Quantitative Understanding in Biology Module III: Linear Difference Equations Lecture III: A First Look at Eigenvectors

In our work on linear dynamic systems, we have shown that a general, two-variable linear system can be written in the form…

$$\begin{pmatrix} x_{n+1} \\ y_{n+1} \end{pmatrix} = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} \begin{pmatrix} x_n \\ y_n \end{pmatrix}$$

This system can be solved iteratively when the initial conditions x_0 and y_0 are specified. Such a system is fully described by six parameters: a_{11}, a_{12}, a_{21}, a_{22}, x_0, and y_0.

More generally, and more compactly, a linear system of arbitrary size can be written in vector and matrix notation as…

$$\boldsymbol{x}_{n+1} = \boldsymbol{M} \cdot \boldsymbol{x}_n \qquad \text{Initial Conditions: } \boldsymbol{x}_0$$

If this system has p state variables, then **M** is a p x p matrix, and **x** is a vector of length p. The system is defined by $p^2 + p = p\,(p + 1)$ parameters. For the 2 x 2 case, p = 2 and there are, of course, six parameters.

We have seen that the general solution to the two-variable system can be written as…

$$x_{n+1} = A_1\lambda_1^n + A_2\lambda_2^n$$
$$y_{n+1} = B_1\lambda_1^n + B_2\lambda_2^n$$

Like its difference equation counterpart, this system also has six parameters: A_1, A_2, B_1, B_2, λ_1, and λ_2. We've seen that the eigenvalues (λs) are completely specified by the matrix in the difference equation representation of the system.

We mentioned in passing that the As and Bs would be dependent on the initial conditions of the system; we'll be digging a bit deeper into these As and Bs now.

It is important to realize that there is no more information in the difference equation representation of a system and its corresponding solution in terms of As, Bs, and λs. Anything you might want to know about the system can be answered by either representation. The answers to some questions you might have (e.g., what is the long-term behavior of the system) might be more obvious when the system is written on one form or the other, but this is a matter of convenience of interpretation, not new information. The fact that both systems are fully defined by six parameters is an indication that there is no new information in the second representation.

Further reasoning along these lines tells us that the As and Bs in the above solution cannot be determined by the initial conditions alone. After all, the initial conditions represent two 'pieces' of information about the whole system, while the As and Bs together hold four 'pieces' of information. The extra two pieces of information needed to determine the As and Bs are, not surprisingly, found in the matrix **M** (there is no other place where this information could come from, after all).

From our two variable linear system you can show that the ratio A_1/B_1 is solely determined by the elements of **M**. We won't derive this conclusion here, but you can consult a text on linear algebra if you want a proof. Similarly, the ratio A_2/B_2 is also fixed solely by the matrix **M**. Those two ratios use up all of the information in **M**, and the rest of the system is defined by the initial conditions.

Now, if A_1/B_1 is fixed to a value determined by **M**, then the *direction* of the vector $\begin{pmatrix} A_1 \\ B_1 \end{pmatrix}$ is fixed. Here the term 'direction' doesn't include a sign, so (2, 2) is said to point in the same direction as (-2, -2). We'll call this vector $\mathbf{v}_1$, and since we really know about it is its direction, we'll (arbitrarily choose to write it such that its magnitude, or norm, is one. In other words, for our two variable system, the vector $\mathbf{v}_1$ really only has *one* 'piece' of information embedded in it, which is its direction.

If we apply analogous reasoning in defining $\mathbf{v}_2$ to embody information about the direction of the vector $\begin{pmatrix} A_2 \\ B_2 \end{pmatrix}$, then we can write the solution to our two variable linear system of difference equations as…

$$\begin{pmatrix} x_n \\ y_n \end{pmatrix} = k_1 \boldsymbol{v}_1 \lambda_1^n + k_2 \boldsymbol{v}_2 \lambda_2^n$$

The really profound point here is that both the **v**s and the λs are determined solely by the matrix **M**, while the k's embody information about the initial conditions. We say that each eigenvalue (λ_i) have a corresponding eigenvector ($\mathbf{v}_i$). These eigenpairs come only from the matrix defining the system, and not from the initial conditions.

This solution can be generalized beyond a two parameter system. It is written as…

$$\boldsymbol{x}_n = \sum k_i v_i \lambda_i^n = k_1 \boldsymbol{v}_1 \lambda_1^n + k_2 \boldsymbol{v}_2 \lambda_2^n + k_3 \boldsymbol{v}_3 \lambda_3^n + \cdots$$

Note that for a three parameter system, each eigenvector represents two 'pieces' of information. You can specify the direction of a vector is 3D space with only two numbers (e.g., latitude and longitude). So the three eigenvalues represent three 'pieces' of information and three eigenvectors represent six 'pieces' of information. These are solely determined by the nine values in the 3 x 3 matrix in the difference equation formulation. The three ks in the solution will be determined with the addition specification of the three initial conditions of the system.

Inspecting the solution above, you can see that the fact that the eigenvectors are determined solely by **M** has profound implications. Most importantly, the eigenvector corresponding to the dominant eigenvalue will give you the long term ratio of the state variables in the system. This long-term ratio is determined solely by the matrix, not the initial conditions. More generally, you can think of the

evolution or trajectory of a dynamical system as a linear combination of these characteristic vectors, where the weights vary over time with a growth or decay governed by their corresponding eigenvalues.

Some Worked Examples

Typically, eigenvalues and eigenvectors are computed numerically using a computer. This is essential for systems with large matrices. In MATLAB, these are computed together using commands as shown in the following example:

```
>> alpha = 0.07;
>> beta = 0.05;
>> gamma = 25;
>> M = [alpha * gamma, beta * (1 - alpha); gamma, 0]

M =

    1.7500    0.0465
   25.0000         0

>> [V,D] = eig(M)

V =

    0.0902   -0.0205
    0.9959    0.9998


D =

    2.2636         0
         0   -0.5136
```

Notice that two matrices, V and D, are defined at once when you use this syntax. The diagonal elements of the matrix D contain the eigenvalues, and each column of the matrix V is the corresponding eigenvector. In the example above, which revisits our plants and seeds model from the first lecture in this section, the dominant eigenvalue is 2.2636, and the corresponding eigenvector is $\begin{pmatrix}0.0902\\0.9959\end{pmatrix}$. We know from the eigenvalue that our model population of annual plants and seeds will grow in an unbounded fashion, and we now know by inspecting the eigenvector that, in the long term, the ratio of seeds to plants will be 11:1 (0.9959 / 0.0902 = 11.04).

Let's revisit our model of molecular evolution of nucleotide sequences. In the simplest model, where all possible mutations are equally likely, the eigenvalues and eigenvectors are computed as follows…


```
>> a = 0.01;
>> M = [ 1-3*a a a a; a 1-3*a a a; a a 1-3*a a; a a a 1-3*a]

M =

    0.9700    0.0100    0.0100    0.0100
    0.0100    0.9700    0.0100    0.0100
    0.0100    0.0100    0.9700    0.0100
    0.0100    0.0100    0.0100    0.9700

>> [V,D] = eig(M)

V =

    0.3770   -0.7570    0.1866    0.5000
   -0.8445   -0.0443    0.1866    0.5000
    0.3668    0.6286    0.4693    0.5000
    0.1007    0.1727   -0.8426    0.5000


D =

    0.9600         0         0         0
         0    0.9600         0         0
         0         0    0.9600         0
         0         0         0    1.0000
```

Here you can see that all of the values of the state variables (the probabilities) in the eigenvector corresponding to the dominant eigenvalue are equal. Note that when MATLAB computes eigenvectors, the norm is one, whereas for a Markov model we need to renormalize so that the sum is one…

```
>> V(:,4)/sum(V(:,4))

ans =

    0.2500
    0.2500
    0.2500
    0.2500
```

Exercise: Consider a model where a pair of forward and reverse mutation rates is not equal. Can you explain these results…


```
>> M = [ 1-4*a a a a; 2*a 1-3*a a a; a a 1-3*a a; a a a 1-3*a]

M =

    0.9600    0.0100    0.0100    0.0100
    0.0200    0.9700    0.0100    0.0100
    0.0100    0.0100    0.9700    0.0100
    0.0100    0.0100    0.0100    0.9700

>> sum(M)

ans =

     1     1     1     1

>> [V,D] = eig(M)

V =

   -0.3961   -0.7071    0.0000    0.0000
   -0.5941    0.7071    0.8165   -0.0020
   -0.4951    0.0000   -0.4082   -0.7061
   -0.4951    0.0000   -0.4082    0.7081


D =

    1.0000         0         0         0
         0    0.9500         0         0
         0         0    0.9600         0
         0         0         0    0.9600

>> V(:,1)/sum(V(:,1))

ans =

    0.2000
    0.3000
    0.2500
    0.2500
```

Let's revisit one more model we looked at briefly in the second lecture. We saw that a system with the matrix M = $\begin{bmatrix} 0.8 & -0.05 & -0.05 \\ 0.05 & 1 & 0 \\ 0 & 0.05 & 1 \end{bmatrix}$ exhibited a long-term decay with a periodic behavior. A 3D plot of the trajectory of the system (see notes from previous lecture) showed that after a short time, the system spiraled in a plane. You can understand this behavior a bit better when you look at the eigenvalues and eigenvectors.


```
>> M = [0.8 -0.05 -0.05; 0.05 1.0 0; 0 0.05 1.0]

M =

    0.8000   -0.0500   -0.0500
    0.0500    1.0000         0
         0    0.0500    1.0000

>> [V,D] = eig(M)

V =

   0.9650            -0.2114 - 0.0845i  -0.2114 + 0.0845i
  -0.2535            -0.0839 + 0.4362i  -0.0839 - 0.4362i
   0.0666             0.8665             0.8665


D =

   0.8097                  0                  0
        0             0.9952 + 0.0252i        0
        0                  0             0.9952 - 0.0252i
```

Note here that when eigenvalues are complex, the terms in the corresponding eigenvectors are also complex, and also come in complex-conjugate pairs. This occurs in such a way that the end result will always be real numbers. While an intuitive interpretation of complex eigenvectors may be illusive, you can see from the results above is that the norm of the real eigenvalue is much smaller than those of the complex eigenvalues. This tells us that after a short time, the first eigenvector will have little weight (because 0.8097^n will diminish more quickly than the others), and we'll be effectively left with a system described by the remaining two eigenpairs. Since a linear combination of any two vectors define a plane, we can deduce that this system will be confined to a plane after the first term dies away, and that we should see rotation in the plane because the remaining eigenpairs are complex.

One Last Note

For completeness, we need to note that there is a case we don't consider in this course. If you see two identical eigenvalues, the mathematics and general form of the solutions are different. We don't worry about this because, in many cases, the parameters in the matrix M are not known exactly, and to obtaining perfectly equal eigenvalues for a general matrix is very unlikely. However, in some cases nature arranges thing just so, and the structure of the matrix may dictate equal eigenvalues. If you run into such a case, you'll need to refer to a text to learn how to handle it.

