Linking the hierarchical decision-making process of fruit choice and the phenotypic selection strength on fruit traits by birds

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Abstract

Aims
Animals in search of fleshy fruits forage mostly according to the number of available fruits and then select individual fruits based on reward quality or advertised subtle traits. This hierarchical pattern of fruit choice would be translated into patterns of selection strength mediated by frugivores on fruit display traits. Thus, frugivores would exert higher selection pressures on fruit crop size and lower selection pressures on within-plant variation of phenotypic traits (infructescence, fruit and seed size). However, no attempt to link this behavioral mechanism of hierarchical trait selection to natural selection patterns has been made. Therefore, we sought to determine the relationship between the hierarchical decision-making process of fruit choice and patterns of natural selection on fruit traits.

Methods
We recorded bird visits and measured fruit-related traits (fruit size, fruit diameter and seed weight) in a natural population of *Psychotria carthagenensis*, a bird-dispersed treelet, in a Yungas forest from Argentina. To assess phenotypic selection patterns on fruit display traits, we performed multivariate selection analysis, and to explicitly identify a hierarchy of fruit trait choice we used a classification tree as a predictive model.

Important Findings
Selection patterns on fruit display traits were in agreement with a hierarchical process of fruit choice made by birds. The strength of directional selection on the total number of fruits in a plant (i.e. fruit crop size) was nearly two times higher than on fruit size, and the classification tree analysis supported this hierarchical pattern. Our results support previous evidence that seed dispersers shape fruit crop size with higher intensity than subindividual fruit traits. Also, high levels of subindividual phenotypic variation of fruit display traits may be explained by relaxed selection pressures exerted by frugivores. Empirical studies also show that this pattern may constitute a general phenomenon among other plant–animal interactions.

Keywords: plant–animal interactions, seed dispersal, selection gradients, subindividual variation

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INTRODUCTION

A central challenge of evolutionary ecology is to understand the mechanisms of selection in natural populations and the causes of variation in selection strength, which natural selection shapes the phenotype. Selection strength varies broadly in time and space, although the causes of this variation are still poorly understood (Kingsolver *et al.* 2001, 2012; Siepielski *et al.* 2009, 2013). Research attempts to answer this question have been focused on the type of trait under selection, on the characteristics of the selection agent and on the conflicts between different selection pressures. The premise is that the way by which the selection agent acts on the target trait determines the strength of selection.

In plant–animal interactions, the basic morphological, behavioral and functional differences between the interacting organisms and the multiplicity of interactions are typical sources of variation of the selection strength exerted by animals on plant phenotypic traits (Herrera 2009; Siepielski *et al.* 2009). In plant–pollinator mutualisms, it is well known that the number of flowers a plant displays represents a major target of pollinator-mediated selection, while for other floral display traits selection strength is generally lower (Benitez-Vieyra *et al.* 2006, 2010; Gómez 2000; Harder and Johnson 2009; Naug and Arathi 2007; Sandring and Agren 2009; Schiestl and Johnson 2013). In a study on the adaptive value of the signal–reward correlation in *Turnera ulmifolia*, Benitez-Vieyra *et al.* (2010) proposed that pollinator's foraging decisions follow a hierarchical pathway, where flower number is the trait of higher hierarchy, a pattern mirrored by the pattern and strength of selection. They also proposed that in spite of the learning capabilities of pollinators, which promote a higher fit between signal and reward, the hierarchical selection pattern gives advantages to plants to upkeep subindividual variation of floral traits (Benitez-Vieyra *et al.* 2010). However, the ecological and evolutionary consequences of the hierarchical animal-mediated selection on plant phenotype are still poorly known.

In mutualistic interactions of fleshy-fruited plants and seed-dispersing birds, and despite empirical evidence of bird-mediated selection on fruit display traits (Jordano 1995; Palacio *et al.* 2014; Sobral *et al.* 2010a, 2013), we still lack a general view to explain the ways by which birds exert selection pressures on different components of fruit display. From a behavioral perspective, Sallabanks (1993) proposed that frugivores face a hierarchical decision-making process of fruit choice. Frugivorous birds may first use extrinsic plant traits (habitat type, availability of fruiting plant species) when choosing among individual plants and then use intrinsic plant traits (fruit crop size, fruit size; Jordano and Schupp 2000; Sallabanks 1993). Nevertheless, a handful of attempts to link this hierarchical process of fruit choice to natural selection patterns on fruit display traits have been made among seed dispersal mutualisms. Some intuitive relationship between the behavioral and the selection process is expected. For instance, considering an individual plant as a foraging patch, fruit-eating behavior should be affected by covariation between fruit display traits (Palacio *et al.* 2015; Sobral *et al.* 2010a). Therefore, phenotypic variation of fruit display traits and selection strengths on fruit display traits might result from correlations between traits of different levels (whole plant and individual fruit levels) and fruit trait choices by frugivores under a nested rather a random process.

In this study, we explored patterns of bird-mediated selection in a natural population of the two-seeded tree *Psychotria carthagenensis* (Rubiaceae) in a Yungas forest. Specifically, we (i) estimated the type, direction and strength of phenotypic selection on fruit display traits exerted by birds and (ii) determined the hierarchical structure of traits under bird-mediated selection (fruit crop size and individual fruit-level traits).

MATERIALS AND METHODS

Study area and species

The study was carried out at the Parque Biológico Sierra de San Javier, Tucumán province, northwest Argentina. This is a 14 000-ha protected area with subtropical Andean mountain forests, which corresponds to the phytogeographic province of Yungas (Cabrera 1976). The study site (26°47′S, 65°20′W, corresponding to 'Selva Pedemontana', 640 m.a.s.l.) is characterized by a mosaic of old growth and secondary forests resulting from relatively recent land use disintensification (Ayup *et al.* 2014). Native-dominated secondary forests are characterized by pioneer species such as *Parapiptadenia excelsa*, *Solanum umbellatum*, *Heliocarpus americanus* and *Tecoma stans*. Exotic-invaded secondary forests present a high proportion of the exotic species *Ligustrum lucidum*. The understory is strongly dominated by the shrub *P. carthagenensis* (Ayup *et al.* 2014). Climate is subtropical with dry winters (July–September) and wet summers (December–March; Hunzinger 1997). Average annual rainfall varies between 1300 and 1500 mm, and average annual temperature is 18°C (Hunzinger 1997).

Psychotria (= *Uragoga*) *carthagenensis* Jacq. (Rubiaceae) is a shrub or small tree 1–4 m in height, dominant in the understory of wet tropical and subtropical forests up to 1400 m.a.s.l., from Mexico to Argentina and Uruguay (Hamilton 1989). It produces 0.5-cm white flowers in panicle inflorescences. The reproductive system varies between populations (Faria *et al.* 2012). The population studied is longistylous monomorphic and insect-pollinated self-compatible, with insects of the family Apidae as primary pollinators (Benavídez *et al.* 2013). It produces fleshy drupes red when ripe, 4.4–9.7 mm in diameter, and mainly dispersed by birds (Ordano *et al.* 2011). The bird assemblage that consumes fruits of *P. carthagenensis* includes *Turdus rufiventris*, *Thraupis sayaca*, *Chlorospingus ophthalmicus*, *Elaenia obscura*, *Catharus ustulatus*, *Turdus nigriceps* and *Atlapetes citrinellus* (Blendinger *et al.* 2012; Giannini 1999; Pacheco and Grau 1997; Ruggera *et al.* 2014). In the study area, *P. carthagenensis* is an important source of nourishment, as it is one of few species fruiting in the drier months, including winter (Blendinger *et al.* 2012; Pacheco and Grau 1997).

Bird observations and fruit display trait measurements

Fieldwork was carried out in August–September 2012 in a 200 × 300 m plot, during peak bird fruit consumption activity in the study area (Blendinger *et al.* 2012). The study plot was split into a grid of 150 cells of 20 × 20 m each, and 17 cells were randomly selected. Within each cell, three or four plants were randomly selected as focal plants. We observed bird fruit-eating behavior at each focal plant for periods of three continuous hours within the first 4 h after sunrise.

Observers remained at least 4 m from the focal plant. During each observation period, bird species, the number of visits per hour (visitation rate) and the number of fruits consumed per visit at each focal plant were recorded. We considered a visit legitimate if a bird completed its foraging bout by eating at least one fruit. If we observed bird visits in plants not selected from the beginning, we also recorded fruit consumption behavior and measured fruit display traits.

We selected five infructescences (one per cardinal point and that from the apex) and counted the number of fruits per infructescence and the number of infructescences per plant. The total number of fruits in a plant (i.e. fruit crop size) was estimated as the average number of fruits per infructescence multiplied by the number of infructescences. Although this estimation method serves practical purposes, it assumes a linear relationship in fruit distribution within a plant. Given that fruits are arranged on infructescences in our plant system, variation in the number of fruits per infructescence may be perceived by birds as a signal itself. Consequently, we also evaluated variance (uncertainty) in the number of fruits per infructescence within plants. At the end of focal plant observations, five fruits per plant were collected (one per cardinal point and that from the apex). For each fruit, fresh weight and seed fresh weight were measured with an Ohaus Discovery 114C scale to the nearest 0.1 mg, and fruit diameter was measured on scaled photographs of the fruits using the software ImageJ 1.4g (imagej.nih.gov/ij/). Fruit photographs were taken with a Canon EOS 550D digital camera (12.0 megapixels).

Data analysis

Phenotypic selection analyses

We estimated the pattern and strength of bird-mediated phenotypic selection on fruit crop (unique measure), mean and coefficient of variation of fruit traits (subindividual-level measures; number of fruits per infructescence, diameter and seed weight). Due to the low number of visitations registered, visited or non-visited plant was used as the measure of fitness. Individual relative fitness was estimated as the individual fitness measure divided by the population mean fitness, and fruit display traits were standardized to a mean of 0 and a variance of 1. The directional selection differential (S_i) was estimated as the covariance between relative fitness and each standardized trait and the disruptive/stabilizing selection differential (C_{ii}) as the covariance between relative fitness and the squared deviation of each standardized trait (Brodie *et al.* 1995). To assess the direction and magnitude of selection on a specific trait independent of the indirect effect of other traits, we used a multivariate selection approach, following Morrissey and Sakrejda (2013). This unifies multiple regression models to obtain selection gradients (Lande and Arnold 1983) and spline-based estimations to obtain smooth functions of the relationship between fitness and phenotypic traits (Schluter 1988). Significant linear gradients (β_i) indicate that selection favors either a phenotypic mean increase (if positive) or decrease (if negative). Significant non-linear selection gradients (γ_{ii} and γ_{ij}) indicate non-linear selection against extreme phenotypes (stabilizing selection), non-linear selection against intermediate trait values (disruptive selection) or correlational selection on a given combination of traits (Lande and Arnold 1983). For the multivariate selection approach, we fitted two separate models including mean and subindividual variation in fruit traits (following Herrera 2009) due to power restrictions encountered for sample size. The first model included fruit crop size, coefficient of variation in the number of fruits per infructescence and fruit diameter (mean and coefficient of variation), whereas the second model included fruit crop size, coefficient of variation in the number of fruits per infructescence and seed diameter (mean and coefficient of variation). We used binomial error structure with a logit link function due to the binary nature of the fitness measure (0 = visited plant, 1 = non-visited plant). Standard errors and significance for selection differentials and gradients were estimated using 1000 bootstrap replicates (Morrissey and Sakrejda 2013).

Classification trees

Although the multivariate selection approach leads to direct comparisons between selection magnitudes on different traits (Lande and Arnold 1983), selection gradients would be difficult to interpret as the result of hierarchy of trait selection (only partially through the correlational gradient). Instead, to infer how birds may hierarchically exert selection pressures on fruit display traits, we used classification trees (Breiman *et al.* 1984). These are non-parametric classifiers, which predict class membership by recursively partitioning a data set into more homogeneous groups (Breiman *et al.* 1984). The result is a dichotomously branching tree, which shows both the hierarchy of importance of predictors as well as the nature of interactions between predictors. Since classification trees suffer from several statistical problems, such as overfitting, we determined the optimal level of tree complexity by performing cross-validation (James *et al.* 2013).

All analyses and graphs were run in R v.3.2.1 (www.R-project.org) using the packages mgcv (Wood 2006), gsg (Morrissey and Sakrejda 2013), visreg (CRAN.R-project.org/package=visreg) and tree (CRAN.R-project.org/package=tree).

RESULTS

Bird observations

We recorded five bird species that visited focal plants (11 out of 72 plants) of *P. carthagenensis* in 47 h of observation. We also recorded 14 visits (mean = 0.065 ± 0.172 individual birds per hour) and 33 fruit consumption events (mean = 0.153 ± 0.506 fruits per hour). The species recorded were *Turdus rufiventris* (six visits), *Syndactyla rufosuperciliata* (four visits), *Atlapetes citrinellus* (two visits), *Chlorospingus ophthalmicus* (one visit) and *Arremon flavirostris* (one visit).

Bird-mediated phenotypic selection

Both univariate and multivariate selection analyses showed positive directional selection on fruit crop size and mean fruit diameter (Tables 1–3). The multivariate approach showed, in addition, positive correlational selection on the interaction between fruit crop size and fruit diameter (Table 2; Fig. 1). Disruptive selection gradients were also significant for fruit crop size, mean fruit traits (fruit diameter and seed weight) and subindividual variation in fruit traits (fruits per infructescence, fruit diameter and seed weight; Tables 1–3). However, these indicated that fitness functions were non-linear, as they

had only one phenotypic optimum (Phillips and Arnold 1989; Fig. 2). For subindividual variation in fruit diameter, the disruptive selection gradient indicated a negative directional selection pattern (Fig. 2a), whereas for mean and subindividual variation in seed weight and subindividual variation in fruits per infructescence disruptive selection gradients indicated positive directional selection patterns (Fig. 2b and c).

Hierarchical levels of bird-mediated selection

The classification tree showed that fruit crop size and mean fruit diameter were the most important variables that

Table 1: univariate phenotypic selection on fruit display traits in a *Psychotria carthagenensis* population (*n* = 72 plants)

Trait	S_i (SE)	C_{ii} (SE)
Fruit crop size	0.492 (0.251)*	0.020 (0.574)
CV fruits/infructescence	0.229 (0.306)	0.280 (0.405)
Mean fruit diameter	0.851 (0.346)*	1.367 (0.769)*
Mean seed weight	−0.229 (0.269)	−0.067 (0.345)
CV fruit diameter	−0.306 (0.258)	−0.136 (0.348)
CV seed weight	−0.134 (0.297)	0.143 (0.402)

Standardized directional selection differentials (S_i), stabilizing/disruptive selection differentials (C_{ii}) and standard errors are shown. Standard errors and significance of selection differentials were estimated using 1000 bootstrap samples. Abbreviations: CV = coefficient of variation, SE = standard error.
*$P < 0.05$.

Table 2: multivariate phenotypic selection on fruit display traits (fruit crop size and fruit size) in a *Psychotria carthagenensis* population (*n* = 72 plants)

Trait	β_i (SE)	γ_{ii} or γ_{ij} (SE)
Fruit crop size	1.026 (0.344)*	1.043 (0.782)
CV fruits/infructescence	0.273 (0.264)	0.220 (0.345)
Mean fruit diameter	0.492 (0.265)*	0.017 (0.206)**
CV fruit diameter	−0.149 (0.297)	0.058 (0.315)*
Fruit crop size × CV fruits/infructescence		0.315 (0.314)
Fruit crop size × mean fruit diameter		0.548 (0.285)*
Fruit crop size × CV fruit diameter		−0.173 (0.345)
Mean fruit diameter × CV fruit diameter		−0.053 (0.202)
Mean fruit diameter × CV fruits/infructescence		0.097 (0.291)
CV fruit diameter × CV fruits/infructescence		−0.031 (0.147)

Standardized directional selection gradients (β_i), stabilizing/disruptive selection gradients (γ_{ii}), correlational selection gradients (γ_{ij}) and standard errors are shown. Gradients were estimated from a generalized additive model; standard errors and significance of selection gradients were estimated using 1000 bootstrap samples (see Morrissey and Sakrejda (2013) for details). Abbreviations: CV = coefficient of variation, SE = standard error.
*$P < 0.05$, **$P < 0.01$.

Table 3: multivariate phenotypic selection on fruit display traits (fruit crop size and seed size) in a *Psychotria carthagenensis* population (*n* = 72 plants)

Trait	β_i (SE)	γ_{ii} or γ_{ij} (SE)
Fruit crop size	1.348 (0.332)**	1.928 (0.998)
CV fruits/infructescence	0.253 (0.267)	0.046 (0.457)*
Mean seed weight	0.304 (0.289)	0.067 (1.212)**
CV seed weight	0.295 (0.305)	0.063 (0.122)*
Fruit crop size × CV fruits/infructescence		0.352 (0.319)
Fruit crop size × mean seed weight		0.421 (0.290)
Fruit crop size × CV seed weight		0.408 (0.377)
Mean seed weight × CV seed weight		0.065 (0.208)
Mean seed weight × CV fruits/infructescence		0.056 (0.740)
CV seed weight × CV fruits/infructescence		0.054 (0.138)

Standardized directional selection gradients (β_i), stabilizing/disruptive selection gradients (γ_{ii}), correlational selection gradients (γ_{ij}) and standard errors are shown. Gradients were estimated from a generalized additive model; standard errors and significance of selection gradients were estimated using 1000 bootstrap samples (see Morrissey and Sakrejda (2013) for details). Abbreviations: CV = coefficient of variation, SE = standard error.
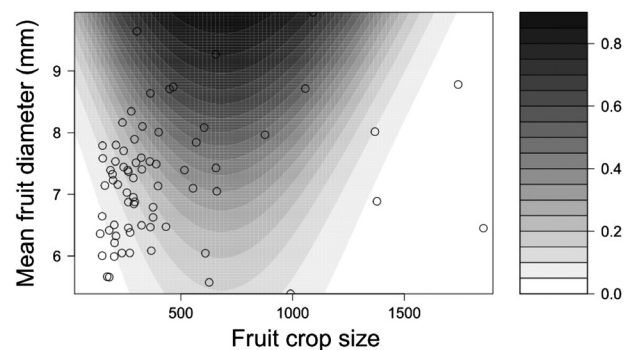*$P < 0.05$, **$P < 0.01$.

Figure 1: phenotypic selection surface for probability of bird visitation (gray scale) as a function of fruit crop size and fruit diameter in a *Psychotria carthagenensis* population (*n* = 72). Predictions are derived from a generalized additive model conditional on the coefficient of variation of fruits per infructescence and fruit diameter. Open circles represent observed values.
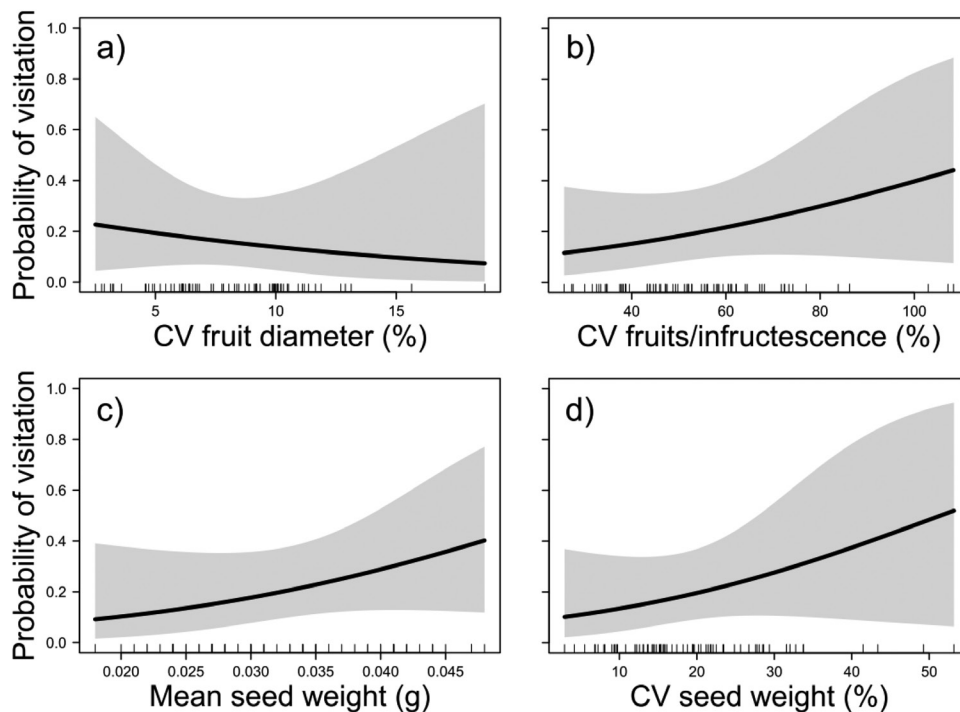
Figure 2: bird-mediated selection on fruit display traits in a *Psychotria carthagenensis* population (*n* = 72). Lines depict the fit of generalized additive models conditional on the mean of the following explanatory variables: (**a**) fruit crop size, mean fruit diameter and coefficient of variation of fruits per infructescence; (**b**) fruit crop size, mean seed weight and coefficient of variation of seed weight; (**c**) fruit crop size, coefficient of variation of seed weight fruits per infructescence; and (**d**) fruit crop size, mean seed weight and coefficient of variation of fruits per infructescence. Shaded regions depict 95% confidence intervals and the vertical black lines in the *x* axis show the observed values of the explanatory variable.
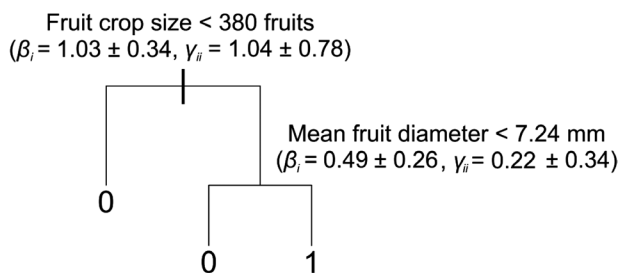

Figure 3: classification tree of bird-mediated selection on fruit display traits in a *Psychotria carthagenensis* population (*n* = 72). The threshold defined by each variable corresponds to the left-hand branch. Zero values represent plants classified as non-visited ones, and the one value represents plants classified as visited ones. Standardized directional (β_i) and stabilizing/disruptive (γ_{ii}) selection gradients ± standard errors are shown.

explained bird-mediated selection (Fig. 3). In particular, individual plants seem to be first discriminated by fruit crop size (favoring large fruit crops) and then by mean fruit diameter (favoring large fruits). In contrast, subindividual variation in fruit traits did not appear in the final tree.

DISCUSSION

We found that birds exert selection pressures on fruit display traits according to a hierarchical process of fruit choice.

From a behavioral perspective, our correlative results suggest that birds first choose larger fruit crops and then choose fruit size. From a micro-evolutionary perspective, this hierarchical decision-making process was supported by noticeable differences in strength of directional selection, being nearly two times higher for fruit crop size than for fruit size. This result is consistent with previous studies (Brown and Morgan 1995; Jordano 1995; Sallabanks 1993). The hierarchical pattern of phenotypic selection linked to a behavioral decision-making process of fruit choice may represent a widespread phenomenon among seed dispersal mutualisms.

In his seminal work, Sallabanks (1993) found that *Turdus migratorius* first selected among *Crataegus monogyna* fruit crops and then selected fruits within crops according to fruit size. In an experiment with captive *Nucifraga columbiana*, Christensen *et al.* (1991) found that birds first selected artificial plants with higher *Pinus edulis* cone number, and within high-cone number plants, selected cones with higher seed number. In an another experiment, Giles and Lill (1999) found that relative artificial fruit abundance was more important than fruit color in captive *Zosterops lateralis* preferences, and when fruits of two colors were equally abundant, sugar concentration influenced fruit choice. Finally, in trial experiments with wild and naïve *Turdus merula* and *Crataegus monogyna* fruits, Sobral *et al.* (2010b) found that birds chose display size (number of fruits) over fruit size, and when birds were offered same

display sizes, they chose large fruit sizes. This mixed evidence indicates that Sallabank's premise of hierarchical fruit choice is a common phenomenon deserving deeper research.

In agreement with the hierarchical mechanism of fruit trait choice, most evidence suggests that fruit crop size may be more important to birds than subindividual traits (e.g. fruit and seed size, nutrient content, color; Foster 1990; Izhaki 2002; Ortiz-Pulido et al. 2007). This can be explained by the fruit crop size hypothesis (Howe and Estabrook 1977; Izhaki 2002; Snow 1971), which states that the number of fruits a plant displays represents a prominent signal for frugivores. Therefore, fruit crop size is expected to be a major target of bird-mediated phenotypic selection relative to other fruit traits. In the only three studies that have analyzed bird-mediated phenotypic selection patterns on fruit crop size and subindividual fruit traits, Jordano (1995), Sobral et al. (2010a) and Palacio et al. (2014) found higher selection strengths on fruit crop size relative to fruit and seed size in *Cerasus mahaleb*, *Crataegus monogyna* and *Celtis ehrenbergiana*, respectively. In *P. carthagenensis*, fruit crop size was the most important trait under selection, and there was also positive correlational selection on the combination of fruit crop size and fruit diameter. This suggests that birds favored larger fruit crop sizes and larger fruits simultaneously, reinforcing the idea that selection patterns may be the result hierarchical decision on the fruit trait choice process.

Subindividual variation in infructescence, fruit and seed size was also a target of bird-mediated selection in *P. carthagenensis*. In particular, there was selection against fruit diameter variation and in favor of seed weight and infructescence size variation. From the bird's perspective, selection against variation in fruit reward offered by plants would reduce time and energy costs, as well as predation risk (Herrera 2009). However, response to variable rewards (risk aversion or risk proneness; Kacelnik and Bateson 1996) depends on a range of factors, including the energetic status of the forager, the mean offered reward and the number of options between an animal is choosing (see Shafir 2000 and Bateson 2002 for reviews). As a consequence, other types of phenotypic selection patterns (positive directional, stabilizing or disruptive selection) on subindividual variation should also be expected among seed dispersal mutualisms. From the plant's perspective, subindividual variation in reward would reduce fruit production costs, allowing an increase in the number of fruits produced and thus offering a window of opportunity for plants (Herrera 2009; Ordano et al. 2011). In considering the adaptive value of subindividual variation in fruit traits, Herrera (2009) and Sobral et al. (2010a, 2013) found that birds exerted selection pressures against variation in fruit size in *Phillyrea latifolia* and *Crataegus monogyna*, respectively. In contrast, Palacio et al. (2014) found no selection pressures acting on subindividual variation in different fruit traits (fruit diameter, pulp-to-seed ratio and sugar concentration) in *Celtis ehrenbergiana*, which may represent an underlying level of selection. Part of the subindividual variation in fruit and seed

traits may be also the result of different selection pressures exerted by a functional diverse species assemblage (Ordano et al. 2011; Palacio et al. 2015; Siepielski and Benkman 2010). In particular, differences on morphology (e.g. beak size) of different bird species may increase variation of different fruit and seed traits (e.g. Jordano 1984; Siepielski and Benkman 2010; Wheelwright 1985). Although subindividual variation in fruit traits has been found to be relatively high in *P. carthagenensis* (56.2–84.5% relative to between-plant variation, Ordano et al. 2011), birds also exerted positive selection on subindividual variation in seed weight. This suggests a by-product of indirect selection with other correlated traits (Palacio et al. 2014), such as mean pulp-to-seed ratio ($r = 0.340$, $n = 72$). The relative low correlations between traits linked to costs (e.g. seed size) and benefits (e.g. fruit size, pulp-to-seed ratio) for frugivores would have important positive consequences for plants, as it would hinder birds to predict seed load based on visual signals, such as fruit size (Palacio et al. 2014).

Given that birds move among plants to choose resources, it is expected that the ecological context and time–spatial scales also play a role on fruit choice by birds and, consequently, on the strength of selection on fruit display traits. For instance, the premise that birds choose fruit traits following a hierarchy of spatial scales may be a particular case or subcomponent of the fruit-tracking hypothesis, in which frugivores track fruit resources through hierarchical decisions on fruit quantity and reward (Burns 2004; Rey 1995). García and Ortiz-Pulido (2004) proposed that foraging decisions of fruit trait selection may be explained by resource tracking at different spatial and temporal scales. They found that fruit tracking in *Juniperus communis* and *Bursera fagaroides* depended on the scale of study and were partly explained by differences in fruit availability among patches and spatial distribution of patches between populations (García and Ortiz-Pulido 2004). This variation in fruit–frugivore patterns among sites or geographical regions could be the context for local adaptation or geographical mosaics of co-evolution, an idea seldom under direct testing (Amico et al. 2011; Sobral et al. 2013; Thompson 1994).

As many animals make foraging decisions in a hierarchical fashion, the hierarchical decision-making process of resources may be a general pattern in other plant–animal interactions (Herrera 2009). In an ecological study, Gass and Montgomerie (1981) showed that the migrant pollinator *Selasphorus rufus* first selects habitats within large geographical areas, then among patches of flowers within habitat and then individual flowers within patches. The micro-evolutionary approach searching for hierarchy in natural selection arose later in the literature. A review addressed by Harder and Johnson (2009) revealed that the intensity of natural selection on floral display (in this case the number of flowers) is usually higher than on other reproductive traits. Contemporaneous empirical work supported this general view. In two insect-pollinated

plants, *Cyclopogon elatus* and *Turnera ulmifolia*, Benitez-Vieyra et al. (2006, 2010) found that pollinators first promote larger floral displays, and second, plants with higher levels of reward. In plant–herbivore interactions, herbivores would also choose food resources following a hierarchy of scales (Senft et al. 1987; Weisberg and Bugmann 2003), with evolutionary consequences similar to other plant–animal interactions. For instance, herbivore-mediated selection has been shown to be higher on plant size (as a visual cue for herbivores) than on other individual-level traits in several plant species, such as *Claytonia virginica* (Frey 2004), *Ipomoea hederacea* (Stinchcombe 2005) and *Datura stramonium* (Valverde et al. 2015). Consistent with this empirical evidence, major differences between plants and animals, basically movement and modularity (synthesized by Herrera 2009), seem unveil a general hierarchical pattern on the relationship between resource choice by animals and the strength of animal-mediated selection on plant traits.

Previous detailed reviews on patterns of natural selection strength (Kingsolver et al. 2001, 2012; Siepielski et al. 2009, 2013) and the scarce available studies on hierarchical processes in plant–animal interactions highlight the potential for research about the relationship between the patterns of resource choice by animals and the strength of natural selection on plant traits. Our study reveals that the hierarchical mechanism of foraging decisions made by animals would have important ecological and evolutionary consequences for the interaction between animals and plants. A hierarchy of selection strength on plant traits may promote differential variation within-plant traits and ultimately drive natural selection patterns on plant populations.

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