Introduction to Evolutionary Dynamics
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Lecture - 35
Evolutionary game theory – 2

Welcome everyone. We will continue our discussion from the last lecture and develop and work towards development of a frame work in which we can analyze evolution or coexistence of multiple genotypes in an environment. And this particular field of analysis is called evolutionary game theory. So, just to recap from where we had finished last time: in 2 species environment where 2 distinct genotypes are coexisting.

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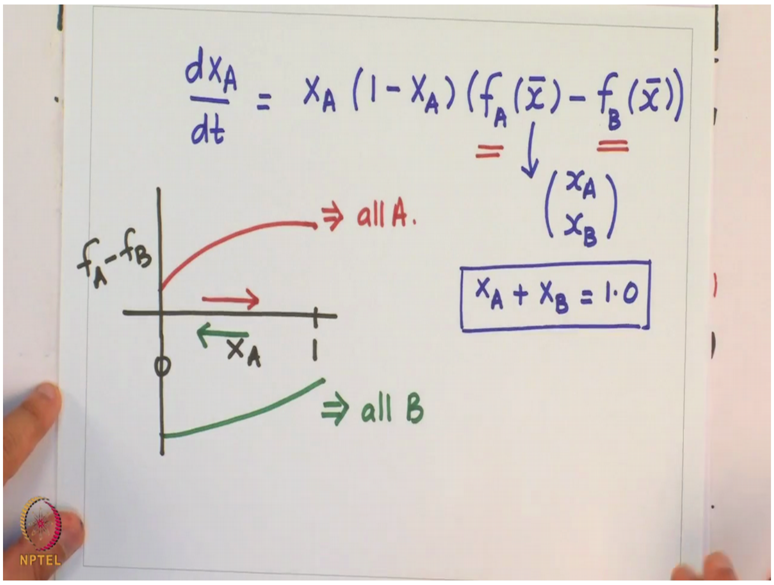

Our dynamical equation which captured the dynamics associated with frequency of one particular genotype which can be represented as: d X A by d t is equal to X A times 1 minus X A times f of A as a function of X minus f of B as a function of X, where the vector X is just the composition of the population in environment at that particular instant.

So, when we are talking of 2 particular genotypes the vector X will comprise of X A component which represents a frequency of individuals belonging to genotype A and X B which is frequency of individuals belonging to genotype B, and X B we also know that X A plus X B is equal to 1 at all times. So, essentially the vector X is just 1 variable X A and 1 minus X A because of that is true because of this linear relationship that we know exists between X A and X B.

And then we had talked about the steady states associated with the system and the steady states are X A equal to 0 X A equal to 1 which corresponds to no A and all B and all A and no B. And any particular composition of the population such that f A of X is equal to f B of X, which implies any such composition where fitness of A is equal to fitness of B would also constitute as a steady state associated with the system.

So, then there are different relationships that can exist between f A and f B; and if I am looking at X A going from 0 to 1 and on the y axis I have f A minus f B then we discussed a couple of cases. In case number 1 f A minus f B was always greater than 0, for all values of X and this implied that in the environment it was all A. And in the other case that we did f A minus f B was always less than 0, irrespective of what composition of the population we worked at f A minus f B were always less than 0. And this corresponds to a situation where any nonzero composition associated with the 2 genotypes moves to a situation where there is all B and no A.

So, this particular condition ensures that the system moves in this direction towards X A equal to 0 and f A minus f B greater than 0 ensures that system moves in this direction towards X A equal to 1 which is all a this moves in this direction just all B. So, we did these 2 compositions, but then we recognized that there could be other scenarios such that we are not commenting yet on the structure of these functions- we do not know what kind of functions these are these linear or non-linear functions. So, there could be compositions which are defined by this vector X such that f A of X is equal to f B of X.

Now, let us imagine that one of those structures; again we are not commenting yet on the mathematical nature of f A and f B of x, but what we will what we will assume sort of is should f A and f B curve intersect the X axis at any given composition any given nonzero and non one value of X A what would the nature of the steady states associated with that situation look like.

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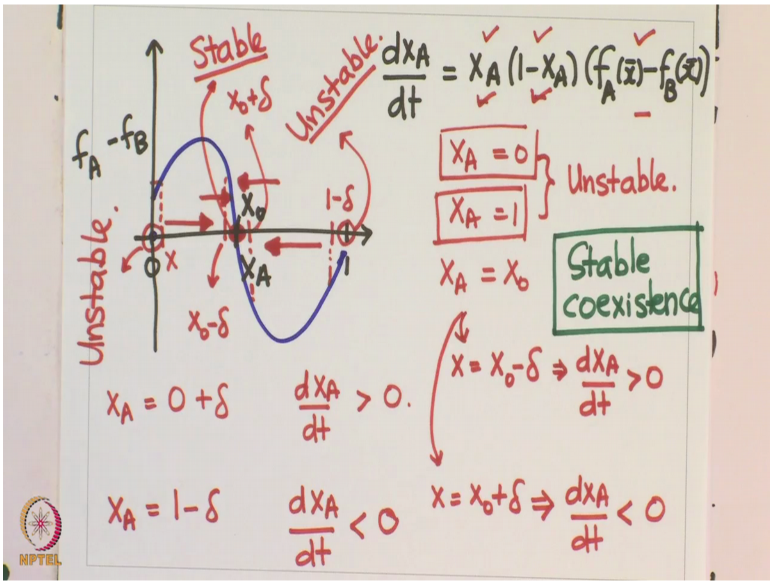

So, for example, if we if we take a case like this again our X axis represents X A it goes from 0 to 1 and y axis is f A minus f B each of these remember is a function of X A on the X axis. And now if the graph associated with this looks something like this maybe that s what the graph looks like.

So, now we want to comment on what s the fate of this system given that the dynamics is defined by d X A by d t equals X A times 1 minus X A times f A of X minus f B of x. So, we know the form associated with the first 2 terms, but this third one we are not comment on the on the mathematical framework which defines this, but let us say this term looks like this as X is varied. So, what is clearly evident here that there exists a certain X naught below which when the composition of the population is such that the a type individuals are less than X naught then f A minus f B is greater than 0 which means in this section of the graph individuals are fitter than individuals B and vice versa that in this composition of the population where X A is from X naught 1 its f B which is more than f A and hence f A minus f B is less than 0.

So, what happens in a scenario such as this and that can be easily seen from the analysis that we have been doing. So, far that let us look at. So, first thing to recognize is that there are 3 steady states X A equals 0 because this term is 0 X A equals 1 because this term is 0 and X A equals X naught because at that value of X naught this term is equal to 0 and we want to comment on the stability associated with each of these 3 each of these

3 terms. So, again we follow the standard procedure let us to study the first one let us introduce a disturbance such that X A is equal to 0 plus delta which means bring a value of X into this point at this point X is a small value delta which is positive and if delta is positive; that means, this quantity is positive.

Since delta is small 1 minus X A is always positive unless X A is equal to 1, but we know that X A is much smaller than 1. In this case which is just equal to delta and for this particular composition of the population f A minus f B is at this value which is greater than 0. So, all of these greater than 0 for X A greater than 0; hence d X A by d t is greater than 0 at X equal to delta which means we are increasing time X A increases and we move in this direction which is away from the steady state that we started with hence this particular point is unstable.

Similarly, we can look at the next steady state which is X A equal to 1 and the disturbance that we introduced now is X A equal to 1 minus delta which means we bring the system to somewhere there which is 1 minus delta now starting from this point we looked that at X A equal to 1 minus delta X A is positive 1 minus X A is always positive unless X A is equal to 1, but X A is not equal to 1 X A is 1 minus delta. So, this is positive and at this particular point f A minus f B can be seen is negative here which means d X A by d t is less than 0 because it is a product of 2 positive and 1 negative numbers d X A by d t is less than 0. And hence starting from this point the system moves in this direction hence this point is also unstable.

So, X A equal to 0 and X A equal to 1 are both unstable points while it is also evident from these graphs that any deviation in this region moves the moves the system in this particular direction any deviation from this point in this direction moves the system towards X naught. So, we can see that deviations from either side bring the system towards X naught then hence intuition implies that X naught should be a steady state stable steady state associated with the system, but let us just go and actually explicitly check for stability of X equal to X naught and if we do that we will introduce deviations from X equal to X naught on either side and track which way does the system move once its disturbed from its steady state X equal to X naught.

So, let us let us introduce a first deviation where X is equal to X naught minus delta if that is the case; that means, this is the X that I am talking about X naught minus delta and at X naught minus delta X A is positive 1 minus X A is positive and f A minus f B at this point is also positive. So, all 3 factors are positive which implies d X A by d t at X naught minus delta is greater than 0 which means system moves in this direction towards the point that it was disturbed from.

Similarly if the disturbance that is introduced here is X equals X naught plus delta which means now I am talking of s disturbance which is here this is X naught plus delta at X naught plus delta X A is positive 1 minus X A is positive and f A minus f B in this case happens to be less than 0 and if it is less than 0 it means the system moves in this direction again towards the point that it started from towards the steady state that we are talking about here which is X equal to X naught hence at this point d X A by d t is less than 0 and you get a case where you have this particular point X equal to X naught as our stable steady state.

So, of the 3 steady states that we have in system X A equal to 0 X A equal to 1 and X A equal to X naught 2 of them 2 of the steady states are unstable and the one which accounts for nonzero frequencies associated with both genotypes is actually the stable steady state. And hence this type of a system which would exhibit f A minus f B such like we just described is actually is actually said to be a representative of a case where there is stable coexistence of multiple genotypes because the only steady state which is associated with the system actually ensures that both genotypes coexist in the environment and not one of them is eliminated.

Like what happened in the previous 2 cases that we that we discussed and the case that we had started this discussion last time around when we started talking about evolutionary game theory of the case where there is a cheater of there is a mutant bacteria a cheater in the population which does not commit cellular resources towards production of an enzyme which is responsible for breakdown of a polymer that the bacteria are then going to use for energy is a case which is represented by this sort of a framework where there is a stable population, because we saw that if the if the mutant population goes down very small then the mutant is actually more fit than the parent genotype.

But if the mutant is everywhere and there are only a few parent genotype individuals left in the population in that case mutants fitness is less than the parent and somewhere in between in between these 2 extreme there lies a particular frequency of the mutant genotype such that the fitness associated with both the genotypes exactly meet each other. And that is the stable steady state that we are looking at in an analysis such as this, alright. So, that is stable coexistence there is one more case regarding this that we want to talk about and let me let me sketch that out.

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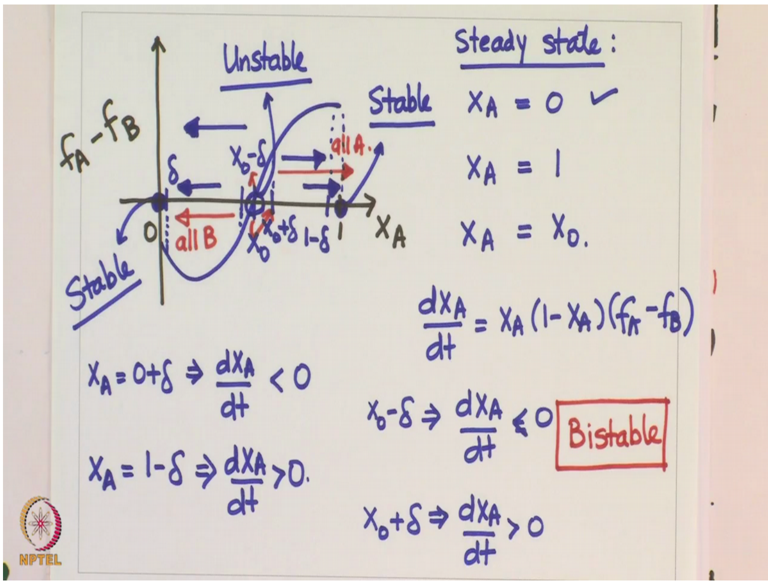

First again, so, X axis is X A which goes from 0 to 1 and y axis is f A minus f B and now my graph looks something like this. So, it starts with a negative value which means that f A is less fit f A is less than f b; that means, a is less fit as compared to B at this particular population composition. However, if there are mostly a s in the population because these this region here represents high values of X a; that means, there are lots of a s and very few B s in a scenario such as that its f A which is more than f B and hence f A minus f B is a positive and in between there is one particular point where the fitnesses of the 2 genotypes exactly match each other.

So, again we do a similar analysis we know that our steady states are going to be X A equals 0 X A equals 1 and X A equals X naught. So, again first let me write down the equation once more these are both functions of X like we have been talking about. So, far this is the relationship that is biographic given graphically here. So, if we look at X A equal to 0 we disturb the system bring it to X A equals 0 plus delta again we are only introducing the positive deviation the negative deviation does not really make any sense for us. So, this is delta.

And at this point X A is positive 1 minus X A is positive, but f A minus f B at this point is less than 0 hence as the system moves forward in time the composition of the population moves in this direction towards the point that it was deviated from this implies d X A by d t is less than 0. And hence this particular point, in this case is stable what you should note at this point is that what we have just shown by changing the nature of f A minus f B graph the point X A equal to 0 has basically switched its stability in the case that we just finished X A equal to 0 was an unstable steady state, but in this case X A equal to 0 represents a stable steady state associated with the system, alright.

So, this one is done, let us talk about X A equal to 1. So, again we disturb the system and bring it to a state 1 minus delta which is somewhere over here and at this point at this particular point X A is greater than 0 1 minus X A is greater than 0 and f A minus f B is greater than 0 which means system moves in this direction again towards the point that we disturbed the system from towards X A equal to 1.

Hence, this point is also stable and this d X A by d t is greater than 0 and our last intermediate point which is again we will disturb it 2 ways, but intuition here or this analysis of the other 2 steady states associated with the system sort of suggest that X naught should be an unstable steady state, because the systems want to move away from that system because the system wants to move away from this particular steady state.

So, X naught if we deviate at X naught to X naught minus delta which is somewhere over here then again at this point d X A by d t is equal to positive; positive times negative which means a negative number which is what is here d X A by d t is negative. Hence, the system moves in this direction away from the steady state that we are talking about X naught. Similarly X naught plus delta; this particular location implies d X A by d t is positive times a positive number hence greater than 0. And that means, the system moves in this particular direction away from the steady state that we started with which confirms that X equal to X; X A equal to X naught is an unstable steady state.

So, the difference between this case and the previous one is just that the steady state associated with the system have switched stabilities. Now the points which were unstable in the previous analysis have become stable and vice versa. So, what is this system like this is actually called. So, the previous one was called coexistence of (Refer Time: 19:29) because the stable steady state corresponded to a situation where both the genotypes had a nonzero frequency associated with them here the stable steady states are those which are associated with one of the genotypes going extent and one of them taking over the population; however, depending on where you start your system from that that is the determining factor as to which particular genotype goes extinct and which particular survives.

For instance if we look at this point X naught if we see here and any disturbance brings the system to X naught minus delta if the system is existing at X equal to X naught and any disturbance brings the system to X naught minus delta what will happen is that the dynamics of the system will ensure that the system moves in this direction towards X A equal to 0 which means towards all b.

However, if that initial fluctuation or disturbance to the system was such that it moves it to X naught plus delta then from here the system prefers to move in this particular direction towards X A equal to 1 which is all a. So, in a scenario like this what is happening is that the initial disturbance if the system is existing at X; X A equal to X naught it is the initial disturbance which decides which direction does the system move to and that particular disturbance which could be a random fluctuation that happens in the environment decides the fate of the 2 species which are involved.

So, the starting point of an analysis such as this is the key determining factor which decides what happens to the genotypes and hence this type of a framework is called a bi stable system because this system exhibits 2 stable steady states and which one you land up on is decided by where you start your system from. So, if you are operating at X equal to X naught your starting point is decided by which way does the disturbance that enter the system push; push the system and from there on the dynamics of the system take over and take you to one stable steady state or not.

So, these are four scenarios associated with this type of an analysis and just to summarize it could give you four different type of results all A all B coexistence of the 2 or a bi stable system in theory you could also have more complex forms of these relationships for instance, it is not inconceivable that you might have X A looking something like this.

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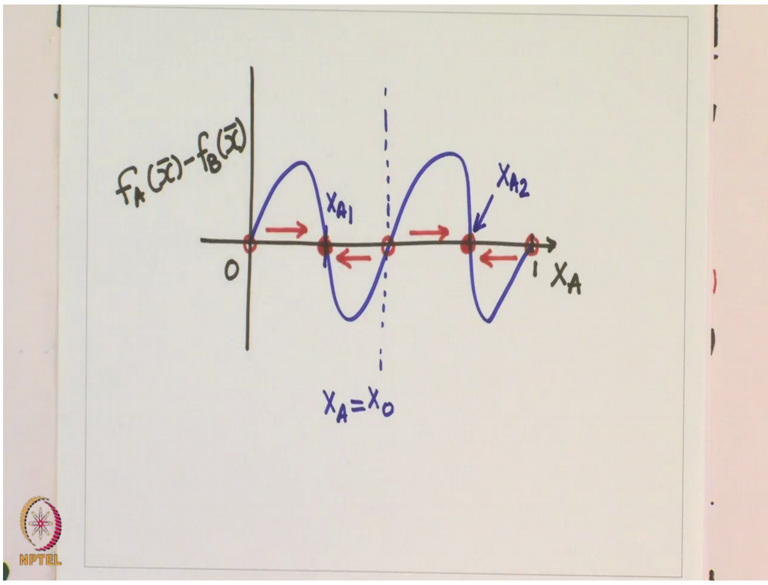

So, if your graph looks something like this now you have lots of stable steady states now you have lots of steady states associated with the system X A equal to 0 and 1 always exist and in addition you have these four intermediate states and what you should show is that in a scenario such as this; this represents a stable steady state this is an unstable this is a stable steady state this is an unstable steady state.

So, this a if f A minus f B exhibited a form such as this then what you are talking about is coexistence, but coexistence could also happen 2 different ways in this system and again that is decided by what was your starting point if the starting point of the system which had an f A minus f B defined like this was let us say this point is X A equal to X naught if the starting point of the system was between X A equal to 0 and X A equal to X naught then the coexistence happens at this particular steady state let us call this X A 1 whereas, if the starting point was between X A equal to 0 and X A equal to 1 then the system is going to converge to this stable steady state which also ensures coexistence, but at X A equal to X A 2.

So, again these systems can exhibit different dynamics depending upon the precise nature of f A minus f B curve. So, the next question that we have for us is that how do we actually arrive at analytical natures analytical expressions for this f A minus f B expressions that we might have and in order to do that we need to understand something called a payoff matrix which comes from a game theory which comes from the field of the game theory and the way we are going to look at is in a (Refer Time: 24:46) contest think of it like this.

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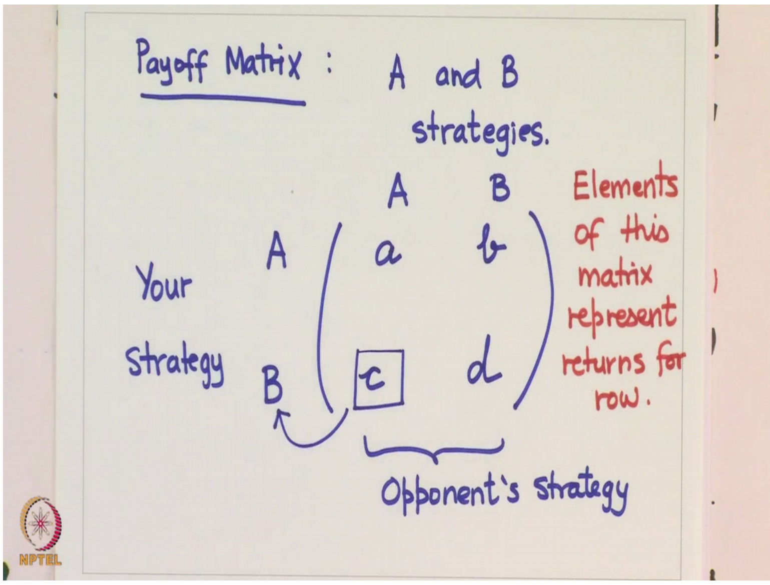

So, we want to define what is called a payoff matrix and before in the context of before we talk in the context of before we talk in the context of microbial populations let us talk in terms of game theory let us imagine that you have a 2 player game and the strategies which are available to 2 players are called strategy a and strategy B these are the 2 strategies that are available to the 2 players and the payoff matrix is defined as the following you have strategy a and B competing against strategy a and B and the way its defined is that if strategy a. So, if you are playing.

So, let us say this is your strategy and the columns represent opponent strategy and the way you define this is this elements of this payoff matrix define what is your payoff how much do you stand to gain or lose if you are playing the row strategy and the opponent was playing the column strategy for instance if you are playing a and the opponent was also playing with strategy a your payoff would be small a on the other hand if you are playing strategy a and the opponent was playing strategy B your payoff would be small B if you are playing strategy B and opponent was playing strategy a then your payoff would be c and if both of you are playing strategy d strategy B then your payoff would be d.

So, again what is important to note is that elements of this matrix represent returns for row. So, these are the strategies whose elements are being represented here. So, which means your; the returns that you are going to get when you play this game. So, if you are playing with strategy d opponent is playing with strategy c this c return represents your return when you are playing B and opponent is playing A; it does not talk about what does the opponent get when a when it is playing with a, alright.

So, that s this is what is called payoff matrix. And in the next lecture onwards we will start to use this framework of a payoff matrix from game theory to incorporate a scenario where microbial populations which we will treat as 2 players here can be analyzed in a framework which is very similar to this payoff matrix from game theory.

Thank you.