


Spring 2016

Nutrient Cycling in the Amazon: A Comparison of Soil Characteristics, Insects, Root Types and Decomposition Rates between Varzea and Terra Firme habitats in the Ecuadorian Amazon

Mira Ensley-Field

SIT Graduate Institute - Study Abroad

Follow this and additional works at: https://digitalcollections.sit.edu/isp_collection

 Part of the [Biosecurity Commons](#), [Environmental Monitoring Commons](#), [Systems Biology Commons](#), and the [Terrestrial and Aquatic Ecology Commons](#)

Recommended Citation

Ensley-Field, Mira, "Nutrient Cycling in the Amazon: A Comparison of Soil Characteristics, Insects, Root Types and Decomposition Rates between Varzea and Terra Firme habitats in the Ecuadorian Amazon" (2016). *Independent Study Project (ISP) Collection*. 2324. https://digitalcollections.sit.edu/isp_collection/2324

This Unpublished Paper is brought to you for free and open access by the SIT Study Abroad at SIT Digital Collections. It has been accepted for inclusion in Independent Study Project (ISP) Collection by an authorized administrator of SIT Digital Collections. For more information, please contact digitalcollections@sit.edu.

Nutrient Cycling in the Amazon:

A Comparison of Soil Characteristics, Insects, Root Types and Decomposition Rates between
Varzea and Terra Firme habitats in the Ecuadorian Amazon



View of Rio Napo from Monkey Island

Mira Ensley-Field

Academic Director: Silva, Xavier

Project Advisor: Vargas, Hector

Macalester College

Biology

South America, Ecuador, Orellana

Submitted in partial fulfillment of the requirements for Ecuador: Comparative Ecology and
Conservation, SIT Study Abroad, Spring 2016

Index

Abstract.....	3
Acknowledgments.....	4
Introduction.....	4
Materials and Methods.....	8
Results.....	10
Discussion and Conclusion.....	15
Future Research.....	24
Bibliography.....	26

Abstract:

Decomposition and nutrient cycling form the basis of every ecosystem. Nutrient availability in the soil affects plant species composition, richness, and productivity. The Amazon rainforest is known for its unusually fast nutrient cycle, but many aspects lack detailed study and analysis. This comparative study carried out in the Ecuadorian Amazon had four primary objectives related to understanding the nutrient cycle in the Amazon; 1.) analyze soil characteristics, 2.) assess insect diversity in the leaf litter layer, 3.) examine root characteristics, and 4.) measure the decomposition rate between Varzea and Terra Firme habitats alongside the Rio Napo. Forty 0.25 x 0.25m quadrats were set up in each site to examine soil characteristics and insect diversity. The organic horizon, clay content, dry leaf litter weight, and soil moisture capacity were measured and hypothesis tests were then performed to analyze potential differences between sites. Varzea forest had a deeper organic horizon, less clay, and higher soil moisture capacity as compared to Terra Firme. There was no significant difference between the amount of leaf litter in each ecosystem. The leaf strata was also collected in both sites and insect diversity analyzed. Terra Firme had significantly more insects per unit area as well as more diversity within orders. Ten 25m transects were used to gather data on root types present in each ecosystem. Varzea had significantly more prop roots than Terra Firme forest. Lastly, an attempt was made to measure the decomposition rate using the tethered leaf method, but no significant difference was found. A better understanding of the nutrient cycle in the Amazon will both add to ecological theory and understanding as well as potentially help predict and mitigate human impacts on this ecosystem. The nutrient cycle is an incredibly important way of understanding an ecosystem and many parts of the nutrient cycle in the Amazon remain elusive and are in need of further study.

Resumen:

Descomposición y el ciclo de nutrientes es el fundación de cada ecosistema. La disponibilidad de nutrientes en el suelo afecta la composición, riqueza, y productividad de plantas que afecta todo el ecosistema. La Amazonia es conocido por su ciclo de nutrientes rápido, pero mucho aspectos falta estudia detallado y análisis. Ese estudio comparativo hecho en la Amazonía Ecuatoriana tuvo cuatro objetivos primarios relacionados con el ciclo de nutrientes en la Amazonia; 1.) analizar característicos de suelo, 2.) evaluar la diversidad de insectos en la hojarasca, 3.) examinar característicos de raíces, y 4.) medir la tasa de descomposición entre la Varzea y Terra Firme hábitats cerca del Rio Napo. Cuarenta 0.25x 0.25m cuadrados fueran colocados en los dos sitios para examinar características de suelo y la diversidad de insectos. El horizonte orgánico, contenido de arcilla, peso seco de hojarasca, y capacidad de humedad de suelo fueran medidos y exámenes de hipótesis hechos para analizar diferencias potenciales entre sitios. Los bosques de Varzea tienen un horizonte orgánico de más profundidad, menos arcilloso, y una capacidad de humedad más alto comparado con el Terra Firme. No había una diferencia significativa entre el peso seco de la hojarasca en cada ecosistema. La hojarasca fuera colectada y analizada en los dos ecosistemas también. Terra Firme tuvo más insectos en cada cuadrado y también más diversidad de órdenes. Diez 25m transectos fueron usado para colectar data en tipos de raíces presentes en cada ecosistema. Varzea tuvo significativamente más raíces de “prop” comparado con el Terra Firme. Finalmente, un intento fuera hecho para medir la tasa de descomposición usando el método de tethered leaf, pero no diferencia significativa fuera encontrado. Un entendimiento mejor del ciclo de nutrientes en la Amazonia añadirá a teoría ecológico y además, potencialmente a ayudar a predecir y mitigar impactos humanos en ese ecosistema. Muchos partes del ciclo de nutrientes en la Amazonia ya están elusivo y necesitan más investigaciones.

ISP Topic Codes: 601, 609, 614
Keywords: Nutrient Cycling, Decomposition, Insect Diversity

Acknowledgements:

There are many people without whom this project would not have been successful. Many thanks to Hector Vargas, my project advisor, for his extensive background knowledge on the ecosystems of the Amazon rainforest, advice, encouragement, and assistance in finding and setting up study sites. He consistently went above and beyond all expectations and was an invaluable resource and mentor throughout the project. Martina Vargas lent me a scale which was enormously useful, and was a source of encouragement throughout the study. I owe many thanks to Julian Marvelas for transportation assistance to and from study sites and rescue from venomous spiders. I am furthermore extremely indebted to Xavier Silva, who assisted in identification of insects as well as extensive help with establishing field methodology ahead of time and sharing his incredible knowledge on this ecosystem. Javier Robayo also assisted in establishing field methodology and sparked my interest in the many physiological adaptations of plants to nutrient poor and inundated ecosystems. And I never would have made it without Gabriel Oppler, Marie Lilly, Paulina Arcuri, Juliana Hitchins, and Kyla Hood who all assisted me in data collection and basic living necessities following an injury for which I am very grateful.

Introduction:

Amazon Rainforest:

The Amazon is the world's largest tropical rainforest, spread across 5,500,000 hectares and nine countries and its importance and significance is hard to overstate. For biologists, the Amazon represents an amazing hotspot for biodiversity, a resource by which to understand and analyze countless new and novel species and ecosystem processes in a way simply not possible in other ecosystems throughout the world. It contains an estimated 10% of the entire world's known biodiversity, meaning one in every ten species comes from the Amazon (World Wildlife Fund). A hectare in a temperate forest in North America may contain 30 different species of tree. A hectare in the Amazon contains 40-100 species, and some sites have been found to have 300 or more tree species in a single hectare (Kricher 1997). The staggering biodiversity of the Amazon can make its true extent difficult to estimate. For instance, scientists believe there to be 75,000 total tree species, 15,000 animals species, and 2.5 million insect species present in the Amazon, but only a fraction of each have been described (Desonie). For scientists therefore, the Amazon remains a crucial resource for investigation, with much potential for discovery.

The Amazon is not just important to conservationists and scientists interested in unlocking the mysteries of ecology and evolution and discovering and preserving unique species. The Amazon is a crucial part of the global climate system containing 25% of the world's total terrestrial biomass (Jobbagy and Jackson 2000). Deforestation of the Amazon, starting in the mid 1850's

accounts for 1.5% of the total increase in CO₂ levels (Life Science Weekly) and continued deforestation is a source of CO₂ entering our atmosphere every year. Thus conservation of the Amazon does not just benefit conservationists and scientists, it literally affects everyone on the planet and especially people living in areas vulnerable to climate change.

And it is finally important not to overlook the many people who live in the Amazon. The Amazon is perhaps most famous for its biodiversity and is often seen through an ecological or environmental lens, but a significant number of human beings also call this place home. Nearly 22% of the Amazon is the territory of indigenous people, with an estimated 600,000 people living there (The Nature Conservancy).

Despite its enormous importance to scientists, the global climatic system, indigenous peoples, not to mention the countless tourists who visit each year to experience first-hand this incredible ecosystem, threats to the Amazon are abundant and serious. Human activities such as petroleum, agriculture, and hunting are pose great threats to this ecosystem (Bass 2010). Nearly 14% of the Amazon rainforest has already been deforested, and the process of deforestation is still taking place with an estimated 2,000,000 hectares lost every year (Flora and Fauna International).

According to estimates based on satellite imagery by the FAO, Ecuador, where this study took place, is currently deforesting 1.8% of its rainforests every year, or 200,000 hectares, the highest rate in any Latin American country (FAO 2015). It should be noted however, that the figure from the Ecuadorian government puts estimates significantly lower, at only 62,000 hectares per year (Latin America Herald Tribune). The primary causes of deforestation in Ecuador are expanding agriculture and agroindustry, logging, mining, infrastructure, and petroleum activity (Silva 2016) all of which are serious concerns in the Amazon.

The Amazon Rainforest is one of the most biodiverse places on earth, but it's worth noting that is biodiversity is highest in the western Amazon in Ecuador, where this study was carried out. Thousands of years ago during the Pleistocene, climatic variation resulted in large global temperature changes. While the Amazon basin was never covered in glaciers like other parts of the world, the Ice Age lowered the temperature by several degrees centigrade. Though still comparatively warm, this had the important effect of changing the climate system from wet and humid to dryer and cooler. Thus the lush Amazonian forests were converted to tropical savannah in most of the Amazon. In Ecuador however, the rain shadow effect due to the Andes Mountains as well as the eastern trade winds conserved the humidity and rainfall. Thus, in this part of the Amazon, the lush and dense forests remained and did not lose species as happened in other parts of the Amazon (Silva lecture 2016, Kricher 1997).

Nutrient Cycling:

Nutrient cycling is the process by which nutrients are exchanged through trophic levels and leave and enter ecosystems. Unlike energy and biomass which travel and diminish up trophic levels, nutrients are recycled after passing through trophic levels, with occasional influxes and outputs. The nutrient cycle of an ecosystem can be slow or fast and it governs the amount of nutrients available for uptake. Nutrient availability forms the basis of every ecosystem as it can limit the growth of plants, affecting Net Primary Productivity as well as species richness and composition.

Net Primary Productivity, the amount of carbon produced by an ecosystem, is an area of utmost importance in the light of the carbon cycle and its impacts on the climate system. Scientists are very interested in understanding which ecosystems have the highest Net Primary Productivity and why rates are different. One hypothesis is that, especially among terrestrial systems, there is a K, N, and/or P limitation (Cleveland et al 2011). Amazonian soils tend to be lacking relatively more in P compared to N (McGroddy et al 2004, Reich & Oleksyn 2004, Townsend et al 2007, Cleveland et al), but whether this lack is limiting Net Primary Productivity has yet to be conclusively established (Cleveland et al 2011).

Many studies have investigated the relationship between species richness and nutrient availability, and at times the results are occasionally counterintuitive. Vermeer et al found in a study published in 1983 an optimum curve where the availability of nutrients correlate with increased species richness up to a point before declining. While a wider nutrient availability can increase the number and type of species that can survive in an ecosystem, a very large amount of available nutrients is accompanied by relatively low species richness. Increased competition for scarce resources in the soil is perhaps able to increase species richness by providing selection pressures that lead to increased niche partitioning, but an abundance of nutrients available for uptake can allow a few specialists in high nutrient microhabitats to dominate. A study carried out in the Costa Rican rainforest found that sites with lower nutrient availability, the sites with the seeming poorest growing conditions, had the highest species richness (Huston 1980).

Nutrient availability is clearly a crucial piece of understanding an ecosystem. To understand nutrient availability, a thorough understanding of soil characteristics and how nutrients are returned and uptaken from the soil is necessary. Litter decomposition, depending on the quality of leaf litter, can return varying amounts of P and K in addition to carbon to soil. Litter decomposition rates are complicated and highly influenced by soil temperature, soil moisture, litter quality, as well as the health and diversity of decomposers (Karberg et al 2008). The Amazon has one of the highest decomposition rates in the world, precisely because of the constant rain, the high humidity, and the high temperatures (Kricher, 1997) but little research has been done on estimating the decomposition rate, especially in different parts of the Amazon. Therefore, the overall functioning of the flow of nutrients in the Amazon remains poorly understood.

Soil Characteristics in the Amazon:

Soil in the Amazon was deposited very early and originated from sediment, but due to the warm and humid climate has been leached over the centuries until it is now nutrient poor. While high amounts of rainfall can aid in the decomposition of leaves and returning nutrients to soil, over time it leads to leaching. It can also drive nutrients lower and deeper through soil and make them less bioavailable. Leaching and high rainfall also has a tendency to make soils more acidic (Kricher, 1997). Nutrient poor soil is often assumed to be correlated with low net primary productivity and species richness, but it is not always so and certainly not in the Amazon. Vermeer et al found in a study published in 1983 an optimum curve where the availability of nutrients correlate with increased species richness up to a point before declining. Increased competition for scarce resources in the soil is perhaps able to increase species richness by

providing selection pressures that lead to increased niche partitioning. Additionally, low nutrient availability, such as is in the case of the Amazon, does not mean there are no life-sustaining nutrients. It can also mean that nutrients are tied up in biomass and that there is a rapid nutrient cycle. The Amazon is a particularly interesting place to study nutrient cycling therefore, because the nutrient cycle is incredibly fast, nutrient availability incredibly low, yet Net Primary Productivity and species richness incredibly high.

Though nutrients have been leaching out of the soil for thousands of years, there is also an important source of nutrients for the Amazon. The global climate system and winds bring in dust from the Sahara that settles and adds nutrients such as phosphorous and nitrogen to the Amazon which have an important effect (Bristol et al 2010).

Additionally, Varzea forest is close to sedimentary rivers originating from the Andes, and thus has a tendency towards richer soil in terms of nutrients (Herrera et al 1978, Wittman et al 2006, Assis et al 2015). Though seasonal flooding in the Igapo can drain the soil of important nutrients, the opposite effect has been observed in the Varzea, located next to sediment rich white waters. One study calculated an estimated 8100g/m² of sediment were added annually to Varzea forest after flooding (Irmiler 1979). Terra Firme forest, located elevationally above Varzea does not receive these influxes of nutrients from flooding.

Study site:

This study was carried out on Monkey Island, a 115 ha (284 acre) nature reserve owned by Sumak Allpa in the Orellana province near Coca located in the Napo River between Coca and Limoncocha. Primary Varzea was examined on Monkey Island, and Primary Terra Firme on the bank next to the island.



Varzea and Terra Firme have a number of known differences and similarities. Both are warm, humid, and have high rainfall. They are located next to each other and thus share many species, however each ecosystem can also be distinguished based on differential frequency of species composition of plants, and a number of other physical characteristics. Varzea have more heliconias and palms, and the understory layer tends to be thicker. Terra Firme forests have more taller and older trees, especially Kapoks and trees in the Meliaceae family. The easiest way to distinguish these two ecosystems, lacking botanical expertise in these areas however, is that Terra Firme forest is hilly, constantly going up and down and located at least half a kilometer from the river whereas Varzea is flat and next to the river (Vargas 2016).

The general focus of this study was a better understanding of the incredible yet unusual nutrient cycling processes in the Amazon by comparing two ecosystems; Terra Firme and Varzea. There were four specific goals to provide a structured and multifaceted way to look at nutrient cycling processes. First was to compare soil characteristics between Terra Firme and Varzea forest and heterogeneity within each ecosystems. By necessity, this was done with somewhat minimal equipment. Soil characteristics measured include organic horizon depth, dry leaf litter weight, clay content, and moisture capacity of the soil. The next specific goal was to see if there were any differences in insects in the leaf strata between these two ecosystems, a way to look at any potential differences in the insect community primarily responsible for the breakdown of organic matter into soil. Thirdly, to examine any potential differences in root adaptations, specifically prop roots and buttress roots, which both have theorized strategic adaptations that allow them to take advantage of physical characteristics in their respective environments. Lastly, to experimentally determine the decomposition rate and compare it between the two ecosystems.

Materials and Methods:

Materials:

- 0.25 x 0.25m quadrat
- Measuring tape
- Small shovel
- Scale
- 8 or more airtight bags for collecting samples
- 8 or more large containers for drying samples
- Thermometer
- Humidity meter
- Lens
- Camera
- Soap
- 4 or more graduated cylinders
- Twine
- Tape
- Sharpie
- Field notebook

Soil Characteristics Study:

Eleven 3x3m plots were set up in primary Varzea and Terra Firme forest. Each 3x3 m plot contained four 0.25 x 0.25m quadrats. The relative humidity, temperature, and organic horizon depth were taken on site at each of the smaller quadrats. The organic horizon was determined by digging down and measuring from the top of the leaf litter layer to where the soil color changed from darker to lighter. The leaves that fell more than 50% in the quadrats were also gathered as well as a small amount of soil underneath the leaf litter layer and placed in separate, labeled plastic bags. The leaf litter and soil was then left to dry in glass aquariums in a greenhouse. After 6-24 hours, depending on weather conditions, the dry weight of the leaf litter was taken and the moisture carrying capacity of the soil was tested. To test soil moisture capacity of soil, a known weight of thoroughly dry soil was mixed with a known weight of water. I used around twice as much water as soil to ensure that the saturation point of the soil would be reached. After waiting for the soil and water to mix, the water and soil was poured over a mesh that trapped the soil and the water passed through a funnel into another container. The excess water not held by the soil was then measured and the water captured by the soil then could be determined. Finally, the soil was mixed with a 5% soap solution (see Whiting 2015), shaken and mixed for ten minutes, and left out in plastic bottles until the sediment and clay ratios had settled and could be recorded. The depth of the clay layer and of the total sediment in the bottle was recorded and converted later to a percent. A total of 80 quadrats between the two sites were sampled for each of these variables.

Insect Study:

Immediately after collection, the leaf litter from each quadrat was sifted through in a large glass aquarium. All leaves and leaf matter was placed on one side, and each large leaf or leaf fragment examined for insects and placed on the opposite side of the container. After all large leaf material had been moved, and all insects on leaves recorded, the very broken up leaves were gently brushed across the container to the center as I watched for fleeing insects. After no more movement was observed, the leaf matter would be pushed to the opposite side of the aquarium and this process was continued until all leaf matter had been examined. All observed insects were recorded, and unknown insects were photographed to be identified later. Insects that were not successfully identified were marked as “unknown” when entered into final spreadsheets.

Root Type:

Ten 25m transects were set up in the Terra Firme and Varzea forest. For 1m on each side, every tree with a dbh over 10cm was recorded as having normal, prop, or buttress root types. Care was taken to run transects only in primary Terra Firme and Varzea forest, and to not allow transects to overlap or intersect with trails.

Decomposition Rate:

The tethered leaf method was used to estimate the decomposition rate in the Varzea and Terra Firme forest. Three plant species were selected and ten leaves were split into two groups,

weighed, labeled, and distributed across the forest floor and left to decompose for 24 hours. They were then collected and their final weights compared with the initial ones.

Results:

Soil Characteristics results:

Examination of soil characteristics between Varzea and Terra Firme forest revealed a number of significant differences. The organic soil horizon was 31.4% deeper in the Varzea compared to the Terra Firme with an average depth of 3.583 versus 1.699 cm. Varzea has a significantly lower clay composition and a correspondingly greater silt composition, having nearly 334% less clay, with a value just shy of 3% compared to the 8.3% encountered in Terra Firme. There was not enough evidence to establish a significant difference between the weight of dry leaf litter in either ecosystem, they both had similar dry weights with 48.2g on average in Varzea and 53.1g in Terra Firme. The moisture carrying capacity of the soil was found to be significantly higher in the Varzea compared to Terra Firme. The average soil moisture capacity in the Varzea was 0.6238 grams of water per gram of soil, and only .5083 in Terra Firme (see Table 1). In addition to being correlated with ecosystem type, there is also a significant relationship between the moisture carrying capacity of soil and its clay content (see Figure 2)

Ecosystem	Varzea	Varzea Standard Deviation	Terra Firme	Terra Firme Standard Deviation	% Difference in Value between Terra Firme and Varzea	P value
Organic Horizon (cm)	3.5825	2.064087	2.4575	1.699002	31.40265178	0.00944
Amount of Clay (%)	2.935	1.549284	12.7325	8.328431	-333.8160136	1.97E-10
Amount of Silt (%)	97.065	1.549284	87.27	8.328431	10.09117602	2.00E-10
Leaf Litter (g)	48.187	19.9302	53.125	24.85567	-10.24757715	0.33
Soil Moisture Capacity (g of H2O/g of soil)	0.6238	0.1930549	0.50825	0.1309509	18.51703407	0.00245

Table 1: Summary of Differences in Soil Characteristics between Terra Firme and Varzea Forest

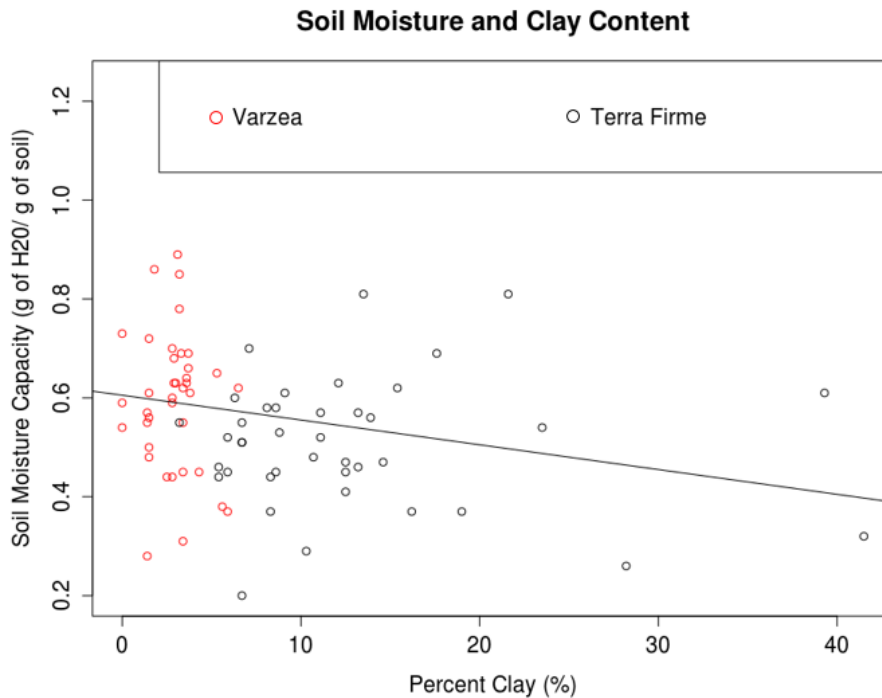


Figure 2: Soil Moisture and Clay Content

Another interesting thing to note is the standard deviations, which are high between both ecosystems on many of the variables, most notably the organic horizon and leaf litter measurements. Even within the same ecosystem, there is a highly varied amount of leaf litter and highly varied depth to the soil horizon. The organic horizon depth for Varzea was 3.5835 and the standard deviation was 2.064 with values ranging from as high as 8.2cm to as low as only 1cm. The Terra Firme also exhibited large variation, with a mean of 2.4575, a standard deviation of 1.699 and depths ranging from 6 to 0.1cm.

Insect Study Results:

Results from the insect study indicate that insects are more abundant and more diverse in Terra Firme compared with Varzea. More individual insects were found in Terra Firme, 662 individuals compared to only 435 as well as more orders of insects (see Table 2). In total, 20 m² of leaf strata were analyzed for insects, 10m² in Terra Firme and 10m² in Varzea. Of the 1097 total insects found, 39.65% were found in Varzea and 60.35% in Terra Firme. Of the 16 total orders found, all were present in Terra Firme, but two orders (Phasmida and Opiliones) were not encountered in Varzea.

Ecosystem	Varzea	Terra Firme
Total Number of Insects	435	662
Total Number of Insects Ant Colonies Excluded	285	562
Total Orders Encountered	14	16
Avg Insects per quadrat	10.875	16.55
Avg Orders per quadrat	3.625	4.475

Table 2: Insects and Orders of Insects in Varzea and Terra Firme Forest

Ranked in order of their abundance in Varzea forest, the 16 encountered orders and the number of insects captured from each order are listed below in Table 3 (for a breakdown of insect by individual quadrat, see Appendix section B). It is important to note a total of 17 insects were not identified, and they could be from different orders.

If ant colonies (defined as quadrats where 50 or more ants were found) are included, there is no significant difference between the number of insects found in Varzea and Terra Firme (p value=.179). If ant colonies are removed, the difference does become significant with a p value of 9.83e-05. Removing ant colonies is justified as capturing even part of a single ant colony can easily add 50-100 insects to one ecosystem, when the encounter with the colony was largely due to chance. Two ant colonies were found in Varzea, and only one in Terra Firme.

	Varzea Number of Individuals	Varzea Percent of Total Individuals (%)	Terra Firme Number of Individuals	Terra Firme Percent of Total Individuals (%)
Hymenoptera	284	65.29	380	57.40
Araneae	25	5.75	30	4.53
Isopoda	24	5.52	32	4.83
Diplopoda	20	4.60	22	3.32
Coleoptera	18	4.14	33	4.98
Acari	14	3.22	17	2.5
Diplura	13	2.99	73	11.03
Isoptera	8	1.84	4	0.60
Diptera	5	1.15	13	1.96
Orthoptera	4	0.92	12	1.81
Mollusca	4	0.92	1	0.15
Collembola	4	0.92	0	0.00

Pseudoscorpionida	2	0.46	6	0.91
Turbellaria	2	0.46	2	0.30
Phasmida	0	0.00	1	0.15
Opiliones	0	0.00	4	0.60
Unknown	4	0.92	13	1.96

Table 3: Total Individuals and Percent of Total Individuals between Varzea and Terra Firme

Most differences and variations in frequencies of insects of different orders are slight, constituting only a few percent. The two exceptions are the Diplura and Hymenoptera orders. Individuals from the order Diplura comprised less than 3% of total individuals in the Varzea forest, but over 11% in the Terra Firme. 65% of individuals in the Terra Firme are ants, but only 57% in the Varzea, another seemingly large difference. A hypothesis test between the differences in each ecosystem (Table 4) sheds light on the matter. When ant colonies are included, there is no significant difference between Hymenoptera in the Varzea and Terra Firme. When the colonies are excluded however, a significant difference appears. More ant colonies were found in the Varzea, and this skewed the data despite a clear trend of more ants overall in the Terra Firme. Though a few differences approach the level of significance, the only truly significant results are that of the Hymenoptera and the Diplura order.

	Average Individuals in Varzea	Average Individuals in Terra Firme	p-value
Coleoptera	0.450	0.825	0.150000
Hymenoptera	7.100	9.500	0.526409
Hymenoptera colonies excluded	3.526	7.05	0.011
Araneae	0.625	0.750	0.515000
Diplopoda	0.500	0.550	0.805520
Pseudoscorpionida	0.050	0.150	0.311000
Diptera	0.125	0.325	0.455900
Acari	0.350	0.425	0.652237
Mollusca	0.100	0.025	0.170000
Orthoptera	0.100	0.300	0.110903
Isoptera	0.200	0.100	0.512000
Turbellaria	0.008	0.005	1.000000
Ispodoa	0.600	0.800	0.361000
Diplura	0.325	1.825	0.000017
Phasmida	0.000	0.025	0.320000
Collembola	0.100	0.000	0.206000
Opiliones	0.000	0.100	0.099100
Phasmida	0.000	0.025	0.320000

Table 4: Hypothesis Test between Differences in Insect Encounters by Order in Varzea and Terra Firme

Roots results:

The Varzea forest had significantly fewer “normal” roots compared to the Terra Firme forest and significantly more “prop” roots. And although the data suggests there is likely a higher amount of buttress roots in the Terra Firme forest, the results are not quite significant and therefore inconclusive. In any case the observed difference between buttress roots in the two ecosystems was relatively small, only a 5.5% differences where the difference in prop roots was over 20%. The density of trees with a dbh greater than 10cm was higher in the Terra Firme, with an average of 0.326 trees per m² compared to 0.274 in Varzea, but again this slight difference did not make the cutoff value for significance.

	Percent Normal Roots	Percent Buttress Roots	Percent Prop Roots	Density (trees/m ²)
Varzea	59.0	9.8	31.2	0.274
Terra Firme	76.7	15.3	8	0.326
Significance	0.000939	0.0587	0.000036	0.07801

Table 5: Root Types and Tree Densities by Ecosystem

Decomposition Results:

The tethered leaf method was employed to estimate the decomposition rates of leaves between the Varzea and Terra Firme forest (Karberg et al 2008). After two weeks of leaving leaves in either ecosystem, the only retrievable part was the string and tape marking each bundle, and a few remaining petioles (see Figure 3). The rest of the leaves had entirely decomposed. While this does say many things about the incredible speed of the decomposition process, it makes it rather difficult to compare between the Varzea and Terra Firme. A back-up set of leaves was then produced to try again to measure the decomposition rate on a shorter time scale, and this time left for only three days. Nonetheless, a similar problem occurred. Though a few leaves were recoverable, more than half of the leaves were not and had decomposed entirely, or decomposed from the petiole and were no longer findable. A 24 hour study was initiated at the very end of the study, and in that time period all leaves were recoverable. The average decomposition rate in the Varzea was 9.52%/day and 15.15%/day in the Terra Firme. These are based on a very small sample size and no significant difference can be detected.



Figure 3: Empty Leaf Tether

	Varzea Init Weight (g)	Varzea Final Weight (g)	Change in Weight (g)	Change in Weight as %	Terra Firme Init Weight (g)	Terra Firme Final Weight (g)	Change in Weight (g)	Change in Weight as %
a	11	11	0	0	11	8	3	27.3
b	14	13	1	7.1	20	19	1	9.1
c	20	17	3	21.4	21	20	1	9.1

Table 6: Decomposition over 24 hours between Varzea and Terra Firme. Average change in weight was 9.52% per day for Varzea and 15.15% per day for Terra Firme.

Discussion and Conclusion:

Organic Layer:

The organic layer is defined as a layer of soil composed of 20-30% decaying organic material and it is typically darker in color than layers underneath (Turenne.) My measurements for the organic layer included the leaf litter scattered on top, usually no more than a few centimeters or less. A paper published in 2002 examined leaf litter and organic horizons in Wisconsin forests, and found that the leaf litter and first organic horizon combined had an average depth of 5.65cm (Gundale 2002). This contrasts to what I found in the Amazon rainforest, where the means of these two layers were 3.58cm for Varzea and 2.458 cm for Terra Firme. Though I was unable to find estimates in the scientific literature on the depth of the soil organic layer for the Amazon, it is widely agreed upon that the Amazon is characterized by an extremely thin organic horizon (Kricher, 1997). In light of that, the estimates I found for each ecosystem based on 40 sample sites do make sense but more research is definitely needed in this area. In other parts of the world, leaf litter layers are monitored closely because they can often offer clues as to effects of invasive species, such as in Illinois where they are used to see effects on invasive earthworms (Heneghan et al 2007). A more complete understanding of the usual litter layer in parts of the Amazon could also be very useful. For instance, most of the petroleum blocks in the Amazon have gas flares where they burn off any gas produced in the extraction process because it is easier than trapping it. But around these sites are hundreds of insects burnt to a crisp, attracted by the flame during the night and then killed. The death of so many insects could be having detrimental effects in other parts of the ecosystem, and effects may show up in places such as the leaf litter layer, but without a solid understanding of the usual functioning of the leaf litter, such effects are impossible to notice.

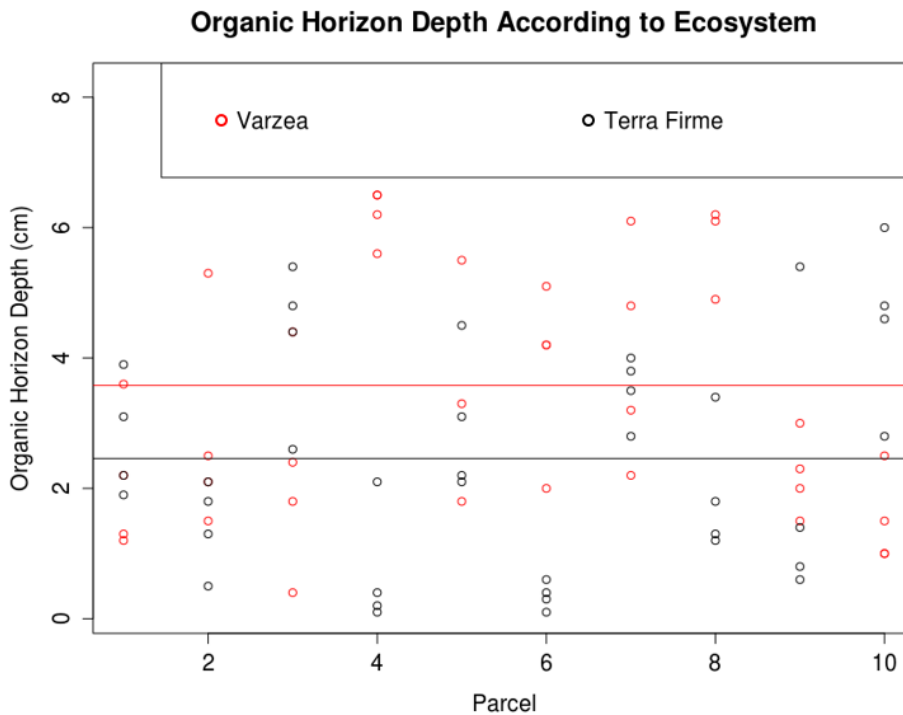


Figure 4: Organic Horizon Depth According to Ecosystem. Red dots signify Varzea and the red line the average value, 3.58cm. Black dots signify Terra Firme with the black line being the average value, 2.458cm.

I found a significant difference between the soil organic layer in the Varzea and Terra Firme, though both are thin in comparison to other parts of the world. There are several implications in a differing organic layer of soil. One is that decomposition and uptake of nutrients in the organic layer is taking place more quickly in Terra Firme forest. It could also be that while decomposition rates are similar, more leaf fall in Terra Firme results in a deeper organic layer. Without an accurate estimate of leaf fall or decomposition it is difficult to be certain what could be causing this phenomenon. Leaf fall and decomposition, it is important to note, are both variables that can change over the course of a year. Many trees in both ecosystems occasionally shed all their leaves, though the phenology of this follows no clear pattern. Trees of the same species located only a few meters apart can differ tremendously in when their leaves fall (Vargas, 2016). Likewise, decomposition can change drastically according to climatic variation. High temperatures and high humidity and rainfall are all key factors in decomposition rates (Karberg et al 2008). A study that sampled sites over a longer time period than three weeks could help control some of these factors.

Of additional interest is the high variability, even within ecosystems from one quadrat site to another of organic horizon depth. As previously noted, both Varzea and Terra firme have high standard deviations (2.064 and 1.699 respectively) and large ranges (1-8.2cm and 0.1-6cm respectively). Though not obvious, close examination of Figure 4 can beg the question whether individual parcels are correlated with one another. That is, is it possible that the red or black dots within the same parcel are more closely related to one another than the rest of the red or black dots overall. When the data is divided and examined according to parcels (located 3m from each

other), there are a hints that auto-correlation, or predicting a variable based on geographical proximity to a nearby variable, is a strong influence (see appendix section A for complete results of this test). While not true of every parcel, there are still a handful of parcels that show more similarity within their own 3m x 3m grid compared to all other data points parcel than is likely if only random factors were affecting the distribution of leaf litter or the organic horizon. However, only 7 of a total of 20 parcels show this statistically significant auto-correlation according to these characteristics.

Measuring the depth of the organic layer involved digging down through the leaf litter and a little farther so that I could be sure of a distinct color change. It was oftentimes surprisingly difficult to dig even 6-8cm deep in Terra Firme. I encountered what is often referred to as the 'root matt.' Krichler, author of *A Neotropical Companion*, emphasizes that in many cases trees in the Amazon are not growing in the soil so much as they are growing on the soil. The soil is so nutrient poor that an extensive root system permeates the organic horizon and leaf litter layer and dense matts of roots can be encountered at very shallow depths. I noticed this phenomenon in almost every quadrat in the Terra Firme, digging down was a constant struggle. And I frequently found roots mixed only centimeters below the surface alongside barely decomposed leaves. This observation, of more roots present at very shallow depths, coupled with the thinner organic layer could suggest that the nutrient cycle is occurring more quickly in Terra Firme, with trees uptaking nutrients very early on in the decomposition process. But it could also be a result of poorer soil beneath the organic horizon that necessitates shallower roots.

Clay and Silt Content:

Another significant difference between Terra Firme and Varzea forest was the clay composition of the soil. The sand/silt/clay ratio methodology I used (Whiting 2016) should have resulted in three distinct layers, but an issue quickly became apparent. First is that the silt and sand did not separate and were not distinguishable. This was not a huge issue as it was the clay component that was of most interest to this study. However, even with only the clay component, it appears that the method is likely to be undercounting clay. When soil that appears to be almost entirely clay is mixed with solution, shaken, and allowed to settle, a deceptively shallow layer of clay forms as much of the clay is still stuck together and not at the top. This error leads me to believe that not only are the clay percentages severely underestimated, but any differences between the study sites would be underestimated as well. Future research should test a clay-sorting methodology before beginning the study with soils of known composition. Despite these drawbacks, as the same methodology was used for both ecosystems, measurements are still useful for comparative purposes.

Percent Clay Content of Soil According to Ecosystem

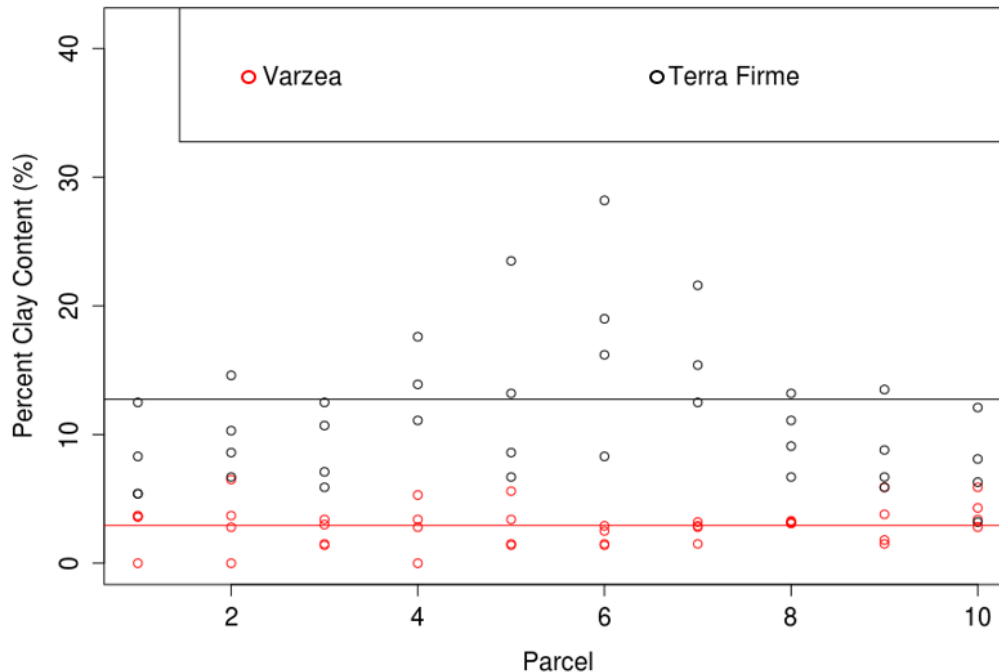


Figure 5: Percent Clay Content of Soil According to Ecosystem. Red dots signify Varzea and the red line the average value, 2.935%. Black dots signify Terra Firme with the black line being the average value, 12.7325%

Comparatively, the results clearly show that Terra Firme forest has far more clay than Varzea. The test confirmed this, but it was visually obvious as well. The soil beneath the organic horizon in the Varzea tends to be grey and brownish, but the soil beneath the Terra Firme is more orange and reddish.

Another interesting observation was the clay patchiness found in the Terra Firme. Many quadrats had soil that was almost entirely clay, others seemed to have more silt. It seemed that soils high in clay were more frequent on the steep slopes common in the Terra Firme, while the siltier soils were more common on hill crests, troughs, and in general on less steep places. Future studies could attempt to see if there was indeed soil variation related to topography and slope. Perhaps hill crests have less leaching of leaves and other organic materials during heavy rain, allowing them to have more silt and leaf matter in their soil, while soils on steep slopes are never able to accumulate soil as it is constantly washed away by the rain.

Root Results:

This study did find many suggestive differences between root adaptations of trees in these two ecosystems. The two habitats had similar abundances of buttress roots, but the Varzea had significantly more prop roots. The believed adaptation benefit of buttress roots is enhanced ability to uptake nutrients concentrated in the shallow soil layers and increased anchorage despite

how shallow the roots spread out in the ground (Newberry et al 2008), while prop roots are believed to be adaptations for ecosystems that face repeated flooding.

The higher percentage of prop roots in Varzea forests (see Figure 6) was expected as Varzea forest floods more often and prolonged time underwater can be a significant environmental stressor (Irmiler 1979).

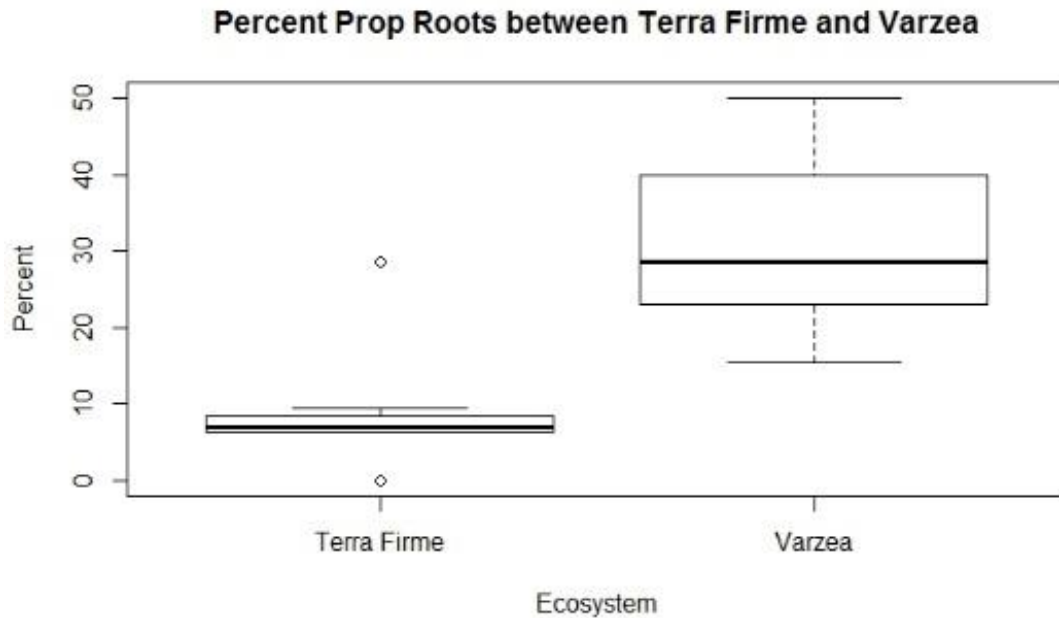


Figure 6: Percent Prop Roots between Terra Firme and Varzea

Though not quite making the threshold of significance, there was a small difference between the abundance of buttress roots between the two ecosystems with more buttress roots in the Terra Firme forest. This result makes sense in that both ecosystems are nutrient poor and thus one would expect this adaptation to be advantageous in both. Perhaps the Terra Firme forest is slightly more nutrient poor as has been found in previous studies (Herrera et al 1978, Wittman et al 2006, Assis et al 2015) which would make this adaptation slightly more beneficial.

As mentioned earlier, the “root matt” was a clear and ubiquitous characteristic and difference between the Terra Firme and Varzea forest. Looking only at the roots of trees with dbh over 10cm limited the scope of this study significantly in this regard. The “root matt” absent in Varzea that becomes readily apparent in Terra Firme is an important root adaptation characteristic that went beyond the extent of this study but that certainly merits further attention and research.



Figure 7: Photo taken of classic buttress roots found in the top soil layers and are believed to be adapted to nutrient poor ecosystems



Figure 8: Photo taken of a tree exhibiting prop roots, found commonly in inundated areas and more common in Varzea than Terra Firme

Insect results:

The most abundant insect order found by far was Hymenoptera. Ants dominated in both ecosystems, constituting a majority of total individuals captured. This is of little surprise; the dominance and abundance of ants in the Amazon is well-established (Wilkie et al 2009, Wilkie et al 2010). There was a higher amount of Hymenoptera found in the Terra Firme, but the difference was only significant if any colonies were not included. The random encounter of an ant nest in a quadrat, as happened three times throughout this study, can heavily bias these results as it can easily add 50-100 individuals to one data set. By chance, two ant colonies were encountered in Varzea, and only one in Terra Firme. Arachnids, Isopods, Diplopods, and Coleopteras were also common in both ecosystems. Aside from arachnids, many of these orders do indeed play important roles as decomposers in ecosystems (Zimmer et al 2002). It is important to note that although this study aimed to investigate decomposers by targeting the leaf strata, simply being present in the leaf strata does not mean an individual plays an important role in decomposition, as is likely the case for arachnids.

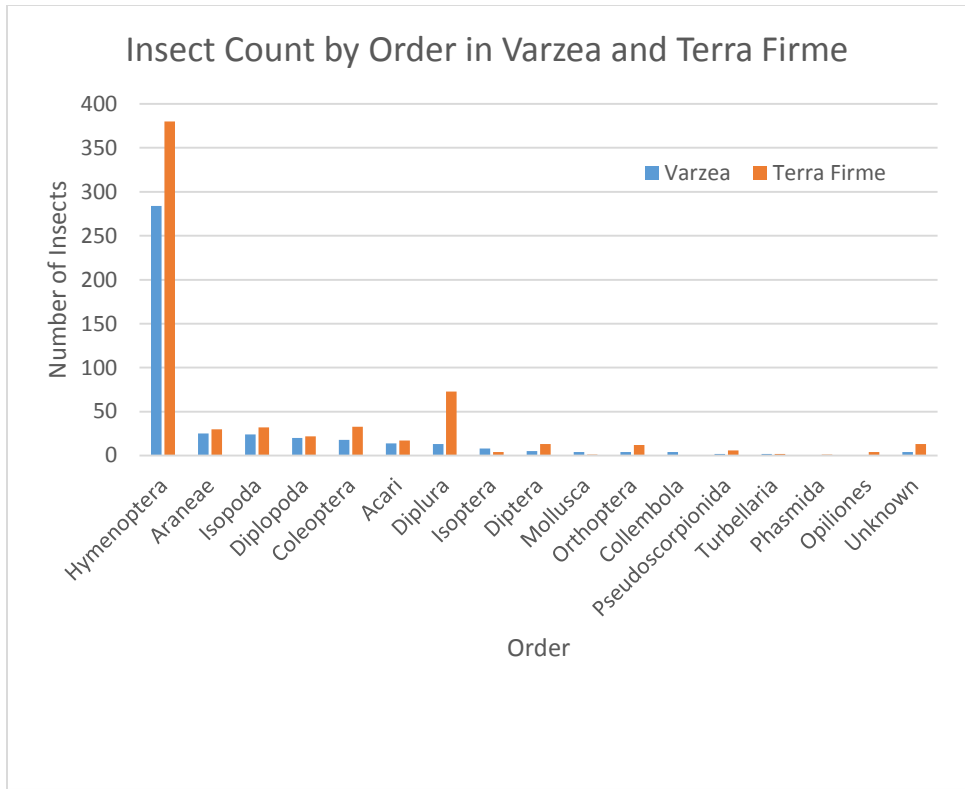


Figure 9: Insect Count by Order in Varzea and Terra Firme

Diplura were only common in the Terra Firme. Though it is tempting to presume this result is meaningful, the number of hypothesis tests run should also be taken into account. With 16 orders being examined for significance and the standard threshold of 5% being used, there is a chance of committing a Type 1 error, or interpreting a significant relationship where none exists. In this case, it would mean rejecting the null hypothesis; that differences in insect counts happened due to chance, when in fact the null hypothesis was true. This study is very preliminary and more research is needed to establish whether there is indeed a significant difference between these two ecosystems.

Another interesting insight can be made by where in the leaf strata insects had a tendency to be found. Diplopods (millipedes) for instance, were almost almost found on larger, less decomposed leaves. Often, they were easy to miss as they would cling and hide in furled leaves. Individuals in the Diplura and Collembola family also displayed this tendency, though they were frequenters of smaller, more fragmented leaves as well. Beetles and isopods also stuck out for their behavioral response in the sorting containers. Both were very still and hid under leaves, but when leaves were picked up and examined they were prone to making mad dashes across the aquarium towards the other side.

Overall, though leaf litter weight was similar between the two ecosystems, Terra Firme tended to have larger leaves that had not yet been broken up, whereas the Varzea leaf litter had a few larger leaves, but more shredded leaves were present underneath. The leaf strata in Terra Firme

was also often coexisting alongside extremely shallow roots and often fungus and mushrooms. Mushrooms, fungi, and roots were encountered in Varzea, but much less frequently.

Only a limited amount of studies on faunal decomposers of the Amazon are present and accessible. One author, Irmiler (1979) in a study of flooding regions of Igapo and Varzea found high representation of Annelida, Arthropoda, Mollusca, Coleoptera, Oligochaeta, Heteroptera, and Pseduoscorpionida, I also found many arthropods, coleopteran, and a few pseudoscorpions and mollusks. I did not find Annelida, Oligochaeta, or Heteroptera, and I suspect his difference may be that I was focusing on terrestrial decomposing organisms in the leaf strata, and my study sites were never inundated. Though the incredible insect diversity of the Amazon is well-known, and not just to the scientific community, studies combining insect diversity with understanding the nutrient cycle and decomposition process are still uncommon.

Decomposition Rate:

The decomposition rate I found was based off a far smaller sample size and time frame than originally imagined. Though I did come up with values, 1.33g/day for Varzea and 1.67g/day for Terra Firme, these are based on a very small sample size and no significant difference can be detected. The tethered leaf methodology for measuring the decomposition rate offers several advantages over other techniques, such as its availability to larger macroinvertebrates and its use in short-term studies. Nonetheless, it largely failed to provide good estimates for this particular study. Leaf fragmentation occurs rapidly for decomposing leaves in the Amazon, as I learned after two attempts to measure the decomposition rate. The first attempt took place over two weeks. Within two weeks, all tethered leaves had entirely decomposed making measurements impossible. The second attempt left leaves in their respective habitats for only three days. Yet within only three days, most of my samples had decomposed from their petioles, again making data collection impossible. Compounding to this issue was the problem that due to an injury, I was no longer able to collect and place my own samples, making additional tests very difficult. The third and final attempt therefore, involved only three plant species and 24 hours.

Even for comparative purposes, the results of this part of the study remain inconclusive. An important lesson to be learned here is that methods that work in other regions throughout the world may not work in the Amazon. Though unsuccessful, perhaps this can serve to emphasize the need for more experimental research on leaf litter decomposition, an essential component of understanding the nutrient cycle of ecosystems (Cleveland et al 2011).

Limitations and Sources of Error:

Though some were already touched upon, this study had several important limitations and sources of error that should explicitly be noted.

Within the soil characteristics component of this study, many considerations that should be taken into account when interpreting this study. Different authors often define “organic horizon” differently. Care should always be taken when comparing organic horizons from different papers as they can mean different things. In my study, the organic horizon included both the sparse leaf layer on top, up to the point where the soil changed color and texture. There are also potential

sources of error with the accuracy of my measurements. Difficult lighting and imprecise digging or mixing of soil layers while digging can easily add imprecision and error to this measurement. Furthermore, following an injury, the last organic horizon measurements for each ecosystem were taken by a different researcher, and it is possible that this led to slightly different measurements at the end of the study. In the design of this study, it was hoped soil moisture could be recorded using a hydrometer. Unfortunately, materials were limited and instead air humidity and temperature were taken at every site. These measurements were not included in any analysis because they were primarily a function of time of day. In future, switching times of day for different ecosystems could cut down on this error if these variables were of interest, but better still is to have equipment to be able to take soil temperature and humidity. Problems with the clay and silt settling technique were already touched upon but are worth emphasizing. Though for comparative purposes, the measurements are sound and results clear, I would advise future studies to test soil ahead of time to perfect this method. In this study, leaves and soil were dried in aquariums in a greenhouse. While leaves and soil seemed dry by the time they were measured, it is worth keeping in mind the humidity in the Amazon rarely dropped under 80% and that a clay oven would be preferable for ensuring complete dryness of all samples. Lastly, I used a scale that was accurate to 1g, while this was suitable for these two measurements, a higher degree of precision could only help and is highly recommended if available.

One large part of this study involved finding and correctly identifying all insects in the leaf litter strata of all quadrats. Prior to the sifting method, I attempted to separate insects from leaves using Berlese funnels. Unfortunately, small leaf litter as well as small insects both fell through the mesh and landed in the alcohol where it was exceedingly difficult to differentiate dead insects from specs of dirt. Additionally, time and space constraints with the Berlese method made for slow processing of leaf samples. Results from the first few days using the Berlese method were not included in final data as they appeared to be drastically undercounting insects. It was more time effective and more accurate to sift through leaf matter immediately upon returning to the greenhouse and watching for movement. Nonetheless, this methodology can introduce some sources of error. First is that extremely small insects are still difficult to see. Waiting and watching for movement helped me see several extremely small insects, but it is likely that others escaped detection and were never counted. Likewise, insects that do not move when exposed to light are also more likely to escape detection. Although I examined all leaves and leaf remnants collected, tiny insects can often impersonate inanimate specs of dirt quite successfully. Thus very small and immobile insects were likely undercounted. Furthermore, several times while gathering leaf litter from a quadrat, I noticed an insect, commonly millipedes, grasshoppers, and beetles escaping. When this happened I would make a note but it is likely that insects that ran when I approached were also undercounted in this study.

The timing of collection is also a factor. Terra Firme data collection usually happened in the morning, and Varzea in the afternoon. If certain insects change locations between these two time periods, they may be over or underrepresented. Likewise, as I had only a short period of time to collect data, I was often collecting samples in adverse conditions such as rain. Ideally, one would conduct a study over a long enough time period that data collection could halt during rain and thus eliminate weather as a potential source of error. Again, it is quite possible that certain species change location depending on the weather which could lead to over and underrepresentation. It is also quite likely that I missed counting several important decomposers

that are only active in the leaf litter at night, or certain times around dawn and dusk. Data collection during the dark was not possible for my study, but could be a way to include more orders that actually are present and important in the decomposition of leaves. Finally, many insects, especially very small insects are not only difficult to count, they are difficult to identify. The ability to collect samples and examine under more powerful lenses could have greatly cut back on potential errors in identification, as would a stronger background in herpetology. I received a great deal of help from Xavier Silva in identifying insects, but oftentimes insects were too small to take pictures of, and pictures too blurry to be conclusive. A stronger camera and lens are therefore highly recommended for future experiments.

Methods for measuring decomposition were largely taken from Karberg et al 2008. I first attempted, as in the paper to tether leaves and let them decompose for two weeks. After two weeks, there were no leaves left, only the labels used to tether together. I then tried to leave them for three days, and many leaves were not recoverable. Leaves were again left out, this time for only one day, and were recoverable, but unfortunately the sample size at this point had been severely reduced. The incredibly fast nutrient cycle in the Amazon therefore makes some traditional methodology of measuring decomposition unusable and this should be taken into consideration when designing a study. Other methodologies that may work better are the litterbag technique or screen cohort method, which better control leaf fragmentation.

Future research:

Nutrient cycling in the Amazon is a relatively understudied area of research and there are many directions future research could take. Though this study only examined Varzea and Terra Firme forest, it could easily be expanded to include Moretal and Igapo as well as primary and secondary forests. The comparison of soil characteristics could likewise be expanded to include nitrogen, phosphate, potassium, as well as soil humidity, soil temperature, and pH. The leaf decomposition component of this study using the tethered leaf methodology can and should be expanded upon in further studies. Though many ecosystems and places in the world can find weeklong and longer decomposition rate estimates using this method, in the Amazon it is only usable in the extremely short term. Future studies should attempt to find other methods that can find estimates over longer time periods. This is necessary as litter decomposition is faster during the emergent phase of Varzea forest (Irmeler 1979) and in a short time window, it is also likely that normal climatic variation could affect the calculation as well. It would also additionally be helpful to compare decomposition with different methods such as litterbags, and cohort layered screens (Karberg et al 2008).

Another interesting direction future research could take is comparing the decomposition process. In the Terra Firme forest, I found a common pattern of spiderweb fungus on leaves that I saw only a few times in the Varzea (see Figure 8). I was unable to find anything in the scientific literature about what this fungus might be and why it is so common in Terra Firme, and it would be an



Figure 10: Typical Decomposition of large leaf in Terra Firme

interesting topic for further investigation. There also are a number of trees, such as the Ceiba, that will drop all their leaves at once resulting in a large availability of leaves. These infrequent but large influxes of leaf litter might have different fungal and insect specialists than the more frequent but less copious leaf fall elsewhere.

Another interesting and practical direction research could take is establishing normal baselines of litter weights, organic horizon depths, insect communities, and decomposition rates as a way to notice changes that may take place in this ecosystem. The Amazon faces an enormous number of threats related to human activities, such as agriculture, oil, and logging, (Bass 2010) and understanding how these activities may impact this ecosystem through the nutrient cycle will help create a more holistic picture of human impacts in this ecosystem.

Another budding area of research is the role of faunal diversity in litter decomposition. Temperature, rainfall, and litter quality are three important and widely recognized factors that influence the decomposition rate, but faunal diversity of the decomposer community is increasingly being recognized as the fourth important factor (Karberg et al 2008).

Understanding the functioning of the nutrient cycle of an ecosystem is a crucial part of understanding an ecosystem as a whole. More scientific research even on basic features of different ecosystems in the Amazon like leaf litter amounts and organic horizon depths, can serve as important factors in assessing the health of sites, but is not possible if no baseline measurements are known. A more complete understanding of the role of the decomposer insect community in the nutrient cycle can not only add to basic knowledge of this ecosystem, but again serve as a potential way to notice any impacts, human or natural, that may affect insect populations. Evaluations of root characteristics and other adaptations common in the Amazon yet rare in the rest of the world can provide clues and increase our understanding of adaptation strategies. Lastly, though the decomposition rate of the Amazon is understood to be fast, more research into how its speed differs between ecosystems and times of year can add greatly to our understanding of the flow of nutrients in this ecosystem. This is especially important as a way of determining limiting factors on the Net Primary Productivity of the Amazon, which is critically important given its global status as a major carbon sink. Despite the hard work of many scientists and the significant number of studies and investigations already done, the Amazon and its incredible diversity and complexity remain a frontier for scientific investigations

Bibliography:

- "Amazon rainforest losses impact on climate change, study shows." *Life Science Weekly*. University of Edinburgh. April 21, 2015. Print.
- Assis, R. L., Haugaasen, T., Schöngart, J., Montero, J. C., Piedade, M. T., & Wittmann, F. (2015). Patterns of tree diversity and composition in Amazonian floodplain paleo-várzea forest. *Journal Of Vegetation Science*, 26(2), 312-322. doi:10.1111/jvs.12229
- Bass MS, Finer M, Jenkins CN, Kreft H, Cisneros-Heredia DF, et al. (2010) Global Conservation Significance of Ecuador's Yasuni National Park. *PLoS ONE* 5(1): e8767. doi:10.1371/journal.pone.0008767
- Bristow, C. S., K. A. Hudson-Edwards, and A. Chappell (2010), Fertilizing the Amazon and equatorial Atlantic with West African dust. *Geophys. Res. Lett.*, 37, L14807, doi:[10.1029/2010GL043486](https://doi.org/10.1029/2010GL043486).
- Cleveland, C. C., Townsend, A. R., Taylor, P., Alvarez-Clare, S., Bustamante, M. M. C., Chuyong, G., Dobrowski, S. Z., Grierson, P., Harms, K. E., Houlton, B. Z., Marklein, A., Parton, W., Porder, S., Reed, S. C., Sierra, C. A., Silver, W. L., Tanner, E. V. J. and Wieder, W. R. (2011). Relationships among net primary productivity, nutrients and climate in tropical rain forest: a pan-tropical analysis. *Ecology Letters*, 14: 939–947. doi:10.1111/j.1461-0248.2011.01658.x
- Desonie, Dana. *Biosphere: Ecosystems and Biodiversity Loss*. New York: Chelsea House, 2008. Print.
- Gundale, Michael J. Influence of Exotic Earthworms on the Soil Organic Horizon and the Rare Fern *Botrychium Mormo*. *Conservation Biology* 16.6 (2002): 1555-561. Doi: 0.1046/j.1523-1739.2002.01229
- Heneghan, Liam, James Steffen, and Kristen Fagen. (2007). "Interactions of an Introduced Shrub and Introduced Earthworms in an Illinois Urban Woodland: Impact on Leaf Litter Decomposition." *Pedobiologia* 50.6 (2007): 543-51. doi:10.1016/j.pedobi.2006.10.002.
- Herrera, R., Jordan, C., Klinge, H., Medina, E. (1978). Amazon Ecosystems, Their Structure and Functioning with Particular Emphasis on Nutrients. *Interciencia* 3(4):223-232. Doi:10.1086/283696. 0.500
- Huston, Michael. (1980.) "Soil Nutrients and Tree Species Richness in Costa Rican Forests". *Journal of Biogeography* 7.2 (1980): 147–157. DOI: 10.2307/2844707
- "Indigenous Communities Ensuring a Thriving, Sustainable Future." *The Nature Conservancy*. The Nature Conservancy, n.d. Web. Retrieved May 6, 2016 from <http://www.nature.org/ourinitiatives/regions/southamerica/brazil/placesweprotect/amazon-indigenous-communities.xml>

Irmiler, U. (1979). Considerations on Structure and Function of the "Central-Amazonian Inundation Forest Ecosystem" with Particular Emphasis on Selected Soil Animals. *Oecologia*, 43(1): 1-18. doi: 4215938

Jobbagy, E. & Jackson, R. (2000). The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecol. Appl.*, 10, 423–436. Doi: 10.1890/1051-0761

Karberg, Noah J., Neal A. Scott, and Christian P. Giardina.. Field Measurements for Forest Carbon Monitoring. Netherlands. Springer Science+Business Media B.V., 2008. Print.

Kricher, J (1997). *A Neotropical Companion: An introduction to the animals, plants, and ecosystems of the new world tropics*. Princeton, NJ: Princeton University Press. Print.

"Latin American Herald Tribune - Ecuador Has One of Latin America's Highest Deforestation Rates." *Latin American Herald Tribune*. Oct 3, 2011. Print.

McGroddy, M.E., Daufresne, T. & Hedin, L.O. (2004a). Scaling of C:N:P stoichiometry in forests worldwide: Implications of terrestrial Redfield-type ratios. *Ecology*, 85, 2390–2401. DOI: 10.1890/03-0351

Minor, M. (n.d.). Soil Bugs - An illustrated guide to New Zealand soil invertebrates. Retrieved March 31, 2016, from <http://soilbugs.massey.ac.nz/key.php>

Newbery, David M., Sarah Schwan, George B. Chuyong, and Xander M. Van Der Burgt. (2008). Buttress Form of the Central African Rain Forest Tree *Microberlinia bisulcata*, and Its Possible Role in Nutrient Acquisition. *Trees* 23.2: 219-34. Doi: 10.1007/s00468-008-0270-3

Reich, P.B. & Oleksyn, J. (2004). Global patterns of plant leaf N and P in relation to temperature and latitude. *Proc. Natl Acad. Sci. USA*, 101, 11001–11006. Doi: 0.1073/pnas.0403588101

Silva, Xavier. 24 February 2016. Amazon Lecture. SIT Ecuador: Comparative Ecology and Conservation.

"The Amazon Rainforest." *Flora and Fauna International*. N.p., n.d. Retrieved May 29, from <http://www.fauna-flora.org/explore/amazon-rainforest/>

Townsend, Lee. "Recognizing Insect Larval Types." *Entomology*. University of Kansas, n.d. Retrieved May 4, 2016 from <https://entomology.ca.uky.edu/ef017>

Turenne, Jim. "O - Horizons." O - Horizons. *Society of Soil Scientists*, n.d. Retrieved May 5, 2016 from <http://www.nesoil.com/properties/horizons/index.htm>

Townsend, A.R., Cleveland, C.C., Asner, G. & Bustamante, M.M.C. (2007). Controls of foliar N:P ratios in tropical rain forests. *Ecology*, 88, 107–118. DOI: 10.1890/0012-9658

Vargas, Hector. Personal Interview. May 3d, 2016

Vermeer, J., Berendse, F. (1983). The Relationship between Nutrient Availability, Shoot Biomass and Species Richness in Grassland and Wetland Communities. *Vegetation*, 53(2) 121-126. DOI:10.1016/j.jnc.2012.12.008

Wilkie, K., Mertl, A., Traniello, J. (2009). Diversity of ground-dwelling ants (Hymenoptera: Formicidae) in primary and secondary forests in Amazonian Ecuador. *Myrmecological News* 12 139-147. doi:10.1371/journal.pone.0117853

Wilkie, K., Mertl, A., Traniello, J.. (2010). Species Diversity and Distribution Patterns of the Ants of Amazonian Ecuador. *PLoS ONE* 5(10): e13146. doi:10.1371/journal.pone.0013146

Whiting, David. "Estimating Soil Texture: Sand, Silt or Clayey?" Estimating Soil Texture: Sand, Silt or Clayey. *Colorado State University Extension*, 2015. Retrieved March 31, from <http://www.ext.colostate.edu/mg/Gardennotes/214.html>

Wittmann, F., Schöngart, J., Montero, J. C., Motzer, T., Junk, W. J., Piedade, M. T. F., Queiroz, H. L. and Worbes, M. (2006). Tree species composition and diversity gradients in white-water forests across the Amazon Basin. *Journal of Biogeography*, 33: 1334–1347. doi:10.1111/j.1365-2699.2006.01495.x

Zimmer, M. "Is Decomposition of Woodland Leaf Litter Influenced by Its Species Richness?" *Soil Biology and Biochemistry* 34.2 (2002): 277-84. doi: 10.1016/S0038-0717(01)00173-0