Fruit selection by Andean forest birds: influence of fruit functional traits and their temporal variation

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ABSTRACT

Fruit selection, *i.e.,* the consumption of fruits disproportionately to their availability, results from the interaction between diet preferences and ecological factors that modify them. We assessed the importance of functional fruit traits to explain fruit selection by birds in Andean subtropical forests, taking into account temporal variation in trait distribution in the assembly of available fruits. During 2 yr, we measured the abundance of ripe fruits and their consumption by birds in a 6-ha plot during 11 bimonthly samplings, and we used 17 phenological, morphological, and nutritional traits to characterize fruits selected by four bird species. Fruit selection was pervasive year-round, highly variable over time and across bird species. Fruit species were selected over time periods shorter than their ripening phenology, and the selection of fruits with particular traits was specific to the fruit-eating species. Maximization in pulp reward per consumed fruit seems to be the main driving force behind fruit selection, indicating that birds select fruits with traits that directly affect net energy gain. Our results can be interpreted in a framework of a hierarchy of foraging decisions, under which the spatiotemporal context of the fruiting environment modifies the relative intake rates of a particular fruit, while the ability to discriminate fruit contents becomes increasingly important on a smaller dimension. We show that fruit-selection properties are contingent on specific fruit traits and particular spatiotemporal conditions, which modify the structure of mutualistic interactions.

Abstract in Spanish is available with online material.

Key words: Andean forests; feeding selection; fruit shape; fruit-eating birds; functional trait; Neotropics; nutrient content; pulp-to-seed ratio.

MOST FRUIT-EATING BIRDS INCLUDE A WIDE RANGE OF FRUIT IN THEIR DIETS AND OFTEN SELECT CERTAIN FRUIT SPECIES that are consumed in greater proportions to their availability over alternative diet options (Fleming & Estrada 1993, Dennis *et al.* 2007). Bird foraging decisions leading to fruit-selection patterns can provide insights into the ecology and physiology of the consumers, such as adaptations in their digestive physiology, abilities to discriminate nutrients, and nutritional requirements that they need to meet. Moreover, these decisions are relevant due to their potential consequences on the evolution and ecology of plants being consumed. Non-random patterns of fruit consumption render the fruit-eating birds potential selective agents, which can lead to phenotypic selection of fruit traits associated to seed dispersal (Lomáscolo *et al.* 2010, Sobral *et al.* 2010, Palacio *et al.* 2014). Among the ecological implications of fruit selection by birds, differences in the seed-dispersal effectiveness provided by fruit-eating birds across plant species might affect plant demography and local patterns of vegetation diversity (Jordano 2000, Schupp *et al.* 2010). These implications are particularly important in tropical and subtropical forests, where interactions between plants and

their seed dispersers involve up to 90 percent of woody plant species and a large proportion of birds which feed on fruits (Fleming *et al.* 1987, Kissling *et al.* 2009).

Diet 'preferences' of birds, *i.e.*, increased consumption of certain food item given equal access to alternative foods (Johnson 1980, Bolser *et al.* 2013), can be related to physiological capacities (Lepczyk *et al.* 2000, Wilson & Downs 2012) and nutritional requirements (Herrera 1982, Wheelwright 1988) of consumers and to fruit traits, such as concentration and type of nutrients (Levey 1987, Avery *et al.* 1999), secondary compounds (Cipollini & Levey 1997, Catoni *et al.* 2011), energy content (Wilson & Downs 2011), color (Avery *et al.* 1995, Schaefer *et al.* 2008), and size (Sobral *et al.* 2010). Fruit preferences are usually determined in controlled studies in aviaries, while field studies typically evaluate fruit selection. Unlike preference, food 'selection' is the process by which an animal chooses among different resources and consumes them disproportionately to their availability (Johnson 1980). It results from the interaction between diet preferences and several factors that modify them (Martin 1985, Bolser *et al.* 2013), including consumer abilities, trophic morphology (*e.g.*, gape size) and its constraints on feeding behavior (Moermond & Denslow 1985, Moran & Catterall 2010), the arrangement and spatial distribution of fruits (Denslow 1987, Sasal & Morales 2013,

Smith & McWilliams 2014), the availability of alternative resources (Saracco *et al.* 2005, Blendinger & Villegas 2011), the temporal variation of fruit types (Herrera 1982), and interactions with other fruit-eating animals (Carlo 2005).

Fruits with fleshy pulp are an important resource in the diets of many species of birds. They provide water, energy in the form of simple carbohydrates and lipids, nutrients such as protein, and micronutrients such as vitamins and minerals (Karasov & Martinez del Rio 2007). The composition and concentration of nutritional compounds are highly variable between fruit species (*e.g.*, Herrera 1987, Pannell & Koziol 1987, Blendinger *et al.* 2015). Under the assumption that individuals select those types of resources that meet the most adequate set of conditions to satisfy their living requirements (Stephens & Krebs 1986, Manly *et al.* 2002), it is expected that fruit selection is based on nutritional features (Levey & Martinez del Rio 2001). Owing to multiple factors that could modify fruit availability, studies on bird diets in the wild do not show a clear relationship between fruit selection and fruit traits such as preference studies in aviaries do. This promoted the idea that fruit selection is less dependent on fruit characteristics than on spatiotemporal contingencies and contextual circumstances such as the composition and abundance of the fruit assemblage (Johnson *et al.* 1985, Jordano 1988, Whelan & Willson 1994). Despite the influence of the environmental context, fruit-eating birds can be very consistent over time in their criteria of fruit selection (Herrera 1998). Therefore, the importance of particular fruit traits on bird decisions leading to resource selection remains as an open question in the extensive literature on frugivory.

Our aim is to determine the importance of fruit functional traits (*i.e.*, phenological, morphological, and chemical characteristics which might indirectly impact species fitness via their interaction with seed dispersers) to explain fruit selection by birds in Southern Yungas Andean forests of Argentina. These forests host around 240 plant species primarily dependent on birds and bats to disperse their seeds; seed dispersal by birds often depends on small-sized perching birds in Tyrannidae, Turdidae, and Thraupidae families (Malizia 2001, Blendinger & Giannini 2010, Ruggera *et al.* 2016). To understand patterns of fruit selection by birds and identify their driving mechanisms, (1) we investigate fruit selection by the most common fruit-eating bird species, comparing fruit availability and fruit consumption during 2 yr of bimonthly samplings. Then, (2) we assess if fruit traits related to the quantity and quality of resources influence the selection of fruits by birds. First, we explore the distribution of fruit selection by birds in the multidimensional space of fruit traits. Second, we compare the consumption and availability of fruits in terms of nutritional, morphological, and phenological traits to determine if single functional traits may explain fruit selection by birds. Since fruit selection occurs in a changing context of combinations of co-fruiting species (Herrera 1998, Saracco *et al.* 2005), we take into account the temporal variation in the distribution of fruit traits. We expect that particular fruit traits—or combinations of traits—above the level of fruit species are responsible for fruit-eating bird behaviors that lead to diet selection patterns.

METHODS

STUDY AREA.—We conducted this study in Parque Sierra de San Javier, Tucumán province, northwest Argentina. This is a 14,000 ha protected area with Andean forests known as Southern Yungas. Climate is subtropical with dry winters (May to September) and wet summers (November to March). Average annual rainfall varies between 1300 and 1500 mm across the mountain ranges, of which 80 percent is concentrated in summers; average annual temperature is 19°C (Minetti *et al.* 2005). The study site (26°30′ S, 65°40′ W, 970 m asl) belongs to the lower montane forest, a multi-layered mature forest including deciduous and evergreen species. Canopy varies between 15 and 30 m high, and it is dominated by emergent species like *Ocotea porphyria* (Lauraceae) and *Blepharocalyx salicifolius* (Myrtaceae). The upper tree layer is mainly composed by *Parapiptadenia excelsa* (Fabaceae), *Myrcianthes pungens* (Myrtaceae), *Pisonia zapallo* (Nyctaginaceae), and *Terminalia triflora* (Combretaceae). The lower tree layer, between 5 and 12 m high, is dominated by *Piper tucumanum* (Piperaceae), *Eugenia uniflora* (Myrtaceae), *Allophylus edulis* (Sapindaceae), and *Solanum riparium* (Solanaceae). Understory vegetation is dense and strongly dominated by *Psychotria carthagenensis* (Rubiaceae), a shrub reaching up to 4 m high. The most common vines and epiphytes are *Cissus striata* (Vitaceae), *Celtis iguanaea* (Cannabaceae), *Aechmea distichantha* (Bromeliaceae), and *Rhipsalis floccosa* (Cactaceae). We used a 200 × 300 m plot (6 ha), split in a grid of 150 cells of 20 × 20 m each, where we carried out 11 bimonthly samplings between September 2008 and June 2010. Each sampling period lasted 3 d on the first week of the 2-mo, when we measured the abundance of ripe fruits and fruit consumption by birds as summarized below.

RIPE FRUIT ABUNDANCE.—We performed exhaustive searches of fruiting plants (trees, shrubs, vines, and epiphytes) and counted ripe fruits of each individual plant. During each sampling period, we recorded all ripe fruits of bird-dispersed plants in each 20 × 20 m cell. We counted ripe fruits per plant from 1 to 10 in units, from 11 to 100 in tens, from 101 to 1000 in hundreds, and for more than 1000 in thousands of fruits. Given the extremely high density of *Psychotria carthagenensis*, its fruit abundance was estimated counting fruits in five 4-m^2 quadrats randomly located in each cell and extrapolated to the surface area of the cell. We estimated fruit abundance of epiphytic plants by direct counting whenever possible; alternatively, we assigned to these plants the average value for the species during the corresponding sampling period. We determined fruit ripeness of all species based on previous observations about the condition in which fruits are usually eaten by birds. All observers were trained and their performance compared prior to the sampling to reduce observer bias in fruit counting and determination of fruit ripeness. Fruit abundance was expressed as dry mass of ripe fruit pulp and calculated for each species as the recorded number of ripe fruits times the mean pulp dry mass in grams. We obtained pulp dry mass of each species from healthy fresh ripe fruits, dried at 60°C for 72 h (Blendinger *et al.* 2015).

FRUIT CONSUMPTION BY BIRDS.—We recorded fruit consumption by birds during the same sampling periods than fruit abundance (11 sampling periods, 3 d of observation in each one). Starting 30 min after sunrise and within the next 4 h, each one of five observers traversed a block of 10 × 2 contiguous 20 × 20 m cells, walking slowly and recording all fruit-eating birds. We sampled a total of 50 h per period (550 h considering the whole study). Since bird activity varies throughout the day, we minimized temporal biases by sampling each cell at two different times (early in the morning and mid-morning) in subsequent days. In each cell, we recorded every event of fruit consumption seen, noting the species of bird and fruit. A fruit consumption event was defined as a visit of a bird to a plant in which it was observed eating at least one fruit. In a few cases with restricted visibility, we also included birds that entered into a part of the plant with ripe fruit and that remained in there for a length of time consistent with fruit consumption (Saracco et al. 2005, Blendinger et al. 2012). We did not count the number of fruits consumed because limited visibility inside the forest prevented their reliable quantification. We considered consecutive visits to different plants as separate events; likewise, we considered each individual of a flock consuming fruits a separate frugivory event. Although this approach might cause some pseudoreplication, we believe this would have only a minor effect on the results because most times, interaction records corresponded to one individual bird eating fruits on one individual plant (Ruggera et al. 2016).

FRUIT SELECTION.—We obtained enough data of fruit consumption to analyze fruit selection by four bird species: Rufous-bellied Thrush (*Turdus rufiventris*; 66.2 g body mass), Sayaca Tanager (*Thraupis sayaca*; 30.7 g), Common Bush-Tanager (*Chlorospingus ophthalmicus*; 16.6 g), and Golden-rumped Euphonia (*Euphonia cyanocephala*; 16.3 g). *Turdus rufiventris* is a 'gulper' that swallows whole fruits, while the other three species are 'pulp mashers'; *i.e.*, they pluck fruits and process them with the bill, discarding the peel and some seeds (Blendinger & Villegas 2011, Ruggera et al. 2016).

We analyzed fruit selection by each bird species in sampling periods with at least five events of fruit consumption. Plant species with one or two consumption events in a sampling period were used in all analyses but not to assess fruit selection of those plant species. For every available fruit species (r), we calculated Manly's index of selection (α), which measures the frequency of use of a fruit species (f_r) in relation to its relative availability (g_r), with n_R the number of available fruit species.

$$\alpha = \frac{\frac{f_r}{g_r}}{\sum_{j=1}^{n_R} \frac{f_j}{g_j}}$$

The denominator is a scaling factor that sums up the numerators of every available resource. Thus, calculated alphas range from 0 to 1 and the alpha selection indices of all available resources sum up to 1. Under the assumption of no selection, every available resource would have an alpha of $1/n_R$. Values above $1/n_R$ indicate some degree of selection, with 1 being the most extreme case in which a bird species consumes only one resource (Manly et al. 2002, Pledger et al. 2007).

FRUIT TRAITS.—Traits used to characterize the nutritional quality of fruits were concentration of total sugars (sugars) (g of glucose/100 g dry weight), proteins (mg BSA [bovine serum albumin]/100 g dry weight), total polyphenols (mg GAE [gallic acid equivalents]/100 g dry weight), and essential minerals: Ca, Na, K, Fe, Mg, and P (mg/100 g dry weight). A full explanation of laboratory techniques used to calculate each nutrient type is provided in Blendinger et al. (2015). We also considered the length of the fruiting phenology (number of sampling periods with ripe fruits) and the following morphological traits: fruit mass (mean mass of the whole fresh fruit in *g*), fruit width (mean equatorial diameter of fruit in mm), fruit shape (fruit length/fruit width), seed number (mean number of seeds per fruit), seed mass (mean mass of a single seed in mg), total seed mass (mean mass of seeds per fruit in mg), and pulp-to-seed ratio (fruit mass/total seed mass). Hereafter, each trait will be referred to as follows: sugars, proteins, phenols, Ca, Mg, Na, K, P, Fe, fruiting phenology, fruit whole mass, fruit width, fruit shape, seed number, seed mass, total seed mass, and pulp-to-seed ratio.

STATISTICAL ANALYSES.—To evaluate the statistical significance of fruit selection by bird species in each sampling period, we used a null model of frugivory based on resamplings of fruit consumption assuming that fruits were taken randomly (*i.e.*, consumption in the null model was affected by fruit abundance but not by fruit selection). Thus, fruit samples were taken from a multinomial distribution in which the probability of consuming each fruit species was proportional to its relative abundance (g_r). To build the distribution of the null model, we performed 10,000 resamplings of random fruit consumption (Manly et al. 1993, Gotelli & Graves 1996). We evaluated the deviation of the observed fruit consumption from the expected theoretical diet with a single metric (Bray Curtis dissimilarity index) to avoid multiple inferences on single datasets. As distances cannot attain negative values, we considered that the observed composition of fruit consumption significantly deviated from a random pattern whenever it exceeded the value of the 95th percentile. When this criterion was attained, we evaluated resource selection individually. So we compared the observed frequency of use of each resource (f_r) with the distribution of its simulated consumptions and we took a significance level of 0.05 corrected by the sequential Bonferroni method (Pledger et al. 2007). We evaluated selection of fruits consumed at least three times to reduce the noise of occasional fruit consumption.

We used principal component analysis (PCA) to reduce the multiple dimensions of fruit functional traits. We conducted two separate PCAs, one with nutritional traits and one with morphological traits. All fruit variables except fruit shape and pulp-to-seed ratio were log_{10}-transformed before the analysis. We used the first two principal components (PC 1 and PC 2) of each PCA to interpret the major nutritional and morphological trends

in the assembly of consumed fruits. To explore the distribution of fruit species selected by bird species in the multidimensional space of consumed fruits, we used surface graphics denoting the frequency of fruit selection (*i.e.*, number of sampling periods in which a fruit was selected) on the plane defined by the first two PCs of nutritional and morphological traits, respectively.

To evaluate the statistical significance of fruit traits used to explain consumption patterns by each bird species, we compared the observed average traits with simulations obtained through 10,000 randomizations. In every randomization, we simulated random events of fruit consumption to obtain an average value of every functional trait. The simulated number of fruit consumption events in a specific sampling period was the same as the number of consumption events observed for the bird species; the probability of consuming a fruit species depended on the fruit relative abundance. We recorded the average of functional traits of fruits consumed in every simulation. Observed values significantly higher or lower than expected by chance (above the 97.5th percentile or below the 2.5th percentile) indicated that the fruit-eating species consumed fruits with high (or low) values of a given fruit trait. All analyses were conducted using the R environment (R Development Core Team 2013).

RESULTS

In 1269 interactions between 18 bird species and 22 plant species, 89 percent corresponded to *T. rufiventris, T. sayaca, C. ophthalmicus,* and *E. cyanocephala.* We recorded the consumption of fruits by *T. sayaca* and *C. ophthalmicus* in 11 sampling periods, in 10 by *T. rufiventris,* and in six by *E. cyanocephala.* Species richness of ripe fruits reached extreme values in June (five species) and November to January (13 species) (Table S1). The mean pulp dry mass was 855.6 g/ha (range: 41.2 g/ha in February to 4327.5 g/ha in September). *Psychotria carthagenensis* accounted for 62.3 percent of total pulp dry mass, followed by *Celtis iguanaea* (7.8%), *Piper tucumanum* (7.5%), *Ocotea porphyria* (6.2%), and *Duranta serratifolia* (5.4%); each of the remaining 17 species accounted for <5 percent of total pulp dry mass recorded throughout the study (Table S1). The length of the fruiting phenology showed a noteworthy variation across species, 9 percent of the species (*P. tucumanum* and *S. riparium*) had fruits in 10 of 11 sampling periods, while 45.5 percent (10 species) fructified in three or fewer sampling periods (Table S1).

FRUIT SELECTION.—The four fruit-eating species altogether selected 13 out of the 22 fruit species they consumed. The number of fruit species selected per sampling period ranged from one species in October to five species in July and December. *Phoradendron falcifrons* was the only fruit species selected by the four fruit-eating species, *Rhipsalis floccosa* was selected by three of them, *Blepharocalix salicifolius, Chamissoa altissima, Myrsine laetevirens,* and *P. carthagenensis* by two species, and the remaining seven (62% fruit species) were selected by a single bird species (Table 1)

Turdus rufiventris selected fruits in 66 percent of the sampling periods in which it was recorded eating fruits, *T. sayaca* in 100 percent, *C. ophthalmicus* in 87 percent, and *E. cyanocephala* in 83

percent. *Turdus rufiventris* selected 5 of the 18 species it consumed (range: 0–2 per sampling period), *T. sayaca* selected 10 of 16 (range: 1–4), *C. ophthalmicus* selected 4 of 13 (range: 0–2), and *E. cyanocephala* selected 2 of 6 (range: 0–2) (Table 1).

FRUIT TRAITS.—The first two components of the nutritional PCA explained 53.6 percent of total variation in the chemical composition of fruits. PC 1 represented a decrease in the concentration of minerals (except K), and PC 2 mainly represented an increase in protein and phenol concentration (Table 2). The first two components of the morphological PCA explained 73.0 percent of the total variation in shape and size of fruits consumed. These two components primarily represented a decrease in fruit size (mass and width) on PC 1 and a decrease in seed number and fruit shape on PC 2; pulp-to-seed ratio had a high and positive factor loading on PC 1 (Table 2).

Frequencies of fruit selection in the multidimensional space of fruit traits varied sharply among fruit-eating species. The ordi-

TABLE 1. *Number of sampling periods in which fruit species were consumed (C) and selected (S) by fruit-eating bird species in a Southern Yungas mountain forest of Argentina. The selected times are emphasized in bold.*

Plant species	Turdus rufiventris		Thraupis sayaca		Chlorospingus ophthalmicus		Euphonia cyanocephala	
	C	S	C	S	C	S	C	S
Ocotea porphyria	3	–	2	–	–	–	–	–
Piper tucumanum	3	–	5	**3**	2	–	–	–
Aechmea distichantha	1	–	2	**1**	–	–	1	–
Cissus striata	1	**1**	–	–	–	–	–	–
Celtis iguanaea	2	–	2	–	3	–	–	–
Urera baccifera	1	**1**	1	–	1	–	–	–
Urera caracasana	–	–	2	**1**	1	–	–	–
Blepharocalix salicifolius	1	–	2	**1**	2	**1**	1	–
Eugenia uniflora	2	**2**	2	–	1	–	1	–
Myrcianthes pungens	1	–	–	–	–	–	–	–
Allophylus edulis	–	–	–	–	1	–	–	–
Cupania vernalis	2	–	2	–	–	–	–	–
Phoradendron falcifrons	4	**1**	6	**5**	6	**3**	6	**5**
Chamissoa altissima	–	–	2	**1**	1	**1**	–	–
Rhipsalis floccosa	–	–	3	**2**	3	**2**	1	**1**
Myrsine laetevirens	1	–	4	**2**	1	–	–	–
Psychotria carthagenensis	6	**2**	6	**1**	4	–	1	–
Duranta serratifolia	1	–	–	–	–	–	–	–
Cestrum lorentzianum	1	–	–	–	–	–	–	–
Cestrum strigillatum	1	–	–	–	–	–	–	–
Solanum riparium	3	–	5	**1**	2	–	–	–
Zanthoxylum coco	1	–	1	–	–	–	–	–

TABLE 2. *Factor loadings of fruit traits and contribution to the variance of the two-first principal components of both principal component analyses on chemical and morphological traits of fruits consumed by bird species across the study period.*

	PCA of chemical traits			PCA of morphological traits		
	PC 1	PC 2		PC 1	PC 2
Eigenvalue	2.63	2.20	Eigenvalue	3.13	1.98
% Total variance	29.2	24.5	% Total variance	44.7	28.3
Factor loadings			Factor loadings		
Sugars	−0.35	0.19	Fruit whole mass	−0.91	−0.31
Proteins	−0.35	0.75	Fruit width	−0.60	0.16
Phenols	−0.01	0.63	Fruit shape	−0.49	−0.70
Ca	−0.66	0.46	Seed number	−0.12	−0.90
Mg	−0.60	0.55	Single seed mass	−0.70	0.61
Na	−0.66	−0.38	Total seed mass	−0.97	0.01
K	0.47	0.47	Pulp-to-seed ratio	0.51	−0.44
P	−0.60	−0.51			
Fe	−0.76	−0.26			

nation of nutritional traits showed that *T. rufiventris* tended to select fruits with average values of minerals and low in protein and phenol concentration; *T. sayaca* tended to select fruits rather

dissimilar in nutritional content; *C. ophthalmicus* tended to select fruits low in proteins and phenols and high in mineral concentration; *E. cyanocephala* did not show a clear selection tendency for fruits with particular nutritional traits (Fig. 1). Assessment of morphological fruit traits showed that *T. rufiventris* tended to select medium-sized round-shaped fruits with one or a few seeds; *T. sayaca* and *C. ophthalmicus* showed a trend to select small-sized fruits with low seed load and high pulp-to-seed ratio; *E. cyanocephala* clearly selected small fruits with a high pulp-to-seed ratio (Fig. 2).

Traits of fruits selected by birds varied across sampling periods and fruit-eating species (Table 3). The main trends seen were as follows. *Turdus rufiventris* selected fruits with a low protein concentration. *Thraupis sayaca*, *C. ophthalmicus*, and *E. cyanocephala* selected fruits with a low concentration of minerals, but differed in that *T. sayaca* selected fruits with high concentrations of sugars, proteins, and phenols, while *C. ophthalmicus* and *E. cyanocephala* selected fruits with average concentrations of macronutrients. The four species selected round small fruits high in pulp-to-seed ratio, but frugivores differed in the importance of seed load, which was high in fruits selected by *T. sayaca* and low in fruits selected by the remaining bird species. *Turdus rufiventris* clearly selected species available during short time periods (Table 3).

FIGURE 1. Color surface graph of the frequency of fruit selection (ratio of number of sampling periods that one fruit species was selected and the total of sampling periods that had ripe fruits) in the space of nutritional fruit traits of fruits consumed by fruit-eating birds in Southern Yungas forests. Empty circles indicate fruit species.
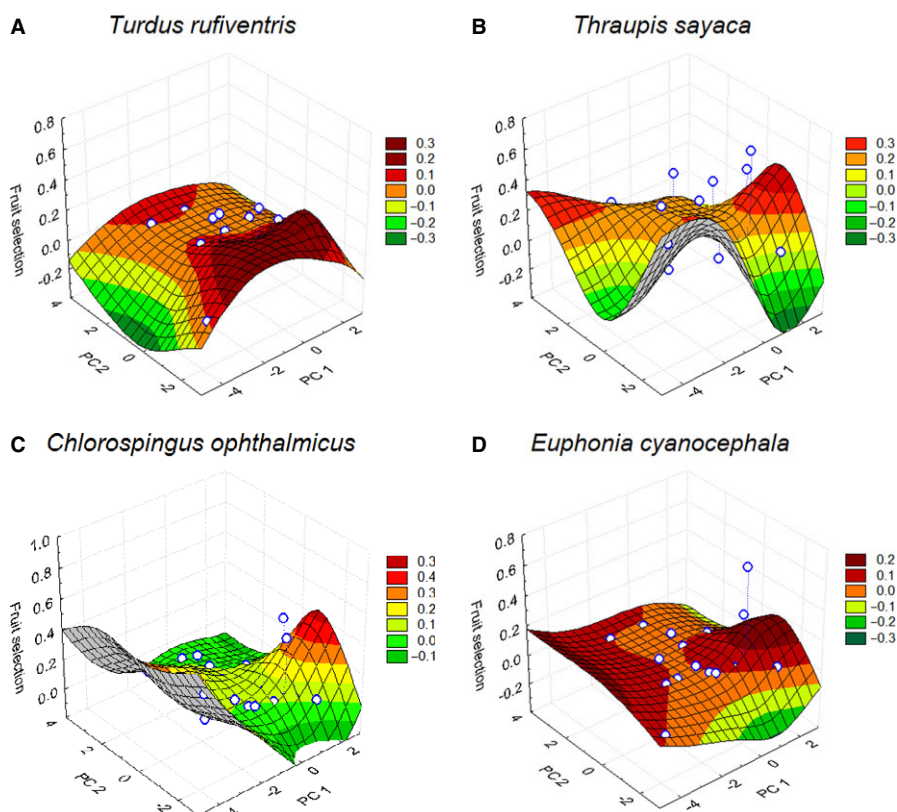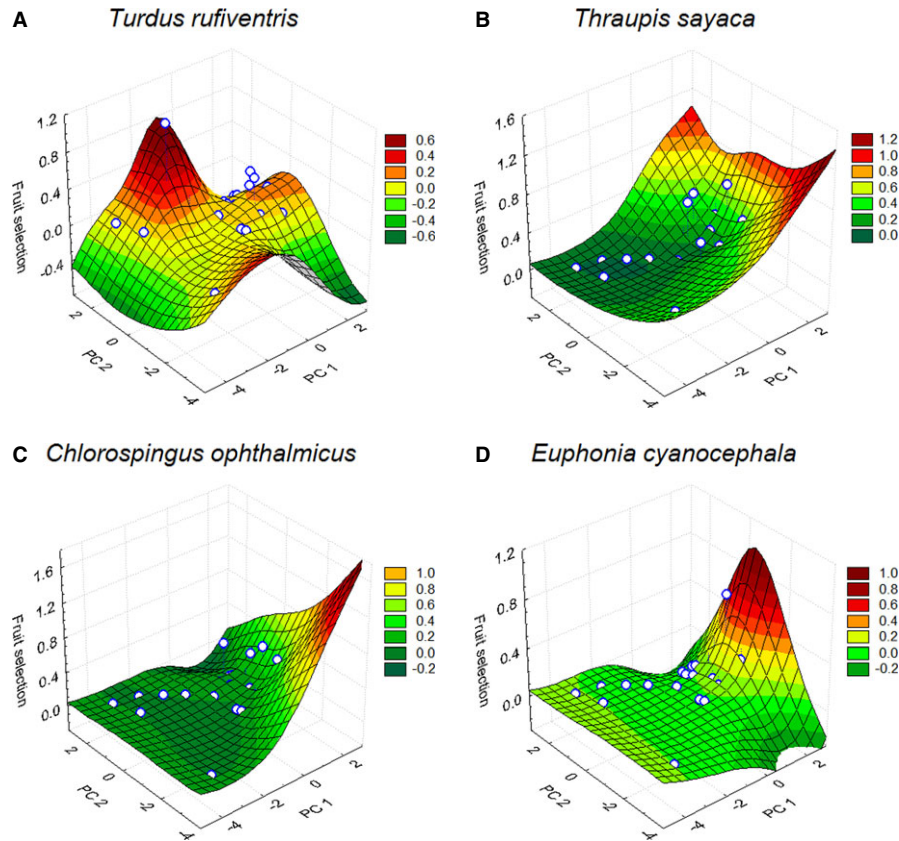
FIGURE 2. Color surface graph of the frequency of fruit selection (ratio of number of sampling periods that one fruit species was selected and the total of sampling periods that had ripe fruits) in the space of morphological fruit traits of fruits consumed by fruit-eating birds in Southern Yungas forests. Empty circles indicate fruit species.

DISCUSSION

The selection of particular fruit species is highly variable in time and is a fairly idiosyncratic behavior of fruit-eating bird species in subtropical Andean forests. Particular fruit species are selected only over short time periods, even when most plant species offer ripe fruits during several months. Given the temporal changing nature that characterizes fruit species abundances and the composition of co-fruiting species, we conclude that fruit selection is highly dependent on the temporal context of fruit availability. Fruits selected by birds depart from the pool of available species in their values of particular functional traits, but the traits relevant to the interaction can change throughout the year when other fruits are selected by birds. The main trend across bird species involves the selection of fruits with high pulp-to-seed ratio. In the context-dependent scenario depicted above, selection of fruits with particular traits might reflect behavioral decisions subordinated to the availability of a very limited pool of fruit types. Moreover, given that temporal variation in fruit-selection criteria is more pronounced between than within bird species, our results suggest that ecological and evolutionary processes acting at the species level play an important role in the selection of fruits with particular functional traits.

Some fruit species were selected once or a few times even when they were available for more time. This can be explained by two not mutually exclusive mechanisms: changes in the market of available fruits and changes in the nutritional demands of fruit-eating birds. In the former case, the selection of a particular fruit species can be determined by costs and benefits related to the abundance and composition of the fruiting environment (Johnson *et al.* 1985, Whelan & Willson 1994). Plant species partially overlap their ripening phenology over time (Table S1), which might influence bird foraging decisions in a temporal, context-dependent way (Burns 2005). Thus, a fruit species that is the best option for a fruit-eating bird at a given moment may not be so for a new context of coexistence with other fruit species. In the second case, selection of different fruit species throughout the year can be driven by seasonal changes in bird requirements related to life history and physiological traits, such as migration, molting, and reproduction (Bairlein & Gwinner 1994, Murphy 1996, Lamperti *et al.* 2014). This implies fine adjustments in foraging behavior to fulfill specific, temporal nutritional requirements, which are feasible due to the bird's ability to discriminate differences in the nutritional content of fruits (Schaefer *et al.* 2003, Schaefer & Schaefer 2006, Wilson & Downs 2011). However, this argument cannot explain why different bird species

TABLE 3. *Summary of the statistical significance of traits of fruits consumed by birds across 2 yr in a Southern Yungas mountain forest, showing observed values significantly lower (−) or higher (+) than expected by chance or not different (0) than expected by chance. We show sampling periods with one or more fruit species selected by the fruit-eating species. The selected times (+) are emphasized in bold.*

	Turdus rufiventris							*Thraupis sayaca*									*Chlorospingus ophthalmicus*						*Euphonia cyanocephala*				
	Nov	Jan	May	Jul	Dec	Apr	Sep	Nov	Jan	May	Jul	Oct	Dec	Apr	Jun	Sep	Sep	Nov	Jan	Jul	Oct	Dec	Sep	Jan	May	Oct	Dec
Chemical traits																											
Sugars	−	0	−	0	0	0	+	0	+	+	0	+	+	+	+	+	0	−	+	0	+	−	0	0	+	+	0
Proteins	−	−	0	−	−	0	+	0	+	−	+	+	+	+	0	+	0	0	0	0	0	0	0	0	0	0	0
Phenols	0	−	0	−	+	0	+	0	0	0	+	+	+	+	+	+	+	0	−	0	0	−	0	0	0	0	0
Ca	−	+	+	+	−	+	−	−	+	+	−	−	−	+	−	−	−	−	0	−	−	−	−	0	−	−	−
Mg	−	+	0	0	−	+	−	−	+	0	−	−	−	−	−	−	−	−	+	−	−	−	−	0	−	−	−
Na	−	+	+	+	−	+	−	−	+	+	−	−	0	+	+	−	−	−	+	−	−	0	−	+	0	−	−
K	−	−	+	+	−	+	−	−	−	+	−	−	−	+	0	−	−	−	−	0	−	−	−	0	0	−	−
P	−	+	0	0	−	0	−	−	+	0	−	−	−	−	0	−	−	−	+	0	−	−	−	+	−	−	−
Fe	0	+	+	0	0	+	−	−	+	+	+	−	−	+	+	−	−	0	+	−	0	+	−	+	0	0	−
Morphological traits																											
Fruit whole mass	0	−	−	−	0	−	+	0	0	−	0	−	0	+	+	+	−	0	−	−	−	−	−	−	−	−	−
Fruit width	+	−	−	−	−	0	+	0	−	−	−	−	0	−	−	+	−	−	−	−	−	−	−	−	−	−	−
Fruit shape	−	−	−	−	−	0	+	0	0	0	−	−	0	+	+	+	−	0	0	−	−	0	−	−	−	−	0
Seed number	−	−	−	0	−	0	+	0	0	0	0	−	+	−	+	+	−	0	−	−	−	0	−	−	−	−	0
Seed mass	+	0	−	0	0	0	−	−	0	+	+	−	0	−	−	−	−	0	0	−	−	0	−	0	−	−	−
Total seed mass	+	−	−	−	0	0	+	0	0	−	0	−	0	+	+	+	−	0	−	−	−	−	−	−	−	−	−
Pulp-to-seed ratio	−	0	+	0	0	+	+	+	0	+	0	+	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+
Fruiting phenology	−	−	+	0	−	−	+	+	0	−	+	+	0	+	0	+	+	0	−	+	+	0	+	−	0	+	+

select fruits with extremely divergent nutritional traits in the same period of time (*i.e.*, during the same stage of their life cycle). Both explanatory mechanisms of temporal variation in the selection of fruit species, the influence of the market of available fruits and bird's ability to adjust consumption to specific requirements, may be interpreted in a framework of a hierarchy of foraging decisions (Kotliar & Wiens 1990, Searle *et al.* 2006), which determines fine scale-dependent rates of nutrient and energy gain. In a larger dimension, the spatiotemporal context of the fruiting environment modifies the relative intake rates of a particular fruit species, while the ability to discriminate fruit contents becomes increasingly important at a smaller dimension. Studies on nutrient preferences and analyses of functional traits of fruits selected by birds should help in understanding the importance of both mechanisms in fruit selection.

In Blendinger *et al.* (2015), we observed a preponderance of food quantity over nutritional quality of fruits to explain fruit tracking and proposed that nutrient content in fruits may play an important role in fruit consumption decisions once birds adjust their abundances to the overall resource quantity. Although field studies suggested a minor role of particular nutrient on fruit selection by birds (Foster 1987, Levey 1987, Whelan & Willson 1994), we expected that nutrient content in fruits to be important to explain general patterns of fruit-eating bird's diet, given the ability of birds to discriminate concentrations and types of proteins, lipids, and simple sugars (Bosque & Calchi 2003, Schaefer *et al.* 2003, Wilson & Downs 2011). However, despite the fact that all fruit-eating bird species selected fruits with high values of some particular nutrient sometime in the year, the main driving force behind fruit selection in subtropical Andean forests seems to be maximization in the pulp reward per consumed fruit. Our results suggest that even at the level of short-term foraging decisions involved in fruit selection, birds select fruits with traits that directly affect net energy gain. For birds that maximize foraging efficiency, high pulp-to-seed ratio is an indicator of good-quality fruit (Nagar *et al.* 2013). It has been suggested that diet's optimization strategies to meet daily energy requirements may differ between functional groups of birds with different feeding methods, with their morphological abilities an ultimate determinant of these differences (Moermond & Denslow 1985, Wheelwright 1985, Foster 1987). Maximization in net energy gain seems to be a common strategy to all fruit-eating species here studied, no matter their size or mode of fruit handling and ability to discard seeds. Namely, fruits with high pulp-to-seed ratio were selected both by 'pulp mashers' and the 'fruit gulper' species, which differed by as much as four times in body mass.

Most bird species in this study (*T. rufiventris*, *T. sayaca*, and *C. ophthalmicus*) are core species in seed-dispersal networks of subtropical Yungas Andean forests, whose activity deeply impacts the demography of fleshy-fruited plants and can be responsible for major ecological and evolutionary effects on the plants they consume (Ruggera *et al.* 2016). The selection of fruits positively influences seed-dispersal effectiveness a plant receives by increasing the number of seeds moved away (Rodríguez-Pérez & Traveset 2010, Schupp *et al.* 2010). If this effect is not modified at subsequent recruitment stages, it could lead to a relative increase in densities of

plants bearing fruits with specific fruit traits, such as high pulp-to-seed ratio. Moreover, if selection for fruits with higher 'pulpiness' observed at the community level occurs also at the plant population level, then fruit-eating birds may exert evolutionary selection on this fruit trait in a given plant species. Non-random patterns of fruit consumption can lead to phenotypic selection of fruit traits associated with seed dispersal (Jordano 2000, Burns & Lake 2009, Lomáscolo *et al.* 2010, Sobral *et al.* 2010). The selection for fruits with high pulp-to-seed ratio found in our study at an ecological scale gives support to the hypothesis that frugivores are responsible for evolutionary selection pressures toward larger pulp rewards in subtropical Andean forests fruits. Edwards (2006) proposed that plant-disperser mutualisms promote the optimization of a trade-off between seed mass and pulp mass, where the plant investment in pulp is large enough to produce high-reward fruits to attract seed dispersers and ensure seed dispersal, but not committing resources needed for other demands. Thus, to clearly show phenotypic selection by fruit 'pulpiness', future studies must search for fitness differentials in plant populations linked with individual variation in fruit pulp-to-seed ratio.

In summary, fruit selection is a pervasive bird behavior year-round in subtropical Andean forests, shown in contrasting conditions such as periods of fruit scarcity (fall), of maximum fruit abundance (winter), and of maximum fruit diversity (late spring and summer). In these forests, fruit-eating birds tend to select fruit species characterized by similar combinations of some morphological and nutritional traits, such as the relative amount of pulp or low protein content. Nonetheless, neither a certain fruit species nor such specific nutritional or design traits are consistently selected throughout the year. The only exception is the selection of fruits with high pulp-to-seed ratio, denoting a foraging strategy focused on the maximization of energy gain as a major driving mechanism of fruit selection. Knowledge of the mechanisms promoting fruit selection might contribute to a better understanding of the role of fruit-eating animals in determining the composition and structure of plant communities. Accordingly, answering why and how bird–fruit interactions vary through time could allow the development of predictive models of community structure based on ecological mechanisms (Poisot *et al.* 2015). We show that interspecific interactions are not a stochastic process, since all the bird species included in this study select fruits. However, selection patterns are species-specific, suggesting that a given fruit species has different nutritional and caloric consequences for fruit-eating birds that differ in behavior and body mass. Moreover, fruit species selected by individual bird species change over time, denoting that the traits that determine an interaction and the strength of links between interacting species are contingent upon particular conditions, such as the presence of other species with ripe fruits, which modify the structure of the mutualistic interactions.

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SUPPORTING INFORMATION

Additional Supporting Information may be found with online material:

TABLE S1. *Fruiting phenology and fruit abundance of plant species growing in a 6-ha plot in Southern Yungas mountain forests.*

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