E. Consumer-Resource Model

- GLV model describes effective pairwise interaction between species, doesn't address mechanistic origin.
- "Random interaction" leads to global instability for large number of interacting species (May, 73).
- Incorporate more realistic interactions:
  - Competition for nutrients (Sec E)
  - Collaboration to scavenge (Sec F)

Want to know:
- Combinations of environmental parameters yielding coexistence/extinction/dominance ("ecological phase diagram")
- Combinations of physiological parameters yielding coexistence/extinction/dominance for given range of environment -> fitness landscape

→ focus on planktonic/microbial systems where the effect of nutrient on growth reasonably understood.

→ focus on exponential growth and neglect stationary phase + cell death
Continuous culture of single species

Common scenario:

- Nutrient influx \( j_0 \) at rate \( \mu \)
- Death at rate \( \mu \)

Mimicked by a chemostat:

- Nutrient of \( CMC \) dripping in at rate \( \mu \) \( (j_0 = \mu \cdot n_0) \)
- Medium (and cells) removed at rate \( \mu \)

\[
\begin{align*}
\frac{dp}{dt} &= r(n)p - \mu p \\
\frac{dn}{dt} &= n_0 \mu - n \mu - r(n)p/y
\end{align*}
\]

Monod growth law:

\[
r(n) = \frac{n}{n + K}
\]

Yield:

\[
Y = \frac{8p}{5n}
\]

A) Steady state:

- \( p(t) \rightarrow p^* \geq 0 \)
- \( n(t) \rightarrow n^* \leq n_0 \)

Constraint:

\[
S^* = (n_0 - n^*) \cdot Y \quad \text{(mass conservation)}
\]

Check:

\[
\frac{dp}{dt} + Y \cdot \frac{dn}{dt} = \mu \cdot [(n_0 - n(t))Y - p(t)]
\]

Fixed pt:

- \( r(n^*) = \mu \)

\[
\mu = \frac{n^*}{n^* + K} \Rightarrow \frac{n^*}{K} = \frac{\mu}{n_0 - \mu}
\]

Further, \( S^* > 0 \rightarrow n^* < n_0 \)

\[
\Rightarrow \frac{n_0}{K} > \frac{\mu}{n_0 - \mu} > 0
\]

Note: \( j_0 = \mu n_0 \quad \text{environmental} \quad n_0, K, \mu \quad \text{physiological} \)
General rule: chemostat culture "washes out" if $\mu$ too large or $n$ too small.

$$\tau(n) = \frac{\tau_0 n}{n + k}$$

Common: $\mu << \tau_0$

$$n^* << k$$

- Can linearize Model:

$$\tau(n) = \frac{\tau_0 n}{k} = \gamma n$$

(Will work with $\mu = \tau_0$ throughout, and use $\tau(n) = \gamma n$)

Criteria for stable chemostat culture becomes

$$\frac{n_0}{K} > \frac{\mu}{\tau_0 \cdot \mu} = \frac{\mu}{\tau_0} \rightarrow \mu < \gamma n_0$$

or $\mu < \sqrt{\gamma \cdot \tau_0}$ i.e., death rate < geo. mean of nutrient influx x uptake

$\rightarrow$ lone dimensionless parameter $\gamma = \frac{\mu K}{\tau_0 n_0} = \frac{\mu}{\gamma n_0}$

$\rightarrow$ Stability of chemostat requires $\gamma < 1$

Note that $\frac{n^*}{n_0} \approx \frac{\mu K}{\tau_0 n_0} = \gamma$

- from mass conservation $P^* = (n_0 - n^*) \gamma$
- also get $\frac{P^*}{P_0} = 1 - \gamma$ where $P_0 \equiv n_0 \gamma$ is max density

$\rightarrow$ can est $\gamma$ (hence $k$) from $\frac{n^*}{n_0} \approx \frac{P^*}{P_0}$
• Chemosat most stable when \( \gamma < 1 \)

In this limit, \( \frac{\gamma^*}{n_0} \approx \gamma < 1 \).

\[ p^* = (n_0 - n^*) Y \approx n_0 Y = p_0 \]

\( \rightarrow \) nutrient input mostly goes to biomass

• Opposite limit \( \gamma \to 1 \) (approaching wash out)

\[ \frac{\gamma^*}{n_0} \approx \gamma \to 1, \]

\[ p^* = (n_0 - n^*) Y = (1 - \gamma) p_0 \to 0 \]

\( \rightarrow \) low density approx quantitatively valid

(difficult to work with experimentally)

b) Dynamics

\[ \dot{p} = (r(n) - \mu) p = (\nu n - \mu) p \]

\[ \dot{n} = \mu(n_0 - n) - r(n)p/y = \mu(n_0 - n) - \nu n p / y. \]

\[ \text{Compare to the damped predator-prey system (Sec. A3)} \]

\[ \dot{p} = r p (1 - p / \alpha) - b p q \quad \text{nutrient (n) \rightarrow prey (p)} \]

\[ \dot{q} = c p q - \mu q \quad \text{cell (p) \rightarrow predator (q)} \]

\[ c \equiv v; \ b \equiv v / Y. \]
main difference:
- prey replicates at rate \( r_p(1-p/p_0) \)
- nutrient injected at rate \( \mu n_0 \) & diluted at \( \mu n \).

- Make dimensionless:
  \[
  \frac{n}{n_0} = u, \quad \frac{\rho}{\gamma n_0} = \nu, \quad \gamma n_0 \cdot t = \tau, \quad \frac{\mu}{n_0} = \zeta
  \]

\[
\begin{align*}
\frac{du}{d\tau} &= \gamma(1-u) - \nu u \\
\frac{d\nu}{d\tau} &= \nu \tau - \gamma \nu
\end{align*}
\]

- Perturbative analysis around \( u^*, \nu^* \)
  \[
  \lambda = \left\{ -\zeta, -1 + \zeta \right\} < 0 \quad (\text{if} \ \zeta < 1)
  \]

  In real time unit: \( \lambda \cdot n_0 = \left\{ -\mu, \mu - n_0 \right\} \)

  \( \rightarrow \) Instability as \( \mu \to n_0 \)
  \( \text{(washout)} \)

  \( \rightarrow \) Instability as \( \mu \to 0 \)
  \( \text{(reflects batch culture growth)} \)

  \( \Rightarrow \) vary chemostat setting by \( n_0 \)
  \( \text{while keep } \mu \ll n_0 \text{ const.} \)
For $\eta \to 1$,

- Fast mode: $\lambda_1 = -\eta = -1$.
- Slow mode: $\lambda_2 = 1 - \eta$

To find the fast/slow mode by solving for eigenvectors,

$$M \left( \begin{array}{c} x_i \\ y_i \end{array} \right) = \lambda_i \left( \begin{array}{c} x_i \\ y_i \end{array} \right) \Rightarrow \left( \begin{array}{cc} 1 - \eta & -\eta \\ -\eta & 0 \end{array} \right) \left( \begin{array}{c} x_i \\ y_i \end{array} \right) = \lambda_i \left( \begin{array}{c} x_i \\ y_i \end{array} \right)$$

For $\eta \to 1$, $\lambda_1 = -\eta$ is the fast mode

$$\Rightarrow (1-\eta)x_1 = -\eta y_1 \quad \Rightarrow (1-\eta)x_1 + \eta y_1 = 0$$

$\lambda_2 = 1 + \eta$ is the slow mode

$$\Rightarrow (1-\eta)x_2 = -(1+\eta)y_2 \quad \Rightarrow x_2 + y_2 = 0$$
\[ \text{Slow direction:} \]
\[
\dot{u} + \dot{\nu} = 1 \quad \text{or} \quad \frac{\dot{S}(t)}{Y} + \dot{\nu}(t) = n_0 \quad (\text{mass conserved})
\]

Recall from original eqns: \[
\dot{\nu} = (\nu n - \mu) \nu \\
\dot{n} = \mu(n_0 - n) - \nu n p / Y.
\]

\[ \Rightarrow \frac{\delta}{\delta t} (\nu S(t) + n(t)) = \mu (n_0 - n - p / Y) \]

\[ \Rightarrow \text{dynamics quickly converges to } \frac{\dot{S}(t)}{Y} + \dot{n}(t) = n_0 \]

Next, take this condition as a constraint and determine the dynamics of \( P(t) \):

\[ \Rightarrow \text{use } \dot{n}(t) = n_0 - \frac{\dot{S}(t)}{Y} \text{ in eqn for } P(t): \]

\[ \dot{\nu} = (\nu n - \mu) \nu = (\nu n_0 - \mu - \nu p / Y) \nu \]

\[ \Rightarrow \text{recover logistic growth eqn.} \]

\[ \dot{S} = r (1 - S / S_0) S \]

with \[ r = \nu n_0 - \mu = \nu n_0 (1 - \gamma) \]

\[ \hat{S} = \frac{(\nu n_0 - \mu) Y}{\nu} = S_0 (1 - \gamma). \]

\[ \Rightarrow \text{Approach to fixed point: } P(t) = \hat{S} + 8 \hat{p}(t) \]

\[ \dot{S} \hat{p} = -r \hat{S} \hat{p} = -\nu n_0 (1 - \gamma) \hat{S} \hat{p} \]

\[ \uparrow \text{slow} \]
Why is logistic growth recovered here?
- leading order expansion in $\delta$ when $\delta \propto (1-z)$ is small
- cost: long relaxation time: $r^{-1} \propto 1/(1-z)$

Not realistic to operate chemostat close to washout; expect results to be semi-quantitatively captured by logistic growth model (or generalized LV for multiple species)