5. Epidemic modelling

To model spread of infectious diseases in a population, need to make assumptions about how disease is spread, how it affects individuals, etc. Simplest model: SIR model.

- Closed population. Individuals do not enter population, and leave only by death due to disease.
- Population in 3 compartments: Susceptible, Infective, or Removed (cured and now immune, or dead).
- No spatial effects (uniform mixing), and no heterogeneity in activity (important in, e.g., STDs such as AIDS).
- Negligible incubation time.
- Susceptibles move into Infective class at rate proportional to number of contacts between Susceptibles and Infectives.
- Infectives removed at some rate γ into Removed class.

$$\frac{dS}{dt} = -\beta SI \qquad \beta > 0$$

$$\frac{dI}{dt} = \beta SI - \gamma I \qquad \gamma > 0$$

$$\frac{dR}{dt} = \gamma I$$

5.1.1 SIR epidemic: Model equations

$$\frac{dS}{dt} = -\beta SI \qquad \beta > 0 \tag{1}$$

$$\frac{dI}{dt} = \beta SI - \gamma I \qquad \gamma > 0 \tag{2}$$

$$\frac{dR}{dt} = \gamma I \tag{3}$$

(Kermack & McKendrick (1927)). Solve subject to initial conditions

$$S(0) = S_0 > 0, \quad I(0) = I_0 > 0, \quad R(0) = 0.$$

- We define an epidemic to occur if $I(t) > I_0$ for some $t > 0$. Thus an epidemic will occur if $dI/dt > 0$ at $t = 0$.
- Note: adding (1)–(3) gives conservation of population, $S + I + R = N$, constant, and can eliminate one of variables from model.

5.1.2 Nondimensionalise model

$$\frac{dS}{dt} = -\beta SI \qquad \beta > 0$$

$$\frac{dI}{dt} = \beta SI - \gamma I \qquad \gamma > 0$$

$$\frac{dR}{dt} = \gamma I$$

$$S + I + R = N, \quad \text{constant}$$

Dimensions:

- S, I, R numbers; scale with N: $(S, I, R) = N(u, v, w)$
- γ has dimensions t^{-1}. Thus $t = \tau/\gamma$ gives suitable nondimensionalisation of time (could also have used a timescale based on β).
- Model then becomes

$$\left.\begin{aligned} \frac{du}{d\tau} &= -r^* uv \\ \frac{dv}{d\tau} &= (r^* u - 1)v \\ w &= 1 - u - v \end{aligned}\right\} \quad r^* = \frac{\beta N}{\gamma}$$

- r^* is called the basic reproductive rate of infection = mean no. of secondary cases of infection caused by a single infected case in a population without immunity.

5.1.3 Phase plane analysis

$$\frac{du}{d\tau} = -r^* uv \tag{4}$$

$$\frac{dv}{d\tau} = (r^* u - 1)v \tag{5}$$

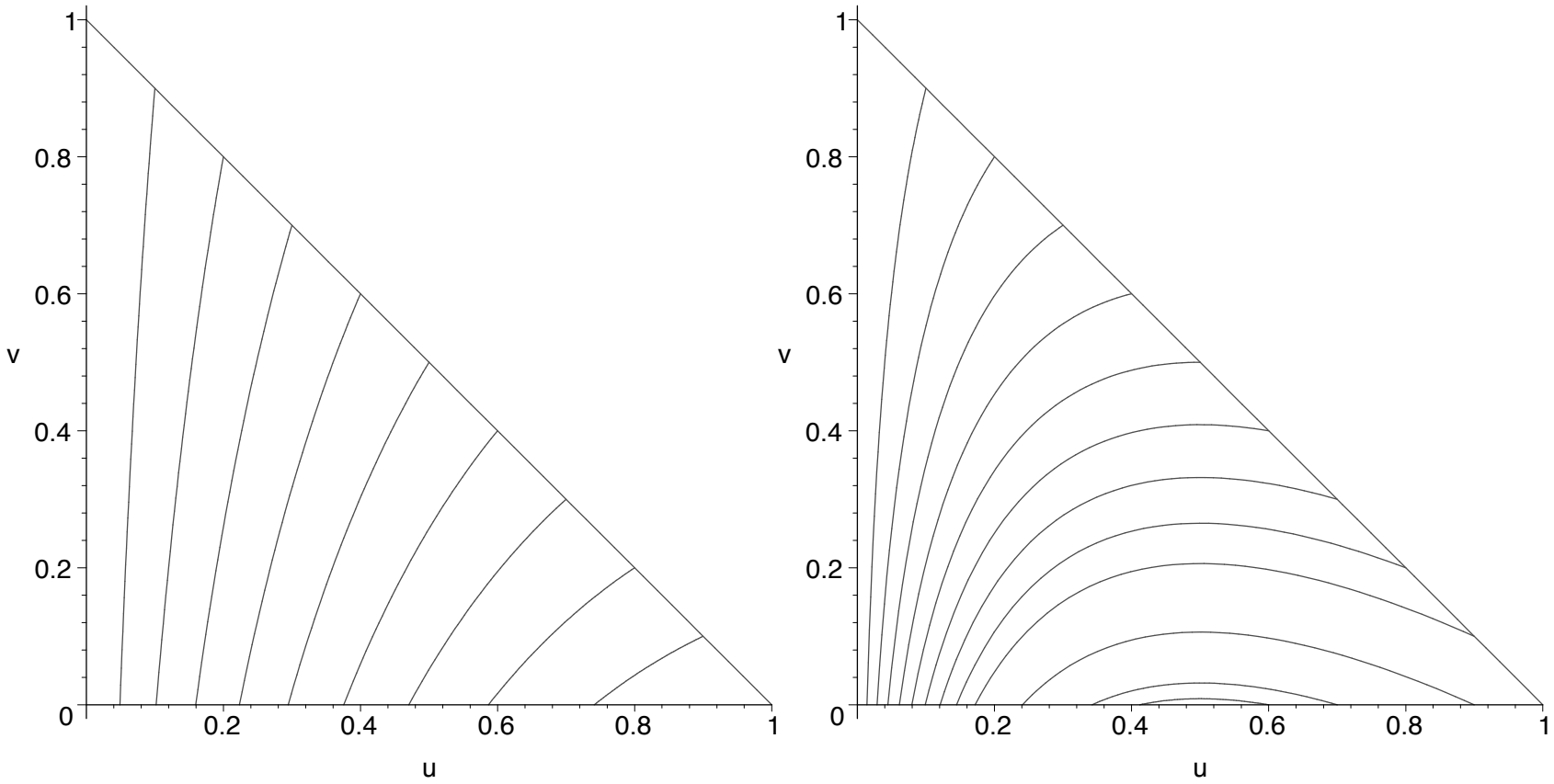
$$w = 1 - u - v \tag{6}$$

- Since $w \geq 0$, clearly $u + v \leq 1$ by (6)
- If $w(0) = 0$ (no-one immune/dead initially) all initial states for system (4), (5) satisfy $u_0 + v_0 = 1$.
- Eqns for u and v independent of w, thus can plot phase-plane for the (u, v) system in triangular domain $D = \{u \geq 0, v \geq 0, u + v \leq 1\}$.
- As for the predator-prey system, phase paths can be plotted directly, by dividing eqns (4), (5) to obtain separable ODE for $v(u)$, with solution

$$v = \frac{1}{r^*} \ln(u/u_0) - u + v_0 + u_0. \tag{7}$$

- Different choices of initial conditions correspond to different phase paths within D.

Phase trajectories (Maple)



Phase trajectories of the system for two different values of r^*

What if we don't have access to Maple??

$$\left.\begin{aligned} \frac{du}{d\tau} &= -r^* uv \\ \frac{dv}{d\tau} &= (r^* u - 1)v \end{aligned}\right\} \quad u + v \leq 1 \tag{8}$$

- Alternative approach to obtain the phase portrait is to determine the critical points, their type, and the nullclines of the system (8).
- Critical points:

$$(u, v) = (u_0, 0) \qquad u_0 \in [0, 1] \text{ arbitrary.}$$

- Every point on u-axis is a possible equilibrium of the system (non-standard case).
- Consider the critical point $(u_0, 0)$. Linearise, writing

$$u = u_0 + \epsilon x(\tau) + O(\epsilon^2), \quad v = \epsilon y(\tau) + O(\epsilon^2), \qquad 0 < \epsilon \ll 1$$

- Local behaviour of system satisfies

$$\dot{\boldsymbol{x}} = A\boldsymbol{x}, \quad A = \begin{pmatrix} 0 & -r^* u_0 \\ 0 & r^* u_0 - 1 \end{pmatrix} \qquad \boldsymbol{x} = (x, y)^T.$$

Linearised system

$$\dot{\boldsymbol{x}} = A\boldsymbol{x}, \quad A = \begin{pmatrix} 0 & -r^* u_0 \\ 0 & r^* u_0 - 1 \end{pmatrix}$$

- Solutions $\boldsymbol{x} = \boldsymbol{x}_0 e^{\lambda \tau}$
- Eigenvalues of linearised system are

$$\lambda_1 = 0, \ \lambda_2 = r^* u_0 - 1.$$

- Two cases:
  - If $r^* < 1$ then $\lambda_2 < 0$ for all $u_0 \in [0, 1]$ and the critical points are all neutrally stable.
  - If $r^* > 1$ then for $0 \leq u_0 < 1/r^*$ critical points are again neutrally stable, while for $1/r^* < u_0 \leq 1$ they are unstable ($\lambda_2 > 0$).
- Next determine nullclines of system to determine turning-points of phase trajectories.

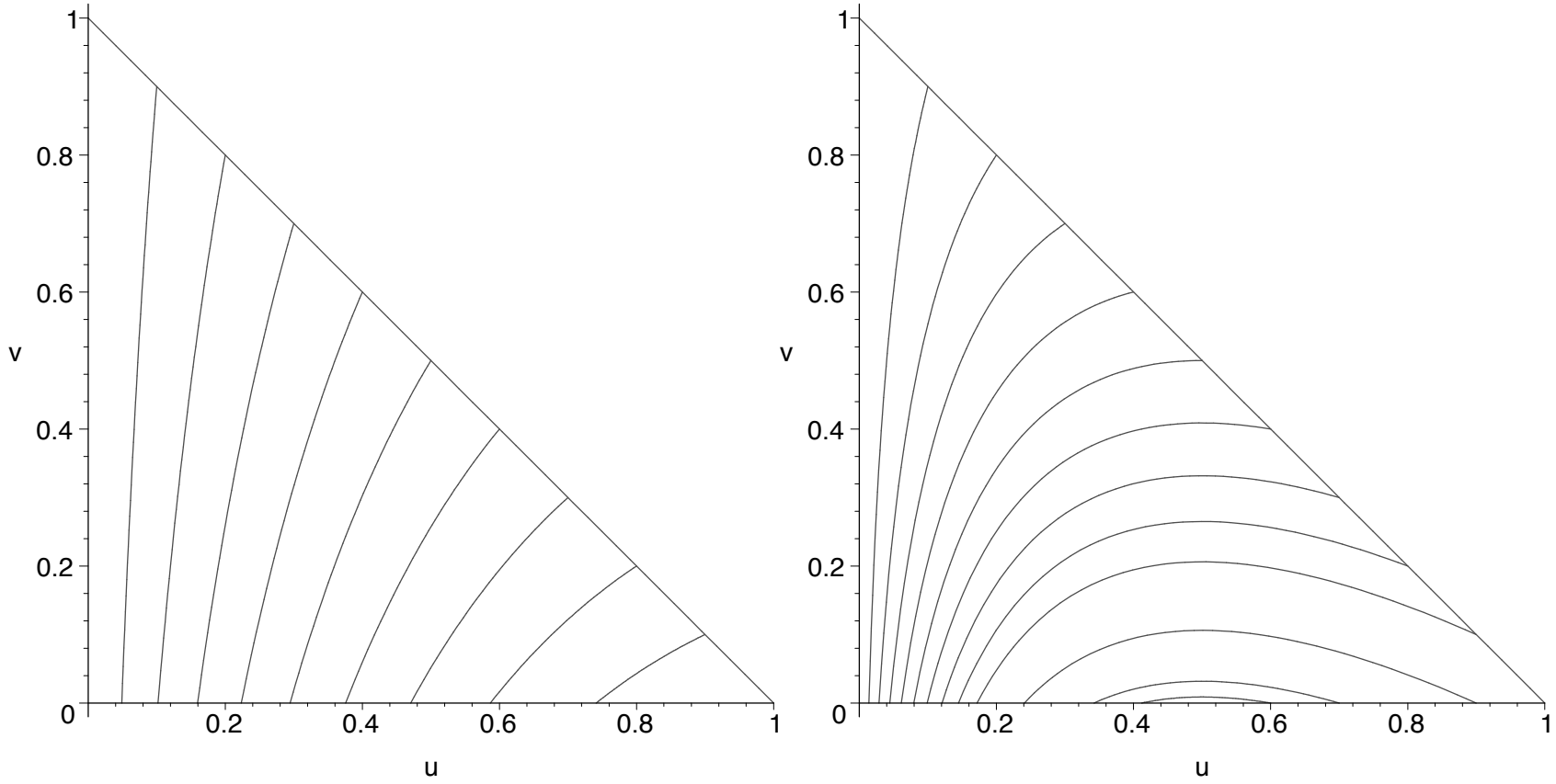
Nullclines of system

$$\left.\begin{aligned} \frac{du}{d\tau} &= -r^* uv \\ \frac{dv}{d\tau} &= (r^* u - 1)v \end{aligned}\right\} \quad u + v \leq 1$$

- Nullclines $\dot{u} = 0$ given by the lines $u = 0$, $v = 0$
- Nullclines $\dot{v} = 0$ given by $u = 1/r^*$, $v = 0$
- That $v = 0$ is a nullcline for both variables reflects its exceptional nature as a line of critical points, already analysed. Take care when plotting!
- Line $u = 0$ also slightly exceptional – it is a nullcline $\dot{u} = 0$ so phase paths must cross it vertically, but it is itself vertical – so it must be a phase path, on which ODE for u satisfied trivially, and $\dot{v} = -v < 0$.
- For the nullcline $u = 1/r^*$ ($\dot{v} = 0$), again two cases:
  - If $r^* < 1$ then nullcline $u = 1/r^*$ lies outside physically-relevant domain D and has no significance. $\dot{v} < 0$ everywhere in D.
  - If $r^* > 1$ then nullcline lies partly within physical domain D, and phase trajectories cross this vertical line horizontally.
  - In the latter case $r^* > 1$: In $u > 1/r^*$ we have $\dot{v} > 0$, while in $u < 1/r^*$ we have $\dot{v} < 0$.

Phase trajectories (sketch based on analysis)

Noting also that $\dot{u} \leq 0$ everywhere, can now sketch phase paths.



Phase trajectories of the system for two cases $r^* < 1$, $r^* > 1$

Interpretation of phase diagram

- Each individual phase trajectory represents a solution of the system.
- Which trajectory the solution follows is dictated by initial conditions imposed.
- For $r^* < 1$ both v (infectives) and u (susceptibles) decrease monotonically in time until $v = 0$ and $u = u_\infty$ $(0 < u_\infty < u_0)$.
  - Since v decreases monotonically to zero, there is no epidemic, outbreak dies away.
  - Value of u_∞ can be found by setting $v = 0$ in explicit expression for phase paths with given values of r^*, u_0, v_0 (slide 5).
- For $r^* > 1$, if the initial number of susceptibles $u_0 > 1/r^*$ then although u again decreases monotonically (to $u_\infty \in (0, 1/r^*)$), v initially increases to some v_{max} (epidemic), before decreasing ultimately to zero.
  - Value of v_{max} found by setting $u = 1/r^*$ (the nullcline on which phase paths horizontal) in explicit expression for phase-paths with given values of r^*, u_0, v_0 (equation (7), slide 5).

5.1.4 Infection control

Can prevent epidemics if $r^* = \beta N/\gamma < 1$. Hence 3 possible control mechanisms:

1. Increase γ (rate of removal of infectives)
2. Decrease β (pairwise infectious contact rate)
3. Decrease effective value of N (decrease total population).

Foot and mouth epidemic employed all 3 tactics.

1. Infected animals slaughtered (increase γ)
2. Disinfectant and movement controls reduced β
3. Slaughtering potential infection carriers (esp. those adjacent to infected farms) effectively reduced N.

Infection control (ctd)

Another strategy is to vaccinate.

- Vaccination essentially removes a proportion p of initial susceptible class to the removed class (that is, $w(0) = p$).
- Assuming $r^* > 1$, so that an epidemic will potentially occur in an unvaccinated population, after vaccination initial numbers of susceptibles and infectives satisfy

$$u_0 + v_0 = 1 - p.$$

- To avoid epidemic require $u_0 < 1/r^*$, since then all phase trajectories have v monotone decreasing.
- Thus to be sure of avoiding an epidemic we must vaccinate such that

$$1 - p < 1/r^* \quad \Rightarrow \quad p > 1 - 1/r^*.$$

- Assuming a perfect vaccine, this is the proportion of the population we must vaccinate to avoid an epidemic.

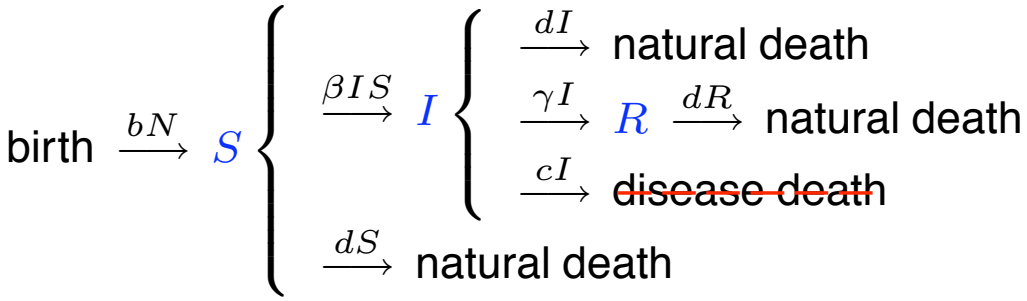
5.2 SIR endemic model

- Endemic disease: one that is always present in a population.
- SIR epidemic model: implicitly assumed that duration of epidemic sufficiently short that the population does not change much due to natural births and deaths during epidemic.
- Endemic: interested in disease progress over long times – many generations sometimes – so must include the "natural" population dynamics too.
- Consider population N with per capita birth rate b, and per capita death rates c (from disease) and d (other causes).
- Assume c, d constant, and that disease not transferred from mother to foetus, so all new births enter susceptible class. Schematically:

$$\text{birth} \xrightarrow{bN} S \begin{cases} \xrightarrow{\beta IS} I \begin{cases} \xrightarrow{dI} \text{natural death} \\ \xrightarrow{\gamma I} R \xrightarrow{dR} \text{natural death} \\ \xrightarrow{cI} \text{disease death} \end{cases} \\ \xrightarrow{dS} \text{natural death} \end{cases}$$

- How might the population approach an endemic steady state?

5.2.1 No death from disease (non-fatal)



- Steady state in this case requires natural births to balance natural deaths.
- Let $b = d$ and $c = 0$. Then the above schematic leads to model equations

$$\begin{aligned} \frac{dS}{dt} &= bN - \beta IS - bS, \\ \frac{dI}{dt} &= \beta IS - \gamma I - bI, \\ \frac{dR}{dt} &= \gamma I - bR. \end{aligned}$$

- Easily verified that $N = S + I + R$ is constant for this model.
- Scale population classes with N as before.
- Now however scale time with $1/(\gamma + b)$ to reflect the different rate at which infectives now leave the I-class.

5.2.2 Nondimensionalisation much as before...

$$\begin{aligned}
\frac{dS}{dt} &= bN - \beta IS - bS, \\
\frac{dI}{dt} &= \beta IS - \gamma I - bI, \\
\frac{dR}{dt} &= \gamma I - bR,
\end{aligned}$$

$$(S, I, R) = N(u, v, w), \qquad t = \frac{\tau}{\gamma + b},$$

leads to

$$\left.\begin{aligned}
\frac{du}{d\tau} &= \hat{b}(1-u) - r^* uv \\
\frac{dv}{d\tau} &= (r^* u - 1)v \\
\frac{dw}{d\tau} &= \hat{\gamma} v - \hat{b} w
\end{aligned}\right\} \quad \hat{b} = \frac{b}{(\gamma + b)}, \quad \hat{\gamma} = \frac{\gamma}{(\gamma + b)}, \quad r^* = \frac{\beta N}{\gamma + b}.$$

- Note that $\hat{\gamma} = 1 - \hat{b}$, so just 2 parameters in model.
- Again, r^* is defined to be the basic reproductive rate of infection.

5.2.3 Steady states and linear stability

$$\left.\begin{aligned} \frac{du}{d\tau} &= \hat{b}(1-u) - r^* uv \\ \frac{dv}{d\tau} &= (r^* u - 1)v \\ w &= 1 - u - v \end{aligned}\right\} \quad \hat{\gamma} = 1 - \hat{b}. \tag{9}$$

- Again $w = 1 - u - v$ uncouples from the system leaving a pair of ODEs to be solved for u and v on domain $D = \{u \geq 0, v \geq 0, u + v \leq 1\}$.
- Critical points of (9) at

$$(u_c, v_c) = \begin{cases} (1,0) & \text{(disease-free state)} \\ (\frac{1}{r^*}, \hat{b}(1 - \frac{1}{r^*})) & \text{(disease remains endemic in population).} \end{cases}$$

- Endemic steady state exists only if $r^* > 1$.
- Linearising about first critical point, find that eigenvalues at $(1,0)$ are

$$\lambda_1 = -\hat{b}, \quad \lambda_2 = r^* - 1,$$

so the disease-free state is stable if $r^* < 1$ (stable node) and unstable if $r^* > 1$ (saddle).

Endemic steady state stable when it exists ($r^* > 1$)

$$\begin{aligned} \frac{du}{d\tau} &= \hat{b}(1-u) - r^* uv \\ \frac{dv}{d\tau} &= (r^* u - 1)v \end{aligned}$$

- At endemic steady state critical point $(1/r^*, \hat{b}(1-1/r^*))$ eigenvalues are

$$2\lambda_{1,2} = -\hat{b}r^* \pm \hat{b}r^* \left(1 - \frac{4}{\hat{b}r^*} + \frac{4}{\hat{b}r^{*2}}\right)^{1/2}.$$

- For stability require real part of both eigenvalues to be negative, that is,

$$\text{stable} \iff \left(1 - \frac{4}{\hat{b}r^*} + \frac{4}{\hat{b}r^{*2}}\right) < 1 \iff r^* > 1.$$

- If unstable, critical point lies outside domain of interest and is irrelevant.
- If stable, it will either be a stable spiral (if square-rooted quantity is imaginary) or a stable node. We have

$$(\hat{b}r^* - 2)^2 \begin{matrix} < \\ > \end{matrix} 4(1-\hat{b}) \equiv 4\hat{\gamma} \quad \Rightarrow \quad \begin{matrix} \text{stable spiral} \\ \text{stable node} \end{matrix}$$

Nullclines

$$\begin{aligned}\frac{du}{d\tau} &= \hat{b}(1-u) - r^* uv \\ \frac{dv}{d\tau} &= (r^* u - 1)v\end{aligned}$$

- As usual, further information about phase-plane can be extracted by considering nullclines of system:

$$\dot{u} = 0 \quad \text{on} \quad v = \frac{\hat{b}(1-u)}{r^* u} \qquad \text{(hyperbola)}$$

$$\dot{v} = 0 \quad \text{on} \quad v = 0, \quad u = \frac{1}{r^*} \qquad \text{(straight lines).}$$

- Note that $v = 0$ is a solution trajectory of the system, on which $\dot{u} = \hat{b}(1-u)$.
- Endemic steady state critical point at $(1/r^*, \hat{b}(1 - 1/r^*))$ provided $r^* > 1$.
- Typically in endemic diseases $\gamma \gg b$ (people removed from I-class much more quickly by recovery than by natural death), thus $\hat{b} = b/(\gamma + b) \ll 1$.
- Proportion of population who have the disease in the endemic steady state is therefore usually small.

5.2.4 Worked example

$$\left.\begin{aligned}\frac{du}{d\tau} &= \hat{b}(1-u) - r^* uv \\ \frac{dv}{d\tau} &= (r^* u - 1)v\end{aligned}\right\} \quad \hat{b} = 0.1,\ r^* = 5. \tag{10}$$

- Critical points at $(u_c, v_c) = (1, 0), \quad (u_c, v_c) = (0.2, 0.08)$
- Critical point at $(1, 0)$: Write $(u, v) = (1 + \epsilon x, \epsilon y)$ and seek solutions $\boldsymbol{x} = \boldsymbol{r}\exp(\lambda\tau)$. Linearised problem:

$$\mathbf{0} = \begin{pmatrix} -\hat{b} - \lambda & -r^* \\ 0 & r^* - 1 - \lambda \end{pmatrix} \boldsymbol{r}$$

which leads to eigenvalues and (unnormalised) eigenvectors

$$(\lambda_1, \lambda_2) = (-\hat{b}, r^* - 1) = (-0.1,\ 4), \quad \text{saddle-point}$$
$$\boldsymbol{r}_1 = (1, 0)^T, \quad \boldsymbol{r}_2 = (r^*, 1 - \hat{b} - r^*)^T = (5, -4.1)^T.$$

- Eigenvectors give directions in which phase-paths enter or leave saddle-point.
- Since $\lambda_1 < 0$, phase paths along $+\boldsymbol{r}_1$ enter the critical point. Note $-\boldsymbol{r}_1$ is outside physical region.
- $\lambda_2 > 0 \Rightarrow$ paths along $-\boldsymbol{r}_2$ leave critical point. Note $\boldsymbol{r}_2$ is outside physical region.

Worked example (ctd)

$$\left.\begin{aligned}\frac{du}{d\tau} &= \hat{b}(1-u) - r^* uv \\ \frac{dv}{d\tau} &= (r^* u - 1)v\end{aligned}\right\} \quad \hat{b} = 0.1,\ r^* = 5.$$

- Critical point at $(u_c, v_c) = (0.2, 0.08)$: Linearising gives eigenvalues

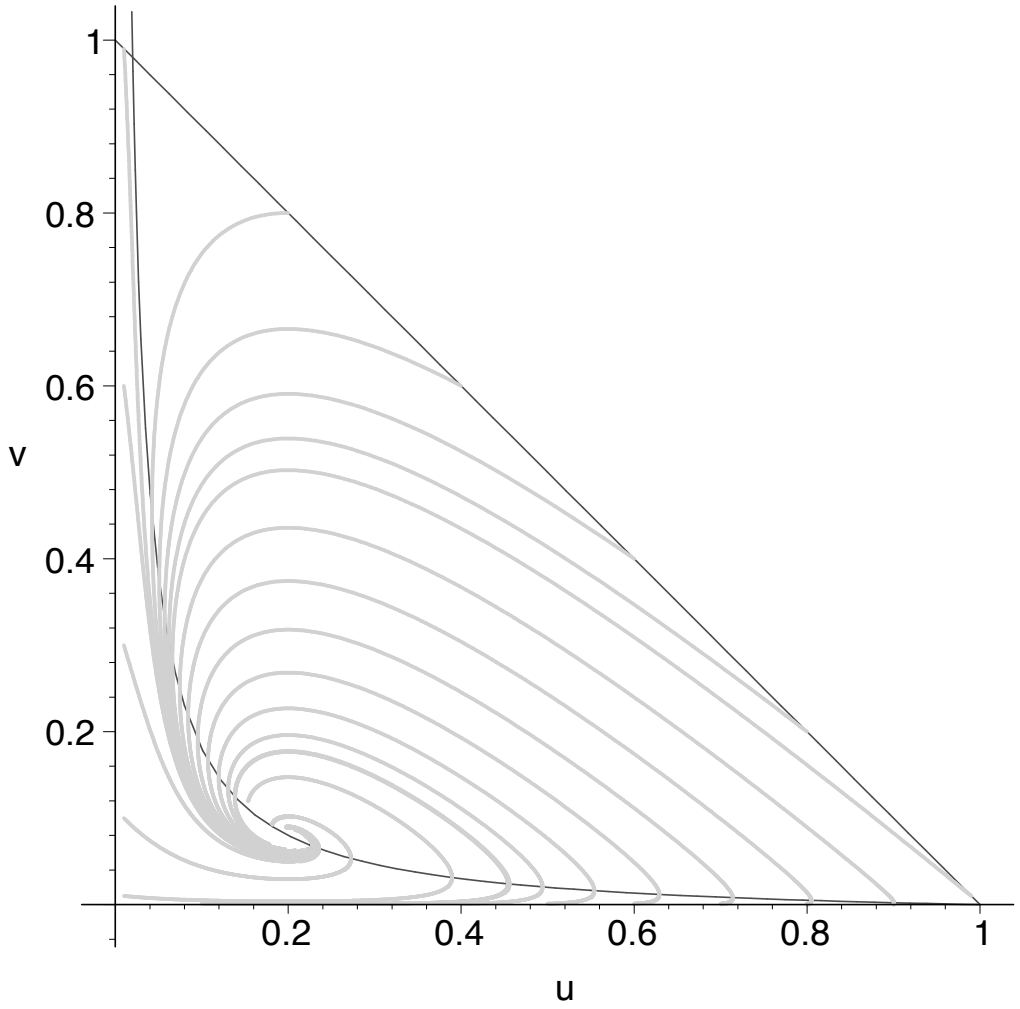
$$\lambda_{1,2} = -0.25 \pm 0.581i, \quad \text{stable spiral}$$

- Next consider nullclines of the system:

$$\begin{aligned}\dot{u} = 0 \quad &\text{on} \quad v = 0.02(1/u - 1) \qquad \text{(hyperbola)} \\ \dot{v} = 0 \quad &\text{on} \quad v = 0, \quad u = 0.2, \qquad \text{(straight lines).}\end{aligned}$$

- Hyperbola is easily sketched, since it must pass through the two critical points, and asymptote to the v axis as $u \to 0$.
- Putting all this information together we can sketch the phase plane.

The phase plane



Phase paths, together with the nullcline $\dot{v} = 0$. Since this nullcline lies very close to u-axis near critical point $(1, 0)$ it is difficult to distinguish where the phase-paths turn over near this saddle point. That $u = 1/r^* = 0.2$ is also a nullcline $\dot{u} = 0$ is also easily seen.

5.2.5 Vaccination against endemics

- Again assume a non-fatal disease, and suppose the vaccination strategy is to vaccinate a proportion p of susceptibles at birth.
- Governing equations are replaced by

$$\begin{aligned}\frac{dS}{dt} &= b(1-p)N - \beta IS - bS \\ \frac{dI}{dt} &= \beta IS - \gamma I - bI \\ \frac{dR}{dt} &= bpN + \gamma I - bR\end{aligned}$$

and again $N = S + I + R$ is constant.

- With scalings as before

$$(S, I, R) = N(u, v, w), \quad t = \frac{\tau}{\gamma + b},$$

we obtain

$$\begin{aligned}\frac{du}{d\tau} &= \hat{b}(1-p) - \hat{b}u - r^* uv \\ \frac{dv}{d\tau} &= (r^* u - 1)v \\ \frac{dw}{d\tau} &= \hat{b}p + \hat{\gamma}v - \hat{b}w.\end{aligned}$$

Steady states

$$\frac{du}{d\tau} = \hat{b}(1-p) - \hat{b}u - r^*uv \tag{11}$$

$$\frac{dv}{d\tau} = (r^*u - 1)v \tag{12}$$

- Steady states of system (11), (12) given by

$$(u_c, v_c) = (1-p, 0), \quad (u_c, v_c) = \left(\frac{1}{r^*}, \hat{b}(1-p-\frac{1}{r^*})\right).$$

- For successful vaccination, want disease-free state to be stable, and nontrivial endemic state to be unstable, so that disease ultimately dies out.
- Stability results may be read off directly from non-vaccinated case if we note that rescaling $u = (1-p)U$, $v = (1-p)V$, $R^* = (1-p)r^*$ leads to system

$$\frac{dU}{d\tau} = \hat{b}(1-U) - R^*UV,$$

$$\frac{dV}{d\tau} = (R^*U - 1)V$$

exactly equivalent to unvaccinated case.

Stability results from previous analysis

$$\frac{dU}{d\tau} = \hat{b}(1-U) - R^*UV$$
$$\frac{dV}{d\tau} = (R^*U - 1)V$$

- Rescaling $\longrightarrow$ system identical to unvaccinated case.
- Thus we have stability of disease-free state and instability of endemic state if

$$R^* = r^*(1-p) < 1 \quad \Rightarrow \quad p > 1 - \frac{1}{r^*} \tag{13}$$

- If $R^* > 1$ the converse is true.
- Condition (13) holds trivially if $r^* < 1$ — in this case endemic steady state does not exist in non-vaccine model — so no need to vaccinate.
- Condition (13) gives minimum fraction of the population that must be vaccinated to avoid endemic disease.

Real data

Data exists from which values of r^* (and hence critical value of p) may be estimated, for many common diseases. Some examples (see Britton):

Infection	r^*	p
Smallpox	3 to 5	0.67 to 0.8
Measles	12 to 13	0.92
Whooping cough	13 to 17	0.92 to 0.94
Rubella	6 to 7	0.83 to 0.86
Chickenpox	9 to 10	0.89 to 0.9
Diphtheria	4 to 6	0.75 to 0.83
Scarlet fever	5 to 7	0.8 to 0.86
Mumps	4 to 7	0.75 to 0.86
Poliomyelitis	6	0.83

5.3 Criss-cross infection: STDs

Consider a simple model for gonorrhoea transmission. Make the following assumptions.

- Criss-cross infection – only males infect females, and vice-versa
- Incubation period short compared with length of infection.

Schematically,

$$\left.\begin{array}{rccc} \text{Males} & S & \rightleftharpoons & I \\ & & \nwarrow\!\!\searrow & \\ \text{Females} & \tilde{S} & \rightleftharpoons & \tilde{I} \end{array}\right\} \quad \text{no acquired immunity.}$$

- Further assume that male and female populations closed.
- Simplest model equations are then

$$\frac{dS}{dt} = \underbrace{-rS\tilde{I}}_{\text{infection}} + \underbrace{aI}_{\text{recovery}} \qquad \frac{dI}{dt} = rS\tilde{I} - aI$$

$$\frac{d\tilde{S}}{dt} = \overbrace{-\tilde{r}\tilde{S}I}^{\text{infection}} + \overbrace{\tilde{a}\tilde{I}}^{\text{recovery}} \qquad \frac{d\tilde{I}}{dt} = \tilde{r}\tilde{S}I - \tilde{a}\tilde{I}$$

- Can show that

$$S + I = N, \quad \tilde{S} + \tilde{I} = \tilde{N}, \qquad N,\ \tilde{N} \text{ constant.}$$

5.3.1 Model equations

$$\frac{dS}{dt} = -rS\tilde{I} + aI \qquad \frac{dI}{dt} = rS\tilde{I} - aI$$

$$\frac{d\tilde{S}}{dt} = -\tilde{r}\tilde{S}I + \tilde{a}\tilde{I} \qquad \frac{d\tilde{I}}{dt} = \tilde{r}\tilde{S}I - \tilde{a}\tilde{I}$$

$$S + I = N \qquad \tilde{S} + \tilde{I} = \tilde{N} \qquad N,\ \tilde{N} \text{ constant.} \tag{14}$$

- Using (14) can then reduce model to a pair of ODEs for infected M and F populations:

$$\frac{dI}{dt} = r(N - I)\tilde{I} - aI$$

$$\frac{d\tilde{I}}{dt} = \tilde{r}(\tilde{N} - \tilde{I})I - \tilde{a}\tilde{I}$$

- Steady states (exercise):

$(I, \tilde{I}) = (0, 0),\ (I^*, \tilde{I}^*)$, where $I^* = \dfrac{N\tilde{N} - \rho\tilde{\rho}}{\tilde{N} + \rho},\ \tilde{I}^* = \dfrac{N\tilde{N} - \rho\tilde{\rho}}{N + \tilde{\rho}}, \quad \rho = \dfrac{a}{r},\ \tilde{\rho} = \dfrac{\tilde{a}}{\tilde{r}}$

(nontrivial st.st. only realistic if $N\tilde{N} > \rho\tilde{\rho}$).

5.3.2 Linear stability of steady state $(0, 0)$

Near $(0, 0)$ approximate (linearised) equations are

$$\frac{dI}{dt} = rN\tilde{I} - aI, \quad \frac{d\tilde{I}}{dt} = \tilde{r}\tilde{N}I - \tilde{a}\tilde{I}$$

so usual procedure of seeking solutions $(I, \tilde{I}) = \boldsymbol{R}\exp(\lambda t)$ gives eigenvalue problem

$$0 = \begin{vmatrix} -a-\lambda & rN \\ \tilde{r}\tilde{N} & -\tilde{a}-\lambda \end{vmatrix}$$

$$\Rightarrow \quad 2\lambda = -(a+\tilde{a}) \pm \left[(a+\tilde{a})^2 + 4a\tilde{a}\left(\frac{N\tilde{N}}{\rho\tilde{\rho}} - 1\right)\right]^{1/2}.$$

Hence stability depends on the value of $N\tilde{N}/(\rho\tilde{\rho})$.

- If $N\tilde{N}/(\rho\tilde{\rho}) < 1$ then both eigenvalues are negative: $(0, 0)$ is stable and in fact is the only steady state, so infection dies out in population.
- If $N\tilde{N}/(\rho\tilde{\rho}) > 1$ then one eigenvalue is positive and one is negative: $(0, 0)$ is unstable (saddle). In this case the nontrivial steady state $(I^*, \tilde{I}^*)$ exists and must be analysed.

Linear stability of $(I^*, \tilde{I}^*)$

- Assume $N\tilde{N}/(\rho\tilde{\rho}) > 1$ and linearise about the steady state, writing $I = I^* + \epsilon x$, $\tilde{I} = \tilde{I}^* + \epsilon\tilde{x}$, where $0 < \epsilon \ll 1$.
- Usual procedure leads to eigenvalue problem for λ, the growth-rate of $(x,\, \tilde{x})$:

$$0 = \lambda^2 + \lambda(\tilde{r}I^* + r\tilde{I}^* + a + \tilde{a}) + a\tilde{a}\left(1 - \frac{N\tilde{N}}{\rho\tilde{\rho}}\right) + r\tilde{a}\tilde{I}^*\left(1 + \frac{N}{\tilde{\rho}}\right) + \tilde{r}aI^*\left(1 + \frac{\tilde{N}}{\rho}\right).$$

- Writing this quadratic as $\lambda^2 + B\lambda + C = 0$, the formula gives the solutions as

$$2\lambda_{1,2} = -B \pm \sqrt{B^2 - 4C},$$

- Hence solutions are stable ($\Re(\lambda) < 0$) if $C > 0$. A little algebra reveals

$$C = -a\tilde{a}\left(1 - \frac{N\tilde{N}}{\rho\tilde{\rho}}\right) > 0,$$

and the nontrivial steady state is stable, when it exists, while the trivial steady state is unstable.

5.3.3 Interpretation

- The parameter

$$\frac{N\tilde{N}}{\rho\tilde{\rho}} \equiv \frac{N\tilde{N}r\tilde{r}}{a\tilde{a}}$$

  combines the effects of the promiscuity of the population as a whole and the infectiveness of the disease.
- In terms of individual model parameters, $1/\tilde{a}$ is the average period of infection of a female. rN is the no. of males contacted who get the disease if all males are susceptible ($I = 0$), per infected female.
- Similarly for females infected by males.
- It follows that

$$\frac{rN}{\tilde{a}} \sim \text{No. of infectives produced per infected female,}$$

$$\frac{\tilde{r}\tilde{N}}{a} \sim \text{No. of infectives produced per infected male.}$$

- The product of these two parameters must be > 1 for the disease to persist.
- Some data exists for these parameters. USA 1973: $N\tilde{N}/(\rho\tilde{\rho}) \approx 1.127 > 1.$

5.4 Overview of disease-spread modelling

- Epidemic models: Disease outbreak duration short compared with natural birth and death processes, hence natural birth and death neglected.
  - Compartment model – SIR, susceptibles, infectives, removed.
  - Basic reproductive rate of infection r^* determines whether or not epidemic occurs. If $r^* > 1$ have epidemic, otherwise not.
  - Possible control strategies considered, specifically vaccination.
- Endemic models: Interested in situations where disease can persist indefinitely in a population, hence natural birth and death processes important on such long timescales.
  - Steady state population if birth rate balances death rate – assumed this, giving modified SIR model.
  - Again find a critical parameter r^*, which determines whether or not disease can remain endemic in population (nontrivial stable steady state).
  - Vaccination again studied as a means of eliminating the endemic steady state.
- Criss-cross infection models considered in 2 closed populations. Again criterion can be derived in terms of model parameters that predicts whether or not disease can persist, or must die out.