Biological Waves: Single Species Models

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Fisher–Kolmogoroff equation

$$\frac{\partial u}{\partial t} = r u(1-u) + D \Delta u$$

$r, D = \text{const.}$ $\quad u = N/K$

$$\Delta = \frac{\partial^2}{\partial x^2} + \frac{\partial^2}{\partial y^2} + \frac{\partial^2}{\partial z^2},$$

in one-dimension

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

$$t \to rt \qquad x \to x\sqrt{\frac{r}{D}}$$

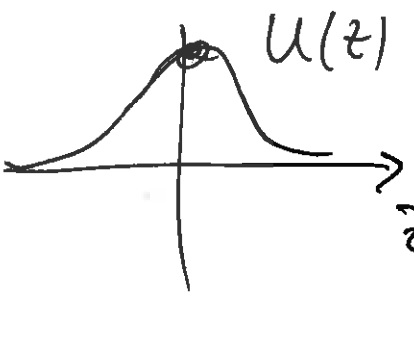
$$\boxed{u_t = u(1-u) + u_{xx}}$$

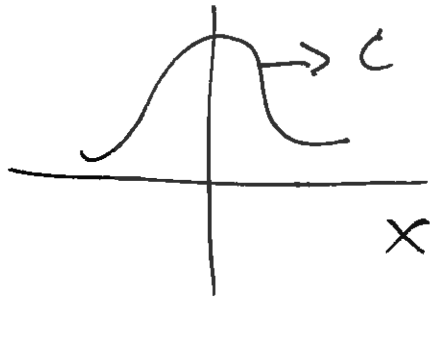
Nonlinear PDE

Travelling wave solution

$u(x,t) = U(x - ct), \quad c = \text{const.}$

$z = x - ct \quad u(x,t) = U(z)$





$z = x - ct$

Fix x, $c>0 \Rightarrow t = -\infty$ $\quad z = \infty$ 'past'

$t = +\infty$ $\quad z = -\infty$ 'future'

$$u_t = \frac{\partial u}{\partial t} = \frac{dU}{dz}\underbrace{\frac{\partial z}{\partial t}}_{(-c)} = -cU'(z)$$

$$u_x = \frac{\partial u}{\partial x} = \frac{dU}{dz}\underbrace{\frac{\partial z}{\partial x}}_{1} = U'(z)$$

$$u_t = u(1-u) + u_{xx}$$

$$-cU' = U(1-U) + U'' \qquad \underline{\text{ODE}}$$

$$\boxed{U'' + cU' + U(1-U) = 0}$$

Two constant solutions $U=0$, $U=1$

Linearize near $U=0$ and $U=1$

$U = 0 + n$, n - 'small', $n^2 \to 0$

$$n'' + cn' + n(1-n) = 0$$

$$n'' + cn' + n - \cancel{n^2} = 0 \qquad n = n_0 e^{\lambda z}$$

$$n_0\lambda^2 e^{\lambda z} + cn_0\lambda e^{\lambda z} + n_0 e^{\lambda z} = 0$$

$\lambda^2 + c\lambda + 1 = 0$ characteristic equ.

$$\lambda^2 + c\lambda + 1 = 0$$

$$\lambda = \frac{-c \pm \sqrt{c^2-4}}{2}$$

$\cancel{u = n} = n_0 e^{-\frac{c}{2}}$

$\underline{\text{I}}$ $\quad c^2 - 4 \geq 0$

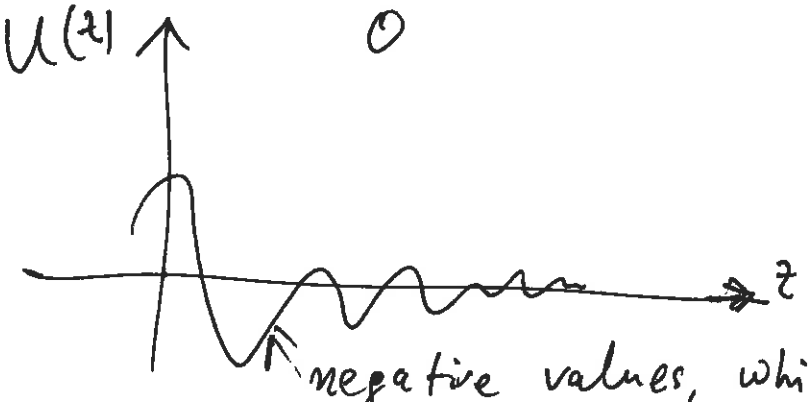
Two negative roots $\lambda_1, \lambda_2 < 0$

$$u = n_{01} e^{\lambda_1 z} + n_{02} e^{\lambda_2 z} \to 0$$

$u = 0$ is a stable equilibrium

$\underline{\text{II}}$ $\quad c^2 - 4 < 0$ complex roots

$$u = n_0 \underbrace{e^{-\frac{c}{2}z}}_{\downarrow\, 0} \cos\left(\sqrt{4-c^2}\, z + \varphi_0\right)$$



negative values, which are not possible.

Case II not possible.

Case I: $c^2 - 4 \geq 0 \Rightarrow \boxed{c \geq 2}$

$$\boxed{c_{min} = 2}$$

$$U = 1 \Rightarrow U = 1 + n, \qquad |n| \ll 1$$

$$U'' + cU' + U(1-U) = 0$$

$$n'' + cn' + (1+n)(\cancel{1} - \cancel{1} - n) = 0$$

$$n'' + cn' - n - \cancel{n^2} = 0$$

$$n'' + cn' - n = 0, \qquad n = n_0 e^{\lambda z}$$

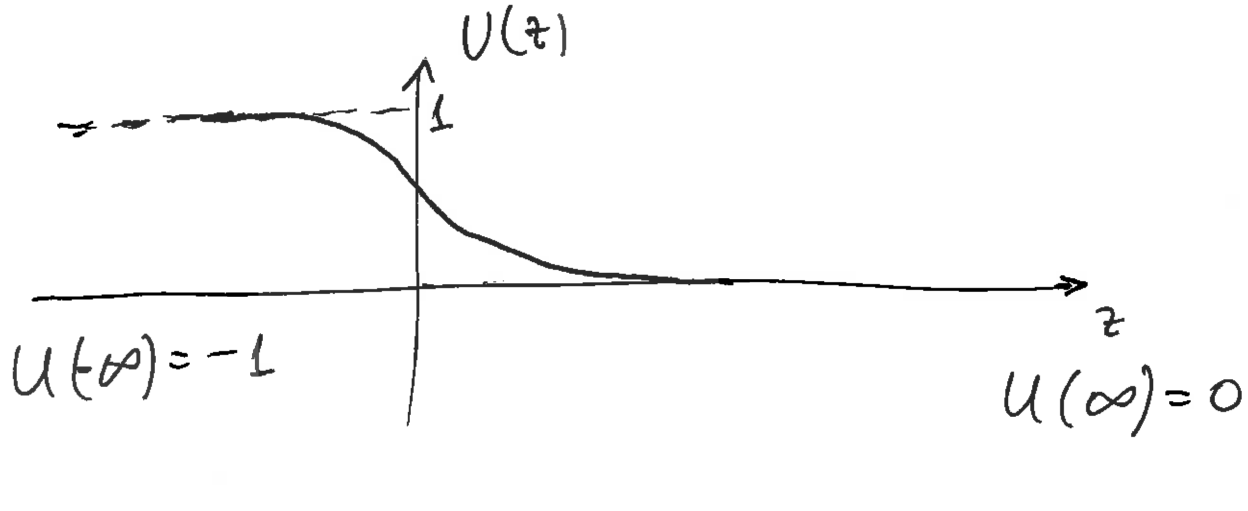
$$\lambda^2 + c\lambda - 1 = 0$$

$$\lambda_\pm = \frac{1}{2}\left(-c \pm \sqrt{c^2+4}\right)$$

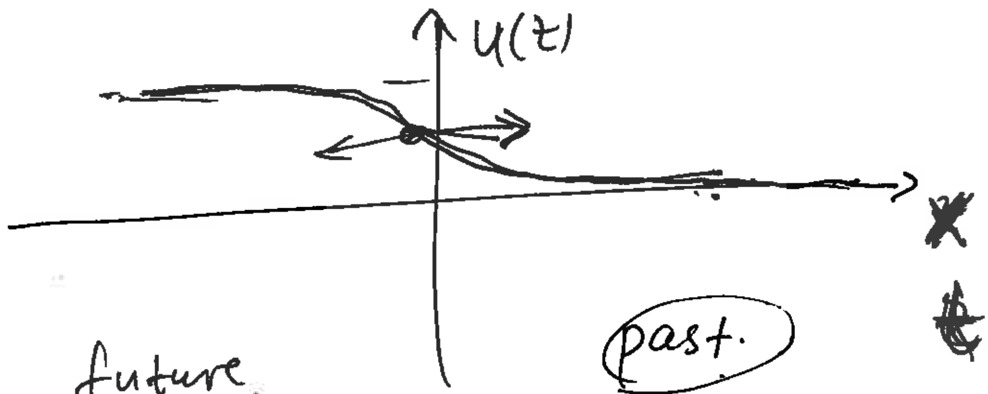
$$n = n_{01}\underset{\substack{\downarrow\\ 0}}{e^{\lambda_- z}} + n_{02}\underset{\substack{\downarrow\\ \infty}}{e^{\lambda_+ z}}$$ <u>unstable</u>

$$n = n_{01}\underset{\substack{\downarrow\\ 0}}{e^{\lambda_- z}} + n_{02}\underset{\substack{\downarrow\\ \infty}}{e^{\lambda_+ z}} \rightarrow \infty$$

$U(z) = 1$ is unstable equilibrium



$\boxed{z = x - ct}$



$u(-\infty) = 1.$ $\quad u(\infty) = 0$ (stable)

$\boxed{c \geq 2}$ $\quad c_{min} = 2$

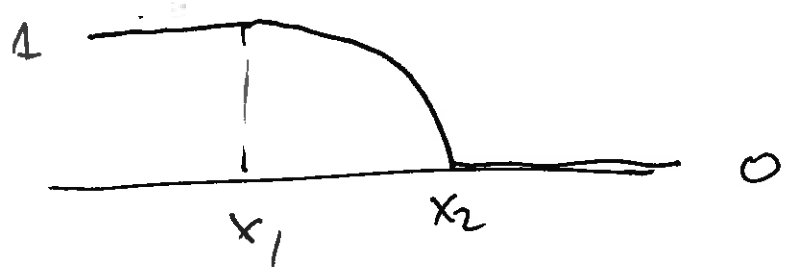
$x \to x\sqrt{\frac{r}{D}} \quad t \to rt$

$1 = \left[\frac{x}{t}\right] \to \frac{\sqrt{\frac{r}{D}}}{r} = \frac{1}{\sqrt{rD}}$ c dim.

$$\boxed{c_{min} = 2\sqrt{rD}}$$

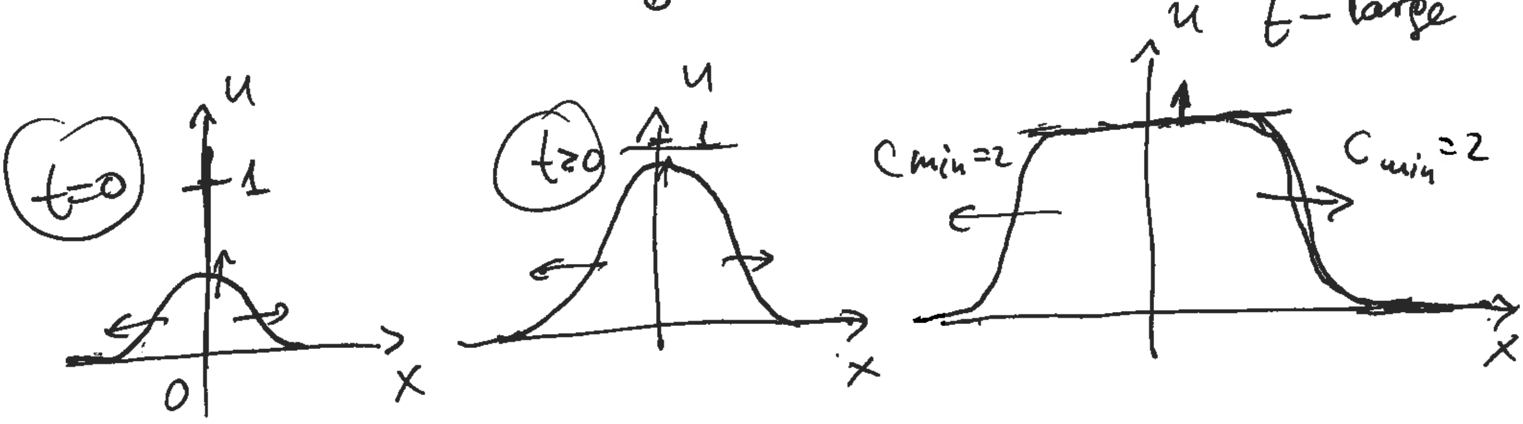
Kolmogoroff:

$u(x,0) = \begin{cases} 1, & x < x_1 \\ 0 & x > x_2 \end{cases}$



Then $u(x,t)$ is a travelling wave with $c = 2 = c_{min}$

c depends on $u(x,0)$ at $\pm\infty$



$$u_t = u(1-u) + u_{xx}, \qquad x \to -x$$

$U(x-ct)$ is solution so is $U(x+ct)$

$$-x-ct = -(x+ct), \qquad \pm c$$

$$\lim_{t\to\infty} u(x,t) = \lim_{z\to-\infty} U(z) = 1 \qquad z = x - ct$$

Asymptotic solution

$c \geq 2$, $\varepsilon = \dfrac{1}{c^2} < \dfrac{1}{c_{min}^2} = \dfrac{1}{4} = 0.25$

$$U'' + cU' + U(1-U) = 0$$

$$U(z) = g(\xi), \quad \xi = \frac{z}{c} = \sqrt{\varepsilon}\, z$$

$$g(\xi) = g_0(\xi) + \varepsilon g_1(\xi) + \varepsilon^2 g_2(\xi) + \cdots$$

$$g(-\infty) = 1, \quad g(\infty) = 0, \quad g(0) = \tfrac{1}{2}$$

$$U(z) = g(\xi) \quad , \quad \xi = \frac{z}{c}$$

$$\frac{dU}{dz} = \frac{dg}{d\xi} \cdot \frac{d\xi}{dz} = \frac{1}{c} g' = \sqrt{\varepsilon} \frac{dg}{d\xi}$$

$$\frac{dU}{dz} = \sqrt{\varepsilon} \frac{dg}{d\xi}$$

$$U'' + cU' + U(1-U) = 0$$

$$\varepsilon \frac{d^2 g}{d\xi^2} + \cancel{c} \cdot \frac{1}{\cancel{c}} \frac{dg}{d\xi} + g(1-g) = 0$$

$$\varepsilon \frac{d^2 g}{d\xi^2} + \frac{dg}{d\xi} + g(1-g) = 0$$

$$g = g_0 + \varepsilon g_1 + \varepsilon^2 g_2 + \cdots$$

$$\varepsilon (g_0'' + \varepsilon g_1'' + \cdots) + (g_0' + \varepsilon g_1' + \cdots) +$$
$$+ (g_0 + \varepsilon g_1 + \cdots)(1 - \underline{g_0} - \underline{\varepsilon g_1} - \cdots) = 0$$

$$0 = \varepsilon g_0'' + \cancel{\varepsilon^2 g_1''} + \underline{g_0'} + \varepsilon g_1' + \underline{g_0} + \varepsilon g_1 - \underline{g_0^2} - \varepsilon g_1 g_0 - \varepsilon g_0 g_1 + \cdots$$

$\boxed{\varepsilon^0}$ $\quad g_0' + g_0(1-g_0) = 0 \longrightarrow$ solve for g_0

$\boxed{\varepsilon^1}$ $\quad g_0'' + g_1' + g_1 - 2g_0 g_1 = 0 \longrightarrow$ solve for g_1

$\vdots$

$$g_0(\xi) = \frac{1}{1+e^{\xi}}$$

$$u(z) = \frac{1}{1+e^{z/c}} + O(\varepsilon)$$

$$(*) \quad g_1' + \underline{(1-2g_0)}\, g_1 = - g_0''$$

$$\boxed{y' + P(\xi)\, y = Q(\xi) \quad - \text{ linear } 1^{st} \text{ order}}$$

$$1 - 2g_0$$

$\boxed{\text{Eq. for } g_0}$: $g_0' + g_0(1-g_0) = 0$

$$g_0' + g_0 - g_0^2 = 0 \quad \Rightarrow \quad g_0'' + g_0' - 2 g_0 g_0' = 0$$

$$g_0'' + \underline{(1-2g_0)}\, g_0' = 0$$

'Trick' $\boxed{1 - 2g_0 = - \frac{g_0''}{g_0'}}$

$$g_1' - \frac{g_0''}{g_0'}\, g_1 = - g_0'' \qquad \Big| \cdot \frac{1}{g_0'}$$

$$\frac{g_1' g_0' - g_0'' g_1}{(g_0')^2} = - \frac{g_0'' \cdot A}{g_0' A} \qquad \left[\frac{g_1}{g_0'}\right]' = \left(- \ln|A g_0'|\right)'$$

$$\frac{g_1(\xi)}{g_0'} = - \ln|A g_0'| \quad \Rightarrow \quad \boxed{g_1(\xi) = - g_0' \ln|A g_0'|}$$

$$g_0 = \frac{1}{1+e^{\xi}} \, , \quad g_0' = -\frac{e^{\xi}}{(1+e^{\xi})^2}$$

$$g_1 = -g_0' \ln |A g_0'|$$

$$g_1(\xi) = \frac{e^{\xi}}{(1+e^{\xi})^2} \ln \frac{A e^{\xi}}{(1+e^{\xi})^2} \qquad \underline{g_1(0) = 0}$$

$$g_1(0) = \frac{1}{2^2} \ln\left(\frac{A}{2^2}\right) \Rightarrow A = 2^2 = \underline{\underline{4}}$$

$$\boxed{g_1(\xi) = \frac{e^{\xi}}{(1+e^{\xi})^2} \ln \frac{4e^{\xi}}{(1+e^{\xi})^2}} \qquad \xi = \frac{z}{c}$$

$$U(z) = g_0 + \varepsilon g_1 + O(\varepsilon^2) \qquad \varepsilon = \frac{1}{c^2}$$

$$U(z) = \frac{1}{1+e^{z/c}} + \frac{1}{c^2} \cdot \frac{e^{z/c}}{(1+e^{z/c})^2} \ln \left[\frac{4e^{z/c}}{(1+e^{z/c})^2}\right] + O\left(\frac{1}{c^4}\right)$$

$$\boxed{\underline{c \geq 2}}$$

Density-Dependent Diffusion Models

$$\frac{\partial u}{\partial t} = f(u) + \frac{\partial}{\partial x}\left[D(u)\frac{\partial u}{\partial x}\right]$$

Typically $f(u)$ has zeroes at $u=0$ & $u=1$

$$f(u) = u^p(1-u^q) \quad , \quad p,q>0$$

$$D(u) = D_0 u^m \quad , \quad D_0, m > 0$$

$$\frac{\partial u}{\partial t} = r u^p(1-u^q) + D_0 \frac{\partial}{\partial x}\left(u^m \frac{\partial u}{\partial x}\right)$$

$$\frac{\partial u}{\partial t} = u^p(1-u^q) + \frac{\partial}{\partial x}\left(u^m \frac{\partial u}{\partial x}\right)$$

An example of an exact solution

take $\underline{p=1, \quad m=0}$

$$\frac{\partial u}{\partial t} = u(1-u^q) + \frac{\partial^2 u}{\partial x^2} \quad , \quad q>0$$

$$u = U(z) \quad , \quad z = x-ct \quad , \quad U(-\infty)=1, \quad U(\infty)=0$$

$$L(U) = U'' + cU' + U(1-U^q) = 0$$

$$U(z) = \frac{1}{(1+ae^{bz})^s} \qquad \underline{a, b, s > 0}$$

$$U = \frac{1}{(1+ae^{bz})^s} = (1+ae^{bz})^{-s}$$

$$U' = \frac{-sabe^{bz}}{(1+ae^{bz})^{s+1}} = -sab\,\frac{e^{bz}}{(1+ae^{bz})^{s+1}}$$

$$U'' = -sab\,\frac{be^{bz}(1+ae^{bz})^{s+1} - e^{bz}(s+1)(1+ae^{bz})^{s}\,abe^{bz}}{(1+ae^{bz})^{2s+2}}$$

$$U'' = -sab^2(1+ae^{bz})^{-s-2}e^{bz}\left[1+\cancel{ae^{bz}} - (s+\cancel{1})ae^{bz}\right]$$

$$U'' = -sab^2e^{bz}(1+ae^{bz})^{-s-2}(1-sae^{bz})$$

$$U' = -sabe^{bz}(1+ae^{bz})^{-s-1}$$

$$U = (1+ae^{bz})^{-s}$$

$$U'' + cU' + U(1-U^q) = 0$$

$$-sab^2e^{bz}(1+ae^{bz})^{-s-2}(1-sae^{bz})$$
$$-\,c\,sabe^{bz}(1+ae^{bz})^{-s-1} + \underline{(1+ae^{bz})^{-s}} - \underline{(1+ae^{bz})^{-s(q+1)}}$$

$$\cancel{\frac{1}{(1+ae^{bz})}}$$
$$(1+ae^{bz})^{-s-2}\left[-sab^2e^{bz}(1-sae^{bz}) - csabe^{bz}(1+ae^{bz}) + (1+ae^{bz})^2 - (1+ae^{bz})^{2-sq}\right] = 0$$

$$e^0,\ e^{bz},\ e^{2bz} \qquad \boxed{2-sq = 0,1,2}$$

$2 = sq \quad , \quad s = \frac{2}{q}, \frac{1}{q}, \cancel{sq = 0}$. $\quad \frac{s > 0}{q > 0}$

Consider $\quad s = \frac{1}{q} \qquad sq = 1$

$$-sab^2 e^{bz} + s^2a^2b^2 e^{2bz} - csabe^{bz} - csa^2be^{2bz}$$
$$+ \cancel{1} + 2ae^{bz} + a^2e^{2bz} - \cancel{1} - ae^{bz}$$

e^{bz} | $\quad -sab^2 - csab + 2a - a = 0$

$$-sb\cancel{a}(b+c) + \cancel{a} = 0 \qquad a > 0$$
$$\boxed{1 = sb(b+c)}$$

e^{2bz} | $\quad s^2a^2b^2 - csa^2b + a^2 = 0$

$$s^2b^2 - csb + 1 = 0$$
$$sb(sb-c) = -1 = -sb(b+c)$$

$$\underline{sb}(sb-c) + \underline{sb}(b+c) = 0$$
$$sb(sb - \cancel{c} + b + \cancel{c}) = 0$$
$$sb^2(s+1) = 0 \qquad \text{Not possible!}$$

$s = \frac{1}{q}$ not possible.

$\underline{sq = 2}$

$$-sab^2e^{bz} + s^2a^2b^2e^{2bz} - csabe^{bz} - csa^2be^{2bz}$$
$$+ \cancel{1} + 2ae^{bz} + a^2e^{2bz} - \cancel{1} = 0$$

$e^{bz}|$
$$-sab^2 - csab + 2a = 0$$
$$-s\cancel{a}b(b+c) + 2\cancel{a} = 0$$
$$\boxed{2 = sb(b+c)}$$

$e^{2bz}|$
$$s^2a^2b^2 - csa^2b + a^2 = 0$$
$$sb(sb-c) + 1 = 0$$
$$2sb(sb-c) + 2 = 0$$
$$2sb(sb-c) + sb(b+c) = 0$$
$$sb(2sb - 2c + b + c) = 0$$
$$(2s+1)b - c = 0$$
$$(2s+1)b = c \Rightarrow \boxed{b = \frac{c}{1+2s}}$$

$$s = \frac{2}{q}, \quad b = \frac{q}{[2(q+2)]^{1/2}}, \quad c = \frac{q+4}{[2(q+2)]^{1/2}}$$

$q = 1$ Fisher – Kolmogoroff

$s = 2$, $b = \frac{1}{\sqrt{6}}$ $c = \frac{5}{\sqrt{6}} = 2.04 > \underline{\underline{2}}$

$U(0) = \frac{1}{2} \Rightarrow \underline{a = \sqrt{2} - 1}$

$$U(z) = \frac{1}{\left(1 + (\sqrt{2}-1)\, e^{z/\sqrt{6}}\right)^2}$$

$c = \frac{5}{\sqrt{6}}$ – works for specific <u>speed</u>!