MID-CANOPY HEIGHT AND LEAF THICKNESS ARE CORRELATED TO CATERPILLAR (LEPIDOPTERA) HABITAT CHOICE IN AN EASTERN USA, TEMPERATE, OAK-HICKORY FOREST

by

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Abstract: Mechanical and chemical plant structures are important factors in determining herbivorous insect assemblages. During the summer of 2017, 2015 caterpillars (Lepidoptera), classified as either shelter builders or exposed feeders, were collected by hand from 40 felled trees in an oak-hickory temperate forest located in Toms Brook (Shenandoah County, Virginia, eastern USA). Preserved caterpillars were identified by morphological and molecular characteristics. I explored whether there are statistical relationships between caterpillar abundance and plant mechanical traits, such as leaf thickness, leaf toughness, and relative tree height. As a group, caterpillars were concentrated in the relative middle height of each trees' canopy. Leaf thickness - but not leaf toughness - was correlated to overall caterpillar abundance. Specifically, shelter builders were more abundant on thicker leaves, and, in contrast, exposed feeding caterpillars were more abundant on thinner leaves. Whether caterpillars are shelter builders or exposed feeders, it appears that their presence within a tree varies substantially, and that this variation is related, in part, to relative canopy location and to leaf thickness. Also, these results support the hypothesis that leaves in the relative upper canopy, as defined by a relative tree height formula, experience reduced herbivory possibly due to abiotic factors, such as decreased water availability and increased exposure to UV radiation both of which reduce their nutritional content and palatability.

Key Words: leaf toughness, leaf thickness, relative tree height, Lepidoptera

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Executive Summary

This project was built on much of what I learned in my principles and methods of ecology (PME), conservation biology, and quantitative methods courses. PME taught me how to see ecosystems on a small scale. It taught me that caterpillars are vital ecosystem engineers that shape the behavior of animals across the food chain. Through what I've learned during my time with the Smithsonian, and PME, I was able to integrate my background in botany and entomology holistically. My conservation biology class was also of tremendous benefit. It helped me learn the basics of R, which was the foundation of this project. It also taught me about population dynamics, which were often apparent when monitoring the fluctuation of caterpillar incidences.

My quantitative methods class taught me the fundamentals of ecological statistics, and it eventually showed me how to apply complex equations to environmental dilemmas. This was used throughout my project, with simple formulas like relative tree height, and complex formulas involving Poisson modeling. Gaining experience in applying ecological theory to mathematical modeling is a skill that I will take with me for the rest of my professional life. If there is one thing that all three of these courses have taught me it's that environmental science truly is interdisciplinary; a complex weaving of biological sciences and advanced statistics is necessary to fully understand the impact of modern environmental problems.

Preface

I would like to thank Bryce Corrigan for his guidance in helping me navigate R. His expertise was necessary to create the best statistical models to represent my data. I would also like to credit the Smithsonian-Mason School of Conservation, Smithsonian Conservation Biology Institute (SCBI), Smithsonian National Museum of Natural History (NMNH), Czech Academy of Sciences, and Johns Hopkins University for providing the necessary resources to complete this project. I would like to thank Dr. Greg Lamarre, who helped me with the conceptualization of this project, and I would like to thank Dr. Carlo Seifert, whose caterpillar data perfectly complimented my plant data. Special credit is also reserved for other members of my Smithsonian team: these include Erika Gonzalez-Akre, Scott Miller, Vojtech Novotny, Kristina Teixeira, and Martin Volf. Mitch Catron and Ryan Fallon were of techical assistance.

Introduction

Plants have various direct defense mechanisms mediated by either mechanical protection on the plant surface (trichomes, thorns, spines, thicker leaves, etc.) and/or the production of defensive chemical compounds (terpenoids, alkaloids, anthocyanins, phenolics, quinones, etc.) to either counter or delay the effects of herbivores (Lambert et al. 2008, War 2012). Recent studies suggest that leaf mechanical traits, including toughness and trichome density, are better predictors of plant strength than percentage of oxidized phenolics (López-Carretero et al. 2016). Although leaf mechanical traits contribute significantly to defense from insect herbivores (Hanley et al. 2007), little is known about which mechanical traits contribute most to defense for different feeding guilds.

Abiotic factors have major impacts on leaf mechanical properties. (He et al. 2019) examined dominant woody species in a subtropical evergreen forest in China focusing on photosynthetic rates, mechanical properties, and leaf lifespan. Plants were assigned to two distinct categories: shade-tolerant and light-demanding species. The study's initial hypothesis stated that shade-tolerant species had higher leaf mechanical strength and leaf lifespan, yet lower photosynthetic rates than light-demanding species. This is associated with a tradeoff, in which photosynthetic capabilities are reduced to increase physical strength (Onoda et al. 2017).

The study location (Toms Brook, Virginia, eastern USA) is in a shaded area. It is full of intermediate to high shade tolerant trees including *Acer rubrum*, *Carya glabra*, *C. tomentosa*, *Cornus florida*, *Fraxinus americana*, *Nyssa sylvatica*, *Ostrya virginiana*, *Quercus alba, Q. rubra*, and *Ulmus americana* (Burns and Honkala 1990-1991). This should lead to strong mechanical biomass that records high leaf thickness and toughness.

In tropical systems, leaf toughness increases with tree height and plants adapt to herbivory and environmental stress by strengthening physical and chemical defense systems. Leaves in the upper canopy are consistent with adaptation to physically stressful conditions, such as high herbivore pressure and strong light; this results in the development of high cell wall thickness (Kenzo et al. 2022). Leaves with high toughness are often characterized by having low water content, thick cell walls, and hardness or stiffness (Nardini 2022). Chewing on tougher leaves is not energy efficient, as the physical and diluting effect of cell walls deter herbivores. Additionally, toughness has been shown to slow nutrient intake and assimilation, both of which are crucial to herbivore performance and survival (Clissold et al. 2009). Tough leaves give plant protection to herbivore pressures and physically stressful environments, such as strong wind and precipitation (Onoda et al. 2011). Leaf toughness has been found to vary by height. In the forest canopy, increased toughness may be a contributor to plant protection since herbivore pressure and physical stress would be higher than it would in the forest understory (Yoneyama and Ichie 2019). For example, in a study involving 103 trees in a tropical rainforest in Malaysia it was found that leaves became tougher in the upper canopy (Kenzo et, al 2022). This might suggest that, as relative tree height increases, so does leaf toughness.

Similar results were found in temperate systems. In another study examining resistance and tolerance to herbivory in eleven tree species in a temperate forest it was found that traits related to the physical reinforcement of leaves (leaf toughness and fiber content) were negatively associated with herbivory. Conversely, it was found that chemical defenses including secondary metabolites (flavanols, gallic acid, tannins, and terpenoids) were not associated with reduced herbivory (Salgado-Luarte 2022). The strength of plant adaptations is often attributed to resistance-tolerance trade-offs. This assumes finite resource allocation for both physical and chemical defenses. Consequently, it has resulted in an optimization of resistance at the expense of tolerance, or vice versa (Mauricio et al. 1995). It is common for plants to implement a mixed defense strategy, one which seeks a balance between the two to maximize plant fitness. This study isolated the physical defense component of resistance-tolerance trade-off. Physical traits tend to be less costly to produce long-term, and they have also been observed to be more effective in deterring herbivory (Carmona et al. 2011).

Leaf thickness is a quantitative characteristic associated with the ability of plants to occupy dry, high irradiance environments. Thick leaves maintain water potential in droughts (Coneva and Chitwood 2018). Thickness is determined by plant anatomy, which includes the number, size, and arrangement of leaf cells that differ among species (Giuliani et al. 2013). Leaf thickness, along with toughness, is a function of leaf structural traits, which often vary by species and leaf position on the plant (Afzal et al. 2017). Factors such as light exposure, temperature, and age can all alter thickness measurements. The factors in this study will present varying levels of shade in summer, high temperatures, and aged (mature) leaves. Factors like leaf lifespan have been positively correlated with cellulose and toughness in shade-tolerant trees (Kitajima et al. 2012). Additionally, toughness, measured as punch resistance, and cellulose content were determined to be the two best traits in explaining species difference in herbivory rates and leaf lifespan amongst 46 tropical tree species (Coley 1983).

In this study, I tested the hypothesis that increased leaf height in the canopy as well as increased leaf mechanical defenses (leaf thickness and leaf toughness) are inversely correlated with herbivore abundance.

Methods

Herein, I present a comprehensive canopy sampling of indicators of leaf strength, leaf toughness and thickness, among 16 sympatric tree species native to the eastern USA (Table 1), aiming to explore the relationship between insect herbivory and leaf mechanical defenses on a vertical scale. Specifically, I focused on investigating: 1) the correlation between leaf mechanical traits and insect occurrence and 2) the significance of structural characteristics such leaf thickness and leaf robustness on leaf herbivory vertical stratification.

Table 1. Species of tree, average number of leaves collected per species, and percentage of the total leaves collected in this study.

Species, authority (number of trees examined)	Interval samples	Average number of leaves	Percent of the total leaf examined
Quercus alba Linnaeus (5)	3, 8, 8, 8, 10	370	19.6%
Carya tomentosa Sargent (8)	2, 3, 3, 4, 4, 5, 6, 6	330	17.4%
Quercus rubra Linnaeus (5)	5, 5, 5, 6, 8	290	15.3%
Acer rubrum Linnaeus (3)	3, 6, 9	180	9.5%
Fraxinus americana Linnaeus (3)	4, 5, 5	140	7.4%
Carya glabra Miller (2)	4, 6	100	5.4%
Prunus serotina Ehrhart (2)	4, 5	90	4.8%
Quercus montana Willdenow (1)	7	70	3.7%
Ulmus americana Linnaeus (2)	3, 3	60	3.2%
Amelanchier arborea (F. Michaux) Fernald (2)	3, 3	60	3.2%
Sassafras albidum (Nuttall) Nees (2)	2, 3	50	2.6%
Ostrya virginiana (Miller) K. Koch (1)	4	40	2.1%
Quercus velutina Lamarck (1)	4	40	2.1%
Nyssa sylvatica Marshall (1)	3	30	1.6%
Cornus florida Linnaeus (1)	2	20	1.1%
Prunus avium Linnaeus (1)	2	20	1.1%

This sampling effort falls within the scope of a global project on plant-herbivore food webs (Volf et al. 2017, Novotny 2010) where a selective group of insect feeders (Lepidoptera) are thoroughly sampled on a vertical profile.

Study site

The study was conducted in two forested 0.1 ha plots in Toms Brook, Virginia, USA (38°55.548' N, 78°25.465' W) located in an agricultural setting in the Shenandoah Valley with intense logging in the surroundings through the year (Figures 1 and 2). Mean annual temperature and precipitation in this region is 4.9 °C and 879 mm, respectively (Burton et al. 2012). Each sampled tree was given an ID number based off the initials of its scientific name and the number of which that species was felled (AR-08 stands for *Acer rubrum*, the eighth tree felled etc.). Data was collected from June 5th through August 8th, 2017.

Figure 1. Map of the United States. The study was conducted in Toms Brook, Virginia (red dot).

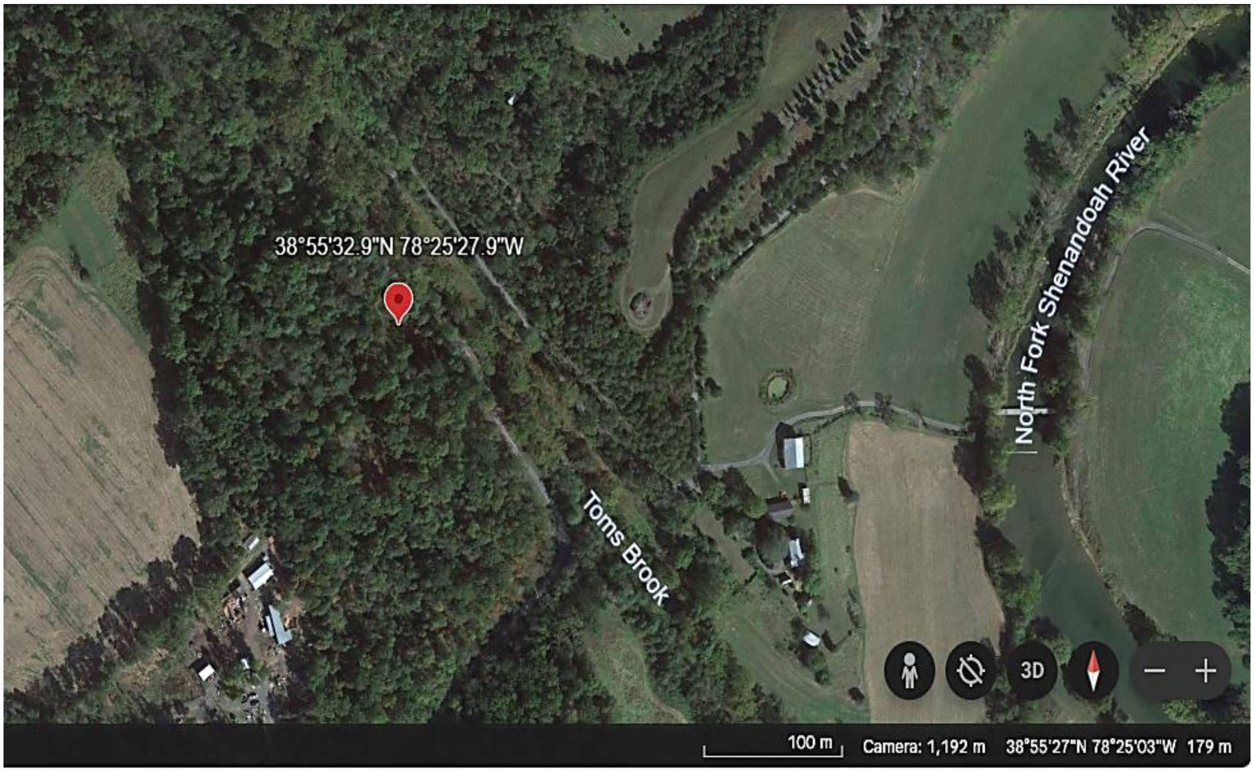

Figure 2. Google Earth image of the site location of Figure 1.

Leaf sampling and crown measurements

Through a series of coordinated tree felling with a local logging company I measured total tree height, diameter at breast height (DBH), height and width of crown (defined at the start of the first major branch up to the treetop), estimated total leaf area and leaf biomass (following Volf et al. 2017), and estimated total insect leaf herbivory. Leaves were collected between June and August 2017 from 40 trees ranging between 6.7 and 30.7 m height. I sampled leaves at uniform intervals (2 m) from base to top of the tree crown. For each individual tree, 10 individual mature leaves or leaflets (fully expanded and structurally developed) were randomly collected at each height interval (modified from López-Carretero et al. 2016) summing 30 to 100 leaves per tree depending on tree height. Multiple branches at the same interval were randomly sampled to compensate for potential data variability from factors such as light and water stress. The thickness and toughness measurements for these leaves were not done on each individual leaf a caterpillar was found. Leaves were sealed in plastic bags and fresh processed the same day of collection or stored overnight at 2°C and allowed to reach room temperature before measuring traits. 1,890 total leaves were collected.

Leaf mechanical traits

I measured leaf thickness (mm) using a digital caliper (Figure 3, Mitutoyo 500-196-30, accuracy ±0.001”/0.02 mm, Mitutoyo, Kawasaki, Japan) on each lamina close to the apex, avoiding primary and secondary leaf venation. Uniform measurements were taken near the top left of each leaf, to assure minimal variation. Measurements were repeated on a measured leaf if a significant outlier was recorded. Ten leaves were sampled, and each height interval was recorded as the average of all ten specimens, in order to assure higher accuracy.

Figure 3. Pictured above is the Mitutoyo 500-193-30 Digimatic Caliper -CD-12"ASX digital caliper (Aurora, Illinois, USA).

To estimate leaf toughness, I applied the punch test using a Mecmesin BFG 500N force gauge (Figure 4, TE, Long Branch, USA) (attached to a Mecmesin lever-operated test stand (ValuTest-L model) (TE, Long Branch, USA). Two sections of the tissue in each of the 10 leaves were sampled between the main vein and the margin in the apical region in the adaxial surface; the measurements were then averaged. Consistent force was applied with the lever during each tissue cut to assure that the data was not skewed.

Figure 4. Pictured above is the Mecmesin force gauge (BFG, stand not illustrated; Mecmesin, Sterling, Virginia, USA).

Insect collection

A total of 2015 caterpillars, across 40 individual trees, belonging to 123 taxa (113 identified to species and 10 identified only to genus), were collected throughout all our leaf samples. Caterpillar taxonomy was recorded along with feeding guilds. In all, 2015, caterpillars were examined providing an overall glimpse of insect diversity, regardless of their location on the tree (Appendix 1).

Figure 5. Common caterpillars collected in this study. A. *Psilocorsis reflexella* (image by Dotted Leaftier, *Psilocorsis reflexella*, caterpillar, on F… | Flickr. B. *Machimia tentoriferella* (image by Colin Gillette gold-striped leaftier | Colin Gillette | Flickr) that became the dominant species in the exclusionary models. C. *Symmerista albifrons* (image by Kim Fleming, Red-humped Oakworms | *Symmerista canicosta* or *Symmerista alb*… | Flickr. D. *Anisota senatoria* (image by Cody Hough, *Anisota senatoria* | Orange-tipped Oakworm (*Anisota senatoria*… | Flickr). Images retrieved from Flickr and used by permission of the photographers.

Once the caterpillars were captured, they were separated into two different feeding guilds - exposed feeders and shelter builders. Exposed feeders were defined as caterpillars living free on the foliage. Shelter builders were defined as leaf rollers, leaf tier, or webbers (Seifert et al. 2020). Total incidences were also recorded and modeled; this is defined as the basic presence of caterpillars. The tree species and number were recorded with each extraction. Relative tree height was generated to address major tree size differences. This was particularly effective when comparing tall trees like *Quercus alba* and small trees like *Cornus florida*. Relative tree height utilized the mean tree height per height interval; this allowed much smaller trees to have their thickness and toughness values more evenly distributed. The date of sampling, tree height at the point of extraction were also included. The insects were sampled via tree felling. Tree felling presented a significant limitation on insect extraction; much of the larvae was lost in the process due to the collision with the ground. However, this method does possess an advantage over conventional methods like canopy cranes – increased maneuverability.

Rank abundance

Rank abundance curves were generated using Excel to display which species were most prominent.

Vertical insect abundance

Insects typically prefer younger leaves. They are usually softer, with higher nutrient quality, but sometimes this is complicated due to higher levels of chemical defense (Coley 1983). Mature leaves' physical qualities often make the energy cost too high for herbivores to invest in. Higher canopy leaves have several qualities that increase the likelihood of deterring herbivores, largely due to their increased sun exposure: they include thicker, tougher, of lower water content, and possess higher concentrations of secondary metabolites than leaves developing in the shaded understory (Murakami et al. 2005). Lepidoptera were collected from leaves, branches, and stems immediately after the tree felling. Sampled caterpillars were morphotyped, photographed, and stored in ethanol to allow for later DNA barcoding; this is how species identification was determined (Seifert et al. 2020).

Chemical defenses must be acknowledged when considering insect herbivory on smaller, less developed leaves. Younger leaves are targeted more heavily by both temperate and tropical insect herbivores, suggesting a trend that transcends ecosystems (Coley and Barone 1996). Given their anatomical deficiencies, young leaves are more likely to invest in chemical defenses than mechanical ones. Consequently, secondary chemicals tend to be much more highly concentrated in young leaves than mature ones. Observations tend to show a pattern of simultaneous increases in leaf toughness and decreases in secondary chemical concentration. Generalists are more sensitive to secondary chemicals than specialists, which may encourage larger caterpillars to select leaves that have lower concentrations, regardless of nutrient content or mechanical defenses (Barton et al. 2019). Throughout the course of this study, it was discovered that exposed feeders were much more common than shelter builders. This might indicate that feeding requires less energy than shelter building.

Exclusionary models

Psilocorsis reflexella, *Symmerista albifrons*, and *Anisota senatoria* were the most common caterpillar species collected. These three species would be excluded in caterpillar abundance models, to remove species that could potentially skew the results. *Psilocorsis reflexella* is mainly found on oaks, which is their preferred host. This explains their high abundance pattern, since most of the trees sampled in this study were oaks. *Symmerista albifrons* are highly gregarious caterpillars, especially in their first instars; this is why they are so numerous in their tree presence. *Anisota senatoria* is also heavily reliant on oaks, which explains its heavy incidence as well.

Machima tentoriferella is a highly polyphagous species, and it became the main species driver after the exclusion. This versatility was reflected in our study – *Quercus rubra*, *Quercus velutina, Quercus alba*, *Fraxinus americana*, *Carya glabra*, *Carya tomentosa*, *Prunus serotina, Nyssa sylvatica*, *Cornus florida*, *Acer rubrum*, *Amelanchier arborea*, *Prunus avium*, *Quercus montana*, and *Ostrya virginiana* were all hosts to this species, totaling 14 out of the 16 possible species.

Data analyses

Statistical analyses were conducted using R software (R Development Core Team 2023). A Generalized Linear Model (GLM) analysis was used to identify the significance and strength of the relationship between leaf thickness, leaf toughness, and relative tree height, amongst three caterpillar categorizations – overall, exposed feeders, and shelter builders. GLM was deemed more effective than a Linear Model (LM) since it allowed for Poisson modeling, which is helpful with count data and makes it easy to run a regression (Penn State University 2018, no date; van

Oijen 2020). Every individual caterpillar represented a count. All caterpillar counts were estimated under the parameter of a 2-meter height interval. All host plant species were included in this generalized model. For leaf mechanical traits, a line of best fit was included to establish a clear indication of the strength of the relationship between two variables amongst the scatter plots. Incidence rate ratio (IRR), confidence interval, and p-values were run for total incidence, exposed feeder, and shelter builder for leaf thickness, toughness, and relative tree height. Incidence rate ratios compare incident rates between two different groups. It provides a metric to explain if exposure to a variable (tree species) increases or decreases the rate of some incidence (caterpillar count). Confidence interval describes the probability that an estimate falls between a certain percentage. A narrower confidence interval indicates stronger, more reliable data. A p-value is a probability score that determines the statistical significance of an observed effect. A p-value less than 0.05 indicates statistical significance. When running the GLM models, the caterpillar total dipped from 2,015 to 1,743; this was due to the relative tree height formula establishing lower and upper bound limitations, this will be explained further in the limitations section. The plant data was unaffected by this change. The code, in R, used in this research is included in Appendix 2.

Botanical specimens overview

This study shows that foliage further on the canopy displays greater leaf toughness and thickness due to increased exposure to abiotic factors such as UV radiation and precipitation. Subsequently, this study, in combination with data from a previous study (Seifert et al. 2020), indicates that the abundance of Lepidoptera inversely correlates with canopy height. Studies suggest that caterpillars are deterred by thick cuticles and tough leaf margins (War 2012). Therefore, herbivory will be much more frequent on lower lying leaves that are on average thinner and softer. Furthermore, tree species that have smooth leaf margins, such as *Carya tomentosa* should be less resistant to insect predation than tough leaf margin species like *Quercus alba* (Powell et al. 2022). *Quercus* and *Carya* were the most abundant tree genera with *Quercus alba* and Carya *tomentosa* being the most common species sampled (Table 1).

There was a total of 1,890 individual leaves collected. *Quercus* is among the most common genera of trees in Virginia, which lessens the concerns of their high representation in this study. *Carya is* one of the most common genera in Virginia, so its high presence is also of reduced concern. *Acer,* although not to the extent of *Quercus* and *Carya,* is another one of the more common genera of trees in Virginia, and their sampling size reflects that. *Fraxinus*, although once incredibly abundant, have had entire populations decimated by the Emerald Ash Borer, *Agrilus planipennis* Fairmaire, 1888 (Coleoptera: Buprestidae), in this past decade (Anonymous 2023a). Despite this, it was of average abundance in this forest. *Prunus* also displayed average abundance. *Nyssa, Ostrya, Amelanchier*, *Sassafras*, *Cornus*, and *Ulmus* are lesser common genera in the state of Virginia, so their minimal representation is not of concern. There are several reasons attributed to their lower abundance. *Ulmus,* for example, was once incredibly common throughout the state of Virginia, but that was before Dutch Elm Disease affected their mortality rate (Brasier and Buck 2001). *Sassafras* is common in the Shenandoah Mountain region. However, *Sassafras* is often smaller and struggles to find the light exposure needed to grow into mature trees (Anonymous 2015). They typically reach maturity by growing in forest gaps, which eliminates the shade provided by dense canopies.

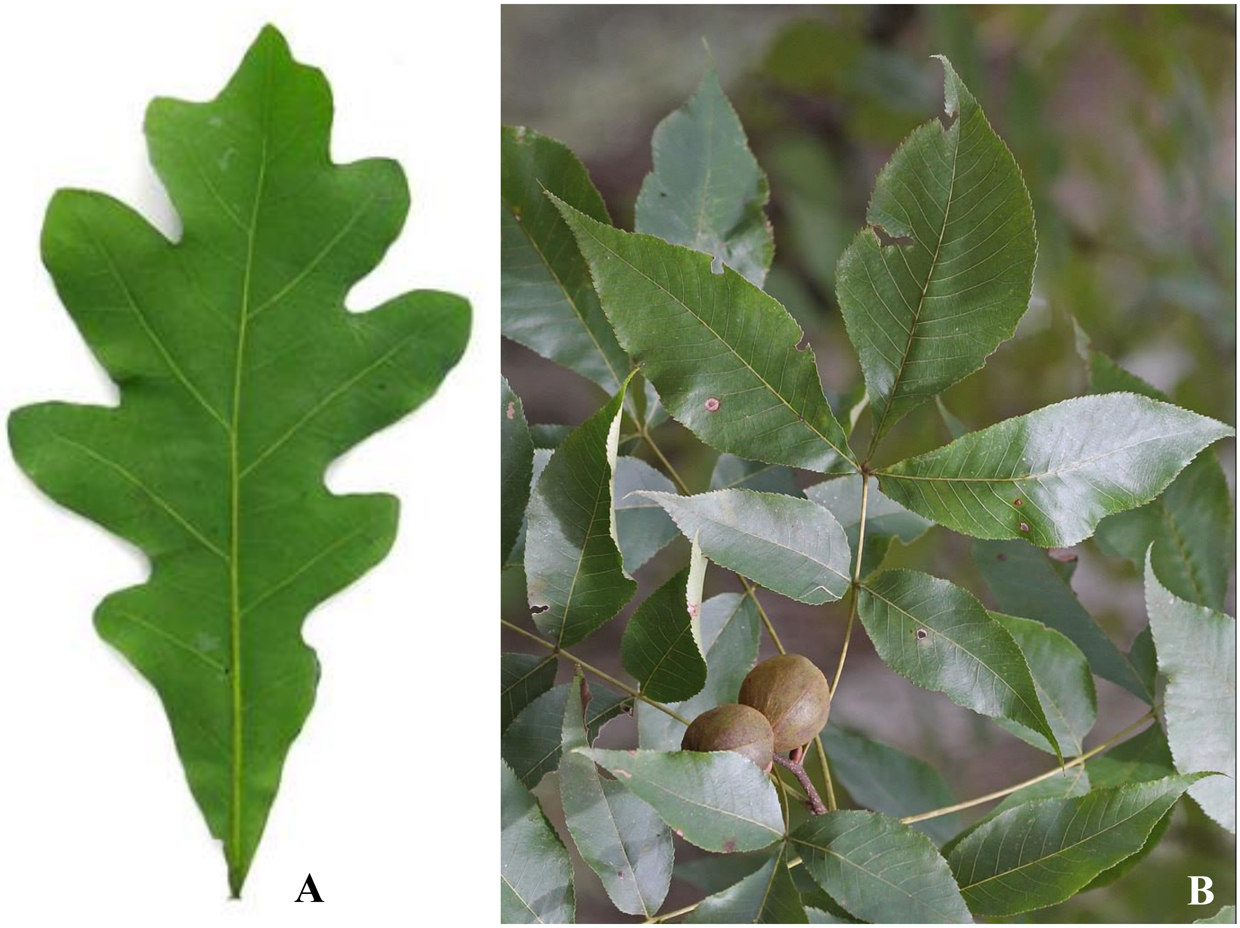

Figure 6. A. Leaf of *Quercus alba,* https://www.flickr.com/photos/evelynfitzgerald/3928463012 . B. Leaf of *Carya glabra*, another common species at the study site, https://www.flickr.com/photos/38514062@N03/15136237414.

Host-plant records

The relationship between herbivores and host plants can reflect the quality of plants as food sources. Plant nutrient composition (Scriber and Feeny 1979), defenses (Courtney 1981), and phenology (Wood and Keese 1990) all play major roles in determining herbivore assemblages. Furthermore, it has been shown that parasitism of specific species of Lepidoptera is highly host-plant dependent. This would indicate that the pattern of host-plant interactions could be species specific among caterpillars and that certain species of parasitoids could further modulate these insect – host plant interactions tree species (Lill and Ricklefs 2002).

Results

New host plant records

During this study, three new host plants records for the family Tortricidae were discovered. *Acleris chalybeana* (Fernald, 1882) was found on *Acer rubrum*. This is a new host plant record for the United States and Canada. *Acleris comariana* (Lienig and Zeller, 1846) was also found on *Acer rubrum*. This is a new host plant record for the entire United States. *Gretchena deludana* (Clemens, 1864) was found on *Carya glabra.* This is a new host plant record for the eastern United States.

Effect of leaf thickness, leaf toughness, and relative tree height on caterpillar distribution

Figures 7 to 9 are generalized linear models that represent an estimate of caterpillar abundance in two-meter intervals on the tree canopy across three different variables: leaf thickness, leaf toughness, and relative tree height. Counts (y axis) are total caterpillar abundance (Figure 7), exposed feeder abundance (Figure 8), and shelter builder abundance (Figure 9). Tick marks (x axis) represent individual counts in the original data (1,743) for a variable (leaf thickness, leaf toughness, relative tree height, respectively). Each tick represents a one caterpillar.

Figure 7 represents the total number of all caterpillars (exposed feeders and shelter builders) that occur through the estimation at every two meters height intervals for average leaf thickness.

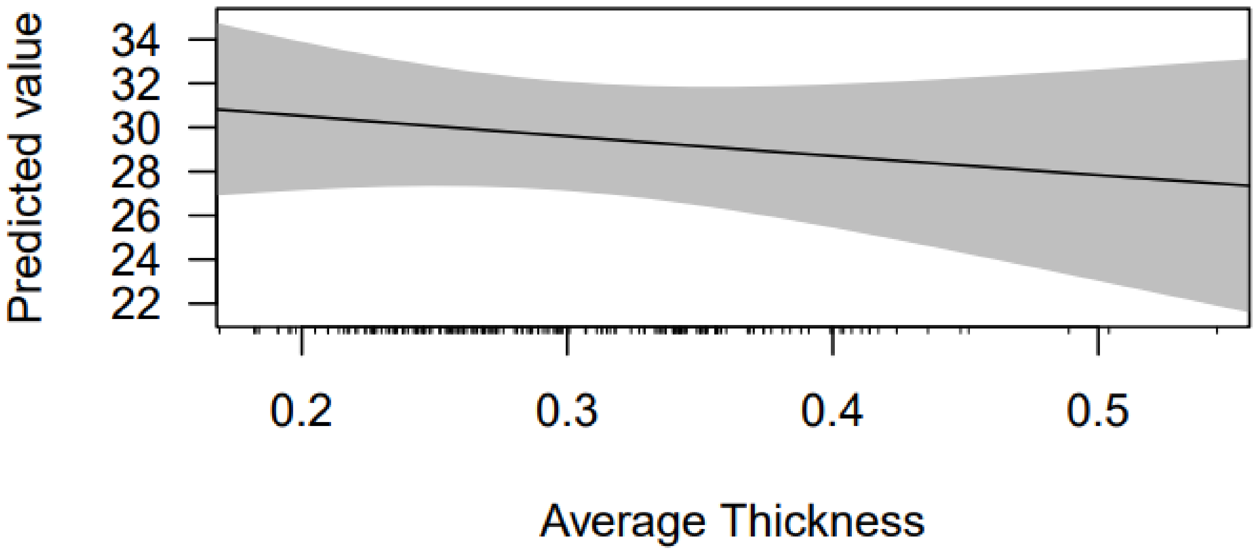

Figure 7. Estimated abundance (predicted value) of all caterpillars by average leaf thickness every two meters height interval estimation. Gray area represents the 95% confidence interval. The dark line represents the line of best fit. The $p = 0.418$, suggesting that there is no significant statistical relationship between leaf thickness and overall caterpillar abundance.

Figure 8 represents the total number of caterpillars (exposed feeders and shelter builders) that occur through the estimation at every two meters height intervals of average leaf toughness.

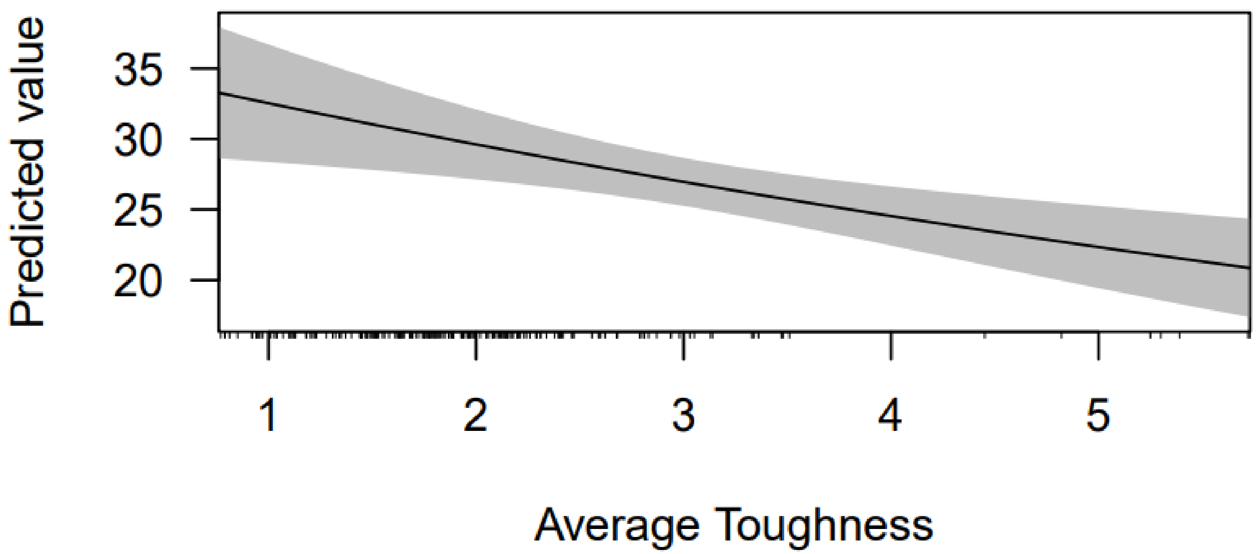

Figure 8. Estimated abundance (predicted value) of all caterpillars by average leaf toughness every two meters height interval estimation. The gray area represents the 95% confidence interval. The dark line represents the line of best fit. The p = 0.001, suggests that there is a significant statistical relationship between leaf toughness and overall caterpillar abundance.

Figure 9 represents the total number of caterpillars (exposed feeders and shelter builders) that occur through the estimation at every two meters height intervals of relative tree height.

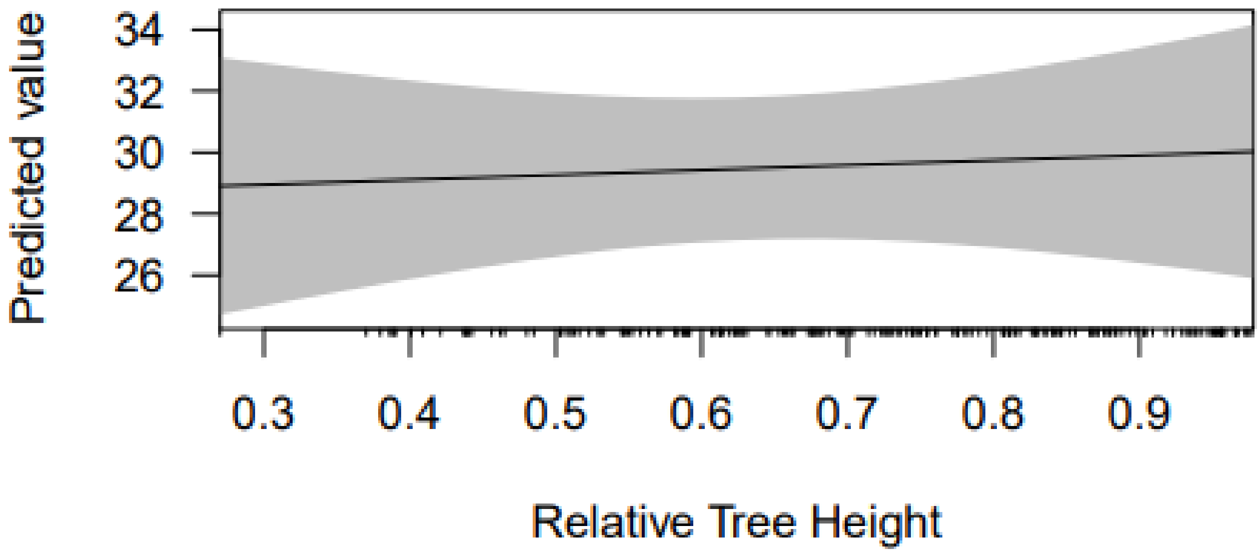

Figure 9. Estimated abundance (predicted value) of all caterpillars by relative tree height every two-meter height interval estimation. The gray area represents the 95% confidence interval. The dark line represents the line of best fit. The $p = 0.750$ suggests that there is no significant statistical relationship between relative tree height and overall caterpillar abundance.

In Figures 10 to 12, I present the exposed feeder models. This represents the overall abundance of exposed feeding caterpillars that occur at every two meters height interval estimation across three variables (leaf thickness, leaf toughness, and relative tree height).

Figure 10 represents the total number of exposed feeding caterpillars that occur through the estimation at every two meters height interval of leaf thickness.

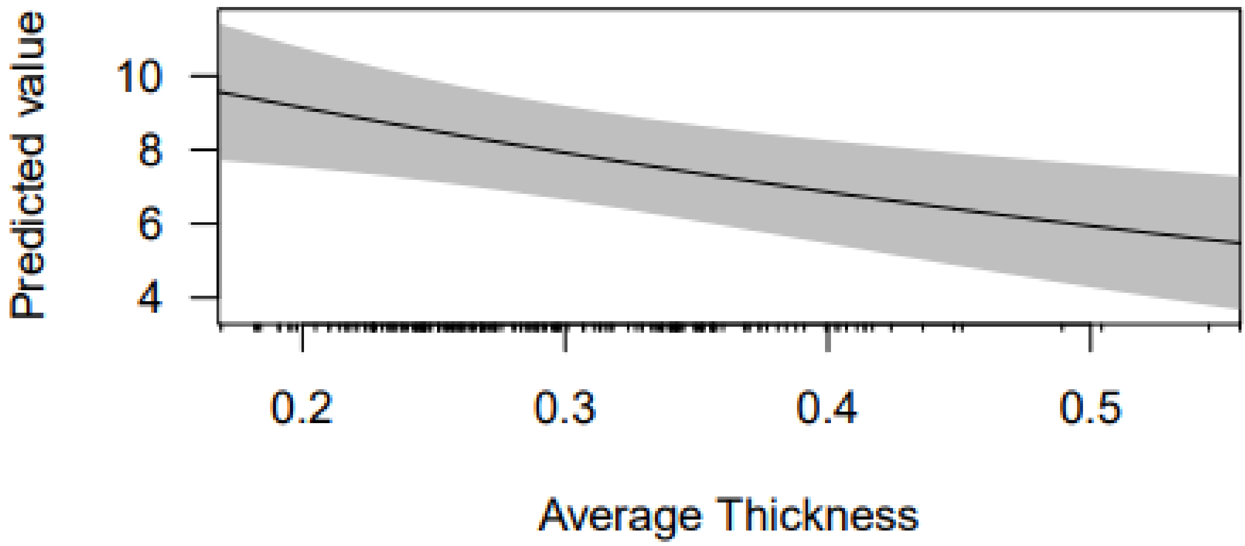

Figure 10. Estimated abundance (predicted value) of all exposed feeding caterpillars by average leaf thickness every two-meter height interval estimation. The gray area represents the 95% confidence interval. The dark line represents the line of best fit. The $p = 0.006$, suggests that there is a significant statistical relationship between leaf thickness and exposed feeder caterpillar abundance.

Figure 11 represents the total number of exposed feeding caterpillars that occur through the estimation at every two meters height interval of leaf toughness.

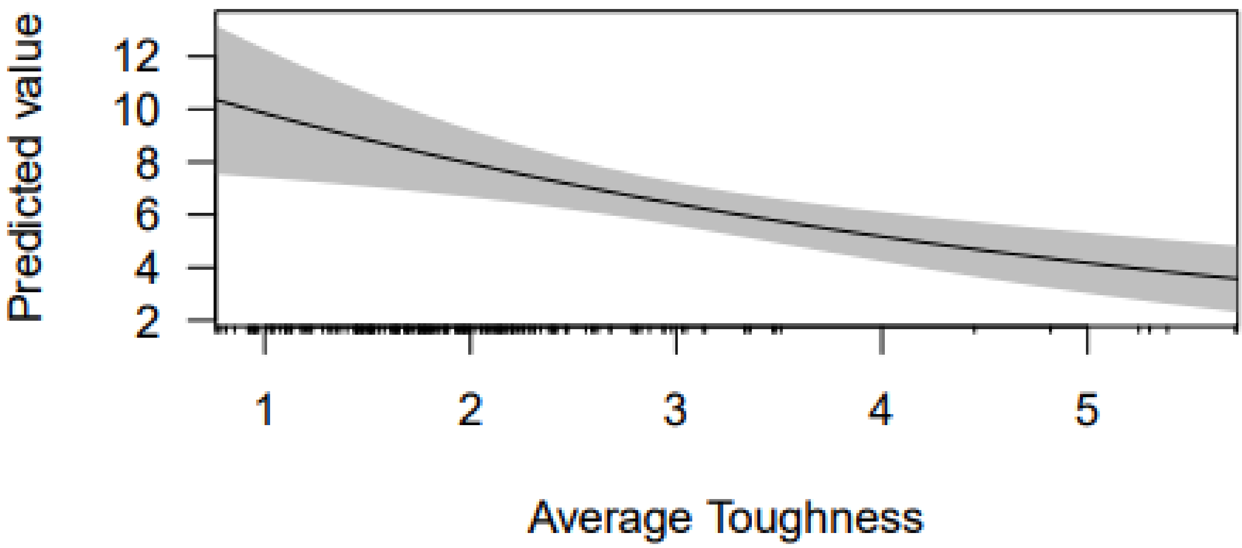

Figure 11. Estimated abundance (predicted value) of exposed feeding caterpillars by average leaf toughness every two meters height interval estimation. The gray area represents the 95% confidence interval. The dark line represents the line of best fit. The p = 0.001 suggests that there is a significant statistical relationship between leaf toughness and caterpillar abundance.

Figure 12. represents the total number of exposed feeder caterpillars that occur through the estimation at every two-meter height interval of relative tree height.

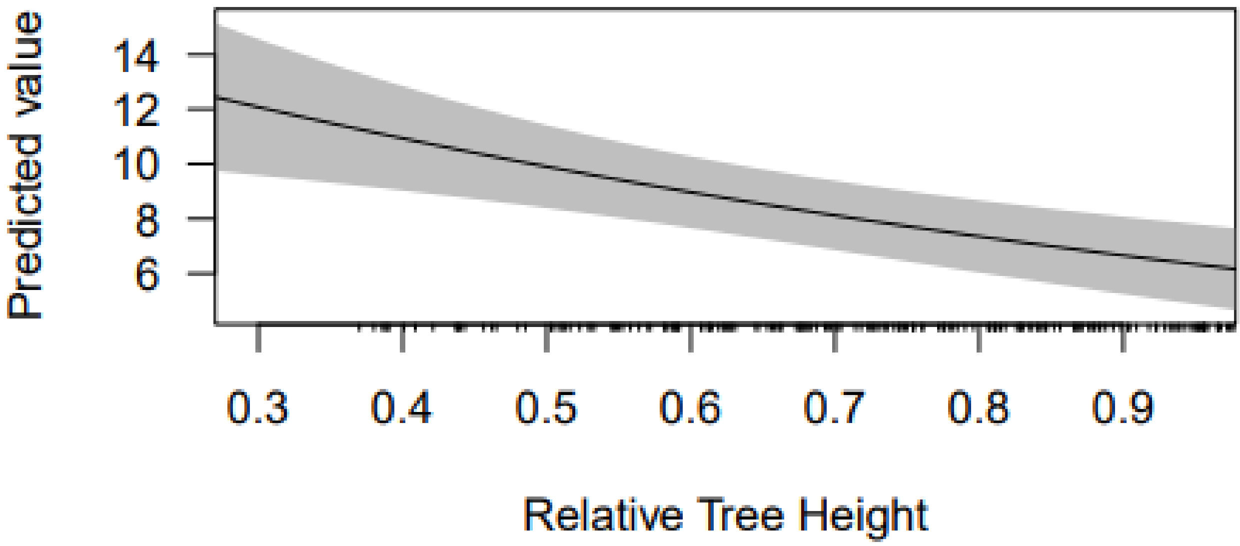

Figure 12. Estimated abundance (predicted value) of exposed feeding caterpillars by average relative tree height every two-meter height interval estimation. Gray area means 95% confidence interval. Dark lines mean line of best fit. The $p = < 0.001$ suggests that there is a significant statistical relationship between relative tree height and caterpillar abundance.

In Figures 13 to 15, I present the shelter builder models. This represents the abundance of shelter building caterpillars that occur at every two-meter height interval estimation across three variables (leaf thickness, leaf toughness, and relative tree height).

Figure 13 represents the total number of shelter building caterpillars that occur through the estimation at every two-meter height interval of leaf thickness.

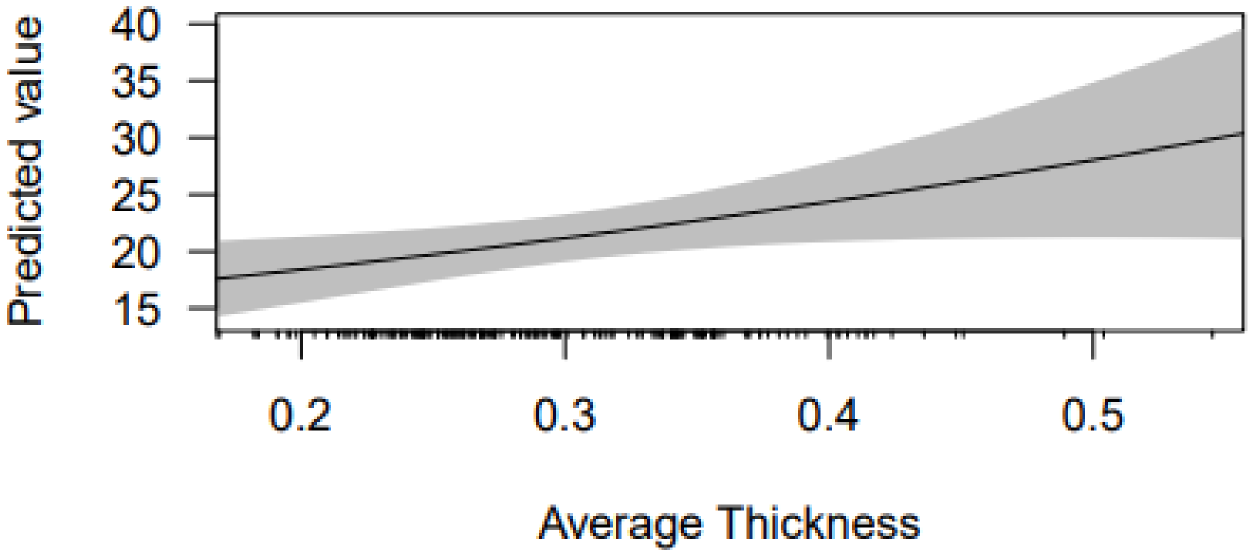

Figure 13. Estimated abundance (predicted value) of shelter building caterpillars by average leaf thickness every two-meter height interval estimation. The gray area represents the 95% confidence interval. The dark line represents the line of best fit. The p = 0.017 suggests that there is a significant statistical relationship between leaf thickness and caterpillar abundance.

Figure 14 represents the total number of exposed feeding caterpillars that occur through the estimation at every two-meter height interval of leaf toughness.

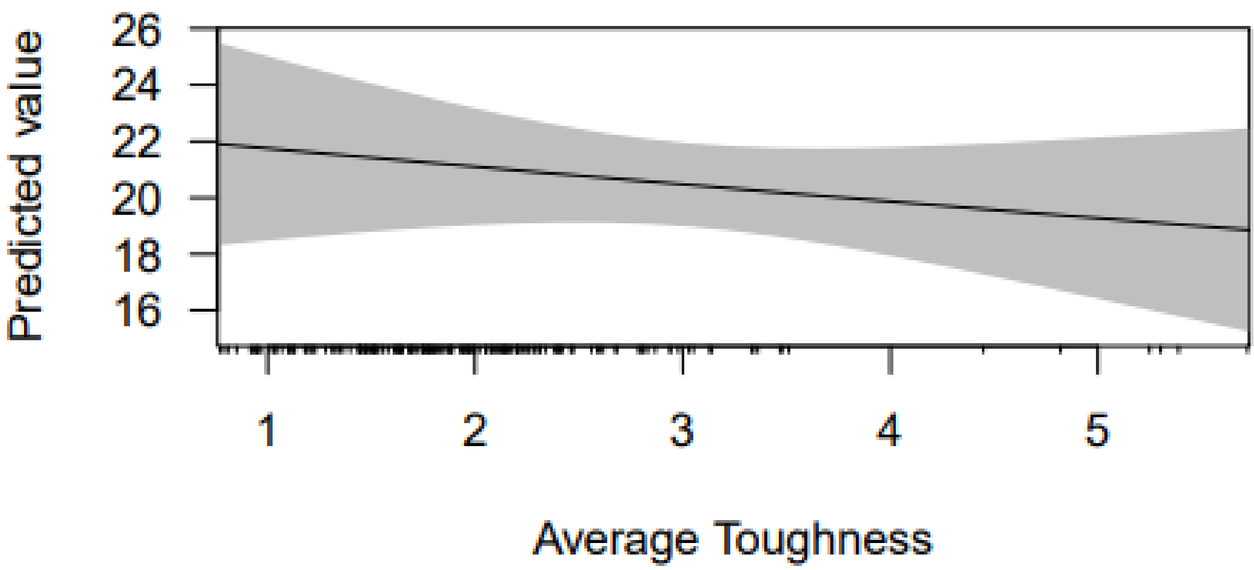

Figure 14. Estimated abundance (predicted value) of shelter building caterpillars by average leaf toughness per two-meter height interval estimation. The gray area represents the 95% confidence interval. The dark line is the line of best fit. The $p = 0.365$ suggests that there is no significant statistical relationship between leaf toughness and caterpillar abundance.

Figure 15 represents the total number of shelter building caterpillars that occur through the estimation at every two-meter height interval of relative tree height.

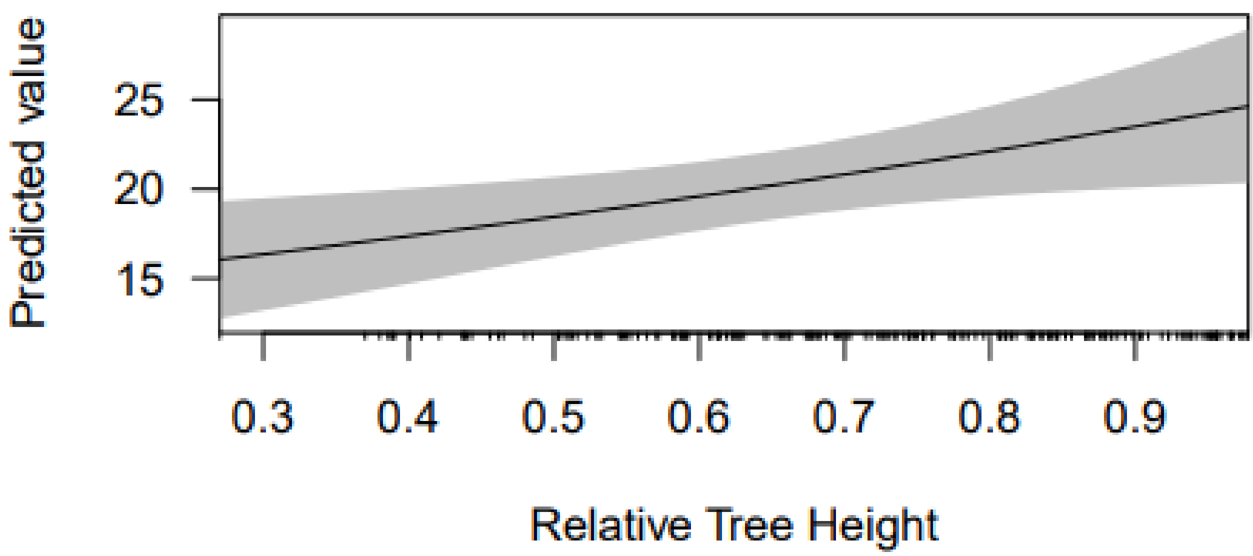

Figure 15. Estimated abundance (predicted value) of shelter building caterpillars by relative tree height every two-meter height interval estimation. The gray area represents the 95% confidence interval. The dark line is the line of best fit. The p = 0.011 suggests that there is a significant relationship between relative tree height and caterpillar abundance.

Generalized Linear Models (GLM)

A generalized linear model (GLM) is a generalization of a linear regression. It provides a framework for comparing how several variables affect different continuous variables. A GLM includes multiple linear regressions.

Table 2 provides the results of an overall incidence model. A confidence interval that does not include 1 indicates statistical significance. This is the case with leaf toughness (CI = 0.86-0.96), which had a p = 0.001. An incidence rate ratio lower than one indicates that the incidence of caterpillars is lower in that species of tree or leaf attribute. Oak trees (*Quercus alba*, *Q. montana*, *Q. rubra*) appeared to have the highest IRRs, this reflects their dominance amongst caterpillar inhabiting tree species.

The R^2 Nagelkerke is a measure of the goodness of fit of a logistic regression model. It covers a full range from 0-1. Values closest to 1 represent ideal models. This is a perfect model with perfect goodness of fit.

Table 2. Overall caterpillar incidence model.

	incidence		
Predictors	*Incidence Rate Ratios*	*CI*	*p*
Average Thickness	0.74	0.35 – 1.53	0.418
Average Toughness	0.91	0.86 – 0.96	**0.001**
Relative Tree Height	1.06	0.76 – 1.47	0.750
Amelanchier arborea	0.46	0.17 – 1.00	0.073
Carya glabra	2.74	1.81 – 4.17	**< 0.001**
Carya tomentosa	0.58	0.37 – 0.90	**0.015**
Cornus florida	0.87	0.26 – 2.18	0.798
Fraxinus americana	1.08	0.67 – 1.72	0.749
Nyssa sylvatica	2.94	1.64 – 5.06	**< 0.001**
Ostrya virginiana	0.69	0.26 – 1.50	0.390
Prunus avium	0.48	0.08 – 1.57	0.313
Prunus serotina	1.58	0.97 – 2.54	0.062
Quercus alba	14.50	10.56 – 20.50	**< 0.001**
Quercus montana	3.50	2.29 – 5.38	**< 0.001**
Quercus rubra	7.74	5.64 – 10.94	**< 0.001**
Quercus velutina	0.48	0.14 – 1.19	0.159
Sassafras albidum	0.27	0.06 – 0.74	**0.029**
Ulmus americana	0.38	0.13 – 0.87	**0.040**
Observations	189		
R^2 Nagelkerke	1.000		

Table 3 provides the results of an overall exposed feeder incidence model. A confidence interval that does not include 1 indicates statistical significance; this is the case with leaf toughness (0.72-0.91), which had a p-score of (< 0.001). An incidence rate ratio lower than one indicates that the incident rate of caterpillars is lower in that species of tree or leaf attribute. Oak trees (*Quercus alba*, *Q. rubra*) and *Nyssa sylvatica* (IRR = 4.15) appeared to have the highest IRRs, this reflects their dominance amongst caterpillar inhabiting tree species. An R^2 value was nearly identical to one – indicating good strength of fit.

Table 3. Exposed feeder caterpillar model

	exposed_feeder		
Predictors	*Incidence Rate Ratios*	*CI*	*p*
Average Thickness	0.24	0.09 – 0.67	**0.006**
Average Toughness	0.81	0.72 – 0.91	**< 0.001**
Relative Tree Height	0.37	0.22 – 0.61	**< 0.001**
Amelanchier arborea	0.20	0.05 – 0.83	**0.027**
Carya glabra	1.85	1.07 – 3.19	**0.029**
Carya tomentosa	0.33	0.18 – 0.62	**0.001**
Cornus florida	0.00	0.00 – Inf	0.978
Fraxinus americana	0.62	0.32 – 1.21	0.160
Nyssa sylvatica	4.15	2.25 – 7.64	**< 0.001**
Ostrya virginiana	0.44	0.13 – 1.45	0.179
Prunus avium	0.00	0.00 – Inf	0.978
Prunus serotina	0.77	0.37 – 1.58	0.475
Quercus alba	6.09	4.05 – 9.15	**< 0.001**

Quercus montana	0.70	0.29 – 1.68	0.422
Quercus rubra	9.29	6.34 – 13.62	**< 0.001**
Quercus velutina	0.16	0.02 – 1.20	0.076
Sassafras albidum	0.14	0.02 – 1.03	0.053
Ulmus americana	0.43	0.15 – 1.22	0.112
Observations	189		
R^2 Nagelkerke	0.992		

Table 4 provides the results of an overall shelter builder incidence model. A confidence interval that does not include 1 indicates statistical significance; this was not the case with any of the mechanical leaf properties. An incidence rate ratio lower than one indicates that the incident rate of caterpillars lower in that species of tree or leaf attribute. Oak trees (*Quercus alba*, *Q. montana*, *Q. rubra)* and *Carya glabra* (IRR = 5.67) appeared to have the highest IRRs, this reflects their dominance amongst caterpillar inhabiting tree species. An R^2 value was identical to one – indicating a perfect strength of fit.

Table 4. Shelter builder caterpillar model

	shelter_builder		
Predictors	*Incidence Rate Ratios*	*CI*	*p*
Average Thickness	4.08	1.26 – 12.83	**0.017**
Average Toughness	0.97	0.91 – 1.03	0.365
Relative Tree Height	1.83	1.15 – 2.91	**0.011**
Amelanchier arborea	1.41	0.38 – 4.34	0.570
Carya glabra	5.67	2.81 – 12.69	**< 0.001**
Carya tomentosa	1.36	0.66 – 3.08	0.431

Cornus florida	4.38	1.18 – 13.57	**0.015**
Fraxinus americana	2.64	1.24 – 6.10	**0.016**
Nyssa sylvatica	1.28	0.19 – 4.96	0.754
Ostrya virginiana	1.57	0.35 – 5.26	0.502
Prunus avium	2.14	0.33 – 8.32	0.330
Prunus serotina	4.55	2.12 – 10.54	**< 0.001**
Quercus alba	41.41	22.64 – 87.00	**< 0.001**
Quercus montana	11.31	5.75 – 24.89	**< 0.001**
Quercus rubra	6.99	3.74 – 14.90	**< 0.001**
Quercus velutina	1.61	0.36 – 5.40	0.476
Sassafras albidum	0.75	0.11 – 2.93	0.714
Ulmus americana	0.31	0.02 – 1.64	0.265
Observations	189		
R^2 Nagelkerke	1.000		

Exclusionary models

In the following models the three most abundant caterpillar species were excluded: *Psilocorsis relexella*, *Symmerista albifrons*, and *Anisota senatoria*. These species represented 53% of total caterpillars. This exclusionary model was created to control for potential major variation that these three species might create.

Figure 16 represents the estimated total number of caterpillars that occur every two meters height interval of leaf thickness with the three most dominant species excluded.

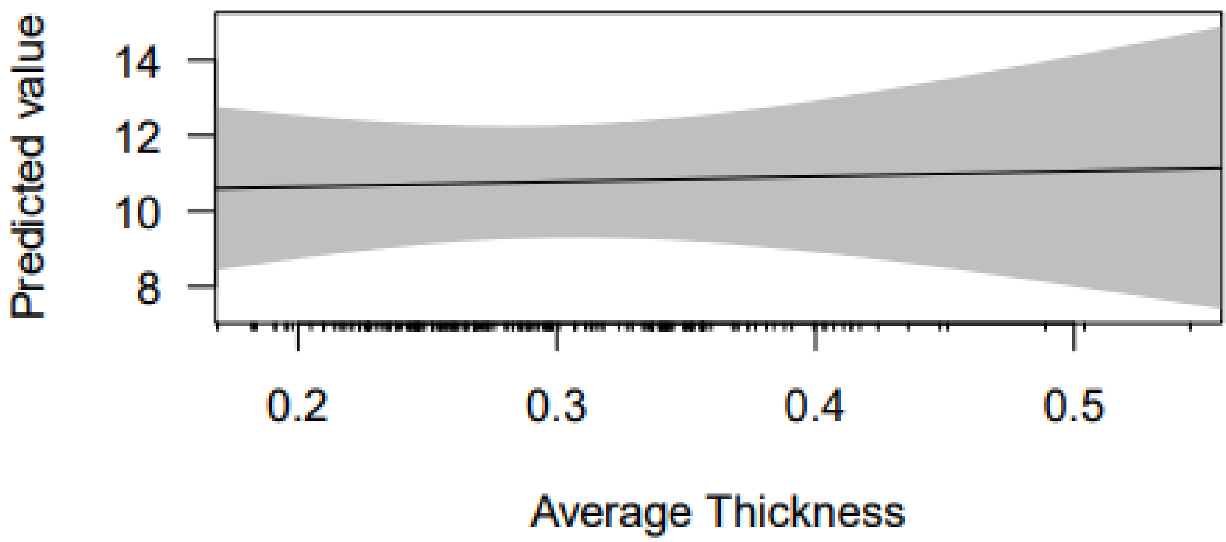

Figure 16. Estimated abundance (predicted value) of overall caterpillars by average leaf thickness every two-meter height interval, excluding the three most abundant species of caterpillars in this study. The gray area represents the 95% confidence interval. The dark line is the line of best fit. The $p = 0.829$ suggests that there is no significant statistical relationship between average leaf thickness and caterpillar abundance.

Figure 17 represents the estimated total number of caterpillars that occur every two meters height interval of leaf toughness with the three most dominant species excluded.

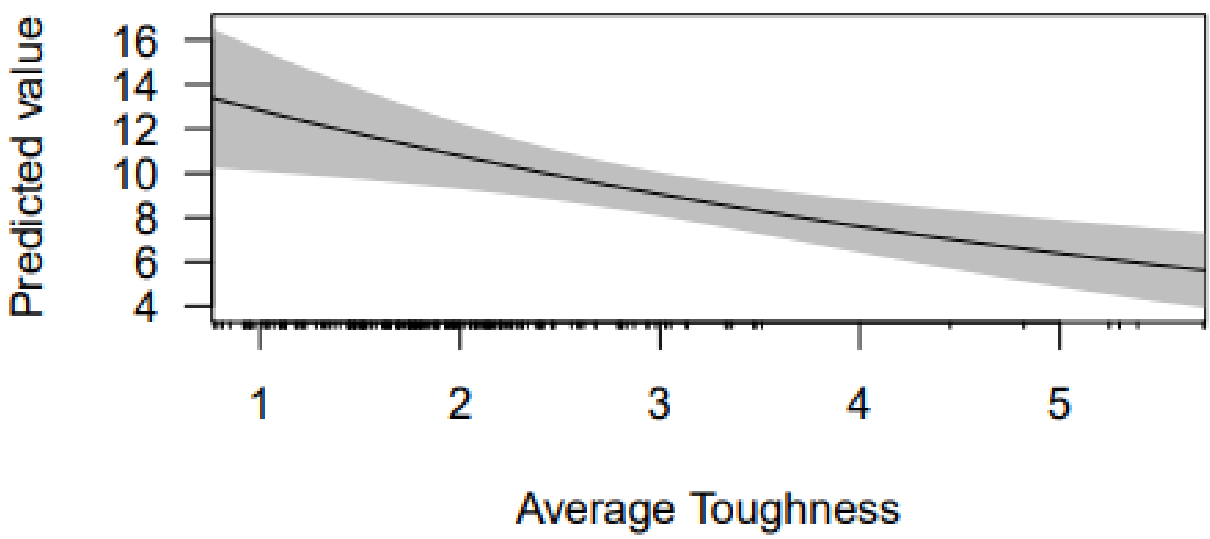

Figure17. Estimated abundance (predicted value) of overall caterpillars by average leaf toughness every two-meter height interval estimation, excluding the three most abundant species of caterpillars in this study. The gray area represents the 95% confidence interval. The dark line is the line of best fit. The $p = 0.001$ suggests that there is a statistically significant relationship between leaf toughness and caterpillar abundance.

Figure 18 represents the total number of caterpillars that occur through the estimation at every two meters height interval of relative tree height with the three most dominant species excluded.

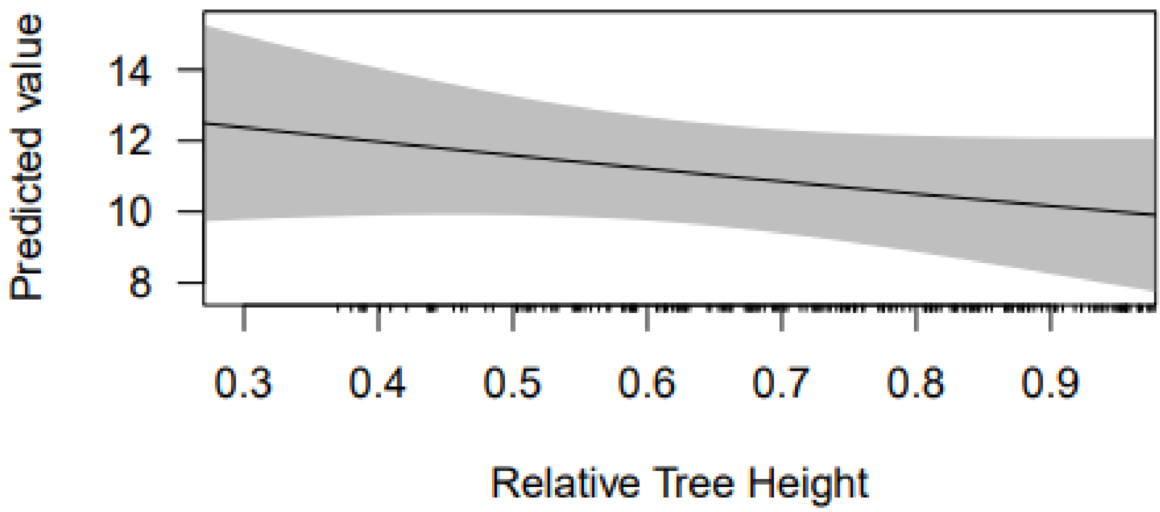

Figure 18. Estimated abundance (predicted value) of overall caterpillars by average relative tree height every two-meter height interval estimation, excluding the three most abundant species of caterpillars in this study. The gray area represents the 95% confidence interval. The dark line is the line of best fit. The $p = 0.201$ suggests that there is no significant statistical relationship between relative tree height and caterpillar abundance.

Figure 19 represents the total number of exposed feeding caterpillars that occur through the estimation at every two-meter height interval of leaf thickness, with the three most dominant species of caterpillars in this study being excluded.

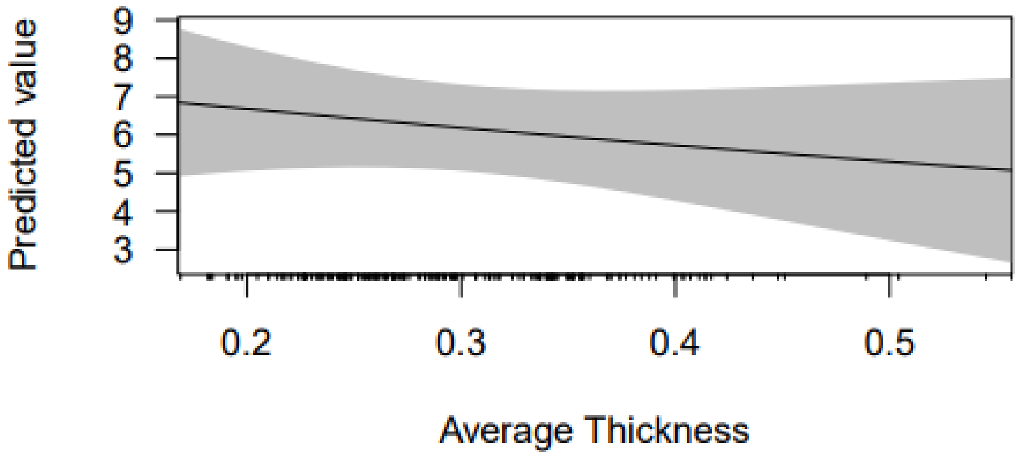

Figure 19. Estimated abundance (predicted value) of exposed feeding caterpillars by average leaf thickness every two-meter height interval estimation, excluding the most abundant species of caterpillars in this study. The gray area represents the 95% confidence interval. The dark line is the line of best fit. The $p = 0.370$ suggests that there is no significant statistical relationship between leaf thickness and caterpillar abundance.

Figure 20 represents the total number of exposed feeding caterpillars that occur through the estimation at every two-meter height interval of leaf toughness, with the three most dominant species of caterpillars in this study being excluded.

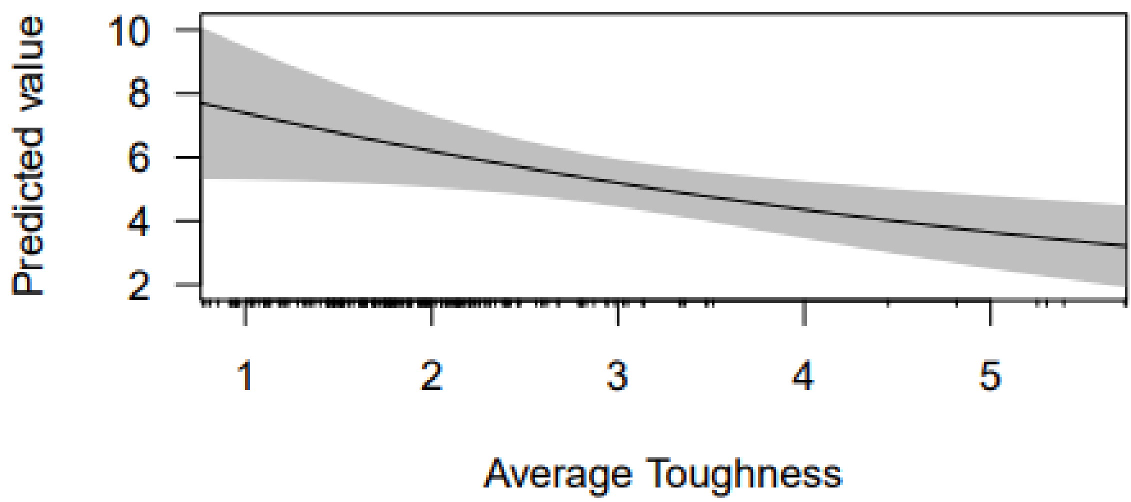

Figure 20. This represents the estimation of exposed feeding caterpillars by average leaf toughness per two-meter height interval, excluding the three most abundant species of caterpillars in this study. The gray area represents the 95% confidence interval. The dark line is the line of best fit. The p = 0.008 suggests that there is a significant statistical relationship between leaf toughness and caterpillar abundance, when the three most abundant species are excluded.

Figure 21 represents the total number of exposed feeding caterpillars that occur through a two-meter height interval estimation of relative tree height, with the three most dominant species of caterpillars being excluded.

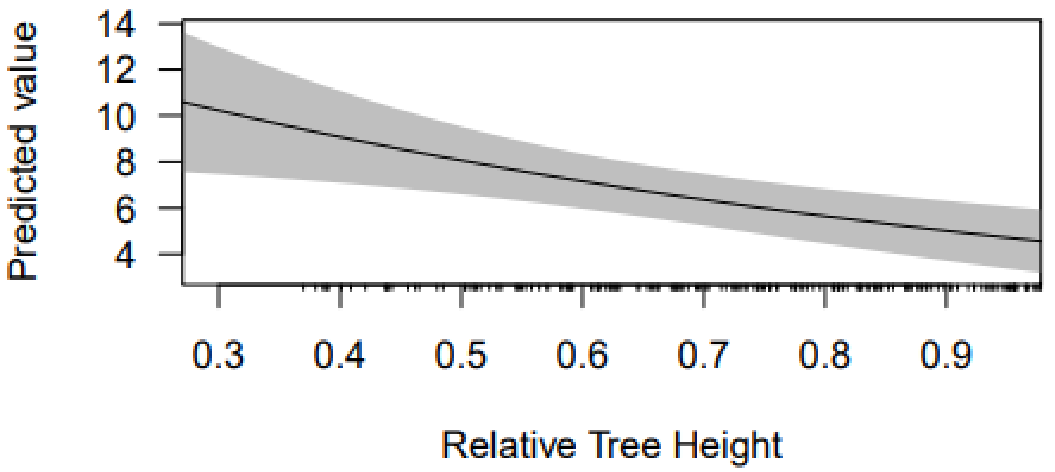

Figure 21. Estimated abundance (predicted value) of exposed feeding caterpillars by relative tree height every two-meter height interval estimation, excluding the three most abundant species of caterpillars in this study. The gray area represents the 95% confidence interval. The dark line is the line of best fit. The $p = 0.001$ suggests that there is a significant statistical relationship between relative tree height and caterpillar abundance.

Figure 22 represents the total number of shelter building caterpillars that occur through the estimation at every two-meter height interval of leaf thickness, with the three most dominant species of caterpillars being excluded.

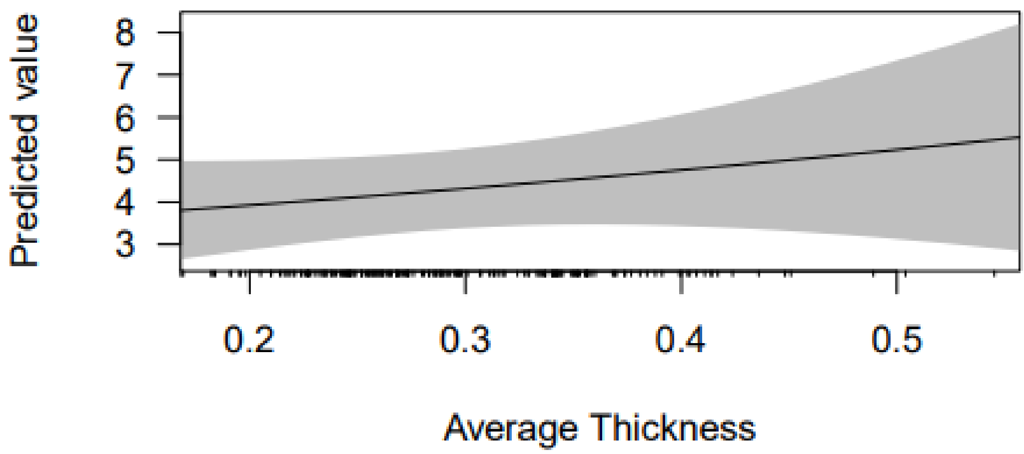

Figure 22. Estimated abundance (predicted value) of shelter building caterpillars by average leaf thickness every two-meter height interval estimation, excluding the three most abundant species of caterpillars in this study. The gray area represents the 95% confidence interval. The dark line is the line of best fit. The $p = 0.259$ suggests that there is no significant statistical relationship between leaf thickness and caterpillar abundance.

Figure 23 represents the total number of shelter building caterpillars that occur through the estimation at every two-meter height interval of leaf toughness, with the three most dominant species of caterpillars being excluded.

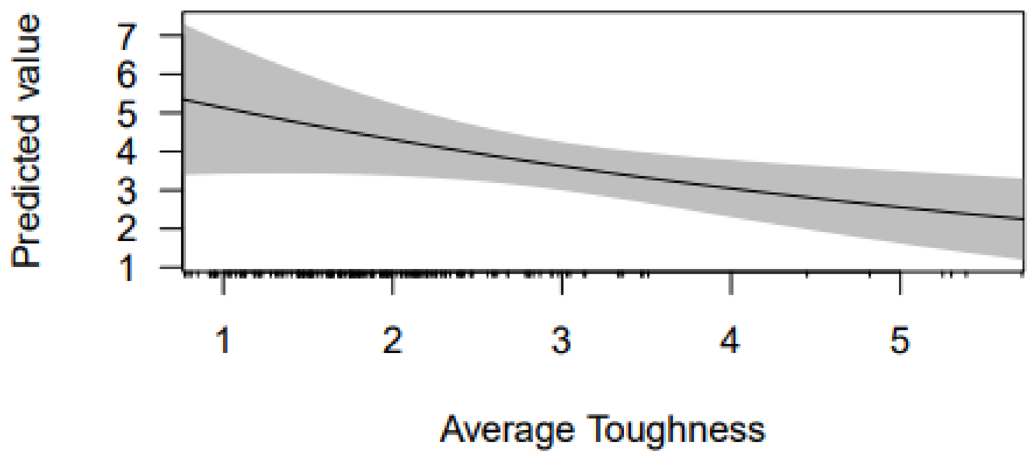

Figure 23. Estimated abundance (predicted value) of shelter building caterpillars by average leaf toughness every two-meter height interval estimation, excluding the three most abundant species of caterpillars in this study. The gray area represents the 95% confidence interval. The dark line is the line of best fit. The $p = 0.026$. suggests that there is a significant statistical relationship between leaf toughness and caterpillar abundance.

Figure 24 represents the total number of shelter building caterpillars that occur through the estimation at every two-meter height interval of relative tree height, with the three most dominant species of caterpillars being excluded.

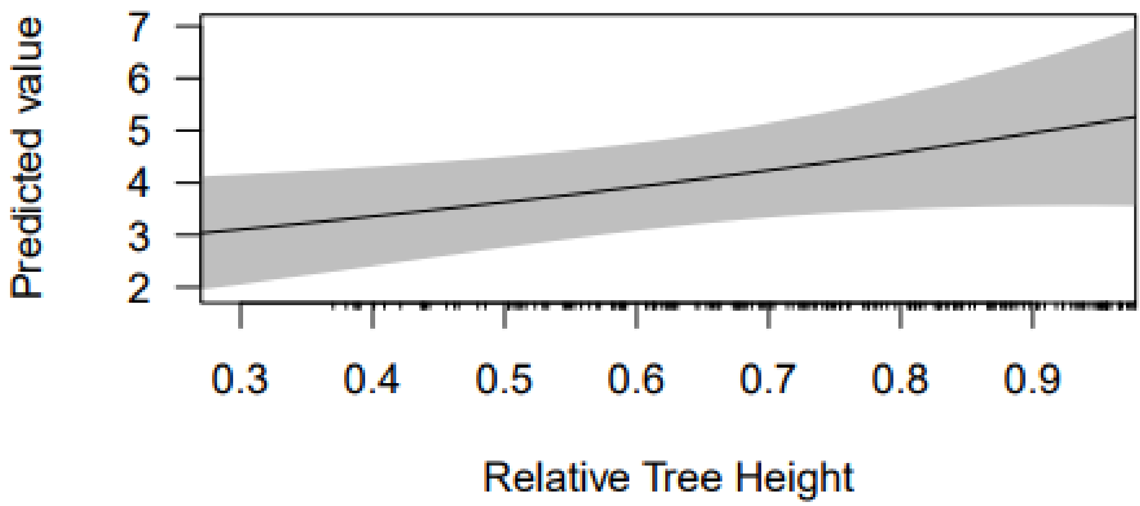

Figure 24. Estimated abundance (predicted value) of exposed feeding caterpillars by relative tree height every two-meter height interval estimation, excluding the three most abundant species of caterpillars in this study. The gray area represents the 95% confidence interval. The dark line is the line of best fit. The $p = 0.044$ suggests that there is a significant statistical relationship between relative tree height and caterpillar abundance, when the three most abundant species are excluded.

Generalized Linear Models (GLM)

Table 5 provides the results of an overall exclusionary incidence model. A confidence interval that does not include 1 indicates statistical significance; this is the case with leaf toughness (CI = 0.76-0.93). An incidence rate ratio lower than one indicates that the incident rate is lower in that species of tree or leaf attribute. Oak trees (*Q. alba*, *Q. rubra*) and *Nyssa sylvatica* (IRR = 3.22) appeared to have the highest IRRs, this reflects their dominance amongst caterpillar inhabiting tree species. An R^2 value was close to one – indicating a good strength of fit.

Table 5. Exclusionary model for overall caterpillar incidence

	incidence_subset		
Predictors	*Incidence Rate Ratios*	*CI*	*p*
Average Thickness	1.14	0.34 – 3.62	0.829
Average Toughness	0.84	0.76 – 0.93	**0.001**
Relative Tree Height	0.72	0.44 – 1.19	0.201
Amelanchier arborea	0.48	0.18 – 1.06	0.098
Carya glabra	2.80	1.84 – 4.29	**< 0.001**
Carya tomentosa	0.58	0.37 – 0.91	**0.017**
Cornus florida	0.93	0.28 – 2.33	0.886
Fraxinus americana	1.13	0.70 – 1.80	0.618
Nyssa sylvatica	3.22	1.79 – 5.56	**< 0.001**
Ostrya virginiana]	0.72	0.27 – 1.58	0.454
Prunus avium	0.49	0.08 – 1.61	0.331
Prunus serotina	1.74	1.07 – 2.83	**0.025**
Quercus alba	5.69	4.02 – 8.25	**< 0.001**
Quercus montana	1.26	0.68 – 2.24	0.435
Quercus rubra	3.14	2.22 – 4.55	**< 0.001**

Quercus velutina	0.52	0.15 – 1.28	0.208
Sassafras albidum	0.29	0.07 – 0.82	**0.042**
Ulmus americana	0.38	0.13 – 0.87	**0.041**
Observations	189		
R^2 Nagelkerke	0.917		

Table 6 provides the results of an overall exposed feeder incidence exclusionary model. A confidence interval that does not include 1 indicates statistical significance; this is the case with leaf toughness (CI = 0.74-0.96) and relative tree height (CI = 0.15-0.61), but not leaf thickness (CI = 0.09-2.49). An incidence rate ratio lower than one indicates that the incident rate is lower in that species of tree or leaf attribute. Oak trees (*Q. alba*, *Q. rubra*) and *Nyssa sylvatica* (IRR = 4.14) appeared to have the highest IRRs, this reflects their dominance amongst caterpillar inhabiting tree species. *Cornus florida* and *Prunus avium* did not have any exposed feeding caterpillars. An R^2 value was close to one – indicating a good strength of fit.

Table 6. Exclusionary model for exposed feeder caterpillars

	exposed_feeder_subset		
Predictors	*Incidence Rate Ratios*	*CI*	*p*
Average Thickness	0.46	0.09 – 2.49	0.370
Average Toughness	0.84	0.74 – 0.96	**0.008**
Relative Tree Height	0.31	0.15 – 0.61	**0.001**
Amelanchier arborea	0.21	0.05 – 0.88	**0.033**
Carya glabra	1.75	1.00 – 3.05	**0.048**
Carya tomentosa	0.33	0.18 – 0.61	**< 0.001**
Cornus florida	0.00	0.00 – Inf	0.986
Fraxinus americana	0.62	0.31 – 1.21	0.159

Nyssa sylvatica	4.14	2.24 – 7.65	**< 0.001**
Ostrya virginiana	0.46	0.14 – 1.51	0.201
Prunus avium	0.00	0.00 – Inf	0.986
Prunus serotina	0.80	0.38 – 1.65	0.542
Quercus alba	4.69	3.08 – 7.13	**< 0.001**
Quercus montana	0.67	0.27 – 1.61	0.367
Quercus rubra	2.20	1.43 – 3.38	**< 0.001**
Quercus velutina	0.17	0.02 – 1.23	0.079
Sassafras albidum	0.15	0.02 – 1.11	0.063
Ulmus americana	0.43	0.15 – 1.24	0.118
Observations	189		
R^2 Nagelkerke	0.878		

Table 7 provides the results of an overall exclusionary shelter builder incidence model. A confidence interval that does not include 1 indicates statistical significance; this is the case with leaf toughness (CI = 0.72-0.97). An incidence rate ratio lower than one indicates that the incident rate is lower in that tree species or leaf attribute. Only one species met that criteria, *Ulmus americana* (IRR = 0.30). Oak trees (*Q. alba*, Q. *rubra*) and *Carya glabra* (IRR = 6.17) appeared to have the highest IRRs, this reflects their dominance amongst caterpillar inhabiting tree species. This R^2 value was the lowest of all models, by far, 0.638. This regression has a less reliable goodness of fit, thus reducing the significance of these trends.

Table 7. Exclusionary model for shelter building caterpillars.

	shelter_builder_subset		
Predictors	*Incidence Rate Ratios*	*CI*	*p*
Average Thickness	2.61	0.47 – 13.22	0.259
Average Toughness	0.84	0.72 – 0.97	**0.026**
Relative Tree Height	2.18	1.03 – 4.68	**0.044**
Amelanchier arborea	1.38	0.37 – 4.27	0.594
Carya glabra	6.17	3.02 – 13.92	**< 0.001**
Carya tomentosa	1.36	0.65 – 3.11	0.428
Cornus florida	4.02	1.07 – 12.56	**0.023**
Fraxinus americana	2.73	1.28 – 6.30	**0.013**
Nyssa sylvatica	1.40	0.21 – 5.45	0.669
Ostrya virginiana	1.54	0.34 – 5.19	0.518
Prunus avium	2.30	0.35 – 8.94	0.289
Prunus serotina	4.71	2.18 – 10.98	**< 0.001**
Quercus alba	9.24	4.77 – 20.16	**< 0.001**
Quercus montana	3.15	1.25 – 8.02	**0.014**
Quercus rubra	6.27	3.28 – 13.56	**< 0.001**
Quercus velutina	1.70	0.38 – 5.73	0.428
Sassafras albidum	0.71	0.11 – 2.78	0.659
Ulmus americana	0.30	0.02 – 1.59	0.252
Observations	189		
R^2 Nagelkerke	0.638		

Incidence for all caterpillars

For the overall total incidence models (shelter builders and exposed feeders), only the declining presence with increased leaf toughness was statistically significant. When the incidence was analyzed by species of tree, *Carya glabra*, *Nyssa sylvatica*, *Quercus alba*, *Q. montana*, and *Q. rubra* had a significant incidence ($p < 0.001$). *Carya tomentosa* (0.015), *Sassafras albidum* (0.029), and *Ulmus americana* (0.040) also had significant incidence.

A. Incidence for all exposed feeders

The incidence of exposed feeding caterpillars was significantly related to leaf toughness, thickness, and relative three height ($p < 0.05$; leaf toughness and relative tree height $p < 0.001$, leaf thickness $p = 0.006$). When the incidence was analyzed by species of tree, *Nyssa sylvatica*, *Quercus alba*, and *Quercus rubra* had a significance incidence ($p < 0.001$) as did *Amelanchier arborea* ($p < 0.027$), *Carya glabra* ($p < 0.029$), and *C. tomentosa* ($p < 0.001$).

B. Incidence for all shelter builders

The incidence of shelter builder caterpillars there was significantly related to leaf thickness and relative tree height. These were modest increases, with p-scores of 0.017 and 0.011 respectively. When shelter builder incidences were analyzed by species of tree, *Carya glabra*, *Prunus serotina*, *Quercus alba*, *Quercus montana*, and *Quercus rubra had a significant incidence (*$p < 0.001$). *Cornus florida* ($p < 0.015$) and *Fraxinus americana* ($p < 0.016$) also had significant incidence.

Overall incidence models, with the most abundant caterpillars removed

Leaf toughness was significant on the incidence exclusion models. When overall incidences were analyzed by species of tree, *Carya glabra*, *Nyssa sylvatica*, *Quercus alba*, and *Quercus rubra*, had a significant incidence ($p < 0.001$). *Carya tomentosa* ($p < 0.017$), *Prunus serotina* ($p < 0.025$), *Sassafras albidum* ($p < 0.042$), and *Ulmus americana* ($p < 0.041$) also had significant incidence.

A. *Incidence for exposed feeders, with the most abundant caterpillars removed*

The incidence of exposed feeders was significantly related to leaf toughness ($p < 0.008$) and relative tree height ($p < .001$) on the exclusion models. When the incidence of exposed feeders was analyzed by species of tree, *Carya tomentosa* ($p < 0.001$), *Nyssa sylvatica* ($p < 0.001$), *Quercus alba* ($p < 0.001$), and *Quercus rubra* ($p < 0.001$) experienced a significant decline; as well as *Amelanchier arborea* ($p < 0.033$) and *Carya glabra* ($p < 0.048$).

B. Incidence for all shelter builders, with the most abundant caterpillars removed

In the shelter builder exclusionary model, there was a significant decrease in caterpillar incidence as leaf toughness per 2M height interval increased; there was also an increase in shelter builder incidence as relative tree height per 2M interval increased. When the incidence of shelter builders per species of tree was analyzed When the incidence of shelter builders by species of trees were analyzed, *Carya glabra*, *Prunus serotina*, *Quercus alba*, and *Quercus rubra* declines were significant ($p < 0.001$), as well as *Cornus florida* ($p < 0.023$), *Fraxinus americana* ($p < 0.013$), and *Quercus montana* ($p < 0.014$).

The trends for both total incidence models (overall caterpillars and most abundant caterpillar excluded) matched – with leaf toughness being the only common statistically significant variable in all models ($p < 0.001$). In both models, the incidence of exposed feeders held heavy significance with toughness ($p < 0.001$) and relative tree height ($p < 0.001$). Leaf thickness was significant on the overall model ($p < 0.006$) but not the exclusionary model. In contrast, the statistical tendencies for shelter builders followed a mixed pattern. In the overall model, leaf thickness ($p < 0.017$) and relative tree height ($p < 0.011$) were positively correlated with caterpillar incidence. In the exclusionary model, caterpillar incidence decreased significantly with increased leaf toughness ($p < 0.026$) and increased significantly ($p < 0.044$) with relative tree height. This suggests that leaf thickness and relative tree height were ideal for caterpillar shelter building, and leaf toughness was often correlated with reduced insect presence, whether it be exposed feeders or shelter builders.

Botanical synopsis

The consistency of the *Quercus* data suggests that their leaves display tremendous plasticity. This suggests that they are remarkably adept at withstanding abiotic stress, which is much more common in temperate than in tropical forests. It may also indicate a potential evolutionary mechanism, generating natural variation in this trait (Coneva and Chitwood 2018). Regarding leaf toughness, it has been found that species that specialize in shaded forest understory or nutrient-poor soils have tougher leaves and longer lifespans (Turner et al. 1993). This would indicate that our two major Oak trees *Quercus alba* and *Quercus rubra* are the most resilient. This is a result of larger cell walls, which provide both stiffness and toughness (Choong 1996). *Quercus* can thrive in nutrient-poor soils for many reasons. They can construct arbuscular and ectotrophic mycorrhizae, with widely diverse fungi that independently evolved for many generations. This allows individual trees to form mycorrhizal symbiosis with partners adapting to divergent conditions and accessing a wide array of resources. Furthermore, *Quercus* has deep roots, which allows them access to water resources deep in the groundwater. This provides a source of hydration that can be accessed during prolonged droughts and periods of extremely dry surface soils (Bose et al. 2021).

Leaf toughness has often been noted as the best predictor for caterpillar leaf preference. Additionally, generalist caterpillar oak leaf preference was coupled to its feeding performance (Pearse 2011). *Carya tomentosa* is also worth examining regarding leaf toughness. This is likely the result of trichome density, which this species is widely known to have in abundance. These trichomes can delay the onset of feeding. They show a strong correlation of reduced herbivory in the first and second instar stages of caterpillar development (Kariyat et al. 2018). Caterpillar presence would be much lower since their only reliable hosts would be in their third stage of development.

Discussion

There is a clear indication that mechanical properties impact insect herbivory. It appears that caterpillars are less likely to prey on the highest areas of a tree, but that is generally only observed near the canopy's highest part. This may result from a relative unpalatability of the basal leaves due to their physical strength.

Shelter building as a function of leaf toughness is a variable that followed a complex relationship. Shelter builders act as ecosystem engineers that alter the physical structure of the environment, which in turn impacts resource availability for associated species (Reinhardt and Marquis 2023). Shelter building has a greater dependence on the ontogenetic stage of caterpillars, as it is often restricted to the later larval instars (Gaston and Valladares 1991). This might explain its relationship with relative tree height, which recorded a sharp increase in both the overall and exclusionary model. This mixed results with tougher leaves could be attributed to several reasons: increased time and energy spent on building, an increased risk of parasitoid attack because of increased visual and chemical cues (Abarca et al. 2014).

It is only in their later instars that Lepidoptera larvae possess the capabilities to build trenched shelters. This is a result of the development of their mandibles, which are essential in cutting and crafting leaves. Shelter building caterpillars protect them from predators (Abarca et al. 2014).

Rank abundance

Rank abundance curves were generated to display which species were most abundant. *Psilocorsis reflexella* is the species with the highest representation followed by list the next three in order (the ones that have 100 or more). The shape of this rank abundance curve (Figure 25) is typical of most biological systems studied (Avolio et al. 2019).

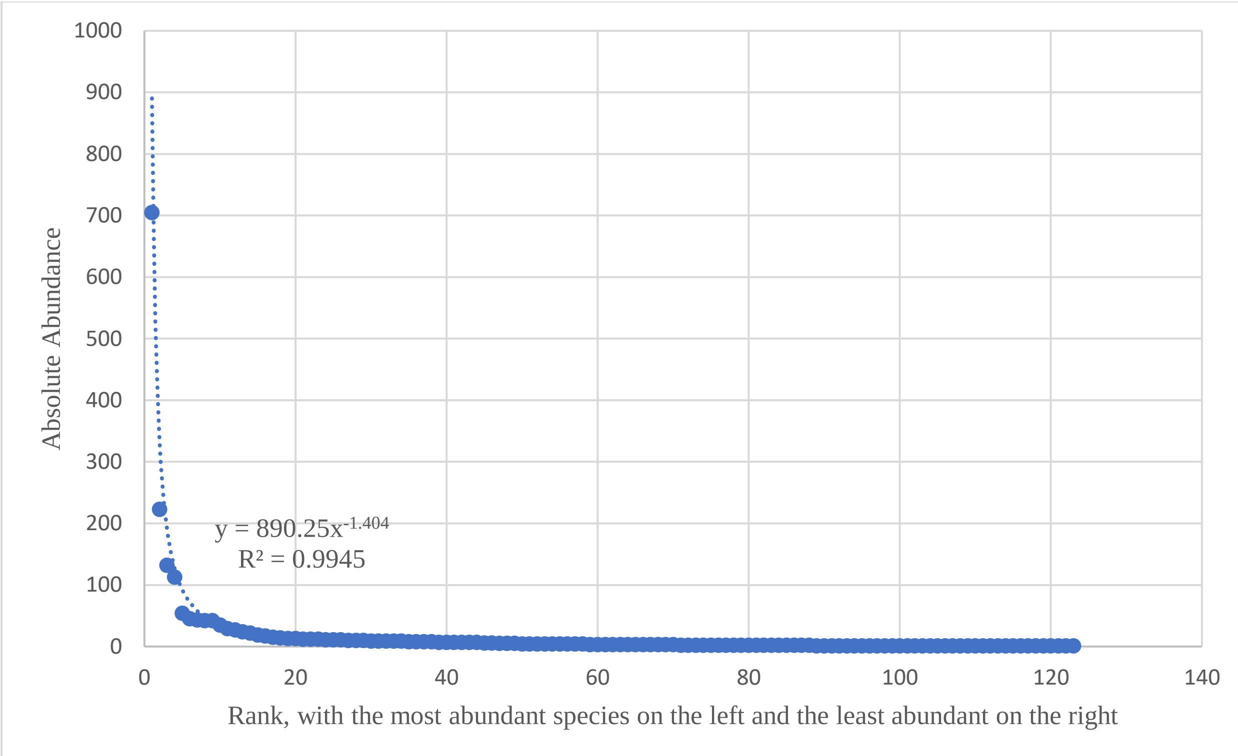

Figure 25. Rank abundance of the species of caterpillars found in this study with the most abundant species on the left and the least abundant to the right.

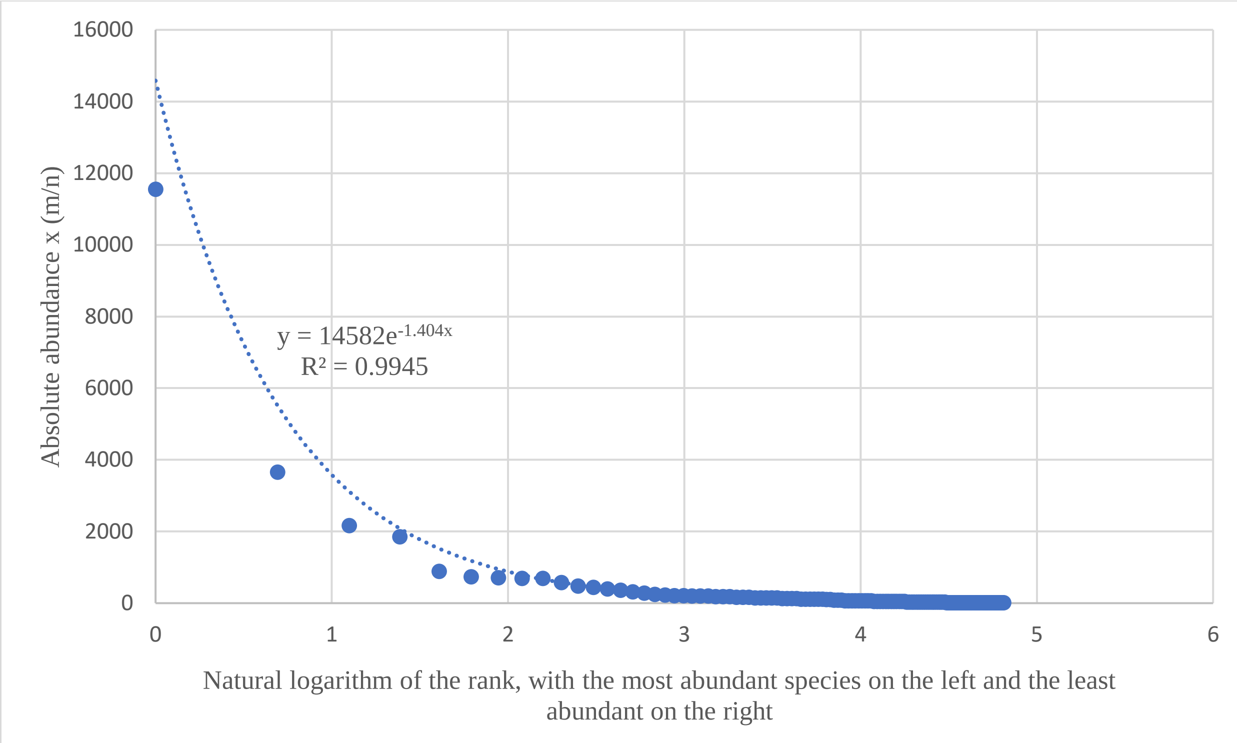

Figure 26. Natural logarithm of rank abundance. In this plot, m means the total number of caterpillars collected, 2015, and n means the total number of species based on the caterpillars, 123.

What is the meaning of these curves and the significance of this study to community ecology? In a theoretical study and as a first approximation McArthur's (1957) suggested that transforming rank abundance curves by taking the logarithm of the rank would reveal three types of resource use:

1) Nonoverlapping niches – the environment is compared with a stick of unity length on which points are thrown randomly. The stick is then broken at these points, and the lengths of the resulting segments are proportional to the abundance of the species.

2) Overlapping niches – the environment is compared with a stick, but each species becomes independent of the others. Each species' abundance is determined by the distance between a pair of points thrown randomly onto the stick.

3) Niches particulate, not continuous – the abundance-determining factor is accumulated as independent discrete units by different species. Species are then compared with urns into which units of abundance are tossed on independent random throws, with each urn having a probability.

Figure 26 supports the overlapping niche hypothesis. It set two basic parameters – the number of individuals, and the number of species along two-meter height intervals. There is a large niche overlap between the caterpillars, a prediction supported by the large overlap in host-plants of the caterpillars. King (1964) and Avolio et al. (2019) stress the limitations of McArthur (1957) models by stressing the importance of hypothesis I. Hypothesis I matches observations more effectively than hypothesis II or III. Its only parameters are the number of individuals and number of species. This simplicity makes it ideal for homogenous communities, which is the case with this study, through its strict inclusion of caterpillars. Hypothesis I works well because niches rarely overlap; and they are more discrete than continuous.

Community ecology emphasizes that forest health is of the utmost importance. Insects are great bioindicators, and by studying their patterns it provides insight into the potential impacts on both long-term and short-term environmental health (Chowdhury et al. 2023). Caterpillars are in the center of food webs. Many species of predators and parasitoids attack and eat them. Therefore, the populations of these natural enemies depend on an abundance of caterpillars (Koptur and Marquis 2022). Caterpillars prey on primary producers (plants), which makes them primary consumers; they help deliver energy and nutrients across the food chain. A healthy ecosystem is one in which plant and insect life both flourish in symbiosis, this requires the implementation of well-informed forestry practices. By studying these deciduous forests, proper conservation practices will be established.

These forests must also be studied through the lens of climate change. Climate change can have a tremendous impact on leaf mechanical traits. A 2020 study examining leaf traits of 515 species in 210 experiments mimicked abiotic factors such as climate warming, drought, elevated CO_2, and nitrogen deposition (Cui et al. 2020). The results indicated that warming increases leaf photosynthesis in cold environments but decreases leaf photosynthesis in warmer environments. These negative effects may result from warming-induced water deficits, or the excessive temperatures pushing the leaf specimens beyond optimum points. Water shortage and drought can cause leaves to wilt irreversibly, which can decimate herbivore populations (Kramp et al. 2022). As herbivores are faced with changing morphological features, it is possible for them to adjust their feeding patterns.

Leaf thickness has a strong correlation between growth and relative water content. As temperatures continue to increase in this temperate deciduous forest, there is growing concern of extended periods of dehydration, and a subsequent loss in leaf nutrient content. Factors such as short leaf lifespans and leaf toughness played a major role in climate adaptation. Drought also presents threats to forest health due to the increased risk of wildfires. Wildfires can annihilate vast hectares of forest, and the risks of such events are rapidly increasing in these Virginia habitats (Anonymous 2023b). Monitoring other mechanical traits, such as leaf toughness, can also offer a glimpse into climate change. Shorter living leaves – that are less tough - have a greater ability to replace drought-damaged tissues, and build defense with new, acclimated leaves. On the other hand, tree species with longer lifespans – and tougher leaves – fared poorly in drought recovery, due to their low organ turnover rates (Song et al. 2022).

Limitations of this study

1. This study represents the results of a correlation study of one moment in time. A longer-term study may show significant differences in how species partition their habitat (King 1964, Avolio et al. 2019).
2. Besides leaf toughness and thickness, I did not study other anatomical characteristics, such as cell wall fiber content, tissue density, and the average toughness of the veins, etc. All these traits enhance plants' resistance to natural enemies, which increases plants' survival and may offset the energy of producing tougher leaves (Westbrook 2011). The cost of producing tougher leaves would be worth examining further.
3. Full tree height should be included in a future study since leaf toughness traits have occasionally been observed not to be correlated with relative growth rates (Westbrook 2011).
4. Trichome density might have been a measurement that may have benefitted this study, since the tiny hairs make caterpillars less likely to chew on the leaves (Rupesh 2018).
5. Additionally, studies in caterpillar predators might have helped to understand the location of the caterpillars, along with locomotion following eclosion (larvae emerging from the eggs). Examining these trends at both temperate and tropical sites may illuminate any herbivory patterns.

6. Some of the caterpillars were collected below the crown making them ineligible for the plant data. Future studies may benefit from extending plant measurements below the crown, since it is common for caterpillars to occupy these areas during their early stages of development. Additionally, when accounting for larger trees, particularly *Quercus*, the greater heights were excluded to offset the height disparities in smaller trees; this eliminated caterpillar incidents at the top of the tree. Two quartiles were set (25-75%) as lower and upper bounds to establish the relative tree height formula; this limited the caterpillar data between 59.1 and 86.7% of total tree height. This took the caterpillar total from 2,015 to 1,743.
7. Future research could focus specifically on the impact of chemical defenses. Such chemical defenses may render predators more susceptible to natural enemies like endoparasitoids, while providing necessary protection against generalist predators (Lampert 2015).
8. Future modeling could utilize a negative binomial regression and/or robust standard errors. This will address any issues of overdispersion that come with heteroscedasticity. Adding an extra parameter will further test the validity of these findings.

Conclusion

Leaf mechanical defenses had a major impact on insect abundance. Variables like leaf toughness showed a strong correlation in the deterrence of caterpillars, but only as it pertained to exposed feeders. There was no strong correlation between leaf toughness and shelter builders. Variables like leaf thickness carried significance, as they did correlate with enhanced exposed feeder deterrence. Furthermore, leaf thickness revealed an interesting relationship with shelter builders; shelter building increased as leaf thickness increased. Relative tree height showed several strong relationships. It was linked with reduced herbivory as height increased. It also offered stronger habitat for shelter builders, as shelter builder incidences increased with height.

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Appendix 1. Caterpillars examined in this study and some of their traits.

Family	Species and Authorship	Caterpillar is External Feeder or Shelter Feeder	Number of Caterpillars Collected
Blastobasidae	*Asaphocrita busckiella* (Dietz, 1910)	exposed feeder	1
Bucculatricidae	*Bucculatrix packardella* Chambers, 1873	exposed feeder	4
Bucculatricidae	*Bucculatrix recognita* Braun, 1963	exposed feeder	2
Bucculatricidae	*Bucculatrix* sp. AAB1987	exposed feeder	2
Bucculatricidae	*Bucculatrix* sp. AAH4716	exposed feeder	1
Bucculatricidae	*Bucculatrix* sp. ADL1829	exposed feeder	4
Crambidae	*Palpita magniferalis* (Walker, 1861)	shelter builder	13
Depressariidae	*Antaeotricha schlaegeri* (Zeller, 1854)	shelter builder	9
Depressariidae	*Machimia tentoriferella* (Clemens, 1860)	shelter builder	113
Depressariidae	*Psilocorsis quercicellia* (Clemens, 1860)	shelter builder	24
Depressariidae	*Psilocorsis reflexella* (Clemens, 1860)	shelter builder	705
Depressariidae	*Rectiostoma xanthobasis* (Zeller, 1876)	shelter builder	12
Depressariidae	*Semioscopis packardella* (Clemens, 1863)	shelter builder	1
Erebidae	*Allotria elonympha* (Hubner, 1823)	exposed feeder	9
Erebidae	*Dasychira obliquata* (Grote and Robinson 1866)	exposed feeder	4
Erebidae	*Dasychira tephra* (Hubner, 1809)	exposed feeder	13

Erebidae	*Halysidota tessellaris* (J. E. Smith, 1797)	exposed feeder	42
Erebidae	*Hypena abalienalia* (Walker, 1859)	exposed feeder	1
Erebidae	*Hypena baltimoralis* (Guenee, 1854)	exposed feeder	2
Erebidae	*Hypena palparia* (Walker, 1861)	exposed feeder	2
Erebidae	*Hyperstrotia nana* (Hubner, 1818)	exposed feeder	11
Erebidae	*Hyperstrotia secta* (Grote, 1879)	exposed feeder	12
Erebidae	*Hyphantria cunea* (Drury, 1773)	exposed feeder	1
Erebidae	*Orgyia definita* (Packard, 1865)	exposed feeder	11
Erebidae	*Orgyia leucostigma* (J. E. Smith, 1797)	exposed feeder	6
Erebidae	*Panopoda carneicosta* Guenée, 1852	exposed feeder	7
Erebidae	*Panopoda rufimargo* (Hubner, 1818)	exposed feeder	22
Erebidae	*Parallelia bistriaris* (Hubner, 1818)	exposed feeder	12
Gelechiidae	*Arogalea cristifasciella* (Chambers, 1878)	shelter builder	7
Gelechiidae	*Chionodes fuscomaculella* (Chambers, 1872)	shelter builder	10
Gelechiidae	*Dichomeris georgiella* (Walker, 1866)	shelter builder	1
Gelechiidae	*Pseudotelphusa quercinigracella* (Chambers, 1872)	shelter builder	9
Gelechiidae	*Pseudotelphusa querciphaga*	shelter builder	2
Gelechiidae	*Trypanisma prudens* Clemens, 1860	shelter builder	3
Geometridae	*Anacamptodes defectaria* Guenée, 1857	exposed feeder	3
Geometridae	*Besma quercivoraria* (Guenée, 1857)	exposed feeder	2
Geometridae	*Campaea perlata* Guenée, 1858	exposed feeder	3

Geometridae	*Euchlaena amoenaria* (Guenée, 1857)	exposed feeder	2
Geometridae	*Eupithecia swettii* Grossbeck, 1907	exposed feeder	1
Geometridae	*Eutrapela clemataria* (J. E. Smith, 1797)	exposed feeder	4
Geometridae	*Hydriomena bistriolata* (Zeller, 1872)	shelter builder	9
Geometridae	*Hydriomena* sp._ADN0943	shelter builder	1
Geometridae	*Hydriomena transfigurata*	shelter builder	1
Geometridae	*Hypagyrtis unipunctata* (Haworth, 1809)	exposed feeder	45
Geometridae	*Lambdina fervidaria* Hübner, 1827	exposed feeder	19
Geometridae	*Lomographa vestaliata* (Guenee, 1857)	exposed feeder	3
Geometridae	*Macaria bisignata* Walker, 1866	exposed feeder	1
Geometridae	*Melanolophia signataria* (Walker, 1860)	exposed feeder	2
Geometridae	*Nemoria bistriaria* Hübner, 1818	exposed feeder	2
Geometridae	*Protoboarmia porcelaria* (Guenée, 1857)	exposed feeder	7
Geometridae	*Speranza pustularia* (Guenée, 1857)	exposed feeder	2
Gracillariidae	*Caloptilia paradoxa* (Frey and Boll, 1873)	shelter builder	1
Gracillariidae	*Parornix dubitella* (Dietz, 1907)	shelter builder	2
Hesperiidae	*Erynnis juvenalis* (Fabricius, 1793)	shelter builder	11
Lasiocampidae	*Tolype velleda* (Stoll, 1791)	exposed feeder	1
Limacodidae	*Apoda y-inversum* (Packard, 1864)	exposed feeder	4
Limacodidae	*Euclea delphinii* (Gray, 1832)	exposed feeder	7

Limacodidae	*Isa textula* (Herrich-Schäffer, [1854])	exposed feeder	1
Limacodidae	*Lithacodes fasciola* (Herrich-Schäffer 1854)	exposed feeder	2
Limacodidae	*Natada nasoni* (Herrich-Schäffer, [1854])	exposed feeder	10
Limacodidae	*Parasa chloris* (Herrich-Schaffer, 1854)	exposed feeder	1
Megalopygidae	*Megalopyge crispata* (Packard, 1864)	exposed feeder	3
Mimallonidae	*Lacosoma chiridota* Grote, 1864	shelter builder	5
Noctuidae	*Acronicta afflicta* Grote, 1864	exposed feeder	7
Noctuidae	*Acronicta americana* Harris, 1841	exposed feeder	4
Noctuidae	*Acronicta hasta* Guenée, 1852	exposed feeder	3
Noctuidae	*Acronicta increta* (Morrison, 1875)	exposed feeder	1
Noctuidae	*Acronicta lobeliae* (Guenée, 1852)	exposed feeder	4
Noctuidae	*Acronicta modica* Walker, 1856	exposed feeder	37
Noctuidae	*Acronicta ovata* Grote, 1873	exposed feeder	17
Noctuidae	*Acronicta morula* Grote and Robinson, 1868	exposed feeder	1
Noctuidae	*Acronicta radcliffei* Harvey, 1875	exposed feeder	1
Noctuidae	*Acronicta tristis* Smith, 1911	exposed feeder	15
Noctuidae	*Acronicta vinnula* Grote, 1864	exposed feeder	1
Noctuidae	*Anterastria teratophora* Herrich-Schäffer, 1854	exposed feeder	1
Noctuidae	*Balsa labecula* (Grote, 1880)	exposed feeder	2
Noctuidae	*Charadra deridens* (Guenée, 1852)	exposed feeder	2

Noctuidae	*Morrisonia confusa* (Hubner, 1831)	shelter builder	27
Noctuidae	*Morrisonia latex* Guenée, 1852	shelter builder	9
Noctuidae	*Morrisonia micens* (Hübner, [1831])	shelter builder	1
Noctuidae	*Polygrammate herbraeicum* Hübner, 1818	exposed feeder	10
Nolidae	*Baileya ophthalmica* (Guenée, 1852)	exposed feeder	3
Nolidae	*Meganola phylla* (Dyar, 1898)	exposed feeder	3
Nolidae	*Datana* sp. AAA7653	exposed feeder	1
Notodontidae	*Coelodasys unicornis* (J. E. Smith, 1797)	exposed feeder	1
Notodontidae	*Heterocampa guttivitta* (Walker, 1855)	exposed feeder	14
Notodontidae	*Heterocampa obliqua* Packard, 1864	exposed feeder	2
Notodontidae	*Heterocampa umbrata* Walker, 1855	exposed feeder	1
Notodontidae	*Lochmaeus bilineata* (Packard, 1864)	exposed feeder	3
Notodontidae	*Macrurocampa marthesia* (Cramer, 1780)	exposed feeder	35
Notodontidae	*Nadata gibbosa* (J. E. Smith, 1797)	exposed feeder	43
Notodontidae	*Paraeschra georgica* (Herrich-Schäffer, 1855)	exposed feeder	2
Notodontidae	*Peridae angulosa* (J. E. Smith, 1797)	exposed feeder	1
Notodontidae	*Symmerista albifrons* (J. E. Smith, 1797)	exposed feeder	223
Papilionidae	*Papilio troilus* Linnaeus, 1758	exposed feeder	1
Pyralidae	*Canarsia ulmiarrosorella* (Clemens, 1860)	shelter builder	1
Pyralidae	*Oneida lunulalis* Hulst, 1889	shelter builder	3

Pyralidae	*Salebriaria engeli* (Dyar, 1906)	shelter builder	4
Pyralidae	*Pococera* sp. AAA3814	shelter builder	2
Pyralidae	*Pococera* sp. AAA4979	shelter builder	5
Pyralidae	*Pococera* sp. ABY6852	shelter builder	8
Pyralidae	*Salebriaria tenebrosella* (Hulst, 1887)	shelter builder	5
Saturniidae	*Actias luna* (Linnaeus, 1758)	exposed feeder	1
Saturniidae	*Anisota senatoria* (J. E. Smith, 1797)	exposed feeder	132
Saturniidae	*Dryocampa rubicunda* (Fabricius, 1793)	exposed feeder	8
Sphingidae	*Amorpha juglandis* (J. E. Smith, 1797)	exposed feeder	7
Sphingidae	*Ceratomia amyntor* (Geyer, 1835)	exposed feeder	1
Sphingidae	*Ceratomia undulosa* (Walker, 1856)	exposed feeder	8
Tortricidae	*Acleris chalybeana* (Fernald, 1882)	shelter builder	3
Tortricidae	*Acleris comariana* (Lienig and Zeller, 1846)	shelter builder	1
Tortricidae	*Acleris nivisellana* (Walsingham, 1879)	shelter builder	2
Tortricidae	*Amorbia humerosana* Clemens, 1860	shelter builder	1
Tortricidae	*Ancylis* sp. AAA8534	shelter builder	54
Tortricidae	*Argyrotaenia mariana* (Fernald, 1882)	shelter builder	6
Tortricidae	*Argyrotaenia* sp. 01	shelter builder	1
Tortricidae	*Argyrotaenia velutinana* (Walker, 1863)	shelter builder	1
Tortricidae	*Choristoneura rosaceana* (Harris, 1841)	shelter builder	1

Tortricidae	*Gretchena deludana* (Clemens, 1864)	shelter builder	42
Tortricidae	*Pandemis limitata* (Robinson, 1869)	shelter builder	4
Tortricidae	*Phaecasiophora niveiguttana* Grote, 1873	shelter builder	3
Tortricidae	*Platynota idaeusalis* (Walker, 1859)	shelter builder	1
Tortricidae	*Pseudexentera oregonana* (Walsingham, 1879)	shelter builder	1
		Total	**2015**

Appendix 2. The code for R used in this study.

This appendix has the entire code in R developed for the statistical analyses herein presented.

```
setwd("~/SCBI Plant and Insect Project")
#RawData_LeafTraits_Jul1222 <- read_excel("RawData_LeafTraits_Jul1222.xlsx")
#Caterpillar_data_Thomas_Final <- read excel("Caterpillar_data_Thomas_Final.xlsx",
#  col_types = c("text", "text", "text",
#     "text", "text", "text", "text", "text",
#      "text", "text", "text", "numeric",
#      "numeric", "text", "numeric", "numeric"))
load("LeafTraits.RData")
load("Caterpillar.RData")
library(ggplot2)
#A scatterplot with leaf toughness and thickness by tree species
#plot(RawData_LeafTraits_Jul1222$Relative_Tree_Height[RawData_LeafTraits_Jul1222$Scientifi
    c_Name=="Acer rubrum"],RawData_LeafTraits_Jul1222$`Average
    Thickness`[RawData_LeafTraits_Jul1222$Scientific_Name=="Acer rubrum"])
#Ignore pdf("Leaf Touhgness by Relative Tree Height.pdf")
par(mfrow=c(4,4))
for (sn in unique(RawData_LeafTraits_Jul1222$Scientific_Name)) {
  # Scatterplot for our variables plot(`Average Toughness` ~ Relative_Tree_Height,
    data=RawData_LeafTraits_Jul1222[RawData_LeafTraits_Jul1222$Scientific_Name==sn,])
  fit <- lm(`Average Toughness` ~ Relative_Tree_Height,
    data=RawData_LeafTraits_Jul1222[RawData_LeafTraits_Jul1222$Scientific_Name==sn,])
  # line of best fit abline(fit)
  # The same as above but with ggplot which gives us a confidence envelope
  ggplot(RawData_LeafTraits_Jul1222[RawData_LeafTraits_Jul1222$Scientific_Name==sn,],
      aes(x = Relative_Tree_Height, y = "Average Toughness")) +
   geom_point() +
   stat_smooth(method = "lm")
  }
#Use a loop instead aggCat <- aggregate(Count~`Tree-Nr.`+Guild+`Tree
    species`,data=Caterpillar_data_Thomas_Final,FUN=sum)
RawData_LeafTraits_Jul1222$incidence <- NA
RawData_LeafTraits_Jul1222$exposed_feeder <- NA
RawData_LeafTraits_Jul1222$shelter_builder <- NA
for (tn in unique(RawData_LeafTraits_Jul1222$Tree_Number)) {
```

```
 on_tree <- Caterpillar_data_Thomas_Final[tn==Caterpillar_data_Thomas_Final$`Tree-Nr.`,]
 lbub <-
    as.data.frame(t(matrix(unlist(lapply(strsplit(unique(RawData_LeafTraits_Jul1222$Canopy_H
    eight.m),"-",fixed=TRUE),function(x)
    gsub("\\[|\\]","",x))),nrow=2,dimnames=list(c("lb","ub")))))
 for (i in 1:nrow(lbub) ){
  lb <- lbub$lb[i]
  ub <- lbub$ub[i]
  at_height <- on_tree[(on_tree$`Height (m)`>lb)&(on_tree$`Height (m)`<=ub),]
  RawData_LeafTraits_Jul1222$incidence[RawData_LeafTraits_Jul1222$Tree_Number==tn &
    RawData_LeafTraits_Jul1222$Canopy_Height.m==paste0("[",lb,"-",ub,"]")] <-
    sum(at_height$Count)
  exposed_feeder_at_height <- at_height[at_height$Guild=="Exposed feeder",]

    RawData_LeafTraits_Jul1222$exposed_feeder[RawData_LeafTraits_Jul1222$Tree_Number=
    =tn & RawData_LeafTraits_Jul1222$Canopy_Height.m==paste0("[",lb,"-",ub,"]")] <-
    sum(exposed_feeder_at_height$Count)
  shelter_builder_at_height <- at_height[at_height$Guild=="Shelter builder",]

    RawData_LeafTraits_Jul1222$shelter_builder[RawData_LeafTraits_Jul1222$Tree_Number==
    tn & RawData_LeafTraits_Jul1222$Canopy_Height.m==paste0("[",lb,"-",ub,"]")] <-
    sum(shelter_builder_at_height$Count)
    }
}

#Aggregate to merge in caterpillar abundance data
#Use a loop instead aggCat <- aggregate(Count~`Tree-Nr.`+Guild+`Tree
    species`,data=Caterpillar_data_Thomas_Final,FUN=sum)
RawData_LeafTraits_Jul1222$incidence_subset <- NA
RawData_LeafTraits_Jul1222$exposed_feeder_subset <- NA
RawData_LeafTraits_Jul1222$shelter_builder_subset <- NA
for (tn in unique(RawData_LeafTraits_Jul1222$Tree_Number)) {
 on_tree <- Caterpillar_data_Thomas_Final[tn==Caterpillar_data_Thomas_Final$`Tree-Nr.` & !(
    Caterpillar_data_Thomas_Final$`Species name`%in%c("Psilocorsis reflexella" , "Anisota
    senatoria", "Symmerista albifrons")), ]
 lbub <-
    as.data.frame(t(matrix(unlist(lapply(strsplit(unique(RawData_LeafTraits_Jul1222$Canopy_H
    eight.m),"-",fixed=TRUE),function(x)
    gsub("\\[|\\]","",x))),nrow=2,dimnames=list(c("lb","ub")))))
 for (i in 1:nrow(lbub) ){
  lb <- lbub$lb[i]
```

```
  ub <- lbub$ub[i]
  at_height <- on_tree[(on_tree$`Height (m)`>lb)&(on_tree$`Height (m)`<=ub),]

    RawData_LeafTraits_Jul1222$incidence_subset[RawData_LeafTraits_Jul1222$Tree_Number
    ==tn & RawData_LeafTraits_Jul1222$Canopy_Height.m==paste0("[",lb,"-",ub,"]")] <-
    sum(at_height$Count)
  exposed_feeder_at_height <- at_height[at_height$Guild=="Exposed feeder",]

    RawData_LeafTraits_Jul1222$exposed_feeder_subset[RawData_LeafTraits_Jul1222$Tree_N
    umber==tn & RawData_LeafTraits_Jul1222$Canopy_Height.m==paste0("[",lb,"-",ub,"]")] <-
    sum(exposed_feeder_at_height$Count)
  shelter_builder_at_height <- at_height[at_height$Guild=="Shelter builder",]

    RawData_LeafTraits_Jul1222$shelter_builder_subset[RawData_LeafTraits_Jul1222$Tree_Nu
    mber==tn & RawData_LeafTraits_Jul1222$Canopy_Height.m==paste0("[",lb,"-",ub,"]")] <-
    sum(shelter_builder_at_height$Count)
    }
 }

#Starting initial exploratory analysis here
mod <- glm(incidence ~ `Average Thickness` + `Average Toughness` + `Relative_Tree_Height` +
    `Scientific_Name`, family="poisson", data=RawData_LeafTraits_Jul1222)
summary(mod)
summary(RawData_LeafTraits_Jul1222$`Average Toughness`)
summary(RawData_LeafTraits_Jul1222$`Average Thickness`)
library(MASS)
mod <- glm.nb(y ~ x1 + x2 + x3, data=RawData_LeafTraits_Jul1222)
mod <- glm(incidence ~ `Average Thickness` + `Average Toughness` + `Relative_Tree_Height`,
    family="poisson", data=RawData_LeafTraits_Jul1222)
summary(mod)
install.packages("lme4")
library(lme4)
mod <- glmer(incidence ~ `Average Thickness` + `Average Toughness` + `Relative_Tree_Height` +
    (1|`Scientific_Name`), family="poisson", data=RawData_LeafTraits_Jul1222)
summary(mod)
unique(RawData_LeafTraits_Jul1222$Relative_Tree_Height)
#Exploratory interactions below
mod <- glmer(incidence ~ `Average Thickness` + `Average Toughness` +`Relative_Tree_Height` +
    `Average Thickness` * `Relative_Tree_Height` + (1|`Scientific_Name`), family="poisson",
    data=RawData_LeafTraits_Jul1222)
summary(mod)
```

```
mod <- glmer(exposed_feeder ~ `Average Thickness` + `Average Toughness`
    +`Relative_Tree_Height` + `Average Thickness` * `Relative_Tree_Height` +
    (1|`Scientific_Name`), family="poisson", data=RawData_LeafTraits_Jul1222)
summary(mod)
mod <- glmer(shelter_builder ~ `Average Thickness` + `Average Toughness`
    +`Relative_Tree_Height` + `Average Thickness` * `Relative_Tree_Height` +
    (1|`Scientific_Name`), family="poisson", data=RawData_LeafTraits_Jul1222)
summary(mod)
mod <- glmer(exposed_feeder ~ `Average Thickness` + `Average Toughness`
    +`Relative_Tree_Height` + `Average Toughness` * `Relative_Tree_Height` +
    (1|`Scientific_Name`), family="poisson", data=RawData_LeafTraits_Jul1222)
summary(mod)
mod <- glmer(shelter_builder ~ `Average Thickness` + `Average Toughness`
    +`Relative_Tree_Height` + `Average Toughness` * `Relative_Tree_Height` +
    (1|`Scientific_Name`), family="poisson", data=RawData_LeafTraits_Jul1222)
summary(mod)
mod <- glmer(exposed_feeder ~ `Average Thickness` + `Average Toughness`
    +`Relative_Tree_Height` + `Average Toughness` * `Relative_Tree_Height` + `Average
    Thickness` * `Relative_Tree_Height` + (1|`Scientific_Name`), family="poisson",
    data=RawData_LeafTraits_Jul1222)
summary(mod)
mod <- glmer(shelter_builder ~ `Average Thickness` + `Average Toughness`
    +`Relative_Tree_Height` + `Average Toughness` * `Relative_Tree_Height` + `Average
    Thickness` * `Relative_Tree_Height` + (1|`Scientific_Name`), family="poisson",
    data=RawData_LeafTraits_Jul1222)
summary(mod)
#gg predict
install.packages("devtools")
library(ggeffects)
#how to install ggeffects. Only run once
#install.packages("devtools"); library(devtools);
    remotes::install_github("strengejacke/ggeffects")
#install.packages("ggpubr")
library(ggeffects)
library(dplyr)
library(ggpubr)
summary(RawData_LeafTraits_Jul1222$Relative_Tree_Height)
#2 quartiles came from here. 0.5910-0.8670
mod <- glmer(exposed_feeder ~ `Average Thickness` + `Average Toughness`
    +`Relative_Tree_Height` + `Average Toughness` * `Relative_Tree_Height` + `Average
```

```
    Thickness` * `Relative_Tree_Height` + (1|`Scientific_Name`), family="poisson",
    data=RawData_LeafTraits_Jul1222)
lowplot <-  plot(ggpredict(mod, terms=list(`Average Thickness`=(10:50)/100), condition =
    c(Relative_Tree_Height = .5910)))
highplot <- plot(ggpredict(mod, terms=list(`Average Thickness`=(10:50)/100), condition =
    c(Relative_Tree_Height = .8670)))
mod
summary(mod)
ggarrange(lowplot, highplot)
summary(RawData_LeafTraits_Jul1222$Relative_Tree_Height)

install.packages("margins")
library(margins)
install.packages(c("mfx","sjPlot"))
library(mfx)
library(sjPlot)
install.packages("MASS")
library(MASS)
#Let's look at just the linear model
par(mfrow=c(1,1))
mod <- glm(incidence ~ `Average Thickness` + `Average Toughness` + `Relative_Tree_Height` +
    `Scientific_Name`, family="poisson", data=RawData_LeafTraits_Jul1222)
mod2 <- glm.nb(incidence ~ `Average Thickness` + `Average Toughness` + `Relative_Tree_Height`
    + `Scientific_Name`, data=RawData_LeafTraits_Jul1222)
pchisq(2 * (logLik(mod) - logLik(mod2)), df = 1, lower.tail = FALSE)
modirr <- poissonirr(incidence ~ `Average Thickness` + `Average Toughness` +
    `Relative_Tree_Height` + `Scientific_Name`, data=RawData_LeafTraits_Jul1222)
summary(mod)
modirr
tab_model(mod)
cplot(mod,"Average Thickness", main = "Total Incidence by Average Thickness")
mod2irr<-negbinirr(incidence ~ `Average Thickness` + `Average Toughness` +
    `Relative_Tree_Height` + `Scientific_Name`, data=RawData_LeafTraits_Jul1222)
mod2irr
tab_model(mod2)
cplot(mod2,"Average Thickness", main = "Total Incidence by Average Thickness")

#Specific incidences
mod <- glm(exposed_feeder ~ `Average Thickness` + `Average Toughness` +
    `Relative_Tree_Height` + `Scientific_Name`, family="poisson",
    data=RawData_LeafTraits_Jul1222)
```

```
mod2 <- glm.nb(incidence ~ `Average Thickness` + `Average Toughness` + `Relative_Tree_Height`
    + `Scientific_Name`, data=RawData_LeafTraits_Jul1222)
pchisq(2 * (logLik(mod) - logLik(mod2)), df = 1, lower.tail = FALSE)
modirr <- poissonirr(exposed_feeder ~ `Average Thickness` + `Average Toughness` +
    `Relative_Tree_Height` + `Scientific_Name`, data=RawData_LeafTraits_Jul1222)
summary(mod)
modirr
tab_model(mod)
cplot(mod, "Average Thickness", main = "Exposed Feeder Incidence by Leaf Thickness")

mod <- glm(shelter_builder ~ `Average Thickness` + `Average Toughness` +
    `Relative_Tree_Height` + `Scientific_Name`, family="poisson",
    data=RawData_LeafTraits_Jul1222)
mod2 <- glm.nb(incidence ~ `Average Thickness` + `Average Toughness` + `Relative_Tree_Height`
    + `Scientific_Name`, data=RawData_LeafTraits_Jul1222)
pchisq(2 * (logLik(mod) - logLik(mod2)), df = 1, lower.tail = FALSE)
modirr <- poissonirr(shelter_builder ~ `Average Thickness` + `Average Toughness`. +
    `Relative_Tree_Height` + `Scientific_Name`, data=RawData_LeafTraits_Jul1222)
summary(mod)
modirr
tab_model(mod)
cplot(mod, "Average Thickness", main = "Shelter Builder Incidence by Leaf Thickness")

#Now Toughness
mod <- glm(incidence ~ `Average Thickness` + `Average Toughness` + `Relative_Tree_Height` +
    `Scientific_Name`, family="poisson", data=RawData_LeafTraits_Jul1222)
mod2 <- glm.nb(incidence ~ `Average Thickness` + `Average Toughness` + `Relative_Tree_Height`
    + `Scientific_Name`, data=RawData_LeafTraits_Jul1222)
pchisq(2 * (logLik(mod) - logLik(mod2)), df = 1, lower.tail = FALSE)
modirr <- poissonirr(incidence ~ `Average Thickness` + `Average Toughness` +
    `Relative_Tree_Height` + `Scientific_Name`, data=RawData_LeafTraits_Jul1222)
summary(mod)
modirr
tab_model(mod)
cplot(mod, "Average Toughness", main = "Total Incidence by Average Toughness")

mod <- glm(exposed_feeder ~ `Average Thickness` + `Average Toughness` +
    `Relative_Tree_Height` + `Scientific_Name`, family="poisson",
    data=RawData_LeafTraits_Jul1222)
mod2 <- glm.nb(incidence ~ `Average Thickness` + `Average Toughness` + `Relative_Tree_Height`
    + `Scientific_Name`, data=RawData_LeafTraits_Jul1222)
```

```
pchisq(2 * (logLik(mod) - logLik(mod2)), df = 1, lower.tail = FALSE)
modirr <- poissonirr(exposed_feeder ~ `Average Thickness` + `Average Toughness` +
    `Relative_Tree_Height` + `Scientific_Name`, data=RawData_LeafTraits_Jul1222)
summary(mod)
modirr
tab_model(mod)
cplot(mod, "Average Toughness", main = "Exposed Feeder Incidence by Leaf Toughness")

mod <- glm(shelter_builder ~ `Average Thickness` + `Average Toughness` +
    `Relative_Tree_Height` + `Scientific_Name`, family="poisson",
    data=RawData_LeafTraits_Jul1222)
mod2 <- glm.nb(incidence ~ `Average Thickness` + `Average Toughness` + `Relative_Tree_Height`
    + `Scientific_Name`, data=RawData_LeafTraits_Jul1222)
pchisq(2 * (logLik(mod) - logLik(mod2)), df = 1, lower.tail = FALSE)
modirr <- poissonirr(shelter_builder ~ `Average Thickness` + `Average Toughness` +
    `Relative_Tree_Height` + `Scientific_Name`, data=RawData_LeafTraits_Jul1222)
summary(mod)
modirr
tab_model(mod)
cplot(mod, "Average Toughness", main = "Shelter Builder Incidence by Leaf Toughness")
#Now RTH
mod <- glm(incidence ~ `Average Thickness` + `Average Toughness` + `Relative_Tree_Height` +
    `Scientific_Name`, family="poisson", data=RawData_LeafTraits_Jul1222)
mod2 <- glm.nb(incidence ~ `Average Thickness` + `Average Toughness` + `Relative_Tree_Height`
    + `Scientific_Name`, data=RawData_LeafTraits_Jul1222)
pchisq(2 * (logLik(mod) - logLik(mod2)), df = 1, lower.tail = FALSE)
modirr <- poissonirr(incidence ~ `Average Thickness` + `Average Toughness` +
    `Relative_Tree_Height` + `Scientific_Name`, data=RawData_LeafTraits_Jul1222)
summary(mod)
modirr
tab_model(mod)
cplot(mod, "Relative_Tree_Height", main = "Total Incidence by Relative Tree Height",xlab =
    "Relative Tree Height")

mod <- glm(exposed_feeder ~ `Average Thickness` + `Average Toughness` +
    `Relative_Tree_Height` + `Scientific_Name`, family="poisson",
    data=RawData_LeafTraits_Jul1222)
mod2 <- glm.nb(incidence ~ `Average Thickness` + `Average Toughness` + `Relative_Tree_Height`
    + `Scientific_Name`, data=RawData_LeafTraits_Jul1222)
pchisq(2 * (logLik(mod) - logLik(mod2)), df = 1, lower.tail = FALSE)
```

```
modirr <- poissonirr(exposed_feeder ~ `Average Thickness` + `Average Toughness` +
    `Relative_Tree_Height` + `Scientific_Name`, data=RawData_LeafTraits_Jul1222)
summary(mod)
modirr
tab_model(mod)
cplot(mod, "Relative_Tree_Height", main = "Exposed Feeder Incidence by Relative Tree Height",
    xlab = "Relative Tree Height")

mod <- glm(shelter_builder ~ `Average Thickness` + `Average Toughness` +
    `Relative_Tree_Height` + `Scientific_Name`, family="poisson",
    data=RawData_LeafTraits_Jul1222)
mod2 <- glm.nb(incidence ~ `Average Thickness` + `Average Toughness` + `Relative_Tree_Height`
    + `Scientific_Name`, data=RawData_LeafTraits_Jul1222)
pchisq(2 * (logLik(mod) - logLik(mod2)), df = 1, lower.tail = FALSE)
modirr <- poissonirr(shelter_builder ~ `Average Thickness` + `Average Toughness` +
    `Relative_Tree_Height` + `Scientific_Name`, data=RawData_LeafTraits_Jul1222)
summary(mod)
modirr
tab_model(mod)
cplot(mod, "Relative_Tree_Height", main = "Shelter Builder Incidence by Relative Tree Height",
    xlab = "Relative Tree Height")
#Incidences end
summary(mod)
summary(mod)
#end looking at linear model

mod <- glmer(shelter_builder ~ `Average Thickness` + `Average Toughness`
    +`Relative_Tree_Height` + `Average Toughness` * `Relative_Tree_Height` + `Average
    Thickness` * `Relative_Tree_Height` + (1|`Scientific_Name`), family="poisson",
    data=RawData_LeafTraits_Jul1222)
summary(mod)
mod2 <- glmer(shelter_builder ~ `Average Thickness`  +`Relative_Tree_Height` + `Average
    Thickness` * `Relative_Tree_Height` + (1|`Scientific_Name`), family="poisson",
    data=RawData_LeafTraits_Jul1222)
summary(mod2)
anova(mod, mod2) # Significance of anova test ends here

# Now let's look at exposed feeders

lowplot <-  plot(ggpredict(mod2, terms=list(`Average Thickness`=(10:50)/100), condition =
    c(Relative_Tree_Height = .5910)))
```

```
highplot <- plot(ggpredict(mod2, terms=list(`Average Thickness`=(10:50)/100), condition =
    c(Relative_Tree_Height = .8670)))
mod2
summary(mod2)
ggarrange(lowplot, highplot)
sum((Caterpillar_data_Thomas_Final$Count))

#linear models for counts of subset incident
mod <- glm(incidence_subset ~ `Average Thickness` + `Average Toughness` +
    `Relative_Tree_Height` + `Scientific_Name`, family="poisson",
    data=RawData_LeafTraits_Jul1222)
modirr <- poissonirr(incidence_subset ~ `Average Thickness` + `Average Toughness` +
    `Relative_Tree_Height` + `Scientific_Name`, data=RawData_LeafTraits_Jul1222)
summary(mod)
modirr
tab_model(mod)
cplot(mod,"Average Thickness", main = "Total Incidence by Average Thickness")

#Specific incidences (SUBSET)
mod <- glm(exposed_feeder_subset ~ `Average Thickness` + `Average Toughness` +
    `Relative_Tree_Height` + `Scientific_Name`, family="poisson",
    data=RawData_LeafTraits_Jul1222)
modirr <- poissonirr(exposed_feeder_subset ~ `Average Thickness` + `Average Toughness` +
    `Relative_Tree_Height` + `Scientific_Name`, data=RawData_LeafTraits_Jul1222)
summary(mod)
modirr
tab_model(mod)
cplot(mod, "Average Thickness", main = "Exposed Feeder Incidence by Leaf Thickness")

mod <- glm(shelter_builder_subset ~ `Average Thickness` + `Average Toughness` +
    `Relative_Tree_Height` + `Scientific_Name`, family="poisson",
    data=RawData_LeafTraits_Jul1222)
modirr <- poissonirr(shelter_builder_subset ~ `Average Thickness` + `Average Toughness` +
    `Relative_Tree_Height` + `Scientific_Name`, data=RawData_LeafTraits_Jul1222)
summary(mod)
modirr
tab_model(mod)
cplot(mod, "Average Thickness", main = "Shelter Builder Incidence by Leaf Thickness")

#Now toughness (SUBSET)
#linear models for counts of subset incident
```

```
mod <- glm(incidence_subset ~ `Average Thickness` + `Average Toughness` +
    `Relative_Tree_Height` + `Scientific_Name`, family="poisson",
    data=RawData_LeafTraits_Jul1222)
modirr <- poissonirr(incidence_subset ~ `Average Thickness` + `Average Toughness` +
    `Relative_Tree_Height` + `Scientific_Name`, data=RawData_LeafTraits_Jul1222)
summary(mod)
modirr
tab_model(mod)
cplot(mod,"Average Thickness", main = "Total Incidence by Average Thickness")

#Specific incidences (SUBSET)
mod <- glm(exposed_feeder_subset ~ `Average Thickness` + `Average Toughness` +
    `Relative_Tree_Height` + `Scientific_Name`, family="poisson",
    data=RawData_LeafTraits_Jul1222)
modirr <- poissonirr(exposed_feeder_subset ~ `Average Thickness` + `Average Toughness` +
    `Relative_Tree_Height` + `Scientific_Name`, data=RawData_LeafTraits_Jul1222)
summary(mod)
modirr
tab_model(mod)
cplot(mod, "Average Thickness", main = "Exposed Feeder Incidence by Leaf Thickness")

mod <- glm(shelter_builder_subset ~ `Average Thickness` + `Average Toughness` +
    `Relative_Tree_Height` + `Scientific_Name`, family="poisson",
    data=RawData_LeafTraits_Jul1222)
modirr <- poissonirr(shelter_builder_subset ~ `Average Thickness` + `Average Toughness` +
    `Relative_Tree_Height` + `Scientific_Name`, data=RawData_LeafTraits_Jul1222)
summary(mod)
modirr
tab_model(mod)
cplot(mod, "Average Thickness", main = "Shelter Builder Incidence by Leaf Thickness")

#Now toughness (SUBSET)
mod <- glm(incidence_subset ~ `Average Thickness` + `Average Toughness` +
    `Relative_Tree_Height` + `Scientific_Name`, family="poisson",
    data=RawData_LeafTraits_Jul1222)
modirr <- poissonirr(incidence_subset ~ `Average Thickness` + `Average Toughness` +
    `Relative_Tree_Height` + `Scientific_Name`, data=RawData_LeafTraits_Jul1222)
summary(mod)
modirr
tab_model(mod)
cplot(mod, "Average Toughness", main = "Total Incidence by Average Toughness")
```

```
mod <- glm(exposed_feeder_subset ~ `Average Thickness` + `Average Toughness` +
    `Relative_Tree_Height` + `Scientific_Name`, family="poisson",
    data=RawData_LeafTraits_Jul1222)
modirr <- poissonirr(exposed_feeder_subset ~ `Average Thickness` + `Average Toughness` +
    `Relative_Tree_Height` + `Scientific_Name`, data=RawData_LeafTraits_Jul1222)
summary(mod)
modirr
tab_model(mod)
cplot(mod, "Average Toughness", main = "Exposed Feeder Incidence by Leaf Toughness")

mod <- glm(shelter_builder_subset ~ `Average Thickness` + `Average Toughness` +
    `Relative_Tree_Height` + `Scientific_Name`, family="poisson",
    data=RawData_LeafTraits_Jul1222)
modirr <- poissonirr(shelter_builder_subset ~ `Average Thickness` + `Average Toughness` +
    `Relative_Tree_Height` + `Scientific_Name`, data=RawData_LeafTraits_Jul1222)
summary(mod)
modirr
tab_model(mod)
cplot(mod, "Average Toughness", main = "Shelter Builder Incidence by Leaf Toughness")

#Now RTH (SUBSET)
mod <- glm(incidence_subset ~ `Average Thickness` + `Average Toughness` +
    `Relative_Tree_Height` + `Scientific_Name`, family="poisson",
    data=RawData_LeafTraits_Jul1222)
modirr <- poissonirr(incidence_subset ~ `Average Thickness` + `Average Toughness` +
    `Relative_Tree_Height` + `Scientific_Name`, data=RawData_LeafTraits_Jul1222)
summary(mod)
modirr
tab_model(mod)
cplot(mod, "Relative_Tree_Height", main = "Total Incidence by Relative Tree Height", xlab =
    "Relative Tree Height")

mod <- glm(exposed_feeder_subset ~ `Average Thickness` + `Average Toughness` +
    `Relative_Tree_Height` + `Scientific_Name`, family="poisson",
    data=RawData_LeafTraits_Jul1222)
modirr <- poissonirr(exposed_feeder_subset ~ `Average Thickness` + `Average Toughness` +
    `Relative_Tree_Height` + `Scientific_Name`, data=RawData_LeafTraits_Jul1222)
summary(mod)
modirr
tab_model(mod)
```

```
cplot(mod, "Relative_Tree_Height", main = "Exposed Feeder Incidence by Relative Tree Height",
    xlab = "Relative Tree Height")

mod <- glm(shelter_builder_subset ~ `Average Thickness` + `Average Toughness` +
    `Relative_Tree_Height` + `Scientific_Name`, family="poisson",
    data=RawData_LeafTraits_Jul1222)
modirr <- poissonirr(shelter_builder_subset ~ `Average Thickness` + `Average Toughness` +
    `Relative_Tree_Height` + `Scientific_Name`, data=RawData_LeafTraits_Jul1222)
summary(mod)
modirr
tab_model(mod)
cplot(mod, "Relative_Tree_Height", main = "Shelter Builder Incidence by Relative Tree Height",
    xlab = "Relative Tree Height")
#Sum by all caterpillar species
write.csv(aggregate(Count~`Species
    name`,data=Caterpillar_data_Thomas_Final,FUN=sum,na.rm=TRUE),row.names=FALSE,file=
    "Species Counts of Caterpillars.csv")
```