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 \( s \).
- Produces its own nutrient \( n \) (e.g., fix \( \text{CO}_2 \), degrade \( \text{chitin} \)).

\[
\dot{s} = r(n)s - ms, \quad \dot{n} = s_0 \frac{n}{n+k}
\]

\[
\dot{n} = \frac{gs}{\text{production} \; \text{rate}} - \mu n - r(n)s/\gamma
\]

Take \( \dot{n} = 0 \) (rapid eqn of \( n \)).

\[
\dot{s} = \frac{\mu n}{\gamma - r(n)}/\gamma = \frac{n\gamma r(n)}{\gamma \gamma r(n) - 1} = \frac{\mu Y_{0} (n+k)}{r_{0} (n+k - 1)}
\]

\[
= \frac{\mu (n+k)}{(s - r(n)\gamma) + Y\frac{K}{n}}
\]

Two cases:

i) \( s \gg r_{0}/\gamma \) (bottleneck = uptake)

Insert \( n(p) \) into eqn for \( s \)
for small \( n \approx 0 \):
\[
\dot{n} = r(n) - n - \mu n = \left( \frac{r_0}{K} \right) n - \mu n
\]

\( p = \frac{\mu c K}{n_0} \)

\( p \to 0 \) if \( p(0) < P_0 = \frac{r_0}{K} \)

for \( p > P_0 \), increase in \( p \) \to increase in \( n \)
\[
\dot{n} = r_0 n - \mu n
\]

\( \dot{n} = r_0 n - \mu n \to \dot{n}(t) = e^{(r_0 - \mu)t} \)

\( \Rightarrow \) even at high production rate \( r_0 \), growth of population occurs only for sufficiently large initial pop size.

Why: nutrient production requires \( p \) (\( n \approx 0 \) for small \( p \))

\( p \approx r_0 n \) (bottleneck = production)

\( \dot{n} = \frac{\gamma n (n - c)}{c} - \mu n - r(n) \)

\( \frac{\dot{n}}{n} = \frac{\gamma n - c}{c} - \mu \)

\( \dot{n} \to 0 \) as \( n \to n^* = \frac{cK}{\gamma c - \mu} \)

\( n^* = \frac{cK}{\gamma c - \mu} \)

Cyclical where production = consumption

(Will show below this is the steady state curve where cells grow)
For $\gamma \ll \gamma_0 / Y$, \( \frac{\gamma}{K} \ll 1 \), can approximate \( r(n) \approx \frac{r_0 n}{K} \).

Corresponding growth rate: \( r(n^*) = \frac{r_0 n^*}{K} = \gamma Y \approx \gamma^* \).

\[
\dot{\gamma} = \gamma (\mu + \frac{r_0}{\gamma Y} \gamma)
\]

\[
\rho = [\frac{\gamma^*}{\mu} \rho(n) - \mu] \rho
\]

\[
= \left( \frac{\gamma^*}{\mu} \frac{\rho}{\rho + \gamma^*} - \mu \right) \rho
\]

\[
\sigma^* = \gamma Y
\]

\[
\sigma = \gamma Y - \mu
\]

\[
\Rightarrow \text{pop survives only if } \gamma Y > \mu.
\]

Note 1: batch culture growth: Allee effect manifested as an in-itec-dependent lag period.

Note 2: \( \gamma \) treated so far as fixed quantity. It is actually regulated and GR dependent.

\[
\gamma^* = \gamma Y K / r_0 \quad \text{Set by cell increasing} \gamma \text{ increases } \gamma^* \text{ increases growth but also invite "cheaters" how to set } \gamma \text{ (in presence of exogenous } \gamma) ?
\]
b) Multiple species: "Cheaters" (parasitism) 
- 2 species, 1 nutrient

\[ \begin{align*}
\dot{P}_1 &= r_1(n) P_1 - \mu S_1 + r_2(n) P_2 - \mu S_2 \\
\dot{P}_2 &= r_2(n) P_2 - \mu S_2
\end{align*} \]

\[ \hat{n} = \dot{P}_1 - \mu n - c_1(n) \frac{P_1}{Y} - c_2(n) \frac{P_2}{Y} \]

produced only by species 1 (called "producer")

Consider \( \gamma Y < c_1^0 \rightarrow n^* < k_1 \) use \( c_1(n) = \frac{c_1^0 n}{K_1} \equiv n \cdot c_1^0 \)

. rapid equil of \( n (n = 0) \),

\[ \gamma \hat{P}_1 = n^* \left[ \mu + (\nu_1 \nu_1 + \nu_2 \nu_2) / \gamma \right] \]

\[ n^* = \frac{\gamma \hat{P}_1 \gamma}{\mu \gamma + \nu_1 \nu_1 + \nu_2 \nu_2} \]

from \( \dot{P}_1 = (\gamma \cdot n - \mu) \hat{P}_1 \),

the critical pt for the growth of \( P_1 \) is at

\[ n^* (P_1, P_2) = \frac{\mu}{\nu_1} \] (where \( \hat{P}_1 = 0 \))

\[ \frac{\mu \gamma + \mu \nu_1 P_1 + \mu \nu_2 P_2}{n} = \gamma \cdot P_1 \]

\[ P_2 = \frac{\mu \gamma + \mu \nu_1 P_1}{\mu + \mu \nu_2} \]

\[ P_2 = \frac{\gamma \cdot P_1}{\gamma \cdot Y - \mu} \]

\[ \rightarrow \text{uptake by Sp} \ 2 \ (i.e. \nu_2 > 0) \]

Increases threshold for growth of Sp \( 1 \)
b) Multiple species: "Cheaters" (parasitism)
- 2 species, 1 nutrient

\[ \dot{p}_1 = r_1(p_1 - mp_1) \]
\[ r_i(p) = \frac{r_i^0 n}{n + Ki} \]

\[ \dot{p}_2 = r_2(p_2 - mp_2) \]

\[ \dot{n} = r_1 p_1 - \mu n - \frac{r_1(p_1)}{Y} - \frac{r_2(p_2)}{Y} \]

Produced only by species 1 (called "producer")

Consider \( Y Y << r_1^0 \rightarrow n^* \ll K \); use \( r_1(n) = \frac{r_1^0 n}{K_i} \equiv n \cdot n \)

Rapid equil. \( \gamma n (\nu = 0) \),

\[ \dot{p}_1 = \gamma \left[ n + (\nu_1 p_1 + \nu_2 p_2) / Y \right] \]

\[ n^* = \frac{\dot{p}_1 \gamma}{\mu Y + \nu_1 p_1 + \nu_2 p_2} \]

From \( \dot{p}_1 = (\gamma, n - \mu) p_1 \),

The critical pt for the growth of \( p_1 \) is at

\[ n^*(p_1, p_2) = \mu / Y \] (where \( \dot{p}_1 = 0 \))

\[ \frac{\Delta}{\gamma} - \mu Y + \mu p_1 + \mu \frac{\nu_2}{\gamma} p_2 = \gamma p_1 \]

\[ p_2 = \frac{\Delta \cdot \mu Y + \mu \frac{\nu_2}{\gamma} p_2}{\gamma \cdot Y - \mu} \]

\( \rightarrow \) uptake by sp 2 (i.e. \( \nu_2 > 0 \))

Increases threshold for growth of sp 1
Next, \( \dot{p}_2 = (\nu_2 n^2 - \mu) \cdot p_2 \)

\[ h(p_1, p_2) = \frac{\nu_1}{\nu_2} = \frac{\nu_1}{\nu_2} \cdot \frac{Y - \mu}{\nu} \]

\[ p_i = \frac{\nu_1}{\nu_2} \cdot Y + \mu p_2 \]

\[ \text{Phase flow:} \]

\[ p_1 = p_1 \left[ \gamma_1 \cdot \frac{\nu_1}{\mu + \nu_1 p_1 + \nu_2 p_2} - \mu \right] \]

\[ p_2 = p_2 \left[ \frac{\nu_1}{\mu + \nu_1 p_1 + \nu_2 p_2} - \mu \right] \]

for \( \nu_1 > \nu_2 \),

\[ \dot{p}_2 > 0 \text{ where } \dot{p}_1 = 0 \]

\[ \dot{p}_2 < 0 \text{ where } \dot{p}_1 = 0 \]

\[ \rightarrow \text{ Allee effect involves combo of } p_1(0), p_2(0) \]

\[ \rightarrow \text{ Sp} 2 \text{ enlarges the region of extinction (hence parasites)} \]

\[ \dot{p}_1(0) > p_i^c = \frac{\mu \cdot \mu Y}{\nu(Y - \nu)} \]  
[find boundary in this]

\[ \text{growth phase:} \]

at \( \text{con} \ n^* \),

\[ \lambda_1 = \nu_1 n^* - \mu > \lambda_2 = \frac{\nu_1}{\nu_2} n^* - \mu \]

\[ p_1 \propto e^{\lambda_1 t} \Rightarrow p_2 \propto e^{\lambda_2 t} \]

\[ \n^* = \frac{\gamma_1 p_1(t) Y}{\mu Y + \nu_1 p_1(t) + \nu_2 p_2(t)} \]

\[ \rightarrow \text{ Sp} 2 \text{ gets a free ride at } \lambda_2 = \frac{\nu_1}{\nu_2} \cdot \frac{Y - \nu}{\nu} \]

\[ \Rightarrow \text{ does not affect growth of sp} 1 \text{ (in growth phase)} \]
for \( v_2 \geq v_1 \),

\[
\begin{align*}
\dot{p}_2 &> 0 \text{ where } \dot{p}_1 = 0 \\
\dot{p}_1 &< 0 \text{ where } \dot{p}_2 = 0
\end{align*}
\]

\( \Rightarrow \) excitable dynamics

for \( p_1(0) > p_1^c \), \( p_2(0) > 0 \). Eventually headed for extinction

\( \Rightarrow \) increasing \( v_2 \) increases fitness of cheater; but too much will make it extinct (blackjack)

Assume growth phase exists. \( N = n^* \).

then \( \lambda_2 = v_2 n^*-\mu > \lambda_1 = v_1 n^*-\mu \) if \( v_2 > v_1 \)

\( \Rightarrow \)

\( n^* = \frac{\lambda_1 p_1(t)}{\lambda_2 + v_1 p_1(t) + v_2 p_2(t)} = \frac{n_1}{v_2} e^{(\lambda_1-\lambda_2)t} \rightarrow 0 \)

This scenario can be anticipated from 2-species on one nutrient in chemostat.

- Species with large \( v \) survives.

- If \( v_2 > v_1 \), then \( p_1 \rightarrow 0 \) but \( p_2 \) cannot exist alone

\( \Rightarrow \) no stable state if \( v_2 > v_1 \)
Cross-feeding of self-generated essential nutrients

- Species 1, 2 generates nutrient A, B respectively
- Each species need both nutrients to grow (e.g. $A = \text{carbon}, B = \text{Fe}$)

\[
\begin{align*}
\dot{p}_1 &= \left( r_1(n_0, n_3) - \mu \right) p_1 & n_0 &\xrightarrow{\text{diagram}} n_A \\
\dot{p}_2 &= \left( r_2(n_0, n_3) - \mu \right) p_2 & n_0 &\xrightarrow{\text{diagram}} n_B \\
\dot{n}_A &= Y_{\text{A}} p_1 - \mu n_A - r_1(n_0, n_3) p_1 / Y_A - r_2(n_0, n_3) p_2 / Y_A \\
\dot{n}_B &= Y_{\text{B}} p_2 - \mu n_B - r_1(n_0, n_3) p_1 / Y_B - r_2(n_0, n_3) p_2 / Y_B \\
\end{align*}
\]

Growth function: (from Sec IIA2)

\[ r_i = \left( \frac{1}{V_{iA} n_A} + \frac{1}{V_{iB} n_B} \right)^{-1} \]

For $n_A \ll K_{x_i}$ (for $Y_A \ll g_i / Y_A$)

- $\dot{p}_1 | p_1 = 0 \rightarrow \mu = \frac{1}{V_{iA} n_A} + \frac{1}{V_{iB} n_B}$
- $\dot{p}_2 | p_2 = 0 \rightarrow \mu = \frac{1}{V_{2A} n_A} + \frac{1}{V_{2B} n_B}$

- Fixed pt solns generically exist if $V_{iA} \neq V_{iB}$
- Expect Allee effect (since $S_i$ needed to generate $X_i$)
  - 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

\[ \dot{P}_1 = (\gamma_1(n_1, n_2) - \mu) P_1 \]

\[ \dot{P}_2 = (\gamma_2(n_1, n_2) - \mu) P_2 \]

\[ \dot{n}_A = \gamma_{1A} P_1 - \mu n_A - \gamma_1(n_1, n_2) P_1 / n_A - \gamma_2(n_1, n_2) P_2 / n_A \]

\[ \dot{n}_B = \gamma_{2B} P_2 - \mu n_B - \gamma_1(n_1, n_2) P_1 / n_B - \gamma_2(n_1, n_2) P_2 / n_B \]

Take small-\(\mu\) limit: \(\gamma_1' = \gamma_2' = \mu \ll \gamma_{1A}\)

\[ \dot{n}_A = 0 \rightarrow n_A = \gamma_{1A} P_1 / \mu \]

\[ \dot{n}_B = 0 \rightarrow n_B = \gamma_{2B} P_2 / \mu \]

\[ \gamma_1' = \left( \frac{1}{\gamma_{1A} n_A} + \frac{1}{\gamma_{2B} n_B} \right)^{-1} = \left[ \frac{\mu}{\gamma_{1A} \gamma_{2B} P_1} + \frac{\mu}{\gamma_{1A} \gamma_{2B} P_2} \right]^{-1} \]

\[ \gamma_2' = \left( \frac{1}{\gamma_{1A} n_A} + \frac{1}{\gamma_{2B} n_B} \right)^{-1} = \left[ \frac{\mu}{\gamma_{1A} \gamma_{2B} P_1} + \frac{\mu}{\gamma_{1A} \gamma_{2B} P_2} \right]^{-1} \]

\[ \dot{P}_1 = \gamma_1' \left[ \frac{1}{\gamma_{1A} \gamma_{2B} P_1} + \frac{1}{\gamma_{1A} \gamma_{2B} P_2} \right] - \text{effective GLV eqn} \]

\[ \frac{\dot{P}_1}{P_1} = 0 \Rightarrow \frac{1}{\gamma_{1A} \gamma_{2B} P_1} + \frac{1}{\gamma_{1A} \gamma_{2B} P_2} = \frac{1}{\mu^2} \]

\[ \frac{\dot{P}_2}{P_2} = 0 \Rightarrow \frac{1}{\gamma_{1A} \gamma_{2B} P_1} + \frac{1}{\gamma_{1A} \gamma_{2B} P_2} = \frac{1}{\mu^2} \]

\[ \gamma_{1A} > \gamma_{2A}, \; \gamma_{2B} > \gamma_{1B} \]

\[ \gamma_{1A} < \gamma_{2A}, \; \gamma_{2B} < \gamma_{1B} \]

\[ \Rightarrow \text{Why asymmetric? Need to look at high density state} \]
growth phase:
- Expect \( P_1(t) = P_1^* e^{\lambda_1 t} \), \( P_2(t) = P_2^* e^{\lambda_2 t} \) for large \( t \) with \( \lambda_1 = \lambda_2 > \mu \).
- If not, one of the nutrients will be depleted and \( \dot{P}_1, \dot{P}_2 \to 0 \) (since both nutrients are essential).

\[
\dot{P}_A = \gamma_{1A} P_1 - \mu P_A - \gamma_{2}(n_A, n_B) P_1/Y_A - \gamma_{2}(n_A, n_B) P_2/Y_A
\]
\[
\dot{P}_B = \gamma_{2B} P_2 - \mu P_B - \gamma_{1}(n_A, n_B) P_1/Y_B - \gamma_{1}(n_A, n_B) P_2/Y_B
\]

E.g., if \( \lambda_1 > \lambda_2 \), then \( \dot{P}_B \to 0 \). \( P_1/Y_B \to P_2^* = 0 \).

- For \( \lambda_1 = \lambda_2 \equiv \lambda \), must have \( \dot{P}_A > 0, \dot{P}_B > 0 \)
such that \( \gamma_{1}(n_A^*, n_B^*) = \gamma_{2}(n_A^*, n_B^*) = \gamma^* \), with \( \lambda = \gamma^* - \mu \).

Plug \( P_1(t) = P_1^* e^{\lambda_1 t} \) and \( P_2(t) = P_2^* e^{\lambda_2 t} \) (large \( t \)) into nutrient flux equs:

\[
\dot{P}_A = 0 \implies \mu P_A^* Y_A = [\gamma_{1A} Y_A - \gamma^* P_1^*] e^{\lambda_1 t}
\]

\[
\implies (\gamma_{1A} Y_A - \gamma^*) P_1^* = r^* P_2^*
\]

Similarly, \( (\gamma_{2B} Y_B - \gamma^* P_2^*) = r^* P_1^* \)

\[
\gamma^* = \left[ \left( \gamma_{1A} Y_A \right)^{-1} + \left( \gamma_{2B} Y_B \right)^{-1} \right]^{-1} < \min(\gamma_{1A} Y_A, \gamma_{2B} Y_B)
\]

\( (\dot{P}_A^*, \dot{P}_B^*) \) fixed from \( \gamma_1(n_A^*, n_B^*) = \gamma_2(n_A^*, n_B^*) = \gamma^* \)

Note: no dependence on \( V_{ia} \).
Stability? \( \mu = r^* \), so that \( \frac{p_1}{p_2} \to \frac{p_1^*}{p_2^*} \)

\[
\begin{align*}
\dot{p}_1 &= (r_1(n_a,n_b) - r^*) p_1 \\
\dot{p}_2 &= (r_2(n_a,n_b) - r^*) p_2
\end{align*}
\]

\[
\begin{align*}
Y_{A1A} &= (\delta_{1A} Y_A - r_1(n_a,n_b)) p_1 - r_2(n_a,n_b) p_2 \\
Y_{A1B} &= -r_1(n_a,n_b) p_1 + (Y_{2B} Y_B - r_2(n_a,n_b)) p_2
\end{align*}
\]

deviation from \( n_a, p_i^* \)?

Use Tilman's approach:

**Rabbits:**

\[
\begin{align*}
\dot{p}_1 &= 0 \quad \rightarrow \quad r_1(n_a,n_b) = r^* \\
\dot{p}_2 &= 0 \quad \rightarrow \quad r_2(n_a,n_b) = r^*
\end{align*}
\]

**Nutrient dynamics:**

\[
\begin{pmatrix}
Y_A n_A \\
Y_B n_B
\end{pmatrix}
= \begin{pmatrix}
Y_{1A} Y_A - r \\
-r
\end{pmatrix}
J_1
+ \begin{pmatrix}
- r \\
Y_{2B} Y_B - r
\end{pmatrix}
J_2
\]

**Steady state:** \( \frac{p_1}{J_1} + \frac{p_2}{J_2} = 0 \)
Perturbation from steady state:

Suppose $s_1$ increases from $p_1$.

Then $\dot{n}_A > 0$, $\dot{n}_B < 0$.

This moves system in region with $\dot{p}_1 < 0$, $\dot{p}_2 > 0$

→ restores perturbation in $p_1$

Suppose $V_{1A} < V_{2A}$, $V_{2B} < V_{1B}$

- Increase of $s_1$ leads to $\dot{n}_A > 0$, $\dot{n}_B < 0$

- System moves into region with $\dot{p}_1 < 0$, $\dot{p}_2 < 0$

→ further increase of $p_1$

Fixed at unstable → system collapses (extinction)

⇒ this asymmetry arises from production asymmetry

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