

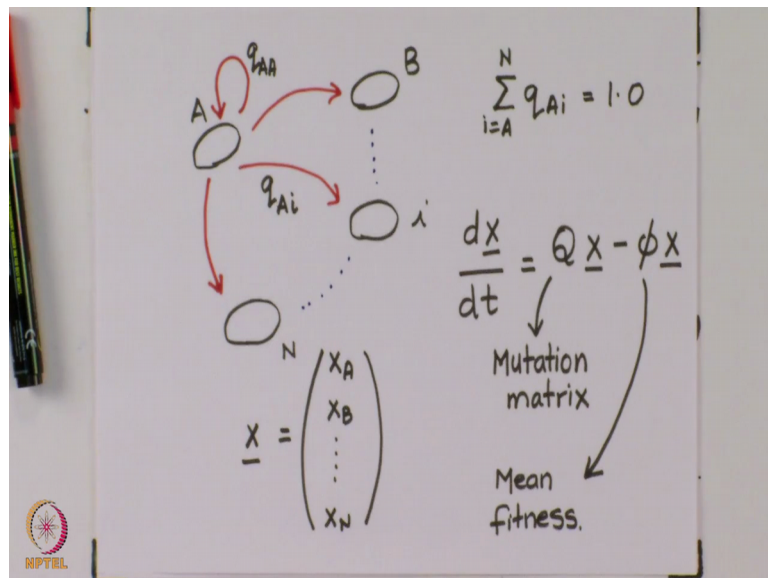
Introduction to Evolutionary Dynamics
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Lecture - 11
Modelling Mutations – 3

Hi and welcome to the next lecture of the course Evolutionary Dynamics, and we are going to continue our discussion from last time, we were discussing one particular aspect of any evolutionary process which is selection and the particular case we are dealing with is we have N distinct genotypes of a bacterial species coexisting in an environment where the total number of individuals in the environment has been constraint to K , no genotype has any advantage over the other they all have identical fitnesses which is another term be used for growth rates.

So, all N genotypes are going with the same growth rate and for the sake of simplicity, we will quieted that particular growth rate value to be equal to 1 and we saw that last time that this process can be represented graphically as shown in the picture here.

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So, what we have is this graph and each of the circle represents a particular genotypes. So, if you focus on particular genotype A when a bacterium of this particular genotype divides, it could either lead to a genotype which is identical to its own and which happens in the case when there are no mutations or if there is a mutation that happens, it

would lead us to one of the other $N - 1$ genotypes and the probability that when a divides and it gives me and the progeny also has genotype A is given by q_{AA} . The probability that when genotype A divides the progeny has a genotype i gives me is defined by the variable q_{Ai} a divides and the progeny is of genotype i. And now it is important to realize as we saw last time that $\sum_i q_{Ai}$; i varies from A to N equals 1.

Because if these represent probabilities then after any division event, the progeny has to belong to one of the N genotypes which are associated with the system here and hence the sum of those probability is associated with generation associated with the fact that the progeny belongs to genotype i when summed over all i this number has to be equal to 1 and we saw that this dynamical system can be represented as $\frac{dX}{dt} = qX - \phi X$ and X here is a vector quantity which is represented by $X_A X_B$ going all the way up to X_N q is what is called the mutation matrix. And I refer you to the last lecture for its definition and ϕ is the variable that we have been talking about. So, the course of this through the course of this video series ϕ is the mean fitness of the of the individuals in the bacteria and in our case because all in genotypes have the same identical fitness ϕ which represents the mean fitness associated with the culture at any given point remains constant with time that does not change that is because no matter what is the composition of the population at any given point in time.

Since all genotypes have the identical fitness the mean fitness of the culture also remains identical. So, ϕ represents that and then now we have this differential equation and now if you are interested in analyzing the steady state of this thing steady state.

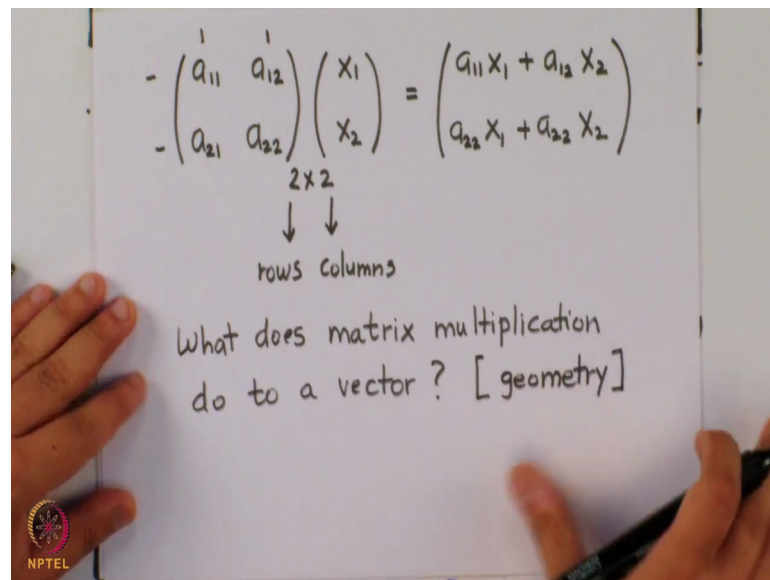
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$$\text{At steady state: } \frac{d\mathbf{X}}{dt} = 0$$
$$Q\mathbf{X} - \phi\mathbf{X} = 0$$
$$\phi = 1 \quad \rightarrow \quad Q\mathbf{X} = \mathbf{X}$$
$$Q\mathbf{X} - \mathbf{X} = 0$$

So, we have at steady state of the system the quantity $d\mathbf{X}$ upon $d\mathbf{t}$ is equal to 0 which gives me the equation that $q\mathbf{X}$ minus $\phi\mathbf{X}$ should be equal to 0 and since we had taken ϕ because we know all genotypes have identical fitness we take ϕ equal to 1 which is the mean fitness and that is given by the fact that all individual genotypes also have fitness equal to 1 our equation reduces to $q\mathbf{X}$ minus \mathbf{X} equals 0 where q is a matrix and \mathbf{X} is a vector. So, this is the equation that way that we are interested in solving which gives us which tells us that if we have n distinct genotypes which are equal in fitness, but are mutating among themselves what is the composition of the population at steady state because we have put $d\mathbf{X}$ by $d\mathbf{t}$ equal to 0 and I again emphasize that when we say $d\mathbf{X}$ by $d\mathbf{t}$ \mathbf{X} here is a vector which represents derivative of the composition of the population and it says it is comprised of n distinct derivatives.

So, now let us go back to this and see how do we solve this equation $q\mathbf{X}$ minus \mathbf{X} equal to 0 and to do that first we have to realize that this equation can be rewritten as $q\mathbf{X}$ equals \mathbf{X} where again \mathbf{X} is a vector and q is a matrix. So, given the mutational matrix q for any system with n distinct genotypes, I have to find an \mathbf{X} such that when that \mathbf{X} vector is multiplied by the mutation matrix, I get \mathbf{X} back that is essentially the problem that that we have to solve here and to be able to comment more on the solution of the system we have to take help from linear algebra and we will spend the next few minutes talking about some matrix multiplication matrix multiplications with vectors and their associate properties. So, when we do this.

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The image shows a whiteboard with handwritten mathematical notation. At the top, a 2x2 matrix is written as $\begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}$. Below the matrix, the text "2x2" is written, with two arrows pointing down to the words "rows" and "columns". To the right of the matrix is a column vector $\begin{pmatrix} x_1 \\ x_2 \end{pmatrix}$, followed by an equals sign and another column vector $\begin{pmatrix} a_{11}x_1 + a_{12}x_2 \\ a_{21}x_1 + a_{22}x_2 \end{pmatrix}$. Below the matrix and vector, the text "What does matrix multiplication do to a vector? [geometry]" is written. In the bottom left corner, there is a small circular logo with the text "NPTEL" below it.

Let us matrices come in different sizes are a to cross 2 matrix would look something like this say its elements are a 11, a 12, a 21, a 22 and this is represented as a 2 cross 2 matrix this to here represents the number of rows. So, there are 2 rows and this 2 represents the number of columns these are the 2 columns. So, this is a 2 cross 2 system.

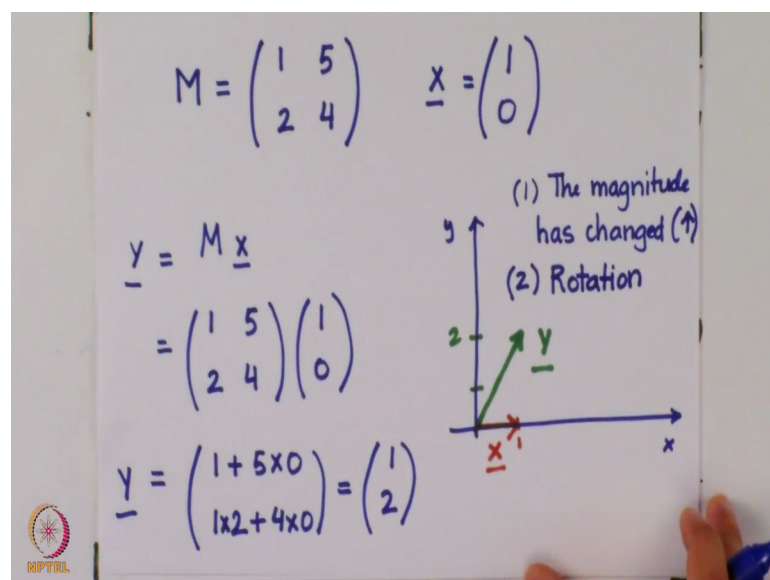
Now, when this matrix divides with a vector which is X 1, X 2, the rules of multiplication between a matrix and a vector are that this would give me a vector whose elements are the first element is given by the first row of the matrix times the column vector. So, this is a 11 times X 1 plus a 12 times X 21 and the second element is given by a 21 times X 1 plus a 22 times X 2 and this is my resultant vector i; which I get up on multiplication of a matrix and a vector and it is important to realize that this multiplication event is only permitted if the number of columns of the matrix is equal to the number of rows of the vector associated that you are trying to that you are trying to multiply. So, given this we want to understand that what happens when a vector multiplies with a matrix.

What does a matrix multiplication due to a vector and we are particularly interested in an analyzing the geometry associated with this process we see on our nodes here that a vector when multiplied by this matrix gives me another vector. So, we want to understand the relationship between these two vectors the one that multiplies with the matrix and the one that we get post multiplication. We want to understand what is the

relationship between these two vectors and we are interested in the studying that relationship because that is what is happening in my mutational event that we are trying to model a vector multiplied by a matrix gives me another vector and I want to study the relationship what between these two vectors in general.

So, let us do this with the help of an example we are interested in understanding what does matrix multiplication due to a vector and we are interested with the perspective with that we will take to analyze this is will look at the geometry associated with this process alright let us do this with the help of an example. So, we will pick a 2 cross 2 matrix and we will pick a vector associated vector multiply the two and see where that takes us.

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The image shows a handwritten derivation of the matrix multiplication $\underline{y} = M \underline{x}$ and a corresponding 2D coordinate system diagram.

Matrix and Vector Definition:

$$M = \begin{pmatrix} 1 & 5 \\ 2 & 4 \end{pmatrix} \quad \underline{x} = \begin{pmatrix} 1 \\ 0 \end{pmatrix}$$

Calculation:

$$\underline{y} = M \underline{x}$$

$$= \begin{pmatrix} 1 & 5 \\ 2 & 4 \end{pmatrix} \begin{pmatrix} 1 \\ 0 \end{pmatrix}$$

$$\underline{y} = \begin{pmatrix} 1 + 5 \times 0 \\ 1 \times 2 + 4 \times 0 \end{pmatrix} = \begin{pmatrix} 1 \\ 2 \end{pmatrix}$$

Diagram:

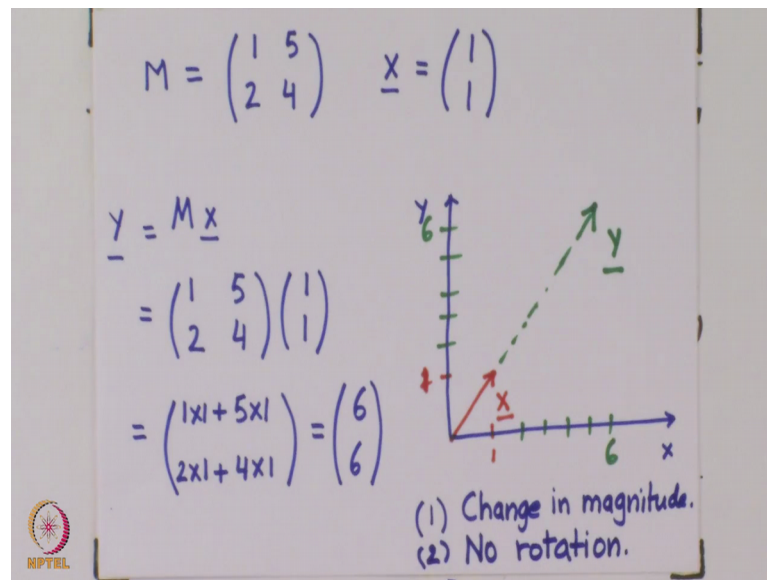
The diagram shows a 2D coordinate system with x and y axes. A red vector \underline{x} is drawn along the positive x-axis, starting from the origin and ending at the point (1, 0). A green vector \underline{y} is drawn from the origin to the point (1, 2). Annotations next to the diagram state: (1) The magnitude has changed (\uparrow) and (2) Rotation.

So, the matrix that we will take let us call that M and let us say the elements associated with that matrix are 1 5 2 and 4 and let us say that the vector X that we are talking about is simply 1 0. So, the first thing that we want to note is that where does this vector lie on the 2 dimensional plane if this is X if this is Y where does 1 0 vector lie and that is easy to analyze the first component is 1. So, this is 1, the second component is 0. So, 1 0 is just this vector. So, this is the vector X that I am talking about whose first component is one second component is 0 these X and Y are just dummy variables you can choose them to be anything. So, that is where my vector lies in this 2 dimensional space this is 2 dimensional space, because the dimensions of my vector are equal to 2 the number of elements associated with the vector are equal to 2.

Now, what happens when I multiply this with my matrix what let us say that I call Y equals M times X and I get this to be equal to $\begin{bmatrix} 1 & 5 \\ 2 & 4 \end{bmatrix}$ times $\begin{bmatrix} 1 \\ 0 \end{bmatrix}$ and as we had done in our last slide this is 1 times 1 plus 5 times 0 and the second element is 2 times 1 which is 2 times 1 plus 2 times 0 plus 4 times 0 and that gives me $\begin{bmatrix} 1 \\ 2 \end{bmatrix}$. So, my Y vector is equal to $\begin{bmatrix} 1 \\ 2 \end{bmatrix}$. Let us try and plot this on the same graph and see what has happened to my vector X when multiplied with this matrix M and what has happened you will realize is that the first element remains unchanged that still equal to 1, but the second element which was one which was 0 here has become 2. So, the second element is one 2 and my resultant vector is this; this is the vector Y that have if you are asked to comment on this that what is happened to vector X upon multiplication with the matrix M we can see from our example that we have taken here that 2 events have happened one is my vector X has gotten enlarged its now much bigger in an absolute sense the magnitude of the vector has increased and the second thing that is happened is the vector has gotten rotated its initially it was a lied along the X axis, but now the vector is in the X Y plane with both the X component and the Y component equal to non 0.

So, 2 things that have happened here is that first the magnitude has changed in our case it has increased, but in general the magnitude could decreases well and second thing that has happened is that there has been a rotation of the vector in the X Y plane the initial vector was pointing along the X axis, but now we have a vector which lies in the X Y plane where none of the 2 components is A 0. So, these are the 2 things that a matrix has done 2 vector X, but surprisingly if we do this example again.

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Let us take the same matrix again M which is equal to 1 2 5 4 and choose our X differently this time and choose X to be 1 1, right. So, remember in the example that we just did, my X vector was 1 0 and what I got after the multiplication with the matrix M was 1 2.

Now, what I am doing is I am redoing the whole exercise, but having choosing X as 1 1. So, again before we multiply we want to see where does X lie this is element 1 X this is Y and 1 1 will lie one unit along the first dimension second unit along the one along the second dimension and this is 1 1. So, this is my vector X , now what happens when we multiply this lets again say that Y equals M times X and that gives me 1 5 2 4 times 1 1 which is just equal to 1 times 1 plus 5 times 1 1 times 1 plus 5 times 1 in the second element is 2 times 1 plus 4 times 1 which is equal to 6 6, let us try and plot our just obtained vector Y and see what has happened to it when the vector X was multiplied Y matrix M and how has Y change in relation to the original vector X that we started with remember in our last example 2 events had happened upon multiplication of vector X with matrix Y 1 was that are resultant vector Y had become enlarge its magnitude had increased in the second thing that had happened was that there was a rotation in the X Y plane of vector X giving us the resultant vector Y .

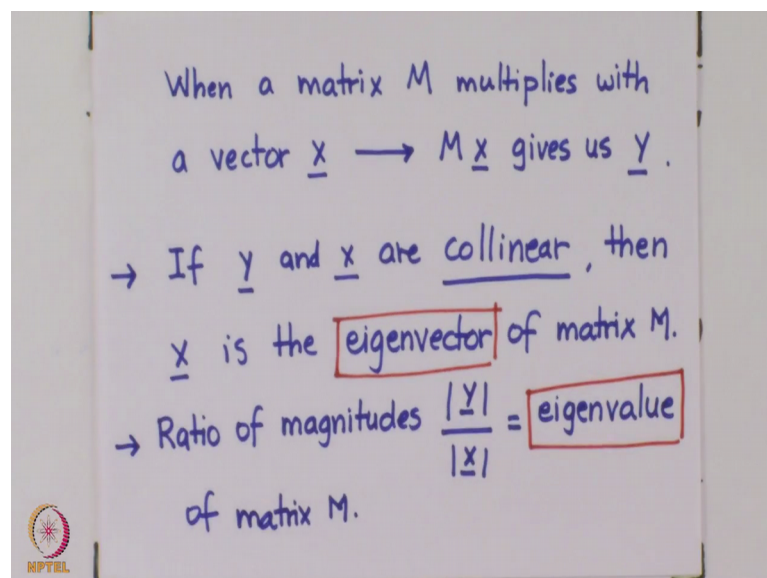
Now, let us plot other vector Y that we have just obtained and see what has happened in relation what is happened to this Y in relation to the X that which was started with. So,

now, if we look at this again \underline{Y} is 6 6. So, it is six dimensions here; 6 units 1 2 3 4 5 6; 6 units in the first dimension and similarly 6 units in the second dimension and if you plot these the resultant vector that we get is 6 6, this is my vector \underline{Y} and now a curious thing has happened that the same matrix when multiplied with another vector \underline{X} , there seems to have been no rotation this time and then the only effect that has that can be seen here is just the change in magnitude and in this case there is no rotation event that has happened, right.

So, the two examples that we have done today shows 2 different things the first one showed that there was a change in magnitude and rotation and the second one there was no rotation, but only change in magnitude. So, matrix does different operations to different initial vectors that are being multiplied to it depending on the initial vector \underline{X} that is multiplying with a vector you may have different things happened to that vector when multiplied by the matrix M that we are interested in and keep at the back of the you are mind that this whole analysis is being done we are doing this exercise to understand what does a mutational matrix q that we have due to a vector \underline{X} .

Because we want to understand the relationships q times \underline{X} equal to \underline{X} . So, now, that we know this we want to I want to talk about a couple of definitions.

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So, and when so the definitions go as follows that when a matrix M multiplies with a vector \underline{X} and the resultant of this multiplication M times \underline{X} such that M times \underline{X} gives us

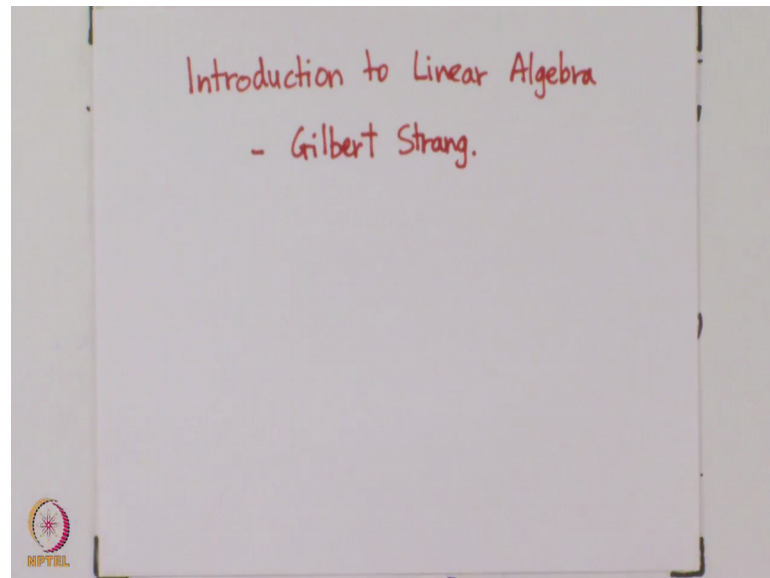
vector Y if Y and X are collinear then X is the eigenvector of matrix M and the second thing that we want to say here is that the ratio of magnitudes magnitude of vector Y divided by magnitude of vector X is equal to is refer to as the eigenvalue of matrix M .

So, we were introduced 2 concepts here one is called eigenvector and the second one is called eigenvalue, what are these? So, again let us go through this definition again when a matrix multiplies with a vector X $M X$ gives us Y . So, Y is equal to $M X$ and now if Y and X are collinear by collinear you mean what you want to say is that Y and X between Y and X there has been no rotation event happened if there was no there has no rotation between Y and X then X is said to be the eigenvector of matrix M eigenvector represents a direction in which when any vector in that particular direction is multiplied with the matrix M there is no rotation happened and the resultant vector is collinear with the direction that you had started with.

So, eigenvectors are important in that context that they do know i any vector in the direction of the eigenvector does not get rotated, but we get the same direction back, but remember even though X and Y are pointing in the same direction here their magnitude change and by the factor by which the magnitude changes. So, this was $1 \ 1$ which became $6 \ 6$. So, the vector has gotten enlarged by a factor of six this factor by which the resultant vector Y has either i become enlarged or gotten shrunk is called the eigenvalue associated with that eigenvector.

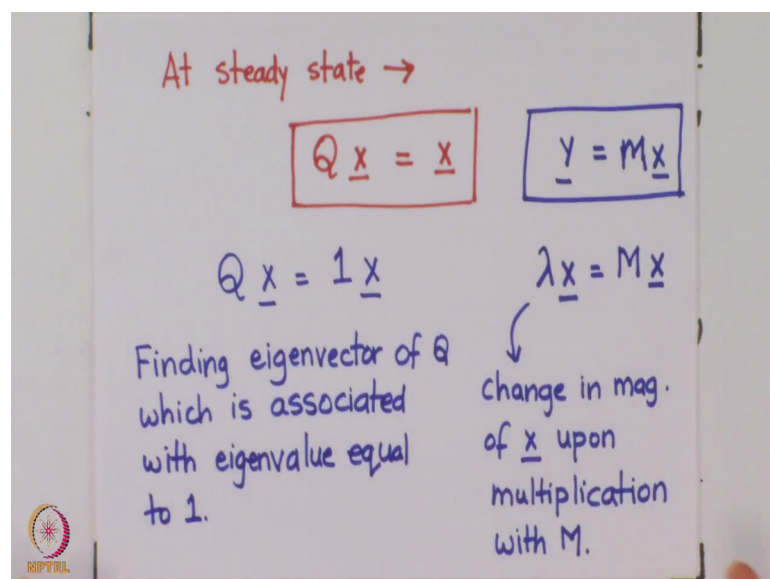
So, eigenvector and eigenvalues are important in that context. So, now, we have an eigenvalue and eigenvector and an idea of eigenvector and eigenvalue associated with matrices what we want to do now is use this information in the context that we were talking about for all of you who are interested in exploring linear algebra associated with geometry.

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There is an excellent book which is called introduction to linear algebra by Gilbert Strang, it is a very easy read and it is very very clear and it makes you visualize linear algebra in geometry and make things very very easy to understand. So, now, we want to understand what we have just talked about in the context of the biological example that we being talking about we understand eigenvalues we understand eigenvectors we understand matrix multiplication with a vector.

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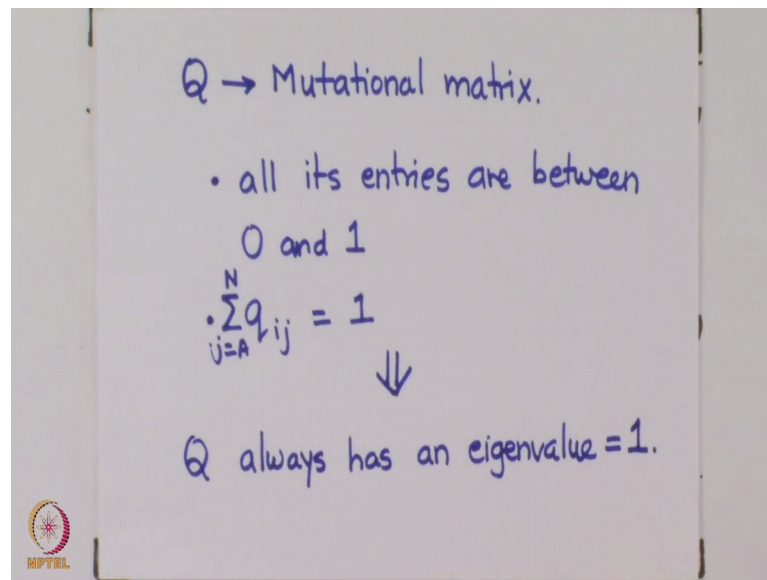


Now, let us see what does all of this mean in the context of the biological example of mutations happening that we been talking about remember at steady state what I am interested in solving in my $n \times n$ genotype model at steady state I know that q times X is equal to X that is what I am interested in solving and what we have solved just now is that Y is equal to M times X what we are.

So, what we have just seen in linear algebra is that Y equals $M X$ and that when Y and X are collinear. That means, there is no rotation event that has happened this can be written as λ times X equals $M X$ where λ is the change in magnitude of X upon multiplication with M this is not true in general this is only true for a very specific class of vectors which are called eigenvector because when you multiply a direction which is pointing in the direction of the eigenvector you get back the same direction and the only difference is that the original vector is either shrunk or enlarge by a factor λ which is called the eigenvalue if λ is bigger than one. That means, the resultant vector has become enlarged if λ is less than one; that means, a result 2 vector has become short.

So, what does this mean what this means for $q X$ equals X is the following that we are interested in solving $q X$ equals one times X which means because we want this matrix multiplication to give the same vector back no change in magnitude hence λ will be equal to 1 here; that means, I am interested in finding eigenvector of q which is associated with eigenvalue equal to 1 that is what I am interested in. I am interested in that eigenvector of matrix q which is associated with eigenvalue equal to 1 which gives the same vector, but which gives the same direction back and also that back direction should not be enlarged or should not be shrunk and what comes in handy here is the following result that q is not just any matrix.

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But it is actually a very special type of a matrix q satisfies the following properties q which is the mutational matrix satisfies the following properties that A all its entries are between 0 and 1 which is true because all entries of q any entry q_{ij} represents probabilities and probabilities have to be between 0 and 1. So, all entries of q r between 0 and one and. Secondly, $\sum q_{ij}$ summation over j is equal to 1 which means in this case that when a genotype i is dividing it could resultant any one of the N genotypes and the summation of probabilities of this transition equal to 1 which when both these properties are satisfied what linear algebra tells us is that q always has an eigenvalue equal to 1.

Because these 2 properties are satisfied we are guaranteed that this matrix q mutational matrix always has an eigenvalue one which is great because one is the eigenvalue for which we want to find the corresponding eigenvector which gives me the solution to the mutational problem that I started with. So, given the structure of matrix q if I know how the transitions between the different genotypes are taking place I can easily now go ahead and find the eigenvector corresponding with the eigenvalue equal to 1 for that matrix Q and that gives me the steady state makeup of the population among these n genotypes.

So that is that, and that concludes our discussion on the three tenets of the three evolutionary processes reproduction mutation and selection we close this introductory

description of these 3 processes now. And next lecture onwards we will start with something different which are consequence basis and fitness landscapes.

Thank you.