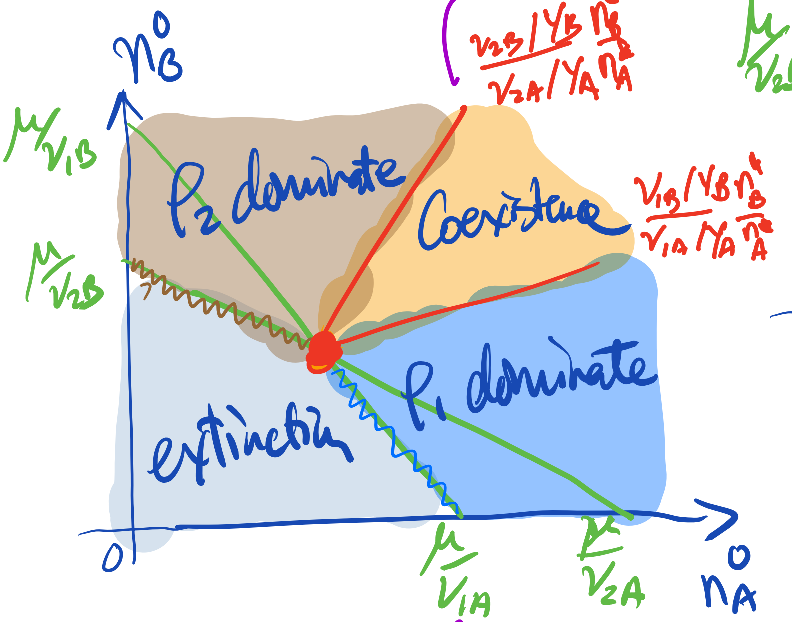
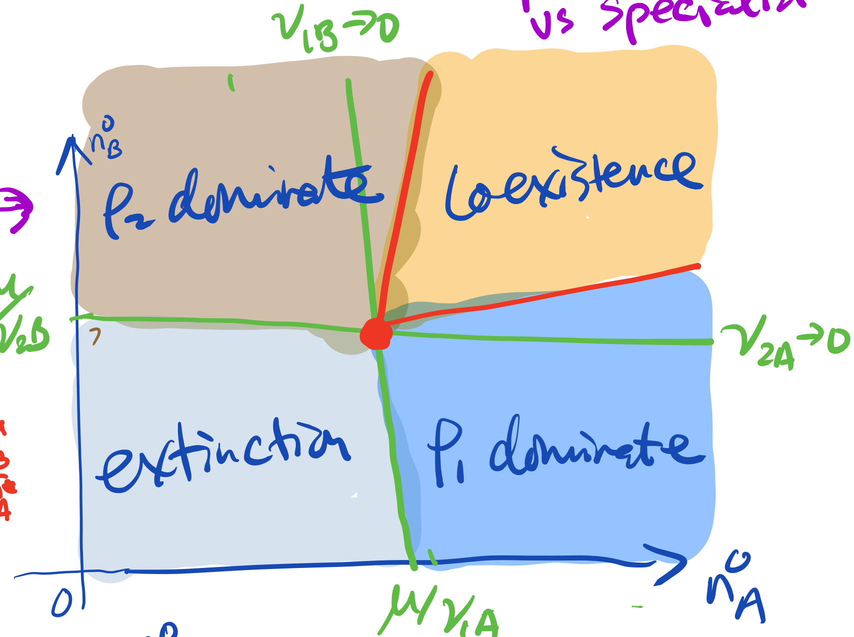
B3. phase diagram and feasibility space

a) Ecological phase diagram (for 2 species)

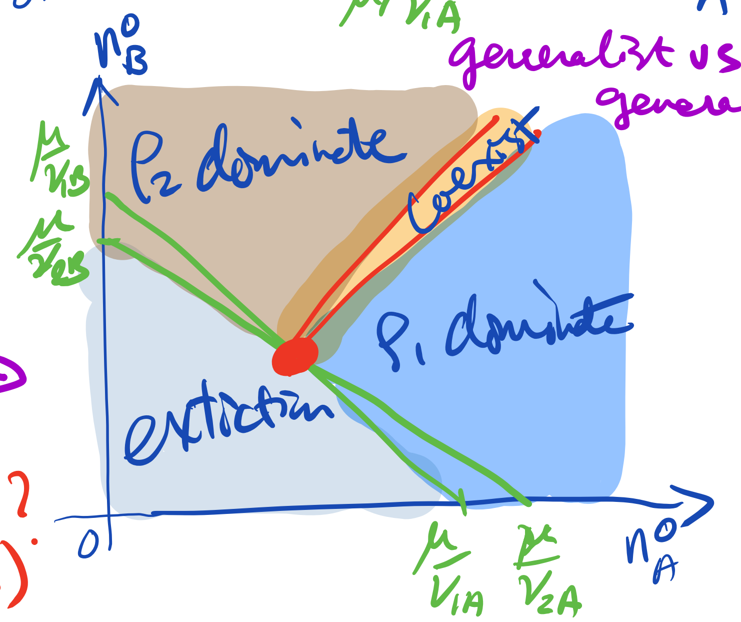
Strong orthogonal nutrient pref
broad coexist. regime



specialist vs specialist



generalist vs generalist



Similar nut. pref.
narrow coexist regime

$\Rightarrow$ phenotypical landscape ?
for fixed environment (n_A^0, n_B^0).

* Algebraic analysis:

$$\begin{bmatrix}\rho_1^* \\ \rho_2^*\end{bmatrix} = \begin{bmatrix} \dfrac{(n_A^0-n_A^*)\cdot Y_A}{1-\nu_{1B}/\nu_{2B}} + \dfrac{(n_B^0-n_B^*)\cdot Y_B}{1-\nu_{1A}/\nu_{2A}} \\[2ex] \dfrac{(n_A^0-n_A^*)\cdot Y_A}{1-\nu_{2B}/\nu_{1B}} + \dfrac{(n_B^0-n_B^*)\cdot Y_B}{1-\nu_{2A}/\nu_{1A}} \end{bmatrix} = \begin{bmatrix} \dfrac{j_A/\mu}{1-\nu_{1B}/\nu_{2B}} + \dfrac{j_B/\mu}{1-\nu_{1A}/\nu_{2A}} \\[2ex] \dfrac{j_A/\mu}{1-\nu_{2B}/\nu_{1B}} + \dfrac{j_B/\mu}{1-\nu_{2A}/\nu_{1A}} \end{bmatrix}$$

where $j_\alpha = \mu(n_\alpha^0 - n_\alpha^*)\, Y_\alpha$ = flux of nutrient α assimilated

Note: $\rho_1^* + \rho_2^* = (j_A + j_B)/\mu$ (mass conservation) let $\psi_i \equiv \rho_i^* / (\rho_1^* + \rho_2^*)$: frac. abundance of sp. i

$f_\alpha \equiv \dot{j}_\alpha / (\dot{j}_A + \dot{j}_B)$: frac. assim. flux for nutrient α

then $\psi_1 = f_A \frac{1}{1 - \nu_{1B}/\nu_{2B}} + f_B \frac{1}{1 - \nu_{1A}/\nu_{2A}}$ from mass conservation

$$\psi_1 = \frac{f_A}{1 - m_B} + \frac{f_B}{1 - m_A}$$

where $m_\alpha \equiv \frac{\nu_{1\alpha}}{\nu_{2\alpha}}$ is uptake preference of species 1 for nutrient α rel. to species 2 for α

note: different from $m_1 = \frac{\nu_{1A}/Y_A}{\nu_{1B}/Y_B}$ used earlier

In limit $\mu \to 0$ (to emphasize competition): $n_\alpha^* \ll n_\alpha^0$

$$\dot{j}_\alpha = \mu (n_\alpha^0 - n_\alpha^*) Y_\alpha \simeq \mu n_\alpha^0 Y_\alpha$$ ← environmental parameter.

then $f_\alpha = \frac{\dot{j}_\alpha}{\dot{j}_A + \dot{j}_B} = \frac{n_\alpha^0 Y_\alpha}{n_A^0 Y_A + n_B^0 Y_B}$ involves only env. parameters

- condition for coexistence: $1 > \psi_1 > 0$

→ find $\psi_1(m_A, m_B; f_A, f_B)$ such that $1 > \psi_1 > 0$.

- if $m_A > 1$, $m_B > 1$, $\psi_1 < 0$
- if $m_A < 1$, $m_B < 1$, $\psi_1 > 1$

} no coexistence

- for $m_A > 1 > m_B$ or $m_A < 1 < m_B$

$\psi_1 > 0$: $\frac{f_A}{1 - m_B} > \frac{f_B}{m_A - 1}$,

$f_A m_A - f_A > f_B - m_B f_B$ → $\boxed{f_A m_A + f_B m_B > 1}$

$\psi_1 < 1$: $\dfrac{f_A}{1-m_B} + \dfrac{f_B}{1-m_A} < 1$

$\cancel{f_A} - m_A f_A + \cancel{f_B} - m_B f_B > \cancel{1} - m_A - m_B + m_A m_B$

$m_A f_B + m_B f_A > m_A m_B \rightarrow$ $\boxed{\dfrac{f_A}{m_A} + \dfrac{f_B}{m_B} > 1}$

→ Ecological phase diagram: range of f_A given (m_A, m_B)

$m_A > 1 > m_B$ (or $m_B > 1 > m_A$)

$f_A m_A + (1-f_A) m_B > 1$

if $m_A > 1 > m_B$ then $f_A > \dfrac{1-m_B}{m_A - m_B}$

(if $m_A < 1 < m_B$, then $f_A < \dfrac{m_B - 1}{m_B - m_A}$)

$f_A m_A^{-1} + (1-f_A) m_B^{-1} > 1$

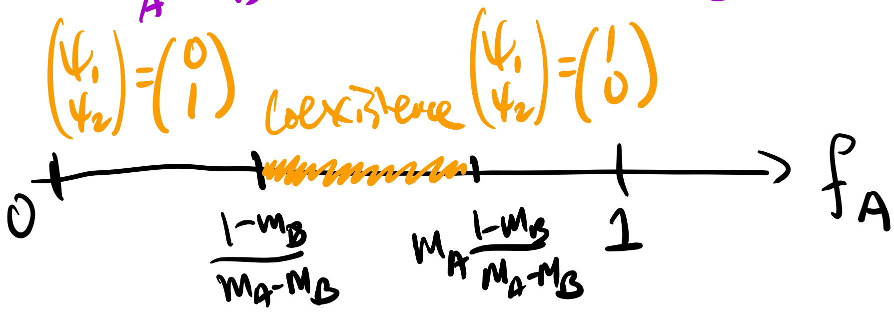
if $m_B > 1 > m_A$, then $f_A > \dfrac{1-m_B^{-1}}{m_A^{-1} - m_B^{-1}} = \dfrac{m_A(m_B-1)}{m_B - m_A}$

(if $m_A > 1 > m_B$, then $f_A < \dfrac{m_B^{-1} - 1}{m_B^{-1} - m_A^{-1}} = \dfrac{m_A(1-m_B)}{m_A - m_B}$)

for $m_B < 1 < m_A$: $\dfrac{1-m_B}{m_A - m_B} < f_A < m_A \dfrac{1-m_B}{m_A - m_B}$

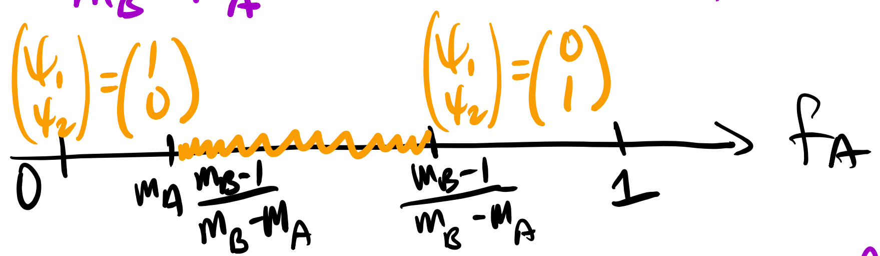
m_B: v_{1B}/v_{2B} $\quad$ m_A: v_{1A}/v_{2A}

Sp1 specializes in A
Sp2 specializes in B



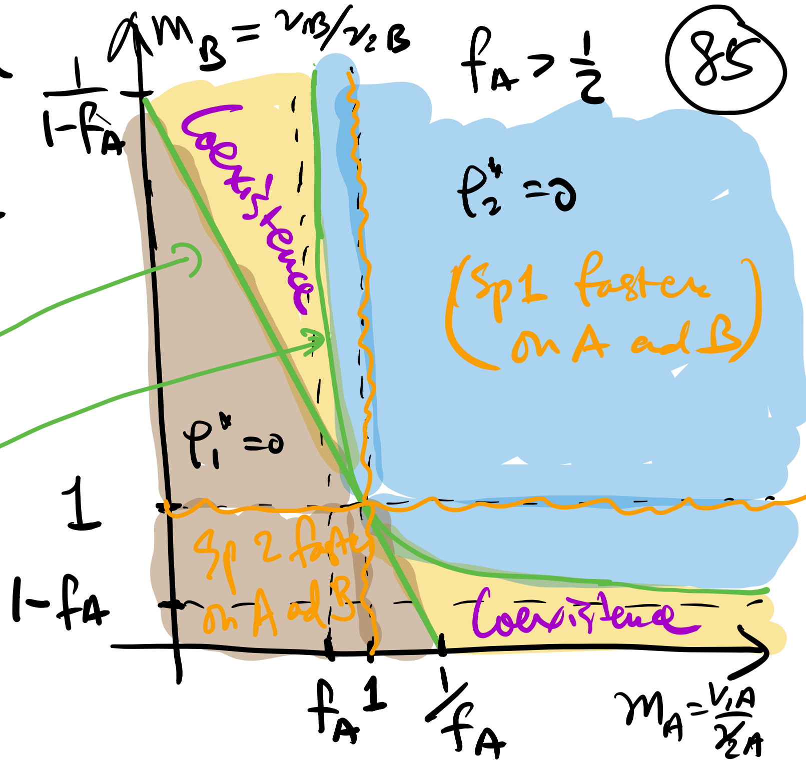
for $m_A < 1 < m_B$: $\dfrac{m_A(m_B-1)}{m_B - m_A} < f_A < \dfrac{m_B - 1}{m_B - m_A}$

Sp1 specializes in B
Sp2 specializes in A



⇒ Coexistence occurs for intermediate range of f_A
but meaning of condition obscure (see later)

b) phenotypical phase diagram for coexistence for fixed f_A



$\psi_1 > 0$: $m_A f_A + m_B f_B > 1$

$\psi_1 < 1$: $\frac{f_A}{m_A} + \frac{f_B}{m_B} > 1$

- Conditions favorable for coexistence: large m_A and small m_B (Sp 1 prefers A, Sp 2 prefers B) or vice versa = niche specialization

- For a given f_A, species can change genetic parameter (m_A, m_B) to drive the other species to extinction! Thus, phenotypical phase diagram has element of "fitness landscape" (but $\psi \neq$ fitness)

  [note: reality more challenging as f_A is variable]

- however, trivial effect from overall scale of $\nu_{i\alpha}$: If $\nu_{1A} > \nu_{2A}$ & $\nu_{1B} > \nu_{2B}$: $\rho_2^* \to 0$
  $\nu_{2A} > \nu_{1A}$ + $\nu_{2B} > \nu_{1B}$: $\rho_1^* \to 0$

  → overall scale of $\nu_{i\alpha}$ constrained?

Hypothesis: Constraint in resource uptake

(Parfait et al, 2017)

$$\nu_{i\alpha} = \nu_\alpha^0 \cdot \eta_{i,\alpha}$$

$\sum_\alpha \eta_{i\alpha} = 1$

allocation of catabolic enzyme is constrained

enzymatic properties for a given nutrient is invariant across species

$$\Rightarrow \psi_1 = \frac{f_A}{1-\frac{\nu_{1B}}{\nu_{2B}}} + \frac{f_B}{1-\frac{\nu_{1A}}{\nu_{2A}}} = \frac{f_A}{1-\frac{\eta_{1B}}{\eta_{2B}}} + \frac{f_B}{1-\frac{\eta_{1A}}{\eta_{2A}}}$$

$\eta_{1B} = 1-\eta_{1A}$

$\eta_{2B} = 1-\eta_{2A}$

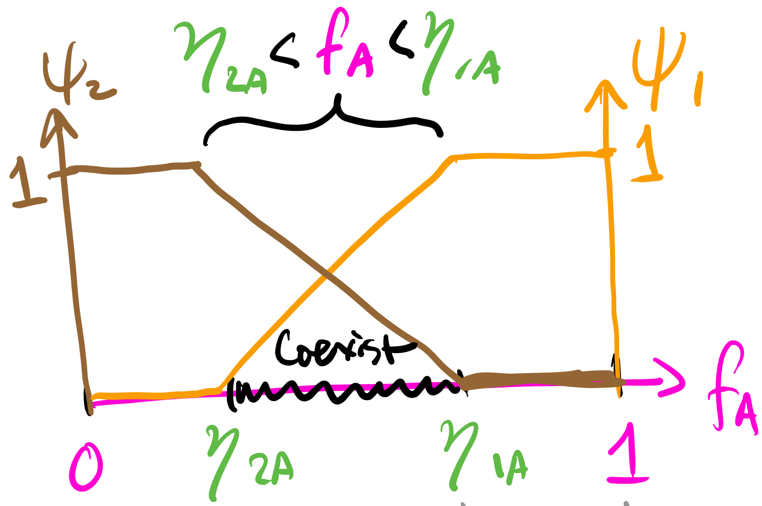
$f_B = 1-f_A$

$$= \frac{f_A - \eta_{2A}}{\eta_{1A}-\eta_{2A}}$$

Ecological phase diagram

$\eta_{1A} > \eta_{2A}$

(Sp. 1 invests more in nutrient A than Sp 2)



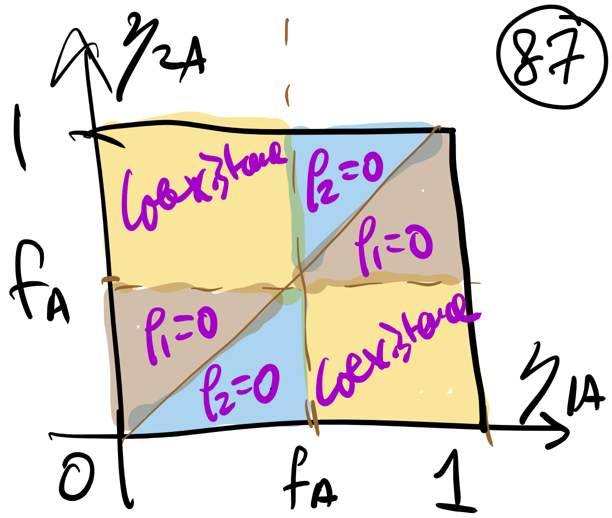
nutrient is B-rich
Sp1 made wrong investment.

nutrient is A-rich
Sp1 invest more in A

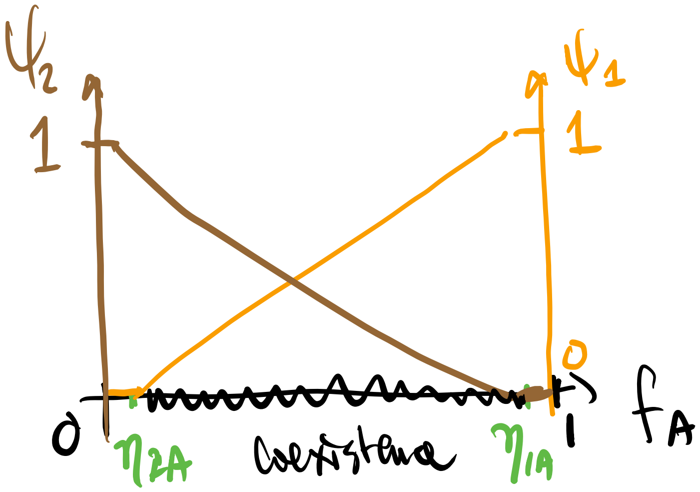
feasibility space (fixed f_A)

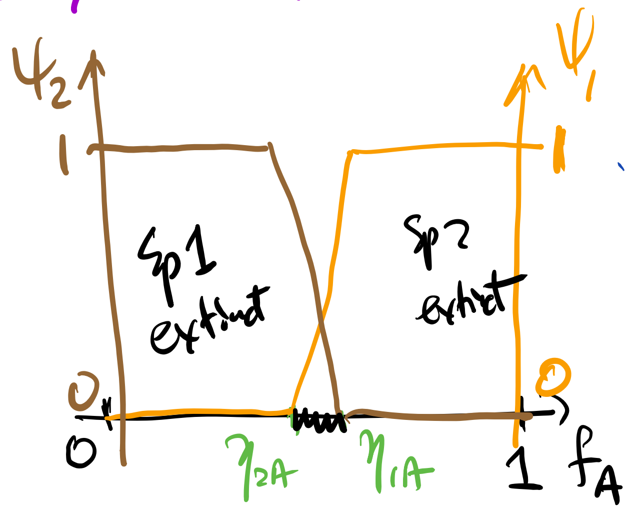
$\eta_{2A} < \eta_{1A}$: $\eta_{2A} < f_A < \eta_{1A}$

$\eta_{1A} < \eta_{2A}$: $\eta_{1A} < f_A < \eta_{2A}$



- Coexistence favored if $\eta_{2A} \to 0$, $\eta_{1A} \to 1$
  or $\eta_{2A} \to 1$, $\eta_{1A} \to 0$





- Starting from $\eta_{2A} \simeq 0$, $\eta_{1A} \simeq 1$
  if η_{2A} increases toward f_A, sp 2 removes sp 1
  or if η_{1A} decreases toward f_A, sp 1 removes sp 2.

- however, if $\eta_{1A} \to f_A$ + $\eta_{2A} \to f_A$, then each sp. risks extinction if f_A fluctuates

$\Rightarrow$ given a distribution of f_A
what is the evol. stable dist of η_1, η_2?

Generalization to 3 (or more) nutrients (A,B,C)

$$\begin{cases} \dot{\rho}_i = \left(\sum_\alpha \nu_{i\alpha} n_\alpha - \mu\right)\rho_i = \left(\sum_\alpha \nu^0_\alpha \eta_{i\alpha} n_\alpha - \mu\right)\rho_i \\ \dot{n}_\alpha = \mu\left(n^0_\alpha - n_\alpha\right) - \sum_i \nu^0_\alpha \eta_{i\alpha} n_\alpha \rho_i / Y_\alpha \end{cases}$$

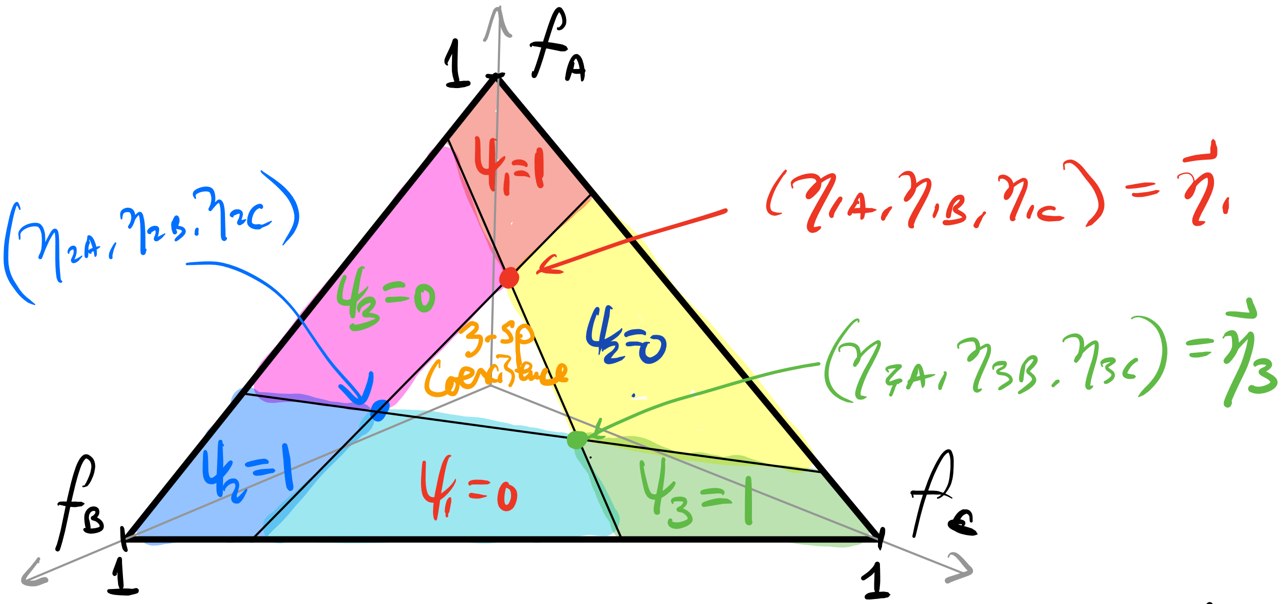
* Consider 3 species ρ_1, ρ_2, ρ_3 with nutrient uptake rates

$\nu_{1\alpha} = \nu^0_\alpha \eta_{1\alpha}$, $\nu_{2\alpha} = \nu^0_\alpha \eta_{2\alpha}$, $\nu_{3\alpha} = \nu^0_\alpha \eta_{3\alpha}$ $\left(\sum_\alpha \eta_{i\alpha} = 1;\ 6 \text{ independent } \eta\text{'s}\right)$

phase space: $f_\alpha = n^0_\alpha Y_\alpha / \sum_\alpha n^0_\alpha Y_\alpha$, with $f_A + f_B + f_C = 1$

→ Can represent results succinctly in simplex

(Posfai et al, 2017; work out in HW)



- each position in this space represents the value of $\{f_\alpha\}$
- Strain property shown as colored dots ($f_\alpha = \eta_{i\alpha}$)
- colored regions: phases of partial coexistence

⇒ phase boundary obtained simply by connecting $\overline{\eta_1 \eta_2}$, $\overline{\eta_2 \eta_3}$, $\overline{\eta_3 \eta_1}$

* Important observation by Posfai et al

for the class of constrained CR model $\nu_{i\alpha} = \nu_\alpha^0 \eta_{i\alpha}$

fixed point condition:

$$\dot{\rho}_i = 0 = \rho_i^* \cdot \left(\sum_\alpha \nu_\alpha^0 \eta_{i\alpha} n_\alpha^* - \mu \right)$$

$$\dot{n}_\alpha = 0 = \mu (n_\alpha^0 - n_\alpha^*) - \sum_i \nu_\alpha^0 \eta_{i\alpha} n_\alpha^* \rho_i^* / Y_a$$

if $n_\alpha^* = \mu / \nu_\alpha^0$,

then $\sum_\alpha \eta_{i\alpha} = 1$ guarantees $\dot{\rho}_i = 0$ if $\rho_i^* \neq 0$

for arbitrary # species (even if $N_C > N_R$)

$$\dot{n}_\alpha = 0 \rightarrow n_\alpha^0 Y_\alpha = \sum_i \eta_{i\alpha} \rho_i^* \qquad (n_\alpha^* \ll n_\alpha^0)$$

or $\sum_i \eta_{i\alpha} \psi_i^* = f_\alpha$ (feasability condition)

→ can show for each species $j \notin \{1,2,3\}$ whose $\eta_{j\alpha}$ lies in the white region defined by $\eta_{1\alpha}, \eta_{2\alpha}, \eta_{3\alpha}$

that $\psi_j > 0$ and $\dot{\rho}_j = 0$

→ with many species, the coexistence region is specified by the "complex hull" of all $\eta_{i\alpha}$

→ 3 "keystone" sp. with $\eta_{i\alpha} = (1,0,0), (0,1,0), (0,0,1)$ would suffice to support the coexistence of infinite # of intermediate species.