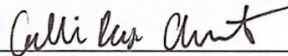


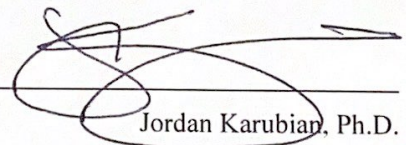
UNDERSTANDING HOW FRUITING NEIGHBORHOOD AND PLANT TRAITS AFFECT  
FRUGIVORY IN NORTHWESTERN ECUADOR

AN HONORS THESIS  
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Callie Rose Chenevert. Understanding How Fruiting Neighborhood and Plant Traits Affect Frugivory in Northwestern Ecuador.

(Professor Jordan Karubian, Ecology and Evolutionary Biology)

## **ABSTRACT**

Seed dispersal services are important in maintaining healthy forest ecosystems, yet there is still a lot that is not fully understood in the plant-frugivore relationship, such as how the fruiting neighborhood, plant traits, and fruit traits interact and affect frugivory. Additionally, not all frugivore species remove fruit from plants equally, with gape size being a limitation for fruit selection among avian frugivores. We explored how the fruiting neighborhood and palm traits such as height, crop size, and nutrition content influenced the fruit removal rate as well as the number of fruits removed per frugivore visit in an understory palm in the neotropics. Additionally, we compared the frugivore communities between two understory palm species to identify how and why frugivore communities may differ. We found that the fruiting neighborhood has a significant negative effect on both frugivory metrics, but palm height is the only other significant factor that affects the fruit removal rate, while sucrose and fruit/seed size both affect the number of fruits removed per frugivore visit. We also found that the frugivore communities differed significantly between the two understory palms, consistent with the idea that a frugivore's gape size limits the frugivore's selection in fruit. The results from our study provide more insight into how palm traits influence frugivore removal of a palm's fruits.

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## TABLE OF CONTENTS

Abstract.....	ii
Acknowledgements.....	iii
Table of Contents.....	iv
List of Tables.....	vi
List of Figures.....	vii
Introduction.....	1
Methods.....	7
Study Site.....	7
Study Species.....	7
Frugivore Community Characterization.....	8
Palm Neighborhood, Plant Characteristics, and Fruit and Seed Data.....	9
Analysis.....	10
Drivers of intraspecific variation in fruit removal services.....	10
Comparison between the understory palms <i>Synechanthus warscewiczianus</i> and <i>Prestoea decurrens</i> .....	12
Results.....	13
Data Summary.....	13
Drivers of Intraspecific Variation in Fruit Removal Services.....	14
Interspecific Comparison.....	17
Discussion.....	21
Conclusion.....	25

References.....27

Appendix .....37

**LIST OF TABLES**

Table 1. Factors predicted to affect frugivore behavior.....	6
Table 2. Model averaged coefficients for fruit removal rate and fruits removed per visit for <i>S. warscewiczianus</i> .....	17
Table 3. Frugivore community comparison.....	19

## LIST OF FIGURES

Figure 1. Map of FCAT.....	13
Figure 2. Best fit model of predictors for fruit removal rate.....	15
Figure 3. Best fit model of predictors for number of fruits removed per visit.....	16
Figure 4. Comparison of frugivore communities between palm species.....	20
Figure 5. Comparison of fruiting neighborhood and palm height and crop size between palm species.....	20
Supplementary figure S1. Comparison of pulp to seed ratios across focal <i>S. warscewiczianus</i> palms.....	37
Supplementary figure S2. Comparison of sucrose content across focal <i>S. warscewiczianus</i> palms.....	37
Supplementary figure S3. Comparison of water mass across focal <i>S. warscewiczianus</i> palms.....	38
Supplementary figure S4. Comparison of visitation and removal rate, and species richness and diversity between two palm species.....	38

## INTRODUCTION

In the tropics, seed dispersal is an important process that allows seeds to escape distance- and density-dependent mortality caused by heightened concentrations of plant pathogens and predation risk beneath the parent plant (Nathan and Casagrandi 2004; Bagchi et al. 2010). As such, seed dispersal is important for promoting gene flow, colonization of new habitats, and establishing the plant community composition (Whelan et al. 2008). In tropical systems, most tree species are reliant on birds and mammals to disperse their seeds (Howe & Smallwood 1982). Additionally, many birds and mammals in these ecosystems are often equally reliant on these fruits as a food source (Peres 2000; Diaz-Martin et al. 2014). Because of the importance of seed dispersal mutualisms in tropical forests, decades of ecological work have been dedicated to identifying factors that influence frugivore visitation and fruit removal (Howe & Smallwood 1982; Schupp 1993; Schupp et al. 2019). The environment of the fruiting plants and the surrounding habitat available to frugivores, physical plant characteristics such as height and crop size, as well as morphological and chemical fruit properties have all been found to contribute to variation in rates of frugivore visitation and fruit removal (Flörchinger et al. 2010; Crestani et al. 2019; Schupp et al. 2019). Understanding how these different factors influence frugivory and their relative importance in determining interactions important for seed dispersal services remains an active area of research (Schupp et al. 2019; Pizo et al. 2021; Rojas et al. 2021). A more comprehensive understanding of different drivers of frugivore foraging behavior will not only provide insight into the determinants of seed dispersal patterns and plant community composition (Crestani et al. 2019; Tonos et al. 2022), but also the evolutionary history of seed dispersal mutualisms and plant traits

(Martínez Del Río et al. 1992; Crestani et al. 2019; Lei et al. 2021). Lastly, knowledge regarding determinants of frugivore foraging preferences can allow us to better anticipate how ongoing patterns of fragmentation and land use change may affect frugivory and seed dispersal processes in the future (Cazetta et al. 2019; Wang et al. 2023).

In nature, there is rarely a uniform distribution of equally available fruit. Our understanding of how variation in resource availability (i.e. neighborhood fruiting density and fruit crop size) may affect frugivore foraging decisions and fruit removal services has been traditionally informed by the optimal foraging theory (Charnov 1976; Pizo and Almeida-Neto 2009). The optimal foraging theory explores how animals decide what food to consume, especially when considering the abundance, quality, and spatial distribution of food and the associated costs of traveling to food sites (Krebs 1977). When fruit is abundant, then it is expected that a frugivore will become satiated and will not remove all fruit in the area (Hampe 2008). Plants with larger crop sizes are generally expected to receive more visitation and fruit removal services (Howe & Estabrook 1977; Ortiz-Pulido & Rico-Gray 2000); however, studies show this relationship is not always present and may vary with factors such as taxa and local competition among plants (Laska & Stiles 1994; Flörchinger et al. 2010). Additionally, when there is an abundance of resources, frugivores should exhibit foraging preferences and select the most nutritionally rewarding option (Krebs 1977). Therefore, factors such as the neighborhood fruiting density and the crop size on individual palms are important to consider, but there are also individual-level variations among plants' fruits that can encourage or discourage frugivory (Schupp et al. 2019).

Current work on factors influencing frugivory in tropical forests has focused on factors related to the frugivore's immediate habitat when foraging, such as fruiting neighborhood density, plant height, and plant fruit crop size, and results have been mixed (Schupp et al. 2019). Some studies have found that a higher fruiting density in an area results in more competition among the fruiting trees and thus lowers the rate of seed dispersal for individual trees (Smith and McWilliams 2014; Lamperty et al. 2021), while other studies have found that higher fruiting density attracts more frugivores and may compensate for the higher level of competition among trees (Carlo and Morales 2008). Additionally, trees with larger crop sizes have been found to attract more frugivores and thus experience higher rates of seed dispersal (Howe and Estabrook 1977; Hampe 2008; Schupp et al. 2019), although this is not always the case, with Laska & Stiles (1994) finding no relation between crop size and fruit removal rate. Plant height has also been found to be positively correlated with the proportion of fruits removed (Vissoto et al. 2022) and is typically positively correlated with the crop size (Flörchinger et al. 2010; Guerra et al. 2017). However, it cannot be assumed that height always has a positive correlation with fruit removal, as canopy and understory plants have been found to have very different frugivore community compositions, thus resulting in different frugivore behaviors, which may affect their feeding behaviors (Schleuning et al. 2011).

In addition to the fruiting neighborhood and individual plant traits, fruit traits such as morphology and chemistry can influence foraging decisions. However, the extent to which individual plants vary in fruit traits such as seed and fruit size, pulp to seed ratio, sugar, and water content and the importance of these factors in influencing foraging behaviors and fruit removal services is not well understood. Wheelwright (1993) found

that larger fruits were removed more often than smaller fruits within *Ocotea tenera*, an avian-dispersed tree species in the tropics. Additionally, frugivorous birds have been found to select fruits as wide as their gape width, possibly to maximize foraging efficiency (Burns 2013). In addition to being able to eat larger fruits, birds with larger gapes have been found to have more varied diets than small-gaped frugivores (Wheelwright 1985; Naniwadekar et al. 2019). Therefore, fruit size may attract frugivores to some extent, but it can also be a limiting factor if the fruit is too large for the bird's gape. Additionally, many studies have found that within a species, as the fruits get larger, the pulp-to-seed ratio slightly increases (Jordano 1995; Martínez et al. 2007; Pizo & Almeida-Neto 2009). Frugivorous birds prefer larger fruits with smaller seeds, likely to obtain more energy and nutrients (Sobral et al. 2010; Lei et al. 2021). Two nutrients that are important in avian-dispersed fruits are water and sugar. While water is important for birds, they cannot store much water (Nisbet et al. 1963). Therefore, it is not likely that avian-dispersed fruits will be high in water. Also, sugar has been found to be an important nutrient that can influence frugivory and seed removal (Levey 1987). Although some birds are unable to assimilate sucrose efficiently (McWhorter et al. 2021), Crestani et al. (2019) found that frugivorous birds prefer fruits with intermediate levels of sucrose around 7%. Because of the physiology of frugivorous birds and their role as seed dispersers, it is important to understand how nutrients may influence frugivory.

The objective of this study was to comprehensively test the relative importance of various factors thought to affect frugivory within a plant species and to examine how a subset of these factors may translate into differences in fruit removal services between two generally co-fruiting understory palm species in northwestern Ecuador with differing

fruit sizes. *Prestoea decurrens* is an understory palm with small-medium sized fruits (~14mm), and *Synechanthus warscewiczianus* is an understory palm with medium-large sized fruits (~20mm). We examined the fruit removal rate, defined as the number of fruits removed across 30 days, as well as the number of fruits removed per visit as proxies for seed dispersal services (Holbrook and Loiselle 2009; Schupp et al. 2010). An overview of our hypotheses are shown in Table 1. We expect the variables we examined to affect fruit removal rate and number of fruits removed per visit similarly, so they are grouped together as fruit removal in Table 1. We do not expect higher fruiting neighborhood density to result in more removal events due to competition among palms (Smith and McWilliams 2014; Lamperty et al. 2021). Plant height is expected to be positively associated with fruit removal because taller palms are more visible and safer from terrestrial predators (Vissoto et al. 2022). Palms with larger crop sizes are expected to have more removal events because they are a reliable food source for frugivores (Schupp et al. 2019; Lamperty et al. 2021). We also expect frugivores to prefer intermediate levels of sucrose because while it is one of three dominant sugars commonly present in fruit pulp and utilized by frugivores as an energy source (Lotz and Schondube 2006; Crestani et al. 2019), they cannot digest it as effectively as glucose or fructose and high levels may serve even as a frugivore deterrent (Martínez del Rio and Restrepo 1993; Crestani et al. 2019). Avian frugivores in particular are expected to prefer fruits low in water content to reduce the amount of unnecessary weight consumed (Nisbe et al. 1963; Moermond and Denslow 1985; Ramos-Robles et al. 2018). We also expect frugivores to select fruits with the highest pulp to seed ratio to obtain more nutrients per fruit handled (Pizo & Almeida-Neto 2009; Sobral et al. 2010; Dias Da Silva et al. 2020). Lastly, although frugivores are

not expected to always eat the largest fruits their gape size will allow (Wheelwright 1985), we expect gape size to be a limiting factor on the diameter of the fruits they consume and to therefore be the main driver of differences in frugivore communities between the two understory palm species.

**Table 1.** Summary of expected effects of variables on fruit removal. + indicating a positive effect on fruit removal; - indicating a negative effect on fruit removal; ~ indicating an intermediate effect on fruit removal.

<b>Variable</b>	<b>Expected effect on fruit removal</b>	<b>Reasoning</b>
Fruiting neighborhood density	-	Studies have found a negative effect with fruiting neighborhood and frugivory (Smith and McWilliams 2014; Lamperty et al. 2021)
Plant height	+	Studies have found taller trees experience higher rates of frugivory (Vissoto et al. 2022)
Crop size	+	Studies have found crop size to be positively associated with frugivory (Schupp et al. 2019)
Sugar content	~	Avian frugivores have been found to prefer intermediate levels of sucrose in fruit (Crestani et al. 2019)
Water content	-	Birds do not want to fly with a lot of water weight (Nisbet et al. 1963)
Pulp:seed ratio	+	Birds have been found to select for fruits with more pulp and smaller seeds (Sobral et al. 2010)
Fruit size (diameter)	~	Birds will select the largest fruits, but will be limited by their gape size (Wheelwright 1985)

## METHODS

### I. Study Site

This study took place at the Fundación para la Conservación de los Andes Tropicales (FCAT) research station in northwestern Ecuador in the Mache-Chindul Ecological Reserve (Figure 1). FCAT is within the Chocó biogeographic region, which has been identified as a biodiversity hotspot that hosts more than 400 endemic vertebrate species and over 2,000 endemic plant species (Myers et al. 2000). Although there is considerable disturbance within the Mache-Chindul Reserve, data was only collected in primary forests. Data was collected June-October in 2022 and 2023 during the dry season.

### II. Study Species

We selected two focal understory palm species that fruit synchronously, *Prestoea decurrens* and *Synechanthus warscewiczianus* (Arecaceae). We focus on palms in part because of these species' accessibility for our study (both are common throughout the region and consumed by multiple frugivores), but also because palms represent one of the most dominant plant families in Neotropical forests (ter Steege et al. 2013), and thus insights into factors influencing frugivore foraging and fruit removal from our study species represents an opportunity to advance our knowledge of factors influencing seed dispersal and regeneration for an exceptionally ecologically important plant group. *Prestoea decurrens* is approximately 5.2 meters tall on average, and each fruit has only one round seed approximately 13-14mm in diameter (Chenevert, unpublished data). *Synechanthus warscewiczianus* averages 4.1 meters in height, and also has only one seed

per fruit which are ovoid and approximately 22-23mm long and 18-19mm wide (Chenevert, unpublished data). Additionally, mature *P. decurrens* fruits are dark purple and mature *S. warscewiczianus* fruits are bright red in appearance.

### III. Frugivore Community Characterization

We collected data across nine one-hectare plots (Figure 1c). Within each plot, we identified and mapped all canopy and understory palm species and assigned each palm a unique number. Focal palms for this study were selected based on their fruiting availability. We recorded frugivory interactions via camera traps (Bushnell and Browning) that were focused on infructescences on 77 individual palms, 42 of which were *P. decurrens* and 35 of which were *S. warscewiczianus*. The cameras recorded 10 seconds each time motion was detected. To understand if limitations in gape size predict differences in frugivore communities between the two focal palm species, we divided frugivores by gape size and categorized them as small, medium, or large. Thrushes (*Turdidae spp.*) and squirrels (*Sciurus spp.*) were categorized as small gape frugivores. Rufous motmots (*Baryphthengus martii*) and crested guans (*Penelope purpurascens*) were grouped as medium gape frugivores. Toucans (*Ramphastos spp.*) and pale mandibled aracaris (*Pteroglossus erythropyglus*) were classified as large gape frugivores.

We analyzed the footage for all frugivore interactions with every focal palm. For each frugivore interaction, the palm and plot number were recorded, along with the frugivore's species, their behavior, the number of seeds removed, and the date and time. The frugivore's behavior was closely observed to see whether the frugivore dropped the

fruit, ate the fruit, or left the focal palm with the fruit before eating it, but these were all considered removal events.

#### IV. Palm Neighborhood, Plant Characteristics, and Fruit and Seed Data

In 2023, additional methods were implemented to better understand factors influencing frugivory in our study species. In a subset of 5 of our 9 study plots, we estimated fruit availability in focal individuals surrounding neighborhoods by recording all co-fruiting palms, not just our focal species, in a 35-meter radius of each focal palm. Additionally, we estimated palm height and crop size (the number of fruits on the focal palm) and collected fruits from each focal palm and measured: fruit weight, length, and width, seed weight, length, and width, water weight, and sugar content. Our goal was to sample 20 fruits per focal individual, 10 when camera traps were first placed and another set of 10 when the cameras were retrieved to avoid removing a significant number of fruits and potentially impacting frugivore behavior. The number of viable fruits we were able to obtain per individual varied from 10-35. All fruits collected from the focal palms were cleaned with water and then dried. Once dried, we weighed each fruit and recorded their length and diameter. We then removed the seed from the fruit, cleaned it, and also recorded its weight, length, and diameter. For the first ten fruits collected, we would place the pitted fruits in a drying oven overnight. Once fully dried, the fruits were weighed, and the difference was recorded as the fruit's water weight. For the next ten fruits collected, we squeezed a few drops of the fruit's juice onto a portable refractometer and recorded the Brix percentage, which measures dissolved sucrose in juice (Jaywant et al. 2022).

## V. Analysis

All statistical analyses were done in R version 4.3.2 (R Core Team 2023). We examined 3 metrics that are indicative of seed-dispersal services: frugivore visitation rate, frugivore fruit removal rate, and the number of fruits removed by frugivores during each foraging bout (Carlo and Morales 2008; Holbrook and Loiselle 2009; Raji and Downs 2022). Visitation and fruit removal rates were estimated by summing the number of visits or the number of fruits removed per focal palm, then dividing those values by the number of camera trap days recorded for that palm. This rate was then multiplied by 30 to gain an approximation of monthly visitation and fruit removal rates. All analyses were performed on both visitation and fruit removal rates and because the majority of our results were qualitatively identical regardless of which metric (visitation or fruit removal rate) was the response variable, we present only fruit removal rate results here. We also assessed differences in the number of fruits removed per foraging visit by frugivores because this can provide additional insights into factors affecting frugivore foraging behavior and satiation which also have consequences for dispersal services and patterns (Saracco et al. 2005; Holbrook and Loiselle 2009).

### *i. Drivers of intraspecific variation in fruit removal services*

We tested if the neighborhood density of co-fruiting palms, palm height, fruit crop size, fruit and seed size and weight, the seed-to-pulp ratio, water weight, and sucrose concentration are predictors of (1) fruit removal rates and (2) the number of fruits removed per visit with. All fruit and seed size and weight metrics that we measured were

highly correlated with one another except for sucrose concentration and the pulp-to-seed ratio, but no plant characteristics (e.g. crop size) were correlated with any fruit or seed variables or to each other. Because of the high positive correlation between fruit and seed size and mass data, we used a Principal Component Analysis with the ‘prcomp’ function (R Core Team 2023) and found the first two Principal Components (PC1 and PC2) accounted for 92% of variance. To assess the effects of fruit and seed size and mass on frugivory, we therefore use PC1 and PC2 together in our models in place of modeling each of the 8 separate variables measured (see full description of these variables above in Methods section IV) (Flörchinger et al. 2010).

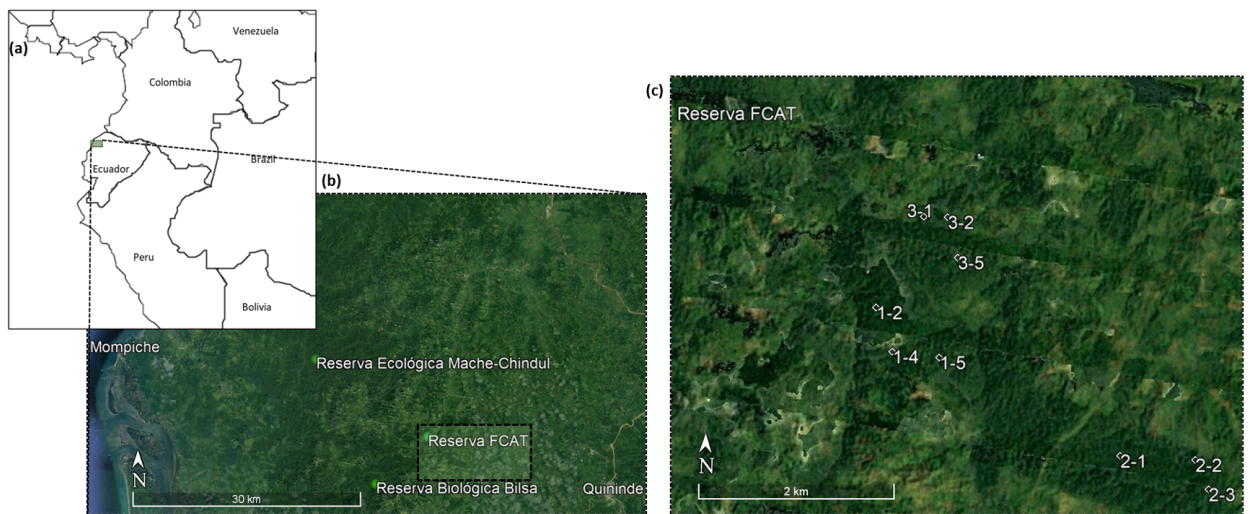
For models with the response variable of fruit removal rate, we used a Gamma distribution with log link functions, with the exception of the model examining the effect of pulp-to-seed ratio on fruit removal rate, for which we used a Tweedie distribution in order to pass model validation steps. For models that had the number of fruits removed per visit as the response variable we used negative binomial distributions and palm ID as our random effects. We used the ‘dharma’ package (Hartig and Lohse 2022) to validate all models. We used the ‘Anova’ function in the ‘car’ package on our models to produce the likelihood-ratio Chi-square and  $p$  values that we report (Fox 2016; Fox et al. 2022). Finally, we performed a model selection analysis using the ‘dredge’ function in the ‘MuMin’ package (Bartoń 2023). We constructed one global model for each frugivory response variable (fruit removal rate and the number of fruits removed per visit) consisting of palm crop size, height, number of fruiting palms in a 35m radius, sucrose concentration, pulp-to-seed ratio, and the fruit and seed size index represented by PC1 and PC2. We used a Gamma distribution with a log link function with the fruit removal

rate response variable while the number of fruits removed per visit was analyzed with a negative binomial distribution and included the random effect of palm ID. Through the dredge function we obtained the best models based on lowest Aikake Information Criterion (AICc) scores after comparing all possible combinations of variables as fixed effects (we did not include interaction terms). We then used model averaging across the subset of top models (those within 2 delta AICc of each other) using the ‘model.avg’ function in the ‘MuMin’ package to compute model averaged coefficients.

ii. Comparison between the understory palms *Synechanthus warscewiczianus* and *Prestoea decurrens*

To assess if differences in frugivore community composition existed between the two understory palm species, we computed pairwise Horn-Morisita dissimilarity values between all focal palms and ran a Permutational Multivariate Analysis of Variance (PERMANOVA) using the ‘adonis2’ function in the ‘vegan’ package (Oksanen et al. 2022). Using the ‘glmmTMB’ package, we compared visitation and fruit removal rates between the two palm species using lognormal models and the number of fruits removed per frugivore visit with a negative binomial mixed model with the fixed effect of palm species, the interaction effect between palm species and frugivore species, and the random effect of palm ID. We computed species richness and diversity according to the Inverse Simpson’s index for each palm species using lognormal models to assess differences between palm species. To analyze differences between the two palm species in potential predictors of variation in frugivore community composition and fruit removal services, we used a lognormal model to compare height between the two species, a

Gamma model with a log link function to compare crop size, and a negative binomial model to compare the number of fruiting palms in a 35m radius of focal palms; each of these models had the sole fixed effect of palm species. As with previously mentioned models, we used the ‘dharma’ package (Hartig and Lohse 2022) for model validation and the ‘Anova’ function in the ‘car’ package to compute likelihood-ratio Chi-square and  $p$  values (Fox 2016; Fox et al. 2022).



**Figure 1.** A map of our study sites at the FCAT reserve within the Mache-Chindul Ecological Reserve, located in northwestern Ecuador.

## RESULTS

### I. Data Summary

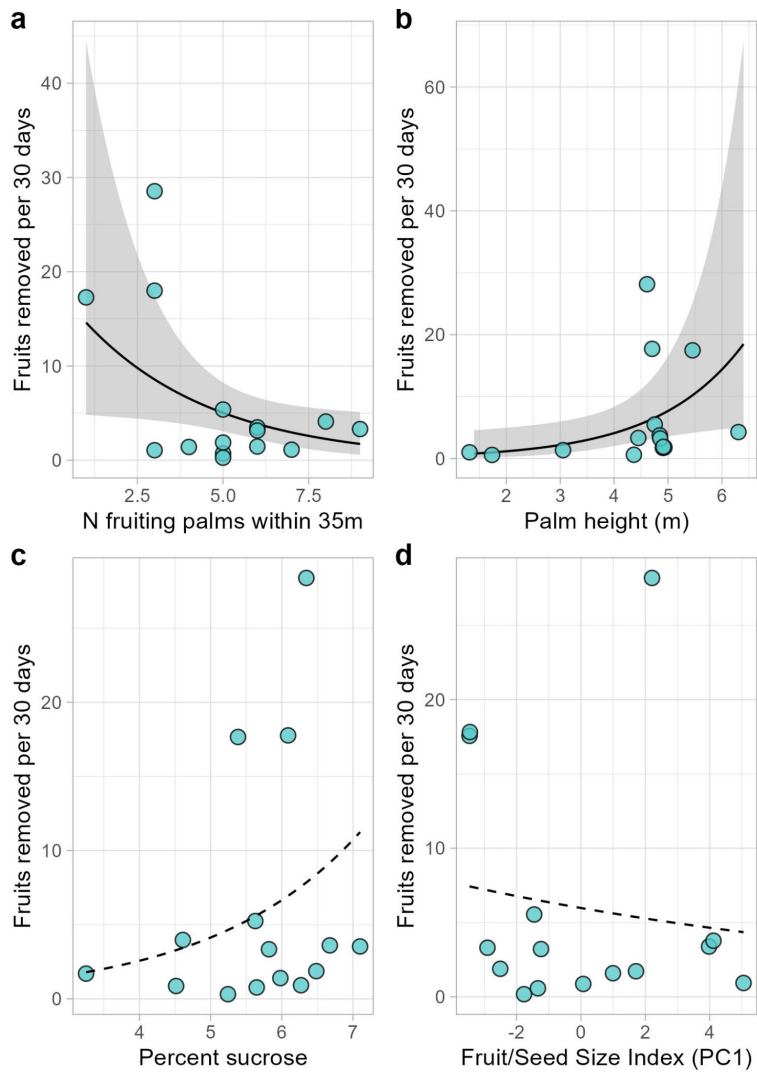
*Prestoea decurrens* was our initial study species in 2022, with 31 *P. decurrens* sampled that year and only 1 *S. warscewiczianus*. In 2023, we introduced *S. warscewiczianus* as an equal focus of the study due to an uncharacteristically low abundance of fruiting *P. decurrens*. In 2023, 12 *P. decurrens* were studied and 34 *S.*

*warscewiczianus*. Camera traps were deployed for 15.4 days at a time per palm on average (we aimed for approximately 2 weeks per individual per deployment for both years of the study). Cumulatively, we recorded 1,229 camera trap days for *P. decurrens* and 1,314 for *S. warscewiczianus*. There were 252 total plant-frugivore interactions recorded, with 162 interactions from *P. decurrens* and 90 interactions recorded from *S. warscewiczianus*. Within fruits collected from *S. warscewiczianus* palms, there was significant variation in the pulp to seed ratio, sucrose content, and water mass (S1; S2; S3).

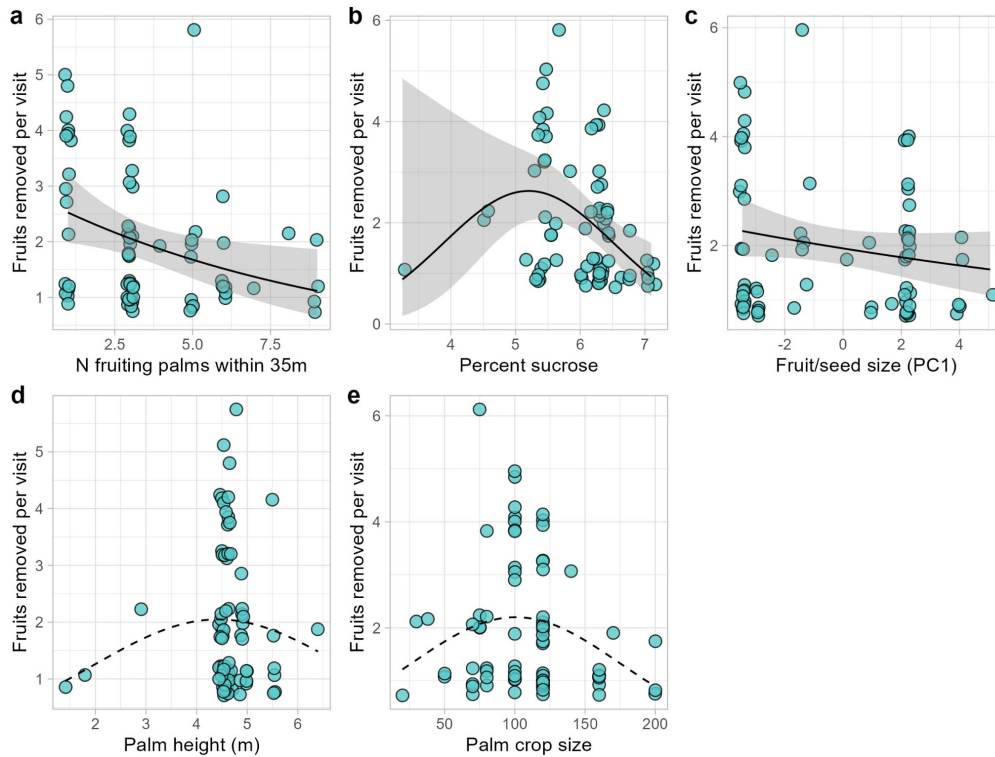
## II. Drivers of Intraspecific Variation in Fruit Removal Services

We examined how the fruiting neighborhood, palm height, crop size, sucrose content, and PC1 and PC2 (fruit and seed size indices) influenced the fruit removal rate and number of fruits removed per visit for *S. warscewiczianus* palms. The dredge model selection procedure examining drivers of fruit removal rate yielded support for 3 top models (i.e. within 2 AICc units of one another). Model average results from these top three models indicate an overall positive association between fruit removal rates and palm height, while the density of surrounding co-fruiting palms within 35m of the focal palm had a negative effect on fruit removal rates (Table 2; Figure 2). Additionally, the averaged estimates from top models indicated a weak, near-significant positive effect of sucrose content on fruit removal rate. Similarly, averaged top models for the number of fruits removed per visit by frugivores indicate a significant negative relationship with fruiting neighborhood palm density (35m radius around focal palms), and a weak, near-significant positive relationship with palm height (Table 2; Figure 3). Unlike fruit

removal rate, the number of fruits removed per visit had a significant negative relationship with both sucrose content and fruit/seed size index (PC1) (Table 2; Figure 3).



**Figure 2.** The top traits to predict fruit removal rate, the number of fruits removed per 30 days, for *S. warszewiczianus* were (a) the fruiting neighborhood, (b) palm height, (c) sucrose content, and (d) pulp to seed ratio. The shaded areas around trend lines represents the standard error. For sucrose and pulp to seed ratio, the lines are dashed and without a standard error because these were not found to be significant in the models. Fruit removal information was collected across all frugivore species, and this information is not frugivore species specific.



**Figure 3.** The top traits to predict the number of fruits removed per visit for *S. warscewiczianus* were (a) the fruiting neighborhood, (b) sucrose content, (c) the fruit/seed size index (PC1), (d) palm height, and (e) crop size. The shaded areas around trend lines represents the standard error. For palm height and crop size, the lines are dashed and without a standard error because these were not found to be significant in the models. Fruit removal information was collected across all frugivore species, and this information is not frugivore species specific.

**Table 2.** Model averaged (conditional average) coefficients, standard errors (SE), and associated z and p values for the two response variables. Significant predictors are in bold.

Response	Variable	Estimate	SE	Z value	p
30 day fruit removal rate	<b>Palm height</b>	<b>0.69</b>	<b>0.15</b>	<b>4.18</b>	<b>&lt;0.001</b>
	<b>N fruiting palms in 35m radius</b>	<b>-0.34</b>	<b>0.08</b>	<b>3.71</b>	<b>&lt;0.001</b>
	Sucrose concentration	0.37	0.17	1.89	0.06
	Pulp to seed ratio	-0.75	0.41	1.58	0.11
N fruits removed per frugivore visit	<b>N fruiting palms in 35m radius</b>	<b>-0.28</b>	<b>0.11</b>	<b>2.60</b>	<b>0.009</b>
	<b>Sucrose concentration</b>	<b>-0.64</b>	<b>0.25</b>	<b>2.5</b>	<b>0.01</b>
	<b>Fruit/seed size index PC1</b>	<b>-0.14</b>	<b>0.07</b>	<b>2.11</b>	<b>0.03</b>
	Height	0.84	0.45	1.84	0.07
	Crop size	0.01	0.01	1.29	0.20

### III. Interspecific Comparison

There were significant differences in certain palm characteristics between *P. decurrens* and *S. warscewiczianus*. It was found that *S. warscewiczianus* palms grew in areas with a significantly lower fruiting neighborhood than *P. decurrens* palms (Figure 5) (Gamma GLM,  $X^2 = 33.85$ ,  $p < 0.001$ ). The two palm species also differed significantly in height, with *P. decurrens* tending to be taller (Figure 5) (Gamma GLM,  $X^2 = 30.27$ ,  $p < 0.001$ ). Fruit crop size was found to be significantly larger for *P. decurrens* (Figure 5) (Gamma GLM,  $X^2 = 8.08$ ,  $p = 0.004$ ). Fruits from *P. decurrens* weighed 1.39g on average (sd = 0.19), had an average length of 13.38mm (sd = 0.74), and an average diameter of 13.14 (sd = 0.57). Fruits from *S. warscewiczianus* weighed 3.18g on average

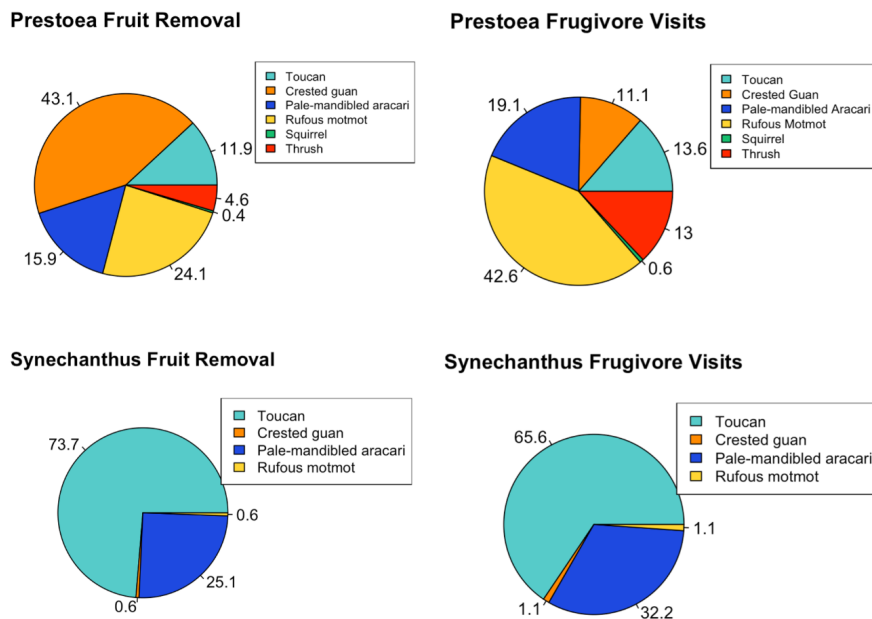
(sd = 1.02), had an average length of 22.69mm (sd = 3.31), and an average diameter of 18.17mm (sd = 2.27).

Frugivore communities differed significantly between *Prestoea decurrens* and *Synechanthus warscewiczianus* (PERMANOVA based on Horn-Morisita community dissimilarity indices, DF = 1, Sum of Squares = 1.15,  $R^2 = 0.10$ ,  $F = 3.95$ ,  $p = 0.01$ ), with toucans and pale-mandibled aracarís being the dominant visitors to *S. warscewiczianus* while *P. decurrens* palms had visits from many additional frugivore species (Table 3; Figure 4). *Prestoea decurrens* had significantly more frugivore visits relative to *S. warscewiczianus* (Table 3; S4) (Lognormal GLMM,  $X^2 = 4.36$ ,  $p = 0.04$ ). Additionally, there was a significant difference in removal rate between the two palm species, with *P. decurrens* having a higher removal rate (S4) (Gamma GLM,  $X^2 = 15.26$ ,  $p < 0.001$ ), as well as a significantly higher number of fruits removed per visit (Negative Binomial GLMM,  $X^2 = 5.54$ ,  $p = 0.02$ ). There is also a statistically significant difference in the frugivore species richness between the two palm species, with *P. decurrens* palms having a higher frugivore richness than *S. warscewiczianus* (Table 3; S4) (Lognormal GLMM,  $X^2 = 11.57$ ,  $p < 0.001$ ) as well as Inverse Simpsons species diversity indices (Lognormal GLMM,  $X^2 = 10.45$ ,  $p = 0.0012$ ). Toucans, crested guans, aracarís, and rufous motmots visited both focal palm species. However *P. decurrens* saw most of their visits from rufous motmots, followed by pale-mandibled aracarís, toucans, and crested guans, while *S. warscewiczianus* saw toucans as their most frequent frugivore visitor, followed by pale-mandibled aracarís, and only one visit from a crested guan and rufous motmot (Table 3; Figure 4). Large frugivores (i.e. toucans and guans) removed on average

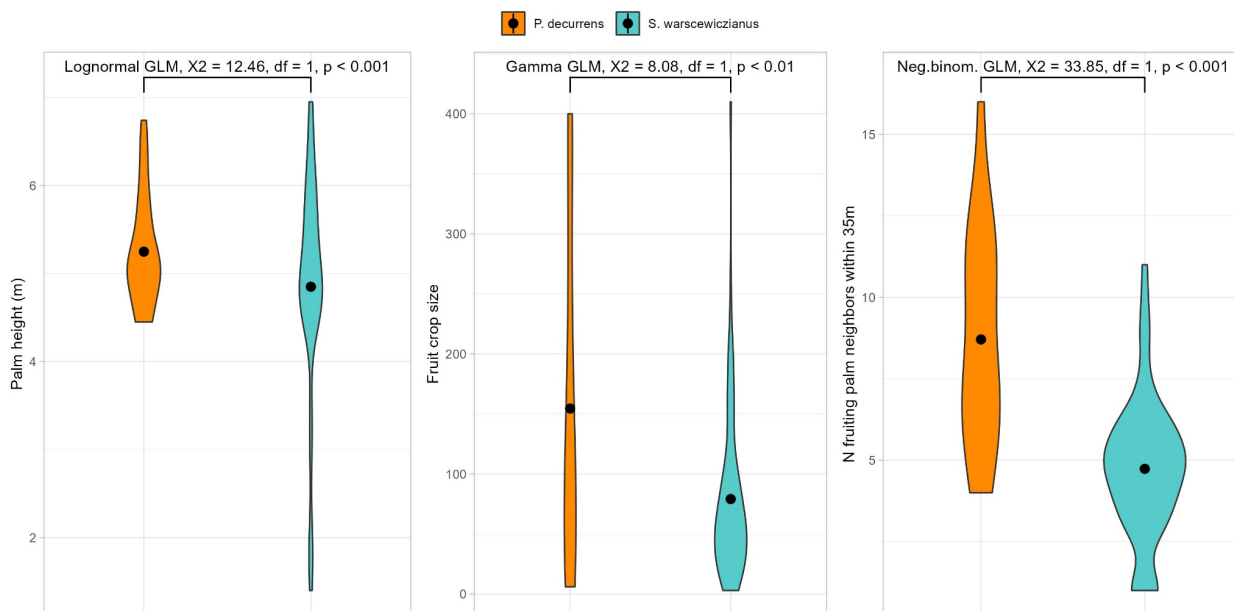
approximately 4 fruits per recorded visit (mean = 4.2 fruits), while the other small- to medium-sized frugivores removed on average 2 fruits per visit (mean = 1.9 fruits).

**Table 3.** Frugivore community composition across the understory palms, as well as the total number of visits and average number of fruits removed per visit per frugivore species.

<b>Frugivore species</b>	<b><i>P. decurrens</i> total visits</b>	<b><i>S. warszewiczianus</i> total visits</b>	<b><i>P. decurrens</i> mean # fruits removed per visit</b>	<b><i>S. warszewiczianus</i> mean # fruits removed per visit</b>
Toucan	22	59	2.68	2.12
Crested guan	18	1	13.11	1.00
Pale-mandibled aracari	31	29	2.81	1.48
Rufous motmot	69	1	1.90	1.00
Squirrel	1	0	2.00	<i>NA</i>
Thrush	21	0	1.24	<i>NA</i>



**Figure 4.** Comparison of the frugivore community between *P. decurrens* and *S. warscewiczianus* as well as the frugivores' relative visitation and fruit removal between focal palm species.



**Figure 5.** Differences in the palm height, fruit crop size, and fruiting neighborhood between *P. decurrens* and *S. warscewiczianus*.

## DISCUSSION

We explored how plant and fruit traits influence frugivory within an understory palm species, and also compared how the frugivore community differs between two normally co-fruiting understory palm species. Our results generally agreed with our predictions about neighborhood and plant trait effects on frugivory, and we correctly predicted that there would be a difference in frugivore communities between two understory palm species. However, we did not expect the predictors for fruit removal rate and number of fruits removed per visit to differ for frugivore foraging behavior with *S. warscewiczianus* palms. Height and the density of surrounding fruiting palms were the most important predictors of fruit removal rate, showing a positive and negative relationship, respectively. This suggests palm crops higher off the ground are favored by frugivores and that fruiting neighborhood density can have a dilution effect on seed dispersal services for individual palms. Interestingly, with the exception of fruiting palm neighborhood density, we found that the number of fruits removed per visit by frugivores was affected by a different set of predictors than the overall fruit removal rate was. While the most important predictor of the number of fruits consumed per visit by frugivores was still the density of the surrounding fruiting palm neighborhood, sucrose content, and our first Principal Component (PC1) reflecting fruit size and weight were also significant drivers. When we examined differences between *Prestoea decurrens* and *Synechanthus warscewiczianus* in fruit removal services and frugivore communities, results indicate that likely a combination of slightly taller palms, larger crop sizes, and smaller fruits lead to *P. decurrens* having a more speciose and diverse frugivore community and possibly a greater fruit removal and visitation rate. Taken together, our results provide insight into

factors affecting individual frugivore foraging decisions with implications for seed dispersal services at the level of the individual plant, as well as how co-fruiting understory palm species that differ in several of these key drivers can gain different frugivore communities and dispersal services, potentially reflecting different evolutionary strategies for gaining effective seed dispersal.

We found that the fruiting neighborhood had a negative effect on frugivory, likely due to competition among avian-dispersed plants (Saracco et al. 2005; Hopson et al. 2020). This supports findings from other studies that found lower rates of frugivory when there were more fruiting plants nearby (Smith and McWilliams 2014; Hopson et al. 2020; Lamperty et al. 2021). Fruiting neighborhood can affect seed dispersal efficacy in different ways; e.g., fruits removed from denser fruiting neighborhoods have been found to be dispersed shorter distances than fruits removed from more isolated plants (Carlo and Morales 2008; Morales et al. 2012). While we did not measure dispersal distance after fruits were removed from our focal palms, it is important to consider how the fruiting neighborhood influenced frugivore and seed dispersal services consequently. Additionally, it is important to note that we looked at the fruiting neighborhood in a 35m radius, while others have examined the fruiting neighborhood in larger ranges (Carlo and Morales 2008), and others considered smaller ranges between 7-25m (Guerra et al. 2017; Hopson et al. 2020; Jayanth et al. 2024). Therefore, it's possible that at different radii, the fruiting neighborhood has different effects on frugivory. The fruiting neighborhood's negative relationship with fruit removal rate and fruits removed per visit suggest that a high fruiting neighborhood dilutes the focal palm and increases competition among plants, and it also appears to have potential effects on seed dispersal services.

We had hypothesized that the trends for removal rate would be very similar to the trends for fruits removed per frugivore visit, as they are both similar metrics used to quantify frugivory, but we found that different factors influence the metrics. Taken together, our results suggest that frugivore decisions are scale-dependent. We found that the fruit removal rate increases with plant height and decreases with the density of other fruiting palms in the neighborhood. This would suggest that fruit removal rate provides more insight on why a bird would choose a focal palm, since these more visually obvious traits seem to be the most important drivers. At a more individual scale, the number of fruits removed per visit was best predicted by the fruiting neighborhood, sucrose content, and the fruit and seed size index. The predictors for fruit removal rate differ from the predictors for the number of fruits removed per visit, and this seems to suggest that fruits removed per visit best explains a bird's decision to eat fruit once they select a focal palm. Because fruit-specific traits are important only for the fruits removed per visit, it implies that sucrose and fruit and seed size are the main factors that encourage or deter a bird from eating fruit from the focal palm they've selected. Conversely, the fruit removal rate only considers the number of fruits removed in a 30 day period, which provides insight into the bird's decision to select the focal palm but does not predict how much fruit the bird will eat from the focal palm. When explaining the optimal foraging theory, Krebs (1977) states that birds should be able to identify the most nutritious fruit that will be the easiest to handle, and they will choose these fruits even when less nutritious fruits are more abundant in the area. Our results support the optimal foraging theory and suggest that more visually apparent traits such as the fruiting neighborhood and palm height are most influential in focal palm selection, but not for fruit selection. By exploring how

environmental and plant traits influence frugivory on both a larger and more individualistic scale, we gain more insight into frugivore foraging behavior.

Previous studies examining the relationship between sucrose and frugivory have given mixed results. Although previous studies found sucrose to be a deterrent for many frugivorous birds (Martínez del Río et al. 1995), we found an ideal sucrose range for the frugivores around 6%. This supports findings from Crestani et al (2019), who found that frugivores preferred fruits with intermediate levels of sucrose between 5-10%. As expected, however, the fruit/seed size index was negatively associated, though only slightly, with the number of fruits removed per visit, presumably because larger sizes of fruits and seeds would satiate frugivores faster.

In addition to gaining more insight into how intraspecific traits affect frugivory, we found significant differences in the frugivore community between the understory palm species, as well as differences in frugivore behavior. *Prestoea decurrens* palms were found to have a significantly higher frugivore species richness than *S. warscewiczianus*. This difference in species richness may be due to the difference in the palms' fruit sizes. Wheelwright (1985) discusses how plants with smaller fruits are visited by a more diverse community of frugivores than plants with large fruits and attributes this difference in frugivore community to the birds' gape sizes, since birds are unable to ingest fruits larger than their gape's width. In addition to having a higher frugivore species richness, *P. decurrens* experienced a higher amount of frugivory than *S. warscewiczianus*. One study found that in addition to a lower water content and longer fruiting periods, plants with fruits less than 14 mm experience more frugivory than fruits larger than 14mm (Ramos-Robles et al. 2018). *Prestoea decurrens* palms have an average

fruit length and diameter just less than 14mm, again suggesting that the fruit size is an important factor in influencing frugivory. Other studies have found that fruit diameter and bill width were highly correlated (Bender et al. 2018), supporting our findings where the main frugivores removing fruits for *P. decurrens* palms were crested guans and rufous motmots, which were classified as our medium gape frugivores. Conversely, the main frugivores for *S. warscewiczianus* were overwhelmingly from toucans and pale mandibled aracaris, which were classified as our large gape frugivores. Therefore, we believe that fruit size is the most important trait for a plant's frugivore community and may also influence frugivory.

Potentially due to an El Niño event in 2023, fewer *P. decurrens* palms were producing fruit at our study sites, so we decided to pivot and introduce *S. warscewiczianus* into our study as a second focal palm. Because *S. warscewiczianus* was not initially intended to be a focal palm, we only had one observation from the 2022 field season. Therefore, it is possible that many of the environmental and plant trait results only explain frugivore preferences in times of different climatic conditions (Wright et al. 1999).

## CONCLUSION

By exploring the palm-frugivore relationship in the Neotropics, we have gained important insight into how frugivores decide which palms to eat fruit from as well as how many fruits they will eat. It is becoming increasingly important to understand the plant-frugivore relationship as anthropogenic disturbances are negatively affecting seed dispersal services and the associated frugivore communities (Markl et al. 2012). By

learning more about frugivore preferences and palm fruiting strategies, we can better anticipate how seed dispersal will be affected by ecological disruptions. Future studies that aim to explore the frugivore community and the palm traits that affect frugivory may want to incorporate additional palm species into their study to examine how patterns of annual fruiting, differences in seasonality, and differences in understory and canopy species may affect frugivory. Similarly, future studies should look to examine how different levels of disturbance may also affect frugivory and the frugivore community. Lastly, future studies should consider observing fructose or glucose if studying avian dispersed plants, as these sugars may be more readily absorbed by avian frugivores.

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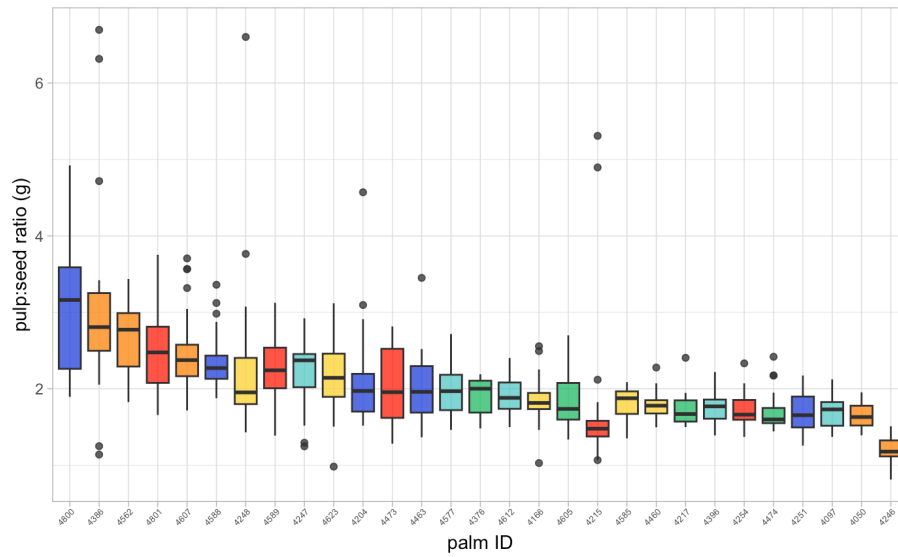
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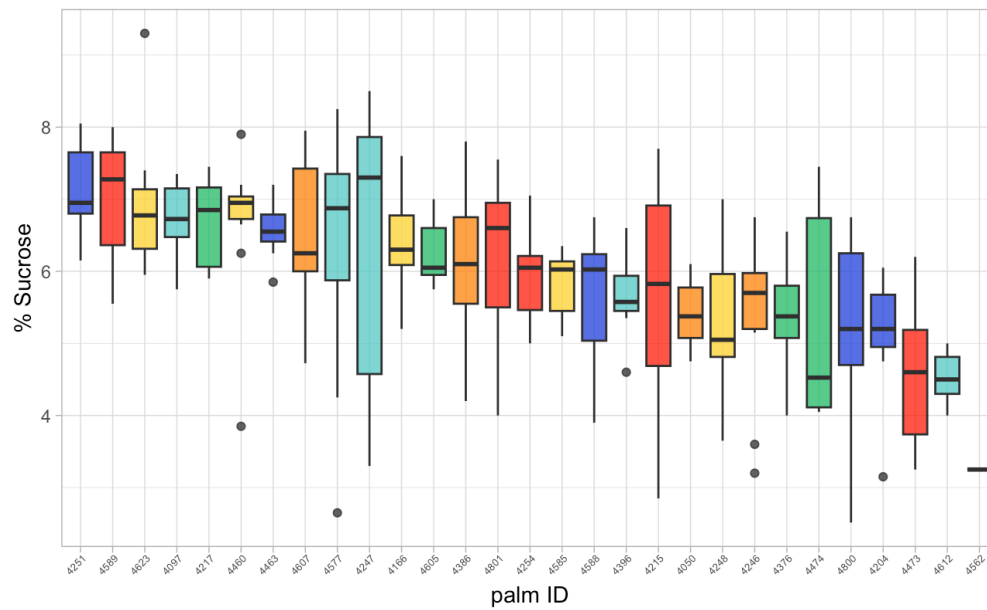
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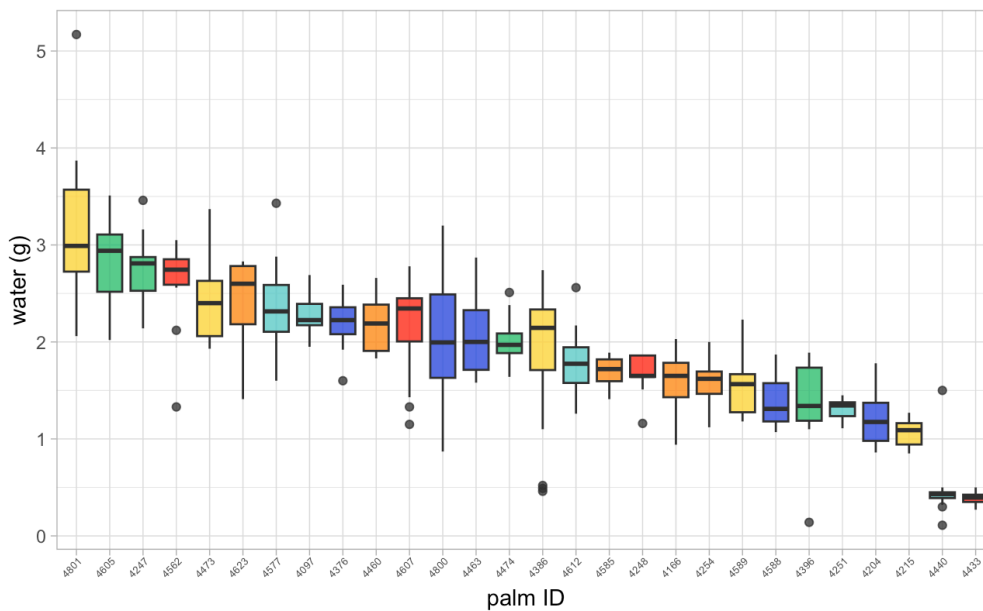
## APPENDIX



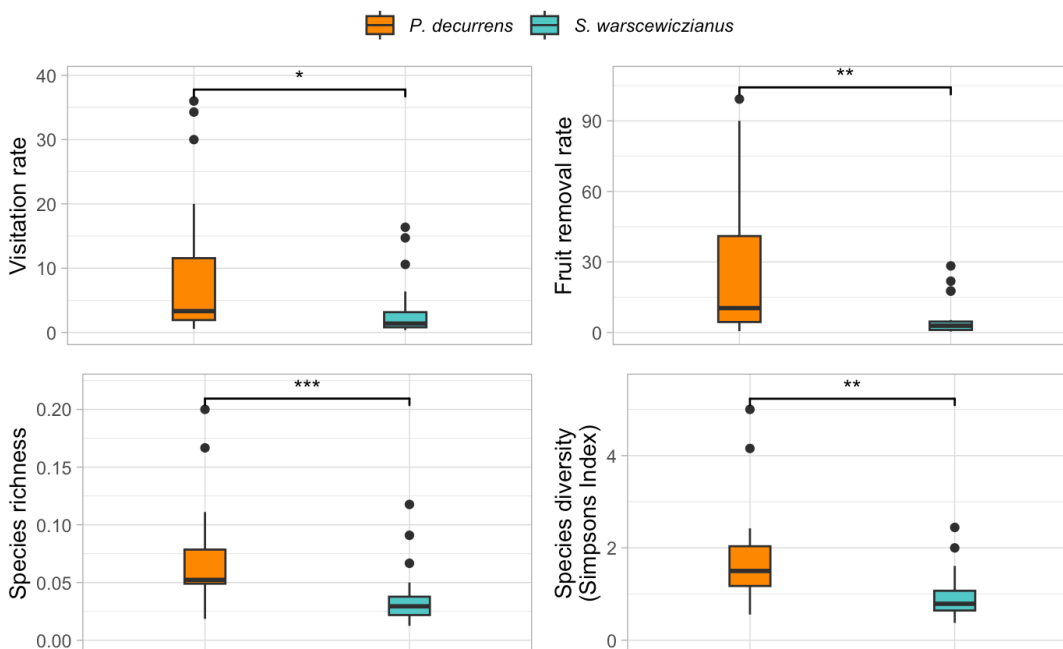
**Supplementary figure S1.** Comparison of the pulp to seed ratio (g) found in all fruits across the focal *S. warscewiczianus* palms studied.



**Supplementary figure S2.** Comparison of the sucrose content (Brix %) found in all fruits across the focal *S. warscewiczianus* palms studied.



**Supplementary figure S3.** Comparison of the water mass (g) found in all fruits across the focal *S. warscewiczianus* palms studied.



**Supplementary figure S4.** Comparison of visitation, removal rate, species richness, and species diversity between *S. warscewiczianus* and *P. decurrens* palms. Significance is indicated by asterisks.