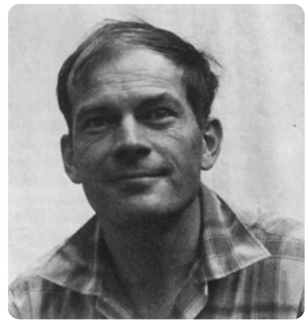
# B2. Stability in generalized CR model

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"

→ We reconstruct below MacArthur's work.

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

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

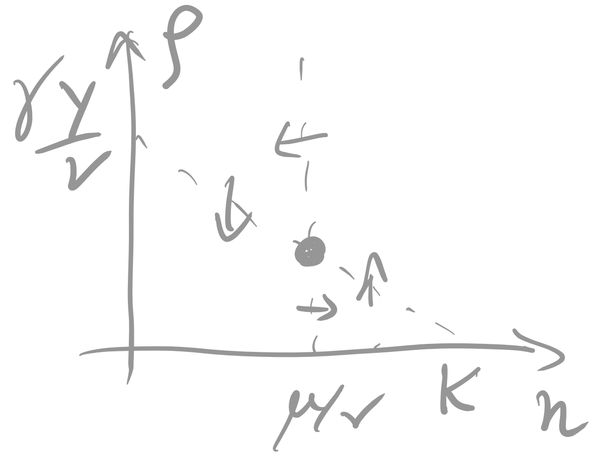
$n$ = prey
$\rho$ = predator

Steady-state: $\nu n^* = \mu$

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

→ fixed point $\rho^* = \gamma \frac{Y}{\nu}(1 - \mu/\nu K)$

is stable if $\mu/\nu < K$ ($\rho^*>0$)




General $N_R, N_c$:

fixed pt $\rho_i^* = \sum_j A^{-1}_{ij} r_j$ 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

a) Solve for fixed pt of many-species system

$\dot{n}_\alpha = 0 \rightarrow \quad \gamma_\alpha \left(1 - \frac{n_\alpha}{K_\alpha}\right) = \sum_i \nu_{i\alpha} \rho_i / Y_\alpha$

$n_\alpha \neq 0 \qquad n_\alpha = K_\alpha - \sum_i \nu_{i\alpha} \rho_i \underbrace{\left(K_\alpha / \gamma_\alpha Y_\alpha\right)}_{\sigma_\alpha}$

Note: MacArt assumed nutrient to relax with faster time scale; full system studied by Case & Casten (1979).

Substitute into eqn for $\rho_i$

$$\dot{\rho}_i = \sum_\alpha \nu_{i\alpha} \rho_i n_\alpha - \mu_i \rho_i$$

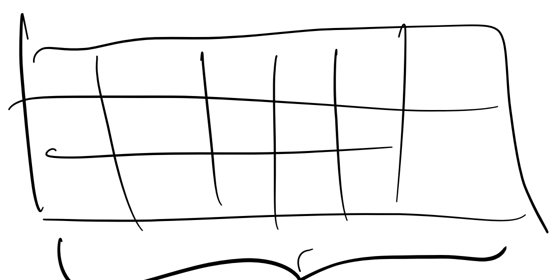
$$= \sum_\alpha \nu_{i\alpha} \rho_i \left(K_\alpha - \sum_j \nu_{j\alpha} \rho_j \sigma_\alpha\right) - \mu_i \rho_i$$

$$\dot{\rho}_i = \underbrace{\left(\sum_\alpha \nu_{i\alpha} K_\alpha - \mu_i\right)}_{r_i} \rho_i - \sum_{j\alpha} \underbrace{\nu_{i\alpha} \nu_{j\alpha} \sigma_\alpha}_{A_{ij}} \rho_i \rho_j$$

$\rightarrow$ effective gLV system

note: $\rho_i$, $i = 1, \cdots N_c$

$n_\alpha$, $\alpha = 1, \cdots N_R$, (will see generic sol'n requires $N_c \leq N_R$)

$\nu_{i\alpha}$  $\}\, N_c$

$N_R$

$A_{ij} = \sum_\alpha \nu_{i\alpha} \nu_{j\alpha} \sigma_\alpha$ is $N_c \times N_c$ (outer product)

Steady state: $r_i = \sum_j A_{ij} \rho_j^*$

$$\longrightarrow \quad \rho_i^* = \sum_j A^{-1}_{ij} r_j$$

(provided that $A_{ij}$ invertible) - see below

b) Stability of fixed pt:

Next show that $\rho_i^* = \sum_j A^{-1}_{ij} r_j$ is the <u>global</u> fixed point of the gLV eqn:

$$\frac{d}{dt}\rho_i = r_i \rho_i - \sum_j A_{ij} \rho_i \rho_j$$

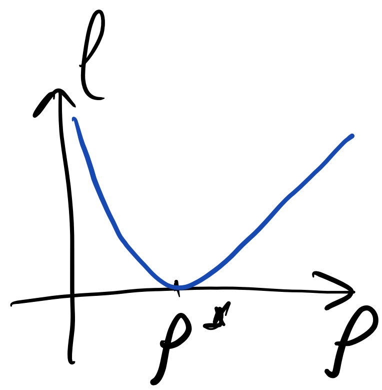
where $A_{ij} = \sum_\alpha V_{i\alpha} V_{j\alpha} \sigma_\alpha$

→ Construct "Lyapunov function":

$$L(t) = \sum_i \underbrace{\left[ (\rho_i(t) - \rho_i^*) - \rho_i^* \ln \frac{\rho_i(t)}{\rho_i^*} \right]}_{l_i(t)}$$

Property of each term $l_i$:

$$\left.\begin{aligned} \frac{dl}{d\rho} &= 1 - \frac{\rho^*}{\rho} \\ \frac{d^2 l}{d\rho^2} &= \frac{\rho^*}{\rho^2} > 0 \end{aligned}\right\} \quad \begin{aligned} &\frac{dl}{d\rho} = 0 \text{ at } \rho = \rho^* \\ &l(\rho^*) = 0 \end{aligned}$$



$\longrightarrow$ $\ell(\rho)$ has single minimum at $\rho^*$

$\therefore$ $L = \sum_i \ell_i$ has one global min at $\rho_i = \rho_i^*$

for $\rho_i > 0$, $\rho_i^* > 0$

Next, look at $dL/dt$

$$\frac{dL(t)}{dt} = \sum_i \left[ \frac{d\rho_i}{dt} - \frac{\rho_i^*}{\rho_i} \frac{d\rho_i}{dt} \right]$$

use gLV for $\frac{d\rho_i}{dt}$

$$\downarrow\; = \sum_i \left[ \left( r_i - \sum_j A_{ij} \rho_j \right) \left( \rho_i - \rho_i^* \right) \right]$$

$$= \sum_{ij} A_{ij} (\rho_j^* - \rho_j) (\rho_i - \rho_i^*)$$

used $r_i = \sum_{ij} A_{ij} \rho_j^*$

Now use the form $A_{ij} = \sum_\alpha v_{i\alpha} v_{j\alpha} \sigma_\alpha$

$$\frac{dL}{dt} = -\sum_\alpha \sigma_\alpha \sum_{ij} v_{i\alpha} v_{j\alpha} (\rho_i - \rho_i^*)(\rho_j - \rho_j^*)$$

$$= -\sum_\alpha \sigma_\alpha \left( \sum_i v_{i\alpha} (\rho_i - \rho_i^*) \right)^2 \leq 0$$

$\Rightarrow$ $L(t)$ always decreasing until $\rho_i(t) = \rho_i^*$ where $L(t) = 0$. i.e. <u>global attractor</u>!

$\Rightarrow$ only pending on the existence of $\rho_i^* > 0$

c) Solve for fixed point (feasibility)

- Start with $r_i = \sum_j A_{ij} \rho_j^*$

$\tilde{\nu}_{j\alpha} = \sigma_\alpha^{1/2} \nu_{j\alpha}$
$= \left(\frac{K_\alpha}{\gamma_\alpha Y_\alpha}\right)^{1/2} \nu_{j\alpha}$

$= \sum_{j\alpha} \sigma_\alpha \nu_{i\alpha} \nu_{j\alpha} \rho_j^*$
$= \sum_{j\alpha} \tilde{\nu}_{i\alpha} \tilde{\nu}_{j\alpha} \rho_j^*$

matrix notation: $A = \tilde{\nu} \times \tilde{\nu}^T$
where $(\tilde{\nu}^T)_{\alpha i} = \tilde{\nu}_{i\alpha}$

$\tilde{\nu}_{i\alpha}$: Consumption rate of $\underbrace{\text{resource } \alpha}_{N_R \text{ (\# col.)}}$ by $\underbrace{\text{Consumer } i}_{N_C \text{ (\# row)}}$

$A = \tilde{\nu} \times \tilde{\nu}^T$: symmetric square matrix $(N_C \times N_C)$

Linear Algebra:

rows are independent

If matrix $\tilde{\nu}$ is full rank with $N_C \le N_R$

then $A = \tilde{\nu} \times \tilde{\nu}^T$ is invertible

$\Rightarrow \rho_i^* = \sum_j A^{-1}_{ij} r_j$

where $A^{-1} = (\tilde{\nu} \times \tilde{\nu}^T)^{-1}$, $r_i = \sum_\alpha \nu_{i\alpha} K_\alpha - \mu_i$

Special case: $N_R = N_C$, $\rho_i^* = \sum_\alpha \nu^{-1}_{\alpha i} \gamma_\alpha Y_\alpha - O(\mu)$

cf. The random matrix perspective:

(connect to May's work — Cui et al, 2019)

Effective gLV system:

$$\frac{d}{dt}\rho_i = r_i \rho_i - \sum_{j=1}^{N_c} A_{ij}\, \rho_i \rho_j$$

where $A_{ij} = \sum_\alpha \nu_{i\alpha} \nu_{j\alpha} \sigma_\alpha$

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

$$\delta\rho_i \equiv \rho_i - \rho_i^* .$$

$$\frac{d}{dt}\delta\rho_i = -\rho_i^* \sum_j A_{ij}\, \delta\rho_j$$

Community matrix $M_{ij} = -\rho_i^* A_{ij}$

R. May: $M_{ij} = R_{ij} - \delta_{ij}$

random non-neg elements of var $= \sigma^2$

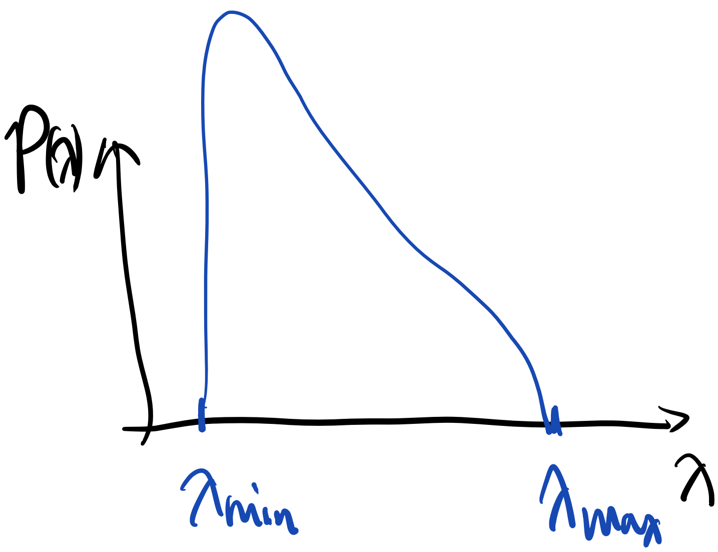
→ largest eigenvalue $= -1 + \sigma\sqrt{N_c} > 0$ for $N_c \gg 1$.

For the CR model, $A = \nu \cdot \nu^T$

$\nu_{i\alpha}$ = iid, non neg. (var $= \sigma_\nu^2$) → Wishart matrix

eigenvalue dist (Marchenko-Pastur dist — for Gaussian dist of $\nu_{i\alpha}$)

$$P(\lambda) = \frac{N_R/N_c}{2\pi\sigma_\nu^2 \lambda}\sqrt{(\lambda_{max}-\lambda)(\lambda-\lambda_{min})}$$




$$\lambda_{min} = \sigma_v^2 \left(1 - \sqrt{N_c/N_R}\right)^2$$

$$\lambda_{max} = \sigma_v^2 \left(1 + \sqrt{N_c/N_R}\right)^2.$$

$\rightarrow$ $\lambda \geq 0$ as long as $N_c \leq N_R$ even as $N_c, N_R \to \infty$.

Relation to community matrix $M$:

largest eigenvalue of $M_{ij}$

$=$ - smallest eigenvalue of $A_{ij} = -\lambda_{min}$

$\rightarrow$ Community matrix is stable as $N_c, N_R \to \infty$, as long as $\frac{N_c}{N_R} < 1$.

$\rightarrow$ in practice, even if $N_c = N_R$, feasible sol'n ($p_i^* > 0$) involves $N_c^* < N_R$.

* Recent study (Cui et al, 2019) showed numerically that for large random consumption matrix $V_{i\alpha}$, typically ~50% of $V_{i\alpha}$ exhibit coexistence.

( no analytical result on this so far )