

# Bird responses to forest loss are influenced by habitat specialization

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## Abstract

**Aim:** Due to intrinsic differences in the sensitivity to habitat grain among species, studies performed at different extent are necessary to understand the consequences of forest loss and fragmentation. Using a large database, we explored the responses of birds to changes in forest cover and the role of habitat specialization in the strength of this response.

**Location:** Southern Atlantic forest of Argentina, Brazil and Paraguay.

**Methods:** We used data on bird occurrences recorded in 1,384 point counts (2004–2011), estimated forest cover and number of forest fragments in two radii (60 and 960 m), centred at each point count. For each bird species, we extracted the geographical and altitudinal range as two indirect measures of habitat specialization. We used general linear model and Akaike information criterion to explore the influence of the type of habitat, the amount of habitat and fragmentation pattern on the probability of species occurrence and the influence of habitat specialization on the strength of response.

**Results:** Of the 28 species analysed, 15 (55%) responded either to forest loss or the number of fragments, either positively or negatively. In these 15 species, the probability of occurrence of 67% was better explained by a specific extent (either 60 or 960 m). The strength of the response to forest loss decreased with both the geographical and the altitudinal range of species.

**Main conclusions:** Our study shows that a large proportion of species responded to forest loss at a specific extent and that the magnitude of the response is related to species specialization. A single-extent approach to multispecies studies may not be enough to preserve the whole community due to differences in sensitivity to habitat grain. Maintaining forest cover at multiple extents and managing anthropogenic habitats to increase their suitability for native species are essential to preserve communities in highly fragmented landscapes such as the Atlantic forest.

## KEYWORDS

Atlantic forest, birds, extent, forest loss, grain, habitat cover, habitat specialization

## 1 | INTRODUCTION

Loss of natural habitats due to human activities is considered the primary factor of species extinctions world-wide (Pimm et al., 2014). Species extinction, or decline, and habitat loss are mainly a consequence of four non-exclusive mechanisms (Banks Leite et al., 2010;

Estavillo et al., 2013; Fahrig, 2002; Lundberg & Moberg, 2003): (1) declines in the patch size of suitable habitats below the minimum area requirements of species; (2) reduction of the functional connectivity among remaining patches; (3) patches become dominated by edge effects, with a decrease in habitat quality; and (4) changes in the nature and extent of biotic interactions.

The type (positive or negative), magnitude and grain (defined as a function of how animals exploit resource patchiness in environments, sensu MacArthur & Levins, 1964) of response to forest loss strongly differ among species within the same assemblage (Henle et al., 2014); changes in habitat cover may lead species to either decrease, increase or maintain their local abundance (Betts et al., 2014; Devictor et al., 2008; Julliard et al., 2006). Among species affected (either negatively or positively) by changes in habitat cover, the magnitude of change creates a gradient of response, from species exhibiting small changes in abundance to species exhibiting large changes, which presumably reflects intrinsic differences in the ecological requirements or ecological niche of species (Reif et al., 2015). The characteristics and breadth of the ecological niche of each species will influence the species capacity to exploit different types of habitats (degraded native habitats or new habitats created by human activities) and, consequently, the type and magnitude of their response to forest loss. Species requiring specific resources from undisturbed natural habitats will often be negatively affected, while species with broader requirements should be able to tolerate changes and might even increase in abundance (Cerezo et al., 2010; Devictor et al., 2010; Reif et al., 2015). Moreover, niche breadth is a key component explaining the geographical range of species; a reduced niche breadth is typical of species with restricted geographical distribution while a broad niche breadth is typical of species inhabiting different ecosystems and large geographical ranges (Brown, 1984; Slatyer, Hirst, & Sexton, 2013).

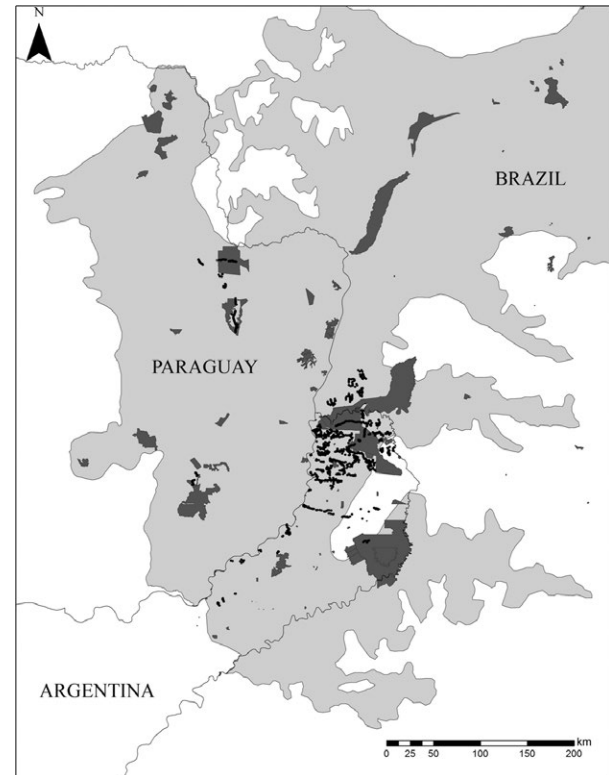
The sensitivity to habitat grain is also highly variable among species (Betts et al., 2014). The individual responses determine the minimum area requirements of species (Pe'er et al., 2014a) and, when summed up across species, are expected to shape species assemblages and communities (among other factors shaping community composition). As a consequence, different species will respond to habitat disturbance at different extent and such extent should be consistent with the species ecological requirements.

In this study, we addressed the question of how habitat specialization (estimated through the geographical and altitudinal range of species) operates in shaping species responses to forest loss. We also aimed to determine how these responses vary with the spatial extent of habitat cover. To explore the qualitative and quantitative components and the extent of species response to forest loss, we used a large database of presence/absence of birds collected in the southern Atlantic forest of Argentina, Brazil and Paraguay (one of the most threatened ecosystems in the world (Butchart et al., 2010)) over 10 years. Studies dealing with patterns and processes of species response are highly necessary to improve ecosystem management and species conservation.

## 2 | METHODS

### 2.1 | Study area and sampling design

We gathered our data in surveys conducted in extensive areas in the southern semi-deciduous Atlantic forest of Argentina, Brazil and Paraguay (Figure 1). This area includes large remnants of native forest of



**FIGURE 1** Study area in the southern Atlantic forest of Argentina, Brazil and Paraguay. Large native forest remnants are depicted in dark grey; sampled areas (bird point counts) are marked in black

more than 100 km<sup>2</sup> (mainly in protected areas of Argentina and Paraguay) and a wide range of forest fragments of different size (between 0.1 and 1,000 ha), shape and degree of isolation (57–1,401 m, with a median of 85.5 m; Zurita & Bellocq, 2010). Native forest covered 40% of the study areas (Zurita & Bellocq, 2010). A detailed description of the landscape structure and configuration can be found in Zurita and Bellocq (2010). In addition to the native forest, predominant land uses include commercial tree plantations for wood and pulp production (mainly Pine), agriculture (annual crops such as tobacco and corn), open pastures for cattle and Yerba mate (*Ilex paraguariensis* A. St.-Hil.) plantations, with 19.2%, 10.6%, 10.8% and 4.9% of the productive area, respectively. The number of point counts per habitat reflects, approximately, the relative cover of each habitat at the landscape scale (native forest and land uses) (Zurita & Bellocq, 2010).

Within the study area, we established 1,384 point counts between 2004 and 2011 (each point count was visited once). In each year, point counts were separated by at least 500 m and, at each point, we sampled birds within a 50 m fixed radius. We considered all visual and audio records within the sampling radius (Colin, 2000). Observations were performed between sunrise and 10:00 a.m. during the breeding season (September–January). To reduce the probability of double counting (recording the same individual more than once on the same point count), we only considered the presence/absence per point count. As point counts were randomly performed in the study area among years, we expected that other factors (weather conditions, etc.) would represent a random bias on the dataset. The same

trained observer (G.Z.) performed all point counts, minimizing the biases associated with observer differences in species identification. In case of unclear identification, a directional microphone was used to record singing birds and later compared the recording with the public xeno-canto database ([www.xeno-canto.org](http://www.xeno-canto.org)). We followed the BIRDLIFE CHECKLIST V7.0 for species nomenclature (BirdLife 2015).

## 2.2 | Data analysis

Thematic maps were used for our analysis based on earlier mapping performed with Landsat 5 TM Images (Zurita & Bellocq, 2010). Each Landsat image corresponded to the same year as the field survey was conducted, to increase the consistency between field data and satellite images. Around each point count sampled, we delineated two circular areas (radius of analysis) to explore the response of species to forest cover at different extent: 60 and 960 m. To reduce the dependence between both radii, we calculated a ring instead of a circular area for the 960 m radius (60–960 m) (Wiegand & Moloney, 2004). The selected radii were consistent with the territory size of the species included in the analysis (Hansbauer et al., 2008) and, consequently, with the species sensitivity to habitat grain. Within each radius or ring around a point, we calculated the proportional native forest cover (native forest area/total area) and the number of forest fragments. Point counts included the full range of forest covers (0%–100%) in all radii, with 48.6% of the points occurring in native forests, 33.5% in tree plantations, 7.1% in cattle pastures, 7.3% in annual crops and 3.5% in Yerba mate plantations. All analyses were performed in R (R Core Team 2014).

### 2.2.1 | Forest cover and radii of analysis

To explore the influence of the extent of analysis (60 radius and 960 ring) on forest cover, we performed a nonparametric Friedman analysis using the radius as the independent variable and forest cover as the dependent variable.

### 2.2.2 | Species response to forest loss

For each of the species sampled, we extracted the geographical range size and the altitudinal range (max–min altitude) (BirdLife International 2016). Both variables were considered an indirect measure of niche breadth or species specialization (Brown, 1984; Slatyer et al., 2013). To explore factors affecting the probability of species occurrence (at the 60 radius and the 960 ring), we performed a binomial regression analysis (general linear models—GLM) with presence/absence (1 and 0) of species on bird point counts as the dependent variable and the proportional forest cover, the number of forest fragments and the type of habitat at the point count as independent variables. We defined type of habitat as a categorical variable with three categories: (1) native forest points, (2) open-habitat points (cattle pastures, annual crops and recent plantations) and (3) intermediate and mature tree plantation points (non-native forest). Habitat categories were defined based on a previous study identifying the suitability of the different types of land uses in the study area (Zurita & Bellocq, 2012).

Only species recorded in at least 5% of sampling points (more than 69% of records) were considered in the analysis. Due to the large number of statistical regressions, we applied a conservative Holm–Bonferroni correction with an alpha significance level of 0.05. For each species showing a corrected significant association between the probability of occurrence and forest cover or the number of fragments, we selected the main radius or ring of response by calculating the Akaike information criterion for each model and comparing the Akaike weight between models (probability of a better model) (Appendix S1); we only considered a better fit when the Akaike weight between models was higher than 0.9 (more than 90% of probability).

We extracted the slope of the binomial regression, that is, the rate of change in the probability of species occurrence, as a quantitative measure of the species response to forest loss and hereafter referred to as the strength of response.

### 2.2.3 | Factors explaining birds' response to forest loss

To explore the influence of habitat specialization or niche breadth (geographical and altitudinal range) to the quantitative response to forest loss (strength of response), we performed a GLM analysis using the geographical and altitudinal range as explanatory variables and the strength of response to forest loss as dependent variables.

## 3 | RESULTS

### 3.1 | Forest cover and radii of analysis

Changing the extent of analysis (60 m radius and 960 m ring) affected the estimated forest cover per sampling point (Kruskal–Wallis = 1,383,  $p < .01$ ). The same subset of points, on average, increased from a median cover of 29.1% at 60 m to 37.6% when a 960-m ring was used.

### 3.2 | Species response to forest loss

On the 1,384 bird point counts conducted, we obtained 6,903 records of 229 different species (Appendix S1). We recorded 66.8% individuals in native forests, 22.1% in tree plantations, 6.8% in cattle pastures, 2.6% in annual crops and 1.7% in Yerba mate plantations. A total of 28 species had at least 70 (more than 5%) records in the 1,384-point database and were consequently included in our statistical analyses (Appendix S2). The binomial GLM analysis indicated that the probability of occurrence of all species (28) showed a significant association with explanatory variables. After the Horn–Bonferroni correction for multiple comparisons, 27 of the 28 species remained significant (Appendix S2). Among these 27 species, the type of habitat (native forest, non-native forest and open habitats) at the sampling point was the primary factor affecting the probability of occurrence (all 27 species were associated with this explanatory variable), whereas forest cover and the number of forest fragments influenced the probability of occurrence of 15 species (Appendix S2). Of the 15 species showing a significant response to forest cover or the number of fragments,

**TABLE 1** Species response to forest cover in the southern Atlantic forest of Argentina, Brazil and Paraguay

Species	Akaike weight	Best radius/Ring	Geographical range (km <sup>2</sup> )	Altitudinal range (m)
<i>Ammodramus humeralis</i>	1.00	960	8,730,000	1,100
<i>Cyanocorax chrysops</i>	0.98	960	2,830,000	2,800
<i>Dysithamnus mentalis</i>	0.70	60–960	4,410,000	1,900
<i>Hypoedaleus guttatus</i>	0.98	960	1,210,000	900
<i>Leptotila verreauxi</i>	1.00	960	15,500,000	2,800
<i>Mackenziaena severa</i>	0.98	60	955,000	1,400
<i>Megarynchus pitangua</i>	0.73	60–960	13,200,000	1,900
<i>Pitangus sulphuratus</i>	0.99	60	16,100,000	1,600
<i>Sittasomus griseicapillus</i>	0.86	60–960	12,000,000	2,000
<i>Synallaxis ruficapilla</i>	1.00	60	1,180,000	1,400
<i>Poecilotriccus plumbeiceps</i>	0.77	60–960	1,470,000	2,000
<i>Troglodytes aedon</i>	0.76	60–960	21,500,000	4,000
<i>Turdus rufiventris</i>	0.94	960	5,030,000	2,200
<i>Vireo olivaceus</i>	0.95	960	11,600,000	1,500
<i>Zonotrichia capensis</i>	0.99	60	12,700,000	3,500

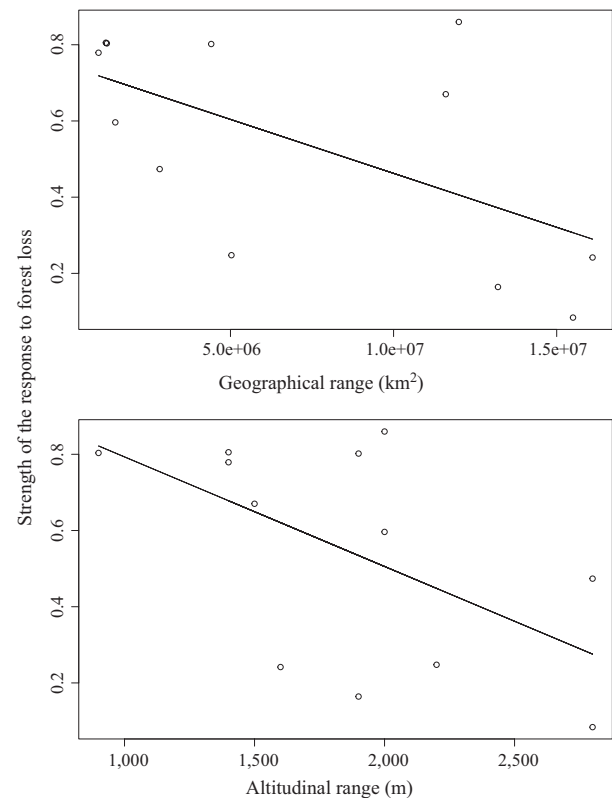
five showed a similar fit to both distances (60–960 m) (Akaike weight < 0.9), six species fitted better to the 960-m ring and four fitted better to the 60 m radius (Table 1).

### 3.3 | Factors explaining birds' response to forest loss

Of the 15 species showing a significant association with forest cover or the number of fragments, 12 were forest species (Table 1) and were included in the analysis to relate the strength of the response to forest loss (i.e., the slope of the binomial regression for each species) to species specialization (geographical and altitudinal range) (Figure 2). The strength of response to forest loss showed a linear decrease with the geographical and altitudinal range of species ( $t = 2.3$  and  $t = 2.2$ ,  $p < .05$  in both cases) (Figure 2). In other words, the strength of the response to forest loss increased with species specialization (smaller geographical and altitudinal range).

## 4 | DISCUSSION

Our study offers a link between species specialization, sensitivity to habitat grain and strength of response to forest loss—a link which should be anticipated based on theoretical studies but with little empirical evidence. Our analyses were performed using individual observation sites, and at a scale that should be relevant for the response of animals to the surrounding landscape (i.e., the area of the individual's home range). Hence, this scale is very relevant to predict the impacts of habitat loss on species persistence (Betts et al., 2014). In the present study, most species were sensitive to changes in habitat cover to a specific extent. Therefore, we believe that multi-extent studies are necessary to understand the response of complete species assemblages to the alteration of native habitats by humans, and offer mitigation strategies that suit the needs of entire communities. A single-extent



**FIGURE 2** The strength of response to increases in forest loss declines with the geographical (upper figure) and altitudinal range (lower figure) of species in the southern Atlantic forest of Argentina, Brazil and Paraguay

approach will probably either over- or underestimate the response of species to changes in habitat cover and fragmentation pattern.

Analyses of point-pattern data on tropical and subtropical ecosystems often ignore small-scale habitat structures in favour of

landscape-scale analyses, primarily due to logistic limitations such as sample size. However, here we showed that the response of several species to forest loss and fragmentation was best explained by landscape structure at the smallest scales. Using small-scale analyses would better match both the small scale of human production in rural areas, and the actual grain of the species' sensitivity to the habitat (Cattarino et al., 2014). Also, it is possible that previous studies in the Atlantic rain forest have not considered the impact of forest loss at individual scale (Boscolo & Metzger, 2009; Pardini et al., 2010; Uezu et al., 2005; Zurita & Bellocq, 2010).

The geographical range has been proposed as a proxy of the ecological niche breadth and reflects the capacity of species to exploit new resources (Brown, 1984; Devictor et al., 2010; Reif et al., 2015; Slatyer et al., 2013; Vázquez & Simberloff, 2002). Species that are able to exploit a broad range of resources colonize and exploit anthropogenic habitats, whereas species depending on resources that are exclusive to native forests are more sensitive to forest loss. This is true for bird communities in the Atlantic forest of Brazil (Morante-Filho et al., 2015) and was confirmed in this study. The configuration and quality of the remaining native habitats in the landscape, as well as the management strategies of anthropogenic habitats for conservation purposes, become critical, especially in landscape structures close to the proposed thresholds for species extinction (15%–30% forest cover) (Fahrig, 2002; Pardini et al., 2010; Zurita & Bellocq, 2010). Mobile species could extend their territory to reach other habitat patches or include suitable anthropogenic habitats, partially compensating for the loss of forest (Hansbauer et al., 2008). The replacement of forest specialists that decline with forest loss by open-habitat species is considered as the simplest explanation for the changes observed in patterns of species richness and composition across landscapes with differing levels of forest loss (Estavillo et al., 2013; Pardini et al., 2010; Zurita & Bellocq, 2010).

Our results offer insights to understand species responses to forest loss from the finer scales of landscape configuration. Conservation planning requires better understanding of the spatial characteristics of species' decline and replacement, and forest conservation strategies must use the right approach to mitigate impacts of forest loss and fragmentation. Considering that species show a specific sensitivity to habitat grain, it is evident that the extent to which forest is lost matters. The fact that several species show a response to forest loss at a small extent (60 m) indicates that fine-grain structures may determine the behaviour and viability of several forest species. Such findings are critical in the light of the strong pressures to decrease corridor widths, as recently performed with the update of the Forest Code in Brazil (reducing legal demand for riparian vegetation to merely 15 m (Arima et al., 2014)). Our results confirm the concern that, at such narrow widths, most forest species will be lost. Conservation of native forest at small scales should be combined with landscape and regional conservation of native forest over thresholds of species extinction to maintain viable populations.

The Atlantic forest is one of the most diverse and threatened ecosystems in the world (Butchart et al., 2010). The landscape has been proposed as the most appropriate spatial scale for conservation management to preserve native biodiversity (Teixeira et al., 2009),

as endorsed by larger-scale agreements such as the Convention for Biodiversity ("ecosystem approach"). Our results indicate, however, that conservation strategies ignoring fine-scale protection will most likely fail to safeguard most bird species (see also Banks Leite et al., 2010). Native forest protection and restoration should therefore be consistent with both the scale of land use and the target species, and landscape planning needs to focus on the conservation of entire communities in terms of both habitat requirements and connectivity (Pe'er et al., 2014a).

This study demonstrates the need to predict and mitigate the impact of forest loss across spatial scales in the long term, with special emphasis on the fine scales to which individual animals respond. Addressing the needs of species and communities requires a more profound understanding of the species' ecological requirements, their behaviour in different types of habitats and the physiological constraints to their responses. Detailed studies at the individual level, including movement patterns (telemetry), nesting and feeding behaviour, as well as biotic and abiotic interactions in heterogeneous landscapes, can shed further light on species' needs and improve our capacity to devise effective conservation strategies across species and landscapes.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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