Introduction to Evolutionary Dynamics

Prof. Supreet Saini
Department of Chemical Engineering
Indian Institute of Technology, Bombay

Lecture - 34
Evolutionary game theory - 1

Hi everyone. We will change glares in the course and last few lectures we have devoted to deriving an expression for speed of evolution in an analytical form. And making some assumptions we were able to come up with an order of; we were able to come up with expressions that would give us order of magnitude estimates for speed of evolution and simple micro (Refer Time: 00:37) experiment that we might be doing.

We will talk about a different aspect associated with evolutionary analysis and this is called evolutionary game theory, and the simplest way to understand this is that so far we have been talking about fitness of a particular genotype. In a sense that the fitness of a genotype is independent of what are the biological entities that are surrounding it.

But very often what happens is that one particular genotype is interacting with another genotype present in the environment. And hence the fitness associated with this particular genotype is closely linked to what all other genotypes are present in the environment in that sense fitness of genotype a is not just dependent on a itself or is not just a constant associated as completely opposite to this fitness of genotype a is actually dependent on the frequencies of genotypes a b c an however, many genotypes that are present in the environment and also what are the relative frequencies associated with this genotypes in the environment.

So, fitness becomes a complex thing to analyze in a setting like this and that is what we will spend the next few lectures in this course on, and trying to come up with systems as to try to come up with an analysis and understand how do we look at the systems and understand them.

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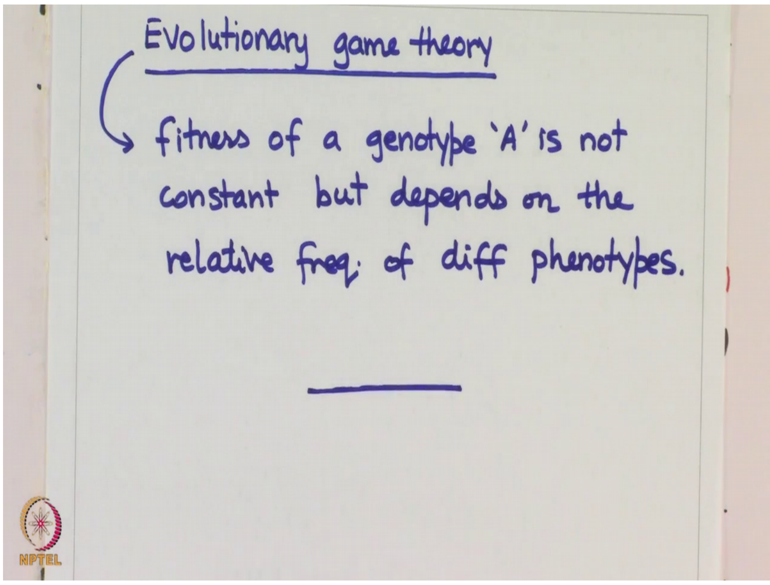

So, let us start this thing and this particular section is going to be called evolutionary game theory and the premise behind this is that the fitness of a genotype, let us say A is not constant, but depends on the relative frequencies of the different phenotypes that are present in the environment. So, that is evolutionary game theory and now we are going to have these genotypes which are going to be constantly interacting with each other, and their fitness will be dependent on the sum total of what is the current composition of the population at any particular instant.

But what that also means is that a particular genotype is going to want to try and acquire mutations any mutation that increases it is fitness. So, if I am genotype A I am going to try any mutation in my geno, which makes me take advantage of other genotypes in a better way will lead to increase in my own fitness and hence I will change my genotype so that I can exploit other genotypes better. Similarly other genotypes any mutation in them which make use of what I am offering to the environment better is going to favorable and selected for and hence those genotypes are going to change and evolve strategies as well.

So, you have this constant evolution of strategies between these two particular genotypes and that s a sort of dynamics that we are interested in in analyzing under evolutionary game theory.

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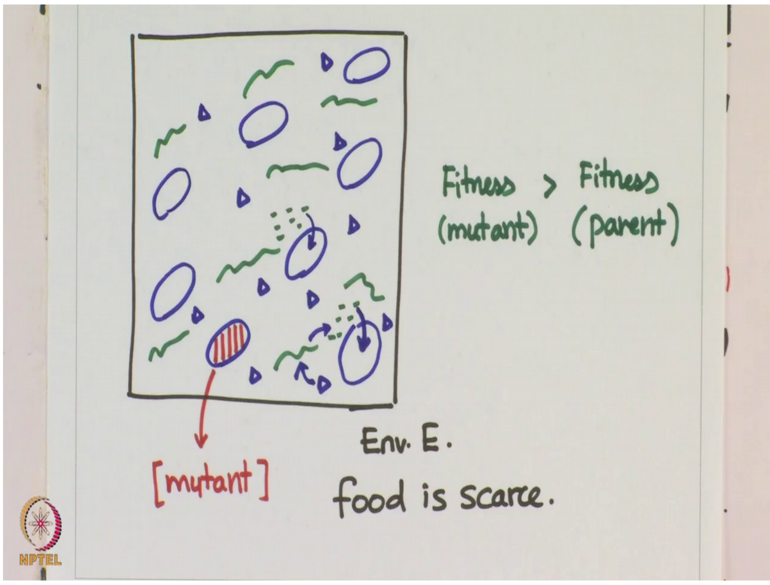

So, let us start with an example associated where something like this might play out. Let us imagine an environment where food is scarce. So, this is my environment E and in this environment food is scarce and the only food that is sort of available is these polymers in the environment which cannot be directly used by bacteria.

So, these are polymers which are not directly used by bacteria and what is going to happen is that and these are the bacteria which are present in the environment, and these extracellular polymers cannot be used up by the bacteria. But what s going to happen is that the bacteria in the environment are going to produce an enzyme and these enzymes are produced in the cytoplasm of the bacteria and released outside the cell and the job of these enzymes is to breakdown these polymers into little monomers.

So, the polymer gets broken down because of this extracellular enzyme, and that broken monomer is then taken up by the bacteria and used for growth. So, this is the scenario that we have and all particular individuals in the population belong to this particular genotype. Now what might happen is one way to look at this is that every single individual in this population paying a certain cost in terms of the energy investment that it is making towards production of this enzyme, which is not directly benefiting the producer.

The enzyme which is produced is not breaking down the polymer outside just for my sake, but the enzyme that I am secreting is going to break is going to go into the environment and break the polymer and that the broken monomers can be used by any individual belonging to the population. So, in that sense the enzyme that I am making by using my own private goods and I am releasing into the environment is doing a public benefit in the sense that it breaks down the polymer and creates monomers which can be used by any individual in the population.

So, this is a private investment that I am making, but the benefits associated with this private investment are public in nature in the sense that any individual belonging to the species can use the monomers which are broken down by this enzyme. So, that s the setting that we have and of course, every every particular enzyme molecule which is released into the environment is doing the same, and bacteria taking up this monomers and using them for growth purposes, but what s going to happen is that let us imagine that one of the bacteria living in the environment acquires a mutation. So, this is my mutant in the population now, and what this mutant is doing is that it has picked up a genetic mutation which no longer leaves it capable of producing that enzyme.

So, this particular mutant is not producing the enzyme, but it still retains the capability of picking up the monomers from the environment and using them for energy. Now imagine this particular this one mutant bacteria in a pool of normal bacteria every single individual is paying a certain metabolic cost towards production and release of the enzyme into the media; however, the mutant that we are talking about here is paying no cost towards production of enzyme, but is only the is only reaping the benefits of the enzyme that has been produced by others.

So, in a setting such as this because my mutant is not paying any cost in terms of production of enzyme and every other individual in the population is paying that metabolic cost towards production of this enzyme, fitness of the mutant is more than fitness of what we call the parent genotype. Now we have seen what happens when something like this happens. Now we have two distinct genotypes in the environment, the mutant genotype and the parent genotype and the mutant has a fitness more than the parent, because it is not paying any cost towards production of a public good, the enzyme which helps provide food for every individual in the population.

Because there is fitness differential selection will take over and the frequency of the mutant is going to increase in the environment. And now, because the mutant is fitter than the while type; thus, the way selection will act as the numbers associated with the mutant are going to increase and while type are going to get the parent genotype is going to get sort of eliminated from the environment and if that happens.

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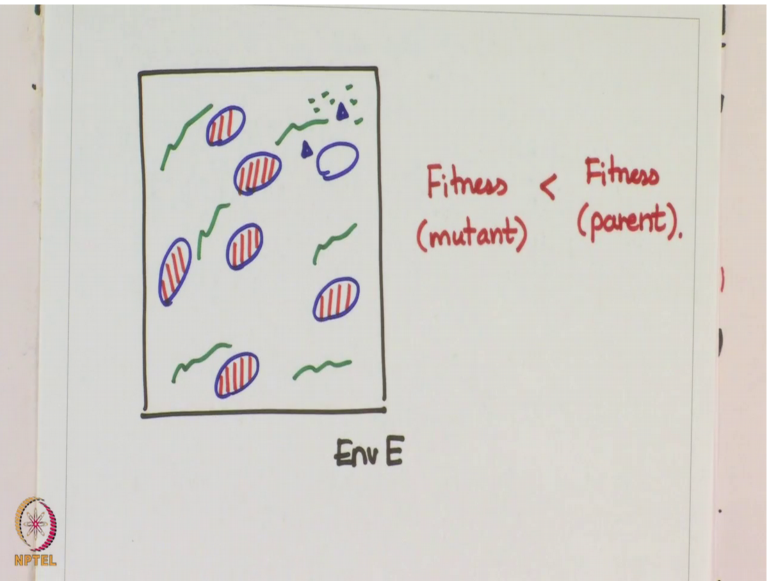

Let us take a look at the picture that will be offered when that s the case after selection has acted for a while the environment is going to look something like this. So, this is the same environment E, this environment has food resources these are the polymers that cannot be broken down by the mutants or the while type, but can be broken down by the enzymes that are produced by the wild type, and these are the bacteria now.

And because selection has acted for a while most of these bacteria belong to the mutant genotype let us imagine the scenario in this case to be something like this where most genotypes are mutants and only this one parent genotype survives. Now this parent genotype is still producing the enzyme, but of course, because there is only one producer of the enzyme the enzyme production will not be very much and as a result the polymer that is broken down only been the missinity of this of the location where this parent genotype individual still exists.

So, now in this case what s going to happen is that because this setting like this has been arrived at most of the benefit that s obtained from breaking down this polymer is going to be derived by this parent genotype only these mutants are not going to see the monomer at all and are going to get selected against where as these mutants may see some amount of monomer associated with the polymer because of their physical proximity with the parent genotype.

But as a result of all of this what this means is that in this case now the fitness of the mutant is now less than fitness of the parent, and what this sort of illustrates is that if you were to start with an environment that we started with, there was only one mutant and everybody else belonged to the parent genotype was producing the enzyme. In that case fitness of mutant was more than fitness of parent. And eventually, this environment transitions itself to the second environment that we do selection acts on the two genotypes, and we have mutant population which now dominates over the parent genotype and in this case fitness of mutant is less then fitness of parent.

So, what all of this illustrates is that change in frequency, the frequency of the mutants in our example went up and the frequency of the parent genotype went down. And this change in frequency what it resulted in was that the fitness of mutant which was more than fitness of the parent to begin with, now became less than parent and this change was facilitated just by changing the genetic makeover or the genetic or just by the frequencies associated with the various genotypes that are present in the environment. Again fitness in this sense is a concept associated with, the frequencies associated with the different genotypes in the environment and they are not fixed in nature.

So, how do we look at that? Remember in the first few lectures of course, we when we started dynamics capturing dynamics in a mathematical form we would write. So, again let us go back to our simplest example that we started with two particular genotypes and we will call them a and b.

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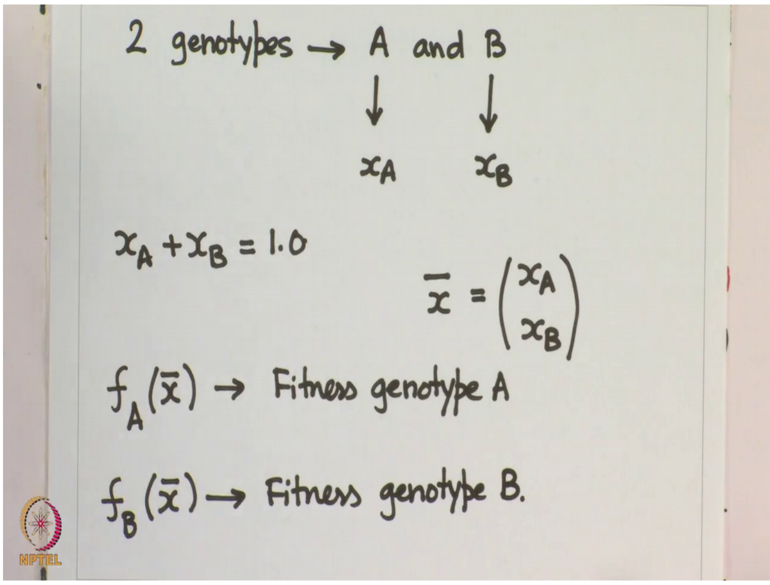

So, if we have two genotypes, let us call them A and B, let the frequency of individuals belonging to genotype a be x A, frequency of individuals belonging to genotype B be x B then we know that x A plus x B is equal to 1 and what that means, is that the composition of the population of the environment is denoted by this vector x which is x A and x B. If there are more genotypes this vector would just have more components, but for our example this vector denotes the composition of the population at any given instant and time.

Also because fitness is now a concept which is dependent on frequency is a not and not a constant, fitness of A is given by is given by fitness of A, but this is a variable which is dependent on composition of the population and composition is defined by the vector x hat. Similarly fitness of B will be a variable quantity which is dependent on the vector x this is fitness of genotype A and fitness of genotype B ok.

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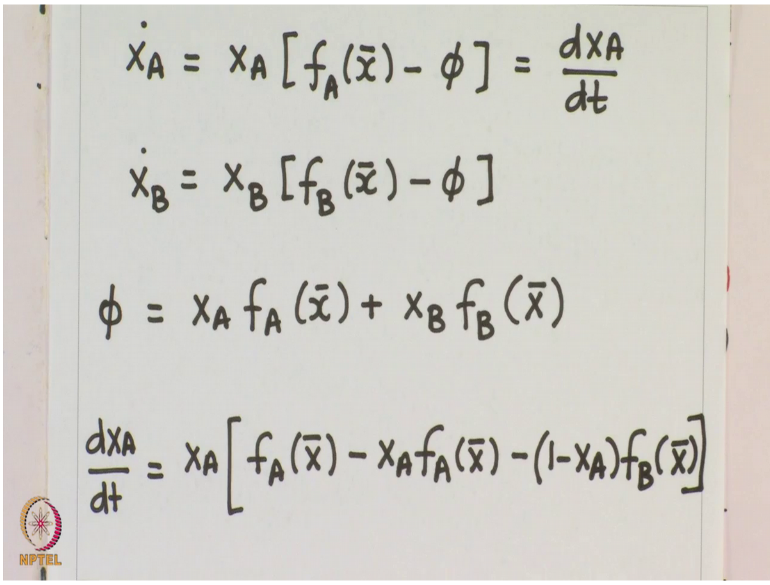

So, if we have this then we can write that x A dot is just equal to x A into fitness of genotype A which is f A function of vector x minus phi, and x B is just equal to x B dot which is just this is just x A dot is just short form d x A by d t the rate of change of frequency of individual number of individuals belonging to genotype A, x B dot is just d x B by d t is equal to x B f B x minus phi and phi of course, is the mean fitness associated with this environment which is just going to be equal to x A times f A x, plus x B times f B x.

So, we can simplify this further we can plug this value of phi in the first expression that we have here and get d x A by d t is equal to x A into f A into x minus x A into f A x minus I am going to write x B as 1 minus x A times f B into x that is the expression that we get.

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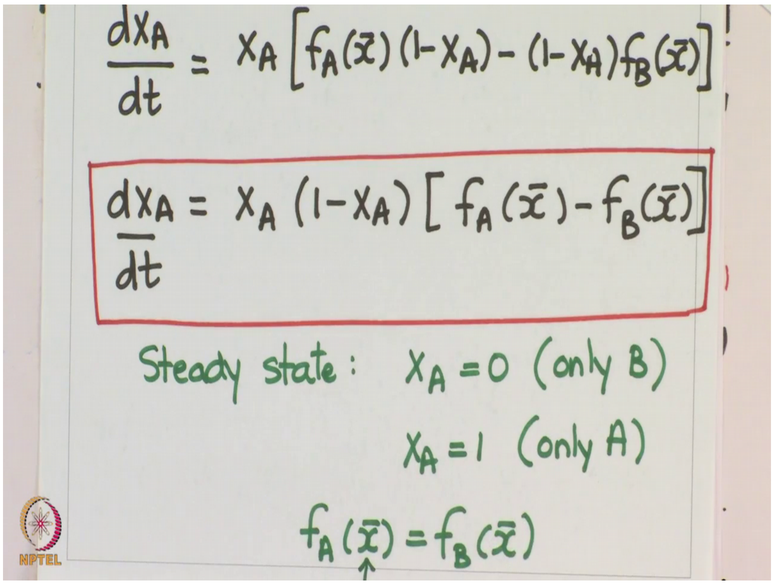

And we can simplify this further and write this as d x A by d t equals x A into f A x into 1 minus x A minus 1 minus x A times f B x, which can be simplified as x A times 1 minus x A times f A x minus f B x; that is the dynamical x equation which derives which defines the dynamics of these two genotypes where fitness is not a constant, but a function of the composition of the population. So, if we have this now the next thing associated with this is just going to be the analysis of the steady states and the stabilities associated with this system.

So, again we will use the standard strategy that we have been doing so far what are the steady states of the system and steady state by just looking at this we can tell is equal to x A equal to 0, which means that it is only B in the environment or x A equals one which implies that there is only A in the environment or any such scenario any such composition such that f A of x is equal to f B of x, what we mean by that is these are the two compositions of the environment where d x A by d t is equal to 0.

But these are intuitive in the intuitive in the sense that this this particular value x A equal to 0 is talking about the case where there is only B in the environment and x A equal to 1 talks about the case where there is only A in the environment. So, these are steady states, but in addition we also have another steady state which is given by that composition x such that f A of x is equal to f B of x, which means those compositions where fitness of A is exactly matched by fitness of genotype B and now. So, we may need to solve for these fitness's depending on what are the exact expressions of these. Now let us think about this a little more imagine a case where f A x minus f B x looks something like this.

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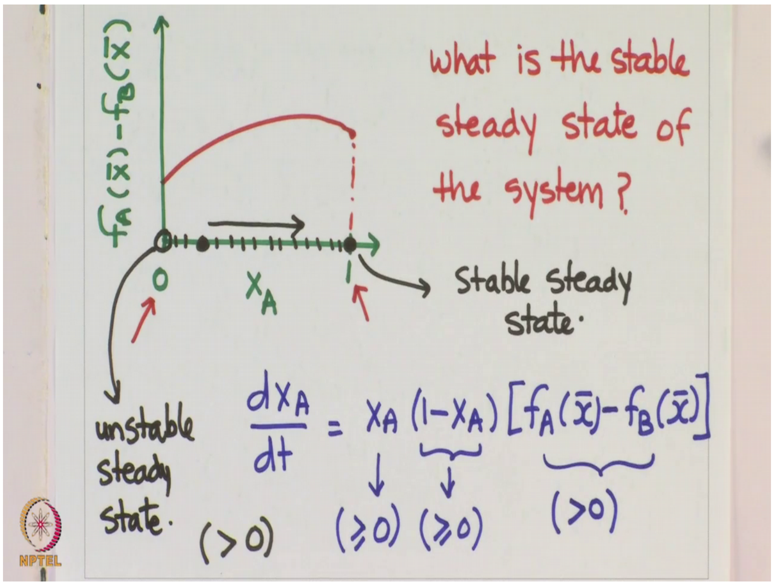

So, I am going to plot this is x and on the y axis I have f A of x minus f B of x and let us say this is x A this is 0 and this is one. So, again let us imagine. So, this will be all A s this will be all B s and this is f A and x B at every particular f A x minus f B x at all particular values of the variable x A.

So, if this quantity looks something like this. So, imagine that as x A varies from 0 which represents a scenario that there are only B s in the environment, and goes towards x A equals one which represents the scenario that there are only A s in the environment if the quantity f A x minus f B x which is the difference between fitness of genotypes A and B that expression looks like this which is not constant, but is changing with composition if that looks like this what is the stable steady state of the system. So, in one sense we have already talked about this. So, maybe pause the video for a minute.

So, think about this system and continue thereafter oh what you should realize here is that our equation that we are working with is the following just d x A by d t is equal to x A times 1 minus x A times f A x minus f B x and what this tells me is that x A is a quantity which is always greater than equal to 0 this is equal to 0 when x A is equal to 0, but otherwise is always greater than 0. So, it is a positive quantity 1 minus x A is an expression which is always greater than equal to 0 because by definition x A cannot exceed any exceed one.

So, 1 minus x A is equal to 0 when x A is equal to 1, but is otherwise between 0 and 1 and is always positive; and f A minus f B is in this case given to me by this expression which tells me that f A x minus f B x is type of a function which is always greater than 0. So, what that tells me is that this expression d x A by d t is actually never less than 0, but could only be equal to 0 or greater than 0 it is only equal to 0 at two particular values x A equal to 0 x A equal to 1.

But at any other value of x A at any other value of x A between these two extremes if my system was present at any of these two values my d x A by d t will be a positive number times a positive numbers times another positive number; that means, d x A by d t will be greater than 0 as long as x A is not equal to 0 and x A is not equal to 1 for any other value of x A d x A by d t is greater than 0. And what that means, is if my system is at this place then d x A by d t is greater than 0 which means as time increases x A increases and hence my system moves in this direction and eventually it stops at x A equal to 1 because that s the value where d x A by d t is equal to 0. So, this is the stable steady state associated with the system and x A equal to 0 is the unstable steady state. So, this is analysis of stability using something that we have already done in the course before.

But if you think about this this makes a lot of intuitive sense let us take a look at the kind of a function that f A x minus f B x is. If we look at this graph then f A x minus f B x is always greater than 0 what; that means, because this graph f A x minus f B x is always greater than 0 and that greater than 0 is independent of the composition of the environment. So, no matter what is the composition of the environment f A x minus f B x is always greater than 0.

What that means, is that if I were to start my environment with a composition anywhere on this scale fitness of A minus fitness of B is greater than 0 and what that means, is that fitness of A is more than fitness of B and what; that means, is that selection is going to act and select for genotype a and remove genotype b because f A minus f B is a positive numbers which implies f A is more than f B. So, a is growing at a great which is greater than the rate at which genotype B is growing and that fact is independent of the composition of the population in the setting that we are talking about right here. And if A is fitter than B irrespective of the composition it is only natural to expect that selection would totally eliminate B from the population and eventually you will have only A s survive in the population which is what our stability analyzes is telling us right here ok.

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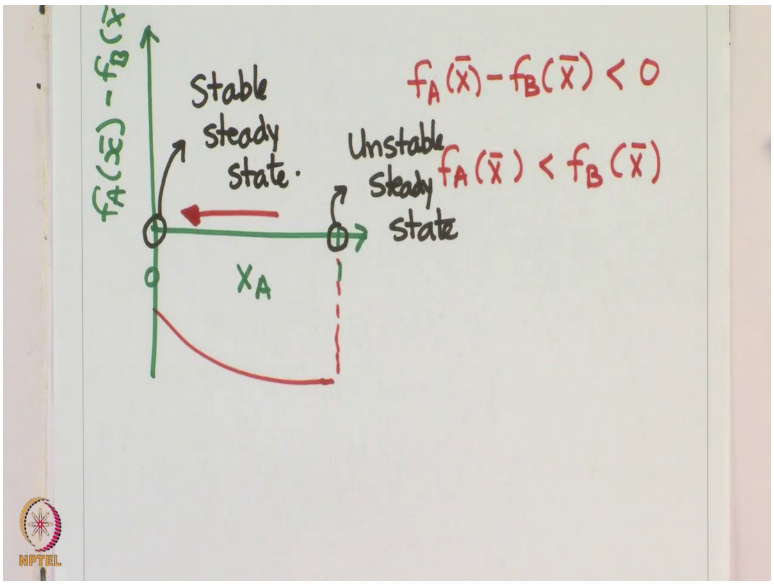

So, let us quickly take a look at the converse of this situation as well if f A minus f B was a graph which look like this, this is x A going from 0 to 1, and now if my graph look something like this what that tells me is that f A x minus f B x is always less than 0 and this fact is independent of the composition of the environment which tells me that f A x is less than f B x independent of the composition, and if B is fitter than a then selection should automatically act and ensure that A is driven out of the population. So, if we do the stability analysis I leave that as an exercise for you if you do that analysis the population should move towards left and approach 0.

And what that tells me in terms of my steady state associated with my system is that x A equal to 1 is an unstable steady state and x A equal to 0 is my stable steady state. So, when we started this discussion we said that there are three types of steady states that might occur in the system and those three types of steady states are x A equal to 0 x A equal to 1 and also all those points where any such composition which ensures that f of A is equal to f of B will also be a steady state according to this situation because if this is satisfied for any composition of x then d x A by d t will be equal to 0 because this quantity then becomes equal to 0. But so far the two examples that we have done which is this this one where f A x minus f B x is always greater than 0.

And the other one where f A x minus f B x is always less than 0 do not offer us any such example where any such composition where f A x is equal to f B x for a particular composition associated with the environment. And that is something that we will start within the next lecture.

Thank you.