

An Introduction to Evolutionary Biology

Prof. Sutirth Dey

Biology Department, Population Biology Lab

Indian Institute of Science Education and Research (IISER) Pune

Week 9 Lecture 43

Evolution of reproductive isolation

Hi, so in our last discussion, we looked at the various ways in which reproductive isolation can occur between groups or species. And then we asked the question of how exactly these mechanisms of reproductive isolation can evolve. Now, why is that a big question? That is a big question because reproductive isolation requires that some individuals either do not mate at all or only mate under certain conditions. If they mate, the offspring are going to be infertile or the offspring are going to have a lesser amount of fitness. Now, understand that when such a thing happens, Then the fitness of both the individuals who are, you know, taking part in reproduction, as well as the entire population, drops. Now, all else being equal, organisms are freely exchanging genes and selection when it is trying to maximize the fitness of the individuals, Then such a situation, or rather anything that reduces the fitness of the population or the individual, is not going to be promoted. So, if that is the case, how exactly will reproductive isolation mechanisms evolve? So, that is not a very easy question and frankly speaking the answer is that somehow the ability to exchange genes have to be reduced. Once it starts getting reduced, then all kinds of other mechanisms can happen, but at the first step there has to be some reduction in the ability to exchange genes. And the simplest way by which it happens is some kind of geographical isolation.

Geographic isolation can happen in multiple ways. The most well-studied one is what is

known as the allopatric mode of speciation. Now, what is that? Now, allopatric: the word "allo" means other, and "patric" refers to "pater," which basically means homeland. So, it is like another homeland. So, this is the case where the formation of a new species occurs.

Because a single population somehow gets subdivided into two or more geographically isolated populations. Now, how exactly can that happen? Now, it can happen in two major ways: either if you have what is known as vicariance or if you have dispersal. So, what are these things? So, vicariance is the scenario in which you have a population. So, let us look at this example. Suppose you have an original population and somehow a geographical barrier rises in the way.

Somewhere inside the population, within the range of that population and the geographical barrier, it can be. in the form of a mountain range, a river, or some kind of upliftment of land, or you know, somehow the land going down and forming some kind of valley, or whatever, or, you know, in many cases, sea level changes. So, when you have a geographical barrier coming up like this, Then populations that are on either side of the geographical barrier are no longer able to exchange genes. And when that happens, the two habitats might end up becoming slightly different. Selection might lead to different outcomes; there can be different kinds of mutations that might arise in these populations.

Ultimately, all of this will lead to reproductive isolation such that at some point, one species will separate. You will end up with two different species. So, you know there are quite a few well known examples of vicariates, I am just giving you one. So, you know that you have North America and then you have South America. These two continents are connected by a land bridge, which is known as the Isthmus of Panama.

That is what I am showing you over there. Now, it turns out that the isthmus of Panama did not exist at all times. So, there was a time when the Atlantic Ocean and the Pacific Ocean were actually connected in that place. And then about 3 million years or so ago,

the isthmus of Panama slowly rose from, you know, below the sea. And when that happened, when it formed a landmass, then the Atlantic and the Pacific Oceans got separated from each other.

As a result of that, the environment on both sides actually changed. So, there were differences in terms of tidal fluctuations, water temperature, and the clarity of the water. How much salinity was there on the two sides? All these factors varied across the two sides. So, obviously, the species that were previously continuously distributed on both sides of the isthmus, Now they have become separated, and they have started evolving differently. And this has actually been observed in multiple taxa.

But I am going to show you in the context of a taxon where it has been studied very well. These are known as snapping shrimps. The genus is *Alpheus*. Now, this is a very interesting organism. So, you can see that one limb of it is highly enlarged.

So, what it does is it has a mechanism over there by which it is able to compress air and then release it at a very high pressure. And as a result, it is almost like a bullet of water that goes and strikes, you know, prey and stuns it. It is not a bullet; it is more like a pressure wave that goes and strikes the prey and stuns it. And in the process, there is a massive snapping sound that is created, which is why these are known as snapping shrimps. Now, it turns out that there are many species of this particular thing, but there are seven pairs of sister species.

So, what are sister species? Sister species are species that are very, very closely related to each other. The most closely related species to each other in some senses. And there are seven such pairs on either side of the Atlantic and Pacific. And it turns out that if you look at these sister species at the genetic level, there is quite a bit of similarity. But because of this vicariance event, they have ended up becoming reproductively isolated from each other.

Even if you bring them together, and you know that in nature or under laboratory

conditions they are not going to be able to mate. So, this is one way of achieving allopatric speciation. The other way of achieving allopatric speciation is through dispersal. So, what is dispersal? So, basically, when a small group of individuals migrates to a new isolated habitat, they effectively creating a new geographically separated population is when you have the dispersal mode of allopatric speciation. So, for example, when you have, let us say, an island being colonized by some organisms from somewhere.

So, this is exactly similar to the vicariance mode that we saw, except that instead of having a specific geographical barrier. You know, in separating the two subpopulations, the barrier is essentially distance. Just the fact that they are, you know, quite a bit away from each other—that is it. Now, again, there are a few very well-known examples of this, and the one that I am going to share with you is related to an island. You know, somewhere that is not an island, it is actually a group of islands about 1100 kilometers west of South America.

I am sure you can recognize which one is about the famous Galapagos Islands. So, this is where Darwin went and saw his tortoises and, more importantly, the finches. So, if you look at the Galapagos finches, there are about 18 species of finches. They are also known as Darwin's finches, and I am showing you just four of those 18 species over here. And what is more important is the fact that all of them are supposed to have descended from just one migration event which happened about 1 or 2 million years ago. And that migration event happened from the mainland, and after that, there were multiple speciation events. But the main thing that I am talking about is the fact that. The original thing was a dispersal event that subsequently led to all these 18 species or so. Now, instead of giving you the details myself, I am going to request that you watch a particular video.

This video, again, is one of the, you know, HHMI videos. This is about the work of Peter and Rosemary Grant, who spent more than 50 years studying these birds. In you know their natural habitat on the Galapagos Islands. So, this is a very, very famous piece of

work. As a matter of fact, this is one of the most well-known pieces of modern work in evolutionary biology.

I strongly recommend that you look at it not only to understand how new species arise, how the Galapagos finches arose, but also how one can visualize the effects of selection in nature and see the selection work right in front of one's eyes. And after that, I also want you to look at one more video, which is this one set in the Galapagos Islands. The grants were able to document the birth of a new species, interestingly, again due to a migration event. And so these were the so-called big birds, and I do not think they have named the species yet, but, What happened was that one bird migrated to the Galapagos Islands, and it had a very different song. Therefore, it should not have been recognized by the existing species over there, but somehow there was freak female on the Galapagos island female finch which ended up mating with this migrant finch and Somehow, all the babies that were produced were fertile. Then they have ended up establishing a new species, a new population. So, have a look at this particular link that I am showing you at the bottom. Also, look at the, you know, there is a video over there; see that video, but there is also a write-up over there. It describes in very simple language what exactly these people saw; absolutely brilliant stuff.

So that was about the dispersal mode of allopatric speciation. Now the question is how exactly allopatry leads to reproductive isolation, and this is, you know, roughly speaking, what happens. Once the subpopulations get isolated, gene flow ceases. There is no more migration, and after that, these separated populations start diverging. Why do they diverge? They diverge because of a bunch of things that can happen together or, you know, separately.

So, first of all, the environments are slightly different, as I showed you in the case of the isthmus of Panama, you know, arising. And because the environments are different, the selective pressures in the new environments are slightly different. Of course, they are now, you know, evolving independently. So the mutations that arise and decrease in frequency are also different, and more importantly, Particularly if the populations are

small or smallish, there is an effect of genetic drift, and as you remember. Genetic drift, you know, the effect of it cannot be predicted; it is, quote unquote, random with respect to fitness.

So, because of that, the populations also end up diverging. Over sufficient time, these differences may end up accumulating within the populations. Such that it might lead to reproductive isolation. Now, what kind of differences are we talking about? And basically, you know all the mechanisms that we dealt with in the context of both premating and postmating. And I mean prezygotic and postzygotic reproductive isolation.

So, for example, the structure of the genitals can end up diverging. There might be behavioral differences; for example, in terms of courtship songs, courtship dances, or whatever mating rituals, and so on. There can be biochemical differences, or as we pointed out, you know, due to selection, mutation, etc. The differences might even be at the genetic level. So, the other three things we have already dealt with in the previous lecture, but I will just say a few things about them what kind of, or rather, how differences at the genetic level can potentially lead to reproductive isolation? So, what I am going to talk about is known as the Dobzhansky-Müller model. Dobzhansky is Theodosius Dobzhansky, and Muller is Hermann J. Muller; we have met both of these people in our previous discussions. So, what they suggested was that if you have an ancestral population, this is a highly simplified cartoon model. So, suppose you have an ancestor, and let us say the ancestor you know has two loci.

And let us assume that the ancestor's genetic makeup is $A_1A_1B_1B_1$. Now, at some point, there is a geographic separation that happens: dispersal, vicariance, whatever. Again, population 1 is $A_1A_1B_1B_1$, and population 2 is also $A_1A_1B_1B_1$. But now let us assume that genetic divergence has started happening, because of which let us say that in population 1, the A_1 allele is replaced by the A_2 allele, whereas in population 2, the B_1 allele is replaced by the B_2 allele. Now, because of this, what is happening? The A_2 allele only evolves in the presence of B_1 , and the B_2 allele only evolves in the presence of A_1 .

So, B2 has never met A1, and A2 has never met B1. Now, because of this, the epistatic effects might be such that, when, for whatever reason, Now these populations are coming back into contact with each other, and they are hybridizing. Then you have some of the hybrids; they are going to have A1B1 or A2B2, you know, coming in conjunction with each other. And because A2 has never evolved with B1 and B2 has never evolved with A1, There can be potential negative epistatic effects when these alleles come into contact with each other. This might end up reducing the fitness of the hybrids.

So, this is, you know, how it works and how it is described that DMIs. Dobzhansky-Muller incompatibilities describe the negative epistatic interactions that occur. Between different alleles of different genes with divergent or different evolutionary histories. Now, do we have any reason to believe that such a thing even works? Do we have any examples? Of course, we do.

So, I will give you just one example again. So, this is about a species of Mexican swordtail fish, whose genus is *Xiphophorus*. So, these two species diverged from each other about 250,000 generations ago. And it turns out that these are the two specific species we are talking about: *Birchmanni* and *Malinche*. Now, if you look at the *Birchmanni* species, some of them, not all, have a black spot here on the tail.

Malinche has nothing like that. So, you can see they are, you know, physically or morphologically very different from each other. Now, when you mate these two species, you get a hybrid; then some of the hybrids are going to inherit the allele for this caudal spot. Now, it turns out that this caudal spot actually has zero effect on the fitness of the *Birchmanni*. However, when the caudal spot allele finds itself in a hybrid, it occurs in a rather high proportion of the hybrids. It ends up developing malignant tumors, and people have actually figured out which gene is responsible for this.

This is due to a gene that is known as the *xmrk* gene. Essentially, it is a melanoma receptor tyrosine-protein kinase. So, here is a situation where this particular allele of this

gene is perfectly benign and harmless. When it finds itself in the Birchmanni background, but the moment it gets into a hybrid background with some genes from Malinche, Then it ends up causing the tumor and thereby greatly reducing the fitness of the hybrids. So, we talked about allopatric speciation; I gave you some examples, but those might be, you know, specific cases.

Do we really have evidence to believe on a large scale that allopatric speciation can occur? And essentially what I am asking is whether distance or separation can be a major factor in terms of organisms diverging from each other. And it turns out that we do have a couple of, you know, predictions that have very nice empirical support. So, we will look; actually, there are quite a few. I am just giving you two of them. So, let us first grasp the logic, you know, then we can understand what exactly is being done here.

So, if geographical isolation plays a big role in creating reproductive isolation, Then, populations of the same species that are further away from each other, what will we predict? We predict that such populations should be more differentiated than populations that are close by. Why? Because the further away you are from each other, the lower the chance of exchanging genes. The lower the chance of exchanging genes, the more differentiated you are going to be, and therefore, Obviously, you know distance and differentiation will be positively correlated with one another. Do we have any evidence to support this? So, in order to check this out, Tillay et al. investigated the mating behavior of pairs of wild salamander populations some names, you know, *Desmognathus ochrophaeus*, are separated by different geographical distances. So, what they did was take males and females from many, many populations, which were separated from one another by different distances. So, what they did was say it is a humongous experiment. So, they took males and females from all these populations, brought them to the lab, and then Essentially, males of one population mated with females of, you know, different populations. which are all coming from different distances and vice versa, which means they kept the female constant and then gave them males from different populations.

So, essentially they created a bunch of mating pairs where the males and the females

were from different populations. which were geographically separated to varying degrees. And then they tried to see in what fraction of the cases mating was happening. So, yeah, this is the species *Desmognathus*. What you have here on the x-axis is the geographical distance in kilometers between the populations. And what you have on the y-axis is the sexual isolation index. So, basically, the higher the sexual isolation index, the lower the probability that they are going to meet. And what you can see is a very clear positive correlation between the two variables. The greater the geographical distance, the greater the sexual isolation, which means that the less likely they are to meet. So, this shows us that what we predict from allopatric speciation that distance should be correlated with isolation, It looks like we have a validation for that. So, another prediction that can be made in the context of allopatric speciation is regarding the island populations.

Now, we are saying that allopatric speciation depends on gene flow. Now, of course, gene flow in many cases is correlated with the dispersal distance, but, It is also related to how dispersive the species are. So, suppose let us say you have a snail on one side, and let us say you have a bird on the other side. Obviously, the distance that the snail can move, and therefore, The distance that you know is required for gene flow is very different.

Much smaller for the snail compared to, let us say, the bird. So, now instead of talking in terms of distance, we are going to talk in terms of gene flow. Which explicitly takes into account the dispersal propensity of the organisms. So, the idea is that if you talk about a continent, which is a huge landmass, then of course, You know it is difficult to figure out who is going from where to where and how speciation is happening. But if you think about island populations, then you can be more sure that if you have two sister species, Then they have essentially arisen from a common ancestor because it is an island population, right? So, it is very unlikely that they would have come from a different place.

So, I mean I will qualify that as I go forward. So, the point here is that if you have island populations, Then species that have greater gene flow should require more area for speciation. versus species that have a lesser amount of gene flow, they should require

relatively less area. So, what Kisel and Barraclough did was look at different pairs of sister species and, through genetic mechanisms, etc. They made sure that they were species which most likely had originated on the islands. And then they essentially ask the question that if you know they are also using genetic methods, they figured out the rate of gene flow.

I mean, we did not discuss it over here; there is something known as F_{st} , through which you can get the measure of gene flow. So, they asked the question of what the minimum area required for a sister species to be found is. So, what is the smallest island on which, let us say, I have found a snail to speciate? What is the smallest area of the island in which, let us say, I have found a bird to speciate? So, that is the data that they obtained by, you know, crawling through an enormous amount of literature. And that is what has been plotted over here. So, on the x-axis, we have $1/F_{st}$, which is essentially increasing gene flow going from left to right.

And on the y-axis, we have the minimal island size in which a speciation event has been observed for that group of organisms. And they have taken, you know, snails, and these are flowering plants and small birds. These are lizards, ferns, insects, mammals, and specifically, these are bats. Now what you can clearly see is that there is a very nice, positive relationship. In other words, the minimal island size that allows speciation is small in taxa that have limited gene flow, like snails, etc whereas if you look at those species that are able to migrate much more and therefore generally have greater gene flow, they require much larger islands in order to speciate. Showing that gene flow is related to the rate of speciation. So, that was about allopatric speciation. So there is a special case of allopatric speciation known as peripatric speciation. So, what is the special case? So normally, when you talk about allopatric speciation, people think that the populations that are getting separated are reasonably large, not too small, let us say.

But there can be a special type of allopatric speciation where new species arise from small isolated populations. which is on the periphery of the larger ancestral species' range. In other words, we are talking about very, very small populations. which are

geographically not very far away from the ancestral range, but there is some kind of barrier nonetheless. So, the main thing over here is the fact that one of the populations, the subpopulation, is going to be much, much smaller than the main one, such that genetic drift actually is what is going to play a major role in this speciation. So, in the other case, in the allopatric case, typically it's mutation selection. Those are the ones that are supposed to be more important; drift plays a relatively lesser role. In this particular case, drift is supposed to be a major mechanism.

So, as you can see, this is not a very, you know, clean distinction or anything. which is why many people do not even talk about peripatric speciation separately. They simply say that, okay, this is just allopatric speciation, one more type; that is about it, and that is how you should also look at it. So, this geographical isolation that we are talking about can happen in three ways. What are the three ways? One is that you know about dispersal. So, you have the original population; a small number of those go and settle somewhere close to the original range.

But after they go there, dispersal more or less stops, because of which this small isolated population is on the periphery. For the range of the original population, this one diverges and ends up forming a new species. The other way in which it can happen, which is what is known as centrifugal speciation, is where you have the original population, and then, for whatever reason, the original population expands its range. So, the members are now found over a larger area, and then for whatever reason Bad environment or whatever, the range again contracts back. But while it contracts back, it leaves a small subpopulation somewhere within the broad range area of, you know the expanded range, but it is outside the original range. And again, there is no gene exchange between these two subpopulations, and at some point, speciation ends up happening. So, this is centrifugal speciation, and the third one is exactly like, you know, the vicariant situation wherein. You have an original population, and within that range, some barrier is created because of which a small population exists. You know, it gets separated out, and then this little population speciates and becomes a new thing.

So, as you can see, it is conceptually extremely similar to allopatric. Now, because of this, it is very, very difficult to distinguish between an example of peripatric speciation and allopatric speciation. So, one way you can do this is by thinking about what the signature of drift in the genome is. But then the problem is how do you know that it did not speciate allopatrically in a large, you know, population size? And then subsequently underwent drift, whereas it speciated right at the beginning with a small population via drift. So, these are frankly tough things to do, and even the example that I am going to show you is reasonable.

But it is not absolutely 100% foolproof. So, this is an example that is related to this tree, a species of tree known as the *Picea* spp. These are spruce trees, and they are found in many places, but I am primarily going to talk about spruce trees in North America. So, there you have two different species of *Picea*; one is known as *Picea rubens*, the red spruce tree. And the other is known as *Picea mariana*, the black spruce tree. So as you can see, these are conifers, and the shape and color of the cones are very, very different from each other.

Now people have done a lot of phylogeny and genetic studies on these two species, and they have figured out. That the geographical range of the red spruce tree is actually much smaller than that of the black spruce tree. And if you look at their sequences, you realize that there is a very high degree of genetic similarity between the two taxa. which suggests that they are very closely related to each other. But if you look at the genetic differences between the two, you realize that the genetic diversity of the red spruce tree is actually far lower than the black spruce tree, both in terms of nuclear and mitochondrial DNA. So, this suggests that most likely this red spruce tree came from the black spruce population like a founder event. Also, the red spruce possesses no unique mitochondrial haplotypes. Everything that it has is a subset of the black spruce mitochondrial haplotypes. Which again suggests that it is like a small subset that has broken off from the black spruce tree.

Thus, all this evidence together suggests that the red spruce speciated peripatrically from a black spruce population. Based on how much divergence there is, people have

estimated that this most probably occurred due to glaciation. Because of this, a small subpopulation of the red spruce ancestor was separated from the main black spruce population.

Great. So, we talked about the first mode of geographical isolation: allopatric speciation. A special case of allopatric speciation is peripatric speciation. So, now we are going to look at a second type of geographical isolation. Or something that leads to a mode of speciation known as parapatric speciation. So, what is it? So, in this particular case, there is reproductive isolation happening between the two populations. They are there; there is geography involved, but there is no barrier, and these populations are actually exchanging genes.

But they are not doing so freely. So, what do I mean by all these things? So, essentially, parapatric speciation occurs when the populations are continuously distributed. But the divergence happens because there is reduced gene flow, and much of the time, this reduced gene flow occurs. Because there is an environmental gradient over the geographical range. So, because of this gradient in different regions of the geographical range.

Selection operates on separate things, and because of that, there is, you know, a lack of gene flow. So, just to give you a diagrammatic representation of the whole thing, Let us assume that we have time going from left to right. So, you have the original population, and then, for whatever reason, a cline gets set up; an environmental gradient gets set up. And when the environmental gradient is set up in different regions, different kinds of things, you know. Different suits of traits are being selected for, which has led to the original traits being present in one area. New traits in another area, and this is the important bit: there is going to be an area somewhere in the middle where the hybrids are going to be. And over time, the fitness of the hybrids, if reduced compared to both the sites, will decline. They end up having lower fitness and just disappear, which leads to speciation. So, the main thing that is happening here is that this is predicting that there will be hybrid zones. In a large fraction of instances between the two populations where

the two speciating populations meet. So do we have evidence for this? So there would not be any barrier, there would not be any distance, but Because there is a change in the environmental gradient, because of which There will be low fitness in the middle, and because of that, speciation will happen.

That is the whole idea. So just to say that you know in more concrete terms, unlike allopatric speciation, no absolute physical barriers completely preventing gene flow. Populations are still adjacent to each other; they may still interbreed at the borders. But it is this gradient that is creating distinctive selective pressures in adjacent areas. Individuals will typically mate with their geographical neighbors because of that. There is going to be limited gene flow where you know the gradient is changing the hybrid zone, so to speak.

And when these diverging populations meet, hybrid zones will be formed. but these hybrids will end up having reduced fitness Because their traits are neither well-suited for this side of the environmental gradient. Nor is it well-suited for the other side of the environmental gradient. And it is this reduced fitness in the hybrid zone that will reinforce the selection against interbreeding.

Therefore, reproductive isolation is going to evolve. Slightly complicated, but let me show you an example. Hopefully, that will make it clear. So this example is from the mines, you know, in the UK. So you know that whenever mining happens, the soil in the neighboring area gets thoroughly contaminated. And in this particular case, the soils were contaminated with very high levels of heavy metals.

Specifically, zinc and lead, and this had happened for about the last 100 years. So the soils were in really bad condition, but near them there were pastures, and those pastures had reasonably good soils. So it turns out that there was this species of grass known as sweet vernal grass. And these grasses, some populations, have adapted to grow in highly contaminated areas. Whereas other populations of the same grasses were growing in the less contaminated areas.

So, these populations adapted to grow in the contaminated areas. They actually changed quite a lot, and more specifically, what changed was their flowering time. So, these metal-adapted populations were flowering much earlier than the non-metal-tolerant plants. And as a result of this, there was a very strong prezygotic isolation. That happened between the metal-tolerant and the non-tolerant populations.

And this prezygotic isolation has been maintained for more than 40 years. So, just think back to all the cases that we have discussed so far. There was geographical isolation that occurred, which led to the evolution of reproductive isolation. But then what happens if the geographical isolation breaks down? Maybe you know the river that had started flowing again; it changes its course. And now the populations again come into contact with each other, or, Maybe you know that the populations have again undergone some range expansion for whatever reason and in another area of their range now again they have come into contact with each other. What is going to happen when this is what is known as secondary contact? So, what is going to happen if there is a secondary contact? So, what are the possible outcomes of secondary contact? One outcome may be that reproductive isolation has not really evolved. So, when there is secondary contact, they again freely exchange genes with one another. And then again, they meld back to form a single population. So, as if the entire divergence had not really happened, they are back to square one or what might happen is that some amount of divergence has occurred. which has made one population more adapted to or more competitive than the other, Then the two populations might end up competing with one another. One population might drive the other population to extinction. This is what is known as competitive exclusion. A third possibility is that you know what we were talking about in the context of parapatric speciation.

When these two populations meet, the diverged populations hybridize in the zone where they are meeting. but there is reinforcement of the reproductive isolation simply because the hybrids have lower fitness. So, in other words, everybody from one population who has a tendency to mate with, you know, individuals of the other population. Their fitness

goes down, and therefore, the tendency to avoid the other population increases. that is what gets selected for which ultimately obviously leads to reinforcement of the reproductive isolation or the fourth thing that can happen is that the populations meet. The fitness of the hybrids is low, but that does not lead to reinforcement. In other words, the two populations, you know, just maintain their distinctive identity except for a narrow zone in the middle. Where the hybrids are, there is some mild gene flow happening, but the rest of the identity remains as it is. So, until now, everything we talked about was speciation in the context of geographical isolation. But can we have speciation without any geographical isolation? It turns out that we indeed can. And this is what, in technical language, is known as sympatric speciation. So, allopatric, I said, was other homeland; sympatric is sym, i.e., same patric, i.e., homeland, so same homeland. When they are in the same geographical area, how can this happen? So, suppose you have an original population, and then something changes inside a subset of the population. Due to this, although they are in the same geographical area, one group stops or reduces exchanging genes with the other group. And when that happens, that is when you have the formation of a new species. Even though the two groups are still in contact with each other, this is what sympatric speciation is.

Now, obviously, what we are trying to say is that there is a reduction in gene flow. But that is happening in the absence of geographical barriers. So what kinds of factors can lead to that? Turns out there are three major factors. One that we have already discussed is polyploidy. You know polyploidy is when the entire chromosomal number changes, and although it is somewhat uncommon in animals, It is actually very, very common in plants, where it accounts for about 15% of all the speciation events. The other thing that can happen is sexual selection, where the males' or females' preference for certain traits can You know one group can make them very, very different from another group that does not have that preference.

And the third thing, of course, is some kind of habitat differentiation or resource partitioning. Where the environment in which the organisms exist, some individuals specialize. You know, in one part of the habitat, some individuals specialize in another

part of the habitat. We will look at examples of all three, one by one. An example of polyploidy in plants we have already dealt with, you know, remember? The speciation in the primroses in Kew Gardens, *Primula kewensis*, was something that had been artificially induced.

But, as it turns out, polyploidy in plants is very, very common under natural conditions. So we will look at a very famous example. So there is a species of plant known as the "goatsbeard." So in the early 1900s, three species of this 'goatsbeard' were introduced into North America from Europe. And for this, all three species have a haploid species number of $n=6$. So, what species are these? So these are, you know, the three species called *Tragopogon dubius*, *Tragopogon pratensis*, and *Tragopogon porrifolius*.

Now, around the 1950s, people, as the scientists, suddenly started seeing. Two new species of this particular plant, *Tragopogon*, were discovered, and they were like, "Where the hell did this come from?" And when they looked up at the chromosomes and at the molecular level, they realized that one of them. *Tragopogon miscellus* had actually arisen due to hybridization between *Pratensis* and *dubius*. and the other one, *T. mirus*, had arisen due to a hybridization event between *dubius* and *porrifolius*.

So, essentially, these two have $n=12$, which is double what was happening for the three parental species. So this is allopolyploidy, where two different organisms, two different species come together to lead to a polyploid hybrid. And as a result, this is also an example of hybrid speciation, where two different species come together. And in one step, form a new species that is not fertile and reproductively isolated from the parental species.

So this is a sympatric example number one. The other way in which sympatric speciation can occur is through sexual selection. And we are going to talk about this particular lake called Lake Victoria. This is one of the largest lakes in the world. As you can see, it is somewhere in eastern or central eastern Africa, and it has many claims to fame. but one of its major claims to fame is that it has an amazing fish diversity.

So, if you look at this particular Lake Victoria, there is a particular kind of fish called cichlids. It has more than 500 species of cichlids alone. Now we are going to come back to these 500 species of cichlids later on, but right now I am telling you a different story. Now, unfortunately, the number of species has gone down quite a bit in Lake Victoria. That is because humans, at some point, decided to introduce a new fish called Nile perch over there.

That fish turned out to be invasive and extremely aggressive. and ended up just, you know, outcompeting many of the existing, you know, cichlids, but we still have quite a few. Now, among the ones that are still alive, there are two existing species that are very, very closely related to each other. But I mean, in these species, the females look very, very similar to each other.

You will be very hard pressed to distinguish them, you know, based on morphology alone. But if you look at the males, they look very different. How different? Let me just show you. So this is *Pundamilia pundamilia*, and you can see that it is a bluish-grey kind of color, and this is *Pundamilia nyererei*. So this, as you can see, is very, very brightly colored. Now it turns out that in both of these species the females of the species They have a very, very strong preference for the color of their own males.

So, in other words, *Pundamilia pundamilia* females will only prefer males that are bluish-grey in color. *Pundamilia nyererei* females are only going to prefer males that are this color. Although these two species are sympatric, they are unable to exchange any genes. The females are simply not going to mate with you, know? *Pundamilia* females are not going to mate with *Nyererei* females and vice versa. Very interestingly, people have shown that this choice is heritable and This selection, because the choice is heritable, the selection for this trait is still extremely strong.

In other words, *Pundamilia nyererei* females prefer males that are, you know, more red compared to males of their own species, which are less red. which means that there is

very strong selection for the *nyererei* to become redder and redder. because of which the divergence from *Pundamilia pundamilia* is going to increase even more. So, this is an example in which sexual selection is driving reproductive isolation. And then the third example is that of sympatric speciation through habitat differentiation.

And the specific example that I am going to share with you is this particular fly called the railroad worm. Of course, the worm refers to its larval stage, which is called *Rhagoletis pomonella*. So, it turns out that this fly in North America originally only used to lay its eggs on a particular fruit known as the hawthorn fruit. But somewhere around the 1850s, apple trees were introduced in North America, and when that happened, In some places, some of these flies shifted over to apples, and when that happened, They ended up adapting to the apples, and that actually had very interesting consequences. So, two populations started emerging: one that was specializing in hawthorn and the other that was specializing in apples.

And how did it work? It turns out that the fruit the host, the apples, mature earlier compared to the hawthorns. And because the apples may have matured earlier, the flies that were adapting to the apples. They shifted their timing of emergence and started emerging earlier. So, what I am showing you here are dates. What I am showing you here is the number of males that were captured during one hour of sampling.

So, here is the fly, and this red one is showing you those flies that are specialized in the apple fruit. And you can see that the peak emergence of these guys is here in this zone. whereas these are flies that specialize in the hawthorn fruit. Note that their peak emergence is much later, and more importantly, there is very little overlap, just a small overlap over here. Now you will think that that much is enough for inbreeding sorry interbreeding but no turns out that Something else has also evolved: the females have developed a preference for laying eggs only on the kind of fruit on which they grew up and also seeking mates only on that fruit. In other words, the populations that have adapted to apples will lay their eggs only on the apples. And they will mate with males that are only there on the apples. So, even if some of the hawthorn flies, male flies, are

coming out while the apples are still around, they are not going to go there. And you know males are also seeking mates on the preferred host fruit, which is why they are not going to go there.

And even if they go, you know the females are going to lay their eggs only on the apples. They will not lay eggs on the hawthorn, and vice versa. So, this behavioral isolation on top of temporal isolation has essentially ended up further reducing gene flow. And because of this, these two flies have started to become genetically differentiated. You can find a lot of differences, although it is not yet reproductively isolated. So, if you can bring them together in the lab they will end up mating and producing fertile offspring, But it looks like they are going in that direction.

Great. Now, temporal separation is one way by which organisms can lead to reproductive isolation under sympatric speciation. There is another way that is known as character displacement. Now, what is that? So, let me give you the definition first. So when similar species, or you know groups, populate diverging populations of the same species. When they live in the same area sympatrically, the differences in their traits become more pronounced.

But when their distributions do not overlap, then these distinctions fade or disappear, which essentially means That their trait distributions start overlapping. Now, how does this happen? Let me just show you through a cartoon. So let us assume that we have two species, and what you are seeing in green and blue is the phenotypic distribution of the traits. So, in this particular case, the trait is the size of the bill. So let us assume that these two populations are in totally different areas and the fitness function looks somewhat like this. Now, when these are in different areas, the fitness function, even if it is, you know, like this in the overlapping zone, It does not really matter for this species.

However, when you put them in the same region, Then individuals whose bill sizes are going to be, you know, intermediate are going to face a problem. And because of which they are going to diverge, they are going to, you know, differentiate. Their trait

distributions are not going to overlap to that extent. So, I know this is probably a little confusing. So, let me explain the same thing to you with an example. And, this character displacement can be another way to reinforce reproductive isolation after allopatric speciation. So how does that work? Let me explain this to you with an example, which is in the context of the Galapagos finches again. So here we have two species: one is called *fuliginosa* and the other is called *fortis*; these are the ground finches. These are two islands, Los Hermanos and Daphne Major, and what we are showing you. Are the distributions of the bill sizes at Los Hermanos, where only *Fuliginosa* works, I mean, is found? And for Daphne Major, where only *fortis* is found, bill size is very, very important for these birds because the bill size determines what kind of food they can eat and with what efficiency. Now observe the fact that when the birds are found on their own, Then there is a substantial overlap between the distribution of their bill sizes, which means That they are essentially eating whatever resources they want to eat, and accordingly, their bill sizes have evolved. However, now you look at the same two birds, and you see them on an island called Santa Cruz. Where both birds are found together.

Now, when that happens, note that the overlap between the distributions of the two bill sizes has actually almost disappeared. It is a very small overlap. Essentially, what is happening is, of course, this is assuming that. It is known that the resources are similar across all three islands. So, essentially what is happening here is that, you know, when they are found singly on an island, They are eating whatever resources they find best to eat, you know, most physiologically suitable for them. But when they are forced to be together, they kind of partition away the resources and one set of resources *Fuliginosa* is feeding on or using, another set of resources *Fortis* is using. Because of this, the fitness function is such that it has completely separated out their trait distributions. So, this is what is known as character displacement, and you know the one-sentence summary of this is. That the distribution of build depths overlaps in allopatry, which means that When they exist away from each other, but not in sympatry, which means when they are together. So, this is another way, you know, which is different from the temporal isolation way in which you know sympatric populations might end up separating their niches, which then might end up having. You know the different selection pressures on the two

populations, which will reinforce. Whatever reproductive isolation might have set in due to allopatry. So, before we finish this topic, remember I told you about Lake Victoria, right? And I told you that I would get back to it.

So, it turns out, and this is something we have already discussed in the last discussion. There is a phenomenon known as adaptive radiation. What is adaptive radiation? Remember, we were talking about the fact that you know. Different species, you know, have different rates of formation of new species, and there is this special phenomenon where there is an extremely rapid diversification of a single ancestral species into many new forms. And when that happens in a very small amount of time in a rather small space, you suddenly get an explosion of species.

And there are three major features of this phenomenon called adaptive radiation. First, as I said, speciation happens very, very rapidly. Second, there is an enormous phenotypic divergence; thus, there are many different forms or traits that are created. And third, these forms or traits are very often specialized, you know, to their ecology. In other words, they often end up using different niches in the environment. And one of the questions that one obviously asks is that. What kind of scenarios can lead to this kind of adaptive radiation, and the answers are very simple? Typically, this happens when a new resource becomes available or a new habitat is colonized where there is little initial competition from the existing species. In other words, where the species are free to explore the various possibilities in the environment. And the kind of opportunities that we are talking about, for example, the colonization of new island chains. So, if you remember the HHMI video when, you know, Peter Grant explicitly talks about the fact that there was a migration event into the Galapagos Islands, and because the Galapagos Islands at that point were empty, these birds had all the niches free to them, you know, for themselves, and they ended up radiating adaptively into those niches. So, the Galapagos Islands are a major example of this. Sometimes what happens is that, due to geological events or other kinds of celestial events, there are mass extinctions and when there are mass extinctions, the major competitors are all dead; that is when the guys who got left out. They often end up conquering all those niches or adapting to those niches. And perhaps the biggest example

of that is the adaptive radiation of mammals. This happened after the extinction of the dinosaurs due to a meteorite impact.

And finally, sometimes what happens is that there are evolutionary novelties. Some groups are able to create a new trait that then allows them to explore and exploit certain niches. Which were not available to them earlier. So, for example, you know about the evolution of flight in birds, insects, and bats. These animals were able to exploit certain parts of the environment that earlier nobody was able to exploit. And once they started exploiting that, then they, you know, kind of speciated very easily and very rapidly into those things.

So remember Lake Victoria; we were talking about the cichlid fish. So, there is this excellent study by Meier et al. I have taken the photograph you know from there. So Meier et al. showed that in a span of about 1,500 years, which is, you know, less than a blink of an eye. In the context of evolutionary history, more than 500 species have evolved in Lake Victoria and its surrounding areas. And this, so people have always asked this question, you know why? What exactly happened? This is the greatest example of adaptive radiation in vertebrates in terms of the number of species that is known on this planet. So these people figured out that there were actually two different lineages of cichlid fishes.

One was evolving in the upper Nile area, and the other was evolving in the Congo area in two different river systems. And somehow they had been doing that for, you know, more than a million years. And then we are still not sure what exactly happened, but somehow these two lineages came together in the Lake Victoria region, I mean Lake Victoria has a few other lakes around it. So, we are not saying Victoria per se, but that region. So, they came together and hybridized. And when they hybridized, this hybridization event occurred because it led to a massive amount of genetic variation. That had separately accumulated in two different areas and came together. And therefore, this ended up facilitating the subsequent adaptive radiation in that area through recombination and all kinds of other evolutionary processes that we talked about. And that is what led to all

these species. I mean, just look at this; there are more than 500 species. I am showing you about 10 or 12 over here. But just look at the variation in form, just look at the variation in size, in terms of color and function. There is a huge functional difference between these species. And this is just one group; this is just the cichlid fish; there are other groups as well. So, this is one of the most mind-blowing examples of speciation known to human beings.

The other example that has been extremely well studied and is almost as beautiful is in the context of the vangas of Madagascar. So, these are a group of birds. You find them; actually, the group is found in different places, but when you look at the vangas of Madagascar, They are a bit special because there are only 40 species; well, I should not say only 40, but still, 40 species. But there are 21 genera, which tells you that most of these are actually endemic there. They are found nowhere else, which is true. And if you look at their, you know, molecular data and you do the phylogeny, You realize that all these populations arose from one single founding population. Just one, and that ended up diverging, radiating into this enormous diversity that you are seeing in front of you. And again, this is not complete diversity; this is just a part of the diversity.

And, very interestingly, all these species, or most of them, actually eat insects. In spite of that, if you look at the shape of their bills, they are very different. Why is that so? Because although they eat insects, the way they eat them is slightly different. So, for example, look at the bill of this one; this is a very long and protruding kind of bill. So, this one actually uses it to probe the holes and other things inside the trees and rocks, and take the insects out whereas, look at this guy; consider the fact that the beak is somewhat heavy. So, this one actually strips the bark off and looks at the insects below it. So, although many of them are insect eaters, In spite of that, the way they eat the insects and the place from which they eat the insects differs. And because of that, their bill shapes, the bill morphologies, are very, very different. So, again, a superb example of how evolution can lead to, you know, endless forms most beautiful.

Now, whatever we have discussed so far, most of the time we have talked about things at the organismal level. We said that things would happen at the levels of genes, etc., but we

did not really go too much into that depth. But while all these things are happening at the organismal level, At the mechanistic level, at the level of the genes, new things have to happen. New genes need to emerge somewhere. So that you know, a flightless bird or a flightless organism does not develop flight, right? So, how exactly is the genome changing? What exactly is happening at the sequence level? Such that we see all these enormous, you know, diversification and speciation processes happening? So, that is the next big question that we are going to tackle, but that is something that will happen only next week. See you then. Bye.