II. 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, 72)
- incorporate more realistic interactions:
  - → competition for nutrients (Sec IIB)
  - → collaboration to scavenge (Sec IIC)

want to know

- combinations of environmental parameters yielding coexistence/extinction/dominance ("ecological phase diagram")
- combo 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

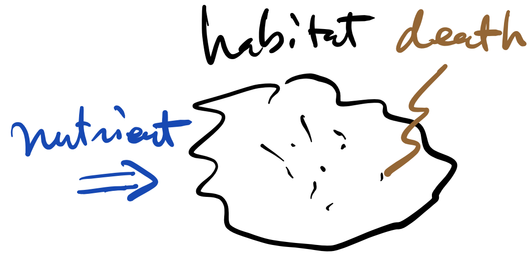
⇒ focus on exponential growth and neglect stationary phase + cell death

A1. Continuous culture of single species

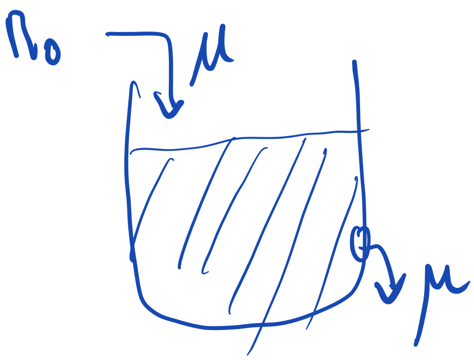
Common scenario:

nutrient influx j_0

death at rate δ



Mimicked by a chemostat:



- nutrient of conc n_0 dripping in at rate μ $(j_0 = \mu \cdot n_0)$
- medium (incl cells) removed at rate μ

$$\begin{cases} \dfrac{d\rho}{dt} = r(n)\rho - \mu\rho \\ \dfrac{dn}{dt} = n_0\mu - n\mu - r(n)\rho/Y \end{cases}$$

- Monod growth law: $r(n) = r_0 \dfrac{n}{n+K}$
- Yield: $Y = \dfrac{\delta\rho}{\delta n}$

a) Steady state: $n(t) \to n^* \le n_0$ nutrient in medium

$\rho(t) \to \rho^* \ge 0$

Constraint (indept of $r(n)$): $\rho^* = \underbrace{(n_0 - n^*)}_{\text{consumed nutrient}} Y$ (mass conservation)

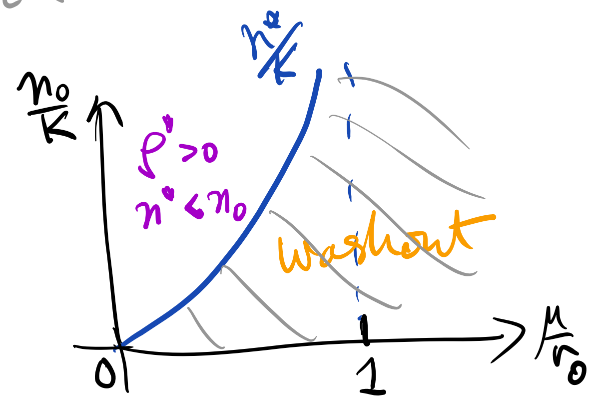
Check: $\dfrac{d\rho}{dt} + Y \cdot \dfrac{dn}{dt} = \mu \cdot \left[(n_0 - n(t))Y - \rho(t)\right]$ ✓

fixed pt: $r(n^*) = \mu$

$\to \dfrac{\mu}{r_0} = \dfrac{n^*}{n^*+K} \to \dfrac{n^*}{K} = \dfrac{\mu}{r_0 - \mu}$

further, $\rho^* > 0 \to n^* < n_0$

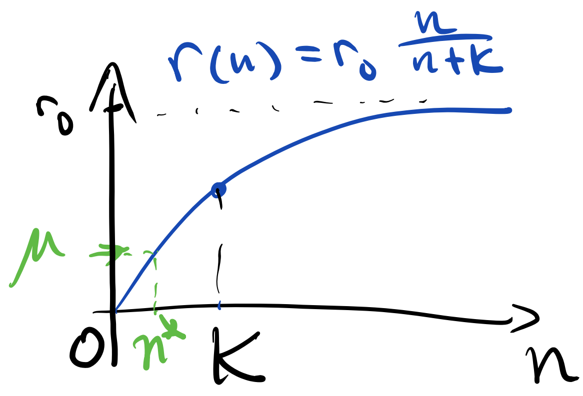
$\Rightarrow \dfrac{n_0}{K} > \dfrac{\mu}{r_0 - \mu} > 0$



Note: $j_0 = \mu n_0$: environmental

r_0, K, μ: physiological

general rule: chemostat culture "washes out" if μ too large or n_0 too small.



Common: $\mu << r_0$

$\rightarrow n^* << K$.

- Can linearize Monod:

$r(n) \simeq \frac{r_0 n}{K} \equiv \nu n$ ← r_0/K

(Will work with $\mu << r_0$ throughout, and use $r(n) = \nu n$)

Criterion for stable chemostat culture becomes

$\frac{n_0}{K} > \frac{\mu}{r_0 - \mu} \simeq \frac{\mu}{r_0} \rightarrow \mu < r_0 n_0/K = \nu n_0$

[For nutrient influx j_0, death rate $= \delta$.
$\rightarrow \delta < \nu \cdot j_0/\delta$ or $\delta < \sqrt{\nu \cdot j_0}$; i.e. death rate < geo mean]

$\rightarrow$ lone dimensionless parameter $\eta = \frac{\mu K}{r_0 n_0} = \frac{\mu}{\nu n_0}$

$\rightarrow$ stability of chemostat requires $\eta < 1$

[Note that $\frac{n^*}{K} = \frac{\mu}{r_0 - \mu} \overset{\mu << r_0}{\simeq} \frac{\mu}{r_0} \rightarrow \frac{n^*}{n_0} \simeq \frac{\mu K}{r_0 n_0} = \eta$

from mass conservation $\rho^* = (n_0 - n^*) Y$

also get $\frac{\rho^*}{\rho_0} = 1 - \eta$ where $\rho_0 \equiv n_0 Y$ is max density

$\rightarrow$ can est η (hence K) from $\frac{n^*}{n_0}$ or $\frac{\rho^*}{\rho_0}$]

- chemostat most stable when $\eta \ll 1$

in this limit, $\frac{n^*}{n_0} \simeq \eta \ll 1$.

$$\rho^* = (n_0 - n^*) Y \simeq n_0 Y \equiv \rho_0$$

$\rightarrow$ nutrient inflow mostly goes to biomass

(difficult to measure n^*, $\rho_0 - \rho^*$)

- opposite limit $\eta \to 1$ (approaching wash out)

$$\frac{n^*}{n_0} \simeq \eta \to 1,$$

$$\rho^* = (n_0 - n^*) Y = (1-\eta) \rho_0 \longrightarrow 0$$

(difficult to maintain experimentally)

b) Dynamics (relationship to logistic growth model)

$$\dot{\rho} = (r(n) - \mu) \rho = (\nu n - \mu) \rho$$

$$\dot{n} = \mu (n_0 - n) - r(n) \rho / Y = \mu (n_0 - n) - \nu n \rho / Y .$$

[Compare to the damped predator-prey system (Sec A3)

$$\dot{p} = r p (1 - p/\tilde{p}) - b p q$$

$$\dot{q} = c p q - \mu q$$

nutrient (n) $\leftrightarrow$ prey (p)

cell (ρ) $\leftrightarrow$ predator (q)

$c \leftrightarrow \nu$; $b \leftrightarrow \nu / Y$.

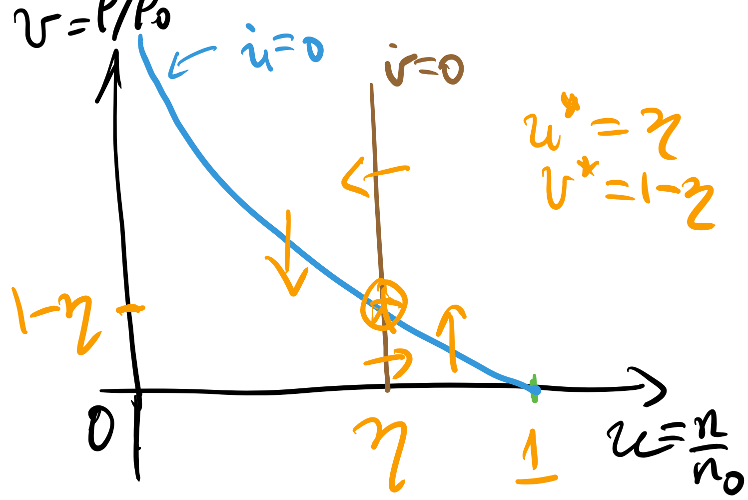
main difference:

- prey replicates at rate $r\cdot(1-\rho/\tilde{\rho})$
- nutrient injected at rate $\mu(n_0-n)$

- Make dimensionless:

$$\frac{n}{n_0}=u,\quad \frac{\rho}{n_0 Y}=v,\quad \nu n_0 t=\tau,\quad \frac{\mu}{\nu n_0}=\eta$$

$$\begin{cases} \dfrac{du}{d\tau} = \eta\cdot(1-u) - uv \\[2ex] \dfrac{dv}{d\tau} = uv - \eta v \end{cases}$$

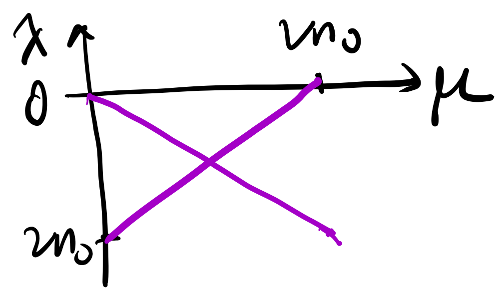


- perturbative analysis around u^*, v^*

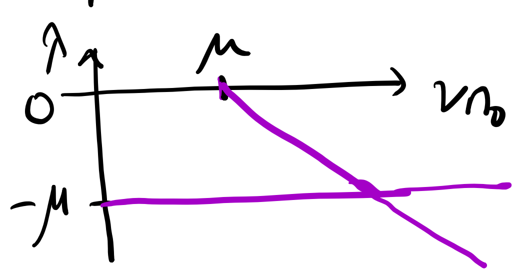
$$\lambda=\{-\eta,\ -1+\eta\}<0 \quad \text{for } \eta<1$$ (see next page)

in real time unit: $\lambda\cdot\nu n_0=\{-\mu,\ \mu-\nu n_0\}$

→ instability as $\mu\to\nu n_0$ (washout)



→ instability as $\mu\to 0$ (reflects batch culture growth)



⇒ vary chemostat setting by n_0 while keep $\mu \ll r_0$ const.

* perturbation: $u = u^* + x$
$v = v^* + y$

$u^* = \eta$
$v^* = 1-\eta$

$$\frac{dx}{d\tau} = \eta(1-u^*-x) - (u^*+x)(v^*+y)$$
$$= -\eta x - v^* x - u^* y = -x - \eta y$$

$$\frac{dy}{d\tau} = (u^*+x)(v^*+y) - \eta(v^*+y)$$
$$= v^* x = (1-\eta)x$$

$$\frac{d}{d\tau}\begin{pmatrix} x \\ y \end{pmatrix} = M \begin{pmatrix} x \\ y \end{pmatrix}, \quad M = \begin{pmatrix} -1 & -\eta \\ 1-\eta & 0 \end{pmatrix}$$

$$\det\left[M - \lambda I\right] = 0 \rightarrow \lambda(\lambda+1) + \eta(1-\eta) = 0$$

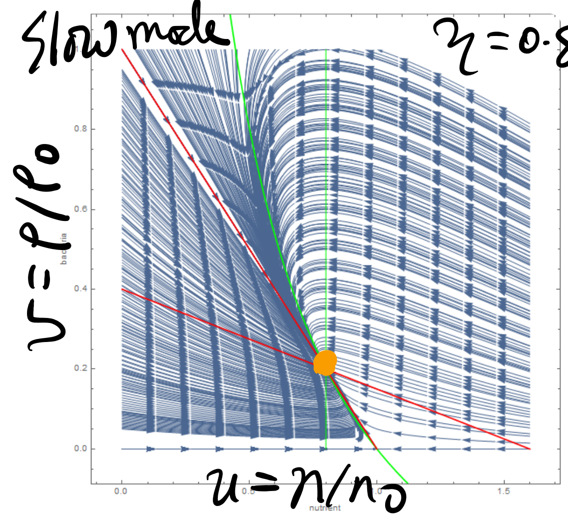
$$\lambda = -\frac{1}{2} \pm \sqrt{\frac{1}{4} - \eta + \eta^2} = -\frac{1}{2} \pm \left|\frac{1}{2} - \eta\right|$$

$$= \begin{cases} -\eta, -1+\eta & \eta < \frac{1}{2} \\ -1+\eta, -\eta & \eta > \frac{1}{2} \end{cases} = -\eta, -1+\eta$$

For $\eta \to 1$,

fast mode: $\lambda_1 = -\eta \simeq -1$.

slow mode: $\lambda_2 = 1-\eta$



→ Find fast/slow mode by solving for eigenvectors

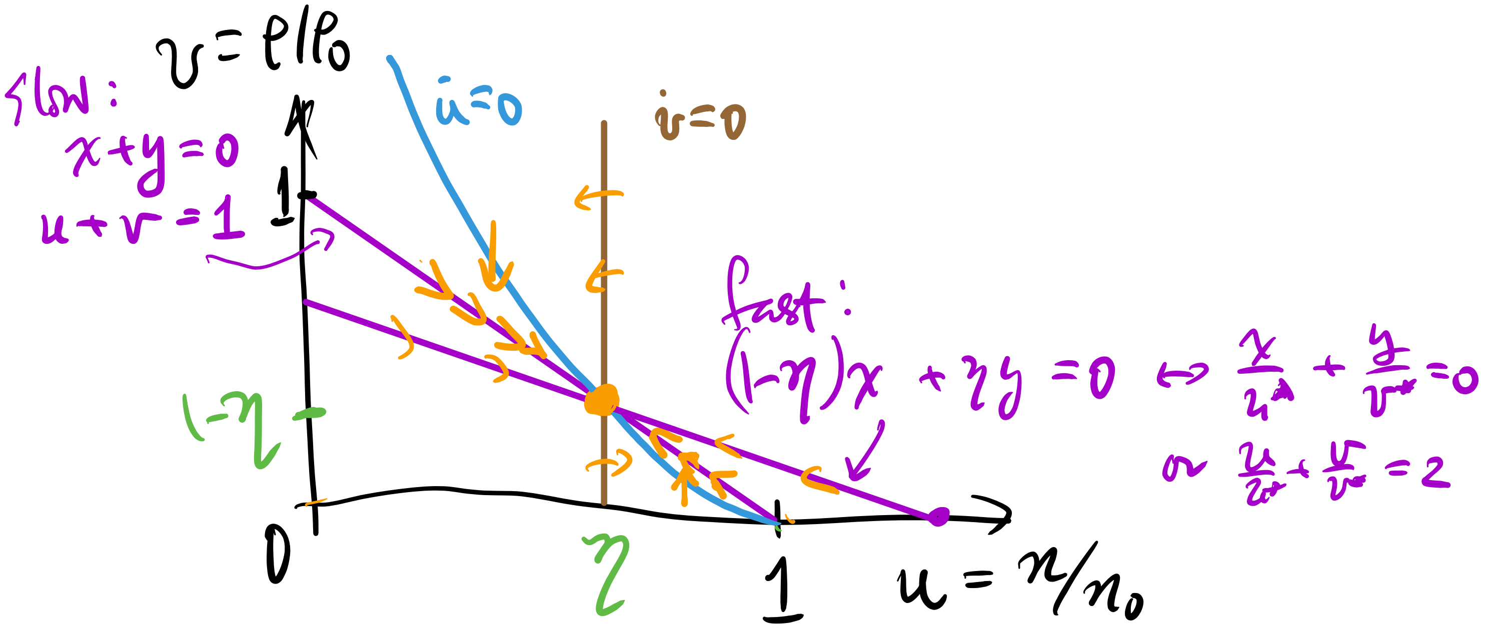
$$M\begin{pmatrix}x_i\\ y_i\end{pmatrix} = \lambda_i\begin{pmatrix}x_i\\ y_i\end{pmatrix} \to \begin{pmatrix}-1 & -\eta\\ 1-\eta & 0\end{pmatrix}\begin{pmatrix}x_i\\ y_i\end{pmatrix} = \lambda_i\begin{pmatrix}x_i\\ y_i\end{pmatrix}$$

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

$\to (1-\eta)x_1 = -\eta y_1$ or $\boxed{(1-\eta)x_1 + \eta y_1 = 0}$

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

$\to (1-\eta)x_2 = (-1+\eta)y_2$ or $\boxed{x_2 + y_2 = 0}$



$\Rightarrow$ Slow direction:

$u + v = 1$ or $\boxed{\rho(t)/\gamma + n(t) = n_0}$ (mass conservation)

Recall from original eqns: $\dot{\rho} = (\nu n - \mu)\rho$

$\dot{n} = \mu(n_0 - n) - \nu n \rho/\gamma$.

$$\Rightarrow \frac{d}{dt}(\rho/\gamma + n) = \underset{\uparrow\ \text{fast}}{\mu}(n_0 - n - \rho/\gamma)$$

$\Rightarrow$ dynamics quickly converges to $\frac{\rho(t)}{\gamma} + n(t) = n_0$

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

$\rightarrow$ use $n(t) = n_0 - \rho(t)/\gamma$ in eqn for $\rho(t)$:

$$\dot{\rho} = (\nu n - \mu)\rho = \left(\nu(n_0 - \rho/\gamma) - \mu\right)\rho$$

$\rightarrow$ recovers logistic growth eqn.

$$\dot{\rho} = r(1 - \rho/\tilde{\rho})\rho$$

with $r = \nu n_0 - \mu = \nu n_0 (1 - \eta)$

$$\tilde{\rho} = \frac{(\nu n_0 - \mu)\gamma}{\nu} = \rho_0(1 - \eta).$$

$\rightarrow$ Approach to fixed point: $\rho(t) = \tilde{\rho} + \delta\rho(t)$

$$\dot{\delta\rho} = -r\,\delta\rho = -\underbrace{\nu n_0 (1-\eta)}_{\text{slow}}\,\delta\rho$$

Why is logistic growth recovered *here*?

- leading order expansion in $\tilde{\rho}$ when $\tilde{\rho} \propto (1-\eta)$ is small
- cost: long relaxation time: $r^{-1} \propto \frac{1}{1-\eta}$

[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)]