III Southern-Summer School on Mathematical Biology

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Lecture V

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Outline

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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...
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 $\rho(\vec{x}, t)$ for density. It is a function of time and **space**.

In some contexts, we use the term **concentration**.
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?
The Fickian diffusion law states that:

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

\[
\vec{J} = -D \vec{\nabla} \rho \equiv -D \left( \frac{\partial \rho}{\partial x}, \frac{\partial \rho}{\partial y} \right)
\]

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

\[
J \sim - \frac{\partial \rho}{\partial x}
\]
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
    \[ \frac{\partial \rho}{\partial t} = - \frac{\partial J(x, t)}{\partial x} = D \frac{\partial^2 \rho}{\partial x^2} \]
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 \( \rho \) 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 $\rho(x, 0)$.
There is a distinctive solution: a Gaussian function.
In one dimension we have, for $t > 0$:

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

where $Q$ is a constant.

It is a Gaussian that "widens" with time.
Corresponds to an initial condition concentrated in $x = 0$.
Here is a plot.
Gauss: plots

Solution to the 1D diffusion equation
Gauss: 2D plot

Solution to the 2D diffusion equation
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 extension occupied by the population.
- Let’s be more specific: we want the extension of the region containing 95% of the population.
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.**
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:

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

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

- Let us again look at the problem of a population released at a point \((x = 0)\).
- Suppose it obeys the Fisher-Kolmogorov equation (and not anymore the simple diffusion equation).
- No explicit formula.
- But look at the plot:
We can see that there is a wave-front. And it moves with speed $v = 2\sqrt{aD}$. 

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.
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, a 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 follows, we see the expansion of the muskrat's range around Prague over 17 years.
Muskrat

1905
Muskrat

1909
Muskrat

1913
Muskrat

1917
Muskrat

1921
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!
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?
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.
In 2000, a new species of Hantavirus was discovered, being the etiological agent of 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.
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

Online Resources

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

Thank you for your attention