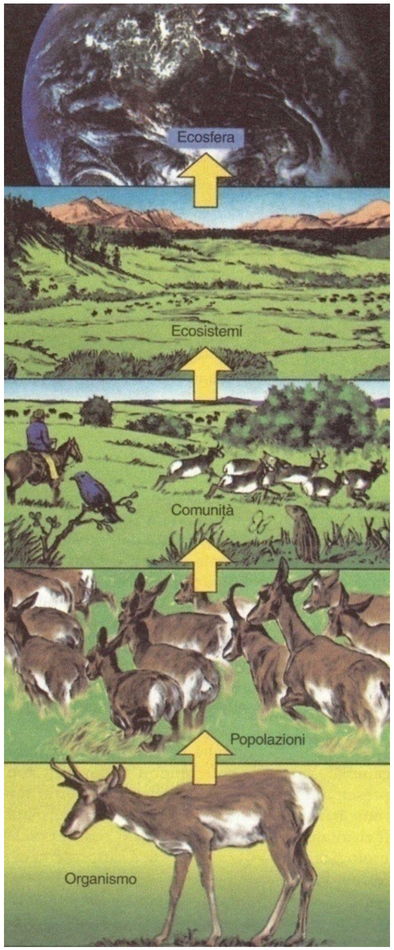
# The importance of space in biological problems




⋮

Solar system

Earth

Biosphere

Biome

Ecosystem

Population

Organism

Organ

Tissue

Cell

Molecule

⋮

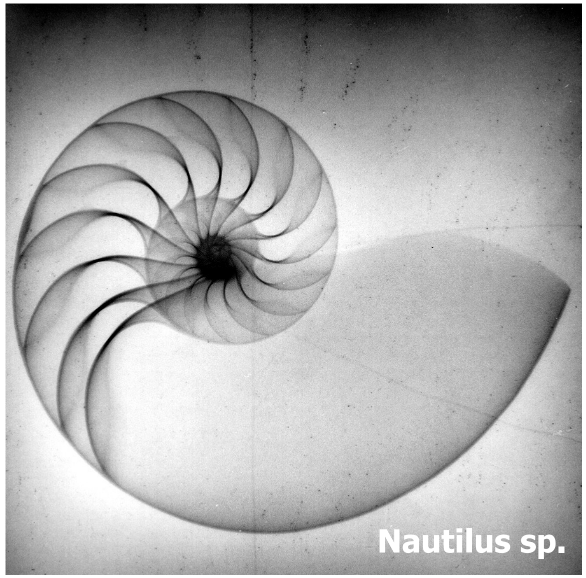
Biosphere level

Population level

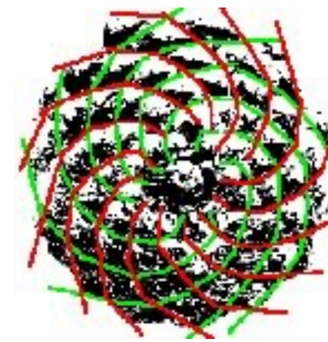
Individual level

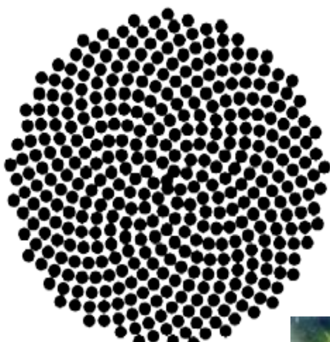
space does matter at every scale of aggregation in biology

# Individual level: patterns of growth



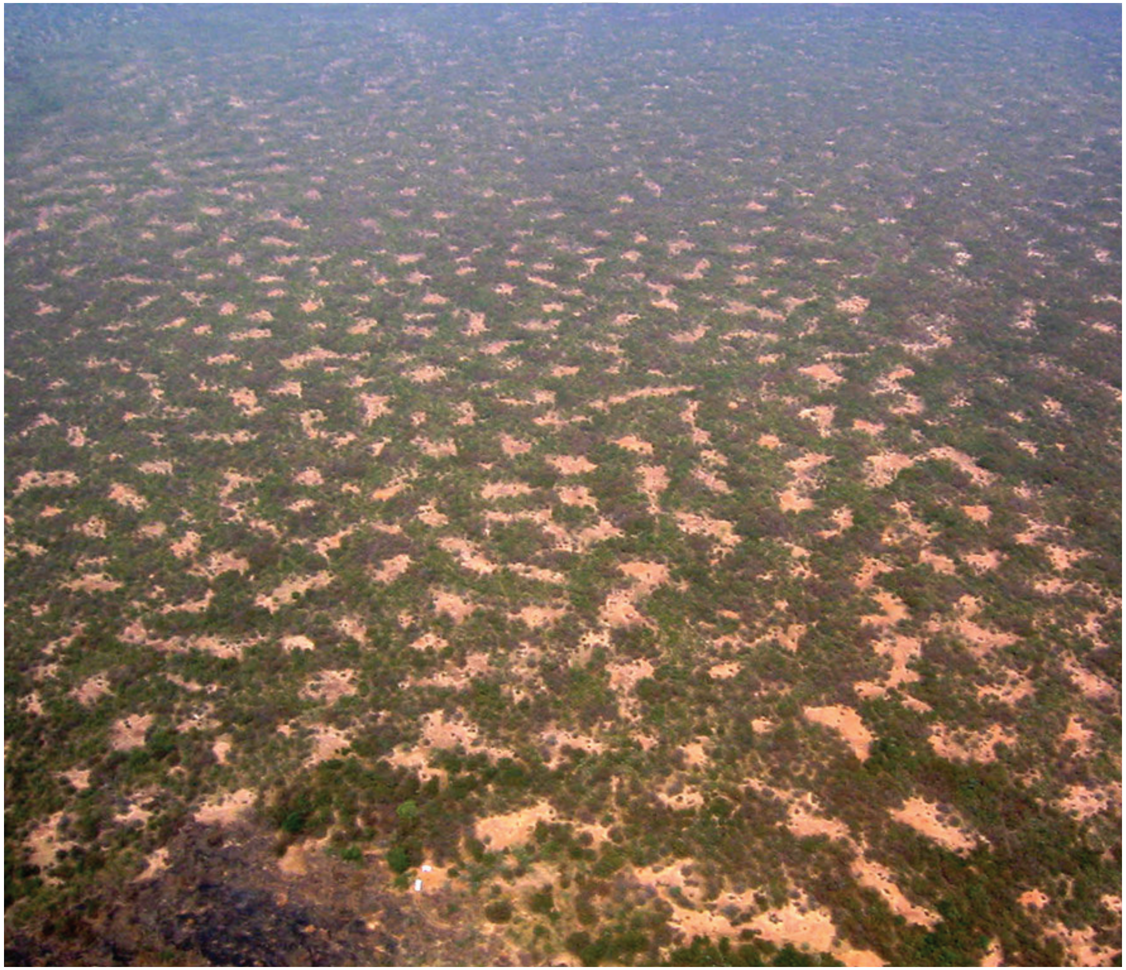

Pinus
ponderosa





Helianthus
annuus

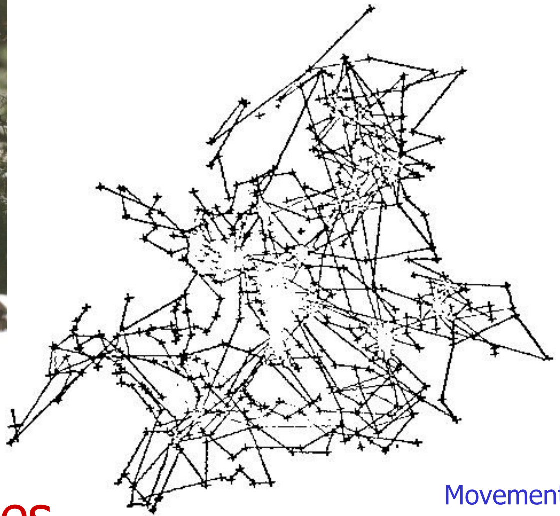
# Ecosystem level: the tigerbush pattern



Benin-Niger National Park

# From the individual to the population level

Red fox (*Vulpes vulpes*)

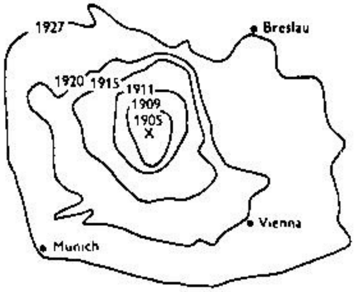


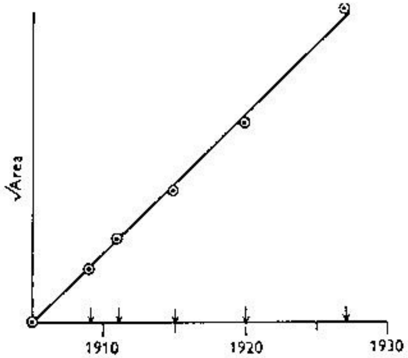
Movements of a red fox
from telemetry (Sniff and Jensen 1969)

**Lagrangian** approaches
follow individuals

e.g., random walks

**Eulerian** approaches
describe spatial densities

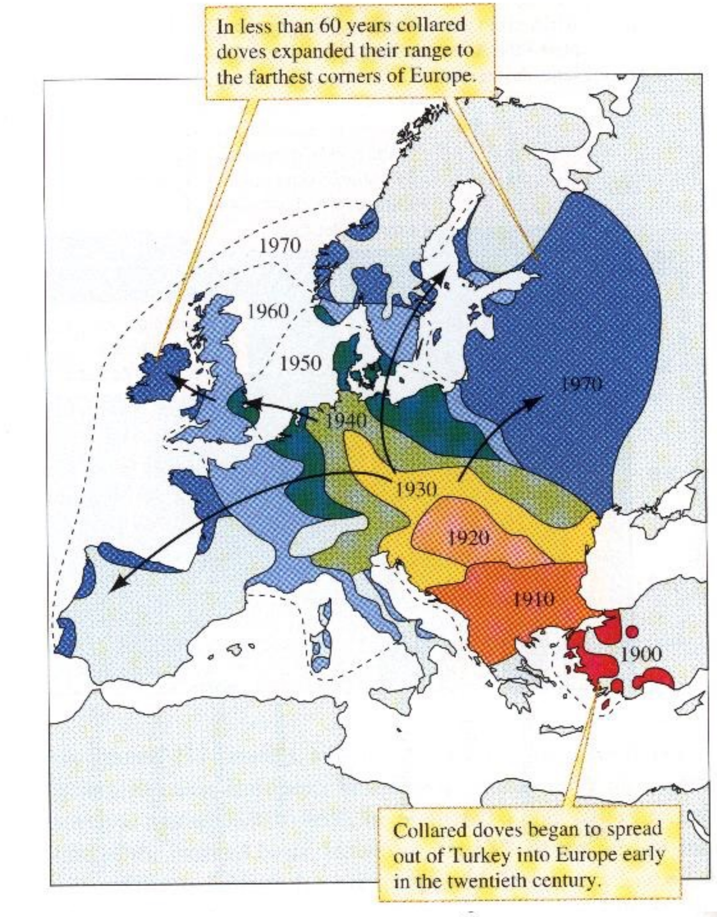


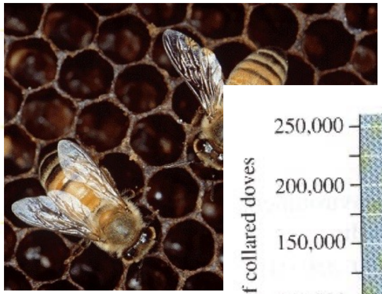

Skellam 1951

Muskrat (*Ondatra zibethica*)

# Population level: waves of species

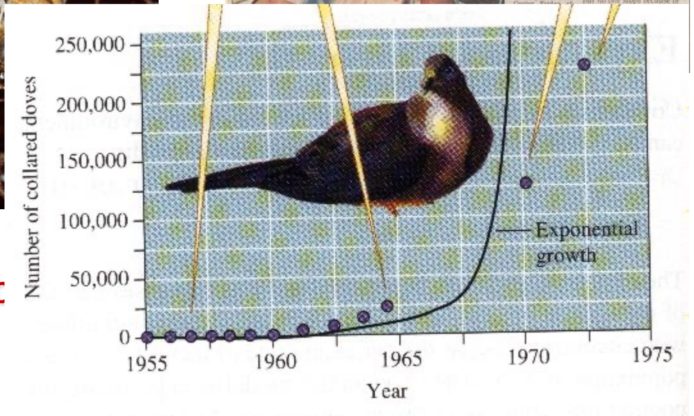



Apis mellifera
(European bee)

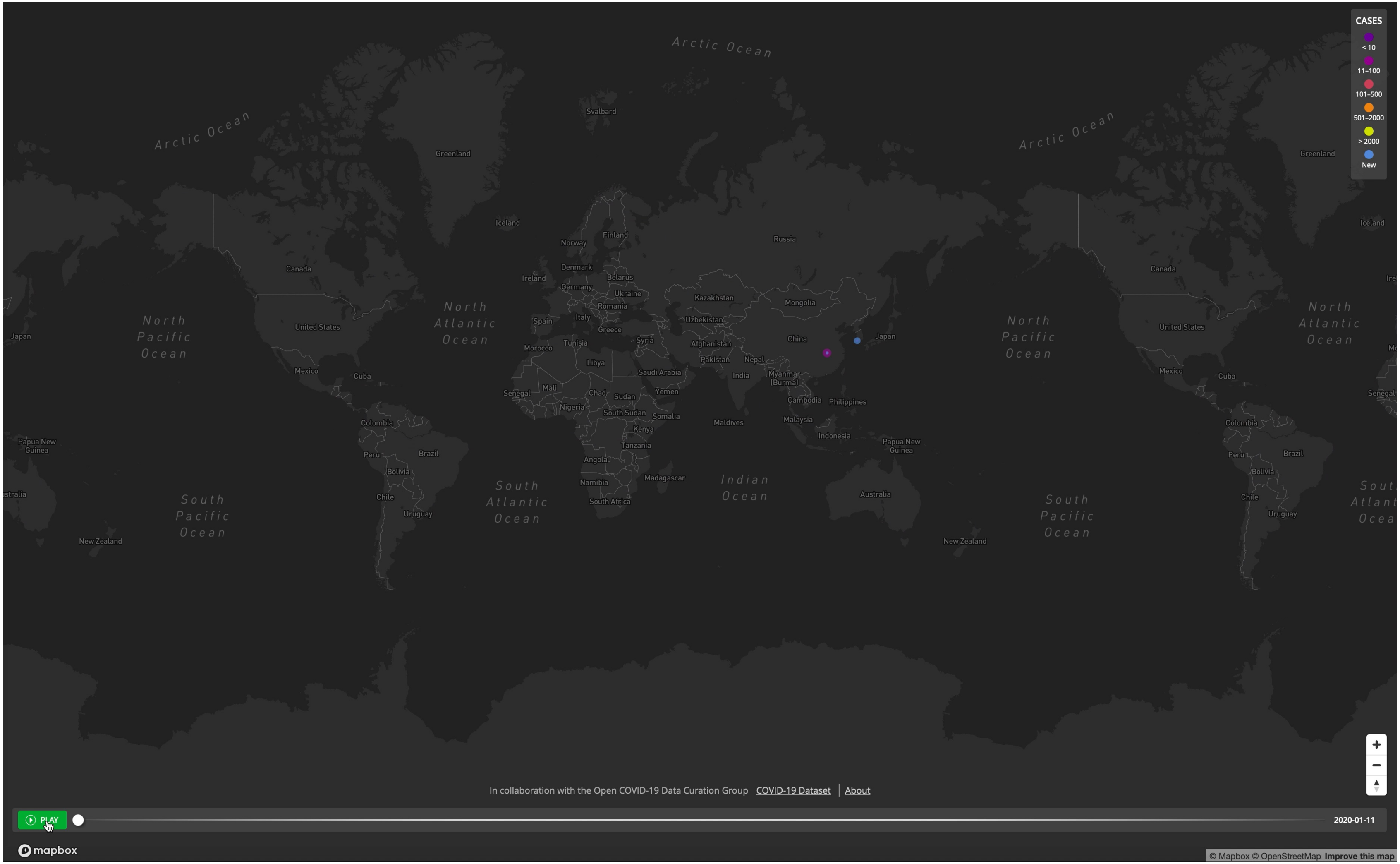


Streptopelia decaocto
(Collared dove)

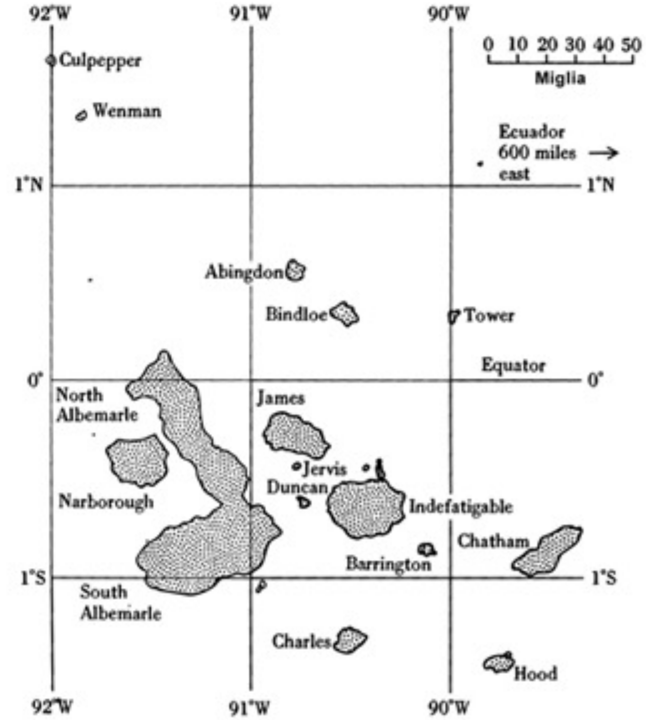
Apis mellifera
(Killer b

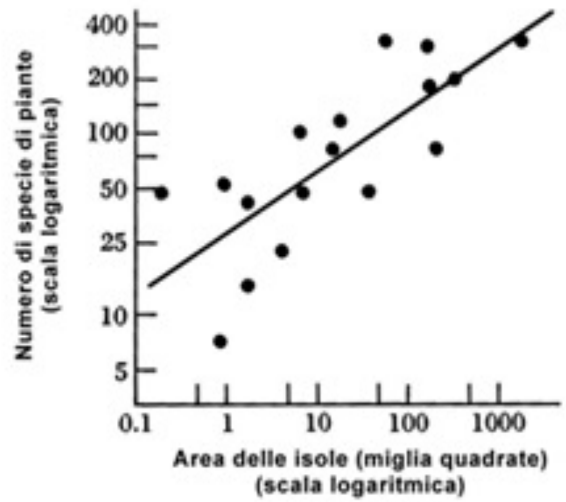


# COVID-19 (SARS-CoV-2) diffusion all over the world (January-May 2020)

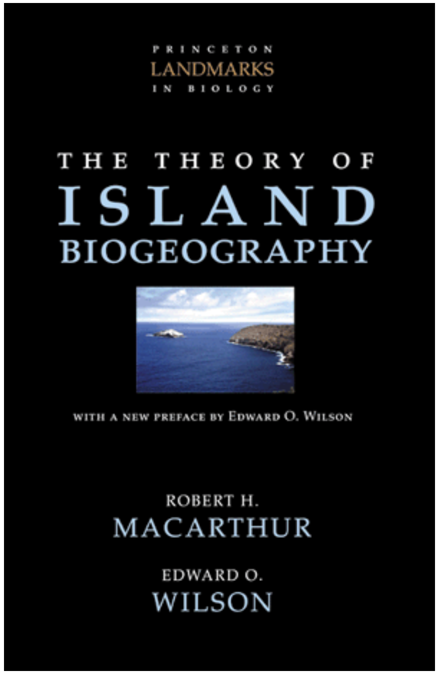


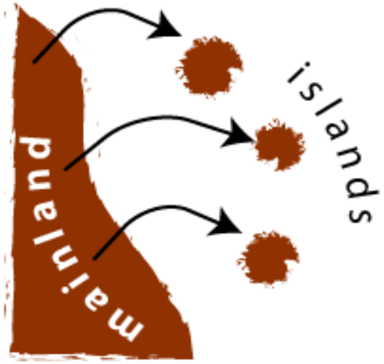
# The area effect

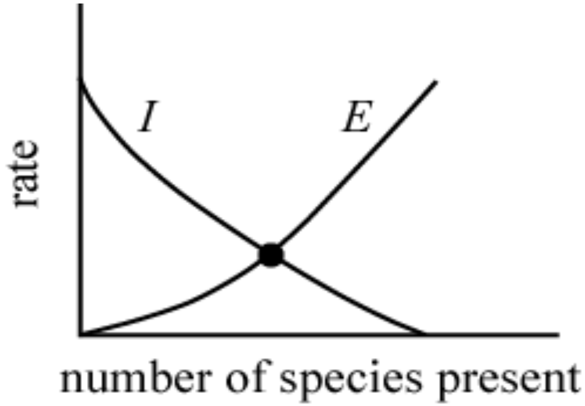


# Island biogeography



# Populations are often spatially subdivided

The patchiness

Andrewartha

*A natural population occupying any considerable area will be made up of a number of ... local populations or colonies. In different localities the* [demographic] *trends may be going in different directions at the same time.*

(Andrewartha and Birch 1954
*The Distribution and Abundance of Animals*, p. 657)

and *The balance of Nature*

Slobodkin

*Despite this enormous variation in reproductive patterns, each female adult animal alive now — in every species, in almost every location — will be replaced by precisely one female alive a generation from now. If this were not the case, the size of animal populations would be changing permanently and strikingly at a much greater rate than any existent evidence indicates.*

(Slobodkin 1962
*Growth and Regulation of Animal Populations*, p. 657)

# Discrete populations as subpopulations

with a reply

*Over the five years 1960 — 64, a casual observer wandering along the ridge find* Euphydryas editha *butterflies on the wing there every spring.* "How precise is the control of natural populations" *he might say,* "for are there not butterflies here every year?" *He might even guess at the number of butterflies present each year. He could then add up is estimates, divide by the number of years, and come up with an average on a chart of his yearly estimates he would find the average presented as a straight line parallel to the time axis. It could not, of course, be otherwise.* "Nature" *he would say,* "keeps the average size of this population constant."

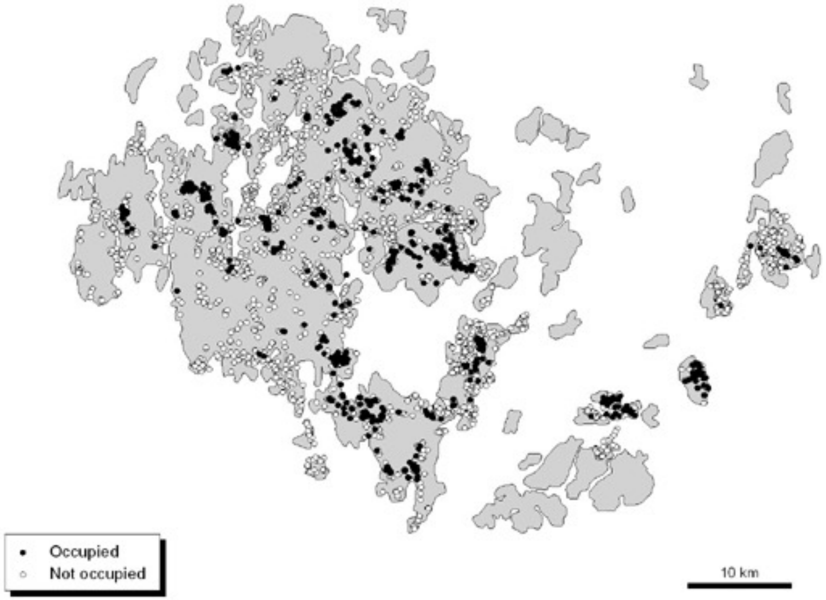
*Only if our observer had taken the trouble to determine that the ridge was actually occupied by three discrete populations of* E. editha *would we have found out what was actually going on: that, in fact, he had witnessed one population increase steadily in size, another fluctuate in size, and the third decrease to extinction*

(Ehrlich 1962
*Evolution* 19:327 — 336)

# A very much studied case

Ilkka Hanski

Glanville fritillary butterfly
(*Melitaea cinxia*)



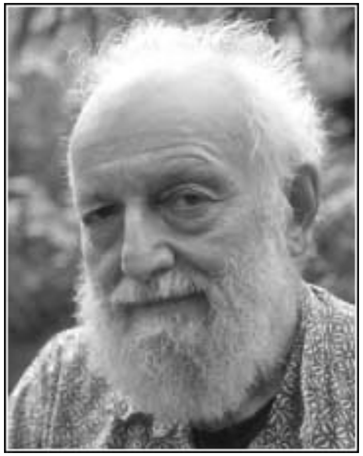

Åland Islands (Finland)

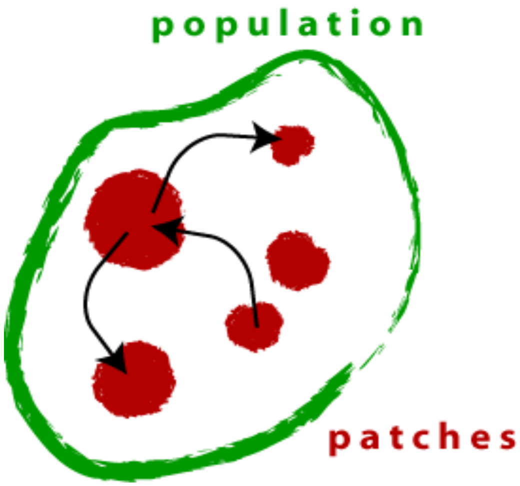
# Metapopulations: populations of populations

to the metapopulation concept (Levins, 196?)

*Since the area over which control is sought is much greater than that of the local population, the control strategy* must *be defined for* a population of populations *in which* local extinctions are balanced by emigration from other populations.

(Levins 1969
*Bulletin of the Entomological Society of America* 15:237-240)





## Euphydryas editha



362 THE AMERICAN NATURALIST

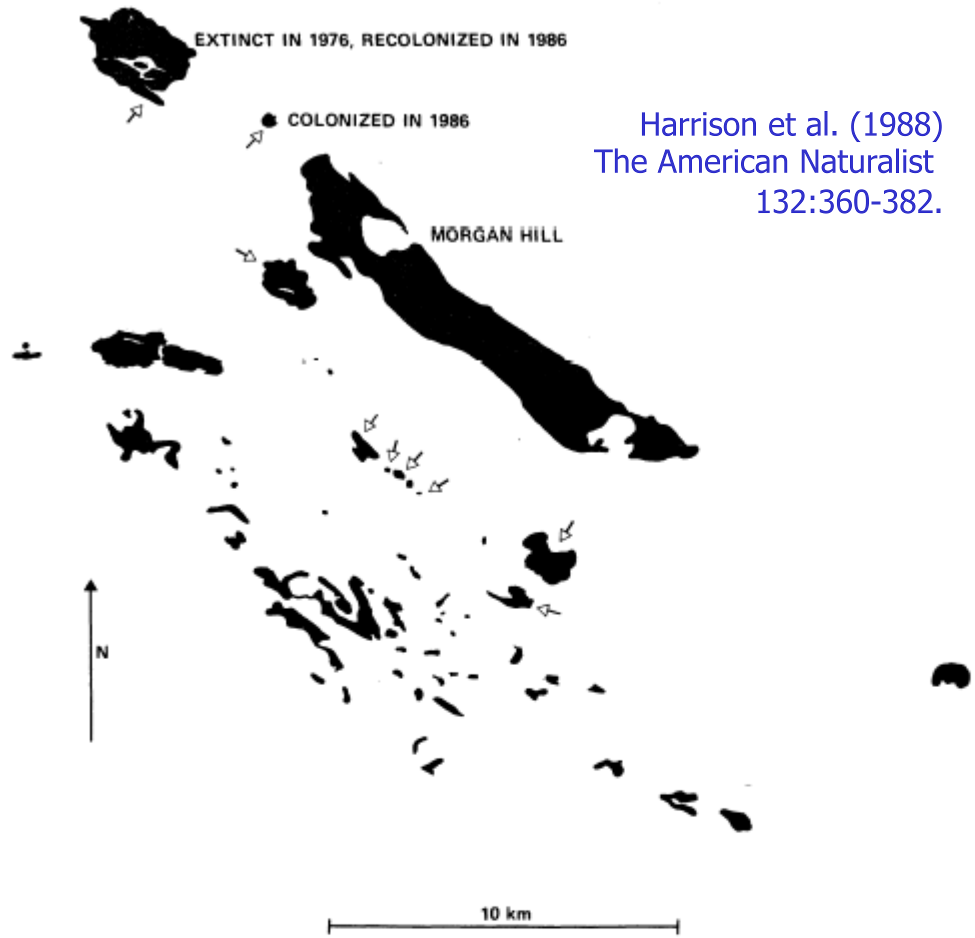
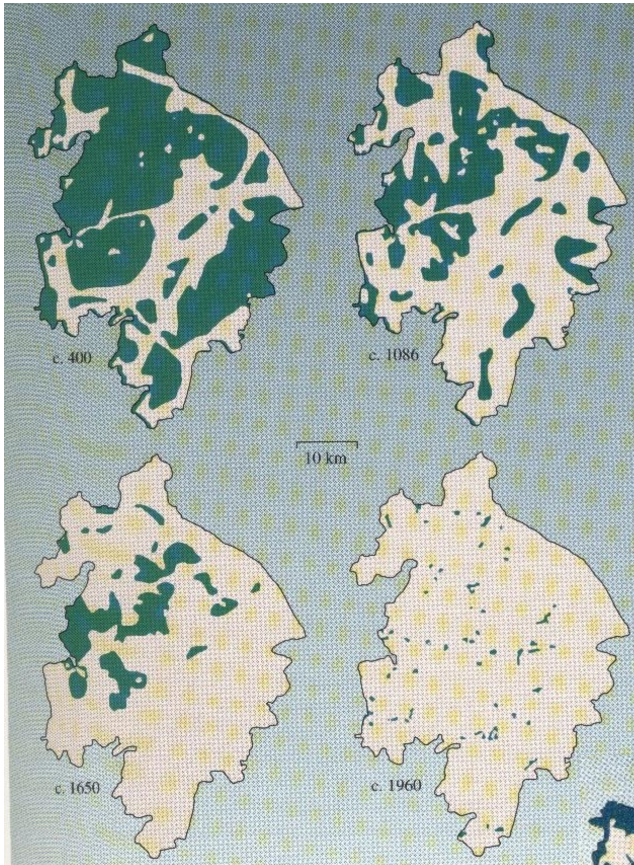



FIG. 1.—Distribution of serpentine grasslands in southern Santa Clara County, California, and butterfly populations in 1987. Population MH is located on the large patch labeled "Morgan Hill." Arrows indicate the locations of the seven small populations measured by the mark-recapture technique in 1987. Two additional patches at the upper left, colonized in 1986, also support populations.

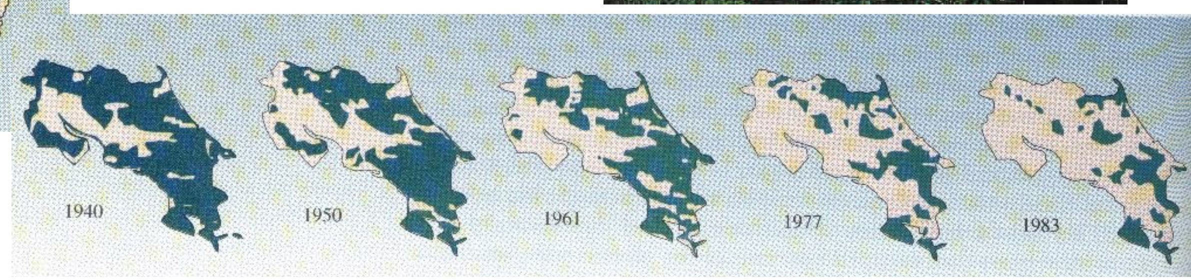
Harrison et al. (1988)
The American Naturalist
132:360-382.

# The influence of man: habitat fragmentation




Forests in England


Brazil

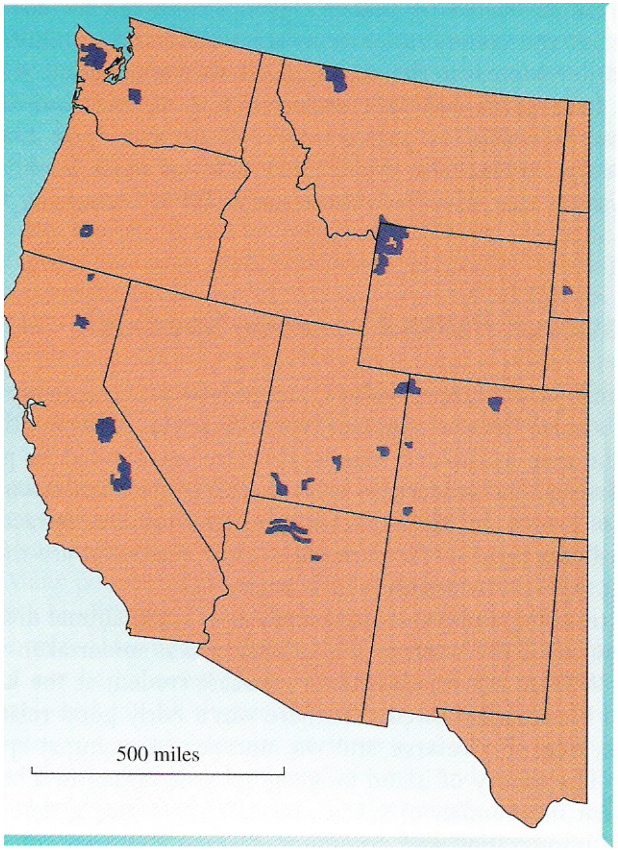


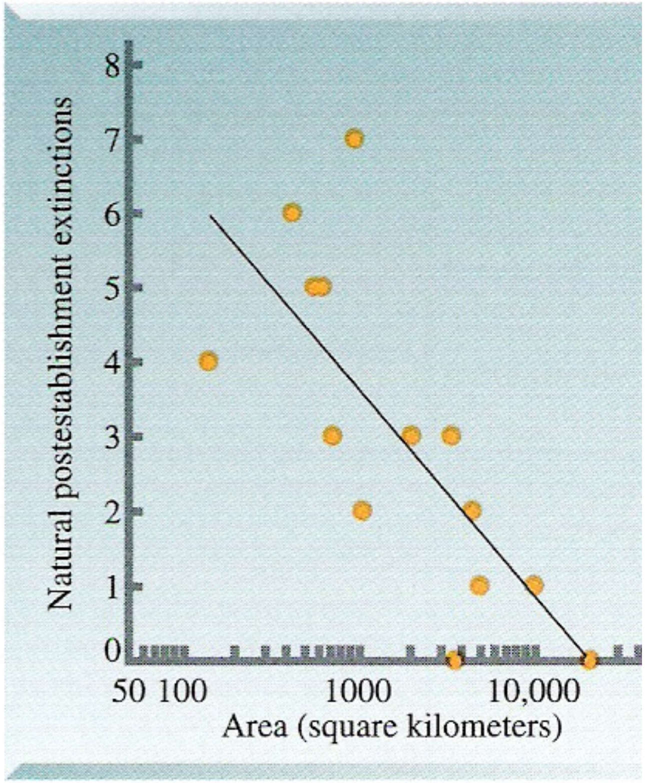

Forests in Costarica

# The monk seal

*Monachus monachus*


# Reserve area and extinction

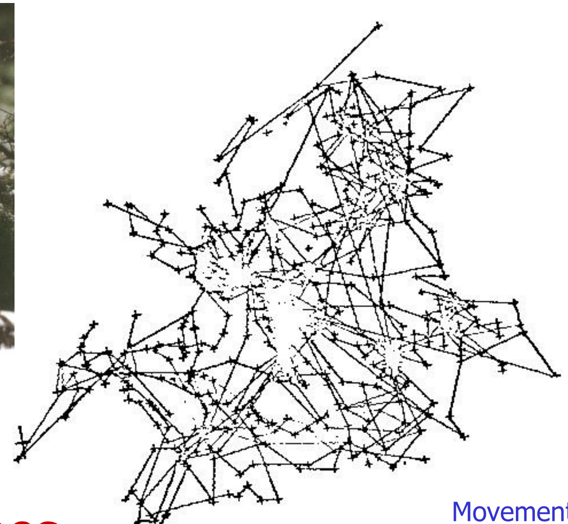



National parks in western USA

# Analysing the movement of organisms and the consequences on their spatial distribution

Red fox (*Vulpes vulpes*)

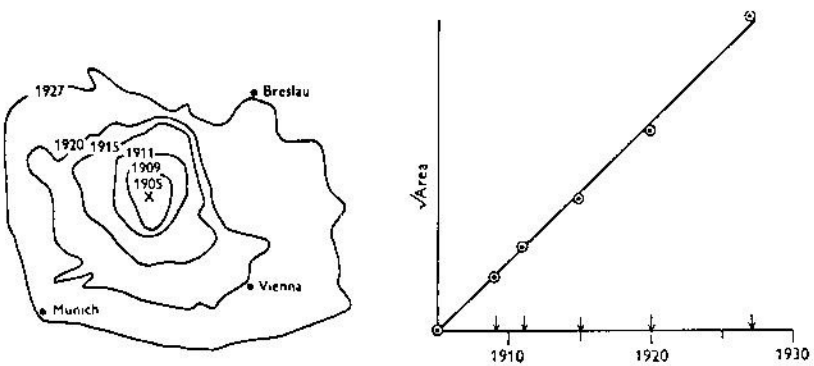


Movements of a red fox
from telemetry (Sniff and Jensen 1969)

**Lagrangian** approaches
follow individuals

e.g., random walks

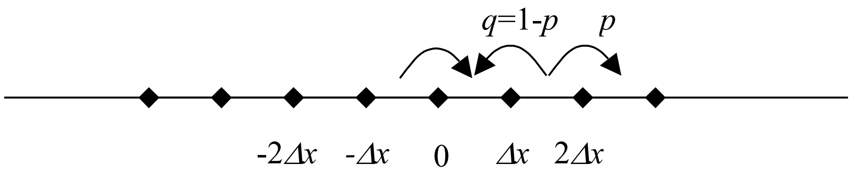
**Eulerian** approaches
describe spatial densities




Skellam 1951

Muskrat (*Ondatra zibethica*)

# The diffusion-advection equation




Random walk

$p$ = Prob. moving right

- $n(x,t)\,\Delta x$ = No. of organisms between $x$ and $x+\Delta x$ at time $t$
- $p\,n(x,t)\,\Delta x$ = No. of organisms moving from $x$ to $x+\Delta x$ in time interval $\Delta t$
- Letting $\Delta x$ and $\Delta t$ tend to zero <u>suitably</u> we get

$$\frac{\partial n}{\partial t} = -v\frac{\partial n}{\partial x} + D\frac{\partial^2 n}{\partial x^2}$$

advection (transport, drift)

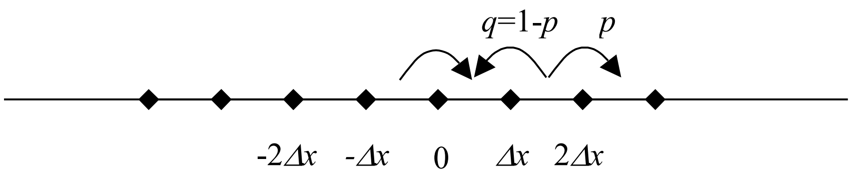
$v$ = velocity

diffusion

$D$ = diffusion coefficient

# The diffusion approximation (1)

How can we obtain the diffusion-advection equation from random walk?




$p$ = Prob. moving right

1st assumption: particle number is very large

$n(x,t)$ = particle concentration

Mass balance:

$$n(x,t + \Delta t)\,\Delta x = p\, n(x-\Delta x,t)\,\Delta x + (1-p)\, n(x+\Delta x,t)\,\Delta x$$

Expanding both sides we get

$$n(x,t)+\frac{\partial n}{\partial t}\Delta t+O(\Delta t^2)=p\left[n(x,t)-\frac{\partial n}{\partial x}\Delta x+\frac{1}{2}\frac{\partial^2 n}{\partial x^2}\Delta x^2+O(\Delta x^3)\right]+$$

$$+(1-p)\left[n(x,t)+\frac{\partial n}{\partial x}\Delta x+\frac{1}{2}\frac{\partial^2 n}{\partial x^2}\Delta x^2+O(\Delta x^3)\right]$$

# The diffusion approximation (2)

Dividing by $\Delta t$ we get

$$\frac{\partial n}{\partial t} + \frac{O(\Delta t^2)}{\Delta t} = (1-2p)\frac{\partial n}{\partial x}\frac{\Delta x}{\Delta t} + \frac{1}{2}\frac{\partial^2 n}{\partial x^2}\frac{\Delta x^2}{\Delta t} + \frac{O(\Delta x^3)}{\Delta t}$$

Let $\Delta x$ and $\Delta t$ tend to zero in the following way (2nd assumption)

$\frac{\Delta x}{\Delta t} =$ absolute movement speed of a single particle ➔ $\infty$

$\frac{1}{2}\frac{\Delta x^2}{\Delta t} \to D$ = finite positive constant = diffusion coefficient

$(2p-1)\frac{\Delta x}{\Delta t} = p\frac{\Delta x}{\Delta t} + (1-p)\frac{-\Delta x}{\Delta t} =$ average population velocity ➔ $v$, a finite constant

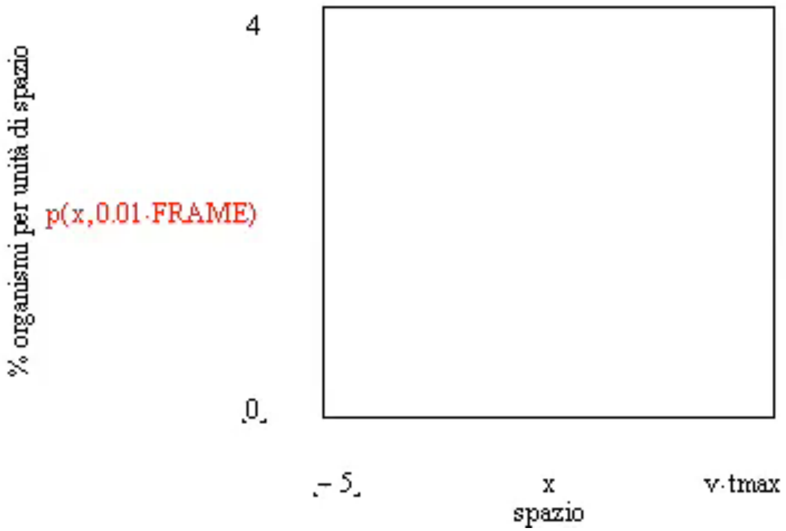
Since $\Delta x / \Delta t$ ➔ $\infty$ advection velocity (drift) is finite only if $p$ ➔ 1/2

$$\boxed{\frac{\partial n}{\partial t} = -v\frac{\partial n}{\partial x} + D\frac{\partial^2 n}{\partial x^2}}$$

# Safe tracer in a river

# Pure diffusion in one dimension

- We can get rid of drift by switching to spatial coordinate travelling at speed $v$ : $u(x,t) = n(x+vt,t)$
  $u$ satisfies equation of pure diffusion $$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2}$$



# Pure diffusion in one dimension

- $n(x,t)$ = concentration in $x$ at time $t$

$$\frac{\partial n}{\partial t} = D \frac{\partial^2 n}{\partial x^2}$$

$$n(x,t) \geq 0 \quad \forall x \qquad t \geq 0$$

- with suitable
  - initial conditions $n(x,0) = n_0(x)$
  - boundary conditions in space

# Boundary and initial conditions

- **Infinite domain** (-∞,+∞), Cauchy problem
  - Initial conditions

    $n(x,0) = n_0(x)$
  - Solution must be bounded (otherwise not unique)

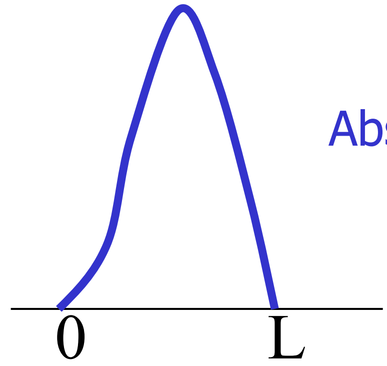
$$\int_{-\infty}^{+\infty} n(x,t)dx = \int_{-\infty}^{+\infty} n_0(x)dx = \text{Initial number}$$

- **Bounded domain**
  - Space domain is bounded: in one dimension a finite interval $[0, L]$
  - Initial conditions

    $n(x,0) = n_0(x)$ given

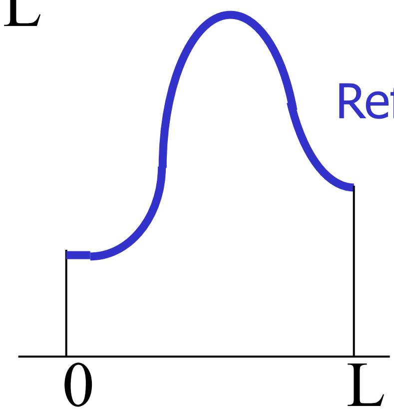
1. Unsuitable habitat outside domain (absorbing boundary, Dirichlet problem)
2. No flux through the boundary (reflecting boundary, Neumann problem)
3. Environment is a circle or a sphere or a torus, (periodic conditions, Dirichlet problem)

$$n(0,t) = n(L,t) = 0$$




Absorbing barrier

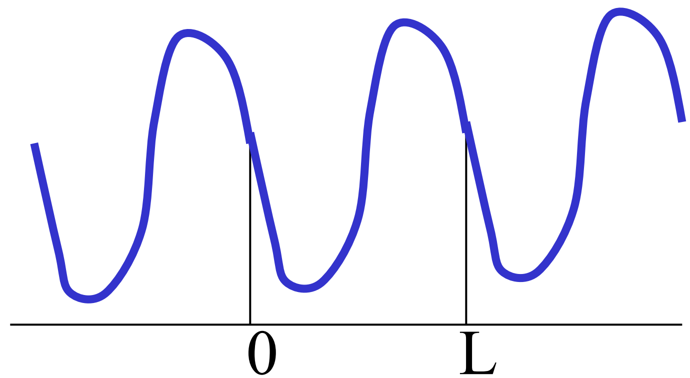
$$\frac{\partial n}{\partial x}(0,t) = \frac{\partial n}{\partial x}(L,t) = 0$$

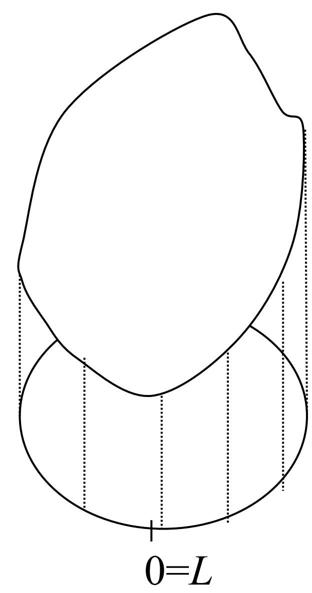



Reflecting barrier

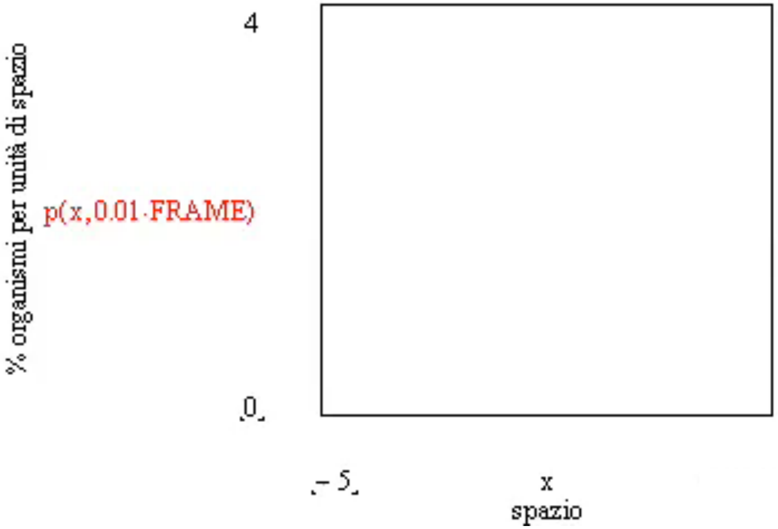
$$n(0,t) = n(L,t)$$

Periodic conditions



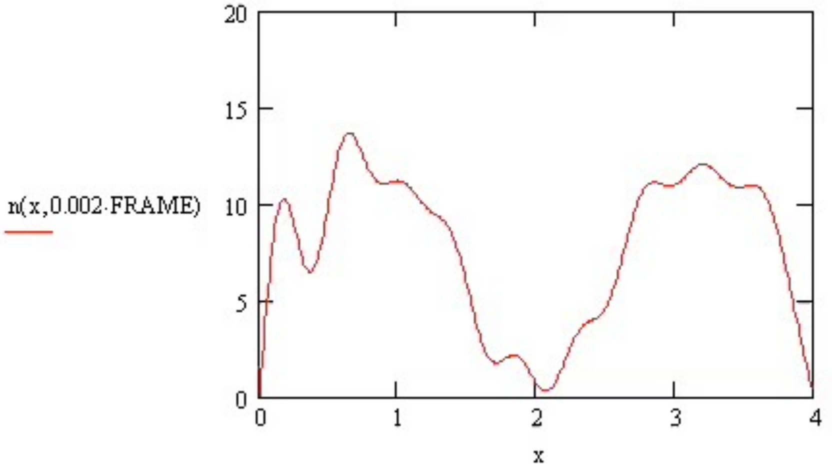



# Simulating diffusion (and drift)

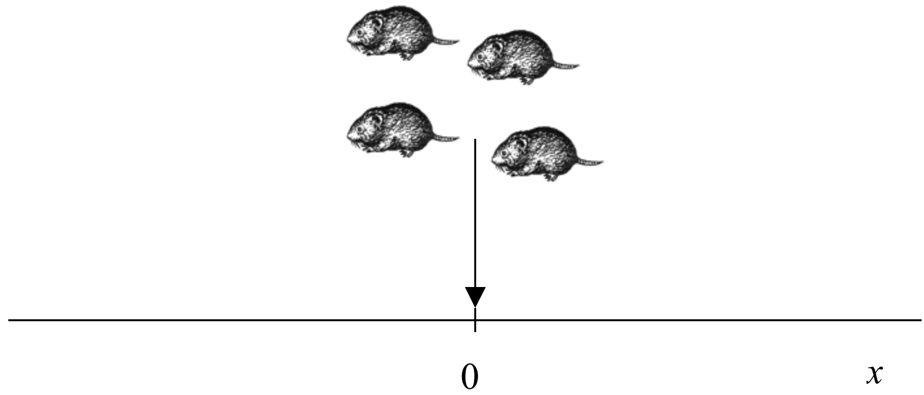



Diffusion and drift in unbounded habitat

Diffusion in bounded habitat (absorbing barrier)



# Diffusion in infinite domain (no barriers)




$N$ organisms are released in a given location and move

$p(x,t) = n(x,t)/N$ = fraction of organisms per unit space

$$\int_{-\infty}^{+\infty} n(x,t)\,dx = N \quad \text{for any } t$$

$$\int_{-\infty}^{+\infty} p(x,t)\,dx = 1$$

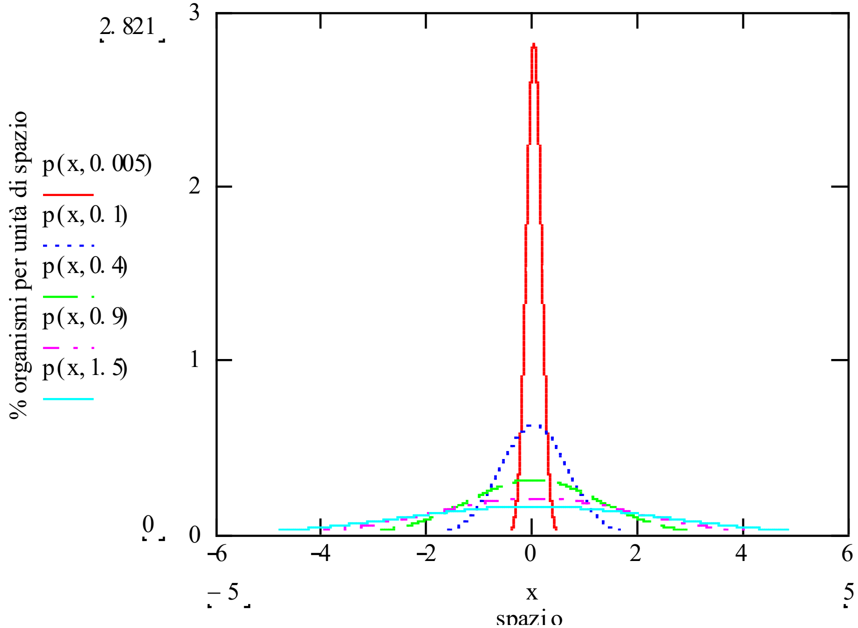
$$n(x,t) = Np(x,t)$$

$$p(x,t) = \frac{1}{\sqrt{4\pi Dt}} \exp\left(-\frac{1}{2}\frac{x^2}{2Dt}\right)$$

SOLUTION!

Normal distribution

# Solution properties




Standard deviation $\sigma_x = \sqrt{2Dt}$

Average distance from release point

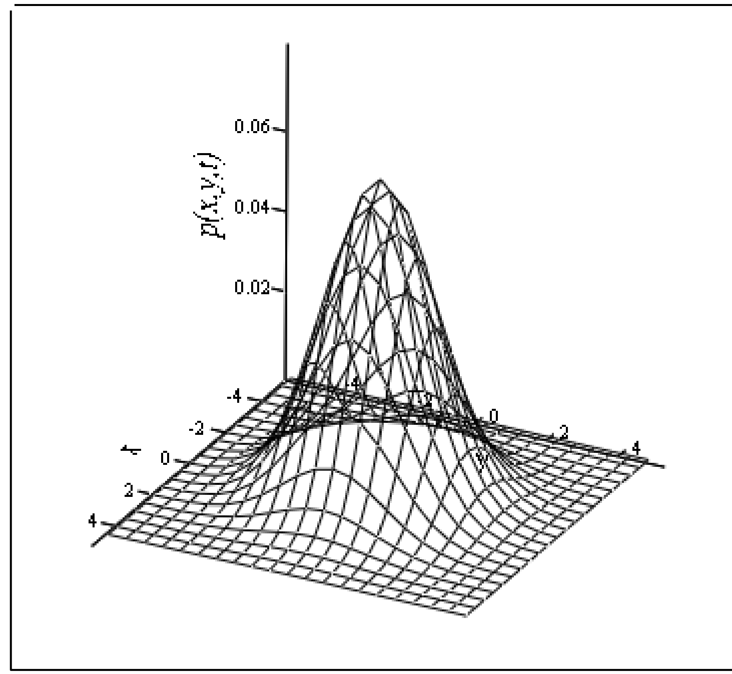
$$E\left[|x|\right] = \int_{-\infty}^{+\infty} |x|\, p(x,t)\, dx = 2\int_{0}^{+\infty} x p(x,t)\, dx = \sqrt{\frac{4Dt}{\pi}} = 1.128\sqrt{Dt}$$

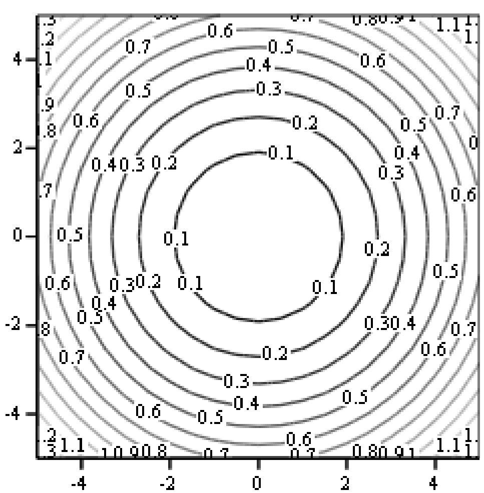
# Diffusion in 2 dimensions (isotropic)

Release $A$ organisms at 0

$$n(x,y,t) = \frac{A}{4\pi Dt} \exp\left(-\frac{1}{2}\frac{x^2+y^2}{2Dt}\right)$$

fraction outside circle of radius $R$ = $\exp\left(-\frac{R^2}{4Dt}\right)$




Area containing 99% of organisms at different times

α = fraction outside $R$

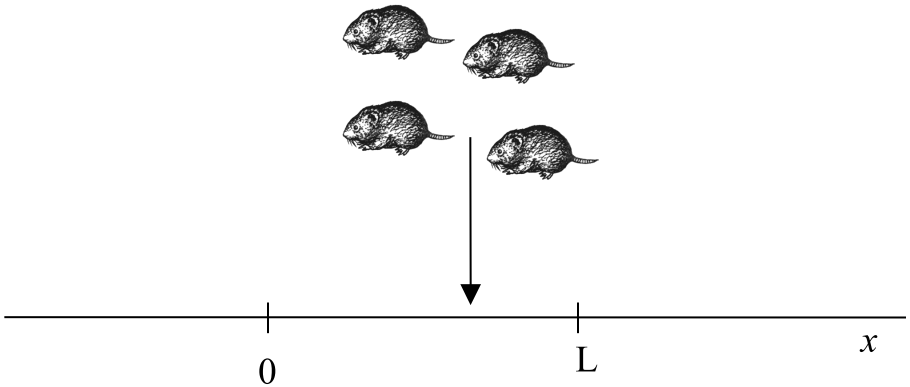
$$R_\alpha = 2\sqrt{\ln(1/\alpha)}\sqrt{Dt}$$

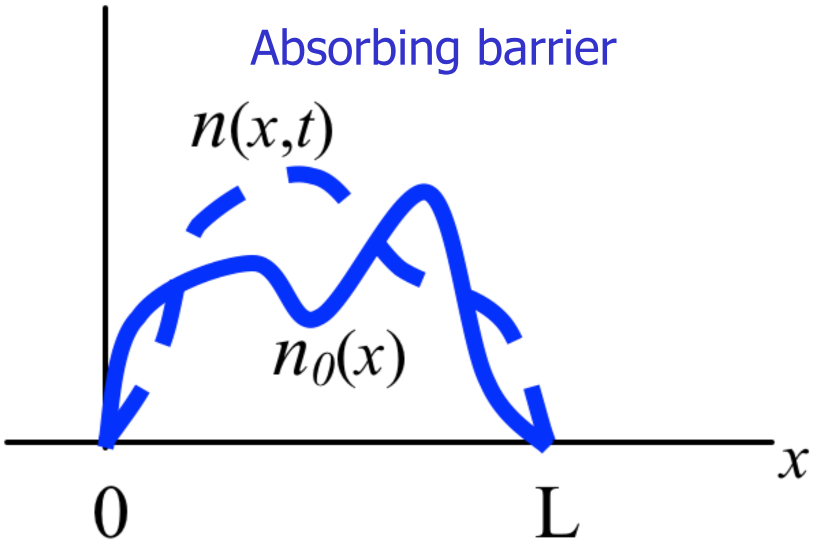
$$R_{0.01} = 4.292\sqrt{Dt}$$

$$\text{"}velocity\text{"} \div \sqrt{D/t}$$

Velocity is decreasing with time

# Diffusion in a bounded domain (e.g. island)



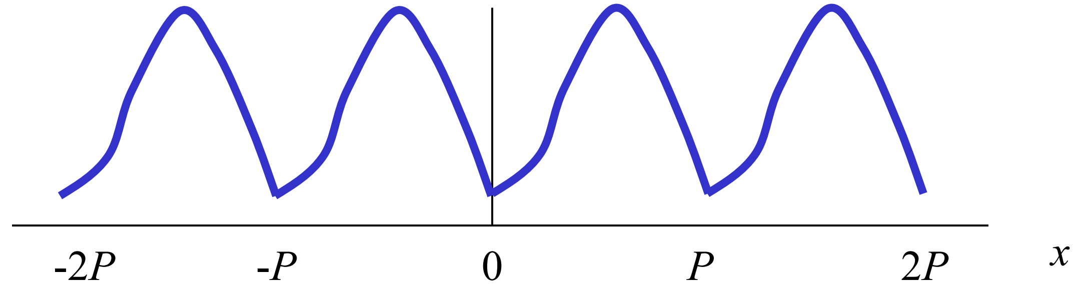

$$\frac{\partial n}{\partial t} = D\frac{\partial^2 n}{\partial x^2}$$

$n(x,0) = n_0(x)$

$n(0,t) = n(L,t) = 0$

# Fourier series

- Periodic and continuous function *f*(*x*)



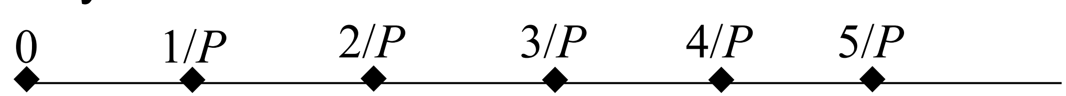

$$f(x)=\frac{a_0}{2}+\sum_{k=1}^{\infty} a_k \cos\left(\frac{2\pi k}{P}x\right)+b_k \sin\left(\frac{2\pi k}{P}x\right)$$

$$a_k=\frac{2}{P}\int_0^P f(x)\cos\left(\frac{2\pi k}{P}x\right)dx=\frac{2}{P}\int_{-\frac{P}{2}}^{\frac{P}{2}} f(x)\cos\left(\frac{2\pi k}{P}x\right)dx$$

$$b_k=\frac{2}{P}\int_0^P f(x)\sin\left(\frac{2\pi k}{P}x\right)dx=\frac{2}{P}\int_{-\frac{P}{2}}^{\frac{P}{2}} f(x)\sin\left(\frac{2\pi k}{P}x\right)dx$$

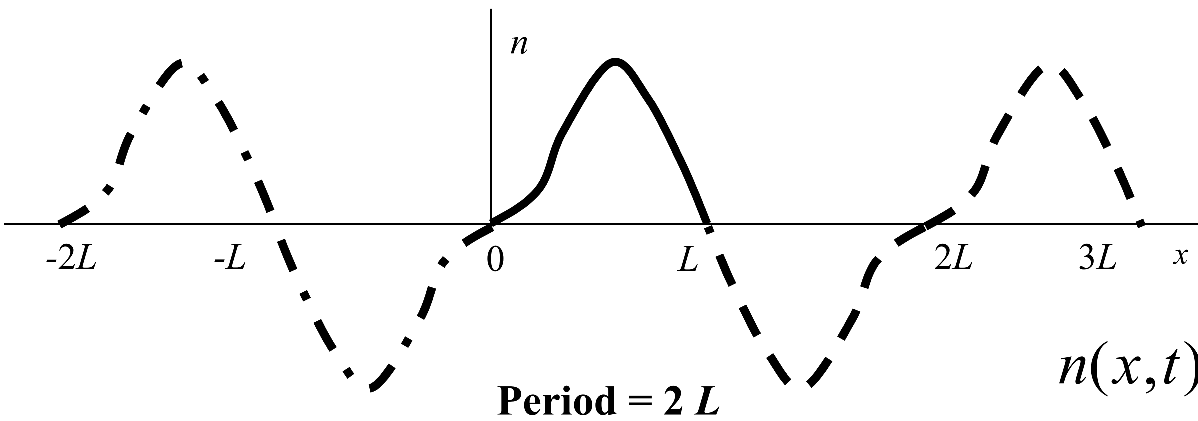
$$\frac{a_0}{2}=\frac{1}{P}\int_0^P f(x)dx=mean\ \ value$$

- *k*/*P* = frequency
- 2π*k*/*P* = angular frequency
- *k* = wave number




spatial frequency

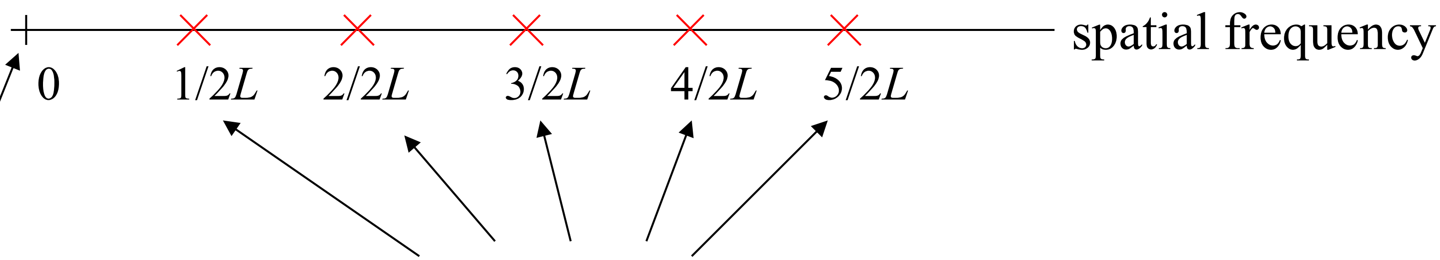
# Absorbing boundary




$$n(0,t) = n(L,t) = 0$$

for any $t$

$$n(x,t) = \sum_{k=1}^{\infty} B_k(t) \sin\left(\frac{\pi k}{L} x\right)$$

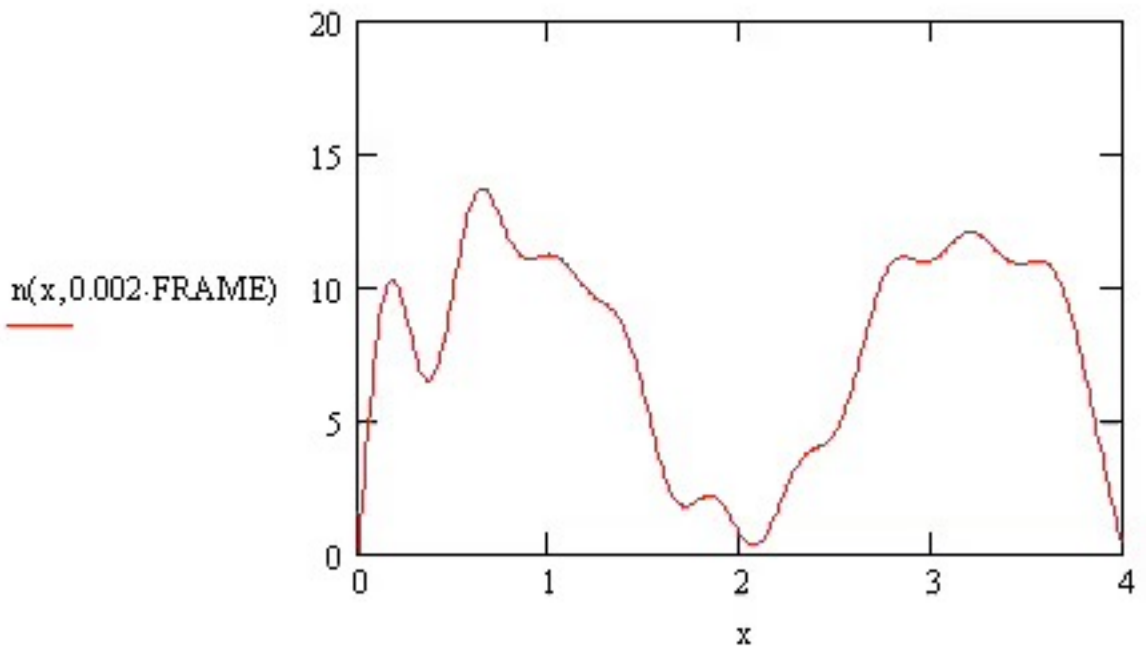



Excited modes

This mode is not excited because boundary is absorbing

$$B_k(t) \div \exp(-D\eta_k^2 t) \quad \eta_k = \frac{\pi k}{L}$$

# Simulation of diffusion in finite habitat with absorbing boundary



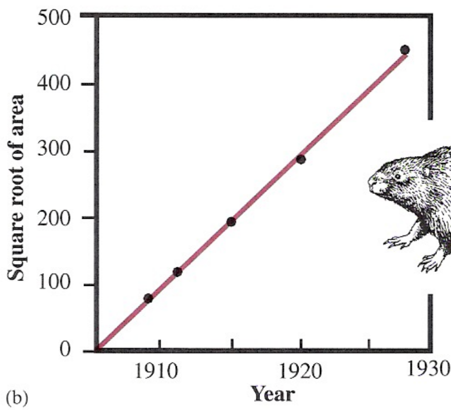

$n(x,t) \rightarrow 0$ for $t \rightarrow \infty$

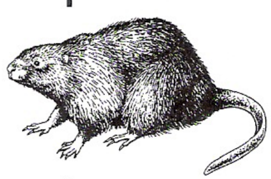
Modes of smaller wavelength $\rightarrow$ 0 more rapidly

$$B_k(t) \div \exp(-D\eta_k^2 t) \quad \eta_k = \frac{\pi k}{L}$$

# Muskrat invasion

*Ondatra zibethica*



Skellam 1951

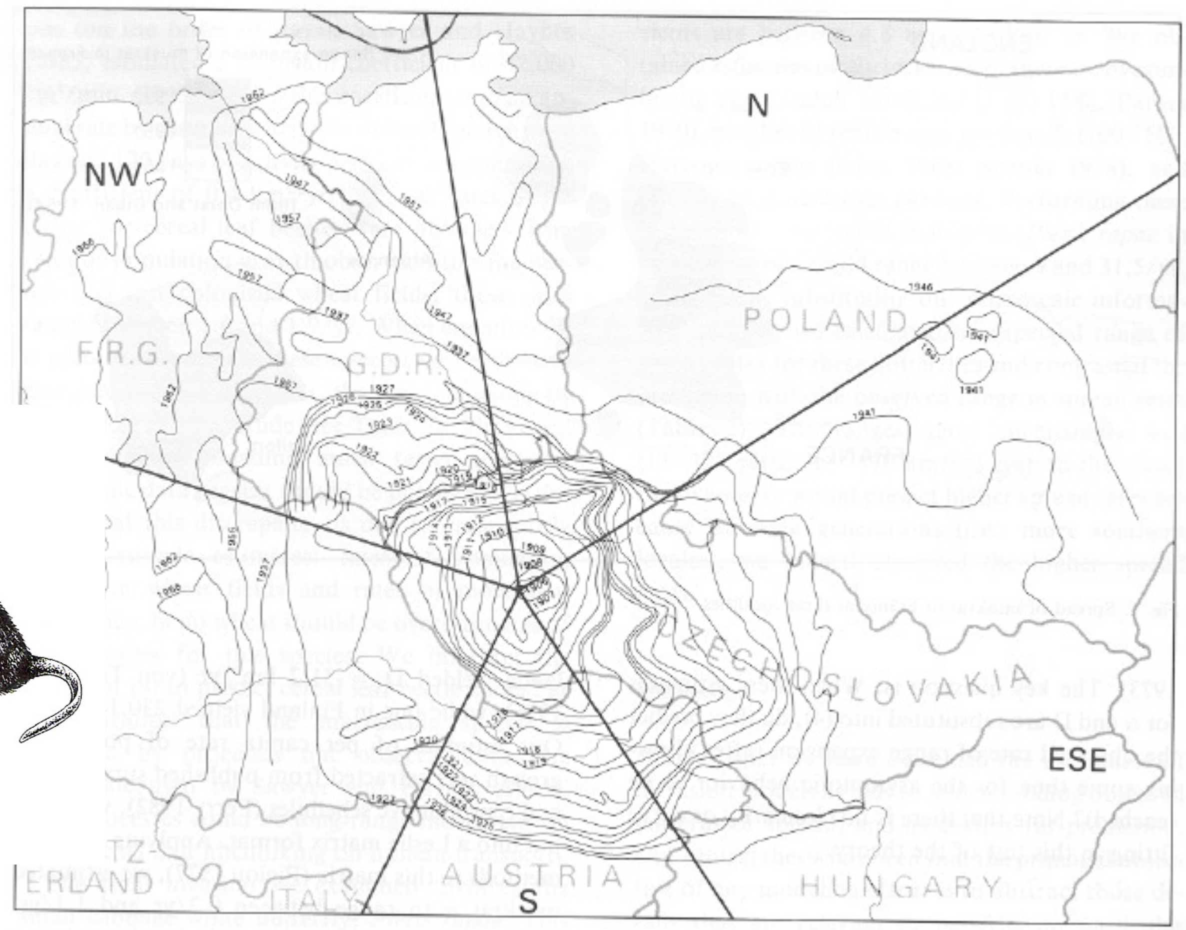



*Fig. 1.* Spread of muskrat from Prague in five sectors. The S/ESE and ESE/N boundaries roughly separate the eastern European plain; the N/NW boundary distinguishes spread down the Oder River from spread down the Elbe River; the NW/W and W/S boundaries isolate the poorly known W sector.

# Reaction-Diffusion equation

$$\frac{\partial n}{\partial t} = \underbrace{\nu n}_{\text{BIRTHS}} - \underbrace{\mu n}_{\text{DEATHS}} + \underbrace{D \frac{\partial^2 n}{\partial x^2}}_{\text{DIFFUSION}}$$

$$n(x,t) \geq 0$$

Possible assumptions on reaction terms

- $\nu$ = constant $\mu$ = constant $r = \nu - \mu$ = constant

First-order reaction, Malthusian (exponential) growth

- $\nu$ and $\mu$ depend on local concentration $n$

  $\nu - \mu = R(n(x,t))$ = per capita rate of increase

$$\frac{\partial n}{\partial t} = R(n)n + D \frac{\partial^2 n}{\partial x^2}$$

# Infinite domain – Malthusian demography

$$\frac{\partial n}{\partial t} = rn + D\frac{\partial^2 n}{\partial x^2}$$

$r$ = instantaneous rate of increase

Guess: $n(x,t)$ grows exponentially

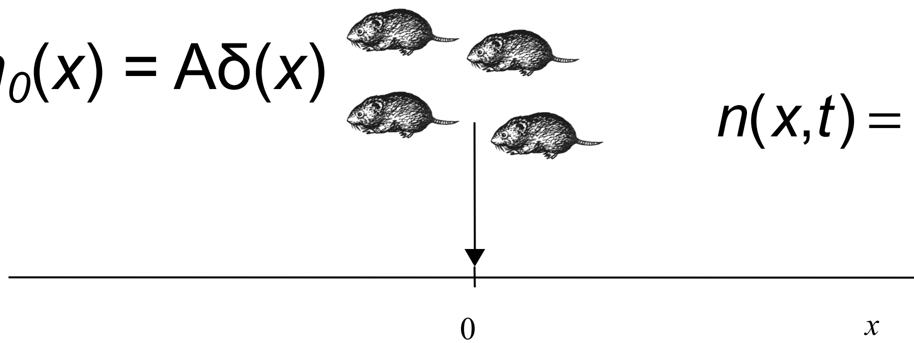
Introducing
$z(x,t) = \exp(-rt)\, n(x,t)$
one obtains

$$\frac{\partial z}{\partial t} = -r\exp(-rt)n(x,t) + \exp(-rt)\frac{\partial n}{\partial t} = -rz + \exp(-rt)\left[D\frac{\partial^2 n}{\partial x^2} + rn\right] = D\frac{\partial^2 z}{\partial x^2}$$

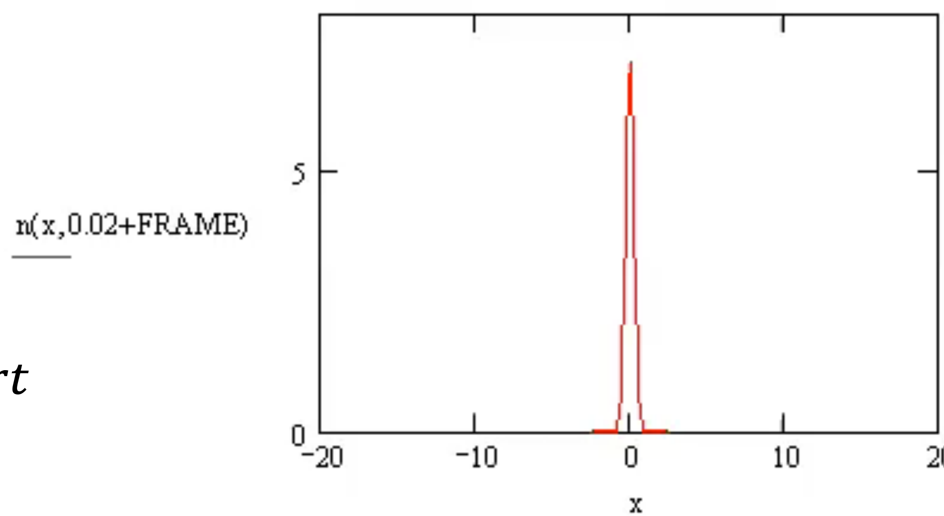
Therefore $n(x,t) = z(x,t)\exp(rt)$ with $z(x,t)$ satisfying pure diffusion model

# Simulation of diffusion and Malthusian growth in infinite domain

$$n_0(x) = A\delta(x)$$




$$n(x,t) = \frac{A}{\sqrt{4\pi Dt}} \exp\left( -\frac{1}{2}\frac{x^2}{2Dt} \right) \exp(rt)$$




$$\int_{-\infty}^{+\infty} n(x,t)\,dx = N_0 e^{rt}$$

# Infinite domain: diffusion and growth in 2 dimensions

Release *A* organisms at origin of *x*-*y* plane

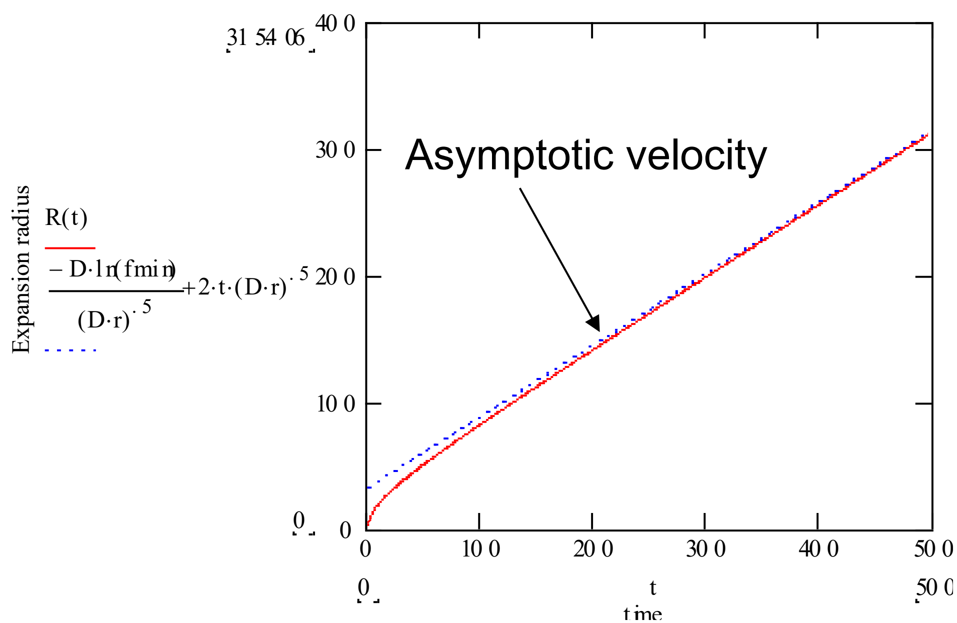
$$n(x,y,t) = A\frac{1}{4\pi Dt}\exp\left(rt - \frac{1}{2}\frac{x^2+y^2}{2Dt}\right)$$

$$\textit{fraction of A outside radius } R_t = \alpha = \exp\left(rt - \frac{1}{2}\frac{R_t^2}{2Dt}\right)$$

$$R_t^2 = 4Drt^2 - 4Dt\ln\alpha$$

prevailing term

$$R_t = \sqrt{4Drt^2 - 4Dt\ln\alpha} \rightarrow \sqrt{4Drt^2} = 2t\sqrt{Dr} + \text{constant}$$




Expansion speed = $2\sqrt{rD}$

Contrast with pure diffusion!

# Grey squirrels and Argentine ants expansion

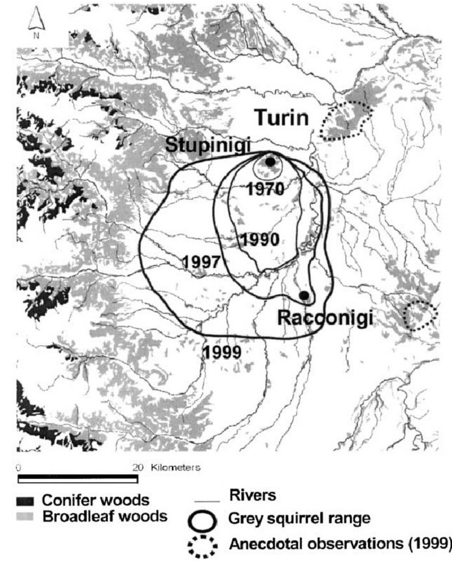



Fig. 2. Grey squirrel expansion in the 1970–1999 period. Distribution in 1970, 1990 and 1997 defined from data published in Wauters et al., 1997b (modified). Distribution in 1999 defined on the basis of hair-tube data.

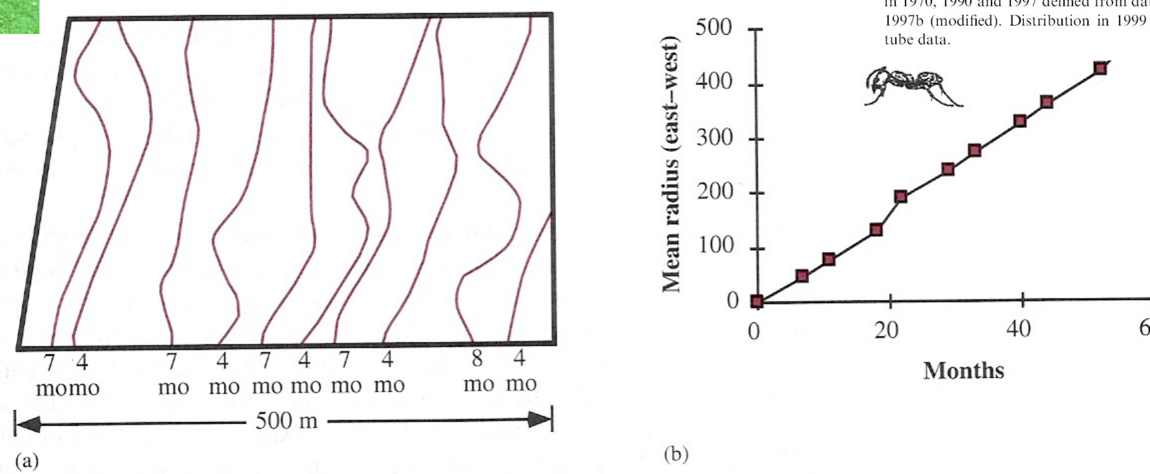
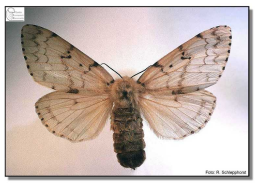



*Figure 2.11*
(a) The spread of Argentine ants across an old field. Each contour gives the approximate limit of the ants at various times. Time is expressed in months since the last census. (b) The positions in the east–west direction are averaged (across the north–south direction), and these averages are plotted as a function of elapsed time in months. Again we see an approximate linear increase in the occupied radius over time. Modified from Erickson (1971).

# Expansion speeds of different species

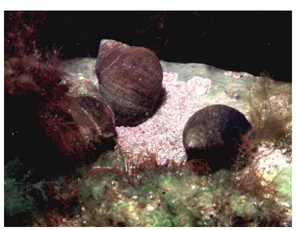
$$velocity \rightarrow 2\sqrt{Dr}$$

*Impatiens*

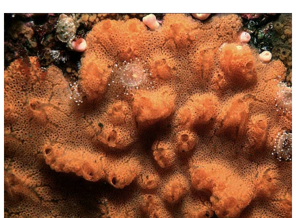


*Lymantria*

*Sciurus*



*Littorina*



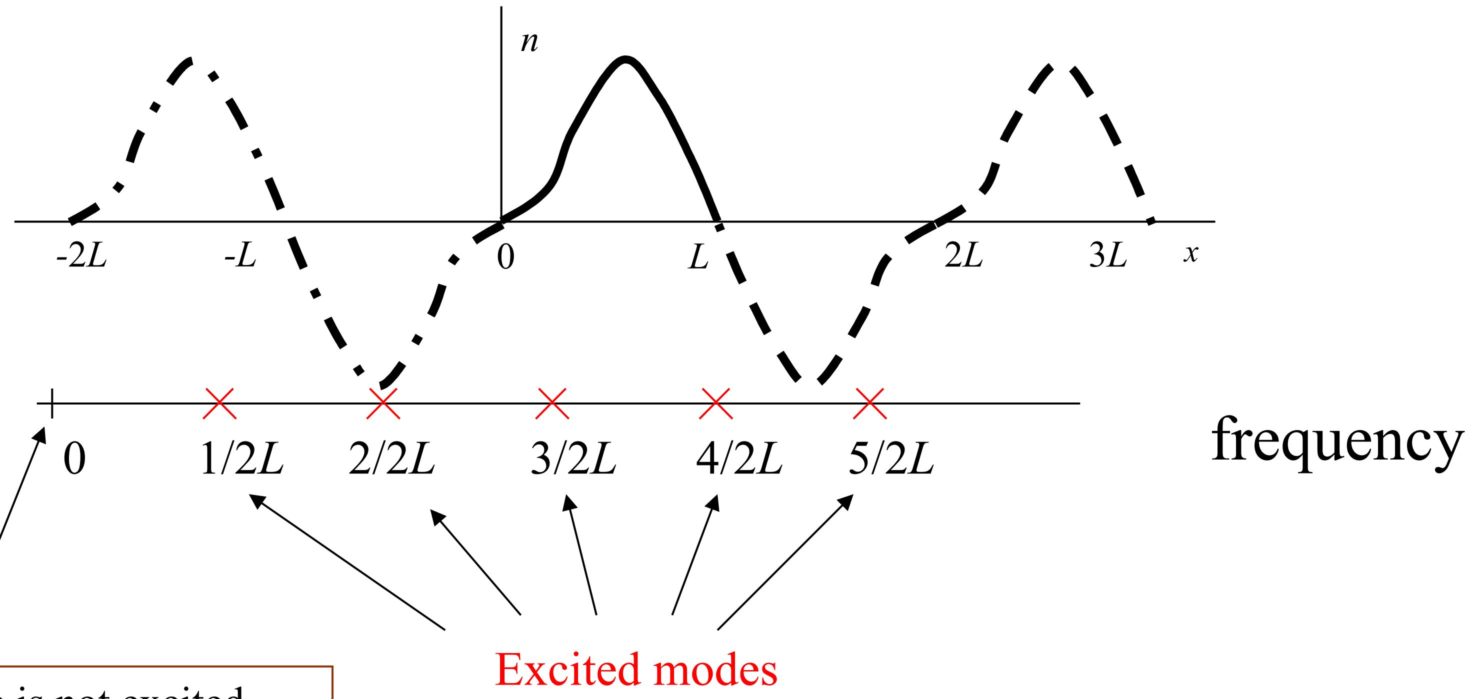
*Botrylloides*

*Table 2.1.* The Observed Rates of Range Expansion for Some Biological Invasi
from Grosholz (1996).

| Species | Latin name | Observed velocity of s (km/yr) |
|---|---|---|
| *Terrestrial species* | | |
| Weedy plant | *Impatiens glandulifera* | 9.4–32.9 |
| Gypsy moth | *Lymantria dispar* | 9.6 |
| Cabbage butterfly | *Pieris rapae* | 14.7–170 |
| Cereal leaf beetle | *Oulema melanopus* | 26.5–89.5 |
| Muskrat | *Ondatra zibethica* | 0.9–25.4 |
| Grey squirrel | *Sciurus carolinensis* | 7.66 |
| Collared dove | *Streptopelia decaocto* | 43.7 |
| European starling | *Sturnus vulgaris* | 200 |
| Plague bacterium (in human host) | *Yersinia pestis* | 400 |
| *Marine Species* | | |
| Tunicate | *Botrylloides leachi* | 16 |
| Bryozoan | *Membranipora membranacea* | 20 |
| Crab | *Carcinus maenas* | 55 |
| Crab | *Hemigrapsus sanguineus* | 12 |
| Barnacle | *Elminius modestus* | 30 |
| Snail | *Littorina littorea* | 34 |
| Mussel | *Mytilus galloprovincialis* | 115 |
| Mussel | *Perna perna* | 95 |

# Absorbing boundary

Question: Introduce *N* organisms in an island of size *L*. Will the population grow or become extinct?




This mode is not excited because boundary is absorbing (mean value =0)

Rates of eponential increase = $r - D\dfrac{\pi^2 k^2}{L^2}$

Rate is maximum for wave number $k$ = 1

# The critical size

If $r < D\pi^2/L^2$ , then $r < Dk^2\pi^2/L^2$ for any $k$

$$\Downarrow$$

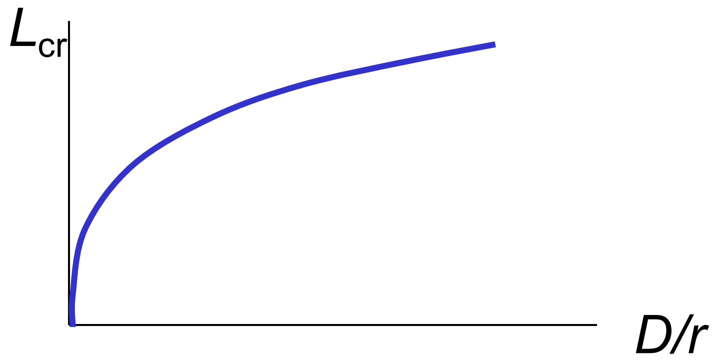
$$n(x,t) \rightarrow 0 \text{ for } t \rightarrow \infty$$

Therefore $L < L_{cr} = \pi\sqrt{\dfrac{D}{r}}$ implies extinction

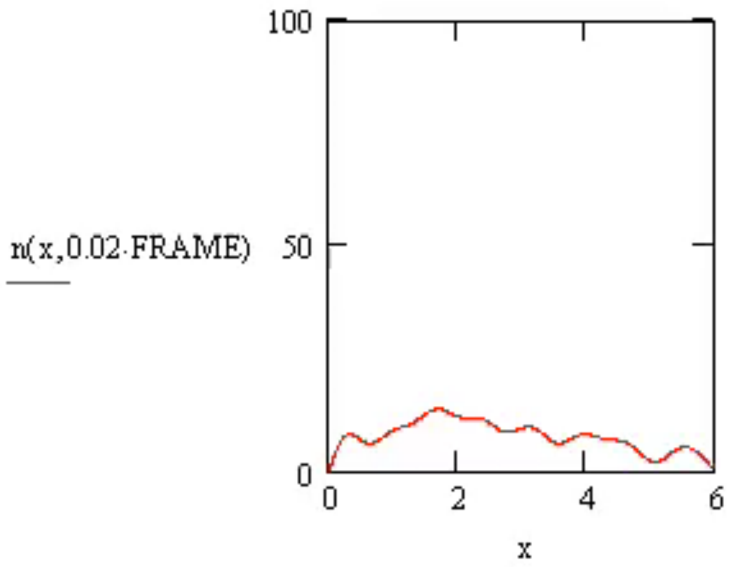
Reaction can go on / population can establish in the island only if

$r > 0$ and $L > L_{cr}$.

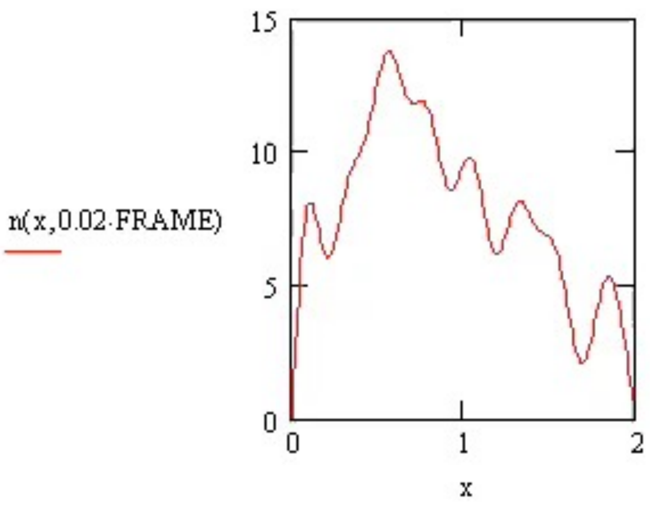
Threshold depends on the ratio of dispersal coefficient to population increase rate



# Simulation of diffusion and Malthusian growth in bounded habitat with absorbing boundary (island)




$$L > L_{cr}$$




$$L < L_{cr}$$

# Diffusion and reaction in 2D or 3D

- Extensions are fairly obvious. Diffusion coefficients can be equal for different directions (isotropy) or different for different directions (anisotropy).
- Basically, nothing changes from a qualitative viewpoint
- For instance: isotropic case in 2D

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

critical patch/island area

$A_{cr} = c_0 \pi^2 D/r$

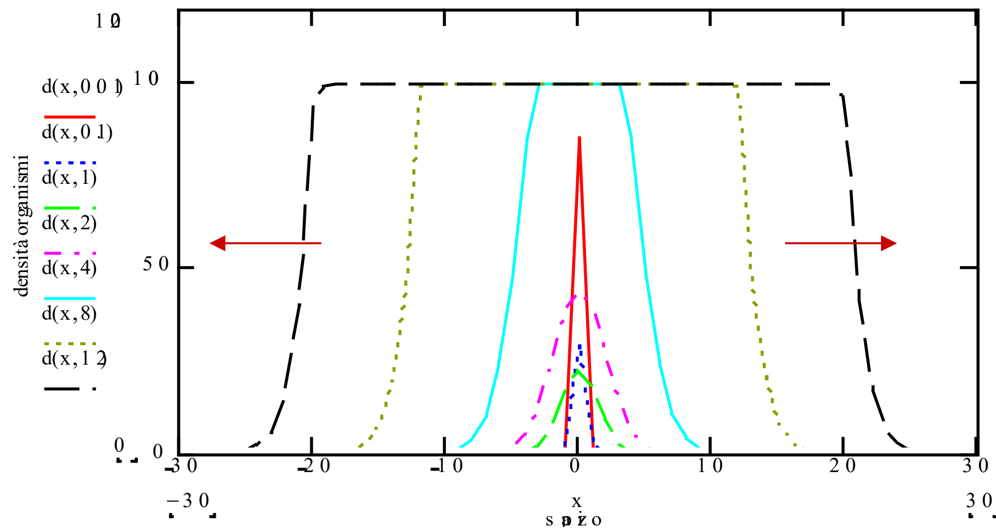
with $c_0$ = 1.84 for circular patch

$c_0$ = 2 for square patch

# Diffusion and demographic growth with density dependence

$R(n(x,t))$ = per capita rate of increase (e.g. logistic = $r(1-n/K)$)

Speed of wavefront = $2\sqrt{DR(0)}$



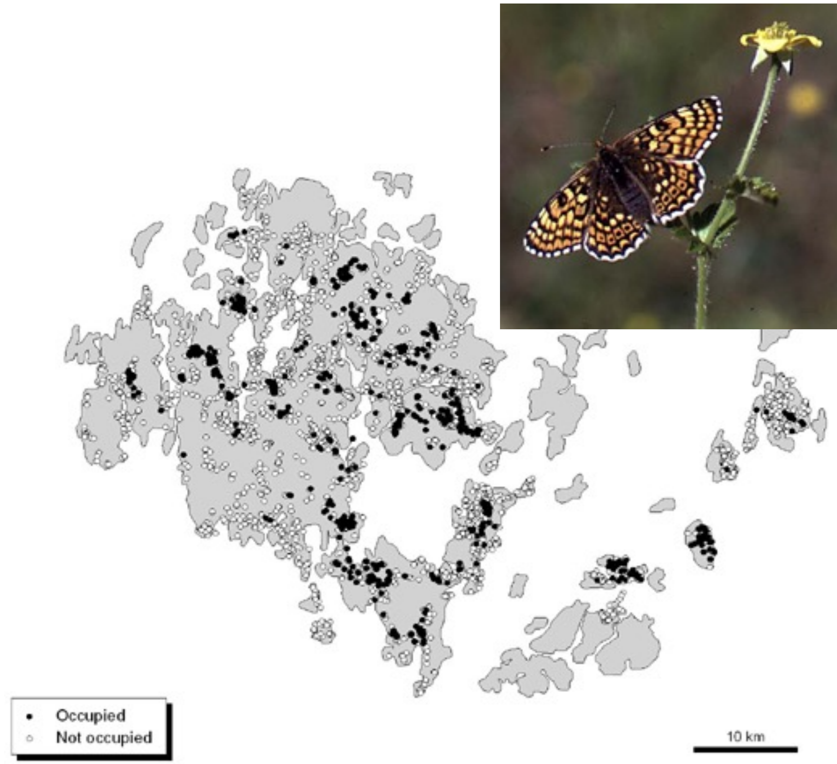

Critical patch size

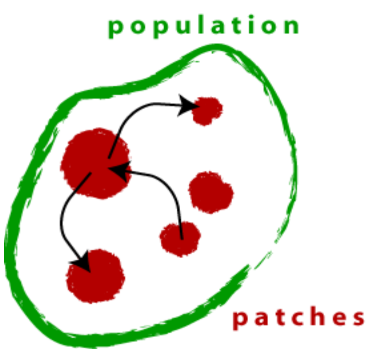
$$L_{cr} = \pi\sqrt{D/R(0)} \quad \text{one-dimensional habitat}$$

$$A_{cr} = 1.84\pi^2 \frac{D}{R(0)} \text{ circular patch}$$

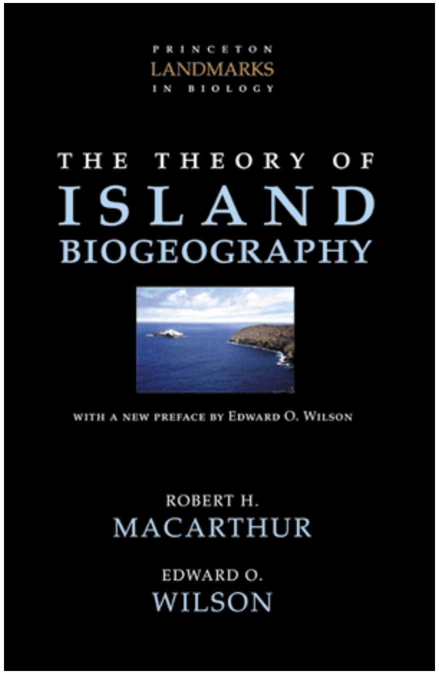
$$A_{cr} = 2\pi^2 \frac{D}{R(0)} \text{ square patch}$$

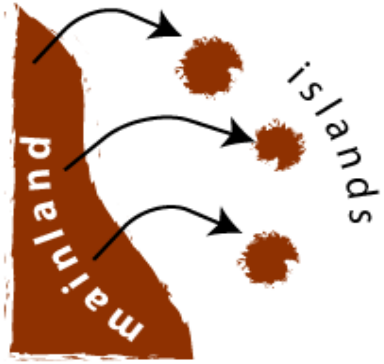
# Dynamics of metapopulations

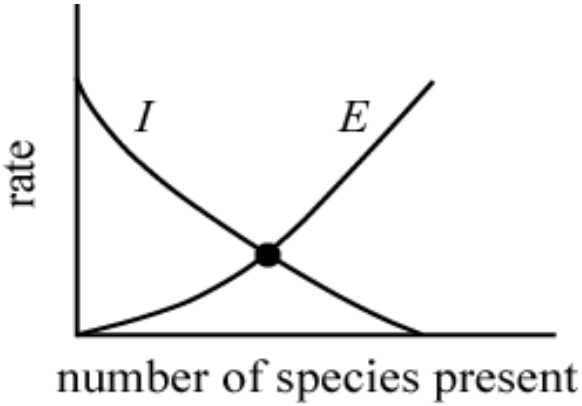



# Island biogeography and …



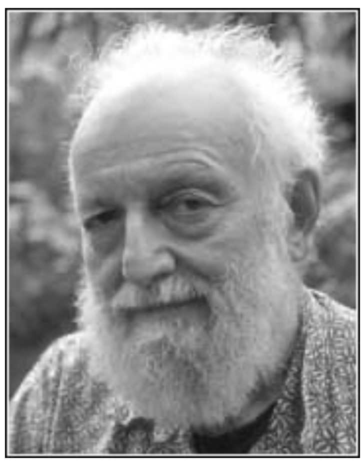



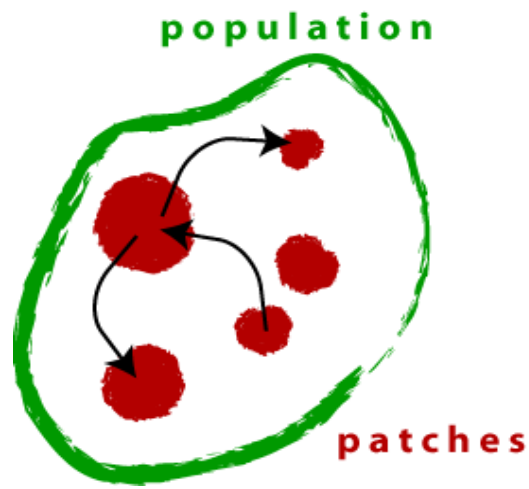
# …the metapopulation paradigm

Since the area over which control is sought is much greater than that of the local population, the control strategy must be defined for a population of populations in which local extinctions are balanced by emigration from other populations.

Levins 1969
*Bulletin of the Entomological Society of America* 15:237-240



Levins



# Islands and metapopulations

The next step is the assertion that the distribution of many species even on the mainland is insular. Mountain tops, lakes, individual host plants, a fallen log, a patch of vegetation, a mammalian gut, or, less obviously, a region of optimal temperature or humidity are all islands for the appropriate organisms. Therefore the insular model is much more broadly applicable.

Levins 1970
*Some Mathematical Questions in Biology* (p. 78)

Habitat fragmentation

ecosystems management

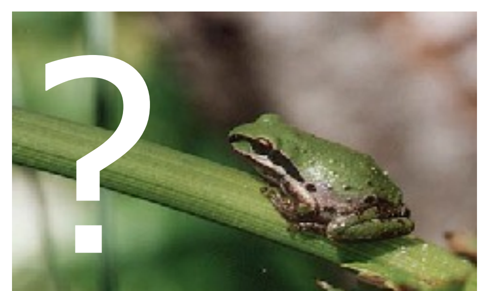
islands

land use

ephemeral environments

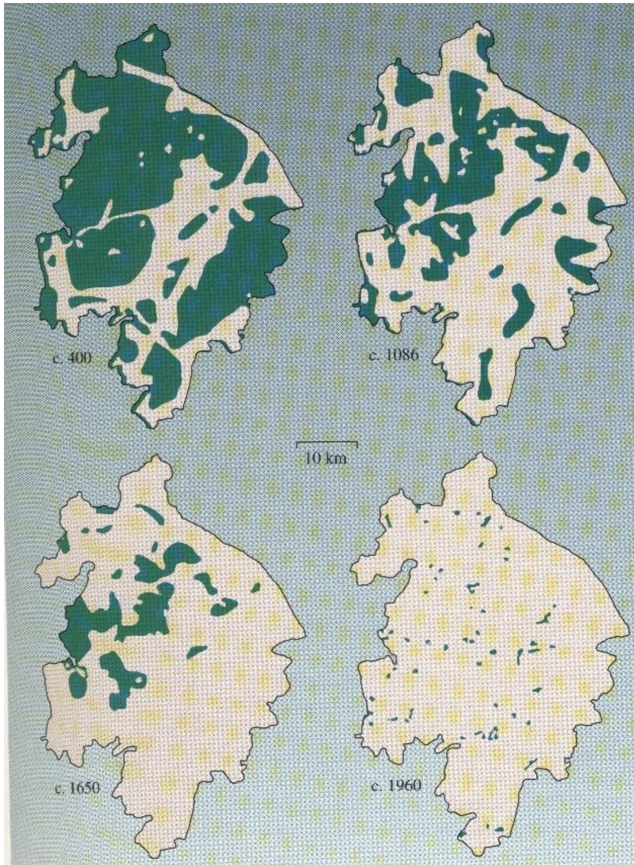
Aerial view of an oil road in Ecuador


*Six Rivers National Forest,* California



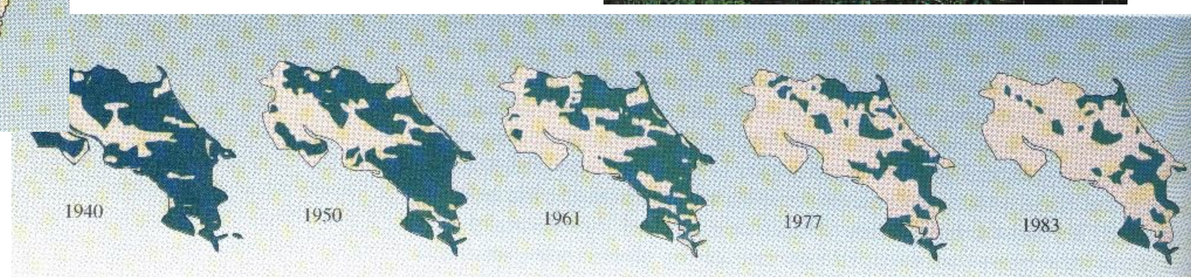

*Pseudacris regilla*

# Habitat fragmentation




Forests in England


Brazil

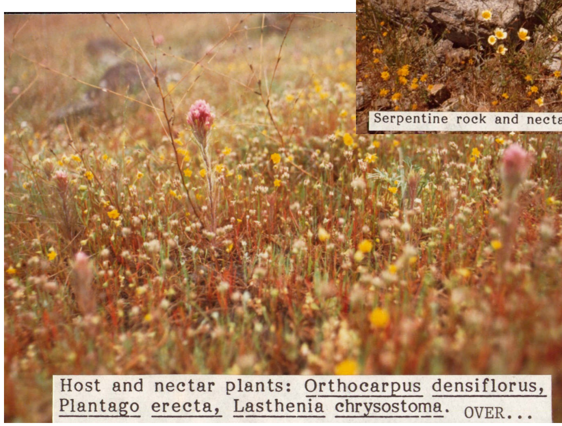



Forests in Costarica

# Habitat fragmentation


# Natural habitat can be patchy

*Euphydryas editha*



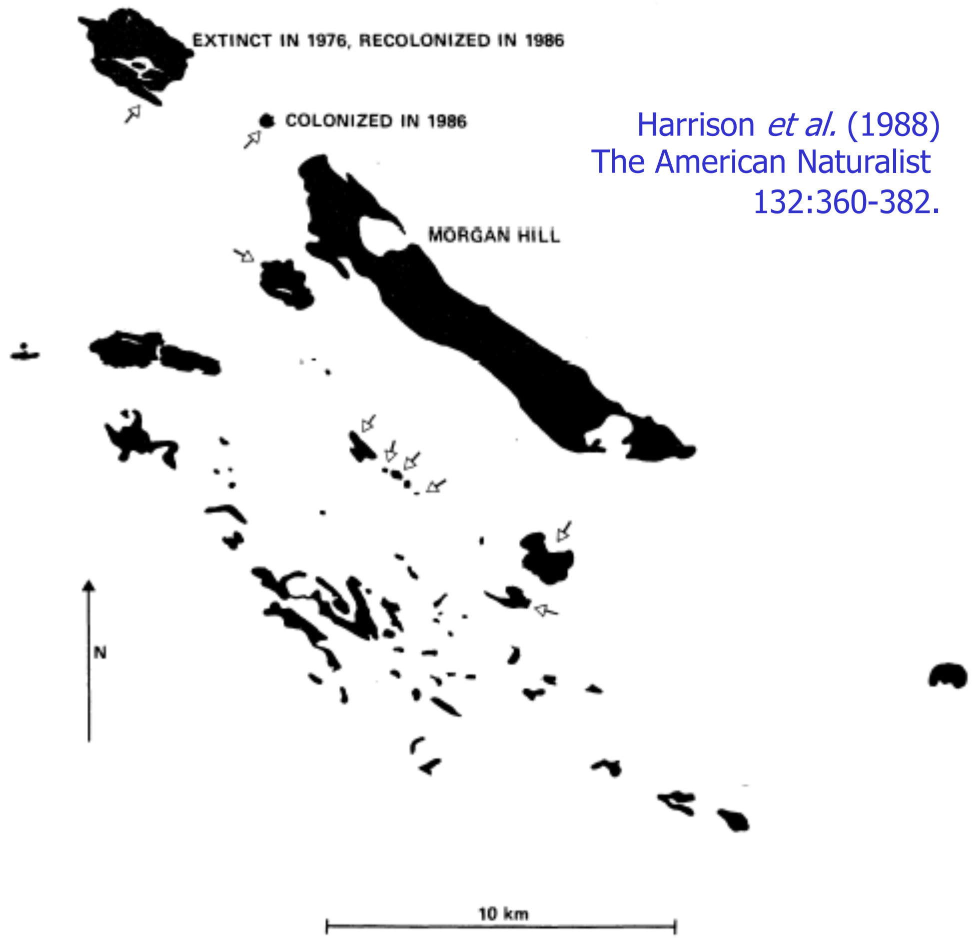
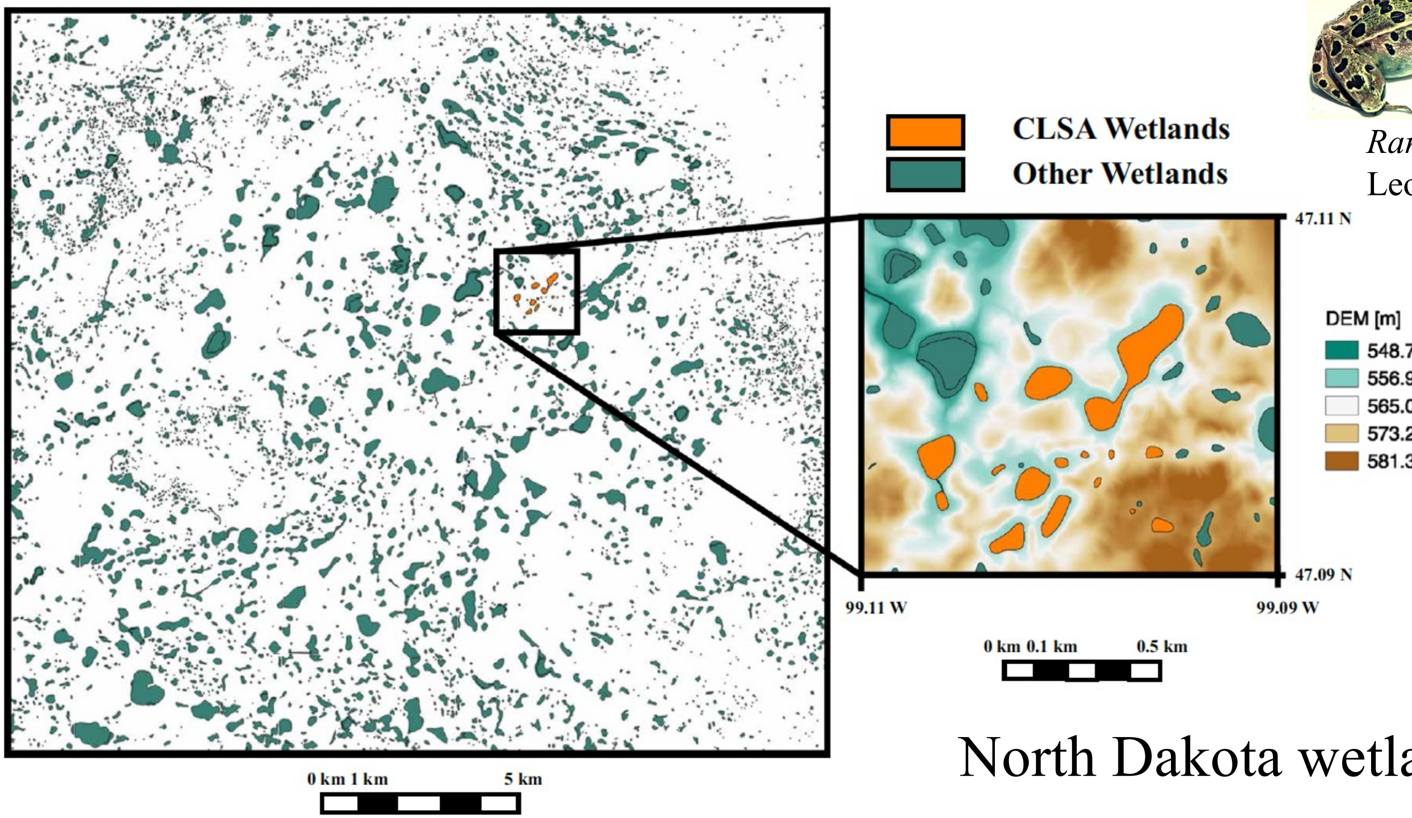




Fig. 1.—Distribution of serpentine grasslands in southern Santa Clara County, California, and butterfly populations in 1987. Population MH is located on the large patch labeled "Morgan Hill." Arrows indicate the locations of the seven small populations measured by the mark-recapture technique in 1987. Two additional patches at the upper left, colonized in 1986, also support populations.

Harrison *et al.* (1988)
The American Naturalist
132:360-382.

# Another example



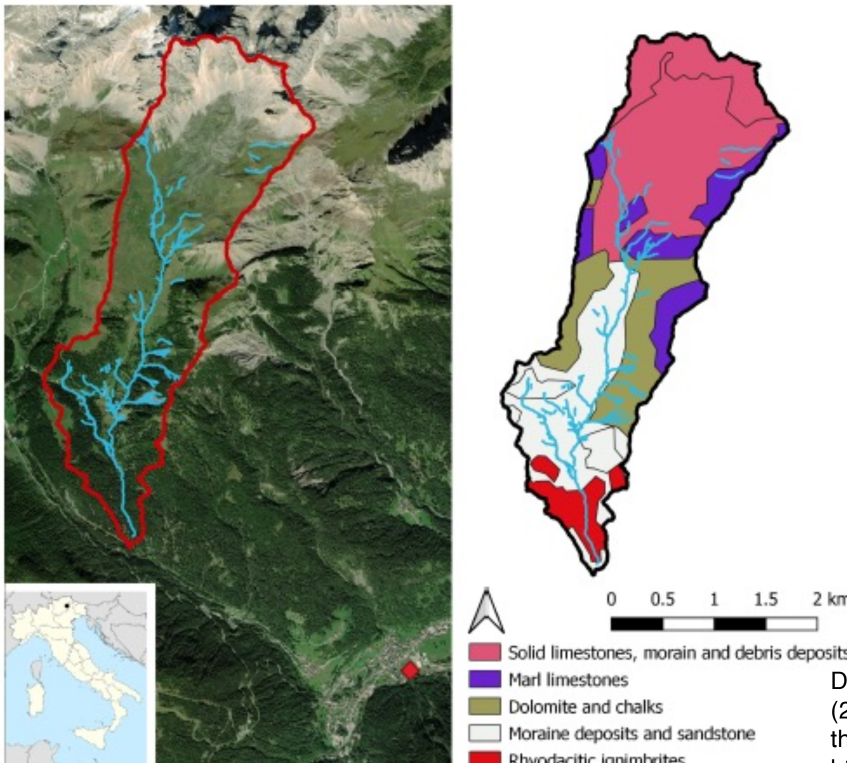

*Rana pipiens*
Leopard frog

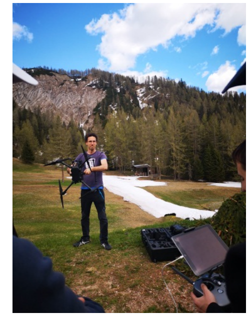
North Dakota wetland (USA)

L. E. Bertassello et al. Persistence of amphibian metapopulation occupancy in dynamic wetlandscapes. Landscape Ecology (2022) https://doi.org/10.1007/s10980-022-01400-4

Cottonwood Lake
Study Area

# Habitat may vary

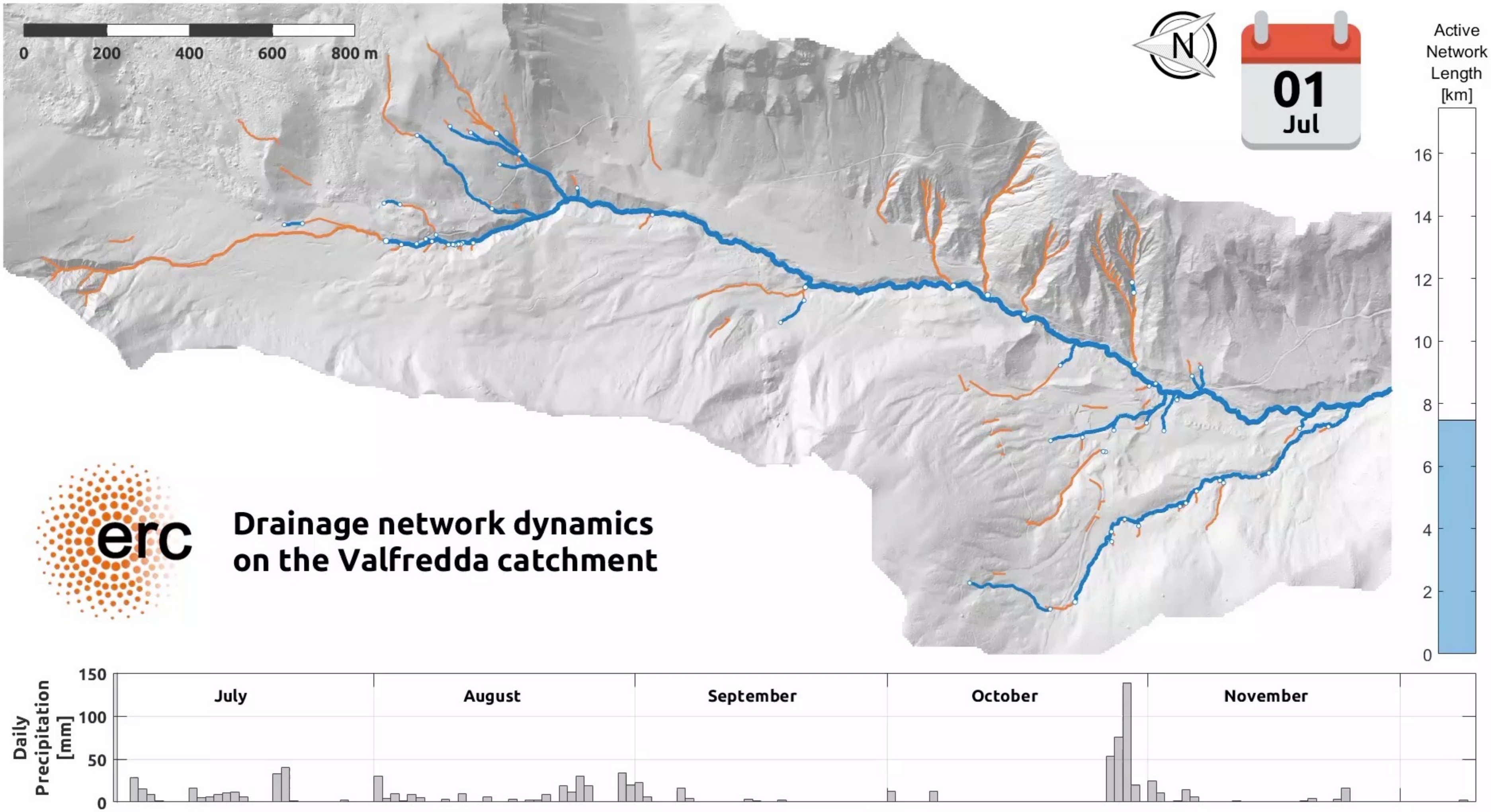


Durighetto, N., Vingiani, F., Bertassello, L. E., Camporese, M., & Botter, G. (2020). Intraseasonal drainage network dynamics in a headwater catchment of the Italian Alps. Water Resources Research, 56, e2019WR025563. https://doi.org/10.1029/2019WR025563

Valfredda (Dolomiti bellunesi)

*Salamandra atra*



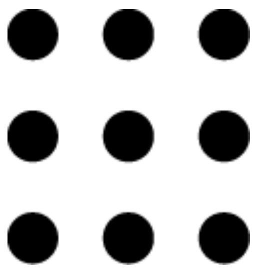

N. Durighetto. G. Botter (2020). Time-lapse visualization of spatial and temporal patterns of stream network dynamics. Hydrological Processes. 2021;35:e14053

# How many variables? The problem of scale

+

Describing the habitat...

theoretical

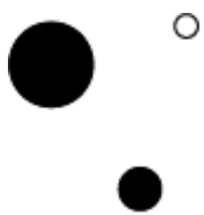


realistic

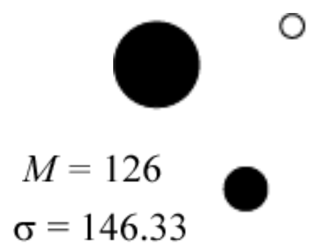
landscape


...and the local demography

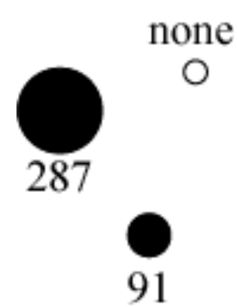
boolean



intermediate




discrete individuals

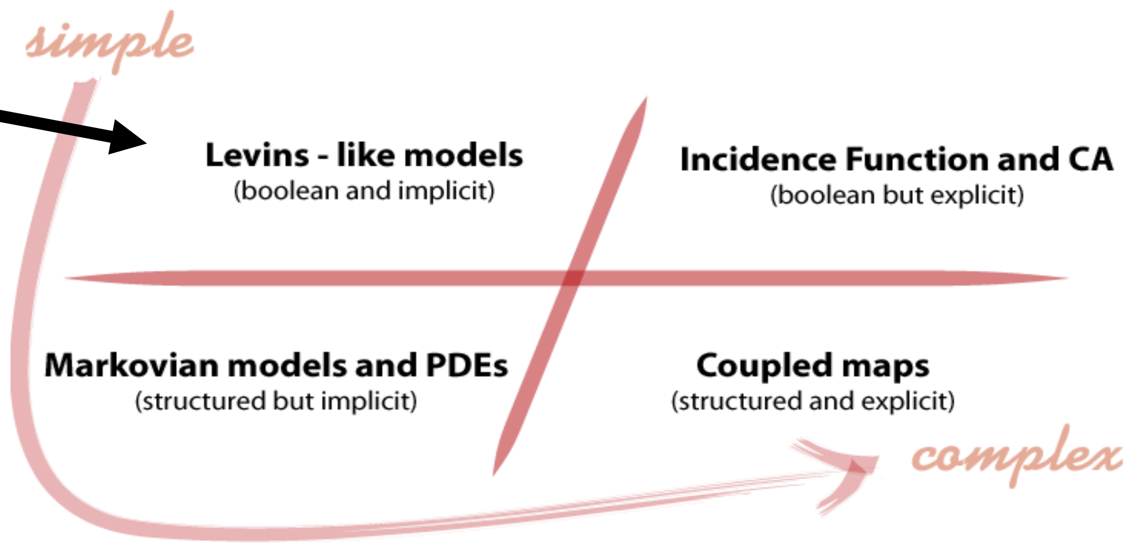


# Models of metapopulation dynamics

## Several possibilities

- ✓ local demography description
  **boolean** vs **structured**
- ✓ habitat description
  **implicit** vs **explicit**

Will deal with boolean models only



# Thinking spatially in a boolean way

## Two shifts in our usual frame of reference

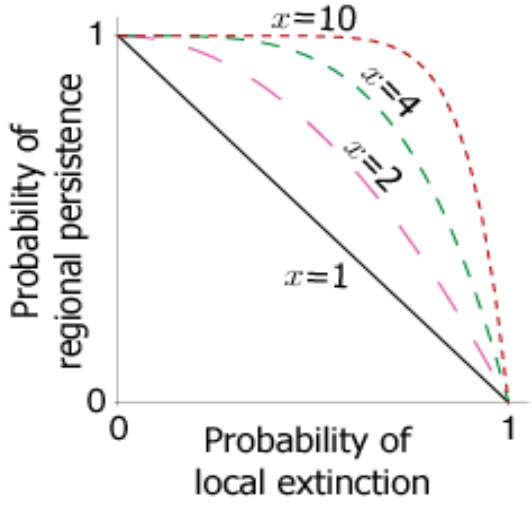
population size ➔ population persistence

local scale ➔ regional scale

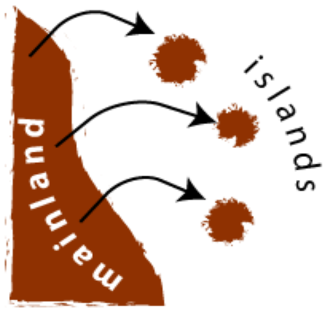
## Multiple patches decrease the risk of extinction: an example

$\tau$ = probability of local extinction measured on a yearly scale

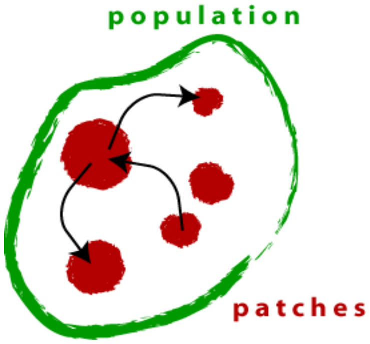
- Suppose we have a single population in which $\tau = 0.7$.
- What is the probability $P_n$ that such a population will persist for $n$ years?
- $P_n = (1 - \tau)^n$
- Now imagine we have $x$ identical populations, i.e. $x$ patches ($\tau = 0.7$). What is the probability of regional persistence for one year?
- P(ext all local pop)= $\tau^x$ Prob(persistence)= $1 - \tau^x$



# Simple approaches (spatially implicit and boolean)




What is the simplest model for the dynamics of patch occupancy?




## Main underlying hypotheses

- Homogeneous patches
- No spatial structure
- No time lags
- Large number of patches

$p$ = proportion of occupied patches

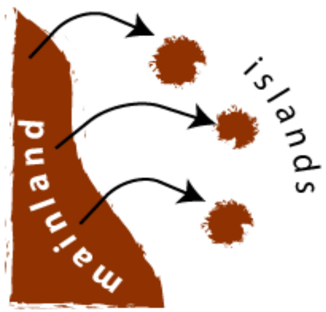
$C'(p)$ = colonization rate = proportion of sites successfully colonized per unit time

$E'(p)$ = extinction rate = proportion of sites that go extinct per unit time

$$\frac{dp}{dt} = C' - E' = C\left(p\right)\left(1 - p\right) - E\left(p\right)p$$

- $C(p)$ = probability of colonization of one empty patch per unit time
- $E(p)$ = probability of extinction of one occupied patch per unit time

# Version 1: The island-mainland model

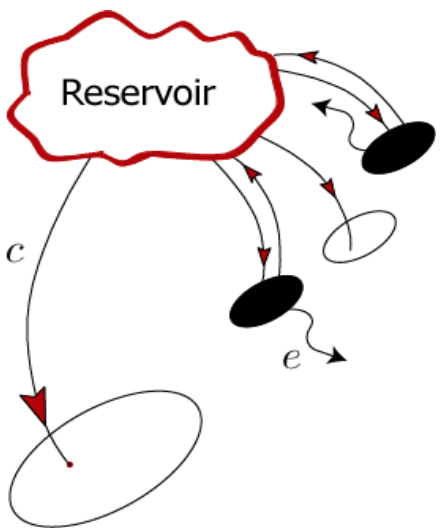



$$\begin{cases} C(p) = c \\ E(p) = e \end{cases}$$

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

- Is there any equilibrium?
- What is the main property?

# Version 2: *The* metapopulation model

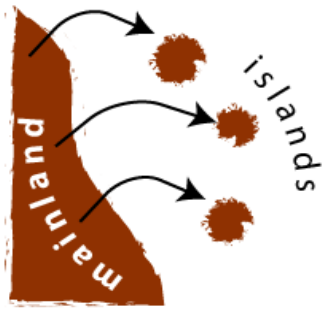



$$\begin{cases} C(p) = cp \\ E(p) = e \end{cases}$$

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

- Similarity with the logistic equation
- Is there any equilibrium?
- The persistence-extinction boundary

# Version 1: The island-mainland model

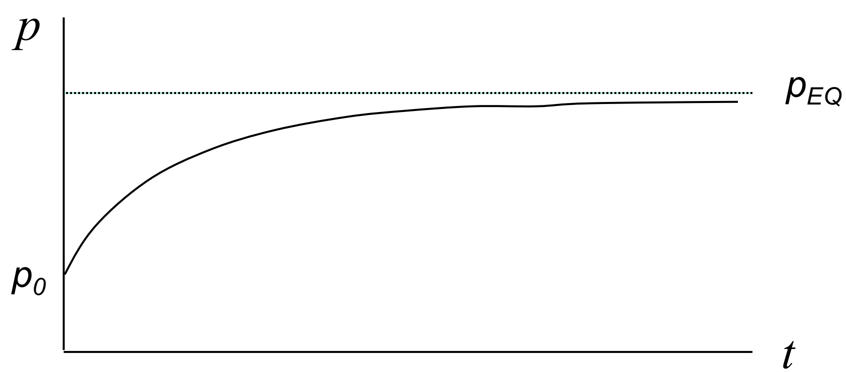



$$\begin{cases} C(p) = c \\ E(p) = e \end{cases}$$

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

- Is there any equilibrium?
- What is the main property?

- Linear equation: solution is exponential
- $dp/dt = c - (e+c)p$
- Equilibrium $dp/dt = 0 \rightarrow p_{EQ} = c/(e+c)$

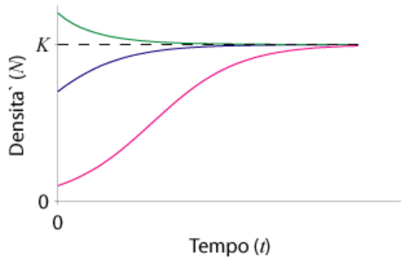



Exponential converges as exp(-($e$+$c$)$t$)

# Version 2: *The genuine* metapopulation model

$$\frac{dp}{dt} = cp(1-p) - ep = (c-e)p - cp^2 = (c-e)p\left(1 - \frac{p}{(c-e)/c}\right)$$

$$\frac{dN}{dt} = \dot{N} = rN - bN^2 = rN\left(1 - \frac{b}{r}N\right) = rN\left(1 - \frac{N}{K}\right)$$




- Similarity with the logistic equation

*c*-*e* replaces *r*; $(c - e)/c = 1 - e/c$ replaces *K*

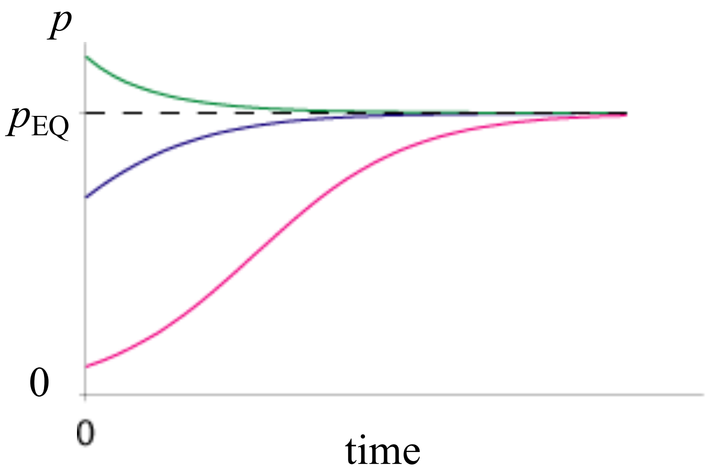
- Is there any equilibrium?

$p_{EQ} = 0$ if $c < e$

$p_{EQ} = 1 - e/c$ otherwise

In fact, if $c < e$ then $1 - e/c < 0$

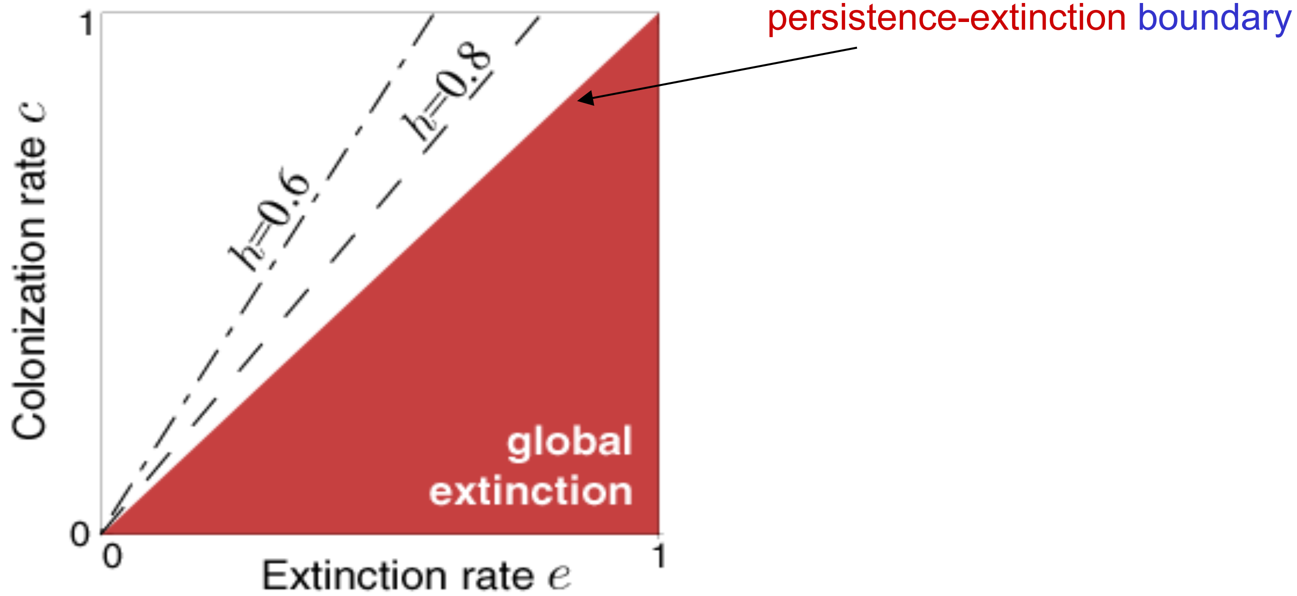
Also, for *p* small the derivative $dp/dt$ is $< 0$



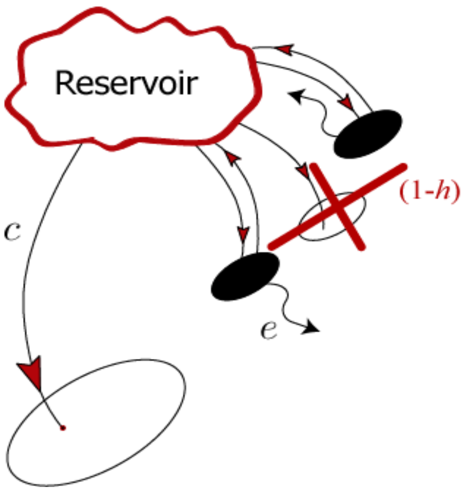
# Version 2: *The genuine* metapopulation model

- The persistence-extinction boundary in the parameter plane *c*–*e* is where there is a switch from metapopulation persistence to metapopulation extinction.

It is thus $c = e$



# Incorporating habitat destruction in Levins' model



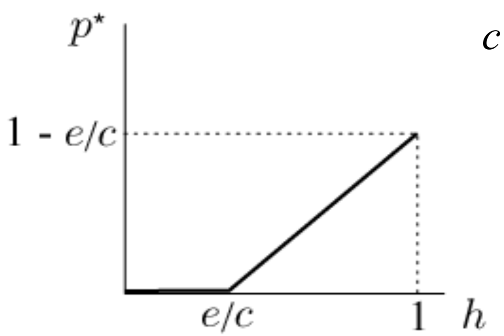

$h$ = proportion of remaining suitable habitat out of the original habitat

$h$ - $p$ = fraction of empty suitable patches

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

at the equilibrium...

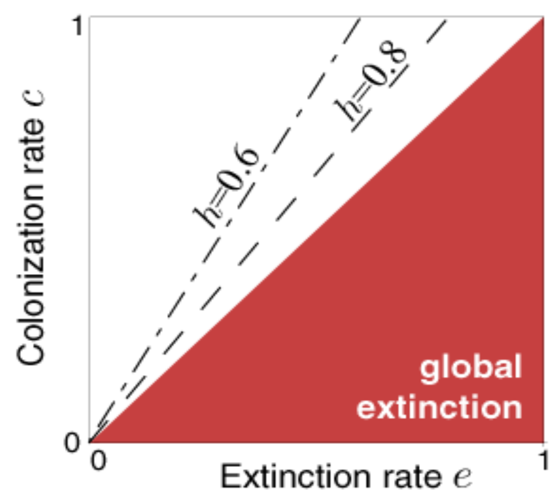
$$p^* = \begin{cases} h - \dfrac{e}{c} & \text{if } h > e/c \\ 0 & \text{otherwise} \end{cases}$$




...and the persistence-extinction boundary

$c > e/h \rightarrow$ persistence

$c = e/h$ pers.ext. boundary

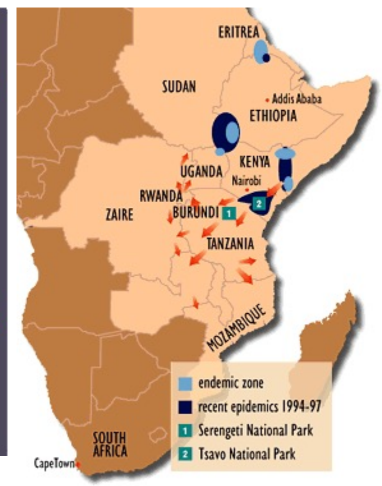


# Disturbances are important: environmental catastrophes

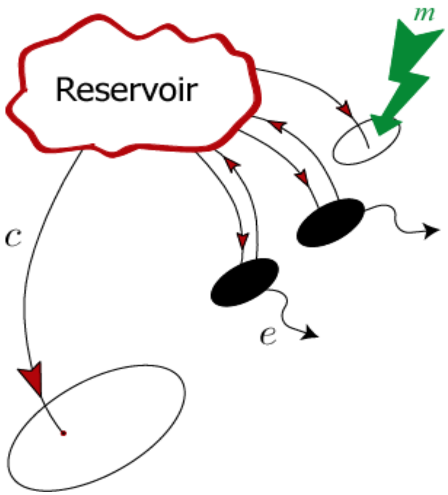
floods

forest fires


rinderpest


# Incorporating environmental catastrophes in Levins' model



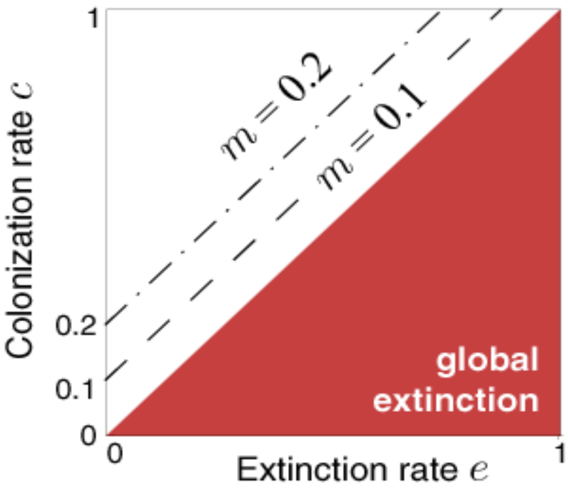

$m$ = rate of occurrence of catastrophes wiping out occupied patches

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

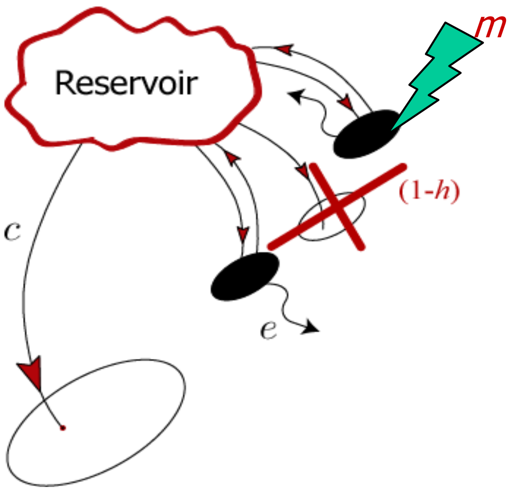
At equilibrium...

$$p^* = \begin{cases} 1 - \dfrac{e+m}{c} & \text{if } c > e+m \\ 0 & \text{otherwise} \end{cases}$$

...and the persistence-extinction boundary

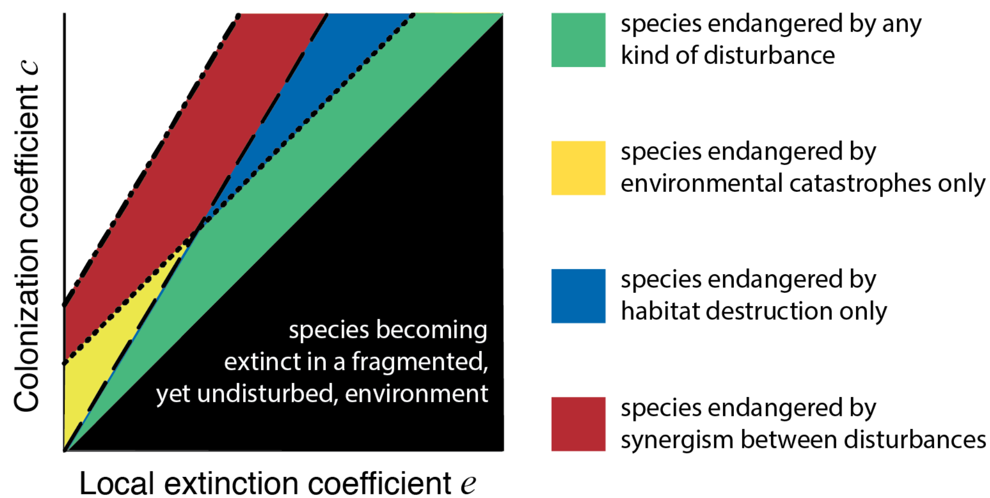


# The synergistic effects of habitat destruction and environmental catastrophes




$$\frac{dp}{dt} = cp(h-p) - (e+m)p$$

## Persistence-extinction boundary



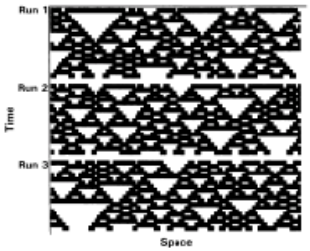

## At equilibrium

$$p^* = \begin{cases} h - \dfrac{e+m}{c} & \text{if } h > \dfrac{e+m}{c} \\ 0 & \text{otherwise} \end{cases}$$

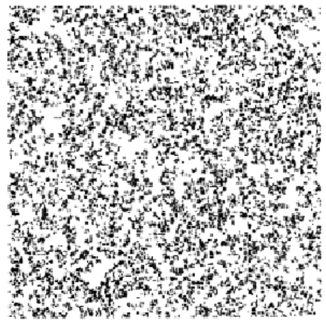
$c > (e+m)/h \rightarrow$ persistence

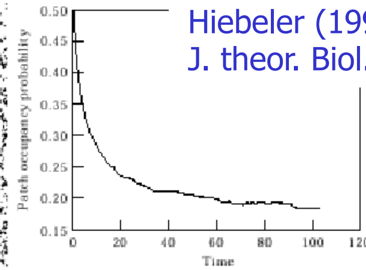
# Other approaches (a quick review)

## Presence-absence CA




Molofsky (1994)
Ecology 75:30

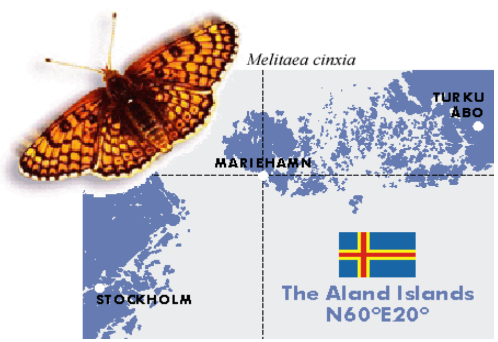





Hiebeler (1997)
J. theor. Biol. 187:307

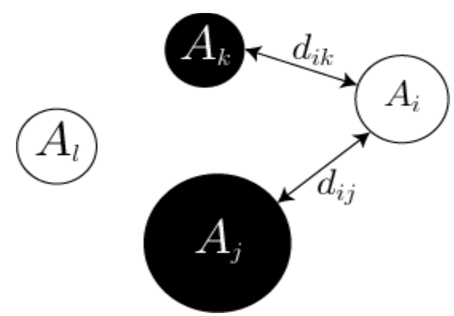
+ spatially explicit
+ very flexible
– boolean

## The **S**patially **R**ealistic **L**evins




Hanski and Ovaskainen (2000)
Nature 63:151

$$\frac{dp_i}{dt} = C_i(\mathbf{p})(1 - p_i) - E_i p_i$$




+ realistic landscapes

+ patch specific extinction and colonization functions

- boolean

# Other approaches (a quick review)

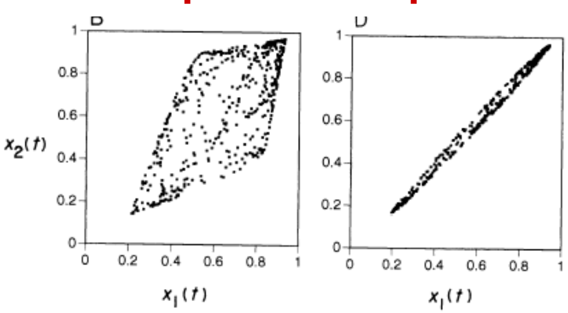
## PDE

Gyllenberg and Hanski (1993) Am. Nat. 142:17

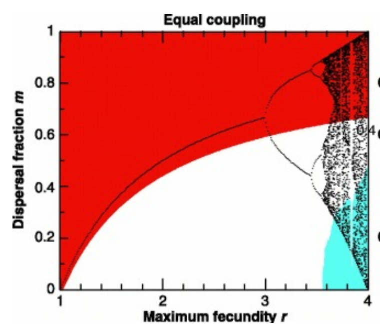
$$\frac{\partial}{\partial t}p(t,x,y) + \mu(x,y)p(t,x,y) = -\frac{\partial}{\partial x}\left\{\left[g(x,y) - \gamma(x,y) + \alpha\psi(y)D(t)\right]p(t,x,y)\right\}$$

+ different patch areas ($y$)
+ structured ($x$)
– spatially implicit

## Coupled maps




Hastings (1993) Ecology 74: 1362
Allen *et al.* (1993) Nature 364:229

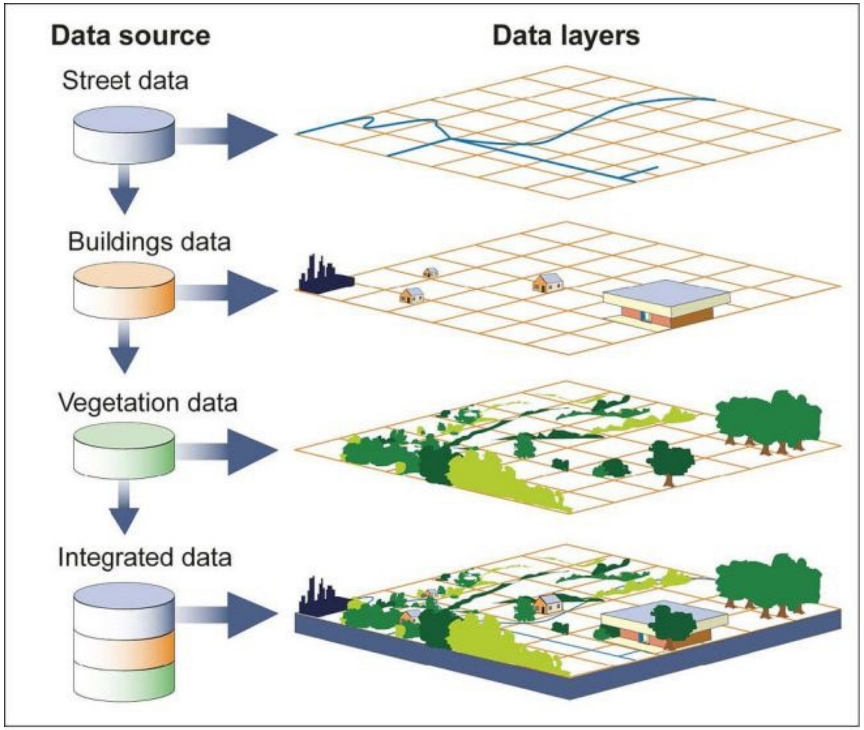



Earn *al.* (2000) Science 290:1360

+ spatially explicit
+ structured
– no discrete individuals

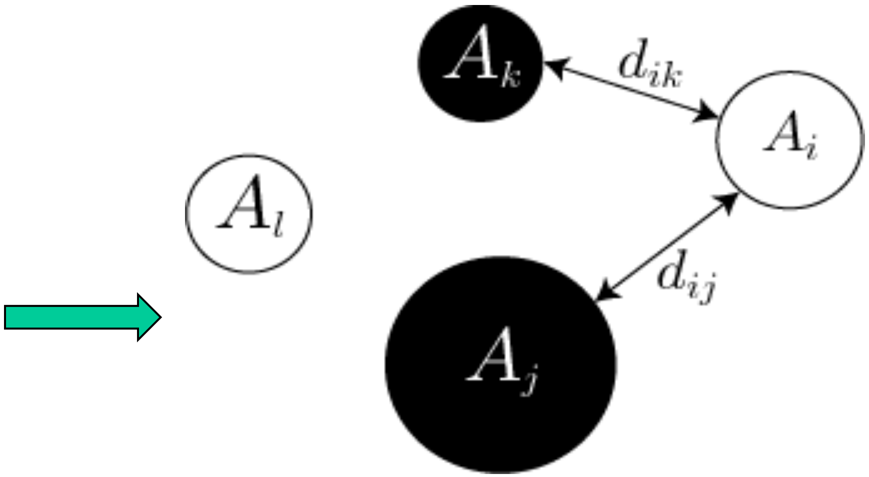
# The spatially realistic Levins model (Hanski 2000)

Ilkka Hanski



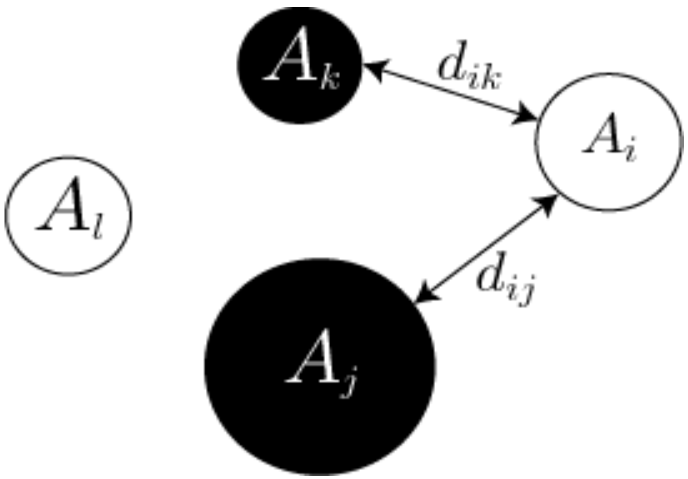

Source: GAO.

Geographic Information System




Patch areas, centroids, distances

# The spatially realistic Levins model (Hanski 2000)




$$\frac{dp_i}{dt} = C_i(\mathbf{p})(1 - p_i) - E_i p_i$$

$p_i =$ probability that patch $i$ is occupied

$A_i =$ area of patch $i$

$E_i =$ extinction rate $= \dfrac{e}{A_i}$

$C_i =$ colonization rate $= c\sum_{j \neq i}^{n} l_{ji} A_j p_j$

$l_{ji} =$ probability that propagule from $j$ reaches patch $i =$ a function of distance $d_{ji}$ $\quad l_{ii} = 0$

$l_{ji} = L\exp(-\alpha d_{ji})$ exponential dispersal kernel

$1/\alpha =$ average dispersal distance

# The condition for metapopulation persistence (Hanski 2003)

$m_{ij} = l_{ij} A_i A_j$ for $j \neq i$ $\quad m_{ii} = 0 \quad m_{ij} = m_{ji}$

$M = \left[ m_{ij} \right] =$ symmetric migration matrix

$$\dot{p}_i = \frac{c}{A_i} \left[ \sum_{j \neq i}^{n} m_{ji} p_j \left(1 - p_i\right) - \frac{e}{c} p_i \right]$$

$\lambda_M =$ dominant eigenvalue of $M =$ metapopulation capacity

Condition for persistence

$$\lambda_M > \frac{e}{c}$$

$p_i = 0$ for all $i$ is an equilibrium
Is this equilibrium stable or unstable? If unstable, metapopulation can persist

# The condition for metapopulation persistence (Hanski 2003)

Discard quadratic terms (linearization around *p*=0)

$$\dot{p}_i = \frac{c}{A_i}\left[\sum_{j\neq i} m_{ji} p_j - \frac{e}{c} p_i\right]$$

$$p = \begin{bmatrix} p_1 \\ p_2 \\ . \\ p_n \end{bmatrix} \qquad A = \begin{bmatrix} A_1 & 0 & 0 & 0 \\ 0 & A_2 & . & 0 \\ . & . & . & . \\ 0 & 0 & . & A_n \end{bmatrix} \qquad M = \begin{bmatrix} 0 & m_{12} & \dots & m_{1n} \\ m_{12} & 0 & \dots & m_{2n} \\ . & . & . & m_{n-1,n} \\ m_{1n} & m_{2n}\dots. & m_{n-1,n} & 0 \end{bmatrix}$$

$$I == \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & 1 & . & 0 \\ . & . & . & . \\ 0 & 0 & . & 1 \end{bmatrix}$$

$$\dot{p} = cA^{-1}\left(M - \frac{e}{c} I\right) p = Bp$$

*p*=0 is unstable if at least one eigenvalue of *B* is positive

# Eigenvalues and eigenvectors of a matrix

$$B = \begin{bmatrix} b_{11} & b_{12} & \cdots & \cdots & b_{1n} \\ b_{21} & b_{22} & \cdots & \cdots & b_{2n} \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ b_{n1} & b_{n2} & \cdots & \cdots & b_{nn} \end{bmatrix} \qquad p = \begin{bmatrix} p_1 \\ p_2 \\ \vdots \\ p_n \end{bmatrix}$$

$$Bp = \lambda p$$

If there exists $p \neq 0$ satisfying the equation, $\lambda$ is an eigenvalue of *B* and *p* is the corresponding eigenvector

$$(B - \lambda I)p = 0$$
$$det(B - \lambda I) = 0$$

This is a polynomial of degree *n* equated to 0. The equation has *n* complex solutions that are the eigenvalues of *B*. The corresponding *p*'s are the eigenvectors associated to the eigenvalues. The eigenvalue with the largest real part is the dominant eigenvalue. **If *B* is symmetric all the eigenvalues are real and the dominant eigenvalue is the largest one.**

# The condition for metapopulation persistence (Hanski 2003)

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Is this equilibrium stable or unstable? If unstable, metapopulation can persist