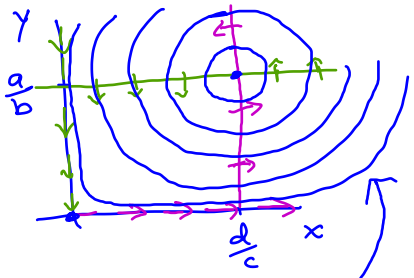
Lotka-Volterra (Predator-Prey)

Lecture 1 (rushed)

$x' = ax - bxy$
$y' = cxy - dy$
x grows exp unless y is around.
y dies out exp " x is around.
x is converted into y with stochiometry c:b (think "limiting nutrient")

Phase plane

$x' = 0$ for $x = 0$ or $y = \frac{a}{b}$
$y' = 0$ for $x = \frac{d}{c}$ or $y = 0$



First degeneracy:
- two nullclines of the same equation cross

Second degeneracy:
- infinite family of periodic solutions.

Trajectories

Define $Y(x)$ so that $Y(x(t)) = y(t)$

$$\frac{dY}{dx} = \frac{dy}{dt} \Big/ \frac{dx}{dt} = \frac{cxy - dy}{ax - bxy} = \frac{Y(cx-d)}{x(a-bY)}$$

$$\left(\frac{a}{Y} - b\right)\frac{dY}{dx} = \frac{cx-d}{x} = c - \frac{d}{x}$$

$a \ln y - by = cx - d \ln x + R$

$H(x,y) = a\ln y - by - cx + d\ln x$ (hence closed loops)

Solutions are level curves of H with density increasing to ∞ near the axes).

Talk about biology of unfolded model.
Also, non-dimensionalize both systems (after all this analysis)

Stability analysis

$$J = \begin{pmatrix} a-by & -bx \\ cy & cx-d \end{pmatrix}$$

$J_{(0,0)} = \begin{pmatrix} a & 0 \\ 0 & -d \end{pmatrix}$ ← always saddle

$J_{(\frac{d}{c}, \frac{a}{b})} = \begin{pmatrix} 0 & -\frac{bd}{c} \\ \frac{ca}{b} & 0 \end{pmatrix}$ ← always center (at a Hopf with no bifurcation parameter)

↳ the bifurcation diagram must look like
with an infinite set of periodic solutions at the bifurcation (degenerate, neither supercrit. nor subcrit) but we don't have a bifurcation parameter!!
— Must unfold!!

Unfolding - exp. growth of prey is unrealistic. Try decreasing growth rate constant

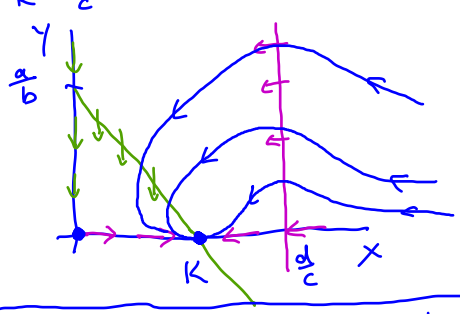
$a \to a(1 - \frac{x}{K})$ (logistic)

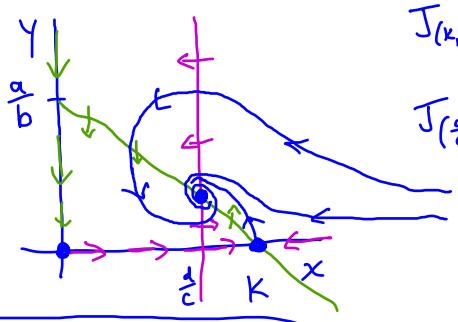
$x' = ax(1 - \frac{x}{K}) - bxy$
$y' = cxy - dy$

Phase plane
$x' = 0$ when $x = 0$ or $y = \frac{a}{b}(1 - \frac{x}{K})$
$y' = 0$ when $x = \frac{d}{c}$ or $y = 0$

Two cases: $K < \frac{d}{c}$ and $K > \frac{d}{c}$

$K < \frac{d}{c}$





Stability analysis

$$J = \begin{pmatrix} a - \frac{2ax}{K} - by & -bx \\ cy & cx-d \end{pmatrix}$$

$J_{(0,0)} = \begin{pmatrix} a & 0 \\ 0 & -d \end{pmatrix}$ ← saddle

$J_{(K,0)} = \begin{pmatrix} -a & -bK \\ 0 & cK-d \end{pmatrix}$ ← stable node $K < \frac{d}{c}$, saddle $K > \frac{d}{c}$

$J_{(\frac{d}{c}, \frac{a}{b}(1-\frac{d}{cK}))} = \begin{pmatrix} -\frac{ad}{cK} & -\frac{bd}{c} \\ \frac{ca}{b}(1-\frac{d}{cK}) & 0 \end{pmatrix} = A$

$\operatorname{tr} A < 0$, $\det A = ad(1 - \frac{d}{cK})$

$K < \frac{d}{c} \Rightarrow \det A < 0$ but $y < 0$ so who cares.

$K > \frac{d}{c} \Rightarrow \det A > 0$ so stable node or spiral

To see the Hopf, $L = \frac{1}{K}$ gives Hopf at $L = 0$. K doesn't go all the way through.

Hopf as $K \to \infty$.

Lotka-Volterra nondimensionalization

Lecture 2 – students did PP in groups

$x' = ax\left(1-\frac{x}{K}\right) - bxy = ax(1-Lx) - bxy$

$y' = cxy - dy$

x scales: $\frac{d}{c}, K, \cdots$

y scales: $\frac{a}{b}, \frac{d}{b}, \frac{cK}{b}$

Avoid having scales or non-bifurcation parameters change with bifurcation parameter(s).

$x = \frac{d}{c}X, \quad y = \frac{a}{b}Y$

$\frac{d}{c}x' = \frac{ad}{c}X\left(1-\frac{d}{cK}X\right) - b\frac{d}{c}\frac{a}{b}XY$

$x' = aX(1-LX) - aXY$

$\frac{a}{b}y' = c\frac{d}{c}\frac{a}{b}XY - d\frac{a}{b}Y$

$y' = dXY - dY$

$\tau = at$

$\dot{X} = X(1-LX) - XY$

$\dot{y} = -\delta Y(1-X)$

(Original L-V model: $\dot{X} = X(1-Y)$, $\dot{y} = -\delta Y(1-X)$)

$L = \frac{d}{cK}$

$\delta = \frac{d}{a}$

Competitive L-V

$x' = px\left(1-\frac{x+ry}{K_x}\right)$

$y' = qy\left(1-\frac{sx+y}{K_y}\right)$

Time scales: p, q

x scales: K_x, rK_y

y scales: K_y, sK_x

This model will come back when we talk about evolution.

$x = K_x X, \quad y = K_y Y, \quad \tau = pt$

$\dot{X} = X\left(1-X-\frac{rK_y}{K_x}Y\right) = X\left(1-X-\frac{Y}{\alpha}\right)$

$\dot{y} = \frac{q}{p}Y\left(1-\frac{sK_x}{K_y}X - Y\right) = \delta Y\left(1-\frac{X}{\beta}-Y\right)$

$\alpha = \frac{K_x}{rK_y}$ (ratio of x scales / ratio of time scales)

$\delta = \frac{q}{p}$, $\beta = \frac{K_y}{sK_x}$ (ratio of y scales)

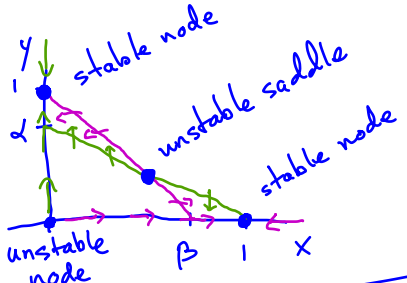
Phase plane

$\dot{x} = 0$ when $X = 0$ or $Y = \alpha(1-X)$

$\dot{y} = 0$ when $Y = 0$ or $Y = 1 - X/\beta$

4 cases:

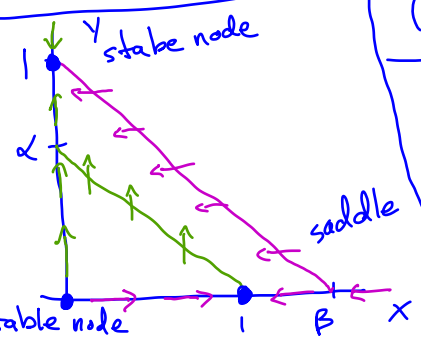
(i)



$\alpha < 1 \Rightarrow$ y has greater impact on x growth than x does

$\beta < 1 \Rightarrow$ x has " " " y " "

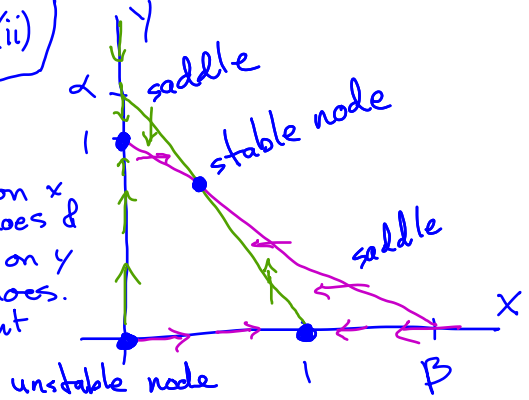
(ii) $\alpha < 1$, $\beta > 1$



(iii) $\alpha > 1$, $\beta < 1$ reverse of (ii)

(iv) $\alpha > 1$, $\beta > 1$

$\Rightarrow$ y has less impact on x growth than x does & x has less impact on y growth than y does. That is, overlapping but distinct niches.



Epidemiology models

Lecture 3

SIS $S' = -\beta SI + \gamma I$

$I' = \beta SI - \gamma I$

(Predator-prey with no growth for S and stoichiometry 1:1)

Recovery from infection returns you to the susceptible pool

$S + I = N$

$I' = \beta I(N-I) - \gamma I = \beta I(N - \frac{\gamma}{\beta} - I)$

If $N - \frac{\gamma}{\beta} < 0$, infection does not spread. If $N - \frac{\gamma}{\beta} > 0$, logistic growth to $N - \frac{\gamma}{\beta}$ carrying capacity. Restate inequality: $R_0 = \frac{\beta N}{\gamma} > 1 \Rightarrow$ epidemic

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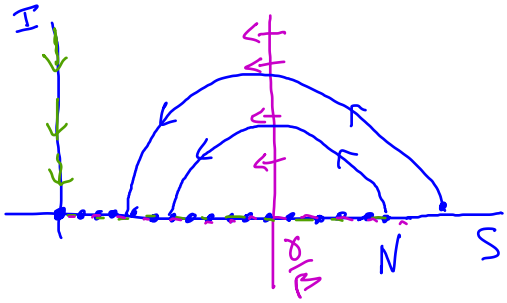
SIR $S' = -\beta SI$ Recovery leads to immunity.

$I' = \beta SI - \gamma I$

$R' = \gamma I \leftarrow$ integrate after solving for S & I.

$S' = 0$ for $S = 0$ or $I = 0$. $I = 0$ is a continuum of steady states

$I' = 0$ for $S = \frac{\gamma}{\beta}$ or $I = 0$



$\frac{dI}{dS} = \frac{\beta SI - \gamma I}{-\beta SI} = -1 + \frac{\gamma}{\beta S} \Rightarrow \bar{I}(S) = -S + \frac{\gamma}{\beta}\ln S + C$ (max at $S = \gamma/\beta$)

All solutions are heteroclinics. Biologically interesting one starts at $S = N, I = 1$. But $I = 1$ is a low number regime. "Does the epidemic take off?"

If $N < \gamma/\beta$ then no (deterministically) or equivalently, $R_0 = \frac{\beta N}{\gamma} < 1 \Rightarrow$ no epidemic.

But even if $R_0 > 1$, the infection might die out by chance (stochastic dynamics)

Nondimensional SIS

$I' = \beta I(N-I) - \gamma I$

$I = Ny$

$I' = Ny'$

$Ny' = \beta Ny(N - Ny) - \gamma Ny$

$y' = \beta Ny(1-y) - \gamma y$

$\tau = \gamma t$

$\dot{y} = \frac{\beta N}{\gamma} y(1-y) - y$

$= R_0 y(1-y) - y = R_0 y\left(1 - \frac{1}{R_0} - y\right)$

Nondimensional SIR

$\begin{cases} S' = -\beta SI \\ I' = \beta SI - \gamma I \end{cases}$

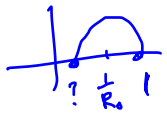
$S = Nx$, $I = Ny$ (no reason to break nice stoichiometry)

$\tau = \gamma t$

$\begin{cases} N\dot{x} = -\frac{\beta}{\gamma} N^2 xy \\ N\dot{y} = -\frac{\beta}{\gamma} N^2 xy - Ny \end{cases}$

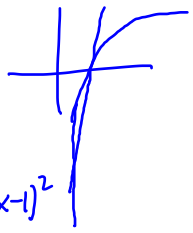
$\begin{cases} \dot{x} = -R_0 xy \\ \dot{y} = R_0 xy - y \end{cases}$

$$Y = -X + \frac{1}{R_0}\ln X + 1$$



$$-X + \frac{1}{R_0}\ln X + 1 = 0 \Rightarrow X = 1 \text{ and } \cdots X = X_p$$

$$\ln x = R_0(x-1)$$



For $R_0 \approx 1$ $(R_0 > 1)$

$X_p \approx 1$ so $\ln x \approx (x-1) - \frac{1}{2}(x-1)^2$

$$x - 1 - \frac{1}{2}(x-1)^2 = R_0(x-1)$$

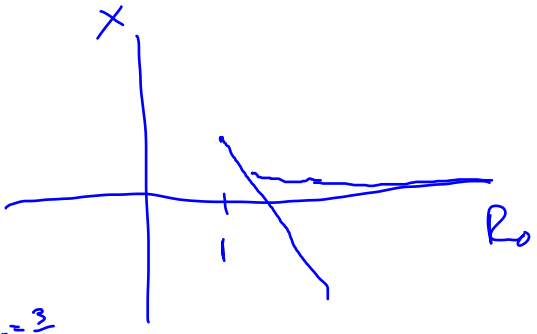
$$1 - \frac{1}{2}(x-1) = R_0$$

$$\frac{1}{2}(x-1) = 1 - R_0$$

$$X = 1 + 2(1-R_0) = 3 - 2R_0$$

$$= 1 - 2(R_0 - 1)$$

Bad by $R_0 = \frac{3}{2}$



For $R_0 >> 1$, $X_p \approx 0$ so

$$\ln x = R_0(x-1)$$

$$X = e^{R_0(x-1)} \approx e^{-R_0}\left(1 + R_0 X + \frac{R_0^2 X^2}{2}\right)$$

$$\frac{R_0^2}{2}X^2 + (R_0 - e^{R_0})X + 1 = 0$$

$$\frac{R_0^2}{2}X^2 - (e^{R_0} - R_0)X + 1 = 0$$

$$X = \frac{e^{R_0} - R_0 - \sqrt{(e^{R_0}-R_0)^2 - 4\frac{R_0^2}{2}}}{R_0^2} = \frac{e^{R_0}-R_0}{R_0^2}\left(1 - \sqrt{1 - \underbrace{\frac{2R_0^2}{(e^{R_0}-R_0)^2}}_{\text{small}}}\right)$$

$$\sqrt{1-\varepsilon} \approx 1 - \frac{1}{2}\varepsilon$$

$$= \frac{e^{R_0}-R_0}{R_0^2}\left(1 - \left(1 - \frac{R_0^2}{(e^{R_0}-R_0)^2}\right)\right)$$

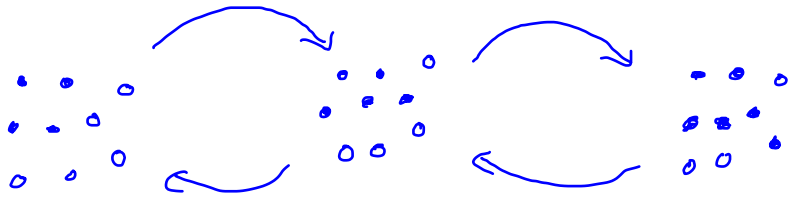
$$= \frac{1}{e^{R_0} - R_0} \approx e^{-R_0}$$

Plot $R(R_0)$: $N(1-e^{-R_0})$

$$e^{-\frac{3}{2}} \approx 0.22 << 1$$

Add vaccination calculation $\frac{N_{vac}}{N} = 1 - \frac{1}{R_0}$

Stochastic SIS



$X(t)=n-1$ $\quad$ $X(t)=n$ $\quad$ $X(t)=n+1$

$\beta \cdot S \cdot I$ – prob that one particular infected individual infects one particular susceptible individual per unit time.

γ – prob that one infected individual recovers per unit time.

$p_n(t) = \text{Prob}(X(t)=n)$

$$p_n(t+\Delta t) = p_{n-1}(t)\cdot \text{Prob}(\text{step right} \mid X(t)=n-1) + p_n(t)\cdot \text{Prob}(\text{no step} \mid X(t)=n) + p_{n+1}(t)\cdot \text{Prob}(\text{step left} \mid X(t)=n+1)$$

$$\left.\begin{aligned} \text{Prob}(\text{step right} \mid X(t)=n-1) &= \beta\cdot(n-1)(N-(n-1))\,\Delta t \\ \text{Prob}(\text{no step} \mid X(t)=n) &= 1-\beta n(N-n)\Delta t - \gamma\cdot n\,\Delta t \\ \text{Prob}(\text{step left} \mid X(t)=n+1) &= \gamma(n+1)\Delta t \end{aligned}\right\} \text{Transition matrix for discrete time process.}$$

$$p_n(t+\Delta t) \approx p_{n-1}(t)\cdot\beta(n-1)(N-(n-1))\Delta t + p_n(t)\cdot(1-\beta\cdot n\cdot(N-n)\Delta t - \gamma\cdot n\cdot\Delta t) + p_{n+1}(t)\gamma(n+1)\Delta t$$

$$\frac{p_n(t+\Delta t)-p_n(t)}{\Delta t} \approx p_{n-1}(t)\cdot\beta(n-1)(N-(n-1)) - p_n(t)(\beta n(N-n)+\gamma\cdot n) + p_{n+1}(t)\gamma\cdot(n+1)$$

$$\downarrow$$

$$\frac{dp_n}{dt} = \begin{bmatrix}\beta(n-1)(N-(n-1)) & -(\beta\cdot n\cdot(N-n)+\gamma n) & \gamma(n+1)\end{bmatrix}\cdot\begin{bmatrix}p_{n-1}(t)\\ p_n(t)\\ p_{n+1}(t)\end{bmatrix}$$

$n=0,\cdots,N$ (where β terms are omitted in the $n=0$ equation and $\gamma(n+1)$ is omitted from the $n=N$ eqn.)

$$\bar{p}' = A\bar{p}, \quad A = \begin{pmatrix} \ddots & & 0 \\ & \ddots & \\ 0 & & \ddots \end{pmatrix}, \quad p_1(0)=1,\ p_n(0)=0 \ (n\neq 1).$$

Steady state and evalues

(1) $p_0' = \gamma p_1 \Rightarrow p_1^{ss}=0 \Rightarrow p_2^{ss}=0 \cdots$.

(2) $\sum_{n=0}^{N} p_n'(t) = 0$ so $\sum_{n=0}^{N} p_n(t) = \sum_{n=0}^{N} p_n(0) = 1 \Rightarrow p_0^{ss} = 1-\sum_{n=1}^{N} p_n^{ss} = 1$

(3) $\bar{p}$ is bounded because $\sum_{n=0}^{N} p_n(t) = 1$ so all evalues of A are ≤ 0 and one is 0 (columns add to zero but not if you omit a row).

(4) Therefore $\bar{p} = \begin{pmatrix}1\\0\\\vdots\\0\end{pmatrix}$ is the only steady state (that sums to 1) and it's stable.

Exploring parameters

There are 4 scales for population size: 1, the IC (if not 1), $N-\gamma/\beta$, N.

Because of 1, their is no rescaling to do.

Time scales: $1/\gamma$ (average recovery time), $\frac{1}{\beta N}$ (average time from first infection to second infection in a pop.) i.e. $S\approx N$

Their ration $R_0 = \frac{\beta N}{\gamma}$ determines spread or no spread.

Fixing N determines whether there is a regime in which determinism works.

Fixing R_0 (and hence β) controls if and how quickly that regime is reached.

When is the Logistic ODE a good approximation? (Never if we let $t\to\infty$!)

Solving the Kolmogorov Eq.

Instead of solving $\bar{p}' = A\bar{p}$ where $\bar{p} = \begin{pmatrix} p_0(t) \\ \vdots \\ p_N(t) \end{pmatrix}$, solve $\bar{p}_*' = B\bar{p}_*$ where $\bar{p}_* = \begin{pmatrix} p_1(t) \\ \vdots \\ p_N(t) \end{pmatrix}$.

Then use $p_0(t) = 1 - \sum_{n=1}^{N} p_n(t)$.

Solution: $\bar{p}_*(t) = e^{At} \cdot \bar{p}_{IC}$ where $\bar{p}_{IC}$ is IC. e.g. $\bar{p}_{IC} = \begin{pmatrix} 1 \\ 0 \\ \vdots \\ 0 \end{pmatrix}$ means one initial infected.

Show $\bar{p}(t)$ for a range of N and R_0 values.

Can we link this description to the ODE? Let $y = \sum_{n=0}^{N} n p_n(t)$ (expected value of $x(t)$)

$$y' = \sum_{n=1}^{N} n p_n'(t) = \sum_{n=1}^{N} n\left[\beta(n-1)(N-(n-1))p_{n-1} - (\beta n(N-n)+\gamma n)p_n + \gamma(n+1)p_{n+1}\right]$$

$$= \sum_{n=1}^{N} n\beta(n-1)(N-(n-1))p_{n-1} - \sum_{n=1}^{N} n\beta n(N-n)p_n - \sum_{n=1}^{N} n\gamma n p_n + \sum_{n=1}^{N} n\gamma(n+1)p_{n+1}$$

$$= \sum_{n=1}^{N} (n-1)\beta(n-1)(N-(n-1))p_{n-1} - \sum_{n=1}^{N} n\beta n(N-n)p_n - \sum_{n=1}^{N} n\gamma n p_n + \sum_{n=1}^{N} (n+1)\gamma(n+1)p_{n+1}$$

$$+ \sum_{n=1}^{N} \beta(n-1)(N-(n-1))p_{n-1} \qquad - \sum_{n=1}^{N} \gamma(n+1)p_{n+1}$$

$$= \sum_{n=0}^{N-1} \beta n^2(N-n)p_n - \sum_{n=1}^{N} \beta n^2(N-n)p_n - \sum_{n=1}^{N} \gamma n^2 p_n + \sum_{n=2}^{N+1} \gamma n^2 p_n + \sum_{n=0}^{N-1} \beta n(N-n)p_n - \sum_{n=2}^{N+1} \gamma n p_n$$

$$= \sum_{n=1}^{N} \beta n(N-n)p_n - \sum_{n=1}^{N} \gamma n p_n = \beta N y - \sum_{n=1}^{N} \beta n^2 p_n - \gamma y = \beta N y - \beta\left(y^2 + \mathrm{Var}(x(t))\right) - \gamma y$$

$$\therefore \quad y' = \beta y(N-y) - \gamma y - \beta\,\mathrm{Var}(x(t))$$

Thus we get an equation for the first moment (mean) that depends on the first and second moment. Provided $\mathrm{Var}(x(t)) \ll y^2$, we can ignore the Var term. Otherwise, we might be able to get an equation for $z = \mathrm{Var}(x(t))$. This is known as a moment-closure approximation.

Show $y \pm \sqrt{z}$ over top the $\bar{p}(t)$ solution image.

Gillespie

If some event occurs randomly but with a constant rate λ, independent of "clock" time t,

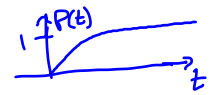
$Q(t+\Delta t) = $ Prob(event has not occured by $t+\Delta t$) = Prob(event has not occured by t) · Prob(event does not occur during $(t, t+\Delta t)$)

Prob(event occurs in $(t, t+\Delta t)$) $\approx \lambda \Delta t$ so

$Q(t+\Delta t) = $ Prob(event has not occured by $t+\Delta t$) $\approx Q(t) \cdot (1 - \lambda\Delta t)$

$$\frac{Q(t+\Delta t) - Q(t)}{\Delta t} \approx -\lambda Q(t) \quad \Longrightarrow \quad \frac{dQ}{dt} = -\lambda Q \Longrightarrow Q(t) = e^{-\lambda t}$$

$P(t) = $ Prob(event occured by t) $= 1 - e^{-\lambda t}$ ← Cumm. distribution



$p(t) = P'(t) = \lambda e^{-\lambda t}$ ← Prob. density

How to pick a t from this distr.?

Probability Inverse Transform: If $P(t)$ is the CDF for variable T, i.e. $P(t) = \mathrm{Prob}(T \le t)$, then r.v. $S = P(T)$ has a uniform distribution, and vice versa (if S is uniform then $T = P^{-1}(S)$ has CDF $P(t)$)

Proof: $\mathrm{Prob}(S \le s) = \mathrm{Prob}(P(T) \le s) = \mathrm{Prob}\left(T \le P^{-1}(s)\right) = P\left(P^{-1}(s)\right) = s$ Q.E.D.

So $y = 1 - e^{-\lambda t} \rightsquigarrow t = -\frac{1}{\lambda}\ln(1-y)$. So generate $y \sim U(0,1)$ and use $t = -\frac{1}{\lambda}\ln(1-y)$ (or equiv. $t = -\frac{1}{\lambda}\ln y$).

For Gillespie, every possible event gets a t; next event is smallest of those. Wipe slate, repeat.

Stochastic simulation methods

① Fixed time step: State at t is $I(t) \in \mathbb{N}$. Fix Δt.

$$I(t+\Delta t) = I(t) + \begin{cases} 1 & \text{if someone gets infected in } \Delta t \\ 0 & \text{if nothing happens in } \Delta t \\ -1 & \text{if someone recovers in } \Delta t \end{cases}$$

Must choose Δt small enough to avoid multiple events because rate changes as soon as an event occurs. So $\Delta t \ll \frac{1}{\text{fastest rate}}$ to ensure "never" more than one event. Often gives zero events. $\lambda_I = \beta I(N-I)$, $\lambda_R = \gamma I$

$Q(s) = e^{-\lambda s} \approx 1 - \lambda s$ for $s \ll \lambda$

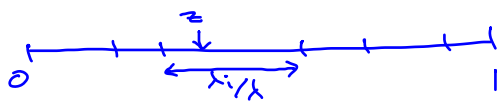
$\text{Prob}(\text{no event in } (t, t+s)) \approx 1 - \lambda s$

$\text{Prob}(\text{event in } (t, t+s)) \approx \lambda s$

For $s = \Delta t$ $\text{Prob}(\text{event in } \Delta t) \approx \lambda \Delta t$. Generate $T \sim U(0,1)$. If $T < \lambda \Delta t$, event occurs. Otherwise, not. If stochastic event is fastest, this wastes time. Better to find t_{next} so that on average, time steps are $\frac{1}{\lambda}$. If deterministic processes are faster, use ODE solve's Δt to check for intermediate stochastic events.

② Gillespie – First reaction method

n steps
- Use current state to find $\lambda_1, \lambda_2, \cdots, \lambda_n$, rates for reactions $1, \cdots, n$.
- Generate $\tau_1, \tau_2, \cdots, \tau_n$ using $\tau = -\frac{1}{\lambda}\ln(y)$.
- Let $\Delta\tau = \min(\tau_i)$ and update state and repeat

– Direct method

2 steps
- Find $\lambda_1, \lambda_2, \cdots, \lambda_n$ $\lambda = \sum \lambda_i$. Generate $\Delta\tau = -\frac{1}{\lambda}\ln(y)$.
- Determine which reaction by choosing another $z \sim U(0,1)$ and seeing which interval it lies in: