Part II: Mathematical Biology - Revision Notes

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1. Deterministic Systems

1.1. Single population models

1.1.3. Populations with age structure

Notations

$n(a,t)$: Number of individuals with age n at time t.

$N = \int_0^\infty n(a,t)da$: Total population at time t.

$b(a)$: Birth rate from individuals with age a.

$\mu(a)$: Death rate from individuals with age a.

$n(a+\delta t, t+\delta t) = n(a,t) - \mu(a) \cdot \delta t \cdot n(a,t) \ + \ O(\delta t^2)$

Also, by Taylor expansion,

$n(a+\delta t, t+\delta t) = n(a,t) + \delta t \frac{\partial n}{\partial a} + \delta t \frac{\partial n}{\partial t} + O(\delta t^2)$

Comparing and dividing by δt:

$$\frac{\partial n}{\partial a} + \frac{\partial n}{\partial t} = -\mu(a) n(a,t)$$

Boundary condition: Number of newborn babies satisfies

$$n(0,t) = \int_0^\infty b(a) n(a,t) da$$

Normal node solutions

Set $n(a,t) = r(a)e^{\gamma t} \implies r'(a) = -(\mu(a)+\gamma)\ r(a)$

$$r(a) = r(0)e^{-\gamma a}e^{\int_0^a \mu(s)ds}$$

$$n(a,t) = r(0)e^{\gamma(t-a)}e^{\int_0^a \mu(s)ds}$$

By boundary condition, we have

$$1 = \int_0^\infty b(a)e^{-\gamma a}e^{-\int_0^a \mu(s)ds}da := \phi(\gamma)$$

So if we can find a γ s.t. $\phi(\gamma) = 1$, then we have a valid normal node solution.

$\phi(\gamma)$ strictly decreasing $\implies$ $\phi(\gamma) = 1$ has a unique solution.

$$\phi(0) = \int_0^\infty b(a)e^{-\int_0^a \mu(s)ds}da$$

$\phi(0) > 1 \implies \gamma > 0 \implies$ growth
$\phi(0) < 1 \implies \gamma < 0 \implies$ decay

Biological interpretation of $\phi(0)$: mean number of offspring from one individual.

1.2. Discrete time

1.3. Multi-species models

1.3.1. Competition models

$$\dot{N}_1 = r_1 N_1 (1 - \frac{N_1}{K_1} - b_{12}\frac{N_2}{K_2})$$
$$\dot{N}_2 = r_2 N_2 (1 - \frac{N_2}{K_2} - b_{21}\frac{N_1}{K_1})$$

Physical interpretation of each term:

Each species along has a simple logistic dynamics with linear growth ($r_1 N_1$ and $r_2 N_2$);

Negative quadratic terms mean each species has some stable equilibrium sizes (K_1 and K_2; the carrying capacity);

Terms with b_{12} and b_{21}: interactions between species. If the negative interaction terms are not too big, then two species will coexist at some stable equilibrium value; if too big, one species will win out.

Rescaling: $M_1 = \frac{N_1}{K_1}$, $M_2 = \frac{N_2}{K_2}$, $\tau = r_1 t$.

$$\frac{dM_1}{d\tau} = M_1(1 - M_1 - b_{12}M_2)$$
$$\frac{dM_2}{d\tau} = \rho M_2(1 - M_2 - b_{21}M_1)$$

where $\rho = \frac{r_2}{r_1}$.

1.3.2. The predator-prey models

$$\frac{dN}{dt} = N(a - bP)$$
$$\frac{dP}{dt} = P(cN - d)$$

After rescaling,

$$\dot{u} = u(1 - v)$$
$$\dot{v} = -\alpha v(1 - u)$$

1.3.3. Chemical kinetics models

$$\mathrm{E} + \mathrm{S} \underset{k_2}{\overset{k_1}{\rightleftharpoons}} \mathrm{C}$$
$$\mathrm{C} \xrightarrow{k_3} \mathrm{E} + \mathrm{P}$$

$\dot{s} = -k_1 es + k_2 c$
$\dot{e} = -k_1 es + k_2 c + k_3 c$
$\dot{c} = +k_1 es - k_2 c - k_3 c$
$\dot{p} = +k_3 c$

Initial conditions: $s(0) = s_0$, $e(0) = e_0$, $c(0) = 0$, $p(0) = 0$

Invariant quantities: $\dot{e} + \dot{c} = 0$, $\dot{s} + \dot{c} + \dot{p} = 0$.
$\implies e + c = e_0$, $s + c + p = s_0$.

Hence, four equations reduce to two:
$\dot{s} = -k_1(e_0 - c)s + k_2 c$
$\dot{c} = +k_1(e_0 - c)s - k_2 c - k_3 c$

Rescaling: $u = \frac{s}{s_0}$, $v = \frac{c}{e_0}$ and suitable time rescaling gives:
$u' = -u + (u + \mu - \lambda)v$
$\epsilon v' = u - (u + \mu)v$

1.3.4. Epidemic models

S: Susceptible, I: Infected, R: Recovered

$\dot{S} = -\beta IS$
$\dot{I} = +\beta IS - \nu I$
$\dot{R} = \quad\quad +\nu I$

β=transmission rate, ν=recovery rate

Total population size remain constant: $N = S + I + R$. Hence
can determine R from $R = N - S - I$.

When can an epidemic happen?

$$\dot{I}(0) = [\beta S(0) - \nu]I(0)$$

Assumptions: Initially one or a few infected are introduced,
i.e. $I(0) > 0$; starting from nearly everyone susceptible, and only a very small number infected, i.e. $S(0) \approx N$.

Epidemic possible if and only if $\dot{I}(0) > 0$, i.e. $R_0 = \frac{\beta}{\nu}N > 1$.

Interpretation of R_0 (reproduction ratio): R has expon-
-ential distribution of time, with expected time to recovery $\frac{1}{\nu}$,
i.e. duration of an infection. β is the rate that one individual infects each susceptible. Hence, R_0 is the mean number of infected from one infection.

Vaccination

Assume a proportion p of the population is vaccinated. Then
$S(0) = (1-p)N$,

$$\frac{\beta}{\nu}S(0) = \frac{\beta}{\nu}(1-p)N = (1-p)R_0 > 1$$

for an epidemic to be possible.

Epidemic and final size

Consider $\frac{dI}{dS} = \frac{\dot{I}}{\dot{S}} = -1 + \frac{N}{R_0}\frac{1}{S}$ (Note: $\frac{dI}{dS} > -1$)

Integrating wrt S: $I = -S + \frac{N}{R_0}\log S + C$

Putting initial conditions:

$$I(t) - I(0) = -(S(t) - S(0)) + \frac{N}{R_0}\log\frac{S(t)}{S(0)} \quad (*)$$

where $I(0) \ll N$, $S(0) \approx N$.

(Diagram: trajectories in (S, I) plane)

By differentiating $(*)$, we see that trajectories have a maximum number of infected as $S = \frac{N}{R_0}$.

Define: σ =proportion of the population that escape the epidemic and actually never get infected.

Moral: σN is the left-most S-intercept in the diagram.

$$0 = -[\sigma N - NB] + \frac{N}{R_0}\log(\frac{\sigma N}{N})$$

$$\sigma - \frac{1}{R_0}\log\sigma = 1$$

(Diagram for σ as a function of R_0).

Extended epidemic model

In long term, consider natural births and deaths: let μ be the constant birth/death rate per capita.

$$\dot{S} = -\beta IS - \mu S + \mu N$$

$$\dot{I} = \beta IS - \nu I - \mu I$$

$$\dot{R} = \nu I - \mu R$$

(normally ignore the equation for R).

New reproduction ratio: $R_0 = \frac{\beta}{\nu+\mu}N$.

Consider $\nu \gg \mu$, i.e. the recovery rate is far higher than the natural death rate, i.e. the infectious period is much shorter than host lifetime.

$\exists$ a FP with disease present: $S^* = \frac{N}{R_0}$, $I^* = \frac{\mu}{\beta}(R_0 - 1)$.
This is a stable focus with $\omega \approx \sqrt{\mu\nu(R_0-1)}$ and period $T \approx \frac{2\pi}{\sqrt{\mu\nu(R_0-1)}}$.

$(\mu\nu)^{-1/2}$: geometric mean of host lifetime and disease infectious period.

1.3.5. Excitable systems

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

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

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

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

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

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

$var(N) = \lambda t$

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

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

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

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 $B(x) = \sum_r r^2 W$

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 $|x| \to \infty$.

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:

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

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:

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

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

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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:

$$F(x) = \sin(\frac{n\pi x}{L}),\ \ n = 1, 2, ...$$

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

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

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

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 $|x| \to \infty$.

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

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

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

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

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

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

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 $x \to \infty$.

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

Solve A by integration.

3.2. Travelling waves in reaction-diffusion systems