



Department of  
Integrative Biology  
UNIVERSITY OF WISCONSIN-MADISON

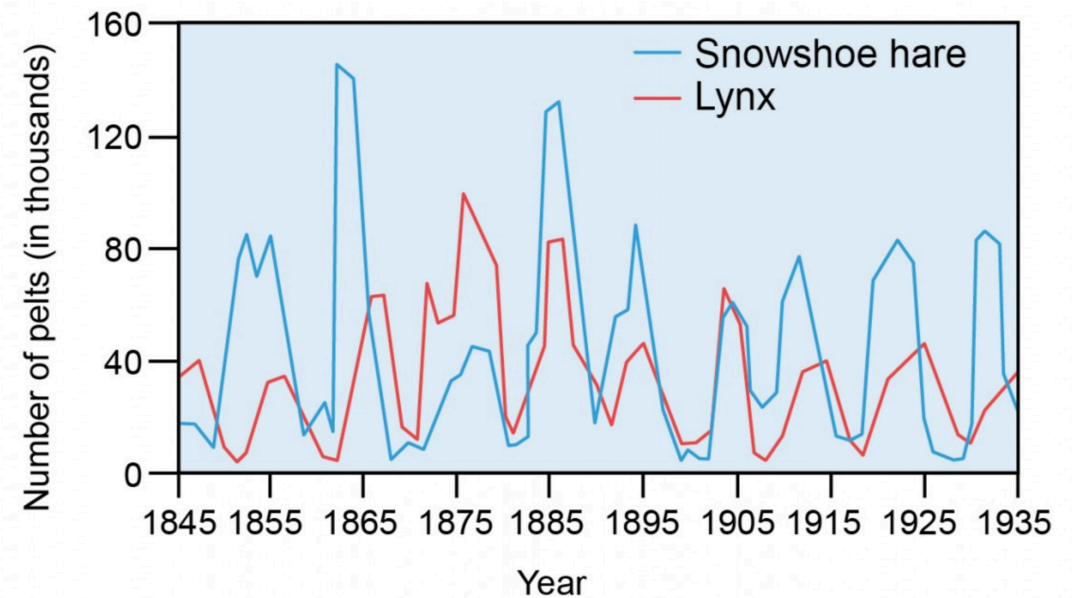
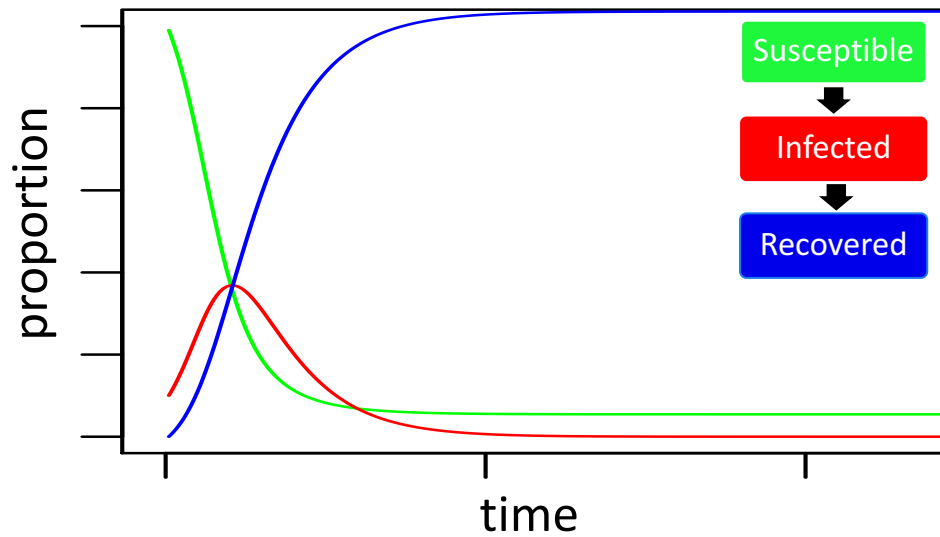


# Spatial mechanistic models

Tanjona Ramiadantsoa  
with materials from Atte Molainen

# Previously

- Variable of interest is population size through time

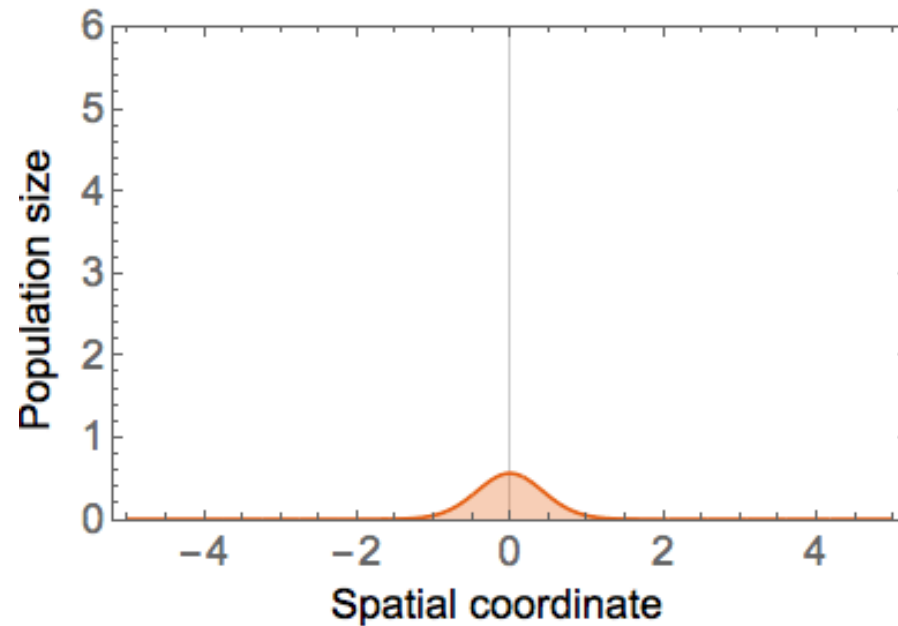


# Spatial model

- Now, we are interested in population size **both through time and through space**

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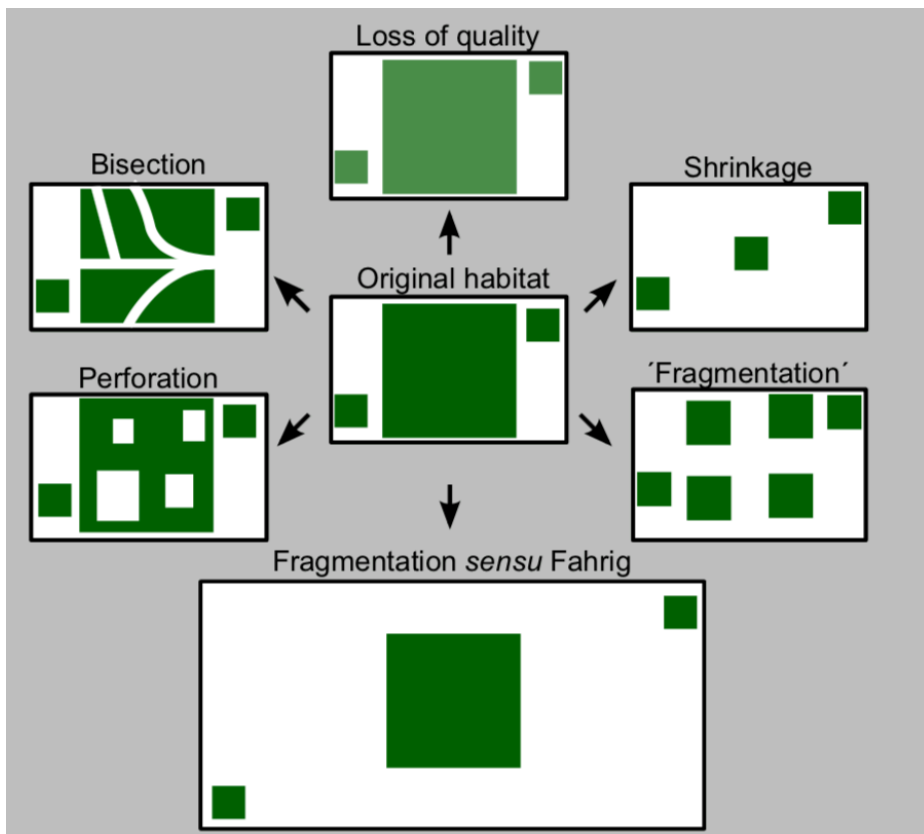




# Spatial model

## Two necessary additions

### Landscape structure



### Dispersal



# Outline

- Metapopulation paradigm
- Levins' (spatially implicit) metapopulation model
- Spatially realistic metapopulation model
- Software demonstration: SPOMSIM

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# Model system for metapopulation

Glanville fritillary butterfly  
(*Melitaea cinxia*)

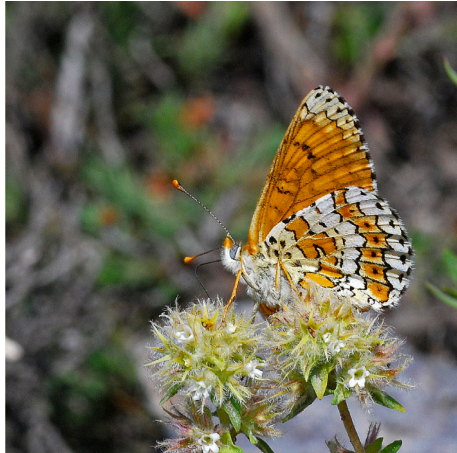
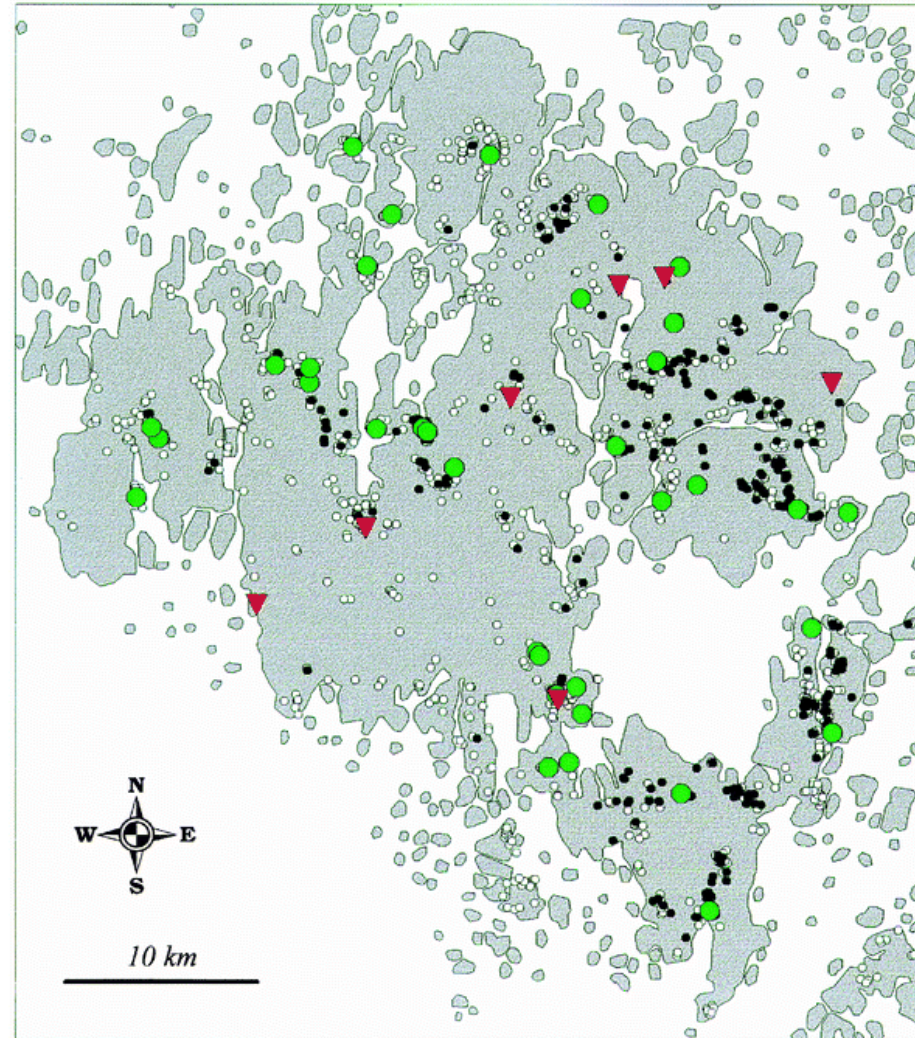


Photo: Hannu Aarnio



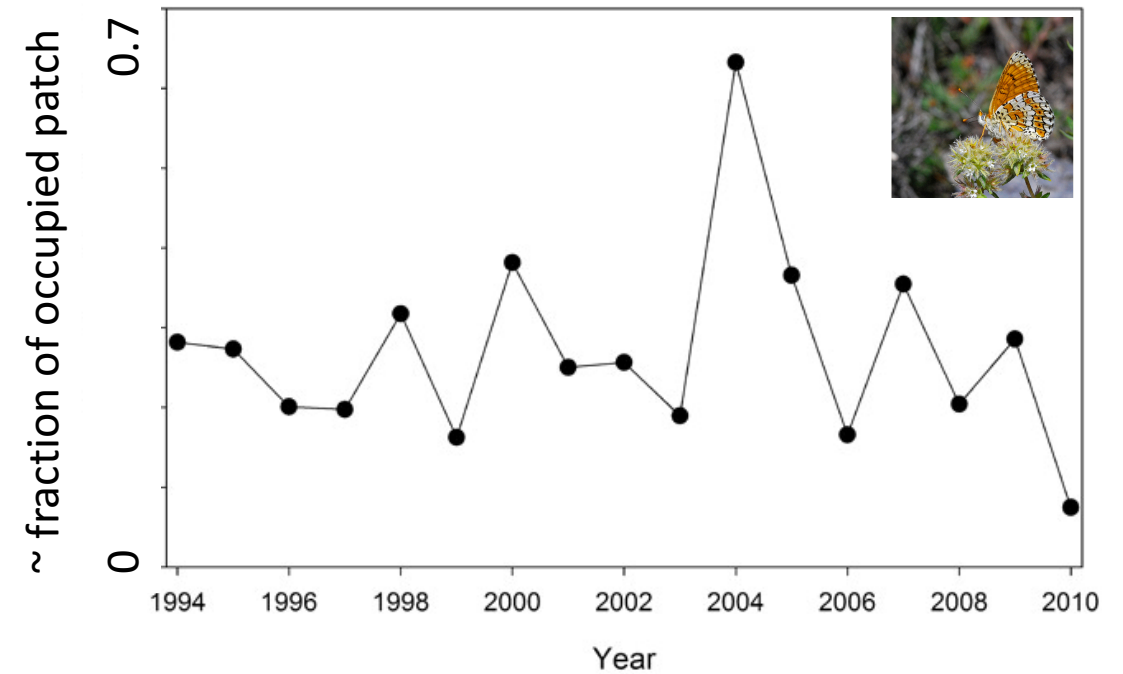
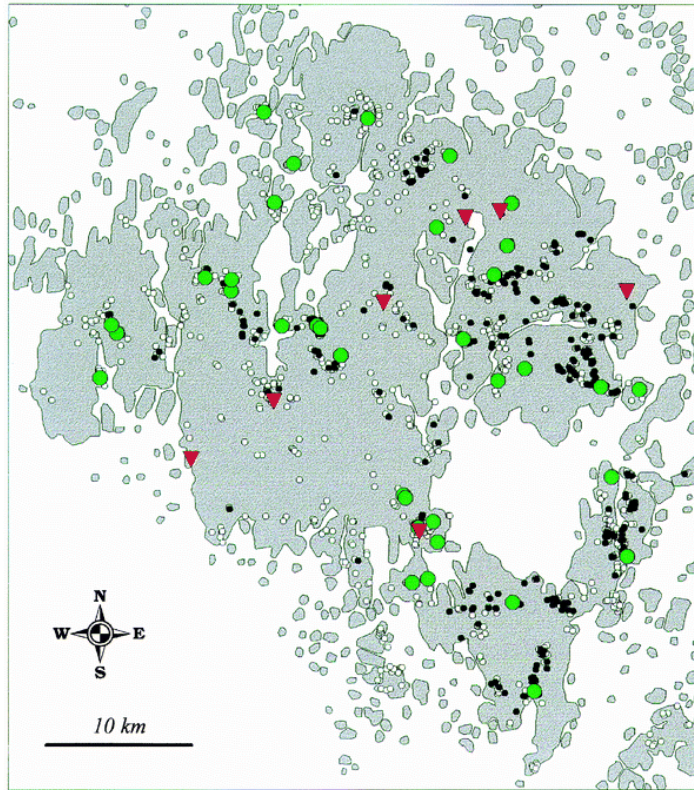
Saccheri et al. 1998

Ilkka Hanski





# Metapopulation dynamics

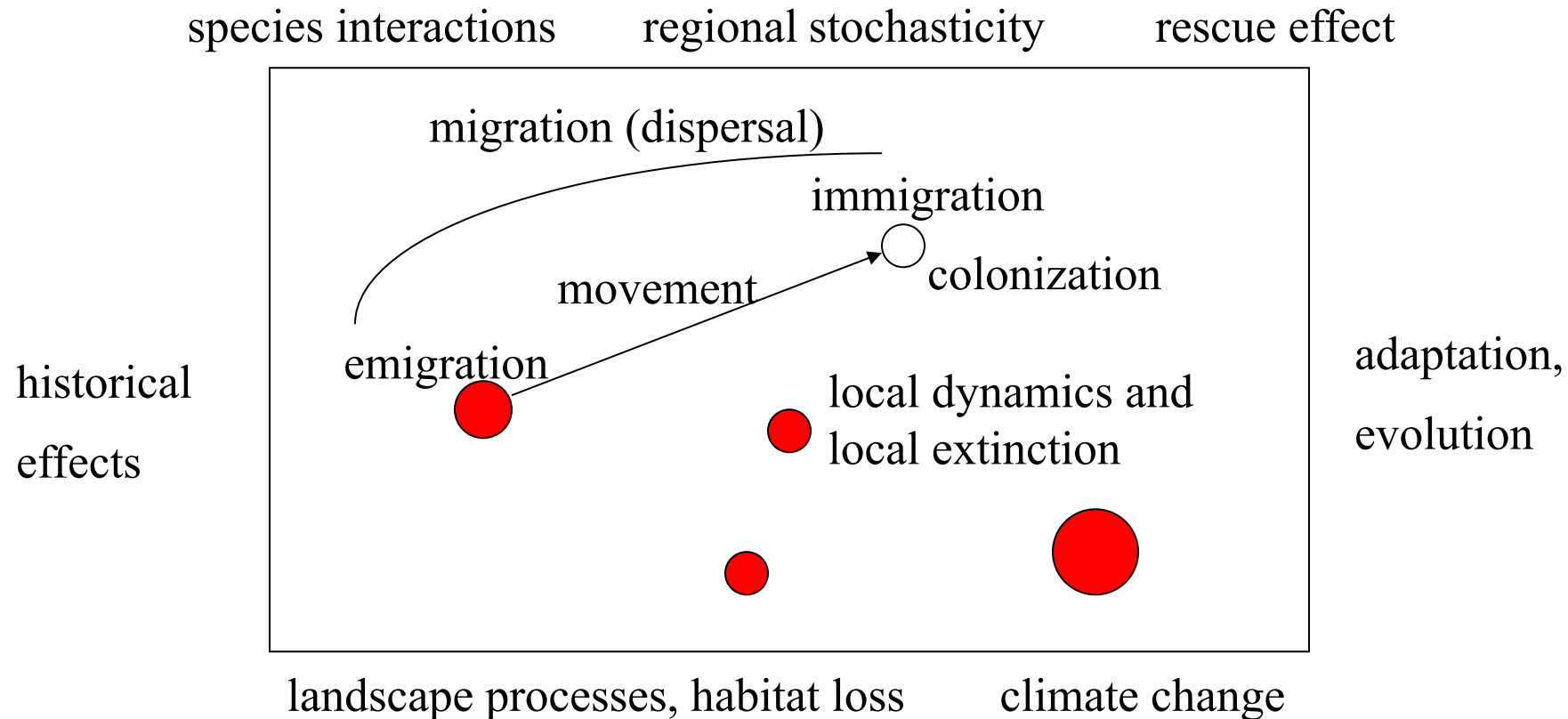


# Metapopulation paradigm

Historically, ecologists mainly focus on local processes

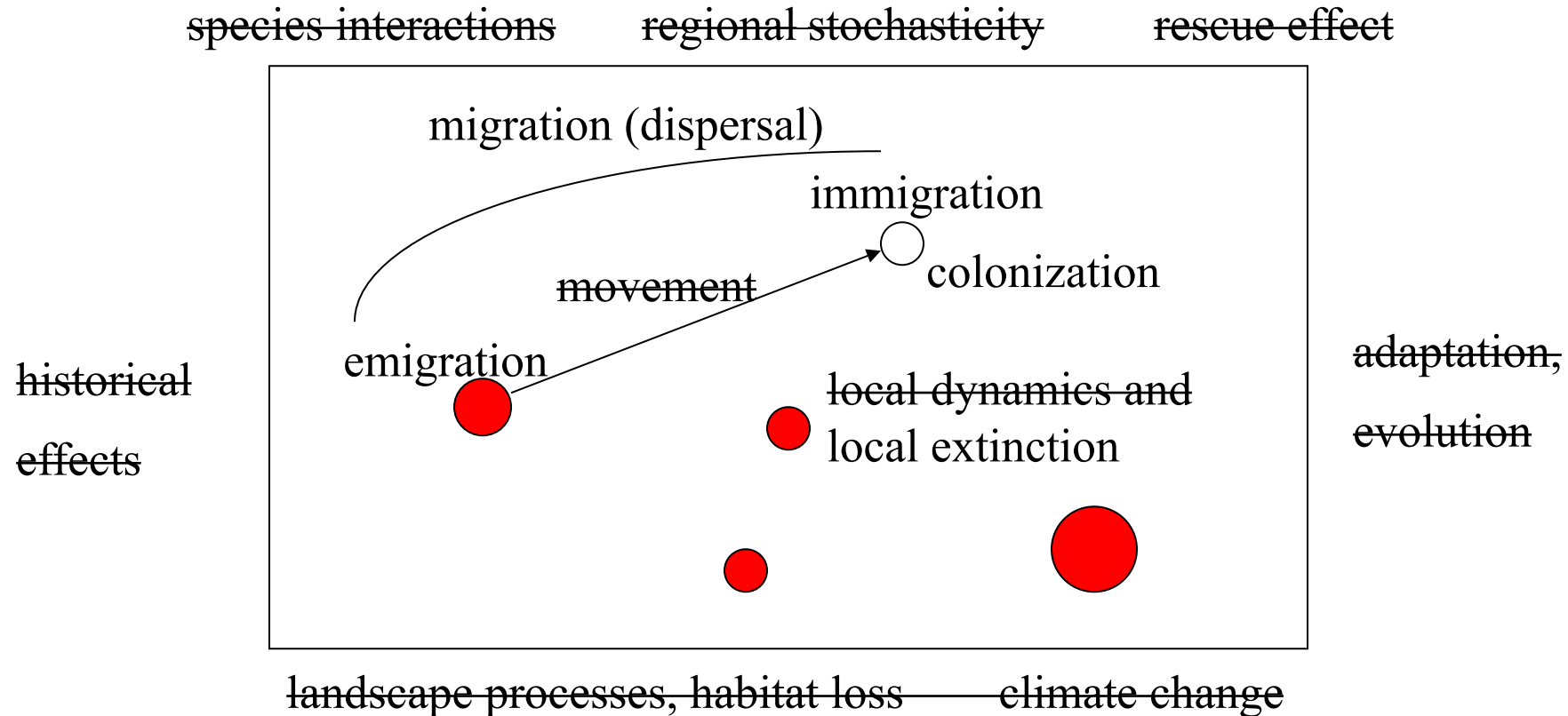
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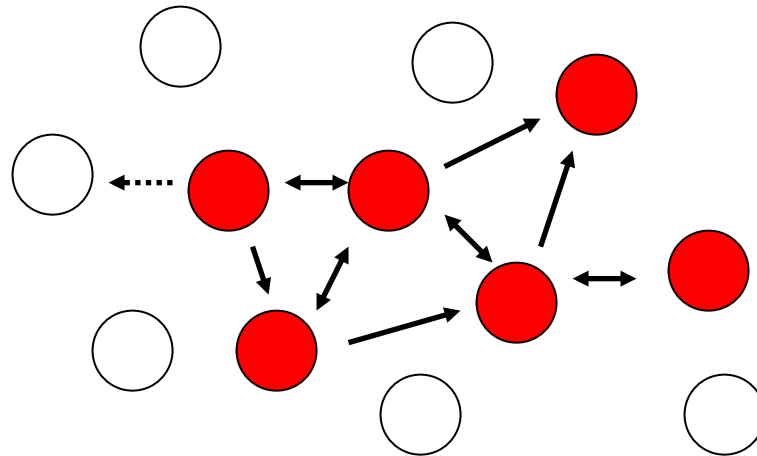
# Outline

- Metapopulation paradigm
- **Levins' (spatially implicit) metapopulation model**
- Spatially realistic metapopulation model
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# The concept of metapopulation (Levins 1969)



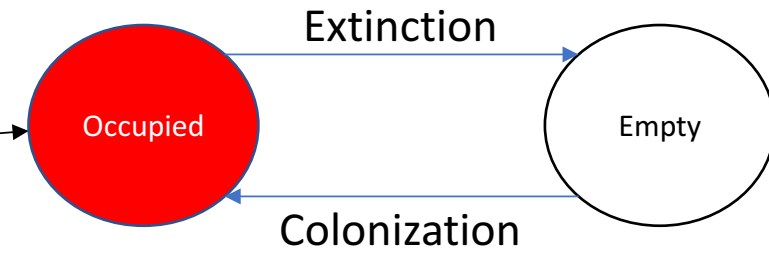
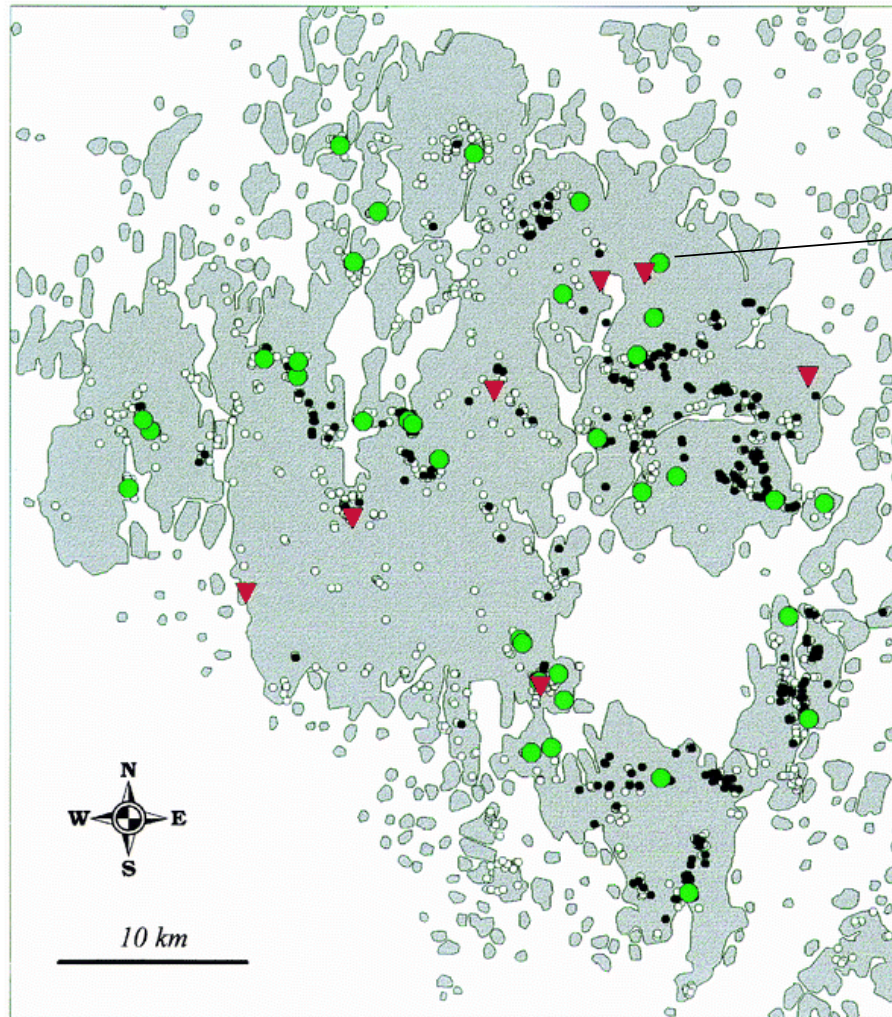
Richard Levins



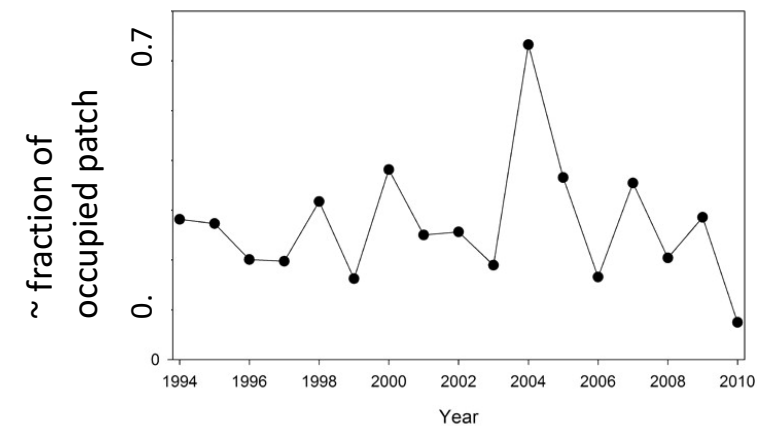
⇒ We only ask whether the patch is empty or occupied (occupancy model)

“a set of local populations connected by migration”

# Conceptual model



We are interested in the fraction of occupied patch  $p$



# Levins' (spatially implicit) deterministic model

Spatial implicit model

- 1- All patches have the same probability of going extinct
- 2- All patches are equidistant to each other
- 3- Infinitely many patches (removes stochasticity)

Let  $p$  the fraction of occupied patch in the landscape

- Extinction happens at a rate  $e$
- Colonization happens at a rate  $cp$

$$\frac{dp}{dt} = \underbrace{cp(1-p)}_{\text{All colonizations}} - \underbrace{ep}_{\text{All extinctions}}$$

Empty patches

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Empty patches

- Equilibria

$$\begin{aligned}\frac{dp}{dt} = 0 &\Leftrightarrow cp(1-p) - ep = 0 \\ &\Leftrightarrow p^* = 0 \text{ or } p^* = 1 - \frac{e}{c}\end{aligned}$$

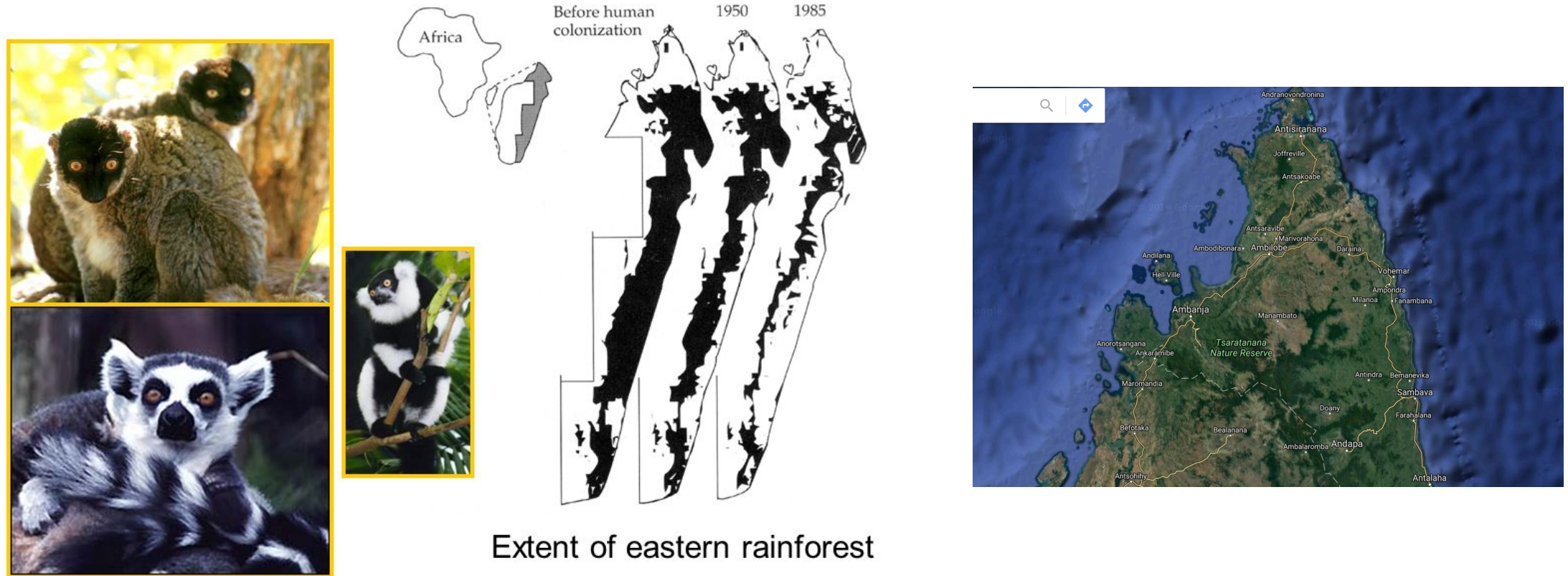
- Persistence if  $p^* > 0$ , i.e.

$c > e$  (does it make sense?)



# Habitat destruction and extinction threshold

## DEFORESTATION AND HABITAT FRAGMENTATION IN MADAGASCAR



# Habitat destruction and equilibrium

- If we destroy the habitat, so that  **$h$  fraction remains**, the remaining part available for colonization is  $h - p$

$$\frac{dp}{dt} = cp(h - p) - ep$$

- The new equilibrium is

$$p^* = 1 - \frac{e/c}{h}$$

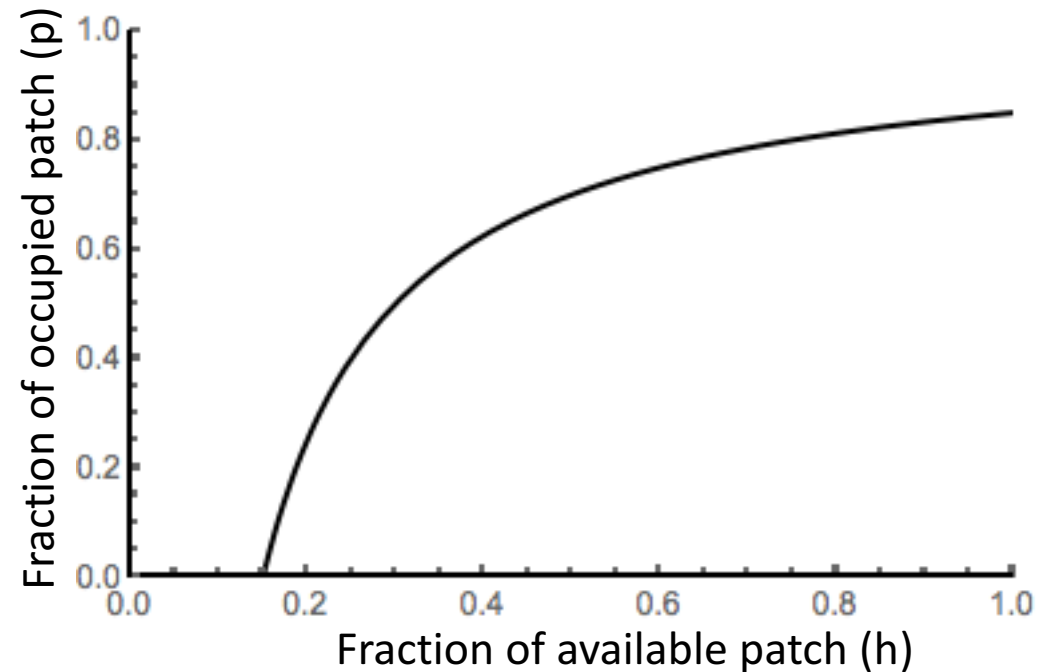
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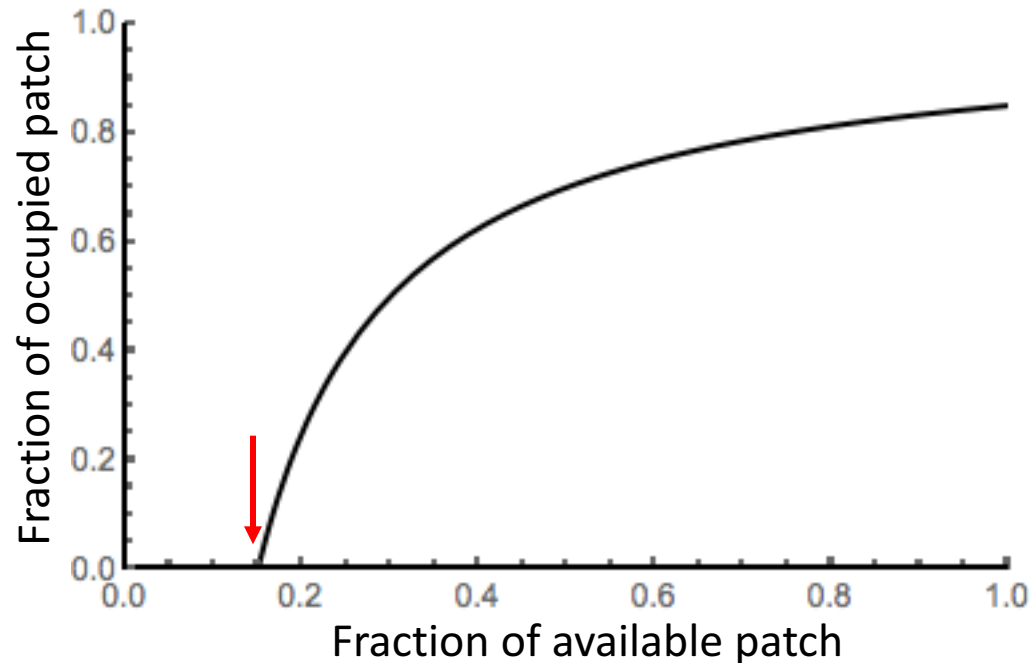
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# Habitat destruction and extinction threshold



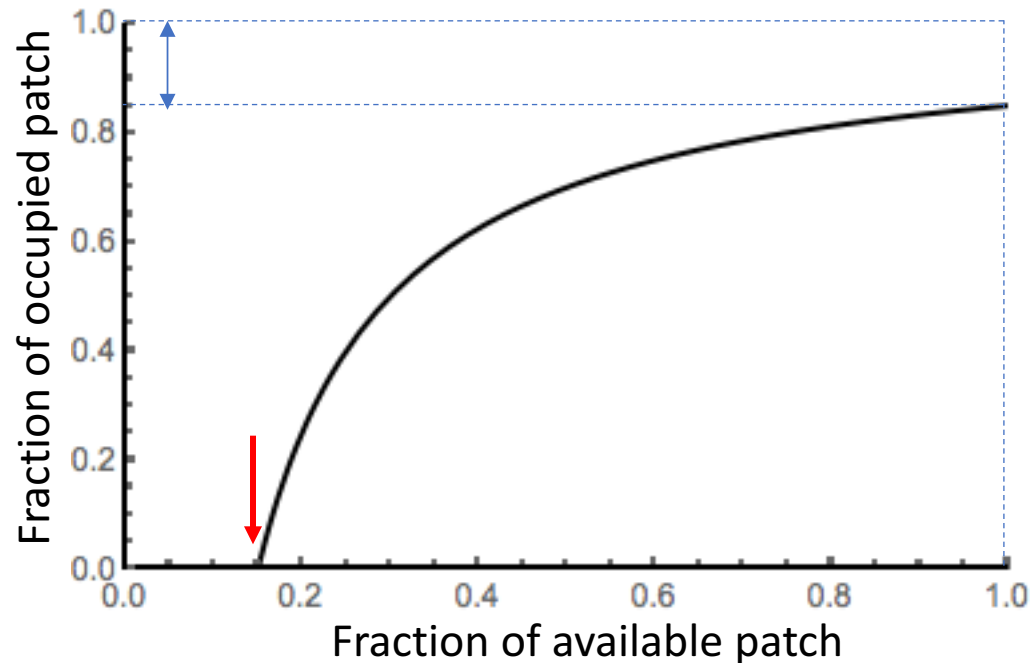
The extinction threshold (↓) is the minimum amount of habitat necessary for the persistence of the metapopulation

$$p^* = 1 - \frac{e/c}{h} > 0$$

i.e.

$$h > e/c$$

# Habitat destruction and extinction threshold



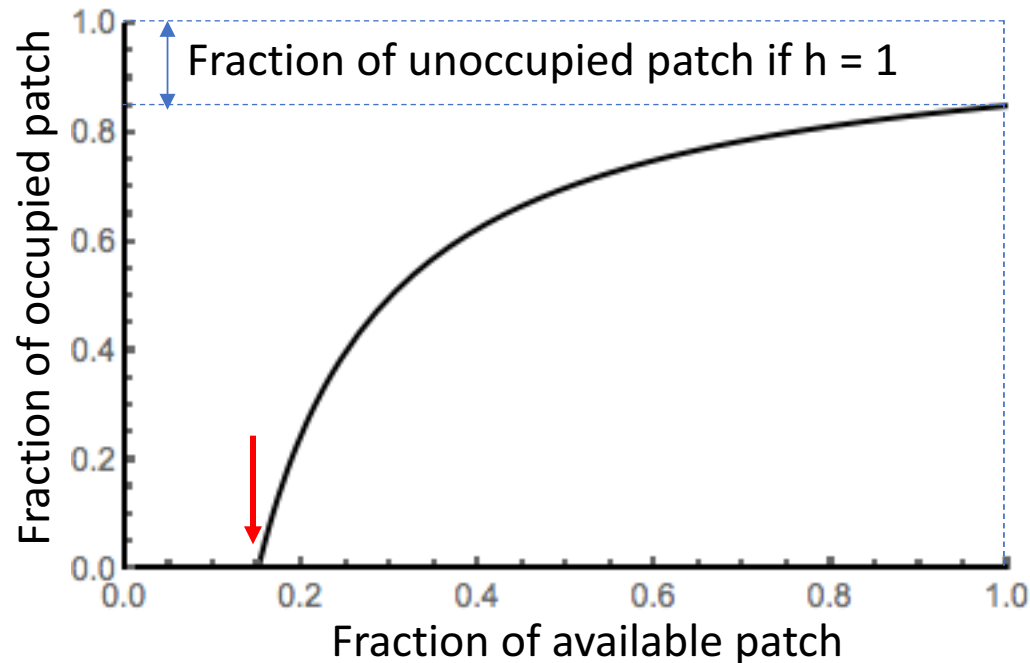
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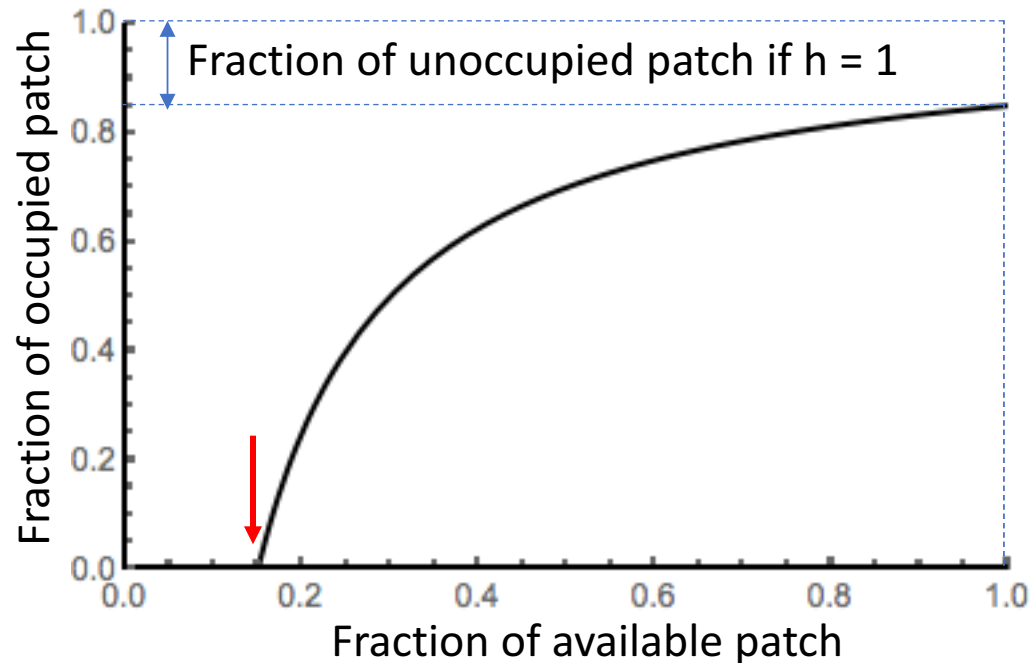
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The extinction threshold (↓) is the minimum amount of habitat necessary for the persistence of the metapopulation

$$p^* = 1 - \frac{e/c}{h} > 0$$

i.e.

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The extinction threshold = the fraction of unoccupied patch at equilibrium when all patches are available

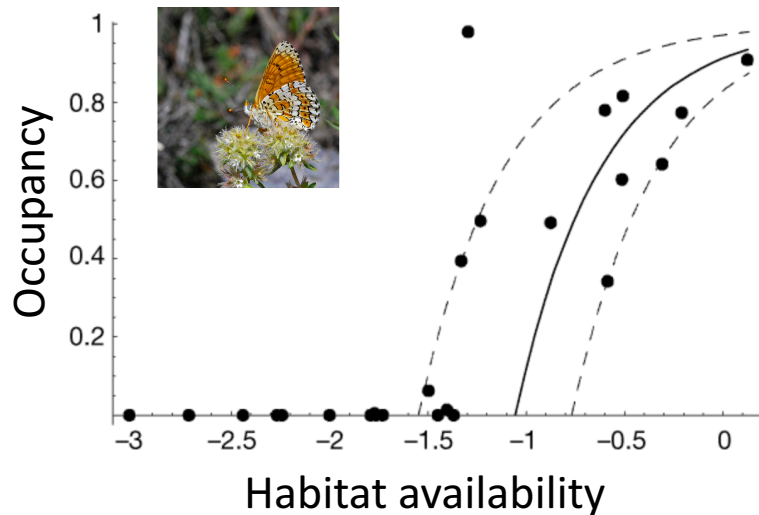
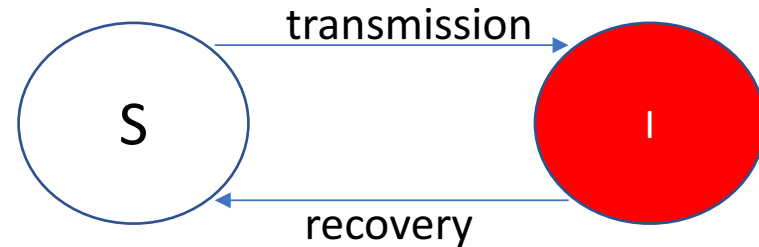
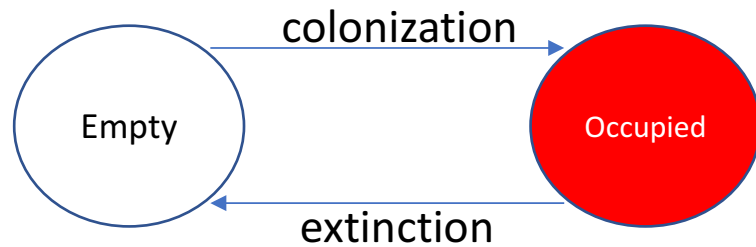
# Ecology vs. Epidemiology



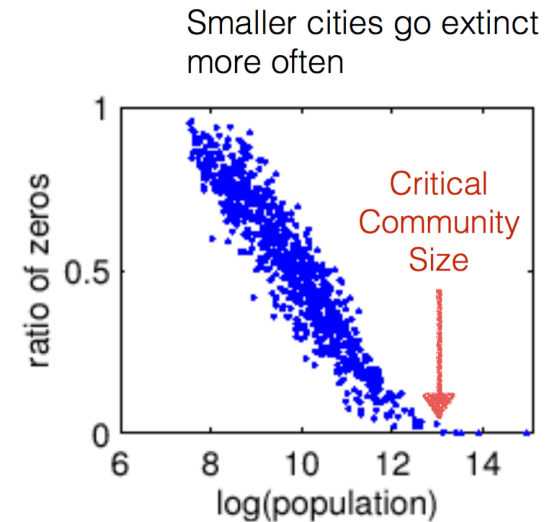
# Ecology ~ Epidemiology



# Metapopulation ~ Epidemiology: SIS



Hanski & Ovaskainen, 2000, *Nature*



Grenfell et al., 2001, *Nature*



# Metapopulation ~ Epidemiology: SIS

## Metapopulation

- The fraction of occupied patch at equilibrium is

$$p^* = 1 - \frac{\text{extinction rate}}{\text{colonization rate}} = 1 - \frac{e}{c}$$

- If  $h$  is the fraction of suitable patches, the metapopulation goes extinct if

$$h < \frac{e}{c}$$

## SIS

- The fraction of infected individuals at equilibrium is

$$p^* = 1 - \frac{\text{recovery rate}}{\text{transmission rate}} = 1 - \frac{\gamma}{\beta}$$

- If  $h = 1 - p_c$  is the fraction of unvaccinated individual, the disease is eradicated if

$$h < \frac{\gamma}{\beta} = \frac{1}{R_0}$$

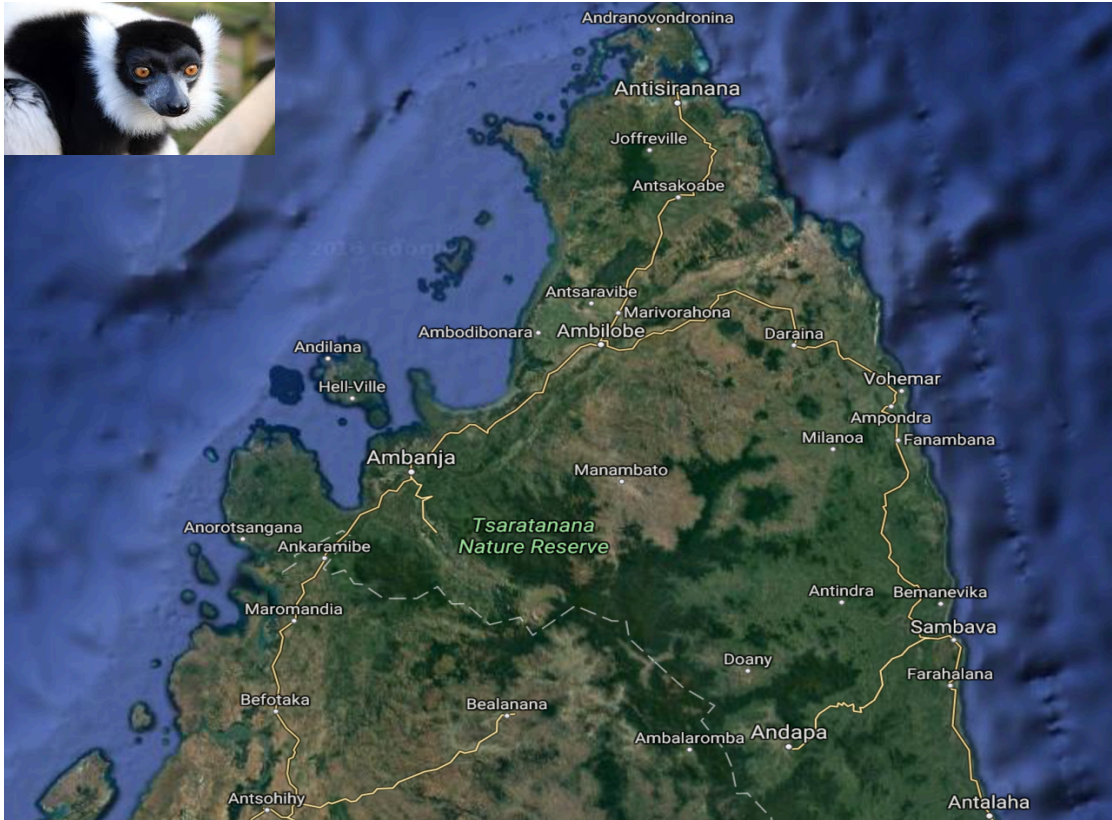


# Outline

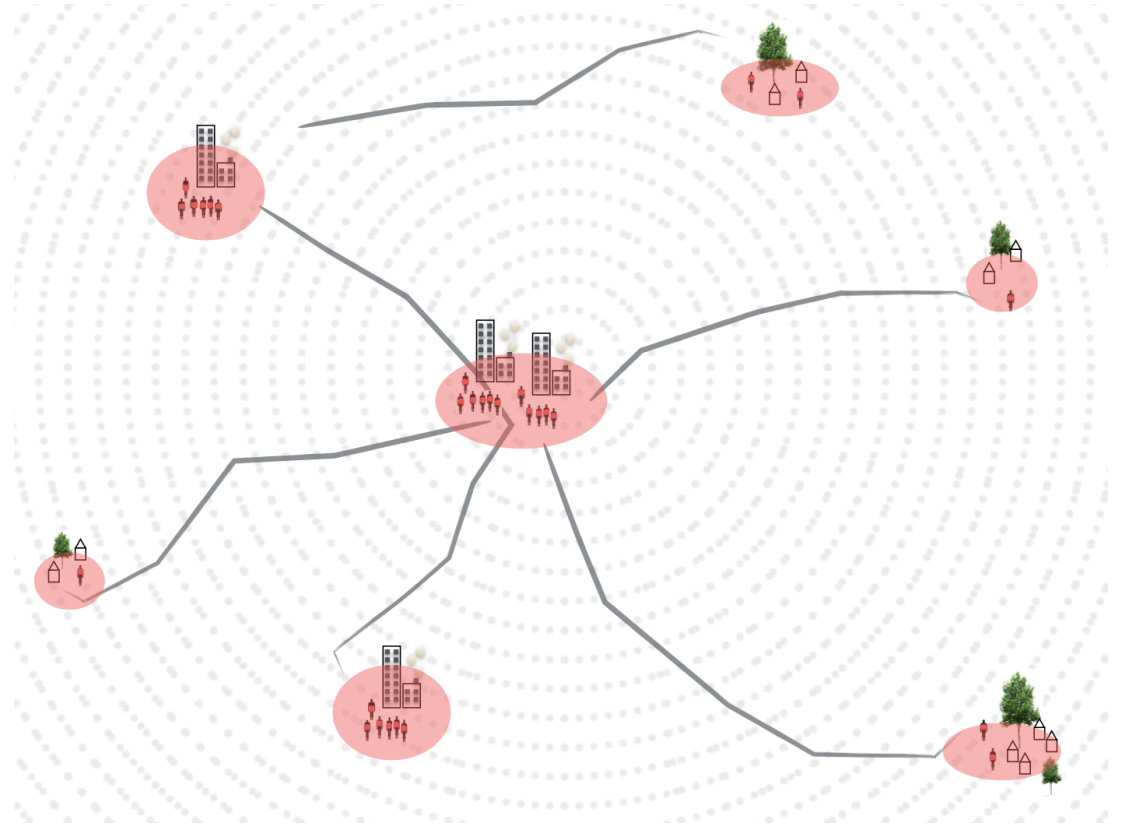
- Metapopulation paradigm
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- **Spatially realistic metapopulation model**
- Software demonstration: SPOMSIM

# Spatially realistic metapopulation model

## Ecology

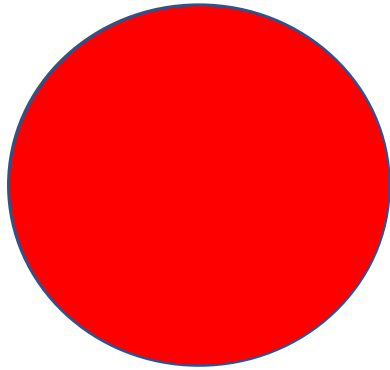


## Epidemiology



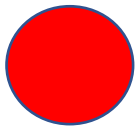
# Extinction as a function of patch size

Large patch => large population size



=> Low probability of extinction

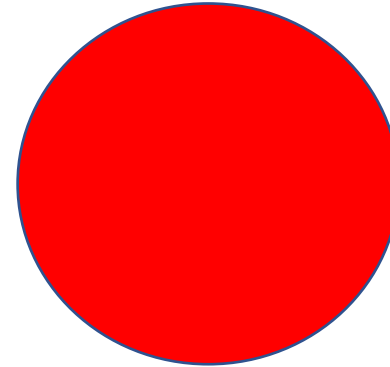
Small patch => small population size



=> High probability of extinction

# Recovery as a function of human 'condition'

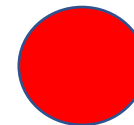
Strong person => ...



=> Quick recovery



Weak person => ...

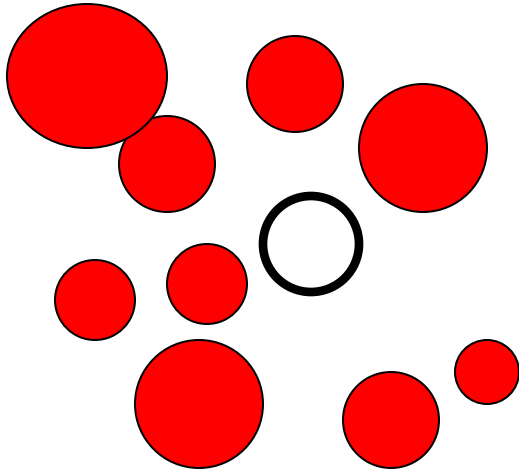


=> Slow recovery



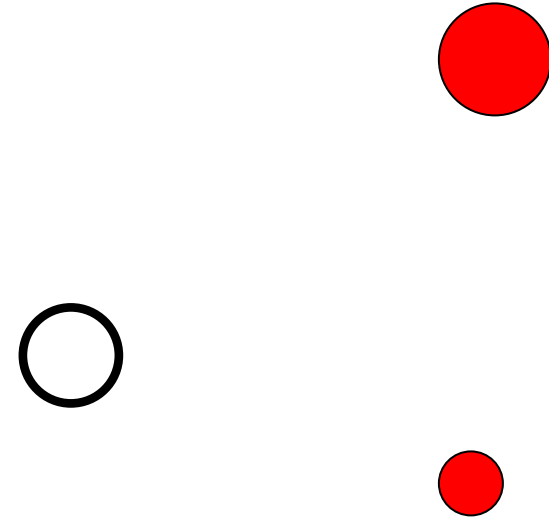
Colonization of an empty patch:  
general idea = scales with *connectivity*. Heuristically:

Well-connected focal patch  
(many close-by occupied  
neighbours)



⇒ **High** probability of  
being colonized

Poorly connected  
focal patch

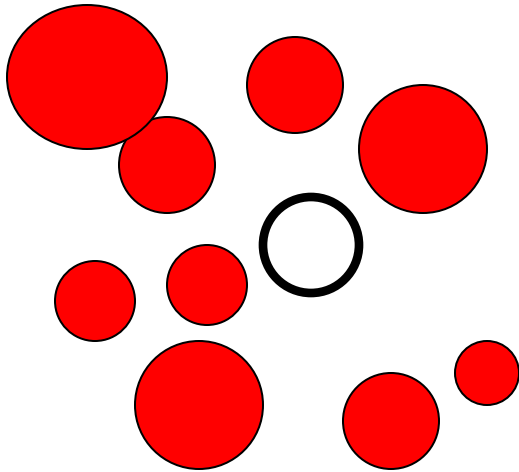


⇒ **Low** probability of  
being colonized

# Epidemiology

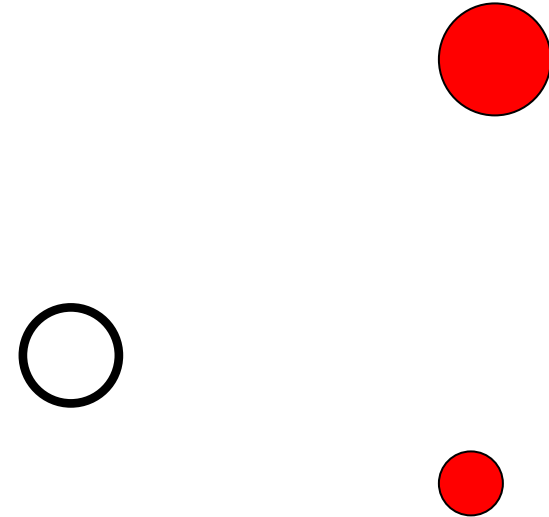
Infection of an healthy person:  
general idea = scales with *connectivity*. Heuristically:

Well-connected focal healthy  
person  
(many sick persons close-by)



⇒ **High** probability of  
being infected

Poorly connected  
focal health person



⇒ **Low** probability of  
being infected

# A little bit of math: functional forms

## Extinction (recovery) probability

- Assume patch  $i$  of size  $A_i$  is occupied, the probability of local extinction is

$$prob_e(A_i) = 1 - e^{-e/A_i}$$

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## Extinction (recovery) probability

- Assume patch  $i$  of size  $A_i$  is occupied, the probability of local extinction is

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## Colonization (transmission) probability

- Assume patch  $i$  of size  $A_i$  is empty, the probability of local colonization is

$$prob_c(A_i) = 1 - e^{-c \psi(A_i)}$$

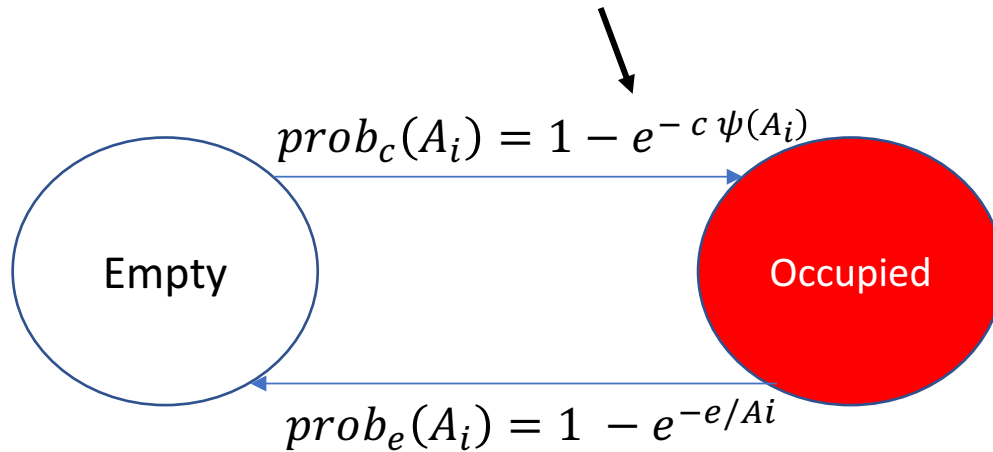
- $\psi(A_i)$  represents the connectivity of the patch  $i$

$$\psi(A_i) = A_i \sum_{A_j \in source} A_j e^{-\kappa d_{ij}}$$

- $e^{-\kappa d_{ij}}$  is called a dispersal kernel

# Simulation

Remember that  $\psi$   
depends on the proximity  
to your sick neighbors



‘for’ loop for each time step

- If patch 1 is empty, it has a probability  $prob_c(A_1)$  to be colonized for next year
- If patch 1 is occupied, it has a probability  $prob_e(A_1)$  to go extinct for next year

Repeat that procedure for all the patches in the system and we get the next state of the metapopulation





# Extinction threshold in the realistic model

- In the Levins' model, the equilibrium was

$$p^* = 1 - \frac{e/c}{h}$$

# Extinction threshold in the realistic model

- In the Levins' model, the equilibrium was

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- In the realistic model, we have a similar relationship

$$p^* = 1 - \frac{e/c}{\lambda_M}$$

- $\lambda_M$  summarizes the role of dispersal, landscape structure, and the dominant eigenvalue of a something called “landscape” matrix.
- $\lambda_M$  is called the **metapopulation capacity**

# Outline

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# SPOMSIM: Stochastic Patch Occupancy Model Simulation



Available online at [www.sciencedirect.com](http://www.sciencedirect.com)

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Ecological Modelling 179 (2004) 533–550

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[www.elsevier.com/locate/ecolmodel](http://www.elsevier.com/locate/ecolmodel)

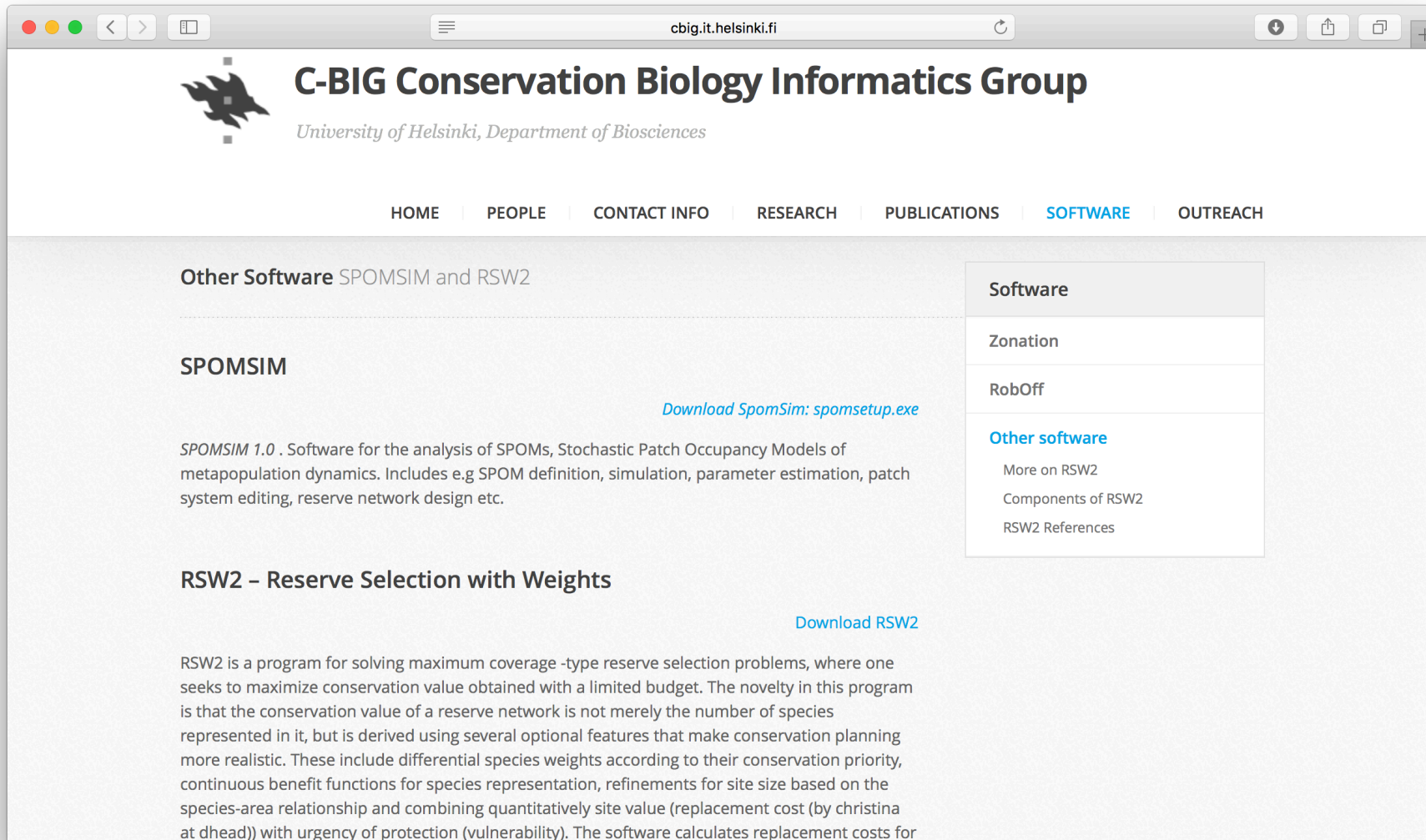
## SPOMSIM: software for stochastic patch occupancy models of metapopulation dynamics

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*Department of Biological and Environmental Sciences, Metapopulation Research Group, University of Helsinki,  
PO Box 65 (Viikinkaari 1), Helsinki FIN-00014, Finland*

Received 7 July 2003; received in revised form 29 March 2004; accepted 29 April 2004

# SPOMSIM: Stochastic Patch Occupancy Model Simulation



The screenshot shows a web browser window with the URL `cbig.it.helsinki.fi`. The page header features the C-BIG logo and the text "C-BIG Conservation Biology Informatics Group" and "University of Helsinki, Department of Biosciences". A navigation menu includes links for HOME, PEOPLE, CONTACT INFO, RESEARCH, PUBLICATIONS, SOFTWARE (highlighted), and OUTREACH.

The main content area is titled "Other Software SPOMSIM and RSW2". It contains two sections:

- SPOMSIM**: Includes a link to "Download SpomSim: `spomsetup.exe`". The description states: "SPOMSIM 1.0 . Software for the analysis of SPOMs, Stochastic Patch Occupancy Models of metapopulation dynamics. Includes e.g SPOM definition, simulation, parameter estimation, patch system editing, reserve network design etc."
- RSW2 – Reserve Selection with Weights**: Includes a link to "Download RSW2". The description states: "RSW2 is a program for solving maximum coverage -type reserve selection problems, where one seeks to maximize conservation value obtained with a limited budget. The novelty in this program is that the conservation value of a reserve network is not merely the number of species represented in it, but is derived using several optional features that make conservation planning more realistic. These include differential species weights according to their conservation priority, continuous benefit functions for species representation, refinements for site size based on the species-area relationship and combining quantitatively site value (replacement cost (by christina at ahead)) with urgency of protection (vulnerability). The software calculates replacement costs for

A sidebar on the right titled "Software" contains links for "Zonation", "RobOff", and "Other software". The "Other software" section includes links for "More on RSW2", "Components of RSW2", and "RSW2 References".

# Conclusions

Spatial models are needed when:

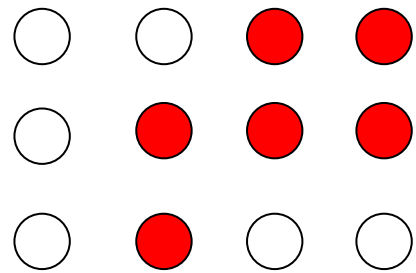
- the question involves both the distribution and abundance of a species/disease
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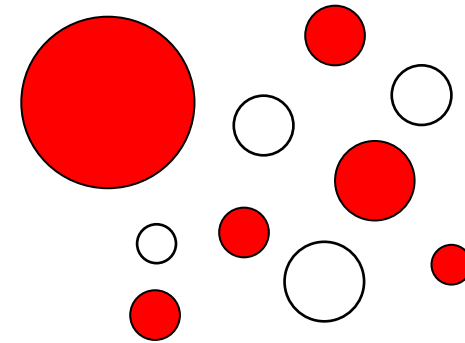
Spatially implicit: homogenous



$$\text{Habitat quality} > \frac{\text{extinction rate}}{\text{colonization rate}}$$

$$\text{Susceptible} > \frac{\text{recovery rate}}{\text{transmission rate}}$$

Spatially realistic: heterogeneous



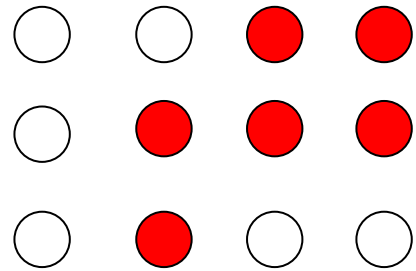


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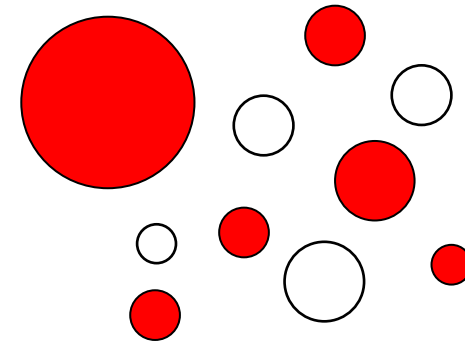
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Metapopulation theory helps to understand dynamics of population in a fragmented landscape