II B. CR Model of Competition & Coexistence

1. Two-Species Interaction

a) 2-species growing on a single substrate

chemostat with dilution rate μ

$$\dot{\rho}_1 = r_1(n)\rho_1 - \mu\rho_1$$

$$\dot{\rho}_2 = r_2(n)\rho_2 - \mu\rho_2$$

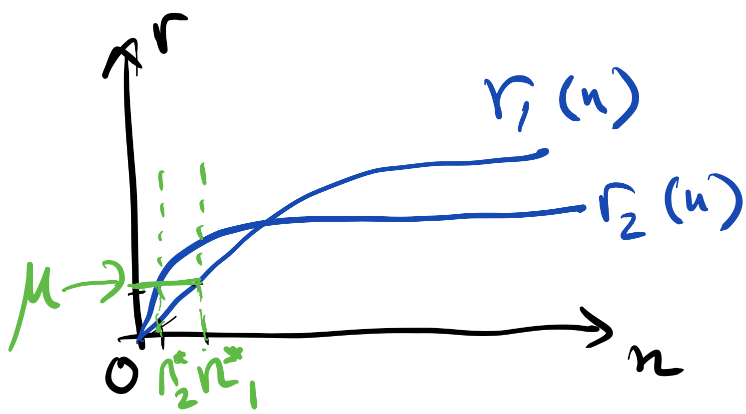
$$r_i(n) = r_i^0 \frac{n}{n+K_i}$$

$$\dot{n} = \mu(n_0 - n) - r_1(n)\rho_1/Y - r_2(n)\rho_2/Y$$

Steady state:

$\mu = r_1(n^*)$, $\mu = r_2(n^*)$

→ cannot be satisfied simultaneously unless $r_1(n) = r_2(n)$



Sol'n: $\mu = r_i(n^*)$, with $\rho_i \neq 0$, while $\rho_{j\neq i} = 0$.

→ i.e. only one species survives in steady state

HW: Surviving species is one with lower n_i

⌈approach: Assume one of the species goes extinct, e.g. $\rho_2 = 0$.

check for stability for small $\rho_2 > 0$.⌋

b) two species (of densities ρ_1 ρ_2) growing on two nutrients (of concentrations n_A, n_B)

- chemostat with dilution rate μ.
- nutrient influx ($j_A^0 = \mu n_A^0$, $j_B^0 = \mu n_B^0$)

Uptake of multiple nutrients:

- substitutable (e.g. glucose vs. glycerol)
- essential (e.g. glucose + ammonium)

Substitutable nutrients:

- Many substrates co-utilized; GR approx additive

i.e. $r_i(n_A, n_B) \simeq r_i^0 \frac{n_A}{K_{i,A}} + r_i^0 \frac{n_B}{K_{i,B}}$

$\equiv \nu_{iA} n_A + \nu_{iB} n_B$

[ref: Hermsen et al MSB 2014]

- some combo of substrates hierarchically utilized

e.g. $r_i(n_A, n_B) = \max\{ r_i(n_A), r_i(n_B) \}$

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

→ will focus on substitutable, co-utilized nutrients

Dynamical equations:

$$\dot{\rho}_1 = (\nu_{1A} n_A + \nu_{1B} n_B)\rho_1 - \mu \rho_1$$

$$\dot{\rho}_2 = (\nu_{2A} n_A + \nu_{2B} n_B)\rho_2 - \mu \rho_2$$

Y_α can be scaled out

$\nu_{i\alpha}/Y_\alpha = \tilde{\nu}_{i\alpha}$

$n_\alpha Y_\alpha = \tilde{n}_\alpha$

$$\dot{n}_A = \mu(n_A^0 - n_A) - \nu_{1A} n_A \rho_1 / Y_A - \nu_{2A} n_A \rho_2 / Y_A$$

$$\dot{n}_B = \mu(n_B^0 - n_B) - \nu_{1B} n_B \rho_1 / Y_B - \nu_{2B} n_B \rho_2 / Y_B$$

assumption made: yield is species independent

(but different substrate can contribute quite differently to biomass, e.g. glucose has 6C, glycerol only 3C)

* Steady state soln (and $\rho_1^* \neq 0$, $\rho_2^* \neq 0$)

$\dot{\rho}_1 = 0$. $\quad \nu_{1A} n_A + \nu_{1B} n_B = \mu$

$\dot{\rho}_2 = 0 \quad \nu_{2A} n_A + \nu_{2B} n_B = \mu$

$$\begin{bmatrix} \nu_{1A} & \nu_{1B} \\ \nu_{2A} & \nu_{2B} \end{bmatrix} \begin{bmatrix} n_A \\ n_B \end{bmatrix} = \begin{bmatrix} \mu \\ \mu \end{bmatrix}$$

Recall linear algebra

$$M \cdot \begin{bmatrix} x_1 \\ x_2 \end{bmatrix} = \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} \rightarrow \begin{bmatrix} x_1 \\ x_2 \end{bmatrix} = M^{-1} \cdot \begin{bmatrix} b_1 \\ b_2 \end{bmatrix}$$

$$M = \begin{bmatrix} m_{11} & m_{12} \\ m_{21} & m_{22} \end{bmatrix}$$

$$M^{-1} = \frac{1}{\det M} \begin{bmatrix} m_{22} & -m_{12} \\ -m_{21} & m_{11} \end{bmatrix}$$

$$\begin{bmatrix} n_A^* \\ n_B^* \end{bmatrix} = \frac{1}{\det(\nu)} \begin{bmatrix} \nu_{2B} & -\nu_{1B} \\ -\nu_{1A} & \nu_{1A} \end{bmatrix} \begin{bmatrix} \mu \\ \mu \end{bmatrix} = \frac{\mu}{\det(\nu)} \begin{bmatrix} \nu_{2B} - \nu_{1B} \\ \nu_{1A} - \nu_{2A} \end{bmatrix} \sim O(\mu/\nu)$$

Note: nutrient levels set by ν_{ij} and μ. not dependent on ρ_i, nor n_i^0 (cf. chemostat)

ρ_1^*, ρ_2^* found from $\dot{n}_A = 0, \dot{n}_B = 0$

$$\nu_{1A} n_A^* \rho_1^* + \nu_{2A} n_A^* \rho_2^* = \mu (n_A^0 - n_A^*) Y_A$$

$$\nu_{1B} n_B^* \rho_1^* + \nu_{2B} n_B^* \rho_2^* = \mu (n_B^0 - n_B^*) Y_B$$

$$\underbrace{\begin{bmatrix} \nu_{1A} & \nu_{2A} \\ \nu_{1B} & \nu_{2B} \end{bmatrix}}_{\nu^T} \begin{bmatrix} \rho_1^* \\ \rho_2^* \end{bmatrix} = \mu \begin{bmatrix} \left(\frac{n_A^0 - n_A^*}{n_A^*}\right) Y_A \\ \left(\frac{n_B^0 - n_B^*}{n_B^*}\right) Y_B \end{bmatrix},$$

$$\begin{bmatrix} \rho_1^* \\ \rho_2^* \end{bmatrix} = \frac{\mu}{\det(\nu^T)} \begin{bmatrix} \nu_{2B} & -\nu_{2A} \\ -\nu_{1B} & \nu_{1A} \end{bmatrix} \cdot \begin{bmatrix} \ \end{bmatrix} = \frac{\mu}{\det(\nu^T)} \begin{bmatrix} \nu_{2B} \frac{n_A^0 - n_A^*}{n_A^*} Y_A - \nu_{2A} \frac{n_B^0 - n_B^*}{n_B^*} Y_B \\ -\nu_{1B} \frac{n_A^0 - n_A^*}{n_A^*} Y_A + \nu_{1A} \frac{n_B^0 - n_B^*}{n_B^*} Y_B \end{bmatrix}$$

from above: $n_A^* = \mu(\nu_{2B} - \nu_{1B})/\det(\nu) \rightarrow 1/n_A^* = \det(\nu)/[\mu(\nu_{2B} - \nu_{1B})]$

$n_B^* = \mu(\nu_{1A} - \nu_{2A})/\det(\nu) \quad\quad 1/n_B^* = \det(\nu)/[\mu(\nu_{1A} - \nu_{2A})]$

$$\begin{bmatrix} \rho_1^* \\ \rho_2^* \end{bmatrix} = \begin{bmatrix} \frac{\nu_{2B}(n_A^0 - n_A^*) Y_A}{\nu_{2B} - \nu_{1B}} - \frac{\nu_{2A}(n_B^0 - n_B^*) Y_B}{\nu_{1A} - \nu_{2A}} \\ \frac{-\nu_{1B}(n_A^0 - n_A^*) Y_A}{\nu_{2B} - \nu_{1B}} + \frac{\nu_{1A}(n_B^0 - n_B^*) Y_B}{\nu_{1A} - \nu_{2A}} \end{bmatrix};$$

$\det \nu = \det \nu^T$

Note 1: $\rho_1^* + \rho_2^* = (n_A^0 - n_A^*) Y_A + (n_B^0 - n_B^*) Y_B$ — mass conservation

Note 2: if $\mu \to 0$, then $n_A^*, n_B^* \to 0$ (little nutrient left

ρ_1^0, ρ_2^* depend on $(n_A^0 Y_A, n_B^0 Y_B)$ & $\nu_{i\alpha}$

Note 3: if $n_A^0 - n_A^* \to 0$, $n_B^0 - n_B^* \to 0$ (i.e. $n_A^0 \to \frac{\mu(\nu_{2B} - \nu_{1B})}{\nu_{1A}\nu_{2B} - \nu_{1B}\nu_{2A}}$)

then $\rho_1^* \to 0$, $\rho_2^* \to 0$ (washout limit of chemostat)

Goal: Understand dependence of Coexistence ($\rho_1 > 0, \rho_2 > 0$) vs. dominance ($\rho_1 > 0, \rho_2 = 0$ or vice versa) or extinction ($\rho_{1,2} = 0$) for diff environmental parameters ($j_A^0 = \mu n_A^0$, $j_B^0 = \mu n_B^0$) and genetic parameters ($\nu_{i\alpha}$, μ)

- find fixed points (if $\rho_i \leq 0$, then no coexistence)
- if $\rho_A > 0$, $\rho_B > 0$ exist, determine stability
  - unstable in one direction: phase transition (multi-modality)
  - Stable: Coexistence occurs
    - $\rightarrow$ basin of attraction?

A simple limit (weak interaction case):

specialist vs specialist

$n_A \rightarrow \rho_1$

$n_B \rightarrow \rho_2$

$\nu_{1A} \gg \nu_{2A}$

$\nu_{2B} \gg \nu_{1B}$

$\rightarrow$ coexistence. (if not washed out)

Q: as Interaction is turned on, to what extent is coexistence stable?

generalist vs specialist

$n_A \rightarrow \rho_1$

$n_B \rightarrow \rho_2$

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

$\nu_{1B} \ll \nu_{1A}, \nu_{1B}$

??

generalist vs generalist

$n_A \rightarrow \rho_1$

$n_B \rightarrow \rho_2$

all $\nu_{i\alpha}$ comparable ??

$\rightarrow$ General analysis of stability (around $\rho_1^*, \rho_2^*, n_A^0, n_B^*$)

4x4 matrix – not intuitive

$\rightarrow$ Short-cut:

effective dynamics of n_A, n_B (Tilman)

c) Tilman's graphical analysis of coexistence (Tilman 1980)

$$\dot{\rho}_1 = (\nu_{1A} n_A + \nu_{1B} n_B)\rho_1 - \mu\rho_1 = f_1(n_A, n_B)\rho_1$$

$$\dot{\rho}_2 = (\nu_{2A} n_A + \nu_{2B} n_B)\rho_2 - \mu\rho_2 = f_2(n_A, n_B)\rho_2$$

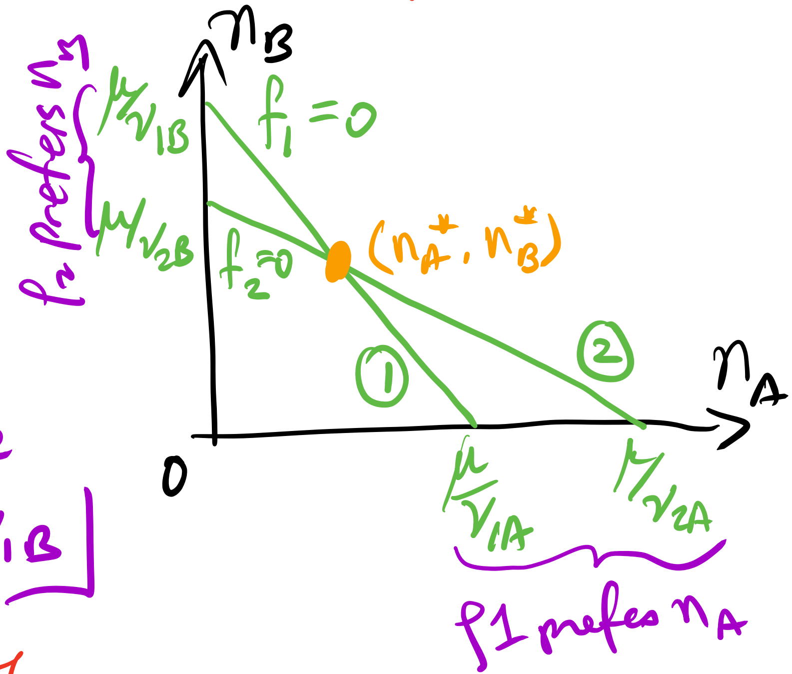
$$\dot{n}_A = \mu(n_A^0 - n_A) - (\nu_{1A}\rho_1 + \nu_{2A}\rho_2)\, n_A / Y_A$$

$$\dot{n}_B = \mu(n_B^0 - n_B) - (\nu_{1B}\rho_1 + \nu_{2B}\rho_2)\, n_B / Y_B$$

Tilman: Analyze dynamics in (n_A, n_B) plane

first, $\dot{\rho}_1 = 0$, $\dot{\rho}_2 = 0$

$$\begin{cases} \nu_{1A} n_A + \nu_{1B} n_B = \mu & (1) \\ \nu_{2A} n_A + \nu_{2B} n_B = \mu & (2) \end{cases}$$



[Note: plot shows the case with $\nu_{1A} > \nu_{2A}$, $\nu_{2B} > \nu_{1B}$]

→ focus on the effect of ρ_1 and ρ_2 on nutrient n_A, n_B:

$$\begin{pmatrix} \dot{n}_A \\ \dot{n}_B \end{pmatrix} = \mu\underbrace{\begin{pmatrix} n_A^0 - n_A \\ n_B^0 - n_B \end{pmatrix}}_{\vec{J}_0} - \rho_1 \underbrace{\begin{pmatrix} \nu_{1A} n_A / Y_A \\ \nu_{1B} n_B / Y_B \end{pmatrix}}_{-\vec{J}_1} - \rho_2 \underbrace{\begin{pmatrix} \nu_{2A} n_A / Y_A \\ \nu_{2B} n_B / Y_B \end{pmatrix}}_{-\vec{J}_2}$$

At steady state ($\dot{n}_A=0$, $\dot{n}_B=0$),

the above becomes $\mu \vec{J_0} + \rho_1^* \vec{J_1} + \rho_2^* \vec{J_2} = 0$, a statement of balance between nutrient source $\vec{J_0}$ and sink ($\vec{J_1}, \vec{J_2}$)

subject to $\rho_1^* \cdot \rho_2^* > 0$

- this flux balance can be represented graphically in (n_A, n_B) plane
- the graphical representation also gives a glimpse of the dynamics of (n_A, n_B)

Pick arbitrary point ($\hat{n}_A, \hat{n}_B$) in (n_A, n_B) plane

$\vec{J_0}$: pointing from ($\hat{n}_A, \hat{n}_B$) to (n_A^0, n_B^0)

$\vec{J_1}$: pointing downward from ($\hat{n}_A, \hat{n}_B$) with slope $\dfrac{\gamma_{1B}\, \hat{n}_B / Y_B}{\gamma_{1A}\, \hat{n}_A / Y_A}$

$\rightarrow$ look for a function $n_B(n_A)$ passing through ($\hat{n}_A, \hat{n}_B$)

with slope $= m_1 \dfrac{\hat{n}_B}{\hat{n}_A}$, $m_1 = \dfrac{\gamma_{1B}/Y_B}{\gamma_{1A}/Y_A}$

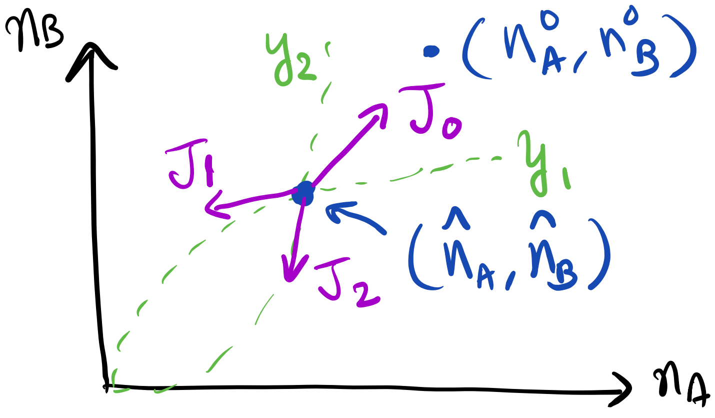
$$\frac{dn_B}{dn_A} = m_1 \frac{n_B}{n_A} \rightarrow n_B = c\, n_A^{m_1} \text{ or } \boxed{n_B = \hat{n}_B \left(\frac{n_A}{\hat{n}_A}\right)^{m_1}}$$

$\Rightarrow \vec{J_1}$: tangent of $n_B = \hat{n}_B \left(\frac{n_A}{\hat{n}_A}\right)^{m_1}$

Similarly, $\vec{J_2}$ is tangent of $n_B = \hat{n}_B \left(\frac{n_A}{\hat{n}_A}\right)^{m_2}$

take $m_1 < 1$ (ρ_1 better at consuming n_A)

$m_2 > 1$ (ρ_2 better at consuming n_B)

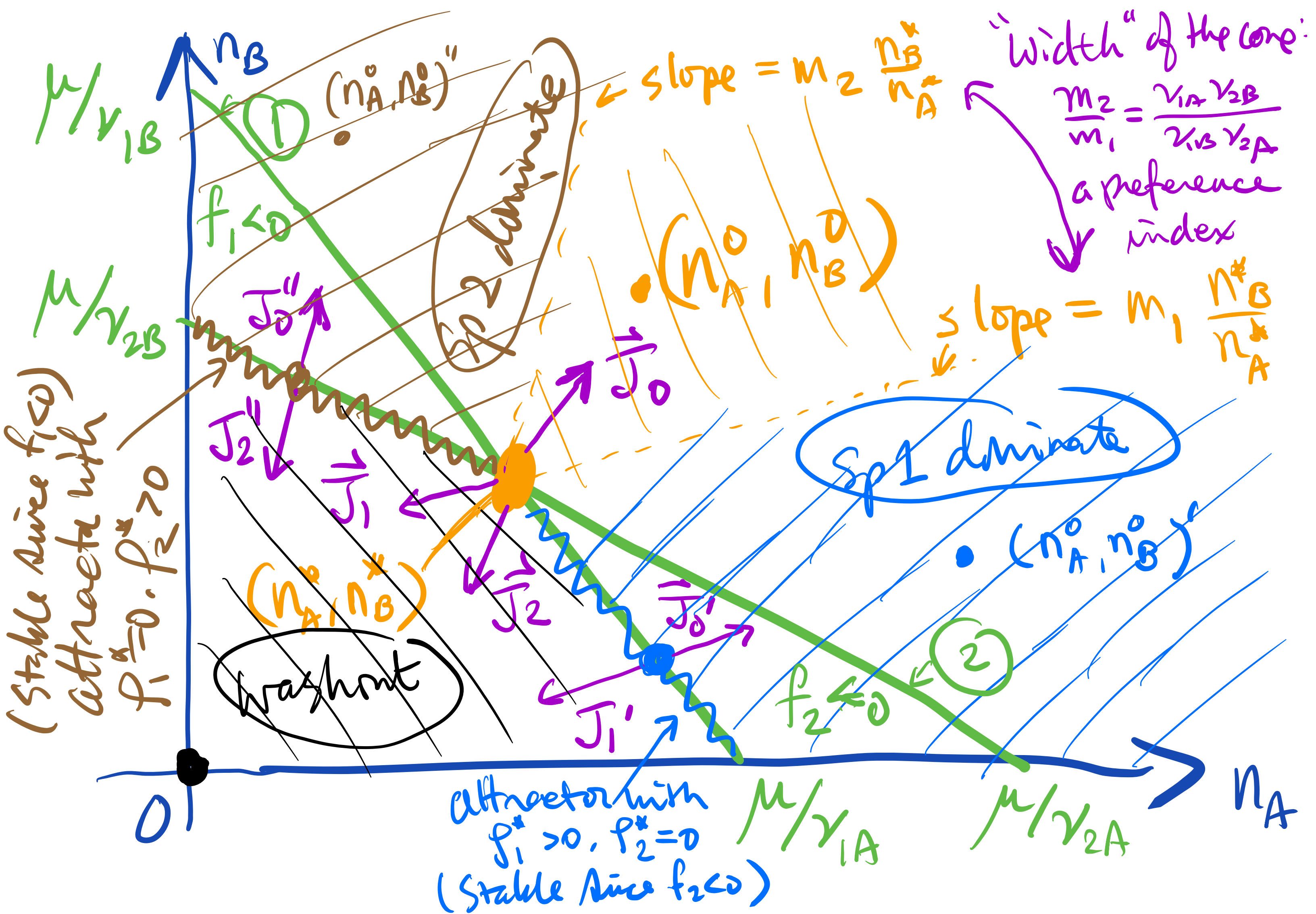


$m_1 = \dfrac{\nu_{1B}/Y_B}{\nu_{1A}/Y_A}$, $m_2 = \dfrac{\nu_{2B}/Y_B}{\nu_{2A}/Y_A}$

- determine the direction of the "flow field" $(\vec{J}_1, \vec{J}_2)$ for every $(\hat{n}_A, \hat{n}_B)$
- magnitude adjusted by ρ_1, ρ_2

Now, combine with growth isoclines $f_1(n_A, n_B) = f_2(n_A, n_B) = 0$

* first look at vicinity of fixed pt, i.e., $(\hat{n}_A, \hat{n}_B) = (n_A^*, n_B^*)$



- for habitat (n_A^0, n_B^0) in orange zone, $\rho_1^*, \rho_2^* > 0$ such that $\rho_1^* \vec{J}_1 + \rho_2^* \vec{J}_2 = \mu J_0$
- for habitat in light blue zone, $\rho_2^* = 0$
- for habitat in brown zone, $\rho_1^* = 0$
- for habitat in black zone, $\rho_1^* = 0$, $\rho_2^* = 0$

(for $\nu_{2A} > \nu_{1A}$ and $\nu_{1B} > \nu_{2B}$, just switch $A \leftrightarrow B$)

[The phase boundary of coexistence can be obtained algebraically from .

$$\dot{n}_A = 0 \to \nu_{1A} n_A^* \rho_1^* + \nu_{2A} n_A^* \rho_2^* = \mu (n_A^0 - n_A^*) Y_A$$

$$\dot{n}_B = 0 \to \nu_{1B} n_B^* \rho_1^* + \nu_{2B} n_B^* \rho_2^* = \mu (n_B^0 - n_B^*) Y_B$$

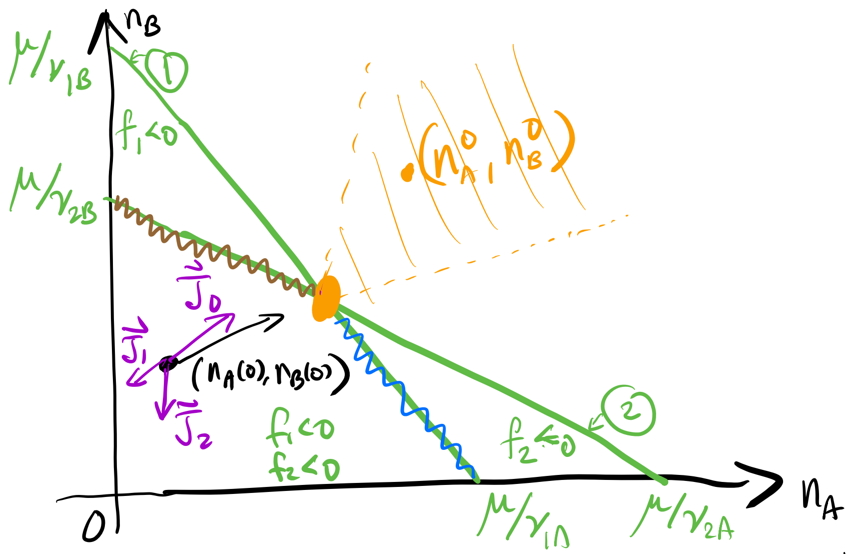
Sol'n:
$$\begin{bmatrix} \rho_1^* \\ \rho_2^* \end{bmatrix} = \frac{\mu}{\det(\nu^T)} \begin{bmatrix} \nu_{2B} \frac{n_A^0 - n_A^*}{n_A^*} Y_A - \nu_{2A} \frac{n_B^0 - n_B^*}{n_B^*} Y_B \\ -\nu_{1B} \frac{n_A^0 - n_A^*}{n_A^*} Y_A + \nu_{1A} \frac{n_B^0 - n_B^*}{n_B^*} Y_B \end{bmatrix}$$

Condition for $\rho_1^* \geq 0$: $\nu_{2B} \frac{n_A^0 - n_A^*}{n_A^*} Y_A \geq \nu_{2A} \frac{n_B^0 - n_B^*}{n_B^*} Y_B$

$$\Rightarrow \frac{n_B^0 - n_B^*}{n_A^0 - n_A^*} \leq \frac{\nu_{2B} Y_A}{\nu_{2A} Y_B} \frac{n_B^*}{n_A^*} = m_2 \frac{n_B^*}{n_A^*} \checkmark$$

Similarly, $\rho_2 \geq 0 \Rightarrow \frac{n_B^0 - n_B^*}{n_A^0 - n_A^*} \geq m_1 \frac{n_B^*}{n_A^*}$ ✓]

* Next look at different initial condition for (n_A^0, n_B^0) within the allowed cone.



→ Starting from the black point $(n_A(0) < n_A^*, \; n_B(0) < n_B^*)$, dynamics leads to smaller $\rho_1 \, \rho_2$ (since $f_1 < 0$, $f_2 < 0$), driving the black point towards fixed pt (orange)

⇒ will show in Sec. II B2 that all fixed points with $\rho_1^* > 0$, $\rho_2^* > 0$ are stable (i.e., all eigenvalues < 0) so no phase transition; all init cond converge to f.p.

⇒ diagram above can be taken as "ecological phase diagram" (gives the fate of system for environmental parameter (n_A^0, n_B^0, μ))

⇒ Advantage of Tilman's approach is ease of generalization to other growth functions $r_i(n_A, n_B)$ HW