



Conserving nest trees used by cavity-nesting birds from endangered primary Atlantic forest to open farmland: Increased relevance of excavated cavities in large dead trees on farms



Eugenia Bianca Bonaparte^{a,b,*}, José Tomás Ibarra^{c,d}, Kristina L. Cockle^{a,b,e}

^a Instituto de Biología Subtropical, CONICET- Universidad Nacional de Misiones, Bertoni 85 Puerto Iguazú, Misiones 3370, Argentina

^b Proyecto Selva de Pino Paraná, Vélaz Sarsfield & San Jurjo S/N, San Pedro, Misiones 3352, Argentina

^c ECOS (Ecology-Complexity-Society) Laboratory, Centre for Local Development (CEDEL), Pontificia Universidad Católica de Chile, Villarica, Chile

^d Millennium Nucleus Centre for the Socioeconomic Impact of Environmental Policies (CESIEP) & Centre of Applied Ecology and Sustainability (CAPES), Pontificia Universidad Católica de Chile, Santiago, Chile

^e Department of Forest and Conservation Sciences, University of British Columbia, 2424 Main Mall, Vancouver, BC V6T 1Z4, Canada

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ABSTRACT

Understanding nest-site selection is critical to conserving tree-cavity-nesting wildlife, but nest-sites may vary across landscapes. We examine variation in the characteristics of trees and cavities used by cavity-nesting birds from globally-threatened primary Atlantic Forest to open farmland with isolated trees. We predicted that nests would occur in the largest trees available, but that secondary cavity nesters (non-excavators) would increase their use of bird-excavated cavities and dead and exotic trees in open farmlands. We used a stratified case-control design and 20 random plots to assess variation in characteristics of trees and cavities (used and available) across gradients of canopy cover and distance to forest edge in subtropical Argentina. For secondary cavity nesters, nest cavities were more likely to occur in larger-diameter trees across all stand conditions, but more likely to occur in dead trees as canopy cover declined (i.e., in open farmland; $n = 123$ nest trees). For primary excavators, nest cavities were more likely to occur in dead (vs. live) trees, with larger diameter, regardless of stand conditions ($n = 54$ nest trees). Available cavities declined from 4/ha in primary forest to 0.4/ha in open farmland. Cavities were increasingly excavated origin in open farmland, including both available cavities and those used by secondary cavity nesters, which indicates that avian excavation may partly compensate for the loss of decay-formed cavities when large trees are cleared. As forest landscapes shift toward a predominance of agroecosystems, dead trees and primary cavity nesters may take on important roles in conserving cavity-nesting communities and their ecosystem functions. However, nest cavities declined in height and depth, and increased in entrance size toward open farmland, raising the possibility that birds increasingly use suboptimal cavities as forest cover declines.

1. Introduction

Nest-site selection theory has a long-standing history in forest ecology and management, and it is helpful for assessing the condition of ecological communities under global and regional changes (e.g. Bergmanis et al., 2019; Newell and Rodewald, 2011). Among the many forest birds that nest in tree cavities globally, about 26% of species can excavate their own cavities (primary excavators), and must select a suitable substrate for excavation; the rest (secondary cavity nesters or non-excavators) select a nest site among existing cavities formed by primary excavators or by tree decay (van der Hoek et al., 2017). Suitable cavities and substrates can limit breeding density (Newton, 1994;

Saunders et al., 2020), and may become increasingly scarce as primary forest landscapes are replaced by logged forest and agroecosystems (Aitken and Martin, 2012; Ibarra and Martin, 2015; Manning and Lindenmayer, 2009; Politi et al., 2010), leading to declines in populations of cavity-nesting birds, many of which have key roles in seed dispersal, local culture, and ecotourism (e.g., toucans, parrots, hornbills, quetzal; Anderson 2017; Bennett et al. 1997; Renton et al. 2015). However, the nest-site requirements of cavity-nesting species, and the processes involved in cavity formation, may vary across habitats, allowing cavity nesters to reproduce even in highly-modified environments (Bonaparte and Cockle, 2017; Manning et al., 2006b; Monterrubio-Rico et al., 2009). As native forest cover declines in many

* Corresponding author at: Instituto de Biología Subtropical, CONICET- Universidad Nacional de Misiones, Bertoni 85 Puerto Iguazú, Misiones 3370, Argentina.
E-mail addresses: ebbonaparte@gmail.com (E.B. Bonaparte), jtbarra@uc.cl (J.T. Ibarra), kristinacockle@gmail.com (K.L. Cockle).

regions, conservation of cavity-nesting communities will increasingly depend on understanding how their ecology varies across such landscapes.

Predominant characteristics of nest cavities vary across regions, and most cavity nesters outside of North America rely primarily on non-excavated (i.e., decay-formed or “natural”) cavities (Cockle et al., 2011a). Nest-cavity characteristics can also vary within regions in response to variation in habitat characteristics (Chen et al., 2011; Cornelius, 2008; Nickley and Bulluck, 2019) and species composition (Lawrence et al., 2017; Schlossberg and King, 2010; Strubbe and Matthysen, 2009). For example, in Chile, secondary cavity-nesting thorn-tailed rayaditos (*Aphrastura spinicauda*) selected the largest trees of one species in primary forests, but showed no such preference in isolated patches (Cornelius, 2008). In Italy, when cavities in native trees became scarce, some cavity-nesting birds shifted to artificial cavities in exotic tree species (Zapponi et al., 2015). Non-excavated cavities require many years of decay in large, old, trees (Gibbons and Lindenmayer, 2002; Zheng et al., 2016), and when such trees are removed from the landscape, secondary cavity nesters might increasingly rely on cavities generated by primary excavators (Cockle et al., 2019; Remm and Löhms, 2011). Many primary excavators can produce a cavity in smaller or exotic trees within a few weeks (De la Peña and Salvador, 2016; Pakkala et al., 2017; van der Hoek and Martin, 2018) and can increase their rates of excavation in response to cavity scarcity (Norris and Martin, 2012; Wiebe, 2016). Thus, flexibility in nest site selection may allow birds to nest in otherwise unsuitable landscapes. However, whereas some forest species can adjust to landscape modifications, others maintain nest-site preferences that may restrict their reproduction to areas that meet certain thresholds of key resources (Berl et al., 2015; Poulin et al., 2008). A major challenge in designing conservation policies for cavity-nesting communities in human-altered landscapes is that for most such communities, it is not known how converting primary forest to logged forest or agriculture will affect nest-site use and selection (van der Hoek et al., 2017).

Understanding cross-landscape variation in nest-site characteristics is critical to maintaining cavity-nesting communities in areas with high levels of deforestation, such as the Atlantic Forest, a humid subtropical forest in southeastern Brazil, northern Argentina and eastern Paraguay. The Atlantic Forest is among the five most diverse and threatened ecosystems in the world (Myers et al., 2000), and by 2009 around 88% of its original cover had disappeared or had suffered deep modifications (Ribeiro et al., 2009). In primary Atlantic Forest of Argentina, 73% of nests of cavity-nesting birds were in living trees; secondary cavity nesters made 94% of their nests in non-excavated cavities, preferring high, deep cavities, in trees with less crown touching other vegetation (Cockle et al., 2011a, 2019). Compared to non-excavated cavities, excavated cavities occurred in trees that were 25% smaller in diameter and had eight times the odds of being dead (Cockle et al., 2012). Other than a few records of native birds using exotic tree species on farms (Bonaparte and Cockle, 2017; Cockle et al., 2012), little is known about how nest-tree and cavity characteristics may vary from primary forest to open farmland.

Here, we examined variation in tree characteristics (tree size, condition [live/dead], % of crown touching other vegetation) and cavity characteristics (cavity origin, height, depth, entrance size) according to stand conditions (% canopy cover and distance to forest edge) that reflected the transition from primary Atlantic Forest to open farmland. First, we used a case-control study to investigate variation in the effect of tree characteristics on nest cavity occurrence along the gradient from primary forest to open farmland. Second, to explore potential mechanisms and implications of these patterns of nest-tree use along the same gradient, we examined variation in the characteristics of used and available cavities. Changes in the trees and cavities used for nesting from primary forest to open farmland can arise because of changes in (1) characteristics of available cavities, (2) nest-site preferences of bird species that are present across all stand conditions, or (3) the pool of bird species (if nest site requirements of new species differ from those of

the species they replaced). Here we examined the overall pattern of tree and cavity use by the cavity-nesting community across stand conditions, and assessed changes in cavity availability as a potential mechanism. We predicted that, (1) across the gradient, nest cavities would consistently be more likely to occur in the largest trees, (2) across the gradient, excavators would consistently prefer dead trees, and (3) toward open farmland, given the likely decline in density of large old trees, available cavities and cavities used by secondary cavity nesters would increasingly be excavated, low in dead trees.

2. Methods

2.1. Study area

Our study area was chosen to encompass approximately 90% of the remaining critically endangered Paraná pine (*Araucaria angustifolia*) mixed Atlantic Forest in Argentina (Kershaw and Wagstaff, 2001; Thomas, 2013), that comprises most of the San Pedro Important Bird Area (San Pedro IBA AR123, Appendix A; Bodrati et al. 2005; Birdlife International 2019). It covered high-elevation terrain within San Pedro department, Misiones province (26°36'S, 54°01'W; 500–700 m a.s.l., 1200–1400 mm annual precipitation). Natural vegetation was mixed forest with laurel (*Nectandra* and *Ocotea* spp.), guatambú (*Balfourendron riedalianum*) and Paraná pine (Cabrera, 1976). The study area included both public and private land, and presented a mosaic of small (mean: 38 ha) family farms with patches and corridors of forest, scattered native trees, and planted native and exotic trees, as well as two provincial parks, with varying histories of selective logging and other uses (Varns, 2012). Seventy-three cavity nesting bird species breed in our study area and 24 of them are endemic to the Atlantic Forest. During the main breeding season (September to December) we searched for bird nests in tree cavities at Cruce Caballero Provincial Park (400 ha primary forest; 200 ha logged forest; 2015–2017); at Araucaria Provincial Park (90 ha logged forest; 2015–2017); and at 24 farms (logged forest and isolated trees; 2015–2018; Appendix A). Farms were selected for a related research project using the snowball method (Newing, 2010), whereby each participant family was asked to refer another farming family who might like to participate in an interview. After each interview, we obtained the farmers' permission to search for nests on their farm during the following breeding seasons.

2.2. Nest searching and habitat measurements

We found nests by observing adult birds, listening for nestlings, inspecting apparent cavities, and re-checking cavities used in previous years. To confirm the presence of eggs or nestlings, we inspected cavities using video camera inspection systems custom-made from parts purchased at 3rd Eye Electronics Co. and transmitting to a DVR (MCV8-LED cameras with lighting reduced, mounted in the end of 1.5-cm diameter, 1–3 m long flexible silicon tubing, and MC901A cameras with two LEDs mounted within 30-cm rigid polycarbonate tubes). Cameras were mounted on a 15- or 22-m telescoping pole, or carried up to the cavity using single-rope climbing. For 21 inaccessible cavities, nests were confirmed by watching the activity of adults (i.e. long periods inside the cavity consistent with incubation bouts, visits to the cavity with food in the beak).

Once the nest fledged or failed (depredated or abandoned by adults), we took measurements of the nest cavity, tree, and stand conditions. At cavity scale, cavity origin was determined as non-excavated (irregular entrance and interior) or excavated (bird observed excavating, wood chips, or regular entrance and interior; Cockle et al., 2011b). We used metric tapes to take cavity depth (distance from the entrance sill to the cavity floor), entrance diameter (the smaller diameter of the entrance opening used by the birds), and cavity height (from the entrance sill to the ground). Cavity measurements were taken by climbing a ladder (up to 9 m) or using single-rope climbing. When neither of these systems was feasible, we measured cavity entrance and height using 1-cm markings placed on the camera and the telescoping

pole, and estimated cavity depth using DVR images, following Bonaparte & Cockle (2017).

At the tree scale, we determined tree species and condition (live or dead), measured diameter at breast height (DBH, using a diameter tape), and estimated the percent of the tree's crown touching other trees or lianas. At the stand scale, we assessed canopy cover around the tree by visually estimating canopy cover in a 30-m radius, then taking the mean of four densiometer measurements (in four cardinal directions, 10 m away from the nest-tree trunk, farther if necessary to exclude the crown of the nest tree itself; Lemmon, 1956). Visually-estimated canopy cover was highly correlated with final densiometer value ($r = 0.86$) and was used only to generate expected densiometer values for 21 cases that lacked densiometer measurements. We regressed densiometer value against visually-estimated cover for the 510 cases with complete data, and used the resulting equation (canopy cover = $16.53 + 0.86 \times$ estimated cover, adjusted $R^2 = 0.74$) to generate expected densiometer values for the 21 missing cases. Final values of canopy cover (used as predictors to model nest cavity occurrence) were densiometer values, either measured (510 cases) or expected (21 cases). We used Google Earth® images to measure the distance from the nest tree to the nearest forest edge (normally seen as a clear-cut line between forest and a new land cover, e.g. open cropland). For nest trees inside the forest, we measured from the nest tree to the edge of the nearest cleared area > 5 ha, and assigned a positive value. For nest trees in open farmland, we measured to the edge of the nearest forest patch > 5 ha and assigned a negative value. We used the closest available images to the nesting attempt, normally within 2 years, and paid special attention to changes in surrounding land use in the years before and after nests were found to ensure we measured a representative value of distance to edge.

We used a stratified case-control sampling design (Keating and Cherry, 2004) to examine tree-level factors influencing nest-cavity occurrence along the gradient from primary forest to open farmland, represented by our two independent stand-level habitat measurements: distance to edge and percent canopy cover. For every nest tree, we measured two control trees in random directions, 20 to 100 m away. Control trees needed to meet the condition of DBH > 20 cm, but did not need to contain a cavity. We took the same tree- and stand-level measurements at control trees as at nest trees.

To study the number and characteristics of available cavities in primary forest, logged forest, and farms, we used data from 20 randomly located plots, 1.44 ± 1.46 ha (mean \pm SD; range: 1.0–7.1 ha) in size (Appendix A; 8 of the forest plots were included in Cockle et al., 2010). Five plots were in primary forest and the remaining 15 were in stands that varied in human impact, including lightly-logged forest, secondary forest, cropland, and cattle paddocks. In 2006–2008, 2011, or 2013, two to four observers searched for potential cavities (entrance \geq 2 cm wide but interior depth unknown). We accessed these potential cavities using a ladder or single-rope tree climbing. We deemed a cavity suitable for nesting (“available cavity”) when its depth was \geq 5 cm (vertically or horizontally). We took the same measurements of these available cavities as for nest cavities. Additionally, we estimated percent canopy cover (for the whole plot and 30 m around each cavity-bearing tree) and measured distance to the nearest forest edge using Google Earth® (see above).

2.3. Statistical analyses

We conducted all analyses using R 3.6.1 (R Core Team, 2019). To examine variation in the factors influencing nest-cavity occurrence across stand conditions, we used the clogit command in the ‘survival’ package (Therneau and Grambsch, 2000) to create two sets of *a priori* conditional logistic regression models for comparison (within each set) using a model selection approach (Appendix B). Conditional logistic regression is an extension of logistic regression used to assess conditional probability of a rare condition (in this case, nest occurrence), stratified by cases. Conditional logistic regression can be interpreted in terms of

odds ratios and is suitable for case-control studies, such as ours, in which the proportion of cases in the sample is determined by the sampling protocol rather than the probability of occurrence in the population (Cameron, 2006; Keating and Cherry, 2004). The response variable for all models was tree status (nest tree vs. control tree). Our first set of models was designed to test for changes, along the gradient in stand conditions, in the effect of tree-level factors on occurrence of nest-cavities used by secondary cavity nesters. In this first set, all models included, as predictor variables, three tree-level measurements (DBH, tree condition, and crown touching), but models varied in their inclusion of interactions between tree- and stand-level variables (distance to edge, canopy cover; Appendix B). We performed correlation tests and no pair of variables included in the models was significantly correlated. Our second set of models, for primary excavators, was limited by a smaller sample size. As we wished to understand the role of primary excavators in production of suitable tree cavities, we limited the predictors in this model set to (1) stand-scale variables (canopy cover and distance to edge), (2) tree-scale variables that showed a significant effect on nest-cavity occurrence for secondary cavity nesters, and (3) their interactions (Appendix B). In conditional logistic regression models, nest trees were considered only once even when they were used in different years and/or by different species. To facilitate interpretation of interaction terms, we standardized continuous predictor variables (DBH, crown touching, distance to edge, and canopy cover), by subtracting the mean and dividing by the standard deviation. We used the ‘MuMin’ package (Barton, 2019) to calculate Akaike’s Information Criterion corrected for small sample sizes (AICc) and Akaike weight (w_i), and used these to rank models within each set. We focused on the model with lowest AICc but also report parameter estimates for other models with $\Delta AICc < 2$. We calculated the area under the curve of the receiver operating characteristic (AUC) for each model using the ‘ROCR’ package (Sing et al., 2005) to evaluate classification performance independent of cutoff values; values of AUC > 0.8 indicate good performance.

To assess variation in number of available cavities from primary forest to open farmland, we employed two generalized linear models (quasi-Poisson family, log link) with the number of cavities in random plots as the response variable, \ln (plot size) as an offset, and canopy cover and distance to edge (from the center of the plot to the nearest forest edge) as independent variables. We calculated the coefficient of determination (R^2_V) for both quasi-Poisson models, using the ‘rsq’ package (Zhang, 2020, 2017).

To evaluate variation across stand conditions in the characteristics of cavities used by birds and all available cavities, we employed a series of generalized linear models in which response variables were cavity characteristics and predictor variables were either distance to edge or canopy cover. First, to examine how the origin (excavated vs. non-excavated) of cavities used by secondary cavity nesters and available cavities in plots varied across stand conditions, we employed generalized linear models (binomial family, logit link) in which the response variable was cavity origin. We calculated AUC using the ‘ROCR’ package (Sing et al., 2005) for model diagnosis. Second, to examine how cavity dimensions varied across stand conditions for (1) cavities used by secondary cavity nesters, (2) cavities used by primary excavators, and (3) available cavities in plots, we used generalized linear models (Gamma family, identity link) with cavity depth, entrance diameter and cavity height as response variables. We used the package DHARMA (Hartig, 2019) for graphical model diagnosis. We plotted original data and predicted values with 95% confidence intervals using the visreg package (Breheny and Burchett, 2017) to visually evaluate how distance to edge and canopy cover influenced origin and dimensions of used and available cavities.

3. Results

Across primary forests, logged forests and open farmlands, we found 212 nests of 44 cavity-nesting bird species (Appendix C),

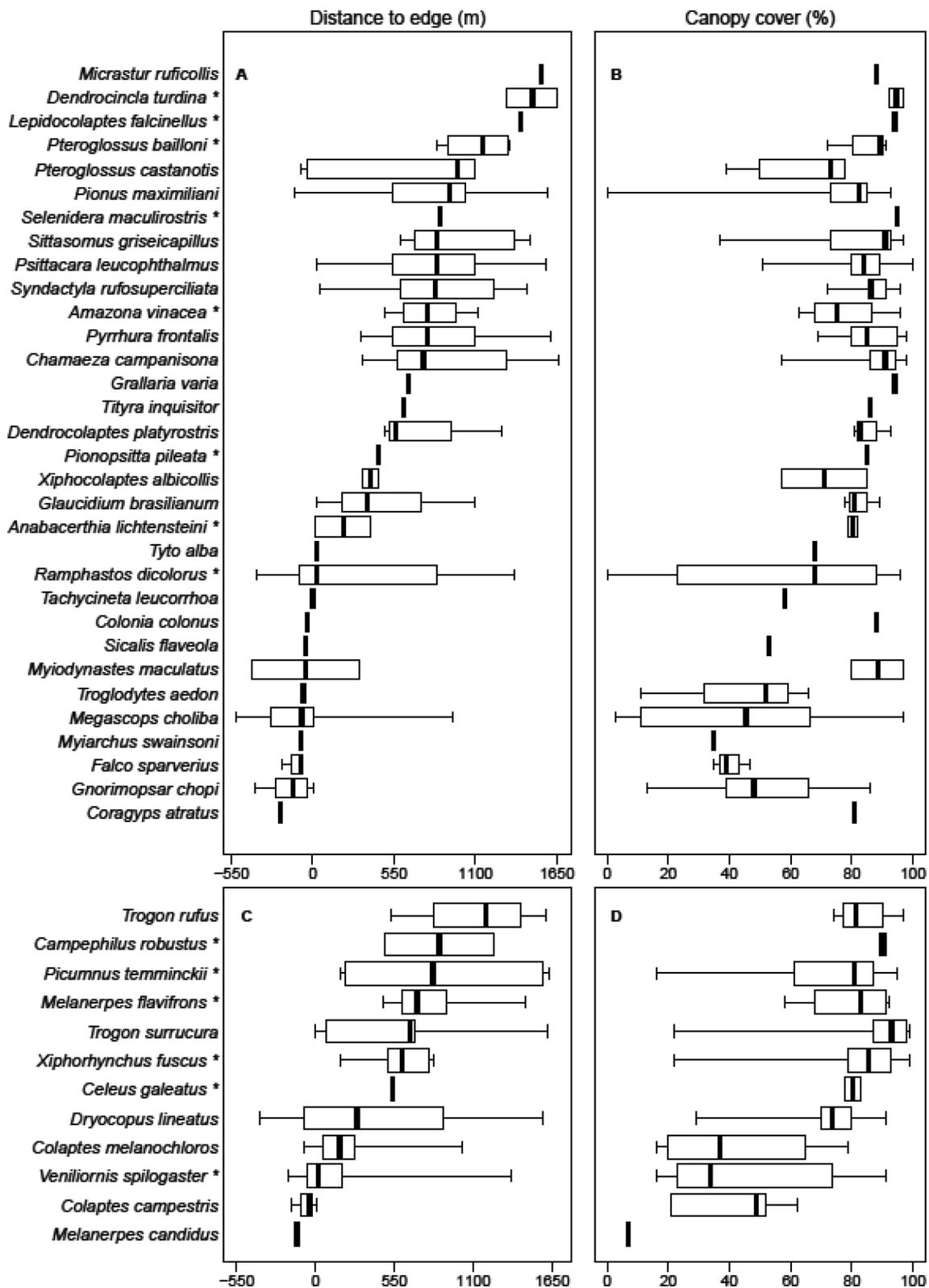


Fig. 1. Distance to edge and canopy cover for all nest trees found of secondary cavity nesters (A, B) and primary excavators (C, D) in the Atlantic Forest of Argentina, 2015 to 2018. Species are ordered according to median distance to forest edge. Positive values of distance to forest edge indicate nest trees inside the forest, negative values indicate isolated nest trees outside the forest. Percent canopy cover was the mean of densiometer measurements, 10 m from the nest tree in the four cardinal directions. Asterisks indicate species endemic to the Atlantic Forest.

ranging from 515 m outside of the forest to 1666 m inside the forest edge and from 0% to 100% canopy cover around the nest tree (Fig. 1). Specifically, we found 123 nest trees used by 32 species of secondary cavity nesters and 54 nest trees used by 12 species of

primary excavators. We found 14 Atlantic Forest endemic species nesting in primary forest, and three of these species (*Ramphastos dicolorus*, *Picumnus temminckii* and *Veniliornis spilogaster*) also nested on farms (Fig. 1).

3.1. Nest cavity occurrence

Nests occurred in (at least) 34 species of native trees and three species of exotic trees (Appendix C). Nests in exotic trees represented 2% of all nests found and 3% of all nest trees used (vs. 4.7% of control trees); all of them in farmlands. We found cavities in 3% of native control trees, but none in exotic control trees. DBH of nest trees was 63.0 ± 29.6 cm (mean \pm SD) in parks ($n = 121$) and 47.7 ± 19.6 cm on farms ($n = 50$); while DBH of control trees was 29.7 ± 5.9 cm for exotic species ($n = 16$, all of them on farms), 44.5 ± 20.6 cm for native species in parks ($n = 242$), and 36.1 ± 15.5 cm for native species on farms ($n = 84$). We found 4.0 ± 1.6 available cavities / ha in primary forest, 1.6 ± 1.2 cavities / ha in logged forest, and 0.4 ± 0.5 cavities / ha in open farmland.

Among models predicting whether trees would harbor a cavity used for nesting by a secondary cavity nester, two models had $\Delta AICc < 2$. The top-ranked model included interactions between tree-level variables and canopy cover, and the second-ranked model included only tree-level variables (no interactions; Table 1). In the top-ranked model for secondary cavity nesters, the odds of nest cavity occurrence increased with increasing DBH and were higher for dead than live trees, but there was an interaction between tree condition and canopy cover whereby occurrence of nests in dead trees was more pronounced in open farmland (stands with lower canopy cover) than in closed forests (Table 2). Percent of crown touching other vegetation had odds ratios whose 95% confidence intervals overlapped 1 in all models for secondary cavity nesters (Table 2), so we did not include this predictor in models for primary excavators.

In the set of models predicting whether trees would harbor a cavity used for nesting by a primary excavator, two models had $\Delta AICc < 2$. The lowest AICc model included canopy cover and its interactions with tree-level variables (DBH and tree condition; Table 1), but all of the interaction terms had odds ratios whose 95% confidence intervals overlapped 1 (Table 2). The second lowest AICc model included only DBH and tree condition. For primary excavators, the odds of nest cavity occurrence increased with DBH and decreased with canopy cover, and were higher for dead than living trees (Table 2).

3.2. Characteristics of nest cavities and cavities available in random plots

The number of available cavities increased by a factor of 1.15 ($e^{0.0014 \times 100}$) for each additional 100 m inside forest edge ($b \pm SE = 0.0014 \pm 0.0004$; $t = 3.48$; $P = 0.003$; $R^2 = 0.51$) and by a factor of 1.32 ($e^{0.028 \times 10}$) for each 10% increase in canopy cover ($b \pm SE = 0.028 \pm 0.007$; $t = 3.89$; $P = 0.001$; $R^2 = 0.62$).

Cavity origin changed with distance to the forest edge and canopy

Table 1

Conditional logistic regression models predicting occurrence of nest cavities used by secondary cavity nesters and primary excavators in the Atlantic Forest of Argentina, and their corresponding number of parameters (k), log-likelihood (logLik), difference in Akaike's Information Criterion (corrected for small sample size; AICc) between the given model and the lowest AICc model ($\Delta AICc$), Akaike weight (w_i) and area under the curve of the receiver operating characteristic (AUC; a measure of model classification performance). For all models, the response variable was use of the tree for nesting (nest vs. control). For secondary cavity nesters, lowest AICc = 201.6; $n = 123$ cases (246 controls). For primary excavators, lowest AICc = 76.12; $n = 54$ cases (108 controls). DBH: diameter at breast height. Tree condition: live or dead. Crown touching: percent of crown touching other trees or lianas. Canopy cover: mean of four densiometer measurements around the tree (percent). Distance to edge: distance from the tree to nearest forest edge (positive values indicate trees inside the forest and negative values indicate trees outside the forest).

Models	k	logLik	$\Delta AICc$	w_i	AUC
<i>Secondary cavity nesters</i>					
DBH, tree condition, crown touching, canopy cover, DBH \times canopy cover, tree condition \times canopy cover, crown touching \times canopy cover	7	-93.31	0.00	0.51	0.84
DBH, tree condition, crown touching	3	-98.13	0.87	0.33	0.82
DBH, tree condition, crown touching, distance to edge, DBH \times distance to edge, tree condition \times distance to edge, crown touching \times distance to edge	7	-94.78	2.93	0.12	0.83
DBH, tree condition, crown touching, canopy cover, distance to edge, DBH \times canopy cover, tree condition \times canopy cover, crown touching \times canopy cover, DBH \times distance to edge, tree condition \times distance to edge, crown touching \times distance to edge	11	-91.34	5.46	0.03	0.84
<i>Primary excavators</i>					
DBH, tree condition, canopy cover, DBH \times canopy cover, tree condition \times canopy cover	5	-32.44	0.00	0.64	0.90
DBH, tree condition	2	-36.70	1.51	0.30	0.87
DBH, tree condition, distance to edge, DBH \times distance to edge, tree condition \times distance to edge	5	-34.90	4.93	0.05	0.88

Table 2

Parameter estimates (b) with standard errors (SE), odds ratios (OR) and their 95% confidence intervals for the top-ranked conditional logistic regression models (lowest AICc) predicting use of trees for nesting by secondary cavity-nesting birds ($n = 123$ cases and 246 controls) and primary excavators ($n = 54$ cases and 108 controls) in the Atlantic Forest of Argentina. Bold indicates predictor variables with odds ratios whose confidence intervals do not overlap 1. Odds ratios > 1 indicate a positive effect of the parameter on nest cavity occurrence, and odds ratios < 1 indicate a negative effect.

Parameter	$b \pm SE$	OR (95% CI)
<i>Secondary cavity nesters</i> ^a		
DBH (cm)	1.022 \pm 0.178	2.78 (1.96–3.94)
Crown touching (%)	-0.229 \pm 0.796	0.80 (0.57–1.10)
Tree condition (live)	-2.173 \pm 0.562	0.11 (0.04–0.34)
Canopy cover (%)	-1.808 \pm 0.837	0.16 (0.03–0.85)
DBH \times canopy cover	-0.165 \pm 0.201	0.85 (0.57–1.26)
Crown touching \times canopy cover	0.108 \pm 0.176	1.11 (0.79–1.57)
Tree condition (live) \times canopy cover	1.840 \pm 0.841	6.30 (1.21–32.71)
<i>Primary excavators</i> ^b		
DBH	1.149 \pm 0.390	3.16 (1.47–6.78)
Tree condition (live)	-4.018 \pm 1.068	0.02 (0.01–0.15)
Canopy cover	-2.947 \pm 1.434	0.05 (0.01–0.87)
DBH \times canopy cover	-0.529 \pm 0.447	0.59 (0.25–1.42)
Tree condition (live) \times canopy cover	2.384 \pm 1.413	10.84 (0.68–172.81)

^a Estimate, SE, P , OR and 95% CI for the second-best model ($\Delta AICc = 0.87$) for secondary cavity nesters: DBH, $b = 0.94$, SE = 0.17, OR = 2.55, 95% CI = 1.85–3.53; Crown touching, $b = -0.21$, SE = 0.15, OR = 0.81, 95%CI = 0.60–1.09; Tree condition (live), $b = -1.75$, SE = 0.42, OR = 0.17, 95% CI = 0.08–0.39.

^b Estimate, SE, OR and 95% CI for the second-best model ($\Delta AICc = 1.51$) for primary excavators: DBH, $b = 0.95$, SE = 0.35, OR = 2.59, 95% CI = 1.31–5.10; Tree condition (live), $b = -2.82$, SE = 0.58, OR = 0.06, 95% CI = 0.02–0.19.

cover, for both (1) cavities used by secondary cavity nesters and (2) available cavities in random plots (Table 3, Fig. 2A, C, Fig. 3A, C). For each 10% increase in canopy cover, the odds of having a non-excavated origin increased by a factor of 2.0 for cavities used by secondary cavity nesters (OR = 1.07), and by a factor of 1.8 for available cavities in random plots (OR = 1.06; Table 3). For each 100-m increase in distance inside the forest edge, the odds of having a non-excavated origin increased by a factor of 1.22 for cavities used by secondary cavity nesters (OR = 1.002), and by a factor of 2.23 for available cavities in random plots (OR = 1.01; Table 3). An excavated origin was assigned to 40.6% of nest cavities used by secondary cavity nesters in open farmland (vs. 7.3% in primary forest), and to 33.3% of available cavities in plots in open farmland (vs. 10% in primary forest).

Table 3

Generalized linear models predicting cavity origin (Binomial family, logit link) and cavity dimensions (height, depth, entrance diameter; Gamma family, identity link) as a function of stand conditions (canopy cover and distance to forest edge) for cavities used by secondary cavity nesters, cavities used by primary excavators, and available cavities, in the Atlantic Forest of Argentina. Distance to edge increases within the forest and decreases outside of the forest. Canopy cover was the mean of four densiometer measurements around the nest tree for cavities used by secondary cavity nesters and primary excavators, and was visually estimated for available cavities in random plots. Bold indicates parameters (*b*) that differ significantly from 0 at $\alpha = 0.05$.

Predictor Variables	Response Variables	Canopy cover (%)				Distance to edge (m)			
		Cavity origin ^b	Cavity height (m)	Cavity depth (m)	Entrance diameter (cm)	Cavity origin ^c	Cavity height (m)	Cavity depth (m)	Entrance diameter (cm)
<i>Secondary cavity nesters</i> (n = 140)	b	0.068	0.100	0.483	0.005	0.002	0.004	0.021	−0.001
	SE	0.013	0.021	0.127	0.017	0.001	0.001	0.005	0.001
	Test statistic ^a	5.28	4.87	3.81	0.27	4.76	4.33	4.21	−2.08
	P	< 0.001	< 0.001	< 0.001	0.791	< 0.001	< 0.001	< 0.001	0.039
<i>Primary excavators</i> (n = 58)	b	−	−0.034	−0.061	0.003	−	−0.001	− 0.008	4.19 e-4
	SE	−	0.024	0.053	0.012	−	0.001	0.002	5.99 e-4
	t	−	−1.44	−1.15	0.26	−	−0.59	− 3.91	−0.70
	P	−	0.154	0.255	0.794	−	0.556	< 0.001	0.487
<i>Cavities available in random plots</i> (n = 48)	b	0.059	0.056	0.575	−0.012	0.008	0.006	−0.033	2.80 e-4
	SE	0.020	0.023	0.447	0.031	0.003	0.002	0.041	0.002
	Test statistic ^a	3.01	2.42	1.29	−0.38	2.43	3.12	−0.81	0.15
	P	0.003	0.020	0.205	0.704	0.015	0.003	0.425	0.880

^a Z for cavity origin models (Binomial family), t for cavity dimensions models (Gamma family). ^b Model AUC for secondary cavity nesters = 0.81; model AUC for cavities in random plots = 0.92. ^c Model AUC for secondary cavity nesters = 0.80; model AUC for cavities in random plots = 0.93.

Cavities used by secondary cavity nesters increased in height and depth, and decreased in entrance diameter, with increasing canopy cover and distance into the forest (Table 3, Fig. 2D, G, J, Fig. 3D, G). On average, nest cavities of secondary cavity nesters measured 13.0 ± 6.6 m in height, 56.1 ± 42.3 cm in depth, and 7.3 ± 4.5 cm in entrance diameter in primary forest, versus 7.8 ± 4.1 m in height, 31.0 ± 13.6 cm in depth, and 8.5 ± 3.4 cm in entrance diameter in open farmland. Cavities used by secondary cavity nesters showed a greater variation in depth (both deep and shallow cavities) in primary forest compared to farms (shallower cavities only; Figs. 2G, 3G). Among cavities occupied by secondary cavity nesters, those with an excavated origin measured 9.6 ± 6.7 m in height, 38.7 ± 36.1 cm in depth, and 8.2 ± 3.2 cm in entrance diameter, versus 12.0 ± 5.9 m in height, 52.1 ± 38.3 cm in depth, and 7.4 ± 4.5 cm in entrance diameter for non-excavated cavities. In contrast, nest cavities used by primary excavators always had an excavated origin (Table 3, Figs. 2B, 3B) and decreased in depth with increasing distance inside the forest edge (27.5 ± 9.8 cm on farms versus 21.9 ± 11.3 cm in primary forests; Table 3, Fig. 2H), while other characteristics did not vary along gradients of canopy cover or distance to edge (Table 3, Figs. 2E, K, Fig. 3E, H, K). Across the gradient from primary forest to farms, available non-excavated cavities were generally deeper and more variable in depth (74.3 ± 129.1 cm, range: 13–799 cm) compared to available excavated cavities (20.6 ± 7.8 cm, range 15–34) and the nest cavities of primary excavators (23.1 ± 11.3 cm, range: 7–45 cm; Figs. 2I–H, 3I–H).

Available cavities in random plots increased in height with increasing distance inside the forest edge and canopy cover (Table 3, Figs. 2F, 3F). Available cavities were 10.6 ± 5.5 m high in primary forest, vs. 6.6 ± 4.3 m high on farms. Cavity depth and diameter did not vary significantly across stand characteristics (Table 3), and deep cavities were scarce, even in primary forest (Figs. 2I, 3I).

4. Discussion

The factors associated with nest-cavity occurrence, as well as the characteristics of used and available cavities, varied along disturbance gradients from globally-threatened primary Atlantic Forest to open farmland, especially for secondary cavity nesters, which implies that findings from forest habitats will not necessarily identify the key components that allow communities to persist in agroecosystems. For

secondary cavity nesters, occurrence of a nest-cavity was associated with the largest trees (> DBH) across all stand conditions, but increasingly associated with dead trees in open farmland, consistent with our prediction that dead trees become more important as sources of nest cavities as forest cover declines. Primary excavators consistently nested in the largest dead trees and in areas with lower canopy cover across all stand conditions. Cavity availability declined from primary forest to open farmland (lower canopy cover and further outside forest edges), in concordance with findings from other regions (e.g. Schaaf et al., 2020; Walankiewicz et al., 2014). Although our previous work identified old living trees with non-excavated cavities as critical for conserving biodiversity of cavity nesters in primary Atlantic Forest (Cockle et al., 2011a, 2011b, 2019), available cavities and those used by secondary cavity nesters were increasingly of excavated origin in open farmland, pointing to an increased role of excavators in producing the few cavities available on farms. Our finding that changes in the characteristics of nest trees and cavities used by secondary cavity nesters generally mirrored the changes in characteristics of available cavities along the gradient from primary forest to open farmland, suggests that variation in the pool of cavities available drives much of the variation in the trees and cavities used for nesting. On farms, this pool of available cavities is largely conditioned by the nest site preferences and cavity characteristics of primary excavators. Exotic trees provided a few nest sites to birds in farmlands; however, the small proportion of nests in exotic trees, and the smaller size of these trees, suggests that they are not currently an important resource for the cavity-nesting community.

Although primary excavators play a minor role as nest cavity producers throughout many old-growth forests of South America (Altamirano et al., 2017; Cockle et al., 2019, 2011a), our study supports the hypothesis that they can become more important in modified landscapes (Kikuchi et al., 2013; Politi et al., 2009; Remm and Löhms, 2011), possibly helping to maintain ecosystem functions of cavity-nesting communities (Ibarra et al., 2017, 2020). Some secondary cavity-nesting species may avoid excavated cavities (Wesołowski, 2007), but we found that use of excavated cavities by secondary cavity nesters was roughly proportional to their availability on farms and in forest, and many species of secondary cavity nesters in our system used both excavated and non-excavated cavities. An increasing reliance on excavated cavities in open farmland (versus non-excavated cavities in primary forest), likely explains, in part, the shifts in cavity and nest-tree characteristics exhibited by secondary cavity

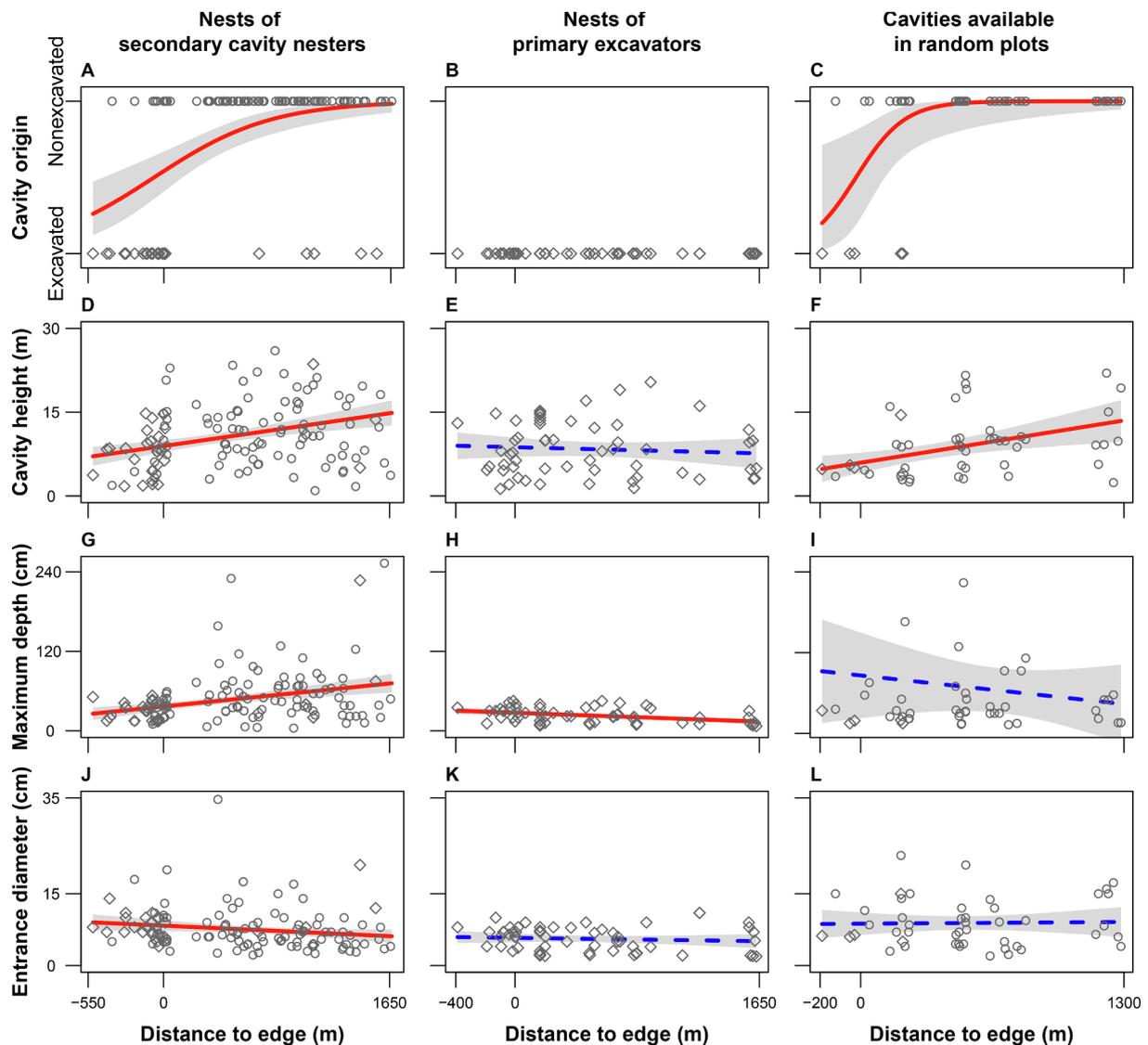


Fig. 2. Variation in origin (excavated, diamonds, vs. non-excavated, circles) and dimensions (height, depth and entrance diameter) of cavities used by secondary cavity nesters ($n = 140$; A, D, G, J), used by primary excavators ($n = 58$; B, E, H, K), and available in random plots ($n = 48$; C, F, I, L), according to distance to the nearest forest edge, in the Atlantic Forest of Argentina. Lines indicate predicted values of Generalized Linear Models and grey shading indicates 95% confidence bands; broken lines indicate non-significant regressions. Positive distances to forest edge indicate nest trees inside the forest and negative values indicate trees outside the forest. An extreme depth value for a cavity in a plot (799 cm deep and 519 m to forest edge) is not shown here but was included in the models.

nesters across stand conditions (e.g., toward shallower cavities and dead trees in farmland).

Tree- and cavity characteristics (not stand-level characteristics) have been reported as the primary determinants of nest survival and cavity persistence in our study area (Cockle et al., 2015, 2017), which suggests that cavity-nesting birds can successfully breed on farms, for multiple years, if they can find an optimal cavity. However, we found that with declining forest cover secondary cavity nesters increasingly used dead trees and lower excavated cavities, with larger entrances, characteristics associated with higher rates of nest failure and cavity loss (Cockle et al., 2015, 2017; Li and Martin, 1991; Wesołowski, 2007), which may indicate an increasing usage of suboptimal, short-term cavities in agroecosystems. Stand-, tree- and cavity-level factors, as well as changes in the predator and cavity-nester communities, may have complex and interacting effects on the fitness trade-offs faced by secondary cavity-nesting birds in modified landscapes (Cornelius, 2008; Dhondt, 2012). Our results show that secondary cavity nesters use deeper cavities in stands with higher canopy cover and further inside forest edges, and this could be the result of an increased availability, in primary forest, of deep, non-

excavated cavities, which many secondary cavity nesters may prefer (Cockle et al., 2011b).

Contrasting with secondary cavity nesters (which are constrained by the presence of existing cavities), primary excavators maintained the same nest site preferences from primary forest to open farmlands. Our finding that primary excavators preferred larger dead trees is consistent with previous results in the same study area and elsewhere (Altamirano et al., 2017; Basile et al., 2020; Berl et al., 2015; Cockle et al., 2011b; Gutzat and Dormann, 2018; van der Hoek and Martin, 2018). Tree size and condition are likely associated with wood decay and optimal hardness for cavity excavation (Jackson and Jackson, 2004; Lorenz et al., 2015; Schepps et al., 1999), and this relationship is probably consistent regardless of surrounding habitat. The negative effect of canopy cover on the occurrence of nests of primary excavators might indicate a preference for nest sites with low cover, as shown for some species of North American woodpeckers (Cooke and Hannon, 2012; Latif et al., 2015; Nickley and Bulluck, 2019; Vierling, 1997). However, low canopy cover around excavator nests might also be related to death and collapse of the branches of large nest trees (which can break the surrounding canopy when they fall), death of neighboring trees because

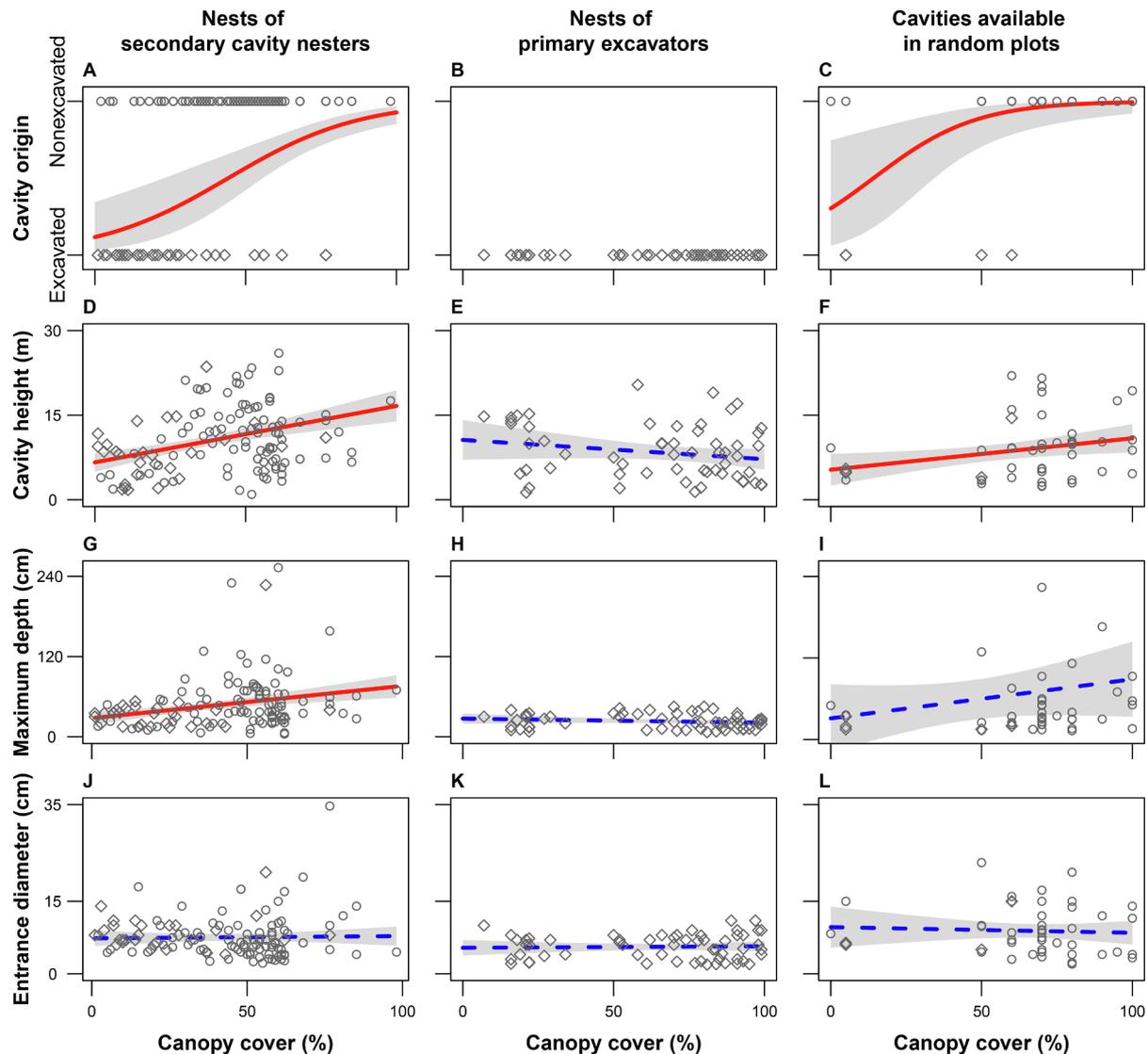


Fig. 3. Variation in cavity origin (excavated, diamonds, vs. non-excavated, circles) and dimensions (height, depth and entrance diameter) of cavities used by secondary cavity nesters ($n = 140$; A, D, G, J), used by primary excavators ($n = 58$; B, E, H, K), and available in random plots ($n = 48$; C, F, I, L), according to canopy cover, in the Atlantic Forest of Argentina. Lines indicate predicted values of Generalized Linear Models and grey shading indicates 95% confidence bands; broken lines indicate non-significant regressions. Canopy cover for cavities used by secondary cavity nesters and primary excavators was the mean of four densiometer measurements around the nest tree, while canopy cover for available cavities in random plots was estimated visually. An extreme depth value for a cavity in a plot (799 cm deep at 80% canopy cover) is not shown here but was included in the models.

of the same agent that killed the nest tree (e.g. strong winds or pest), or higher detectability of nests in open areas (clearings inside the forest or isolated trees on farms) than nests surrounded by other trees. Decreasing cavity depth towards primary forest is likely explained by increased abundance and diversity of small or weak primary excavator species such as black-throated trogon (*Trogon rufus*), surucua trogon (*Trogon surrucura*) and ochre-collared piculet (*Picumnus temminckii*), which produce shallower cavities than the true woodpeckers that comprise the only primary excavators in open farmland (e.g., campo flicker *Colaptes campestris*; Appendix C). Although we found that cavities made by primary excavators in dead trees are an important resource for secondary cavity nesters in open farmland, excavated cavities have a shorter permanence before collapsing or falling (vs. non-excavated cavities in living substrates; Cockle et al., 2017; Wesółowski, 2011), and thus special attention is needed to ensure an ongoing supply of trees suitable for excavation on farms.

The cavity-nesting community varied in composition across stands in our study, with several species found nesting only inside forest with high canopy cover (e.g., plain-winged woodcreeper

Dendrocincla turdina) and other species found only outside of the forest in open areas (e.g., American kestrel *Falco sparverius*). Such species are likely constrained by thresholds of minimum habitat characteristics, such that their nest-site selection is in turn constrained by the higher-level selection of home range (Johnson, 1980; Jones, 2001). Although our small sample size for each species prevented us from performing species-specific analyses, several species, such as red-breasted toucan (*Ramphastos dicolorus*; Perrella and Guida 2019) and tropical screech-owl (*Megascops choliba*; Menq and Anjos 2015), were found across all stand conditions from primary forest to open farmlands and the variation in their nest-site selection could be studied in more detail with a larger sample size. Although we found some Atlantic Forest endemic species nesting outside forest edge and in stands with low canopy cover on farms, only 21% of endemic species we found nesting used trees in farmlands. Our finding that many forest-dwelling cavity-nesters can reproduce in open farmland is likely dependent on the small scale of farms in our study area, which allows individual birds to include both forest and open farmland within their home range. We would not expect to find

many of these species far from forest edge, in the much more extensive agro-industrial areas of the Atlantic Forest region in Paraguay and Brazil.

5. Recommendations for management and future research

In the short term, sustainable management of trees for birds to nest on family farms in the Atlantic Forest should include retention of large native trees (even when they currently do not bear a cavity) because such trees provide opportunities for cavity formation throughout their lifespan. While living, they are prone to heart rot and formation of non-excavated cavities via branch fall, as well as excavated cavities in dead branches. When they die and decay further, the main stems and remaining branches of these trees can be excavated by a succession of primary excavators. To conserve cavity-nesting birds in the long term, active recruitment of younger native trees is also needed, through protection of naturally regenerated seedlings and planting of scarce important species such as Paraná pine and grapia *Apuleia leiocarpa*. In addition to their benefits as nest sites for cavity-nesters, native trees or forest patches throughout farms can offer additional key resources for wildlife (e.g., food, roost sites), reinforce forest regeneration (as seed producers) and provide important ecosystem services (soil protection, regulation of temperatures, and water retention; Gómez-Cifuentes et al., 2020; Manning et al., 2006a).

Tropical and subtropical forests harbor most of the world's ~ 1880 cavity-nesting bird species, yet these communities remain little-studied even as the forests are converted to agroecosystems (van der Hoek et al. 2017). Our study shows that characteristics of trees and cavities used for nesting vary across stand conditions in the Atlantic Forest; future work should assess the role of landscape characteristics in driving nest-patch selection by cavity-nesters. Although cavity-excavation by woodpeckers may allow some secondary cavity nesters to occupy otherwise unsuitable agroecosystems, future research should examine the extent to which primary excavators support a diversity of cavity nesters and their services in seed dispersal, local culture and ecotourism, in these highly modified landscapes. Ideally, future studies can identify the key biological mechanisms that determine the production of excavated cavities in agroecosystems, including woodpecker abundance and diversity, but also their ability to regulate cavity supply by increasing excavation rates in response to scarcity (Drever and Martin, 2010; Remm and Löhms, 2011; Wiebe, 2016). Moreover, we suggest that tree and cavity characteristics used by secondary cavity nesters in open farmland could be suboptimal, associated with low nest survival and cavity persistence, and an important line of future research is to examine fitness consequences of the variation in nest site

characteristics across habitats (Jones, 2001). Finally, we indicated some variation in the species pool of cavity nesters across the gradient we studied, but our small sample size limited broader inference about species turnover. In future, effects of forest loss on endemic species reproduction, community structure, interspecific relationships and functional traits should be specifically assessed to improve our understanding of how to manage for cavity-nesting bird communities, and their ecosystem functions, across a range of tropical and subtropical landscapes.

CRedit authorship contribution statement

Eugenia Bianca Bonaparte: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Data curation, Writing - original draft, Writing - review & editing, Visualization, Project administration, Funding acquisition. **José Tomás Ibarra:** Conceptualization, Validation, Writing - review & editing, Supervision, Funding acquisition. **Kristina L. Cockle:** Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Writing - original draft, Writing - review & editing, Visualization, Supervision, Project administration, Funding acquisition.

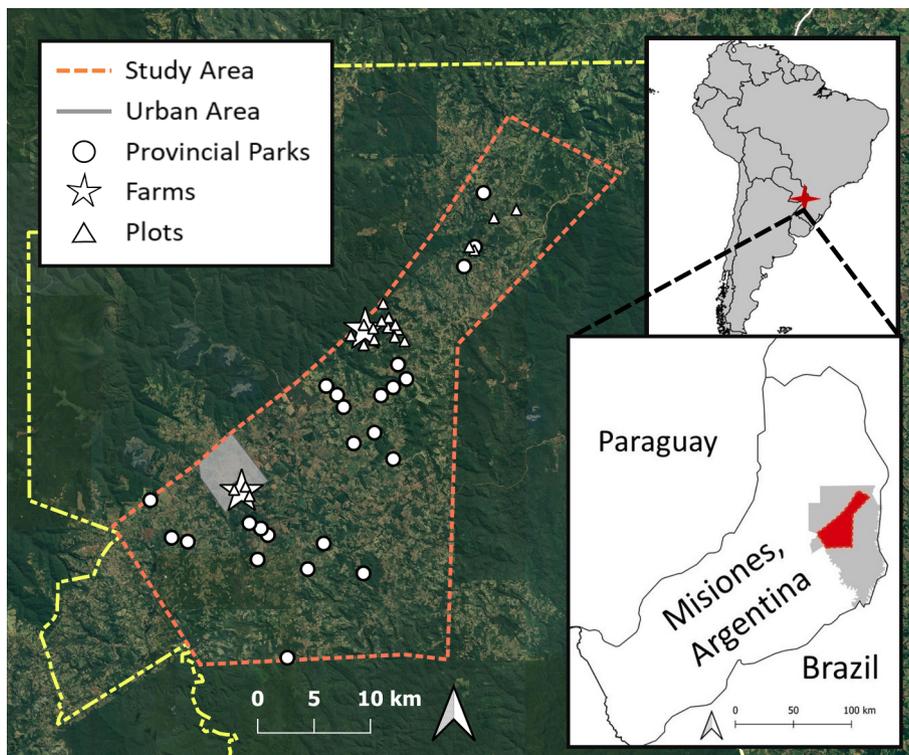
Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix



Appendix A. Study area in San Pedro department (grey shaded inside Misiones Province, Argentina), comprising 90% of *Araucaria angustifolia* forests in the country and most of San Pedro Important Bird Area. White stars show Cruce Caballero (northern circle) and Araucaria Provincial Parks, white circles show farms where we searched for active nests, and white triangles show random plots.

Appendix B. A priori hypotheses represented by conditional logistic regression models to explain changes in nest-site preferences of cavity-nesting birds along a habitat gradient from primary Atlantic Forest to open farmland, in Argentina. For all models, the response variable was tree status (nest tree vs. control tree).

Hypotheses	Predictor Variables
H1 Nest-tree preference does not vary across site conditions.	DBH ¹ , tree condition ¹ , crown touching ³ (without interactions).
H2 Nest-tree preference varies across site conditions at the scale of immediate tree surroundings.	DBH, tree condition, crown touching, canopy cover ⁴ , DBH × 10-m canopy cover, tree condition × 10-m canopy cover, crown touching × 10-m canopy cover.
H3 Nest-tree preference varies across site conditions at a scale beyond the immediate tree surroundings.	DBH, tree condition, crown touching, distance to edge ⁵ , DBH × distance to edge, tree condition × distance to edge, crown touching × distance to edge.
H4 Nest-tree preference varies at both immediate and larger scales.	Global model, includes all variables and interactions in previous models.

¹ DBH: diameter at breast height. ² Tree condition: live or dead. ³ Crown touching: percent of crown touching other trees or lianas. ⁴ 10-m canopy cover: mean of four densiometer measurements around the tree (percent). ⁵ Distance to edge: distance from the tree to nearest forest edge. Positive values indicate trees inside the forest and negative values indicate trees outside the forest.

Appendix C. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2020.118440>.

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