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Forest fragmentation negatively affects common bird species in subtropical fragmented forests

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ABSTRACT

Forest fragmentation threatens bird species throughout the world. Previous studies suggest that the sensitivity of bird species to forest fragmentation is related to food abundance, and that this could be a key factor in understanding demographic changes. We assessed the relationship between forest fragment size, isolation and food abundance and the abundance of seven common species of birds in southern Chaco forests of Argentina, which use different food items, and are involved in different ecosystem processes. The relative abundance of *Turdus amaurochalinus* (Creamy-bellied Thrush) and *Saltator aurantiirostris* (Golden-billed Saltator) significantly decreased with patch size reduction, whereas the relative abundance of *Taraba major* (Great Antshrike) decreased with patch isolation and increased with arthropod abundance. *Chlorostilbon lucidus* (Glittering-bellied Emerald), *Elaenia parvirostris* (Small-billed Elaenia), *Polioptila dumicola* (Masked Gnatcatcher) and *Zonotrichia capensis* (Rufous-collared Sparrow) appeared to be resilient to forest fragmentation. Body size was a good predictor of bird sensitivity, as only the largest species were negatively correlated with forest fragmentation. Previous work suggests that birds inhabiting Chaco forests may be resilient to forest fragmentation. This needs to be reconsidered in the light of our results since the abundance of three out of seven common bird species was negatively related to forest fragmentation.

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Body size; food abundance; isolation; patch size; species-specific response

Introduction

Land-use change is considered one of the major threats to biodiversity (Sala *et al.* 2000; Fischer and Lindenmayer 2007). The expansion of agricultural frontiers in the past decades has resulted in extensive deforested areas (Grau and Aide 2008; Hansen *et al.* 2013). One example of this is the Chaco subtropical forest in South America, which represents the most extensive seasonally-dry forest on the continent, and which currently has an alarming rate of forest loss and fragmentation (Hoyos *et al.* 2013; Cáceres 2015).

Birds are considered to be sensitive to the forest fragmentation process (Zanette *et al.* 2000; Lampila *et al.* 2005), principally in tropical regions (Bregman *et al.* 2014). However, not all bird species are equally affected (Renjifo 1999; Henle *et al.* 2004). Particularly in subtropical regions, the responses of bird species to forest fragmentation seem to be highly idiosyncratic (Bregman *et al.* 2014). Several studies suggest that forest patch size and isolation are two factors that strongly affect the persistence of bird populations in fragmented forests (Franken and Hik 2004; Uezu *et al.* 2005). While population size and probability of extinction depend on the patch area, re-colonisation depends on the isolation (Franken and Hik 2004; Martensen *et al.* 2008). Specifically, patch size reduction can affect bird population size by means of food shortage (Burke and Nol 1998; Zanette *et al.* 2000), and increased nest parasitism and nest predation (Andrén 1992).

Because the forest fragmentation process can affect food abundance for birds (Zanette *et al.* 2000), the analysis of that variable in the forest fragmentation context would help to better understand the response of birds to such environmental changes. Food shortage can negatively impact the survival of adult and young birds, ultimately causing changes in population densities (see Martin 1987; Zanette *et al.* 2000). For example, forest fragmentation has led to a shortage of arthropods, fruits or flowers (Zanette *et al.* 2000; Aguilar and Galetto 2004; Cagnolo *et al.* 2006), which are important food resources for a variety of bird species. However, the responses of avian species to forest fragmentation depend on species traits, such

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The supplemental material for this article can be accessed here.

as dispersal ability, social behaviour, etc., and hence on their landscape perception (see Henle *et al*. 2004; Melorose *et al*. 2006; Lees and Peres 2009). In this sense, body size is an important trait that can affect the response of species to forest fragmentation. In general, large bird species are more sensitive to the forest fragmentation process than small species (Henle *et al*. 2004; Barbaro and Van Halder 2009).

Particularly in the Chaco region, bird species are negatively impacted by changes in land use (Schrag *et al*. 2009; Mastrangelo and Gavin 2014). In general, bird species richness has been the most studied indicator and it is negatively related to patch isolation and edge effect (Mastrangelo and Gavin 2014) and positively related to patch size (Bucher *et al*. 2001). Nevertheless, small Chaco forest fragments (1 ha or less) still host a rich avifauna (Dardanelli *et al*. 2006). Previous studies highlight that this general trend of change in bird species richness in relation to forest fragmentation does not mirror species-specific responses (Dardanelli *et al*. 2006; Calamari 2014).

Given the complexity of bird responses to forest fragmentation in relation to specific habitat requirements and landscape perceptions, studies at the species level are needed to understand responses to fragmentation (Didham *et al*. 2012). So, in the present work we assess the relationship between forest fragmentation and the relative abundances of common bird species that use different food items in the semi-arid Chaco forest in Córdoba, Argentina. Common species are fundamental to the structure of most assemblages and they contribute substantially (relative to other less common species) to different ecosystem functions (Gaston and Fuller 2007). Moreover, that a species is characterised as 'common' does not mean that it is resilient to ecological disturbances, such as forest fragmentation (Gaston and Fuller 2007). However, studies focusing particularly on common species and their response to ecological disturbances have received little attention (Gaston 2008). Based on what we stated previously, we hypothesised that the relative abundance of common bird species is affected by the forest fragmentation process. Specifically, we predicted that (i) both reduction of forest patches size and the increase of their isolation will be negatively related to the relative abundance of common bird species, yet large species will be more sensitive than small species, and (ii) food abundance will be positively associated with the relative abundance of common bird species.

To address those predictions, we studied seven bird species with different diets (e.g. Blake and Loiselle 1991; Blendinger and Ojeda 2001; de la Peña 2001; de la Peña and Pensiero 2003). *Chlorostilbon lucidus* (which feeds mainly on nectar), *Elaenia parvirostris* and *Turdus amaurochalinus* (which feed mainly on fleshy fruits, at least during the summer), *Polioptila dumicola* and *Taraba major* (which feed mainly on arthropods), and *Zonotrichia capensis* and *Saltator aurantiirostris* (which feed mainly on seeds). Because these bird species are involved in different ecosystem processes (i.e. seed dispersal, pollination, etc.) and are common in the region (Yzurieta 1995), understanding their responses to forest fragmentation can help to predict the potential effects of forest fragmentation on ecosystem functioning (Gaston and Fuller 2007; Galetti *et al*. 2013; Bregman *et al*. 2014).

Materials and methods

Study area

We conducted the study in a semi-arid Chaco forest in Córdoba, Argentina, in a region transformed into an agricultural ecosystem (Figure S1). Forests are restricted to patches surrounded by a matrix of different crops, usually soybean or maize in summer and wheat in winter (Grilli and Galetto 2009). All the forest patches have a complex structure, with arboreal, shrubby, and herbaceous strata. Moreover, there are some epiphytes and vine species. Forest patches present mostly native trees species (for details, see Ferreras and Galetto 2010; Grilli *et al*. 2014).

We estimated the relative abundance for each bird species and the abundance of food items generally consumed by those species across a gradient of forest patch sizes ($n = 14$) and isolation distances. Because the effect of patch size on the bird population can change with the landscape context, to better understand the tendencies and achieve more representative results we have replicated the size gradient of fragments sampled in two landscapes (areas of 12 × 12 km), located 40 km apart from each other. They are mostly similar in their plant composition, yet have some differences in the amount of forest cover (Santo Domingo: −31.18° S, −64.26° W, 48.6% of forest cover and Tinoco: −31.10° S, −63.87°, 11.4% of forest cover; Figure S1a, b respectively). In each landscape we selected a group of seven patches between 0.4 and >800 ha, where we conducted bird surveys and food abundance assessments (Table 1; Figure S1). In each forest patch, we estimated isolation as the mean distance to the three closest woodland patches of any size (Radford and Bennett 2004).

Bird surveys

We conducted bird surveys throughout two seasons (summer 2011–2012 and summer 2012–2013) using

Table 1. Description of each forest patch sampled: location (latitude and longitude), size, isolation and estimated abundance of arthropods, fruits, flowers and seeds (see details in the 'Materials and methods' section)

L	FP	Lat.	Long.	Patch size (ha)	Patch isolation (m)	Mean (min–max) arthropod abundance (mg arthropods/100g vegetation)	Mean (min–max) fruit abundance (*n*)	Mean (min–max) flower abundance (*n*)	Mean (min–max) seed abundance (g per sample)
SD	1	−31.184° S	−64.255° W	0.4	38.1	0.061 (0.012–0.157)	43 221 (12 073–114 771)	990 (4–2604)	1.22 (0.92–1.56)
	2	−31.196° S	−64.285° W	0.7	332.5	0.142 (0.022–0.830)	24 214 (80–36 869)	7529 (18–29 192)	1.83 (0.95–3.87)
	3	−31.215° S	−64.271° W	1.6	98.1	0.069 (0.006–0.244)	15 275 (389–42 031)	286 (0–826)	2.06 (1.01–2.82)
	4	−31.175° S	−64.217° W	13.6	38.1	0.046 (0.009–0.137)	9457 (675–25 968)	567 (4–2700)	1.38 (0.72–2.46)
	5	−31.186° S	−64.258° W	18.0	38.8	0.085 (0.007–0.208)	32 665 (57–82 637)	151 (1–536)	0.84 (0.65–1.12)
	6	−31.208° S	−64.261° W	18.9	51.6	0.038 (0.006–0.073)	8841 (35–25 291)	6437 (105–37 163)	1.51 (0.92–2.22)
	7	−31.179° S	−64.263° W	495.1	27.4	0.066 (0.008–0.318)	10 907 (1996–20 895)	489 (4–1842)	0.80 (0.44–1.13)
TC	8	−31.107° S	−63.894° W	0.5	1722.7	0.039 (0.001–0.147)	16 740 (698–87 377)	48 (0–158)	1.15 (0.62–1.60)
	9	−31.078° S	−63.838° W	1.4	275.5	0.03 (0.002–0.0815)	9307 (56–40 410)	60 (1–132)	0.73 (0.31–1.64)
	10	−31.148° S	−63.898° W	1.8	159.9	0.026 (0.007–0.082)	15 547 (739–34 010)	54 (0–215)	0.88 (0.53–1.13)
	11	−31.090° S	−63.855° W	11.5	649.3	0.077 (0.007–0.197)	3335 (96–12 255)	60 (0–183)	0.92 (0.34–2.14)
	12	−31.063° S	−63.864° W	16.5	308.5	0.045 (0.004–0.196)	37 098 (175–143 270)	519 (13–2775)	0.96 (0.52–1.82)
	13	−31.144° S	−63.894° W	16.8	191.7	0.030 (0.003–0.099)	16 420 (9563–27 408)	16 (0–52)	0.58 (0.41–0.89)
	14	−31.108° S	−63.865° W	830.2	18.8	0.071 (0.002–0.219)	5568 (0–18 081)	4255 (1–23 530)	0.70 (0.28–1.18)

L = landscape, FP = forest patches, SD = Santo Domingo, TC = Tinoco. The resource abundance is shown as the mean value of the six plots per patch and the minimum and maximum values registered in each forest patch (see details in the 'Materials and methods' section).

fixed-radius point counts, carried out between 6:00 a.m. and 10:00 a.m. and from 5:00 p.m. to 8:00 p.m. We recorded the relative abundance of all bird species seen or heard within a 50 m radius, during a period of 10 min. We did not include birds flying over the area. At each of the 14 forest patches, we conducted 47 point counts (a total of 658 points), visiting them between six to eight times during both seasons. The location of each point was selected randomly using ArcGis 9.3 software and then located in the field with a Global Positioning System (GPS). Visits to each site were separated from each other by a minimum of 3 weeks to reduce the probability of double counts, particularly in the small forest patches. However, to test whether the lack of independence among point counts in those small patches could alter the results, for the different bird species we carried out bootstrap analyses in which the 47 point counts per forest patch were selected randomly (with replacement). With the new data frame resulting from the bootstrapped data, we conducted the data analyses (as explained in the 'Data analysis' section below). This process was repeated 1000 times. Then we compared the *p*-value distribution of variables included in the best model per bird species with the observed *p*-values. We found concordance (graphically and analytically) between bootstrapped and observed *p*-values for all the seven bird species (for more detail see Figure S2).

We chose data on seven bird species (already enumerated in the introduction) present in most fragments – at least in four of the seven patches within each landscape – to perform statistical analyses. The nomenclature follows Remsen *et al.* (2016) (available online at http://www.museum.lsu.edu/~Remsen/SACCCountryLists.htm).

Food abundance

We estimated the abundance of arthropods, fruit, flowers (i.e. indirectly nectar) and seeds in six plots (15 m × 15 m; four in the summers of 2011–2012 and two in the summer of 2012–2013) within each one of the 14 forest patches (a total of 84 food abundance plots). The plot location was selected randomly within the forest patches, following the same methodology as that used to select the bird point count locations.

Abundance of arthropods

We used the 'branch clipping' technique described by Johnson (2000) to quantify the abundance of arthropods in each plot. Briefly, we clipped two branches (45 cm long) from trees of two common woody species (*Celtis ehrenbergiana* and *Acacia caven*) present in all of the 14 forest patches (total of sample per patch = 2 branches clipped of *C. ehrenbergiana* + 2 branches clipped of *A. caven* * 6 plot = 24 branches). To standardise clipped vegetation, each sample was expressed as the total biomass of arthropods per 100 g of clipped vegetation (wet mass) (Johnson and Sherry 2001).

Fruit abundance

At each 15 m × 15 m plot we counted the total number of fruits per plant in all the plant species with fleshy fruits (including trees, shrubs, vines and herbaceous species) potentially eaten by birds (Ponce *et al.* 2012; Díaz Vélez *et al.* 2015). When fruit abundance was very high, the amount of fruit produced per individual was obtained by counting the number of fruits on three representative branches of the plant and then multiplying the mean fruit number per branch by the total number of branches with fruits (Ferreras and Galetto 2010). Fruit abundance is expressed as the mean number of fruits per plot in each forest patch.

Nectar abundance

We used the number of available open flowers potentially visited by hummingbirds as an indirect indicator of nectar abundance (Galetto and Bernardello 2003; McKinney *et al.* 2012). The same methodology described for the estimation of fruit abundance was used to estimate the number of flowers per plot (expressed as the mean number of flowers per plot in each forest patch).

Seed abundance

At each plot we collected four soil core samples (15 cm diameter), one at each corner of the 15 m × 15 m plot, which were combined in a single sample per plot. We only sampled soil immediately below the surface (at a depth of 3 mm) in order to represent the potential soil seed bank available for small passerines (Robinson and Sutherland 1999; Moorcroft *et al.* 2002). In the laboratory, we sifted the samples and analysed them under a stereoscopic magnifying glass. We quantified seed biomass (expressed as mean seed biomass per sample per forest patch), considering seeds between 0.55 mm and 3.42 mm. Seeds larger or smaller than this range were not included in the analysis because they are not usually consumed by small granivorous birds (Blendinger and Ojeda 2001).

Data analysis

Prior to the statistical analysis, we averaged the relative abundance of each species among all the point counts conducted within a given patch, resulting in a unique relative abundance value for each bird species at each patch.

To test the relationship between patch size, isolation, and food abundance and relative abundance per bird species, we used linear models ($n = 14$) for which landscape was included as a fixed factor (block). Because the response variable is continuous (relative abundance), we assumed that the error structure had a Gaussian distribution. The abundances of *Chlorostilbon lucidus, Turdus amaurochalinus, Polioptila dumicola* and *Taraba major* were square root transformed to agree with the model assumptions whereas those of *Elaenia parvirostris, Zonotrichia capensis* and *Saltator aurantiirostris* were not transformed because they met model assumptions. We performed a full model (with all the explanatory variables) for each bird species. Model selection was done using the drop 1 function in program R (R Core Team 2016; according to Zuur *et al.* (2009), detailed in Table S1). Explanatory variables (patch size, isolation or food abundance) were not collinear to each other (VIF value <3; Zuur *et al.* 2009). We performed a spatial autocorrelation test (Zuur *et al.* 2009) using the GSTAT package (Pebesma 2004) in program R (R Core Team 2016), yet we did not observe autocorrelation patterns with residuals for the models.

To test for the relationship between body size and bird response to forest fragmentation, we performed a within-study meta-analysis (Milner *et al.* 2010). We considered the six passerine birds studied here. *Chlorostilbon lucidus* was not included because it belongs to a different taxonomic order (Apodiformes). We decided not to include different taxonomic orders in this analysis because the relationship between body size and bird sensitivity to forest fragmentation may be strongly affected by phylogenetic relationships (Cotgreave and Harvey 1992; Sodhi *et al.* 2004). Species were grouped in two sets relative to their body mass (see Barbaro and Van Halder 2009): large passerine species (>50 g: *T. amaurochalinus, T. major* and *S. aurantiirostris*; Salvador 1988; Zimmer and Isler 2003), and small passerine species (<20 g: *E. parvirostris, P. dumicola, Z. capensis*; Salvador 1988). For each bird species, we calculated the effect size Fisher's *r*-to-*z* transformation and standard errors (for both patch size and isolation). We then performed a fixed model analysis using the metafor package (Viechtbauer 2010) in R program (R Core Team 2016).

Results

We recorded a total of 2416 individuals of the seven focal bird species. The most abundant species was *Zonotrichia capensis* (with 664 individuals), followed by *Saltator aurantiirostris* (620), *Chlorostilbon lucidus* (417), *Elaenia parvirostris* (314), *Turdus amaurochalinus* (197), *Polioptila dumicola* (147) and *Taraba major* (61). In Table 1 we show a summary of abundance of food items that can potentially be consumed by bird species, recorded at each forest patch.

For each bird species we obtained the relationship between its relative abundance and the different explanatory variables (patch size, isolation and food abundance; Table 2). The relative abundance of *T. amaurochalinus* and *S. aurantiirostris* was negatively correlated with patch size reduction (Table 3; Figure 1). In particular, patch size was strongly correlated with the relative abundance of *T. amaurochalinus*, a species not detected in three of the smallest forest patches (Figure 1). The relative abundance of *T. major* was negatively correlated with patch isolation (Table 3; Figure 2). On the other hand, the relative abundance of *C. lucidus, E. parvirostris, P. dumicola* and *Z. capensis* was not correlated with any of the explanatory variables considered (Table 3). Moreover, there were other biologically interesting relationships, although non-significant. Patch area was positively correlated with relative abundance of *T. major*; furthermore, this species was not detected in two small forest patches (Figure 1). Isolation was negatively correlated with relative abundance of *C. lucidus, T. amaurochalinus* and *S. aurantiirostris* (Figure 2). Food abundance did not explain relative abundance variation in most bird species except for *T. major*: its relative abundance was positively correlated with arthropod abundance (Table 3).

Table 2. Slopes and standard errors for each of the three explanatory variables resulting from the full model per bird species

Explanatory variables	Slope	SE
Chlorostilbon lucidus		
Logarea	−0.024	0.074
Logisolation	−0.154	0.156
Flower	0.00002	0.00002
Elaenia parvirostris		
Logarea	0.098	0.118
Logisolation	0.009	0.230
Fruit	0.0000008	0.000007
Turdus amaurochalinus		
Logarea	0.152	0.047
Logisolation	−0.002	0.092
Fruit	0.000001	0.000002
Polioptila dumicola		
Logarea	0.004	0.084
Logisolation	−0.127	0.184
Arthropods	0.426	2.328
Taraba major		
Logarea	0.012	0.040
Logisolation	−0.209	0.087
Arthropods	2.193	1.102
Zonotrichia capensis		
Logarea	−0.062	0.177
Logisolation	−0.153	0.388
Seed	−0.232	0.463
Saltator aurantiirostris		
Logarea	0.207	0.107
Logisolation	−0.420	0.234
Seed	0.142	0.279

Body size was correlated with bird sensitivity to forest fragmentation considering the six passerine birds studied here. In particular, an increase in patch size was correlated with an increase in the relative abundance of the largest species, whereas an increase in patch isolation was correlated with a decrease in the relative abundance of these species (Figure 3). The smallest species were not correlated with any of the forest fragmentation proxies (Figure 3).

Discussion

Our results showing that three of seven bird species common to the Chaco forest are negatively related to forest fragmentation highlight the severity of forest fragmentation in the remaining semi-arid forests of central Argentina, the southernmost distribution of the Chaco. This is worrying, since birds inhabiting temperate regions are usually more resilient to forest fragmentation than tropical birds (Bregman *et al.* 2014).

Food abundance was not correlated with bird abundance except for *T. major*. The abundance of this species was positively correlated with arthropod abundance. This particular trend for *T. major* agrees with those previously found for other insectivorous birds in fragmented forests (Burke and Nol 1998; Zanette *et al.* 2000). In general, the absence of clear relationships between mean food abundances per forest patch and the relative abundances of the birds studied here can be explained because most species in the study region are not specialists and can supplement their diets with other items (de la Peña 2001).

Body size seems to be linked with the response of bird populations to forest fragmentation, considering the six passerine species studied. This pattern was previously reported showing that large bird species are more sensitive than smaller ones to forest fragmentation (Barbaro and Van Halder 2009). Body size may affect bird responses to the forest fragmentation process because, in general, larger species have broader

Table 3. Summary of statistics for the explanatory variables included in the final model explaining the relative abundance of birds for each avian species. Each landscape was used as a fixed effect (block); *p*-values in bold indicate a statistically significant relationship ($p < 0.05$)

Species	Explanatory variable	Estimates	SE	*t*-value	*p*-value
Chlorostilbon lucidus	Flower	0.00002	0.00002	1.121	0.286
Elaenia parvirostris	Logarea	0.091	0.068	1.342	0.206
Turdus amaurochalinus	Logarea	0.148	0.027	5.396	**0.0002**
Polioptila dumicola	Logisolation	−0.126	0.11	−1.149	0.274
Taraba major	Logisolation	−0.227	0.056	−4.007	**0.002**
	Arthropods	2.284	1.009	2.263	**0.047**
Zonotrichia capensis	Seed	−0.257	0.33	−0.78	0.451
Saltator aurantiirostris	Logarea	0.319	0.077	4.111	**0.001**

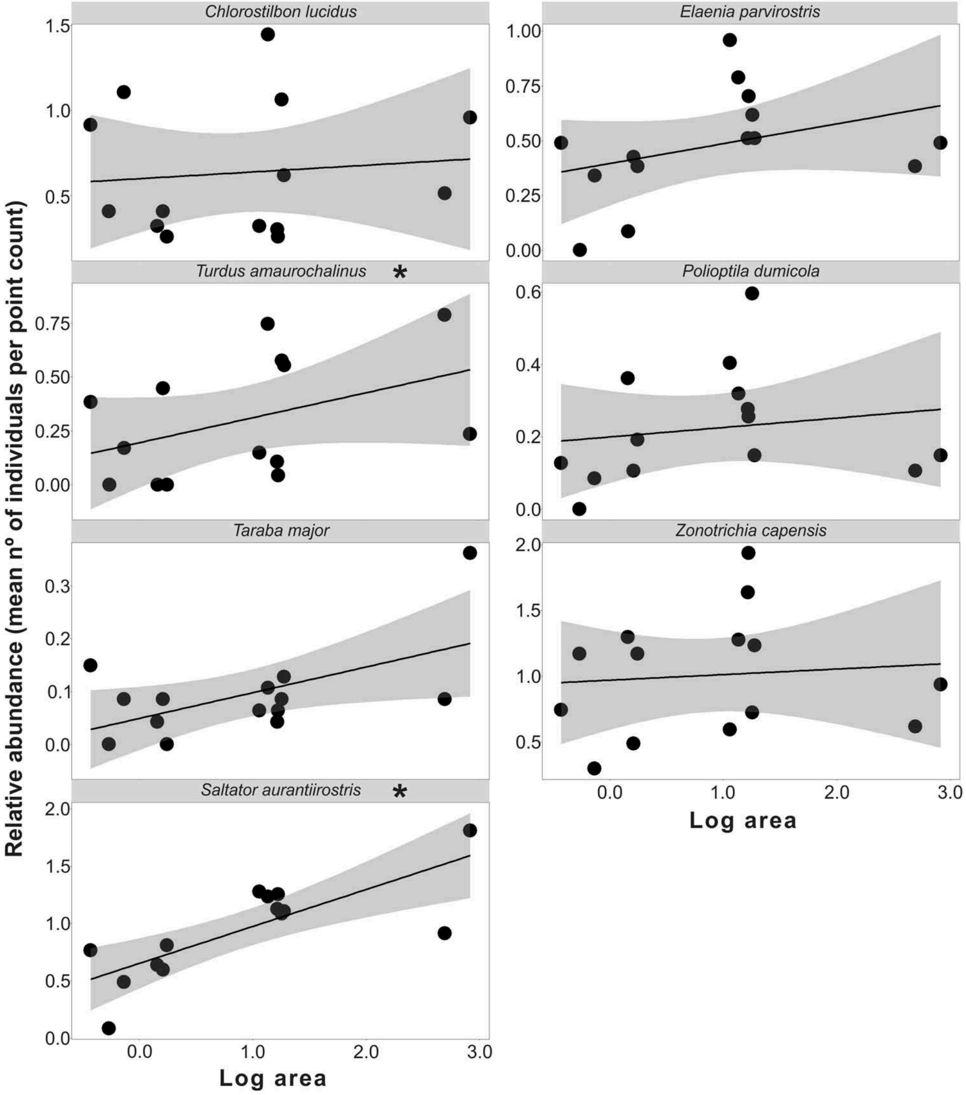

Figure 1. Relationship between patch size and relative abundance for each of the seven bird species considered in this study, across 14 patches of semi-arid Chaco forest in Córdoba, Argentina. Confidence intervals of 95% are shaded in grey. Asterisks indicate a statistically significant relationship ($p < 0.05$).

area requirements and a wider home-range than smaller ones (Renjifo 1999; Dardanelli *et al.* 2006; Barbaro and Van Halder 2009). Consequently, as forest patches become smaller, large species are more prone to get in contact with edges, open areas, or other unsuitable habitat (Van Houtan *et al.* 2006).

Species-specific responses

Marsden *et al.* (2001) found that *T. amaurochalinus* was a common species in continuous forest but not in fragments. The negative correlation between forest fragmentation and *T. amaurochalinus* relative abundance (see Figure 1) is of special concern as this species is a seed disperser of several native woody plant species of Chaco forests (de la Peña 2001; Sánchez Hümöller 2008; Ponce *et al.* 2012). Although *E. parvirostris* (effective seed dispersers but small-gape species; Marini and Cavalcanti 1998; Ponce *et al.* 2012) seem to be resilient to forest fragmentation in the Chaco region, small species cannot entirely replace the functional role of other larger frugivorous birds, such as *T. amaurochalinus* (Montaldo 2005; see also Galetti *et al.* 2013). This is because large-gape birds can disperse plant species that produce large fruits, which cannot be consumed and dispersed by small-gape birds (Galetti *et al.* 2013).

The relative abundance of *T. major* was negatively correlated with patch isolation and positively by arthropod abundance. In general, understorey insectivorous birds have poor dispersal ability, which makes them more sensitive to forest fragmentation,

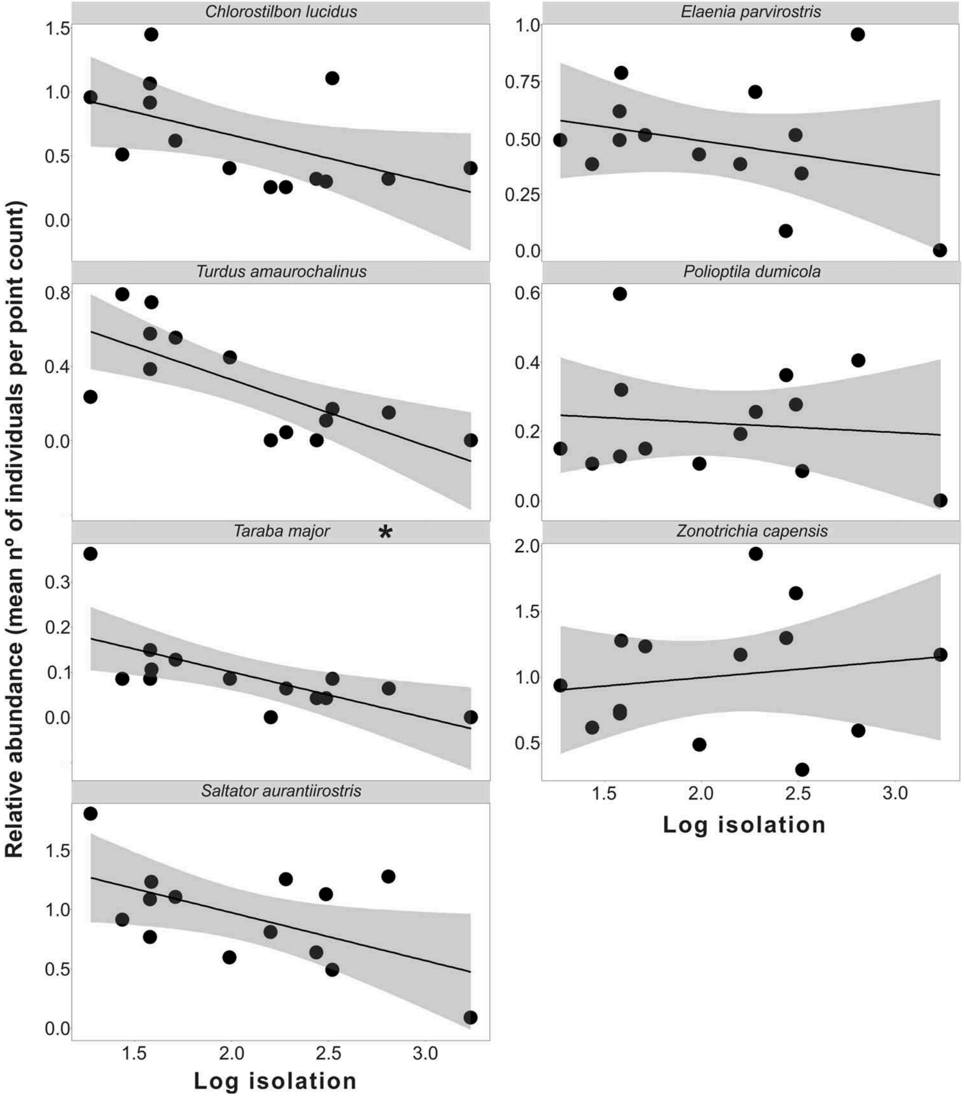

Figure 2. Relationship between patch isolation and relative abundance for each of the seven bird species considered in this study, across 14 patches of semi-arid Chaco forest in Córdoba, Argentina. Confidence intervals of 95% are shaded in grey. The asterisk indicates a statistically significant relationship ($p < 0.05$).

particularly to forest isolation (Kattan *et al.* 1994; Stouffer and Bierregaard 1995; Marini 2001). Moreover, the Thamnophilidae family (*T. major* is included) is particularly sensitive to fragmentation (Renjifo 1999). The positive relationship of *T. major* relative abundance with food abundance may also be due to its poor dispersal ability. Therefore, changes in its abundance could depend more on food variations at the patch scale compared to the other bird species. For example, frugivorous and nectarivorous birds would be able to track changes in food distribution at a larger scale, given the patchy distribution of their food both spatially and temporally (Lees and Peres 2009; Tobias *et al.* 2013; Bregman *et al.* 2014).

Saltator aurantiirostris was negatively correlated with patch size reduction, showing a strong abundance–patch size relationship, which may be due to the low dispersal ability of this species (Blendinger and Ojeda 2001; Díaz Vélez *et al.* 2015). Previous studies support the idea that the patch size effect is more relevant than other factors (such as isolation) for species with a restricted dispersal capacity (Uezu and Metzger 2011). This seems to happen when the distance among patches is greater than the species' dispersal ability. As a result, the population becomes completely (or largely) isolated and depends exclusively on the intrinsic characteristics of the patch (e.g. patch size; Uezu and Metzger 2011).

One of the major consequences of patch size reduction is the increase in the patch edge-area ratio. Therefore, the edge effect could also explain

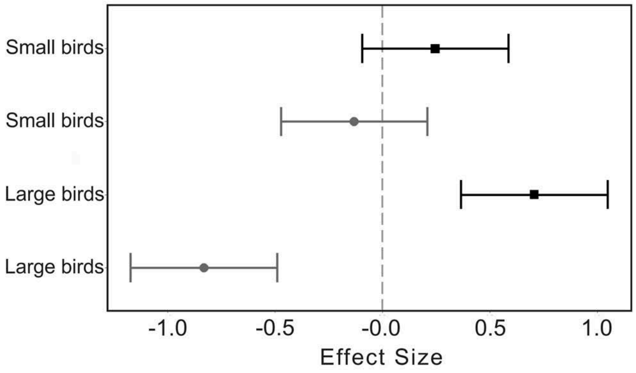

Figure 3. Effect size of patch size (black bar) and patch isolation (grey bar) on relative abundance of the three small species and the three large species. Positive values show a positive relationship between patch size and the relative abundance of each group species and a positive relationship between isolation and the relative abundance of each group species. Negative values show negative relationships between patch size and isolation and relative abundance. The vertical dashed line shows when the effect is equal to zero.

the negative impact of patch size reductions on the relative abundances of *T. amaurochalinus* and *S. aurantiirostris*, and the absence of *T. major* in two small patches. Several biotic and abiotic conditions dramatically change in (and near) forest edges (Ewers and Banks-Leite 2013). An increase in nest predation and parasitism at the forest edge relative to the forest interior has been reported elsewhere (Paton 1994; Manolis *et al.* 2002) but also for species in the Chaco forest of Córdoba (Dardanelli 2006).

A bird study based on presence–absence data on a gradient of fragmentation in the semi-arid Chaco forests of Córdoba conducted 10 years ago showed that *T. amaurochalinus, T. major*, and *S. aurantiirostris* can be found in small forest fragments and consequently these species were categorised as tolerant to forest fragmentation (Dardanelli *et al.* 2006). When considering relative abundances in a gradient of forest patches, we found here that these species are negatively related to forest fragmentation. The disparity in the conclusions for these species could be related to methodological differences between studies. Moreover, temporal differences in data collection may indicate population decline of these species since deforestation is an ongoing process in the study region (Hoyos *et al.* 2013; Cáceres 2015) and the negative effects of the fragmentation process on bird populations can be increasing. A time lag in the responses of the bird species to forest fragmentation could explain different trends during the process of land-use changes (Uezu and Metzger 2016).

Small forest patches are crucial

Even though small forest patches (less than 2 ha; see Table 1; Figure S1) in the Chaco region support low relative abundances of some species (and in certain cases lack some species), they seem to maintain species of a variety of feeding guilds (Dardanelli *et al.* 2006; our data). Therefore, these forest patches could be important elements in bird metapopulation persistence at the landscape level (see Radford and Bennett 2004) and help to maintain ecological processes (i.e. pollination, seed dispersal; Díaz Vélez *et al.* 2015). Moreover, due to the high forest loss in the Chaco subtropical forest and the current high rates of deforestation in central Argentina (Cáceres 2015), each forest patch represents a critical and unique possibility to maintain viable bird populations (Turner and Corlett 1996; Dardanelli *et al.* 2006; our data).

Our results provide evidence of the complexity of the responses of different bird species to forest fragmentation, showing that they are differentially correlated to patch isolation or patch size (see Watson *et al.* 2005; Didham *et al.* 2012). Studies that simultaneously consider several bird species and include data collected across landscapes are crucial for a better understanding of the forest fragmentation effects on bird populations.

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