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The cumulative effects of hurricanes on *Eleutherodactylus* frogs and *Anolis* lizards within the Canopy Trimming Experiment, El Yunque National Forest

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By

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DEDICATION

I dedicate this thesis to my grandparents, Harry and Stella Harris, from whom I gained my love of nature and ecology.

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Abstract

On September 20th, 2017, Hurricane Maria stuck Puerto Rico as a Category 5 storm. Hurricanes are large-scale common occurrences in the Caribbean, and are the most significant natural disturbance involved in altering the forest structure of the Luquillo Mountain range of Puerto Rico. Climate change is expected to result in more frequent major hurricanes (Category 3 or higher). When Hurricane Hugo hit Puerto Rico in 1989, it was the first major hurricane to hit the island in nearly 60 years; the island has been hit by three major hurricanes since Hugo. The effects of multiple hurricanes on assemblages of Puerto Rican herpetofauna are not well known.

We compared pre- and post-Hurricane population data sets of the two most abundant vertebrates in the forest, *Eleutherodactylus* frogs and *Anolis* lizards. Population data was collected from four plots within the Canopy Trimming Experiment, a long-term ecological study at El Verde Field Station, El Yunque National Forest. Two plots were considered “control” plots and had been exposed only to Hurricane Maria. Two plots were “treatment” plots, and in addition to Hurricane Maria, were exposed in 2014 to a simulated hurricane via canopy removal and tree branch placement on the forest floor. Our findings indicate that multiple hurricanes have muted effects on herpetofaunal populations when comparted to a single hurricane, as populations have less time to recover between hurricanes, thus dampening the cycle of population decrease and subsequent recovery. Thus, a climate regime of more frequent hurricanes may result in novel population dynamics for Puerto Rican *Anolis* lizards and *Eleutherodactylus* frogs.

Chapter 1

Introduction

Hurricanes are large-scale common occurrences in the Caribbean (Walker et al., 1991), and are the most significant natural disturbance involved in altering the forest structure of the Luquillo Mountain range of Puerto Rico (Brokaw et al., 2012). The damage caused by hurricanes opens the forest canopy and accelerates the canopy turnover rate in the Luquillo Mountains compared to tropical forests that are not affected by these systems. In 1989, Hurricane Hugo opened the forest canopy and decreased canopy height at LTER by 50% or more (Brokaw and Grear, 1991). The most significant structural impacts of hurricanes on the forests of Puerto Rico are the opening/destruction of the canopy, the deposition of large amounts of organic debris matter on the forest floor (Ostertag et al., 2003), and the subsequent change in foliage profiles in the forest, as seedlings increase their density at the ground level in response to the increase in available light (Brokaw and Greer, 1991). Essentially, hurricanes remove vegetative habitat from the canopy and place it at lower levels of the forest.

These changes in forest structure have the potential to impact two herpetofaunal groups within the Luquillo forest- the assemblages of diurnal *Anolis* lizards and populations of the nocturnal frog *Eleutherodactylus coqui.* Both require certain habitats to thrive. Anole species of the Greater Antilles islands will nearly always fall into one of six “ecomorphs”- grass, twig, trunk-ground, trunk, truck-crown, crown giant (Losos, 2009). Each ecomorph has a particular morphology that is related to the habitat or niche the species utilizes (Williams, 1972). Although a habitat generalist (Beard et al., 2003), populations of *E. coqui* are limited by the availability of appropriate nesting sites (Woolbright, 1996). Therefore, any changes in the structure of the forest will likely impact populations of both genera.

Changes to the populations of anoles and coquis are likely to have cascading effects on the entire food web. Anoles are the most abundant vertebrate in the forest of El Verde (Reagan and Waide, 1996). Just one species, *Anolis stratulus*, may account for as much as 55.7 kg/ha of total biomass in the forests. Likewise, Stewart and Woolbright (1996) estimate a density 20,000 frogs per hectare at El Verde field station (350m asl), making them the most abundant nocturnal vertebrate. Both are predatory dietary generalists; anoles consume all manner of arthropods, neonate frogs, other anoles, and in the case of *Anolis cuvieri*, fledgling birds (Henderson and Powell, 2009). Some species are also frugivorous and nectivorous (Herrel et al., 2004). *Eleutherodactylus coqui* is an equally opportunistic consumer, have been found to feed on over 100 different species of animals from 60 different families (Henderson and Powell, 2009). Both anoles and coquis are in turn prey for other anoles, frogs, arachnids, centipedes, birds, and snakes (Henderson and Powell, 2009). Owing to their commonness and abundance, changes to the populations of *Anolis* and *Eleutherodactylus* are likely to have effects on species at both higher and lower tropic levels. Understanding the impacts that common, destructive events such as hurricane have on these animals is an essential piece of the puzzle to understanding the impacts of hurricane on the forest ecosystem as a whole.

The body of research concerning the impact of hurricanes on the herpetofaunal assemblages of the subtropical wet forests at the Luquillo Experimental Forest comes from studying the aftermath of Hurricanes Hugo and Georges, as well at the Canopy Trimming Experiment initiated in 2005. Hurricane Hugo made landfall in Puerto Rico on September 18th, 1989 as a Category 3 hurricane (Scatena, 1991); Georges hit on September 19th, 1998 as a

Category 2 storm. The Canopy Trimming Experiment simulated the two most common impacts of a hurricane on the structure of the forests of Puerto Rico- the opening of the canopy by branch removal of trees, and the deposition of organic debris on the forest floor (Sheils et al., 2015). This experiment allowed for these two variables to be studied independently of one another as well as in tandem.

Reagan (1991) found that Hugo had a significant short-term impact on anole assemblage composition, with the ground/understory species abundance of anoles shifting dramatically from a dominance of *Anolis gundlachi* pre-hurricane to *Anolis stratulus* post-hurricane. In a survey conducted September of 1981, *A. gundlachi* accounted for 83% of all anoles encountered in the forests at El Verde; *A stratulus* represented a mere 2% of anoles, presumably because the majority were in the canopy, out of view of observers. In October of 1989, *A. gundlachi* comprised only 13% of all anoles observed at ground/understory level, and *A. stratulus* accounted for 51% of all observed anoles. *A. evermanni*, another canopy species, increased from representing 12% of anole abundance pre-hurricane to 35% post hurricane. *Anolis gundlachi* did not constitute a majority of observed anoles until a year later, in a survey conducted in October of 1990; even then, it comprised only a slight majority- 38% of the abundance as opposed to 33% for *A. stratulus* and 26% for *A. evermanni*.

These results, as well as Reagan's (1991) observation that no anoles were observed higher than three meters from the ground suggest that anole habitat usage was laterally compressed, with canopy anoles such as *Anolis stratulus* forced to the lower levels of the forest after the removal of the canopy by Hurricane Hugo. *A. gundlachi*, an understory anole typical of shaded-closed canopy forests, is less heat resistant than other anole species, and appeared to compensate for the increased heat and light penetration into the understory by utilizing protected habitat that was much closer to the ground.

Woolbright (1991) found that Hurricane Hugo led to an increase in the density of adults of *Eleutherodactylus coqui*. Surveys of two $20m^2$ plots conducted from 1987 to 1989 revealed a relatively steady adult population of *E. coqui*, with 40-80 individuals per $20m^2$. One year after the hurricane, adult coquis reached 150-160 per $20m^2$ plot. This increase in individuals came at the expense of body size, with observed males averaging 3mm smaller post hurricane. Conversely, the population of juvenile *E. coqui* experienced a marked decline. Juvenile populations fluctuated pre-hurricane, from a high of approximately 250 per $20m^2$ plot in 1987 to a low of 80 juveniles in 1989. However, a year after Hurricane Hugo made landfall, juvenile coqui populations were still at a record low, with fewer than 40 juveniles identified in either of the two $20m^2$ plots in the study. Woolbright hypothesized that a subsequent period of extreme dryness after Hurricane Hugo caused a die-off of juvenile coquis. However, those that survived were more likely to reach adulthood (perhaps due to reduced resource competition?), as evidenced by the subsequent increase in adult coquis within the study area.

However, the findings of surveys for *Eleutherodactylus coqui* conducted during the CTE study (Klawinksi et al, 2014) differed from Woolbright's observations. The CTE study consisted of twelve $20m^2$ plots that were given different treatments that mimicked one or both of the most common impacts of a hurricane to the forests of El Verde- the opening of the canopy and the deposition of leaf litter, branches, and other organic debris on the forest floor. Four plots ("No Trim, No Debris") consisted of controls, and received no treatment. Four plots ("Trim, Debris") had the canopy trimmed in a manner simulating the damage to the canopy caused by Hurricane Hugo, and had the subsequently generated organic debris deposited on the forest floor within the plots. Four plots ("Trim, No Debris") had the canopy trimmed but the debris was removed and placed in the last four plots, which did not have the canopy trimmed ("No Trim, Debris").

The authors expected that canopy openness would have a detrimental effect on *Eleutherodactylus coqui* abundance, but that forest-floor debris accumulation would have a beneficial effect on coqui abundance. Expected levels of coqui abundance were therefore assumed to be found, from highest levels to lowest, in this order: "No Trim, Debris" Plots > "Trim, Debris" > "No Trim, No Debris" > "Trim, No Debris". However, results showed that regardless of debris, trimming the canopy resulted in a significant reduction of coquis compared to plots where the canopy was not trimmed (Klawinksi et al., 2014). Two possible explanations for these findings were given. The first is scale- previous research into the impacts of hurricanes on *Eleutherodactylus* frogs occurred after an actual hurricane. The forests of Puerto Rico were more or less homogenous in their canopy openness. In the CTE study, the canopy was opened only in small plots; it is likely that frogs simply moved from less-ideal conditions within the open-canopy plot to closed-canopy forest outside of the plot.

The second possible reason for a difference in results between the CTE study and previous research is structure. The canopy debris that was deposited within some of the plots after trimming was much more compressed and uniform in distribution than debris deposited by a real hurricane (Klawinksi et al., 2014). It is possible that the lack of complex habitat that would have been generated by more random distribution of litter and branches after a hurricane was one reason the CTE debris treatments failed to yield an increase in coqui populations.

Chapter 2

Research Motivation and Questions

As previously discussed, research on the effects of hurricanes on *Eleutherodactylus coqui* populations have yielded mixed results. Woolbright (1991) found *E. coqui* abundance to increase after Hurricane Hugo; however, after Hurricane Georges (1989), an increase in *E. coqui* abundance at one site in the Cordilla Central seems to be due to a decrease in other species of *Eleutherodactylus*, rather than an increase in *E. coqui* (Vilella and Fogarty, 2005). Yet at another site, an increase in *E. coqui* was the cause of the higher abundance of the species. Lastly, the CTE study found that the increase of organic debris on the forest floor in the hurricane simulation did not lead to an increase in *E. coqui* numbers, in direct contrast to Woolbright's (1991) findings. Clearly, there is room for more inquiry into the dynamics of hurricane-induced changes in frog populations.

While the effects of hurricanes on anole assemblages has also been studied, there are fewer studies specifically focused on Puerto Rican anoles than for coquis. Reagan's study (1991) stands as the definitive work for understanding how anoles are impacted by canopy removal after the storm. Anoles were not studied in the Canopy Trimming Experiment.

The need for additional research is underscored by the changing dynamic in Caribbean weather patterns. While research is still underway regarding the relationship between climate change and hurricanes, some models suggest that strong hurricanes (Category 4 and 5) will become more frequent due to warming waters (Tsuboki, 2015; Emanuel, 2005; Webster et al., 2005). If hurricanes are a dominant factor in the structure of Puerto Rican forests, then more frequent and stronger hurricanes may shift the forest recovery process, structure, and plant/animal communities in unforeseen ways.

Most recently, Hurricane Maria made landfall in Puerto Rico near Yabucoa Harbor on September 20th, 2017 as an exceptionally strong Category 4 storm with maximum sustained winds of 250 km/hour (Feng et al., 2018; Lin et al., 2018). The storm traveled in a Northwestern direction diagonally across the island, a pathway that maximized the time that the system was over land, causing massive damage. The forests of the island were heavily impacted, with an estimated 23-31 million tree deaths resulting from the storm (Feng et al., 2018); the forests at El Yunque lost a majority of their canopy, drastically altering the structure of the forest. Hurricane Maria was an exceptionally damaging storm, more so than Hugo or Georges. The aftermath of Maria has generated opportunities to study how the forests of Puerto Rico, as well as their floral and faunal assemblages, respond to the abrupt environmental changes brought out by strong hurricanes.

Considering the prominent role that both anoles and coquis play in the food web of El Verde, as well as the possibility that powerful hurricanes will become more common in the Caribbean, hurricane-induced change to these assemblages is an important subject of investigation, as changes in the populations of either are likely to have direct impacts on other animal species in the forest. Hurricane Maria has presented such a research opportunity. Using the CTE plots, we can determine if there are significant differences between *Anolis* and *Eleutherodactylus* populations that have encountered only one hurricane versus those that have been impacted by two hurricanes in a relatively short time frame. Those animals within the CTE control plots (A1, B1, C4) were never subjected to the treatment, and have only been impacted by Hurricane Maria. Those animals within the CTE plots of "Trimming, Debris" (hereafter referred to as “Treatment”) have been subjected to a simulated hurricane, most recently in 2014 (time of the most recent trimming), and then again during Maria.

After reviewing the available literature, we post the following questions:

- Did Hurricane Maria impact *Eleutherodactylus coqui* population size, population composition, microhabitat use in the CTE plots?
- Does the CTE treatment of a simulated hurricane (Trim, Debris) pre-Maria further impact *Eleutherodactylus coqui* population size, population composition, and/or microhabitat use?
- Does Hurricane Maria impact *Anolis spp.* population size, population composition, microhabitat use, and average perch height in the CTE plots?
- Does the CTE treatment of a simulated hurricane (Trim, Debris) pre-Maria further impact *Anolis spp.* population size, population composition, microhabitat use, and average perch height?

Methods

Study Site

This study took place within the Luquillo Experimental Forest, at the El Verde Field Station within the boundaries of the El Yunque National Forest. We selected six of the twelve plots previously established for the Canopy Trimming Experiment, three control plots that had not been altered during the experiment (A1, B1, C4) and three plots that had their canopies trimmed and the subsequent debris placed on the forest floor during the CTE (A3, B2, C2). Each plot is $30m^2$. However, in order to minimize edge effects, within each $30m^2$ plot is a smaller $20m^2$ plot, offset by five meters from each side of the larger plot. Each $20m^2$ plot contains three 20 meter long, 0.3 meter wide transects spaced 4.7 meters apart from each other. These transects were used for the anole and coqui visual encounter surveys. All plots are located in tabonuco forest, between 343 and 476 meters asl. More detailed descriptions of the plots, as well as the methodology of the original canopy trimming experiment, can be found in (Sheils et al., 2014).

Frequency and timing of data collection

There were four sampling periods during this study- December 2017 (Three months post-Maria), March 2018 (Six month post-Maria), June 2018 (Nine months post-Maria) and September 2018 (One year post-Maria). For each sampling period, each plot was counted three times on different days, in an attempt to account for short-term fluctuations in anole and frog activity due to weather variations. All surveys for *Anolis* lizards were conducted in the mornings, between 7:00 and 12:00. All surveys for *Eleutherodactylus* frogs were conducted between 19:00 and 24:00, but never before 10 minutes after sunset. Plots C2 and C4 were not counted during the March 2018 and June 2018 sampling periods.

Anolis and Eleutherodactylus count data collection methods

We collected data using two methodologies that utilized the same number of man-hours. When LTER interns were available, data was collected by a group of three researchers- two observers and one recorder. At the start of each transect count, the two observers stood shoulder-to-shoulder outside the plot at the end of the transect to be surveyed. The recorder followed behind the two observers the entirety of the survey. The recorder will mark the start time and tell the observers to start. Observers spent 15 minutes surveying each transect (a total of 45 minutes or 1.5 man-hours per plot). When LTER interns were unavailable, one person conducted the counts, doubling the amount of time spent surveying each transect, to ensure that the plots were surveyed with the same number of man-hours regardless of how many people were collecting data.

During surveys, observers walked transect line, visually searching for animals up to 2.0 meters from the transect on either side; we did not actively disturb the habitat looking for animals that are not immediately visible. We collected the following data for both *Eleutherodactylus* frogs and *Anolis* lizards: Species, Age (adult/juvenile), and Substrate. For anoles, we also gauged the approximate height at which we first observed the anole, in 0.5 meter increments (e.g. 0-0.5, 0.5-1.0, 1.0-1.5, etc.). A complete description the classification of species, sex, age, and substrate is included as Appendix A.

Foliage profile data collection methods

In order to obtain the understory foliage profile, we utilized a similar methodology as Brokaw and Grear (1991). First, each 30m^2 plot (including borders) was demarcated into a grid every five meters, for a total of 49 points for data collection. The three 20 meter long transects, as well as the borders of the 20m^2 area of study accounted for 25 of the 49 data collection points. At each point, we raised a PVC pipe with half-meter demarcations. When vegetative matter-alive or dead- touched the pipe, it was recorded within the appropriate height interval. Unlike Brokaw and Grear (1991), we only measured the foliage profile to five meters from the ground level.

Anolis and Eleutherodactylus data analysis methods

Anolis and *Eleutherodactylus* population estimates are presented as the average of the total number of individuals, adults, and juveniles of the three day/night sampling events per sampling period, per plot. Data is presented in this manner in order to show overall population trends of *Eleutherodactylus* and *Anolis spp*. for the entire year of sampling post-Hurricane Maria. For *Eleutherodactylus* and *Anolis* microhabitat use, population composition, and *Anolis* height, data from the six plots was combined into two groups- “Control” (A1, B1, C4) and “Treatment”

(A3, B2, C2). In order to provide the most robust data possible for data analysis, the March 2018 and June 2018 counts were excluded, as C block was not sampled at these times. For population composition, this data was then presented as the percent of the average of the three day/night sampling events per sampling period. For microhabitat use, this data is presented as the percentage of the total number of *Eleutherodactylus* or *Anolis spp.* observed over the course of the three days of data collection during a given sampling period. For *Anolis* height, all height observations made for a given species were given a numerical designation (an anole observed at 2.5-3.0 meters was listed at 2.75 meters, for example) to allow for calculation. The total height observations made for a given species over the course of a three day sampling period were then summed and averaged by the total number of anoles of that species observed over the three day sampling.

We used three factor ANOVA for data analysis. The dependent variables tested are:

- *Anolis spp./Eleutherodactylus coqui* population
- *Anolis spp*./*Eleutherodactylus coqui* population composition
- *Anolis spp./Eleutherodactylus coqui* microhabitat use
- *Anolis spp.* average perch height

These variables were analyzed against the following independent variables:

- Sampling period (time pre- or post- Hurricane Maria)
- CTE treatment (Control/Treatment)
- Block (location)

For both *Anolis* and *Eleutherodactylus*, the March 2018 and June 2018 counts were excluded from the ANOVA analysis due to lack of data for C block. ANOVA tables for every analysis in this study are included in Appendix B.

Environmental Data Analysis

Temperature and humidity data was obtained from the US Forest Service. The data loggers for the USFS take a temperature/humidity reading every 30 minutes. USFS provided us with the average of the 30 minute readings for the mornings (for anoles) and evenings (for coquis). We then selected the data for each day of each sampling period and averaged it by the number of days per sampling period (n=3).

Litterfall data is collected every two weeks by LTER staff. We obtained the average of total leaf litter for each plot, and present the total amount of leaf litter accumulated over an eight week period (four collections of leaf litter data). The foliage profile was analyzed as percent coverage at a given height. Temperature, humidity, and litterfall data was also analyzed via three-way ANOVA.

Chapter 3

Abiotic Factors Results

Due to an error with the data logger in plot A3, no temperature or humidity data is available for that plot for September 2018. Although block C was not sampled in March 2018 or June 2018, we used temperature and humidity data stored in the data logger of each plot from the same time period as the sampling dates for Blocks A and B to determine temperature and humidity averages for C block for those sampling periods. Nighttime temperatures for all plots were higher in December 2016 (pre-Maria) than December 2017 with the exception of plot B2 (Fig. 1). In December 2016, the highest temperature recorded was 22.14°C in plot A3, the lowest was 21.58°C in B2. In December 2017, plot B2 had the highest recorded temperature for the sampling period, 21.86°C, and the lowest temperature was 20.96°C, in plot A1.

Generally speaking, average temperatures were low in December 2017, peaked in June 2018, and began to drop again in September 2018. The highest recorded temperature in September 2018 was 24.75°C in plot A1; the lowest was 23.67°C in C4. No clear pattern emerges in regards to differences in temperature between control plots and treatment plots.

Nocturnal humidity levels in each plot dropped between December 2016 (pre-Maria) and December 2017 (post-Maria). In December of 2017, the highest humidity level was in C4, at 98.33%. A3 contained the lowest humidity level for December 2017, at 91.6%. In December 2017 the highest humidity levels were in B2 at 94.97%, with C2 having the lowest, 89.33%. Humidity was the lowest in all plots in March 2018 (maximum 93.57% in B2, minimum 83.27% in C2), during a dry period of weather. Humidity levels had rebounded by September of 2018, with B2 having the highest nocturnal humidity at 98.87%, and A1 having the lowest humidity, 90.57%.

Diurnal temperature and humidity levels during the *Anolis* sampling are included as Fig. 2. Temperatures were lowest in December 2017, rising until June 2018, and decreasing in September 2018, with the exception of plot A1, which continued to rise. In December 2018, the highest recorded temperature was 22.49°C in plot C2, the lowest was 21.20°C in C4. December 2017. In June, the highest temperature was 25.48°C in A3, the lowest was 24.38°C in B1. In September 2018, plot A1 continued to rise to 25.99°C. The lowest recorded temperature in September 2018 was in plot B2, 23.87°C.

For the ANOVA analysis of temperature and humidity, the sampling period of September 2018 was excluded for both anoles and coquis, due to the lack of data for A3 for that sampling period. Temperature and humidity analysis for *Eleutherodactylus coqui* included pre-hurricane data from December 2016; analysis for *Anolis spp*. did not. For nocturnal temperature averages, there were highly significant differences between sampling periods ($F_{3,6}$= 68.67, p= 4.91E-05) and between blocks ($F_{2,6}$= 12.31, p=0.008). There were also mild interactions between sampling period and block ($F_{6,6}$=4.72, p=0.04). There were no significant differences between treatments. Nocturnal humidity levels followed a similar pattern. There were highly significant differences between sampling period ($F_{3,6}$= 59.32, p=7.5E-05) and block ($F_{2,6}$= 26.00, p=0.001). For humidity, the interactions between treatment and block were much more highly significant than for temperature ($F_{2,6}$= 22.06, p=0.002).

For diurnal temperature during anole counts, there were highly significant differences between sampling periods ($F_{2,4}$= 49.72, p=0.001), but not between treatments or blocks. This held true for diurnal humidity levels as well, with moderately significant differences between sampling periods ($F_{2,4}$= 13.14, p=0.02) only.

The litterfall values given represent eight weeks of litterfall accumulation prior to the sampling period (Fig. 3). In December of 2016, all three control plots contained significantly more litter than treatment plots. In the control plots, the highest amount of litterfall was 250.36 grams in A1; the lowest amount was in C4 at 183.29 grams. In the treatment plots, the highest amount of litterfall was in C2 at 135.12 grams, the lowest amount was 72.19 grams in B2. In December 2017, three months after Hurricane Maria, all plots contained lower amounts of litterfall, but treatment plots contained slightly more (B2, 58.82 grams; A3, 51.51 grams; C2, 35.14 grams) than the corresponding control plots (B1, 35.81 grams; A1, 35.06 grams; C4, 18.59 grams). This trend continued through September 2018, with treatment plots A3, B2, and C2 containing 161.15, 100.83, and 65.83 grams of litter, respectively, and the control plots A1, B1, and C4 (control) containing 70.14, 75.36, and 58.5 grams, respectively. ANOVA analysis of litterfall from December 2016 to September 2018 shows a significant difference between sampling periods ($F_{4,8}$= 15.38, p=0.0008) and a mildly significant difference between blocks ($F_{2,8}$=4.9, p=0.04). In spite of the noted differences in amount of litterfall between control and treatments, this difference was not statistically significant. There were, however, highly significant interactions between sampling period and treatment ($F_{4,8}$= 6.35, p=0.01).

Foliage profiles are presented by block (Fig. 4a-4c). For blocks A and B, profiles for March 2018 and September 2018 are provided. For block C, only September 2018 is provided, as block C was not sampled in March 2018. For all plots, the majority of foliage coverage is at 2.0 meters or below, with the maximum amount of coverage for each plot being at the 0-0.5 meter interval, ranging from 75 to 100% coverage in each plot. As of September 2018, all plots are still largely uncovered at heights above 1.5-2.0 meters.

In both March and September 2018, treatment plots had a slightly higher percent coverage at a higher height than the corresponding control plot. In March 2018, A1 (control) had no height intervals above 20% coverage with the exception of the 0-0.5 meter interval. A3 had greater than 20% coverage at 1.0-1.5 meters and a greater than 40% coverage at 0.5-1.0 meters in March 2018. By September 2018, the highest height interval to reach more than 20% coverage in A1 was 1.0-1.5, with 0-0.5 meters still being the only height interval above 40% coverage. In A3, there was a greater than 20% coverage (nearly 25%) at the height interval of 4.0-4.5 meters, and 1.0-1.5 was the highest height interval with more than 40% coverage.

B block showed a similar trend. In March 2018, the highest height in B1 to contain more than 20% coverage was 1.0-1.5 meters; the only height interval to contain more than 40% coverage was 0-0.5meters. In B2, the height interval of 3.0-3.5meters contained more than 20% coverage, and 1.0-1.5 meters contained more than 40%. In September 2018, both plots showed less coverage at some height intervals than before, but the treatment plot of B2 showed more coverage at higher intervals than B1, with B2 having a greater than 20% coverage at 3.0-3.5 meters and a greater than 40% coverage at 1.0-1.5 meters, vs B1 with a greater than 20% coverage at 0.5-1.0 meters and a greater than 40% coverage at 0-0.5 meters.

For C block, only September 2018 data is available, but the treatment plot C2 has more coverage at higher levels than the control plot C4. C2 contained greater than 20% coverage at 4.0-4.5 meters, whereas the highest height interval with more than 20% coverage in C4 is 1.5-2.0 meters. For both plots, the height interval of 0.5-1.0 is the highest with more than 40% coverage.

***Eleutherodactylus* and *Anolis* count results**

Eleutherodactylus coqui was the only frog visually observed in the CTE plots during the study, with the exception of a single male *Leptodactylus albilabris*, which we observed every night in A3 during the sampling in September 2018. At every sampling period, in every plot, we heard calls of *Eleutherodactylus hedricki*- an arboreal species- in the canopy, out of view of our team. No other frog calls were heard during the completion of this study.

Five species of *Anolis* were observed within the CTE plots during the study- *Anolis krugi, A. cuvieri, A. evermanni, A. gundlachi, and A. stratulus*. Of those five species, *A. krugi* and *A. cuvieri* were not observed in significant numbers to allow for data analysis. *A. krugi* was observed in B block, never more than a single individual per daily count per sampling period. We observed a single adult male *A. cuvieri* on a small shrub in CTE plot C2 during the December 2017 count. This individual was emaciated, with rib, waist, and tail bones visible under the skin. Another adult male was observed in a similar condition outside of B2 prior to the start of a nighttime coqui count in December 2017. Finally, we encountered a dead, emaciated *A. cuvieri* in A3 during the March 2018 coqui count. It had not been there during the anole count earlier that morning. As *A. evermanni, A. gundlachi*, and *A. stratulus* were the three species observed with regularity, data analysis was restricted to those three species.

Eleutherodactylus coqui

Population

Population trends of *E. coqui* (Fig. 5) for A1 (control) and A3 (treatment) are similar, as are the trends for C4 (control) and C2 (treatment). For all blocks, the number of coquis observed in December 2016 (pre-Hurricane Maria) within the treatment plots were equal to or less than the number of coquis in control plots. In blocks A and B, treatment plots contained more total coquis than control plots. By September 2018, all treatment plots had more coquis than control plots. All plots in blocks A and B experienced a decrease in the number of coquis observed in March 2018, corresponding with a period of drier weather.

Block A consistently yielded the least amount of coquis, both in A1 (control) and A3 (treatment). In December 2016, A1 and A3 yielded n= 24.67 +/-2.96 and n= 22.33 +/-4.05 coquis, respectively. The first post-Maria count, in December 2017, A1 coquis were n= 20.33 +/-6.56 and A3 was n= 27.00 +/-1.53. By September 2018, the populations between the two plots continued to widen, with Al yielding n= 19.33 +/-2.18 coquis, and A3 yielding n= 29.33 +/-2.90.

B block and C block were more comparable in coqui numbers. In B block, December 2016 coquis were n=58.67+/-13.13 and n=41.00 +/-2.13, in B1 and B2 respectively. In December 2017, three months after Hurricane Maria, B1 yielded n=30.67 +/-3.18 and B2 yielded n=34.67 +/-2.9. By September 2018, B2 coquis had returned to pre-Hurricane levels, with n= 43.67 +/-2.18. B1 coquis, however, had not yet recovered, with n= 34.33 +/-7.44.

In C block, pre-hurricane December 2016 coqui populations in C4 were n= 34.33 +/-8.95 and in C2 were 38.67 +/-2.33. In December 2017, C4 contained n= 33.67 +/-1.0 total coquis, and C2 contained n=40.00 +/-0.67 total coquis, comparable to pre-hurricane levels. In Sept of 2018, the two plots yielded nearly identical amounts of coquis, with n= 43.33 +/- 4.63 in C4 and n= 44.67 +/-7.68 in C2.

ANOVA analysis of the December 2016, December 2017, and September 2018 sampling periods showed that neither the sampling period nor the CTE treatment influenced total coqui population within the six plots. Variation in coqui populations was best explained by differences among the blocks ($F_{2,4}$= 12.43, p= 0.02).

Population composition

In both control and treatment plots, juveniles comprised the majority of the pre-Maria *E. coqui* population (71.39% control, 64.05% treatment; Fig. 6). In December 2017, three months post-Maria, the number of juveniles had fallen, accounting for 42.12% (Control) and 49.65% (Treatment) of the coqui populations. In September of 2018, one year post-Maria, the juvenile population had continued to decline, to 32.99% of the Control population and 36.54% of the Treatment population. ANOVA analysis found that sampling period (time) had a highly significant influence on population composition (for adults, $F_{2,4}$= 56.54, p=0.001; for juveniles, $F_{2,4}$= 57.6, p= 0.001). Analysis found that CTE treatment (Control vs Treatment) did not have a statistically significant impact on the population composition of *E. coqui*, nor were there statistically significant differences between blocks A, B, and C. However, there was a significant interaction effect of CTE treatment and block to account for differences in population composition (for adults, $F_{2,4}$= 10.88, p=0.02; for juveniles, $F_{2,4}$= 11.05, p=0.02), indicating that on a localized scale, there are differences in population composition between the control and treatment plots of a given block.

Microhabitat use

Microhabitat data is presented as a percentage of coquis observed utilizing one of four types of habitat- hurricane debris, tree trunks, non-woody vegetation, and the ground (See Appendix A). In the control plots, adult *E. coqui* utilized the ground the most both before the hurricane and immediately after (Fig. 7a). In December 2016 (total adults n=99), 49.49% of adult coquis used the ground, compared to 26.26% utilizing non-woody vegetation and 24.24% utilizing tree trunks. In December 2017 (n=112), with the addition of a new classification of habitat (hurricane debris), 50.89% of adult coquis utilized the ground, 20.54% utilized hurricane debris, 16.07% utilized non-woody vegetation, and 12.5% utilized tree trunks. By September 2018 (n=187), microhabitat use had shifted dramatically, with only 17.11% of adult coquis utilizing the ground. The largest percentage, 35.29%, utilized non-woody vegetation, followed by 25.67% and 21.93% utilizing hurricane debris and tree trunks, respectively.

In contrast, a majority (57.27%) of adult *Eleutherodactylus coqui* in treatment plots utilized non-woody vegetation in December 2016 (n=110), followed by 23.64% using tree trunks and 19.09% using the ground. This shifted post-hurricane during December 2017 sampling period (n=144), with 34.03% utilizing the ground, 31.25% utilizing non-woody vegetation, 27.78% utilizing tree trunks, and 6.95% using hurricane debris. By September 2018 (n=244), a slight majority of adults (54.02%) were again utilizing non woody vegetation. 21.88% utilized tree trunks, 14.29% used the ground, and the use of hurricane debris increased only slightly, to 9.82% of adults.

ANOVA analysis of adult *Eleutherodactylus coqui* microhabitat use reveals that in regards to the use of hurricane debris, there were no significant differences between the sampling periods, CTE treatments, or blocks. There were statistically significant difference for use of tree trunks between sampling periods ($F_{2,4}$= 10.79, p=0.02) and a mildly significant difference for the use of tree trunks between blocks ($F_{2,4}$= 7.58, p=0.04). There were significant interactions between all three independent variables for tree trunk use, with interactions between sampling period and CTE treatment being highly significant ($F_{2,4}$= 21.37, p=0.007) sampling period and block ($F_{4,4}$= 12.11,p=0.02), and CTE treatment and block ($F_{2,4}$= 12.62, p=0.02). For non-woody vegetation, the only statistically significant difference was between CTE treatments ($F_{1,4}$= 14.19, p=0.02). Adult *E. coqui* use of the ground between sampling periods was strongly significant

($F_{2,4}$= 15.94, p=0.01); differences between CTE treatments were moderately significant ($F_{1,4}$=13.99, p=0.02).

In December of 2016, juveniles in both control and treatment plots showed a preference for non-woody vegetation (Fig. 7b), with 78.57% of juveniles in the control plots (total juveniles n=252) and 75.90% in treatment plots (n=195) using this microhabitat. In the control plots, the remaining juveniles utilized the ground (18.25%), with only 3.17% utilizing tree trunks. The remaining juveniles in the treatment plots were more evenly split among microhabitat use, with 13.85% using tree trunks and 10.26 utilizing the ground.

During the first post-Maria sampling, in December 2017 (control juvenile n=115; treatment juvenile n=142), use of non-woody vegetation decreased among juveniles, to just 30.43%. At this sampling, just over half (51.30%) were encountered on the ground, 9.57% were found on hurricane debris, and 8.70% were found on tree trunks. A similar shift in habitat use occurred in the treatment plots, but not nearly to the extent as in the control plots. In December 2017, the use of non-woody vegetation among juvenile coquis dropped to 58.45%, and the percent of juveniles found on the ground increased to 23.94%. Tree trunks were utilized by 15.49% of juvenile coquis; just 2.11% utilized hurricane debris.

One year after Hurricane Maria, in September 2018 (control juvenile n=98; treatment juvenile n=126), a majority of juvenile coquis in both control and treatment plots returned to using non-woody vegetation; 57.14% of juveniles in the control plots and 82.54% of juveniles in the treatment plots. Of the remaining juveniles in the control plot, 18.57% were observed on hurricane debris, 12.24% on tree trunks, and 12.24% on the ground. In the treatment plots, 7.94% used tree trunks, 5.56% were observed on the ground, and 3.79% utilized hurricane debris. For juvenile *Eleutherodactylus coqui*, there was a strongly significant difference between sampling periods for the use of hurricane debris ($F_{2,4}$= 16.75, p=0.01). There were no statistically significant differences for juvenile use of tree trunks between any of the independent variables. Differences between CTE treatments in juvenile use of the ground were moderately significant ($F_{1,4}$= 13.04, p=0.02).

Juvenile use of non-woody vegetation showed the most variation. There were highly significant differences between sampling periods ($F_{2,4}$=54.45, p=0.001) and CTE treatments ($F_{1,4}$= 33.65, p=0.004), as well as mildly significant differences between blocks ($F_{2,4}$= 7.59, p=0.04). Additionally, there was moderate interaction between sampling period and CTE treatments ($F_{2,4}$= 10.67, p=0.02).

***Anolis spp*.**

Population

Population trends of *Anolis evermanni*, *A. gundlachi*, and *A. stratulus* within each plot are presented by block (Figs. 8a-8c). *A. evermanni* was the least abundant anole in every plot at every sampling period, with the exception of CTE plot C2 during September 2018. In December 2017, three months post-Maria, all treatment plots contained fewer *A. evermanni* than corresponding control plots. No matter the treatment, *A. evermanni* was the least common anole. The highest number of encountered *A. evermanni* in the control plots was n= 10.67 +/- 1.2 in C4; the highest number for *A. evermanni* in treatment plots was in B2, at n=4.67 +/- 1.76. By September 2018, the population of *A. evermanni* had fallen in every plot with the exception of C2, which not only rose but surpassed the number of *A. stratulus* found in the plot. ANOVA analysis on the population of *A. evermanni* found that none of the independent variables accounted for differences in population between December 2017 and September 2018. However, the differences in treatments were only mildly statistically non-significant ($F_{1,2}$= 18.36, p=0.0503).

Overall, the population of *A. gundlachi* increased in all three control plots between December 2017 and September 2018. In A1 and B1, the population was actually highest in June 2018. In A1, 3.33 +/- 2.85 *A. gundlachi* were observed in December. In June 2018, that number rose to 11.33 +/- 2.03 before falling to 6.67 +/- 2.40 in September 2018. Similarly, in B1, 7.33 +/- 3.53 *A. gundlachi* were observed in December 2017, rising to 20.00 +/- 0.29 in June 2018 and falling to 13.67 +/- 2.73 in September 2018. As C block was not sampled in March or June 2018, there is no way to determine if this trend holds for all three CTE control plots. Furthermore, C4 had the lowest number of *A. gundlachi* in the entire study, with 1.00 +/- in December 2017, rising to 4.00 +/- in September 2018.

Population trends for *A. gundlachi* in the CTE treatment plots do not appear to follow a particular pattern. In A3, *A. gundlachi* slowly climbed from 3.37 +/- 1.20 in December 2017 to 10.33 +/- 0.66 by September 2018. Conversely, in B2, there were 12.33 +/- 2.72 observed A. gundlachi in December 2018, falling slightly to 8.67 +/- 0.88 in September 2018. *A. gundlachi* remained relatively unchanged in C2, falling only slightly from 7.00 in December 2017 to 6.33 in September 2018. ANOVA analysis on the population of *A. gundlachi* found that none of the independent variables accounted for differences in population between December 2017 and September 2018

Anolis stratulus was the most commonly encountered anole in A block, for both the control (A1) and treatment (A3) plots. The number of *A. stratulus* has decreased in all plots since December 2017. Plot A3 has consistently contained the most *A. stratulus* with 26.00 +/- 0.77 in December 2017, rising to 31.00 +/- 2.03 in March 2018, before falling to 22.67 +/- 4.80 in

September 2018. ANOVA analysis showed that for *A. stratulus*, there was a moderately significant difference between blocks ($F_{2,2}$= 53.84, p=0.02); *A. stratulus* was the most commonly encountered anole in A block at every sampling period, but within B block, it was the second most common anole at all sampling periods except one. C block had a nearly identical population trend in both plots for *A. stratulus*. There were also moderate interactions between treatment and block ($F_{2,2}$= 34.58, p=0.03); in A block, the population trend of *A. stratulus* was similar between A1 (control) and A3 (treatment). However, within B block, the *A. stratulus* population within B2 (treatment) initially rose between December 2017 and March 2018, before steadily declining in June and September 2018. This is in contrast to B1 (control), where *A. stratulus* declined between December 2017 and March 2018, then remaining relatively stable thereafter.

Population composition

For all three species, adults comprised the majority of encountered anoles in both control and treatment plots in December 2017 (Fig. 9a- 9c). In September 2018, the populations of *A. evermanni* and *A. stratulus* had shifted to majority juvenile in both control and treatment plots. *A. evermanni* increased juvenile population from 20.9% (total anoles n=67) to 69.39% (total anoles n= 49) in control plots, and from 45.83% (n=24) to 78.57% (n=28) within the treatment plots. ANOVA analysis showed that the sampling period (time) was responsible for variation in the population composition (for adults, $F_{1,2}$= 33.85, p=0.03. For juveniles, $F_{1,2}$=34.25, p=0.03). Analysis yielded no statistically significant relation between *A. evermanni* population composition and either CTE treatment or block.

A. stratulus in the control plots increased from a December 2017 population consisting of 38.38% (total anoles n=99) juveniles to 61.22% juveniles in September 2018 (total anoles n=75). In the treatment plots, juvenile *A. stratulus* accounted for 25.4% of the population (total anoles n=42) in December 2017, rising to 79.37% (total anoles n=21) in September 2018. The population composition of *A. stratulus* was influenced by all three factors- sampling period (for adults, $F_{1,2}$= 245.9, p=0.004; for juveniles, $F_{1,2}$= 229.26, p=0.004), CTE treatment (for adults, $F_{1,2}$= 32.5, p=0.03; for juveniles, $F_{1,2}$= 29.88, p=0.3), and by block (for adults, $F_{2,2}$= 157.7, p=0.006; for adults, $F_{2,2}$= 147.4, p=0.007).

Anolis gundlachi population composition trended in the opposite direction of *A. evermanni* and *A. stratulus* for both control and treatment plots. As with *A. evermanni* and *A. stratulus*, the population of *A. gundlachi* was majority adult in December 2017. However, the percentage of juveniles decreased further in September 2018. In the control plots, juveniles decreased from 34.29% of the population (total anoles n= 35) in December to 21.15% of the population (total anoles n=79) in September 2018. In the treatment plots, *A. gundlachi* juveniles decreased from 45.31% of the population (total anoles n= 126) in December 2017 to 10.00% (total anoles n=111) in September 2018. Sampling period (for adults, $F_{1,2}$= 23.31, p=0.04); for juveniles, $F_{1,2}$= 23.06, p=0.04) and block (for adults $F_{1,2}$= 34.30, p=0.03; for juveniles, $F_{2,2}$= 33.77, p=0.03) moderately influenced the population composition of *A. gundlachi*, but CTE treatment did not. The differences in block can be explained from the continued lack of juvenile *A. gundlachi* in both plots of Block A. At no sampling period did the percentage of juveniles ever rise above 10%, compared to B block, where in December 2017, the percentage of juveniles in in B block were 50.0% and 32.43% in B1 and B2, respectively.

Perch height

All species of anoles in the control plots slightly increased their average perch height between December 2017 and September 2018 (Fig. 10). *Anolis evermanni* went from an average height 1.17 +/0.15 meters in December 2017 (n=64) to 1.61 +/-0.22 meters in height in

September 2018 (n=50). *Anolis gundlachi* increased from 0.63 +/-0.2 meters in December 2017 (n=26) to 1.07 +/-0.09 meters in September 2018 (n=79). *Anolis stratulus* increased from a height of 0.72 +/-0.07 meters in December 2017 (n=99) to 1.09 +/-0.12 meters in September 2018 (n=75).

In the treatment plots, *Anolis evermanni* actually decreased in encountered height, from 1.77 +/-0.20 meters in December 2017 (n=31) to 1.60 +/-0.14 meters in September 2018 (n=31). Perch height for *Anolis evermanni* was moderately influenced by sampling period ($F_{1,2}$= 49.84, p=0.02), and significantly by block ($F_{2,2}$= 98.31, p=0.01), as well as by interactions between sampling period and CTE treatment ($F_{1,2}$= 20.67, p=0.05). Interactions between CTE treatment and block ($F_{2,2}$= 131.61, p=0.01) had a high influence on perch height, but interactions between sampling period and block ($F_{2,2}$= 72.45, p=0.007) were the most significant influence to *A. evermanni* perch height. Although overall *A. evermanni* decreased in perch height, there was actually an increase in perch height over time for *A. evermanni* in both plots of blocks A and C; however, decrease in block B between December 2017 and September 2018 was enough to offset this increase when averaging the heights by treatment.

Anolis gundlachi increased in average perch height, from 0.71 +/-0.10 meters in December 2017 (n=62) to 1.28 +/-0.09 meters in September 2018 (n=90). For *Anolis gundlachi*, sampling period had a significant impact on perch height ($F_{1,2}$= 120.56, p=0.008). Interactions between CTE treatment and block were mildly influential on *A. gundlachi* perch height ($F_{2,2}$= 22.90, p=0.04).

Anolis stratulus remained virtually unchanged, with an averaged perch height of 1.39 +/-0.09 meters in December 2017 (n=142) and an average perch height of 1.38 +/-0.09 meters in

September 2018 (n=89). None of the independent variables, nor interactions between them, accounted for variation in *A. stratulus* perch height

Microhabitat use

In the control plots, a majority of *Anolis evermanni* (Fig. 11a) utilized tree trunks in both December 2017 and September 2018. In December 2017 (n=61), 60.66% of observed *A. evermanni* used trunks, compared to 22.95% utilizing hurricane debris, 14.75% using non-woody vegetation, and 1.64% using the ground. In September of 2018 (n=46), use of tree trunks had declined just slightly, to 56.52%. The use of non-woody vegetation increased to 31.61%, while the percentage of *A. evermanni* using hurricane debris decreased to 10.87%. No *A. evermanni* utilized the ground in September 2018.

Within the treatment plots, in December 2017 (n=31), 58.06% of *A. evermanni* utilized tree trunks, 25.81% used non-woody vegetation, 9.68% were observed on the ground, and 6.45% used hurricane debris. By September 2018 (n=89), use of tree trunks had fallen to just 33.33% of *A. evermanni*, with a majority (63.33%) using non-woody vegetation, 3.33% observed on the ground, and none using the hurricane debris.

In both control and treatment plots, a majority of *Anolis gundlachi* (Fig. 11b) used tree trunks for both sampling periods. In the control plots, December 2016 (n=33) 56.55% of *A. gundlachi* used tree trunks, whereas hurricane debris, ground, and non-woody vegetation were each utilized by 15.15% of all observed *A. gundlachi*. In September 2016 (n=79), tree trunk use among *A. gundlachi* decreased slightly, to 49.37%. Hurricane debris was utilized by 22.78% of A. gundlachi, 21.25% utilized non-woody vegetation, and 6.33% utilized the ground.

In the treatment plots, in December 2017 (n=74), 47.30% of *A. gundlachi* were observed on tree trunks, 21.62% were observed on the ground, 17.57% were observed on non-woody vegetation, and 13.51% were observed on hurricane debris. By September 2018 (n=92), the percentage of *A. gundlachi* observed on tree trunks increased to 63.04%, and the percentage of A. gundlachi using non-woody vegetation increased to 23.91%. The use of hurricane debris as a perch decreased to 8.70% of observed *A. gundlachi* in September 2018; the percentage of *A. gundlachi* observed on the ground also decreased, to 4.35%.

Microhabitat use by *Anolis stratulus* (Fig. 11c) was more evenly proportioned among the different categories of microhabitat than *A. evermanni* and *A. gundlachi*. In the control plot, one category of microhabitat was never used by a majority of the observed *A. stratulus*. In December 2017 (n=94) 38.80% of *A. stratulus* utilized hurricane debris, 27.66% utilized tree trunks, 20.11% were observed on non-woody vegetation, and 13.38% used the ground. September 2018 (n=75) showed a similar distribution of microhabitat used, with 41.33% of *A. stratulus* were observed on hurricane debris, 24.00% were observed on tree trunks, 20.00% were observed on non-woody vegetation, and 14.67% were observed on the ground.

In the treatment plots, *Anolis stratulus* showed different preferences for microhabitat. In December 2017 (n=132), a slight majority (53.79%) of *A. stratulus* were observed on tree trunks. Both hurricane debris and non-woody vegetation were utilized by 21.21% of *A. stratulus*, and 3.79% used the ground. In September 2018 (n=89), 41.57% of *A. stratulus* were observed on non-woody vegetation, 34.83% on tree trunks, 21.35% on hurricane debris, and 2.25% were observed on the ground.

ANOVA analysis did not reveal any significant correlation between any of the independent variables and microhabitat use for any of the species, with one exception. Sampling period had a slight ($F_{1,2}$= 22.11, p=0.04) influence on *A. evermanni* use of non-woody vegetation.

Chapter 4

Discussion

Eleutherodactylus coqui

We did not observe the significant post-hurricane increase in population of *Eleutherodactylus coqui* that Woolbright (1991) observed with Hurricane Hugo. Woolbright found that coqui populations within El Verde increased to four times their pre-hurricane levels at one year after Hurricane Hugo. Our data shows that although there were fluctuations, total coqui numbers remained relatively constant. ANOVA analysis showed that there were differences between populations of coquis in different blocks, however, coqui populations subjected to different CTE treatments or sampling periods were not statistically different, suggesting that local dynamics within the blocks were the primary influencing factor for coqui population trends for this study.

We did find a highly significant difference in population compositions between different sampling periods, indicating that the hurricane did impact the coqui population composition, specifically by reducing the number of juveniles in a given plot. These findings are similar to those observed by Woolbright (1991), which showed juvenile *Eleutherodactylus coqui* densities lower than pre-Hugo densities. Our study findings differ, however, in that Woolbright recorded that *E. coqui* juvenile densities were on the rebound one year after Hurricane Hugo. Our findings show that, as a percentage of the population, *E. coqui* juveniles are continuing to decline after Hurricane Maria.

There were no significant differences between blocks or treatments, but the significant *interaction* between blocks and treatments suggests that on a localized scale, coqui populations are impacted by CTE treatment, but the extent of the impact is influenced by dynamics within the different blocks. Juvenile population trends within C block are nearly identical. In B block, juvenile population trends are erratic; juveniles actually comprised a majority of coquis found during the March 2018 count. In A block, the percentage of juveniles in the treatment block show an apparent lag trend to the juveniles in the control plot. The continued decrease of juveniles in all plots is likely due in part to environmental factors such as temperature and humidity. There was decrease in humidity between the pre-Maria count of December 2016 and the post-Maria count of December 2017, as well as a further lowering of humidity during a dry weather period at the March and June 2018 sampling events. There was also as a seasonal rise in temperature between December 2017 and September 2018. This is consistent with Woolbright's (1991) findings which identified a post-Hugo drought as a factor in decreased juvenile populations.

Continued monitoring and data collection may identify long-term post-Maria trends in *Eleutherodactylus coqui* populations not revealed in this study. Woolbright found that alteration to the physical structure of the forest by Hurricane Hugo was the major factor influencing abundance of *Eleutherodactylus coqui* for several years after the storm. The initial increase of adult frogs within a year of the storm was a result of both an increase of refuge sites created by the deposition of branches, fallen trees, and other debris on the forests floor, as well as a reduction in the number of predators (Woolbright 1991). Subsequent increases in population were partially sustained by the addition of yet more habitat by the regrowth of vegetation (Woolbright, 1996).

Similar to the variation in *Eleutherodactylus coqui* population trends between blocks, Vilella and Fogarty (2005) observed localized differences in coqui relative abundance at study sites in Maricao and Guilarte state forests after Hurricane Georges struck in 1998. When measured as relative abundance, it first appears that *E. coqui* populations increased at every site, with relative abundance of coquis increasing from 46.3% to 69.2% in Maricao and from 69.1% to 73.9% in Guilarte in 1999. However, different local factors were responsible for the increase in abundance. The decline of other species of frogs seems to be partially responsible for the increase in coqui relative abundance after Hurricane Georges, as there was not a significant difference in mean sample size of *E. coqui* in Maricao from 1998 to 1999, but significantly fewer individuals of all other species of *Eleutherodactylus* were recorded post-Georges in 1999 (Vilella and Fogarty, 2005). Conversely, at Guilarte, all but one species of *Eleutherodactylus* (*E. brittoni*) showed an increase in the number of individuals observed post-Georges, but *E. coqui* showed the largest increase.

Vilella and Fogarty compared their findings to Woolbright's research on coqui populations in El Verde post-Hugo, and concluded that habitat generalists such as *E. coqui* do not experience long-term population reductions from hurricanes, while habitat specialists such as *E. richmondi* may be more susceptible to post-hurricane weather changes that may alter microhabitat conditions necessary for these species. Generally speaking, they concluded that hurricanes tend to cause a short-term decrease the overall species richness of Puerto Rican *Eleutherodactylu*s assemblages, and favor stabilization or increase of adult *E. coqui* on account of additional habitat space created by the deposition of debris on the forest floor (Walls et al., 2013). Our findings in this study indicate that within the CTE plots, regardless of treatment, coqui population trends were stabilized, but did not increase, similar to Vilella and Fogarty's (2005) findings at their study site in Maricao.

Differences in microhabitat usage by *E. coqui* within the control plots vs the treatment plots is best explained by the physical structure of the plots before and after the hurricane. Within the control plots, adult *E. coqui* overwhelmingly used the ground both in December 2016 prior to Hurricane Maria, and in December 2017, three months after the storm hit. This is likely due to a lack of understory vegetation resulting from the closed canopy within these plots. In September 2018, a year after the hurricane, the non-opened canopy had allowed for significant regrowth of vegetation in the understory, allowing adult *E. coqui* additional microhabitat.

In contrast, the treatment plots contained a thicker understory and more non-woody vegetation to use pre-Maria, as a result of the CTE trimming in 2014. The subsequent drop in use of non-woody vegetation in December 2017 was likely due to the partial destruction of the understory by the hurricane. Trends show that non-woody vegetation is a preferred habitat for adult *E. coqui*. By September 2018, a majority of *E. coqui* were once again using the non-woody vegetation in the treatment plots. In the control plots, the *E. coqui* use of non-woody vegetation saw a steady incline as understory plants grew as a result of Hurricane Maria opening the canopy. While the percentage of adult *E. coqui* utilizing non-woody vegetation was not a majority of encountered frogs (35.29%), it was the highest percentage of the four microhabitat categories.

Of note is the fact that adult coquis within the control plots utilized hurricane debris more than adult *E. coqui* in treatment plots. This is likely due to the fact that there was more hurricane debris within the control plots as a result of the closed canopy. The treatment plots had been trimmed in 2014, so there was less organic material in the canopy available to be deposited on the forest floor. This can be inferred from the litterfall data. Though litterfall itself is not significantly different between control and treatment plots, control plots accumulated larger quantities of litterfall than treatment plots in December 2016. By December 2017, three months post-Maria, the amount of litterfall accumulated in control plots and treatment plots was nearly identical, with treatment plots accumulating slightly more. This suggests that control plots had proportionally larger amounts of damage to the canopy, which would correlate with a larger amount of debris being deposited on the forest floor by the storm. Additional hurricane debris was added to one of the control plots in September 2018. In B1, a large tree that was killed in Hurricane Maria but initially remained standing fell into the plot sometime between June 2018 and September 2018, damaging other trees as it fell and depositing a substantial amount of fresh debris into the plot to be utilized as additional habitat.

Trunk use by adult *Eleutherodactylus coqui* differed significantly between sampling periods, between blocks, and statistically significant interactions were found between all three independent variables. In December 2017, three months post-Maria, use of tree trunks declined in the control plots but increased slightly in the treatment plots. It is likely that differences between the blocks and within plots account for the selection of tree trunks as microhabitat. During data collection, we observed that *E. coqui* were rarely observed completely out in the open; those utilizing tree trunks seemed to prefer trees with vines or other vegetation as concealment, and the trees in A1 (control), B2 (treatment), and C4 (control) were relatively devoid of vines compared to their block counterparts.

Juvenile *Eleutherodactylus coqui* overwhelmingly utilized non-woody vegetation as microhabitat when it was available. A majority of juveniles in both control and treatment plots used non-woody vegetation before the hurricane, as well as one year after in September 2018, when understory vegetation had begun to regrow, and both reduced their usage significantly in December 2017. There was a significant difference in juvenile usage of non-woody vegetation between treatments; the closed-canopy control plots contained less non-woody vegetation at the understory level before the hurricane than the open-canopied treatment plots.

There was also a significant difference of juvenile use of non-woody vegetation between blocks, which we attribute to localized variations in the amount of non-woody vegetation within a particular block. There is a possibility that the type of vegetation may play a role as well. Woolbright (1996) observed that at five years after Hugo, *E. coqui* was more abundant at sites with the tree species *Cecropia schrebriana*, as the fallen leaves provide nesting sites. Different types of non-woody vegetation will also provide differing type of habitat; a fragile *Ipomea* vine and a sturdy *Heleconia* are both non-woody vegetation, but provide very different microhabitats. More detailed classifications of microhabitat types in future studies may help explain differences in use by both juvenile and adult *Eleutherodactylus coqui*.

From December 2017 to September 2018, hurricane debris was the second most utilized microhabitat for juveniles in the control plots, but not treatment plots. As with adult *E. coqui* debris use, this trend is likely due to the relative lack of debris in the treatment plots. Trends also indicate that hurricane debris is a better microhabitat for adults than juveniles. At every count, regardless of treatment, a higher percentage of adults utilized hurricane debris than did juveniles. Though both adults and juveniles preferred non-woody vegetation, adults are more likely to use the debris generated by hurricanes. One possible explanation for this is that the debris provides habitat requirements that are specific to adults, such a calling and nesting sites.

Anolis spp.

As we do not have pre-Maria data, we cannot make comparisons for pre- and post-Hurricane *Anolis spp*. populations. However, we do know that prior to the hurricane, *Anolis gundlachi* was the most commonly encountered anole at the understory/ground level of the forest. Similar to Reagan's (1991) study on the effects of Hurricane Hugo on *Anolis* lizards, in December 2017, three month post-Maria, *Anolis gundlachi* was the least common anole in the forest at understory/ground level, and *A. stratulus*, usually found in the canopy, was the most common anole.

Anolis evermanni was the least abundant anole in every plot at nearly every sampling period, similar to Reagan's observations (1991). Considering that overall population of *A. evermanni* fell with each count in the study, but the percentage of juveniles within the population rose, it is likely that *A. evermanni* adults were the first to recolonize the canopy after Hurricane Maria. The increase in juvenile *A. evermanni* may partially explain the slight shift towards the use of understory non-woody vegetation as a microhabitat in September 2018. Even with this slight shift, *Anolis evermanni* overwhelmingly preferred tree trunks as microhabitat, and was the anole species with the highest average perch height at every sampling period. Considering the relative scarcity of *A. evermanni* in the understory, and that differences in CTE treatment were found to be only mildly insignificant on the population of *A. evermanni*, it is likely that assessing the canopy of the plots will yield more robust trends regarding hurricane impacts on this species.

Similar to Reagan, we found that immediately after the hurricane, *Anolis gundlachi* was no longer the most common anole in the understory, though we do not have pre-Hurricane Maria data to make exact comparisons. The exact factors influencing post-Hurricane *A. gundlachi* population trends remain unclear- *A. gundlachi* in the control plots increased between December 2017 and September 2018 (peaking in June 2018 for A1 and B1), again in a similar manner to Reagan's observations. However, the three different treatment plots yielded three different results- a slight increase in *A. gundlachi* numbers, a decrease, and a holding pattern. This suggests that multiple hurricanes, along with local environmental and habitat factors, may have an effect on the total population of the shade-loving *A. gundlachi*, but ANOVA analysis yielded no significant differences between control and treatment plots. Furthermore, there was no significant differences between *A. gundlachi* populations between blocks or sampling periods.

Trends break down even further when examining *Anolis gundlachi* populations by block. Although *A. gundlachi* was usually encountered in lower numbers than *A. stratulus*, similar to Reagan (1991), in block B this was not the case, with *A. gundlachi* being the most common anole in both plots at all counts, with the exception of the March 2018 sampling period in B2.
Unlike the other two anole species, *Anolis gundlachi* was the only anole to experience a continued decrease in the juvenile population between December 2017 and September 2018. The continued decline of juveniles may be linked to the increase in temperature over time, as well as the periods of lower humidity during March and June 2018. *Anolis gundlachi* is sensitive to dehydration, and at higher elevations where temperatures are lower, it has been shown to avoid open habitats that provide proper temperature in favor of closed-canopy habitats that are sub-optimal for temperature, but prevent dehydration. As with *Eleutherodactylus coqui*, we posit that the open canopy of the post-Maria forest created an environment detrimental to juvenile *A. gundlachi*.

As with *Anolis evermanni*, *A. gundlachi* was usually observed on tree trunks, no more than 1.28 meters in height. During sampling events, we observed that even in plots where the canopy was opened to the extent that most of the plot was insolated, adult *A. gundlachi* would be encountered on most trees. In areas of intense sunlight, the animal would remain in whatever shade was available, usually on the lowest regions of the tree trunk. *A. gundlachi* is known to non-randomly select woody perches over non-woody plants and even Sierra palms (Rodríguez-Robles et al., 2005). This pattern holds true even after alteration of the habitat by hurricane.

Competition between *Anolis evermanni* and *A. gundlachi* cannot be ruled out as a possible influencing factor on population trends for both species. Leal et al. (1998) found that in spite of apparent segregation of shared habitat, competition did occur between the two species. This competition occurred in spite of spatial segregation of habitat; the study suggested that the two species are separated at approximately two meters in height, with *A. gundlachi* occupying trunks at lower than two meters, and *A. evermanni* inhabiting areas on trunks above two meters. As both of these species had average heights below two meters for the entirety of the study, it is likely that any competition would be intensified in a post-hurricane environment with a disturbed food web.

Anolis stratulus microhabitat use was more evenly distributed at all counts compared to *A. evermanni* and *A. gundlachi*. This cosmopolitan use of habitat may partially account for its success immediately after the hurricane, where it traded the structure of the canopy for the newly created structures on the forest floor comprised of hurricane debris and rapidly growing non-woody vegetation. *A. stratulus* used hurricane debris, and used it more consistently, than *A. evermanni* and *A. gundlachi*. If hurricane debris is a preferred habitat for *A. stratulus* post-hurricane, then this may explain why there was a significant difference in population between blocks. Block B, where *A. stratulus* was not as frequently observed, had noticeably less hurricane debris than Block A or Block C. In Block A, both the control and treatment plots had a large Tabonuco (*Dacryodes excelsa*) tree that had fallen into the plot. During sampling, we always observed numerous *A. stratulus*, both adults and juveniles, on these trees.

The population composition of *Anolis stratulus* went from majority adult in December 2017 to majority juvenile in September 2018, in both treatment and control plots. The change was more distinct in treatment plots, where the September 2018 population was 79.37% juvenile.

This corresponds with a shift from the use of tree trunks to the use of non-woody vegetation in the treatment plots, similar to the majority-juvenile population of *A. evermanni* in September 2018. In the control plots, the use of tree trunks by *A. stratulus* declined slightly, but there was no corresponding increase in the use of non-woody vegetation. As shown in the foliage profiles, the treatment plots contained more vegetative habitat at lower heights than the control plots. Interestingly, *A. stratulus* did not increase in perch height in the treatment plots between December 2017 and September 2018, and made only a slight increase in height in the control plots. Foliage profiles show that, overall, treatment plots gained more habitat at higher levels of the forest (4.0 meters and higher).

A. stratulus is a canopy-dwelling anole. Taken together, these trends- an increase in juveniles, a shift towards non-woody vegetation in the treatment plots, the lack of a perch height increase, and the foliage profile differences- indicate that, as with *A. evermanni*, adult *A. stratulus* are recolonizing the canopy as suitable habitat becomes available at those levels of the forest, and that the previously trimmed treatment plots sustained less damage in Hurricane Maria, providing more canopy habitat earlier than the control plots. The juveniles remained in the understory.

Conclusions, Limitations, and Future Research

Eleutherodactylus coqui populations did not experience a significant drop after Hurricane Maria, regardless of CTE treatment. As with previous research, we observed a decline in juveniles. This decline continued one year after the hurricane, likely due to a post-Maria dry period, lower humidity levels, and a seasonal increase in temperature. Both adult and juvenile coquis utilized non-woody vegetation when it was available, though adults were more likely to use other habitats. The treatment plots contained more non-woody vegetation before the hurricane, and recovered this vegetation more quickly after the hurricane, owing to the already opened canopy allowing for a thicker understory to establish pre-Maria.

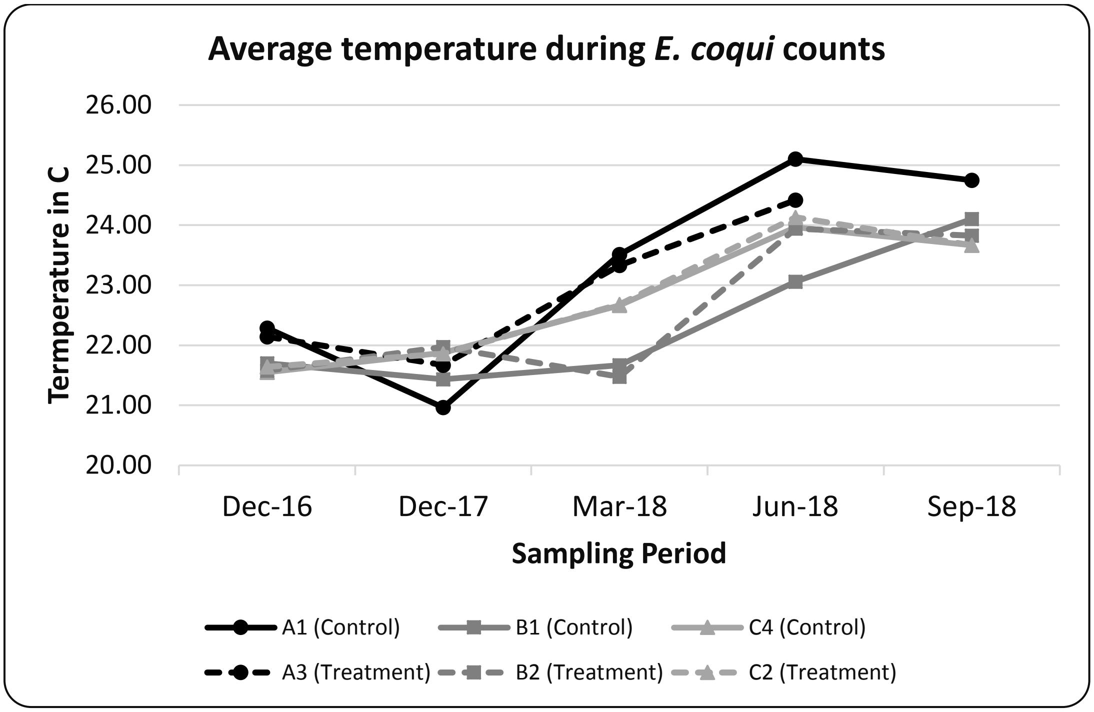
Anolis evermanni and *A. gundlachi* both preferred tree trunks after Hurricane Maria, which may have led to competition between the two species. *A. evermanni* was usually the least encountered species in a given sampling period, and adults likely began recolonizing the canopy before *A. stratulus*. CTE treatment did not have a significant impact on either *A. evermanni* population, population composition, microhabitat use, or perch height.

Anolis gundlachi saw a decline in juveniles throughout the study, likely due to similar reasons as the decline in juvenile coquis- a post-Maria dry period and an increase in temperature, leading to increased risk of dehydration. The effects of hurricanes on *Anolis gundlachi* do not appear evenly distributed throughout the forest, and depend heavily on local conditions, as evidenced by *A. gundlachi* being the most common anole in block B, as well as reports that an assessment on the Mt. Britton trail, also located within El Yunque, did not yield a single *A. gundlachi* 14 months after Hurricane Maria (Winchell, 2018). CTE treatment did not have a significant impact on either *A. gundlachi* population, population composition, microhabitat use, or perch height.

Anolis stratulus was the only anole to be directly influenced by CTE treatments, and then, only in regards to population composition, as the understory of the treatment plots supported a larger percentage of juveniles. *Anolis stratulus* was more likely to utilize hurricane debris than either *A. evermanni* or *A. gundlachi*. As with *A. gundlachi*, localized environmental conditions play a role in determining the post-hurricane population trends and microhabitat use of *A. stratulus.*

This study had several limitations that emphasize the need for future research. Our largest limitation is the lack of pre-Maria anole data. We recommend continued sampling of anoles and coquis to form more robust data sets for comparison in subsequent hurricanes and other disturbance events. We did not focus on percentage of male and female adults, as classification of animals was done visually, without capture, and at a distance of up to two meters from the transect. Furthermore, there would be a likelihood of overrepresentation of males with this methodology, as male coquis and male anoles are easier to ensure a positive identification for a distance, via a call or dewlap display. Focus on male/female interactions and trends for coquis and anoles may reveal information than a simple adult vs juvenile methodology cannot. Lastly, given the different trends between blocks for *A. gundlachi* and *A. stratulus*, future research should include more focus on measuring environmental differences at the local level, and how that impacts how *Eleutherodactylus* and *Anolis* populations respond to hurricanes.

Figures



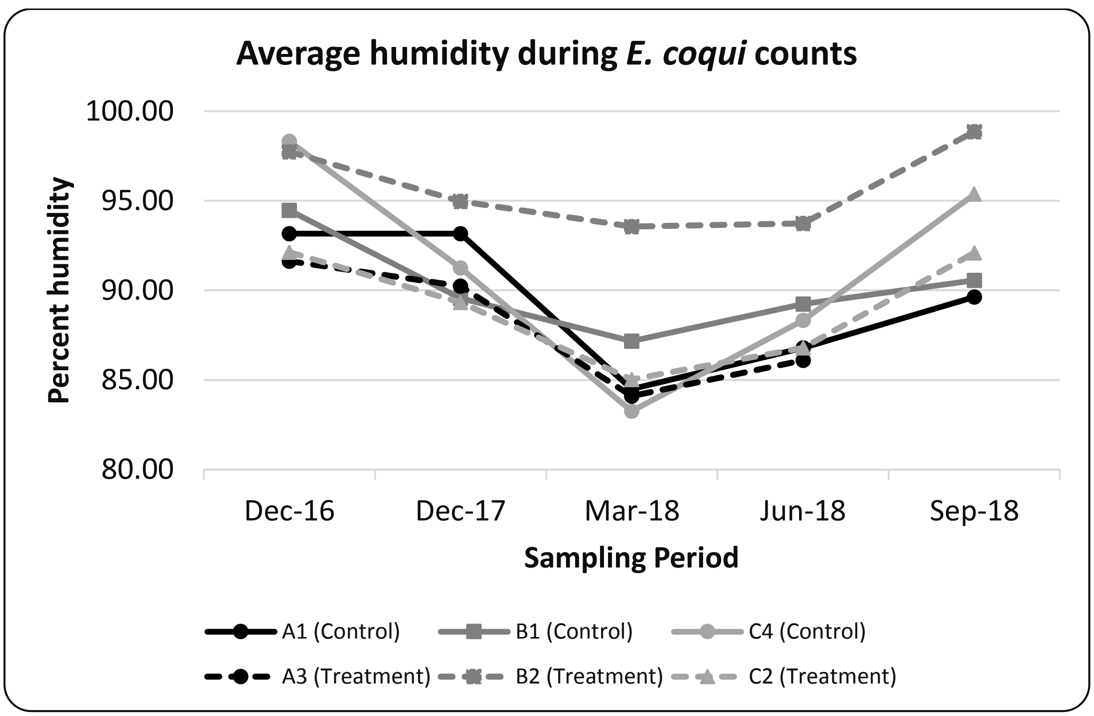
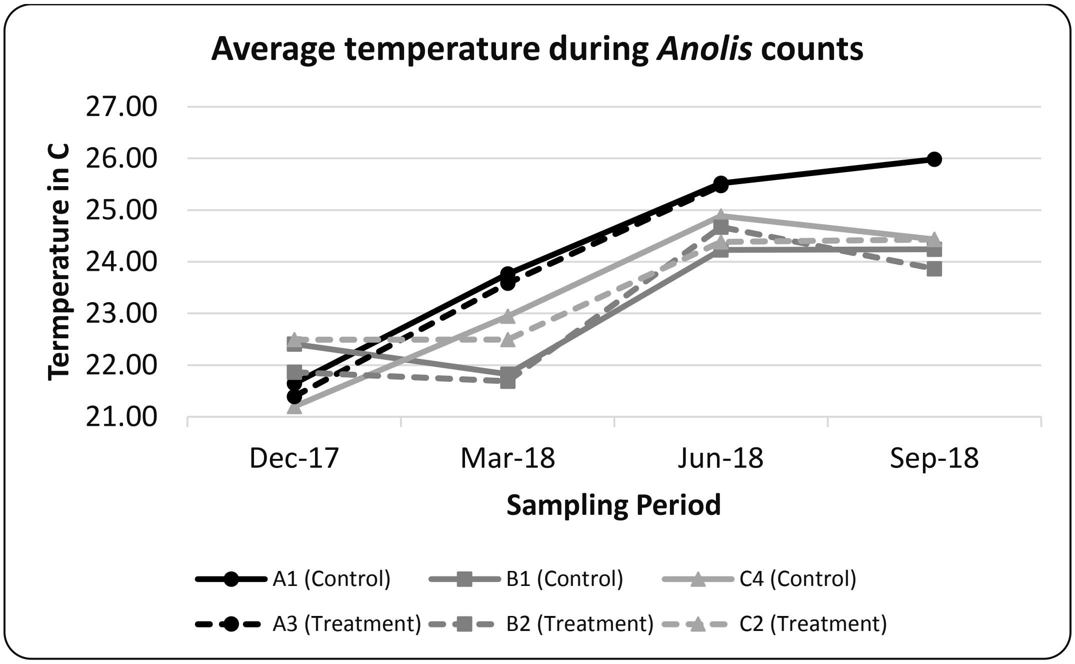


Figure 1. Temperature and humidity levels during *Eleutherodactylus coqui* (nocturnal) sampling periods.



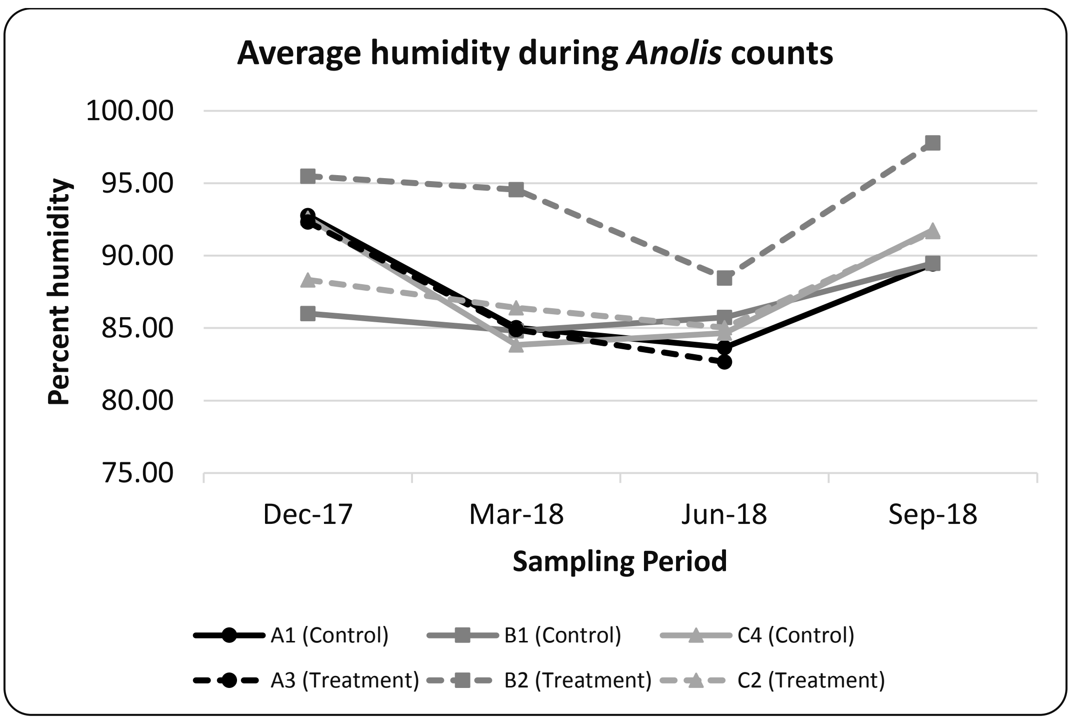


Figure 2. Temperature and humidity levels during *Anolis* (diurnal) sampling periods.

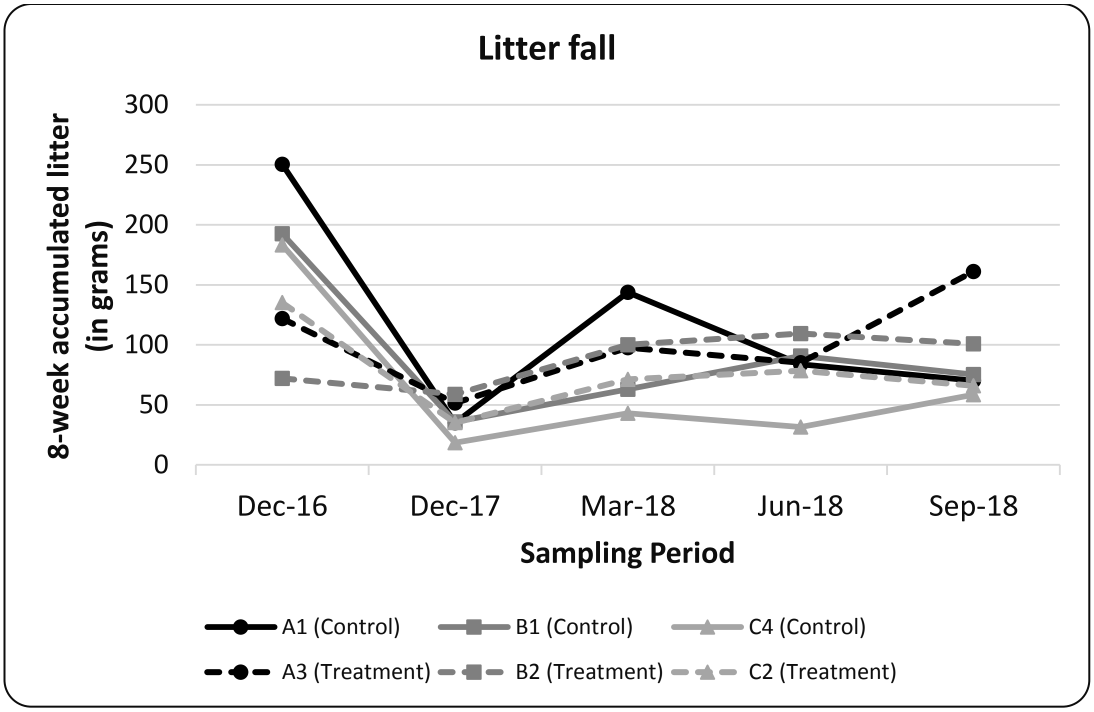
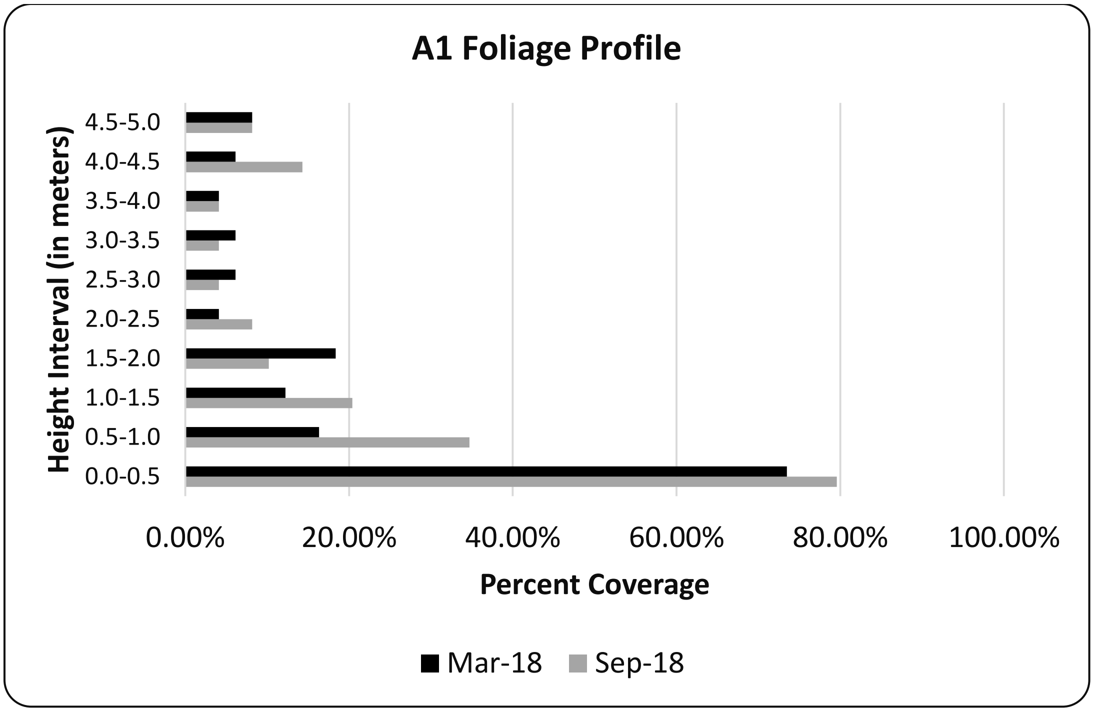


Figure 3. Litter fall in Canopy Trimming Experiment plots during sampling periods



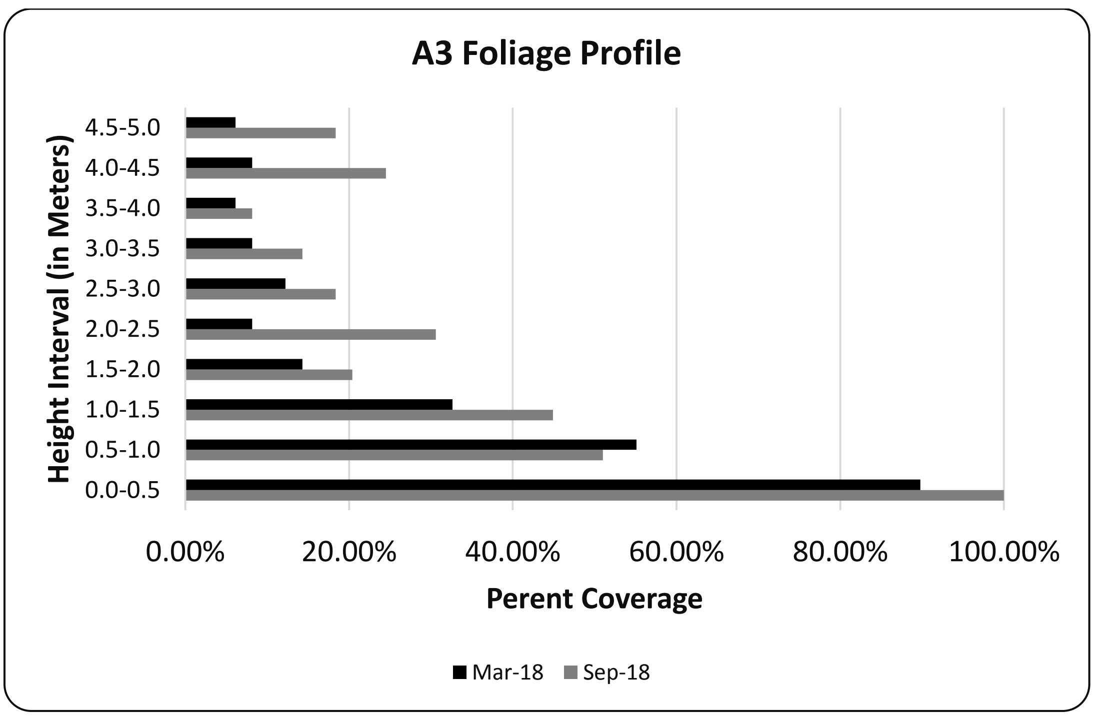
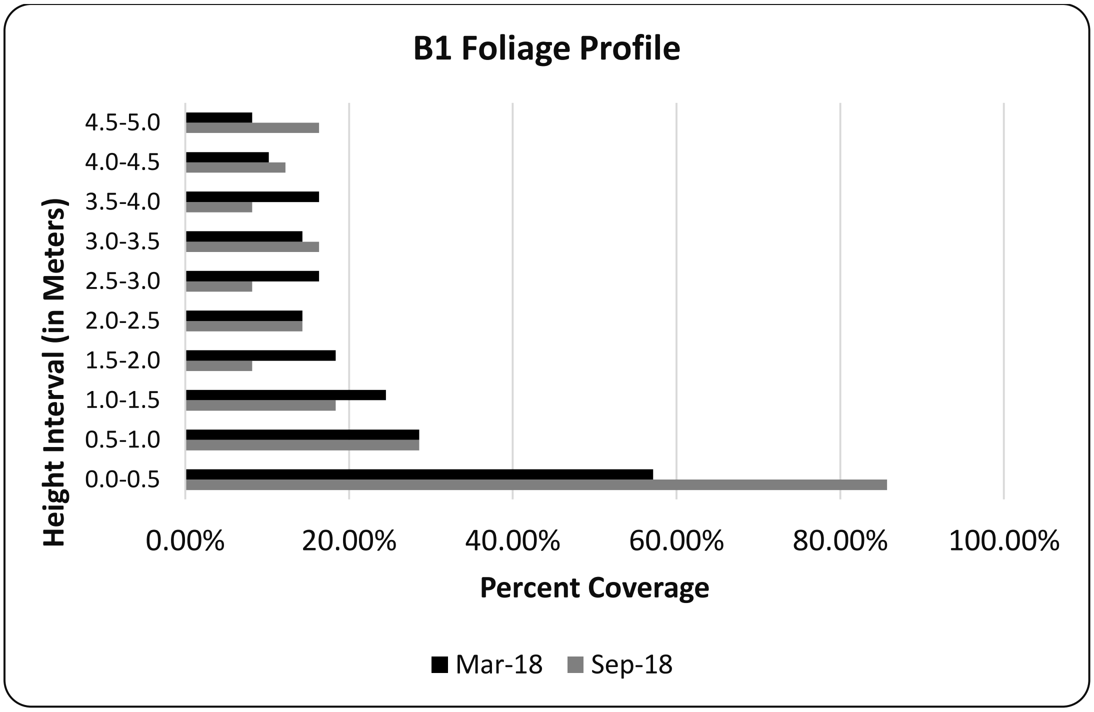


Figure 4a. Foliage profile of block A



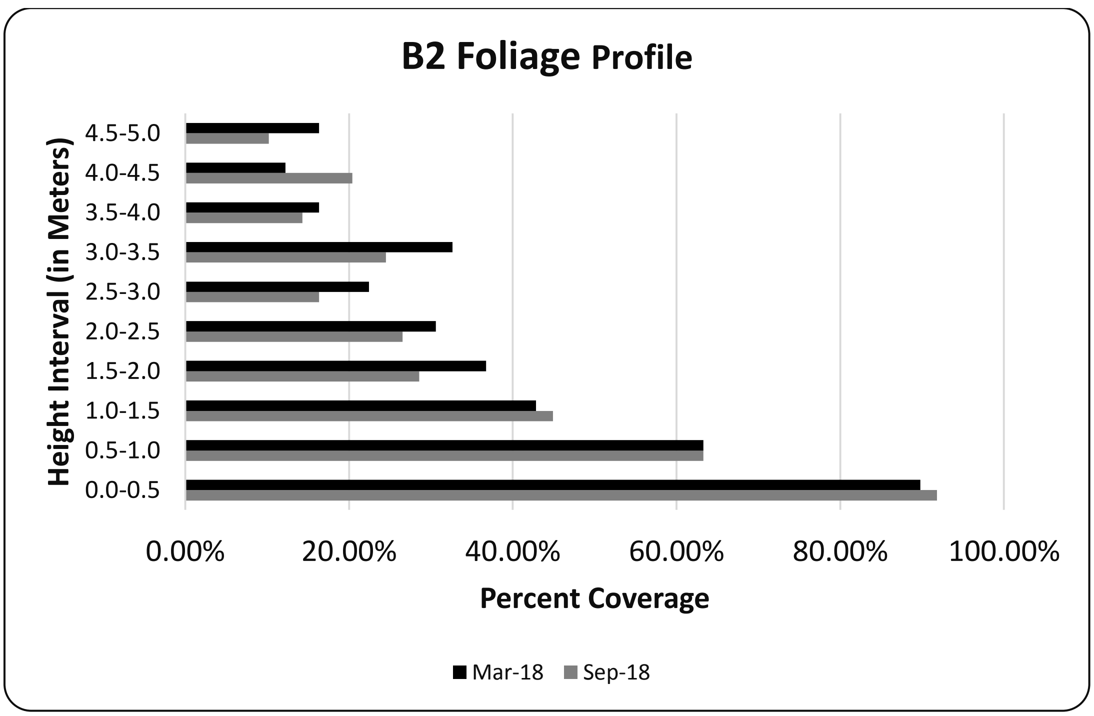
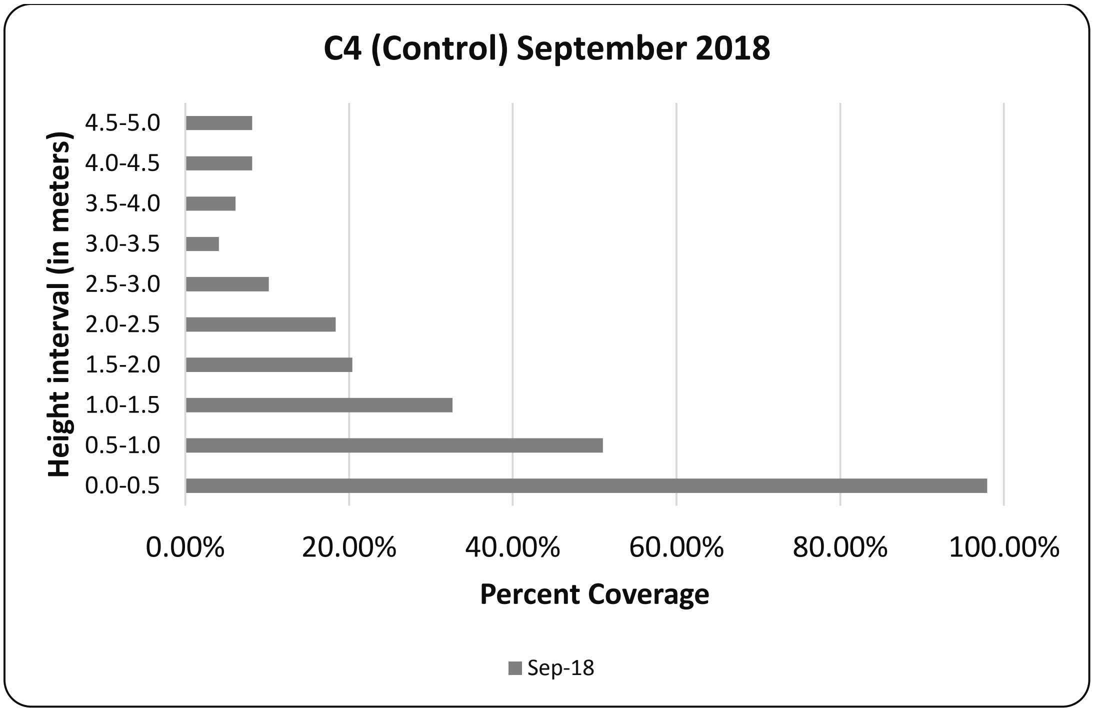


Figure 4b. Foliage profile of block B



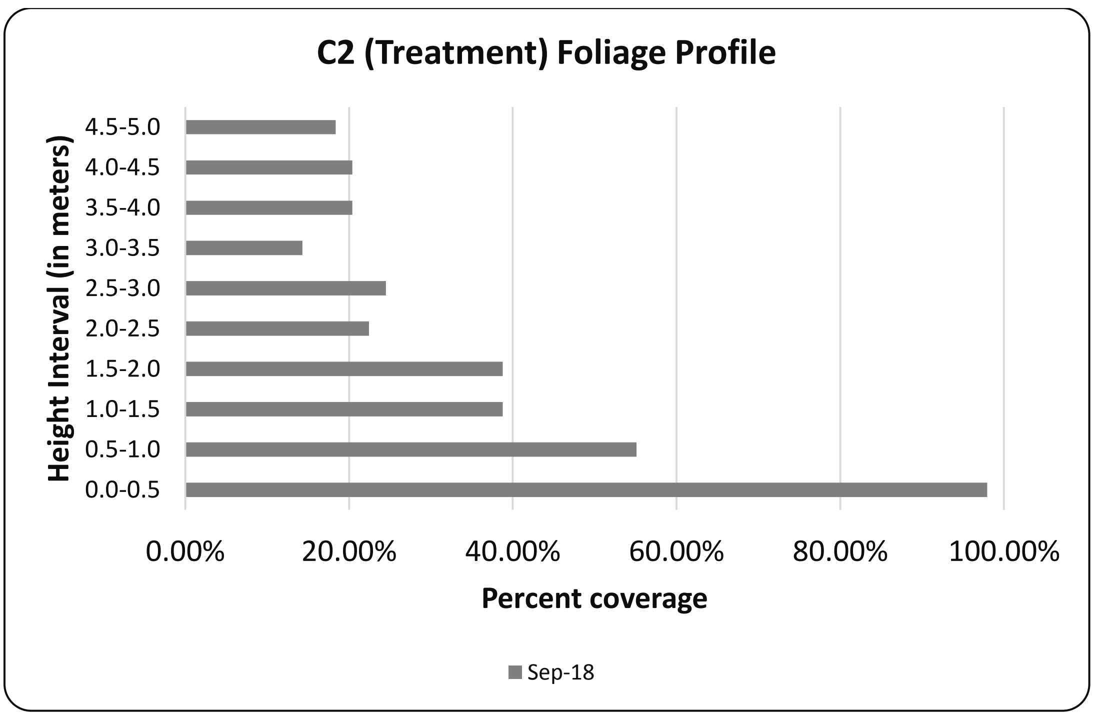


Figure 4c. Foliage profile of block C.

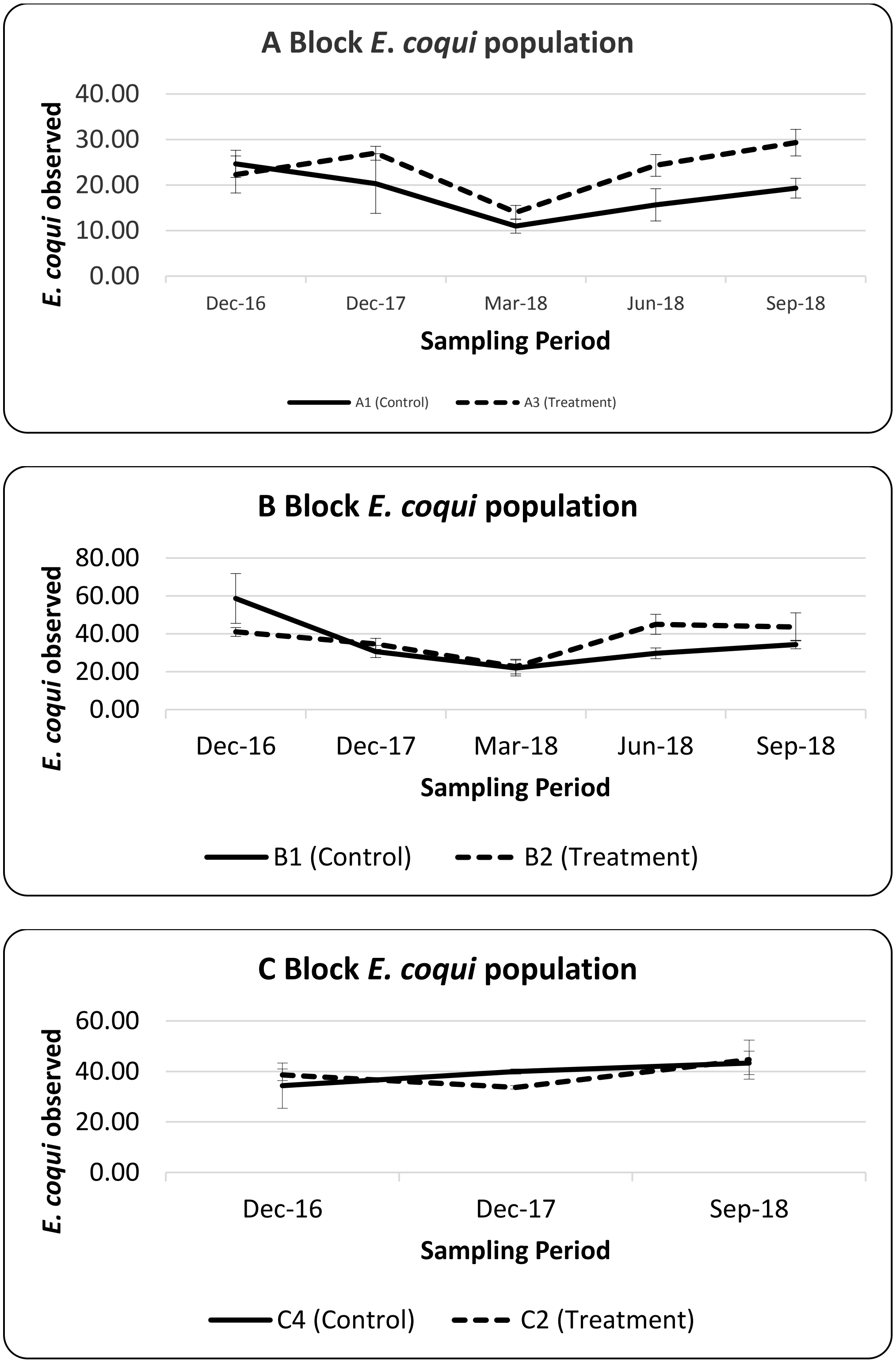


Figure 5. Pre- and post-Hurricane Maria population trends of *Eleutherodactylus coqui* within the Canopy Trimming Experiment Plots.

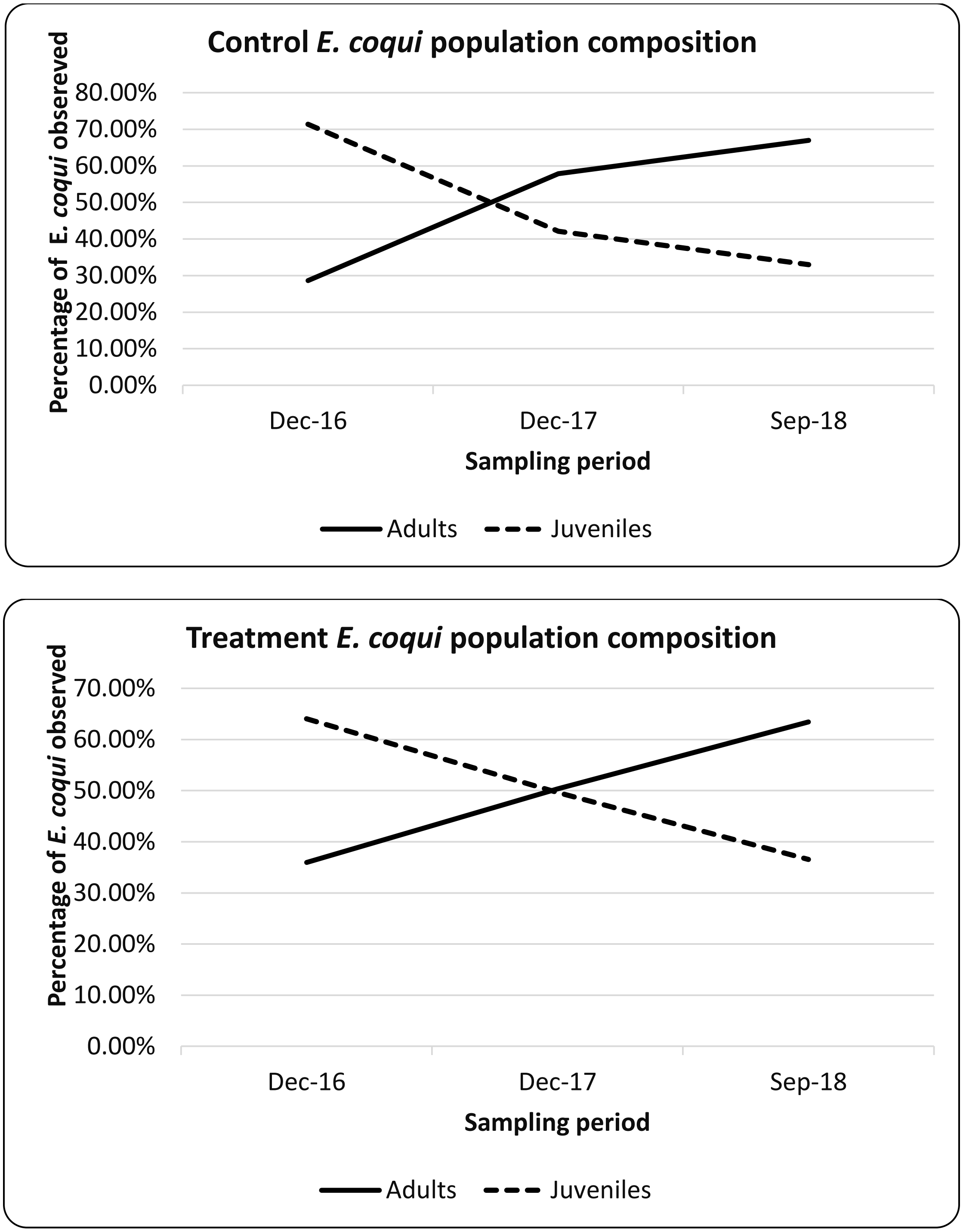
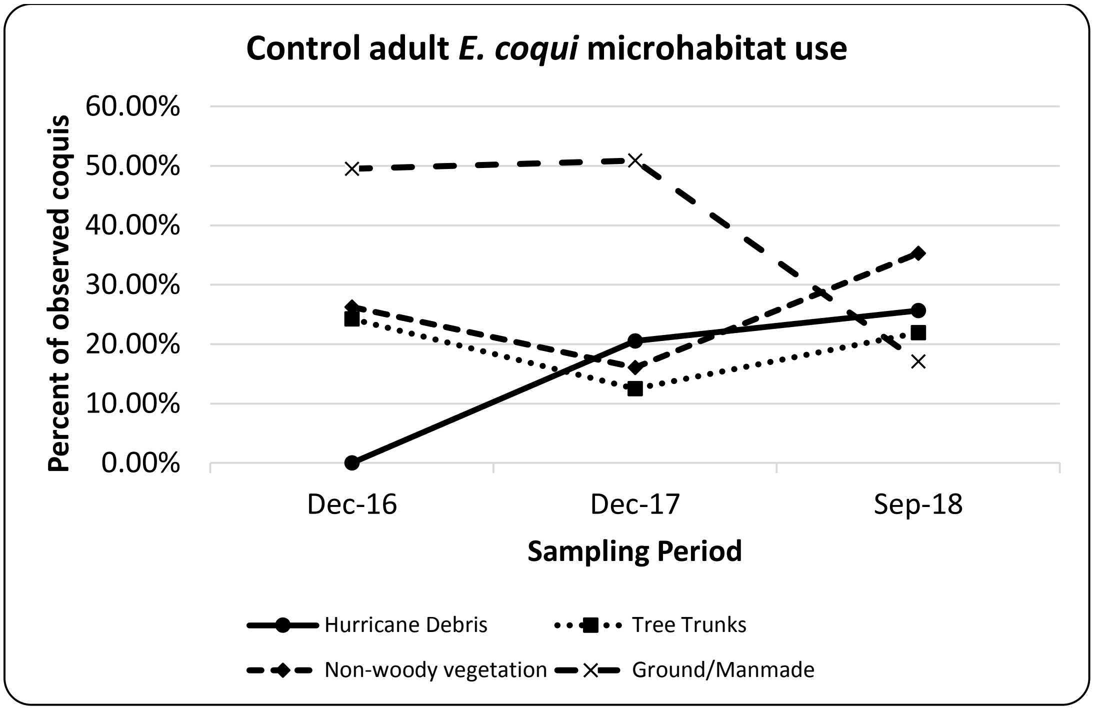


Figure 6. Pre- and post-Hurricane Maria population composition trends of *Eleutherodactylus coqui* within the Canopy Trimming Experiment.



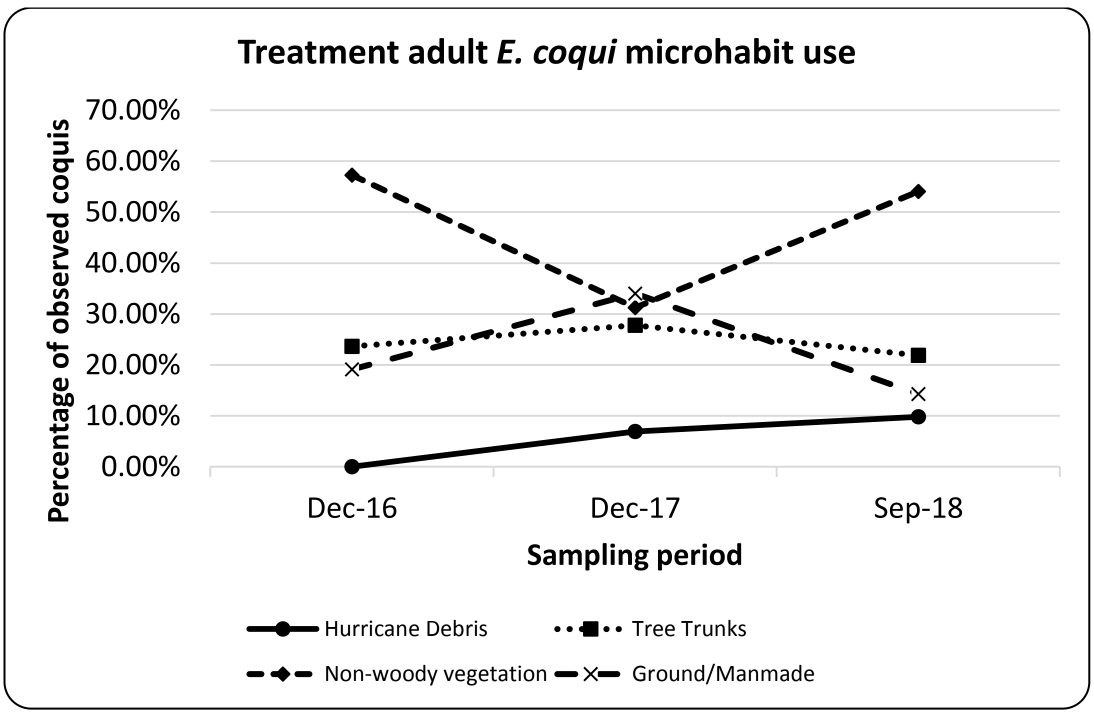
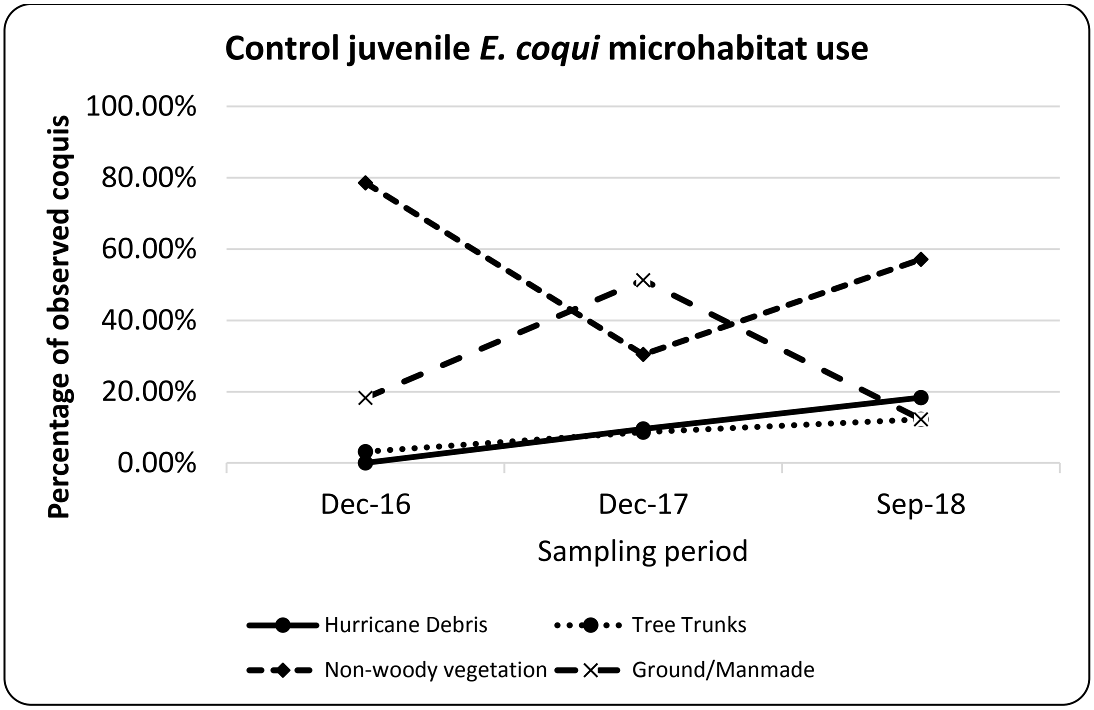


Figure 7a. Use of microhabitats by adult *Eleutherodactylus coqui* within the Canopy Trimming Experiment.



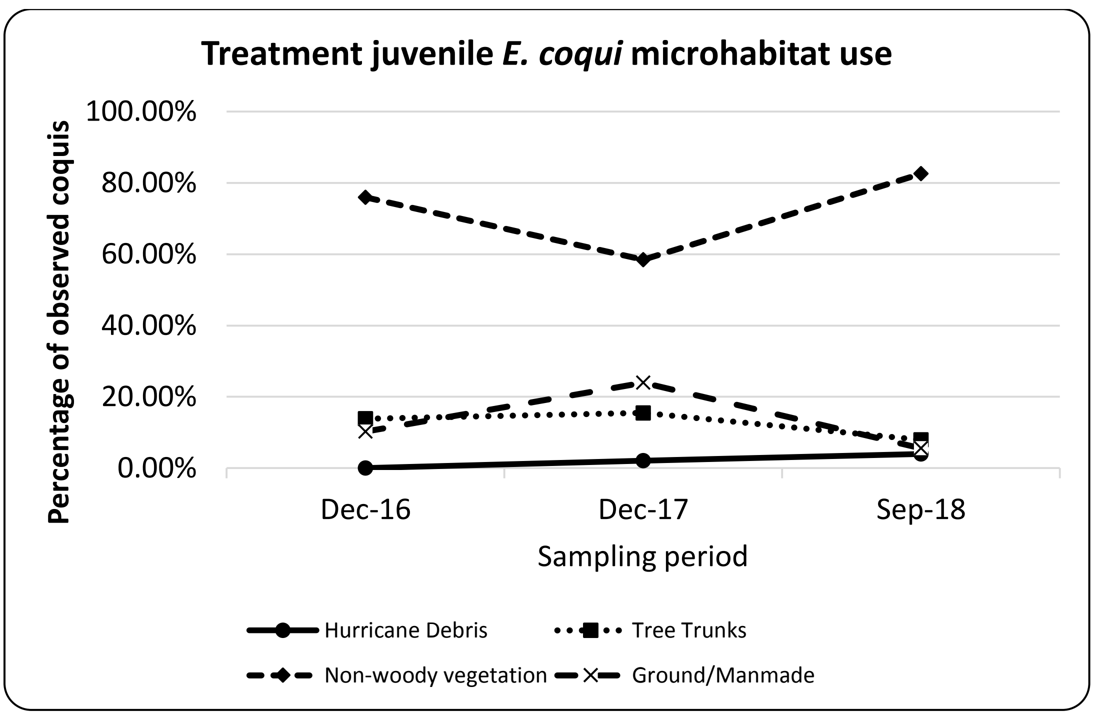
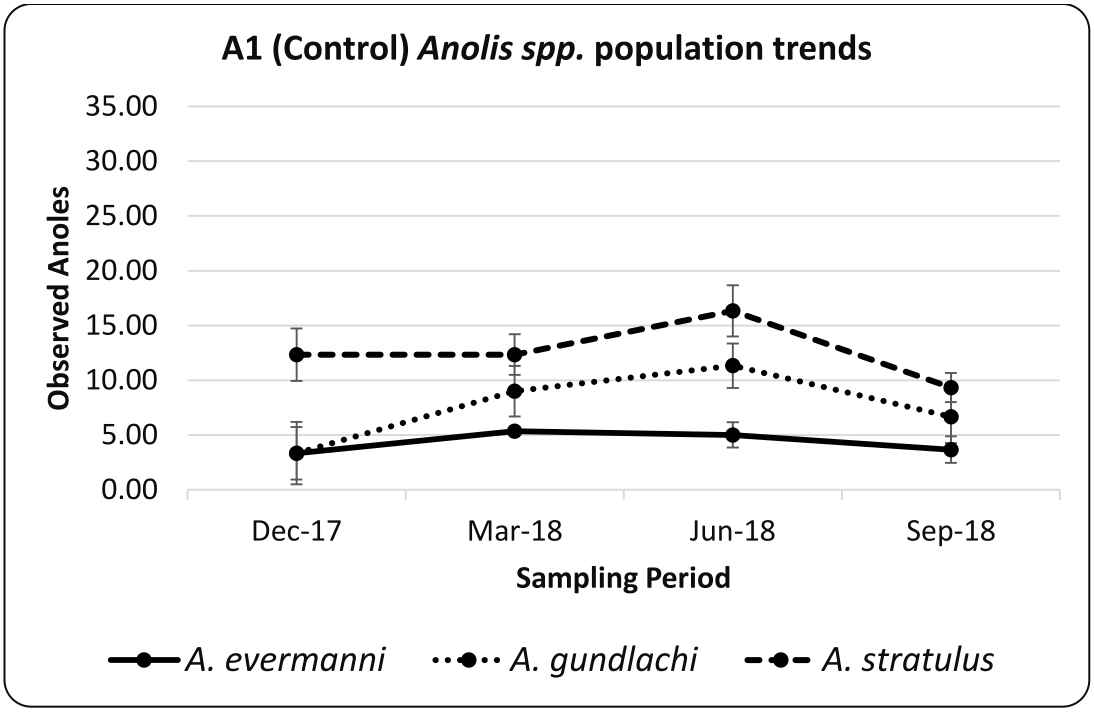


Figure 7b. Use of microhabitats by juvenile *Eleutherodactylus coqui* within the Canopy Trimming Experiment.



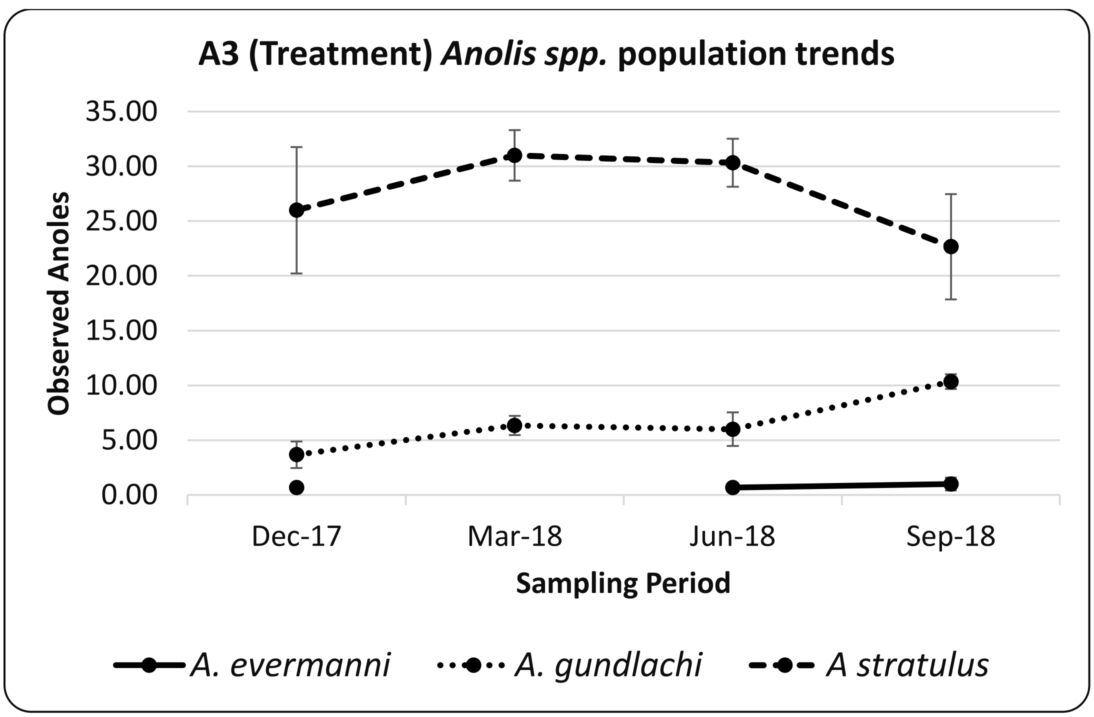
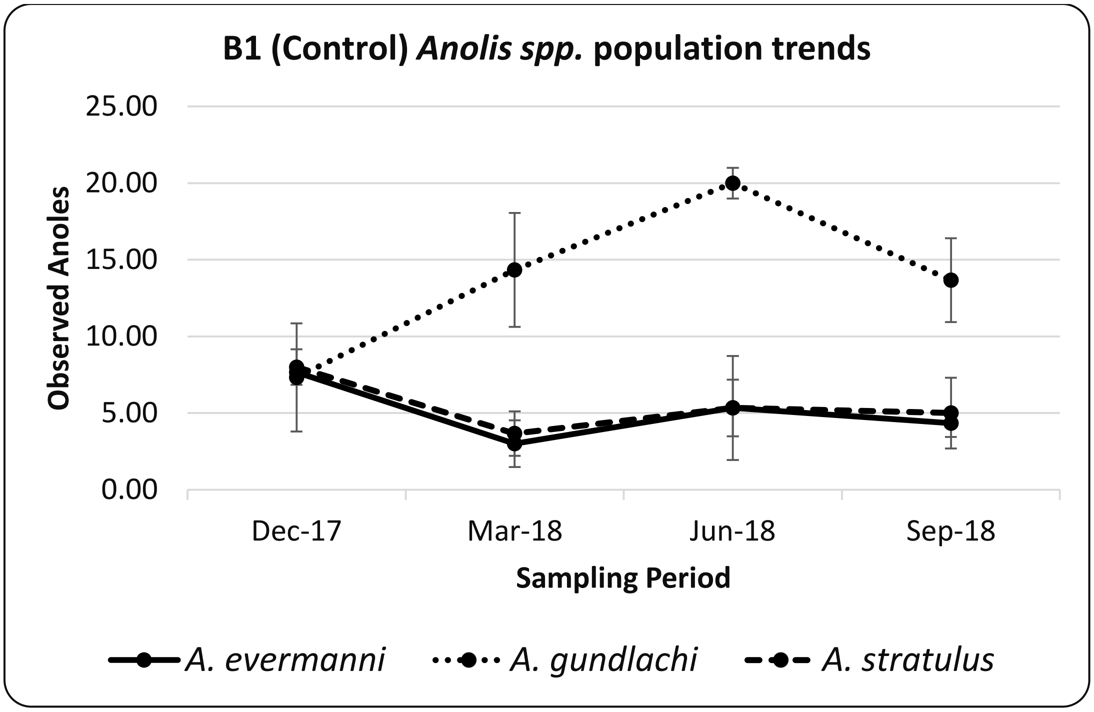


Figure 8a. Population trends of *Anolis spp*. within block A of the Canopy Trimming Experiment



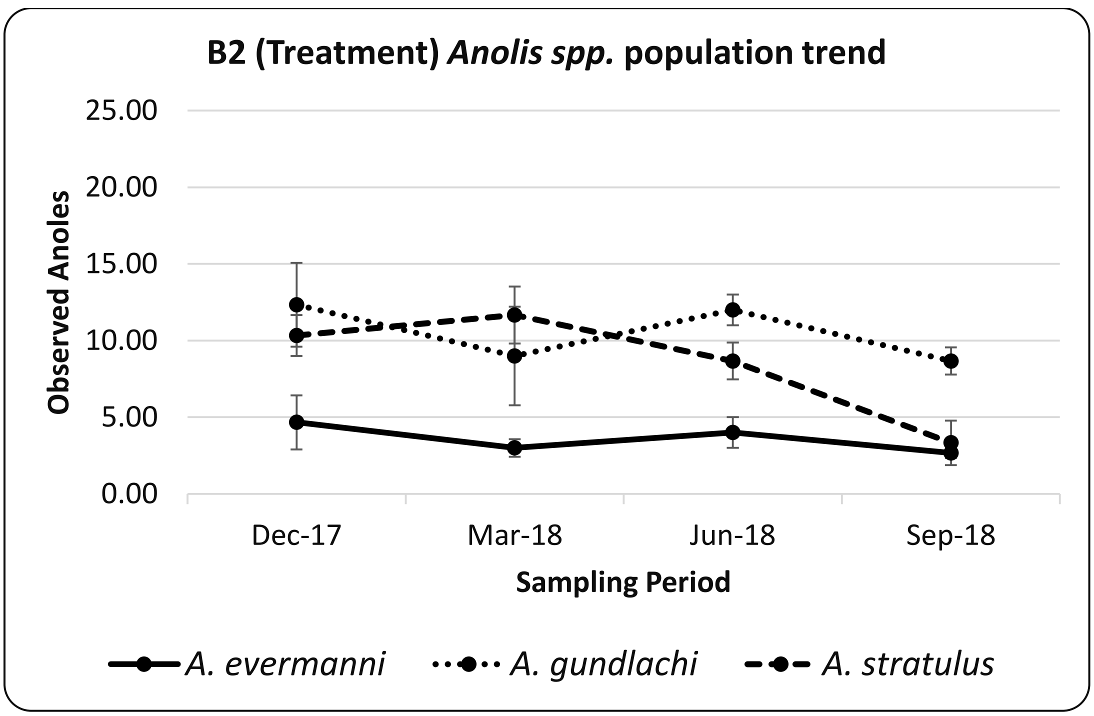
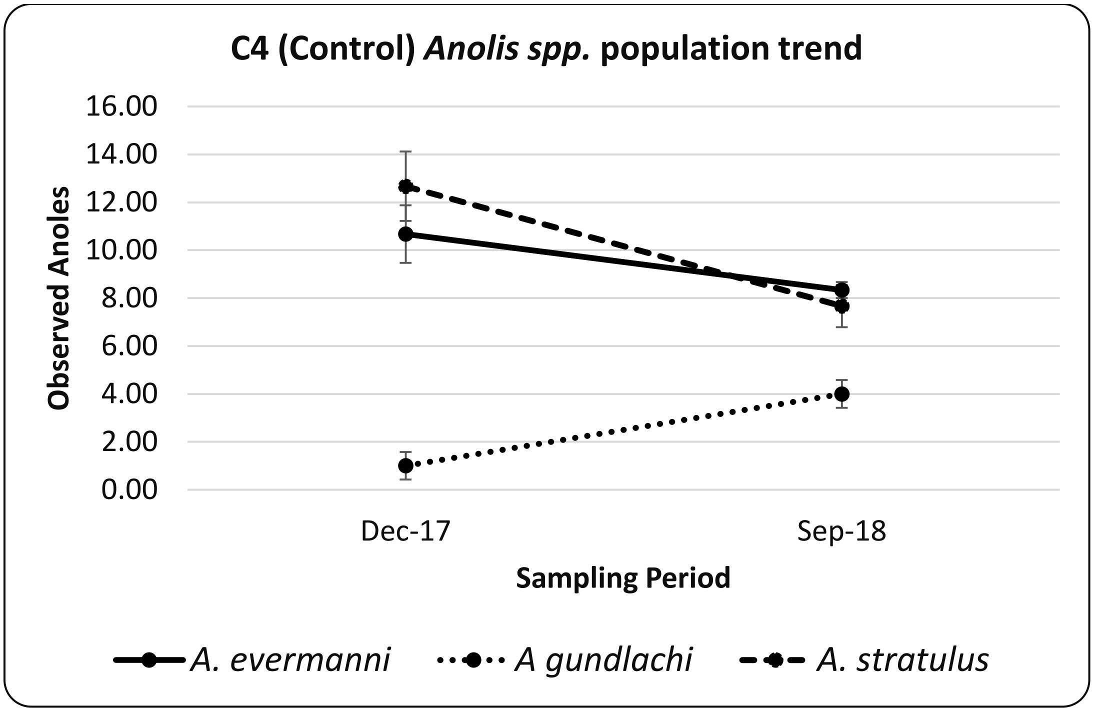


Figure 8b. Population trends of *Anolis spp*. within block B of the Canopy Trimming Experiment



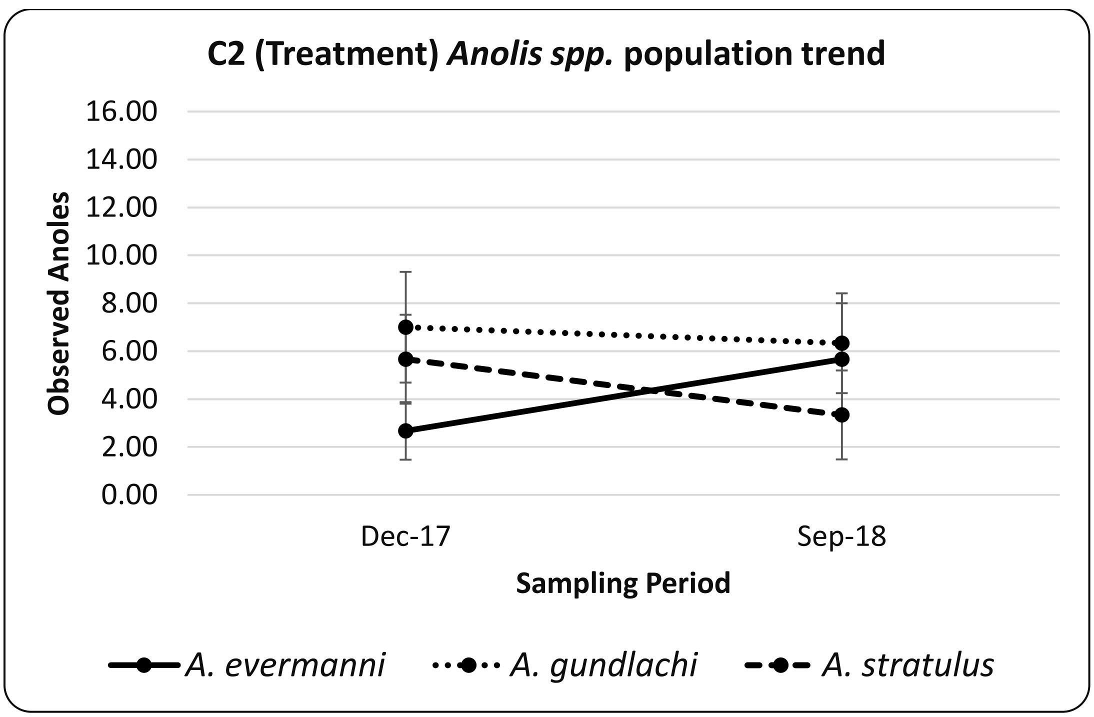
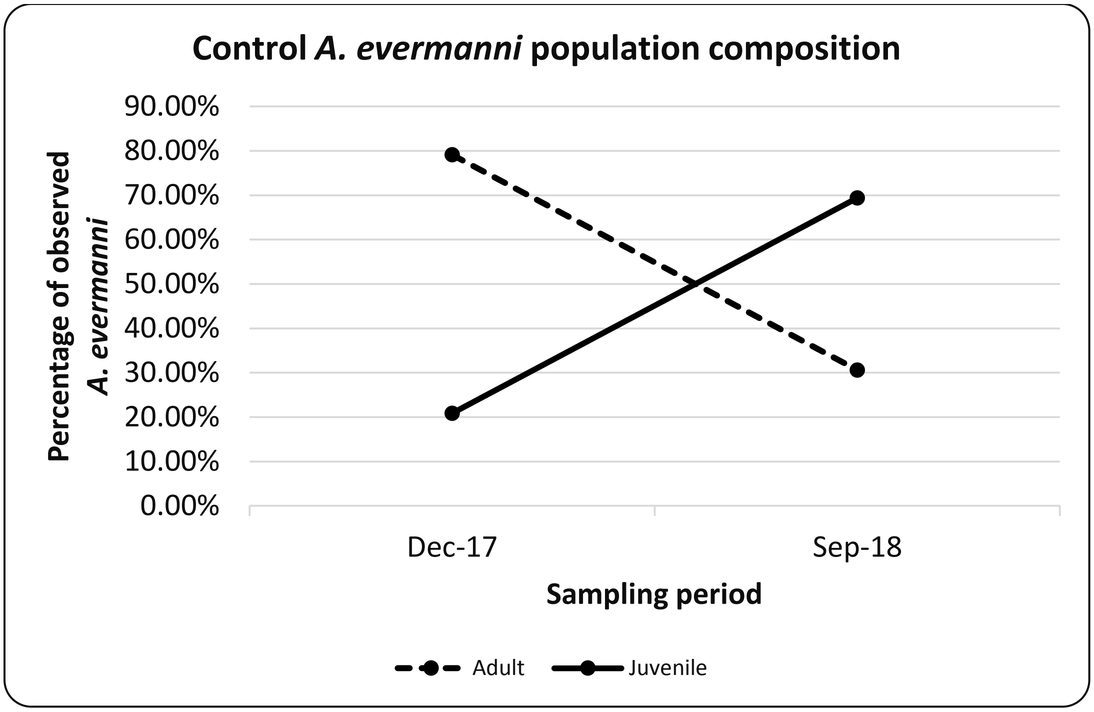


Figure 8c. Population trends of *Anolis spp*. within block C of the Canopy Trimming Experiment



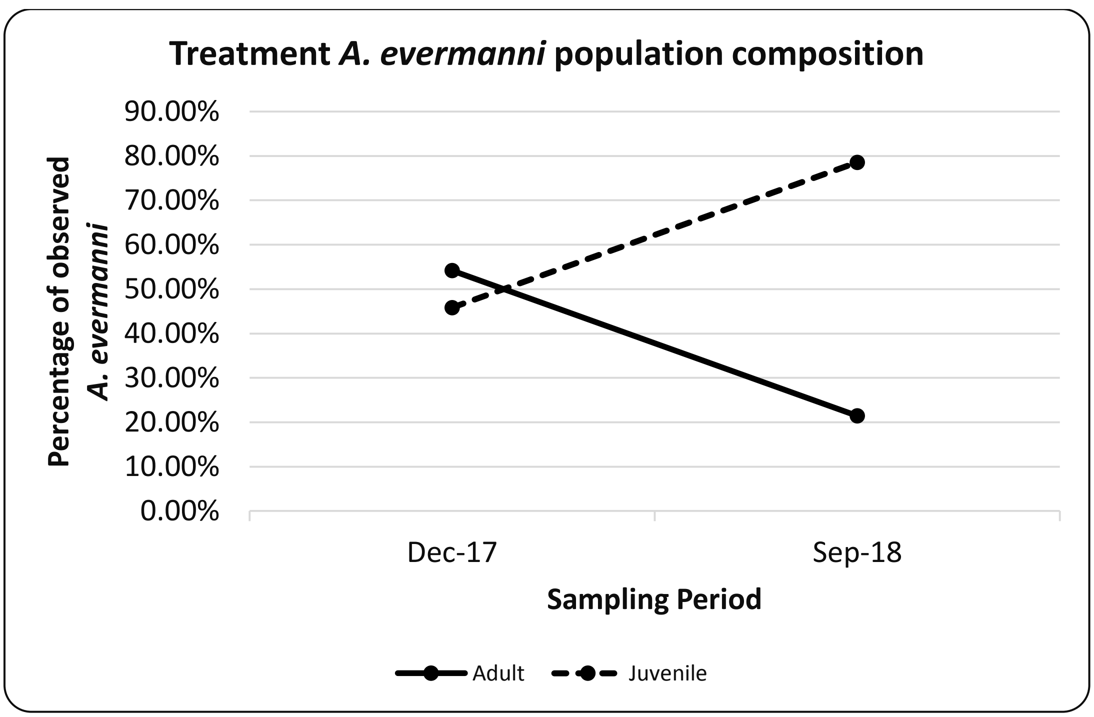


Figure 9a. Post-Hurricane Maria population composition trends of *Anolis evermanni* within the Canopy Trimming Experiment.

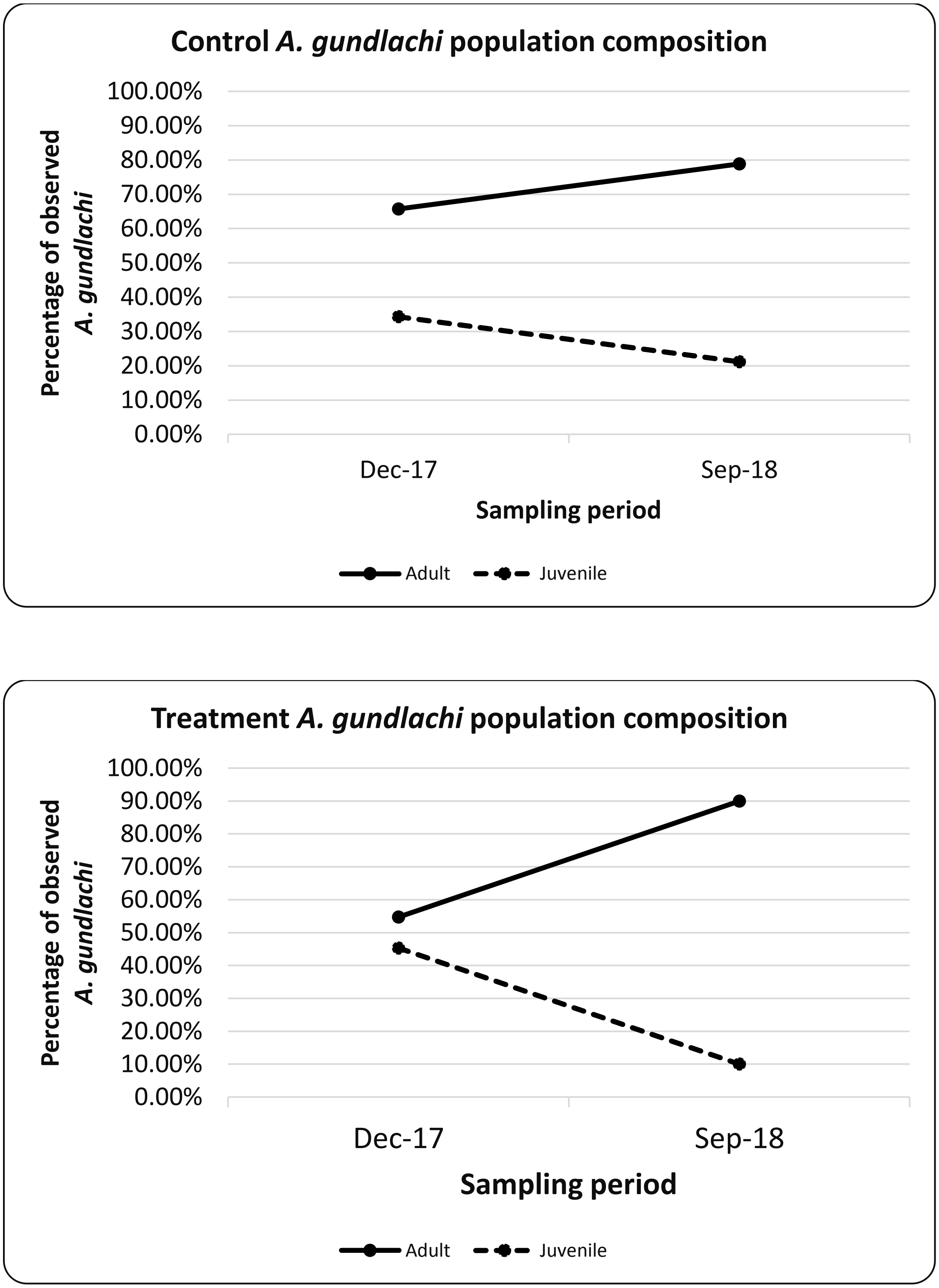


Figure 9b. Post-Hurricane Maria population composition trends of *Anolis gundlachi* within the Canopy Trimming Experiment.

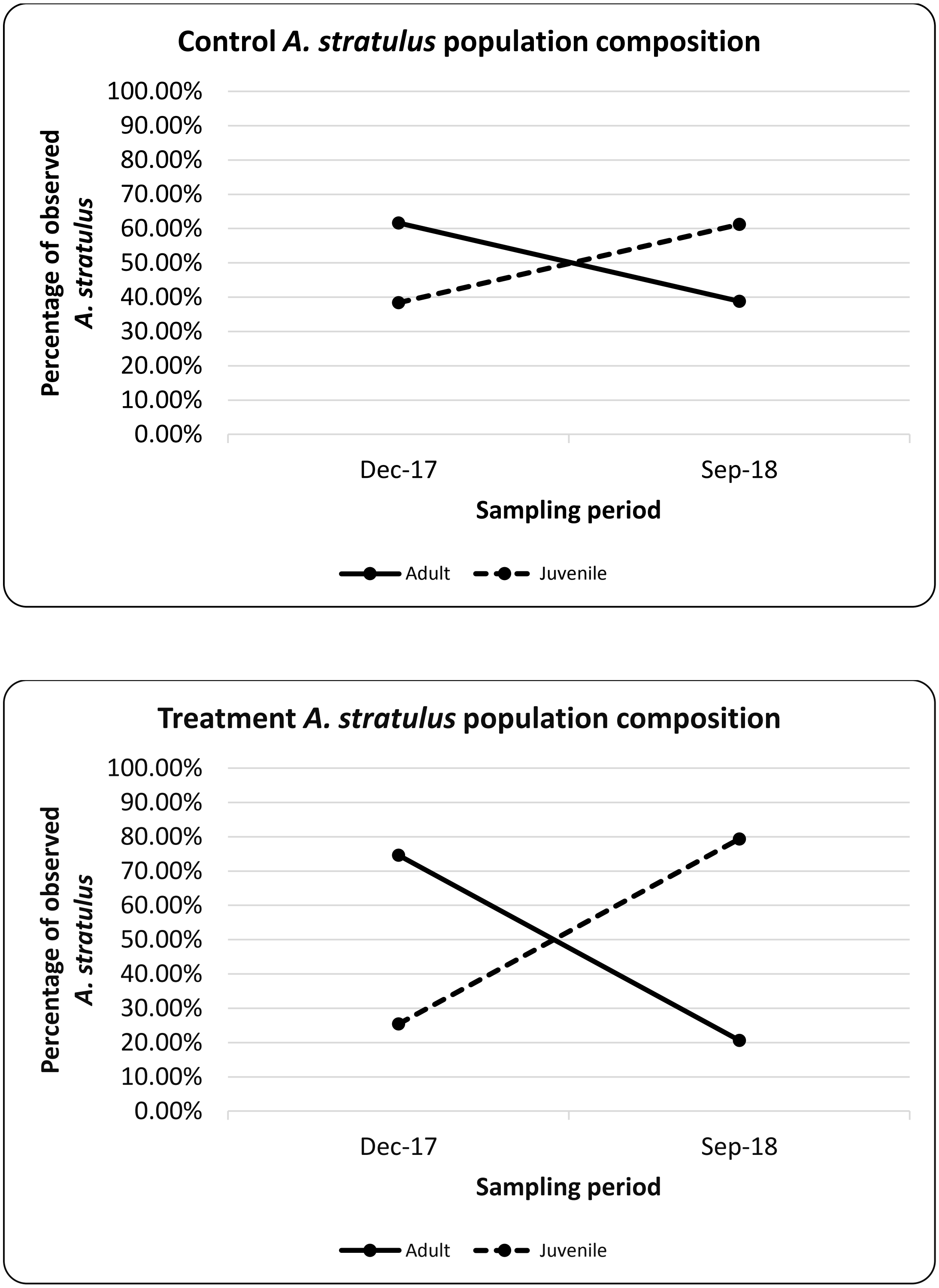


Figure 9c. Post-Hurricane Maria population composition trends of *Anolis stratulus* within the Canopy Trimming Experiment.

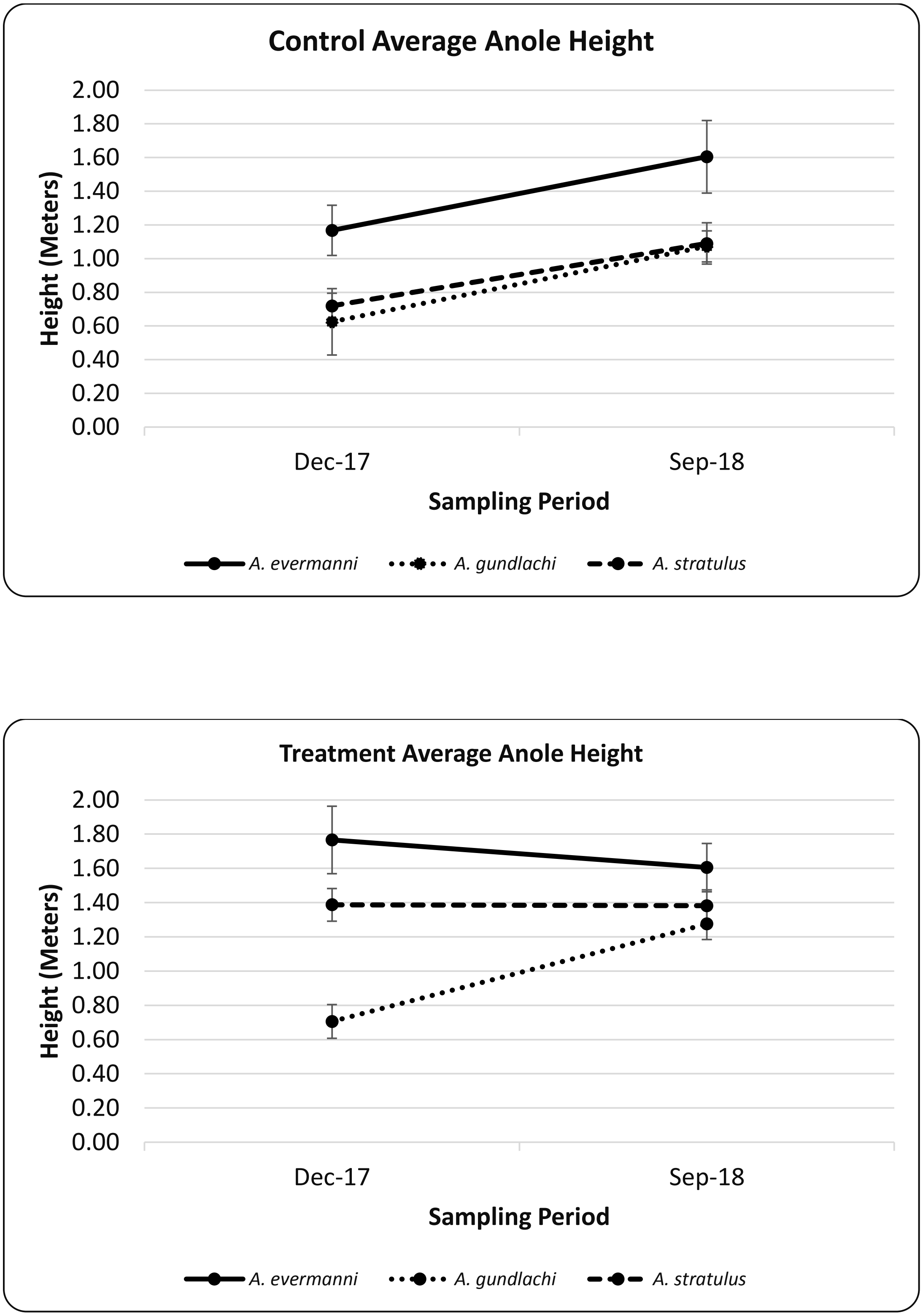
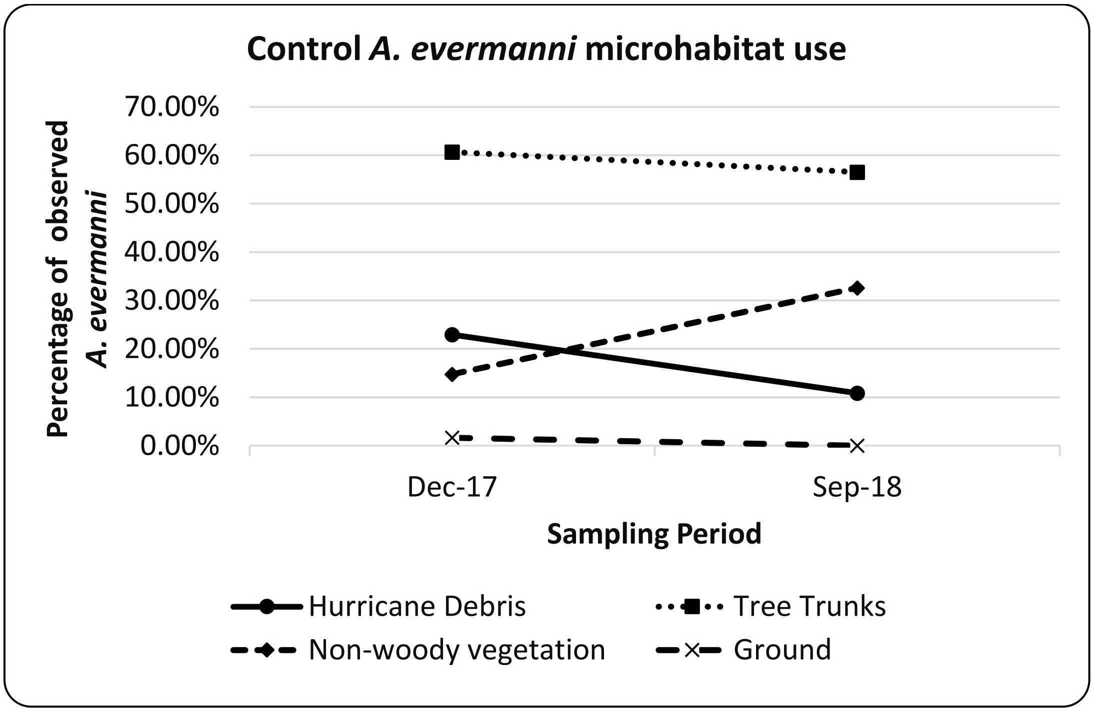


Figure 10. Average anole height within the Canopy Trimming Experiment.



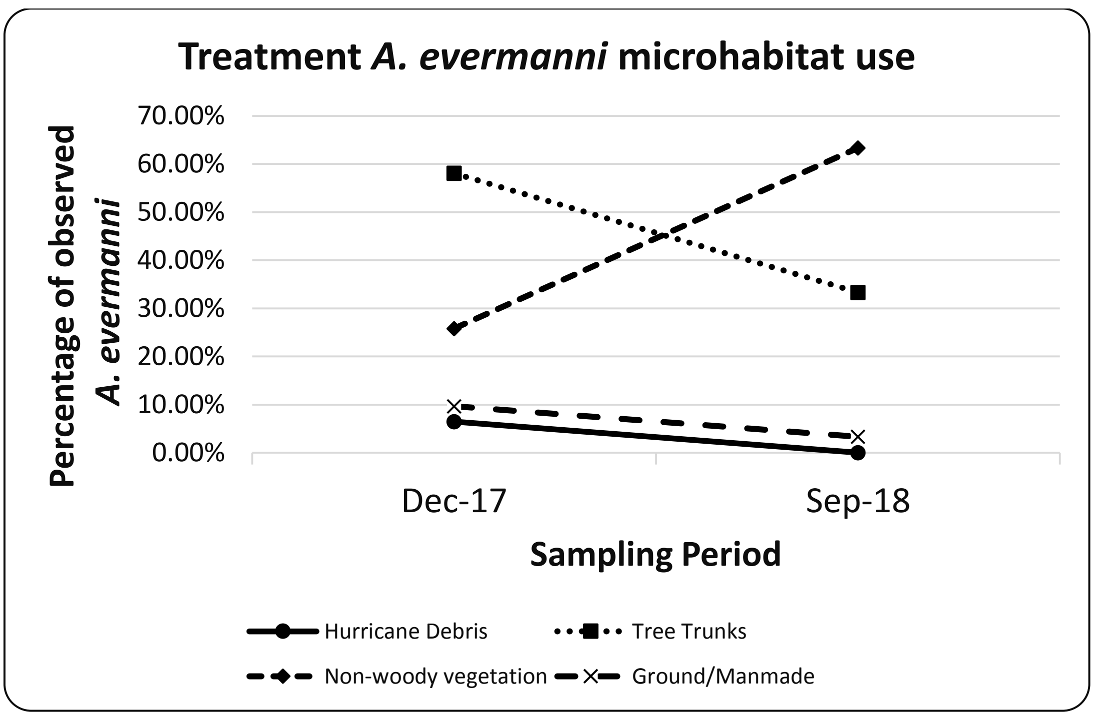
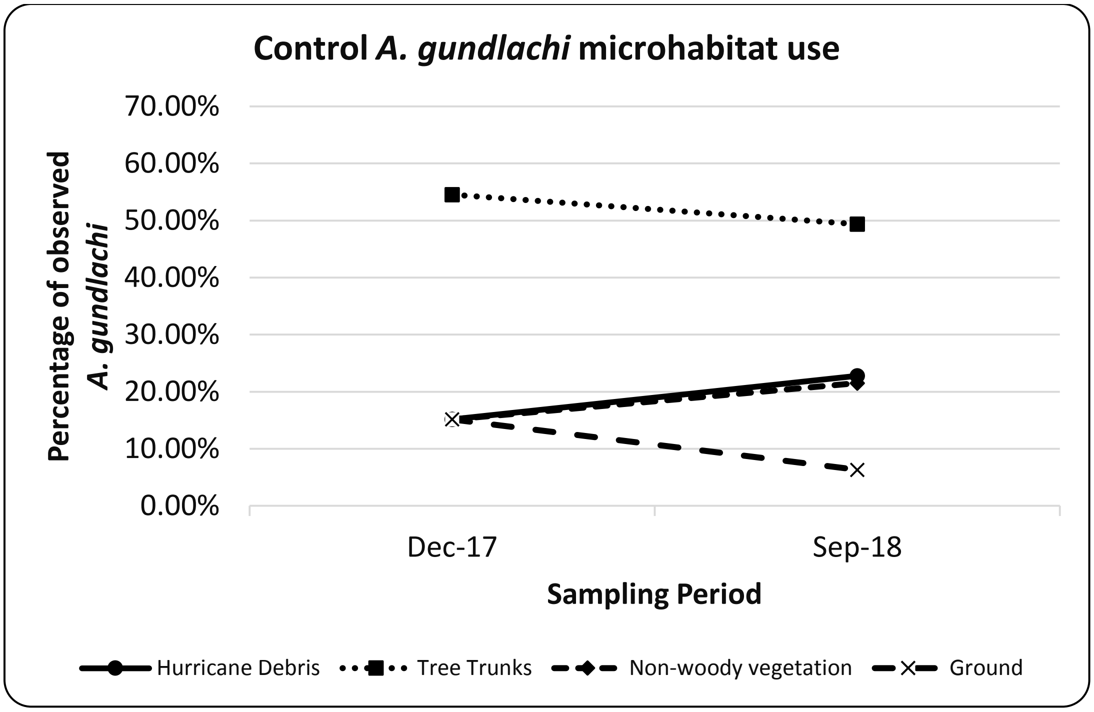


Figure 11a. Use of microhabitats by *Anolis evermanni* within the Canopy Trimming Experiment.



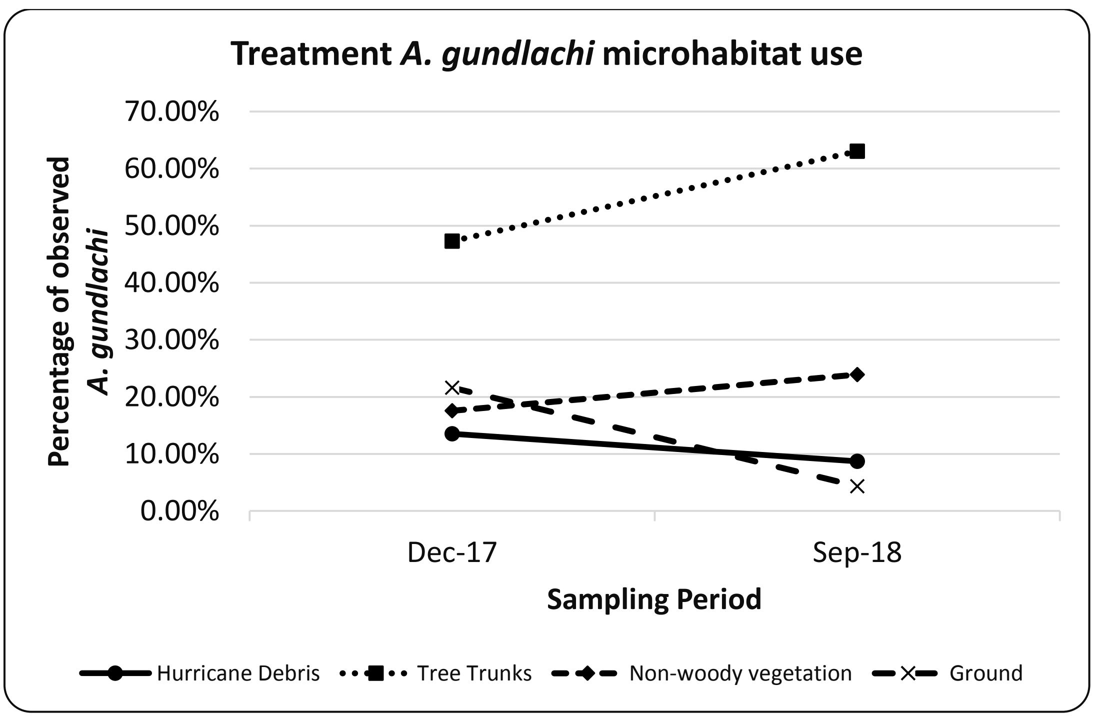
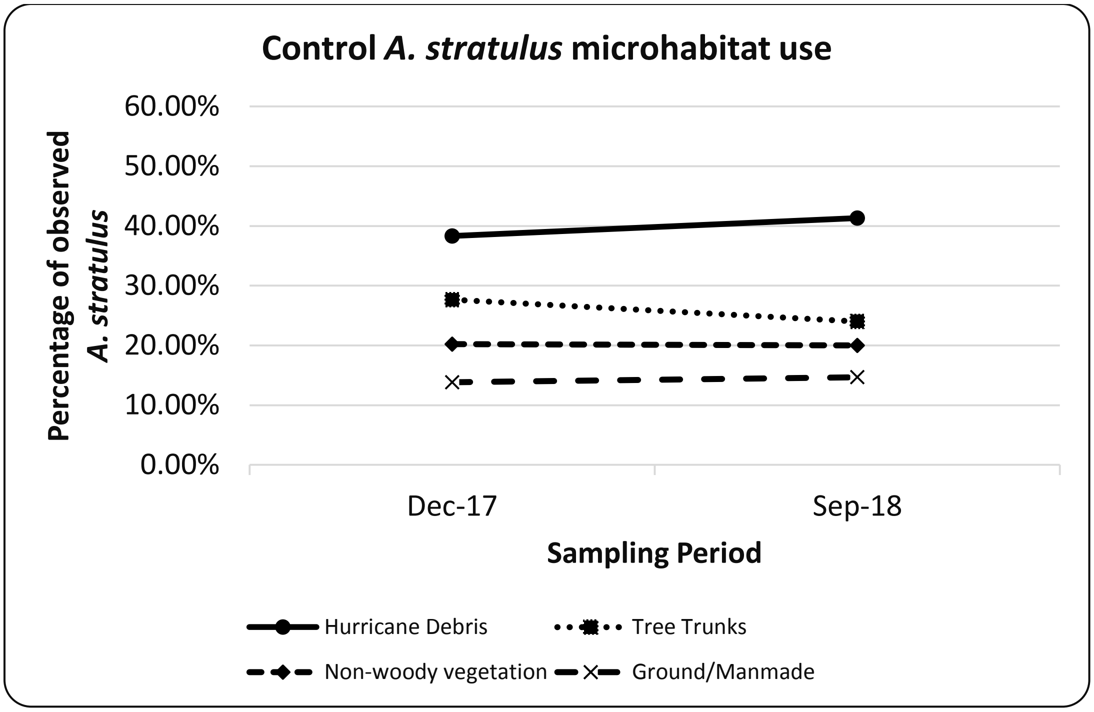


Figure 11b. Use of microhabitats by *Anolis gundlachi* within the Canopy Trimming Experiment.



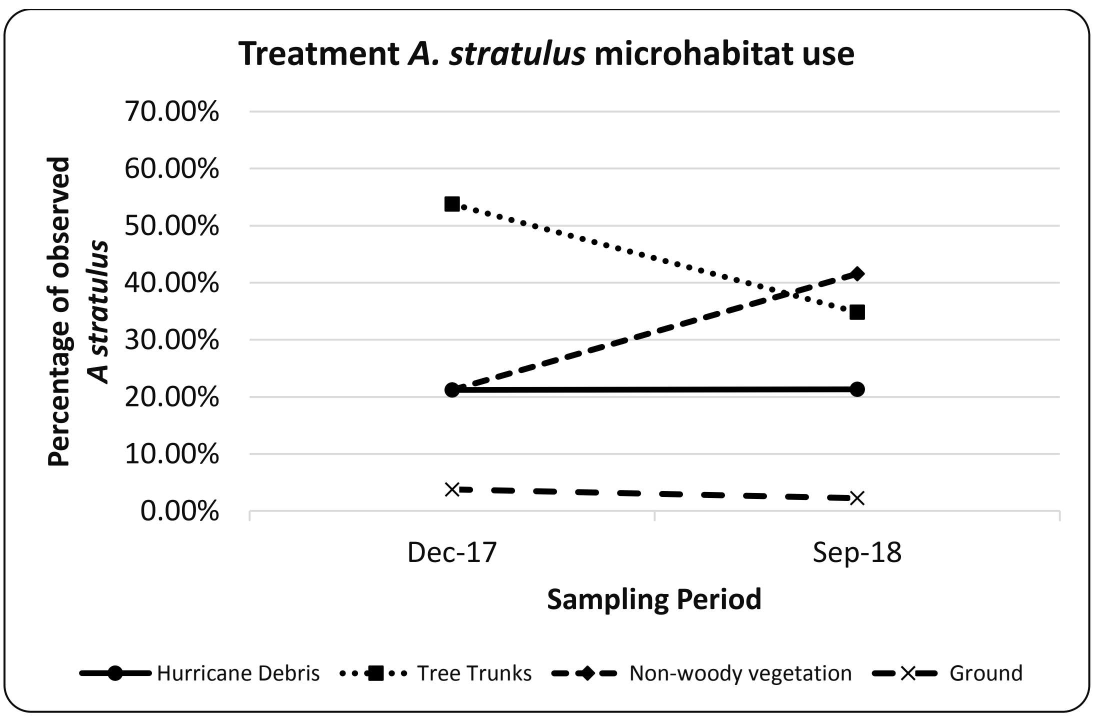


Figure 11c. Use of microhabitats by *Anolis stratulus* within the Canopy Trimming Experiment.

Appendices

Appendix A: Data Categories

Age

Animals were classified as either adult or juvenile. Because identification was made via visual observations, we did not use a more nuanced classification system with additional age classes (such as neonate and sub-adult). Anoles that were not yet large enough to show sexually dimorphic characteristics were classified as juvenile. Those that displayed such characteristics were classified as adults.

For *Eleutherodactylus coqui*, individuals that were less than 20mm in SVL (based on visual estimation) were classified as juveniles, those above 20mm were classified as adults.

Microhabitat/substrate

The same categories of microhabitat were used for both anoles and coquis. They are as follows:

<u>Hurricane Debris</u>- Any woody vegetation deposited on the ground of the plots which resulted from damage due to Hurricane Maria was placed under this classification. This includes fallen live trees, fallen snags, and piles of branches broken from the canopy.

<u>Trunks</u>- This category includes the tree trunks of all standing trees, of all species, with a DBH greater than 2.5cm and a height of more than 1.5 meters. It also includes dead, defoliated, but still standing "snags".

<u>Non-woody vegetation</u>- This category encompasses ferns and lianas, as well as broadleaf shrubs, tree saplings not yet 1.5 meters in height, and palm leaves.

<u>Ground</u>- This category was used for all animals observed on the forest floor, rocks, or on manmade PVC pipes used to denote the plot/transect boundaries.

Appendix B: ANOVA Calculation Results Tables

ANOVA				Alpha	0.05	
	SS	*df*	*MS*	*F*	*p-value*	*sig*
Sampling Period	22.77785	3	7.592616	68.66585	4.91E-05	yes
Treatment	0.046699	1	0.046699	0.422335	0.539843	no
Block	2.723264	2	1.361632	12.31428	0.007518	yes
Sampling Period x Treatment	0.254985	3	0.084995	0.768675	0.552076	no
Sampling Period x Block	3.131159	6	0.52186	4.719578	0.040409	yes
Treatment x Block	0.125951	2	0.062975	0.569535	0.593648	no
Within	0.66344	6	0.110573			
Total	29.72335	23	1.292319			

ANOVA of temperature during *Eleutherodactylus coqui* sampling

ANOVA				Alpha	0.05	
	SS	*df*	*MS*	*F*	*p-value*	*sig*
Sampling Period	233.8561	3	77.95202	59.31809	7.5E-05	yes
Treatment	1.550417	1	1.550417	1.179799	0.319096	no
Block	68.33815	2	34.16907	26.00117	0.001107	yes
Sampling Period x Treatment	12.73199	3	4.243997	3.229496	0.103202	no
Sampling Period x Block	29.00407	6	4.834012	3.678472	0.069021	no
Treatment x Block	57.98111	2	28.99056	22.06055	0.001716	yes
Within	7.884815	6	1.314136			
Total	411.3466	23	17.88464			

ANOVA of humidity during *Eleutherodactylus coqui* sampling

ANOVA				Alpha	0.05	
	SS	*df*	*MS*	*F*	*p-value*	*sig*
Sampling Period	29.05911	2	14.52956	49.71976	0.001495	yes
Treatment	0.007307	1	0.007307	0.025005	0.882018	no
Block	1.879469	2	0.939734	3.215746	0.147037	no
Sampling Period x Treatment	0.131644	2	0.065822	0.225241	0.807804	no
Sampling Period x Block	3.432433	4	0.858108	2.936424	0.160817	no
Treatment x Block	0.058284	2	0.029142	0.099723	0.907269	no
Within	1.168916	4	0.292229			
Total	35.73717	17	2.102186			

ANOVA of temperature during *Anolis* sampling

ANOVA				Alpha	0.05	
	SS	*df*	*MS*	*F*	*p-value*	*sig*
Sampling Period	125.6544	2	62.82722	13.1341	0.017464	yes
Treatment	20.26722	1	20.26722	4.236886	0.108653	no
Block	21.64333	2	10.82167	2.262282	0.220179	no
Sampling Period x Treatment	9.114444	2	4.557222	0.952693	0.4588	no
Sampling Period x Block	27.79111	4	6.947778	1.452441	0.363205	no
Treatment x Block	61.10481	2	30.55241	6.387016	0.056865	no
Within	19.13407	4	4.783519			
Total	284.7094	17	16.74761			

ANOVA of humidity during *Anolis* sampling

ANOVA				Alpha	0.05	
	SS	*df*	*MS*	*F*	*p-value*	*sig*
Sampling Period	44989.53	4	11247.38	15.3851	0.000795	yes
Treatment	31.49825	1	31.49825	0.043086	0.84075	no
Block	7220.862	2	3610.431	4.938647	0.040101	yes
Sampling Period x Treatment	18564.76	4	4641.19	6.348604	0.013312	yes
Sampling Period x Block	5214.051	8	651.7564	0.891526	0.562518	no
Treatment x Block	689.937	2	344.9685	0.471877	0.640149	no
Within	5848.454	8	731.0567			
Total	82559.1	29	2846.865			

ANOVA of Litterfall

ANOVA				Alpha	0.05	
	SS	*df*	*MS*	*F*	*p-value*	*sig*
Sampling Period	107.6673	2	53.83365	1.303793	0.366467	no
Treatment	4.856806	1	4.856806	0.117627	0.748889	no
Block	1026.599	2	513.2994	12.43156	0.019206	yes
Sampling Period x Treatment	110.4843	2	55.24217	1.337906	0.359014	no
Sampling Period x Block	266.3068	4	66.5767	1.612416	0.327402	no
Treatment x Block	32.56324	2	16.28162	0.394323	0.697741	no
Within	165.1602	4	41.29004			
Total	1713.637	17	100.8022			

ANOVA for total coquis observed

ANOVA				Alpha	0.05	
	SS	*df*	*MS*	*F*	*p-value*	*sig*
Sampling Period	0.32494	2	0.16247	56.64157	0.001163	yes
Treatment	0.007729	1	0.007729	2.69468	0.176028	no
Block	0.01968	2	0.00984	3.430517	0.135637	no
Sampling Period x Treatment	0.010555	2	0.005278	1.83996	0.271273	no
Sampling Period x Block	0.006208	4	0.001552	0.54109	0.716736	no
Treatment x Block	0.062402	2	0.031201	10.87755	0.024121	yes
Within	0.011474	4	0.002868			
Total	0.442989	17	0.026058			

ANOVA for *E. coqui* population composition, percent adults

ANOVA				Alpha	0.05	
	SS	*df*	*MS*	*F*	*p-value*	*sig*
Sampling Period	0.326312	2	0.163156	57.60482	0.001126	yes
Treatment	0.007564	1	0.007564	2.670766	0.177546	no
Block	0.019347	2	0.009673	3.415343	0.136398	no
Sampling Period x Treatment	0.01046	2	0.00523	1.846593	0.270338	no
Sampling Period x Block	0.006588	4	0.001647	0.581519	0.693824	no
Treatment x Block	0.062592	2	0.031296	11.04961	0.023489	yes
Within	0.011329	4	0.002832			
Total	0.444194	17	0.026129			

ANOVA for *E. coqui* population composition, percent juveniles

ANOVA				Alpha	0.05	
	SS	df	MS	F	p-value	sig
Sampling Period	0.107604	2	0.053802	6.438476	0.056174	no
Treatment	0.048985	1	0.048985	5.861961	0.072673	no
Block	0.037326	2	0.018663	2.233383	0.223195	no
Sampling Period x Treatment	0.025094	2	0.012547	1.501516	0.326248	no
Sampling Period x Block	0.054568	4	0.013642	1.632521	0.323264	no
Treatment x Block	0.037609	2	0.018805	2.250349	0.221417	no
Within	0.033425	4	0.008356			
Total	0.344611	17	0.020271			

ANOVA for adult *E. coqui* microhabitat use, percentage utilizing hurricane debris

ANOVA				Alpha	0.05	
	SS	*df*	*MS*	*F*	*p-value*	*sig*
Sampling Period	0.032963	2	0.016482	10.79196	0.024445	yes
Treatment	0.001184	1	0.001184	0.775409	0.428278	no
Block	0.02315	2	0.011575	7.579047	0.043593	yes
Sampling Period x Treatment	0.065277	2	0.032638	21.37108	0.007323	yes
Sampling Period x Block	0.073999	4	0.0185	12.11331	0.016559	yes
Treatment x Block	0.038555	2	0.019278	12.62263	0.018707	yes
Within	0.006109	4	0.001527			
Total	0.241237	17	0.01419			

ANOVA for adult *E. coqui* microhabitat use, percentage utilizing tree trunks

ANOVA				Alpha	0.05	
	SS	*df*	*MS*	*F*	*p-value*	*sig*
Sampling Period	0.182158	2	0.091079	6.384618	0.056898	no
Treatment	0.20246	1	0.20246	14.1924	0.019651	yes
Block	0.041702	2	0.020851	1.461653	0.333805	no
Sampling Period x Treatment	0.023188	2	0.011594	0.81274	0.505593	no
Sampling Period x Block	0.060382	4	0.015095	1.058183	0.478804	no
Treatment x Block	0.069751	2	0.034875	2.444756	0.202472	no
Within	0.057062	4	0.014265			
Total	0.636702	17	0.037453			

ANOVA for adult *E. coqui* microhabitat use, percentage utilizing non-woody vegetation

ANOVA				Alpha	0.05	
	SS	*df*	*MS*	*F*	*p-value*	*sig*
Sampling Period	0.232881	2	0.11644	15.94601	0.01242	yes
Treatment	0.102152	1	0.102152	13.98927	0.020117	yes
Block	0.043349	2	0.021674	2.968213	0.162054	no
Sampling Period x Treatment	0.045949	2	0.022975	3.146258	0.151035	no
Sampling Period x Block	0.07446	4	0.018615	2.549251	0.193416	no
Treatment x Block	0.084162	2	0.042081	5.762833	0.066377	no
Within	0.029209	4	0.007302			
Total	0.612162	17	0.03601			

ANOVA for adult *E. coqui* microhabitat use, percentage utilizing the forest floor

ANOVA				Alpha	0.05	
	SS	*df*	*MS*	*F*	*p-value*	*sig*
Sampling Period	0.114271	2	0.057136	16.75166	0.011376	yes
Treatment	0.005941	1	0.005941	1.741699	0.257388	no
Block	0.024733	2	0.012367	3.625807	0.126383	no
Sampling Period x Treatment	0.009457	2	0.004729	1.386352	0.348816	no
Sampling Period x Block	0.084582	4	0.021145	6.199655	0.052517	no
Treatment x Block	0.020497	2	0.010249	3.004764	0.159696	no
Within	0.013643	4	0.003411			
Total	0.273124	17	0.016066			

ANOVA for juvenile *E. coqui* microhabitat use, percentage utilizing hurricane debris

ANOVA				Alpha	0.05	
	SS	*df*	*MS*	*F*	*p-value*	*sig*
Sampling Period	0.006171	2	0.003086	0.534666	0.622613	no
Treatment	0.005236	1	0.005236	0.907257	0.394781	no
Block	0.009455	2	0.004727	0.819119	0.503307	no
Sampling Period x Treatment	0.00846	2	0.00423	0.732946	0.535547	no
Sampling Period x Block	0.012595	4	0.003149	0.545568	0.714163	no
Treatment x Block	0.009418	2	0.004709	0.815943	0.504443	no
Within	0.023085	4	0.005771			
Total	0.07442	17	0.004378			

ANOVA for juvenile *E. coqui* microhabitat use, percentage utilizing tree trunks

ANOVA				Alpha	0.05	
	SS	*df*	*MS*	*F*	*p-value*	*sig*
Sampling Period	0.356908	2	0.178454	54.45149	0.001255	yes
Treatment	0.110293	1	0.110293	33.65368	0.004391	yes
Block	0.049734	2	0.024867	7.587686	0.043514	yes
Sampling Period x Treatment	0.069909	2	0.034954	10.66559	0.024935	yes
Sampling Period x Block	0.00934	4	0.002335	0.712501	0.624729	no
Treatment x Block	0.013308	2	0.006654	2.030343	0.24625	no
Within	0.013109	4	0.003277			
Total	0.622603	17	0.036624			

ANOVA for juvenile *E. coqui* microhabitat use, percentage utilizing non-woody vegetation

ANOVA				Alpha	0.05	
	SS	*df*	*MS*	*F*	*p-value*	*sig*
Sampling Period	0.15549	2	0.077745	6.640541	0.053577	no
Treatment	0.15272	1	0.15272	13.04449	0.022522	yes
Block	0.046451	2	0.023226	1.983809	0.252036	no
Sampling Period x Treatment	0.032615	2	0.016307	1.392885	0.347474	no
Sampling Period x Block	0.064051	4	0.016013	1.367723	0.384457	no
Treatment x Block	0.029957	2	0.014979	1.279397	0.371939	no
Within	0.046831	4	0.011708			
Total	0.528116	17	0.031066			

ANOVA for juvenile *E. coqui* microhabitat use, percentage utilizing the forest floor.

ANOLES

ANOVA				Alpha	0.05	
	SS	*df*	*MS*	*F*	*p-value*	*sig*
Sampling Period	1.340008	1	1.340008	0.692436	0.492872	no
Treatment	35.53521	1	35.53521	18.36247	0.050379	no
Block	43.86815	2	21.93408	11.33422	0.081075	no
Sampling Period x Treatment	3.707408	1	3.707408	1.915767	0.30054	no
Sampling Period x Block	6.010017	2	3.005008	1.552809	0.391725	no
Treatment x Block	5.404817	2	2.702408	1.396443	0.417285	no
Within	3.870417	2	1.935208			
Total	99.73602	11	9.066911			

ANOVA for total *Anolis evermanni* observed

ANOVA				Alpha	0.05	
	SS	*df*	*MS*	*F*	*p-value*	*sig*
Sampling Period	18.77501	1	18.77501	1.691751	0.323057	no
Treatment	12.66908	1	12.66908	1.141566	0.397194	no
Block	76.36815	2	38.18408	3.440634	0.225193	no
Sampling Period x Treatment	8.926875	1	8.926875	0.80437	0.464437	no
Sampling Period x Block	9.377817	2	4.688908	0.422501	0.702987	no
Treatment x Block	8.67815	2	4.339075	0.390979	0.718918	no
Within	22.19595	2	11.09798			
Total	156.991	11	14.27191			

ANOVA for total *Anolis gundlachi* observed

ANOVA				Alpha	0.05	
	SS	*df*	*MS*	*F*	*p-value*	*sig*
Sampling Period	46.68908	1	46.68908	16.78341	0.054737	no
Treatment	22.22241	1	22.22241	7.988332	0.105703	no
Block	299.536	2	149.768	53.83738	0.018236	yes
Sampling Period x Treatment	0.232408	1	0.232408	0.083544	0.799757	no
Sampling Period x Block	1.79705	2	0.898525	0.322995	0.755861	no
Treatment x Block	192.4204	2	96.21021	34.58487	0.028102	yes
Within	5.563717	2	2.781858			
Total	568.461	11	51.67828			

ANOVA for total *Anolis stratulus* observed

ANOVA				Alpha	0.05	
	SS	*df*	*MS*	*F*	*p-value*	*sig*
Sampling Period	0.355696	1	0.355696	33.84898	0.028295	yes
Treatment	0.114856	1	0.114856	10.93002	0.080586	no
Block	0.170525	2	0.085262	8.113783	0.109724	no
Sampling Period x Treatment	0.04788	1	0.04788	4.556416	0.16636	no
Sampling Period x Block	0.085565	2	0.042782	4.071277	0.197189	no
Treatment x Block	0.064405	2	0.032202	3.064457	0.246035	no
Within	0.021017	2	0.010508			
Total	0.859944	11	0.078177			

ANOVA of *Anolis evermanni* population proportion, percent adults

ANOVA				Alpha	0.05	
	SS	*df*	*MS*	*F*	*p-value*	*sig*
Sampling Period	0.356041	1	0.356041	34.24676	0.02798	yes
Treatment	0.115052	1	0.115052	11.0666	0.079708	no
Block	0.171849	2	0.085924	8.264869	0.107935	no
Sampling Period x Treatment	0.048514	1	0.048514	4.666461	0.163346	no
Sampling Period x Block	0.085914	2	0.042957	4.131938	0.194858	no
Treatment x Block	0.063531	2	0.031765	3.055436	0.246583	no
Within	0.020793	2	0.010396			
Total	0.861693	11	0.078336			

ANOVA of *Anolis evermanni* population proportion, percent juveniles

ANOVA				Alpha	0.05	
	SS	*df*	*MS*	*F*	*p-value*	*sig*
Sampling Period	0.041419	1	0.041419	23.30824	0.040326	yes
Treatment	0.010384	1	0.010384	5.843603	0.136857	no
Block	0.121896	2	0.060948	34.29826	0.02833	yes
Sampling Period x Treatment	6.75E-06	1	6.75E-06	0.003799	0.956461	no
Sampling Period x Block	0.044282	2	0.022141	12.45976	0.074296	no
Treatment x Block	0.020221	2	0.01011	5.689552	0.149487	no
Within	0.003554	2	0.001777			
Total	0.241762	11	0.021978			

ANOVA of *Anolis gundlachi* population proportion, percent adults

ANOVA				Alpha	0.05	
	SS	*df*	*MS*	*F*	*p-value*	*sig*
A	0.041536	1	0.041536	23.06186	0.040731	yes
B	0.010325	1	0.010325	5.732846	0.138976	no
C	0.121662	2	0.060831	33.77472	0.028757	yes
A x B	5.33E-06	1	5.33E-06	0.002961	0.96155	no
A x C	0.044111	2	0.022056	12.24573	0.075496	no
B x C	0.020323	2	0.010162	5.641928	0.150559	no
Within	0.003602	2	0.001801			
Total	0.241566	11	0.021961			

ANOVA of *Anolis gundlachi population* proportion, percent juveniles

ANOVA				Alpha	0.05	
	SS	*df*	*MS*	*F*	*p-value*	*sig*
Sampling Period	0.13632	1	0.13632	245.9172	0.004041773	yes
Treatment	0.018019	1	0.018019	32.50526	0.029413669	yes
Block	0.174845	2	0.087422	157.7072	0.006300913	yes
Sampling Period x Treatment	2.41E-05	1	2.41E-05	0.043446	0.854188673	no
Sampling Period x Block	0.000925	2	0.000462	0.834035	0.545245902	no
Treatment x Block	0.003992	2	0.001996	3.600722	0.217357208	no
Within	0.001109	2	0.000554			
Total	0.335233	11	0.030476			

ANOVA of *Anolis stratulus* population proportion, percent adults

ANOVA				Alpha	0.05	
	SS	*df*	*MS*	*F*	*p-value*	*sig*
A	0.135894	1	0.135894	229.2604	0.004334	yes
B	0.01771	1	0.01771	29.87783	0.031878	yes
C	0.174746	2	0.087373	147.4029	0.006738	yes
A x B	1.87E-05	1	1.87E-05	0.031632	0.875221	no
A x C	0.001013	2	0.000507	0.854632	0.53919	no
B x C	0.004001	2	0.002001	3.375088	0.228567	no
Within	0.001186	2	0.000593			
Total	0.334569	11	0.030415			

ANOVA of *Anolis stratulus* population proportion, percent juveniles

ANOVA				Alpha	0.05	
	SS	*df*	*MS*	*F*	*p-value*	*sig*
Sampling Period	0.360533	1	0.360533	49.84332	0.019479	yes
Treatment	0.008533	1	0.008533	1.179724	0.39089	no
Block	1.4222	2	0.7111	98.30876	0.01007	yes
Sampling Period x Treatment	0.149633	1	0.149633	20.68664	0.045096	yes
Sampling Period x Block	1.904067	2	0.952033	131.6175	0.00754	yes
Treatment x Block	1.048067	2	0.524033	72.447	0.013615	yes
Within	0.014467	2	0.007233			
Total	4.9075	11	0.446136			

ANOVA of *Anolis evermanni* average encountered height

ANOVA				Alpha	0.05	
	SS	*df*	*MS*	*F*	*p-value*	*sig*
Sampling Period	1.104133	1	1.104133	120.5605	0.008193	yes
Treatment	0.064533	1	0.064533	7.046406	0.117437	no
Block	0.03395	2	0.016975	1.853503	0.350446	no
Sampling Period x Treatment	0.004033	1	0.004033	0.4404	0.575191	no
Sampling Period x Block	0.027617	2	0.013808	1.507734	0.398766	no
Treatment x Block	0.419517	2	0.209758	22.90355	0.041835	yes
Within	0.018317	2	0.009158			
Total	1.6721	11	0.152009			

ANOVA of *Anolis gundlachi* average encountered height

ANOVA				Alpha	0.05	
	SS	*df*	*MS*	*F*	*p-value*	*sig*
Sampling Period	0.048133	1	0.048133	1.705344	0.321591	no
Treatment	0.246533	1	0.246533	8.734573	0.097954	no
Block	0.306017	2	0.153008	5.421022	0.155738	no
Sampling Period x Treatment	0.1587	1	0.1587	5.622675	0.141149	no
Sampling Period x Block	0.081817	2	0.040908	1.449365	0.408269	no
Treatment x Block	0.030117	2	0.015058	0.53351	0.652099	no
Within	0.05645	2	0.028225			
Total	0.927767	11	0.084342			

ANOVA of *Anolis stratulus* average encountered height

ANOVA				Alpha	0.05	
	SS	*df*	*MS*	*F*	*p-value*	*sig*
Sampling Period	0.007854	1	0.007854	0.587525	0.523491	no
Treatment	0.067951	1	0.067951	5.083059	0.152866	no
Block	0.007611	2	0.003806	0.284677	0.778406	no
Sampling Period x Treatment	0.00014	1	0.00014	0.010479	0.927805	no
Sampling Period x Block	0.060917	2	0.030459	2.278456	0.305022	no
Treatment x Block	0.001006	2	0.000503	0.037608	0.963755	no
Within	0.026736	2	0.013368			
Total	0.172215	11	0.015656			

ANOVA of *Anolis evermanni* microhabitat use, percentage utilizing hurricane debris

ANOVA				Alpha	0.05	
	SS	*df*	*MS*	*F*	*p-value*	*sig*
Sampling Period	0.226875	1	0.226875	4.985104	0.155206	no
Treatment	0.04344	1	0.04344	0.954511	0.431608	no
Block	0.047891	2	0.023946	0.526154	0.655242	no
Sampling Period x Treatment	0.07332	1	0.07332	1.611061	0.332058	no
Sampling Period x Block	0.204869	2	0.102434	2.250779	0.307619	no
Treatment x Block	0.007441	2	0.003721	0.081752	0.924426	no
Within	0.091021	2	0.045511			
Total	0.694858	11	0.063169			

ANOVA of *Anolis evermanni* microhabitat use, percentage utilizing tree trunks

ANOVA				Alpha	0.05	
	SS	*df*	*MS*	*F*	*p-value*	*sig*
Sampling Period	0.38092	1	0.38092	22.10594	0.042382	yes
Treatment	0.164268	1	0.164268	9.53296	0.090833	no
Block	0.001732	2	0.000866	0.050261	0.952144	no
Sampling Period x Treatment	0.085345	1	0.085345	4.952843	0.155993	no
Sampling Period x Block	0.188856	2	0.094428	5.479942	0.154322	no
Treatment x Block	0.013249	2	0.006624	0.384425	0.722322	no
Within	0.034463	2	0.017232			
Total	0.868834	11	0.078985			

ANOVA of *Anolis evermanni* microhabitat use, percentage utilizing non-woody vegetation

ANOVA				Alpha	0.05	
	SS	*df*	*MS*	*F*	*p-value*	*sig*
Sampling Period	0.00267	1	0.00267	2.42276	0.259869	no
Treatment	0.00407	1	0.00407	3.693081	0.194583	no
Block	0.013538	2	0.006769	6.141777	0.140021	no
Sampling Period x Treatment	0.001102	1	0.001102	1	0.42265	no
Sampling Period x Block	0.00534	2	0.00267	2.42276	0.292162	no
Treatment x Block	0.00814	2	0.00407	3.693081	0.21308	no
Within	0.002204	2	0.001102			
Total	0.037064	11	0.003369			

ANOVA of *Anolis evermanni* microhabitat use, percentage utilizing the forest floor

ANOVA				Alpha	0.05	
	SS	*df*	*MS*	*F*	*p-value*	*sig*
Sampling Period	0.094164	1	0.094164	2.226294	0.274209	no
Treatment	0.06322	1	0.06322	1.494694	0.346009	no
Block	0.18515	2	0.092575	2.188724	0.313605	no
Sampling Period x Treatment	0.093104	1	0.093104	2.201233	0.276157	no
Sampling Period x Block	0.007075	2	0.003537	0.083632	0.922822	no
Treatment x Block	0.172001	2	0.086	2.033281	0.329676	no
Within	0.084593	2	0.042296			
Total	0.699306	11	0.063573			

ANOVA of *Anolis gundlachi* microhabitat use, percentage utilizing hurricane debris

ANOVA				Alpha	0.05	
	SS	*df*	*MS*	*F*	*p-value*	*sig*
Sampling Period	0.024843	1	0.024843	7.233718	0.1149	no
Treatment	2.13E-05	1	2.13E-05	0.006212	0.944356	no
Block	0.086509	2	0.043254	12.59468	0.073558	no
Sampling Period x Treatment	0.042245	1	0.042245	12.30088	0.072558	no
Sampling Period x Block	0.01535	2	0.007675	2.234786	0.309139	no
Treatment x Block	0.015829	2	0.007914	2.304474	0.30262	no
Within	0.006869	2	0.003434			
Total	0.191666	11	0.017424			

ANOVA of *Anolis gundlachi* microhabitat use, percentage utilizing tree trunks

ANOVA				Alpha	0.05	
	SS	*df*	*MS*	*F*	*p-value*	*sig*
Sampling Period	2304.918	1	2304.918	0.994055	0.423797	no
Treatment	2330.043	1	2330.043	1.004891	0.421711	no
Block	4612.803	2	2306.402	0.994695	0.50133	no
Sampling Period x Treatment	2320.077	1	2320.077	1.000593	0.422536	no
Sampling Period x Block	4652.608	2	2326.304	1.003278	0.499182	no
Treatment x Block	4656.994	2	2328.497	1.004224	0.498946	no
Within	4637.406	2	2318.703			
Total	25514.85	11	2319.532			

ANOVA of *Anolis gundlachi* microhabitat use, percentage utilizing non-woody vegetation

ANOVA				Alpha	0.05	
	SS	*df*	*MS*	*F*	*p-value*	*sig*
Sampling Period	0.005125	1	0.005125	0.260165	0.660723	no
Treatment	0.05044	1	0.05044	2.56038	0.250707	no
Block	0.019334	2	0.009667	0.490702	0.670825	no
Sampling Period x Treatment	0.00264	1	0.00264	0.134025	0.749393	no
Sampling Period x Block	0.081331	2	0.040665	2.064195	0.32635	no
Treatment x Block	0.108017	2	0.054008	2.741493	0.267273	no
Within	0.039401	2	0.0197			
Total	0.306288	11	0.027844			

ANOVA of *Anolis gundlachi* microhabitat use, percentage utilizing the forest floor

ANOVA				Alpha	0.05	
	SS	*df*	*MS*	*F*	*p-value*	*sig*
Sampling Period	0.019441	1	0.019441	0.879155	0.447414	no
Treatment	0.33634	1	0.33634	15.21006	0.0599	no
Block	0.074754	2	0.037377	1.690273	0.37171	no
Sampling Period x Treatment	0.017101	1	0.017101	0.773335	0.471941	no
Sampling Period x Block	0.035912	2	0.017956	0.812011	0.551873	no
Treatment x Block	0.060813	2	0.030406	1.375043	0.421045	no
Within	0.044226	2	0.022113			
Total	0.588586	11	0.053508			

ANOVA of *Anolis stratulus* microhabitat use, percentage utilizing hurricane debris

ANOVA				Alpha	0.05	
	SS	*df*	*MS*	*F*	*p-value*	*sig*
Sampling Period	0.081345	1	0.081345	8.843246	0.09692	no
Treatment	0.066901	1	0.066901	7.273004	0.114381	no
Block	0.061276	2	0.030638	3.330739	0.230907	no
Sampling Period x Treatment	0.038081	1	0.038081	4.139913	0.178865	no
Sampling Period x Block	0.034671	2	0.017336	1.884593	0.346669	no
Treatment x Block	0.034792	2	0.017396	1.89117	0.345881	no
Within	0.018397	2	0.009199			
Total	0.335465	11	0.030497			

ANOVA of *Anolis stratulus* microhabitat use, percentage utilizing tree trunks

ANOVA				Alpha	0.05	
	SS	*df*	*MS*	*F*	*p-value*	*sig*
Sampling Period	0.042483	1	0.042483	8.403739	0.101245	no
Treatment	0.056856	1	0.056856	11.24699	0.078576	no
Block	0.021765	2	0.010883	2.152729	0.317186	no
Sampling Period x Treatment	0.054675	1	0.054675	10.81549	0.081339	no
Sampling Period x Block	0.034214	2	0.017107	3.383957	0.228104	no
Treatment x Block	0.04139	2	0.020695	4.09378	0.196318	no
Within	0.01011	2	0.005055			
Total	0.261494	11	0.023772			

ANOVA of *Anolis stratulus* microhabitat use, percentage utilizing non-woody vegetation

ANOVA				Alpha	0.05	
	SS	*df*	*MS*	*F*	*p-value*	*sig*
Sampling Period	0.028227	1	0.028227	0.762598	0.474601	no
Treatment	0.001323	1	0.001323	0.035743	0.867494	no
Block	0.040437	2	0.020219	0.546238	0.646731	no
Sampling Period x Treatment	0.010443	1	0.010443	0.282135	0.648393	no
Sampling Period x Block	0.002446	2	0.001223	0.033035	0.968022	no
Treatment x Block	0.032614	2	0.016307	0.440553	0.694178	no
Within	0.074029	2	0.037014			
Total	0.189518	11	0.017229			

ANOVA of *Anolis stratulus* microhabitat use, percentage utilizing the ground

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