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: νq = 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 predation problem (Sec A2) is obtained by setting νq = constant.

* Make dimensionless (Same notation as in Sec A3)

$$u = P/\tilde{P}, \quad v = \frac{\nu q}{r}, \quad \frac{P_K}{\tilde{P}} = \kappa$$

$$\tau = r\cdot t, \quad \frac{\delta}{\nu\tilde{P}} = \eta$$

max predator growth rate (when prey at carrying capacity)

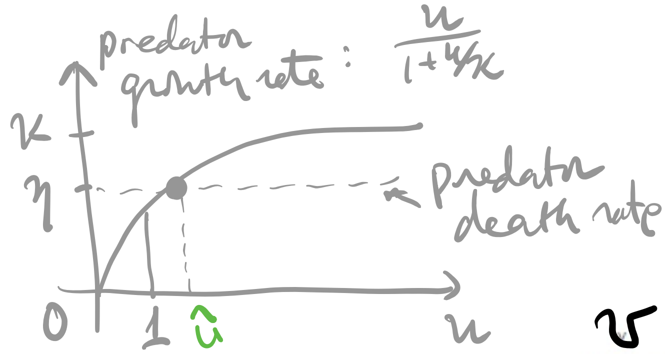
$$\begin{cases} \dfrac{du}{d\tau} = u(1-u) - \dfrac{uv}{1+u/\kappa} = f(u,v) \\[2ex] \dfrac{r}{\delta}\dfrac{dv}{d\tau} = \dfrac{v}{\eta}\left(\dfrac{u}{1+u/\kappa} - \eta\right) = g(u,v) \end{cases}$$

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

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

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

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



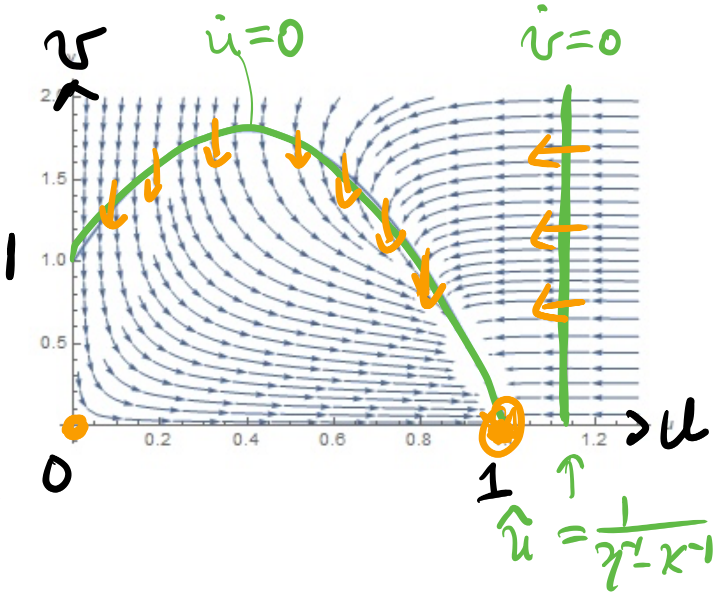
predator extinct if $\eta > \kappa$

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

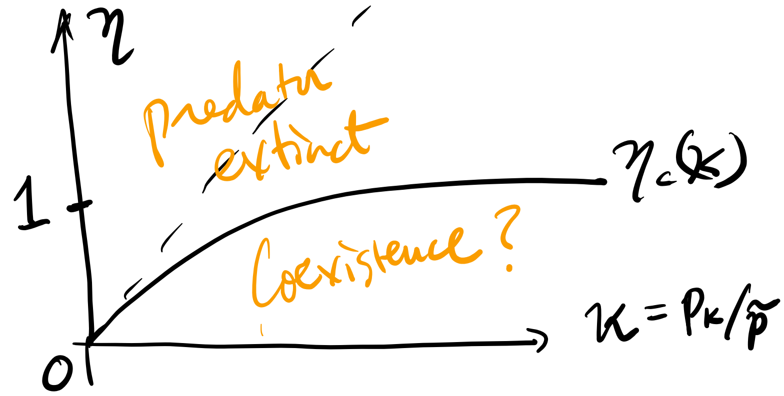
then $u^*=1, v^*=0$ is only nontrivial f.p.

$\rightarrow$ predator extinct,

prey at carrying capacity



* Overview of phase diagram

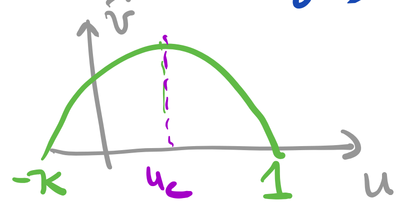


Next, the regime $\eta < \eta_c(\kappa) = \frac{\kappa}{1+\kappa}$ where $u^* = \hat{u} = \frac{1}{\eta^{-1} - \kappa^{-1}} < 1$

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

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

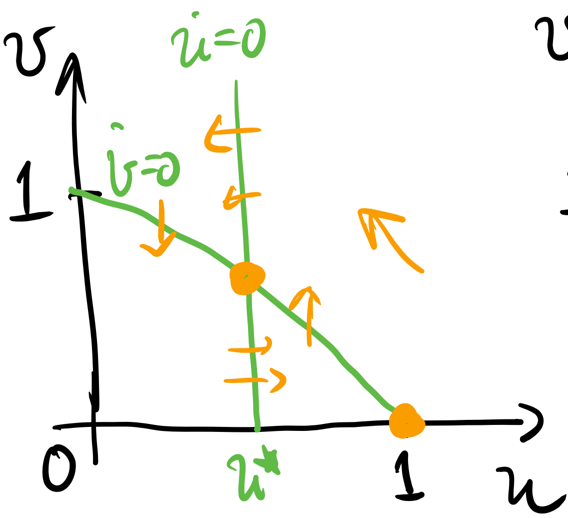
max: $\left.\frac{d\hat{v}}{du}\right|_{u_c} = 0 \to u_c = \frac{1-\kappa}{2}$

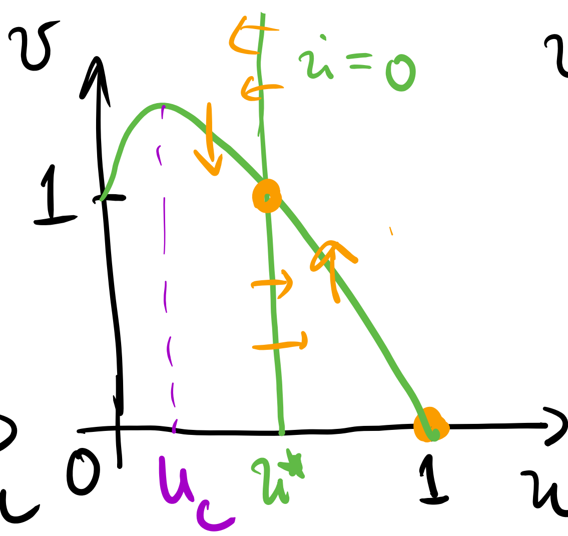


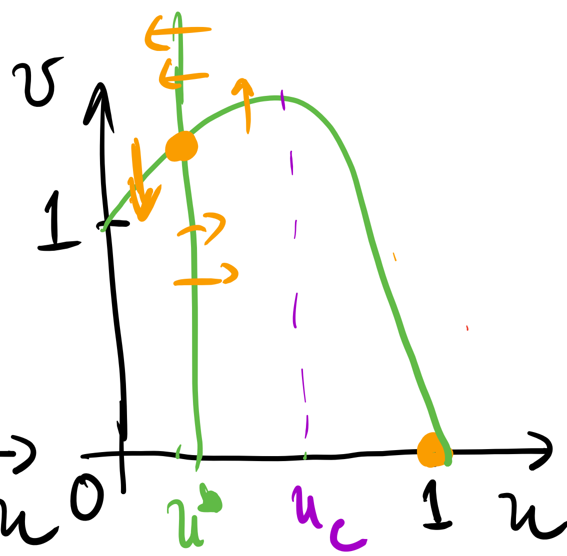
Case ①: $\kappa > 1 \to u_c < 0$

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

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



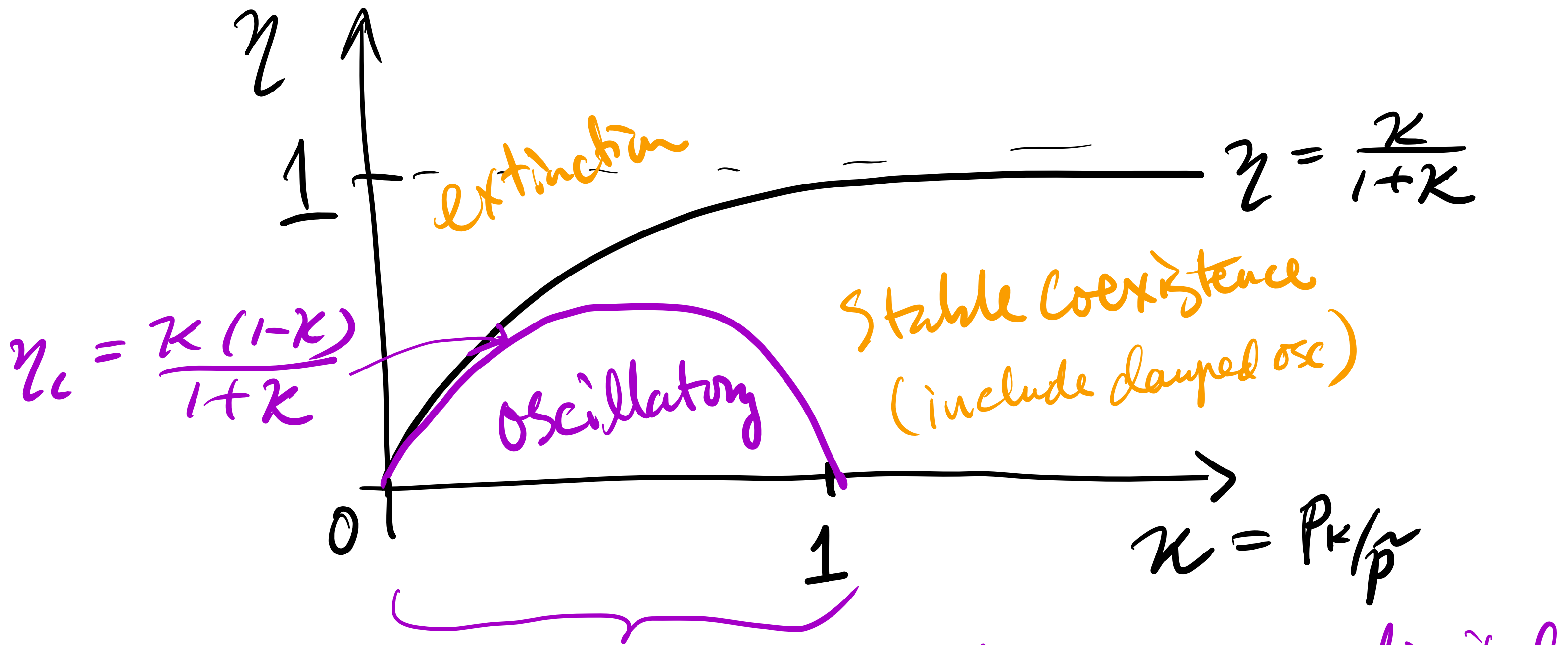




$\to$ $u^* = u_c$ occurs at $\frac{1}{\eta_c^{-1} - \kappa^{-1}} = \frac{1-\kappa}{2}$

$$\eta_c^{-1} = \frac{2}{1-\kappa} + \kappa^{-1} = \frac{1+\kappa^{-1}}{1-\kappa} \quad \text{or} \quad \eta_c = \frac{\kappa(1-\kappa)}{1+\kappa}$$

Will show below that case (3) $\to$ stable limit cycle



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

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

predator death limited

* Algebraic analysis:

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

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

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

$$\frac{dv}{d\tau} = \frac{\delta}{r} g(u,v)$$

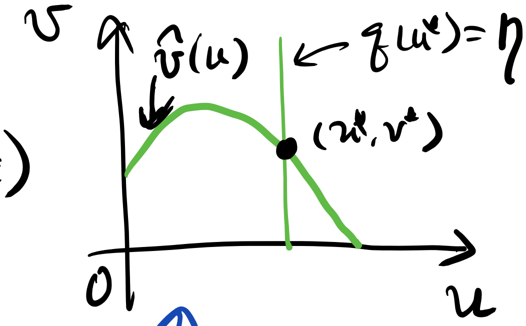
$f(u,v) = p(u) - v\, q(u)$ | $p(u) = u\cdot(1-u)$

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

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

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

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



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

Evaluate derivative at fixed pt:

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

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

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

$$\frac{\partial g}{\partial u} = \frac{1}{\eta} v^* q'$$

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

$$M = \begin{pmatrix} \eta \frac{d\hat{v}^*}{du} & -\eta \\ \frac{\delta}{r} \frac{v^*}{\eta} q' & 0 \end{pmatrix}$$

$$\det(M - \lambda I) = 0 \rightarrow \boxed{\lambda^2 - \eta \frac{d\hat{v}^*}{du} \lambda + \frac{\mu}{r} v^* q' = 0}$$

$$\lambda = \frac{\eta}{2}\frac{d\hat{v}^*}{du} \pm \sqrt{\underbrace{\left(\frac{\eta}{2}\frac{d\hat{v}^*}{du}\right)^2 - \frac{\delta}{r} v^* q'}_{\Delta}}$$

$$q(u) = \frac{u}{1+u/\kappa}; \quad q' = \frac{1+\cancel{u/\kappa} - \cancel{u/\kappa}}{(1+u/\kappa)^2} > 0 \Rightarrow \Delta < \left(\frac{\eta}{2}\frac{dv^*}{du}\right)^2$$

$$\hat{v}(u) = \frac{p(u)}{q(u)} = (1-u)(1+u/\kappa)$$

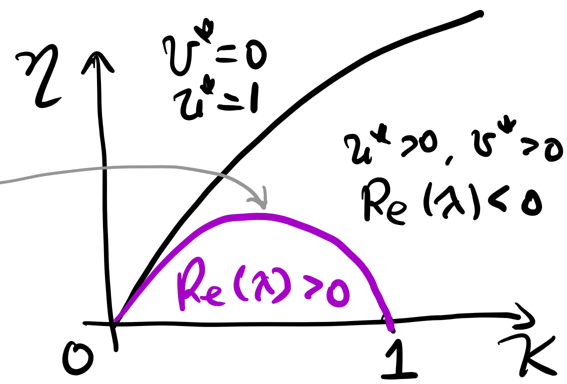
$$\frac{d\hat{v}^*}{du} = \frac{2}{\kappa}\Big(\underbrace{\frac{1-\kappa}{2}}_{u_c} - u^*\Big) = \frac{2}{\kappa}(u_c - u^*)$$

- if $\frac{d\hat{v}^*}{du} < 0$ (for $u^* > u_c$), $\lambda = -\left|\frac{\eta}{2}\frac{dv^*}{du}\right| \pm \sqrt{\Delta}$, $Re\,\lambda < 0$

→ (u^*, v^*) is stable

Condition: $u^* > u_c$,

$\frac{1}{\eta^{-1}-\kappa^{-1}} > \frac{1-\kappa}{2} \to \eta > \kappa\frac{1-\kappa}{1+\kappa}$



→ further calculate Δ to find regimes for stable coexistence ($\Delta>0$) or damped osc ($\Delta<0$)

- if $\frac{d\hat{v}^*}{du} > 0$ ($u^* < u_c$), $\lambda = \left|\frac{\eta}{2}\frac{dv^*}{du}\right| \pm \sqrt{\Delta} > 0$

→ to show the limit cycle, need to show $\Delta < 0$

* Calculate the determinant $\Delta = \left(\frac{\eta}{2}\frac{d\hat{v}^*}{du}\right)^2 - \frac{\delta}{r} v^* q'$

$\frac{dv^*}{du} = \frac{2}{\kappa}\left(u_c(\kappa) - u^*\right)$;

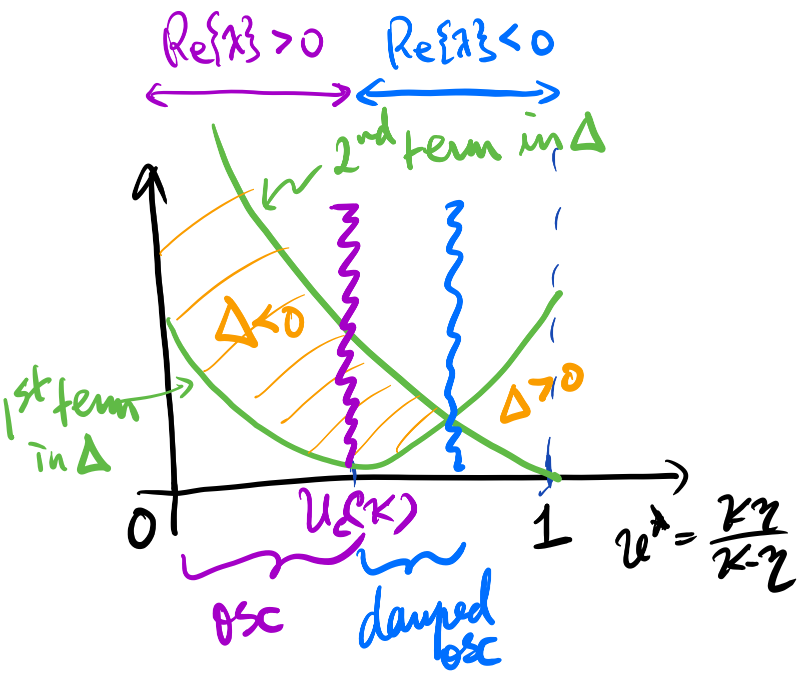
$u^* = \frac{1}{\eta^{-1} - \kappa^{-1}}$

$q' = \frac{1}{(1 + u^*/\kappa)^2} \longrightarrow q' = (\eta/u^*)^2$

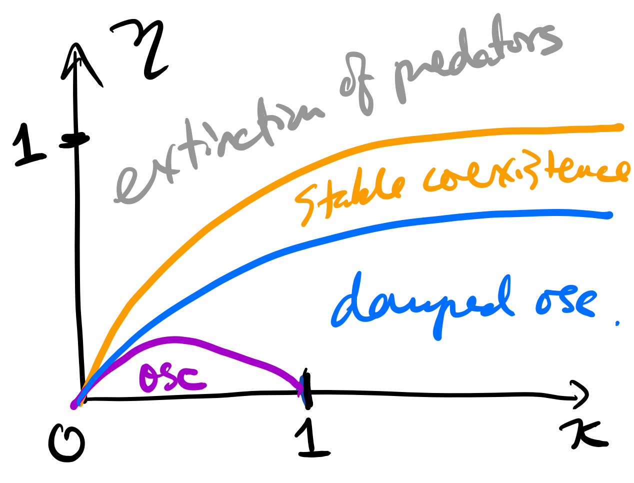
$v^* = \frac{p(u^*)}{q(u^*)} = \frac{u^*(1-u^*)}{\eta}$; 2^{nd} term in $\Delta = \frac{\delta}{r}\eta \frac{(1-u^*)}{u^*}$

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

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

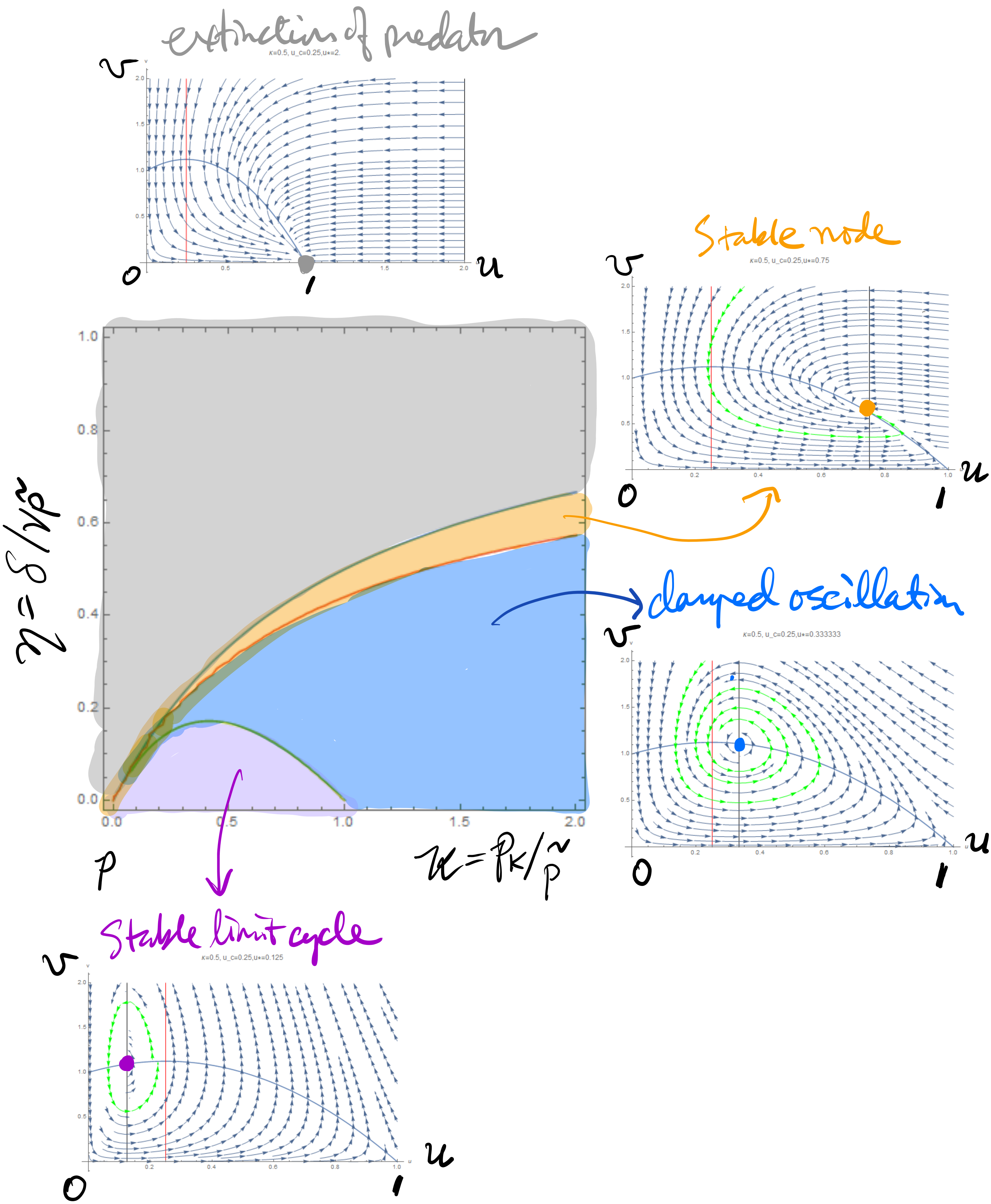


Final phase diagram



* finally, for large u, v, $\dot{u} = -u^2 - \# v$; $\dot{v} = -\# v$

Poincare-Bendixson Theorem: Stable limit cycle for $\Delta < 0$ and $Re(\lambda) > 0$.


extinction of predator
κ=0.5, u_c=0.25,u*=2.
Stable node
κ=0.5, u_c=0.25,u*=0.75
damped oscillation
κ=0.5, u_c=0.25,u*=0.333333
Stable limit cycle
κ=0.5, u_c=0.25,u*=0.125
$\eta = \delta/\nu\tilde{p}$
$\kappa = p_K/\tilde{p}$
v
u
0
1