Evolutionary Dynamics
Supreet Saini
Chemical Engineering
Indian Institute of Technology Bombay
Week 07
Lecture 31

Hi, let's start with the next video. So in the last video, we saw this marbles-in-a-jar game. And in this one, what we are going to try and do is build a parallel between the game we just saw—marbles in a jar—and how an evolutionary process proceeds. So to understand that, we are going to go back to the game and draw one particular manifestation of how it may proceed.

So this is the number of jars in the game. In evolution, I am going to write the corresponding evolution terms in blue and the game that we played in black. This will be the number of generations. On the y-axis in the game, we plotted the number of marbles, which varied from 0 to n. But in evolution, this is going to be the number of individuals. n in this case will be the population size.

In the marbles-in-a-jar game, we started with different colors. Let us draw just a few colors so that we can look at this. Two, three, four. Let us do six. So in the marbles-in-a-jar game, each of these represented marbles of different colors.

In evolution, each of these colors represents a different genotype. So if you are talking about bacteria, then these are all genotypes that are different from each other—six of them—with respect to carrying a mutation at different places in the genome; there could even be more than one mutation. They carry mutations in different places in the genome. And hence, they are non-identical. In the marbles-in-the-jar game, we said that each marble is identical to every other in all respects except color.

So let me write this rule in black. Marbles were identical except in color. Except in color and equally likely to be drawn. In evolution, what that means is that—so if I drew, let us go back to the marbles game— If I drew a red marble, what that meant was that a red marble made it to the next generation or the next jar.

In this case, if I pick a red-colored individual, that red-colored individual produces progeny in the next generation. And since the probability with which I am drawing an individual is random and no individual has a greater chance of being drawn from this population, we say all individuals are equally likely to produce offspring in the next generation. What that also means is that natural selection is absent because natural selection automatically means that some individuals are more likely to make it to the next generation. Their fitnesses are different.

And hence, when I'm talking about representation in the next generation, some individuals are more likely to be represented compared to others. But that's not the case here. So this means that natural selection in this game is absent. So what happens in this case? As was exactly done in the marbles-in-a-jar game, as we move to the next generation, I might get this red color drawn twice.

The orange color might also be drawn twice, and then light blue is drawn once and purple is drawn once. What that means is that this color expanded from 1 to 2, orange also expanded from 1 to 2, green collapsed from 1 to 0, light blue remained the same from 1 to 1, dark blue collapsed from 1 to 0, and purple remained from 1 to 1. What that means is that the structure of the population—the genotypes that were available in the population—changed with time as I transitioned from generation number one to generation number two. The green-colored genotype is lost from the population, and so on and so forth. Some have increased in frequency, and as a result, some have decreased in frequency.

So these changes are taking place. Very importantly, in the absence of natural selection. Hence, we must realize that natural selection is not the only force that brings about evolutionary change. As we move forward in time, let us do a few more manifestations of this. Let us imagine that in the next generation, red increases to 4.

Orange increases to 3. No, it is at 2, 3, 4, 5, 6. Red increases to 4. Orange is at 1. And light blue is also at 1.

So what has happened now is that red has expanded again from 2 to 4. Orange has shrunk from 2 to 1. And blue has remained at 1. And maybe in the next generation, what happens is that only red is picked. We can all imagine playing this game and an outcome like this coming into being.

Maybe it won't take four generations. Maybe it will take a few more generations or a few more jars to happen. But eventually, this will happen. So what has happened here is, From the context of evolution, in a few generations, the following has happened.

In a few generations most of genetic diversity lost. In fact, all colors or all genotypes except one type of genome have been lost from the population. Only one genotype survives. Interestingly, Although only one genotype survives, the identity of that genotype is not constant.

If I play this game again, maybe in the next iteration, the green color will be the one which represents the genotype that takes over the population. So, identity of the surviving genotype. Identity of surviving genotype is different in different trends. And lastly, all of this change is happening in absence of natural selection. What that tells us, these are extremely important manifestations of how evolutionary process might proceed.

What that tells us, the last point, is that natural selection is not the only driving force for evolutionary change. There is some other force of evolution, some other change, some other force which is driving evolutionary processes also. And in this case, that force is drift. So, let us write in that means natural selection not the only force driving evolutionary change. If natural selection was the only force which was driving evolutionary change, then as we proceeded from one generation to the next one, there would be no change in the frequencies of different genotypes or different colors that we see.

Because of natural selection, even though there were different genotypes, since each had an equal chance of being drawn, their fitnesses were exactly the same as each other. So natural selection did not have any variation in fitness to act on. The genotypic variation was there, but it did not manifest as phenotypic or fitness variation for selection to act on. Hence, in the example we discussed, if natural selection was the only force acting, no evolutionary change would take place. And this change that occurred is due to the force of chance events.

So, the force that drove change is called chance, or in evolutionary literature, it is called drift. Remember that in this game, we started with n different genotypes. Every individual in the starting population carried a different genotype. And by the time this game ended, n-1 genotypes had gone extinct. And only one genotype remained.

This genotype, which occupies the entire population—for example, in this case, the red genotype—is the only one that remains in the population. And there is no other genotype remaining in the population. That means the mutations that the red genotype was carrying—let us imagine that this was the red genotype and these were the mutations it carried. These were the unique mutations that the red genotype carried. And now, since we have reached a stage where every individual carries those two mutations in the population, we say that these two mutations

these two mutations have been fixed in the population. Alternatively, they are also referred to as that these mutations, the two mutations in the red genotype are have reached fixation. So we'll say one genotype, this has become fixed in the population. And that's a technical term used in evolution.

Let us go back for a minute here and let us discuss a couple more things. One is that what is the probability that the color that got fixed or the genotype or color that was fixed was let us not say was let us say is yellow or orange is orange. So, we have only started playing the game. So, let us imagine that we do not know what happens in generations 2, 3, 4.

We are just starting from generation 1 and we have 6 individuals each with a different genotype. And what we are asking is that we don't know the outcome of the game that will play out later on as we start playing. But at t equal to 0, when we are at generation 1, the question we are asking is that what is the probability that in this manifestation, this run of the game, orange individual, orange genotype is the one that reaches fixation. And it's impossible to answer because any one of these six colors could win. So we can't really answer that.

But we can also think of it another way. We know if the game starts with these six different colors—five, six—we know that the game will only end when one of these six colors reaches fixation. There is no other color. Five colors have been eliminated. Now, out of those five, five colors need to be eliminated.

What is the chance for any one of these colors to win? Since fitness is not different among individuals or in the marble scheme, each marble is equally likely to be drawn. There is an equal probability that red will go to fixation, an equal probability that orange will go to fixation, and green and blue, and so on. So, there is an equal probability of every one of these genotypes reaching fixation. And there are six of them.

And we know that one of them will reach fixation. Hence, the probability that the orange one will win is simply equal to 1 upon 6. This question is exactly the same as asking: I am going to roll a die. What is the probability that I will see a 4? Now, the possible outcomes are only six, and I am asking what is the probability of seeing one of those six outcomes.

I also know that each one of those 6 outcomes is equally possible. It is the same idea here: I am starting with 6 different genotypes. There are only 6 different outcomes possible in this game, which are green going to fixation, red going to fixation, and so on and so forth. Each one of those colors can reach fixation.

Those are the only six possible outcomes in this game. Starting from that idea, each one of these outcomes is equally likely. Just as I am equally likely to see a 4 as compared to a 3 on a die, it is equally likely that green might go to fixation and equally likely that orange might reach fixation. And so on and so forth. Hence, the probability that orange goes to fixation is 1 in 6.

Let us explore one more idea behind this marbles-in-a-jar analogy of the evolutionary process before we wrap up this lecture. Imagine in one run of this, so now this is generations. And this is population. Population, this goes from 0 to n. In one manifestation of this, I am playing this game where there are only four colors.

This is what I'm starting with, and I'm beginning to play this game. And of course, just as we defined the rules, we only stop when one color takes over. When only one color remains. So if that is the case, then it's going to take a certain amount of time for all the other three colors to get eliminated. Let's imagine that the time taken, in terms of the number of generations for the n-1 colors or genotypes,

to get eliminated, let us call that T bar 1. The bar represents an average because if you play this game, you can very well imagine that in some instances, the other three colors might become extinct in five generations. Sometimes it may take 10 generations. Sometimes it may take 20 generations. So there is not a fixed answer that you would get every time.

But if you play this enough times and take an average, you would get some average generation time. At the end of which, you only have one color left in the population. We will compare this scenario with the same scenario. But the only difference is that now, instead of having three colors at the starting point, I have—let me just draw it with one color.

I in this case I had four genotypes. In this case, I do not have 4 genotypes, but 400 genotypes at generation 1. In this case also, the fate of the population is going to be the same. Diversity is going to be lost. The number of different genotypes remaining after a few generations is going to be fewer than 400 because many will be lost in the first few generations.

At the end of which, the eventual fate of the game is the same that only one genotype is going to remain. If that is the case, then let us say that the average time for elimination of the 399 genomes in this case is equal to T2 bar. Take a 15 second pause and intuitively try to guess that what is which number is greater? Is T1 greater or T2 greater? In one case, we are asking for the population size is only 4.

In the other case, the population size is 400. So, n is equal to 4, n is equal to 400 here. In this case, from n equal to 4, where there are 4 different genotypes, we are asking for the average time that it takes for this to go from 4 genotypes to 1 genotype. And in this case, we are asking the average time to go from 400 genotypes to only 1 genotype, and that is T2 bar. Which one of the two feels greater?

Maybe let us take 10 seconds to think about it. So it should be apparent from this that T2 bar is going to be much bigger compared to T1 bar. What that means is that this intuitive realization brings us to an important point in evolutionary biology: small populations are much more susceptible much more susceptible to evolutionary change by the action of drift or chance compared to large populations.

This tells us that natural selection and drift act differently, and one of the variables which changes the effectiveness of how these two forces act is population size. Chance is much stronger in smaller population sizes compared to larger ones, and as we'll see, natural selection acts much more effectively in larger populations compared to smaller ones. So the goal of this video was to convey that the game we called Marbles in a Jar can be easily extended to this idea of population change because of the action of chance only. It is very important to note that evolutionary change in these two cases—whether it is marbles in a jar or populations—is brought about without the action of natural selection. Because in this game, for instance, every genotype had the same chance of being drawn.

So there was no advantage that one color had over the other when we started out. Each was equally likely. Yet we saw that some of the colors reached extinction very fast, and eventually one of the colors will reach fixation or become fixed in the population. And all of this evolutionary change is happening in the absence of natural selection, only because of chance events. And in the next video, we'll begin a much more formal discussion about how to handle the case where chance and natural selection are both combined together.

What does theory tell us about those ideas? So, in the first part of the course, we discussed only natural selection, which told us that even if one beneficial mutant arose, it would take over the population eventually. That's not true because drift also acts in conjunction with natural selection. Through this marbles-in-a-jar game, we have demonstrated how powerful drift is in bringing about evolutionary change by simply eliminating genotypes, even though there was no natural selection acting. And going forward, in the next video onward, we will combine natural selection and drift and see how they act together.

And we'll start with that analysis in the next video.