II. Population Dynamics in Spatially Extended Systems

A. Spatial range expansion

1. Diffusion equation

If individuals perform random walk, then the local density $p(R, t)$ evolves according to the diffusion equation

$$\frac{\partial p}{\partial t} = D \nabla^2 p(R,t) ; \text{ initial condition } p(R,t=0) = p_0(R)$$

boundary condition: $p(R=\infty, t) = 0$

So the diffusion equation:

Fourier transform: $\hat{p}(k,t) = \int d^3R \overrightarrow{p}(R,t) e^{ik \cdot R}$

can obtain $p$ from $\hat{p}$: $p(R,t) = \int \frac{d^3k}{(2\pi)^3} \hat{p}(k,t) e^{-ik \cdot R}$

insert $\hat{p}$ into diff. equa:

$$\frac{\partial \hat{p}}{\partial t} = \frac{1}{2} \nabla^2 \frac{\partial \hat{p}}{\partial \omega}$$

$$\hat{p}(k,t) = \frac{1}{(2\pi)^3} \hat{p}(k,t) e^{-ik \cdot R}$$

$\hat{p}(k,t) = \hat{p}(k,t=0) \cdot e^{-D k^2 t}$

$\hat{p}(k,t=0) = \int d^3R p_0(R) e^{ik \cdot R}$

for each mode $k$: $\frac{\partial \hat{p}(k,t)}{\partial t} = -D k^2 \hat{p}(k,t)$
Consider initial cond where \( \hat{p}_0(\vec{r}) = N_0 \delta^3(\vec{r}) \) 
(i.e. \( N_0 \) individuals placed in a small volume at \( t = 0 \))

then \( \hat{p}(\vec{r}, t=0) = N_0 \), \( \hat{p}(\vec{r}, t) = N_0 e^{-\Delta k^2 t} \)

**Inverse transform:**

\[
\hat{p}(\vec{r}, t) = \int \frac{d^3k}{(2\pi)^3} \hat{\phi}(\vec{k}, t) e^{-i\vec{k} \cdot \vec{r}} = N_0 \int \frac{d^3k}{(2\pi)^3} e^{-\Delta k^2 t - ik \cdot \vec{r}}
\]

\[
= N_0 \int \frac{dk_x}{2\pi} e^{-\Delta k_x^2 t - ik_x x} \int \frac{dk_y}{2\pi} e^{-\Delta k_y^2 t - ik_y y} \int \frac{dk_z}{2\pi} e^{-\Delta k_z^2 t - ik_z z}
\]

\[
= N_0 \left( \frac{1}{4\pi \Delta t} e^{-\frac{x^2}{4\Delta t}} \right) \left( \frac{1}{4\pi \Delta t} e^{-\frac{y^2}{4\Delta t}} \right) \left( \frac{1}{4\pi \Delta t} e^{-\frac{z^2}{4\Delta t}} \right)
\]

\( p(\vec{r}, t) = N_0 \left( \frac{1}{4\pi \Delta t} \right)^{3/2} e^{-\frac{x^2}{4\Delta t}} \) — *spreading Gaussian*

plot along \( x \)-axis

\( \Rightarrow \) the width of the density distribution expands

\( \langle x^2 \rangle = \int d^3r x^2 \hat{\phi}(\vec{r}, t) = 2D \Delta t; \) \( W \sim \sqrt{D \Delta t} \)

\( \Rightarrow \int d^3r \hat{\phi}(\vec{r}, t) = \hat{\phi}(\vec{k} = 0, t) = N_0, \) *unchanged*
2. Range expansion for growing population

- Logistz growth of well-mixed population
  \[ \frac{dp}{dt} = r p \left( 1 - \frac{p}{K} \right) \]

- Allow random spatial movement
  Starting from localized initial spatial dist \( p_0(x) \)

- Study in 1d for illustration

\[ \frac{\partial p(x,t)}{\partial t} = D \frac{\partial^2 p}{\partial x^2} + r p \left( 1 - \frac{p}{K} \right) \]

Fisher-Kolmogorov Equation (1937)

Dimensionless form: \( u = \frac{p}{\bar{p}} \), \( \tau = ct \), \( \xi = \frac{x}{\sqrt{D} t} \)

\[ \frac{\partial u}{\partial \tau} = \frac{\partial^2 u}{\partial \xi^2} + u (1-u) \]

**a) Look for propagating soln:**

\[ u(\xi, \tau) = \frac{y}{1 + \frac{y}{c \sqrt{D} \tau}} \quad \text{where} \quad \frac{y}{1 + \frac{y}{c \sqrt{D} \tau}} \]

\[ v = c \sqrt{D} \tau \]

\[ \frac{du}{d\tau} = \frac{dy}{d\zeta} \quad \frac{du}{d\xi} = -c \frac{dy}{d\zeta} \]

\[ \frac{d^2 y}{d\zeta^2} + c \frac{dy}{d\zeta} + y \cdot (1-y) = 0 \quad \text{(3)} \]

\[ \Rightarrow \text{What is the propagating speed } c \text{ or } v = c \sqrt{D} \tau ? \]
find $c$ such that $y(z) > 0$ exist with $y(z \to -\infty) = 1$, $y(z \to \infty) = 0$.

- Can visualize $\Theta$ as Newton's eqn of motion for a "particle" at "position" $y$ at "time" $z$

\[ U(y) \]

\[ \frac{d^2 y}{dz^2} = -c \frac{dy}{dz} - y(1-y) \]

Friction: $F(y) = -\frac{dU}{dy}$

\[ U(y) = \frac{y^2}{2} - \frac{y^3}{3} \]

- Expect two types of motion:
  - If "friction" ($c$) is small, get "damped oscillation" around $y=0$ (unphysical since $y$ cannot be $-ve$)
  
  - If friction ($c$) suff large (over damped)
    then expect $y(z) > 0$

$\Rightarrow$ a range of allowed $c$?
• Quantify the above conditions by doing linear stability analysis around \( y = 0 \) (front)

For \( y < 1 \), \[ \frac{d^2 y}{dx^2} = -c \frac{dy}{dx} - y. \]

Let \( y = y e^{\lambda z} \), \( \lambda^2 - c\lambda + 1 = 0 \)

\[ \lambda = \frac{c \pm \sqrt{c^2 - 4}}{2} \rightarrow \begin{cases} \frac{c + \sqrt{c^2 - 4}}{2} & c < 2 \\ \frac{c - \sqrt{c^2 - 4}}{2} & c \geq 2 \end{cases} \]

\( c < 2 \): Damped oscillations; \( c \geq 2 \): Stable

\( \Rightarrow \) Propagating soln exist for \( c \geq 2 \)

\( c \geq 2 \), \( y \sim A e^{-\lambda_+ z} + B e^{-\lambda_- z} \geq B e^{-\lambda_- z} \) (since \( \lambda_- < \lambda_+ \))

\( u(3, t) = y(3-ct) \propto e^{-\lambda_- (3-ct)} \)

\[ = e^{-\lambda_- \frac{x-c\sqrt{D}rt}{\sqrt{D}t}} = e^{-\lambda_- (x-ct)} \]

Allowed speed: \( v = c \sqrt{D} \geq 2 \sqrt{D} r \)

Steepness of front:

\[ \kappa = \frac{\lambda_-}{\sqrt{D}} = \frac{c}{\sqrt{D}} \left( \frac{c}{2} \right)^{2-\frac{c^2}{2}} \leq \sqrt{\frac{c}{D}} \]
b) Selection of propagating speed

In general, propagating speed \(c\) can depend on the initial profile \(u(3, t=0)\).

- Examine the soln at the front
  (\(u^2\) term can be neglected at front)

\[
\frac{\partial u}{\partial t} = u + \frac{x^2}{\partial^2_x} u
\]

Suppose initial cond is \(u(3,0) = u_0 e^{-x^3}\) for \(t>0\), look for traveling soln

\(u(3, t) = u_0 e^{-\lambda(3-c t)}\)

Then \(\lambda c = 1 + \lambda^2\)

\(\Rightarrow c = \lambda + \frac{1}{\lambda}\)

\[
\begin{align*}
\frac{dc}{d\lambda} &= 1 - \frac{1}{\lambda^2} \\
\frac{d^2c}{d\lambda^2} &= \frac{2}{\lambda^3} > 0 \\
\Rightarrow & \text{at most one min} \\
\frac{dc}{d\lambda} &= 0 \Rightarrow \lambda^* = 1 \\
\Rightarrow & c(\lambda^*) = 2
\end{align*}
\]

\(\Rightarrow\) Speed depends on steepness of initial profile \(u\)
Stability of propagating front with different slopes

Heuristics given below: formal solve via stability analysis.

\[ e^{-\lambda (\xi - c t)} (\lambda = 1) \]

\[ \rightarrow c = 2 \]

\[ \rightarrow C = C_{\text{min}} = 2 \]

"Marginal Stability"

the above does not apply to broader init cond.

Thus for any init cond \( U(\xi,0) \)

such that \( U(\xi,0) = 0 \) for \( \xi > \xi_0 \)

(i.e. init pop confined to a certain region \( \xi < \xi_0 \))

then eventually the speed of the front

approaches \( C = C_{\text{min}} = 2 \) or

\[ v^* = 2\sqrt{Dc} \]

(validation for mytobacteria population, Cremer 2019)

\[ u \sim e^{-\lambda (\xi - 2t)}; \lambda(c=2) = 1 \]

\[ \kappa \quad \text{Steepness} \quad \kappa = \lambda \frac{1}{\sqrt{D}} = \frac{1}{\sqrt{D}} \]
3. Spatial spread of epidemics

Recall the SIR model (from I.A3)

\[
\begin{align*}
\frac{dS}{dt} &= -rS\cdot I \\
\frac{dI}{dt} &= rS\cdot I - \mu I \\
\frac{dR}{dt} &= \mu I
\end{align*}
\]

\(r\): infection rate/suscep.  
\(\mu\): removal rate  
\(\text{Note:} \frac{dS}{dt} + \frac{dI}{dt} + \frac{dR}{dt} = 0 \Rightarrow S(t) + I(t) + R(t) = N\)

Add 1d diffusion coupling to S and I (R inert)

\[
\begin{align*}
\frac{dS}{dt} &= -rS\cdot I + D\frac{\partial^2 S}{\partial x^2} \\
\frac{dI}{dt} &= rS\cdot I - \mu I + D\frac{\partial^2 I}{\partial x^2}
\end{align*}
\]

Make dimensionless: Initial suscep. pop So

\[
S_0 = S', \quad I_0 = I', \quad \zeta = \frac{\sqrt{S_0}}{D}; \quad \frac{\mu}{D} = \frac{1}{\zeta}
\]

\[
\begin{align*}
\frac{dS'}{dt} &= -S'\cdot I' + \frac{\partial^2 S'}{\partial x^2} \\
\frac{dI'}{dt} &= +S'\cdot I' - rS'\cdot I' + \frac{\partial^2 I'}{\partial x^2}
\end{align*}
\]

Invasion of infection into suscep. pop?
Look for propagating solution of the form
\[ S'(z, t) = u(z-c t) \]
\[ I'(z, t) = v(z-c t) \]

then \[ \frac{d^2 u}{dz^2} + c \frac{du}{dz} - u v = 0 \] \hspace{1cm} (1) \hspace{1cm} 0 \leq u(-\infty) < u(\infty) = 1

\[ \frac{d^2 v}{dz^2} + c \frac{dv}{dz} + (u - \delta) v = 0 \] \hspace{1cm} (2) \hspace{1cm} v(-\infty) = v(\infty) = 0

dynamics at the front:

\[ u \approx 1. \rightarrow \text{solve } v(z) \text{ from (2)} \]
then solve \( u(z) \) from (1).

(2) \[ \frac{d^2 v}{dz^2} + c \frac{dv}{dz} + (1-\delta') v = 0. \]

Try \( v = e^{\lambda z} \): \[ \lambda^2 - c \lambda + (1-\delta') = 0. \]

\[ \lambda = \frac{c}{2} \pm \sqrt{(\frac{c}{2})^2 - (1-\delta')} \]

- \( v(z \to \infty) = 0 \) requires \( \lambda_+ > 0 \) or \( \Delta < \left(\frac{c}{2}\right)^2 \)
  \( \rightarrow c_0 > 1 \) (cf. threshold work in See IA.3)

- Osc. Soln. not allowed since \( v \geq 0 \)

\[ \Rightarrow c \geq 2 \sqrt{1-\delta'} \]

Stability argument:

\[ c = 2 \sqrt{1-\delta'} \]

(1) \[ \frac{d^2 u}{dz^2} + c \frac{du}{dz} - \frac{1}{2} u v = 0 \] \hspace{1cm} \( \rightarrow u(z) = 1 - \# e^{-\lambda z} \)
4. Predator–prey chase: “wave of pursuit”
Recall Lotka–Volterra eqn (with logistic growth of prey)
\[
\begin{align*}
\frac{dp}{dt} &= r p (1-p/\P) - \nu pq \\
\frac{dq}{dt} &= \nu pq - \mu q
\end{align*}
\]
\( p \): prey, \( q \): predator
\( \P \): carrying capacity
in prey
\( \nu \): death rate of predator
\( \mu \): death rate of predator
\( \nu_{\text{max}} \)

• Make dimensionless:
\( u = p/\P, v = q \nu r, \tau = rt, a = \nu \P r, \eta = \mu/\nu \)
\[
\begin{align*}
\frac{\partial u}{\partial \tau} &= u (1-u-v) \\
\frac{\partial v}{\partial \tau} &= a v (u-\eta)
\end{align*}
\]
coexistence if \( \eta < 1 \)

• Include “diffusion” of \( p \) and \( q \) (1d):
\[
\begin{align*}
\frac{dp}{dt} &\to \frac{\partial p}{\partial \tau} = \ldots + D_p \frac{\partial^2 p}{\partial x^2} \\
\frac{dq}{dt} &\to \frac{\partial q}{\partial \tau} = \ldots + D_q \frac{\partial^2 q}{\partial x^2}
\end{align*}
\]
dimensionless: \( z = \sqrt{D_{\nu} / \nu} \)
\( D = D_p / D_q \)
\[
\begin{align*}
\frac{\partial u}{\partial \tau} &= u (1-u-v) + D \frac{\partial^2 u}{\partial x^2} \\
\frac{\partial v}{\partial \tau} &= a v (u-\eta) + \frac{\partial^2 v}{\partial x^2}
\end{align*}
\]
\( \rightarrow \) predator–prey dynamics in coexistence regime?
Suppose $u/v$ in coexistence for $t \to -\infty$
(i.e. $u^*(x, t) = \eta$, $v^*(x, t) = 1 - \eta$)
and $u \to 1$, $v \to 0$ for $t \to +\infty$.

How fast does predator spread?

We can expect the following

\[ u = \eta \text{, prey} \]
\[ v = 1 - \eta \text{, predator} \]

Look for traveling wave of the form

\[ u(z, t) = u(z - ct), \quad v(z, t) = \sqrt{v(z - ct)} \]

\[ D \frac{d^2 u}{dz^2} + c \frac{du}{dz} + u(1 - u - v) = 0 \quad ① \]
\[ \frac{d^2 v}{dz^2} + c \frac{dv}{dz} + a v(u - \eta) = 0 \quad ② \]

Boundary conditions: \quad $U(-\infty) = \eta$, $U(+\infty) = 1$
\quad $V(-\infty) = 1 - \eta$, $V(+\infty) = 0$

For simplicity, set $D = 0$, i.e., prey is immotile

(e.g. prey = plankton, predator = herbivore)

(Similar results obtained for $D \neq 0$, [Dubin, 1984])
look at leading first \((z \to \infty)\)

\[ V(z) = v_0 e^{-\lambda z} ; \quad U(z) = 1 - u_0 e^{-\lambda z} \]

work out eqs (1) + (2) to leading order in \(u_0, v_0\)

\[
c\lambda u_0 + u_0 - v_0 = 0
\]

\[
\lambda^2 v_0 - \lambda c v_0 + a(1-\eta) v_0 = 0
\]

\[
\begin{bmatrix}
1 + c\lambda & -1 \\
0 & \lambda^2 - c\lambda + a(1-\eta)
\end{bmatrix}
\begin{bmatrix}
u_0 \\
v_0
\end{bmatrix} = 0
\]

\[
\text{det} [ ] = 0 \quad \rightarrow \quad \lambda_1 = -\frac{1}{c}
\]

\[
\lambda_1 = -\frac{1}{c}
\]

\[
\lambda_2, 3 = \frac{c}{2} \pm \sqrt{\left(\frac{c}{2}\right)^2 - a(1-\eta)}
\]

Sol'n \(\lambda = -\frac{1}{c}\): Sol'n blows up for \(z \to \infty\); unphysical

Sol'n \(\lambda_2, 3\): must have \(c^2 \geq 4a(1-\eta)\)

(Otherwise, osc. Sol'n would have \(U < 0\) )

since \(\eta < 1\), must have \[c \geq \sqrt{4a(1-\eta)}\]

\[\rightarrow\] marginal stability: \(c = \sqrt{4a(1-\eta)}\)
Next, consider the limit \( z \to -a \).

Let \( U(z) = \gamma + u_0 e^{x^2} \)
\[ V(z) = 1-\gamma - v_0 e^{x^2} \]

then
\[ c \lambda u_0 + \gamma \cdot (-u_0 + v_0) = 0 \]
\[ -x^2 v_0 - c \lambda v_0 + a (1-\gamma) u_0 = 0 \]

\[
\begin{bmatrix}
  c \lambda - \gamma & 2 \\
  a(1-\gamma) & -c \lambda - x^2
\end{bmatrix}
\begin{bmatrix}
  u_0 \\
  v_0
\end{bmatrix} = 0
\]

\[
\det \left[ \begin{array}{cc}
  c \lambda - \gamma & 2 \\
  a(1-\gamma) & -c \lambda - x^2
\end{array} \right] = 0 \Rightarrow \left( c \lambda - \gamma \right) x (c+\lambda) + a \gamma (1-\gamma) = 0
\]

\( p(x) \)

to see how \( S \) and \( \theta \) depend on parameters,
let's \( p(0) \) for various values of \( a \).

\( a = 0 \) : \( p_0(x) = 0 \) for \( x_1 = -c, \lambda_2 = 0, \lambda_3 = \gamma / c \)

\( a > 0 \) : \( p(x) = p_0(x) + a \gamma (1-\gamma) \)
\[ \begin{align*}
\rightarrow \text{ for } 0 < a < a^*, \quad &\lambda_1 < 0 \quad \text{(incompatible with b.c.)} \\
&\lambda_2, \lambda_3 > 0 \quad (\text{OK}) \\
\text{for } a > a^*, \quad &\lambda_1 < 0 \quad \text{(incompatible with b.c.)} \\
&\lambda_{2,3} = \text{Complex with } \Re \lambda_{2,3} > 0 \\
&\text{damped oscillatory sol'n}
\end{align*} \]

(Note: osc. sol'n around \( U^* = y, V^* = 1-y \) is OK)

\[ \begin{align*}
0 < a < a^* \\
\rightarrow \text{ expect propagating wave if } 0 \text{-dim dynamics exits limit cycle.}
\end{align*} \]
5. Trigger wave:

$U = "order\ parameter" \ of\ a\ bistable\ system$

$\frac{dy}{dt} = \gamma y (a-y) (y-b) \quad g(y) = -\frac{dy}{dx}$

E.g.: Magnetization (ferromagnet)
Mitoic wave, chromosome mod,...

Spatially coupled dynamics:

$\frac{2u}{\delta t} = D \frac{2u}{\delta x^2} + \gamma y (a-y) (y-b)$

$\gamma = \frac{\delta t \delta x}{\delta \xi}$; \( \delta \xi = \sqrt{\frac{D}{\delta t}} \delta x \rightarrow \frac{2u}{\delta \xi} = \frac{2}{\delta \xi^2} u \ + \ y (a-y) (y-b)$

Propagation from stable to metastable phase ("trigger wave")

$U(x, t) = g(x - \gamma t)$

$\Rightarrow \frac{d^2y}{dz^2} = -\gamma \frac{dy}{dz} - y(a-y)(y-b)$ (4)

$g(y) = -\frac{dy}{dx}$

$U(y)$

Mechanical analogy: a ball rolling down from a, move pass ori, and stop exactly at b.
"dissipation energy", proportional to $c$,

must be exactly equal to $\Delta U \equiv U(a) - U(b)$

(unique criterion for prop. speed $c$)

\[ d^2 \frac{dy}{dz} = -c \left( \frac{dy}{dz} \right)^2 - \frac{dU}{dy} \cdot \frac{dy}{dz} \]

\[ \int_{-\infty}^{\infty} dz \left( \frac{dy}{dz} \right)^2 = -c \int_{-\infty}^{\infty} dz \left( \frac{dy}{dz} \right)^2 - \int_{-\infty}^{\infty} dz \frac{dU}{dz} \]

\[ \left. \left( \frac{dy}{dz} \right)^2 \right|_{-\infty}^{\infty} = 0 \]

\[ c \int_{-\infty}^{\infty} dz \left( \frac{dy}{dz} \right)^2 = U(-\infty) - U(\infty) = U(a) - U(b) \]

\[ \Rightarrow \quad c \propto U(a) - U(b) \]

Thermodynamic potential $(U(a) - U(b) = -\Delta G)$

is the driving force for propagation
Analysis of trigger wave dynamics:

\[ \frac{\partial u}{\partial t} = \frac{\partial^2}{\partial z^2} u + (u-u_1) \cdot (u_2-u) (u-u_3) \]

\( g(u) : u_1 < u_2 < u_3 \)

Let \( u(z,t) = y(z-t) \)

\[ \frac{\partial^2}{\partial z^2} y + c \frac{\partial y}{\partial z} + (y-u_1) \cdot (u_2-y) \cdot (y-u_3) = 0 \]

\( g(y) = -f(y) = \frac{dy}{dz} \)

Solve:

\[ \frac{dy}{dz} = \alpha (y-u_1) \cdot (y-u_3) \cdot h(y) \]

\[ \frac{d^2 y}{dz^2} = \frac{dy}{dz} \cdot h(y) = \frac{dy}{dz} \cdot \frac{dh}{dy} \]

\[ = \frac{dy}{dz} \cdot \alpha (y-u_1+y-u_3) \]

\[ = \alpha^2 (y-u_1) (y-u_3) \cdot (2y-u_1-u_3) \]

\[ L(u) = (y-u_1) (y-u_3) \cdot \left[ \alpha^2 (2y-u_1-u_3) + c \alpha + (u_2-y) \right] \]

\[ [ ] = 0 \rightarrow 2\alpha^2 = 1 \]

\[ \alpha = \pm \frac{1}{\sqrt{2}} \]

\[ \alpha^2 (u_1+u_3) = c \alpha + u_2 \]

\[ c = \frac{1}{2 \alpha} (u_1+u_3 - 2u_2) \]

\( y(z) \) from direct integration:

\[ \frac{dy}{dz} = \alpha (y-u_1) (y-u_3) \]

\[ y(z) = \frac{u_3+u_1}{1 + e^{2 \alpha (u_1-u_3) (z-z_0)}} \]

\( z_0 \) is arbitrary shift of z-axis

\[ y(z) = \frac{u_1+u_3}{2} + \frac{u_1-u_3}{2} \tanh \left( \frac{\alpha (u_1-u_3) (z-z_0)}{2} \right) \]
boundary condition: \( y(z \to -\infty) = u_3 \)
\( y(z \to +\infty) = u_1 \) \( \exists \ \alpha > 0 \),

\[ C = \frac{1}{\sqrt{2}} (u_1 + u_3 - 2u_2) \]

\( \Rightarrow \) propagation to the right if \( \frac{u_1 + u_3}{2} > u_2 \)
left if \( \frac{u_1 + u_3}{2} < u_2 \)

Direction of propagation:

\[ U(u_3) - U(u_1) = \int_{u_1}^{u_3} dy f(y) = \int_{u_1}^{u_3} (y-u_1)(u_2-y)(y-u_3) \]

\[ = -\frac{1}{12} (u_3-u_1)^2 \left[ (u_2-u_1)^2 - (u_3-u_1)^2 \right] \]
\[ = \frac{1}{12} (u_3-u_1)^2 (u_1 + u_3 - 2u_2) \]

\[ C = \frac{6E}{(u_3-u_1)^3} \left[ U(u_3) - U(u_1) \right] \]

\( \Rightarrow \) propagation from stable to metastable state

Why does the system know about metastability even though the dynamics is deterministic?

Existence of Lyapunov function

\[ \dot{X}[u] = \int dx \left[ \frac{1}{2} D \left( \frac{\partial u}{\partial x} \right)^2 - U(u) \right] \]

\[ \frac{\partial u}{\partial t} = -\frac{S}{8u(x_0)} \dot{X}[u] \]

Can show \( \frac{dL}{dt} < 0 \) except when \( u \) solves PDE.