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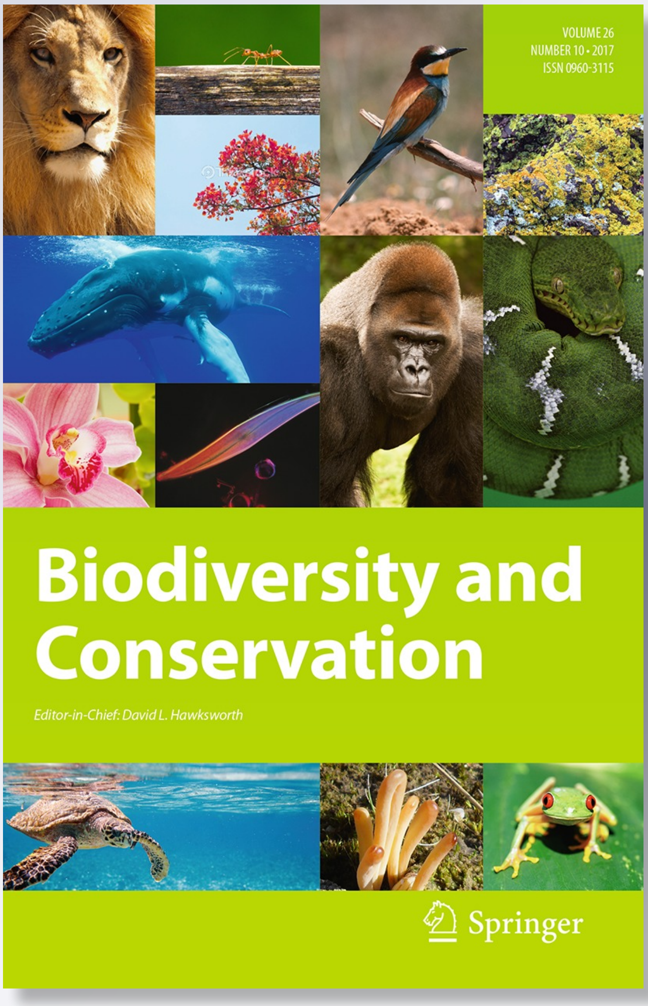

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ORIGINAL PAPER

The conservation value of tree decay processes as a key driver structuring tree cavity nest webs in South American temperate rainforests

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Abstract South American temperate rainforests, a global biodiversity hotspot, have been reduced to nearly 30% of their original extent and most remaining stands are being degraded. Cavity-nesting vertebrate communities are dependent on cavity-bearing trees and hierarchically structured within nest webs. Evaluating the actual degree of cavity dependence (obligate, non-obligate) and the preferred attributes of trees by cavity nesters is critical to design conservation strategies in areas undergoing habitat loss. During three breeding seasons (2010–2013), we studied the cavity-nesting bird community in temperate rainforests of Chile. We found the highest reported proportion of tree cavity nesters (n = 29 species; 57%) compared to non-cavity-using birds for any forest system. Four species were excavators and 25 were secondary cavity nesters (SCNs). Among SCNs, ten species were obligate and 15 were non-obligate cavity nesters. Seventy-five percent of nests of SCNs were located in cavities produced by tree decay processes and the remaining 25% were in cavities excavated mainly by *Pygarrhichas albogularis* and *Campephilus magellanicus*. Nest web structure had a low dominance and evenness, with most network interactions occurring between SCNs and large decaying trees. Tree diameter at breast

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height (DBH) was larger in nest-trees (57.3 cm) than in available trees (26.1 cm). Cavity nesters showed a strong preference for dead trees, both standing and fallen (58% of nests). Our results stress that retaining large decaying and standing dead trees (DBH > 57 cm), and large fallen trees, should be a priority for retention in forest management plans in this globally threatened ecosystem.

Keywords Bird community · Cavity nesters · Chile · Forest conservation · Habitat degradation · Standing dead trees

Introduction

Habitat loss and degradation is the principal cause leading to species endangerment globally (Pimm et al. 2006; Rybicki and Hanski 2013). In forests worldwide, increasing rates of habitat degradation (i.e. decrease in the quality of forest attributes at the stand-level) may limit the populations of more than 1878 bird species that require or use cavities for nesting or roosting (Newton 1994; Cockle et al. 2011a; Van der Hoek et al. 2017). 13% of these species are currently considered globally threatened, and some of them have already gone extinct, mostly due to the loss and degradation of key habitat attributes (e.g. large decaying and standing dead trees; Lammertink et al. 2011; Van der Hoek et al. 2017).

Cavity-nesting bird communities are hierarchically structured within nest webs (Martin and Eadie 1999). In nest webs, two guilds exist depending on how tree cavities are obtained (Martin et al. 2004): "excavators" or primary cavity nesters (PCNs) and "non-excavators" or secondary cavity nesters (SCNs) (Fig. 1). SCNs nest in either excavated cavities or in those produced by tree decay processes. Among SCNs, the degree of dependence on tree cavities compared to other nesting types varies among species along a continuum from obligate (required to breed) to incidental cavity nesters (opportunistically use a tree cavity for nesting, Gibbons and Lindenmayer 2002). A higher proportion of

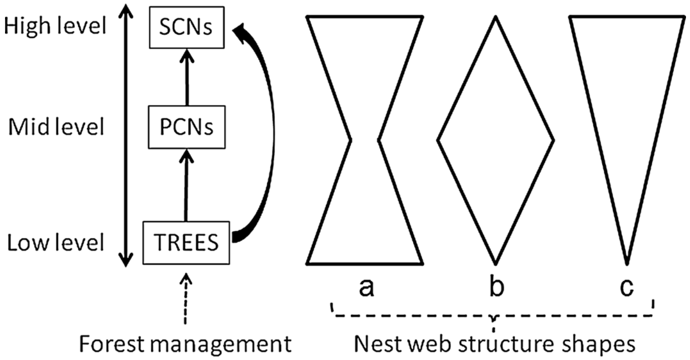

Fig. 1 Representation of nest web structure composed by "nest web levels", including: tree species (*lowest level*), primary cavity nesters (*PCNs*, *mid level*), and secondary cavity nesters (*SCNs*, *highest level*). Different reported nest web shapes depicting how the number of species at different levels interact in the web: **a** low species diversity at mid level of the nest web for Atlantic forests of Argentina (Cockle et al. 2012); **b** high species diversity at mid level of the nest web, observed in Florida, USA (Blanc and Walters 2008b); and **c** inverse structure observed in northern temperate forests of Canada, with more species diversity at high level (Martin et al. 2004)

obligate cavity nesters may make a community more vulnerable to habitat degradation as these species cannot switch to an alternative nesting substrate such as river banks, termitaria, or branches to build open cup nests (Ibarra and Martin 2015a; Newton 1998). Although knowing the proportion of obligate to non-obligate (i.e. animals that use both tree cavities and other nest site types) cavity nesting vertebrates may be important for conservation and forest management, the degree of tree cavity-dependence has hardly been reported for most cavity-nesting communities.

A suite of nest web studies conducted mostly in the northern hemisphere has elucidated the ecological factors, including key biotic interactions and habitat attributes, structuring cavity-nesting communities (Blanc and Walters 2008a; Martin et al. 2004; Cockle et al. 2012). Understanding nest web composition and structure can be an important conservation management tool for environmental agencies charged with protecting forest biodiversity (Ruggera et al. 2016). For example, in temperate forests of British Columbia (Canada), Martin et al. (2004) found that a community of over 20 cavity-nesting bird species was strongly structured, in a bottom-up manner, by the availability of cavities in Trembling Aspen trees (*Populus tremuloides*; 95% of nests in this tree species) (Fig. 1, shape c). This cavity-nesting community showed a strong preference for excavated cavities (90% of nests, Aitken and Martin 2007; Cockle et al. 2011a) and live unhealthy trees (Martin et al. 2004). In longleaf pine (*Pinus palustris*) forests in Florida (United States), eight PCNs and six SCNs composed a nest web of 14 species (Blanc and Walters 2008b). Here, more than 99% of nests used by SCNs were located in cavities excavated chiefly by northern flickers and red-cockaded woodpeckers (*Picoides borealis*), with 73% of nests situated in standing dead trees or snags (Blanc and Walters 2008a, b; Fig. 1, shape b). In contrast, in Atlantic forests of Argentina, Cockle et al. (2011a, b) described a nest web for 69 cavity-nesting birds (12 PCNs and 57 SCNs), which used mostly cavities created by tree decay processes (80% of nests; Fig. 1, shape a).

Forest management plays a potentially strong role in structuring nest webs, mainly because it modifies the availability of critical large decaying trees and snags (Zarnowitz and Manuwal 1985; Gibbons et al. 2002; Drever et al. 2008) (Fig. 1). For example, tree diameter at breast height (DBH) and cavity availability were disproportionally important for a cavity-nesting bird community inhabiting forests under timber production in Australia (Gibbons et al. 2002; Gibbons and Lindenmayer 2002). In Canada, Edworthy and Martin (2013) found that persistence of tree cavities decreased from 15 to 9 years in harvested forests compared to unharvested forests. Evaluating the preferred attributes of nest-trees by cavity nesters in areas subject to high rates of forest degradation is important as forests are chronically short of large decaying trees and snags globally (Cockle et al. 2011a; Müller et al. 2016).

Temperate rainforests of South America are classified among the 35 most critically endangered eco-regions in the world because only 30% of the original vegetation remains (Myers et al. 2000). These forests, which are isolated by more than 1000 km from other forested areas in the continent, support a relatively low bird species richness ($\sim$51 species) but many are endemics (41%; Vuilleumier 1985). Despite the global relevance of southern temperate rainforest biodiversity, current knowledge on the composition and structuring factors of the cavity-nesting community inhabiting these ecosystems is rudimentary, as well as the degree of tree cavity dependence and stand-level structural attributes preferred for nesting. The historical use of fire to open agricultural and livestock areas, selective logging of native forests, and the expansion of pine plantations in the last four decades, have been the main factors driving the loss of temperate rainforests of South America (Veblen et al. 1992; Echeverria et al. 2006; Caviedes and Ibarra 2017).

In this study we (i) describe the composition of the cavity-nesting bird community, reporting the degree of tree cavity dependence for endemic and non-endemic cavity nesters, (ii) compare the relative importance of tree decay and excavation processes in structuring the nest web, and (iii) determine the utilization and preferred attributes of nest-trees in South American temperate rainforests. For this, we conducted a nest web analysis of the cavity-nesting bird community that explicitly outlines the links and interactions that must be understood to predict how the community will respond to further degradation of temperate rainforests of South America.

Methods

Study area

Temperate rainforests of South America occur in both sides of the Andean range, forming a narrow but latitudinally extensive strip of land between 35° and 55°S (Armesto et al. 1998). The main weather characteristics of southern temperate rainforests are cool summers and average annual precipitation >2000 mm distributed throughout the year. We conducted our study in 20 forest stands (each with an area of at least 20 ha) in the La Araucanía Region, Chile (39°16′S, 71°48′W). The surveyed stands included nine second-growth forests (40–80 years), subjected to selective logging, and 11 old-growth forests (>200 years) within protected areas. Second-growth forests were dominated by broadleaf species including *Lophozonia obliqua*, *Nothofagus dombeyi*, and *Laurelia sempervirens*. Old-growth stands were mixed conifer-broadleaf forests dominated by *Saxegothaea conspicua*, *Laureliopsis philippiana*, and *N. dombeyi* or by the conifer *Araucaria araucana* and *Nothofagus pumilio*. The understory in both second- and old-growth stands was mostly dominated by bamboo species (*Chusquea* spp.), *Rhaphithamnus spinosus*, different species of *Azara* and *Berberis*, and tree saplings.

Nest searching and monitoring

Over three breeding seasons (2010–2011, 2011–2012, and 2012–2013), from October 1 to February 28 (6 h per day, 6 days per week), we searched for occupied cavities in each forest stands. We followed the protocol for nest localization and monitoring of Martin and Geupel (1993), observing adult behaviour and looking for evidence of recent wear around cavity entrance (Martin et al. 2004; Cockle et al. 2011b). We also followed adults and searched for nests of species generally considered to be open-cup nesters to assess if they used cavities.

We checked the interior of cavities apparently used for nesting. Lower cavities (<2 m high) were checked directly using a flashlight with a mirror and higher cavities (>2 m high) were checked using a wireless monitoring system with a telescopic pole that reached up to 15 m high (Martin et al. 2004; Huebner and Hurteau 2007; Cockle et al. 2011b). When cavities were above 15 m high, we determined if the cavity contained an active nest from the ground, looking for signs of active nesting (e.g. feeding nestlings or removing fecal sacs). We considered a cavity as active when at least one egg or nestling was present in the cavity. For each nest we recorded: breeding species, origin of the cavity (decay-formed or excavated), tree species, and excavator species (in the case the cavity was excavated). We then assigned a unique numbered code for the nest, the cavity, and the nest-tree for monitoring the cavity use across the three breeding seasons. The status of each cavity-nest was checked every 3–4 days to determine the fate of the nest (depredated, number of hatched eggs, number of fledglings) and to determine when cavities were available again for further nesting attempts.

We also conducted a literature review to include nesting information for other cavity-nesting bird species present in our study area but for which we did not find nests. We only included nests from published studies (i.e. thesis and scientific papers) conducted in either the central valley or Andean locations of southern temperate rainforests. We used, for nest web analysis, studies that explicitly mention the SCN species, the tree species and the PCN species (in the case of cavities produced by excavation) involved in the nesting event (e.g. Beaudoin and Ojeda 2011; Carneiro et al. 2013; Díaz and Kitzberger 2013; Figueroa and Corales 2003; Jiménez and White 2011; Ojeda et al. 2007; Wallace 2010). Ornithological books, which did not report this information (e.g. Martínez and González 2004; Altamirano et al. 2012), were used only to complement the species composition of cavity-nesting bird community inhabiting temperate rainforests of South America.

Nest web structure

We classified each cavity-nesting bird as primary cavity nester (PCNs) or secondary cavity nester (SCNs) to construct a hierarchical nest web diagram (sensu Martin and Eadie 1999). We quantified the frequency of interactions between different species of trees, PCNs, and SCNs. A nest web is a quantitative interspecific network in which species that produce cavities (trees and PCNs) are linked to species that use these cavities (SCNs; Cockle et al. 2012). Lines in the nest web diagram represent species interactions. For example, for any species A and B, where A is a cavity consumer and B is a cavity producer (tree or excavator), an interaction occurs when an individual of species A uses a cavity produced by species B. Furthermore, we included tree decay classes in the nest web diagram to depict the nesting substrate selected for nesting by cavity nesters in relation to tree species. Decay classes ranged from 1 to 5 where 1 was a live healthy tree; 2 was a live unhealthy tree; 3 was a recently dead tree; 4 was an old dead tree; and 5 was a naturally fallen tree (modified from Edworthy et al. 2012; Thomas et al. 1979).

Nest-tree attributes and preferences

When each nesting season was over, we quantified nest-tree attributes including tree species, diameter at breast height (DBH, cm), and decay class. Preference is considered the observed pattern of utilization of habitat attributes in contrast to their availability (Jones 2001). To determine preference for specific attributes of nesting-trees, we systematically established a grid of 40 vegetation plots (0.04 ha, radius = 11.2 m) in each forest stand. Each plot was separated by 30 m. For each tree with DBH $\geq$ 12.5 cm present in the vegetation plot, we recorded: species, DBH, and decay class.

Data analysis

We considered each nest as an independent data point (Martin et al. 2004). Because of small sample size in old-growth stands, we pooled all nests for the analysis. We classified each cavity-nesting bird according to its degree of dependence on tree cavities for nesting: obligate, when the species depends strictly on cavities for nesting (>90% of found nests were in tree cavities); facultative, when the species may nest in tree cavities or other substrates (e.g. ground, shrubs) (10.1–90% of found nests in tree cavities); marginal, when the species is chiefly an open-cup nester, but sometimes nests in tree cavities (1–10% found nests in tree cavities); and incidental, when the species was an open-cup nester, but opportunistically may use cavities for nesting (<1% found nests in tree cavities). This classification integrated our own field data with information sourced from field guides and ornithological books (Goodall et al. 1957; Fjeldså and Krabbe 1990; Martínez and González 2004; Altamirano et al. 2012).

We assessed the nest web dominance and evenness to describe the diversity of interactions between bird species and tree species, and between bird species (e.g. a SCN using a cavity excavated by a PCN). Dominance was calculated as the total number of interactions between the two species that interacted most often, divided by the total number of interactions counted for all species (Sabatino et al. 2010; Cockle et al. 2012). The evenness was calculated using the PIE index (Probability of Interspecific Encounter) (Hurlbert 1971):

$$PIE = \sum_{i=1}^{s} \left(\frac{\mathrm{N}_i}{\mathrm{N}}\right)\left(\frac{\mathrm{N}-\mathrm{N}_i}{\mathrm{N}-1}\right)$$

where S is the total number of links in the network, N is the total number of interactions in the network, and N_i is the interaction frequency of the link i. PIE values close to 0 indicate a particular dominant link (almost all interactions occur between one pair of species), and a PIE value of 1 indicates equal partitioning of interactions frequencies in the web (each pair of species interacts the same number of times as each other pair of species) (Hurlbert 1971; Sabatino et al. 2010).

All tree attributes, excluding decay class, are presented as mean ± standard deviation (SD). Decay class is a categorical and rank variable; thus, we present the median and range of its values. To determine the importance of tree attributes (i.e. tree decay and DBH) predicting whether a tree would be used for nesting by a cavity-nesting bird, we fitted generalized linear mixed effect models, with a binary response variable (used or not used tree) and logit link function (Quinn and Keough 2002). Tree decay and DBH were included as fixed effects, and site identity and tree species were fitted as random effects. The mixed effects models, through random effects, allowed us to include tree attributes within the same sites and/or tree species considering any inherent capacity for each site and/or tree species to hold lower or higher numbers of nests (Drever and Martin 2010). To assess the strength of evidence for each tested model, we ranked models using Akaike's information criterion corrected for small sample sizes (AICc) and Akaike model weights (Burnham and Anderson 2002; Johnson and Omland 2004). The model showing the lowest AICc value is the best supported by the data, while the highest weight indicate the best explanatory power (Burnham and Anderson 2002). Chi square was employed to examine the significance of the preference of tree species. One-way ANOVA was used to compare the tree DBH of nesting versus non-nesting trees for each of the most selected tree species. All analysis were conducted using R version 3.3.2 (R Core Team 2017).

Results

Species composition and degree of cavity dependence

We recorded a total of 29 bird species nesting in tree cavities in temperate rainforests of Chile, including species for which we did not find nests (i.e. 10 additional species from literature review), belonging to six orders and 15 families (Table 1). Furnariidae was the most represented family with five species. Cavity-nesting bird species comprised 57% of the avian community in South American temperate rainforests. Twenty-five (86.2%) species were secondary cavity nesters (SCNs) and four (13.8%) were primary cavity nesters (PCNs). From the total species, nine (31%) were endemic to southern temperate rainforests. Among SCNs, ten species (40%) were obligate and 15 (60%) were non obligate cavity nesters. Non obligate cavity nesters included six (24%) facultative, five (20%) marginal, and four (16%) incidental SCNs (Table 1; Fig. 2). Two passerines (*Zonotrichia capensis* and *Spinus barbata*) were not previously described in the literature using cavities for nesting.

Nest web structure: tree decay versus excavation processes

We found 263 nests belonging to 19 bird species. Nests were located in 172 different trees and 215 different cavities. One hundred seventy-two nests (71% of 242 nests, excluding 19 nests in banks and two in unknown tree species) were located in trees belonging to the Nothofagaceae family. Ten tree species were used for nesting, including: *N. dombeyi* (NOTDOM, n = 102 nests), *L. obliqua* (LOPOBL, n = 40 nests), *Gevuina avellana* (GEVAVE, n = 34 nests), *N. pumilio* (NOTPUM, n = 30 nests), *Eucryphia cordifolia* (EUCCOR, n = 13 nests), *Persea lingue* (PERLIN, n = 11 nests), *Dasyphyllum diacanthoides* (DASDIA, n = 4 nests), *Saxegothaea conspicua* (SAXCON, n = 4 nests), *Luma apiculata* (LUMAPI, n = 3 nests), and *Lomatia hirsuta* (LOMHIR, n = 1 nest). We added from the literature review 156 nests, four bird species (i.e. *Strix rufipes*, *Enicognathus ferrugineus*, *Enicognathus leptorhynchus*, and *Anas flavirostris*), and two tree species *Araucaria araucana* (ARAARA) and *L. sempervirens* (LAUSEM) into the nest web composition and structure (Fig. 3).

One hundred fifty-eight (75%) nests of SCNs (non-excavators) were in cavities produced by tree decay processes (e.g. crevices, decay wood, broken branches). The remaining 25% were in excavated cavities. Eleven out of the total of 18 SCNs (61%) never used excavated cavities for nesting. Furthermore, none of the SCN species nested exclusively in excavated cavities. Only three species of SCNs used excavated cavities as their main (>50%) nesting substrate.

All PCNs produced cavities that were used later by SCNs. Within excavated cavities, those excavated by *Pygarrychas albogularis* and *Campephilus magellanicus* were the most used by SCNs for nesting. Twenty-one (68%) cavities used by breeding *Tachycineta meyeni* were produced by PCNs. From this, 18 (86%) nests were in cavities excavated by *P. albogularis*. Three nests (60%) of *S. rufipes* and 31 nests (57%) of *E. ferrugineus* were located in cavities produced by *C. magellanicus* (from literature review: Beaudoin and Ojeda 2011; Díaz and Kitzberger 2013). From the 71 links and 427 interactions recorded, the most frequent were between *C. magellanicus* and *N. pumilio* (54 interactions), and between *A. spinicauda* and *N. dombeyi* (39 interactions). The network dominance was low (0.124) and the PIE index indicated a high evenness (0.952).

Table 1 Species names, code, and degree of tree cavity dependence by cavity-nesting bird community in temperate rainforests of South America

Species		Species code	Tree cavity dependence[c]
Scientific name	Common English name		
Primary cavity nesters			
Veniliornis lignarius[b]	Striped woodpecker	VENLIG	O
Colaptes pitus	Chilean flicker	COLPIT	O
Campephilus magellanicus	Magellanic woodpecker	CAMMAG	O
Pygarrhychas albogularis[b]	White-throated treerunner	PYGALB	O
Secondary cavity nesters			
Chloephaga poliocephala[a]	Ashy-headed goose	CHLPOL	I
Anas flavirostris[a]	Speckled teal	ANAFLA	M
Milvago chimango	Chimango caracara	MILCHI	M
Falco sparverius[a]	American kestrel	FALSPA	O
Enicognathus ferrugineus[a,b]	Austral parakeet	ENIFER	O
Enicognathus leptorhynchus[a,b]	Slender-billed parakeet	ENILEP	O
Tyto alba[a]	Barn owl	TYTALB	O
Bubo magellanicus[a]	Magellanic horned-owl	BUBMAG	F
Strix rufipes[a,b]	Rufous-legged owl	STRRUF	O
Glaucidium nana	Austral pygmy-owl	GLANAN	O
Cinclodes fuscus	Bar-winged cinclodes	CINFUS	F
Cinclodes patagonicus	Dark-bellied cinclodes	CINPAT	M
Aphrastura spinicauda[b]	Thorn-tailed rayadito	APHSPI	O
Leptasthenura aegithaloides	Plain-mantled Tit-spinetail	LEPAEG	O
Pteroptochos tarnii[b]	Black-throated huet-huet	PTETAR	F
Scelorchilus rubecula[b]	Chucao tapaculo	SCERUB	F
Scytalopus magellanicus	Magellanic tapaculo	SCYMAG	F
Elaenia albiceps[a]	White-crested elaenia	ELAALB	I
Tachycineta meyenii	Chilean swallow	TACMEY	O
Pygochelidon cyanoleuca	Blue-and-white swallow	PYGCYA	M
Troglodytes aedon	Southern house wren	TROAED	O
Turdus falcklandii	Austral thrush	TURFAL	F
Zonotrichia capensis	Rufous-collared sparrow	ZONCAP	I
Phrygilus patagonicus[b]	Patagonian sierra-finch	PHRPAT	M
Spinus barbatus[a]	Black-chinned siskin	SPIBAR	I

[a] Species classified as cavity-nester by literature review (Ojeda and Trejo 2002; Martínez and González 2004; Beaudoin and Ojeda 2011; Jiménez and White 2011; Peña-Foxon et al. 2011; Altamirano et al. 2012; Carneiro et al. 2013). *Spinus barbatus* was recorded by the authors nesting in a tree cavity in an Andean location, but out of the study area

[b] Endemic species (Vuilleumier 1985; Rozzi et al. 1996)

[c] *O* Obligate, depends strictly on tree cavities for nesting (>90% of nests in tree cavities); *F* facultative, when the species may nest in tree cavities or other substrates (e.g. ground, shrubs) (10.1–90% of nests in cavities); *M* marginal, when the species is chiefly an open-cup nester, but may occasionally nest in tree cavities (1–10% nests in tree cavities); *I* incidental, when the species was an open-cup nester, but opportunistically may use cavities for nesting (<1% nests in tree cavities) (Altamirano and Ibarra unpubl. data)

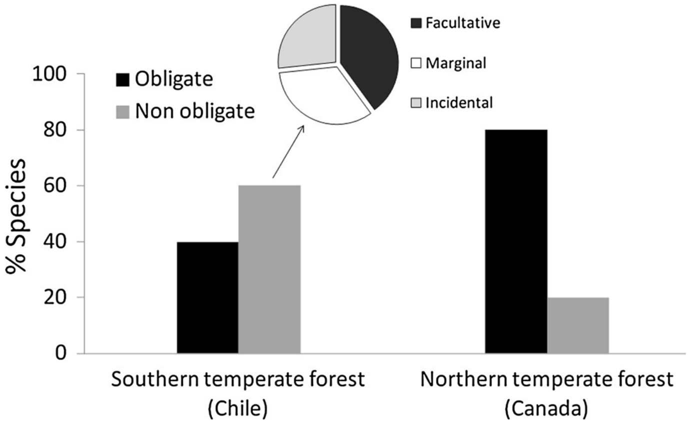

Fig. 2 Degree of tree cavity dependence by secondary cavity-nesting birds in southern (this study) and northern temperate forests (Martin unpublished data). *Black bars* show the percentage of obligate cavity nesters (>90% of found nests were in tree cavities). *Gray bars* show the percentage of non-obligate cavity nesters. *Circle chart* shows the percentage of species, within non-obligate cavity nesters, which are facultative (10.1–90% of nests in tree cavities), marginal (1–10% of nests in tree cavities), and incidental (<1% of nests were in tree cavities) cavity nesters in South American temperate rainforests

Tree utilization and preferences

Nothofagus dombeyi was the main tree species used for nesting; this tree species was also utilized disproportionally more than its availability ("preferred", $X^2 = 10.56$; $p < 0.001$). The same pattern was found for *G. avellana* ($X^2 = 19.18$; $p < 0.0001$). Seventy-nine percent of the cavity nests present in *G. avellana* belonged to either *Troglodytes aedon* (16 nests) or *A. spinicauda* (11 nests). In contrast, *L. obliqua* was utilized disproportionally less in relation to its availability ("avoided", $X^2 = 4.74$; $p = 0.03$). We did not find any preference or avoidance in the utilization of *E. cordifolia* ($X^2 = 1.58$; $p = 0.21$) and *N. pumilio* ($X^2 = 1.20$; $p = 0.27$), as they were utilized proportionally to their availability (Fig. 4a).

The occurrence of cavity-nests in trees was best predicted by a model including DBH and tree decay (Table 2). The probability that trees are used for nesting by cavity-nesting birds was positively associated with diameter at breast height (DBH, $b_{(\mathrm{DBH})} = 0.04$, $SE = 0.001$, $z = 9.41$, $p < 0.001$). Birds used trees ranging from 11.6 to 193.8 cm DBH. *Colaptes pitius*, *Pteroptochos tarnii*, and *Glaucidium nana* used the largest trees, while *Veniliornis lignarius*, *P. albogularis*, and *T. aedon* used the smallest trees (Table 3). Mean DBH of nest-trees differed significantly between nesting bird species ($F = 4.40$; $p < 0.001$; Table 3). Trees used for nesting were significantly larger (mean DBH ± SD = 57.26 ± 34.88 cm) than those available in their stands (mean ± SD = 26.11 ± 19.99 cm; $F = 350.80$; $p < 0.01$; Fig. 4b). We found that DBH for all trees used for nesting were larger than those available in their stands: *N. dombeyi* (mean DBH = 79.4 vs. 29.4 cm; $F = 325.49$; $p < 0.01$), *L. obliqua* (mean DBH = 39.9 vs. 25.9 cm; $F = 29.38$; $p < 0.001$), *G. avellana* (mean DBH = 21.4 vs. 14.8 cm; $F = 75.56$; $p < 0.001$), *N. pumilio* (mean DBH = 60.2 vs. 46.5 cm; $F = 9.33$; $p < 0.01$), and *E. cordifolia* (mean DBH = 42.8 vs. 21.5 cm; $F = 34.73$; $p < 0.001$) (Fig. 4b). The mean diameter of fallen trees used for nesting was 66.12 ± 39.33 cm.

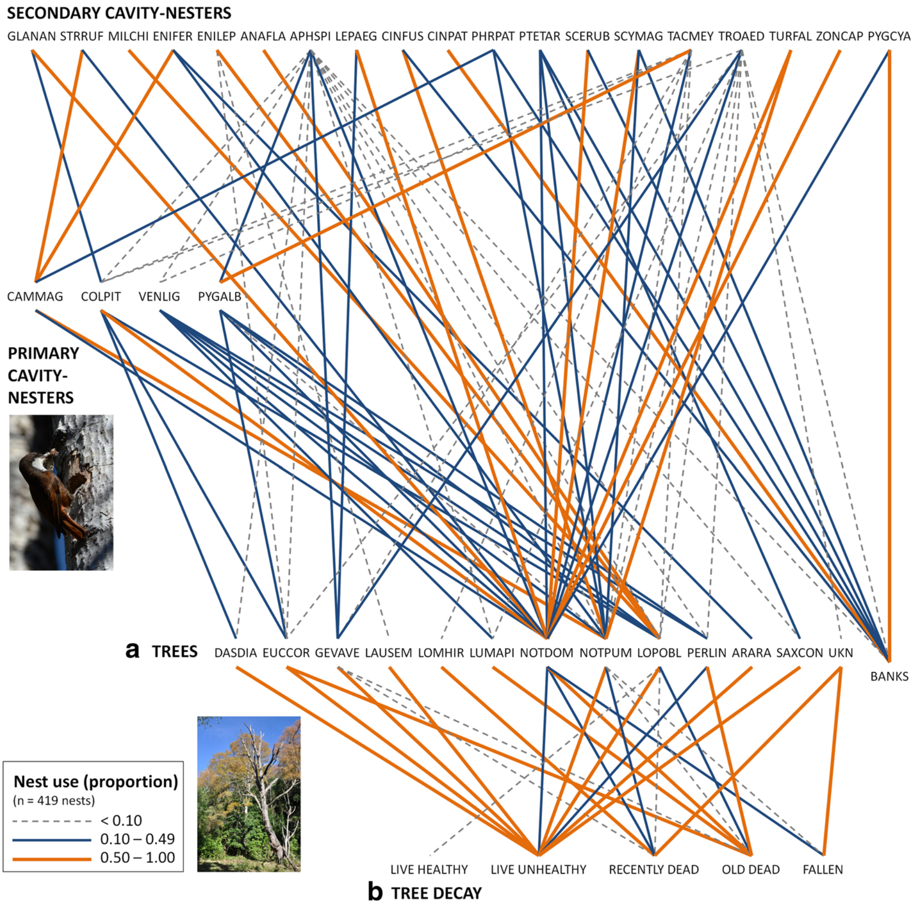

Fig. 3 Nest web structure in southern temperate rainforests. The diagram is divided in two parts: **a** above the tree species level, showing links between secondary cavity-nesters, primary cavity-nesters, and tree species, and **b** below the tree species level, showing the links between tree species and tree decay. The frequency of the relationship is indicated by three types of lines: *thick lines* (more than 50% of nests), *thin lines* (between 10 and 49% of nests), and *dashed lines* (less than 10% of nests). Sample size includes nests from our literature review. See Table 1 for codes of bird species and text for codes of tree species. (Color figure online)

Tree decay class strongly predicted the occurrence of cavity-nests in trees (Table 2). Tree decay increased the probability that trees are used by cavity-nesting birds for nesting, being positively associated with each tree decay category, excepting with live healthy trees. Snags and fallen trees (this last decay class only used by SCNs) were the most common nest substrate (58%; Fig. 4c). Among tree decay classes, and considering the availability of each decay class in forest stands, birds showed a strong preference for the two most advanced stages of tree decay: fallen trees ($b_{(\text{tree decay } 5)} = 7.30$, SE $= 1.149$, $z = 6.35$, $p < 0.001$) and old dead trees ($b_{(\text{tree decay } 4)} = 6.87$, SE $= 1.041$, $z = 6.60$, $p < 0.001$). For example, *Scelorchilus rubecula* and *Scytalopus magellanicus* nested in cavities available chiefly in fallen trees (91%). Live unhealthy trees ($b_{(\text{tree decay } 2)} = 3.91$,

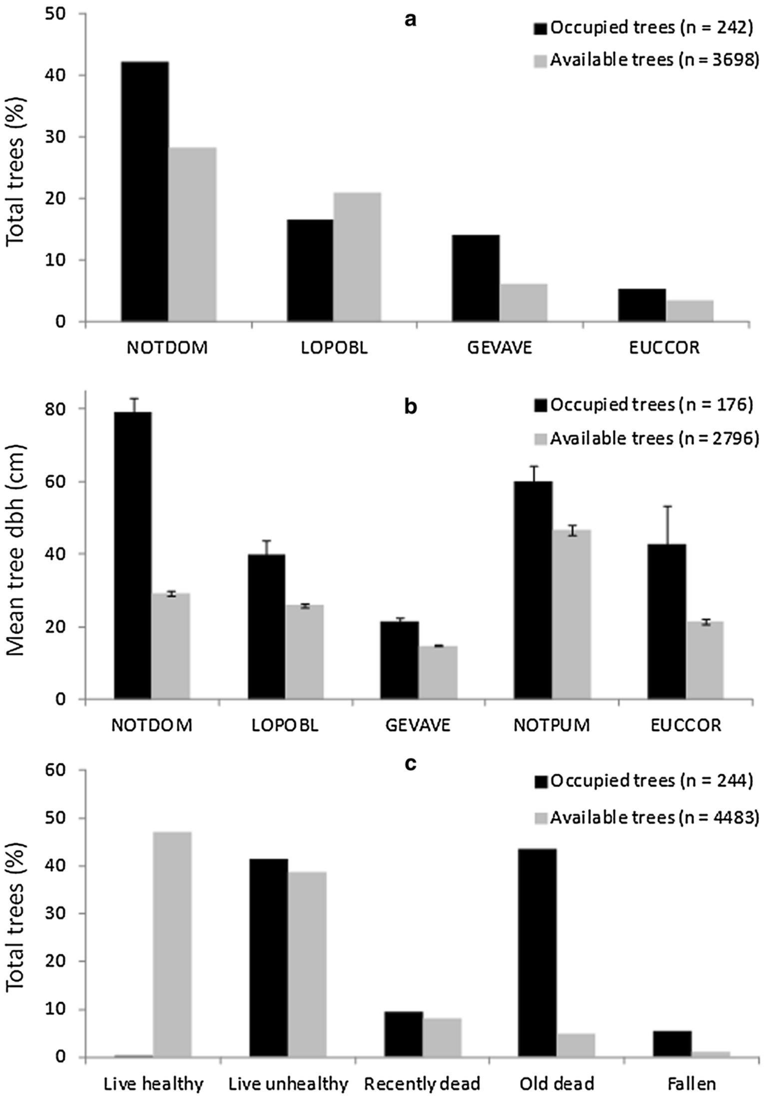

Fig. 4 Nest-tree attributes preferred (i.e. utilization in relation to their availability) by secondary cavity nesters in temperate rainforests of South America. **a** Species, **b** diameter at breast height (DBH), and **c** decay class. *Error bars* indicate standard error. See text for codes of tree species and decay classes

SE = 1.024, $z = 3.82$, $p < 0.001$) and recently dead trees ($b_{(\text{tree decay 3})} = 2.98$, SE = 1.081, $z = 2.76$, $p < 0.01$) were also preferred by cavity-nesting birds. For example, *P. tarnii* nested in cavities available mostly in live unhealthy trees (86%). Live healthy trees were the most abundant tree decay class in the area, but were used for nesting only once out of 263 nests (avoided, $b_{(\text{tree decay 1})} = -11.07$, SE = 1.51, $z = -7.33$, $p < 0.001$) (Fig. 4c). Most birds nesting in live trees used a dead section of the main trunk or a dead branch as nest substrate (83%).

Table 2 Ranking of generalized linear mixed effect models (binary function) predicting whether trees would be used for nesting as a function of tree decay and trees DBH by the cavity-nesting bird community in South American temperate rainforests

Predictor variables	*k*	LogLik	AICc	ΔAIC	Weight
Tree decay + DBH	**8**	**−397.39**	**810.82**	**0.00**	**1**
Tree decay	7	−452.78	919.59	108.77	0
DBH	4	−533.20	1074.41	263.59	0
Null model	3	−597.86	1201.72	390.90	0

The best model in bold

Discussion

High proportion of cavity nesters in the temperate rainforest bird community

Our nest web analysis of the cavity-nesting community described the links and interactions among birds, cavities, and trees in temperate rainforests of South America. This forest bird community shows one of the highest reported proportion of tree cavity nesters (57% of the bird community) for any forest system. For example, 25–30% of the bird community relies on tree cavities in the Pacific northwest (Bunnell et al. 1999), 50% in southeastern Oregon (Dobkin et al. 1995), 32–43% in northeastern Colorado (Sedgwick and Knopf 1986), 15% in central Venezuela (Gibbs et al. 1993), and 33% in both central Costa Rica and northern Belize (Gibbs et al. 1993). Contrary to temperate forests in the northern hemisphere (Gibbs et al. 1993), we found half the proportion of primary cavity nesters (PCNs) in southern temperate forests at the same latitude (39° LS; 29 vs. 14% of the cavity-nesting bird community for the northern and southern hemispheres, respectively).

Our findings show that most cavity nesters (60%) from temperate rainforests of South America do not strictly depend on tree cavities for nesting. This result contrasts with the high degree of tree cavity dependence in temperate forests in Canada, where 80% of cavity nesters are obligate (Martin unpublished data). This high contrast between temperate areas may be associated with the higher proportion of resource generalist species in relation to resource specialists in temperate rainforests of South America (Vuilleumier 1985; Jaksic and Feinsinger 1991). Forest degradation will likely play a stronger detrimental effect over obligate cavity-nesters (40% of the southern temperate rainforests bird community) as they are species highly specialized on a specific nesting resource (Devictor et al. 2008). In fact, most obligate cavity nesters in southern temperate rainforests show the highest degrees of habitat specialization among the avian community and are known to be strongly affected by habitat loss and degradation in southern temperate forests (Ibarra and Martin 2015b).

Cavities produced by tree decay as the key driver structuring the Andean nest web

The nest web in southern temperate rainforests shows an A shape (Fig. 1), with higher number of species in both extremes of the nest web (i.e. trees and secondary cavity nesters, SCNs). This result is similar to the shape of the nest web reported for subtropical Atlantic forests (Cockle et al. 2012). However, although birds nest in 12 tree species in southern temperate rainforests, 71% of the network depends on three tree species from the same

Table 3 Nest-tree attributes for cavity nesting birds, from our field study, in the temperate rainforest of South America

Species	*Nothofagus dombeyi*			*Lophozonia obliqua*			*Gevuina avellana*		
	DBH	Decay class		DBH	Decay class		DBH	Decay class	
	Mean ± SD	Median (range)	n	Mean ± SD	Median (range)	n	Mean ± SD	Median (range)	n
Primary cavity nesters									
Veniliornis lignarius									
Colaptes pitus	181.1	2 (2)	1						
Campephilus magellanicus	133.7	2 (2)	1						
Pygarrhychas albogularis	102.4	2 (2)	1	29.6 ± 14.6	4 (1–4)	10			
Secondary cavity nesters									
Milvago chimango				64.6	4 (4)	1			
Glaucidium nana	113.2	3 (3)	2	83.3	2 (2)	1			
Cinclodes fuscus									
Aphrastura spinicauda	75.5 ± 25.9	4 (2–5)	49	35.1 ± 10.8	4 (2–4)	16	18.0 ± 4.4	2 (2–4)	11
Leptasthenura aegithaloides	69.4 ± 2.7	4 (4)	2				23.5	2 (2)	1
Pteroptochos tarnii	193.8	3 (2–4)	2						
Scelorchilus rubecula	72.0 ± 34.7	5 (4–5)	6						
Scytalopus magellanicus	61.3 ± 51.1	5 (5)	4						
Tachycineta meyenii	106.1 ± 32.9	3 (2–4)	13	29.7 ± 13.6	4 (2–4)	6	26.2	2 (2)	1
Pygochelidon cyanoleuca	126.4	5 (5)	1						
Troglodytes aedon	60.5 ± 17.9	4 (2–4)	16	60.1 ± 23.3	2 (2–4)	5	22.7 ± 7.6	2 (2–3)	16
Turdus falcklandii	42.4	4 (4)	1						
Zonotrichia capensis	75.3	2 (2)	1						
Phrygilus patagonicus	61.3	3 (3)	1						

Table 3 continued

Species	*Nothofagus dombeyi*			*Lophozonia obliqua*			*Gevuina avellana*		
	DBH	Decay class		DBH	Decay class		DBH	Decay class	
	Mean ± SD	Median (range)	n	Mean ± SD	Median (range)	n	Mean ± SD	Median (range)	n
Primary cavity nesters									
Veniliornis lignarius	43.2	2 (2)	1				26.9	3 (2–4)	2
Colaptes pitus							181.1	2 (2)	1
Campephilus magellanicus							133.7	2 (2)	1
Pygarrhychas albogularis	51.4 ± 30.5	3 (2–4)	2	16.1 ± 1.2	4 (4)	3	35.9 ± 27.5	4 (1–4)	20
Secondary cavity nesters									
Milvago chimango							64.6	4 (4)	1
Glaucidium nana							103.2 ± 17.5	3 (2–3)	3
Cinclodes fuscus	63.6 ± 7.9	2 (2)	2				63.6 ± 7.9	2 (2)	3
Aphrastura spinicauda	60.9 ± 23.2	2 (2–4)	9	65.0 ± 43.4	2 (2–4)	5	58.5 ± 31.4	4 (2–5)	102
Leptasthenura aegithaloides							54.1 ± 26.6	4 (2–4)	3
Pteroptochos tarnii	81.8 ± 38.5	2 (2)	2				104.4 ± 47.2	2 (2–4)	8
Scelorchilus rubecula							72.0 ± 34.7	5 (4–5)	7
Scytalopus magellanicus	63.9	5 (5)	1				62.0 ± 41.8	5 (5)	6
Tachycineta meyenii	60.6 ± 19.5	2 (2–3)	5	43.9 ± 45.7	4 (2–4)	3	71.9 ± 42.9	3 (2–4)	31
Pygochelidon cyanoleuca							126.4	5 (5)	3
Troglodytes aedon	49.4 ± 17.6	2 (2–4)	5	25.8 ± 0.0	4 (4)	2	41.9 ± 21.9	2 (2–5)	54
Turdus falcklandii	69.3	3 (3)	1				55.9 ± 19.0	3.5 (3–4)	2
Zonotrichia capensis							75.3	2 (2)	1
Phrygilus patagonicus	61.3	3 (3)	1				61.3	3 (3)	3

DBH diameter at breast height, *n* is the number of occupied nests. Decay classes were modify from Thomas et al. (1979), where 1 represents live healthy trees, 2 live unhealthy trees, 3 recently dead trees, 4 old dead trees, and 5 fallen trees family (Nothofagaceae). On the other hand, the proportion of tree species used by cavity nesters in southern temperate rainforests is relatively larger (50% out of 24 tree species, Altamirano 2014) in comparison to the 27 tree species and one palm (20% out of 132 tree species) recorded for Atlantic forests (Ribeiro et al. 2009; Cockle et al. 2012).

Despite the relatively low richness (n = 29 species) in our cavity-nesting community, there is a comparable diversity of ecological functions in relation to other cavity-nesting communities with two to three times more species (e.g. Cockle et al. 2011a, b; Gibbons and Lindenmayer 2002). For example, among PCNs, our forests support two small-bodied excavators (26 g, *P. albogularis* and 40 g, *V. lignarius*), one mid-sized excavator (125 g, *C. pitius*) and one large excavator (260 g, *C. magellanicus*) (Cofre et al. 2007; Ibarra and Martin 2015b). This condition makes our nest web vulnerable to species loss: if one of the excavator species is lacking, all of an excavated cavity size spectrum might be lost (Ibarra and Martin 2015b). In contrast to North American forests in British Columbia (Canada) and Florida (United States) (Martin et al. 2004; Blanc and Walters 2008a), our results suggest a relatively high evenness in the interactions among trees, SCNs, and PCNs. In southern temperate rainforests, a relatively wide distribution of links generates a low dominance index (0.12 vs. 0.24 for northern temperate forests of Canada, and 0.43 for longleaf pine forests; Cockle et al. 2012). However, our dominance index was 4.5 times higher than the one reported for Atlantic forests (0.028; Cockle et al. 2012), likely related to a network depending mostly on only three tree species from the family Nothofagaceae for nesting. The dominance index found in this study is equivalent to the one found in subtropical piedmont forests (0.12; Ruggera et al. 2016), where also a few number of tree species are mainly used by cavity-nesting birds.

Similar to a cavity-nesting community in Atlantic forests (80% of cavity-nests in Argentina; Cockle et al. 2011a, 2012), we found that decay-formed cavities in southern temperate forests were much more utilized by cavity nesters (75% of nesting cavities) compared to excavated cavities. This result contrasts with cavity-nesting communities in North America. In temperate forests of Canada, only 10% of cavities used by SCNs were produced by tree decay (Aitken and Martin 2007). In longleaf pine forests of United States, <1% of nests were in cavities produced by tree decay (Blanc and Walters 2008b).

Excavated cavities can be produced at relatively higher rates and have similar persistence to those produced by tree decay in northern temperate forests (Edworthy et al. 2012). In contrast, high quality cavities for cavity nesters generated by tree decay require long-term periods to be produced (Lindenmayer et al. 1993; Koch et al. 2008a). For example, in Australia more than 100 years are necessary to form a non-excavated cavity and more than 200 years for large cavities (>10 cm of entrance diameter, Gibbons et al. 2002; Koch et al. 2008a, b). To understand the underlying mechanisms behind the importance of tree decay processes in producing nest-cavities in southern temperate rainforests, future studies should assess cavity persistence because it has been proposed as the main factor explaining a higher use of cavities produced by either tree decay or excavation for different forest systems (Cockle et al. 2011a). Anyhow, cavity availability and breeding success in cavities produced either by tree decay or excavation in forest stands, may also play a strong role in cavity selection by cavity-nesters (Robles and Martin 2013). Therefore, future assessments on the relative importance of quantity (availability plus persistence) and quality (breeding success) of cavities created by both tree decay and excavation processes may untangle the underlying drivers behind our results for southern temperate ecosystems.

The importance of large decaying and dead trees

Our findings support the hypothesis that large decaying trees are exceptionally important stand-level attributes for cavity-nesting birds (Gibbons et al. 2002; Díaz et al. 2005; Cockle et al. 2011b; Robles and Ciudad 2012; Caviedes and Ibarra 2017), determining whether bird species are present or not in some areas (Politi et al. 2009; Ibarra and Martin 2015b). Cavity-nesting species showed a strong preference for large decaying trees of all tree species utilized for nesting. Because our system is highly dependent on non-excavated cavities, tree DBH may explain the increase in number of cavities per tree and in cavity volume in forests (as was found in New Zealand forests; Blakely et al. 2008). On the other hand, PCNs have been proposed to play a much more important role as cavity producers in forests with a low number of decay-formed cavities (e.g. second-growth forest stands; Remm and Lõhmus 2011). As our data base comes mainly from second-growth forests, probably cavity-nesting bird communities breeding in old-growth forests rely even more on non-excavated cavities, because these forests contain the highest density of decay-formed cavities (as was found in North America and European forests; Remm and Lõhmus 2011; Wesołowski and Martin 2017). However, future studies contrasting nest web composition and structure between old-growth and second-growth forests may provide valuable insights on how tree-cavity networks of southern temperate rainforests vary across forests of different ages.

We found a key role of snags and fallen trees for cavity nesters. This result contrasts to temperate forest of Canada (Martin et al. 2004), where 55% of cavity-nesting birds nest in living trees, but is similar to longleaf pine forest in Florida where 73% of cavity-nesting birds nests in snags (Blanc and Walters 2008a, b). Southern temperate rainforests contain a high density of snags (Carmona et al. 2002) but, as we found in our study, they are in much lower proportion than living trees. The strong preference for snags by cavity nesters may be associated with the high number of cavities available in these trees (Boyle et al. 2008) and the softer wood to produce cavities by excavators (Thomas et al. 1979). The strong preference for fallen trees showed by the cavity-nesting bird community in southern temperate rainforest has no comparison with any previous nest web study (Martin et al. 2004; Blanc and Walters 2008b; Cockle et al. 2012; Ruggera et al. 2016). Among all previous nest web studies, the maximum utilization rate of fallen trees has been reported for temperate forests of Canada (1% of the nests, Martin et al. 2004). In our study area, in forest stands where understory birds such as the tapaculos (Rhinocryptidae, *S. rubecula* and *S. magellanicus*) avoid the forest edge and nest in the forest interior, they use almost exclusively cavities available in fallen trees. Thus, these species may be considered “fallen tree specialists”, similar to what has been reported for other taxa showing a strong selection of fallen trees for breeding (e.g. Diptera, Rotheray et al. 2001).

Implications for forest bird conservation

Nest web analyses provide insights into both the forces determining community structure and the potential effects of forest degradation on cavity-nesting communities (Blanc and Walters 2007; Cockle et al. 2012). Our study suggests that certain forest management schemes reducing the availability of large decaying trees, snags, and naturally fallen trees can be detrimental for cavity-nesting communities (Drever and Martin 2010; Politi et al. 2010; Caviedes and Ibarra 2017), as they directly decrease the availability of tree cavities and their persistence (Edworthy and Martin 2013). Recently, Ibarra and Martin (2015a, b) recommended the maintenance of multi-aged forest stands with a variety of tree sizes (mean DBH = 37.6 ± 12.5 cm), including living trees and snags, to protect bird species of conservation concern in southern temperate forests. Here, we are more conservative and recommend forestry schemes to maintain a full range of diameter classes, especially large trees (DBH > 57 cm) for benefiting cavity nesters. We also suggest maintaining a high number of large fallen trees with a diameter larger than 65 cm.

Forest management schemes should not only consider the presence of snags and fallen trees, but also ensure the retention of all classes of tree decay (Cockle et al. 2011a). This consideration will secure a continuous supply of cavities from trees that currently have many cavities to trees that will provide many cavities in the future. Worldwide, the great majority of forest policies specify a lower diameter limit of trees to be harvested (as the case of Argentina; Cockle et al. 2011a), generally protecting younger trees and discouraging the presence of large decaying trees and snags (Lindenmayer et al. 2014; Müller et al. 2016). In Chile, the national forestry policy only superficially mentions tree DBH and does not consider snags and fallen trees (Law number 20 283; CONAF 2014). Even more, the Chilean forestry policy indicates that woody debris (e.g. fallen trees) with diameter >3 cm can be removed from managed areas. Mandatory limits on the harvest of trees should go beyond protecting only young trees. These should also establish harvest limits for large decaying trees, snags, and limit the removal of fallen trees. We encourage the Chilean Forestry Service (CONAF), forestry companies, and forestry certification agencies to incorporate these recommendations in forest management plans.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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