# Population ecology - exec

## Matrices and difference/differential equations

Pavel Fibich

Department of Botany, Faculty of Sciences, Univ. South Bohemia
pavel.fibich@prf.jcu.cz

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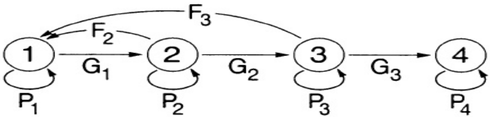
# Why?

Recapitulation of basic math covering matrices, differential ($\delta$R) and difference ($\Delta$R) equations for mathematical modelling used in Population Ecology.

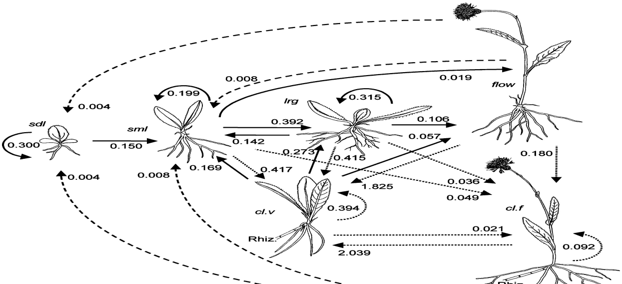
- Matrix models are often used to describe transitions between years, between size stages.
- $\delta$R and $\Delta$R are usefull for describing relationships and evolution in time in continuous and discrete time steps.

Solutions can be stable size/stage distributions in the population (how will population look like after some time).

# Example – Matrix

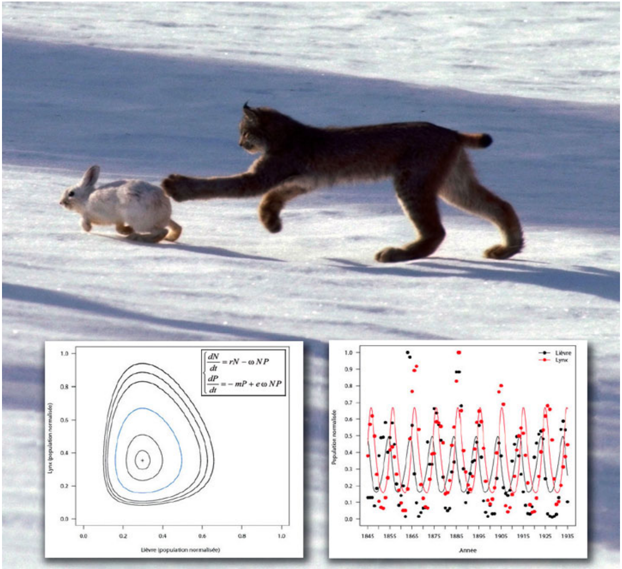



$$\begin{pmatrix} 0 & F_2 & F_3 & 0 \\ G_1 & P_2 & 0 & 0 \\ 0 & G_2 & P_3 & 0 \\ 0 & 0 & G_3 & P_4 \end{pmatrix}$$



# Example – Differential equation





# Vector and Matrix

**Vector** is a quantity characterized by size and direction, denoted as $\vec{x}$. It is order an object of $n$ numbers $x_i$. Eg.: $\vec{x}^{31}, \vec{y}^{21}, \vec{z}^{14}$

$$\vec{x} = \begin{pmatrix} 3 \\ a * b \\ i \end{pmatrix}, \vec{y} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}, \vec{z} = (5\ 3\ 9\ 1)$$

**Matrix** is characterized by the number of rows and columns, contains vectors. Eg. $A^{32}$, $E^{33}$

$$A = \begin{pmatrix} 3 & -1 \\ -1 & 0 \\ 1 & 8 \end{pmatrix}, E = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{pmatrix}$$

Elements can be indexed, $a_{ij}$ $i$-th row and $j$-th column.
Are usefull to describe linear transition, solving ordinary $\delta$R, for describing set of linear equations, ...

# Operations

Vectors can be

- $\vec{a}^{21} + \vec{b}^{21} = \vec{x}^{21}$ summed,
- $\vec{a}^{31} * c = \vec{x}^{31}$ multiplied by one value,
- $\vec{x}^{m1} * \vec{y}^{1n} = A^{mn}, \vec{x}^{1n} * \vec{y}^{n1} = c$ multiplied between themselves, ...

Matrices can be

- $A^{mn} + B^{mn} = C^{mn}$ summed,
- $A^{mn} * c = C^{mn}$ multiplied by one value,
- $A^{mn} * \vec{b}^{n1} = \vec{c}^{m1}$ multiplied by vector,
- $A^{mn} * B^{nk} = C^{mk}$ multiplied between themselves,
- $(A^{mn})^T = A^{nm}$ transposed,
- $A^{-1}$ inverted, ...

# Matrix operations

Sum is cumutative. $A^{mn} + B^{mn} = C^{mn}$

$$\begin{pmatrix} 3 & -1 & 1 \\ -1 & 0 & 1 \\ 1 & 8 & 2 \end{pmatrix} + \begin{pmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{pmatrix} = \begin{pmatrix} 4 & -1 & 1 \\ -1 & 1 & 1 \\ 1 & 8 & 3 \end{pmatrix}$$

Multiplying by vector is cumutative. $A^{mn} * c = C^{mn}$

$$\begin{pmatrix} 3 & -2 & 0 \\ 2 & 1 & 5 \\ 3 & 3 & 1 \end{pmatrix} * 3 = \begin{pmatrix} 9 & -6 & 0 \\ 6 & 3 & 15 \\ 9 & 9 & 3 \end{pmatrix}$$

# Matrix operations



Matrix multiplication is not cumutative. For $A^{mn} * \vec{b}^{n1} = \vec{c}^{m1}$ it is defined as $c_{ij} = \sum_{k=1}^{n} a_{ik} * b_{kj}$

$$\begin{pmatrix} 2 \\ -1 \end{pmatrix} * \begin{pmatrix} 5 & -2 \end{pmatrix} = \begin{pmatrix} 10 & -4 \\ -5 & 2 \end{pmatrix}$$

$$\begin{pmatrix} 3 & -1 & 1 \\ -1 & 0 & 1 \end{pmatrix} * \begin{pmatrix} 2 \\ 1 \\ 0 \end{pmatrix} = \begin{pmatrix} 5 \\ -2 \end{pmatrix}$$

$$\begin{pmatrix} 3 & -1 \\ -1 & 0 \\ 1 & 8 \end{pmatrix} * \begin{pmatrix} 2 \\ 1 \end{pmatrix} = \begin{pmatrix} 5 \\ -2 \\ 10 \end{pmatrix}$$

The same equation applies for matrices multiplication. In R, you can easily use $\% * \%$ operator for matrix multiplication.

# Matrix operations in R



## In R

```
> v1<-c(2,-1)
> v2<-c(5,-2)
> v1 %*% t(v2)
     [,1] [,2]
[1,]   10   -4
[2,]   -5    2
> m1<-matrix(c(3,-1, -1,0, 1,1),nrow=2)
> v3<-c(2,1,0)
> m1 %*% v3
     [,1]
[1,]    5
[2,]   -2
```

# Simplify information from matrix

Looking for a characteristic of matrix by one or few numbers. **Determinant** noted det A, $|A|$

- matrix *n x n* got one number,
- absolutely it is scaling of volume of linear transformation given by the matrix
- Sarrus algorithm (only for sizes 2x2 and 3x3), else Leibniz equation

**Characteristic equation** given by $|A - \lambda * E| = 0$, eg.

$$A = \begin{pmatrix} 3 & -1 \\ 2 & 0 \end{pmatrix}$$

$$0 = |A - \lambda * E| = \begin{vmatrix} 3 - \lambda & -1 \\ 2 & -\lambda \end{vmatrix} = \lambda^2 - 3 * \lambda + 2$$

# Eigenvalues and eigenvectors



**Eigenvalues** are solutions of characteristic equation, denoted $\lambda_i$. **Eigenvector** is vector $\vec{u}$ satisfying equation

$$(A - \lambda * E) * u = 0$$

Eigennumber belongs to eigenvector. Or

$$A * \vec{u} = \lambda * \vec{u}$$

$\vec{u} \neq 0$ is the eigenvector and $\lambda$ is the eigenvalue.

Eigenvectors are used as characteristics of stable (age, ...) structure for transitional matrix in ecology.

# Eigenvalues and eigenvectors



$$A = \begin{pmatrix} 3 & -1 \\ 2 & 0 \end{pmatrix}$$

$$0 = |A - \lambda * E| = \begin{vmatrix} 3-\lambda & -1 \\ 2 & -\lambda \end{vmatrix} = \lambda^2 - 3 * \lambda + 2$$

Solutions of equation are $\lambda_1 = 2, \lambda_2 = 1$, and corresponding eigen vectors

$$\begin{pmatrix} 3-\lambda_1 & -1 \\ 2 & -\lambda_1 \end{pmatrix} * u_1 = \begin{pmatrix} 1 & -1 \\ 2 & -2 \end{pmatrix} * u_1$$

solution is the vector $u_1 = \begin{pmatrix} 2 \\ 2 \end{pmatrix}$. Similarly one can find eigenvector for eigenvalue $\lambda_2$.

# Power iteration

Fast method for finding eigenvalue and eigenvector without analytical solving determinant. This method will find only dominant (biggest) eigenvalue and corresponding eigenvector. Iterative approach

$$b_{k+1} = \frac{Ab_k}{||Ab_k||}$$

Starts with nonzero $b_0$ (initial population structure) that is multiplied by transitional matrix $A$ in time steps $k = 0...$ $||$ denotes normalization.

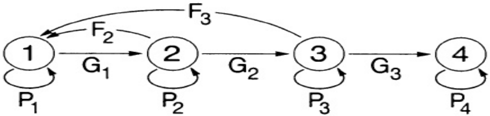
Useful for big matrices, although it can converge slowely. Google (PageRanks), Twitter (recommendations) and Šuspa are using it.

# Power iteration

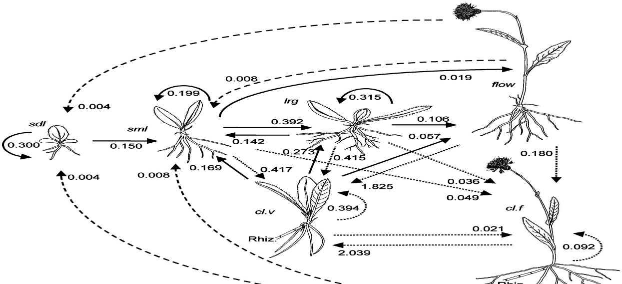
## In R

```
> A<-matrix(c(3, 2, -1, 0),nrow=2)
> x0<-rnorm(2); thresh<-1e-22
> pit<-function(A, x0) {
+    m0<-x0[which.max(abs(x0))]
+    x1<-A %*% (x0 / m0)
+    m1<-x1[which.max(abs(x1))]
+    if(abs(m1 - m0) < thresh) {
+       return(m1) } else { pit(A, x1) } }
> ev1<-pit(A, x0);
> A1<-A - diag(2)*ev1
> ev2<-ev1 + pit(A1, x0)
> c(ev1,ev2)
[1] 2 1
```

# Example




$$\begin{pmatrix} 0 & F_2 & F_3 & 0 \\ G_1 & P_2 & 0 & 0 \\ 0 & G_2 & P_3 & 0 \\ 0 & 0 & G_3 & P_4 \end{pmatrix}$$



# Matrices summary

- Matrices contains rows and columns
- Several basic operations can be made with them
  - comutativity is not always satisfied
  - sizes of elements must correspond
- Math software allows easy work with matrices
- Eigenvector and eigenvalues of matrix are often used in ecology to describe stable (age, size, . . . ) structure.

**Q?**

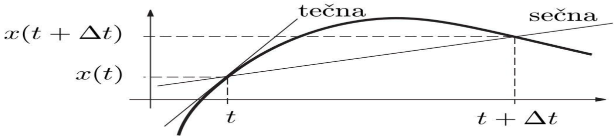
# Equations

**Slope** $k$ of a line $x = k * t + q$

- describes ratio of change of $x$ during change of $t$
- $k$ defines if $(x)$ is in-(de)creasing or non independent on $t$

**Derivative** of function $x(t)$ describes change of $x(t)$ according the change of parameter $t$

- denoted as $\frac{dx}{dt}$ or more commonly just by $x'$ (if we know argument for sure)
- $x'(t) = \frac{dx}{dt} = \lim_{\Delta t \to 0} \frac{x(t+\Delta t) - x(t)}{\Delta t}$
- it is also slope of tangent (tecna in Czech)
- for example, speed is derivative of distance by time



# Differential equation ($\delta$R)



$\delta$R is equation having form

$$y'(t) = f(t, y)$$

where the solution is a function $y$. Deriative ($y'$) and function alone are in the equation. **Solution** (integral) of $\delta$R is any function $y$ that satisfies $\delta$R.

Examples of differential equations:

- $y' = r * y$, with solution $y(t) = y_0 * e^{r*t}$
- $dy/dt = r * y(1 - y/K)$, with solution $y(t) = \frac{K*y_0}{y_o+(K-y_o)*e^{-r*t}}$

These $\delta$R have infinitive number of solutions, therefore we should specify **initial conditions** $y(t_0) = y_0$ (eg. $y(0) = 5$). **Right side of $\delta$R describes change of $y$ (change of population size $y$).**

# To solve $\delta R$



How to solve $y' = f(t, y)$, $y(t_0) = y_0$?

- **analytically** by integration (can be complex or unresolvable)
- numerically to get proximative solution by several methods:
  - Euler,
  - Runge-Kutta,
  - Predictor-Corrector, …

# To solve $\delta R$ analytically



$\frac{dy}{dt} = r * y$, where $r = b - d$ (*b*irth - *d*eath). $r$ growth of population and $y$ size of population.
Solving by separation of variables in $\frac{dy}{r*y} = dt$ and integration

$$\int \frac{dy}{r * y} = \int dt$$

$$\frac{1}{r} ln\ y = t + C$$

then $y$

$$ln\ y = r * (t + C)$$

$$y = e^{r*(t+C)} = e^{r*c} * e^{r*t} = K * e^{r*t}$$

Now we can apply initial conditions $y(t_0) = y_0$ a $t = 0$

$$y_0 = K * e^0 = K$$

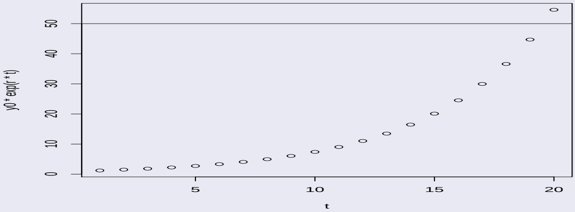
Finally, we have a solution $\delta R$ in form $y = y_0 * e^{r*t}$.

# Analytical solution $\frac{dy}{dt} = r * y$ is $y = y_0 * e^{r*t}$



## In R, r=0.2

```
> t<-1:20;y0<-1;r<-0.2
> plot(y0*exp(r*t)~t); abline(h=50)
```

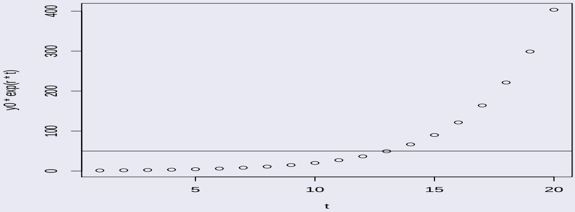


# Analytical solution $\frac{dy}{dt} = r * y$ is $y = y_0 * e^{r*t}$



## In R, r=0.3

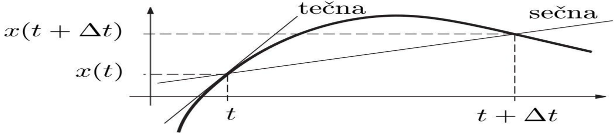
```
> t<-1:20;y0<-1;r<-0.3
> plot(y0*exp(r*t)~t); abline(h=50)
```



# Euler's method – numerical solution $\delta R$



$y' = f(t, y)$ is approximated by a **tangent.**
Go in discrite steps $\Delta t$. In point $(t_0, y_0)$, integral curve have tangent having slope $f(t_0, y_0)$. By changing integral curve by tangent, $y$ is changed by $\Delta y = f(t_0, x_0) * \Delta t$.
For short steps $\Delta t$ is this approximation mostly acceptable.



# Euler's method - numerical solution



For $(t_0 + \Delta t)$ we get

$$y(t_0 + \Delta t) = y_0 + f(t_0, y_0) * \Delta t$$

And generally

$$y_{t+1} = y_t + f(t_n, y_n) * \Delta t$$

It is the easy, but not so accurate method. By decreasing $\Delta t$ one can improve precision, but then it requires more steps.

# Euler's method – example



Euler's method on $y' = f(t, y) = r * y * (1 - y/K)$ with initial concitions $t_0 = 1, y_0 = 1, r = 0.1, K = 10, \Delta t = 1$

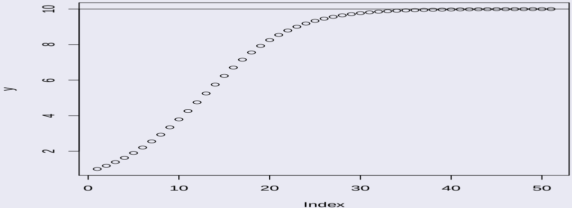
| $t$ | $y$ | $\Delta y$ |
|---|---|---|
| $t_0$ | $y_0$ | $\Delta y_0 = f(t_0, y_0) * \Delta t$ |
| $t_1 = t_0 + \Delta t$ | $y_1 = y_0 + \Delta y_0$ | $\Delta y_1 = f(t_1, y_1) * \Delta t$ |
| $t_2 = t_1 + \Delta t$ | $y_2 = y_1 + \Delta y_1$ | $\Delta y_2 = f(t_2, y_2) * \Delta t$ |
| $\dots$ | $\dots$ | $\dots$ |

# Euler's method – example

## Euler's method on $y' = f(t, y) = r * y * (1 - y/K)$

### In R, r=0.2

```
> dt<-1;y0<-1;r<-0.2;K=10
> y<-c(y0)
> for(s in 1:50)
+   y<-c(y, y[s]+r*y[s]*(1-y[s]/K)*dt)
> plot(y);abline(h=K)
```



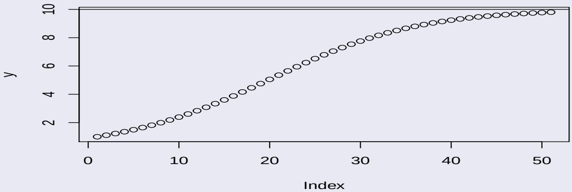
# Euler's method – example



Euler's method on $y' = f(t, y) = r * y * (1 - y/K)$

## In R, r=0.12

```
> dt<-1;y0<-1;r<-0.12;K=10
> y<-c(y0)
> for(s in 1:50)
+   y<-c(y, y[s]+r*y[s]*(1-y[s]/K)*dt)
> plot(y);abline(h=K)
```



# Other methods for numerical solution *DR*



Eg. Runge-Kutta and Predictor-Corrector are much more precise and available in mathematical software.

- Commercial - Matlab, Maple, Mathematica
- Free - R, Maxima, SciLab, Octave,...

# Symbolic solver – example



## In R, symbolic solution of the logistic growth

```
> library(deSolve)# loads the library
> ti<-seq(from=0, to=10, by = 0.01)
> params<-c(r=1.5,K=10); state<-c(x=0.1)
> lgr<- function(t, state, params){
+   with( as.list(c(state, params)),{
+         dx <- r*x*(1-x/K)
+         return(list(dx)) }) }
> out <- ode(y=state,times=ti,func=lgr,
                 parms=params)
> plot(out[,2]~out[,1],xlab="time",
        ylab="pop size")
> abline(h=params[2])
```

# Difference equation ($\Delta R$)



$\Delta$R are discrete form of differential equations ($\delta$R). Changes are **discrete** not continuous as in $\delta$R (eg. like in Euler's method).
$\Delta R$ has form

$$y_{n+1} = f(y_n),$$

where the **solution** is any a sequence $y = \{y_n\}_{n=1}^{\infty}$, satisfying the equation $\Delta R$.
**Fixed point** (FP) of $f$ is number $y^*$ that satisfies $f(y^*) = y^*$.

# Difference equation - example



Arithmetic sequence is defined by a recursive equation

$$a_{n+1} = a_n + \Delta$$

Difference is $a_{n+1} - a_n = \Delta$.
Solution is

$$a_n = a_0 + n * \Delta$$

# Transformation of $\delta R$ to $\Delta R$



By setting change of differential equation as a discrete, we can approximate $DR$ by $\Delta R$.

$$dy/dt \approx \frac{y_{t+\Delta t} - y_t}{\Delta t}$$

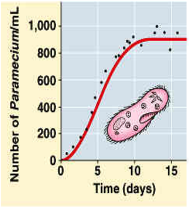
For example for $y' = r * y * (1 - y/K)$ a $\Delta t = 1$

$$y_{n+1} = y_n + r * y_n * (1 - y_n/K)$$

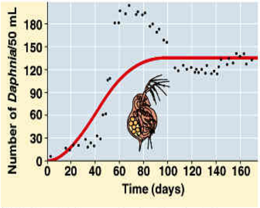
like in the Euler's method.

# Examples

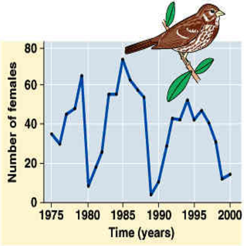





(a) A *Paramecium* population in the lab

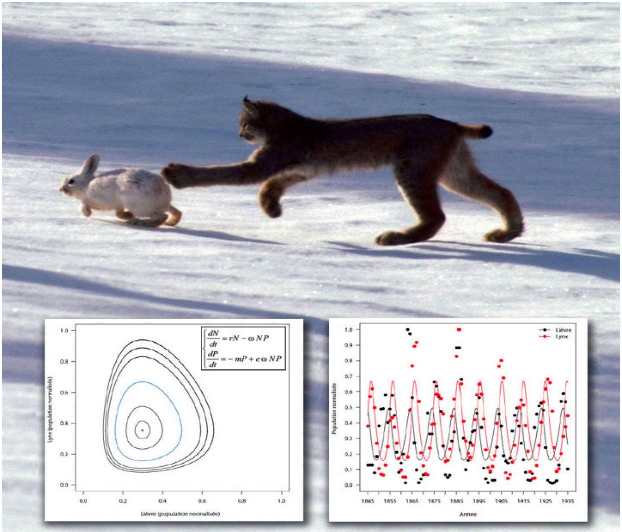



(b) A *Daphnia* population in the lab




(c) A song sparrow population in its natural habitat

# Lynx follows snowshoe



# Summary of equations



- $\delta$R describes continuous change (eg. in time) and solution is a function.
- $\delta$R can be solved analytically or numerically, defines discrete dependence, solution is sequence.
- With the solution can help mathematical software (it is not necessary to do math on paper).
- $y' = r * y$ exponential growth (unlimited).
- $y' = r * y * (1 - y/K)$ logistic growth (limited by carrying capacity of environment $K$).

Any questions or comments?

# References and Questions



- Caswell H., *Matrix Population Models*, Oxford University Press, 2006.
- Pastor J., *Mathematical Ecology of Populations and Ecosystems*. Wiley-Blackwell, 2008.
- Kot M., *Elements of Mathematical Ecology*. Cambridge University press, 2001.