

Avian responses to forest fragmentation during the breeding and non-breeding seasons

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Forest fragmentation represents a threat to several bird species worldwide. Several factors can change across seasons (e.g. bird perception of the landscape, weather conditions, biotic interactions), which can modify the response of bird populations to forest fragmentation. However, most studies have been conducted only during the breeding season. Here we assessed the relationship between forest fragmentation (patch area and patch isolation) with population abundances of resident species during both the breeding and the non-breeding seasons. Bird population abundances (all species in the community, subsets of forest and habitat generalist species and for individual species) were estimated across a gradient of area-isolation in a semi-arid forest in Córdoba, Argentina. Population abundance of the overall avian community and of the subset of forest species declined with patch area reduction independently of the season. By contrast, the subset of habitat generalist species was not affected by patch area reduction or by the increase in patch isolation, either during the breeding or during the non-breeding season. When the analyses were carried out for individual species, we found four forest species and one habitat generalist species whose responses (the relationship between population abundance and patch area or with isolation) were different between breeding and non-breeding seasons. The negative effects of forest fragmentation were found mainly during the breeding season. Our results suggest that reduction of patch area may lead to a reduction of more than 65% of the population abundance of forest bird species, during both the breeding and the non-breeding season. Therefore, there is an urgent need to conserve large forest patches within the region as irreplaceable elements for the conservation of populations of several species.

Keywords: generalist, habitat, isolation, patch area, seasonal effects, specialist.

Birds are one of the most frequently studied groups in the context of forest fragmentation (Turner 1996, Bennett *et al.* 2006, Fardila *et al.* 2017). However, bird responses to forest fragmentation have been examined mostly during the breeding season (spring–summer), disregarding other periods

of the year (Nour *et al.* 1999, Murgui 2007, Caprio *et al.* 2009, Fraixedas *et al.* 2015). Consequently, our understanding of forest fragmentation effects on bird populations is partial and mainly restricted to the reproductive period (Nour *et al.* 1999). Several processes that affect bird populations may change seasonally, including food availability, predation risks, habitat use, movement patterns and territoriality, so bird population responses to forest fragmentation may vary accordingly (Keller & Yahner 2007, Lenz *et al.* 2015). For example, edge effects on nest predation and brood parasitism risk are restricted to the breeding season. Similarly,

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during the breeding season, birds tend to be restricted to local ecological conditions or within territories, whereas during the non-breeding season, many bird species show less territorial defence (Nour *et al.* 1999) and may have increased home-range sizes (Wiktander *et al.* 2001, Lenz *et al.* 2015). Therefore, during the non-breeding season, isolated or small forest patches not suitable for reproduction are more likely to be visited and used (Nour *et al.* 1999, Murgui 2007). On the other hand, because small forest patches have limited capacity to buffer abiotic conditions (Murgui 2007), the effects of patch area reduction on bird populations could be more evident during the winter, when weather conditions are more severe than during the breeding season in temperate and subtropical regions (Nour *et al.* 1999, Murgui 2007). Consequently, it is important to compare fragmentation patterns for birds in both breeding and non-breeding seasons better to understand forest fragmentation effects on bird populations (Nour *et al.* 1999, Murgui 2007).

Previous studies have not shown clear patterns in bird population responses to forest fragmentation across different seasons (Nour *et al.* 1999, Caprio *et al.* 2009, Naoe *et al.* 2011, 2012). Some authors have reported negative responses of birds to forest fragmentation only during the breeding season (i.e. a decrease of bird abundance in fragmented forests relative to a continuous forest reserve, Naoe *et al.* 2011, and a greater occurrence and persistence in continuous forest than in forest patches, Lenz *et al.* 2015). On the other hand, Caprio *et al.* (2009) found that bird abundance was influenced by forest fragmentation, considering a combination of several landscape-level predictors of forest fragmentation, but only during the non-breeding season. Other authors have detected consistent trends across seasons (i.e. a decrease of bird richness and occurrence in association with an increase in the degree of forest fragmentation, Nour *et al.* 1999, or a decrease of species richness with a reduction of patch area, Murgui 2007, Yamaura *et al.* 2009). However, Morgado *et al.* (2010) observed avian population declines in relation to habitat fragmentation (i.e. habitat amount and patch area) that were more pronounced during the non-breeding period. This variety of responses observed in different periods of the year highlights the need to study patterns of population change in the forest fragmentation context during both the breeding and the non-breeding seasons to

formulate a more complete assessment of the effect of forest fragmentation on bird populations (Siffczyk *et al.* 2003, Robb *et al.* 2008). To assess possible variations of avian responses to forest fragmentation across seasons, it is necessary to study resident species in the same sites but during different times of the year.

In addition to seasonal changes in bird responses to forest fragmentation, specific life history traits may also affect changes in population abundances in relation to forest fragmentation (Henle *et al.* 2004, Dardanelli *et al.* 2006, Bregman *et al.* 2014, Morante-Filho *et al.* 2015). In this sense, forest specialists in general are more prone to decline as a response to habitat fragmentation (because their needs are restricted to forest habitats) than habitat generalist species, which are able to use open areas, degraded or treeless areas, and are less sensitive or even favoured by forest fragmentation (Asefa *et al.* 2017).

Forests of the Chaquean dominium in South America, in which the phytogeographical regions of the Chaco forest and the Espinal are included (Lewis *et al.* 2009), are one of the most endangered worldwide as a result of forest clearance and fragmentation, mostly due to agricultural expansion (Hansen *et al.* 2013, Schmidt 2015). Both phytogeographical regions are characterized by woodland and grassland vegetation distributed as a mosaic across the landscape (Bucher 1982, Cabido *et al.* 2018). Woody vegetation in the Chaco forest is dominated by *Schinopsis* spp. and *Aspidosperma quebracho-blanco*, whereas the Espinal is dominated by species of *Prosopis* (Bucher 1982, Cabido *et al.* 2018). In the most austral distribution of these forests (located in Cordoba province), land conversion has been so high that more than 1 000 000 ha of seasonal, semi-arid forest has been lost between 1970 and 2000, a loss of 85% of the original Chaco forest in the province (Zak *et al.* 2004, Hoyos *et al.* 2013). Despite this scale of forest loss and fragmentation, forest remnants still host a great diversity of birds (Dardanelli *et al.* 2006, Giraudo *et al.* 2006, Salvador *et al.* 2016, Table S1). Small forest patches (approximately 1 ha) can host most of the bird species found in larger patches (approximately 300 ha), suggesting that such a community is resilient to forest fragmentation (Dardanelli *et al.* 2006). However, a recent study showed that common bird species were considerably less abundant in smaller and more isolated patches (Verga *et al.* 2017).

We tested the hypothesis that forest fragmentation (measured as patch area reduction and increase of patch isolation) will be negatively related to population abundance of bird species but that this effect will vary between breeding and non-breeding seasons. However, because previously reported trends of avian populations in response to forest fragmentation in different seasons are unclear, we were unable to make specific predictions. Recognizing this uncertainty, we describe changes in population abundances of different assemblages (the overall avian community, subsets of forest species and of habitat generalist species) and of individual species separately, to assess bird population changes in relation to forest fragmentation during both the breeding and the non-breeding seasons.

METHODS

Study area

The study area is included in the Chaquean dominium (Lewis *et al.* 2009), particularly in an ecotone between semi-arid Chaco Forest and Espinal, Córdoba, Argentina. The climate is seasonal, with precipitation concentrated in the warm season (50–200 mm monthly) and scarce during the winter (0–70 mm monthly). The mean temperature is approximately 23 °C in summer and 11 °C in winter (Gavier & Bucher 2004). The study area has been transformed into an agricultural ecosystem. Currently, natural vegetation is restricted to forest patches of different size and degree of isolation immersed in an agricultural matrix (Fig. S1): mainly soybean *Glycine max* and maize *Zea mays*

in the summer and wheat *Triticum aestivum* during the winter (Grilli & Galetto 2009). Forest patches have been isolated for at least 40 years (González *et al.* 2018). During the winter, some fields have only the stubble of the summer cultures. Dominant trees species within the forest patches are *Prosopis nigra*, *Prosopis alba*, *Celtis ehrenbergiana*, *Geoffroea decorticans*, *Senegalia praecox* and *Aspidosperma quebracho-blanco*. In addition, some exotic tree species such as *Ulmus* spp., *Melia azedarach*, *Broussonetia papyrifera*, *Gleditsia triacanthos*, *Morus* spp. and *Ligustrum lucidum* are common. The most common native shrub species are *Vachellia caven*, *Schinus fasciculatus*, *Jodina rhombifolia*, *Porlieria microphylla* and *Condalia microphylla* (Ferrerías *et al.* 2008, Ferrerías & Galetto 2010, Grilli *et al.* 2014). The sites selected for study shared a similar vegetation structure to minimize possible effects of vegetation heterogeneity on the response variables. In other words, all the forest patches have a complex structure, with arboreal, shrubby and herbaceous strata (Grilli *et al.* 2013, Díaz Vélez *et al.* 2015). Moreover, forest patches are not managed for timber production or other purposes.

We selected forest patches representing a combined gradient of patch area (from 0.4 to 830 ha) and isolation (from 20 to 1700 m). Specifically, the areas of the forest patches were 0.4, 0.5, 0.7, 1.4, 1.6, 1.8, 11.5, 13.6, 16.5, 16.8, 18.0, 18.9, 495 and 830 ha in size. We estimated patch isolation as the average distance between a patch and the three closest woodland patches of any size (Radford & Bennett 2004). We conducted avian surveys in a total of 14 forest patches. Seven forest patches were located within the Estancia Santo Domingo (31.18°S, 64.26°W) and seven were located within

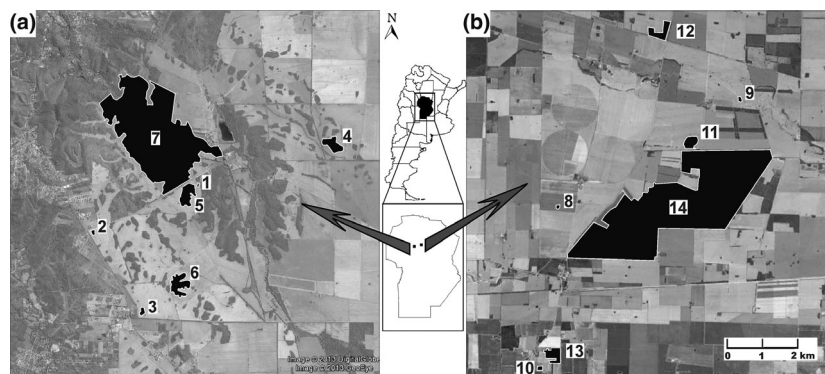


Figure 1. Location of the study area in Córdoba province (shaded in black), Argentina. The black rectangles within the map show the location of the two regions: (a) Santo Domingo, and (b) Comuna Tinoco. The forest patches sampled are indicated in black.

the Comuna Tinoco (31.10°S, 63.87°W) (Fig. 1). Both regions are in the centre of Cordoba Province, 40 km apart (Verga *et al.* 2017).

Bird surveys

We conducted surveys during two consecutive breeding seasons (from December 2011 to early April 2012, and December 2012 to early April 2013) and two non-breeding seasons (from July to early September during the winters of 2012 and 2013). We estimated abundance of bird species by means of fixed-radius point counts, conducted between 06:00 and 10:00 h and between 17:00 and 20:00 h. We recorded the presence and abundance of all birds seen or heard at each point within a 50-m radius, during a period of 10 min. We did not include birds flying over the area. We conducted 20 point counts per patch during the summer (12 point counts in 2011–2012 and eight in 2012–2013) and 16 point counts per patch during the winter (eight per season during 2012 and 2013). We randomly selected the location of each point using ARCGIS 9.3 software (ESRI 2009) and then accessed the point in the field with a Global Positioning System. Overall, we conducted 504 counts throughout the study.

Data analysis

To compare changes in bird abundances in response to forest fragmentation between seasons, we selected bird species based on two criteria: first, from the overall number of species registered during the surveys (total species registered = 83, see Table S1 for details), we selected those species that are resident in the area (Dardanelli *et al.* 2006, Salvador *et al.* 2016). In addition, we selected only those species that were recorded in at least three of the 14 forest fragments (in both seasons), in order to allow statistical comparisons in the species-by-species analysis (see below). After applying these two criteria, 28 species were included in the analysis, which we now refer to as the overall species complement of the avian community. Of those 28 species, 12 were considered habitat generalists (species that occur both in woodlands and in open areas) and 16 were considered forest species (Dardanelli *et al.* 2006, Salvador *et al.* 2016, Table 1). We refer to forest species as those that occur mainly in the forest but are not necessarily restricted to it, because they

Table 1. Model selection process based on AIC criterion. Final models are indicated in bold (the one with the lowest AIC value).

Species	Model	AIC
Species groups		
Overall species	Model 1	135.9
	Model 2	134.1
	Model 3	140.9
Forest species	Model 1	83.7
	Model 2	83
	Model 3	90.7
Habitat generalist species	Model 1	124.8
	Model 2	123.9
	Model 3	127.7
Forest species		
<i>Crypturellus tataupa</i>	Model 1	−23.6
	Model 2	−24.2
	Model 3	−5.7
<i>Leptotila verreauxi</i>	Model 1	11.9
	Model 2	11
	Model 3	11.5
<i>Colaptes melanochloros</i>	Model 1	−55.4
	Model 2	−57.7
	Model 3	−55.9
<i>Thamnophilus caerulescens</i>	Model 1	−8
	Model 2	−10.2
	Model 3	1.3
<i>Taraba major</i>	Model 1	−10
	Model 2	−6.8
	Model 3	−11.6
<i>Pseudoseisura lophotes</i>	Model 1	−14.4
	Model 2	−17.6
	Model 3	−11.5
<i>Stigmatura budytoides</i>	Model 1	−23.4
	Model 2	−23.9
	Model 3	−20.8
<i>Serpophaga subcristata</i>	Model 1	−25.2
	Model 2	−21.8
	Model 3	−16.7
<i>Phytotoma rutila</i>	Model 1	16
	Model 2	14
	Model 3	12.7
<i>Cyclarhis gujanensis</i>	Model 1	−8.8
	Model 2	−11.6
	Model 3	0.8
<i>Polioptila dumicola</i>	Model 1	5.5
	Model 2	2.9
	Model 3	1.8
<i>Sicalis flaveola</i>	Model 1	25.6
	Model 2	25.4
	Model 3	22
<i>Coryphospingus cucullatus</i>	Model 1	−1.9
	Model 2	−4.6
	Model 3	−3.1
<i>Poospiza nigrorufa</i>	Model 1	−62.3
	Model 2	−63.2
	Model 3	−64.2

(continued)

Table 1. (continued)

Species	Model	AIC
<i>Thraupis bonariensis</i>	Model 1	15.1
	Model 2	12
	Model 3	11.4
<i>Saltator aurantirostris</i>	Model 1	20.5
	Model 2	20.2
	Model 3	24.7
Habitat generalist species		
<i>Patagioenas maculosa</i>	Model 1	45.2
	Model 2	43.4
	Model 3	50.9
<i>Patagioenas picazuro</i>	Model 1	13.1
	Model 2	9.2
	Model 3	14.5
<i>Zenaida auriculata</i>	Model 1	33.8
	Model 2	33.1
	Model 3	33.8
<i>Columbina picui</i>	Model 1	39.6
	Model 2	37.5
	Model 3	36.3
<i>Myiopsitta monachus</i>	Model 1	41.6
	Model 2	38
	Model 3	42.1
<i>Furnarius rufus</i>	Model 1	-15.1
	Model 2	-16.8
	Model 3	-14.9
<i>Pitangus sulphuratus</i>	Model 1	9.4
	Model 2	8.2
	Model 3	9.2
<i>Troglodytes aedon</i>	Model 1	4.2
	Model 2	3.9
	Model 3	5
<i>Zonotrichia capensis</i>	Model 1	16.2
	Model 2	12.9
	Model 3	12.5
<i>Agelaioides badius</i>	Model 1	31.9
	Model 2	29.4
	Model 3	28
<i>Molothrus bonariensis</i>	Model 1	14
	Model 2	14.6
	Model 3	16.1
<i>Molothrus rufoaxillaris</i>	Model 1	20.9
	Model 2	17
	Model 3	17.1

Some final models for particular species (i.e. *Crypturellus tataupa*, *Poospiza nigrorufa*, *Serpophaga subcristata* and *Troglodytes aedon*) were selected based on the model assumptions, because, although there was another model with lower AIC value, it did not comply with model assumptions.

are also able to use other elements of the landscape but at a lower frequency (Yzurieta 1995, Salvador *et al.* 2016).

We calculated a single measure of per-patch abundance for (1) all birds, (2) all forest specialist and generalist birds separately, and (3) each

species independently, by dividing the total count in each patch by the number of point counts undertaken ($n = 20$ for the breeding season, and $n = 16$ for the non-breeding season). We collapsed all the data of abundance into a single value (i.e. mean abundance) because point counts within each forest patch were not independent (to avoid pseudoreplication). In summary, we worked with a mean per-patch abundance corresponding to data collected across two breeding seasons, and with a mean per-patch abundance calculated from data collected across the two non-breeding seasons.

To test the relationship between forest fragmentation and bird abundance (for all birds, for forest specialists and habitat generalists, and for individual species), and to examine whether these relationships were different between seasons, we used linear mixed models. Because we conducted surveys in the same 14 forest patches during both the breeding and the non-breeding seasons, we included in the model the identity of such forest patches as a random effect (Zuur *et al.* 2009). That is, the use of a random effect in a mixed model allowed us to specify that data collected during the breeding season in a forest patch are not independent of data collected during the non-breeding season in the same forest patch. To minimize the unexplained error in the models, we considered the regions (with two levels: Santo Domingo and Tinoco) as a fixed, categorical effect (block). This term was considered an additive factor in the models because explanatory data analyses suggested no interaction between region and fragmentation parameters. Because point counts within a forest patch were summarized in a single value (mean abundance), the response variable became a continuous variable. Therefore, models were run with a Gaussian distribution of the errors. To meet model assumptions, we log-transformed (\log_{10}) abundances of the three groups of species (i.e. overall species, forest species, and habitat generalist species). In the species-by-species analyses, we transformed (\log_{10} or square root) the population abundances for some species to meet assumptions. In summary, for the three groups of species and for each bird species individually, we tested three models:

Model 1: abundance \sim patch area + patch isolation + patch area * season + patch isolation * season

Model 2: abundance ~ patch area + patch area * season

Model 3: abundance ~ patch isolation + patch isolation * season

In all models, the relationship between the response variable (abundance) and the different explanatory variables is symbolized by ~, * symbolizes an interaction term and + indicates an additive effect.

In model 1, we tested the main effect of patch area (covariate: area in ha), patch isolation (covariate: distance in m) and the interaction between both factors with the season (categorical effect). In model 2, we tested only the main effect of patch area and its interaction with the season. In model 3, we tested only the main effect of isolation and its interaction with the season.

For each group of species and for each bird species we selected the model with the lowest Akaike information criterion (AIC) value (Table 1). However, for four species (see Table 1 for details), the model with the lowest AIC value did not meet model assumptions (i.e. normality or homogeneity). In such cases, we compared the three models (1, 2 and 3) and selected the model which best matched the model assumptions, which is also a valid selection criterion (Zuur *et al.* 2009). That is, if the inclusion of some omitted variable improves the model assumption (i.e. normality, homogeneity or independence distribution of residuals), we included the variable in the final model (Zuur *et al.* 2009). Table 1 shows the AIC value for each of the three models per bird species, and we have marked in bold which of the three models were selected as the final one. We checked for spatial autocorrelation in the residuals of the models. For that, we followed Zuur *et al.* (2009). The models for the three groups of species and for 26 of 28 studied species did not show spatial autocorrelation. However, the models for two species, Blue-and-yellow Tanager *Thraupis bonariensis* and Saffron Finch *Sicalis flaveola*, did show spatial autocorrelation. Therefore, we included the autocorrelation structure in the models for those species (Zuur *et al.* 2009). We used the free software R (R Core Team 2016 version 3.2.5) for data analysis, using the nlme package (Pinheiro *et al.* 2015) to run the mixed models and the MuMIn package (Bartoń 2016) to obtain the AIC values.

Based on the species-by-species analysis, for those species which showed an interaction between forest fragmentation and season, we

constructed a scatter plot showing the relationship between its abundance and forest fragmentation (patch area or isolation) during both the breeding season and the non-breeding season, to visualize how this relationship changed across seasons.

The avian taxonomy follows Gill and Donsker (2019).

RESULTS

We registered 4205 individuals of the 28 selected species. We found effects of forest fragmentation for two groups of species (overall species and forest species; Table 2, Fig. 2). Patch area was the only explanatory variable selected in the best models for all three groups of species (overall species, forest species and habitat generalist species), whereas patch isolation was not selected in any case. Patch area was positively related to total population abundance over all species, independently of the season (Table 2, Fig. 2). Similarly, patch area was positively related to population abundance of forest species in both seasons. However, the interaction term between patch area and season was marginally significant ($P = 0.058$; Table 2). Patch area was not significantly related to population abundance of habitat generalist species in any of the seasons (Table 2, Fig. 2).

When we considered responses of individual species to forest fragmentation, we found idiosyncratic patterns. The population abundances of some forest species, such as Green-barred Woodpecker *Colaptes melanochloros*, Variable Antshrike *Thamnophilus caerulescens*, Brown Cacholote *Pseudoseisura lophotes*, Greater Wagtail-Tyrant *Stigmatura budytoides* and Rufous-browed Peppershrike *Cyclarhis gujanensis*, were positively related to patch area, independently of the season (Table 2). Similarly, the relationship between forest patch area and population abundance of other forest species, such as Tataupa Tinamou *Crypturellus tataupa* and Golden-billed Saltator *Salta-tor aurantirostris*, was positive, yet stronger during the breeding than during the non-breeding season (Table 2, Fig. 3). On the other hand, the relationship between patch isolation and population abundance for Great Antshrike *Taraba major* was negative and stronger during the breeding than during the non-breeding season (Table 2, Fig. 3). Finally, the relationship between patch isolation and population abundance for Saffron Finch *Sicalis flaveola* was positive, yet stronger during the non-breeding season (Table 2, Fig. 3).

Table 2. Relationship between the explanatory variables selected in the best model and population abundance for overall species, and the subsets of forest species and habitat generalist species, and for each individual species.

Species	Estimates	se	t-value	P-value
Species groups				
Overall species				
Patch area (log)	1.844	0.663	2.781	0.017
Season × Patch area (log)	0.703	0.674	1.043	0.317
Forest species				
Patch area (log)	1.003	0.267	3.744	0.003
Season × Patch area (log)	0.558	0.266	2.092	0.058
Habitat generalist species				
Patch area (log)	0.84	0.532	1.58	0.142
Season × Patch area (log)	0.145	0.619	0.235	0.818
Forest species				
<i>Crypturellus tataupa</i>				
Patch area (log)	0.084	0.047	1.79	0.103
Patch isolation (log)	0.096	0.093	1.033	0.325
Season × Patch area (log)	0.154	0.061	2.504	0.029
Season × Patch isolation (log)	0.048	0.108	0.442	0.666
<i>Leptotila verreauxi</i>				
Patch area (log)	0.159	0.074	2.136	0.055
Season × Patch area (log)	0.069	0.072	0.949	0.361
<i>Colaptes melanochloros</i>				
Patch area (log)	0.059	0.0201	2.937	0.013
Season × Patch area (log)	−0.035	0.028	−1.26	0.231
<i>Thamnophilus caerulescens</i>				
Patch area (log)	0.245	0.047	5.167	0.0003
Season × Patch area (log)	−0.057	0.061	−0.944	0.363
<i>Taraba major</i>				
Patch isolation (log)	−0.141	0.091	−1.548	0.149
Season × Patch isolation (log)	−0.237	0.103	−2.281	0.041
<i>Pseudoseisura lophotes</i>				
Patch area (log)	0.137	0.041	3.307	0.007
Season × Patch area (log)	0.008	0.053	0.161	0.874
<i>Stigmatura budytoides</i>				
Patch area (log)	0.106	0.036	2.882	0.014
Season × Patch area (log)	−0.07	0.052	−1.346	0.202
<i>Serpophaga subcristata</i>				
Season × Patch area (log)	−0.031	0.081	−0.383	0.709
Season × Patch isolation (log)	0.056	0.104	0.537	0.601
<i>Phytotoma rutila</i>				
Patch isolation (log)	−0.214	0.137	−1.554	0.148
Season × Patch isolation (log)	0.034	0.176	0.195	0.847
<i>Cyclarhis gujanensis</i>				
Patch area (log)	0.104	0.045	2.287	0.043
Season × Patch area (log)	0.123	0.064	1.908	0.08
<i>Poliophtila dumicola</i>				
Patch isolation (log)	−0.194	0.113	−1.709	0.115
Season × Patch isolation (log)	0.060	0.145	0.415	0.685
<i>Sicalis flaveola</i>				
Patch isolation (log)	0.463	0.092	4.994	< 0.001
Season × Patch isolation (log)	−0.412	0.130	−3.151	0.004
<i>Coryphospingus cucullatus</i>				
Patch area (log)	0.058	0.053	1.101	0.294
Season × Patch area (log)	−0.061	0.063	−0.958	0.356
<i>Poospiza nigrorufa</i>				
Patch area (log)	−0.008	0.018	−0.485	0.636
Season × Patch area (log)	0.004	0.024	0.177	0.861

(continued)

Table 2. (continued)

Species	Estimates	se	t-value	P-value
<i>Thraupis bonariensis</i>				
Patch isolation (log)	-0.152	0.139	-1.091	0.286
Season × Patch isolation (log)	0.040	0.184	0.220	0.827
<i>Saltator aurantirostris</i>				
Patch area (log)	0.146	0.09	1.62	0.133
Season × Patch area (log)	0.267	0.082	3.254	0.006
Habitat generalist species				
<i>Patagioenas maculosa</i>				
Patch area (log)	0.445	0.133	3.346	0.006
Season × Patch area (log)	-0.114	0.129	-0.883	0.394
<i>Patagioenas picazuro</i>				
Patch area (log)	0.186	0.07	2.637	0.023
Season × Patch area (log)	-0.134	0.073	-1.82	0.093
<i>Zenaida auriculata</i>				
Patch area (log)	0.026	0.115	0.229	0.822
Season × Patch area (log)	0.106	0.100	1.061	0.309
<i>Columbina picui</i>				
Patch isolation (log)	-0.153	0.212	-0.721	0.485
Season × Patch isolation (log)	-0.028	0.257	-0.109	0.914
<i>Myiopsitta monachus</i>				
Patch area (log)	0.148	0.112	1.321	0.213
Season × Patch area (log)	0.083	0.145	0.57	0.578
<i>Furnarius rufus</i>				
Patch area (log)	-0.011	0.044	-0.256	0.802
Season × Patch area (log)	0.094	0.046	2.038	0.064
<i>Pitangus sulphuratus</i>				
Patch area (log)	-0.04	0.069	-0.58	0.573
Season × Patch area (log)	0.106	0.072	1.479	0.164
<i>Troglodytes aedon</i>				
Patch area (log)	-0.154	0.078	-1.981	0.075
Patch isolation (log)	-0.238	0.153	-1.55	0.152
Season × Patch area (log)	0.128	0.101	1.264	0.232
Season × Patch isolation (log)	0.263	0.179	1.472	0.168
<i>Zonotrichia capensis</i>				
Patch isolation (log)	-0.192	0.152	-1.266	0.236
Season × Patch isolation (log)	0.121	0.137	0.888	0.392
<i>Agelaioides badius</i>				
Patch isolation (log)	0.241	0.181	1.333	0.209
Season × Patch isolation (log)	-0.164	0.232	-0.709	0.491
<i>Molothrus bonariensis</i>				
Patch area (log)	0.119	0.092	1.288	0.226
Patch isolation (log)	0.194	0.183	1.063	0.312
Season × Patch area (log)	-0.271	0.121	-2.237	0.046
Season × Patch isolation (log)	-0.409	0.213	-1.92	0.081
<i>Molothrus rufoaxillaris</i>				
Patch area (log)	0.021	0.082	0.262	0.797
Season × Patch area (log)	-0.05	0.081	-0.615	0.549

P-values in bold indicate a statistically significant relationship. 'Estimates' indicate the slope of the relationship between the explanatory variable and the response variable. The estimates of the interaction term indicate how much stronger (if the value was positive) or weaker (if the value was negative) is this relationship during the breeding season relative to the non-breeding season. Therefore, a significant relationship between patch area or isolation and season means that the relationship between forest fragmentation (patch area or isolation) and population abundance is different between the seasons.

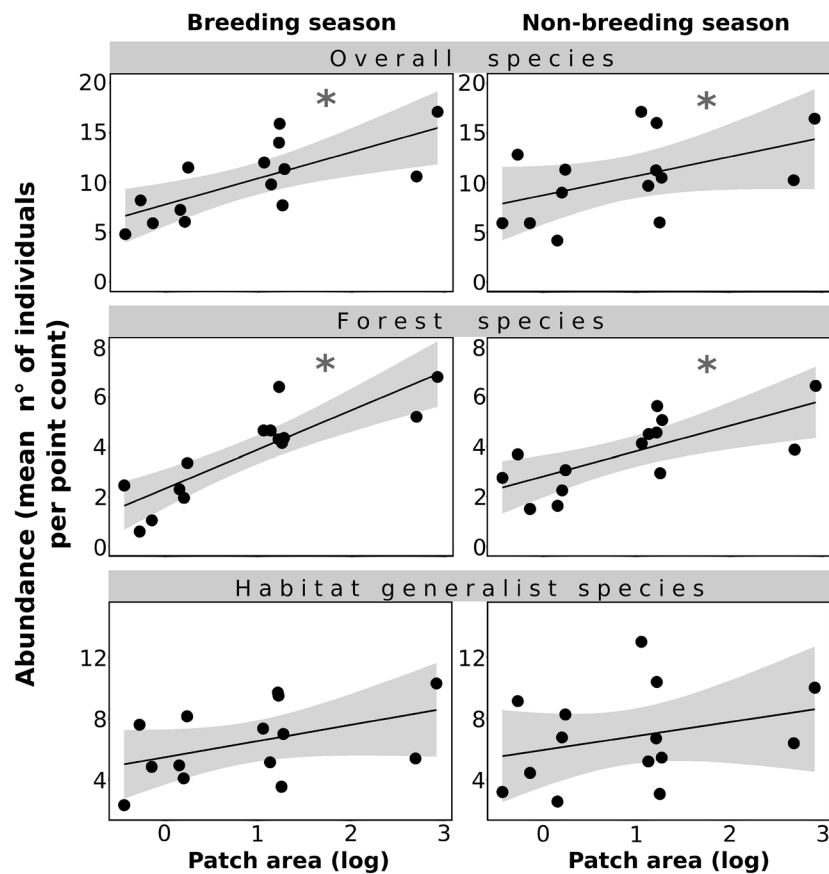


Figure 2. Relationship between forest patch area and population abundance of three groups of bird species (overall species, forest species and habitat generalist species), both during the breeding season (three plots located on the left hand side of the figure) and during the non-breeding season (three plots located on the right hand side of the figure). An asterisk indicates a statistically significant relationship ($P < 0.05$; see Table 2). Confidence intervals of 95% are shaded in grey.

The species-by-species analysis for habitat generalists showed that the population abundances of Spot-winged Pigeon *Patagioenas maculosa* and Picazuro Pigeon *Patagioenas picazuro* were positively related to patch area, independently of the season (Table 2). On the other hand, the relationship between patch area and population abundance for Shiny Cowbird *Molothrus bonariensis* was different across seasons: a negative relationship was observed only during the breeding season. That is, the species was more abundant in smaller patches than in larger patches during the breeding season (Table 2, Fig. 3).

DISCUSSION

Most bird species in this study are relatively common, both locally and regionally (Yzurieta 1995, Salvador *et al.* 2016). However, summed

abundance over all species was negatively related to patch area during both the breeding and the non-breeding seasons. It is important to highlight negative responses of common bird species to forest fragmentation because several studies in conservation biology generally focus on rare or threatened species, disregarding common ones (Gaston 2008, Gaston & Fuller 2008). Moreover, it is important to point out that the size of the smallest patches in this study closely represents the mean area of forest patches in the northwest (7.3 ha) and northeast of Cordoba province (1.5 ha; Hoyos *et al.* 2013). Therefore, the decrease in population abundance in relation to forest fragmentation observed locally for common bird species in the study area may be evidence of a generalized situation that the avifauna faces across the Chaco region.

At the broadest level of analysis (considering the overall species studied in the community),

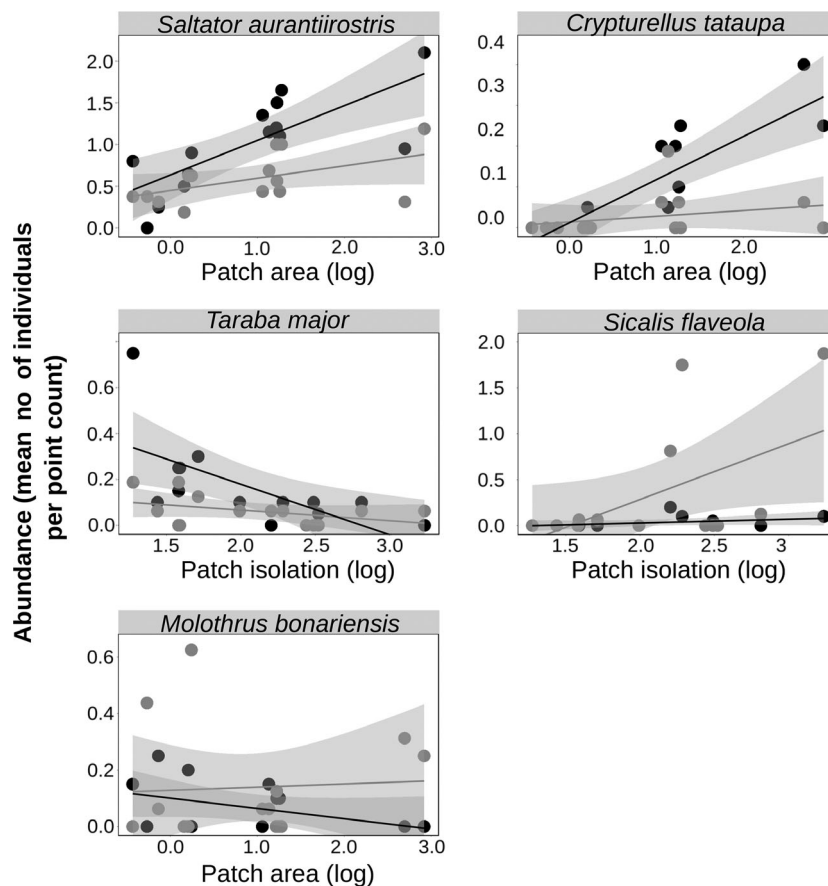


Figure 3. Relationship between forest fragmentation (patch area or patch isolation) and population abundance for those species which showed a differential response across seasons. Black dots and lines represent abundances during the breeding season, and grey dots and lines represent abundances during the non-breeding season. Confidence intervals of 95% are shaded in grey.

forest fragmentation seems to affect bird populations independently of season. Several studies suggest that patch area reduction is one of the main factors explaining population declines in the context of forest fragmentation (Watson *et al.* 2004, Bregman *et al.* 2014, Modest *et al.* 2016). Patch area reduction can lead to food shortage, which in turn can negatively affect bird population abundances (Zanette *et al.* 2000, but see Verga *et al.* 2017). Moreover, the reduction of patch area is correlated with an increase of the patch edge–area ratio. Many environmental conditions change near the forest edges, such as temperature, moisture, vegetation structure and biotic interaction (Ewers & Banks-Leite 2013), and these can negatively affect bird populations (Banks-Leite *et al.* 2010).

At a lower level of analysis, the fact that we found different responses of bird populations to forest fragmentation depending on them being

forest or habitat generalist species was as expected (Morante-Filho *et al.* 2015, Asefa *et al.* 2017). Habitat generalist species appear to be resilient to forest fragmentation, possibly because they are able to use different elements of the landscape, such as open areas, isolated trees or even the agriculture matrix. However, it was less expected that only some forest species would respond differently to forest fragmentation between seasons. Species that showed a different response to forest fragmentation seem to be more sensitive during the breeding season (Golden-billed Saltator, Great Antshrike, Tataupa Tinamou and Saffron Finch). This pattern could be explained by different factors. For example, the increase of the spatial range of daily movements during the non-breeding season (Wiktander *et al.* 2001, Lenz *et al.* 2015) implies that the probability of individual occurrences in an isolated or small forest patch would

be greater during that season than during the breeding season. Hence, during the non-breeding season, it is expected that the effect of patch area reduction or patch isolation on bird population would be weaker than in the breeding season (Evans *et al.* 2013, Lenz *et al.* 2015).

The seasonal changes in the matrix used by some species may also be important in understanding seasonal differences in bird responses to forest fragmentation. During the winter there are some agricultural fields without crop production, so the matrix is composed of stubble fields. This type of matrix can offer food resources, such as seeds and invertebrate fauna, which are consumed by granivorous–insectivorous bird species (Moorcroft *et al.* 2002, Whittingham *et al.* 2006). Therefore, there are species that use stubble fields as an alternative foraging area during the non-breeding season (Moorcroft *et al.* 2002). For example, Golden-billed Saltator (whose response to forest fragmentation was weaker during the non-breeding season), forages on stubble fields near forest patches at this time of year (E. G. Verga pers. obs.). This expansion of the foraging habitat during the winter could ameliorate the negative effects of patch area reduction or isolation, relative to the summer when birds spend most of their time within forest patches.

Shiny Cowbird was another species for which we found a different response to forest fragmentation between seasons. The species showed greater abundance in smaller forest patches, yet this pattern was observed only during the breeding season (see Table 2 and Fig. 3 for details). Shiny Cowbird is a generalist brood parasite which lays eggs in the nests of at least 232 different avian species (Reborada *et al.* 2003). Our results suggest that the incidence of brood parasitism may be greater in small forest patches, where this species is more abundant (Dardanelli *et al.* 2006). Furthermore, our results provide additional support for the hypothesis that a key mechanism to explain bird population decline in fragmented forests is brood parasitism (Paton 1994, Robinson *et al.* 1995, Stratford & Robinson 2005).

Interestingly, there were no bird species or groups of species studied here that only showed a negative population response to forest fragmentation during the non-breeding season. However, in this study, we have considered only a local scale (patch level). Therefore, we do not know whether bird responses are weaker during the non-breeding

season or whether birds may be responding at a larger spatial scale that we did not consider. As birds tend to increase the distances travelled and the size of their home-range during the winter (Wiktander *et al.* 2001, Lenz *et al.* 2015), the spatial scale of response to forest fragmentation may also change throughout the year. Future studies could assess the scale of effect, that is, the spatial extent at which landscape structure has the highest correlation with the response variable (e.g. population abundance; for details of the study design see Jackson & Fahrig 2015), and could assess whether this scale of effect is greater during the non-breeding season.

CONCLUSIONS AND CONSERVATION REMARKS

Chaco forest is one of the regions most threatened by agricultural expansion worldwide (Hansen *et al.* 2013, Schmidt 2015) and its rate of forest clearance shows an increasing trend in the last 30 years (Vallejos *et al.* 2015). In this context of accelerated habitat loss, all forest patches, including the smallest ones, are of conservation value. However, considering that overall bird abundance is lower in smaller patches during both the breeding and the non-breeding seasons, major conservation efforts should be focused on the largest forest patches. Moreover, larger forest patches harbour three times greater population abundances of forest species compared with smaller ones (see Fig. 2 for details). Because mean patch area in the study region is relatively small (between 1.5 and 7 ha; Hoyos *et al.* 2013), there is an urgent necessity to conserve the remnant large patches of native forest in the area. However, we should not discount the conservation value of smaller patches as, at least during the non-breeding season, such patches may also be important elements to maintain the population of some bird species in fragmented landscapes. Additionally, restoration efforts with native vegetation should be carried out to increase the mean size of forest patches.

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Data availability statement

The data that support the findings of this study are available from the corresponding author (E.G.V) upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Landscape of the study area, where forest patches of different size are immersed in an agricultural matrix.

Table S1. Total avian species registered in the study area, during both the breeding and the non-breeding seasons, within the 14 studied patches.