Mathematical Models of Organism Movement and Dispersal

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Biologically Inspired Mathematics

Not Mathematical Biology or BioMathematics

Biologically Inspired Mathematics

Survey of well-known and maybe not-so-well-known results

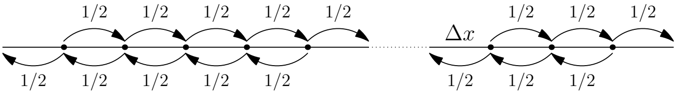
Survey of mathematics motivated by organism movement, dispersal, population growth

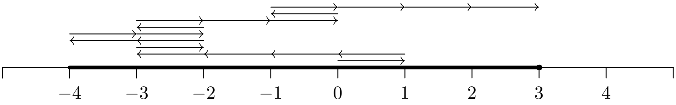
Caution: Hand-waving over constants and changes of variables

Simplest Model

Bernoulli (Coin Flip) model

Discrete Time/Discrete Space/One-Dimensional





Pass to Limit

Speed up, zoom out, scale appropriately:

$\Delta t \to 0$, $\Delta x \to 0$, $[\Delta x]^2/\Delta t \to D$

$x \in \mathbb{R}$, $t \geq 0$

$u(x,t) =$ distribution of population over x

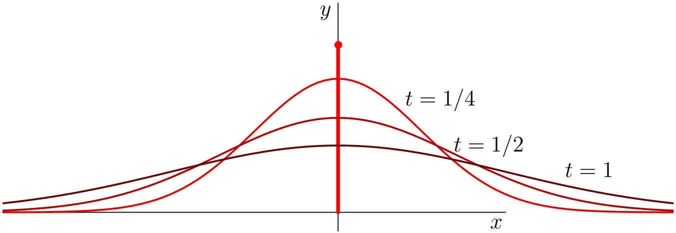
Diffusion (Heat) Equation:

$$u_t = \frac{1}{2} D u_{xx}$$

Problem – Infinite Speed of Spread

Solution:

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



Note $u(x,t) > 0$ for all x, and $t > 0$.

Fisher or KPP Equation

Ronald Fisher (1937), *The wave of advance of advantageous genes*,

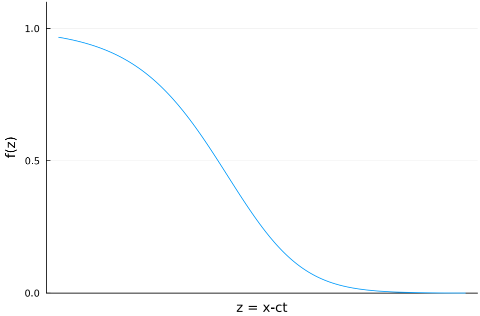
A. Kolmogorov, I. Petrovskii, and N. Piskunov. (1937) *A study of the diffusion equation with increase in the amount of substance* (slight generalization)

Add Logistic Growth, obtain Reaction-Diffusion Equation:

$$u_t = \frac{1}{2} D u_{xx} + r u (1 - u)$$

Traveling Wave Solutions

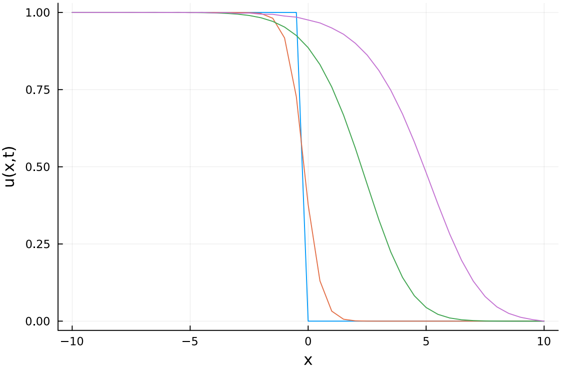
Solutions of the form $u(x, t) = f_c(x - ct)$ exist for *all* $c \geq \sqrt{2Dr}$



All solutions with compact support initial data converge to the wave with the minimum speed.

Problem – Infinite Speed of Spread

Solution with Heaviside initial data:



Note $u(x,t) > 0$ for all x, and $t > 0$.

Better Model for Movement

Continuous Time/Continuous Space

- Motivated by E. coli "Run and Tumble" or "Run and Turn"
- Alternating sequence of "runs" and "tumbles"
- Run: organism propels itself in a fixed direction for a random time
- Tumble: organism remains stationary, reorients for the next run
- wild-type E. coli: run duration is exponentially distributed with a mean of about 1 second

Run-and-Tumble in Flagellates

- E. coli,
- Salmonella typhimurium,
- Bacillus subtilis (soil and gut bacterium)
- Chlamydomonas reinhardtii (green alga with 2 flagella)
- Synechocystis (unicellular freshwater cyanobacteria)

Correlated Random Walk

Simple Continuous Time/Continuous Space/One-Dimensional Model: Goldstein (1951), Kac, (1974), McKean (1967), Segel (1978)

- Particles move left or right along line at speed s
- At random times (Poisson process, rate λ), reverses direction.
- $u^+(x,t)$ is probability density of particles moving right at t.
- $u^-(x,t)$ is probability density of particles moving left at t.

Simplest example of a *random evolution*.

Equations for Density Evolution

$$\frac{\partial u^+}{\partial t} + s\frac{\partial u^+}{\partial x} = -\lambda u^+ + \lambda u^-$$
$$\frac{\partial u^-}{\partial t} - s\frac{\partial u^-}{\partial x} = \lambda u^+ - \lambda u^-$$

Let $u(x,t) = u^+(x,t) + u^-(x,t)$ be the total density at x and t.

Rearrange into Telegrapher's Equation: (slightly modified, $\frac{1}{2}D = s^2$)

$$u_{tt} + 2\lambda u_t = \frac{1}{2}Du_{xx}$$

Tangent: What's Telegraphy Have to Do with It?

Heaviside, 1876, with prior work by Kelvin (Wm. Thomsen)

First undersea (Atlantic) telegraph cables about 1855 worked poorly. Weak signals, "blurred" signals in contrast to land based telegraphy. Why?

$$LCu_{tt} + (RC + GL)u_t + GRu = u_{xx}$$

- R: Resistance of copper line
- L: Inductance around copper line
- C: Capacitance between copper line and seawater
- G: Conductance of Insulator between copper line and seawater

Tangent: What's Telegraphy Have to Do with It?

$$u_{tt} + 2\lambda u_t = \frac{1}{2} D u_{xx}$$

Rough Physical Interpretation: Combines Inertia/Mass (Inductance) and Friction (Resistance) with spatial distribution.

The solution of the telegrapher's equation has finite speed of propagation, damping and dispersion (blurring).

Compare with the solution of the finite-speed wave equation and a dispersing diffusion equation.

Add in Logistic Growth

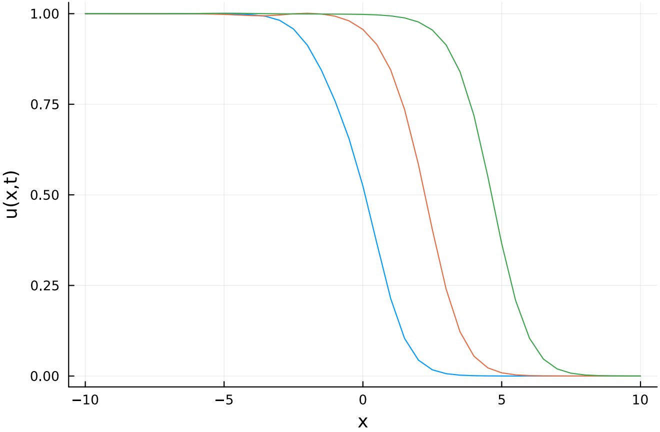
Telegrapher-Fisher Equation

$$u_{tt} + u_t = \frac{1}{2} D u_{xx} + ru(1-u)$$

- Traveling wave solutions exist for *bounded* range of speeds.
- Minimal speed of T-F is less than "natural hyperbolic speed" and mimimal Fisher speed.

Traveling Wave Solutions

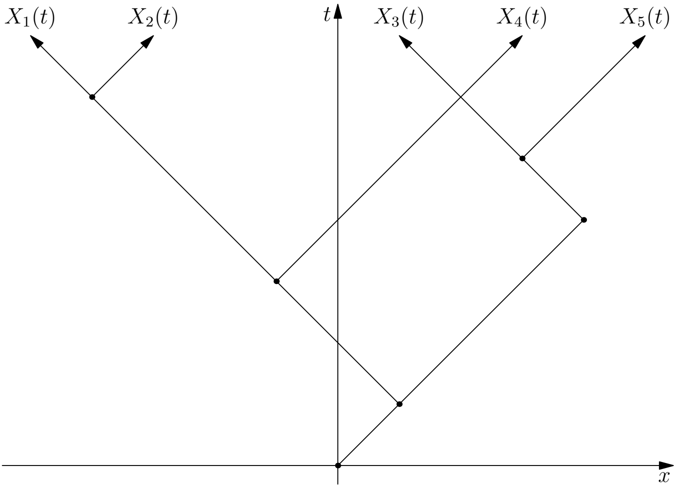
Finite Cut-off starting from Heaviside initial data



Stochastic Birth-Death Process

- Particle(s) on real line moving and reproducing in continuous time
- Speed is constant s, initial direction is $\epsilon_0 = \pm 1$, (coin flip)
- Particle reverses direction as Poisson process with parameter a
- Particle dies and splits into 2 daughter particles as Poisson process with parameter b.
- Daughter particles evolve according to similar rules.
- Every process is independent of all others.
- Binary branching random evolution.

Schematic diagram of Branching Random Evolution



Telegrapher-Fisher-Like Equation

Keep track of the position of the right-most particle at time t:

$$u(x,t) = \Pr[x \geq \max_{1 \leq j \leq n(t)} X_j(t)]$$

Note Heaviside initial data:

$$u(x,0) = \begin{cases} 1 & x \geq 0 \\ 0 & x < 0 \end{cases}$$

$$u_{tt} + ((2a+2b) - 4bu)u_t = s^2 u_{xx} + (-b^2 - 2ab)u + (b^2 + 2ab)u^2$$

Propagation of Support

$u(x,t)$ is probability of the position of the right-most particle at time t.

Starting from Heaviside initial condition, $u(x,t) = 1$ on $[st, \infty]$ with a jump discontinuity along $x = st$.

Theorem

For the binary branching process, the jump discontinuity is

$$u(st,t) - u(st-,t) = \frac{a\mathrm{e}^{-at}}{a + b(1-\mathrm{e}^{-at})/4}$$

and always goes to zero.

Roughly: The dispersal and growth spreads with speed s.

Generalization to Ternary Branching Random Evolution

3 Daughter particles at each splitting with $a = 2b$

$$u_{tt} + 6b(1 - u^2)u_t + 5b^2(u - u^2) = s^2 u_{xx}$$

Equation for a contiuum of coupled van der Pol-like oscillators.

Similar discontinuity for the ternary branching random evolution, but the discontinuity doesn't go to zero if $b > 2a$.

Spatial Jump Models of Movement

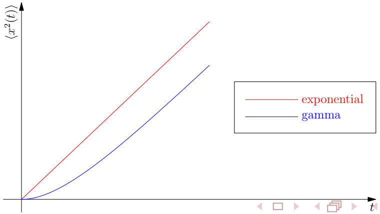
- Jump Process (kangaroo process) in $\mathbb{R}^n$
- Generalizes the coin flip model
- Generalizes Chapman-Kolmogorov to continuous time, continuous space
- $n(\mathbf{x}, t)$ number of organisms at $(\mathbf{x}, t)$

$$n(\mathbf{x}, t) = \hat{\Phi}(t) F(\mathbf{x}) + \int_0^t \int_{\mathbb{R}^n} \phi(t - \tau) T(\mathbf{x}, \mathbf{y}) n(\mathbf{y}, \tau) \, \mathrm{d}\mathbf{y} \, \mathrm{d}\tau$$

Mean squared displacement depends on waiting time distribution.

Mean-Squared Displacement

- $\phi(t) = \lambda \mathrm{e}^{-\lambda t}$ (exponential wait between jumps) gives $\langle x^2(t) \rangle = \text{const} \cdot t$.
- Roughly, mean-squared displacement is same as diffusion equation.
- $\phi(t) = \lambda^2 t \mathrm{e}^{-\lambda t}$ (Gamma wait between jumps) gives $\langle x^2(t) \rangle = \text{const} \cdot \left(t - \frac{1}{2\lambda}(1 - \mathrm{e}^{-2\lambda t})\right)$.
- Roughly, mean-squared displacement is same as telegraph equation.



Velocity Change Models of Movement and Growth

Generalization of the telegraph process

$$\frac{\partial p}{\partial t} + \nabla \cdot (\mathbf{v}p) = \\ -\lambda p + \int T(\mathbf{v}, \mathbf{v}')p(\mathbf{x}, \mathbf{v}', t)\,d\mathbf{v}' + kr(n)p$$

Mean-squared displacement matches some experimental and observational data for cells, micro-organisms, insects.