

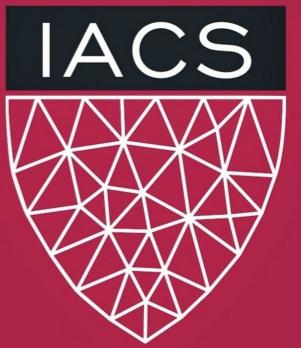
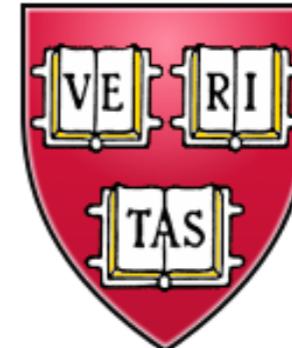
Statistical Fluctuations in Evolutionary and Population Dynamics

Thiparat Chotibut

SUTD Brain Lab Meeting

September 23, 2016

PHYSICS



Statistical Fluctuations in Evolutionary and Population Dynamics

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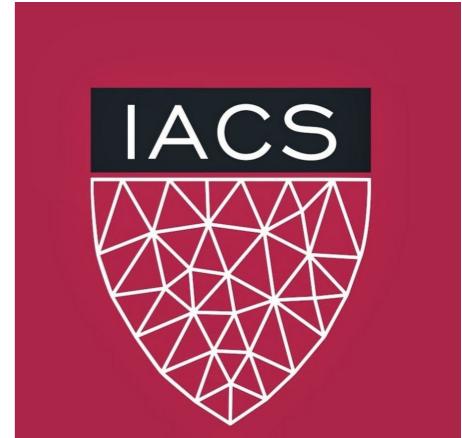
September 23, 2016

In collaboration with



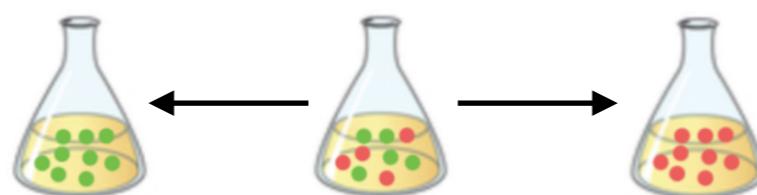
David R. Nelson
Physics Department, Harvard

Sauro Succi
IACS, Harvard

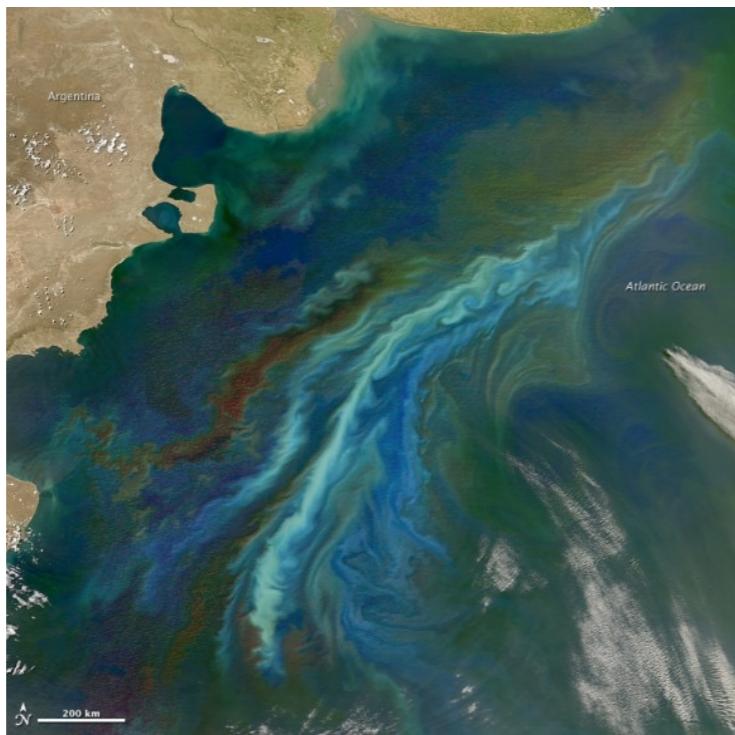


Outline

Part 1: Evolutionary Dynamics with Fluctuating Population Sizes



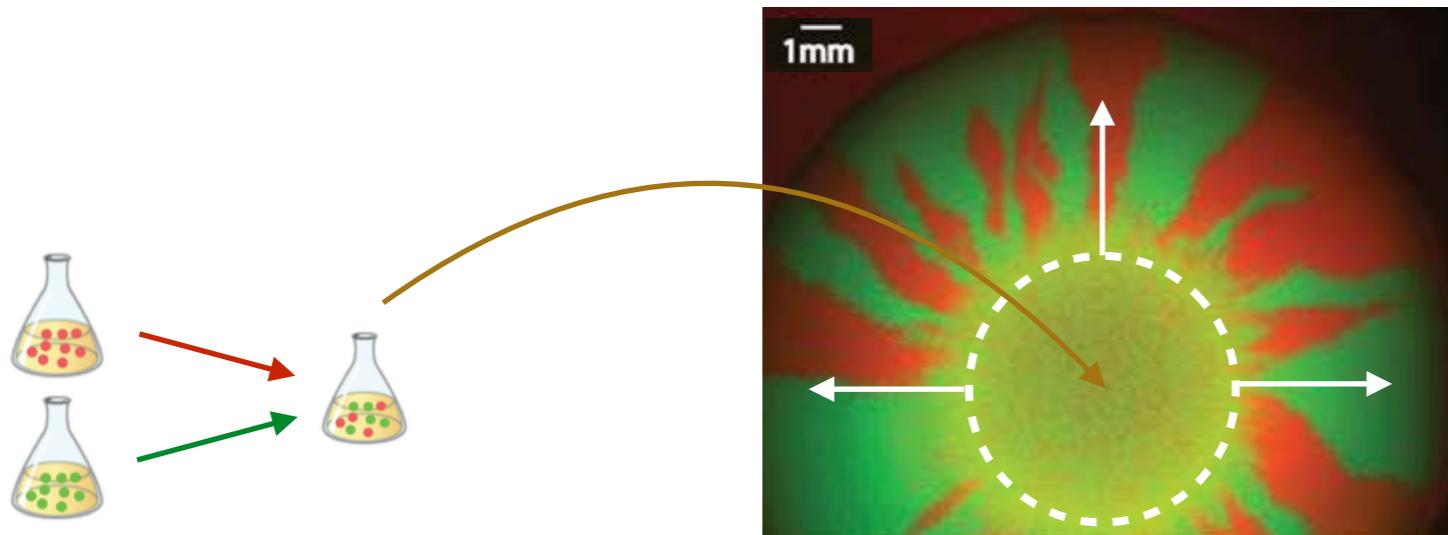
Part 2: Striated Populations in Disordered Environments with Advection



Part 1: Evolutionary Dynamics with Fluctuating Population Sizes

Motivation: Competition Experiments

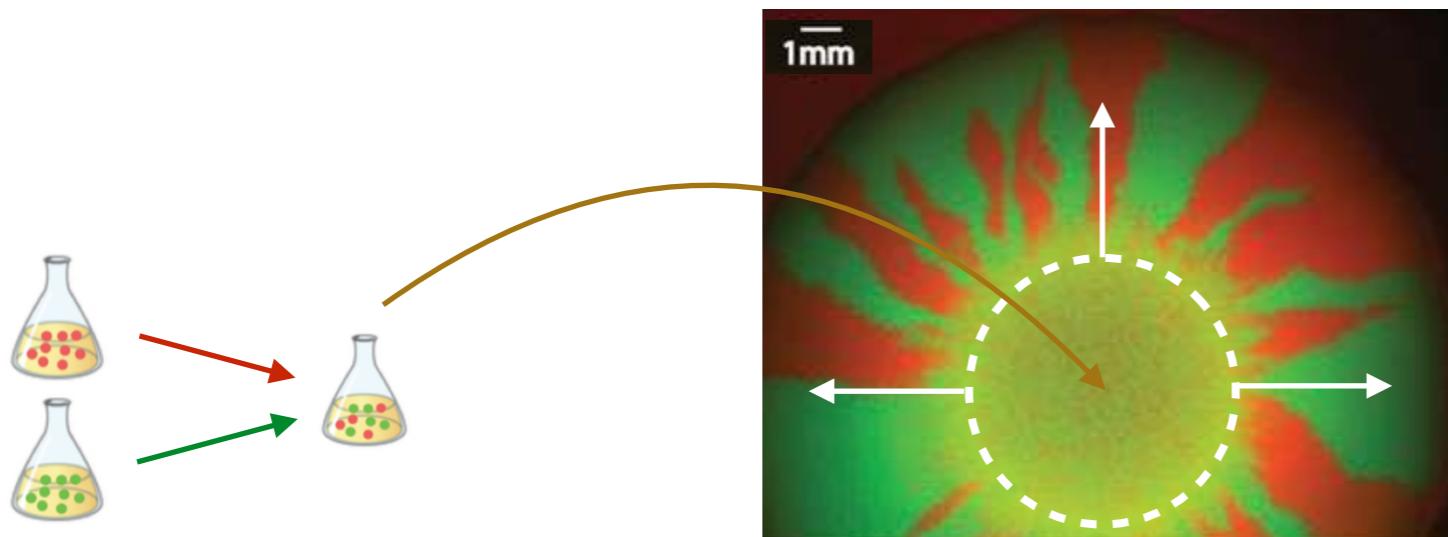
Spatial Range Expansion
Competition of *neutral* strains of *E.Coli*



O. Hallatschek and D. R. Nelson, Evolution **64**, 193 (2010)

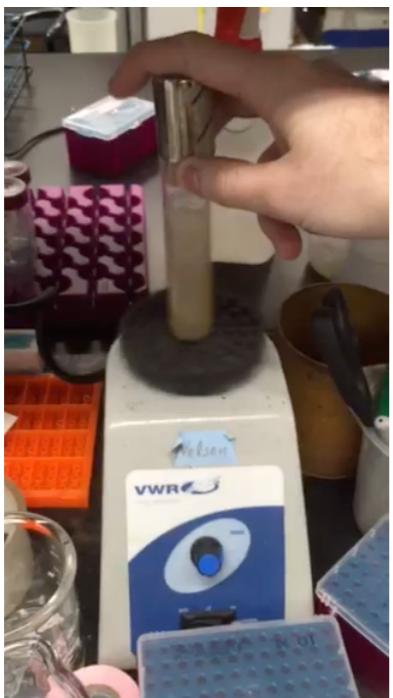
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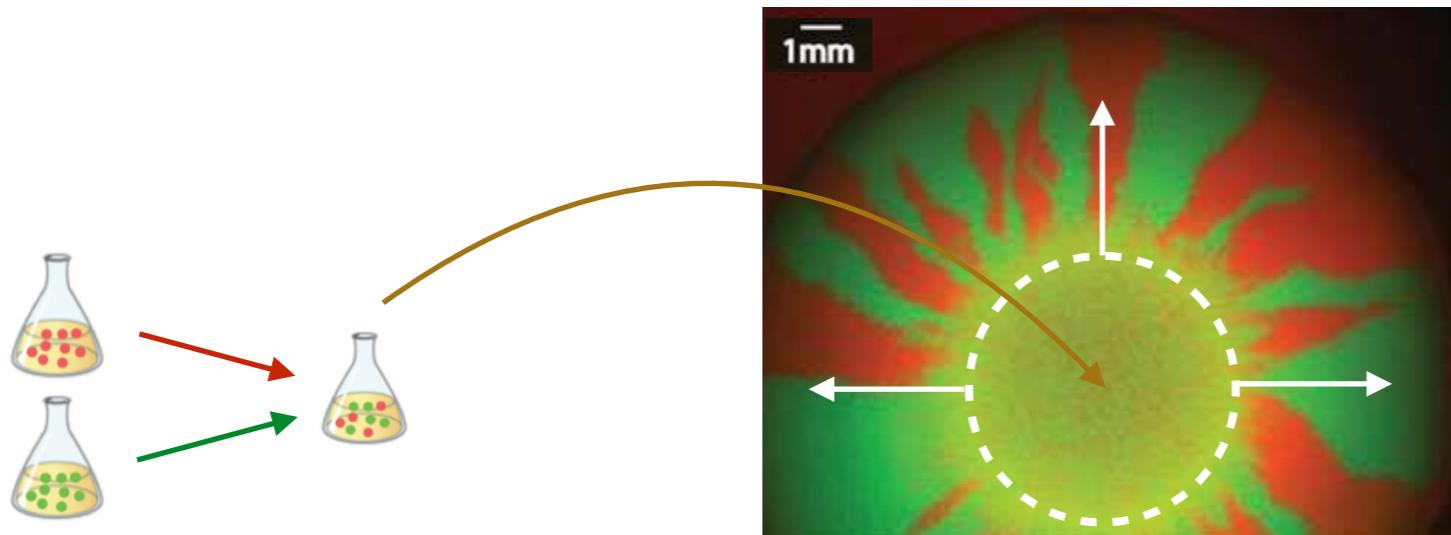
Well-mixed Environments



Molecular and Cellular Biology Lab, Harvard

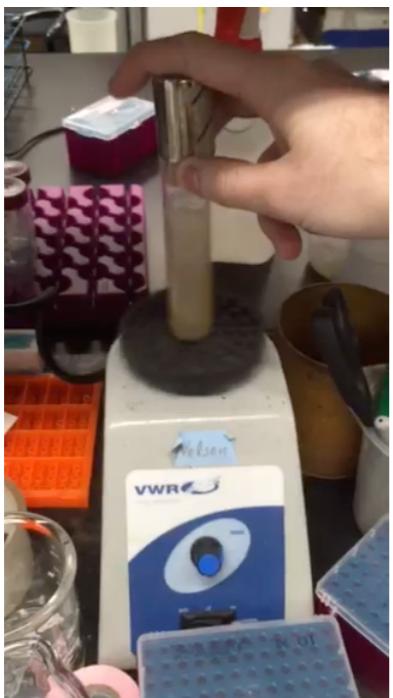
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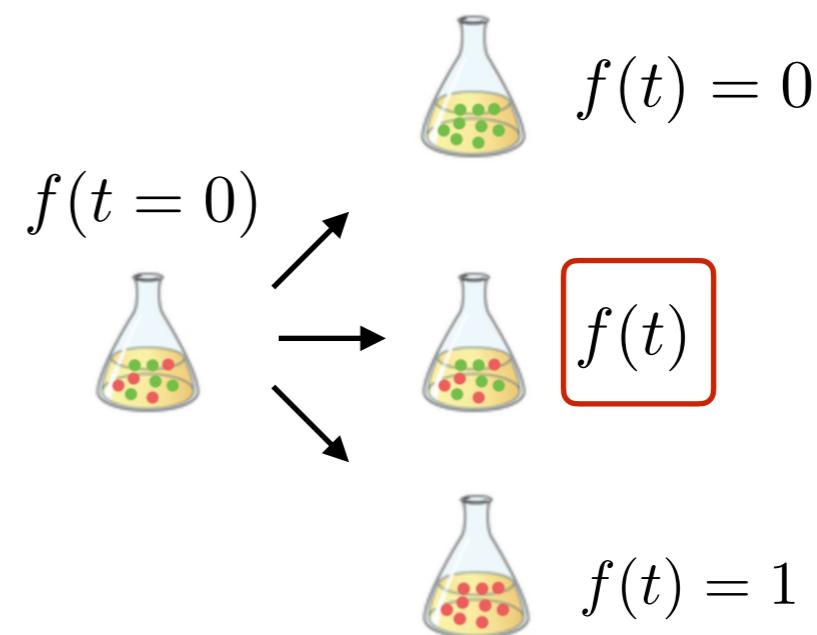


O. Hallatschek and D. R. Nelson, Evolution 64, 193 (2010)

Well-mixed Environments



Genetic compositions (frequency $f(t)$) change over time.



Molecular and Cellular Biology Lab, Harvard

Frequency-dependent Natural Selection: Replicator Dynamics

deterministic time evolution:

$$\frac{df_i}{dt} = [w_i(\mathbf{f}) - \bar{w}(\mathbf{f})] f_i$$

fitness of species i:

$$w_i(\mathbf{f}) \equiv 1 + \sum_j a_{ij} f_j$$

mean fitness of all interacting species

$$\bar{w}(\mathbf{f}) = \sum_j f_j w_j(\mathbf{f})$$

determined from the sum of mean background fitness (set to 1)
and the payoff a_{ij} from interacting with species j

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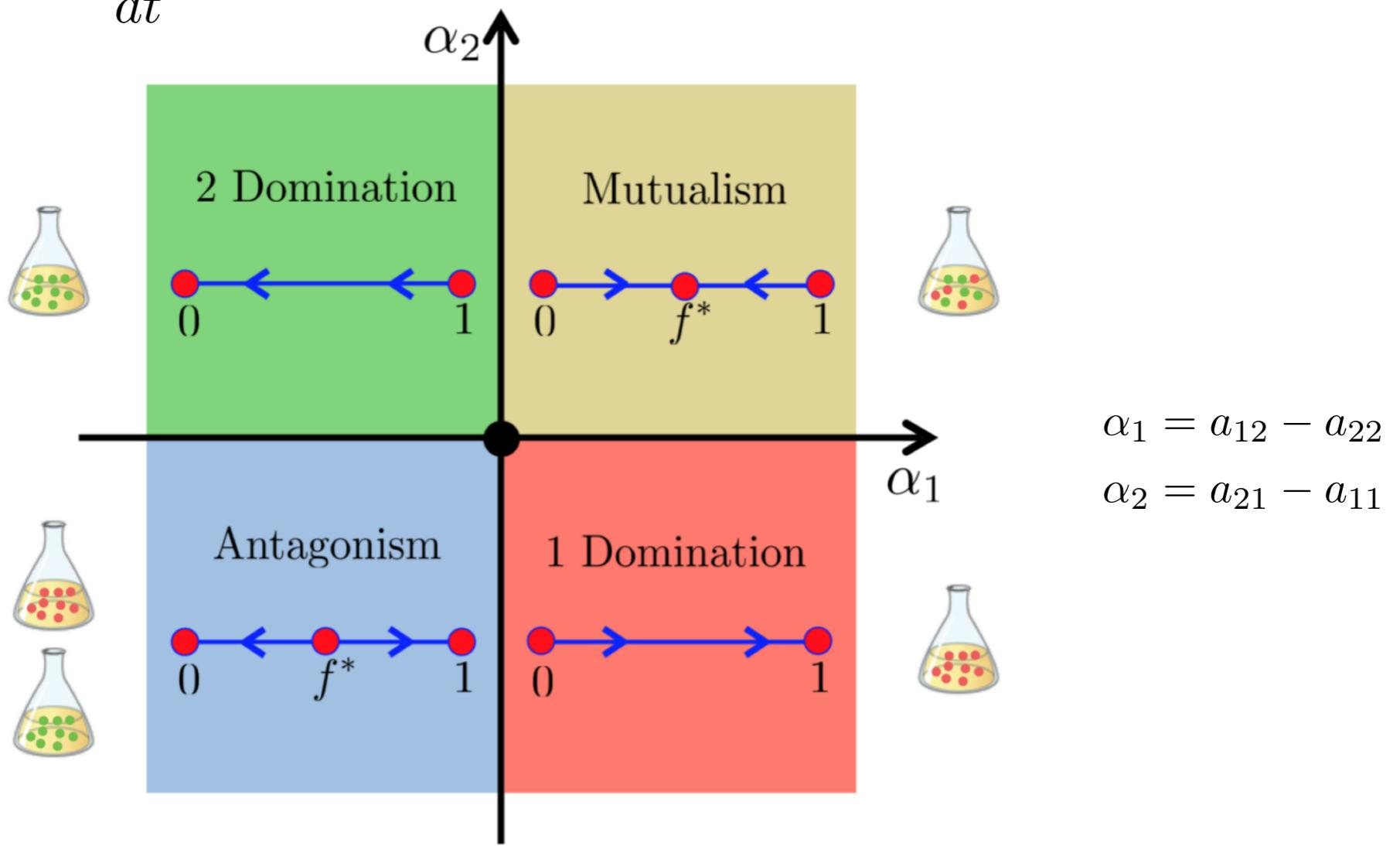
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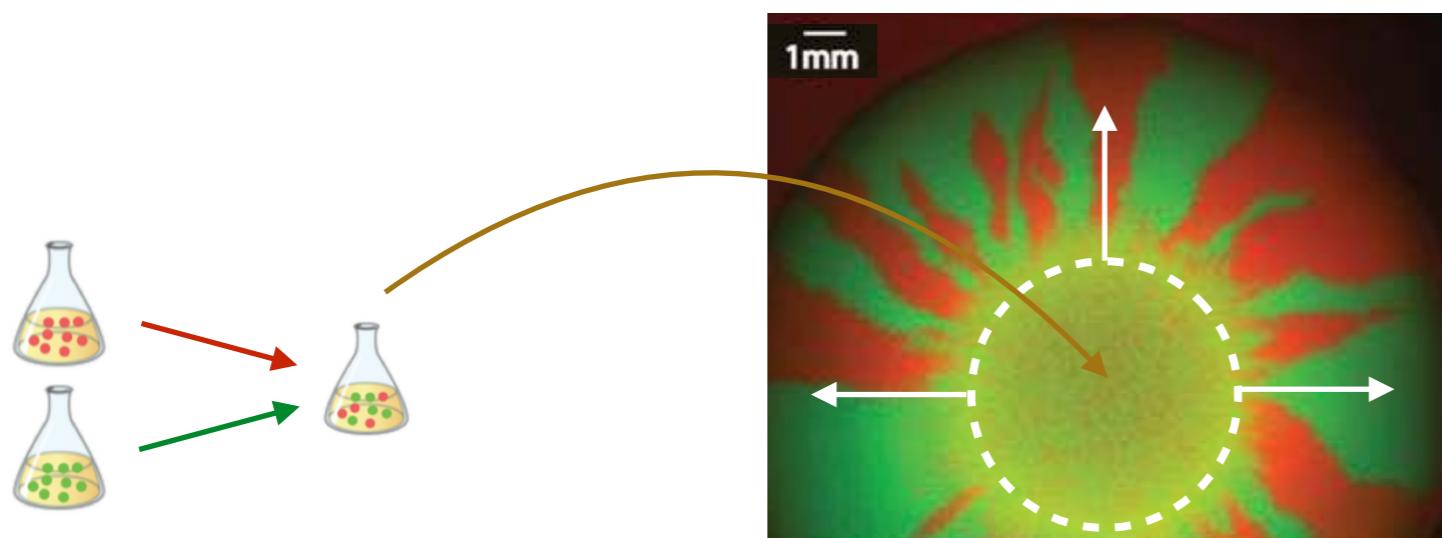
determined from the sum of mean background fitness (set to 1)
and the payoff a_{ij} from interacting with species j

For 2-Species Competition, $\frac{df}{dt} = [\alpha_1(1-f) - \alpha_2 f](1-f)f \equiv v_E(f)$



Fluctuations in Reproduction Rates: Genetic Drift

Genetic drift can destroy the coexistence of *neutral* variants by chance!

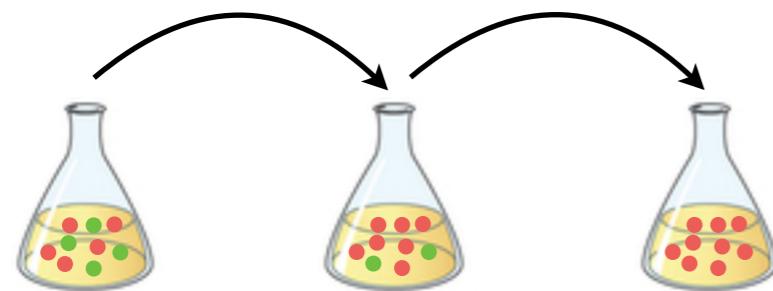


O. Hallatschek and D. R. Nelson, Evolution **64**, 193 (2010)

Fluctuations in Reproduction Rates: Genetic Drift

The Wright-Fisher Model or the Moran Model of Genetic Drift

The population size N is assumed *fixed*.
 f is updated by samplings with replacement.



In the form of Langevin's equation,

$$\frac{df}{dt} = \sqrt{\frac{2D_g(f)}{N}} \Gamma(t)$$

$$D_g(f) = f(1 - f) \quad \text{Genetic Drift Coefficient}$$

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

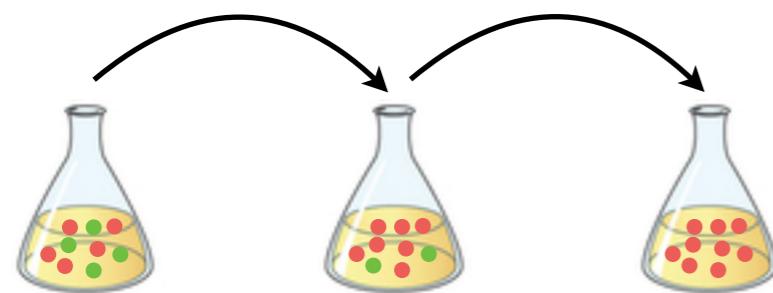
W. J. Ewens, *Mathematical Population Genetics*: (2004)

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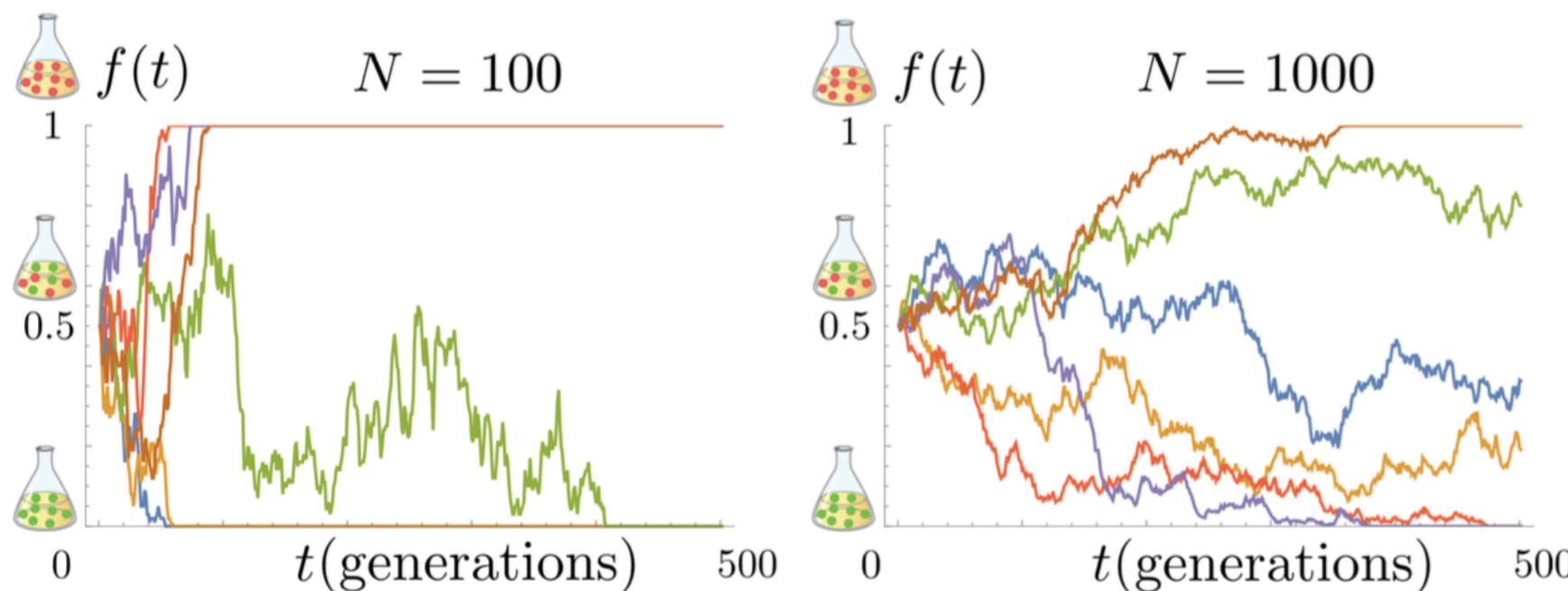
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The effect of genetic drift is more pronounced at smaller N .



W. J. Ewens, *Mathematical Population Genetics*: (2004)

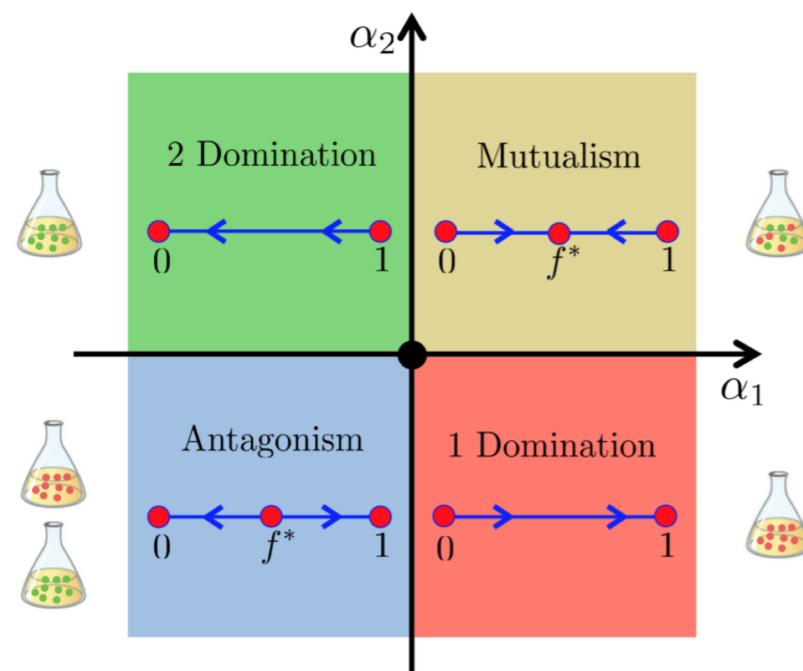
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The fate of coexistence depends on replicator dynamics and genetic drift

$$\frac{df}{dt} = v_E(f) + \sqrt{\frac{2D_g(f)}{N}}\Gamma(t)$$

Natural Selection (deterministic)

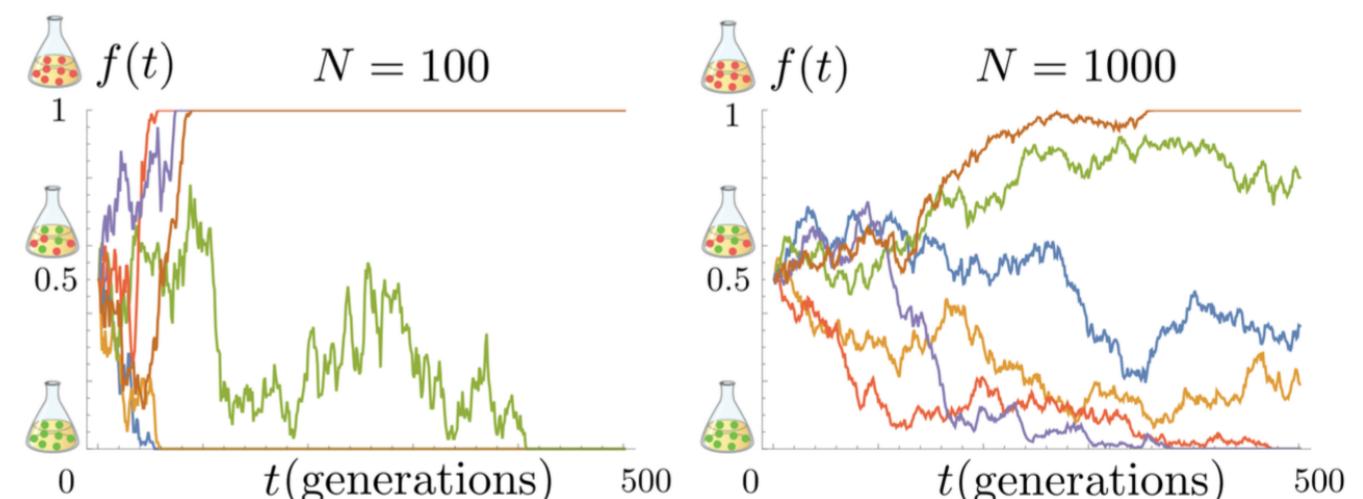
$$v_E(f) = [\alpha_1(1-f) - \alpha_2 f](1-f)f$$



Genetic Drift (stochastic)

$$D_g(f) = f(1-f)$$

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



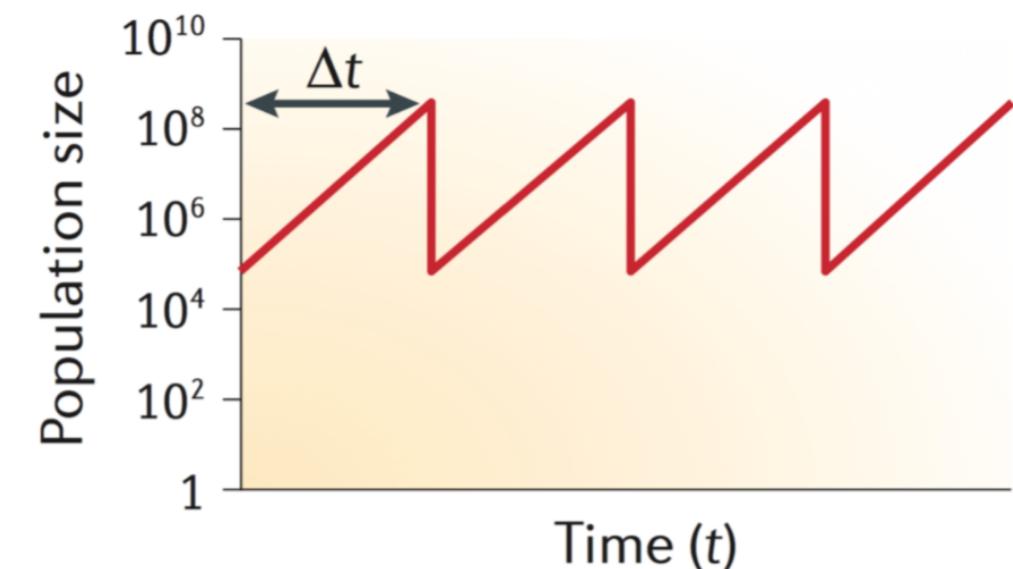
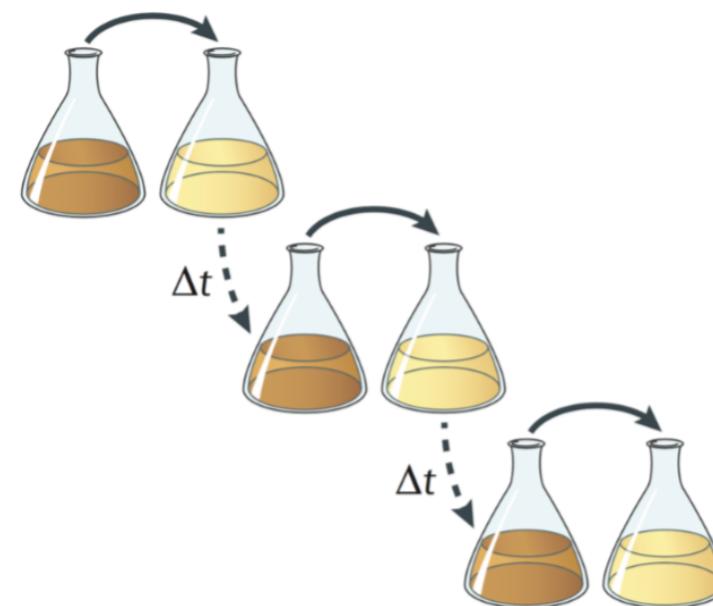
$f = 0$ and $f = 1$ are the **absorbing states**.

Two important well-studied quantities: the **fixation probability** $u(f)$ and the **mean fixation time** $\tau(f)$

Replicator dynamics with genetic drift assume a *strictly fixed population size N*

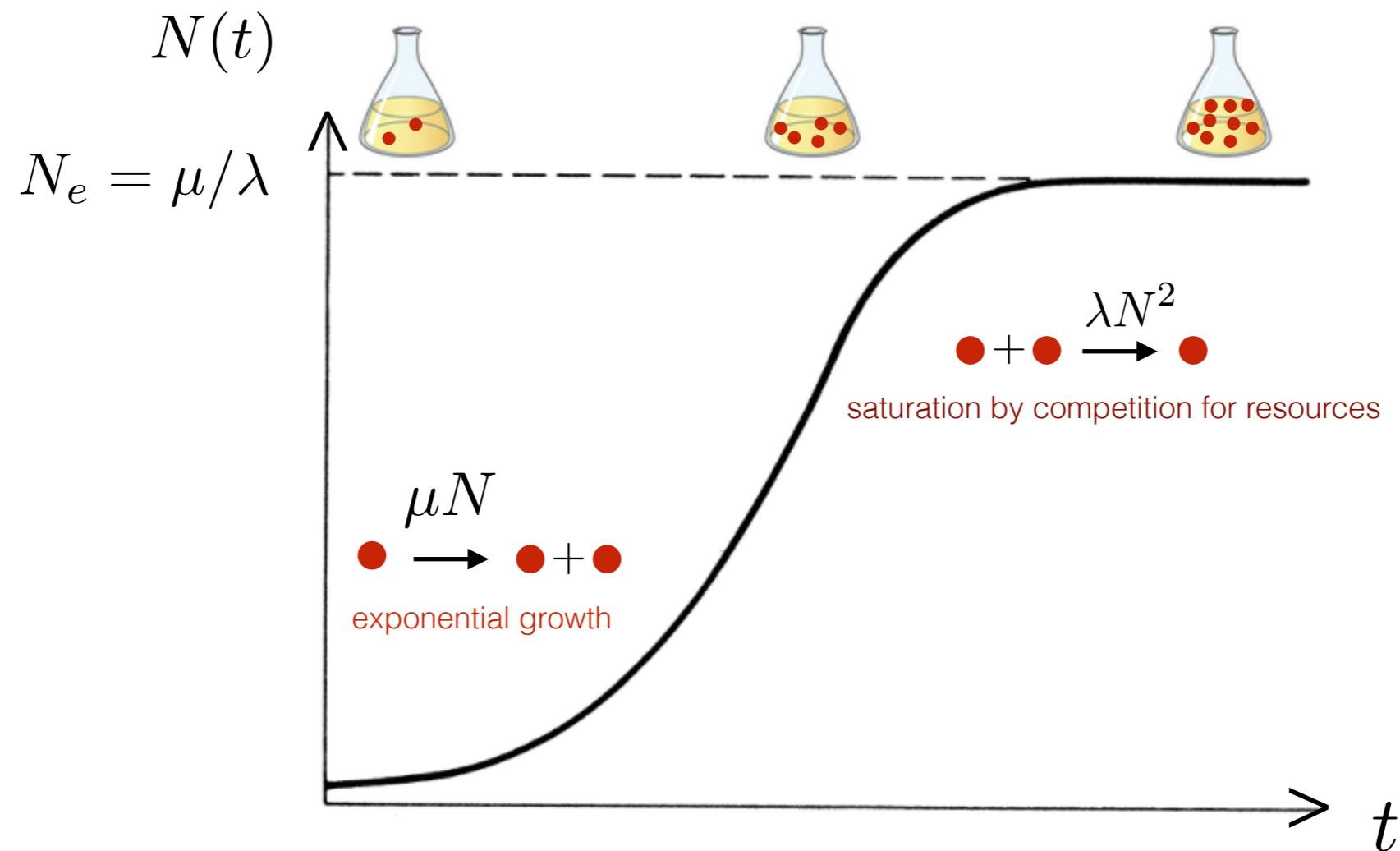
$$\frac{df}{dt} = v_E(f) + \sqrt{\frac{2D_g(f)}{N}}\Gamma(t)$$

This is rarely the case in experimental evolution !



S. F. Elena and R. E. Lenski, Nature Reviews Genetics 4, 457 (2003)

Logistic growth of population size in a well-mixed environment



$$\frac{dN}{dt} = \mu N - \lambda N^2$$

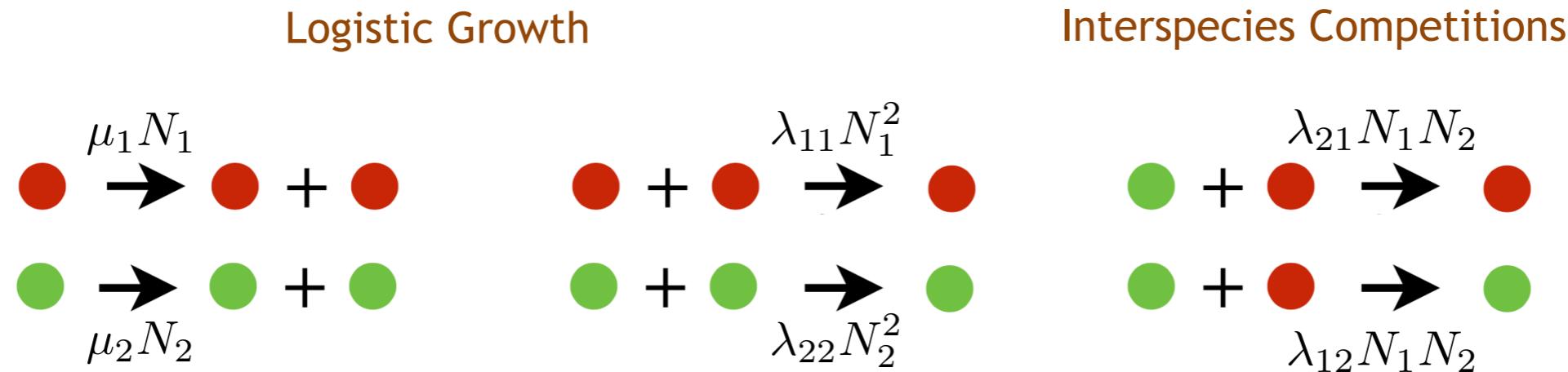
$$= \mu N \left(1 - \frac{N}{N_e}\right)$$

Experiments in yeast show good fit to the simple model; see

J.M.Smith, *Evolutionary Genetics*, (1998).

R. Pearl and L. Slobodkin, Q. Rev. Biol. **51**, 6 (1976).

Simple model for 2-species competition: Competitive Lotka-Volterra Model



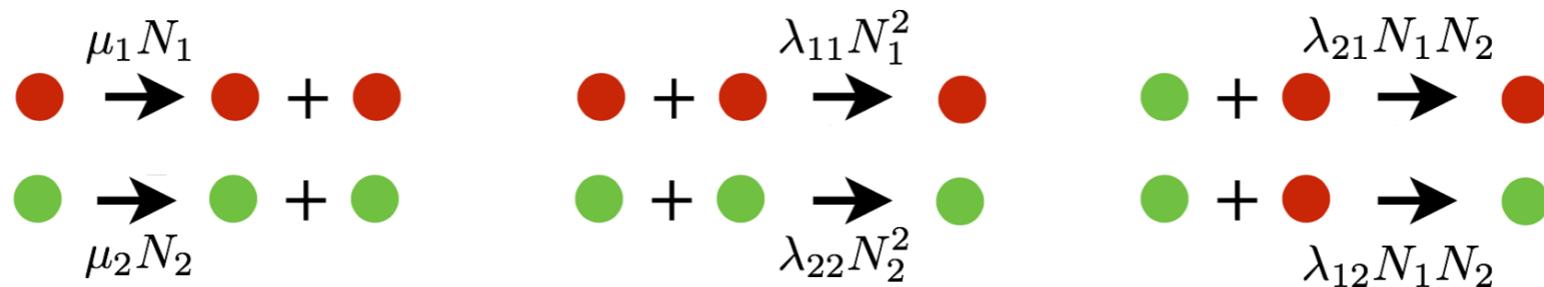
N_1 = the number of species 1

N_2 = the number of species 2

The population size $N_T \equiv N_1 + N_2$ is a *dynamical* variable

We study the *stochastic dynamics* of this competition model!

Deterministic Dynamics of the Competitive Lotka-Volterra Model



$$\frac{dc_1}{dt} = [\mu_1 c_1(1 - c_1 - c_2) + \mu_1 \beta_1 c_1 c_2]$$

$$\frac{dc_2}{dt} = [\mu_2 c_2(1 - c_1 - c_2) + \mu_2 \beta_2 c_1 c_2]$$

$c_i(t) = N_i(t)/N$ are the normalized population size

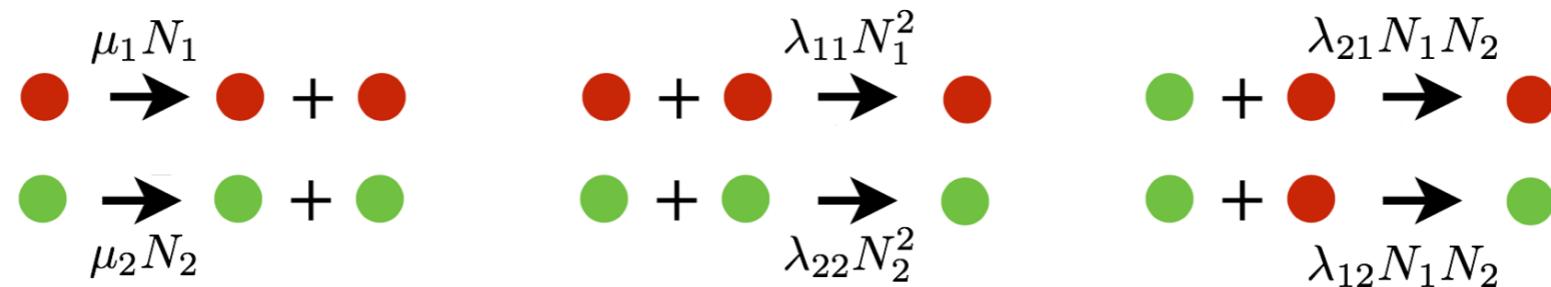
$N = \left(\frac{\mu_1}{\lambda_{11}} \right) = \left(\frac{\mu_2}{\lambda_{22}} \right)$ is the carrying capacity (assumed equal)

$\beta_i \equiv 1 - \left(\frac{\lambda_{ij}}{\lambda_{jj}} \right) \left(\frac{\mu_j}{\mu_i} \right)$ control the structure of the dynamical systems

The population size is dynamical: $N_T(t) = (c_1(t) + c_2(t))N \equiv c_T(t)N$

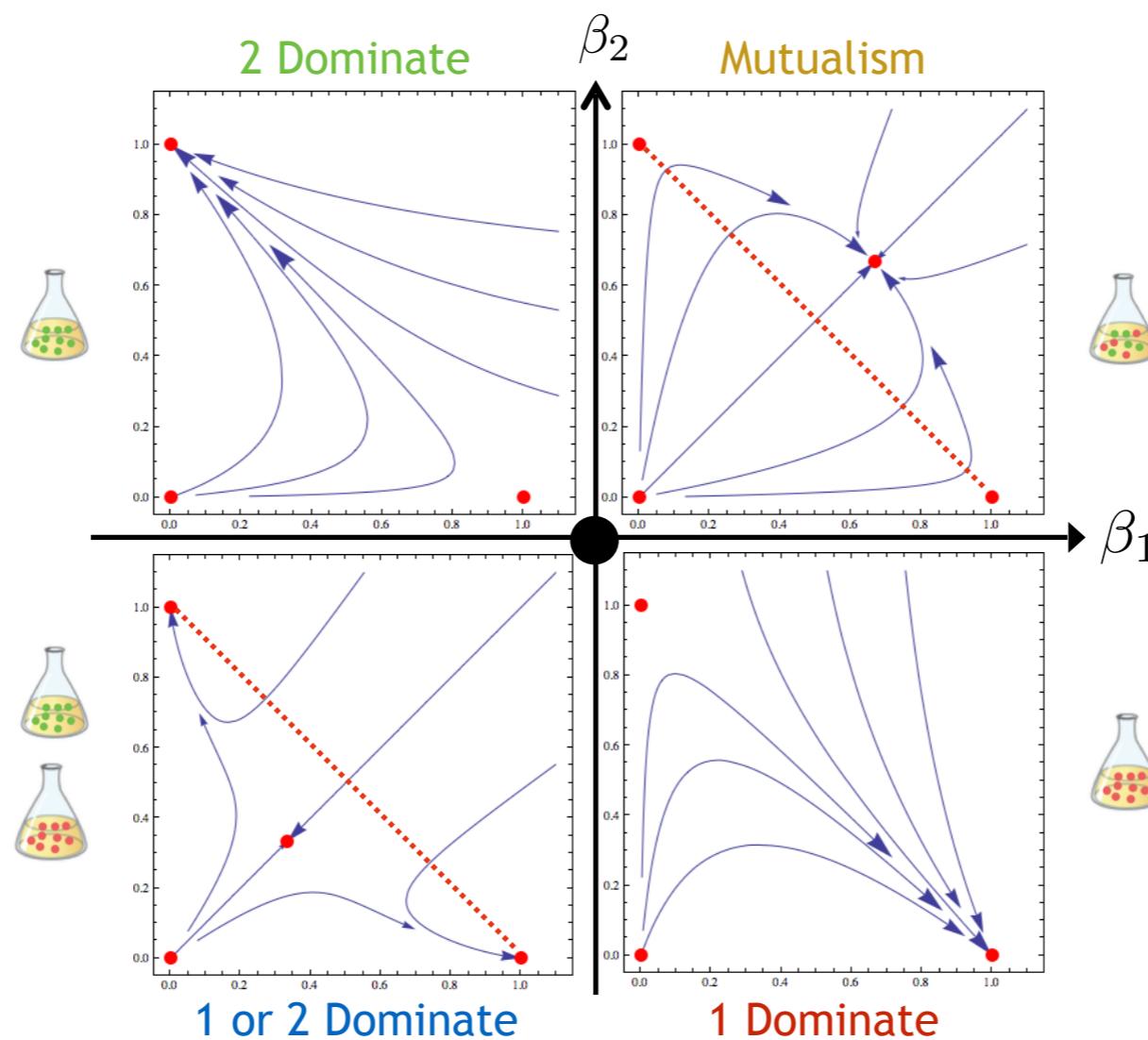
The fraction is given by $f(t) = c_1(t)/(c_1(t) + c_2(t))$

Competition scenarios resemble those of the replicator dynamics, but the population size is dynamical

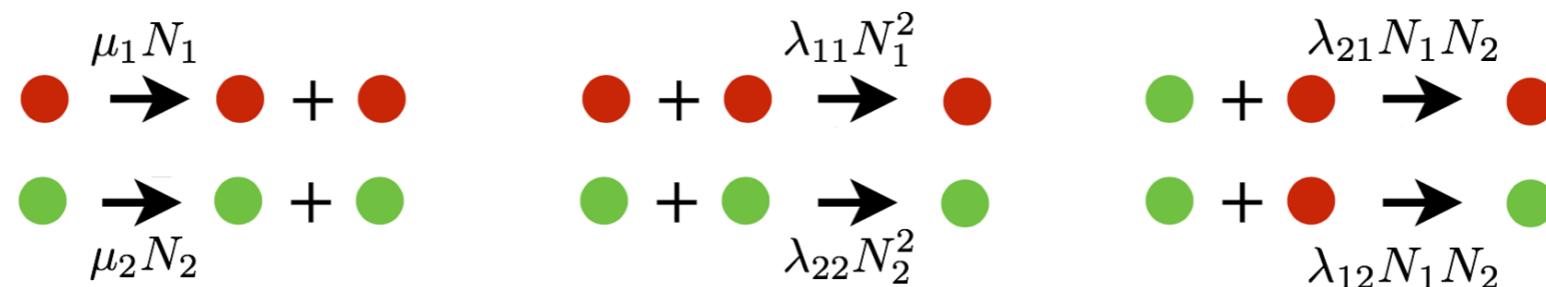


$$\frac{dc_1}{dt} = [\mu_1 c_1(1 - c_1 - c_2) + \mu_1 \beta_1 c_1 c_2]$$

$$\frac{dc_2}{dt} = [\mu_2 c_2(1 - c_1 - c_2) + \mu_2 \beta_2 c_1 c_2]$$

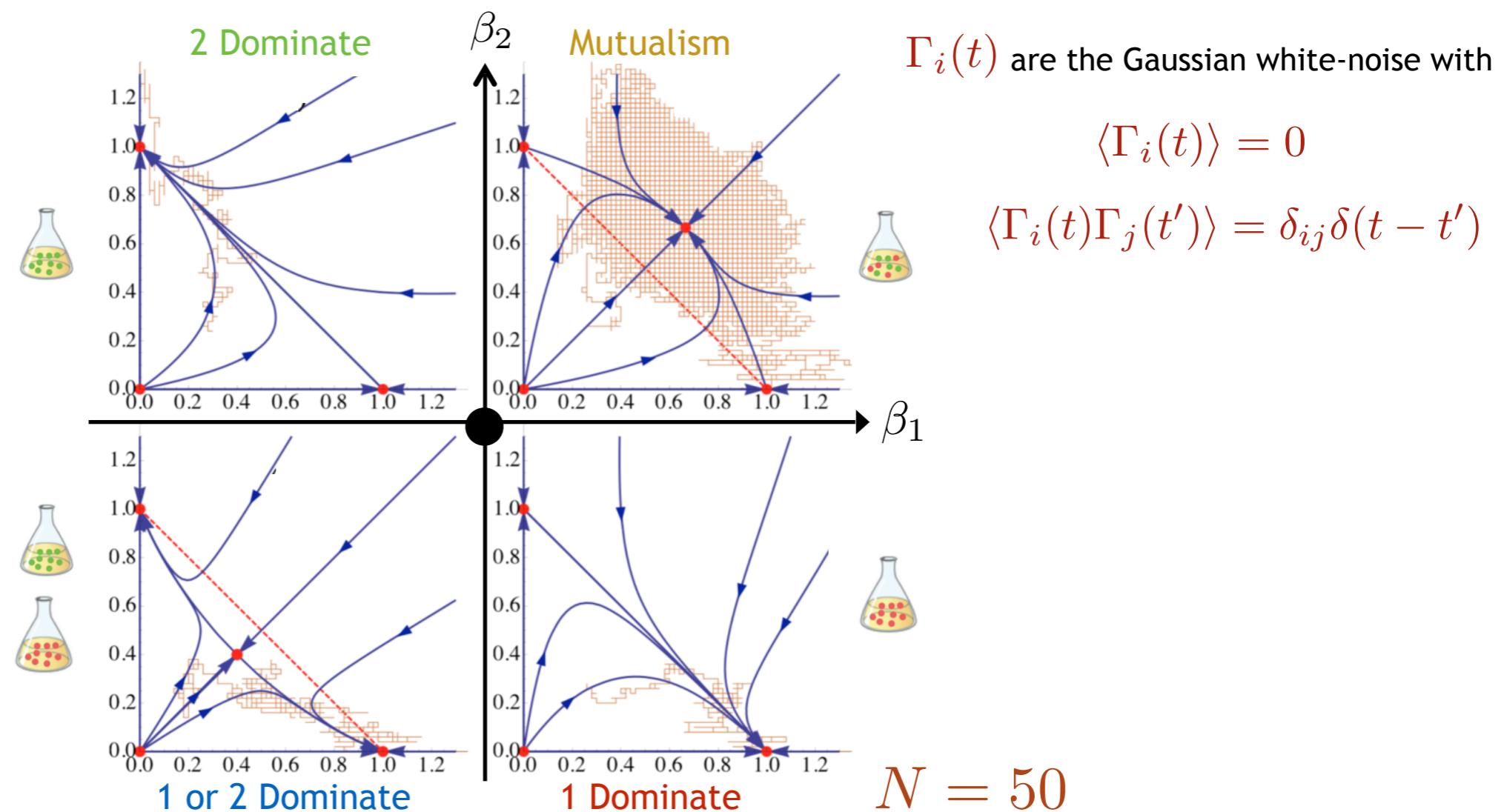


Stochastic Dynamics in the Large N Limit: from Markov Process to Ito Stochastic Differential Equation



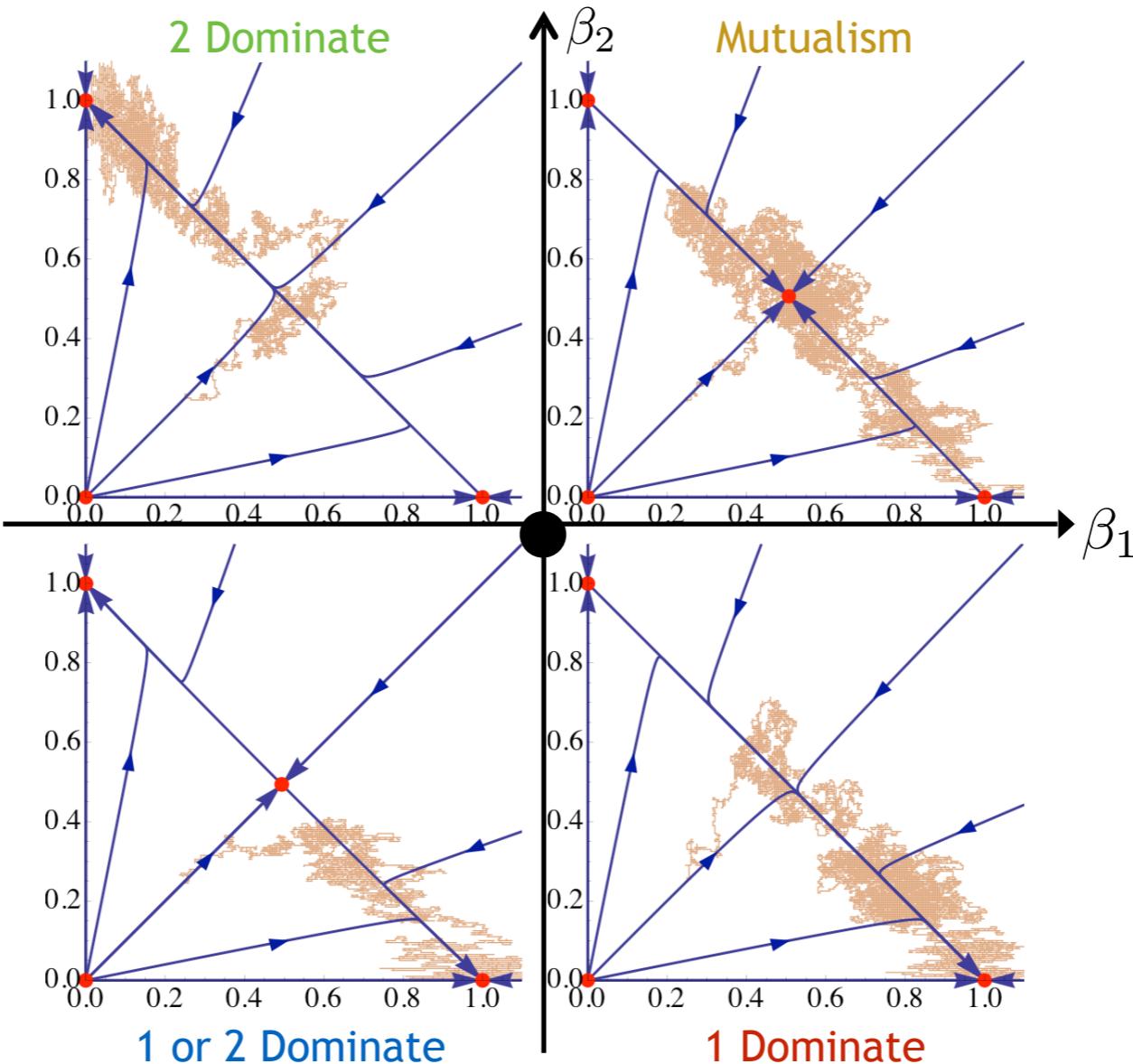
$$\frac{dc_1}{dt} = [\mu_1 c_1(1 - c_1 - c_2) + \mu_1 \beta_1 c_1 c_2] + \sqrt{\frac{\mu_1 c_1(1 + c_1 + c_2) - \mu_1 \beta_1 c_1 c_2}{N}} \Gamma_1(t)$$

$$\frac{dc_2}{dt} = [\mu_2 c_2(1 - c_1 - c_2) + \mu_2 \beta_2 c_1 c_2] + \sqrt{\frac{\mu_2 c_2(1 + c_1 + c_2) - \mu_2 \beta_2 c_1 c_2}{N}} \Gamma_2(t)$$



The limit $O(|\beta_i|) \ll 1$ and $\mu_1 = \mu_2 = \mu$

Fluctuations at long times are *constrained* near the equilibrium population size $c_T = 1$



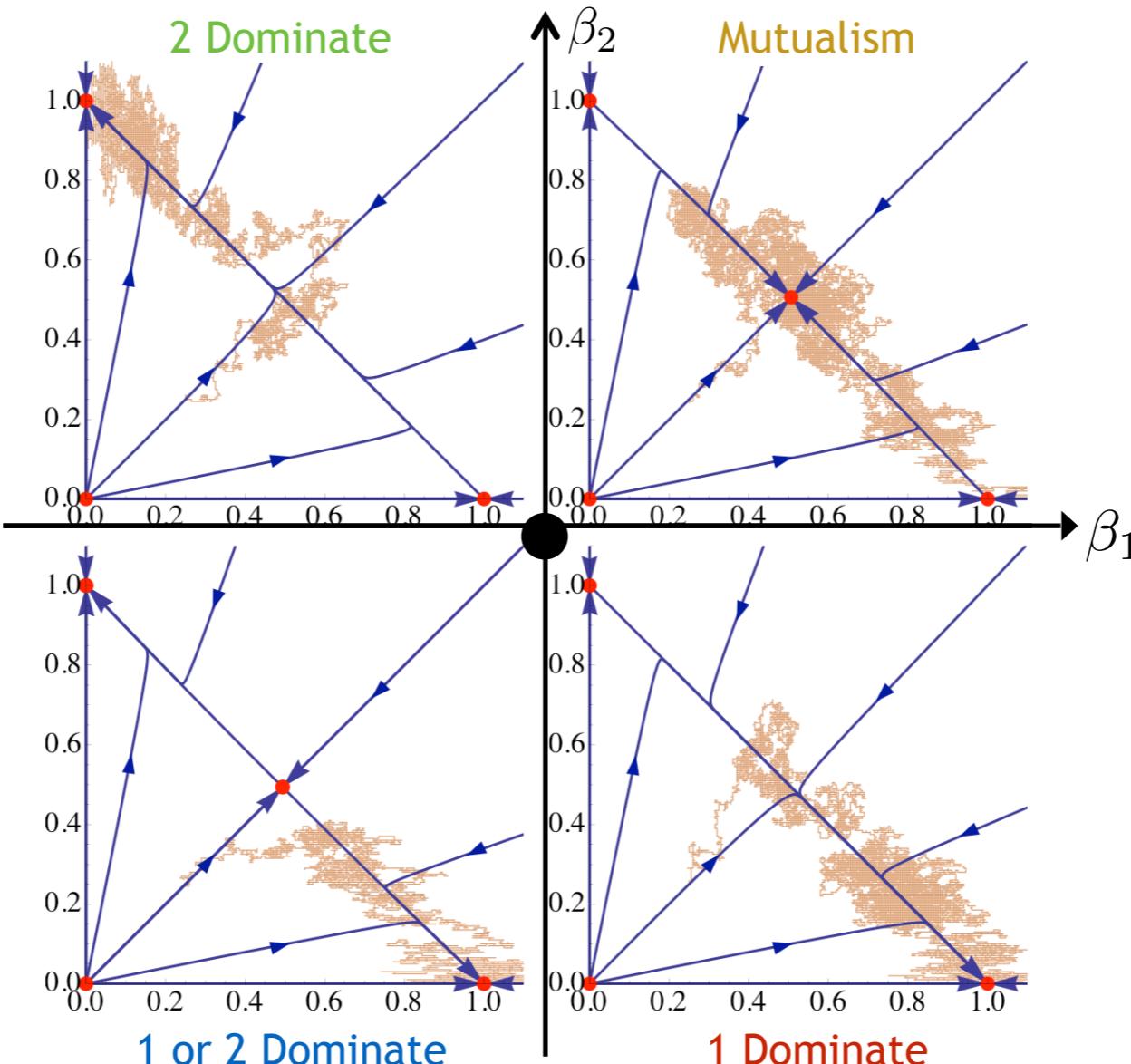
$N = 100$

At long times ,

$$N_T(t) = c_T(t)N \approx N$$

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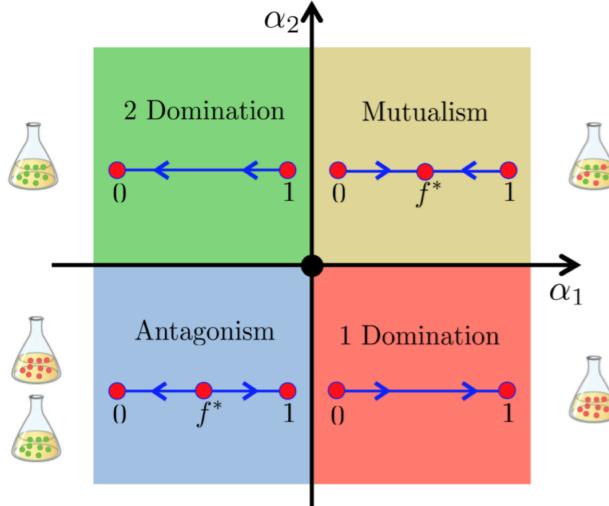


$N = 100$

At long times ,

$$N_T(t) = c_T(t)N \approx N$$

When $c_T \approx 1$, recover **replicator dynamics** with **genetic drift** and **independently fluctuating population sizes!**



$$v_E(f) = [\alpha_1(1-f) - \alpha_2 f](1-f)f$$

$$\alpha_i = \beta_i$$

$$\frac{df}{dt} = \mu v_E(f)c_T + \sqrt{\frac{\mu D_g(f)}{N}} \left(\frac{1+c_T}{c_T} \right) \Gamma_f(t),$$

$$\frac{dc_T}{dt} = \mu v_G(c_T) + \sqrt{\frac{\mu c_T(1+c_T)}{N}} \Gamma_{c_T}(t),$$

$$f(t) = c_1(t)/c_T(t)$$

$$c_T(t) = c_1(t) + c_2(t)$$

$$D_g(f) = f(1-f)$$

logistic growth of population size
that equilibrates at 1

$$v_G(c_T) = c_T(1-c_T)$$

$$v_E(f) = [\alpha_1(1-f) - \alpha_2 f](1-f)f$$

$$\alpha_i = \beta_i$$

New phenomena can arise if evolutionary and population size dynamics are coupled

Example: *quasi-neutral* evolution

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neutral at the equilibrium size ($\beta_1 = \beta_2 = 0$)

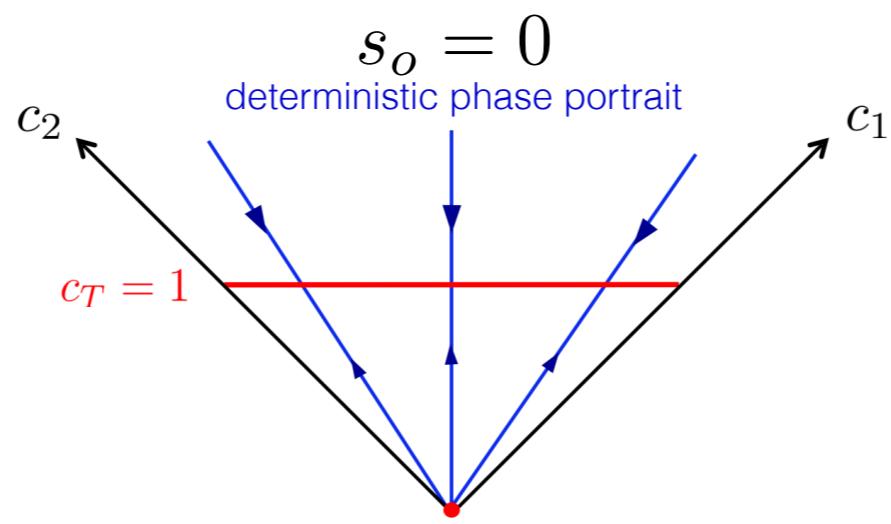
New phenomena can arise if evolutionary and population size dynamics are coupled

Example: *quasi-neutral* evolution

neutral at the equilibrium size ($\beta_1 = \beta_2 = 0$)

selective advantage in the dilute limit: $\left(\frac{\mu_1}{\mu_2} \right) = 1 + s_o$ with $s_o > 0$

neutral evolution without fluctuations



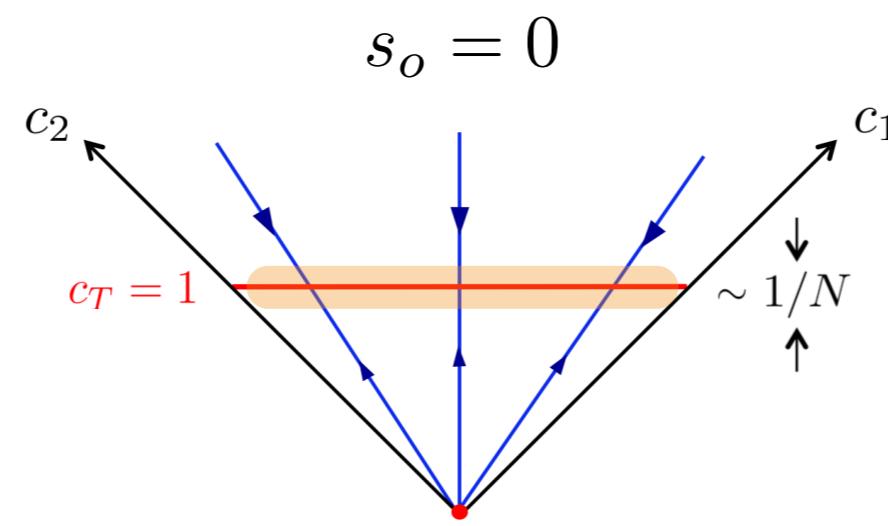
$$\frac{df}{dt} = 0$$

neutral evolution

$$\frac{dc_T}{dt} = v_G(c_T) = c_T(1 - c_T)$$

logistic growth of population size

neutral evolution with fluctuations



$$\frac{df}{dt} = \sqrt{\frac{D_g(f)}{N} \left(\frac{1 + c_T}{c_T} \right)} \Gamma_f(t)$$

genetic drift near $c_T = 1$ with $D_g(f) = f(1 - f)$

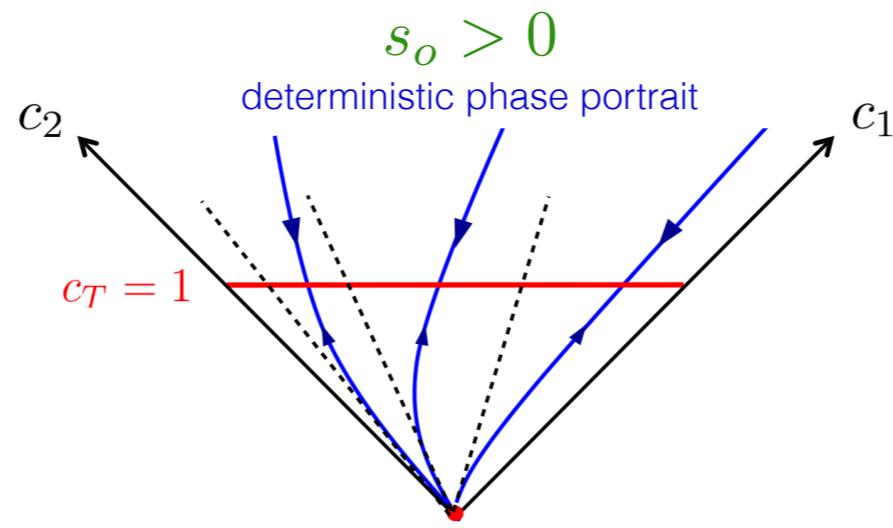
$$\frac{dc_T}{dt} = v_G(c_T) + \sqrt{\frac{c_T(1 + c_T)}{N}} \Gamma_{c_T}(t)$$

population size follows logistic growth

$$v_G(c_T) = c_T(1 - c_T)$$

and fluctuates independently near $c_T = 1$

quasi-neutral evolution without fluctuations



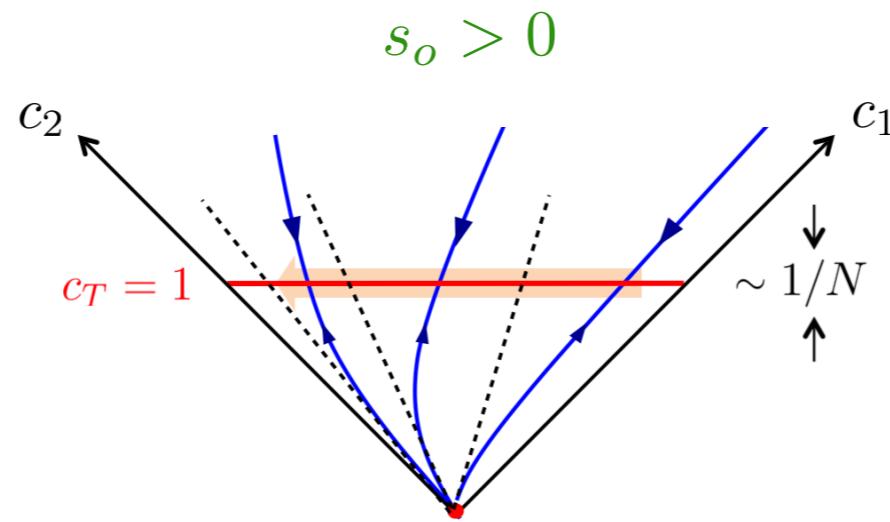
$$\frac{df}{dt} = v_R(f, c_T) = s_0 f (1 - f) [(1 - c_T)] \quad \text{evolutionary dynamics}$$

$$\frac{dc_T}{dt} = (1 + s_o f) v_G(c_T) \quad \text{population size dynamics}$$

} coupled

quasi-neutral evolution with fluctuations

Fluctuations-induced selection arises near $c_T = 1$



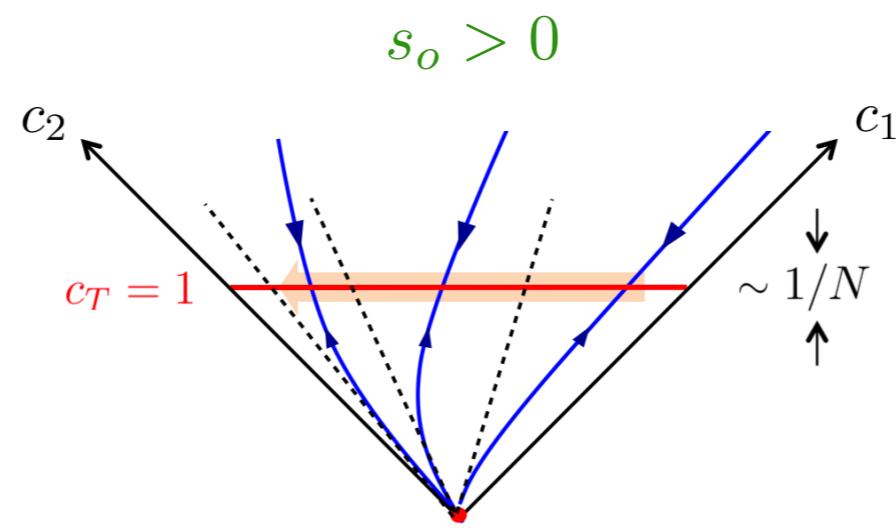
$$\frac{df}{dt} = v_R(f, c_T) + \sqrt{\frac{D_g(f)}{N} \left(\frac{1+c_T}{c_T} \right) \left(1 + s_o(1-f) \right)} \Gamma_f(t),$$

$$\frac{dc_T}{dt} = (1+s_o f) v_G(c_T) + \sqrt{\frac{c_T(1+c_T)}{N}} (1+s_o f) \Gamma_{c_T}(t),$$

$$v_R(f, c_T) = s_o f (1-f) \left[(1-c_T) - \frac{1}{N} \left(\frac{1+c_T}{c_T} \right) \right]$$

Evolutionary dynamics near $c_T = 1$ *disfavors* the fixation of species with *reproductive advantage* near the origin.

Solving for the fixation probability and the mean fixation time in 2D
starting from an arbitrary $\mathbf{c} = (c_1, c_2)$?



Solving for the fixation probability and the mean fixation time in 2D
 starting from an arbitrary $\mathbf{c} = (c_1, c_2)$?

The fixation probability $u(\mathbf{c})$:

$$0 = \sum_{i=1}^2 \left(v_i(\mathbf{c}) \partial_{c_i} u(\mathbf{c}) + \frac{1}{2N} D_i(\mathbf{c}) \partial_{c_i}^2 u(\mathbf{c}) \right)$$

$$u(c_1, 0) = 1 \text{ and } u(0, c_2) = 0$$

The mean fixation time $\tau(\mathbf{c})$:

$$-1 = \sum_{i=1}^2 \left(v_i(\mathbf{c}) \partial_{c_i} \tau(\mathbf{c}) + \frac{1}{2N} D_i(\mathbf{c}) \partial_{c_i}^2 \tau(\mathbf{c}) \right)$$

$$\tau(c_1, 0) = 0 \text{ and } \tau(0, c_2) = 0$$

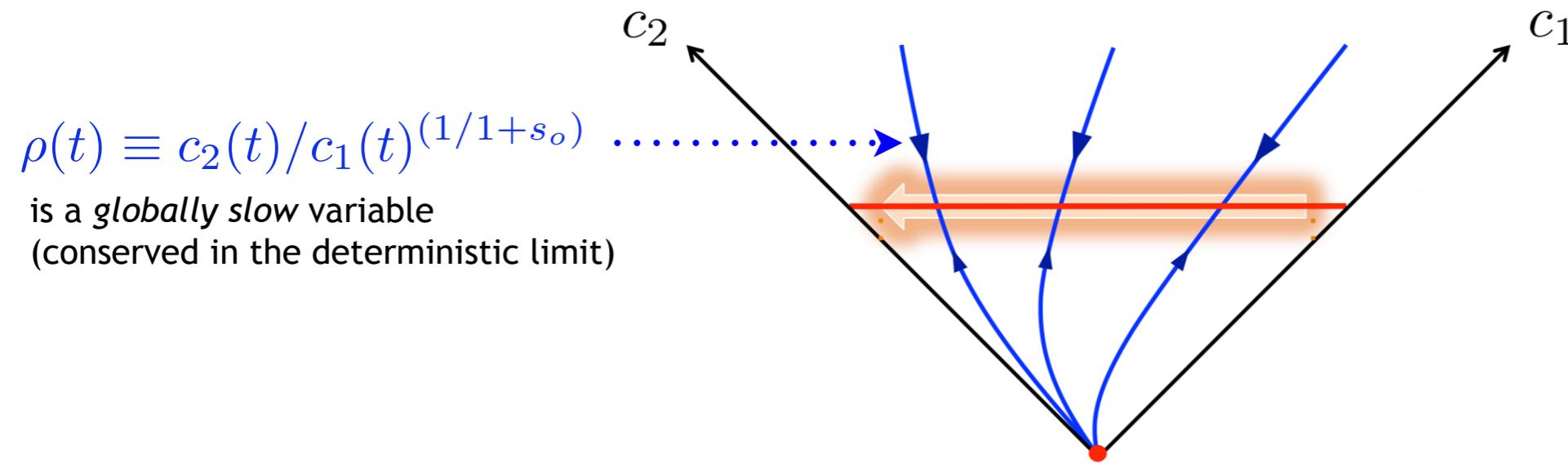
$$v_1(\mathbf{c}) = \mu_1 c_1 (1 - c_1 - c_2) + \mu_1 \beta_1 c_1 c_2,$$

$$v_2(\mathbf{c}) = \mu_2 c_2 (1 - c_1 - c_2) + \mu_2 \beta_2 c_1 c_2,$$

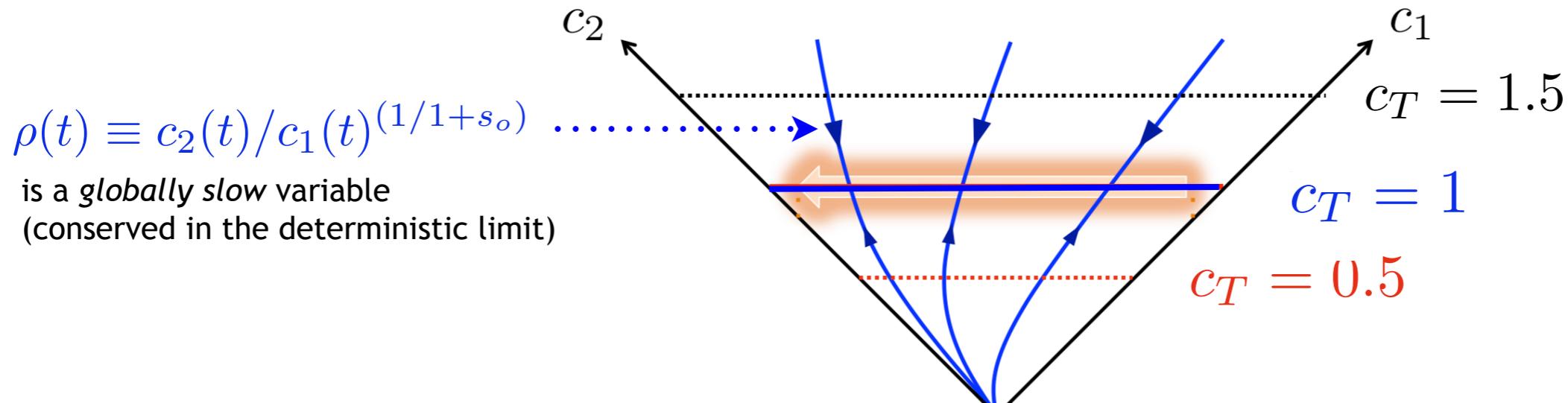
$$D_1(\mathbf{c}) = \mu_1 c_1 (1 + c_1 + c_2) - \mu_1 \beta_1 c_1 c_2,$$

$$D_2(\mathbf{c}) = \mu_2 c_2 (1 + c_1 + c_2) - \mu_2 \beta_2 c_1 c_2$$

Adiabatic elimination of the fast population size variable leads to
a *one-dimensional* effective dynamics in the slow variable $\rho(t) \equiv c_2(t)/c_1(t)^{(1/1+s_o)}$



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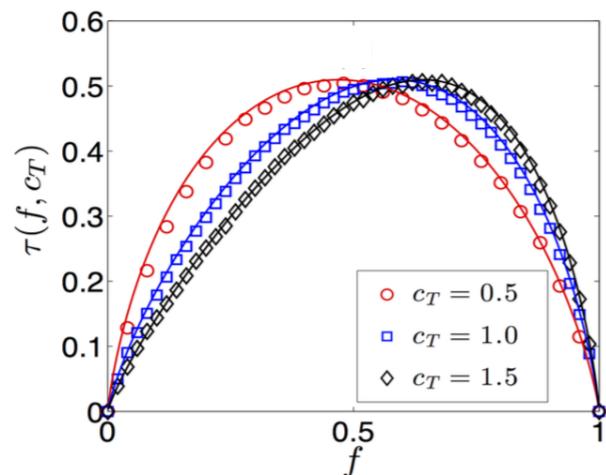
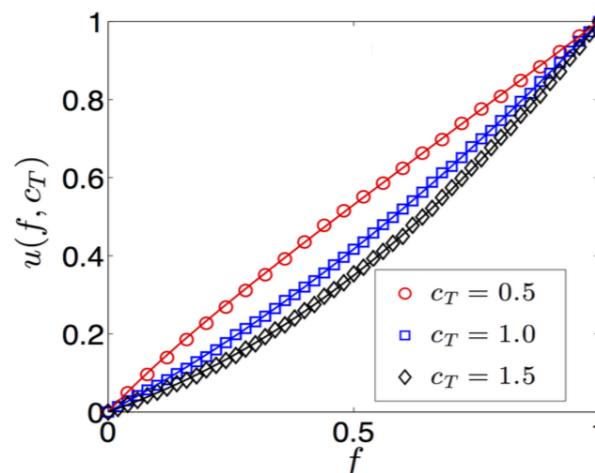
$\rho(t) \equiv c_2(t)/c_1(t)^{(1/1+s_o)}$
is a *globally slow* variable
(conserved in the deterministic limit)

can solve for the **fixation probability** $u(f, c_T)$ and **the mean fixation time** $\tau(f, c_T)$
in an **arbitrary population size** as an effectively one dimensional problem in ρ .

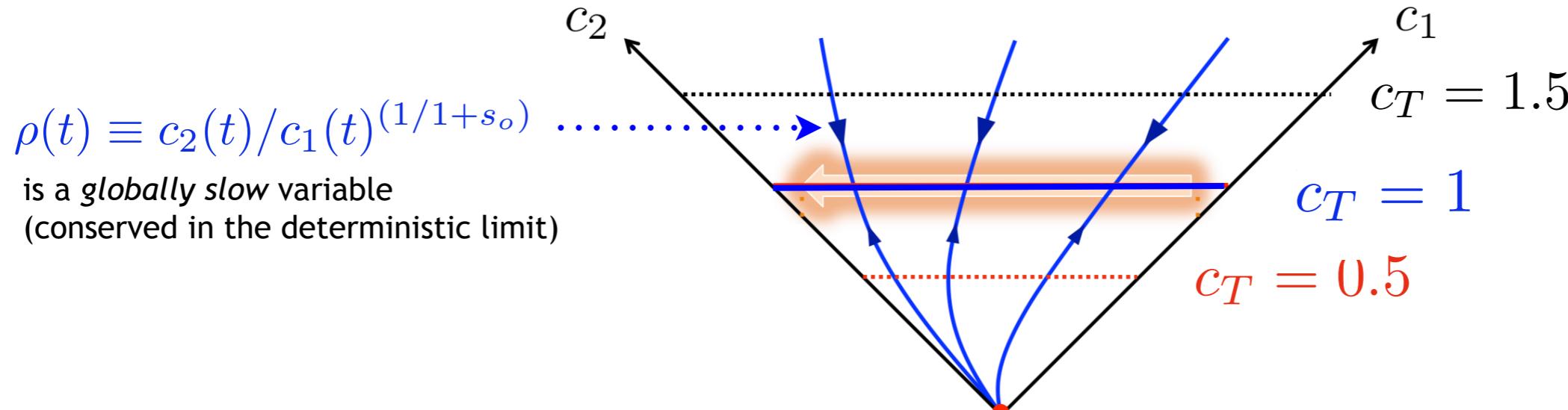
The fixation probability

$$N = 100 \\ s_o = 1$$

The mean fixation time



Adiabatic elimination of the fast population size variable leads to a *one-dimensional* effective dynamics in the slow variable $\rho(t) \equiv c_2(t)/c_1(t)^{(1/1+s_o)}$



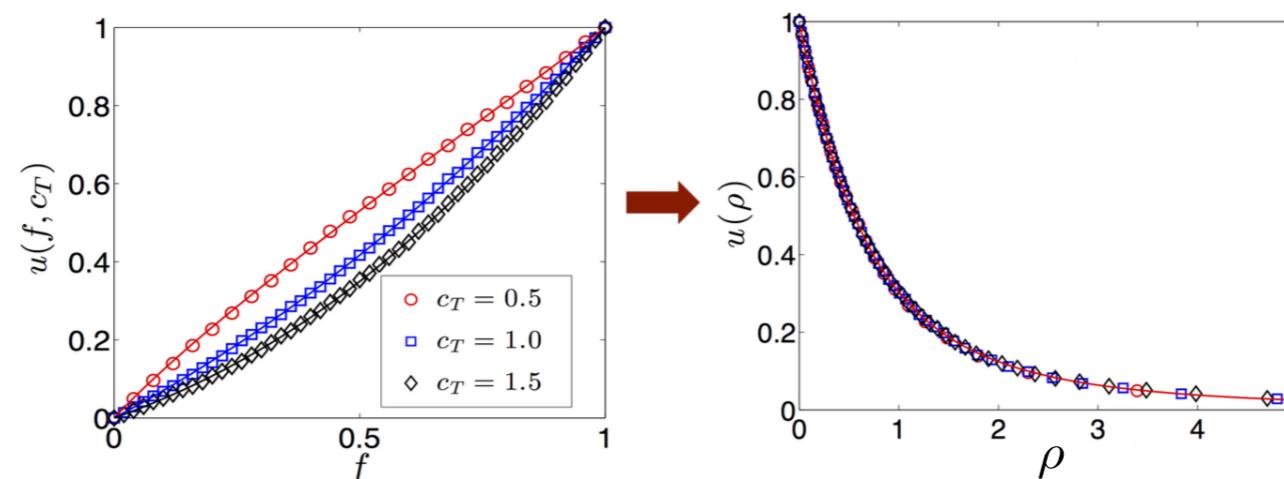
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The fixation probability

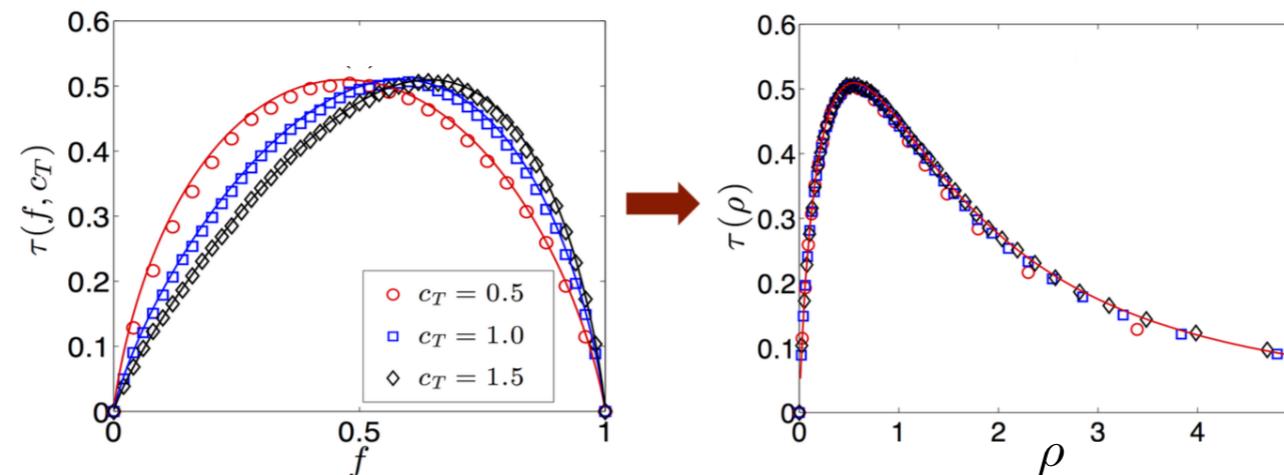
$$N = 100$$

$$s_o = 1$$

The mean fixation time

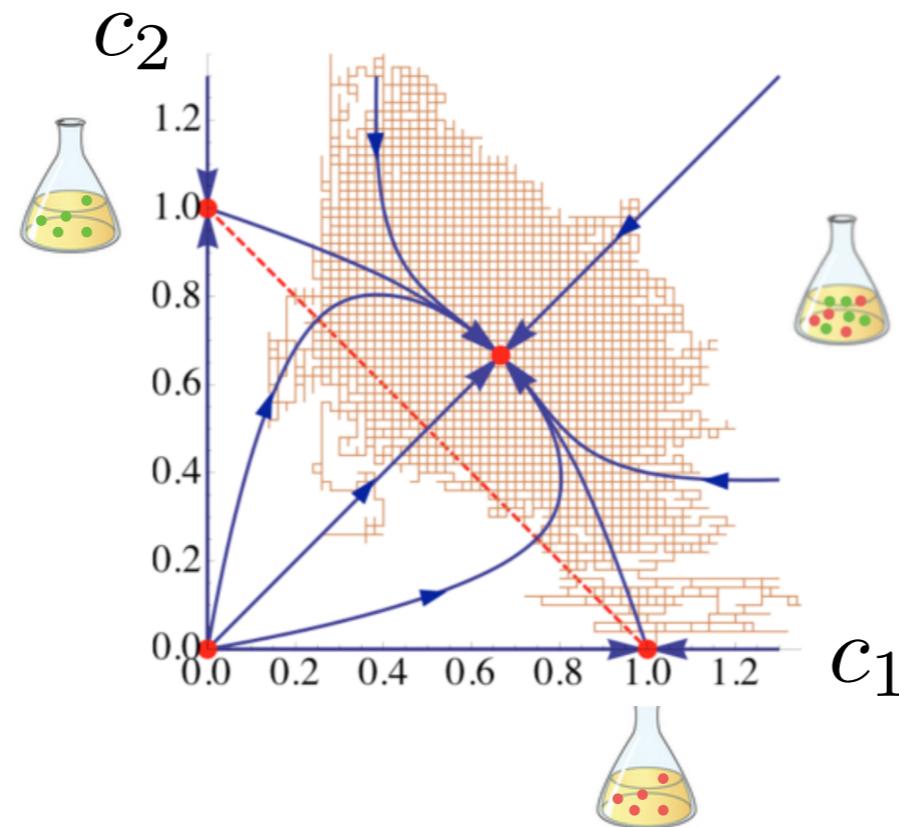


Data collapse when plotted as a function of ρ



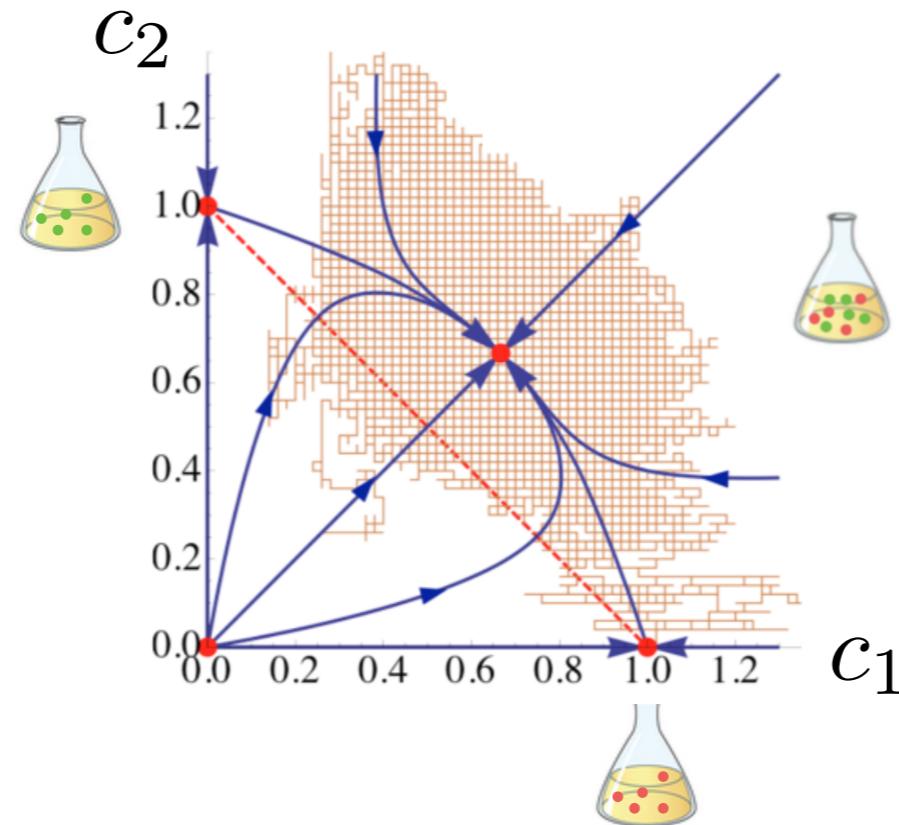
Another limit where the replicator dynamics with genetic drift fails: strong mutualism

The population size no longer fluctuates around the fixed equilibrium line



Another limit where the replicator dynamics with genetic drift fails: strong mutualism

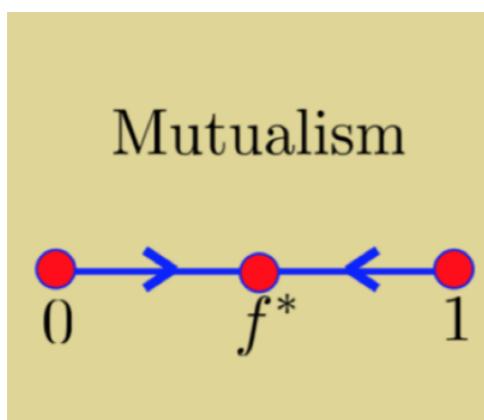
The population size no longer fluctuates around the fixed equilibrium line



The fixed population size model

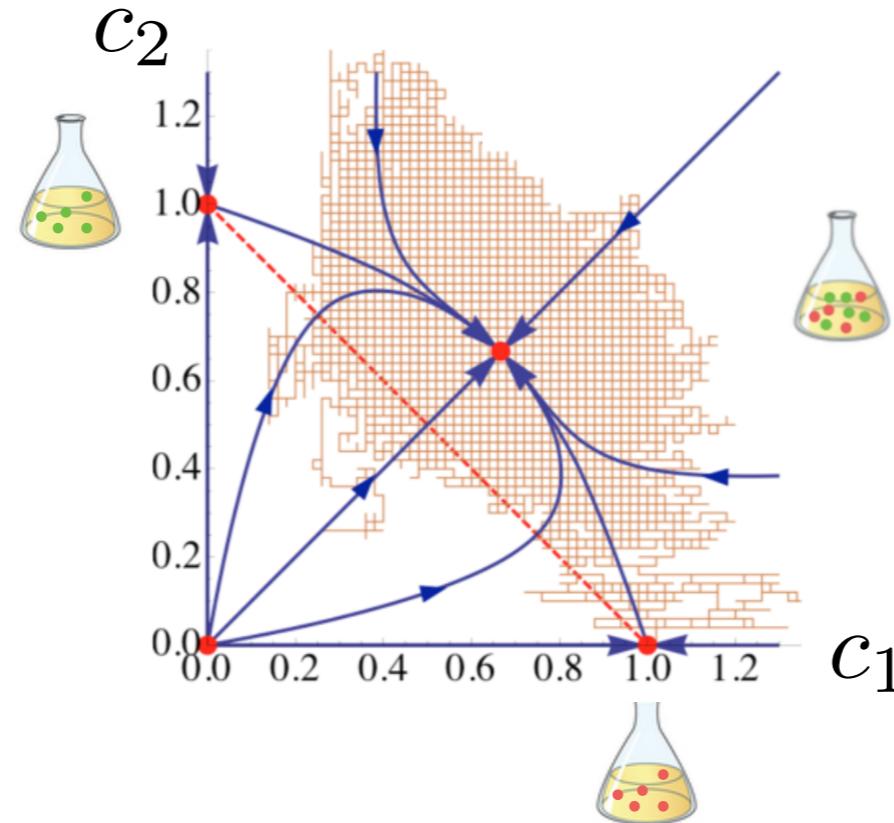
$$\frac{df}{dt} = \mu \tilde{\beta} f(1 - f)(f^* - f) + \sqrt{\frac{2\mu}{N} D_g(f)} \Gamma_f(t)$$

$$\bar{\beta} = (\beta_1 + \beta_2) , \quad f^* = \beta_1 / (\beta_1 + \beta_2)$$



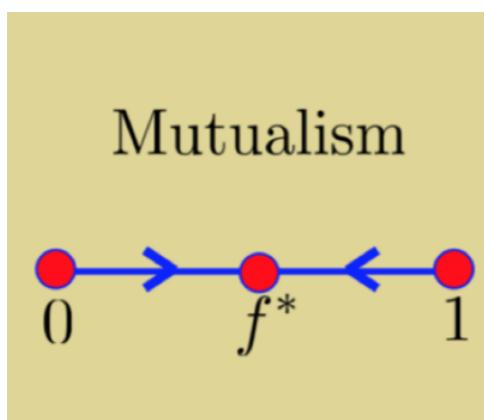
Another limit where the replicator dynamics with genetic drift fails: strong mutualism

The population size no longer fluctuates around the fixed equilibrium line



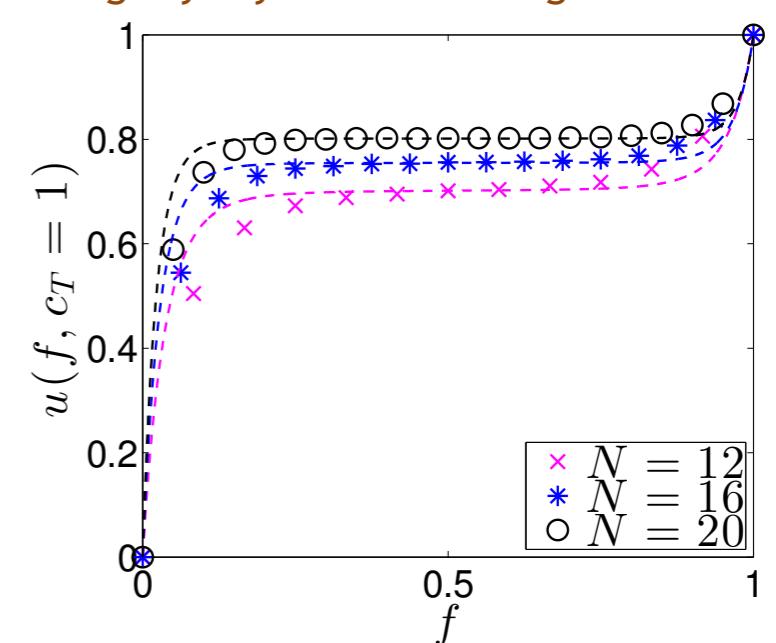
The fixed population size model **fails** to predict the fixation probability near the absorbing boundaries:

$$\frac{df}{dt} = \mu \tilde{\beta} f(1-f)(f^*-f) + \sqrt{\frac{2\mu}{N} D_g(f)} \Gamma_f(t)$$



$$u(f) = \frac{\int_0^f e^{\frac{N\tilde{\beta}}{2}(f^*-f)^2} df}{\int_0^1 e^{\frac{N\tilde{\beta}}{2}(f^*-f)^2} df}$$

$\beta_1 = 0.75$ $\beta_2 = 0.7$ $f^* \approx 0.52$
slightly asymmetric strong mutualism



Solving for the fixation probability and the mean fixation time in 2D
 starting from an arbitrary $\mathbf{c} = (c_1, c_2)$?

The fixation probability $u(\mathbf{c})$:

$$0 = \sum_{i=1}^2 \left(v_i(\mathbf{c}) \partial_{c_i} u(\mathbf{c}) + \frac{1}{2N} D_i(\mathbf{c}) \partial_{c_i}^2 u(\mathbf{c}) \right)$$

$$u(c_1, 0) = 1 \text{ and } u(0, c_2) = 0$$

The mean fixation time $\tau(\mathbf{c})$:

$$-1 = \sum_{i=1}^2 \left(v_i(\mathbf{c}) \partial_{c_i} \tau(\mathbf{c}) + \frac{1}{2N} D_i(\mathbf{c}) \partial_{c_i}^2 \tau(\mathbf{c}) \right)$$

$$\tau(c_1, 0) = 0 \text{ and } \tau(0, c_2) = 0$$

$$v_1(\mathbf{c}) = \mu_1 c_1 (1 - c_1 - c_2) + \mu_1 \beta_1 c_1 c_2,$$

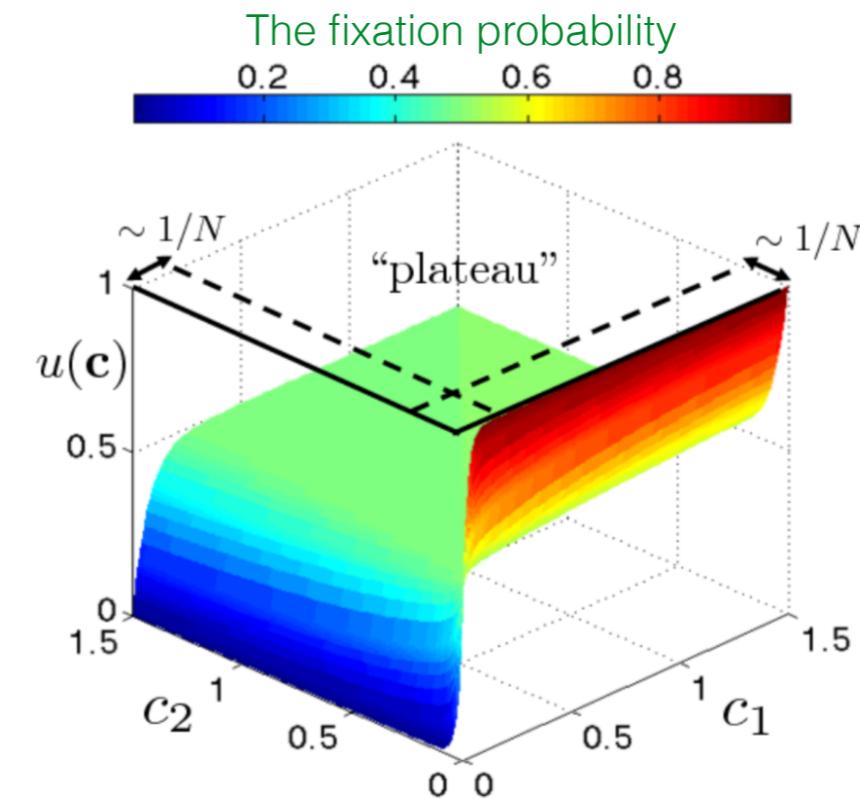
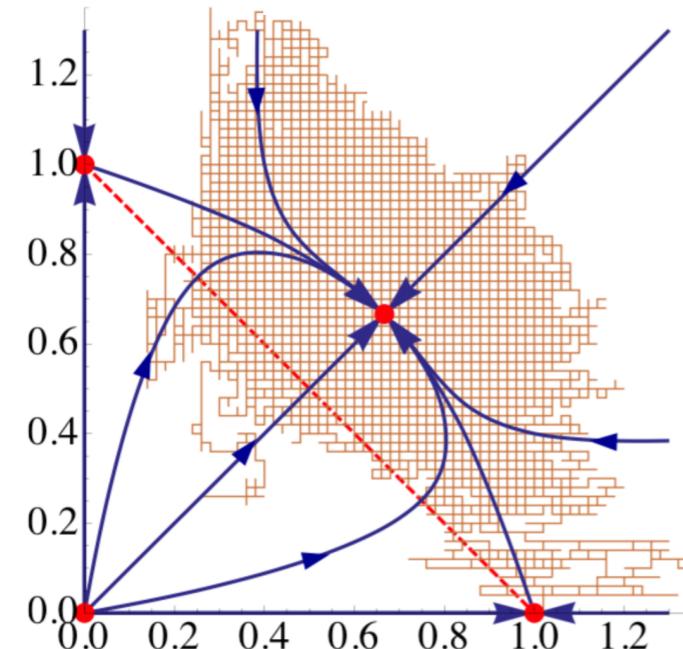
$$v_2(\mathbf{c}) = \mu_2 c_2 (1 - c_1 - c_2) + \mu_2 \beta_2 c_1 c_2,$$

$$D_1(\mathbf{c}) = \mu_1 c_1 (1 + c_1 + c_2) - \mu_1 \beta_1 c_1 c_2,$$

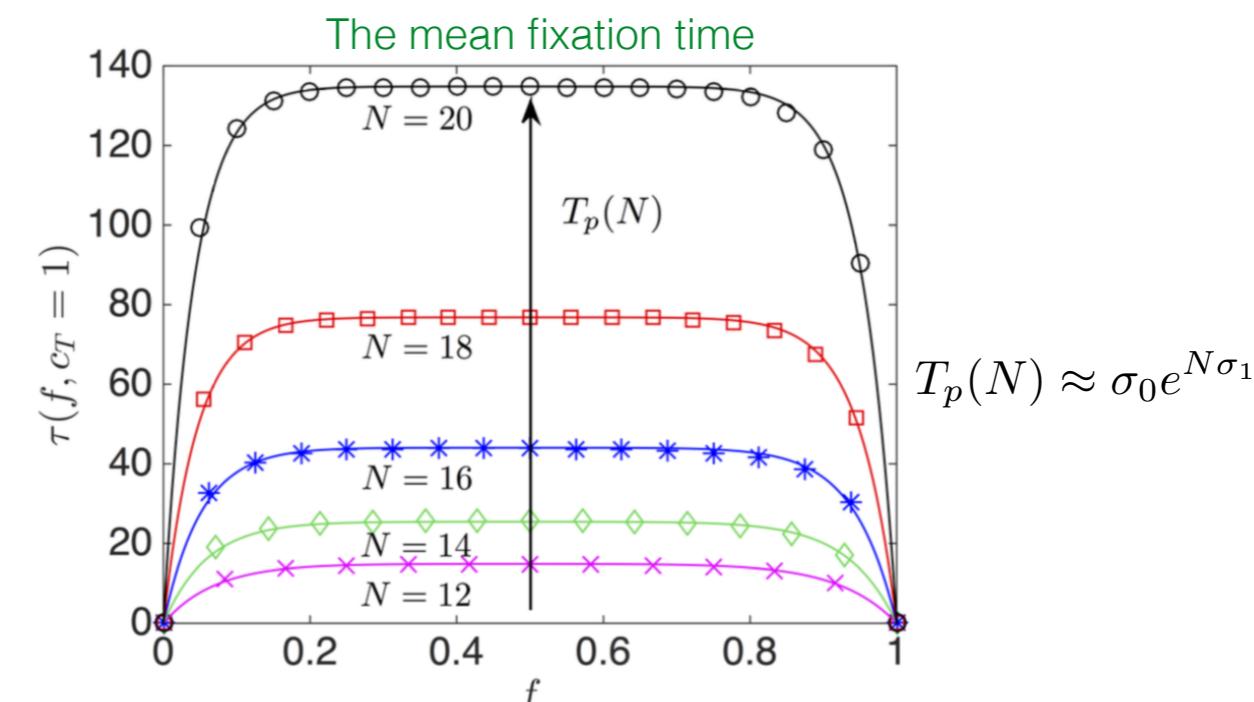
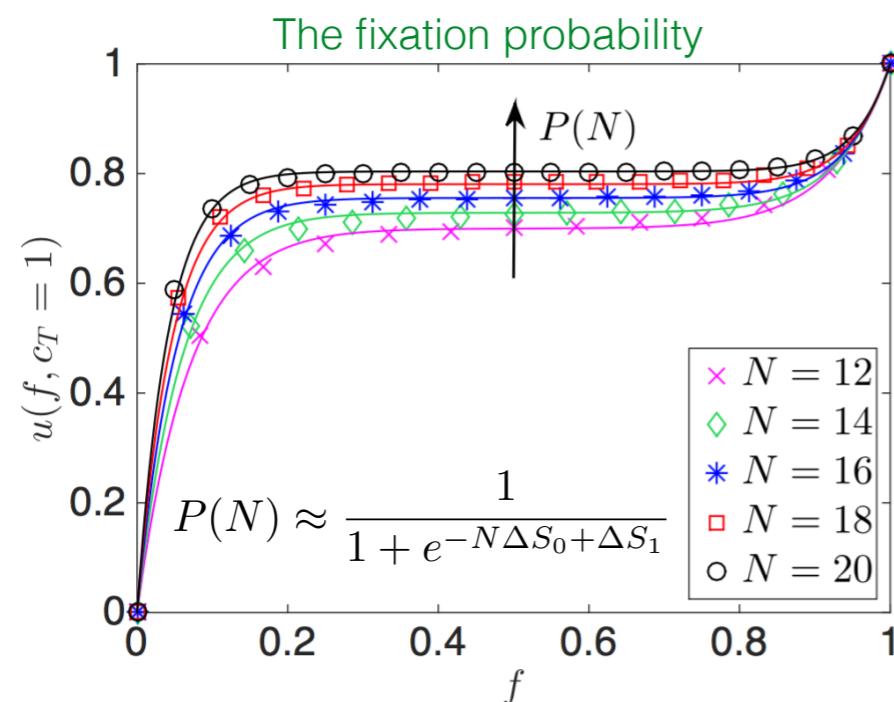
$$D_2(\mathbf{c}) = \mu_2 c_2 (1 + c_1 + c_2) - \mu_2 \beta_2 c_1 c_2$$

The fixation probability and the mean fixation time for strong mutualism: large deviation in 2D

Using matched asymptotic expansions, we get an excellent agreement between simulation and theory.
 symmetric strong mutualism: $\beta_1 = \beta_2 = 0.5$

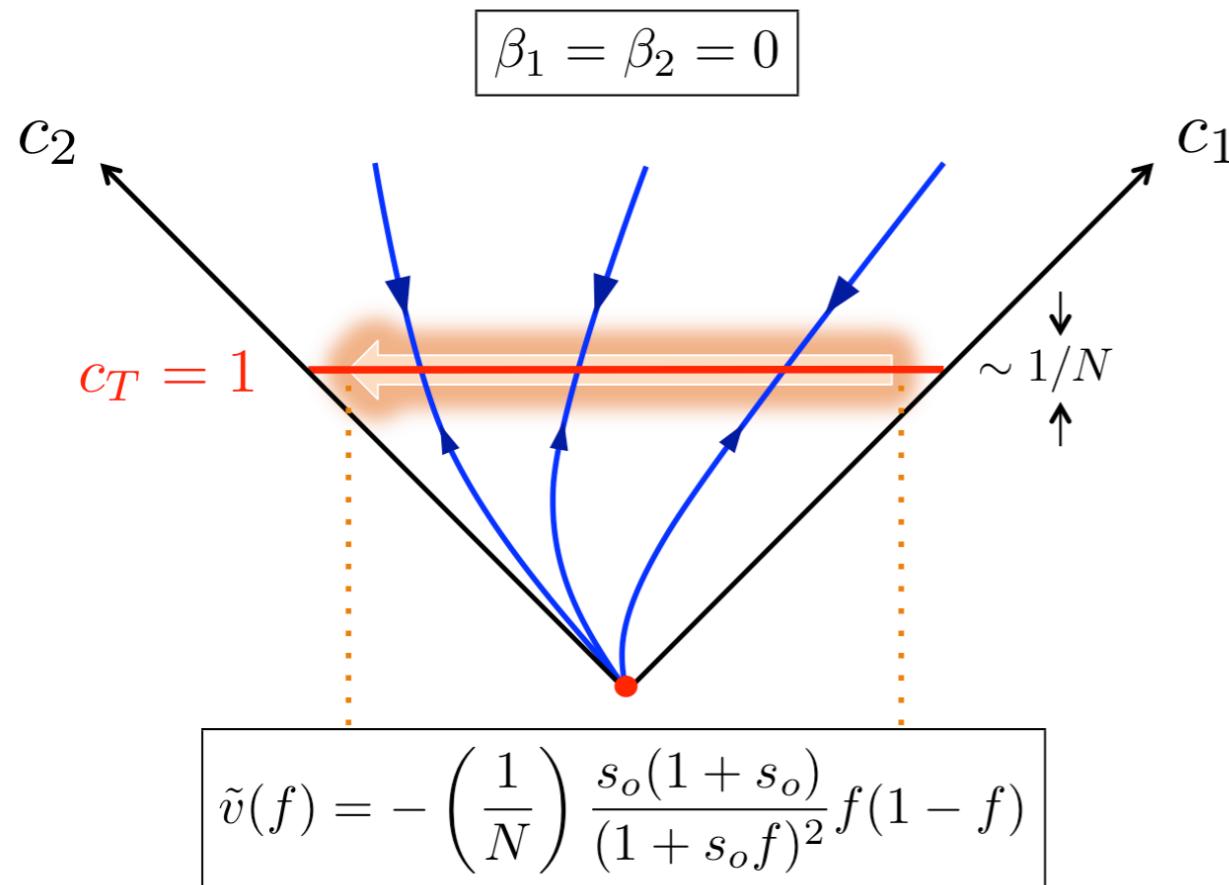


slightly asymmetric strong mutualism: $\beta_1 = 0.75$ $\beta_2 = 0.7$ $f^* \approx 0.52$

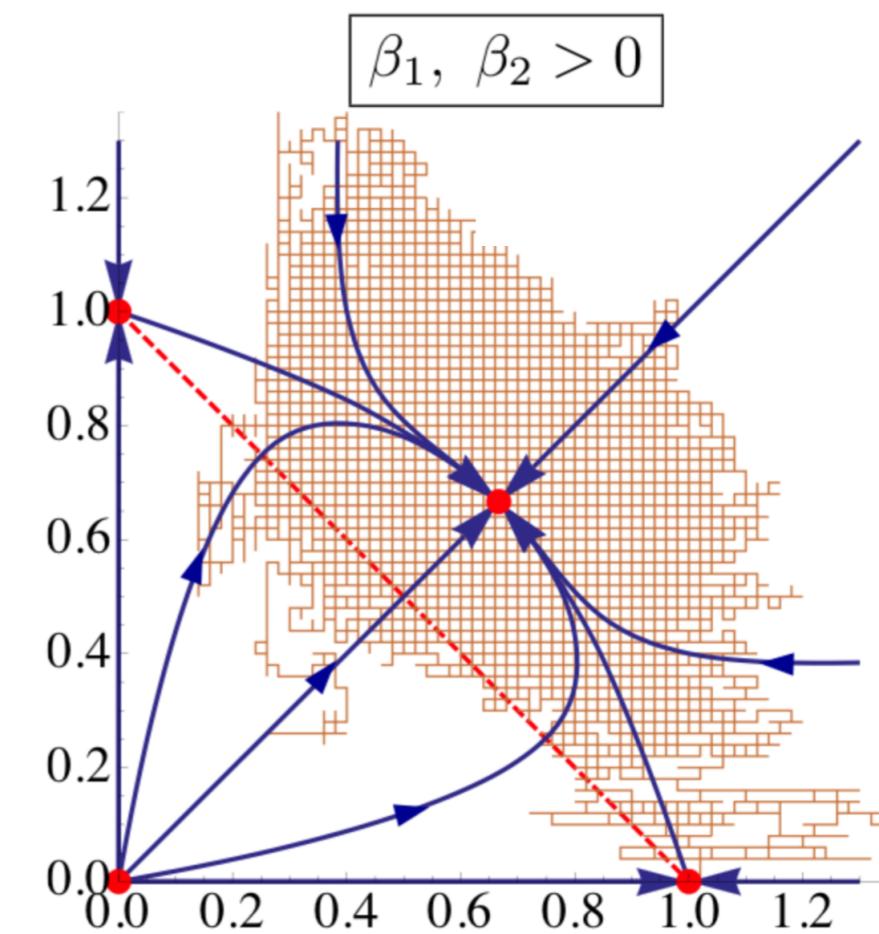


Conclusion of part 1: population size fluctuations are important in a well-mixed system!

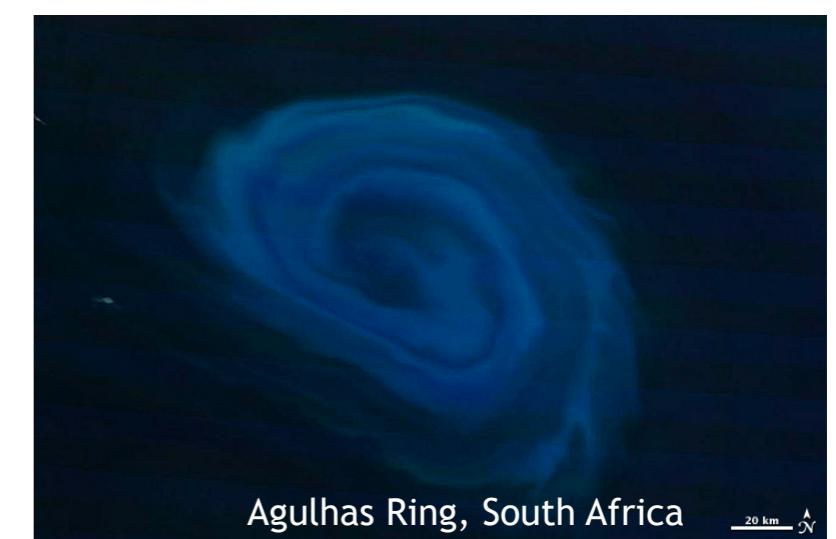
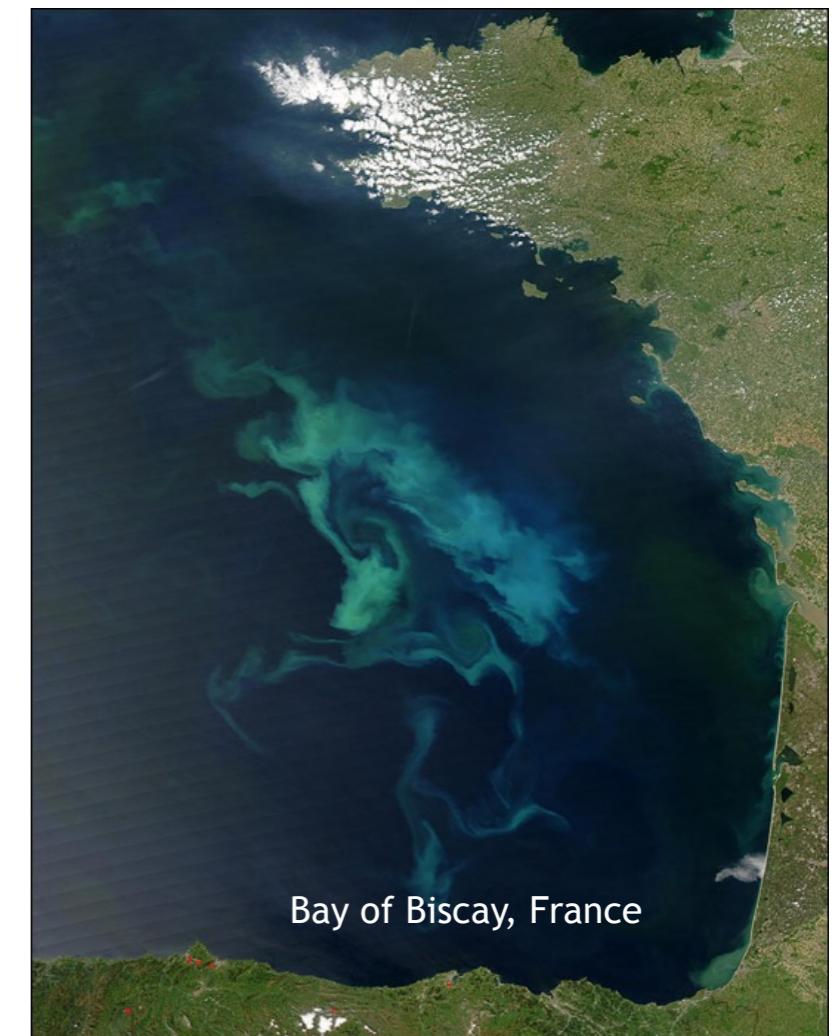
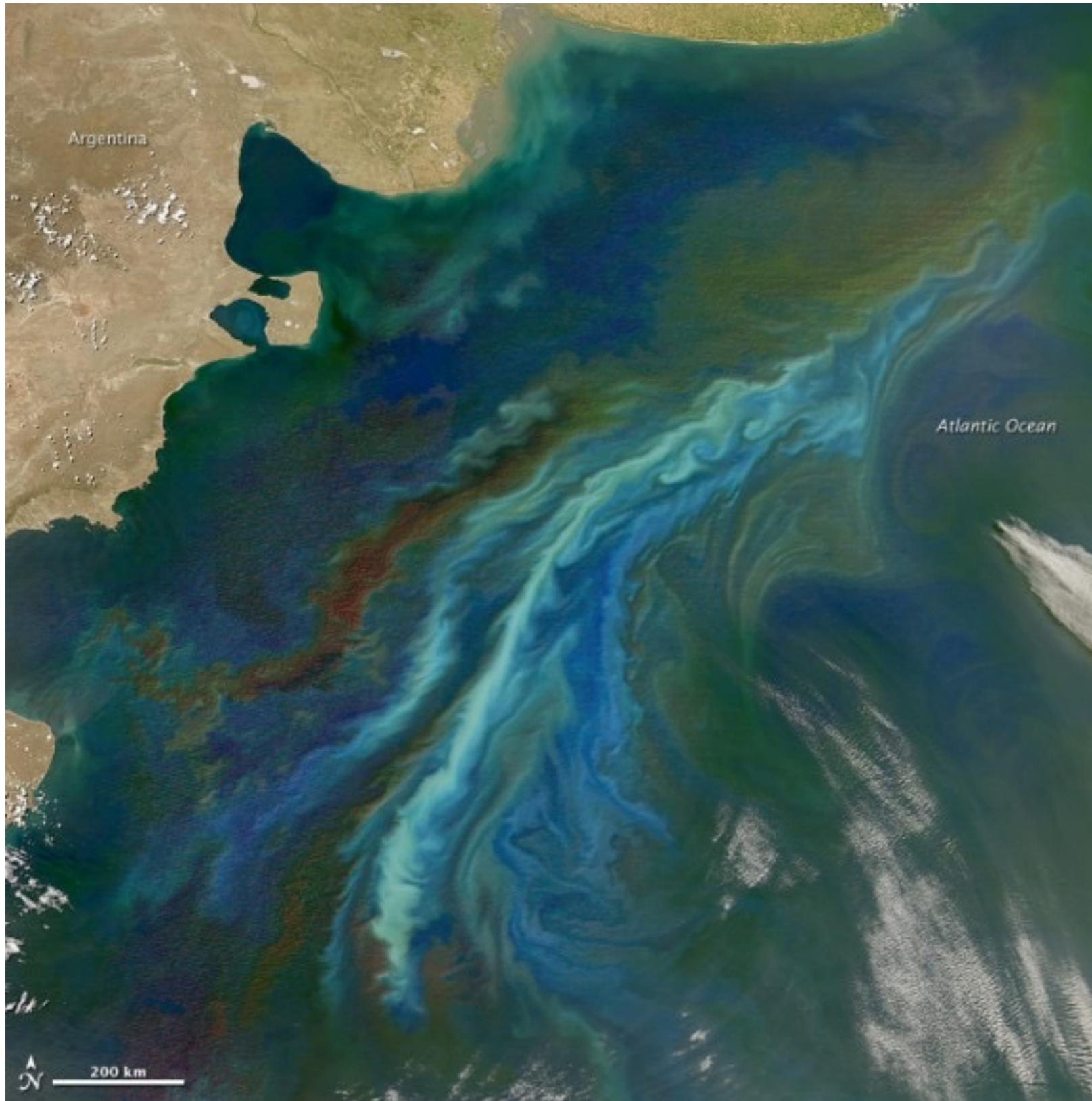
Quasi-neutral Evolution



Strong Mutualism



Part 2: Striated Populations in Disordered Environments with Advection



Standard Spatial Model of Population Growth (Range Expansion)

Fisher-Kolmogorov-Petrovsky-Piscounov (FKPP) equation:

$$\partial_t c = D \nabla^2 c + a_0 c - b c^2$$

Diffusion Logistic Growth

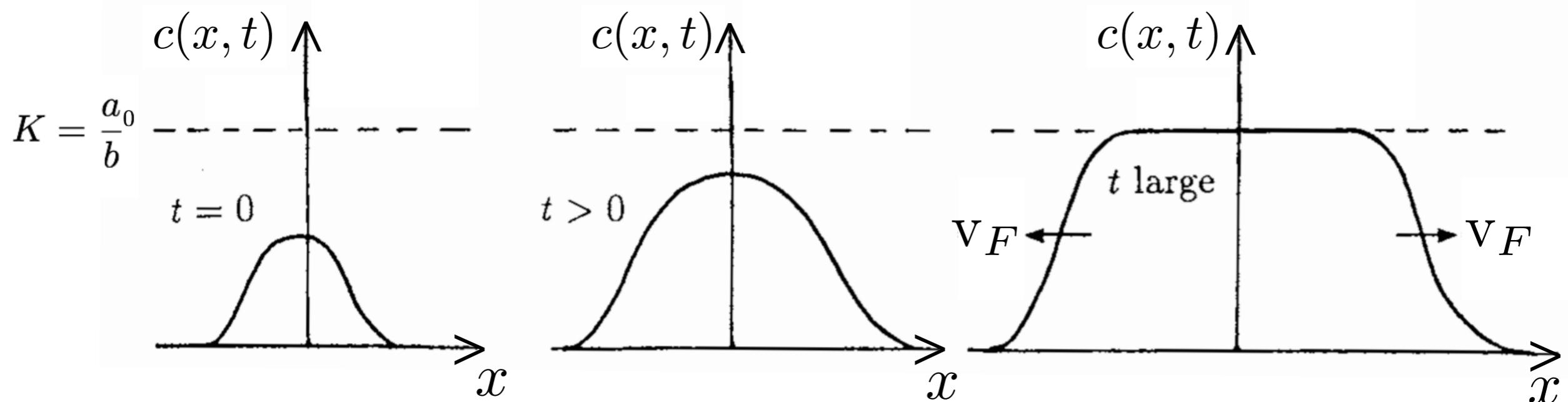
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Diffusion Logistic Growth

1D behavior of $c(x, t)$:



Typical (minimal) propagation Fisher's velocity: $V_F = 2\sqrt{D a_0}$

Steady state at long times is **featureless** determined by the local carrying capacity K .

Spatial Variations in Growth Environments



Spatial Population Dynamics with Spatial-dependent Growth Rates

FKPP equation with a spatially quenched random growth rate:

$$\partial_t c = D \nabla^2 c + a(\mathbf{x})c - bc^2$$

Spatial-dependent Growth Rates

Experiments of bacteriophage T7 populations diffusing and reproducing on disordered E.Coli lawn

the yellow fluorescent labeled region are susceptible *E. Coli* populations (favorable growth habitats) while the red fluorescent labeled rhombus are resistant *E. coli* populations (less favorable growth habitats.)



Marine Populations in Disordered Environments with Advection

FKPP equation with a spatially quenched random growth rate and constant advection:

$$\partial_t c + \mathbf{v} \cdot \nabla c = D \nabla^2 c + a(\mathbf{x})c - bc^2.$$

Fluid Advection

Spatially Quenched *Fluctuating* Growth Rates

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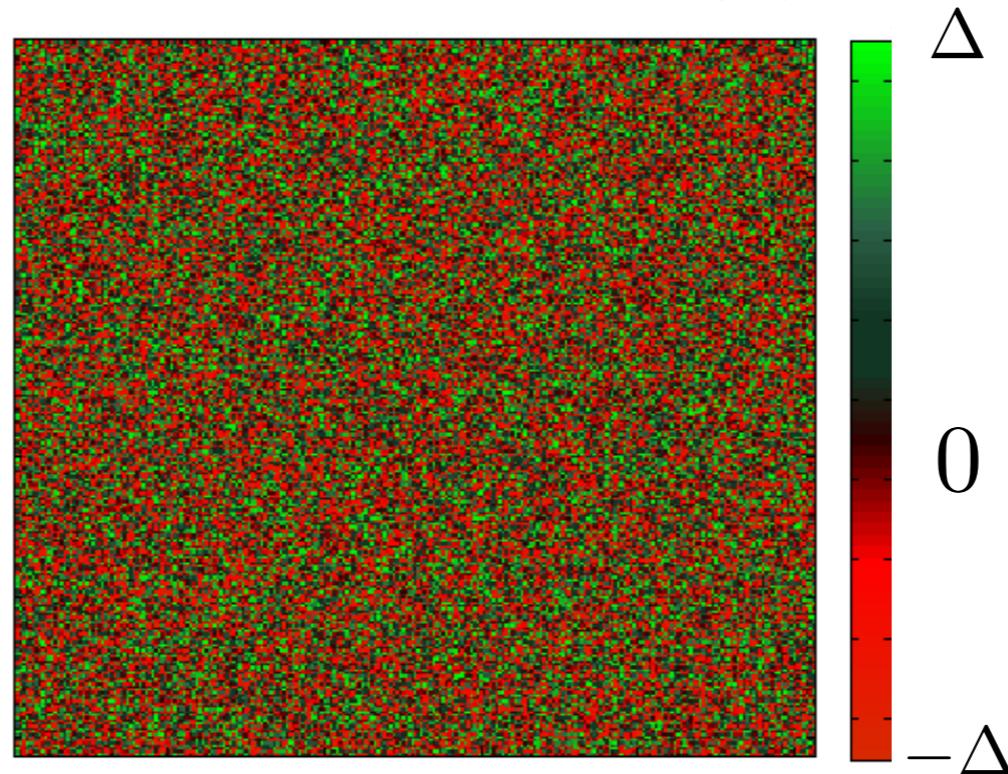
Fluid Advection

Spatially Quenched *Fluctuating* Growth Rates

Spatially Quenched Random Growth Landscape:

$$a(\mathbf{x}) = a_0 + \delta a(\mathbf{x}) \quad , \quad \langle \delta a(\mathbf{x}) \rangle = 0 \quad , \quad \langle \delta a(\mathbf{x}) \delta a(\mathbf{x}') \rangle \propto \Delta^2 \delta^d(\mathbf{x} - \mathbf{x}')$$

A 2D realization of $\delta a(\mathbf{x})$

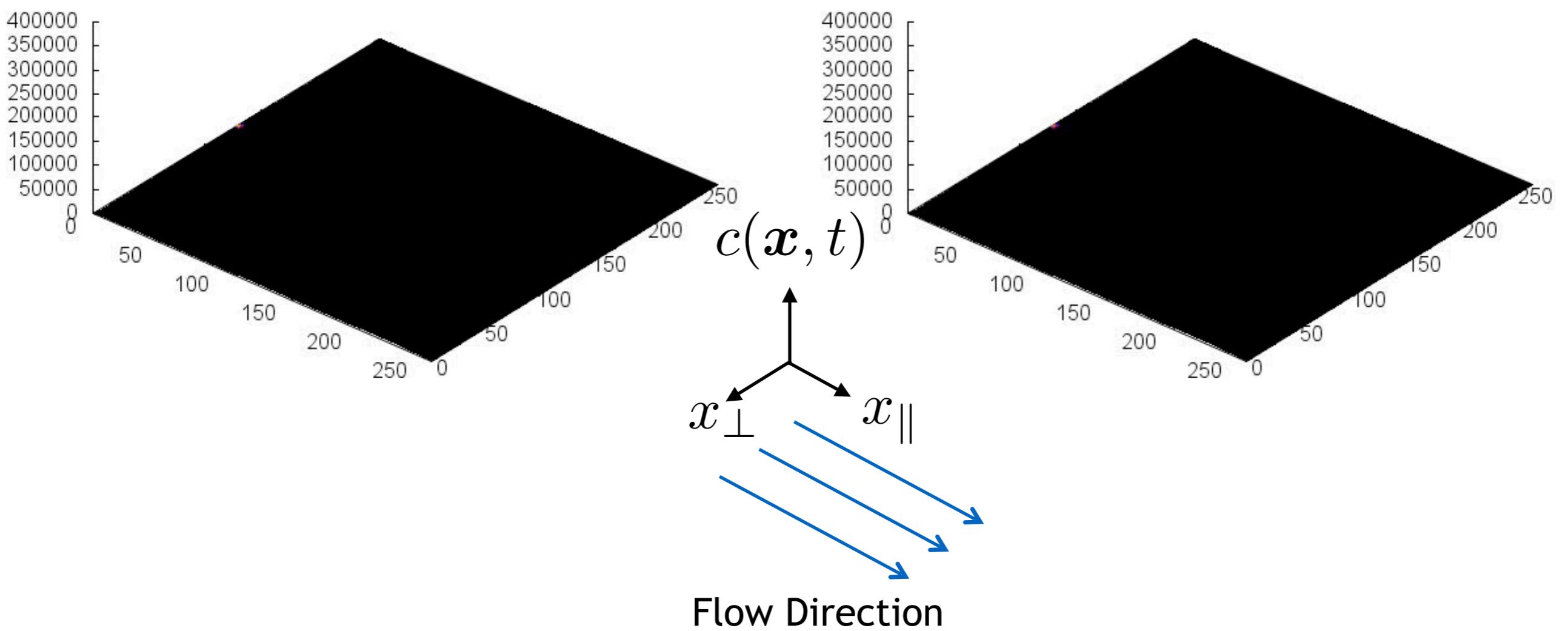


How does a simple constant flow and fluctuations in the growth environment affect the population structure?

Approach to Steady State Populations in Disordered Environments with Advection

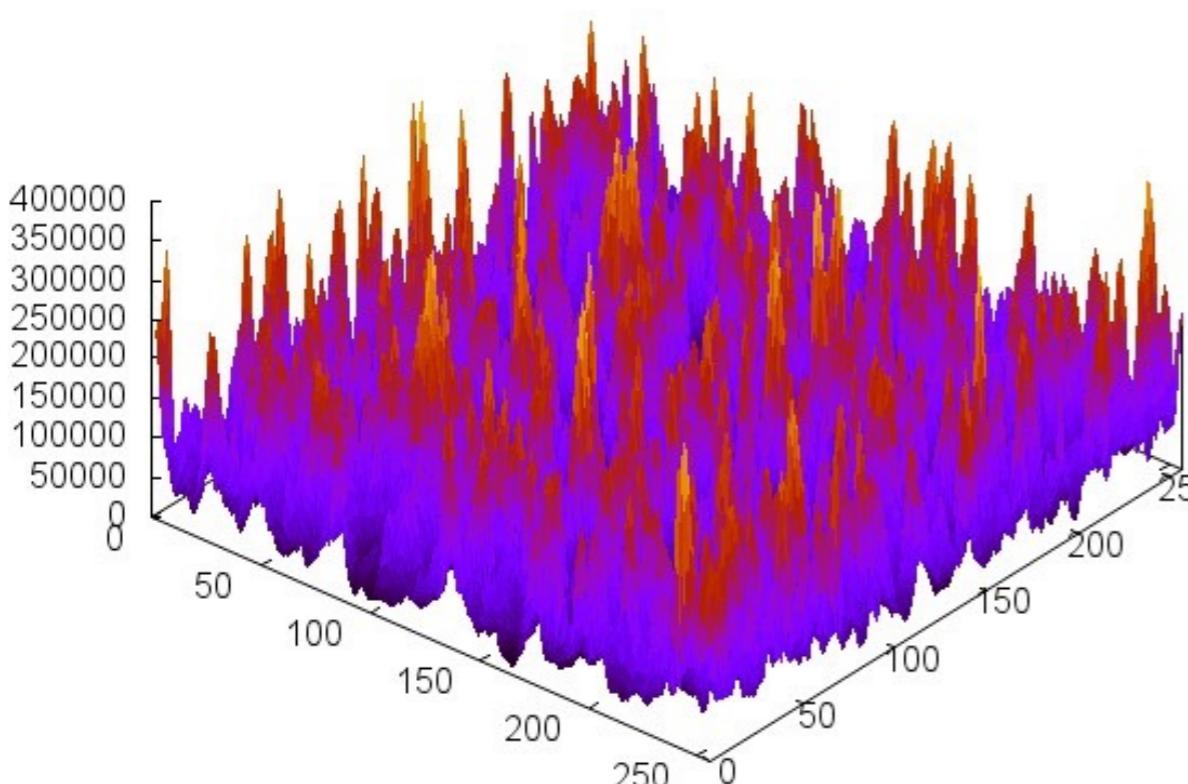
$$v = 0$$

$$v = 0.8v_F$$

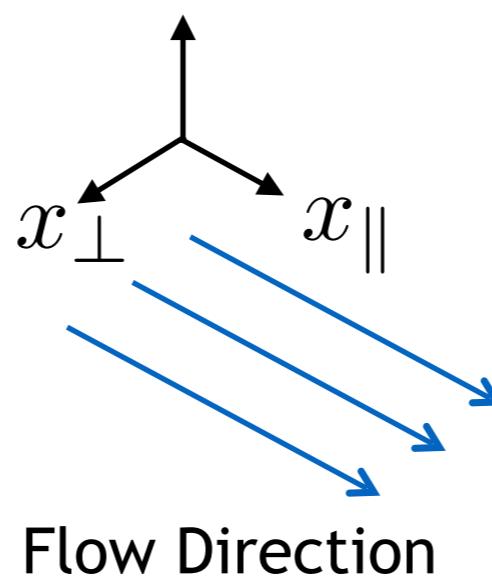
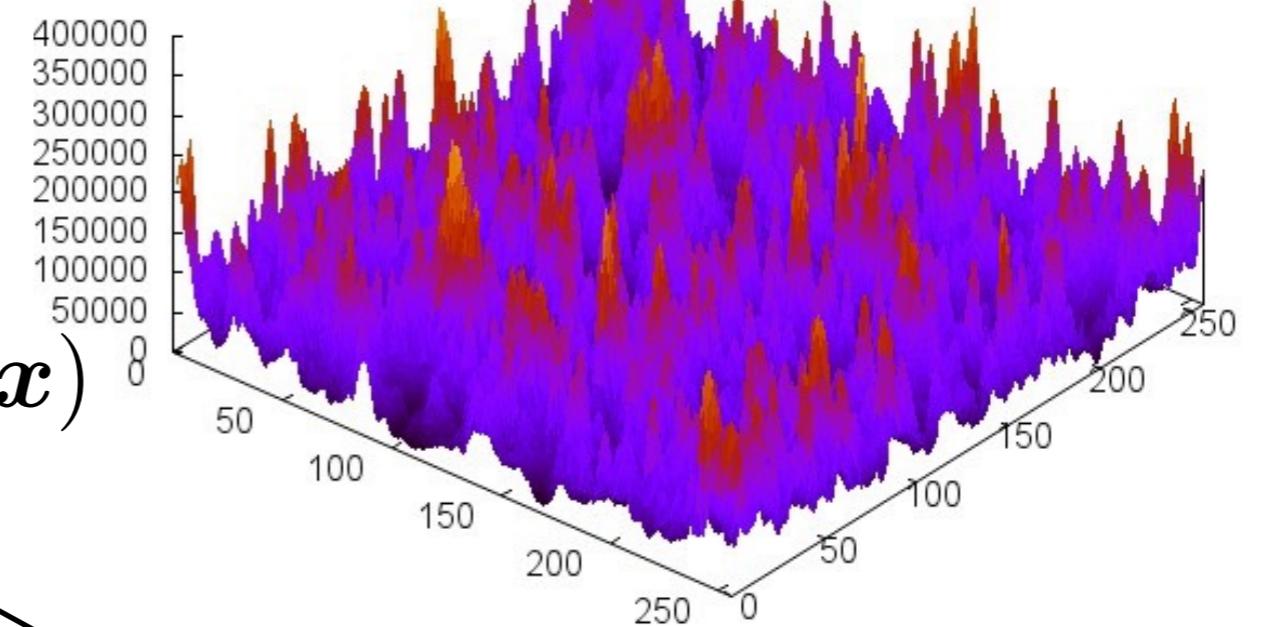


Approach to Steady State Populations in Disordered Environments with Advection

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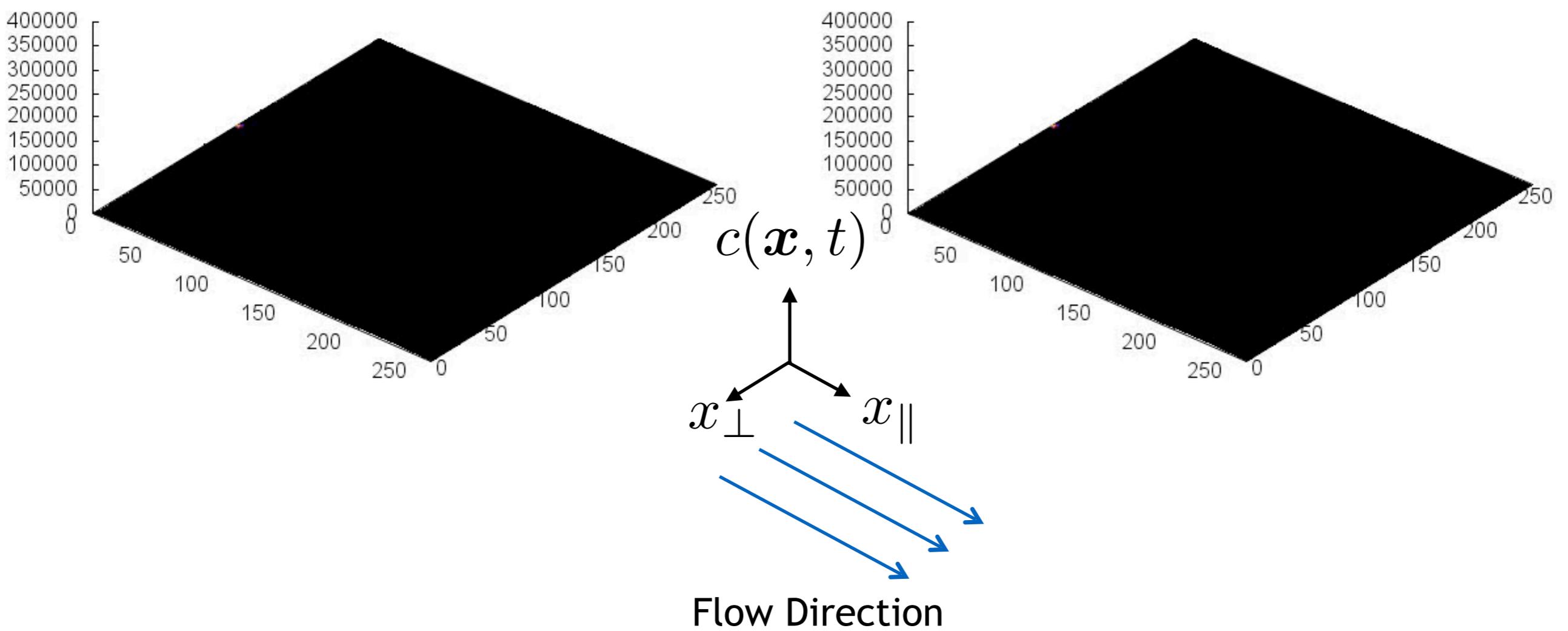
$v = 0.8v_F$



Approach to Steady State Populations in Disordered Environments with Advection

$$v = 1.3v_F$$

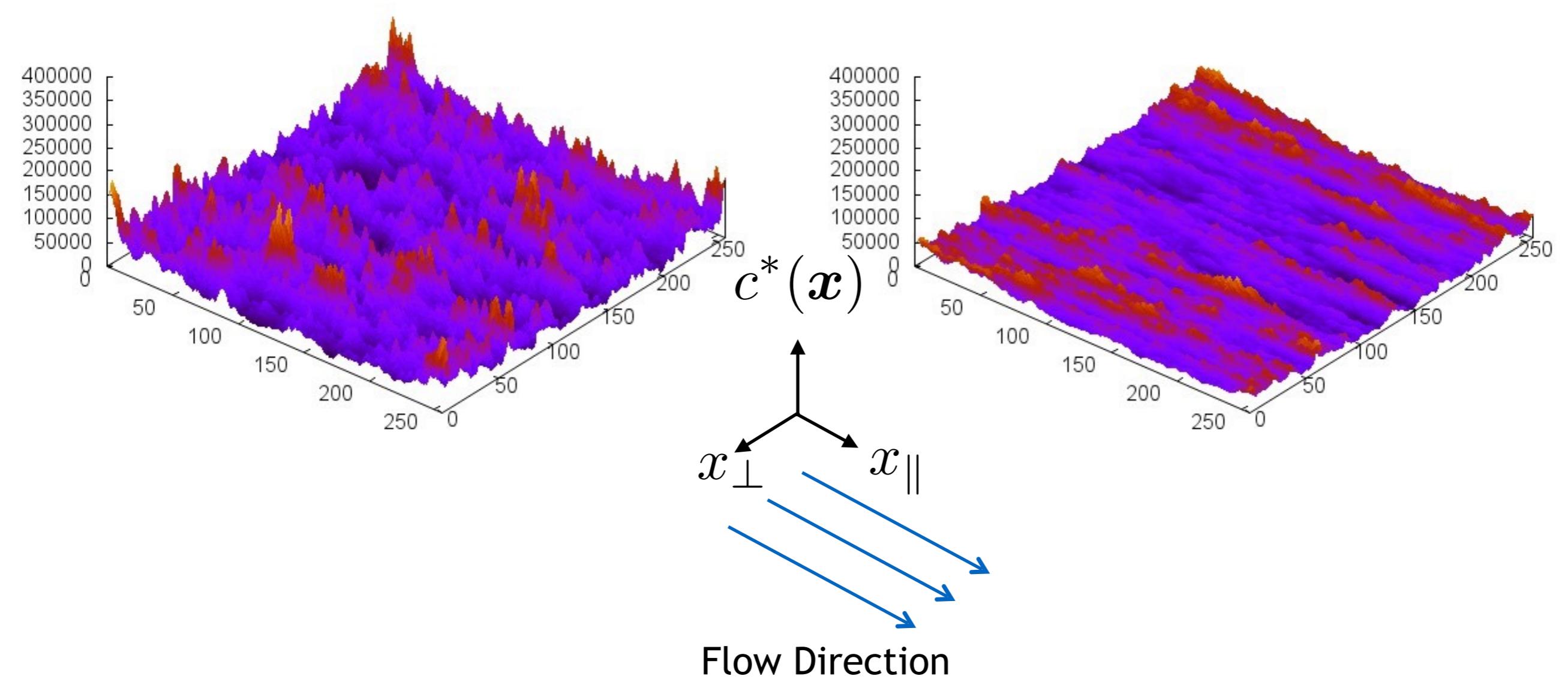
$$v = 3v_F$$



Approach to Steady State Populations in Disordered Environments with Advection

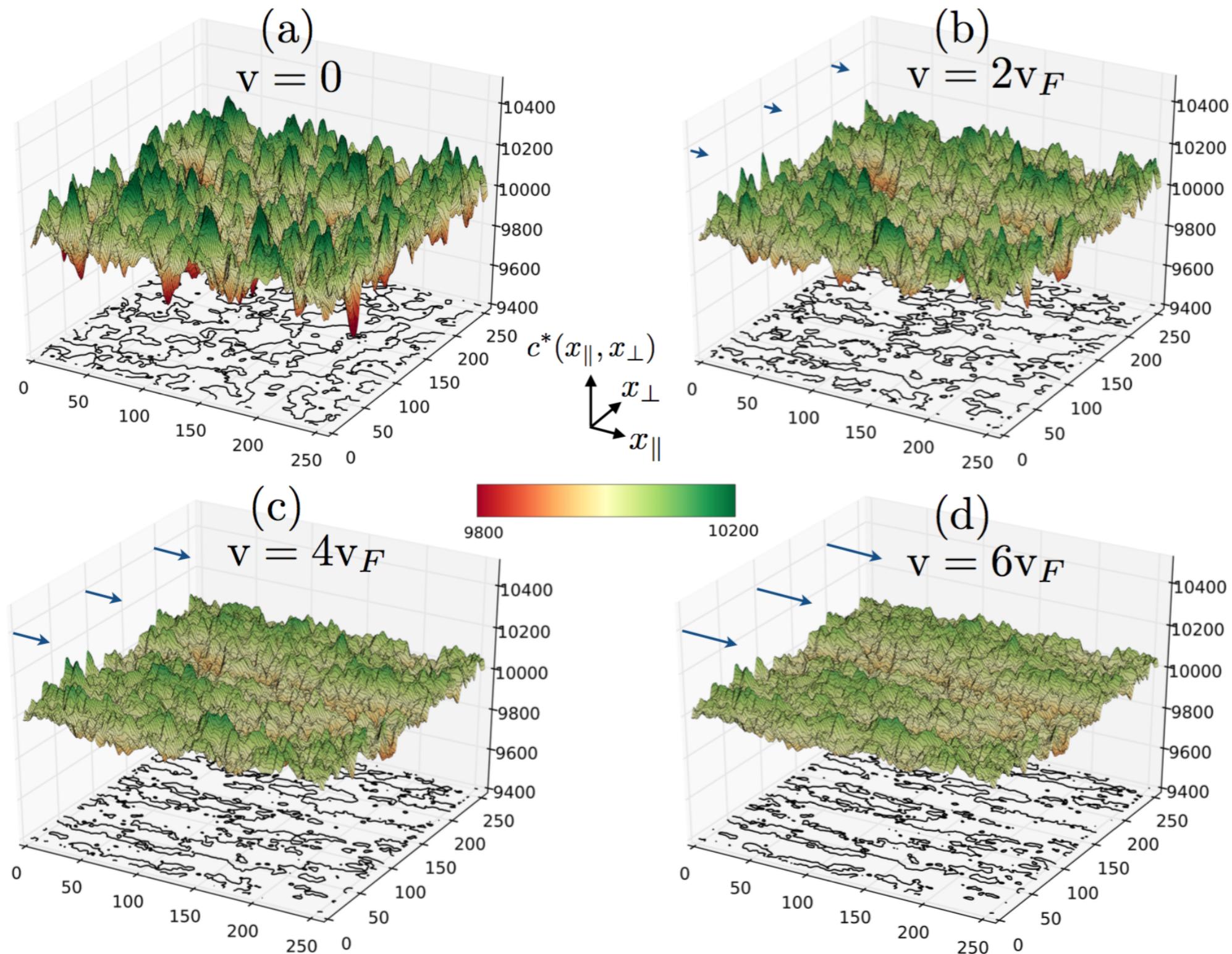
$$v = 1.3v_F$$

$$v = 3v_F$$



Advection and uncorrelated *fertile* growth landscape lead to correlated *striations* of *steady-state*

$$a_0 > 0$$
$$\delta a(\mathbf{x})/a_0 \ll 1$$



Understanding the Emergent Correlations

The steady states $c^*(\mathbf{x}) \equiv c(\mathbf{x}, t \rightarrow \infty)$ are governed by the nonlinear partial differential equation:

$$0 = D\nabla^2 c^*(\mathbf{x}) - \mathbf{v} \cdot \nabla c^*(\mathbf{x}) + a(\mathbf{x})c^*(\mathbf{x}) - bc^{*2}(\mathbf{x})$$

For weak growth rate fluctuations $\delta a(\mathbf{x})/a_0 \ll 1$, regard $c^*(\mathbf{x})$ as a **response** to growth perturbation

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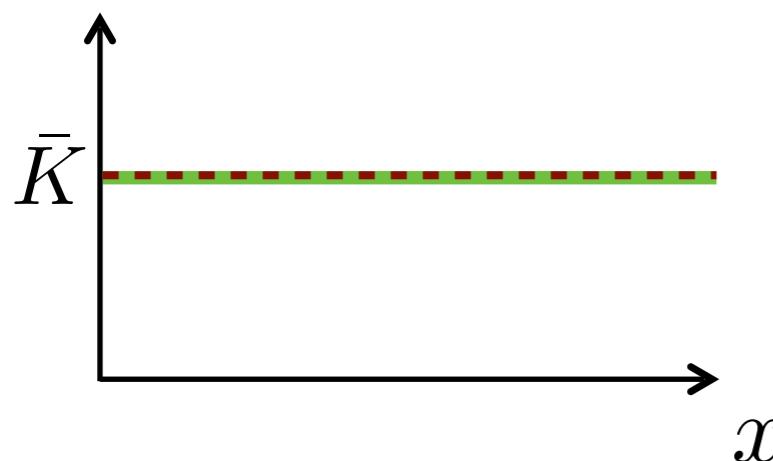
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uniform growth rates

$$a(\mathbf{x}) = a_0$$

$$c^*(\mathbf{x}) = \bar{K} = a_0/b$$



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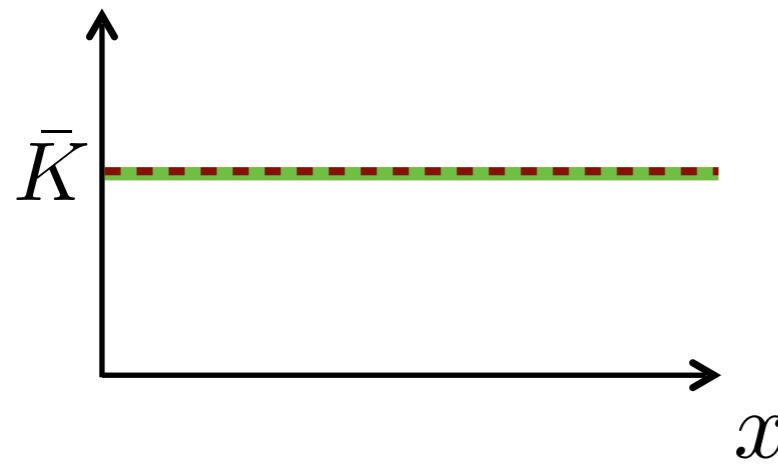
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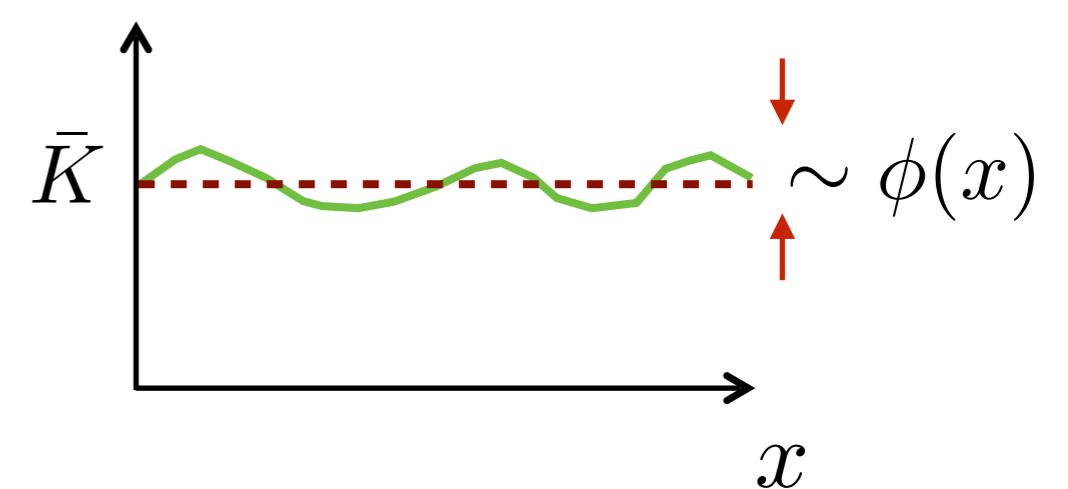
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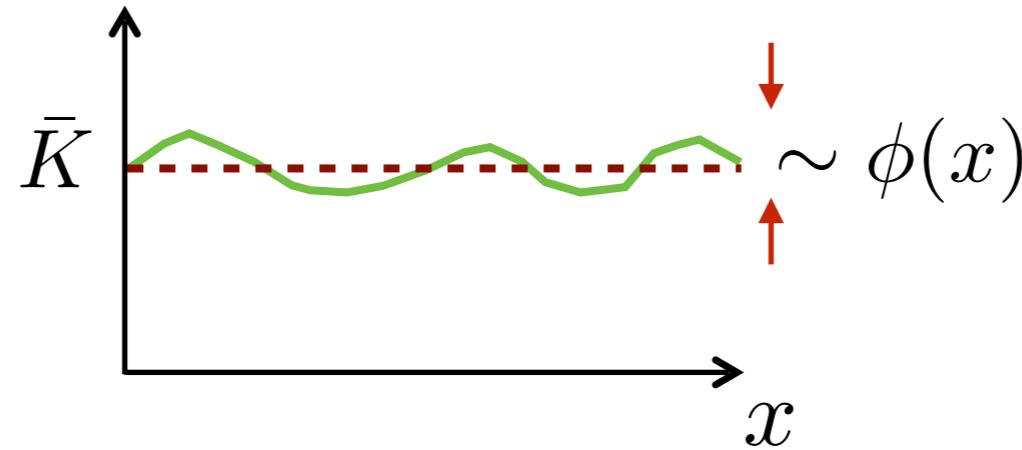
fluctuating growth rates

$$a(\mathbf{x}) = a_0 + \delta a(\mathbf{x})$$

$$c^*(\mathbf{x}) \equiv \bar{K}(1 + \phi(\mathbf{x}))$$



Understanding the Emergent Correlations: Linear Response Approximation



The steady-state density fluctuations $\phi(\mathbf{x}) \equiv [c^*(\mathbf{x}) - \bar{K}]/\bar{K}$ is governed by:

$$(-D\nabla^2 + \mathbf{v} \cdot \nabla + a_0) \phi(\mathbf{x}) = \delta a(\mathbf{x}) + [\delta a(\mathbf{x})\phi(\mathbf{x}) - a_0\phi^2(\mathbf{x})]$$

Can solve for $\phi(\mathbf{x})$ perturbatively, the leading order is the linear response equation:

$$(-D\nabla^2 + \mathbf{v} \cdot \nabla + a_0) \phi^{(0)}(\mathbf{x}) = \delta a(\mathbf{x})$$

Density fluctuations are the linear response to growth rate perturbations.

Non-dimensionalized Linear Response Equation and the Green's Function

$$\left(-\tilde{\nabla}^2 + 2\tilde{\mathbf{v}} \cdot \tilde{\nabla} + 1 \right) \phi(\tilde{\mathbf{x}}) = U(\tilde{\mathbf{x}})$$

$\tilde{\mathbf{x}} \equiv \mathbf{x}/\xi_D,$
 $\tilde{\mathbf{v}} \equiv \mathbf{v}/2\sqrt{D a_0}$
 $U(\mathbf{x}) \equiv \delta a(\mathbf{x})/a_0,$
 $\xi_D \equiv \sqrt{D/a_0},$

For a *point-like growth hot spot* $U(\tilde{\mathbf{x}}) \sim \delta^d(\tilde{\mathbf{x}}),$

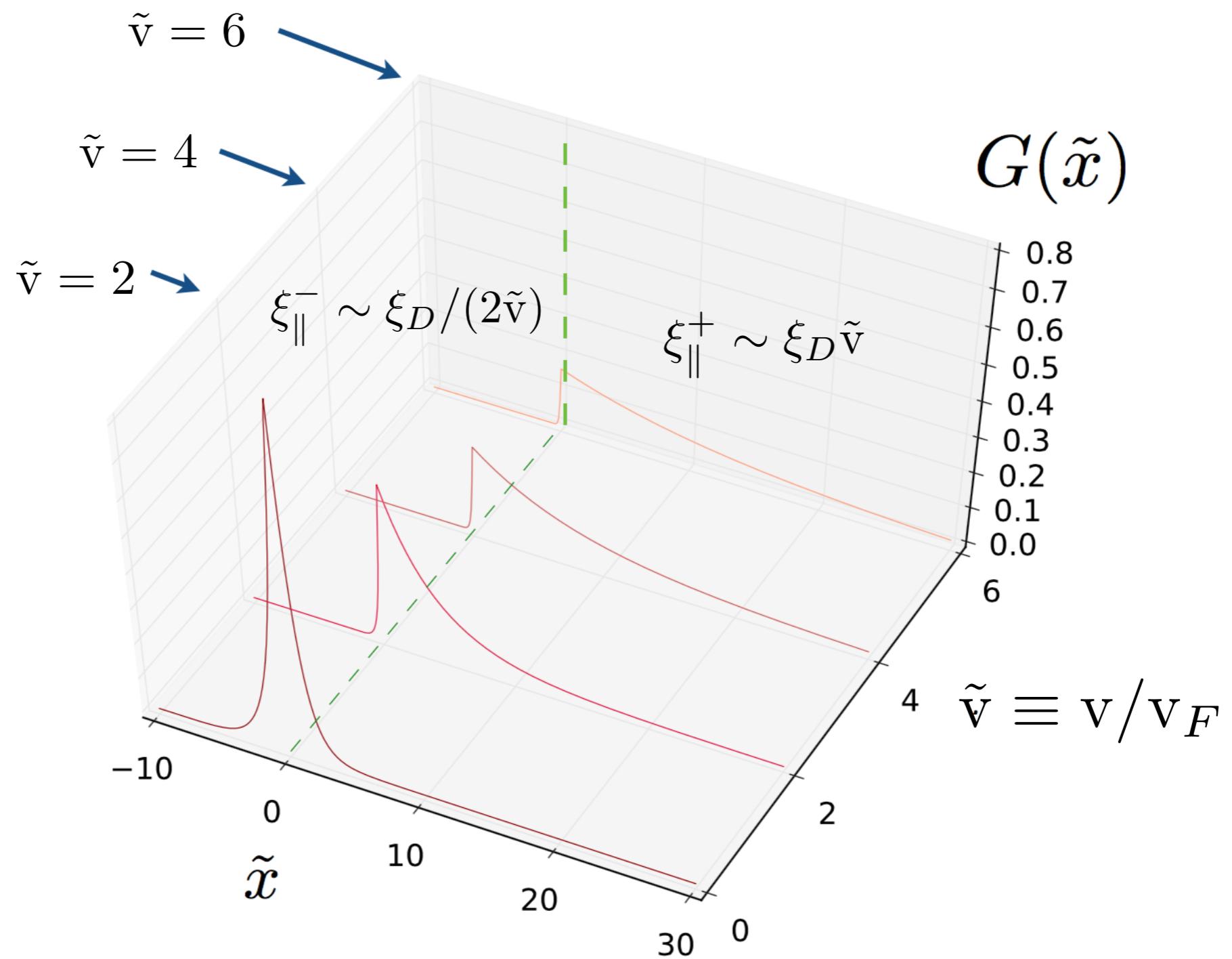
the density response is the Green's function $G(\tilde{\mathbf{x}})$, *exactly solvable in d-dimensions*:

$$G(\tilde{\mathbf{x}}) = \exp(\tilde{\mathbf{v}} \tilde{\mathbf{x}}_{\parallel}) G_{\tilde{\mathbf{v}}}(\tilde{\mathbf{x}})$$

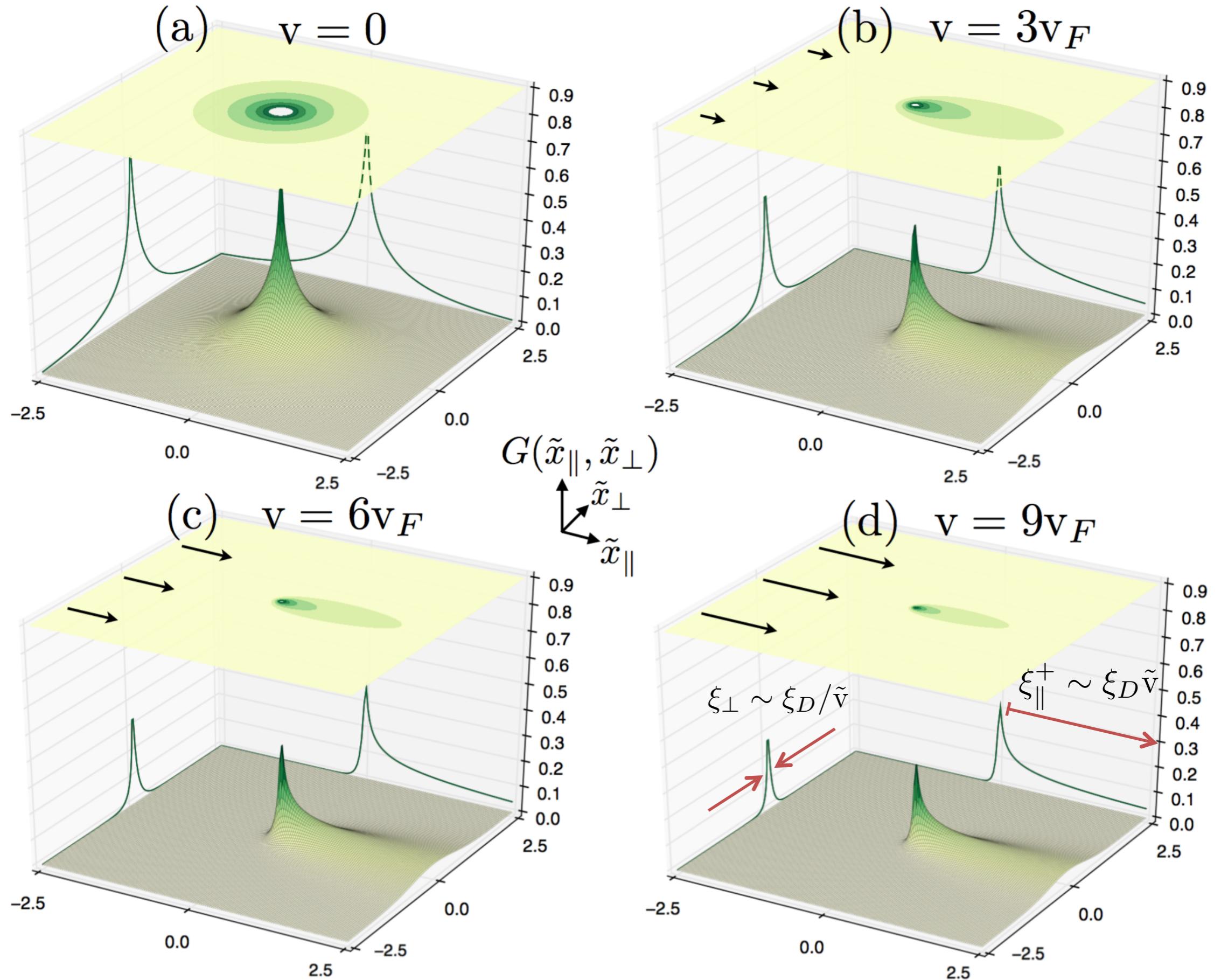
$$G_{\tilde{\mathbf{v}}}(\tilde{\mathbf{x}}) = \frac{\Delta}{\bar{a}} \left(\frac{l}{\sqrt{\pi} \xi_D} \right)^d$$

$$\times \left[\left(\frac{|\tilde{\mathbf{x}}|}{\sqrt{1 + \tilde{\mathbf{v}}^2}} \right)^{1-d/2} K_{1-d/2} \left(\sqrt{1 + \tilde{\mathbf{v}}^2} |\tilde{\mathbf{x}}| \right) \right].$$

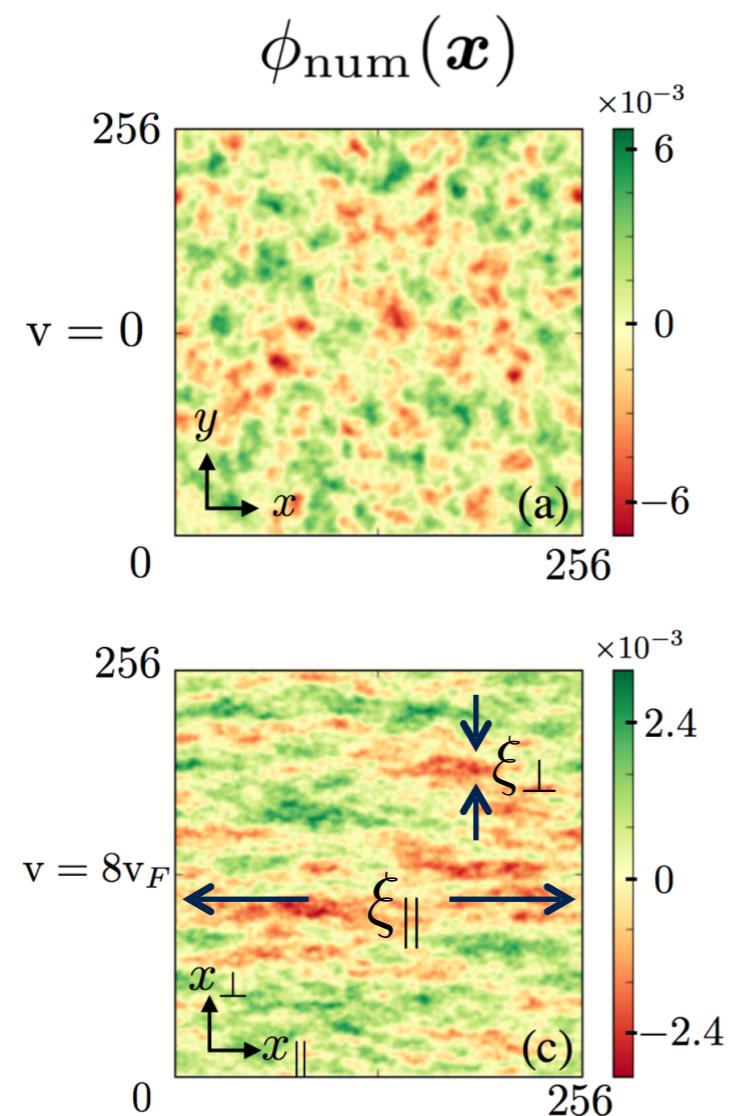
One dimensional reaction-diffusion-advection response to a growth hot spot



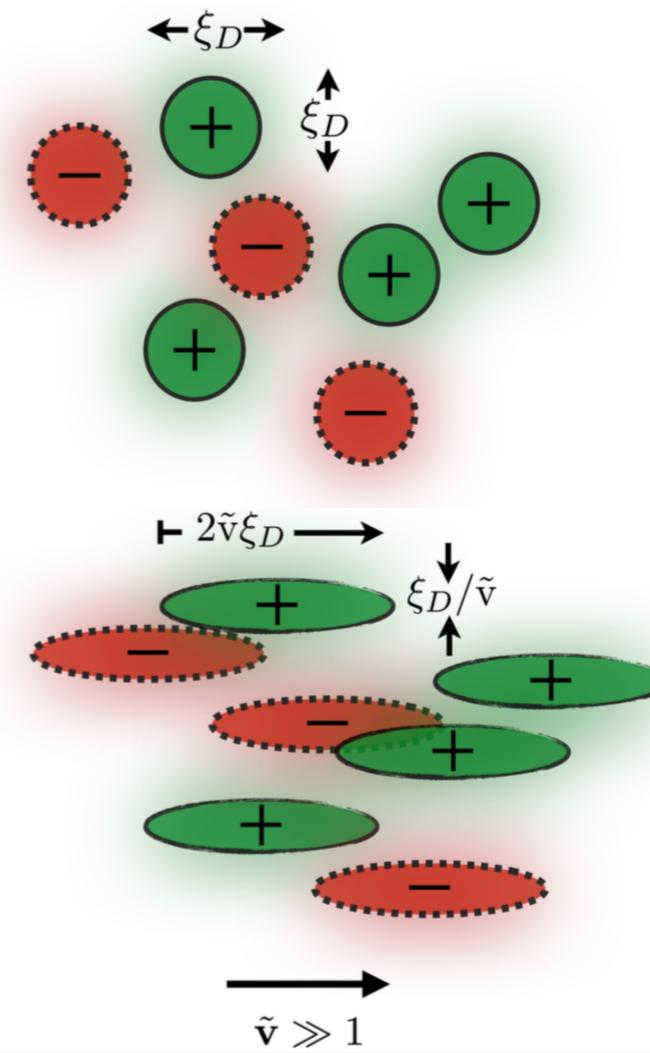
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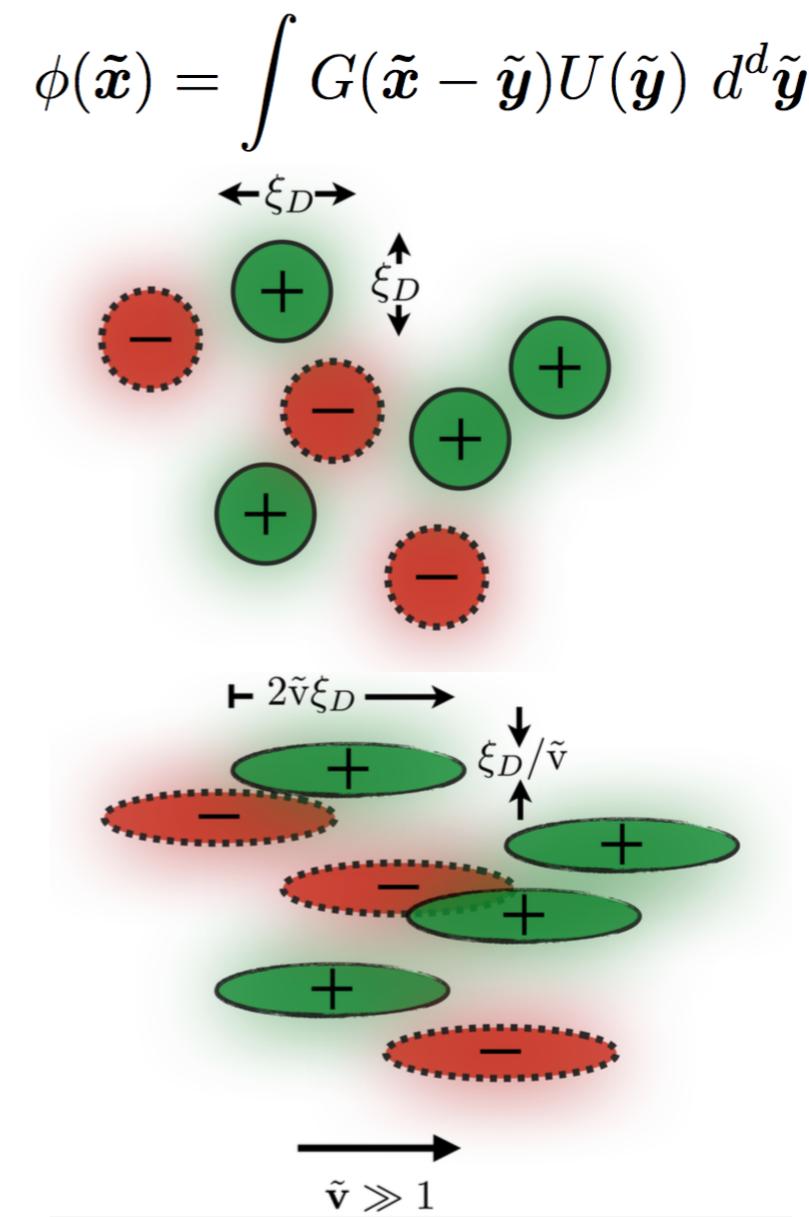
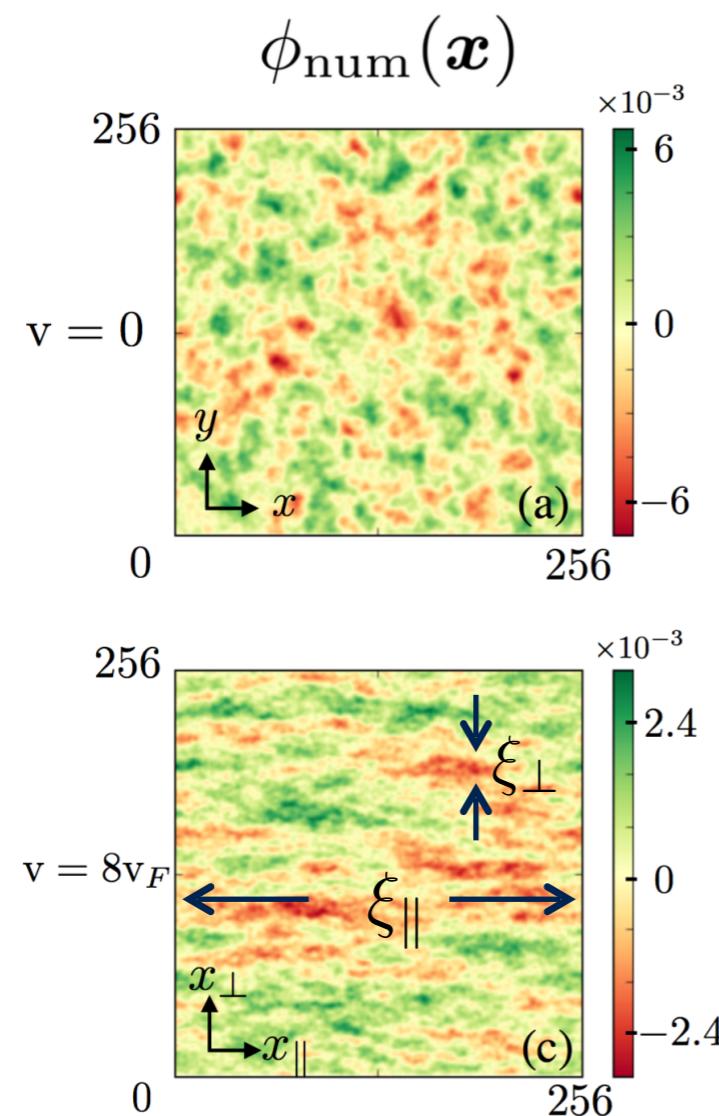
Density fluctuations from the superposition of the responses from uncorrelated growth disorder



$$\phi(\tilde{\mathbf{x}}) = \int G(\tilde{\mathbf{x}} - \tilde{\mathbf{y}}) U(\tilde{\mathbf{y}}) d^d \tilde{\mathbf{y}}$$



Density fluctuations from the superposition of the responses from uncorrelated growth disorder

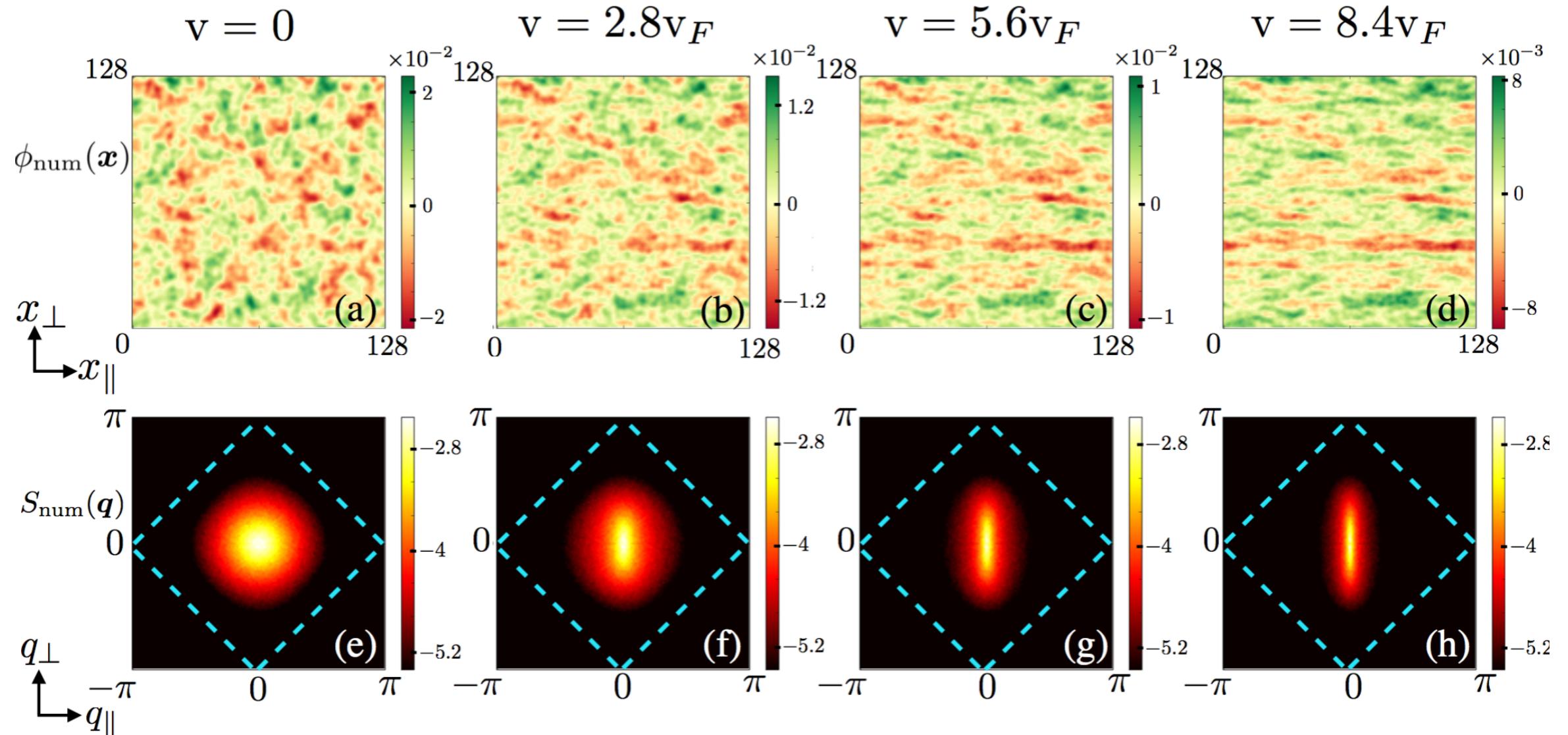


In $d \geq 2$, uncorrelated disorder leads to a finite velocity-independent transverse correlations, given by the diffusive localization length ξ_D , and the longitudinal correlations length diverges linearly with the advection speed.

$$\lim_{\tilde{v} \rightarrow \infty} \langle \phi(\tilde{x}_\parallel, 0) \phi(\mathbf{0}) \rangle \sim \left(\frac{|\tilde{x}_\parallel|}{2\tilde{v}} \right)^{1/4} K_{-1/4} \left(\frac{|\tilde{x}_\parallel|}{2\tilde{v}} \right), \quad \lim_{\tilde{v} \rightarrow \infty} \xi_\parallel = \xi_v = \frac{v}{a_0},$$

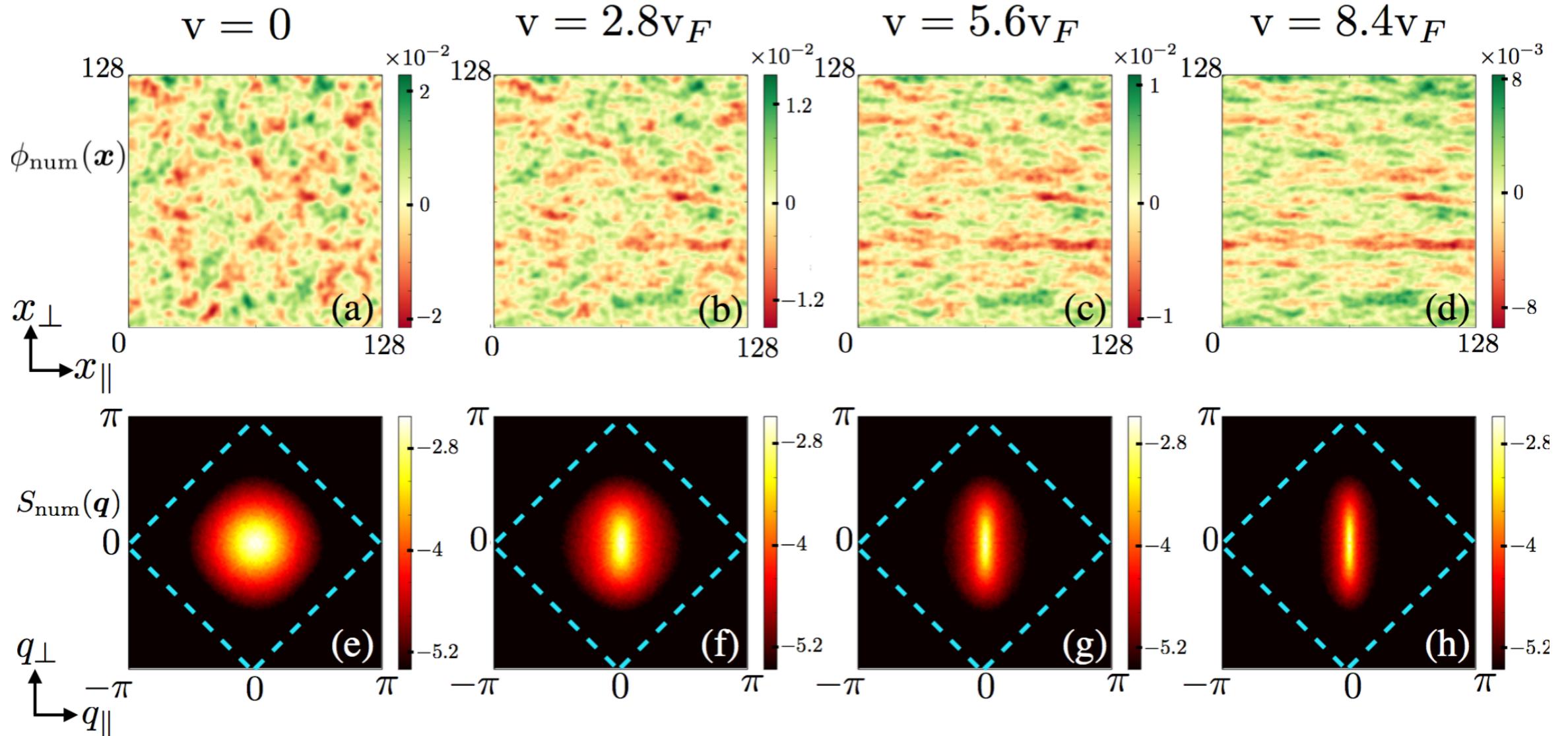
$$\lim_{\tilde{v} \rightarrow \infty} \langle \phi(0, \tilde{x}_\perp) \phi(\mathbf{0}) \rangle \sim \frac{e^{-|\tilde{x}_\perp|}}{\tilde{v}}, \quad \lim_{\tilde{v} \rightarrow \infty} \xi_\perp = \xi_D = \sqrt{\frac{D}{a_0}}.$$

Statistics of correlations from the *structure factor*



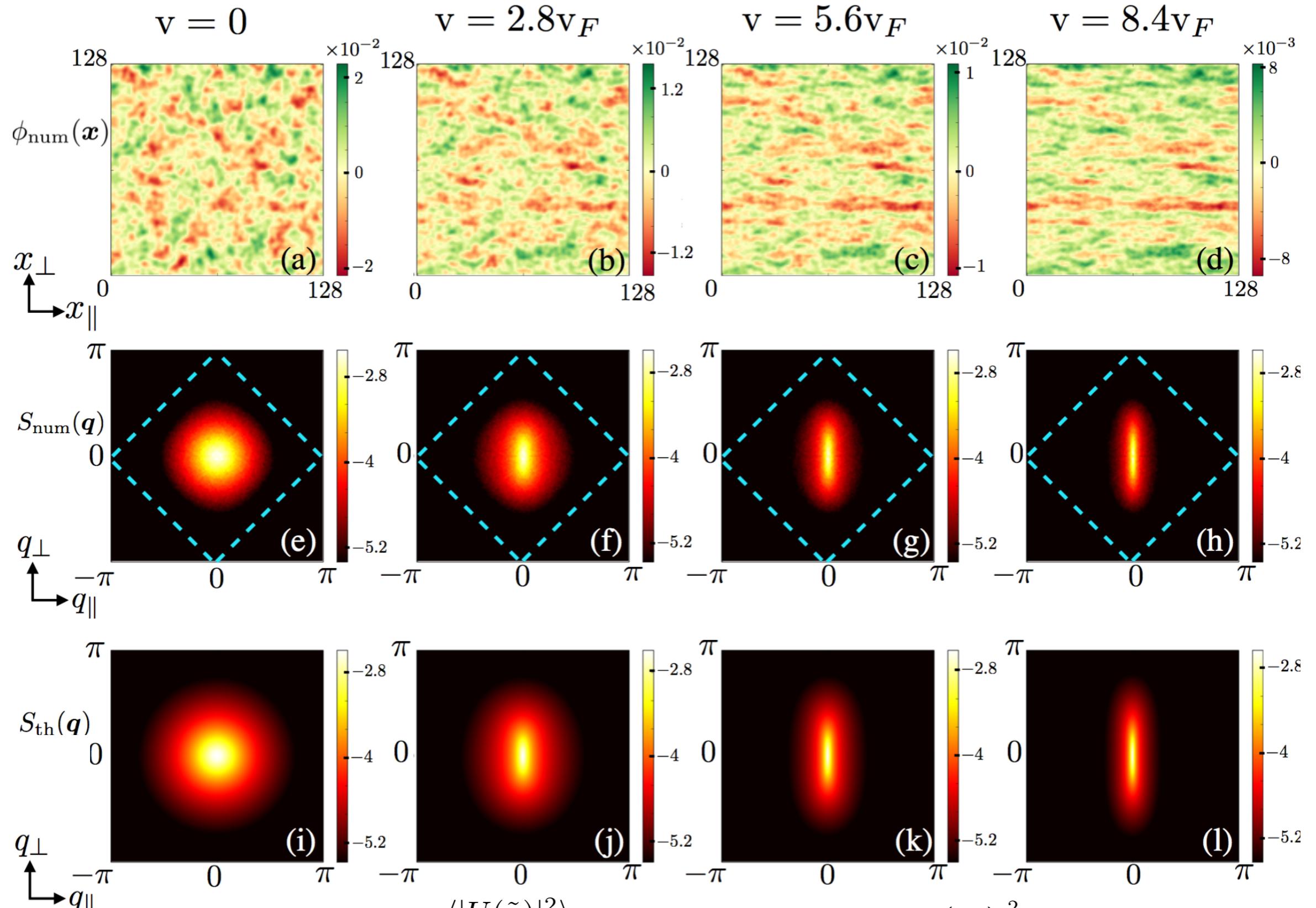
$$S(\tilde{\mathbf{q}}) = \langle |\phi(\tilde{\mathbf{q}})|^2 \rangle$$

Statistics of correlations from the *structure factor*



$$S(\tilde{\mathbf{q}}) = \langle |\phi(\tilde{\mathbf{q}})|^2 \rangle = \frac{\langle |U(\tilde{\mathbf{q}})|^2 \rangle}{\left[(\tilde{q}_{\parallel}^2 + \tilde{q}_{\perp}^2 + 1)^2 + 4\tilde{v}\tilde{q}_{\parallel}^2 \right]} \quad \text{where} \quad \langle |U(\tilde{\mathbf{q}})|^2 \rangle \sim \left(\frac{\Delta}{a_0} \right)^2 \quad \text{for uncorrelated noise}$$

Theoretical predictions of the structure factor agree with numerical steady states at long wavelengths



$$S(\tilde{\mathbf{q}}) = \langle |\phi(\tilde{\mathbf{q}})|^2 \rangle = \frac{\langle |U(\tilde{\mathbf{q}})|^2 \rangle}{[(\tilde{q}_\parallel^2 + \tilde{q}_\perp^2 + 1)^2 + 4\tilde{v}\tilde{q}_\parallel^2]} \quad \text{where} \quad \langle |U(\tilde{\mathbf{q}})|^2 \rangle \sim \left(\frac{\Delta}{a_0} \right)^2 \text{ for uncorrelated noise}$$

Conclusion of Part 2: Striated Populations in Disordered Environments with Advection

$$\partial_t c + \mathbf{v} \cdot \nabla c = D \nabla^2 c + a(\mathbf{x})c - bc^2.$$

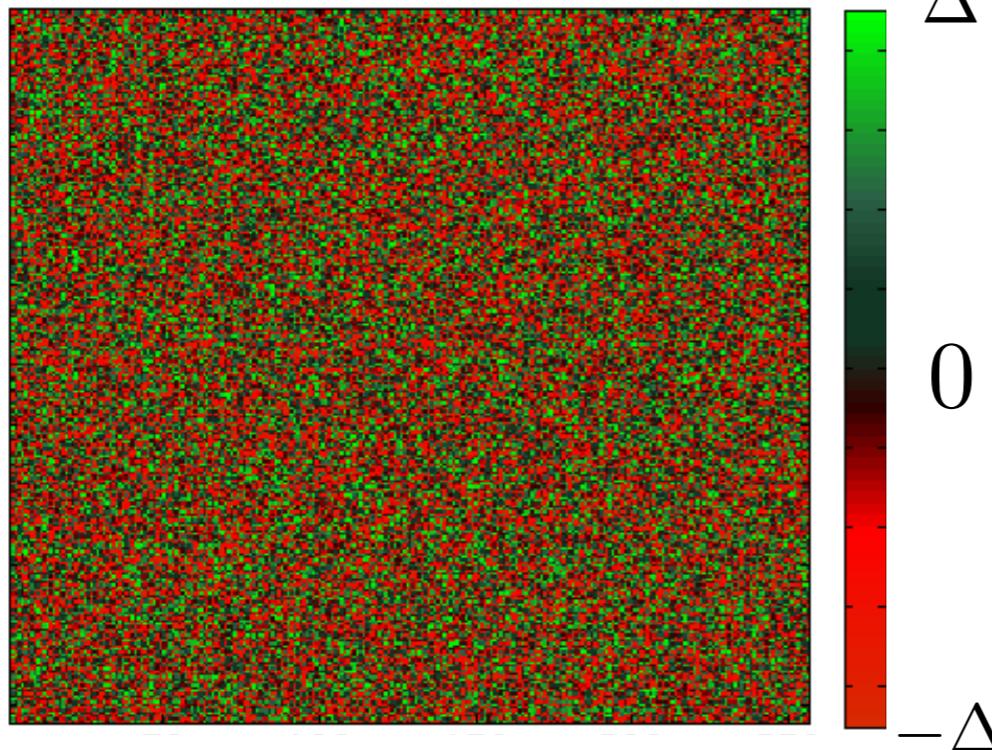
Fluid Advection

Spatially Quenched *Fluctuating Growth Rates*

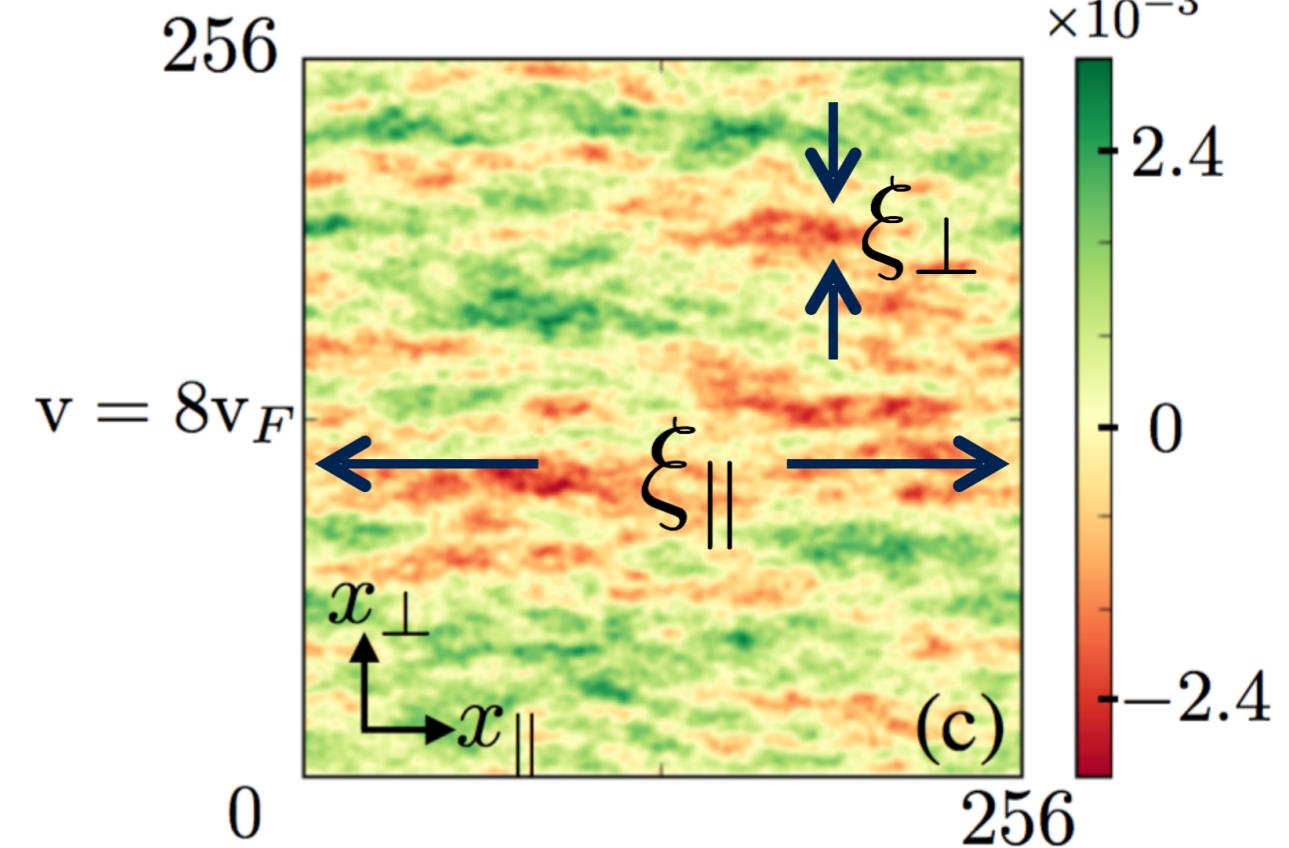
Although the growth disorder can be spatially *uncorrelated*, *correlated population structures* with striations *emerge naturally* at sufficiently strong advection

Spatially Quenched *Uncorrelated* Growth Landscape

A 2D realization of $\delta a(\mathbf{x})$



Correlated “Growth Seascape”



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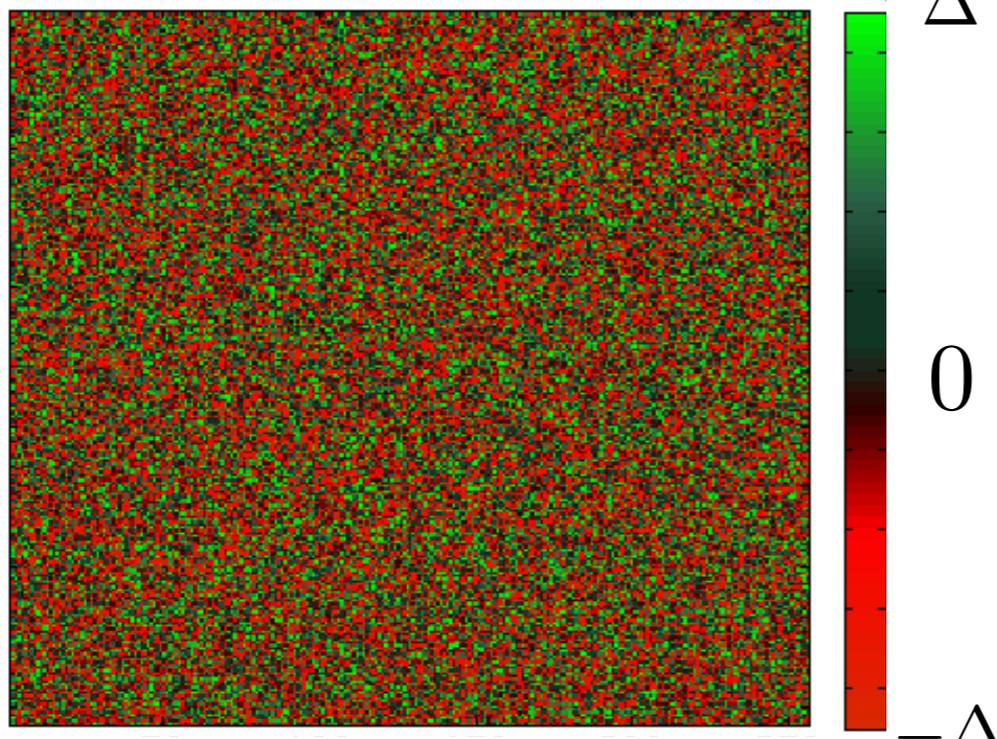
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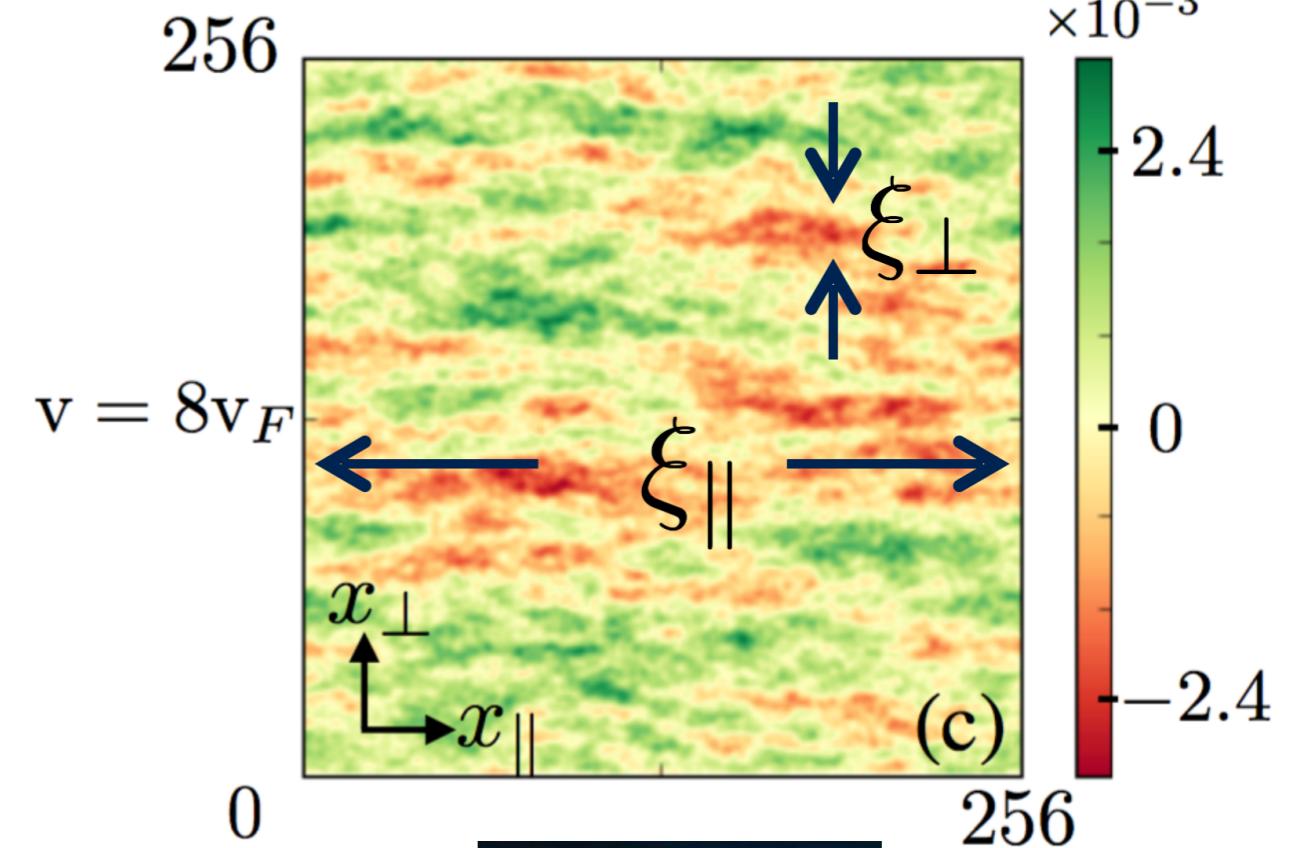
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Thank You!