THE IMPACT OF TROPHIC GUILD ON THE DIVERSITY OF COLEOPTERA

by

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ABSTRACT

Biodiversity is said to increase the productivity and stability of the various ecological processes that keep the environment as a whole functioning properly (Naeem et al., 1999). I compared the biodiversity of three target beetle families (Scarabaeidae, Chrysomelidae and Carabidae) in Yasuni National Park of the Amazon rainforest in Ecuador in two different forest types, seasonally flooded forest (varzea) and dry forest (terre firme) to 1) to determine whether one forest type would be more diverse than the other; and 2) test the hypothesis that herbivores are more diverse than predators or detritivores. No significant differences were found between the herbivores, detritivores and predators in dry and seasonally flooded forest. Scarabaeidae: Aphodiinae and Scarabaeinae were more abundant than Chrysomelidae (herbivores) which were more abundant than Carabidae, which roughly followed predictions of energy transference up the feeding trophic levels. However species richness was highest in Chrysomelids, followed by the scarabs with the fewest species recorded within the Carabidae. This result suggests that herbivores are most diverse because of the high diversity of plant life in the tropics.

Chapter 1

INTRODUCTION

According to the Convention on Biological Diversity, biodiversity is "the variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are a part; this includes diversity within species, between species, and of ecosystems" (Encyclopedia of Earth, 2007).

The environment, and the ecosystems that comprise it, are complex and multi- faceted, and many processes influence the success, stability, and productivity of any given ecosystem. Everything from plant productivity to water quality depends on a stable ecosystem, and these conditions are not only important to animals and plants, but also to the welfare of human beings. The successful function of ecosystem processes is controlled by the diversity of the flora and fauna in a given ecosystem (Naeem et al., 1999). Therefore, it is critical to better understand these complicated interactions through the measurement and surveillance of biodiversity at different levels.

Insects are well known as the most diverse multicellular taxon of life. As such, insect diversity is important in the assessment of the overall species diversity of a given area (Carlton et al., 2004). Within the class Insecta, the order Coleoptera is by far the largest; the beetles represent a fifth of all living organisms and a fourth of all animals, and thus "epitomize diversity" (Evans and Bellamy, 2000). Beetles occupy numerous niches, and their environmental roles and habits are just as diverse as their

numbers. Therefore, they are an important taxon of organisms with which to test hypotheses about the origin and maintenance of diversity.

This project was conducted at the Yasuni Research Station (created 1994), located in the Orellana province of Ecuador (76°24'1.8"W; 0°40'16.7"S). It is located within Yasuni National Park (created 1979), found in the northwestern Amazon Basin, and is considered to be one of the most diverse forests in the world, with tens of thousands of invertebrates present (Yasuni Research Station, 1999). At the Yasuni Research Station, two distinct types of forest exist adjacent to each other; terra firme, which is relatively stable and un-flooded forest, and varzea ("flooded forests" in Portuguese).

Beetles fall mostly into three general guilds: detritivores, such as members of the Scarabaeinae, Geotrupidae, and Silphidae; herbivores such as members of the Chrysomelidae, Cetoniinae, and Curculionidae; and carnivores such as most members of the families Carabidae and Staphylinidae, and Cleridae. Members of each guild fill specific niches; therefore, knowing which guilds are more diverse can lead to insight about the need for redundancy within particular ecosystem roles. For example, large numbers of a single species within a guild indicates a less complicated niche structure whereas high diversity in a guild indicates more complicated and multi-faced niche structure.

The objectives of this project were two- fold. First I wanted to determine if the three guilds studied differed in diversity and abundance. I also wanted to determine whether habitat impacts the diversity of beetle guilds by comparing guilds within varzea and terra firme. Several hypotheses were addressed by this study. First I hypothesized that the most diverse taxa and the lowest abundance would be found

within the herbivore guild based on the necessity for specialists to decrease competition and to feed on the vast variety of plant taxa in the Amazon rain forest without succumbing to their numerous phytochemical defenses. Moreover, I predicted that the least diverse taxa with the greatest abundance would be found within the detrivores, represented by select members of the family Scarabaeidae, because specialized adaptations are not required to eat detritus and because detritus is abundant in the Amazon. An alternative hypothesis is that the transfer of energy up trophic levels rather than feeding specificity will be the main determinant of diversity and the abundance of guild members. Finally, I hypothesized that herbivores will dominate other guilds in both habitats.

For the sake of feasibility, select families of Coleoptera were selected as "representatives" of the three guilds being studied. Herbivores were represented by the family Chrysomelidae. Detritivores were represented by the Scarabaeidae subfamilies Scarabaeinae and Aphodiinae. Dung beetles (Scarabaeidae: Scarabaeinae) are a very widespread taxon, and feed on a variety of detritus besides dung, such as fungi, decaying leaves, and fruit (Maleque et al., 2009), also making them an ideal detritus guild member to survey. Carnivores were represented by the family Carabidae. It should be noted that, although the vast majority of carabid beetles are predatory, there are taxa that are known to be seed and grass feeders; thus identification of carabid tribes was necessary to ensure that only carnivorous taxa were counted. Nonetheless, carabid beetles were a good choice for this type of survey, because they are easy to sample (Maleque et al., 2009), have good taxonomic keys available (Abdullah et al., 2008), and have been used successfully for a variety of indicator studies (Rainio and Niemela, 2003).

Chapter 2

MATERIALS AND METHODS

2.1 Review of Sampling Methodology

2.1.1 Pitfall Trap

Pitfall traps (Figure 1) are a very useful method for surveying terrestrial organisms because they are cheap and require little labor (Luff, 1975). Larger glass traps, as opposed to plastic or metal traps, are the most efficient containers for pitfall traps (Luff, 1975). A mason jar is buried with the lip of the jar flush with the ground, allowing insects that walk on the ground to fall into the trap. A smaller removable plastic cup, with the same lip width as the glass jar, is placed in the glass jar and filled with about 1.5 inches of a preservative to allow for easy specimen removal without compromising the trap. A mixture of ethylene glycol and water has been shown to have the highest capture efficiency as opposed to water, ethanol-water, ethanol-glycerin, or brine (Schmidt et al., 2006); however, due to the toxicity of ethylene glycol, eco-friendly propylene glycol was considered as an acceptable substitute in my study. A thin metal sheet can be elevated over the trap to prevent rain and falling debris from filling the trap, and bait such as carrion or dung wrapped in cheesecloth may be suspended from this elevated cover to attract target groups (such as carrion beetles [Silphidae] or dung beetles [Scarabaeidae: Scarabaeinae]). Barriers constructed between the pitfall traps have been shown to increase yield, especially of

singleton taxa (Hansen and New, 2005). Based on the size of the sampling sites, the cumbersomeness of the most effective barriers, and the use of other sampling practices, barriers were excluded from this project. When more than one pitfall is used per site, it has been shown that a higher number of beetle 'morphospecies' is represented when the traps are farther apart (five to ten meters apart as opposed to one meter apart) (Ward et al., 2001).

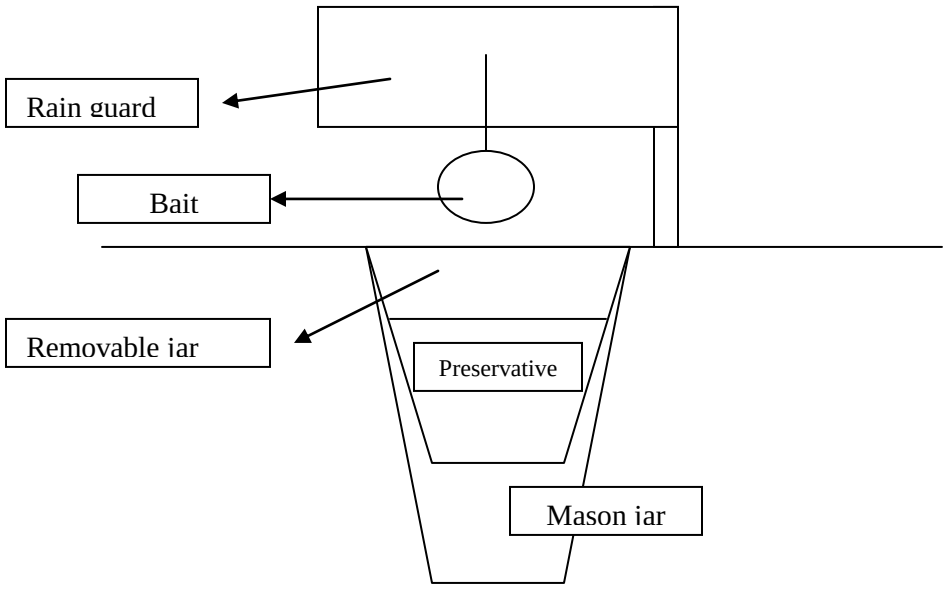

Figure 1. Pitfall trap design

2.1.2 Sweep netting

Sweeping is a commonly used method of sampling, allowing for the rapid capture of a large number of specimens in a given area. A net was swung through the vegetation for a designated number of 'swings.' This method allowed for the capture

of insects perching, feeding, or crawling on the vegetation through which the net was swung, especially herbivorous insects on their host plants. Sorting sweep samples can be labor intensive due to the large number of specimens collected this way, especially when there is a need to separate target taxa from the bulk of the sample.

2.1.3 Mercury vapor lighting

Many insect taxa are attracted to the wavelengths given off by black lights and mercury vapor lights. A white sheet, usually about the size of a bed sheet, was suspended on twine and draped down over the ground (to collect insects falling off of the sheet). A light source was then set up clamped to a nearby tree, near the sheet, giving the attracted insects a place to perch. Light trapping is a very popular means of attracting insects; however due to the sheer numbers attracted to the trap, searching for and separating desired taxa can be very tedious, especially in the tropics.

2.1.4 Trophy Hunting

Trophy hunting is a sampling method less random than the other three that was used in this project. It involved the active searching of desired specimens in the given sampling areas of each site, including but not limited to, specimens perching on trees or actively flying through the sample area. It was meant to account for specimens unattainable in sweep samples and pitfalls traps and unlikely to be attracted to light traps. Although the efficiency of this method is debatable, it allowed for 'odds and ends' specimens to be collected that would otherwise be unaccounted for by the other sampling methods. This sampling method is more useful for sampling certain taxa that are more active, such as members of the orders Lepidoptera, Hymenoptera and Diptera.

2.2 Sampling Site Selection

This project took place during the month of January 2010 at the Yasuni Research Station in Ecuador. Three separate sampling sites were selected for both the varzea and terra firme habitats. Sampling sites were chosen with a mixture of shaded and canopy breached areas, so that a slight dappling effect was present at each site. Recent studies have suggested that abiotic plant factors "are important predictors of insect herbivore community composition" (Schwab and Raghu, 2006). Sunlight is a precious resource; as such, it has been suggested that biodiversity is very high where the sunlight can breach the canopy, both because of the diversity of flora competing for sunlight and the variations in nutrients associated with floral life form diversity (Bigelow, 1993), and because the leaves of plants from high light environments tend to have more nitrogen and other nutrients than leaves from less sunny environments (Field & Mooney, 1986). Because of the relatively low nutritional value of an herbivorous diet, herbivorous insects are attracted to more nutrient-rich plants, possibly accounting for the large number of specialists that focus their efforts on plants with higher nutrient content (Elser et al., 2000). Various studies have shown that higher nitrogen and phosphorous levels increase the survival and fecundity of some herbivorous insects, such as Lepidoptera (Myers and Post, 1981).

A central point was determined at each site, and a ten- meter radius was measured to form a twenty- meter diameter circular sampling site (Figure 2).

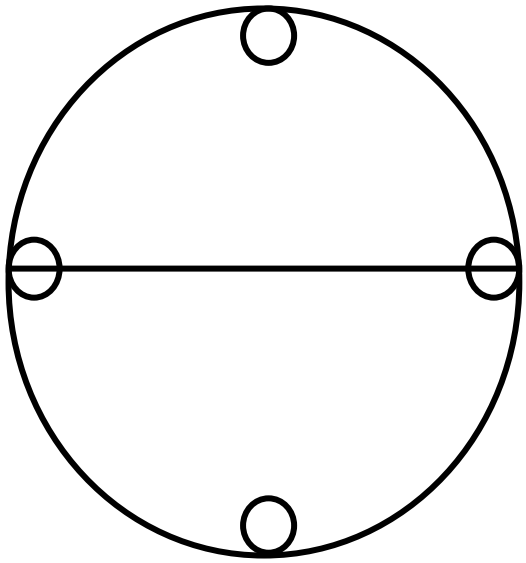

Figure 2. Sampling site layout. Each small circle represents a pitfall trap, placed at each of the four cardinal directions.

2.3 Usage of Sampling Methods

Each site was sampled in four ways, as follows:

PITFALL TRAPS: Four pitfall traps were set at the four cardinal directions of each sampling site when pitfall samples were scheduled to be collected. Pitfall samples were collected three times per site, and collected three days following deployment. When not in use, collection jars were placed upside down in their holes.

SWEEP SAMPLES: Sweep samples were collected three times per site, with one hundred sweep 'swings' per sample within the sampling area. These samples were taken on the days that that pitfall samples were picked up

'TROPHY HUNTING:' Each site was actively searched for more conspicuous taxa. These samples were taken three times per site, immediately after sweep samples were taken.

MERCURY VAPOR LIGHTING: At each site a mercury vapor light, powered by a portable generator, was set up for one hour, beginning at 6:30pm as the sun set and ending at 7:30pm. Light samples were taken once per site. Lighting was quantified by using the phases of the moon; all six sites were sampled around the new moon, with the three varzea sites sampled on three different moon phases before the new moon, and the three terra firme sites sampled on the three concurrent moon phases after the new moon.

2.4 Calculating Plant Biomass at the Sample Plots

For each of the three research plots located in both the varzea and terra firme habitats, a survey of herbaceous and woody plant biomass was conducted once during the project. Herbaceous plant biomass was collected within four randomly placed 1 by 1 square meter plots within each sampling site by counting the number of herbaceous plant stems that occurred within the sampling area, estimating an average number of stems from the four areas, and then extrapolating to obtain an estimated number of herbaceous plants found within the entire sampling site.

Woody plant biomass was estimated by counting the trunks of all woody plants found within the entirety of each of the sampling areas. Each trunk was placed into one of three different size categories: those trunks 0 to 2 centimeters in diameter, 2 to 4 centimeters in diameter, or greater than 4 centimeters in diameter. Trunk diameters were estimated by sight and not measured individually. A total woody plant

count for each site was determined by adding the numbers of each of the three categories of woody plant size for each site.

2.5 Abundance and Species Richness

All Coleoptera were collected and preserved for identification. On return to University of Delaware, all target specimens were mounted, labeled, and identified to the family level and then to morphospecies. The data was compiled in a species-by-sample abundance matrix.

'Morphospecies' identification can provide richness estimates equitable to those generated with species identifications (Oliver and Beattie, 1996), and is a superior method of data collection to leaving specimens at the order, family, or even subfamily level (Grove, 2003).

For this project, a voucher label was given to each specimen. On the voucher label is a morphospecies code used as a reference name for that taxon. The code consists of a letter (S for Scarabaeidae, L for Chrysomelidae, or G for Carabidae) and a number, starting with 1 for each family, each representing a different morphospecies. For each family, varzea habitat samples were analyzed first. The first new terra firme species encountered for each family was given the number following the last species of that family recorded in the varzea habitat. For example, the last scarab species of the varzea was given the number 9, so the first new scarab species for the terra firme habitat was given the number 10. Species that occurred in both the terra firme and varzea habitats were given the same number. If there was more than one representative of the same family, each received the same number on their voucher label.

Samples were also compared between the varzea and terra firme habitats by the number of specimens of each target family collected from each sampling method, in order to determine which sampling methods are effective for collecting each family.

2.6 Data Analysis

The data was analyzed using the EstimateS program (Coldwell, 2006) to compute nine species richness estimators (ACE, ICE, Chao1, Chao2, Jack1, Jack2, Bootstrap, MMRuns and MMMeans) for both the varzea and terra firme habitats to determine which habitat type had greater species richness (Colwell and Coddington, 1994).

Simpson's Diversity Index and a Shannon's Diversity Index were also calculated for each habitat type through EstimateS. Then Simpson's Diversity Index was also calculated for each family within each habitat type.

A one-way ANOVA calculation was also used to determine whether or not the differences in species richness and abundance were significant between the guilds and between the two habitat types.

Chapter 3

RESULTS

3.1 Plant Biomass of the Sample Plots

Herbaceous plant biomass was similar between the varzea and terra firme habitats. The varzea sites had a total of 12,874 herbaceous plants, overall 539.5 more than the combined totals of the terra firme sites, a 4.2% difference (Table 1). V1 site had the most herbaceous plant biomass, 6201.5 stems, followed by TF1 site, with 5338 stems (Table 1). Although the varzea sites showed higher herbaceous plant counts, the difference does not appear to be significant. The average stem counts for each habitat have a noticeably low, medium, and high value (Table 1).

Table 1. Herbaceous plant biomass collected and extrapolated for each sampling site

	Average 1 Square Meter Herb Stem Count	314 Square Meter Site Stem Count Extrapolation
V1	19.75	6201.5
V2	7.75	2433.5
V3	13.50	4239.0
V Site	~	12874.0
TF1	17.00	5338.0
TF2	12.50	3925.0
TF3	9.75	3061.5
TF Site	~	12334.5

Woody plant biomass did not differ greatly either between the varzea and terra firme habitats, although the difference was more noticeable, relatively speaking, when compared to the herbaceous plant counts. The terra firme sites had a total of 447 woody plants, 73 more than the varzea sites, a 16.3% difference (Table 2). TF2 site had the highest overall woody plant count of 181 plants, followed by V1 site with 158 woody plants (Table 2). There seemed to be many more small (and probably younger) woody plants (0-2 cm) in the terra firme sites: 258 when compared to the 164 total of the varzea sites, but more larger (and probably older) woody plants in the varzea habitats: 97 compared to the 75 total of the terra firme sites (Table 2). Medium sized plants seemed to be more evenly distributed between the varzea and terra firme habitats (Table 2).

Table 2. Woody plant biomass collected and extrapolated for each sampling site.

	Woody Plants 0-2cm	Woody Plants 2-4cm	Woody Plants >4cm	Total Woody Plants
V1	83	52	23	158
V2	38	39	42	119
V3	43	22	32	97
V Site	164	113	97	374
TF1	58	39	18	115
TF2	107	41	33	181
TF3	93	34	24	151
TF Site	258	114	75	447

3.2 Abundance and Species Richness

Over the course of the project, 162 specimens were collected for the three target groups (Table 3). The varzea habitat produced 94 specimens, 26 more than the terra firme habitat, a 27.7% difference. Although the varzea habitat had a higher specimen count, both the varzea and terra firme habitats followed a similar trend in family representation: the most specimens were collected in the family Scarabaeidae, followed by the family Chrysomelidae, with the fewest in the family Carabidae. This difference is more noticeable in the terra firme specimen count. Almost every species was represented by a specimen count between 1 and 5; the noticeable exception occurred in species S8, which was collected 43 times in the varzea habitat and 31 times in the terra firme habitat (all during a mercury vapor light collection session) (Table 4).

Table 3. Specimens collected in each of the three beetle families.

	Varzea	Terra Firme	Overall Total
# Scarabaeidae Specimens	56	49	105
# Chrysomelidae Specimens	24	16	40
# Carabidae Specimens	14	3	17
TOTAL	94	68	162

Table 4. Species and specimens collected.

Morph	#Specimens	Location	Site Number
Scarabaeidae			
S1	1	V	V2PF1

-Table 4 continued-			
S2	3	V	3V2PF1
S3	1	V	V2PF1
S4	1	V	V2PF1
S4	4	TF	2TF3HG, TF2HG, TF1PF1
S5	1	V	V2PF1
S6	4	V	V1T3, V3T1, V1S2, V1T2
S7	1	V	V1HG
S8	43	V	38V2HG, 5V3HG
S8	31	TF	23TF2HG, 4TF3HG, 4TF1HG
S9	1	V	V2HG
S10	4	TF	2TF2T2, TF2T1, TF3S2
S11	1	TF	TF2HG
S12	1	TF	TF1T2
S13	1	TF	TF3PF1
S14	1	TF	TF3PF1
S15	1	TF	TF1T2
S16	2	TF	TF3PF1, TF3PF3
S17	1	TF	TF3PF3
S18	1	TF	TF3T2
S19	1	TF	TF2HG
Chrysomelidae			
L1	1	V	V3T2
L2	2	V	V3S1, V3T2
L3	1	V	V3S2
L4	1	V	V3S1
L5	1	V	V2S2
L6	1	V	V2T1
L7	1	V	V2S3
L8	1	V	V2T2
L9	1	V	V2S2
L10	2	V	2V2S2
L11	2	V	2V2S2

-Table 4 continued-			
L11	1	TF	TF3T2
L12	4	V	4V2HG
L13	1	V	V3S2
L14	1	V	V2S2
L15	1	V	V2S2
L16	1	V	V1S2
L17	1	V	V3S3
L18	1	V	V3S1
L19	2	TF	2TF1T1
L20	1	TF	TF3T1
L21	1	TF	TF1S2
L22	2	TF	2TF2S1
L23	1	TF	TF1T2
L24	1	TF	TF2HG
L25	1	TF	TF1S1
L26	1	TF	TF1T1
L27	1	TF	TF1S1
L28	1	TF	TF2HG
L29	2	TF	2TF1S1
L30	1	TF	TF2HG
Carabidae			
G1	7	V	5V1PF1, V2PF3, V2PF1
G2	1	V	V2PF2
G3	1	V	V1PF1
G4	1	V	V3PF1
G5	1	V	V1T2
G6	1	V	V3S1
G7	2	V	2V2HG
G8	1	TF	TF2PF3
G9	1	TF	TF3PF3
G10	1	TF	TF3S3

62 species total were collected for the project, 34 of which were found in the varzea habitat, 6 more than were found in the terra firme habitat, a 17.6% difference (Table 5). Both the varzea and terra firme habitats had a similar species distribution, although this differed from the total specimen distribution. The most

species were found within the family Chrysomelidae, followed by the family Scarabaeidae, with the fewest within the family Carabidae (Table 5). This trend is more noticeable in the varzea habitat. Interestingly, only 3 of the 62 species occurred in both the varzea and terra firme habitats (Table 6).

Table 5. Species collected in each of the three beetle families.

	Varzea	Terra Firme	OVERALL TOTAL
# Scarabaeidae Species	9	12	21
# Chrysomelidae Species	18	13	31
#Carabidae Species	7	3	10
TOTAL	34	28	62

Table 6. Number of species found in both varzea and terra firme habitats.

	Number of Species Found in both Varzea and Terra Firme
Scarabaeidae	2 (#4, #8)
Chrysomelidae	1 (#11)
Carabidae	0
TOTAL	3

3.3 Effectiveness of Collecting Methods

It is important to make note of what sampling methods were the most effective in collecting specific families. Mercury vapor lighting and pitfall traps were the most effective method of collecting scarabs, while sweeping was the least

effective; chrysomelid beetles were collected most frequently by sweeping and trophy hunting and never in pitfall traps; and carabids were most often collected with pitfall traps, but still sporadically seen with the other three sampling methods (Tables 7-8).

Table 7. Comparison of collecting method in varzea

	Scarabaeidae	Chrysomelidae	Carabidae
Sweep	1	16	1
Trophy	3	4	1
Pitfall Trap	7	0	10
Hg Light	45	4	2

Table 8. Comparison of collecting method in terra firme

	Scarabaeidae	Chrysomelidae	Carabidae
Sweep	1	6	1
Trophy	6	7	0
Pitfall Trap	6	0	2
Hg Light	36	3	0

3.4 Data Analysis: Diversity Indexes and Species Accumulation Curves

The EstimateS program was used to determine which of the two habitats was richer as a whole, using all the target specimens collected for the project. The varzea habitat was richer than the terra firme habitat, with a 35.2% higher average estimator value (Table 9). These estimators were then plotted (omitting MMRuns, which behaved erratically), with observed species on a species accumulation curve to

determine the validity of this conclusion. Figures 3 and 4 both show a linear accumulation of species for each of the estimators graphed, except for MMMeans which behaved erratically. Because these estimators progress linearly instead of leveling off, which is what would happen if collections had accurately sampled existing species in each site, the validity of the estimators in determining habitat richness is questionable here.

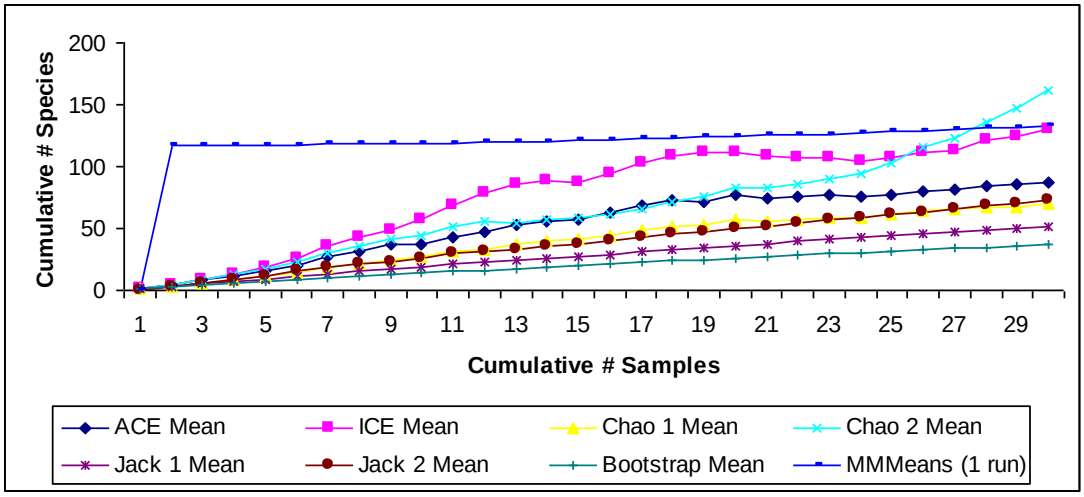

Figure 3. Species richness estimators for the varezea habitat.

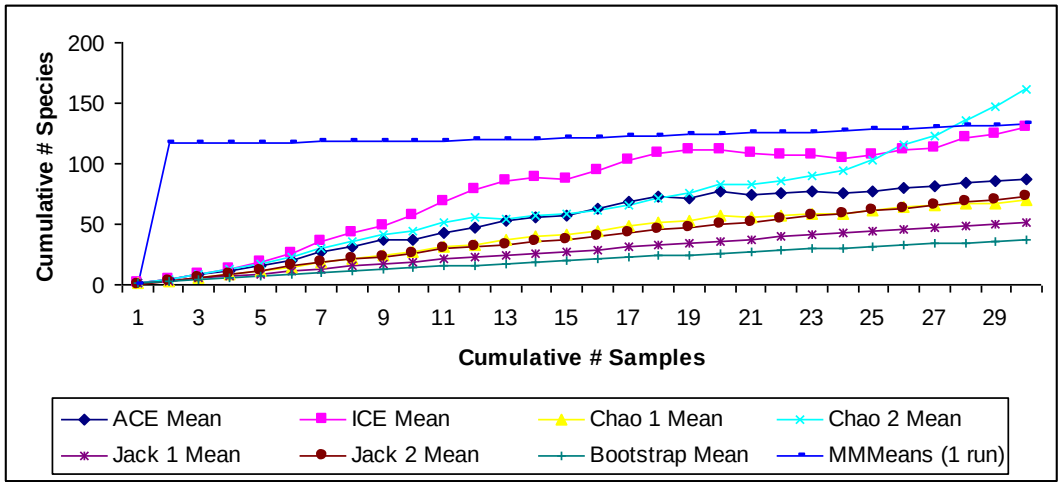

Figure 4. Species richness estimators for the terra firme habitat.

Table 9. Richness estimator values for both varzea and terra firme

Species Richness Estimator	Diversity Index Value Varzea	Diversity Index Value Terra Firme
ACE	116.28	87.72
ICE	209.64	130.34
Chao 1	94.00	70.00
Chao 2	174.17	161.40
Jack 1	63.00	51.20
Jack 2	89.20	72.70
Bootstrap	45.16	36.93
MMRuns	309.54	94.60
MMMeans	191.26	132.86
AVERAGE	143.5833	93.08333

The EstimateS program calculated Simpson's Reciprocal Index, which was used to calculate Simpson's Index and Simpson's Diversity Index. Simpson's Index has a range of 0 to 1: 0 represents infinite diversity and 1 represents no diversity. For Simpson's Index of Diversity, 0 represents no diversity and 1 represents infinite diversity. Both the varzea and terra firme habitats were similarly diverse (Table 10)

Shannon's Diversity Index was also calculated, and showed similar diversity in each habitat (Table 10). This index can range from 0 to about 4.6; however, values lying in the middle of this range are considered ambiguous and therefore not very helpful in determining the diversity of a site.

Table 10. Diversity indexes for varzea and terra firme sites

	Total Varzea	Total Terra Firme
Simpson's Index (D)	0.2155	0.2110
Simpson's Index of Diversity (1-D)	0.7845	0.7890
zSimpson's Reciprocal Index (1/D)	4.64	4.74
Shannon Diversity Index (H)	2.47	2.41

Diversity indexes were further calculated for each family within both the varzea and terra firme habitats. The low numbers of specimens and species make the value of these indices questionable but they can still be used to view trends and make general observations. Simpson's index for the family Chrysomelidae was small, indicating a very high level of diversity in both habitats (Tables 11-12) while the family Scarabaeidae was less diverse in each habitat. The data for the family Carabidae is difficult to interpret because it had both the smallest number of

specimens and species. An index could not be determined by EstimateS for the Carabids in the terra firme habitat because of limited data (Table 12).

Table 11. Diversity Indexes for target families in varzea habitat

	Scarabaeidae	Chrysomelidae	Carabidae
Simpson's Index of Diversity (1/D)	1.69	30.67	4.14
Simpson's Index (D)	0.5917	0.0326	0.2415
Simpson's Index of Diversity (1-D)	0.4083	0.9674	0.7585

Table 12. Diversity indexes for target families in terra firme habitat

	Scarabaeidae	Chrysomelidae	Carabidae
Simpson's Index of Diversity (1/D)	2.46	40	|
Simpson's Index (D)	0.4065	0.025	|
Simpson's Index of Diversity (1-D)	0.5935	0.975	|

A one-way ANOVA analysis comparing the number (Figure 5) and abundance (Figure 6) of species in each trophic guild in the varzea habitat found no significant differences among guilds for either parameter (Species: $F_{2,6}$=0.888, P=0.46: Abundance: $F_{2,6}$=0.781, P=0.5).

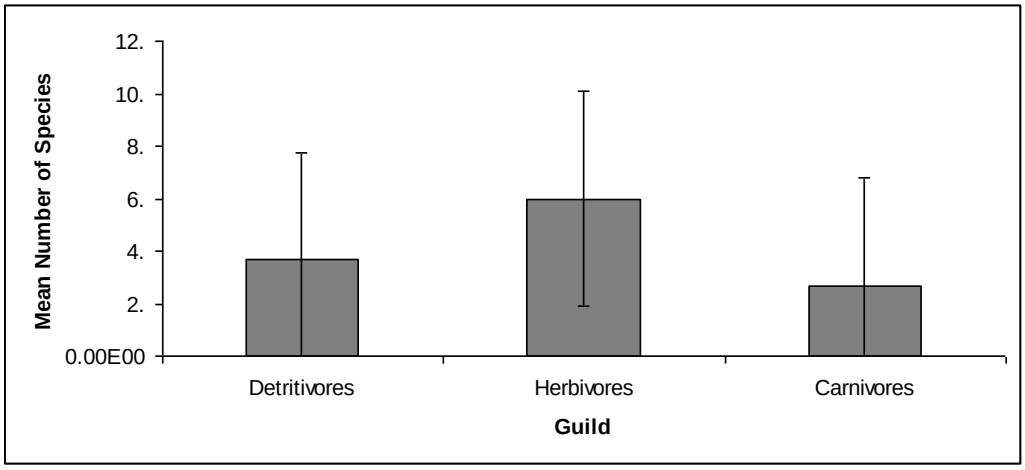

Figure 5: Mean number of species for each guild, varzea habitat

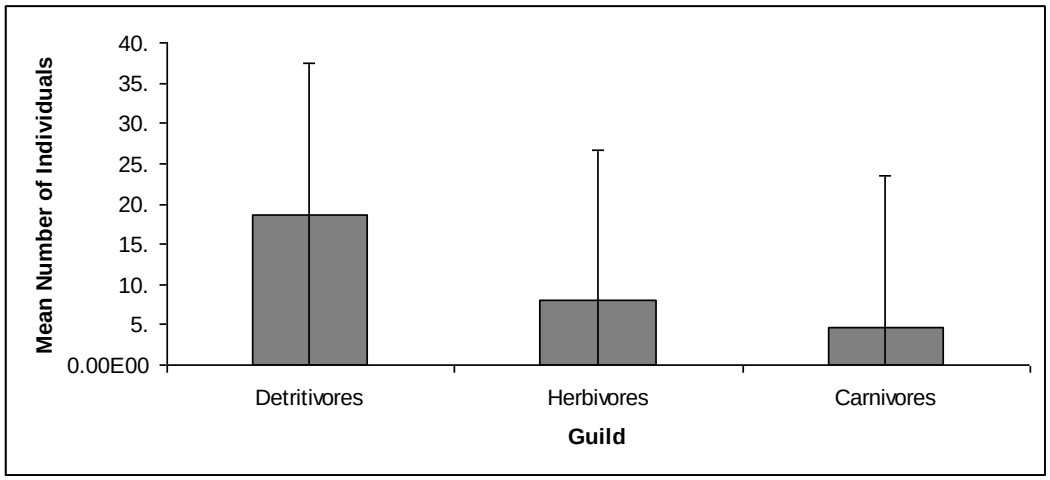

Figure 6: Mean number of individuals for each guild, varzea habitat

The total number of species found in each guild in the terra firme habitat showed marginal differences (ANOVA: $F_{2,6}$=4.457, *P*=0.065; Figure 7) as did the guilds in abundance ($F_{2,6}$=3.942, *P*=0.081; Figure 8)

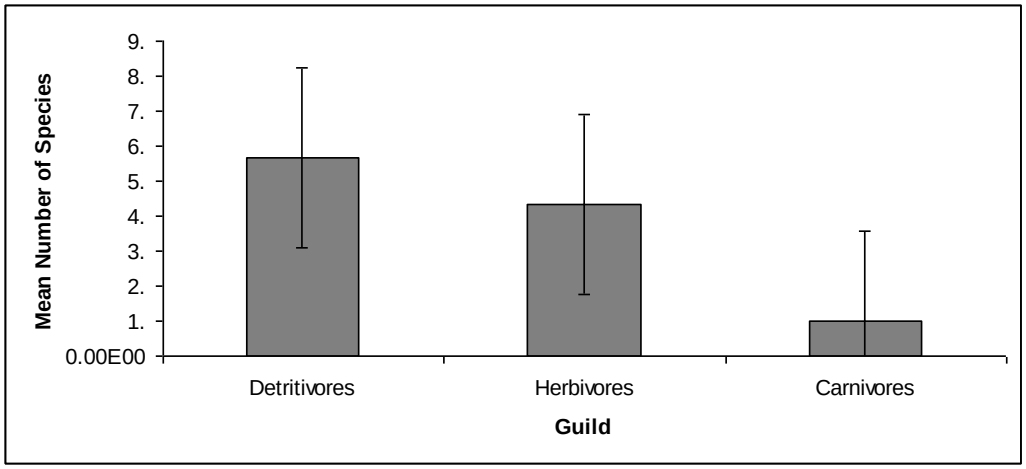

Figure 7: Mean number of species for each guild, terra firme habitat

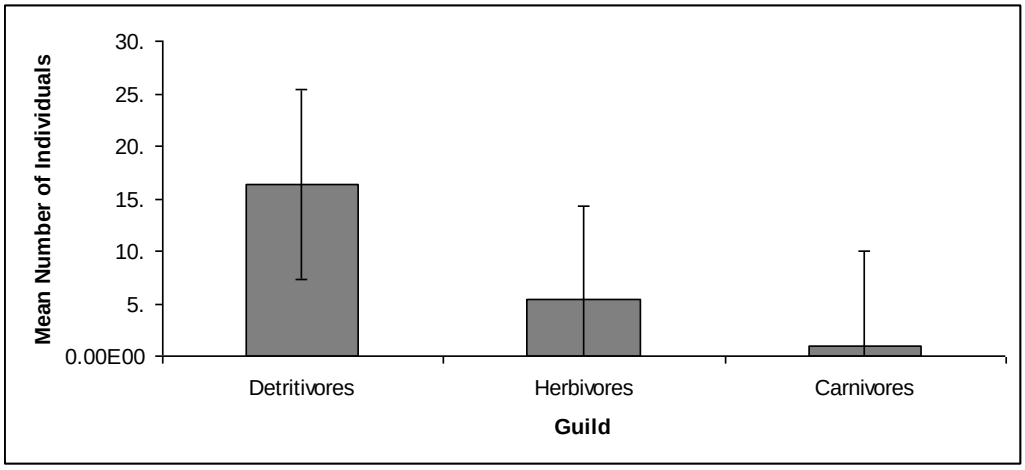

Figure 8: Mean number of individuals for each guild, terra firme habitat

A one- way ANOVA was used to compare the species richness of guilds in each habitat (Figure 9). There were no significant differences between the detritivore guild ($F_{1,4}$=0.947, *P*=0.386), or the herbivore guild ($F_{1,4}$=0.305, *P*=0.61), but the carnivore guild had marginally fewer individuals at the terra firme site ($F_{1,4}$=.6.25, *P*=0.067). Error bars are standard error of the mean.

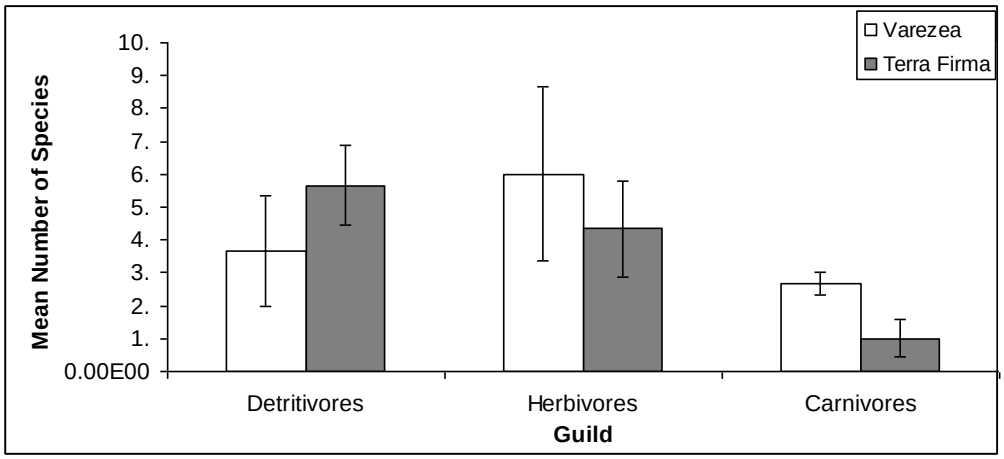

Figure 9: Comparison of the mean number of species for each guild between habitats

Similarly, the abundance of each guild was compared individually between habitats (Figure 10). There were no differences in abundance between habitats for the detritivore guild ($F_{1,4}$=0.024, *P*=0.885), or the herbivore guild ($F_{1,4}$=0.348, *P*=0.587), but the carnivore guild had marginally fewer individuals at the terra firme site ($F_{1,4}$=5.5, *P*=0.079). Error bars represent for the standard error of the mean.

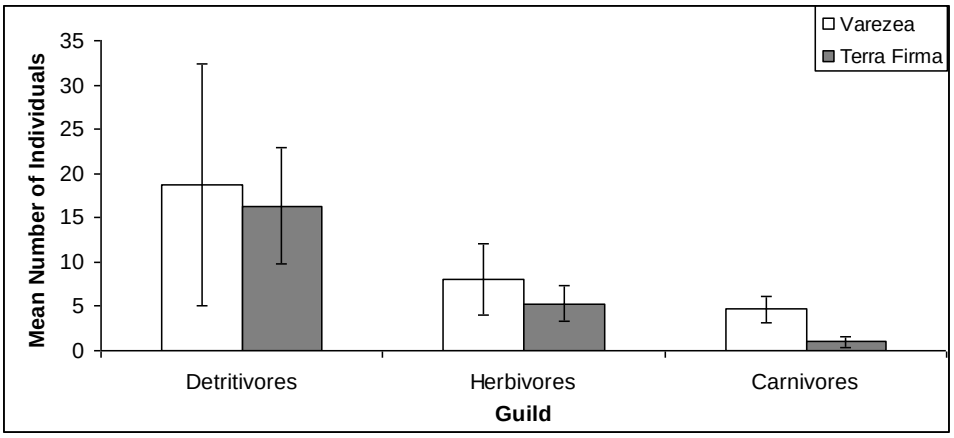

Figure 10: Comparison of the mean number of individuals for each guild between habitats

Chapter 4

DISCUSSION

The five largest beetle families are Curculionidae, Staphylinidae, Chrysomelidae, Carabidae, and Scarabaeidae. All five families are extremely diverse and each one generally falls into the same feeding trophic level, with the exception of the scarabs, which can either be detritivores or herbivores. It should be noted that the subfamilies Aphodiinae and Scarabaeinae of the family Scarabaeidae are well known for their detritivorous lifestyles and were therefore the only scarabs used for the project to represent detritivores. For the purpose of this project, the families Carabidae, Chrysomelidae, and Scarabaeidae were each chosen to represent a guild, based on the expectation that they would: 1.) be the most commonly encountered families in the understory; and 2.) be the easiest to identify to morphospecies. In retrospect, to improve the comparison of guild diversity in Coleoptera, all five families should have been included in the study. This was not done in the project designed because: 1) of the difficulty in identifying species in the families Staphylinidae and Curculionidae; 2) of the expectation that carabids would be more numerous than staphylinids and chrysomelids would be more numerous than curculionids with the sampling methods used; and 3) the time-frame of the project, which would have been difficult to keep if identification of the staphylinids and curculionids were included. Therefore, this project can only be used to make observations for these three families in relation to guild, not each guild as a whole. What is interesting to note is that a large number of staphylinid beetles was collected at the light traps for two of the terra firme sites.

Because of this, it is difficult to simply assume that the observations for the three target taxa will follow the same pattern for other groups; it may only be an observation seen in relation to the three families surveyed.

Simpson's and Shannon's diversity indexes suggest that both are similarly diverse, and that overall diversity is consistent throughout the understory. It also appears that plant biomass is similar between the two forest types and by extrapolation similar within the region. However, the main objective of this project was to compare abundance and species richness in the three target families, each representing a general feeding guild. Because of the low number of both specimens and individuals collected, abundance and species means were not found to be significantly different at the alpha $P < 0.05$ value for any guild in either of the habitats. However, both abundance and species richness for each guild in the terra firme habitat were marginally different at the alpha $P < 0.1$ level. When comparing the individual guilds among forest habitat, the carnivore guild, which had the lowest number of specimens, was statistically significant at the alpha $P < 0.1$ level for both mean number of species and individuals. The lack of power in the statistical analyses is attributed to the low number of replicates for the two habitat types, and thus the low number of samples collected. In the future, a larger number of research plots for each habitat would need to be sampled in order to test the hypotheses adequately.

Although the low number of specimens collected made it difficult to draw statistically significant conclusions, some general observations can be made. The most interesting observation was the difference between the numbers of specimens collected versus number of species. Detritivores were most abundant, followed by a 62% decrease in the number of target herbivores, and consequently followed by a 57.5%

decrease in the number of target carnivores. A different observation was seen for species richness. Herbivores had the most species, with a 32.3% decrease in the number of target detritivores species, and consequently followed by a 52.4% decrease in the number of target carnivore species. Again, because only 162 specimens were collected for the three target groups, these observations are not statistically significant. Both of these observations do support the hypothesis, if only weakly.

There was one exception to the general pattern in species richness. The greatest mean number of species was found in the herbivore guild in the varzea habitat; however, abundance in the varzea and both species richness and abundance in the terra firme followed a different trend, with the highest means in the detritivore guild, followed by the herbivore guild, and with the lowest in the carnivore guild. It was hypothesized that the herbivore guild would contain the most species, but this was not the case in terra firme habitat. Individual means across the three guilds followed the trend hypothesized.

When the hypothesis was developed, different factors were taken into account in order to make an educated guess as to what groups would be richer and/ or more abundant.

Because of the sheer availability of detritus, a high abundance of detritivores is to be expected; however, richness is also relatively high in certain situations. Although detritus is a widely available resource, there is still some specificity in the detritivore guild, and the presence and/or abundance of certain types of detritus can have an effect on a variety of factors within the detritivore population, such as abundance or distribution (Yang 2006), as well as detritivore growth rate and

feeding activity (Swan and Palmer 2006). The high richness of scarabs collected is therefore most likely due to a high variety of detritus availability.

Herbivore diversity seems to rely on a number of complicated flora- based factors. Although plant species diversity has been considered to be an important indicator of herbivorous taxa diversity (Donoso et al. 2010, Novotny et al. 2006), Scherber et al. has suggested that this is not as important as noting the presence of certain plant functional groups (2006). Therefore although it is generally accepted that there is a high level of plant diversity and therefore herbivore diversity in the tropics, plant identification may prove to be necessary in future diversity surveys to compare the diversity of herbivores between habitat types or to explain the reasoning behind the presence or absence of certain groups of taxa, which may be due to the lack of certain plant types or groups. For example, the distribution of certain herbivorous ladybird beetles has been determined to rely on the distribution of specific food plants, limiting the ladybird beetles' presence in certain areas (Koizumi et al. 1999).

Describing the predator dynamics in an ecosystem can be difficult. It has been suggested that predator distribution may be due to habitat specialization as opposed to feeding specialization or availability, meaning that carnivore abundance and/ or richness may not be significantly correlated to either herbivore or detritivore abundance or richness (Woodock and Pywell 2009). The habitats that were sampled may have been more favorable for smaller predators, which could explain the large number of staphylinid beetles collected versus the low number of carabid beetles. Vegetation structure and density have been suggested to be important indicators of carabid beetle richness instead of food availability (Brose 2003).

For sake of thoroughness, four different collection methods were implemented at each site, and repeated during three different sampling periods. The exception to this was the mercury vapor lighting method, which was difficult to implement and quantify at the same time, thus this was limited to one sampling period per site. Every time a sampling method was implemented, every member of Coleoptera was collected. Despite the variety of collecting methods and numerous sampling periods, the collection of not only the target groups, but all insects, yielded low total specimen numbers. There were many different factors that could shed some light on this low number of samples collected.

First, there were some limitations in regards to the sampling methods. Four different methods were chosen to take into account the different life styles and habits of the taxa being studied. Sweeping and trophy hunting was geared toward the collection of the herbivorous family Chrysomelidae, whereas the pitfalls and mercury vapor lighting were considered more appropriate for collecting scarabs and carabids. Each of these methods was limited in some way in their implementation during the course of this project.

The most limited sampling method was the pitfall trapping. As opposed to the other methods used, pitfall trapping has been very thoroughly tested in the literature for the efficiency of various aspects of the trap (Luff, 1975; Hansen and New, 2005; Schmidt et al., 2006; Ward et al., 2001). Preservative, jar type, placement of jars in relation to each other, and size of jars are all aspects that have been tested to reach a general consensus of the most efficient way to pitfall trap. Pitfall traps are usually very high-yielding traps, which to my surprise was not the case during the project. Glass jars are considered much more effective than plastic or metal because

they are more effective in preventing insects from escaping the trap (Luff, 1975). This experiment used thick plastic colored cups because of the difficulty of transporting glass mason jars to the research station, which could have been a factor in increasing the chances of insects escaping once they had fallen in. Another factor in the efficiency of pitfall traps is the preservative used. The ability for a preservative to kill the trapped insects as quickly as possible without evaporating or diluting quickly is crucial to the trap's success. Whereas a mixture of ethylene glycol and water has been shown to have the highest capture efficiency as a medium (and probably by extension even the use of propylene glycol as an eco- friendly alternative), substances such as water, ethanol- water, ethanol- glycerin, or brine seem to be much less effective (Schmidt et al., 2006). For this project, a soap and water mixture was used to prevent the use of hazardous chemicals in the park; however, this was ineffective. Traps were left out for three days, and on numerous occasions, especially if it had rained, no specimens were collected because the water levels had become flush with the mouth of the jar. In a few instances live dytiscid diving beetles had taken up residence during the three day period.

Sweeping and trophy hunting were also difficult to implement. The sample areas were chosen deep in the jungle to prevent any biases from human interactions more closely located to the research station, but the forest this far out was extremely dense. It was very difficult to move around the sites well and even more difficult to maneuver a sweep net to collect properly. Many of the plants have enormous leaves, which made it even more difficult to sweep. Trophy hunting was also limited by the density of the forest. Trophy hunting was implemented immediately after sweep sampling as a way to locate and collect the insects that had

disturbed but missed by the sweep sampling. These methods were primarily aimed at the collection of chrysomelids. Because of this, the methods seemed to be slightly more effective when used in conjunction with one another. A fair number of chrysomelids were collected from the trophy hunts. But again, sweeping is considered to be one of the highest yielding methods of collecting insects, and so I was surprised when a few sweep samples yielded no insects, let alone the target groups.

Perhaps the most difficult sampling method to use was the mercury vapor lighting. First this method required the most work to use; a power source to run the vapor light was needed, which was a forty pound generator, along with a gasoline/oil mixture to keep it running. Second this method required constant attention when used, which was difficult at night because it was considered safer to have a guide present so far down the trail and they normally were preparing for bed around 9:00pm. Thirdly, standardizing the lighting method for six different sampling periods was difficult. Weather is unpredictable and some insects are more active in particular weather patterns. The weather also affects the temperature and humidity levels. Moon phase is another factor, because some insects are more active during different phases of the moon. In the end, it was decided that the lighting would take place from 6:30 to 7:30pm, in order to sample while the sun set and into the night, and on concurrent moon phases. On more than one occasion, the generator would cut out and require restarting, especially during rainy nights. This made the amount of time lighting inconsistent between the different sampling periods.

The six sampling methods took place within a time frame near the new moon; that is, the three varzea samples were done on three moon phases before the new moon, and the terra firme samples were done on the three moon phases after the

new moon that were the same phase as the varzea samples. The samples were all taken on the trail immediately next to the sample site, because of the difficulty of setting up a collection sheet properly in the heart of the jungle. V1 site happened to be sampled while it rained, as was TF1. Both of these samples had the poorest yield of specimens. V2 site, V3 site, and TF3 site were done on clear night, whereas TF2 site was done on a cloudy night. Again these differing weather patterns could have had a large effect on the yield of the lighting samples. However, it could be that lighting is not a very productive method of insect collection when implemented that deeply in the jungle. My sampling sites were deep in the forest in areas that were very dense. I have found that I have the most luck on forest edges when lighting in Delaware; it may be that the density of the jungle inhibits the visibility of the mercury vapor light, or any light for that matter, and thus its ability to attract insects. It would be interesting to see the yield if a lighting sample was taken on a forest edge or clearing and comparing that yield to a dense jungle sample.

Another factor to consider is the time of year. January in that region of the Amazon is the 'intermittent phase' where the dry season is becoming the wet season. Because of the small time frame and the abrupt season change, it may be that many taxa are not at their most diverse during this period. It is worth noting that the study was performed during a record long dry spell for that region of the Amazon, where it hadn't rained for about two weeks (mid-December 2009 to the first week in January 2010).

The rainforest can be broken up into different habitat levels; including an understory and a canopy. Because only the understory was sampled the project was not a thorough sampling of guild diversity in the forest as a whole. Perhaps certain

families are more diverse in the canopy than in the understory, in which case the project is only a representation of trends in a certain part of the rainforest.

In conclusion, this project has made me realize the extreme difficulty in studying biodiversity, especially in relation to insects. Even when working with a numerous group, this project has also shown me that biodiversity is not something easily quantified at all; trends are very difficult to find as a whole, and the methodology used to measure it is difficult to implement successfully.

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