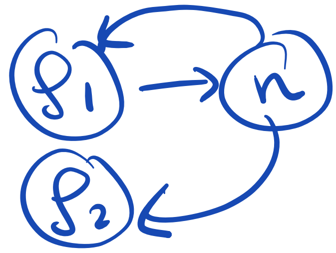
c) Multiple species: "Cheaters" (parasitism)

– 2 species, 1 nutrient



$$\dot\rho_1 = r_1(n)\rho_1 - \mu\rho_1 \qquad r_i(n) = r_i^0 \frac{n}{n+K_i}$$

$$\dot\rho_2 = r_2(n)\rho_2 - \mu\rho_2$$

$$\dot n = \gamma_1\rho_1 - \mu n - r_1(n)\rho_1/Y - r_2(n)\rho_2/Y$$

↖ produced only by species 1 (called "producer")

Consider $\gamma Y \ll r_i^0 \;\to\; n^* \ll K$; use $r_i(n) \simeq \frac{r_i^0 n}{K_i} = \nu_i n$

· rapid equil of n ($\dot n = 0$).

$$\gamma_1\rho_1 \cong n^*\left[\mu + (\nu_1\rho_1 + \nu_2\rho_2)/Y\right]$$

$$n^* \simeq \frac{\gamma_1\rho_1 Y}{\mu Y + \nu_1\rho_1 + \nu_2\rho_2}$$

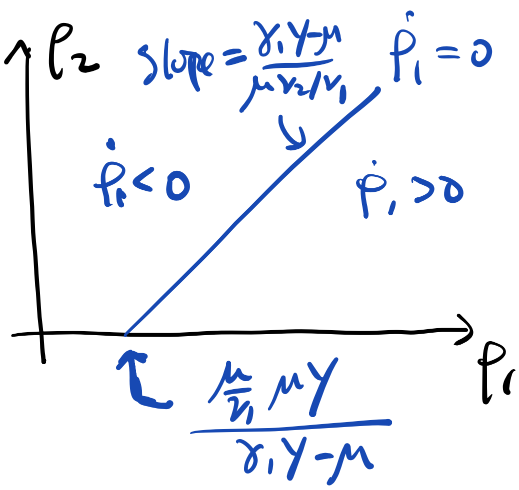
from $\dot\rho_1 = (\nu_1 n - \mu)\rho_1$,

the critical pt for the growth of ρ_1 is at

$n^*(\rho_1^c, \rho_2^c) = \mu/\nu_1$ (where $\dot\rho_1/\rho_1 = 0$)

$$\gamma_1\rho_1^c Y = \frac{\mu}{\nu_1}\cdot\mu Y + \mu\rho_1^c + \mu\frac{\nu_2}{\nu_1}\rho_2^c$$

$$\rho_2^c = \frac{(\gamma_1 Y - \mu)\rho_1^c - \frac{\mu}{\nu_1}\mu Y}{\mu\nu_2/\nu_1} \qquad (1)$$



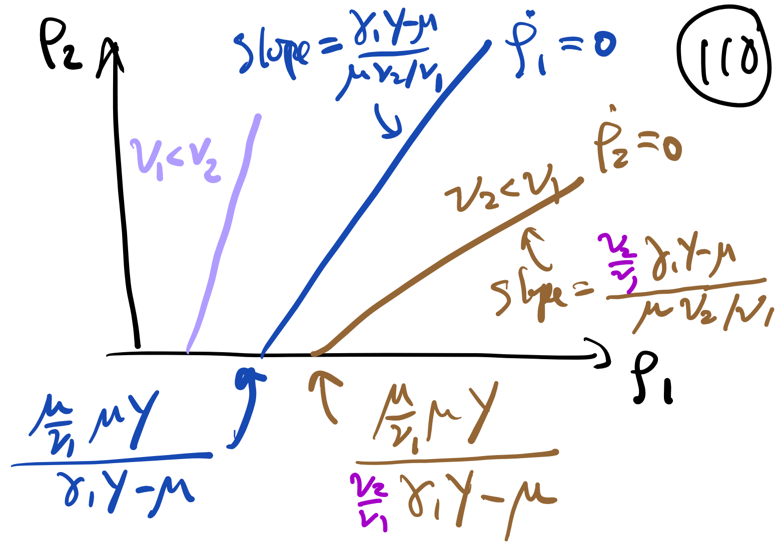
→ uptake by Sp 2 (i.e. $\nu_2 > 0$)

increases growth threshold for sp 1

Next, $\dot{\rho}_2 = (\nu_2 n^* - \mu)\cdot \rho_2$

$$n^*(\rho_1^c, \rho_2^c) = \frac{\mu}{\nu_2} = \frac{\mu}{\nu_1}\cdot\frac{\nu_1}{\nu_2}$$

$$\rightarrow \rho_2^c = \frac{\left(\frac{\nu_2}{\nu_1}\gamma_1 Y - \mu\right)\rho_1^c - \frac{\mu}{\nu_1}\mu Y}{\mu \nu_2/\nu_1}$$



phase flow:

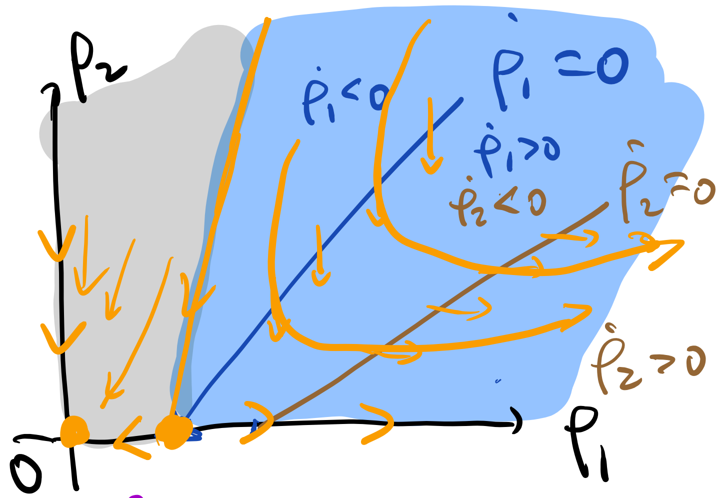
$$\dot{\rho}_1 = \rho_1\left[\nu_1 \frac{\gamma_1 \rho_1 Y}{\mu Y + \nu_1\rho_1 + \nu_2\rho_2} - \mu\right]$$

$$\dot{\rho}_2 = \rho_2\left[\nu_2 \frac{\gamma_1 \rho_1 Y}{\mu Y + \nu_1\rho_1 + \nu_2\rho_2} - \mu\right]$$

for $\nu_1 > \nu_2$, $\dot{\rho}_1 > 0$ where $\dot{\rho}_2 = 0$

$\dot{\rho}_2 < 0$ where $\dot{\rho}_1 = 0$

$\nu_1 > \nu_2$



→ Allee effect involves combo of $\rho_1(0), \rho_2(0)$

→ Sp 2 enlarges the region of extinction

$\rho_1(0) > \rho_1^c(\rho_2 = 0) = \frac{\mu}{\nu_1}\mu Y/(\gamma_1 Y - \mu)$ [find boundary in HW]

growth phase:

at conc n^*, $\lambda_1 = \nu_1 n^* - \mu > \lambda_2 = \nu_2 n^* - \mu$

$$\rho_1 \propto e^{\lambda_1 t} \gg \rho_2 \propto e^{\lambda_2 t}$$

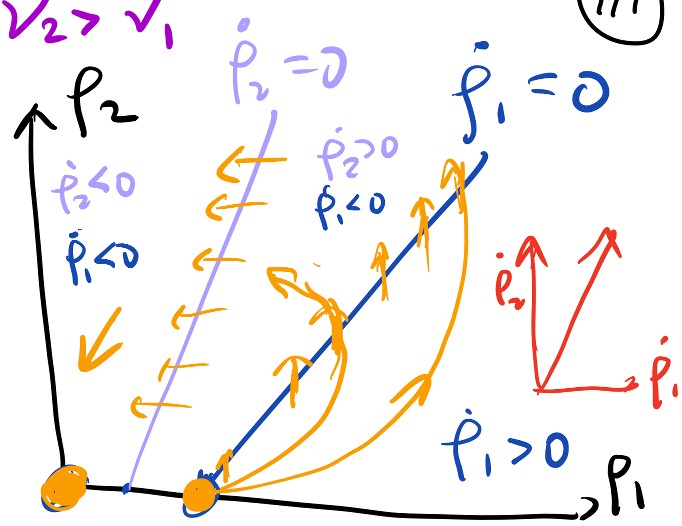
$$\rightarrow n^* = \frac{\gamma_1 \rho_1(t) Y}{\mu Y + \nu_1 \rho_1(t) + \nu_2 \rho_2(t)} \overset{t\to\infty}{=} \frac{\gamma_1 Y}{\nu_1}$$

⇒ Sp 2 gets a free ride at $\lambda_2 = \frac{\nu_2}{\nu_1}\gamma_1 Y - \nu$.

⇒ does not affect growth of sp 1 (in growth phase) for $\nu_2 > \nu_1$,

$\dot{\rho}_2 > 0$ where $\dot{\rho}_1 = 0$

$\dot{\rho}_1 < 0$ where $\dot{\rho}_2 = 0$



$\Rightarrow$ excitable dynamics

for $\rho_1(0) > \rho_1^c$, $\rho_2(0) > 0$.

eventually headed for extinction

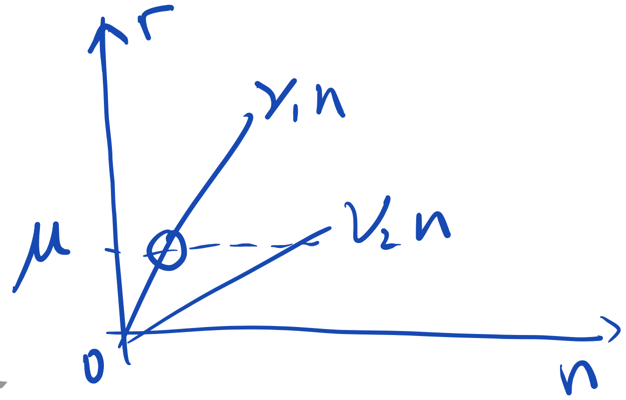
$\Rightarrow$ increasing ν_2 increases fitness of cheater; but too much will drive sp2 extinct (blackjack)

[Assume growth phase exists. $n = n^*$.

then $\lambda_2 = \nu_2 n^* - \mu > \lambda_1 = \nu_1 n^* - \mu$ if $\nu_2 > \nu_1$

$$\rightarrow n^* = \frac{\gamma_1 \rho_1(t)}{\mu Y + \nu_1 \rho_1(t) + \nu_2 \rho_2(t)} \simeq \frac{\gamma_1}{\nu_2} e^{(\lambda_1 - \lambda_2)t} \rightarrow 0$$

This scenario can be anticipated from 2-species on one nutrient in chemostat.



- Species with large ν survives.
- If $\nu_2 > \nu_1$, then $\rho_1 \to 0$ but ρ_2 cannot exist alone

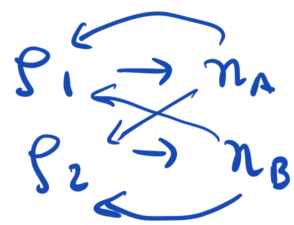
$\Rightarrow$ no stable state if $\nu_2 > \nu_1$]

d) Cross-feeding of self-generated essential nutrients (112)

- Species 1, 2 generates nutrient A, B respectively
- each species need <u>both</u> nutrients to grow (e.g. A = carbon, B = Fe)

$$\dot{\rho}_1 = \left(r_1(n_A, n_B) - \mu\right)\rho_1$$

$$\dot{\rho}_2 = \left(r_2(n_A, n_B) - \mu\right)\rho_2$$



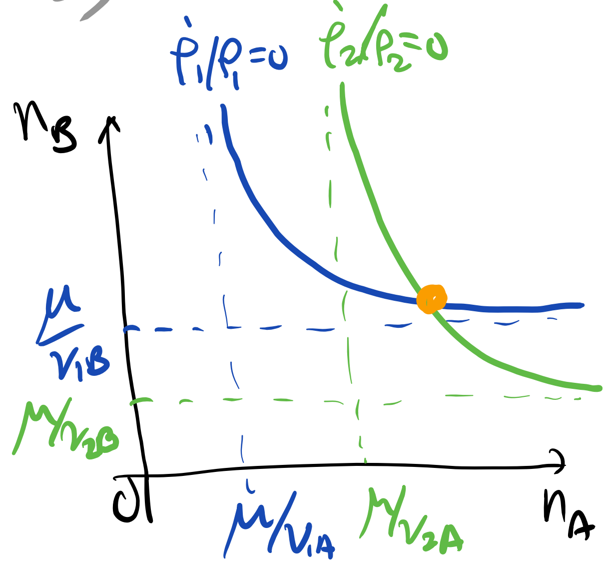
$$\dot{n}_A = \gamma_{1A}\rho_1 - \mu n_A - r_1(n_A, n_B)\rho_1 / Y_A - r_2(n_A, n_B)\rho_2 / Y_A$$

$$\dot{n}_B = \gamma_{2B}\rho_2 - \mu n_B - r_1(n_A, n_B)\rho_1 / Y_B - r_2(n_A, n_B)\rho_2 / Y_B$$

growth function: (from Sec II A1)

$$r_i \simeq \left(\frac{1}{\nu_{iA} n_A} + \frac{1}{\nu_{iB} n_B}\right)^{-1}$$

for $n_\alpha \ll K_{\alpha_i}$ (for $\gamma_\alpha Y_\alpha \ll r_i^0$)



$$\dot{\rho}_1/\rho_1 = 0 \rightarrow \frac{1}{\mu} = \frac{1}{\nu_{1A} n_A} + \frac{1}{\nu_{1B} n_B}$$

$$\dot{\rho}_2/\rho_2 = 0 \rightarrow \frac{1}{\mu} = \frac{1}{\nu_{2A} n_A} + \frac{1}{\nu_{2B} n_B}$$

- fixed pt soln generically exist if $\nu_{1\alpha} \neq \nu_{2\alpha}$
- expect Allee effect (since ρ_i needed to generate n_α)
  - → fixed point = saddle point (phase transition)

- work out dynamics at saddle pt
- work out steady state at high densities.

★ Workout dynamics around nontrivial fixed point

$$\left.\begin{aligned}\dot{\rho}_1 &= \left(r_1(n_A,n_B)-\mu\right)\rho_1\\ \dot{\rho}_2 &= \left(r_2(n_A,n_B)-\mu\right)\rho_2\end{aligned}\right\} \quad r_i \simeq \left(\frac{1}{\nu_{iA} n_A} + \frac{1}{\nu_{iB} n_B}\right)^{-1}$$

$$\dot{n}_A = \gamma_{1A}\rho_1 - \mu n_A - r_1(n_A,n_B)\rho_1/Y_A - r_2(n_A,n_B)\rho_2/Y_A$$

$$\dot{n}_B = \gamma_{2B}\rho_2 - \mu n_B - r_1(n_A,n_B)\rho_1/Y_B - r_2(n_A,n_B)\rho_2/Y_B$$

take small-μ limit (emphasizing interaction): $r_1 = r_2 = \mu \ll \gamma Y$

$$\dot{n}_A = 0 \to n_A \simeq \gamma_{1A}\rho_1/\mu; \quad \dot{n}_B = 0 \to n_B \simeq \gamma_{2B}\rho_2/\mu$$

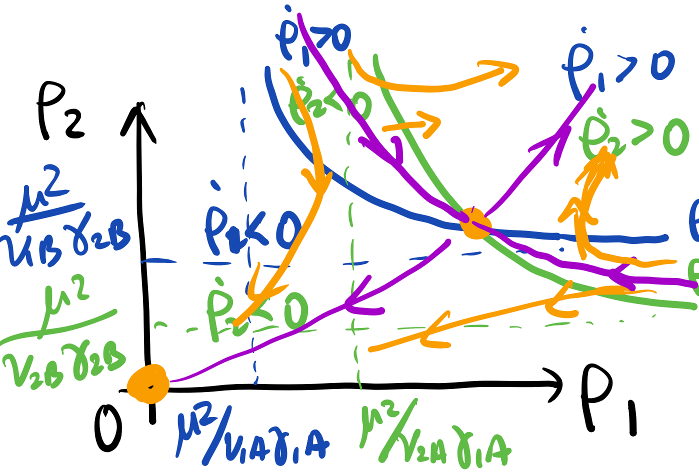
$$r_1 = \left(\frac{1}{\nu_{1A} n_A} + \frac{1}{\nu_{1B} n_B}\right)^{-1} = \left[\frac{\mu}{\nu_{1A}\gamma_{1A}\rho_1} + \frac{\mu}{\nu_{1B}\gamma_{2B}\rho_2}\right]^{-1}$$

$$r_2 = \left(\frac{1}{\nu_{2A} n_A} + \frac{1}{\nu_{2B} n_B}\right)^{-1} = \left[\frac{\mu}{\nu_{2A}\gamma_{1A}\rho_1} + \frac{\mu}{\nu_{2B}\gamma_{2B}\rho_2}\right]^{-1}$$

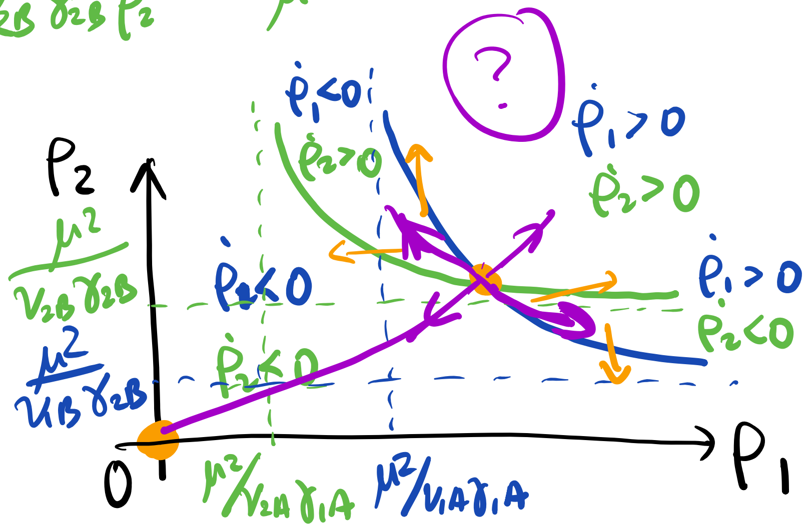
$$\dot{\rho}_1 = \rho_1\left[\frac{1}{\mu}\left(\frac{1}{\nu_{1A}\gamma_{1A}\rho_1} + \frac{1}{\nu_{1B}\gamma_{2B}\rho_2}\right)^{-1} - \mu\right]$$

$$\dot{\rho}_1/\rho_1 = 0 \Rightarrow \frac{1}{\nu_{1A}\gamma_{1A}\rho_1} + \frac{1}{\nu_{1B}\gamma_{2B}\rho_2} = \frac{1}{\mu^2}$$

$$\dot{\rho}_2/\rho_2 = 0 \Rightarrow \frac{1}{\nu_{2A}\gamma_{1A}\rho_1} + \frac{1}{\nu_{2B}\gamma_{2B}\rho_2} = \frac{1}{\mu^2}$$



$\nu_{1A} > \nu_{2A}, \ \nu_{2B} > \nu_{1B}$



$\nu_{1A} < \nu_{2A}, \ \nu_{2B} < \nu_{1B}$

$\Rightarrow$ why asymmetric? need to look at high density state

* growth phase:
  - expect $\rho_1(t) = \rho_1^* e^{\lambda_1 t}$, $\rho_2(t) = \rho_2^* e^{\lambda_2 t}$ for large t with $\lambda_1 = \lambda_2 > \mu$.
  - if not, one of the nutrients will be depleted and $\rho_1, \rho_2 \to 0$ (since both nutrient are essential)

$$\dot{n}_A = \gamma_{1A}\rho_1 - \mu n_A - r_1(n_A, n_B)\rho_1/Y_A - r_2(n_A, n_B)\rho_2/Y_A$$

$$\dot{n}_B = \gamma_{2B}\rho_2 - \mu n_B - r_1(n_A, n_B)\rho_1/Y_B - r_2(n_A, n_B)\rho_2/Y_B$$

e.g. if $\lambda_1 > \lambda_2$, then $\dot{n}_B \xrightarrow{t\to\infty} -r_1\rho_1/Y_B \to n_B^* = 0$

  - for $\lambda_1 = \lambda_2 \equiv \lambda$, must have $n_A^* > 0$, $n_B^* > 0$ such that $r_1(n_A^*, n_B^*) = r_2(n_A^*, n_B^*) = r^*$, with $\lambda = r^* - \mu$

→ plug $\rho_1(t) = \rho_1^* e^{\lambda t}$ and $\rho_2(t) = \rho_2^* e^{\lambda t}$ (large t) into nutrient flux eqns:

$$\dot{n}_A = 0 \to \mu n_A^* Y_A = [(\gamma_{1A} Y_A - r^*)\rho_1^* - r^*\rho_2^*]e^{\lambda t}$$

$$\to (\gamma_{1A} Y_A - r^*)\rho_1^* = r^*\rho_2^*$$

Similarly, $(\gamma_{2B} Y_B - r^*)\rho_2^* = r^*\rho_1^*$

$$\boxed{r^* = \left[(\gamma_{1A}Y_A)^{-1} + (\gamma_{2B}Y_B)^{-1}\right]^{-1}} < \min(\gamma_{1A}Y_A, \gamma_{1B}Y_B)$$

(n_A^*, n_B^*) fixed from $r_1(n_A^*, n_B^*) = r_2(n_A^*, n_B^*) = r^*$

Note: no dependence on $V_{i\alpha}$

Stability? set $\mu = r^*$, so that $\rho_1 \to \rho_1^*$, $\rho_2 \to \rho_2^*$ (115)

$$\dot{\rho}_1 = \left(r_1(n_A, n_B) - r^*\right)\rho_1$$
$$\dot{\rho}_2 = \left(r_2(n_A, n_B) - r^*\right)\rho_2$$
$$Y_A \dot{n}_A = \left(\gamma_{1A} Y_A - r_1(n_A, n_B)\right)\rho_1 - r_2(n_A, n_B)\rho_2$$
$$Y_B \dot{n}_B = -r_1(n_A, n_B)\rho_1 + \left(\gamma_{2B} Y_B - r_2(n_A, n_B)\right)\rho_2$$

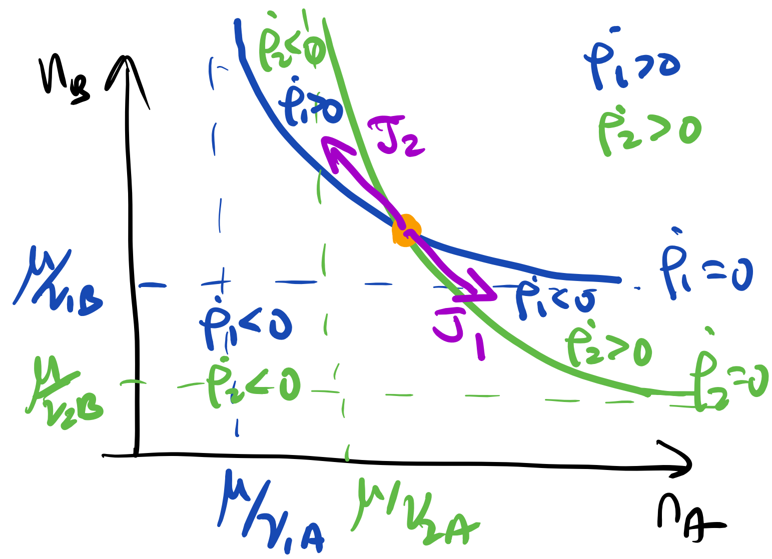
deviation from n_α^*, ρ_i^* ?

Use Tilman's approach: $\nu_{1A} > \nu_{2A}$, $\nu_{2B} > \nu_{1B}$

Isoclines:

$\dot{\rho}_1/\rho_1 = 0 \to r_1(n_A, n_B) = r^*$

$\dot{\rho}_2/\rho_2 = 0 \to r_2(n_A, n_B) = r^*$



nutrient dynamics:

$$\begin{pmatrix} Y_A \dot{n}_A \\ Y_B \dot{n}_B \end{pmatrix} = \rho_1 \underbrace{\begin{pmatrix} \overset{+ve}{\gamma_{1A} Y_A - r} \\ -r \end{pmatrix}}_{J_1} + \rho_2 \underbrace{\begin{pmatrix} -r \\ \underset{+ve}{\gamma_{2B} Y_B - r} \end{pmatrix}}_{J_2}$$

Steady state: $\rho_1^* J_1 + \rho_2^* J_2 = 0$

perturbation from steady state:

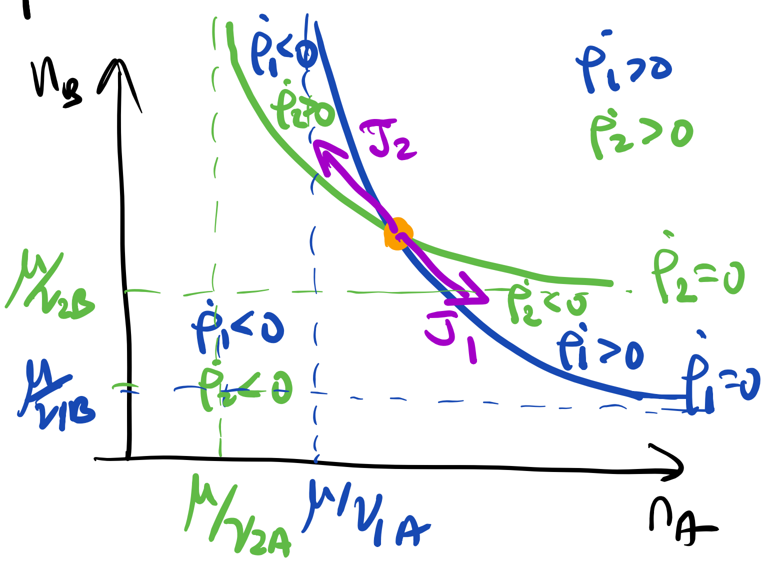
Suppose ρ_1 increases from ρ_1^*

then $\dot{n}_A > 0$, $\dot{n}_B < 0$.

this moves system in region with $\dot{\rho}_1 < 0$, $\dot{\rho}_2 > 0$

→ restores perturbation in ρ_1

Suppose $\nu_{1A} < \nu_{2A}$, $\nu_{2B} < \nu_{1B}$



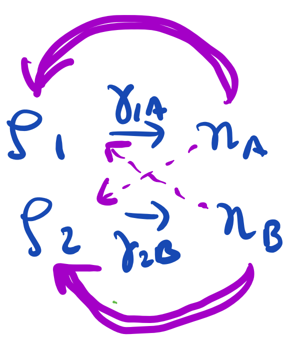
- Increase of ρ_1 leads to $\dot{n}_A > 0$, $\dot{n}_B < 0$
- System moves into region with $\dot{\rho}_1 > 0$, $\dot{\rho}_2 < 0$

→ further increase of ρ_1

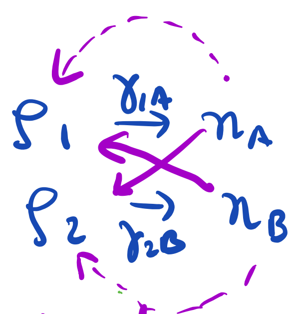
fixed pt unstable → system collapses (extinction)

⇒ this asymmetry arises from production asymmetry

Stable



Unstable



(extinction due to overactive cheaters)

HW: production + crossfeeding of sub. nutrients (different!)