Evolutionary Dynamics

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Week 01
Lecture 05

Thank you. Hi, welcome to the fifth video of this course. What we'll discuss now are a few concepts and ideas about natural selection that Darwin did not understand. What we discussed in the last video were three elements of natural selection as Darwin proposed them. And it's quite remarkable that while this was done in the first half of the 19th century, eventually published in 1859, these ideas have remarkably stood the test of time for the last 160 to 170 years.

And these ideas have not only stood the test of time but have actually been strengthened by all the experimental evidence that we have available to us now. There is one idea that Darwin describes, which is called fitness. And fitness is an idea that, in a modern understanding of evolutionary biology, takes a very different meaning compared to what Darwin meant. When Darwin talks about the Origin of Species, it is a remarkably easy book to read. And if you read that, Darwin talks about the fitness of an organism.

And when he talks about fitness, he means how well an organism is able to fit into the environment in which the organism is growing. So there might be a horse that is very well adapted to live in a particular environment. A camel is well adapted to live in a desert, but a horse is not, and so on and so forth. So when Darwin talks about fitness, he talks about the fit that an organism is, how fit an organism is to live in a particular environment.

And the analogy often used is that this is like how well a glove fits your hand, which is the same as how Darwin means that how fit is and what is the fit between an individual and a particular environment in which that individual is living. That has been sort of the historical context in which the word fitness is used. But in a more modern understanding of the word, the word fitness has quantitative meanings. And for sexually reproducing organisms, the word fitness is simply quantified as the number of offspring I leave behind. So if I, as an individual, do not have any offspring, then my fitness is zero.

And it's just as simple as that. So there are these quantitative meanings to the word fitness that have come over time for asexually reproducing organisms. And we'll be spending most of the time in our course discussing actually reproducing organisms. Fitness can be given a quantitative meaning in a variety of contexts. And we'll spend a lot of time describing these contexts as we move forward with the course.

So I will not spend time on it right now. But for sexually reproducing organisms, it's simply the number of offspring that I have. You would have heard that. J.B.S. Haldane once remarked that I will gladly lay down my life to save two siblings.

And what he meant by that is that what is relevant for evolutionary change is how many copies of my gene are allowed to progress to the next generation. So if I am here, then one copy of my genes is there in today's generation because I am carrying it. But I share 50 percent of my genes with my sibling. So if I save two siblings, then statistically speaking, two siblings are carrying it because the genetic identity between two siblings is 50 percent. Then two siblings living is equivalent to one copy of my genes existing in today's generation.

So I am also carrying one copy of my genes. Two siblings of mine are also carrying one copy of my genes. So evolutionarily speaking, it doesn't really matter whether I survive or they survive. My genes have an equal chance of being propagated to the next generation. And that's the idea.

The idea that Haldane is referring to is this one. All right. Before we discuss some examples of natural selection, I want to spend a few minutes discussing ideas which Darwin wasn't very sure about. So while natural selection is an idea that has flourished and we have numerous examples of natural selection acting, there are a few things that Darwin wasn't quite sure about. Remember that the origin of species came in 1859 and

It was in 1859, and all of this is to see how remarkable an intellectual leap this was. We just have to think about the fact that the material basis of heredity, which is the DNA structure, was only published in the year 1953. So Darwin had natural selection figured out 100 years before we actually knew what the structure of DNA looked like. So this was a remarkable intellectual leap. So it's no surprise that he didn't know many details associated with the process. We'll discuss three limitations in Darwin's understanding.

He was aware of two, and he wasn't quite right about the third one. The first one that Darwin did not know, and he knew that this was a problem with the theory, was that he did not know what the mechanism of inheritance was. So the issue is that I, as an individual, have a trait value X naught. And when I have an offspring, the offspring also has, in the next generation, this trait value X naught. How is this information of that value of that trait communicated from one generation to another?

What is the material basis for inheritance? This was a big problem for Darwin. There was no material basis. There were ideas floating around well before Darwin's time. Around the end of the 18th century, the French naturalist Lamarck gave a series of lectures which were published in a book of his in 1809.

And in this book, we've all heard of this Lamarckian inheritance, the idea of the use and disuse of organs. And that's how information gets propagated from one generation to another. The Lamarckian idea was obviously wrong in the context that he was proposing it. And Darwin, in Origin of Species, acknowledges that there is no mechanism which explains how this could act. While the observations were right, there was no mechanistic explanation, and this was a problem.

In the later life of Darwin, he proposed an idea called pangenesis. And we won't spend time on this as a mechanistic explanation of how inheritance might work. This idea was completely wrong, and it was surprisingly Lamarckian in how Darwin proposed that it could work. So this was a big problem that Darwin faced. The second issue was that there was a problem with something called blending inheritance.

Blending inheritance is relevant for sexually reproducing organisms only. And we are talking about the middle of the 19th century. So there isn't really any work going on with asexually reproducing organisms. Bacteria and other microbes as a model system to study evolution came on the scene much, much later. So essentially, his observations are drawn from sexually reproducing organisms.

And the problem that Darwin is faced with, and he does not have any answer to, is the following. What he notices in the wild is that if you look at a wild population and you look at any trait X, and again this is the percentage of the population, then this trait will exhibit some sort of variation. And very often, this is a normal distribution. The normal distribution was also described around the same time. So this will be the distribution that this trait exhibits in this population.

However, this distribution, Darwin notices, remains constant over generations. So this is an empirical observation of him noticing populations in the wild which, year after year, exhibit the same distribution. So this distribution remains constant over time. However, he also knows that blending inheritance is a concept. What is blending inheritance?

Darwin also notices that in a distribution like this, X percentage population. In a distribution like this, if two individuals mate, let us say, because we are talking about sexually reproducing organisms, hence we have biparental inheritance. Let us say if one individual is from this block and the other individual is from this block, and if these two mate, the idea is what will be the offspring's trait value. What will be the offspring's trait value?

And again, through empirical evidence, just by noticing the laws of how this proceeded in actual populations, Darwin knew that, by and large, if two individuals of phenotype X1 and X2 mate with each other, the phenotype of the offspring is best described as X1 plus X2 divided by two, which is just the arithmetic mean of the two parents. Now, if that is the case, and mating is random in this population, then this idea is blending inheritance, where the trait of the offspring is a blend between the two parents who mated to produce this offspring. So that's blending inheritance. If you add to blending inheritance the idea that mating is random in this population, which means this individual could mate with this individual from this block, two individuals from this block could mate with each other, or this individual from this block could mate with this individual, and so on and so forth.

Mating is completely random. If mating is completely random and blending inheritance operates like this, then statistically, it's very easy to show that in the next generation, this distribution will look something like this. So this is, let's say, generation G1. In generation G2, this distribution would look something like this. Let me just bring this down.

So if you compare these two distributions, what you will notice is that they have the same mean. If I take the arithmetic mean of this distribution and this distribution, that arithmetic mean is this X naught. So, they have the same mean. However, the spread around the mean is much greater here. The spread is much narrower here.

It is almost like coming from G1 to G2. The population has become concentrated at the mean phenotype. The spread around the mean is much smaller in the G2 generation. As a result of that, the standard deviation around the mean in G2 is the standard deviation in G1 divided by 2. And you can imagine what the consequences of this are.

If this is allowed to propagate for more and more generations, then what that means is that these two rules will still hold, which means the mean of the population will remain at the value that we started with. But the standard deviation associated with the trait value in this population just keeps on shrinking with time. And if that shrinking happens as populations go through generations, what that means is that variation in the population is reducing. That is a natural consequence of these two rules: one, there is blending inheritance. Second, that this mating is random.

If these two ideas hold, then the natural consequence is that variation is reducing. And from empirical evidence, Darwin knew that this is right and this is also observed in nature. So, these two are right. So, now you have a conflicting idea that variation is reducing, and this idea has to be balanced with this contradictory observation that variation actually remains constant with generations.

So, while if I am looking at individuals mating, I see that blending happens. If a particular pair mates, the offspring is a blend of the two. I also see that mating is random. So, that is at an individual level. These two hold.

However, if I look at a statistical distribution of population through generations, then I know that the distribution in the population is maintained. Variation is not lost. But these two, if true, mean that variation should be lost. So Darwin was at a loss to explain, in the scenario where these two rules are active, what is happening to the population that despite variation getting reduced, variation remains constant, which means that going from these rules to maintaining the same distributions, there must be mechanisms involved. There must exist these mechanisms which maintain, which add to the variation so that overall variation is not lost from the population.

As I go through generations, the overall variation remains at the level that we started with. There is no substantial change in it. And how all of this is happening, how these two rules have to be combined together with this particular observation was also a problem that Darwin didn't really have an answer to. The third idea has to deal with What type of distribution, what type of variation in a population is responsible for evolutionary change?

And this debate was a huge one in the decades that came after the publication of Origin of Species. On one hand, Origin of Species was published in 1859, and this was a constant source of debate for the next 50 years until it was resolved in the 1910s by a classical paper published by Ronald Fisher, an English statistician. And the problem is as follows. There is one argument which says that, okay, we started with the assumption that for a trait X, and if you look at the percentage population again, this variation will exist in a population. There was one argument,

a line of argument that this change, this continuous change, is sufficient for evolutionary change. Like in the example that we studied in the previous lecture, the argument goes that if these individuals are more fit, then they will produce more offspring compared to these individuals. And as a result, as we move from generation to generation, evolutionary change will take place, ensuring that the population moves in this particular direction. These phenotypes are lost from the population, and this phenotype eventually wins in the population. It seems clear now, but at the time, this was actually not clear at all.

On the other side of the debate was the argument that this is not true because the variation that exists on the left, the variation that we are talking of, this continuous variation, will be lost because of blending. What we saw on the previous slide. This will be lost because of blending. Hence, this sort of continuous variation, because this continuous variation will be lost because of blending, is irrelevant as far as evolutionary change is concerned. So, the idea here is that we have this population and there is this distribution, and blending will ensure that this distribution keeps on shrinking from one generation to another.

So, standard deviation keeps reducing by half, and very soon, because of blending and random meeting, as we saw in the previous slide, this distribution will shrink and keep on shrinking, and this variation will be lost as a result. And because blending will make sure that this variation is lost, this variation is not the type of variation that is responsible for evolutionary change. So, people who argued this particular explanation. To them, evolutionarily, the relevant explanation. Change that we must have is something like this.

That you have a population which exhibits continuous variation, but this change is really irrelevant because blending will make sure that all of this collapses. For evolutionary change, you must have one or very few individuals who come into the population. We'll discuss mechanisms how. Who come into the population, which exhibit a value that is far, far from the population's distribution. And only this type of variation, discontinuous variation,

because it exists in discontinuity with the rest of the population, only this discontinuous variation is relevant for evolutionary change. So, we have these two competing ideas for a good 50 years about what type of variation is responsible for evolutionary change. So, something as innocuous as what we started with in the previous lecture, that variation must exist, was actually a huge contentious issue for half a century as to. The subtlety associated with the argument is that not any variation would do. What is the nature of that variation that must exist for evolutionary change to take place?

So, of course, Darwin was aware of these issues, and there is a lot of literature and discussion that happened around these ideas. But primarily, this particular debate was there because all of this debate was happening in the absence of the knowledge of the mechanistic issues as to what are the molecules involved in the transmission of information from one generation to another and so on and so forth. So that's three ideas about which Darwin wasn't quite right. The other Darwin wasn't quite sure. The one issue that Darwin wasn't quite right about was simply estimating the time it would take for evolutionary change to take place.

According to Darwin, evolution was a really, really slow process. And it would be very hard for a human being to estimate, to sort of actually see evolutionary change play out in his or her lifetime. So this takes so evolutionary timescale is much, much greater than the time that a human life is. And hence, he said that it would be hard for us to do experiments or study evolutionary change within a lifetime just because of the time constants involved with the evolutionary process. And this is one idea where I think Darwin has been proved wrong.

With the amount of evidence that we have for evolutionary change taking place, we now know that evolutionary change can be fairly rapid. And the COVID in the past few years is actually a great example because we started with a viral sequence that the pandemic started with. But what are the variants that are prevalent now in the population or even just a few months after the pandemic started? Those variants had changed from the ancestral population, and the virus had exhibited evolutionary change. And human populations also responded to these ideas.

And there are a lot of human genetic studies as to which populations were more susceptible, which populations were less susceptible to an infection via COVID, and so on and so forth. So evolutionary change can be very, very rapid. Another example of rapid evolutionary change is antibiotic resistance that has evolved. When antibiotics were first discovered in the first half of the 20th century, They were considered a great boon.

In fact, industrial production of antibiotics really only started with World War Two, where the Allied forces had soldiers getting injured on the field and who were then prone to infections. And these infections would become systemic and lead to death. And antibiotics were just a great tool that helped ward off those infections. And at the time, what was thought was that there are these disease-causing agents that we are fighting against. And we now have access to these fantastic chemicals, antibiotics, that we can just pop in, and we can control their growth rates and where they grow.

They don't grow, and so on and so forth. What was not realized at the time was how quickly bacteria would adapt to the environment that they were asked to live in now and develop resistance against these antibiotics. And today we know there are many, many strains of pathogenic bacteria that are resistant to antibiotics. Numerous antibiotics that we clinically use. And this evolution of antibiotic resistance has been a fairly rapid process.

And in one of the first experiments that we will study in the course in a couple of weeks' time, will be precisely this: how can we study the evolution of resistance in a lab setting? And the time constants associated with that process are remarkably fast. All it takes is a couple of weeks for a bacterial species to become a thousand-fold more resistant to an antibiotic than its ancestor was. And two weeks is all it takes for that process to happen.

We will continue our discussion with some examples of natural selection. Thank you.