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Effects of Fruiting Neighborhood, Plant Traits, and Fruit Traits on Frugivore Visitation and Fruit Removal for an Understory Palm

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ABSTRACT

Seed dispersal services are key to maintaining healthy forest ecosystems, yet our understanding of the factors that influence visitation and frugivory between conspecific plants remains incomplete. Although fruiting neighborhood, plant traits, and fruit traits have been shown to individually influence frugivory, few studies have concurrently evaluated the relative importance of these factors. We address this knowledge gap by simultaneously assessing multiple factors thought to influence frugivory. Specifically, we evaluated how the fruiting neighborhood, defined as the number of fruiting palms in a 35 m radius, and relevant traits at the level of individual plants (e.g., height, crop size) and fruits (e.g., fruit and seed size, water and sucrose content) influenced frugivore visitation and the number of fruits removed per visit in a common understory palm in Northwestern Ecuador, *Synechanthus warscewiczianus*. A higher number of conspecific fruiting neighbors exhibited a decrease in visitation, suggesting competition among palms that share frugivore mutualists for dispersal services. However, the number of fruits removed per frugivore visit appeared to be affected by crop size and fruit traits of individual palms. Larger crop and fruit sizes were positively associated with the number of fruits removed per visit and indicates frugivore satiation is not a main determinant of fruit consumption during visits. Taken together, our results suggest larger-scale factors like fruiting neighborhood may affect a frugivore's decision to visit a palm, yet finer-scale fruit traits may drive fruit removal once a palm is selected, thereby influencing variation in seed dispersal services at the individual plant level.

RÉSUMÉ

La dispersión de las semillas es muy importante para mantener ecosistemas bosques saludables, sin embargo, nuestra comprehensión de los factores que influyen la visitación y la frugivoría entre plantas conspecíficos no esta completo. Aunque el vecindario de frutar, atributos de las plantas, y atributos de las frutas ha estado mostrado a influir frugivoría, pocos estudias han evaluado la importancia relativa de estes factores juntos. Atendemos esta brecha de conocimiento con evaluando en lo mismo tiempo muchos factores se piensa a influir frugivoría. Específicamente, evaluamos como el vecindario de frutar, define como la numera de las palmas con frutas en un área de 35 m, y atributos relevantes para la planta individua (por ejemplo, alta, numero de frutas) y frutas (por ejemplo, la tamaña de las frutas y las semillas, el agua y el sucre en las frutas) influyeron la visitación de los frugívoros y el numero de las frutas sacadas cada visite en una palma sotobosque y común en el noreste de Ecuador, *Synecanthus warscewiczianus*. Una numero mas alta de vecinos frutando de miso especie causaron una reducción en visitación, sugiriendo

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competencia entre palmas que compartir frugívoras mutualistas para servicios de dispersar. Sin embargo, la numera de las frutas sacadas cada visite pareció ser afectado del tamaño de la cosecha y atributas frutas de palmas individuas. Las cosechas mas grandes y frutas más grandes fueron asociadas positivamente con la numera de las frutas sacadas cada visite e indica frugívora satisfacción no es una determinante mejor de consumición de las frutas durante visites. Junto, nuestras resultadas sugieren que factores en una escala más grande como el vecindario de frutar quizás afecta las decisiones de las frugívoros a visitar una palma, pero, cosas más finas como atributos de las frutas quizás manejar de sacar de las frutas después de la palma esta seleccionada para visitar, influyendo variedad en servicios de la dispersión de las semillas en el nivel individuo de las plantas.

1 | Introduction

Ingestion and dispersal of seeds by animals shapes tropical forest plant communities by determining the spatial pattern of seed deposition and by influencing propagule survival probability and plant population genetics (Janzen 1970; Connell 1970; Fine and Lohmann 2018; Razafindratsima and Dunham 2015; Lamperty et al. 2025). Variation in frugivore behaviors can create scenarios in which not all plant individuals of the same species receive equal seed dispersal services (Brehm and Mortelliti 2022; Tonos et al. 2022). Such intraspecific variation in the receipt of seed dispersal services can have far reaching effects on plant populations and community compositions, particularly in tropical forests where most species are animal-dispersed (Howe and Smallwood 1982). Identifying factors that influence frugivore visitation and fruit removal is therefore an important component of understanding the underlying mechanisms that determine plant recruitment patterns in hyperdiverse tropical systems (Howe and Smallwood 1982; Schupp 1993; Peres 2000; Diaz-Martin et al. 2014; Schupp et al. 2019).

Existing work highlights a complex and dynamic set of factors that can affect frugivore behavior with consequences for seed dispersal services, such as a plant's local environment (Mahoney et al. 2018), the abundance of other nearby fruiting plants (the 'fruiting neighborhood') (Guerra et al. 2017), characteristics including plant height and fruit crop size (Saracco et al. 2005), and morphological and chemical fruit properties (Flörchinger et al. 2010; Crestani et al. 2019; Schupp et al. 2019). However, most studies focus on one or a limited subset of these factors at once, and the field is characterized by contradictory or context-dependent findings (Schupp et al. 2019; Jayanth et al. 2024). Comprehensive assessments that concurrently evaluate how both fine-scale (e.g., intraspecific variation of fruit traits) and larger-scale (e.g., heterogeneity in the fruiting neighborhood) factors influence frugivory are needed to better understand seed dispersal mutualisms in tropical forests.

Among the factors that may contribute to frugivore foraging behaviors, the density of the surrounding fruiting neighborhood has received considerable attention as a potential driver of variation in frugivore visitation and seed dispersal (Schupp et al. 2019; Jayanth et al. 2024; Prasad and Sukumar 2010). A range of effects have been reported that are likely context-dependent. For example, frugivores can mediate indirect interactions between co-fruiting neighbors in a beneficial, facilitative way whereby per capita seed dispersal services increase with greater neighborhood fruiting availability (e.g., Guerra et al. 2017), which may occur in a resource-limited landscape in which a dense fruiting patch attracts more frugivores than a low-density patch. Alternatively, frugivore-mediated interactions between fruiting neighbors can be competitive, whereby plants receive fewer seed dispersal services in higher-density fruiting neighborhoods because visitation and fruit removal at the scale of individual plants become diluted (e.g., Smith and McWilliams 2014; Hopson et al. 2020). Between conspecific neighbors in particular, mutualist-mediated competition for services can be expected if the plant species has a small assemblage of possible mutualistic partners (Manasse and Howe 1983; Albrecht et al. 2015). Likewise, if heterospecific neighbors also share overlapping assemblages of frugivore mutualists, and if dispersers are limited across the landscape, this is expected to lead to indirect competition between heterospecific neighbors and decreased per capita dispersal services (Donoso et al. 2017). However, conspecific and heterospecific neighborhood fruiting density may also correlate with facultative indirect interactions, particularly if many generalist frugivores are drawn into a high resource patch, which could increase visitation probability to all conspecific and nonspecialist fruiting plants in the neighborhood (Moeller 2004; Nottebrock et al. 2017; Santos et al. 2018). The context-dependency of fruiting neighborhood effects on per capita dispersal may also be shaped by the broader landscape of fruiting availability (Smith and McWilliams 2014; Vissoto et al. 2022). For example, some studies report no evidence of a relationship between the density of fruiting conspecifics and frugivore visitation (Pizo and Almeida-Neto 2009) or find the importance of other factors such as crop size are more important in driving intraspecific variation in the receipt of seed dispersal services (Blendinger and Villegas 2011).

In addition to the surrounding context of the fruiting neighborhood, plant traits such as height and fruit crop size have also been found to influence frugivory. Studies indicate a positive relationship between plant height, frugivore richness, and visitation rate (Vissoto et al. 2022; González-Varo et al. 2023). Crop size is also often positively associated with plant height (Flörchinger et al. 2010; Guerra et al. 2017). As with plant height, crop size has been found to positively influence frugivore visitation (Blendinger and Villegas 2011; Guerra et al. 2017) as well as fruit removal (Ortiz-Pulido et al. 2007). However, some research has found no significant relationship between crop size and fruit removal (Laska and Stiles 1994). These studies highlight the ways in which phenotypic variation between individual conspecific trees may influence frugivore foraging behaviors, which in turn shapes downstream dispersal services.

At an even finer scale, fruit traits may also influence frugivory. Interspecific studies have found water content to influence frugivore choices, with many avian frugivores preferring fruits lower in water content to reduce the amount of unnecessary weight consumed; however, not much is known at the intraspecific level. (Nisbet et al. 1963; Moermond and Denslow 1985;

Ramos-Robles et al. 2018). Sucrose can also influence fruit consumption by exerting a moderating effect on fruit removal, as avian frugivores appear to prefer fruits with intermediate sucrose concentrations (Lotz and Schondube 2006; Crestani et al. 2019; del Martínez Rio and Restrepo 1993; McWhorter et al. 2021). However, this relationship is not well understood, as most frugivorous birds are unable to hydrolyze sucrose and prefer monosaccharides such as glucose or fructose (del Martínez Rio et al. 1995; Levey and Martínez del Rio 2001). Despite sucrose not being easily digestible for most avian frugivores, it can be associated with fruit ripeness via the color of the fruit and therefore is still a valuable visual cue for frugivores when foraging (Luo et al. 2019; Durán-Soria et al. 2020). While this body of work points to a potential role for fruit traits in shaping frugivory, much remains to be learned about this relationship as well as its relative importance compared to fruit neighborhood and plant traits such as height and crop size.

The effectiveness that a frugivore has as a seed disperser is often broken down into two components: quantity and quality (Schupp 1993; Schupp et al. 2010). From the plant's perspective, quantity is comprised of both the number of visits by frugivores that an individual plant receives and the number of fruits removed during foraging, while quality is determined in large part by handling and treatment (e.g., chewing, gut passage) and spatial patterns of seed deposition (Schupp 1993; Schupp et al. 2010). In the present study we focus on the quantity components of seed dispersal effectiveness by passively recording visitation and removal at focal trees using motion-activated camera traps. Our particular focus is how the rate of frugivore visitation and fruit removal per visit relate to plant, fruit, and neighborhood traits for *Synechanthus warscewiczianus*, an understory palm commonly found throughout our study area in northwestern Ecuador's critically threatened Chocó ecoregion (Browne and Karubian 2016). We investigate this by evaluating both the number of frugivore visits a palm received and the number of fruits removed during those visits as functions of the surrounding fruiting neighborhoods, palm height, palm crop size, as well as fruit and seed weight, size, and nutritional metrics. We expect that avian frugivores are capable of simultaneously integrating neighborhood, plant, and fruit cues to determine which palm to visit and how many fruits to remove in order to optimize their foraging efficiency. We hypothesize that broader patterns of resource availability (e.g., fruit neighborhood) exert stronger effects on visitation, whereas fruit traits (e.g., water content) will exert stronger effects on fruit removal among foraging frugivores.

2 | Methods

2.1 | 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 S1). FCAT is a privately owned reserve of approximately 700-ha (250–550 m a.s.l.), with approximately 2.5 m rain per year (Clark et al. 2006). The study site is located within the Chocó biogeographic region, a biodiversity hotspot that hosts more than 400 endemic vertebrate species and over 2000 endemic plant species (Myers et al. 2000). Although there is considerable disturbance within the Mache-Chindul Reserve, data were only collected in intact forests from June–October (dry season).

We collected data across five, 1-ha plots that have previously been established for research on canopy palms at the FCAT Reserve. Within each plot, all canopy palms were already marked and mapped. For the current study, we identified, marked, and mapped all understory palm species within the five study plots, assigning each individual a unique numbered tag. The focal palm species for this study was *Synechanthus warscewiczianus*, and individuals were selected based on their fruiting availability. However, we included all palm species within the plots (understory and canopy) for our assessment of the fruiting neighborhood. There was no set minimum distance between focal palms.

2.2 | Study Species

Synechanthus warscewiczianus palms average 4.1 m in height and have only one seed per fruit. The fruits are ovoid and have an average length of 22.8 mm ±2.3 (range: 19.4–28.6) and average width of 14.8 mm ±1.4 (range: 12.2–17.1) and an average crop size of 72 fruits (range: 6–250). The fruits are bright red when mature.

We focus on palms in part because of the species' accessibility for our study (they 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; Browne and Karubian 2016). Thus, insights into factors influencing frugivore foraging and fruit removal from our study species represent an opportunity to advance our knowledge of factors influencing seed dispersal and regeneration for an exceptionally ecologically important plant group (Browne and Karubian 2016; Lueder et al. 2022).

2.3 | Frugivore Community Characterization

We selected 34 focal *S. warscewiczianus* palms across the landscape within the five 1 ha plots in FCAT reserve's contiguous forest (Figure S1). We had an average of 13.2 palms ±3.6 sampled in each plot (range: 8–16). We recorded frugivore visits and interactions with fruits (detailed below) on focal palms via motion-activated camera traps (Bushnell and Browning), placed approximately 5 m from focal palms and focused on infructescences with ripe fruit. Cameras recorded 10 s each time motion was detected. Focal palms were checked approximately every 2 weeks to ensure fruits were still present, and if most fruits were gone, the camera trap was relocated to a new focal palm. Camera trap deployment length was never less than 15 days, and mean deployment length was 38 ± 22 (SD) days.

We reviewed camera trap footage and recorded each visiting frugivore species and its interactions with fruits. We considered the following actions to be "removal" events: the frugivore dropped the fruit, ingested the fruit, or left the focal palm with the fruit in its beak. A visit was classified as any time a frugivore known to remove fruits from our focal species (based on this study's data) was perched on the branch with the infructescence, regardless of

whether they interacted with the fruit. Of our 34 focal palms, 14 received visits, while 17 had no visits recorded. We include all palms (including those with no recorded visits) in our analyses because a lack of visits could be a reflection of frugivore foraging preferences (or aversions) in response to the predictor variables we investigate in the present study. However, fruits removed per visit exclude palms that received 0 visits due to the nature of this metric.

2.4 | Fruiting Neighborhood, Plant Characteristics, and Fruit and Seed Data

To estimate fruiting neighborhood resources, we counted all palms that presented mature fruit within a 35 m radius of each focal palm when the camera traps were being placed. The palms in the 35 m radius are comprised of conspecific and heterospecific palms. Due to the relatively large fruit size (22.4 mm length and 14.8 mm diameter) of our focal species, we expect the frugivore community of *S. warscewiczianus* to be composed of large-bodied generalists capable of also consuming the fruits of most of the other co-fruiting palms. We focused solely on palms for our measures of fruiting neighborhood. In addition to *S. warscewiczianus*, the palm species comprising the fruiting neighborhood were: *Prestoea decurrens* (fruits 6.5–8 mm in diameter), *Bactris gasipaes* (fruits 10–15 mm in diameter), *Socratea exorrhiza* (fruits 20 mm in diameter), *Oenocarpus bataua* (fruits 20–25 mm in diameter), and *Iriartea deltoidea* (fruits 20–28 mm in diameter) (Henderson and De Nevers 1988; Henderson 1990; Wyatt and Silman 2004; Silva De Souza et al. 2012; Soares et al. 2022). A single *Attalea colenda* (fruits 45–50 mm in length) palm was also fruiting in one of the focal palm's neighborhoods (Blicher-Mathiesen and Balslev 1990). However, we do not expect overlap to exist between frugivore communities of this species and *S. warscewiczianus* due to its large fruit size and largely terrestrial seed dispersal, and we excluded it from our analyses.

To characterize tree traits, we estimated palm height and crop size (the number of fruits on the focal palm). Palm height was measured with a rangefinder while crop size was estimated visually by counting the fruits on one branch and multiplying it by the number of racemes with fruit on the focal palm unless there was a visually apparent difference between the amount of fruit on each branch.

To quantify fruit and seed traits relevant to frugivory, we collected a minimum of 10 fruits from each focal palm and measured several physical and nutritional qualities. 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. Ultimately, the number of viable fruits we were able to obtain per individual was on average 19 ± 6.3 (range: 10–35). First, we recorded overall fruit mass (seed included), then pulp and seed mass separately and used these data to compute pulp-to-seed ratios. We also measured length and width for fruits and seeds. We recorded water mass for the first 10 fruits collected from each focal palm by placing fruits in a drying oven overnight and taking the difference in pulp mass pre- and post-drying. Then we calculated water content as a percentage from the total fruit's weight. For an additional 10 fruits collected from each focal palm, 2–4 drops of the fruit's juice were squeezed onto a portable refractometer and recorded the Brix percentage, which measures dissolved sucrose in liquid (Jaywant et al. 2022). Although avian frugivores do not have a high sucrase activity compared to other diet niches such as nectivores (del Martínez Rio et al. 1992; McWhorter et al. 2021), we decided to look at sucrose because it is known to be positively associated with fruit ripeness in some cases (Luo et al. 2019; Durán-Soria et al. 2020).

2.5 | Analysis

All statistical analyses were done in R version 4.4.2 (R Core Team 2024), and all predictors were scaled and centered prior to analysis. We tested two response variables that are indicative of quantitative aspects of seed-dispersal services: (1) frugivore visitation (the number of frugivore visits at a focal palm) and (2) the number of fruits removed by each frugivore during visits (Carlo and Morales 2008; Holbrook and Loiselle 2009; Schupp et al. 2010; Raji and Downs 2022). Water content data was lacking for 3 palms, therefore we constructed models using a truncated dataset ($n = 25$ palms). To assess drivers of variation in frugivore visitation, our analysis included palms that received no visits. Models examining visitation used a negative binomial distribution and included an offset term as the logarithm of camera trap days to account for variation in sample size between individual palms. Palms that received visits ($n = 16$) were used to assess predictors of the number of fruits that frugivores removed per visit. The number of fruits removed per visit by frugivores was modeled with a Conway-Maxwell-Poisson (COM-Poisson) mixed-effects model with the random effect of palm ID; COM-Poisson was selected after negative binomial and Poisson failed residuals diagnostics tests.

Fruit and seed values varied between palms (Figure 1) and our analysis used mean values of the examined traits per focal palm. Pearson correlation coefficients showed high collinearity between fruit length, fruit diameter, seed length, seed diameter, seed mass, wet pulp mass, and cumulative fruit + seed mass (Figure S2). To address this, these variables were used in a principal component analysis (PCA) (Pearson 1901; Hotelling 1933; Jolliffe and Cadima 2016). The first principal component (PC1) accounted for the majority of the variance (79.42%) and was included in models as a fruit and seed size metric (Figure S2) (Jolliffe and Cadima 2016). Additionally, we limited our fruiting neighborhood predictors to (1) conspecific fruiting neighbors and (2) heterospecific fruiting neighbors to avoid using collinear terms (e.g., total fruiting neighbors, conspecific fruiting neighbors, and fruiting understory palms were all highly collinear) (Figure S3).

Model comparison and selection were based on the lowest Akaike Information Criterion (AIC) values, which reflect a tradeoff between model complexity (increases AIC) and fit (decreases AIC) (Burnham and Anderson 2002). Models were constructed using the "glmmTMB" package (Brooks et al. 2022) and validated using the "DHARMa" package to check residuals, zero-inflation, and overdispersion (Hartig and Lohse 2022). Models were structured to test hypothesized effects of neighborhood, plant, and fruit traits and moved from simple to more complex. Fixed effects were added in the order in which they are described below; when the addition of a fixed effect improved

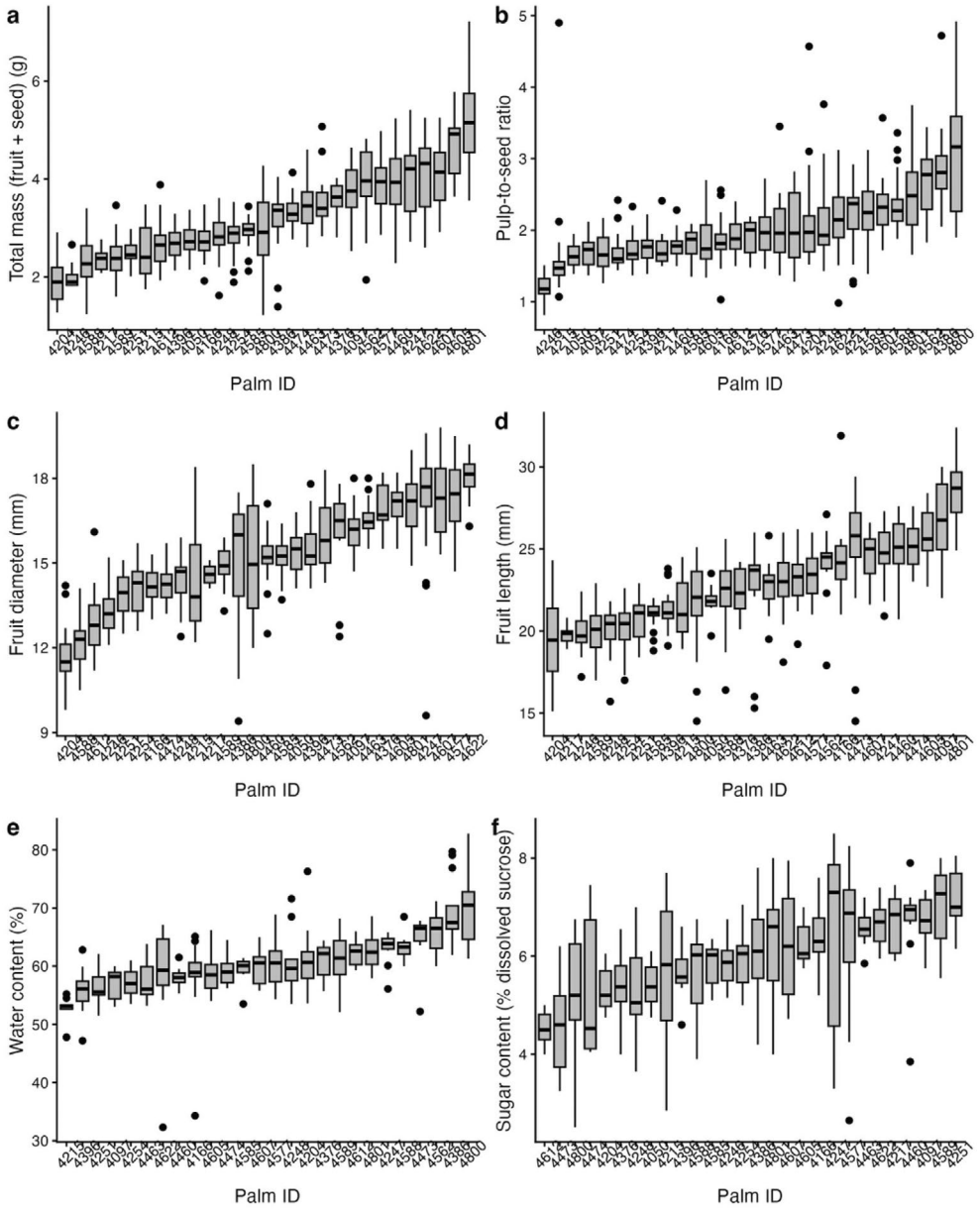


FIGURE 1 | Inter-individual variation across focal palms in fruit-specific traits expected to influence frugivory, including (a) total fruit mass (g), (b) pulp-to-seed ratio, (c) fruit diameter (mm), (d) fruit length (mm), (e) water content (%), and (f) sugar content (% dissolved sugar). See Table S1 for the mean, SD, minimum, and maximum value for each trait.

model fit (resulted in a lower AIC value), it remained in subsequent models; otherwise, it was dropped from our model progression towards greater complexity.

2.5.1 | Testing Fruiting Neighborhood Effects

First, we constructed a simple model with the total number of all co-fruiting neighbors as the only fixed effect to test if, regardless of species, a denser fruiting neighborhood attracts more frugivores to an area and thereby facilitates an increase in visitation or if fruiting neighbors dilute the number of visits individuals receive (akin to competition), resulting in decreased visitation at the individual level. We then tested if effects on visitation from co-fruiting neighbors depend on species identity by breaking co-fruiting neighbors into two fixed effects in our model: heterospecific and conspecific fruiting individuals. Due to the complete overlap in frugivore assemblages for trees of the same species, we expected conspecific neighbors, more so than heterospecific neighbors, to influence visitation. This model progression was repeated for our second response variable as well (the number of fruits removed per visit), with the expectation that if frugivore visitation is affected by fruiting neighborhood density at all, this effect would mirror the effect on fruit removal for the same reasons.

2.5.2 | Testing Individual Palm Traits

We then tested if the individual traits of height and crop size had an effect on visitation and on the number of fruits removed per visit. First, palm height was added as a fixed effect

to our best fit model from above for each response variable (visitation and fruits removed during foraging). Because many frugivore species large enough to consume fruits whole from our study species are primarily canopy species, we hypothesized that height could lead to greater visitation as well as extended foraging activity (i.e., more fruits removed per visit). We subsequently investigated if incorporating fruit crop size, also a factor that could attract greater visitation and fruit removal by offering greater foraging efficiency, improved each model's fit.

2.5.3 | Testing Fruit Traits

Finally, we tested if adding fixed effects for fruit and seed size (PC1), pulp-to-seed ratio, sucrose content, and water content improved our models. If frugivore foraging choices are influenced by variation in the fruit characteristics at individual palms, we would expect that larger fruits, as well as higher pulp-to-seed ratios, would result in increased visitation because this trait should increase foraging efficiency. In contrast, we hypothesized that the number of fruits removed per visit would be lower in relation to these traits due to satiation occurring faster after consuming fewer fruits, unless foraging bouts are limited by something other than satiation. Sucrose content could be a draw or a deterrent to avian frugivores, depending on factors such as their ability to digest sucrose and their dietary needs (Luo et al. 2019; Durán-Soria et al. 2020), as could water content, depending on if it is a limited resource in this environment. Fruit traits were added to our model progression one at a time sequentially in the order described above and were only kept in the model progression if their addition improved model fit.

3 | Results

3.1 | Frugivore Community

Cumulatively, we recorded 85 frugivore visits over 1290 camera trap days, with most individual *S. warscewiczianus* palms receiving less than three visits, while one focal palm received over 5× the mean number of visits per individual received (mean = 2.5 per palm, standard deviation = 5.3, range = 0–26 visits per focal palm).

The seed disperser community we recorded visiting *S. warscewiczianus* consisted of four species, all relatively large avian frugivores: toucan (*Ramphastos spp*), pale-mandibled aracari (*Pteroglossus erythropygius*), crested guan (*Penelope purpurascens*), and rufous motmot (*Baryphthengus martii*). It should be noted while both *Ramphastos swainsonii* and *R. brevis* are present in the study area, we were unable to confidently distinguish between the two on camera traps and therefore grouped them together under *Ramphastos* spp. (Table 1). These two *Ramphastos* species and *P. erythropygius* dominated visitation and fruit removal, accounting for 98.6% of all fruit removal events that we recorded. The variables we assessed as potential drivers of frugivore visitation and fruit removal varied substantially between focal palms, including fruit and seed traits (e.g., fruit diameter, sugar content, and seed and fruit mass) from mature fruits (Figure 1, Table 2, Figures S4 and S5, Table S1).

TABLE 1 | For each frugivore recorded visiting *S. warscewiczianus*: The cumulative number of visits across all focal palms, the mean number of fruits removed per visit (including instances of visits with 0 recorded fruit removal) and standard deviation (SD), and the cumulative number of fruits that species removed during the study.

Species	Total visits	Mean fruits removed per visit	SD	Total fruits removed during study
Toucan (*Ramphastos spp*)	63	1.89	1.43	119
Pale-mandibled aracari (*Pteroglossus erythropygius*)	20	1.40	0.88	28
Crested guan (*Penelope purpurascens*)	1	1.00	—	1
Rufous motmot (*Baryphthengus martii*)	1	1.00	—	1

3.2 | Visitation

Our top model based on lowest AIC included only the fixed effect of conspecific fruiting neighborhood density (Table 3). The second-ranked model included only the fixed effect of total fruiting neighborhood density, which was highly collinear with conspecific fruiting neighborhood density (Table 3, Figure S3). Both were negatively related to visitation and marginally nonsignificant (Table 4, Figure 2). Our null model ranked 3rd and was within two AIC of our top two models (Table 3). See Table S2 for a complete list of ranked models.

3.3 | Fruits Removed Per Frugivore Visit

The best-fit model for predicting the number of fruits removed per visit by frugivores included both the fixed effects of PC1 (fruit and seed size) and water content (Table 5). The second best-fit model only included PC1, while the third only included crop size. Our null model was ranked 5th and was within two AIC of the top model (Table 5). The number of fruits removed per visit was positively associated with PC1 and negatively related to fruit water content (Table 6, Figure 3a,b). Crop size, which was the sole fixed effect in our 3rd best-fit model, was also positively correlated with fruits removed per visit (Table 6, Figure 3c).

4 | Discussion

Assessing the factors that may influence frugivore foraging preferences among individuals of the same plant species is a key part of understanding what determines variation in seed

TABLE 2 | Mean, standard deviation (SD), minimum, and maximum values of focal palm fruiting neighborhood and fruit trait data. Sample size reflects the number of focal palms in this study for which we had data for each trait/factor. This includes a subset of the fruit and seed traits measured in this study. A complete table of fruit and seed traits measured can be found in Table S1.

Trait/Factor	Mean	SD	Min	Max	Sample size
35 m radius neighborhood					
N fruiting palms	5.49	2.82	1.00	11.00	34
N fruiting conspecifics	3.90	2.71	0.00	10.00	34
N fruiting understory palms	4.18	2.60	0.00	10.00	34
N fruiting canopy palms	1.31	1.60	0.00	6.00	34
N fruiting heterospecifics	1.58	1.75	0.00	6.00	34
Plant traits					
Height (m)	4.85	1.27	1.40	6.95	34
Crop (*N* fruits)	72.43	55.90	6.00	250.00	32
Total mass (fruit + seed) (g)	3.20	0.80	1.88	5.13	29
Water content (%)	60.49	3.92	52.4	69.8	26
Fruit traits					
Brix (% dissolved sucrose)	5.97	0.68	4.52	7.16	28
Fruit diameter (mm)	15.25	1.60	11.65	18.00	29
Fruit length (mm)	22.75	2.31	19.4	28.6	29
Pulp-to-seed ratio	2.02	0.40	1.19	3.11	29

TABLE 3 | Top 3 models ranked by ascending AIC values. Null and full models are also shown; our null model was the 3rd ranked model, while our full model was 18th (the lowest fit of all models run). The first column gives the response, subsequent columns give degrees of freedom (df), log-likelihood, AIC, delta AIC (dAIC), and model weight. See Table S2 for a complete AIC-ranked list of models run.

	Response~fixed effect(s)	df	log-likelihood	AIC	dAIC	Weight
	Visits~conspecific fruiting neighbors	3	−46.90	99.79	0	0.12
	Visits~all fruiting neighbors	3	−46.94	99.88	0.09	0.12
Null model	Visits~1	2	−48.21	100.43	0.63	0.09
Full model	Visits~all fruiting neighbors + height + crop size + PC1 + pulp-to-seed ratio + water content + sucrose content	10	−45.80	111.61	11.81	0.00

dispersal services and plant propagation success (Schupp et al. 2019; Messeder and Silveira 2025). A range of factors including the surrounding fruiting neighborhood and variation in plant and fruit traits between individuals are all thought to influence frugivore foraging behaviors and therefore seed dispersal services (Schupp et al. 2019), but the relative effects of these factors on visitation and fruit removal are not well understood because they are rarely studied concurrently. To address this, we simultaneously assessed how factors ranging from fruit traits (e.g., size) and plant traits (e.g., height) to neighborhood effects may influence two aspects of frugivory: visitation and fruit removal during visits in a large-seeded understory palm, *Synechanthus warscewiczianus*. We found substantial inter-individual variation in palm height and crop size and several fruit metrics; yet our results indicate that only the fruiting neighborhood influenced frugivore visitation. Specifically, the conspecific fruiting neighborhood was associated with a decrease in frugivore visitation—a pattern indicative of frugivore-mediated competition for visitation between neighboring fruiting plants. However, once frugivores arrived at a palm, plant- and fruit-specific traits that may be more nutritionally/energetically relevant appeared to shape decisions about time and energy invested in actual fruit removal. This was evidenced by positive associations between both fruit and crop sizes with the number of fruits removed per visit by frugivores, while water content appeared to be associated with lower fruit removal per visit to a focal palm. Our findings suggest that avian frugivores may assess the fruiting neighborhood when determining which individual to visit, but once visitation has occurred, foraging decisions at that specific individual plant may then be influenced by finer-scale traits such as fruit size.

TABLE 4 | Outputs of the top three models and full model examining predictors of visitation. The first column gives AIC-based ranking, the second gives fixed effects of each model with subsequent columns showing for each: Maximum-likelihood estimate, standard error (SE), *z*-value, and *p*-value. Note the full model includes conspecific neighbors and heterospecific neighbors as main fixed effects to avoid collinearity with the 'all fruiting neighbors' term, which is the sum of heterospecific + conspecific fruiting neighbors.

Response: Number of visits					
Model	**Fixed effect(s)**	**Estimate**	**SE**	***z***	***p***
1	(Intercept)	−2.77	0.29	−9.49	< 0.001
	Conspecific fruiting neighbors	−0.45	0.26	−1.71	0.09
2	(Intercept)	−2.77	0.29	−9.43	< 0.001
	All fruiting neighbors	−0.52	0.31	−1.67	0.09
3 (Null)	(Intercept)	−2.68	0.31	−8.64	< 0.001
18 (Full)	(Intercept)	−2.79	0.31	−8.88	< 0.001
	Conspecific fruiting neighbors	−0.26	0.36	−0.72	0.47
	Heterospecific fruiting neighbors	0.03	0.69	0.05	0.96
	Height	0.14	0.37	0.39	0.70
	Crop size	0.33	0.45	0.73	0.46
	PC1 (fruit & seed size)	0.07	0.22	0.31	0.76
	Pulp-to-seed ratio	−0.40	0.74	−0.54	0.59
	Sucrose content	0.39	0.35	1.11	0.27
	Water content	0.55	0.72	0.77	0.44

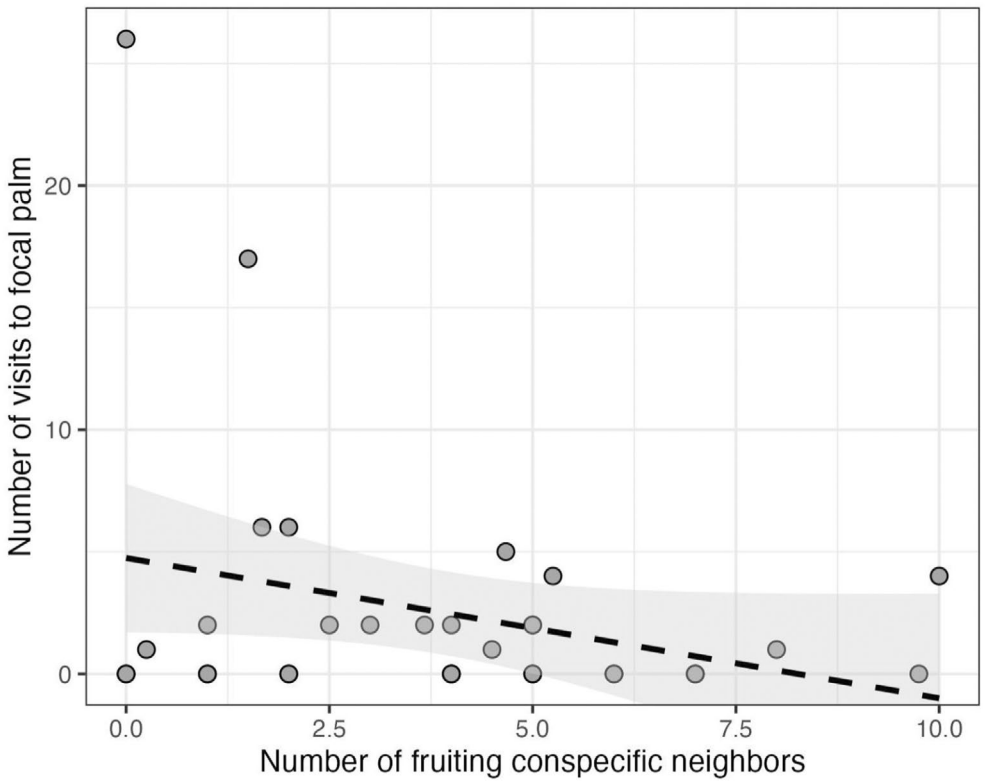


FIGURE 2 | The number of conspecific fruiting neighbors within a 35 m radius was the best predictor of frugivore visitation based on lowest AIC. The dashed line indicates a marginally nonsignificant relationship (negative binomial mixed effects model, conspecific fruiting neighborhood density: Estimate = −0.45 ± 0.26 SE, $Z = -1.71$, $p = 0.09$).

TABLE 5 | Top 3 models ranked by ascending AIC values. Null and full models are also shown; our null model was the 5th best-fit model, while our full model was 11th. The first column gives the response, subsequent columns give degrees of freedom (df), log-likelihood, AIC, delta AIC (dAIC), and model weight. See s Table S3 for a complete AIC-ranked list of models run.

	Response ~ fixed effect(s)	df	log-likelihood	AIC	dAIC	Weight
	Fruits removed~PC1 (fruit & seed size) + water	5	−89.59	189.18	0	0.16
	Fruits removed~PC1	4	−90.60	189.19	0.02	0.16
	Fruits removed~crop size	4	−90.69	189.34	0.21	0.15
Null model	Fruits removed~1	3	−91.93	189.87	0.69	0.12
Full model	Fruits removed~all fruiting neighbors + height + crop size + PC1 + pulp-to-seed ratio + water content + sucrose content	11	−85.44	192.89	3.71	0.03

TABLE 6 | Outputs of the top three models plus the null and full models examining predictors of fruits removed per frugivore visit. The first column gives AIC-based ranking, the second gives fixed effects of each model with subsequent columns showing for each: Maximum-likelihood estimate, standard error (SE), *z*-value, and *p*-value. Non-intercept fixed effects with *p*-values <0.05 are bolded. Note the full model includes conspecific neighbors and heterospecific neighbors as main fixed effects to avoid collinearity with the 'all fruiting neighbors' term, which is the sum of heterospecific + conspecific fruiting neighbors.

Response: Fruits removed per frugivore visit					
Model	**Fixed effect(s)**	**Estimate**	**SE**	***z***	***p***
1	(Intercept)	0.21	0.15	1.48	0.14
	PC1 (fruit & seed size)	0.13	0.07	1.84	0.07
	Water	−0.14	0.10	−1.44	0.15
2	(Intercept)	0.22	0.15	1.40	0.16
	PC1	0.13	0.08	1.68	0.09
3	(Intercept)	0.16	0.17	0.99	0.32
	Crop size	0.31	0.20	1.59	0.11
5 (Null)	(Intercept)	0.22	0.17	1.32	0.19
11 (Full)	(Intercept)	0.16	0.15	1.08	0.28
	Conspecific fruiting neighbors	0.22	0.19	1.14	0.26
	Heterospecific fruiting neighbors	0.23	0.42	0.55	0.58
	Height	0.51	0.27	1.89	0.06
	Crop size	**0.52**	**0.25**	**2.09**	**0.04**
	PC1	**0.22**	**0.11**	**2.13**	**0.03**
	Pulp-to-seed ratio	0.04	0.31	0.14	0.89
	Sucrose content	−0.07	0.12	−0.62	0.54
	Water content	−0.09	0.32	−0.30	0.77

Our results suggest that some frugivore-mediated competition between neighboring plants for visitation exists in our study system. This effect is what we would expect if the landscape is not particularly resource-limited in terms of fruit availability (Smith and McWilliams 2014). More specifically, the decrease in visitation that we found in response to greater fruiting neighborhood density was driven by conspecific fruiting neighbors. This apparent existence of competition for services from mutualistic partners is consistent with what we would expect if a species has a limited number of viable partners (frugivores in our case) present across the landscape (Manasse and Howe 1983; Albrecht et al. 2015). In our case, while we do not have information on the local abundances of frugivore mutualists for our focal species, our results do show that at our study site, *S. warscewiczianus* is notably limited in disperser diversity. We found only two consistent visitors: toucans and aracaris (though a single guan and a single motmot each removed one fruit during our study). The lack of an effect from heterospecific fruiting neighbors in our

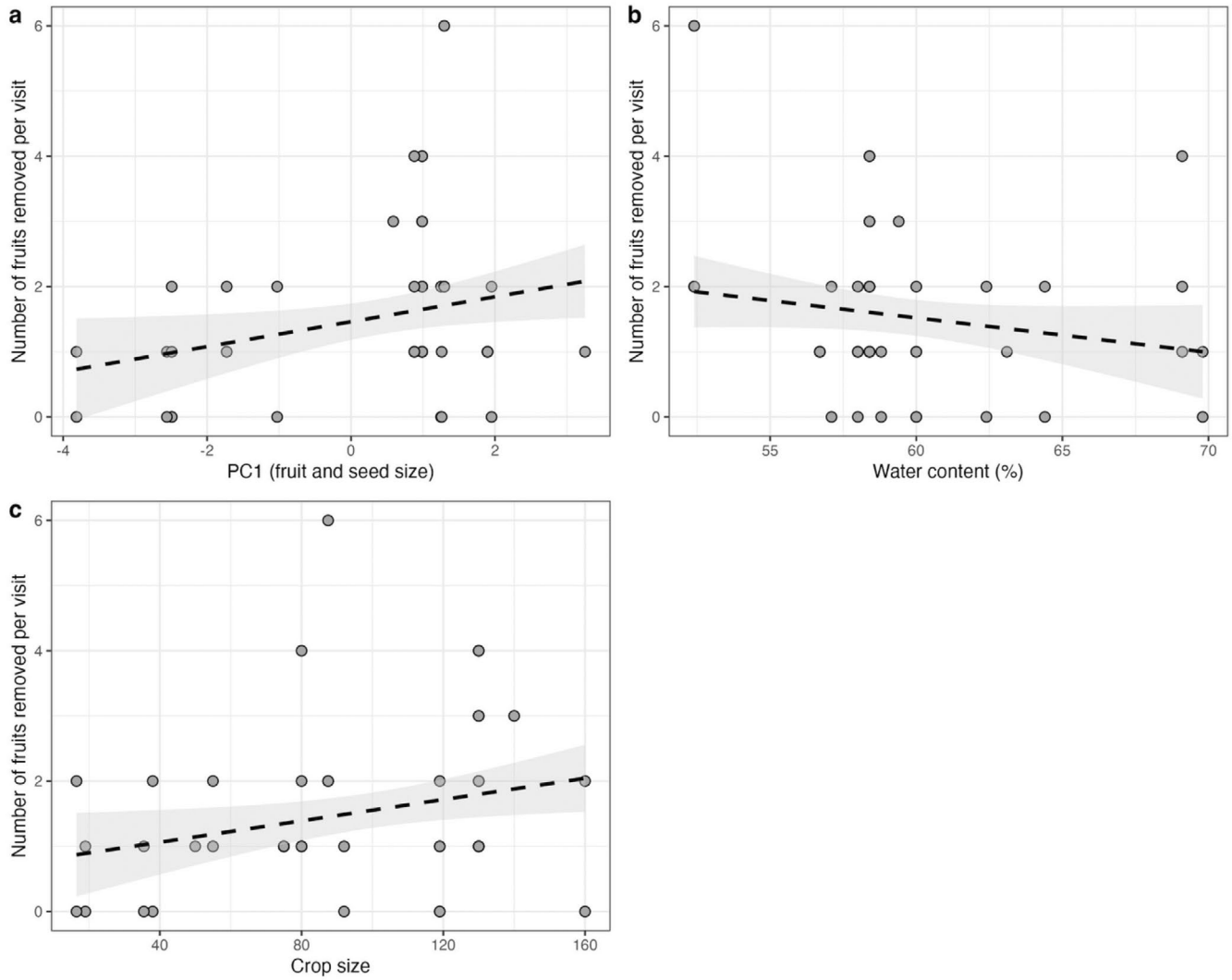


FIGURE 3 | Predictors involved in top ranked models based on AIC (Table 5). In our top model (COM-Poisson mixed effects model: Number of fruits removed ~ PC1 + water content), PC1 (fruit and seed size) showed a marginally nonsignificant relationship with fruit removal (Estimate = 0.13 ± 0.07, $Z = 1.84$, $p = 0.07$) while water content had a nonsignificant negative relationship with fruit removal (Estimate = −0.14 ± 0.10, $Z = -1.44$, $p = 0.15$). Crop size, which was the sole fixed effect in our 3rd best fit model, had a nonsignificant positive relationship with the number of fruits removed per visit (COM-Poisson mixed effects model, crop size Estimate = 0.31 ± 0.20, $Z = 1.59$, $p = 0.11$).

study could reflect low overlap between mutualistic partners between our focal species and its heterospecific neighbors or could be evidence that *S. warscewiczianus* produces more desirable fruits relative to other fruiting plants across the landscape at the time of our study.

While the relatively large-bodied frugivores documented in our study are likely to travel across much farther ranges than the 35 m scale we used in measuring the influence of fruiting neighborhoods, we note that spatial scale can greatly influence detected neighborhood effects. Related studies have examined the influence of fruiting neighborhoods on frugivory across a range of neighborhood sizes, from relatively large (100–150 m) to small (7–25 m) (Carlo and Morales 2008; Pizo and Almeida-Neto 2009; Moreira et al. 2017; Guerra et al. 2017; Hopson et al. 2020; Vissoto et al. 2022; Jayanth et al. 2024). It is possible that at different radii, the fruiting neighborhood may have different effects on frugivory, and the appropriate spatial scale to use when assessing neighborhood effects is at least partially dependent on frugivore mobility and ranges. Future studies should evaluate radii of different sizes to better understand the effects of different scales, particularly given findings such as a simulation study by Carlo and Morales (2008) which suggests nonlinear neighborhood effects and the existence of an optimal scenario for fruit removal exists, beyond which the effect of increasing neighborhood fruiting density becomes negative. Existing studies on fruiting neighborhood effects also use different criteria for inclusion in the neighborhood, such as conspecific individuals only or a suite of functionally similar plant species. This too can influence detected effects; for example, visitation to our focal species was only influenced by conspecific and not heterospecific fruiting neighbors. Lastly, we also note that neighborhood effects on visitation and fruit removal measured at the parent plant do not necessarily translate into intraspecific variation in effective seed dispersal services and successful propagation. For example, fruits removed from denser fruiting neighborhoods have been found to be dispersed shorter distances than fruits removed from more isolated plants (Morales et al. 2012). This

suggests that fruiting plants in less-dense neighborhoods benefit from greater visitation in systems such as ours and receive a higher quality and likelihood of long-distance dispersal services from frugivores.

Interestingly, in contrast to visitation, we found that traits specific to individual palms influenced how many fruits frugivores consumed during a foraging visit. Our results indicate that frugivores invested more effort in foraging at palms that had relatively larger crop sizes and larger fruit sizes. From the plant's perspective, this means individuals are being rewarded with increased seed dispersal services for investing more resources in fruit production at two scales: number of fruits produced (crop size) and the size of the fruits themselves (evidenced by PC1 and also pulp-to-seed ratio appearing in top ranked models). From the perspective of the frugivore mutualists in our system, the positive association between fruits removed during visits and the size and availability of fruits on that specific plant could mean that satiation is not the determining factor in foraging intensity. This could reflect scenarios such as low fruit availability across the landscape but could also be evidence that *S. warscewiczianus* produces fruits that are exceptionally desirable to the limited number of species that are large enough to consume it in our system.

In addition to fruit size, we found that water content could also be a determinant of fruit removal during foraging bouts. We found evidence of a potential negative relationship between water content in fruits and the number of fruits removed per visit. We posit that this could be an indication of frugivores preferring larger fruits that contain more nutrients but less unnecessary weight from the fruits' water content. Other work has also noted negative relationships between avian frugivores and fruits with higher water content (Ramos-Robles et al. 2018), similar to the present study. However, water availability in the broader landscape may change seasonally, and if water were to become a more limited resource, the negative relationship we detected between the number of fruits consumed and fruit water content would be expected to reverse. Therefore, we believe that further research on varying environmental factors as well as plant and fruit traits is needed to better understand how they influence frugivore foraging behavior across different landscapes and frugivore species.

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 (Brodie and Gibbs 2009; Markl et al. 2012). By learning more about frugivore preferences, we can better anticipate how seed dispersal will be affected by ecological disruptions. Forest fragmentation threatens many ecosystem services including seed dispersal, as smaller fragments of forest have been found to have smaller-bodied frugivores with smaller gape widths (Bovo et al. 2018). As a result, fragmented forests can lead to a loss of frugivore species diversity and a subsequent decline in plant diversity for plants that produce larger fruits. Most of the frugivores that we recorded visiting *S. warscewiczianus* were in the family *Ramphastidae*, with only two other frugivore species being represented once each. Although future studies should be conducted to better understand the frugivore community of *S. warscewiczianus*, our preliminary findings suggest that *S. warscewiczianus* fruits rely on a small range of species for seed dispersal services, making this frugivore-palm relationship specialized and vulnerable to disruption. Future studies that aim to explore the frugivore community and the palm traits that affect frugivory may want to examine the impact that different levels of disturbance may have on the plant-frugivore relationship and frugivore community, as previous studies have found different impacts across different types of disturbances as well as time passed between disturbance events (Mahoney et al. 2018; Lamperty et al. 2021; Rossi et al. 2025). Similarly, other studies should incorporate additional palm species into their study to examine how patterns of annual fruiting, differences in seasonality, and differences between understory and canopy species may affect frugivory. 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 and may be stronger drivers in frugivory.

The extent to which frugivore preferences for certain trait characteristics affect dispersal success, particularly relative to more obvious factors such as fruiting neighborhood, remains unresolved (Zhang and Wang 2024). The fruit traits we evaluated (water and sugar content, seed and fruit sizes) exhibited substantial inter- and intraindividual variation (e.g., Obeso and Herrera 1994; Zhang and Wang 2024). Our results provide additional insight into frugivore behavior and show that avian frugivores may be capable of assessing their environment to select a focal palm for foraging. However, once at their selected palm, plant- and fruit-specific traits become the most important drivers for fruit removal. These results highlight the importance of assessing multiple traits across large and small scales to understand frugivore foraging preferences.

Author Contributions

Callie Rose Chenevert: conceptualization, methodology, formal analysis, investigation, data curation, writing – original draft, visualization, fieldwork funding acquisition. **Therese Lamperty:** conceptualization, methodology, software, validation, formal analysis, writing – review and editing, supervision. **Domingo Cabrera:** methodology, investigation, data curation. **Jordan Karubian:** conceptualization, methodology, validation, resources, writing – review and editing, visualization, supervision, project administration.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and code that support the findings of this study are openly available in GitHub (https://github.com/Jlamperty/Syne-Frugs-Biotropica).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** (a) Location of study region within northwestern Ecuador highlighted by rectangle and (b) enlarged study region with 1-ha study plots outlined and focal palm locations shown. **Figure S2:**. Correlogram with Pearson correlation coefficients (given in white within boxes) of fruit and seed-related traits investigated. Orange indicates negative relationships between variables and purple indicates positive relationships. Darker shades indicate stronger relationships. **Figure S3:** Correlogram with Pearson correlation coefficients (given in white within boxes) of fruiting palm neighborhood data (i.e., co-fruiting palms within a 35 m radius of focal palms). Orange indicates negative relationships between variables and purple indicates positive relationships. Darker shades indicate stronger relationships. **Figure S4:**. Variation in neighborhood traits expected to influence frugivory, including (a) total fruiting neighborhood in a 35 m radius, (b) fruiting conspecifics in a 35 m radius, (c) fruiting heterospecifics in a 35 m radius, (d) fruiting understory palms in a 35 m radius, and (e) fruiting canopy palms in a 35 m radius. These are the averages of each value, as the number of fruiting palms sometimes varied across camera deployments. **Figure S5:**. Variation in fruit traits expected to influence frugivory, including (a) crop size estimate and (b) focal palm height. **Table S1:** Mean, standard deviation, and range for all fruit and seed traits measured from focal palms. **Table S2:**. Models compared based on AIC to test predictors of visitation to focal palms. **Table S3:** Models compared based on AIC to test predictors of fruits removed per frugivore visit to focal palms.