# Linear models of structured populations 

Matthew Macauley<br>Department of Mathematical Sciences<br>Clemson University<br>http://www.math.clemson.edu/~macaule/

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## Motivation: Population dynamics

Consider a population divided into several groups, such as

- children and adults
- egg, larva, pupa, adult

For example, consider a population of insects

$$
\mathrm{Egg} \longrightarrow \text { Larva } \longrightarrow \text { Adult } \longrightarrow \text { Dead }
$$

$E_{t}=\#$ eggs at time $t$
$L_{t}=\#$ larve at time $t$
$A_{t}=\#$ adults at time $t$

## An example

Suppose we have the following data:

- $4 \%$ of eggs survive to become larvae
- $39 \%$ of larvae make it to adulthood
- The average adult produces 73 eggs each
- Each adult dies after 1 day


We can write this as a system of difference equations:

$$
\left\{\begin{array}{l}
E_{t+1}=73 A_{t} \\
L_{t+1}=.04 E_{t} \\
A_{t+1}=.39 L_{t}
\end{array} \quad\left[\begin{array}{ccc}
0 & 0 & 73 \\
.04 & 0 & 0 \\
0 & .39 & 0
\end{array}\right]\left[\begin{array}{c}
E_{t} \\
L_{t} \\
A_{t}
\end{array}\right]=\left[\begin{array}{c}
E_{t+1} \\
L_{t+1} \\
A_{t+1}
\end{array}\right]\right.
$$

By back-substitution, or inspection, we can deduce the following:

$$
A_{t+3}=(.39)(.04)(73) A_{t}=1.1388 A_{t}
$$

Thus, this is just exponential growth. But what if instead of dying, $65 \%$ of adults survive another day?

A slighly more complicated example
Suppose we have the following data:

- $4 \%$ of eggs survive to become larvae
- $39 \%$ of larvae make it to adulthood

■ The average adult produces 73 eggs each

- Each day, 35\% of adults die.


This yields a more complicated system of difference equations:

$$
\left\{\begin{array}{l}
E_{t+1}=73 A_{t} \\
L_{t+1}=.04 E_{t} \\
A_{t+1}=.39 L_{t}+.65 A_{t}
\end{array} \quad\left[\begin{array}{ccc}
0 & 0 & 73 \\
.04 & 0 & 0 \\
.65 & .39 & 0
\end{array}\right]\left[\begin{array}{l}
E_{t} \\
L_{t} \\
A_{t}
\end{array}\right]=\left[\begin{array}{c}
E_{t+1} \\
L_{t+1} \\
A_{t+1}
\end{array}\right] .\right.
$$

## Questions

- Best way to solve this?
- What is the growth rate?
- What is the long-term behavior?

■ How much effect does changing the initial conditions have?

## Another example

Consider a forest that has 2 species of trees, $A$ and $B$. Let $A_{t}$ and $B_{t}$ denote the population of each, in year $t$.

When a tree dies, a new tree grows in its place (either species).
Each year:

- $1 \%$ of the $A$-trees die
- $5 \%$ of the $B$-trees die
- $25 \%$ of the vacant spots go to species $A$
- $75 \%$ of the vacant spots go to species $B$


This can be written as a $2 \times 2$ system:

$$
\left\{\begin{array}{l}
A_{t+1}=.99 A_{t}+(.25)(.01) A_{t}+(.25)(.05) B_{t} \\
B_{t+1}=.95 B_{t}+(.75)(.01) A_{t}+(.75)(.05) B_{t}
\end{array} \quad\left[\begin{array}{ll}
.9925 & .0125 \\
.0075 & .9875
\end{array}\right]\left[\begin{array}{l}
A_{t} \\
B_{t}
\end{array}\right]=\left[\begin{array}{l}
A_{t+1} \\
B_{t+1}
\end{array}\right]\right.
$$

## Solving systems of difference equations

One way to solve $\mathbf{x}_{t+1}=P \mathbf{x}_{t}$ :

$$
\begin{aligned}
& \mathbf{x}_{1}=P \mathbf{x}_{0} \\
& \mathbf{x}_{2}=P \mathbf{x}_{1}=P\left(P \mathbf{x}_{0}\right)=P^{2} \mathbf{x}_{0} \\
& \mathbf{x}_{3}=P \mathbf{x}_{2}=P^{3} \mathbf{x}_{0}
\end{aligned}
$$

## A better method

Find the eigenvalues and eigenvectors of $P$.
Then write the initial vector $\mathrm{x}_{0}$ using a basis of eigenvectors.

Suppose $\mathbf{x}_{0}=c_{1} \mathbf{v}_{1}+c_{2} \mathbf{v}_{2}$. Then

$$
\begin{aligned}
\mathbf{x}_{1} & =P \mathbf{x}_{0}=P\left(c_{1} \mathbf{v}_{1}+c_{2} \mathbf{v}_{2}\right)=c_{1} \lambda_{1} \mathbf{v}_{1}+c_{2} \lambda_{2} \mathbf{v}_{2} \\
\mathbf{x}_{2} & =P \mathbf{x}_{1}=P^{2} \mathbf{x}_{0}=P\left(c_{1} \lambda_{1} \mathbf{v}_{1}+c_{2} \lambda_{2} \mathbf{v}_{2}\right)=c_{1} \lambda_{1}^{2} \mathbf{v}_{1}+c_{2} \lambda_{2}^{2} \mathbf{v}_{2} . \\
& \vdots \\
\mathbf{x}_{t} & =P^{t} \mathbf{x}_{0}=c_{1} \lambda_{1}^{t} \mathbf{v}_{1}+c_{2} \lambda_{2}^{t} \mathbf{v}_{2} .
\end{aligned}
$$

An example, revisted
Let us revisit our "tree example", where $P=\left[\begin{array}{ll}.9925 & .0125 \\ .0075 & .9875\end{array}\right]$.
The eigenvalues and eigenvectors of $P$ are

$$
\lambda_{1}=1, \quad \mathbf{v}_{1}=\left[\begin{array}{l}
5 \\
3
\end{array}\right], \quad \lambda_{2}=.98, \quad \mathbf{v}_{2}=\left[\begin{array}{c}
1 \\
-1
\end{array}\right] .
$$

Consider the initial condition $\mathrm{x}_{0}=\left[\begin{array}{c}A_{0} \\ B_{0}\end{array}\right]=\left[\begin{array}{c}10 \\ 990\end{array}\right]$.

## First step

Write $\mathbf{x}_{0}=c_{1}\left[\begin{array}{l}5 \\ 3\end{array}\right]+c_{2}\left[\begin{array}{c}1 \\ -1\end{array}\right]$, i.e., solve $P \mathbf{c}=\mathbf{x}_{0}$ :

$$
\left[\begin{array}{cc}
5 & 1 \\
3 & -1
\end{array}\right]\left[\begin{array}{l}
c_{1} \\
c_{2}
\end{array}\right]=\left[\begin{array}{c}
10 \\
990
\end{array}\right] .
$$

$$
\mathbf{c}=P^{-1} \mathbf{x}_{0}=-\frac{1}{8}\left[\begin{array}{cc}
-1 & -1 \\
-3 & 5
\end{array}\right]\left[\begin{array}{c}
10 \\
990
\end{array}\right]=\left[\begin{array}{c}
125 \\
-615
\end{array}\right]
$$

Thus, our initial vector is $\mathbf{x}_{0}=\left[\begin{array}{c}10 \\ 990\end{array}\right]=125\left[\begin{array}{l}5 \\ 3\end{array}\right]-615\left[\begin{array}{c}1 \\ -1\end{array}\right]$.

## An example (cont.)

## Solving for $\mathbf{x}_{t}$

Once we have written $\mathbf{x}_{0}=c_{1} \mathbf{v}_{1}+c_{2} \mathbf{v}_{2}$, the solution $\mathbf{x}_{t}$ is simply

$$
\mathbf{x}_{t}=P^{t} \mathbf{x}_{0}=c_{1} \lambda_{1}^{t} \mathbf{v}_{1}+c_{2} \lambda_{2}^{t} \mathbf{v}_{2}
$$

In our example, $\mathbf{x}_{0}=125\left[\begin{array}{l}5 \\ 3\end{array}\right]-615\left[\begin{array}{c}1 \\ -1\end{array}\right]$, and so

$$
\mathbf{x}_{t}=125(1)^{t}\left[\begin{array}{l}
5 \\
3
\end{array}\right]-615(.98)^{t}\left[\begin{array}{c}
1 \\
-1
\end{array}\right]=\left[\begin{array}{c}
625-(615)(.98)^{t} \\
375+(615)(.98)^{t}
\end{array}\right]
$$

The long-term behavior of this system is

$$
\lim _{t \rightarrow \infty} \mathbf{x}_{t}=125\left[\begin{array}{l}
5 \\
3
\end{array}\right]=\left[\begin{array}{l}
625 \\
375
\end{array}\right]
$$

Notice that this does not depend on $\mathbf{x}_{0}$ !

