III Southern-Summer School on Mathematical Biology

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Lecture V

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Outline

Space

- Up to this point, all models that we have studied assume implicitly that all individuals are in certain region of space.
- This region has been supposed not to be very important .
- We think of homogeneous regions.
- Well-mixed populations.
- **HOWEVER...**
- Individuals move, generating possibly the spatial redistribution of the population.
- And space may be heterogeneous due to several factors :
  - climate
  - soil
  - vegetation
  - composition
  - salinity....

Density

- Let us consider a population in space.
- Let space be homogeneous. How do populations spread over space?.
- First point: we will not speak of number of individuals.
- Instead we will speak of **density** of individuals.
- The number of individuals per unit space.
- The usual notation is r $\rho(\vec{x}, t)$ for density. It is a function of time and **space**.
- In some contexts, we use the term **concentration**.

Diffusion

- Our main hypothesis is that individuals move **randomly.**
- In some sense, they behave as molecules in a gas.
- If we look at such population from a space scale much larger than the typical scale of the movement of the individuals we will see the macroscopic phenomenon called **diffusion**.
- Particles in a gas obey Fick's law.
- We will assume the same for a population.
- **So, what's Fick's law?**

Fick

- The Fickian diffusion law states that:
  - The flux $\vec{J}$ of "material"(animals, cells,..) is proportional to to the gradient of the density of the material:

$$\vec{J} = -D\vec{\nabla}\rho \equiv -D(\frac{\partial\rho}{\partial x}, \frac{\partial\rho}{\partial y})$$

  - where we took a two-dimensional space.
  - But to simplify the calculations let us consider the one-dimensional case:

$$J \sim -\frac{\partial\rho}{\partial x}$$

Mass/number of individuals conservation

- Let us impose a conservation law:
  - *The rate of change in time of the quantity of individuals in a region of space is equal to the flux through the borders.*
- that is, (in one dimension, $(x_0 - x_1)$ being the size of the region):

$$\frac{\partial}{\partial t} \int_{x_0}^{x_1} \rho(x,t) dx = J(x_0,t) - J(x_1,t)$$

The diffusion equation

$$\frac{\partial}{\partial t}\int_{x_0}^{x_1}\rho(x,t)dx = J(x_0,t) - J(x_1,t)$$

- We can write the previous equation in a differential form:
  - Take $x_1 = x_0 + \Delta x$.
  - So that for $\Delta x \to 0$:
    - $\int_{x_0}^{x_1}\rho(x,t)dx \to \rho(x_0,t)\Delta x$
    - $J(x_1,t) \to J(x_0,t) + \Delta x \left(\frac{\partial J(x,t)}{\partial x}\right)_{x=x_0}$
  - Which implies::

$$\frac{\partial \rho}{\partial t}\Delta x = -\Delta x \left(\frac{\partial J(x,t)}{\partial x}\right)$$

  - and using Fick's law

$$\frac{\partial \rho}{\partial t} = -\frac{\partial J(x,t)}{\partial x} = D\frac{\partial^2 \rho}{\partial x^2}$$

SAIFR

The diffusion equation

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

- The above equation is known as the diffusion equation.
- In two dimensions we would have:

$$\frac{\partial \rho}{\partial t} = D \nabla^2 \rho$$

where $\nabla^2 \rho \equiv \frac{\partial^2 \rho}{\partial x^2} + \frac{\partial^2 \rho}{\partial y^2}$

- It is the same equation that describes heat diffusion if ρ is taken as temperature.
- Let us recall some facts about it.

Diffusion Equation

- The diffusion equation is a *partial differential equation*, a **PDE**.
- It is linear, and the coefficients are constants.
- It can be solved **analytically**.

Mathematical comment

- In order to speak of a solution of a differential equation, we need to specify supplementary conditions.
- In the case of the diffusion equation we should give an initial condition $\rho(x, 0)$ and the values of either $\rho(x, t)$ or $\frac{\partial \rho(x,t)}{\partial x}$ at the borders or for $x \to \pm\infty$.
- To solve it analytically, means that we can find a formula connecting $\rho(x, t)$ to $\rho(x, 0)$.

Gauss

- There is a distinctive soolution: a **Gaussian** function.
- In one dimension we have, for $t > 0$:

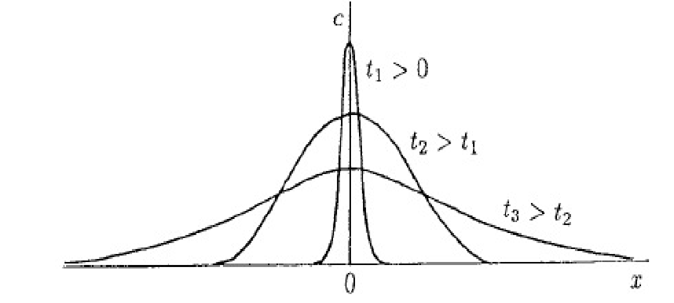
$$\rho(x,t) = \frac{Q}{2(\pi D t)^{1/2}} e^{-x^2/(4Dt)}$$

where Q os a constant.

- It is a Gaussian that "widens"with time.
- Corresponds to an initial condition concentrated in $x = \mathbf{0}$.
- Here is a plot.

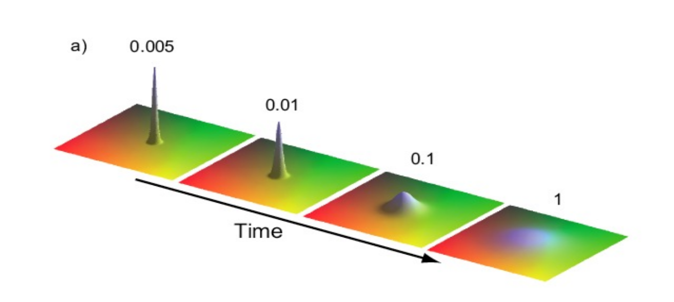
Gauss: plots

Solution to the 1D diffusion equation



Gauss: 2D plot

Solution to the 2D diffusion equation



Diffusion, biology

Let us put some biology in this lecture!

- Let us give a biological sense to all that.
- Suppose that at $t = 0$ a population of N individuals is released at $x = 0$.
- After a certain amount of time we want to know the the extension occupied by the population.
- Let's be more specific: we want the extension of the region containing 95% of the population.

Diffusion, biology

- Knowing the density of a population allows us to calculate the total population in a given area. In the 1D case, we have:

$$\text{Population between } -L \text{ and } L = N_L = \int_{-L}^{+L} \rho(x,t)dx.$$

- If we use the Gaussian for $\rho(x,t)$,perform the integral, we obtain that 95% of the population is a region of size $2\sqrt{2Dt}$.
- Which grows in time proportional to $t^{1/2}$.
- Or, at a speed which goes like $t^{-1/2}$. Decreasing.

Diffusion + Growth

- The previous case corresponds to a non-growing population.
- Let us incorporate growth:

$$\frac{\partial \rho}{\partial t} = D\frac{\partial^2 \rho}{\partial x^2} + a\rho(x,t)$$

- Still linear.
- But, as we already learning, some saturation mechanism should become relevant for large enough populations Say:

$$\frac{\partial \rho}{\partial t} = D\frac{\partial^2 \rho}{\partial x^2} + a\rho(x,t) - b\rho^2(x,t)$$

Fisher-Kolmogorov

$$\frac{\partial \rho}{\partial t} = D\frac{\partial^2 \rho}{\partial x^2} + a\rho(x,t) - b\rho^2(x,t)$$

Figura : Robert. A. Fisher

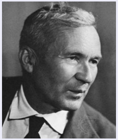


Figura : Andrei N. Kolmogorov

- The above equation is called Fisher-Kolmogorov equation.
- It is the simplest equation with diffusion, growth and self-regulation of a species.
- It is nonlinear.
- It is a representative of the class of **"reaction-diffusion"** equations.
  - This name comes from chemistry.
- The 2D version is obvious:

$$\frac{\partial \rho}{\partial t} = D\nabla^2\rho + a\rho - b\rho^2$$

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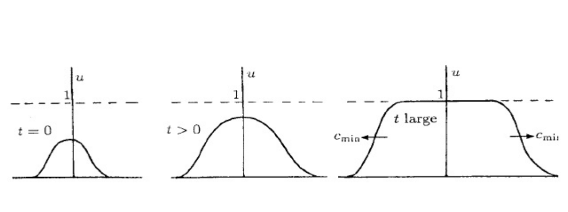
Fisher-Kolmogorov

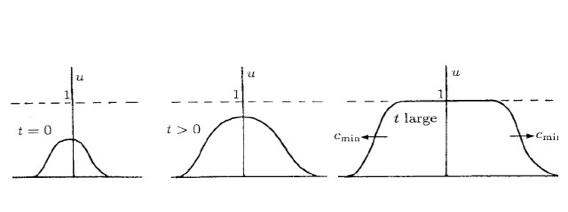
$\frac{\partial \rho}{\partial t} = D\frac{\partial^2 \rho}{\partial x^2} + a\rho(x,t) - b\rho^2(x,t)$

- Let us again look at the problem of a population released at a point ($x = \mathbf{0}$).
- Suppose it obeys the Fisher-Kolmogorov equation (and not anymore the simple diffusion equation).
- No explicit formula.
- But look at the plot::



Fisher-Kolmogorov

$$\frac{\partial \rho}{\partial t} = D\frac{\partial^2 \rho}{\partial x^2} + a\rho(x,t) - b\rho^2(x,t)$$



- We can see that there is a wave-front. And it moves with speed $v = \mathbf{2}\sqrt{aD}$. **Constant.**
- In the case of simple diffusion the speed decreased with time.
- This pattern can be made the basis of experimental verification.
- Our observations should concentrate on the front's speed. .

Skellam

- The speed does not depend on b.
- Therefore, the constant wavefront speed is not related to density dependence. The nonlinear term is there to avoid infinities.
- A equation

$$\frac{\partial \rho}{\partial t} = D\frac{\partial^2 \rho}{\partial x^2} + a\rho(x,t)$$

  is called the Skellam equation.

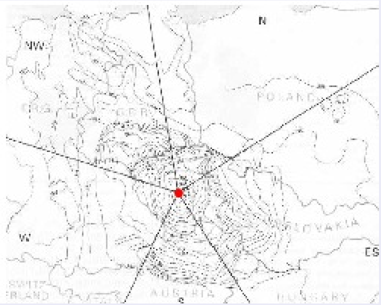
The classic example

Muskrat

- The muskrat, an species native of North-america, was introduced in Europe.
- In 1905, five individuals were introduced in Prague.
- Today, there are millions in Europe
- In what follow, we see the expansion of the muskrat's range around Prague over 17 years..

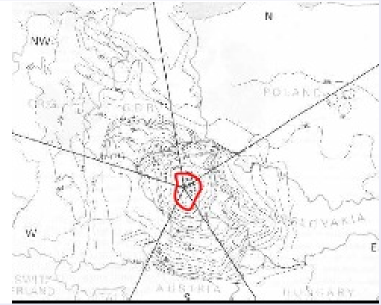
Muskrat

1905



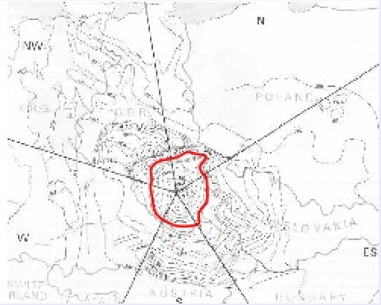
Muskrat

1909



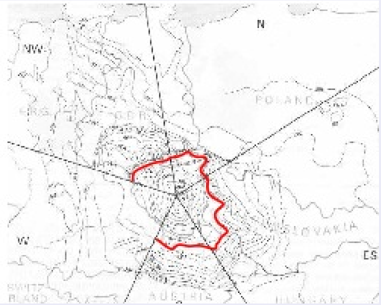
Muskrat

1913



Muskrat

1917

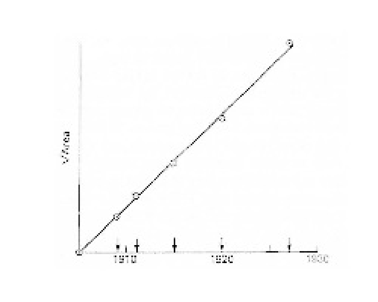


Muskrat

1921

Skellam !

- From these observations we can estimate the speed of invasion as a function of time.
- Here it is:



- A straight line. Constant speed. *Skellam dixit!* REJOICE!.

Micro X macro

- From the theory of the Brownian motion we can see D as the mean square displacement per unit of time.
- We could try to track individuals and calculate it .
- Beware!, it is likely that you get a wrong value for D. Too large.
- Why?

Home range effects

- Many species have home ranges.
- This comes from several factors: the need to find food, the need to find shelter .
- This slows down the diffusion process.
- In general, a mechanistic study of D is difficult. In most studies it is taken as a phenomenological constant.

Example: Hantavirus

- In 2000, a new species of Hantavirus was discovered, being the etiological agent of f a respiratory syndrome. It is fatal in up to 60% of cases
- The host is *Oligoryzomys fulvescens*. Take a look at him:

- Where you find the rat, you find the Hantavirus
- The disease "follows"the spread of the rat.

Hantavirus II

- The diffusion of the hosts is well modeled by the usual models,.
- But D is *small*.
- *Oligoryzomys fulvescens* has a limited home-range.
- The population spreads through juvenile migrants.
- A statistically rare event.
- But determinant for the spatial redistribution of the population.
- The diffusion coefficient appearing in the equations is a proxy of all these processes.

Bibliography

- J.D. Murray: *Mathematical Biology I e II* (Springer, 2002)
- N.F. Britton: *Essential Mathematical Biology* (Springer, 2003).
- R.S. Cantrell e C. Cosner: *Spatial Ecology via Reaction-Diffusion Equations* (Wiley, 2003).
- A. Okubo e S.A. Levin: *Diffusion and Ecological Problems* (Springer, 2001).
- P. Turchin: *Quantitative Analysis of Movement* (Sinauer, 1998)

Online Resources

- http://www.ictp-saifr.org/mathbio3
- http://ecologia.ib.usp.br/ssmb/

Thank you for your attention