Spatial Ecology: Lecture 1, metapopulations

II Southern-Summer school on Mathematical Biology

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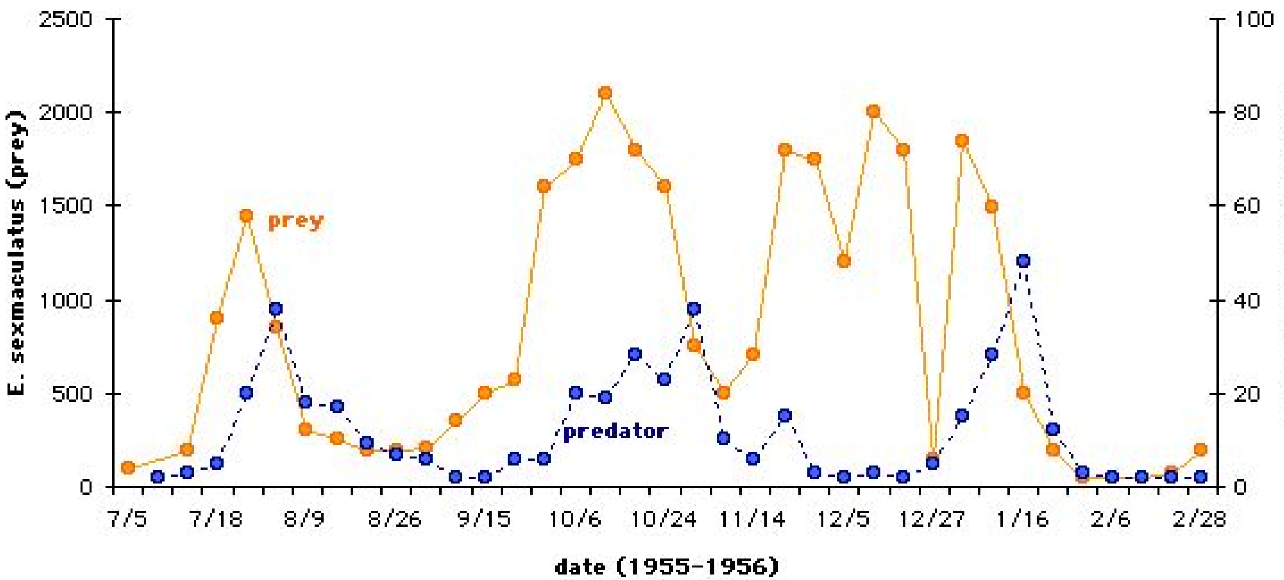
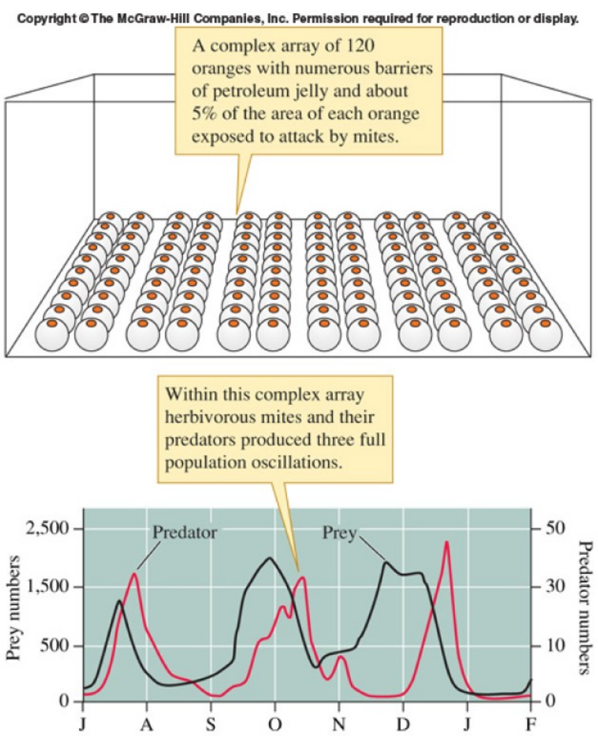
Overview

- Lecture 1: Metapopulations
- Lecture 2: Reaction-diffusion models: invasion and persistence
- Lecture 3: Reaction-diffusion models: spatial patterns
- Lecture 4: Integrodifference equations

Why include space?

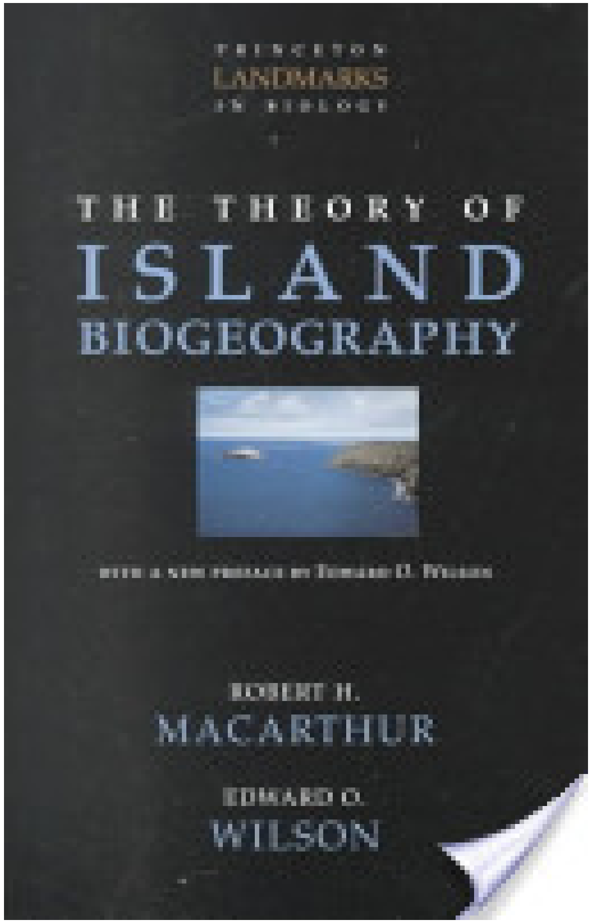
- Both the theory and experiments can be difficult, but…….
- **Huffaker (1958)** spatial heterogeneity allowed persistence





Why include space?

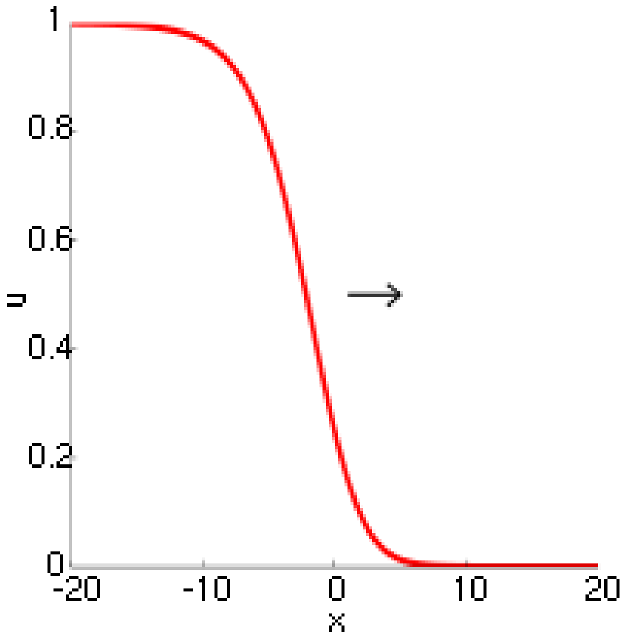
- **Mac Arthur- Wilson (1967)** Theory of island biogeography



- Human expansion was leading to fragmentation, resulting in species extinction.
- The spatial patterning of fragments is important for patterns of diversity

Why include space?

- **Skellam (1951)** Spread of novel organisms and genotypes into an environment



- Dispersal dynamics
- Effective population sizes
- Rate and spatial patterning of invasions

Why include space?

- **Hutchinson (1961) Paradox of the plankton**
- “Many more plankton species coexist in a supposedly homogeneous habitat than permitted under the competitive exclusion principal of Gause”

One explanation: Spatial refuges

Why include space?

- **Turing (1952) Pattern formation** Random movement and population dynamics can give spatial variation in density in the absence of environmental heterogeneity (Segal & Jackson 1972)

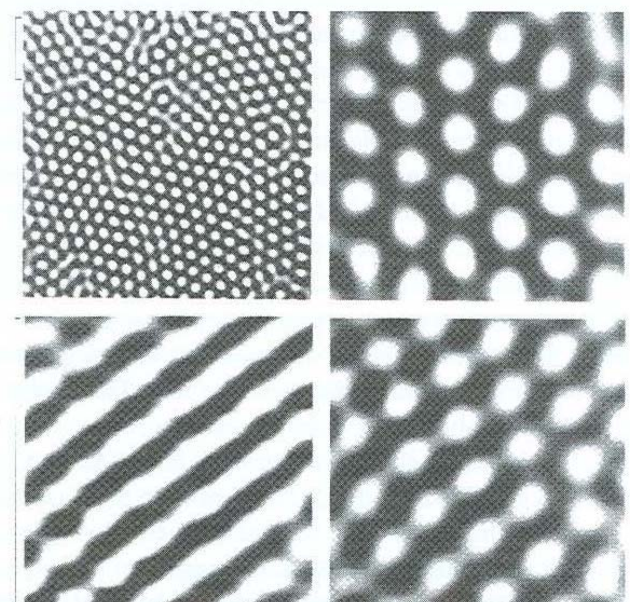
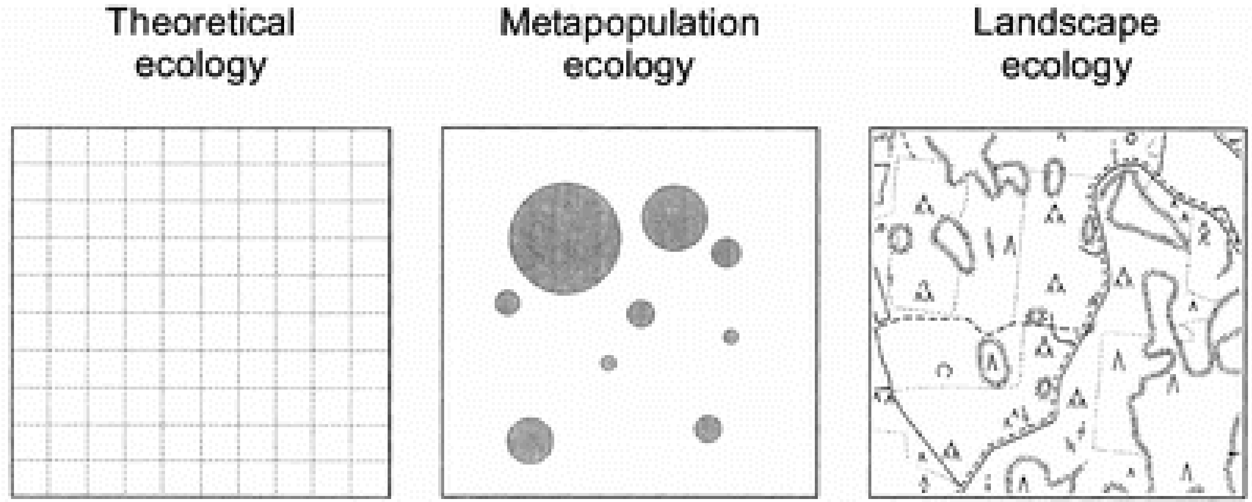


Figure 1 **Different types of Turing patterns in the chloride-iodide-malonic-acid (CIMA) chemical reaction.**
Reprinted with permission from Ouyang and Swinney, 1991.

Approaches to large-scale spatial ecology

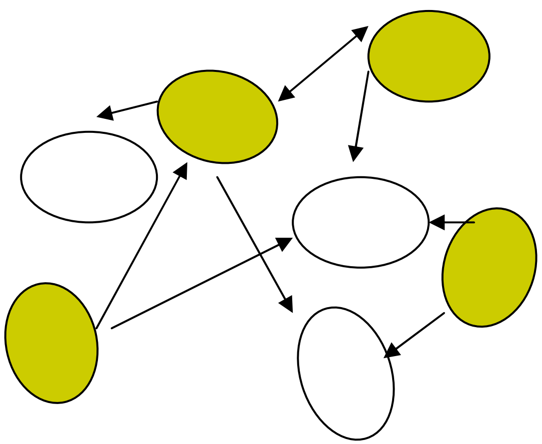


- Landscape ecologists: Describing complex structures of real landscapes. Study the movement of individuals and resources in them
- Theoretical ecologists: Generally assume homogeneous or discrete space. Focus, how population dynamic processes can generate complex dynamics and spatial patterns without landscape heterogeniety
- Metapopulation ecology: Idealised habitat patches. Species occur in local populations connected by migration. Focus, persistence

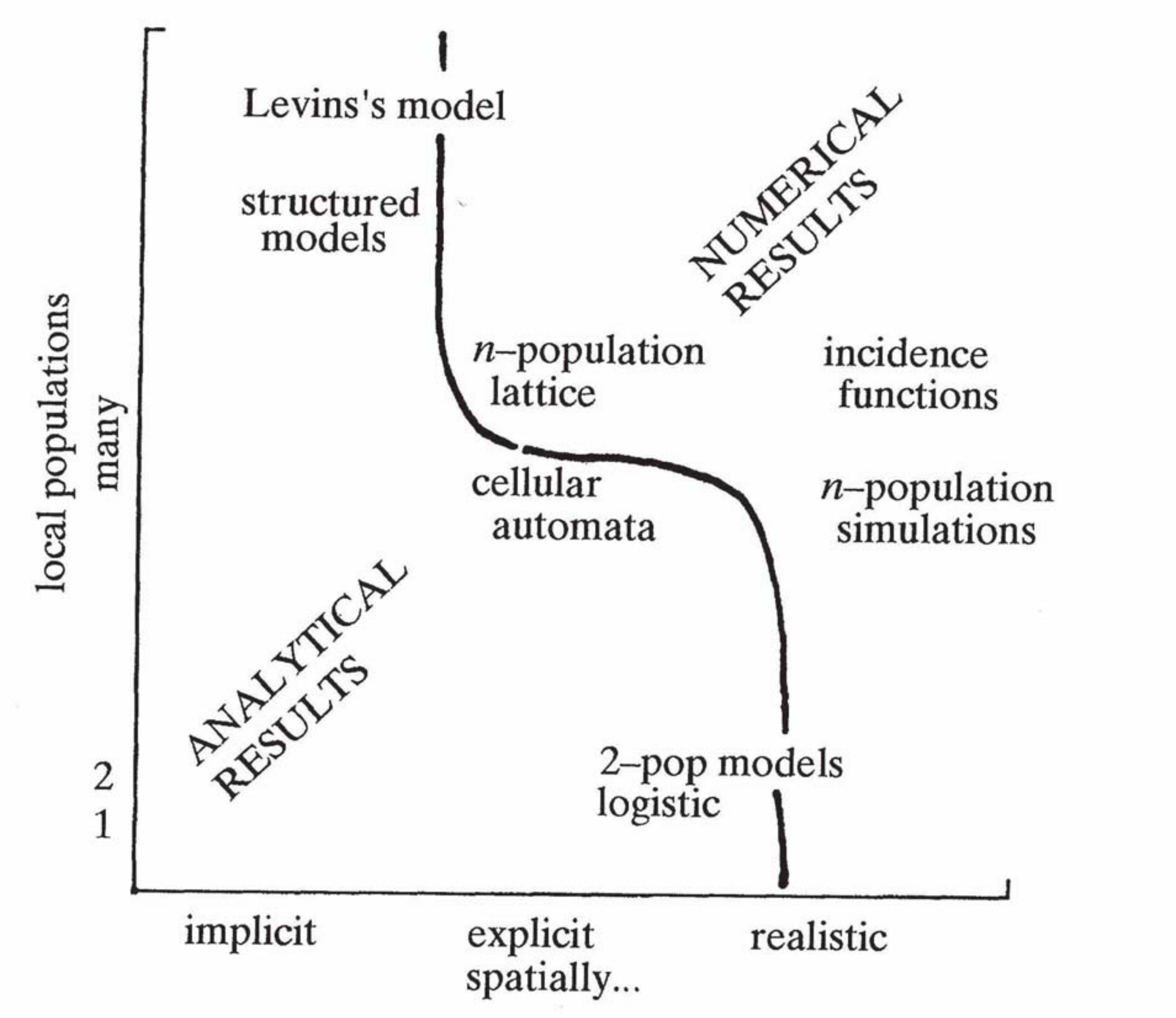
Metapopulation modelling

- ***Metapopulation*** is a population of unstable local populations, which can persists in a balance of local extinctions and colonisations*.*

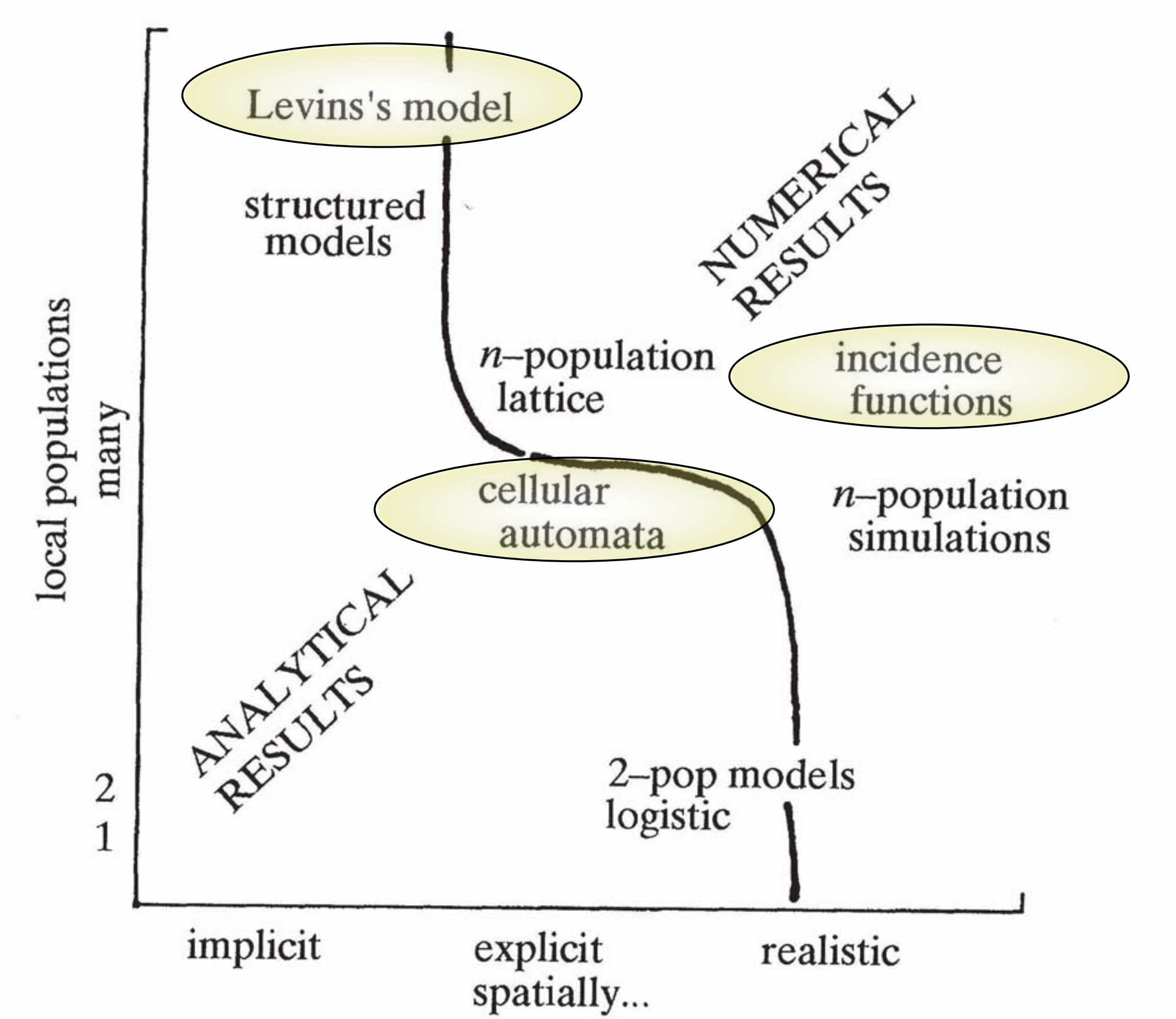
- **Basic assumptions:**
  - Habitat occurs in discrete patches (local populations)
  - Local population extinction is a recurrent event *(not rare)*
  - Patch dynamics are asynchronous



Types of metapopulation models



Types of metapopulation models



Levins' metapopulation model

- p=fraction of occupied patches

$$\frac{dp}{dt} = \underbrace{cp}_{\substack{\text{Rate of}\\\text{emigration}\\\text{depends on \#}\\\text{of occupied patch}}} \underbrace{(1-p)}_{\substack{\text{Colonisation of}\\\text{empty patch}}} - \underbrace{ep}_{\substack{\text{Extinction of a}\\\text{local popualtion}}}$$

  - c is large if patches are close
  - e is small if habitat patches are large

- **Assumptions:**
  - Infinite number of patches (>100 is fine)
  - Patches are the same size, and equally accessible
  - Timescale is on the scale of the colonisation and extinction, local dynamics are ignored.

Levins' metapopulation model

- p=fraction of occupied patches

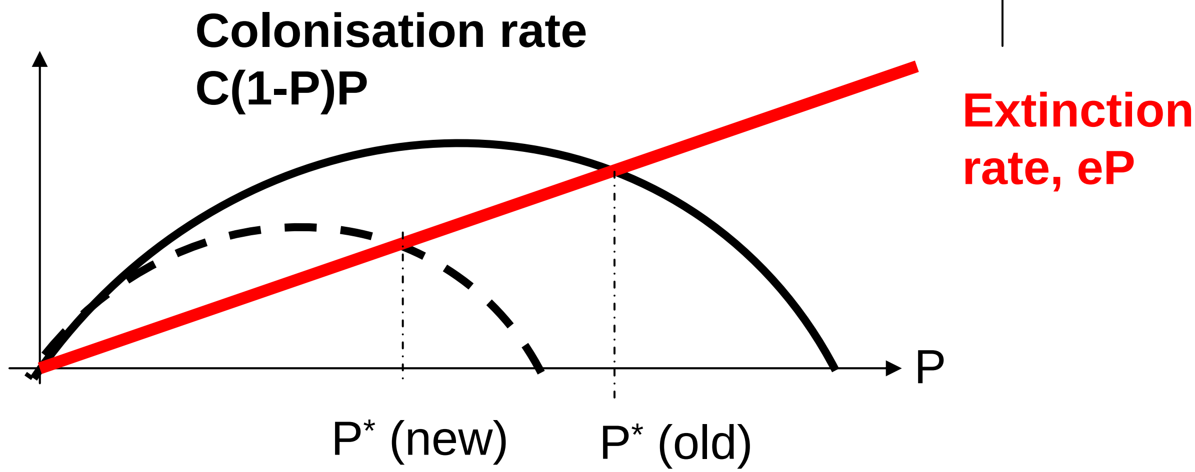
$$\frac{dp}{dt} = \underbrace{cp}_{\substack{\text{Rate of} \\ \text{emigration} \\ \text{depends on \#} \\ \text{of occupied patch}}} \underbrace{(1-p)}_{\substack{\text{Colonisation of} \\ \text{empty patch}}} - \underbrace{ep}_{\substack{\text{Extinction of a} \\ \text{local popualtion}}}$$

- Steady state: p^{*}=1-e/c
- Never get 100% occupation.
- If e/c >=1 there is extinction, extinction can happen before all the habitat has gone.

Patch destruction and shrinkage

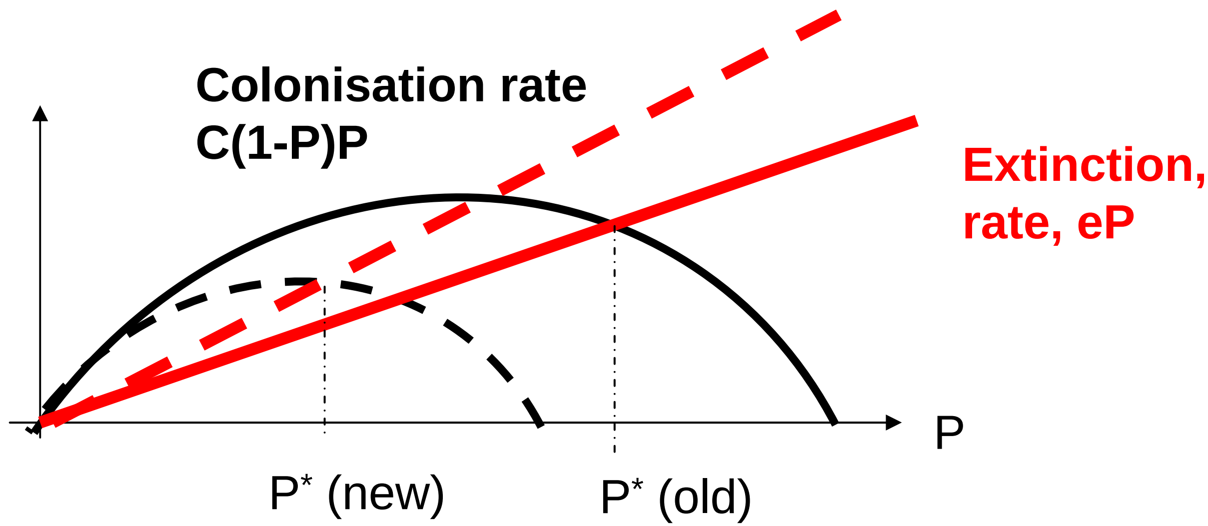
1. Removing patches reduces c.

Result, P^* decreases

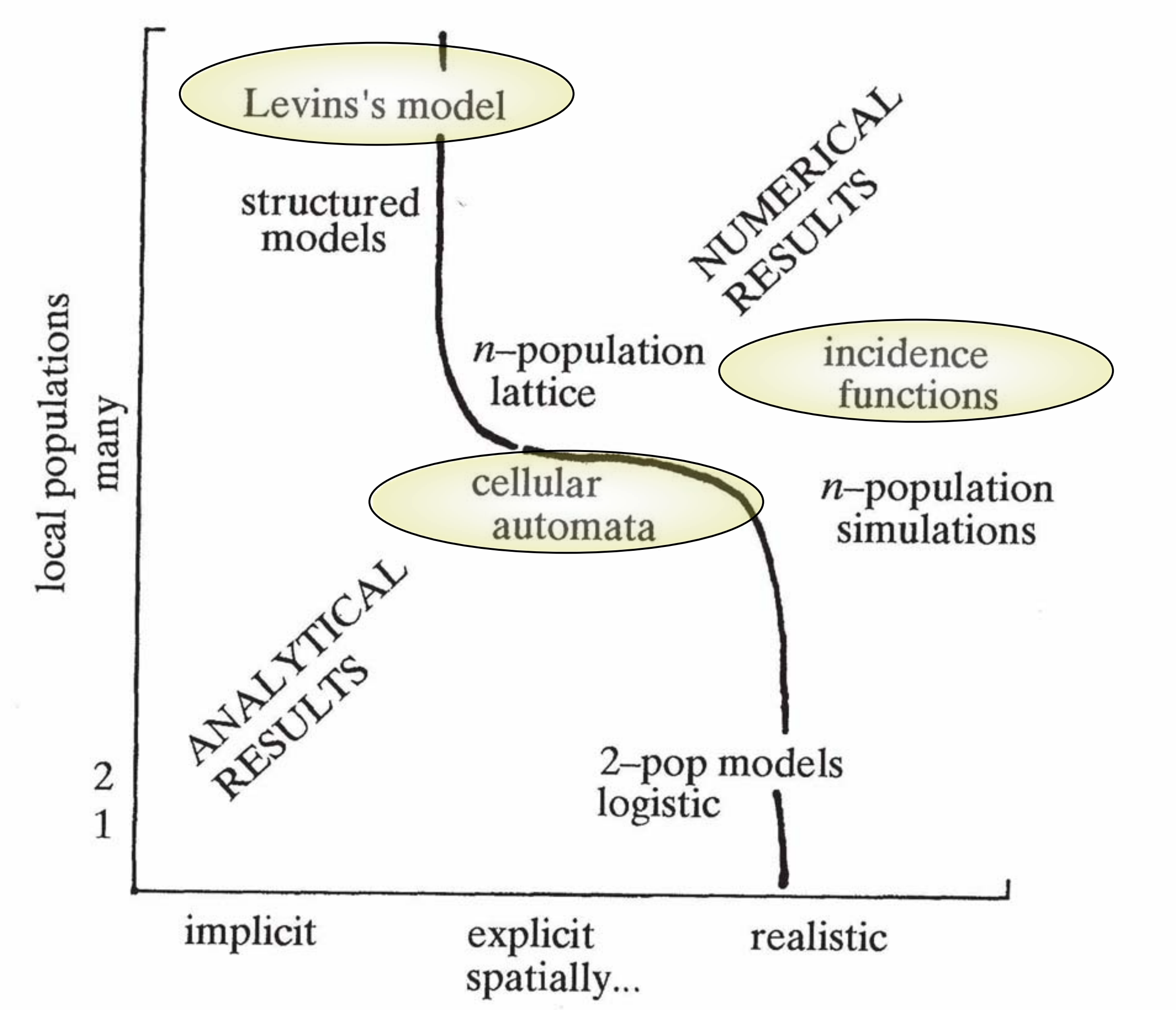


2. Reducing patch area reduces c and increases e

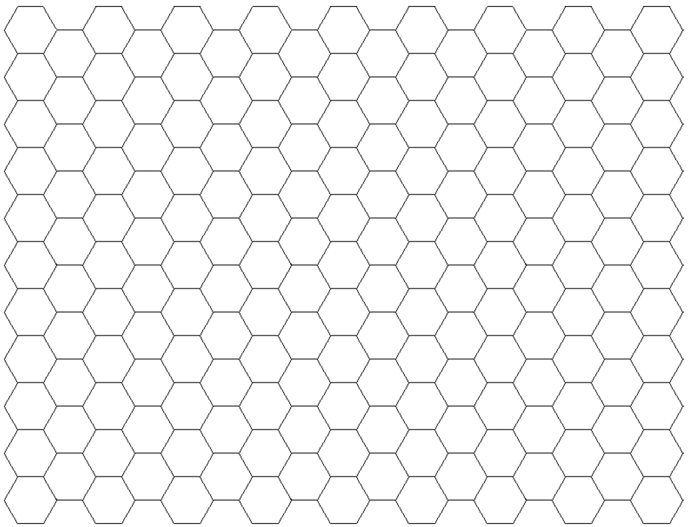
Result, P^* decreases

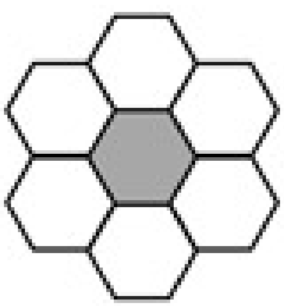


Types of metapopulation models: What about patch distance?



Cellular automata / individual based models:





6 neighbors,

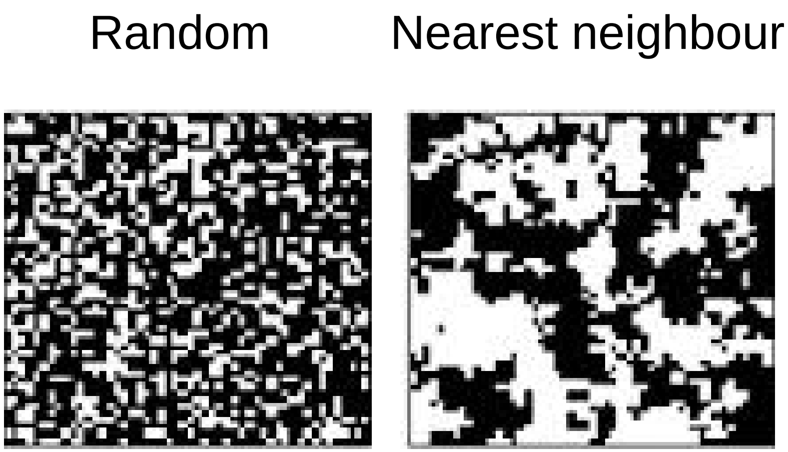
- c dt = prob an occupied site *colonises* and sends out a propagule
- e dt = prob a site goes *extinct*
- New propagules are sent to a neighbourhood of the parent cell (with 1-cell , 2-cells etc)
- Algorithm:
  1. Randomly pick a site. Generate a uniform random number x
  2. Occupied -> colonises

$$0 \le x \le \frac{c}{c+m}$$

  3. Occupied -> empty if

$$\frac{c}{c+m} \le x \le 1$$

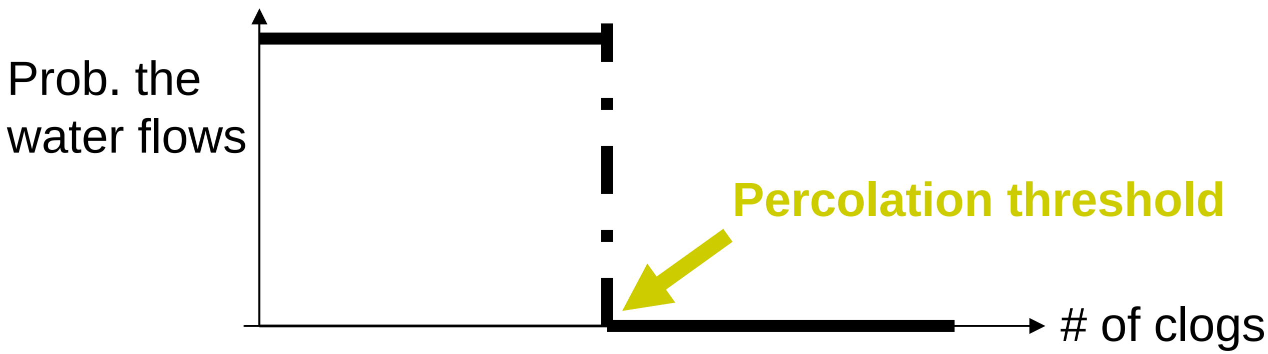
Cellular automata: dispersal range

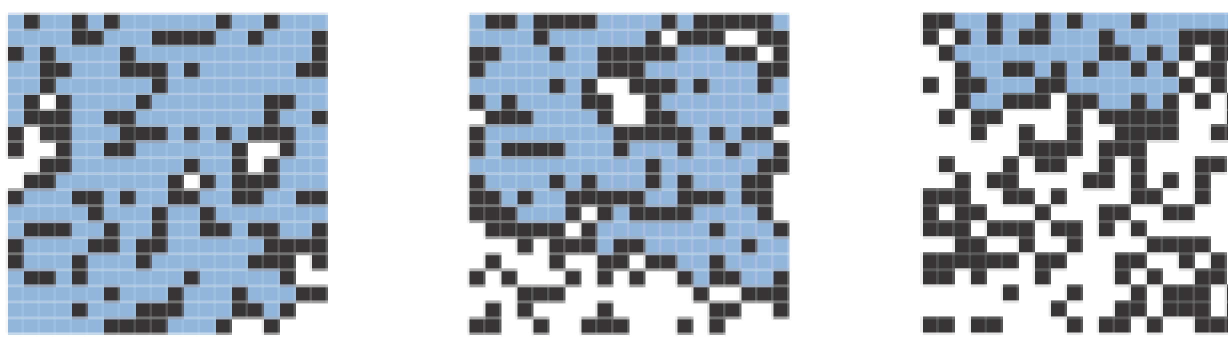


- Clumping in nature is not necessarily due to the environment
- Size of the neighbourhood effects equilibrium number of occupied sites
  - more likely to land on a neighbour is dispersal is local
  - Local dispersal -> Lower equilibrium density
  - Large dispersal -> Higher equilibrium density

A digression: Percolation

- Percolation: How flow responds to “clogs” (barriers) in the substrate.



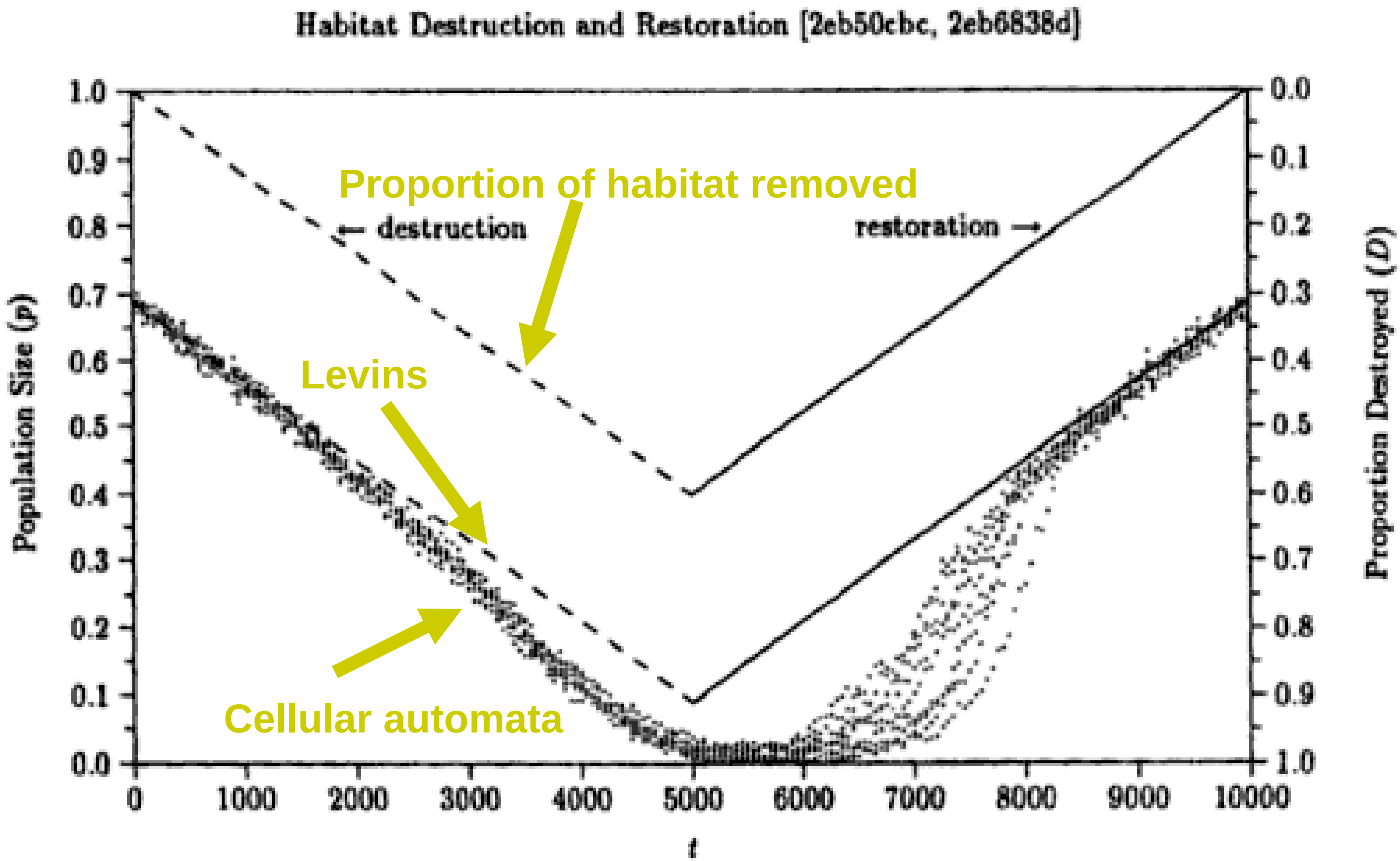


Percolation is less probable as the site vacancy probability decreases

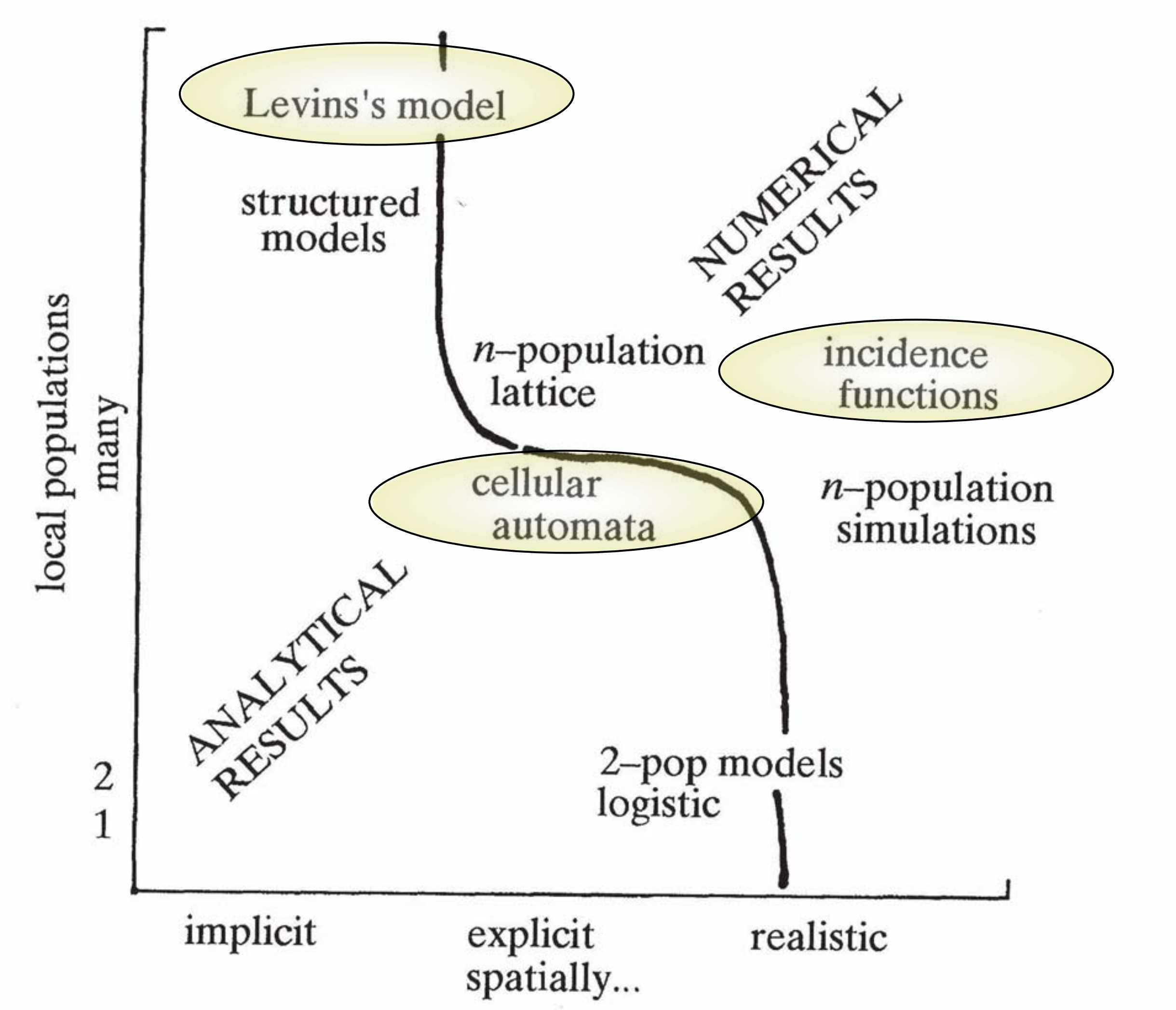
Effect of habitat destruction and restoration

- “flow” – dispersal and reproduction of the population
- “clogs” – destroyed habitat
- **Model:** Random destruction of habitat
  - Compare cellular automata model to levins’

Effects of habitat distruction and restoration: Hysteresis!

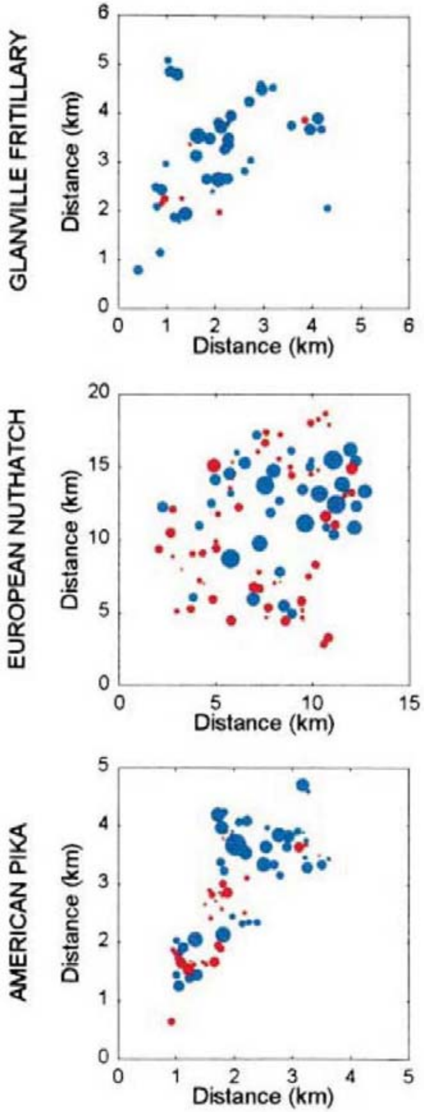


Types of metapopulation models: What about patch size and location?



Incidence Functions and data

- Objective: Understand patterns in patch occupancy data
- The following example focuses on: Patch area and patch isolation effects
- Question: How do changes in the network (e.g. remove 3 largest patches) effect occupancy patterns and metapopulation persistence?



Incidence function model (IFM)

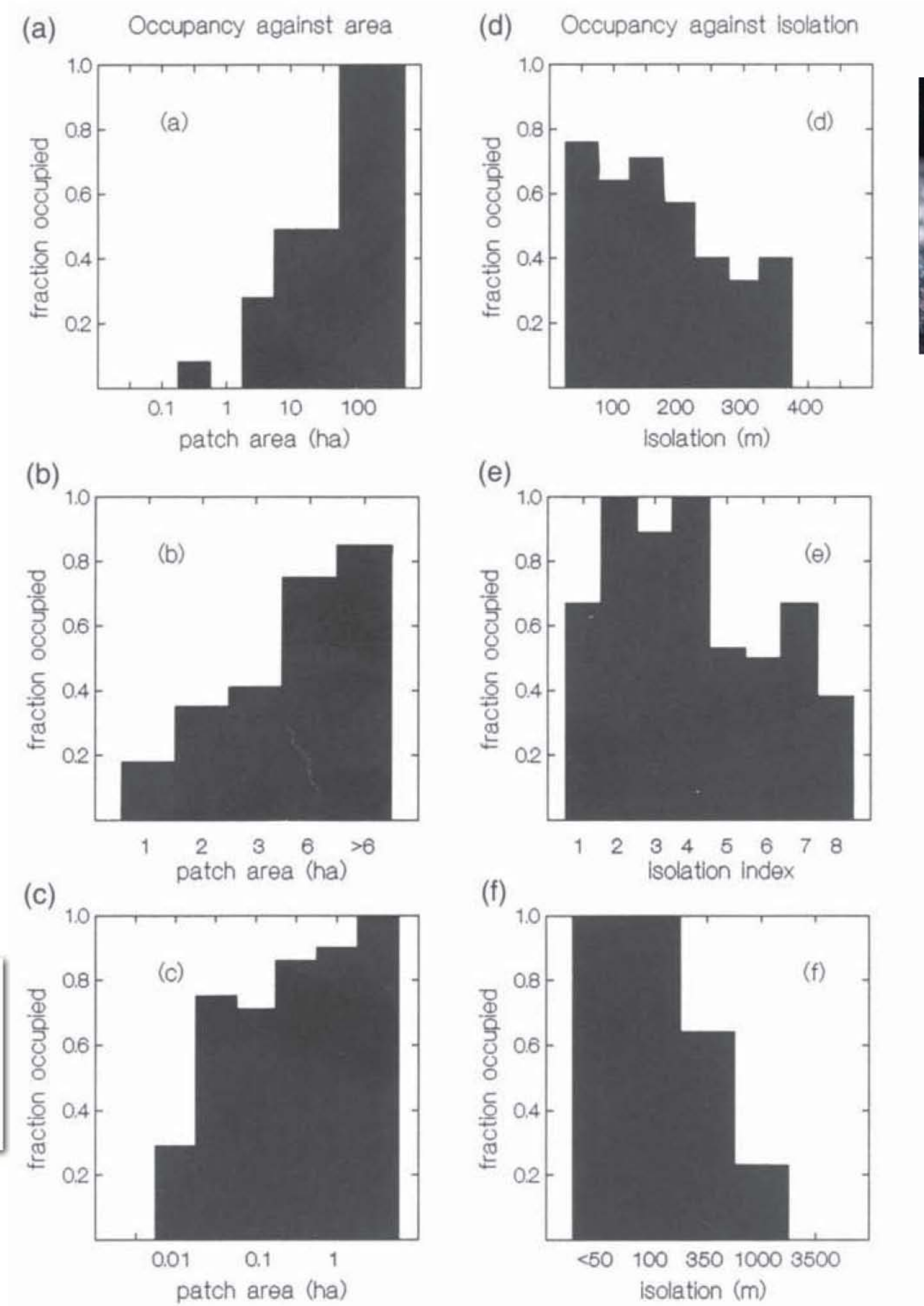
- ***Ilkka Hanski,*** leading expert on metapopulations, works at the interface between theory and data

- Model assumptions:
  - Finite number of patches
  - Patches can be of different sizes with unique spatial coordinates
  - Localised spatial interaction
  - Patches need to be large enough to support local breeding populations, BUT not too large that local extinction is rare

Incidence Function Models: Data

1. Experimentally determine habitat and non-habitat. *Caution: Not finding a species in a location does not mean is in non-habitat*
2. Locate patches on a spatial grid and obtain a snap shot of the occupancy data
3. Measure patch area and patch isolation to check if there is an effect on occupancy

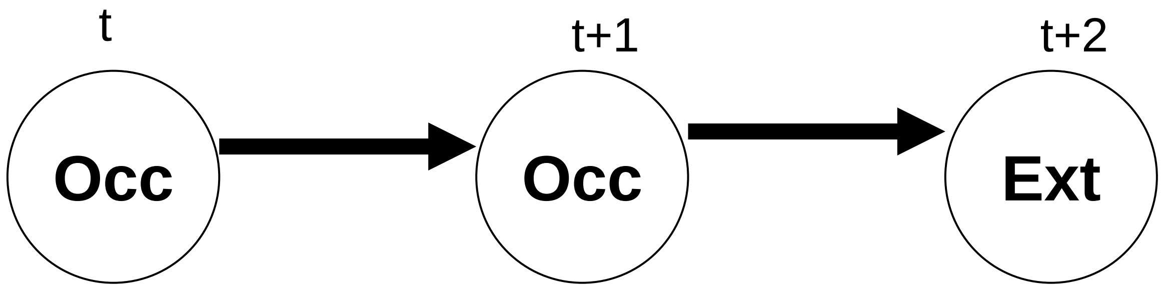
Caution: Choose isolation measure carefully, shortest distance to another patch ignores viscosity of the matrix



(a) Occupancy against area
(d) Occupancy against isolation
(a)
fraction occupied
1.0
0.8
0.6
0.4
0.2
0.1
1
10
100
patch area (ha)
(d)
fraction occupied
100
200
300
400
isolation (m)
(b)
fraction occupied
1
2
3
6
>6
patch area (ha)
(e)
fraction occupied
1
2
3
4
5
6
7
8
isolation index
(c)
fraction occupied
0.01
0.1
1
patch area (ha)
(f)
fraction occupied
<50
100
350
1000
3500
isolation (m)

Incidence function model: The Model!

- Markov chain model: Two states, **O**ccupied and **E**mpty is extended to a metapopulation of connect patches



- **Incidence function** (key to linking model to the data): *Long term* probability patch i is occupied

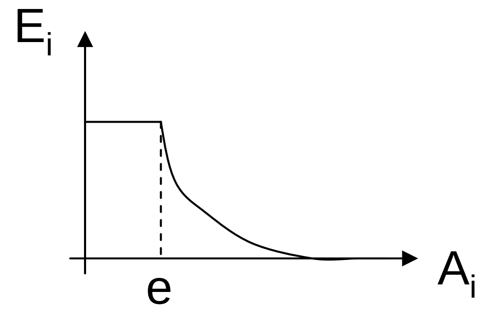
$$J_i = \frac{C_i}{C_i + E_i - \underbrace{E_i C_i}_{\substack{\text{rescue effect} \\ \text{occupation of extinct area}}}}$$

C_i probability of colonisation $\quad$ E_i is probability of extinction

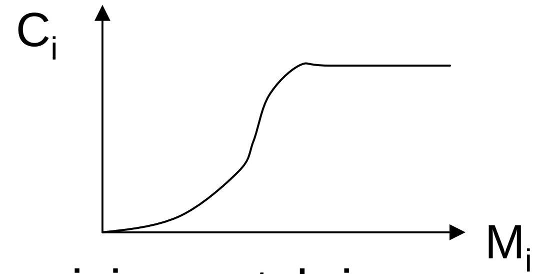
Relating E_i and C_i to the landscape

- A_i =area of patch i

$$E_i = \min\left(1, \frac{e}{A_i^x}\right)$$

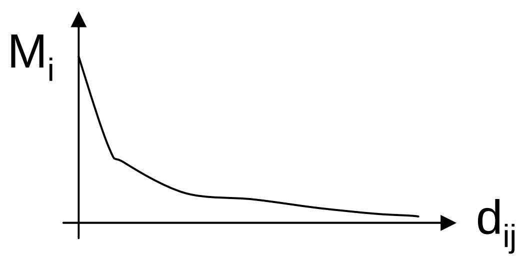


$$C_i = \frac{M_i^2}{y^2 + M_i^2}$$



- M_i =expected number of migrants arriving patch i

$$M_i = \beta S_i = \beta \sum_{j \neq i} p_j \exp\left(-\alpha d_{ij}\right) A_j$$



- p_j =0 if patch empty, 1 if patch occupied
- d_{ij}= distance from patch i to patch j

Incidence function and data

- Substitute all the expressions into J_i

$$J_i = \left(1 + \frac{ey'}{S_i^2 A_i^x}\right)^{-1} \qquad \text{where } y' = \left(\frac{y}{\beta}\right)^2$$

- Link from to model to field data: Using logistic regression or nonlinear least squares

$$\ln\left(\frac{J_i}{1 - J_i}\right) = -\ln(ey') + 2\ln(S_i) + x\ln(A_i)$$

- A_i, S_i and J_i are from the data for each patch. We estimate the constants e, y' and x (common parameters for all the patches)

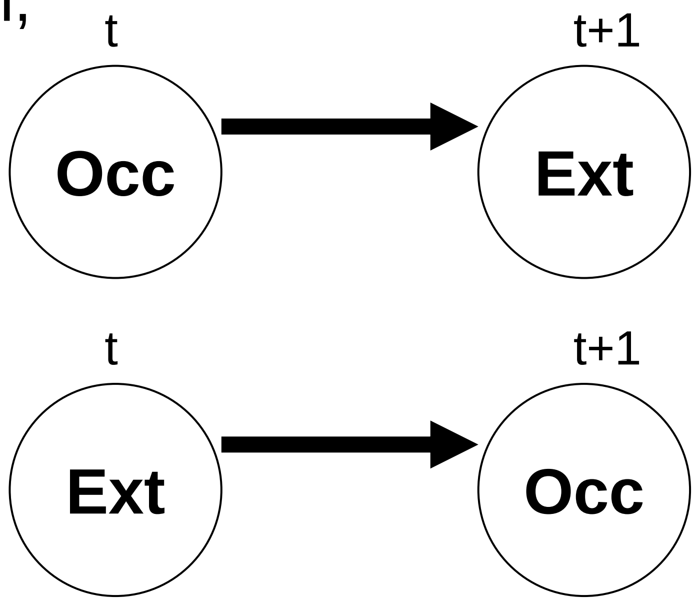
Assumptions and difficulties

- **Assumes M_i (Migrant to patch i) is constant, at steady state**
  - Numerics say this assumption is fine and generally holds
- **Assumes the data is at a stochastic steady state**, so if the size of the metapopulation (number of local populations) shows a long term increasing or decreasing trend, this approach will not work.
  - Stochastic steady state is difficult to test for.
- **e and y' cannot be estimated independently**.
  - So we need to find e independently, we can estimate the patch area A_0 such that

    $E = e (A_0)^{-x} = 1$ **(Critical patch size)**

Iterate the model

- We now know all the parameters, so we know the colonisation and extinction probability for each patch.
- Randomly choose a patch i, let X be a random variable then,



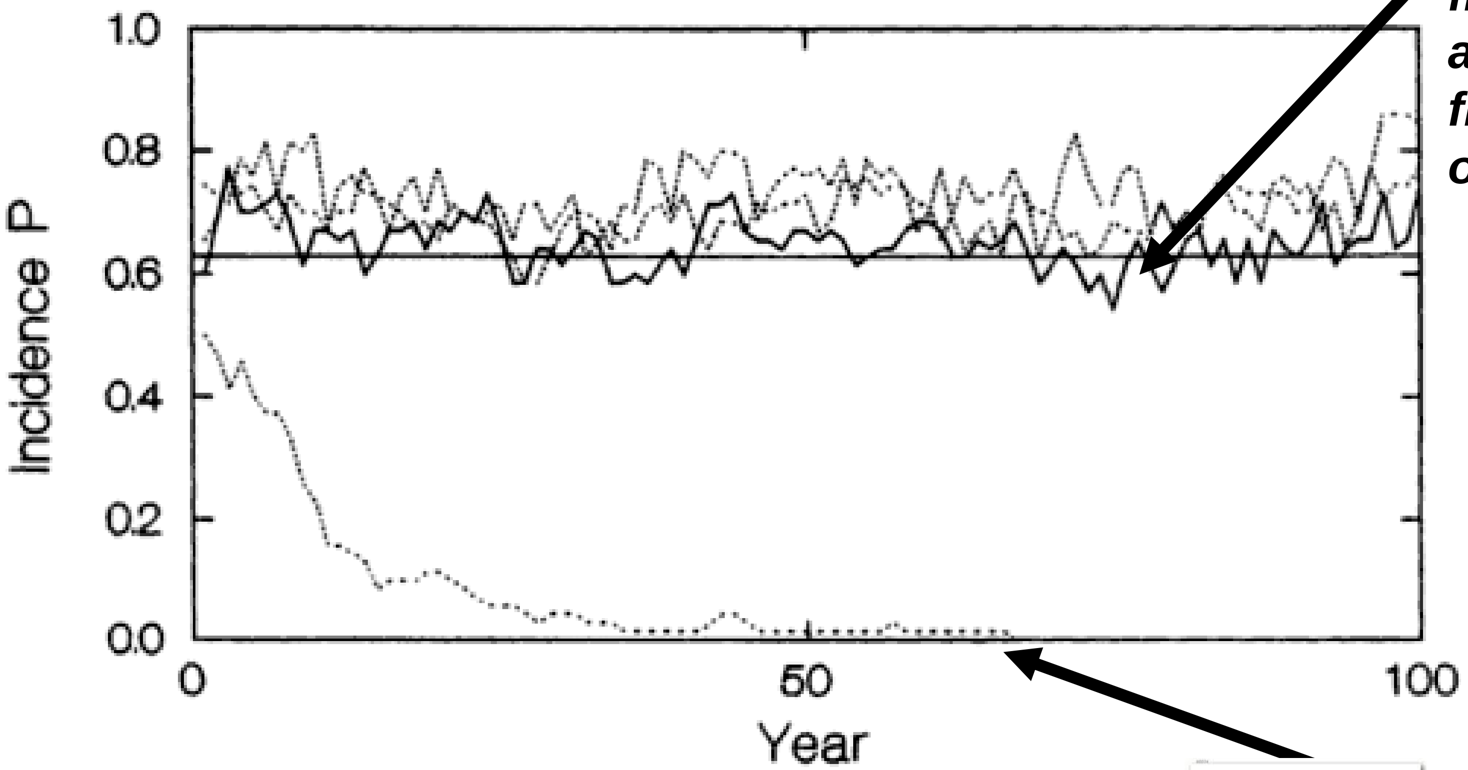
If $X<C_i$

If $X<E_i\,(1-C_i)$

(includes rescue effect)

- Now update p_i = indicator of if patch i is occupied…. Repeat

Model predictions for real metapopulations



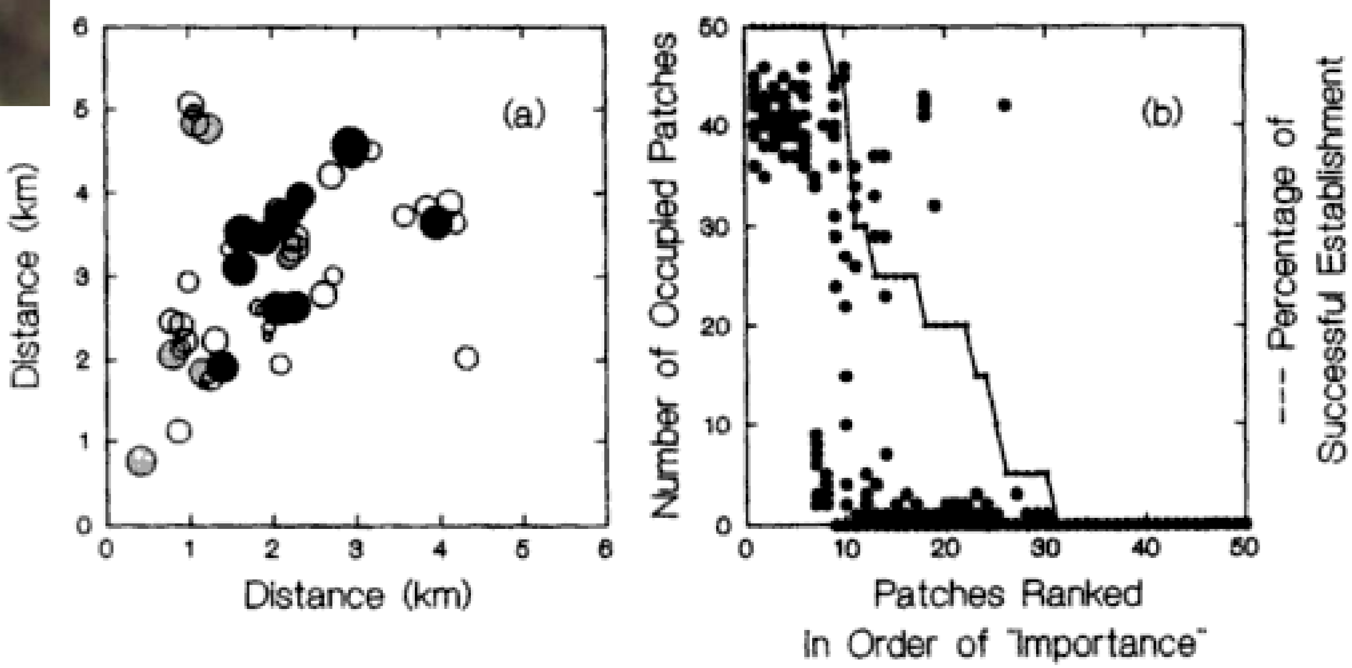
Melitea diamina ***fluctuates around observed fraction of occupied patches***

Hesperia comma ***Rapidly extinct***

Ranking patches in order of importance

- Taking each patch in term introduce an occupied patch and see if the population can reinvade the network

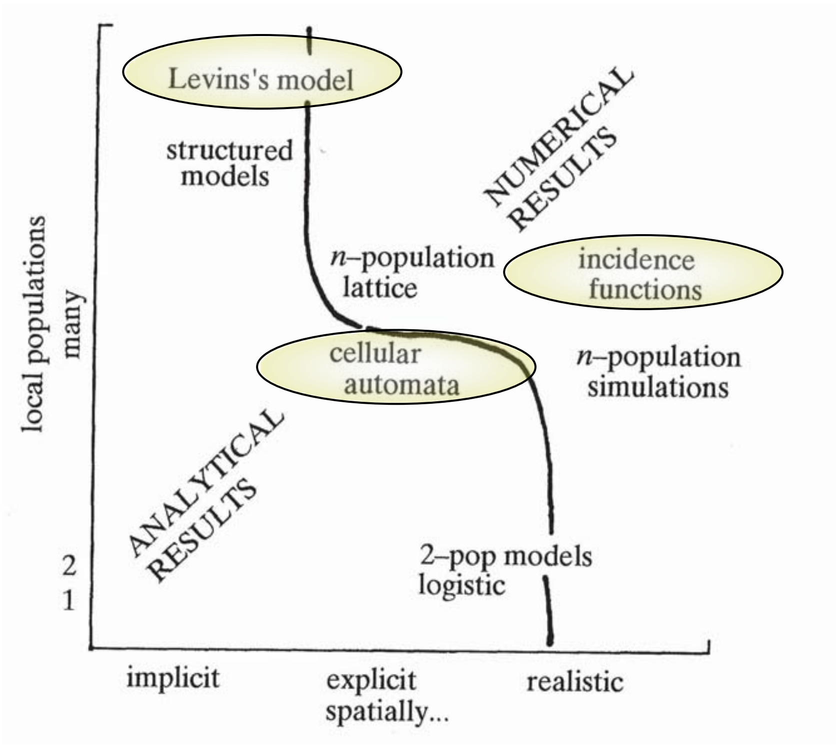
Glanville fratillary butterfully



Extensions

- IFM can be easily extended to include the effects of other environmental factors, apart from patch area and isolation, on the extinction and colonisation probabilities, e.g.
  - Patch quality could effect extinction rate
  - Habitat type may effect emigration and immigration rates (e.g. abundance of nectar flowers reduces emigration from, increase immigration to a habitat for Glanville fratillary)

Summary



- Metapopulations can answer questions about persistence - important for conservation.
- Good connection to data

- Patch isolation questions:
  - When can populations pass through corridors?
  - How do populations move through matrix?
- Patch area questions:
  - What is the critical patch size for a viable population?
  - How does patch are relate to extinction probability? Local population dynamics?

References

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