Systems of Differential Equations, see 5.5, 5.6, 5.7

So far, only single populations $\dot{x} = f(x)$. Now interacting populations, i.e. each variable influences the other.

Example 1: Newton's law of cooling: H: heat A: ambient

$$\frac{dH}{dt} = \alpha(A - H) \quad \text{but A might change as well:}$$

$$\frac{dA}{dt} = \alpha_2(H - A) \qquad \alpha, \alpha_2 > 0$$

Typically $\alpha_2 < \alpha$ (size of ambient is smaller than object).
If $\alpha_2 = 0$, we get the single equation back. $\frac{\alpha}{\alpha_2} \sim \frac{\text{size of object}}{\text{size of room}}$

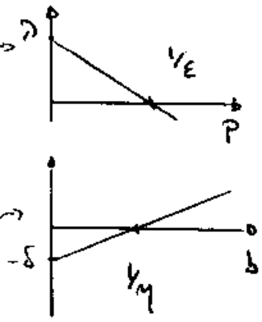
Example 2: Romeo and Juliet:

$$\frac{dR}{dt} = aR + bJ$$
$$\frac{dJ}{dt} = cR + eJ$$

a: influence of R on itself b: influence of J on R
c: - " - R on J e: influence of J on J

Example 3: Predator and Prey

$$\frac{db}{dt} = (\lambda - \varepsilon p)\, b$$
$$\frac{dp}{dt} = (-\delta + \eta b)\, p$$

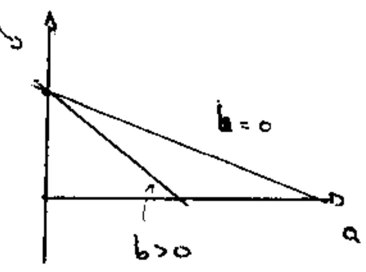


λ: prey growth rate
ε: kill rate at encounter
δ: death rate of predator without prey
η: conversion of prey into predator biomass

the term $p \cdot b$ reflects the "principle of mass action". The probability of encounter between p and b is proportional to the product.

<u>Example 4</u>: Competition $\frac{da}{dt} = \mu\left(1 - \frac{a+b}{K_a}\right)a$

$\frac{db}{dt} = \rho\left(1 - \frac{a+b}{K_b}\right)b$



μ, ρ: growth rates
K_a, K_b: carrying capacity for single species

Competitor reduces growth rate (net growth rate)

<u>Question</u>: How to analyze this? What will happen?

Reminder for single Equations: explicit solution — phase line — stability test
For systems: no ↓ phase plane ↓ yes

<u>Phase plane: Nullclines, Equilibria, direction arrows</u>

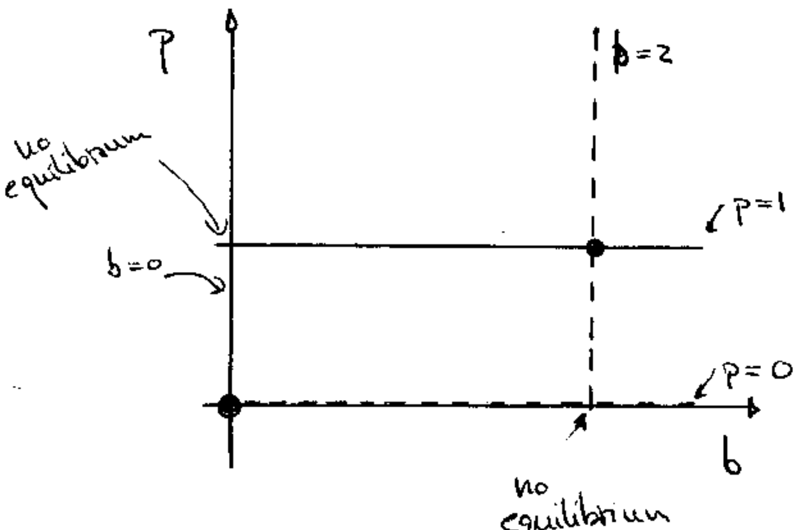
Recipe

- Nullcline: When does one of the species not change?
- Equilibria: When do both species not change?
- Direction arrow: How do the two species change?

<u>Example</u>: Predator - Prey: $\frac{db}{dt} = (1-p)b \quad \frac{dp}{dt} = (-1+\frac{1}{2}b)p$

Prey nullcline, prey no change, $\frac{db}{dt} = 0 \Rightarrow b=0$ or $p=1$. ———

Predator nullcline, $\frac{dp}{dt} = 0 \Rightarrow p=0$ or $b=2$ - - - - - - -

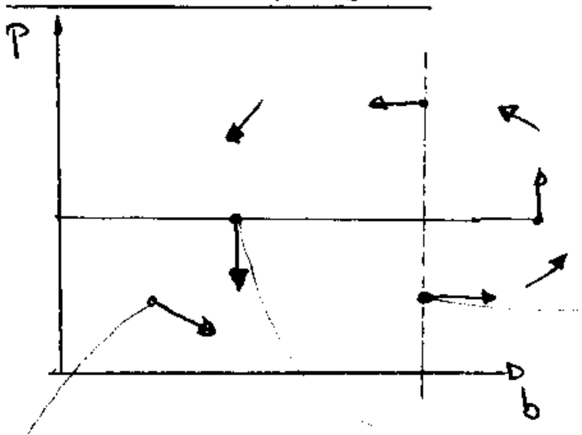


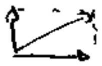
Equilibria: $\frac{db}{dt} = 0$ <u>and</u> $\frac{dp}{dt} = 0$

$\Rightarrow$ Intersection of nullclines

$(0,0)$ and $(2,1)$

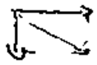
Direction arrows



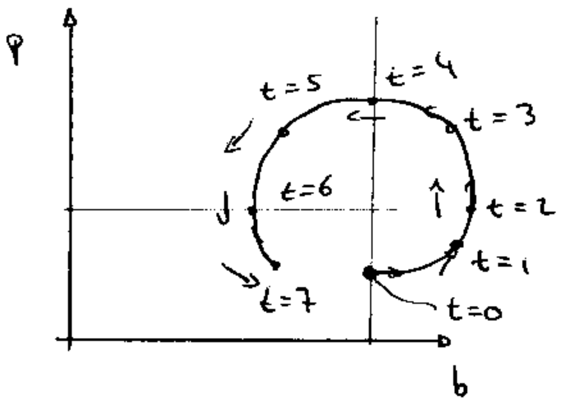
1) Pick a point
2) Find $\frac{db}{dt}$, $\frac{dp}{dt}$ the sign
3) draw  at that point.

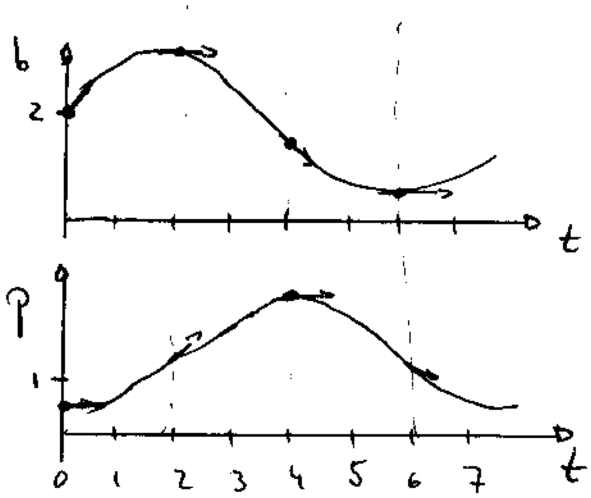
→ know: $\frac{dp}{dt} = 0$ $\quad \frac{db}{dt} > 0$ since $p < 1$

→ know: $\frac{db}{dt} = 0$, $\frac{dp}{dt} < 0$ since $b < 2$

→ here: $\frac{db}{dt} > 0$ and $\frac{dp}{dt} < 0$ 

Solution curves





⇒ No explicit solution, but a good idea of how solutions behave.

<u>Note</u>: the sign $\frac{db}{dt}$ or $\frac{dp}{dt}$ changes only when crossing a null cline.

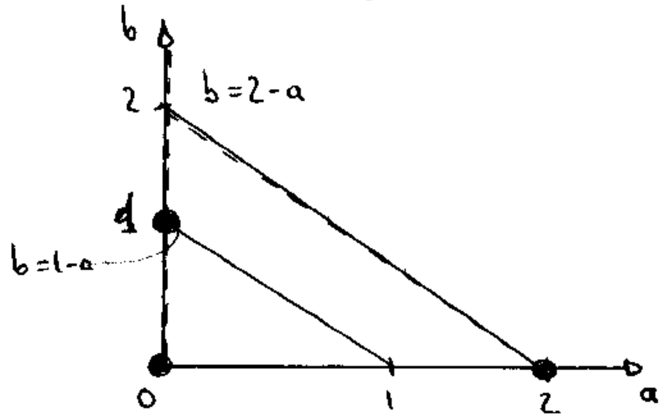
⇒ Nullclines divide the phase plane into regions with arrows pointing in similar directions

Example for Competition

$$\frac{da}{dt} = 2\left(1 - \frac{a+b}{2}\right)a \qquad \frac{db}{dt} = 2\left(1-(a+b)\right)b$$

Nullclines: $\frac{da}{dt} = 0 \Leftrightarrow a = 0$ or $a+b = 2$ $\quad (b = 2-a)$

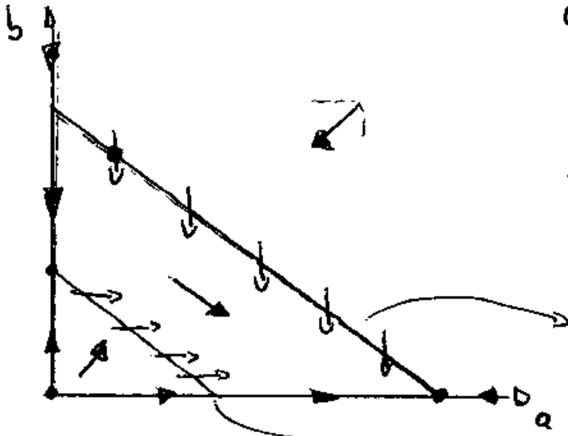
$\frac{db}{dt} = 0 \Leftrightarrow b = 0$ or $a+b = 1$ $\quad (b = 1-a)$



Equilibria: $(0,0)$, $(0,1)$, $(2,0)$

note: No coexistence equilibrium

Direction arrows



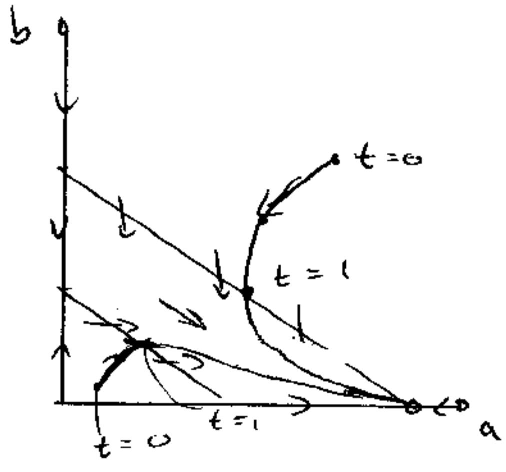
on $a=0$ and $b=0$ we have the single species phase-line diagram.

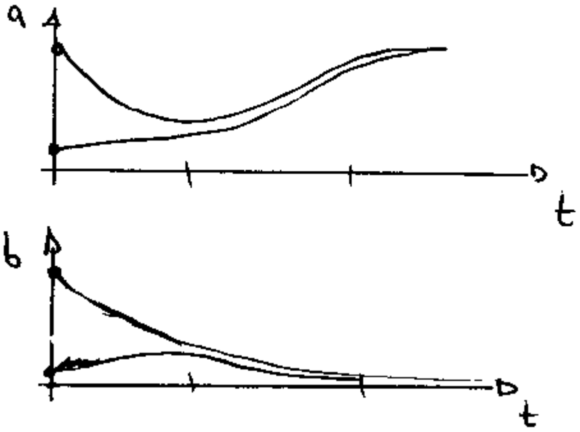
on $\frac{da}{dt} = 0$: arrows are $\begin{cases} \text{up if } \frac{db}{dt} > 0 \\ \text{down if } \frac{db}{dt} < 0 \end{cases}$

if $a+b = 2$ then $1-(a+b) = -1 < 0$

if $a+b = 1$ then $1 - \frac{a+b}{2} = \frac{1}{2} > 0$

Solution curves





Linear Systems (see Romeo and Juliet)

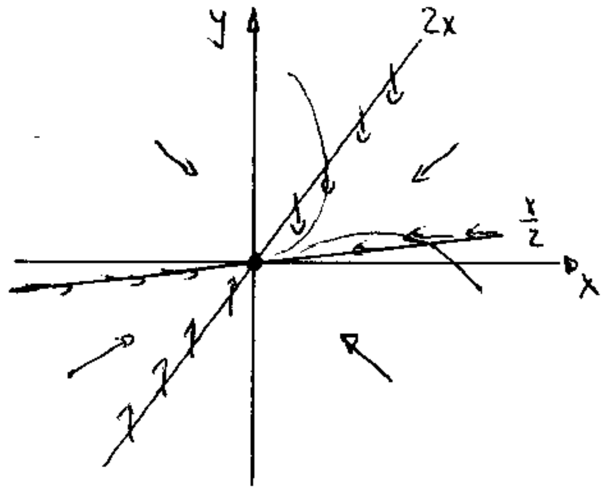
$$\frac{dx}{dt} = ax + by \qquad \frac{dy}{dt} = cx + ey \qquad \text{or} \quad \frac{d}{dt}\begin{bmatrix} x \\ y \end{bmatrix} = \begin{bmatrix} a & b \\ c & e \end{bmatrix}\begin{bmatrix} x \\ y \end{bmatrix} = A\begin{bmatrix} x \\ y \end{bmatrix}$$

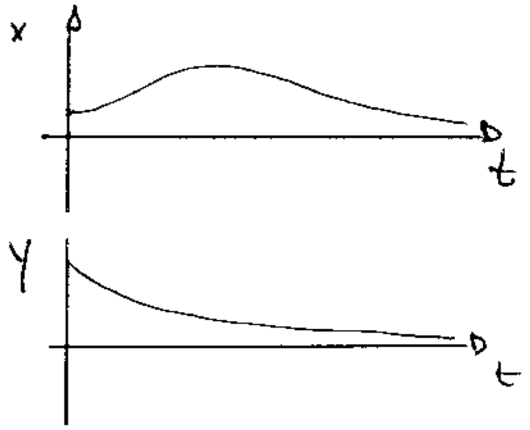
Example 1: (Cautious love) $A = \begin{bmatrix} -1 & \frac{1}{2} \\ \frac{1}{2} & -1 \end{bmatrix}$

$$\dot{x} = -x + \frac{y}{2} \qquad x\text{-nullcline} \Rightarrow y = 2x$$
$$\dot{y} = \frac{x}{2} - y \qquad y\text{-nullcline} \Rightarrow y = \frac{x}{2}$$

On $y = 2x$: $\dot{y} = \frac{x}{2} - y = \frac{x}{2} - 2x = -\frac{3}{2}x \begin{cases} <0 \text{ if } x>0 \\ >0 \text{ if } x<0 \end{cases}$

On $y = \frac{x}{2}$: $\dot{x} = -x + \frac{y}{2} = -x + \frac{x}{4} = -\frac{3}{4}x$





$\text{tr} A = -2$, $\det A = \frac{3}{4}$

eigenvalues $(a-\lambda)(e-\lambda) - cb = 0 \Leftrightarrow \lambda^2 - (a+e)\lambda + ae - bc = 0$

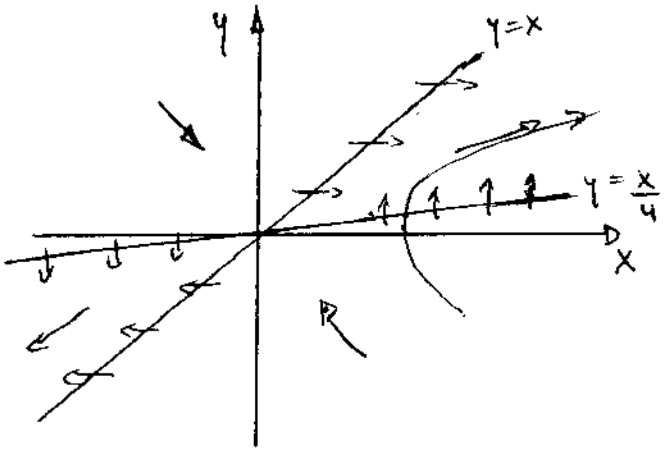
$$\Leftrightarrow \lambda = \frac{a+e}{2} \pm \sqrt{\frac{(a+e)^2}{4} - ae + bc}$$
$$= \frac{\text{tr} A}{2} \pm \sqrt{\frac{(\text{tr} A)^2}{4} - \det(A)}$$

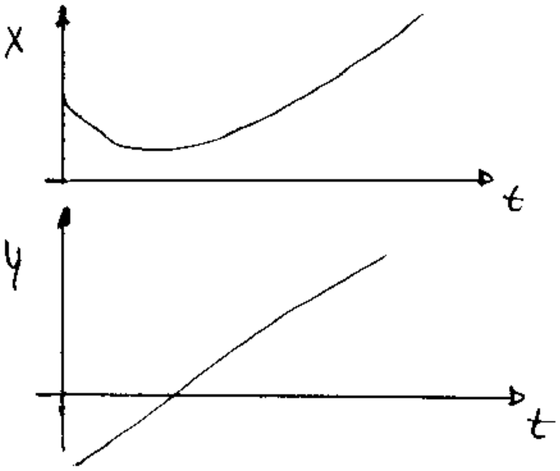
So $\left.\begin{aligned} \lambda_1 &= -1 + \sqrt{1-\tfrac{3}{4}} = -1 + \tfrac{1}{2} = -\tfrac{1}{2} \\ \lambda_2 &= -1 - \sqrt{1-\tfrac{3}{4}} = -1 - \tfrac{1}{2} = -\tfrac{3}{2} \end{aligned}\right\}$ both <0

<u>Example 2</u> (more exciting) $A = \begin{bmatrix} -1 & 4 \\ 1 & -1 \end{bmatrix}$

$\dot{x} = -x + 4y$ $\quad$ x nullcline $\Rightarrow y = \frac{x}{4}$ $\quad$ $\frac{dy}{dt} = x - y = x - \frac{x}{4} = \frac{3}{4}x$

$\dot{y} = x - y$ $\quad$ y nullcline $\Rightarrow y = x$ $\quad$ $\frac{dx}{dt} = -x + 4y = -x + 4x = +3x$





$\mathrm{tr}\, A = -2$

$\det A = 1 - 4 = -3$

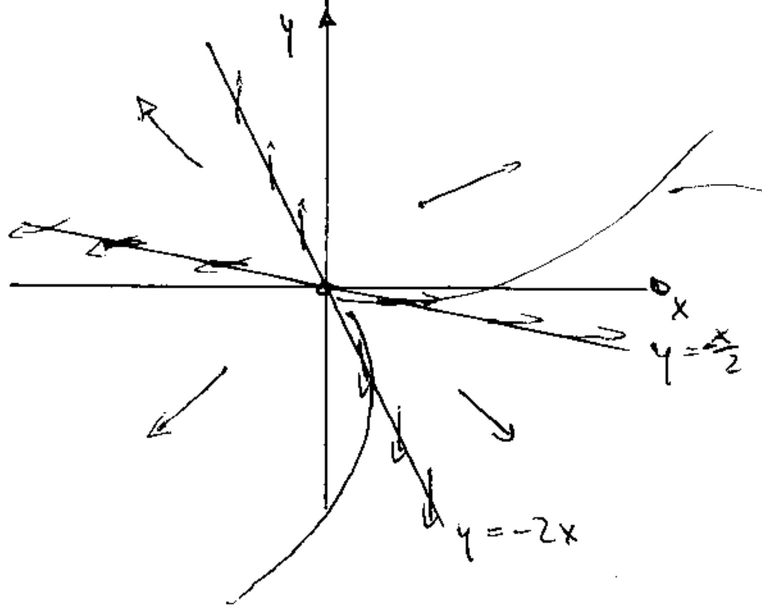
$$\lambda = \frac{\mathrm{tr} A}{2} \pm \sqrt{\frac{(\mathrm{tr} A)^2}{4} - \det A} = -1 \pm \sqrt{1+3} = -1 \pm \sqrt{4} = -1 \pm 2$$

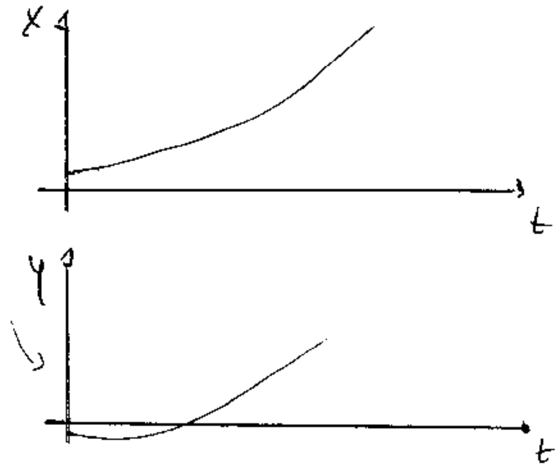
$$\Rightarrow \lambda_1 = 1 > 0 \;, \quad \lambda_2 = -3 < 0$$

<u>Example 3</u> (self excitement) $A = \begin{bmatrix} 1 & 1/2 \\ 1/2 & 1 \end{bmatrix}$

$\dot{x} = x + \frac{y}{2}$ $\quad$ x nullcline $y = -2x$ $\quad$ $\frac{dy}{dt} = \frac{x}{2} - 2x = -\frac{3}{2}x$

$\dot{y} = \frac{x}{2} + y$ $\quad$ y nullcline $y = -\frac{x}{2}$ $\quad$ $\frac{dx}{dt} = x - \frac{x}{4} = \frac{3}{4}x$





$\operatorname{tr} A = 2 \quad \det A = 1 - \frac{1}{4} = \frac{3}{4}$

$$\lambda_1 = 1 + \sqrt{1-(1-\tfrac{1}{4})} = 1 + \sqrt{\tfrac{1}{4}} = 1 + \tfrac{1}{2} = \tfrac{3}{2} > 0$$
$$\lambda_2 = 1 - \sqrt{1-\tfrac{3}{4}} = \qquad = 1 - \tfrac{1}{2} = \tfrac{1}{2} > 0$$

<u>Result:</u> If $\frac{(\operatorname{tr} A)^2}{4} - \det A > 0$, then λ_1, λ_2 are real.

If $\lambda_1, \lambda_2 < 0$ then 0 is stable.
If at least one of the two $\lambda_1 > 0$ or $\lambda_2 > 0$, then 0 is unstable.

[Note: Compare with single species: if $f' > 0$ unstable
$f' < 0$ stable]

<u>Note:</u> If λ is an eigenvalue of A with eigenvector v, i.e.

$$A v = \lambda v = \lambda \begin{bmatrix} v_1 \\ v_2 \end{bmatrix}$$

then

$$x(t) = e^{\lambda t} v_1, \quad y(t) = e^{\lambda t} v_2$$

is a solution of the differential equation $\frac{d}{dt}\begin{bmatrix} x \\ y \end{bmatrix} = A \begin{bmatrix} x \\ y \end{bmatrix}$

$$\frac{dx}{dt} = \lambda e^{\lambda t} v_1, \quad \frac{dy}{dt} = \lambda e^{\lambda t} v_2, \text{ so}$$

$$\frac{d}{dt}\begin{bmatrix} x \\ y \end{bmatrix} = \lambda e^{\lambda t}\begin{bmatrix} v_1 \\ v_2 \end{bmatrix} = e^{\lambda t} A \begin{bmatrix} v_1 \\ v_2 \end{bmatrix} = A \begin{bmatrix} e^{\lambda t} v_1 \\ e^{\lambda t} v_2 \end{bmatrix} = A \begin{bmatrix} x \\ y \end{bmatrix}$$

Note: If $Av = \lambda v$ and λ is real, then $\begin{bmatrix} x \\ y \end{bmatrix} = e^{\lambda t} v$ is a solution of $\frac{d}{dt}\begin{bmatrix} x \\ y \end{bmatrix} = A\begin{bmatrix} x \\ y \end{bmatrix}$, $v = \begin{bmatrix} v_1 \\ v_2 \end{bmatrix}$

Compare this to $\frac{d}{dt}x = ax$ has solution $x(t) = e^{at}x_0$

$$\begin{bmatrix} x \\ y \end{bmatrix} = e^{\lambda t}\begin{bmatrix} v_1 \\ v_2 \end{bmatrix} \Rightarrow \frac{d}{dt}\begin{bmatrix} x(t) \\ y(t) \end{bmatrix} = \lambda e^{\lambda t}\begin{bmatrix} v_1 \\ v_2 \end{bmatrix} = e^{\lambda t}\lambda\begin{bmatrix} v_1 \\ v_2 \end{bmatrix} = e^{\lambda t}A\begin{bmatrix} v_1 \\ v_2 \end{bmatrix}$$
$$= A\begin{bmatrix} e^{\lambda t}v_1 \\ e^{\lambda t}v_2 \end{bmatrix} = A\begin{bmatrix} x(t) \\ y(t) \end{bmatrix}$$

Similar if λ is not real, but we need to know something about complex numbers. We don't have enough time to do this here. Instead, we do linearized stability test.

Remember: $\frac{dx}{dt} = f(x)$, $f(x^*) = 0$ steady state. Then
x^* is stable if $f'(x^*) < 0$
x^* is unstable if $f'(x^*) > 0$.

Want to find a similar criterion for 2-D systems. Use linear approximation and Jacobi-matrix.

Remember Competition equations on 59. $\frac{da}{dt} = f(a,b) = 2\left(1 - \frac{a+b}{2}\right)a$

$\frac{db}{dt} = g(a,b) = 2(1-(a+b))b$

Jacobi matrix: $J = \begin{bmatrix} \frac{\partial f}{\partial a} & \frac{\partial f}{\partial b} \\ \frac{\partial g}{\partial a} & \frac{\partial g}{\partial b} \end{bmatrix} = \begin{bmatrix} 2-2a-b & -a \\ -2b & 2-2a-4b \end{bmatrix}$

$E_1 = (0,0) \rightarrow J(0,0) = \begin{bmatrix} 2 & 0 \\ 0 & 2 \end{bmatrix}$ $\quad \lambda_1 = \lambda_2 = 2 > 0$ unstable

$E_2 = (0,1) \rightarrow J(0,1) = \begin{bmatrix} 1 & 0 \\ -2 & -2 \end{bmatrix}$ $\quad \lambda_1 = 1,\ \lambda_2 = -2$ unstable

$E_3 = (2,0) \rightarrow J(2,0) = \begin{bmatrix} -2 & -2 \\ 0 & -2 \end{bmatrix}$ $\quad \lambda_1 = \lambda_2 = -2 < 0$ stable

Competing species

$$\frac{da}{dt} = 2(1-a-2b)a, \qquad \frac{db}{dt} = 2(1-3a-b)b$$

a-nullcline: $\frac{da}{dt} = 0 \iff a=0$ or $1-a-2b=0 \iff a=0$ or $b = \frac{1-a}{2}$

b-nullcline: $\frac{db}{dt} = 0 \iff b=0$ or $1-3a-b=0 \iff a=0$ or $b = 1-3a$

steady states: $E_1 = (0,0)$, $E_2 = (1,0)$, $E_3 = (0,1)$, $E_4 = \left(\frac{1}{5}, \frac{2}{5}\right)$

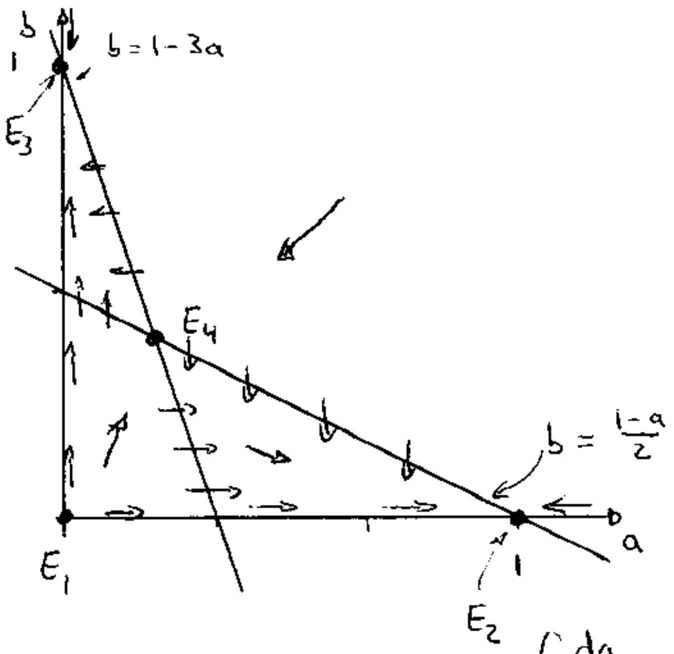
to compute E_4: set $b = \frac{1-a}{2} = 1-3a$ and solve for a

$$\frac{1-a}{2} = 1-3a \rightarrow 1-a = 2-6a \rightarrow 5a = 1 \rightarrow a = \frac{1}{5}$$

then substitute $b = 1-3a = 1 - \frac{3}{5} = \frac{2}{5}$.

Phase plane

Consider only $a, b \geq 0$.



$\frac{da}{dt} > 0 \iff 1-a-2b > 0 \iff b < \frac{1-a}{2}$

$\frac{db}{dt} > 0 \iff 1-3a-b > 0 \iff b < 1-3a$

Linearized stability:

$$\begin{cases} \frac{da}{dt} = f(a,b) = 2(1-a-2b)a \\ \frac{db}{dt} = g(a,b) = 2(1-3a-b)b \end{cases}$$

Find the Jacobimatrix:

$$\begin{bmatrix} \frac{\partial f}{\partial a} & \frac{\partial f}{\partial b} \\ \frac{\partial g}{\partial a} & \frac{\partial g}{\partial b} \end{bmatrix} = \begin{bmatrix} 2-4a-4b & -4a \\ -6b & 2-6a-4b \end{bmatrix} = J(a,b)$$

Evaluate the Jacobimatrix

at $E_1=(0,0) \to J(0,0)=\begin{bmatrix} 2 & 0 \\ 0 & 2 \end{bmatrix}$

this has eigenvalues $\lambda_1=\lambda_2=2>0 \to$ unstable

at $E_2=(1,0) \to J(1,0)=\begin{bmatrix} -2 & -4 \\ 0 & -4 \end{bmatrix}$ eigenvalues $\left.\begin{matrix}\lambda_1=-2 \\ \lambda_2=-4\end{matrix}\right\} \Rightarrow$ stable

at $E_3=(0,1) \to J(0,1)=\begin{bmatrix} -2 & 0 \\ -6 & -2 \end{bmatrix}$ eigenvalues $\left.\begin{matrix}\lambda_1=-2 \\ \lambda_2=-2\end{matrix}\right\} \to$ stable

at $E_4=\left(\frac{1}{5},\frac{2}{5}\right) \to J\left(\frac{1}{5},\frac{2}{5}\right)=\begin{bmatrix} 2-\frac{4}{5}-\frac{8}{5} & -\frac{4}{5} \\ -\frac{12}{5} & 2-\frac{6}{5}-\frac{8}{5} \end{bmatrix}=\begin{bmatrix} -\frac{2}{5} & -\frac{4}{5} \\ -\frac{12}{5} & -\frac{4}{5} \end{bmatrix}$

trace $=-\frac{6}{5}$, det $=\frac{8}{25}-\frac{48}{25}=-\frac{40}{25}$

$\lambda=-\frac{3}{5}\pm\sqrt{\left(\frac{36}{25}\right)\cdot\frac{1}{4}-\left(-\frac{40}{25}\right)}=-\frac{3}{5}\pm\sqrt{\frac{9}{25}+\frac{40}{25}}=-\frac{3}{5}\pm\sqrt{\frac{49}{25}}=-\frac{3}{5}\pm\frac{7}{5}$

$\Rightarrow \lambda_1=-2,\quad \lambda_2=\frac{4}{5}>0 \quad \Rightarrow$ unstable

The corresponding eigenvectors are $v_1=\begin{bmatrix}1\\2\end{bmatrix}$ $v_2=\begin{bmatrix}2\\-3\end{bmatrix}$

<u>Result</u>: There are 4 possible outcomes in the competition system (see page 59 and also exercises I.4 and I.5)

(1) Species a wins

(2) Species b wins

(3) Species a and b can coexist

(4) The winner depends on the initial conditions

Paradox of enrichment

prey: $\frac{db}{dt} = b\left(1 - \frac{b}{K}\right) - p\sqrt{b}$ K: carrying capacity of b.

predator: $\frac{dp}{dt} = -p + p\sqrt{b}$

b-nullcline: $\frac{db}{dt} = 0 \iff b = 0$ or $b\left(1-\frac{b}{K}\right) = p\sqrt{b}$

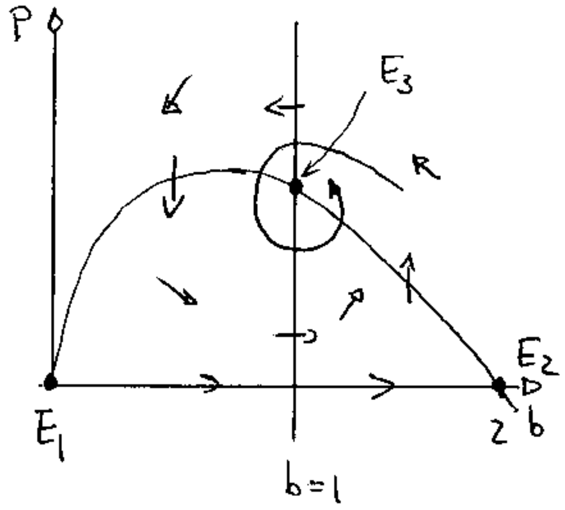
$\iff b = 0$ or $p = \left(1 - \frac{b}{K}\right)\sqrt{b}$

p-nullcline: $\frac{dp}{dt} = 0 \iff p = 0$ or $\sqrt{b} = 1 \iff p = 0$ or $b = 1$.

steady states: $E_1 = (0,0)$, $E_2 = (K, 0)$, $E_3 = \left(1, 1 - \frac{1}{K}\right)$

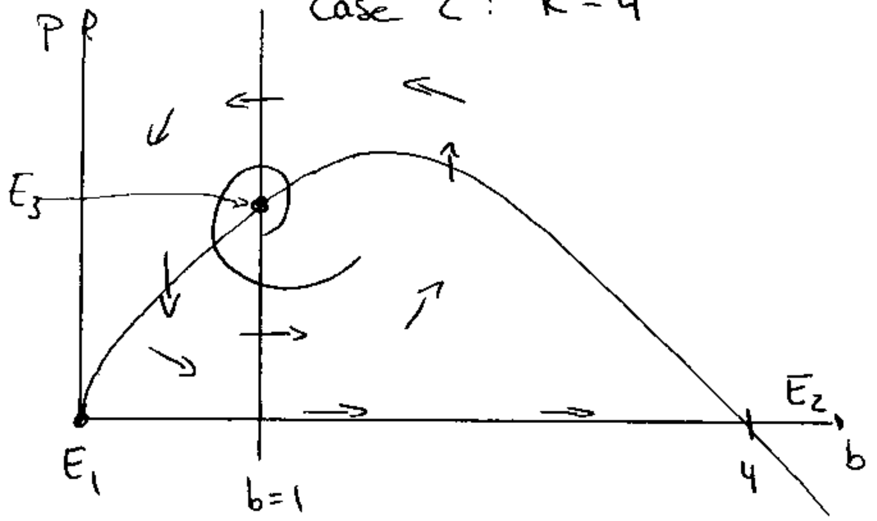
for E_3: put $b = 1$ into the condition $p = \left(1 - \frac{b}{K}\right)\sqrt{b}$

Case 1: $K = 2$



looks like E_3 is stable

Case 2: $K = 4$



looks like E_3 is unstable.

Find the Jacobimatrix

$$J(b,p) = \begin{bmatrix} 1 - \frac{2b}{K} - \frac{p}{2\sqrt{b}} & -\sqrt{b} \\ \frac{p}{2\sqrt{b}} & \sqrt{b} - 1 \end{bmatrix}$$

At E_3 for $k=2$: $E_3=(1,\frac{1}{2})$

$$J(1,\tfrac{1}{2})=\begin{bmatrix}-\frac{1}{4} & -1\\ \frac{1}{4} & 0\end{bmatrix}\qquad tr=-\frac{1}{4}\qquad det=\frac{1}{4}$$

$$\lambda=-\frac{1}{8}\pm\sqrt{\left(\frac{1}{4}\right)^2\cdot\frac{1}{4}-\frac{1}{4}}=-\frac{1}{8}\pm\sqrt{\frac{1}{64}-\frac{16}{64}}=-\frac{1}{4}\pm\sqrt{-\frac{15}{64}}$$

$\to \lambda$ is not real, trace is negative $\to E_3$ is stable.

For $k=4$: $E_3=(1,\frac{1}{4})$

$$J(1,\tfrac{1}{4})=\begin{bmatrix}\frac{3}{8} & -1\\ \frac{1}{8} & 0\end{bmatrix}\qquad tr=\frac{3}{8}\qquad det=\frac{1}{8}$$

$$\lambda=\frac{3}{16}\pm\sqrt{\frac{9}{64}\cdot\frac{1}{4}-\frac{1}{8}}=\frac{3}{16}\pm\sqrt{\frac{9}{256}-\frac{32}{256}}=\frac{3}{16}\pm\sqrt{-\frac{23}{256}}$$

λ is not real, trace is positive $\to E_3$ is unstable.