DR MARIANO ORDANO (Orcid ID : 0000-0003-0962-973X)

Article type   : Standard Paper

Section: Plant-Animal Interactions
Editor: Natalia Norden

The role of trait combination in the conspicuousness of fruit display among bird-dispersed plants

Mariano Ordano[1,6*], Pedro G. Blendinger[2], Silvia B. Lomáscolo[2], Natacha P. Chacoff[2], Mariano S. Sánchez[3], M. Gabriela Núñez Montellano[4], Julieta Jiménez[2], Román A. Ruggera[5], Mariana Valoy[6]

1 Unidad Ejecutora Lillo (UEL), Fundación Miguel Lillo (FML) and Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Miguel Lillo 251, T4000JFE San Miguel de Tucumán, Tucumán, Argentina.

2 Instituto de Ecología Regional (IER), Universidad Nacional de Tucumán (UNT) and Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), CC 34, 4107 Yerba Buena, Tucumán, Argentina.

3 Instituto de Biología Subtropical (IBS), nodo Iguazú, Universidad Nacional de Misiones (UNaM) and Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Bertoni 85, N3370BFA, Puerto Iguazú, Misiones, Argentina.

4 Instituto de Bio y Geociencias del NOA (IBIGEO), Universidad Nacional de Salta (UNSA) and Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), 9 de Julio 14, A4405BBB, Rosario de Lerma, Salta, Argentina.

5 Instituto de Ecorregiones Andinas (INECOA), Universidad Nacional de Jujuy (UNJu) and Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Alberdi 47, Y4600DTA, San

Salvador de Jujuy, Jujuy, Argentina.

6 Fundación Miguel Lillo, Miguel Lillo 251, T4000JFE San Miguel de Tucumán, Tucumán, Argentina.

*Corresponding Author: Unidad Ejecutora Lillo (UEL), Fundación Miguel Lillo (FML) and Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Miguel Lillo 251, T4000JFE San Miguel de Tucumán, Tucumán, Argentina. E-mail: maordano@lillo.org.ar

Running Headline: Plants bet on fruit display conspicuousness

Summary

- In visually-driven seed dispersal mutualisms, natural selection should promote plant strategies that maximize fruit visibility to dispersers. Plants might increase seed dispersal profitability by increasing conspicuousness of fruit display, understood as a plant strategy to maximize fruit detectability by seed dispersers.
- The role of different plant traits in fruit choice and consumption by seed dispersers has been broadly studied. However, there is no clear evidence about the importance of the traits that increase conspicuousness of fruit display. Because strategies to maximize conspicuousness of fruit display are diverse, and usually are expected to be costly, we would expect that individual plant species will produce an efficient combination of traits.
- We explored this prediction with 62 fleshy-fruited plant species of a subtropical Andean forest (Southern Yungas), and using a large dataset of fruit consumption by birds (4,476 records). Conspicuousness of fruit display was characterized by both fruit and plant traits including chromatic contrast, size, exposure, aggregation, and crop size of fruits. We also considered phylogenetic effects on phenotypic variation.
- Fruit consumption was explained by fruit chromatic contrast depending on fruit crop size. These traits revealed low phylogenetic effects, with the exception of four plant clades at different levels in the phylogenetic tree. Negative correlations between pairs of traits support

our assumption that fruit display traits are costly, suggesting natural selection favours parsimonious evolutionary pathways.

- Plant species seem to rely on conspicuousness of fruit display by a combination of traits that might minimize costs of fruit display. This appears adaptively relevant to improve communication with mutualistic animals, to increase fruit consumption in a community context and, ultimately, to enhance the profitability of seed dispersal.

Keywords: plant-animal communication, plant-animal interaction, seed dispersal mutualism, signal amplification, subtropical Andean forests.

Introduction

One of the most frequently asked questions in plant-animal mutualisms is whether frugivores select for conspicuous fruit displays. Yet, there are wide gaps in our knowledge on the main strategies used by plant species to attract seed dispersers (Stournaras, Prum & Schaefer 2015). It is still poorly understood which traits make fruit display more conspicuous to frugivores, and how those traits varied throughout the evolutionary history of fleshy-fruited plants. The inter-specific variation in fruit traits is partially explained in the context of the dispersal syndrome hypothesis, whereby non-random suites of phenotypic plant traits across distantly related taxa have converged due to selection by particular groups of frugivores (van der Pijl 1972; Lomáscolo et al. 2010; Valido, Schaefer & Jordano 2011). Frugivores most probably detect fruits based on a holistic perception of fruits and the whole fruiting plant, and not due to specific fruit traits. Hence, we focus on the concept of conspicuousness of fruit display, defined as a plant strategy resulting from the combination of traits at the fruit and whole plant levels. This strategy is expected to maximize fruit detectability by seed dispersers. How plants increase seed dispersal profitability by means of conspicuousness of fruit display, and how these plant traits are phylogenetically related are pending questions in the evolutionary ecology of seed dispersal.

Among seed-dispersing animals, fruit-eating birds have been recognized as a key group. Because fruit choice by birds relies on visual perception (Schaefer & Ruxton 2011), conspicuousness of fruit display should be essential in plant-bird communication. Schmidt, Schaefer & Winkler (2004) formally defined the contrast hypothesis, which says that conspicuousness of the diaspore determines fruit choice, and predicts that diurnal dispersers choose fruit colours based on their conspicuousness and not on colour itself. Nevertheless, most studies have neglected the importance of trait combination to achieve conspicuousness and increase fruit consumption.

A plant's main strategy should be to increase the magnitude of their signals to communicate with vision-biased seed dispersers (Schaefer & Ruxton 2011). Therefore, conspicuousness of fruit display might function as a signal amplifier. An increment in signal resolution and power would modify signal detection and evaluation by recipients (Hasson 2000; Berglund & Rosenqvist 2003; Harper 2006). Signal amplification may be achieved at the level of the dispersal unit (i.e. the diaspore or fruit), at the level of the whole plant, or both (Stournaras & Schaefer 2017). In a plant community context, where dispersal is often limited (Ehrlen & Eriksson 2000) signal amplification is particularly important because the most distinguishable signals will be easier to remember and recognize by seed dispersers (Guilford & Dawkins 1991; Stournaras, Prum & Schaefer 2015).

At the individual fruit level, signals change at ripening. The change in colour and contrast against its background as fruits ripen constitutes an important signal to attract seed dispersers and/or deter antagonists (Sumner & Mollon 2000; Kelber, Vorobyev & Osorio 2003; Schaefer, Schaefer & Vorobyev 2007; Schaefer & Braun 2009; Burns 2015). In fact, forest birds detect more readily fruits with a high chromatic contrast against their background (Schmidt, Schaefer & Winkler 2004; Cazetta, Schaefer & Galetti 2009; Cazetta et al. 2012). Also, signal amplification at the fruit level can be achieved by increasing its exposed surface via increased size (Valenta et al. 2015).

At the plant level, fruit display will depend on crop size, and on whether fruits are solitary or grouped, scattered within the foliage or exposed (Denslow et al. 1986; Jordano 2000; Herrera 2002; McCall & Walck 2014). The number of fruits and their arrangement on the plant enhance conspicuousness, influencing the ability of birds to detect them and their foraging decisions. Fruit clumps are easily noticeable by birds improving foraging efficiency in terms of decreasing search, travel time, and predation risk (Sallabanks 1993; Ortiz-Pulido, Albores-Barajas & Díaz 2007; Palacio et al. 2017). In spite of knowing the role played by different plant traits on fruit consumption (Howe & Estabrook 1977; Alcántara et al. 1997; Blendinger, Loiselle & Blake 2008; Palacio, Lacoretz & Ordano 2014, Blendinger et al. 2015), there is no strong evidence yet on how different combinations of traits affect conspicuousness of fruit display.

The role of frugivores in the evolution of fruit display has been contentious, and the debate has not yet ended (Jordano 1995a; Lomáscolo et al. 2010; Harrison et al. 2012; Stournaras & Schaefer 2017). Phylogenetic effects are important to explain present-day phenotypic variation in fruit traits such as fruit and seed mass, colour and nutrient content among fleshy-fruited plants (Jordano 1995a; Särkinen et al. 2013). If conspicuousness of fruit display favours seed dispersal by birds, we therefore should be able to see their effects in the evolutionary history of traits that compose conspicuousness.

In this study, we expand the contrast hypothesis proposed by Schmidt, Schaefer & Winkler (2004). We propose that fruit conspicuousness is enhanced at both the fruit and plant levels. Also, phenotypic variation of traits that are relevant to conspicuousness of fruit display could be affected by phylogenetic effects. Therefore, it is necessary to differentiate the effects of common ancestry on phenotypic variation of traits. Since the production of the fruit display is costly (Herrera 2009; Schaefer & Ruxton 2011), which probably constrains the expression of plant traits, we propose that conspicuousness should be magnified by particular low-cost trait combinations. We tested the expanded contrast hypothesis using a large dataset of fruits consumed by birds in a subtropical Andean forest ecosystem. Then, we considered the following traits as mechanisms to amplify signalling of the fruit display: chromatic contrast, size, exposure, aggregation, and crop size. Specifically, we (1) characterized the inter-specific variation in fruit colour and chromatic contrast using avian vision models (e.g., Endler & Mielke, 2005); (2) determined the relevance of the plant traits by modelling which trait combination best explained fruit consumption by birds at the community level; (3) explored the phylogenetic effects for the relevant traits identified in (2); and, (4) assessed if trait combinations unveil underlying cost constrains by exploring the relationships between the plant traits that define conspicuousness of fruit display.

Materials and methods

STUDY AREA

We conducted this study in the subtropical Andean forest known as Southern Yungas, which grows on the eastern slope of the Andes from Bolivia to NW Argentina (Brown et al. 2001). Our study area comprised localities at the southernmost region of the Southern Yungas (between 26° and 27° S), characterized by a strong altitudinal gradient that includes the following three forest types: Montane Forest (“Selva Montana”), which is subdivided into Lower Montane Forest (“Selva Basal”; 700-1,000 m.a.s.l.) and Upper Montane Forest (“Selva de Mirtáceas”, 1,000-1,500 m.a.s.l.); and Cloud Forest (“Bosque Montano”, 1,500 to 2,500 m.a.s.l.). The weather is subtropical with one dry (May to September, includes austral winter) and one wet (November to March, includes austral summer) season. Average annual rainfall varies between 1,300 and 1,500 mm across the mountain range and average annual temperature is 19 ºC (Minetti, Bobba & Hernández 2005).

FRUIT DISPLAY TRAITS

We characterized the fruit display of 97 plant species (Appendix S1). We sampled ripe fruits over the entire altitudinal and latitudinal gradients of the study area. Healthy ripe fruits were collected in field trips during 2014 and 2015 to measure fruit colour. Fruit ripeness of all species was determined on the basis of previous records about the condition in which fruits were usually eaten by birds. Remaining traits were obtained from several information sources (Giannini 1999; Ruggera, Álvarez & Blendinger 2011; Blendinger et al. 2012; Ruggera 2013; Ruggera, Gómez & Blendinger 2014; Blendinger et al. 2015). Overall, our study assumes that including samples from different sources does not affect the characterization of fruits at the species level. We measured five display traits to characterize conspicuousness of fruit display. Sample size of each display trait varied within species according to the specificities of each trait and the availability of information, as follows:

(1) *Fruit chromatic contrast* was quantified after recording reflectance of the fruit and the structure over which it was displayed (Appendix S2). Because the leaves of the same plant are the structures closest to fruits, they often represent an acceptable estimation of the fruit background (Camargo et al. 2014). In the case of our study, the background of the fruit was composed by leaves. Whenever possible according to what was explained above, we quantified the colour of five fruits and five leaves from each of four individuals from each plant species (Appendix S1). Fruits collected in the field were put in sealed plastic bags and stored in the fridge until colour was quantified in the laboratory no later than three days after collection. Specifically, we scanned the exocarp of the fleshy reward of the diaspore and the leaves collected close to the fruits. In order to consider fruit colour according to the visual system of fruit consumers (Endler & Mielke 2005), we characterized fruit colour based on birds' visual system, which is classified as either violet-sensitive (VS) or ultraviolet-sensitive

(UVS), according to the sensitivity peak of the pigment type that absorbs the shortest wavelengths within the 300-700 nm wavelength range (Vorobyev & Osorio 1998). We calculated the chromatic contrast or chromatic distance (ΔS) between fruits and leaves as defined below. For both fruits and leaves, these measurements represented the reflectance mean values of all the samples taken from a given plant species. The chromatic distance was expressed in units of just noticeable differences (JNDs). We considered a discrimination threshold of 4 JND, with < 4 JND indicating that animals cannot distinguish between the two colours compared; and values > 4 JND indicating that animals are able to discriminate the compared spectra (Schaefer, Schaefer & Vorobyev 2007; Stournaras, Prum & Schaefer 2015; Appendix S2).

(2) *Fruit size* of each plant species, defined by fruit mass, was measured for each whole fresh fruit with a digital scale to the nearest 0.1 mg (Denver Instrument APX-200, USA) for up to 20 fruits per species from different individuals (Appendix S1). All fruits of each species collected in the field were stored in a common container and, once in the laboratory, we drew fruits from this common pool. Only ripe and healthy fruits were measured.

(3) *Fruit aggregation* expresses the mean number of fruits found in relatively discrete and distinguishable groups. Mean values were obtained by counting the number of fruits that appeared in clumps from up to ten independent records per plant species, from photos taken in the field and from direct observations at the study area. For species with insufficient information, we consulted additional pictures and descriptions available in the literature, as well as images available in reliable websites (Appendix S1).

(4) *Fruit exposure* refers to the disposition of the fruit (either solitary or clumped) with respect to the branch that supports it and its contiguous foliage. We defined two broad categories of fruit exposure: "unexposed" includes sessile fruits, without an elongated pedicellum, and fruits that grew amongst the foliage; and "exposed" fruits includes fruits

supported by an elongated pedicellum, either hanging down from the branch (pendulous) or erect, and terminal fruits disposed entirely away from the foliage.

(5) *Fruit crop size* was estimated as the mean number of ripe fruits per plant for each species, estimated from an average of 5.5 plant individuals per species (up to 20 plant individuals per species). Plants were randomly selected during field trips for fruit collection, encompassing the entire fruiting season. In plants with numerous infructescences (e.g. *Myrsine* spp., *Sambucus nigra*, *Phytolacca bogotensis*, *Urera* spp.) we estimated the mean number of fruits in up to 20 infructescences and multiplied by the number of infructescences on the plant. Due to the large intra-specific variation in crop size to typify a plant species, we used the per-species mean values over all individuals measured to classify fruit species into five categories: 1 = 1 to 10 fruits; 2 = 11 to 100; 3 = 101 to 1,000; 4 = 1,001 to 10,000; 5 > 10,000 (Blendinger et al. 2012).

FRUIT CONSUMPTION BY BIRDS

We compiled a database of 4,476 records of fruit consumption by 50 bird species in the study area. These records were not all directly comparable to each other, as they were obtained from different data sets collected with different sampling methods and sampling efforts. Databases constitute systematic direct observations at a fruiting tree (Blendinger et al. 2012; Ruggera 2013; Blendinger et al. 2015), opportunistic observations (Ruggera, Álvarez & Blendinger 2011; Ruggera, Gómez & Blendinger 2014) and identification of seeds in faeces collected from birds trapped in mist-nets (Giannini 1999; Ruggera 2013). Therefore, to make records comparable, we processed the raw data by a multi-step process (modified from Giannini & Kalko 2005). First, we grouped data from different sources in 18 datasets according to the following attributes: geographical location defined by latitude and membership to continuous mountain ranges, forest type, season and sampling technique

(Appendix S3). Second, we calculated the proportion of each fruit species (p_i) in the diet of each bird species (b) per dataset (d), with p_{ibd} values ranging from 0 (a fruit species not consumed by the bird species) to 1 (the only fruit species consumed by the bird species in a given dataset). This allowed us to incorporate into the fruit consumption estimation the fact that consumption frequency of a fruiting species depends on the other fruits available in the dataset. Finally, we obtained a single value of consumption of each fruit species (FC_i) by the community of fruit-eating birds in Southern Yungas forests, by the sum of all the p_i values recorded in the 18 datasets, using the following equation:

$$FC_i = \sum_{d=1}^{n=18} \sum_{b=1}^{n} p_i$$

Therefore, our estimation of fruit consumption (FC_i) is a relative frequency of fruit consumption for each plant species by the community of fruit-eating birds of the Southern Yungas. The combination of relative frequencies recorded at different local communities gave a regional perspective of the importance of each fruit species to the community of fruit-eating birds as a whole. The final dataset, with complete information for all traits of the fruit display, resulted in 62 plant species.

DATA ANALYSIS

In order to characterize the inter-specific variation in fruit colour and chromatic contrast using avian vision models we first included all 97 plant species for which we had fruit colour data. The tetrahedral colour space and colourspan were obtained from bird visual models ran with the package pavo (Maia et al. 2013) for R (R Development Core Team 2016) using the *vismodel*, and *tcs* functions. To estimate the chromatic contrast (ΔS) we used the function *coldist* for each plant species in the dataset (Appendix S2). For the second goal of the study, to determine the importance of the different traits related to fruit conspicuousness on fruit consumption by birds, we used a general lineal model (GLM) procedure. Fruit consumption was the response variable while traits denoting fruit conspicuousness (chromatic contrast between fruit and foliage, crop size, fruit size, fruit exposure and fruit aggregation) were considered as predictor variables. The model was based on a dataset that compiled 62 plant species for which we had data on consumption by birds and on fruit characteristics (Appendix S1 and Appendix S3). The response variable (fruit consumption) was log-transformed to warrant an error distribution that complied with normality assumptions (inspection of relationships with predicted values and deviance residuals, Cook's distance, and Shapiro-Wilk test; W = 0.979, *P* = 0.38). Explanatory variables were standardised as the observed value minus their mean, divided by two times their standard deviation, according to Gelman & Hill (2007). The initial model considered all the simple explanatory variables and all their first order interactions. We selected the best model by using a stepwise procedure (function *steps* in R) using a Gaussian error structure. The algorithm estimates the AIC for all the possible models (models with all the interactions, with double interactions, with simple effects and with no effects) and selects the model with the lowest AIC (Venables & Ripley 2002) (Appendix S4). The result of this procedure is expected to reveal the trait, or combination of traits, that best explains fruit consumption and therefore may be adaptively relevant.

Third, we estimated phylogenetic effects on fruit traits revealed as determinant for fruit consumption by the GLM procedure explained above, using Canonical Phylogenetic Ordination (CPO), a phylogenetic comparative method derived from linear regression models (Giannini 2003). This analysis was done because plant taxa may have variable degrees of statistical dependence due to common ancestry or phylogenetic inertia (Blomberg & Garland 2002; Giannini 2003). We used a main matrix including plant species and their data on relevant fruit traits, and an external phylogenetic matrix composed of the nested set of clades of the taxa included in the main matrix (Giannini 2003). Clades' significance was individually assessed using 9,999 unrestricted Monte Carlo permutations testing at $P < 0.01$. A forward stepwise selection of clades from the tree matrix was then performed to obtain a reduced tree matrix that maximally explained the variation in the main matrix without redundancy (Giannini 2003). We constructed the meta-tree of plants from trees stored in Phylomatic (Webb & Donoghue 2005) and R package *taxize* (Chamberlain & Szöcs 2013), and additional sources for unresolved relationships (Appendix S5). Canonical Phylogenetic Ordination was performed using CANOCO 4.5 (ter Braak & Šmilauer 2002).

Finally, we assessed the relationship among all fruit traits determining conspicuousness of fruit display (Appendix S1) with Pearson's product-moment correlations for the continuous variables (fruit chromatic contrast, crop size, fruit size and fruit aggregation), and with a Kruskal-Wallis test for the binary variable of fruit exposure. To avoid potential problems of lack of independence between species (our data points) due to common ancestry, we randomly chose one species from each of the clades that showed some phylogenetic effects in CPO, combined them with all the other species in our data set, and ran the analysis. We repeated this 1000 times choosing each time a random combination of species from the clades showing phylogenetic effects. We recorded the value of the corresponding statistical estimator in each run and saved them in a vector. We then calculated a confidence interval (CI) for all the statistics to see whether they contained zero. Because the distribution of our test statistics was not normal, a regular CI would not accurately describe the range of data that we needed. Therefore, we calculated a bootstrap CI. This was done by withdrawing 1,000 data points with replacement 1,000 times, and then identifying the 0.025 and the 0.975 quantiles of that distribution. In the same way, the *p-value* was calculated as twice the minimum proportion of the target statistic that resulted below or above zero (Appendix S6). Except when indicated otherwise, all analyses were run in R 3.2.4 (R

Development Core Team 2016).

Results

FRUIT COLOUR SPACE AND INTER-SPECIFIC VARIATION IN FRUIT CHROMATIC CONTRAST

There was a distinctive pattern of fruit colour among the 97 plant species surveyed (Appendix S1). The volume of the colourspan was 0.0263, with most plant species occupying the long-wave and short-wave spaces of the tetrahedron (Figure 1). Fruit chromatic contrast showed great variation (range = 3.39 – 107.46, mean = 17.77, SD = 16.96). Almost all fruit species had contrast values distinguishable by birds (only three species showed < 4 JND; Appendix S1).

FRUIT CONSUMPTION BY BIRDS AND PLANT CONSPICUOUSNESS STRATEGIES

The variables that best explained fruit consumption were crop size and fruit chromatic contrast (Table 1). The interaction between crop size and fruit chromatic contrast was marginally significant and both variables were selected in the final model. Fruit consumption increased for larger crop size, but only when associated to higher fruit chromatic contrast (Table 1, Figure 2).

PHYLOGENETIC EFFECTS

Four clades were significant at $P < 0.01$ (Table 2) in a tree matrix according to the CPO analysis (Table 2). On one hand, phylogenetic effects for crop size were found in three clades, and explained 42.8 % of variation in this trait ($F = 7.083$; $P = 0.0095$; Table 2). The model successively incorporated, (1) a clade that included the families Rubiaceae, Boraginaceae, Verbenaceae and Solanaceae, hereafter Asterid I; (2) a clade that included three species of the genus *Urera*, hereafter Urticaceae; and (3) a clade that included three species of the genus *Rhipsalis*, hereafter Cactaceae (respectively, clades number 83, 107 and 76 in Figure 3). The Urticaceae and Cactaceae clades showed smaller mean crop size values (0.4 and 0.8, respectively) (Appendix S1) than the overall mean (1.4), while the Salicaceae clade showed a larger mean crop size value (2.7) than the overall mean (clade 102 in Figure 3, including genera *Xylosma* and *Prockia*). On the other hand, the Sapindaceae clade (number 120 in Figure 3, including genera *Cupania* and *Allophylus*) explained 27.1 % of variation in fruit chromatic contrast ($F = 15.896$; $P = 0.0032$; Table 2). The mean value of fruit chromatic contrast in the Sapindaceae clade (31.7) was higher than the overall mean (12.4) (Appendix S1).

RELATIONSHIPS BETWEEN FRUIT DISPLAY TRAITS

All traits were significantly correlated when compared pairwise (Table 3). At the fruit unit level, fruit chromatic contrast increased with fruit size. Fruit size was negatively associated to fruit aggregation and crop size. Species with exposed fruits showed larger fruit size than unexposed ones. Fruit aggregation was positively related to crop size, and the more exposed fruits were more aggregated. Finally, exposed fruits were associated to smaller crop size (Table 3).

Discussion

Fleshy-fruited plants seem to enhance conspicuousness by specific trait combinations, which serve as a strategy to increase fruit consumption. Our test showed that high chromatic contrast combined with large crop size induces higher consumption in comparison to plant species with high contrast and low crop size. So, there seems to be a combination of traits that increases consumption. Our study also showed that there were weak phylogenetic effects on fruit display traits. These results reinforce the premise that frugivore-mediated selection shapes fruit display traits. In addition, the potential trade-offs unveiled by significant and negative relationships between fruit display traits suggest that natural selection promotes low-cost strategies in plant communities.

Wheelwright (1985) proposed that frugivore-mediated selection promoted inter-specific variation in fruit colour and increased fruit conspicuousness. After him, Schmidt, Schaefer & Winkler (2004) formalised the contrast hypothesis. Both views were centred on the individual fruit unit. Here, we found that the combination between high fruit chromatic contrast and large crop size increases consumption, probably due to the amplification of the signal to frugivores with vision-biased perception. Almost all fruits studied here are conspicuous (JND higher than birds' visual threshold) at the level of the dispersal unit. Therefore, once a fruit becomes ripe and turns a certain colour, with a resulting chromatic contrast against its background, traits at the plant level gain adaptive relevance.

Our results highlight two main premises for further testing. Firstly, visually-driven frugivores initially exert selection on crop size, assuming that this is the first variable detected by birds. Secondly, fruit consumption depends on the interaction between two traits, one at the fruit level and one at the plant level. It is known that the evolution of complex displays involves one or two modes of signal perception (Rowe 1999, Hebets & Papaj 2005). In seed dispersal mutualisms that involve frugivorous birds, fruit display signals involve traits at fruit and plant levels, both of which fall within a unique sensorial mode, the visual perception. A further line of research might improve our knowledge about interaction between plants and frugivorous birds asking for the inter-specific variation in the use of plant signals and/or cues by birds when they choose fruits for consumption (see Corlett 2011). Plants that invest in conspicuousness might allow the production of reliable information, increasing signal recognition (Cazetta et al. 2012). The association between crop size and fruit chromatic contrast could have evolved to intensify conspicuousness by a signal amplification process. Similar hypotheses were considered in the study of sexual displays (Zuk et al. 1992), animal contests (Deag & Scott 1999) signal advertising (Marples et al. 1994), or signal reliability (Harper 2006), but were not considered so far for seed dispersal mutualisms.

Schaefer & Schmidt (2004) indicated that fleshy-fruited plants might produce signals that increase fruit consumption at a low production cost, which are sufficiently detectable by frugivores (i.e., over a minimal perceptual threshold in the context of the foliage). They also suggested that signals that improve detectability are more effective and have a lower cost than signals indicating quality. Following these premises, natural selection will favour a low-cost trait combination. In our study, when chromatic contrast was high, fruit consumption increased in species with larger crop sizes. However, when chromatic contrast was low, crop size was irrelevant to explain consumption. This might be interpreted as an outcome of constraints due to production cost. It has been argued that plants produce an excessive number of fruits and usually, at the end of the season, they still bear abundant unconsumed fruits, and therefore, incur in a waste of energy and nutrients (Jordano 1995a). This apparent fruit waste may be compensated if plants with larger crop size experience greater fruit consumption, which increases seed dispersal effectiveness in comparison to plants with smaller crops (Blendinger, Loiselle & Blake 2008; Blendinger et al. 2015, 2016). In addition, the negative correlation between fruit and crop size and the positive relationship between fruit size and exposure found in our study, suggest that investing on conspicuousness is costly. Moreover, the significant relationship that we found among chromatic contrast, arrangement of fruits, and fruit size suggest that fruit display is costly. All these interpretations are research lines that demand more attention.

For a given species, chromatic contrast may be a fixed trait upon which natural selection acted in the past. This may be a common scenario, given that intra-specific variation in fruit colour is often negligible compared to inter-specific colour variation. The underlying causes of trait fixation may be related to nutrient recognition (Janzen 1983; Blendinger et al. 2015, 2016), phylogenetic constraints (Jordano 1995b), natural selection driven by seed dispersers (Lomáscolo, Speranza & Kimball 2008), phenotypic integration of traits constituting a dispersal unit (Valido, Schaefer & Jordano 2011), deterrence of antagonists (Lev-Yadun, Ne'eman & Izhaki 2009) or protection from solar radiation (Burns 2015). Our results seem to mirror a process where the amplitude of the signal becomes relevant to enhance fitness. In our study, only four out of 57 clades had strong phylogenetic effects on crop size and fruit chromatic contrast. These two traits showed weak phylogenetic effects across the rest of the tree, which might mean that their evolution is potentially driven by natural selection. Nevertheless, two points indicate that our analysis could have been affected by taxonomic biases, and phylogenetic effects might be more important than revealed by our study. First, we detected phylogenetic effects in clades including two highly diverse families, Rubiaceae and Solanaceae (Davis et al. 2009; Weese & Bohs 2007). The evolution of these large lineages of plants is complex. For example, in Rubiaceae, fleshy fruits evolved 12 times independently (Bremer et al. 1995) whereas in Solanaceae, they evolved three times (Knapp 2002). In the Neotropics, both families are highly diverse and are common shrubs and treelets in lowland humid forests (Olmstead 2013, ter Steege et al. 2013). Second, some lineages that showed non-significant phylogenetic effects (e.g., the clade including the genera *Rhipsalis*, *Chamissoa* and *Muehlenbeckia*) have poor representation in the Yungas forests. Therefore, further assessment of phylogenetic effects in conspicuousness of fruit display could be better understood in a broader taxonomic context. At the scale of our study, our interpretation is that crop size and chromatic contrast are adaptively interdependent traits as we did not find phylogenetic effects for both traits in the same clade. Given the developmental constraint exerted by flowering evolution, crop size could have evolved earlier, further constraining the evolution of fruit chromatic contrast and conspicuousness of fruit display.

Overall, our study suggests that plants may communicate profitably with frugivores by means of signal amplification based on a combination of fruit display traits. Here, we promote a more integrative view of fruit display. Specifically, conspicuousness of the fruit display may be the main strategy that drives communication between fleshy-fruited plants and frugivores (Stournaras & Schaefer 2017). In some specific clades, conspicuousness traits may also be driven by phylogenetic effects. Whether our findings apply to other seed-dispersal mutualisms and whether qualitative effectiveness of seed dispersal (*sensu* Schupp, Jordano & Gómez 2010) is increased via enhanced conspicuousness and their relationship with fruit display quality (i.e., nutrients), are still pending questions in the evolutionary ecology of seed dispersal.

Authors' contributions

The article is the final product of an initiative originated within a discussion group, and consequently all authors made substantial, rather equitable, contributions to the conception of the objectives and sampling design, data acquisition and processing, and drafting the final versions of the manuscript. In addition, Mariano Ordano incorporated co-authors' suggestions to complete the final version. Mariano Ordano, Pedro Blendinger, Silvia Lomáscolo, Natacha Chacoff and Mariano Sánchez did most of data analysis.

Acknowledgments

We thank T. Rojas, A. Amado and M. Roy for comments on a previous draft; E. Martin, S. Benítez-Vieyra, A.A. Cocucci, P. Schliserman, F. Bernacki, A. Benavidez, J.A. González, R. Piacentini, J. Cruceño, G.M. Salum, F. Iñón, for laboratory and field aid; and S. Benitez-

Vieyra, T. Klausch, and *stackoverflow* contributors for R programming tips. We thank staff of Dirección de Flora, Fauna Silvestre y Suelos (A. N. Palacios), Tucumán province, Argentina, and Parque Sierra de San Javier for fieldwork authorisations and logistical support. This research was partially supported by a CONICET scholarship given to R.A.R., FONCyT (PICT 2013-1280 to P.G.B.), CONICET (PIP 11420110100395 to M.O.), and Fundación Miguel Lillo. The authors declare that they have no conflict of interest.

Data accessibility

Appendix S1 to S6 (Data summaries, details for methods, meta-tree and R scripts): uploaded as online supporting information.

Data summaries deposited in the Dryad Digital Repository; doi:10.5061/dryad.0kh67

References

Alcántara, J.M., Rey, P.J., Valera, F., Sánchez-Lafuente, A.M. & Gutiérrez, J.E. (1997) Habitat alteration and plant intra-speciffic competition for seed dispersers. An example with *Olea europaea* var. *sylvestris*. *Oikos*, **79**, 291-300.

Berglund, A., & Rosenqvist, G. (2003) Sex role reversal in pipefish. *Advances in the Study of Behavior*, **32**, 131-167.

Blendinger, P.G., Loiselle, B.A. & Blake, J.G. (2008) Crop size, plant aggregation, and microhabitat type affect fruit removal by birds from individual melastome plants in the Upper Amazon. *Oecologia*, **158**, 273-283.

Blendinger, P.G., Ruggera, R.A., Núñez Montellano, M.G., Macchi, L., Zelaya, P.V., Álvarez, M.E., Martín, E., Osinaga Acosta, O., Sánchez, R. & Haedo, J. (2012) Fine-tuning the fruit-tracking hypothesis: spatiotemporal links between fruit availability and fruit consumption by birds in an Andean mountain forest. *Journal of Animal Ecology*, **81**, 1298-1310.

Blendinger, P.G., Jiménez, J., Macchi, L., Martín, E., Sánchez, M.S., & Ayup, M.M. (2015) Scale-dependent spatial match between fruits and fruit-eating birds during the breeding season in Yungas Andean forests. *Biotropica*, **47**, 702-711.

Blendinger, P.G., Martín, E., Osinaga Acosta, O., Ruggera, R.A. & Aráoz, E. (2016) Fruit selection by Andean forest birds: influence of fruit functional traits and their temporal variation. *Biotropica* **48**, 677-686

Blomberg, S.P. & Garland, T. (2002) Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. *Journal of Evolutionary Biology*, **15**, 899-910.

Bremer, B., Andreasen, K. & Olsson, D. (1995) Subfamilial and tribal relationships in the Rubiaceae based on the rbcL sequence data. *Annals of the Missouri Botanical Garden*, **82**, 383-397.

Brown, A.D., Grau, H.R., Malizia, L.R. & Grau, A. (2001) *Argentina*. In M. Kappelle & A.D. Brown (Ed.). *Bosques Nublados del Neotrópico*, pp. 623-659. Instituto Nacional de Biodiversidad, Santo Domingo de Heredia.

Burns, K.C. (2015) The colour of plant reproduction: macroecological trade-offs between biotic signaling and abiotic tolerance. *Frontiers in Ecology and Evolution*, **3**, 118.

Camargo, M.G.G., Cazetta, E., Morellato, L.P.C. & Schaefer, H.M. (2014) Characterizing background heterogeneity in visual communication. *Basic and Applied Ecology*, **15**, 326-335.

Cazetta, E., Schaefer, H.M. & Galetti, M. (2009) Why are fruits colorful? The relative importance of achromatic and chromatic contrasts for detection by birds. *Evolutionary Ecology*, **23**, 233-244.

Cazetta, E., Galetti, M., Rezende, E.L. & Schaefer, H.M. (2012) On the reliability of visual communication in vertebrate-dispersed fruits. *Journal of Ecology*, **100**, 277-286.

Chamberlain, S. & Szöcs, E. (2013) *taxize* - taxonomic search and retrieval in R. *F1000Research*, **2**, 191.

Corlett, R. T. (2011) How to be a frugivore (in a changing world). *Acta Oecologica*, **37**, 674-681.

Davis, A.P., Govaerts, R., Bridson, D.M., Ruhsam, M., Moat, J. & Brummitt, N.A. (2009) A global assessment of distribution, diversity, endemism, and taxonomic effort in the Rubiaceae. *Annals of the Missouri Botanical Garden*, **96**, 68-78.

Deag, J.M. & Scott, G.W. (1999) 'Conventional' signals in avian agonistic displays: integrating theory, data and different levels of analysis. *Journal of Theoretical Biology*, **196**, 155–162

Denslow, J.S., Moermond, T.C. & Levey, D.J. (1986) *Spatial Components of Fruit Display in Understory Trees and Shrubs*. In A. Estrada & T.H. Fleming (Ed.) *Frugivores and Seed Dispersal*, pp. 37-44. Springer, Netherlands.

Ehrlen, J. & Eriksson, O. (2000) Dispersal limitation and patch occupancy in forest herbs. *Ecology*, **81**, 1667-1674

Endler, J.A. & Mielke, P.W. (2005) Comparing entire colour patterns as birds see them. *Biological Journal of the Linnean Society*, **86**, 405-431.

Gelman, A. & Hill, J. (2007) *Data Analysis Using Regression and Multilevel/Hierarchical Models*. Cambridge University Press, New York.

Giannini, N.G. (1999) *La interacción de aves-murciélagos-plantas en el sistema de frugivoría y dispersión de semillas en San Javier, Tucumán, Argentina*. Doctoral Dissertation, Universidad Nacional de Tucumán, Tucumán.

Giannini, N.P. (2003) Canonical phylogenetic ordination. *Systematic Biology*, **52**, 684-695.

Giannini, N.G. & Kalko, E.K.V. (2005) The guild structure of animalivorous leaf-nosed bats of Barro Colorado Island, Panama, revisited. *Acta Chiropterologica*, **7**, 131-146.

Guilford, T., Dawkins, M.S. (1991) Receiver psychology and the evolution of animal signals. *Animal Behavior*, **42**, 1-14.

Harper, D.G.C. (2006) Maynard Smith: amplifying the reasons for signal reliability. *Journal of Theoretical Biology*, **239**, 203-209.

Harrison R.D., Ronsted, N., Xu, L., Rasplus, J.Y. & Cruaud, A. (2012) Evolution of fruit traits in *Ficus* Subgenus *Sycomorus* (Moraceae): To what extent do frugivores determine seed dispersal mode? *PLoS ONE*, **7(6)**, e38432

Hasson, O. (2000) *Knowledge, Information, Biases and Signal Assemblages*. In Y. Espmark, T. Amundsen & G. Rosenqvist (Eds.) *Animal Signals: Signalling and signal design in animal communication*, pp. 445-463. Tapir Academic Press, Trondheim.

Hebets, E.A., & Papaj, D.R. (2005) Complex signal function: developing a framework of testable hypotheses. *Behavioral Ecology and Sociobiology*, **57**, 197-214.

Herrera, C.M. (2002) *Seed Dispersal by Vertebrates*. In C.M. Herrera & O. Pellmyr (Ed.) *Plant-animal Interactions, An Evolutionary Approach*, pp. 185-208. Blackwell, Oxford.

Herrera, C.M. (2009) *Multiplicity in Unity: Plant Subindividual Variation and Interaction with Animals*. The University of Chicago Press, Chicago.

Howe, H.F. & Estabrook, G.F. (1977) Intraspecific competition for avian dispersers in tropical trees. *American Naturalist*, **111**, 817-832.

Janzen, D.H. (1983) *Physiological Ecology of fruits and their Seeds: Physiological Plant Ecology*. In O.L. Lange, P.S. Nobel, C.B. Osmond, & H. Ziegler (Ed.) *Encyclopedia of Plant Physiology*, pp. 625-655. Springer-Verlag, Berlin.

Jordano, P. (1995a) Frugivore-mediated selection on fruit and seed size: Birds and St. Lucie's Cherry, *Prunus mahaleb*. *Ecology*, **76**, 2627-2639.

Jordano, P. (1995b) Angiosperms fleshy fruits and seed dispersers: a comparative analysis of adaptation and constraints in plant-animal interactions. *American Naturalist*, **145**, 163-

191.

Jordano, P. (2000) *Fruits and Frugivory*. In R.S. Gallagher (Ed.) *Seeds: The Ecology of Regeneration in Plant Communities*, pp. 125-165. CAB International, Wallingford.

Kelber, A., Vorobyev, M. & Osorio, D. (2003) Animal colour vision - behavioural tests and physiological concepts. *Biological Reviews*, **78**, 81-118.

Knapp, S. (2002) Tobacco to tomatoes: a phylogenetic perspective on fruit diversity in the Solanaceae. *Journal of Experimental Botany*, **53**, 2001-2022.

Lev-Yadun, S., Ne'eman, G. & Izhaki, I. (2009) Unripe red fruits may be aposematic. *Plant Signaling & Behavior*, **4**, 836-841.

Lomáscolo, S.B., Speranza, P. & Kimball, R. (2008) Correlated evolution of fig size and color supports the Dispersal Syndromes hypothesis. *Oecologia*, **156**, 783-796.

Lomáscolo, S.B., Levey, D.J., Kimball, R.T., Bolker, B.M. & Alborn, H.T. (2010) Dispersers shape fruit diversity in *Ficus* (Moraceae). *Proceedings of the National Academy of Sciences*, **107**, 14668-14672

Maia, R., Eliason, C.M., Bitton, P.P., Doucet, S.M. & Shawkey, M.D. (2013) *pavo*: an R package for the analysis, visualization and organization of spectral data. *Methods in Ecology and Evolution*, **4**, 906-913.

Marples, N.M., van Veelen, W. & Brakefield, P.M. (1994) The relative importance of colour, taste and smell in the protection of an aposematic insect Coccinella septempunctata. *Animal Behaviour*, **48,** 967-974.

McCall, L.J. & Walck, J.L. (2014) Dispersal characteristics of two native and two nonnative fleshy-fruited sympatric shrubs. *Castanea*, **79**, 88-99.

Minetti, J.L., Bobba, M.E. & Hernández, C. (2005) *Régimen espacial de temperaturas en el Noroeste de Argentina*. In J.L. Minetti (Ed.) *El clima del noroeste Argentino*, pp. 141-161. Laboratorio Climatológico Sudamericano, Editorial Magna, Argentina.

Olmstead, R.G. (2013) Phylogeny and biogeography in Solanaceae, Verbenaceae and Bignoniaceae: a comparison of continental and intercontinental diversification patterns. *Botanical Journal of the Linnean Society*, **171**, 80-102.

Ortiz-Pulido, R., Albores-Barajas, Y.V. & Díaz, S.A. (2007) Fruit removal efficiency and success: influence of crop size in a neotropical treelet. *Plant Ecology*, **189**, 147-154.

Palacio, F.X., Lacoretz, M. & Ordano, M. (2014) Bird-mediated selection on fruit display traits in *Celtis ehrenbergiana* (Cannabaceae). *Evolutionary Ecology Research*, **16**, 51-62

Palacio, F.X., Valoy, M., Bernacki, F.G., Sánchez, M.S., Núñez-Montellano, M.G., Varela, O. & Ordano, M. (2017) Bird fruit consumption results from the interaction between fruit-handling behaviour and crop size. *Ethology Ecology & Evolution*, **29**, 24-37.

R Development Core Team. (2016) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.

Rowe, C. (1999) Receiver psychology and the evolution of multicomponent signals. *Animal Behaviour*, **58**, 921-931.

Ruggera, R.A. (2013) *Equivalencia ecológica en mutualismos de dispersión-frugivoría y su relación con la estructura y función de las comunidades en las Yungas australes*. Doctoral Dissertation, Universidad Nacional de Tucumán, Tucumán.

Ruggera, R.A., Álvarez, M.E. & Blendinger, P.G. (2011) Dieta de la Pava de Monte Alisera (*Penelope dabbenei*) en un bosque montano del noroeste de Argentina. *Ornitologia Neotropical*, **22**, 615-621.

Ruggera, R.A., Gómez, D. & Blendinger, P.G. (2014) Frugivory and seed dispersal role of the Yellow-striped Brush-Finch (*Atlapetes citrinellus*), an endemic emberizid of Argentina. *Emu*, **114**, 343-351.

Sallabanks, R. (1993) Hierarchical mechanisms of fruit selection by an avian frugivore. *Ecology*, **74**, 1326-1336.

Särkinen, T., Bohs, L., Olmstead, R.G., & Knapp, S. (2013) A phylogenetic framework for evolutionary study of the nightshades (Solanaceae): a dated 1000-tip tree. *BMC Evolutionary Biology*, **13**, 214. DOI: 10.1186/1471-2148-13-214

Schaefer, H.M. & Braun, J. (2009) Reliable cues and signals of fruit quality are contingent on the habitat in black elder (*Sambucus nigra*). *Ecology*, **90**, 1564-1573.

Schaefer, H.M. & Schmidt, V. (2004) Detectability and content as opposing signal characteristics in fruits. *Proceedings of the Royal Society of London B: Biological Sciences*, **271**, S370-S373.

Schaefer, H.M. & Ruxton, G. (2011) *Plant-animal Communication*. Oxford University Press, Oxford.

Schaefer, H.M., Schaefer, V. & Vorobyev, M. (2007) Are fruit colors adapted to consumer vision and birds equally efficient in detecting colourful signals? *American Naturalist*, **169**, S159-S169.

Schmidt, V., Schaefer, H.M. & Winkler, H. (2004) Conspicuousness, not colour as foraging cue in plant-animal interactions. *Oikos*, **106**, 551-557.

Schupp, E.W., Jordano, P., & Gómez, J. M. (2010) Seed dispersal effectiveness revisited: a conceptual review. *New Phytologist*, **188**, 333-353.

Stournaras, K.E., Prum, R.O & Schaefer, H.M. (2015) Fruit advertisement strategies in two Neotropical plant–seed disperser markets. *Evolutionary Ecology*, **29**, 1-21.

Stournaras, K.E. & Schaefer, H.M. (2017) Does flower and fruit conspicuousness affect plant fitness? Contrast, color coupling and the interplay of pollination and seed dispersal in two *Vaccinium* species. *Evolutionary Ecology*, **31**, 229-247.

Sumner, P. & Mollon, J.D. (2000) Chromaticity as a signal of ripeness in fruits taken by primates. *Journal of Experimental Biology*, **203**, 1987-2000.

ter Braak, C.J.F. & Šmilauer, P. (2002) CANOCO Reference Manual and CanoDraw for

Windows User's Guide: Software for Canonical Community Ordination (version 4.5). Microcomputer Power, Ithaca NY, USA.

ter Steege, H. et al. [120 authors] (2013) Hyperdominance in the Amazonian tree flora. Science, 342.

Valenta, K., Brown, K.A., Melin, A.D., Monckton, S.K., Styler, S.A., Jackson, D.A. & Chapman, C A. (2015). It’s not easy being blue: Are there olfactory and visual trade-offs in plant signalling? *PLoS ONE*, **10**, e0131725.

Valido, A., Schaefer, H.M.& Jordano, P. (2011) Colour, design and reward: phenotypic integration of fleshy fruit displays. *Journal of Evolutionary Biology*, **24**, 751-760.

van der Pijl, L. (1972) *Principles of Dispersal in Higher Plants*. Springer-Verlag, Berlin.

Venables, W.N. & Ripley, B.D. (2002) *Modern Applied Statistics with S*. Springer (4th ed), New York.

Vorobyev, M. & Osorio, D. (1998) Receptor noise as a determinant of colour thresholds. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **265**, 351-358.

Webb, C.O. & Donoghue, M.J. (2005) Phylomatic: tree assembly for applied phylogenetics. *Molecular Ecology Notes*, **5**, 181-183.

Weese, T.L. & Bohs, L. (2007) A three-gene phylogeny of the genus *Solanum* (Solanaceae). *Systematic Botany*, **32**, 445-463.

Zuk, M., Ligon, J.D. & Thornhill, R. (1992) Effects of experimental manipulation of male secondary sex characters on female mate preference in red jungle fowl. *Animal Behaviour*, **44**, 999-1006.

Supporting Information

Additional Supporting information may be found in the online version of this article.

Appendix S1. List of plant species and traits.

Appendix S2. Methods for collection and analysis for data on fruit reflectance.

Appendix S3. Bases and criteria for fruit consumption data.

Appendix S4. Competing models in the GLM procedure.

Appendix S5. Construction of the phylogenetic tree.

Appendix S6. R script for estimating relationships between fruit display traits.

Table 1. Estimated coefficients and their standard error (SE) for the selected model after a stepwise procedure applied by means of a general lineal model, where fruit consumption was the response variable, and fruit chromatic contrast, fruit size, crop size, fruit exposure and fruit aggregation were the predictor variables. See Methods and Appendix S4 for details.

Parameters	Estimate (SE)	*t*	*P*
Intercept	2.7445 (0.2987)	9.188	< 0.00001
Fruit chromatic contrast (FCC)	-0.0434 (0.0213)	-2.034	0.0465
Fruit crop size (FCS)	-0.0569 (0.1964)	-0.290	0.7732
FCC × FCS	0.0290 (0.0149)	1.943	0.0569

Table 2. Results of the Canonical Phylogenetic Ordination for 62 plant species. The two plant traits that resulted significant in the general lineal model were considered significant for each clade at *P* < 0.01 (bold); *F*, statistic value of permutations test; V%, percent of explained variation. The clades are numbered as in Figure 3. The clades denoted with an asterisk were not included in the forward stepwise selection process (*P* > 0.01). The total variation explained by the final model (after forward stepwise selection) was 42.8 % for crop size and 27.1% for fruit chromatic contrast.

Test	Trait	Clade	*F*	*P*	V%
Individual	Fruit crop size	83	10.082	**0.0015**	18.9
		107	8.895	**0.0079**	17.0
		85	7.045	0.0149	13.8
		87	6.614	0.0161	13.0
		99	5.211	0.0336	10.5
		82	4.765	0.0333	10.4
		98	4.691	0.0404	9.6
		106	4.567	0.0446	9.3
		76	4.245	0.0761	8.7
		95	4.245	0.0647	8.7
	Fruit chromatic contrast	120	15.896	**0.0032**	27.1
		119	6.111	0.0234	11.9
		80	5.696	0.0250	11.3
		79	2.856	0.0833	5.8
		99	1.709	0.2061	3.6
		110	1.608	0.2170	3.4

		98	1.537	0.2221	3.2
		116	1.396	0.2355	3.0
		70	1.098	0.3027	2.3
		74	0.952	0.3290	2.1
Forward stepwise	Fruit crop size	83, 107	7.654	**0.0056**	31.8
		83, 107, 76	7.083	**0.0095**	42.8
		75*	4.743	0.0532	
	Fruit chromatic contrast	120	15.896	**0.0032**	27.1
		80*	8.380	0.0240	

Table 3. Correlation and Kruskal-Wallis tests performed on fruit display traits of 62 plant species of the Southern Yungas. LCI: lower confidence interval, UCI: upper confidence interval, *P*: *p*-value according to bootstrapping (see Methods and Appendix S5 for details).

Correlation tests

	fruit size	fruit aggregation	fruit crop size
fruit chromatic contrast	**0.134**	**-0.175**	**-0.133**
LCI	0.133	-0.176	-0.136
UCI	0.135	-0.174	-0.130
P	0.002	<0.001	<0.001
fruit size		**-0.143**	**-0.288**
LCI		-0.144	-0.289
UCI		-0.143	-0.287
P		<0.001	<0.001
fruit aggregation			**0.419**
LCI			0.417
UCI			0.422
P			<0.001

Kruskal-Wallis tests

	fruit chromatic contrast	fruit size	fruit aggregation	fruit crop size
fruit exposure	**0.107**	**7.420**	**1.225**	**1.718**

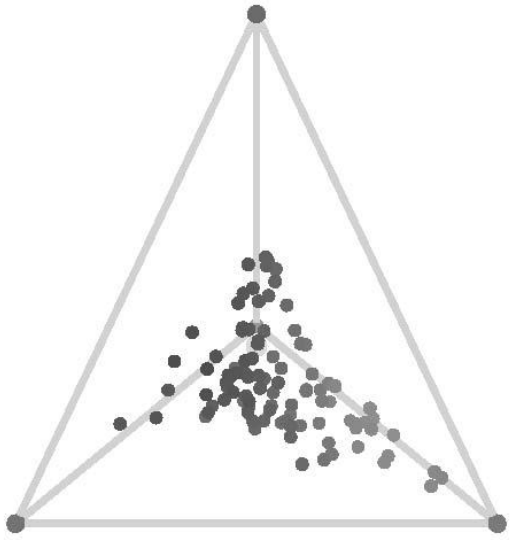
LCI	0.103	7.380	1.214	1.688
UCI	0.112	7.461	1.236	1.754
P	<0.001	<0.001	<0.001	<0.001
conclusion for plants with exposed fruits	higher fruit chromatic contrast	larger size	higher aggregation	smaller crop size
exposed mean	13.40	0.94	42.41	3.27
exposed SD	8.10	1.85	94.31	0.86
unexposed mean	12.56	0.23	7.80	3.46
unexposed SD	6.53	0.30	12.27	0.88

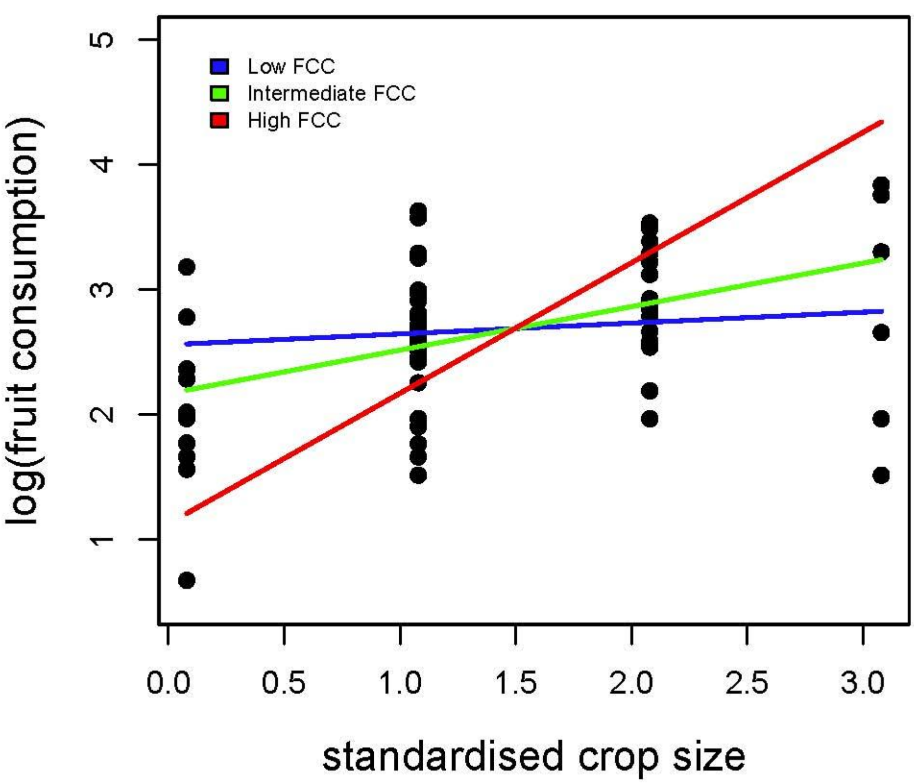
Figure legends

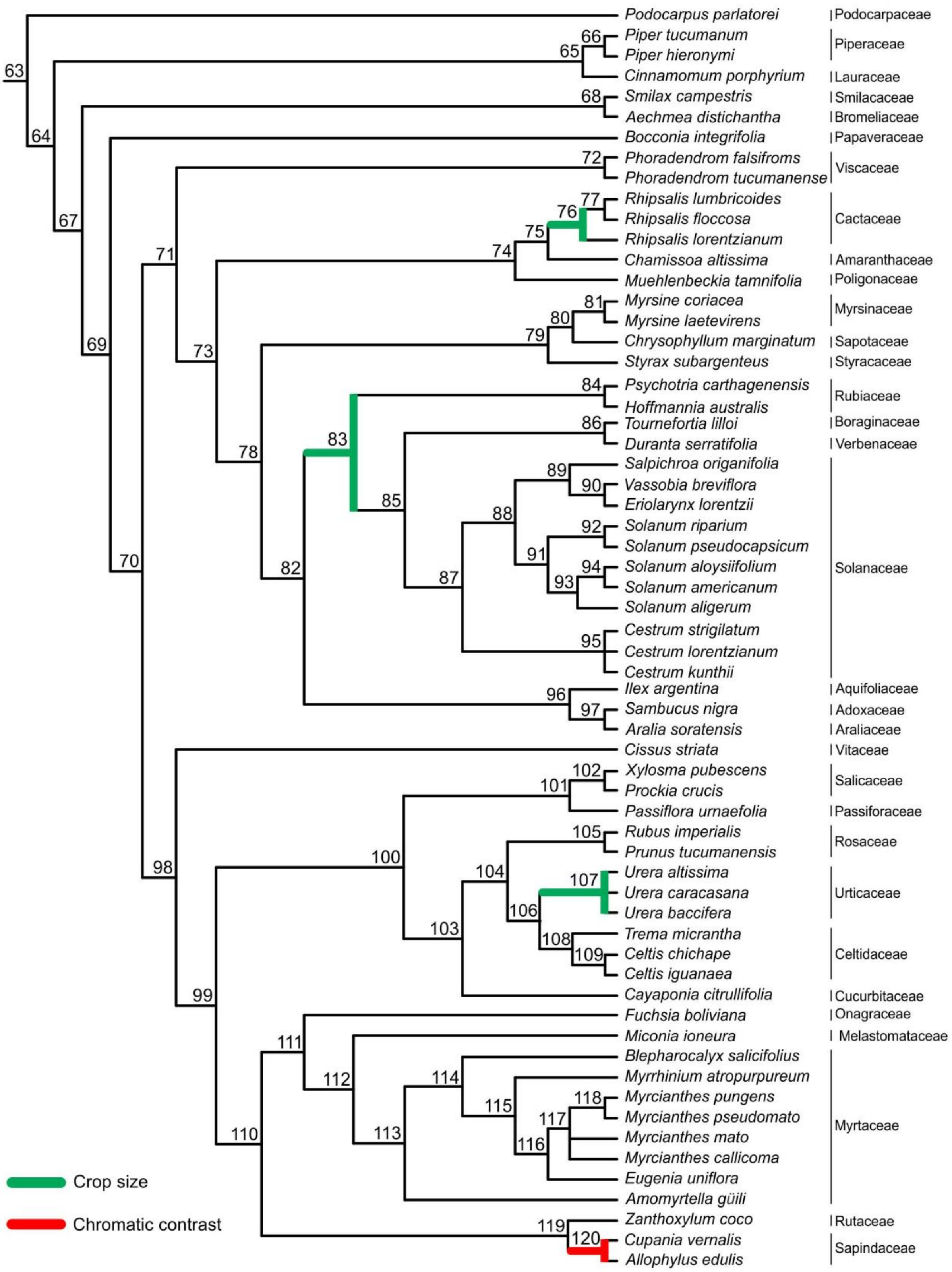
Figure 1. Fruit colour variation in the avian sensory colour space of 97 plant species in a subtropical Andean montane forest of NW Argentina. Each point represents the fruit colour average of one plant species. Location of each point is determined by the relative stimulation of each of the four types of cones: uv, s, m, and l. Cone excitation is maximized at the respective vertex of the tetrahedron.

Figure 2. Relationship between fruit consumption and fruit crop size for different values of fruit chromatic contrast. Relationship for low fruit chromatic contrast in blue (= 3), for intermediate in green (= 12) and high fruit chromatic contrast in red (= 36). Fruit consumption is increased only when higher fruit chromatic contrast is associated to larger crop size (right side of red line). On the contrary, when fruit chromatic contrast is high but crop size is small, fruit consumption is low (left side). On the other hand, low fruit chromatic contrast does not promote greater fruit consumption in spite of a larger crop size (blue line).

Figure 3. Composite cladogram of plants representing phylogenetic relationships between plants of the Southern Yungas evaluated in our study. Groups used in the Canonical Phylogenetic Ordination (CPO) analysis are noted on the tree as nodes 63 to 120. The coloured branches of the tree represent those clades that resulted significant (see Methods and Table 2 for details).




Low FCC
Intermediate FCC
High FCC
log(fruit consumption)
1
2
3
4
5
0.0
0.5
1.0
1.5
2.0
2.5
3.0
standardised crop size


63
64
65
66
67
68
69
70
71
72
73
74
75
76
77
78
79
80
81
82
83
84
85
86
87
88
89
90
91
92
93
94
95
96
97
98
99
100
101
102
103
104
105
106
107
108
109
110
111
112
113
114
115
116
117
118
119
120
Podocarpus parlatorei
Piper tucumanum
Piper hieronymi
Cinnamomum porphyrium
Smilax campestris
Aechmea distichantha
Bocconia integrifolia
Phoradendrom falsifroms
Phoradendrom tucumanense
Rhipsalis lumbricoides
Rhipsalis floccosa
Rhipsalis lorentzianum
Chamissoa altissima
Muehlenbeckia tamnifolia
Myrsine coriacea
Myrsine laetevirens
Chrysophyllum marginatum
Styrax subargenteus
Psychotria carthagenensis
Hoffmannia australis
Tournefortia lilloi
Duranta serratifolia
Salpichroa origanifolia
Vassobia breviflora
Eriolarynx lorentzii
Solanum riparium
Solanum pseudocapsicum
Solanum aloysiifolium
Solanum americanum
Solanum aligerum
Cestrum strigilatum
Cestrum lorentzianum
Cestrum kunthii
Ilex argentina
Sambucus nigra
Aralia soratensis
Cissus striata
Xylosma pubescens
Prockia crucis
Passiflora urnaefolia
Rubus imperialis
Prunus tucumanensis
Urera altissima
Urera caracasana
Urera baccifera
Trema micrantha
Celtis chichape
Celtis iguanaea
Cayaponia citrullifolia
Fuchsia boliviana
Miconia ioneura
Blepharocalyx salicifolius
Myrrhinium atropurpureum
Myrcianthes pungens
Myrcianthes pseudomato
Myrcianthes mato
Myrcianthes callicoma
Eugenia uniflora
Amomyrtella güili
Zanthoxylum coco
Cupania vernalis
Allophylus edulis
Podocarpaceae
Piperaceae
Lauraceae
Smilacaceae
Bromeliaceae
Papaveraceae
Viscaceae
Cactaceae
Amaranthaceae
Poligonaceae
Myrsinaceae
Sapotaceae
Styracaceae
Rubiaceae
Boraginaceae
Verbenaceae
Solanaceae
Aquifoliaceae
Adoxaceae
Araliaceae
Vitaceae
Salicaceae
Passiforaceae
Rosaceae
Urticaceae
Celtidaceae
Cucurbitaceae
Onagraceae
Melastomataceae
Myrtaceae
Rutaceae
Sapindaceae
🟩 Crop size
🟥 Chromatic contrast