

An Introduction to Evolutionary Biology

Prof. Sutirth Dey

Biology Department, Population Biology Lab

Indian Institute of Science Education and Research (IISER) Pune

Week 1 Lecture 5

Beyond Darwinism: Modern Synthesis_EES

Hi, welcome back. So, in our last discussion, we looked at Darwin's theory and Darwin's logic. And I said that the reaction to his theory was rather electrifying. And although Darwin's theory was able to explain a large number of things, There are also several things that Darwin's theory cannot explain. And very interestingly, Darwin himself, you know, discusses a large number of these things in his book. And essentially talks about the various ways in which his theory could fail.

Various kinds of observations, which, if true, would lead to a failure of his theory. Again, this is a shining example of how good science is to be done. Because nowadays most people, when they write papers, They do not really talk about, you know, what the ways are in which their theory can be wrong. Most people are like, "Here is my theory, and this is the best thing since sliced bread.

But that is not exactly how science is done. For science, one always needs to take into account the possibility that one's theory might be wrong; therefore, One might actually, one should perhaps pay more attention to what will happen. And in how many ways can your theory be wrong? So, anyway, let us look at what the major objections to Darwin's theory are. And as I said, many of these were part of his own book. Now, the point to be noted is that I will only deal with a few of these objections right now.

That is because right now we are more, you know, looking at the history of the subject. We will come back to a few other objections in some of the later modules. Many of the objections that we are discussing regarding Darwin were actually resolved in his later works. And some of the others were resolved much later. However, again there is not anything over here that, to the best of my knowledge, remains unresolved even today.

So, there are objections to Darwin's theory. The first thing to remember is that Darwin takes variation across traits as an observation. In other words, he takes it as a given. But then, what causes this variation in traits within a population? Why is it that some people say they are 6 feet tall, others are 5 feet tall, and others, you know, everything else in between? Now, unfortunately, Darwin, at that point in time, had no real answer to this question. However, today, when we have understood a lot about genes and how they express, How environments affect that expression, etcetera, etcetera; we actually have a lot more information.

I cannot really say that we know everything there is to know about it. But definitely, we know a lot more than Darwin knew about it. This was a major one. Darwin explicitly said that evolution is a very, very slow process. Now, he also said that starting from just one or two life forms, the entire biodiversity is both extinct.

And you know existing species which together represent millions and millions of species, He assumes that all this biodiversity has been generated through that slow process. So, then obviously the question is whether we had enough time for this to happen? Remember when all this was being discussed, people thought that the Earth was perhaps a few thousand. or at most you know a few billion years old. However, Darwin really did not believe that. He actually believed that the Earth was a few billion years old.

However, during the same time, there was this famous physicist, Lord Kelvin. Who did some experiments, basically measuring the temperature at the surface of the Earth? And based on what was known about how Earth cools, he estimated that Earth was much, much younger. He basically estimated that Earth was a few million years old, and

therefore his point was that Look, there could not have been sufficient time spent on the surface of the Earth. For all that biodiversity to arise through that slower process. As I said, Darwin did not really believe this, but then Darwin was not a physicist.

So, he did not really have any way to counter this argument. However, later, much later, people figured out the flaw in, you know, Lord Kelvin's arguments. And more importantly, the process of radioactive dating was invented, and once that happened. And people got good estimates of the age of the Earth; it was clear that Earth actually is a pretty ancient planet. Definitely a few billion years, and therefore, people thought that perhaps the time component was working out.

There was sufficient time. Of course, today we understand that. You know Darwin was not entirely correct in thinking that evolution is a very slow process. There are many times when evolution can be extremely fast. Species can form over just one generation, and so on and so forth.

Some of these we are going to talk about in the next module when we discuss the evidence for evolution. But at least you know, even if it is slow. The Earth is pretty ancient; that is the main point I am trying to convey to you here. The next objection to Darwin's theory was why there are major gaps in the fossil record. Now, why is that an objection? Remember, Darwin says that species change very slowly.

All species come from pre-existing species, which basically means that If you are finding two species today, there have to be intermediate forms between the two species. So for example suppose you say that human beings have arisen from ape-like ancestors, Then you need to be able to find fossils, which are, or maybe other existing organisms. which are intermediates between humans and ape-like ancestors. You cannot have a one step you know, change so Darwin said going from ape to humans. So if that is the case, remember this is what we are talking about 170 years back.

At that point in time, we did not really have fossil records that were very complete. We

essentially had something here and then something else. Which is, you know, quite a bit different from the previous one, and so on. So how does the fact that fossil records are extremely, you know, discontinuous? Square with Darwin's claim that things are happening continuously and that everything is arising from a pre-existing form. So Darwin made two arguments in his book.

His first argument is that, look, we have not really found all the fossils that are there to be found. So please, please, please go around and start looking for more fossils. Incidentally, this argument proved to be correct, and today, obviously, we do not have continuous, you know. Every single intermediate form for any divergence. But today, the fossil records are much more complete than in Darwin's time, which again suggests that, you know, in many cases, the intermediates that were hypothesized were actually found, you know, when people looked for them.

The second reason that Darwin gave is that fossilization is a very, very difficult process. There are so many things that need to happen in precisely the correct way before you obtain a fossil. So, normally, whenever an organism dies, what happens? It gets eaten by other organisms, and it gets decomposed by the bacteria, right? Therefore, a vast majority of the organisms that die never really form fossils. So, Darwin argued that only those organisms that died but were not decomposed were covered up in a certain way. And then the correct conditions of temperature, covering, and pressure, etc., happened. Only they became fossilized, and therefore, it is no wonder that we do not really have fossils for all the intermediate forms. Again, this is a pretty decent argument. And nobody has really questioned this part, that fossilization is indeed a very difficult and, you know, special process. Then, I mean, there are, as I said, many other objections. But then came what is one of the most critical objections, which is related to the mechanism of inheritance.

Remember, for natural selection to happen, it is crucial that organisms are able to pass their traits to their offspring. So, if a tall parent is not able to pass the trait of tallness at least to some degree to their baby, then natural selection cannot happen. So, that means that the entire process of inheritance is central to the process of natural selection;

therefore, Obviously, everybody asked how inheritance happens. Now, here things really became problematic because Darwin, although initially favoring the inheritance of acquired traits, But you know, again, he was aware of the fact that that does not really work. So, he came up with what is known as a blending theory of inheritance which basically meant that you know of organisms for every trait They passed some part of their body to, you know, the germ cells. And the sperm and the ova, and then in the offspring, you know these traits get blended. So, you have, let us say, a tall mother and, let us say, a short father; then the traits are going to get blended. and the offspring is going to be intermediate between the heights of the father and the mother. Offspring's height is going to be intermediate.

However, this is something that was immediately objected to by a very brilliant engineer named Fleming Jenkins. This is the person who invented cable cars, but he was also a very well-respected scientist. And he argued that, look, suppose you have a tall dad or a tall mom and a short dad or a short mom, Then if the organism, the offspring, is intermediate between the two, Then obviously its value is going to be somewhere in the middle. Now in the next generation, this organism is supposed to breed with somebody else again. And again, it comes to something in the middle in the next generation.

Then, over time, there is going to be a regression towards the mean. In other words, over time, all the variation that is present in the population is going to disappear. And everybody is going to go toward some kind of mean value over all the extremes. You know to go towards a mean value rather than going towards an extreme value. If that happens, then all the variation in the population is essentially going to get lost.

If every trait is getting blended every generation. And if there is no variation left in the population, then natural selection as a process will cease to operate. Now, Darwin actually had no answer to this particular criticism, and this was a very, very strong criticism. So if you look at the reactions to what Darwin spoke, there was a lot of diversity in those reactions. There were many people who focused on all the things that Darwin's theory could explain and were convinced that evolution through natural

selection was a big deal. There were many people who accepted that species can change. Remember, this is a departure from the original; you know God created everything in its present formulation. However, not everybody accepted that species would necessarily have to change slowly. There were lots of people who thought that, yeah, changes happened, but they can happen extremely fast—the so-called saltation.

And the most important bit in Darwin's theory, which is the importance of natural selection, is what people really contested. Many people thought that natural selection was perhaps not as important as you know. Darwin is making it out to be saltationism, which is, you know, sudden change within one generation from one form to another. This was, for many people, a much better alternative to the gradual evolution that Darwin was talking about. And finally, the religious reaction to this entire situation was also extremely varied.

There were some people who essentially did not really see this as an affront to their religion. But there were a lot of other people who were very perturbed. A lot of the perturbation was coming explicitly from Darwin's assertion that humans might have an animal origin. God did not really create humans as something special.

God did not create humans in His own image. Humans are just well basically another ape-like creature. Very interestingly, Carolus Linnaeus, when he created his original classification, he had explicitly recognized that human beings were very close to the apes. So, in that sense, you know Darwin was not the first person to think that humans are perhaps just modified apes, but yeah. So, finally, anyway, Carolus Linnaeus ended up creating a special genus called Homo for human beings. Although you know, if you look at it properly, there was not much reason for him to create that thing.

Basically, it was created more to placate the, you know, people. With a religious bent of mind, human beings have to be a special creation. So, anyway, this particular set of human beings who were worried about, you know, the ape origins of humans. They actually had a field day with Darwin, and you know caricatures like this were extremely

common in newspapers. In books and in all kinds of places for several years after Darwin's theory.

Now, as I said, a crucial piece of this entire puzzle was the mechanism of inheritance. Without that, it was very difficult to establish natural selection as a proper mechanism. And this actually gets resolved by the work of this man, Gregor Johann Mendel, and his laws of inheritance. Now Mendel proposes his theory in a paper read in 1865. His paper was published in 1866, 16 years before Darwin's death.

And yet, there is no evidence to believe that Darwin ever came to know of Mendel's work during his lifetime. If Darwin had come to know of Mendel's work, then given how sharp he was, Given how deeply he had thought about it, he would most probably have figured out that You know this is the missing piece for his work, but that didn't happen. So this is one of those great "what ifs" of, you know, the history of science. As it happened, Mendel's work was largely ignored by the scientific community until 1900. When two people, Hugo de Vries and Carl Correns, independently rediscovered these principles.

And when they were trying to publish it, they realized that Mendel had already talked about these principles. And therefore, they published their papers but explicitly acknowledged Mendel as the person who thought of it first. Of course, Mendel's inheritance laws have many components. But the major component that was important in this context was the fact that what Mendel called factors, today we call genes. Mendel's theory explicitly said that the factors do not blend; the factors pass as they are as discrete units across generations.

Now the moment Mendel says that, it means that the traits do not blend in their offspring. And if they do not blend into the offspring, then variation is going to be maintained. Of course, selection is going to, you know, reduce variation; that is a different ball game. But by itself, the process of inheritance is not going to kill the variation. And you know this realization that this is solving a huge problem in Darwin's theory.

This realization actually completely revitalized you know the work on Darwin and his work. So prior to this, between 1859 and 1900, as I pointed out, you know. There were lots of opposition to natural selection as a major mechanism of evolution. But after 1900, things became much better, and Between 1900 and 1950, an enormous amount of work occurred in the context of evolutionary biology. A lot of this work happened in the domain of mathematics, or rather, theoretical evolutionary biology.

Again, many, many names; I am just quoting three of the most famous. This is Ronald Fisher, this is J.B.S. Haldane, and this is Sewall Wright. And the work of these people and hundreds of people around them. Established a very formal mathematical basis for the process of evolution. As a matter of fact, amongst all the sub-disciplines of biology, Evolution is perhaps one of the most highly mathematized fields, along with neurobiology, perhaps. So, people were able to show and predict so many things just based on the theory alone. Now, while all this stuff was happening in the realm of theory, An enormous amount of work also happened in the context of experiments both in the field and in the laboratory.

Again, hundreds and hundreds of names, and these are, you know, people making great contributions. I have just chosen three people. So, you know that this on the left-hand side is J. Ledyard Stebbins. So he actually ended up doing a lot of work on the evolution of plants. In the middle, you have G. G. Simpson. So this person was a paleontologist, and he did a lot of work on fossils. He was an expert on mammals, but his primary focus was the rate of evolution, which is what he contributed to. And this person we have already met, this is Theodosius Dobzhansky, and he did a lot of work on *Drosophila*. But he also did some very important work on natural populations as well. and played a major role in crystallizing the theory as we are going to see.

So, all this stuff that happened between 1900 and, say, 1950 or so, These came out in the form of books, these came out in the form of papers, and in 1942, There was a very famous book written called "Evolution: The Modern Synthesis" by a person named Julian Huxley. So, around that time, you know this book is the shining example, but this is not

the only book that contributes to the crystallization. There were at least 5 or 6 other major books that are also recognized as being very important. So, there was a synthesis of Darwin's insights combined with What was derived from the geneticists, the theoreticians, the experimentalists, the paleontologists, and the ecologists? Pretty much everybody in science, except to some extent the embryologists, is what we today call a developmental biologist. Somehow, their points of view did not get properly integrated into the whole picture but the insights from all the other fields were incorporated, and you had what is known as the modern synthesis. which is essentially a bunch of you know interconnected statements that talk about how evolution happens. As I pointed out, although this name comes from a particular book by Julian Huxley, In reality, the insights are coming from the work of hundreds, if not thousands, of people roughly between that period. Now, what you study in textbooks is what we are going to talk about, you know. Over this course, primarily, is this modern synthesis with some minor changes here and there.

Of course, what I talked about is from the 1940s to the 1950s, but roughly around the 1950s. And later is when molecular biology and biochemistry start making enormous amounts of advances; superb work happens. So, for example, you know this is Frederick Sanger; he figured out how to sequence proteins and DNA. And the first thing that he does is he actually ends up doing it for multiple species and studying these species. and tries to see what kind of patterns he gets; essentially, he gets similar patterns to those that the anatomists got.

If you have species that, let us say, have very similar form and function to each other. Then their proteins and their DNA were often very close to each other, very similar to each other. Similarly, there was a man called Charles Sibley. He realized that you can actually use DNA and protein data to do taxonomy. So, until that point, taxonomy was primarily based on morphological features.

But now he said, "Let us look at the molecular data and see what kind of taxonomy we can do," one of the pioneers in the field. And then, of course, you have Linus Pauling and

Emily Zuckerkandl. So they were the ones who proposed that if you have, you know, differences in protein sequences, Then, assuming that these differences are occurring at a constant rate, You can actually use the amount of difference to predict when exactly these species diverge from each other. So, in other words, when was the common ancestor from which the divergence happened? And then, of course, you know that this kind of data can then be verified with fossil data to see whether it is making sense or not and spiral alert it does. Most of the time, there is a pretty reasonable match. So, over the last 75 years, which means, you know, after the modern synthesis. An outstanding amount of information has been generated related to. DNA sequence, protein sequence, molecular genetics, molecular taxonomy, evolutionary ecology.

Basically, every single sub-area of biology. And the interesting information is that, because of this, the modern synthesis itself has undergone several modifications. So what was proposed in the 1940s to 50s is not the precise form of the modern synthesis that we evolutionary biologists use today. However, this is the important bit: there has been no major structural change. Certain new forces have been added.

So, for example, you know Darwin thought natural selection was the force. By the time the modern synthesis came in, People realized that natural selection is one of the four major forces of evolutionary biology. Today, people are asking if there are some other forces that also need to be considered. Similarly, you know, in terms of variation, all this information about DNA sequences, protein sequences, molecular genetics, etc. that has actually led us to a lot of understanding about how variation is generated, how the variation is transmitted. But the overall picture of how evolution is supposed to operate really has not changed, and more importantly, There is no new information among the, you know, petabytes and petabytes of information that has been generated over the last 75 years, which is inconsistent with the existing theory. When I said existing theory, I meant modern synthesis in its present form. So, however, in spite of this, in the early 2000s, there were some evolutionary biologists. Who started asking the question, "What is the modern synthesis?" with some little modifications here and there? Is it enough to explain all the data that we have, or do we need a major overhaul of this synthesis? And this

program, you know, of a potential overhaul is what they called the extended synthesis.

And this generally is, you know, rooted or directed to this very famous book. edited by, you know, Massimo Pigliucci and Gerd B. Müller, which came out, I think, in 2016, if I am not mistaken. So, there is right now a lot of debate in the field about whether incremental changes are enough. A totally new theory called the extended evolutionary synthesis is needed. Now please understand one thing: this debate is not about whether evolution happened or not.

Both sides of this are populated by people who accept that evolution has happened. All that the debate is trying to do is ask whether we need to change the way we look at evolution or not. And if yes, by how much? Some people are saying that the modern synthesis suggests the change is going to be very little. The other guys are saying that no, no, no, the change might have to be pretty large, and that is it. It is only about the magnitude of the change. And to the best of our understanding, until now, whatever changes have been proposed are not large in magnitude.

They are relatively small in magnitude, but that is where the debate is. So, overall, this time in, you know. The field of evolutionary biology is perhaps a very exciting time to be an evolutionary biologist. Because, as I showed you, you know evolution right now encompasses the entire science of biology, and therefore, Theories of evolution talk about it requiring one to have an overall view. Overall, you know how to hold on to the entire subject in a way that no single sub-discipline of biology allows you to do. So, if that is the case, what is it that makes EES so controversial? If both sides are in agreement over the broad strokes, why should one be worried? Or why should there be a debate that really needs to be? And more importantly, you know if we are saying that most of the things have already been answered.

Then does that mean there are no unanswered questions in evolutionary biology? Obviously not. There are lots of questions that remain to be answered, but what are those questions? So, we will invite a prominent evolutionary biologist from India to discuss the

two issues that I have flagged above. But before we go there, we have unfinished business. What is our unfinished business? Remember that in the very first discussion when we were talking about the alien. We said that there are two questions that need to be resolved, and I said that in order to resolve those two questions, First, we need to understand how exactly you know the history of evolutionary thought.

The evolution of evolutionary thought happened. So, now that we have done that, I know I would not say that we have done a very thorough job. but we have an overall picture of how evolutionary thought evolved, and with that information, Now we will go back to our two questions, but that will happen in our next discussion.