## Linear models of structured populations

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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

$$\mathsf{Egg} \longrightarrow \mathsf{Larva} \longrightarrow \mathsf{Adult} \longrightarrow \mathsf{Dead}$$

 $E_t = \#$  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

73 E .04 L .39 A .96 Dead

We can write this as a system of difference equations:

$$\begin{cases} E_{t+1} = 73A_t \\ L_{t+1} = .04E_t \\ A_{t+1} = .39L_t \end{cases} \qquad \begin{bmatrix} 0 & 0 & 73 \\ .04 & 0 & 0 \\ 0 & .39 & 0 \end{bmatrix} \begin{bmatrix} E_t \\ L_t \\ A_t \end{bmatrix} = \begin{bmatrix} E_{t+1} \\ L_{t+1} \\ A_{t+1} \end{bmatrix}.$$

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

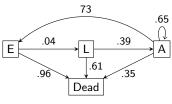
$$A_{t+3} = (.39)(.04)(73)A_t = 1.1388A_t$$

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:

$$\begin{cases} E_{t+1} = 73A_t \\ L_{t+1} = .04E_t \\ A_{t+1} = .39L_t + .65A_t \end{cases}$$

$$\begin{bmatrix} 0 & 0 & 73 \\ .04 & 0 & 0 \\ .65 & .39 & 0 \end{bmatrix} \begin{bmatrix} E_t \\ L_t \\ A_t \end{bmatrix} = \begin{bmatrix} E_{t+1} \\ L_{t+1} \\ A_{t+1} \end{bmatrix}.$$

## 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?

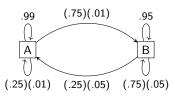
### Another example

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:

$$\begin{cases} A_{t+1} = .99A_t + (.25)(.01)A_t + (.25)(.05)B_t \\ B_{t+1} = .95A_t + (.75)(.01)A_t + (.75)(.05)B_t \end{cases}$$

$$\begin{bmatrix} .9925 & .0125 \\ .0075 & .9875 \end{bmatrix} \begin{bmatrix} A_t \\ B_t \end{bmatrix} = \begin{bmatrix} A_{t+1} \\ B_{t+1} \end{bmatrix}$$

# Solving systems of difference equations

One way to solve 
$$\mathbf{x}_{t+1}=P\mathbf{x}_t$$
: 
$$\mathbf{x}_1=P\mathbf{x}_0$$
 
$$\mathbf{x}_2=P\mathbf{x}_1=P(P\mathbf{x}_0)=P^2\mathbf{x}_0$$
 
$$\mathbf{x}_3=P\mathbf{x}_2=P^3\mathbf{x}_0$$
 .

#### A better method

Find the eigenvalues and eigenvectors of P.

Then write the initial vector  $\mathbf{x}_0$  using a basis of eigenvectors.

Suppose 
$$\mathbf{x}_0 = c_1 \mathbf{v}_1 + c_2 \mathbf{v}_2$$
. Then 
$$\begin{aligned} \mathbf{x}_1 &= P \mathbf{x}_0 = P(c_1 \mathbf{v}_1 + c_2 \mathbf{v}_2) = c_1 \lambda_1 \mathbf{v}_1 + c_2 \lambda_2 \mathbf{v}_2 \\ \mathbf{x}_2 &= P \mathbf{x}_1 = P^2 \mathbf{x}_0 = P(c_1 \lambda_1 \mathbf{v}_1 + c_2 \lambda_2 \mathbf{v}_2) = c_1 \lambda_1^2 \mathbf{v}_1 + c_2 \lambda_2^2 \mathbf{v}_2 \,. \end{aligned}$$
$$\vdots$$
$$\mathbf{x}_t &= P^t \mathbf{x}_0 = c_1 \lambda_1^t \mathbf{v}_1 + c_2 \lambda_2^t \mathbf{v}_2 \,. \end{aligned}$$

## An example, revisted

Let us revisit our "tree example", where  $P = \begin{bmatrix} .9925 & .0125 \\ .0075 & .9875 \end{bmatrix}$ .

The eigenvalues and eigenvectors of P are

$$\lambda_1=1, \ \textbf{v}_1=\begin{bmatrix} 5\\ 3 \end{bmatrix}, \qquad \lambda_2=.98, \ \textbf{v}_2=\begin{bmatrix} 1\\ -1 \end{bmatrix}\,.$$

Consider the initial condition  $\mathbf{x}_0 = \begin{bmatrix} A_0 \\ B_0 \end{bmatrix} = \begin{bmatrix} 10 \\ 990 \end{bmatrix}$ .

# First step

Write 
$$\mathbf{x}_0 = c_1 \begin{bmatrix} 5 \\ 3 \end{bmatrix} + c_2 \begin{bmatrix} 1 \\ -1 \end{bmatrix}$$
, i.e., solve  $P\mathbf{c} = \mathbf{x}_0$ :

$$\begin{bmatrix} 5 & 1 \\ 3 & -1 \end{bmatrix} \begin{bmatrix} c_1 \\ c_2 \end{bmatrix} = \begin{bmatrix} 10 \\ 990 \end{bmatrix}.$$

$$\mathbf{c} = P^{-1}\mathbf{x}_0 = -\frac{1}{8} \begin{bmatrix} -1 & -1 \\ -3 & 5 \end{bmatrix} \begin{bmatrix} 10 \\ 990 \end{bmatrix} = \begin{bmatrix} 125 \\ -615 \end{bmatrix}$$

Thus, our initial vector is  $\mathbf{x}_0 = \begin{bmatrix} 10 \\ 990 \end{bmatrix} = 125 \begin{bmatrix} 5 \\ 3 \end{bmatrix} - 615 \begin{bmatrix} 1 \\ -1 \end{bmatrix}$ .

# 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,  $\mathbf{x}_0 = 125 \begin{bmatrix} 5 \\ 3 \end{bmatrix} - 615 \begin{bmatrix} 1 \\ -1 \end{bmatrix}$ , and so

$$\textbf{x}_t = 125(1)^t \begin{bmatrix} 5 \\ 3 \end{bmatrix} - 615(.98)^t \begin{bmatrix} 1 \\ -1 \end{bmatrix} = \begin{bmatrix} 625 - (615)(.98)^t \\ 375 + (615)(.98)^t \end{bmatrix}.$$

The long-term behavior of this system is

$$\lim_{t\to\infty}\mathbf{x}_t=125\begin{bmatrix}5\\3\end{bmatrix}=\begin{bmatrix}625\\375\end{bmatrix}\;.$$

Notice that this does not depend on  $x_0!$