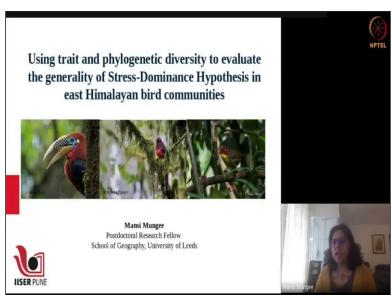
Basic Course in Ornithology Dr. Mansi Mungee Postdoctoral Research Fellow School of Geography University of Leeds, UK

Lecture 30 Macroecology - Case Study _ LIVE

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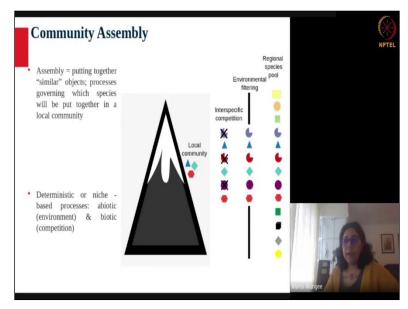
So, like I was saying. So, the case study that I am discussing today is sort of an extension of my PhD work in which I will be addressing important ecological hypothesis known as the stress dominance hypothesis or the SDH. The original study like Umesh mentioned also involves an evaluation of SDH for hawkmoths followed by a subsequent comparison between hawkmoths and birds which were both the primary taxa focus during my PhD.

But well today is all about the birds and I will restrict myself to just SDH and birds of a small region in the eastern Himalayas. I will start with a brief overview of community assembly and some basics of trait and phylogenetic diversity. And how the three can be used together to test the SDH in natural ecological communities and finally, I will use a data set of birds from my PhD to test this particular hypothesis.

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So, we will start with some basics and before I begin actually, I want to just mention that community assembly and functional diversity and phylogenetic diversity are really vast and mutually non-exclusive subject areas in their own right. And I am covering only aspects of these topics which are relevant for understanding and exploring the SDH. But I believe there is some additional reading that has been shared with you all or will be circulated which should help you navigate these subjects a little more deeply. So, I will start with the basics, community assembly. (Refer Slide Time: 01:48)



Very simply assemblies just means in plain English putting together or a collection of similar objects, in the context of ecology, community assembly refers to a set of processes or mechanisms

which determine which species will be observed in any given area or a local community. Now, even without any background just intuitively, I think we can all come up with an exhaustive list of these processes.

If I just ask a simple question, why is the species found here and not there? Is it the environment or the abiotic factors or is it the presence or absence of another species such as a competitor or a symbiote or a predator which are the biotic factors. Or is it simply a random or a chance historical dispersal event which has introduced the species to this location. And one of the most fundamental goals in ecology is to understand and quantify the relative importance of these different assembly processes or mechanisms.

Very broadly these assembly processes can be classified as either niche based or deterministic and neutral processes. And I will talk only about the niche based processes today, which are relevant for understanding the SDH. So, the niche based processes themselves are of two types - abiotic and biotic like I mentioned and both of these can be best illustrated with the help of a schematic that I have shown to the right here.

So, in this cartoon, I will be using the example of a mountain system or an elevation gradient to elucidate a lot of my concepts because my case study will also be along an elevational gradient eventually. So, if you consider this hypothetical mountain system in the outermost panel is a regional species pool (which is basically just all the species that are found across the entire elevational gradient of this mountain system).

From this regional species pool, there are certain species which will be able to coexist in a local community (which is the community of birds found at a specific elevation or a given narrow elevational belt). What determines the composition of this local community given a regional larger species pool is the question that we are trying to address here. Now there are these two sets of sort of hierarchical filters that are commonly used to determine the composition of a local community.

First is environmental filtering, because the species that are found across the entire elevational range will have different adaptations to survive at the abiotic conditions of the different elevations.

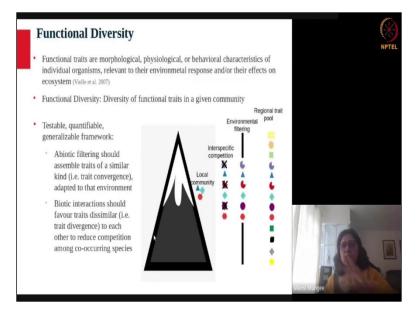
So, the species that can survive at the highest and the lowest elevations will be filtered out and only the ones which can actually effectively colonize the intermediate elevations will be selected by this first set of filtering.

Now, because all these species are very similar to each other, in the sense that they all exhibit characteristic or features that are needed to survive in this relatively homogeneous environmental conditions of a specific elevational belt. The inter-specific competition will further rule out certain species which are too similar to each other. And in ecology, we refer to this as something known as a niche overlap.

So, species which have which exhibit high niche overlap will be rejected by this second set of filtering and you will finally get a local community which is essentially a trade-off between species which are similar environmentally and not too similar ecologically to minimize competition between themselves. And these two filters are known as environmental filtering and inter-specific competition.

And a lot of community ecology is actually centered around understanding and quantifying the relative importance of these two processes of community assembly and how these change along elevational or other environmental gradients. Now, this is all nice and good as a conceptual framework but how do you actually go about quantifying or testing some of these given a natural community or an empirical data set. And this is where the concepts of functional diversity and phylogenetic diversity come into play.

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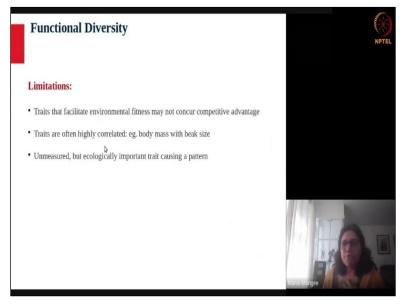
So, we will start with functional diversity and to first understand functional diversity, we need to understand functional traits. So, very simply functional traits are defined as a morphological, physiological or behavioral characteristic of individual organisms relevant to their environmental response which is your environmental filtering and or their effects on ecosystem properties or other species which is your inter-specific competition.

And functional diversity is just the diversity of functional traits in a given community. So, all this simply means is that now instead of asking the question why are these species found here? I am instead asking why are these beak sizes found here for instance. And if we translate the functional trait concept to our previous schematic you have the outermost panel as now a regional trait pool as opposed to a regional species pool.

And you have a local community which consists of a certain selection of traits which are selected by the environment to help those species survive and colonize a given environmental condition and which are not too similar to each other to minimize inter-specific competition. So, the advantage of using traits instead of species as the unit of investigation is first that traits are measurable. And secondly, we now have a testable and a quantifiable framework to assess the relative importance of environmental filtering versus inter-specific competition. Because if environmental filtering dominates, if this filter dominates then the traits of the local community will be very similar to each other more similar to each other as compared to a random sample from the regional trait pool. Whereas, if inter-specific competition dominates then the traits of a local community will be more dissimilar to each other as compared to a random sample from the regional trait pool.

And this simple phenomenon of studying patterns and traits similarity and dissimilarities along environmental gradients has actually become one of the most important analytical benchmarks in modern community ecology. But of course, like other analytical developments this has its limitations.

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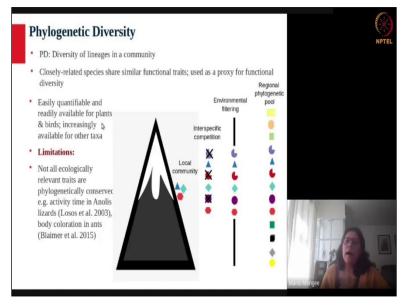
And we will come to that now. So, first, in the previous example we assumed that both the filters or both the mechanisms that is environmental filtering and inter-specific competition they will act upon the same trait. That is if we consider beak size, we are assuming that the environment will determine the beak sizes and so, will the competitive interactions but this is actually very difficult to assess in reality.

It may well happen that if a trait x is more important for survival given the abiotic conditions then another trait why is important for resource competition for example body size and beak size. Body size may actually be more important for environmental filtering but beak size for resource competition. So, the two processes are not acting on the same trait. So, using the same trait you cannot sort of a priori predict to understand both the processes.

Second and actually more important is that if you use more than one traits, they may actually just be very correlated and mask the pattern of one trait by the other. So, for again the instance of beak size and body size, we know that there is allometric relationship between different traits of species. A larger bird will also have a larger beak size. So, body size is actually correlated highly with beak size.

And thus if we use them separately how robust will our observations be given that one is actually just mimicking the pattern of the other. And finally it is impossible to measure all functional traits. So, what if the pattern that we observe is getting masked by the importance of another trait that we have not measured. But because they are correlated, we are getting one pattern even though the other trait which was not measured is being completely ignored.

So, to address some of these issues, the concept of phylogenetic diversity has been introduced and is used.



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So, after species and functional diversity, phylogenetic diversity is the third dimension of biodiversity and is increasingly used as a surrogate or a complementary metric to quantify the

diversity of a region. It represents the diversity of lineages in a given community. To give a very simple example, if you consider two communities and they both consist of ten species they will have identical species richness.

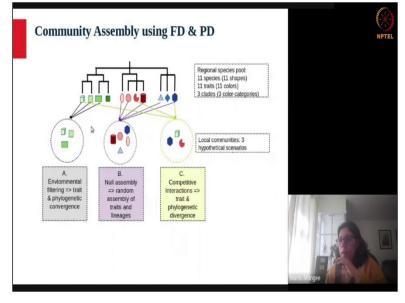
But they can have very different phylogenetic diversities, if those ten species are from the same genus in one case but they are from 10 different genera in the other case. So, you will have a higher diversity of phylogenies in the second case and thus this particular community may be more important from conservation viewpoint in certain scenarios. Now the simple rationale for using phylogenetic diversity as a surrogate for functional diversity is that traits are conserved across the phylogeny which means that closely related species have more similar traits to each other than distantly related species.

This is very intuitive because you know Warbler are more similar in body size to other Warbler than Hornbills or Magpies. For instance, and because phylogenetic trees are now readily available for many taxa specially for birds and plants. You can simply use phylogenetic similarity instead of measuring traits for all species and going back to my favorite mountain system schematic. So, instead of a regional trade pool you now have a regional phylogenetic pool and environmental filtering is selecting for species which are closely related because they all share similar traits which help them colonize a given environmental conditions. And inter-specific competition will reject species or will not allow certain species to persist which are too similar to each other or which exhibit high niche overlap. And you finally have a local community which is again a trade-off between being too similar and being similar as compared to the regional pool.

So, again there are certain caveats to using phylogenetic diversity. First, was the first assumption that we made which is that closely related species will also have similar traits. This actually is not always true in nature and there are two classical examples to this, one is the activity time in certain lizards and the second is body coloration in ants. So, it is actually very important to test that the traits that you are using are actually closely related are actually more similar to each other for closely related species.

So, the best given all these caveats of functional diversity and phylogenetic diversity the best approach ideally is to use both of these together to inform the relative importance of community assembly mechanisms. And the usage of both of these together can again be best illustrated with the help of a schematic.

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So, here I have shown a regional species pool, which consists of 11 species in three distinct clades. The species within a clade have all very similar traits. So, the different shades of a colour represent the different traits and the different colour categories themselves represent different clades. So, now in the instance of strong environmental filtering, you will expect the communities to exhibit trait and phylogenetic convergence.

That is the species that will inhabit this particular community will all have very similar traits and they will all be from a single clade or a very narrowly or very closely related. This is because the environment has selected for specific traits and those traits are phylogenetically conserved that is they are similar in closely related species. In the other extreme, under the instance of competitive interactions, the competition will ensure that very closely related species are actually not coexisting because otherwise they will compete for limiting resources.

And thus, you get a scenario in which the species come from different the species comprise of different traits and therefore they come from distinct lineages. And you can actually test for the

similarity or dissimilarity of traits within a community with a randomly assembled community to inform whether the observed patterns of traits is actually clustered or over dispersed as compared to your random community.

So, now we have a conceptual framework of under what conditions environmental filtering dominates and under what conditions competitive interactions dominate and how you can actually test for some of these things. The next obvious question is can you make certain predictions of how these two processes will vary along a elevational gradient or environmental gradient and this is where the stress dominance hypothesis comes along.

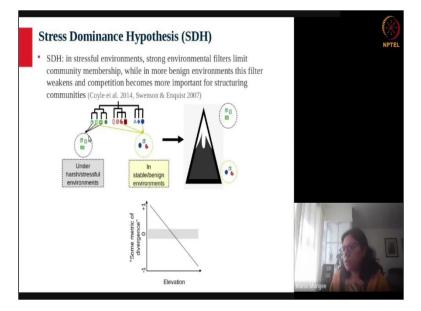
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So, the stress dominance hypothesis or the SDH, it makes an important and explicit prediction that the strength of environmental filtering should increase towards the highest elevations. Because very simply, the abiotic conditions are stressful and therefore only species with very specific adaptations should be able to survive in such conditions whereas in the more benign or stable conditions of the lowest elevations competition becomes more important.

And since the external pressures from environment are minimized species can actually invest in developing more competitive strategies as opposed to simply survival.

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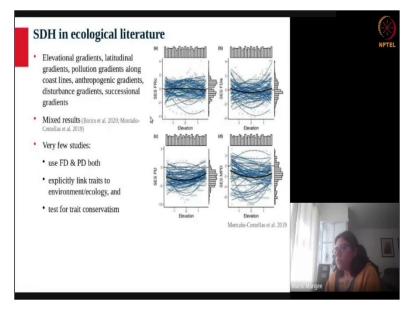


And we can look at this in the form of a schematic again. So, we had a scenario of strong environmental filtering where the species within a local community exhibit similar traits and they are also from and they are also phylogenetically conserved and this scenario is expected towards the higher elevations whereas a diverged pattern such as this one is expected at the lower elevations. And this is something that is commonly tested using certain metric of divergence which many metrics are available.

And they basically just calculate some measure of distance between the traits or phylogenies of all the co-occurring species within a local community and that metric itself can be plotted against elevation. So, a positive value of that metric represents over dispersion which is this scenario and a negative value of the same metric represents clustering or convergence which is this scenario, which means the traits are very similar to each other and when the metric has measured phylogenetic diversity then the lineages are very close to each other.

And this pattern is what is known as the stress dominance hypothesis, that is your metric of divergence should actually decrease with elevation. Now throughout this talk, I have used the example of a mountain system as the stress gradient. But tests of SDH have been extensively conducted along many different kinds of stress gradient, I think I have noted yeah.

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So, elevational gradients are one kind of stress gradients, there are latitudinal gradients where you expect higher latitudes to be more stressful in terms of temperature or productivity. Pollution gradients along coastline, they can be anthropogenic gradients and disturbance gradients and successional gradients where again the productivity decreases along the gradient of succession. This figure on the right actually represents a meta-analysis or a study which has shown stress which has shown patterns of trait and phylogenetic clustering along different mountain systems in the world.

So, the top two figures correspond to metrics of trait divergence and the bottom two plots correspond to phylogenetic divergence and this was tested along 46 elevational gradients (I think). And you can see the histograms on the right they show that most of these are clustered around zero which means that most of the elevation communities along elevational gradients did not exhibit any pattern.

So, the stress dominance hypothesis was actually ruled out as a general mechanism or a general pattern. However, one important point to note here is that very few studies have actually used phylogenetic and functional diversity both, very few studies have explicitly linked traits to the environment or the ecology. Because I mentioned that it is important to know whether the trait you are using is more meaningful for environmental filtering or does it play a more important role in a species competitive strategies.

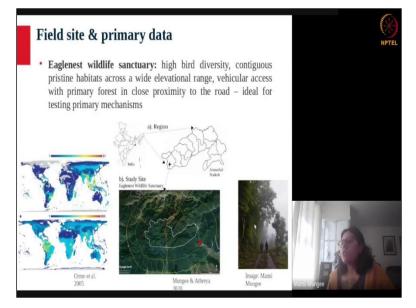
And finally explicit tests for trait conservatism, which means that you need to actually test whether the traits that you are using are conserved across the phylogeny. That is are the closely related species actually exhibiting more similar traits as compared to distantly related species. And in the next section, I finally demonstrate the use of a systematic data set of birds from along a broad elevational gradient in the eastern Himalaya to address some of these issues and test for SDH in these bird communities.

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So, I shall start with a quick overview of the struggle of the study region and the sampling protocols and the primary data that was collected.

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So, this study was done in Eaglenest wildlife sanctuary, the figure on the bottom leftmost panel is a famous one I believe. It shows it sort of puts the region study region in a global context and it shows the top panel shows the threatened species diversity, bird species and the bottom panel shows the number of species bird species. And in both scenarios, you can see that eastern Himalayas ranks very high on a global scale on a global index.

And Eaglenest wildlife sanctuaries nested within this larger east Himalayan global biodiversity hotspot. So, within this region Eaglenest itself is a very small protected area roughly around 220 square kilometers. It is unique in spanning more than 3000 meters in elevation. It has a motorable road providing access to some of the highest elevations and more importantly the primary forest occurs in very close proximity to this road.

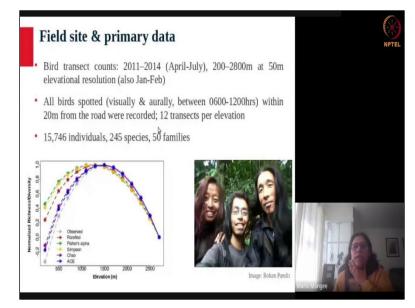
So, you can actually drive up to 2000 meters and just get out of your vehicle and start counting birds and this orange line that you see here that is the Eaglenest road it goes right up to the pass which is the highest point and then down again. There are some other unique features to Eaglenest one of which is that the distance the straight line distance aerial distance between the lowest and the highest elevation points in Eaglenest is roughly just about 20 kilometers.

But the temperature difference is more than 20 degrees, which is actually equivalent to a latitudinal difference of 20 degrees or more than 2000 kilometers. So, you will actually have to walk 2000

kilometers across a latitudinal gradient to experience the same shift in temperature that you can see here in Eaglenest at 20 kilometers. So, this steep elevational gradient presents an exciting opportunity to test SDH.

Because the environment changes sharply and you can therefore expect the strength of environmental filtering to change sharply. Further, because the bird diversity is so, high in this region you can expect competitive strategies or competitive interactions to play a very important role in determining coexistence here. So, all these factors make Eaglenest sort of an ideal location to test the SDH.

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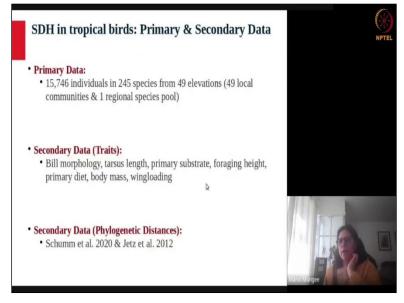
So, coming to the primary data as I mentioned before my PhD was a comparative study between several community and species level properties across hawkmoths and birds. And the primary data related to the bird component of my species was actually collected by this remarkable birder Rohan Pandith who is this guy in the middle here. So, Rohan was a project student in the lab and he conducted really impressive and exhaustive transit surveys.

During 2011-2014 at 50 meter elevational resolution which means that he went he walked along the Eaglenest road he stopped at every 50 meter gain in elevation and he conducted a transit count of 200 meters along the road and counted all birds visually and orally between 6 a.m and 12 p.m.

and he kept shifting between these time zones to cover the entire time track for each transit. He did this 12 times for each elevational band.

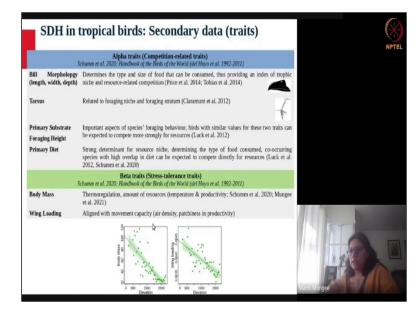
So, there were 12 transits in duplicates. So, 12 into 2 at each 50 meter band which gave me an impressive data set of around 15700 individuals in 245 species and 50 families. So, this is what the plot of species richness versus elevation looks like I have used multiple indices this is just to give you an idea of what the distribution is like. So, I have used this data set to test for the presence of SDH or the conformity to SDH in this region.

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And now the raw ingredients for needed for a comprehensive test of the stress dominance hypothesis are first is the species data, second is the trait data and finally the phylogenetic data. So, the primary data comprises of 245 species and more than 15000 individuals from 49 elevations. So, basically, I have 49 local communities and one regional species pool which consists of 245 species.

I compiled a set of secondary data consisting of the following traits which I will talk about in the next slide and finally a phylogenetic tree was compiled based on again existing literature. (**Refer Slide Time: 24:44**)



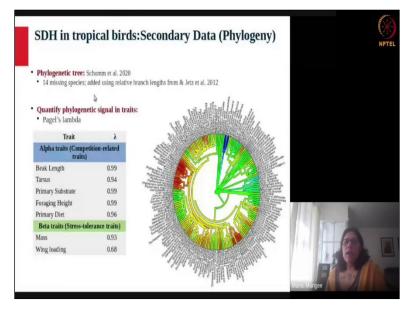
So, these are some of the traits that were compiled bill morphology which is bill length width and depth. Beak morphology is important in birds it determines the type and size of food that can be consumed. So, species that exhibit very similar beak morphology can be expected to be strong competitors and thus beak morphology was classified as a competition related trait or alpha trait. So, I classified all the traits into two categories alpha and beta.

Depending on whether I expect them to play a stronger role in competitive interactions or in environmental filtering. The next rate was tarsus length, which is related to foraging niche and foraging stratum again species with similar foraging niche and stratum are expected to be strong competitors. Similarly primary substrate foraging height and primary diet these are all related to competitive strategies in birds.

And body mass and wing loading were chosen as metrics of beta traits because I expect body mass and wing loading to play a stronger role in allowing birds to navigate the abiotic conditions such as temperature and air density which changes rapidly along the elevational gradient. And of course, the first step was to check that the traits that I am using as response trait or beta traits are actually responding to the environment or no.

Which is why I assessed the variation of body mass and wing loading with elevation and I found a very strong response at the level of communities the birds in that region exhibit a strong decline in body mass and wing loading as you go higher. So, which gives me confidence that the traits that I am choosing are actually robust beta traits that is their environment is actually selecting for specific traits at specific elevations.

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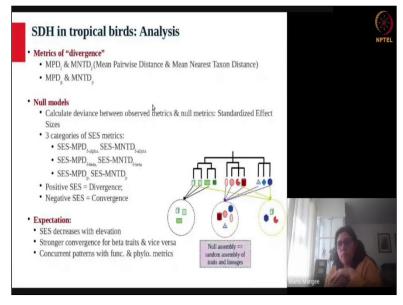


So, moving on to the phylogenetic tree, so the phylogenetic tree for birds of the region has been assembled previously by a Schumm et al and there were 14 missing species which were added from another source. Now I mentioned previously that it is important to make sure that the traits that you are using are actually phylogenetically conserved that is you need to make sure that closely related species actually also have similar traits.

So, this can be assessed by something known as a lambda metric which basically gives the metric itself varies between 0 and 1 and gives you the degree to which traits are phylogenetically conserved. So, all the traits were tested using pages lambda and they showed high phylogenetic convergence here and here you can see I think this is wing loading across the tips of the phylogeny.

So, the colours represent absolute values and you can see that similar coloured tips, the terminal nodes actually are more pluck clustered across the phylogeny. So, the oranges here are together the blue here is together in here which means that closely related species are also exhibiting similar wing loading or similar traits. So, I have used wing loading which is actually one of the least conserved traits in my collection here.

So, now the raw ingredients that I need for testing SDH is ready which is basically my primary data my traits and my phylogenetic data. I will move on to the analytical or the statistical section. (**Refer Slide Time: 28:13**)



So, the next is of course the selection of the metric of divergence and there is a whole suite of metrics available in the ecological literature and I have chosen these two particular ones called MPD and MNTD. We do not need to go into the details of this all you need to remember is that there were two metrics which were used for functional and phylogenetic diversity for calculating divergence within local community.

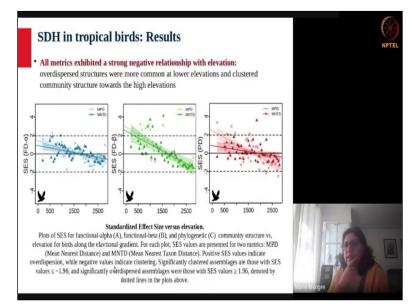
So, basically if I go back to the schematic, all I have done is I have calculated MPD and MNTD for each local community along the elevational gradient and I have calculated the deviance of that metric with a randomly assembled community. And I have tried to assess how that deviance changes along the elevational gradient. So, there are three categories. So, the deviance itself is a standardized metric and it is expected it is expected to reduce with elevation.

So, it does not really matter whether the metric itself is coming from alpha traits or beta traits or phylogenetic diversity. The point is that the metric should decrease with elevation. So, a positive value of the metric indicates divergence and a negative value indicates convergence. And the metric itself should decrease with elevation. I should also expect like I mentioned earlier I should

expect stronger convergence for beta traits because environmental filters select for beta traits and I should expect stronger divergence for alpha traits.

And because I have tested for phylogenetic conservatism, I expect concurrent patterns between functional and phylogenetic metrics.

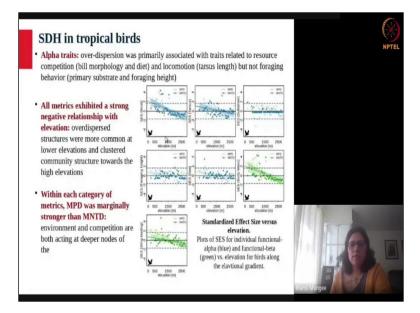
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So, coming to the results for the birds of Eaglenest. So, now if you see here, these are three plots the first one shows my metric of divergence for functional alpha traits which is my competition related traits. The second one is for functional beta traits and the third one is for phylogenetic diversity. You can see that in all three scenarios there is a strong negative slope that is the metric of divergence actually declines with elevation as expected.

The strongest response was for functional beta traits. Overall, all communities were more over dispersed as compared to under dispersed and all exhibited a negative decline with elevation. Now, if you recall earlier, I actually expected a higher divergence of alpha traits but on the contrary, I am getting a higher divergence of beta traits whereas beta traits should have actually given me high under dispersion towards the higher elevations.

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So, to look at this a little more closely, I assessed individual traits in my next figure here instead of using multivariate alpha and beta traits. So here, I can see in blue are all my alpha traits and I can see here that over dispersion that is positive SES values are actually most related to beak and tarsus and there is really no change in the SES of substrate and very weak association between foraging height and diet.

So, much of the signal that I was getting in my alpha traits was coming just from beak sizes. And similarly, if I look at beta traits in fact if you look at alpha traits beak again there is really no signal after about 1500 meters. So, at higher elevations these are just really not responding which is what something I would expect for an alpha trait. There was divergence at lower elevation but the environmental filtering is really making no effect at the highest elevation.

So, for the beta trait contrary to my expectation I did not expect I did not find any convergence at the highest elevation but I did find divergence at the lower elevations. But overall, all metrics exhibited a strong negative relationship with elevation.

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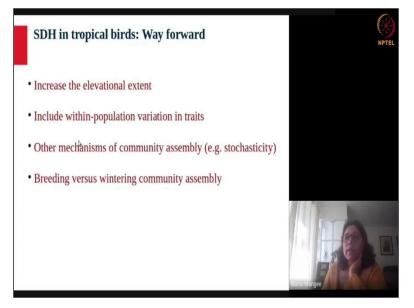


And more importantly, what I observed was that communities in general are more over dispersed than clustered. Which means that for the bird communities of Eaglenest overall competitive interactions seem to be playing a more important role as compared to environmental filtering. And this is an important study because in previous studies a lot of people have remarked that for avian communities worldwide

environmental filtering seems to be a more pronounced mechanism at elevations above 3000 meters which was really lacking in my study. Most of my all my samples were up till 2800 meters and it appears like at that elevational extent competitive interactions seem to be playing a predominant role. Overall, I still think that the communities of birds and Eaglenest conform to SDH because of the strong negative slope that I see in all of the traits.

And all the metrics of diversity which means that the strength of environmental filtering is definitely decreasing with elevation.

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And finally, there are certain things that I expect to do in the future some of which is increase the elevational extent and see actually whether environmental filtering extends beyond the elevation beyond 2800 meters. The second is to use within population variation in traits that is to characterize traits at the level of individuals in the community as opposed to species mean traits which I have used here.

Then I have talked only about the niche based processes of community assembly. There are other mechanisms which I did not talk about which I hope to cover in the future such as the random events that I was talking about. And finally, Rohan has also collected a similarly impressive data set of birds from the wintering season that is January and February which I hope to include in this analysis in the future and see whether the mechanisms actually exhibit a similar pattern in the wintering season as well as they do in the breeding season and yeah I think this is about it. Thank you.