Spatial clustering of interacting random walkers

Els Heinsalu

National Institute of Chemical Physics and Biophysics
Tallinn, Estonia

in collaboration with:

Emilio Hernández-García & Cristóbal López
IFISC (CSIC-UIB), Palma de Mallorca, Spain

- models where the birth and death processes occur are inspired by population biology (individual based models), but can be used to investigate also other problems in different fields such as condensed matter physics, chemical kinetics, or sociology (agent based models)
- in most of such systems also the diffusion has an important role
- the simplest model which takes these three processes into account is the Brownian bug model, often considered in the context of population dynamics, in particular to address plankton distribution – Young, Roberts, Stuhne, Nature **412**, 328 (2001)
- in the simple Brownian bug model there is no interaction/competition between the organisms, but more sophisticated models take into account also the competition

Non-interacting bug models

- $N(t)$ organisms modelled as point-like particles (bugs):

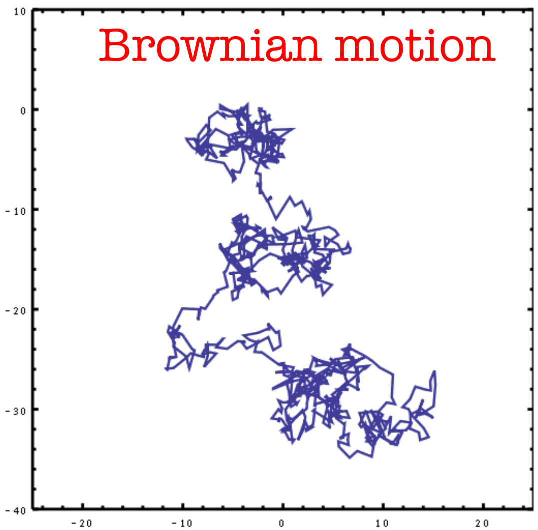
1) reproduce at rate $r_b = const$, giving rise to an offspring close to the parent, or die at rate $r_d = const$
2) perform independent Markovian continuous time random walk

- if the CTRW is Brownian motion ⟶ Brownian bug model

$$p(\tau) = \exp(-\tau / \tilde{\tau})$$

$$\varphi(\ell) \propto \exp[-\ell^2 / (2\tilde{\ell}^2)]$$

$$\langle \ell \rangle, \langle \ell^2 \rangle = finite$$



Non-interacting bug models

- ***N(t)*** organisms modelled as point-like particles (bugs):

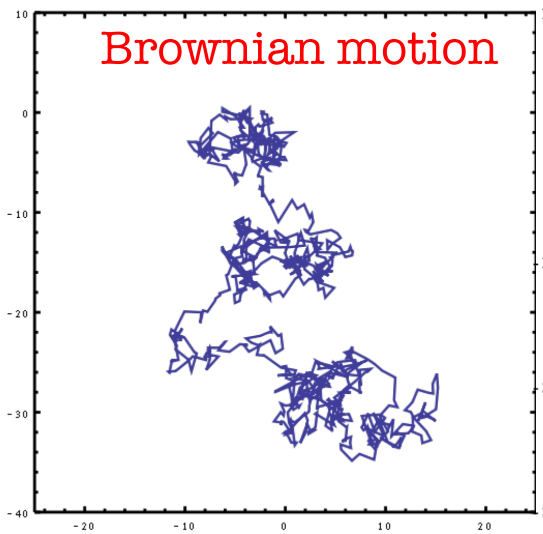
1) reproduce at rate $r_b = const$, giving rise to an offspring close to the parent, or die at rate $r_d = const$
2) perform independent Markovian continuous time random walk

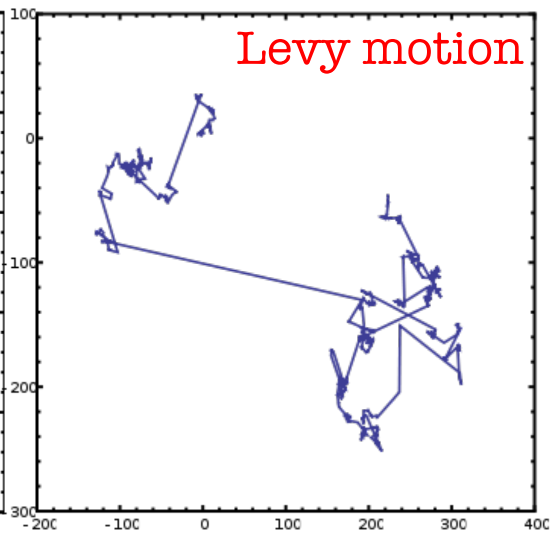
- if the CTRW is Brownian motion → Brownian bug model
- many systems are characterized by anomalous diffusion, e.g. the bacterial motion is found to be described by Levy statistics, as well as the movement of spider monkeys in search of food
  → Levy bug model

$$p(\tau) = \exp(-\tau / \tilde{\tau})$$

$$\varphi(\ell) \propto \exp[-\ell^2 / (2\tilde{\ell}^2)]$$

$$\langle \ell \rangle, \langle \ell^2 \rangle = finite$$





$$\varphi_\mu(\ell) \propto \tilde{\ell}^{\mu} |\ell|^{-\mu-1}$$

$$\ell \to \pm\infty \quad (|\ell| >> \tilde{\ell})$$

$$0 < \mu < 2$$

$$\langle \ell \rangle = finite$$

$$\langle \ell^2 \rangle = \infty$$

modelling in terms of continuous concentration field:

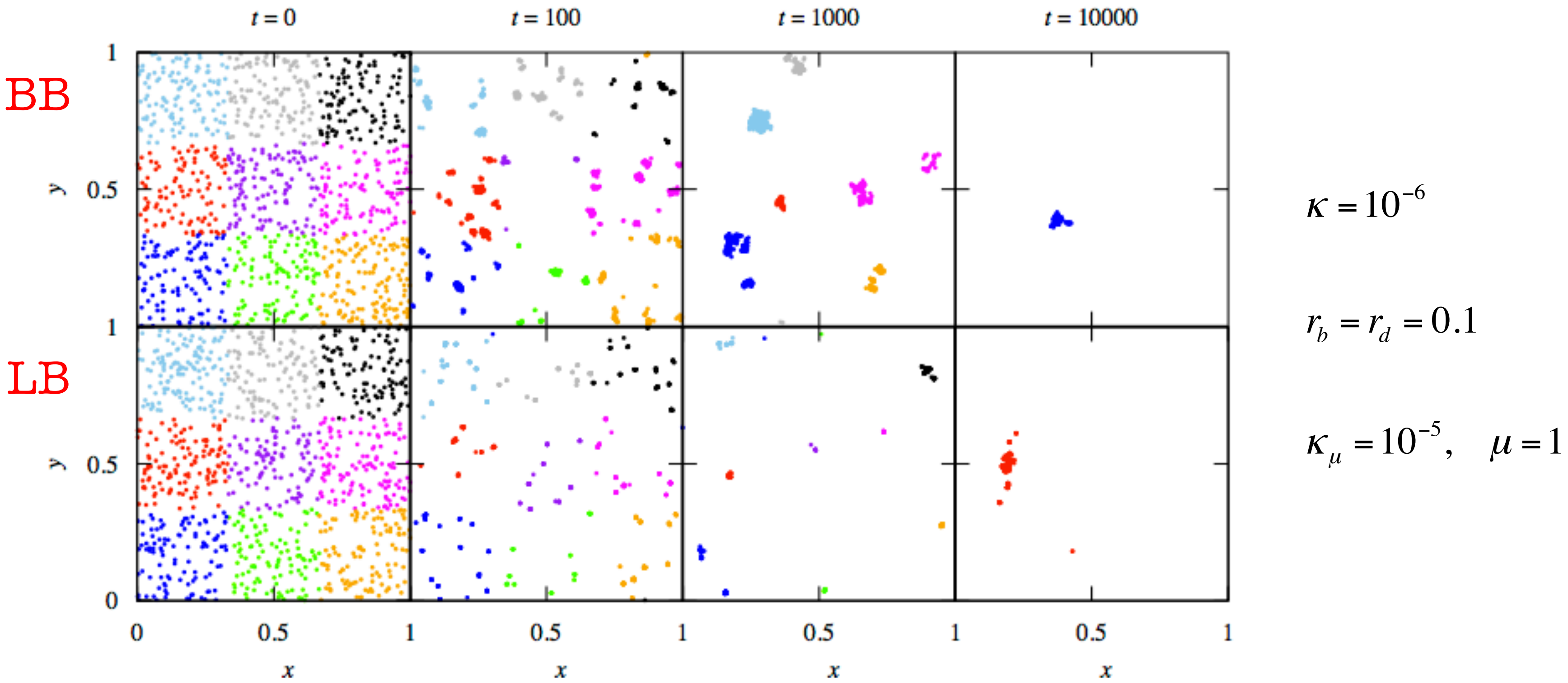
$$\frac{\partial}{\partial t} N(x,t) = (r_b - r_d) N(x,t) + \kappa_\mu \nabla^{2/(3-\mu)} N(x,t)$$

$$N(t) = N(t_0) \exp[(r_b - r_d)(t - t_0)]$$

- if $r_b > r_d$ – population explodes exponentially (finite probability for extinction that depends on $N(t_0)$ and decreases with increasing $r_b - r_d$)
- if $r_b < r_d$ – extinction with probability 1
- if $r_b = r_d$ – taking average over many realizations $\langle N(t) \rangle = N(t_0)$

κ_μ – generalized diffusion coefficient: $\kappa_\mu = \tilde{\ell}^\mu / (2\tilde{\tau}), \quad \mu \in (0,2]$

∇^γ - fractional diffusion operator



- for small values of diffusion coefficient clustering appears due to the reproductive correlations: newborns are close to the parents
- continuous deterministic description does not predict/explain the appearance of the clustering because the birth is assumed to be homogeneous
- after some time the system consists of particles coming from a single ancestor
- the final state is complete extinction; typical lifetime is proportional to N_0
- center of mass motion is similar to the one of single bugs

Globally interacting bug models

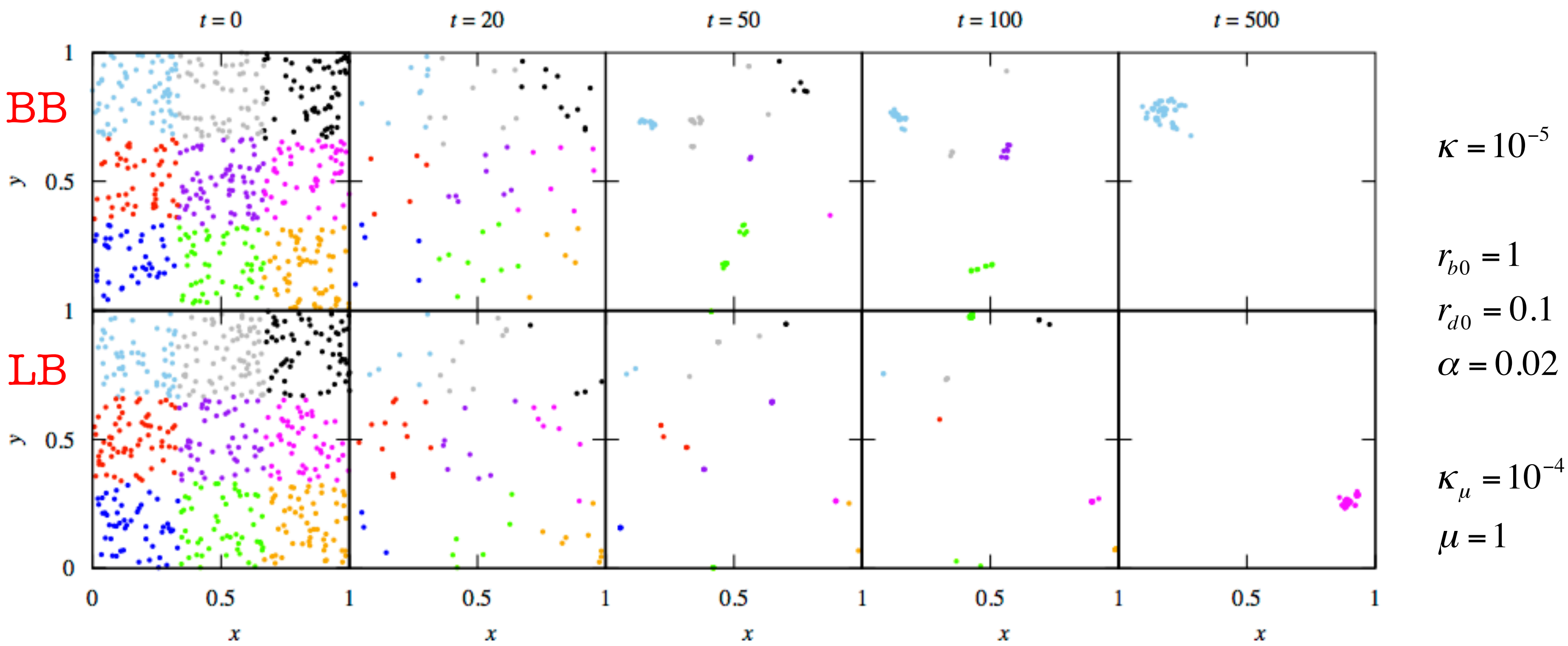
in more realistic models the birth and/or death rate of an organism depends e.g. on the competition for resources, i.e. on the number of other bugs in the system, $N(t) - 1$

in the most simple case the dependence can be assumed liner:

$$r_b = const \qquad \longrightarrow \qquad r_b = \max\{0, r_{b0} - \alpha[N(t)-1]\}$$

$$r_d = const \qquad\qquad\qquad r_d = r_{d0} + \beta[N(t)-1]$$

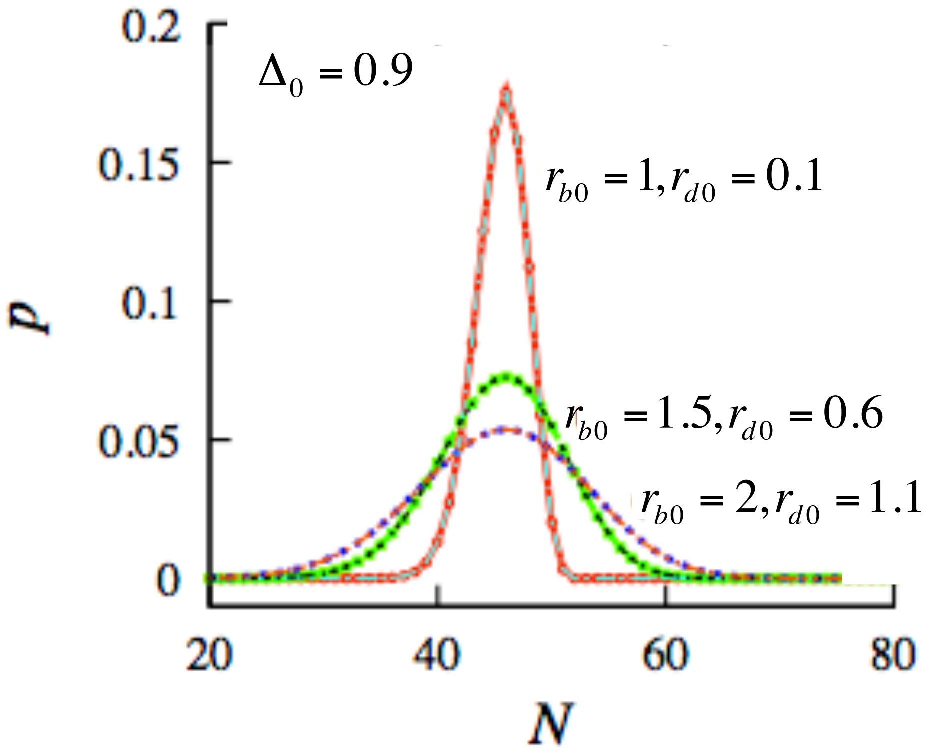
- $\alpha \geq 0$, $\beta \geq 0$
- $r_{b0} > r_{d0}$ is always assumed, otherwise the system becomes extinct with probability 1
- in the following $\beta = 0$ i.e. $r_d = r_{d0}$
- the critical size of the system is therefore $N^* = (r_{b0} - r_{d0})/\alpha + 1$:
  for $N(t) < N^*$ the reproduction is more probable, whereas
  for $N(t) > N^*$ the death becomes more probable than reproduction



- also now clustering appears due to the reproductive pair correlations
- after some time the system consists of particles coming from a single ancestor
- center of mass motion undergoes the same type of diffusion as the individual bugs of the system
- the final state is complete extinction due to the fluctuations

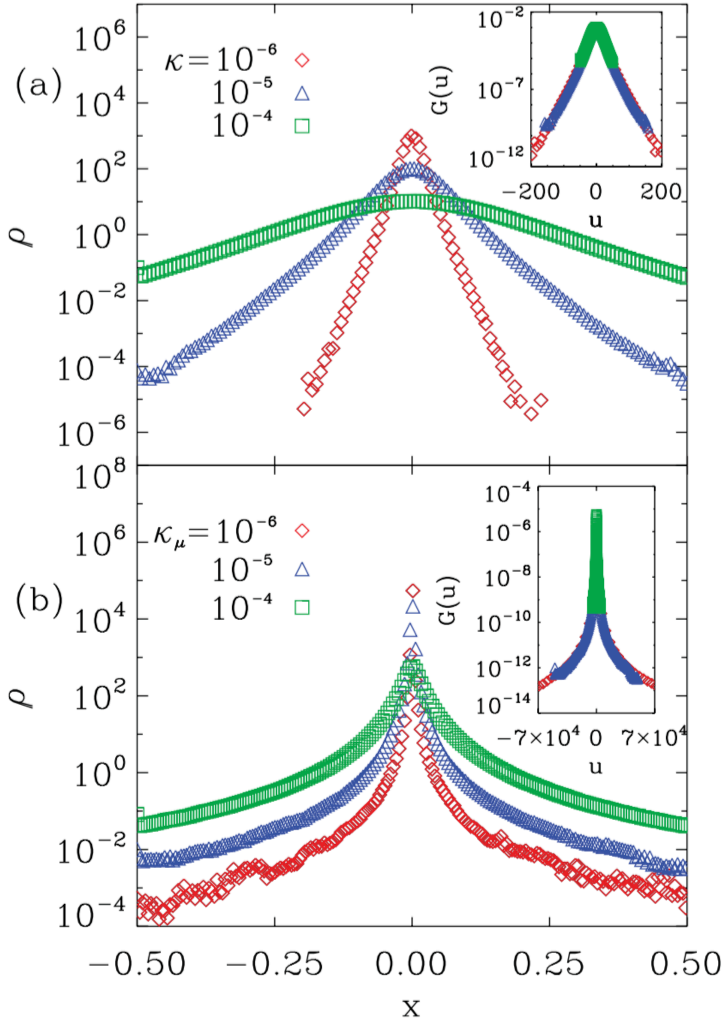
- the average number of organisms fluctuates around the critical value $N^* = (r_{b0} - r_{d0})/\alpha + 1$, depending for a fixed α only on the difference $\Delta_0 = r_{b0} - r_{d0}$
- the fluctuations of $N(t)$ depend on the values of r_{b0} and r_{d0}

the probability distribution of the number of individuals from the simulations time series:

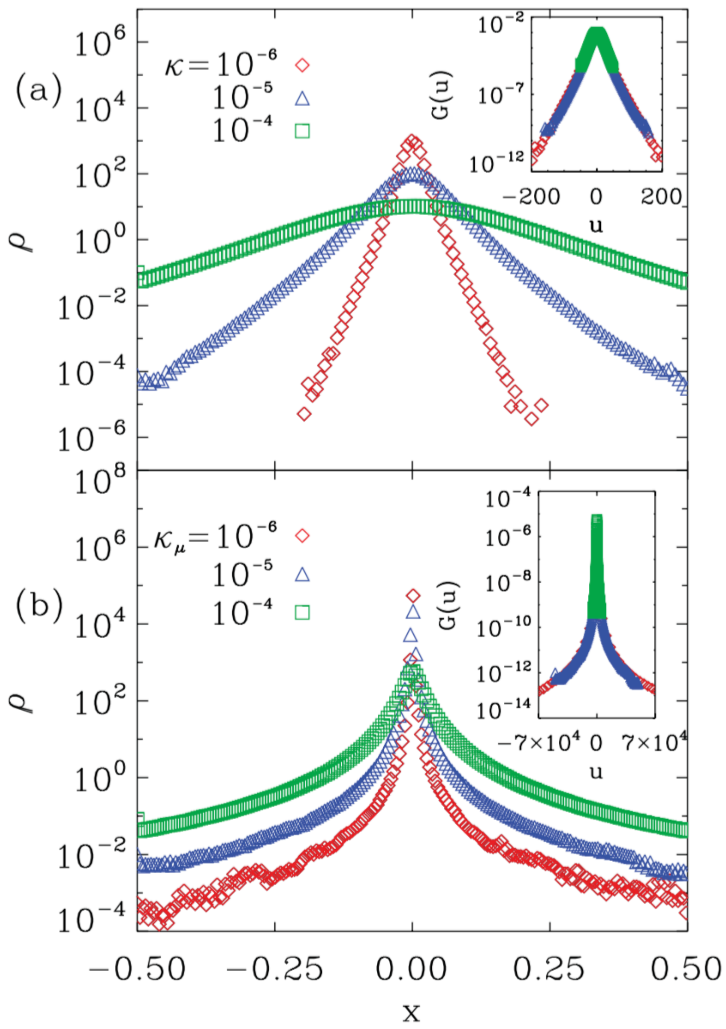


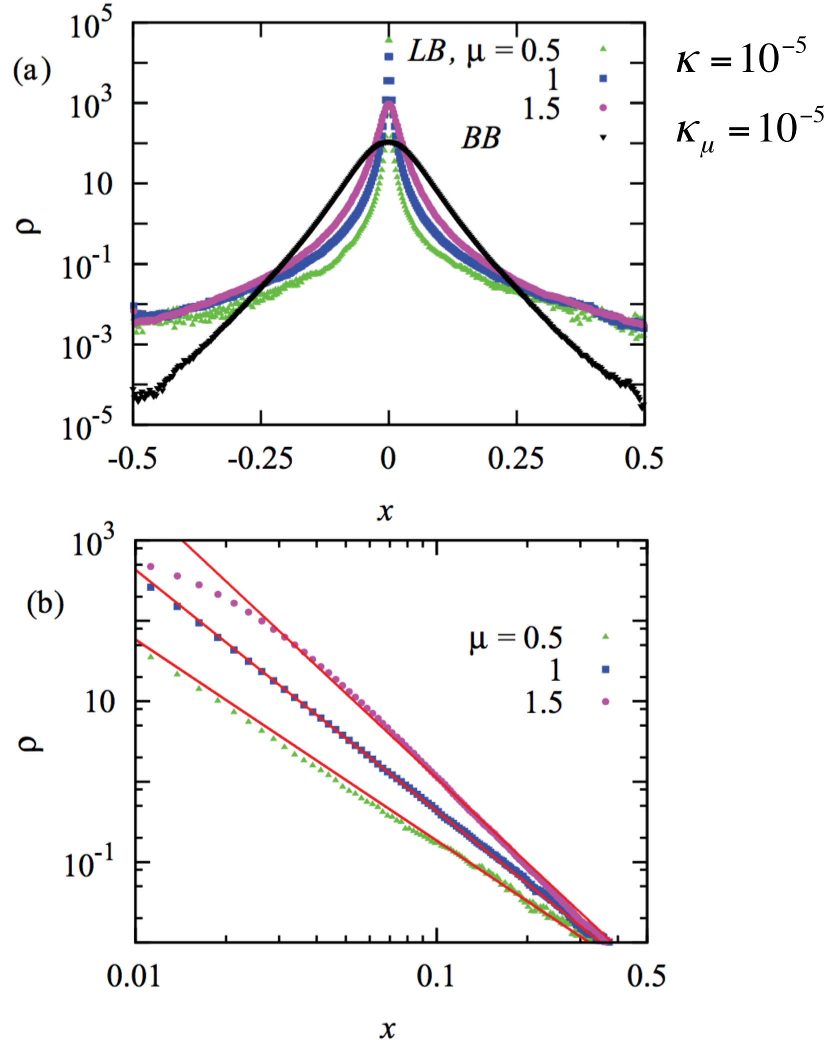
- for larger rates the fluctuation get larger implying that there is an enhanced probability for the system to become extinct
- in the context of ecological colonies this means that the increase of the death rate due to some change in the rate due to some change in the ecosystem, leads the colony to extinction more probably, even if the equilibrium size remains the same

the cross section of the 2-dimensional particle density of the average cluster:



the cross section of the 2-dimensional particle density of the average cluster:
for Brownian bugs, the tail of the average cluster is approximately exponential





the tails of ρ in the case of the Levy bug systems:
solid lines correspond to fitting curves $\sim x^{-(2+\mu)}$

Bug models with non-local finite-range interaction

in even more realistic models the organisms do not compete with all other organisms of the population, but only with the ones in a certain neighborhood, i.e. the birth and/or death rate of a particle $\boldsymbol{i}$ depend on the number of neighbors N_R^i within a given distance R:

$$r_b = \max\{0, r_{b0} - \alpha[N(t)-1]\} \qquad \longrightarrow \qquad r_b^i = \max\{0, r_{b0} - \alpha N_R^i\}$$

$$r_d = r_{d0} + \beta[N(t)-1] \qquad \longrightarrow \qquad r_d^i = r_{d0} + \beta N_R^i$$

- $\alpha \geq 0$, $\beta \geq 0$
- $r_{b0} > r_{d0}$ is always assumed, otherwise the system becomes extinct with probability 1
- in the following $\beta = 0$, i.e. $r_d = r_{d0}$
- the critical number of neighbors is therefore $N_R^* = (r_{b0} - r_{d0})/\alpha$:
  for $N_R^i < N_R^*$ the reproduction is more probable, whereas
  for $N_R^i > N_R^*$ the death becomes more probable than reproduction

mean-field approximation to the dynamics of the density of particles (***D*** – set of points within a distance smaller than ***R***):

$$\frac{\partial \rho(x,t)}{\partial t} = \rho(x,t)\left[\Delta_0 - \alpha \int_D dy\, \rho(y,t)\right] + \kappa_\mu \nabla^{2/(3-\mu)} \rho(x,t)$$

spatial diffusion

net growth of the population

non-local contribution associated to the saturation due to the interaction within a distance ***R***

- the uniform solution becomes unstable for small κ_μ and large Δ_0, leading to periodic pattern with periodicity of the order ***R***
- the anomalous exponent μ has only a very light influence on the periodicity of the pattern

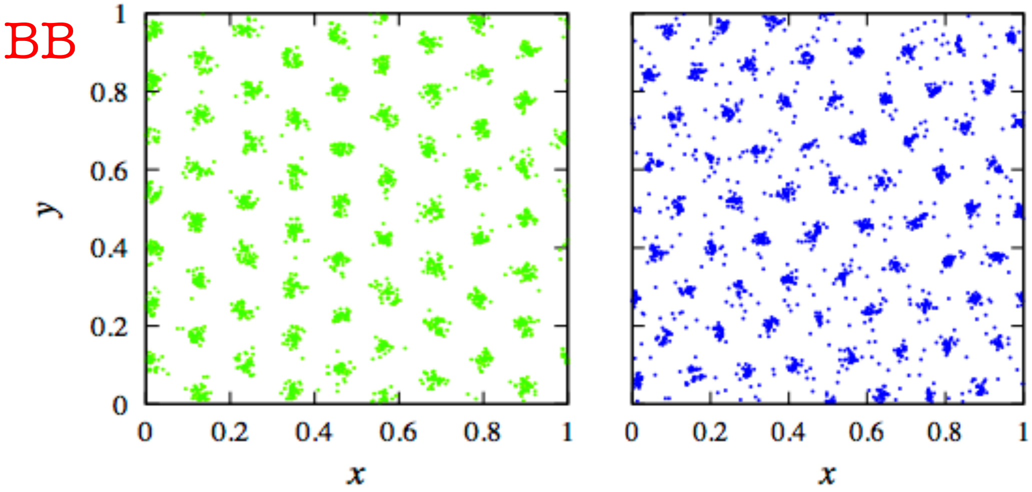
- r_{d0} should be small enough otherwise the number of particles is fluctuating too much and the stationary state (periodic pattern) is not reached

$$r_{b0} = 1, \quad \alpha = 0.02, \quad r_{d0} = 0.1, \quad R = 0.1$$

$$\kappa = 10^{-5}, \quad \langle N \rangle_B = 2555$$

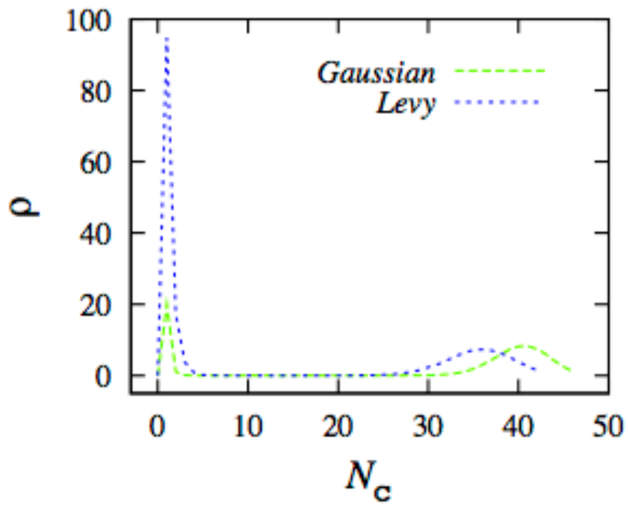
$$\kappa_\mu = 56 \times 10^{-5}, \quad \mu = 1, \quad \langle N \rangle_L = 2565$$

BB

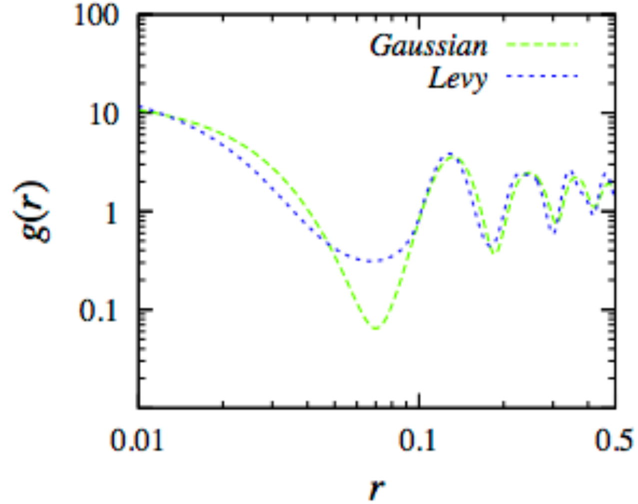


LB

distribution of cluster sizes:

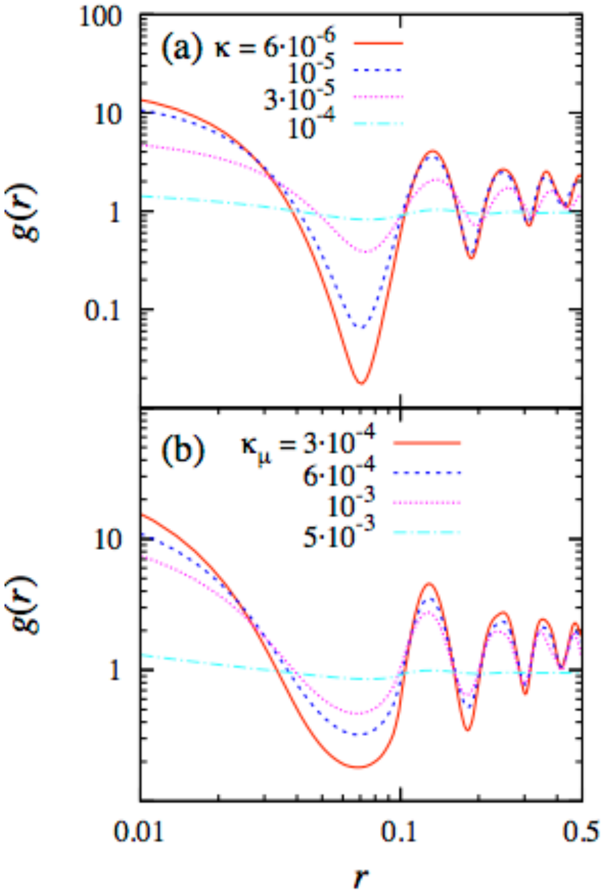


radial distribution function:

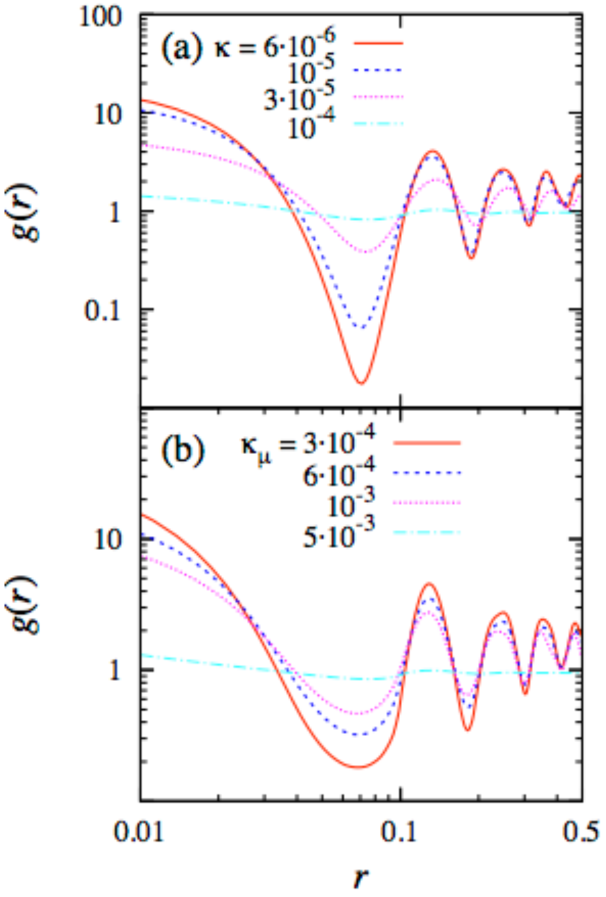


- an hexagonal pattern is formed with periodicity of the order ***R***
- the mean-field approximation is proper to describe the periodicity in the bug models with non-local finite-range interaction
- the large-scale collective behavior of the systems is much more strongly influenced by the competitive interaction then by the type of spatial motion performed by the organisms
- in the case of Levy bugs there are many single organisms between the clusters

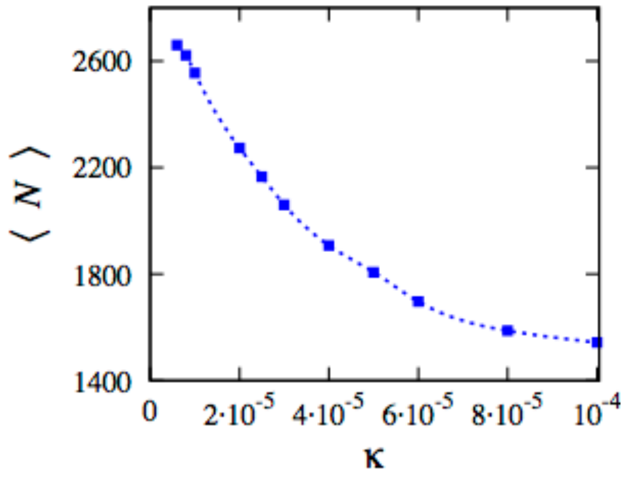
radial distribution function:

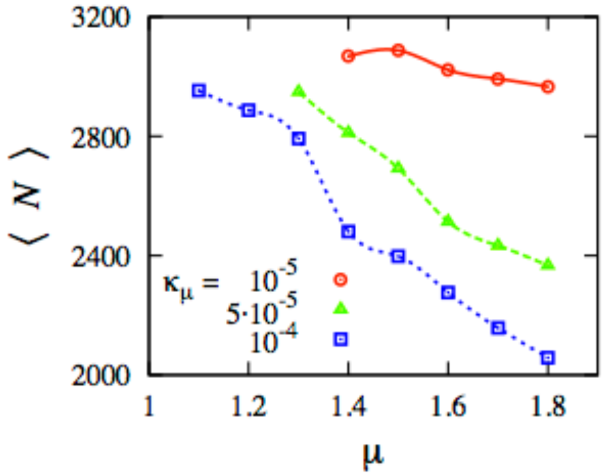


radial distribution function:

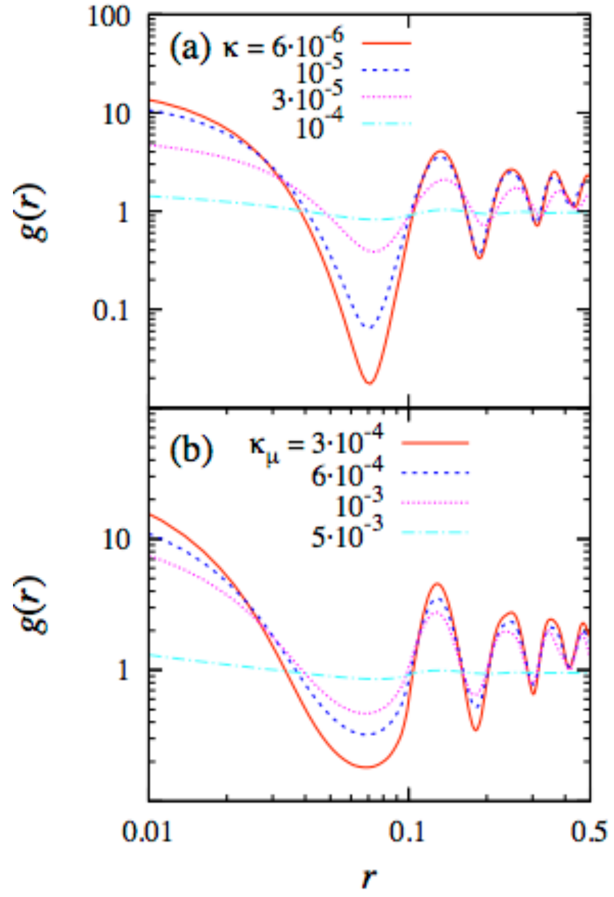


average number of bugs:

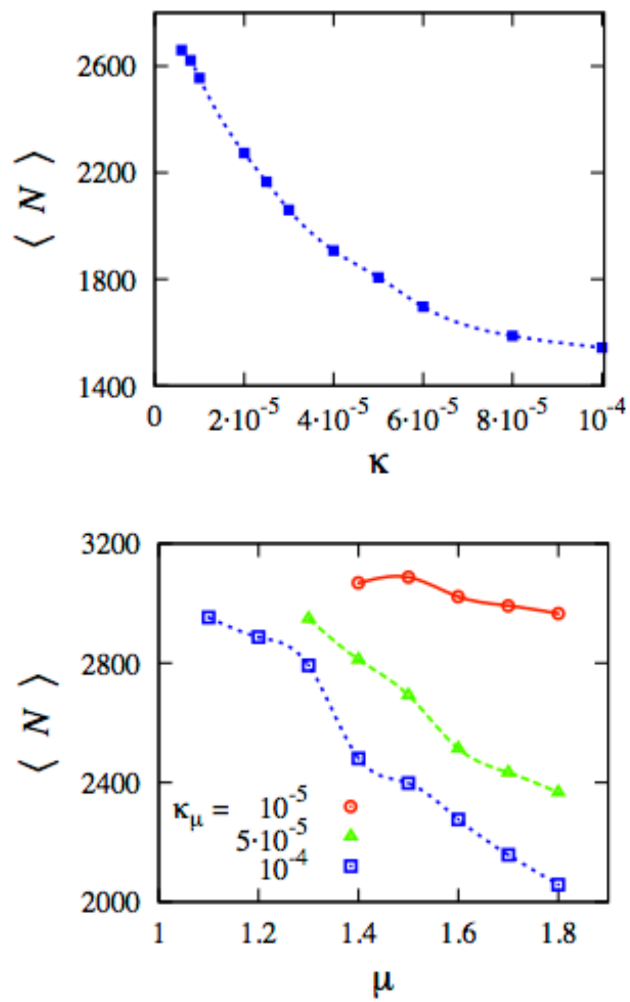




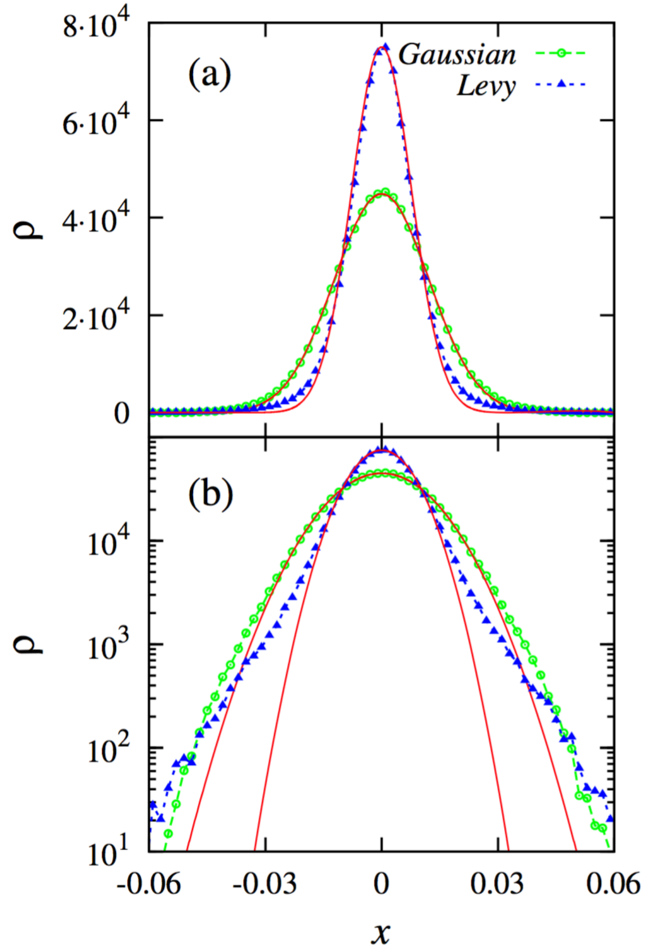
radial distribution function:



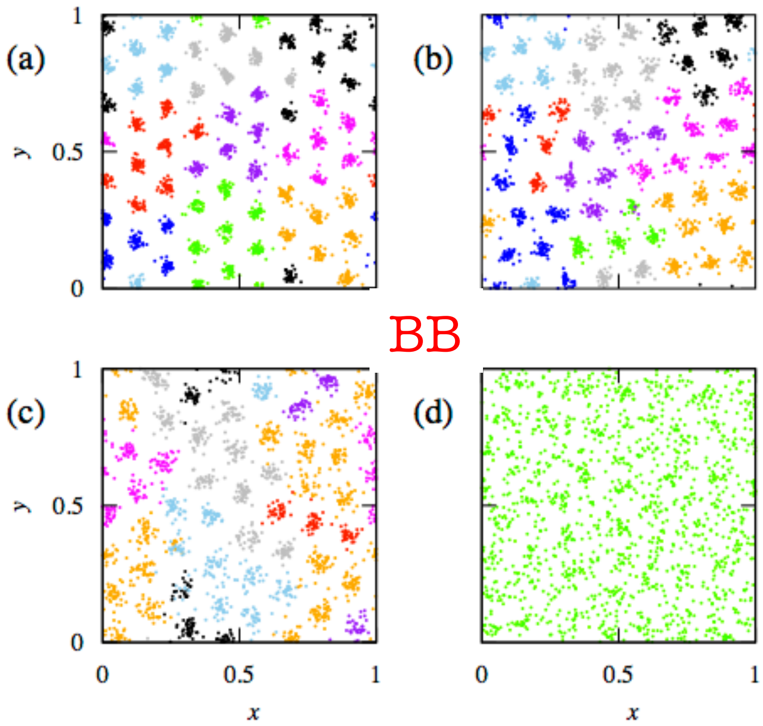
average number of bugs:



the cross section of the 2D particle density of the average cluster:

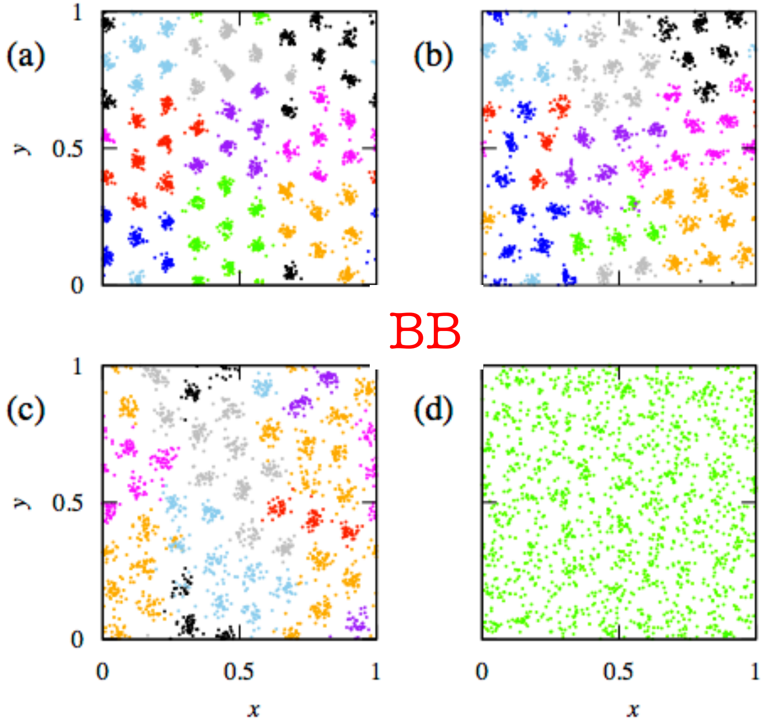


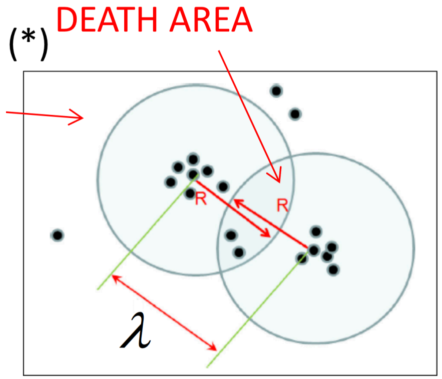
the central part of the average cluster is well fitted by a Gaussian function; the decay in the Levy case is close to exponential



$(a)\ \kappa = 10^{-5}$, $(b)\ \kappa = 2\times 10^{-5}$

$(c)\ \kappa = 4\times 10^{-5}$, $(d)\ \kappa = 10^{-4}$





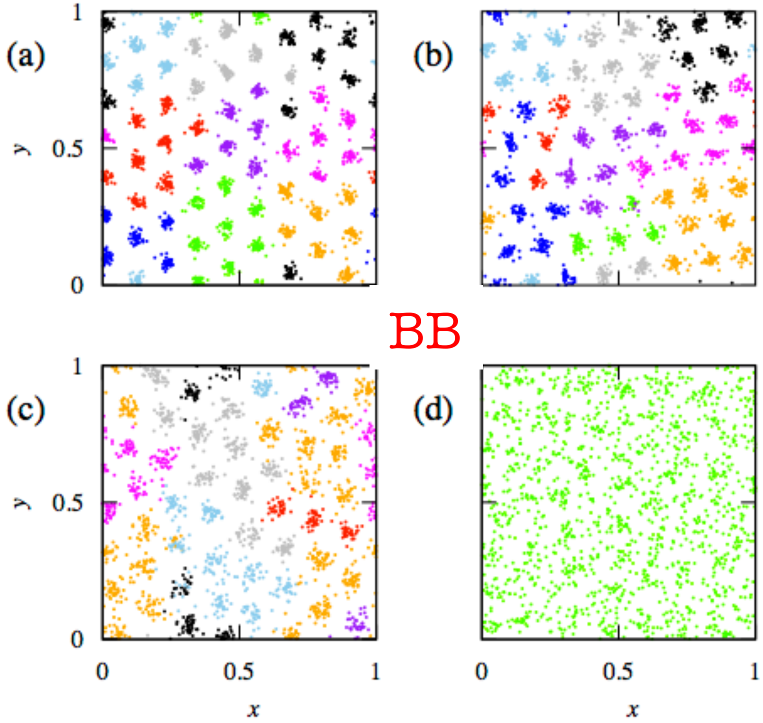
$(a)\,\kappa = 10^{-5}$, $\quad (b)\,\kappa = 2\times10^{-5}$

$(c)\,\kappa = 4\times10^{-5}$, $\quad (d)\,\kappa = 10^{-4}$

$(a)\,\kappa_\mu = 10^{-4}, \mu = 1$, $\quad (b)\,\kappa_\mu = 10^{-3}, \mu = 1$

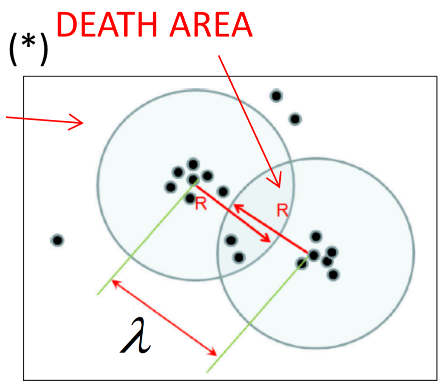
$(c)\,\kappa = 10^{-4}, \mu = 1.5$, $\quad (d)\,\kappa = 5\times10^{-5}, \mu = 1.5$

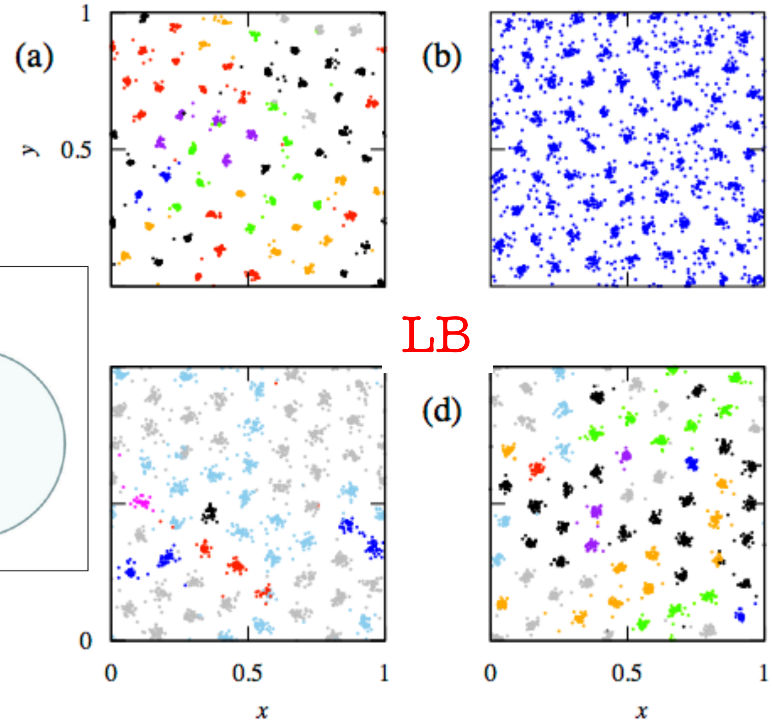
- organisms that are out of clusters, have more neighbors and thus the death is more probable in the inter-cluster space
- in the case of Brownian bugs this means that for low diffusivity the mixing of different families is very small
- if the diffusivity is high, in the end there is only one family present



$(a)\ \kappa = 10^{-5}$, $(b)\ \kappa = 2\times10^{-5}$

$(c)\ \kappa = 4\times10^{-5}$, $(d)\ \kappa = 10^{-4}$





$(a)\ \kappa_\mu = 10^{-4}, \mu = 1$, $(b)\ \kappa_\mu = 10^{-3}, \mu = 1$

$(c)\ \kappa = 10^{-4}, \mu = 1.5$, $(d)\ \kappa = 5\times10^{-5}, \mu = 1.5$

- organisms that are out of clusters, have more neighbors and thus the death is more probable in the inter-cluster space
- in the case of Brownian bugs this means that for low diffusivity the mixing of different families is very small
- if the diffusivity is high, in the end there is only one family present; in the case of Levy bugs this is always so due to the long jumps

Conclusion:

- we have investigated systems where the individuals are modeled as Brownian or Levy random walkers which interact in a competitive manner
- though the models studied describe rather living organisms, such as animals or bacteria, competition and spatial diffusion are important also in plant ecology for the development of vegetation patterns
- we have observed that mixing of families and their competition is greatly influenced by the type of spatial motion; in the recent works we have been investigating the competition between the individuals with different diffusion coefficients
- small modifications allow to investigate very different systems; does not have to be (only) the birth or death rate, but can be any quantity, e.g. the choice of the language that one speaks depending on what is the language spoken in the local community

References:

- E. Heinsalu, E. Hernandez-Garcia, C. Lopez,
  Spatial clustering of interacting bugs: Levy flights versus Gaussian jumps,
  Europhys. Lett. **92**, 40011 (2010)
- E. Heinsalu, E. Hernandez-Garcia, C. Lopez,
  Competitive Brownian and Levy walkers,
  Phys. Rev. E 85, 041105 (2012)
- E. Hernández-García, E. Heinsalu, C. López,
  Spatial patterns of competing random walkers,
  Ecol. Complex. 21, 166 (2015)