



The Strength and Drivers of Bird-Mediated Selection on Fruit Crop Size: A Meta-Analysis

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In seed-dispersal mutualisms, the number of fruit a plant displays is a key trait, as it acts as a signal for seed dispersers that entails fruit removal and exportation of reproductive units (fruit crop size hypothesis). Although this hypothesis has gained general acceptance, forces driving the shape and strength of natural selection exerted by birds on fruit crop size remains an unresolved matter. Here, we propose that ecological filters promoting high functional equivalence of interacting partners (similar functional roles) translate into similar selection pressures on fruit crop size, enhancing selection strength on this trait. We performed a meta-analysis on 50 seed-dispersal systems to test the hypothesis that frugivorous birds exert positive selection pressure on fruit crop size, and to assess whether different factors expected to act as filters (fruit diameter, fruit type, fruiting season length, bird functional groups, and latitude) influence phenotypic selection regimes on this trait. Birds promote larger fruit crop sizes as a general pattern in nature. Short fruiting seasons and a high proportion of species belonging to the same functional group showed higher selection strength on fruit crop size. Also, selection strength on fruit crop size increased for large-fruited species and toward the tropics. Our results support the hypothesis that fruit crop size represents a conspicuous signal advertising the amount of reward to visually driven interacting partners, and that both plant and bird traits, as well as environmental factors, drive selection strength on fruit display traits. Furthermore, our results suggest that the relationship among forces impinged by phenology and frugivore functional roles may be key to understand their evolutionary stability.

Keywords: frugivory, mutualism, phenotypic selection, plant-animal interactions, seed dispersal

INTRODUCTION

A major challenge in evolutionary ecology is to understand how mutualistic interactions between plants and animals drive the evolution of plant phenotype (Strauss and Irwin, 2004). Among plant traits involved in mutualistic interactions, the fruits that plants display are a major target of natural selection. Generally, these structures advertise the amount of reward (for example, the larger the fruit, the higher the reward) to their interacting partners (Snow, 1971; Schaefer and Ruxton, 2011). Under this scenario of signal-reward correlation (Benitez-Vieyra et al., 2010), the expected outcome is directional selection on the number of fruit (Snow, 1971; Carr, 1992; Ortiz-Pulido and Rico-Gray, 2000), as well as other fruit and seed traits (e.g., size, color, water and nutrient content, coat thickness; Jordano, 2000; Herrera, 2002). However, this selection regime may be modified by

different factors, such as the costs of fruit production or selection pressures imposed by antagonistic interactors (Jordano, 1987; Parciak, 2002; Russo, 2003; Burns, 2015; Muñoz et al., 2017). In this sense, the underlying mechanism of the evolution of repeated plant structures (leaves, flowers, and fruits) is still poorly understood (Herrera, 2009, 2017).

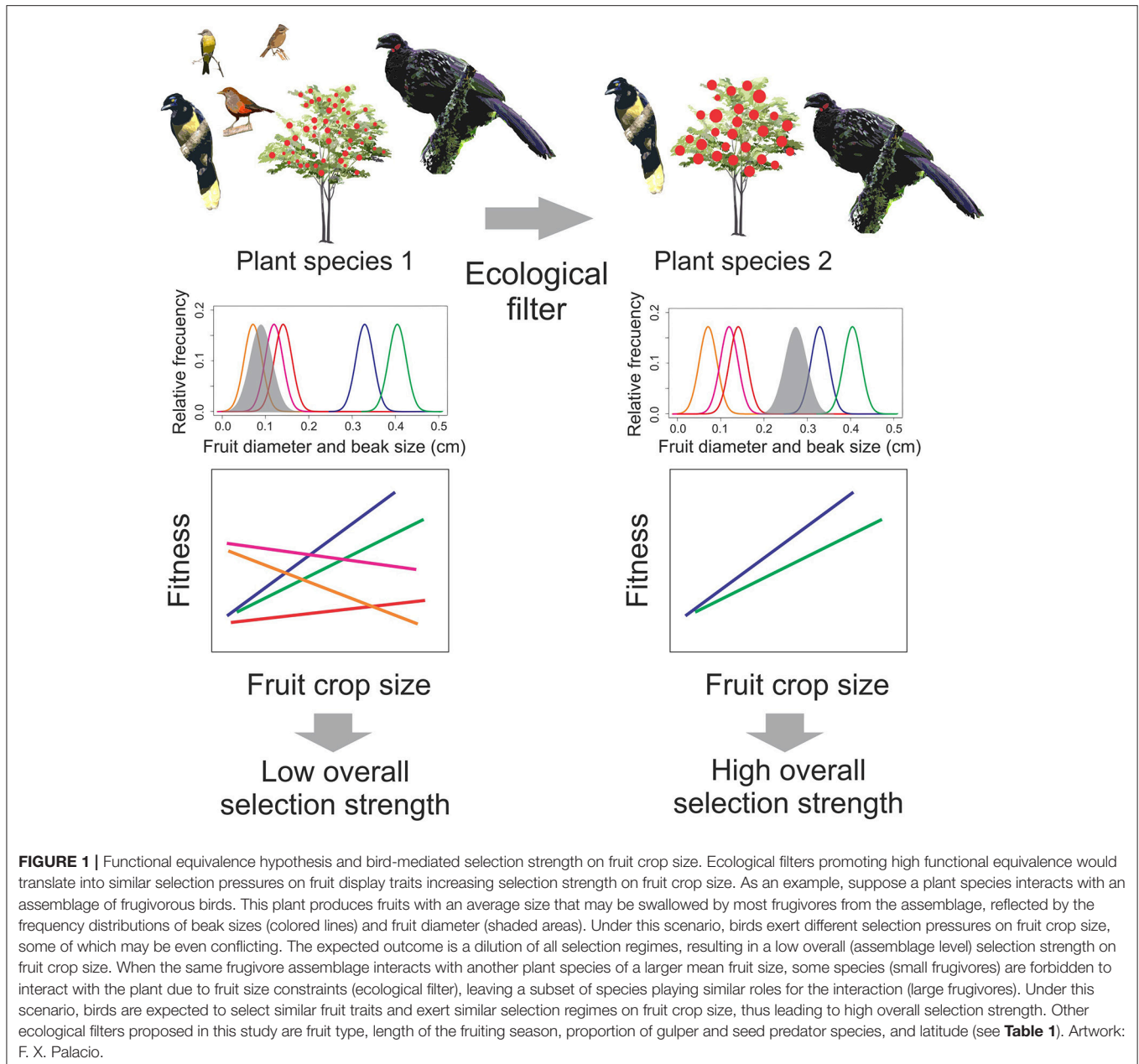
In seed dispersal mutualisms, frugivores act as natural selection agents on different fruit display traits (e.g., fruit and seed size, nutrient content, color), including the number of ripe fruits (i.e., fruit crop size; Jordano, 1995; Sobral et al., 2010; Palacio et al., 2017a). Indeed, fruit crop size has been advocated as the principal target of bird-mediated selection (Snow, 1971; Howe and Estabrook, 1977). In his seminal work, David Snow proposed that plants offering a relatively high number of fruit should increase fruit removal (the “fruit crop size hypothesis”; Snow, 1971; McKey, 1975; Howe and Estabrook, 1977). Several surrogates for fruit removal have been used to test this hypothesis, mainly the number of fruit removed, the proportion of fruit removed and bird visitation rate (Davidar and Morton, 1986; Foster, 1990; Ortiz-Pulido and Rico-Gray, 2000). The fruit crop size hypothesis also assumes that fruit removal bears a positive relationship with effective seed dispersal away from the mother plant (Howe and Estabrook, 1977). Although there is field experimental evidence supporting this hypothesis (Christensen et al., 1991; Ortiz-Pulido et al., 2007), evidence from field studies have had mixed results. For instance, in a qualitative review, Carr (1992) found positive linear relationships between fruit crop size and removal (number of fruit removed) in 18 out of 19 temperate and tropical seed dispersal systems. By contrast, only 3 out of 19 seed dispersal systems showed a positive relationship between fruit crop size and removal (proportion of fruit removed), whereas no relationships in the remaining 16 were found. Further, the shape and intensity of bird-mediated selection on fruit crop size may vary within plant populations in different selection episodes. Foster (1990), for instance, found a positive relationship between fruit crop size and bird visitation in 1 year, but found no relationship in previous years in a population of *Allophylus edulis*. Similarly, Ortiz-Pulido and Rico-Gray (2000) found that the covariation between fruit crop size and bird visitation varied drastically from non-significant to positive in a population of *Bursera fagaroides*. These studies have proposed multiple ecological factors to explain fruit removal by birds and their potential evolutionary consequences on seed dispersal (see also Jordano, 2000; Herrera, 2002 for reviews). However, there has not been as yet a quantitative review of the relationship between fruit crop size and fruit removal, nor of the drivers of variation in selection regimes on fruit crop size to disentangle their underlying mechanisms.

As we see it, factors characterizing seed dispersal systems (Snow, 1971; Howe and Estabrook, 1977) that will drive the shape and intensity of selection on fruit crop size fall into three categories: (1) plant traits, such as plant size, fruit size, pulp and nutrient content, and fruiting phenology (Wheelwright, 1993; Burns, 2004, 2005; Sobral et al., 2010; Palacio et al., 2014); (2) bird assemblage traits, related to the functional role of frugivores (Galetti et al., 2013; Morales et al., 2013; Dehling et al., 2016;

Palacio et al., 2017b), and (3) environmental or abiotic factors (Hampe, 2003; Márquez et al., 2004; Sobral et al., 2013). We hypothesized that the strength of selection on fruit crop size stems from ecological filtering by constraining certain bird species to interact with a plant population. Basically, ecological filters promoting high functional equivalence (i.e., species with similar roles for the interaction) would translate into similar selection pressures on fruit display traits (Zamora, 2000; Strauss and Irwin, 2004; hereafter “functional equivalence hypothesis”; **Figure 1**).

There are two central processes increasing selection strength on fruit crop size. The first is related to the fruit crop size itself. Fruit crop size is a key trait for conspicuousness and fruit consumption by birds (Ordano et al., 2017; Palacio et al., 2017a), so plants with more fruits are consumed more. Fruit consumption by birds leads to a positive effect on seed germination, because seed gut passage increases the probability of successful seed dispersal (Traveset and Verdú, 2002; Verdú and Traveset, 2004). If we also consider that fruit crop size is a heritable trait (Wheelwright, 1993; Hancock, 2008), its evolutionary rate will increase with increased selection strength. The second process is that increased functional equivalence involves several species and hence more interacting individuals. Although seed dispersal effectiveness is usually highly variable between species (Ruggera et al., 2016), increased abundance of fruit-consuming species results in a greater number of fruit removed and seeds dispersed (Blendinger, 2017). Therefore, interaction strength will increase, which predicts an increase in the strength of selection (selection intensity for standardized values; Benkman, 2013). A greater number of individuals interacting and playing the same role (i.e., functional equivalent species) will lead to higher interaction strength. The regime (or shape) of the relationship between the interaction strength and the selection intensity will be thus a function of the interacting fruit-consuming birds. If a subset of species after events of ecological filtering is composed by a higher proportion of effective seed dispersers, selection intensity will increase. On the other hand, if the subset of species is composed by a higher proportion of seed predators or non-effective seed dispersers, selection on fruit crop size will be weakened. Altogether, the positive feedback among generations leads selection to a run-away process, increasing the strength of selection on fruit crop size.

Filters such as large fruits (physical constraints on fruit-handling and ingestion; Wheelwright, 1985; Levey, 1987), low pulp-to-seed ratio fruits (benefit-cost ratio based on optimal foraging; Hegde et al., 1991), short fruiting seasons (reduced temporal species overlap; Howe and Estabrook, 1977; Ting et al., 2008), and high latitudes (environmental constraints; Kissling et al., 2009), would restrict some bird species' ability to interact with a plant species. This would leave as interacting partners those species with similar functional roles (increased functional equivalence), promoting higher selection strength on fruit crop size, particularly effective seed dispersers (**Figure 1**). In other words, these factors would filter bird species on the basis of ecological traits reflecting resource use, increasing both



functional equivalence and selection strength on fruit crop size (**Figure 1**). This idea is partly analogous to the “environmental or niche filtering hypothesis” in community ecology, which proposes that coexisting species are more similar to one another than would be expected by chance because environmental conditions act as a filter allowing a set of species traits to persist (Zobel, 1997; Laliberté et al., 2014; Kraft et al., 2015). Under this premise, a high interaction frequency of species belonging to the same functional group, such as gulper, pulp consumer, or seed predator species (differences in fruit choice criteria; Levey, 1987; Foster, 1990; Palacio et al., 2017b) will also promote higher selection strength on fruit crop size. However, this hypothesis assumes that the filtered subset of bird species

includes species with positive consequences on plant fitness, i.e., effective seed dispersers, yet there could also be non-legitimate seed dispersers or even a combination of seed predators and seed dispersers.

Although each of these factors propose specific ecological predictions (**Table 1**), little attempt has been made to quantitatively synthesize the patterns of phenotypic selection on fruit crop size related to them. Here, we assessed the strength of bird-mediated phenotypic selection on fruit crop size with a meta-analysis. First, we evaluated the widespread assumption about whether birds exert selection pressures on fruit crop size. We then evaluated how much variation in the strength of phenotypic selection on fruit crop size

TABLE 1 | Ecological hypotheses and predictions proposed for bird-mediated phenotypic selection strength on fruit crop size.

Factor	Hypothesis	Expected selection strength on fruit crop size	References
Fruit size (plant trait)	Fruit size imposes physical constraints to ingestion reducing the number of frugivore species	Higher for large fruits	(Wheelwright, 1985; Levey, 1987)
Fruit type (plant trait)	Frugivores maximize benefit-cost ratios. Fruits with numerous seeds (berries) have higher pulp-to-seed ratios relative to drupes and arils	Higher for drupes and arils	(Jordano, 1995; Witmer and Van Soest, 1998; Levey and Martínez del Río, 2001)
Fruiting season (plant trait)	Peaked fruiting seasons reduce the number of frugivores relative to extended fruiting seasons	Higher for short fruiting seasons	(Howe and Estabrook, 1977)
Fruit-handling behavior (bird assemblage trait)	Gulpers (swallow fruits whole), pulp consumers (mash or peck fruits), and seed predators (crush and destroy seeds) represent functional groups that respond to fruit crop size	Higher for high proportion of a functional group	(Levey, 1987; Foster, 1990)
Latitude (environmental factor)	Frugivore richness increases toward the tropics. Also, fruiting seasonality increases with latitude	Higher toward the poles	(Herrera, 1985; Ting et al., 2008; Kissling et al., 2009)

Between brackets the type of factor to which each factor belongs (plant trait, bird assemblage trait, or environmental factor) is shown.

is accounted for plant traits (fruit type and size, length of the fruiting season), bird assemblage traits (fruit-handling behavior) and environmental factors (latitude). Under the premise of signal-reward correlation, our main predictions are that (1) birds exert positive directional selection on fruit crop size, and (2) ecological filters leading to high functional equivalence of the frugivores (large fruits, fruit types with low pulp-to-seed ratio, short fruiting phenologies, similar fruit-eating behavior, high latitudes) promote higher selection strength.

MATERIALS AND METHODS

Search and Selection Protocol

We carried out a review of the literature available at the database ISI Web of Science (Thompson Scientific, 2009) using “fruit,” “crop,” “selection,” and “birds” as keywords to find published papers in any year (until 1 September 2015) or language. We then checked out the references of these studies to find earlier publications. With this list and the studies carried out by us and collaborators (Palacio et al., 2017a,b) we completed a list of 100 references (Tables S1, S2, Figure S1). We used the Pearson product-moment correlation coefficient as effect size measure to determine the strength and direction of bird-mediated selection on fruit crop size. Although directional selection is properly measured using the standardized directional selection differential i , which represents the covariance between relative fitness (mean = 1) and a standardized phenotypic trait (mean = 0, variance = 1; Brodie et al., 1995), the advantage of Pearson’s correlation is that it is widespread as a statistical descriptor, and well-developed meta-analytical methods exist (Hedges and Olkin, 1985). Moreover, r is proportional to i : $r = i/\sqrt{I}$, where I is the variance in relative fitness (i.e., opportunity for selection) and is a measure of the power to detect directional selection (Hersch and Phillips, 2004). We therefore selected studies that reported data on fruit crop size and any of three quantitative estimators deemed as surrogate for fitness

measures (Brodie and Janzen, 1996; McGraw and Caswell, 1996; Kingsolver et al., 2001; Schupp et al., 2010): bird visitation rate, the number of fruit removed or the proportion of fruit removed. References without this information were excluded (Figure S1).

We defined a visit as the event in which a bird approached a plant and consumed at least one fruit. Several studies have widely used these three fitness components to assess bird-mediated selection on fruit display traits (e.g., Jordano, 1995; Martínez et al., 2007; Sobral et al., 2010; Palacio et al., 2014). We also assumed a positive covariation between short-term dispersal success (a fitness component) and long-term plant fitness (McGraw and Caswell, 1996; Muñoz et al., 2017). Values for Pearson’s r were also obtained from one tail P -values when sample size was known (Rosenthal and DiMatteo, 2001), and Spearman’s ρ were converted into Pearson’s r following Rupinski and Dunlap (1996) as: $r = 2\sin(\rho \times \pi/6)$. In several cases, we were able to compute r from raw data. In those studies that raw data were not reported, we estimated approximate values by processing published plots with DATA THIEF III version 1.6 (Tummers, 2010). The final database and the complete list of corresponding references are shown as Supplementary Material (Tables S1, S2).

Effect Sizes and Publication Bias

Correlation coefficients were transformed to Zr using Fisher’s algorithm (Hedges and Olkin, 1985). A single mean effect size was computed for species with more than one effect size by averaging Zr values (Rosenthal and DiMatteo, 2001) to account for dependence among species. Once we obtained and transformed effect sizes per species, we computed mean effect sizes for the three fitness components (bird visitation rate, number, and proportion of fruit removed). Within-species variances were computed as $1/(n-3)$, where n is sample size (Hedges and Olkin, 1985). For comparative purposes, and whenever possible, we computed standardized directional selection differentials. Overall effect sizes were considered

statistically significant if 95% confidence intervals did not include zero.

We assessed publication bias both graphically, by funnel plots, and statistically by rank correlations between effect sizes and samples variances (Begg and Mazumdar, 1994). Spearman's rank correlations between effect size and sampling variance were non-significant for the proportion of fruit removed ($\rho = -0.050$, $P = 0.779$), but it was significant for the bird visitation rate ($\rho = 0.450$, $P = 0.040$) and the number of fruit removed ($\rho = 0.511$, $P = 0.003$), indicating the presence of publication bias (Figure S2). We therefore used the Copas selection model (Copas, 1999) to correct mean effect sizes. This model has two components: a model for the effect size, and a "selection" model that gives the probability that study i is published. A Pearson correlation between these two components estimated by maximum likelihood quantifies the magnitude of publication bias; the stronger the correlation, the higher the probability that more extreme effect sizes are published.

Phylogenetic Relationships Between Plant Species

Phylogenetic relationships may lead to non-independence in effect sizes, due to shared phylogenetic history among taxa (Lajeunesse, 2009). We therefore constructed phylogenetic hypotheses using S.Phylomaker, based on the megaphylogeny of vascular plants PhytoPhylo (Qian and Jin, 2016; Figure S3). This phylogeny includes all extant families of gymnosperms and angiosperms, provides ages of all branches, and includes five times as many genera and 55 times more species than does the newest version of angiosperm supertrees derived from Phylomatic (i.e., tree version R20120829; Webb and Donoghue, 2005). We estimated phylogenetic signal in effect sizes with Pagel's λ according to a Brownian motion model of evolution where $\lambda = 0$ indicates no phylogenetic signal, and $\lambda = 1$ indicates high phylogenetic signal (Pagel, 1999). P -values were computed with 999 randomizations of species across the tips of the phylogeny. Pagel's λ values for correlations between fruit crop size and visitation rate, the number of fruit removed and the proportion of fruit removed were $\lambda = 1.000$ ($P = 0.151$), $\lambda = 0.325$ ($P = 1.000$), and $\lambda = 0.406$ ($P = 1.000$), respectively. This indicates that no effect size expressed phylogenetic inertia, and a phylogenetically controlled meta-analysis is thus unnecessary (Lajeunesse, 2009; Chamberlain et al., 2012).

Factors Affecting Phenotypic Selection on Fruit Crop Size

To test for the heterogeneity of effect sizes we used Cochran's Q , which is computed as the weighted sum of squared differences between individual study species and the mean effect size (Hedges and Olkin, 1985). As a complement, we also computed the I^2 index to quantify the degree of heterogeneity in a meta-analysis, which measures the percentage of the total variability in effect sizes due to between-studies heterogeneity (Higgins and Thompson, 2002; Huedo-Medina et al., 2006). We then assessed the influence of factors on mean effect sizes to explain variation in phenotypic selection on fruit crop size. We fitted mixed-effects

models using both categorical (fruit type: aril, drupe, or berry) and continuous variables (length of the fruiting season, mean fruit diameter, proportion of gulper, pulp consumer and seed predator species, and latitude) as fixed effects. Mixed- or random-effects meta-analysis assumes that the studies analyzed represent a random sample of effect sizes by including a component of between-study variation (study-specific random effect) into the uncertainty of the effect size parameters and their estimates (Hedges and Olkin, 1985). We selected these variables since most studies included information on these factors. The proportion (relative richness) of gulpers, pulp consumers, and seed predators were used instead of interaction frequency, as most studies did not report the latter. We considered "fleshy fruit" as any fleshy diaspore (dispersal unit of seeds plus fleshy structures covering the seeds; Herrera, 2002), so aril was categorized as a fruit type. Regarding bird foraging behavior, we categorized gulpers as species that swallow fruits whole, pulp consumers as those that mash or peck fruits, and seed predators as those that crush and typically destroy seeds (Foster, 1987; Levey, 1987). The length of the fruiting season and fruit diameter were log-transformed due to right-skewed distributions. The proportion of gulper and pulp consumer species were highly correlated ($r < -0.90$), so we only included the former. To assess the importance of explanatory variables, we adopted an information-theoretic approach based on Akaike's Information Criterion corrected for small sample sizes (AICc), which allows identifying best models given a certain set of plausible hypotheses (Johnson and Omland, 2004; Burnham et al., 2011). We fitted four non-nested main models per fitness component (bird visitation rate, number and proportion of fruit removed), which represented a trade-off between the classification of factors proposed here (plant traits, bird assemblage traits and environmental factors) and differences in sample sizes: a "plant trait" model 1 (fruit type + fruit diameter), a "plant trait" model 2 (length of the fruiting season), a "bird assemblage trait" model (proportion of gulper species + proportion of seed predator species), and an "environmental model" (latitude). For each of the four main models, all the possible nested models were ranked based on their AICc, and those models with the lowest AICc in a range such that $\Delta AICc < 2$ were identified as the best models. To complement this analysis and test the support of our results, we fitted a model for bird visitation rate, number and proportion of fruit removed including all variables.

All analyses were performed in R 3.4.2 (R Core Team, 2017), using the packages phytools (function *phylosig*; Revell, 2012), metafor (function *rma*; Viechtbauer, 2010), metasens (function *copas*; Schwarzer et al., 2016), and glmulti (function *glmulti*; Calcagno, 2013).

RESULTS

Bird Mediated-Selection on Fruit Crop Size

Data of 50 plant species from 27 families (44 published and 5 unpublished studies) met the selection criteria to assess phenotypic selection on fruit crop size (see Figures S3, S4). Most families were represented by 1 or 2 species, but Rosaceae,

Burseraceae, and Myristicaceae were represented by 7, 6, and 5 species, respectively. The median number of plants monitored per species within a publication was 17 (mean = 43.7, $SD = 61.9$, range = 5–278). Most species were represented by only one study; only data for *Olea europaea* (Oleaceae), *Virola surinamensis* (Myristicaceae), and *Crataegus monogyna* (Rosaceae) were available from 2, 3, and 4 studies, respectively. All continents (except for Asia and Antarctica) were represented in the meta-analysis, with most data from the Americas (31 studies) and Europe (12 studies; Figure S4). Significant positive effects (z -transformed values) of bird-mediated selection on fruit crop size were detected for bird visitation rate (mean bias-uncorrected effect size = 0.584, $n = 21$, 95% CI = 0.385–0.783; mean bias-corrected effect size = 0.400, $n = 21$, 95% CI = 0.188–0.613) and the number of fruit removed (mean bias-uncorrected effect size = 1.640, $n = 32$, 95% CI = 1.390–1.890; mean bias-corrected effect size = 1.300, $n = 32$, 95% CI = 1.181–1.419), but not for the proportion of fruit removed (mean bias-uncorrected effect size = 0.098, $n = 34$, 95% CI = –0.017 to 0.213; mean bias-corrected effect size = 0.097, $n = 34$, 95% CI = –0.011 to 0.211). Moreover, between-species heterogeneity was high (bird visitation rate $I^2 = 80.10\%$, number of fruit removed $I^2 = 94.59\%$; proportion of fruit removed $I^2 = 71.94\%$) and significant for the three overall effect sizes (bird visitation rate $Q = 73.573$, $df = 20$; number of fruit removed $Q = 497.432$, $df = 31$; proportion of fruit removed $Q = 98.103$, $df = 33$; all P 's < 0.0001). These results therefore justified our subsequent analyses of factors explaining variation in bird-mediated selection on fruit crop size.

Directional selection differentials were consistent with results using Pearson's correlation as effect size. Differentials showed positive directional selection for the three fitness components (bird visitation rate, number, and proportion of fruit removed). Selection strength on fruit crop size was stronger for the number of fruit removed (median = 1.030, range = 0.033–2.336, $n = 31$) and bird visitation rate (median = 0.473, range = –0.483–1.581, $n = 23$), and it was lowest for the proportion of fruit removed (median = 0.041, range = –0.261 to 0.586, $n = 36$). It should be noted that selection differentials measure both direct selection on a given phenotypic trait and indirect selection through correlations with other traits (Lande and Arnold, 1983), so these values should be interpreted with some caution.

Factors Affecting Phenotypic Selection on Fruit Crop Size

Both plant (length of the fruiting season, mean fruit diameter) and bird (proportion of species belonging to the same functional group) traits, as well as environmental factors (latitude) explained variation in bird-mediated selection on fruit crop size (Tables 2, 3, Figure 2). For the three fitness measures higher selection strength was detected in plants with shorter fruiting seasons and higher proportion of gulper species (Table 3, Figure 2). Also, for the proportion of fruit removed, higher selection strength was detected in plants with larger fruits (Table 3, Figure 2). For the number and proportion

of fruit removed, the proportion of seed predators explained variation in phenotypic selection on fruit crop size but showed opposite trends (Table 3, Figure 2). In particular, seed-dispersal systems with higher proportion of seed predators showed either higher or lower selection strength on fruit crop size for the proportion and number of fruit removed, respectively. Finally, selection strength increased toward the equator for bird visitation rate (Table 3, Figure 2). Models with all variables gave similar qualitative results despite their low sample size (Table S3).

DISCUSSION

As Snow (1971) proposed in the first study on the evolutionary ecology of seed dispersal by birds, our meta-analysis suggests that fruit crop size represents a prominent target of bird-mediated selection, and that birds promote larger fruit crop sizes as an overall pattern in nature. After Snow (1971), numerous authors have found a positive association between fruit crop size and fruit removal (Howe and Vande Kerchove, 1981; Davidar and Morton, 1986; Jordano, 1987; Murray, 1987; Foster, 1990; Carr, 1992; Sallabanks, 1992; Laska and Stiles, 1994; Ortiz-Pulido and Rico-Gray, 2000; Palacio et al., 2017b; see also Tables S1, S2). Although the underlying mechanism of this hypothesis is still unclear, it has been traditionally assumed that frugivores perceive fruit display as a signal that determines fruit choice and, consequently, fruit removal (Snow, 1971; Murray, 1987; Willson and Whelan, 1990; Schmidt et al., 2004; Ordano et al., 2017). For instance, in a recent study of fruit traits of 62 plant species of a subtropical Andean forest, Ordano et al. (2017) found that fruit consumption was explained by a positive interaction between fruit crop size and chromatic contrast, supporting the idea that conspicuousness of fruit display acts as a strong signal for visually driven frugivores. However, this hypothesis remains contentious, as several studies have shown no evidence that fruit's signals (e.g., color) are adapted to maximize fruit conspicuousness (Schaefer et al., 2007; Burns et al., 2009; Stournaras and Schaefer, 2017). In this sense, our results do support the hypothesis that fruit crop size represents a conspicuous signal at the plant level that increases fruit detectability, but also reveals the need to assess the interplay with other fruit traits advertising rewards to seed dispersers.

Moreover, the positive directional selection regime on fruit crop size depended on the fitness component. In particular, both the number of fruit removed and visitation rate would be fitness components of fruit removal under selection pressures, contrary to the proportion of fruit removed. This agrees with a few studies quantifying the three fitness components within the same study system (Howe and De Steven, 1979; Howe and Vande Kerchove, 1979; Howe, 1980) and supports the view that bird behavior promotes absolute rather than proportional dispersal success (Davidar and Morton, 1986; Izhaki, 2002; Stournaras and Schaefer, 2017). From a theoretical perspective, the proportion of fruit removed has been considered a benefit-cost ratio for the plant, since it relates the reproductive investment to the number of dispersed seeds (Herrera, 1991; Willson and Whelan,

TABLE 2 | Set of models relating explanatory variables with bird-mediated selection on fruit crop size.

Fitness component	Model	Submodel	logL	k	AICc	ΔAICc	w _i	
Bird visitation rate	"Plant trait" 1	Null	-14.51	2	33.69	0.00	0.73	
		Mean fruit diameter (log)	-14.50	3	36.42	2.73	0.19	
		Fruit type	-12.15	5	38.30	4.61	0.07	
		Fruit type + mean fruit diameter (log)	-12.08	6	42.15	8.47	0.01	
	"Plant trait" 2	Length of the fruiting season (log)	-11.09	3	29.78	0.00	0.88	
		Null	-14.51	2	33.69	3.90	0.12	
	"Bird assemblage trait"	Proportion of gulper species	-10.21	3	28.01	0.00	0.69	
		Proportion of gulper species + Proportion of seed predator species	-10.15	4	31.16	3.15	0.14	
		Proportion of seed predator species	-11.92	3	31.45	3.44	0.12	
		Null	-14.51	2	33.69	5.68	0.04	
	"Environmental"	Null	-14.51	2	33.69	0.00	0.72	
		Null	-14.51	2	33.69	0.00	0.72	
Number of fruit removed	"Plant trait" 1	Absolute latitude	-14.09	3	35.59	1.90	0.28	
		Null	-29.63	2	63.68	0.00	0.57	
		Mean fruit diameter (log)	-29.42	3	65.73	2.05	0.20	
		Fruit type	-28.22	4	65.97	2.29	0.18	
		Fruit type + mean fruit diameter (log)	-28.21	5	68.82	5.14	0.04	
	"Plant trait" 2	Length of the fruiting season (log)	-19.99	3	47.24	0.00	1.00	
		Null	-34.48	2	73.37	26.13	0.00	
	"Bird assemblage trait"	Proportion of gulper species	-17.98	3	43.56	0.00	0.48	
		Proportion of seed predator species	-18.12	3	43.84	0.28	0.42	
		Proportion of gulper species + Proportion of seed predator species	-17.96	4	46.78	2.94	0.10	
		Null	-34.48	2	73.37	29.54	0.00	
	"Environmental"	Null	-34.48	2	73.37	0.00	0.77	
		Absolute latitude	-34.47	3	75.81	2.43	0.23	
	Proportion of fruit removed	"Plant trait" 1	Mean fruit diameter (log)	-6.69	3	20.19	0.00	0.92
			Fruit type	-8.86	5	25.72	5.54	0.06
			Null	-12.31	2	29.01	8.82	0.01
			Fruit type + mean fruit diameter (log)	-5.31	6	29.86	9.68	0.01
		"Plant trait" 2	Length of the fruiting season (log)	-5.02	3	17.25	0.00	1.00
Null			-12.31	2	29.01	11.76	0.00	
"Bird assemblage trait"		Proportion of gulper species + Proportion of seed predator species	-1.85	4	14.56	0.00	0.73	
		Proportion of seed predator species	-4.70	3	16.99	2.44	0.21	
		Proportion of gulper species	-6.00	3	19.60	5.04	0.06	
		Null	-12.31	2	29.01	14.45	0.00	
"Environmental"		Null	-12.31	2	29.01	0.00	0.76	
		Absolute latitude	-12.23	3	31.27	2.26	0.24	

Log-likelihood (logL), number of model parameters (k), Akaike Information Criterion corrected for small sample sizes (AICc), and Akaike weights (w_i) are shown. The null model represents the intercept-only model. The "plant trait" model 1 includes fruit type and mean fruit diameter, the "plant trait" model 2 includes length of the fruiting season (i.e., phenology), the "bird assemblage trait" model includes the proportion of gulper species and the proportion of seed predator species, and the "environmental" model includes latitude.

1993). Our results suggest that the number of fruit removed is the principal fitness component, at least at this reproductive stage. From the plant's perspective, fruit production should be maximized at the limit of the costs of fruit production to guarantee seed dispersal in a competitive scenario for seed dispersers (Howe and Estabrook, 1977; Albrecht et al., 2015; Donoso et al., 2017). It is worth mentioning that a greater dispersal success (absolute and relative) does not necessarily entails greater recruiting success, due to uncoupling between

successive recruitment stages (Jordano and Herrera, 1995; Wang and Smith, 2002; Palacio et al., 2014; but see Blendinger et al., 2011).

Factors Affecting Bird-Mediated Selection Strength on Fruit Crop Size

The functional equivalence hypothesis proposes that different ecological filters (e.g., phenology, plant traits, environmental factors) remove species and leave those with similar trait values

TABLE 3 | Effects of explanatory variables on bird-mediated selection on fruit crop size.

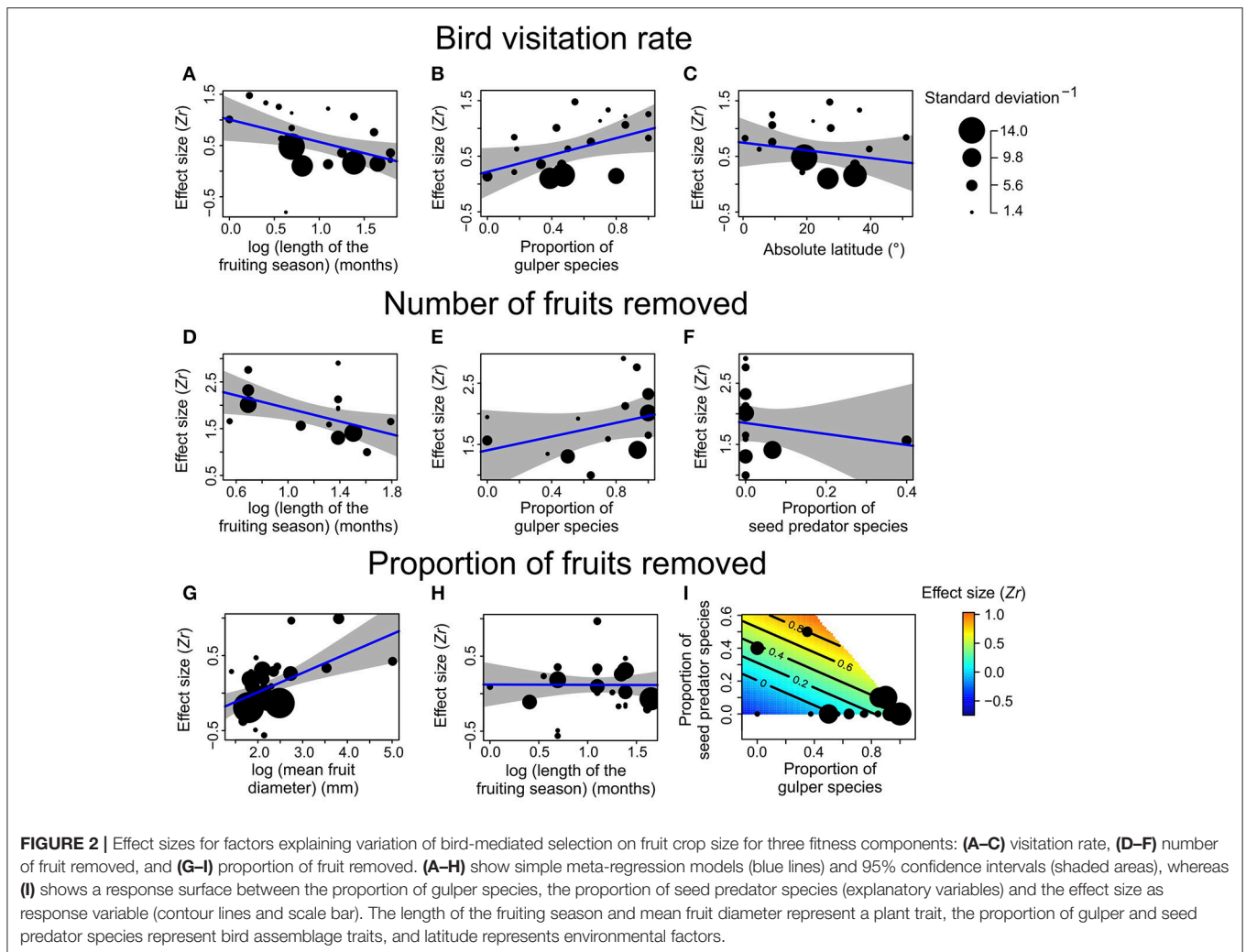
Fitness component	Model	Number of species	Parameter	Estimate	Standard error
Bird visitation rate	"Plant trait" 1	21	Intercept	0.580	0.099
	"Plant trait" 2	19	Intercept	0.995	0.201
			Length of the fruiting season (log)	-0.434	0.174
	"Bird assemblage trait"	19	Intercept	0.213	0.209
			Proportion of gulper species	0.752	0.356
	"Environmental"	21	Intercept	0.580	0.099
"Environmental"	21	Intercept	0.749	0.207	
		Absolute latitude	-0.007	0.008	
Number of fruit removed	"Plant trait" 1	31	Intercept	1.573	0.116
	"Plant trait" 2	23	Intercept	2.184	0.320
			Length of the fruiting season (log)	-0.415	0.271
	"Bird assemblage trait"	19	Intercept	1.418	0.372
			Proportion of gulper species	0.447	0.448
	"Bird assemblage trait"	19	Intercept	1.888	0.143
Proportion of seed predator species			-1.001	1.423	
"Environmental"	31	Intercept	1.639	0.126	
Proportion of fruit removed	"Plant trait"1	33	Intercept	-0.509	0.165
			Mean fruit diameter (log)	0.260	0.069
	"Plant trait" 2	24	Intercept	0.122	0.145
			Length of the fruiting season (log)	-0.004	0.124
	"Bird assemblage trait"	19	Intercept	-0.369	0.251
			Proportion of gulper species	0.689	0.276
"Environmental"	34	Intercept	1.825	0.601	
				0.097	0.058

For each of the four main models, best set of models in terms of Akaike's Information Criterion corrected for small sample sizes are shown ($\Delta AIC_c < 2$). The "plant trait" model 1 includes fruit type and mean fruit diameter, the "plant trait" model 2 includes length of the fruiting season (i.e., phenology), the "bird assemblage trait" model includes the proportion of gulper species and the proportion of seed predator species, and the "environmental" model includes latitude.

and functional roles, promoting similar selection regimes on plant traits (Zamora, 2000). Several studies have found an increase in selection strength resulting from an increase in the abundance of species with shared functional traits. For instance, Alcántara et al. (2007) found that ant assemblages with similar-sized species exerted similar selection pressures on elaiosome and seed size in 12 populations of *Helleborus foetidus*. In another study, Galetti et al. (2013) found that the functional extinction of large-gape seed dispersers correlated with an evolutionary reduction of seed size in 22 populations of *Euterpe edulis* in the Atlantic Forest from Brazil. In this case, defaunation acted as a filter on large species changing the evolutionary trajectory of seed size (Galetti et al., 2013). These studies suggest that changes in the abundance of functionally equivalent interacting partners stemming from ecological filters may be an important evolutionary force driving phenotypic trait variation, and therefore deserves further research.

For the three fitness components studied, two plant and bird traits (fruiting phenology and fruit-handling behavior) consistently played a role in bird-mediated selection strength on fruit crop size. As predicted by the functional equivalence

hypothesis, factors that would filter bird functional traits promoted higher selection strength on fruit crop size. The timing of fruiting has been shown to play a role in regulating the abundance and diversity of frugivores in many communities (Fenner, 1998; Burns, 2004; Albrecht et al., 2015). A fruit display in a short time period would decrease assemblage diversity relative to extended fruiting seasons, acting as a temporal filter and increasing selection strength on fruit crop size (McKey, 1975; Howe and Estabrook, 1977; Howe, 1993; Fenner, 1998). Higher proportions of species from the same functional group also supported the functional equivalence hypothesis, under the idea that an increase in the proportion of species with shared functional traits promotes higher selection pressure on fruit traits. One limitation of our approach is that we considered the effects of legitimate seed dispersers and seed predators on plant fitness as equivalent. It is known that the effect of fruit removal by seed dispersers and predators are opposite in all aspects of plant recruitment, in which seed predators have a detrimental effect on plant fitness, contrary to seed dispersers (Levey, 1987; Schupp et al., 2010; but see Loayza and Knight, 2010; Tella et al., 2015). From our results, we can only assert that both gulpers and seed predators favor larger fruit crop sizes



but, under the assumption that seed predators negatively affect fitness, higher proportion of seed predators entails a negative directional selection pattern on fruit crop size. This highlights the role of antagonistic interactions in shaping fruit display traits in multispecies assemblages (e.g., Alcántara and Rey, 2003; Gómez, 2004; Martínez et al., 2007; Siepielski and Benkman, 2007).

Another plant trait, i.e., mean fruit diameter, also explained variation in selection strength on fruit crop size. In particular, larger fruits promoted higher selection strength on fruit crop size for the proportion of fruit removed. Fruit size is considered a key trait at the fruit unit level in mutualistic interactions of frugivores and fleshy-fruited plants, as it constraints fruit-handling behavior and fruit consumption by seed dispersers (“the fruit size hypothesis”; Wheelwright, 1985; Levey, 1987). Under this hypothesis, it would be expected a decrease of frugivore richness with increased fruit size (Wheelwright, 1985; Jordano, 2000). Indeed, plant species of our database with the largest mean fruit sizes (*Aglaia flavida*: 150 mm, *Pinus edulis*: 45 mm) were consumed by one and two frugivores, respectively. In contrast, mean frugivore richness per plant species in those systems ranging from 1 to 10 mm in fruit diameter was 10.2 ± 6.4 bird

species. Therefore, larger fruits would promote higher strength on fruit crop size, as a result of coupled selection pressures of a reduced bird assemblage (Herrera, 1985). A latitudinal effect on phenotypic selection on fruit crop size would also be expected, as both frugivore richness (Kissling et al., 2009) and fruiting seasons (Ting et al., 2008) increases toward the tropics which, interestingly, is explained by the same climatic variable (actual evapotranspiration). Nonetheless, we found a negative latitudinal trend of selection strength on fruit crop size, although of low magnitude. A possible explanation is that an unmeasured variable covaries with latitude that decreases selection strength toward the tropics. Recently, Dalsgaard et al. (2017) found opposed latitudinal patterns of network-derived measures of specialization and dietary specialization in bird-frugivore interactions. In particular, the proportion of obligate frugivores increased toward the tropics, but frugivorous birds divided the niche of fruiting plants more finely at high latitudes (Dalsgaard et al., 2017). Higher proportion of obligate frugivores within a seed-dispersal assemblage (potentially fulfilling similar functional roles; Loiselle et al., 2007) may drive higher selection strength on fruit crop size, an idea that deserves further research.

Finally, phylogenetic relationships played a minor role in bird-mediated selection strength on fruit crop size. Indeed, no phylogenetic signal was detected for any fitness component. This also supports the fruit crop size hypothesis, which states that birds promote positive selection on fruit crop size, regardless of plant identity.

Evolutionary Consequences of Selection Imposed by Frugivores on Fruit Crop Size

Several conditions have been advocated to constrain reciprocal coadaptation among plants and seed dispersers, leading to diffuse coevolution (Wheelwright and Orians, 1982; Howe, 1984; Herrera, 1985; Tewksbury, 2002): (1) low selection intensity of dispersers on fruit traits, (2) inconsistent spatiotemporal bird-mediated selection, (3) antagonistic selection by fruit or seed predators, (4) correlations among fruit traits that prevent the evolution of mutual adaptations, and (5) differences in evolutionary rates between plants and dispersers. Two of these conditions, however, are not supported by our results. First, selection coefficients on fruit crop size fell within the range of other reported values of phenotypic selection in natural populations, yet for the number of fruit removed it would be considerably strong (most linear gradients range between -1 and $+1$, $|\text{median}| = 0.16$; Kingsolver et al., 2001). Therefore, fruit crop size represents a phenotypic trait under strong selection. Furthermore, it has shown to be highly heritable ($h^2 = 83.0\text{--}99.0\%$; e.g., Manju and Sreelathakumary, 2002; de Moraes et al., 2005; Denton and Nwangburuka, 2011; Meena and Bahadur, 2014) indicating a strong response to selection. Second, we did not find strong negative correlations among fruit crop size and other fruit traits that may prevent reciprocal adaptations. Indeed, we found only positive correlations between fruit crop size and other fruit traits, such as mean fruit diameter ($r_{\text{Psychotria carthagenensis}} = 0.11$, $n = 72$; $r_{\text{Vassobia breviflora}} = 0.10$, $n = 27$; $r_{\text{Jodina rhombifolia}} = 0.28$, $n = 17$; $r_{\text{Passiflora caerulea}} = 0.35$, $n = 8$) and mean sugar concentration ($r_{\text{Psychotria carthagenensis}} = 0.03$, $n = 72$; $r_{\text{Vassobia breviflora}} = 0.22$, $n = 27$). Other studies in natural conditions have found no associations between fruit crop size and other fruit level traits (Michaels et al., 1988; Martínez et al., 2007; Palacio et al., 2014; but see Sallabanks, 1993). Although an increase in fruit production could compromise fruit quality (fruit size, pulp mass, nutrient content), this has been shown under experimental conditions (Barone et al., 1994; Berman and DeJong, 1996; Naor et al., 1999, 2008; Stopar et al., 2002; Roussos et al., 2011). Negative correlations between fruit crop size and other fruit traits may be obscured by the fact that fruit crop size is a complex trait constrained by several factors (Lee, 1988) including resource availability (Lescourret and Génard, 2003), plant age (Mechlia and Carroll, 1989; Marshall et al., 2010), flower display and pollination service (Herrera, 1991; Cunningham, 2000; Benavidez et al., 2013; Stournaras and Schaefer, 2017). The interaction between different factors affecting fruit crop size may reduce correlations with other fruit traits, potentially relaxing indirect selection on fruit crop size in nature (e.g., Jordano, 1995; Sobral et al., 2010; Palacio et al., 2014). By

contrast, counteracting selection pressures exerted by seed predators may dilute the overall selection pressure imposed on fruit crop size, favoring the process of diffuse coevolution (Herrera, 1985). Our results support this idea, as an increase in the proportion of seed predators favored large fruit crops. Finally, seed dispersers may shape the evolution of seed size and number, as a result of a trade-off between fruit crop size, seed size, and seed number (Smith and Fretwell, 1974; Eriksson and Jakobsson, 1999; Sadras, 2007). In particular, fruit crop size is positively correlated with the total seed number of a plant, but seed number within a fruit is negatively correlated with mean seed size (Westoby et al., 1992; Parciak, 2002; Sadras, 2007). Therefore, selection on large fruit crop sizes should promote lower mean seed size. This suggests that seed dispersal may be more important than seed size for successful offspring recruitment (Parciak, 2002), although the existence of conflicting selection by other selection agents (e.g., seed predators) might explain the occurrence of an optimal seed size in some plant species without invoking a seed number-size trade-off (Gómez, 2004).

CONCLUDING REMARKS AND PROSPECTS

As Snow (1971) proposed in his seminal study, the number of fruit a plant displays is a key trait subject to bird-mediated natural selection. The positive directional selection on fruit crop size would be a common regime in nature, and the strong intensity on this trait suggests that it may be more important than other fruit display traits (e.g., Jordano, 1995; Sobral et al., 2010; Palacio et al., 2017a). Moreover, both plant and bird traits play major roles in natural selection regimes on fruit crop size. As we have shown, the strength of selection on fruit crop size is driven mainly by plant fruiting phenology and functional equivalence. Being the first meta-analysis on this matter, it opens new questions and suggests there are still important gaps of studies measuring phenotypic selection on fruit crop size in natural populations, the first step in understanding its evolution (Endler, 1986).

After 45 years of the fruit crop size hypothesis, only four studies have reported selection coefficients of natural selection on fruit crop size (Jordano, 1995; Sobral et al., 2010; Palacio et al., 2014, 2017a). Future studies should report selection coefficients not only on fruit crop size (linear and quadratic selection), but also on combinations of fruit crop size with other fruit traits (correlational selection). This information would give us a broader picture of the patterns and causes of bird-mediated phenotypic selection on fruit crop size, as well as the relationship between fruit crop size and individual fruit level traits.

Overall, as the main ecological consequence, the maximization in fruit production would increase seed dispersal. As an evolutionary one, birds would impose constraints on fruit display development, providing plants enhanced opportunities for the evolution of reproductive assurance mechanisms. Furthermore, the relationship among forces impinged by phenology and frugivore functional roles may be key to understand their evolutionary stability.

AUTHOR CONTRIBUTIONS

FP and MO: Contributed substantially to the conception and design of the study; FP: Performed the meta-analysis and wrote the first draft of the manuscript. Both authors contributed to ideas and revisions.

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