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Selection on fruit traits is mediated by the interplay between frugivorous birds, fruit flies, parasitoid wasps and seed-dispersing ants

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Abstract

Every organism on Earth must cope with a multitude of species interactions both directly and indirectly throughout its life cycle. However, how selection from multiple species occupying different trophic levels affects diffuse mutualisms has received little attention. As a result, how a given species amalgamates the combined effects of selection from multiple mutualists and antagonists to enhance its own fitness remains little understood. We investigated how multispecies interactions (frugivorous birds, ants, fruit flies and parasitoid wasps) generate selection on fruit traits in a seed dispersal mutualism. We used structural equation models to assess whether seed dispersers (frugivorous birds and ants) exerted phenotypic selection on fruit and seed traits in the spiny hackberry (*Celtis ehrenbergiana*), a fleshy-fruited tree, and how these selection regimes were influenced by fruit fly infestation and wasp parasitoidism levels. Birds exerted negative correlational selection on the combination of fruit crop size and mean seed weight, favouring either large crops with small seeds or small crops with large seeds. Parasitoids selected plants with higher fruit fly infestation levels, and fruit flies exerted positive directional selection on fruit size, which was positively correlated with seed weight. Therefore, higher parasitoidism indirectly correlated with higher plant fitness through increased bird fruit removal. In addition, ants exerted negative directional selection on mean seed weight. Our results show that strong selection on phenotypic traits may still arise in perceived diffuse species interactions. Overall, we emphasize the need to consider diverse direct and indirect partners to achieve a better understanding of the mechanisms driving phenotypic trait evolution in multispecies interactions.

KEYWORDS

Acromyrmex lundii, *Celtis ehrenbergiana*, frugivory, plant–animal interactions, *Rhagoletotrypeta pastranai*, seed dispersal, selection gradients, structural equation model, *Utetes anastrephae*

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1 | INTRODUCTION

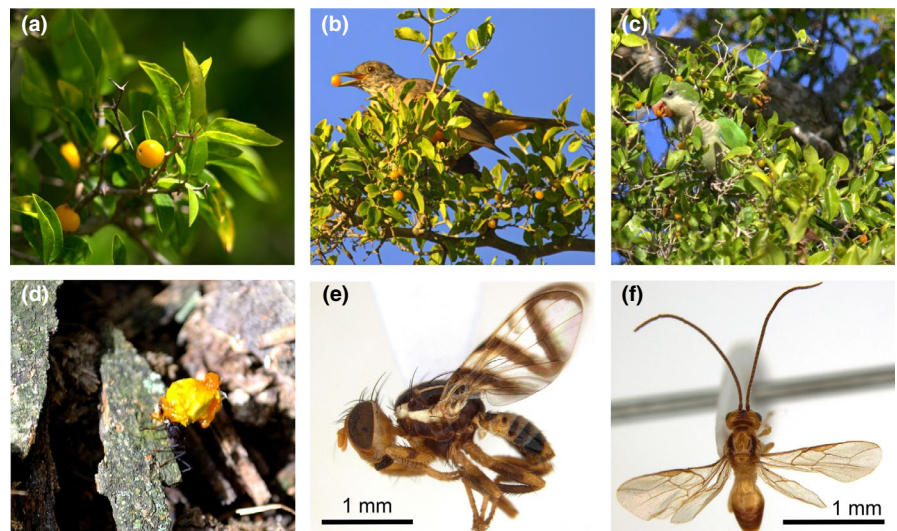
One unifying goal in evolutionary biology is to understand how interactions between species shape the evolution of their phenotypes and in turn how this mediates species interactions (Agrawal, 2001; Thompson, 1999). However, disentangling how species may alter the evolution of traits of their interacting partners has been challenging, because species typically interact both directly and indirectly through interactions mediated by other species (Ohgushi, Schmitz, & Holt, 2012; Strauss & Irwin, 2004; terHorst et al., 2015; Walsh, 2013). Although ecologists have long acknowledged the complexity of species interactions in nature, studies in the evolution of biotic interactions have classically focused on the reductionist view of direct, pairwise interactions (Møller, 2008; Strauss & Irwin, 2004). Over the last several decades, nevertheless, there has been an increase in studies assessing how multispecies interactions affect both the ecological and evolutionary outcomes of interactions that could have not been achieved by looking at pairwise interactions alone (Beduschi, Tschardtke, & Scherber, 2015; Craig, Itami, & Horner, 2007; Siepielski & Benkman, 2004; Start, Weis, & Gilbert, 2019).

Like every organism, plants must deal with multiple mutualists and antagonists throughout their life cycle (Lawton, 1999), including herbivores, pathogens, mycorrhizal fungi, parasites, pollinators, seed dispersers and seed predators (Van Dam, 2009). The species involved in these interactions are taxonomically and ontogenetically diverse, use different parts of the plant and vary in their impacts on plant fitness (Strauss & Irwin, 2004). In turn, each of these species interact with other species that do not directly interact with the plant (e.g. plant–herbivore–parasite or plant–pollinator–predator interactions), resulting in complex interaction networks that can generate cascading effects (Harvey, Van Dam, & Gols, 2003; Singer, Farkas, Skorik, & Mooney, 2012; Tschardtke, 1992). However, the influence of other species and other trophic levels on mutualisms has received much less attention than other types of interactions (Bronstein & Barbosa, 2002; see Strauss & Irwin, 2004 for a review).

Like most plant structures, fruits and seeds contend with multiple different interactions simultaneously or at different points in their life cycles, which often generate conflicting selection pressures that constrain the evolution of fruit and seed traits. This occurs because plants face trade-offs in attracting seed dispersers while also attracting antagonists, which have been shown to modulate selection on fruit and seed traits (Cazetta, Schaefer, & Galetti, 2008; Herrera, 1984; Manzur & Courtney, 1984; Whitney & Stanton, 2004). For instance, birds often favour large seeds during the dispersal stage in fleshy-fruited plants, but seed size is also often under opposing selection by seed predators (Alcántara & Rey, 2003; Gómez, 2004; Martínez, García, & Obeso, 2007). As another example, predispersal seed predators favour increased seed defences in pine species, conflicting with selection exerted by birds for traits that promote seed dispersal (Siepielski & Benkman, 2007a). These studies have provided valuable knowledge about the effects of different species on shaping phenotypic selection on plant traits, yet how plants amalgamate the combined effects of multiple mutualists and antagonists remains still poorly understood.

Endozoochorous seed dispersal is classically treated as a textbook example of mutualism, in which nutrients in the fleshy pulp (nutrition benefit) are exchanged for seed dispersal services provided by animals (transportation benefit). Nevertheless, this interaction has been shown to be much more complex than previously thought, as the outcomes of the interaction are expected to be influenced by the presence of other species and trophic levels in several ways (Bronstein & Barbosa, 2002). First, this mutualism may be altered by antagonists of one of the partners. For instance, fruits often attract frugivorous insects interfering with seed dispersal by making plants less attractive to birds (Traveset, Willson, & Gaither, 1995; Valburg, 1992). Second, seed dispersal may be altered by other mutualists of one of the partners. As an example, plants may attract more seed dispersers when neighbouring plants bear fruit simultaneously, enhancing plant fitness (Guerra et al., 2017; Morales, Rivarola, Amico, & Carlo, 2012; Sargent, 1990). Third, seed dispersal

FIGURE 1 Spiny hackberry (*Celtis ehrenbergiana*) and its multiple interactors. (a) spiny hackberry fruits are consumed and dispersed by several frugivorous birds, including (b) rufous-bellied thrush (*Turdus rufiventris*) and (c) monk parakeet (*Myiopsitta monachus*); (d) leaf-cutting ants (*Acromyrmex lundii*) are secondary seed dispersers; (e) the fruit fly *Rhagoletotrypeta pastranai* oviposits its larvae in the fruit, which are attacked by (f) the parasitoid wasp *Utetes anastrephae*. Photo credits: F. X. Palacio (a–c), and F. Luque (d). (e) and (f) taken from Palacio, Lacoretz, Pérez, and Ordano (2019)



may be altered by exploiters of the mutualism (Bronstein, 2001). For instance, pulp-consuming birds often ingest fruit rewards without dispersing seeds (Schupp, 1993; but see Loayza & Knight, 2010), or ants may either enhance or decrease seed dispersal depending on dispersal syndrome, plant and ant species characteristics (Penn & Crist, 2018). These examples of different multispecies and multitrophic interactions unveil some of the complexity in interaction networks, whose ecological and evolutionary influences on the outcome of beneficial pairwise interactions have seldom been addressed.

Therefore, we investigated how multispecies interactions between plants, frugivorous birds, ants, fruit flies and parasitoid wasps shape selection on fruit and seed traits in the spiny hackberry (*Celtis ehrenbergiana*; Figure 1). To this end, we assessed how phenotypic selection on fruit and seed traits by seed dispersers was influenced by fruit flies and parasitoid wasps (Figure 2). Specifically, we addressed the following questions: (a) Do different mutualistic seed dispersers (birds and ants) exert different selection pressures on fruit and seed traits? And (b) how is selection imposed by dispersers influenced by antagonistic fruit flies and parasitoids? Given the nature of these direct and indirect interactions and the presence of multiple potentially conflicting selection pressures, diffuse selection on fruit and seed traits, as a general outcome, was expected. Thus, we predicted that the impact of different interactors on plant fitness would depend on the presence or absence of other species (Siepielski & Benkman, 2004; Strauss, Sahli, & Conner, 2005; Thompson, 2009). More specifically, parasitoids were expected to exert selection on fruit and seed traits similar to that exerted by fruit flies (e.g. if fruit flies select large fruits to oviposit larvae, it is expected that parasitoids also select large fruits, as a by-product of fruit fly selection). Birds, in turn, were expected to select against those fruit and seed traits selected by fruit flies and, indirectly, by parasitoids. Ants were also expected to select fruit and seed traits selected by birds. Overall, multiple interactors are expected to create indirect effects on phenotypic selection on fruit and seed traits, leading to nonadditive and diffuse selection (Strauss et al., 2005; terHorst et al., 2015).

2 | MATERIALS AND METHODS

2.1 | Study area

The study was carried out at 'Estancia San Isidro' (35°09'S, 57°23'W) located in the Biosphere Reserve 'Parque Costero del Sur', north-eastern Buenos Aires province, Argentina. The area is composed of native and alien grasslands, and native forest patches, with nearly 9% forest cover (Goya, Placci, Arturi, & Brown, 1992). Forest patch size ranges between 0.02 and 1.77 ha (Palacio, 2016), and dominant native tree species are *C. ehrenbergiana*, *Scutia buxifolia*, *Jodina rhombifolia* and *Schinus longifolia* (Goya et al., 1992). The climate is wet temperate, with mean minimum and maximum temperatures of 6.0 and 26.0°C, respectively. Annual mean rainfall is 926 mm, with most precipitation occurring in January and February, but without a noticeable dry season.

2.2 | Natural history of the study system

Our focal plant is the spiny hackberry *C. ehrenbergiana* (Cannabaceae)—a thorny andromonoecious tree, found in dry forests and scrubs from the southern United States to central Argentina (Berg & Dahlberg, 2001). It produces actinomorphic, hermaphroditic or male flowers, 4.0 mm wide (Romanczuk & del Pero de Martínez, 1978), and is characterized as an insect- and wind-pollinated self-compatible species (Torretta & Basilio, 2009). Fruits are one-seeded fleshy drupes, 8.5 ± 0.6 mm wide (Palacio, Lacoretz, & Ordano, 2014; Figure 1a). Fruiting occurs mainly from February to April, and it is one of few species fruiting in the dry months (Murriello, Arturi, & Brown, 1993). Both fruits and seeds are involved in several mutualistic and antagonistic interactions. Seeds are primarily consumed and dispersed by birds, including *Turdus rufiventris*, *Mimus saturninus*, *Zonotrichia capensis*, *Agelaioides badius*, *Paroaria coronata*, *Pitangus sulphuratus*, *Elaenia parvirostris* and *Icterus pyrrhopterus* (Palacio et al., 2014). Birds

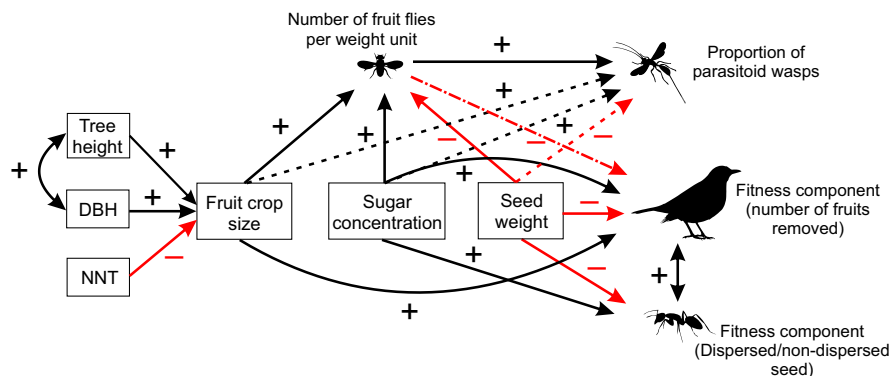


FIGURE 2 Hypothesized causal relationships between plant traits, fruit and seed traits, frugivorous birds, ants, fruit flies and parasitoid wasps. One-headed arrows represent causal relationships between variables, and the two-headed arrow represents a correlation. Signs and colours indicate expected positive (black lines) or negative (red lines) relationships. The full model includes all arrows, whereas Model A includes all arrows except for the dash-dotted arrow, and Model B includes all arrows except for the dashed arrows. DBH: diameter at breast height; NNT: nearest neighbour tree

either swallow entire fruits or peck the pulp discarding the seeds and the remaining pulp, often in locations suitable for germination (Figure 1b; Palacio et al., 2014).

After seeds reach the ground by primary dispersal or natural fall, they are subject to secondary dispersal by ants (i.e. diplochory; Vander Wall & Longland, 2004). Although armadillos (Bolković, Caziani, & Protomastro, 1995) and foxes (Varela, Cormenzana-Méndez, Krapovickas, & Bucher, 2008) also consume spiny hackberry fruits, the latter typically represent a small amount of their diets. One of the main ant seed dispersers at our study site is the native leaf-cutting ant *Acromyrmex lundii* (Hymenoptera: Formicidae), who are often observed carrying seeds to their nests (Figure 1c) and are considered fungus farmers (Mason et al., 2017; Mehdiabadi & Schultz, 2010). Interestingly, seeds have no specialized structures to attract ants (elaiosome or other edible appendage attached to the seed), and the reward is presumably represented by the sugary pulp of the fruit (mean sugar concentration 22.5 ± 3.1 °Bx; Palacio et al., 2014) or by the available biomass for fungus growing (i.e. fruit size). However, information about seed dispersal by ants, as well as their effects on plant establishment survival in the spiny hackberry, remains poorly known. In other systems, nevertheless, ants are known to be important secondary seed dispersers (e.g. Bieber, Silva, & Oliveira, 2013; Camargo, Rodrigues, Piratelli, Oliveira, & Christianini, 2019; Christianini & Oliveira, 2010; Levey & Byrne, 1993).

In addition, spiny hackberry fruits are attacked by the fruit fly *Rhagoletotrypeta pastranai* (Diptera: Tephritidae), a specialist on *Celtis* (Norrbom, 1994; Ovruski, Norrbom, Schliserman, & Aluja, 2005; Figure 1d). Fruit flies oviposit one egg per fruit inside the fruit pulp, and percentage infestation levels are highly variable (mean \pm standard deviation = $18.2 \pm 32.1\%$; Palacio et al., 2019). Only one fruit fly larva is typically found per fruit (only once, a fruit with two larvae out of 2,447 fruits was found; F. X. Palacio unpublished data). In turn, *Utetes anastrephae* (Hymenoptera: Braconidae) is a generalist koinobiont endoparasitoid (the parasitoid allows the host to continue its development and does not kill the host until the parasitoid larva pupates) ranging from Florida (USA) to Argentina (Sivinski, Aluja, & López, 1997; Wharton & Marsh, 1978), which attacks late-instar larvae of *R. pastranai* (Palacio et al., 2019; Figure 1e). Only one parasitoid is found per fruit fly larvae. Parasitoids emerge after 1–2 months, whereas fruit flies emerge after a 12-months diapause period (Palacio et al., 2019).

2.3 | Plant, fruit and seed traits

We mapped all mature trees across 10 forest patches ($N = 80$ trees). For each tree, we measured tree height, diameter at breast height (DBH) and the distance to the nearest reproductive tree (plant traits). We also measured the following fruit and seed traits: total number of ripe fruits per tree (i.e. fruit crop size), sugar concentration and seed weight. In three randomly selected 0.120 m^3 cubes within the tree crown, we directly counted the number of ripe fruits (with its

characteristic orange-yellow colour; Figure 1a). Fruit crop size was estimated by extrapolating the mean number of ripe fruits per cube to the total tree crown volume. The latter was estimated assuming an ellipsoid, volume = $(4/3) \pi abc$, where a , b and c are the three longest orthogonal semi-axes of the tree crown (Palacio et al., 2014). We collected 10 fruits per tree ($N = 800$ fruits). Pulp and seed fresh weight were measured in the field with an Ohaus scale to the nearest 0.01 g. Total sugar concentration per individual fruit was measured in the field to the nearest 0.25 °Brix with a Reichert hand-held refractometer (0–50 °Bx). We then computed mean seed weight and mean sugar concentration per tree.

2.4 | Plant-animal and animal-animal interactions

At the beginning of the fruiting season, between 24 and 28 February 2014, we randomly selected 56 of the 80 trees. Four branches per tree were tagged, and four other branches were both tagged and enclosed with fine-mesh bags (2-mm mesh; 40×30 cm bags) to prevent bird fruit removal and control for dropped fruits (Ortiz-Pulido, Albores-Barajas, & Díaz, 2007). On each unbagged branch, we recorded the number of fruits at the beginning of the season (F_b) and the number of remaining fruits at the end of the season (F_e), between 28 March and 1 April 2014. On each bagged branch, we recorded the number of fruits at the beginning of the season (F_i) and the number of fallen fruits at the end of the season (F_f). We then computed the mean initial number of fruits for both bagged and unbagged branches at the beginning of the season (mF_b and mF_i) and the mean number of remaining fruits at the end of the season (mF_e). The mean proportion of fallen fruits per bagged branch (mPF_f) was computed as $mpF_f = mF_f/mF_i$ to account for differences in the number of fruits within bagged branches, and the mean number of fallen fruits per unbagged branch (mF_f) was estimated as $mF_f = mF_i \times mpF_f$. The expected number of fruits removed per (unbagged) branch (mF_r) was then estimated as $mF_r = mF_b - mF_e - mF_f$. The mean proportion of fruits removed per branch (mPF_r) was computed as $mPF_r = mF_r/mF_i$. Finally, the number of fruits removed per tree (F_r) was estimated as the product between fruit crop size (F_c , as defined above) and the mean proportion of fruits removed as $F_r = F_c \times mPF_r$. Given that each fruit encloses only one seed, fruit removal equals seed removal. Fruit removal was used as a surrogate for tree fitness (Jordano, 1995; Palacio & Ordano, 2018; Siepielski & Benkman, 2007a; Sobral, Guitián, Guitián, & Larrinaga, 2013) in the context of selection by bird and ants, under the assumption that trees with a higher number of seeds dispersed would have greater potential for dispersal and germination of their seeds (Primack & Kang, 1989; Siepielski & Benkman, 2007a, 2008a; see Section 4). Although the proportion of fruits removed may be a better surrogate of fitness for plants whose reproductive output is size-dependent (Jordano, 1995; Siepielski & Benkman, 2007b; but see Palacio & Ordano, 2018), we used the number of fruits removed as a fitness component because tree size and fruit crop size were included as covariates in the statistical models (see below).

In addition, we used ant seed removal as another tree fitness component. Since it is unknown whether ants choose spiny hackberry seeds over fruits, we first carried out a cafeteria experiment in the field between 28 February and 01 March 2014. Cafeteria experiments analyse consumption of food items when offered simultaneously and allow for food preferences to be assessed (Krebs, 1989). We collected 12 fruits per tree from 54 trees ($N = 648$ fruits) and randomly allocated each fruit to one of three treatments simulating the three most common conditions in which fruits and seeds are encountered on the ground (Bieber et al., 2013): intact fruits (no marks or holes of any kind), fruits with the pulp partially removed (approx. a half of fruit volume using a jackknife simulating the mark left by pulp consumers) and clean seeds (pulp manually removed with a jackknife and a paper towel to mimic fruit passage). The three treatments were placed in three random corners of a white cardboard sheet (10×10 cm) on the leaf litter under each tree. Each treatment received four fruits or seeds. We set the experiment at 08:00 hr and recorded the number of fruits or seeds removed after 10 hr, which was a sufficient period of time for seed removal. After checking the sheets, we also visually searched for the presence of ants carrying seeds within a 1-m radius. Because the experiment was carried out under natural conditions, we did not control for the number of ants per replicate. However, we here simply assume that ant seed dispersal increases plant fitness by dispersing seeds away from the mother plant and reducing both predation and fungal attack on ripe fruits that fall on the ground (Janzen, 1970; Connell, 1971; Andersen, 1988; Oliveira, Galetti, Pedroni, & Morellato, 1995; Giladi, 2006).

To measure fly infestation levels and the proportion of parasitoids per tree, we sampled 70 of the 80 trees between 28 March and 01 April 2014. To this end, we collected 4–20 fruits per tree ($N = 950$ fruits) and reared fruit flies and parasitoids in the laboratory. Fruit samples of the same tree were placed in closed styrofoam vessels (750 cc) with a mesh at the top and damp sand (50 g, 5–10 water drops) in the bottom as a pupation substrate under natural conditions, as detailed in Palacio et al. (2019). One vessel per sampled tree was used (i.e. 70 vessels). For each sampled tree, we measured mean fruit weight with an Ohaus scale to the nearest 0.01 g. Fruit infestation levels and parasitism values were quantified as the number of pupae per 100 g of fruit (100 g \sim 295 fruits) and the proportion of emerged parasitoids relative to the number of pupae per tree, respectively. We quantified fruit fly infestation levels as the number of pupae per weight unit, because infestation is fruit size-dependent (reviewed by A. Benavidez et al. unpublished manuscript). Moreover, the number of pupae per 100 g of fruit was strongly correlated with the proportion of pupae per tree ($r = .93$, $N = 70$, $p < .0001$).

2.5 | Data analysis

To analyse whether ants preferred seeds over fruits in experimental trials, we fitted a generalized linear mixed model (GLMM; Harrison et al., 2018) using the three fruit/seed treatments as the explanatory variable and fruit/seed removal as the response variable. The patch

and the sheet nested within the patch were included as random effects. We used a binomial error distribution (number of fruits/seeds removed relative to the total number of diaspores) and a logit-link function.

The relationships between fruit fly infestation and mean fruit weight, and between the proportion of parasitoids and mean fruit weight were assessed using GLMMs with a Gaussian error structure (identity link function) and binomial error structure (logit-link function), respectively. Patch identity was included as a random effect.

To estimate the regime and strength of phenotypic selection on fruit and seed traits, as well as direct and indirect effects of fruit flies and parasitoids on plant fitness, we used piecewise structural equation models (SEM; Scheiner, Mitchell, & Callahan, 2000; Shipley, 2009). A SEM combines multiple predictor and response variables into a single framework; it is built a priori based on biological knowledge and allows for testing complex direct and indirect relationships between variables (Grace, 2006; e.g. Figure 2). A piecewise SEM allows fitting different error distributions and nonindependent observations, and, since each causal relationship is solved separately, it may fit smaller datasets compared to a traditional SEM (Lefcheck, 2016). Individual relative fitness components (bird fruit and ant seed removal) were estimated as each individual fitness measure divided by its population mean fitness, and traits were standardized to a mean of 0 and a variance of 1 prior to analyses. Therefore, the standardized path coefficients are vectors of partial regression coefficients and thus equivalent to selection gradients comparable among traits and populations (Scheiner et al., 2000; Wood & Brodie, 2016). Although the effect of increased seed dispersal on survival and establishment is unknown in our study system, we assumed that a higher dispersal delivery increased the probability for a seed to reach a suitable site and thus the probability of seed survival and seedling recruitment (Jordano & Herrera, 1995; Primack & Kang, 1989; Siepielski & Benkman, 2008a). We included forest patch identity as a random effect.

We developed three competing a priori hypotheses based on our understanding of the relationships between plants, fruit and seed traits, seed removal, fruit infestation and parasitoids (Figure 2). The initial full SEM hypothesized that both birds (Palacio et al., 2014; Palacio & Ordano, 2018; Siepielski & Benkman, 2007a) and ants (Alcántara et al., 2007; Manzaneda, Rey, & Alcántara, 2009) act as agents of selection on fruit and seed traits, so we connected the two fruit traits (fruit crop size and mean sugar concentration) and mean seed size to bird fruit removal, and mean sugar concentration and mean seed size to ant seed removal (Figure 2). The number of fruits produced is often a function of plant size and neighbour density (Minor & Kobe, 2019), so we included a path connecting tree height, DBH and the distance to the nearest neighbour to fruit crop size, as well as a correlation between tree height and DBH. Fruit flies are highly selective of fruit traits, such as fruit crop size, fruit colour, size and shape, because these are critical for oviposition and larva survival (Jordano, 1987; Poyet et al., 2015; Prokopy, 1968; Prokopy, Cooley, & Papaj, 1993). We therefore included paths connecting fruit and seed traits to infestation levels (Figure 2). In turn, birds may

also respond to fruit infestation by rejecting low attractive or unhealthy fruits (García, Zamora, Gómez, & Hódar, 1999; Janzen, 1977; Valburg, 1992), so we included a path between fruit infestation and bird fruit removal. Parasitoids are highly specialized predators, which rely on chemical, visual and mechanical cues to find their hosts (Godfray, 1994; Wajnberg, Bernstein, & Van Alphen, 2008). We thus included paths from fruit traits and fruit infestation to the proportion of parasitoids per plant (Figure 2). Finally, we added a correlation between both fitness components. Shipley's tests of directed separation were used to test the assumption that there are no missing relationships among unconnected variables (Shipley, 2009).

The initial full SEM was compared to a set of two alternative nested models built by constraining some paths to zero. Model A considered that birds find it difficult to discriminate against infested fruits. Thus, we removed the path between fruit infestation and bird fruit removal. Model B hypothesized that the proportion of parasitoids is mainly driven by infestation levels rather than by fruit and seed traits. Thereby, we removed those paths from fruit and seed traits to the proportion of parasitoids. Significant standardized linear paths indicate that selection favours either a phenotypic mean increase (if positive) or decrease (if negative). Significant standardized nonlinear paths indicate nonlinear selection against extreme phenotypes (stabilizing selection), nonlinear selection against intermediate trait values (disruptive selection) or correlational selection on a given trait combination (Lande & Arnold, 1983; Scheiner et al., 2000). Given that fruit crop size showed a right-skewed distribution, we fitted a SEM with only linear terms and a SEM with linear, quadratic and cross-product (interaction) terms for each hypothesis to obtain unbiased estimates of linear and nonlinear selection, respectively (Scheiner et al., 2000). This is because the full model (with linear, quadratic and interaction terms) gives biased linear selection coefficients, unless phenotypic traits meet multivariate normality (Lande & Arnold, 1983). Correlations between a given trait and its square were also included (Scheiner et al., 2000). Given that quadratic selection is a necessary, but not sufficient, condition to infer stabilizing or disruptive selection (Phillips & Arnold, 1989), we visually inspected plots between fruit traits and fitness when a significant quadratic path was found. The strength of indirect effects was computed as the product between coefficients of direct effects along a given path (Grace, 2006).

Due to the particular landscape structure of our study area, that is, small forest patches immersed in a grassland matrix, a patch effect on natural selection patterns is expected. That is, selection is expected to be more similar within than between patches. Although we cannot be certain of the factors accounting for this variation, this patch effect can illustrate the importance of latent environmental factors underlying how selection operates under specific spatial contexts and scales. We therefore quantified the proportion of variance explained by the fixed effects only and the combined fixed and random effects as the marginal R^2_{GLMM} and the conditional R^2_{GLMM} , respectively, following Nakagawa, Johnson, and Schielzeth (2017). Both linear and quadratic models were compared using Akaike's information criterion corrected for small sample sizes

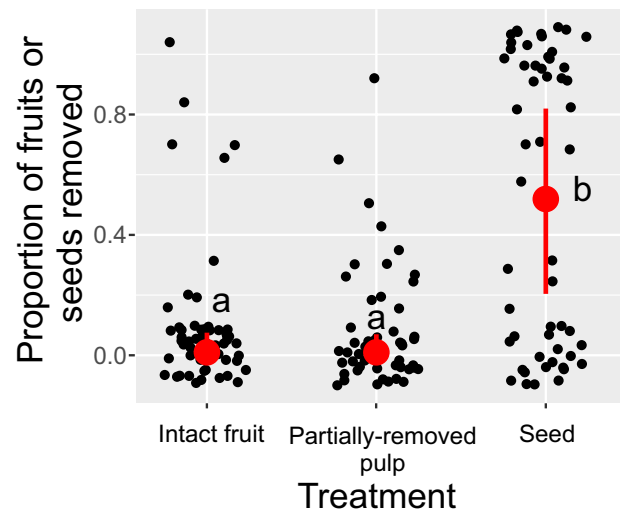


FIGURE 3 Results of cafeteria experiments (control [intact fruit], partially removed pulp and seed) on ant fruit/seed removal. Red points and lines depict estimates and 95% confidence intervals of a generalized linear mixed model (see Section 2). Jittered points (individual seeds/fruits) are also shown. Different letters indicate statistically significant differences ($p < .05$) between treatments

(AICc; Shipley, 2013). Best linear and nonlinear models were evaluated using Shipley's test of directed separation, which yields Fisher's C statistic that can be compared with a chi-square distribution (Shipley, 2009). Model fit is considered poor when Fisher's C has a $p < .05$ (Shipley, 2009). To visualize the shape of fitness surfaces, we used nonparametric cubic splines (one trait) and thin-plate splines (two traits; Morrissey & Sakrejda, 2013).

All graphs and analyses were performed in R 3.5.2 (R Core Team, 2018) using the packages lme4 (Bates, Maechler, Bolker, & Walker, 2015), piecewiseSEM (Lefcheck, 2016), nlme (Pinheiro, Bates, DebRoy, & Sarkar, 2018), mgcv (Wood, 2017), fields (Nychka, Furrer, Paige, & Sain, 2017) and ggplot2 (Wickham, 2016).

3 | RESULTS

The cafeteria experiment showed significant differences between treatments (GLMM: $F_{2,157} = 63.05$, $p < .0001$). In particular, ants removed almost six times more seeds than fruits, whereas no differences in removal between intact and partially removed pulp fruits were detected (mean proportion of intact fruits removed = 0.09 ± 0.24 , mean proportion of fruits with the pulp partially removed = 0.09 ± 0.21 , mean proportion of seeds removed = 0.53 ± 0.47 ; Figure 3). Overall, the model accounting for both fixed and random effects explained more than 80% of the variation in ant seed/fruit removal (conditional $R^2_{\text{GLMM}} = .82$ vs. marginal $R^2_{\text{GLMM}} = .26$), indicating a strong patch effect on ant seed dispersal.

Fruit fly infestation was relatively low (mean = 29.85 pupae/100 g, standard deviation = 39.28 pupae/100 g, mean percentage infestation level = 12.86%, standard deviation = 14.56%, $N = 70$). The proportion of parasitoids per tree was also relatively

low (18.00%, standard deviation = 31.98%, $N = 70$). Rearing experiments showed that both fruit fly infestation (GLMM: $F_{1,67} = 13.38$, marginal $R^2_{\text{GLMM}} = .030$, conditional $R^2_{\text{GLMM}} = .059$, $p = .0002$, estimate $\pm SE = 4.54 \pm 1.24$) and the proportion of parasitoids (GLMM: $F_{1,67} = 4.32$, marginal $R^2_{\text{GLMM}} = .034$, conditional $R^2_{\text{GLMM}} = .034$, $p = .037$, estimate $\pm SE = 4.80 \pm 2.31$) per plant were positively related to mean fruit weight.

Both the linear and nonlinear Model B were the best models and had good fit to the data (Table 1), and no missing paths were statistically significant (all p 's $> .05$). Moreover, the inclusion of a random component accounting for patch identity increased explained variation in infestation levels and ant seed removal (conditional $R^2_{\text{GLMM}} = .09$ and 0.31 vs. marginal $R^2_{\text{GLMM}} = .01$ and 0.11 , respectively), indicating a patch effect on these response variables. Both models showed that DBH and tree height were positively correlated (path coefficient = 0.466 , $p < .0001$), and these positively affected fruit crop size (DBH path coefficient $\pm SE = 0.288 \pm 0.114$, $p = .014$, tree height path coefficient $\pm SE = 0.243 \pm 0.115$, $p = .038$; Figure 4a). Birds exerted positive directional selection on fruit crop size (path coefficient $\pm SE = 0.686 \pm 0.288$, $p = .022$), indicating that tree size (height and DBH) was also indirectly selected by birds (indirect DBH path coefficient = 0.198 , indirect tree height path coefficient = 0.167). Both SEMs A and B indicated that the proportion of parasitoids was positively determined by fruit infestation levels (path coefficient $\pm SE = 0.266 \pm 0.118$, $p = .028$; Figure 4). By contrast, fruit and seed traits did not account for variation in fruit infestation or parasitoidism levels.

Ants exerted directional selection against mean seed weight (path coefficient $\pm SE = -0.226 \pm 0.105$, $p = .038$; Figure 4a). In addition, Model B also showed that birds exerted negative correlational selection on the combination of fruit crop size and seed weight (path coefficient $\pm SE = -1.047 \pm 0.414$, $p = .016$; Figure 4b), favouring either large crops with small seeds or small crops with large seeds (Figure 5a). Therefore, plants with large crops and small seeds were favoured by both seed dispersers, but those plants with small crops were only favoured by birds if they had large seeds, presumably due to a positive correlation between seed and pulp weight ($r = .40$, $N = 800$, $p < .0001$). When looking at total (direct and indirect) phenotypic

selection on seed weight, selection exerted by birds and ants was conflicting (Figure 5b). Summaries of best linear and quadratic model coefficients are available as Tables S1 and S2, respectively.

4 | DISCUSSION

4.1 | The diffuse nature of selection mediated by multiple species

Our results show that multispecies interactions represent complex systems and that both direct and indirect effects play significant roles in generating phenotypic selection on fruit and seed traits. Birds exerted negative correlational selection on the combination of fruit crop size and mean seed weight, favouring either large crops with small seeds or small crops with large seeds. In turn, ants exerted negative directional selection on mean seed weight. This suggests that the impact of ant-mediated selection on plant fitness depends on bird-mediated selection, resulting in diffuse selection (Strauss & Irwin, 2004; Strauss et al., 2005). In particular, one scenario (large crops–small seeds) favoured diplochory by enhancing plant fitness, whereas another (small crops–large seeds) led to disruptive selection on seed size. In addition, parasitoids selected plants with higher fruit fly infestation levels, and fruit flies positively selected mean fruit size, which positively correlated with mean seed weight. Therefore, higher parasitoidism indirectly led to higher plant fitness through increased seed dispersal, despite birds not responding to fruit fly infestation (e.g. no path between fruit fly and birds). This suggests either that fruit fly infestation levels are too low to affect bird consumption behaviour or that birds may not discriminate between infested and noninfested fruits. The latter is supported by the observation that no external damage by fruit flies is evident at least by human visual perception. Overall, any adaptive evolutionary responses to selection imposed from the rich community of interacting species on this single species likely represent the combined effects of multifarious selection.

4.2 | Bird- and ant-mediated selection on fruit and seed traits

The fitness surface of bird-mediated selection showed two peaks: (a) small fruit crop sizes with large seeds and (b) large fruit crop sizes with small seeds. Both peaks could be the result of different selection regimes exerted by a diverse frugivorous bird assemblage, whose species vary in morphology (e.g. gape limitation), fruit-eating behaviour and foraging preference (Palacio, Girini, & Ordano, 2017; Palacio et al., 2014). In other words, birds are expected to select optimal fruit trait combinations, rather than isolated traits (Palacio, Girini, et al., 2017; Sobral, Larrinaga, & Guitián, 2010). In particular, the first trait combination would be selected by pulp consumers who only peck the pulp, for which seed size does not represent an energetic cost (Levey, 1987; Palacio, Valoy, et al., 2017). Although this fruit-handling

TABLE 1 Comparison of piecewise structural equation fits for both linear and nonlinear models

Model	Fisher's C	df	p	AICc	K	ΔAICc
Full linear	42.95	36	.198	270.9	30	60.5
A linear	41.35	38	.326	228.9	29	18.5
B linear	45.23	42	.339	210.4	27	0.0
Full quadratic	49.77	52	.562	720.9	40	288.5
A quadratic	52.98	56	.590	534.0	39	101.6
B quadratic	58.54	60	.529	432.4	36	0.0

Abbreviations: AICc, Akaike's information criterion corrected for small sample sizes; df, degrees of freedom; K, number of parameters; ΔAICc , difference between AICc of the candidate model and the lowest AICc value among all models being compared.

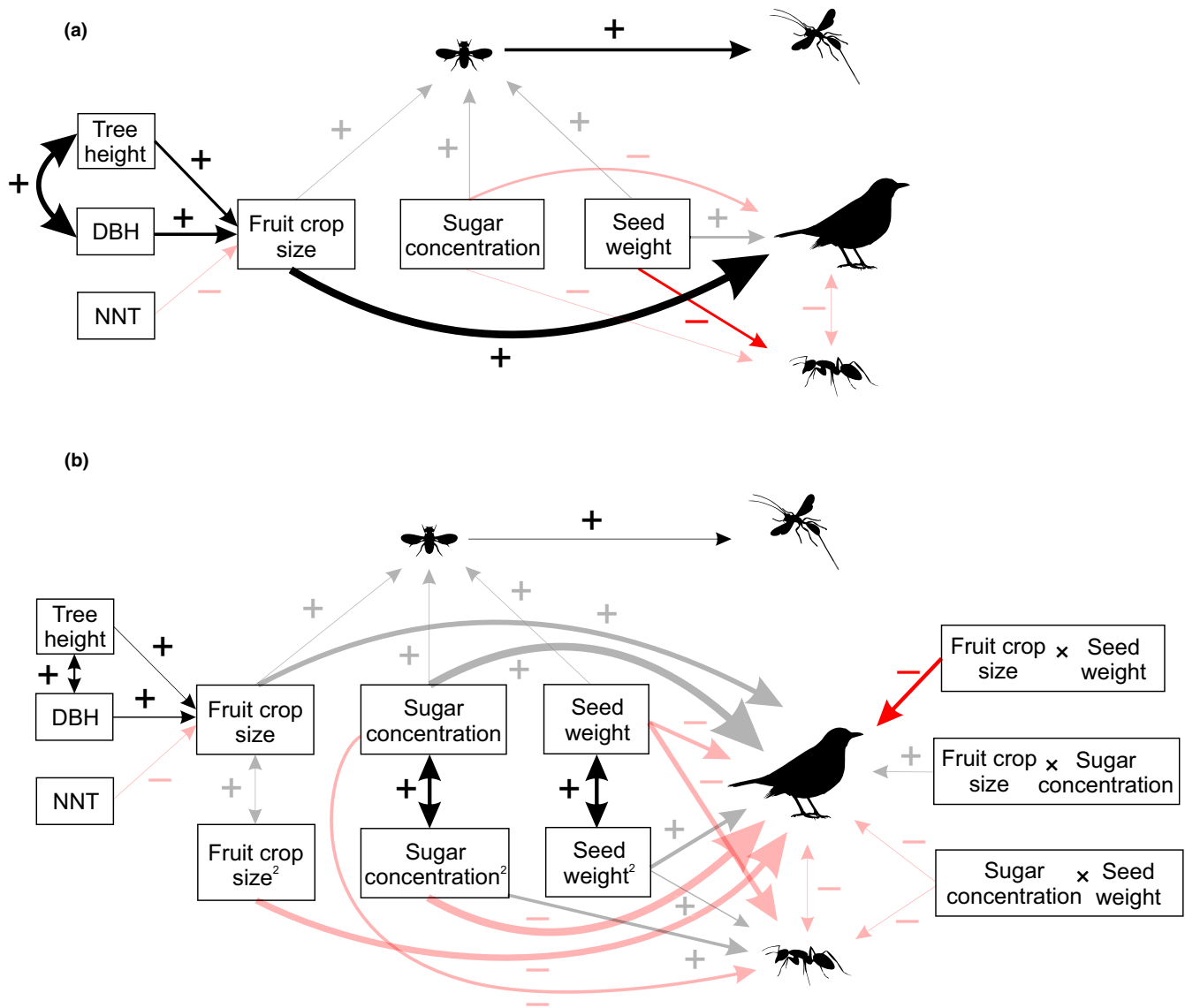


FIGURE 4 Best piecewise structural equation (SEM) models for the relationships between tree size, neighbour density, fruit and seed traits, bird fruit removal, ant seed removal, fruit fly infestation and proportion of parasitoids (black silhouettes). (a) Best linear SEM model (Table S1) and (b) best nonlinear SEM model (Table S2) are shown. The width of the arrow is proportional to the path (one-headed arrows) or correlation coefficient (two-headed arrows). Black and red indicate positive and negative relationships, respectively, whereas solid and translucent colours depict significant and nonsignificant paths, respectively. Signs indicate positive (+) or negative (−) relationships. DBH: diameter at breast height; NNT: nearest neighbour trees

behaviour is expected to have detrimental effects on seed recruitment, secondary dispersal by ants would relax this effect by dispersing fallen seeds. As our experiments showed, ants removed almost six times more seeds than either intact or pecked fruits, which supports the hypothesis that ants can act as seed dispersers. Moreover, ants exerted negative directional selection on seed size. This was expected, as body size constrains seed dispersal distances in ants (Gómez & Espadaler, 2013; Ness, Bronstein, Andersen, & Holland, 2004). The complementary seed dispersal ants provide seems to be particularly relevant in some fleshy-fruited plants, in which diplochory allowed seed removal of up to 83% of fallen diaspores in *Xylopia aromatica* (Christianini & Oliveira, 2010) and a 42% increase in seed dispersal effectiveness in *Erythroxylum ambiguum* compared to dispersal by birds

alone (Camargo et al., 2019). Our results (53% of seeds removed) fall within this range and highlight the potential and overlooked impact ants may have on seed dispersal. It should be noted that ants can act not only as mutualists, but also as antagonists by eating harvested seeds (Levey & Byrne, 1993; Penn & Crist, 2018). Moreover, seed germination on ant nests can be lower than that on the surrounding-site soil (Varela & Perera, 2003). Therefore, further studies are needed to assess the impacts of ant-mediated dispersal on seed removal, establishment and viability (Giladi, 2006).

On the other hand, the large crops–small seeds combination would be favoured by gulpers who swallow fruits whole, for which seed size is expected to be selected against (Levey, 1987; Palacio, Valoy, et al., 2017). As a result, ants would provide a redundant seed

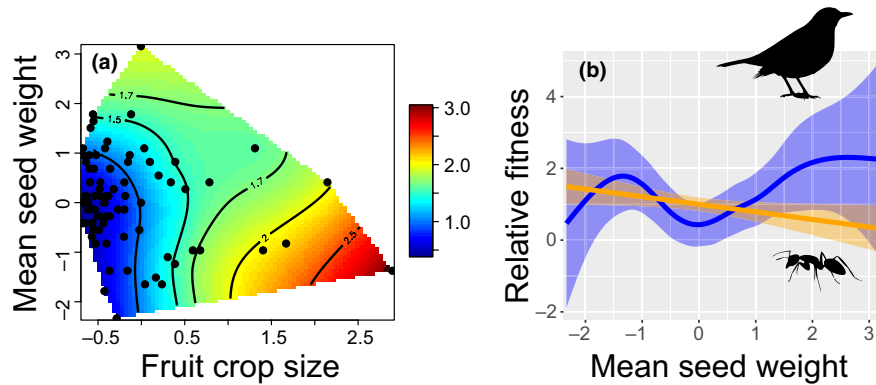


FIGURE 5 Bird- and ant-mediated phenotypic selection on fruit display traits. (a) Response surface (thin-plate splines) showing bird-mediated correlational selection between standardized fruit crop size and mean seed size. Black circles represent individual trees. Lines and scale bars depict predicted relative fitness. (b) Conflicting selection exerted by birds (blue line) and ants (orange line) on mean seed weight. Contour lines and bands depicting predictions and 95% confidence intervals from cubic splines are shown

dispersal delivery, enhancing plant fitness. In this sense, dispersed seeds are slightly but significantly heavier (around 8.5%) than nondispersed seeds in this population (Palacio et al., 2014), suggesting that large seeds are favoured by overall selection, but to such an extent of barely outweighing other counteracting selection pressures. Both trait combinations under selection suggest a trade-off between fruit number and size and that seed dispersers may shape the evolution of seed size and number. Moreover, fruit crop size is a highly heritable trait in fleshy-fruited plants (broad-sense heritability = 83.0%–99.0%; see Palacio & Ordano, 2018 and references therein) which, coupled to a strong phenotypic selection, suggests a strong response to selection. Small seeds would presumably experience low dispersal probability, but also low predation (Martínez et al., 2007). By contrast, large seeds will presumably experience high dispersal probability, but then will be selected against by post-dispersal seed predation, leading to stabilizing selection (Martínez et al., 2007; Gómez, 2004). The spiny hackberry is an interesting system to study from this perspective, because it produces only one seed per fruit, allowing to tease apart the effect of seed number within fruits on the size–number trade-off. Thus, fruit crop size equals the total number of seeds produced, and a negative correlation between fruit crop and seed size is expected. Interestingly, we found no plants with relatively large crops and large seeds (see Figure 5a), suggesting a potential trade-off between seed size and number. However, a non-significant negative effect size between fruit crop and mean seed size was found ($r = -.15$, $N = 80$, $p = .17$), suggesting that other factors, such as plant size, age, climate and resource availability, correlate with seed size (Jakobsson & Eriksson, 2000; Wulff, 1986).

4.3 | Seed removal as an early-stage fitness component

The main limitation of our study is that we have only quantified two fitness components at an early plant life stage: fruit removal by birds and seed removal by ants. As in many studies of long-lived plants, fruit and

seed removal have been largely used as fitness components in the context of animal-mediated selection (Fontúrbel & Medel, 2017; Jordano, 1995; Martínez et al., 2007; Palacio et al., 2014; Siepielski & Benkman, 2007a, 2008b; Sobral et al., 2013), under the assumption that increased seed delivery increases the probability of reaching suitable conditions, and thus seed survival and recruitment (Jordano & Herrera, 1995; Primack & Kang, 1989; Siepielski & Benkman, 2008a). Nevertheless, growing evidence shows that conflicting selection may act on post-dispersal stages of recruitment. For instance, Alcántara and Rey (2003) found that small seeds of *Olea europaea* (Oleaceae) had higher bird-mediated dispersal probabilities, but after dispersal, large seeds had higher survival probabilities. In other two studies, Gómez (2004) and Martínez et al. (2007) found that large seeds of *Quercus ilex* (Fagaceae) and *Crataegus monogyna* (Rosaceae), respectively, had higher dispersal probabilities, but large seeds had higher post-dispersal predation probabilities and thus lower survival probabilities. Despite the presence of conflicting selection, the cumulative effects of selection may still be significant as selection acting through one fitness component can influence the distribution of phenotypic traits during subsequent bouts of selection (Jordano & Herrera, 1995; Martínez et al., 2007). An appropriate analysis of plant fitness would require knowledge of the multiple sequential dispersal stages involved in the plant life cycle (Wang & Smith, 2002), yet achieving this would be extremely challenging for long-lived trees and indeed we are not aware of any study quantifying animal-mediated selection on fruit and seed traits using fitness components from seed removal to adult plant recruitment (but see Siepielski & Benkman, 2008a). To our knowledge, most studies have analysed between two and four fitness components (e.g. Fontúrbel & Medel, 2017; Gómez, 2004; Martínez et al., 2007) and rarely up to six (Alcántara & Rey, 2003).

4.4 | Strong selection pressures may exist in diffuse interactions

There is a long-held notion that multispecies assemblages of seed dispersers prevent reciprocal adaptation between plants and

seed dispersers, leading to diffuse co-evolution (Herrera, 1985; Tewksbury, 2002; Wheelwright & Orians, 1982). One of the arguments to support this statement is that frugivores exert low and inconsistent selection pressures on fruit traits, because many potential selective agents coexist (Herrera, 1985; Wheelwright & Orians, 1982). Nevertheless, growing evidence has shown that seed-dispersing animals may exert strong and consistent selection pressures on fruit and seed traits (Jordano, 1995; Martínez et al., 2007; Palacio & Ordano, 2018; Sobral et al., 2013). It should be noted that we have no data on traits under selection on seed dispersers (e.g. bird bill traits or ant body size), and we have only estimates of selection imposed by each agent, not evolutionary responses. Moreover, we still lack studies addressing the potential for temporal and spatial variation in selection on fruit crop size as well. Yet, selection on the latter trait could vary spatially (e.g. high variation in fruit crop size among populations) and temporally (e.g. absence of selection during very small fruit crop years), both of which could affect the opportunity for selection. Indeed, selection can be strong and drive trait evolution only during infrequent years of large seed production (Siepielski & Benkman, 2007b). Although we quantified phenotypic selection in only one episode, our results show that strong selection pressures on fruit traits may be exerted by seed dispersers in the presence of multiple interactions. What remains unknown is how these varying selection pressures generate differences in adaptive evolution across the landscape.

A second constraint argued for reciprocal adaptation between plants and seed dispersers is that antagonist-mediated selection relaxes total selection exerted on fruit and seed in post-dispersal stages, favouring diffuse co-evolution (Herrera, 1985; Wheelwright & Orians, 1982). For instance, several studies have found that large seeds are more likely to be dispersed or established, but also to be attacked by seed predators (Alcántara & Rey, 2003; Gómez, 2004; Manzaneda et al., 2009; Siepielski & Benkman, 2007a). Even in the presence of conflicting selection, however, total selection may be still significant (Martínez et al., 2007), increasing phenotypic trait variation at the population level (Siepielski & Benkman, 2010). In the spiny hackberry, ants exerted conflicting selection on seed size imposed by birds in one partial selective scenario. Regardless of the categorical label put to interactors participating in the system (mutualist or antagonist), our results show that counteracting selective pressures on plant traits arise from interspecific differences in scaling effects, behaviour and foraging preferences on fruit traits (Morales, García, Martínez, Rodríguez-Pérez, & Herrera, 2013; Peters, Oberrath, & Böhning-Gaese, 2003). Overall, our results suggest that strong selection on traits may still arise, even in what are often perceived as diffuse species interactions, highlighting the evolutionary potential of phenotypic trait variation in multispecies interactions.

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DATA AVAILABILITY STATEMENT

The dataset "Data from: Selection on fruit traits is mediated by the interplay between frugivorous birds, fruit flies, parasitoid wasps, and seed-dispersing ants" has been approved for publication in Dryad. Data <https://doi.org/10.5061/dryad.gxd2547hn>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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