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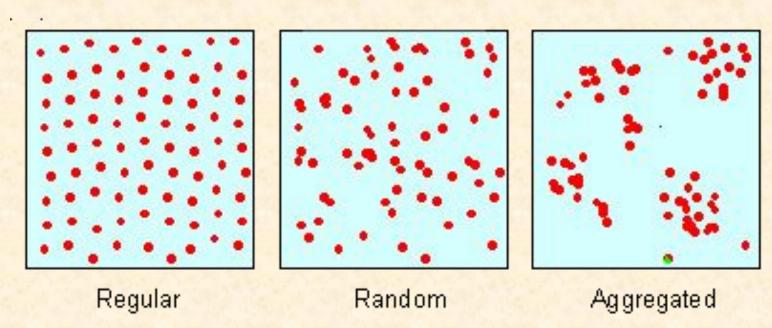
Spatial ecology - describes changes in spatial pattern over time

- 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 discrete 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:  $\mu > \sigma^2$ 

#### Random distribution

described by hypothetical Poisson distribution

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

 $\mu$ .. 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
- $\blacktriangleright$  observed and expected frequencies are compared using  $\chi^2$  statistics
- for random distribution:  $\mu = \sigma^2$

### Aggregated distribution

described by hypothetical negative binomial distribution

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

 $\mu$ .. 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

 $\blacktriangleright$  approximate value of k:

$$k \approx \frac{\mu^2}{\sigma^2 - \mu}$$

• for aggregated:

$$\mu < \sigma^2$$

#### Coefficient of dispersion (CD)

$$CD = 1 \dots random distribution$$

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

# Dispersal

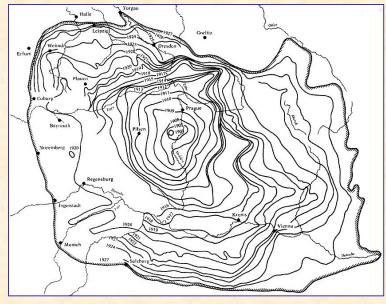
- Geographic range radius of space containing 95% of individuals
- expansion increase in geographic range
- individual makes blind random walk
- random walk of a population undergoes diffusion in space
- diffusion (Brownian motion) model in 2dimensional space:

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

- radial distance moved in a random walk is related to  $\sqrt{time}$ 

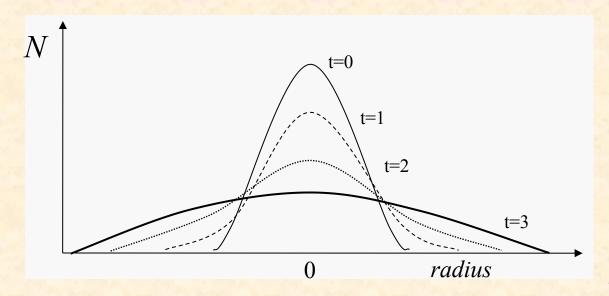
D.. diffusion coefficient (distance<sup>2</sup>/time)





Spread of muskart in Europe

## Pure dispersal



- assuming all individuals are dispersers
- range expanses linearly with time
- no reproduction

 $N_0$ .. initial density

 $\rho$  .. radial distance from point of release (range)

- Diffusion model
- solved to2dimensionalGaussian distribution

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

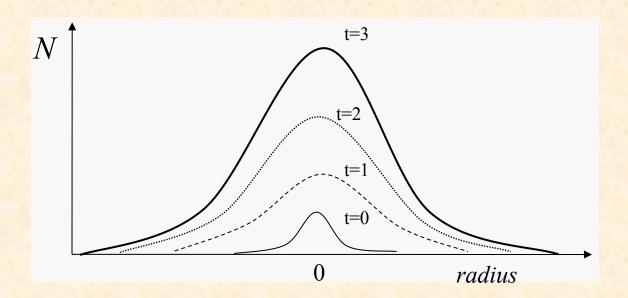


$$\rho = \sqrt{4Dt}$$



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

## Dispersal + population growth



- · Skellam's model
- includes diffusion and exponential population growth

r.. intrinsic rate of increase

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

c - expansion rate [distance/time]

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

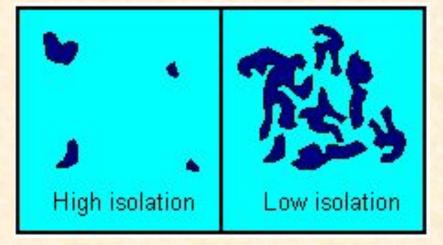
## Metapopulation ecology

▶ 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 subpopulation and focus on fraction of sub-population sites occupied

#### Levin's model

- assumptions
- sub-populations are identical in size, distance, resources, etc.
- extinction and colonisation are independent of p
- many patches are available
- natality and mortality is ignored
- p.. proportion of patches occupied
- m.. colonisation (immigration) rate proportion of open sites colonised per unit time
- e.. extinction (emigration) rate proportion of sites that become unoccupied per unit time

$$\frac{\mathrm{d}p}{\mathrm{d}t} = mp(1-p) - ep$$

• equilibrium is found for  $\frac{dp}{dt} = 0$ 

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

- sub-populations will persist  $(p^* > 0)$  only if colonisation is larger than extinction (m > e)
- all patches can be occupied only if e = 0
- K .. is fraction of patches
- defined by balance between m and e
- ▶ metapopulations are found in insects, *Daphnia*, frogs, birds
- rescue-effect model, incidence model

