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Arthropod Assemblages at the Intersection of Epiphyte and Soil Habitats: An assessment of understory level nonvascular epiphyte communities and their connectivity within a tropical montane rainforest

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SIT Study Abroad

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An assessment of understory level nonvascular epiphyte communities and their connectivity within a tropical montane rainforest.

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Abstract:

Canopy arthropods communities represent a disproportionate amount of global species richness (Stuntz 2001). Understanding arthropod composition and connectivity of lower epiphyte communities is important in understanding how canopy arthropods communities are formed and will respond to change (Floren and Linsenmair 1998). As such this study examined arthropod assemblages living within nonvascular epiphyte communities (epiphyte mats) living directly upon lower trunk regions of 24 trees in a tropical montane rain forest within the Santa Lucia Nature Reserve in Pichincha, Ecuador. Trees were assessed for size, epiphyte diversity, and epiphyte coverage before arthropod sampling within the epiphyte mats. Soil assessments were taken as well to compare community structure at the zone of intersection between the two habitats. No direct correlation was found between size, epiphyte diversity, or coverage on the diversity of arthropods within the mats, however this meant that population density and species richness density was very strongly negatively correlated with surface area. Arthropod communities differed significantly between soil samples and epiphyte samples, including in morphospecies present and proportional composition of arthropod orders.

Resumen

Comunidades de artrópodos doseles representan una cantidad desproporcionada de la riqueza de especies global (Stuntz 2001). El entendimiento de composición y conectividad de artrópodos en comunidades de epifitos bajos es importante en el entendimiento como comunidades artrópodos doseles forman y responden a cambios (Floren y Linsenmair 1998). Esta investigación examinó colecciones de artrópodos viviendo dentro comunidades de epifitas no vasculares (epifita mats) viviendo directamente sobre los troncos de 24 árboles en un bosque nublado dentro de la Reserva Natural de Santa Lucia en Pichincha, Ecuador. Se evaluaron los árboles por tamaño, diversidad de epifitas, y cobertura de epifitas antes de muestreo de artrópodos dentro de las epifitias mats. Evaluaciones del suelo se tomaron para comparar estructura comunitaria a la zona de intersección entre estos dos hábitats. No se encontró ninguna correlación directa entre tamaño, diversidad de epifitas, ni cobertura en la diversidad de artrópodos dentro del substrato compuesto de las epifitas. Sin embargo, significó que densidad de población y riqueza de especies fue correlacionada muy fuertemente negativamente con el área superficie. Comunidades de artrópodos se difirió considerablemente entre muestras de suelo y epifitas, incluyendo en presencia de morfoespecies y en composición proporcional de ordenes artrópodos.

Acknowledgements:

I'd like to first start by thanking my program directors Xavier Silva, Ana Maria Ortega, and Diana Serrano, for their continued support and knowledge throughout this program. Next, I'd like to specially thank project advisor Holger Beck for introduction to the reserve, and guidance in site selection and methodology. Niki Melnick was an invaluable friend and ally in this project, helping with laboratory work of sorting and identifying insects. Furthermore, I'd like to give a heartfelt thank you to the staff at Santa Lucia, specifically Denis Merino, Graciela Santos, and Ruth for all their logistical and moral support throughout my stay in Santa Lucia and Nanegal; Freddy for the amazing food; and to Noé Morales, Leyder Riascos, and Luis Miño for their hard-work and friendship at the lodge.

Introduction:

Tropical montane rain forests, colloquially known as cloud rainforests, boast some of the highest biodiversity rates in the world. These ecosystems can be equated to "keystone ecosystems" in their contributions to water cycling carbon storage, and biodiversity. (Yanoviak 2006). Epiphyte -plants that germinate and spend their lives living on other plants (Zotz 2016)- play critical roles in each of these processes. Cloud forests can contain staggeringly high rates of epiphytes and can in some sites can exceed that of all other types of vegetation combined (Kelley et al. 1994).

These epiphytes play exceptionally important roles in supporting and promoting the diversity of arthropods within these ecosystems. Epiphytes transform landscapes and add structural and resource diversity of arboreal habitats (Angon et al 2009), serving as secondary foundation species for countless species of amphibians, mammals, birds, and arthropods (Solis et al .2021) by providing nurseries, feeding areas, and sanctuaries from predators or environmental pressures (Angelini and Silliman 2014). Due to their multifaceted role as foundational species, biodiversity within epiphyte communities can rival that of the entire tree canopy (Elwood and Foster 2004). Studies on biodiversity within epiphyte communities have sparked conversations about revising estimates on global biodiversity of arthropod species (Elwood and Foster 2004).

Due to their ecological importance, biodiversity of epiphytes and the communities they support has become a popular topic for research. Studies of arthropod diversity nearly universally focus on canopy level arthropod communities. Canopy level epiphyte dwelling arthropod communities are tremendously important and hold an immensely high rate of diversity and richness. This research dogma is driven in large part because tropical forest canopies contain most of the world's global biodiversity (Stuntz 2001). Moreover, the primary methodology of canopy arthropod assessment, fogging, is relatively easy and captures an effectively large amount of canopy arthropod diversity. However, these methods are flawed in the fact that they do not adequately sample the diversity found living within nonvascular epiphyte assemblages (Yanoviak 2003b). As such, non-vascular assemblages are very understudied. Few studies exist on these communities, known as epiphyte mats, but once again they are focused only on canopy epiphyte communities (Yanoviak *et al.* 2006, 2003a). This paradigm means that epiphyte communities in forest understory layers are very understudied, and overreliance of fogging means that dynamics of continuation and distribution of arthropods within these ecosystems are unknown.

Epiphytes are considered microhabitats, and generally considered to contain their own unique faunal assemblages (Stuntz 2001). However, because of the lack of information on non-canopy epiphytes it's unclear how arthropod diversity varies along the tree. Therefore, its difficult to make assessments about how these canopy communities are related to the rest of the forest ecosystem. Because these epiphyte communities support such a large portion of global biodiversity, understanding how their communities form and respond to change is critical especially as threats to these ecosystems increase (Yanoviak *et al.* 2006, Pounds *et al.* 1999, Lawton *et al* 2001, Thomas *et al* 2004). However, looking only at canopy communities is insufficient to capture an accurate image of how these communities form and respond to change (Floren and Linsenmair 1998). As such, knowledge of population dynamics and community of epiphyte communities in the understory is critical in the assessment of the formation and function of epiphyte communities throughout all forest canopy layers.

The principal objective of this study is to generate a novel description of the makeup of nonvascular epiphyte assemblages (hereafter: epiphyte mats) within tree understories and to assess connectivity of these communities to the soil habitat. These assemblages of epiphyte mats can serve as connective tissue, covering tree from soil to canopy. By focusing specifically on the lower level of the tree where the trunk

intersects the ground, we hope to capture a picture of how epiphyte communities are composed and influenced by their connecting soil. As reforestry projects attempt to generate healthy secondary forests and guide them into healthy primary forests, information about the connectivity of these ecosystems to their surroundings is critically important. Therefore, by providing a description of the population dynamics within this zone of intersection between the soil and epiphyte habitats, this study aims to provide information on how arthropod assemblages in nonvascular epiphyte communities are formed. This information on how these communities are composed and differ from their surroundings sheds light on how important processes, such as colonization and recovery, are driven.

Methods

Study Site

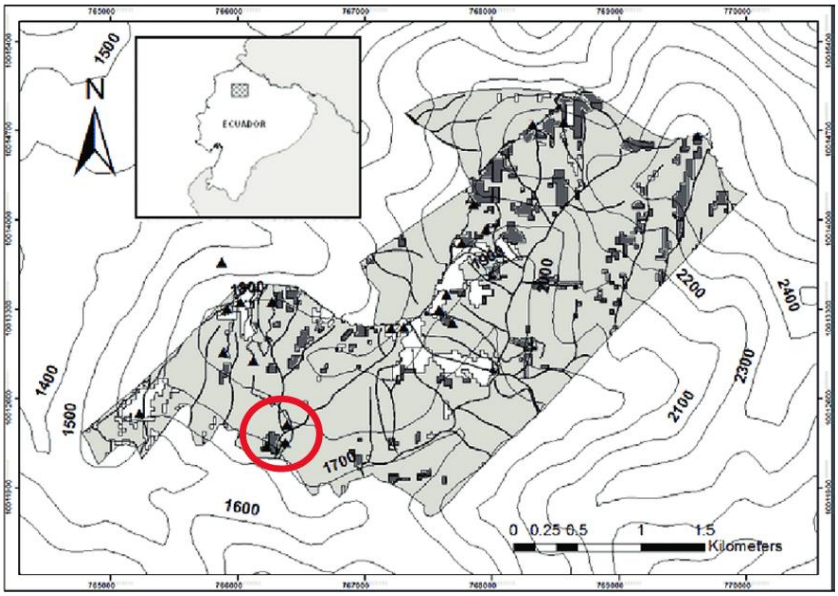

Figure 1: Elevation Map of Santa Lucia Cloud Forest Reserve. Red circle indicates study site at 1750m. Black contour lines show elevation, white shading shows silvopasture, gray shading shows primary forest, dark gray shows secondary.

Note: Map by Tolhurst et al, 2016.

Santa Lucia Cloud Forest Reserve is an approximately 730ha forest preserve located in the southern region of the choco-andino conservation corridor in Pichincha, Ecuador, containing approximately 80% primary forest and 15% secondary and scattered silvopastures (Tolhurst *et al.* 2016). This study took place in an approximately 200 meter long transect of primary forest at 1750m elevation. The site was chosen specifically for its constant elevation for the duration of the transect, to minimize the any confounding effects of altitudinal changes. Sampling occurred for 10 days between November 15th – November 30th. This period is typically the end of the dry season and start of the rainy season, but weather during this time was unusually dry, with no rain in the three weeks leading up to the study. Intermittent rain occurred during the study, but general weather conditions were constant during sampling hours.

Tree Selection

In this study, 24 trees were sampled across the length of the transect. All trees were free standing, mature canopy level trees with presence of nonvascular epiphyte communities. Trees with excessive climbers obscuring the central trunk were not sampled, neither were trees with extensive vegetative connections to other trees to avoid connectivity as confounding variables. Trees were selected based on these categories across the transect, sampling every eligible tree available within the first 10 meters to either side of the

transect. If two eligible trees were within 2 meters of each other, only the larger tree was sampled to avoid oversampling a geographically small area.

Sampling Procedure

Trees were divided into two sampling ranges based on height: 1-2m and 3-4m (hereafter: Low and high ranges). Within each zone, epiphyte communities upon the tree were evaluated for epiphyte diversity before sampling. For each range, data was taken on: estimated total percent coverage of epiphytes, number of fern morphospecies, number monocot morphospecies, number of dicot morphospecies, number of bromeliads, and tree circumference. This data was used to generate estimates on epiphyte diversity and surface area within each range.

Arthropod sampling started in the soil and progressively moved upwards across zones to avoid contamination of lower samples from arthropods fallen from other zones. Sampled of each zone occurred for five minutes, for a total of 15 minutes of arthropod collection. Longer times were proposed, but accumulation of samples generally slowed enough by minute 4 that a 5-minute sample was sufficient. Soil samplings occurred by hand in a 1m radius around the base of the tree. For five minutes, detritus on the soil was moved and examined and upper soil layers were disturbed with a knife to expose arthropods. Arthropods seen were collected using forceps into a 100mL plastic jar. For smaller arthropods harder to catch, the surrounding soil was scooped into the jar to capture. At the end of the five minutes, the rest of the jar was filled with 100mL of soil detritus for dissection in the lab. Large specimens that would not fit within the container or survive the return were photographed and recorded in the field and released.

Epiphyte arthropod sampling also occurred by hand. Epiphytes were first visually examined for surface dwellers that might leave once sampling began. Then, epiphyte mats were examined by a combination of scraping using a gallon sized sealable plastic bag upwards against the trunk or brushing the mat downwards, causing arthropods to fall inside the bag as the sample continued. This method collected arthropods living within both the vegetative and humic portion of the epiphyte mat (Yanoiak 2003a, 2006). Epiphyte mats were sampled using this method for the entire surface area of the tree along the 1m range, typically 3-4 times within the time allotted. After the five minutes, once again large arthropods were removed from the bag and identified in the field, while the rest of the contents in the bag, including epiphyte material and living samples were stored in a 100mL plastic jar. Additional epiphyte material would be collected if needed to fill the jar completely to ensure every sample captured the same quantity of epiphyte material. This procedure was identical for both epiphyte ranges, but sampling in the high range occurred on a 3-meter wooden ladder.

Mature bromeliads were collected from trees when present for laboratory dissection. If several bromeliads were present, the largest was chosen for sampling.

Laboratory work

In the lab, jars were emptied and examined in large plastic bowls. Soil and epiphyte material was dissected using forceps to further dislodge arthropods. Arthropods captured were placed into petri dishes for finer identification and to take photos. Each morphospecies was assigned a name and recorded, along with its population. Species to small to adequately examine by hand were examined underneath a 60x electronic microscope and photographed using the HiView microscope software.

Statistical Analysis

Microsoft Excel and R were both utilized for data analysis. Excel was used for graph making and analysis of statistical significance using Two Sample Z Tests for difference in proportion, and for Chi-Squared

statistical analysis. R program packages iNEXT and DIVO were utilized to estimate diversity indices for each site (Shannon and Simpson) and between sites (Sorenson, Horn, Jaccard).

Results:

1. *Initial statistics and site makeups*

Over 775 arthropods representing 180 unique morphospecies across 21 orders were collected and identified during the 10 days of sampling. Of these arthropods, the vast majority (405 individuals, 120 morphospecies) were found living within the nonvascular epiphyte matt directly upon the tree trunk between 1-4m in height. The second largest source were from the soil samples (232 individuals, 76 morphospecies), and the remaining from the bromeliad samples.

Epiphyte mats contained very high rates of arachnids, specifically typical spiders of the order Araneae which make up nearly 30% of the epiphytes total species richness. Other notable orders present in high richness include Hemiptera, Coleoptera, and Diptera. Araneae consisted of nearly 40% of total population within epiphyte communities.

Summary of Observations (All substrates)			
CLASS	Order	SPECIES RICHNESS	POPULATION
ARACHNIDA	ARANEAE	44	205
	OPLILIONES	10	33
	PSEUDOSCORPIONES	1	4
CHILOPODA	SCOLOPENDROMORPHA	3	6
DIPLOPODA	POLYDESMIDA	12	25
	JULIFORMIA	1	1
INSECTA`	APTERYGOTA	1	11
	BLATAREA	7	24
	COLEOPTERA	15	62
	DERMAPTERA	2	3
	DIPTERA	7	22
	HEMIPTERA	16	27
	HOMOPTERA	6	9
	HYMENOPTERA	11	143
	ORTHOPTERA	12	13
	THYSANOPTERA	1	1
	ZYGENTOMA	3	18
MALACOSTRACA	ONISCIDEA	5	41
ENTOGNATHA	COLLEMBOLA	1	49
UNCATEGORIZED	LARVAE	21	77
Total		179	774

Figure 2: Summary of arthropod observations during the 10-day observation period.

Using iNEXT statistical analysis (Figure 3), general diversity statistics for each of the four substrate categories (soil, low, high, and bromeliads) were generated. In general, the substrates were consistent in their overall biodiversity rankings, as they followed the same order from most diverse to least: Low epiphyte mat, high epiphyte mat, soil, bromeliads. within each diversity assessment (Richness, Shannon, and Simpson). The bromeliads in general underperformed expectations, with several bromeliads sampled resulting in no arthropods entirely, most likely due to general immaturity of bromeliad samples. Although not unusual (Stuntz et al 2002) they were excluded from the rest of the statistical analysis due to insufficient sampling.

iNEXT Diversity Report For Sampling Sites			
Assemblage	Diversity	Observed	Estimator
BR	Species richness	32	75.68
H		67	146.78
L		84	172.93
S		62	112.81
BR	Shannon diversity	10.59	15.06
H		39.95	59.60
L		47.56	68.17
S		25.13	33.14
BR	Simpson diversity	4.19	4.32
H		22.84	25.98
L		29.63	33.51
S		11.74	12.34

Figure 3: iNEXT diversity report for each of the four sampling substrates. Br = Bromeliad; L = “Low” 1-2m, H = “High” 3-4m, S = soil

Using the predicted richness values generated by the iNEXT rarefaction assessment, total species coverage was predicted and shown in Figure 4. In general, coverage in each site was very similar, with an average coverage of 0.48 and a standard deviation of only 0.047, implying that the sampling methods captured a roughly equal estimate of diversity within each site, ensuring that each site is equal in terms of completeness of data. However, this coverage value also implies that completeness of data is low, with only approximately 50% of global species captured. The rarefaction curve (Figure 5) and the effort curve (Figure 6) of accumulation within epiphyte mats showed a steady continuation in morphospecies accumulation throughout the duration of the investigation, with showed no signs of decrease. Average accumulation of new morphospecies per site within the mats was very high, at 2.5 species per site for an average of 5 new morphospecies per tree sampled. 58% of morphospecies were singletons, only occurring once.

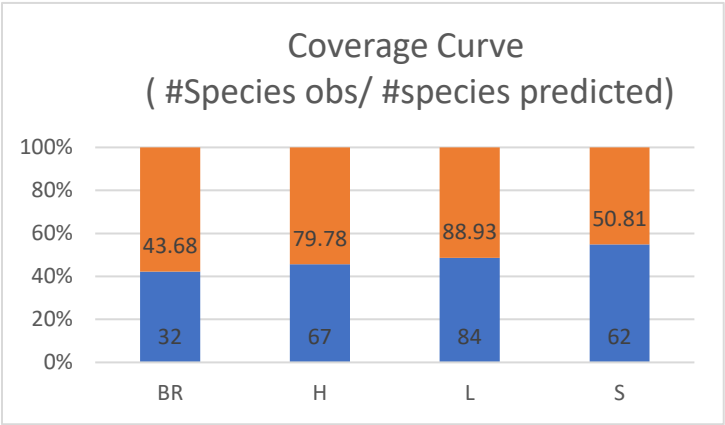

Figure 4: Coverage curve. Blue represents proportion of predicted species observed, orange represents predicted species not observed, numbers inside provide numerical counts for species observed and predicted species unobserved

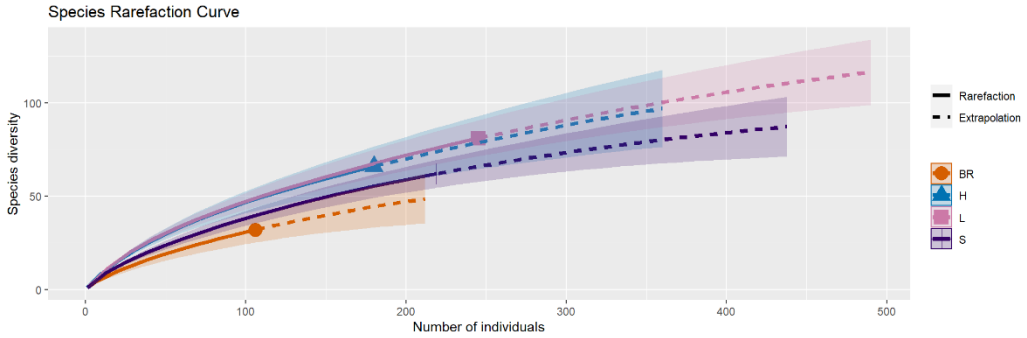

Figure 5: iNEXT generated rarefaction curve. Displays projected species accumulation for each of the four substrate categories based on observed richness and diversity

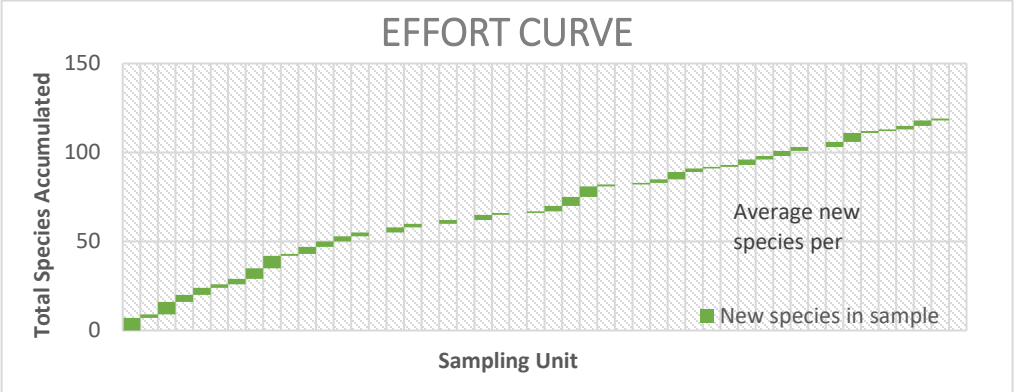

Figure 6: Effort Curve. Displays accumulation of species within epiphyte mats over the 48-sample study. Green vertical bars represent new species per sample

2. Factors influencing the diversity and makeup of the epiphyte microcosm

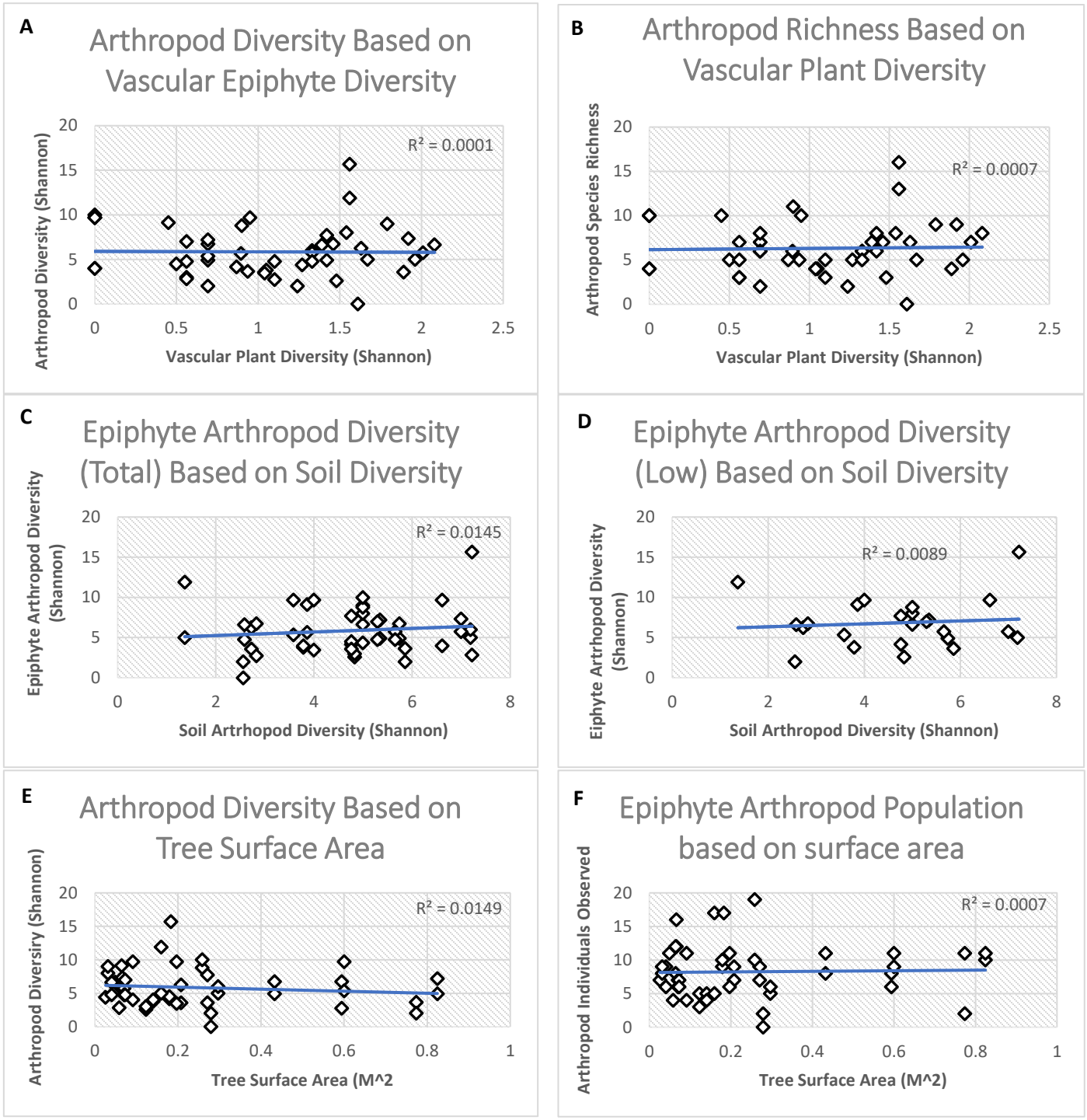

Figure 7: Variables measured to predict diversity of arthropod dwelling epiphytes. **A/B:** Observed Epiphyte arthropod diversity (Shannon) and richness (number species) predicted by the Shannon diversity of surrounding vascular epiphyte community. **C:** Observed Epiphyte arthropod diversity (Shannon) for entire tree (low and high ranges) predicted by the diversity of soil arthropods from corresponding soil sample (Shannon). **D:** Observed Epiphyte arthropod diversity (Shannon) for low range only predicted by the diversity of soil arthropods from corresponding soil sample (Shannon). **E/F:** Observed Epiphyte arthropod diversity (Shannon) and population predicted by the total surface area of the tree, calculated using circumference at center of each sample range.

Diversity within the epiphyte mat samples showed a large spread in variability, with an average Shannon index of 5.85 and standard deviation of 2.85. Approximately 30% of the Shannon diversity scores fell outside of the one standard deviation and combined with the slightly bell-shaped histogram in Figure 8 suggests that these distributions may follow a normal distribution.

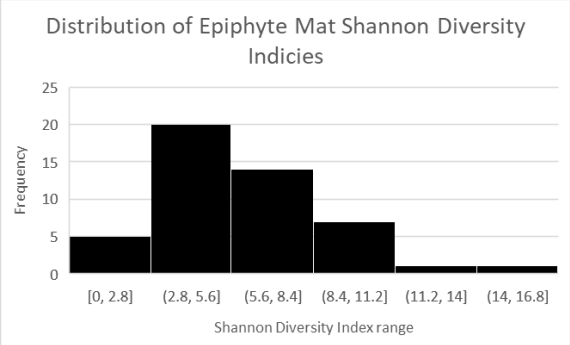

Figure 8: Histogram of Shannon diversity frequencies from epiphyte mat sites.

Median arthropod diversity increased slightly along with the coverage categories from 25-50%, 50-75+, to 75%+, implying a trend between epiphyte coverage and arthropod diversity although this trend was not significant (Figure 9). Nonvascular epiphyte diversity also failed a predictor of arthropod diversity, with no discernable trend in any direction detected and an R squared of nearly zero as shown in figure 7A and B.

Furthermore, arthropod diversity within the soil of the tree was not an accurate measurement of epiphyte arthropod diversity (Figure 7C). Trends did not improve when comparing only the "low" sample diversity with soil, shown in Figure 7D.

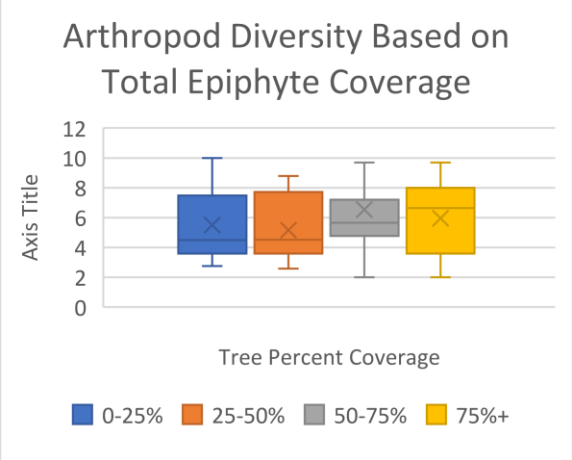

Figure 9: Distribution of arthropod diversity for each category of % tree surface area covered by epiphyte mats

Finally, the data showed no influence between arthropod diversity (Shannon and raw Population) and surface area of the tree (Figures 7E and F). Initially, errors in methodology were suspected as the cause. Because each sample was the same time, perhaps the time was insufficient to capture an equitable proportion of the population of trees with large surface areas compared with the small trees. To test this, an independent coverage curve was created (figure 10) based specifically on surface area to ensure that coverage was not biased by surface area. The coverage assessment showed that coverage of species was constant and independent of surface area, implying that these findings are not the result of error, and that arthropods are spatially distributed within epiphytes in ways not initially expected.

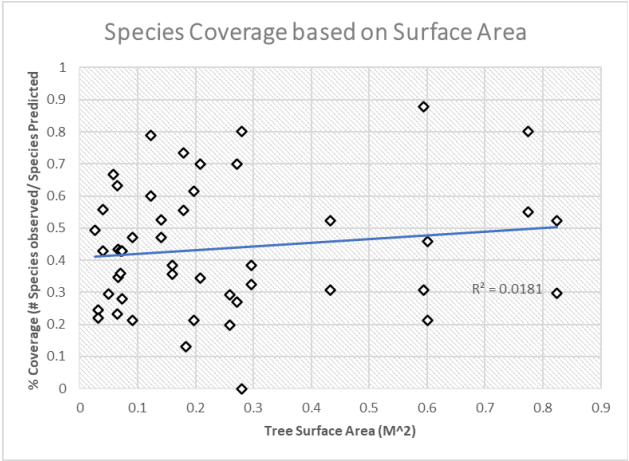

Figure 10: Species coverage by Surface area. Coverage calculated using observed species divided by projected species populations using iNEXT rarefaction

3. Geospatial distributions of arthropods within and between trees

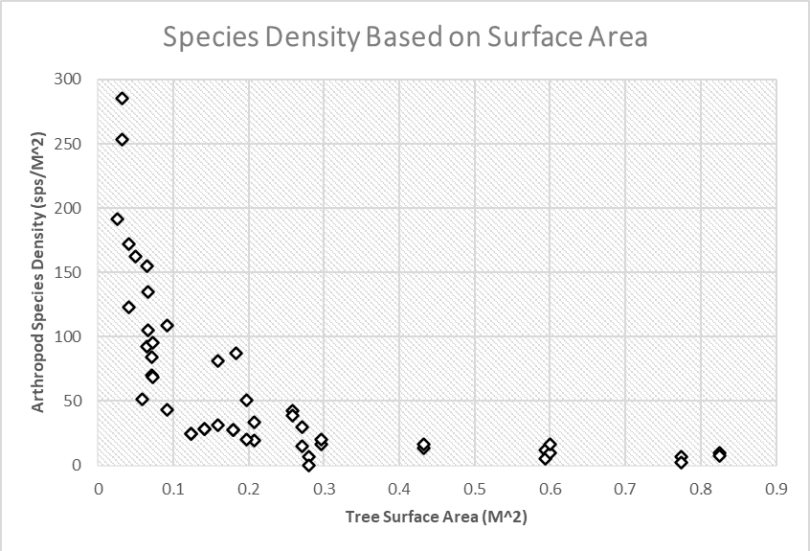

Fig 11: Species Density (number of observed per M^2) plotted against corresponding surface areas of trees (calculated using circumference at center of each sampling range). Species density calculated using the total number of species observed in the sample, divided by the surface area of the sample tree.

Although diversity and population were not directly correlated with surface area, population density and species richness density were very strongly related with surface area. Because population and richness were not correlated with surface area, density is very strongly negatively correlated with tree surface area. Once again, coverage was not correlated with surface area, reinforcing these results (Figure 11).

Arthropod communities varied considerably in composition between trees. Due to the high rate of species accumulation and singletons, average community beta diversity between trees was high. Trees were spaced as evenly as possible but could be irregularly spaced due to specificity in tree requirements. Two groups of trees were specially chosen with the spatial analysis in mind at either end of the transect. Each group contained three trees of equitable size and epiphyte coverage, equally spaced in a triangle of approximately 7 meters between each tree. Using these sites, beta diversity was calculated without the confounding variable of distance between trees. Average inter-tree beta diversity using Sorenson, Horn, and Jaccard indices within these trees was very low, at 0.1689, 0.2075, and 0.0941 respectively. These sites also offered the ability to compare the effect of spatial distribution between sites. Average beta diversity comparing trees between groupings was lower than the diversity within the groupings, although not by a significant margin.

4. Examining the continuity between epiphyte and soil communities

Despite a roughly equivalent amount of soil surface and tree surface sampled, cumulative epiphyte sampling contained approximately 1.75 times more individuals (405 compared to 232) and 1.58 times more species present. As seen in figure 3, epiphyte samples also contain higher diversity indices (Shannon and Simpson).

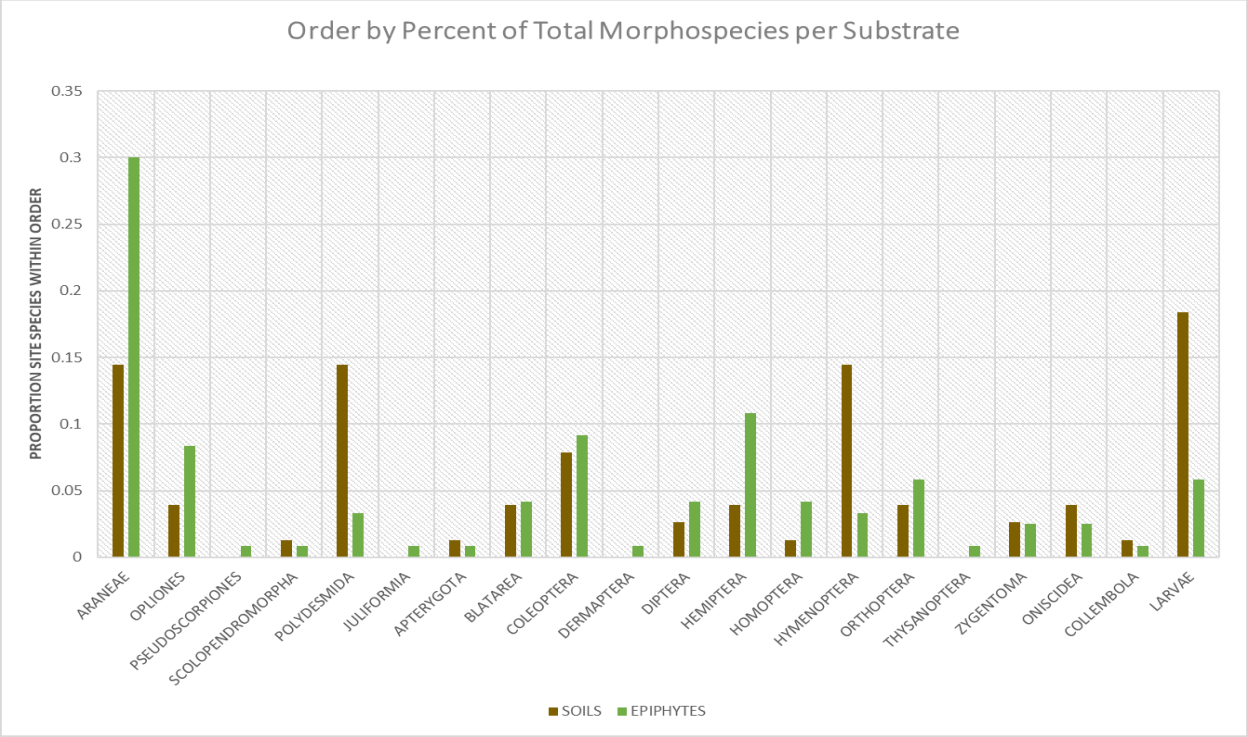

Figure 12: Observed orders by percent of total morphospecies within each substrate. Shows the weighting of each order by the number of morphospecies it contains specific to each substrate (#morphos per substrate seen within order/ total morphos seen in substrate)

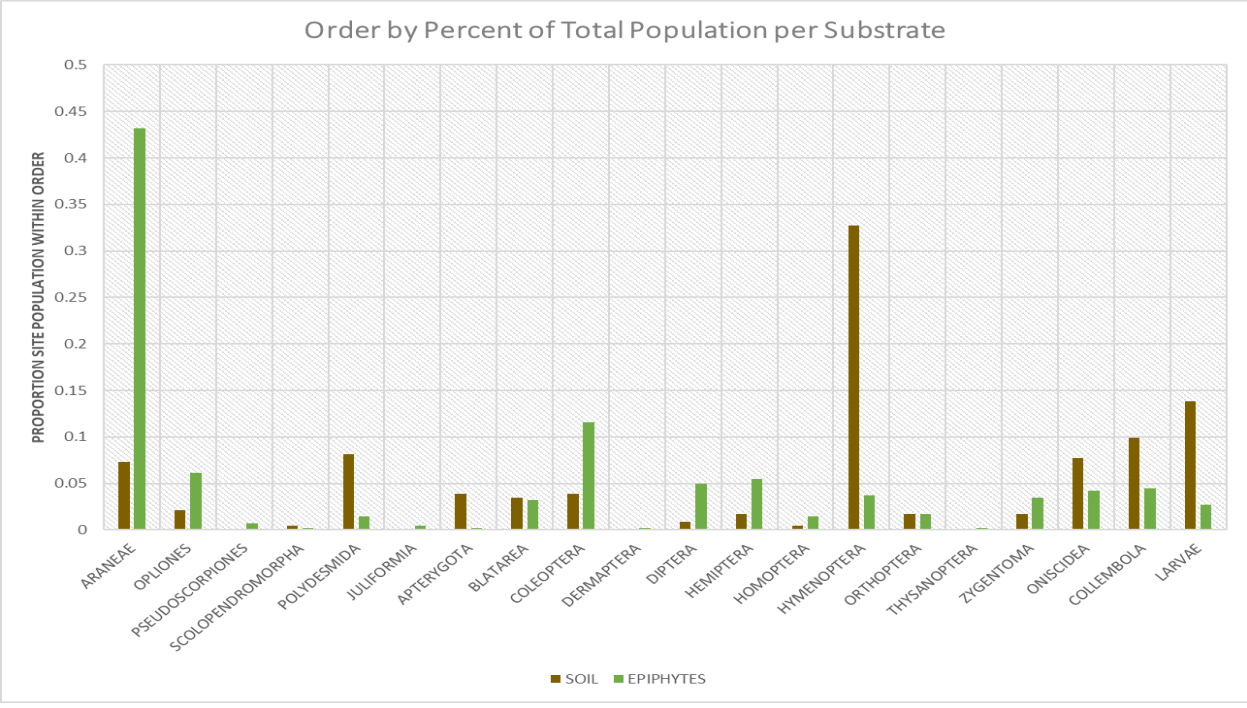

Figure 13: Observed orders by percent of total population within each substrate. Shows weighting of each order by the number of individuals contained specific to each substrate (# individuals per substrate within order/ total population of each susbtrate)

The two communities differed greatly in distribution of species by order, as shown in figure 12. Most notably, epiphyte mats contained higher rates of arachnids, specifically typical spiders of the order Araneae (30% in Epiphytes, 15% in soil). Soil substrate was also similarly occupied by Hymenopteran species, with another 15% of species present (<5% in epiphytes). Population breakdown by order also differed considerably between the two sites (Figure 13). Araneae consisted of nearly 40% of total population within epiphyte communities, while in the soil typical spiders only made up approximately 8% of total population. In a similar vein, Hymenopterans dominated the soil by population, making up nearly 35% of total population.

TWO SAMLE Z TEST FOR DIFFERENCE IN PROPORTIONS BETWEEN SOIL AND EPIPHYTES, P = 0.05				
CLASS	ORDER	ORDER % RICHNESS	ORDER % RICHNESS (RAREFACTED	ORDER % POPULATION
ARACHNIDA	ARANEAE	2.48	2.62	9.50
	OPLIONES	1.20	0.90	2.30
	PSEUDOSCORPIONES	0.80	0.44	1.31
CHILOPODA	SCOLOPENDROMORPHA	0.33	1.64	0.40
DIPLOPODA	POLYDESMIDA	2.86	1.87	4.20
	JULIFORMIA	0.80	0.61	1.07
INSECT	APTERYGOTA	0.33	0.44	3.55
	BLATAREA	0.08	0.22	0.16
	COLEOPTERA	0.31	1.38	3.31
	DERMAPTERA	0.80	0.61	0.76
	DIPTERA	0.56	0.53	2.71
	HEMIPTERA	1.72	2.97	2.28
	HOMOPTERA	1.13	1.67	1.22
	HYMENOPTERA	2.86	6.16	10.08
	ORTHOPTERA	0.58	1.84	0.00
	THYSANOPTERA	0.80	0.61	0.76
	ZYGENTOMA	0.06	0.29	1.27
	ONISCIDEA	0.57	0.50	1.90
	LARVAE	2.78	4.25	5.36
ENTOGNATHA	COLLEMBOLA	0.33	0.44	2.71

Figure 14: Two sample Z tests for community composition of orders. Proportional abundance of orders by percent richness (% of total morphospecies) and percent population (% of total individuals per substrate) between the two substrates were compared using a 2 sample Z test for difference of proportions, at 95% confidence level. Orders by percent richness were calculated using both observed values and rarefacted values (iNEXT) for accuracy. Green represents significant differences between the two communities.

The proportion of orders Araneae, Polydesmidae and Hymenoptera by total morphospecies observed was significantly different between the soil and epiphyte samples using a 2 Sample Z Test at a 95% confidence level. To improve this estimate, a second Z test was performed using iNEXT rarefaction data of predicted species present by order. Araneae and Hymenoptera remained statistically significant, while Polydesmidae failed to provide meaningful differences. Order by percent total population revealed more distinct differences, as orders Araneae, Opiliones, Polydesmida, Apterygota, Coleoptera, Diptera, Hemiptera, Hymenoptera and Collembola (50% of all orders observed) showed significant differences in proportion of total population between the two substrates (Figure 14). A Chi squared goodness of fit test was used to create a wholistic comparison of the community compositions of two substrates. Order by percent morphospecies resulted a X^2 value of 124.68 for observed proportions and 327.17 for rarefacted values, both significant for df=19 and critical value of 30.14.

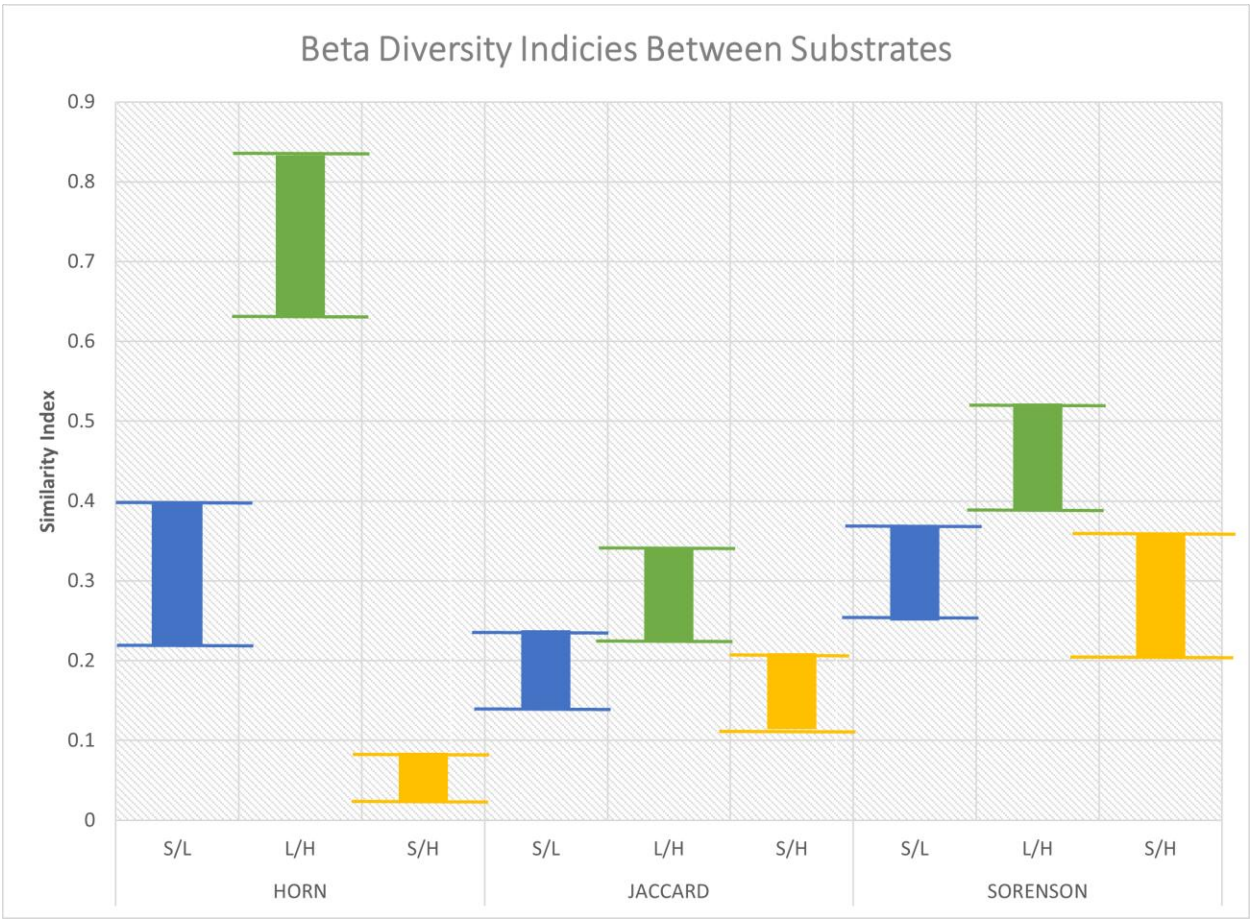

Figure 15: Beta Diversity indices for Horn, Jaccard, and Sorenson indices across substrate ranges. Beta similarity indices compare aggregate populations between sites for each substrate range (Soil = S, Low = L, High = H), and generated using the DIVO programming package in R. Actual beta similarity scores are not shown, but upper and lower quantile of beta indices are shown for comparison of significance. Lack of overlap between upper and lower quantiles indicates significantly high beta diversities and significant differences in the morphospecies makeup between the two substrates.

Beta diversity (Sorenson, Horn, and Jaccard) between samples within trees (Low to high) were lower (higher similarity indices, lower beta diversity) than beta diversity values between soil and either epiphyte substrate by significant margins (except Horn S/L and L/H). Beta diversity showed no significant difference between beta diversity between S/L and S/H.

Discussion

1. *Epiphyte arthropod communities are diverse and vary considerably between trees.*

Epiphyte mats contained the highest rate of diversity, population, and richness of all substrate types examines within this study, even outperforming bromeliads. Species accumulation within these mats continued steadily and at a high rate. The inability of the study to reach an asymptote within the coverage curve or within the accumulation curve is a testament to the incredibly diversity within the study ecosystem. Diversity observed in this ten-day observation period has actually surpassed that of yearlong studies in quantity of morphospecies and orders, with 180 morphospecies compared to 89, although studies took place within different substrates (Stuntz *et al*. 2002). Due to this high rate of accumulation, trees generally shared a low degree of similarity in terms of B diversity, but most followed a similar breakdown of order, with Araneae spiders being the dominant order in most samples. Insectivores dominated guild structure within these samples, with a wide array of arachnids and assassin bugs found. The high population of insectivores implies a large degree of top-down population pressure. Furthermore, the high rates of insectivores implies either an under sampling of smaller prey insects or a high degree of predation within the insectivore guild. Both are entirely plausible, and it is likely that both are occurring. Springtails (order Collemba) were nearly ubiquitous within samples, but were difficult to capture, count, and identify, and as such are underrepresented. Predation within insectivores is extremely likely and was even directly observed on several occasions within the spiders in the sample.

2. *Distribution of spiders*

Within these epiphyte mat communities, typical spiders was the most dominant order by both richness and population. The most numerous morphospecies (Morpho name: Tiger Spider) within the study was a single hunting spider that was found within nearly 65% of sites and was frequently found in high populations of 1-3 individuals within each sample. Nearly every sample contained at least some kind of hunting spider, and these spiders were visually observed hunting silverfish within these matt communities. Web building spiders were also frequently found, although they were typically much more localized, and found as singletons much more often.

Juveniles were also found in nearly every sample. Within the Tiger Spider morphospecies, nearly 25% of the total observations were categorized as juveniles. Within the web building spiders, morphospecies ID was sometimes difficult or impossible due to the extremely small size of some samples, assumed to be juveniles as well. Nearly 50% of all observed spiders were assumed to be juveniles, classified either as spiders smaller than the average size of their morphospecies or spiders small enough to need a hand lens to identify. Epiphytes are known for their roles are nurseries (Angelini and Siliman 2014), and this high rate of juveniles indicates that these epiphyte mat ecosystems serve as important nurseries for spider populations.

3. *Inability to predict epiphyte arthropod diversity*

Epiphyte diversity was highly variable. Some samples resulted in eight new species or a Shannon diversity nearly two standard deviations above the mean, while others could capture no species entirely. However, none of the variables measured in this study could adequately assess the cause of this variation site to site. Although epiphyte diversity is thought to increase overall canopy arthropod diversity by adding habitat complexity (Angon *et al.* 2009, Benzing 1990, Gentry and Dodson 1987), the results between arthropod diversity and vascular epiphyte diversity do not support this statement in this case. It's important to consider in this situation that the majority of studies regarding broad scale effects of epiphytes on arthropod diversity are canopy assessments that utilize fogging, and therefore are not

effective at determining where within the canopy arthropods are living (Yanoviak 2003b) As such, the boost in localized diversity epiphytes provide (Stuntz et al 2002) may not be shared with local nonvascular assemblages. According to this data, this seems to be the case as no correlation whatsoever was detected between the two variables.

Furthermore, the lack of a conclusive trend between percent coverage and diversity came as a surprise, as raw epiphyte coverage was predicted to be the primary driver of arthropod diversity. Considering that these samples were taken directly from the epiphyte mats, higher habitat space was assumed to correlate strongly with diversity. The inability to provide a conclusive trend may be a result of the methodology as coverage was measured in categories instead of individual estimates, as such analysis was limited to simple quartiles and a stronger regression analysis was unavailable. This use of categorical assessment also further limited the ability to associate percent coverage with other factors, namely surface area, to create a stronger covariance assessment.

There are a myriad of factors that could affect the diversity within these communities, most notably phorophyte characteristics could be very important. Although herbivory within epiphytes is noted and important (Schmidt and Zotz 2000), true herbivores are uncommon in epiphyte mats. Most "herbivores" found within epiphytes are granivores and sap suckers (Stuntz et al 2002). As such, the foundational primary consumers within these microhabitats may be highly dependent on phorophyte characteristics such as sap and bark type. Furthermore, phorophyte characteristics cause considerable variation on actual epiphytes present including nonvascular assemblages such as mats (Caceres et al 2007), and therefore could lead to a cascade effect on the arthropods present.

4. Non-Spatial Limitations on Arthropod Communities

The pattern provided by the data on species density within the epiphyte mats is novel and surprising, as it implies that arthropod species aren't taking full advantage of epiphytic resources. This raises many interesting questions regarding how these communities form and how they are maintained. Lower epiphyte mats seem to support a similar maximum number of species, regardless of surface area available. Once again, methodology errors were thought to be the source, but the predicted species coverage based on surface area provides evidence that the methodology sampled an equal proportion of species present independent of surface area. Because this trend isn't caused by a simple methodology limit, it raises interesting questions regarding the spatial distributions of epiphyte dwelling arthropods. The lack of variation within population and richness based on available habitat space implies that there is some form of a carrying capacity within these communities that is independent of surface area. The distribution of the population densities flattens asymptotically very fast by $0.3m^2$ (max of $0.83m^2$), trees between 0.15 and $0.3m^2$ decrease dramatically, with the smallest trees containing the highest density of arthropods.

Because population in the asymptotic section doesn't appear to change as trees increase in size, this pattern suggests that perhaps these locations are colonized by primary successors until they reach carrying capacity early on, then perhaps followed by the insectivores later that impose a top down carrying capacity. This theory is guided by two pieces of evidence from the study, the availability of habitat space on the larger trees and the very large proportion of insectivores within the sample population. Primarily, because the density is so low on the larger trees it is likely that the limiting factor is not a bottom-up issue of resource availability. Second, the large proportion of insectivores compared to primary consumers within these habitats implies a very heavy top-down pressure. Insectivores comprised nearly half of all feeding guilds within this sample, and in similarly related studies (Stuntz et al 2002, Angilini and Siliman 2014). Therefore, top-down ecological pressure imposed by this top-heavy tropic chain could suppress

further growth in the form of direct population growth and further colonization (Bruno and Cardinale 2008).

5. *Epiphytes as independent, non-continuous microhabitats*

The results of the soil/ tree diversity comparisons are compelling and important. Soil communities and trunk epiphyte communities differ in significant and drastic manners. The significant difference in beta diversity indices between the substrates similarities implies that these epiphyte communities are more homogenous with other epiphyte communities than they are with their adjacent soils. In other words, the diversity of morphospecies found within the epiphyte mats are distinctly unique from the soil that they are directly contiguous with, signaling that these mats serve as an independent, unique microhabitat that is not directly overlapped by soil habitats. This statement is even more supported by the distribution of unique species per substrate that the number of unique species in the epiphyte mats are higher than the number of species shared between the two substrates. Furthermore, the lack of strong overlap between S/L and L/H and the roughly equivalent Beta diversity between S/L and S/H implies that there is not a strong gradient of distribution between these zones. If diversity was indeed shared to a significant amount between the two habitats, we would see the influence of soil diversity on the diversity of the low epiphyte zone. This is notably absent in the data, with R^2 values of near 0 between arthropod diversity within soils and epiphytes. The data indicates that species makeup is not the same between the two habitats; creating a convincing argument that even at the point of intersection, the organisms that make up these two habitats deliberately choose and prefer to live in their respective habitat, despite the close proximity.

Beyond species makeup these habitats differ tremendously in the way in which they are composed as well. Analyzing the makeup of orders within these two habitats reveals drastic differences in their composition as well. Specifically, by percent of total species, the two zones differed significantly in composition of Araneae and Hymenoptera, the two orders with the highest richness and population in the epiphyte and soil habitats respectively. Furthermore, over 50% of orders differed significantly in percent of total population. More wholistically, Chi-squared analysis demonstrates that these two communities differ significantly in the wholistic makeup of their species and population by order. These strong differences in makeups of orders imply that these communities not only are composed of unique species, but also fundamentally within the makeup of their communities, indicating a higher degree of organizational differences and independence between the two habitats.

These differences could be the result of a numerous factors. Epiphyte mats are composed of both living tissue and humic soil underneath, and microdistributuions of arthropods exist between these layers (Yanoiak 2003a). This arboreal soil with can contain vastly different chemical properties than terrestrial soil, including pH and cation content (Nadkarni *et al.* 2002). Soil arthropods are known to exhibit strong preferences for soil characteristics (Delgado-Baquerizo *et al.* 2020, Lavelle *et al.* 2006), therefore the chemical differences between these soils could make arboreal soil non-ideal habitats for general terrestrial soil arthropods, while serving as perfect niches for species specializing in these conditions. Other physical conditions could be at play. For instance, as arboreal soil is typically much thinner and generally highly variable (Yanoiak 2003a), larger detritivores may be excluded from these zones as they are unable to effectively burrow and gather sufficient resources, as seen in the difference in Polydesmidae between the two habitats (Figures 12 and 13).

These results have important implications, as they demonstrate that the diversity within epiphyte dwelling arthropods are not a continuation or gradient of the soil habitat. This is especially important as this study focuses on the zone where these two habitats intercept. Epiphyte arthropod communities are unique from those of the soil, with significantly different compositions of orders by richness and population, as well as

distinctly different casts of morphospecies living within them. This has been known to be the case within canopy arthropods (Fagan and Winchester 1999), but this assessment at the start of the point of intersection may in fact be novel. Because of the academic focus on arthropod assemblages within canopy epiphytes, data is lacking on the gradient of overlap between epiphyte communities and their soil counterparts differs. However, this data suggests that the degree of overlap between these two communities is little, and that epiphyte mat community makeup is comprised of an independent, and unique arthropod assemblages that begins the point of intersection.

Conclusion:

Epiphytes are tremendously important in the diversity of arthropods. This fact has been long known in the case of canopy arthropods, but this study demonstrates that this fact also extends throughout understory epiphyte layers. To properly conserve the epiphyte ecosystems that remain, and to promote regrowth of forests into successful and thriving secondary forests, it is important to understand the dynamics of population distributions of these microhabitats. The results from this study suggest that epiphyte communities at the base of trees are already independently constructed microhabitats at the point of intersection, and that continuity within the tree is much stronger. This implies that epiphyte arthropod diversity is not sourced from the soil, and colonization takes place by some other means. If true, sources of epiphyte arthropod diversity may be internal, with self-sustaining populations of permanent residents making up the majority of epiphyte dwelling arthropods. This would mean that colonization likely takes place laterally from tree to tree, as proposed by, rather than ground up, making preservation of primary forests neighboring secondary forests of critical importance for recovery of arboreal arthropod assemblages.

Works cited

Angelini, C., & Silliman, B. R. (2014). Secondary foundation species as drivers of trophic and functional diversity: evidence from a tree—epiphyte system. *Ecology*, *95*(1), 185–196. http://www.jstor.org/stable/23597282

Benzing, D. (1990). *Vascular Epiphytes: General Biology and Related Biota* (Cambridge Tropical Biology Series). Cambridge: Cambridge University Press. doi:10.1017/CBO9780511525438

Benzing, D. H. (1994). HOW MUCH IS KNOWN ABOUT BROMELIACEAE IN 1994? *Selbyana*, *15*(1), 1–7. http://www.jstor.org/stable/41759854

Brosnan, V., & Ellis, C. (2020). EPIPHYTE RESPONSE TO WOODLAND HABITAT CONDITION ASSESSED USING COMMUNITY INDICATORS: A SIMPLIFIED METHOD FOR SCOTLAND'S TEMPERATE RAIN FOREST. *Edinburgh Journal of Botany*, *77*(3), 519-541. doi:10.1017/S096042862000013X

Bruno, J. F., & Cardinale, B. J. (2008). Cascading Effects of Predator Richness. *Frontiers in Ecology and the Environment*, *6*(10), 539–546. http://www.jstor.org/stable/20441019

Cáceres, Marcela & Lücking, Robert & Rambold, Gerhard. (2007). Phorophyte specificity and environmental parameters versus stochasticity as determinants for species composition of corticolous crustose lichen communities in the Atlantic rain forest of northeastern Brazil. Mycological Progress. 6. 117-136. 10.1007/s11557-007-0532-2.

Cruz-Angón, A., Baena, M., & Greenberg, R. (2009). The contribution of epiphytes to the abundance and species richness of canopy insects in a Mexican coffee plantation. *Journal of Tropical Ecology*, *25*(5), 453-463. doi:10.1017/S0266467409990125

Déleg, Jorge & Gradstein, S. & Aragón, Gregorio & Giordani, Paolo & Benítez Chavez, Angel. (2021). Cryptogamic epiphytes as indicators of successional changes in megadiverse lowland rain forests of western Amazonia. Ecological Indicators. 129. 1470-160. 10.1016/j.ecolind.2021.107890.

Delgado-Baquerizo, M., Reich, P.B., Trivedi, C. *et al*. Multiple elements of soil biodiversity drive ecosystem functions across biomes. *Nat Ecol Evol* **4**, 210–220 (2020). https://doi.org/10.1038/s41559-019-1084-y

Ellwood, M., Foster, W. Doubling the estimate of invertebrate biomass in a rainforest canopy. *Nature* **429**, 549–551 (2004). https://doi.org/10.1038/nature02560

Fagan, L. L., & Winchester, N. N. (1999). Arboreal Arthropods: Diversity and Rates of Colonization in a Temperate Montane Forest. *Selbyana*, *20*(1), 171–178. http://www.jstor.org/stable/41760019

Floren, A., & Linsenmair, K. E. (1998). DIVERSITY AND RECOLONIZATION OF ARBOREAL FORMICIDAE AND COLEOPTERA IN A LOWLAND RAIN FOREST IN SABAH, MALAYSIA. *Selbyana*, *19*(2), 155–161. Retrieved from https://journals.flvc.org/selbyana/article/view/120493

Gentry, A. H., & Dodson, C. (1987). Contribution of Nontrees to Species Richness of a Tropical Rain Forest. *Biotropica*, *19*(2), 149–156. https://doi.org/10.2307/2388737

Higuera, Diego & Martinez, Eliana. (2006). Sequestration and storage capacity of carbon in the canopy oak trees and their epiphytes in a Neotropic Cloud Forest, Colombia. 11.

LAWTON, R. O., U. S. NAIR, R. A. PIELKE, SR., AND R. M. WELCH. 2001. Climatic impact of tropical lowland deforestation on nearby montane cloud forests. Science 294: 584-587.

P. Lavelle, T. Decaëns, M. Aubert, S. Barot, M. Blouin, F. Bureau, P. Margerie, P. Mora, J.-P. Rossi,Soil invertebrates and ecosystem services,European Journal of Soil Biology,Volume 42, Supplement 1,2006,Pages S3-

S15,ISSN 1164-5563,https://doi.org/10.1016/j.ejsobi.2006.10.002.
(https://www.sciencedirect.com/science/article/pii/S1164556306001038)

Nalini M. Nadkarni, Douglas Schaefer, Teri J. Matelson, Rodrigo Solano,Comparison of arboreal and terrestrial soil characteristics in a lower montane forest, Monteverde, Costa Rica, Pedobiologia, Volume 46, Issue 1,2002,Pages 24-33,ISSN 0031-4056,https://doi.org/10.1078/0031-4056-00110.
(https://www.sciencedirect.com/science/article/pii/S0031405604701195)

Nieder, J., Engwald, S., & Barthlott, W. (1999). Patterns of Neotropical Epiphyte Diversity. *Selbyana*, *20*(1), 66–75. http://www.jstor.org/stable/41760009

Pounds, J., Fogden, M. & Campbell, J. Biological response to climate change on a tropical mountain. *Nature* **398**, 611–615 (1999). https://doi.org/10.1038/19297

Richardson, B. A. (1999). The Bromeliad Microcosm and the Assessment of Faunal Diversity in a Neotropical Forest. *Biotropica*, *31*(2), 321–336. http://www.jstor.org/stable/2663795

SCHMIDT, G., & ZOTZ, G. (2000). Herbivory in the epiphyte, Vriesea sanguinolenta Cogn. & Marchal (Bromeliaceae). *Journal of Tropical Ecology*, *16*(6), 829-839. doi:10.1017/S0266467400001747

Solis, G., Díaz, A., Mansilla, D., Tejo, C., Tello, F., Craven, D., Kreft, H., Armesto, J. (2022). Trash-basket epiphytes as secondary foundation species: a review of their distribution and effects on biodiversity and ecosystem functions. bioRxiv 2021.06.22.449473; doi: https://doi.org/10.1101/2021.06.22.449473

Stuntz, S., Ziegler, C., Simon, U., & Zotz, G. (2002). Diversity and Structure of the Arthropod Fauna within Three Canopy Epiphyte Species in Central Panama. *Journal of Tropical Ecology*, *18*(2), 161–176. http://www.jstor.org/stable/3068729

THOMAS, C. D., A. CAMERON, R. E. GREEN, M. BAKKENES, L. J. BEAUMONT, Y. C. COLLINGHAM, B. E N. ERASMUS, M. E DE SIQUEIRA, A. GRAINGER, L. HANNAH, L. HUGHES, B. HUNTLEY, A. S. VAN JAARSVELD, G. E MIDG- LEY, L. MILES, M. A. ORTEGA-HUERTA, A. T. PETERSON, 0. L. PHILLIPS, AND S. E. WILLIAMS. 2004. Extinction risk from climate change. Nature 427: 145-148)

Tolhurst, Bryony & Aguirre-Peñafiel, Vanessa & Mafla-Endara, Paola & Berg, Maureen & Peck, Mika & Maddock, Simon. (2016). Lizard diversity in response to human-induced disturbance in Andean Ecuador. Herpetological Journal. 26. 33-39.

Yanoviak, S.P., Nadkarni, N.M. & Gering, J.C. Arthropods in epiphytes: a diversity component that is not effectively sampled by canopy fogging. *Biodiversity and Conservation* **12**, 731–741 (2003). https://doi.org/10.1023/A:1022472912747

Yanoviak, S. P., Nadkarni, N. M., & Rodrigo, S. J. (2007). Arthropod Assemblages in Epiphyte Mats of Costa Rican Cloud Forests. *Biotropica*, *39*(2), 202–210. http://www.jstor.org/stable/30045394

Yanoviak, S.P, Hannah Walker, Nalini M Nadkarni,Arthropod assemblages in vegetative vs. humic portions of epiphyte mats in a neotropical cloud forest,Pedobiologia,Volume 48, Issue 1,2004,Pages 51-58,ISSN 0031-4056,https://doi.org/10.1016/j.pedobi.2003.07.003.
(https://www.sciencedirect.com/science/article/pii/S0031405603000076)

Zotz, Gerhard & Weigelt, Patrick & Kessler, Michael & Kreft, Holger & Taylor, Amanda. (2021). EpiList 1.0: a global checklist of vascular epiphytes. Ecology. 102. 10.1002/ecy.3326.