

Part II: Mathematical Biology - Revision Notes

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1. Deterministic Systems

1.1. Single population models

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2. Stochastic Systems

Write $P(n, t)$ to represent the probability of the population size being n at time t . For simplicity, we write $P(n, t) = p_n$.

$$\phi(s, t) = \sum_{n=0}^{\infty} s^n p_n = \langle s^n \rangle$$

$$\phi(1, t) = 1$$

$\phi(0, t) = p_0$ = probability that the population has die out.

$$\phi(s, 0) = 1$$

2.1. Discrete population sizes

Single populations: Constant probability rate λ of adding one individual to the population

Master equation: $\dot{p}_n = \lambda(p_{n-1} - p_n)$

Try generating function: $\phi(s, t) = \sum_{n=0}^{\infty} s^n p_n = \langle s^n \rangle$

$$\dot{\phi} = (s - 1)\lambda\phi$$

$$\phi = A(s)e^{(s-1)\lambda t}$$

$$\phi(s, 0) = 1 \Rightarrow \phi(s, t) = e^{(s-1)\lambda t}$$

$$\mu = \langle N \rangle = \frac{\partial \phi}{\partial s} \Big|_{s=1} = \lambda t$$

$$\langle N(N-1) \rangle = \frac{\partial^2 \phi}{\partial s^2} \Big|_{s=1} = (\lambda t)^2$$

$$var(N) = \lambda t$$

Import and death model: Same import model as before with a per capita probability death rate β (so the total death rate is βn).

Master equation: $\dot{p}_n = \lambda(p_{n-1} - p_n) + \beta[(n+1)p_{n+1} - np_n]$

$$\phi_t = (s - 1)[\lambda\phi - \beta\phi_s]$$

Try $\phi = e^{(s-1)f(t)} \Rightarrow \phi(s, t) = \exp[\frac{\lambda}{\beta}(s-1)(1 - e^{-\beta t})]$.

$$\langle N \rangle = \frac{\lambda}{\beta}(1 - e^{-\beta t})$$

$$var(N) = \frac{\lambda}{\beta}(1 - e^{-\beta t})$$

Multiple population model

2.2. Continuous population sizes

2.2.1. Fokker-Planck for a single variable

$W(n, r)$ represents the jump rate from n to $n + r$. Use x to represent continuous population size instead of n .

Master equation:

$$\frac{\partial}{\partial t} P(n, t) = \sum_r [W(n-r, r)P(n-r, t) - W(n, r)P(n, t)]$$

Fokker-Planck Equation (FPE):

$$\frac{\partial P}{\partial t} = -\frac{\partial}{\partial x}(AP) + \frac{1}{2}\frac{\partial^2}{\partial x^2}(BP)$$

Derivation: Do Taylor expansion to the master equation and define $A(x) = \sum_r rW$ and $B(x) = \sum_r r^2W$

How expectation of a general function $f(x)$ evolves in time:

$$\frac{d}{dt} \langle f(x) \rangle = \langle Af' \rangle + \frac{1}{2} \langle Bf'' \rangle$$

Derivation: By definition of expectation, then substitute Fokker-Planck equation, and lastly integration by parts with boundary conditions P and $\frac{\partial P}{\partial x}$ tends to 0 as $|x| \rightarrow \infty$.

Time evolution of mean: $\langle x \rangle' = \langle A \rangle$ (time derivative)

Time evolution of variance: $var(x)' = \langle B \rangle + 2cov(A, x)$

2.2.2. Multivariate Fokker-Planck

General master equation:

$$\frac{\partial}{\partial t} P(\mathbf{x}, t) = \sum_{\mathbf{r}} [W(\mathbf{x} - \mathbf{r}, \mathbf{r})P(\mathbf{x} - \mathbf{r}, t) - W(\mathbf{x}, \mathbf{r})P(\mathbf{x}, t)]$$

Multidimensional Fokker-Planck equation:

$$\frac{\partial P}{\partial t} = -\frac{\partial}{\partial x_i}(A_i P) + \frac{1}{2}\frac{\partial^2}{\partial x_i \partial x_j}(B_{ij} P)$$

Time evolution of \mathbf{x} : $\langle \mathbf{x} \rangle' = \langle \mathbf{A} \rangle$

Time evolution of covariance:

$$C'_{mn} = cov(A_m, x_n) + cov(A_n, x_m) + \langle B_{mn} \rangle$$

where $C_{mn} = cov(x_m, x_n) = \langle x_m x_n \rangle - \langle x_m \rangle \langle x_n \rangle$

Behaviour at steady state

Lyapunov equation:

$$\mathbf{aC} + \mathbf{Ca}^T + \mathbf{b} = 0$$

$$a_{ik}C_{kj} + a_{jk}C_{ki} + b_{ij} = 0$$

3. Systems with spatial structure

$C(\mathbf{x}, t)$ is some quantity of interest.

$$\frac{d}{dt} \int_V C(\mathbf{x}, t) dV = \int_V F(\mathbf{x}, t) dV - \int_V \mathbf{J} \cdot \mathbf{n} dS$$

By divergence theorem, we get $\frac{\partial C}{\partial t} = F - \nabla \cdot \mathbf{J}$

There are two types of flux:

1. Advection or active motion: $\mathbf{J} = \mathbf{u}C$ where the stuff moves with velocity \mathbf{u} .
2. Diffusion: $\mathbf{J} = -D\nabla C$

So transport equation becomes:

$$\frac{\partial C}{\partial t} + \nabla \cdot (\mathbf{u}C - D\nabla C) = F(\mathbf{x}, t)$$

3.1. Diffusion and growth

3.1.1. Linear diffusion in finite domain

Basic setup: D constant, $F = 0$, $\mathbf{u} = 0$, one-dimension. So the transport equation is: $\frac{\partial C}{\partial t} = D \frac{\partial^2 C}{\partial x^2}$; In finite linear domain of length L : $x \in [0, L]$; Boundary condition: $C(0, t) = C_0$, $C(L, t) = C_1$.

Steady state solution:

$$0 = D \frac{\partial^2 C}{\partial x^2}$$

Then C is just linear in x :

$$C(x, t) = C^*(x) = C_0 + (C_1 - C_0)x/L$$

General solution:

$$C(x, t) = C^*(x) + \hat{C}(x, t)$$

By linearity:

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

with boundary condition $\hat{C}(0, t) = \hat{C}(L, t) = 0$.

Separation of variables:

$$\hat{C}(x, t) = F(x)G(t)$$

$$\frac{G'(t)}{G(t)} = D \frac{F''(x)}{F(x)}$$

Boundary condition $F(0) = F(L) = 0$ gives:

$$F(x) = \sin\left(\frac{n\pi x}{L}\right), \quad n = 1, 2, \dots$$

$$G(t) = e^{-\lambda_n t} \quad \text{with} \quad \lambda_n = D \frac{n^2 \pi^2}{L^2}$$

$$\hat{C}(x, t) = \sum_{n=1}^{\infty} a_n e^{-\lambda_n t} \sin\left(\frac{n\pi x}{L}\right)$$

$$C(x, t) = C_0 + (C_1 - C_0)x/L + \sum_{n=1}^{\infty} a_n e^{-\lambda_n t} \sin\left(\frac{n\pi x}{L}\right)$$

Add linear growth to finite domain: $\frac{\partial C}{\partial t} = D \frac{\partial^2 C}{\partial x^2} + \lambda C$

Set $C(x, t) = e^{\lambda t} \tilde{C}(x, t)$, then

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

3.1.2. Linear diffusion in an infinite domain

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

with boundary condition that C and $\frac{\partial C}{\partial x}$ tends to 0 sufficiently fast as $|x| \rightarrow \infty$.

Total amount of stuff: $M = \int_{-\infty}^{\infty} C(x, t) dx$.

Check that M is constant: $\frac{dM}{dt} = \frac{d}{dt} \int_{-\infty}^{\infty} C(x, t) dx = \int_{-\infty}^{\infty} \frac{\partial C}{\partial t} dx = \int_{-\infty}^{\infty} D \frac{\partial^2 C}{\partial x^2} dx = [D \frac{\partial C}{\partial x}]_{-\infty}^{\infty} = 0$

Approach 1: Similarity solution

Seek a solution of the form $C(x, t) = \eta f(\xi)$ with $\xi = \frac{x}{\sqrt{Dt}}$ and $\eta = \frac{M}{\sqrt{Dt}}$

Then get $f = Ae^{-\frac{1}{4}\xi^2}$.

$$\int_{-\infty}^{\infty} f d\xi = 1 \implies A = (4\pi)^{-\frac{1}{2}}$$

Approach 2: Sort powers of t

Set $C(x, t) = t^\alpha G(\xi)$ with $\xi = \frac{x}{t^\beta}$.

Substitute this into the diffusion equation to get $\beta = \frac{1}{2}$.

$M = \int_{-\infty}^{\infty} C dx$ to get $\alpha = -\frac{1}{2}$.

Add simple growth to linear diffusion in infinite domain

$$\frac{\partial C}{\partial t} = D \frac{\partial^2 C}{\partial x^2} + \lambda C$$

Set $C(x, t) = e^{\lambda t} \tilde{C}(x, t) \implies \frac{\partial \tilde{C}}{\partial t} = D \frac{\partial^2 \tilde{C}}{\partial x^2}$

3.1.3. Non-linear diffusion

$$D = kC, \quad \frac{\partial C}{\partial t} = \frac{\partial}{\partial x} \left(D \frac{\partial C}{\partial x} \right) = k \frac{\partial}{\partial x} \left(C \frac{\partial C}{\partial x} \right)$$

$$\xi = \frac{x}{(Mkt)^{1/3}}, \quad \eta = \frac{M}{(Mkt)^{1/3}}$$

$$M = \int_{-\infty}^{\infty} C dx \implies \int_{-\infty}^{\infty} F d\xi = 1$$

Substitute new variable gets $-\frac{\eta}{3t}(\xi F)' = \frac{\eta}{t}(FF')' \implies FF' + \frac{1}{3}\xi F = 0$ by noting that LHS goes to zero as $x \rightarrow \infty$.

$$F(\xi) = \begin{cases} A - \frac{1}{6}\xi^2 & \text{for } |\xi| < \sqrt{6A} \\ 0 & \text{otherwise} \end{cases}$$

Solve A by integration.

3.2. Travelling waves in reaction-diffusion systems