Linear algebra and matrix models

One of the major complications of biological systems is that they are structured - not all components which make up the system are the same, and they have different properties which affect how the system behaves. Thus populations are made up of individuals (or in a somewhat different view subpopulations which interact) and these individuals differ in a variety of characteristics which affect how the population changes. This is the basis for demography, in which the future behavior of the population depends upon the age structure. But there are many other types of structure in biological systems than age within a population.

Many systems can be thought of as having compartments or "black boxes" which interact and we may be interested more in the interactions between these boxes than in what happens within each box in detail. The compartments could correspond to various chemical constituents of a system (insulin/glucose), drug levels within different organs, different species in a chemostat, etc.

A basic mathematical method to analyze changes brought about by structure in a system is to use matrices. These are useful as well in hosts of other applications (particularly in multivariate analysis in statistics), but we are going to focus on basic ways they van be used to analyze populations. The idea of a matrix is simple: all it is an ordered array of numbers or variables, arranged into a rectangular form with a certain number of rows and columns. In computer science it is called an array. Examples:

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

is called a 2x2 matrix (2 rows and 2 columns) and

$$B = \begin{bmatrix} 4 & 4 \\ 3 & 0 \\ 5 & 8 \end{bmatrix}$$

$$C = \begin{bmatrix} 4 & -7 & 7 \\ 3 & 0 & -6 \end{bmatrix}$$

so B is 3x2 matrix and C is a 2x3 matrix - the classication is row# x column#. The matrix is made up of elements with the (i,j) element being the one in the ith row and jth column. So $B_{2,1} = 3$ and $C_{3,2} = -6$. The elements can be anything at all, they do not have to be numbers

$$D = \begin{bmatrix} x_n & x_{n+1} \\ y_n & y_{n+1} \end{bmatrix}$$

A vector is an matrix with either one row (called a row vector) or one column (called a column vector).

There are a variety of basic operations you an do with matrices, some of which occur in the same manner as standard algebra and others do not. Generally you have the additional complication that the sizes od the matrices must be appropriate. You can add or subtract two matrices which are of the same size (the number of rows in each matrix is the same as are the number of columns) by just adding or subtracting the equivalent elements

$$A + D = \begin{bmatrix} x_n + 2 & x_{n+1} + 4 \\ y_n + 3 & y_{n+1} \end{bmatrix}$$

Matrix multiplication and division are not at all the same as in standard algebra. These operations are set up in order to make linear algebra useful in the solution of systems of linear equations (one of the main applications). So the idea is to make sure that the system

$$a_1 x_1 + a_2 x_2 + a_3 x_3 = 0$$

$$b_1 x_1 + b_2 x_2 + b_3 x_3 = 0$$

$$c_1 x_1 + c_2 x_2 + c_3 x_3 = 0$$

is handled equivalently to the matrix equation

$$\begin{bmatrix} a_1 & a_2 & a_3 \\ b_1 & b_2 & b_3 \\ c_1 & c_2 & c_3 \end{bmatrix} \begin{bmatrix} x_1 \\ x_2 \\ x_3 \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix}$$

where you multiply the rows of the matrix respectively with the column of the vector to get the equivalent entries in the equations. When we multiply two matrixes, you do it by using the rows of the first matrix and the columns of the second, taking products element by element and adding them up. This means that the number of columns of the first matrix must match the number of rows of the second matrix - you can multiple an ixj matrix with a jxk matrix. This means that in general matrix multiplication is not commutative - $\mathbf{A}\,\mathbf{B} \neq \mathbf{B}\,\mathbf{A}$ except in very special cases.

The identity matrix is a square matrix (same number of rows as columns) with ones on the diagonal and zeros elsewhere - multiplying any square matrix by this gives the same matrix back - $\mathbf{A}\,\mathbf{I} = \mathbf{I}\,\mathbf{A} = \mathbf{A}$.

The inverse of a matrix $\mathbf{A}$ is a matrix $\mathbf{A}^{-1}$ such that when you multiply $\mathbf{A}\,\mathbf{A}^{-1} = \mathbf{I}$.

All the above is set up in order to easily use matrixes to solve linear systems of equations. Suppose you have $\mathbf{A}\,\mathbf{x} = \mathbf{b}$ where **x** is a column vector of unknowns and **b** is a column vector of constants, and **A** is a matrix of constants. Then the solution is $\mathbf{x} = \mathbf{A}^{-1}\,\mathbf{b}$. This means that if you can find the inverse of a matrix then all you need to do is to multiply that inverse times the right hand side in a system of equations to obtain the unknowns. This of course only works for LINEAR equations. Of course not all systems of linear equations have unique solutions which arises if the matrix of coefficients **A** does not have an inverse - in this case the matrix **A** is called singular and it arises if one row of the matrix is a linear combination of the other rows (can be writen as a sum of constants times rows). The determinant of a square matrix is a function of the matrix that assigns 0 to the matrix if it is singular and a non-zero number if it is non-singular. You can think of the determinant as measuring the area (or volume in more than 2 dimensions) that is bounded by the vectors that make up the rows of the matrix.

Eigenvalues and Eigenvectors

These apply to square matrices. Think of a matrix applied to a vector as a transformation that stretches and rotates the vector. For example

$$\mathbf{A}\,\mathbf{x} = \begin{bmatrix} 2 & 3 \\ 0 & -1 \end{bmatrix} \begin{bmatrix} x \\ y \end{bmatrix} = \begin{bmatrix} 2x + 3y \\ -y \end{bmatrix}$$

then the vector (1,0) here gets transformed to a vector (2, 0) and the vector (0,1) gets transformed to the vector (0,-1). So the effect of the transforamtion is to stretch out the x direction by a factor of two and to reverse the y direction with no stretching (rotate it 180 degrees). The eigenvalues are 2 and -1, correponding to this stretching and squeezing, and the eigenvectors associated with this are (1,0) and (0,1) which indicates the directions in which the stretching and rotation occurs.

In general for any matrix **A**, the eigenvalues λ are numbers such that

$$\mathbf{A}\,\mathbf{v} = \lambda\,\mathbf{v} \tag{1}$$

where **v** is the eigenvector associated with the eigenvalue. Think of the eigenvector as giving a direction such that if you were headed that way then the effect of the transformation is to keep you headed that way but just stretched or squeezed. In the context of population growth, this corresponds to a structure of the population which is not changing - sort of an equilibrium structure. So the population may be growing or declining, but the structure doesn't change. Eigenvalues are found by solving (1), typically by looking for values of λ such that the determinant of $\mathbf{A} - \lambda\,\mathbf{I}$ is zero. Eigenvectors are always known only up to a constant factor - they are directions not magnitudes.