Basic Course in Ornithology
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Lecture -29
Macroecology

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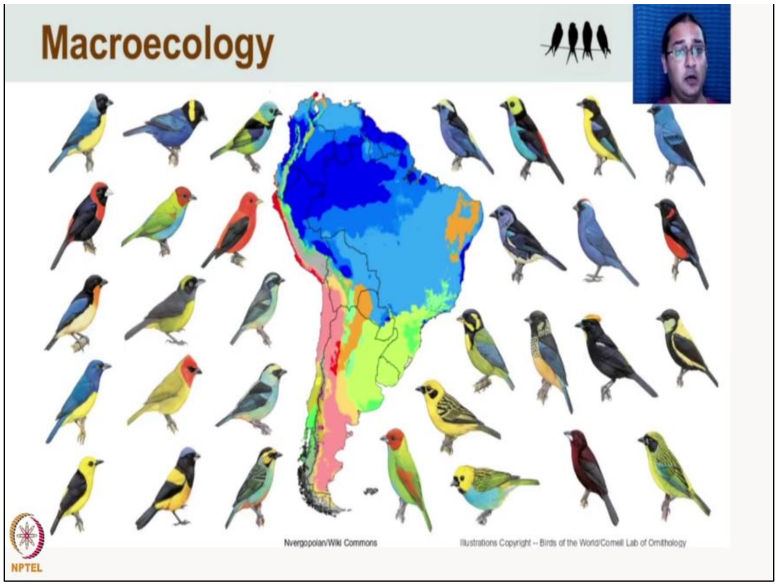

Welcome back to basic ornithology where today we will be talking about macroecology. Macroecology looking at patterns of species richness and patterns of species diversity across large pattern scales, across continents, across the world. For example, why are there so, many species of Tanagers in South America? Why are some species of Tanagers found in certain areas of South America?

Why is the species diversity of Tanagers high in some parts of the Andes versus parts of the Amazon basin. So, macroecology deals with the distribution of species and diversity across very very large pattern scales.

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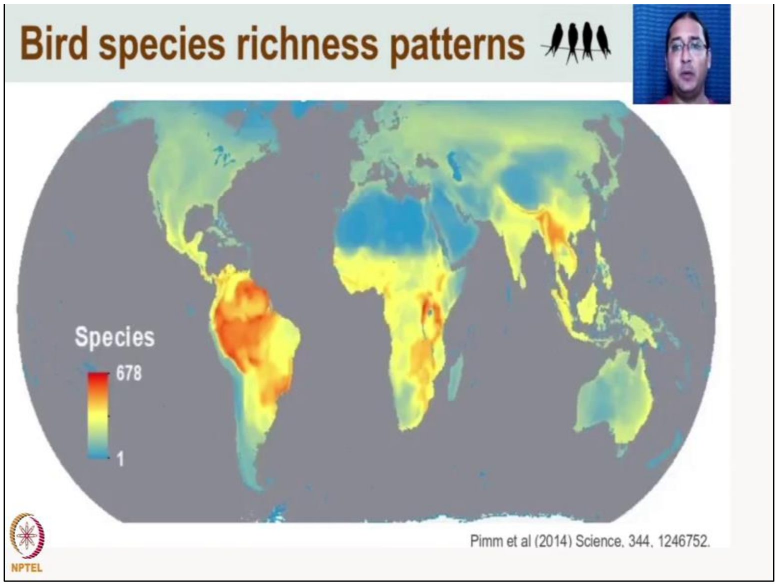

For instance, if you look at bird species richness patterns across the world. This is a map of the world showing you the number of species that breed at a particular location. And you know you could have very very low bird species breeding bird species richness near the poles (polar areas) whereas if you come to the tropics the Amazon basin and the Andes, Central Africa the Eastern Arc Mountains, Southeast Asia.

and the Himalayas, you actually find very very high number of species in these tropical areas. macroecology is the field of ecology that asks why do we see these species patterns. Why are there so, many more species in the tropics than there are at higher latitudes in the polar areas? What is the reason why we see these large scale patterns of diversity in the world?

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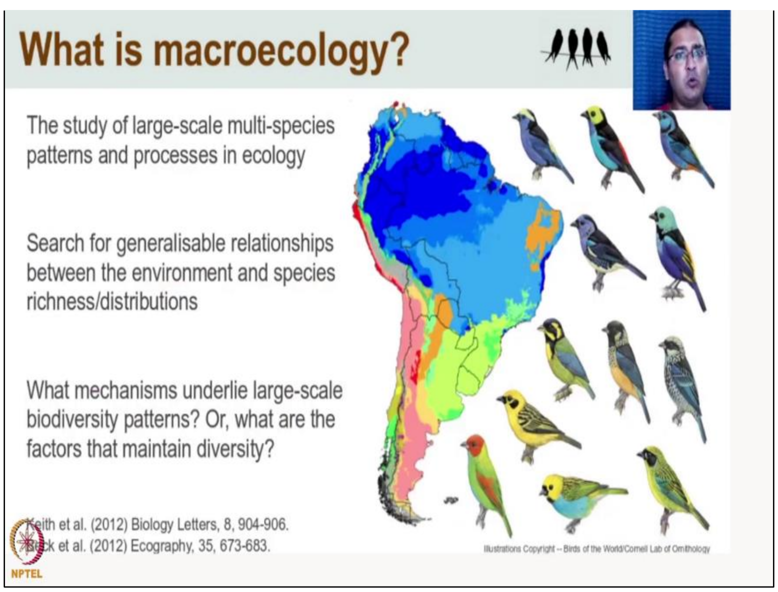

So, what is macroecology? Macroecology is the study of very very large scale multi-species patterns and processes. In ecology, it searches for relationships between the environment for example: temperature, rainfall and species richness distributions that can be generalized. So, it is searching for let us say a relationship between wherever temperatures are high you have high species richness wherever temperatures fluctuate a lot more you have lower species richness.

So, searching for these kinds of explanations for why we see these large scale species richness and species biodiversity patterns. And it asks what are these mechanisms what is the processes that maintain diversity what are the processes that encourage there to be high number of species at a particular location or what are the processes that discourage species coexistence and reduce the number of species that are present at a particular location.

So, this is what the field of macroecology is. It is a very very interesting field, it is very very ripe for for a lot more research, it is a field that is evolving very very rapidly and very very exciting research opportunities in the field of macroecology.

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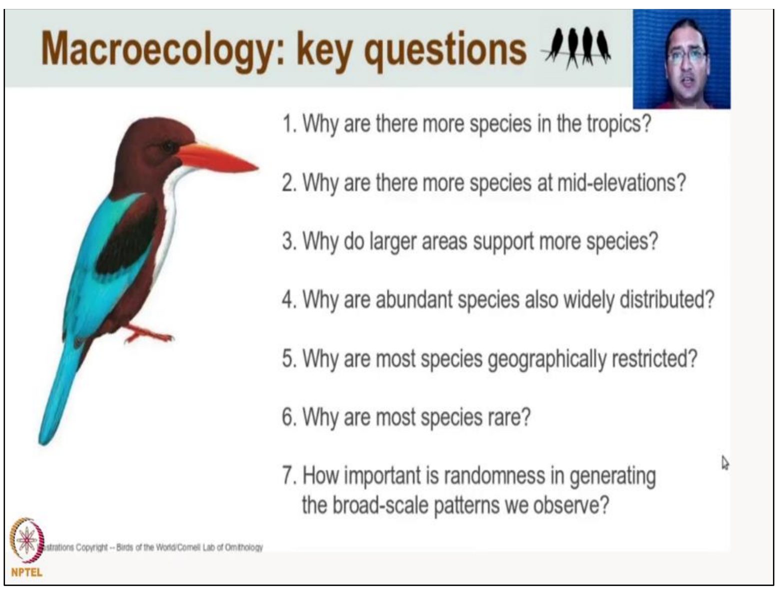

So, some of the questions that macroecology asks like we talked briefly about why are there more species in the tropics. Why are there more species at mid elevations if you go to mountains often you tend to find that species at mid elevations the communities at middle elevations have a high number of species whereas low elevation and high elevation communities have fewer species.

Why do larger areas support more species? Why are there more species on large islands than there are on small islands? For example: what is the relationship between the population size of the species and is geographical range. Why are abundant species species that have large population densities high population densities. Why are they also widely distributed why do they have large geographic ranges why.

But why are most species though geographically restricted why do most species have small distributions why are more species rare. Overwhelmingly, if you look at bird species across the world most species are rare there are very few common species compared to the number of rare species which so, why are these species rare and are there any random mechanisms that generate these broad scale patterns that we observe.

So, this is sort of a sampling of the kind of questions that macroecology is asking. It is asking questions about area it is asking questions about a species abundance in geographic range sizes. Asking questions about commonness and rarity. Asking why these patterns in commonness and rarity emerge and asking these questions about diversity across large gradients like latitude and elevation.

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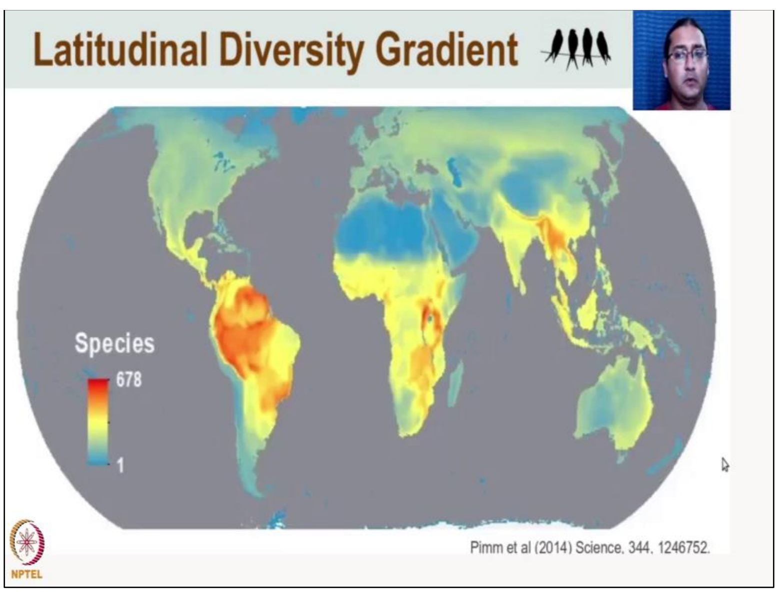

One of the most consistent patterns that you see across the world is what is called the latitudinal diversity gradient. So, the latitude at the equator is zero, the latitude at the north pole and the south pole are 90 degrees north and 90 degrees south. And this latitudinal diversity gradient you see on all continents. Whereas as you go closer to the equator the number of species increases as you move further away from the equator towards the poles, the number of species declines.

Again, this is the same map that we looked at earlier which shows you a colour coding of the world based on the number of breeding bird species that are found in any given location. And you can see that obviously the tropical regions, tropical areas have the maximum number of species they are showing up as a dark red. Whereas as you move away from the tropical regions either towards the north or towards the south, the number of breeding bird species reduces until you get to the poles where the number of breeding bird species is very very low.

So, the latitude diversity gradient is something that has been known and observed for a long long time. It is perhaps one of the first patterns that early ecologists recognize that this tropics have far more species and as you move away from the tropics you have fewer and fewer species.

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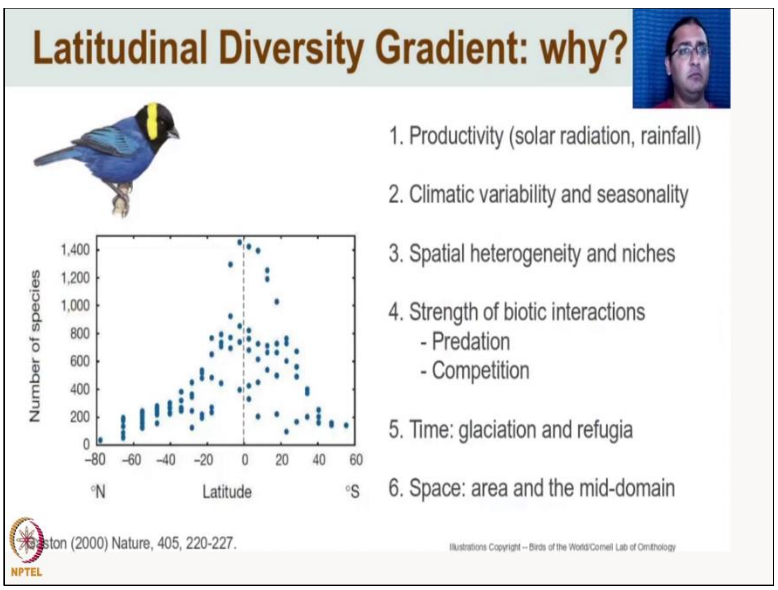

And it is been a subject that has received intense speculation why do you have this latitude diversity gradient? Why are there more species of tropics? Here is a graph showing you from South America, the number of bird species that you see with with latitude and you can see that at the equator zero degrees is where you see about a 1400 bird species, if you move towards the left that is going north in the Americas or move towards the right going south towards the Americas.

In the Americas you see this decline in the number of species until when you reach 80 degrees north you have no bird species breeding there at all and when you get to about 60 degrees south you might have about 150 bird species that are found in that location. So, the tropics are massively diverse and there are more than about 120 various explanations that people have come up with for why you see this latitudinal diversity gradient of course, we cannot get into all of them but we look at some of these.

Some of the explanations that people have given is that the tropics are more productive. They receive a lot more sunlight, they receive a lot more rainfall. So, there is more energy in the tropics and therefore that is what allows a large number of species to exist. There is climatic variability, spatial heterogeneity and niches might be more in the tropics whereas climatic variability is low the strength of biotic interactions is thought to be higher in the tropics things like predation and competition are thought to be of higher magnitude in the tropics than they are further away.

There are historical reasons for why you see this latitudinal diversity gradient and there are issues of space. The tropics simply have more land than the higher latitudes to be able to support these species. Now all of these are not standalone explanations. The likely reason for the latitudinal diversity gradient is going to be probably a combination of all of these factors to different extents in different locations.

And the importance of each of these in various parts of the world is likely to vary slightly giving rise to this latitudinal diversity gradient.

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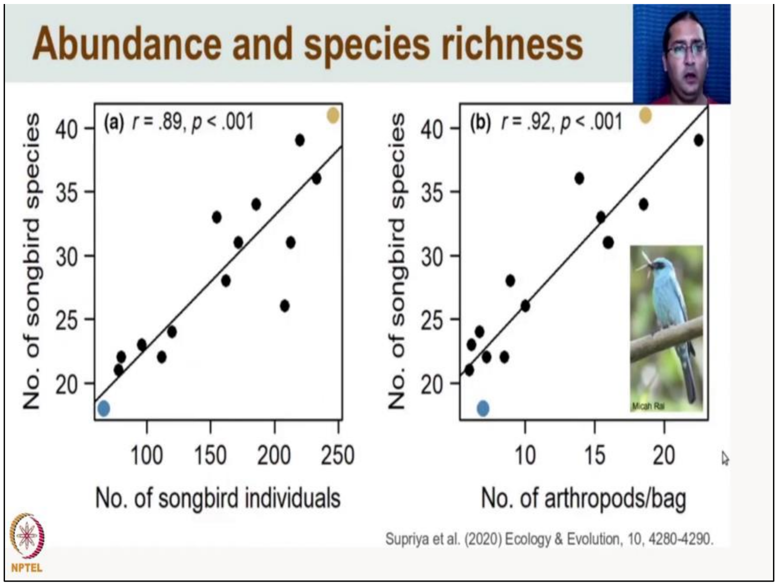

A few of the very important relationships to keep in mind when we are talking about macroecology and macro-ecological patterns, because these will appear repeatedly as explanations for diversity are these relationships. The relationship between the number of individuals in a location and the number of species and the relationship between resource availability and the number of individuals that an area can support.

What you see over here are graphs of the bird community of songbirds from the eastern Himalayas and you have the number of individual songbirds on the x axis in the first graph and the number of species of songbirds on the y-axis. So, if an area supports a greater number of individuals of songbirds (of birds), it is also likely to support more bird species. So, the greater the number of individuals in a location the greater the number of species in that location as well and that depends on the resources.

So, if you have a resource availability which is on the x axis which is arthropod density and all these birds are eating arthropods and the number of songbird species on the y axis. You see that as arthropod density or as the resource availability becomes higher the number of species in that location is also high. So, there is a relationship between resource availability and the number of individuals (individual birds) that a location can support.

The greater the availability of resources the more the number of individuals in that location the greater the number of individuals or the higher the population at that location, the greater the number of species in that area as well. So, there is a relationship between resource availability, the number of individual birds that a location can support and the number of species therefore that a location can support and all of these are positively correlated with each other.

This is the first relationship to remember that higher resources lead to high number of individuals high number of individuals means more species in a locality.

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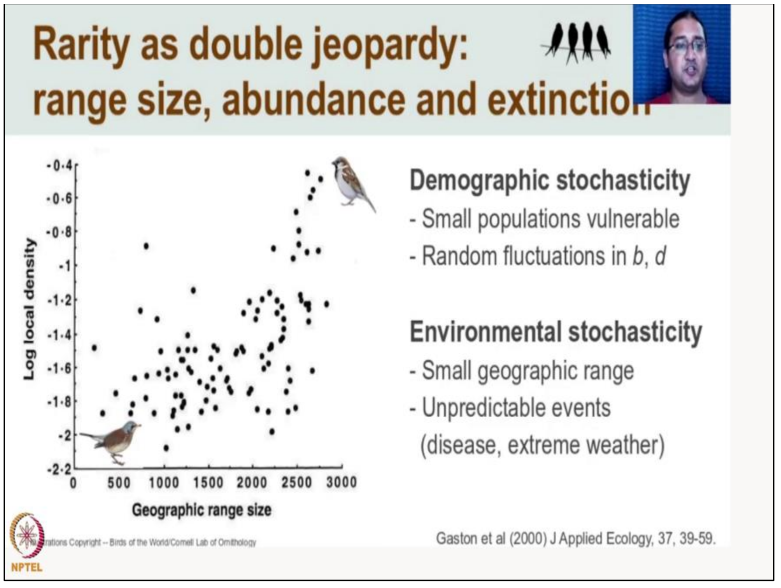

The second relationship is what does rarity entail? And that is what is called double jeopardy. The relationship between range size and abundance. What you see in this graph over here on the is for British birds on the x-axis geographic range size in square kilometers and the local density of birds are the local population sizes of birds on the y-axis. And you see this positive relationship where species that are occur at high densities or have high population sizes are also those that are widely distributed.

They are also bird species that have large geographic ranges. So, rarity both in terms of small range size and in terms of low population sizes acts as double jeopardy because a rare species is now more likely to be vulnerable to both demographic stochasticity and to environmental stochasticity. So, you have species the species that are have small population sizes are also limited to a small geographic range.

Small population sizes are vulnerable to demographic stochasticity which is random fluctuations in birth rates and death rates. So, if one year death rate is very very high a large population would be able to rebound from that mortality and that loss of individuals. But a small population might not be able to rebound in abundance from demographic stochastically leading to a population crash.

So, this population which is made up of a lower number of individuals is vulnerable to demographic scarcity. But because this population which is made up of a small number of individuals is also likely to be restricted to one geographic location it is also vulnerable to environmental stochasticity. So, extreme events let us say an epidemic or extreme weather like a cyclone. If a bird species is widely distributed then a cyclone in one part of the range of the species is not going to affect the entire population.

But if the species is very very local then it has a very small geographical range then a single extreme event in its range can cause the species to go extinct. So, rarity operates as double jeopardy because of this relationship between geographic range size and population size. Species that are very very abundant have large geographic range sizes they are less vulnerable to both demographics to stochasticity and environmental stochasticity.

Species that are rare are rare because they are found in a small geographical area but they are also rare because they have small population sizes and therefore, they are vulnerable to both demographic stochasticity and environmental stochasticity.

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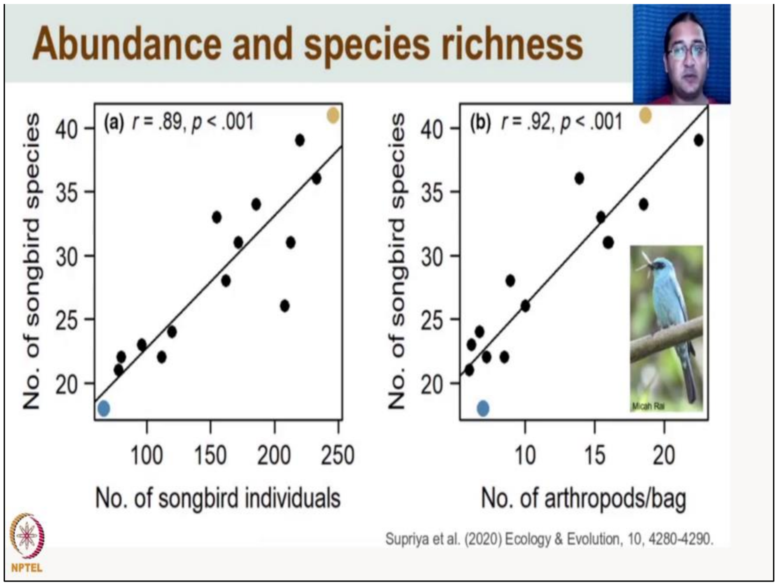

So, these two relationships the relationship between resource availability and species richness and the relationship between abundance and range size are key in understanding some of the mechanisms that have been invoked to explain macroecological patterns.

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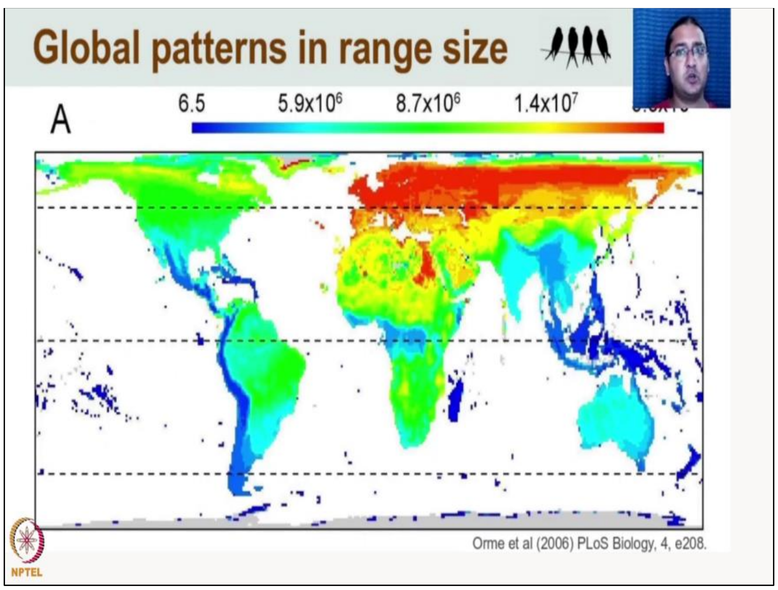

Let us look at the geographical distributions of range size and rarity. This is the global pattern in range size. So, if you if you went to a particular location and you looked at the range size of all the birds in that location and you average the range size, let's say I went to north America to a particular location in north America and I looked at the entire bird community there and I looked at the range sizes (the geographical range sizes) of each of the birds in that community.

and I averaged the geographic range size of all the birds in that particular location then what I find is red the colour scale is such that blue means very small range sizes and this is in square kilometers. And as you go towards the red you will have larger and larger range sizes of the birds at any particular location. And where do you see the smallest range sizes in the tropics you see the smallest range sizes in the Andes using the smallest range sizes in central Africa you see the smallest range sizes of bird communities in southeast Asia and the Himalayas.

So, the birds in the tropics have smaller ranges. Birds in the tropics especially tropical mountains like the Andes have smaller geographical ranges you go towards the poles birds for example in northern Asia have massive geographical ranges. So, there is a relationship between geographical ranges of birds and latitude. Birds near the equator have smaller range sizes birds further away from the equator have larger range sizes.

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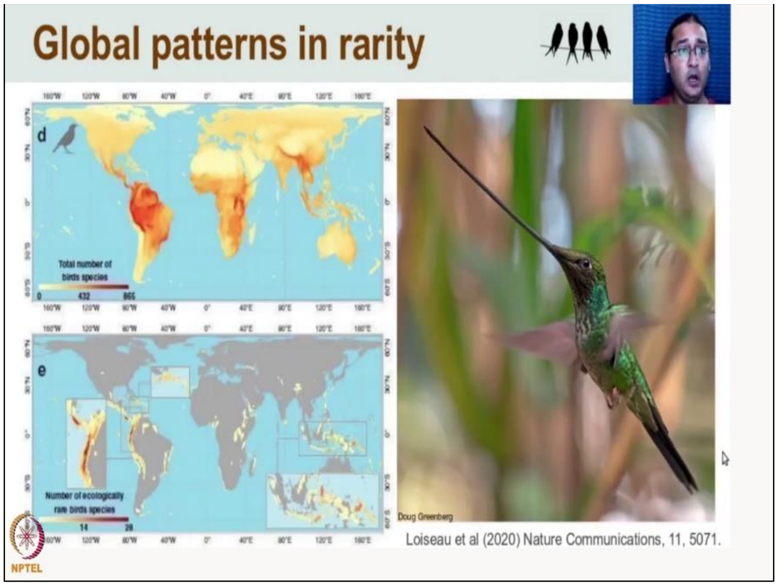

And therefore, you see patterns in rarity. The global patterns in rarity again you look at the total number of bird species, yes they are more in the tropics (that is the panel d), the first panel there are more bird species in the tropics than there are at higher latitudes. If you look at the number of rare species ecologically distinct unique species like this Sword-billed Hummingbird here which is ecologically very very unique.

And you look at the number of ecologically rare species again you find them in the tropics these are species that are highly specialized highly adapted to you know particular kinds of habitats or particular kinds of micro habitats. For instance, the Sword billed Hummingbird is a hummingbird that is uniquely adapted to feed on flowers that have very very long corollas. So, these ecologically rare species are also in the tropics.

So, you have in the tropics species that are ecologically rare and species that have very very small range sizes. So, remembering these relationships, let’s move on to some of the mechanisms or the processes that have been hypothesized to lead to the latitudinal diversity gradient.

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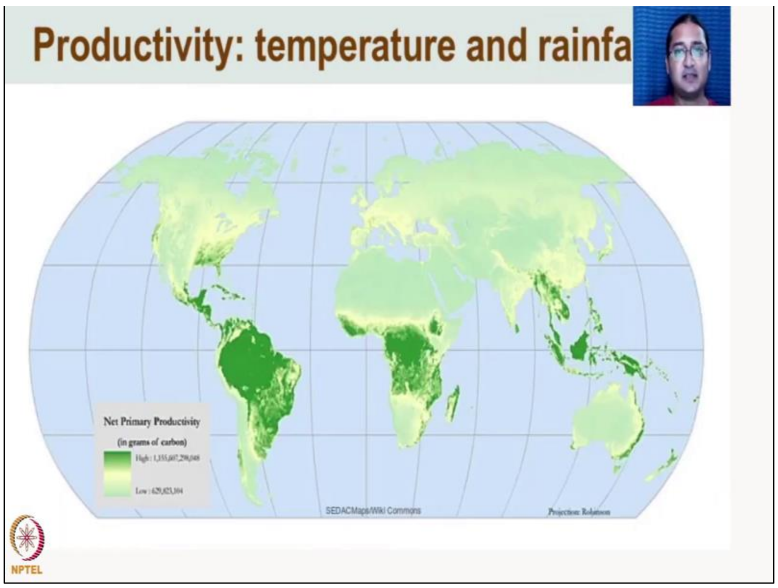

The first is that productivity is high in the tropics, productivity being just simply the amount of solar radiation that the tropics receive, the amount of rainfall that the tropics receive makes resource availability very very high. One of the measures of productivity is what is called net primary productivity which is the conversion of solar radiation to carbon by plants. So, the primary producers which are the plants are converting solar energy into biomass.

And that allows the primary producers… net primary productivity created by primary producers if you look at that across the world then obviously the tropics have the highest net primary productivity. The topics are very very highly productive. And as you move away from the tropics because temperatures come down rainfall comes down solar radiation itself is lower towards the poles that it is in the tropics you see lower productivity at higher latitudes towards north pole and the south pole.

And so, this productivity creates an abundance of resources. Because resources are abundant the number of individuals supported in the bird community is also high. And because the amount of resources is high and it supports a high number of individuals the greater number of individuals means it supports a greater number of species, why is that? If a larger number of individuals is present in in a community,
then because of the larger number of individuals each species would also have a larger population size and that large population size is less vulnerable to extinction. If because of higher productivity because of the availability of resources, there are more individuals because there are more individuals there is a lower chance of stochastic extinction and therefore the tropics can support a greater number of species than temperate areas.

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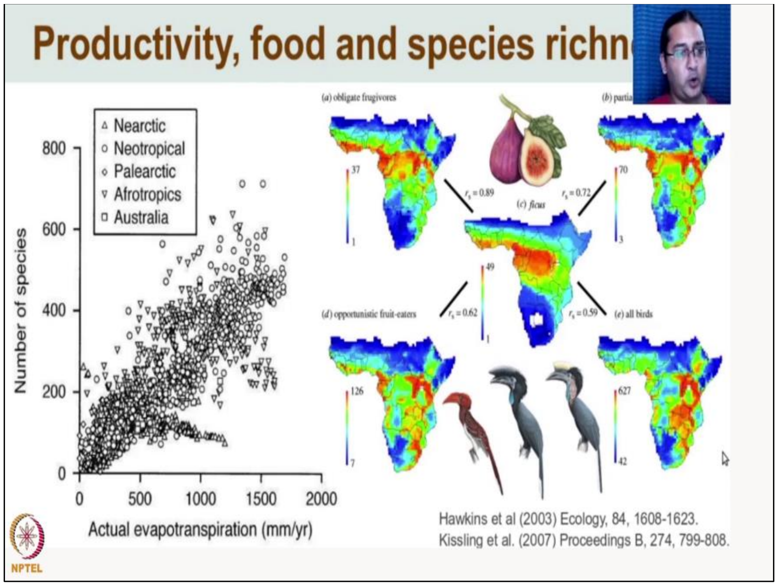

So, let's look at some of these relationships. Does this actually happen? If you look at productivity: look at the graph on the left you have a measure of productivity which is actually evapotranspiration do not worry about what that is it is a measure of productivity. And you look at the number of species there is a very very strong relationship between productivity which is the amount of solar radiation that is converted into biomass high correlation between the productivity and the number of species in in a location.

So, productivity is highly correlated with bird species richness and is that linkage shown where productivity increases resource availability and therefore resource availability increases species richness. If you look at this in Africa, if you look at the pattern of frugivorous birds in Africa (colour-coded there again) you have areas that have large number of frugivorous bird species (bird species that eat fruits) in red or high species richness in red and low species richness in blue.

And if you look at *Ficus* or fig species richness in the (central graph there) central Africa has the highest number of fig species tree species 49 species of figs in central Africa and that correlates very very strongly with the number of frugivorous bird species that are found across the Africa (sub-Saharan Africa). And you see that where *Ficus* species is the highest is also where productivity is the highest and where *Ficus* species richness is the highest is also where the species richness of obligate frugivores, birds that only eat fruits is also highest where *Ficus* species is highest that relationship is not there between *Ficus* and all birds.

So, if you look at all bird species, the highest species diversity or species richness is in the Eastern Arc mountains in Africa towards the east of the African continent and that is not where the Ficus species richness is peaking. So, there is a relationship between the diversity of food availability as well as the diversity of the species that eat this food. And the diversity of food is also closely related to productivity.

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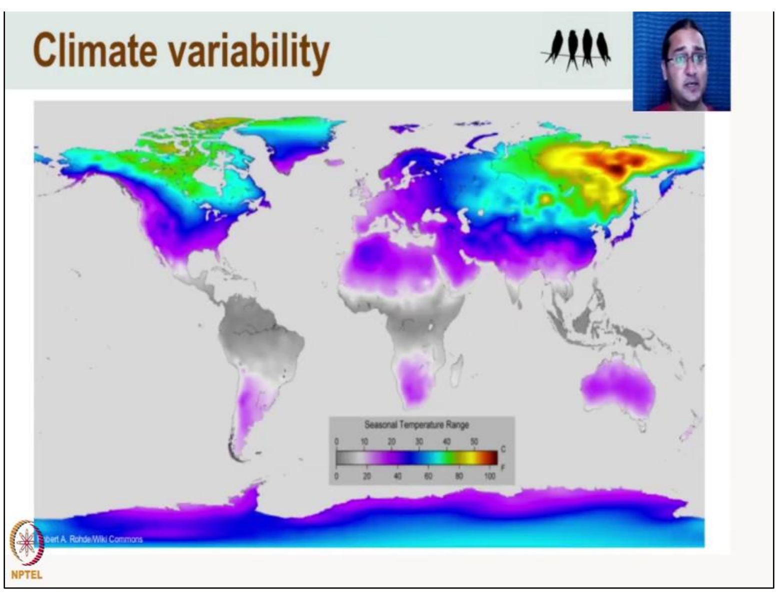

Another hypothesis that has been often advanced is that the tropics are much less seasonal in terms of temperature. So, they are much less climatically variable in terms of temperature. So, if you go to the tropics this is a map of the world colour coded by seasonality or annual temperature variability and the gray areas is where temperature variability is low as you go towards blue and when red the climatic variability is much higher.

And that climatic variability is difference between mean summer temperature and mean winter temperature. You can see that there is hardly any difference between summer and winter in terms of temperatures in the tropics. But as you go higher and higher in latitude, the temperature variability between summer and winter increases. In some places in the higher latitudes the difference between average summer and winter temperature could be as much as 40 degrees Celsius.

So, the hypothesis is that in these areas that are very very have very very low climate variability, resources are also available throughout the year. And because resources are available throughout the year and birds can feed on these resources throughout the year what happens is that birds are able to specialize on certain resources that are available throughout the year. Whereas, at the higher latitudes these resources are not available throughout the year there is a peak in resource availability in summer and then hardly any resource available in winter.

And so, species cannot specialize on certain resources, they have to be more generalist at higher latitudes than in the tropics. And because species can adapt and evolve to specialize on certain resources there is also reduced competition between species and the reduction in competition between species actually also allows for coexistence.

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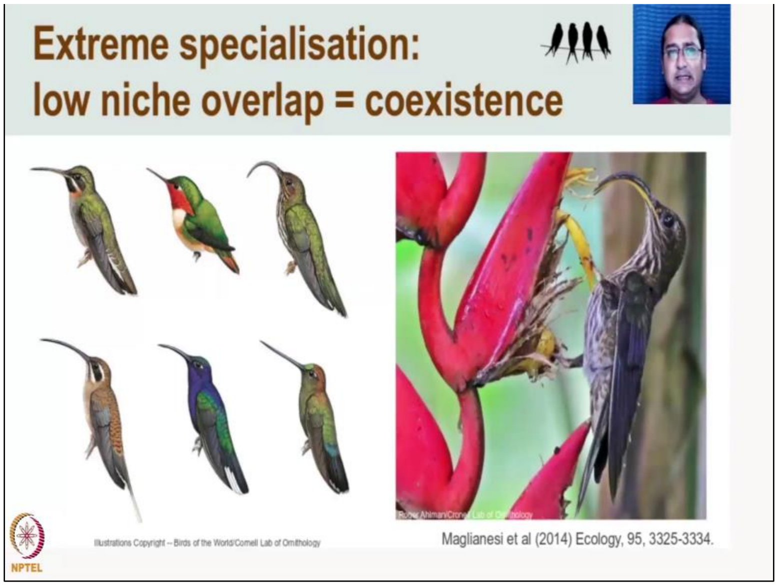

A nice example is these hummingbirds, you see these bills of these hummingbirds they are very very differently shaped and each bill shape is adapted to a certain set of flowers, a certain morphology of flower coronas. So, you have this extreme specialization in hummingbirds which means that they are all specializing on different kinds of flowers and because they are these flowers are in the tropics.

These flowers are available throughout the year and this extreme specialization means that they are not competing for the same flowers and so there is a very little niche overlap between these species that little competition between these species and they are able to coexist in this tropical area because of their extreme specialization.

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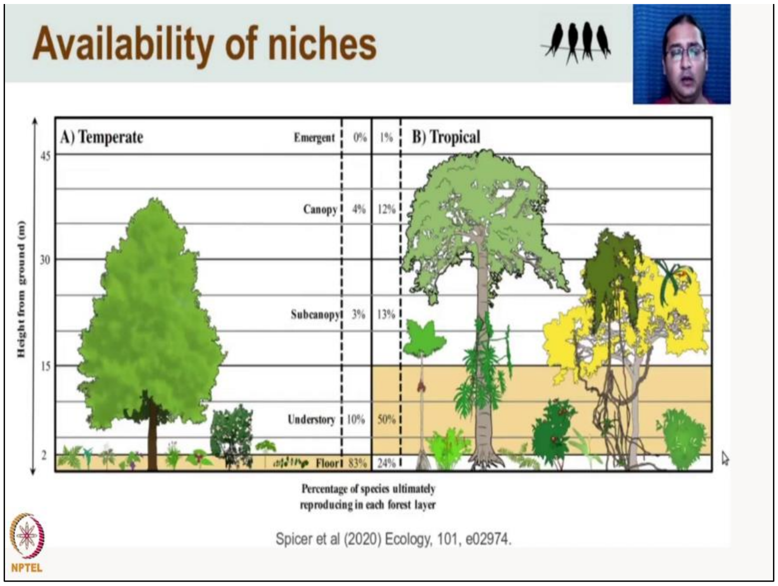

A further explanation that many people have advanced is that there are simply more niches available in the tropics. So, if you compare a tropical forest to a template forest there are just this vegetation at many more levels and many more layers the vegetation is far more complex in tropical forests than it is in temperate forest. And the complexity of vegetation allows birds to specialize in certain niches and exist in this tropical forest areas.

You often see this kind of thing happening in forested areas where certain species of birds will specialize on a certain niche in the forest specialize on a certain structure within the forest. So, there are some species that will feed this degree of specialization you see very very starkly in the birds of the Amazon where species richness is very very high. Some species will only feed on vines (tangled vines), some species are only going to feed on epiphytes which are plants growing on other plants

(plants growing on trees). And so you have this really clear niche differentiation of birds in the tropics where bird species are specializing on certain properties of the vegetation (certain structures of the vegetation). And therefore, that availability of niches allows these species to coexist in the tropics rather than a bird species in temperate forests where the availability of niches is much lower.

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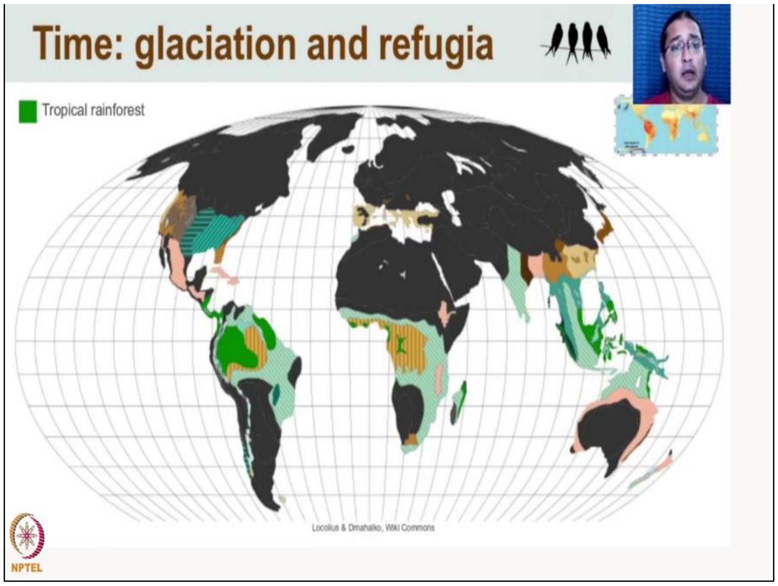

Glaciation is a historical event that has occurred repeatedly. We are today living in an interglacial period that is between two ice ages. When an ice age happens that is the temperature of the earth cools down and ice age happens then what you have is that glaciers occupy a large part of the world. When that happens and the glaciers advance towards the towards the equator the habitats in the world also change.

And during the glacial age when the ice is at its maximum extent (during an ice age) you see that tropical rainforest is present in in these locations this is where tropical rainforest was present during the last ice age. The tropical rainforest is represented by the dark green colour there it is present in south America in the Amazon basin, is present in central Africa and is present in the eastern Himalayas and that is exactly where today we see the largest diversity of species, the highest number of species. It is in these areas that we see the highest number of species.

So, the hypothesis is that when the glaciers advanced, the bird communities retreated to these refugia. The refugia being the areas that had tropical rainforest and in this interglacial period while the glaciers have retreated the birds are now moving out to colonize, recolonize these new habitats that are created. And so, the maximum number of bird species is in these tropical rainforest historical refugia which were the only rainforest available during the ice ages.

And now therefore as they have moved and recolonized areas to different extents from these refugia you also see the species richness decreasing as you move further away from these refugia. And so, this is a historical explanation for why there are more species in the tropics because the tropics had rain forest that during the ice ages and therefore most of the community of these birds retreated to these rainforest refugia.

And as the ice age abated (as the glaciers retreated back towards the poles) different species of birds moved out of these rainforests to different extents leading to this relationship where you have the high species richness in the refugia and as you go further and further away from the refugium you have lower and lower number of species.

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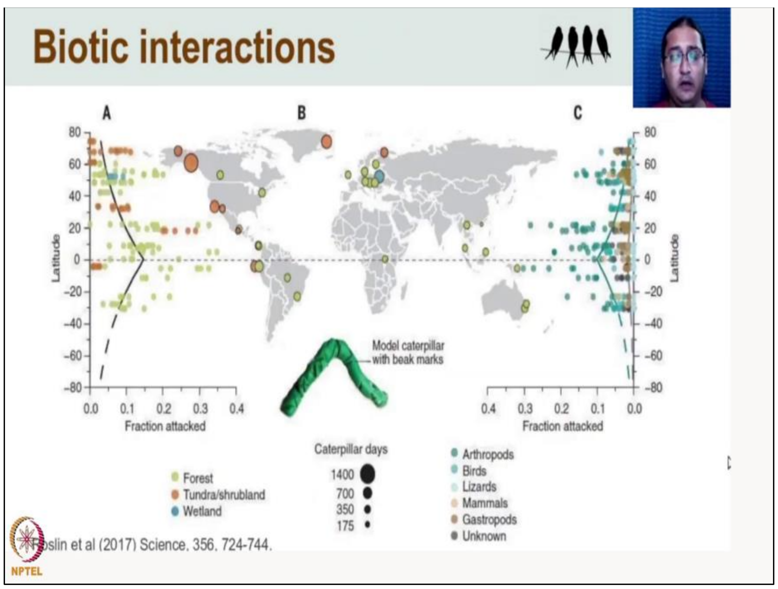

A very very interesting hypothesis for the maintenance of diversity in the tropics is that biotic interactions like predation are higher in the topics. This is not an example with birds but with arthropods. What the authors of this study did was that they made these model caterpillars that they put out into these habitats in the tropics and in temperate areas and they came back after a while to check what was the degree of damage to these model caterpillars. How many of these caterpillars were attacked?

What proportion of these caterpillars were attacked by predators? Those predators being arthropods, birds, lizards, mammals etc etc. And they after a while they looked at these model caterpillars for evidence that they had been attacked. And what you see is that the fraction attacked by predators is highest at the equator and decreases as you go towards the higher latitude. So, about you know 20% to 30% of these model caterpillars were actually attacked at the equator.

Whereas you know almost none of these caterpillars were attacked at the higher latitudes towards the poles. Now, what the hypothesis is, is that because predation is high it keeps population sizes of species low and because it keeps population sizes of species low, there is lower competition between species there is lower inter-specific competition between species because the population sizes of species simply do not reach the threshold for which competitive exclusion occurs.

So, the species two species that are very very similar have population sizes that are kept low by predation and prevent them from having high inter-specific competition therefore allowing these two species to coexist. So, this is an example of a hypothesis that says that biotic interactions in the tropics have a far higher magnitude than biotic interactions like predation at higher elevations and therefore that reduces competition and promotes coexistence between species in the tropics.

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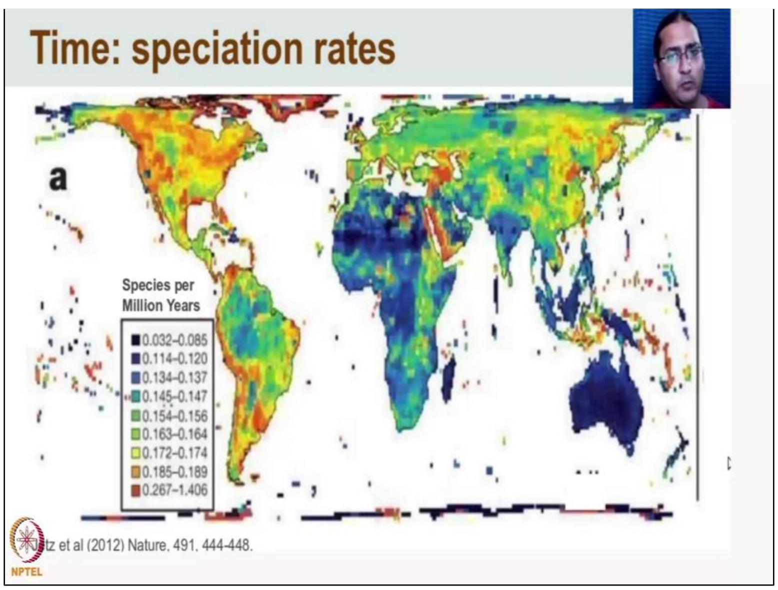

So, up until now we were looking at the probability of a species going extinct in the tropics right because of stochasticity. And a lot of these explanations have to do with the fact that extinction risk in a tropical areas is lower than extinction risk in temperate areas because the number of individuals that tropical areas can support is high therefore the number of species is high species have relatively large population sizes and therefore are less likely to go extinct because of stochastic processes.

A parallel explanation is that speciation rates (this is the number of new species that arise every million years) is this rate at which new species arise is also higher in the tropics than it is at temperate areas. So, there is actually a greater probability of there being new species arising in the tropics than in temperate areas. And this is a map of the world colour coded by speciation rate which is the number of new species being created every million years through the evolutionary process.

There is some evidence but it is not very very clear. It seems like a lot of tropical areas do have higher speciation rates than higher latitudes but that is not necessarily the case throughout the world. For example, Australia is a hotbed of speciation, the belt just below the Sahara is a hotbed of speciation for birds. And there are higher latitudes also that have high speciation rates. So, it is not entirely clear whether speciation rates are driving this latitudinal diversity gradient.

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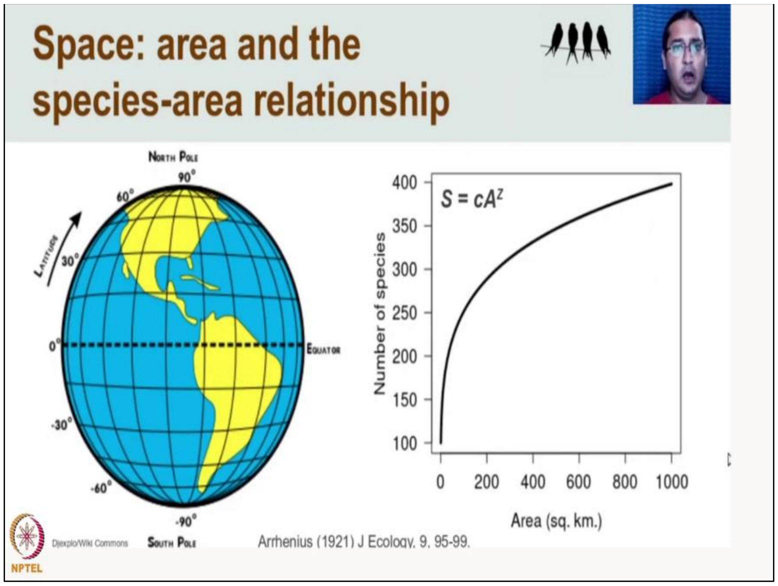

So, we will end with the latitude and the diversity gradient over there some of the explanations for why there are more species in the tropics. And we get to another explanation for this which is space and the species at a relationship which is also much more broadly. It is a relationship not only about the latitude but a much broader relationship as well and a very very important relationship in macro ecology.

So, the tropics simply because of the bulge of the earth have more area and therefore more area supports more species and because more area supports more species, you have higher diversity of species in the tropics than when you go to the poles where the area of the land is very very low. And so, you have a lesser number of species because there is this species relationship. The species area relationship is about 100 years old the formal species area relationship people have been noticing that larger areas support more species for a long long time.

And the relationship between area and species richness often follows what is called a power law, that is the relationship that you see on the graph on the right. Area is on the x-axis and number of species in the y-axis. As area increases, the number of species rises greatly until after a while the the rise in the number of species becomes slower and slower and that follows this relationship, where S is species richness or the number of species C and Z are constants and A is area.

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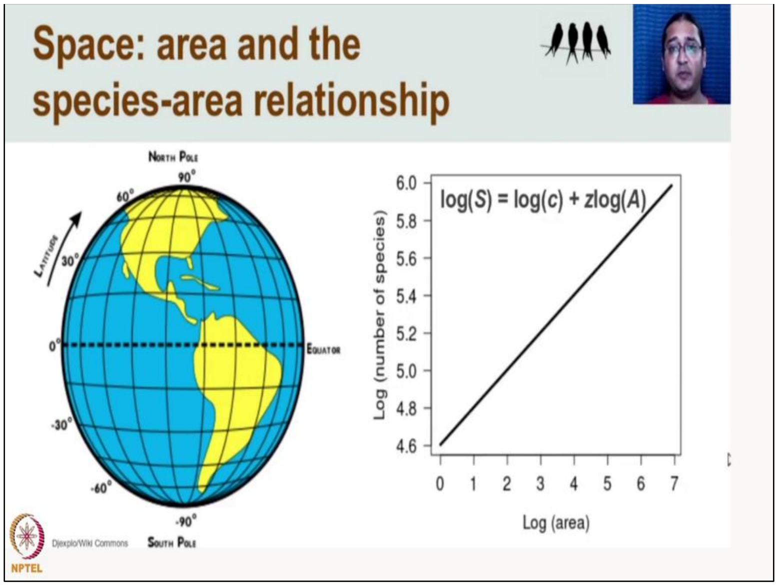

And so, you have this power law relationship and if you convert this to a log log scale then the relationship becomes linear. The relationship between the log of species richness and the log of area then becomes a straight line. But it is been observed over and over again that larger areas do support a greater number of species. And the formalization of this came a lot from the theory of island biogeography.

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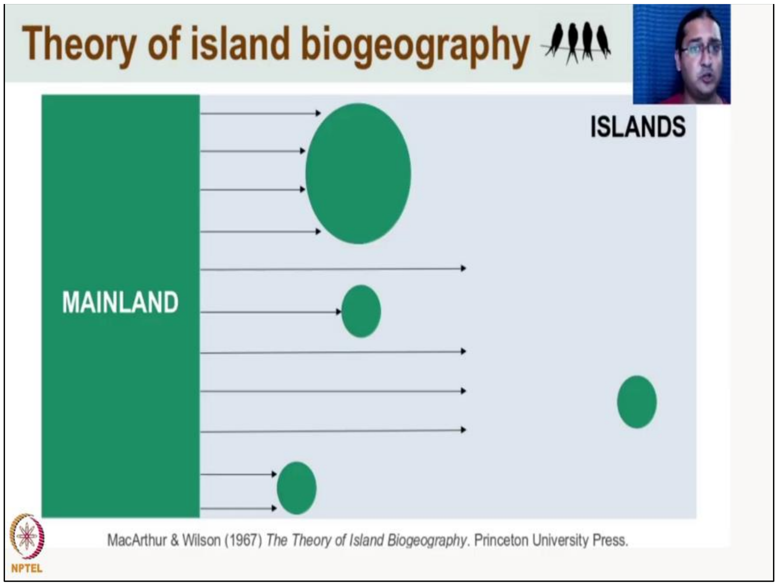

The theory of island biogeography states that islands that are larger and closer to the mainland will have a greater number of species than islands that are small and isolated from the mainland. But let's look at only the area aspect of this and not the isolation aspect of it. Let's look at these two top islands both of these islands are equally distant from the mainland, the top island is large, the island in the middle is small. The larger island will have more bird species than the smaller island.

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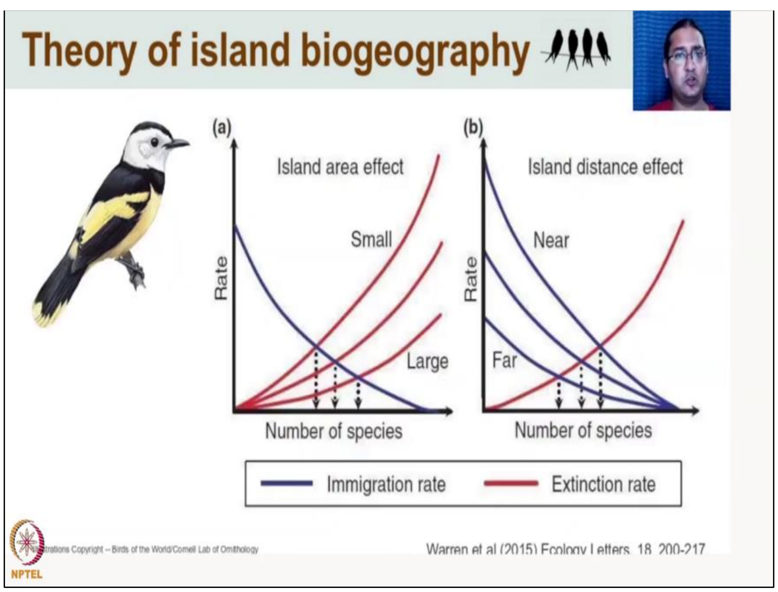

And the reason for this according to the theory of island biogeography is the effect that island area has on extinction rate. Now just look at panel a here not panel b that is the isolation effect of the distance effect, we are looking at the species area relationship or islands. If two islands are at the same distance from the mainland exactly the same distance from the mainland then the rate at which they receive new species from the mainland is not going to change.

The rate at which these new species come into the large island or smaller is not going to be different. But, the extinction rate on small islands is going to be larger higher than the extinction rate on large islands. So, the extinction rate on small islands is going to be larger higher than the extinction grade on large islands which is going to be low. The reason for that is that large islands allow for the presence of large populations.

And large populations have a smaller chance of going extinct but they are less likely to go extinct because of demographics stochasticity whereas small islands support small populations. And because small islands support small populations they are vulnerable to demographics stochasticity, they are vulnerable to extinction and therefore small islands will support a fewer number of species because more of those species are going extinct on the small island.

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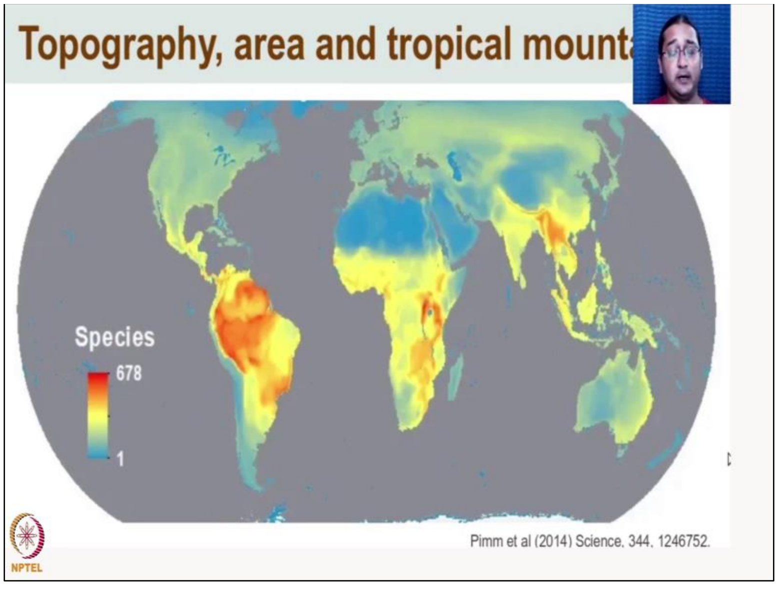

So, that was the species area relationship. Let's talk about mountains and topography in influencing species diversity and species richness. Even within the tropics, if you look at where the number of species is highest, it is in tropical mountains. These hot spots of species richness are in the Andes mountains, in the Eastern Arc mountains of Africa and the Himalayan mountain range. So, even within the tropics the species which is that mountains support is very very high.

That is because you you tend to see that you know you have different species at low elevations, different species at mid elevations, different species at high elevations. So, within a very short distance you can pack in more species on a mountain right you are not actually moving that much in distance from the bottom of a mountain to the top of the mountain in terms of kilometers but because elevation is so, strongly correlated with things like temperature and so on. Bird species occupy different parts of the elevational range and the mountain as a whole can support far more species than an equivalent area of flatland.

So, topography is very important in generating these macroecological patterns and this brings us to the altitudinal diversity gradient.

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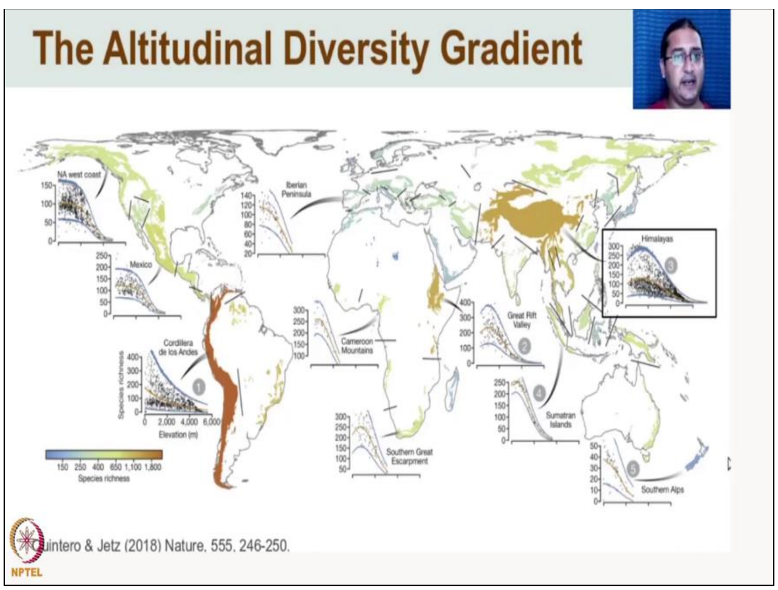

The alternative diversity gradient is the relationship between elevation and species richness. So, all of these relationships here are showing you have elevation on the x-axis (or altitude) of the x-axis and species richness on the y-axis. So, if you look at the American mountains, the west coast Mexican mountains and the Andes the number of species generally reduces as you go to higher and higher elevations.

So, if you go along the x axis from the left to the right, you are going to higher and higher elevations going higher and higher on the mountain and the number of species on the y axis is coming down. But often what you find is this mid elevation hump and I just want you to focus on the Himalayas which is on the right over there, where the number of species actually increases at mid elevations at about 2000 meters and then declines as you go.

So, low elevations have a lower number of species as you move up you have this mid elevation hump you have the highest number of species at about 2000 meters and as you go higher than 2000 meters the number of bird species declines. So, you have this mid elevation hump especially in the Himalayas.

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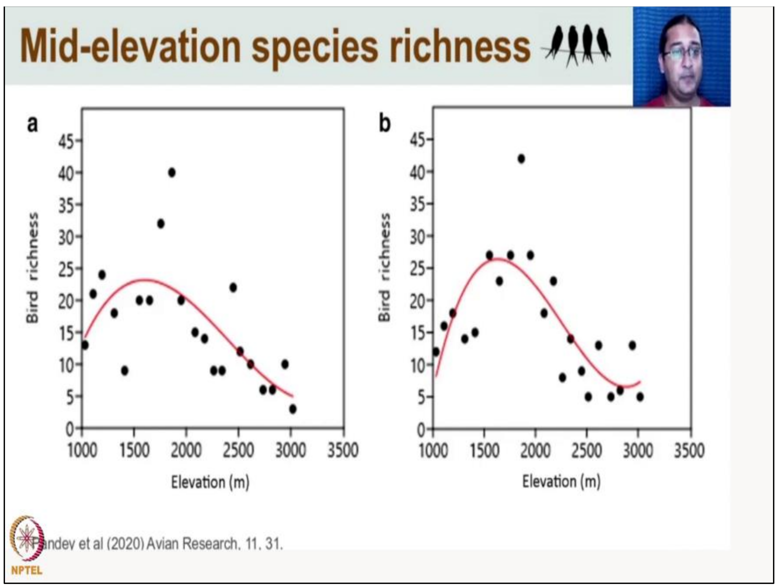

So, here is an example of bird species both in summer and in winter. You can see that as you go higher and higher in elevation which is on the x axis. The bird richness is maximum at 2000 meters in summer and in winter. So, we are seeing that the maximum species richness is at intermediate elevations. Why might that be?

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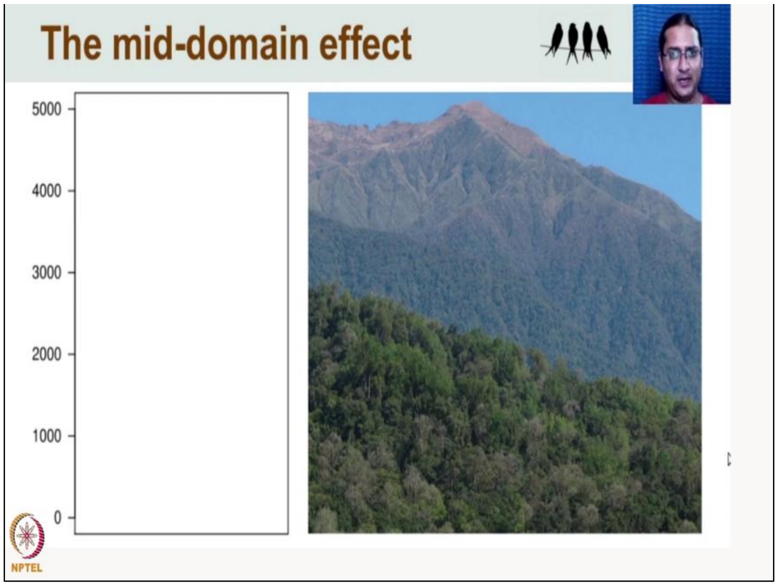

One of the explanations for this mid elevation peak in species richness is what is called the mid-domain effect. The mid domain effect has been around for a while and it is basically saying this it is a random process that generates these mid elevation peaks. So, let's say you have a mountain that goes from zero meters above sea level to 5000 meters above sea level and that is basically what is called a bounded domain.

You cannot go below zero meters you cannot go above the summit of the mountain or the peak of the mountain. So, you cannot go above 5000 meters.

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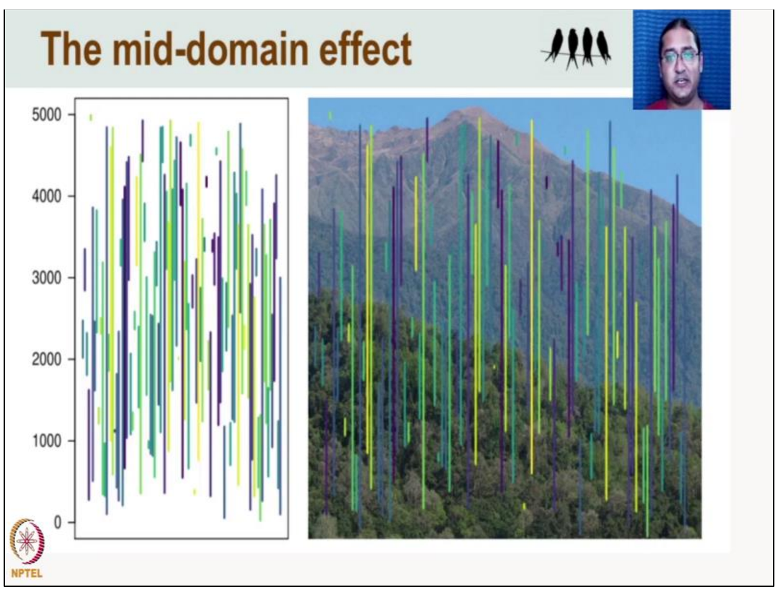

And let’s say you randomly placed elevational ranges of different species on this mountain. So, each of these bars represents one particular species and the elevational range of that species. So, you have some species that are high elevation specialists that are only going to be found at higher elevations. There are some species that are low elevation specialists, some species will have broad elevational ranges other species will have narrow elevational ranges.

The size and the placement of these elevational ranges is completely random. So, you just created random bunch of elevational ranges and overlaid them on this bounded domain which is the altitudinal gradient of the mountain. Note that these ranges are completely random; both the placement and the sizes of the ranges are completely random.

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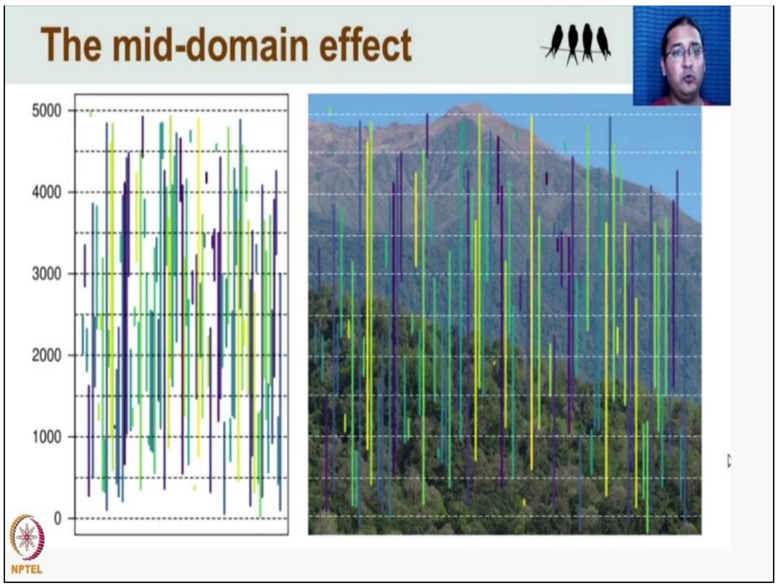

You can ask if you drew a line through these ranges at different elevations how many bird species ranges would they touch (would they overlap with). So, any line through that is going to touch a certain number of ranges and that is the number of species that is found at that elevation right. So, the topmost line is touching one, two, three, four, five, six species and. So, there are six species at that is touching the ranges of six species at 5000 meters.

So, the number of species just from a random process at 5000 meters is you know whatever number of species that are there in that the and so, you see how many ranges are being intersected at each elevation and if you draw the relationship between these two things on from this particular random exercise.

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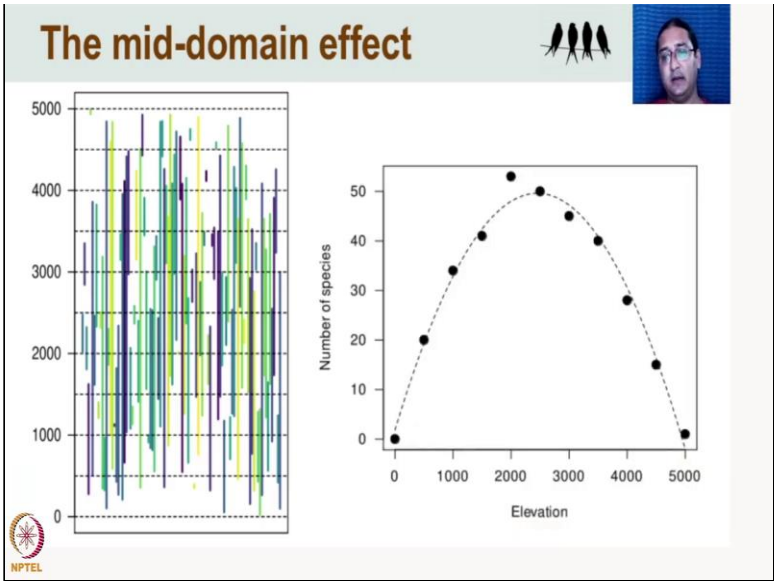

What you see is that you get this mid-domain effect because the maximum number of ranges will overlap at middle elevation. So, from this data itself which I generate randomly for a mountain… for a mountain that goes from zero to 5000 meters just overlay these elevational ranges randomly this is the effect that you get, you get this mid-domain effect because most of the bird species ranges will overlap with each other.

And therefore, most birds will exist or coexist with each other at the mid elevation simply based on a random effect. So, this is what is called the mid-domain effect. The mid-domain effect basically says that the maximum in a bounded domain if you put on place randomly sized elevational ranges in a random manner in a in this bounded domain which is bounded between the low elevation and the peak.

then the maximum number of elevational ranges will overlap at the mid elevation. And if the maximum number of ranges overlap in the mid elevation that means that the maximum number of species also coexist at the mid elevation and this is a completely randomly generated process. There is no biological mechanism that might be creating this mid elevation hump. And a lot of people have argued that the middle elevation hump is simply a result of the maximum overlap of species ranges at the mid elevations.

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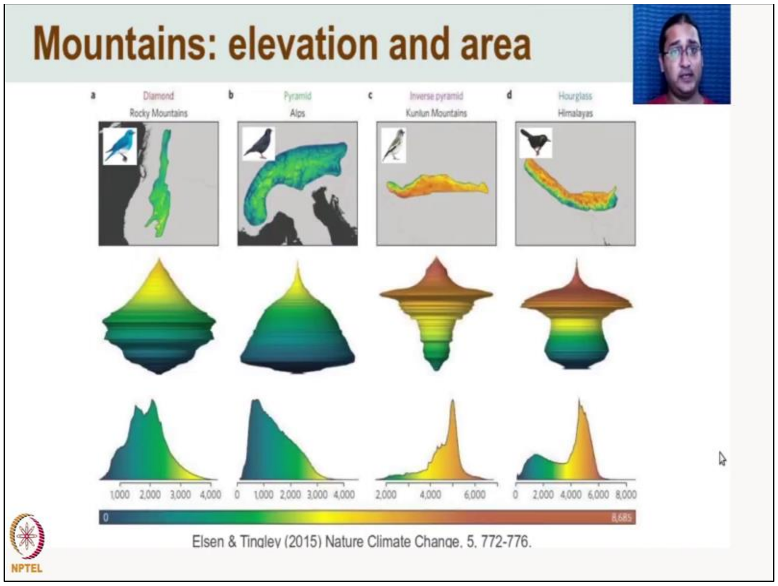

Area as we saw is an important determinant of species richness, the larger the area you have the greater the number of species. And we often imagine mountains to be cones right we often imagine mountains that will have the largest area at the lowest elevations because that if mountains are shaped like cones as you go further up the mountain the area also at the higher elevations reduces.

So, the area at the lowest elevation will be very very high, the area at the highest elevation will be very very low. But, mountains are not necessarily shaped as cones. So, you can have diamond shaped mountains where the area is very low. And so, this is showing you four different mountain ranges: The Rocky Mountains, the Alps, the Kunlun Shan and the Himalayas. And what you see are very very different shape profiles of these mountains.

The Rocky Mountains have very low area at lower elevations, maximum area at mid elevations and then low area again at the highest elevations. So, that what are called diamond shaped mountains. Then you have pyramid shaped mountains, inverse pyramids where actually the maximum area is towards the highest elevations of this mountain range. And the Himalayas which are like an hourglass shaped pattern
where you have a low area at the lower elevations, you have an increase in area at the mid elevations and then as you get to the Tibetan plateau you have the maximum area. And the question is can area on the mountain itself and the species area relationship explain species richness is it

that because area peaks at about 2000 meters in the Himalayas that you see maximum species richness in the Himalayas at 2000 meters.

But if you go further higher up it gets too cold for species you need high species adapted to high climatic variability on the Tibetan plateau and therefore you see a lower number of species there. And area is an interesting potential explanation for the mid domain effect.

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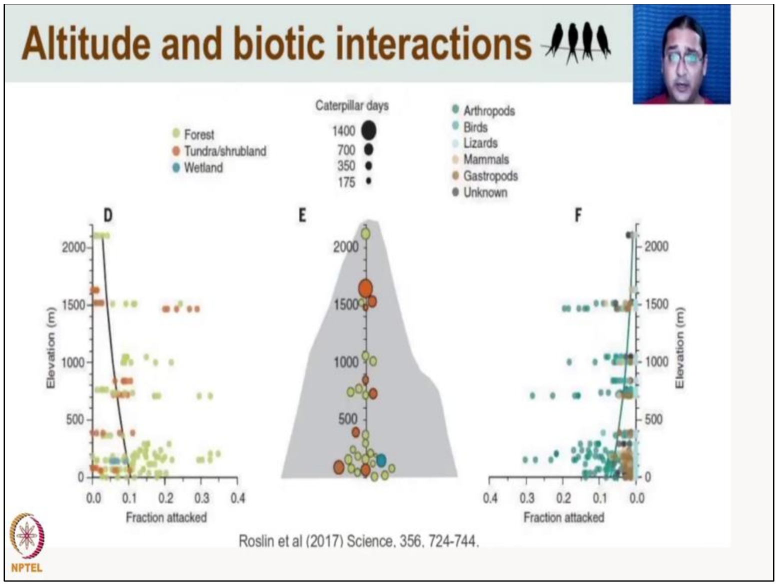

Biotic interactions again like we saw with the latitude and diversity gradient. Biotic interactions again seem to be with those model caterpillars again seem to be highest at low elevations and low at higher elevations. So, the maximum number of model caterpillars attacked is actually at the lowest elevation at about zero meters and has to go higher up the mountain, the predation on caterpillars declines.

Of course, this is an example of insects not with birds, but if biotic interactions are actually very very high at low elevations then it could be that these high biotic interactions are what are leading to smaller populations and less competition between populations and therefore the higher probability of coexistence.

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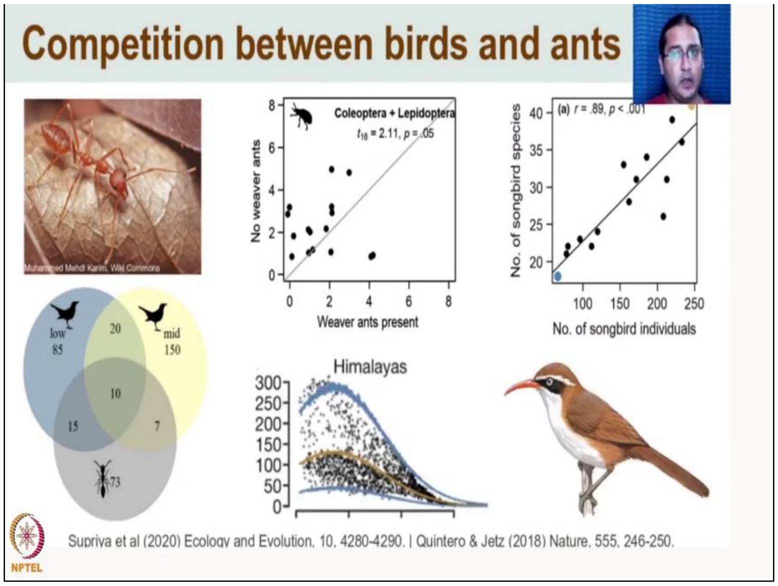

Very very interesting recent work that has come out on a potential explanation for why there are a maximum number of bird species at about 2000 meters in the Himalayas. Again, if you look at the graph at the bottom there you see that the maximum number of bird species in the Himalayas peaks it is maximum at about 2000 meters. And this very interesting piece of work is from the eastern Himalayas where you find the species of ant called *Oecophylla* or the weaver ant.

And *Oecophylla* eats insects and a lot of birds eat insects and so, there is a large amount of dietary overlap between *Oecophylla* and birds. So, if you look at what they are eating and look at that Venn diagram the number of prey items that both the ants are eating and the birds are eating is very very high. So, the birds and the ants are actually potentially competing for the same prey. Now if they are competing for the same prey look at look at the graph in the middle there, where you have weaver ants present and no weaver ants present and the density of insects on a plant.

So, if you look at a tree and you remove all the weaver ants from the tree, what happens. So, where the weaver ants are present and there are no weaver ants you look at that line through the graph that is the one is to one line which means that the number of weaver ants present is equal the number of insects present is equal both when there are weaver ants and there are no weaver ants rights. But most of those points are higher than that one is to one line which means that when you remove weaver ants from from their trees the arthropod abundance actually increases greatly.

Because these ants are not eating those arthropods anymore. They are not eating those insects beetles and moths and butterflies caterpillars. So, in the absence of weaver ants you have much more prey available and we have seen this relationship before where you have more prey or more resources there are more individuals and if there are more individuals there are more species. So, if the weaver ants are actually competing with birds then they are reducing the number of individual birds that can be supported where they are present.

Because they are reducing the number of individuals that can be supported where they are present they are also reducing the number of species of birds that are present in the Himalayas present where they where they occur. And interestingly weaver ants the elevational range of the weaver ants is from the foothills to 1800 meters and beyond 1800 meters is where weaver ants stop.

So, competition with weaver ants comes down and because the ants are no longer competing with birds, 2000 meters where the weaver and stop is where you can support a greater number of individual birds and therefore a greater number of species of birds. So, this is a very interesting (fascinating) explanation for the mid elevation peak in the Himalayas is that ants are actually competing with birds at the lower elevations and reducing species richness whereas where the ants stop is where species richness is the highest.

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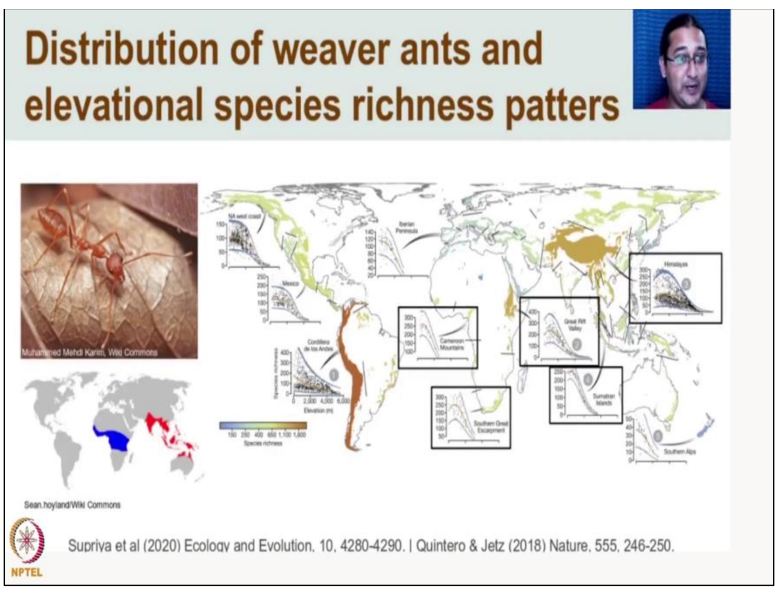

And very interestingly if you look at species richness patterns where *Oecophylla* is present which is basically Africa and Australasia. You see this mid-domain you see this mid-elevation hump where *Oecophylla* is present at the low elevations as a genus you can see the distribution of *Oecophylla* over there which is Africa at the bottom left there which is Africa and Asia, southeast Asia, northern Australia and wherever *Oecophylla* is present the relationship between elevation and species richness seems to be this mid elevation peak.

Whereas in the new world which is the Americas *Oecophylla* is absent there are no *Oecophylla* ants and the maximum number of species is actually at the low elevations and there is a decline in species richness as you go to the higher elevations. So, very very fascinating stuff.

Well! Just to recap, macroecology is asking questions about species issues and diversity patterns at large spatial scales, why are there more species the tropics? what is the relationship between elevation and specie richness? and it actually links lot of ecology across scales.

So, when you have large scale geographic patterns your latitude altitude. You are also looking at the impact of abiotic factors like productivity, what is the distribution of energy and rainfall? What was the historical abiotic environment like? and it is then at the very at the species scale it is looking at things like body size, dispersal ability, rarity, commonness, rarity as double jeopardy and range size and rarity what are the relationships between these and how do all of these things affect extinction risk.

And so macroecology is turning out to be a field that is becoming highly relevant to conservation as well. So, thank you very much I will end here. That was macroecology.