



Individual fruit and crop size effects on seed dispersal differ between plant species offering contrasting rewards

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Abstract

Intraspecific variation in plant traits, such as crop and fruit sizes, can affect frugivore attractiveness to individuals, ultimately influencing plant fitness. Different nutritional rewards offered by plants may attract different sets of seed dispersers, but we know little about how these differences can translate into dispersal effectiveness. Because seed dispersal interactions occur at the individual-level, downscaling from species to individual-based networks may help us link individual traits to plant fitness. Here, we tested whether crop and fruit sizes affected interactions between plant individuals and bird species using individual-based networks for two plant species offering contrasting nutritional rewards: the lipid-rich *Xylopia aromatica* and carbohydrate-rich *Miconia rubiginosa*. To this end, we sampled bird-fruit interactions in 10 individuals per plant species, representing a gradient of crop and fruit sizes in southeast Brazil. Then, we linked those traits to species-level network metrics, number of visits and quantitative effectiveness to examine their influence on seed dispersal. *Miconia* trees with larger fruit crops were more connected and attained higher quantitative effectiveness than trees with smaller fruit crops, whereas for *Xylopia*, trees producing larger fruits showed lower per capita fruit removal. Our findings suggest that traits that shape the selective pressures exerted by frugivores differ among plant species.

Keywords Fitness · Frugivory degree · Individual-based networks; normalized degree · Quantitative effectiveness · Weighted closeness

Introduction

Seed dispersal mediated by frugivores is a crucial ecological process for the persistence of plant populations and communities and to sustaining ecosystem functions (Christian 2001; Rogers et al. 2021). In this mutualistic interaction, frugivores benefit from the edible fruit pulp, while plants rely on animals to disperse their seeds across the landscape. The likelihood and outcomes of these interactions are shaped by both plant and animal traits (Donatti et al. 2011; Mello et al. 2015; Campagnoli et al. 2025). Among plants, individuals usually vary in traits that influence detectability and attractiveness to frugivores, such as crop and fruit sizes (Schupp et al. 2019; Palacio 2019; Vissoto et al. 2022), which may ultimately affect individual plant fitness and population dynamics (Schupp 1995; Jordano 2000).

Larger fruit crop sizes are expected to attract a more abundant and diverse assemblage of frugivores and seed dispersers, as predicted by the fruit crop size hypothesis (Snow 1971). Larger fruit crops would represent a conspicuousness signal that increases fruit detectability and, consequently,

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are a target of animal-mediated fruit selection (Palacio and Ordano 2018). Another plant trait that is expected to influence fruit choices by frugivores is fruit size. Frugivores may visit plants with larger fruits more frequently, maximizing their energy intake, as these fruits offer a greater amount of reward (optimal foraging theory; Pyke et al. 1977). Ultimately, attracting a more abundant and diverse assemblage of dispersers is likely to result in more seeds reaching different microhabitats, generating positive outcomes for recruitment and, consequently, plant fitness (Palacio and Ordano 2018; Isla et al. 2024). Therefore, animal-mediated selection on plant traits potentially acts as a strong evolutionary force, likely favoring certain traits over others.

The strength of selection on plant traits likely depends on various ecological filters (Palacio and Ordano 2018), among them the nutritional reward type displayed by plant species. For instance, plants producing carbohydrate-rich fruits tend to be more attractive to birds that have a higher fraction of their diets composed of fruit (i.e., more frugivorous birds), whereas plant species producing lipid-rich fruits attract frugivorous and also primarily insectivorous birds that opportunistically feed on fruits (Pizo et al. 2021). By attracting more frugivorous birds, plants producing carbohydrate-rich fruits are likely to interact with an assemblage of more functionally equivalent disperser species, intensifying the selection pressure on plant traits, as functionally equivalent species tend to exert similar selective forces (i.e., functional equivalence hypothesis; Palacio and Ordano 2018). Therefore, plant species mostly attracting frugivorous birds may face consistent and directional trait selection due to the similar ecological selectivity imposed by functionally equivalent dispersers. Conversely, plant species visited by a broader range of dispersers (including frugivorous and insectivorous birds) may experience more variable selection due to the greater diversity in disperser traits and behavior.

Although a considerable number of seed dispersal studies use interaction networks at the species-level to understand this ecological function (Donatti et al. 2011; Mello et al. 2015; Schleuning et al. 2015; García et al. 2018), interactions actually take place between plant and animal individuals, rather than species (Bolnick et al. 2011; Clark et al. 2011). Therefore, understanding how traits shape interactions between individual partners is key to unraveling the role of mutualisms in shaping ecological and evolutionary patterns (Bolnick et al. 2011; Quintero et al. 2025). Consequently, a growing number of studies have been focusing on downscaling from species- to individual-based approaches in seed dispersal ecology, as a way of linking plant individual traits to seed dispersal success (i.e., plant fitness) (Guerra et al. 2017; Crestani et al. 2019; Friedemann et al. 2022; Vissoto et al. 2022). However, these studies typically focus on a single plant species, or on plant species sharing

common traits (Blendinger et al. 2008; but see Rehling et al. 2021), whereas different effects of plant traits on bird-mediated selection could emerge across plant species with intrinsic differences, such as nutritional rewards. If the responses of seed dispersers to individual plant traits influence seed dispersal, those traits may be used to guide conservation strategies aiming to conserve the species participating in interactions and, at the same time, the ecological processes they sustain (Valiente-Banuet et al. 2015).

Here, our goal was to understand whether crop and fruit sizes affected interactions between plant individuals and bird species using individual-based networks for two plant species offering contrasting nutritional rewards, the lipid-rich *Xylopia aromatica* and the carbohydrate-rich *Miconia rubiginosa*. To this end, we sampled interactions of birds visiting different plant individuals, representing a gradient of crop and fruit sizes within species. Moreover, because relying solely on the number of interactions between birds and plant individuals is often not enough to estimate the functional outcome of interactions (e.g., Morán-López et al. 2020), we used quantitative effectiveness (Schupp 1993; Schupp et al. 2010) to estimate the amount of seeds effectively dispersed away from the plant crown, which is linked to potential plant fitness (Palacio et al. 2023). We hypothesized that trees (in particular the carbohydrate-rich species) with larger fruits and producing larger crops would increase plant attractiveness and, hence, would interact with more frugivore species, would be more connected in the network, and would have higher quantitative effectiveness, compared to trees with smaller fruits and crops. If this holds true, trees with larger crop and fruit sizes may be the priority to conserve seed-dispersal interactions in plant populations. Finally, we expect bird level of frugivory (i.e., the percentage of bird dependence on fruits) to influence the quantitative effectiveness of seed dispersal, particularly for the carbohydrate-rich plant species.

Methods

Study area and system

The study was conducted from January to June 2019 at the Estação Experimental de Itirapina (22°12'S, 47°51'W), a ca. 200 ha tropical savanna (Cerrado) fragment, located in São Paulo State, Southeast Brazil. Mean annual rainfall and temperature are ca. 1,459 mm and 21.9 °C, respectively. Climate is characterized by a rainy season from October to March and a dry season from April to September. The fragment is covered by Cerrado, a tropical savanna that grows on nutrient poor and well-drained soils and with most plant species resistant to fire. About 62% of trees and shrubs

found in the study area depend on animals for seed dispersal (Mariano et al. 2019) and at least 231 species of birds occur in the surroundings, many of them consuming fruits regularly (e.g., Guans, Tanagers and Euphonias) or opportunistically (e.g., many Flycatchers) (Motta-Junior et al. 2008). More information about the floristics of the study site can be found in Mariano et al. (2019).

We chose two plant species, *Xylopia aromatica* (Lam.) Mart. (Annonaceae) and *Miconia rubiginosa* (Bonpl.) DC (Melastomataceae) (hereafter *Xylopia* and *Miconia*, respectively), which are amongst the most common tree species in the study site (Mariano et al. 2019; Figure S1). Trees of *Xylopia* (2–6 m in height) produce smaller crops (mean $\pm$ SD: $3,554 \pm 770$ seeds) and fruits ripe asynchronously. Ripe *Xylopia* fruits have on average 15 follicles, exposing a pinkish interior containing about 60 arylated seeds, an average of 5 seeds per follicle (Figure S1a). *Xylopia* seeds (dry weight ranging from 24.9 to 41.1 mg) have a bluish tone and present an aril rich in lipids (sugar content = 50.3%, lipid content = 32.9%, retrieved from Christianini and Oliveira 2010). Trees of *Miconia* (2–7 m in height) produce large crops of > 100,000 purple fleshy berries (dry weight ranging from 8 to 29.5 mg), arranged in infructescences (Figure S1b). *Miconia* fruits are rich in carbohydrates (sugar content: 87.3%, lipids: 2.8%, retrieved from Christianini and Oliveira 2009) and contain on average 20 ± 5 seeds (Campagnoli et al. 2025). Fruiting of *Xylopia* and *Miconia* occurs approximately between March and June, and January and April, respectively, and both species are attractive to birds, their primary seed dispersers (Christianini and Oliveira 2009, 2010).

Crop size and fruit weight

We selected 10 plant individuals from each plant species. To ensure spatial independence, plant individuals were at least 10 m apart from one another, and we haphazardly selected individuals amongst those with the most exposed crowns to facilitate fruit crop size estimations and observations of bird visitors. We estimated total fruit crop sizes and ripe fruit crop sizes for each plant individual. Total fruit crop sizes were estimated once at the beginning of the fruiting season of each plant species (i.e., March for *Xylopia* and January for *Miconia*), considering all produced fruits (i.e., ripe and unripe), while ripe fruit crop sizes were estimated once based on the amount of ripe fruits falling beneath plant canopies at the end of the fruiting season (Campagnoli and Christianini 2022).

For each *Xylopia* tree, we estimated fruit crop size by counting the number of fruits in the plant crown, multiplying it by the average number of follicles per fruit (obtained from 30 fruits belonging to six trees), and then multiplying

it by the average number of seeds inside the follicles. The average number of seeds inside the follicles were obtained by counting the number of scars left by the seeds inside a sample of follicles from each tree. For *Xylopia*, each arillate seed is a diaspore, and fruit crop size equals the number of arillate seeds (i.e., diaspores) produced per tree. For each *Miconia* tree, we estimated fruit crop size by counting the number of infructescences with fruits in the plant crown and multiplying them by the average number of fruits contained in 3 to 4 infructescences haphazardly sampled in the same tree. For *Miconia*, each diaspore is a fruit, and fruit crop size equals the number of fruits produced per tree.

To obtain ripe fruit crop sizes, we first calculated the proportion of ripe fruits available for each plant individual for the entire fruiting season by installing 3–4 seed traps underneath the plant canopy. The traps consisted of 0.11–0.15 m² plastic trays lined with 0.2-mm nylon mesh and positioned 20 cm above the ground on four supporting stakes. To prevent ants from removing fruits, each stake was coated with a sticky resin (Tanglefoot). The proportion of fruits ripe, unripe, predated and dropped by primary seed dispersers were estimated based on the amount of fruits from each category reaching the traps at the end of the fruiting season. We then multiplied estimated total crop sizes by the proportion of ripe fruits to obtain an estimate of ripe fruit crop sizes. This measure is a conservative estimate of the actual number of ripe fruits, given that some were removed by primary dispersers from the plant canopy (Campagnoli and Christianini 2022). However, the measure provides a minimum estimate for the number of ripe fruits produced per tree. For *Xylopia*, we only had these data for 8 individuals. To estimate the average diaspore weight per tree, we measured the dry weight of 5–40 fruits for each of ten *Miconia* trees and 4–15 arillate seeds for each of nine *Xylopia* trees. For simplicity, diaspores of *Xylopia* and *Miconia* will hereafter be referred to as fruits.

Focal observations and quantitative effectiveness

We performed focal observations of bird visitors to the same plant individuals in which we estimated crop sizes and fruit weights. Focal observations were performed through all the fruiting season of both plant species, with most sampling hours concentrated at the peak of ripe fruit production (April and March for *Xylopia* and *Miconia* respectively; Table S1). We selected focal individuals each month based on which trees had ripe fruits at that time. Because some individuals exhibited earlier or later ripening than the population peak, they were observed at the beginning or end of the season accordingly. The observations were performed at dawn and dusk, 16 h per tree, totaling 320 h of observations (160 h per species).

During focal observations, we recorded all bird visitors identifying bird species and recording the number of seeds removed, dropped and carried per visit. For *Miconia*, we recorded the number of fruits removed, dropped and carried per visit, and then multiplied it by the average number of seeds contained in fruits. The number of visits to each plant individual was measured as the number of bird individuals visiting each tree and interacting with fruits. We considered a visit every time a bird interacted with a fruit, even when the outcome was not favorable to seed dispersal, i.e., when birds only consumed the pulp and/or dropped the fruits and seeds beneath the plant canopy. We calculated quantitative effectiveness of seed dispersal received by each plant individual belonging to each plant species as the total number of bird visits received during observations multiplied by the average number of seeds removed per visit by all bird species. Furthermore, to understand the role of bird species to overall quantitative effectiveness of plant species, we calculated quantitative effectiveness provided for plant species by each bird species. This number was given by the total number of visits a bird species made to each plant species, multiplied by the average number of seeds they removed per visit. It is worth mentioning that fruit removal is generally considered a reliable proxy for estimating plant fitness (Palacio et al. 2023).

To understand the contributions of each plant individual and bird species to quantitative effectiveness, we built three effectiveness landscapes per plant species (Schupp et al. 2010) with the number of visits in the X-axis and the number of seeds dispersed per visit in the Y-axis. The first two landscapes accounted for the effects of crop size and fruit weight on plant-level effectiveness. Because we expected the bird level of dependence on fruits to affect quantitative effectiveness, the third landscape accounted for bird contributions considering their frugivory level (i.e., the percentage of the bird diet composed of fruits, retrieved from Wilman et al. 2014). Because species of the genus *Elaenia* are difficult to distinguish in the field, we grouped them together and used the average frugivory level of species recorded at the study site.

Individual-based networks

We built two individual-based plant-frugivore networks, one for each plant species, linking the individual trees with the bird species visiting them. Each individual-based network was represented by an adjacency matrix $A = [a_{ij}]$, where a_{ij} indicates the number of visits recorded between bird species i and plant individual j . Then, for each individual-based network, we calculated the normalized degree of each plant individual as a measure of its interaction richness. Specifically, the normalized degree was calculated as the number

of bird species a plant individual interacted with, divided by the total number of bird species in the individual-based network. Normalized degree varies from 0 to 1, and values closer to 1 represent plant individuals visited by a larger number of bird species. In addition, we used weighted closeness centrality as a measure of plant individual centrality. Specifically, closeness centrality estimates the distance of a node to all other nodes in the network, giving an idea of how connected each node is to other nodes in the network and hence their influence within the network. Weighted closeness is a variation of closeness that accounts for the strength of connections in a weighted network. Weighted closeness varies from 0 to 1, with values closer to 1 representing more central plant individuals, closer to the other network nodes. In our case, we used interaction frequency (i.e., number of bird species visits to each plant individual) to weigh the networks.

Data analysis

To understand the effects of crop size and fruit weight on plant individuals' normalized degree, weighted closeness, number of visits and quantitative effectiveness, we used generalized linear models (GLM) and linear models (LM). We performed a separate model for each plant species, as we assumed plant species behave independently, and because separate models may provide more accurate estimates for species individually. For each plant species, we performed five models with crop size and fruit weight as predictor variables. We first modeled the normalized degree of each plant individual using a GLM with beta error distribution, as normalized degree is a proportional variable. However, model assumptions were not met with the *Miconia* model. Therefore, we decided to use a GLM with a binomial error distribution (for consistency, we also used a GLM with binomial error distribution to model the normalized degree of *Xylopia*). Because the normalized degree represents the proportion of realized interactions, it can be treated as a binomial response (i.e., the number of bird species that interacted with a plant individual vs. the number of bird species that did not interact with a plant individual). The second model was a GLM with the weighted closeness of each plant individual as the response variable and beta error distribution. The third model was a GLM with the number of visits received by plant individuals as our response variable, Poisson error distribution (for *Miconia*) and negative binomial error distribution (for *Xylopia*). The fourth model was a LM with quantitative effectiveness received by plant individuals as our response variable. We log-transformed quantitative effectiveness to fulfil the normality and homoscedasticity assumptions of the fourth model. The fifth model was a GLM with quantitative effectiveness divided by crop size

as the response variable and beta error distribution. This ratio served as a proxy for the proportion of fruits removed relative to each tree's investment in fruit production (i.e., quantitative effectiveness per capita). To assess whether the availability of ripe fruits across the fruiting season was a stronger predictor compared to total crop size (ripe and unripe fruits) for the response variables, we refitted all of the above models using ripe fruit crop size instead of total crop size as a predictor.

To understand whether crop size and fruit size were negatively correlated, we performed two additional LMs, one for each plant species. With those models, we wanted to understand whether the selected plant traits were sending mixed signals to birds. The models had crop size as the response variable and fruit weight as the predictor. We used the lme4 (Bates et al. 2015) and the glmmTMB (Brooks et al. 2017) R packages to build our models and tested the normality, homoscedasticity and overdispersion of models using the DHARMA R package (Hartig 2016). All statistical analyses were carried out in R version 4.3.0 (R Core Team 2025).

Results

Total fruit crop size ranged from 2,694 to 4,972 for *Xylopia* trees and 7,505 to 280,815 for *Miconia* trees (Table S2). Plant fruits ranged from 24.9 to 41.1 mg for arillate seeds of *Xylopia* and 8 to 29.5 g for fruits of *Miconia* (Table S2). We recorded 199 interactions between 18 bird species and 10 *Xylopia* trees, and 43 interactions between seven bird species and six *Miconia* trees (Fig. 1). Four trees of *Miconia*, producing comparatively fewer fruits (7,505–179,746 fruits), received no bird visits during focal observations. In general, individual interaction niches of our fruiting trees were narrower than those of their populations (i.e., considering all individuals sampled) supporting a degree of individual specialization, in particular for the lipid-rich *Xylopia* (Figure S2).

We found that larger crops of *Miconia* attracted a larger number of bird species (i.e., attained higher normalized degree, $z=2.29$, $p=0.02$, Table S3, Fig. 2c), while no such pattern was found for *Xylopia* trees (Table S3, Fig. 2a). Fruit weight did not affect normalized degree in *Xylopia*, nor in *Miconia* trees (Table S3, Fig. 2c, d). *Miconia* trees with larger fruit crops had higher values of weighted closeness, i.e., were more connected to visitors and other plant individuals within the network, compared to plants producing smaller crops ($z=2.82$, $p=0.005$, Table S3, Fig. 2g), while no pattern was found for *Xylopia* trees (Table S3, Fig. 2e). Fruit weight did not affect weighted closeness of *Xylopia*, or *Miconia* (Table S3, Fig. 2f, h).

Larger fruit crop sizes positively affected the number of visits ($z=3.03$, $p=0.002$, Table S3, Fig. 2k) and the

quantitative effectiveness of *Miconia* trees ($t=4.0$, $p=0.005$, Table S3; Fig. 2o), but not of *Xylopia* trees (Table S3; Fig. 2i, m), whereas fruit weight did not affect the number of visits or quantitative effectiveness of any plant species (Table S3, Fig. 2j, n, l, p). Interestingly, quantitative effectiveness per capita reinforced that trees producing larger fruit crops, but not heavier fruits (Table S3, Fig. 2t), had a higher proportion of their seeds removed by dispersers for *Miconia* trees ($z=3.20$, $p=0.001$, Table S3, Fig. 2s). Conversely, crop size did not affect *Xylopia*'s quantitative effectiveness per capita (Table S3, Fig. 2q), though fruit weight had a negative effect on quantitative effectiveness per capita ($z=-2.82$, $p=0.005$, Table S3, Fig. 2r), indicating plants producing larger seeds were less removed per unit of crop size.

The models using ripe fruit crop size, instead of total crop size, produced qualitatively similar results from the previous models, with the same predictor variables influencing the same response variables (Table S4). The only exception was that fruit weight also showed a negative effect on the number of visits for *Xylopia* trees (Table S4). Furthermore, there was no significant relationship between crop size and fruit weight for *Miconia* or *Xylopia* (Table S3), indicating that those two traits are unlikely to create such conflicting signals to frugivorous birds visiting those plant species.

Considering the contribution of bird species to the quantitative effectiveness, two highly frugivorous bird species, *Stilpnia cayana* and *Thraupis sayaca*, accounted for 60% of the total quantitative effectiveness of *Miconia* trees, with all bird visitors reaching an average frugivory degree of 70% (Fig. 3f). In contrast, for *Xylopia*, the same quantitative effectiveness (60%) was distributed among four bird species with an average of 52% frugivory degree (Fig. 3e).

Discussion

Our study provides insights into how plant traits differentially influence bird foraging decisions and plant fitness in individuals from two plant species with contrasting nutritional rewards. Overall, *Miconia* trees producing larger fruit crops attracted more bird species, were more central in the interaction network and attained higher number of visits and quantitative effectiveness of seed dispersal, compared to trees with smaller fruit crops. The four *Miconia* trees that did not attract any visitors produced, on average, 50% fewer fruits than those trees that attracted frugivores, reinforcing the idea that fruit crop size is a crucial trait to enhance successful seed dispersal for individual plants. Contrary to our expectations, *Xylopia* trees with larger fruit crop sizes did not attract more bird species (see Christianini and Oliveira 2010 for a similar result), nor were they more central in the interaction network or attained higher number of visitors or

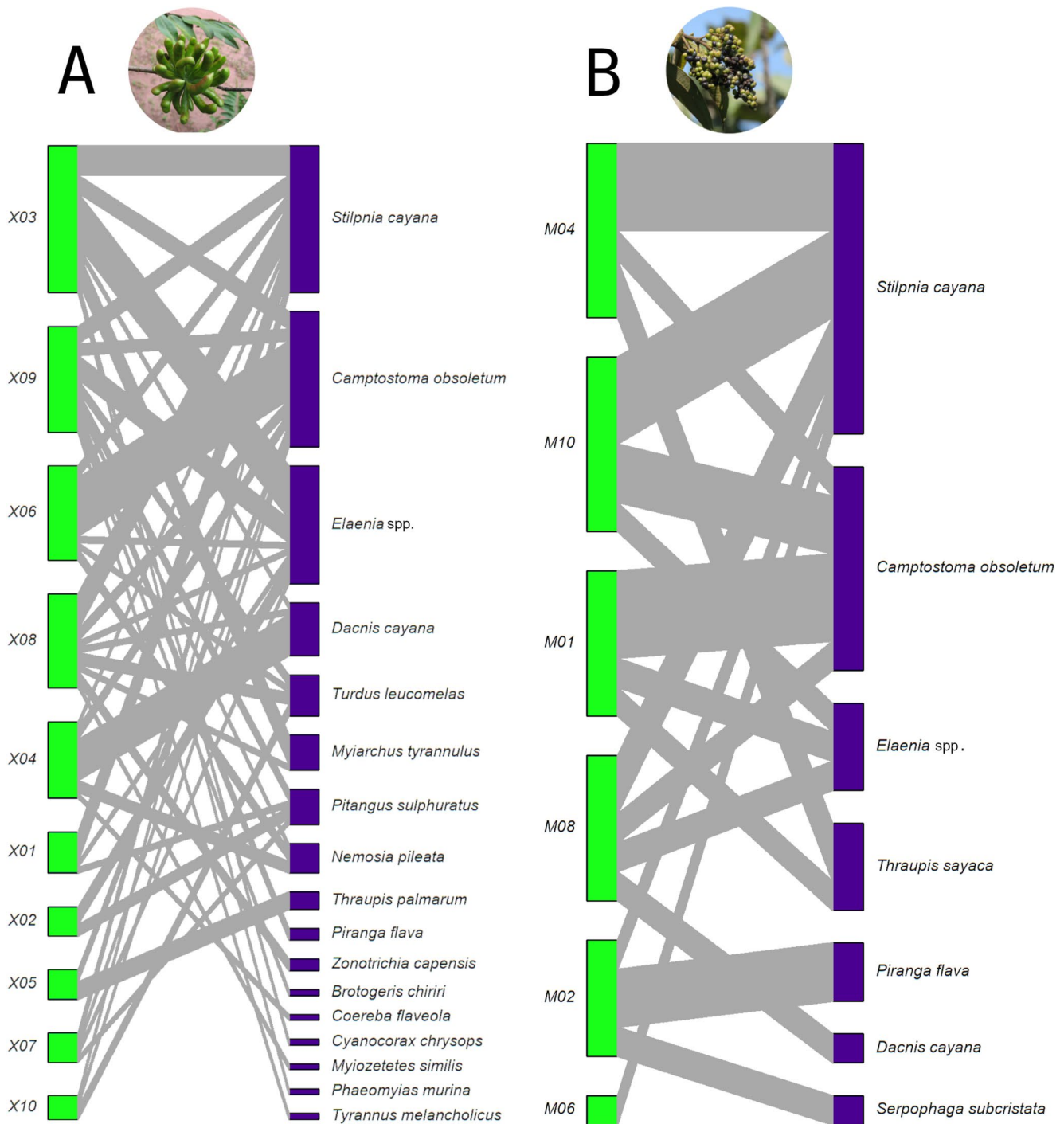


Fig. 1 Individual-based networks weighted by the number of visits received by *Xylopia* (A) and *Miconia* (B) trees. Four *Miconia* individuals are not represented in the network because they did not receive any bird visitors. Bird species and individual plants in each network

are ordered based on their level of connection to partners (i.e., more connected bird species/plant individuals in the top and less connected bird species/plant individuals in the bottom)

quantitative effectiveness, compared to trees with smaller crop sizes. However, *Xylopia* individuals with heavier fruits had lower quantitative effectiveness per capita, indicating lower fruit removal per crop size.

The strong effect of fruit crop size on bird choice of *Miconia* trees are in line with other studies indicating that larger fruit crops are often a strong visual signal for frugivores (Ortiz-Pulido and Rico-Gray 2000; Palacio et al. 2017; Palacio and Ordano 2018), affecting fruit removal. The positive

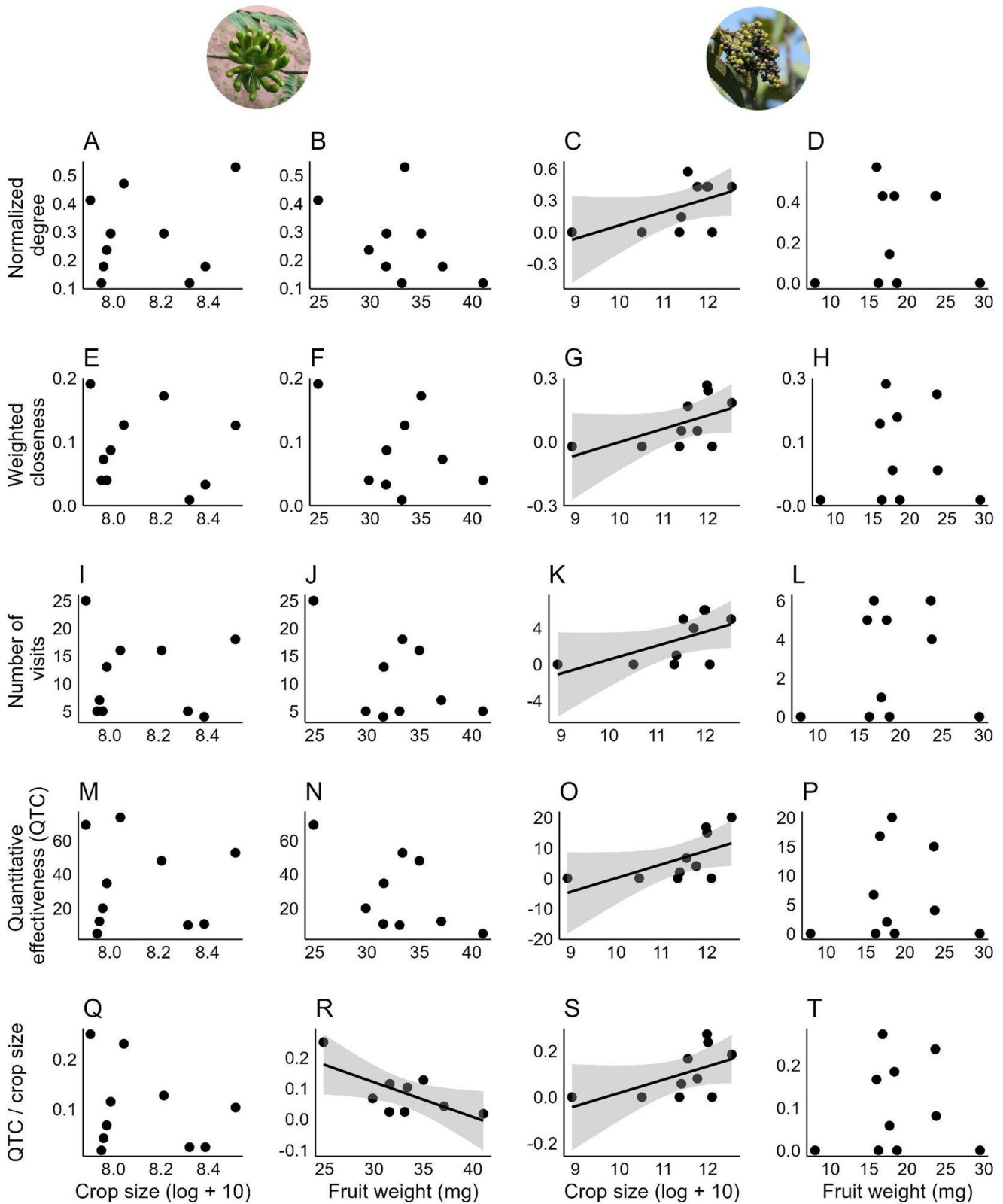
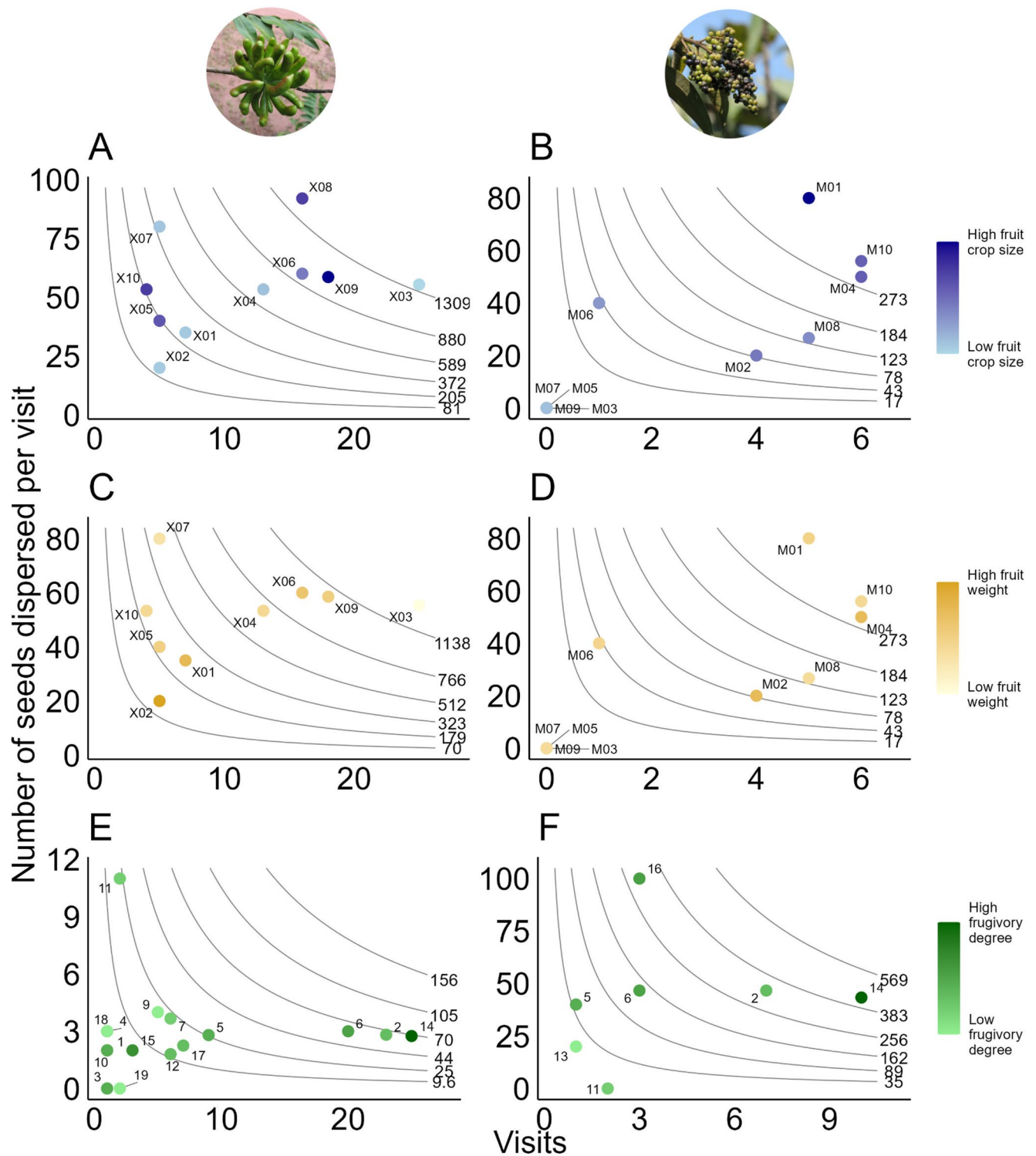


Fig. 2 Crop size and fruit weight relationships with normalized degree (A–D), weighted closeness (E–H), number of visits (I–L), quantitative effectiveness (M–P), and quantitative effectiveness–crop size ratio (Q–T) for *Xylopia* (the two leftmost columns) and *Miconia* (the two rightmost columns) trees. Lines represent significant relationships, and

shaded areas represent the standard errors associated with model predictions. Total crop size was log-transformed to improve the visibility of results, while the quantitative effectiveness per capita was standardized to proportions to avoid extremely small numerical values



effects of fruit crop size on fruit removal may depend on a trade-off between the energy invested to produce a high amount of fruits and the per capita chance of removal of those fruits. Large crops clearly remained advantageous for *Miconia* in both absolute (i.e. the total number of seeds dispersed) and in relative (i.e. the per capita chance of seed

dispersal) terms. Therefore, our results support the idea that seed dispersers may prioritize fruit crop sizes for *Miconia* plant selection before other traits, such as fruit weight (Palacio et al. 2017).

Contrary to the patterns observed for *Miconia*, fruit crop size did not explain bird choices of plant individuals of

Fig. 3 Quantitative effectiveness landscapes for *Xylopia* and *Miconia* trees (A–D) and bird species consuming their fruits (E–F). In (A–D), the X-axis corresponds to the number of visits received by each plant individual, while the Y-axis corresponds to the average number of seeds dispersed away from the plant crown per visit. Color gradient refers to fruit crop sizes (A, B) and fruit weights (C, D), with darker colors representing larger fruit crop sizes and heavier fruit weights and lighter colors representing smaller fruit crop sizes and lighter weights. In (E–F), the X-axis corresponds to the number of times each bird species visited individuals of plant species, while the Y-axis corresponds to the average number of seeds dispersed per visit by each bird species. Color gradient refers to species' frugivory level (assigned following Wilman et al. 2014), with darker colors representing higher levels of frugivory, and lighter colors representing lower levels of frugivory. In (C), the absence of a point labeled X08 refers to a plant individual from which fruit weight could not be retrieved. In all landscapes, the isoclines represent all the different combinations of X and Y that multiplied give the same values of quantitative effectiveness. Bird species in (E–F): 1 - *Brotogeris chiriri*, 2 - *Camptostoma obsoletum*, 3 - *Coereba flaveola*, 4 - *Cyanocorax chrysops*, 5 - *Dacnis cayana*, 6 - *Elaenia* spp., 7 - *Myiarchus tyrannulus*, 8 - *Myiozetetes similis*, 9 - *Nemosia pileata*, 10 - *Phaenopygia murina*, 11 - *Piranga flava*, 12 - *Pitangus sulphuratus*, 13 - *Serpophaga subcristata*, 14 - *Tangara cayana*, 15 - *Thraupis palmarum*, 16 - *Thraupis sayaca*, 17 - *Turdus leucomelas*, 18 - *Tyrannus melancholicus*, 19 - *Zonotrichia capensis*

Xylopia. The range of variation in crop size among *Xylopia* trees was only twofold, against a 37-fold variation for *Miconia* (Table S2), and the lower variance in crop size among *Xylopia* trees may have reduced the chance of detecting potential effects of crop size on dispersal success. Furthermore, *Xylopia* trees attracted more birds that consume fruits occasionally compared to birds attracted by *Miconia*, including insectivorous species that performed 360% more visits to *Xylopia* (46 visits) than to *Miconia* (10 visits). This pattern is consistent with the lipid-rich diaspores of *Xylopia*, which tend to attract insectivores (Pizo et al. 2021), capable of processing high-lipid loads more easily than strict frugivores (Levey & Martínez del Río 2001). Because insectivores are less dependent on fruits, selection on crop size in *Xylopia* is likely weaker and more diffuse (Zamora 2000; Palacio and Ordano 2018). This lack of relationship between crop size and patterns of visitation may reflect asymmetrical dependence patterns, with *Xylopia* plants being dependent on insectivorous birds to disperse their seeds, while insectivorous species interact opportunistically with *Xylopia* plants (Quintero et al. 2023). Therefore, differences in nutritional rewards and the set of dispersers attracted by each plant species may partially explain the different influence of fruit crop size between plant species. Future research incorporating more plant species could further investigate the potential differences in bird foraging decisions associated with contrasting nutritional rewards.

Fruit weight was the only plant trait explaining part of bird choices in *Xylopia* individuals, with heavier fruits experiencing lower per capita removal. Because birds visiting *Xylopia* trees are mostly small passerines (average

body mass: 38.4 g, Wilman et al. 2014), larger fruits impose higher handling and gut constraints, reducing birds' ability to successfully manipulate and swallow them, and resulting in many seeds being dropped beneath the plant canopy. Additionally, because lipid-rich fruits are more demanding for birds to process in the gut (Levey & Martínez del Río 2001; Quintero et al. 2020), birds may limit the number of large fruits they consume. Although our study provides valuable insights into fruit trait selection by birds, future work would benefit from directly measuring and comparing the traits of fruit removed by birds to those available on trees.

Other plant traits, not addressed by our study, could play a role in bird selection of *Xylopia* fruiting trees. For instance, birds can visually detect nutritional differences among fruits from different plant individuals through chromatic cues associated with nutrient content and may exhibit preferences for specific nutrient levels, which can vary among individual plants (Cazetta et al. 2012; Crestani et al. 2019). In *Xylopia*, a large amount of ripe fruits available at the time of frugivore visitation could create a chromatic contrast between the bluish seeds and the pinkish inner walls of the follicles, possibly predicting bird visitation (Ordano et al. 2017; Palacio and Ordano 2018; Figure S1). Although we did not observe an effect of the entire fruiting season ripe fruit crop size on *Xylopia* visitation patterns, it remains to be tested whether ripe fruit crop size at the specific time of visitation would have a different effect.

The presence of neighboring intraspecific (Blendinger et al. 2008; Guerra et al. 2017; Li et al. 2022; Vissoto et al. 2022) or interspecific (Carlo 2005; Vissoto et al. 2022) fruiting plants, as well as the characteristics of the surrounding environment (García 2001; Friedemann et al. 2022; Li et al. 2022; Vissoto et al. 2022) could also contribute to differential patterns of fruit removal by birds. Frugivores may use a hierarchical foraging strategy by initially selecting Cerrado patches where fruiting trees are clustered and subsequently choosing specific plants according to traits such as fruit abundance, fruit size, or visual cues. Therefore, neighborhood effects may depend on the scale at which they are estimated, and, at the immediate vicinity scale (e.g., nearest trees), such effects may lead to increases or decreases in seed removal, depending on whether facilitation or competition for dispersers occurs among plants (Carlo and Morales 2008). Facilitative effects may occur if a tree is surrounded by intraspecific plants that increase attractive fruiting displays to frugivores (Albrecht et al. 2015). Nevertheless, individual plants may compete for frugivores once birds reach the fruiting patch. Facilitative effects may also occur if frugivores look for neighboring heterospecific fruiting plants to complement specific nutrients on their diets (Blendinger et al. 2022). The mechanisms governing

facilitation and competition in our dispersal system remain poorly understood and will require targeted experimental designs to be properly evaluated.

Bird foraging choices on fruit crop size may also vary depending on the intensity of fruit production by plant population in specific years (Ortiz-Pullido & Rico-Gray 2000). For instance, when most plant individuals produce many fruits in a fruiting season, further increases in crop size may not attract more visitors, whereas if few fruits are produced within the population, an individual plant could increase its dispersal efficiency by producing larger crops. In studies conducted at the same site, but in a different fruiting season, we also found evidence supporting the fruit crop size hypothesis for *Miconia*, but not for *Xylopia* (Christianini and Oliveira 2009, 2010). Therefore, although the current study entails one fruiting season only, our results are consistent with known bird foraging behavior and selection patterns at our study site.

A caveat of our measure of quantitative effectiveness is that it only focuses on one type of disperser (birds), even though secondary dispersal by ants is important for the regeneration of both plant species in Cerrado (Christianini and Oliveira 2009, 2010). Ants may partially compensate for the waste of fruits fallen beneath parental plants, especially from those with smaller crop sizes (Christianini and Oliveira 2009). Patterns of bird and ant foraging decisions on fruit traits may then be conflicting, and the combined effects of both disperser agents may be different from patterns found when looking solely at bird choices (Palacio et al. 2020). Furthermore, antagonistic interactions such as pre-dispersal seed predation, may increase with crop size in *Xylopia* trees (Christianini 2017), also playing a role in plant species trait selection. Therefore, the net effect of individual plant attributes on seed dispersal is complex, and future studies should consider the choices of different interaction partners to unravel trait selection mechanisms.

Our results indicate that fruit crop size likely plays a greater role in bird foraging decisions for individuals of a carbohydrate-rich fruited plant (*Miconia*), while fruit weight influences bird visitation patterns for the lipid-rich *Xylopia*. Therefore, restoration and conservation programs should target *Miconia* plants with large fruit crops and *Xylopia* trees with low fruit weight, as this would likely promote their seed dispersal and benefit their frugivorous partners. Finally, our study highlights that individual plant variation in crop and fruit traits observed across plant species, and their consequences for seed dispersal, may be easily overlooked when interactions are recorded at the species level. Thus, investigating the relationship between species traits and interaction patterns at the individual level may provide valuable insight to our understanding of community assembly.

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Data availability Data can be found in <https://doi.org/10.6084/m9.figshare.29959226>.

Declarations

Competing interests The authors declare no competing interests.

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