B. Generalized Lotka-Volterra Model. 22

$$\frac{\partial \rho_i}{\partial t} = r_i \rho_i + A_{ij} \rho_i \rho_j \; ; \quad r_i > 0 \text{ (not predator-prey)}$$

- simple, generic formulation of multi-species interaction

  ($A_{ij} < 0$ competition
  $A_{ij} > 0$ cooperation)

- wide range of dynamical behaviors
- not mechanistic

  (more mechanistic-based models, e.g., Consumer-Resource Model → effective gLV with restricted parameter space)

- small density expansion.
  (higher-order term can be important)

⇒ Central problem in ecology: diversity of species

→ strategy: work out 2-species first, then go to N-species

$$\dot{\rho}_1 = r_1 \rho_1 \left(1 - \rho_1/\tilde{\rho}_{11} - \rho_2/\tilde{\rho}_{12}\right)$$

$$\dot{\rho}_2 = r_2 \rho_2 \left(1 - \rho_1/\tilde{\rho}_{21} - \rho_2/\tilde{\rho}_{22}\right)$$

$\tilde{\rho}_{ij} > 0$; $\tilde{\rho}_{11}, \tilde{\rho}_{22}$: carrying capacities

$\tilde{\rho}_{12}, \tilde{\rho}_{21}$: competitive interaction

(large $\tilde{\rho}_{ij}$ = small interaction) dimensionless variables: $u_1 = \frac{\rho_1}{\tilde{\rho}_{11}}$, $u_2 = \frac{\rho_2}{\tilde{\rho}_{22}}$

dimensionless parameters: $a_{12} = \frac{\tilde{\rho}_{22}}{\tilde{\rho}_{12}}$, $a_{21} = \frac{\tilde{\rho}_{11}}{\tilde{\rho}_{21}}$ strength of interaction

$$\begin{cases} \frac{du_1}{dt} = r_1 u_1 (1 - u_1 - a_{12} u_2) = f_1(u_1, u_2) \\ \frac{du_2}{dt} = r_2 u_2 (1 - a_{21} u_1 - u_2) = f_2(u_1, u_2) \end{cases}$$

($a_{12} > 0$, $a_{21} > 0$ for competition)

* null clines

$$f_1(u_1^*, u_2^*) = 0 \longrightarrow u_1^* = 0 \text{ or } u_1^* + a_{12} u_2^* = 1$$

$$f_2(u_1^*, u_2^*) = 0 \longrightarrow u_2^* = 0 \text{ or } a_{21} u_1^* + u_2^* = 1.$$

* non-trivial fixed pt: $u_1^* = \frac{1 - a_{12}}{1 - a_{12} \cdot a_{21}}$, $u_2^* = \frac{1 - a_{21}}{1 - a_{12} \cdot a_{21}}$

- feasibility: $u_1^* > 0$, $u_2^* > 0$ requires $a_{12} < 1$ & $a_{21} < 1$ or $a_{12} > 1$ & $a_{21} > 1$
- Stability: stable vs unstable fixed pt (coexistence, bistability, limit cycle)

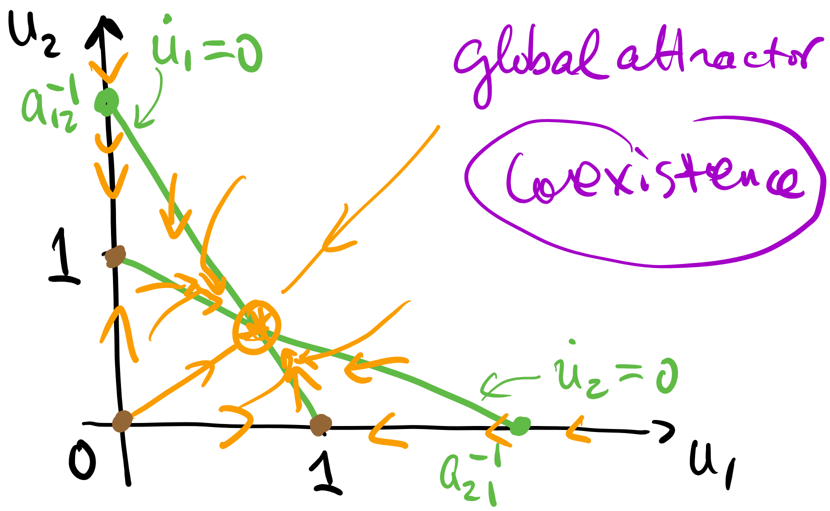
1. Two-species competition ($a_{12} > 0$, $a_{21} > 0$)

Case (i)

$a_{12} < 1$, $a_{21} < 1$

(or $\tilde{\rho}_{ii} < \tilde{\rho}_{i \neq j}$)

weak interaction



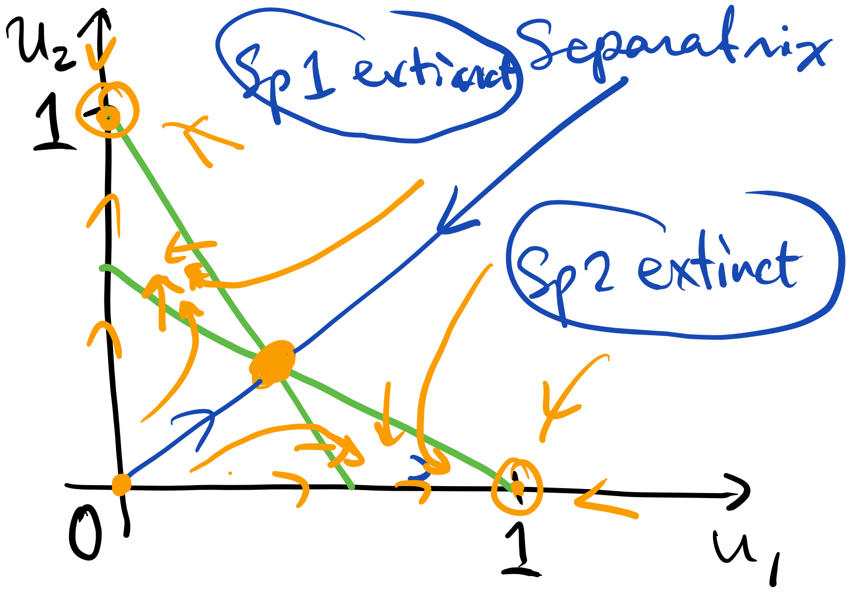
$\Rightarrow$ weak competition merely reduces the values u_1^*, u_2^* from 1 (smaller carrying capacity)

Case (ii)

$a_{12} > 1, \ a_{21} > 1$

(or $\tilde{\rho}_{ii} > \tilde{\rho}_{i \neq j}$)

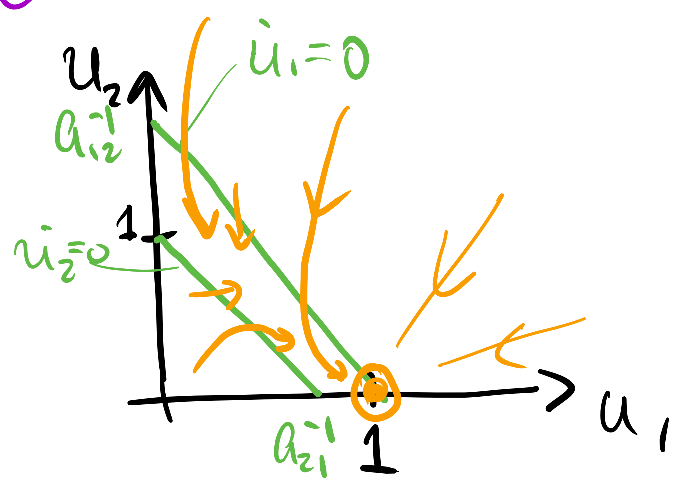
Strong interaction



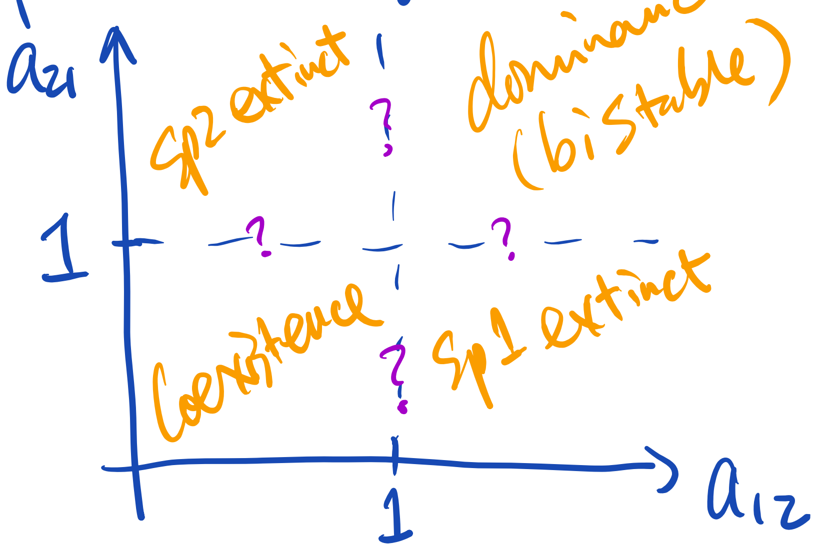
$\Rightarrow$ strong competition drives each other to extinction; determined by init conditions

<u>exclusive dominance</u> (c.f. toggle switch)

Case iii) $a_{12} < 1, \ a_{21} > 1$



phase diagram



Note: phase diagram independent of rate constants r_1, r_2 (no effect on stationary st.)

2. two "cooperating" species ($a_{12} < 0$, $a_{21} < 0$) (25)

$$\begin{cases} \frac{du_1}{dt} = r_1 u_1 (1 - u_1 + |a_{12}| u_2) = f_1(u_1, u_2) \\ \frac{du_2}{dt} = r_2 u_2 (1 + |a_{21}| u_1 - u_2) = f_2(u_1, u_2) \end{cases}$$

* nullclines: $u_1^* = 0$ or $u_1^* - |a_{12}| u_2^* = 1$

$u_2^* = 0$ or $u_2^* - |a_{21}| u_1^* = 1$

* nontrivial fixed point: $u_1^* = \frac{1 + |a_{12}|}{1 - |a_{12}| \cdot |a_{21}|}$; $u_2^* = \frac{1 + |a_{21}|}{1 - |a_{12}| \cdot |a_{21}|}$

Case i) $|a_{12}| \cdot |a_{21}| < 1$

weak cooperativity

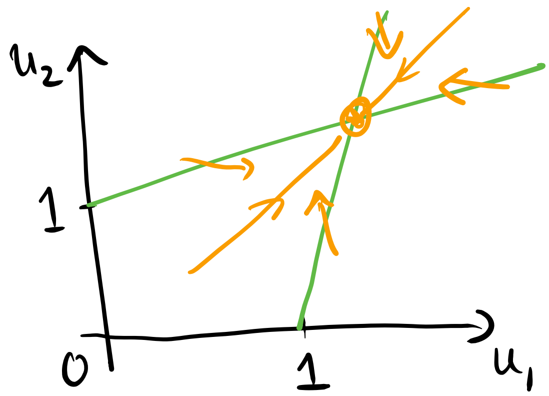
1 ⇄ 2

$\Rightarrow$ moderately increase carrying capacity ($u_1^*, u_2^* > 1$)

$\dot{u}_2 = 0$ $\quad u_2^* = 1 + |a_{21}| u_1^*$

$\dot{u}_1 = 0$ $\quad u_2^* = \frac{1}{|a_{12}|}(u_1^* - 1)$

(nullclines cross since $|a_{21}| < \frac{1}{|a_{12}|}$)

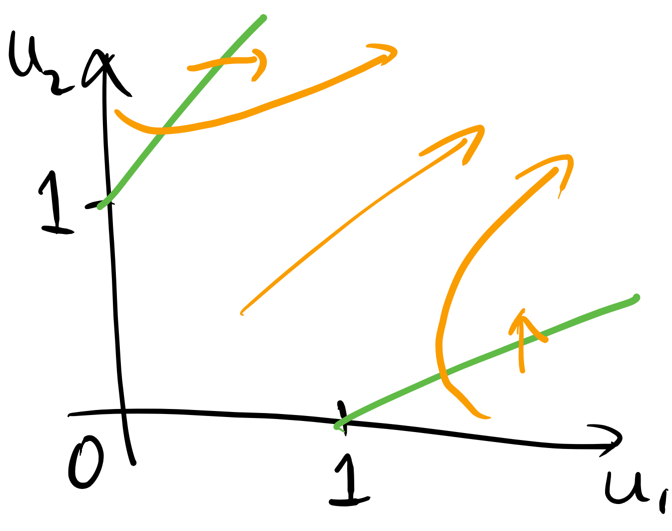


Case ii) $|a_{12}| \cdot |a_{21}| > 1$

strong cooperativity

1 ⇄ 2

$\Rightarrow$ population "blow up"



3. algebraic analysis of stability
(for arbitrary a_{12}, a_{21} with $u_1^* > 0, u_2^* > 0$)

$$\frac{du_1}{dt} = r_1 u_1 (1 - u_1 - a_{12} u_2) = f_1(u_1, u_2)$$

$$\frac{du_2}{dt} = r_2 u_2 (1 - u_2 - a_{21} u_1) = f_2(u_1, u_2)$$

nontrivial fixed pt: $f_1(u_1^*, u_2^*) = 0,\ f_2(u_1^*, u_2^*) = 0$

let $u_1 = u_1^* + x$
$u_2 = u_2^* + y$

$$\begin{pmatrix} \dot{x} \\ \dot{y} \end{pmatrix} = \underbrace{\left.\begin{pmatrix} \frac{\partial f_1}{\partial u_1} & \frac{\partial f_1}{\partial u_2} \\ \frac{\partial f_2}{\partial u_1} & \frac{\partial f_2}{\partial u_2} \end{pmatrix}\right|_{u_1^*, u_2^*}}_{\text{Community matrix } M} \cdot \begin{pmatrix} x \\ y \end{pmatrix}$$

$$\frac{\partial f_1}{\partial u_1} = r_1 (\underbrace{1 - u_1^* - a_{12} u_2^*}_{0} - u_1^*) = -r_1 u_1^*$$

$$\frac{\partial f_1}{\partial u_2} = -r_1 a_{12} u_1^* ; \quad \frac{\partial f_2}{\partial u_1} = -r_2 a_{21} u_2^* ; \quad \frac{\partial f_2}{\partial u_2} = -r_2 u_2^*$$

$$M = \begin{pmatrix} -r_1 u_1^* & -r_1 a_{12} u_1^* \\ -r_2 a_{21} u_2^* & -r_2 u_2^* \end{pmatrix} ; \quad \det(M - \lambda I) = 0$$

$$\lambda^2 + (r_1 u_1^* + r_2 u_2^*)\lambda + (1 - a_{12} a_{21}) r_1 u_1^* r_2 u_2^* = 0$$

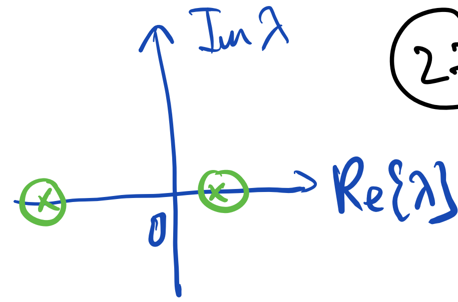
$$2\lambda = -(r_1 u_1^* + r_2 u_2^*) \pm \sqrt{\Delta}$$

$$\Delta = (r_1 u_1^* + r_2 u_2^*)^2 - 4(1 - a_{12} a_{21}) r_1 u_1^* r_2 u_2^*$$

As long as $u_1^* > 0,\ u_2^* > 0$.

- $a_{12} \cdot a_{21} > 1$: $\Delta > (r_1 u_1^* + r_2 u_2^*)^2$

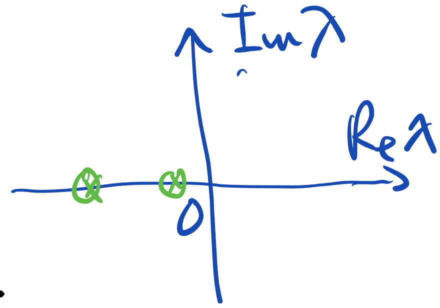
  $\lambda_+ > 0$, $\lambda_- < 0$. bistable



- $0 < a_{12}, a_{21} < 1$:

  $(r_1 u_1^* - r_2 u_2^*)^2 < \Delta < (r_1 u_1^* + r_2 u_2^*)^2$

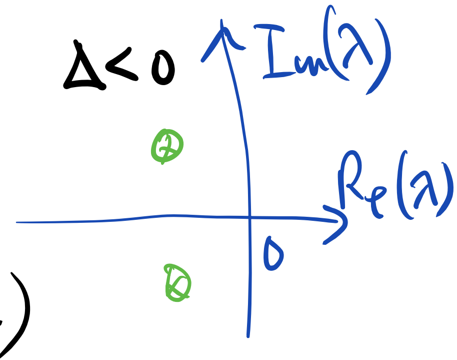
  $\lambda_+ < 0$, $\lambda_- < 0$, stable coexistence



- $\Delta < 0$: $\lambda = -(r_1 u_1^* + r_2 u_2^*) \pm i\sqrt{|\Delta|}$

  for some $a_1 a_2 < 0$

  damped osc



$\Delta = 0 \to$ condition on $(a_{12}, a_{21}, r_1/r_2)$ for the onset of damped osc.

Summary phase diagram: