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Interaction dynamics of avian frugivores and plants in a Chilean Mediterranean shrubland

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ABSTRACT

Studies of plant-frugivore interactions are important for identifying the roles that biotic seed vectors play in seed dispersal, and ultimately plant recruitment. In a subandean shrubland of central Chile, 50% of total flora (14 species) has fleshy fruits dispersed by birds. We examined two aspects of frugivore-plant interaction in this system: the structure of the seed-dispersal network, to predict the effect of hypothetical frugivore species loss for seed dispersal and disperser effectiveness, by analyzing whether birds contribute equally to the removal of seeds from different shrub species. We show that the seed-dispersal network is highly and significantly nested, resulting in a core of interactions among generalist vertebrates and plant species. A reduction in the populations of the three main avian generalists, *Turdus falcklandii*, *Mimus thenca* and *Elaenia albiceps*, would disrupt seed dispersal and natural regeneration for most woody species. Monte Carlo simulations showed that the network was robust to the random loss of frugivorous species but highly sensitive to the loss of generalist species first. Mist-net sampling of birds corroborated that most fruit removal was effected by *E. albiceps* and *T. falcklandii*, highlighting the importance of frugivore species identity on seed dispersal for the maintenance of Mediterranean shrublands.

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1. Introduction

Identifying the roles that individual seed disperser species play in plant recruitment dynamics has relevant implications for theoretical understanding of species interactions and vegetation change, as well as for applied fields, such as conservation and ecological restoration (Jordano, 1987; Loiselle and Blake, 1999; Shea, 2007). The interactions between frugivores and plant species have been represented as networks, where each species (of plant or frugivore) can interact with one or more other species. Hence, the analyses of network structure become a useful tool to examine the consequences of avian species extinctions for seed dispersal and plant community composition (Bascompte et al., 2003; Guimarães et al., 2006; Jordano et al., 2003).

On the other hand, analyzing the interaction dynamics between avian frugivores and plants during seed dispersal, from the perspective of the disperser effectiveness, provides clues to

understanding the ecological consequences of seed dispersal for plant recruitment (Jordano and Schupp, 2000). Disperser effectiveness is the relative contribution that a frugivore makes to plant fitness (Herrera and Jordano, 1981; Schupp, 1993) and depends on the number of seeds dispersed (i.e. quantity component) and the probability that a dispersed seed produces a new reproductive adult (quality dispersal, Herrera and Jordano, 1981; Schupp, 1993).

In Mediterranean-type shrublands of central Chile (locally known as matorral), human impact has greatly altered the cover and distribution of native vegetation (Armesto et al., 2010). Likewise, the regeneration of woody species is generally limited because seed banks are extremely poor or entirely absent from most areas with or without shrub cover, and because woody seedlings are scarce and found restricted to areas under shrub cover (Armesto et al., 1995; Fuentes et al., 1984, 1986; Jiménez and Armesto, 1992). Seed banks are hardly limiting in other Mediterranean-climate regions, where aerial or soil seed banks of woody species are diverse and abundant (Jiménez and Armesto, 1992). The persistent patchy structure of shrubland vegetation in central Chile, with conspicuous open areas between shrub patches may be determined to a large extent by the limited distribution

and longevity of dispersed seeds (Armesto et al., 1995; Fuentes et al., 1986). Despite evidence that seed distribution and availability may strongly limit woody regeneration, only anecdotal information exists on the role of avian frugivores in seed dispersal in the Chilean matorral. Various sites, across a gradient from dry to wet conditions in central Chile have a mean of 14 species, i.e. 34.3% of the total woody flora with fleshy fruits (Hoffmann and Armesto, 1995; Hoffmann et al., 1989). This proportion of fleshy-fruited species is higher than in other Mediterranean ecosystems such as the Californian chaparral (mean of 8 species, 28.5% of the total woody flora) and Australian mallee (mean of 2 species, 8.5% of the flora), but rather lower than the Mediterranean Basin flora (9 species, 56.1%; Hoffmann and Armesto, 1995; Jordano, 2000). In addition, regeneration of Chilean matorral shrubs is severely limited to microsites under bushes in a mosaic of sparse shrub clumps separated by open areas exposed to drought, suggesting limited seed dispersal (Del Pozo et al., 1989). Accordingly, research on bird-mediated seed dispersal is needed to test the hypothesis that recruitment of woody species is limited by the ability of birds to carry seeds between shrub clumps. Open spaces devoid of woody cover, receiving sporadic seed rain, are subjected to greater impacts of summer drought and herbivores making seedling establishment extremely unlikely (Del Pozo et al., 1989; Fuentes et al., 1984, 1986; Holmgren et al., 2000; Jaksic, 2001).

Considering these recruitment limitations, together with the fact that most Mediterranean avian frugivores use covered habitats preferentially to rest, perch and forage, hence avoiding open spaces (Herrera and Jordano, 1981; Izhaki et al., 1991; Johnson and Goodall, 1967; Jordano and Schupp, 2000), our main aim was to identify the main plant–bird interactions that drive seed dispersal dynamics in the Chilean matorral, and to assess the potential roles that disperser species play on seed dispersal. We focus on dispersal-related processes at the source level, i.e. identity of the main seed dispersers, the fleshy-fruited plant species that they feed on and fruit removal patterns by different avian frugivores. Post-dispersal processes at the seed destination site are treated elsewhere (Reid and Armesto, 2010; Reid et al., unpublished manuscript). We first examined the structure of the seed-dispersal network of the Chilean shrubland, identifying the main players (fleshy-fruited plants and fruit-eaters) and their interactions, with the purpose of predicting the effect of hypothetical loss of frugivore species on seed dispersal patterns. Based on previous evidence from other seed-dispersal networks (Bascompte et al., 2003; Jordano et al., 2006), we hypothesized that the structure of the seed-dispersal network of the Chilean matorral would be nested, resulting in a core of interactions among the most generalist plant and frugivore species. Here, few generalist frugivores drive overall seed dispersal in space and specialist species tend to interact with proper subsets of the species that interact with more generalist species.

The hypothesis posed above is relevant on two grounds. First, because the main driver of bird population decline in Chile and elsewhere is land transformation (BirdLife International, 2000; Estades, 2004), and as other Mediterranean-type ecosystems, the Chilean matorral is globally endangered due to land use change (Myers et al., 2000; Sala et al., 2000). Secondly, once the main individual seed dispersers and their food plants are identified, the patterns of fruit removal over time by the main frugivores provide an empirical assessment of how different bird species contribute to overall seed dispersal. We hypothesized that bird species do not contribute equally to seed removal from different shrub species, and that most fruit removal is accounted for by few generalist frugivores.

2. Methods

2.1. Study site

The study was conducted in the Estación de Investigaciones Ecológicas Mediterráneas (EDIEM hereafter) in San Carlos de Apoquindo (33° 23′ S, 70° 31′ W), a presently protected area of 835 ha on the Andean foothills, 20 km east of downtown Santiago, with elevations ranging from 1050 to 1915 m (Appendix 1a, electronic version only). The Chilean matorral is characterized by hot-dry summers and cool and mild rainy winters. Yearly mean rainfall at the study site is 433.6 mm and mean annual temperature is 14.8 °C (EDIEM, four year records). The vegetation, locally known as matorral, is predominantly evergreen sclerophyllous shrubland, strongly influenced by topography, with different vegetation composition and ground cover on polar and equatorial-facing slopes and creeks (Jaksic, 2001). On polar-facing slopes, a thick and nearly continuous evergreen shrub cover (83.6%) is dominated by *Lithrea caustica* (Anacardiaceae), *Quillaja saponaria* and *Kageneckia oblonga* (Quillajaceae). Less represented species are *Retanilla trinervia* (Rhamnaceae), *Azara dentata* (Flacourtiaceae), and *Baccharis* sp. (Asteraceae; Table 1). On equatorial-facing slopes, vegetation cover is more patchy (34.6%) and dominated by *Colliguaja odorifera* (Euphorbiaceae), *L. caustica* and *Baccharis* sp. A dense herbaceous strata of annuals and perennials develops between and under bushes after the winter rains, with invasive European grasses more common in open areas (Arroyo et al., 2000; Holmgren et al., 2000). Today the entire area is mainly devoted to recreational activities (e.g. hiking, mountain-biking, picnics, and horse riding), but occasional low-intensity grazing by horses and cattle still occurs. Until 1982 limited farming and firewood extraction took place in lowland areas (Jaksic, 2001). Of the 28 shrub species present at the site, 14 (50%) have colored small berries, drupes or arillated seeds that remain on the plant when ripe, suggesting that they are dispersed predominantly by frugivorous vertebrates, mainly birds and occasionally mammals (Hoffmann et al., 1989; Jaksic, 2001). The fruiting season is concentrated in the austral summer and fall, from January to May (Jaksic, 2001).

2.2. Plant-frugivore interactions

The seed-dispersal network of San Carlos de Apoquindo was assembled from published information on fruit consumption by birds and mammals, mist-net sampling of birds and their stomach contents, and direct observation of fruit consumption. As the information required to construct the seed-dispersal network was solely qualitative, that is if species interact or not, we included mammals to make the seed-dispersal network as complete as

Table 1
Proportion of ground (%) covered by different shrub species, rock outcrops and open areas (i.e bare ground) on a polar-facing hillside and an adjacent plain in San Carlos de Apoquindo, central Chile.

Cover type	Polar-facing slope	Plain
Azara dentata[a]	5.06	0.75
Acacia caven	0.57	0
Baccharis sp.	1.22	8.63
Colliguaja odorifera	0	1.68
Kageneckia oblonga	15.74	0
Lithrea caustica[a]	35.96	15.01
Maytenus boaria[a]	0	3.34
Quillaja saponaria	16.42	16.87
Retanilla trinervia[a]	8.47	4.57
Schinus polygamus[a]	0.12	3.65
Open areas	16.18	44.22
Rocks	0.26	1.28

[a] berries, drupes or arillated seeds dispersed predominately by birds.

possible. Three mammal species, the foxes *Lycalopex culpaeus*, *L. griseus*, and the introduced European rabbit *Oryctolagus cuniculus*, have shown evidence of frugivory (Castro et al., 1994, 2008; Hoffmann et al., 1989; Silva et al., 2005). As previous information on the identity of avian seed dispersers is limited to a few species (Hoffmann and Armesto, 1995; López-Calleja, 1990; Solar, 1975;), we captured birds using mist nets and analyzed their fecal and regurgitated samples (Loiselle and Blake, 1999). During the months of maximum ripe fruit production (January–May 2006) we weekly set up four to six mist nets from sunrise to noon to obtain fecal samples of captured birds. Nets were set up in an open area in the vicinity of the site where ripe fruit availability was estimated; see section 2.3 and Appendix 1b (electronic version only). Captured birds were placed inside a closed container bag for 10–15 min to obtain fecal and regurgitated samples (Loiselle and Blake, 1999). All samples were kept in paper bags and seeds of fleshy fruits were later identified using a reference collection of all woody species in the area. We used a Zeis Stemi 2000-C magnifying glass to identify the smaller seeds.

To have a monthly measure of fruit consumption, we pooled all the consumed seeds found in bird droppings per month (see Carlo et al., 2003 for a similar method). For one-seeded species (*Schinus polygamus* and *L. caustica*) we counted each seed as one fruit consumed, and for multi-seeded fruits (*A. dentata* and *Cestrum parqui*) we divided the total number of seeds in droppings by the mean number of seeds per fruit, the latter was calculated using a sample of 10 fruits. In this way, we estimated a fruit consumption index (FCI hereafter) as an estimate of monthly consumption of a given plant species by avian frugivores. For the most frequently found plant species in bird feces, *S. polygamus*, we conducted observations of fruit removal by birds in a total of three focal trees to supplement mist-net data. From January to March 2006, during six mornings, we recorded all the birds that perched and picked on fruits of three *S. polygamus* shrubs and recorded the number of fruits consumed.

In addition, to have a measure of the relative abundance of bird species in the area, monthly point-counts were conducted in six 30-m-radius plots (0.28 ha) spaced by at least 200 m to minimize the risk of counting the same individual twice. Bird surveys were conducted monthly from January to May, which corresponds to the austral summer and fall. All birds seen or heard within the circular plots were recorded for an 8-min period. Bird surveys were performed by random order of habitats, from 0800 to 1100 h EST on non-rainy days.

2.3. Fruit abundance

To estimate the abundance of ripe fruits at the site, we counted the number of ripe fruits on five selected marked branches of each shrub species and then multiplied this value by their percent ground cover (Table 1). From these data, we calculated a fruit availability index (hereafter FAI). Counts were repeated three times from January to May 2006, every two months, on three individuals of each of the four most frequently consumed species, *L. caustica*, *A. dentata*, *S. polygamus* and *Cestrum parqui*. The remaining ten shrub species were so rare in cover at the site that they were not included in quantitative analyses. Sampled branches were randomly selected at each of five different heights in the shrub crown (see Jordano and Schupp, 2000 for a detailed description). Percent ground cover of each shrub species was estimated as the projected canopy cover intercepting ten 90-m linear transects, five on a south-facing slope and five on a plain located 150 m away to incorporate local differences in vegetation cover, which varies from almost continuous in the south-facing slope to highly patchy in flat areas previously cultivated (Appendix 1b, electronic version only).

The mean ground-projected cover of these four species was 25.2% for *L. caustica*, 2.9% for *A. dentata*, 1.9% for *S. polygamus* and an arbitrary cover of 0.1% was assigned to *C. parqui* (which did not appear in any of the ten 90 m linear transects). Ground-projected covers of all plant species in the two plots (polar-facing hillside and plain) are shown in Table 1.

2.4. Data analyses

All interactions used to construct the seed-dispersal network are shown in Appendix 2 (electronic version only). To analyze the structure of the seed-dispersal network, we followed the methods of Bascompte et al. (2003), where the level of specialization (or number of recorded interactions among species) was quantified using nestedness N, defined as $N = (100-T/100)$ where T is the matrix temperature, a measure of matrix disorder, with values ranging from $0°$ (perfect nestedness) to $100°$ (perfectly non-nested). Values of N close to 1 indicate high nestedness or strong asymmetrical patterns of specialization, intermediate values imply random interactions among species, and low values of N may indicate compartmentalization (Bascompte and Jordano, 2006). Additionally, we also used a new metric for nestedness based on overlaps and decreasing fill introduced by Almeida-Neto et al. (2008), known as NODF. This metric is highly recommended due to its theoretical consistence and statistical behavior (Almeida-Neto et al., 2008; Ulrich et al., 2009). Furthermore it allows an evaluation of whether and how frugivore species (i.e. columns) and plant species (i.e. rows) contribute to whole-matrix nestedness. Values of NODF may vary from 100 (perfect nestedness) to 0 (compartmented; Almeida-Neto et al., 2008). Matrix temperature was calculated using *Nestedness Temperature Calculator* (Atmar and Patterson, 1993) and NODF was calculated using *Aninhado* software (Guimarães and Guimarães, 2006). Significance of nestedness for T was obtained by comparing the observed values with a benchmark provided by a null model using Random00 model where occurrences are randomly assigned to matrix cells irrespective of the observed total numbers per plant and frugivore species (i.e. equiprobable row and column constraints; Atmar and Patterson, 1993). And for NODF we used two null model algorithms to obtain significance levels, the null model 2 in Bascompte et al. (2003) where the probability of each cell being occupied is the average of the probabilities of occupancy of its row and column. And the EE algorithm (i.e. equiprobable row totals, equiprobable column totals) that preserves the total number of species interactions in the original matrix, but allows both column and row totals to vary freely (Almeida-Neto et al., 2008; Gotelli, 2000). To depict the network structure, plant-frugivore interactions are represented with two sets of nodes (frugivores and plants) and the links between nodes represent two-species interactions (Jordano et al., 2003). The seed-dispersal network was drawn in Pajek (http://vlado.fmf.uni-lj.si/pub/networks/pajek/). To assess the consequences of hypothetical bird species removal on seed dispersal we used Monte Carlo simulations. A Mann–Whitney U-test was used to evaluate differences between random and selected (i.e. most connected frugivorous species) removal of frugivore species on the seed-dispersal network.

To assess whether avian frugivores at the study site contributed evenly to the dispersal of seeds of the four shrub species studied, field data on fruit availability (FAI) and fruit consumption (FCI) were transformed to Log (FAI + 1) and to Log (FCI + 1) respectively to down-weight extremely high abundance and high consumption data.

To compare the roles that individual frugivore bird species play in seed dispersal, we estimated the quantitative component of disperser effectiveness (QCDE hereafter) for *S. polygamus*, the most
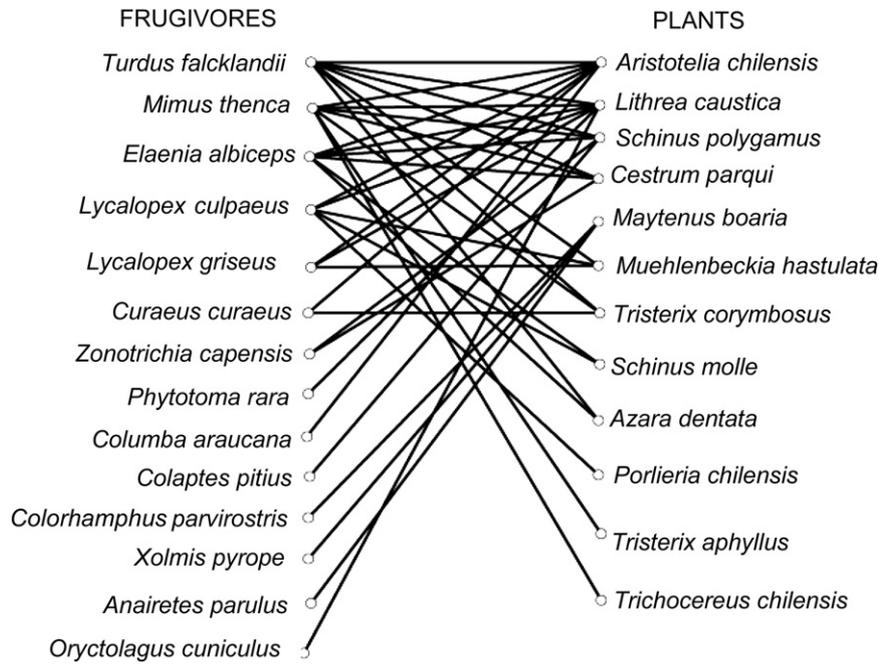
Fig. 1. Bipartite graph depicting the structure of the plant-frugivore network in San Carlos de Apoquindo, a subandean sclerophyllous shrubland in central Chile.

consumed fruit species. For this, we calculated the number of bird visits per hour times the mean number of fruits consumed (for a similar method, see Schupp, 1993).

3. Results

3.1. Seed-dispersal network

The seed-dispersal network in the sclerophyllous shrubland of San Carlos de Apoquindo was significantly nested, $N = 0.81$, $P < 0.01$ and $NODF_{total} = 42.49$, $NODF_{plants} = 49.55$ and $NODF_{frugivores} = 37.38$, $P < 0.04$ and $P < 0.01$ for null model 2 and EE model respectively (Fig. 1). This resulted in a core of generalist interactions among frugivorous vertebrates and plant species. A total of 26 interacting species were recorded, 14 frugivores and 12 plant species, for a total of 40 interactions and 23% matrix fill (Appendix 2, electronic version only). *Turdus falcklandii*, *Mimus thenca* and *Elaenia albiceps* were the main interactors among frugivorous species that drove overall spatial seed dispersal patterns, followed by the foxes *Lycalopex culpaeus* and *L. griseus* (Fig. 1). Monte Carlo simulations showed that the network structure was robust to the random loss of frugivorous species but highly sensitive to the loss of the most generalist (i.e. most connected) frugivorous species first (Fig. 2). The two simulation curves, the former being characterized by an asymptote and the latter by a linear relationship, are significantly different ($U = 46.5$, $P < 0.02$).

3.2. Fruit abundance

The most abundant fruit species during the whole study period was *L. caustica* (Fig. 3a). In January *S. polygamus* followed in abundance, while *A. dentata* and *C. parqui* had 12 times less fruit abundance (Fig. 3a). In March, *A. dentata* followed in fruit abundance, but with less than half of the abundance of *L. caustica*, while *S. polygamus* declined in local fruit abundance towards the end of summer because of fruit removal by birds (S. Reid, pers. obs.). Fruit abundance of *C. parqui* increased from January on; but it always remained much lower than the other species. In May the

ripe fruit availability ranking was the same as in March still, with *L. caustica* as the most abundant species, followed by *A. dentata*, *S. polygamus* and *C. parqui* (Fig. 3a).

3.3. Fruit consumption and seed dispersal

From January to May 2006, we accumulated a total of 193 mist-net captures from 23 bird species and accumulated a total of 337 net-hours. From the mist-net captures we identified a total of 14 interactions not previously reported between avian frugivores and plants in the Chilean matorral, including a total of six avian seed dispersers of five plants species in this Mediterarnean-type shrubland (Table 2; Appendix 2, electronic version only). Five species, *T. falcklandii*, *E. albiceps*, *Colaptes pitius*, *Zonotrichia capensis* and *Colorhamphus parvirostris*, showed evidence of fleshy fruit consumption by the presence of pulp remains and seeds in their
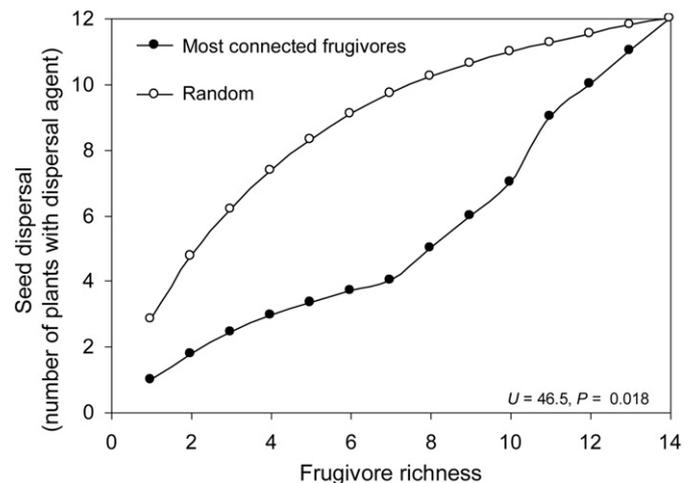

Fig. 2. Monte Carlo simulation curves showing seed dispersal as a function of frugivore species richness for a scenario of random loss of frugivorous species (open circles), and for the loss of the most generalist species (solid circles).
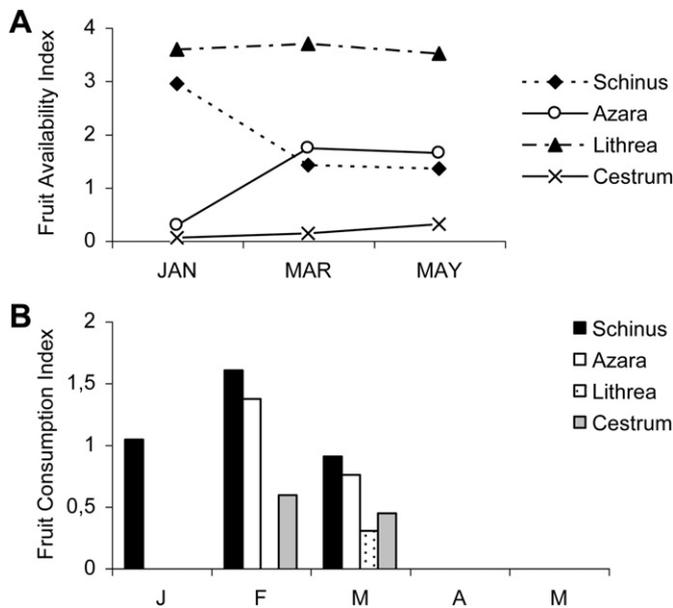
Fig. 3. Monthly abundance of ripe fruits expressed by the value of the fruit availability index (FAI) (A), and rates of consumption of fruits of the main frugivore species expressed by the fruit consumption index (FCI, see methods for details) (B).

fecal samples. In addition, other six species, *Curaeus curaeus* (insectivore-frugivore), *Sturnella loyca* (omnivore), *Callipepla californica* (granivorous exotic species), *Phrygilus gayi*, *P fruticeti* and *Asthenes humicola* (mainly granivores; Johnson and Goodall, 1967) had intact herbaceous seeds in their fecal samples, but not seeds of fleshy-fruited plants. *Mimus thenca*, an important frugivore species in this site, from previous studies (Hoffmann and Armesto, 1995) was not caught in the mist nets, but we observed this bird

consuming fruits of *C. parqui* and *S. polygamus*, and defecating intact seeds (Appendix 2, electronic version only).

The main avian frugivores did not contribute equally to seed dispersal from the major shrub species; and most fruit removal was done by a few generalist frugivore species, specifically *Turdus falcklandii* and *E. albiceps* (Table 3). *Turdus falcklandii* had the highest number of seeds of fleshy fruits found in one fecal sample, 21 seeds of *S. polygamus* and 85 seeds of *A. dentata*, which represented a total of 40 entire fruits, 21 of *S. polygamus* and 19 of *A. dentata*. The most consumed fleshy-fruited species, as inferred from seeds contained in fecal samples from all mist-net captured birds, was *S. polygamus* (56 fruits), followed by *A. dentata* (27 fruits), *C. parqui* (5 fruits), *M. boaria* (4 fruits) and *L. caustica* (1 fruit, Table 3; Fig. 3b). Fruit consumption was maximal in February in correspondence with the greatest local availability of ripe fruits (e.g. see *A. dentata* and *C. parqui*, Fig. 3b).

Visual records of bird visits to fruiting *S. polygamus* showed that *E. albiceps* was the most frequent bird visitor followed by *T. falcklandii* (2.3 visits/hour and 1.3 visits/hour, respectively; Fig. 4). This difference is related to the relative abundance of each bird species, as *E. albiceps* more than doubles *T. falcklandii* abundance in the summer months at this site (12.6% and 5.6% of all birds respectively; Reid, 2008). The QCDE for the most consumed shrub species *S. polygamus*, was highest for *T. falcklandii* and *E. albiceps* (4.4 and 2.6 respectively, Table 3).

4. Discussion

The seed-dispersal network in San Carlos de Apoquindo is significantly nested, resulting in a core of interactions among several generalist vertebrates and plant species. At the same time, specialist fruit-eaters only interact with generalist plant species and there were no interactions among specialist's plants and frugivores. The plant nestedness (i.e. rows), where the dispersal agents of the specialist's plant species constitute proper subsets of the more

Table 2

Bird species captures in mist-nets from January to May 2006 in a sclerophyllous shrubland of central Chile. Relative abundance in the austral summer and fall, total number of captures (n), body mass, gape width, main components of fecal sample mass and number of intact seeds present in the fecal samples are shown. Data are expressed as means ± 1 SD. For seeds, the mean and the range in parentheses are shown in superscripts; the absence of a figure indicates one fecal sample.

Species	Relative abundance (%)[b]	n	Body mass (g)	Gape width (mm)	Fecal sample [c]	Species of seeds dispersed [d]
Callipepla californica	7	13	183.5 ± 14	9.1 ± 1.3	I, P	H 0.2 (0–1)
Sephanoides sephaniodes	12	26	4.7 ± 1.3	3.6 ± 0.8	I	0
Colaptes pitius	0.4	5	152 ± 4.6	15	I	Sp (0–1)
Picoides lignarius	1.6	2	35	10.5	I	0
Upucerthia dumetaria	+	4	41.8 ± 1.3	5.8 ± 0.9	I	0
Aphrastura spinicauda	0.8	1	10	5.7[a]	I	0
Leptasthenura aegithaloides	3.7	2	10	5.3[a]	I	0
Asthenes humicola	6.1	15	23.1 ± 3.5	5 ± 1.2	I, P	H 0.4 (0–3)
Agriornis livida	+	1	85	…	I	0
Xolmis pyrope	2.5	1	30	6.4	I	0
Elaenia albiceps	7.4	16	16.2 ± 4	5.2 ± 1.1	I, P	Sp 1.2 (0–5), Cp 0.5 (0–13), Ad 1.2 (0–16), Lc 0.1 (0–1), Sm 0.1 (0–1)
Anairetes parulus	16	15	7.1 ± 2.2	4.3 ± 0.8	I, P	0
Colorhamphus parvirostris	+	1	10	4.8	I, P	Mb (0–8)
Troglodytes aedon	11	7	10 ± 0	3.4	I	0
Turdus falcklandii	6.1	12	85.2 ± 5.3	13.4 ± 2.7	I, P	Sp 3.4 (0–21), Ad 9.6 (0–85)
Zonotrichia capensis	10	32	20.5 ± 3.1	6.4 ± 0.8	I, P	Sp 0.1 (0–3), Cp 0.1 (0–1)
Curaeus curaeus	1.6	4	108 ± 24.3	9.7[a]	I, P	H 0.3 (0–1)
Sturnella loyca	0.4	2	87.5 ± 24.8	…	I, P	H 1.5 (0–3)
Phrygilus gayi	+	20	21.4 ± 3.2	7.2 ± 0.6	I, P	H 0.2 (0–3)
Phrygilus fruticeti	+	5	33.4 ± 3.2	8 ± 0.6	P	H 5.4 (0–18)
Phrygilus alaudinus	+	2	20.5 ± 0.7	5.9	I, P	0
Diuca diuca	0.4	6	33 ± 2.7	6.8 ± 0.1	P	0
Carduelis barbata	2.5	1	15	6.8	P	0

[a] Taken from Armesto et al. (1987).
[b] A (+) symbol indicates that the species was recorded outside point-counts, so we were unable to estimate its abundance.
[c] I: arthropod remains; P: plant remains.
[d] H: Unidentified herbaceous seed; Sp: *Schinus polygamus*; Cp: *Cestrum parqui*; Ad: *Azara dentata*; Lc: *Lithrea caustica*; Sm: *Schinus molle*; Mb: *Maytenus boaria*.

Table 3
Number of seeds and estimated number of fruits of woody species found in fecal samples of the five main avian frugivores in central Chile.

Plant species	TFALCK[a]	EALBIC	CPITIU	ZCAPEN	CPARV	Total
Schinus polygamus						
Total no. of seeds	37	15	1	3	…	56
Total no. of fruits	37	15	1	3	…	56
Mean no. of seeds (range)	3.3 (0–21)	1.2 (0–5)	1 (0–1)	0.1 (0–3)	…	
QCDE	4.4	2.6	0.3	0.3		
Azara dentata						
Total no. of seeds	106	16	…	…	…	122
Total no. of fruits	23.6	3.6	…	…	…	27.2
Mean no. of seeds (range)	9.6 (0–85)	1.2 (0–16)				
Cestrum parqui						
Total no. of seeds	…	19	…	2	…	21
Total no. of fruits	…	4.2	…	0.4	…	4.6
Mean no. of seeds (range)	…	1.5 (0–13)	…	0.1 (0–2)	…	
Lithrea caustica						
Total no. of seeds	…	1	…	…	…	1
Total no. of fruits	…	1	…	…	…	1
Mean no. of seeds (range)	…	0.1 (0–1)	…	…	…	
Maytenus boaria						
Total no. of seeds	…	…	…	…	8	8
Total no. of fruits	…	…	…	…	4	4
Mean no. of seeds (range)	…	…	…	…	8	
Total no. of fecal samples	11	13	1	23	1	

[a] Species codes are: TFALCK: *Turdus falcklandii*; EALBIC: *Elaenia albiceps*; CPITIU: *Colaptes pitius*; ZCAPEN: *Zonotrichia capensis*; CPARV: *Colorhamphus parvirostris*. QCDE: quantitative component of disperser effectiveness (see methods for details).

generalist plant species, contributes more to overall nestedness than frugivore nestedness. In the latter (i.e. nestedness among columns), fruit species consumed by the specialist frugivorous species would constitute subsets of the more generalist frugivorous species. The high nestedness of this plant-frugivore interaction network in central Chile corroborates recent studies that report highly nested patterns for most seed-dispersal mutualistic networks (Bascompte et al., 2003). This contrasts with the more compartmentalized assemblage structures reported for antagonistic food webs (Dunne et al., 2002). Similar patterns have been documented for other seed-dispersal networks in the Mediterranean Basin, but they differ markedly from the random structure reported for a species-richer Neotropical rainforest in Costa Rica (Jordano et al., 2003; Wheelwright et al., 1984). Although nestedness has been shown to increase with network size, i.e. the total number of interacting plant and animal species (Bascompte et al., 2003), the small network in San Carlos de Apoquindo (26 interacting species and 23% fill) shows an unusually high and significant level of nestedness for a species-poor community. This may be related to the lack of more detailed information about the network, as some bird species were hard or impossible to capture using mist nets, such as the Rhinocryptids *Scelorchilus albicollis* and *Pteroptochos megapodius* closely related to the fruit eating *S. rubecula* and *P. tarnii* in southern temperate rainforests in Chile (Armesto et al., 1987; Johnson and Goodall, 1967). Nevertheless, species additions to the seed-dispersal network in central Chile are unlikely to change network structure, and may increase the level of nestedness (Bascompte et al., 2003). A highly nested structure for the seed-disperal network in the Chilean matorral can provide alternative routes for this system to respond to human disturbances to the landscape (Bascompte et al., 2003). Accordingly, generalists can supplement seed dispersal associated with specialist avian species that may go locally extinct. We suggest this may be happening for the dispersal of *Aristotelia chilensis*, which was in the past dispersed by *Columba araucana*, a bird that has not been recorded for more than 35 years in the study area (Schlatter, 1979); *A. chilensis* is dispersed by six other generalist species, includying the two-species of foxes, *L. culpaeus* and *L. griseus*.

Recent studies have shown that nestedness may emerge as a consequence of the combined effects of the relative species abundance (Krishna et al., 2008; Vásquez et al., 2007), interaction-specific species processes such as forbidden links (i.e. constraints for a given pair of species due to phenological uncoupling, size restrictions or accessibility issues; Jordano et al., 2003), the intensity of dependence on frugivory (Krishna et al., 2008), coevolutionary interactions (Guimarães et al., 2006; Thompson, 2005), phenotypic complementarity (Rezende et al., 2007a; Santamaría and Rodríguez-Gironés, 2007) and past evolutionary history (Rezende et al., 2007b). The network topology in San Carlos de Apoquindo, was constructed solely with qualitative information, that is if species interact or not. This represents a first step to understand the interaction dynamics of frugivores and plants in this Mediterranean-type ecosystem. The current challenge will be to understand the ecological and evolutionary processes that explain these patterns of interaction in time and space. For this,
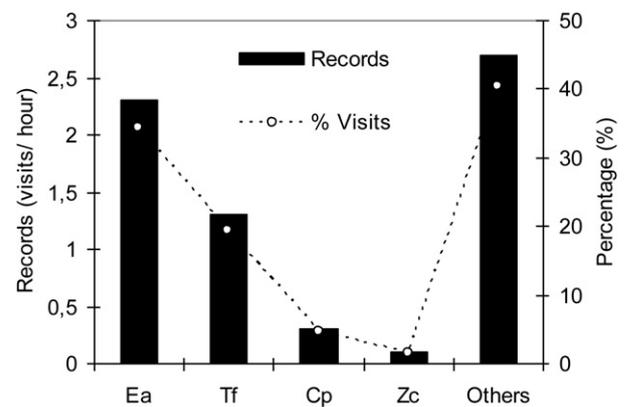

Fig. 4. Bird visitation records to *Schinus polygamus* shrubs expressed as the number of records per hour and the percentage of the total pool of bird species. Bird species recorded are the main frugivores, Ea: *Elaenia albiceps*; Tf: *Turdus falcklandii*; Cp: *Colaptes pitius*; Zc: *Zonotrichia capensis*.

detailed quantitative descriptions of the relationships between traits of interacting pairs of species will be needed.

Our simulations suggest that the current seed-dispersal network is robust to the potential random loss of frugivorous species due to local extinction, but at the same time it is sensitive to the selective loss of the most generalist (i.e., the most connected) species (Fig. 2). The two simulation curves in Fig. 2 remind us of the relationship between an ecological function (here seed dispersal) and biodiversity. The first curve shows an asymptotic function where loss of species is compensated for by others (i.e. redundancy), and the second curve shows a linear relationship, where species contribute to ecosystem functioning in ways that are unique (i.e. singular species; Naeem et al., 2002). We suggest that a reduction in the diversity of generalist avian frugivores, such as *T. falcklandii*, *M. thenca* and *E. albiceps*, and possibly the generalist foxes *L. culpaeus* and *L. griseus*, would greatly disrupt seed dispersal and natural regeneration of numerous woody species in this Mediterranean ecosystem. *T falcklandii* and *E. albiceps*, which are locally abundant during the austral summer-fall period have broad geographic ranges, are habitat generalists and are less likely to decline locally (Cofré et al., 2007), but *M. thenca*, which is endemic to central Chile, is more vulnerable to habitat loss as it nests in open-cup nests in exposed positions of thorny matorral shrubs (e.g. *Echinopsis* sp., *Acacia caven*; Johnson and Goodall, 1967). In sum, our study highlights the importance of frugivore species identity to assess the consequences of changes in frugivore diversity for seed dispersal. We urge that generalist frugivorous species should be given a high priority for research, in an effort to conserve the seed-dispersal networks in these Mediterranean-type ecosystems.

Avian frugivore-plant species interactions that are reported for the first time in this study include the presence of intact seeds of *M. boaria* in fecal samples of a primarily insectivorous species, *Colorhamphus parvirostris*. Only one study mentions that this species eats berries (specifically during the fall and winter months), without specifying whether the seeds were destroyed or defecated intact (Barros, 1920). Observations of *C. parvirostris* in the southern tip of temperate forests range in Chile, in Navarino Island (54° 55′ S, 67° 39′ W) show that this species also consumes arillated seeds of the closely related species *Maytenus magellanica* (McGehee, 2007). Another primarily insectivorous species, the woodpecker *Colaptes pitius* had intact seeds of *S. polygamus* in one fecal sample, and although evidence of frugivory among picids is widespread (Armesto et al., 1987; Stiles, 2000), fruit consumption by this species in a Mediterranean-type ecosystem was undocumented. This indicates fruit consumption may be a relatively opportunistic trait for some species, which include fruits in their diet during the time of the year of maximum fruit availability.

We now discuss fruit consumption of the four focal shrub species in our study, *S. polygamus*, *A. dentata*, *C. parqui* and *L. caustica*. We present for the first time information on differences in fruit consumption rates among the main bird species in the Chilean matorral. Based on fleshy fruit consumption and visitation records for *S. polygamus*, the quantitative component of disperser effectiveness (i.e. QCDE) was highest for *E. albiceps* and *T. falcklandii*, while *C. pitius* and *Z. capensis* were occasional visitors. Although *T. falcklandii* is less abundant than *E. albiceps* (Table 2), the first species contributes more to seed dispersal of *S. polygamus* because it consumes more fruits per visit. In addition, *E. albiceps* emigrates from central Chile around mid-March, which increases the importance of *T. falcklandii* as a local dispersal vector, especially during the austral fall and winter. Similarly, we suggest *T. falcklandii* contributes more to seed dispersal of *A. dentata* because of greater fruit consumption, although the estimation of the QCDE is absent for this species. We propose that fruit consumption (i.e. number of fruits consumed per unit time) is a better proxy for disperser effectiveness

than species abundance in this frugivore assemblage, as it contributes more to the quantitative component of disperser effectiveness. For *C. parqui*, *E. albiceps* was a legitimate seed dispersal agent. In contrast, *Z. capensis* probably was not, as we saw signs of seed predation in some fecal samples. Fruits of *L. caustica* were recorded to be consumed only by *E. albiceps* during our study, but several other seed vectors of this shrub species are known, including the European rabbit *Oryctolagus cuniculus* (Castro et al., 2008), the two fox species of this region, *Lycalopex culpaeus* and *L. griseus* (Silva et al., 2005), and other bird species *T. falcklandii*, *M. thenca* and *Phytotoma rara* (Hoffmann and Armesto, 1995). We attribute this difference to the bias of mist-netting records in the present study. In particular, *M. thenca* was never caught in our mist nets even when using playbacks, despite its presence in the area. In sum, our field results corroborate and extend the conclusion that generalist avian species, specifically *T. falcklandii* and *E. albiceps*, are the major seed dispersers in this rural, suburban landscape of central Chile.

Our discussion is limited to seed dispersal, namely the removal of seeds from source shrubs to an unknown destination (Skarpaas et al., 2007). However, other components of disperser effectiveness, such as events occurring during dispersal or gut treatment, and the sites where seeds are deposited, are important to achieve general conclusions about plant recruitment (Reid and Armesto, 2010; Reid et al., unpublished manuscript). It is well established that the regeneration of woody species is limited by events in the early phases of their life cycle, which in central Chile derive from limited seed dispersal, poor or absent seed banks, and high seedling mortality due to drought and herbivory (Fuentes et al., 1984; Jiménez and Armesto, 1992). To understand the potential importance of seed dispersal patterns for the maintenance or change of the present patch structure of the matorral, we suggest that post-dispersal processes such as seed germination and deposition patterns of dispersed versus non-dispersed seeds should be evaluated (e.g. Nathan and Muller-Landau, 2000; Schupp et al., 2002). Because of high mortality rates and lack of seed banks in most woody species (Armesto et al., 1995; Fuentes et al., 1984; Jiménez and Armesto, 1992), we argue here that seed limitation (*sensu* Levin et al., 2003; Nathan and Muller-Landau, 2000) or the failure of seeds to arrive at suitable sites in sufficient numbers to establish as seedlings, due to insufficient seed dispersal by frugivores, can be a critical and fundamental constraint on seedling recruitment in open areas of the Chilean matorral. Alterations to the bird assemblages could thus have strong impacts on seed dispersal and patch structure and composition, due to changes in the dynamics of seed input.

Appendix 1. Map of the study site San Carlos de Apoquindo in central Chile, with sclerophyllous shrubland associated to the Andean foothills in green (A), and an aerial photo 1: 10 000 of the study site with the location of vegetation plots in the polar-facing slope (top) and plain (bottom) in red and mist-net sites in yellow (B). Constructions belong to the adjacent sports club grounds.

Appendix 2. Frugivore and plant species interaction matrix in San Carlos, a "1" indicates a fruit consumption interaction and a "0" no interaction. A (*) symbol indicates a new interaction (first reported by the present study).

Plant species	Frugivore species													
	Turdus falcklandii	Mimus thenca	Elaenia albiceps	Lycalopex culpaeus	Lycalopex griseus	Curaeus curaeus	Zonotrichia capensis	Pytotoma rara	Columba araucana	Colaptes pitius	Colorhamphus parvirostris	Xolmis pyrope	Anairetes parulus	Oryctolagus cuniculus
Azara dentata	1*	0	1*	0	0	0	0	0	0	0	0	0	0	0
Aristotelia chilensis	1	1	1	1	1	1	0	0	1	0	0	0	0	0
Cestrum parqui	1*	1*	1*	0	0	0	1*	0	0	0	0	0	0	0
Lithrea caustica	1	1	1	1	1	0	0	1	0	0	0	0	0	1
Muehlenbeckia hastulata	1	0	0	1	1	0	0	0	0	0	0	0	0	0
Schinus molle	1*	0	1*	1	0	0	0	0	0	0	0	0	0	0
Schinus polygamus	1*	1*	1*	0	0	0	1*	0	0	1*	0	0	0	0
Tristerix corymbosus	1	1	0	0	0	1	0	0	0	0	0	0	0	0
Trichocereus chilensis	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Tristerix aphyllus	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Porlieria chilensis	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Maytenus boaria	0	0	0	0	0	0	0	0	0	0	1*	1	1	0

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