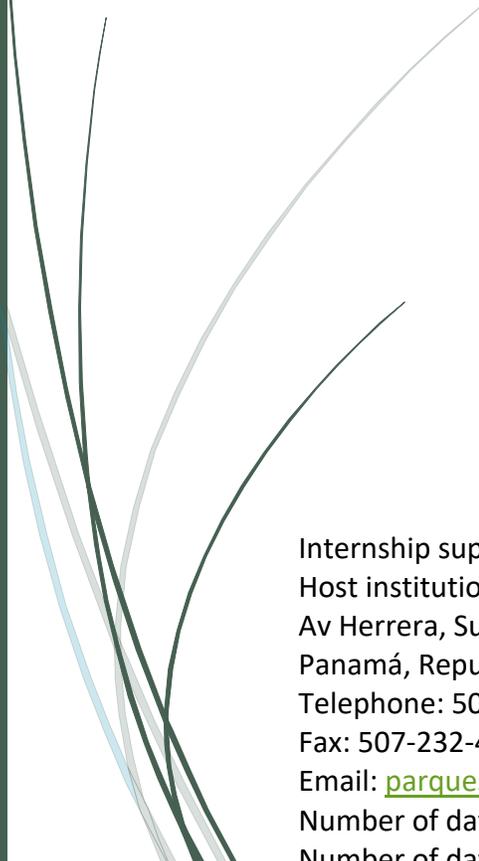




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# Herbivorous Insect Prevalence on Native vs. Introduced Trees in Parque Summit

Tessa Murray



Internship supervisor: Marianne Akers  
Host institution: Parque Municipal Summit  
Av Herrera, Summit, District of Ancon,  
Panamá, Republic of Panama  
Telephone: 507-232-4850  
Fax: 507-232-4854  
Email: [parquesummit@gmail.com](mailto:parquesummit@gmail.com)  
Number of days of research: 21  
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## Introduction

The US government established Parque Municipal Summit in 1923 as an experimental garden; its original intention was to test the ability of Asian and African tropical plants to grow in the Americas. Therefore, most of these plants are nonnative to Panama and deliberately grown for purposes of profit, security, and defense. For example, the garden introduced rubber trees after Japanese powers halted trade with the US (and therefore their rubber supply) during World War II (Blue 2011). Also during World War II, Summit served to train soldiers in military techniques in the jungle, such as the use of tropical plants for food, defense, and camouflage. They introduced 450000 more plants exotic to Panama during this time (Summit 2019).

As part of the Torrijos-Carter treaty, the park's management returned to Panama in 1979 (Summit 2019). Under the mayor of Panama City and a board of directors, the park became the botanical garden, animal refuge, and municipal park as it exists today. Over 150000 people come to Parque Summit each year to enjoy services such as environmental education, recreation, and access to a natural place for urban dwellers (Blue 2011).

My project supervisor, Marianne Akers, is a botanic advisor at Parque Summit who works to promote the public's engagement with the flora of the park. While the majority of Parque Summit's visitors are attracted to the park to view the animals, it is important to draw their attention to the exciting plant life as well. When Marianne began at the park in 2006, she described Parque Summit as more of a plantation for exotic palms than a garden due to its history of American control and experimentation. The park has an estimated distribution of 70% introduced trees to 30% native. Since her arrival at Parque Summit, Marianne has dedicated her efforts to shifting the focus in the park to native plant species. Her reasoning is

that she considers native plants more useful, as many exotic plants' leaves die during the dry season. Not only is this less appealing aesthetically, it also has repercussions in terms of carbon cycling. Instead of continuing photosynthesis and the absorption of carbon dioxide with leaves like native plants do, nonnative plants in the park are more likely to dry up and contribute to greenhouse gas emissions when their leaves fall and decompose. Native plants are also important at Parque Summit because they are already adapted to Panama's climate and therefore need less intensive watering.

As previously discussed, there is a fascinating historical background behind the collection of plants chosen for cultivation in Parque Summit. I believe it is important to recognize the contested legacy of the US influence on Panama that remains in the garden through the distribution of native to nonnative species. My project's intention is to analyze the ecological component of the collection in regard to this distribution. The study seeks to provide insight into the local ecosystem in the garden through comparing insect interactions with native vs. introduced tree species. The research question at hand investigates whether or not there is a positive correlation between native trees and herbivorous insect abundance and diversity.

### Literature Review

Interactions between plants and herbivorous insects have led to evolutionary adjustments for both parties. In tropical forests, leaves grow defenses by having low nutritional quality, greater toughness, and a wide variety of secondary metabolites specific to their co-evolved herbivores (Coley & Barone 1996). In turn, well-adapted insects employ strategies to tolerate, circumvent, or manipulate plant defenses to their advantage (Parker & Gilbert 2007).

This co-evolutionary arms race has implications for situations of plant introductions such as a botanic garden.

The enemy release hypothesis (ERH), first presented by Darwin (1859) and then emphasized by others (Elton 1958, Gillett 1962), predicts the success of nonnative plants in their new environment as attributed to the lack of natural enemies in the invaded area (Maron & Vilà 2001). The ERH demonstrates how natives plant species have a disadvantage because their natural enemies have co-evolved to resist their defenses, while introduced species have different defense mechanisms that insects have not adapted to and cannot resist. Additionally, herbivores are more likely to locate and feed on species with which they are familiar (Parker & Gilbert 2007). In contrast, the biotic resistance hypothesis (BRH) was first developed by Elton (1958) and assumes the defense mechanisms of exotic plants will be not useful in deterring their new herbivorous enemies. Elton's hypothesis explains that species-rich environments such as the tropics are able to use their resources effectively enough to resist intruder species through a combination of predation, competition, parasitism, and disease (1958). Therefore, introduced plant species are suppressed compared to native ones when introduced to a system with high biodiversity such as the tropics (Parker & Gilbert 2007). These two theories are competing, but not mutually exclusive.

Keane et al. wrote a comprehensive report reviewing experimental evidence that tests the ERH. Seven studies confirmed a greater negative impact of natural enemies on introduced host plants compared to exotic species (with impact measured as visible loss of biomass), while the opposite was true for only one study (2002). Another report using existing literature on plants and their herbivores to test the ERH found supporting evidence of less diversity of

herbivorous insects and less damage on exotic plants compared to their native counterparts (Liu & Stiling 2006).

Most recently, a 2016 meta-analysis compiling 68 studies found insect diversity was significantly higher on native than on exotic plants (Meijer et al. 2016). Insect abundance also tended to be higher on indigenous plants, but only in studies using the 'community' approach, that is when introduced species were compared with native counterparts outside of the same species. My experiment in Parque Summit utilizes a community approach as well. Meijer et al. found that the severity of damage to leaves was not different between native and nonnative plants in the majority of studies using the community approach (2016). This study casts some doubt on the seemingly evident ERH, as it suggests that any benefit from invading a novel range may be short-lived: greater evidence supporting ERH tends to be shown in studies with ephemeral plants compared to perennials (such as the trees in this experiment) (Meijer et al. 2016).

This experiment in Parque Summit is unique in that the setting is a tropical botanic garden, where density of each tree species is highly regulated. Exotic species have been introduced intentionally and are not considered invaders with negative impacts in the park. However, Parque Summit has been attributed for the introduction of five species of invasive palm trees in the surrounding forest in Gamboa (Hubbuck & Craft 1995; Svenning 2002). The question of whether the ERH is true for this experiment has local ecological indications: if native trees are more inclined to promote herbivory and diversity of herbivory, they are bolstering biodiversity of the ecosystem as a whole. My hypothesis is that native species suffer greater attack by natural enemies relative to exotic species at the same site: I predict a higher diversity

of insects and higher percentage of leaves damaged will be found on native plants compared to introduced ones.

### Site Description

The park sits at the eastern edge of the Panama Canal, 25 km from Panama City (9°3'59.91" N, 79°38'45.98" W). The elevation of Parque Summit is 90 m asl (Google Earth 2019). The average temperature is 27°C (García et al. 2014). The wet season entails 7 months of heavy rainfall from May to November, and the site averages 2790 mm precipitation annually (World Bank 2016). Parque Summit in its entirety consists of 55 hectares for the botanic garden, with another 195 hectares dedicated to buildings, recreational areas, and animal enclosures (Summit 2019). The main types of vegetation in the park include grassy areas and wooded areas (an array of palms, trees, and bamboo). Along the main paths for visitors, the site undergoes maintenance and landscaping. Lianas are not found on these trees. There are unkempt patches away from the path where native and introduced plants have spread without supervision. The physiognomy which characterizes the park is given by the “tropical rainforest, cleared patches that have been populated with *Saccharum spontaneum*, and introduced herbaceous and mixed plains” (García et al. 2014). The park exists along a major road to Gamboa (Avenida Herrera), but is otherwise surrounded by the highly biodiverse Soberanía National Park, which has an approximate area of 20000 hectares of primary and secondary seasonal tropical lowland forest (García et al. 2014).

# Methodology

Map 1: Parque Municipal Summit

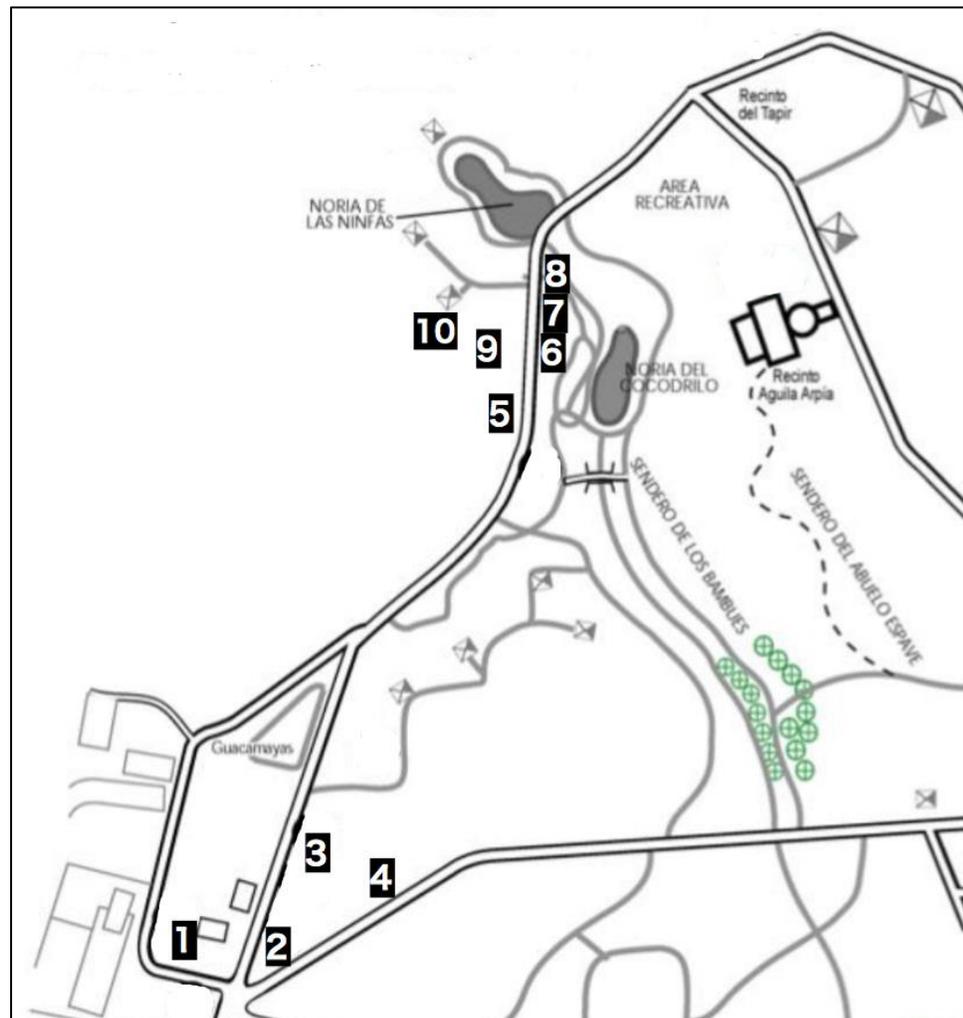


Table 1

	Tree	Common name	Number on map	Height (m)	Diameter (cm)	% Shading at 15:00	Distance from trail (m)
<b>Native</b>	<i>S. apetala</i>	Panama	2	12.66	22	5	5.5
	<i>P. guajaya</i>	Guava	1	6.7	13	0	3.5
	<i>M. chicle</i>	Naisberry	8	17.41	69	10	4.5
	<i>S. macrophylla</i> 1	Mahogany 1	9	27.16	74	5	8
	<i>S. macrophylla</i> 2	Mahogany 2	10	27.66	107	15	16
<b>Introduced</b>	<i>C. verum</i>	Cinnamon	3	8.21	15.5	0	6
	<i>M. papeda</i>	Kaffir Lime	4	10.06	19	5	12
	<i>L. chinensis</i>	Litchi	5	8.94	69	10	3
	<i>C. guianensis</i> 1	Canonball 1	6	13.66	60	10	4
	<i>C. guianensis</i> 2	Canonball 2	7	21.97	89	5	4

My hypothesis is that 1) a higher abundance of leaf damage from herbivory and 2) a higher diversity of herbivorous insects will be present among native trees compared to introduced trees. To investigate this, I established samples of five native and five introduced trees [listed in Table 1]. Four species of each type of tree were chosen, with two trees of the same species sampled for one species of each type. The ten trees are split up with four in one section of the park and six in another [shown in Map 1]. As they are less abundant than the introduced species, I chose native trees first on the basis of having a variety of sizes. As a result, some tall trees and some

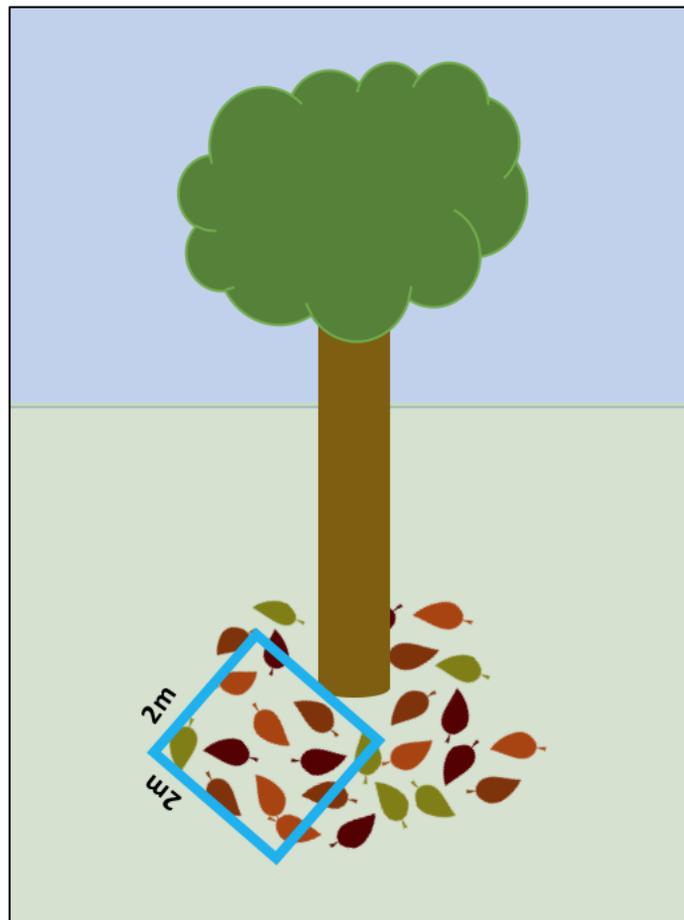


Figure 1

short ones were sampled for the native group. Then the nonnative trees were chosen as similar counterparts to the native ones in terms of height and diameter. The ages of the trees are unknown, but estimated to all be within 10 years of age of each other. None of them are young enough to heavily skew the data (as insects prefer to graze leaves from young trees) (Coley 1983). A phylogenetic tree demonstrating the evolutionary relationship between trees can be found in Appendix A.

For each tree, I created a 2 meter by 2 meter quadrat on the ground starting at the base of the trunk [as shown in Figure 1, and Appendix B]. To randomize the sample, I flipped a

coin to determine the direction from the trunk to collect the sample (assigning North to heads and South to tails, then again with East as heads and West as tails). I counted all of the fallen leaves that came from the coordinating tree within each quadrat as well as any leaves on the trees' branches that are within the first two meters from the base of the trunk.

I did three types of assessments of herbivory: a prevalence census, severity census, and diversity census. In the prevalence census, I recorded presence/absence of markings from herbivorous insects on all leaves observed in the quadrant. The sampling unit acquired with the prevalence census is a percentage of leaves with signs of herbivorous insect damage. As the data collection occurred in the dry season, wind became a significant factor when leaves from other plants blew into the quadrant. To prevent a misrepresentation in the data, I was careful to distinguish leaves in the quadrant that corresponded with the correct tree for the census. Of the leaves observed with herbivory, the severity census recorded the percentage of leaf tissue removed from the total leaf area by herbivores. I estimated these percentages per each leaf visually. Examples of leaves with 10%, 25%, 50%, and 75% damage can be found in Appendices C-G.

As some markings found on leaves appear significantly different than others, I was able to categorize distinct types of damage found on leaves. With the help of my internship professor Dr. Héctor Barrios, these categories were identified to the level of order of insect [see Appendices C-G]. To gauge the diversity of insects grazing on each tree, the sampling unit found for this is order richness of each species per 2 meters squared.

I conducted three trials for each tree, using the aforementioned coin method to randomize a new direction from the stump each time. The prevalence, severity, and diversity

censuses were executed at all three trials at every tree. This data collection culminated with a total of 19093 leaves counted, 4995 of which being leaves with damage that were measured and identified. All methods carried out for the duration of this research project were done in accordance with the Code of Ethics of McGill University [see Appendix H].

### Statistical Analyses Undertaken

I calculated the average of the percentage of herbivory observed per each tree per each trial. After this, I took the average for native trees and compared it to the average of introduced trees. A test of statistical significance was performed using a t-table and the formula for unpaired, two-sided t-test:

$$t = \frac{\bar{x}_1 - \bar{x}_2}{\sqrt{s^2 \left( \frac{1}{n_1} + \frac{1}{n_2} \right)}}$$

$$s^2 = \frac{\sum_{i=1}^{n_1} (x_i - \bar{x}_1)^2 + \sum_{j=1}^{n_2} (x_j - \bar{x}_2)^2}{n_1 + n_2 - 2}$$

where  $\bar{x}_1$  and  $\bar{x}_2$  are the sample means,  $s^2$  is the pooled sample variance,  $n_1$  and  $n_2$  are the sample sizes and  $t$  is a Student  $t$  quantile with  $n_1 + n_2 - 2$  degrees of freedom.

I used Simpson's Diversity Index to measure the diversity of orders present on each tree:

---


$$\text{Simpson's diversity index} = 1 - \frac{\sum_{i=1}^R n_i(n_i - 1)}{N(N - 1)}$$

where R is the total number of orders (order richness),  $n_i$  is the number of individuals of particular order, and N is the total number of individuals. I tested the statistical significance of means for the diversity indices of native and introduced trees using the t-test explained above.

My internship professor Dr. Barrios used JMP to conduct a Principal Components Analysis of every variable measured in the study as well as an ANOVA to assess means of damage per leaf. I calculated the correlations between herbivory and the variables with highest influence on the data detected from the PCA using the Pearson Correlation Coefficient:

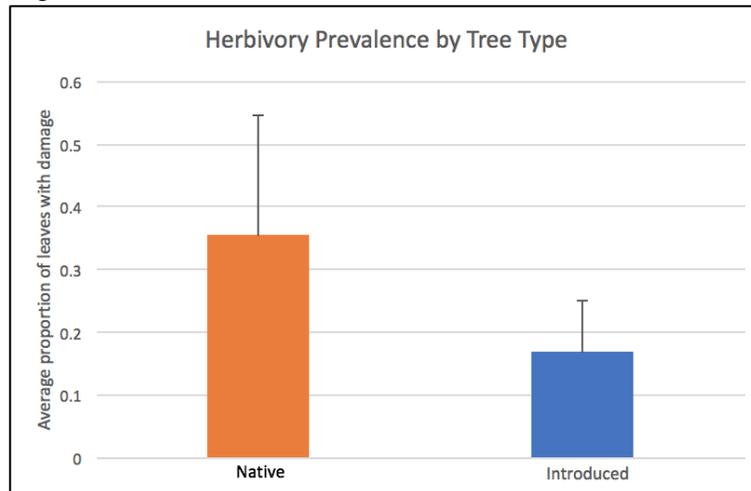
$$r = \frac{n(\sum xy) - (\sum x)(\sum y)}{\sqrt{[n\sum x^2 - (\sum x)^2][n\sum y^2 - (\sum y)^2]}}$$

where r represents the correlation coefficient, n is the sample size, x is whatever variable is currently being tested, and y remains as proportion of herbivory.

## Results

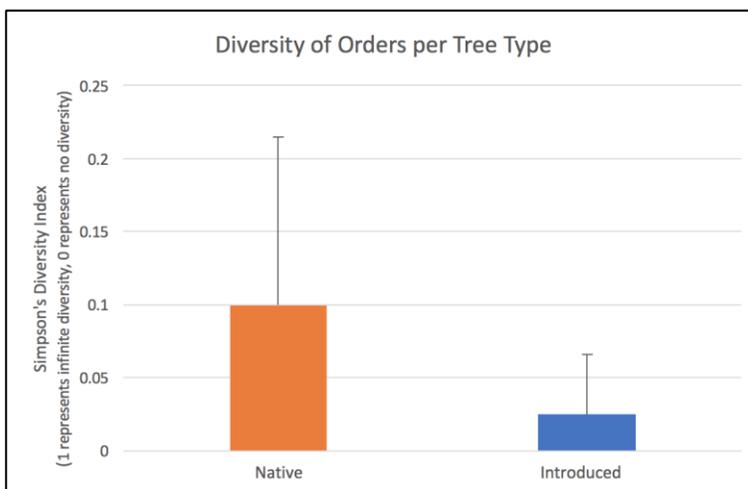
After compiling the means of herbivory prevalence for each tree, I found that on average, 35.49% of leaves collected from native trees contained signs of herbivory, while 16.84% of leaves from introduced trees had signs of

Figure 2



herbivory [shown in Figure 2]. At significance level  $\alpha = 0.05$ , these results do not hold statistical significance. Therefore, I fail to reject the null hypothesis that there was no significant difference between herbivory on native and exotic plants. Taking averages of the computed indices of insect order diversity of both natives and nonnatives resulted in a higher amount of diversity shown on native trees [see Figure 3]. Running a t-test on these means at the significance level of  $\alpha = 0.05$  reveals that this is not sufficient evidence to conclude that there is lower diversity on exotic trees: I fail to reject the null hypothesis that there was no significant difference in diversity of insects on native and exotic plants. These failures to reject the null are perhaps due to the small sample size ( $n=3$ ) and high variance in the data. Given the nature of

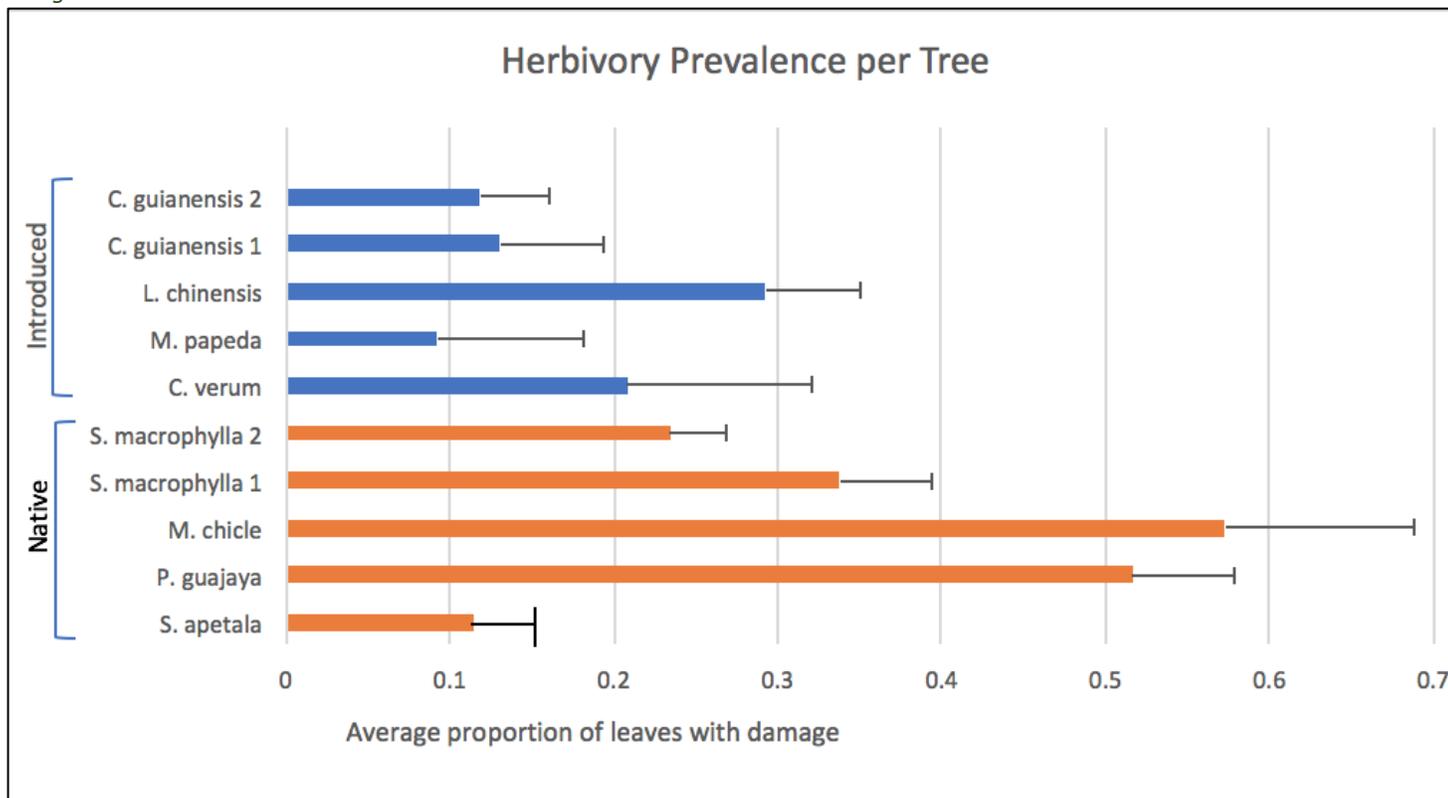
Figure 3



the site, the high variance is difficult to avoid. That is, the location of each tree species is not ideal for a test site and instead distributed for aesthetic and ornamental purposes. There are many variables to account for in the data that are addressed in the PCA. Perhaps repeating

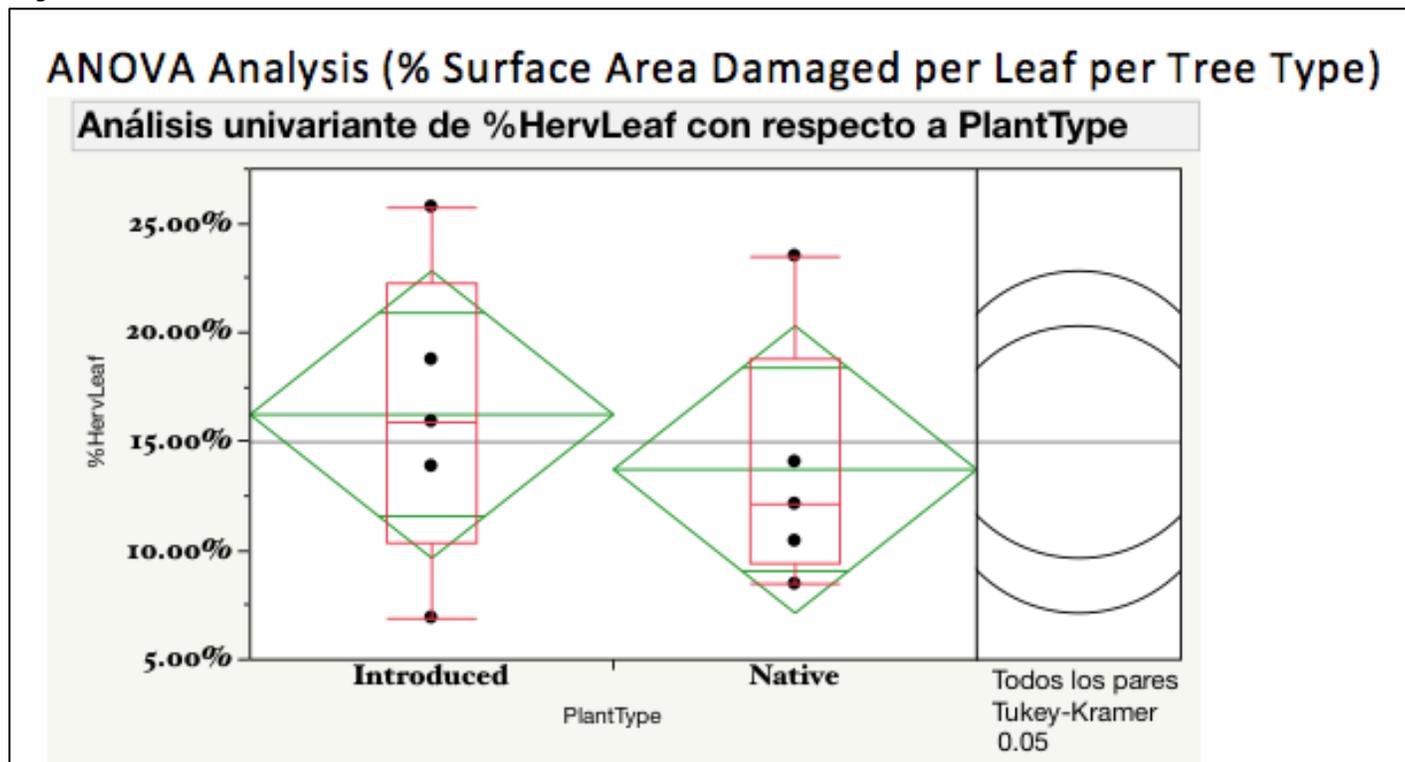
this methodology with a larger sample size may yield a statistically significant result confirming the trend I noticed of greater herbivory and diversity of insects present on native plants.

Figure 4



As seen in Figure 4, over half the leaves collected for two indigenous trees (*M. chicle* and *P. guajaya*) contained damage from herbivory. The exotic tree with the largest amount of observed herbivory was *L. chinensis*, which could possibly be explained by its proximity in the park to the native *S. macrophylla* trees (refer to Map 1). The *S. macrophylla* trees observed 28.58% of herbivory on average, which is similar to *L. chinensis*' 29.25%. A possible explanation for this that could be investigated tests whether a tree of one species growing close to tree of another species (that is commonly used as a food source for insects) could be a disadvantage if insects are observed spilling over to nearby trees when outcompeted.

Figure 5



As previously mentioned, leaves from introduced trees were eaten less overall; but when they are eaten, insects eat a greater surface area of the leaves compared to when they eat leaves from native trees. The average amount of leaf area damaged for introduced trees is 16.24% while the average for native trees is 13.72% [see Figure 5]. This could be congruent with Elton's biotic resistance hypothesis that insects are preferentially damaging potentially invasive plants to protect their habitat. An theory I have for this occurrence is that it could be related to the fact that there tended to be less diversity of herbivorous insects found on exotic trees [See Figure B]. Because there are fewer types of insects that are able to feed on introduced leaves, they suffer from less competition and/or predation while feeding on the leaves and can eat a fuller extent of the leaf. This theory would require an elaborate experiment monitoring insect behavior to confirm.

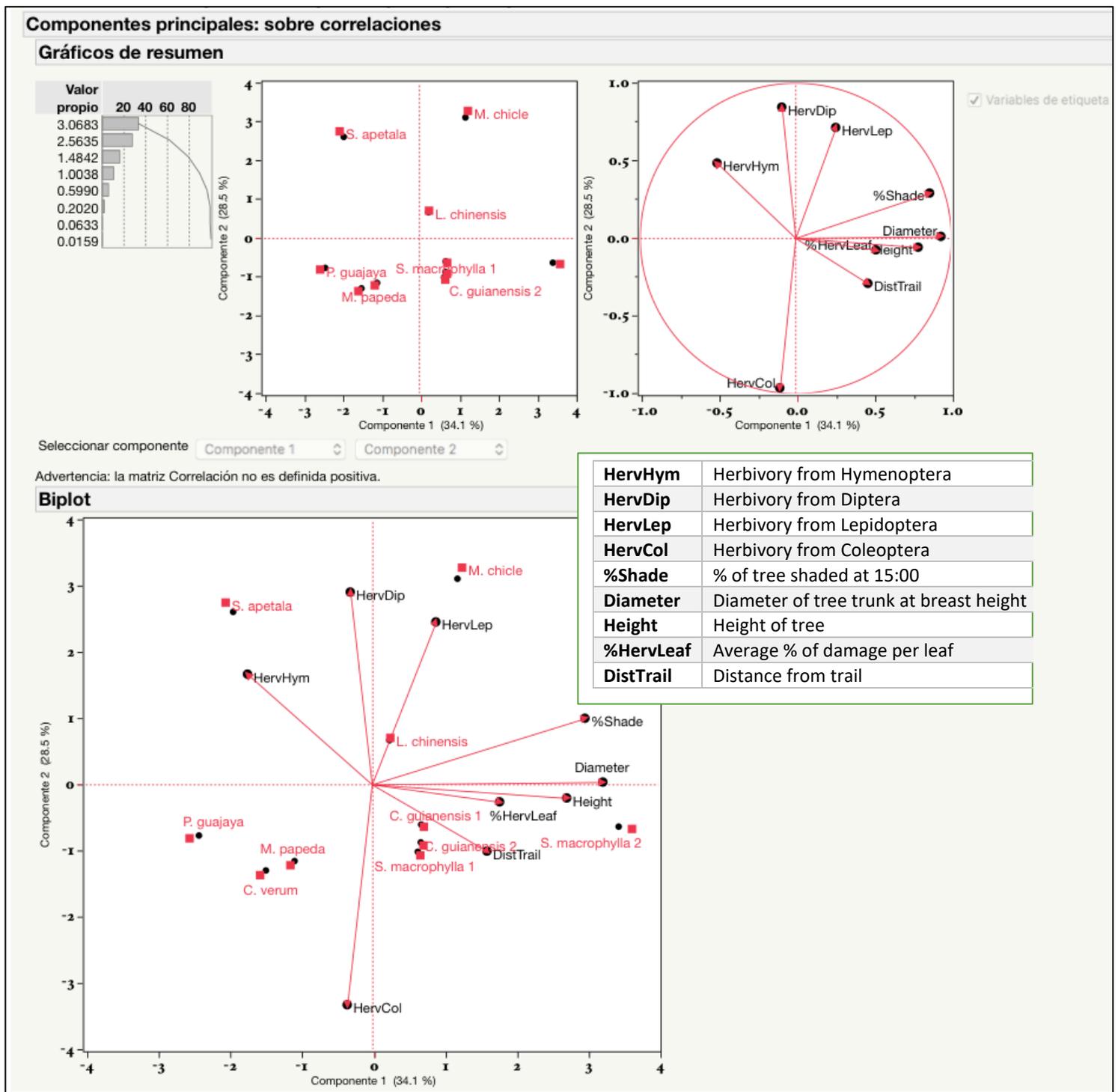


Figure 6

The PCA [Figure 6] shows that the first main component [Componente 1] is the linear combination of the standardized original variables that has the greatest possible variance: 34.1% of the variance is explained by the diameter of tree trunks, % shading on the trees,

Table 2

<u>x,y</u>	Herbivory prevalence
Diameter of tree trunks	r= 0.0319
% shading on trees	r= -0.032
Distance from trail	r= -0.275

distance from the trail, and % of damage per leaf. These are the variables with the greatest influence on herbivory prevalence, and their levels of correlation are exhibited in Table 2. These values are considered to be weak or very weak, however, one interesting

finding is that the distance from the trail has a slight negative correlation with herbivory prevalence. The path is heavily populated with humans and creates a gap between trees in the garden. A possible explanation for the fact that prevalence of insect herbivory decreases further from the path is because here insects are more likely to be predated on, as their predators are mainly birds that would be deterred from approaching the trail. This hypothesis could be tested by comparing sites in the park along the path vs. away from the path.

The slight positive correlation between tree trunk diameter and herbivory prevalence has been a frequently-cited phenomenon due to insects' preference to occupy larger trees with more leaves as a food source and to hide from predators (Basset et al. 1992; Basset et al. 2001; Pratt et al. 2005; Campos et al 2006). The slight negative relationship that exists between percent of tree shaded and herbivory prevalence corresponds with the idea that shade-tolerant species invest more energy in defense against herbivory (Coley & Barone 1996). Nutrients are less available and productivity is lower when light level is reduced. Hence, a shaded leaf has a lower return from photosynthesis than a leaf in the sun, so there is a higher cost to losing a leaf to herbivory. The strongest evidence for this in my study is found through the *S. macrophylla* trees: this species experiences the largest amount of shade for all the trees sampled, has

Distribution of Leaf Damage per Insect Order

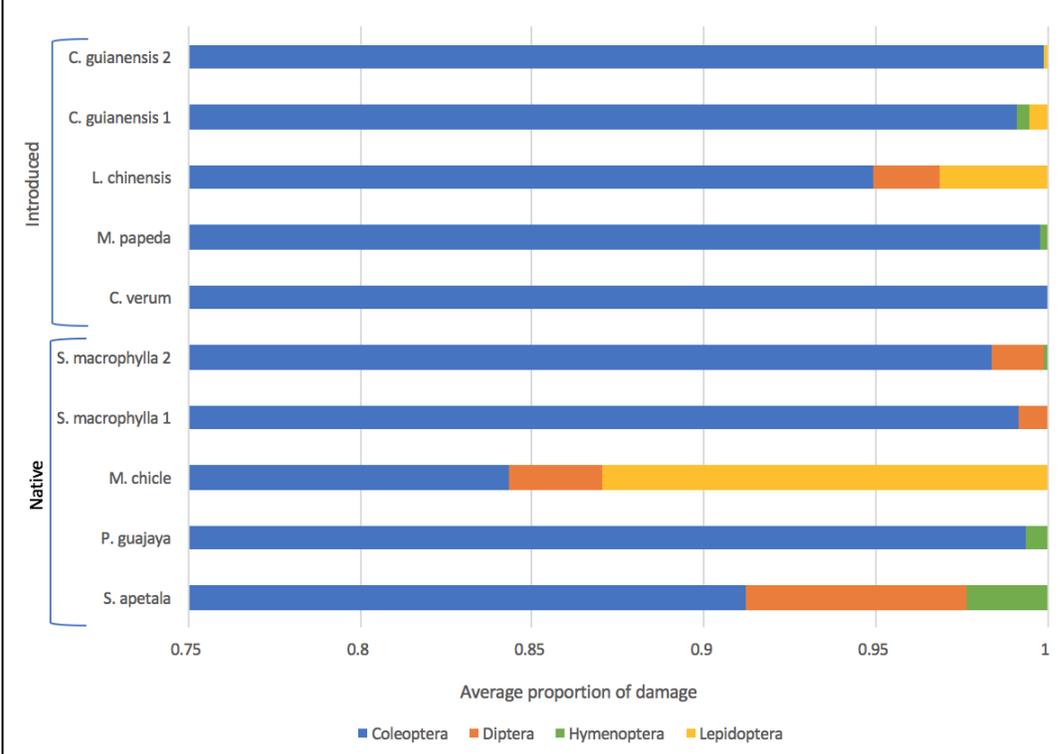


Figure 7

noticeably tough leaves (making grazing more difficult for insects), and experiences from relatively low herbivory compared to the average of native trees (28.58% compared to 35.49%).

Each subsequent principal component

[Componente 2 on Figure D] is the linear combination of the variables that has the greatest possible variance and is uncorrelated with all previously defined components. First, herbivory from the order Coleoptera is the largest and opposite of herbivory from Diptera, Lepidoptera and Hymenoptera. Second, Coleoptera herbivory is associated with the tree species *C. guianensis* (exotic), *C. verum* (exotic), *M. papeda* (exotic), *P. guajaya* (native), and *S. macrophylla* (native). The orders of Hymenoptera, Diptera, and Lepidoptera are associated with *S. apetala* (native), *M. chicle* (native), and *L. chinensis* (exotic). As articulated in Figure 7, markings from Coleoptera were observed as the majority of damage on every species. The other three orders of insects' markings observed (Diptera, Hymenoptera, and Lepidoptera) were found at least once on both native and exotic groups. Thus, there was no evidence in this system of a group of host-specific natural enemies that preferentially

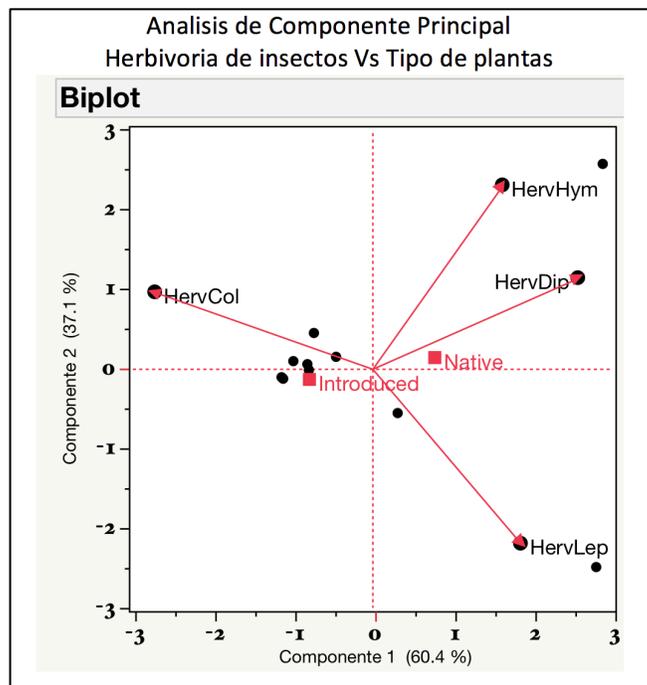
Figure 8

attack native species. As emphasized in Figure 8, the means of native species are more heavily correlated with the orders of insects that are rarer than Coleoptera. This is further indication of increased order-richness on native trees.

### A Note on Sources of Error

There are multiple potential sources of error and imprecisions to acknowledge, as this was a small-scale and short-term experiment. I am

aware of how limited my scope of herbivory is because I could only use leaf litter for samples. The infeasibility of accounting for many other guilds of herbivores (such as phloem and xylem feeders) leaves this study with minimal signification of the complete community of insects and their impact. Attack on leaves from fungi and parrots were observed on some trees but not enough to be analyzed. Additionally, something to note is the possibility that leaves could have been completely eaten by insects, in which case the amount of damage is underestimated. Another aspect not accounted for in this study is the difference in leaf longevity between species. It is impossible to know the time scale over which damage has accumulated on leaves collected under the canopy. Different tropical tree species' leaves can live from 4 months to over 14 years (Coley & Barone 1996). Consequently, the data may be skewed with species of short-lived leaves having lower damage rates. The analysis also does not take into account evolutionary responses of the introduced species, which have been evolving in their new



habitat for almost a century. Finally, this study should be interpreted with caution because herbivory prevalence, severity, and diversity do not necessarily correlate with impact. Further research and experimentation would need to be done to draw any conclusions about the success or failure of native trees in the presence of competing introduced trees in the garden.

## Discussion

Despite the statistical insignificance of my data due to its low sample size, the 19093 leaves I collected during this study eluded to some trends and possible ramifications. First of all, the higher percentage of herbivory noted on indigenous species compared to introduced ones is indicative of preliminary findings supporting the enemy release hypothesis. There are multiple possible interpretations to my second finding that exotic trees incur more damage per leaf. Lastly, the observation of greater diversity on native trees insinuates that the presence of native trees is conducive to a more biodiverse ecological community. Insects are a key component in Parque Summit's ecosystem as they act as pollinators, pest control, nutrient cyclers, as well as a food source for many. When a larger number of orders of insects feed on a certain species of tree, it is more likely for diversity to exist in the next trophic level and so on within that ecological community. It is widely accepted that herbivorous insect diversity and plant diversity are strongly correlated (Kemp et al. 2017). Thus, supporting the growth of indigenous plants will improve biodiversity of the ecosystem as a whole.

Biodiversity conservation is essential in that it makes an ecosystem less susceptible to loss of genetic and species diversity, especially during extreme climate events or other disturbances. Such incidences are becoming ever more foreseeable given the current climate crisis, so biodiversity is of the utmost importance. Parque Summit also has an important role as

it is a part of the watershed of the Panama Canal: maintaining a biodiversity is essential in protecting the land from deforestation and erosion that comes along with the canal. Promoting a biodiverse ecosystem of flora, fauna, and rich soil nutrients in a critical area such as Panama's tropical forests helps create a negative feedback loop: when trees can grow larger and older, more carbon can be sequestered, and greenhouse gasses in the atmosphere are reduced. I recommend further studies that can work to grasp the full extent of the functionality of native plants in Parque Summit.

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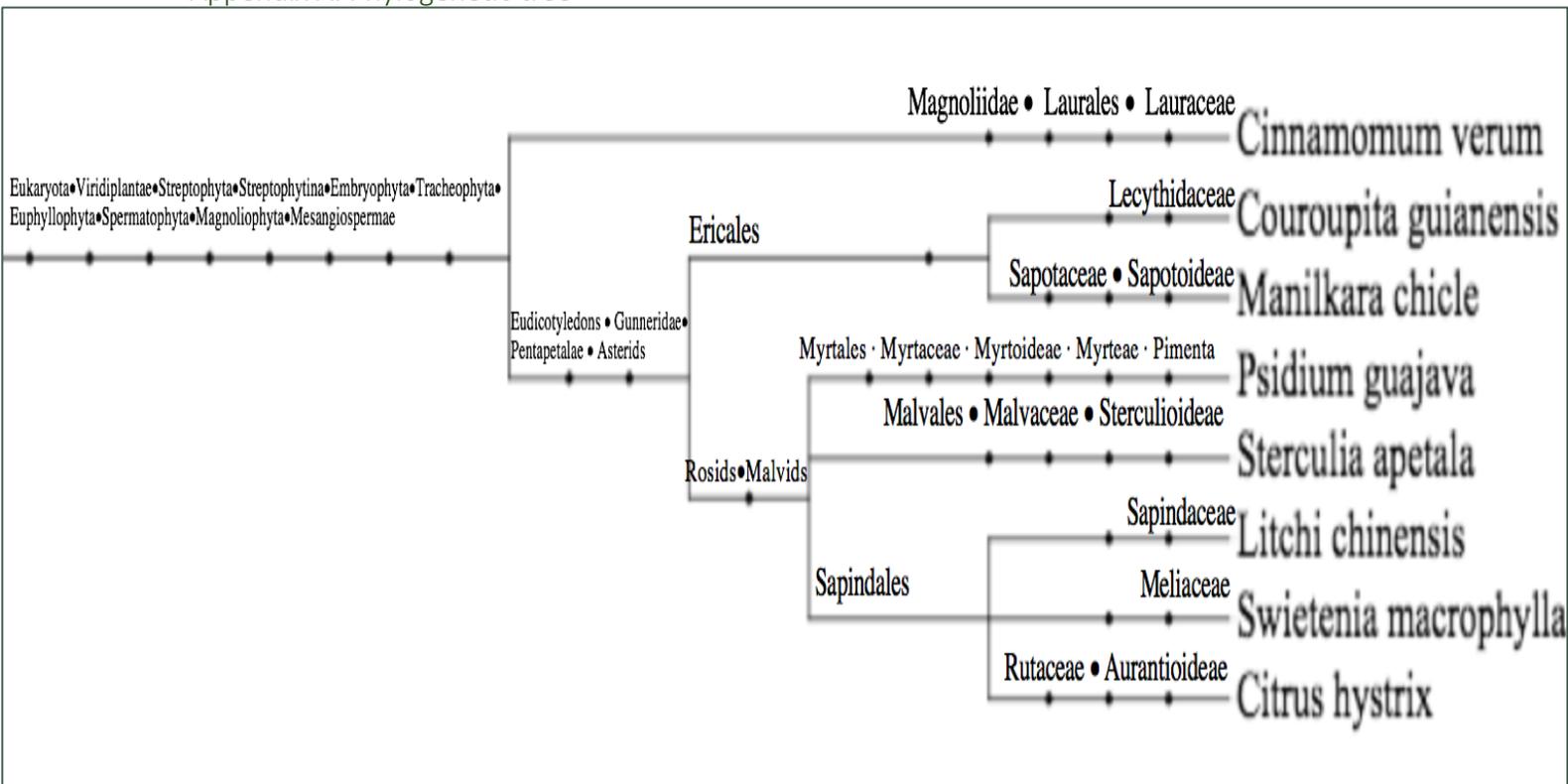
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# Appendix

## Appendix A: Phylogenetic tree



Appendix B: 2m-by-2m quadrat made with Orange Flag Tape



Appendix C: *S. macrophylla* leaf with 10% damage from Diptera



Appendix D: *M. papeda* leaf with 75% damage from Lepidoptera



Appendix E: *M. chicle* leaf with 75% damage from Lepidoptera



Appendix F: *M. chicle* leaf with 50% damage from Hymenoptera



Appendix G: *P. guajaya* leaf with 20% damage from Coleoptera



## Appendix H: Ethical certification

Proof of Ethical Certification in compliance with McGill University's Code of Ethics

**PANEL ON RESEARCH ETHICS**  
*Navigating the ethics of human research*

**TCPS 2: CORE**

## *Certificate of Completion*

*This document certifies that*

**Tessa Murray**

*has completed the Tri-Council Policy Statement:  
Ethical Conduct for Research Involving Humans  
Course on Research Ethics (TCPS 2: CORE)*

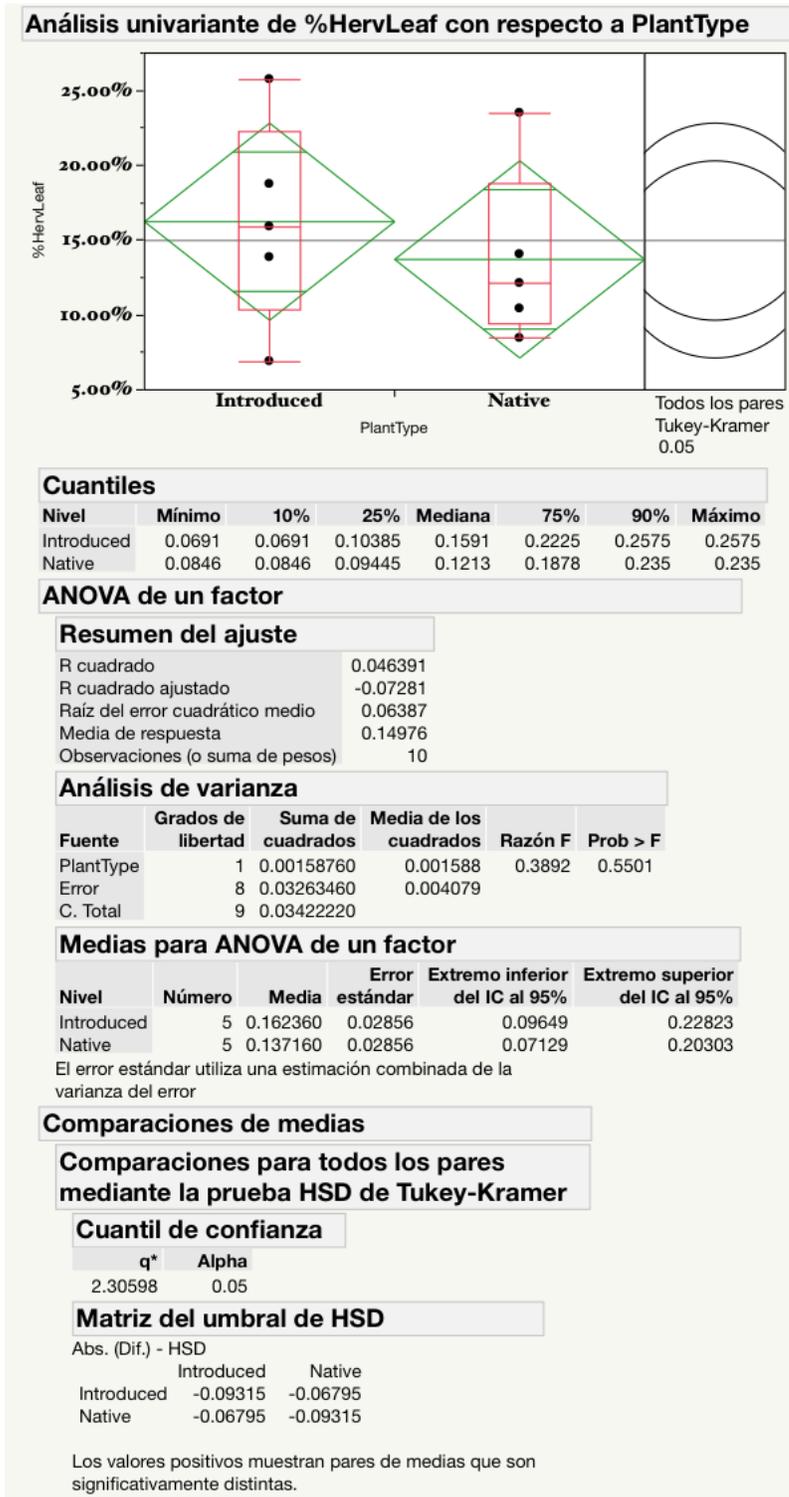
Date of Issue: **16 January, 2019**

## Appendix I: Weather data on collection days

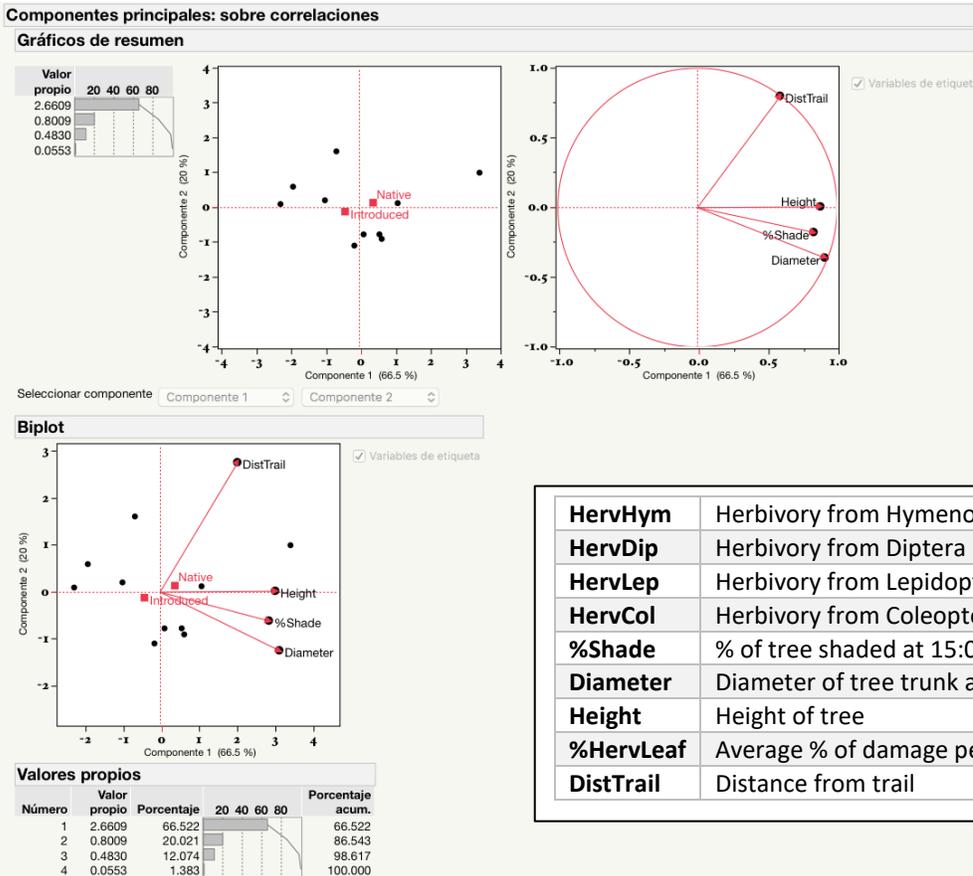
	<b>Temp (°C)</b>	<b>Humidity (%)</b>	<b>Wind (km/h)</b>	<b>Days since last rain</b>
<b>Mar 12 (count 1)</b>	31	54	N 29	1
<b>Mar 13 (count 1)</b>	33	66	N 29	0 (light rain during count)
<b>Mar 16 (count 2)</b>	34	48	N 30	3
<b>Apr 10 (count 3)</b>	32	74	S 8	3
<b>Apr 11 (count 3)</b>	30	68	S 16	4

Appendix J: JMP Analysis  
 Courtesy de Dr. Héctor Barrios

### ANOVA Analysis (% Surface Area Damaged per Leaf per Tree Type)



# Componente principal Tipo de planta y 4 variables



## Analisis de Componente Principal Herbivoria de insectos Vs Tipo de plantas

