Introduction to Evolutionary Dynamics
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Lecture - 22
Role of Randomness in Evolution

Hi, let us start our new lecture on Evolutionary Dynamics and today we will start talking about a different aspect associated with revelation of microbial populations which is associated with randomness in the process of replication and evolution, and what role does that play in dictating the dynamics of evolution of a microbial population.

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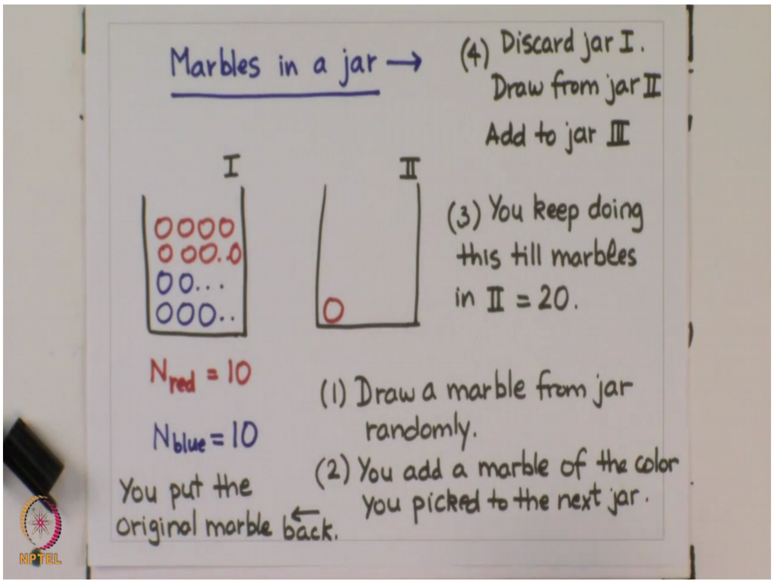

So, we will start our discussion by taking an example not from biology, but an example called marbles in a jar and it is sort of a game and the rules are as follows. Imagine you have a certain jar and you have marbles of 2 different colors present in this jar. Let us say you have some blue marbles and you have some red marbles. Let us say a number of red marbles is equal to 10 and number of blue marbles is the same as the number of red marbles which is equal to 10 and what you do here is, you have another jar which is placed next to it and you put your hand in the original jar and you draw out a marble out of this jar randomly. So, first the rules of the game are that draw a marble from jar randomly and when you do that, there is an equal chance that you are going to draw a red marble or a blue marble because the number of marbles are equal for both colors and there is no reason to expect that marbles of one color are going to be preferentially drawn over the other color. The geometry associated with marbles and everything about them is identical except for the color. So, there is no reason to expect that one color is going to be preferentially drawn as compared to the other one. So, you draw a marble and the chance that you draw a red one is 0.5 and the chance that you draw a blue marble is also equal to 0.5 and what you do after drawing is, you take a look at the color of the marble that you have, that you have picked out and put it back in the jar that you picked it out from, but as you do that, you add a marble of the color that you picked to the next jar and while you do that, you put the original marble back.

So, let me recapture that again. You have 10 red marbles and 10 blue marbles in a jar. What you want to do and marbles are identical to each other in every respect except for their color and you put your hand in this jar and draw out a marble at random. You look at the color of that marble and you put the marble back in the jar from where you picked. Suppose I drew a red marble, then I take a look at its color and put the marble back and I add a red marble to the next jar. So, then because I put the marble that I drew out back in to the jar, the total number of marbles in the original jar remains at 20. So, this number remains at 20 and I keep doing this over and over again. I keep drawing one marble from this pool of 20 marbles and I keep putting a marble of identical or of a color identical to the one that I pick out in every turn and I keep doing this till the numbers of marble in this jar equal 20. So, point one, 2 and the third rule is that you keep doing this. Let say this is jar 1, this is jar 2. You keep doing this till number of marbles in 2 equal 20. So, this one has an identical number of marbles as the first one and you can assume I have drawn the red marbles in at one place and the blue ones, but you can assume that these are well mixed and there is no special preference for one type of marble over the other.

What is personally important to realize is the fact that every time we draw a marble from the first jar, we take a look at its color and we put it back in that jar. That ensures is that the total number of marbles in the first jar never changes and its always equal to 20. So, these are the rules of the game and transition from 20 marbles in jar 1, half red half blue to 20 marbles in jar 2 which would have some number of red and 20 minus that number of blue marbles. We do not know a priori what are those numbers going to be and we keep repeating this. After we are done with this, we start drawing from the jar 2 and put marbles in jar 3 and we forget about the original jar that we started with the jar 1. We do not deal with that anymore.

We start with the 20 marbles in jar 20 and repeat the process. So, the fourth aspect of the game is that once this number of marbles in jar 2 reaches 20 discard jar 1 and draw from jar 2 and using the same rules, add to jar 3 and this process keeps repeating itself over and over again, and we go to higher number of jars as we keep transitioning marbles from one jar to another. So, this game is called marbles in a jar game and the question that we have to ask ourselves is; what is the eventual result of this game. If I want to plot the result or the dynamics of this game in a particular fashion, I would like you to think about what would be the eventual outcome associated with this particular game and then, we will try and answer some questions related to dynamics associated with this game as you transition from jar number I to jar number I plus, one what can we say about the dynamics of that whole process and then, we will talk about that why does this game have where in biology does this game have a parallel and what are the lessons that we can learn from this and apply to biology.

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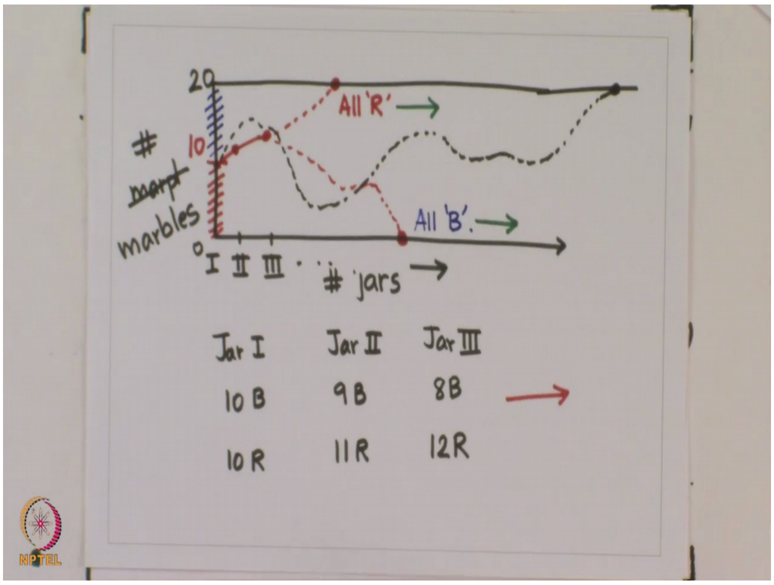

So, first I want to define a representation of results of this game. So, on the y axis I have number of marbles and x axis, here just represents the number of jars that I have used up. I start up with jar 1, then I have jar 2 and 3 and so on and so forth and the way we are going to represent the situation at the I th jar is just by drawing a line. So, the total number of jars in the experiment that I am starting with is equal to 20. I start with 0. This is number of marbles and the way we are going to represent situation at I th jar is by just drawing a line, such as this which tells me and this line is drawn here at 10 and what that tells me here is that everything above this line are blue marbles and everything below this line are red marbles.

So, what this tells me is that at jar number 1, the position was that I had 10 red marbles and 10 blue marbles. Now, suppose I play this game for one round, I transition from jar 1 to jar 2 and I do this exercise of picking a marble and putting an equivalent one in jar 2 and so on and I do that 20 times and I count the number of red ones and the blue marbles that I get in jar 2 and then, I plot this. What would you expect that number to be? You would expect that number to be close to 10 each. If it show if it turns out that in jar 2, you have 10 red and 10 blue that is perfectly possible. You could get 10 each, you could start with 10 each and get 10 each, but it is also perfectly viable, you would not be shocked or you would not be very very surprised if the numbers came out to be 11 blue and 9 red or 9 blue and 11 red. You would not be very surprised if that happened.

So, these minor fluctuations are possible and they can happen as you transition from one jar to another. So, may be in one of the trials of this game in the next round you get 11 red. So, the system moved from 10 red to 11 red. Now, what has happened is that you have in jar 1, you had 10 blue, 10 red in jar 2, you have 9 blue and 11 red. That is just one of the possible outcomes. You could have different outcomes as well. I mean you would not be shocked if you had 8 blue and 12 red.

That is also possible. It is a chance game that we are playing and every time we play the game, we are going to get a different answer. Suppose I do this experiment right here once, I might get in the second jar 10 each, but if I do it again, I might get 11, 9 or 12, 8 or something like that. So, every time I do the experiment, I am going to get a different result associated with the dynamics. So, I moved from 9 to 11, I moved I from 10 each to 9, 11 and in that in this representation I move this red. The number of red marbles can be represented as those below the point and that point has moved from 10 to 11. What happens now as I move from jar 2 to jar 3? When I was moving from jar 1 to jar 2, there was no bias associated with what color I was picking. It was equally likely that I would draw a blue or a red marble, but now when I am moving from jar 2 to jar 3, there is a bias which has been incorporated here. There are more red marbles. The probability of drawing any marble has not changed, any single blue marble is as likely to be picked as any single red marble, but the fact that there are more red marbles now makes more likely that I am going to pick a red marble as compared to a blue marble.

So, chances are that this 9 could become 8 and this could become 12. If that happens, that means from 11 goes up to 12 and this continues for a while and the question that we want to ask ourselves is what is the eventual outcome of this game when no more changes will take place. So, I want you to just pause the video for may be 30 seconds, think about it and then we will continue from there. Think about the fact that what the eventual outcome of this game is that we have. So, defined what is going to happen is that as you move forward in time, as you keep transitioning from one jar to another, you will eventually either reach this point which represents all 20 marbles are red or you will somehow reach this point which means that all red marbles have been eliminated. Number of red marbles are now 0.

So, this corresponds to all red and this corresponds to all blue and no matter how you define this game, these are the only 2 outcomes which are going to ensure that no changes occur after you have reached these positions. So, once you have all red, now you are only drawing from red marbles and there are no blue marbles left in the jar. So, if you are drawing from all red you are going to draw a red marble every single time. That means, you are going to put a red marble in the next jar every single time. There is 0 chance that you are going to add a blue marble because you cannot draw a blue marble because there are no blue marbles left in the previous jar. Hence, it stays like this forever and all blue is the same fate that once you have got rid of all the red marbles in the jar, it stays all blue forever. So, that means these are the only 2 situations possible where the game does not change with time.

It is important to realize that eventually no matter how often you do this experiment or play this game, eventually you will reach one of these 2 states. It could happen at jar number 20, it could happen at jar number 200; it could happen at jar number 2000, but eventually you will reach either all red or all blue. The trajectory is associated with this might vary with every single term. You could have first an increase in red, then you could have decrease, then may be by chance red marbles increase, then it stays somewhat constant for a while, but eventually a chance event is going to drive the system to a point where it is either all red or all blue, but eventually given sufficient times for the game to run, you will either eliminate red marbles or blue marbles. That is the game which is associated with which we call marbles and a game if that is clear, then I would like you to take a guess at what is going to happen in this case.

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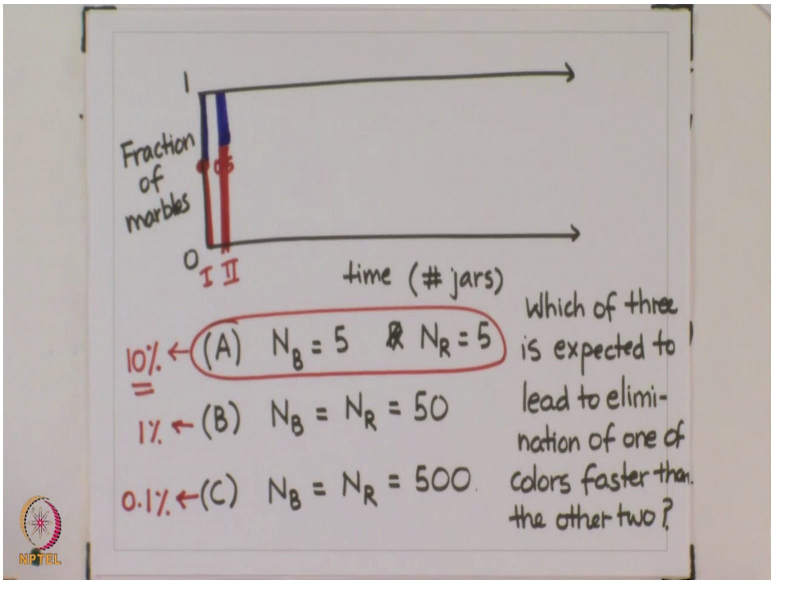

Suppose I am playing the same marbles in a game, marbles in a jar game. These X axis represent time and time is being measured here in number of jars. These represent let say not number of marbles, but fraction of marbles going from 0 to 1 and I am going to put my red marker here which represents that at this point at the start of the game jar number 0 or jar number 1 is what we are starting with a jar number 1. Exactly 50 percent of the marbles are red and 50 percent of the marbles are blue. So, that is what these fractions represent which is just what fraction of marbles belongs to color red and what fraction belong to color blue. If that is the case, then if I am playing this game with three different sizes in terms of number of marbles that I am saying, so in the first trial I am playing with number of blue marbles as 5 number of red marbles is equal to 5.

In the second case I play number of blue marbles is equal to number of red marbles is equal to 50 and in the third case, number of blue marbles equals number of red marbles equals 500. In these three cases, what I want you to do is take a couple of minutes to think about this as answer the following question which of these three is most likely to lead you to a situation, where one of the 2 colors has been eliminated faster than the other two. So, the question that I want you to think about is which of the three is expected to lead to elimination of one of the colors faster than the other 2. So, just take a minute or so and think about this yourselves and try to arrive at an answer from A B and C. So, what should be really apparent to you?

What you should be imagining is playing the game yourselves with 5 marbles, 50 marbles and 500 marbles. If you are playing the game yourselves, it is easy to imagine that with 5 marbles, it is very possible that as you grow from jar number 1 to jar number 2 from 5 each, it goes to 6 4 and as it goes from 5 each to 6 4, what has happened in the terms of change in fraction of marbles, that change of one extra marble. Let us say there is an extra red marble when it comes to the jar number 2. That one extra marble means that this fraction goes up to 0.6 and the blue fraction decreases to 0.4 because there are 6 red and 4 blue marbles now.

What that means is that the transfer of one additional red marble has led to a change in the fraction, total number of fraction marbles by 10 percent. When we are talking of the red marbles, in this scenario if I am dealing with 50 marbles each and the change and in the next generation I have 51 red marbles and 49 blue marbles, the change that has happened is only 1 percent from 50. I have only gone up to 51 percent. So, the change that has happened is 1 percent and the change that has happened here is just 1 out of a 1000 which is 0.1 percent, right. So, the percentage change in terms of frequency associated with marble of each color is much larger when we are dealing with smaller numbers of marbles of each color.

What that means is that this setting with smaller number of marbles is much more likely to go towards one of the colors being eliminated as compared to the other 2 because the relative advantage that red has over blue in this case is only about a percent or so, and given enough time may be the blue marbles can make a comeback and then, try to eliminate red, but the percentage advantage that red has over blue here is 10 percent and it is much harder for blue to make a comeback and sort of into the numbers of red marbles and eventually have all blue and totally eliminated from the population. So, smaller the size, the point being that smaller the size that you are dealing with, easier it is to eliminate one of the 2 colors, in this case as compared to when you are dealing with larger sizes, larger sizes in terms of number of marbles that you have in your game.

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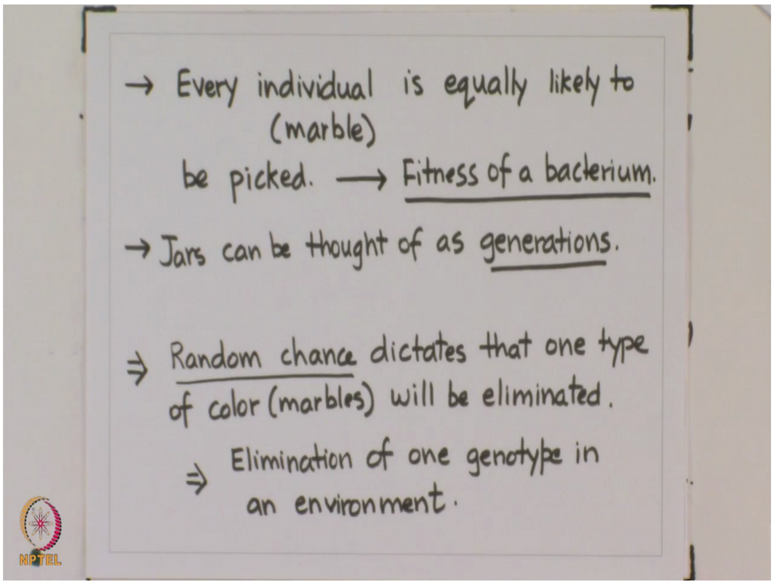

So, that is marbles in a jar game. What is the biological implication of of this game? First of all, the first point you should realize is that we start off with a game where every individual here refers to a marble is equally likely to be picked and the likelihood of being picked can be thought of as equivalent to fitness of an organism because that ensures if I am picking a marble, I am replacing an equivalent marble in the next jar which sort of takes me to the next point that jars can be thought of as generations.

So far in our discussions we have been talking about cases where the population size is held constant which is exactly what marbles in a jar represent. Each jar has a fixed number of marbles associated with it which represent the number of individuals that jar can carry and when I pick an individual randomly from that jar, I am picking an individual for reproduction for giving a progeny which gets passed on to the next generation which is exactly what is happening in marbles in a jar game and chance even dictate which marble dies, which marble propagates the progeny to the next generation, and which marble does not propagate progeny to the next generation.

So, when I am transferring from jar 1 to jar 2 and that transfer is complete because the environment has already reached its carrying capacity equal to 20 marbles, then I forget about the previous generation which has supposedly died and then, it is the turn of jar 1 individuals in jar 1 or generation 1 to propagate their progeny in to the next generation which would be jar 3 in this case, but what is an important insight to this is that while every individual is likely to be picked random chance dictates that one type of color in marbles will be eliminated and the biological implication of this is that in the case of marbles, there was no reason that blue marbles would get picked less often as compared to the red marbles.

The probability associated with picking them was equal, but just by sheer chance we happened to pick red marbles and that led to elimination of blue marbles in our game. In the same way a particular genotype even though it is no less fit than the other genotype that it is surviving in an environment with just because of random chance events can get eliminated from the environment and eventually, you have the other genotype which has no fitness advantage over this. This genotype that we are talking about takes over the entire population and leading to elimination of the other. So, this could lead to the, equivalent could lead to elimination of this random chance of one color of marble or one genotype in an environment as will see in the next few lectures. Random chance plays out has a big impact in dictating the dynamics associated with evolutionary processes and so far we have not talked about them at all.

So far we are saying that one mutant should arise which has a higher fitness than the rest of the population and then, selection acts and that means, that this fitter individual eliminates the rest of the N minus 1 individuals which are at a lower fitness and this fit individual will have in fellow individuals at that higher fitness levels which take over the entire population and low eliminate individuals of lower fitness, but that is not how it always plays out. This first individual that has arisen which is higher in fitness compared to everybody else in the environment has to first overcome this random chance that it might be eliminated just because of the randomness associated with these processes, such as the one which is called such as the one which we just saw in the marbles in a jar game and only after it overcomes that chance of being eliminated, then can fitness effects shall start to dominate over the rest of the population, and that is something that we will be the focus of our discussions in the coming next few lectures.

Thank you.