



Persistence and loss of tree cavities used by birds in the subtropical Atlantic Forest



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ARTICLE INFO

Article history:

Received 30 July 2016

Received in revised form 20 October 2016

Accepted 24 October 2016

Keywords:

Atlantic Forest
Hole-nesting bird
Nest site
Tree hollow
Wood density
Woodpecker

ABSTRACT

An important goal for the conservation of tropical forest biodiversity is to maintain adequate supplies of tree cavities to support diverse communities of cavity-nesting and roosting vertebrates over the long term, especially in human-modified landscapes. The conservation and replacement of nesting cavities depend critically on cavity persistence, which is predicted to decline with increasing anthropogenic impact to the habitat, and to vary according to characteristics of trees and excavators. We used Cox proportional-hazards models to study the factors influencing persistence of 277 cavities used by 43 species of nesting birds in 38 species of trees, across a gradient of human impact in the subtropical Atlantic Forest of Argentina, 2004–2016. Median cavity persistence was 6 years, with 79% of cavity losses caused by the collapse of either the whole tree or the section of the tree holding the cavity. Contrary to predictions, cavity persistence did not vary across habitats (primary forest, degraded forest, farm) or excavator types (true woodpecker vs. weak excavator). Persistence was highest (median > 10 years) for non-excavated cavities in live trunks of healthy trees, and increased with tree size and species-specific wood density. Thus, although logging and conversion to farmland remove most cavities, the cavities that remain in these human-modified habitats provide high quality, multi-annual nest sites for forest birds. Preserving and restoring these cavities should be a priority for conservation of forest vertebrates. The positive effect of species-specific wood density on cavity persistence suggests a trade-off in rates of cavity turnover, whereby cavities are produced early but lost quickly in fast-growing (low wood density) pioneer tree species, and produced late but persist much longer in slow-growing (high wood density) climax species.

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1. Introduction

An important long-term goal for the conservation of forest biodiversity is to maintain adequate supplies of tree cavities to shelter nesting and roosting vertebrates, especially in human-modified landscapes (Lindenmayer et al., 2006; Politi et al., 2012). Most cavity-nesting vertebrates are non-excavators (secondary cavity-nesters) that cannot produce their own cavities, and instead rely on avian excavators and natural decay processes to produce this critical resource (Newton, 1994; Martin and Eadie, 1999; Martin et al., 2004). As a result, populations of non-excavators may frequently be limited by cavity supply, especially in human-altered

landscapes (Newton, 1994; Cockle et al., 2010). To ensure a sufficient supply of nest sites in logged or cleared areas, conservation policies for cavity-nesting vertebrates often include retention of legacy trees. To be effective, such efforts require information about the persistence times of tree cavities under a range of ecological and environmental conditions.

In temperate forests, tree cavities can persist more than 30 years, during which time they can be used by a diverse sequence of vertebrates (Aitken et al., 2002; Wesołowski, 2012). Cavities in temperate forests are typically destroyed by tree fall, breakage, decay of cavity walls, occlusion (growing over), or vertebrate damage (Wesołowski, 2011, 2012; Edworthy et al., 2012). However, persistence of tree cavities varies geographically and according to characteristics of the habitat, trees and cavities, with longer persistence in closed forest and large living trees (Sedgwick and Knopf, 1992; Lindenmayer and Wood, 2010; Cockle et al.,

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2011a; Wesolowski, 2011, 2012; Edworthy et al., 2012; Lindenmayer et al., 2012; Edworthy and Martin, 2013).

Within geographic locations, cavity persistence can vary among tree species (Nielsen et al., 2007). Wesolowski (2012) observed a threefold difference in cavity persistence among tree species at a single site in Poland, and proposed that this variation could be related to species-specific wood hardness. Although not studied specifically for cavity-bearing trees, high wood density appears to convey resistance to both decay and breakage (Chambers et al., 2000; Chave et al., 2009). Decay resistance (durability) also results from secondary chemical compounds in the heartwood, which allow trees of some species to stand >1000 years before collapsing (Scheffer and Cowling, 1966; Loehle, 1987; Hennon et al., 2002; Kurokawa et al., 2003; Oliveira et al., 2005). At a given location, then, we can predict cavity persistence to increase with species-specific wood density and durability.

Cavity persistence has also been linked to excavator species (Wesolowski, 2011; Edworthy et al., 2012). True woodpeckers (Picinae) have morphological adaptations that allow them to excavate cavities into hard wood (Burt, 1930; Spring, 1965; Kirby, 1980; Lorenz et al., 2015). Lacking these adaptations, other species, including piculets (Picumninae), trogons (Trogonidae), and tits (Paridae), must excavate in softer wood, often in advanced stages of decay (Skutch, 1959; Colliars, 1964; Christman and Dhondt, 1997; Steward and Pierce, 2011; Manegold and Töpfer, 2013), which can lead to more rapid collapse of their cavities (Edworthy et al., 2012).

Although most cavity-nesting vertebrates inhabit the tropics and subtropics, little is known about the persistence of tree cavities at these latitudes, where warm conditions favourable for decay organisms may lead to high rates of cavity loss. In the subtropical humid Atlantic Forest of Argentina, 77 species of birds (16 excavators and 61 non-excavators) use tree cavities for nesting (Cockle et al., 2011a, KLC unpubl. data). The Atlantic Forest once covered much of south-eastern Brazil, eastern Paraguay, and north-eastern Argentina, but >85% has been replaced by ranching, agriculture and urbanization, and the region is considered one of the top global priorities for biodiversity conservation (Myers et al., 2000). Previous work showed that persistence was higher for non-excavated cavities than for bird-excavated cavities in the Atlantic Forest (Cockle et al., 2011a). Other factors likely to influence cavity persistence, such as stand context, or characteristics of trees and excavators, have not been studied, to our knowledge, in any tropical or subtropical forest.

Building on work presented in Cockle et al. (2011a), the present study aimed to determine how characteristics of stands, trees, and cavities influenced the persistence of cavities used by birds, and thus their long-term availability to cavity-dependent birds and other vertebrates in the Atlantic Forest. At the stand level, we hypothesized that the removal of neighbouring trees increases the risk of wind throw (Ferreira and Laurance, 1997; Scott and Mitchell, 2005; Mascarúa López et al., 2006), leading to lower persistence of cavities in selectively-logged or cleared areas. At the tree level, we hypothesized that trees would be more stable if they were healthy and larger in diameter, with high-density, durable (decay-resistant) wood. We predicted that cavity persistence would decrease with increasing decay stage, and increase with tree diameter, wood specific gravity (density) and wood durability. At the cavity-level, we hypothesized that high, dead limbs would be unstable. We therefore predicted a negative relationship between cavity persistence and cavity height, higher persistence in living than dead substrates, and higher persistence in tree trunks than in limbs. Additionally, we predicted persistence to be higher for true woodpeckers (Picinae) compared to weak excavators (*Trogon* and *Picumnus* spp.). Finally, we compare our results to cavity

persistence studies from temperate forests of Australia, Europe and North America.

2. Methods

2.1. Study area

We studied tree cavities used by nesting birds in the Atlantic Forest, Misiones province, north-eastern Argentina. Parts of the Atlantic Forest, including Misiones, are located south of the Tropic of Capricorn. However, floristics, physiognomy and fauna unite these southern forests with the northern Atlantic Forests and we therefore include them under the broader category of tropical moist forests (Negrelle, 2002; Oliveira-Filho and Fontes, 2000).

Our study area was a mosaic landscape of primary (unlogged) and logged forest, parks, and small farms from San Pedro (26°38'S, 54°07'W) to Parque Provincial (PP) Cruce Caballero (26°31'S, 53°59'W) and Tobuna (26°27'S, 53°54'W), San Pedro department, and PP Caá Yará (26°52'S, 54°14'W), Guaraní department (Misiones, Argentina). The vegetation is classified as semi-deciduous Atlantic mixed forest with laurels (*Nectandra* and *Ocotea* spp.), guatambú (*Balfourodendron riedelianum*), and Paraná pine (*Araucaria angustifolia*; Cabrera, 1976). Elevation is 520–700 m a. s.l. Annual rainfall is 1900 mm distributed evenly throughout the year.

2.2. Field methods

We studied cavities used for nesting by birds in primary forest, logged forest, and farms, from 2004 to 2016. We found about 90% of nests by observing the behaviour of adult birds (about 6 observer-hours daily from September to December, 2006–2015), from permanent and temporary trails, off-trail, and a grid of transects spaced every 500 m (total 27 km). A few additional nesting trees were shown to us by rangers, farmers, and colleagues, some of whom were studying radio-tagged woodpeckers (2004–2015). When we detected bird activity at a cavity, we inserted a 1.8-cm diameter video camera to confirm nest contents. Cameras were mounted either on the tip of a horizontal rod at the top of a 15-m telescoping pole, or at the end of a 2-m hose which we carried to the cavity via ladder (10 m) or single-rope tree-climbing (any height, if the tree had a sturdy fork). Cavities were included in our study if they contained eggs and/or chicks. About 20% of nest cavities were not accessible using the pole, ladder, or tree climbing. They were observed from the ground for several periods of at least 2 h each, and were included in the study only if bird behaviour indicated the presence of eggs or nestlings. Once used, cavities were revisited every subsequent year until September 2016 to determine their persistence. A cavity was considered “lost” if (1) the tree or cavity-bearing limb had fallen to the ground, (2) the cavity had deteriorated so that it no longer had walls and a bottom, or (3) bark closed off the cavity entrance.

At each nest tree we measured variables expected to affect cavity persistence at the stand, tree and cavity scales. At the stand scale, we assigned the nest to one of three habitat types: primary forest, degraded forest, or farm. To be included in the “primary forest” category, cavities had to be >10 m from vehicle roads or cleared areas, in forest with no history of timber harvesting (Bertolini, 1999, 2000). Cavities were included in the “farm” category if they were in isolated trees within cultivated land or pastures (these trees were 23–474 m from forest edge). All other cavities were included in the “degraded forest” category (i.e., the forest had been selectively harvested for timber, the forest had been cleared and grown back, or the tree was within 10 m of

cleared areas or vehicle roads). We estimated percent canopy cover in a 30-m radius around the nest tree (Cockle et al., 2015). At the tree scale, we measured diameter at breast height (DBH), and determined the decay stage of the tree (live healthy tree, live unhealthy tree, recently dead tree with limbs intact, or long dead tree with only stubs of large limbs or no limbs remaining; Fig. 1; Cockle et al., 2011b). At the cavity scale we classified the type of substrate (live trunk, live limb, dead trunk, or dead limb), and measured cavity height using a 50-m measuring tape from the forest floor to the lower sill of the cavity entrance. For cavities above the reach of our ladder and without a sturdy fork for climbing, we measured cavity height using the telescoping pole (9–15 m), or a laser rangefinder (above 15 m).

To test hypotheses about how tree species influences cavity persistence, we identified living trees to species and assigned values of wood specific gravity (g cm^{-3}) and durability (resistance of

wood to decay: high or low) based on published literature (e.g., Chudnoff, 1984; López et al., 1987; Biloni, 1990; Oliveira et al., 2005; Chave et al., 2006; Zanne et al., 2009; Lorenzi, 2014), averaging values when several were available (Appendix A).

To test hypotheses about how cavity origin influences cavity persistence, we categorized cavities as produced by (1) true woodpeckers (Picinae), (2) weak excavators (*Trogon* or *Picumnus* spp.), or (3) decay processes (non-excavated). Cavities with irregular entrance and interior walls, and cavities that clearly resulted from a limb falling or the tree breaking, were considered non-excavated. Excavators were assigned in 87% of cases by observing the species excavating or using a fresh (recently excavated) cavity. A further 13% of excavated cavities were assigned to true woodpeckers based on internal cavity shape (vertical nest chamber without a long horizontal entrance tunnel) and characteristics of the entrance (circular or oval entrance >3 cm in diameter).



Fig. 1. Examples of nesting cavities (indicated by arrows) in trees at four decay stages in the Atlantic Forest: (A) non-excavated cavity in live trunk of healthy *Ocotea pulchella* in degraded forest at farm edge, (B) cavity excavated by *Veniliornis spilogaster* in dead limb of live, unhealthy *Cedrela fissilis* in primary forest, (C) non-excavated cavity in trunk of a recently dead *Araucaria angustifolia* in primary forest, (D) cavity excavated by *Dryocopus lineatus* in the limb of a long-dead tree in advanced stages of decay, in primary forest.

2.3. Analyses

We used the survival package in R (version 3.2.2) to model cavity persistence and loss (R Core Team, 2015; Therneau, 2015). We used the survfit function to determine median cavity persistence as the time at which a Kaplan-Meier survivorship function (cumulative probability of survival) drops below 0.5. To determine how characteristics of stands, trees, and cavities were related to cavity persistence, we used Cox proportional-hazards models (coxph command) to predict the hazard or risk of failure (probability that a cavity will be lost given that it has persisted to a given point in time) as a log-linear function of covariates. In Cox proportional-hazards models, regression coefficients β are the natural logarithms of the odds of failure. This method allowed us to include cavities that were still usable at the end of the study (right-censored cases; Tabachnick and Fidell, 2001). We used the cox.zph command (survival package) and examined plots of Schoenfeld residuals vs. log(time) to ensure that our data met the assumption of proportional hazards. We examined plots of martingale residuals vs. continuous covariates to ensure that our data met the assumptions of linearity and additivity.

We used three separate sets of Cox proportional-hazards models to test our hypotheses about the factors influencing cavity persistence. To ensure independence of data in these models, we used only the first nest cavity found in each tree. The first set of eight *a priori* models was employed to test competing hypotheses about the main drivers of cavity loss. Each model included a different combination of predictor variables at the scale of stand, tree and/or cavity (Table 1). Because we already knew that decay-formed cavities persisted much longer than excavated cavities (Cockle et al., 2011a), and because cavity origin (decay-formed or excavated) was highly correlated with substrate ($\text{Chi}^2 = 108.5$, $\text{df} = 3$, $p < 0.001$), we omitted cavity origin from this model set and included only substrate. The second set of models was employed to examine the influence of tree species traits on cavity loss, and this dataset was restricted to living trees because we could not identify most dead trees to species. This second set of five models included, as predictor variables, different combinations of decay stage (of the individual tree; healthy or unhealthy), wood specific gravity (of the tree species), and wood durability (of the tree species; Table 1). A third set of two models was employed to examine the influence of cavity producer on cavity persistence and included as a predictor variable only cavity producer (non-excavated, true woodpecker, or weak excavator; Table 1).

We used an information theoretic approach (Burnham and Anderson, 2002) to weigh the support for the models within each set based on their Akaike Information Criterion (corrected for small sample size; AICc) and Akaike weights. If a model had $\Delta\text{AICc} < 2$ we considered it to be well supported by the data. We considered parameters to have a potentially significant influence on cavity persistence if the 90% confidence intervals of their hazard (odds) ratios did not overlap 1. We used 90% confidence intervals rather than 95% confidence intervals to reduce the probability of a Type II error (e.g., failing to detect an existing influence of stand context on the hazard of cavity loss).

3. Results

We monitored a total of 277 nesting cavities in 232 trees, used by 43 species of birds. Over the study period 114 of these cavities were lost to natural causes and 5 were lost because of human actions. Cavities were lost to natural causes when a section of the tree, such as the cavity-bearing limb, broke off below the cavity (45 cavities), when the entire tree fell (34 cavities), when a section of the tree broke off right at the cavity (12 cavities), when the cavity deteriorated even though its supporting structure remained (15 cavities), and when bark grew over the entrance (4 cavities). Four additional cavities were lost to natural causes but we did not determine the exact cause (e.g., whether the branch broke or the cavity deteriorated). Human-driven cavity loss occurred when trees were cut (4 cavities) and when a fire was set to clear regrowth vegetation (1 cavity). Three of the cut trees were removed from a protected area, where they were considered hazardous. The five cavities destroyed by humans were omitted from further analyses.

Overall, median cavity persistence (from the time we found the first nest in a cavity until the cavity was no longer useable) was 6 years ($n = 272$ cavities, 114 losses). Median persistence was also 6 years for the first cavity found in each tree ($n = 227$ cavities, 93 losses), but median persistence for subsequent cavities found in the same trees was 3 years ($n = 45$ cavities, 21 losses). For the remainder of our analyses we include only the first nesting cavity found in each tree.

We studied the influence of stand, tree, and cavity characteristics on the persistence of 227 nesting cavities in separate trees. One hundred and forty nine of these cavities were in primary forest, 61 in degraded forest, and 17 in isolated trees on farms. Canopy cover

Table 1

Cox proportional-hazards models predicting hazard of loss of tree cavities in the Atlantic Forest of Argentina (2004–2016) in relation to (1) stand, tree, and cavity characteristics (first set of models; $n = 227$ tree cavities), (2) tree species traits and decay stage (second set of models; $n = 141$ cavities in living trees), and (3) cavity producer (third set of models; $n = 227$ tree cavities). k = number of parameters, ΔAICc = difference in value of Akaike Information Criterion (corrected for small sample size) between each model and the top model in the set, w_i = Akaike weight. Lowest AICc = 825.8 for the first set of models, 319.4 for the second set, and 858.8 for the third set. Models in the 95% confidence set ($\sum w_i \geq 0.95$) are highlighted in bold.

Model set	Model	Predictor variables	k	ΔAICc	w_i
1.	Constant	–	0	81.7	<0.001
	Stand	Habitat type, % canopy cover	3	78.6	<0.001
	Tree	DBH, decay stage of tree	4	18.1	<0.001
	Cavity	Substrate, cavity height	4	3.5	0.051
	Stand + Tree	Habitat type, % canopy cover, DBH, decay stage of tree	7	16.0	<0.001
	Stand + Cavity	Habitat type, % canopy cover, substrate, cavity height	7	7.2	0.015
	Tree + Cavity	DBH, decay stage of tree, substrate, cavity height	8	0	0.556
	Global	Habitat type, % canopy cover, DBH, decay stage of tree, substrate, cavity height	11	1.0	0.334
2.	Constant	–	0	17.3	<0.001
	Decay stage	Decay stage of tree	1	3.3	0.10
	Wood density	Decay stage of tree, wood specific gravity	2	0	0.53
	Wood durability	Decay stage of tree, wood durability	2	3.0	0.12
	Global	Decay stage of tree, wood specific gravity, wood durability	3	1.6	0.24
3.	Constant	–	0	49.4	<0.001
	Cavity producer	Cavity producer	2	0	1.00

around nest trees ranged from 0 to 100% (mean = 64%, SE = 2%). Tree DBH ranged from 13 to 180 cm (mean = 62 cm, SE = 2 cm). Seventy trees were alive and healthy when we first found a nest, 81 were alive but unhealthy trees, 21 were recently dead, and 55 were in advanced stages of decay.

We found nest cavities in 38 species of living trees (including one cavity in a tree fern *Alsophila procera* and four cavities in *Syagrus romanzoffiana* palms). We obtained values of wood specific gravity and durability for 32 of these species ($n = 141$ cavity trees). Wood specific gravity ranged from 0.40 g cm^{-3} (*Enterolobium contortisiliquum*) to 1.07 g cm^{-3} (*Parapiptadenia rigida*; mean = 0.63 g cm^{-3} , SE = 0.01 g cm^{-3} ; Appendix A).

One hundred and thirty four cavities were produced by decay processes (non-excavated), 74 were excavated by true woodpeckers (*Melanerpes flavifrons*, *Veniliornis spilogaster*, *Colaptes melanochloros*, *C. campestris*, *Cealeus galeatus*, *Dryocopus lineatus*, *Campephilus robustus*), and 19 were excavated by weak excavators (*Trogon surrucura*, *T. rufus*, *Picumnus temminckii*). Fifty-eight of these cavities were in a live trunk, 56 in a dead trunk, 45 in a live limb and 68 in a dead limb. Height of these cavities ranged from 0.9 to 32 m (mean = 12.2 m, SE = 0.4 m).

Over the study period, the most frequently used nest site was a non-excavated cavity in a living branch of a healthy *Apuleia leiocarpa*, which was used 11 times by 5 bird species over an 8-year period. Cavities in living sections of healthy trees comprised 25% of nesting cavities and 39% of cavities used by non-excavator birds.

Within our first set of Cox proportional-hazards models predicting hazard of loss of nesting cavities, the Cavity + Tree Model received the most support from the data. Although the Global Model also received limited support (Table 1), none of the stand-level variables had odds ratios that differed significantly from 1. At the tree level, DBH had a positive influence on cavity persistence, whereby each 1 cm increase in DBH was associated with a 1.3% reduction in the odds of cavity loss (Table 2, Fig. 2A). Also,

compared to live healthy trees, the odds of cavity loss were twice as high for live unhealthy trees, and 3–4 times as high for dead trees (Table 2, Fig. 2B). Median cavity persistence was >10 years in live healthy trees, 6 years in live unhealthy trees, and 2 years for both recently dead trees and dead trees with advanced decay. At the cavity level, compared to cavities in live trunks, the odds of cavity loss were more than twice as high for cavities in live limbs, 8 times as high in dead limbs and 9 times as high in dead trunks (Table 2, Fig. 2B). Median persistence was >10 years for cavities in live trunks, 8 years in live limbs, and 2 years in dead trunks or limbs. Cavity height did not influence persistence (Table 2).

Within our second set of Cox proportional-hazards models, which examined the influence of tree species traits on cavity loss, the Wood Density Model received the most support from the data (Table 1). Although there was limited support for the global model, no additional variables had odds ratios that differed significantly from 1. Each increase of 0.1 g cm^{-3} in wood specific gravity was associated with a 23% reduction in the odds of cavity loss (Table 2, Fig. 2C). In this model set, unhealthy trees had about 4 times the odds of cavity loss compared to healthy trees (Table 2). Wood durability classes did not influence cavity persistence (Table 2).

Within our third set of Cox proportional-hazards models, which examined the influence of cavity producer, hazard of cavity loss did not differ significantly between cavities made by true woodpeckers and weak excavators, but was 4.5 times higher for true woodpeckers compared to non-excavated cavities (Tables 1 and 2, Fig. 2D). Overall, non-excavated cavities persisted a median of >10 years, vs. just 2 years for cavities produced by true woodpeckers and 1 year for weak excavators.

Across seven sites in Australia, North America, South America, and Europe, median cavity persistence varied from 5 years to ~20 years (Table 3). High persistence was consistently associated with cavities in living sections of large, live healthy trees (Lindenmayer et al., 1990, 1997, 2012; Lindenmayer and Wood,

Table 2
Parameter estimates (b) for best supported (lowest AICc, highest Akaike weight) Cox proportional-hazards models of hazard of loss of nesting cavities in the Atlantic Forest of Argentina (2004–2016). Hazard ratio (or odds ratio) = e^b . Hazard ratio represents the change in odds of cavity loss associated with each 1 unit increase in the continuous predictor variable, or a change from the reference condition to the alternate condition if the predictor is categorical. A hazard ratio > 1 indicates that increased values of the predictor variable are associated with a higher hazard of cavity loss (and thus lower cavity persistence). A variable can be considered a significant predictor of cavity loss if the 90% confidence interval for its hazard ratio does not overlap 1. Effect of each predictor on cavity persistence is indicated as positive (+) if the 90% confidence interval for the hazard ratio is below 1, negative (–) if it is above 1, or neutral (0) if it includes 1.

Model/Parameter	b	SE	Hazard ratio (e^b)	90% confidence interval for Hazard Ratio	Effect on cavity persistence
<i>Set 1: Tree + Cavity Model</i>					
DBH (cm)	–0.013	0.0056	0.987	0.978–0.996	+
Decay stage of tree					
Live healthy	0	1			
Live unhealthy	0.82	0.40	2.26	1.18–4.33	–
Recently dead	1.39	0.49	4.01	1.80–8.95	–
Dead with advanced decay	1.14	0.47	3.13	1.45–6.76	–
Substrate					
Live trunk	0	1			
Live limb	0.88	0.49	2.41	1.08–5.37	–
Dead trunk	2.19	0.51	8.91	3.87–20.51	–
Dead limb	2.06	0.48	7.88	3.58–17.35	–
Cavity height (m)	0.020	0.026	1.02	0.98–1.06	0
<i>Set 2: Wood Density Model</i>					
Decay stage of tree					
Live healthy	0	1			
Live unhealthy	1.37	0.38	3.95	2.12–7.35	–
Wood specific gravity (g cm^{-3})	–2.58	1.19	0.076	0.011–0.53	+
<i>Set 3: Producer Model</i>					
Cavity producer					
True woodpecker	0	1			
Weak excavator	0.45	0.32	1.56	0.93–2.62	0
Non-excavated (decay)	–1.51	0.24	0.22	0.15–0.33	+

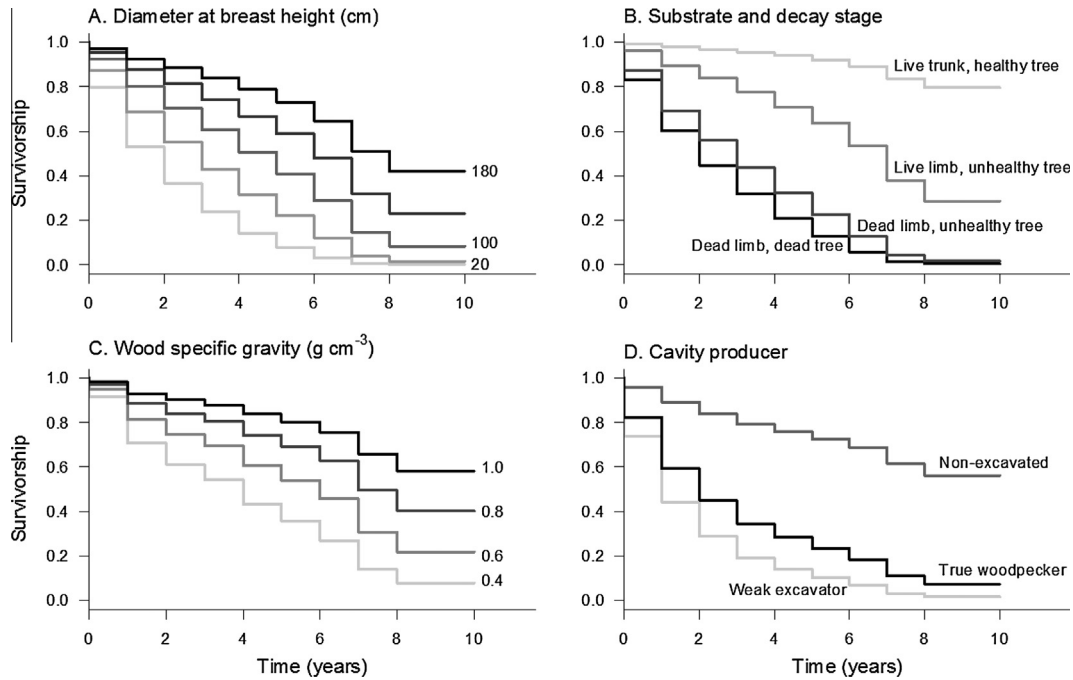


Fig. 2. Kaplan-Meier survival curves generated by the best (lowest AICc; highest Akaike weight) Cox proportional-hazards models predicting hazard of cavity loss in the Atlantic Forest of Argentina (2004–2016). Lines represent predicted probability of cavity survival for varying levels of (A) diameter at breast height (DBH), (B) tree decay stage and cavity substrate, (C) wood specific gravity, and (D) cavity producer. Unless indicated, all other parameters are held constant at their mean or mode (habitat = primary forest, canopy cover = 64%, decay stage = live unhealthy, diameter at breast height = 61.6 cm, substrate = dead limb, cavity height = 12.2 m). (A–B) represent predictions of the global model from the first set of models (n = 227 tree cavities); (C) represents predictions of the wood density model from the second set of models (n = 141 cavities in living trees), and (D) represents predictions of the cavity producer model from the third set of models (n = 227 tree cavities). Increasingly dark shades of grey indicate increasing (A) DBH (in 40-cm increments), (B) decay stage (from live healthy trees to dead trees in advanced stages of decay), and (C) wood specific gravity (in increments of 0.2 g cm⁻³).

Table 3

Influence of stand, tree and cavity characteristics on persistence of tree cavities in six temperate and subtropical forests. Tick marks indicate factors associated with increased cavity persistence, 0 indicates the study found no effect of these factors, and cells are blank if the factor was not included in the study. Sources: 1 - Wesolowski (2011, 2012) (median persistence is the weighted average of values reported in the two studies); 2 - Edworthy et al. (2012) and Edworthy and Martin (2013); 3 - Sedgwick and Knopf (1992); 4 - Nielsen et al. (2007); 5 - Lindenmayer et al. (1990, 1997, 2012) and Lindenmayer and Wood (2010); 6 - Cockle et al. (2011a); this study.

	Poland ¹	British Columbia ²	Colorado ³	Illinois ⁴	South-eastern Australia ⁵	North-eastern Argentina ⁶
Latitude	53°N	52°N	41°N	38°N	37°S	27°S
Biome	Temperate mixed forest	Temperate mixed forest	Temperate broadleaf riparian forest	Temperate broadleaf forest	Temperate Eucalyptus forest	Subtropical mixed forest
Median cavity persistence (years)	11	14	~5	>10	19–24	6
<i>Habitat, tree, and cavity characteristics associated with increased cavity persistence</i>						
Mature forest habitat		✓		0	✓	0
Tree health	✓	✓			✓	✓
Large DBH	✓	✓		✓	✓	✓
Tree species	<i>Quercus robur</i>			<i>Platanus occidentalis</i>		High wood density
Live substrate	✓					✓
Non-excavated cavities	✓					✓
Excavated by strong woodpecker	✓	✓				0

2010; Wesolowski, 2011, 2012; Edworthy et al., 2012; Table 3). However, the influence of forest type and cavity producer varied across sites (Table 3).

4. Discussion

In the Atlantic Forest of Argentina, cavities persisted longest when they were produced by natural decay processes (non-excavated), in the living trunks of large healthy trees. Although both cavity availability and nest density decline strongly in logged Atlantic Forest (compared to primary forest; Cockle et al., 2010),

we found no influence of stand type (primary forest, degraded forest, or open farm) on either nest survival (Cockle et al., 2015) or cavity persistence (this study). Contrasting with the results of studies from temperate forests (Wesolowski, 2011; Edworthy et al., 2012), we also found no influence of excavator group (true woodpecker vs. weak excavator) on cavity persistence in the Atlantic Forest. Instead, our study identified non-excavated cavities in living sections of healthy trees as a key multi-annual resource, expected to last considerably longer than 10 years (Fig. 2B). Living trees are also associated with higher survival of eggs and nestlings in the Atlantic Forest (compared to dead trees; Cockle et al., 2015).

Our results thus highlight the importance of conserving large, living trees with cavities in logged forest and farmland as well as in primary forest.

Our result that stand type and canopy cover did not influence cavity persistence contrasts with studies from temperate forests, where cavity persistence was highest in mature forest (Lindenmayer et al., 2012; Edworthy and Martin, 2013). In the Atlantic Forest, remnant cavity-trees in open farming areas may be exposed to stronger winds, but may be less likely to be pulled or knocked down by lianas and neighbouring trees, compared to trees in continuous forest (Vidal et al., 1997, KLC & AB pers. observ.). Soils within the Atlantic Forest also retain more moisture than those in open pasture (Braga do Carmo et al., 2012), which could promote root decay and tree collapse (Lindenmayer and Wood, 2010). However, it is also possible that the trees most susceptible to wind throw fell shortly after logging, before our study began. Regardless of the mechanisms involved, our study shows that the few cavity-bearing trees currently remaining in logged forest and farms provide high quality, multi-annual nest sites for subtropical forest birds in a global biodiversity hotspot. Preserving and restoring these trees should be a key priority for conservation of vertebrates.

As predicted, cavities persisted longest in tree species with dense wood, which raises the possibility of a trade-off between rates of cavity formation and persistence. We suspect that wood density may be inversely related to the rate of cavity formation, for two reasons. First, high wood densities are produced by slow growth rates (Chave et al., 2009; Wright et al., 2010; Carrasco et al., 2015), and slow-growing trees take longer to reach the size necessary to support a nesting cavity. Second, high wood density may confer resistance to wood-decaying fungi, wood-boring insects, and avian excavators, hindering the formation of cavities (Chave et al., 2009; Kassene et al., 2011; Lorenz et al., 2015). We therefore propose that rates of cavity turnover may vary along a continuum from fast-growing (low wood density) tree species that produce short-duration cavities at a young age, to slow-growing (high wood density) species that produce long-duration cavities, but at a much older age. Importantly, wood density, growth rate, lifespan, and growth form of trees vary with forest succession (Bazzaz and Pickett, 1980; Augspurger, 1984; Poorter et al., 2006). These functional traits merit further study in relation to cavity production and loss. In abandoned pastures and canopy gaps in the Atlantic Forest, for example, fast-growing species with low wood density and high mortality, such as the native pioneer *Solanum granuloso-leprosum* (specific gravity = 0.4 g cm⁻³) or the exotic *Melia azedarach* (0.4 g cm⁻³), may develop short-duration cavities at a young age, providing critical habitat for cavity-nesting birds in the medium-term, even if their cavity turnover rates are high. On the other end of the spectrum, slow-growing *Dipteryx micrantha* trees in climax forests of the Peruvian Amazon (0.9 g cm⁻³) probably take hundreds of years to develop cavities, but these cavities could be useable by macaws and other non-excavators for decades or even centuries (Brightsmith, 2005). We encourage researchers to incorporate functional traits of tree species into studies of cavity availability in tropical and temperate forests, to improve our understanding of how and why cavity persistence and availability vary across geographical regions and habitat types (Table 3), and to identify priorities in habitat restoration for cavity-nesting vertebrates.

Acknowledgements

Many colleagues and field assistants contributed over the years, most recently Carlos Ferreyra, Milka Gómez, Bianca Bonaparte, Facundo Di Sallo, Martjan Lammertink, Max Ciaglo, Carlos Alderete and Bruna Amaral. For access and help at field sites we thank prop-

erty owners in San Pedro department, provincial park rangers, and Ministerio de Ecología y RNR (Misiones). We thank Daryl Cockle for engineering the cameras to monitor nests. Funding and equipment were provided by CONICET, NSERC, Killam Foundation, Rufford Foundation, Columbus Zoo and Aquarium, Ornithological Council, CREOI, British Ornithologists' Union, Oregon Zoo, Lindbergh Foundation, Cleveland Zoo, Explorers' Club, Aves Argentinas, Idea Wild and AMIRBY. Funders had no involvement in the study design; collection, analysis or interpretation of data; report writing; or decision to submit the article for publication.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2016.10.052>.

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