#### Metapopulations

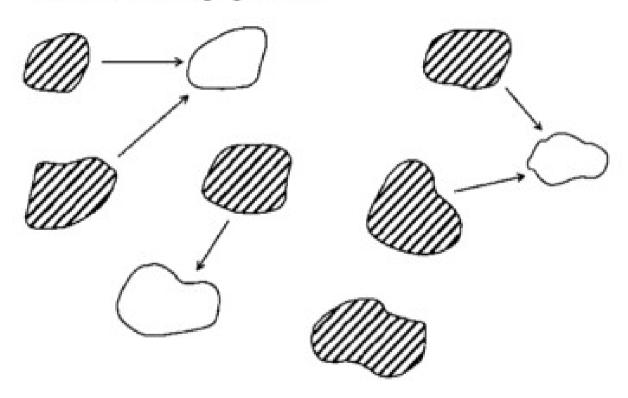
- Populations are "groups of individuals belonging to the same species that live in a shared region at the same time and interbreed".
- However .. most species are comprised of more than a single population
- Small populations are intrinsically more vulnerable to extinction than large populations
- If the "shared region" is a habitat patch within a linked network of similar patches the population may form part of a "metapopulation"

## Metapopulations

- A metapopulation occurs when a species occupies geographically separated patches within a landscape that are interconnected by occasional movements of individuals and gametes
- First metapopulation models constructed Richard Levins in papers published in 1969 and 1970

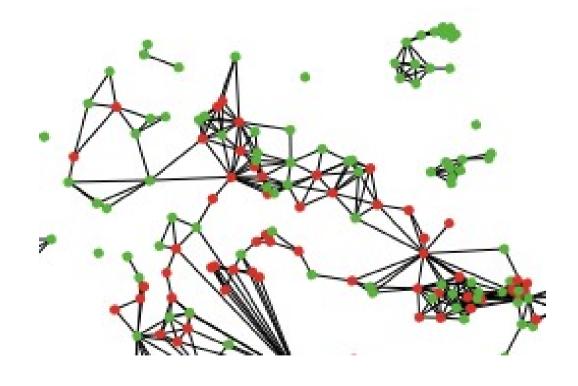
# A metapopulation

(a) Classic metapopulation



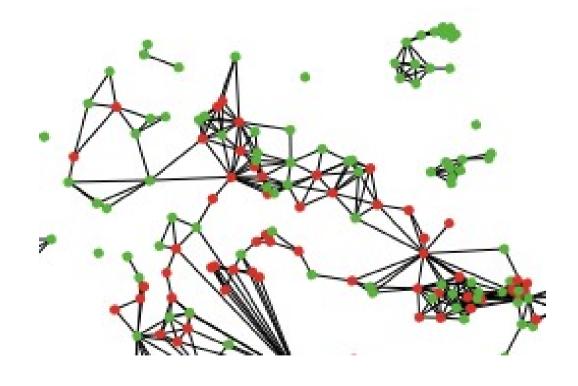
#### Levin's model

$$\frac{dp}{dt} = cp(1-p) - ep$$



#### Levin's model

$$\frac{dp}{dt} = cp(1-p) - ep$$



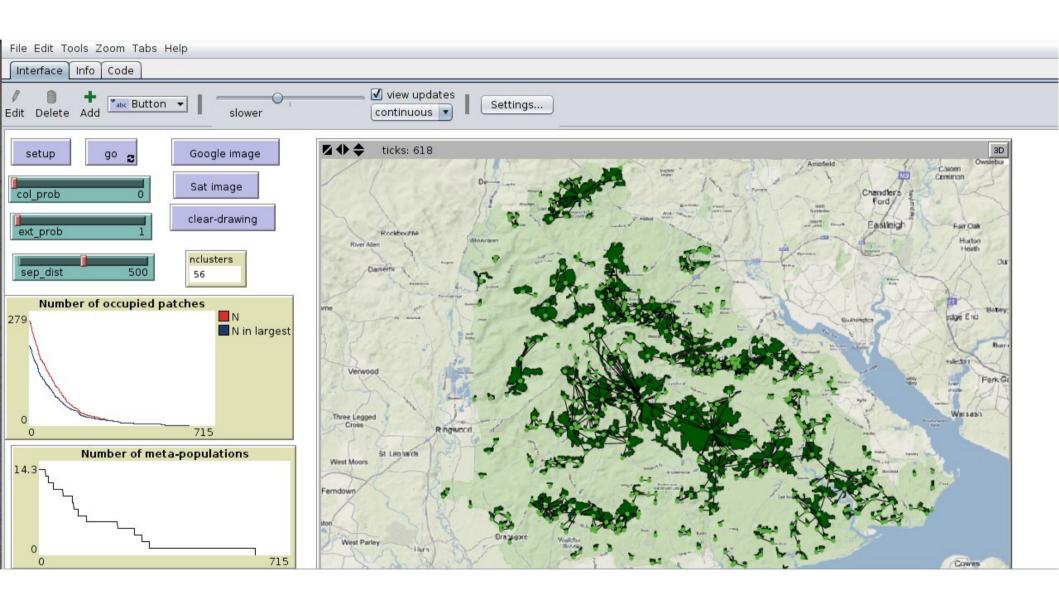
# Understanding the underlying model

- p=proportion of occupied patches
- dp/dt is the rate of change in occupancy
- The last part of the equation is very simple
- The proportion of occupied patches declines by the extinction rate (e) multiplied by the proportion of occupied patches

$$\frac{dp}{dt} = ep$$

# Understanding the model

- If the only process operating on the landscape were extinction (no colonisation) eventually all the populations would become extinct.
- The Levin's model assumes all populations have the same extinction rate
- So, the time to species level extinction depends on the intrinsic rate of population extinction and the number of populations



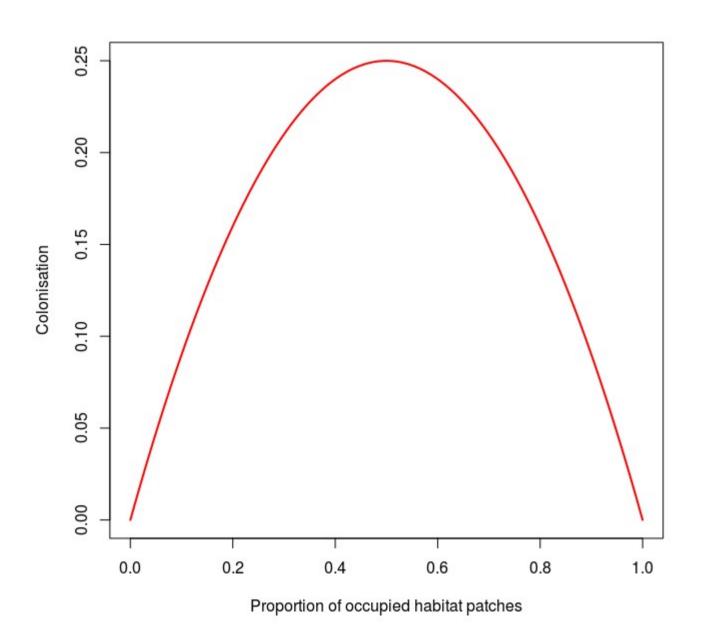
## Understanding the model

- Colonisation (i.e. the founding of new populations) can take place within a network of connected patches
- There will be a balance between extinctions colonisations
- This could result in a sustainable metapopulation

#### Rate of colonisation

- Colonisation requires a source population to provide colonisers
- Colonisation can only take place if there are empty patches of habitat
- Thus colonisation follows a parabolic pattern with a peak occurring when half the patches are occupied

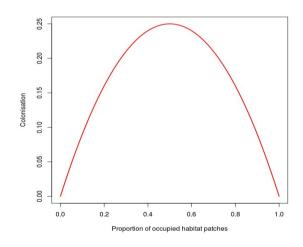
#### Colonisation



#### Levin's equation

 The equation represents colonisation as a constant function of the product of empty patches and occupied patches

$$\frac{dp}{dt} = cp(1-p)$$



## Some simple maths

$$\frac{dp}{dt} = cp(1-p) - ep$$

If there is no change in the number of patches occupied, then

$$\frac{dp}{dt} = 0$$

In other words ..

$$0 = cp(1-p)$$

## Some simple maths

At equilibrium

$$cp(1-p)=ep$$

$$p=1-\frac{e}{c}$$

It is difficult to find a solution where p = 1 (all habitats are occupied) as this implies

$$c = \infty$$

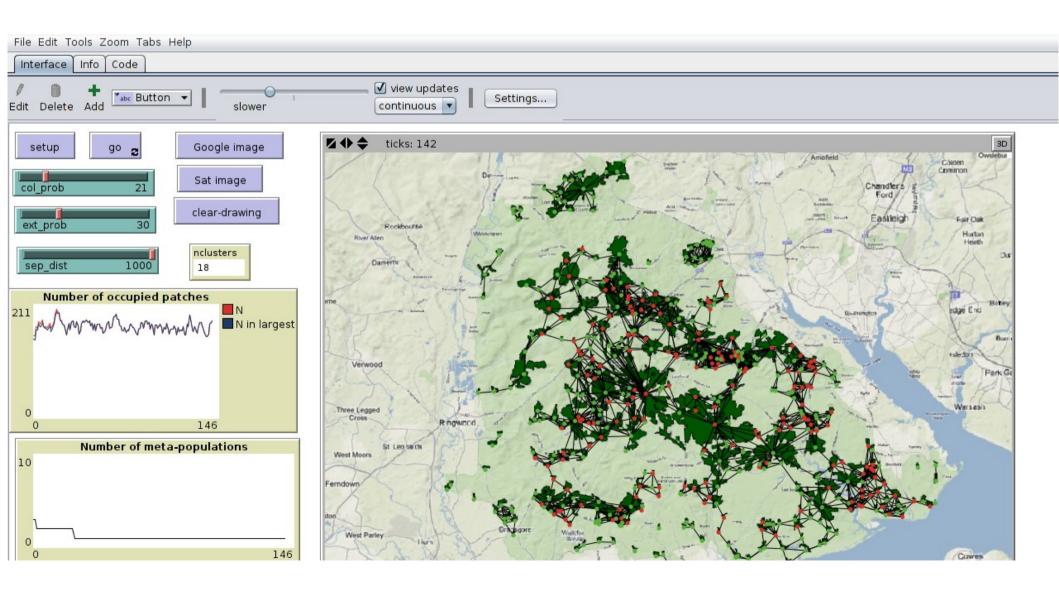
Or

$$e=0$$

# What does this imply?

- Although individual population extinctions may be inevitable, connected habitats can be recolonised
- Recolonisations are most rapid if there are equal numbers of occupied habitats and suitable (unoccupied) habitats
- Metapopulations are dynamic. Some suitable habitats will always be unoccupied (unless there is no extinction or instantaneous recolonisation).

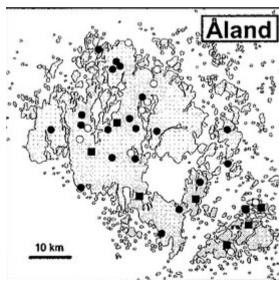
# Metapopulation model



## Classic metapopulation

 Hanski and his colleagues have worked on the Glanville fritillary (*Melitaea cinxia*) for over 30 years







#### Aland islands



## Aland islands



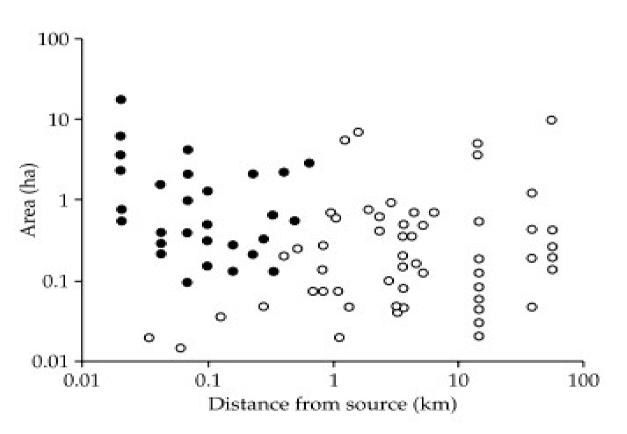
## Model system

- Over 6000 islands
- Network of small meadows
- Ideal system for testing theory
- Hanski found patterns in the empirical system that partly matched the predictions from models
- Concluded that the system does behave as a metapopulation but in a complex manner

# Hanski's four conditions for classic meta-population dynamics

- 1) Habitat patches support local breeding populations,
- 2) No single population is large enough to ensure long-term survival,
- 3) Patches are not too isolated to prevent recolonisation, and
- 4) Local dynamics are sufficiently asynchronous to make simultaneous extinction of all local populations unlikely

#### Silver studded blue



Spatial dynamics of a patchily distributed butterfly species Thomas, CD and Harrison S (1992) Journal of Animal Ecology 61:2

**Figure 10.3** Occupancy of suitable habitat by the silver-studded blue butterfly (*Plebejus argus*) in North Wales in 1990. Most patches larger than 0.1 ha were occupied (filled circle), provided that they were within about 600 m of another occupied patch. Beyond this distance, no patches were occupied (open circle), regardless of patch size. (Redrawn from Thomas and Harrison 1992.)

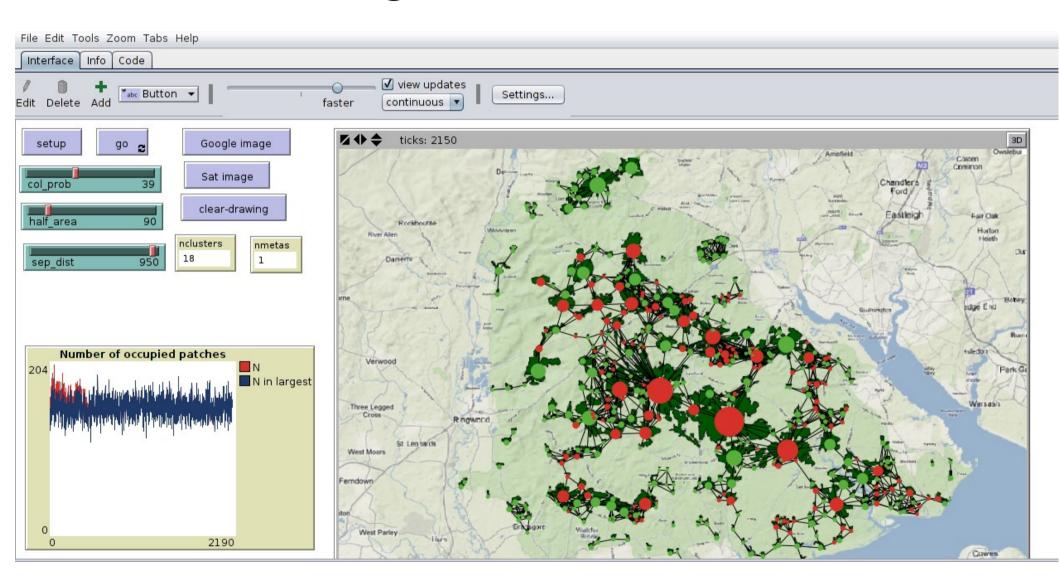
#### Additions to Levin's model

- Levin's original model treated all populations as identical
- Same size, same probability of extinction
- This is obviously not realistic.
- Extinction probability should be made a function of area (population size)
- This adds a "source sink" element to the model

#### Additions to Levin's model

- Each subpopulation has its own birth rate, death rate, and probability of going extinct
- Dynamics depend on interpatch distance, dispersal ability, number of patches
- Collapses if number of patches becomes too small

# Including area in the model

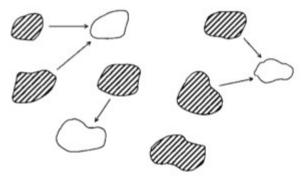


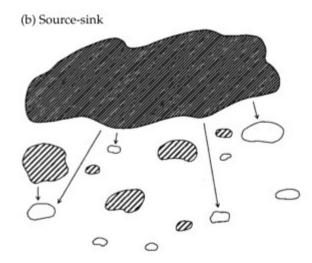
## Source – sink dynamics

- Real metapopulations are always complex
- Large patches tend to act as sources for colonisations
- Small patches tend to act as sinks
- But .. recolonisation of large patches can be the result of the (temporary) survival of populations on small patches

# Source sink dynamics







## Example

- Shoener and Spiller (1987) demonstrated that small populations of Orb web spiders in the Bahamas were constantly becoming extinct
- These small populations were "rescued" by recolonisation from larger populations





## Source sink dynamics

- Complicates analysis of a network
- Small patches of relatively poor habitat may hold populations of the organism if they are close to a source
- In contrast, larger patches of prime habitat may remain unoccupied if distant from a source
- Enhancing connectivity may be especially important.

# Population Viability Analysis

- Sophisticated PVA takes into account spatial elements (eg. RAMAS GIS software)
- Spatial structure of landscapes (fragmentation) often very important
- Population structure may be subdivided spatially
- Human induced habitat fragmentation may play a major role.

# Incorporating metapopulation theory in management

- Interagency Spotted Owl Scientific Committee in US
- Proposed management strategy for spotted owl based on theory
- Metapopulation models have to assume a great deal about owl biology
- US district judge ruled against the plan on the grounds that it carried unacknowledged risks to the owl

#### Conclusions

- Metapopulation models represent simplified abstractions, allowing 'what-if' scenarios to be explored (Harrison 1994).
- It is would be dangerous to assign primacy to any single model in determining conservation policy.
- However, the processes underlying metapopulation dynamics are not controversial and must be recognised
- Connectivity and patch size must influence metapopulation dynamics.
- However precise quantitative predictions based on theory will always be difficult, if not impossible