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SUPPLY OF TREE-CAVITIES IN OLD GROWTH AND SECONDARY FORESTS IN ANDEAN TEMPERATE ECOSYSTEMS OF THE LA ARAUCANÍA REGION, CHILE

Mémoire de Fin d'Études

Hélène JAILLARD

Promotion 2010

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Date: June 23rd 2016

Résumé d'auteur (FR)

NOTICE BIBLIOGRAPHIQUE

AUTEUR : Hélène Jaillard

Promotion 2010

« Offre de cavités dans les arbres des forêts anciennes et secondaires des écosystèmes andéens tempérés de la Région de La Araucanía au Chili »

Mots-clefs : Cavités, forêts tempérées, faune cavernicole

	RESUME D'AUTEUR
PLAN INDICATIF	1. Introduction 2. Matériel et Méthodes 3. Résultats 4. Discussion
BUT DE L'ETUDE	Comparer l'offre de cavités dans les arbres des forêts anciennes par rapport aux forêts perturbées par des activités anthropogéniques, et étudier les facteurs qui influencent l'apparition de cavités dans les arbres des forêts tempérées andines de la Région de la Araucanía au Chili.
MATÉRIEL ET MÉTHODES	Le Diamètre à la Hauteur de la Poitrine (DHP), l'espèce, l'état et le nombre de cavités ont été relevés pour chaque arbre des parcelles d'échantillonnage réparties dans 10 sites d'étude en forêts anciennes ou perturbées. Les densités de cavités ont été calculées pour chaque type de forêts et comparées à l'aide du test de Mann et Whitney. Les facteurs influençant la présence de cavités et le nombre de cavités par arbre ont été déterminés en utilisant des GLMM de type binomial et de type Poisson respectivement.
RESULTATS	Les densités de cavités non-excavées et d'arbres vivants sont supérieures dans les forêts anciennes, mais aucune différence n'a été trouvée entre les deux types de forêts pour les densités de cavités excavées et d'arbres morts. La probabilité d'apparition d'une cavité tout comme le nombre de cavités par arbre est supérieure pour les arbres de grand DHP et dont l'état de décomposition est avancé.
CONCLUSION	Les suivantes recommandations devraient permettre de conserver l'offre de cavités dans les forêts exploitées : les arbres ne devraient pas être coupés avant d'atteindre un DHP de 50 cm. Les arbres tombés naturellement devraient être laissés au sol. Des arbres en état de sénescence peu avancé doivent être conservés sur les parcelles, ainsi que des espèces d'importance économique moindre telles que le lingue et l'avellano car elles constituent une source importante de cavités.

Résumé d'auteur (EN)

BIBLIOGRAPHIC NOTE

AUTHOR : Hélène Jaillard

Promotion 2010

« Supply of tree-cavities in secondary and old-growth forests in Andean temperate ecosystems of the La Araucanía Region, Chile»

Keywords : Cavity-nesters, standing dead trees, temperate forests, tree decay.

	AUTHOR'S SUMMARY
INDICATIVE PLAN	1. Introduction 2. Methods 3. Results 4. Discussion
AIM OF THE STUDY	To compare the supply of cavities in old growth and secondary forests, and analyse the factors that influence the occurrence of cavities and the number of cavities per tree in Andean temperate forests of the La Araucanía Region in Chile.
METHODS	We collected DBH, species, decay and number of cavities for every tree in each sample plots of our 10 study sites in old growth and secondary forests. We calculate cavity densities for each type of forest and compared them using the test of Mann and Whitney. The factors that influence the occurrence of cavities and the number of cavities per trees were analysed using a binomial and a Poisson GLMM respectively.
RESULTS	Non-excavated cavity and living tree densities were much higher in old growth forests, but no significant difference was found for excavated cavity and dead tree densities between the two types of forests. The probabilities of occurrence of cavities, such as the number of cavities per tree are bigger for thick long dead trees.
CONCLUSION	The following recommendations should maintain the supply of cavities in managed forests: trees shouldn't be cut before reaching 50 cm of DBH. Naturally fallen trees should be left on the ground. Trees in early stages of decay should be maintained, such as species of least economical value like the lingue and the avellano because they are important sources of cavities.

Acknowledgements

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Tables Index

Figures Index

Index of Appendixes

Abbreviations and acronyms

ºC : Celsius degrees

AIC : Akaike’s Information Criterion

CONAF : Corporación Nacional Forestal – National Forestry Corporation

DBH : Diameter at Breast Height

GLMM : Generalized Linear Mixed Model

km : kilometers

m.a.s.l.: meters above sea level

Index

1 INTRODUCTION

Tree cavities are an important resource as nesting, roosting and sheltering sites for many species. Throughout the world, more than 1000 bird species, and many mammal, reptile and amphibian species use tree cavities during their life cycle (Bhusal *et al.* 2015). In Andean temperate forests of Southern Chile, the southernmost Global Biodiversity Hotspot, at least 29 bird species, six mammals and two reptiles use cavities for meet their life history requirements (Altamirano & Ibarra, Unpublished data). Tree cavities can be divided in two categories according to how they are generated: excavated cavities are created by the action of an excavating bird (e.g. woodpeckers), while non-excavated cavities are formed by the natural process of tree decomposition, and also the effect of insects, fungi, wind and fire (Altamirano *et al.*, 2012; Cockle *et al*., 2011; Gibbons & Lindenmayer, 2002; Hussain et al., 2013) (Figure 1). A wide range of factors influences the formation and abundance of tree cavities, including the characteristics of the cavity-tree itself such as its size (diameter), age and species (Blakely & Didham, 2008; Fan *et al.*, 2003). Tree size and age, and forest age structure may have a primary role on the occurrence and abundance of tree cavities, older and larger trees being more likely to bear tree cavities than younger and smaller trees (Blakely & Didham 2008; Fan et al. 2003; Hussain et al. 2013).

Tree cavity supply can be reduced in forests under human disturbances that alter the age structure of forests and their associated wildlife, such as deforestation and logging. Reduced availability of tree-cavities is the result of two processes: first, the direct loss of cavity-trees by removal for timber, and second the limited recruitment of trees into cavity-trees cohort (Hussain et al. 2013). Indeed, large-decaying trees are generally targeted in selective logging, as well as dead trees, for their higher commercial value, and in order to reduce hazards such as lightning attraction and falling trees, and foci of infection for healthy trees (Everett & Otter 2004). Young trees are also often harvested before reaching the suitable size or condition for cavity formation (Bhusal *et al.* 2015). Consequently, there are fewer cavities in secondary forests than in old-growth forests. In Europe, Camprodon *et al.* (2008) found that old-growth forests have a major abundance

Figure 1 - Excavated cavity of Magellanic woodpecker (according to size and shape) on a living *Lophozonia obliqua* (left) ; Nest material emerging from a non-excavated cavity due to a wound in a living *Lophozonia obliqua* (right)

of cavities and nests of secondary cavity-nesters than logged forests. In subtropical Atlantic forests, Cockle *et al.* (2010) also found a major abundance of cavities in old-growth than logged forests. Tree harvesting and selective logging may therefore have long-term negative effects on cavity-nesting communities (Bai *et al.*, 2003; Everett & Otter, 2004), since many woodpecker species depend on those large-decaying and standing dead trees (or snags). Furthermore, old living trees and snags provide a key habitat for many species and play an important role in ecosystem functions (Everett & Otter 2004).

Temperate forests are known for their high endemism rate and important role as carbon reservoirs (Neira *et al.*, 2002). Chilean and Argentinean temperate forests are the most austral temperate forests of the world (Armesto *et al.,* 1998). Chile has the greatest temperate forests surface of South America, and more than half of the south hemisphere temperate forests, totaling 13.4 million hectares. The greatest part of these forests extends over more than 2000 km, between 35 and 55 south degrees latitude. Chilean temperate forests form a biogeographic island, isolated by Antarctic to the south, the Andean cordillera to the east, the Pacific Ocean to the west and the Atacama Desert to the north. This isolation explains the biological value but also the fragility of these forests considered as one of the 35 Global Biodiversity Hotspots (Myers 2000). These hotspots are areas that support at least 1500 species of endemic vascular plants, and an area in which at least 70% of the habitat has been lost. Chilean temperate forests are subject to intense anthropogenic disturbances such as logging, fire and cattle ranching that reduce each year their surface in a significant way (Echeverría *et al.* 2006).

It is estimated that the Chilean territory was 45% covered by forests. For 400 years, Chile has seen ¾ of its forests surface disappear (Hoffmann 1997). Nowadays, the major threats to Chilean temperate forests are their conversion to both agriculture land and exotic species plantations (Armesto *et al.* 1998, Neira *et al*. 2002). Indeed, in order to sustain a growing rise of the global demand for timber, native forests are frequently replaced by exotic species plantations of Monterey pines (*Pinus radiata*) or eucalyptus

(*Eucaliptus globulus*), which grow faster and an easier management than native forests (Altamirano & Lara 2010). Cattle ranching is also a practice which has negative impacts on forest composition and structure through the alteration of the regeneration capacity of plants and reduction of the understory density. For example, Zamorano-Elgueta (2012) showed that the regeneration of the monkey-puzzle tree (*Araucaria araucana*), a threatened endemic species, is almost non-existent in presence of intensive cattle ranching.

A guild is a group of species in a community that exploits the same set of resources in a similar manner, although they may not be closely related taxonomically (Root, 1967). Regarding cavity-nesting birds, Martin & Eadie (1999) recognize nesting-guilds according to the way cavity nesters acquire a cavity. Primary cavity-nesters (PCNs) (woodpeckers) are birds that excavate their own cavities. In Andean temperate forests of Southern Chile, the group of PCNs is formed by four species: the magellanic woodpecker (*Campephilus magellanicus*), the Chilean flicker (*Colaptes pitius*), the stripped woodpecker (*Veniliornis lignarius*) and the white-throated treerunner (*Pygarrhichas albogularis*) (Figure 2). Further, secondary cavity-nesters (SCNs) are species not able to create their own cavities, and thus have to use cavities excavated by PCNs or non-excavated cavities. There are strong interdependences between cavity guilds since some species depend partly or entirely on other species (PCNs) to produce a critical resource (Martin & Eadie 1999). Indeed, primary cavity-nesters provide cavities for other cavity-nesting birds species. They can directly affect richness and abundance of cavity-nesters that are not able to create their own cavities and they should there fore be considered as top priority conservation goals (Cockle *et al.* 2011).

However, the proportion of excavated and natural cavities largely differs among different forest types around the world. In North American temperate forests, 90% of secondary cavity-nesters use excavated cavities. On the contrary, in Chilean Andean temperate forest, the great majority (75%) of cavities that are used by secondary cavity-nesting birds, mammals and reptiles are non-excavated cavities (Altamirano & Ibarra, Unpublished data). As in other parts of the world, the high degree of human

Figure 2 – The four primary-excavator birds of temperate forests of Southern Chile : (1) =Stripped woodpecker (*Veniliornis lignarius*), (2)=Chilean flicker (*Colaptes pitiius*), (3)=White-throated treerunner (*Pygarrhichas albogularis*), (4)=Magellanic woodpecker (*Campephilus magellanicus*)

disturbances by tree harvesting and selective logging in Chilean temperate forests may therefore have strong impacts on the cavity supply and the availability of cavity-trees and thus affect the whole cavity-nesting species community. Although tree cavities are a critical component of forest ecosystems worldwide and have been well studied in Europe, North America, Australia and Asia (Bai *et al.*, 2003; Blakely & Didham, 2008; Carlson *et al.*, 1998; Cockle *et al.*, 2011; Fan *et al.,* 2003; Hussain *et al.*, 2013; Wesołowski, 2007), very little is known in about cavity abundance and processes of cavity formation in temperate forests of South America. It is therefore important to evaluate the cavity supply, and study the impacts of forests management policies on this supply and on the cavities formation processes in Andean temperate forests.

Fauna Australis is an organism of the Pontificia Universidad Católica of Chile dedicated to research and education for the conservation of native wildlife of the Chilean temperate forests in the La Araucanía Region. Since 2010, Fauna Australis carry out fieldwork activities during the breeding season. The aim of these field seasons is to collect data on the breeding ecology of cavity-nesting avifauna. Nests of cavity-nesting species were searched and monitored in order to provide fecundity data (Figure 3). Besides the information about reproduction itself, data were collected at three different levels: cavity-level (origin of the cavity, measurements of the entrance…), tree-level (Diameter at Breast Height (DBH), tree decay, number of cavities per tree…) and habitat-level (forest succession, understory cover…). The nest-trees was measured, as well as all the other trees around the nest-tree in an 11.2 meters radius, forming a large database. This database already provided important information about reproduction habits and occurrence patterns of cavity-nesting birds species in previous studies. However, the cavity-tree data of the project had never been specifically analyzed until now. We selected data from the three levels to conduct the present study. We compared cavity availability between secondary and old-growth forests, in order to determine if human activities can reduce cavity supply in temperate forests of Southern Chile. We also examined how the size of trees (Diameter at Breast Height, DBH) and tree-decay influence the occurrence and abundance of cavities per trees in order to better understand the processes of cavity-formation in temperate forests of Chile, and

Figure 3 – Monitor connected to a camera showing the nest of a Rayadito (Aphrastura spinicauda) inside a tree-cavity containing four eggs during the Fauna Australis fielwork for the last breeding saison

understand at which DBH and decay stage trees are more susceptible to hold cavities. The specific objectives of this study were (i) to compare excavated and non-excavated cavity density between secondary and old-growth forests, (ii) examine how DBH and decay are associated with the presence of cavities in trees and (iii) examine the role of DBH and tree decay in the number of cavities per tree in temperate forests of Chile.

2 METHODS

2.1 Study area

The study was conducted in the Municipality of Pucón, La Araucanía Region, Chile. (Figure 4).

The main plant formation in the study area is the Andean temperate forest, which benefits from a cold continental climate with a short dry season from November to February, and abundant rains throughout the year.

The main tree species are avellano (*Gevuina avellana*), olivillo (*Aextoxicon punctatum*), lingue (*Persea lingue*), ulmo (*Eucryphia cordifolia*) roble (*Lophozonia obliqua*), coihue (*Nothofagus dombeyi*), laurel (*Laurelius sempervirens*), tepa (*Laureliopsis philippiana*), mañío (*Saxegotheae conspicua*) and canelo (*Drimys winteri*). The proportion and distribution of each species depend on height above sea level and humidity.

Above 500 meters above sea level (m.a.s.l.), several tree species disappear. Above 750 m.a.s.l., the frequent snowfalls modify radically the vegetation: the roble disappears completely to be remplaced by coihue and associations of mañio and tepa. Above 1000 m.a.s.l., lenga (*N pumilio*) and monkey-puzzle trees (*Araucaria araucana*) dominate forest stands (Hoffmann 1997).

In the region of Pucón, a great number of native species can be observed, which major part has conservation issues due to strong human impacts such as deforestation for example. The most emblematic mammals of Andean temperate forests are the guiña (*Leopardus guigna*), the pudu (*Pudu puda*), the puma (*Puma concolor*), and the monito del monte (*Dromiciops gliroides*) (Hoffmann 1997), a small cavity-nester mammal, which is endemic from Chile.

Andean temperate forests of Chile present an avifauna with a high rate of endemism, and highly threatened by habitat loss and illegal hunting. The most emblematic birds from south of Chile are the chucao tapaculo (*Scelorchilus rubecula*), the black-throated

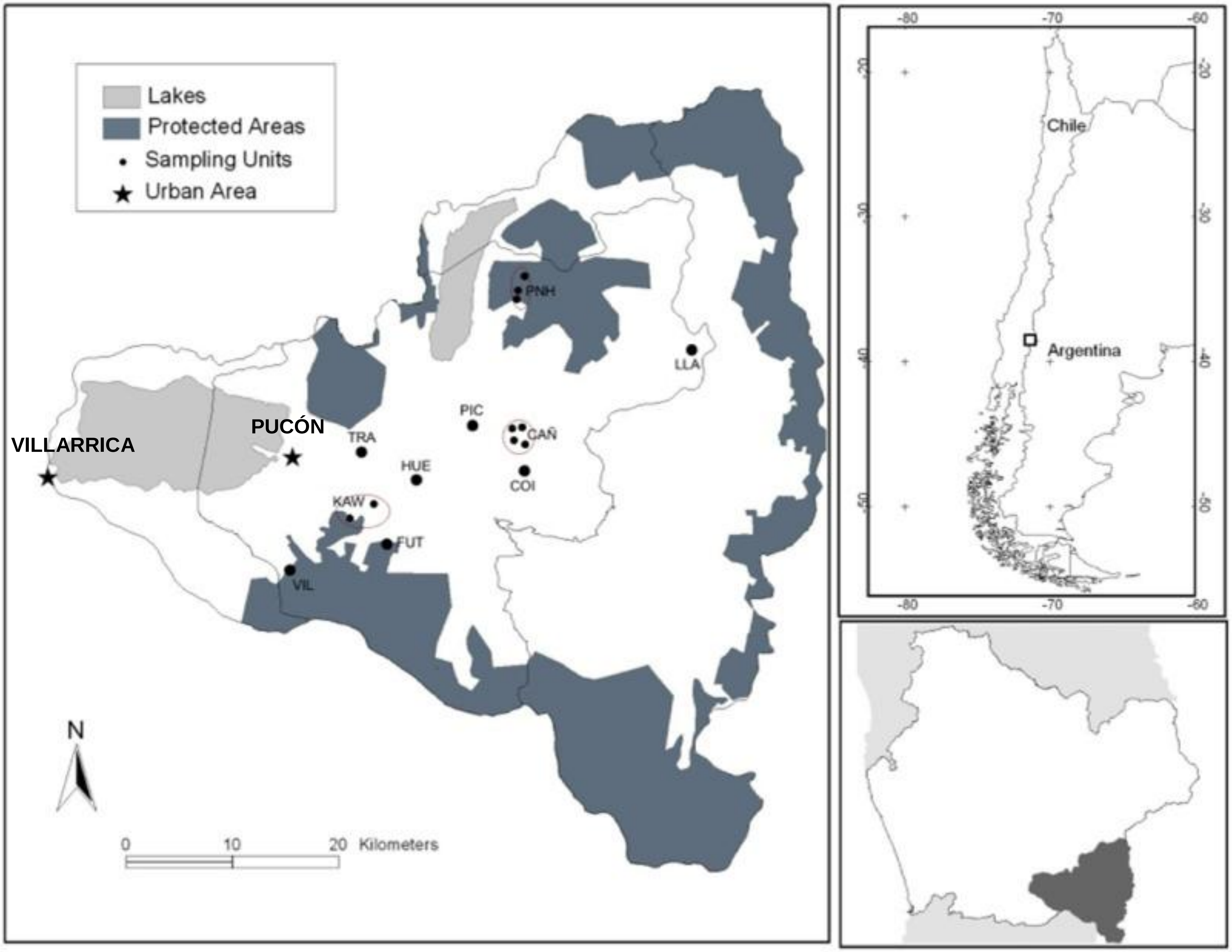


Figure 4 - Map of the study area showing the localization of the ten study sites

huet-huet (*Pteroptochos tarnii*), and the magellanic woodpecker (*C. magellanicus*) (Hoffmann 1997).

2.1.1 Study sites

The study area included ten study sites, chosen according to three criteria: height, human impacts, and forest succession type (Table 1). Three of them are protected areas (public or private): the Cañí nature sanctuary, the Villarrica National Park and the Huerquehue National Park. Coilaco and Llancalil are private properties but with a limited human impact. Those five sites are therefore interesting examples of non-disrupted (or almost non-disrupted) old-growth forests. However, the other five sites (Trancura, Futuro, Kawellauco, Huelemolle and Pichares) are private properties with high human impacts: cattle ranching, logging, presence of many exotic species, roads and houses etc. They are interesting examples of secondary disrupted forests.

Table 1 - Study sites typology: the ten study sites were chosen according to two categories: *lowlands disrupted forests* (low altitude, high human disruption and secondary forest succession) and *old-growth Andean forests* (high altitude, low human disruption and old-growth forest succession

	Lowlands disrupted forests	***Old-growth Andean forests***
Altitude	< 800 m.a.s.l.	> 800 m.a.s.l.
Human impacts (Fire, cattle, logging)	High	Low
Forest succession	Secondary	Old-growth

The ten study sites are described in Table 2, and their localization is showed in Figure 4. Photos of Cañí and Trancura are showed in Figure 5 and 6.

Table 2 - Description of the ten study sites and their main characteristics: name (and three letters code), mean altitude (m.a.s.l.), administration (public or private) and type of vegetation (species and association)

	Code	Name	Mean altitude (m.a.s.l.)	Administration	Vegetation
Old-growth Andean forests	CAÑ	Cañí	1303	Private reserve administrated by the local community	*N. dombeyi,* and at major altitude *N. pumilio* and monkey-puzzle tree association (*A. araucana*)
	COI	Coilaco	852	Private	*N.dombeyi, S. conspicua* and *L. philippiana* association
	LLA	Llancalil	1050	Private	*N.dombeyi, S. conspicua* and *L. philippiana* and at major altitude *N. pumilio* and *A. araucana* association
	VIL	Villarrica	1271	National Park with public administration by CONAF	*N.dombeyi* and at major heights *N. pumilio* pure formation
	PNH	Huerquehue	1251	National Park with public administration by CONAF	*N. dombeyi,* and at major altitudes *N. pumilio* and monkey-puzzle tree association (*A. araucana*)
Low-lands disrupted forests	FUT	Futuro	628	Private	*N.dombeyi,* exotic pine species
	HUE	Huelemolle	457	Private	*N. obliqua* , with *P. lingue, G. avellana, E. cordifolia, A. punctatum*
	KAW	Kawellauco	437	Private	*N.dombeyi*, exotic pine species
	PIC	Pichares	386	Private	*N. obliqua*, with *P. lingue, G. avellana, E. cordifolia, A. punctatum*
	TRA	Trancura	272	Private	*N. obliqua*, with *P. lingue, G. avellana, E. cordifolia, A. punctatum*

Figure 5 - Laguna negra and old-growth forest of *Nothofagus pumilio* and *Araucaria araucana* in the nature sanctuary of Cañí

Figure 6 - Cattle in managed secondary forest of *Lophozonia obliqua* in Trancura study site

2.2 Habitat sampling

To describe the habitat of cavity-nesting birds, data was collected in a circular area within 11,2 meters of every tree where a nest had been found between 2010 and 2016. The table 3 describes the measures that were actually used in the present study.

Table 3 - Data from Fauna Australis fieldworks that are being used in the present study: at cavity-level, the origin of the cavity (excavated and non-excavated) / at tree-level the species diameter and decay class of the tree and number of cavities / at habitat-level, the type of forest succession

	Cavity-level	***Tree-level***	***Habitat-level***
Collected data	Cavity origin	Species Tree diameter Decay class Number of cavities	Forest succession type

For every tree within each 11.2 meters radius sample plots, the species, the DBH (tree diameter), and the tree decay were recorded. Only trees with DBH > 12.5 cm were recorded. The decay class was attributed to each tree according to a scale from 1 for living and healthy trees, to 4 for long dead trees (5 was used for fallen trees). The figure 7 offers a description of each decay class. Each tree was then carefully inspected by at least two persons with binoculars in order to determine the number of cavities. We defined cavity as a hole in the tree with a minimum entrance diameter of 2 cm (Bhusal *et al.* 2015) and a width suspected of being suitable for use by cavity-nester species to nest.

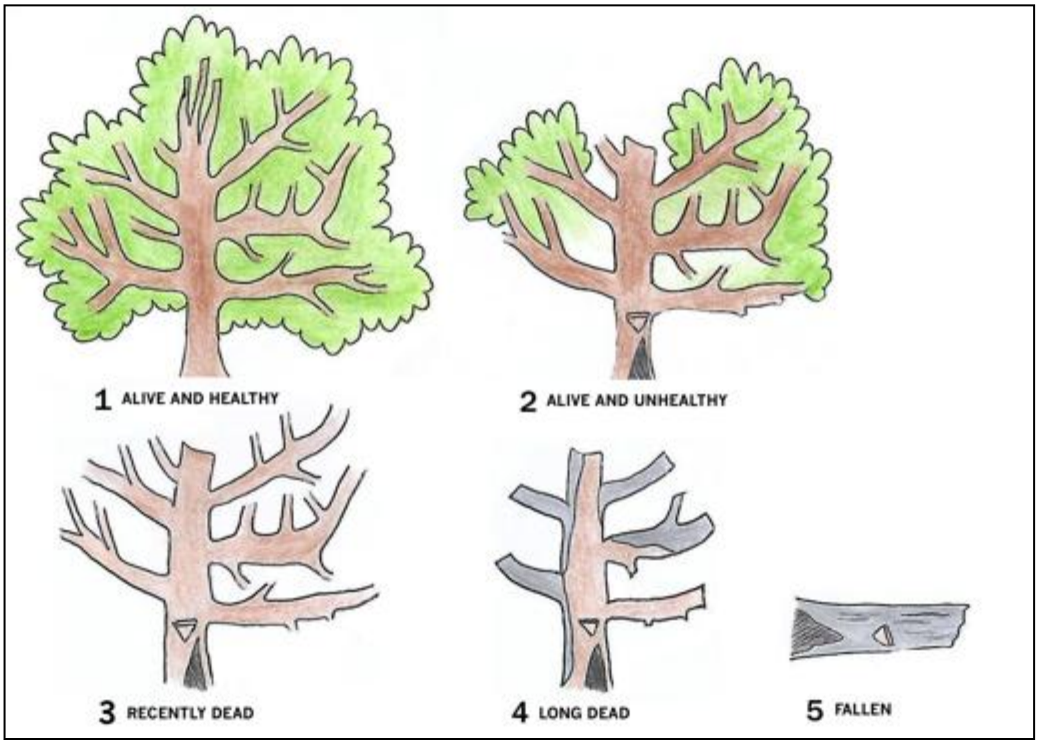


Figure 7 - Tree decay classes: decay class 1 includes alive and healthy trees; decay class 2 includes alive and unhealthy trees (alive with first signs of decay: fungi, feeding holes or mechanical damage and alive with advanced decay: >50% dead branches, broken top); decay class 3 includes recently dead trees (dead trees with major and minor branches intact); decay class 4 includes long dead trees (dead with remnants of major branches, hard and soft wood, bark loss); finally decay class 5 stands for naturally fallen trees.

Regarding the origin, cavities were divided in two categories: non-excavated cavities (formed by natural decomposition of trees) and excavated cavities (formed by the action of a primary cavity-nesting birds). The round symmetrical form of the cavity entrance distinguished excavated cavities, whereas non-excavated cavities present an irregular entrance, and are usually located in a damaged area of the tree (Vázquez & Renton 2015).

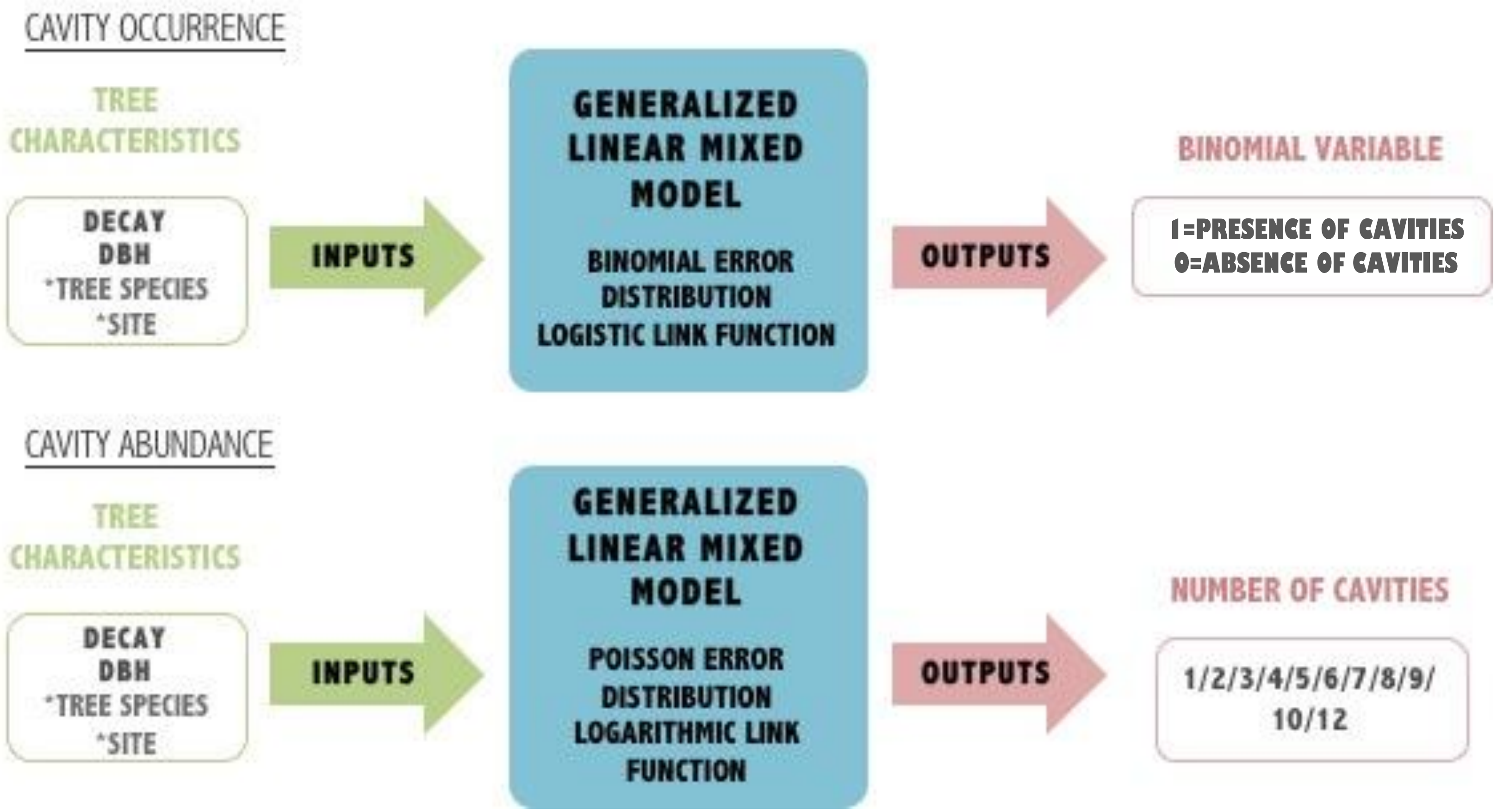


Figure 8 - Analysis of tree cavities occurrence and abundance using generalized linear mixed models (GLMM) ; the factors marked with an (*) were fixed as random terms in the GLMM.

2.1 Data analysis

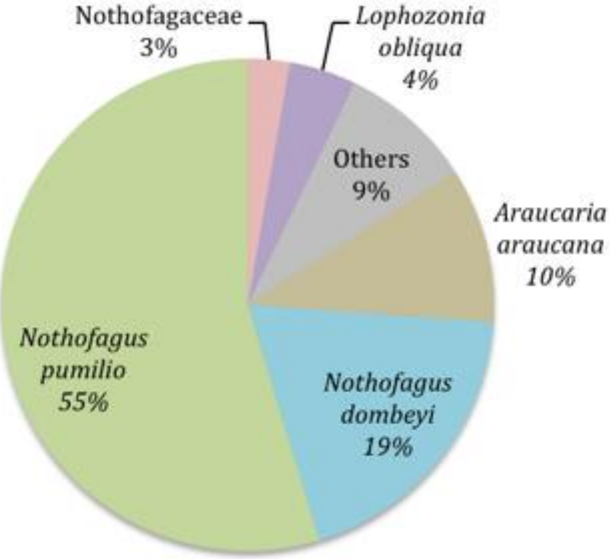
2.1.1 Supply of cavities

To study the potential differences of availability of cavities between the two types of forests we compared a series of density variables we calculated for each sample plots. The number of cavities of all trees within one sample plot was summed to obtain the number of cavities per sample plot. This number was then divided by the area of the sample plots to calculate the density of cavities for each sample plots (number of cavity per hectare (ha)) and then for each type of forest. We used density variables because it allowed comparing data even if the number of plots were different among sites and forest types. The density variables that were analyzed are: (a) number of live trees/ha; (b) number of dead trees/ha; (c) number of cavity trees/ha; (d) total number of cavities/ha; (e) number of excavated cavities/ha; (f) number of natural cavities/ha. The differences for those variables between old growth and secondary sites were examined using the Mann & Whitney's test with R.

2.1.2 Probability of presence of cavities, and abundance of cavities

The characteristics of trees with at least one cavity were used to run two Generalized Linear Mixed Models (GLMM) in R. The first one is a GLMM with a binomial error distribution and a logistic link function (Figure 8). It was used to predict the probability for a tree to hold a cavity according to its characteristics. The binomial dependent variable was the presence of cavities (presence: 1, absence: 0). The second one is a GLMM with a Poisson error distribution and a logarithmic link function (lmer function of the "lme4" package) (Robles *et al.* 2011). It was used to predict the number of cavities per tree according to the characteristics of the tree. The explanatory variables used in those models were tree characteristics variables: (1) tree decay class and (2) DBH; (3) site (10 sites) and (4) tree species (rare species were included in an "Others" category) were fixed as random factor of the GLMM.

The Akaike's Criterion Information (AIC) was calculated and used to rank the different models and select the best models structure (Bhusal *et al.* 2015; Ibarra *et al.* 2014). The models with ΔAIC=0 were the top-ranked models. All the values of parameters estimates and 95% confidence intervals can be found in Appendix 2. Parameters estimates with a 95% confidence interval that do not overlaps zero were considered as relevant parameters for the model explanation.



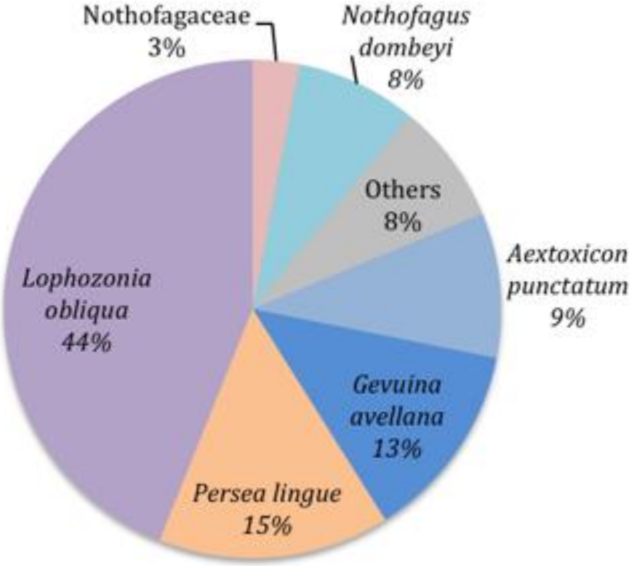


Figure 9 - Tree species composition in old growth (above) and secondarysecondarysecondary (below) forest sites. The species present with a low density were grouped in an « Others » category ; Individuals that couldn't be identified (because of a very advanced decay) but strongly suspected of being *N. dombeyi* or *L. obliqua* were grouped in a « Nothofagaceae » category.

3 RESULTS

3.1 Forest structure and composition

Between 2010 and 2016, a total of 6464 trees were measured, from a total of 296 sample plots: 1412 trees in old growth forest sites (99 sample plots), and 5052 trees in secondary forest sites (197 sample plots).

A total of 28 tree species were found in all sites: 10 in old growth forest sites and 18 in secondary forest sites. Some species are present in both sites types (*Lophozonia obliqua* and *N. dombeyi* for example) but the general composition is radically different. *L. obliqua* was the most common tree species in secondary sites (43,9 % of all trees), while *N. pumilio* was the most common tree species in old growth sites (54,7 % of all trees). In the old growth sites, the second and third most abundant species were *N. dombeyi* and *A. araucana* (19,2 and 10,2 % respectively). In the secondary sites, the next abundant species were *P. lingue* and *G. avellana* (15 and 12,9 % respectively) (Figure 9).

The tree density was calculated for each DBH class in both sites types (Figure 10). The average DBH of secondary forest sites is lower (27,4 cm) than the average DBH of old growth forest sites (44,3 cm), but in old growth sites the standard deviation is more variable.

3.2 Comparison of average densities between sites

3.2.1 Alive and dead tree densities

The density of live trees was much higher in secondary sites, and this difference was significant ($p<0,05$, Table 4), but there was no significant difference between both types of sites for the density of dead trees ($p>0,05$, Table 4) (Figure 11).

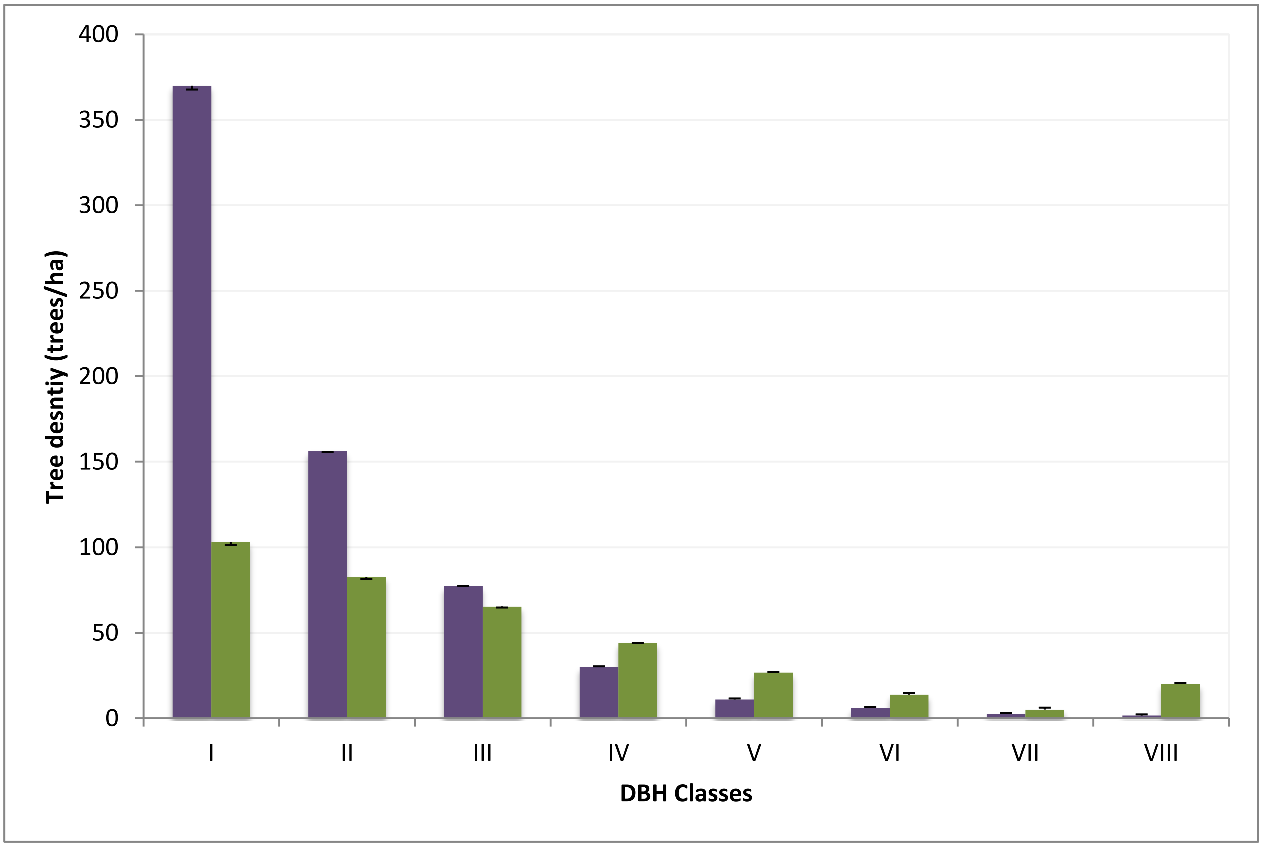


Figure 10 - Tree density for each DBH class in old growth (green) and secondary (purple) study sites. All measured trees were divided into eight DBH classes : (I) 12,5-25 cm ; (II) 25-37,5 cm ; (III) 37,5-50 cm ; (IV) 50-62,5 cm ; (VI) 62,5-75 cm ; (VII) 87,5-100 cm ; VIII >100 cm

3.2.2 Cavity trees

3.2.2.1 Cavity tree density

The density of cavity trees was higher in old growth sites (average of 175 ± 117 ha^{-1}) than in secondary sites (average of 120 ± 89 ha^{-1} (p<0,05 – Table 4). Cavity trees represented 48 % of all trees in old growth forest sites, and 18 % of all trees in secondary forest sites.

3.2.2.2 Cavity trees and decay

In both forest types, more than 60% of cavity trees were alive and unhealthy trees (decay class 2), and more than 15% of cavity trees were long dead trees (decay class 4). However, 75% of old dead trees in secondary forests have at least one cavity, and 85% in old-growth forests.

Dead cavity trees represent 78 and 55% of all dead trees in old growth and secondary forest sites. Live cavity trees represent 43 and 14% of all living trees in old growth and secondary forest sites (Figure 12).

Table 4 - Results of the comparison of average densities between old growth and secondary sites using the test of Mann et Whitney : SE=Standard Error / W=value of the Mann and Whitney constant / p=p-value, to be compared to 0.05

	Old growth (N plots = 99)			**Secondary** (N plots = 197)				
Variables	*Mean density*	±	*SE*	Mean density	±	*SE*	W	p
Live trees/ha	**304.92**	**±**	*245.20*	**589.22**	±	*406.04*	13736	**9.621 e-09**
Dead trees/ha	**57.19**	**±**	*50.26*	**66.63**	±	*62.42*	10396	0.35
Excavated cavities/ha	**53.85**	**±**	*92.95*	**34.15**	±	*62.43*	9222	0.42
Non excavated cavities/ha	**803.19**	**±**	*838.43*	***310.07***	±	*299.07*	3854	**2.2 e-16**
Total cavities/ha	**857.05**	**±**	*860.15*	***344.22***	±	*306.83*	3978	**2.2 e-16**
Cavity trees/ha	**173.61**	±	*117.12*	***119.85***	±	*89.31*	7529	0.001

Figure 11 - Density of live trees, density of dead trees, and total tree density in old growth (left) and secondary (right) sites

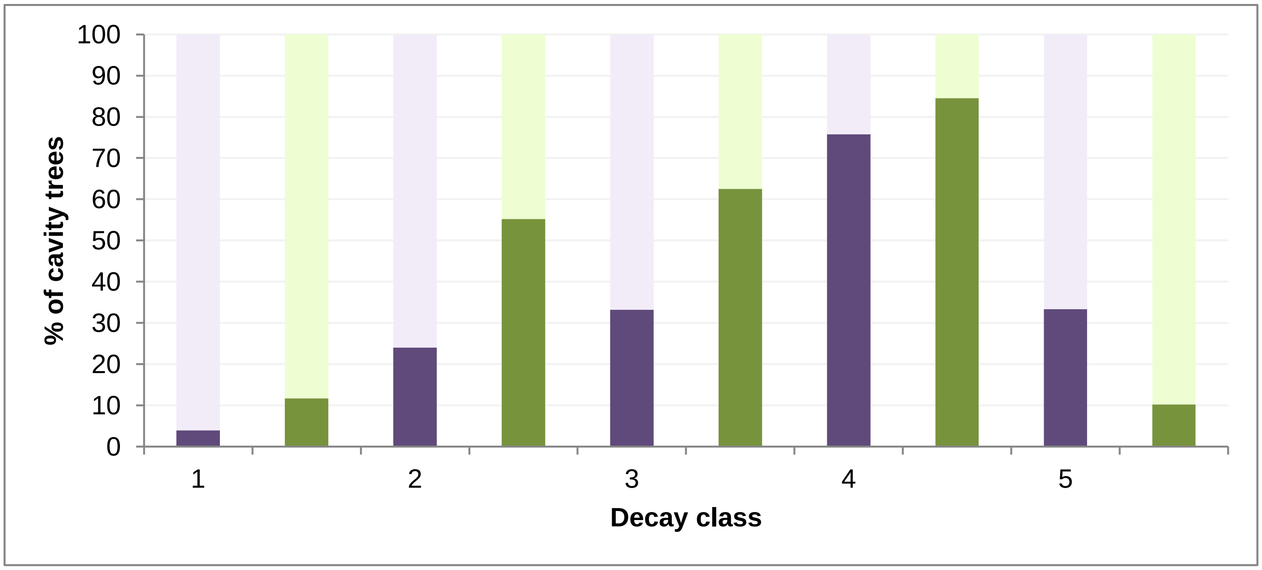


Figure 12 - Percentage of trees having at least one cavity for each decay class in secondary (purple) and old growth (green) forests / 1=alive and healthy ; 2=alive and unhealthy ; 3=recently dead ; 4=long dead ; 5=fallen

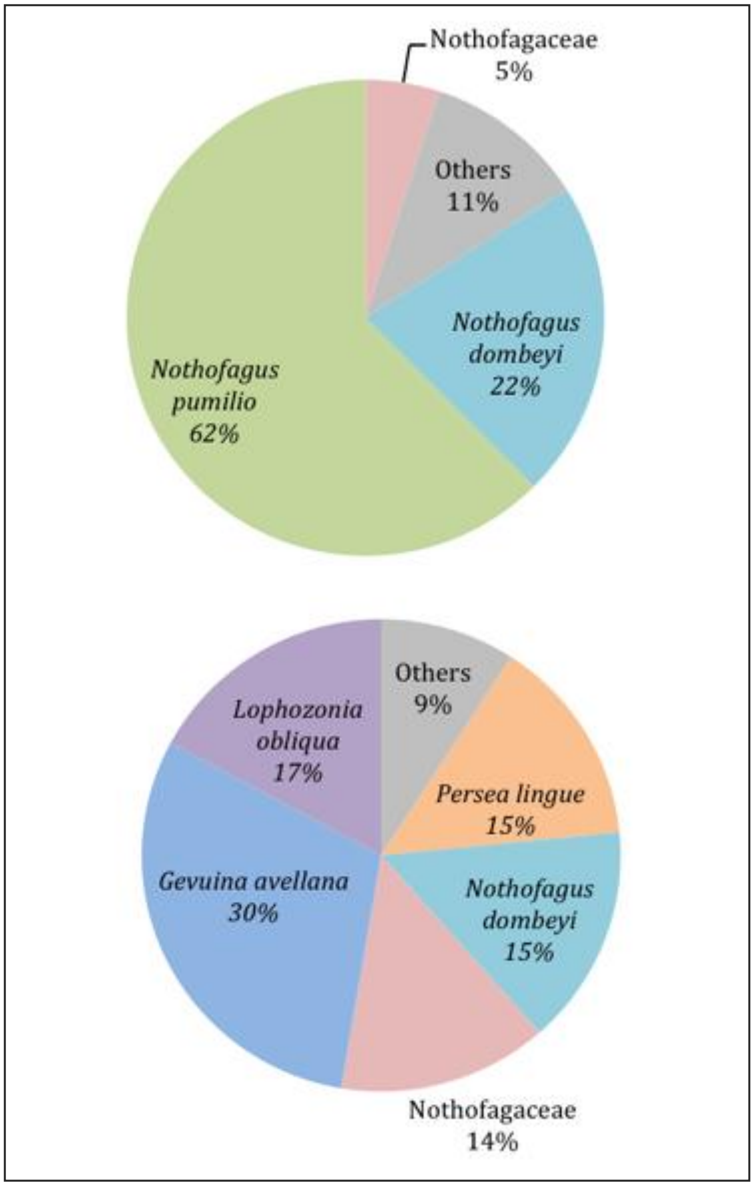


Figure 13 - Cavity tree species composition in old growth (above) and secondary (below) forest sites. The species present with a low density were grouped in an « Others » category ; Individuals that couldn't be identified (because of a very advanced d) but strongly suspected of being *N. dombeyi* or *L. obliqua* were grouped in a « Nothofagaceae » category.

3.2.2.3 Cavity trees and species

In old growth forest sites, the species of cavity tree with the highest density was *N. pumilio*, and the species of cavity tree with the second highest density species was *N. dombeyi*. In secondary forest sites, the most abundant species of cavity trees were *L. obliqua* (26 %) and *G. avellana* (24 %) (Figure 13). The other tree species rarely contained cavities.

3.2.2.4 Cavity trees and DBH

In both forest types, the larger DBH classes have the greatest proportion of trees with at least one cavity. However, in old-growth sites, even low DBH classes (from 25 cm) have 40% of cavity trees. In secondary, those proportions of cavity trees appear from DBH class IV (50 cm of DBH). The proportions of cavity trees are almost equal for largest DBH (Figure 14).

3.2.3 Excavated and non excavated cavity density

The density of total cavities is higher in old growth sites (average of 849 ha^{-1}) compared to secondary sites (average of 344 ha^{-1} ± 307) ($p<0,05$ – Table 4). The difference of density of excavated cavities and non-excavated cavities between secondary and old growth forests was not significant ($p>0,05$ – Table 4). The density of non-excavated cavities was higher in old growth forest ($p<0,05$ – Table 4) (Figure 15).

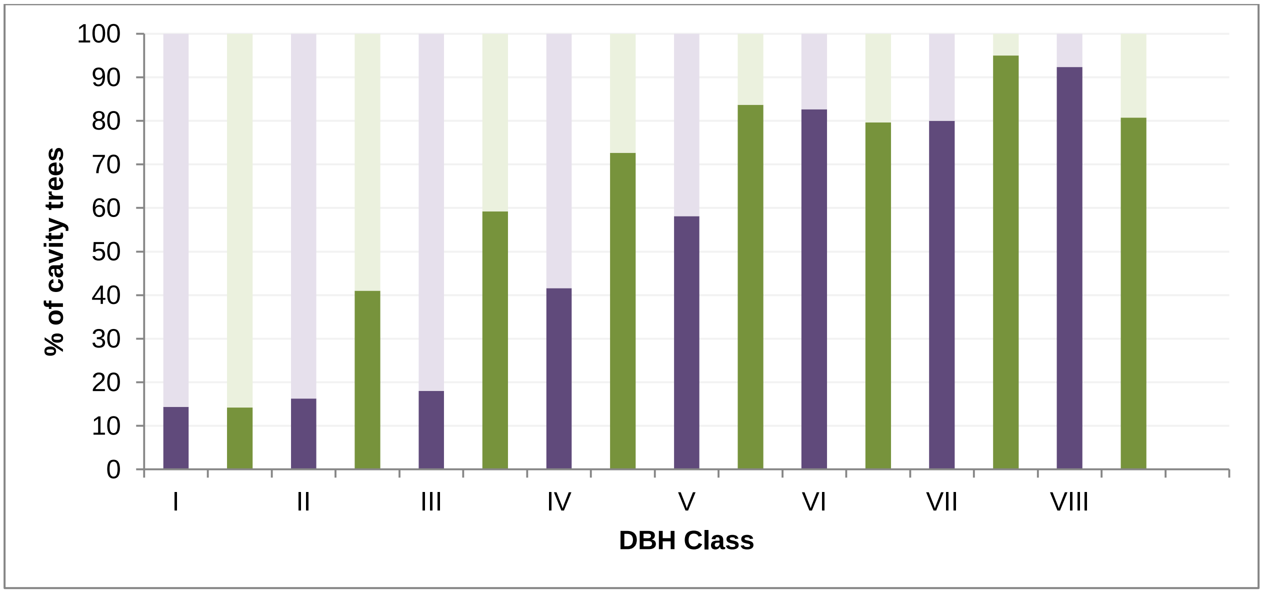


Figure 14 - Percentage of cavity trees for each DBH class in secondary (purple) and old-growth (green) forests

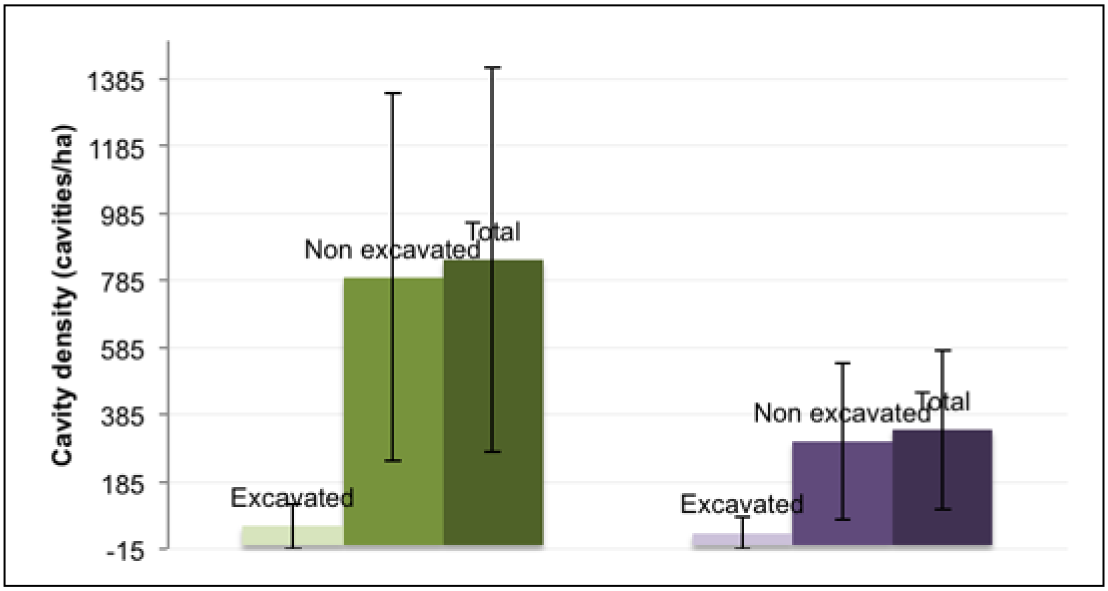


Figure 15 - Density of excavated cavities, non excavated cavities and and total density of cavities in old growth (left) and secondary (right) forest sites

3.3 Cavity occurrence and cavity trees characteristics

For occurrence and abundance of both excavated and non-excavated cavities, the top-ranked models structure included both decay and DBH (blue lines in Table 5). Indeed, the binomial GLMM indicated that trees with at least one cavity (excavated or non-excavated) had significantly larger diameters than non-cavity trees.

Trees with low DBH have a high probability of holding non-excavated cavities, especially trees with advanced decay. However, the probability of holding at least one excavated cavity does not vary much for trees with higher DBH. Alive and healthy trees and fallen trees have almost zero probability of presenting excavated cavity, even for trees with a high DBH (Figure 16, Figure 17).

According to the binomial GLMM, decayed trees were more likely to hold non-excavated and excavated cavities than healthy trees, old dead trees had the highest parameter estimates (with 95% confidence interval that do not overlap zero) and the highest probability of occurrence of non-excavated cavities (Figure 16, Figure 17, Figure 20, Appendix 2).

According to the Poisson error GLMM, the abundance of cavities per tree was associated with DBH and decay. Larger DBH and long dead trees hold higher number of both types of cavities than low DBH and healthy trees. Fallen trees hold the highest number of non-excavated cavities, and lond dead trees hold the highest number of excavated cavities (highest parameters estimates with 95% confidence intervals that do not overlap zero) (Table 5, Figures 18, Figure 19, Appendix 2).

The number of non-excavated cavities per trees is higher (from 0 to 12) than the number of excavated cavities (from 0 to 2) (Figure 18, Figure 19). The probabilities of holding excavated cavities are also very low, since they don’t exceed 0.4, even for trees with high DBH (Figures 17, Figure 21).

Table 5 - Model selection based on Akaike's Information Criterion (AIC) for estimating probability of occurrence and abundance of cavities in Andean temperate forests. The top model set with ΔAIC = 0 is the first blue line. Parameters estimates are listed in Appendix 2 / (Model structure)=description of explicative variables included in the model ; (K)=number of parameters estimated ; (ΔAIC)=difference in AIC values between each model and the lowest AIC model ; (Wt)=AIC model weight

Analysis	**Cavity origin**	**Model structure**	***K***	***AIC***	***ΔAIC***	***Wt***
Occurrence	*Non excavated*	DBH + Decay	8	4544.97	0	1
(Binomial)		DBH	4	4913.15	368.16	0
		Decay	7	4998.89	453.90	0
	Excavated	DBH + Decay	8	1476.55	0	1
		Decay	7	1532.48	55.91	0
		DBH	4	1618.35	141.78	0
Abundance	*Non excavated*	DBH + Decay	9	24172.59	0	1
(Poisson)		DBH	5	24388.76	216.17	0
		Decay	8	25713.18	1540.59	0
	Excavated	DBH + Decay	9	9038.46	0	1
		Decay	8	9188.19	149.73	0
		DBH	5	9194.15	155.69	0

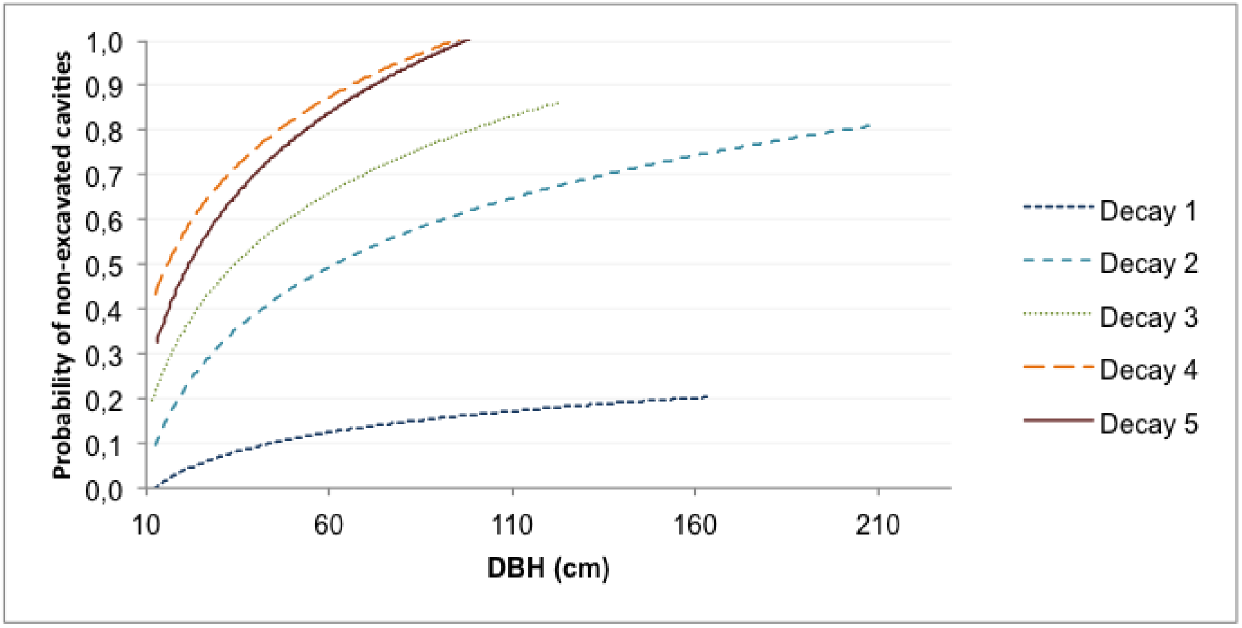


Figure 16 - Trend curves for the probabilities of non-excavated cavities with DBH according to binomial GLMM models in temperate forests of Southern Chile ; Decay 1 = Alive and healthy ; Decay 2 = Alive and unhealthy ; Decay 3 = Recently dead ; Decay 4 = Long dead ; Decay 5 = Fallen.

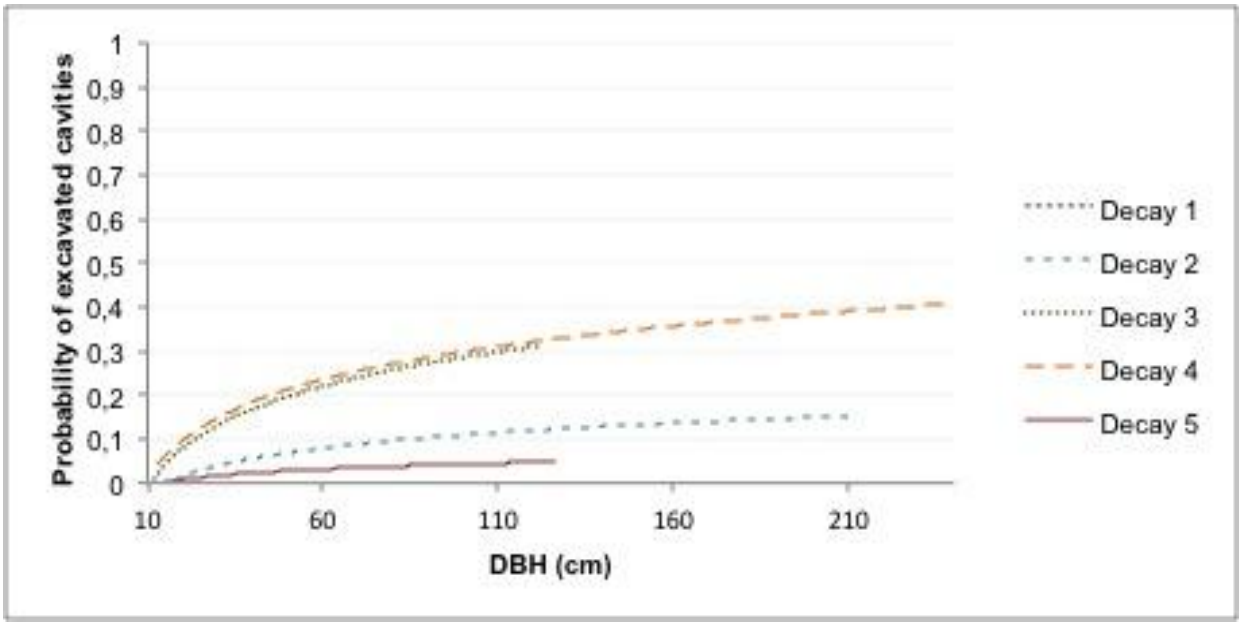


Figure 17 - Trend curves for the probabilities of excavated cavities with DBH according to binomial GLMM models in temperate forests of Southern Chile ; Decay 1 = Alive and healthy ; Decay 2 = Alive and unhealthy ; Decay 3 = Recently dead ; Decay 4 = Long dead ; Decay 5 = Fallen.

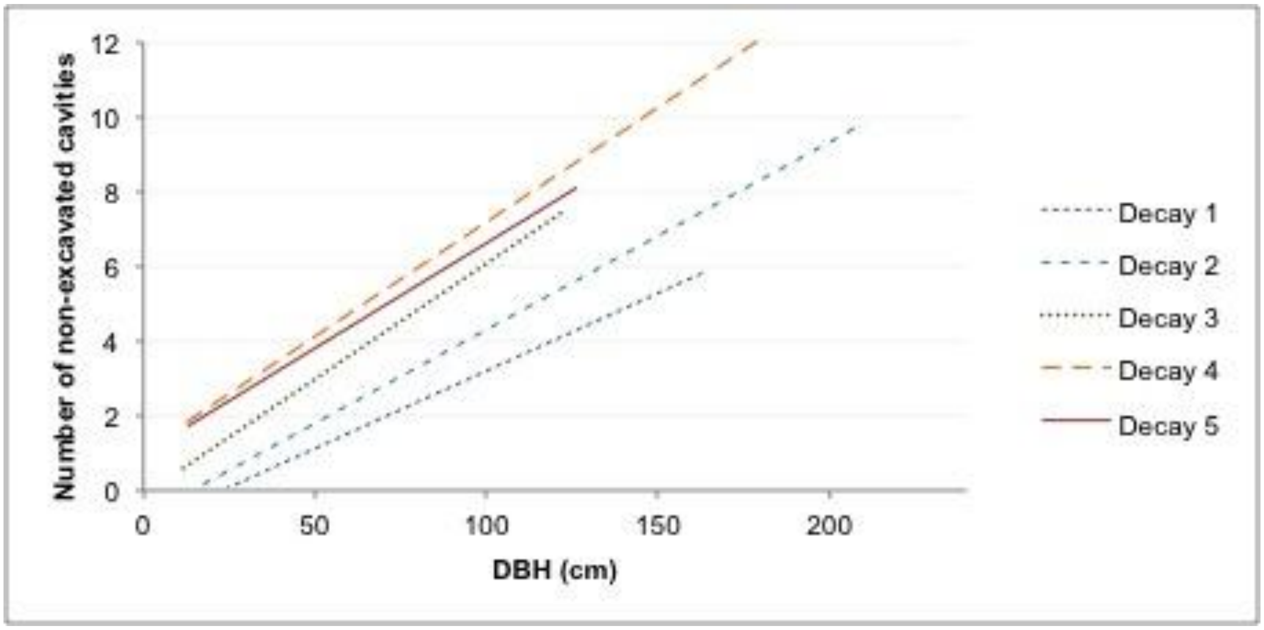


Figure 18 - Trend lines for the number of non-excavated cavities with DBH according to Poisson GLMM in temperate forests of Southern Chile; Decay 1 = Alive and healthy ; Decay 2 = Alive and unhealthy ; Decay 3 = Recently dead ; Decay 4 = Long dead ; Decay 5 = Fallen.

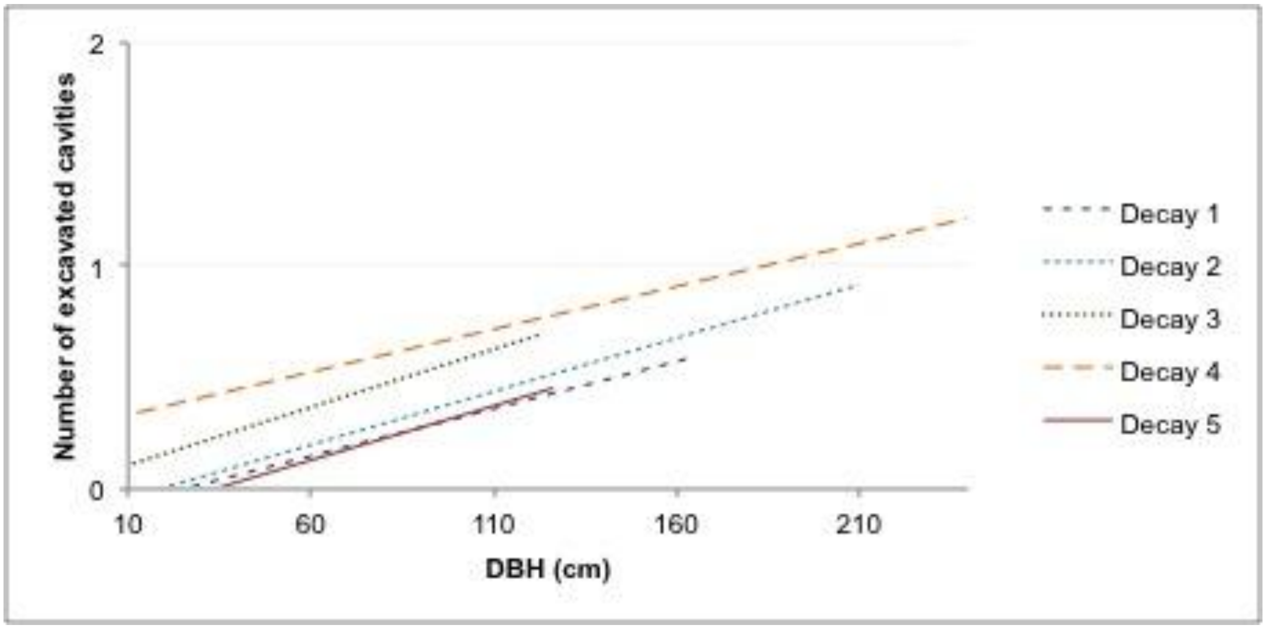


Figure 19 - Trend lines for the number of excavated cavities with DBH according to Poisson GLMM in temperate forests of Southern Chile ; Decay 1 = Alive and healthy ; Decay 2 = Alive and unhealthy ; Decay 3 = Recently dead ; Decay 4 = Long dead ; Decay 5 = Fallen.

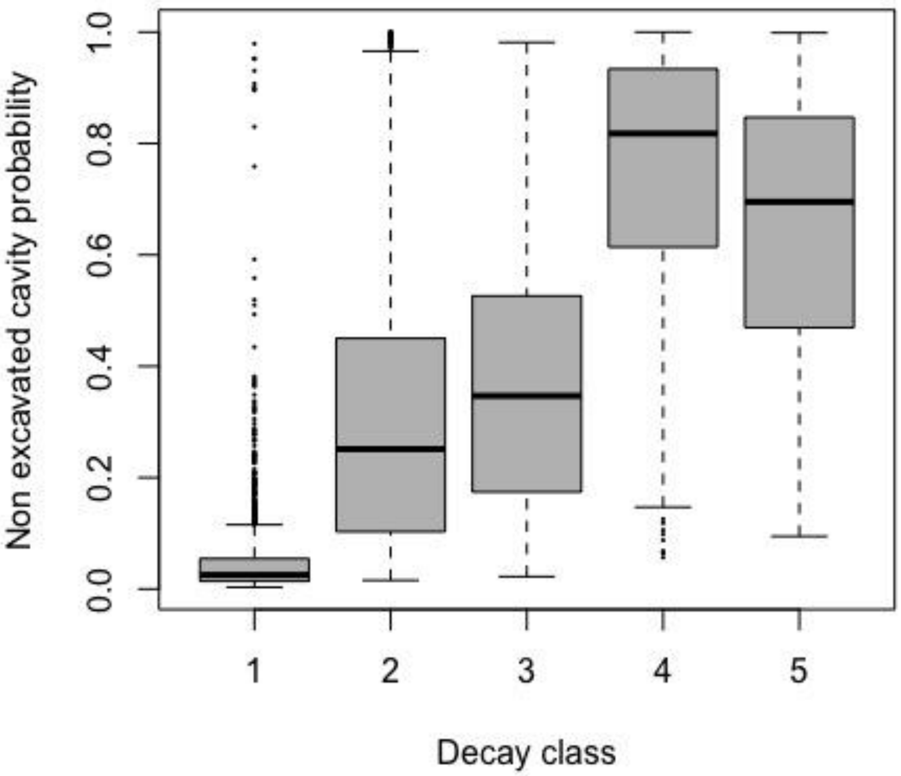


Figure 20 - Probability of occurrence of non-excavated cavities with decay class in temperate forests of Southern Chile; Decay 1 = Alive and healthy ; Decay 2 = Alive and unhealthy ; Decay 3 = Recently dead ; Decay 4 = Long dead ; Decay 5 = Fallen.

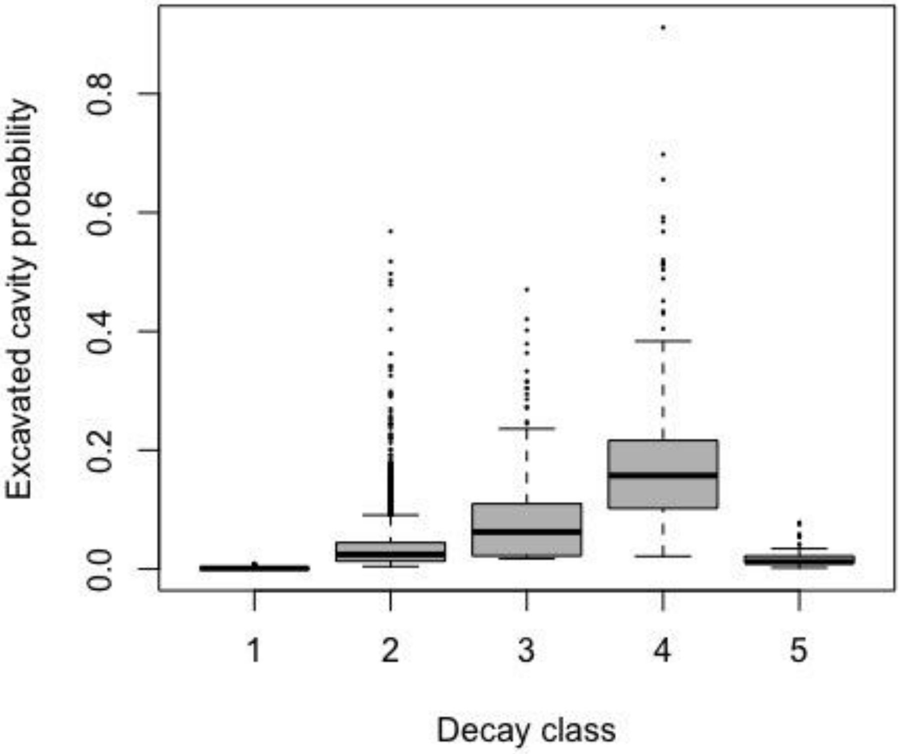


Figure 21 - Probability of occurrence of excavated cavities with decay class in temperate forests of Southern Chile; Decay 1 = Alive and healthy ; Decay 2 = Alive and unhealthy ; Decay 3 = Recently dead ; Decay 4 = Long dead ; Decay 5 = Fallen.

4 Discussion

This study shows striking differences in density of alive trees, density of non-excavated cavities and density of total cavities between old growth and secondary forests in Andean temperate forests of Chile. If the tree density is much higher in secondary forest sites, the dead tree density is the same in both types of forests. The density of cavity trees is much higher in old growth forests. The main species of cavity trees was *N. pumilio*, and Nothofagaceae trees represented almost 90% of cavity trees in old growth forests. In secondary forests however, if Nothofagaceae trees represented almost 50% of cavity trees, a lot of other species were common cavity trees, such as *P. lingue*, and *G. avellana*. The greatest proportion of cavity trees in both sites was represented by long dead trees, and trees with large DBH.

The GLMM analysis allowed us to analyze the tree characteristics that influence the presence and number of cavities. We showed that both DBH and decay are important factors that increase the probability of occurrence of cavities in trees, as well as the abundance of cavities per trees, larger and long dead trees being more likely to hold cavities, and more likely to hold a high number of them. However, DBH and decay seem to be more important explicative factors for non-excavated cavities than excavated cavities.

The database generated with the fieldworks throughout the years is very large, with very unique data for temperate forests of South America, which provided important information about tree-cavities. However, the trees that were measured are the trees located around nest-trees and they might not be a representative sample of the whole forest. It might therefore be questionable to analyze these data and conclude about cavity density for the whole forest. Furthermore, the study sites that were included in the study were not chosen in a rational way with precise methodological criteria of vegetation or altitude for example. Other practical criteria influenced the use of those study sites, like the location, the accessibility, the presence of interesting nests and bird species found in the previous years of the study etc.

The average density of total cavities in our study was 857 ha^{-1} for old growth forests and 344 ha^{-1} for secondary forests, which is much higher than the global average estimated by Remm & Lohmus (2011) of 16 ha^{-1}. The idea of nest-site availability as a limiting factor for cavity-nesting birds dominates thinking in cavity-nester ecology (Wesołowski 2007). However, many studies suggest that there is no nest site limitation in primeval forests: in forests of Central Sweden, a cavity density of 60 ha^{-1} was found, and only 5-9% of them were used (Carlson *et al.* 1998). A surplus of cavities was also observed in old growth Australian forests, where the cavity tree density range from 7 to 27 ha^{-1}. Bai *et al.* (2003) found similar results in deciduous forests of Mongolia, where the cavity density approached 30 ha^{-1}, but where the cavity nest density was only 2,4 ha^{-1}. Finally, the Peruvian rainforest also showed quite low occupancy rates: only 16% of the cavities were actually used (Brightsmith 2005). Our results show a much higher density of non-excavated cavities (803 ha^{-1}). This suggests that there is as well an overabundance of natural cavities in old growth Andean temperate forests of Chile, and that nest site availability is not a limiting factor for cavity-nesting birds in those forests. However a study of cavity occupancy rates would be necessary to confirm this diagnostic, and the fecundity data of the project would allow us to do such study in the future.

Even if the density of non-excavated cavity is higher in old growth forests, there is still a very high density of natural cavities in secondary forests (310 ha^{-1}). This could be due to the high number of old snags that are remnants of fires that occurred several decades ago. Those trees are very important sources of cavities for cavity-nesting birds in managed forests. However, as suggested by Ganey (1999), the trees in latest decay classes are more susceptible to break and their height is reduced, which is less attractive for birds. During the fieldwork, the loss of a few nests in old snags due to an internal collapse showed that they are not safe substrates for birds. Old snags also have less bark cover, which reduces their value for bats that nest and roost under loose bark. Besides, those snags are closer to the end of their useful life than trees in early decay stages: long dead trees have already passed their period of maximum value to wildlife (Ganey 1999). When those trees will fall down, we will assist to a quick diminution of the density of cavity in secondary forests, as the other standing trees haven't the suitable size and decay to form natural cavities yet. This could result in a limitation of nest-site availability for cavity-nesting birds and in the long-term in a diminution of the richness of the cavity-nesting birds (and other cavity-nesting species) community.

In Australian forests, there are no excavating birds, and yet the cavity-nesting avifauna is very diversified, which suggests that the presence of primary cavity-nesters is not always a requirement for non-excavator cavity-nesting birds (Gibbons & Lindenmayer 2002). Similarly, excavated cavities constituted only 22% of those used in old growth forests of Sweden (Carlson *et al.* 1998), and 18% of those used in forests of Mongolia (Bai *et al.* 2003). Yet, in temperate forests of North America, many studies demonstrated that woodpeckers are generally keystone species that provide a great number of cavities (Martin & Aitken 2004). In our study, we found that in both forests types, the density of excavated cavities (54 ha^{-1} for old growth and 34 ha^{-1} for secondary forests) was much lower than the density of non-excavated cavities (803 ha^{-1} for old growth and 310 ha^{-1} for secondary forests). This suggests that woodpeckers don't play a role of keystone species in Andean temperate forests of Chile.

Although the number of cavities we found is very high, a few might actually have the suitable size and characteristics to be used by birds. The number of cavities for each tree was estimated without measures to confirm the suitability of cavities, and without criteria that could help defining which ones are "good" cavities. Suitable cavities therefore may be in short supply for many cavity-nesting birds. It would be important to consider cavity quality when assessing cavity supply (Cornelius *et al*. 2008), in order to avoid an overestimation of cavity density in Andean temperate forests.

The probabilities of occurrence of excavated cavities were slightly higher in long dead trees. The difference would probably be bigger, but these results are biased by the fact that a great number of excavated cavities were found in dead branches of the trees. However, the variable "decay" describes the condition of the tree and not of the branch that actually held the cavity. An excavated cavity can be registered in an alive and unhealthy tree, whereas the actual substrate of the cavity (the branch) was long dead. The decay of the tree and the decay of the substrate were both collected during the fieldwork. It would therefore be interesting to analyze the potential difference in the results using the decay of the substrate instead of the general decay of the tree.

The probability of occurrence of excavated cavities found was very low, even for trees with high DBH and advanced decay. This shows that, even if DBH and decay are parameters that influence the occurrence of excavated cavities, other factors must influence in a significant way the trees that excavator birds choose when they excavate a cavity. Everett & Otter (2004) suggest that the utilization of a tree by excavating birds also depend on the environment around the tree: in managed forests, they found a greater number of excavated cavities as the distance of the tree from the forest cover decreased. They therefore recommend retaining trees in cut blocks within 100 meters of the forest edge.

In both sites, Nothofagaceae trees were the most abundant cavity trees (89% in old growth forests, and 55% in secondary forests). *Nothofagus* trees are therefore playing an important role in cavity formation processes, as suggested by Ojeda *et al*. (2007) and Cornelius *et al.* (2008). In old growth sites, *N. pumilio* represented 63% of cavity trees, suggesting that it is a keystone tree species in high Andean temperate forests, providing both cavities and substrates for excavators (Cornelius 2008). In lowlands secondary forests however, *N. pumilio* does not grow, and the *Nothofagus* trees that are present (*N. obliqua*, now *L. obliqua* and *N. dombeyi*) do not form cavities as easily. The proportions of cavity trees in secondary forests showed that in those forests, other tree species are more important cavity-trees such as *G. avellana* and *P. lingue* since they form cavities early in their life cycle, even with low DBH and decay.

Forest management recommendations

Our results showed that trees with bigger DBH are more likely to hold cavities, and when they do, the number of cavities is higher for thick trees. Forestry schemes should therefore let trees reach a minimum DBH of 50 cm in order to allow the formation of cavities in managed secondary forests. We also showed the importance of tree decay

for the occurrence of both non-excavated cavities and excavated cavities. Fallen trees appear to have the highest
probability of holding non-excavated cavities. It is therefore important in managed forests to let on the ground the naturally fallen trees, since they provide habitat for cavity nesting species. Fallen trees in various stages of decay are also important structures for biodiversity as the fallen tree-soil interface offers a cool and moist habitat for animals and a substrate for microbial and invertebrates activity (Maser & Trappe 1984).

Traditionally, snags are considered as the most important source of cavities, and snag management as an effective way of preserving habitat for cavity nesters (Kenefic & Nyland 2007). In Andean temperate forests of Chile, if snags only represent 15% of cavity trees, the great majority of them have cavities, and our results also showed that long dead trees are more likely to hold cavities, and to hold a greater number of them. They are therefore important sources of cavities for cavity-nesting species, and some of them should be preserved. However, alive and unhealthy trees represent the greatest proportion of cavity trees in both types of forests. Management policies in Andean temperate forests of Chile should then also focus on the conservation of unhealthy living trees. They form a more attractive and a safer substrate for cavity nesting birds since they are less likely to break or fall. Furthermore, their useful life as cavity trees and thus habitat for wildlife will be longer than long dead trees. Healy *et al* (1989) recommend to "retain live and vigorous cavity trees as a mean for maintaining the habitat for cavity-nesting species over an extended period". Finally, after a long period of useful life, they will convert in old snags with a great number of cavities that can still be used by cavity-nesting species.

Our study also highlighted the importance of other common tree species in temperate forests of Southern Chile for the formation of cavities. In managed forests, the *Nothogafus* species (coihue and roble) have the highest density, but other species are more important cavity trees, such as *G. avellana* and *P. lingue*. Although the economic value of the two latter species is lower than *Nothofagus* trees, it is important to maintain those species, and more generally to maintain biodiversity of tree species, in order to maintain a high density of cavities and provide habitat for cavity-nesting species.

Although this study provided important information about cavity supply in Andean temperate forest, it is not sufficient to give a precise image of their use by the cavity-nesting species community. All the fecundity data that was collected during the fieldworks throughout the years should now be used in order to calculate occupancy rate of cavities, assess which trees species and decay classes, and which trees species and decay classes maximize breeding success. Indeed, a great cavity density does not imply a high rate of cavity occupancy. The observation of competitive behaviors for cavities during the fieldwork, and the successive use of the same cavity by different pairs in the same breeding season are both elements that suggest the existence of a strong competition between cavity-nesters (Newton 1994).

APPENDIXES

	Old growth forests (N=1407)			Secondary forests (N=5081)		
Tree species	**Number**	**Mean density**	**%**	**Number**	**Mean density**	**%**
Acacia dealbata (*)	0	0	*0*	2	0,26	*0,04*
Aextoxicon punctatum	0	0	*0*	475	61,22	*9,40*
Araucaria araucana	144	36,93	*10,20*	0	0,00	*0*
Aristotelia chilensis	0	0	*0*	9	1,16	*0,18*
Caldcluvia paniculata	0	0	*0*	4	0,52	*0,08*
Cupressus spp (*)	0	0	*0*	1	0,13	*0,02*
Dasiphyllum diacanthoides	44	11,28	*3,12*	95	12,24	*1,87*
Drimys winteri	0	0	*0*	6	0,77	*0,12*
Eucalyptus globulus	0	0	*0*	9	1,16	*0,18*
Eucryphia cordifolia	0	0	*0*	70	9,02	*1,39*
Gevuina avellana	1	0,26	*0,07*	680	87,63	*13,38*
Laurelia sempervirens	0	0	*0*	45	5,80	*0,89*
Laureliopsis philippiana	45	11,54	*3,19*	6	0,77	*0,12*
Lomatia dentata	0	0	*0*	41	5,28	*0,81*
Lomatia ferruginea	0	0	*0*	1	0,13	*0,02*
Lomatia hirsuta	0	0	*0*	32	4,12	*0,63*
Lophozonia obliqua	62	15,90	*4,39*	2218	285,84	*43,90*
Luma apiculata	0	0	*0*	30	3,87	*0,59*
Myrceugenia exsucca	0	0	*0*	8	1,03	*0,16*
Nothofagus alpina	0	0	*0*	12	1,55	*0,24*
Nothofagus dombeyi	271	69,50	*19,19*	396	51,03	*7,84*
Nothofagus pumilio	769	197,21	*54,66*	0	0	*0*
Nothofagaceae	37	9,49	*2,76*	147	18,94	*2,89*
Persea lingue	0	0	*0*	766	98,72	*15,08*
Pinus radiata (*)	0	0	*0*	12	1,55	*0,24*
Pseudotsuga menziesii (*)	0	0	*0*	1	0,13	*0,02*
Rhaphithamnus spinosus	1	0,26	*0,07*	4	0,52	*0,08*
Saxegothaea conspicua	31	7,95	*2,20*	7	0,90	*0,14*
Weinmannia trichosperma	2	0,51	*0,14*	4	0,52	*0,08*
TOTAL	*1407*	362,10	*100*	*5081*	651,08	*100*

Appendix 1 - Number, mean density and percentage of trees for each tree species found in old growth and secondary forests sites ; exotic species were marked with a (*) ; individuals that couldn't be identified (because of a very advanced decay) but strongly suspected of being *N. dombeyi* or *L. obliqua* were grouped in a « Nothofagaceae » category.

Analysis	**Cavity origin**	**Model structure**	***K***	***AIC***	***ΔAIC***	***Wt***	***Parameter estimates***		***Estimated 95% CI***	
Occurrence	*Non excavated*	**DBH + Decay**	8	4544.97	**0**	1	**dbh: 0.05**		dbh: 0.04 ; 0.05	
							d 2: 1.60	**d 3: 1.97**	d2: 1.39 ; 1.82	d3: 1.62 ; 2.31
							d 4: 2.90	**d 5: 2.57**	d4: 1.62 ; 2.31	d5: 1.82 ; 3.33
		DBH	4	4913.15	368.16	0	**0.05**		0.05 ; 0.06	
		Decay	7	4998.89	453.90	0	**d 2: 1.83**	**d 3:1.89**	d 2: 1.63 ; 2.05	d 3: 1.56 ; 2.12
							d 4: 2.81	**d 5: 1.87**	d 4: 2.45 ; 3.18	d 5: 1.15 ; 2.61
	Excavated	**DBH + Decay**	8	1476.55	**0**	1	**dbh: 0.02**		dbh: 0.02 ; 0.03	
							d 2: 2.99	**d 3: 4.18**	d 2: 2.00 ; 4.40	d 3: 3.11 ; 5.63
							d 4: 4.50	d 5: 2.03	d 4: 3.45 ; 5.94	d 5: -1.01 ; 4.16
		Decay	7	1532.48	55.91	0	**d 2: 3.22**	**d 3: 4.17**	d 2: 2.24 ; 4.63	d 3: 3.10 ; 5.61
							d 4: 4.64	d 5: 2.02	d 4: 3.59 ; 6.07	d 5: -1.01 ; 4.12
		DBH	4	1618.35	141.78	0	**0.02**		0.018 ; 0.029	
Abundance	*Non excavated*	**DBH + Decay**	9	24172.59	0	1	**dbh : 0.05**		dbh : 0.047 ; 0,051	
							d 2: 0.26	**d 3: 0.98**	d 2: 0.18 ; 0.35	d 3: 0.79 ; 1.17
							d 4: 1.35	**d 5: 1.58**	d 4: 1.13 ; 1.57	d 5: 1.11 ; 2.05
		DBH	5	24388.76	**216.17**	0	**0.05**		0.046 ; 0.051	
		Decay	8	25713.18	**1540.59**	0	**d 2: 0.56**	**d 3: 0.89**	d 2: 0.46 ; 0.65	d 3: 0.68 ; 1.11
							d 4: 1.50	**d 5: 0.63**	d 4: 1.26 ; 1.75	d 5: 0.11 ; 1.15
	Excavated	**DBH + Decay**	9	9038.46	**0**	1	**dbh : 0.005**		dbh : 0.004 ; 0.005	
							d 2: 0.03	**d 3: 0.18**	d 2: -0.00 ; 0.05	d 3: 0.12 ; 0.24
							d 4: 0.42	d 5: -0.21	d 4: 0.3 ; 0.48	d 5: -0.16 ; 0.12
		Decay	8	9188.19	**149.73**	0	**d 2: 0.06**	**d 4: 0.45**	d 2: 0.03 ; 0.08	d 3: 0.11 ; 0.23
							d 4: 0.45	d 5: -0.07	d 4: 0.38 ; 0.51	d 5: -0.22 ; 0.08
		DBH	5	9194.15	**155.69**	0	**0.005**		0.004 ; 0.005	

Appendix 2 - Model selection statistics based on Akaike's Information Criterion (AIC) for estimating probability of occurrence and abundance of excavated and non excavated cavities in Andean temperate forets. The top-ranked models (firs blue line) are the with Δ AIC=0. Parameter estimates are listed for each level of each factor in the order of variables under Model structure column, and estimates which 95% confident intervals that do not overlap zero are written in bold font; (K): number of parameters estimated; (*ΔAIC*): difference in AIC values between each model and the lowest AIC model; (Wt): AIC model weight.

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