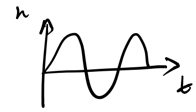
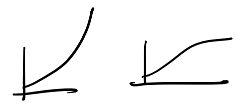
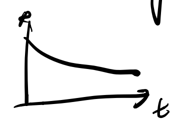
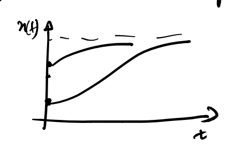
* The study of dynamical systems is the study of how things change over time

→ Mass on a spring $m\frac{d^2x}{dt^2} = -kx$ 

→ population growth $\frac{dx}{dt} = rx$ $\frac{dx}{dt} = rx(1-x/x_{max})$ 

→ fraction of population with a particular allele $\frac{dx}{dt} = sx(1-x)$ 

→ Radioactive decay  $\frac{dx}{dt} = -kx$

* It is the study of deterministic change, which means there is exact repeatability for the same exact conditions for the dynamics, including the initial conditions 

* It is the study of continuous change, where quantities can change infinitesimally over infinitesimal time.

- Sometimes this will be an approximation of the true discrete quantity that is changing
- e.g. population growth:

$$N_{t+1} = 2N_t \Rightarrow N_t = 2^t N_0$$

$$\Rightarrow \frac{dN}{dt} = rN \qquad N(t) = e^{rt} N_0 \qquad r = \ln 2$$

→ When N is large the 2 descriptions are ~ identical.

In general, dynamical equations are expressed in terms of time-derivatives:

$$c_1 \frac{d}{dt}(\text{something}) + c_2 \frac{d^2}{dt^2}(\text{something}) + c_3 \frac{d^3}{dt^3}(\text{something}) + \ldots = f(\text{something})$$

where c_i's are constants.

* We will focus on 1^{st} order systems where the equations are

$$\frac{d}{dt}(\text{something}) = f(\text{something})$$

* Although linear systems are included, the subject is mainly concerned with how to study non-linear systems, where f is a nonlinear function with terms $(\text{something})^n$ where $n > 1$, or $\exp(\text{something})$ which are typically not solvable exactly:

<u>Example</u> Allele frequency dynamics in a diploid population

$$\frac{dx}{dt} = s[h + (1-2h)x]x(1-x)$$ does not have a closed-form solution (i.e. $x(t)$ expressable in terms standard functions)

→ In this case this ODE can be integrated to give $t(x)$, but not inverted to give $x(t)$.

* We will also look at 2D systems of 1^{st} order differential eqns.

$$\frac{d}{dt}(\text{something}_1) = f(\text{something}_1, \text{something}_2)$$
$$\frac{d}{dt}(\text{something}_2) = g(\text{something}_1, \text{something}_2)$$

* However, we will focus on understanding linear systems, as a basis of understanding non-linear systems

* How do we construct a dynamical system?

→ When we look at our system we need to ask what are the elements of our model which cause the (something) we are interested to change?

E.g. population growth of bacteria

1) They divide at a given <u>rate</u> doubling number on division
2) They die at a given <u>rate</u>.

Rule :

Mechanism 1 Mechanism 2

$$\frac{d}{dt}(\text{something}) = (\text{change in number})_1 + (\text{change in number})_2$$

[per unit time] [per unit time]

$$\frac{dN}{dt} = \left(\frac{dN}{dt}\right)_1 + \left(\frac{dN}{dt}\right)_2$$

1) Doubling : rate v : if each member of population adds exactly $v\,\delta t$ then N members will add $\delta N_1 = N v \delta t$.

2) Death : rate k : if each member looses exactly $k\,\delta t$ then N members loose $\delta N_2 = N k \delta t$.

$$\Rightarrow \delta N = \delta N_1 + \delta N_2$$

$$= N v \delta t - N k v \delta t$$

$$= N \delta t\,(v-k)$$

$$\Rightarrow \frac{\delta N}{\delta t} = N(v-k)$$

$\Rightarrow$ In continuous limit, $\lim_{\delta t}\left\{\frac{\delta N}{\delta t}\right\} = \frac{dN}{dt} = N(v-k)$

* Note units of σ & k : rate per second <u>per individual</u> ⇒ to get population level rate need to multiply by N

→ Let's add 3rd mechanism : spontaneous growth.

3) Out of thin air α members of the population are added to the population, per unit time ⇒ in time δt, $\alpha \delta t$ are added.

$$\Rightarrow \frac{dN}{dt} = \left(\frac{dN}{dt}\right)_1 + \left(\frac{dN}{dt}\right)_2 + \left(\frac{dN}{dt}\right)_3$$

$$= \sigma N - kN + \alpha$$

[* <u>Mechanism 3 does not exist</u>! * this is just used as an illustration.]

* α is slightly different : it's units are number of individuals added per unit time, so <u>is not</u> multiplied by N.

* Rates might not be constant, but depend on changing quantity we are modelling

<u>Ex</u> : Logistic growth. : i) growth depends on how much food / resources are available

ii) this depends inversely on the current size of the population; smaller populations have more resources to share than larger populations.

→ It is typical to characterise this limit of resources in terms of the number of individuals that can be supported N_{max}.

$$\Rightarrow \quad r(N) = r\left(1 - \frac{N}{N_{max}}\right) \begin{cases} r & \text{for } N = 0 \\ 0 & \text{for } N = N_{max} \end{cases}$$

→ this is a rate of individuals added per individual per unit time.

$$\Rightarrow \quad \delta N_1 = r(N)\,N = r\left(1 - N/N_{max}\right)N$$

$$\Rightarrow \quad \frac{dN}{dt} = \left(\frac{dN}{dt}\right)_1 + \left(\frac{dN}{dt}\right)_2$$

$$= rN\left(1 - N/N_{max}\right) - kN$$

* N.B. we can mix & match between these different mechanisms of change 1), 2) & 3) & different types of each contribution (e.g. exponential vs logistic growth) to construct our dynamical system or ODE

e.g. Exp. growth + spontaneous (no death) : $\frac{dN}{dt} = rN + \alpha$

Logistic growth (no death) : $\frac{dN}{dt} = rN\left(1 - N/N_{max}\right)$

Only spontaneous : $\frac{dN}{dt} = \alpha$

* These ways of constructing the differential equation are based on the idea of "mass action kinetics" from chemistry

* There are other ways of generating ODE's for example from mechanics physical laws, e.g. Newton's Law

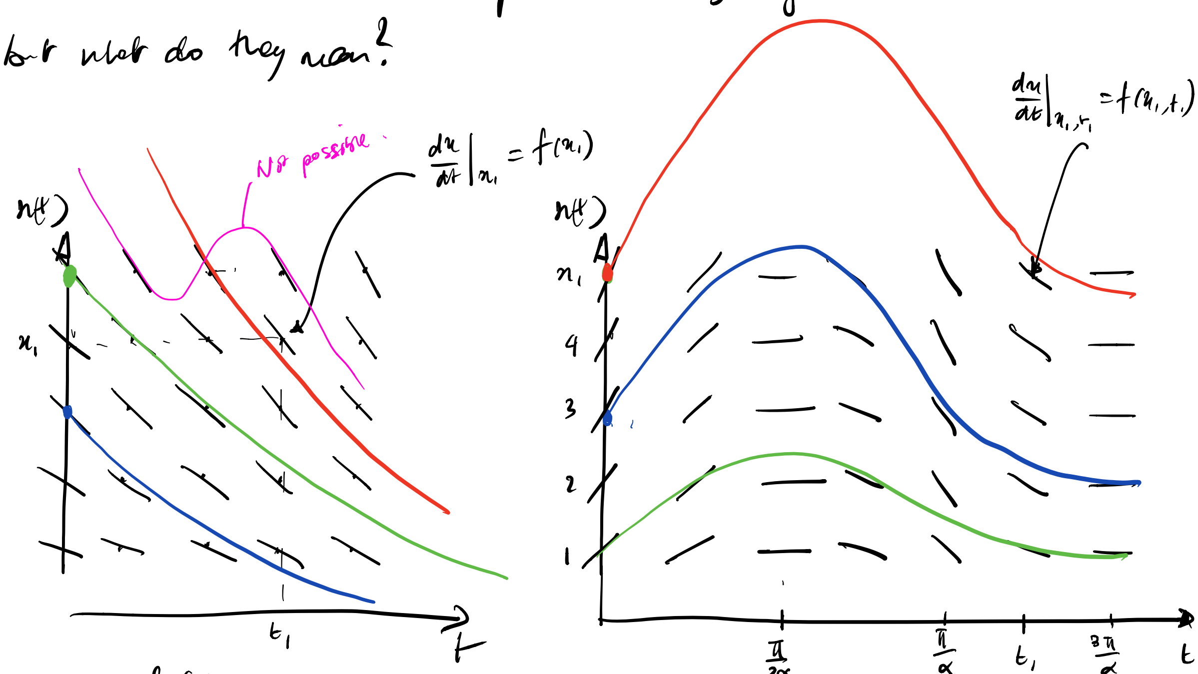
$$(\text{Net force}) = \text{mass} \times \text{accel}^{n}$$

$$F = m\frac{d^2x}{dt^2}$$

1^{st} order differential eqns.

$$\frac{dx}{dt} = f(x) \qquad \text{or} \qquad \frac{dx}{dt} = f(t,x)$$

* We want to solve these eqns f $x(t)$, subject to initial condition $x(0)=x_0$
– but what do they mean?



* Plotting $\frac{dx}{dt} = f(x)$ (or $\frac{dx}{dt} = f(t,x)$) for different values of x & t allows us to visualise the effective flow-field or vector-field
→ like water flowing in pipe or over obstacles. (But point has no momentum!)

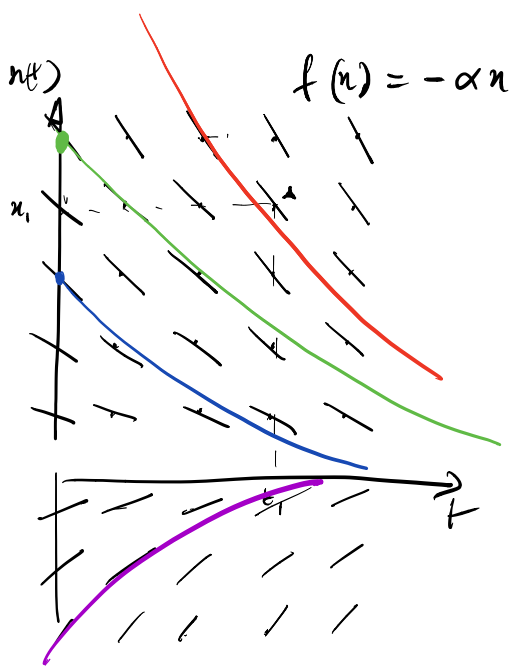
(field is just something that varies continuously in co-ordinate space)

Autonomous 1st order differential eqns.

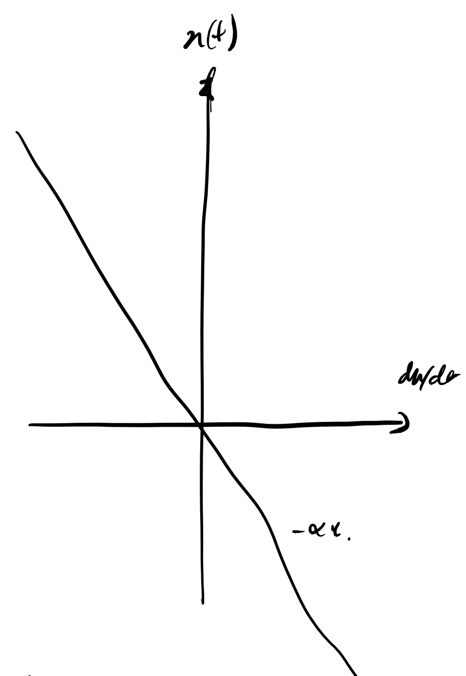
$$\frac{dx}{dt} = f(x)$$

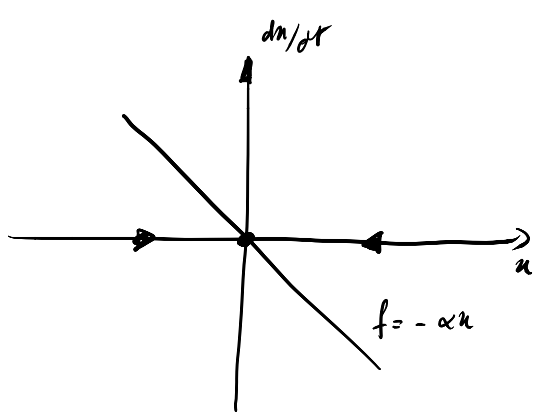
* As flow-field $f(x)$ does not depend on time the time axis in above plots become redundant;

Example $f(x) = -\alpha x \rightarrow \frac{dx}{dt} = -\alpha x$



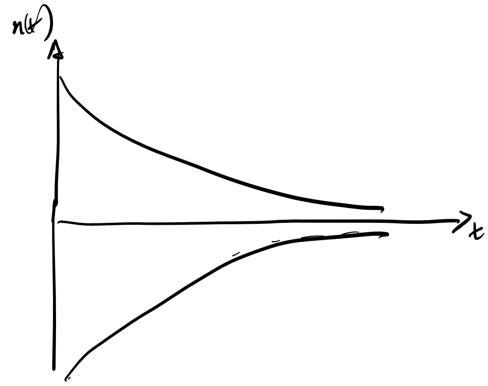
→





* $\frac{dx}{dt} < 0$ for $x > 0$
  → flows cause x to decrease → indicated by arrow on x-axis. ◄
* $\frac{dx}{dt} > 0$ for $x < 0$ ►
* Once it reaches $x = 0$ $\frac{dx}{dt} = 0$
  → nothing changes → this is a "fixed point".

* Qualitative solution curves



* $x>0$: x decreases & $\frac{dx}{dt}$ becomes less & less negative
[$\frac{dx}{dt}$ is increasing $\Rightarrow \frac{d^2x}{dt^2}>0 \Rightarrow$ curves are convex (or concave up)]

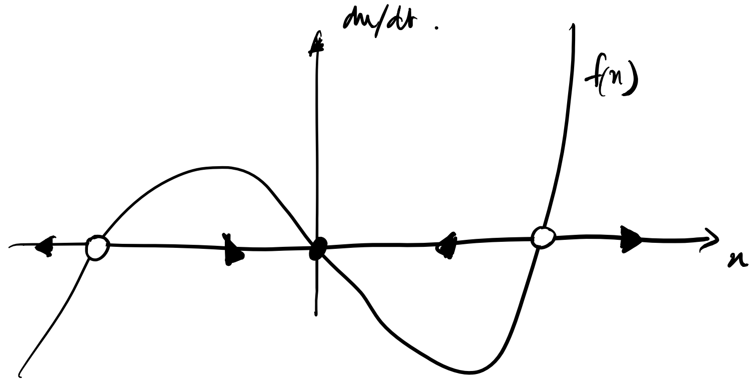
* $x<0$: x increases & $\frac{dx}{dt}$ decreases
[$\frac{dx}{dt}$ is decreasing $\Rightarrow \frac{d^2x}{dt^2}<0 \Rightarrow$ curves are concave (down)]

N.B. We know solution is $x(t) = x_0 e^{-\alpha t}$ $\rightarrow$ Qualitatively, we have drawn curves that are correct..

* However with exact equation we can ask, for example, time t^* to decay to half initial condition?

$$x(t) = \frac{x_0}{2} \Rightarrow x_0 e^{-\alpha t} = \frac{x_0}{2}$$
$$\Rightarrow t^* = -\frac{1}{\alpha}\ln\frac{1}{2} = \frac{1}{\alpha}\ln 2$$

* 1D (1st order autonomous) phase portraits.

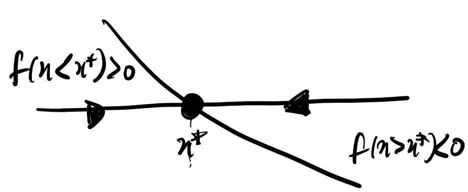


* Fixed points are determined by where $f(x^*) = 0$ or where $f(x)$ crosses the x-axis

* In general, many fixed points $x_1^*, x_2^*, x_3^*, \ldots$ depending on how complicated $f(x)$.

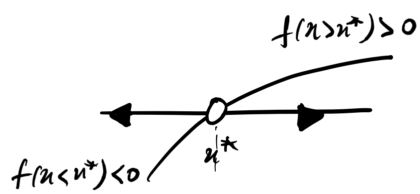
* Stability : How do we determine stability

● stable fixed point



$$\left.\frac{df}{dx}\right|_{x^*} < 0$$

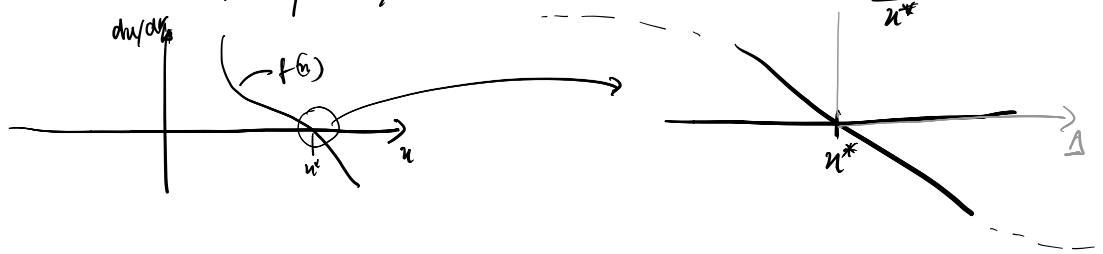
O unstable fixed point.



$$\left.\frac{df}{dx}\right|_{x^*} > 0$$

Proof: (when $\left.\frac{df}{dx}\right|_{x^*} \neq 0$)

if x^* is our fixed point, let $\Delta = x - x^*$ & assume $\frac{\Delta}{x^*} << 1$



$$\frac{d\Delta}{dt} = \frac{d}{dt}(x - x^*) = \frac{dx}{dt} = f(x) = f(\Delta + x^*)$$

$$\Rightarrow \quad \frac{d\Delta}{dt} = f(x^* + \Delta)$$

$$\approx f(x^*) + \Delta \frac{df}{d\Delta} + \frac{1}{2}\Delta^2 \frac{d^2f}{d\Delta^2} + \dots$$

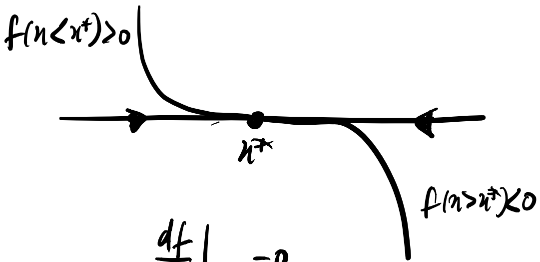
1) $f(x^*) = 0$
2) $\Delta^2 << \Delta$

$$\Rightarrow \quad \frac{d\Delta}{dt} \approx \frac{df}{d\Delta}\Delta$$

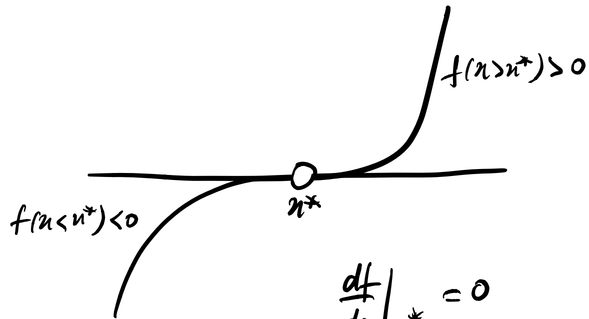
$\Rightarrow$ if $\frac{df}{d\Delta} > 0$ $\quad \Delta$ grows from fixed point $\Rightarrow$ UNSTABLE.

if $\frac{df}{d\Delta} < 0$ $\quad \Delta$ shrinks towards fixed point $\Rightarrow$ STABLE.

Q: What happen if $\left.\frac{df}{dx}\right|_{x^*} = 0$?



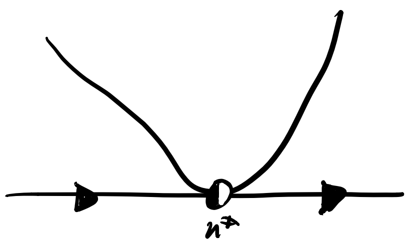
$\frac{df}{dx}\Big|_{x^*} = 0$



$\frac{df}{dx}\Big|_{x^*} = 0$

e.g. $\frac{d\Delta}{dt} = \cancel{\Delta \frac{df}{d\Delta}} + \cancel{\frac{1}{2}\Delta^2 \frac{d^2f}{d\Delta^2}} + \frac{1}{3!}\Delta^3 \frac{d^3f}{d\Delta^3} + \cdots$

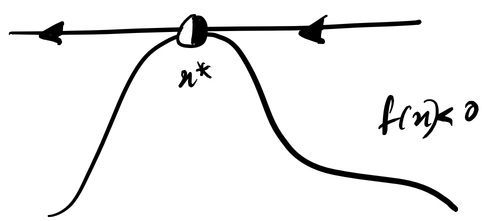
- half-stable fixed point.



f(x)>0

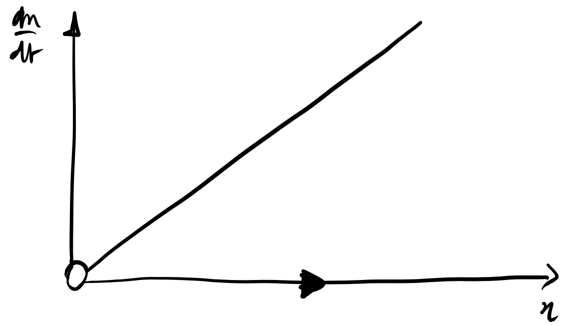
$\frac{df}{dx}\Big|_{x^*} = 0$

$\frac{df}{dx}\Big|_{x^*} = 0$



e.g. $\frac{d\Delta}{dt} \simeq \cancel{\Delta \frac{df}{d\Delta}} + \frac{1}{2}\Delta^2 \frac{d^2f}{d\Delta^2} + \cdots$

* Exponential growth $\quad \frac{dn}{dt} = rn \quad (r>0) \quad \left(\frac{dN}{dt} = rN\right).$



1) Fixed points $\quad \frac{dn}{dt} = 0 \Rightarrow rn = 0 \Rightarrow n^* = 0$

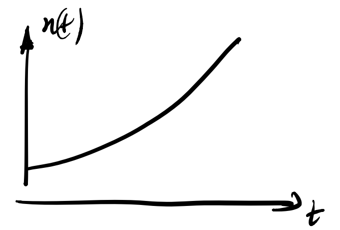
2) Stability $\quad \left.\frac{dn}{dt}\right|_{n=n^*} = r > 0 \Rightarrow$ unstable

$\Rightarrow$ n increases forever for any $n(0) = n_0 > 0$ & monotonically

* Without exact solution difficult to be quantitative;
  e.g. Does population n reach infinity in a finite time?
  Time t^* to double initial population?

$\Rightarrow$ We know that n increases monotonically $\Rightarrow$ from phase portrait $\frac{dn}{dt}$ increases $\Rightarrow \frac{d^2 n}{dt^2} > 0$

$\Rightarrow$ $n(t)$ must be convex (concave up)



* We know solution is $n(t) = n_0 e^{rt}$

$\Rightarrow$ doubling time t^*:

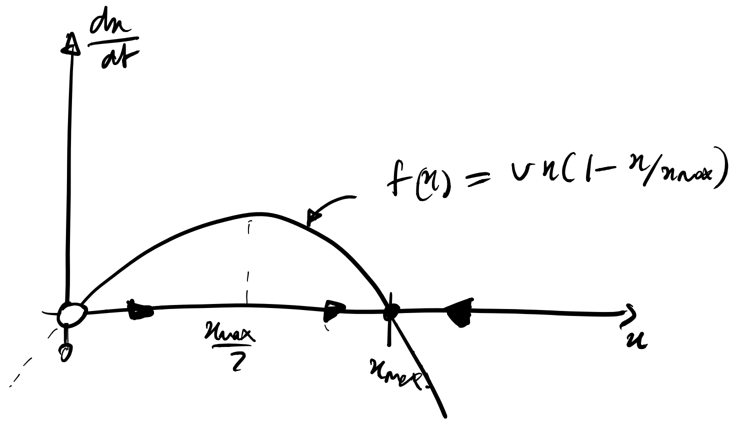
$$n(t) = 2n_0 \Rightarrow \cancel{n_0} e^{rt} = 2\cancel{n_0}$$

$$t^* = \frac{1}{r} \ln(2)$$

* Logistic growth.

$$\frac{dx}{dt} = r x (1 - x/x_{max})$$

1) Fixed points : $x_1^* = 0$ & $x_2^* = x_{max}$.



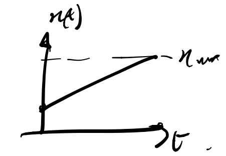
2) Stability (By inspection or :)

$$\left.\frac{df}{dx}\right|_{x_1^*} = r\left(1 - \frac{2x}{x_{max}}\right)\Bigg|_{x_1^*} = r > 0 \quad \text{UNSTABLE}$$

$$\left.\frac{df}{dx}\right|_{x_2^*} = r\left(1 - \frac{2x}{x_{max}}\right)\Bigg|_{x_2^*} = -r < 0 \quad \text{STABLE}$$

→ For all initial conditions (except $x_0 = 0$) we have a single equilibrium solution

Q: What does it mean biologically if $x_0 = 0$?



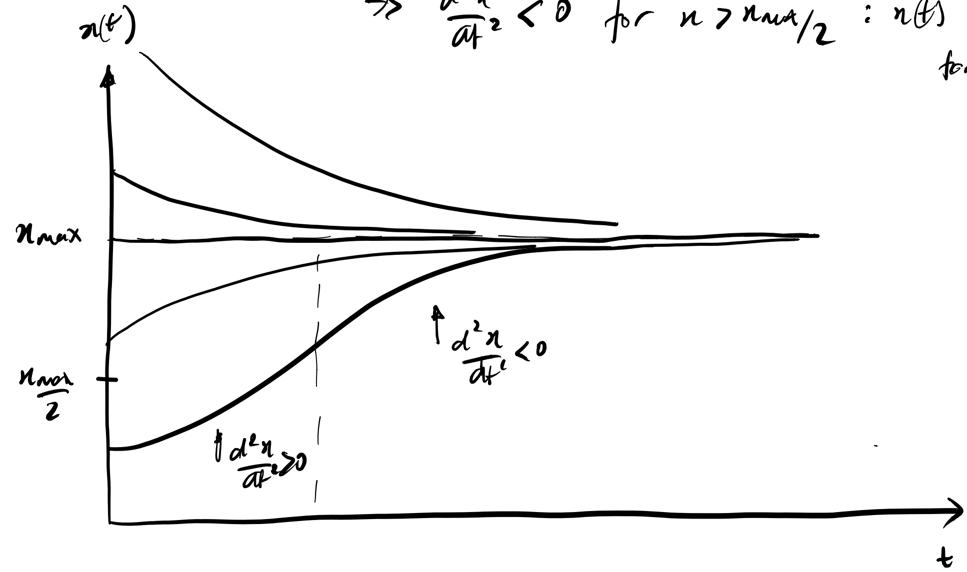
* Can we sketch the solutions ? Are the solutions straight lines ?

1) for $0 < x_0 < \frac{x_{max}}{2}$ $\to$ $\frac{dx}{dt}$ is increasing for $x < \frac{x_{max}}{2}$ $\cup$

$\to$ $\frac{d^2x}{dt^2} > 0$ for $x < x_{max}/2$: $x(t)$ should be convex for $x < \frac{x_{max}}{2}$

$\to$ once $x > x_{max}/2$ $\frac{dx}{dt}$ is decreasing $\cap$

$\to$ $\frac{d^2x}{dt^2} < 0$ for $x > x_{max}/2$: $x(t)$ should be concave for $x > \frac{x_{max}}{2}$



2) for $\frac{x_{max}}{2} < x_0 < x_{max}$: as above $\frac{d^2x}{dt^2} < 0$ $\to$ $x(t)$ is concave.

3) for $x_0 > x_{max}$: As we move towards the fixed point $x^* = x_{max}$ from above $\frac{dx}{dt}$ is increasing $\left(\left| \frac{dx}{dt} \right| \text{ is decreasing} \right)$

$\to$ $\frac{d^2x}{dt^2} > 0$ $\to$ $x(t)$ is convex $\cup$

* Both exponential & logistic growth have exact analytical solutions, which we discuss below

  $\to$ In general, many 1D dynamical systems do not have exact solutions

  $\to$ this approach is the only way to get qualitative behaviour

* Exact solution of logistic differential eqn.

- Using partial fractions can show solution to

$$\frac{dn}{dt} = v n(1 - n/n_{max})$$

is $$n(t) = \frac{e^{vt} n_0 n_{max}}{n_{max} - n_0 + n_0 e^{vt}}$$ (Tutorial Question)

* Limits:

→ limit of $n(t)$ as $t \to \infty$

- for t large $n_0 e^{vt} \gg n_{max} - n_0$

$$\Rightarrow n(t) \to \frac{\cancel{e^{vt}}\cancel{n_0} n_{max}}{\cancel{n_0 e^{vt}}} = n_{max}.$$

→ limit of $n(t)$ for short times:

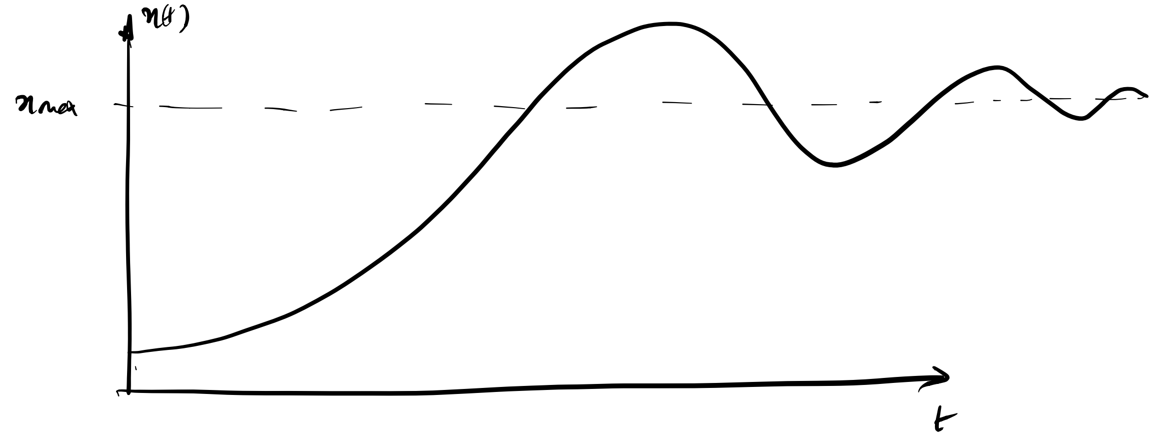
- <u>if</u> $n_0 e^{vt} \ll n_{max} - n_0$

$$\Rightarrow n(t) \approx \frac{n_0 n_{max}}{n_{max} - n_0} e^{vt}$$ → simple exponential growth.

→ if $n_0 > n_{max}/2$, then $n_0 > n_{max} - n_0 \Rightarrow n_0 e^{vt} \ll n_{max} - n_0$ cannot be satisfied!

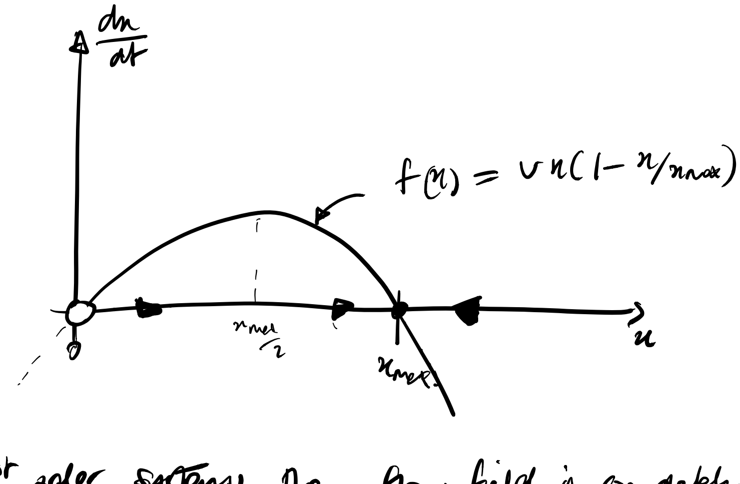
* Impossibility of oscillations in 1D systems (1st order autonomous system)

Q: In the logistic growth model, why doesn't the population size overshoot & then oscillate around the fixed point?



→ Maybe the population doesn't "realise" it's impending limit and temporarily grows beyond the carrying capacity??

→ Phase-portrait



* For autonomous 1st order systems the flow-field is completely specified $f(x)$; in order for there to be oscillations we need flow-field to change direction under different conditions. → we need another degree of freedom
→ oscillations are impossible in 1D autonomic systems

* 2^{nd} order systems

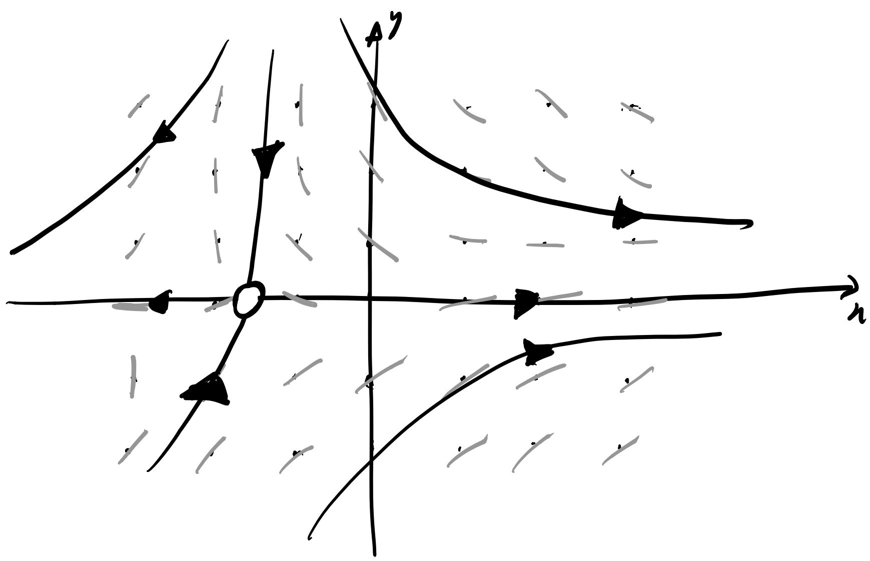
$$\frac{dx}{dt} = \dot{x} = f(x, y)$$

$$\frac{dy}{dt} = \dot{y} = g(x, y)$$

* Again in general it is unlikely that we can find a closed-form analytical solution.

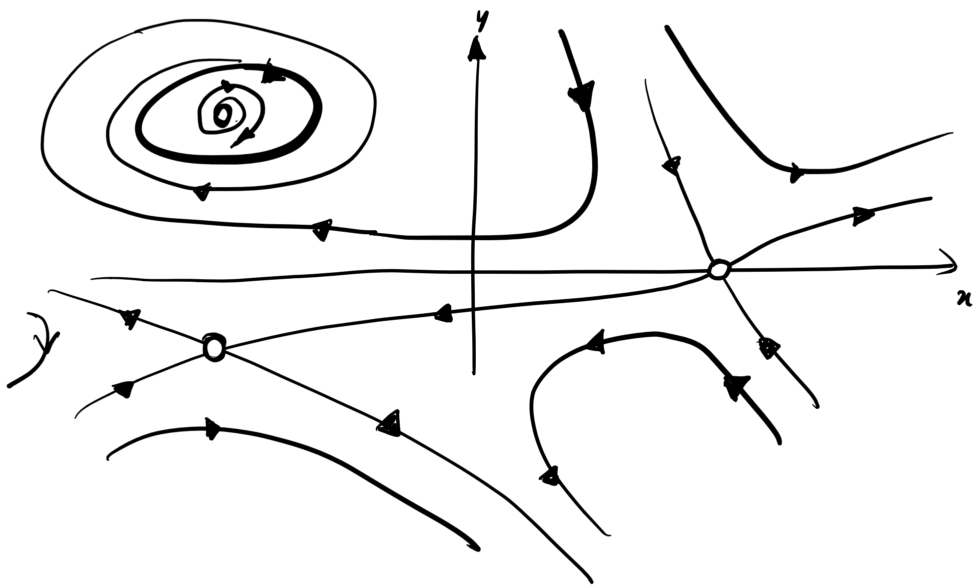
-> We use phase-portraits to gain qualitative understanding of dynamic.

-> we plot the vector $(\dot{x}, \dot{y})$ at a number of points on a x-y axis to indicate the flow field.



-> Each of the black trajectories must follow the local slope in grey.

→ The phase portrait can in principle be very complicated



* We have 1) fixed points which can be stable ● or unstable o

2) Closed orbits (only 2D or above)

where solution is periodic in it $x(t) = x(t+T)$

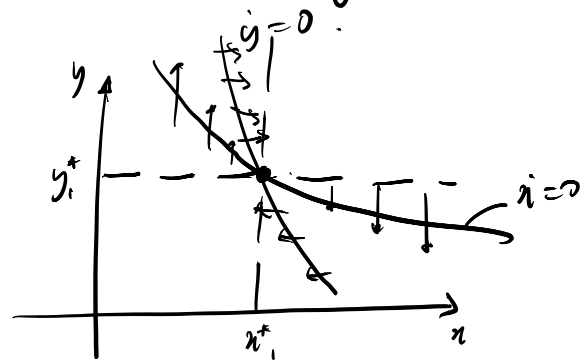
& $y(t) = y(t+T)$

→ As trajectories from within & outside closed orbit converge on it, it is stable.

* The general strategy to understanding such dynamical systems is to analyse the behavior near the fixed points, where behaviour becomes approximately linear.

* Phase Plane analysis of non-linear 2D systems

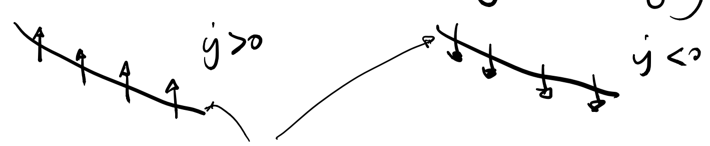
$$\dot{x} = f(x,y)$$
$$\dot{y} = g(x,y)$$



1) Find nullclines :

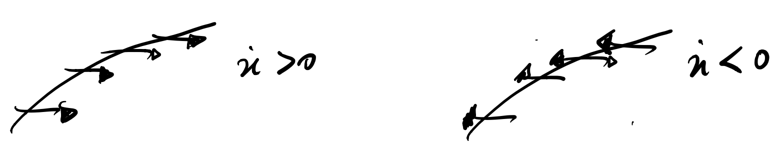
- → these are defined to be the curves for which $\dot{x}=0$ & separately $\dot{y}=0$.
- → On each nullcline the vector field is either all vertical for $\dot{x}=0$ or all horizontal for $\dot{y}=0$.
- → this gives additional information on the qualitative dynamics of the system

2) i) On $\dot{x}=0$ nullcline examine how $\dot{y}$ is changing (is $\dot{y}>0$ or $\dot{y}<0$?)



$\dot{x}=0$ produces a curve $y = F_x(x)$ → plug into eqn for $\dot{y}$

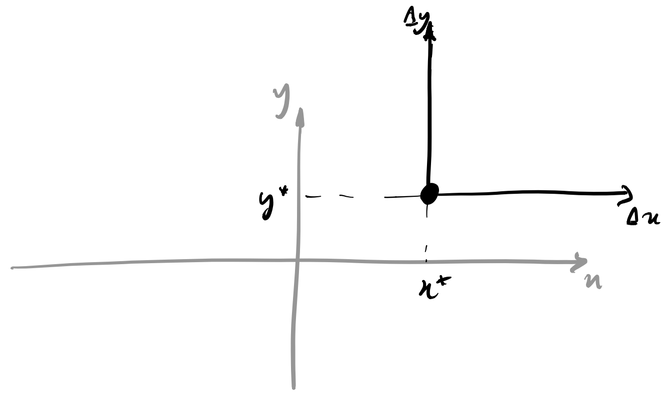
ii) on $\dot{y}=0$ nullcline examine how $\dot{x}$ is changing (is $\dot{x}>0$ or $\dot{x}<0$)



$\dot{y}=0$ produces a curve $y = F_y(x)$ → plug into eqn for $\dot{x}$.

3) For each fixed point calculate effective linearised dynamics near it.

→ This requires expanding the nonlinear function $f(x,y)$ & $g(x,y)$ to linear order about the fixed point x^*, y^*



1D $$f(x) = f(x^*) + \frac{df}{dx}\Big|_{x=x^*}(x-x^*) + \frac{1}{2!}\frac{d^2f}{dx^2}\Big|_{x=x^*}(x-x^*)^2 + \dots$$

$x = x^* + \Delta x \Rightarrow \Delta x = (x - x^*)$

$$f(x^*+\Delta x) = f(x^*) + \frac{df}{dx}\Big|_{x=x^*}\Delta x + \dots$$

$x = x^* + \Delta x \qquad \& \; y = y^* + \Delta y$

$\Rightarrow \dot{x} = \cancel{\dot{x}^*} + \dot{\Delta x} = \dot{\Delta x} \quad \& \; \dot{y} = \cancel{\dot{y}^*} + \dot{\Delta y} = \dot{\Delta y}$

$$\Rightarrow \quad \dot{\Delta x} = f(x^*+\Delta x, y^*+\Delta y) = \underbrace{f(x^*,y^*)}_{=0} + \left(\frac{\partial f}{\partial x}\Big|_{x=x^*, y=y^*}\right)\Delta x + \left(\frac{\partial f}{\partial y}\Big|_{x^*,y^*}\right)\Delta y + \dots$$

$$= \frac{\partial f}{\partial x}\Big|_{x^*,y^*}\Delta x + \frac{\partial f}{\partial y}\Big|_{x^*,y^*}\Delta y + \dots$$

$$\dot{\Delta y} = g(x^*+\Delta x, y^*+\Delta y) = \frac{\partial g}{\partial x}\Big|_{x^*,y^*}\Delta x + \frac{\partial g}{\partial y}\Big|_{x^*,y^*}\Delta y + \dots$$

$$\Rightarrow \dot{\Delta x} = f(x^*+\Delta x, y^*+\Delta y) \approx \frac{\partial f}{\partial x}\bigg|_{x^*,y^*} \Delta x + \frac{\partial f}{\partial y}\bigg|_{x^*,y^*} \Delta y$$

$$\dot{\Delta y} = g(x^*+\Delta x, y^*+\Delta y) \approx \frac{\partial g}{\partial x}\bigg|_{x^*,y^*} \Delta x + \frac{\partial g}{\partial y}\bigg|_{x^*,y^*} \Delta y$$

$\Rightarrow$ **Linear system** as long as we don't let Δx & Δy become too large!

* Matrix form

$$\begin{pmatrix} \dot{\Delta x} \\ \dot{\Delta y} \end{pmatrix} = \underbrace{\begin{pmatrix} \frac{\partial f}{\partial x}\big|_* & \frac{\partial f}{\partial y}\big|_* \\ \frac{\partial g}{\partial x}\big|_* & \frac{\partial g}{\partial y}\big|_* \end{pmatrix}} \begin{pmatrix} \Delta y \\ \Delta y \end{pmatrix}$$

N.B these entries are constants near any fixed point.

$\rightarrow$ this matrix $\underline{\underline{J}}$ is conventionally called the "Jacobian matrix" & also arises when doing a change of variable in differential eqns or evaluating double integrals.

$\rightarrow$ We can use linear analysis of previous section (eigenvectors & eigenvalues) to determine behaviour near <u>each</u> fixed point.

$\rightarrow$ Each of these fixed points will fall into one of the categories discussed depending on the eigenvalues of the Jacobian matrix $\underline{\underline{J}}$.

SIRS epidemic eqns. - model of waning immunity.

S - susceptible to infection

I - infected

R - Recovered & immune to infection

$$\begin{tikzcd}
\boxed{S} \arrow[r, "?"] & \boxed{I} \arrow[r, "?"] & \boxed{R} \arrow[ll, bend left]
\end{tikzcd}$$

1) Infection event $\qquad S + I \rightarrow I + I$

2) Recovery event $\qquad I \rightarrow R$

3) Loosing immunity. $\qquad R \rightarrow S$

→ Need to assign rates to how quickly these events happen.

1) $S + I \rightarrow 2I \; : \; \beta/N$

2) $I \rightarrow R \; : \; \gamma$

3) $R \rightarrow S \; : \; \sigma$

→ Way we write this is as a chemical reaction

$$I + S \xrightarrow{\beta/N} I$$
$$I \xrightarrow{\gamma} R$$
$$R \xrightarrow{\sigma} S$$

For each event what is change in number.

Event.	Change in S	Change in I	Change in R
$S + I \xrightarrow{\beta/N} 2I$	-1	$+1$	0
$I \xrightarrow{\gamma} R$	0	-1	$+1$
$R \xrightarrow{\sigma} S$	$+1$	0	-1

$$\Rightarrow \frac{dS}{dt} = -\frac{\beta}{N} S I + \sigma R$$

$$\frac{dI}{dt} = +\frac{\beta}{N} S I - \gamma I$$

$$\frac{dR}{dt} = \gamma I - \sigma R$$

3x3 system!!!

But $S + I + R = N$ → We can eliminate 1 variable.

→ Let $R = N - (S + I)$

$$\Rightarrow \frac{dS}{dt} = -\frac{\beta}{N} SI + \sigma(N - S - I)$$

$$\frac{dI}{dt} = +\frac{\beta}{N} SI - \gamma I$$

R_0 defined by when epidemic grows

$$\frac{dI}{dt} > 0$$

$$\Rightarrow \frac{dI}{dt} = \frac{\beta}{N} SI - \gamma I$$

$$= \left(\frac{\beta}{N} S - \gamma\right) I > 0.$$

→ Infection level does not change this criterion

$$\Rightarrow \frac{\beta}{N} S - \gamma > 0$$

$$\gamma\left(\frac{\beta S}{\gamma N} - 1\right) > 0.$$

$$\Rightarrow R_e = \frac{\beta S}{\gamma N} > 0 \quad \text{epidemic grows}$$

If whole population is susceptible (say at $t=0$) then $S \approx N$ & $R_e = \frac{\beta}{\gamma} = R_0$

(more generally $R_e = R_0\left(\frac{S}{N}\right)$)

Nullclines

$$\frac{dS}{dt} = 0 \Rightarrow -\frac{\beta}{N} SI + \sigma(N - S - I) = 0$$

$$-\frac{\beta S}{N} I - \sigma I + \sigma(N-S) = 0.$$

$$\Rightarrow -\left(\frac{\beta S}{N} + \sigma\right) I + \sigma(N-S) = 0$$

$$\Rightarrow I = \frac{\sigma(N-S)}{\sigma + \beta S/N}$$

$$\frac{dI}{dt} = 0 \Rightarrow \frac{\beta}{N} SI - \gamma I = 0.$$

$$\frac{\beta S}{N} - \gamma = 0$$

$$\Rightarrow \frac{\beta S}{\gamma N} = 1 \quad \Rightarrow S = \frac{N\gamma}{\beta}$$

$\frac{\beta S}{\gamma N} = R_e$ the effective R-number.

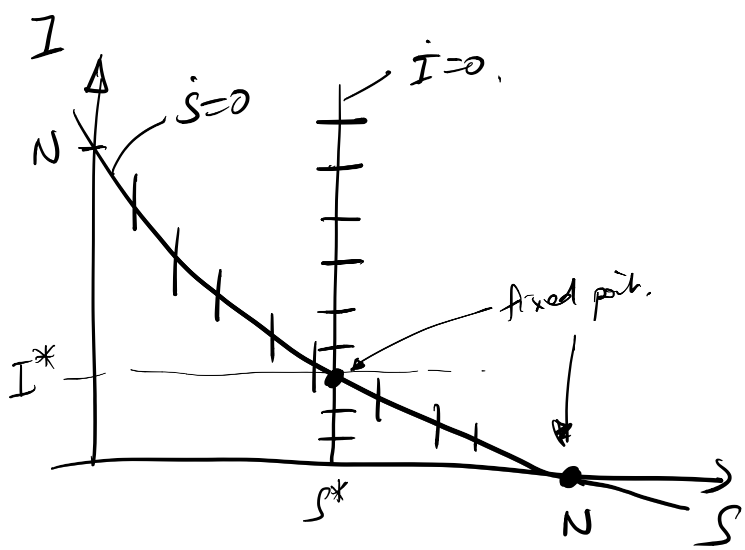
* $\frac{\beta}{\gamma} = R_0$ the R-number when everyone is susceptible.

$\Rightarrow$

$\dot{S} = 0$ nullcline : $I = \dfrac{\sigma(N-S)}{\sigma + \beta S/N}$

$= \dfrac{\sigma(N-S)}{\sigma + \gamma R_0 S/N}$

$\dot{I} = 0$ nullcline : $S = \frac{N\gamma}{\beta} = N/R_0$



* Need to figure out directions of phase flow on the nullclines

1st find fixed point S^* & I^*

1) $\dot{I}=0$ says: $\boxed{S^* = N\gamma/\beta}$ → Plug into $\dot{S}=0$ nullcline.

$$\dot{S}=0 \; : \; I^* = \frac{\sigma(N-S^*)}{\sigma+\beta S^*/N}$$

$$= \frac{\sigma(N - N\gamma/\beta)}{\sigma + \frac{\cancel{\beta}}{\cancel{N}} \times \frac{\cancel{N}\gamma}{\cancel{\beta}}}$$

$$= \frac{\sigma N(1-\gamma/\beta)}{\sigma+\gamma} \qquad R_0 = \beta/\gamma$$

$$\boxed{I^* = \frac{\sigma N(1-1/R_0)}{\sigma+\gamma}}$$

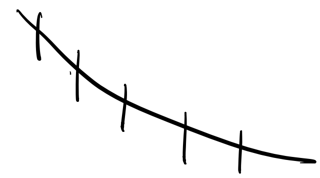
N.B. for $R_0 > 1$ $1/R_0 < 1 \Rightarrow I^* > 0$

$\Rightarrow$ with waning immunity & $R_0>1$ the epidemic is <u>endemic</u>

for $R_0 \leq 1$ $I^* = 0$ → the epidemic goes extinct.
even with waning immunity.

On $\dot{S}=0$. how is I changing?

$\dot{S}=0$ nullcline defined by $I = \dfrac{\sigma(N-S)}{\sigma+\beta S/N}$



$$\frac{dI}{dt} = \left(\frac{\beta S}{N} - \gamma\right) I$$

But I is always +ve ($I>0$) $\Rightarrow$ cannot determine sign $\Rightarrow$ only determined by S.

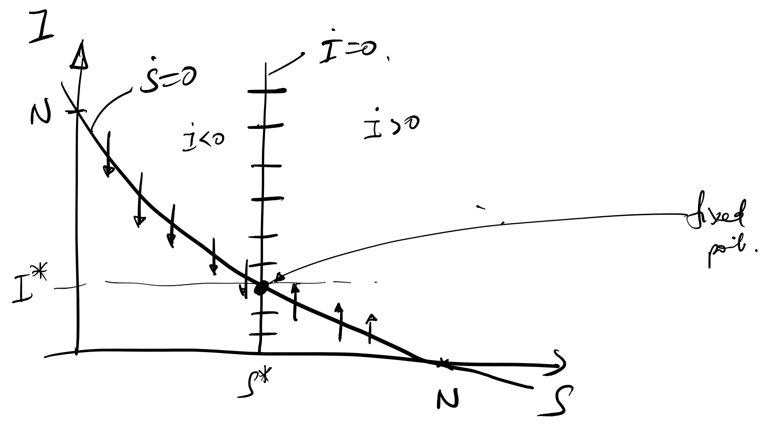
$\Rightarrow$ if $\frac{\beta S}{N} - \gamma > 0$ $\quad \dot{I} > 0$

if $\frac{\beta S}{N} - \gamma < 0$ $\quad \dot{I} < 0$

$\Downarrow$

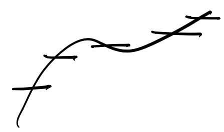
If $S > S^*$ $\quad (R_e > 1)$ then $\dot{I} > 0$

If $S < S^*$ $\quad (R_e < 1)$ then $\dot{I} < 0$



On $\dot{I}=0$ what is S doing?

$\dot{I}=0$



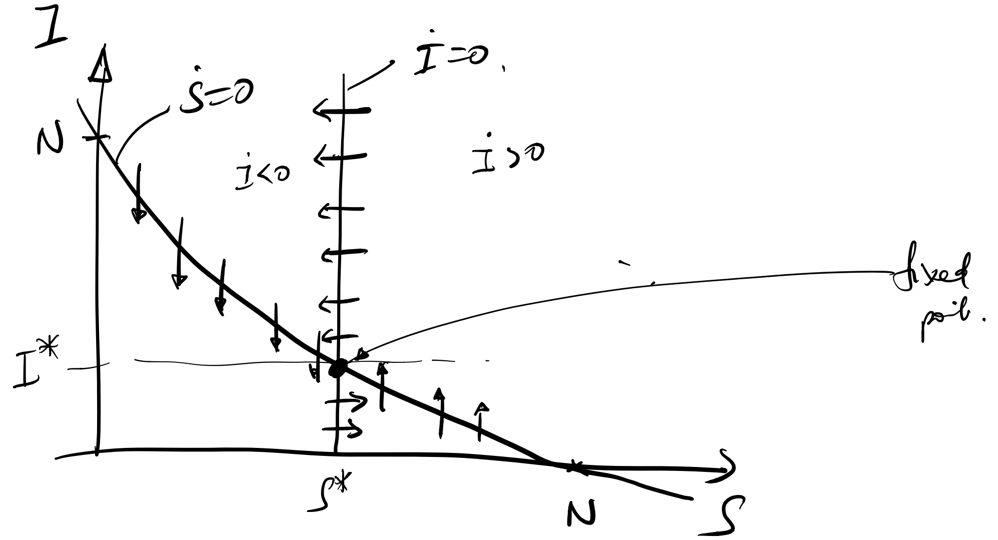
defined by a line $I = F(S)$. Here $S = \frac{N\gamma}{\beta} = S^*$

$$\frac{dS}{dt} = -\frac{\beta S^* I}{N} + \sigma(N - I - S^*)$$

$$= -\left(\frac{\beta S^*}{N} + \sigma\right) I + \sigma(N - S^*)$$

we know if we plug in $I = I^*$ $\frac{dS}{dt} = 0$

$\Rightarrow$ we can see $I > I^*$ $\frac{dS}{dt} < 0$ & $I < I^*$ $\frac{dS}{dt} > 0$



$\Rightarrow$ We expect rotational motion around the fixed point.

→ To examine stability need to analyse dynamics close to fixed point S^* & I^*

→ Calculate matrix of partial derivatives (Jacobian) at the fixed point:

$$\frac{dS}{dt} = -\left(\frac{\beta S}{N} + \sigma\right)I + \sigma(N-S) = f(S,I)$$

$$\frac{dI}{dt} = \left(\frac{\beta S}{N} - \gamma\right)I = g(S,I)$$

$$\underline{\underline{J}} = \begin{pmatrix} \frac{\partial f}{\partial S} & \frac{\partial f}{\partial I} \\ \frac{\partial g}{\partial S} & \frac{\partial g}{\partial I} \end{pmatrix}$$

$$\frac{\partial f}{\partial S} = \frac{\partial}{\partial S}\left(-\left(\frac{\beta S}{N} + \sigma\right)I + \sigma(N-S)\right) = -\left(\sigma + \frac{\beta I}{N}\right)$$

$$\frac{\partial f}{\partial I} = \frac{\partial}{\partial I}\left(-\left(\frac{\beta S}{N} + \sigma\right)I + \sigma(N-S)\right) = -\left(\frac{\beta S}{N} + \sigma\right)$$

$$\frac{\partial g}{\partial S} = \frac{\partial}{\partial S}\left(\frac{\beta S}{N} - \gamma\right)I = \frac{\beta I}{N}$$

$$\frac{\partial g}{\partial I} = \frac{\partial}{\partial I}\left(\frac{\beta S}{N} - \gamma\right)I = \frac{\beta S}{N} - \gamma$$

$$\Rightarrow \quad \underline{\underline{J}} = \begin{pmatrix} \frac{\partial f}{\partial S} & \frac{\partial f}{\partial I} \\ \frac{\partial g}{\partial S} & \frac{\partial g}{\partial I} \end{pmatrix} = \begin{pmatrix} -\left(\sigma + \frac{\beta I}{N}\right) & -\left(\frac{\beta S}{N} + \sigma\right) \\ \frac{\beta I}{N} & \frac{\beta S}{N} - \gamma \end{pmatrix}$$

→ Evaluate Jacobian matrix at the fixed point.

$$\underline{\underline{J}}\Big|_{S=S^*,\, I=I^*} = \begin{pmatrix} -\left(\sigma + \frac{\beta I^*}{N}\right) & -\left(\frac{\beta S^*}{N} + \sigma\right) \\ \frac{\beta I^*}{N} & \frac{\beta S^*}{N} - \gamma \end{pmatrix}$$

$$= \begin{pmatrix} -\left(\sigma + \frac{\beta}{\cancel{N}} \frac{\sigma \cancel{N}(1-\gamma/\beta)}{\sigma+\gamma}\right) & -(\gamma+\sigma) \\ \frac{\beta}{\cancel{N}} \frac{\sigma \cancel{N}(1-\gamma/\beta)}{\sigma+\gamma} & \gamma - \gamma \end{pmatrix}$$

$$= \begin{pmatrix} -\sigma\left(1 + \frac{\beta-\gamma}{\sigma+\gamma}\right) & -(\gamma+\sigma) \\ \frac{\sigma(\beta-\gamma)}{\sigma+\gamma} & 0 \end{pmatrix}$$

$$= \begin{pmatrix} -\sigma\left(\frac{\sigma+\cancel{\gamma}+\beta-\cancel{\gamma}}{\sigma+\gamma}\right) & -(\gamma+\sigma) \\ \frac{\sigma(\beta-\gamma)}{\sigma+\gamma} & 0 \end{pmatrix}$$

$$\boxed{\underline{\underline{J}}\Big|_{S=S^*,\, I=I^*} = \begin{pmatrix} -\sigma\dfrac{(\sigma+\beta)}{\sigma+\gamma} & -(\gamma+\sigma) \\ \sigma\dfrac{(\beta-\gamma)}{\sigma+\gamma} & 0 \end{pmatrix}}$$

Things we can say without explicitly calculating eigenvalues.

1) $Tr(\underline{\underline{J}}) < 0$ as $\sigma > 0$, $\beta > 0$ & $\gamma > 0$

2) Remember $\underline{\underline{A}} = \begin{pmatrix} 0 & -1 \\ 1 & 0 \end{pmatrix}$ → rotation anti-clockwise

i) ⇒ if $\beta - \gamma > 0$ we expect a stable spiral

→ Equivalent to $R_0 > 1$ ⇒ stable spiral.

ii) if $\beta - \gamma < 0$ $(R_0 < 1)$ ⇒ no oscillations

$$Tr(\underline{\underline{J}}) = -\frac{\sigma(\sigma+\beta)}{\sigma+\gamma} \qquad |\underline{\underline{J}}| = 0 - -\cancel{(\gamma+\sigma)}\,\frac{\sigma(\beta-\gamma)}{\cancel{\sigma+\gamma}}$$
$$= \sigma(\beta-\gamma)$$

$\to$ Simplify : $\sigma \ll \gamma \sim \beta$ immunity is "long" lasting.

$$\to Tr(\underline{\underline{J}}) \approx -\sigma\frac{\beta}{\gamma} = -\sigma R_0 \quad \& \quad |\underline{\underline{J}}| = \gamma\sigma(R_0-1)$$

$$\Rightarrow \lambda = \frac{1}{2}\left(-\sigma R_0 \pm \sqrt{\sigma^2 R_0^2 - 4\gamma\sigma(R_0-1)}\right)$$
$$= -\frac{\sigma R_0}{2} \pm \frac{1}{2}\sigma R_0\sqrt{1 - \frac{4\gamma\cancel{\sigma}(R_0-1)}{\sigma^2 R_0^2}}$$
$$= -\frac{\sigma R_0}{2}\left(1 \pm \sqrt{1 - \frac{4\gamma}{\sigma}\frac{(R_0-1)}{R_0^2}}\right)$$

$\Rightarrow$ if $R_0 < 1$ no imaginary part $\Rightarrow$ no oscillations

if $R_0 > 1$ we have criterion for complex eigenvalues

$$\frac{4\gamma}{\sigma}\frac{R_0-1}{R_0^2} > 1$$

$\Rightarrow$ if $\sigma \ll \gamma \Rightarrow \frac{\gamma}{\sigma} \gg 1$ & $R_0 - 1$ is not very small

$$\Rightarrow Im(\lambda) \neq 0$$

for $R_0 > 1$

1) $Re(\lambda) < 0$ → stable

2) $Im(\lambda) \neq 0$ → spiral.