c) Tilman's graphical analysis of Coexistence (D. Tilman, 1980)

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

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

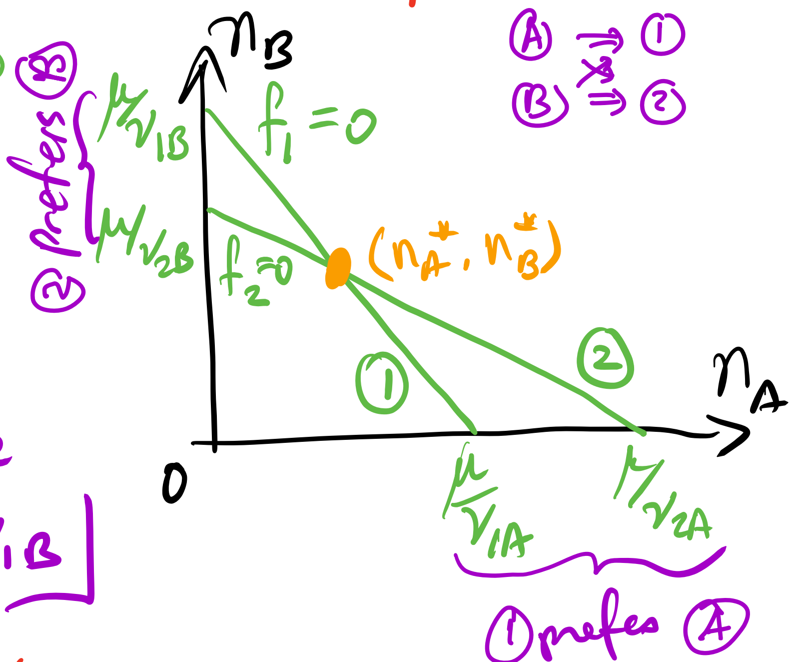
$$\dot{n}_A = \mu(n_A^0 - n_A) - (\nu_{1A}\rho_1 + \nu_{2A}\rho_2)\, n_A / Y_A$$

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

Tilman: Analyze dynamics in (n_A, n_B) plane

first, $\dot{\rho}_1 = 0$, $\dot{\rho}_2 = 0$ with $\rho_1^*, \rho_2^* > 0$ (B)

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



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

→ focus on the effect of sp ① and ② on nutrient Ⓐ + Ⓑ:

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

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 flux-balance between nutrient source $\vec{J}_0$ and sink $(\vec{J}_1, \vec{J}_2)$

- coexistence: can flux balance be obtained at (n_A^*, n_B^*) with $\rho_1^*, \rho_2^* > 0$ (if not, which species dominate?)

- transient: at some $(\hat{n}_A, \hat{n}_B) \neq (n_A^*, n_B^*)$, does the flow take the system to (n_A^*, n_B^*)?

$\Rightarrow$ represent the balance of J_0 and J_1, J_2 graphically in (n_A, n_B) plane:

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

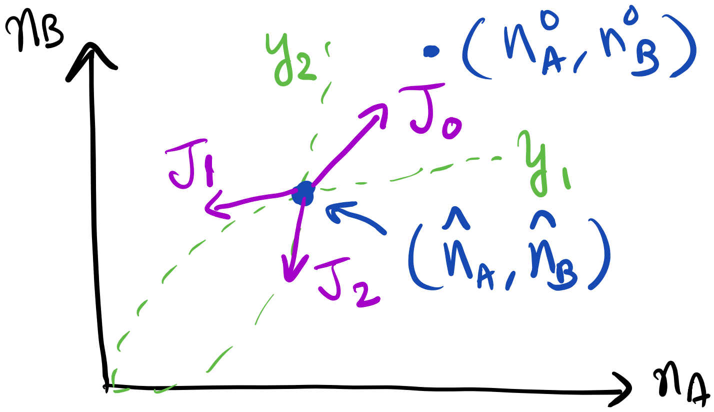
$$\frac{dn_B}{dn_A} = m_1 \frac{n_B}{n_A} \rightarrow n_B = c\, n_A^{m_1} \text{ or } \boxed{n_B = \hat{n}_B \left(\frac{n_A}{\hat{n}_A}\right)^{m_1}}$$

$\Rightarrow \vec{J}_1$: tangent of $n_B = \hat{n}_B \left(\dfrac{n_A}{\hat{n}_A}\right)^{m_1}$

Similarly, $\vec{J}_2$ is tangent of $n_B = \hat{n}_B \left(\dfrac{n_A}{\hat{n}_A}\right)^{m_2}$

take $m_1 < 1$ (① better at consuming Ⓐ)

$m_2 > 1$ (② better at consuming Ⓑ)

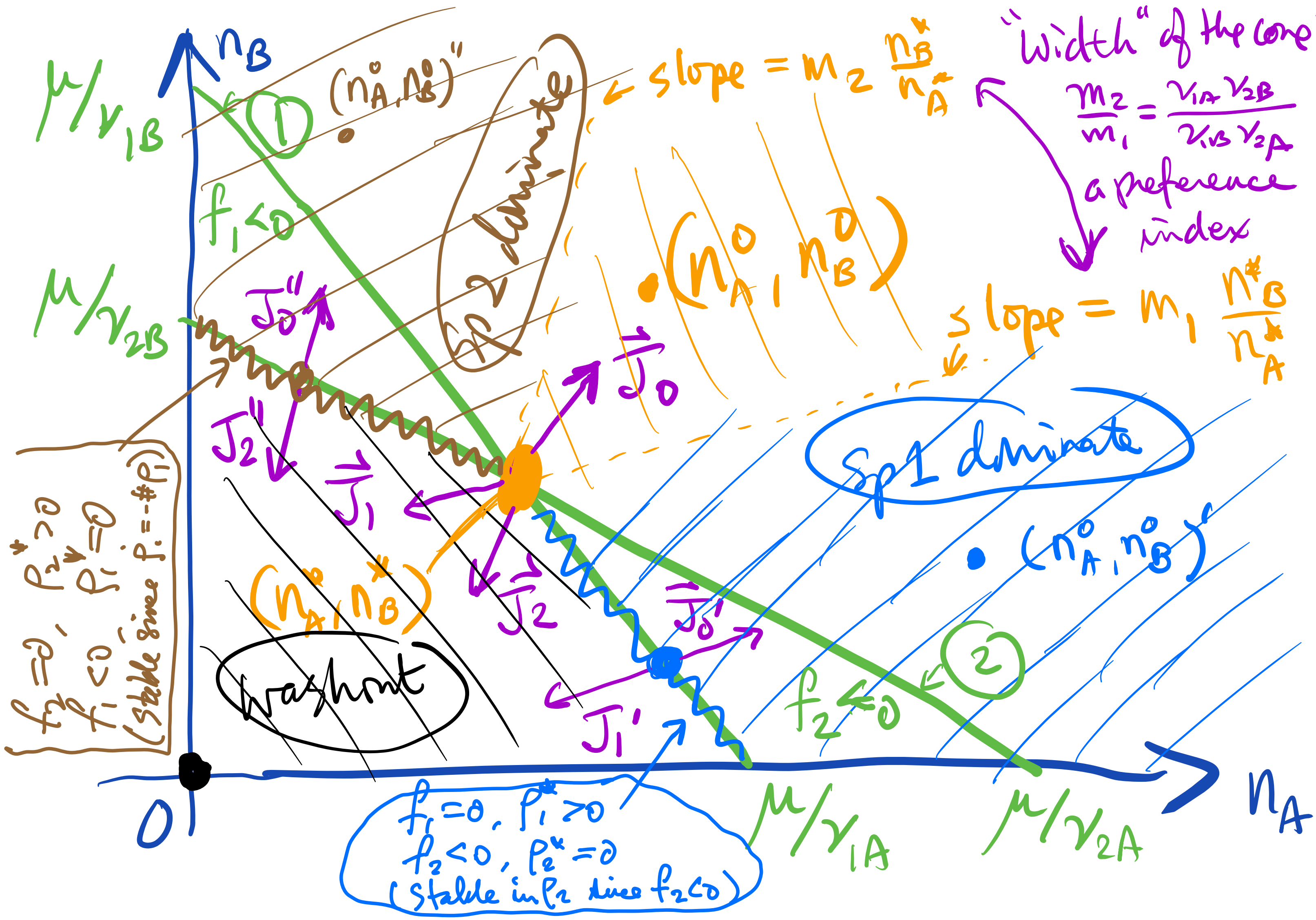


$m_1 = \dfrac{\nu_{1B}/Y_B}{\nu_{1A}/Y_A}$, $m_2 = \dfrac{\nu_{2B}/Y_B}{\nu_{2A}/Y_A}$

- 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 null clines $f_1(n_A, n_B) = f_2(n_A, n_B) = 0$

* 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 cone, $\rho_1^*, \rho_2^* > 0$ 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:

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

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

Sol'n:

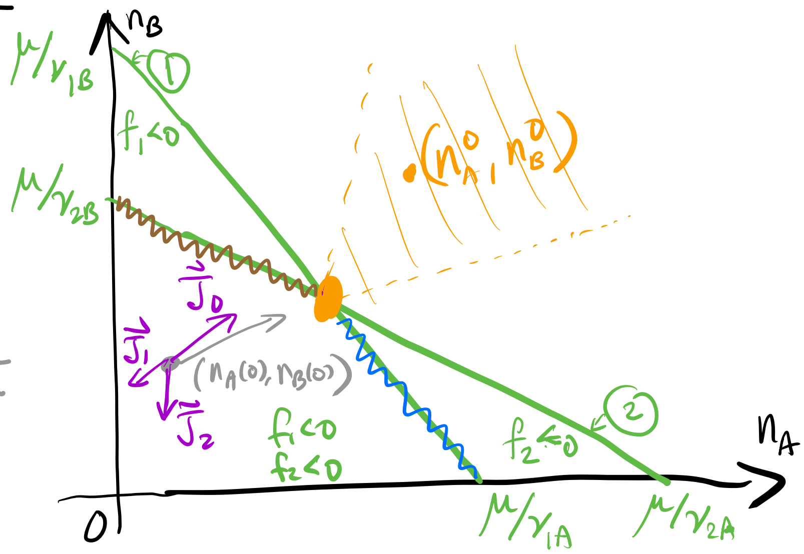
$$\begin{bmatrix} \rho_1^* \\ \rho_2^* \end{bmatrix} = \frac{\mu}{\det(\nu^T)} \begin{bmatrix} \nu_{2B} \frac{n_A^0 - n_A^*}{n_A^*} Y_A - \nu_{2A} \frac{n_B^0 - n_B^*}{n_B^*} Y_B \\ -\nu_{1B} \frac{n_A^0 - n_A^*}{n_A^*} Y_A + \nu_{1A} \frac{n_B^0 - n_B^*}{n_B^*} Y_B \end{bmatrix}$$

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

* Next look at different initial conditions $(n_A(0), n_B(0))$ (72)
for (n_A^0, n_B^0) within coexistence cone for domain of attraction of the fixed pt



- Starting from grey point $(n_A(0) < n_A^*,\ n_B(0) < n_B^*)$
- Suppose $\rho_1(0), \rho_2(0)$ are such that

$$\mu J_0 = \rho_1(0) J_1 + \rho_2(0) J_2$$

→ dynamics leads smaller $\rho_1\ \rho_2$ (since $f_1<0, f_2<0$), driving the grey point towards fixed pt (orange)

⇒ will show in Sec. I 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 towards fixed point.

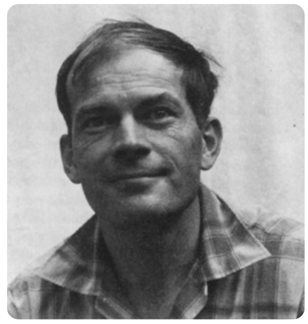
⇒ diagram above can be taken as "ecological phase diagram" (gives the fate of system for environmental parameters (n_A^0, n_B^0, μ))

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

B2. Stability in generalized CR model

Recall generalized Lotka-Volterra model:

$$\dot{\rho}_i = \left(r_i - \sum_j A_{ij}\,\rho_j\right)\rho_i$$



Many-Species CR Model

(Robert MacArthur, 1970)

$$\dot{\rho}_i = \sum_{\alpha=1}^{N_R} v_{i\alpha}\, n_\alpha\, \rho_i - \mu_i \rho_i$$

N_R = # "resources"
N_C = # "consumers"

$$\dot{n}_\alpha = \gamma_\alpha n_\alpha \left(1 - n_\alpha / K_\alpha\right) - \sum_{i=1}^{N_C} v_{i\alpha}\, n_\alpha\, \rho_i \,/\, Y_\alpha$$

Compared to the CR model in Sec. IIB1,

$$\dot{\rho}_i = \left[\sum_\alpha v_{i\alpha}\, n_\alpha - \mu\right]\rho_i$$

$$\dot{n}_\alpha = \mu\left(n_\alpha^0 - n_\alpha\right) - \sum_i v_{i\alpha}\, n_\alpha\, \rho_i \,/\, Y_e$$

nutrient in MacArthur's model "self-generated",

$$\gamma_\alpha n_\alpha \leftrightarrow \mu n_\alpha^0, \quad K_\alpha \leftrightarrow n_\alpha^0$$

- makes mathematics simpler
- no major diff. except for dependence on specific parameters

(see Butler & O'Dwyer, 2018)

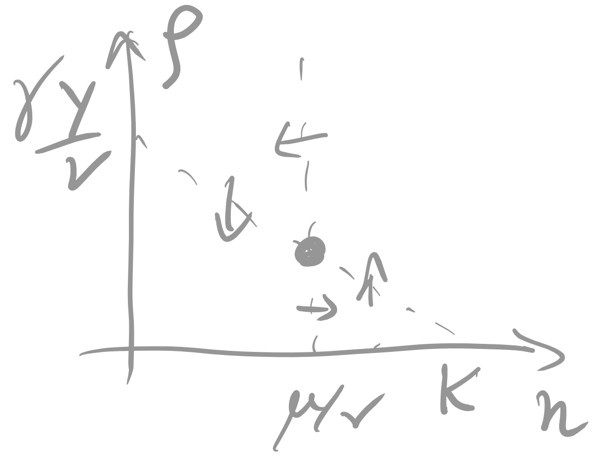
MacArthur showed feasible sol'n ($\rho_i^* > 0, n_\alpha^* > 0$) are global attractor of CR dynamics as long as $N_C \le N_R$, i.e., $\le$ one species/niche = "ecological exclusion principle"

$\rightarrow$ We reconstruct below MacArthur's work.

- recall predator-prey dynamics with carrying cap. (See IA3b)

$$\dot{n} = \gamma \cdot n (1 - n/K) - \nu n \rho / Y \qquad n = \text{prey}$$
$$\dot{\rho} = \nu n \rho - \mu \rho \qquad \rho = \text{predator}$$

Steady-state: $\nu n^* = \mu$
$\gamma \cdot (1 - n^*/K) = \nu \rho^* / Y$



$\rightarrow$ fixed point $\rho^* = \frac{\gamma Y}{\nu}(1 - \mu/\nu K)$
is stable if $\mu/\nu < K$ ($\rho^* > 0$)

General N_R, N_C:

fixed pt $\rho_i^* = \sum_j A_{ij}^{-1} r_j$ is Stable

with $r_i = \sum_\alpha \nu_{i\alpha} K_\alpha - \mu_i$, $A_{ij} = \sum_\alpha \nu_{i\alpha} \nu_{j\alpha} K_\alpha / \gamma_\alpha Y_\alpha$

if $N_R \ge N_C$: Competitive exclusion

$\rho_i^* > 0$: Stability = feasibility