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Araneae Biodiversity in the Amazonian Foothills: An analysis of family and guild presence across habitat types

Rae Lewark
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Araneae Biodiversity in the Amazonian Foothills
An analysis of family and guild presence across habitat types



Lewark, Rae
Academic Director: Xavier, Silva PhD
Project Advisor: Germania Estevez, PhD
Field Advisor: Alex Bentley
Hawaii Pacific University
Environmental Studies
South America, Ecuador, Pastaza Province, Ecominga Rio Anzu
Sumak Kawsay in Situ

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Abstract

The activity of the order *Araneae* within ecosystems is often considered an ecological mystery. Considered top-level trophic predators, spiders act as regulators of insect populations and have influence upon the foundation of the trophic web. In the Ecuadorian Amazonian foothills, it is important to address the lack of knowledge of the biodiversity of spiders in the region. Conducting biodiversity studies across land use gradients can begin to characterize anthropogenic impacts on neotropical spider species. This study quantifies the *araneae* biodiversity in the transition between the Cloud and Amazon forests in Ecuador. Populations in primary forest, secondary forest, cultivated fields and cave systems were analyzed to identify the families and guilds present in the ecosystems. The biodiversity of spider families and guild type were found to diminish with increasing land use impact and the decrease of vegetation complexity.

Resumen

La actividad del orden *Araneae* entre los ecosistemas frecuentemente se considera un misterio. Considera depredadores importantes arañas son reguladores de las poblaciones de insectos y tienen influencia sobre la base de la red trófica. Por las estribaciones de la Amazonia, es importante a enfocar en la falta de información de la biodiversidad de arañas en el región. La realización de más estudios entre los gradientes del uso de la tierra puede empezar a caracterizar los impactos humanos en las arañas de los alotrópicos. Este estudio cuantificó la biodiversidad de *araneae* en la transición del Bosque Nublado y la Amazonian de Ecuador. Las poblaciones de bosque primario, bosque secundario, campos cultivados, y los sistemas de cuevas fueron analizados a identificar las familias y los gremios que se presenten en los ecosistemas. La biodiversidad de las familias y los gremios de arañas se encontraron a disminuir con el crecimiento del uso de tierra y con el decrecimiento de la complejidad de la vegetación.

Acknowledgements

The author would like to extend gratitude to Germania Estevez for advisement and guidance throughout the study, to Alex Bentley for advisement in the field and Ana Maria Ortez, Xavier Silva and Diana Serrano for aid throughout the development and completion of the study. To the staff of Sumak Kawsay in Situ and the fellow Anzu team researchers, Renee Heller, Teo Carr, and Zane Libke for their companionship, their resilience and their constant ability to inspire even in the hardest conditions. To all the representatives of SIT study abroad.

Introduction

Spiders represent a megadiverse order within the arthropod phylum, with 48,262 currently described species (*The World Spider Catalog* 20.5). Spiders pose a taxonomic challenge, as morphological variation within species is abundant and can be due to genetic deviation or geographical difference (Coddington & Levi 1991). The current number of described species is speculated to only constitute 35% of the total spider species present on earth. In comparison to other non-invertebrate groups, spiders and other arachnids represent both a lack of research and an area for new discovery (Pinzon 2010, Brooks 2004.) While research into the ecological importance of spiders is increasing, only an average of 605 new species are described each year. At this rate of description, it would take more than 150 years to develop a sufficient database on the planet's spider biodiversity (Platnick 2013). In the neotropics, where biodiversity is notably higher than temperate regions, research into spider biodiversity is needed and

presents a frontier for the discovery and description of new species. Spiders of tropical regions such as in Ecuador, present an under-explored world of ecological and physiological potential (Basset 2012.) Spider venom contains neurotoxins that are becoming important in neurobiological innovation, studies into properties of spider web for fiber research, and also in the development of less environmentally damaging insecticides (Coddington & Levi 1991). Spiders may benefit the effectiveness of pest control in agroforestry. Increased diversity of spider populations has been found to benefit the mitigation of pest impact on crops. A range of species from different guilds creates an effective network to target pests across their lifecycles. This promotes land management with less chemical impact and focuses on harnessing the natural ecosystem to promote crop productivity (Marc & Conrad 1997).

In order to quantify the impact of land use, spider populations must be thoroughly surveyed. The most effective technique for spider collecting is “nocturnal hand collecting.” This is due to higher probability of encounters in the night hours when many species are more likely to be hunting. This study focused on *hand collecting* as the main sampling method as advised by Rego (2009) when other methods are not available. This method was the focus of the study in order to encounter a range of spiders across guilds and vegetation types, as well as to observe each individual’s ecological interactions and behavior while in their natural environments. Night collecting sessions were a vital component of the study as spiders are often observed in higher quantity in hours of no light in the neo-tropics, with some species exclusively recorded as nocturnally active (Green 1999). This is often due to spider’s main predators being active during day light hours, and in order to hunt spiders must put themselves at risk. Building a web or ambush hunting demands high levels of energy and requires individuals to leave locations where they are safe from predators (Venner 2005). Hunting in low or no light hours decreases the risk of predation and also increases the individual’s potential for catching unsuspecting insects who may not be able to detect the spider’s presence as well at night (Rypstra 1986).

Spiders are considered top level trophic predators within their habitats. Spiders fill the ecological regulator role within their ecosystems, with the capacity to dictate the composition and balance of insect populations (Martin 1982). Throughout the planet’s ecosystems, predators are distinguished as keystone components in overall health. The disproportionate lack of research into spider’s impact on ecosystem functionality draws a stark comparison to predators on larger trophic levels. While small in physical size, spiders have the capacity to act as important control agents in the balance of insect populations (Silva 1992).

Spider families present a diverse range of guilds. Guilds are classified as groups of species who compete for the same resources in an ecosystem. Identifying the guilds present in an ecosystem can lead to a better understanding of the ecological impact spider communities are having on the trophic web. Classifying guilds can also develop an understand of the impact of land use in a habitat. The descriptions of spider guilds by Cardoso et al (2011) characterized spider guilds by 8 definitions: sensing web weavers, sheet web weavers, space web weavers, orb web weavers, specialists, ambush hunters, ground hunters and other hunters.

The stratospheric range of a spider can help identify the taxonomy as well as the guild it belongs to (Yanoviak 2013). Spiders that rely on specific vegetation structure for web building or for hunting will be more vulnerable to changes in vegetation. Spiders who rely on camouflage for hunting may also be negatively impacted by changes in vegetation type (Thery 2002).

Spiders will utilize vegetation structure to build webs, forage, or use ambush hunting. Web building spiders will elect locations of higher insect traffic, in locations where they can attract specific individuals, or locations where they can utilize surprise to entrap prey (Venner 2005).

This study collected specimens across four distinct habitats. Within each habitat a 200m transect oriented around a body of water and a 200m transect in a dry region were sampled. The four ecosystems sampled were primary forest, secondary forest, cultivated fields, and subterranean caves. The first three ecosystem types were selected in order to compare the biodiversity gradient across the region with increasing anthropogenic impact. The cave transects were selected in order to observe the impacts of the ecological pressures of subterranean ecosystems on spider diversity (Mammola & Isaia 2017).

The primary forest transects were considered regions unaltered by anthropogenic activity, with little to no disturbance. The first transect selected was situated in a valley and cut through the path of a stream. The second transect selected was situated along the ride of the same valley, and cut through the forest. Both transects had little to no human impact except for collecting reasons. The structure of vegetation has a significant impact on spiders. As they rely heavily on infrastructure for hunting, areas with more diverse flora will often provide the foundation for diverse spider populations (Schüpbach 2013).

The secondary forest transects were defined as areas where primary forest had been cleared, but had then been abandoned and successional growth was permitted. The first transect selected was oriented close to a river along a stream tributary. The second transect cut through the forest, and crossed the dry portion of the first transects stream. Secondary forest growth is denser while less diverse than primary forests, and if found adjacent to primary forests will often present ideal conditions for spider diversity (Floren & Deeleman-Reinhold 2005).

The cultivated transects were characterized as areas where primary forest had been removed to open the land for agricultural activity. The transects selected were dominated by grasses and some successional forest flora. Cultivated habitats often exhibit patchwork like regions, with the altercations of land causing fragmentation of habitats for the species present. Spiders are adaptive predators, often exhibiting resilience when impacted by habitat disturbance. Often able to adapt, spiders thrive in areas with high insect populations, such as agricultural sites, or habitats around bodies of water. They can adapt their hunting methods, whether web oriented or ambush hunting, to altered ecosystems (Schüpbach 2003). It has been observed however that overall diversity of species will decrease in areas of disturbance impacted by agriculture or other anthropogenic land use. This usually results in a few species thriving and dominating the ecosystem (Cardoso et al 2011).

The caves were characterized as subterranean geological formations. Subterranean habitats create extreme environments, exposing inhabitants to high levels of ecological pressure. Due to low resource availability as well as low light levels, species living in cave ecosystems will often evolve away from their terrestrial counterparts (Mammola & Isaia 2017).

This study aimed to evaluate the biodiversity of spiders in the transitional habitats between the Ecuadorian Cloud Forest and Amazon Forest. By developing an understanding of the species in the region and by sampling various habitats types, the impact of human land use on spider diversity was also evaluated across increasing levels of alteration.

Methods

In the Field

The study was conducted in November, 2019 in the transition between the dry and the wet season in Ecuador. The study site was in the Rio Anzu region of the Pastaza Province, in the Ecominga and Sumak Kawsay biological reserves. Collection sessions were performed for 16 days between the 12th and the 29th of November.

The four habitats sampled were primary forest, secondary forest, cultivated fields, and subterranean caves (caves not mapped). For each type of habitat, excluding the cave systems, two 200m transects were used, one that was oriented around a body of water (wet transect) and one that was not impacted by water (dry transect) (figure 1). The cave transects were evaluated in search hours instead of distance surveyed.

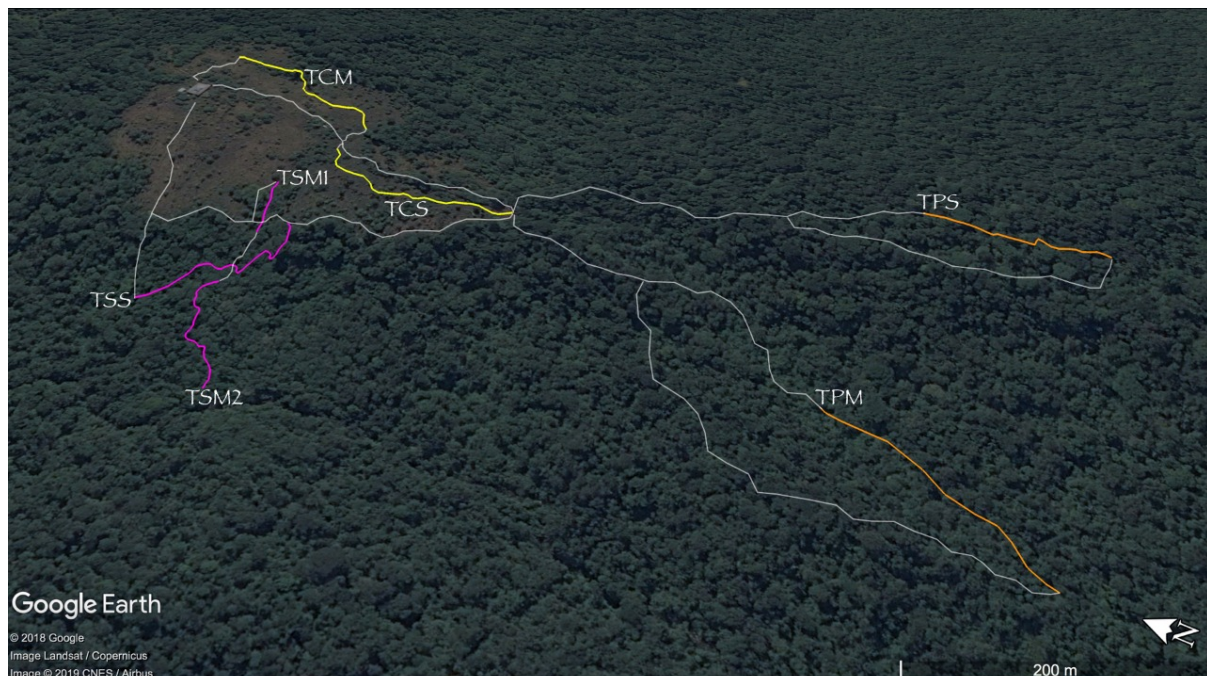


Figure 1. Map of the 6 main transects, TCM=cultivated wet transect, TCS= cultivated dry transect, TSMI and TSM2=secondary wet transects, TSS=secondary dry transect, TPM=primary wet transect, TPS=primary dry transect.

Surveying sessions utilized hand collecting methods, with emphasis on identifying individuals as well as observing behavior and environmental interaction of each morpho-species. When a new individual was encountered it was photographed, the height above ground where it was found was measured, and the type of vegetation or strata was classified. Vegetation or strata classification was broken up into 9 categories: gravel/sand, surface of water, soil bank/wall, leaf litter, root systems, fallen trees/branches, grass, low-level foliage and high-level foliage. The presence of a web and its type was noted, as well as behavior when disturbed, egg sack type, or other notable features that could be used in identification.

As found by Avezedo et al in 2014, *nocturnal hand collecting* is the most effective method for collecting spider specimens above other methods such as *tree beating* or *pitfall traps*. While a combination of the three methods is ideal, *nocturnal hand collecting* is the most successful especially when other options are not accessible. This is due to higher activity of spider species at night compared to the day (Green 1999). This study aimed to map the activity of different spider groups throughout different light levels, and developed collecting schedules in night, day and transitional light sessions. This study utilized hand collecting as the primary sampling technique because *pitfall traps* and *tree beating* either kills individuals or disrupts their natural activity. This inhibits observation to observe of their ecological interaction and behavior in their natural environment.

Fifteen collecting hours were spent in each type of habitat, with even amounts of time spent collecting in transitional hours (sun rise and sunset), day light hours, and night hours. The cave systems were sampled for only an equivalent of three sampling sessions, and not subject to light level specific sampling. A total of 45 search and collection hours were performed in the main three habitat types, and 3 hours and 45 minutes in the cave transects. Each transect was walked slowly, with sweeping visual searches done from side to side of the vegetation or water way. Leaf litter, soil banks, fallen trees, root systems and the undersides of leaves were thoroughly examined at each search interval. Night time sessions utilized both a head lamp and spotting flashlight in visual searches.

Samples were taken at three different levels of light. Day light samples were taken between the hours of 8:00 and 17:00. Night samples were taken between 19:00 and 0:00. Transitional light samples were divided evenly between morning and evening transition hours, with morning sessions taking place within the hours of 5:30 and 7:45, and evening sessions taking place within 17:15 and 18:45. Fifteen hours of collecting in each light level were performed across the three main habitats, with transitional hours broken into 7 hours and 30 minutes for the morning transitions and 7 hours and 30 minutes for the evening transitions.

The application *iNaturalist* was used to organize data during collecting sessions. Each individual was photographed in the field with a macro 10 mm Moment Lens attached to an iPhone XR. If possible, photos were taken of each individual from above to capture the leg and body overall shape, along the dorsal plane to capture shape of the carapace and the abdomen, and from the front to capture the ocular pattern. When a new morpho-species was found it was collected to be preserved and identified outside of the field.

Preservation and Identification

Samples were preserved in a 70% alcohol solution, and photographed with the same lens used in the field. A microscope was used for identification when macro photos were not sufficient for identification. The family of each individual was identified as well as the genus when possible. Identification was based on the descriptions of Jocqué (2007), Wegner (2011), Duperre (2013, 2015, 2016), Brescovit ([no date]), and the *World Spider Catalog 20.5* (2019). Guilds were assigned to each family based on the descriptions of Cardoso et al (2011).

Statistical Analysis

The diversity within each habitat as well as the composite diversity of the region was calculated using the entropy of the *Shannon Diversity Index*, and the inverse *Simpson Diversity Index*. The *Shannon Diversity Index* which accounts for the increase of rare species, as well as the abundance and evenness in the community and functions on an ordinal scale. The entropy was applied in order to avoid unbalanced influence of rare or common groups disproportionately (Jost 2006). The *Gini-Simpson Diversity Index* describes the overall diversity of a community, accounting for richness, evenness and divergence (Solow 1993). The inverse of the formula was applied in order to account for dominance of groups within the sample (Jost 2006).

The *Shannon Index* is calculated as follows, where (p_1) is the quantity of species “1” in respect to the total number of species.

$$= \exp \left(\sum (p_1) |\ln p_1| \right)$$

The *Gini-Simpson Index* is calculated as follows, where n is the total number of individuals in a specific species, and N is number of individuals of the cumulative species:

$$= \frac{1}{\left(\frac{1}{\sum \left(\frac{n}{N} \right)^2} \right)}$$

The *sample completeness* of each habitat type as well as the region as a whole was calculated using the software iNext (Chao et al 2016). This is an important measure to take when studying arachnid populations because they often present high numbers of single or double morpho-species encounters (*singletons* and *doubletons*) (Rego 2009). A *species accumulation curve* was mapped in order to compare the number of species found in a region in respect to the effort used to find them (Chao et al 2016).

The *Jaccard Index* was used to measure the percent similarity of morpho-species between the three main habitats sampled (*primary*, *secondary* and *cultivated*.) The formula operates by dividing the number of shared species by the total number of species, where n equals number of shared species and N equals total number of species between the habitats.

$$\% \text{ similarity} = \frac{n}{N}$$

The samples collected from the cave transects were not statistically comparable to the other habitats as the sampling effort was disproportionate. The results from data sampled from the caves was included in the discussion portion of the study.

Results & Discussion

A total of 1036 spiders were collected across the four habitat types. The total number of individuals could be broken up into 150 morpho-species and 20 families (appendix A). The 20 families could be classified into 8 guilds (table 1). Of the total morpho-species 4 could not be identified and fall into the *unknown* classification.

Table 1. Spider Families found across all habitats designated into guilds.

Guild	Family
Ambush Hunter	<i>Deinopidae</i> <i>Thomisidae</i>
Ground Hunter	<i>Corinnidae</i> <i>Heteropodidae</i> <i>Lycosidae</i>
Orb Weaver	<i>Araneidae</i> <i>Symphytognathidae</i> <i>Tetranychidae</i>
Other Hunter	<i>Anyphaenidae</i> <i>Ctenidae</i> <i>Miturgidae</i> <i>Salticidae</i> <i>Scytodidae</i>
Sensing Web	<i>Theraphosidae</i>
Sheet Web	<i>Agelenidae</i> <i>Pisauridae</i>
Space Web	<i>Pholcidae</i> <i>Theridiidae</i>
Specialist	<i>Dysderidae</i> <i>Gnaphosidae</i>

Of the 150 morpho-species, one from each habitat was found to dominant their respective habitat types. The most dominant morpho-species found in the primary habitat was *Pisauridae gen. sp. 1* (15%), The next most dominant morpho-species were

Pholcidae gen. sp 1. and *Tetranathidae gen. sp. 1* making up 12% and 11% of the total population, respectively.

The most common morpho-species in the secondary habitat was *Pholcidae gen sp 2* which made up 17% of the total morpho-species found in the habitat. The next most dominate morpho-species were *Theridiidae gen. sp. 1* and *Pholcidae gen. sp. 2* which made up 17% and 13% of the total morpho-species found, respectively.

The most common morpho-species found in the cultivated habitat was *Tetranathida leucage sp.* which represented 40% of the total population. The following dominant species were *Theridiidae gen. sp. 1*, and *Pisauridae gen. sp. 2*, making up 11% and 8% of the remaining population, respectively.

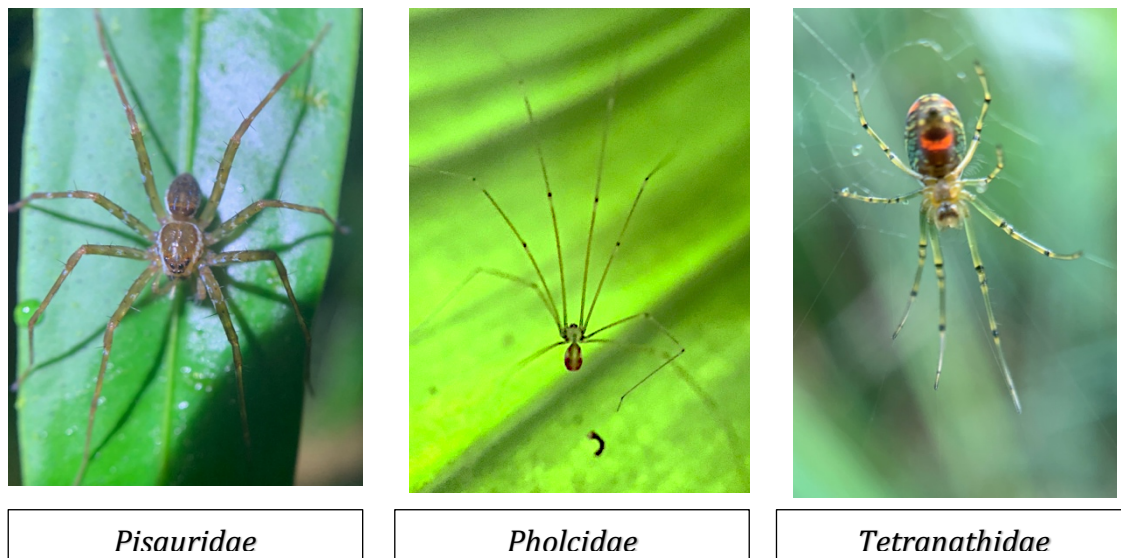


Figure 2. The three most common morpho-species found in each habitat type. From left to right: the most abundant morpho-species in the primary transects, secondary transects, and the cultivated transect.

The most common morpho-species in the secondary habitat was *Pholcidae gen sp 2* which made up 17% of the total morpho-species found in the habitat. The next most dominate morpho-species were *Theridiidae gen. sp. 1* and *Pholcidae gen. sp. 2* which made up 17% and 13% of the total morpho-species found, respectively.

The most common morpho-species found in the cultivated habitat was *Tetranathida leucage sp.* which represented 40% of the total population. The following dominant species were *Theridiidae gen. sp. 1*, and *Pisauridae gen. sp. 2*, making up 11% and 8% of the remaining population, respectively.

Of the three main habitats, the cultivated habitats presented the highest dominance by one morpho-species with a 40% representation of *Tetranathida leucage sp.* This morpho-species is notably adapted to cultivated environments, and are proficient hunters in grass dominated ecosystems (Hall 2019). Similar to spider biodiversity in

other cultivated areas, the most altered environment had the highest dominance of a single morpho-species (Cardoso et al 2011).

Comparison of Diversity

The *Shannon Entropy* calculations showed higher diversity and evenness of the population from the cultivated to the primary habitat gradient (table 2). An increase of 61.31% was found between the cultivated and secondary habitats, and an increase of 29.02% between the secondary and primary habitats. The increase of 72.54% between the cultivated to primary habitats was the most significant change in biodiversity (appendix D).

The *Transformed Gini-Simpson* calculations showed a significant increase of biodiversity when habitat types were less impacted by anthropogenic alteration (table 2). An increase of 67.23% was found between the cultivated and the secondary habitat, and an increase of 33.31% between the secondary and primary habitat. The increase of 78.15% between the cultivated and primary habitats was the most notable in change in biodiversity across the land alteration gradient (appendix D).

Table 2. Diversity values, for each habitat type respectively and for all three combined to represent the regional biodiversity.

Habitat	Shannon Entropy	Gini-Simpson Transformed
<i>Primary</i>	3.86	25.58
<i>Secondary</i>	2.74	17.06
<i>Cultivated</i>	1.06	5.59
Regional	2.88	51.91

The percent similarities between habitats showed the primary and cultivated habitats had the least similarity sharing only 10% morpho-species between them. Secondary and cultivated shared 31% of the total morpho-species, showing the greatest similarity. The primary and secondary habitat showed a slightly lower similarity with 28% of the total morpho-species shared (table 3).

Table 3. Jaccard's Indices between the 3 main habitats sampled.

Habitat Comparison	Shared Morpho-species	Total Morpho-species	Jaccard Indices
Primary to Secondary	30	106	28%
Secondary to Cultivated	34	108	31%
Cultivated to Primary	15	143	10%

Habitats with similar land use impacts shared more morpho-species. Both the secondary and primary transects showed more similarity, as it can be assumed the morpho-species in those habitats rely on more unaltered vegetation structure to survive. Morpho-species in the cultivated regions may be able to cross over to both the secondary and primary habitats, but many of the primary and secondary morpho-

species may be too specialized to their vegetation infrastructure to survive in highly impacted regions (Gollan 2010).

Species Accumulation and Species Coverage

The individuals found across the three main habitats represented from 60% to 75% of the total expected diversity of the region. This leaves an unidentified margin from 35% to 40% of morpho-species not accounted for in the sampling period (figure 3).

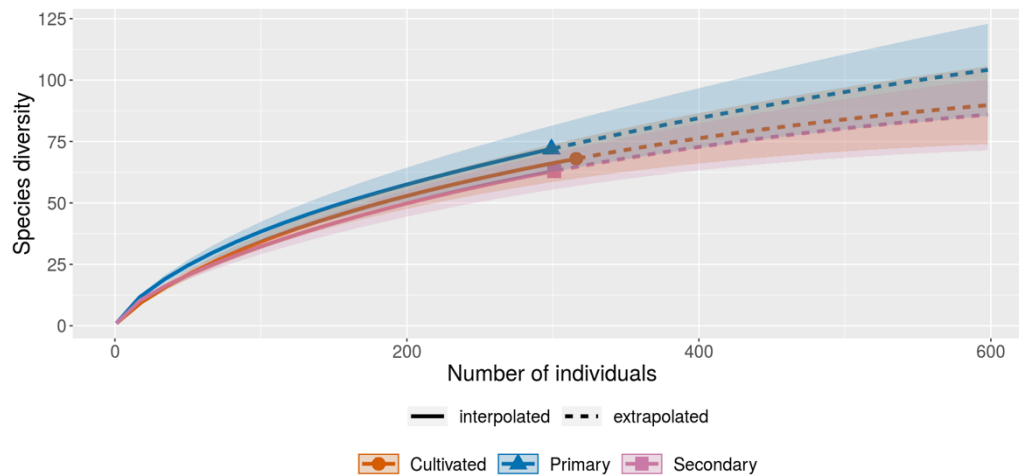


Figure 3. Species Accumulation Curve of the three main habitats: cultivated, primary and secondary. The interpolated line represents data collected and the extrapolated line represents the projection of species and individuals not found in the habitats during the study (Chao et al 2016).

The sampling efforts of the study successfully accounted for around 60% to 75% of the total species in the habitats surveyed. This leaves an unidentified margin from 35% to 40% of the morpho-species not found in the sampling period (figure 4).

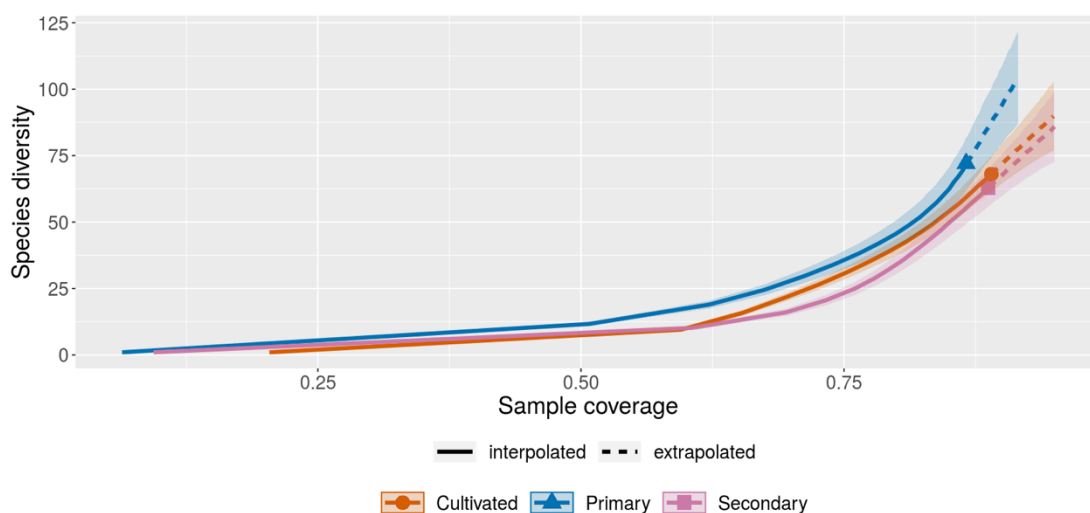


Figure 4. Sample Coverage of the surveys across the three main habitats: cultivated, primary and secondary. The interpolated line represents data collected and the extrapolated line represents the projection of diversity that remains un-surveyed in the habitats (Chao et al 2016).

This result reflects the findings of similar studies where arachnid biodiversity studies of this general size are usually able to account for around 70% of the total regional diversity (Azevedo et al 2014). Due to high variability amongst populations, it is common to encounter a high number of singletons and doubletons while surveying arachnids (Rego 2009).

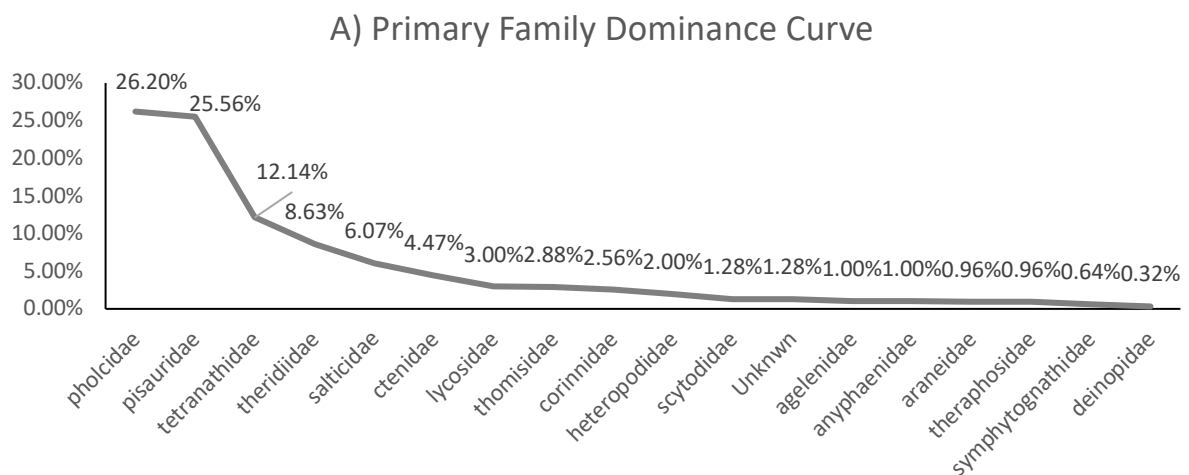
Family Composition

The regional family composition showed the family *Pholcidae* had the greatest abundance representing 23.36% of the total individuals found across habitats. This result is similar to the findings of Moore (2015), who found *Pholcidae* was the most abundant family across altitudes in an adjacent geographical region.



Figure 5. Examples from the 3 most abundant families in the region, a morpho-species from the *Pholcidae*, *Theridiidae* and *Tetranychidae* family.

The families *Theridiidae* and *Tetranychidae* were the second and the third most abundant families representing 18.24% and 17.95% of the total regional population (appendix C.) The family *Theridiidae* was found to be abundant in Ecuadorian Cloud Forests by Robinson (2018), in a study on the biodiversity of spiders across altitude range.



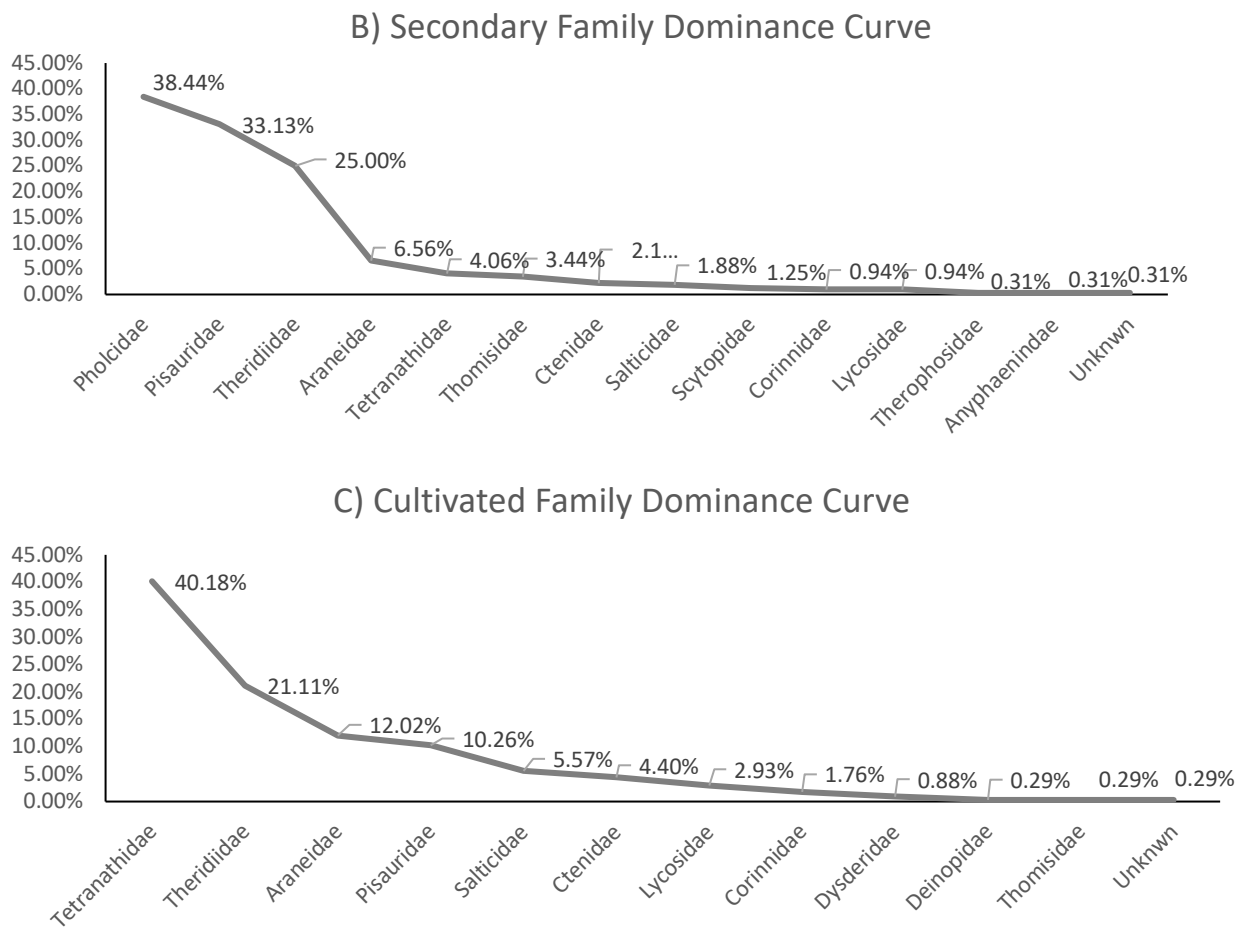


Figure 6. The Family Dominance Curves of each habitat type, exhibiting the families with the greatest representation in the habitat.

The most common family found in the primary habitats was *Pholcidae*, which represented 26.20% of the total individuals found. *Pisauridae* and *Tetranathidae* made up the second and third largest component of the sample, representing 25.56% and 12.14% respectively. The remaining 14 families and the few individuals that could not be classified into families each represented from 0.32% to 8.63% of the total composition (figure 6A).

The most common family in the secondary habitat was *Pholcidae* which represented 38.44% of the total individuals found. *Pisauridae* and *Theridiidae* made up the following highest percentages representing 33.13% and 25% respectively. The rest of the families and the few individuals who could not be identified represented from 0.31% to 6.56% of the individuals in the habitat (figure 6B.)

The most common family in the cultivated habitat was *Tetranychidae* which represented 40.18% of the total individuals found. *Theridiidae* and *Araneidae* made up the following highest percentages representing 21.11% and 12.02% respectively. The rest of the families presented from 0.29% to 10.26% of the individuals in the habitat (figure 6C.)

For both the primary and secondary habitats the *Pholcidae* family dominated the number of individuals in the ecosystem. This finding was similar to the findings of Moore (2015), who found in uncultivated regions the *Pholcidae* family was the most abundant.

The cultivated habitat had the most significant dominance of a single group (*Tetranathidae*) compared to the other habitats which showed almost equal presence of at least two families (figure 6.). The abundance of the *Tetranathidae* family in the cultivated area was so apparent they were considered a part of the third most abundant family in the region (appendix c.)

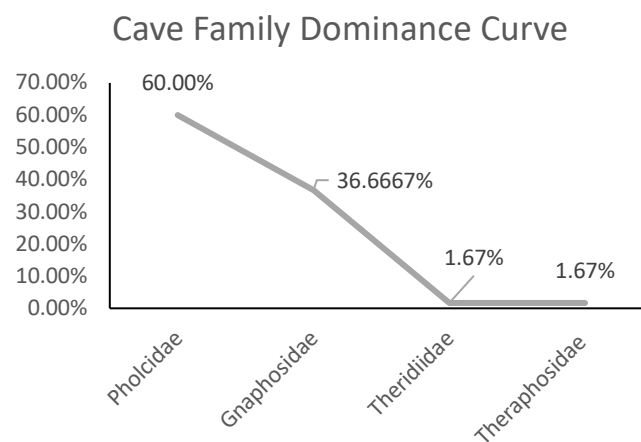


Figure 7. The Cave Habitat Dominance Curve, exhibiting the families with the greatest representation in the habitat

The populations in the cave habitat show a dramatic dominance of two groups. The families *Pholcidae* and *Gnaphosidae* presented 96.67% of the population (figure 7). Compared to the three main transects that had increased ecological resources, the cave habitats could only support a few families. The resources and ecological infrastructure of cave habitats is inhospitable to many organisms, and the presence of a few specialized families is expected under such conditions (Mammola et al 2017).

Guild Composition

Across the region the *space web*, *sheet web* and *orb weaver* guilds were the most abundant. The two most abundant families *Pholcidae* and *Theridiidae* are classified as *space web* builders, while the third most abundant family *Tetranathidae* hunts in the *orb weaver* guild (table 1).

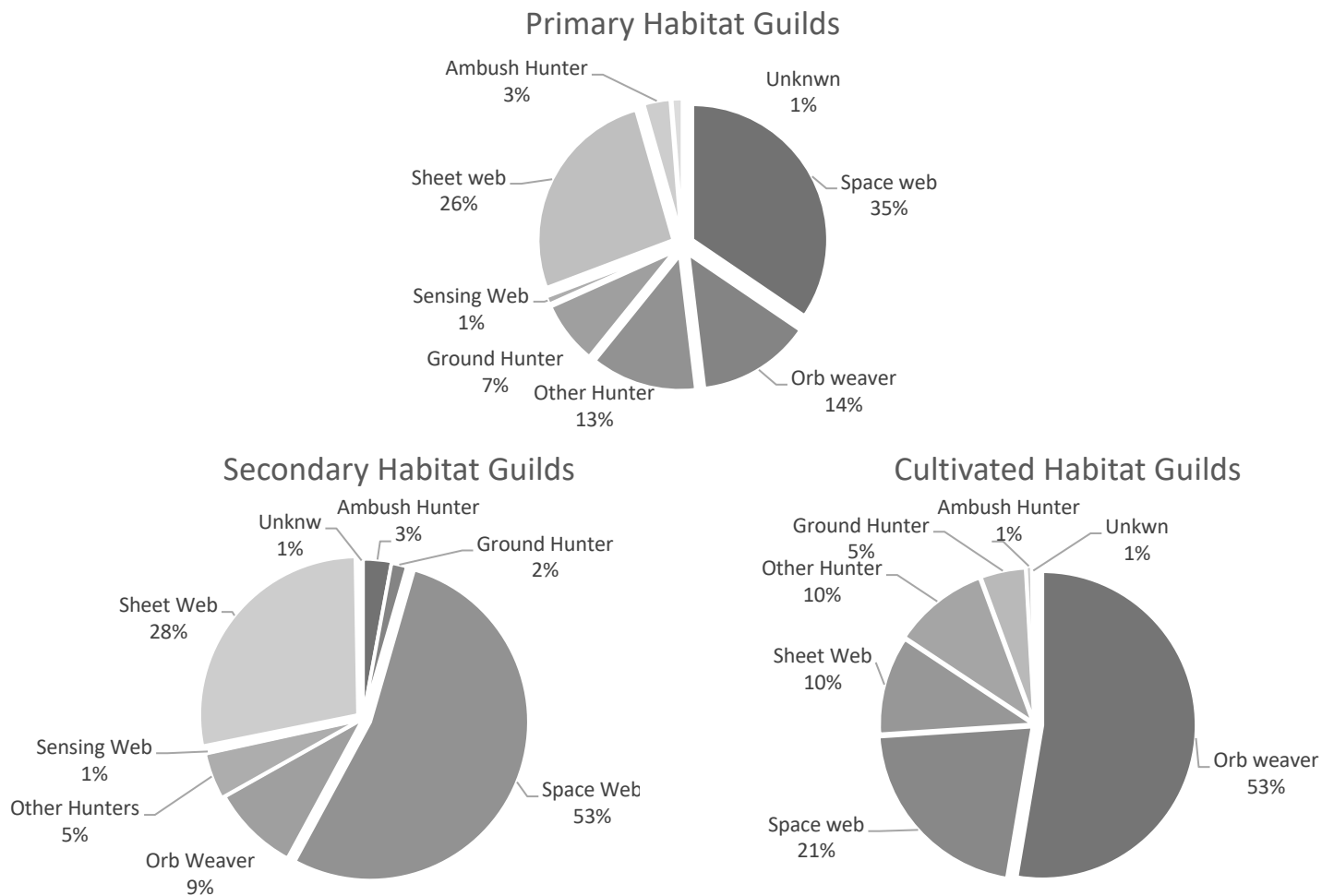


Figure 8. Habitat Guild Composition, displayed in percentages out of the total number of individuals sampled. Chart A represents primary guilds, Chart B represents secondary guilds, and Chart C represents cultivated guilds.

The most abundant guild in the primary habitat were *space web* builders making up 35% of the total guilds represented. The second greatest usage was represented by *sheet web* builders who made up 26% of the individuals in the habitat (figure 8A). The families building space webs include *Pholcidae* and *Theridiidae* (table 1), with *Pholcidae* representing the highest percentage of individuals in the habitat.

The most represented guild in the secondary habitat were *space web* builders, making up 53% of the total individuals in the habitat. The three most abundant morpho-species were classified as *space web* builders. The second most represented guild were *sheet web* builders, making up 28% of the total individuals in the habitat (figure 8B.) The first and third most abundant families in the habitat (*Pholcidae* and *Theridiidae*) were classified in the *space web* guild, while the second most abundant family *Pisauridae* was classified in the *sheet web* guild (table 1).

The most represented guild in the cultivated habitat were *orb weavers*, making up 53% of the total individuals in the habitat. The second most abundant guild was the *space web* builders, making up 21% of the total individuals in the habitat (figure 8C). The most

abundant family in the habitat *Tetranathidae* is classified under the *orb weaver* guild, while the following most abundant families *Theridiidae* and *Araneidae* fall into the *space web* and *orb weaver* guilds, respectively (table 1).

Only 3 guilds were found in the cave transects, with the *specialist* and *space web* guilds making up 99% of guild activity (figure 9). Compared to the guild composition of the three main transects the cave ecosystem presents a high level of ecological stress resulting in only a few guilds being able to adapt to the extreme subterranean environment (Mammola et al 2017.)

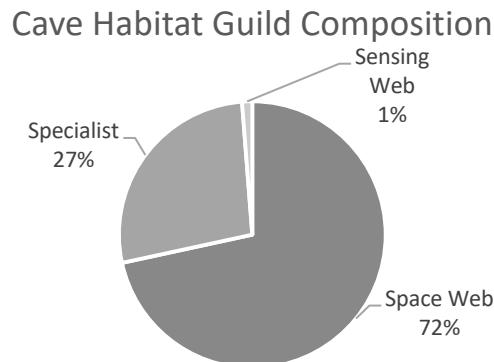


Figure 9. Cave Guild Composition displayed in percentages out of the total number of individuals found.

The richness and evenness of guilds increased from the cultivated to the primary habitat. Habitats with less anthropogenic intervention were able to support a higher range of guilds, resulting in higher measures of biodiversity (table 2). Guilds with more specialized hunting techniques were found to be more represented in more unaltered habitat types (Michalko 2016, Cardoso et al 2011). Habitats with higher ecological pressure (Mammola et al 2017) or increased levels of disruption will only be able to support simplistic guild compositions, as these habitats limit the amount of resources, structure and refuge needed to support complex guild activity (Cardoso et al 2011).

Vegetation and Land Use Impact

The type of vegetation in each habitat could be classified into 9 categories. The 8 guilds could be arranged into the types of vegetation they were found using to hunt.

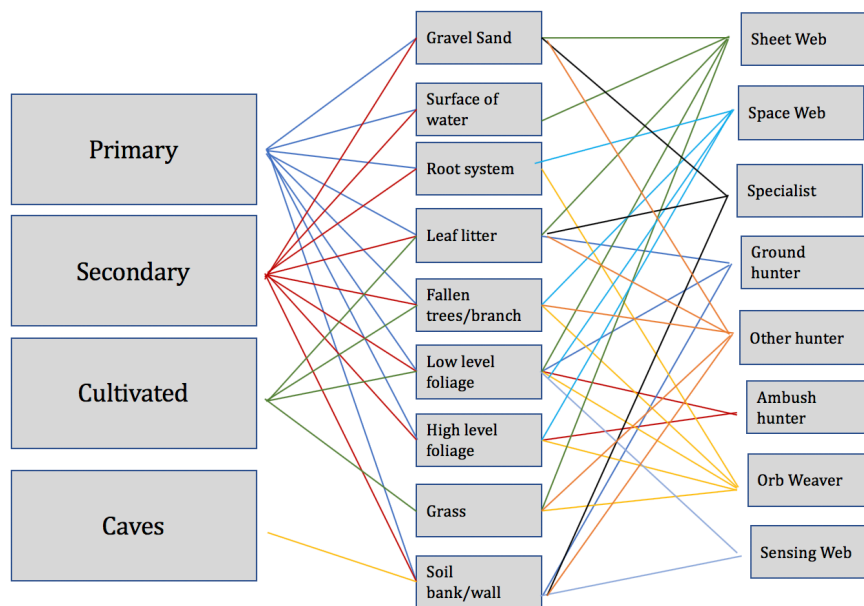


Figure 10. Vegetation and strata present in the four habitats, with designation of type and the guilds found using the infrastructure.

Vegetation variability was found to decrease across the four habitats sampled, paralleling a decrease in the biodiversity and active guilds in the habitat. Both the primary and secondary habitats showed the highest range in vegetation type, while the cultivated habitats had only 4 out of the 9 classifications. The cave ecosystems showed no vegetation and only one strata classification (figure 10).

The species richness, family and guild presence between the main three transects and the cave samples showed a dramatic decrease, with only 6 morpho-species, 4 families and 3 guilds being found throughout the caves surveyed (appendix A.) As the ecological stressors increased, classified in diminishing vegetation variability, the diversity of the spider populations decreased proportionally (Mammola et al 2017). The availability and diversity of vegetation directly impacted the biodiversity present across the region. As vegetation and strata complexity increased the number of active guilds increased. This contributes to the increase of biodiversity as the support of more guild types leads to the presence of more species (Cardoso et al 2011).

As both of the secondary and cultivated habitats had been previously altered and both had varying degrees of dense vegetation type, similar species would find them hospitable. They were also closer together in location, meaning more species had the ability to cross over from habitat to habitat. Spiders in adaptive guilds such as *space web* or *orb weavers* will be able to thrive in varying habitat types, as both rely on vegetation structure but can adapt to varying vegetation to build webs (Schüpbach 2003).

As the primary forest and the cultivated fields had the greatest degree of impact difference, it is expected they would share the least amount of morpho-species (table 3).

The significant difference between anthropogenic impact of unaltered primary forest and cultivated fields would support the assumption that species in primary forest would not find agricultural areas as hospitable (Uetz 1991).

The cultivated transects however showed a relatively high biodiversity measure (table 2). As found by Marc & Canard (1997) agricultural zones with little to no chemical impact will be hospitable to a range of spiders and their respective guilds. They also found higher spider biodiversity in cultivation has the potential to act as an effective pest control, and with the intersection of a range of guilds, can target insects in all of their life stages. The percentage of biodiversity found in the cultivated transects represent a cultivated area with good agroecological management. Cultivated land that has been abandoned to a certain degree will also present higher levels of biodiversity, as the lack of chemical use and consistent disturbance permits spider populations to increase (Martin 1982).

Conclusion

Spider biodiversity around the world, and specifically the *neotropics*, is still a biological frontier to be fully understood (Basset 2012). Presenting a new frontier of new scientific discoveries, spiders display an intriguing range of taxonomy and ecological interactions that rivals comparative top-level predators on other trophic levels (Basset 2012, Silva 1992).

This study found spider biodiversity decreased with increased anthropogenic impact. Primary forests were found to support more spider families and provide infrastructure for increased guild activity. The most impacted regions, the cultivated habitats, showed a decrease in diversity, with a few species dominating the ecosystem. The classification of vegetation type showed that a decrease in variability corresponded to a decrease in biodiversity. In both the cultivated and cave ecosystems (imposing both artificial and natural ecological pressures) fewer families and guilds could be supported. This demonstrates how ecologically mindful land management is vital in preserving spider biodiversity, as increased ecological pressure lessens the resources needed by the more complex guilds.

The unique biodiversity found in the primary forests showed how preservation of pristine environments is vital, especially in the case of spiders where many species have yet to be described (Platnick 2013). The cultivated habitat biodiversity did show how mindful agricultural practices can maintain diverse spider populations, simultaneously creating effective pest control (Jeanneret et al 2003). Spider biodiversity across habitats calls for increased scientific exploration, as knowledge of diversity across trophic levels is necessary when developing complete conservation protocols.

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Appendix A: The number of morpho-species, families, guilds and individuals found in each habitat type.

Habitat	Morpho-species	Families	Guilds	Individuals
<i>Primary Forest</i>	73	17	6	313
<i>Secondary Forest</i>	64	13	7	320
<i>Cultivated Fields</i>	68	11	6	341
<i>Caves</i>	6	4	3	60

Appendix B: The Families and guilds found in each habitat type.

Habitat	Families	Guilds
Primary	<i>agelenidae</i> <i>anyphaenidae</i> <i>araneidae</i> <i>corinnidae</i> <i>ctenidae</i> <i>deinopidae</i> <i>heteropodidae</i> <i>lycosidae</i> <i>pholcidae</i> <i>pisauridae</i> <i>salticidae</i> <i>scytodidae</i> <i>symphytognathidae</i> <i>tetranathidae</i> <i>theraphosidae</i> <i>theridiidae</i> <i>thomisidae</i> <i>Unknwn</i>	<i>Ambush Hunter</i> <i>Ground Hunter</i> <i>Orb weaver</i> <i>Other Hunter</i> <i>Sensing Web</i> <i>Sheet web</i> <i>Space web</i> <i>Unknwn</i>
Secondary	<i>Anyphaenindae</i> <i>Araneidae</i> <i>Corinnidae</i> <i>Ctenidae</i> <i>Lycosidae</i> <i>Pholcidae</i> <i>Pisauridae</i> <i>Salticidae</i> <i>Scytopidae</i> <i>Tetranathidae</i> <i>Theridiidae</i> <i>Therophosidae</i> <i>Thomisidae</i> <i>Unknwn</i>	<i>Ambush Hunter</i> <i>Ground Hunter</i> <i>Orb Weaver</i> <i>Other Hunters</i> <i>Sensing Web</i> <i>Sheet Web</i> <i>Space Web</i> <i>Unknwn</i>

Cultivated

Araneidae
Corinnidae
Ctenidae
Deinopidae
Dysderidae
Lycosidae
Pisauridae
Salticidae
Tetranathidae
Theridiidae
Thomisidae
Unknwn

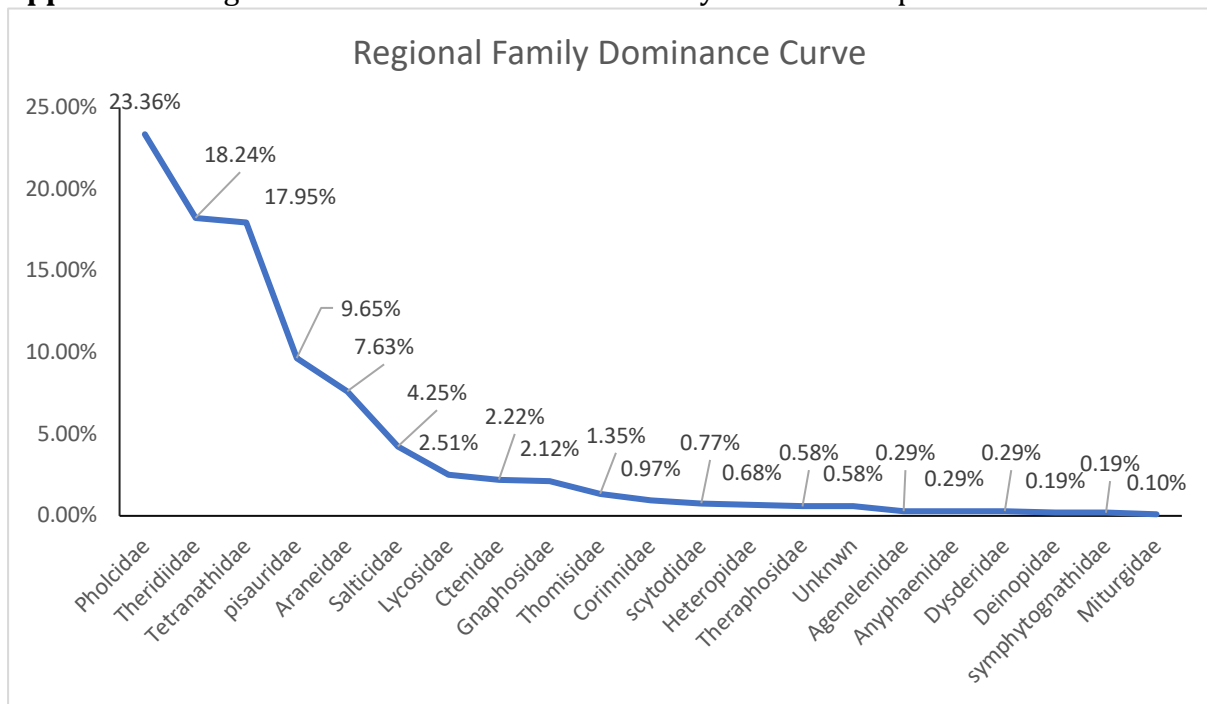
Ambush Hunter
Ground Hunter
Orb weaver
Other Hunter
Sheet Web
Space web
Unknwn

Caves

Gnaphosidae
Pholcidae
Theridiidae
Theraphosidae

Specialist
Space Web
Sensing Web

Appendix C: Regional Dominance Curve and Family Percent Composition



Appendix D: Biodiversity Comparisons

Habitat	Simpson Entropy	Comparison	Difference	% increase
P	3.86	C/S	1.68	61.31%
S	2.74	C/P	2.8	72.54%
C	1.06	S/P	1.12	29.02%
Habitat	Gini-Simpson (transformed)	Comparison	Difference	% increase
P	25.58	C/S	11.47	67.23%
S	17.06	C/P	19.99	78.15%
C	5.59	S/P	8.52	33.31%