

Evaluating Seed Abundance of Palm and Trees species occupying Camera Monitoring Traps during El Niño Southern Oscillation on Barro Colorado Island, Panama

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Introduction

1.1 Context of Study

The Tropical Ecology Assessment and Monitoring Network (TEAM) records terrestrial mammalian fruit-eater (frugivore) presence and activity with camera monitoring sites situated across Barro Colorado Island, Panama. Frugivores, when acting as seed-dispersers, provide an important ecosystem service within a complex plant-animal network (Beaune et al. 2013). Both plant species composition and diversity heavily depends on seed dispersal by frugivores and frugivores heavily depend on fruit-bearing plants for resources (Rivas-Romero and Soto-Shoender 2015). There exists concern for the maintenance of this ecosystem service as habitat loss via forest fragmentation, illegal harvesting and invasive species have resulted in a global decline of frugivores (Sekercioglu et al. 2004). Although much is known about these relationships, past studies have heavily focused on arboreal frugivores (primates, birds, and bats) and little is known about the magnitude of the terrestrial frugivore role (Camargo-Sanabria and Mendoza 2016, Fleming and Kress 2011). This study assessed the abundance of four fruit-bearing tree species and indicators of their productivity at the aforementioned sites. We believe this data will aid in obtaining a comprehensive understanding on this network as well as benefit relevant conservation efforts. Furthermore, this data will enable TEAM to track long-term changes in fruiting production alongside corresponding mammalian activity data.

1.2 Conceptual Framework

Previous studies have illustrated that many Panamanian tree species adjust their energy investments and productivity in response to the annual wet and dry seasons (Kitajima et al. 2005). This ability to adjust, or plasticity, allows for maximum return on investments in times when resources may be limited (Kitajima et al. 2005). Elevated temperatures and reduced rainfall

limits water availability for plants during the dry season, whereas light availability, as cloud coverage increases, is limited during the wet season. These annual cycles manifest temporal differences in fruit abundance which have direct effects on frugivorous populations (Jansen et al. 2008). Beyond this annual cycle, in the tropical Pacific region, lies an influential variable that has major impacts on the relationship held between frugivores and fruit-bearing trees: the El Niño Southern Oscillation.

The El Niño Southern Oscillation (ENSO) is a set of inter-annual fluctuations in atmospheric and oceanic circulation patterns, composed of El Niño, La Niña, and neutral conditions (Jackson 2016). During ENSO, there is an observed reverse of the typical atmospheric pressure gradient in the western Pacific (Jackson 2016). This reverse results in increased rainfall and floods in the west, and drought in the normally wet regions of northern Australia and Indonesia. (Jackson 2016)

In Panama, El Niño events reported by Wright had observed decreases in cloud coverage and rainfall, accompanied by increases in solar irradiance and average temperature. La Niña events are reported to display the opposite phenomenon, with increased cloud coverage and rainfall and decreases in solar irradiance and temperature (Wright 2006). ENSO provides extremes to which trees can either benefit or suffer from. They can gather more energy when there is less cloud cover and more light, but can be subject to forest fires if conditions become too hot or dry (Wright and Calderon 2006).

With an increase in the frequency and intensity of El Niño events (Wright and Calderon 2006) it is important to assess the ability of tree species to adjust to climatic changes. When will those adaptations fail and what is the effect on the animal populations that rely on their fruit? Moreover, since trees rely on seed-dispersers to alleviate themselves of density-related mortality

(Jordano et al. 2010), might there be a positive feedback loop if (1) trees suffer from extreme climatic change (2) seed-dispersing ‘frugivores’ suffer due to lower fruit abundance, and (3) tree populations suffer from lack of seed-dispersal? Of course, if less dispersal occurs or dispersal ranges decrease, tree populations will be limited to their current distribution. Not only could this restrain tree abundance through negative density-dependence; but in the face of climate change, the environment of the current species distribution may undergo a transition from hospitable to inhospitable.

According to Muller-Landau and Hardesty, more than 70% of tropical tree species depend on frugivores for dispersal (2005) and up to 90% of tropical tree species produce fleshy fruits that act as critical resources for mammals (Frankie et al. 1974). As previously mentioned, seed-dispersers affect species distribution and thus directly affect forest composition and diversity (Rivas-Romero and Soto-Shoender, 2015). Disperser movement determines the environment of the next generation of tree species (Jordano et al. 2010) and this movement is controlled by the behaviour, restrictions, and preferences of those animals (Karubian and Durãnes 2009, Côrtes and Uriarte 2012). Different environments will be more favoring than others. As differential survival occurs (natural selection) there is potential for alterations in the genetic make-up of a tree population. Furthermore, this can reverberate into future generations leading to evolution of that species.

Beyond these effects, there exists spatial, temporal, and physical variations in fruit supply that have cascading effects on the distribution and abundance of frugivores (Mourthe 2013). As described by Wien’s et al., the movement of animals influences their risks of predation, the resources they encounter, interactions with conspecifics, and the biotic and abiotic conditions they experience (1995). Also, complexity of fruiting events and the diversity of the

morphological traits of fruit is expected to support more diverse communities of frugivores (Pizo 2002, Lomáscolo et al. 2010, Galetti et al. 2011).

Therefore, the interaction between frugivores and fruit-bearing trees has far-reaching implications for forest structure and composition. As we can see, there are many back-and-forth consequences held between frugivores and fruit producing tree species as their behaviours are dictated by one another as well as influence one another. This study follows a general increase of concern in the scientific community over the dependence between seed dispersal and frugivores during the past three decades (Forget et al. 2011).

1.3 Comparable Past Studies

Two previous studies have been conducted on BCI assessing the relationship between ENSO conditions, fruit-production, and frugivore populations. We believe the results of these studies need to be emphasized as they provide important results pertaining to the relationship in question.

In the first, Wright et al. (1999) recounted 4 famines (1931, 1958, 1970, and 1993) following their severe effects on coatis, peccaries, brocket deer, and agoutis. In 1970-71, dead frugivores could be found every 300m along BCI's forest trails and in 1993-94 some mammal species reportedly died at 5-8 times normal rates.

Wright et al. (1999) reported that each famine occurred during a mild dry season one year following an El Nino event. They successfully identified a two-fold cause that contributes to this observed pattern. First, that El Nino enhances fruit production as plants are provided with more light energy. Second, enhanced fruit production consumes a tree's resource reserves leaving minimal quantities for the consequent fruiting event. Frugivorous populations will prosper in a season of high-fruit production but suffer if a shortage occurs in the consequent season. In fact,

mammal populations increased in size in response to very productive fruiting seasons and declined in consequent seasons of shortage (Milton et al. 2005). Interestingly, Wright et al.'s (1999) model is not fully explained by this two-fold cause. They had suspected a third factor: a mild dry season further limiting fruit production. This was disproved by the two 'rainiest' dry seasons that presented no fruit-shortages (Milton et al. 2005). Thus, potential explanatory variables of the four recorded famines are yet to be identified.

In the second study, Milton et al. (2005) described general relationships between fruiting productivity and mammalian populations. Their findings highlight hidden intricacies of the relationship and possible confounding variables. They discovered that on any given year 20-30% of important tree species have unusually good fruiting seasons while all others have an average or worse season. Moreover, the following season it would be a different 20-30% and those species that comprise this percentage is unpredictable (Milton et al. 2005). Alternatively, measures of seasonal timing of fruiting was predictable (including *D. oleifera*). When monthly rainfall is low, fruit production is high and vice-versa (Milton et al. 2005). Milton et al. (2005) concluded that mammals on BCI can rely on some fruit from most species at predictable times of the year, but the amount and duration of availability was highly unpredictable. Another prediction Milton et al. (2005) confirmed was mammalian population size by fruit production. Within any year, they found that each mammal population could be predicted by the production of a number of fruit species. The lightest mammals were predicted by up to 6 fruit-bearing species, and the heaviest mammals were predicted by only 1. Other significant correlations presented time-lag effects, taking 1 to 2 years to arise. Thus, these correlations are presenting cryptically and may be overlooked without multiple years of monitoring.

Finally, Milton et al. (2005) observed diverse relationships between frugivores and their

food: adult agoutis learn to cache fruits in anticipation of famine to the expense of younger juveniles, arborealism allows red-tailed squirrels earlier access to seeds before they've fallen, diminished breeding activity is practiced in the face of famine (red-tailed squirrels), and incorporation of alternative food sources such as leaves (howler monkeys) or invertebrates and small vertebrates (white-faced monkeys).

These two studies contribute information on both how fruit production on BCI has responded to ENSO and other climatic variations in previous years, as well as how specific mammals on BCI respond to changing fruit production. When starting a long-term study such as ours, we believe it is important to learn from the existing record to help interpret new data and be attuned to resurfacing trends. Moreover, difficulties and successes encountered in the past can be anticipated, planned around, or highlighted.

1.4 Research Objectives

There are 30 motion detection camera-monitoring sites related to the project, positioned in an equidistant grid across the island. Each camera is attached to the base of a tree and records a photo when mammalian movement is detected. This method causes minimal disturbance with greatest likely hood of detecting rarer or cryptic species.

This project specifically assessed the following question: How do factors such as the abundance of fruit-bearing trees and indicators of their productivity vary throughout the island? An understanding of these factors will contribute to a better understanding of any effects they may have on mammalian frugivore activity.

The underlying reasoning for this study is to enable TEAM to track any changes in the long-term alongside mammalian frugivore presence. With the mammalian data TEAM will be

able to assess connections between the two. In the short-term it may be possible to analyze spatial correlations between tree indicators and mammalian activity across the island. For example, there may be distinct areas associated with fruit-poor trees and few mammals or fruitful trees and many mammals.

Our four tree species of interest are *Astrocaryum standleyanum*, *Attalea butyracea*, *Gustavia superba*, and *Dipteryx oleifera*. We have selected these species for their ecological importance as their seeds act as a principal source of food for many mammals on the island (Croat, Milton et al., 2005).

Methods

2.1 Research Design

Our study follows a descriptive, quantitative research design gathering quantitative data of four fruit-bearing tree species on BCI. Information revealing the abundance, distribution and productivity of these species in relation to mammal monitoring traps will enable TEAM to assess potential associations or connections. This study is the start of a long-term assessment. The results obtained reflect a sample of the population and all analysis is a generalization. . Camera locations are equally set across the island in a grid-formation. Moreover, our observation and measurement of our four species of interest at each location addresses the skepticism expressed by Milton et al. about their data collection by randomly placed fruit-fall nets (2005). They reported that could collect data on a wide variety of trees, such collection was not effective at capturing the abundances of few large fruits. This is consistent with those growing out of few, large clusters such as *A. standleyanum*, *A. butyracea*, and *G. superba*. Focussing on a number of individuals of such staple fruit species will provide more useful data for examining fruit-mammal relationships (Milton et al. 2005).

2.2 Study Site

We conducted our study in the tropical lowland moist forest of Barro Colorado Island (BCI), Panama (9°10'N, 75°51'W). BCI is a 1600 ha protected, biological reserve that has been managed by the Smithsonian Tropical Research Institute (STRI) since 1946. It experiences a distinctive four-month dry season spanning December through March and an eight-month wet season April through November. Temperature averages to 26°C during 11 months of the year (expectation of 27°C in April) with annual rainfall averaging at 2600 mm (Wright and Calderon 2006). BCI is a major center for tropical research enabling the execution of long-term, comprehensive studies, and is thus a suitable place to perform our study (Smithsonian Tropical Research Institute).

2.3 Study species

2.3.1 *Gustavia superba* (Common name: Membrillo)

G. superba is an understory-tree abundant in BCI and younger forests (Molofsky and Fisher 1993). According to previous studies, its height ranges from 6 to 10 meters, never surpassing 15m, with a diameter usually under 20 centimeters at breast height (Molofsky and Fisher 1993, Croat (d)). They also reported its flowering season to be from March to June with maturing fruit from June to August, which white-faced monkeys may eat as early as April.

2.3.2 *Attalea butyracea* (Common name: Manca)

A. butyracea is a palm with rings of deep vertical grooves that grows fruit in clusters, growing over 30m tall and 30cm diameter (Croat (b)). It is reported to flower during the rainy season (April to September) and yield mature, green fruits by the middle of the dry season (Croat (b)). Their fruit provides an important food source to white-faced monkeys, agoutis, and vultures

(Croat (b)). *A. butyracea* is reportedly common throughout BCI, but is generally found near the shorelines and in younger forests (Croat (b)).

2.3.3 *Dipteryx oleifera* (Common name: Tonka bean)

D. oleifera is a hard-barked buttressed tree growing up to 40m tall (Croat (c)). Its trunk is a light brown with swaths of copper colour, and its diameter grows over a meter at breast height (Croat (c)). Tomas Croat reported that *D. oleifera* is common to locally abundant throughout BCI. It is reported to flower from May to August yielding mature fruit during Panama's dry season (Croat (c)). White-faced monkeys tend to eat them in that time frame, though they, spider monkeys, and howler monkeys will take them as early as November (Croat (c)). Monkeys feed on the mesocarp and discard the remainder which can still be eaten by other animals. Bats, rodents, coatis, peccaries and beetles are others to eat the fruit (Croat (c)).

2.3.4 *Astrocaryum standleyanum* (Common name: Black palm)

A. standleyanum, easily confused with the genus *Bactris*, is a spiny-trunked palm up to 15m tall with a mature diameter of up to 20 cm at breast height (Croat (a)). It is common in the younger forest, and is generally found on low elevations and very wet regions, being rare in older forest except on steep ravines (Croat (a)). *A. standleyanum* flowers from May to September during the rainy season, with mature, orange fruits in clusters by January, though mature fruits may still be green when animals eat them (Croat (a)). Milton et al. (2005) names them along with the hard-fruit of *A. butyracea* and *D. oleifera* as eaten by agoutis and red-tailed squirrels.

2.4 Method of Data Collection

Camera monitoring traps were located with a GPS device and a map provided by TEAM. An octagonal area with a radius of 25 meters centered at the focal camera tree was surveyed at each site (Figure 1). One quadrat was measured at a time laying two measuring tape lines of 25 meters along the borders for visualization. We alerted the camera to our presence upon arrival to and departure from a site. During the working period, the camera was covered to prevent prolonged human detection. Measurements taken consisted of: (1) basal diameter at breast height, (2) approximate number of fruits and clusters per tree (counted with binoculars from multiple angles and averaged between two independent counts; in the case of *Dipteryx*, we surveyed 3 equidistant 1m x 1m plots 5 meters from the base of the tree for fallen or consumed seeds recording type of predation), (3) direction relative to the central tree, (4) distance relative to central tree and (5) crown illumination on an index of 1-5 (Table 1). Using measurements of distance and angle, aerial sketches were produced to represent the positioning of each tree within each site for future reference by TEAM.

2.5 Method of Data Analysis

Descriptive data analyses and normality assessments were performed on the quantitative data gathered (crown illumination, diameter, number of seeds/clusters) for each species of interest. Three measures of central tendency (sample mean, median, and mode) were calculated to assess the average values for the measurements obtained. To analyze spread, we calculated sample variance, sample standard deviation and confidence intervals about the mean at 95% (only for normally distributed data). Normality of the data was assessed through histogram frequency distributions as well as the Shapiro-Wilk statistical test of normality.

In order to investigate possible relationships or effects between variables, scatterplot graphs were produced in excel. Specifically, we explored any potential effects between CI and number of seeds produced in palm species *A. standleyanum* and *A. butyracea*. Trend lines were generated to visualize how seed production changes as CI changes. The Pearson correlation coefficient (r) was calculated to measure the strength and direction of the linear relationship. The coefficient of determination (R^2) was calculated to measure the proportion of variation in seed production that is explained by CI. For *A. standleyanum* the residuals were plotted and assumptions about the residuals were assessed (normality and homoscedasticity) to determine the next appropriate test. No further analysis was done as the data did not meet the requirements for a simple linear regression test nor the assumptions to test the significance of r . Significance of the slopes and Pearson's value were not tested as the normality assumption was violated for *A. standleyanum* and sample size was violated for *A. butyracea*. Homoscedasticity or homogeneity of variance was violated for both samples as well as confirmed by the Levene's test for equality of variances. All statistical procedures were performed in Excel.

To evaluate species distribution throughout the island, map illustrations, graphs and pie charts were generated. These representations aim to illustrate the percent prevalence of species measured, their varying incidences per site, the extent of seed production per site, and potential explanatory variables such as distinguishing environmental conditions.

All research was carried out following the *Code of Ethics* of McGill University.

Results

We surveyed 19 of 30 TEAM camera sites situated on BCI. Quantitative data, as described in the methods section above, was recorded for 262 individuals. Figure 2 and Table 2 illustrates the

percent prevalence of each species. N = 49 individuals of *A. Standleyanum* and N = 11 individuals of *A. butyracea*. The majority of the individuals measured were *G. superba* (N = 199). Across the 19 sites only two *D. oleifera* were identified (N = 2). Each site hosted a different combination of the four species of interest, with no sites containing all 4 species at once and 2 sites (3-01, 3-11) containing none (as illustrated in Figure 3).

3.1 Preliminary Analysis

Figures 4 and 5 illustrate averages across each species for crown illumination (Figure 4) and diameter (Figure 5). Crown illumination (CI) provides insight into the height of the tree with respect to the surrounding forest canopy. Both measured *D. oleifera* individuals were situated in the upper canopy resulting in a CI of $\bar{x} = 5.0$ (± 0 , 95% CI). *A. butyracea* CI averaged to $\bar{x} = 4.12$ (± 0.349 , 95% CI) and *A. standleyanum* to $\bar{x} = 3.02$ (s.d 1.10), equivalent to medium forest gap and small forest gap positioning respectively. *G. Superba* exhibits the lowest CI of the four species with an average CI of $\bar{x} = 2.61$ (s.d 1.02), positioning equivalent to the edge of a small forest gap. This is confirmed by Molofksy and Fisher (1993) describing *G.superba* as a small understory tree species occurring commonly on BCI.

Baseline diameter measurements were gathered to enable for future assessments of the rates of tree growth. Figure 5 displays the averages of each species *A. Standleyanum* ($\bar{x} = 13.64 \pm 0.498$, 95% CI), *G. Superba* ($\bar{x} = 15.5$, s.d 5.00), *A. Butyracea* ($\bar{x} = 36.9 \pm 3.61$, 95% CI), *D. oleifera* ($\bar{x} = 108$, s.d 82) increasing respectively. Confidence intervals have been reported for normally distributed data and standard deviations for non-normally distributed data. Overall, the diameters measured presented similarly across the 3 measures of central tendency for each species. Large error bars representing standard deviations, such as that observed for *D. oleifera* can be explained sample size (N = 2).

Interestingly, Tomas Croat (a) indicated that *A. standleyanum* grows up to 20cm diameter; but none of ours were over 15 despite our large sample size. Has BCI's population evolved a smaller diameter to compensate in another department requiring the resources? Or are current conditions on BCI not conducive to *A. standleyanum* horizontal growth? Is our sample composed mostly of young trees that have not reached the upper diameters yet, and if so, what happened to the older generation? All of these present possible answers, but of course require more investigation or to be confirmed or denied.

Amount of seeds produced on average per palm are $\bar{x} = 221$ s.d 238 (*A. standleyanum*) and $\bar{x} = 176 \pm 77.9$, 95% CI, s.d 116 (*A. butyracea*) (Figure 6). Error bars in Figure 6 represent standard deviation about the mean. The standard deviations are large for both species indicating considerable spread of the data are the mean. Potential reasoning for this spread is depicted in the data as some palms are producing 0 seeds and others are producing up to 920 seeds. Another possible explanation is that the population is not adequately represented by our sample sizes, as the sample sizes are considerably small for each palm (*A. butyracea* N = 11 and *A. standleyanum* N = 49 where only N = 35 individuals producing seeds for *A. standleyanum*). Of course, it could well be that there is a reason for such a wide distribution. Perhaps the conditions on the island vary enough between the trees that seed production is greatly affected. Tables 3, 4, 5, and 6 display all descriptive statistics calculated per species.

3.2 Assessing Normality

Figures 15 - 26 display histograms of each measure (CI, diameter, number of seeds/clusters, number of individual species abundance per site). Table 7 displays p-values pertaining to the Shapiro-Wilk test of normality. For *A. butyracea* measures of total seeds/tree ($p = 0.728$), total seeds/cluster ($p = 0.609$), CI ($p = 0.788$), and diameter ($p = 0.825$) follow a normal distribution.

No measures of *G. superba* and only the diameter measure ($p = 0.730$) of *A. standleyanum* follows a normal distribution. The *D. oleifera* sample size ($N = 2$) was not sufficient to generate a histogram or perform a Shapiro-Wilk test.

3.3 Assessing Relationships

A. standleyanum scatter plot (Figure 7) relating crown illumination to number of seeds was produced with a trend line of $y = 117.52x - 133.82$, a Pearson r value of $r = 0.5434$ ($R^2 = 0.2953$). The scatter, r and R^2 value indicates a moderate, positive relationship. Assumptions to test the validity of this Pearson value (via t-test) were not met (Table 7). Thus, no strong conclusions can be made from this data. Predicted y -values (number of seeds) were calculated from the x -values (CI) along the trend line. The predicted values were plotted against the residuals (difference between the observed and predicted values) in Figure 8. The residual plot is heteroscedastic showing an increasing trend (not constant variance) and contains very large residual points meaning there is a large difference between predicted and observed values of seed number. The residuals do not follow a normal distribution ($p = 0.038$) and do not have constant variance ($p = 4.9E-12$) as verified by tests Shapiro-Wilk and Levene's (Table 7 and 8 respectively). This data does not meet the assumptions to perform a linear regression analysis.

A. butyracae's scatterplot (Figure 9) of CI and number of seeds produced displayed no strong relationship with a trend line of $y = -6.4534x + 202.88$ and an $R^2 = 0.0008$ ($r = 0.03$). An r value near to 0 indicates no linear relationship. The measures of CI, total number of seeds per tree and the calculated predicted (number of seeds) and residual values all follow a normal distribution ($p = 0.787$, $p = 0.728$, $p = 0.787638$, $p = 0.80$, respectively) (Table 7). Levene's test was performed between CI and total seeds for observed values ($p = 2.7E-05$) and the predicted/residuals ($p = 4.02E-05$). Both violate the assumption of equal variance. Finally, the *A.*

butyracea sample size (N =11) is small. These violations do not allow for testing the validity of the Pearson coefficient or further testing of linear regression.

Overall, our data does not meet the requirements to statistically assess a correlative linear relationship between CI and seed number for palms as both normality and/or equal variance is violated. This is most likely attributed to the sample sizes of the data. In order to better assess this question, more data will need to be collected. Also, it is important to consider that no such linear relationship may exist. Thus, it is potentially useful to consider other forms of relationships and models such as non-linear or additive models. This type of information is important to apprehend if CI does in fact influence seed production. We may expect to find palms with greater seed production in areas permitting higher levels of CI and thus we may expect to find more mammals in those corresponding regions.

3.4 Explanatory Variables

Figures 10 and 11 are maps of BCI illustrating the abundances of each species of interest at each camera location and the total number of seeds present per site, respectively. We have also modified 3 graphs retrieved from GIS STRI Laboratory presenting the location of our camera sites with respect to streams and shoreline, soil types, and forest age zones (Figure 12, 13, and 14 respectively) as these may act as potential factors contributing to the distribution of our species (STRI GIS Laboratory, Baillie et al., 2006). Table 9 (Baillie et al., 2006) describes the soil form and parental type pertaining to the soil map (Figure 13).

3.4.1 Gustavia superba

At least one individual was present at 14 of 19 sites. Our data depicts a concentration of *G. Superba* on the right-hand side of the island. Of those sites either directly beside streams or

farthest away (> 500m), there are both high-densities (>14 individuals) and low-densities (ie. 0); hence no pattern is obvious for that factor (Figure 12). Areas of high-density occur on all soil classes but those with the Andesite trait (shown in olive green and purple, Figure 13 and Table 9). *G. Superba* had high densities in forest of moderate age (level 3 of 5 on Figure 14). Site 3-17 is an outlier as it has 14 individuals located in the oldest forest age level, but this may be potentially explained by recent forest gap formation.

3.4.2 *Attalea butyracea*

Only six sites across the island house *A. butyracea*, most of which are located near the shoreline with two sites, 3-06 and 3-13, located slightly inland (~750 meters). Site 3-06 is the only one of them located directly beside a stream (Figure 12). Areas containing *A. butyracea* are in soil categories pink (Red light clay/Bohio), dark blue (Brown fine loam/Bohio) and mustard (Brown fine loam/Caimito volcanic), and young-to-moderate forest age categories 2 and 3. Seeds only occurred in the pink and mustard soil classes, with the greatest numbers on the pink (500-900 versus 60- 330) (Figure 13, 14 and Table 9).

3.4.3 *Astrocaryum standleyanum*

A. standleyanum appear to have a wide distribution occupying 13 of 19 sites distributed around all the edges of the island and partially inland as well. All inland sites are situated close to a stream (1-19, 3-17, 1-21, 3-06, 3-07, and 3-13) (Figure 12). This is suggestive of a preference for moister environments, attested by Tomas Croat in his description of the species. The sites with *A. standleyanum* fall into all soil categories but Andesite (olive green and purple), and the species is spread throughout forest age categories 5, 4, 3, and 2 (oldest to second youngest level respectively) (Figures 13, 14 and Table 9). This seems to defy Croat's comment that the species

prefers young forest and is rare in old forest, but a more specific analysis would have to be done to test the significance of any trend. The greatest number of *A. standleyanum* seeds were produced at sites 3-20, 3-03, and 1-26, sites relatively close to the shore. However, other sites as close to the shore did not have so many seeds, so no pattern is clear.

3.4.4 Dipteryx oleifera

Only two *D. oleifera* individuals were identified and measured, both at site 3-08. According to the maps, this site is near a stream, close to the shoreline, in forest age level 3, and in soil class dark blue (Brown fine loam/Bohio) (Figure 13, 14, 15, and Table 9). Other individuals were encountered on the island, but not in our designated camera sites. It is possible that the sites merely do not coincide with BCI's many areas of local abundance described by Tomas Croat. This sample size is too small to make inferences about how these environmental factors may influence *D. oleifera* distribution.

All explanatory variables previously mentioned have direct and indirect effects on the forest and thus the species that live within it. For example, our trees of interest and their seeds seem to generally be fewest in areas of the island furthest from the shore, which would also be of higher elevation. But it is difficult to specify or confirm such effects without further and more detailed investigation. Beyond what has already been mentioned, factors such as varying environmental conditions (ex. land cover and forest gaps), proximity to trails or human activity, territorial zoning by top predators, competition, and predation all have the potential to impact frugivore -fruit producing species interactions, whether individually or in combination.

3.5 Improvements and Suggestions

A main consideration is the sufficiency of data on all tree species to allow correlations to be

tested. As we were only able to visit and measure 19 sites out of 30 during our 13 days in the field, it will be of interest to TEAM to plan for more hours of data collection in the seasons to come in order to obtain more data. Additionally, expanding the survey area should also be considered. Some of the sites visited reporting 0 species of interest did in fact house them beyond the designated survey area. This was the case at site 3-11. Surveying a larger area of land will generate more representative results.

Furthermore, since the fruit of our trees are to some extent eaten by arboreal mammals (including monkeys and squirrels (Croat (a, b, c, d)), it may be interesting to include methods of mammal-detection that go above the forest floor, if feasible. Past studies have demonstrated the strengths of arboreal canopy camera monitoring. Rivas-Romero and Soto-Shoender (2015) results demonstrated that camera trapping in the canopy increases the number of frugivores identified including those that may not be identified in a traditional focal tree study (cryptic, arboreal).

Finally, based on past studies of this kind, we suggest that TEAM check not only for current patterns between fruiting and mammal populations, but delayed patterns as well that can take place over one or two years (Milton et al. 2005). Also, according to Wright et al. (1999), a severe dry season during El Niño might predict a famine one year later. By report from farmers interviewed throughout our visit of central and western Panama prior to our study, a severe dry season bringing droughts did occur last year during El Niño conditions. Whether a famine is occurring now or within the next year can be determined by TEAM, allowing them to test Wright et al.'s hypothesis on the cause of famines.

3.6 Product

Two products were delivered to our supervisors, Claudio Monteza and Patrick Jansen, associate scientists of the Smithsonian Tropical Research Institute. The first is our raw dataset containing the measurements for each individual species of interest across the 19 camera sites. This data will be entered into the TEAM public database which is accessible to the scientific and conservation community. The second product is a set of illustrations representing the abundance and distribution at each site visually. These illustrations will aid and guide the repeated surveying of these site in the future (Figure 29).

Conclusion

This project is the beginning of a long-term study by TEAM assessing the response of fruiting trees to ENSO and climate change, including the back-and-forth consequences of frugivore populations particularly during famines. Investigating the frugivore – fruit-bearing species network is critically important. As habitat loss and species extinction rates accelerate, it is becoming crucial to have a comprehensive understanding of this network in order to maximize conservation efforts (Bender et al., 1998, Brooks et al., 2002, Fahrig, 2013). This is especially relevant to the extremely bio-diverse tropical forests of Panama.

This network is endlessly complex. Frugivores and fruit-bearing tree species heavily rely on one another for dispersion and resources. Thus, all behaviors and preferences pertaining to either group will strongly influence each other's survival and fitness. For example, why do frugivores choose certain seeds and what dictates where they are dispersed? For the frugivore, selective consumption behaviour may result from factors such as fruit preference, manipulation

and ingestion (Schupp, 1993, Schupp et al., 2010). Likewise, selective dispersal behavior may reflect a frugivores daily and seasonal habits taking into consideration the social organization and mating systems at play, neighbouring territories, and the ‘home’ boundaries (Karubian and Durãnes, 2009, Côrtes and Uriarte, 2012). Thus, how animals choose to use their habitats, dictated by restrictions and preferences, heavily impacts fruit producing tree species. Similarly, environmental preferences and productivity responses to environmental variation held by trees will directly impact the location and diversity of frugivore assemblages within a community (Pizo 2002, Lomáscolo et al, 2010, Galetti et al., 2011). As we can see, there is a tight link with back-and-forth consequences held between frugivores and fruit producing tree species as their behaviours are dictated by one another as well as influence one another.

Of the sites we visited and measured, *G. superba* was of highest abundance but without seeds this season, as is expected (Croat (d)). Our trees of interest were generally abundant to the North-East of the island, and the amount of fruit producing trees seem to decrease between the shore and further inland zones. We provide maps overlapping the locations of TEAM’s camera-trap sites (Figures 12 – 14, modified from STRI GIS Laboratory) with various habitat distinctions such as forest age, soil class, and proximity to bodies of water, noting apparent possible trends. These factors may act as explanatory variables for better understanding the distribution, abundance and productivity of our focal tree species. These explanatory variables should be considered in the context of the frugivore – fruit-producing tree species network. It is important to understand that the analysis of these patterns are speculative as the sample sizes were too small to make any definitive conclusions about habitat preference.

A correlation between crown illumination and seeds per tree was tried for *A. standleyanum* and *A. butyracea*, but a lack of normality, equal variances, or sufficiency of

sample sizes prevented the testing of the significance of these correlations. We suggest that this be reattempted with more data in the future, or that tests specialized for non-normal distributions be applied.

The distribution of our study's trees of interest across Barro Colorado Island (*Astrocaryum standleyanum*, *Attalea butyracea*, *Dipteryx oleifera*, and *Gustavia superba*) and measures of their productivity can be compared with expected and future values to discern possible challenges that the populations face with respect to natural resources and dispersal opportunities. It will be interesting to evaluate how these measures change with seasonal fluctuations as well as through the ENSO cycle.

Moreover, the resulting understanding that can be gained on these seed-dispersal systems is of great relevance to non-protected areas that are highly fragmented. Fragmented forests strongly influence patterns of species richness and abundance (Fahrig, 2013, Villard and Metzger, 2014) as both recruitment and establishment of tree species are negatively impacted in fragmented forests (Pessoa et al., 2017). Additionally, they are typically more accessible to humans and thus more prone to reoccurring disturbances such as logging (Echeverria et al., 2007), fire (Laurance et al., 2011), and hunting (Canale et al., 2012). Thus, it is extremely important to assess the cascading effects that persist on the mammalian frugivores populations present in fragmented forest as the challenges frugivores face directly impacts the next generation of fruit producing tree species. This linkage between frugivores and fruit producing tree species gives merits to our study as it can be used comparatively to confirm the effects of these additional impacts. Our study and TEAM's larger objective, is thus, more than simply locally relevant as it can illustrate relationships that are being stressed in habitats around the world.

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Figures and Tables

Index	Crown Light Environment
5	Crown +/- exposed completely vertically and laterally (ex. large forest opening)
4	Crown exposed to vertical and some lateral light (ex. medium forest gap)
3	Crown exposed to some vertical light and some lateral light (ex. small forest gap)
2	No vertical light, medium lateral light (ex. edge of small gap)
1	No vertical light, minimal lateral light (ex. forest understory)

Table 1 – Index for Crown Illumination (Davies et al. 1998)

Species	Sites Occupied (of 19)	Individuals Measured (of 260)	Percentage of Species
<i>Astrocaryum standleyanum</i>	12	48	18.4%
<i>Attalea butyracea</i>	6	11	4.2%
<i>Dipteryx oleifera</i>	1	2	0.8%
<i>Gustavia superba</i>	14	199	76.8%

Table 2 – Percentage of species measured and occurrence through total sites visited

<i>Attalea butyracea</i> N = 11	Mean	Median	Mode	Sample Standard Deviation	Sample Variance	Min	Max
CI	4.12	4.25	4.3, 4.65	0.520	0.271	3.1	4.85
Diameter (cm)	36.9	36.6	36.3	5.38	29.0	25.5	45.2
Number of Clusters	1	1	1	0.447	0.2	0	2
Total Seeds/Tree	176	150	No mode	116	13459	0	365

Table 3 – Descriptive statistic of measurements for *A. butyracea*

<i>Dipteryx oleifera</i> N =2	Mean	Median	Mode	Sample Standard Deviation	Sample Variance	Min	Max
CI	5	5	5	0	0	5	5
Diameter	108	108	No mode	82.0	6728	50	166
Total Seeds	61.5	61.5	No mode	33.2	1104	38	85

Table 4 – Descriptive statistic of measurements for *D. oleifera*. *Total seeds is an average between three equidistant 1m x 1m plots

<i>Astrocaryum standleyanum</i> N = 48	Mean	Median	Mode	Sample Standard Deviation	Sample Variance	Min	Max
CI	3.02	3.05	3.05	1.10	1.21	1.05	4.95
Diameter (cm)	13.64	13.7	12.4, 13.1, 13.7, 14	1.69	2.86	10.2	18.8
Number of Clusters	1.73	2	0	1.53	2.33	0	6
Total Seeds/Tree	221	170	0	238	56781	0	920

Table 5 – Descriptive statistic of measurements for *A. standleyanum*

<i>Gustavia superba</i> N = 199	Mean	Median	Mode	Sample Standard Deviation	Sample Variance	Min	Max
CI	2.61	2.75	1.4	1.02	1.05	1	4.8
Diameter *N=226	15.5	14.6	12.4	5.00	24.98	6.37	30.6

Table 6 – Descriptive statistic of measurements for *G. superba*

Shapiro-Wilk p values	<i>Astrocaryum standleyanum</i>	<i>Attalea butyracea</i>	<i>Dipteryx oleifera</i>	<i>Gustavia superba</i>
Total Abundance	0.005	0.005	0.005	0.005
Total Seeds/Tree	0.005	<u>0.728239</u>	insufficient data	all zeros
Seeds/Cluster	0.000837	<u>0.600938</u>	-	-
Clusters/Tree	0.005	0.005	-	all zeros
Crown Illumination	0.038056	<u>0.787638</u>	insufficient data	6.94429E-06
Diameter	<u>0.729922</u>	<u>0.824815</u>	insufficient data	5.27561E-05
Residuals of Seeds/CI relationship	0.038067	<u>0.67989</u>	-	-
Predicted values of seeds (by CI)	<u>0.06</u>	<u>0.787638</u>	-	-

Table 7 – Results from Shapiro-Wilk test of normality. Underlined p-values are normal. P-values < 0.05 reject the null hypothesis of normality. Dashes represent no data.

Levene's Test	CI vs. Total Seeds (Values)	CI vs. Total Seeds (Residuals)
<i>Astrocaryum standleyanum</i>	P = 4.9E-12 (median test for non-normal data)	P = 0.010601 (median test for non-normal residuals)
<i>Attalea butyracea</i>	P = 2.7E-05 (mean test for normal data)	P = 4.02E-05 (mean test for normal residuals)

Table 8 – Results of Levene's Test of equality of variances. All p-values are < 0.05 rejecting the null hypothesis of equal variance

Soil Form and Parental Material	Sites Visited	Trees Measured	Palm Seeds Counted
Brown fine loam, Andesite (M)	3-11	0	0
Brown fine loam, Caimito volcanic, (shallow & stony) (Ho)	3-13	33	604
	3-10	1	39
	1-21	17	194
	1-22	36	748
Brown fine loam, Bohio (S)	3-19	28	64
	3-08	5	0
	3-03	25	3100
	3-07	20	590
Red light clay, Andesite (A)	3-06	6	501
	3-15	1	0
Red light clay, Bohio (F)	1-20	2	0
	1-26	26	2315
	3-01	0	0
	3-17	19	0
Pale swelling clay, Caimito marine sedimentary (Z)	1-25	26	0
	3-20	11	2561
	3-04	2	418
	1-19	2	920

Table 9 – Table assigning camera site codes to soil form and parental geological material, respectively (column 1). Total trees measured per site and corresponding seeds counted illustrated next to their assigned soil class. Color coding corresponds to Figure 13. Table Information retrieved from Semi-detailed soil survey on BCI (Baillie et al., 2006).

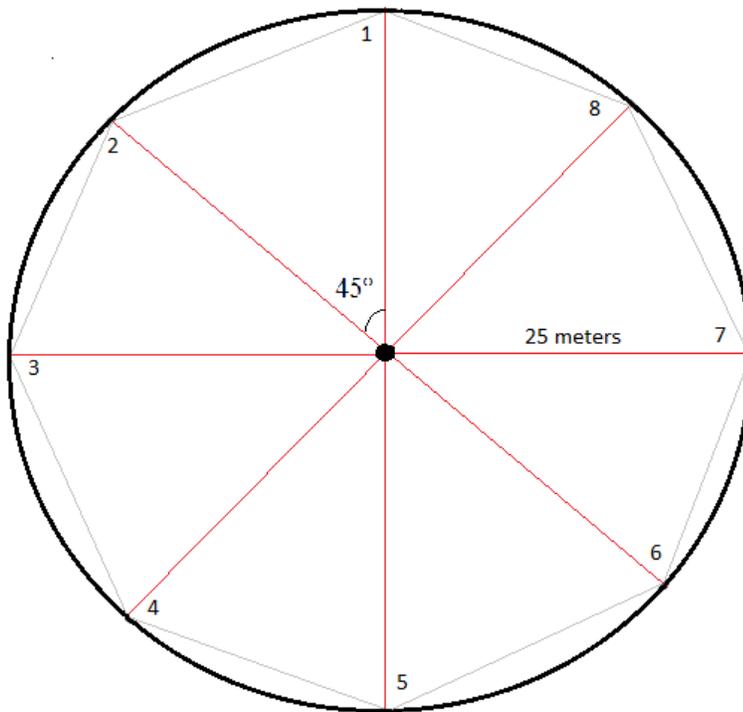


Figure 1 – Representation of our transects

Percent Prevalence of Species Measured

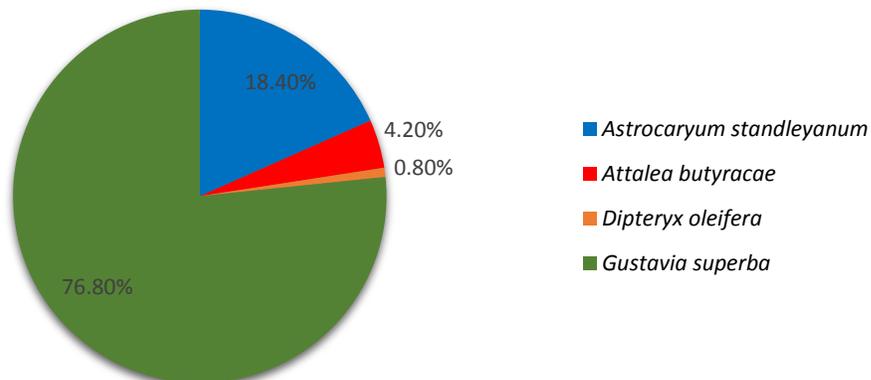


Figure 2 – Percent prevalence of species of interest across 19 TEAM camera sites on Barro Colorado Island, Panama

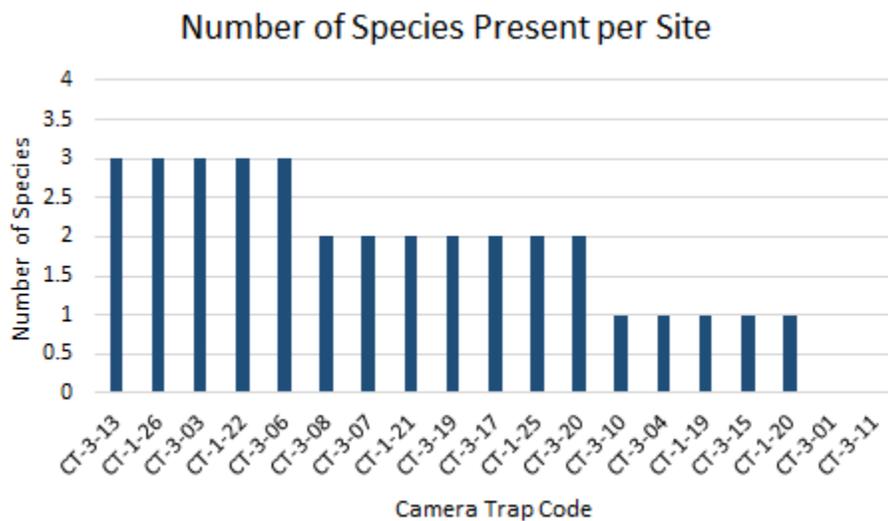


Figure 3 – Graph illustrating the number of species of interest (*D. oleifera*, *G. superba*, *A. butyracae*, *A. standleyanum*) present at each camera site location

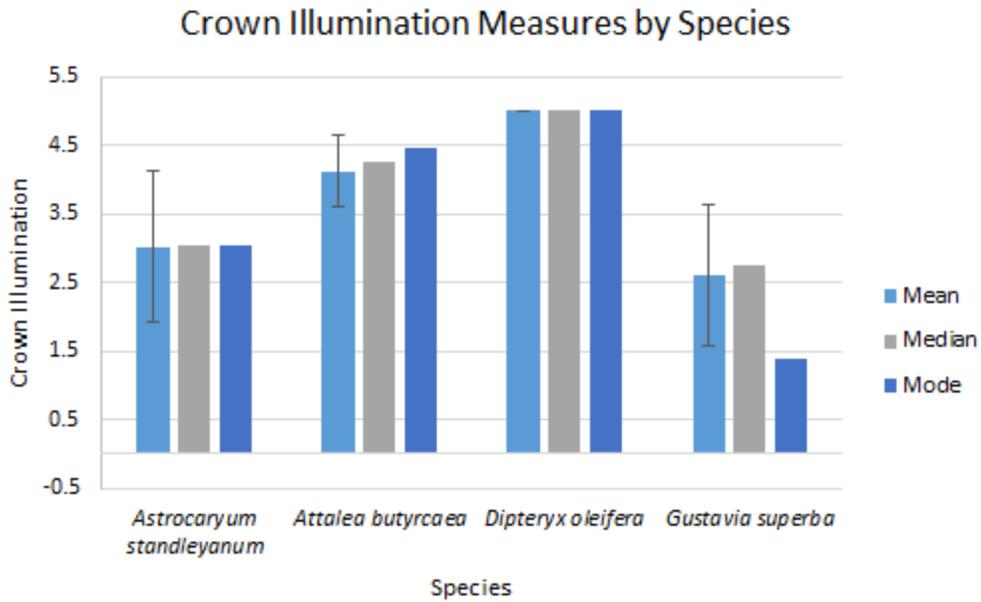


Figure 4 – Means, medians, and modes of crown illumination values by species. Error bars represent standard deviation.

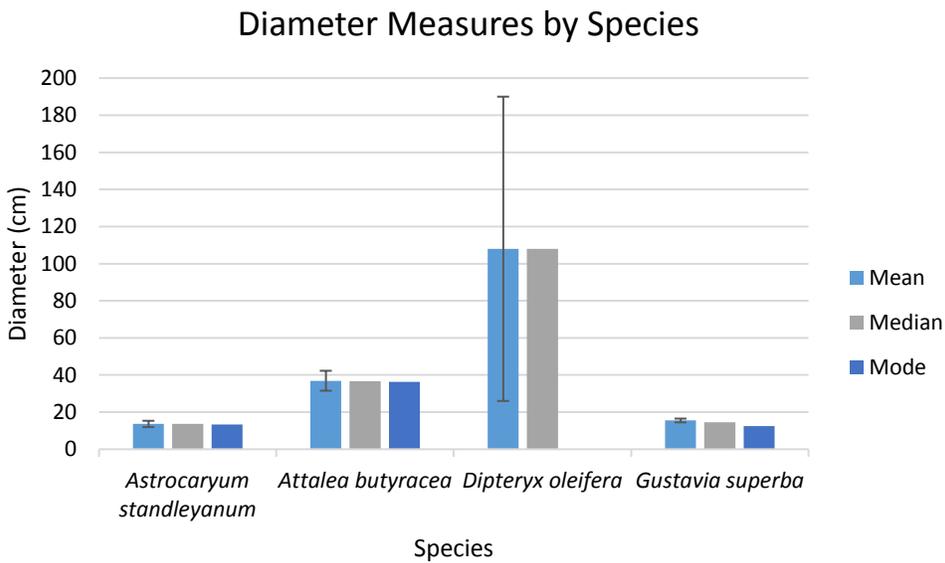


Figure 5 – Means, medians, and modes of diameter values by species. Error bars represent standard deviation.

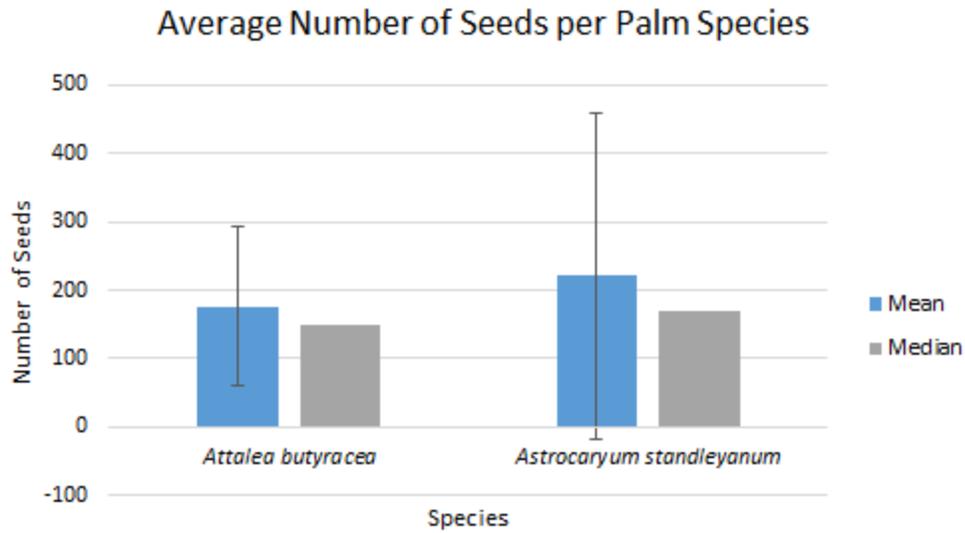


Figure 6 – Mean and median of the average number of seeds per palm (*A. standleyanum* and *A. butyracea*). Error bars represent standard deviation.

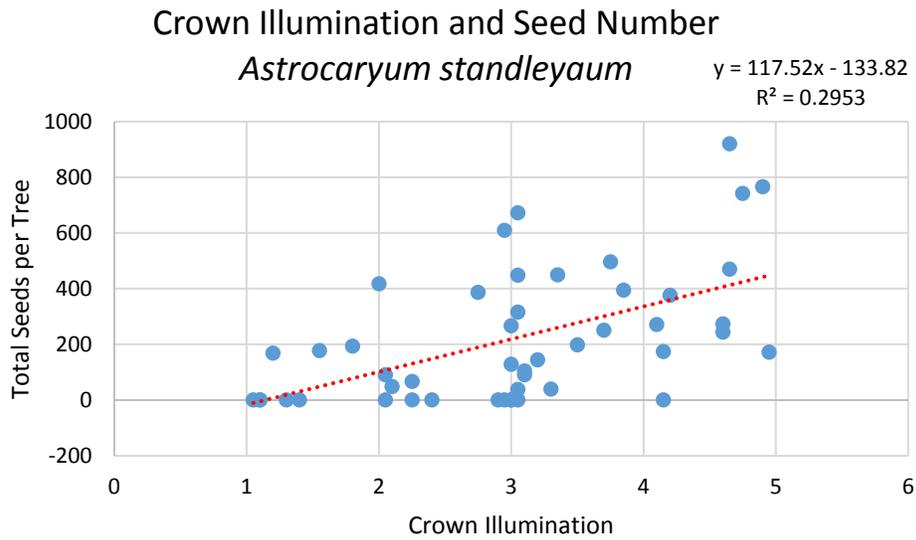


Figure 7 – Scatter plot displaying relationship between the total number of seeds per tree and crown illumination for *A. standleyanum*

Residuals vs Predicted Seed Number *Astrocaryum standleyaum*

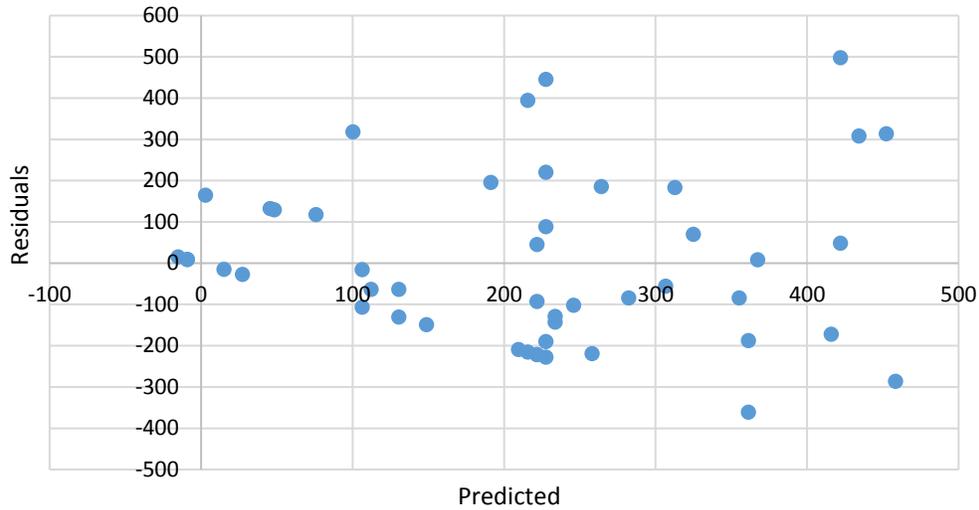


Figure 8 – Plot of residual and predicted values of seed number/*A. standleyanum* tree by observed crown illumination (using equation $y = 117.52x - 133.82$)

Relationship between CI and Seed Number *Attalae butyracea*

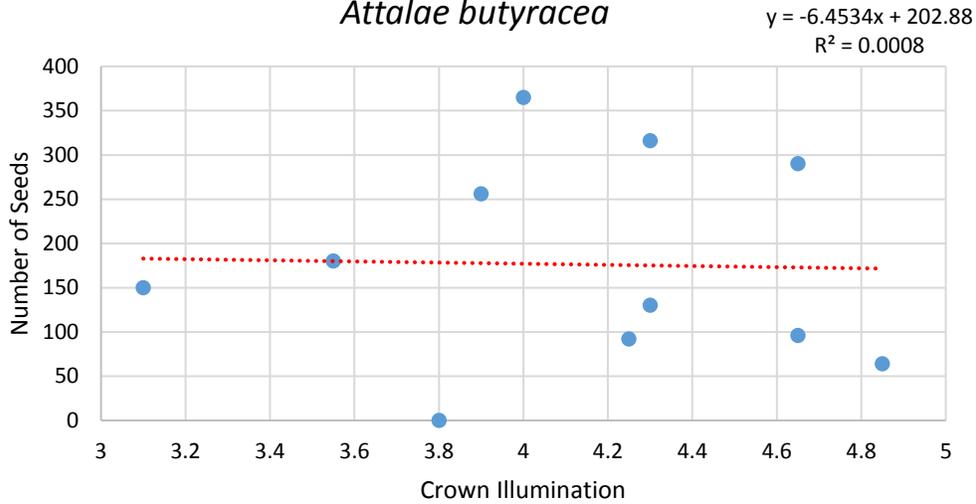


Figure 9 – Scatter plot displaying relationship between the total number of seeds per tree and crown illumination for *A. butyracea*

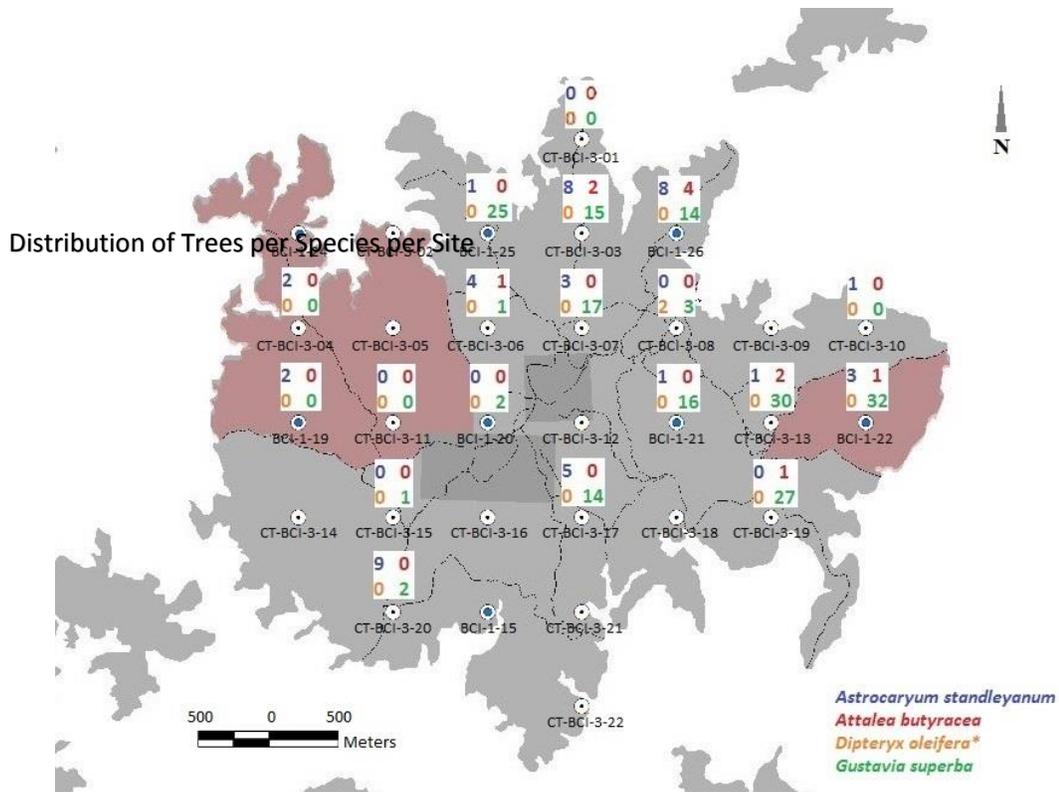


Figure 10 – Map of BCI displaying 30 TEAM camera traps with corresponding number of trees measured per species per site. Color coded.

Distribution of Seeds per Species per Site

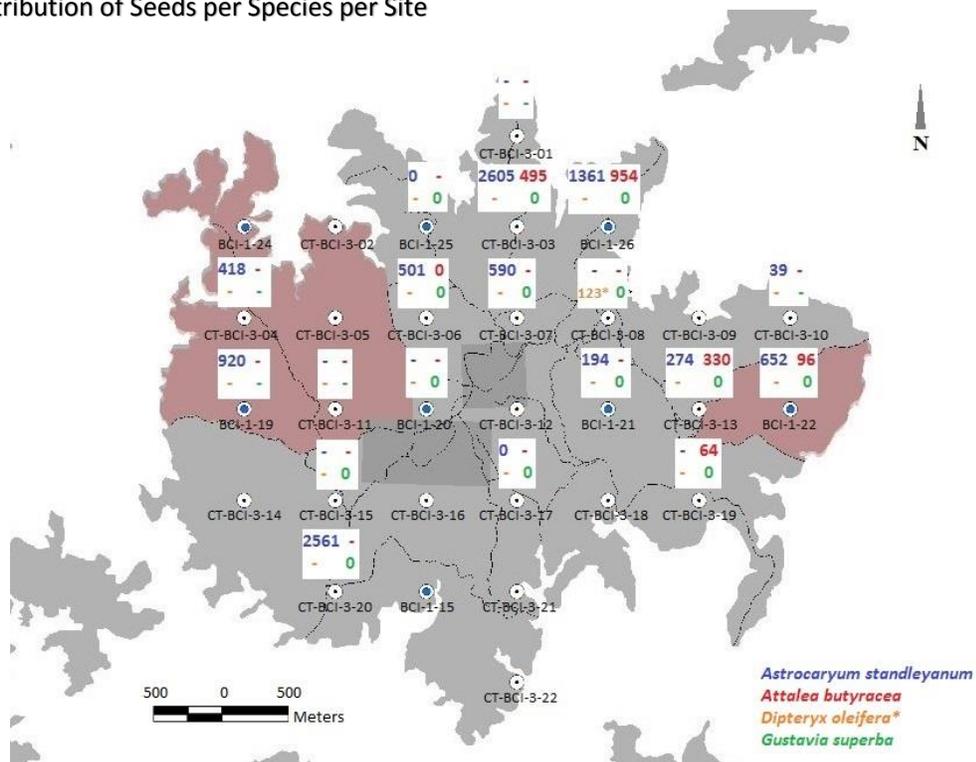


Figure 11 – Map of BCI displaying 30 TEAM camera traps with corresponding number of seeds measured per species per site. Color coded.

Barro Colorado Island
Camera Traps and Streams

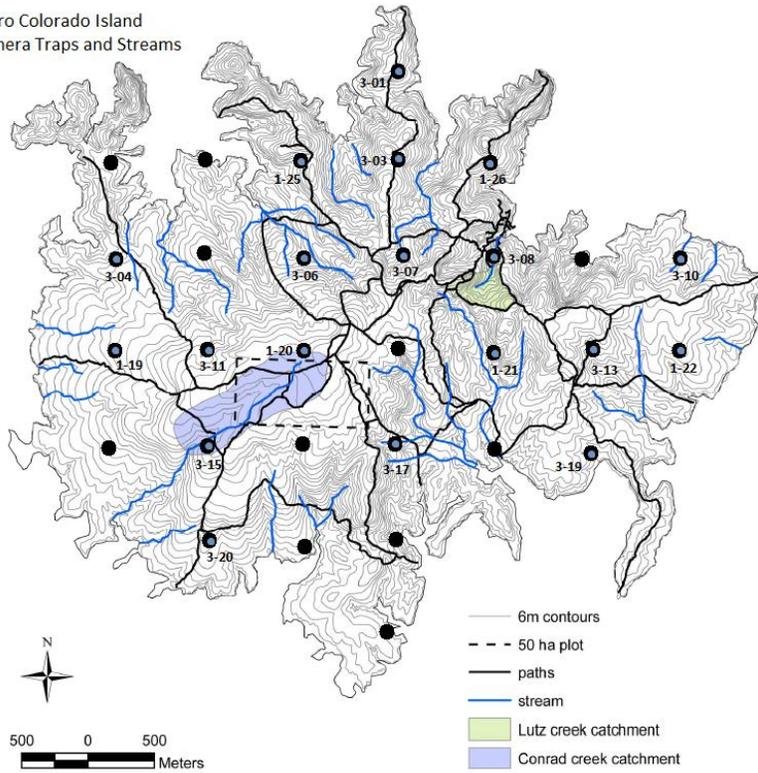


Figure 12 – Modified map of BCI displaying 30 TEAM camera relative to trails and streams. Map retrieved from Semi-detailed soil survey of BCI (Baillie et al., 2006).

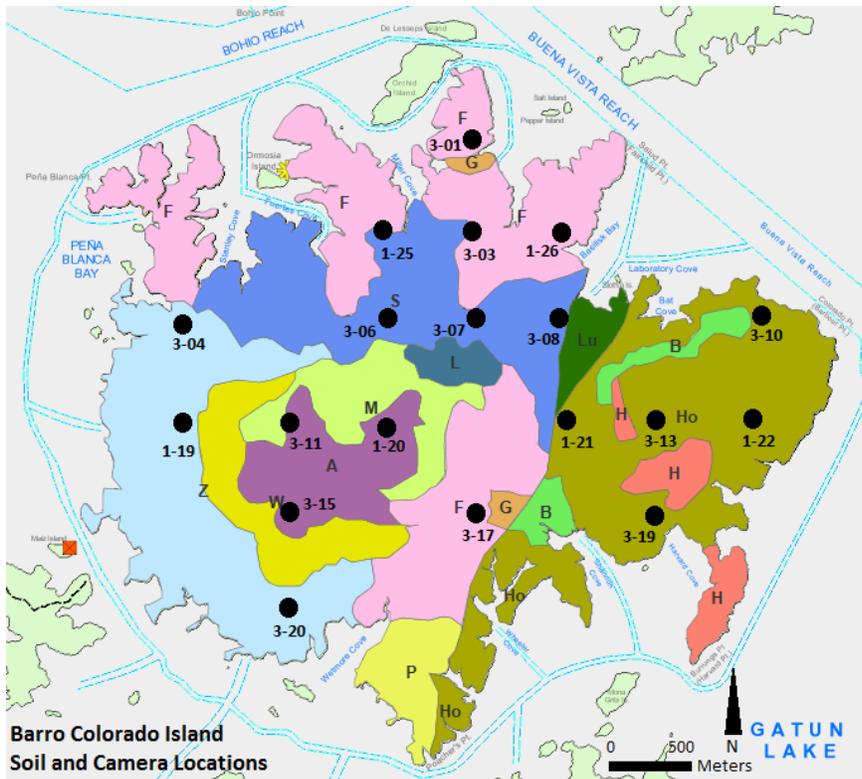


Figure 13 – Modified map of BCI displaying 30 TEAM camera in corresponding soil zones. Soil zones represent soil form and parental material. Details found in Table 9. Map retrieved from STRI GIS Laboratory (Soils of BCI – Feature Layer).

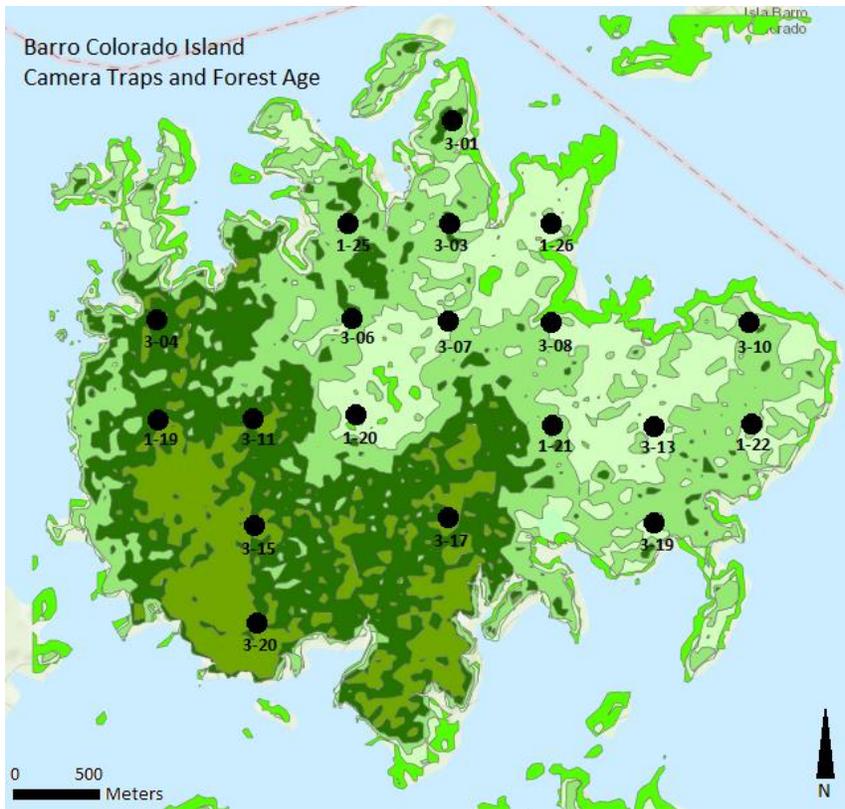


Figure 14 – Map of BCI displaying 30 TEAM camera traps with corresponding forest age region. Range: Level 5 (oldest forest, darkest green) – Level 1 (youngest forest, lightest green). Map retrieved from STRI GIS Laboratory (BCI Forest Age 1927 – Feature Layer).

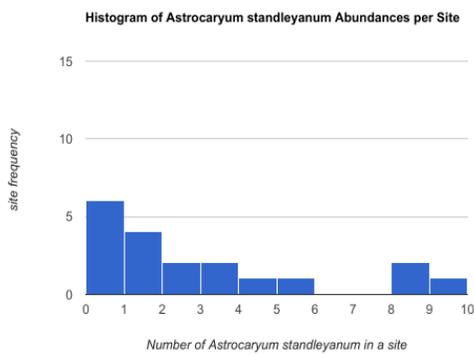


Figure 15 – Histogram of *A. standleyanum* showing frequency distribution of species abundance per site

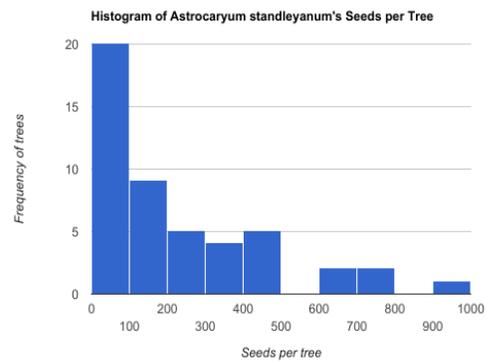


Figure 16 – Histogram of *A. standleyanum* showing frequency distribution of total seeds per tree

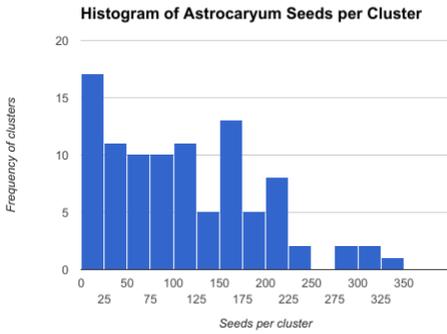


Figure 15 – Histogram of *A. standleyanum* showing frequency distribution of species abundance per site

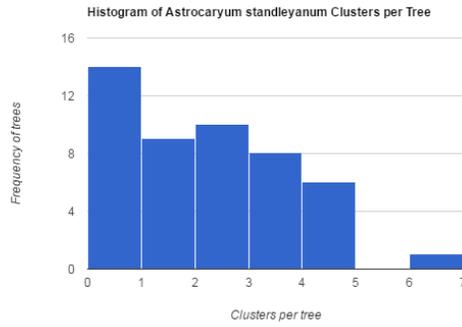


Figure 16 – Histogram of *A. standleyanum* showing frequency distribution of clusters per tree

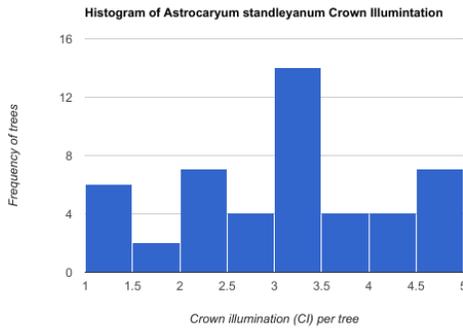


Figure 16 – Histogram of *A. standleyanum* showing frequency distribution of CI values

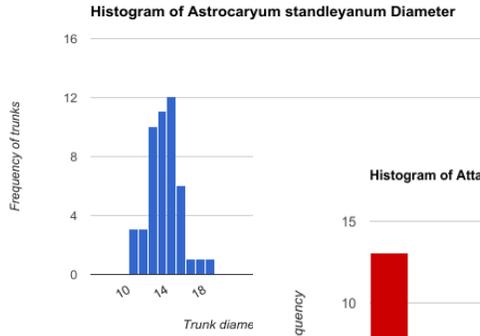


Figure 17 – Histogram of *A. standleyanum* showing frequency distribution of diameters measurements

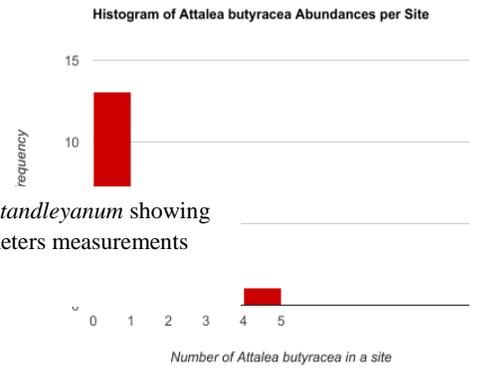
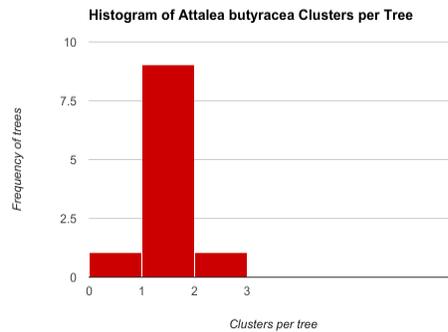
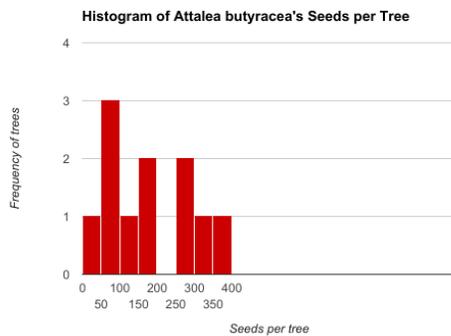


Figure 18 – Histogram of *A. butyracea* showing frequency distribution of species abundance per site



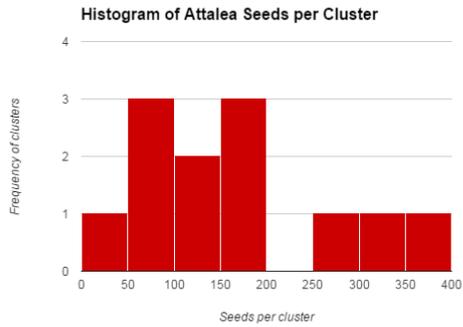


Figure 21 – Histogram of *A. butyracea* showing frequency distribution of total seeds per cluster

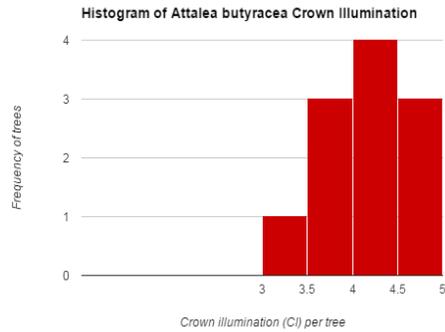


Figure 22 – Histogram of *A. butyracea* showing frequency distribution CI values

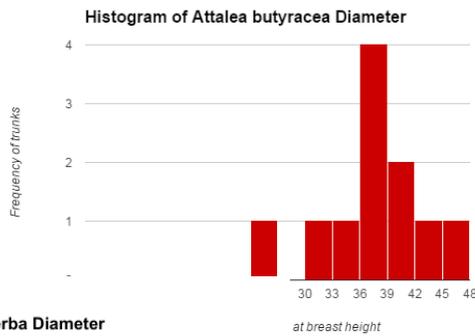


Figure 23 – Histogram of *A. butyracea* showing frequency distribution diameter measurements

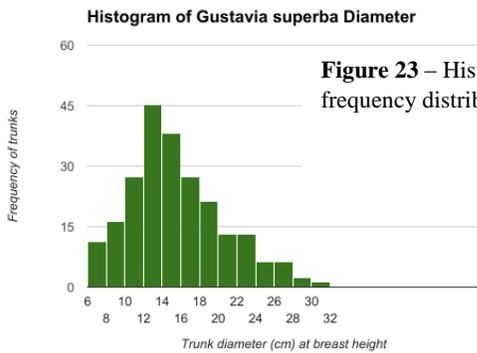


Figure 24 – Histogram of *G. superba* showing frequency distribution of diameter measurements

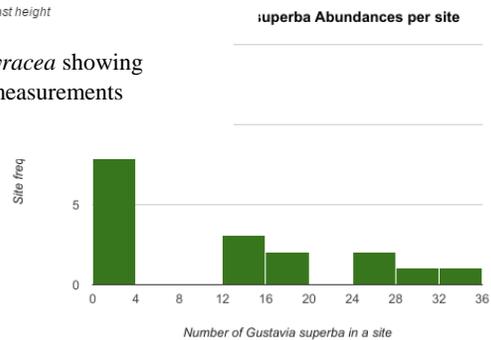


Figure 25 – Histogram of *G. superba* showing frequency distribution of species abundance per site

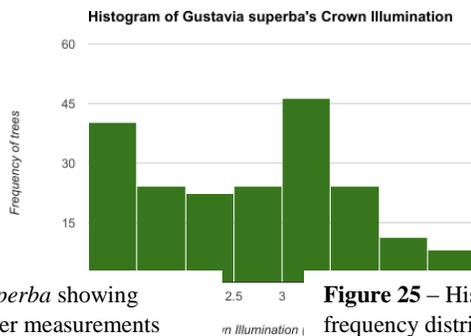


Figure 26 – Histogram of *G. superba* showing frequency distribution of CI values



Figure 27 – Certificate of research ethic course completion (TPCS2: CORE) for Emily McIntosh



Certificate of Completion

This document certifies that

Easton Houle

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

Date of Issue: **30 January, 2017**

Figure 28 – Certificate of research ethic course completion (TPCS2: CORE) for Easton Houle

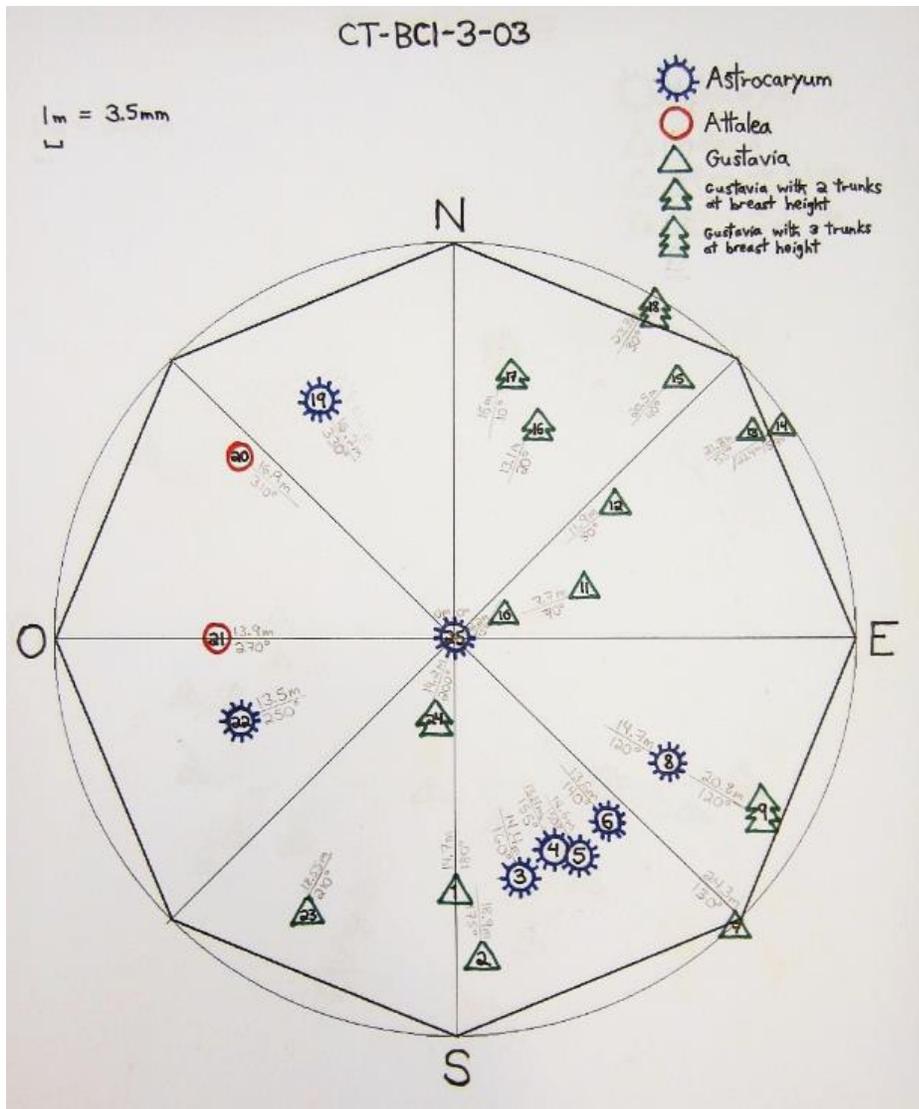


Figure 29 – Example of product 2 for host institution (STRI). Displaying Team site 3-03 distribution and abundance of focal species.