$$\frac{dN}{dt} = N\mathbf{r}$$

Spatial Ecology

“Populační ekologie živočichů“

Stano Pekár

Spatial ecology - describes changes in spatial pattern over time

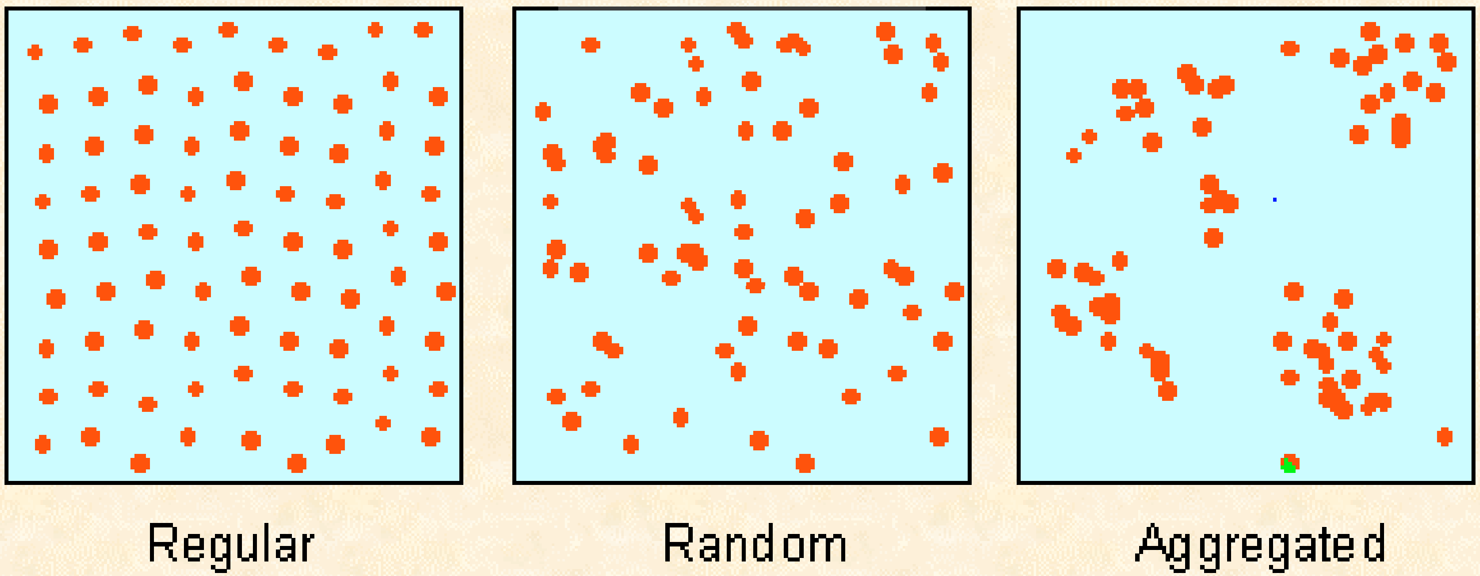
- processes - colonisation / immigration and local extinction / emigration

- local populations are subject to continuous colonisation and extinction
- wildlife populations are fragmented

Metapopulation - a population consisting of many local populations (sub-populations) connected by migrating individuals with discrete breeding opportunities (not patchy populations)

Distribution of individuals

- population density changes also in space
- for migratory animals (salmon) seasonal movement is the dominant cause of population change
- movement of individuals between patches can be density-dependent
- distribution of individuals have three basic models:



- most populations in nature are aggregated (clumped)

Regular distribution

- described by hypothetical uniform distribution

$$P(x) = \frac{1}{n}$$

n .. is number of samples
x .. is category of counts (0, 1, 2, 3, 4, ...)

- all categories have similar probability

- mean: $\mu = \frac{1}{2}(n+1)$

- variance: $\sigma^2 = \frac{1}{12}(n^2 - 1)$

- for regular distribution: $\boxed{\mu > \sigma^2}$

Random distribution

- described by hypothetical Poisson distribution

$$P(x) = \frac{\mu^x e^{-\mu}}{x!}$$

μ .. is expected value of individuals
x .. is category of counts (0, 1, 2, 3, 4, ...)

- probability of x individuals at a given area usually decreases with x

- observed and expected frequencies are compared using χ^2 statistics

- for random distribution: $\boxed{\mu = \sigma^2}$

Aggregated distribution

- described by hypothetical negative binomial distribution

$$P(x) = \left(1 - \frac{\mu}{k}\right)^{-k} \frac{(k+x-1)!}{x!(k-1)!} \left(\frac{\mu}{\mu+k}\right)^{x}$$

μ .. is expected value of individuals
x .. is category of counts (0, 1, 2, 3, 4, ...)
k .. degree of clumping, the smaller k ($\rightarrow$0) the greater degree of clumping

- approximate value of *k:* $$k \approx \frac{\mu^2}{\sigma^2 - \mu}$$

- for aggregated: $\boxed{\mu < \sigma^2}$

Coefficient of dispersion (CD)

$$\boxed{CD = \frac{s^2}{\overline{x}}}$$

CD < 1 … uniform distribution
CD = 1 … random distribution
CD > 1 … aggregated distribution

Dispersal

• **Geographic range** - radius of space containing 95% of individuals
• individual makes blind **random walk**
• random walk of a population undergoes **diffusion** in space

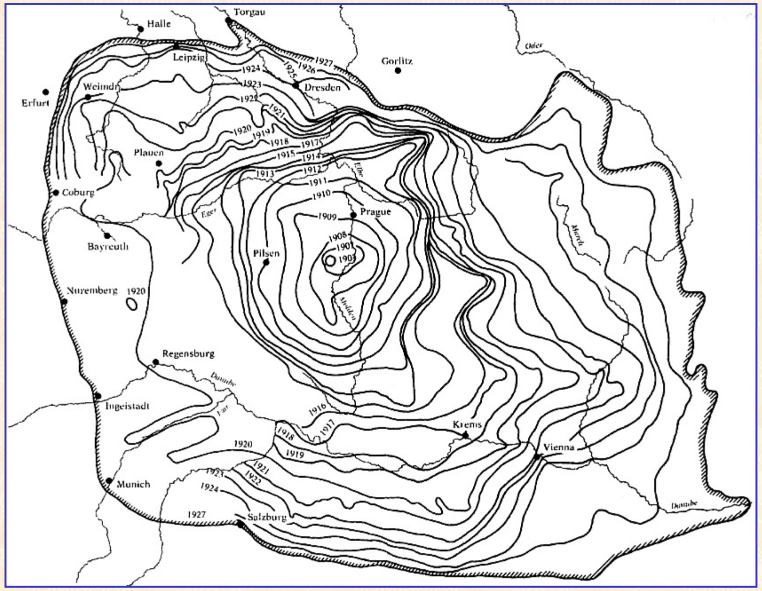
- radial distance moved in a random walk

is proportional to $\sqrt{time}$

- area occupied (radius^2)

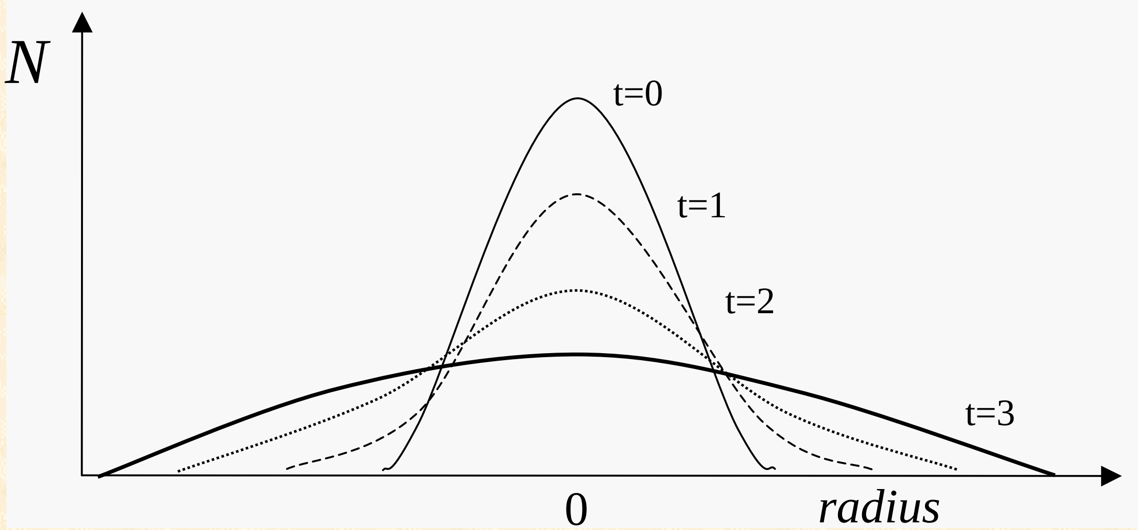
is proportional to *time*

Elton 1958



Spread of muskart in Europe

Pure dispersal



• Difusion model
- solved to 2dimensional Gaussian distribution

$$N(\rho, t) = \frac{N_0}{4\pi Dt}\exp\left(\frac{-\rho^2}{4Dt}\right)$$

$$\boxed{\rho = \sqrt{4Dt}}$$

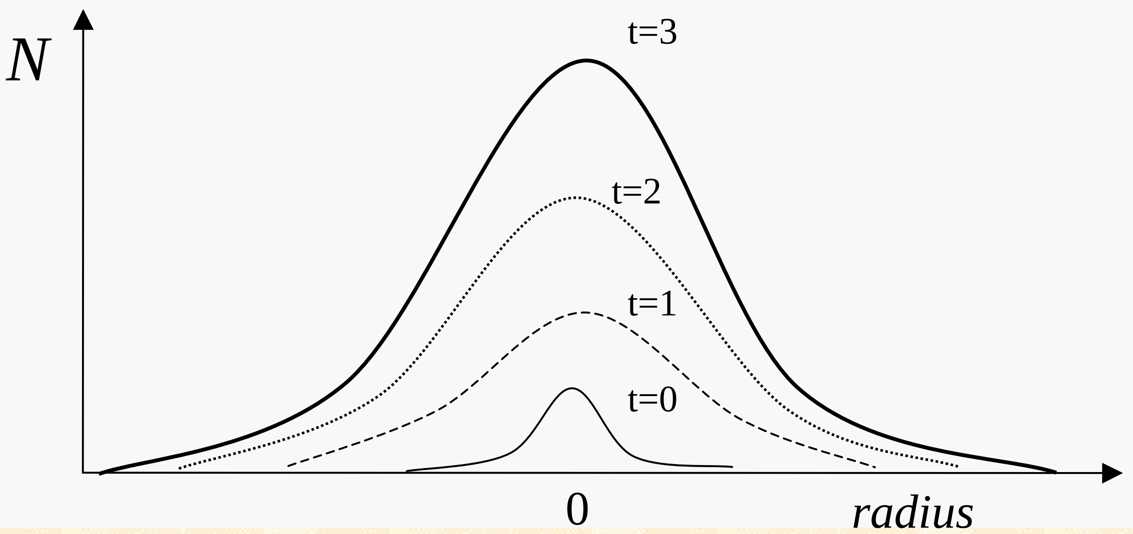
$$\boxed{D = \frac{\rho^2}{4t}}$$

N_0- initial density

ρ .. radial distance from point of release (range)

D - diffusion coefficient (distance^2/time)

Dispersal + population growth



• Skellam's model
- added exponential population growth

$$N(\rho,t)=\frac{N_0}{4\pi Dt}\exp\left(rt-\frac{-\rho^2}{4Dt}\right)$$

r .. intrinsic rate of increase

c - expansion rate [distance/time]

$$\boxed{c = 2\sqrt{rD}}$$

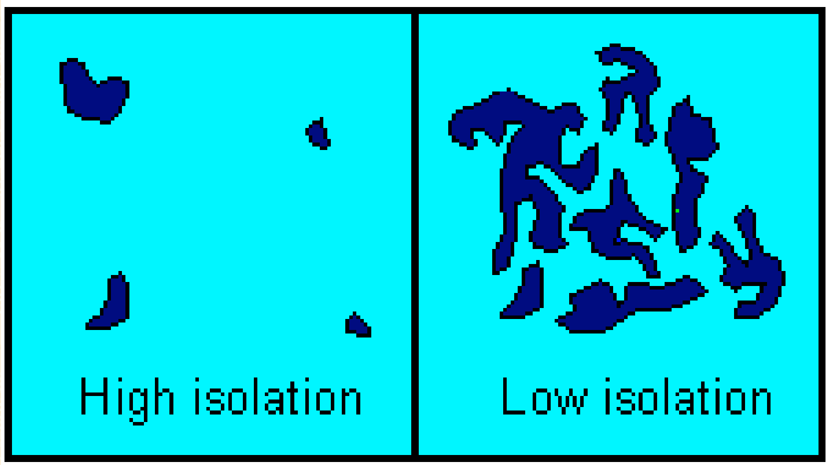
Skellam 1951

Metapopulation ecology

- Levins (1969) distinguished between dynamics of a single population and a set of local populations which interact via individuals moving among populations

- Hanski (1997) developed the theory - suggested *core-satellite* model

- the degree of isolation may vary depending on the distance among patches



- unlike growth models that focus on population size, metapopulation models concern persistence of a population - ignore fate of a single sub-population and focus on fraction of sub-population sites occupied

Levin‘s model

p .. proportion of patches occupied
m .. colonisation rate
e .. extinction rate

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

- assumptions

- sub-populations are identical in size, distance, resources, etc.
- extinction and colonisation are independent of p
- many patches are available

m ..proportion of open sites colonised per unit time

e ..proportion of sites that become unoccupied per unit time

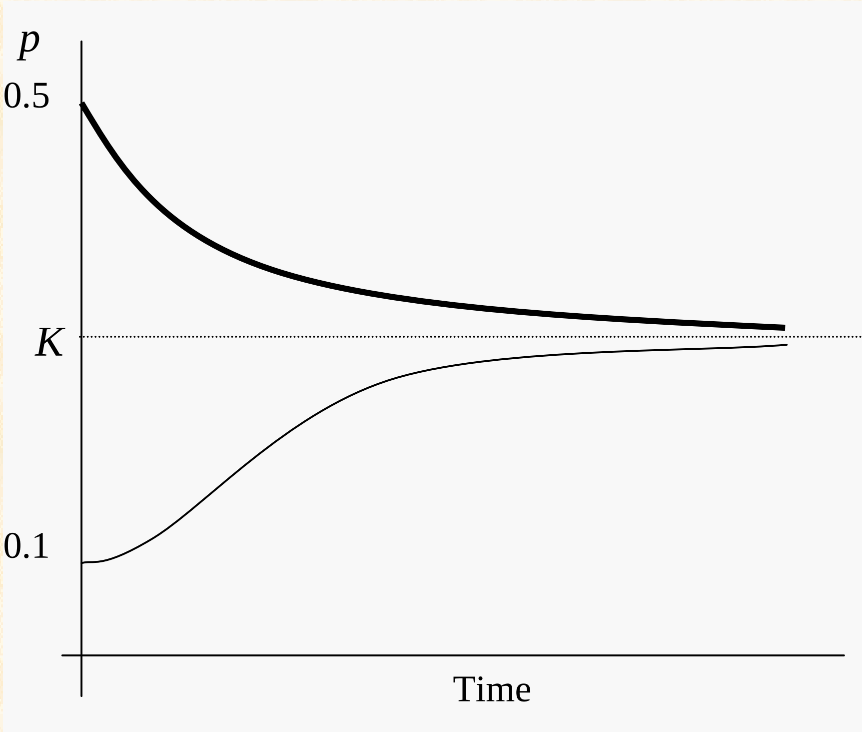
Levin 1969

- equilibrium is found for $dp/dt = 0$

$$p^* = \frac{m-e}{m} = 1 - \frac{e}{m}$$

- sub-populations will persist ($p^* > 0$) only if colonisation is larger than extinction
- all patches can be occupied only if $e = 0$

- K ..is fraction of patches
- defined by balance between m and e



Example 13

In a field the abundance of spiders on leaves was studied. The following counts per leaf were made:

Plant	**Counts**
1	0, 0, 1, 5, 7
2	0, 1, 1, 4, 1
3	0, 0, 2, 0, 0
4	3, 1, 8, 1, 1
5	1, 2, 6, 3, 2

1. What is the distribution of spiders per leaf and per plant?
2. If aggregated, what is the coefficient of dispersion (*CD*) and the degree of aggregation (*k*)?

```
spider<-c(0,0,1,5,7,0,1,1,4,1,0,0,2,3,0,0,1,6,1,1,1,2,6,3,2)
table(spider)
CD1<-var(spider)/mean(spider); CD1
k1<-mean(spider)^2/(var(spider)-mean(spider)); k1

plant<-c(rep(1,5),rep(2,5),rep(3,5),rep(4,5),rep(5,5))
a<-tapply(spider,plant,mean)
CD2<-var(a)/mean(a); CD2
```

Example 14

A dragonfly is spreading along a river. The spreading is anisotropic - faster down the stream than up the stream. During 6 years the dragonfly has spread as follows:

Rok	**Plocha [km2]**	
	po proudu	**proti proudu**
0	0	0
1	3	0.2
2	7	0.5
3	13	1
4	17	1.4
5	26	1.8
6	30	2.2

1. Estimate D in both directions.
2. Estimate expansion rate in both directions if finite growth rate $\lambda = 1.4$.
2. Model the spread using Skellam's model.

```
year<-0:6
po<-c(0,3,7,13,17,26,30)
rho1<-sqrt(po)
plot(year,rho1)
m1<-lm(rho1~year-1)
abline(m1)
m1


pro<-c(0,0.2,0.5,1,1.4,1.8,2.2)
rho2<-sqrt(pro)
plot(year,rho2)
m2<-lm(rho2~year-1)
abline(m2)
m2
```

```
r<-0:50
y<-10*exp(0.34*1-r^2/(4*0.25*1))/(4*pi*0.25*1)
plot(r,y,type="l")
y<-10*exp(0.34*10-r^2/(4*0.25*10))/(4*pi*0.25*10);lines(r,y)
y<-10*exp(0.34*20-r^2/(4*0.38*20))/(4*pi*0.38*20);lines(r,y)
y<-10*exp(0.34*30-r^2/(4*0.38*30))/(4*pi*0.38*30);lines(r,y)
y<-10*exp(0.34*40-r^2/(4*0.38*40))/(4*pi*0.38*40);lines(r,y)
y<-10*exp(0.34*50-r^2/(4*0.38*50))/(4*pi*0.38*50);lines(r,y)
```

Example 15

A population of toads has been split into two sub-populations by a new highway. One has 100 and the other 10 individuals. The first one has exploited its resources so their finite rate of population increase (λ_1) is 0.8. The other has a lot of resources, therefore their λ_2 = 1.2. Is it necessary to built a corridor connecting populations? If so how large it should be in terms of the rate of exchange (d) between sub-populations.

1. Use discrete density-independent models to simulate fate of populations for 20 years that are completely isolated (d = 0).

2. Simulate the dynamics of the two sub-populations for 20 years with various levels of exchange, d = 0.1 to 1.

$$N_{1,t+1} = \lambda_1 N_{1,t}(1-d) + d\lambda_1 N_{2,t} \qquad N_{2,t+1} = \lambda_2 N_{2,t}(1-d) + d\lambda_2 N_{1,t}$$

```
N12<-data.frame(N1<-numeric(1:20),N2<-numeric(1:20))
N12[,1]<-100
N12[,2]<-10

d=0
for(t in 1:20) N12[t+1,]<-{
N1<-0.8*((1-d)*N12[t,1]+0.8*d*N12[t,2])
N2<-1.2*((1-d)*N12[t,2]+1.2*d*N12[t,1])
c(N1,N2)}
matplot(N12, type="l",lty=1:2)
legend(1,200,c("N1","N2"),lty=1:2)

d=0.2
for(t in 1:20) N12[t+1,]<-{
N1<-0.8*((1-d)*N12[t,1]+0.8*d*N12[t,2])
N2<-1.2*((1-d)*N12[t,2]+1.2*d*N12[t,1])
c(N1,N2)}
matplot(N12, type="l",lty=1:2)
legend(1,150,c("N1","N2"),lty=1:2)
```

```
d=0.4
for(t in 1:20) N12[t+1,]<-{
N1<-0.8*((1-d)*N12[t,1]+0.8*d*N12[t,2])
N2<-1.2*((1-d)*N12[t,2]+1.2*d*N12[t,1])
c(N1,N2)}
matplot(N12, type="l",lty=1:2)
legend(15,100,c("N1","N2"),lty=1:2)
```