4. Stability criterion for many-species gLV systems (R. H. May 1972)

Consider a large N-species system, with densities $\{\rho_1(t), \rho_2(t), \cdots, \rho_N(t)\} = \vec{\rho}(t)$

gLV model: $\frac{d\rho_i}{dt} = f_i(\vec{\rho}(t))$

fixed point: $\vec{\rho}^*$ such that $f_i(\vec{\rho}^*) = 0$.

Jacobian matrix: $J_{ij} = \frac{\partial f_i(\vec{\rho}(t))}{\partial \rho_j}$

Community matrix: $M_{ij} = \left.\frac{\partial f_i}{\partial \rho_j}\right|_{\vec{\rho}^*}$

- Stability of fixed point:

  look at eigenvalues of M_{ij}: $\{\lambda_1, \lambda_2, \cdots \lambda_N\}$

  (since M_{ij} are real, $\lambda_k = a \pm ib$)

  $\rightarrow$ fixed pt stable if $\max_k\{\mathrm{Re}\{\lambda_k\}\} < 0$

- Solving for J_{ij} and $\vec{\rho}^*$ complicated

  $\rightarrow$ May (1972): directly look at M_{ij}

take another look at M_{ij} for 2×2 toy system

$$M = \begin{bmatrix} -r_1 u_1^* & -r_1 a_{12} u_1^* \\ -r_2 u_2^* a_{21} & -r_2 u_2^* \end{bmatrix}$$

$$u_1^* = \frac{1-a_{12}}{1-a_{12} \cdot a_{21}}$$

$$u_2^* = \frac{1-a_{21}}{1-a_{12} \cdot a_{21}}$$

Consider $r_1 \sim r_2$, $u_1^* \sim u_2^*$
(i.e. same order of magnitude)

then M has the form

$$M \propto \begin{bmatrix} -1 & a_{12} \\ a_{21} & -1 \end{bmatrix}$$

(a_{ij} could be +ve or -ve)

May generalized M_{ij} to:

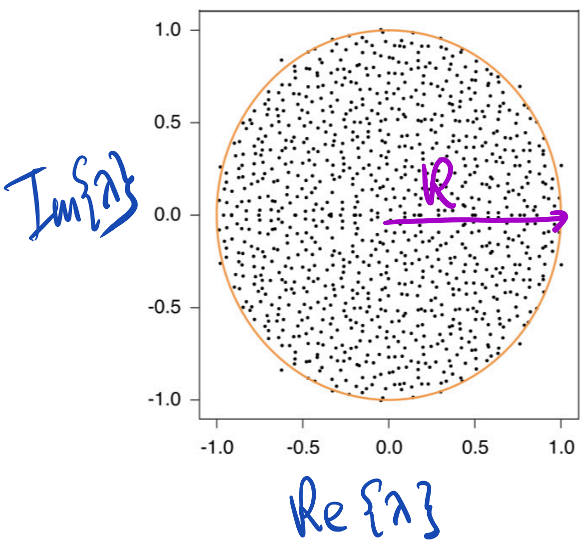
$$M_{ii} = -1, \quad M_{i \neq j} = \begin{cases} 0 & \text{with prob } 1-c \\ \text{random \#} & \text{with prob } c \end{cases}$$

from dist with variance σ^2

attempt to mimic the sparse and random nature of species-species interaction

i) Invoked/guessed "circular law"

for $N \times N$ random matrix A where each matrix element A_{ij} is real and correlated whose distribution has mean $= 0$, var $= \sigma^2$, in the limit $N \to \infty$, eigenvalue λ_k is populated uniformly in a disc in the complex plane, with radius $R = \sigma\sqrt{N}$ (proved for arb. dist. by Terence Tao, 2010)

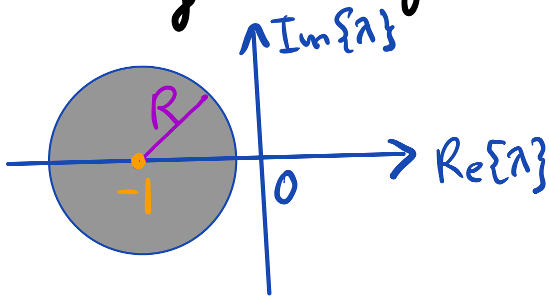


Eigenvalues of a 1000×1000 matrix generated with each element drawn from a Gaussian dist with mean $= 0$ and variance $= 1/1000$

ii) generalization:

- only a fraction c of non-zero entries $\to R = \sigma\sqrt{c \cdot N}$

- $M_{ij} = A_{ij} - \delta_{ij}$, $\lambda \to \lambda - 1$.



$\max \mathrm{Re}\{\lambda\} = R - 1 < 0$

$\Rightarrow R < 1$

or $\sigma\sqrt{cN} < 1$

- Regardless of how sparse the matrix ($C \ll 1$) and how weak the interaction ($\sigma \ll 1$), for sufficiently large N, this system becomes unstable!
- Posed a challenging question for the coexistence of many species in interacting community.

iii) Recent progress (Allesina & Tang, 2010)

include correlation between M_{ij} and M_{ji}

let $\langle M_{ij} M_{ji} \rangle = \rho \sigma^2$. $\langle M_{ij}^2 \rangle = \sigma^2$

+ve correlation
-ve anti-correlation

get "elliptical law"

with $|\mathrm{Re}\{\lambda\}| < (1+\rho)\sigma\sqrt{CN}$

$|\mathrm{Im}\{\lambda\}| < (1-\rho)\sigma\sqrt{CN}$

→ for anti-correlated interactions (e.g. fox/hare)

$\rho < 0$, so $1+\rho < 1$; improved stability

We will see that biologically realistic interaction matrix (e.g. consumer-resource model) can have much different stability criterion

C. Models of Oscillatory dynamics

1. Realistic predator-prey model

- In Sec A3, we saw that oscillatory sol'n of the Lotka-Volterra model was destroyed when carrying capacity of the prey was included. (Small prey pop drives predator to extinction)

→ observed osc in predator/prey systems?
- here: include limited "uptake capacity" by predators
- alternative: stochastic effects at low pop density

$$\frac{dp}{dt} = r\,p\left(1-\frac{p}{\tilde{p}}\right) - \nu q\, p/(1+p/p_K)$$

$$\frac{dq}{dt} = +\nu q\, p/(1+p/p_K) - \delta q$$

Sec A2: $\nu q = \text{const}$

Monod form for "uptake" of prey by predator

Compared to problems we have analyzed:
- the damped predator-prey system of Sec A3 is obtained by taking $p_K \to \infty$;
- the single-species predation problem (Sec A2) is obtained by setting $\nu q = \text{constant}$.

✱ Make dimensionless (Same notation as Sec A3)

$$u = P/\tilde{P} \qquad v = \frac{\gamma Q}{r}, \qquad \frac{P_K}{\tilde{P}} = \kappa$$

$$\tau = r \cdot t, \qquad \frac{\delta}{\gamma \tilde{P}} = \eta$$

max predator growth rate (when prey at carrying capacity)

$$\begin{cases} \dfrac{du}{d\tau} = u(1-u) - \dfrac{uv}{1+u/\kappa} = f(u,v) \\[2ex] \dfrac{r}{\delta}\dfrac{dv}{d\tau} = \dfrac{v}{\eta}\left(\dfrac{u}{1+u/\kappa} - \eta\right) = g(u,v) \end{cases}$$

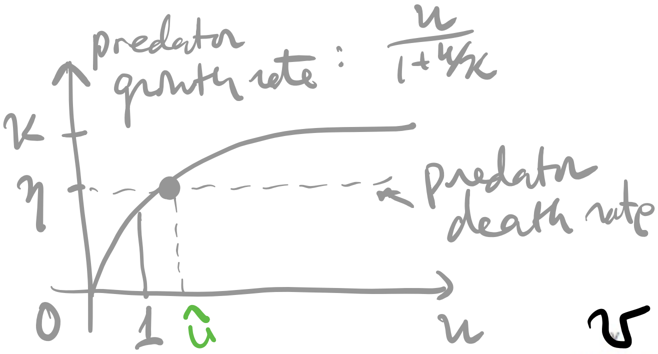
time scale doesn't affect phase boundary but affects eigenvalue.

null clines : $f(u,v)=0$; $u=0$; $v = (1-u)\cdot(1+u/\kappa) \equiv \hat{v}(u)$

$g(u,v)=0$ $\quad v=0,\ u = \eta(1+u/\kappa)$

$\hookrightarrow u = \dfrac{1}{\eta^{-1}-\kappa^{-1}} \equiv \hat{u}$

predator extinct if $\eta > \kappa$

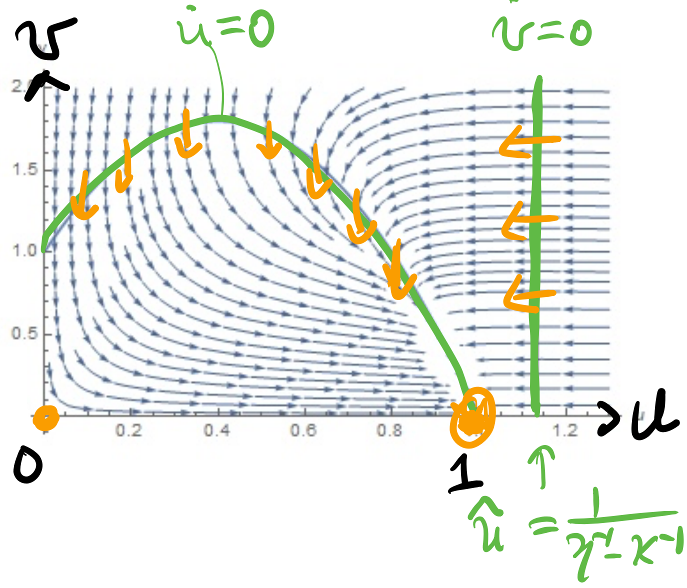


If $\hat{u} > 1$ $\left(\eta^{-1} - \kappa^{-1} < 1, \text{ or } \eta > \frac{\kappa}{\kappa+1}\right)$

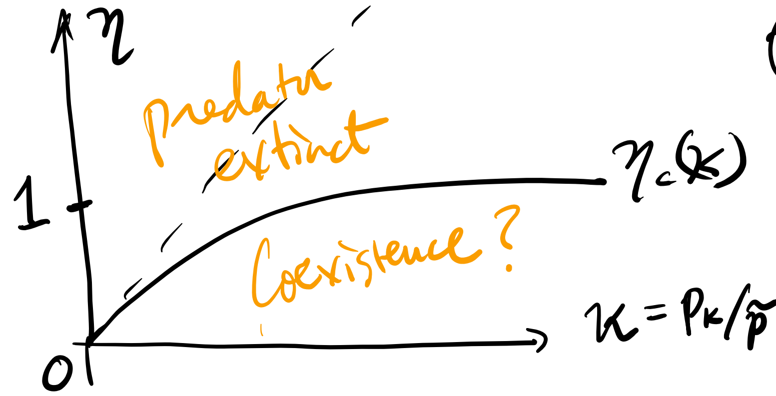
then $u^* = 1, v^* = 0$ is only nontrivial f.p.

→ predator extinct,

prey at carrying capacity



* Overview of phase diagram

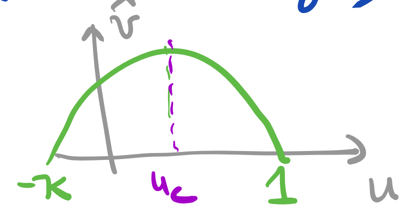


Next, the regime $\eta < \eta_c(\kappa) = \frac{\kappa}{1+\kappa}$ where $u^* = \hat{u} = \frac{1}{\eta^{-1}-\kappa^{-1}} < 1$

$\Rightarrow$ 3 cases depending on the shape of the isocline (controlled by κ)

$$\hat{v}(u) = (1-u)\cdot(1+u/\kappa).$$

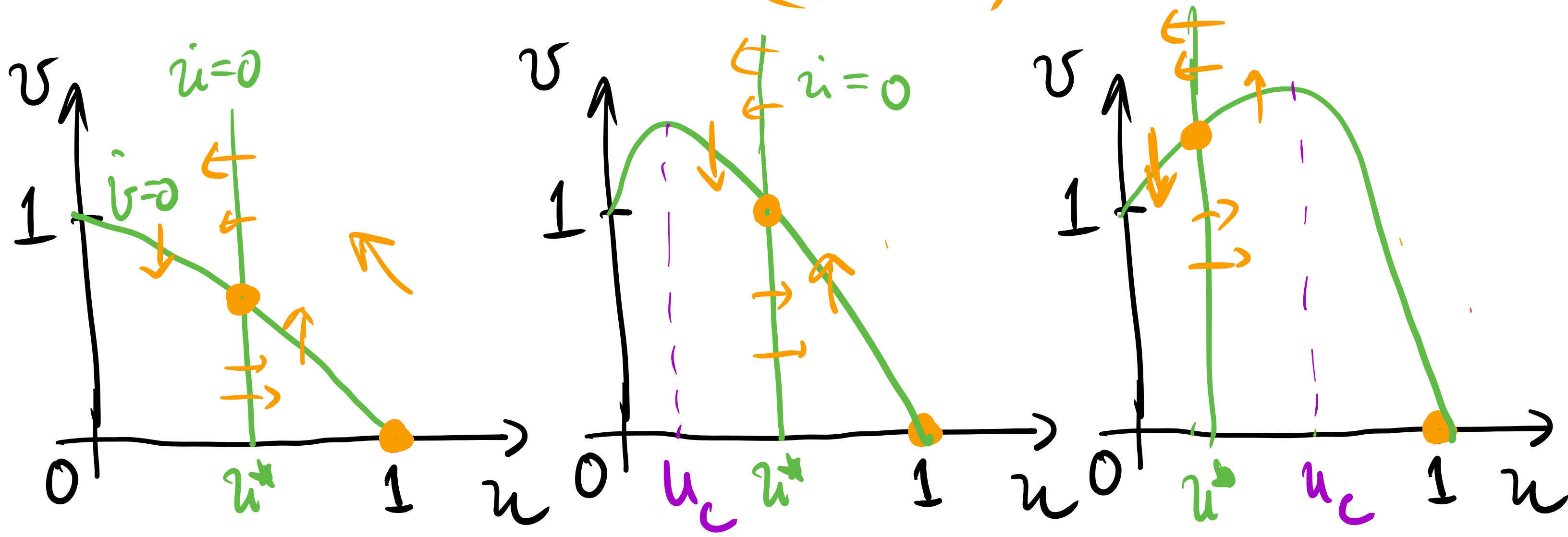
$$\text{max:} \quad \left.\frac{d\hat{v}}{du}\right|_{u_c} = 0 \to u_c = \frac{1-\kappa}{2}$$



Case ①: $\kappa > 1 \to u_c < 0$

Case ②: $\kappa < 1 \to u_c > 0$ $(u^* > u_c)$

Case ③: $\kappa < 1 \to u_c > 0$ $(u^* < u_c)$



will show below that ③ $\to$ stable oscillation

* Algebraic analysis:

Work out the community matrix at fixed pt (u^*, v^*)

Let $u = u^* + x$, $v = v^* + y$

$$\frac{du}{d\tau} = f(u,v) \qquad \frac{dv}{d\tau} = \frac{\delta}{r} g(u,v) \quad \xrightarrow{\text{linearize}} \quad \begin{pmatrix} \frac{dx}{d\tau} \\ \frac{dy}{d\tau} \end{pmatrix} = \underbrace{\begin{pmatrix} \frac{\partial f}{\partial u} & \frac{\partial f}{\partial v} \\ \frac{\delta}{r}\frac{\partial g}{\partial u} & \frac{\delta}{r}\frac{\partial g}{\partial v} \end{pmatrix}_{u^*, v^*}}_{M} \begin{pmatrix} x \\ y \end{pmatrix}$$

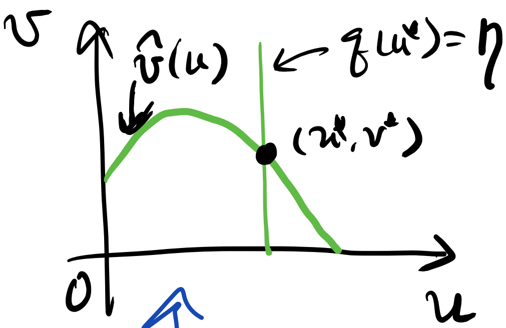
$$f(u,v) = p(u) - v\, q(u) \qquad p(u) = u \cdot (1-u)$$

$$g(u,v) = \left(\frac{1}{\eta} q(u) - 1\right) \cdot v \qquad q(u) = u / (1 + u/\kappa)$$

For the nontrivial fixed pt $(u^* > 0,\ v^* > 0)$

$$\begin{cases} g = 0 \to q(u^*) = \eta \\ f = 0 \to \hat{v}(u) = \dfrac{p(u)}{q(u)} = (1-u)(1+\frac{u}{\kappa}) \end{cases}$$

$$v^* = \frac{p(u^*)}{q(u^*)} = \frac{1}{\eta} p(u^*)$$



Evaluate derivative at fixed pt:

$$\frac{\partial f}{\partial u} = p' - v^* q' = p' - \frac{p(u^*)}{q(u^*)} q'$$

$$= q \cdot \frac{q p' - p q'}{q^2}\bigg|_{u^*} = q(u^*) \frac{d\hat{v}}{du}\bigg|_{u^*} = \eta \cdot \frac{d\hat{v}}{du}\bigg|_{u^*}$$

derivative of $\hat{v}(u)$ at fixed pt.

$$\frac{\partial f}{\partial v} = -q(u^*) = -\eta, \quad \frac{\partial g}{\partial v} = \frac{1}{\eta} q(u^*) - 1 = 0$$

$$\frac{\partial g}{\partial u} = \frac{v^*}{\eta} q'(u^*) = \frac{v^*}{\eta} \cdot \frac{1}{(1+u^*/\kappa)^2} = \frac{v^*}{u^*(1+u^*/\kappa)} = \frac{1-u^*}{u^*}$$

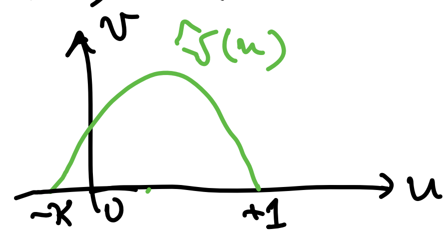
$$\boxed{q(u) = \frac{u}{1+u/\kappa}; \quad q' = \frac{1 + \cancel{u/\kappa} - \cancel{u/\kappa}}{(1+u/\kappa)^2}}$$

$$q(u^*) = \frac{u^*}{1+u^*/\kappa} = \eta$$

$$v^* = (1-u^*)(1+\frac{u^*}{\kappa})$$

Thus, $M = \begin{pmatrix} \eta \left.\frac{d\hat{v}}{du}\right|_{u^*} & -\eta \\ \frac{\delta}{r}\frac{1-u^*}{u^*} & 0 \end{pmatrix}$ where $u^* = \frac{1}{\eta^{-1}-\kappa^{-1}}$

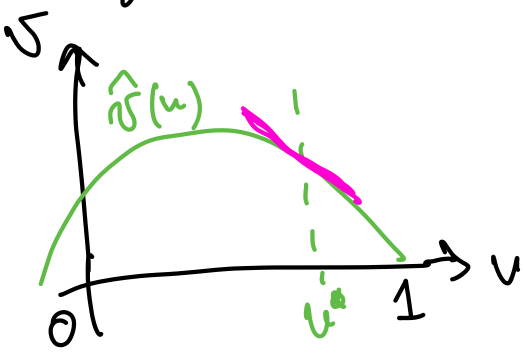
$\hat{v}(u) = (1-u)\cdot(1+u/\kappa)$



$$\det(M-\lambda I)=0 \rightarrow \lambda^2 - \eta \left.\frac{d\hat{v}}{du}\right|_{u^*}\lambda + \frac{\delta}{r}\eta\frac{1-u^*}{u^*} = 0$$

$$\lambda = \frac{\eta}{2}\left.\frac{d\hat{v}}{du}\right|_{u^*} \pm \sqrt{\underbrace{\left(\frac{\eta}{2}\left.\frac{d\hat{v}}{du}\right|_{u^*}\right)^2 - \frac{\delta}{r}\eta\frac{1-u^*}{u^*}}_{\Delta < \left(\frac{\eta}{2}\left.\frac{d\hat{v}}{du}\right|_{u^*}\right)^2 \text{ for } 0<u^*<1}}$$

* for $\left.\frac{d\hat{v}}{du}\right|_{u^*} < 0$ (and $0<u^*<1$).



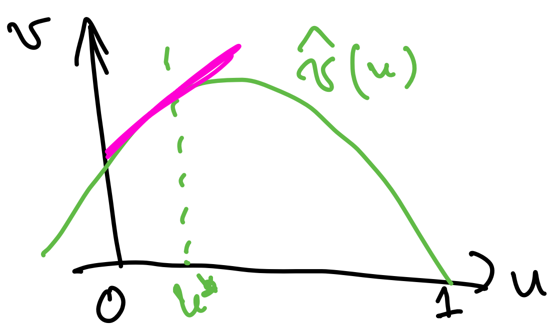
if $\Delta > 0$, $\lambda_\pm < 0$

Stable fixed pt

if $\Delta < 0$, $\lambda = -\frac{\eta}{2}\left|\frac{d\hat{v}}{du}\right| \pm i\sqrt{|\Delta|}$

damped oscillation

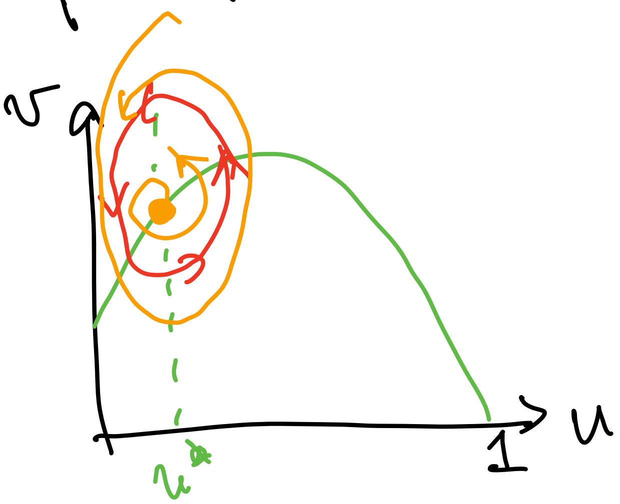
* for $\left.\frac{d\hat{v}}{du}\right|_{u^*} > 0$



it can be shown (p.38) that $\Delta < 0$ if $\left.\frac{d\hat{v}}{du}\right|_{u^*} > 0$

then $\lambda = +\frac{\eta}{2}\frac{d\hat{v}}{du} \pm i\sqrt{|\Delta|}$

phase flow in this case: expanding oscillation



Poincare-Bendixson Theorem: if $Re\{\lambda\}>0$ and $Im\{\lambda\}\neq 0$, and further if u, v are bounded, then 2d flow $\rightarrow$ limit cycle

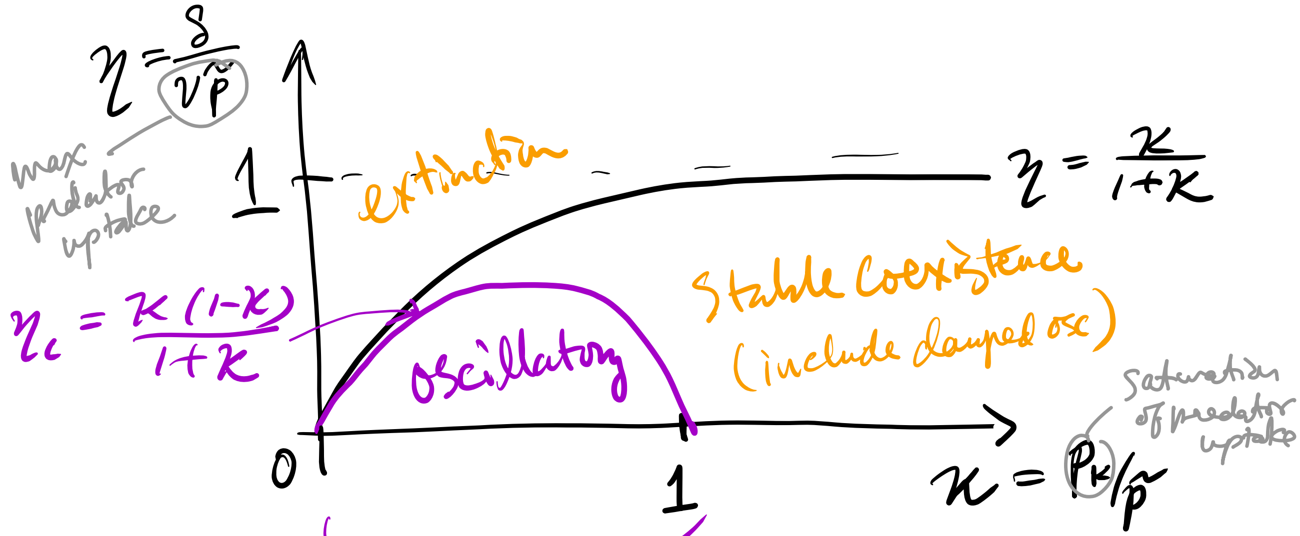
Criterion for stable oscillation: $Re(\lambda)>0$ or $\left.\frac{d\hat{v}}{du}\right|_{u^*}>0$

$$\Rightarrow \left.\frac{d\hat{v}}{du}\right|_{u^*} = -\left(1+\frac{u^*}{\kappa}\right)+\frac{1}{\kappa}\left(1-u^*\right) = \frac{1}{\kappa}-1-\frac{2}{\kappa}u^*$$

$$= \frac{2}{\kappa}\left(u_c - u^*\right) \quad \text{where } u_c = \frac{1-\kappa}{2}$$

$$\Rightarrow \text{Stable osc for } u^* = \frac{1}{\eta^{-1}-\kappa^{-1}} < u_c = \frac{1-\kappa}{2}$$

$$\rightarrow \eta < \eta_c = \frac{\kappa(1-\kappa)}{1+\kappa}$$



$0 < p_K < \tilde{p}$ predator uptake limited

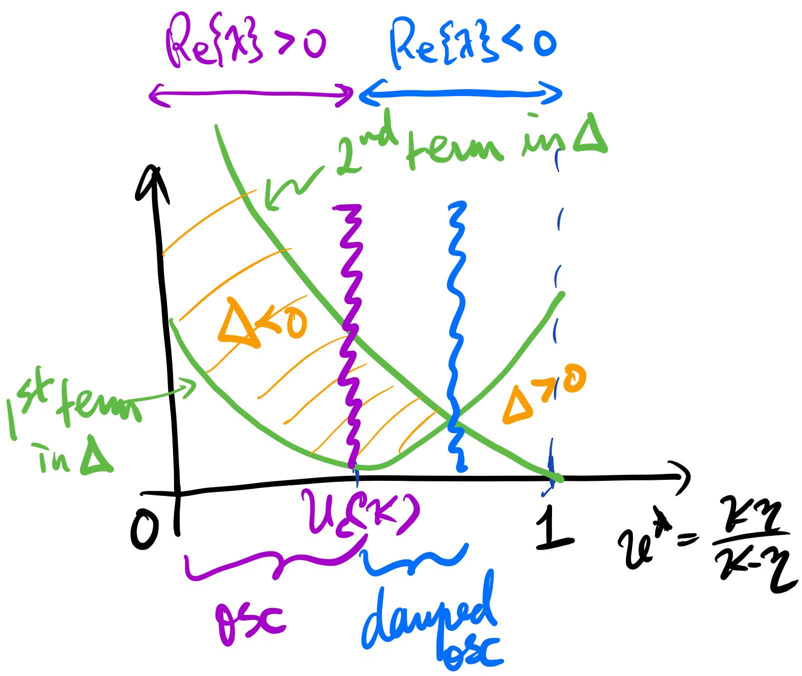
$\eta \ll 1$, or $\delta \ll \nu\tilde{p}$
predator death limited

* Calculate the determinant $\Delta = \left(\frac{\eta}{2}\frac{d\hat{v}}{du}\Big|_{u^*}\right)^2 - \eta\frac{\delta}{r}\frac{1-u^*}{u^*}$ (38)

$$\frac{d\hat{v}}{du}\Big|_{u^*} = \frac{2}{\kappa}\left(u_c(\kappa) - u^*\right);$$

$$\Rightarrow \Delta = \left[\frac{\eta}{\kappa}\left(u_c(\kappa) - u^*\right)\right]^2 - \frac{\delta}{r}\eta\frac{1-u^*}{u^*}$$

- To see how Δ depends on u^*, plot each term in Δ for fixed κ.



Final phase diagram

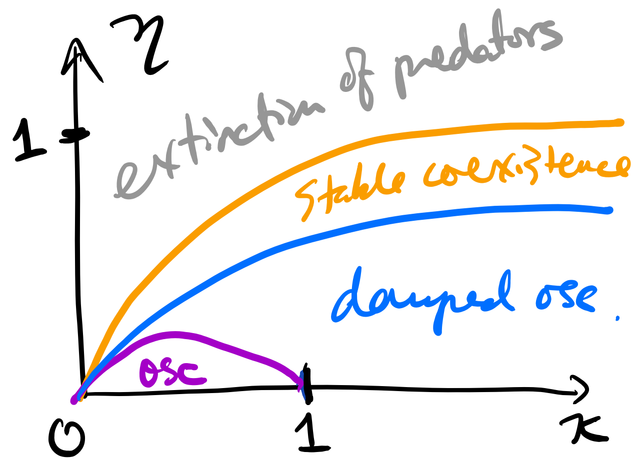


Illustration of numerical flow diagram