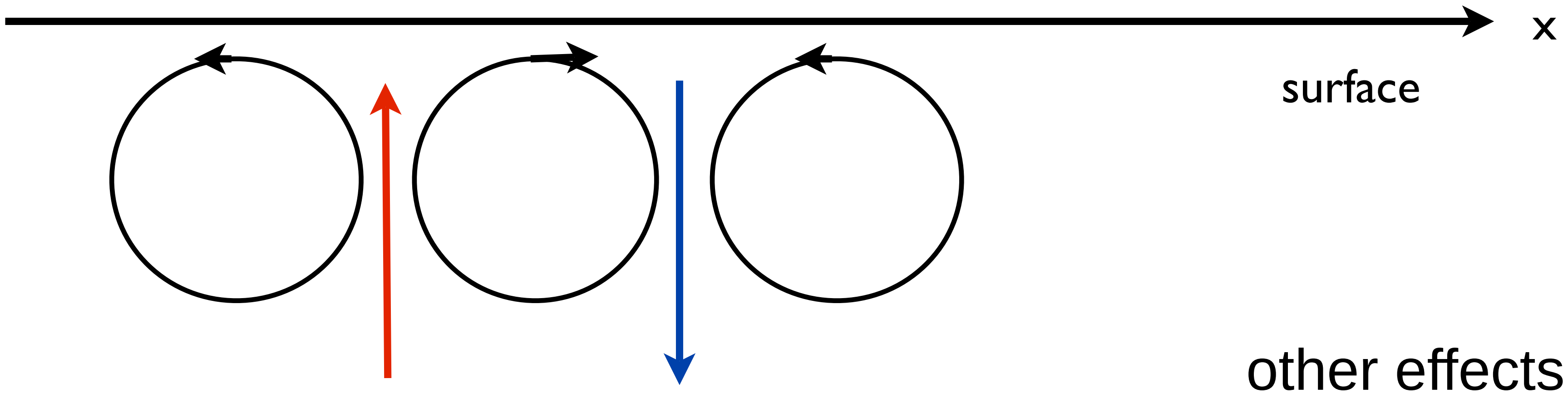
$\mu = 0$




Stochastic fixation

# Overshooting the carrying capacity

forces affecting the density of individuals




Upwelling - large nutrients concentration

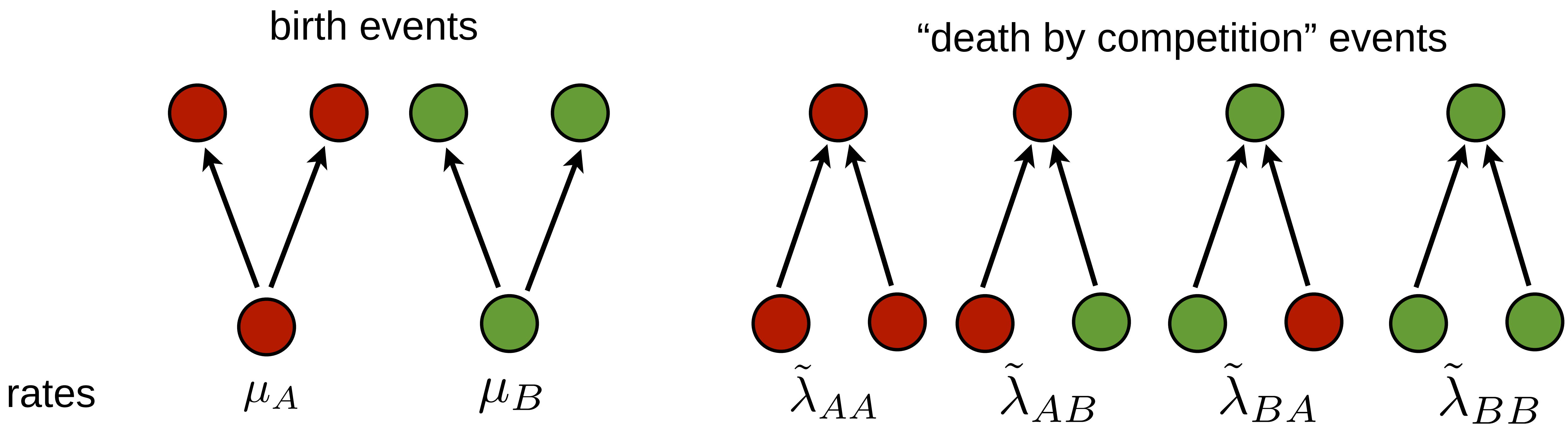
Downwelling - low nutrients concentration

other effects:
- clustering of finite-size particles
- inertial effects
- gyrotaxis (swimming)

$$\partial_t c = -\partial_x [v(x)c] + D\partial_x^2 c + \mu c(1-c) + \sqrt{2c(1-c)/N}\xi$$

Problem: c>1 leads to imaginary noise

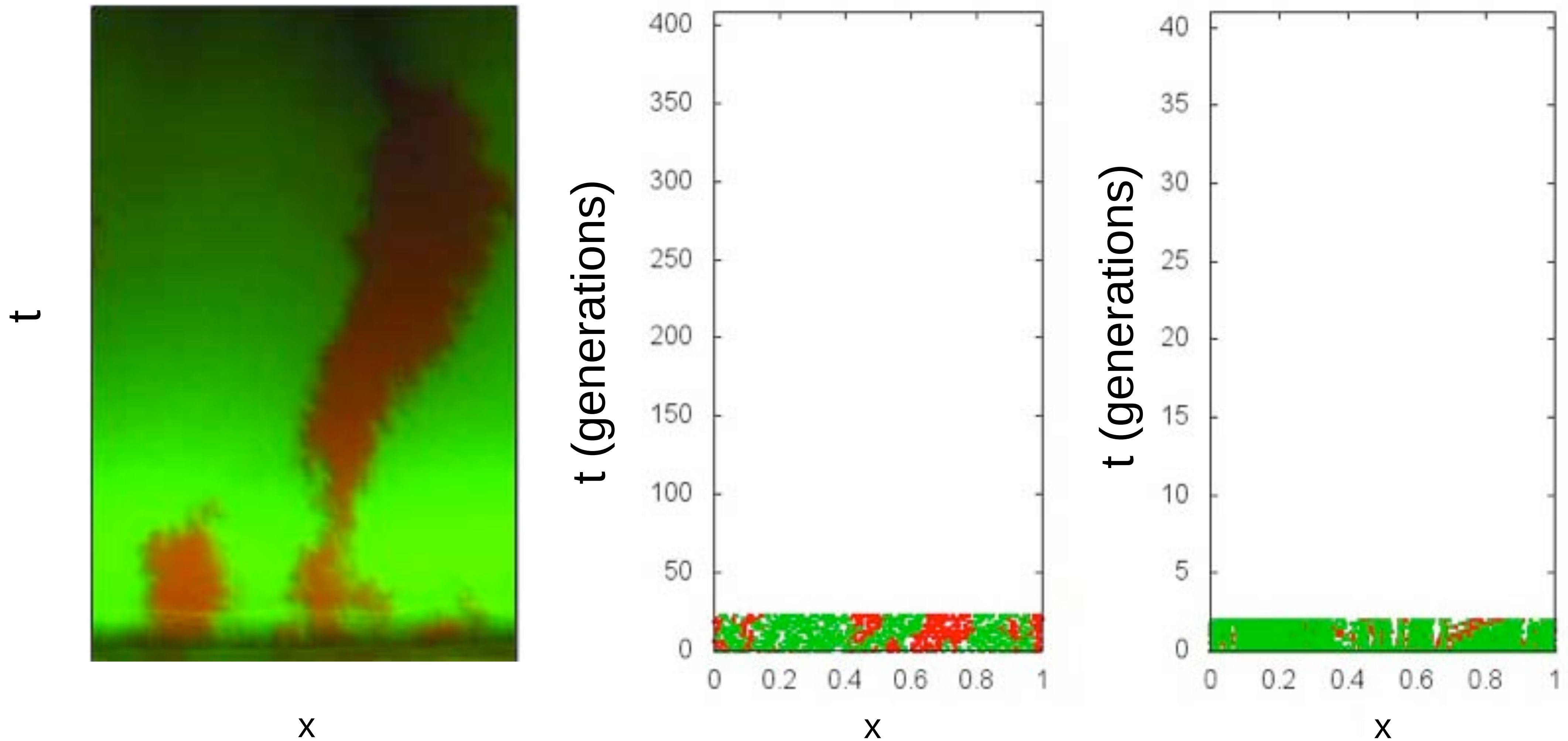
# Particle model



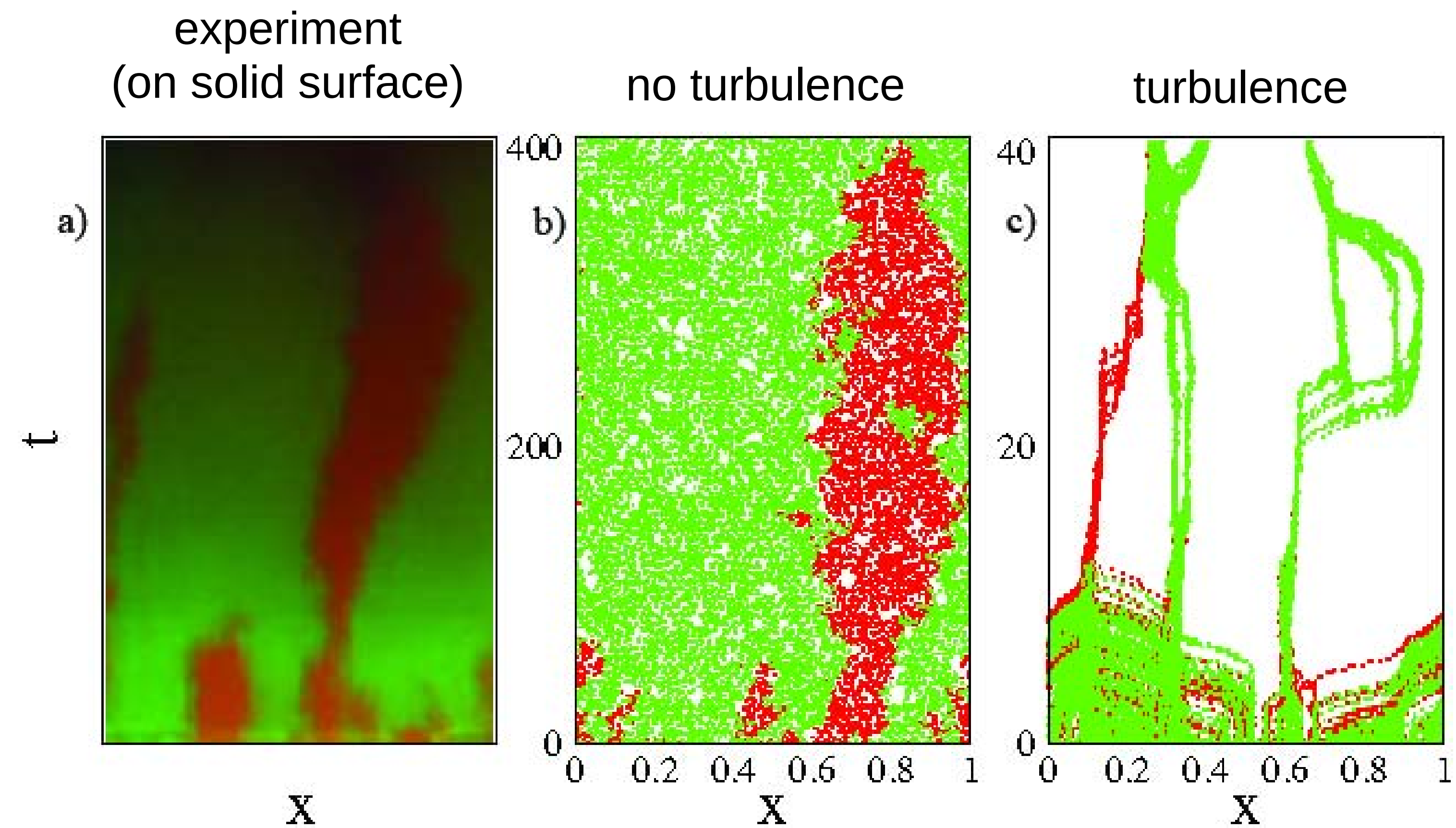

- individuals are advected and diffuse in space (Lagrangian description)
- reaction are implemented like in stochastic chemical kinetics

SP, Benzi, Jensen, Nelson (2012)

experiment (on solid surface) | simulation (no turbulence) | simulation turbulence)



# Eqs. for the densities




equations for the densities of A and B particles, $c_A(x,t)$ and $c_B(x,t)$

fluid transport — diffusion — birth/death processes — number fluctuations

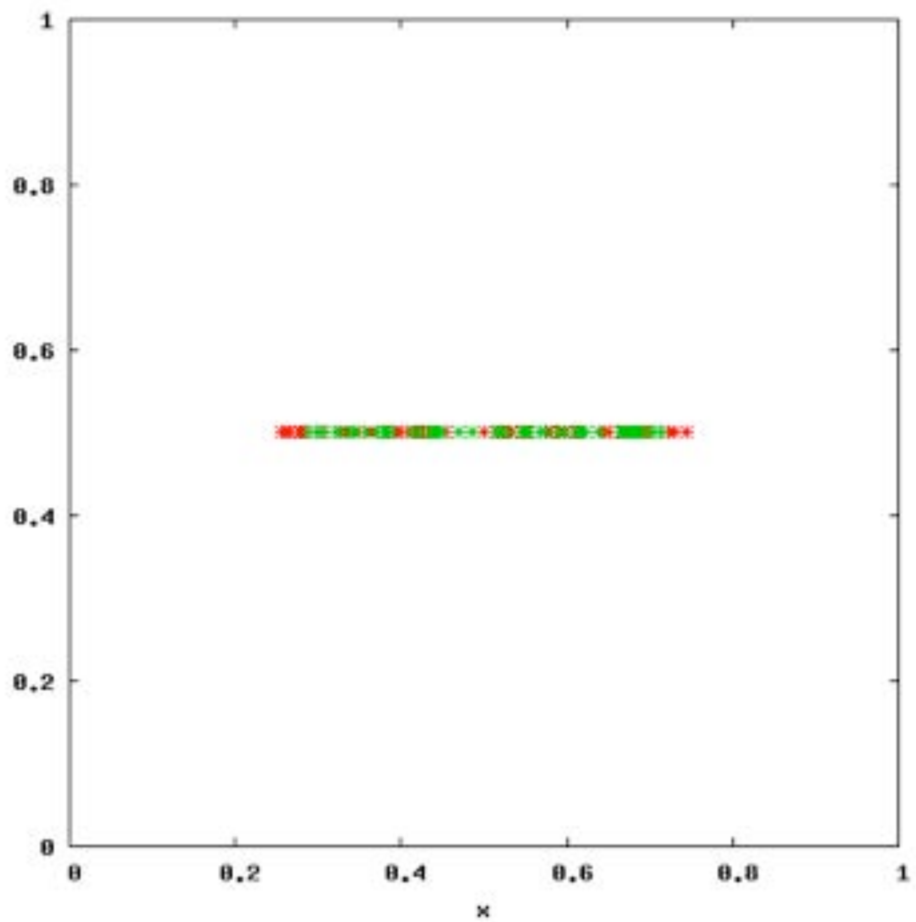
$$\partial_t c_A(x,t) = -\partial_x[v(x,t)c_A] + D\nabla^2 c_A + c_A(\mu_A - \lambda_{AA}c_A - \lambda_{AB}c_B) + \sigma_A \xi(x,t)$$
$$\partial_t c_B(x,t) = -\partial_x[v(x,t)c_A] + D\nabla^2 c_B + c_B(\mu_B - \lambda_{BA}c_A - \lambda_{BB}c_B) + \sigma_B \xi'(x,t)$$

$$\sigma_i^2 = \frac{\mu_i c_i (1 + \lambda_{iA}c_A + \lambda_{iB}c_B)}{N}$$

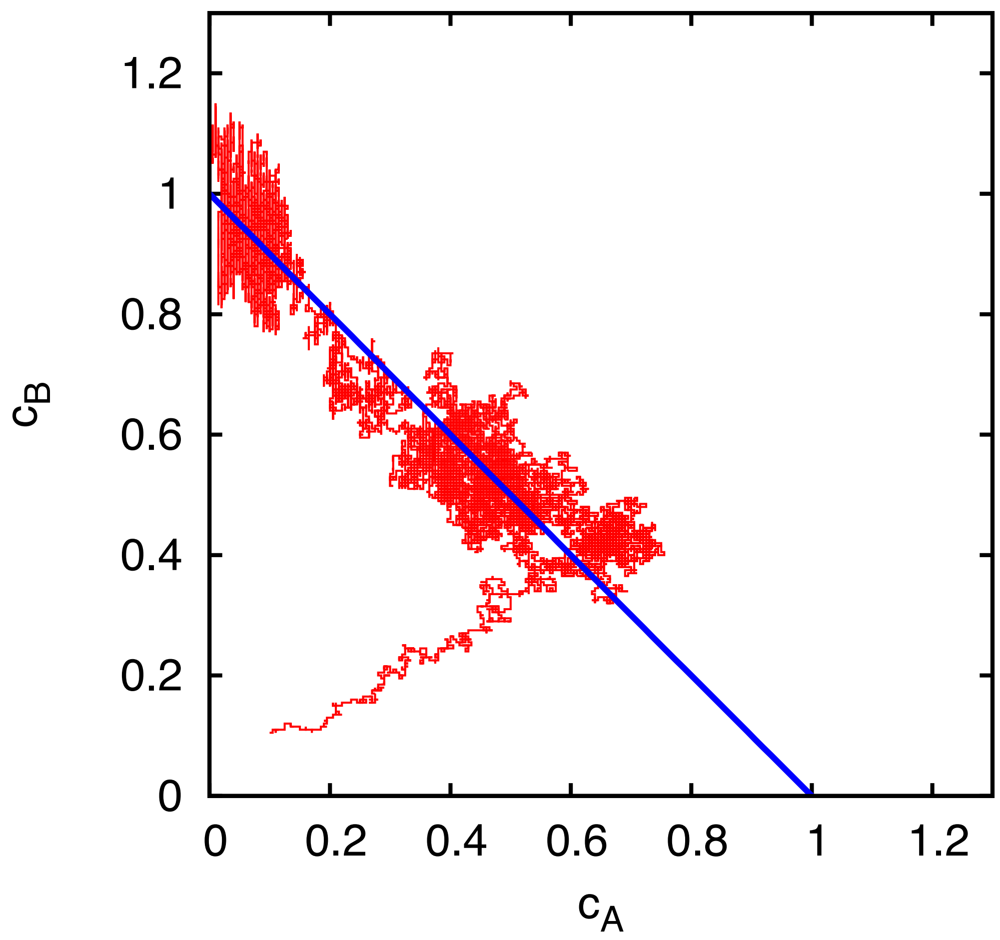
noise is well defined also when c>1

# Example: neutral, no flow

- coarsening dynamics, fixation time is determined by diffusion




$D = 2\ 10^{-4}, \mu = 1$




neutral dynamics:

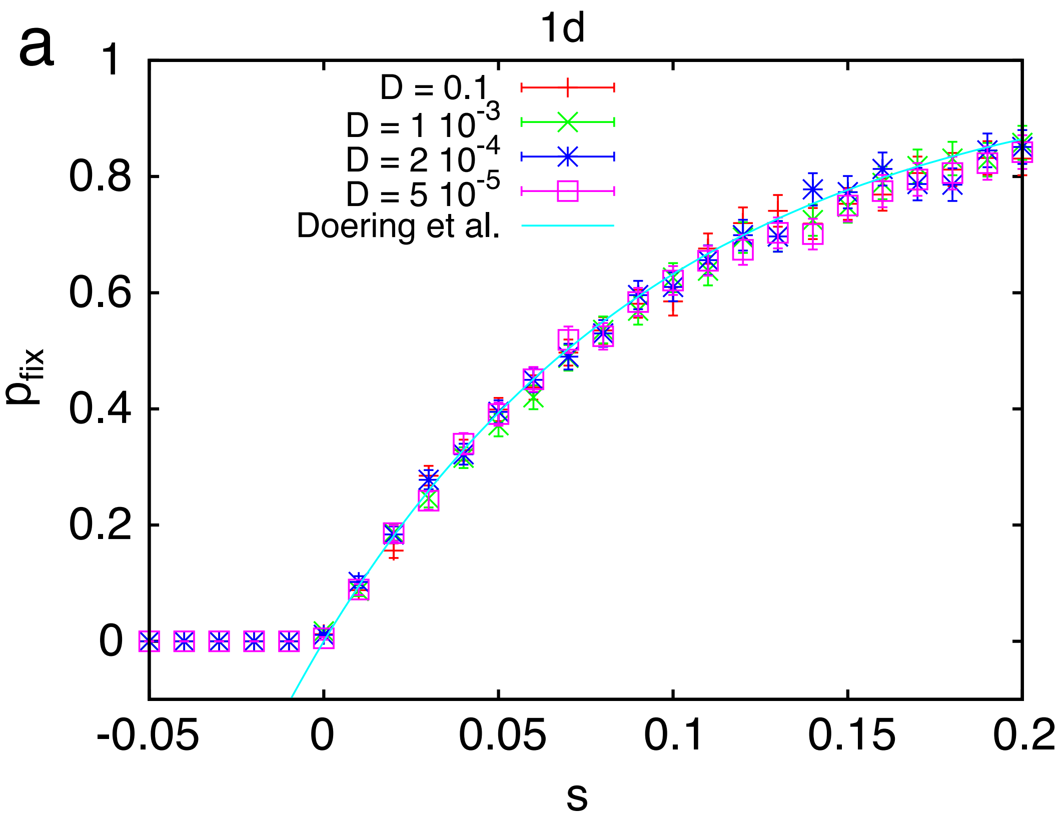
$$
\begin{aligned}
\partial_t c_A(x,t) &= D\nabla^2 c_A + \mu c_A(1 - c_A - c_B) + \sigma_A \xi(x,t) \\
\partial_t c_B(x,t) &= D\nabla^2 c_B + \mu c_B(1 - c_A - c_B) + \sigma_B \xi'(x,t)
\end{aligned}
$$

# Selective advantage

Species A reproduces faster (by a factor s)

$$\begin{aligned}\partial_t c_A(x,t) &= D\nabla^2 c_A + \mu c_A(1+s-c_A-c_B) + \sigma_A \xi(x,t)\\ \partial_t c_B(x,t) &= D\nabla^2 c_B + \mu c_B(1-c_A-c_B) + \sigma_B \xi'(x,t)\end{aligned}$$

stochastic Fisher equation is recovered for the relative fraction $f=c_A/(c_A+c_B)$
- quantitative agreement in absence of flows




Fixation probability

$$p_{fix} = 1 - \exp\left[-sN\int\ dx\ f(x,t=0)\right]$$

(indipendent of spatial diffusion)

SP, Benzi, Perlekar, Jensen, Toschi, Nelson (2013)

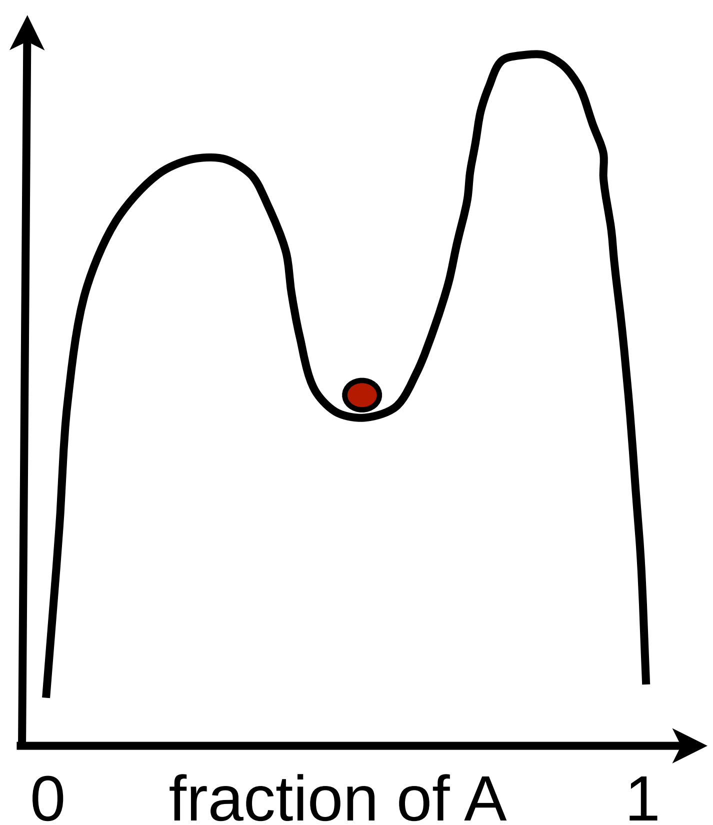
# Mutualism

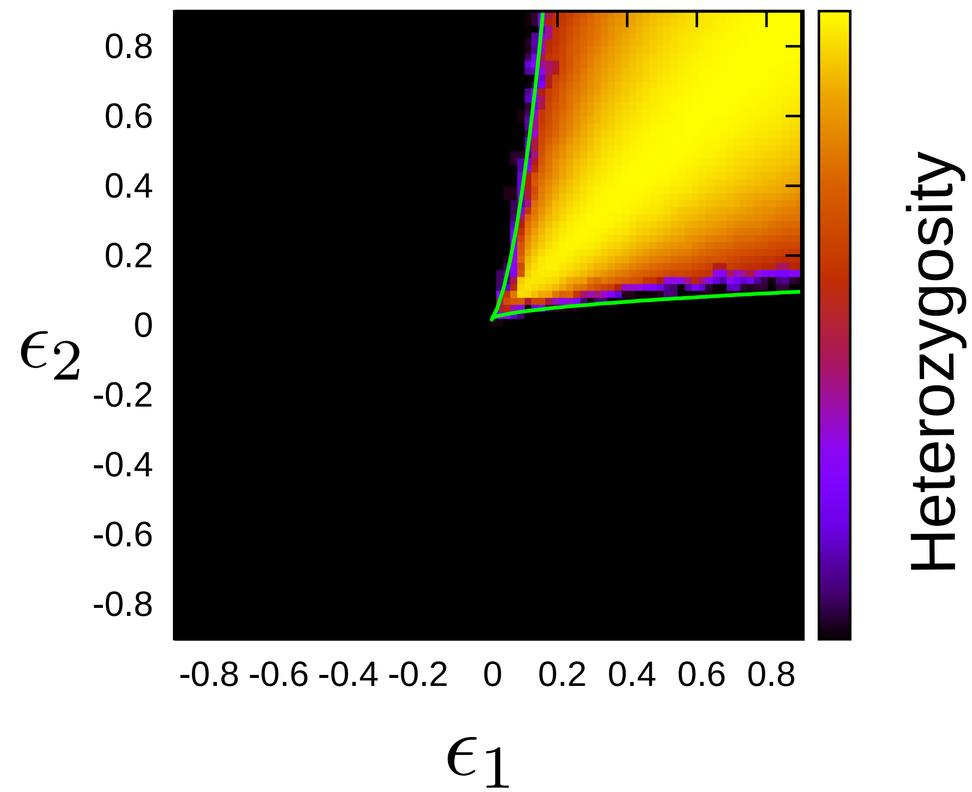
- reduced competition between alleles

$$\frac{d}{dt}c_A = \mu c_A(1 - c_A - c_B) + \epsilon_A c_A c_B + \text{noise}$$
$$\frac{d}{dt}c_B = \mu c_B(1 - c_A - c_B) + \epsilon_B c_A c_B + \text{noise}$$

mean field: exponentially long fixation times

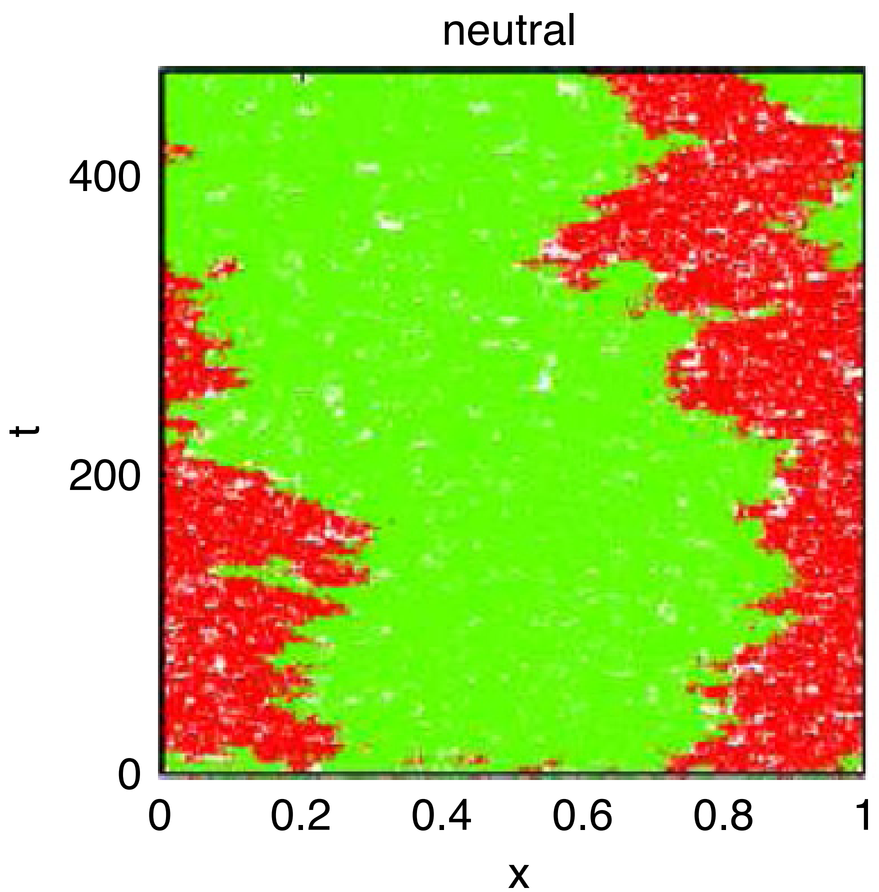
$$t^* \sim \exp\left[\frac{N}{2\mu}\frac{\min(\epsilon_A^2, \epsilon_B^2)}{\epsilon_A + \epsilon_B}\right].$$

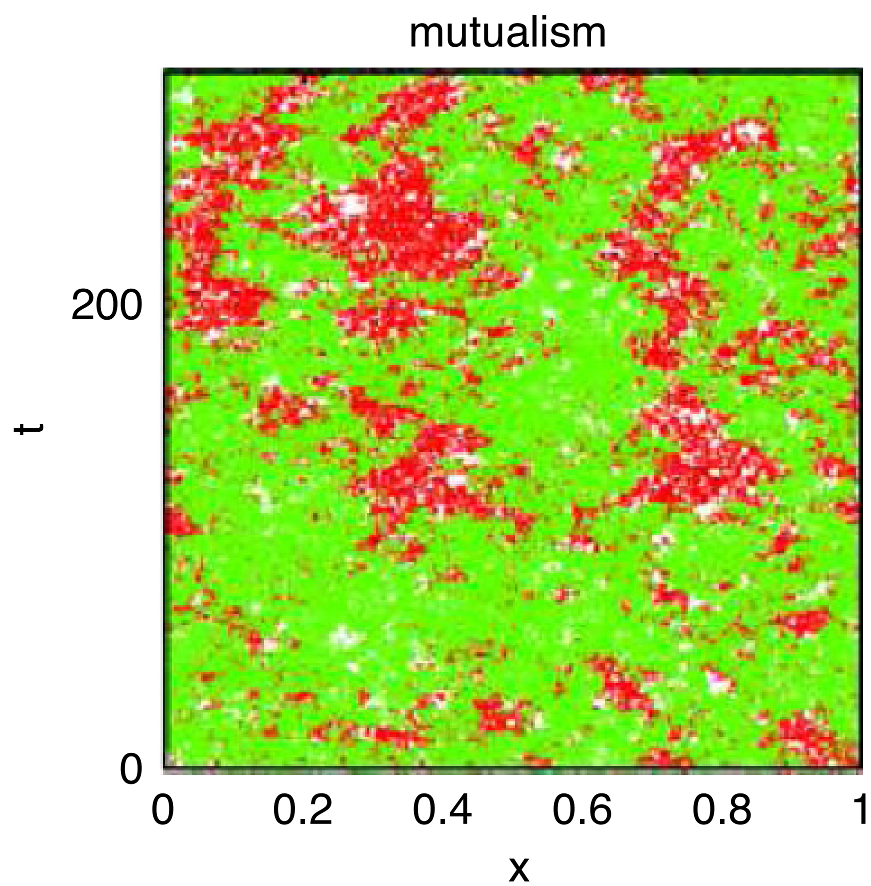


# Mutualism - 1d

$$\partial_t c_A(x,t) = D\nabla^2 c_A + \mu c_A(1 - c_A - c_B) + \epsilon_A c_A c_B + \sigma_A \xi(x,t)$$
$$\partial_t c_B(x,t) = D\nabla^2 c_B + \mu c_B(1 - c_A - c_B) + \epsilon_B c_A c_B + \sigma_B \xi'(x,t)$$



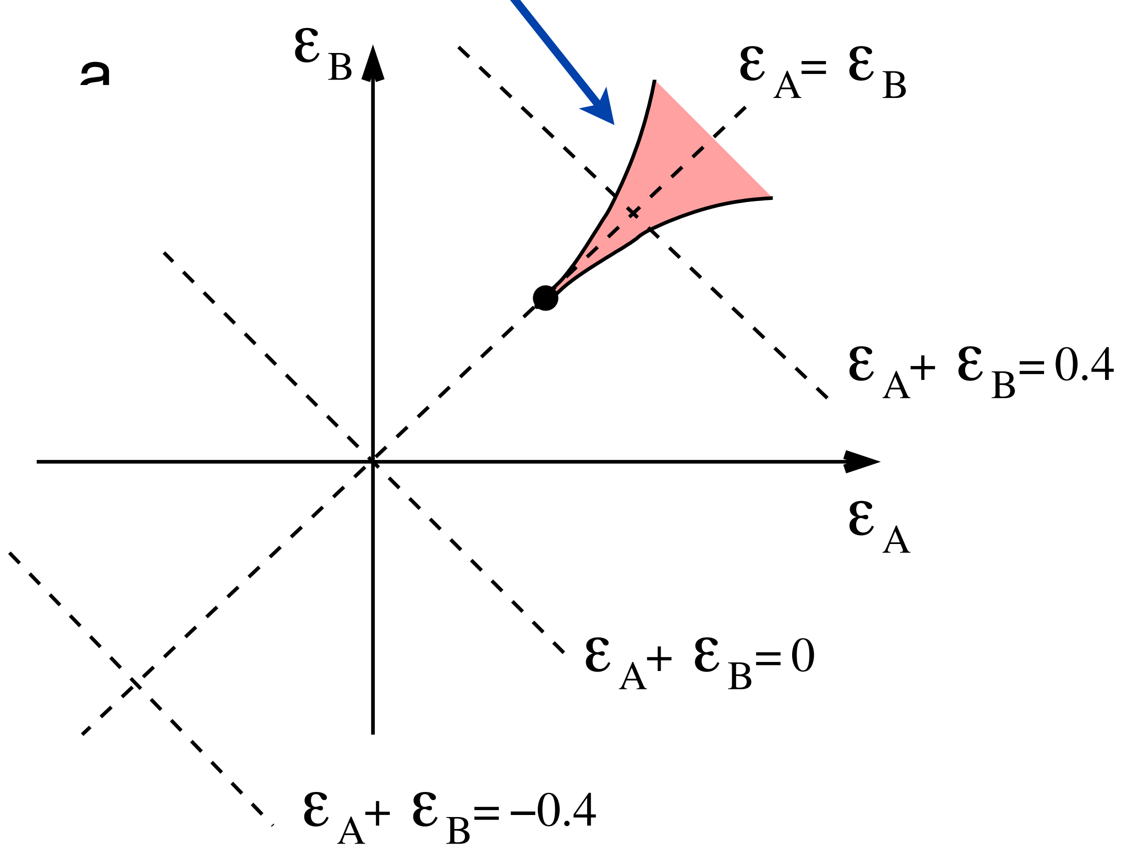



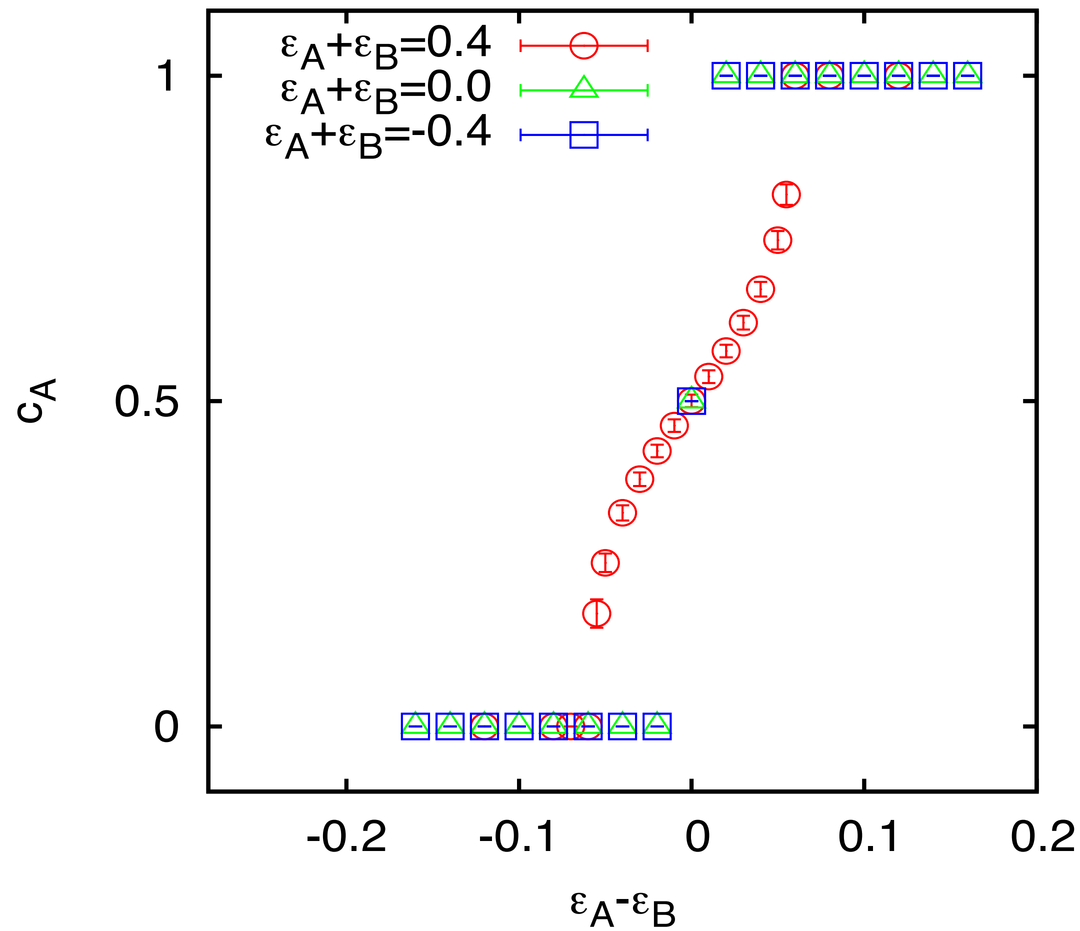

$\epsilon_A = \epsilon_B = 0.7$

# Mutualism - 1d

$$\partial_t c_A(x,t) = D\nabla^2 c_A + \mu c_A(1 - c_A - c_B) + \epsilon_A c_A c_B + \sigma_A \xi(x,t)$$
$$\partial_t c_B(x,t) = D\nabla^2 c_B + \mu c_B(1 - c_A - c_B) + \epsilon_B c_A c_B + \sigma_B \xi'(x,t)$$

stable coexistence region

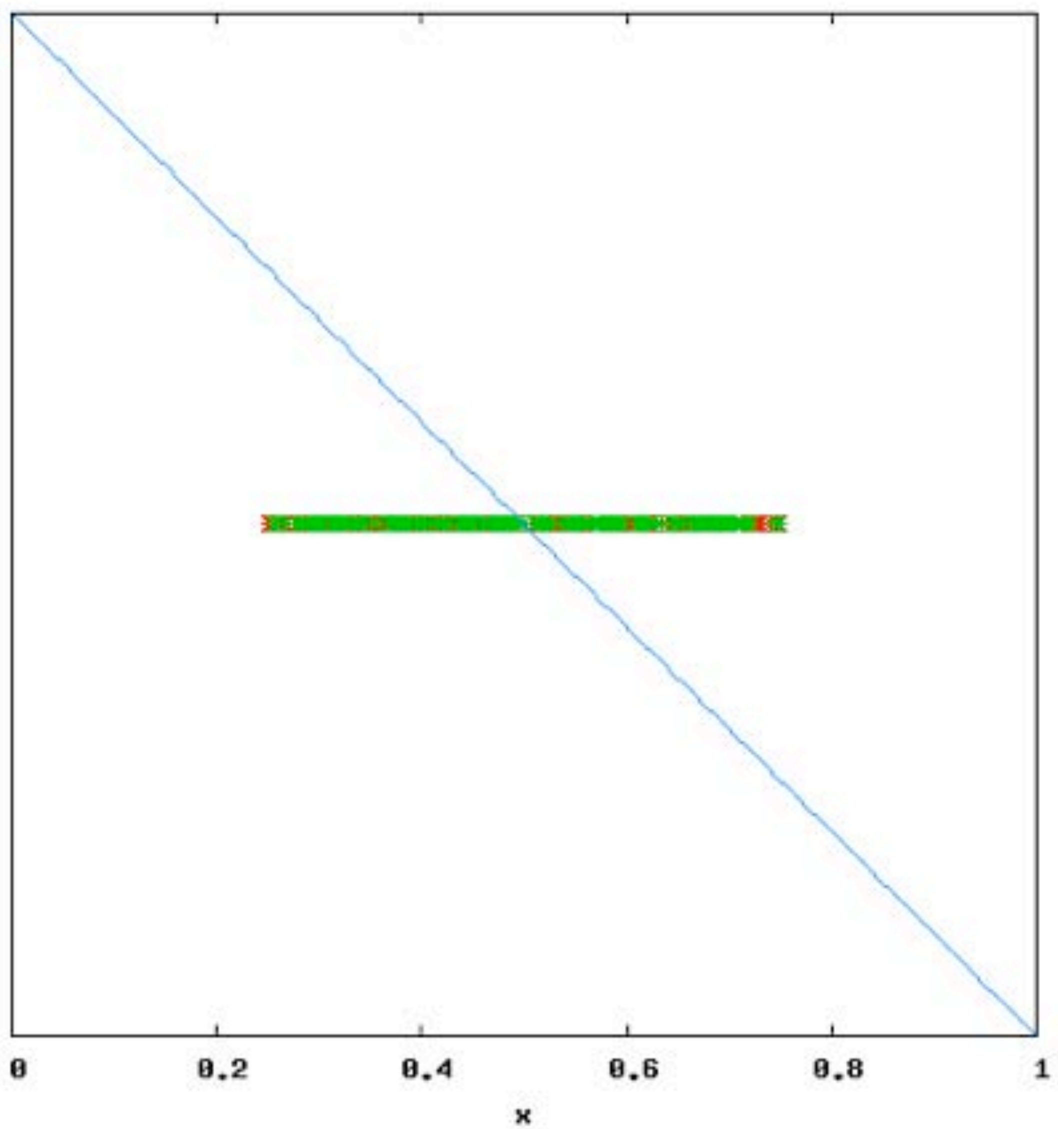



Korolev and Nelson (2011)
SP, Benzi, Perlekar, Jensen, Toschi, Nelson (2013)

# Flows: linear velocity field

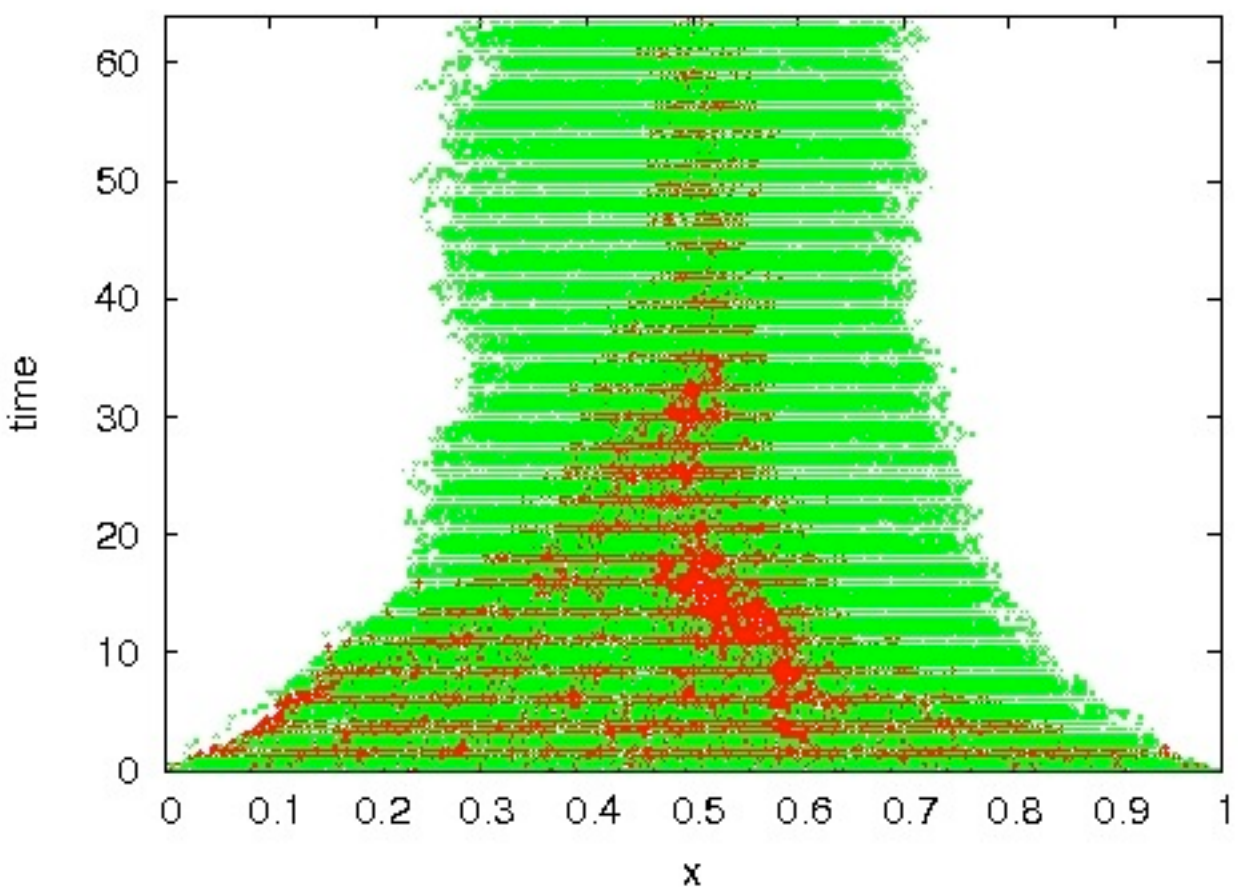
v(x)= -k x $\quad k = 0.075, D = 2\ 10^{-4}, \mu = 1$



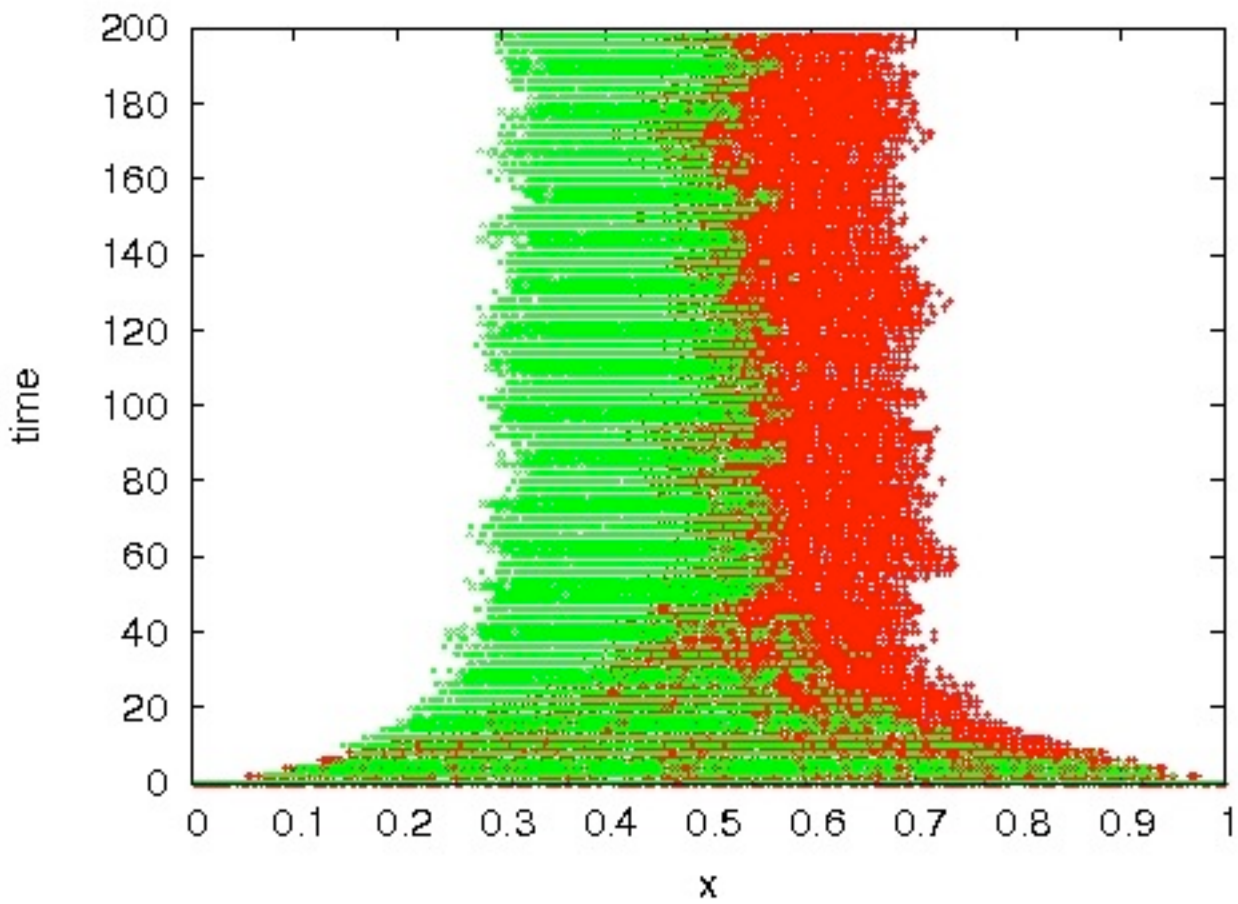

coexistence of neutral species

# Dynamics of boundaries

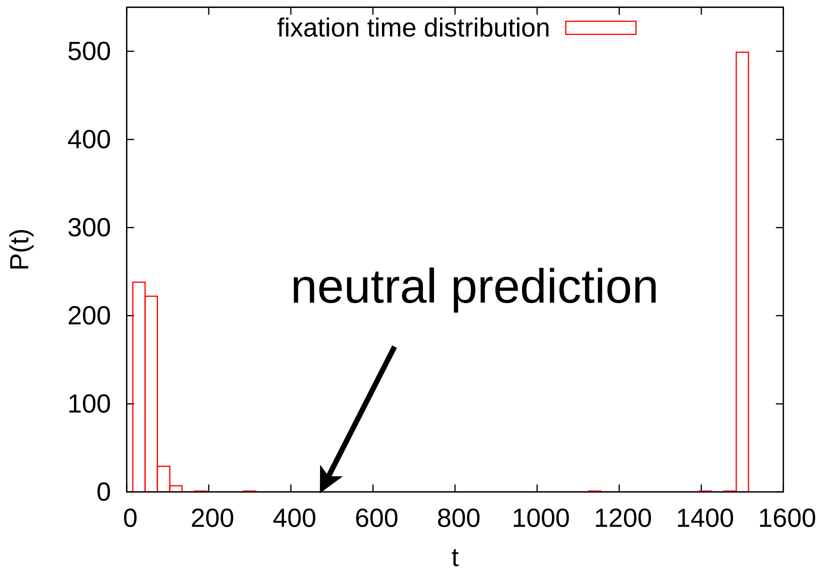
even number of boundaries, fast fixation




odd number of boundaries, demixing

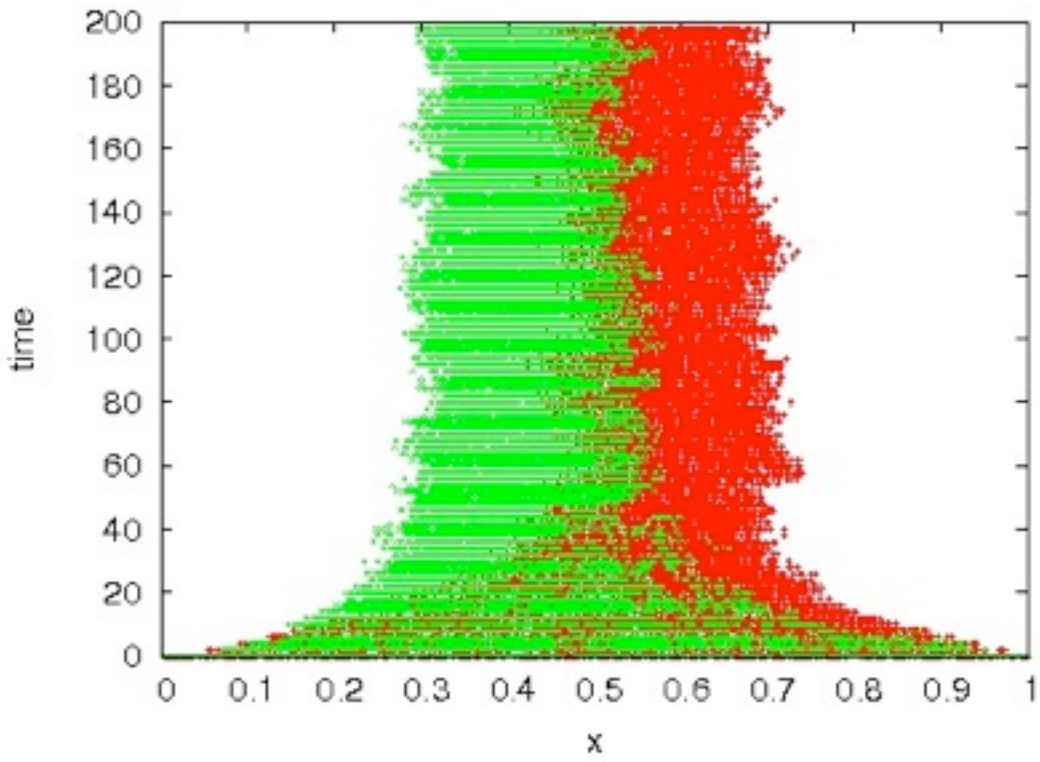



-> bimodal fixation time distribution

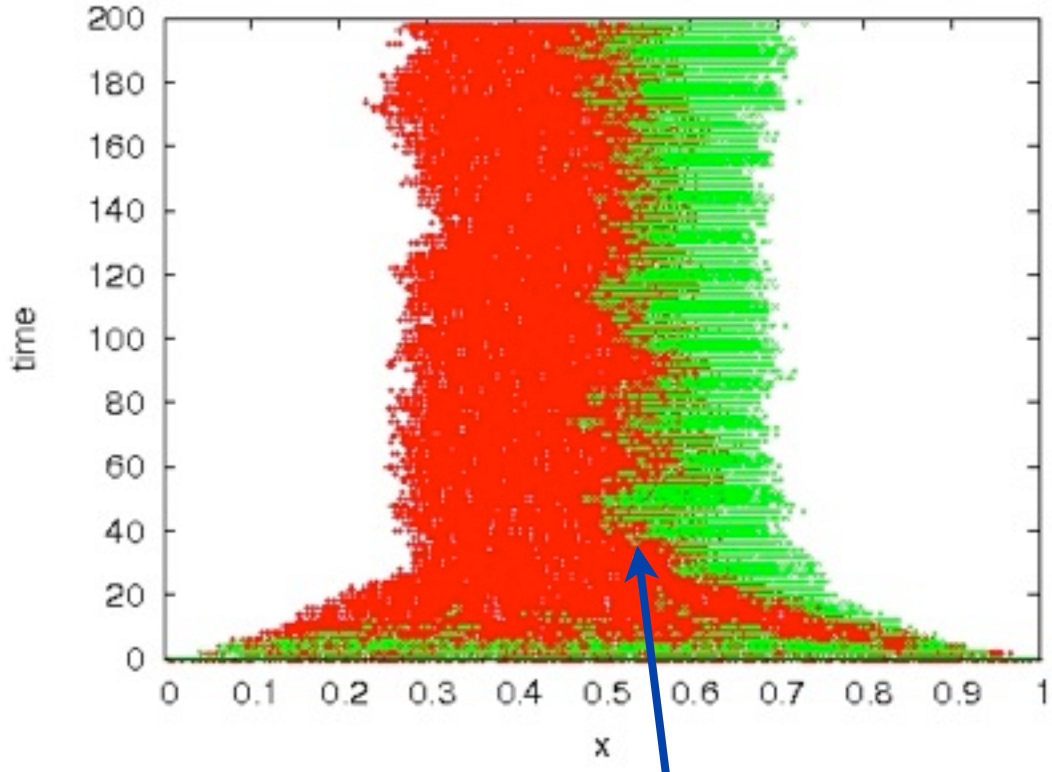


# Linear flow + reproductive advantage

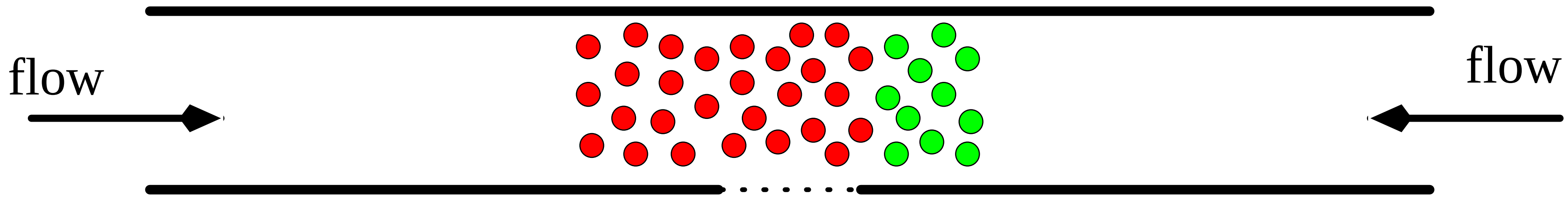
Neutral




Red reproduces 30% faster

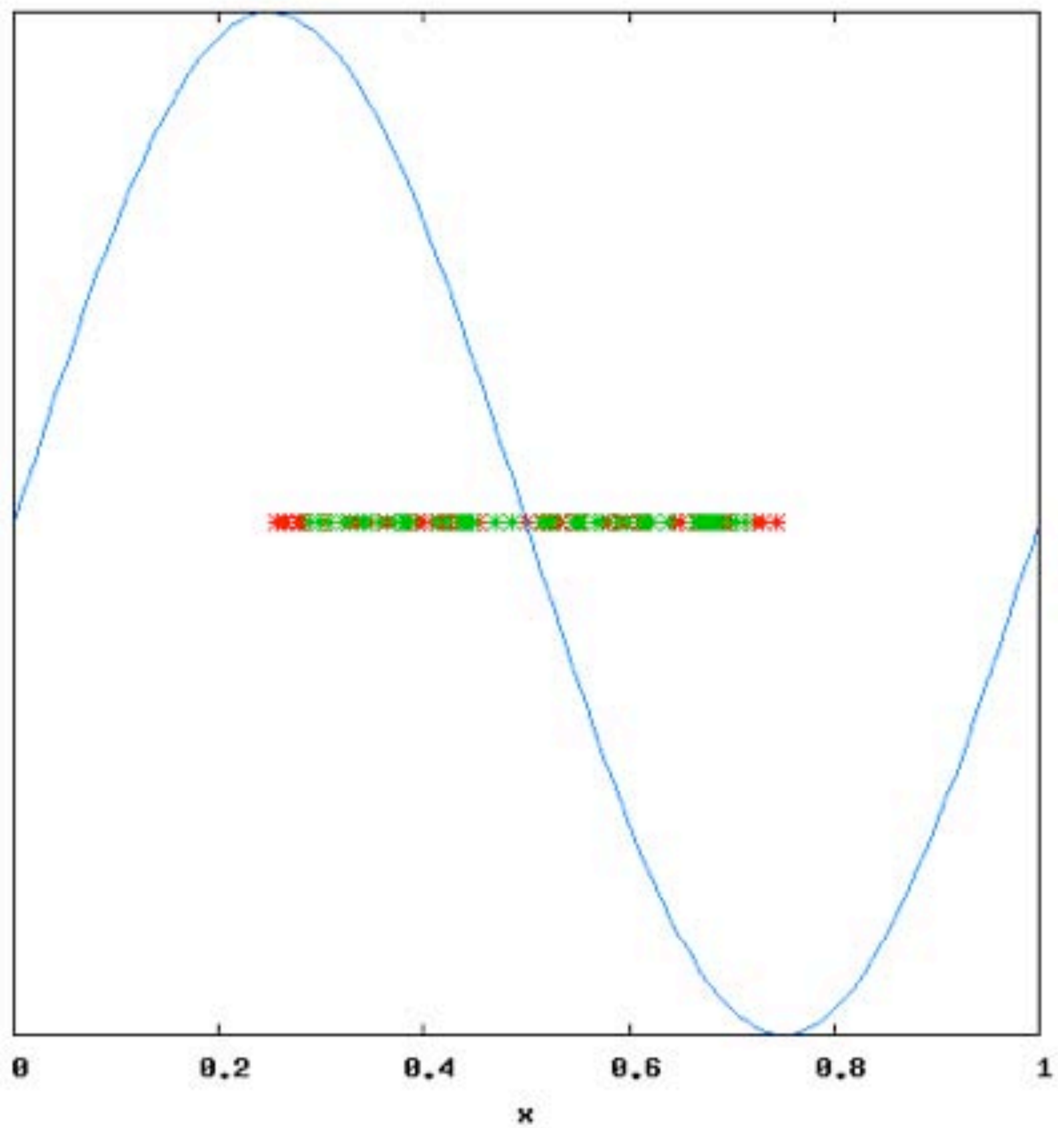



balance between flow and Fisher wave $\delta x = k^{-1}\sqrt{2Ds}$



# Sine wave

v(x)=k sin(x) $k = 10^{-2}, D = 2\ 10^{-4}, \mu = 1$

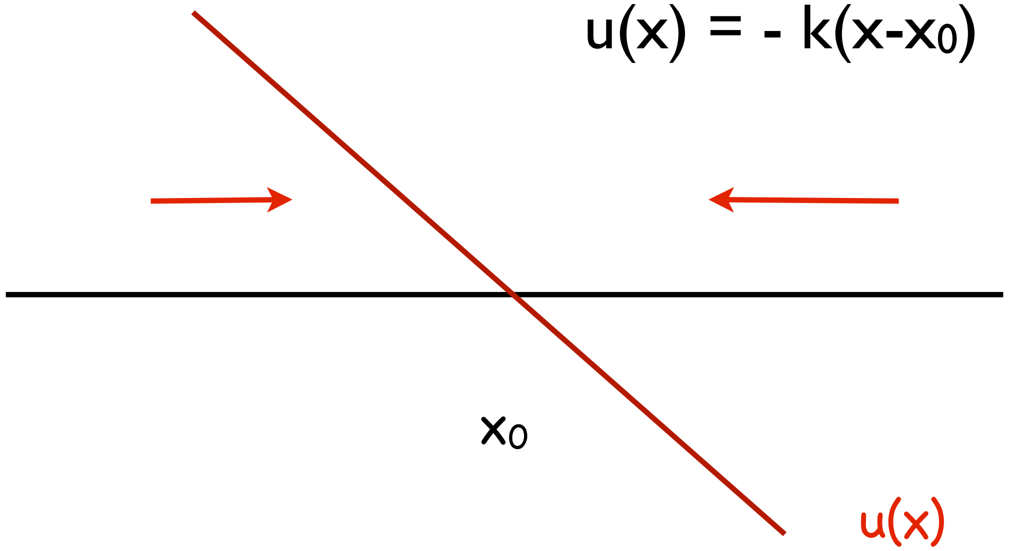



always very short fixation time (never odd number of boundaries)

# Fixation time

## Theory:

$$u(x) = -k(x-x_0)$$



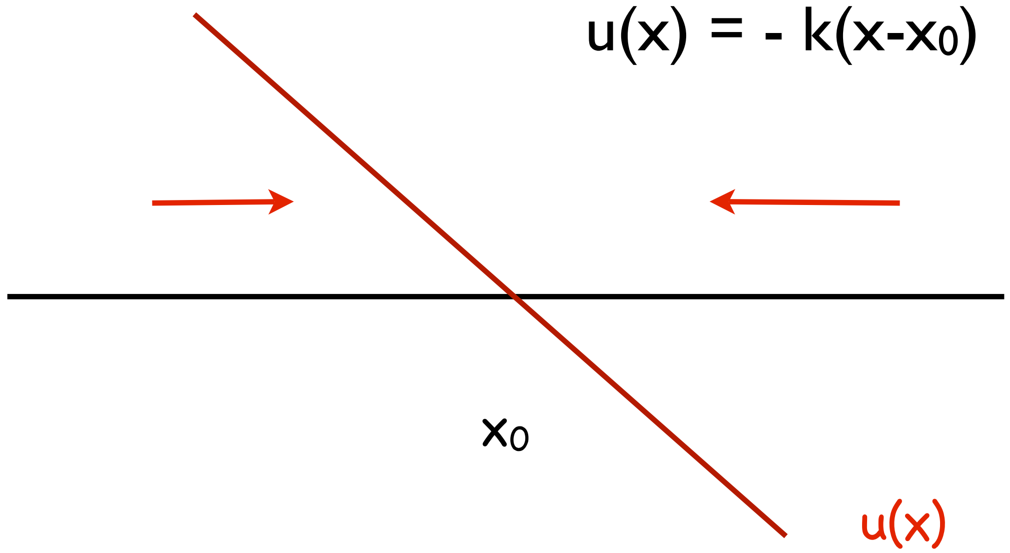

if boundary collapse exponentially, then:

$$\tau_f = \tau_0 + c/k$$

k = average gradient close to the sink

# Fixation time

## Theory:

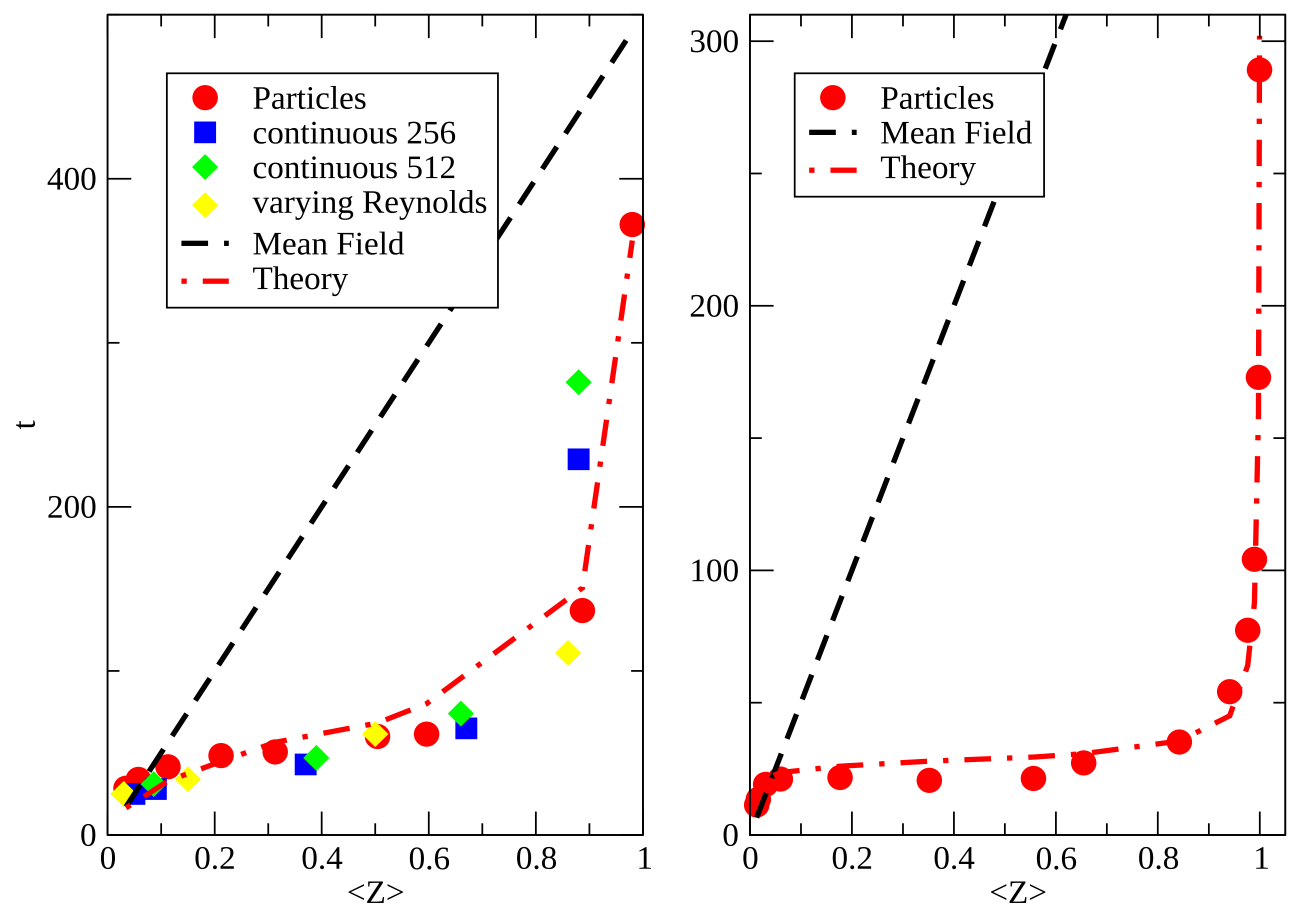



if boundary collapse exponentially, then:

$$\tau_f = \tau_0 + c/k$$

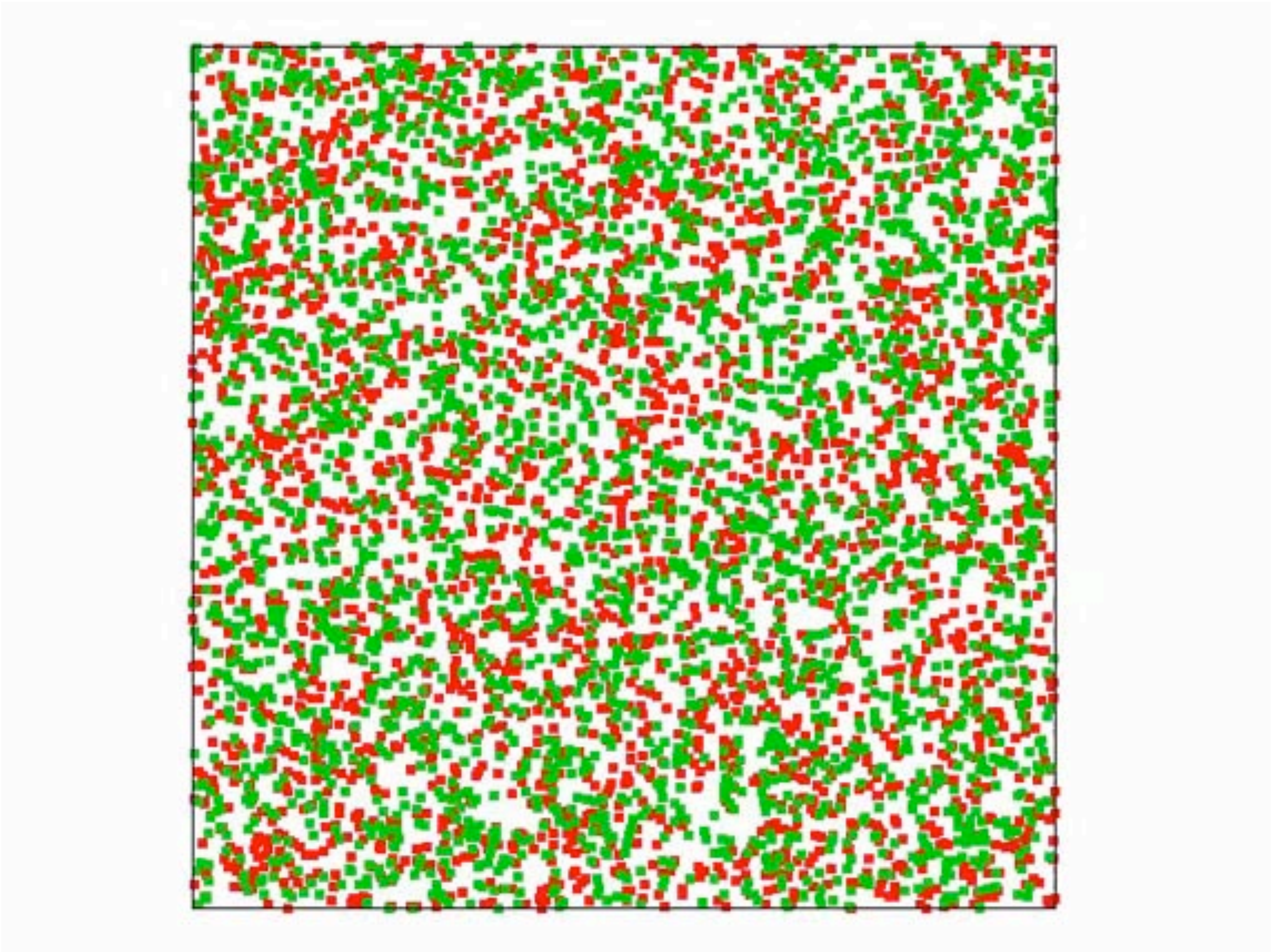
k = average gradient close to the sink

Turbulence V(x) ~ sin(x)




Fixation is much faster than in neutral theory

# 2D dynamics

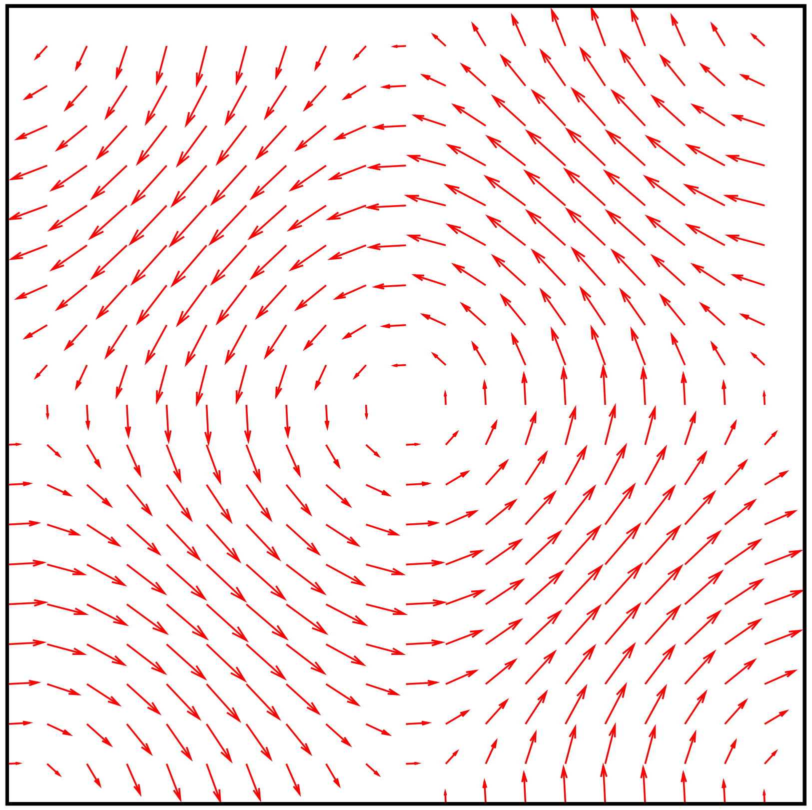


density of interfaces scales as:

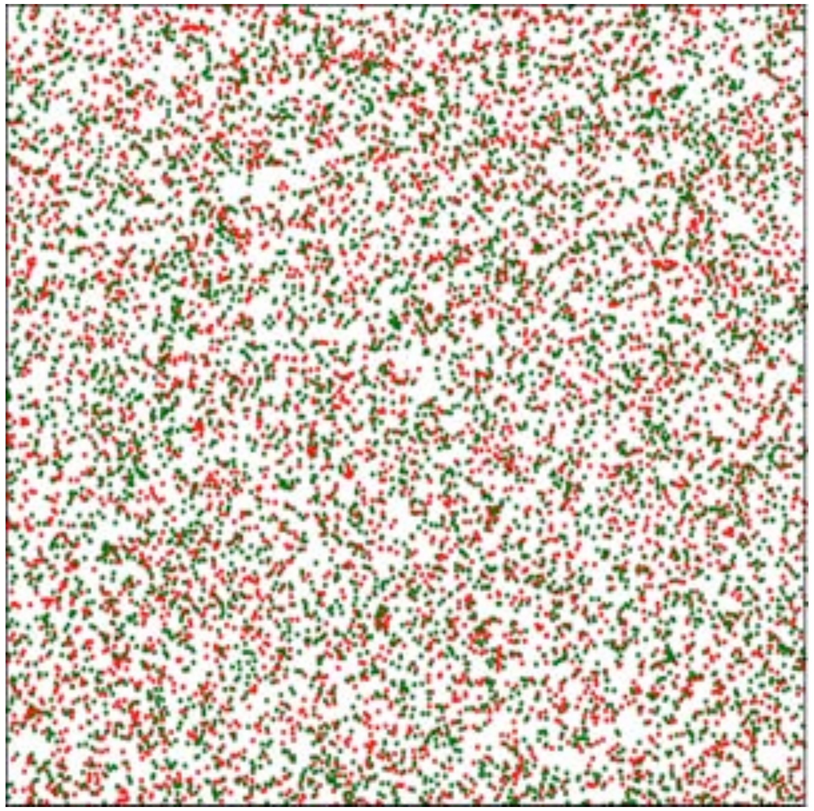
$$1/\sqrt{t} \qquad 1D$$
$$1/\log(t) \qquad 2D$$

-> fixation is a very slow process

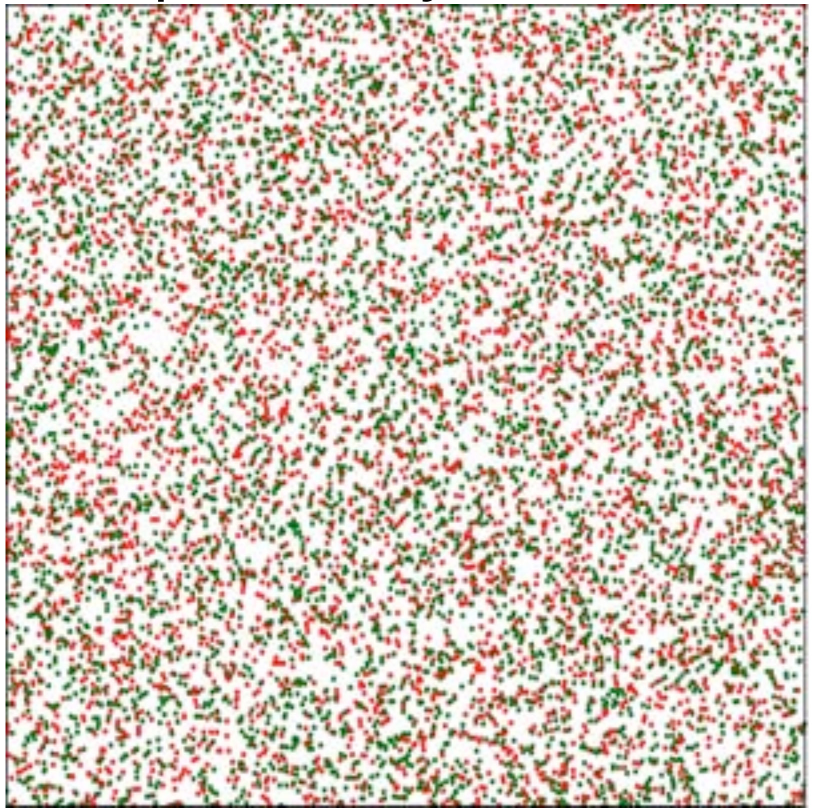
# 2D - steady flow



no compressibility

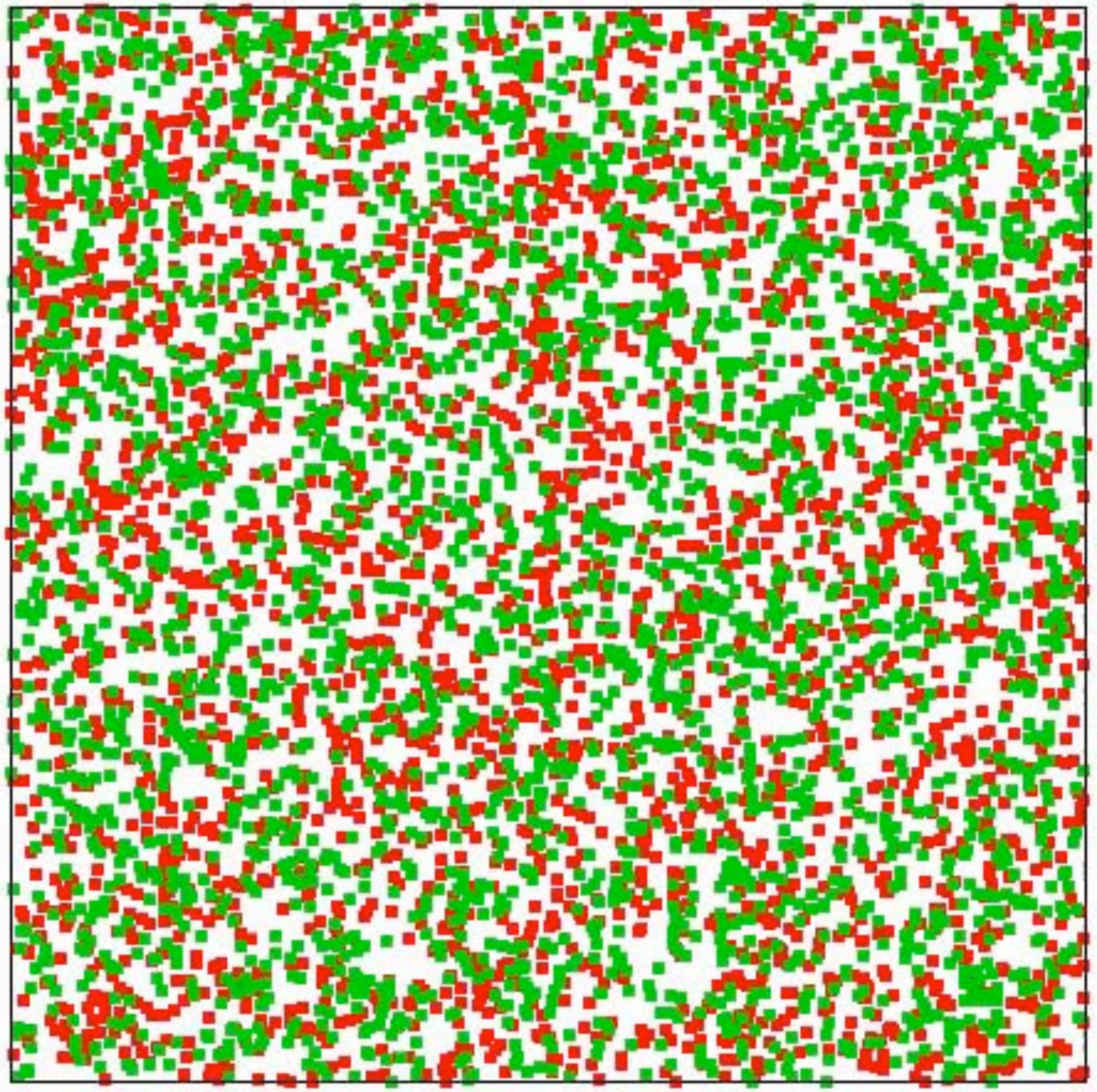


compressibility k=0.0027



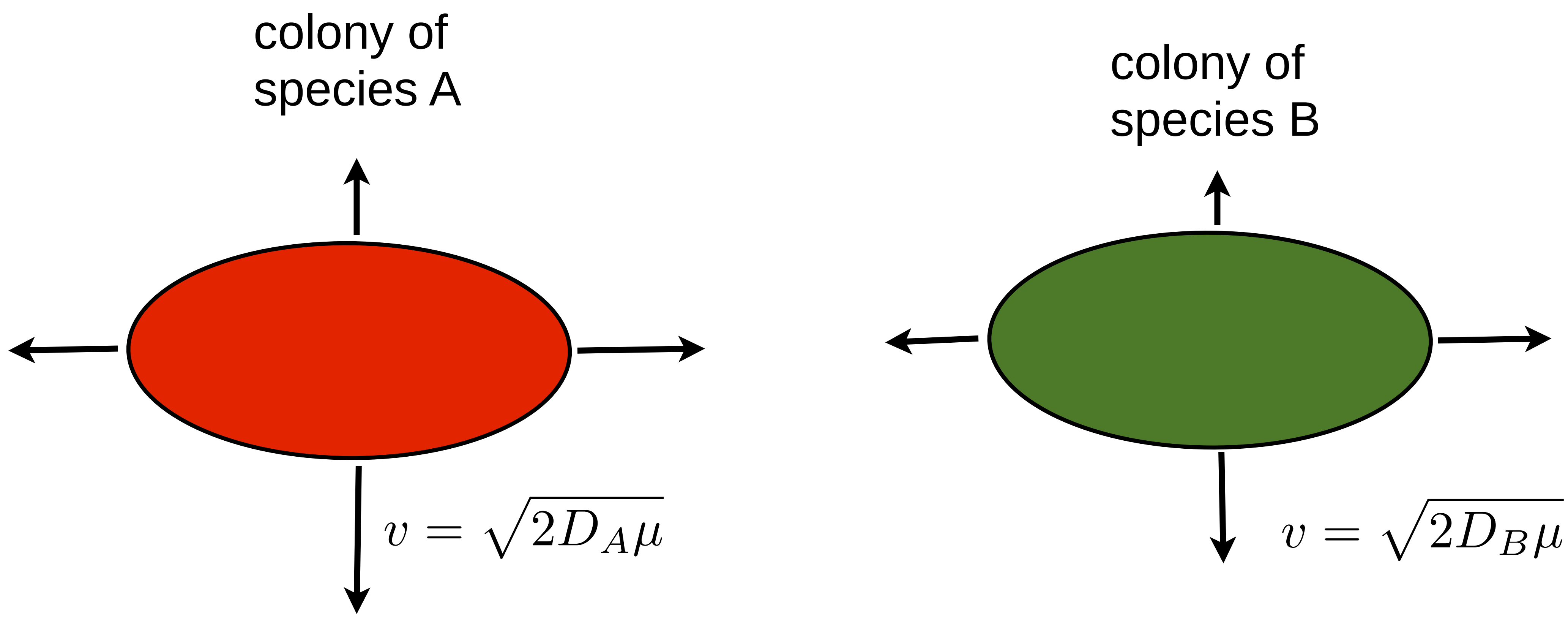
dramatic reduction in number of particles (effective carrying capacity) and fixation times also with small compressibility

# 2D + compressible flow



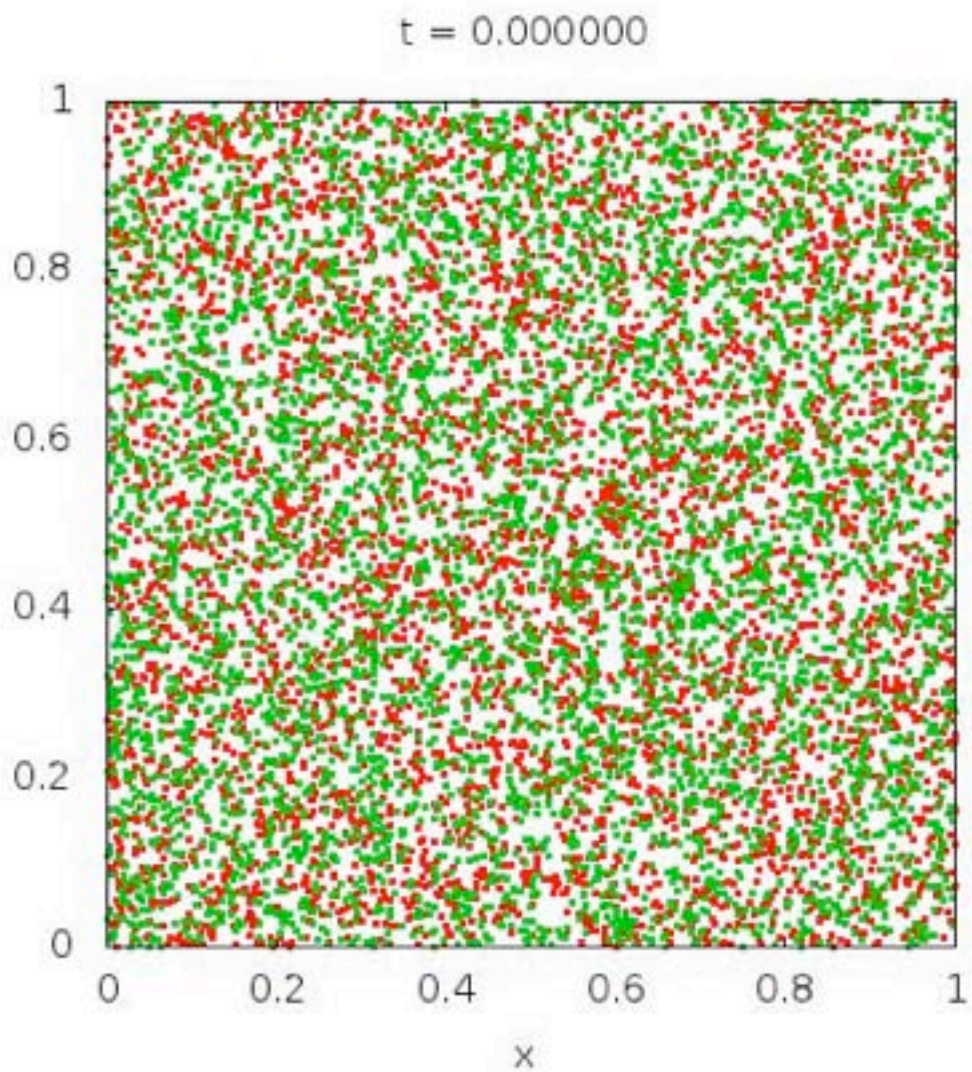
2D “slice” of 3D Navier-Stokes.

# Diffusion determines an advantage

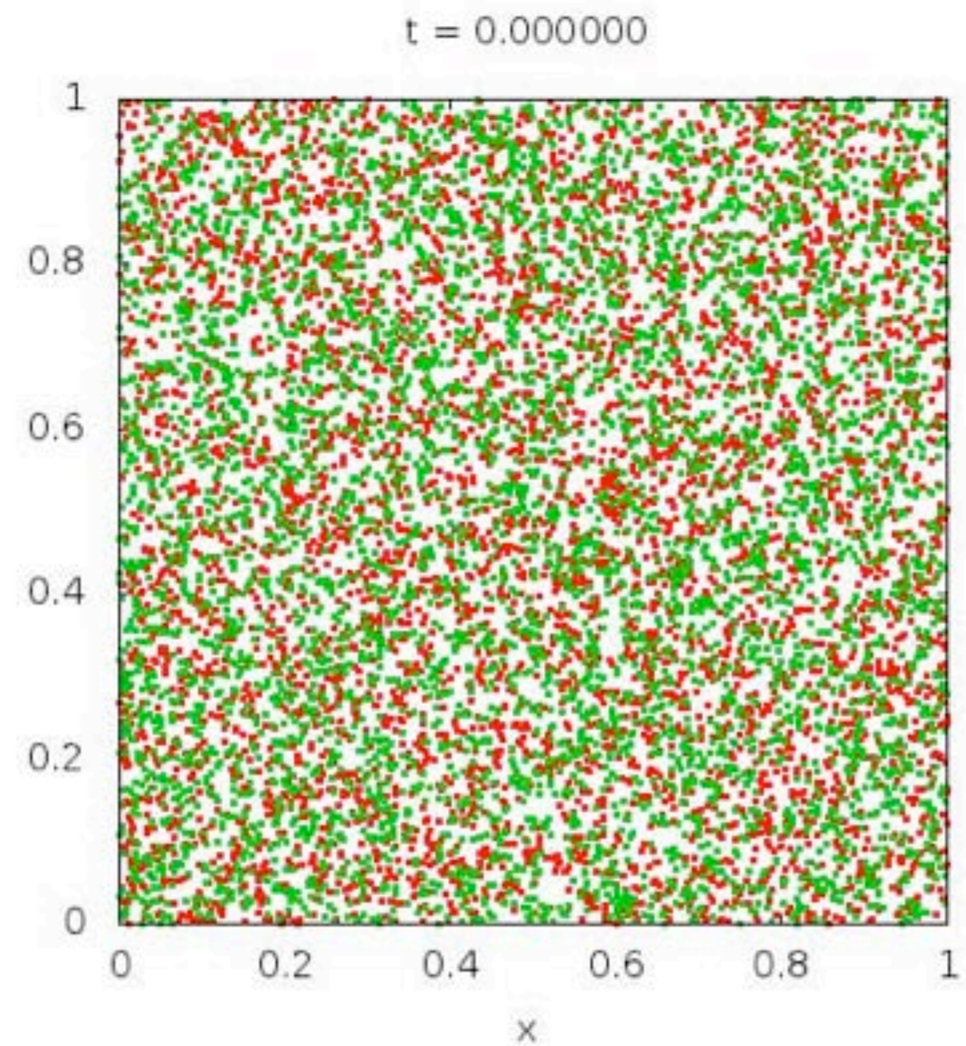



- when two species expand into open space, advantage can be estimated by looking at the difference of Fisher wave speeds

- what happens if they are mixed?



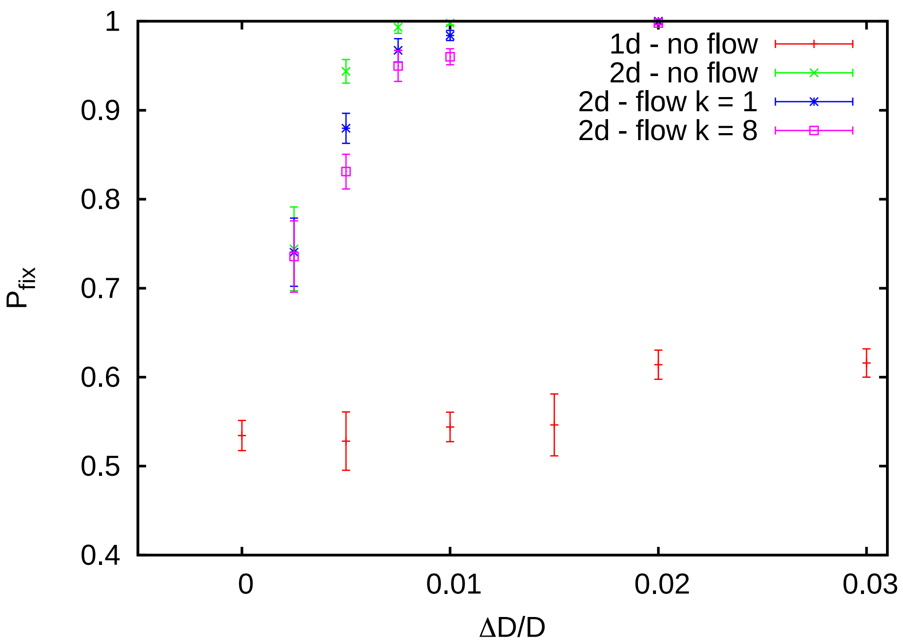

neutral



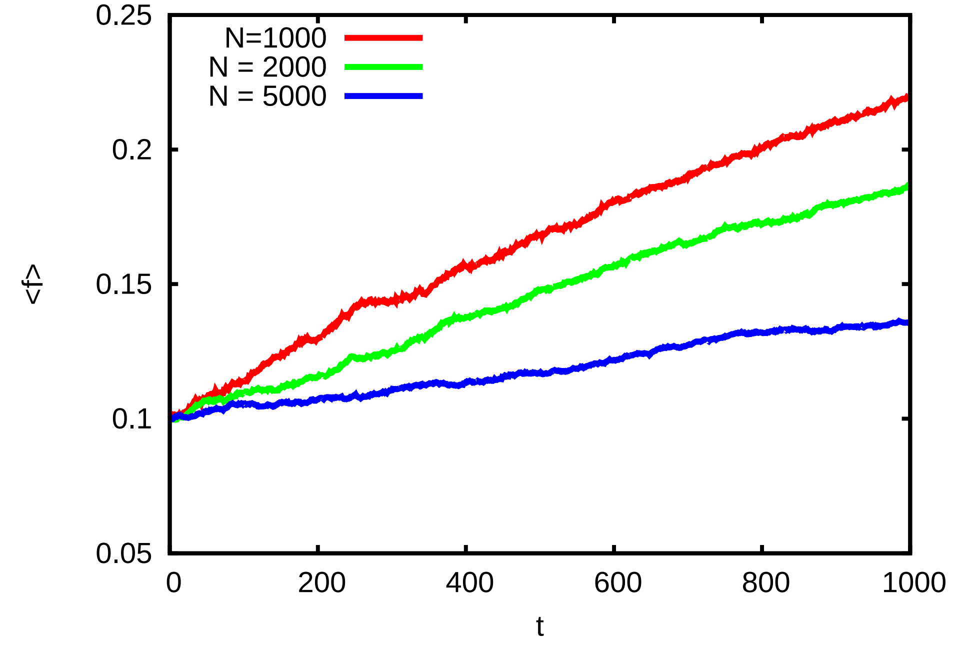

red diffuses 5% faster

SP and R. Benzi , in preparation

# Theory




$\delta D/D = 0.1$

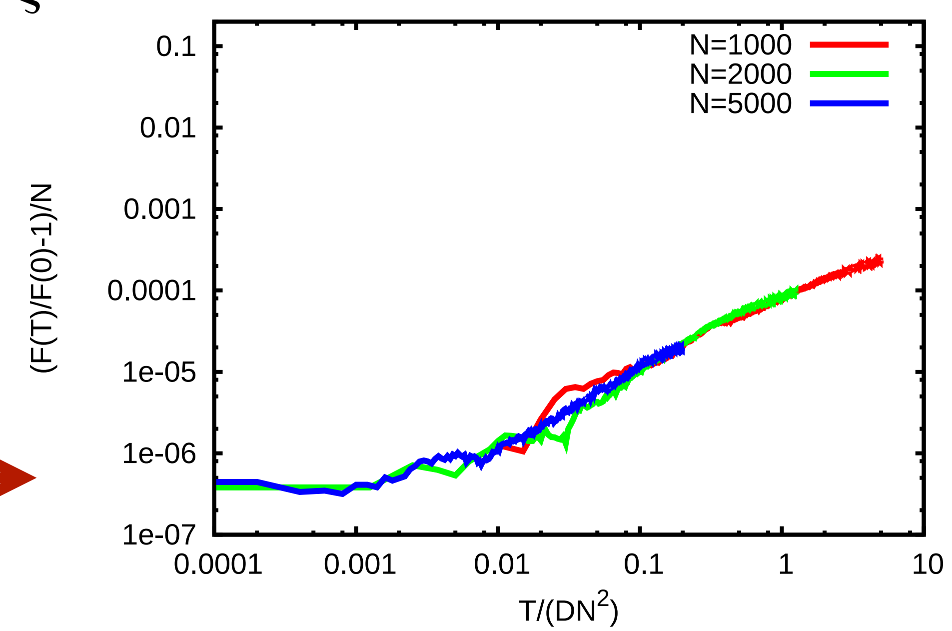



equation for the relative fraction $f=c_A/(c_A+c_B)$

$$\partial_t f = \nabla^2 f + \delta D(1-f)\nabla^2 f + \sqrt{\frac{2\mu f(1-f)}{N}}\xi$$

scaling in N from perturbation theory

$$< f(t) > \approx N\ \delta D\ g[t/(DN^2), D]$$



# Conclusions

- flows can radically change the outcome of competition

- relaxing the assumption of constant total density leads to interesting effects also in the absence of flows