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# Interacting Populations

Volterra-Lotka System (VL)

$N_1$ prey $\qquad$ $N_2$ predator

(more complex: modelling of ecological systems)

$$\frac{dN_1}{dt} = N_1 \left( a - b N_2 \right)$$

$$a, b, c, d > 0$$

$$\frac{dN_2}{dt} = N_2 \left( c N_1 - d \right)$$

$N_1$ without $N_2$: Malthusian growth with $a$

$N_2$ limits growth of $N_1$, rate $b$

$N_2$ without $N_1$: „radioactive" decay with $d$

(no prey $\Rightarrow$ predator disappears)

$N_1$ limits decay of $N_2$, rate $c$

(predator needs prey to survive)

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Dimensionless form:

$$\tau = at \; ; \quad u_1 = \frac{c}{d} N_1 \; ; \; u_2 = \frac{b}{a} N_2$$

$$\alpha = \frac{d}{a}$$

$$\frac{du_1}{d\tau} = u_1(1-u_2)$$
$$\frac{du_2}{d\tau} = \alpha u_2(u_1-1) \qquad \text{(VL)}$$

Only <u>one</u> free parameter $\alpha$
Notice similarity of $1^{st}$ eq. to Verhulst eq.

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Find the Fixed Points (FP):

FP 1: $u_1^* = u_2^* = 0$

FP 2: $u_1^* = u_2^* = 1$

(Condition for FP in this case:
$u_1^*, u_2^*$ is FP of VL system if

$\frac{du_1}{d\tau} = 0$ <u>and</u> $\frac{du_2}{d\tau} = 0$ at $\begin{matrix} u_1 = u_1^* \\ u_2 = u_2^* \end{matrix}$ )

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Next: Stability Analysis for VL system; it is 2D system.

Stability Analysis in the multi-dimensional case:

analogous to one-dim., but vector form:

$$\frac{d\vec{u}}{d\tau} = \vec{f}(\vec{u}) \qquad \begin{pmatrix} \dot{u}_1 \\ \dot{u}_2 \end{pmatrix} = \begin{pmatrix} f_1(u_1, u_2) \\ f_2(u_1, u_2) \end{pmatrix}$$

FP: $\vec{u}^*$ : $\vec{f}(\vec{u}^*) = 0$; FP $\begin{pmatrix} u_1^* \\ u_2^* \end{pmatrix}$ : $\begin{matrix} f_1(u_1^*, u_2^*) = 0 \\ f_2(u_1^*, u_2^*) = 0 \end{matrix}$

Let $\vec{u}(\tau) = \vec{u}^* + \vec{v}(\tau)$ with $|\vec{v}|/|\vec{u}| \ll 1$

We get: $\frac{d\vec{u}}{d\tau} = \frac{d\vec{u}^*}{d\tau} + \frac{d\vec{v}}{dt} = \frac{d\vec{v}}{dt}$

and: $\frac{d\vec{u}}{dt} = \vec{f}(\vec{u}^* + \vec{v}(\tau))$ = Taylor Series

$$= \vec{f}(\vec{u}^*) + D\vec{f}(\vec{u}^*) \cdot \vec{v}(\tau) + \mathcal{O}(\vec{v}^2)$$

To first order: $\frac{d\vec{v}}{dt} = D\vec{f}(\vec{u}^*)\,\vec{v}(\tau)$

What is $D\vec{f}$? Jacobi-Matrix

$$D\vec{f} = \begin{pmatrix} \frac{\partial f_1}{\partial u_1} & \frac{\partial f_1}{\partial u_2} \\ \frac{\partial f_2}{\partial u_1} & \frac{\partial f_2}{\partial u_2} \end{pmatrix}$$

Formal Solution for $\vec{v}(\tau)$
is exponential function:

$$\vec{v}(\tau) = \vec{v}(0) \exp\Big( \underbrace{D\vec{f}(\vec{u}^*)}_{\text{This is a matrix!}} \cdot \tau \Big)$$

What is $\exp(A\tau)$ with matrix $A$?

Ansatz: Series Expansion $\exp(A\tau) = \sum_{n=0}^{\infty} \frac{A^n}{n!} \tau^n$

Right Hand Side is well-defined, if convergent

Let $\vec{x}_i$ be eigenvector (EV) of $A$
with eigenvalue (EW) $\lambda_i$ $\Rightarrow$

$$\underline{A\vec{x}_i = \lambda_i \vec{x}_i} \Rightarrow A^n \vec{x}_i = \lambda_i^n \vec{x}_i \Rightarrow$$

$$\exp(A\tau)\vec{x}_i = \sum_{n=0}^{\infty} \frac{\lambda_i^n}{n!} \tau^n = \underline{\exp(\lambda_i \tau)\vec{x}_i}$$

$\Rightarrow \exp(\lambda_i t)$ is EW of $\exp(A\tau)$ !

Back to our problem:

$$\vec{v}(\tau) = \exp(A\tau)\,\vec{v}(0)$$

with $A = D\vec{f}(\vec{u}^*)$

$\vec{v}(0)$ is our initial condition;

let $\vec{x}_i$ be a system of EV's of $A$;

then we can find $c_i$ with

$$\vec{v}(0) = \sum_i c_i \vec{x}_i \quad \Longrightarrow$$

$$\vec{v}(\tau) = \exp(A\tau) \sum_i c_i \vec{x}_i$$

$$= \sum_i c_i \exp(A\tau)\,\vec{x}_i = \sum_i c_i \exp(\lambda_i \tau)\,\vec{x}_i$$

Now we can conclude:

FP $\vec{u}^*$ is stable, if all $\lambda_i < 0$ –

it means $\lim_{\tau \to \infty} |\vec{v}(\tau)| = 0$

FP $\vec{u}^*$ is unstable, if one $\lambda_i > 0$

it means $\lim_{\tau \to \infty} |\vec{v}(\tau)| = \infty$

Return to Volterra - Lotka System:

$$\overset{\circ}{\vec{u}} = \vec{f}(\vec{u}) = \begin{pmatrix} u_1(1-u_2) \\ \alpha u_2 (u_1 - 1) \end{pmatrix}$$

$$A = \vec{D}f(\vec{u}) = \begin{pmatrix} 1-u_2 & -u_1 \\ \alpha u_2 & \alpha(u_1-1) \end{pmatrix}$$

(i) First FP 1: $u_1^* = u_2^* = 0$

$$A = \begin{pmatrix} 1 & 0 \\ 0 & -\alpha \end{pmatrix}$$

EW: $0 = \det|A - \lambda E| = (1-\lambda)(-\alpha-\lambda)$
(characteristic polynomial)

Solutions: $\lambda_1 = 1$ ; $\lambda_2 = -\alpha$

$\Rightarrow$ FP1 is unstable, since $\lambda_1 > 0$!

(ii) Second FP 2: $u_1^* = u_2^* = 1$

$$A = \begin{pmatrix} 0 & -1 \\ \alpha & 0 \end{pmatrix}$$

EW: $0 = \det|A - \lambda E| = \begin{vmatrix} -\lambda & -1 \\ \alpha & -\lambda \end{vmatrix}$

$$= \lambda^2 + \alpha \Rightarrow \lambda_{1/2} = \pm i\sqrt{\alpha}$$

What is this? Neither $> 0$ nor $< 0$!

Look at solution for perturbation $\vec{v}(\tau)$ near the FP:

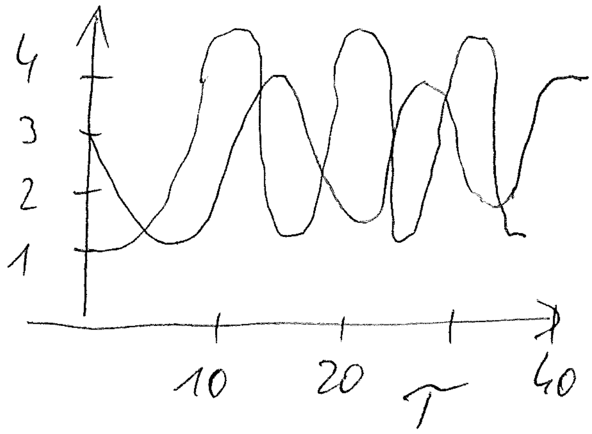
$$\vec{v}(\tau) = \sum_i c_i \exp(\lambda_i \tau) \cdot \vec{x}_i \qquad \left[\vec{v}(0) = \sum_i c_i \vec{x}_i\right]$$

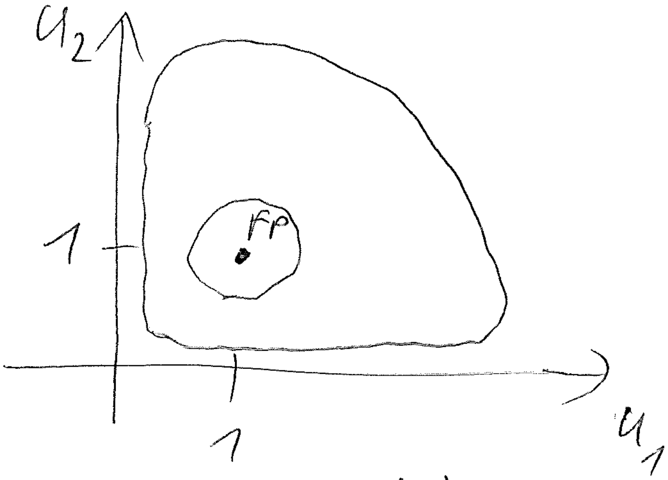
Here:

$$\vec{v}(\tau) = c_1 \exp(i\sqrt{\alpha}\tau)\vec{x}_1 + c_2 \exp(-i\sqrt{\alpha}\tau)\vec{x}_2$$

We have an oscillating solution near the FP – neither does it approach it, nor does it diverge from it!

Schematic Solution of Volterra-Lotka:




$\alpha = 0.5$; $u_1(0) = 1$, $u_2(0) = 3$

$u_1(0) = 1$
$u_2(0) = 2, 3, 4, 5$

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Further generalization:
K predator / K prey species

$$\frac{dN_i}{dt} = N_i \left( a_i - \sum_j b_{ij} P_j \right)$$

$$\frac{dP_i}{dt} = P_i \left( \sum_j c_{ij} N_j - d_i \right)$$

Fixed Points: (i) $N_i^* = P_i^* = 0$
(ii) $a_i = \sum_j b_{ij} P_j^*$ and $d_i = \sum_j c_{ij} N_j^*$

$$A = \left( \begin{array}{c|c} 0 & -N_i^* b_{ij} \\ \hline P_i^* c_{ij} & 0 \end{array} \right)$$

Since $\mathrm{tr} A = \sum_i \lambda_i$
marginal
or unstable!