Spatial population dynamics as point process

How individual-based birth, death, movement, and status change can be translated to dynamical system

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Non-spatial population dynamics

- Non-spatial models focus only on the population size
- Many models are given by Ordinary Differential Equation ODE

Pop. size: $n(t)$

$$\frac{dn}{dt} = \{(b - b'n) - (d + d'n)\}n$$
$$= r\left(1 - \frac{n}{K}\right)n$$

$$\frac{dS}{dt} = -\beta SI + \gamma I$$
$$\frac{dI}{dt} = \beta SI - \gamma I$$

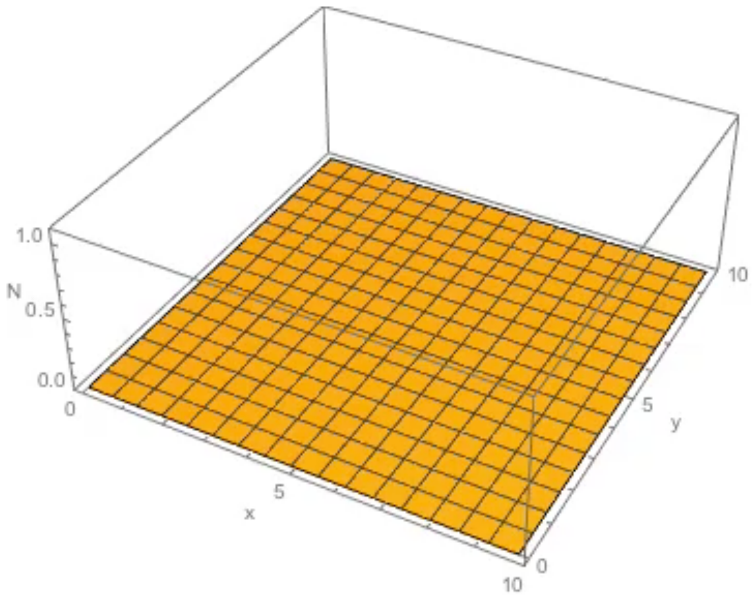
$$\frac{dS}{dt} = -\beta SI$$
$$\frac{dI}{dt} = \beta SI - \gamma I$$
$$\frac{dR}{dt} = \gamma I$$

How to model spatial population dynamics?

- Reaction-diffusion model as Partial Differential Equation PDE
- Dynamics of the population density at time *t* and location **x**

Pop. size: $n(t, \mathbf{x})$

$$\frac{\partial n}{\partial t} = D\left(\frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2}\right) + f(n)$$



$$f(n) = \epsilon(1-n)n$$

Traveling wave

Velocity $2\sqrt{\epsilon D}$

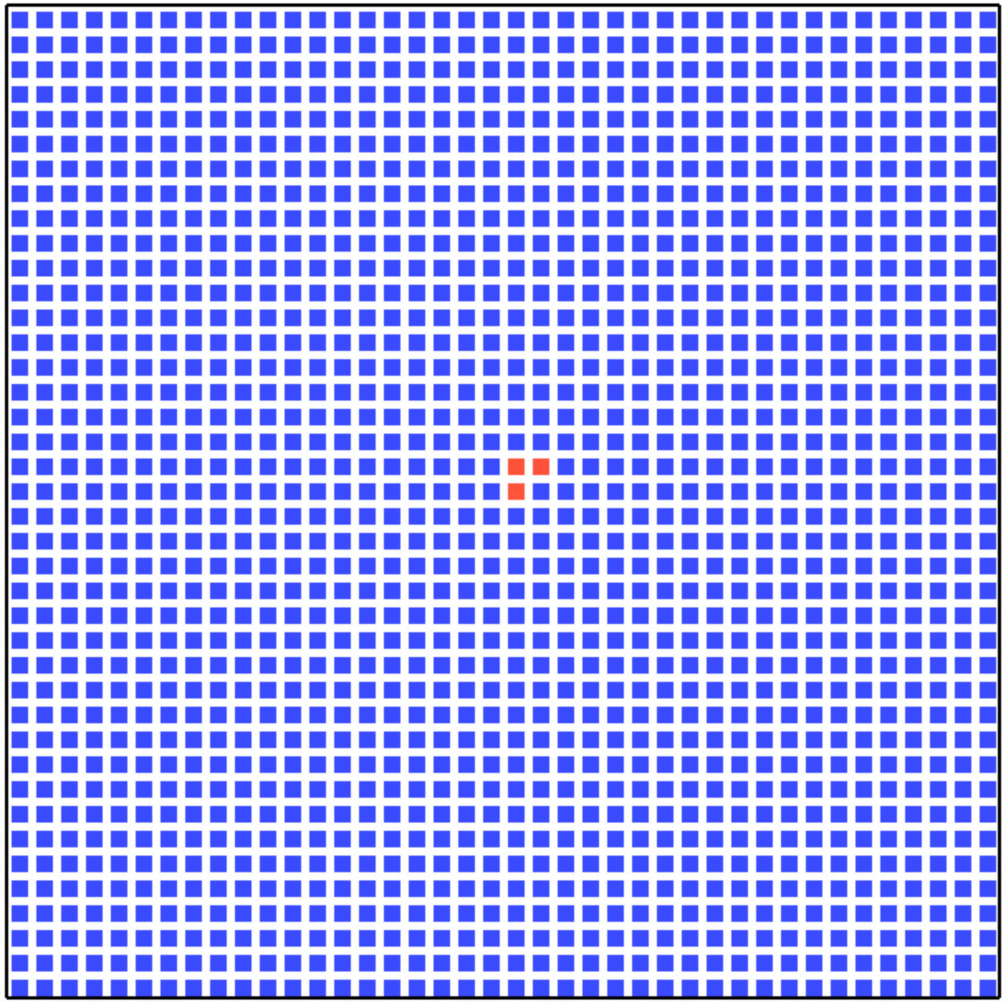
How to model spatial population dynamics?

- Lattice model on a discrete space with cells
- Stochastic transition of a cell between “vacant” and “occupied”
- A vacant site 0 is colonized from adjacent occupied + sites
- An occupied site + goes locally extinct to 0
- How occupied/vacant sites are distributed over space?

0	0	0	0	0
0	+	+	0	0
0	+	0	0	0
0	0	+	0	0
0	0	0	0	0

0 : Vacant
+ : Occupied

Lattice model



Space size L = 40, Rate colonization = 1.2, Rate extinction = 1
t = 0.0534873, Occupied = 3, Vacant = 1597

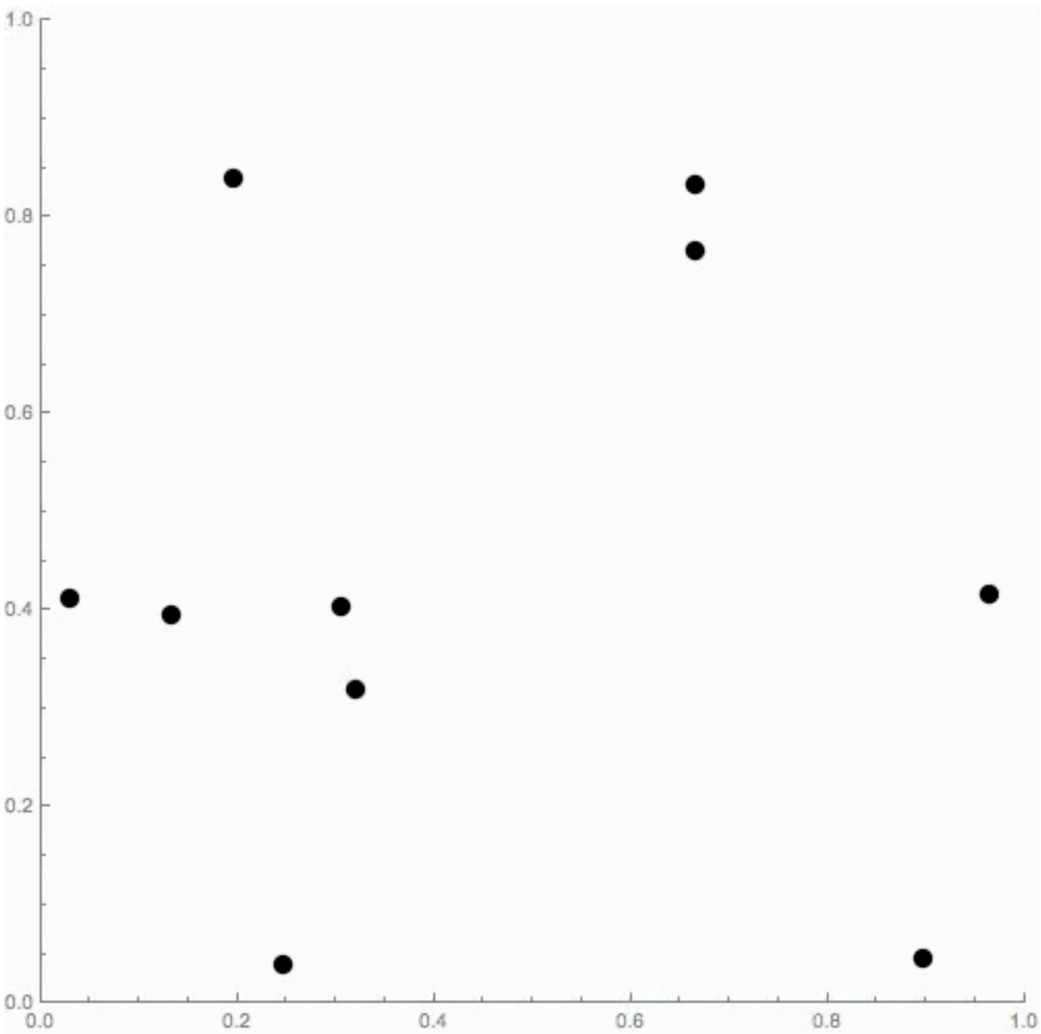
0 : Vacant in blue
+ : Occupied in red

Spatial population dynamics as point process

- A point pattern is a collection of points as individuals
- Each point gives birth, dies, moves and changes its status with a certain rules
- Point pattern dynamics is an individual-based spatial dynamics; each individual has a set of properties that affect birth, death, etc. (age, disease symptoms, etc.)
- A point can be a single cell or a local patch, a city, etc.
- How to analyze point pattern dynamics?
  - Stochastic simulations
  - Analytical approaches to understand simulations

Spatial logistic growth model as a point pattern dynamics

Birth + Death



Competition range σ_c = 1.0, Dispersal range σ_m = 0.03

Law and Dieckmann 2000
Law et al. 2003

Non-spatial logistic model has been extended as PPD as IBM

Each point feels "local density" that determines birth and death rate

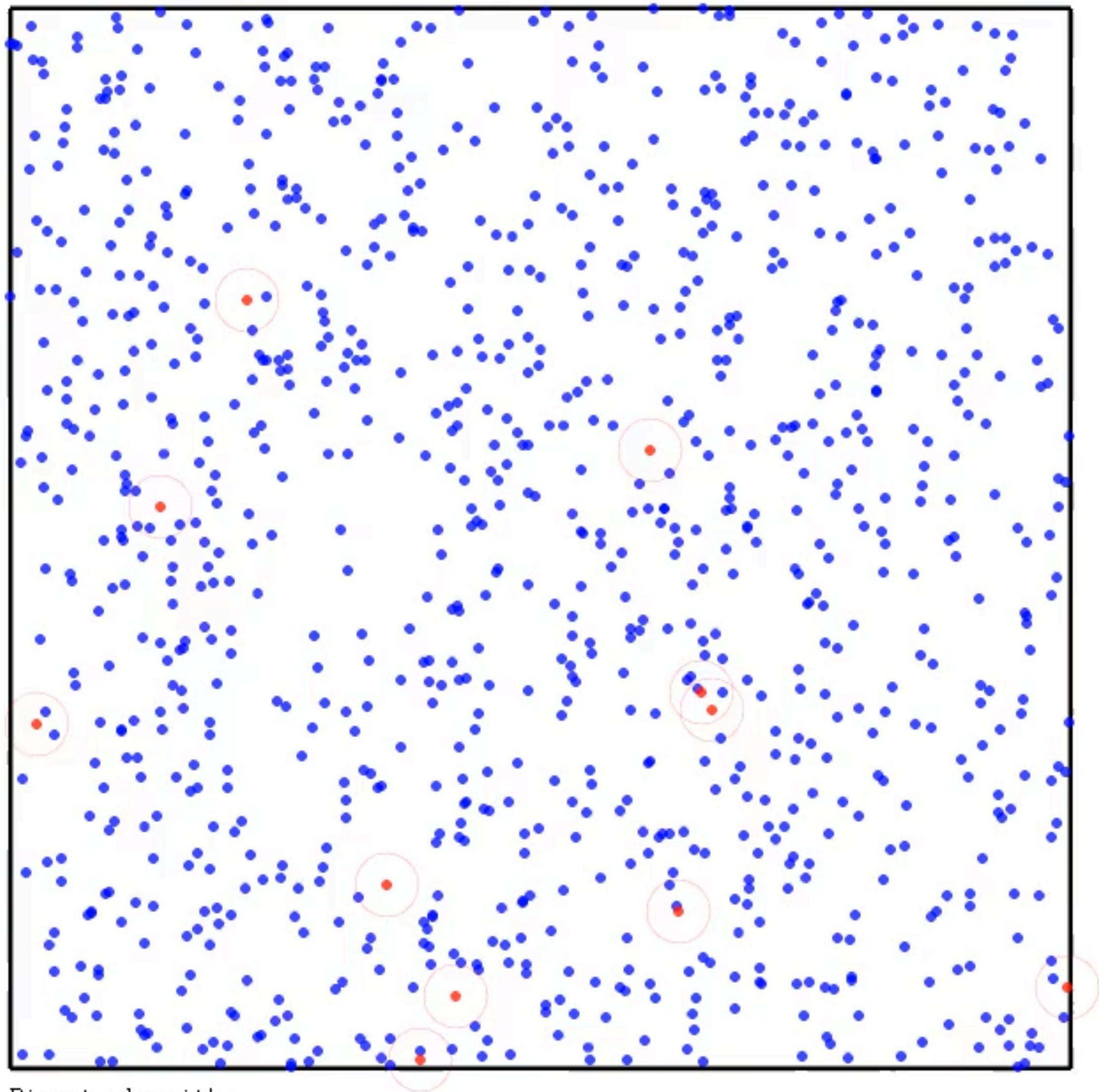
A newly born individual disperses from its parent

Points do not move

Status change

Point pattern SIS model

Hamada and Takasu 2019



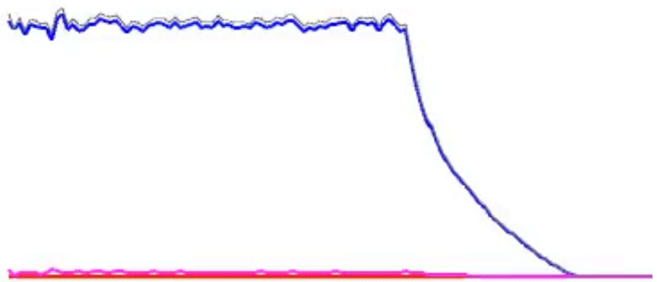
Direct algorithm

Space size L = 1, Range competition = 0.02, Range dispersal = 0.02, Range infection = 0.01, Beta = 1.2, Gamma = 5.1, CELLS = 12

t = 2.29109e-05, pop size total = 1010, S = 999, I = 11, R = 0

Pop. size S, I, R

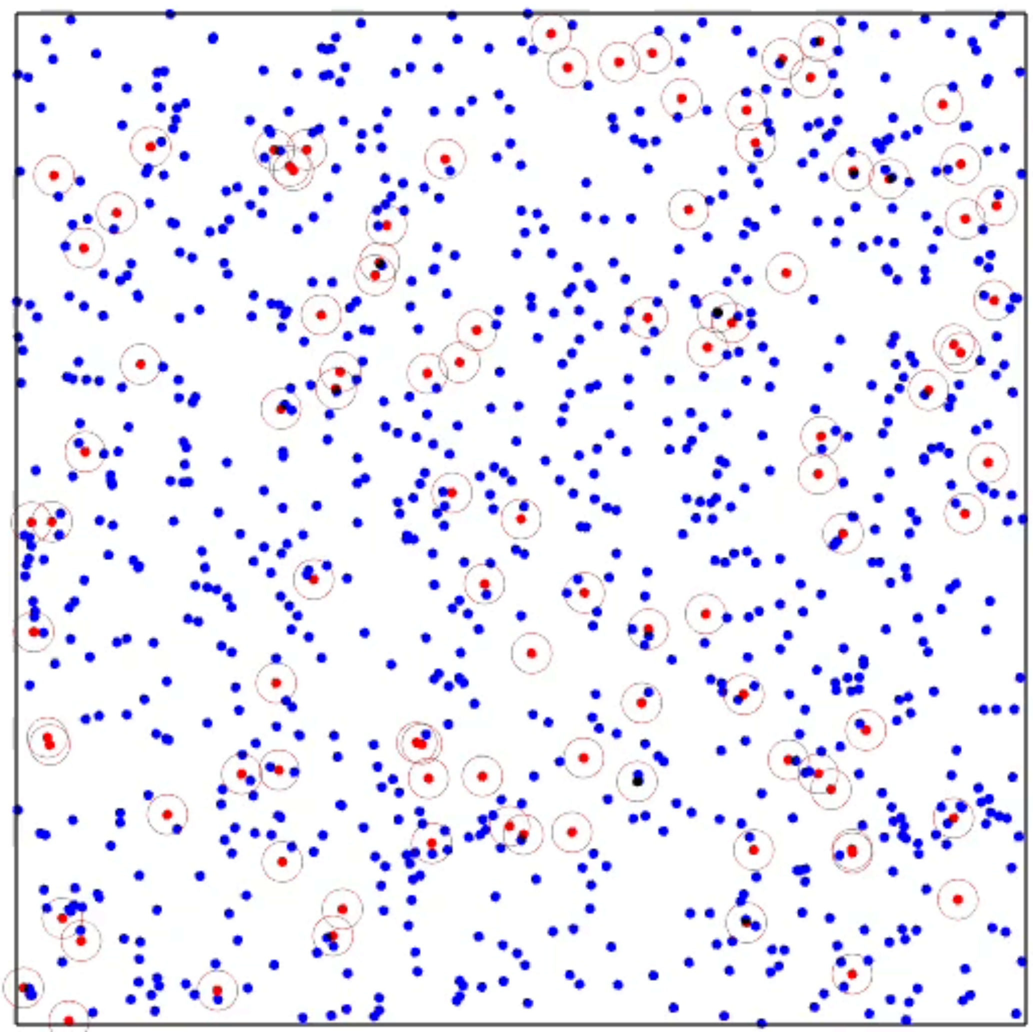
Each point is S or I
Distance dependent infection rate
Points do not move



PCF S-S, I-I, S-I (I-S), and all pairs

Status change + Move

Point pattern SIS model + Movement of points



Susceptible point 0 in blue, Infectious point 1 in red

Space L = 1, CELLS = 25, N = 1000

B0 = 0.01, SD_I = 0.01, GAMMA = 1, M_S = 1, L_S = 0.01, M_I = 0, L_I = 0.01

t = 0.00000000, popS = 900, popI = 100

SIS Point Pattern Dynamics

SIS (Infection + Recovery), Movement

Pop size 0 (blue) and 1 (red)

Updated with time interval 0.1

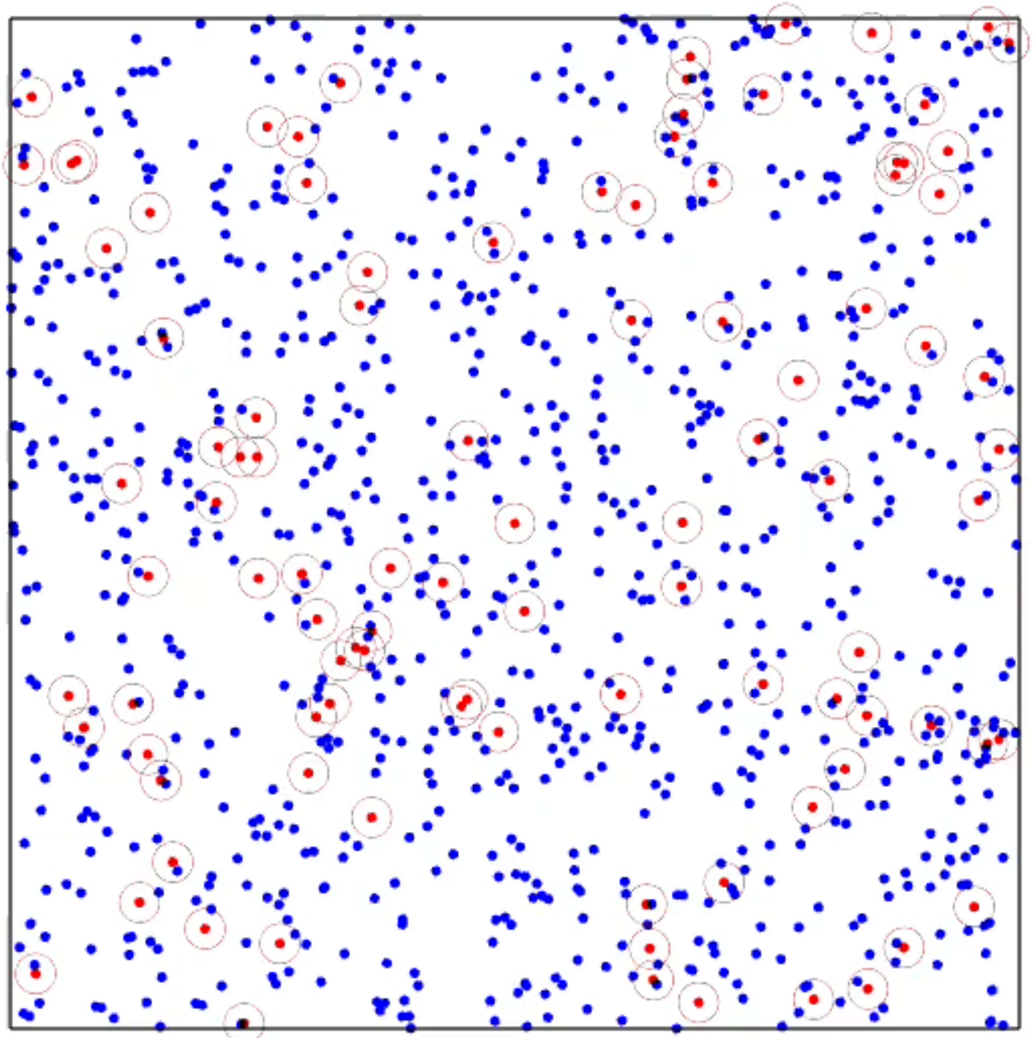
Infection inhibits movement

P.C.F.: 0-0 (blue), 0-1 (purple), 1-1 (red)

Updated with time interval 0.1

Status change + Move

Point pattern SIS model + Movement of points



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Space L = 1, CELLS = 25, N = 1000

B0 = 0.01, SD_I = 0.01, GAMMA = 1, M_S = 0, L_S = 0.01, M_I = 1, L_I = 0.01

t = 0.00000000, popS = 900, popI = 100

SIS Point Pattern Dynamics

SIS (Infection + Recovery), Movement

Pop size 0 (blue) and 1 (red)

Updated with time interval 0.1

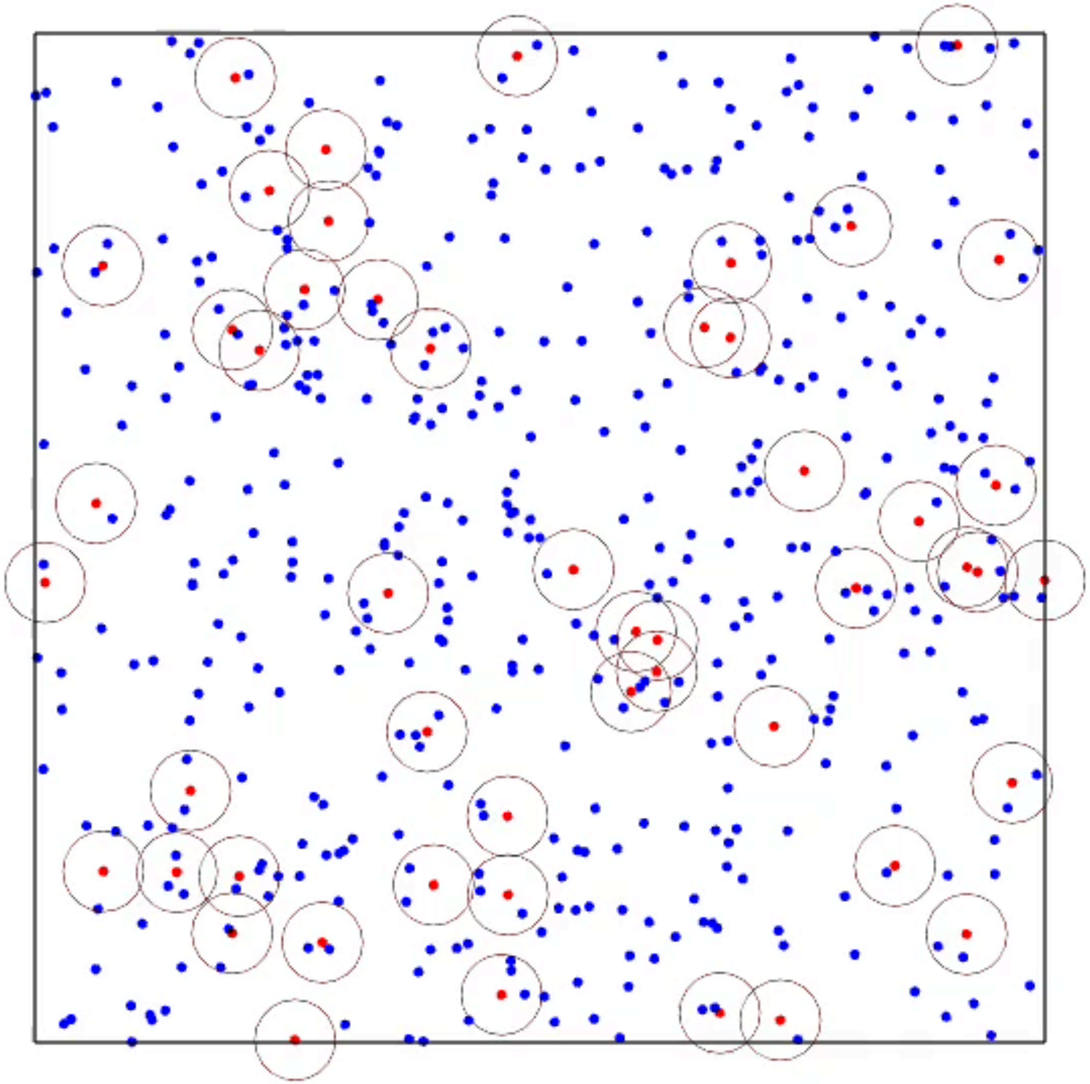
Infection promotes movement

P.C.F.: 0-0 (blue), 0-1 (purple), 1-1 (red)

Updated with time interval 0.1

Status change + Birth + Death

Point pattern SIS model + Birth and Death



Scale birth and death = 1
Space L = 1, CELLS = 12
SIGMA_C = 0.01, SIGMA_D = 0.02, SIGMA_C = 0.02
t = 0.00000000, pop total = 500, S = 450, I = 50

Point Pattern Dynamics with
Spatial logistic + SIS

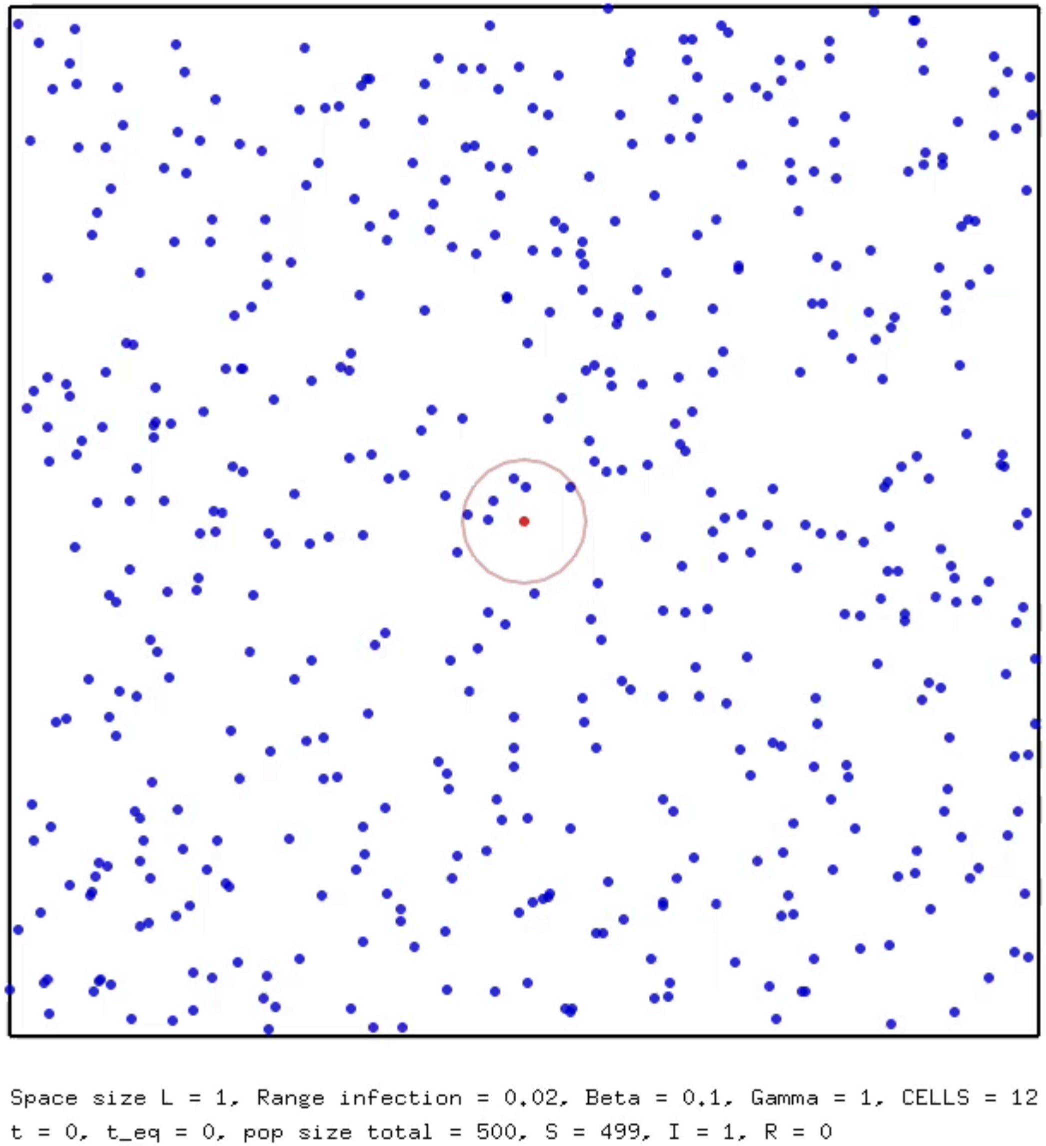
Pop size 0 (blue) and 1 (red)
Updated with time interval 0.1

Birth and death as Law et al. (2003)
+ SIS dynamics

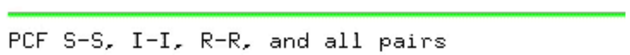
P.C.F.: 0-0 (blue), 0-1 (purple), 1-1 (red)
Updated with time interval 0.1
Max PCF = 0.01

Status change

Point pattern SIR model

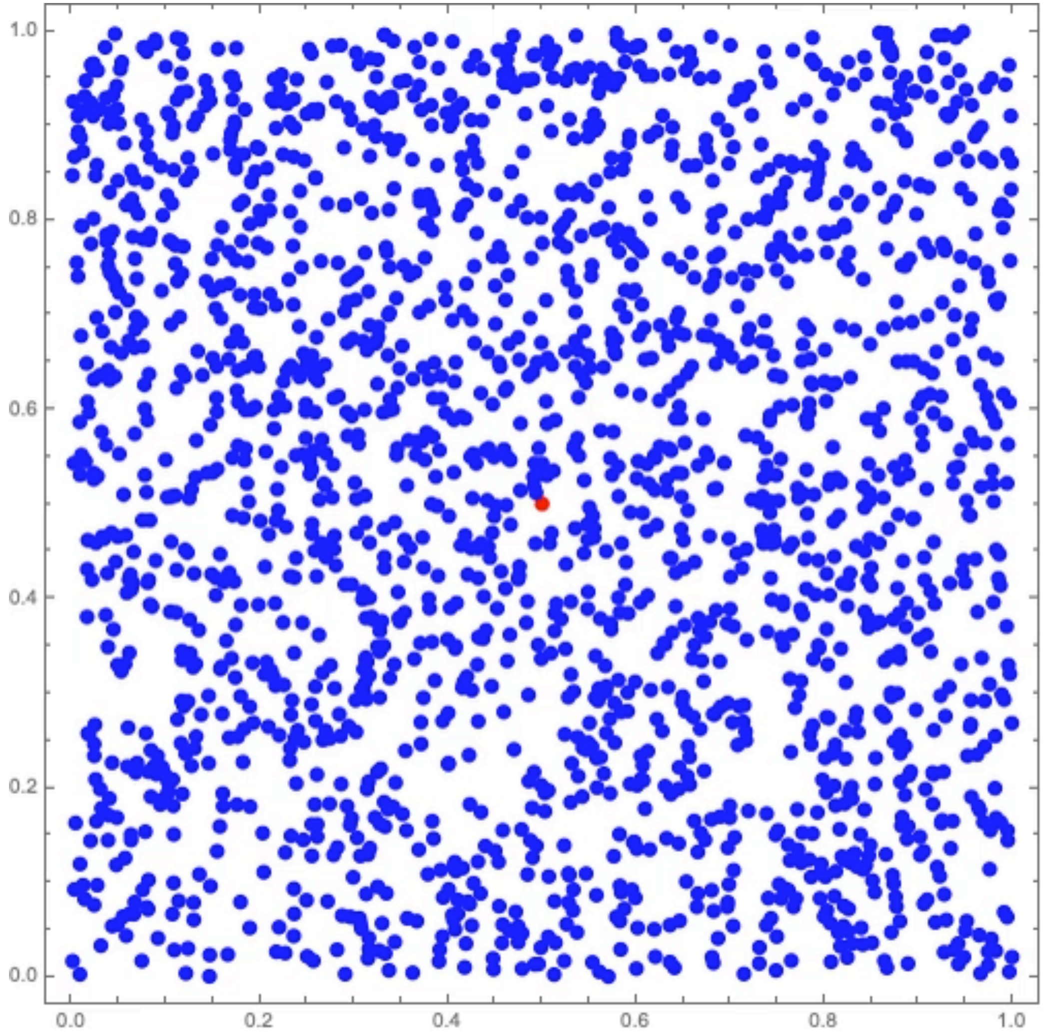


Each point is S or I or R
Distance dependent infection rate
Points do not move



Status change

Example of SIR point pattern dynamics



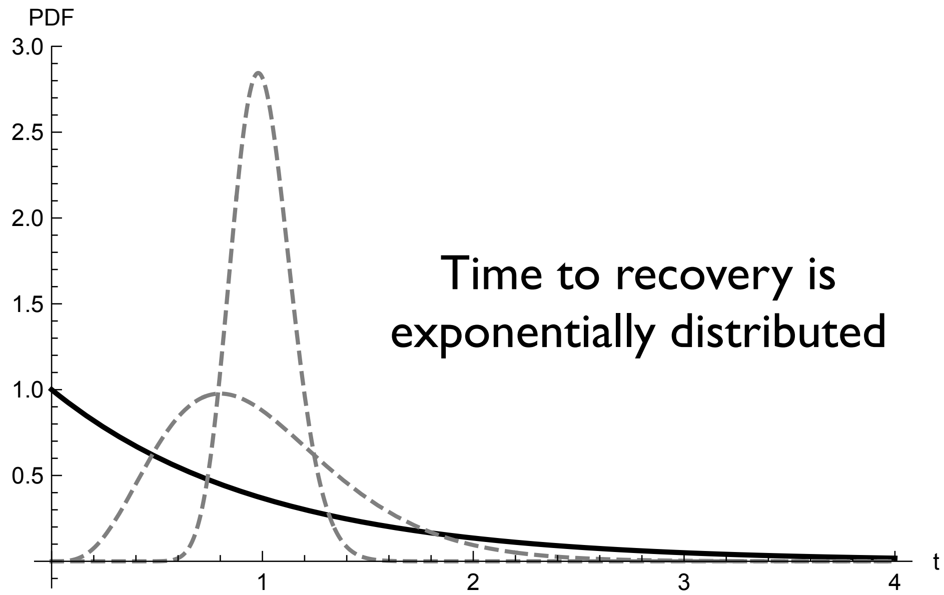
k = 1

Time to recovery is exponential

S in blue

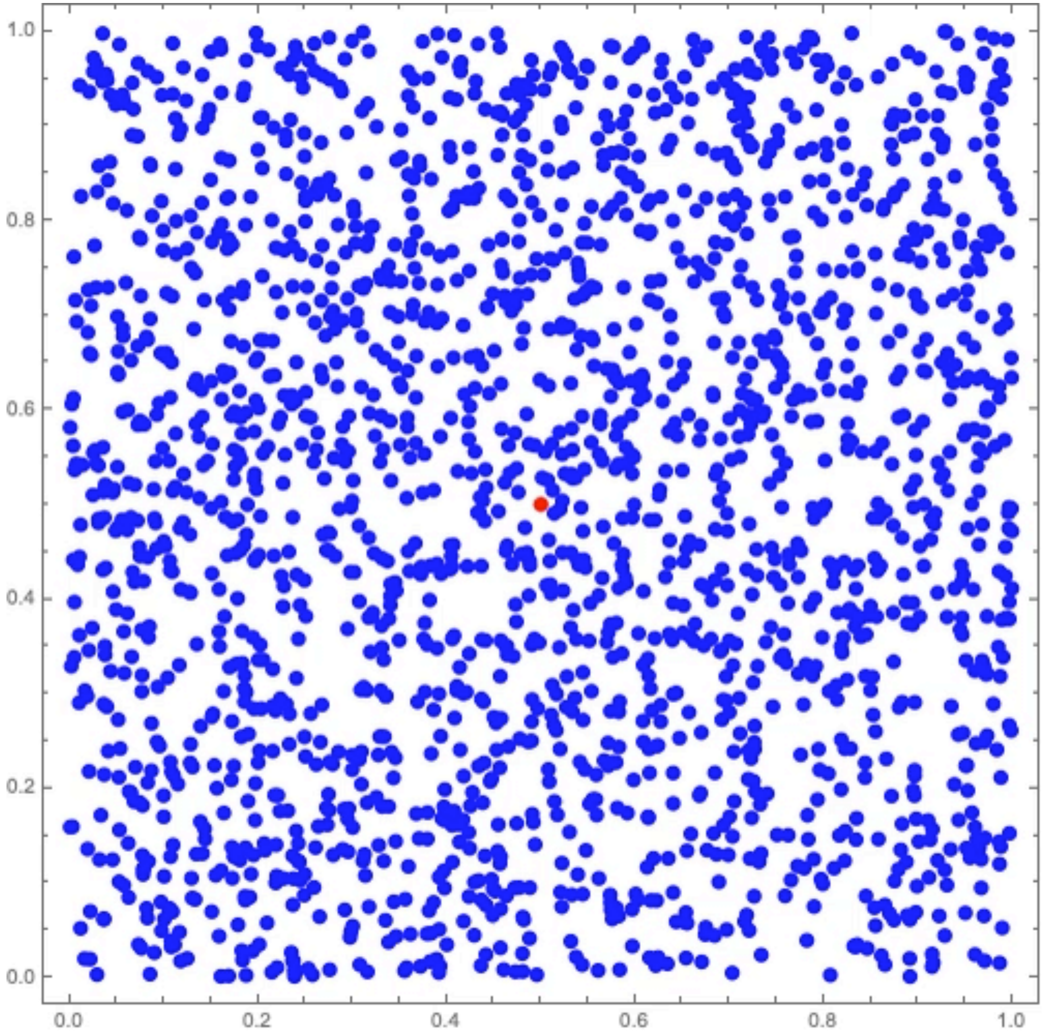
I in red

R in brown



Status change

Example of SIsR point pattern dynamics



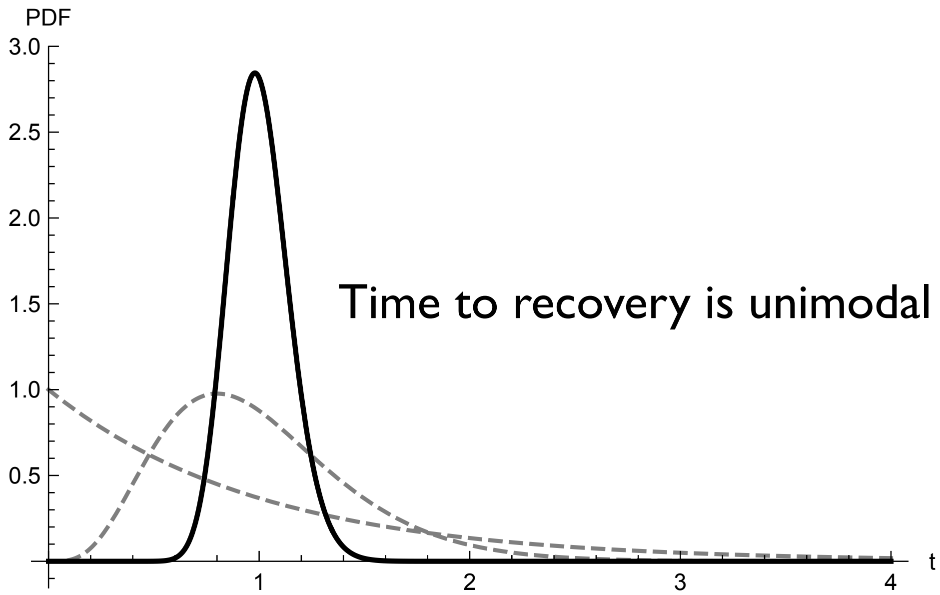
k = 50

Time to recovery is unimodal

S in blue

I in red

R in brown

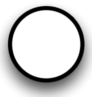


Point pattern

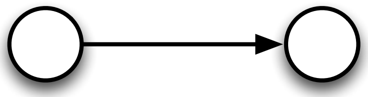
- Spatial arrangement of individuals within an area
- Population density ~ Number of points per unit area
- Spatial structure can be inferred by "pairs" made by two points
- Null model is Complete Spatial Randomness CSR where presence of an individual at a position is independent of other individuals

Quantification of point pattern

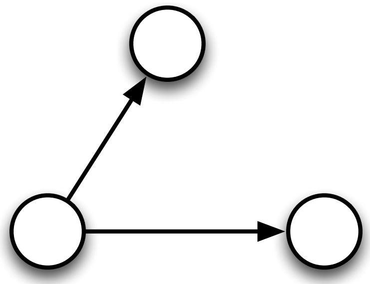
- 1st order (Number of points)
- 2nd order (Number of pairs displaced with a certain distance)
- 3rd order (Number of triplets with a certain configuration)



Number of points
as a scalar



Number of pairs as a
function of a vector

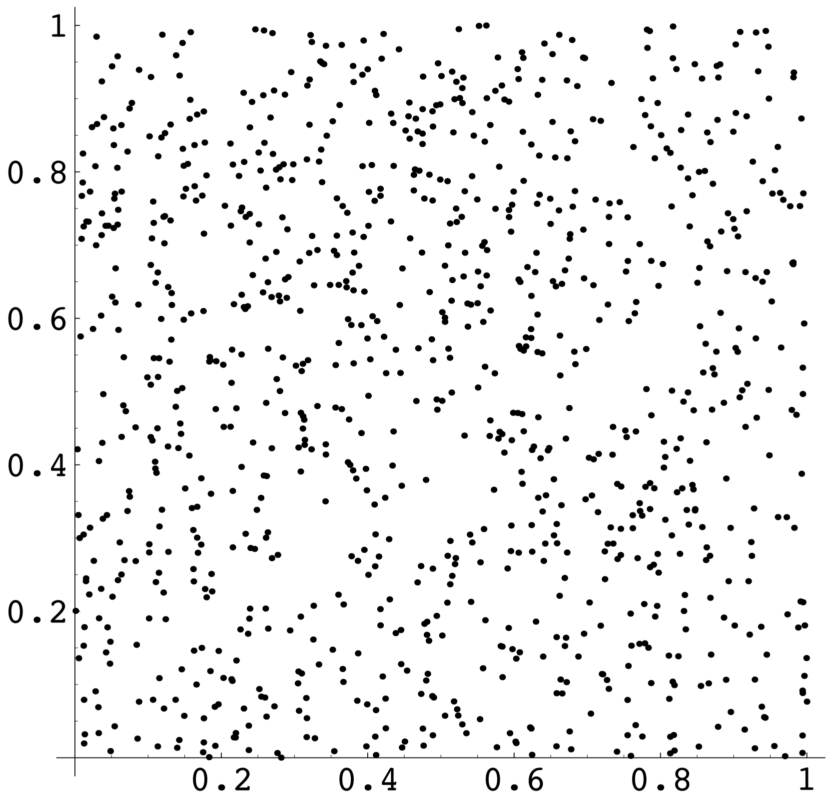


Number of triplets as a
function of two vectors

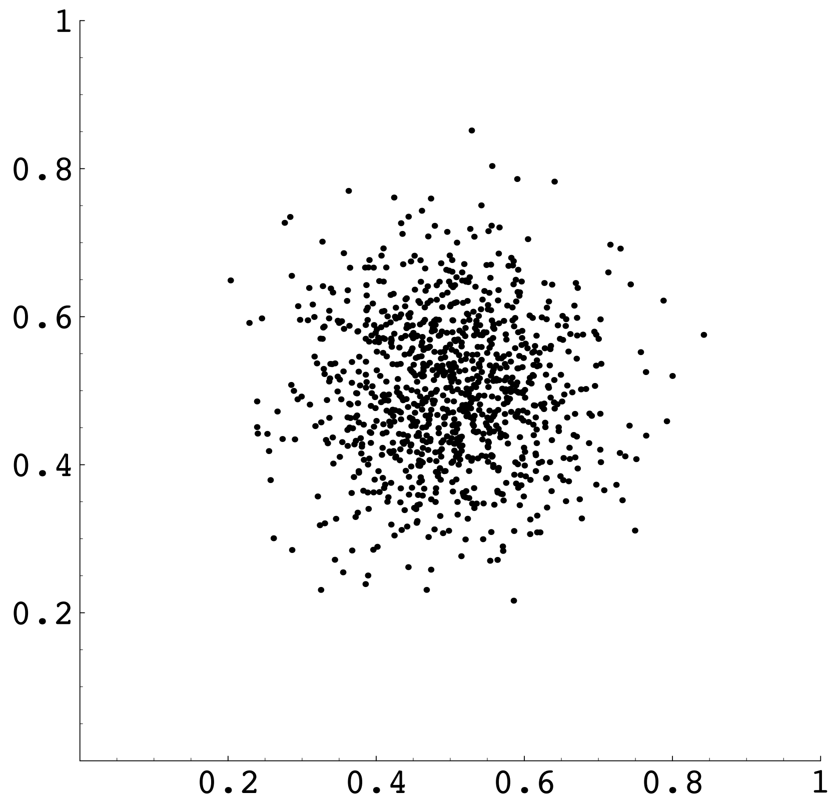
Quantification of a point pattern

- Number of points (1st order structure)
- Number of pairs displaced with a certain distance (2nd order structure)

Homogeneous Poisson (n = 1000)

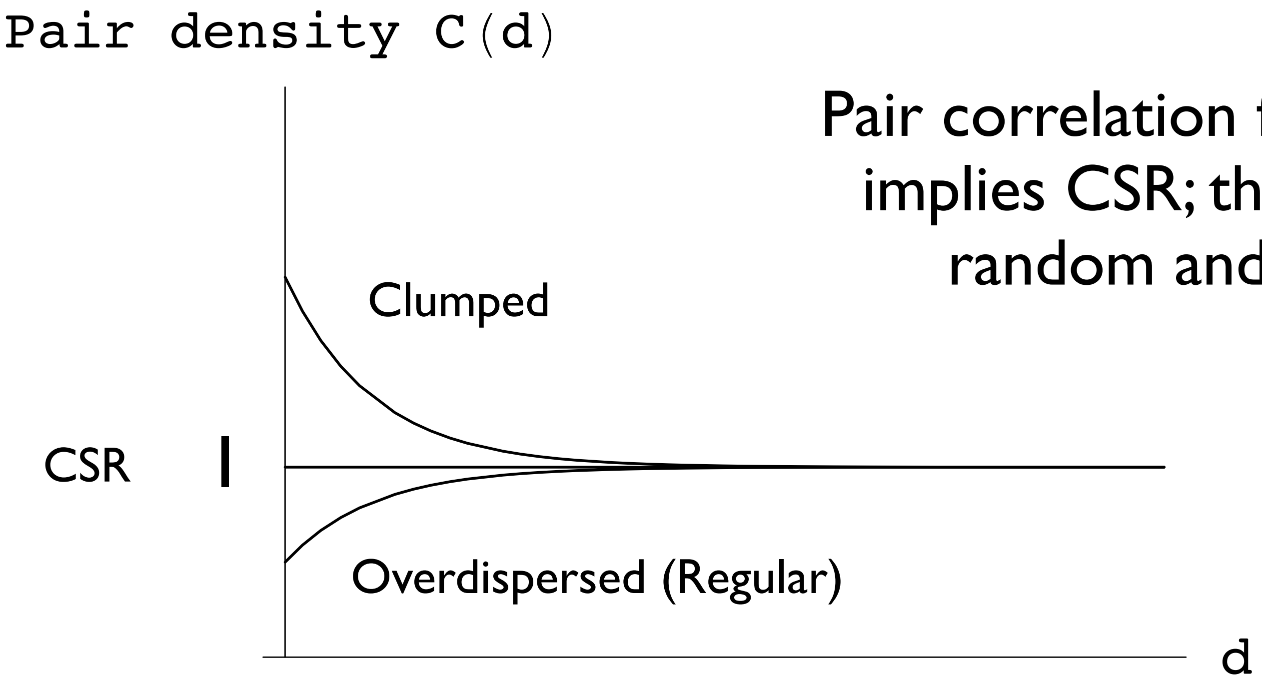


Gaussian (n = 1000)



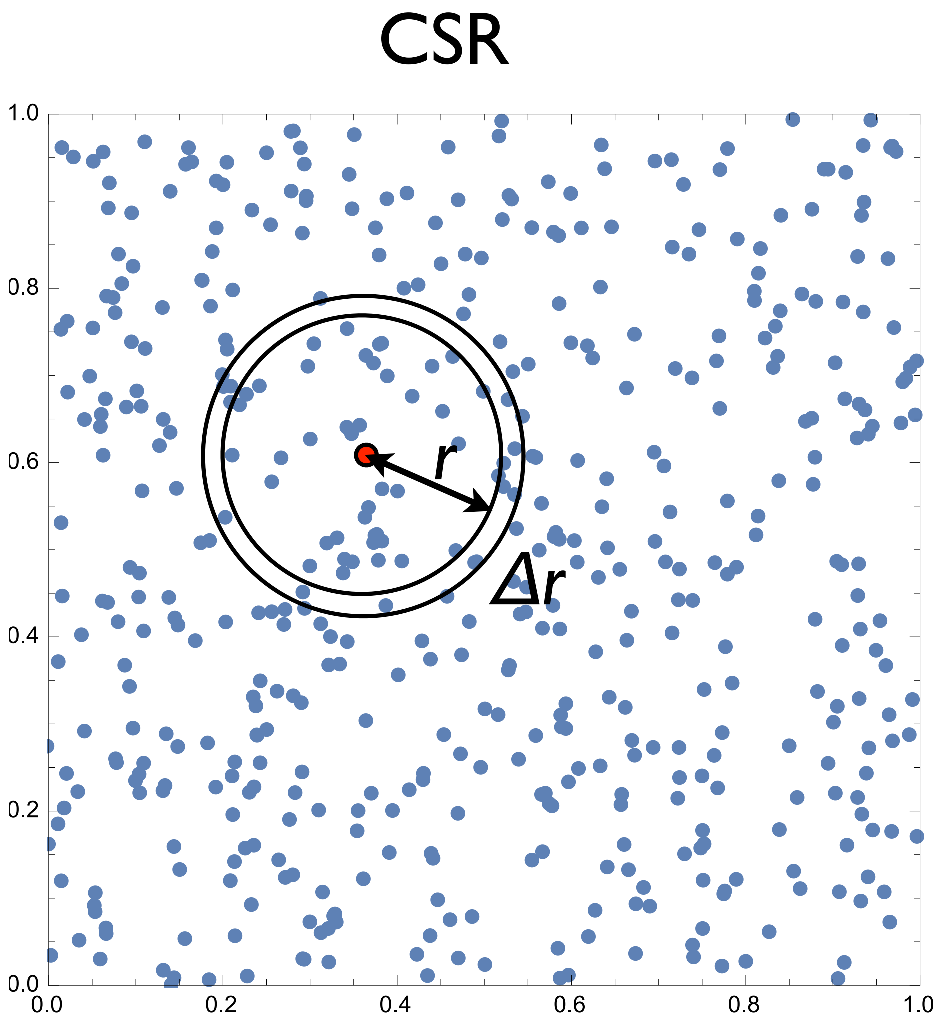
Pair correlation function

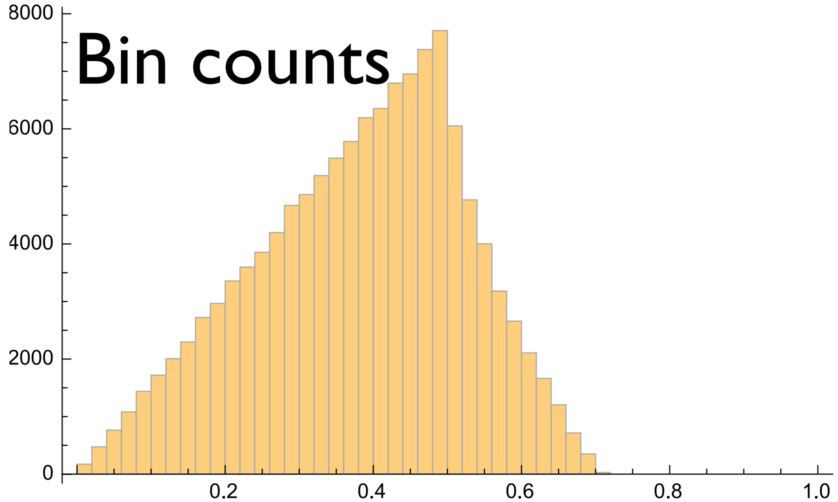
describes the distribution of inter-point distances
(2nd order structure of point pattern)

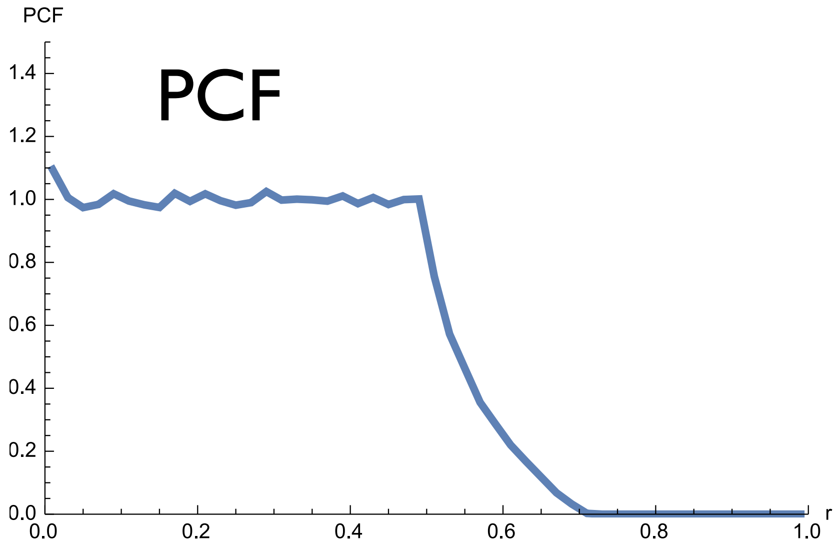


Pair correlation function being flat at 1 implies CSR; the point patten is just random and has no structure

PCF examples

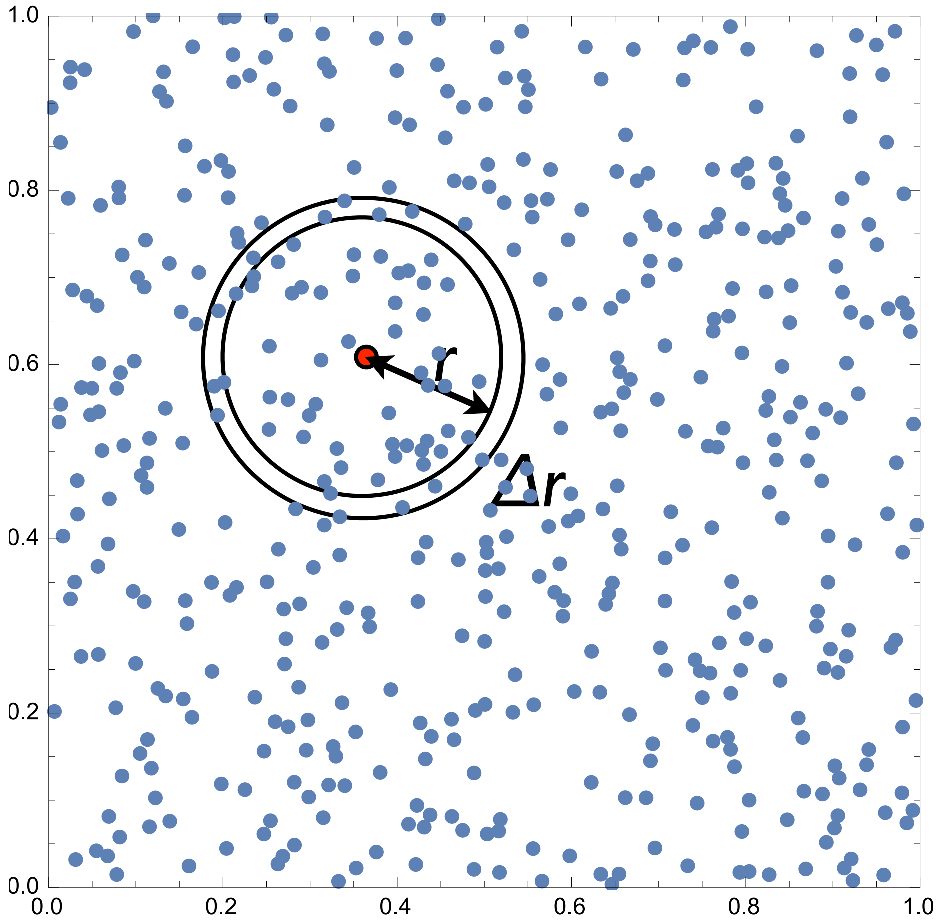


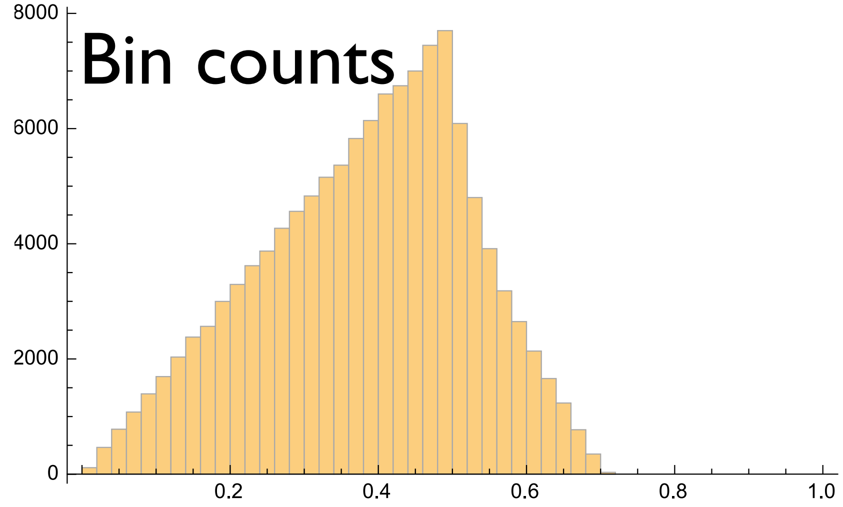


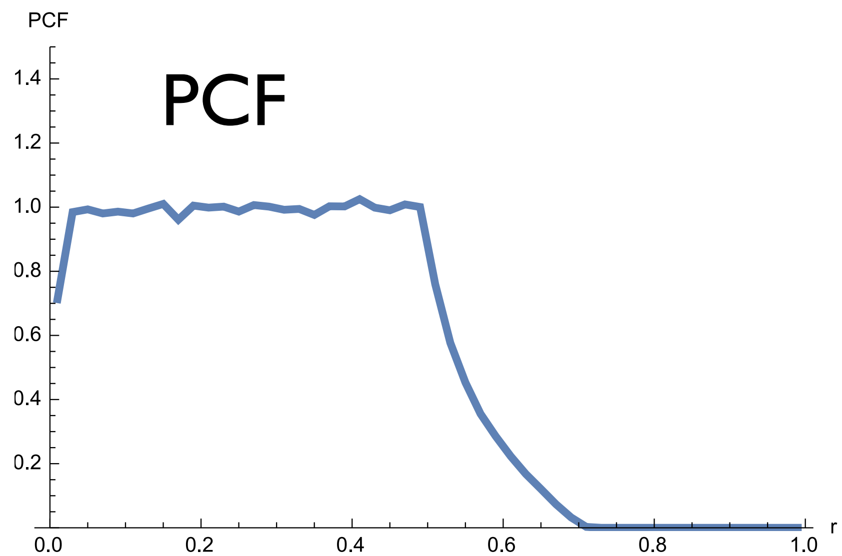


PCF examples

Regular







How to describe point pattern dynamics mathematically?

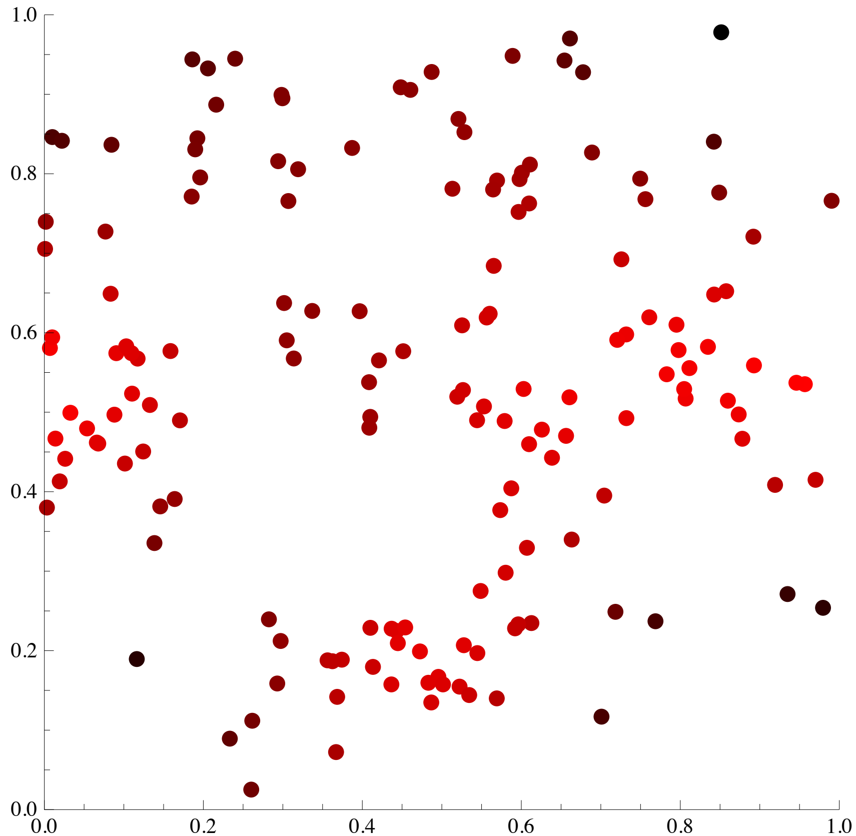
Law and Dieckmann 2000
Law et al. 2003

- An individual is a point on two dimensional space
- Each individual feels "local density"
- Each individual gives birth or dies logistically with rates that depend on its local density
- Newly born individual disperses from its parent

This study revisits the classical logistic growth model in terms of individuals' view point

Visualized example of local densities

- If surrounded by more neighbors, the local density an individual feels becomes higher



Moment dynamics of the IB spatial logistic growth model

Law and Dieckmann 2000
Law et al. 2003

N Density of singlets (individuals)

$$\frac{dN}{dt} = (b - d)N - (b_1 + d_1)\int w_c(\xi)C(\xi)d\xi$$

$w_c(\xi)$: Competition kernel

$C(\xi)$: Density of pairs

When point pattern is CSR, $C(\xi) = N^2$

$$\frac{dN}{dt} = (b - d)N - (b_1 + d_1)N^2$$

Dynamics of the pair density

Birth rate is constant *b* ($b_1 = 0$)

Death rate depends on local density ($d_1 > 0$)

$$\frac{d}{dt}C(\xi) = 2bm(\xi)N \qquad m(\xi) : \text{Offspring dispersal kernel}$$

$$+ 2b \int m(\xi')C(\xi + \xi')d\xi'$$

$$- 2dC(\xi)$$

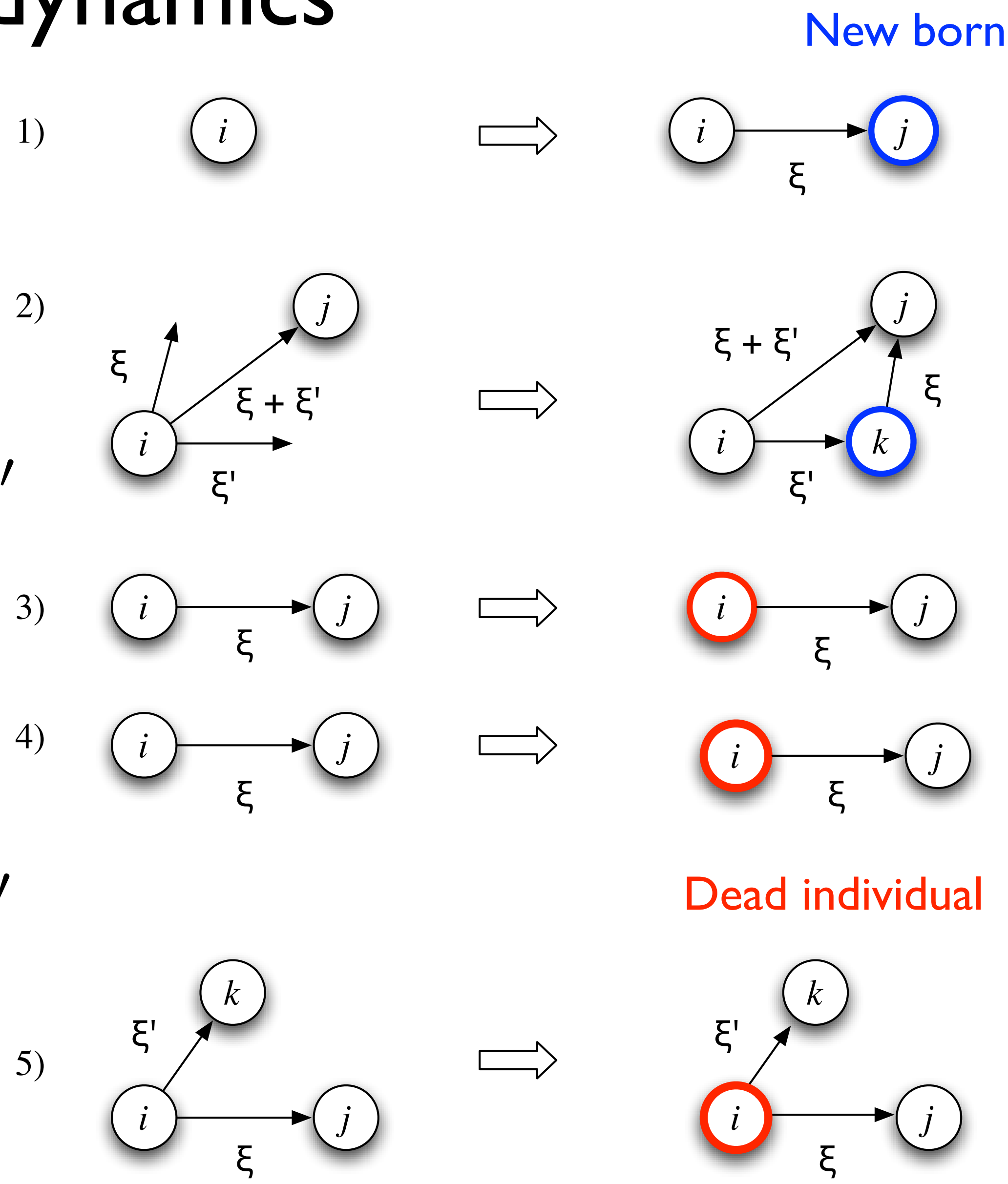
$$- 2d_1 w_c(\xi)C(\xi)$$

$$- 2d_1 \int w_c(\xi')T(\xi, \xi')d\xi'$$

$$T(\xi, \xi') : \text{Triplet density}$$

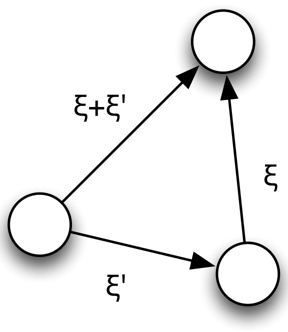
Geometrical interpretation of the pair density dynamics

$$\frac{dC(\xi)}{dt} = 2bm(\xi)N + 2b\int m(\xi')C(\xi+\xi')d\xi' - 2dC(\xi) - 2d_1 w_c(\xi)C(\xi) - 2d_1\int w_c(\xi')T(\xi,\xi')d\xi'$$



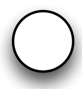
Moment closure

- Density of triplets has to be approximated using the singlet and the pair densities for the moment dynamics to be closed
- How triplet density can be approximated remains an open question
- Several candidates are proposed and evaluated which better explain simulations (Law and Dieckmann 2000, Law et al. 2003)

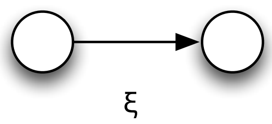


$$T(\xi,\xi') \approx \frac{C(\xi)C(\xi')}{N}$$

N

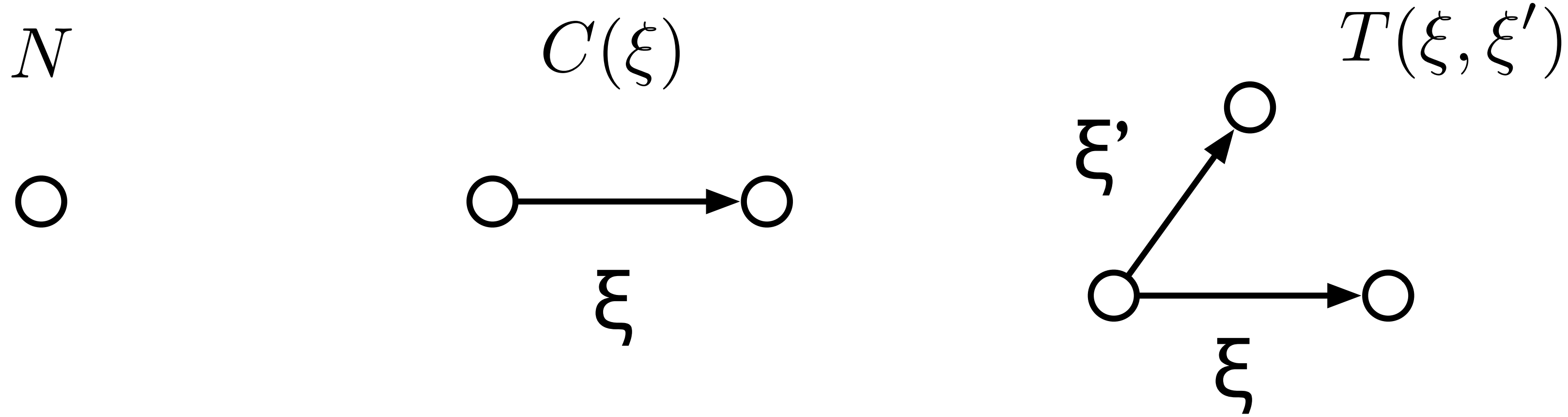


$C(\xi)$



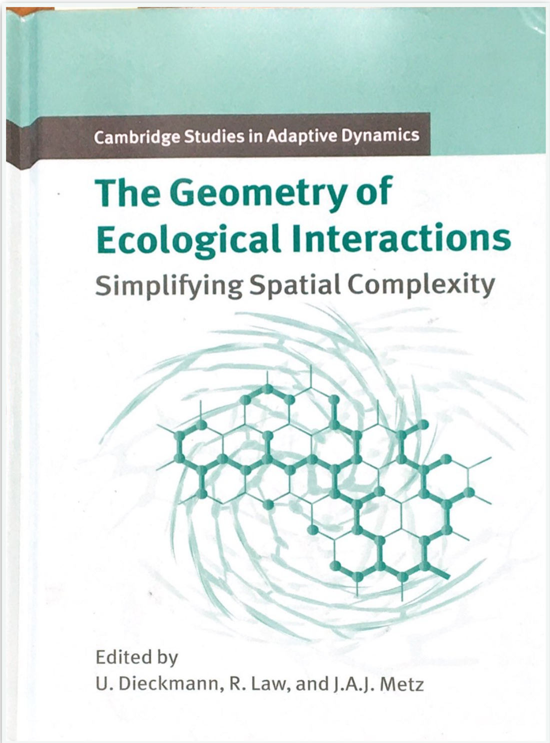
Quantification of a point pattern

- Definition of the moments (1st, 2nd, and 3rd, …)
- 1st moment is the number (density) of points
- 2nd moment is the density of pairs displaced with vector ξ
- 3rd moment is the density of triplets displaced with ξ and ξ'



The Method of Moments - How to derive the moment dynamics

- Bookkeeping an individual's fate (birth, death, and movement) naturally leads to the moment dynamics



The Geometry of Ecological Interactions
Eds. Dieckmann, Law, Metz
Cambridge University Press 2000
Chapter 14, 21

Dynamics of the pair density C(ξ)

How is C(ξ) generated and lost?

$$\frac{d}{dt}C(\xi) = + b \times m^{(b)}(-\xi)N$$
$$+ b \int m^{(b)}(\xi')C(\xi'+\xi)d\xi'$$
$$- b' \times m^{(b)}(\xi) \int w(\xi'')C(\xi'')d\xi''$$
$$- b' \int m^{(b)}(\xi+\xi'')w(\xi'')C(\xi'')d\xi''$$
$$- b' \iint m^{(b)}(\xi')w(\xi'')T(\xi'',\xi'-\xi)d\xi''d\xi'$$

birth

$$- d \times C(\xi)$$
$$- d' \times w(\xi)C(\xi)$$
$$- d' \int w(\xi')T(\xi,\xi')d\xi'$$

death

$$- \int m(x')dx' C(\xi)$$
$$+ \int m(-\xi')C(\xi+\xi')d\xi'$$

movement

$$+ \langle \xi \to -\xi \rangle$$

Simplified dynamics of the moments

Simple birth and death, no density dependency (b_1 = d_1 = 0)

$$\frac{d}{dt}N = (b-d)N$$

$$\begin{aligned}\frac{d}{dt}C(\xi) = &+ b \times m^{(b)}(-\xi)N \\ &+ b\int m^{(b)}(\xi')C(\xi'+\xi)d\xi' \\ &- d \times C(\xi) \\ &- \int m(x')dx'C(\xi) \\ &+ \int m(-\xi')C(\xi+\xi')d\xi' \\ &+ \langle \xi \to -\xi \rangle\end{aligned}$$

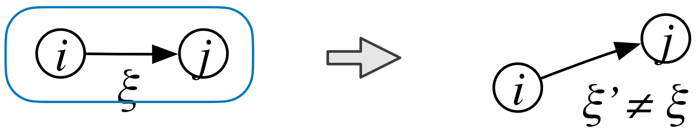
Simplified dynamics of the moments

No birth and no death (b = d = 0)

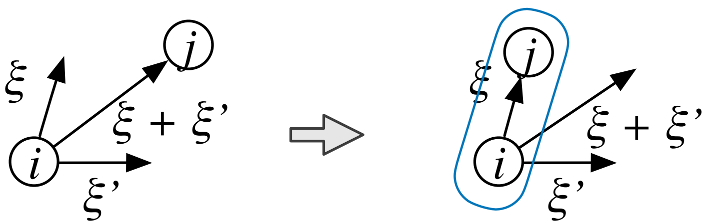
$$N = \mathrm{const.}$$

$$\frac{d}{dt}C(\xi) = -\int m(x')dx'C(\xi) + \int m(-\xi')C(\xi+\xi')d\xi' + \langle \xi \to -\xi \rangle$$

i)



j)

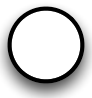


$m(\xi)$: Movement kernel

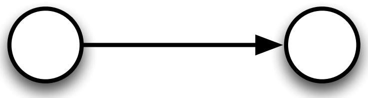
Each points jump-moves with $m(\xi)$ ~ Random diffusion?

The method of moments allows us to derive dynamics of 1st and 2nd order structure

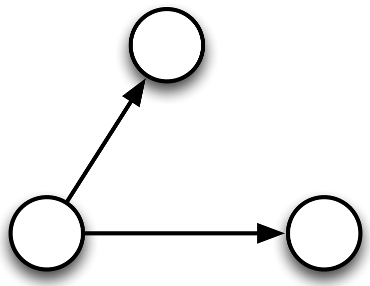
- 1st order (Number of points)
- 2nd order (Number of pairs displaced with a certain distance)
- 3rd order (Number of triplets with a certain configuration)



Number of points as a scalar



Number of pairs as a function of a vector



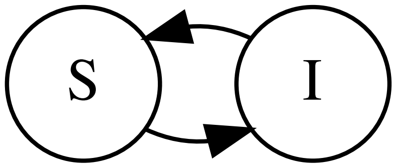
Number of triplets as a function of two vectors

Application to competition, predator-prey models, epidemic models, etc.

- ANY non-spatial population models as ODE can be readily extended to point pattern dynamics
  - Lotka-Volterra competition/predator-prey model
  - Expressions have been derived (Dieckmann and Law 2000)
- Epidemic dynamics SIS, SIR, SEIR, etc., where individuals' "status" change + birth, death, and movement
- With individuality explicitly considered, can we obtain novel insights that models without individuality fail to capture?

SIS point pattern dynamics with movements of points

- SIS point pattern dynamics on a static pattern (no birth and no death of points and points do not move) has been analyzed
  - Hamada and Takasu 2019, Le et al. 2023
- What happens if we allow points to give birth, die, and move?
- Using the method of moments, we derive dynamics of the 1st moment and the 2nd moment



SIS model

$$\frac{dS}{dt} = -\beta SI + \gamma I$$

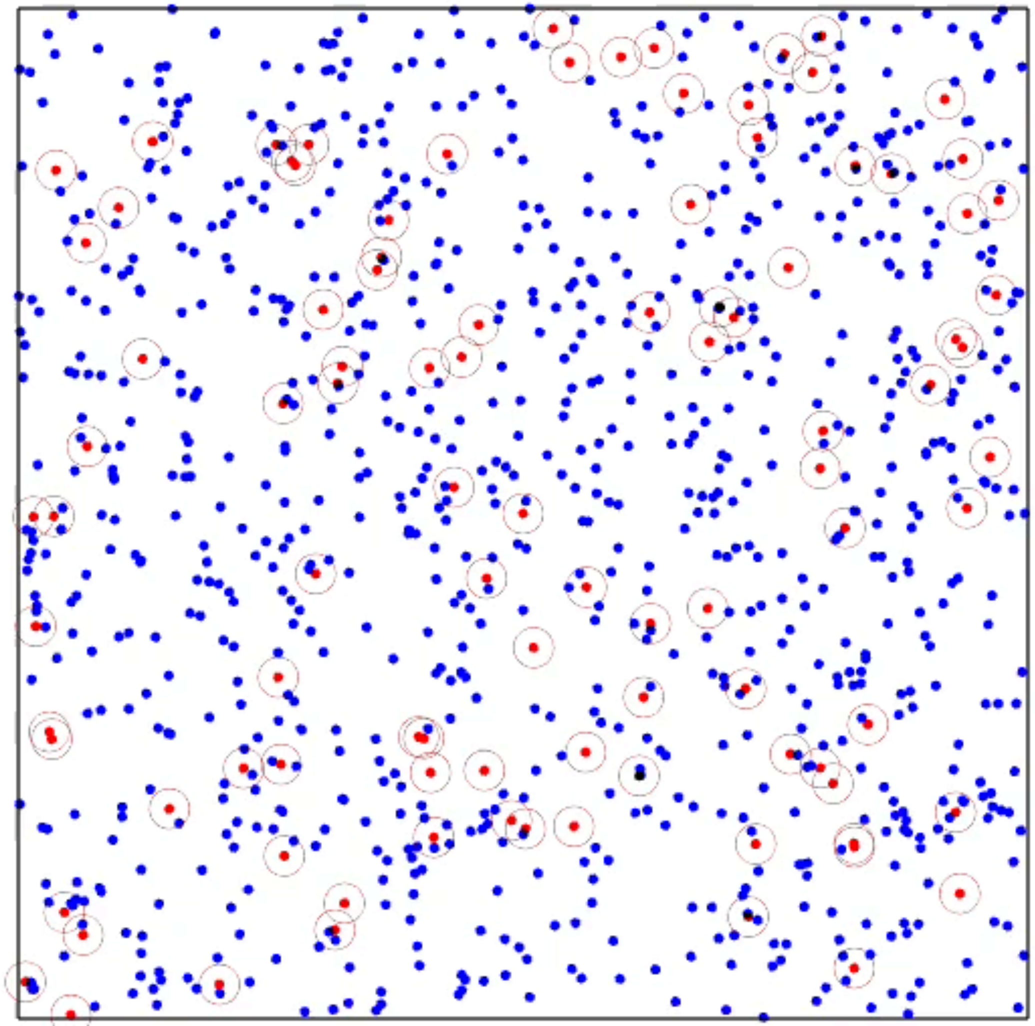
$$\frac{dI}{dt} = \beta SI - \gamma I$$

SIS point pattern dynamics with movements of points

- Each point is either Susceptible S or Infectious I
- Distance dependent infection rate $\beta(\xi)$ (S to I)
- Constant recovery rate γ (I to S)
- Points S and I jump-move with the movement kernel $m_S(\xi)$ and $m_I(\xi)$, respectively
- Simulation by Gillespie algorithm + Analysis using the method of moments

Status change + Move

Point pattern SIS model + Movement of points



Susceptible point 0 in blue, Infectious point 1 in red
Space L = 1, CELLS = 25, N = 1000
B0 = 0.01, SD_I = 0.01, GAMMA = 1, M_S = 1, L_S = 0.01, M_I = 0, L_I = 0.01
t = 0.00000000, popS = 900, popI = 100

SIS Point Pattern Dynamics
SIS (Infection + Recovery), Movement

Pop size 0 (blue) and 1 (red)
Updated with time interval 0.1

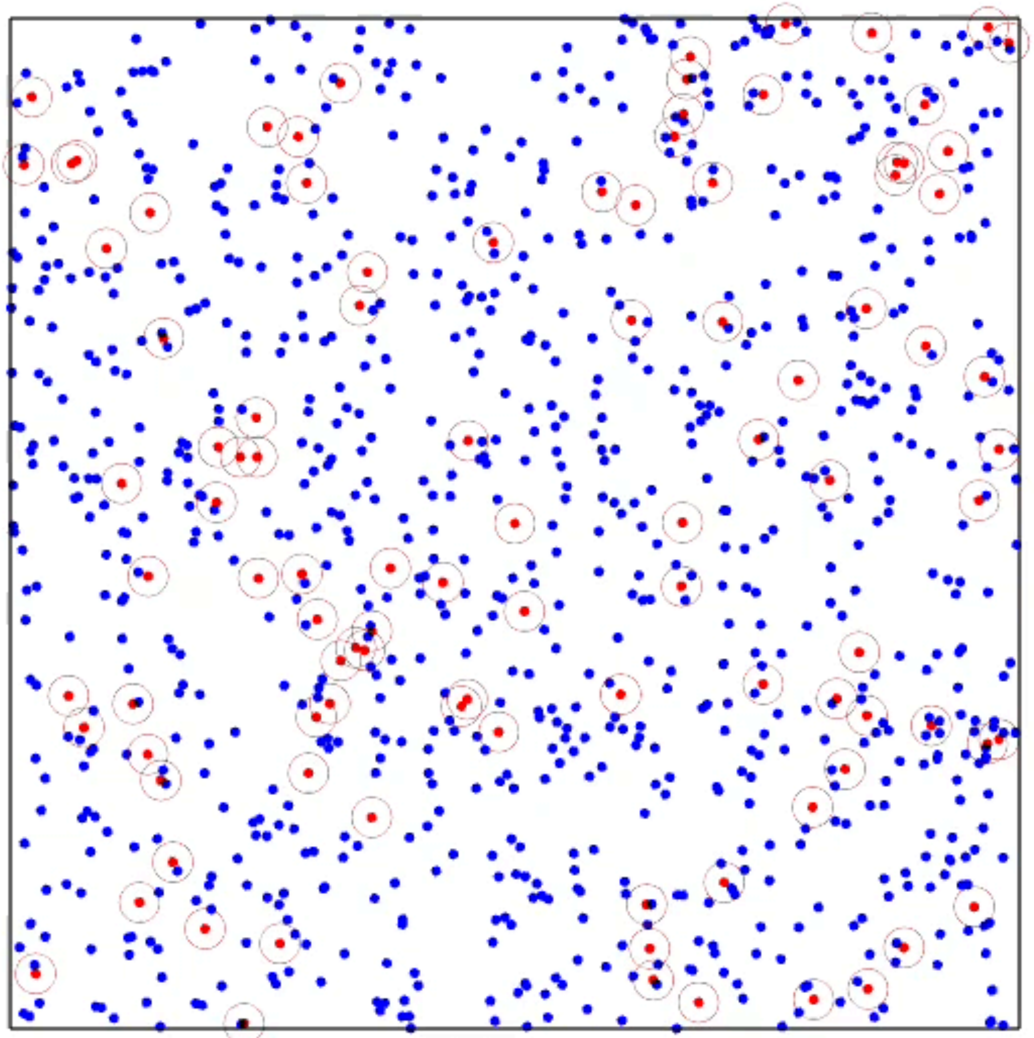
Infection inhibits movement

—> Overall PP becomes clustered

P.C.F.: 0-0 (blue), 0-1 (purple), 1-1 (red)
Updated with time interval 0.1

Status change + Move

Point pattern SIS model + Movement of points



Susceptible point 0 in blue, Infectious point 1 in red

Space L = 1, CELLS = 25, N = 1000

B0 = 0.01, SD_I = 0.01, GAMMA = 1, M_S = 0, L_S = 0.01, M_I = 1, L_I = 0.01

t = 0.00000000, popS = 900, popI = 100

SIS Point Pattern Dynamics

SIS (Infection + Recovery), Movement

Pop size 0 (blue) and 1 (red)

Updated with time interval 0.1

Infection promotes movement

—> PP converges to anti-clustered

P.C.F.: 0-0 (blue), 0-1 (purple), 1-1 (red)

Updated with time interval 0.1

Singlet dynamics

N_S, N_I: Singlet S and I density

$$\frac{d}{dt}N_S = -\int \beta(\xi)C_{SI}(\xi)d\xi + \gamma N_I$$
$$\frac{d}{dt}N_I = \int \beta(\xi)C_{SI}(\xi)d\xi - \gamma N_I$$

$\beta(\xi)$: Infection rate $\quad\quad$ γ: Recovery rate

$C_{SI}(\xi)$: Pair SI density

Pair dynamics

$C_{SS}(\xi), C_{SI}(\xi) = C_{IS}(-\xi), C_{II}(\xi)$: Pair SS, SI, IS, II density

$$\frac{d}{dt}C_{SS}(\xi) = -\int \beta(\xi')T_{SSI}(\xi,\xi')d\xi' - \int \beta(\xi')T_{SSI}(-\xi,\xi')d\xi'$$

$$\cdots$$

Pair dynamics

$C_{SS}(\xi), C_{SI}(\xi) = C_{IS}(-\xi), C_{II}(\xi)$: Pair SS, SI, IS, II density

$$\frac{d}{dt} C_{SI}(\xi) = -\int \beta(\xi') T_{SII}(\xi, \xi') d\xi' + \int \beta(\xi') T_{SSI}(-\xi, \xi') d\xi'$$

$$\cdots$$

Pair dynamics

$C_{SS}(\xi), C_{SI}(\xi) = C_{IS}(-\xi), C_{II}(\xi)$: Pair SS, SI, IS, II density

$$\frac{d}{dt} C_{IS}(\xi) = -\int \beta(\xi') T_{SII}(-\xi, \xi') d\xi' + \int \beta(\xi') T_{SSI}(\xi, \xi') d\xi'$$

$$\cdots$$

Pair dynamics

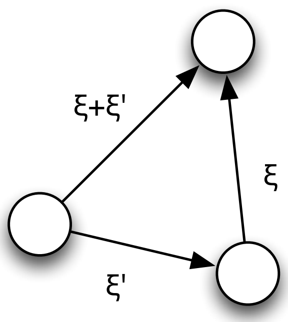
$C_{SS}(\xi), C_{SI}(\xi) = C_{IS}(-\xi), C_{II}(\xi)$: Pair SS, SI, IS, II density

$$\frac{d}{dt}C_{II}(\xi) = \int \beta(\xi')T_{SII}(\xi, \xi')d\xi' + \int \beta(\xi')T_{SII}(-\xi, \xi')d\xi'$$

$$\cdots$$

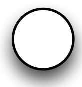
Moment closure

- Density of triplets has to be approximated using the singlet and the pair densities for the moment dynamics to be closed
- How triplet density can be approximated remains an open question
- Several candidates are proposed and evaluated which better explain simulations (Law and Dieckmann 2000, Law et al. 2003)

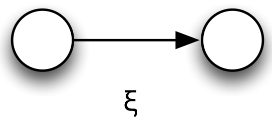


$$T(\xi, \xi') \approx \frac{C(\xi)C(\xi')}{N}$$

N



$C(\xi)$



Equilibrium

- Following Hamada and Takasu 2019, equilibrium pair densities can be analytically derived with a moment closure and some approximation
- Can the derived equilibrium pair densities explain simulation results? - Overall point pattern converges to
  - CSR when $|m_S| = |m_I|$
  - Clustered when $|m_S| > |m_I|$
  - Anti-clustered when $|m_S| < |m_I|$

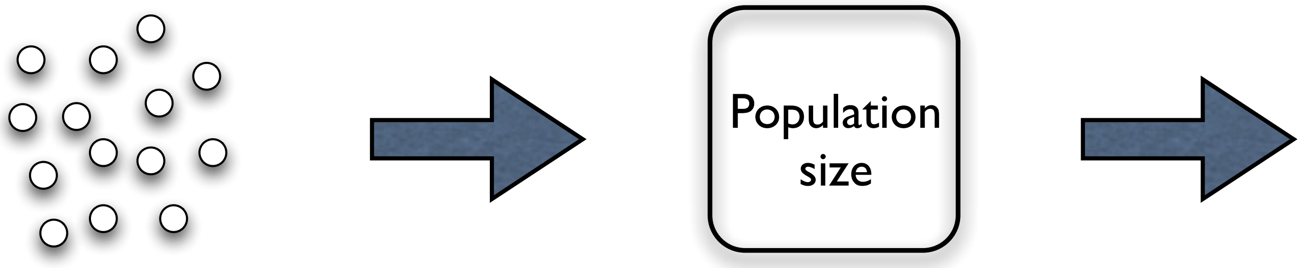
How can we understand the world?

- A big challenge to revisit "equation-based" population dynamics models in terms of "individual-based"

Individual-level

Population-level

Derivation of analytical models to fully understand the dynamics



$$\frac{dn}{dt} = f(n)n$$

$$\frac{\partial n}{\partial t} = \Delta n + f(n)$$

$$n_{t+1} = f(n_t)n_t$$

?

What type of individuals?
How many?
Where?
How do they interact?
IBM!

Observed population dynamics

Mathematical models based on simple assumptions for the sake of mathematics (not necessarily for biology)