# MSc Computational Methods in Ecology and Evolution: Maths for Biology

## Matrices

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[Notation: matrices are upper case bold (e.g. A), and vectors have a single underline (e.g. a)]

### **QUESTION 1**

# Images of basis vectors, and determinants

A matrix is a "table" of numbers, which are defined to act on vectors and transform them in arbitrary ways. We are going to focus on  $2 \times 2$  matrices, which act on 2D vectors in a plane.

a) For each of the following matrices A

$$i) \ \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}; ii) \ \begin{pmatrix} 1 & 0 \\ 0 & -1 \end{pmatrix}; iii) \ \begin{pmatrix} 0 & -1 \\ 1 & 0 \end{pmatrix} iv) \ \begin{pmatrix} 2 & -1 \\ 0 & 1 \end{pmatrix} v) \ \begin{pmatrix} 0 & 0 \\ 0 & 1 \end{pmatrix} vi) \ \begin{pmatrix} 3 & 6 \\ 1 & 2 \end{pmatrix} vi) \ \begin{pmatrix} 1 & 1 \\ 0 & 0.5 \end{pmatrix}$$

calculate the resultant vectors  $\underline{a}_1 = A\underline{e}_1$  &  $\underline{a}_2 = A\underline{e}_2$ , where  $\underline{e}_1 = \left( \begin{smallmatrix} 1 \\ 0 \end{smallmatrix} \right)$  &  $\underline{e}_2 = \left( \begin{smallmatrix} 0 \\ 1 \end{smallmatrix} \right)$  and plot them on an x-y plane. What do you notice about the transformation of vectors  $\underline{e}_1$  &  $\underline{e}_2$ , with respect to the entries in A?

- b) i) Calculate  $|A| = \det A$  for each matrix above and ii) calculate the area of the parallelogram made by two vectors  $\underline{a}_1 \& \underline{a}_2$ ? What do you notice? iii) Comment on the determinant for matrix vi, v & vii and the directions of  $\underline{a}_1 \& \underline{a}_2$ . iv) Why is the sign of determinant of matrix ii) negative?
- c) for the matrix

$$A = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}$$

calculate the resultant vectors  $\underline{a}_1 = A\underline{e}_1$  &  $\underline{a}_2 = A\underline{e}_2$ . What do you notice about the transformation of vectors  $\underline{e}_1$  &  $\underline{e}_2$ , with respect to the entries in A? item i) Calculate  $|A| = \det A$  and \*ii) show that the parallelogram made by  $\underline{a}_1$  and  $\underline{a}_2$  has area = |A|

The vectors  $\underline{e}_1=(\frac{1}{0})$  &  $\underline{e}_2=(\frac{0}{1})$  are known as the basis vectors and the columns of  $\boldsymbol{A}$  represent the *images* of these basis vectors, i.e.  $\boldsymbol{A}=(\underline{a}_1,\underline{a}_2)$ . The determinant is the area of the transformation, of the unit square, represented by  $\boldsymbol{A}$ .

#### **QUESTION 2**

# Eigenvalues and Eigenvectors of Markov matrices

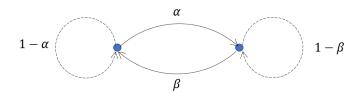


FIG. 1. 2-state Markov process

If we have some system that has only 2-states A and B (e.g. 2-alleles in a population, people are infected with a virus or not, is it raining today or it is dry), and the probability of making a transition only depends on the current state (A or B), then we have a Markov stochastic process. We can then fully describe the stochastic dynamics for  $t \to t+1$  with just two transition probabilities

$$Prob(A \to B) = \alpha$$
  
 $Prob(B \to A) = \beta$ 

and the matrix

$$\mathbf{M} = \begin{pmatrix} 1 - \alpha & \beta \\ \alpha & 1 - \beta \end{pmatrix}$$

describing the change in the probability vector  $\underline{p}_{t+1} = M\underline{p}_t$  is called is Markov matrix (also called a stochastic matrix or a transition matrix). The solution for an initial condition  $p_0$  is

$$\underline{p}_t = \boldsymbol{M}^t \underline{p}_0$$

Consider the Markov matrix

$$\boldsymbol{M} = \begin{pmatrix} 2/3 & 1/2 \\ 1/3 & 1/2 \end{pmatrix}$$

- a) What is the sum of the columns of this matrix and why must this be so?
- b) Let  $\underline{p}_0=(\frac{1}{0})$  and calculate in your favourite numerical software  $\underline{p}_t$  for t=1,2,3,100
- c) Repeat for  $p_0 = \begin{pmatrix} 0 \\ 1 \end{pmatrix}$ . What do you notice in both cases?
- d) Explain your result for b) and c) in terms of the fact that the transition probability for  $A \to B$  is less than the reverse transition  $B \to A$
- e) Let  $\underline{p}_0 = {3/5 \choose 2/5}$  and calculate  $\underline{p}_t$  for t=1,2,3,100. What do you notice? You should find  $\underline{p}_0 = \underline{p}_1 = \underline{p}_2 = \underline{p}_{10} = \underline{p}_{100}$ .
- f) 2x2 square matrices each have at most 2 special vectors that do not change direction under action of the matrix,  $M\underline{v} = \lambda\underline{v}$ , but can be compressed or stretched along this direction by a factor  $\lambda$ . These vectors are called an eigenvectors, and each has an associated eigenvalue, which is the stretch factor. It is clear  $\binom{3/5}{2/5}$  is an eigenvector what is the associated eigenvalue? Let this eigenvalue be  $\lambda_1$ .
- g) Let  $\underline{v} = {1 \choose 1}$  and calculate  $M^t\underline{v}$  for t=1,2,3,100. What do you notice? What is the ratio of values of the elements of each vector between successive time points? What is the eigenvalue for this eigenvector? Let this eigenvalue be  $\lambda_2$ .

h) With the eigenvalues and eigenvectors the solution  $p_{\scriptscriptstyle t}$  can be expressed in a more convenient form

$$\underline{p}_t = \begin{pmatrix} 3/5 \\ 2/5 \end{pmatrix} \lambda_1^t + \gamma \begin{pmatrix} -1 \\ 1 \end{pmatrix} \lambda_2^t$$

where  $\lambda_1$  is often called the leading eigenvalue as it is largest in value. By setting t=0 and with initial condition  $\underline{p}_0=(\frac{1}{0})$  calculate  $\gamma$  and verify this equation for  $\underline{p}_t$  gives the same answer as in part b).

- i) Using this equation, explain intuitively why as t becomes large  $\underline{p}_t o {3/5 \choose 2/5}$ .
- j) Using the methods taught in the lectures calculate the eigenvectors and eigenvalues of M and verify you get the same answer. (Hint: eigenvectors can be normalised arbitrarily: here we want to normalise the first eigenvector, such that it is a probability vector, as it corresponds to the long-time steady state probability.)
- k) If our two states are two alleles/variants in a population which mutate into each other with the same probability of  $\mu$  per generation, what is the Markov matrix for this stochastic process? What are its eigenvalues and eigenvectors? Identify the non-leading eigenvalue and the steady state probability vector and comment on their significance. Discuss whether this system corresponds to evolution in an individual or a population, or both.

(For the last two parts, if you have not been taught how to calculate eigenvalues and eigenvectors yet, they are optional and can be done at a later date.)

#### Circular motion with matrices

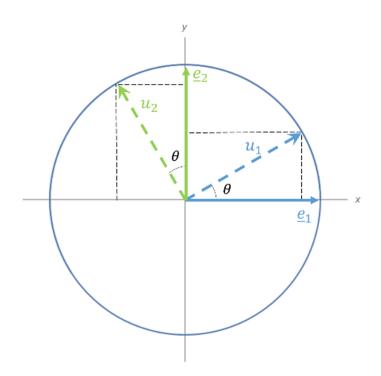


FIG. 2. Unit circle

- a) Above is a figure of the unit circle with the basis vectors each rotated an angle  $\theta$ ; write down the images of the basis vectors  $\underline{u}_1$  &  $\underline{u}_2$  in terms  $\theta$ .
- b) Given this result show that the rotation matrix  $U(\theta)$ , which rotates vectors by angle  $\theta$  is:

$$U(\theta) = \begin{pmatrix} \cos \theta & -\sin \theta \\ \sin \theta & \cos \theta \end{pmatrix}$$

- c) Evaluate the determinant |U|. Explain your result in terms of the answer to Q1.
- d) Evaluate  $U(\theta)$  for  $\theta=0,\pm\pi/2,\pm,\pm3\pi/2,2\pi$ . For each  $\theta$ , what is the corresponding complex number that describes the same rotation ? (Hint: refer back to tutorial from Tuesday, where  $u(\theta)=\cos\theta+i\sin\theta$  is discussed)
- e) What effect does the diagonal matrix

$$\boldsymbol{R} = \begin{pmatrix} R & 0 \\ 0 & R \end{pmatrix}$$

have on the basis vectors  $\underline{e}_1$  and  $\underline{e}_2$ , if R < 1 and if R > 1?? What is the determinant of this matrix?

- f) What would be the corresponding matrix to represent the complex number  $Re^{i\theta}$ , which represents an expansion/contraction of vectors as well as rotation by angle  $\theta$ ?
- g) We want to use the rotation matrix  $U(\omega t)$  to represent the motion of our predator prey species about some fixed point with time-dependent vector given initial values  $x_0$  &  $y_0$  with some  $\omega$  already given. Verify that the following time-dependent vector

$$\begin{pmatrix} x(t) \\ y(t) \end{pmatrix} = \begin{pmatrix} \cos(\omega t) & -\sin(\omega t) \\ \sin(\omega t) & \cos(\omega t) \end{pmatrix} \begin{pmatrix} x_0 \\ y_0 \end{pmatrix}$$

does just this, by showing that  $x^(t)+y^2(t)=x_0^2+y_0^2=R^2. \label{eq:constraint}$ 

- h) Calculate  $U^{-1}(\omega t)$  and show that it is given by  $U(-\omega t)$  explain this result.
- i) Hence, show that

$$\begin{pmatrix} x_0 \\ y_0 \end{pmatrix} = \begin{pmatrix} \cos(\omega t) & \sin(\omega t) \\ -\sin(\omega t) & \cos(\omega t) \end{pmatrix} \begin{pmatrix} x(t) \\ y(t) \end{pmatrix}$$

j) Using your result for the prediction of the number of excess hares and lynxes from question Q1h of the Tuesday tutorial, use this equation to show that 15 years earlier the number of hares and lynxes was  $x_0=80$  and  $y_0=60$ .

Summary of different equivalent ways to describe circular motion with a constant angular velocity  $\omega$ : Initial condition specified by constant radius  $R^2=x_0^2+y_0^2$  and phase delay  $\phi(x_0,y_0)=-\tan^{-1}\left(y_0/x_0\right)$ 

Separate components	Complex separate components	Complex polar form
$x(t) = R\cos(\omega t - \phi)$	$z(t) = R(\cos(\omega t - \phi) + i\sin(\omega t - \phi))$	$z(t) = Re^{i(\omega t - \phi)}$
$y(t) = R\sin(\omega t - \phi)$		

Initial condition specified directly by  $x_0$ ,  $y_0$  ( $z_0 = x_0 + iy_0$ )

Complex separate componer	its Complex Polar	Matrix form		
$z(t) = (x_0 + iy_0)(\cos(\omega t) + i\sin(\omega t))$	$n(\omega t)) z(t) = z_0 e^{i\omega t}$	$\begin{pmatrix} x(t) \\ y(t) \end{pmatrix} = \begin{pmatrix} \cos(\omega t) \\ \sin(\omega t) \end{pmatrix}$	$-\sin(\omega t) \atop \cos(\omega t) \begin{pmatrix} x_0 \\ y_0 \end{pmatrix}$	