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ORIGINAL ARTICLE

Subannual phenology and the effect of staggered fruit ripening on dispersal competition

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Abstract

Seed dispersal mutualisms evolve in complex communities of plants and frugivorous animals, within which indirect interactions such as competition and facilitation can occur. Many tropical plants reproduce subannually in multiple episodes per year. Yet, the consequences of episodic reproduction on interactions with seed dispersers remain largely unexplored. We studied *Guarea guidonia* (Meliaceae), a subannually reproducing tree, to examine temporal variation in seed dispersal within a tropical forested landscape in the central Dominican Republic. We hypothesized that foraging by dispersers would (a) increase with daily ripe fruit set on focal trees, (b) decrease with increasing ripe fruit biomass of neighboring plants, and (c) decrease in response to the fruiting periods of other taxa at the landscape scale. Over 18 months, we tracked the phenology of 24 focal trees and quantified foraging during fruiting phases through repeated observations, simultaneously measuring seed dispersal in traps beneath isolated bird perches across the study landscape. Date was the only clear predictor of frugivore visitation, with early and late peaks in activity during the 5-month fruiting period. The midseason decline in foraging at focal trees matched a decline in *Guarea* dispersal to seed traps independently of fruit abundance. Declines in *Guarea* dispersal were inversely related to peak dispersal of higher quality lipid-rich fruiting species. Our results suggest that multiple flowering episodes and subsequent asynchronous fruit ripening of low-quality fruits can reduce competitive pressure from other higher quality fruiting species, implying that this potential bet-hedging strategy may be an overlooked factor in the evolution of subannual reproduction.

Abstract in Spanish is available with online material.

KEYWORDS
competition, Dominican Republic, frugivory, seed dispersal, subannual phenology, tropical wet forest

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1 | INTRODUCTION

Seed dispersal plays an essential role in the life history of sexually reproducing plants, with diaspore movement acting as an underlying driver of species distribution and community composition (Cain et al., 2000; Hamrick et al., 1993; Levine & Murrell, 2003). Dispersal mutualisms with frugivorous animals are the predominant mode of seed dispersal in many tropical forest ecosystems (Howe & Smallwood, 1982). To increase fitness, plants dependent on this process must attract frugivores that provide effective seed dispersal through the delivery of propagules to suitable habitats (Schupp, 1993; Schupp et al., 2010). Seed dispersal mutualisms, however, rarely occur as obligate pairwise relationships between species but instead are typically networks of interactions among many species within a community (Howe, 1984; Jordano, 1987b). Consequently, spatial and temporal variation in fruit availability often determines the outcome of seed dispersal, since the process is mediated through selective feeding behaviors by frugivores. The abundance of alternative fruit resources within plant neighborhoods leads to competition among fruiting plant species, particularly when dispersal services are limiting, or facilitation when frugivorous animals are attracted to the area (Carlo, 2005; Donoso et al., 2017). Fruiting phenology, therefore, affects both the individual and the community of fruiting species because frugivores adjust their feeding behaviors according to preference and fruit availability (Carlo et al., 2003; Naoe et al., 2018). In contrast to temperate ecosystems, where seed dispersal by frugivores is largely a discrete episodic process with annual cycles (Griz & Machado, 2001; Herrera, 1982; Stiles, 1980; Thompson & Willson, 1979), many tropical forest trees have fruits available year-round with high intra-annual fluctuation of ripe fruit availability that shapes frugivore resource selection (Carnicer et al., 2009; Gleditsch et al., 2017). Much of this variation is driven by plant taxa that reproduce in multiple episodes per year by flowering / fruiting subannually, or even continuously (Newstrom et al., 1994). While various studies have examined the role of heterospecific neighborhood fruits on frugivore-mediated competition and facilitation of seed dispersal (Gleditsch et al., 2017; Rumeu et al., 2019), few have considered how subannual reproduction influences the temporal dynamics of seed dispersal in tropical plant communities.

As a general principle, plants that produce greater quantities of flowers and seeds increase fitness by maximizing the number of propagules dispersed away from the source plant (Blendinger & Villegas, 2011; Murray, 1987; Palacio & Ordano, 2018). Higher quantities of ripe fruits are expected to increase the probability of detection and frequency of dispersal by frugivores (i.e., "the crop size hypothesis," Snow, 1971). Plants, therefore, trade-off costs of growth with the frequency and intensity of reproduction that allows for effective interactions with seed dispersers (Obeso, 2002; Ordano et al., 2017). Two alternative fruit production strategies by bird-dispersed plants have consistently been recognized in tropical forests (Howe & Estabrook, 1977; Howe & Smallwood, 1982; Janzen, 1970; McKey, 1975; Snow, 1971). On the one hand, trees that attract primarily obligate frugivores tend to have larger seeds, energy-rich fruit pulp with high lipid and protein content, lower overall fecundity, and extended periods of ripe fruit availability. On the other hand, trees that attract generalist or facultative frugivores, generally have smaller seeds, high water-content sugary fruits, and relatively high-quantity fruit yields that ripen over a short period (Howe, 1993).

The scale at which frugivorous animals perceive and travel across the landscape is a key determinant of fruit selection and seed dispersal for species that fruit simultaneously (Carlo & Morales, 2008; Morales et al., 2013). Resource tracking, an increase in consumer feeding rate with increasing resource abundance, can be driven by either (i) a numerical response where more consumers are drawn to a resource or (ii) a behavioral response where individual animals increase foraging effort relative to a particular resource (Yang et al., 2008). As predicted by optimal foraging theory, frugivores recruit to patches of high resource density and avoid areas where feeding opportunities are scarce (Blendinger et al., 2015; Reynolds, 2012; Root, 1973). At finer spatial scales, increasing fruit quantity can lead to increased visits from seed dispersers from surrounding areas (Blendinger & Villegas, 2011).

In this study, we investigated temporal variation in seed dispersal interactions between a subannually reproducing tropical tree, *Guarea guidonia* (Meliaceae), and an assemblage of resident frugivorous birds. We monitored the reproductive phenology of a marked population of fruiting trees and conducted focal observations of frugivorous bird foraging activity to test the extent to which seed dispersal depends on fruit availability at three spatial scales: (a) At the scale of individual trees, we hypothesized that the abundance of ripe fruit of the focal tree would have a positive effect on visitation rate from avian seed dispersers; (b) at the scale of neighborhoods, we hypothesized that the abundance of alternative fruit resources would have a negative effect (i.e., competitive) on visits to focal *Guarea* trees; and (c) at the landscape scale, we predicted a negative effect of alternative fruit availability beyond the neighborhood on visits to *Guarea* trees.

2 | METHODS

2.1 | Study area

The study was conducted from March 2016 to August 2017 on a private farm in the foothills of the Cordillera Central of the Dominican Republic near the town of Jarabacoa (500–625 m a.s.l.). The study area was restricted to 180 ha of a mosaic landscape containing remnant and secondary broadleaf forest fragments embedded in a matrix of other cover types, including palm (*Roystonea hispaniolana*) savannas, cattle pastures, pine (*Pinus occidentalis*) stands, and other small-scale subsistence agricultural practices. Mean annual precipitation is 1340 mm, and while winter (Jan–Feb) and summer months (Jun–Aug) are comparatively drier, there is no distinct wet or dry season and mean monthly rainfall is typically >70 mm (https://en.climate-data.org/north-america/dominican-republic/la-vega/jarabacoa-766532/). Previous surveys of this site and surrounding

areas identified 71 woody plant species—including trees, shrubs, and lianas—with nearly all native species producing fleshy fruits (Schubert unpublished). A total of 76 avian species have been documented at the site, with 48 of these known to feed on fruits based on either direct observation or reports from the literature (Table S1).

2.2 | Focal tree species & phenology

We selected *Guarea guidonia* (Meliaceae) as a focal species to investigate temporal patterns in seed dispersal. *Guarea guidonia* (hereafter "*Guarea*") is a large dioecious tree, widespread across the Caribbean and mainland Neotropics (Pennington & Clarkson, 2013). Fertilized flowers develop into lignacious, globular capsules that dehisce after 8–10 months to expose 3–4 seeds with a fleshy, red-orange aril. Seeds are in ovaloid shape, averaging 10.6 mm in length and 6.6 mm in diameter (Liogier, 1978). The fleshy aril accounts for only ~15% of the total seed dry mass and is rich in lipids (Table S2). Phenology data from other studies indicate that this species varies from annual to subannual (Carlo et al., 2003; Zimmerman et al., 2007). Subannual phenology is also well documented from other members of the genus *Guarea* (Bawa et al., 2003; Bullock et al., 1983).

We used ArcMap 10.0 (ESRI, Redlands, CA, USA) to generate 50 random sampling points over ~50 ha of riparian forest fragments, manually classified using hand-drawn polygons, based on satellite imagery (ESRI World Imagery 2016). Each point was visited March–May 2016 to search for the closest *Guarea* tree within 10 m of each point. Only reproductive trees (>12 cm in diameter at breast height [dbh]) that could be unambiguously identified as female (i.e., fruit-bearing, based on a combination of crown and ground surveys for fruit capsules) were selected for the study. Any trees with an obstructed view from surrounding dense vegetation such that <50% of the crown was visible from within 15 m of the tree were excluded. All individuals selected were marked and measured for dbh. A total of 24 female trees were marked for the study. Each tree was visited every 13–15 days (hereafter "biweekly") over an 18-month period, May 2016–October 2017, to record characteristics of reproductive phenology. Recording the presence and condition of flowers enabled us to track the number of flowering episodes and, hence, anticipate the fruit cohorts that would later mature. Observers used standardized 30-s counts to quantify reproductive characteristics in 2–3 non-overlapping sections of the crown (Koenig et al., 1994). Counts were conducted for flowers and fruits with counts performed separately for trees where both flowers and fruits were present. We differentiated among inflorescences and enumerated the number of inflorescences with at least one flower blooming, and we differentiated ripe from unripe fruits based on whether capsules had dehisced and bore at least one red, arillated seed. The seeds were probed from the fruits by birds when first dehiscing, but after several days often hung loosely from the fruits, at which point they soon fell naturally to the ground. Thus, freshly ripe fruits were distinguishable from lingering old fruits whose seeds had already been consumed or had fallen.

2.3 | Foraging observations

We sampled foraging at focal *Guarea* trees from March 18 to August 10, 2017. Observations began following the first detection of ripe fruits during the biweekly phenology censuses, and observations concluded once all mature fruits had begun to rot and had fallen from the crowns of the trees. The fruiting period was divided into four non-overlapping subperiods, each spanning approximately 5 weeks, in which each tree with ripe fruit detected in the surveys was observed once, to distribute observer effort evenly across the population during the fruiting period. Before each foraging observation, the observer quantified the number of ripe and unripe fruits to estimate the density of ripe fruits on the focal tree. Focal foraging observations proceeded with the observer seated quietly from a position 10–15 m away from the tree. Visits from all birds were recorded over the course of a 2-hr period. Observations were subdivided into alternating 30-min intervals in which the observer recorded either (a) the duration of stay of each bird (i.e., arrival and leave times) in the crown of the tree or (b) foraging behavior of individual birds (i.e., failed to remove seed, swallowed, or dropped).

2.4 | Neighborhood plot surveys

To evaluate the effect of neighborhood context on *Guarea* frugivory, we conducted two sets of surveys accompanying each focal observation to record bird and fruit abundance within 15-m radial plots around the focal tree. All stems were identified, measured, and marked at the beginning of the study. Before the foraging observation, we conducted point counts of all potential avian consumers of *Guarea*. Upon arrival at the focal tree, the observer—following a 5-min period of silence to account for potential disturbance to the area—recorded visual and auditory detections of all potentially frugivorous bird species over a 10-min period. Distance of birds from the focal tree was estimated using a rangefinder (Halo XL450, Halo Optics, New Roads, LA, USA). Given that birds detected 15–25 m from the focal tree were likely to stray into the 15-m radius plot after the 10-min count period, we also included those detections in the final analyses of local frugivorous bird abundance.

Following each observation, we conducted surveys in the 15-m circular plots around the focal tree to quantify neighborhood fruit availability. During each fruit survey, the observer surveyed the crown of each plant to quantify fruit abundance. Classification of ripe fruits varied and was based on taxon-specific criteria, including color change (e.g., from green to red/blue/black), stage of dehiscence, and presence of beak marks indicating the fruit had softened enough to be palatable to birds (e.g., *Cecropia schreberiana*). All fruit abundance surveys in neighborhood plots were conducted immediately after the avian focal observation was complete. When possible, we enumerated all fruits in view. However, in cases of exceptionally large fruit sets or plants for which the crown was partially obscured, we counted fruits in 2–3 non-overlapping sections of the crown and estimated the fruit abundance

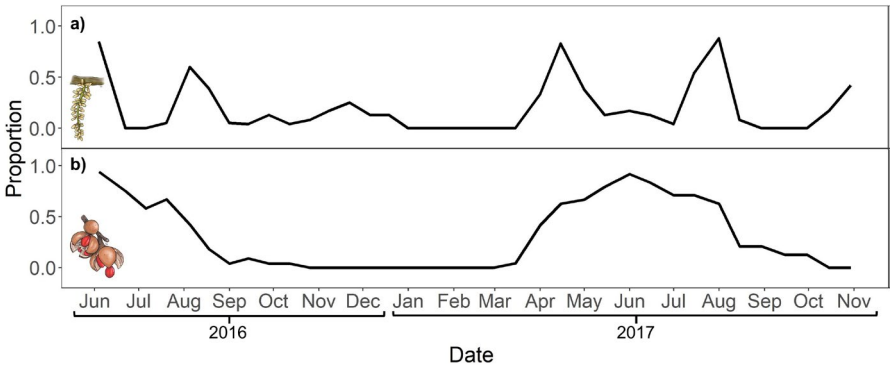

FIGURE 1 (a) Blooming flower and (b) ripe fruit phenology observed in the *Guarea* study population (24 female trees) between June 2016 and October 2017 based on the proportion of individuals displaying reproductive characteristics on each biweekly survey

using a logarithmic fruit abundance index (FAI, i.e., 1 = 1–10, 2 = 11–50, 3 = 51–100, 4 = 101–500, 5 = 501–1,000, 6 = 1,001–5,000, 7 = 5,001–10,000, 8 > 10,000) to quantify both immature and ripe fruits held by each plant (Saracco et al., 2005). To produce a plot-level metric for our analyses, we estimated fruit dry mass using species-specific measurements of these values of fruits collected from the study area and data from the literature, when samples could not be collected for certain species (Jordano, 2007). For each plot survey, we estimated the quantity of fruits by taking the median value within the FAI score range and summed these for all plants with ripe fruits, by species. Estimated totals were then converted to dry species-specific fruit pulp mass (hereafter "neighborhood fruit biomass") to account for large disparities in fruit size among taxa.

2.5 | Landscape seed dispersal patterns

To address whether landscape-level patterns of fruit availability influenced seed dispersal of focal trees, we monitored seed deposition in collection traps as a proxy measure of fruit presence and relative quantity. We deployed 20 screen traps from a PVC frame (0.5 m^2, 1 m tall, 1 mm mesh) in four pasture areas within the boundaries of the study area. Traps were placed haphazardly beneath different types of isolated perches that had no other canopy or perching structure within 10 m. Perch types included palms, dead palms, live fence trees (*Gliricidia sepium*), and mango trees (*Mangifera indica*). Traps in each field were spaced 20–60 m, and all fields were separated by at least 200 m. Seed deposition by gravity occurred only in traps set beneath *R. hispaniolana*, and these seeds were distinguished from seeds dispersed by frugivores based on whether the exocarp of the fruit was removed by digestion or was intact. We visited traps biweekly to collect the contents and enumerate seeds of all species, identified with the aid of a reference collection from the site. Previous field research from a similar agroforestry study area in Puerto Rico showed that seed quantities of most bird-dispersed plants collected from beneath isolated bird perches approximately reflect their abundance in neighboring forest patches, albeit with the most common species slightly underrepresented and some rare species relatively overrepresented (Carlo & Morales, 2016).

2.6 | Data analysis

We used an information-theoretic approach to evaluate candidate models assembled from potential predictor variables of avian frugivore activity at focal study trees. Because the data were overdispersed, we used a hurdle approach to generalized linear mixed models, fitted to a truncated Poisson distribution to evaluate the effects of predictor variables (Martin et al., 2005; Zuur et al., 2009). Hurdle models allowed for separating the process of disperser visits into two parts: (a) whether any visits occurred, and (b) the number of visits for non-zero observations. This was realized by first estimating the probability of a non-zero count, and then separately evaluating the non-zero data using a truncated count model. We considered fixed effects: day-of-year expressed in radians, focal tree ripe fruit count, and neighborhood fruit biomass with *Guarea* and heterospecific taxa considered separately. In addition to examining date with respect to the annual calendar, we considered an additional bimodal effect of date by measuring radians with an origin at the midpoint of the fruiting period recorded for *Guarea*. All models included tree / plot ID and observer ID as random effects. We ranked a priori candidate models using Akaike's information criterion (AICc) values for small sample sizes (Burnham & Anderson, 2002), and we considered all models with ΔAICc < 7 to show support (Burnham et al., 2011). Because the landscape measures of seed dispersal in collection traps were collected continuously and at a sampling frequency independent of the focal foraging observations, we relied on date-related variables in our primary analysis but interpreted their effects relative to trends in seed trap data.

We conducted a second analysis of the effects of neighborhood fruit biomass on local avian abundance. We classified birds as either *Guarea* dispersers or frugivores that do not consume *Guarea*, determined *a posteriori* (Table S1). We used generalized linear mixed models to analyze the effect of *Guarea* and heterospecific neighborhood fruit biomass on each of these two groups of birds. We considered tree / plot ID and observer ID as random factors and used a Poisson distribution. All analyses were conducted using R 3.5.1 (R Development Core Team 2021) with packages "bbmle" (Bolker, 2020) and "glmmTMB" (Magnusson et al., 2017) used for analyses and "ggplot2" (Wickham et al., 2016) used to produce figures.

3 | RESULTS

3.1 | Phenology and seed dispersers

Flowering occurred in the *Guarea* population in eight distinguishable episodes over the 18-month monitoring period (Figure 1). In 2016—the beginning of the reproductive activity that produced the 2017 fruit crop—two large flowering peaks were observed in June and August with a smaller subset of individuals flowering again October–December (Figure 1). Female trees flowered between 1 and 4 episodes in 2016, with 62.5% of trees flowering twice ($n = 24$). Fruits from the 2016 cohort first began maturing in March 2017. Time to fruit maturity from the onset of first bloom ranged from 250 to 344 days (mean 311 ± 21 [*SD*]). The duration of the ripe fruit phase ranged from 58 to 147 days (mean 110 ± 21 [*SD*]), and duration of ripe fruits on the tree was positively predicted by the number of flowering episodes (linear regression: $\beta = 15.395$, $SE = 7.276$, $t = 2.116$, $p = 0.0471$; Figure 2). The multimodal flowering pattern, however, was not reflected at the population level. Instead, we observed a single protracted period of ripe fruit availability (Figure 1).

We recorded 437 detections of 18 frugivorous bird species across all point counts. From 160 hr of foraging observations at focal trees, we recorded 344 visits from 10 frugivorous species (Table S1). Only six species were observed feeding on *Guarea* seeds, with two species feeding on seeds on only a single occasion (Figure S1). Hispaniolan Woodpeckers (*Melanerpes striatus*) were the most frequent seed dispersers at focal trees, accounting for more than half (52.1%) of visits. Black-whiskered Vireos (*Vireo altiloquus*) were the second-most frequent seed dispersers (35.7%). Seed dispersers also varied in their feeding behavior during visits to the tree. Hispaniolan Woodpeckers, Black-whiskered Vireos, and Gray Kingbirds (*Tyrannus dominicensis*) typically only consumed one seed (Figure S2). However, these species showed varying capacities as seed dispersers based on foraging behavior. For example, Hispaniolan Woodpeckers ingested as many as eight seeds in a single visit, while the maximum number of seeds consumed for Black-whiskered Vireos and Gray Kingbirds were four and two, respectively. On the contrary, we recorded only one instance of a Black-crowned Palm Tanager (*Phaenicophilus palmarum*) swallowing seed out of four occasions where we observed feeding behavior, with most foraging attempts resulting in seeds falling to the ground.

3.2 | Drivers of frugivory at focal trees

The abundance of avian frugivores that did not consume *Guarea* exhibited a positive relationship with heterospecific fruits. The best predictor of seed disperser visits, as determined by the best-supported candidate model, was bimodal date (Table 1). Foraging activity of seed dispersers was greatest at the beginning of the *Guarea* fruiting period with a second peak in the final two months (Figure 3). Seed dispersers were less likely to visit trees at the tails of the fruiting period (i.e., closer to beginning and end); however, those trees that did register at least one visit were more likely to have a greater number of visits during these subperiods (Table 2).

Contrary to expectation, we did not detect a positive effect of daily ripe fruit set of focal trees on visits by seed dispersers. The best-supported model did not contain ripe fruit density (Table 1). Similarly, neither heterospecific nor conspecific neighborhood fruit biomass was predictive of seed disperser visits. This lack of influence of neighborhood fruits on seed dispersers was further demonstrated by our findings that showed no relationship between the abundance of these species and neighborhood fruit biomass (Table 3).

3.3 | Seed dispersal & landscape fruit availability

The bimodal pattern of visit frequency by avian seed dispersers to *Guarea* trees corresponded closely with patterns of seed dispersal observed in seed traps (Figure 4). *Guarea* seed deposition in traps increased beginning in late March and peaked in mid-April before a sudden decline. A smaller peak in *Guarea* dispersal was observed in July and early August. The decline in *Guarea* seed dispersal was independent of fruit availability, since the number of trees bearing ripe fruit changed little over this period. This decline in *Guarea* seed dispersal corresponded with large peaks in *Cupania americana* and

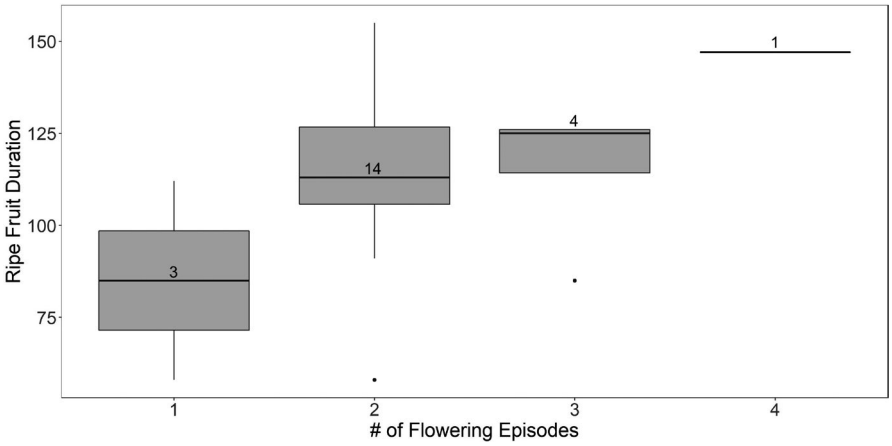

FIGURE 2 Length of the ripe fruit phase of focal trees (i.e., number of days between first and last ripe fruits observed) by flowering frequency. Boxes show interquartile ranges with median line and with vertical lines showing minimum and maximum values. Sample size for each reproduction frequency class shown above the median marker. Two outliers are shown as black dots

Ocotea coriacea, alternative fruit-bearing species fed upon by *Guarea* dispersers.

4 | DISCUSSION

Despite flowering subannually, *Guarea* trees produced ripe fruits continuously over a single extended period. The length of a particular tree's ripe fruit phase related positively to the number of prior flowering episodes, demonstrating that trees with multimodal flowering provided fruits to seed dispersers over a larger temporal window. Counter to expectation, the daily ripe fruit set of focal trees was not predictive of interactions with seed dispersers, suggesting a lack of consistent tracking of *Guarea* by seed dispersers. Even at the neighborhood scale, neither conspecific nor heterospecific ripe fruit biomass was predictive of foraging activity of seed dispersers, suggesting that resource composition did not play a large role in seed dispersal at the scales examined. While fruit availability did not show a pronounced temporal modality, disperser visits to focal trees were markedly bimodal over the fruiting period. Visits peaked late March–early April and again, to a lesser extent, in July. These patterns suggest that bird activity and seed dispersal were controlled by processes at larger spatial scales than the local or neighborhood. By examining the temporal changes in seed deposition across the landscape, our observations indicate that the most likely driver of the midseason decline in *Guarea* seed dispersal was the emergence of ripe fruits of alternative fruiting species over the landscape. Once *Ocotea coriacea* and *Cupania americana* ripened, seed dispersal of *Guarea*, both at the scale of the individual trees and landscape (i.e., in seed traps), decreased precipitously, despite the continued abundance of ripe *Guarea* fruits.

The finding that focal tree daily ripe fruit set had no effect on seed disperser visits contrasts with most field studies that show a positive relationship between tree crop size and fruit removal (Davidar & Morton, 1986; Jordano, 1987a; Ortiz-Pulido & Rico-Gray, 2000; Palacio et al., 2017). In a meta-analysis of seed dispersal field studies of 50 plant species from 27 families, Palacio and Ordano (2018) found broad support for crop size having a positive effect on both visits and fruit removal by frugivorous birds and evidence for strong selection on crop size, a trait known to be heritable (Denton

TABLE 1 AIC table with ranking and relative support of candidate models that predicted the visitation rate of seed dispersers to focal trees

Candidate Model	*k*	ΔAICc	LogLik	Weight
Day from fruit period midpoint	5	0.0	21.9	0.997
Full model	9	11.3	25.3	0.003
Focal tree-ripe fruit density	5	25.4	12.0	<0.001
Calendar day	5	26.4	11.5	<0.001
Heterospecific fruit biomass	5	26.6	11.4	<0.001
Guarea fruit biomass	5	26.7	11.3	<0.001
Intercept	4	37.6	0	<0.001

Note: Tree ID and Observer ID were included as random effects.

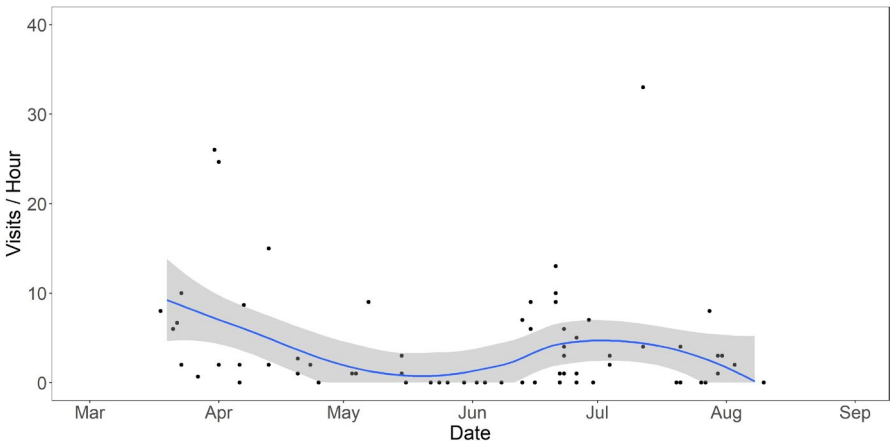

FIGURE 3 Raw data on seed disperser visits to focal trees during the 2017 fruiting period with a fitted smoothing function (loess). The shaded gray region represents standard error. Visits were most frequent in foraging observations conducted near the beginning of the fruiting period when *Guarea* trees were first observed bearing ripe fruits. Visits declined into late May and June before reaching another peak extending through July and August

TABLE 2 Top candidate model (with >99% weight) summary for visit rates of avian seed dispersers to focal study trees based on a generalized linear mixed hurdle model

	Zero-Inflated Model			Conditional Model		
Variable	Estimate	95% CI	*z*-score	Estimate	95% CI	*z*-score
Intercept	−0.080	(−1.932, 1.771)	−0.085	−0.309	(−1.022, 0.405)	−0.848
Day from fruit period midpoint	**−1.873**	**(−3.641, −0.105)**	**−2.077**	**1.1762**	**(0.674, 1.678)**	**4.594**

Note: The zero-inflated component of the model considered the binary result of all data points (i.e., whether or not any seed dispersers visited during focal observation). The conditional model considered the magnitude of the response for all non-zero data (i.e., only observations with at least one visit). Bold print indicates confidence intervals that do not include zero.

TABLE 3 Generalized linear mixed model summaries for the effect of neighborhood fruit biomass of *Guarea* and heterospecifics on *Guarea* dispersers and other frugivorous birds, respectively

	Abundance of *Guarea* Dispersers			Abundance of Other Frugivores		
Variable	**Estimate**	**95% CI**	***z*-score**	**Estimate**	**95% CI**	***z*-score**
Intercept	**0.638**	**(0.263, 1.01)**	**3.34**	**1.624**	**(1.38, 1.87)**	**13.2**
*Guarea*fruit biomass	6.80e−3	(−6.38e−3, 2.00e−2)	1.01	−2.256e−3	(−1.24e−2, 7.90e−3)	−0.435
Heterospecific fruit biomass	4.43e−4	(−2.66e−4, 1.15e−3)	1.22	**6.53e−4**	**(1.64e−4, 1.14e−3)**	**2.62**

Note: Bold print indicates confidence intervals that do not include zero.

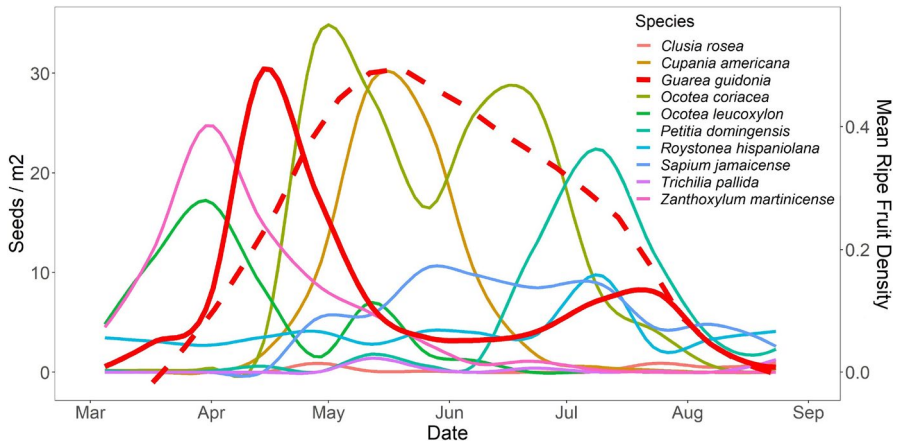

FIGURE 4 Seed quantities sampled from traps ($n = 20$) at 14-day intervals throughout the *Guarea* fruiting period. A smoothing function (loess) was applied to better visualize peaks/troughs in the seed trap data. Displayed is a subset of species known from the diet of the two most important *Guarea* seed dispersers—Hispaniolan Woodpecker and Black-whiskered Vireo. The first peak in *Guarea* dispersal is in early April, but quickly diminishes as *Ocotea coriacea* and *Cupania americana* become the most numerous seeds found in the traps. *Guarea* dispersal reaches a second, smaller peak during the month of July as these two species decline. Mean daily ripe fruit density for the *Guarea* study population is shown for reference (red dashed line) of relative *Guarea* fruit abundance in the study landscape

& Nwangburuka, 2011; Manju & Sreelathakumary, 2006; Meena & Bahadur, 2014; de Moraes et al., 2005). Phenology, however, can potentially mediate selection on crop size, where plant species with shorter fruiting periods experience stronger selection on crop size from interactions with their seed dispersers (Palacio & Ordano, 2018). When compared with plants with annual reproduction that present fruits to dispersers in a single episode, species with subannual reproduction are more likely to experience temporally variable interactions with seed dispersers, obscuring any obvious selection on crop size. Moreover, as evidenced from the *Guarea* phenology data, crop size within the same fruiting period can result from the accumulation of multiple flowering events, presumably decoupling selective pressures on flower and fruit production.

Although our analysis detected no distinguishing effects of neighborhood fruit biomass driving either facilitation of fruit removal or competition among the focal species and other fruiting plants, seed trap data implied interspecific competition among plants at larger spatial scales. There is a general lack of consensus from studies that have considered the indirect effects of plant neighbors on seed dispersal, suggesting that such effects are highly variable and context-dependent by species over space and time (Gleditsch et al., 2017; Smith & McWilliams, 2014). Some of the clearest examples of neighbor-induced competition in tropical environments come from situations in which crowded conspecific neighborhoods lead to lower per capita visits to trees (Manasse & Howe, 1983; Saracco et al., 2005). While it is possible that intraspecific competition at larger spatial scales—particularly during the middle of the fruiting season when *Guarea* is at peak fruit abundance—could have played a role in depressing foraging activities at focal trees, this dynamic would not lead to a decline of *Guarea* seeds in seed traps. Hence, the most parsimonious explanation for the reduced foraging and dispersal of *Guarea*, despite sustained ripe fruit abundance in the population, is interspecific competition.

Fruits of the genera *Guarea*, *Cupania*, and *Ocotea* all contain lipid-rich pulp (i.e., >50% nutritional content, Galetti et al., 2000; Stevenson et al., 2017). Preference for energy-rich lipid nutrients in fruit pulp by frugivorous birds is associated with metabolic demands of migratory birds (Smith & McWilliams, 2010), but it is also a preferred dietary strategy of many tropical birds to meet the high metabolic demands associated with caring for offspring at the nest (Carleton & Smith, 2016; Lamperti et al., 2014). All avian dispersers of *Guarea* at our study site were breeding residents known to feed on *Cupania americana*, *Ocotea coriacea*, *and O. leucoxylon* (Schubert and Walters unpublished). While fruits of these genera have similar lipid content and propagule

size, the per-seed pulp dry mass of *Ocotea* was 6.72 and *Cupania* 3.10 times greater than *Guarea*, respectively (Table S2). Based on seed trap data, these relative values matched the hierarchical fruit preference of these taxa at times when all three fruits were available (Figure 4). Periods of relatively high *Guarea* dispersal corresponded closely with the absence, or low abundance, of these lipid-rich taxa, suggesting that interspecific competition was mediated through resource preference. Ripe *Ocotea* and *Cupania* fruits were relatively abundant and frequent in the neighborhood plots during their respective fruiting phases, recorded at 61% and 52% of plots, respectively. However, we found no evidence that this local-scale availability affected foraging activity at focal *Guarea* trees.

The lack of facilitative or competitive effects at the scales of focal trees or plant neighborhoods is likely manifested by the comparatively stronger temporal variation in fruiting at the landscape scale for *Guarea* seed dispersers. Because *Guarea* dispersers are resident year-round, their breeding phenology implies that fruits are generally fed upon by birds that are either in the process of acquiring a breeding territory, already nesting, or provisioning food to recently fledged offspring. Consequently, frugivorous birds in our study were interacting with fruit resources over relatively confined home ranges as opposed to migratory or nomadic movements that might take place at other times of the year. Hispaniolan Woodpeckers, the most numerous seed disperser at the study site, radio-tagged for a separate study at the site spent most of their time within 800 m of their nest tree during the breeding season but occasionally moved ≥2 km (Schubert unpublished). While little information is available for Black-whiskered Vireos, the next most numerically important seed disperser, movement studies in other vireos have shown that resident vireos in forested environments can readily foray up to 2 km daily (Morton et al., 2010). This range of movement for such avian taxa is consistent with the scale of our study area and point to a generally larger scale of movement and tracking of fruits at a scale much larger than the neighborhood scale used in the present study. Curiously, the bimodal effect of date was manifested by trees with ripe fruits that were less likely to be discovered by seed dispersers early and late in the fruiting period. Trees that were attended were disproportionately more likely to recruit many frugivore visitors. Such a dynamic may suggest a positive feedback response driven by social cues among birds to locate *Guarea* fruits during times when other preferred resources are relatively scarce (Gu et al., 2017; MacDonald et al., 2019).

Previous studies have highlighted the critical role of some tropical plant taxa with protracted phenologies in sustaining frugivore populations in times of low or unpredictable fruit availability in the community (Carlo et al., 2003; Terborgh, 1986; Van Schaik et al., 1993). Extended fruit production as a reproductive strategy is hypothesized to have evolved, in part, as a result of predictable and reliable dispersal by frugivores that specialize on such fruit resources (Carlo et al., 2003; Howe & Estabrook, 1977). Our study, however, highlights apparent resource switching of frugivores from *Guarea* to other more preferred resources. We offer an alternative hypothesis for the adaptive value of extended fruit production. Rather than evolving in the context of reliable frugivore presence and fruit removal, extended fruiting could potentially serve as a form of bet hedging in landscapes where the response of frugivores is highly context-dependent in the phenology and availability of other more preferred fruit resources. By displaying few ripe fruits at any given point in time but extended over a period when other ripe fruits are available, plants with relatively inferior fruit quality may capitalize on temporally unpredictable seed dispersal services. While this bet-hedging strategy of fruit production likely has prevalent effects on tropical forest communities, we urge caution in interpreting a direct evolutionary link between frugivory and phenology, since other environmental conditions such as the presence of pollinators, solar irradiance, and precipitation likely play a large role in fruiting phenology (Van Schaik et al., 1993; Zimmerman et al., 2007). Future work, integrating both community phenology and animal seed dispersal data, especially including the applications of network analyses and long-term data sets, promises to provide a venue for more effectively integrating the various drivers of fruiting phenology.

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CONFLICT OF INTEREST

The corresponding author confirms on behalf of both authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

AUTHOR CONTRIBUTIONS

Both authors contributed to conceptualizing the study, developing methodology, funding acquisition, and writing the manuscript. SCS was responsible for fieldwork, data curation, and analyses. ELW provided oversight and resources.

ETHICAL GUIDELINES

This study was conducted in accordance with Old Dominion University's Institutional Animal Care and Use Committee (IACUC, #16-009).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.5tb2rbp48 (Schubert & Walters, 2021). Data from: Subannual

phenology and the effect of staggered fruit ripening on dispersal competition. Dryad Digital Repository. https://doi.org/10.5061/dryad.5tb2rbp48.

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REFERENCES

Bawa, K. S., Kang, H., & Grayum, M. H. (2003). Relationships among time, frequency, and duration of flowering in tropical rain forest trees. *American Journal of Botany*, *90*(6), 877–887. https://doi.org/10.3732/ajb.90.6.877

Blendinger, P. G., Giannini, N. P., Zampini, I. C., Ordoñez, R., Torres, S., Sayago, J. E., Ruggera, R. A., & Isla, M. I. (2015). Nutrients in fruits as determinants of resource tracking by birds. *Ibis*, *157*(3), 480–495. https://doi.org/10.1111/ibi.12274

Blendinger, P. G., & Villegas, M. (2011). Crop size is more important than neighborhood fruit availability for fruit removal of *Eugenia uniflora* (Myrtaceae) by bird seed dispersers. *Plant Ecology*, *212*(5), 889–899. https://doi.org/10.1007/s11258-010-9873-z

Bolker, B., & R Core Development Team (2020). bbmle: tools for general maximum likelihood estimation. *R package version 1.0.23.1*. https://CRAN.R-project.org/package=bbmle

Bullock, S. H., Beach, J. H., & Bawa, K. S. (1983). Episodic flowering and sexual dimorphism in *Guarea rhopalocarpa* in a Costa Rican rain forest. *Ecology*, *64*(4), 851–861. https://doi.org/10.2307/1937208

Burnham, K. P., & Anderson, D. R. (2002). A practical information-theoretic approach. In *Model selection and multimodel inference* (2nd ed.). Springer.

Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. (2011). AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. *Behavioral Ecology and Sociobiology*, *65*(1), 23–35. https://doi.org/10.1007/s00265-010-1029-6

Cain, M. L., Milligan, B. G., & Strand, A. E. (2000). Long-distance seed dispersal in plant populations. *American Journal of Botany*, *87*(9), 1217–1227. https://doi.org/10.2307/2656714

Carleton, S. A., & Smith, K. G. (2016). Adult nest attendance and diet of nestling Resplendent Quetzals (*Pharomachrus mocinno*) in the Talamanca Mountains of southern Costa Rica. *Ornitología Neotropical*, *27*, 181–188.

Carlo, T. A. (2005). Interspecific neighbors change seed dispersal pattern of an avian-dispersed plant. *Ecology*, *86*(9), 2440–2449. https://doi.org/10.1890/04-1479

Carlo, T. A., Collazo, J. A., & Groom, M. J. (2003). Avian fruit preferences across a Puerto Rican forested landscape: Pattern consistency and implications for seed removal. *Oecologia*, *134*(1), 119–131. https://doi.org/10.1007/s00442-002-1087-1

Carlo, T. A., & Morales, J. M. (2008). Inequalities in fruit-removal and seed dispersal: Consequences of bird behaviour, neighbourhood density and landscape aggregation. *Journal of Ecology*, *96*(4), 609–618. https://doi.org/10.1111/j.1365-2745.2008.01379.x

Carlo, T. A., & Morales, J. M. (2016). Generalist birds promote tropical forest regeneration and increase plant diversity via rare-biased seed dispersal. *Ecology*, *97*(7), 1819–1831. https://doi.org/10.1890/15-2147.1

Carnicer, J., Jordano, P., & Melián, C. J. (2009). The temporal dynamics of resource use by frugivorous birds: A network approach. *Ecology*, *90*(7), 1958–1970. https://doi.org/10.1890/07-1939.1

Davidar, P., & Morton, E. S. (1986). The relationship between fruit crop sizes and fruit removal rates by birds. *Ecology*, *67*(1), 262–265. https://doi.org/10.2307/1938529

de Moraes, M. C., Geraldi, I. O., de Pina Matta, F., & Vieira, M. L. C. (2005). Genetic and phenotypic parameter estimates for yield and fruit quality traits from a single wide cross in yellow passion fruit. *HortScience*, *40*(7), 1978–1981. https://doi.org/10.21273/HORTSCI.40.7.1978

Denton, O. A., & Nwangburuka, C. C. (2011). Heritability, genetic advance and character association in six yield related characters of *Solanum anguivi*. *Asian Journal of Agricultural Research*, *5*(3), 207. https://doi.org/10.3923/ajar.2011.201.207

Donoso, I., García, D., Martínez, D., Tylianakis, J. M., & Stouffer, D. B. (2017). Complementary effects of species abundances and ecological neighborhood on the occurrence of fruit-frugivore interactions. *Frontiers in Ecology and Evolution*, *5*, 133. https://doi.org/10.3389/fevo.2017.00133

Galetti, M., Laps, R., & Pizo, M. A. (2000). Frugivory by toucans (Ramphastidae) at two altitudes in the Atlantic Forest of Brazil. *Biotropica*, *32*(4b), 842–850.

Gleditsch, J. M., Hruska, A. M., & Foster, J. T. (2017). Connecting resource tracking by frugivores to temporal variation in seed dispersal networks. *Frontiers in Ecology and Evolution*, *5*, 98. https://doi.org/10.3389/fevo.2017.00098

Griz, L. M. S., & Machado, I. C. S. (2001). Fruiting phenology and seed dispersal syndromes in caatinga, a tropical dry forest in the northeast of Brazil. *Journal of Tropical Ecology*, *17*(2), 303–321. https://doi.org/10.1017/S0266467401001201

Gu, H., Chen, J., Ewing, H., Liu, X., Zhao, J., & Goodale, E. (2017). Heterospecific attraction to the vocalizations of birds in mass-fruiting trees. *Behavioral Ecology and Sociobiology*, *71*(5), 82. https://doi.org/10.1007/s00265-017-2312-6

Hamrick, J. L., Murawski, D. A., & Nason, J. D. (1993). The influence of seed dispersal mechanisms on the genetic structure of tropical tree populations. *Vegetatio*, *107*(1), 281–297.

Herrera, C. M. (1982). Seasonal variation in the quality of fruits and diffuse coevolution between plants and avian dispersers. *Ecology*, *63*(3), 773–785. https://doi.org/10.2307/1936798

Howe, H. F. (1984). Constraints on the evolution of mutualisms. *American Naturalist*, *123*(6), 764–777. https://doi.org/10.1086/284238

Howe, H. F. (1993). Specialized and generalized dispersal systems: Where does 'the paradigm' stand? *Vegetatio*, *107*(1), 3–13.

Howe, H. F., & Estabrook, G. F. (1977). On intraspecific competition for avian dispersers in tropical trees. *American Naturalist*, *111*(981), 817–832. https://doi.org/10.1086/283216

Howe, H. F., & Smallwood, J. (1982). Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, *13*, 201–228. https://doi.org/10.2307/2097067

Janzen, D. H. (1970). Herbivores and the number of tree species in tropical forests. *American Naturalist*, *104*(940), 501–528. https://doi.org/10.1086/282687

Jordano, P. (1987a). Avian fruit removal: Effects of fruit variation, crop size, and insect damage. *Ecology*, *68*(6), 1711–1723. https://doi.org/10.2307/1939863

Jordano, P. (1987b). Patterns of mutualistic interactions in pollination and seed dispersal: Connectance, dependence asymmetries, and coevolution. *American Naturalist*, *129*(5), 657–677. https://doi.org/10.1086/284665

Jordano, P. (2007). The FRUBASE page. http://pedroj.github.io/FRUBASE/

Koenig, W. D., Knops, J. M., Carmen, W. J., Stanback, M. T., & Mumme, R. L. (1994). Estimating acorn crops using visual surveys. *Canadian Journal of Forest Research*, *24*(10), 2105–2112. https://doi.org/10.1139/x94-270

Lamperti, A. M., French, A. R., Dierenfeld, E. S., Fogiel, M. K., Whitney, K. D., Stauffer, D. J., Holbrook, K. M., Hardesty, B. D., Clark, C. J., Poulsen, J. R., Wang, B. C., Smith, T. B., & Parker, V. T. (2014). Diet selection is related to breeding status in two frugivorous hornbill species of Central Africa. *Journal of Tropical Ecology*, *30*(4), 273–290. https://doi.org/10.1017/S0266467414000236

Levine, J. M., & Murrell, D. J. (2003). The community-level consequences of seed dispersal patterns. *Annual Review of Ecology, Evolution, and Systematics*, *34*(1), 549–574. https://doi.org/10.1146/annurev.ecolsys.34.011802.132400

Liogier, A. H. (1978). *Arboles Dominicanos*. Academia de Ciencias de la República Dominicana.

MacDonald, S. E., Ward, M. P., & Sperry, J. H. (2019). Manipulating social information to promote frugivory by birds on a Hawaiian Island. *Ecological Applications*, *29*(7), e01963. https://doi.org/10.1002/eap.1963

Magnusson, A., Skaug, H., Nielsen, A., Berg, C., Kristensen, K., Maechler, M., van Bentham, K., Bolker, B., Brooks, M., & Brooks, M. M. (2017). Package 'glmmTMB.' R Package Version 1.0.2.1.

Manasse, R. S., & Howe, H. F. (1983). Competition for dispersal agents among tropical trees: Influences of neighbors. *Oecologia*, *59*(2–3), 185–190. https://doi.org/10.1007/BF00378836

Manju, P. R., & Sreelathakumary, I. (2006). Quality parameters in hot chilli (*Capsicum chinense* Jacq.). *Journal of Tropical Agriculture*, *40*, 7–10.

Martin, T. G., Wintle, B. A., Rhodes, J. R., Kuhnert, P. M., Field, S. A., Low-Choy, S. J., Tyre, A. J., & Possingham, H. P. (2005). Zero tolerance ecology: Improving ecological inference by modelling the source of zero observations. *Ecology Letters*, *8*(11), 1235–1246. https://doi.org/10.1111/j.1461-0248.2005.00826.x

McKey, D. B. (1975). The ecology of coevolved seed dispersal systems. In L. E. Gilbert, & P. H. Raven (Eds.), *Coevolution of Animals and Plants* (pp. 159–191). University of Texas Press.

Meena, O. P., & Bahadur, V. (2014). Assessment of genetic variability, heritability and genetic advance among tomato (*Solanum lycopersicum* L.) germplasm. *Bioscan*, *9*(4), 1619–1623.

Morales, J. M., García, D., Martínez, D., Rodriguez-Pérez, J., & Herrera, J. M. (2013). Frugivore behavioural details matter for seed dispersal: A multi-species model for Cantabrian thrushes and trees. *PLoS One*, *8*(6), e65216. https://doi.org/10.1371/journal.pone.0065216

Morton, E. S., Stutchbury, B. J., & Chiver, I. (2010). Parental conflict and brood desertion by females in blue-headed vireos. *Behavioral Ecology and Sociobiology*, *64*(6), 947–954. https://doi.org/10.1007/s00265-010-0910-7

Murray, K. G. (1987). Selection for optimal fruit-crop size in bird-dispersed plants. *American Naturalist*, *129*(1), 18–31. https://doi.org/10.1086/284620

Naoe, S., Masaki, T., & Sakai, S. (2018). Effects of temporal variation in community-level fruit abundance on seed dispersal by birds across woody species. *American Journal of Botany*, *105*(11), 1792–1801. https://doi.org/10.1002/ajb2.1173

Newstrom, L. E., Frankie, G. W., & Baker, H. G. (1994). A new classification for plant phenology based on flowering patterns in lowland tropical rain forest trees at La Selva, Costa Rica. *Biotropica*, 141–159. https://doi.org/10.2307/2388804

Obeso, J. R. (2002). The costs of reproduction in plants. *New Phytologist*, *155*(3), 321–348. https://doi.org/10.1046/j.1469-8137.2002.00477.x

Ordano, M., Blendinger, P. G., Lomáscolo, S. B., Chacoff, N. P., Sánchez, M. S., Núñez Montellano, M. G., Jiménez, J., Ruggera, R. A., & Valoy, M. (2017). The role of trait combination in the conspicuousness of fruit display among bird-dispersed plants. *Functional Ecology*, *31*(9), 1718–1727. https://doi.org/10.1111/1365-2435.12899

Ortiz-Pulido, R., & Rico-Gray, V. (2000). The effect of spatio-temporal variation in understanding the fruit crop size hypothesis. *Oikos*, *91*(3), 523–527. https://doi.org/10.1034/j.1600-0706.2000.910314.x

Palacio, F. X., & Ordano, M. (2018). The strength and drivers of bird-mediated selection on fruit crop size: A meta-analysis. *Frontiers in Ecology and Evolution*, *6*, 18. https://doi.org/10.3389/fevo.2018.00018

Palacio, F. X., Valoy, M., Bernacki, F., Sanchez, M. S., Núñez-Montellano, M. G., Varela, O., & Ordano, M. (2017). Bird fruit consumption results from the interaction between fruit-handling behaviour and fruit crop size. *Ethology Ecology & Evolution*, *29*(1), 24–37. https://doi.org/10.1080/03949370.2015.1080195

Pennington, T. D., & Clarkson, J. J. (2013). A revision of *Guarea* (Meliaceae). *Edinburgh Journal of Botany*, *70*(2), 179–362.

R Core Team (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Reynolds, A. M. (2012). Fitness-maximizing foragers can use information about patch quality to decide how to search for and within patches: Optimal Lévy walk searching patterns from optimal foraging theory. *Journal of the Royal Society Interface*, *9*(72), 1568–1575. https://doi.org/10.1098/rsif.2011.0815

Root, R. B. (1973). Organization of a plant-arthropod association in simple and diverse habitats: The fauna of collards (*Brassica oleracea*). *Ecological Monographs*, *43*(1), 95–124. https://doi.org/10.2307/1942161

Rumeu, B., Álvarez-Villanueva, M., Arroyo, J. M., & González-Varo, J. P. (2019). Interspecific competition for frugivores: Population-level seed dispersal in contrasting fruiting communities. *Oecologia*, *190*(3), 605–617. https://doi.org/10.1007/s00442-019-04434-9

Saracco, J. F., Collazo, J. A., Groom, M. J., & Carlo, T. A. (2005). Crop size and fruit neighborhood effects on bird visitation to fruiting *Schefflera morototoni* trees in Puerto Rico. *Biotropica*, *37*(1), 81–87. https://doi.org/10.1111/j.1744-7429.2005.04040.x

Schubert, S. C., & Walters, E. L. (2021). Data from: Subannual phenology and the effect of staggered fruit ripening on dispersal competition. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.5tb2rbp48

Schupp, E. W. (1993). Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio*, *107/108*, 15–29.

Schupp, E. W., Jordano, P., & Gómez, J. M. (2010). Seed dispersal effectiveness revisited: A conceptual review. *New Phytologist*, *188*(2), 333–353. https://doi.org/10.1111/j.1469-8137.2010.03402.x

Smith, A. D., & McWilliams, S. R. (2014). Fruit removal rate depends on neighborhood fruit density, frugivore abundance, and spatial context. *Oecologia*, *174*(3), 931–942. https://doi.org/10.1007/s00442-013-2834-1

Smith, S. B., & McWilliams, S. R. (2010). Patterns of fuel use and storage in migrating passerines in relation to fruit resources at autumn stopover sites. *The Auk*, *127*(1), 108–118. https://doi.org/10.1525/auk.2009.09139

Snow, D. W. (1971). Evolutionary aspects of fruit-eating by birds. *Ibis*, *113*(2), 194–202. https://doi.org/10.1111/j.1474-919X.1971.tb05144.x

Stevenson, P. R., Cardona, L. M., Acosta-Rojas, D. C., Henao-Diaz, F., & Cárdenas, S. (2017). Diet of oilbirds (*Steatornis caripensis*) in Cueva de Los Guacharos National Park (Colombia): Temporal variation in fruit consumption, dispersal, and seed morphology. *Ornitología Neotropical*, *28*, 295–307.

Stiles, E. W. (1980). Patterns of fruit presentation and seed dispersal in bird-disseminated woody plants in the eastern deciduous forest. *American Naturalist*, *116*(5), 670–688. https://doi.org/10.1086/283657

Terborgh, J. (1986). Community aspects of frugivory in tropical forests. *Frugivores and seed dispersal* (pp. 371–384). Dr. W. Junk Publishers.

Thompson, J. N., & Willson, M. F. (1979). Evolution of temperate fruit/bird interactions: Phenological strategies. *Evolution*, *33*(3), 973–982. https://doi.org/10.1111/j.1558-5646.1979.tb04751.x

Van Schaik, C. P., Terborgh, J. W., & Wright, S. J. (1993). The phenology of tropical forests: Adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics*, *24*(1), 353–377. https://doi.org/10.1146/annurev.es.24.110193.002033

Wickham, H., Chang, W., & Wickham, M. H. (2016). Package 'ggplot2.' *Create Elegant Data Visualisations Using the Grammar of Graphics*. *R Package Version* 3.3.2.

Yang, L. H., Bastow, J. L., Spence, K. O., & Wright, A. N. (2008). What can we learn from resource pulses. *Ecology*, *89*(3), 621–634. https://doi.org/10.1890/07-0175.1

Zimmerman, J. K., Wright, S. J., Calderón, O., Pagan, M. A., & Paton, S. (2007). Flowering and fruiting phenologies of seasonal and aseasonal neotropical forests: The role of annual changes in irradiance. *Journal of Tropical Ecology*, *23*(2), 231–251. https://doi.org/10.1017/S0266467406003890

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). Zero-truncated and zero-inflated models for count data. In *Mixed effects models and extensions in ecology with R* (pp. 261–293). Springer.

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