

Introduction to Evolutionary Dynamics
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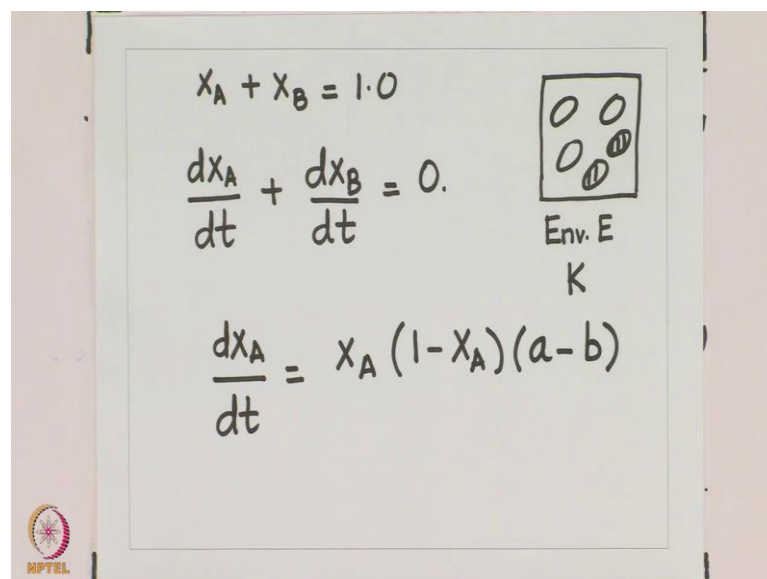
Lecture - 08
Modelling Selection - 3: Two and more species

Hi and welcome to the next lecture of the course; evolutionary dynamics. And so far we have been spending time on capturing the 3 tenets of any evolutionary processes, which is reproduction selection and mutation. We have already completed our discussion on reproduction, and today we will continue our discussion from where we had left of last time talking about selection. So, let us pick up our discussion from where he had left of last time, what we have a 2 bacterial species 2 distinct genotypes A and B, which are constraint in an environment such that their total numbers are said to be equal to a specified number k which is the carrying capacity of the environment.

And now these 2 distinct genotypes are growing at different rates A and B . In our last lecture we had derived the dynamical equation which represents the change in frequencies or the fraction of the total population that belongs to genotype A and genotype b . And where he had left of was trying to comment on the stability of the 2 steady states associated with the dynamics of the system.

So, we will pick our discussion of today from where we had exactly left of last time.

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The image shows a whiteboard with handwritten mathematical equations and a diagram. The equations are:

$$x_A + x_B = 1.0$$
$$\frac{dx_A}{dt} + \frac{dx_B}{dt} = 0.$$
$$\frac{dx_A}{dt} = x_A (1 - x_A)(a - b)$$

To the right of the equations is a diagram consisting of a square box containing five circles. Two circles are shaded with diagonal lines, and three are white. Below the box, the text "Env. E" and "K" are written.

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So, let us just start by recapturing A our scenario that we have an environment E. This environment has a carrying capacity equal to K. And we have 2 distinct genotypes of bacteria in this environment genotype A and genotype b. And the constraints that we are working in are $X_A + X_B = 1$ where X_A and X_B has we have been defined in the last lecture represent the fraction of the population that belongs to genotype A and B. Respectively and then we differentiated this equation to get the result $\frac{dx_A}{dt} + \frac{dx_B}{dt} = 0$ the right hand being a constant. It is derivative gives us a 0 and which gave us this result that the rate of change of the fraction of individuals which belong to genotype A is exactly equal to and opposite in sign to the rate of change of individuals which belong to genotype B and hence this result.

And when we use these 2 results to derive the dynamical equation associated with the system we ended up with the equation $\frac{dx_A}{dt} = X_A (1 - X_A)(a - b)$ where A and B. Are the growth rates associated with the 2 genotypes capital A and capital B? And this is the equation for which we want to comment on the stability of the 2 steady states associated with it.

So, let us take our discussion forward, and if you look at the equation the first thing that we had discussed last time when it comes to analyzing stability of steady states is putting the derivative term equal to 0. And that gives us the points the values associated with X_A where the rate of change of X_A with time is equal to 0.

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$$\frac{dx_A}{dt} = 0 = X_A (1 - X_A)(a - b)$$

$$a > 0 \quad [a \neq b]$$

$$b > 0$$

$$X_A = 0$$

OR

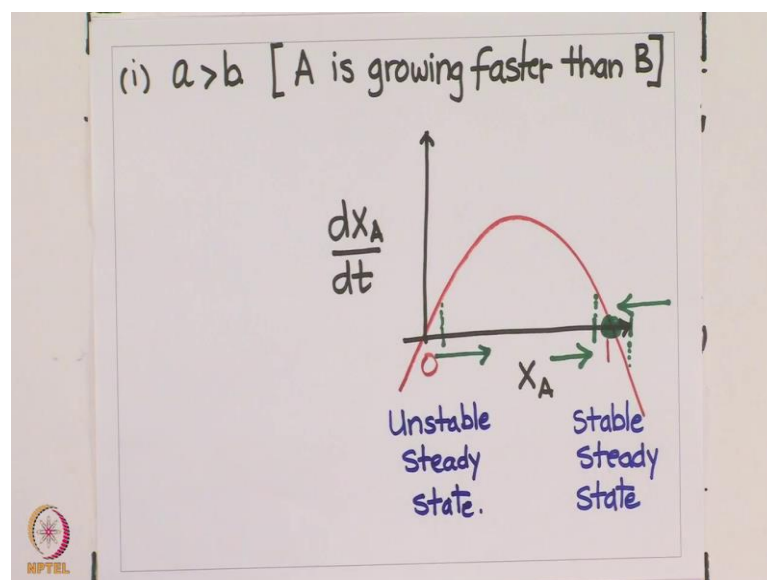
$$1 - X_A = 0 \Rightarrow X_A = 1$$

} Two Steady States

So, when we plug $\frac{dx_A}{dt}$ equal to 0, but we know $\frac{dx_A}{dt}$ is equal to X_A times 1 minus X_A times a minus b . We are working under the consumption that a is greater than 0 this is the growth rate of g of the bacteria with genotype capital A . B it is the growth rate of the bacteria with genotype capital B are both growth rates. So, these are non 0 positive quantities and also that there is a distinct difference in the speed at which these 2 species grow these 2 genotypes grow. So, a is not equal to b . Hence a minus b is either greater than 0 or less than 0 . So, this is a non 0 quantity. So, $\frac{dx_A}{dt}$ is only equal to 0 when either X_A is equal to 0 or $1 - X_A$ is equal to 0 which implies X_A is equal to 1 . And these 2 quantities X_A equal to 0 and X_A equal to 1 are my 2 steady states associated with the system.

After having determine the steady states associated the dynamical process the next step when it comes to commenting on the stability of these steady states is plotting the $\frac{dx_A}{dt}$ against the variable X_A . And first identifying where are the steady state points on this on this curve, and then disturbing the system and checking which way does it move when we disturb it from a steady state in one direction or the other. So, let us just do it, but as we had identified there are 2 distinct cases for doing that in the case that we are dealing with.

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So, case one is when a is greater than b . This represents the case where genotype A is growing faster than B . And when we think about the biology of this problem if you have

2 bacterial genotypes A and B. And A is growing faster than B you would imagine biologically if you were to imagine this process in our head you would imagine that eventually all of A should take over and the genotype capital B should get eliminated. That is what biology microbiology associated with bacterial growth tell us and really the math that we are deriving only make sense if that also leads us to the same answer which we know to be true physiological.

So, we want to plot X_A versus dx_A/dt . And this curve we had discussed last time for $a > b$ looks something like this. This is $X_A = 0$ this is equal to 1. And there are 2 steady states $X_A = 0$ and $X_A = 1$ and we want to comment on their stability. So, again just as we had done last time let us look at $X_A = 1$. Now if I disturb the system to the left I bring it slightly here, what I want to check is what is the sign of dx_A/dt when X_A is at not at steady state value, but slightly to the left of steady state. And I note that slightly to the left of steady state the sign associated with dx_A/dt is positive. Which means X_A increases as time increases and hence the system wants to move towards increasing values of X as we move forward in time.

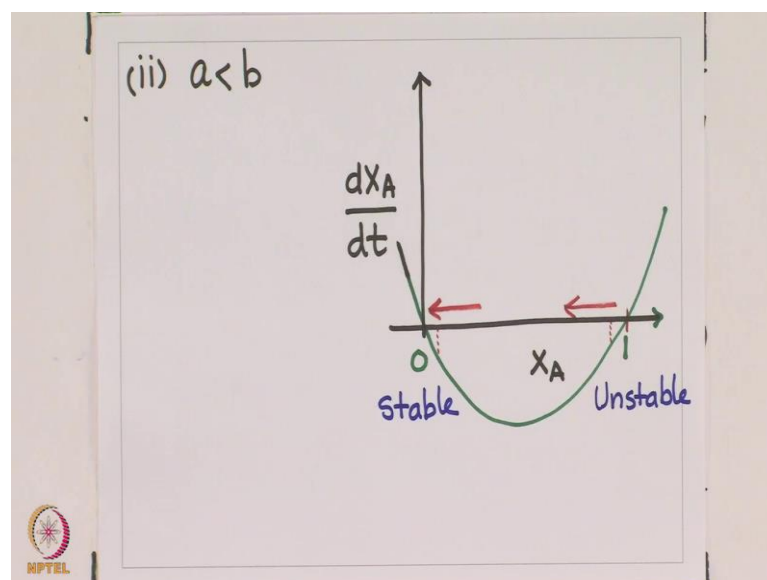
So, approaching from the left hand side if we were to introduce a disturbance to the left of X_A the system wants to move back towards a steady state from which it was disturbed and what happens on the other side if you introduce the disturbance which is to the right of steady state value one at this point the sign associated with dx_A/dt is negative which means as t increases X_A decreases and hence upon introduction of a disturbance which moves a system to the right the system wants to move to the left. So, we see that on introduction of a disturbance on either side the system wants to move back towards the steady state that we disturb it from and hence $X_A = 1$ is a state is a stable steady state.

So, this is a stable steady state and to comment on the stability associated with the second steady state we are only going to disturb it towards positive values because X_A the variable that we are dealing with is fraction of the population belonging to a certain genotype and negative fractions does not have any physical connotation in the system that we are talking about. So, we are only going to disturb it towards the right hand side and see where the system takes us once the disturbance is introduced.

So, when we introduce this disturbance to the right we note that $\frac{dx_A}{dt}$ is positive on the right hand side and hence if the system is at this state as t increases x_A increases and system moves towards the left which means away from the away from the steady state that we had disturbed the system from and hence this is an unstable steady state. So, that completes the mathematical analysis for the case one, but now let us try and take a look at the system and see if this makes any biological sense or not. We knew from biology of the problem that we are dealing with that when a is bigger than b then the a genotypes should take over the B genotype and hence the fraction of the individuals that belong to genotype A should go towards one and we should get eliminated and hence fraction of the population which belongs to genotype B should go towards 0 and that is exactly what this graph is telling us.

It tells us that as we go forward in time if we have any x_A , the system moves towards the right and it approaches x_A value of one which is the entire population belongs to genotype A and x_B which is just equal to $1 - x_A$ gets eliminated and approaches 0. So, this does make a lot of biological sense. Now let us take a look at the second case which is where capital where small a is less than small b where genotype A is going slowly as compared to the genotype B . So, again we do it the exact same way.

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We have small a less than small b . And we are going to plot the same graph, but now I leave it to you to convince yourself that whenever small a is less than small b the shape of the curve is just going to get inverted from what we saw last time.

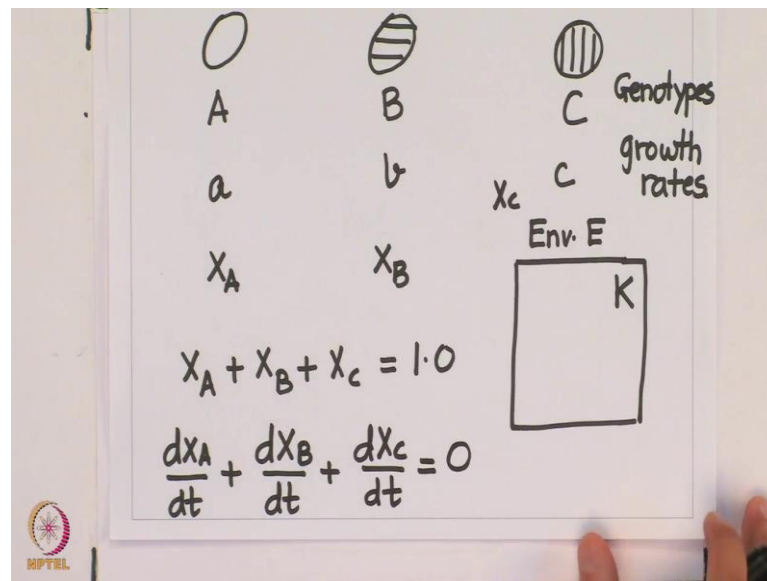
So, in the previous case when small a is bigger than b we have an inverted parabola. And I leave it to you to convince yourself that when small b is less than small a the parabola inverts itself. So, the shape of the curve at this point is going to look you say color. The shape of the curve is going to look something like this. This is the value X_A equal to 0. This is a value X_A equal to 1. And now when we analyze the stability associated with these 2 points, let us look at X_A equal to 1. When we introduce a deviation to the left dx_A by dt is negative hence X_A decreases as we move forward in time the system moves in this direction. At X equal to 0 if we introduce a deviation to the right dx_A by dt is still negative which means X_A decreases with time as we move decreases as we move forward in time.

So, any disturbance in this direction moves the system away from the steady state. And any disturbance in this direction brings the system back towards a steady state that we are started with and help this this steady state. Now becomes unstable whereas X_A becomes stable. So, as compared to the last result that we had where X_A was stable now X_A becomes unstable and in the previous case where X is equal to 0 was unstable X_A equal to 0 become stable. So, all that has happened on switching the signs of A and B . Is that the 2 points have switched their stabilities. And let us also now look at the biology associated with this when small b is bigger than small a ; that means, genotype B is growing faster than genotype A .

Then we imagine the biology to dictate that all of b cell types should take over the population and cell types belonging to genotype A should get eliminated. And that is exactly what we see in in our results where as we have the system any space in the system X_A always move towards the value 0, which means the fraction of individuals belonging to genotype A moves towards 0 and X_B consequently which is just 1 minus X_A always moves towards 1. So, this makes a lot of sense as for as the biology is concerned and that is that is what we want to discuss when it comes to selection between 2 distinct genotypes.

But the problem is that the genotypes multiple types are going to coexist very often and moving more than 2 genotypes is not trivial and then the math becomes difficult and simple analysis such as there is no longer possible when we have more than 2 genotypes associated. So, I will discuss one more distinct one more simple technique to analyze the system when we have 3 genotypes now first I will just quickly write the equations associated with these 3.

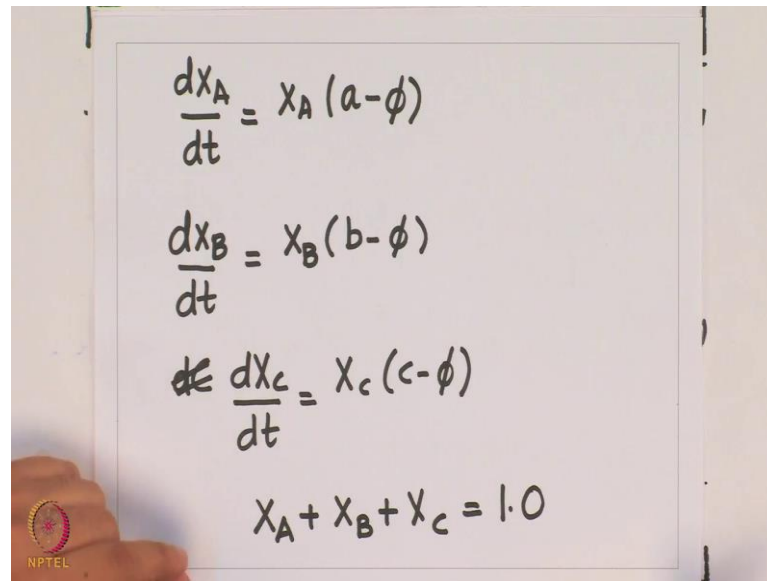
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So, now let us imagine our genotypes are A B and C. Their growth rates are a b c. So, these are genotypes, these are growth rates. And we have the same constraint that this growth is taking place in an environment e with the carrying capacity equal to K.

So, the individuals belonging to each of these 3 species 3 genotypes were added up give me a value equal to k. And again just as just as we had done last time we are not going to be dealing with distinct numbers, but we will be dealing with fraction of the population that belongs to genotype A, and we will call that quantity X A. The fraction of the individuals that belong to genotype B will be fraction X B. And similarly fraction of individuals that belong to genotypes C will be X C and X A plus X B plus X C will always be have to be equal to 1. And when we differentiate with respect to time we get d X A by dt plus dx B by dt plus d X C by dt equal to 0.

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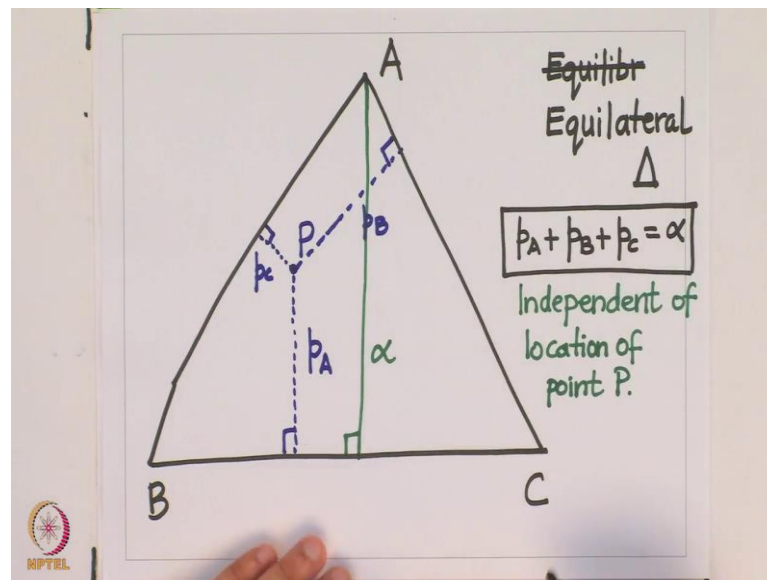
The image shows a whiteboard with handwritten mathematical equations. At the top, the equation is $\frac{dx_A}{dt} = x_A(a - \phi)$. Below it is $\frac{dx_B}{dt} = x_B(b - \phi)$. The third equation is $\frac{dx_C}{dt} = x_C(c - \phi)$, with a small 'd' crossed out before the fraction. At the bottom, the constraint equation is $x_A + x_B + x_C = 1.0$. An NPTEL logo is visible in the bottom left corner of the whiteboard.

And the consequent differential equations that dictate the dynamics of this process can be written as $\frac{dx_A}{dt}$ equals x_A into a minus ϕ where ϕ is an unknown just as we had done last time, $\frac{dx_B}{dt}$ is equal to x_B into b minus ϕ . And $\frac{dx_C}{dt}$ is equal to x_C into c minus ϕ . What had helped me last time when I was only dealing with 2 distinct genotypes is that when we derive the differential equations they were 2 differential equations. And I also had algebraic relationship between those 2 variables such that x_A plus x_B is equal to 1.

Now the problem that I have run into is that I have 3 distinct genotypes hence I have 3 variables x_A , x_B , x_C . And the algebraic equation between these 3 variables is x_A plus x_B plus x_C equals 1. And I can no longer substitute one in the form of another and reduce my system to one differential equation in one variable only which is something I was able to do when I was dealing with 2 species. That is the problem that I have and hence to be able to solve this equation these 3 equations have to be simultaneously solved and ensure that the constraint x_A plus x_B plus x_C is always equal to 1. So, these system of equations have to be solved either via a solver or if these are linear in nature can be solved analytically and the solution arrived at. So, this is analyzing 3 species is not as trivial as how we had analyzed 2 species.

But there is a useful way to represent dynamics of 3 species graphically and that is what I want to talk about next. So, 3 species we have 3 variables x_A , x_B and x_C .

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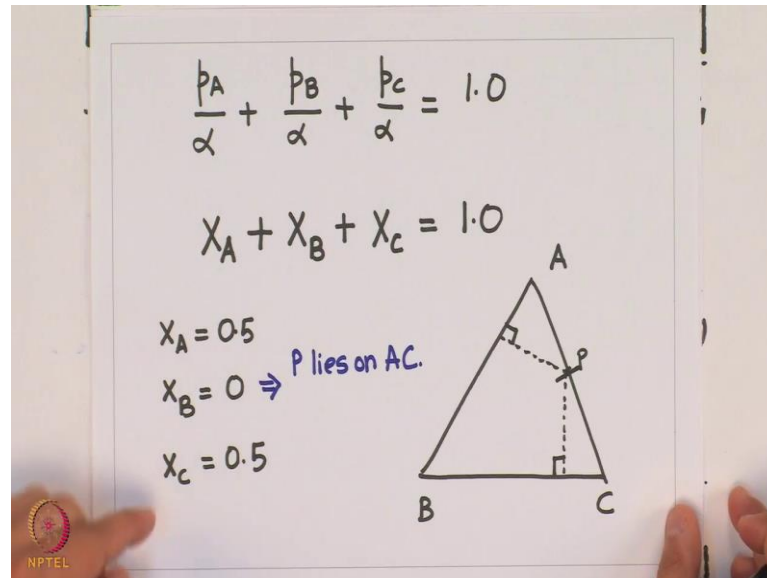


And the composition of this environment can be represented using an equilateral triangle. Let me call this A, B and C, I will explain in just second why this has to be an equilateral triangle for this representation. Now if the composition is at for any point P inside this triangle inside or even on this triangle, what we want to do is we want to drop perpendiculars to the 3 sides. So, perpendicular to the side AB looks like this. Perpendicular to the side BC looks like this and perpendicular to the side AC would look something like this.

Let's call the length associated with these 3 perpendiculars as the one opposite vertex A let us call that PA the perpendicular opposite vertex B let us call that PB and the one opposite vertex C that is call that PC. Let us also define a quantity in this equilateral triangle which is the length of the perpendicular drawn from one vertex to the other side and let us call that alpha. The length of this perpendicular is alpha. An equilateral triangles have this property such that if P is any point on the interior or on the edges of this equilateral triangle PA plus PB plus PC is equal to alpha. This result holds independent of location of point P. This result holds independent of location of point P. The only constraint mean that point P has to be inside or on the edges of the triangle it cannot be outside the tracker.

Once we have this how does this help us this result is a is very useful because it directly related with what we have been talking about. So, far because. So, what I am going to do is being alpha over to the other side.

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And write this as p_A by α p_B by α plus p_C by α equals 1. Now you should begin to see some similarities between the result that we have here for our equilateral triangle and the result we have for our 3 species system X_A plus X_B plus X_C equals 1. So, I am going to write this in this graphical representation of species P a by α for any point P will represent X_A p_B by α for any point P will represent X_B and p_C by α for any point P inside this triangle is going to represent X_C which is equal to 1 and hence I am going to use this equilateral triangle as a as a representation of where is my species located at any particular time.

So, if P is an internal point then this is how you just draw the perpendicular and that will give us the consequent fractions of each type of genotypes which are present in the environment at that particular time. Suppose I want to represent in this triangle suppose I want to represent a composition of an environment such that X_A is equal to 0.5 X_B is equal to 0 X_C is equal to 0.5. So, you should check that X_A plus X_B plus X_C is equal to 1. And how do we represent this point. The way to do that is we know that X_B is equal to 0; that means, I want to locate a point P such that perpendicular to the side which is opposite to vertex B , its length is equal to 0. Because remember the function of

b individuals is given by the length PB divided by capital alpha. And if X_B is equal to 0 which means PB has to be equal to 0. So, PB has to be equal to 0 means that point P lies on line a c right. So, so this this implies that P lies on AC.

Again what I am trying to do here is locate P on this equilateral triangle which represents the 3 species present in the fractions that we have talked about here. And now what we want next is locate a point P on this segment ac such that from that point P the perpendicular drawn opposite the vertex a. So, this perpendicular should be equal in length to the perpendicular drawn to the side which is opposite vertex c which this perpendicular. And that from intuition it should tell you that has to be the midpoint associated with the segment ac because this is an equilateral triangle.

So, given any composition what we can do is we can find a point P which represents the composition associated with the distribution of the genotypes at that particular composition that we have specified. So, equilateral triangle is a useful way to represent when we have 3 or less than 3 distinct genotypes present in an environment. Unfortunately scaling it up to higher number of genotypes becomes difficult because we are constrained by the number of dimensions that we can draw on a planar surface and hence it is not possible. So, that concludes our discussion on selection in a bacterial population.

In the next lecture onwards, we will start with the third tenet of a evolutionary process which is mutations.

Thank you.