Introduction to Evolutionary Dynamics
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Lecture - 24
Dynamics of Moran process without Selection

Hi and let us continue our discussion on the Moran process and the evolutionary dynamics associated with what we can understand from this process. So, last time we had defined the probabilities associated with transition of the system in that delta t time, where we had marked that in that delta t time there is one birth and one death event that has taken place.

What that meant was; that the state of the system which is represented by variable i which is equal to the number of individuals belonging to genotype A; could remain at i if the same genotype was chosen for birth and death or that i could increase to i plus 1 or i could decrease to i minus 1 and each of these transitions had a probability associated with that. So, before we go further let us try to get a sense of these probabilities by understanding some very basic transitions associated with this.

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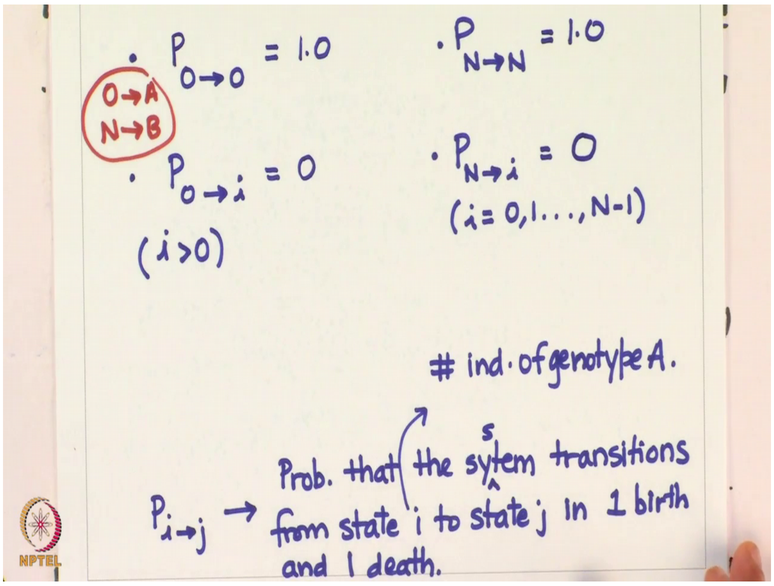

So, again I am going to write some probabilities and what you should do is sort of pause the video and try and think about what transitions we are talking about and come up with the appropriate probability numbers that you think for each of these transitions. So, the first one is that what is the probability that the system transitions from 0 to 0 and again when we are talking these transitions where I write P i to j; what this refers to as is the probability that the system transitions from state i to state j in 1 birth and 1 death.

In that delta t time where 1 birth and 1 death events are taking place; what is the probability that the system transitions from i to j and state i is referred to as the number of individuals of genotype A and similarly state j refers to as what is the state of the system after that transitions and j is the number of individuals of genotype A after this 1 birth and 1 death process have taken place.

So, the first one that I want you to think about is the transition probability that the system starts from 0; ends at 0. The second one is probability system starts from 0; goes to i; the third one is probability of the transition of the system starting from N remaining at N and the fourth is probability of the system when it starts from N goes to i. In this transition we define i to be any number which is greater than 0 and in this one i is equal to any number less than N; so 0, 1 going all the way up to N minus 1.

Again just pause the video for maybe 30 seconds or so, think about these four numbers and we will continue from there. So, what is probability the transition probability 0 to 0 the system is at 0; that means, what; that means, and how we have been defining is that there are 0 number of A genotype individuals; which automatically implies that there are N minus 0, N number of B type individuals and the starting and the ending state of the system are same. So, what is the probability that we start from the state and we remain in this state. Since there are no in A individuals; that means, we cannot ever draw an A individual out of this starting position, we are going to select a B individual for birth, B individual for death; that means, the system remains in the state forever; hence this probability that starting from 0 and remain at 0 is equal to 1.

The second one is starting from 0 you move to i; where i is a number which is bigger than 0. If, we do not have an a individual in the population there is no way that we are going to be able to increase the number of A individuals because the only way the number of individuals of a particular genotype can increase is when we draw that particular genotype to represent a birth process.

Since there are no individuals in the system at this state, we can never draw an individual of genotype A; for birth and hence its numbers can never increase this is equal to 0. This probability is the reverse of that; now we are saying that there are N type of A individuals, 0 type of B individuals. Since all individuals are of type A; they will remain to be of type A because we are not permitting mutations at this stage, this is equal to 1 and last is that since all individuals are of type A, there are no B type individuals.

The number of A individuals cannot come down and this probability is equal to 0. Again maybe spend a few minutes looking at this and convince yourself that all these transition probabilities make intuitive sense and they can be easily thought of in a logical way.

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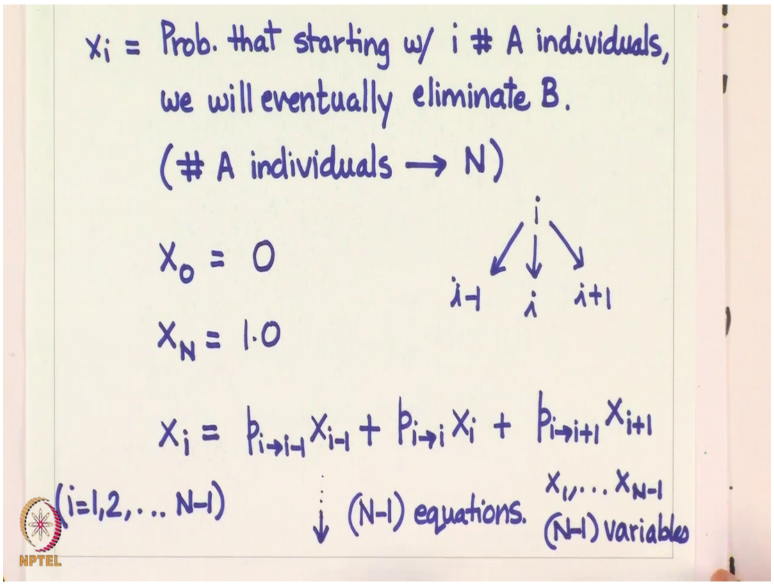

So, now that we have some sense of understanding of probabilities of transitions associated with this process; we are going to, we are interested in a particular quantity which we are going to call X i and this X i is defined as probability that starting with i number of A type individuals, we will eventually eliminate B from the system. What that means is that, the number of A individuals is going to increase and go up to N. What is the probability that I am starting my system with i number of A individuals and this i number should change to N.

That is this probability is represented by X i what; that means, is what is X 0, X 0 is the probability that I start with 0; A individuals; what is the probability that starting with 0, A individuals; the number of A individuals increases to N and I eliminate B from the system and; obviously, since starting number of individuals of A type is 0; this cannot happen; this is just equal to 0.

What is X N? What; that means, is that I am starting with N number of A individuals; what is the probability that I will eliminate B; B is already eliminated because there are N number of A individuals, which implies there are 0 number of B individuals; hence X N is equal to 1 because B is already eliminated. This ensures that there is already no B in the system and hence this transition is always guaranteed.

But interestingly how are we to define the relationship between X i; what is the probability that starting with for any general i not 0 and N; between 0 and N there are N minus 1 values that this variable I can take, so this is valid for i equal to 1 to going all the way up to N minus 1. So, while the values of X naught and X N are very; obviously, clear; the value of X i is not intuitively very clear.

But we know that when we start the system from the state i, it can either go to state i remain there or it can go to the state i plus 1 or it can go to the state i minus 1. We know this from the three transitions that we had studied in the last lecture and derived the appropriate probabilities associated with each of these three translations. We had also seen that starting from i; when we model starting from i; our birth and a death event, there is no way that we can have anything other than these three transitions.

The fate of the system has to belong to one of these three states; once one birth and one death model, one birth and one death process has been accounted for in the system. So, if that is the case starting with X i; that means, my current state is the number of a individuals is equal to i. I transition with probability p i to i minus 1; this is the chance, this represents the chance that starting with I individuals; I move to i minus 1 individuals or my system starting from i could remain at i or I know that starting from i; my system could move to i plus 1.

I am writing these in terms of i because X i is the probability that I am starting with; it is the probability that I am interested in and X i refers to the starting point where there are i number of individuals. Now, starting from X i; if I remain at X i, the probability that after the system remaining at X i, it goes to elimination of B is just going to be equal to X i. There is no difference because the system was at i, so the probability associated with eventually eliminating B was X i; after this particular transition the system remained at X i. Hence the probability associated with elimination of B remains x i; however, if the system transitions from i to i minus 1; the probability associated with elimination of p is no longer X i, but X i minus 1.

Because after this transition which happened from the starting state, the probability associated with is X i minus 1 because after this transition there are only i minus 1 individuals of genotype A. And lastly if starting from state i, the transition that happened was this one going from i to i plus 1; then the probability associated with elimination of A becomes i plus 1. Because now after this transition, the number of individuals of genotype A is i plus 1, so using the fact that I am starting with i and starting with i; there are only three transitions possible; I can build this relationship between X i, X i minus 1 and X i plus 1.

I can write this equation and what is more than that is that I can write this equation for each of this i's; I can put i equal to 1 and write one equation, I can put i equal to 2 and write another equation and so on and so forth; this equation can be written for each of these i's and I have N minus 1 equations, What is the number of variables which are associated here? I know each of these transition probabilities that is something that I have already derived in the last lecture, but what is unknown is all of these X i's.

I know X naught and I know X N and all the in between X i's are what is unknown to me and that is represented by this X i and this I can take a value from X 1 and it can go up to X of N minus 1. So, I can take a value for starting from 1 and go all the way up to N minus 1. So, X 1 to X N minus 1 represent my N minus 1 variables, so what I have here; this is a system of linear equations, I have N minus 1 linear equations and I have N minus 1 variables, I solve these N minus 1 equations for these N minus 1 variables.

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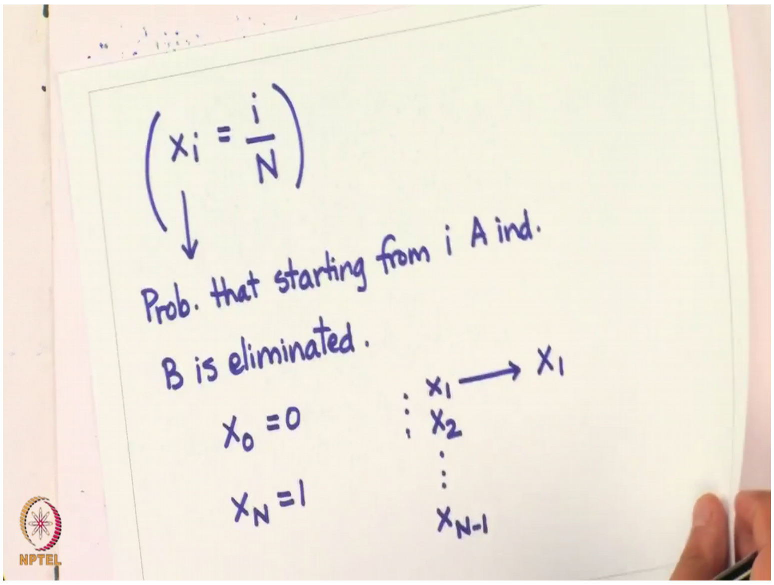

And the answer that I get after solving these equations is simply that X i is just equal to i divided by N. So, the probability that starting from a state that again this represents the fact that the probability that starting from i; A type individuals, B is eliminated; that is the probability that we get and we get this simple expression of X i equal to I by N. We have seen that X naught is equal to 0 and X N is equal to 1.

We have already seen this in the last slide and there are in between N minus 1 quantities starting from X 1 going all the way up to X N minus 1. Of these N minus 1 variables; there is one X i that we are particularly interested in and that particular variable is X 1 because what this physically represents is the following. Imagine you have an environment where the individuals are geno typically identically; all N individuals belong to the same genotype and let us call that same genotype as genotype B, so let us draw that system.

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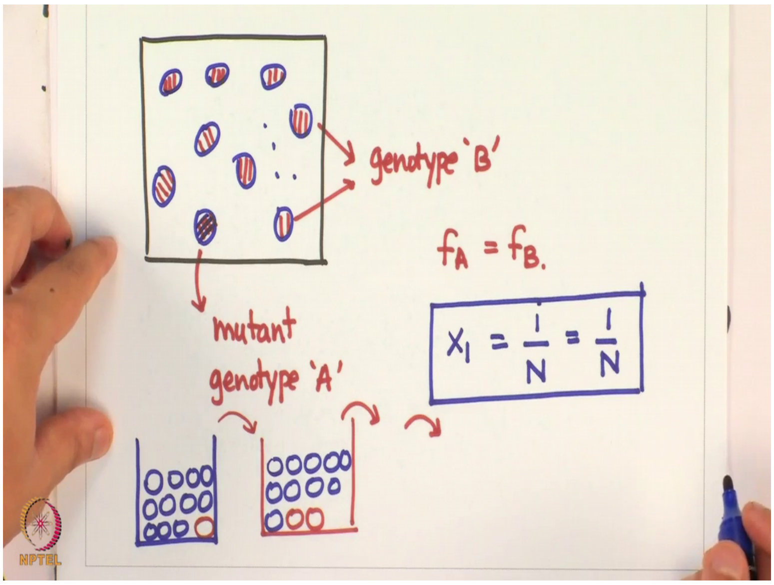

And let us say individuals of genotype B is this and there are N such individuals in this environment p. Now, what happens at a certain time is that one of the individuals while dividing picks up a mutation, if that individual picks up a mutation; the progeny is no longer genotype B, but genotype A. So, this is my mutant which belongs to genotype A and everybody else is the parent genotype which is genotype B. Let us also imagine that the nature of the mutation that has happened is neutral which means that upon conferring this mutant mutation to the progeny, there is no change in the fitness that has happened.

So, the mutant is neither at a fitness advantage or nor at a fitness disadvantage compared to the parent genotype and how we can write that is that f of A is equal to f of B. Both the mutant and the parent genotype are growing at identical rates. In a scenario such as this, the one quantity that we are very interested in is that what is the probability that this single mutant will be able to drive all other B type individuals away from the system, eliminate all of them and eventually ensure that all individuals in the population are of genotype A.

What is the probability that just by random chance; this single mutant cell that arouse is able to eliminate all the other B type individuals that are present in the system; and ensure that every individual in the population is of genotype A and the answer to that in the framework that we have defined is X 1; which is the probability that starting with one individual of genotype A, what is the probability that B is eliminated and that probability is equal to i divided by N and i in this case is 1; hence this is 1 by N.

That is a very important result because when a mutation arises in a system, it is going to lead to a single progeny which is carrying that mutation; so this is 1 by N. In the context of the marbles in a jar game, you should draw the parallel here that imagine these are all the B type marbles and starting off you happen to have just one A type marble and when you are going from one jar to the next one, it is possible that just by random chance you happen to pick the red one more than once.

So, what has happened is that the frequency associated with the red marble has increased and as you transition from jar to jar, the frequency just by random chance can keep on increasing and eventually you might encounter situations where genotype B or the blue marbles in the game that we defined are completely eliminated from the system and it is the red marbles or the mutant genotype A; which takes over the takes over the entire population. This is despite the fact that neither the red marbles or the mutant genotype A had any fitness advantage over their counterparts in each of these 2 respective processes.

Another way to think about the answer that we have got is that X 1 is equal to 1 by N what; that means is, if this is my mutant cell and f A is equal to f B; there is no fitness advantage that once has over the other. Eventually any one of these N cells is likely to eliminate everybody else in the population because they are equally fit every one of these cells is equally likely to eliminate everybody else. Hence the probability of elimination of B is contingent; this is only dependent on the number of A individuals which is present.

The probability of eliminating the remaining N minus 1 cells in a system is equal for every particular individual in this population hence X 1 is just equal to 1 by N. So, that is an important result in the sense that, it gives us an idea of should there be a mutation which is neutral in nature, which does not confer any fitness advantage to an individual; there is still a finite probability that it eliminates all other individuals from the population and establishes itself as the only genotype in the system; this is in the absence of selection. What happens if we were to introduce selection in the system? That is what we are going to talk about next.

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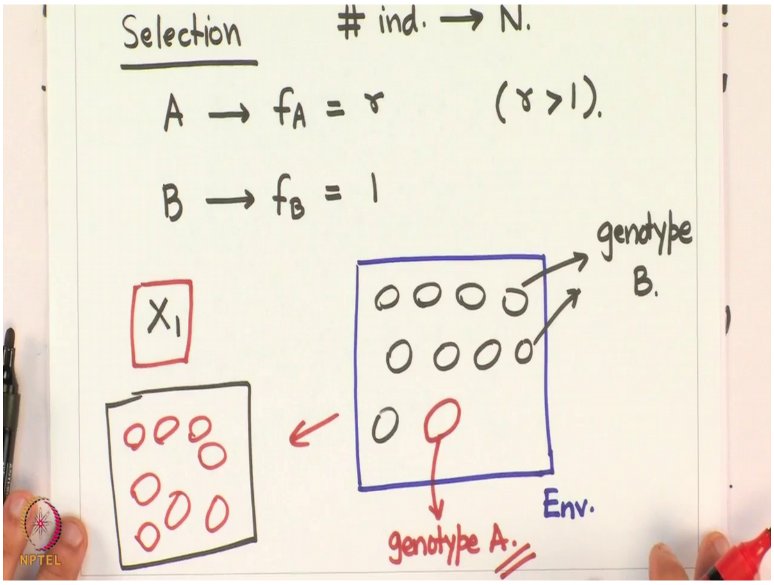

So, now, our 2 genotypes you want to introduce selection and we will say that our 2 genotypes are again A and B the number of individuals in the population remains N, but now what I am going to say is that f A is no longer equal to f B, but f A is equal to r and f B is equal to 1 and r is bigger than 1. So, genotype A is greater than genotype B and again the quantity that we are most interested in here in this analysis is going to be X 1 and let me just reemphasize what that quantity means.

If I have my system; this is environment e and I have N minus 1 individuals of genotype b. So, all these are individuals of genotype B which are growing at rate equal to 1; suddenly one of these individuals acquire some mutation and the progeny belongs to genotype A; which is growing at rate r. So, this is genotype A whose fitness is r; r bigger than 1. What I am interested in is; what is the probability that this one individual mutant is able to eliminate everybody else in the environment and ensure that all of the individuals present in the environment are of this particular genotype.

I am interested in understanding this particular transition that genotype A arose by a mutation; what is the probability that given the fact that A is fitter than genotype B, what is the probability that genotype this one individual is able to replace all B type individuals in the population and the system at some future time starts to look something like this and that probability is represented by the variable X 1. What is important to realize is the fact that if I did not take randomness into account; which is what we are trying to understand here; what is the answer to this question, if there is no genetic drift that we are talking of, there is no randomness associated with the process, what is the answer to this question? What is the value that X 1 takes?

Maybe just pause the video and think about this for 30 seconds and try and see if you can come up with an answer from intuition for the variable X 1 in cases when there is no randomness associated with the system. What you should realize is that starting from this state of the system, where there is only a single mutant; this mutant is going to start eliminating individuals of genotype B and its frequency; the frequency of individuals belonging to this particular genotype will increase with time and eventually it will happen here, the system will reach this state.

As long as it is given that r is bigger than 1; this transition is guaranteed as long as randomness is excluded from our analysis; however, that is not true in nature and randomness does play a big part in dictating the dynamics of the system.

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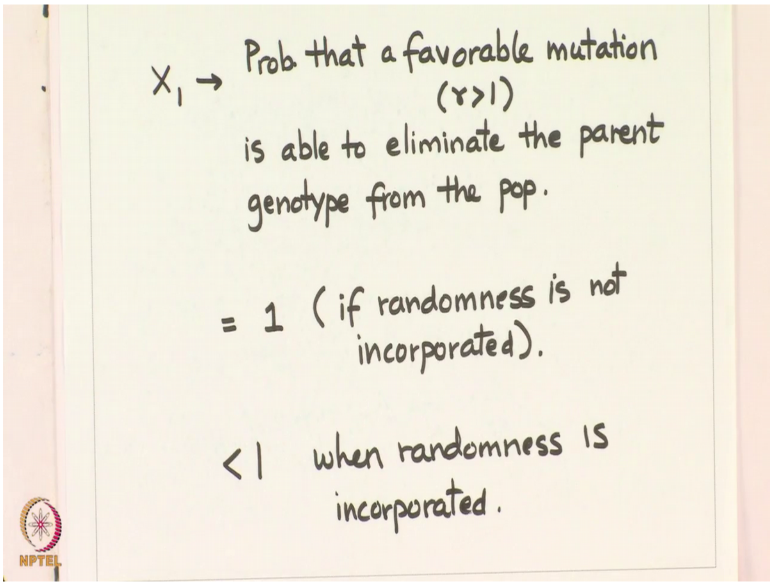

So, the value of X 1 that we are talking about; X 1; I can rewrite is that probability that a favorable mutation. Favorable mutation means r is bigger than 1' the mutant is fitter than the rest of the individuals in the population is able to eliminate the parent genotype from the population and the answer to X 1 is equal to 1, if randomness is not incorporated.

If you go back to the first few lectures of the course, we had discussed the dynamics of system where the relative frequencies of 2 particular genotypes could be anything and starting from their relative frequencies and given their growth rates, we always found out that it is the survival of the fitter genotype that takes place and the less fit genotype is eliminated from the system.

This number is; obviously, going to be less than 1; when randomness is incorporated and what we will do in the next lecture is particularly focus on the aspects associated with how small is this number as compared to 1. Does randomness associated with the system only changed this probability from 1 to 0.99 or does it make a huge difference in terms of the probability associated with survival and the ability of that fitter mutant to eliminate the less fit genotype from the environment that we are interested in. So, we will continue our discussion in regarding development of this expression for X 1 probability in the next lecture.

Thank you.