B. Generalized Lotka-Volterra Model.

$$\frac{\partial \rho_i}{\partial t} = r_i \rho_i + A_{ij} \rho_i \rho_j \qquad (gLV)$$

- simple, generic formulation of multi-species interaction

  $\left(\begin{array}{ll} A_{ij} < 0 & \text{competition} \\ A_{ij} > 0 & \text{cooperation} \end{array} \right)$

- wide range of dynamical behaviors
- not mechanistic

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

- small density expansion.

  (higher-order term can be important)

$\Rightarrow$ Central problem in ecology: diversity of species

1. Two-Species Competition.

$$\dot{\rho}_1 = r_1 \rho_1 \left(1 - \rho_1/\tilde{\rho}_{11} - \rho_2/\tilde{\rho}_{12} \right)$$
$$\dot{\rho}_2 = r_2 \rho_2 \left(1 - \rho_1/\tilde{\rho}_{21} - \rho_2/\tilde{\rho}_{22} \right)$$

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

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

(large $\tilde{\rho}_{ij}$ = small interaction) dimensionless variables: $u_1 = \frac{\rho_1}{\tilde{\rho}_{11}}$, $u_2 = \frac{\rho_2}{\tilde{\rho}_{22}}$, $\tau = r_1 t$

dimensionless parameters: $r = r_2/r_1$, $\underbrace{a_{12} = \frac{\tilde{\rho}_{22}}{\tilde{\rho}_{12}},\ a_{21} = \frac{\tilde{\rho}_{11}}{\tilde{\rho}_{21}}}_{\text{Strength of interaction}}$

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

$$\begin{cases} \frac{du_1}{d\tau} = u_1(1 - u_1 - a_{12}u_2) = f_1(u_1, u_2) \\ \frac{du_2}{d\tau} = r u_2(1 - a_{21}u_1 - u_2) = f_2(u_1, u_2) \end{cases}$$

* null clines

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

$f_2(u_1^*, u_2^*) = 0 \longrightarrow u_2^* = 0$ 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 $a_{12} > 1$ & $a_{21} > 1$
- Stable (coexistence)
- unstable (bistability, limit cycle)

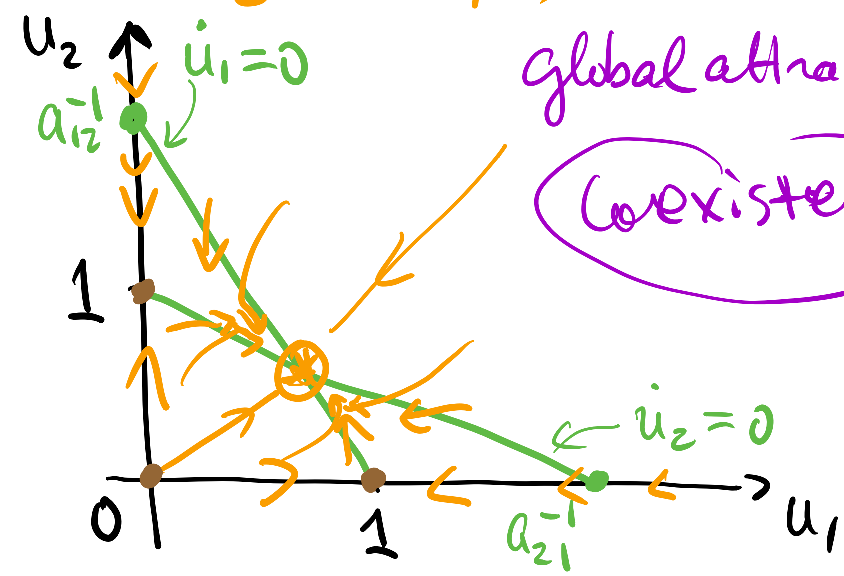
Case (i)

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

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

weak interaction

① ②



Global attractor

Coexistence

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

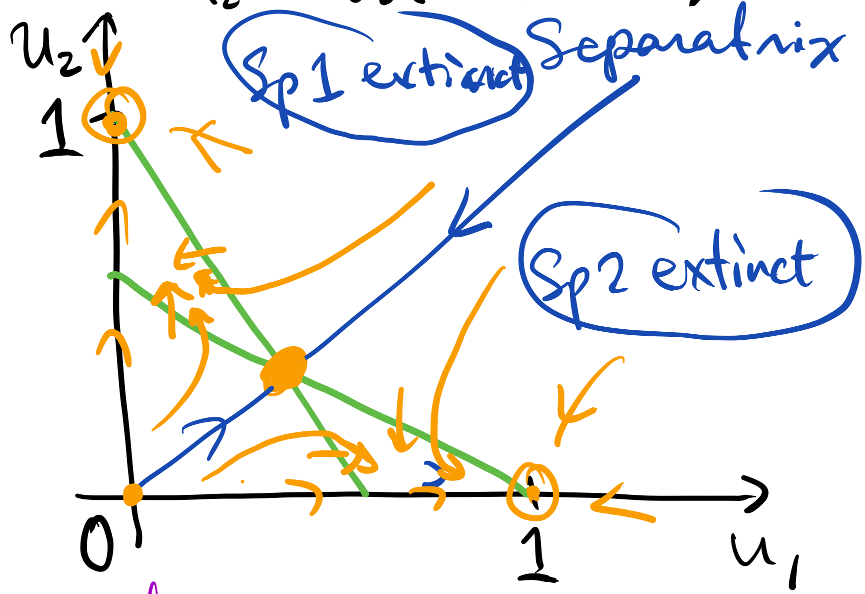
Case (ii)

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

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

Strong interaction

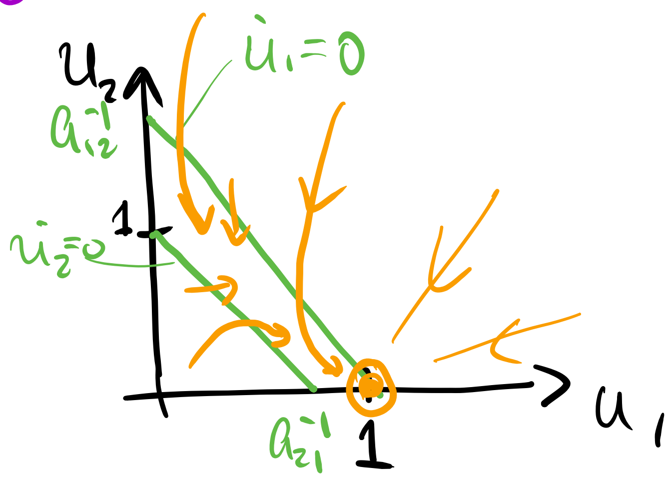
$$\dot{u}_1 = u_1(1-u_1-a_{12}u_2)$$
$$\dot{u}_2 = r u_2(1-a_{21}u_1-u_2)$$



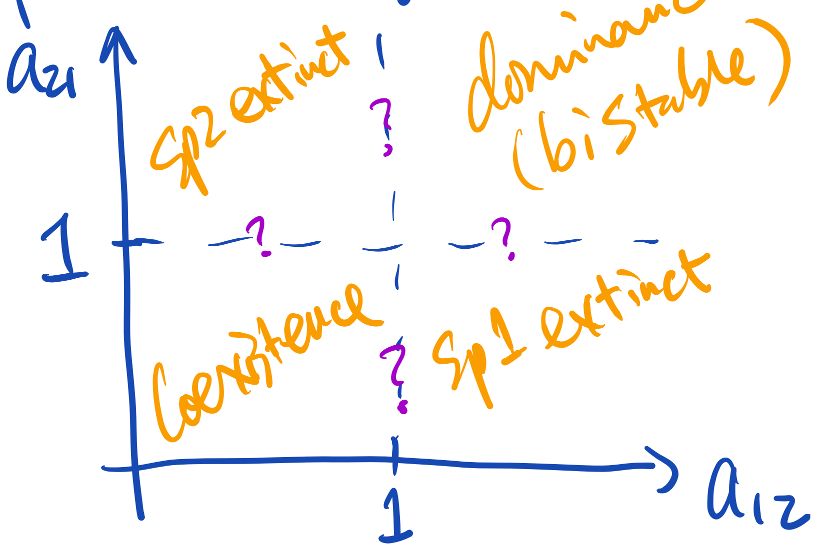
$\Rightarrow$ strong competition drives each other to extinction; determined by init conditions

exclusive dominance (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

$$\dot{\rho}_1 = r_1 \rho_1 \left(1 - \rho_1/\tilde{\rho}_{11} + \rho_2/\tilde{\rho}_{12}\right)$$
$$\dot{\rho}_2 = r_2 \rho_2 \left(1 - \rho_1/\tilde{\rho}_{21} + \rho_2/\tilde{\rho}_{22}\right)$$

dimensionless: $u_1 = \dfrac{\rho_1}{\tilde{\rho}_{11}}$, $u_2 = \dfrac{\rho_2}{\tilde{\rho}_{22}}$ $\tau = r_1 t$

$r = r_2/r_1$, $b_{12} = \dfrac{\tilde{\rho}_{22}}{\tilde{\rho}_{12}}$, $b_{21} = \dfrac{\tilde{\rho}_{11}}{\tilde{\rho}_{21}}$

$$\begin{cases} \dfrac{du_1}{d\tau} = u_1\left(1 - u_1 + b_{12}u_2\right) = f_1(u_1, u_2) \\ \dfrac{du_2}{d\tau} = r u_2 \left(1 - u_2 + b_{21}u_1\right) = f_2(u_1, u_2) \end{cases}$$

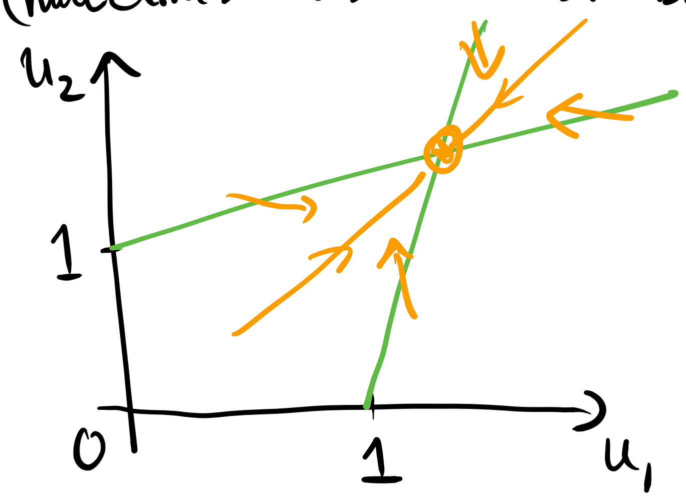
* nullclines: $u_1^* = 0$ or $u_1^* - b_{12}u_2^* = 1$
$u_2^* = 0$ or $u_2^* - b_{21}u_1^* = 1$.

* nontrivial fixed point: $u_1^* = \dfrac{1 + b_{12}}{1 - b_{12} \cdot b_{21}}$ $u_2^* = \dfrac{1 + b_{21}}{1 - b_{12} \cdot b_{21}}$

case i) $b_{12} \cdot b_{21} < 1$
or $\tilde{\rho}_{12}^{-1} \cdot \tilde{\rho}_{21}^{-1} < \tilde{\rho}_{11}^{-1} \cdot \tilde{\rho}_{22}^{-1}$
(weak coop.)

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

$\dot{u}_2 = 0$ $u_2^* = 1 + b_{21} u_1^*$
$\dot{u}_1 = 0$ $u_2^* = \dfrac{1}{b_{12}}(u_1^* - 1)$
(nullclines cross since $b_{21} < \dfrac{1}{b_{12}}$)

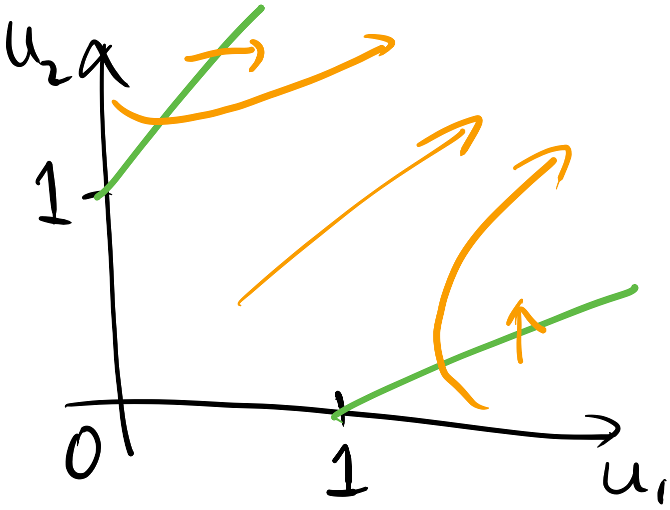


Case ii) $b_{12}\cdot b_{21} > 1$

or $\tilde{\rho}_{12}^{-1}\,\tilde{\rho}_{21}^{-1} > \tilde{\rho}_{11}^{-1}\,\tilde{\rho}_{22}^{-1}$

(Strong cooperativity)

$\Rightarrow$ population "blow up"



* Look at dynamics of

freq $p \equiv \dfrac{u_1}{u_1+u_2}$ and total pop $\bar{u} = u_1+u_2$

$$\frac{dp}{dt} = \frac{1}{u_1+u_2}\frac{du_1}{dt} - \frac{u_1}{(u_1+u_2)^2}\left(\frac{du_1}{dt}+\frac{du_2}{dt}\right) = \frac{u_2\cdot u_1}{(u_1+u_2)^2}\left[\frac{\dot{u}_1}{u_1}-\frac{\dot{u}_2}{u_2}\right]$$

$$= p(1-p)\left[(1-r)+\bar{u}(r+b_{12})-(1+rb_{21}+r+b_{12})p\bar{u}\right]$$

$$\overset{\bar{u}\gg 1}{=} \bar{u}\,p(1-p)\left[(r+b_{12})-(1+rb_{21}+r+b_{12})\,p\right]$$ (neg. freq depd)

$\dfrac{dp}{dt}=0 \rightarrow p^* = \dfrac{r+b_{12}}{1+rb_{21}+r+b_{12}} < 1$ fixed freq.

dynamics for $\bar{u}$: use $u_1 = p^*\bar{u}$. $u_2 = (1-p^*)\bar{u}$.

$$\cancel{p^*}\frac{d\bar{u}}{dt} = \cancel{p^*}\bar{u}\left(1-p^*\bar{u}+b_{12}(1-p^*)\bar{u}\right)$$

$$= \bar{u}\left(1+\bar{u}\,\frac{r(b_{12}\cdot b_{21}-1)}{1+rb_{21}+r+b_{12}}\right)$$

$\sim O(\bar{u}^2 r)$ if $b_{12}\cdot b_{21} > 1$.

$\rightarrow$ blows up in finite time (need higher order terms)

$\rightarrow$ generic problem for gLV description of symbiosis

3. algebraic analysis of stability

(for arbitrary a_{12}, a_{21} with $u_1^* > 0, u_2^* > 0$)

to restore symmetry

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

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

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

let $u_1 = u_1^* + x$

$u_2 = u_2^* + y$

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

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

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

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

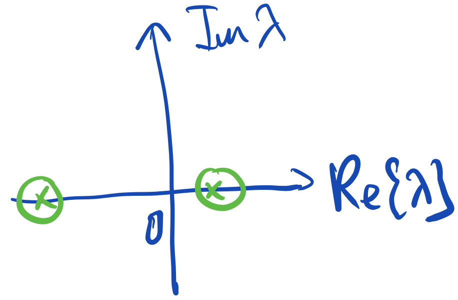
$$\lambda^2 + (r_1 u_1^* + r_2 u_2^*)\lambda + (1 - a_{12} a_{21}) r_1 u_1^* r_2 u_2^* = 0$$

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

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

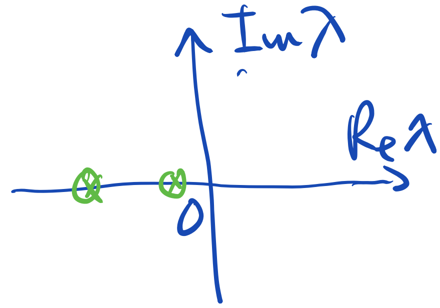
$$= (r_1 u_1^* - r_2 u_2^*)^2 + a_1 a_2 r_1 u_1^* r_2 u_2^*$$

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



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

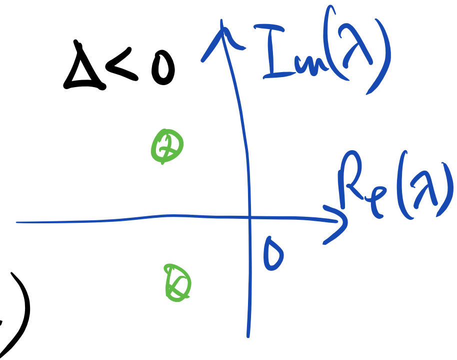
  $\lambda_+ > 0$, $\lambda_- < 0$. <u>bistable</u>



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

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

  $\lambda_+ < 0$, $\lambda_- < 0$, <u>Stable coexistence</u>



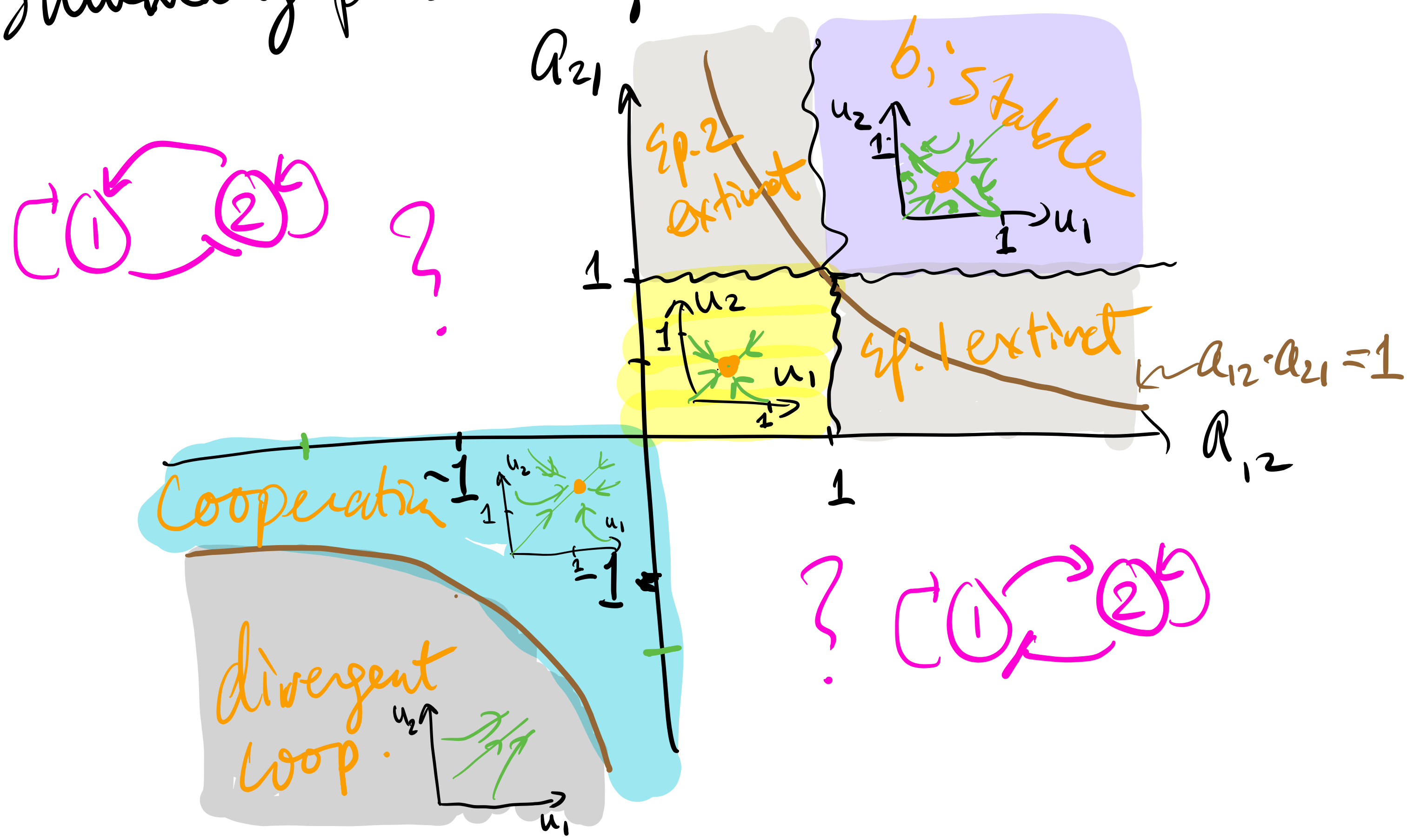
- $\Delta < 0$: $\lambda = -(r_1 u_1^* + r_2 u_2^*) \pm i\sqrt{|\Delta|}$

  for some $a_1 a_2 < 0$

  <u>damped osc</u>

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

Summary phase diagram:



4. Stability criterion for many-species gLV systems (R. H. May 1972)

Consider a large N-species system,
with densities $\{\rho_1(t), \rho_2(t), \cdots, \rho_N(t)\} = \vec{\rho}(t)$

gLV model: $\dfrac{d\rho_i}{dt} = f_i(\vec{\rho}(t))$

fixed point: $\vec{\rho}^*$ such that $f_i(\vec{\rho}^*) = 0$.

Jacobian matrix: $J_{ij} = \dfrac{\partial f_i(\vec{\rho}(t))}{\partial \rho_j}$

Community matrix: $M_{ij} = \left.\dfrac{\partial f_i}{\partial \rho_j}\right|_{\vec{\rho}^*}$

- Stability of fixed point:
  look at eigenvalues of M_{ij}: $\{\lambda_1, \lambda_2, \cdots \lambda_N\}$
  (since M_{ij} are real, $\lambda_k = a \pm ib$)

  $\rightarrow$ fixed pt stable if $\max_k\{\mathrm{Re}\{\lambda_k\}\} < 0$

- Solving for J_{ij} and $\vec{\rho}^*$ complicated

  $\rightarrow$ May (1972): directly look at M_{ij}

take another look at M_{ij} for 2×2 toy system

$$M = \begin{bmatrix} -u_1^* & -a_{12}u_1^* \\ -r u_2^* a_{21} & -r u_2^* \end{bmatrix}$$

$$u_1^* = \frac{1-a_{12}}{1-a_{12}\cdot a_{21}}$$

$$u_2^* = \frac{1-a_{21}}{1-a_{12}\cdot a_{21}}$$

$$r = r_2/r_1$$

Consider $r_1 \sim r_2$, $u_1^* \sim u_2^*$

(i.e. same order of magnitude)

Then M has the form

$$M \propto \begin{bmatrix} -1 & a_{12} \\ a_{21} & -1 \end{bmatrix}$$

(a_{ij} could be +ve or -ve)

May generalized M_{ij} to:

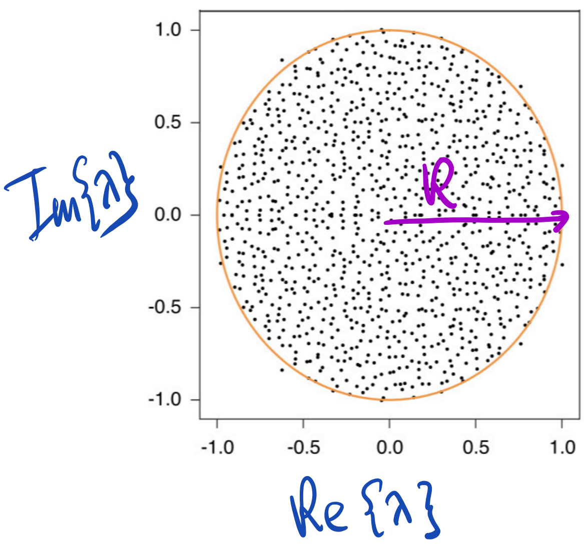
$$M_{ii} = -1, \quad M_{i\neq j} = \begin{cases} 0 & \text{with prob } 1-c \\ \text{random \#} & \text{with prob } c \end{cases}$$

from dist with variance σ^2

attempt to mimic the sparse and random nature of species-species interaction

i) Invoked/guessed "circular law"

for $N\times N$ random matrix A where each matrix element A_{ij} is real and uncorrelated, whose distribution has mean $=0$, var $=\sigma^2$, in the limit $N\to\infty$, eigenvalue λ_k is populated uniformly in a disc in the complex plane, with radius $R=\sigma\sqrt{N}$ (proved for arb. dist. by Terence Tao, 2010)

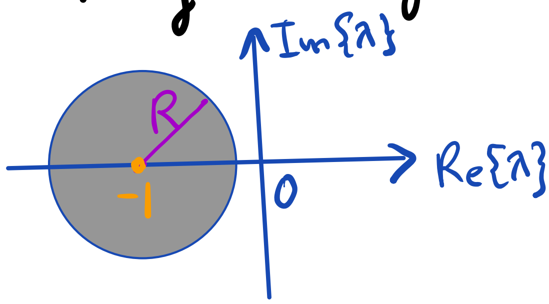


Eigenvalues of a 1000×1000 matrix generated with each element drawn from a Gaussian dist with mean=0 and variance = 1/1000

ii) generalization:

- only a fraction c of non-zero entries $\to R=\sigma\sqrt{c\cdot N}$

- $M_{ij} = A_{ij} - \delta_{ij}$, $\lambda \to \lambda - 1$.



$\max \mathrm{Re}\{\lambda\} = R - 1 < 0$

$\Rightarrow R < 1$

or $\sigma\sqrt{cN} < 1$

- Regardless of how sparse the matrix ($c \ll 1$) and how weak the interaction ($\sigma \ll 1$), for sufficiently large N, this system becomes unstable!
- Posed a challenging question for the coexistence of many species in interacting community.

iii) Recent progress (Allesina & Tang, 2010)

include correlation between M_{ij} and M_{ji}

let $\langle M_{ij} M_{ji} \rangle = \rho \sigma^2$. $\langle M_{ij}^2 \rangle = \sigma^2$

+ve correlation
-ve anti-correlation

get "elliptical law"

with $|Re\{\lambda\}| < (1+\rho)\sigma\sqrt{cN}$

$|Im\{\lambda\}| < (1-\rho)\sigma\sqrt{cN}$

→ for anti-correlated interaction (e.g. fox/hare)

$\rho < 0$, so $1+\rho < 1$; improved stability

We will see that biologically realistic interaction matrix (e.g. Consumer-resource model) can have much different stability criterion