

# Frugivory and seed dispersal role of the Yellow-striped Brush-Finch (*Atlapetes citrinellus*), an endemic emberizid of Argentina

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**Abstract.** The stability and dynamics of multispecies interactions often rely on a small core of species. We examine whether the Yellow-striped Brush-Finch (*Atlapetes citrinellus*), the only species of bird endemic to the Argentinean Yungas, is a core species for seed dispersal. Of 30 species of fleshy fruit consumed, 16 were dispersed through endozoochory. The Yellow-striped Brush-Finch mostly used the ‘cut or mash’ method of handling fruit, in which reasonably large seeds (>0.04 g) were discarded or swallowed equally. Medium-sized and small seeds were more often swallowed than discarded. Although the fruits consumed were mostly understorey species, there was no difference in the consumption of fruit from forest understorey or canopy when total fruit abundance in vertical strata was considered. By using interaction network metrics, we determined that the role of Yellow-striped Brush-Finches in seed dispersal during the rainy season was more important at higher altitudes and in the southern sector of its distribution. Our findings support the idea that the Yellow-striped Brush-Finch must be considered a core seed-disperser of understorey and canopy fruits. Use of network metrics is an effective way to assess the importance of individual species in a network, allowing restoration and conservation efforts to be focussed on environments in which these species occur.

**Additional keywords:** avian frugivory, fruit handling, mutualistic networks, network metrics, species strength, subtropical Andean forests.

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## Introduction

Information on the diet of frugivores is important owing to their role in seed dispersal. Plant populations in tropical and subtropical forests are highly dependent on the mutualistic interactions with frugivores (Fleming 2005). At least 70% of tree species in Neotropical rainforests produce fleshy fruits (Gentry 1993) and rely on fruit-eating birds and mammals to complete their reproductive cycle. Fruit–frugivore mutualism generally involves many plant and animal species interacting in a network (Herrera 1995; Jordano 1995; Bascompte *et al.* 2003), but it is often just a few species that are responsible for most of these interactions and for the connectivity and stability of the network (Bascompte and Jordano 2006; Fortuna and Bascompte 2006; Lewinsohn *et al.* 2006; Burgos *et al.* 2007; Bastolla *et al.* 2009). These few species are considered to make up the core of the network, and are characterised by interaction with many partners (i.e. they are generalists) and by establishing strong links (i.e. interact frequently) with most of them.

Owing to these characteristics, core species are claimed to be capable of driving the evolution and ecology of the entire network (Bascompte *et al.* 2003; Bascompte and Jordano 2006). Despite this importance, studies of mutualistic networks often focus on the core as a whole and disregard the identity and trophic ecology of the species making up that core (see Olesen *et al.* 2007; Alarcón *et al.* 2008; Martín González *et al.* 2010; Donatti *et al.* 2011; Mello *et al.* 2013).

Knowledge of the biology of core species is also important for conservation and restoration of habitats. For example, the interaction between the foraging behaviour of a bird and the spatial distribution of fruit could determine neighbourhood-specific patterns of seed dispersal (Carlo and Morales 2008). Also, the examination of habitat use by core species may help to determine their relative contributions to the maintenance of understorey or canopy structure of forests. Although some consequences of horizontal movements of dispersers have been studied (e.g. differential seedling establishment depending on

microhabitats in which seeds were dropped; Wenny and Levey 1998; Jordano and Schupp 2000; Blendinger *et al.* 2011), the consequences of vertical movements have received less attention (but see Shanahan and Compton 2001; Schleuning *et al.* 2011; Sheldon and Nadkarni 2013).

Dispersal of seeds by birds is ubiquitous in the subtropical Andean forests known as the Austral Yungas, where small passerines are the most abundant frugivores (Giannini 1999; Malizia 2001; Rougès 2003; Blendinger *et al.* 2012). In this study, we examine if the Yellow-striped Brush-Finch (*Atlapetes citrinellus*), an emberizid endemic to north-western Argentina, is an important seed disperser or even a core species in some areas of the Austral Yungas. Based on examination of faecal samples (Blake and Rougès 1997; Giannini 1999; Rougès and Blake 2001; Rougès 2003), Yellow-striped Brush-Finches were classified as primarily insectivorous and granivorous, with frugivory considered less important. Nevertheless, fruit-eating emberizids tend to crush fruits in their bills and discard most of the large seeds and some of the small seeds (e.g. Levey 1987), and the importance of fruit consumption by such species might have been underestimated through faecal examination.

Here we describe the fruit composition of the diet and the behaviour of Yellow-striped Brush-Finches when foraging on fruit, and assess the frugivorous role of this species across its geographical range. Specifically, we examine differential use of vertical strata for fruit consumption, with the prediction that, because Yellow-striped Brush-Finches are primarily an understorey species (Olrog 1984; Ridgely and Tudor 1989), more fruit will be consumed in the understorey than the canopy. Second, we analyse several metrics (importance index, strength index and interaction asymmetry index) frequently used in the study of interaction networks (Silva *et al.* 2002; Bascompte *et al.* 2006; Vázquez *et al.* 2007) to understand the importance of the fruit consumption by Yellow-striped Brush-Finches in relation to coexisting frugivores in local assemblages. Based on previous knowledge of its diet, we predict a minor role of this emberizid compared with other frugivorous birds in local assemblages. To our knowledge, this is the first study that explicitly uses network analyses with quantitative data to determine the role of a single species as a seed disperser in local plant–frugivore communities.

## Methods

### Study area

The forests of the Austral Yungas extend in a long, narrow strip ~50 × 700 km across the eastern lower slopes of the Andes, from south-central Bolivia to north-western Argentina, spanning Catamarca, Tucumán, Salta and Jujuy Provinces of the latter country (Fig. S1 of the Supplementary material). The climate is mostly subtropical with a dry season lasting from May to September, and most rainfall from November to March. Annual rainfall varies from 1000 to 2000 mm depending on elevation and topography (Brown *et al.* 2001). The Argentinean Yungas include the middle and southern sectors of the Austral Yungas (Blendinger and Álvarez 2009; Fig. S1). Altitudinally, three forest types are recognised: premontane forests (400–600 m above sea level (ASL)), montane forests (600–1500 m ASL), and cloud forests (1500–2800 m ASL) (Brown *et al.* 2001). Premontane forests have been extensively modified and were not included in this

study. Montane forests are structurally complex with a dense understorey, a lower canopy, an upper canopy and emergent trees 25–30 m tall. Montane forests can be subdivided into basal montane forests (600–1000 m ASL) and Myrtaceous montane forests (1000–1500 m ASL) (Cabrera 1976). High frequencies of myrtaceous species characterise this last sublevel (e.g. Matos, *Myrcianthes pseudomato*, *M. mato*; Arrayán, *Eugenia uniflora*). Cloud forests are dominated by Pinos del Cerro (*Podocarpus parlatorei*, Podocarpaceae) and Alisos (*Alnus acuminata*, Betulaceae).

We made systematic observations of birds eating fruits at seven localities: three sites in the middle sector of the Austral Yungas, at Chorro de Loros (basal montane forest) and Pozo Verde (myrtaceous montane forest), both in El Rey National Park, and at Santa Bárbara (cloud forest); and at four sites in the southern sector of the Austral Yungas, at La Florida Provincial Park (basal montane forest), Sierra de San Javier Park (basal montane forest), Los Chorizos (myrtaceous montane forest) in Campo de Los Alisos National Park, and at Quebrada del Portugués (cloud forest) (Fig. S1). We also compiled data on fruit consumption by Yellow-striped Brush-Finches from the literature (Blake and Rougès 1997; Giannini 1999; Rougès and Blake 2001), and from our own incidental observations made between 1992 and 2007 in the San Javier Mountain Range (Tucumán Province). Data from the literature and our incidental observations were used to determine the species of fruit in the diet, but were excluded from statistical analyses.

### Study species

The Yellow-striped Brush-Finch (Emberizidae) is one of five species of birds endemic to the Austral Yungas and the only species endemic to the Argentinean Yungas (Blendinger and Álvarez 2009). This poorly known species is more abundant in the southern part of its range (Ridgely and Tudor 1989; Blendinger and Álvarez 2009), particularly in cloud forests above 1500 m ASL (Olrog 1984). Altitudinal movements take place during the dry season (coinciding with the cold months of the austral winter), when part of the population moves to lower elevations, between 450 and 1000 m ASL (Malizia 2001; Rougès and Blake 2001).

### Field work

Field work was carried out from November to February (rainy season) from 2008–09 to 2011–12. Each of the seven localities was visited twice over the whole duration of the study: the first visit in November–December and the second in January–February. At each site, we defined an area of ~50 ha in which we recorded abundance and consumption of fruit. During each visit at each site, 2–3 observers made systematic observations in different directions, to record bird–fruit interactions for 5 h after dawn (0630–1130 or 0700–1200 hours) over 3–4 days, until we had conducted 40 h of sampling. Following Blendinger *et al.* (2012), a bird–fruit interaction consisted of an individual of any frugivorous bird species eating one or more fruits from a single plant. A bird eating more than one fruit from the same individual plant was treated as only one interaction because we could not accurately count how many fruits each individual ate. However, because we were interested in the ecological consequences of

the interaction, consecutive visits to different plants by the same bird were considered separate interactions. In addition, consumption of fruit by different individuals in a flock were considered as separate observations. Although this approach might cause some pseudoreplication, we believe this would have only a minor effect on the results because most observations were of one bird feeding on a single plant (see below). Bird species were classified as frugivorous based on our own observations and those of other investigators (Blake and Rougès 1997; Giannini 1999; Malizia 2001; Rougès and Blake 2001; Blendinger and Álvarez 2009; Blendinger and Villegas 2011; Blendinger *et al.* 2012) (see Table S1 of the Supplementary material).

Systematic observations of bird–fruit interactions were conducted through the ~50-ha area each morning, mostly along trails made by people or cattle and covering the area evenly by the end of the visit. Use of the trails allowed us to reach the different microhabitats in the study sites: old- and secondary-growth forests, gaps, proximity to rivers, ravines and ridges. When possible, we followed individual frugivorous birds until it ate fruit. In most cases (82%,  $n = 2429$  interactions), we recorded only one interaction per bird before we lost sight of it. For each bird–fruit interaction, we recorded the species of bird and fruit, how the fruit was handled and the fate of seeds. Data on interactions by frugivorous species other than Yellow-striped Brush-Finches were used to calculate the network-interaction indices.

To determine abundance of fruit, we used a variable number of 50-m strip-transects (see below). Because the estimation of canopy fruits requires larger sample areas than those needed for estimation of understorey fruits (Blake *et al.* 1990), transects were 20 m wide for trees, epiphytes and lianas, and 4 m wide for herbs and shrubs. Transects were located both parallel and perpendicular to the trails walked during systematic observations of bird–fruit interaction. The transects were at least 50 m apart and distributed throughout the ~50-ha area at each locality. The number of transects sampled per visit varied from 9 to 18 and was determined by a plot of the cumulative number of plant species with ripe fruits at each site. When this reached a plateau (no new species with ripe fruits added in five consecutive transects) we assumed that the given number of transects was an adequate sample. The abundance of ripe fleshy fruit of each individual plant within the transects was estimated using  $8 \times 42$  binoculars. Abundance was estimated using logarithmic intervals: between 1 and 10 fruits were recorded as the exact number of ripe fruits (e.g. 8); between 10 and 100 ripe fruits were recorded as tens (e.g. 30); between 100 and 1000 ripe fruits were recorded as hundreds (e.g. 400); and so forth with each order of magnitude. We transformed fruit amount per area to dry-pulp weight per area ( $\text{g ha}^{-1}$ ) using mean dry-weight data of the pulp of each fruit species (P. G. Blendinger and N. P. Giannini, unpubl. data). The total area monitored was calculated from transect length and width:  $200 \text{ m}^2$  for herbs and shrubs or  $1000 \text{ m}^2$  for trees, epiphytes and lianas, multiplied by the number of transects in that visit. In summary, for each plant species we collected ripe fruits from different parts of the crop of up to 10 individuals; all these fruits were pooled in a single bag. Later in the laboratory, at least 10 fruits were randomly chosen to estimate the mean dry-pulp weight per fruit. Further, the mean number of seeds per fruit and the mean weight of at least 20 individual seeds were estimated with an electronic balance

(APX-200, Denver Instrument, Bohemia, NY, USA), with an accuracy of  $\pm 0.1 \text{ mg}$ .

We determined which fruit species were dispersed from the maternal plants through faecal sample data available in the literature (Blake and Rougès 1997; Giannini 1999; Rougès and Blake 2001). Additionally, we set 5–7 mist-nets (12 m long and mesh-size of 36 mm), which were opened for variable periods of time (18–48 h) at each study site. We held caught birds in a closed plastic container for 10–15 min (Loiselle and Blake 1990) to collect faecal samples, which were kept in small paper envelopes. Faecal samples were examined with a magnifying glass to determine if seeds were entire or had mechanical damage. We identified most seeds from faeces to species level by comparison with a reference collection. Information on fruit consumption from seeds in faeces was used to describe the diet of Yellow-striped Brush-Finches but was excluded from calculation of indices and statistical tests, which were based on systematic observations of fruit consumption only.

### Foraging behaviour

During systematic observations of bird–fruit interaction, when it was possible we recorded how birds ingested the fruit-pulp and whether seeds were discarded or swallowed. Handling methods were based on those of Foster (1987): pluck and swallow, in which the fruit is swallowed whole and seeds regurgitated or defecated; cut or mash, in which the fruit is grasped and the pulp detached from seeds while rolling the fruit in the bill, with seeds generally discarded; and bite, in which the bird eats the pulp while the fruit remains attached to the plant.

We used two strategies to examine differences in consumption of fruits from the understorey (i.e. fruits of all herbs, shrubs, vines and small trees, with most of their fruit-crop below 5 m) and above the understorey, which hereafter considered the canopy. First, we used a Mann–Whitney test to examine differences in fruit-species dependence (see ‘strength index’ in the ‘Frugivorous role’ section following) from the understorey or canopy on fruit consumption by Yellow-striped Brush-Finches. Second, we used a Chi-square contingency table to test for differences in the interaction frequency with fruit species in the understorey and in the canopy. Abundance of fruit was classed as low ( $<388 \text{ g ha}^{-1}$ , the average biomass of fruit species consumed by Yellow-striped Brush-Finches in the fruit-abundance transects) and high ( $>388 \text{ g ha}^{-1}$ ). All tests were run using R (R Development Core Team 2011).

### Frugivorous role

We assessed the role of Yellow-striped Brush-Finches in the frugivorous bird assemblage by calculating three indices with data that were gathered only from our systematic observations. These indices were calculated for all the frugivorous species of bird at each locality. Only Yellow-striped Brush-Finch values are reported, indicating its relative position in comparison to all the frugivorous bird species occurring in each visit.

The importance index ( $I_j$ ) (Murray 2000; Silva *et al.* 2002), weights the contribution of a frugivorous species  $j$ , considering how many species of fruit it feeds on and how many other frugivorous species feed on the same species of fruit. The index  $I_j$  is determined by the equation:

$$I_j = \sum_{i=1}^P \left( \frac{C_{ij}/T_i}{P} \right)$$

where  $C_{ij}=1$  if the bird species  $j$  fed on the fruit species  $i$ , otherwise it is 0;  $T_i$  is the total number of bird species feeding on the fruit species  $i$ ; and  $P$  is the total number of species of fruit that were consumed for the entire frugivorous assemblage. The index  $I_j$  ranges from 0 (a species consuming no fruits at all) to 1 (when that species is the only frugivore in the assemblage).

The strength index ( $S_j$ ) is a quantitative extension of the index  $I_j$ .  $S_j$  can be defined as the sum of dependences of all fruit species relying on the frugivorous species  $j$  (Bascompte *et al.* 2006).

$$S_j = \sum_{i=1}^E d_{ij}$$

and

$$d_{ij} = \frac{f_{ij}}{\sum_{m=1}^J f_{im}}$$

$E$  indicates the number of fruit species consumed by the frugivore  $j$ ;  $d_{ij}$  is the dependence of the fruit species  $i$  on the frugivorous species  $j$ , and can be defined as the fraction of all the animal visits made to that fruit species by the frugivorous species  $j$  alone (Bascompte *et al.* 2006; Vázquez *et al.* 2007);  $f_{ij}$  corresponds to the interaction frequency between the fruit species  $i$  and the frugivorous species  $j$ ;  $J$  is the number of frugivorous species interacting with the fruit species  $i$ . This index was divided by the number of species of fruit consumed by at least one frugivore, so that it goes from 0 (i.e. a negligible frugivorous role of a given frugivore) to 1 (i.e. a high dependence of the fruit assemblage on the fruit consumption by a particular frugivore).

The interaction asymmetry index ( $A_j$ ) is the average value of the dissimilarity between the dependences of the fruits relying on the consumption by the frugivore  $j$  ( $d_{ij}$ , above), and the dependences of that frugivore on the fruits that it feeds on ( $d_{ji}$ ) (Vázquez *et al.* 2007):

$$A_j = \frac{\sum_{i=1}^E (d_{ij} - d_{ji})}{k_j}$$

where  $k_j$  is the number of species of fruit consumed (i.e. the species 'degree'). Values of  $A_j$  close to 1 indicate that the frugivorous species is critically important for removal of fruit from the species of plants that it feeds on, but each of those plants are not essential for the frugivorous diet of that frugivore. Values of  $A_j$  close to  $-1$  indicate the opposite, whereas values close to 0 indicate fairly symmetric effects between the frugivore and the fruits it eats.

## Results

### Dietary composition

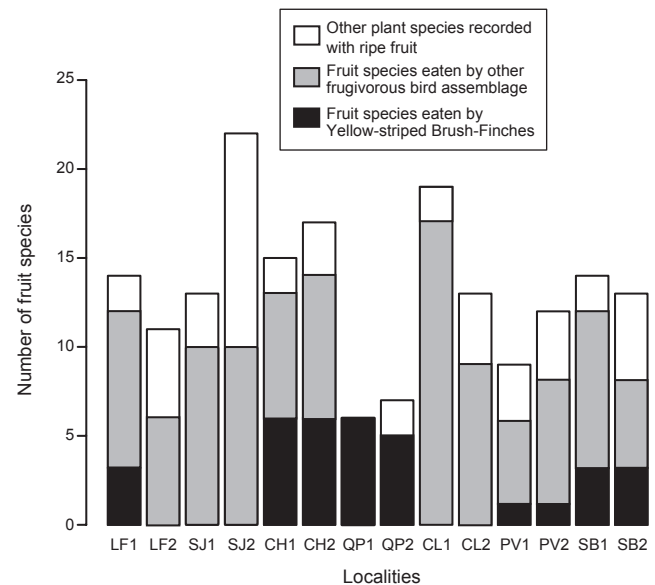
Combining data from this study and published literature, we identified 258 examples of fruit consumption by Yellow-striped Brush-Finches (see Table S2 of the Supplementary material), of 30 species of fruit from 19 families. Seeds of 16 species were swallowed or found in faeces ( $n=164$  faecal samples). No seeds

found in faeces had visible mechanical damage owing to handling in the bill or gut-passage and all looked intact.

In our seven localities we found 71 species of plant with ripe fruits (see Table S3 of the Supplementary material), with 53 observed to be eaten by at least one species of bird and 20 by Yellow-striped Brush-Finches. Frugivores were observed eating 27 species in the understorey ( $6558 \text{ g ha}^{-1}$ ) and 26 species in the canopy ( $5575 \text{ g ha}^{-1}$ ). Yellow-striped Brush-Finches consumed more fruit species from the understorey (13 species, total  $4009 \text{ g ha}^{-1}$ ) than from the canopy (seven species,  $2433 \text{ g ha}^{-1}$ ). Localities in which we observed noticeable fruit consumption by Yellow-striped Brush-Finches were Los Chorizos and Quebrada del Portugués (Fig. 1). In the latter, the Yellow-striped Brush-Finch was the species consuming the highest percentage of fruit species available (100% for the first visit and 71% for the second visit; Fig. 1). Solanaceae was the family comprising the most species in the diet ( $n=6$  species), and the Molle del Cerro (*Schinus gracilipes*, Anacardiaceae) was the most consumed species ( $n=99$  records).

### Foraging behaviour

The method most frequently used by Yellow-striped Brush-Finches was cut or mash (80%,  $n=46$  observations; see Table S2). Whether seeds were eaten or discarded when using this method depended on the size of the seeds (see Table S4). Large seeds ( $>0.04 \text{ g}$ ), such as those of *Myrcianthes pseudomato*, Chal-chal (*Allophylus edulis*) and *Podocarpus parlatorei*, were



**Fig. 1.** Accumulative number of plant species with ripe fruit, number of fruit species eaten by the frugivorous bird assemblage and fruit species consumed by Yellow-striped Brush-Finches, at seven localities in the Austral Yungas, north-western Argentina, from 2008–09 to 2011–12. The number after the locality name denotes whether it is the first visit (November–December) or second visit (January–February) to each locality. Localities: LF, La Florida; SJ, San Javier; CH, Los Chorizos; QP, Quebrada del Portugués; CL, Chorro de Loros; PV, Pozo Verde; SB, Santa Bárbara. In LF2, SJ1 and CL2 the Yellow-striped Brush-Finch was not seen during systematic observations; in SJ2 and CL1 Brush-Finches were seen but not observed eating fruit.

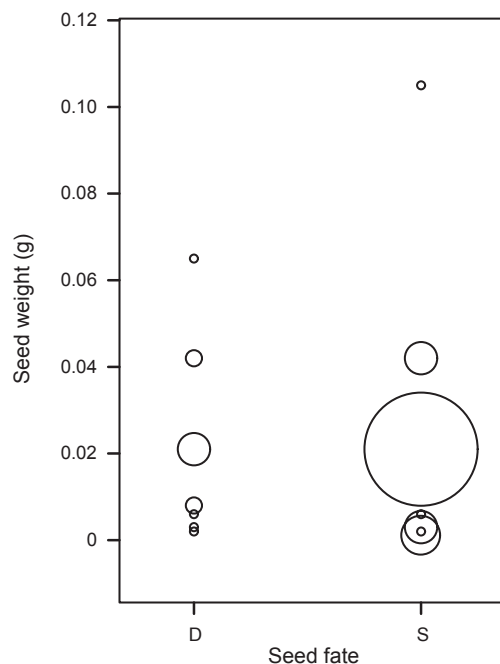


sometimes discarded and sometimes swallowed. Medium-sized and small seeds (those of *Schinus gracilipes*; Zarzamora, *Rubus imperialis*; Liga, *Phoradendron* sp.; *Solanum aligerum*; and Chalchal de gallina, *Vassobia breviflora*) were more often swallowed than discarded (Fig. 2). To a lesser extent, Brush-Finches also used the pluck and swallow method (with two fruit species, 13% of observations). The bite method was seldom observed (with three fruit species, 7% of observations). Indeed, when interacting with *Solanum aloysiifolium*, Yellow-striped Brush-Finches pecked fruits without plucking them from the plants. In only one case, Yellow-striped Brush-Finches used all three feeding methods to handle the same fruit species (Sauco, *Sam-bucus nigra*).

Finches foraged more often in the understorey than in the canopy: 88.9% of the 198 records of foraging on fruit on 66.7% of the 20 fruit species consumed (systematic observations) were in the understorey. This unequal activity was reflected in a greater dependence of understorey fruit species on the Yellow-striped Brush-Finch than canopy fruit species ( $U=161.5$ ,  $P=0.01$ ; Fig. 3). However, when the abundance of fruits per strata was considered, there were no significant differences between interaction frequency in the understorey and above it ( $\chi^2=3.1$ , d.f. = 1,  $P=0.08$ ).

#### The frugivorous role of Yellow-striped Brush-Finches

All three indices (Table 1) revealed a stronger frugivorous role of Brush-Finches in cloud forests than other elevation forests, and a stronger association in the southern sector than in the middle sector. Thus, when moving up on the altitudinal gradient,

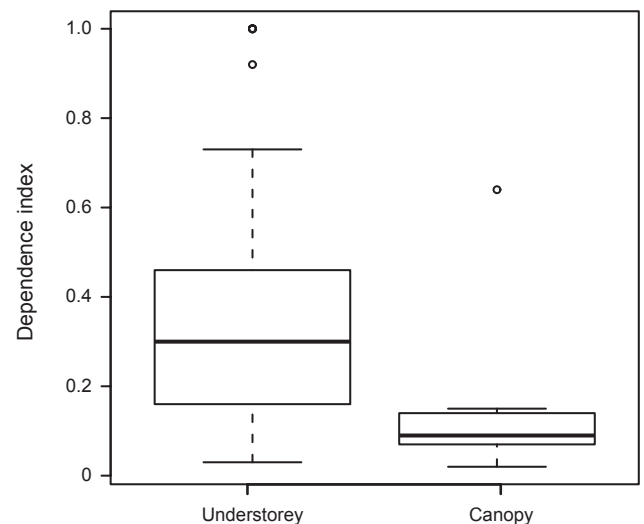


**Fig. 2.** Fates of seeds (i.e. swallowed (S) or discarded (D)) of different weight when consumed by Yellow-striped Brush-Finches using the cut or mash method to manipulate fruits. The circle size corresponds to frequency of observations (range=1–14) in which fate of seeds could be accurately determined.

but especially when moving from the middle to the southern sector: (1) fruits consumed by Yellow-striped Brush-Finches were not eaten by many other frugivores (index  $I$ ); (2) fruit species were more dependent on frugivory by Yellow-striped Brush-Finches, which had a higher interaction frequency with fruits (index  $S$ ); and (3) values of the asymmetry index were closer to 1, meaning that Yellow-striped Brush-Finches strongly influenced its food plants.

#### Discussion

Our results show that Yellow-striped Brush-Finches have a significant frugivorous role, especially in the southern sector of the Austral Yungas forests, where they consumed and potentially dispersed a wide range of fruit species (mainly those with many small-sized seeds), in contrast to our initial predictions. We have shown that this endemic emberizid is a core species in the fruit-seed disperser mutualistic network of the southern sector of the Austral Yungas during the rainy season, but has a minor role as a seed disperser in the middle sector of these forests. This latitudinal trend in the importance as seed disperser could be explained by the higher abundance of the Yellow-striped Brush-Finch in the southern sector of Austral Yungas (Ridgely and Tudor 1989; Blendinger and Álvarez 2009). Abundance has been claimed as one of the main determinants of network structure (Vázquez *et al.* 2009). If species in a community interact at random, interaction probability will greatly depend on relative abundances of species: abundant species will interact with more partners and more frequently, exerting a strong influence on them (Vázquez *et al.* 2007). Because the Yellow-striped Brush-Finch consumes fruits year-round, seed dispersal services provided could be extended to the lower elevation forests, where the species descends during the dry season (Malizia 2001; Rougès



**Fig. 3.** Dependence index values of the understorey fruit species (<5 m) and canopy (>5 m) in the Austral Yungas, north-western Argentina. Dependence is the fraction of visits to a given fruit by Yellow-striped Brush-Finches as a proportion of all animal visits to a given fruit species. The horizontal line in the boxes is the median value; box limits are the first and third quartiles of the distribution; whiskers span the 10–90% range, and circles depict extreme data points.

**Table 1. Frugivorous role of Yellow-striped Brush-Finches**

Importance, Strength, and Asymmetry indices of fruit consumption by Yellow-striped Brush-Finches in the Austral Yungas forests, north-western Argentina. Observations were made at seven localities in either the middle or southern sector of the Austral Yungas, with two visits to each locality, in November–December (first visit, denoted by 1 after locality name), and January–February (second visit, denoted by 2 after locality name). Excluded from the table are localities and visits where Yellow-striped Brush-Finches were not seen consuming fruits (San Javier 2 (127 interactions, 8 frugivorous bird species); Chorro de Loros 1 (162, 14)) or where Brush-Finches were not observed at all (La Florida 2 (187, 11), San Javier 1 (136, 11), Chorro de Loros 2 (184, 18)). Forest types: B, basal montane forest; M, myrtaceous montane forest; C, cloud forest. Values in parentheses in the Importance and Strength columns: the first number shows the position occupied by the Yellow-striped Brush-Finch relative to index values achieved by other frugivorous bird species; the second number refers to the number of frugivorous bird species that consumed fruits during the same visit (Ruggera 2013). Number of interactions is the number of bird–fruit interactions recorded for the frugivorous assemblage, with values for the Yellow-striped Brush-Finch in parentheses

Locality	Forest type	Importance index	Strength index	Asymmetry index	Number of interactions
Southern sector					
La Florida 1	B	0.11 (3°/11)	0.06 (5°/11)	−0.10	124 (6)
Los Chorizos 1	M	0.13 (3°/16)	0.15 (2°/16)	0.15	221 (19)
Los Chorizos 2	M	0.07 (4°/17)	0.10 (4°/17)	−0.01	196 (20)
Quebrada del Portugués 1	C	0.42 (1°/12)	0.63 (1°/12)	0.46	168 (79)
Quebrada del Portugués 2	C	0.41 (1°/11)	0.50 (1°/11)	0.30	174 (61)
Middle sector					
Pozo Verde 1	M	0.02 (11°/14)	0.005 (11°/14)	−0.97	221 (1)
Pozo Verde 2	M	0.03 (10°/14)	0.01 (11°/14)	−0.96	199 (1)
Santa Bárbara 1	C	0.03 (8°/12)	0.02 (8°/12)	−0.39	150 (4)
Santa Bárbara 2	C	0.04 (7°/14)	0.02 (7°/14)	−0.28	180 (7)

and Blake 2001). In fact, several fruits observed as part of the diet of the Yellow-striped Brush-Finch in this study, such as those of Moradillo (*Psychotria carthagenensis*), *Chamissoa altissima*, Ortega Brava (*Urera baccifera*), *Phoradendron* sp. and the invasive Mora Blanca (*Morus alba*), have ripe fruits during the dry season.

The Yellow-striped Brush-Finch was previously considered to be a minor consumer of fruit in local communities (e.g. Giannini 1999; Rougès and Blake 2001; Rougès 2003), an assumption based primarily on its phylogenetic affinities (membership to a family of typical seed-eaters). This study highlights how *a priori* ecological classifications of bird species may wrongly estimate their roles as seed dispersers. Our results suggest that it is necessary to reassess the ecological role of other fruit-eating birds both in the Yungas and other areas where there are still significant gaps in the knowledge of the most basic aspects of the biology and life history of birds.

The few articles assessing vertical distribution of fruit abundance concluded that the understorey of tropical rainforests produces much less fruit than the canopy, and is characterised by specialised associations of fruits with opportunist frugivores having weak interaction strengths (Shanahan and Compton 2001; Schleuning *et al.* 2011). In the subtropical Austral Yungas, similar abundance of fruit in the understorey and canopy could also account for the emergence of core species heavily using the understorey, such as the Yellow-striped Brush-Finch. Our results emphasise the importance of considering vertical stratification of fruit abundance and relative use of these strata by frugivores to understand the dynamic of interaction networks and how it influences the structure of forests.

The effectiveness of seed dispersal can be split to qualitative and quantitative components (Schupp *et al.* 2010). In this

study, we assessed part of the qualitative component by observing fruit-handling methods of the Yellow-striped Brush-Finch, whereas the calculation of network indices pinpoint the importance of this species of bird in the quantitative component. The pluck and swallow method often allows movement of seeds through faeces or regurgitation away from the maternal plant (Janzen 1970; Chapman and Chapman 1995; Jordano and Schupp 2000; but see Santos *et al.* 1999). The cut or mash method, which was more often used by Yellow-striped Brush-Finches, is considered to be less effective in dispersal of seeds because seeds are often discarded below the maternal plant (Foster 1987; Jordano and Schupp 2000; Blendinger and Villegas 2011). Seeds from 16 of >30 species of fruit were dispersed through faeces. Those fruits were often berries with many small seeds. It is probable other similar berries for which we could not observe the fate of seeds or the handling method, such as those of *Rhipsalis floccosa*, *R. lumbricoides* and the invasive *Morus alba*, were also dispersed through faeces. Thus, when fruit is not swallowed, the efficiency of a feeding method is strongly linked to features of the fruit, such as size and numbers of seeds (Manhães 2003).

Species in the Emberizidae are primarily classified as seed predators (Ridgely and Tudor 1989), breaking seeds with the bill or digesting them in the gizzard. Nevertheless, this does not seem to happen with seeds swallowed by the Yellow-striped Brush-Finch. We found that seeds from faeces of Yellow-striped Brush-Finches looked intact (this study) and there are no reports in the literature of evident mechanical damages made during handling in the bill or through gut-passage (Blake and Rougès 1997; Rougès and Blake 2001; Rougès 2003). Although germination trials were not conducted to test for viability, these observations suggest that seeds discarded or defecated by

Yellow-striped Brush-Finches may be viable (D'Avila *et al.* 2010). The prevalent view of a strict frugivore–granivore dichotomy is being replaced by that of a continuum in the contribution to seed dispersal (Wheelwright and Orians 1982; Hulme 2002; Heleno *et al.* 2011). If Yellow-striped Brush-Finches disperse viable seeds, as it probably does, it would fall close to the centre of this continuum, dispersing more than a half (see above) of the fruit species it consumes.

Throughout the literature, several indices of interaction networks have been useful for finding pervasive patterns and the properties of those networks within and across plant–animal systems (e.g. Bascompte *et al.* 2003; Vázquez *et al.* 2007). However, indices of individual species have seldom been reported, even when it may be interesting to compare the relative incidence of core species in their local networks. In this sense, it is expected that the importance index ( $I$ ) could be affected by species richness. Because values of  $I$  of all frugivores in a specific locality add up to 1, species in less-rich assemblages should have higher individual values of  $I$  than in more speciose assemblages. Nevertheless, in this study we obtained high values of  $I$  for the Yellow-striped Brush-Finch in local assemblages with high and low avian species richness. This suggests that the differences in bird richness recorded in the localities that we monitored would not be affecting the conclusions about the greater role as frugivore of this emberizid in the southern sector of the Austral Yungas compared with the middle sector. In a seed-dispersal network in the Atlantic forests (Silva *et al.* 2002), strongly frugivorous species of bird (species of Cotingidae, Pipridae, Thraupidae and Turdidae) showed values of  $I$  in the same range as those of Yellow-striped Brush-Finches in our study (0.02–0.10). Moreover, the highest values recorded in our study (0.41 and 0.42) were almost twice the value recorded for the most important species in the Atlantic forests (Cotingidae: *Carpornis cucullatus*; Silva *et al.* 2002). This difference could be expected owing to the differing frugivore richness in these two communities, ranging from 11–17 species in the Austral Yungas to 48–57 species in the Atlantic forests. Still, communities with fewer frugivores have less redundancy in seed-dispersal services (Loiselle *et al.* 2007). Values of  $I$  reflect this redundancy, highlighting a more essential role of specific frugivores for the maintenance of seed dispersal in the Austral Yungas compared with the Atlantic forests. Furthermore, positive values of the asymmetry index in some localities imply that top-down processes, headed by fruit consumption by Yellow-striped Brush-Finches, could regulate local networks, something atypical in this and other plant–animal interactions (Vázquez *et al.* 2007).

Some recent studies have recognised the importance of identifying core species using qualitative measures (Olesen *et al.* 2007; Martín González *et al.* 2010; Mello *et al.* 2013). However, interaction-frequency data (like those obtained here through direct observation) is not generally reported in such studies, even when they allow the estimation of quantitative indices resulting in more accurate conclusions (Vázquez *et al.* 2005; Bascompte *et al.* 2006; Blüthgen *et al.* 2008). Determination of quantitative indices for species in local network contexts could be a way of maximising conservation and restoration efforts of disturbed environments, focussing on those keystone species that provide the best ecological services to local communities.

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