B4. Constrained CR model:

Recall for single species (i), two nutrients (A, B)

$$w_{iA} M_c^{i,A} = -\dot{n}_A \qquad \Big| \qquad M_c^{i,A} = \eta_{iA} M_c^i \qquad \Big| \qquad \frac{M_c^i}{M^i} = \phi_{max}^i \left(1 - \frac{r_i}{r_c^i}\right)$$

$$w_{iB} M_c^{i,B} = -\dot{n}_B \qquad \Big| \qquad M_c^{iB} = \eta_{i,B} M_c^i$$

$$\hookrightarrow \sum_\alpha \eta_{i,\alpha} = 1 .$$

flux matching: $w_{i,A} M_c^{iA} Y_A + w_{i,B} M_c^{iB} Y_B = r_i M^i$

$$k_c^\alpha = w_\alpha Y_\alpha$$

$$k_c^{iA} \cdot \frac{M_c^{iA}}{M^i} + k_c^{iB} \frac{M_c^{iB}}{M^i} = r_i$$

$$\left(k_c^{iA} \cdot \eta_{iA} + k_c^{iB} \eta_{iB}\right) \frac{M_c^i}{M_i} = r_i$$

$$\left(k_c^{i,A} \cdot \eta_{iA} + k_c^{iB} \cdot \eta_{iB}\right) \phi_{max}^i = \frac{r_i}{1 - \frac{r_i}{r_c^i}} \simeq r_i$$

MM kinetics of uptake proteins:

$$k_c^{i\alpha} = k_{c,max}^{i\alpha} \frac{n_\alpha}{n_\alpha + K_{i\alpha}}$$

for small n_α, $r_i \simeq \overbrace{\underbrace{\frac{k_{c,max}^{iA}}{K_{iA}} \phi_{max}^i}_{\nu_{iA}^0} \eta_{iA}}^{\nu_{iA}} n_A + \overbrace{\underbrace{\frac{k_{c,max}^{i,B}}{K_{iB}} \phi_{max}^i}_{\nu_{iB}^0} \eta_{iB}}^{\nu_{iB}} n_B$

Hypothesis 1: Similar properties for catabolic enzymes for different species in community

(due to, e.g. chemical limit, HGT)

Hypothesis 2: Similar constraint for different species in community

(i.e., Same Φ_{max} for diff. species)

$$\Rightarrow \quad \nu^0_{i,\alpha} = \nu^0_{\alpha} \quad \text{(independent of sp } i\text{)}$$

$$\Rightarrow \quad \nu_{i\alpha} = \nu^0_{\alpha} \cdot \eta_{i,\alpha}$$

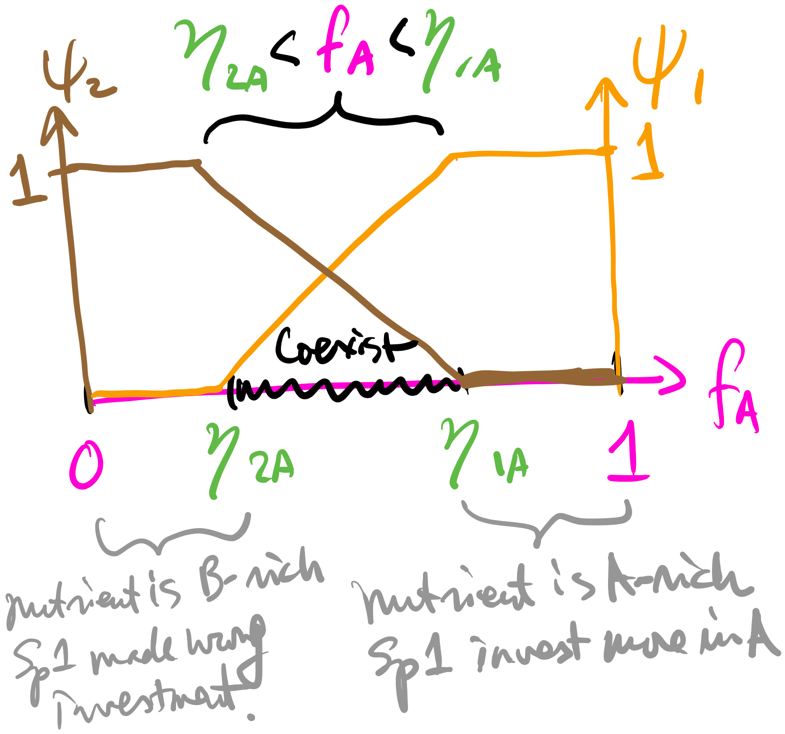
$\eta_{1B} = 1 - \eta_{1A}$
$\eta_{2B} = 1 - \eta_{2A}$

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

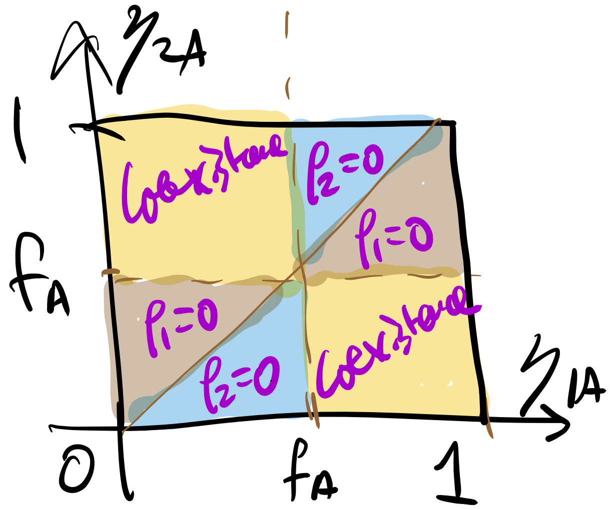
Ecological phase diagram

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

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



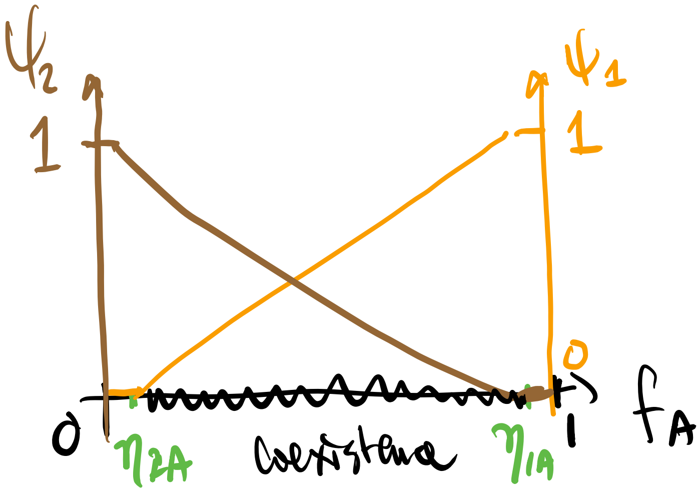
feasibility space (fixed f_A)

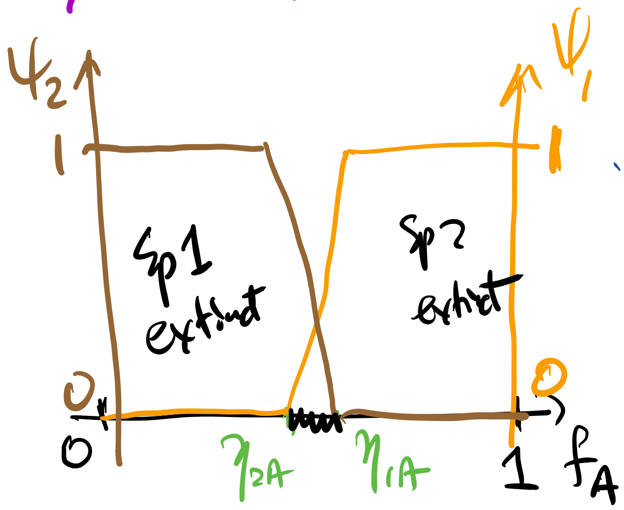


$\eta_{2A} < \eta_{1A}$: $\eta_{2A} < f_A < \eta_{1A}$

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

- 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?

Extend ecological phase diagram to 3 nutrients (A, B, C)

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

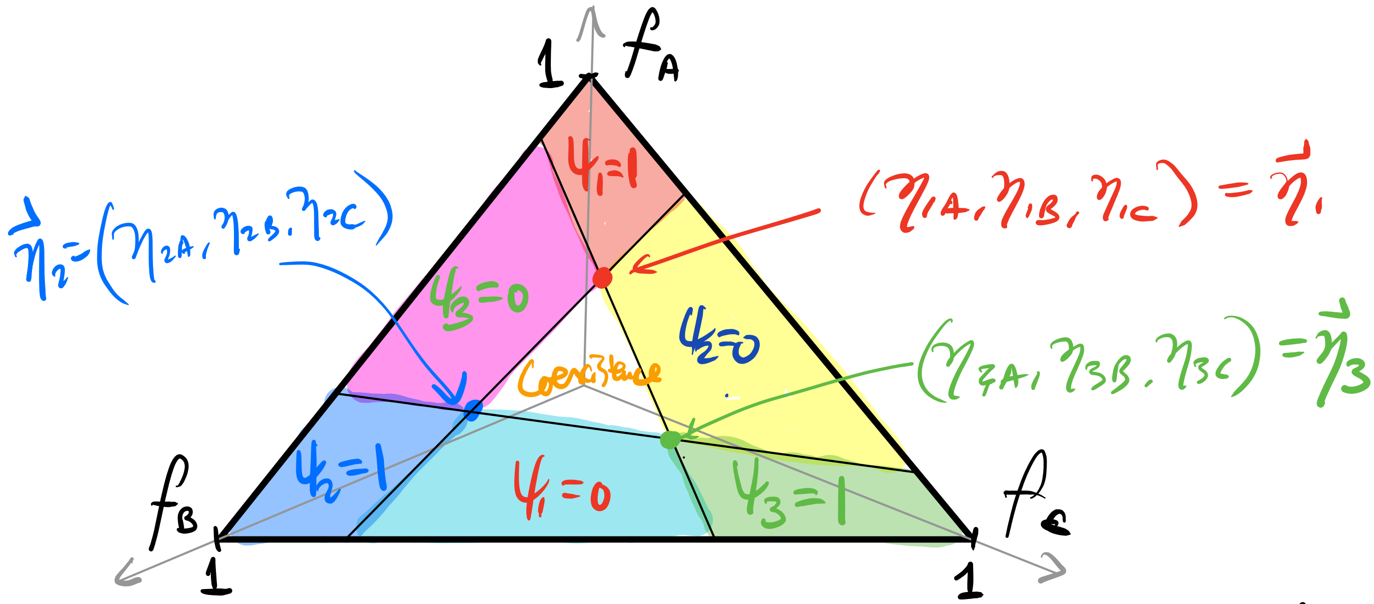
* Consider 3 species ρ_1, ρ_2, ρ_3 with nutrient uptake rates

$\nu_{1\alpha} = \nu_\alpha^0 \eta_{1\alpha}$, $\nu_{2\alpha} = \nu_\alpha^0 \eta_{2\alpha}$, $\nu_{3\alpha} = \nu_\alpha^0 \eta_{3\alpha}$ ($\sum_\alpha \eta_{i\alpha} = 1$; 6 independent parameters)

phase space: $f_\alpha = n_\alpha^0 Y_\alpha / \sum_\alpha n_\alpha^0 Y_\alpha$, 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 $N_c > N_R$)

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

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

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

$\psi_j > 0$, and $\dot{\rho}_j = 0$ satisfied by $\sum_\alpha \eta_{j\alpha} = 1$

→ 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.