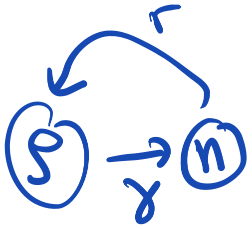
2. Effect of Nutrient Structure

- So far, nutrients are either supplied or self-generated
- below we study the effect of resource structure where certain species produce nutrients for others

→ cheating & cooperation



a) Nutrient production

- one species of density ρ.
- produces its own nutrient n (e.g., fix CO_2, degrade chitin)

$$\dot{\rho} = r(n)\rho - \mu\rho, \quad r(n) = r_0 \frac{n}{n+K}$$

$$\dot{n} = \underbrace{\gamma\rho}_{\text{production; no ext supply}} - \mu n - r(n)\rho / Y$$

γ: nutrient prod. rate

μ: "dilution" rate

($\mu < r_0$ for possibility of existence)

take $\dot{n} = 0$ (rapid eq of n).

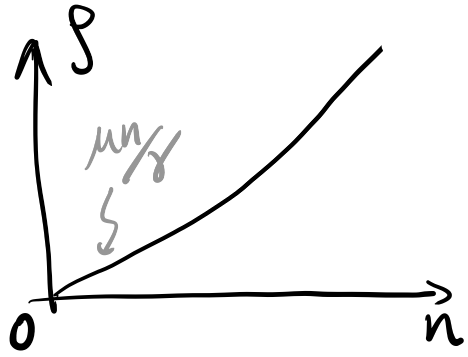
$$\rho = \frac{\mu n}{\gamma - r(n)/Y} = \frac{n\mu Y/r(n)}{\gamma Y/r(n) - 1} = \frac{\mu Y}{r_0}(n+K) \Big/ \left[\frac{\gamma Y}{r_0}\left(1+\frac{K}{n}\right) - 1\right]$$

$$= \frac{\mu(n+K)}{(\gamma - r_0/Y) + \gamma \frac{K}{n}}$$

two cases:

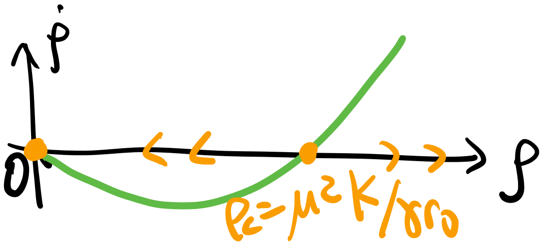
i) $\gamma \gg r_0/Y$ (bottleneck = uptake)

insert $n(\rho)$ into eqn for ρ



for small $n \sim \rho$: $n \simeq \gamma\rho/\mu$

$$\rightarrow \quad \dot{\rho} = r(n)\rho - \mu\rho \simeq \left(\frac{r_0}{K}\frac{\gamma}{\mu}\rho\right)\cdot\rho - \mu\rho$$



Allee effect.

$\rho^* \to 0$ if $\rho(0) < \rho_c = \mu^2 K/\gamma r_0$

for $\rho > \rho_c$, increase in ρ → increase in n.

→ $r(n) = r_0$

$$\dot{\rho} = r_0\rho - \mu\rho \rightarrow \rho(t) \propto e^{(r_0-\mu)t}$$

⇒ even at high production rate γ, growth of population occurs only for sufficiently large init. pop size.

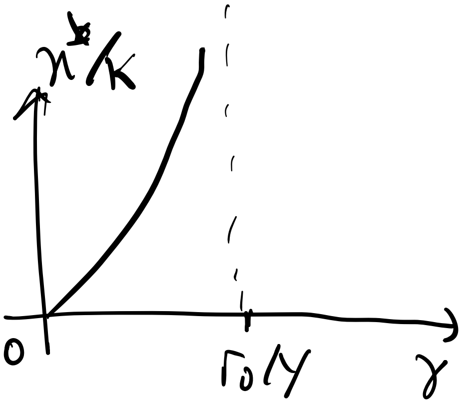
Why: nutrient production requires ρ ($n \propto \rho$ for small ρ)
So $\dot{\rho} \propto r(n)\rho \propto \rho^2$

ii) $\gamma < r_0/Y$ (bottlenecked = production)

$$\dot{n} = \gamma\rho - \mu n - r(n)\rho/Y$$

$$\rho = \frac{\mu(n+K)}{(\gamma - r_0/Y) + \gamma\frac{K}{n}}$$

$$\rho \to \infty \text{ as } n \to n^* = \frac{\gamma K}{r_0/Y - \gamma}$$



↳ conc where production = consumption

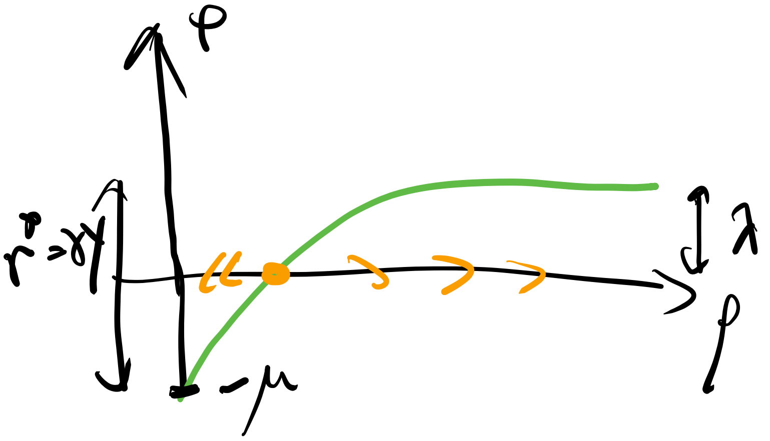
(will show below this is the steady state conc where cells grow) for $\gamma << r_0/Y$, $n^*/K << 1$, Can approx $r(n) \simeq \frac{r_0 n}{K}$

Corresponding growth rate: $r(n^*) \simeq \frac{r_0 n^*}{K} = \gamma Y \equiv r^*$

$\dot{n}=0 \to \gamma \rho = n\left(\mu + \frac{r_0}{KY}\rho\right)$

$$n(\rho) = n^* \cdot \frac{\rho}{\rho+\rho_M} ; \qquad \rho_M = \mu K Y / r_0 .$$

$$\dot{\rho} = \left[\frac{r_0}{K} n(\rho) - \mu\right]\rho$$
$$= \left(r^* \frac{\rho}{\rho + K} - \mu\right)\rho$$



for $\rho(0) > \rho_c$,

- $\rho(t) \propto e^{\lambda t}$, where $\lambda = r^* - \mu = \gamma Y - \mu$.

$\Rightarrow$ pop survives only if $\gamma Y > \mu$.

Note 1: batch culture growth; Allee effect manifested as a init conc-dependent lag period. HW

Note 2: γ treated so far as fixed quantity. it is actually regulated and GR dependent

$n^* = \gamma Y K / r_0$ set by cell

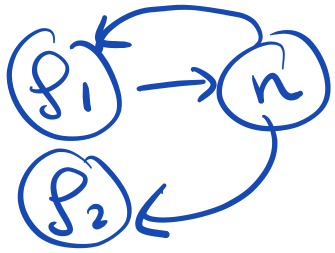
increasing γ increases n^*

→ increases growth but also invite "cheaters"

→ how to set γ (in presence of exogenous n)?

b) Multiple species : "Cheaters" (parasitism)

– 2 species, 1 nutrient



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

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

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

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

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

. rapid equi of n $(\dot n = 0)$.

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

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

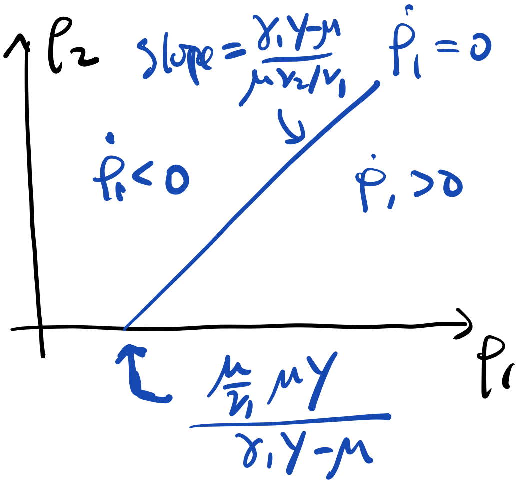
from $\dot\rho_1 = (\nu_1 n - \mu)\rho_1$,

the critical pt for the growth of ρ_1 is at

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

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

$$\rho_1^c = \frac{\frac{\mu}{\nu_1}\cdot\mu Y + \mu\frac{\nu_2}{\nu_1}\rho_2^c}{\gamma_1 Y - \mu} \quad ①$$

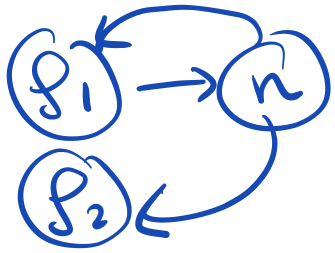


→ uptake by Sp 2 (i.e. $\nu_2 > 0$)

increases threshold for growth of sp 1

b) Multiple species: "Cheaters" (parasitism)

– 2 species, 1 nutrient



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

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

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

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

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

. rapid equi of n ($\dot n = 0$).

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

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

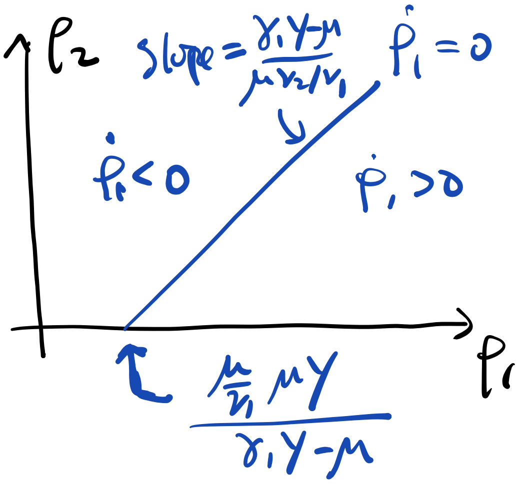
from $\dot\rho_1 = (\nu_1 n - \mu)\rho_1$,

the critical pt for the growth of ρ_1 is at

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

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

$$\rho_1^c = \frac{\frac{\mu}{\nu_1}\cdot\mu Y + \mu\frac{\nu_2}{\nu_1}\rho_2^c}{\gamma_1 Y - \mu} \qquad ①$$

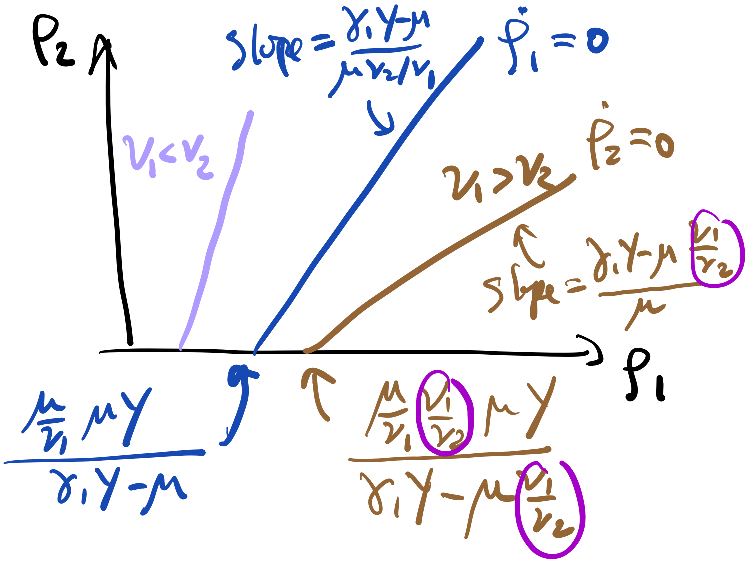


→ uptake by Sp 2 (i.e. $\nu_2 > 0$) increases threshold for growth of sp 1

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

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

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



phase flow:

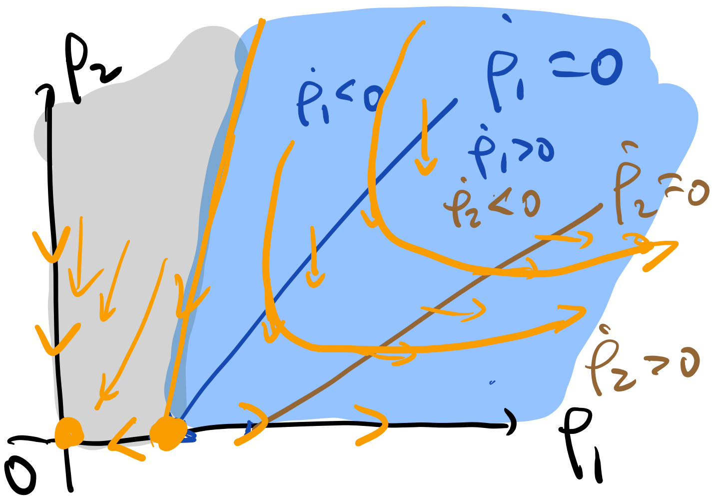
$$\dot\rho_1 = \rho_1\left[\nu_1\frac{\gamma_1\rho_1 Y}{\mu Y + \nu_1\rho_1 + \nu_2\rho_2} - \mu\right]$$

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

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 (hence parasite)

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

growth phase:

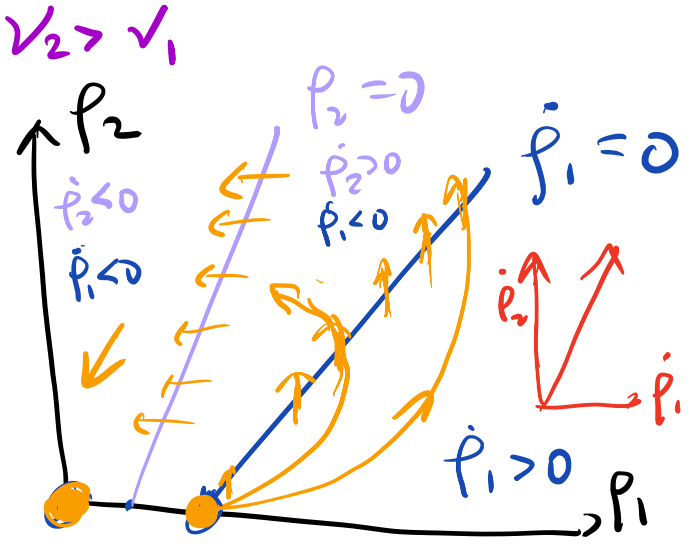
at conc n^*, $\lambda_1 = \nu_1 n^* - \mu > \lambda_2 = \nu_2 n^* - \mu$

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

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

⇒ 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 $\dot\rho_2 = 0$

⇒ excitable dynamics

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

eventually headed for extinction

⇒ increasing ν_2 increases fitness of cheater; but too much will make it extinct (blackjack)

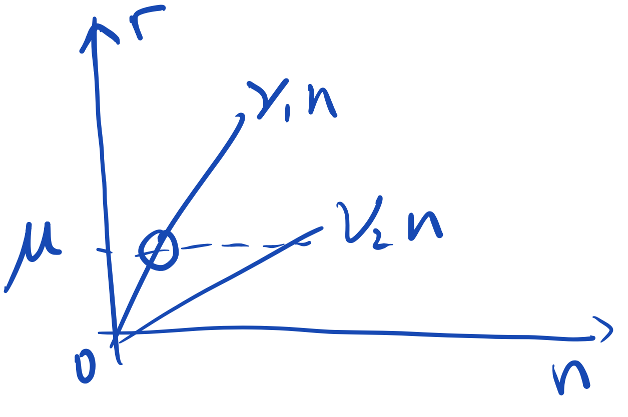
⌈ Assume growth phase exists. $n = n^*$.

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

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

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



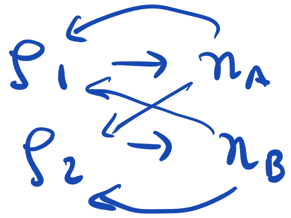
⇒ no stable state if $\nu_2 > \nu_1$ ⌋

c) Cross-feeding of self-generated essential nutrients

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

$$\dot\rho_1 = (r_1(n_A,n_B) - \mu)\rho_1$$

$$\dot\rho_2 = (r_2(n_A,n_B) - \mu)\rho_2$$



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

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

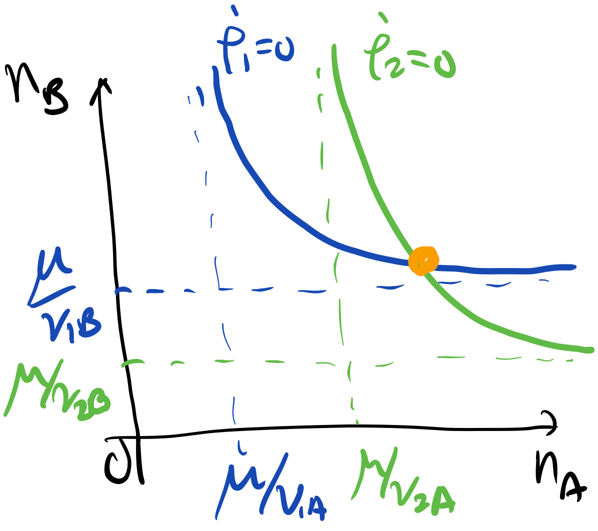
growth function: (from Sec IIA2)

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

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

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

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



- fixed pt soln generically exist if $V_{1\alpha} \neq V_{2\alpha}$
- 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

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

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

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

take small-μ limit: $r_1^* = r_2^* = \mu \ll \gamma$

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

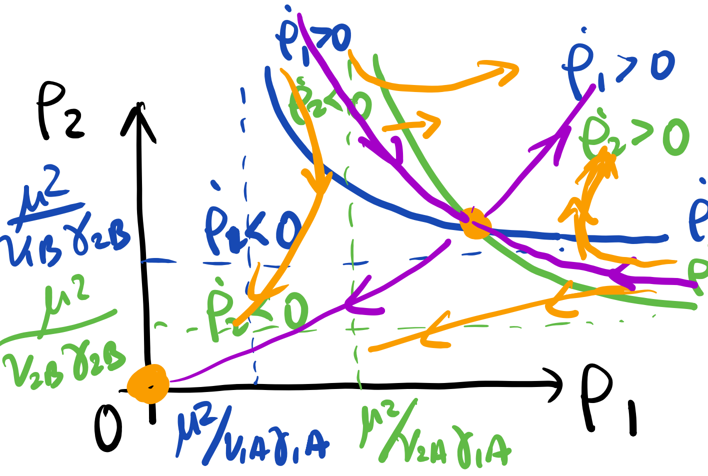
$$r_1 = \left(\frac{1}{\nu_{1A}n_A}+\frac{1}{\nu_{1B}n_B}\right)^{-1} = \left[\frac{\mu}{\nu_{1A}\gamma_{1A}\rho_1}+\frac{\mu}{\nu_{1B}\gamma_{2B}\rho_2}\right]^{-1}$$

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

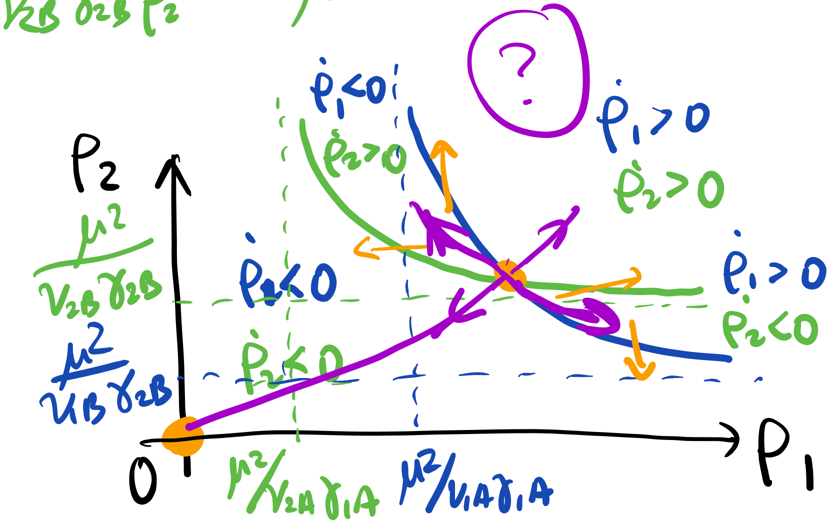
$$\dot\rho_1 = \rho_1\left[\frac{1}{\mu}\left(\frac{1}{\nu_{1A}\gamma_{1A}\rho_1}+\frac{1}{\nu_{1B}\gamma_{2B}\rho_2}\right)^{-1}-\mu\right]$$ — effective gLV eqn

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

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



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



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

$\Rightarrow$ 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 $\rho_1 \to \rho_1^*$
$\rho_2 \to \rho_2^*$

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

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

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

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

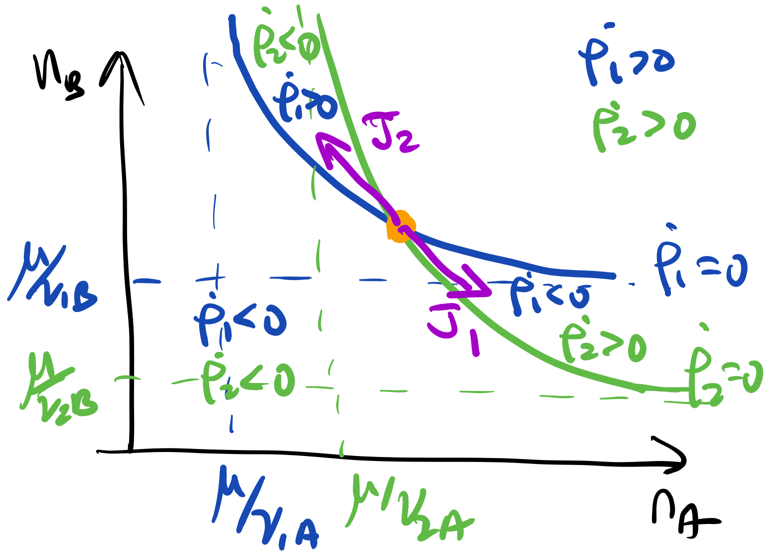
deviation from n_α^*, ρ_i^* ?

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:

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

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

perturbation from steady state:

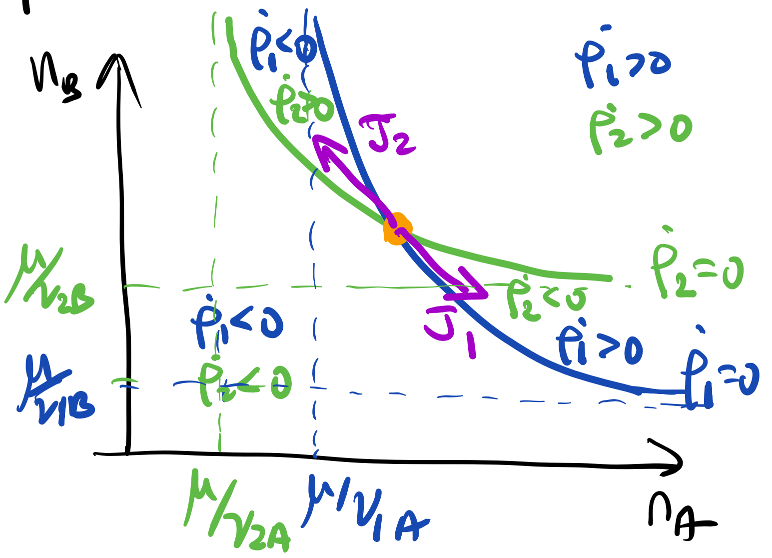
Suppose ρ_1 increases from ρ_1^*

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



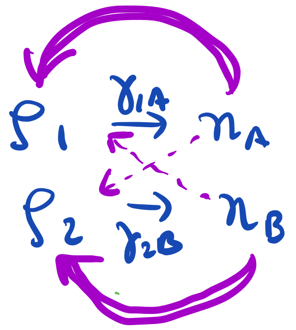
- Increase of ρ_1 leads to $\dot{n}_A > 0$, $\dot{n}_B < 0$
- System moves into region with $\dot{\rho}_1 > 0$, $\dot{\rho}_2 < 0$

→ further increase of ρ_1

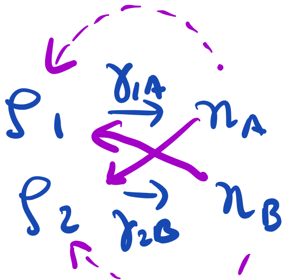
fixed pt unstable → system collapses (extinction)

⇒ this asymmetry arises from production asymmetry

Stable



unstable



(extinction due to overactive cheaters)

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