

Modelling Population Growth

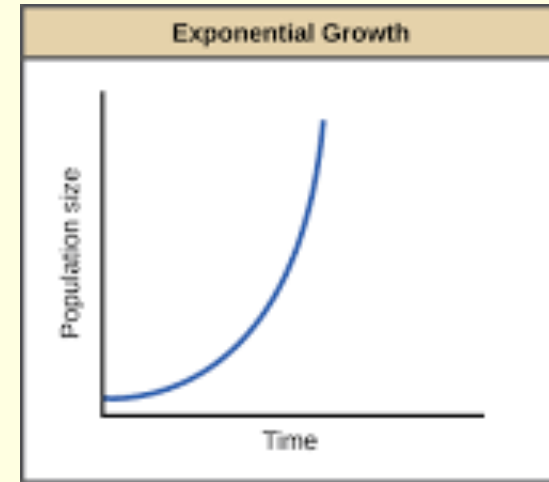
Population Growth in a 2D Spatial Model

Classical (non-spatial) models for population growth

■ Exponential Growth

Typically only for early growth phase

$$\frac{dX}{dt} = aX$$

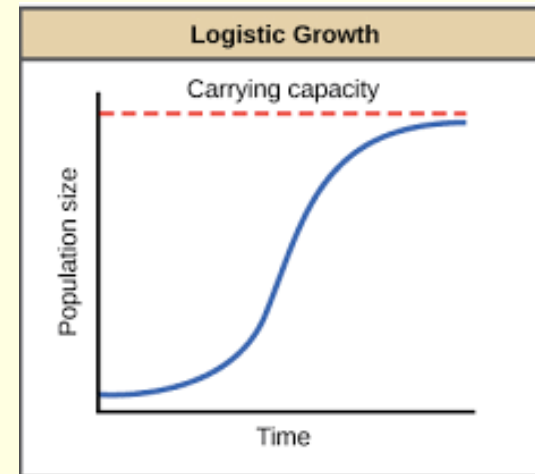


■ Logistic Growth

Providing full description until steady state

$$\frac{dX}{dt} = aX - bX^2$$

$$\frac{dX}{dt} = rX\left(1 - \frac{X}{K}\right)$$



Implementation of growth in a CA model

States:



individual

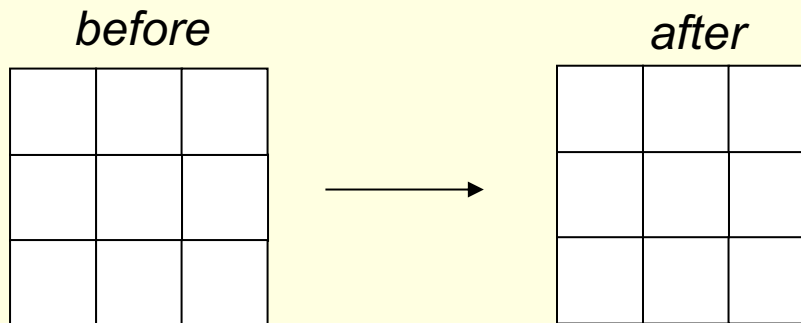


empty

Process: growth ; creating an offspring

Assignment: How could you implement growth of individuals in the model?

Schematic drawing for one cell and its surroundings:



CA model for Population Growth

States:

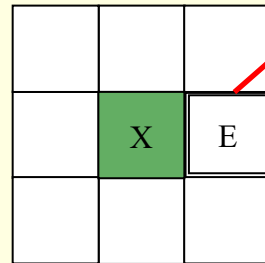


individual



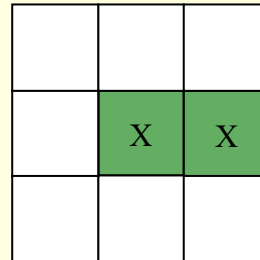
empty

growth:



Select a random neighbour,
and check if the cell is empty

r



r specifies the probability for a birth event ($0 \leq r \leq 1$)

The problem with this implementation is that another full cell might choose the same empty cell for creating an offspring.

Instead, you should make the cell which undergoes the state change the focal cell, so define the process from the empty cell that will be occupied.

CA model for Population Growth

States:



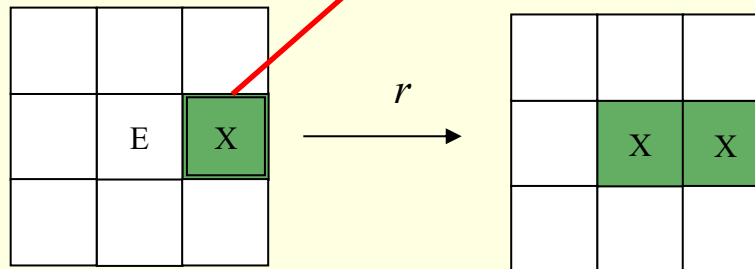
individual



empty

growth:

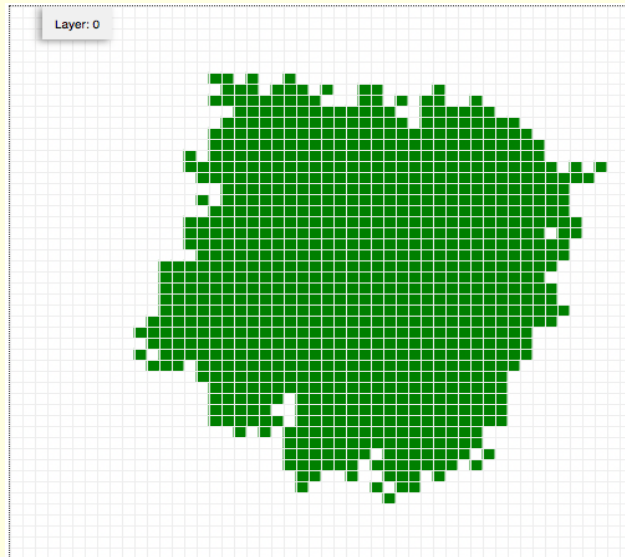
Select a random neighbour, and
check if the cell has an individual



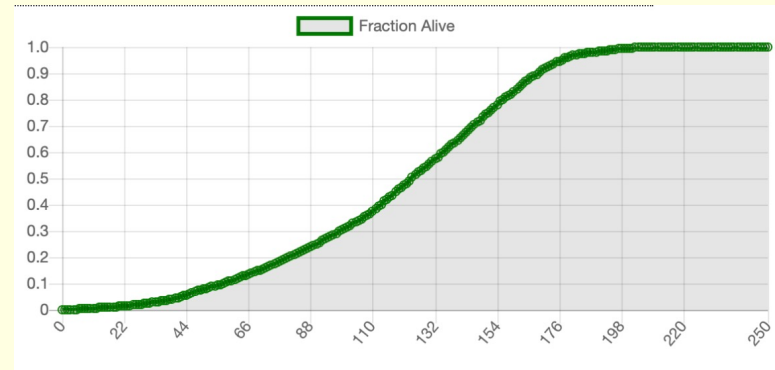
r specifies the probability for a birth event ($0 \leq r \leq 1$)

Note that choosing a random neighbor is mathematically equivalent to using the local density of X. E.g. if 6 out of 8 neighbor cells are occupied, the probability of creating an offspring in the central cell is $6/8 * r$

Run the model for approximately 100 time steps, starting from 2x2 individuals in the middle of the field. Describe the pattern that you observe.



fraction X



Time steps

The population grows in an approximately circular shape (a “clump”; resembling e.g. a bacterial colony). In the middle of the pattern the density already reached steady state, that is, 100% coverage.

Comparing with “Mean Field”

An important question to answer is whether the dynamics of the spatial model differs from the so-called “mean field” model.

In the “mean field” situation, we assume that everything is completely mixed, that is, the probability that individuals are interacting is directly proportional to their density. Note that this is the default assumption in e.g. chemical reaction equations, or more general in ODE’s (ordinary differential equation models)

Question: how could we simulate mean field in our CA model?

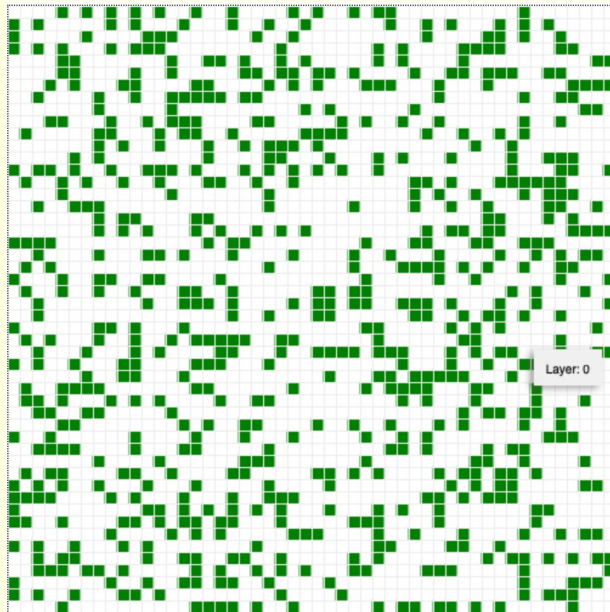
Simulating Mean Field

Solution 1:

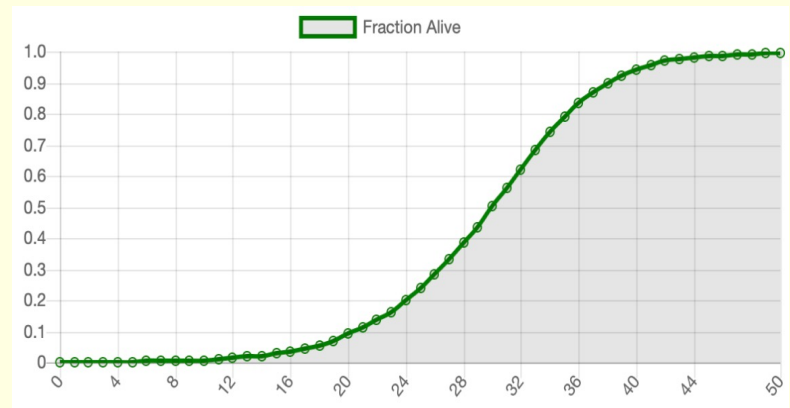
Randomize the field after each time step (quick & dirty)

Solution 2:

Instead of looking at the 8 direct neighbours for the next state function, you look at 8 random cells in the CA



fraction X



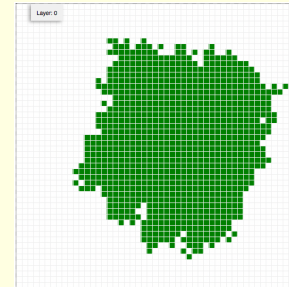
Time steps

Comparing Spatial and Mean-Field

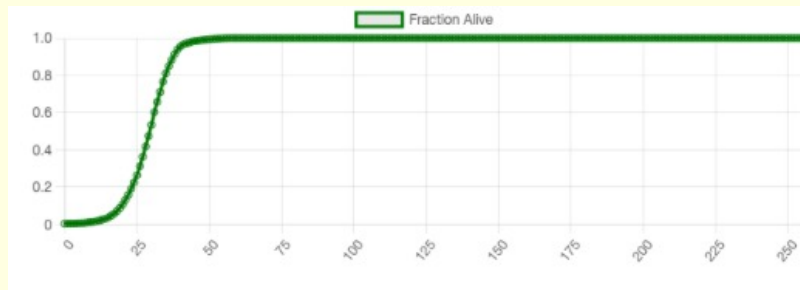
Spatial model:



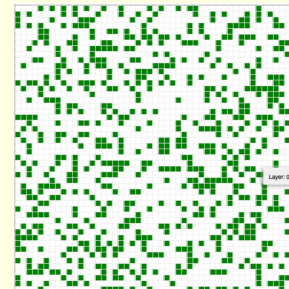
-> timesteps



Mean-Field model:



-> timesteps



Pattern Formation

In the spatial model the population growth rate is severely slowed down compared to the mean field model. This is caused by the clumping of individuals, even at very low global density. Effectively, in the spatial model, the population only expands at the boundary of the growing circular clump.

Note that in the spatial model the time to reach equilibrium depends linearly on the field size, whereas in the mean field situation it only depends on the initial occupied fraction of cells. In the spatial model, the population growth is so to speak limited by the “light speed”, that is, it can only increase by one neighbourhood size within each time step.

The effect of pattern formation

Apparently, pattern formation can have a large effect on the dynamics of a system.

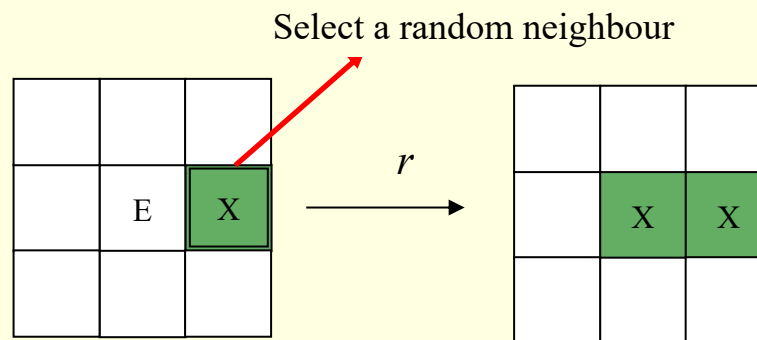
In this example, the patterns only occur in the transient dynamics, but not in the final attractor of the system.

However, for most spatial models the patterns (and their effects on the dynamics) also remain in the attractor of the system

Deriving the mean field equation

We are going to attempt to write down an equation for the expected change in the number of individuals within one time step, that is ΔX_t , where X is the number of individuals and K is the total number of cells in the CA.

growth:



r specifies the probability for a birth event ($0 \leq r \leq 1$)

Deriving the mean field equation

We are going to attempt to write down an equation for the expected change in the number of individuals within one time step, that is ΔX_t , where X is the number of individuals and K is the total number of cells in the CA.

Expected $\Delta X_t = +growth$

$growth = (\# \text{ empty cells}) \cdot (\text{probability of } X \text{ neighbour}) \cdot r$

$$E_t \quad \frac{X_t}{K}$$

$$\Delta X_t = E_t \cdot \frac{X_t}{K} \cdot r \quad \text{Substitute } E_t = K - X_t$$

$$\Delta X_t = (K - X_t) \cdot \frac{X_t}{K} \cdot r = rX_t \left(1 - \frac{X_t}{K}\right) \quad \text{This is logistic growth !}$$

Quantifying the patterns

A first order description of the patterns is to quantify the so-called pairwise correlations, that is to count all neighbouring pairs of cells and determine whether they are of type {XX}, {EE}, or {EX}

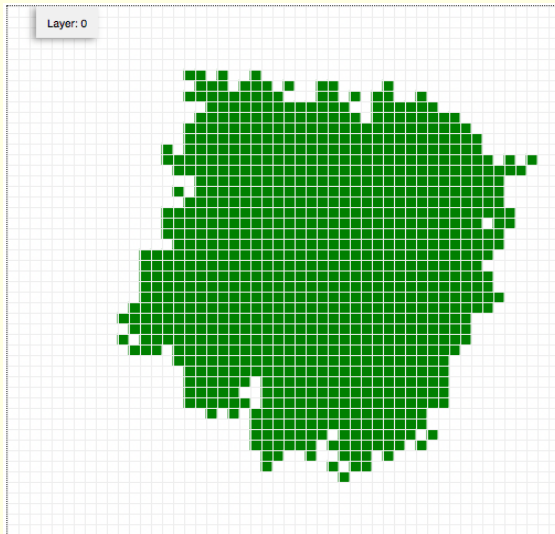
In the mean field model, the expected proportions for these pairs are :

$$\{XX\} = x^2, \{EE\} = (1 - x)^2, \text{ and } \{EX\} = 2x(1 - x)$$

using $x = \frac{X}{K}$ as the fraction of occupied cells

You could compare the observed and expected value for each of the three pairs, and use this in a χ^2 (chi-squared) statistical test to prove that the observed pattern is significantly different from random (but this is typically already obvious from looking at the pattern).

Pairwise correlations



The strongest correlation in the clumpy growth pattern is in the $\{XX\}$ pairs, which in the early growth phase can be up to 50 times more prevalent than expected from the densities (i.c. the mean field).

However, the most relevant correlation is between the $\{EX\}$ pairs, as this correlation is relevant for the growth process. In the above figure the observed $\{EX\}$ pairs are a factor 0.3 lower than expected from mean field, which means that we can accurately predict the next state density of the spatial model in the current time step as

$$\Delta X_t = 0.3 r E_t \frac{X_t}{K}$$

This correction factor however changes during the simulation.

Extending the model

How could you add a **death process** to the model?

States:



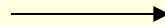
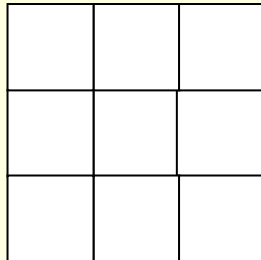
individual



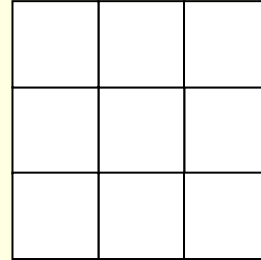
empty

death:

before



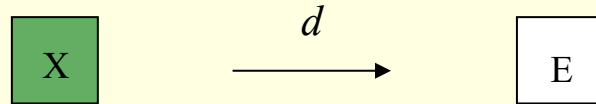
after



Note: think about density dependence of the death process, that is, does the probability that an individual die depend on the (local) density or is probability independent of density.

Adding death of individuals (1)

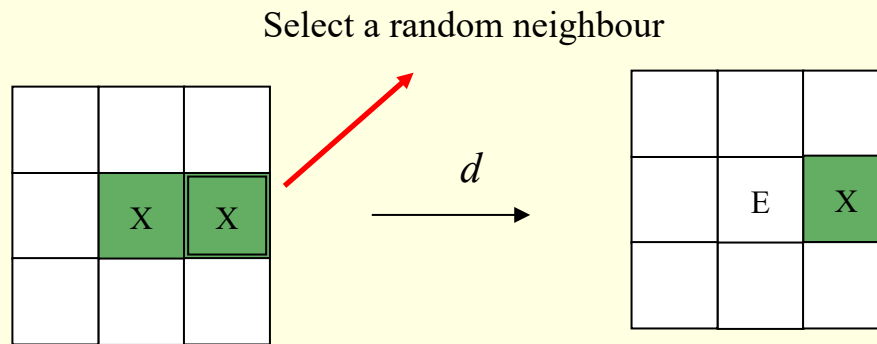
Density independent death:



d specifies the probability for a death event ($0 \leq d \leq 1$)

Adding death of individuals (2)

Density dependent death:



d specifies the probability for a death event ($0 \leq d \leq 1$)