

Large trees and decay: Suppliers of a keystone resource for cavity-using wildlife in old-growth and secondary Andean temperate forests

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Abstract Tree cavities are a keystone resource for many wildlife species worldwide. In Andean temperate forests of South America, many species of birds, mammals and reptiles use cavities to achieve their life history requirements. However, information on cavity supply and drivers of cavity production in these forests remains largely undocumented. We examined the patterns of tree-cavity supply in successional native forests, exploring the potential drivers of cavity occurrence and relative abundances in Andean temperate ecosystems of southern Chile. In 10 forest stands, we established 369 vegetation plots and measured 7951 trees. For each tree, we recorded the species and measured the diameter at breast height (DBH), decay class and number of cavities. While tree density was much higher in secondary than in old-growth forest stands, the density of nonexcavated cavities was higher in old-growth than in secondary forests. Cavity occurrence and relative abundances (number of cavities per tree) were higher in large decaying and standing dead trees (i.e. habitat legacies) than in young healthy trees. Importantly, DBH and decay had a stronger influence on the supply of nonexcavated than excavated cavities. Our results highlight the importance of old-growth forest stands, tree decay processes and habitat legacies for securing a continuous supply of a keystone habitat resource for tree cavity-using wildlife in a global biodiversity hotspot of South America.

Key words: cavity nesters, cavity supply, Chile, habitat legacies, snags, standing dead trees, tree decay.

INTRODUCTION

Tree cavities, epiphytes, mistletoes and canopy-emergent trees are generally considered as critical habitat for a range of species, from invertebrates through birds to mammals, because of their disproportionate contribution to boosting forest biodiversity (Nadkarni & Matelson 1989; Michel & Winter 2009; Díaz *et al.* 2012; Regnery *et al.* 2013a; Griebel *et al.* 2017). In particular, tree cavities are a keystone resource as nesting, roosting and sheltering sites for many wildlife vertebrate species (Martin & Eadie 1999; Cockle *et al.* 2011). Worldwide, at least 1878 bird species and many mammal, reptile and amphibian species utilise tree cavities for achieving their life history needs (van der Hoek *et al.* 2017). Excavated cavities are produced by the action of primary cavity nesters (PCNs; e.g. woodpeckers), while nonexcavated cavities are produced by tree decay processes associated

with the action of insects, fungi, wind, drought and/or fire (Gibbons & Lindenmayer, 2002; Cockle *et al.*, 2011; Hussain *et al.* 2013; Altamirano *et al.* 2017a). Secondary cavity nesters (SCNs) are species not able to create their own cavities and thus rely on cavities generated by either PCNs or decay.

A range of drivers may influence the supply of cavities (including their density or number per ha, occurrence or presence/absence and relative abundances or number of cavities per tree), such as the size and age of cavity trees (Fan *et al.* 2003; Blakely & Didham 2008; Koch *et al.* 2008). At the stand scale, studies have reported higher supply of tree cavities in old-growth than in secondary forests. For example, in European oak forests (Camprodon *et al.* 2008) and subtropical Atlantic forests (Cockle *et al.* 2010), old-growth stands showed higher supply of tree cavities than early successional and logged forests. Similar results were found in forests of Australia (Gibbons & Lindenmayer 1996; Gibbons & Lindenmayer 2002; Koch *et al.* 2008). At the tree scale, large decaying trees are generally considered more

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likely to produce cavities than younger and smaller trees (Fan *et al.* 2003; Blakely & Didham 2008; Hussain *et al.* 2013).

Tree-cavity supply can potentially be reduced by forest loss and degradation because these processes alter the distribution of tree sizes and associated tree-dependent wildlife (Politi *et al.* 2010; Andersson *et al.* 2018). Specifically, direct loss of cavity trees by their removal for timber or other uses, and the limited recruitment of trees into cavity tree cohort have been considered the main causes reducing tree-cavity supply (Hussain *et al.* 2013). Large decaying trees are generally targeted during selective logging because of their high commercial value, and also to reduce hazards such as lightning attraction, tree falls and foci of infection for healthy trees (Everett & Otter 2004; Lindenmayer *et al.* 2012). Standing dead trees (i.e. snags) are commonly considered by the public and forest managers as either 'wasteful', indicative of unhealthy forest condition, or good as firewood; thus, they are frequently the first forest stand-scale component to be removed (Ibarra & Martin 2015). However, large decaying trees and snags can play critical ecological roles as habitat legacies, buffering local species extinction in secondary forest stands (Ibarra *et al.* 2017aa). Tree-cavity supply has been studied in Europe, North and Central America, Australia, Asia and subtropical South America (e.g. Blakely *et al.* 2008; Boyle *et al.* 2008; Koch *et al.* 2008; Cockle *et al.* 2008; Michel & Winter 2009; Politi *et al.* 2010; Edworthy *et al.* 2012; Regnery *et al.* 2013b), but it remains unknown for other globally threatened ecosystems, such as Andean temperate forests of South America. Furthermore, while many of these studies report the supply of tree cavities, only a handful specifically examine the drivers influencing the supply of excavated and nonexcavated cavities.

Andean temperate forests of South America, dominated by several *Nothofagus* species, are considered one of the 35 global biodiversity hotspots because of its high rates of both species endemism and deforestation (Armesto *et al.* 1998; Myers *et al.* 2000). Remaining forest stands showing suitable habitat for cavity-using wildlife, such as sites with large decaying trees and snags, are commonly being degraded and underused by cavity nesters (Vergara & Armesto 2009; Ibarra & Martin 2015). In Andean temperate forests, at least 29 bird species (four primary and 25 secondary cavity nesters), six mammals, three reptiles and one amphibian utilise cavities during their life cycle (Ibarra *et al.* 2014; Altamirano *et al.* 2017a; Altamirano *et al.* 2017b; Novoa *et al.* 2019). These ecosystems show one of the highest reported proportion of cavity-nesting birds (57% of the entire bird community) for any forest system globally (Altamirano *et al.* 2017a). As such, it is critical to understand patterns and processes of tree-cavity supply

so as to inform environmental and forestry agencies charged with the protection of forest biodiversity in this global biodiversity hotspot.

In this paper, we examine the patterns of tree-cavity supply in successional native forests from the Andes of southern Chile, exploring the drivers that potentially influence the density, occurrence and relative abundances of this keystone resource for forest-dwelling vertebrates. Specifically, we (i) compare forest stand-level attributes, including the density of live and dead trees, cavity trees and cavities, between old-growth and secondary forests. We then (ii) examine the potential role of tree size and tree decay class on the occurrence and relative abundances both excavated and nonexcavated cavities in Andean temperate forests. We predicted that (a) Andean old-growth temperate forests will show higher densities of large decaying and dead trees, and thus higher densities of cavities, than secondary forest stands. We further predicted that (b) selected tree parameters, commonly associated with old-growth forest stands, will be positively associated with the supply of both excavated and nonexcavated cavities in native forests of a global biodiversity hotspot from southern Chile.

METHODS

Study area

The study was conducted in the Municipality of Pucón, La Araucanía Region, Chile. The main weather characteristics of Andean temperate forests are cool summers and abundant precipitation throughout the year (>2000 mm). We surveyed ten forest stands, including five old-growth stands (>200 years) inside or surrounding protected areas and five secondary stands (40–80 years old), under selective logging (Altamirano *et al.* 2017a). Midelevation old-growth stands (500–900 m of elevation) were mixed conifer–broadleaf forests dominated by the conifer *Saxegothaea conspicua* and the broadleaf species *Laureliopsis philippiana* and *Nothofagus dombeyi*. High-elevation stands (900–1500 m of elevation) were dominated by *N. pumilio* and the conifer *Araucaria araucana*. Secondary stands were dominated by broadleaf species including *N. dombeyi*, *N. obliqua*, *Laurelia sempervirens*, *Gevuina avellana* and *Persea lingue*.

Vegetation and cavity surveys

To quantify forest stand-level structural attributes and the occurrence and relative abundances of both excavated and nonexcavated cavities, between 2010 and 2017, we randomly deployed 369 vegetation plots (0.04 ha, radius = 11.2 m) across the 10 forest stands (Ibarra *et al.* 2014). For every tree with DBH > 12.5 cm, we recorded the tree species, diameter at breast height (DBH in cm) and decay class. Decay classes assigned were 1 (live healthy tree); 2 (live unhealthy tree); 3 (recently dead tree); 4 (long dead tree); and 5 (naturally fallen tree; modified from

Thomas *et al.* 1979; Edworthy *et al.*, 2012). For each tree, we counted the number of excavated and nonexcavated cavities. To consider a cavity as ‘potentially usable’ by vertebrate cavity nesters, it required to have an entrance diameter ≥ 2.5 cm and an internal chamber, surrounded by sound (not fallen) wood, which could eventually work as an incubation chamber for cavity nesters in our study area. These criteria were based on our knowledge of cavities used by cavity-nesting birds, mammals and reptiles in Andean temperate forests (Ibarra *et al.* 2014; Ibarra *et al.* 2017aa; Ibarra *et al.* 2017b; Altamirano *et al.* 2017a; Altamirano *et al.* 2017b; Novoa *et al.* 2019). To verify these criteria, we inspected reachable cavities with a camera system attached to a 15-m extendible pole.

Data analysis

We first examined differences in forest structural attributes between old-growth and secondary forest stands. For this, we estimated the density (number/ha) of (a) live trees, (b) dead trees (i.e. decay classes 3 to 5), (c) cavity trees (i.e. trees with at least one cavity), (d) all cavities (including excavated and nonexcavated), (e) density of excavated cavities (number/ha) and (f) density of nonexcavated cavities (number/ha). We examined differences between old-growth and secondary forest stands for these attributes using Mann–Whitney tests (Dytham 2011).

We used generalized linear mixed-effects models (GLMMs), with a binomial error distribution and a logistic link function, to predict the probability for a tree to hold a cavity according to tree characteristics. The binomial dependent variable was the occurrence of cavities (presence = 1; absence = 0). We used GLMMs, with a Poisson error distribution and a logarithmic link function (Royle *et al.* 2004), to predict the relative abundances of cavities (number per tree) according to tree characteristics. Mixed-effects models integrate both fixed effects, which explain variation in the response variable, and random effects, which serve as additional error terms to account for correlations among observations within the same group. Fixed effects tested included tree DBH and decay class. We used site identity and tree species as random effects. We included logarithmic terms for tree DBH to account for decelerating or accelerating responses in all tests. We calculated and used Akaike’s information criterion (AIC) to rank and select the most supported models (Burnham &

Anderson 2002; Marques *et al.* 2007). All analyses were conducted using R 3.1.3 (R Core Team 2020).

RESULTS

Forest structural attributes

We measured a total of 7951 trees, corresponding to 1991 trees in old-growth and 5960 trees in secondary forest stands. The density of live trees was 0.42 times higher in secondary forest stands (Table 1), but there was a comparable density of dead trees between old-growth and secondary stands (Table 1; Fig. 1a, b). The density of cavity trees was 0.26 times higher in old-growth stands than in secondary stands (Table 1). Cavity trees (i.e. trees with at least one usable cavity) represented 36% of all trees in old-growth and 16% of all trees in secondary forest stands. In both forest types, more than 60% of cavity trees were live unhealthy trees (decay class 2) and more than 17% were long dead trees (decay class 4). Sixty-four per cent of long dead trees in secondary forests have at least one cavity and 69% in old-growth forests.

In old-growth forest stands, the cavity tree species with the highest density of cavities was *N. pumilio* (66% of all cavities), followed by *N. dombeysi* (16%). In secondary forests, the cavity tree species with the highest density of cavities were *G. avellana* (33%), followed by *P. lingue* and *Nothofagaceae* (both with 14%). Other tree species rarely produced cavities (Fig. 2). In both old-growth and secondary forests, larger trees (DBH) had higher proportions of trees with at least one cavity. The density of total cavities was higher in old-growth (mean $\pm$ SE = 358.4 ± 0.0067 /ha) compared to secondary stands (183.9 ± 0.002 /ha; Table 1). The difference in density of excavated cavities between secondary and old-growth forests was not significant (Table 1). The density of nonexcavated cavities was 0.5 times higher in old-growth than in secondary forest stands (Table 1; Fig. 1c, d).

Table 1. Results for structural attributes and supply of tree cavities between old-growth and secondary forest stands, using the test of Mann and Whitney. SE = standard error; W = value of the Mann and Whitney constant; P = P-value (statistical significance set to be 0.05)

Variables	Old growth (N plots = 130) Mean density $\pm$ SE	Secondary (N plots = 239) Mean density $\pm$ SE	W	P
Live trees/ha	328.88 $\pm$ 19.92	567.36 $\pm$ 25.74	10142	3.5e-08
Dead trees/ha	60.15 $\pm$ 4.72	65.75 $\pm$ 3.93	15012	0.6
Excavated cavities/ha	6.64 $\pm$ 0.0006	8.07 $\pm$ 0.0003	5964708	0.05
Nonexcavated cavities/ha	351.72 $\pm$ 0.0066	175.81 $\pm$ 0.002	7212124	2.2e-16
Total cavities/ha	358.36 $\pm$ 0.0067	183.88 $\pm$ 0.002	7206876	2.2e-16
Cavity trees/ha	140.22 $\pm$ 0.0112	103.78 $\pm$ 0.008	457403	2.2e-16

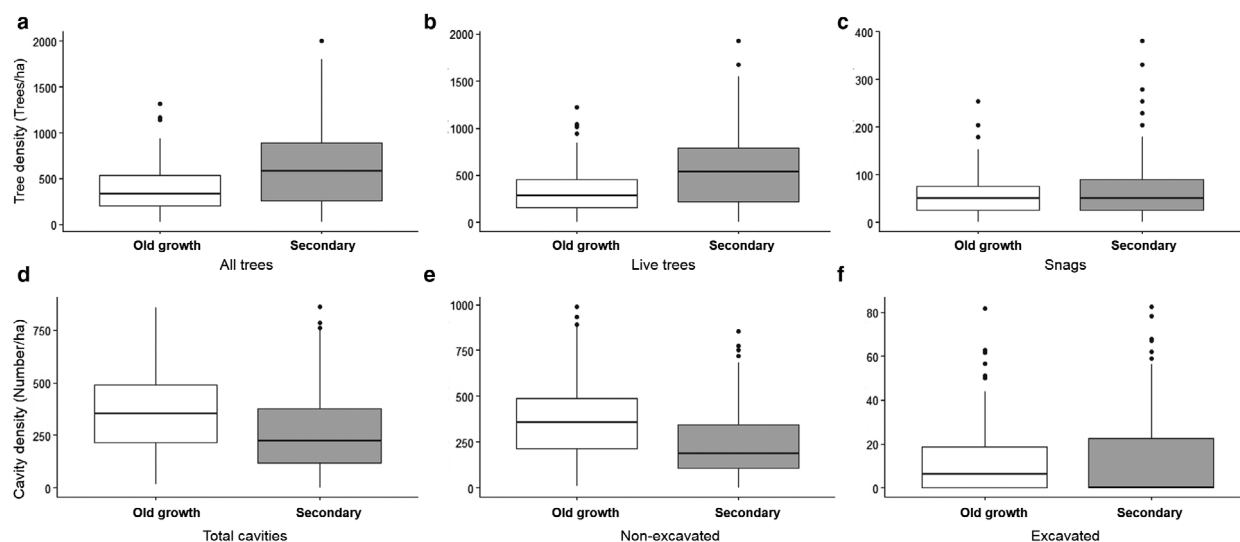


Fig 1. Mean density of (a) total trees, (b) live trees and (c) dead trees or snags in old-growth and secondary forests and mean density (number/ha) of (d) total cavities, (e) nonexcavated cavities and (f) excavated cavities in old-growth and secondary forests. Error bars represent standard error.

The role of tree size and decay on cavity occurrence and relative abundances

For occurrence and relative abundances of both excavated and nonexcavated cavities, the top-ranked models included decay and DBH logarithm (bold lines in Table 2). Binomial GLMMs indicated that trees with at least one cavity (excavated or nonexcavated) had significantly larger diameters than noncavity trees. Live healthy trees and fallen trees had almost zero probability of holding an excavated cavity, even for trees with a high DBH. Trees with low DBH but with advanced decay showed a high probability of holding nonexcavated cavities (Fig. 3). However, the probability of holding at least one excavated cavity did not vary much for trees with relatively high DBH.

According to binomial GLMMs, decayed trees were more likely to hold both nonexcavated and excavated cavities than healthy trees; long dead trees had the highest parameter estimates and the highest probability of occurrence of nonexcavated cavities (Fig. 3). According to Poisson GLMMs, the abundance of cavities per tree was associated with DBH and decay. Larger DBH and long dead trees showed higher abundance of both types of cavities than low DBH and healthy trees. Fallen trees showed the highest number of nonexcavated cavities, and long dead trees showed the highest abundance of excavated cavities (Fig. 4). The abundance of nonexcavated cavities per tree was higher (range = 0–8) than the number of excavated cavities (0–2). The probabilities of holding excavated cavities were relatively low; they did not exceed 0.4 even for trees with high DBH.

DISCUSSION

This study shows important differences in the supply of a keystone habitat resource for tree cavity-using wildlife between old-growth and secondary forests in a global biodiversity hotspot from the southern Andes. We found that tree density was much higher in secondary than in old-growth forest stands and the density of dead trees was comparable for both forest types. However, the density of cavity-bearing trees was much higher in old-growth forests, indicating the importance of these structurally complex stands as habitat for cavity-using wildlife in temperate ecosystems (Zenner 2004; Bunnell 2013; Caviedes & Ibarra 2017; Ibarra *et al.* 2020).

Tree-cavity supply varies widely among forest systems worldwide, although some of these differences can be attributed to different definitions of these habitat resources and to the forest under study. A global meta-analysis reported that, for 133 study areas examined, the median cavity density was 16.2 ha^{-1} , with a maximum of $963 \text{ cavities ha}^{-1}$ (Remm & Löhms 2011). The average density of total cavities in our study was 358 ha^{-1} for old-growth and 184 ha^{-1} for secondary forests, both estimates much higher than the global median reported by Remm and Löhms (2011). This large difference can be explained by at least two factors. First, we considered tree cavities for a broad suite of taxa, including birds, mammals and reptiles, which can potentially use cavities with different characteristics (e.g. entrance size and internal volume) in our study area (Ibarra *et al.* 2014; Altamirano *et al.* 2017a; Altamirano *et al.* 2017b, Ibarra *et al.* 2017b, Novoa *et al.* 2019). These cavity nesters include endemics of

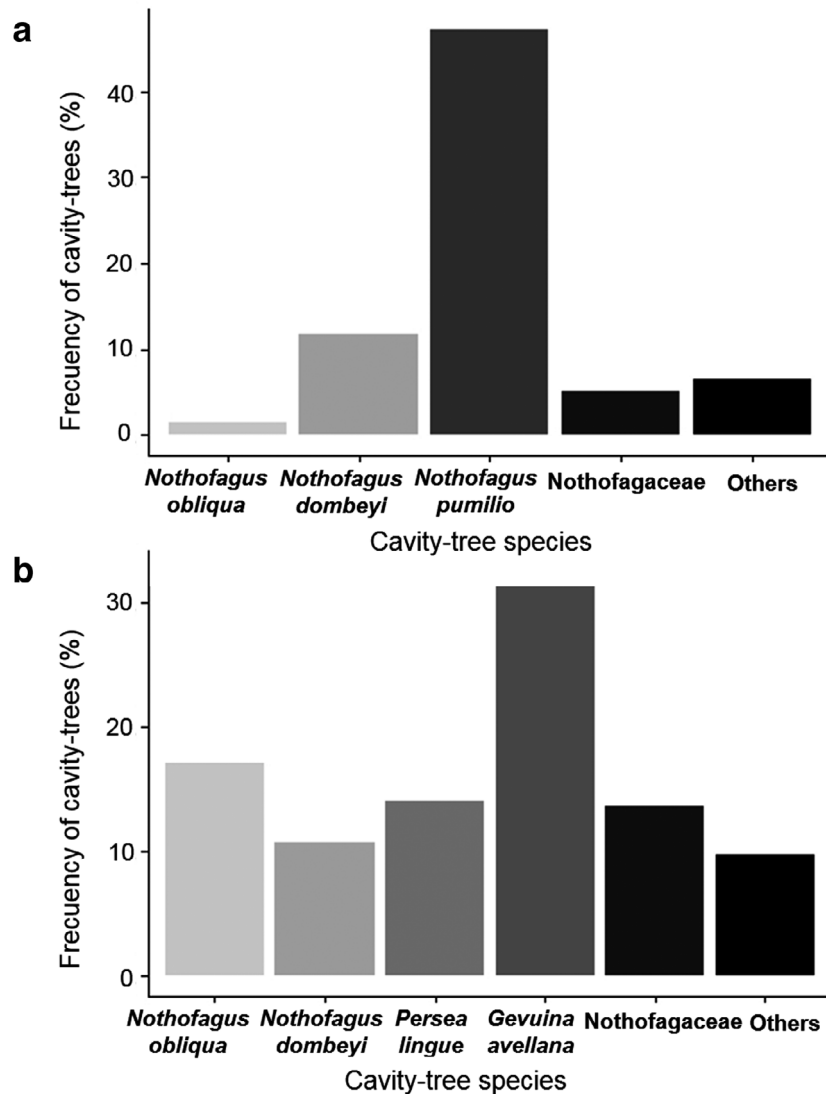


Fig 2. Composition of cavity tree species in (a) old-growth and (b) secondary forest stands. Species present with a low density were grouped in the “Others” category. Individuals that could not be identified at the species level (because of very advanced decay), but strongly suspected to be *Nothofagus dombeyi* or *N. obliqua*, were grouped in the “Nothofagaceae” category.

conservation concern such as the marsupial Austral Opossum (*Dromiciops gliroides*), the Rufous-legged Owl (*Strix rufipes*) and the Magellanic Woodpecker (*Campephilus magellanicus*; Altamirano *et al.* 2019; Ibarra & Martin 2015). Second, our forests are dominated by tree species belonging to the *Nothofagus* genus, which are known to have relatively high rates of wood decay associated with insect attacks, presence of wood-decay fungi, mistletoe infections, wind and drought (Cwielong & Rajchenberg 1995; Veblen *et al.* 1996; Ojeda *et al.* 2007). In distant but comparable temperate forests of New Zealand, decaying *Nothofagus* trees produce up to 963 cavities ha⁻¹ potentially usable by vertebrates (Blakely *et al.* 2008), which was the highest value of cavity density reported

in the global meta-analysis by Remm and Löhms (2011). The main cavity trees in Andean temperate forests were *N. pumilio* and other *Nothofagus* trees, which represented almost 90% of cavity trees in old-growth forests. In secondary forests, however, *Nothofagus* trees decreased in relative importance (nearly 40% of cavity trees) while other species increased in importance as cavity trees such as *P. lingue* and *G. avellana*.

Importantly, even in those systems where cavities seem to be relatively abundant, there may be a shortage of high-quality cavities for wildlife (Löhms & Remm 2005). The idea of nest-site availability as a limiting factor for cavity-nesting birds has a long-standing history in the scientific literature on cavity

Table 2. Model selection based on Akaike's information criterion (AIC) for estimating probability of occurrence and relative abundances of cavities in Andean temperate forests. Model structure = independent variables included in the model; K = number of parameters estimated; Δ AIC = difference in AIC values between each model and the lowest AIC model; Wt = AIC model weight

Analysis	Cavity origin	Model structure	K	AIC	Δ AIC	Wt	Estimated Beta
Occurrence (Binomial)	Nonexcavated	log(DBH) + Decay	5	5453.88	0	1	2.26 + 1.02
		log(DBH)	4	5922.28	468.40	0	2.15
		Decay	4	6249.29	795.41	0	0.92
	Excavated	log(DBH) + Decay	5	1814.43	0	1	1.48 + 0.87
		Decay	4	1919.53	105.10	0	0.785
		log(DBH)	4	1932.99	118.56	0	1.44
Relative abundance (Poisson)	Nonexcavated	log(DBH) + Decay	5	10272.96	0	1	0.46 + 1.69
		log(DBH)	4	10707.80	434.84	0	1.71
		Decay	4	12236.06	1963.10	0	0.43
	Excavated	log(DBH) + Decay	5	913.48	0	1	1.18 + 1.8
		Decay	4	995.54	82.06	0	1.06
		log(DBH)	4	1036.23	122.74	0	1.8

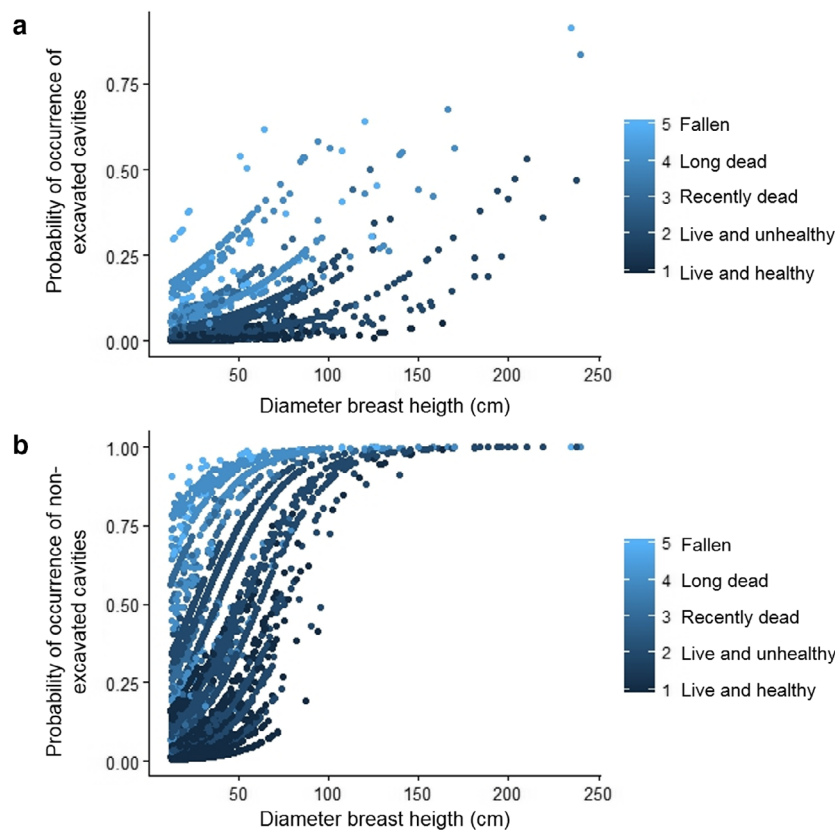


Fig 3. Predicted values for probability of occurrence of cavities per tree as a function of diameter at breast height (DBH in cm) for (a) excavated cavities and (b) nonexcavated cavities, according to tree decay classes.

nester ecology and conservation (Newton 1994, 1998; Martin & Eadie 1999; Wesolowski 2007). However, a suite of studies suggests that there is no nest-site limitation in old-growth forests (Wiebe 2011). For example, a cavity density of 60 ha⁻¹ was found but only 5–9% of them were used in forests of

Central Sweden (Carlson *et al.* 1998). In deciduous forests of Mongolia, Bai *et al.* (2003) reported a cavity density of 30 ha⁻¹ but a cavity nest density of only 2.4 ha⁻¹. Peruvian rainforests also showed low occupancy rates as only 16% of available cavities were utilised (Brightsmith 2005). Our results suggest

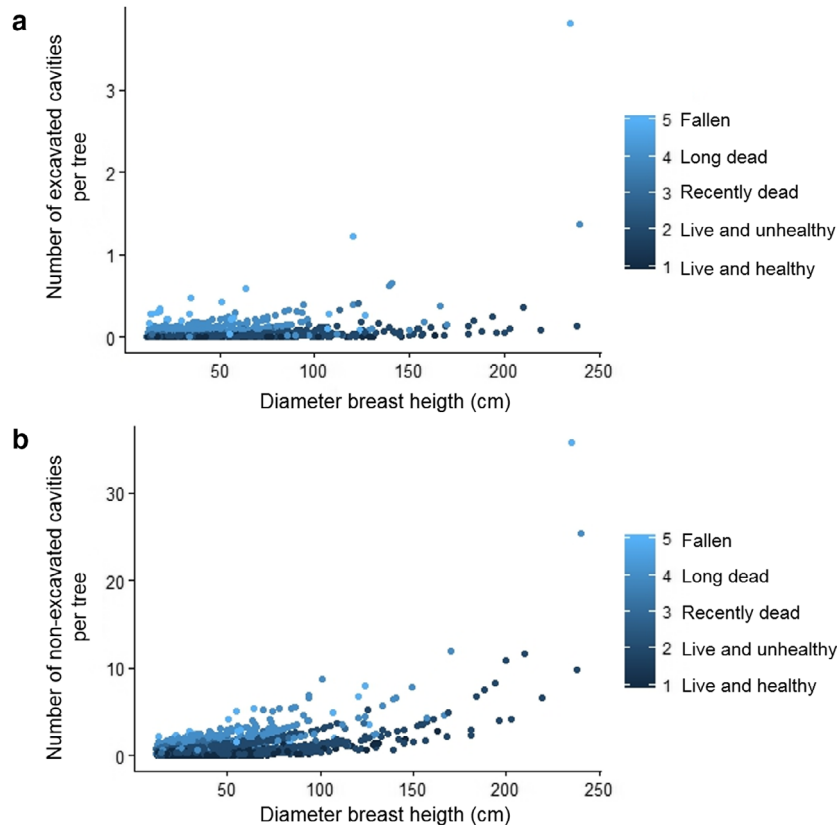


Fig 4. Predicted values for relative abundances of cavities (number per tree) as a function of diameter at breast height (DBH in cm) for (a) excavated cavities and (b) nonexcavated cavities, according to tree decay classes.

that there is a surplus of cavities in old-growth Andean temperate forests, and thus, nest-site availability is likely not a limiting factor for cavity-nesting birds in these forest stands. However, further studies examining occupancy rates in both old-growth and secondary forests are necessary to confirm this hypothesis.

Even when the density of nonexcavated cavity was higher in old-growth forests (352 ha^{-1}), we still found a relatively high density of these cavities in secondary forests (176 ha^{-1}). This result can be explained by the high number of snags that are remnants of fires that occurred nearly eight decades ago in our study system. In the southern Andes, these habitat legacies increase structural complexity (Caviedes & Ibarra 2017) and positively influence nesting site selection of cavity-using wildlife in secondary forest stands (Altamirano *et al.* 2017a). In our secondary forests, trees in advance decay supported a disproportional number of cavities compared to their relative availability. When these habitat legacies fall down, because of their advanced decay, we may observe a dramatic decrease in cavity density in secondary forests as many of the remaining living trees will not have either the size or decay to produce

nonexcavated cavities yet. This may result in a limitation of nest-site supply for several cavity-using vertebrates and a decrease in the population numbers for these species (Cockle *et al.* 2010).

When analysing the mechanisms driving our results, we found that larger trees and those with advanced decay increase the supply of tree cavities. However, both diameter at breast height (DBH) and decay classes of trees had a stronger influence on the supply of nonexcavated than excavated cavities. This finding is important for southern temperate forests because cavity nesters here show a strong preference for nesting in cavities supplied by large decaying and dead trees (58% of nests) and nearly 75% of nests of secondary cavity nesters are located in nonexcavated cavities (produced by tree decay processes; Altamirano *et al.* 2017a). Importantly, high-quality cavities generated by tree decay processes require long periods of time to be produced (Lindenmayer *et al.* 1993; Koch *et al.* 2008). For instance, more than one hundred years are needed to generate nonexcavated cavities and more than two hundred years for large cavities in Australia (Gibbons *et al.* 2002; Koch *et al.* 2008).

In Australian forests, there are no excavators (e.g. woodpeckers) but yet the community of cavity-using wildlife is highly diverse, suggesting that the presence/absence of excavators is not always an indicator of the diversity of secondary cavity-nesting vertebrate species (Gibbons & Lindenmayer 2002). We found that, in both old-growth and secondary forest stands, the density of excavated cavities (7 ha^{-1} and 8 ha^{-1} , respectively) was much lower than the density of nonexcavated cavities (352 ha^{-1} and 176 ha^{-1} , respectively). This suggests that excavation, or at least the supply of excavated cavities, may not play a critical role structuring the community of cavity nesters in Andean temperate forests of Chile. As mentioned earlier, the higher supply of nonexcavated cavities correlates with the fact that 75% of nests of secondary cavity nesters are located in nonexcavated cavities in this system (Altamirano *et al.* 2017a). The occurrence probability of excavated cavities was relatively low, even for trees with high DBH and advanced decay. This suggests that, even if DBH and decay were present in the most supported models as the main drivers that influence the cavity occurrence, other factors, likely occurring across spatial and temporal scales, must influence the tree substrates that excavator species select for excavating a cavity (Everett & Otter 2004; Cockle & Martin 2015).

Snags are frequently considered as keystone habitat attribute because of the disproportionate number of species they support in relation to young healthy trees (Gibbs *et al.* 1993; Caviedes & Ibarra 2017). Thus, snag management is an effective way of conserving habitat for cavity-nesting vertebrates (Bunnell *et al.* 1999; Hannan *et al.* 2019). In Andean temperate forests, snags only represent 15% of cavity trees but most will hold cavities and in greater numbers compared to live trees. As we have shown here and elsewhere (e.g. Ibarra & Martin 2015; Altamirano *et al.* 2017a), snags are critical habitat for cavity-nesting vertebrates in Andean temperate forests and should be maintained. However, snags are frequently considered indicative of 'unhealthy and dirty forest conditions' by landowners and forest managers in Chile and thus the first trees harvested for firewood. Besides the importance of snags, however, we have shown that live unhealthy trees represent the greatest proportion of cavity trees in both old-growth and secondary forests. Forests missing one or more decay classes may result in a severe shortage of cavities in the near future (Cockle *et al.* 2011). Therefore, the National Forestry Service (CONAF) and external forest certification agencies should ideally make mandatory to manage to retain and recruit a variety of decay classes and tree sizes to ensure a continuous supply of cavities through time.

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AUTHOR CONTRIBUTION

José Tomás Ibarra: Conceptualization (equal); Investigation (equal); Project administration (equal); Resources (equal); Supervision (equal); Writing-review & editing (equal). **Fernando Novoa:** Formal analysis (equal); Investigation (equal); Writing-review & editing (equal). **Hélène Jaillard:** Formal analysis (equal); Investigation (equal); Writing-original draft (equal). **Tomás A. Altamirano:** Conceptualization (equal); Investigation (equal); Project administration (equal); Resources (equal); Supervision (equal); Writing-review & editing (equal).

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