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Availability of cavities for avian cavity nesters in selectively logged subtropical montane forests of the Andes

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ABSTRACT

Tree cavities play a critical role in the life history of cavity-using species and thus are an important structural feature of forests. Furthermore, some common forest management practices can have a profound negative effect on cavity quantity and quality. This is the first study to address cavity resources in Neotropical montane forests and with this information we hope to develop approaches to sustainable forest management that will assure the conservation of cavity nesters. Our study design consisted of two treatments (control and harvested forest) in both piedmont and cloud forests of the subtropical montane forests of the Andes. This study indicates that cavities are an uncommon feature even in control sites with only 3% of the trees harboring cavities in both forest types. Even more uncommon are potentially usable cavities for avian cavity nesters: only 0.15% of the trees have a potentially usable cavity in the piedmont forest and only 0.42% in the cloud forest. In logged forests there is a significantly lower density of potentially usable cavities (4.12 vs. 0.51 cavities/ha in piedmont forest and 3.91 vs. 1.64 cavities/ha in the cloud forest). Furthermore, we documented a high loss rate of potentially usable cavities (from 23 to 40%/year) that differs between tree species and DBH classes. More specifically, in the piedmont forest, large, decaying *Calycophyllum multiflorum* have a relatively greater probability of having potentially usable cavities, while in the cloud forest potentially usable cavities are disproportionably found in large, decaying *Blepharocalyx gigantea*. In both forest types, snags are also very likely to harbor a potentially usable cavity. In order for harvested stands in the subtropical montane forest of the Andes to regain some of their ecological value, it is necessary to retain trees that have potentially usable cavities and also trees with the highest probability of becoming usable cavity trees.

1. Introduction

Tree cavities play an important role in the life history of cavity-using species and are an important structural feature of forests (Aitken and Martin, 2008; Drever et al., 2008; Eyre et al., 2010; Harestad and Keisker, 1989; Hunter and Schmiegelow, 2011; Lindenmayer et al., 1993; Newton, 1994; Raphael and White, 1984; Renton and Brightsmith, 2009; Spies et al., 1988; Steeger and Hitchcock, 1998). However, some common forest management practices can have a profound negative effect on cavity quantity and quality, and attention is needed to maintain cavity trees in harvested stands and by reserving some stands from harvest (Cornelius et al., 2008; Drever et al., 2008; Fan et al., 2004; Graves et al., 2000; Martin and Eadie, 1999). Furthermore, the management of tree cavities is challenged by their dynamic nature; i.e., the cavity resource changes over time as cavity trees fall, new cavities are created, and cavity availability changes through decay or structural changes, and all of these may vary in response to factors such as disturbance and stand age (Drever et al., 2009; Fan et al., 2003b; Lindenmayer et al., 1993; Raphael and Morrison, 1987). Moreover, cavity development is a relatively uncommon and poorly understood process governed by stochastic processes that lead to tree injury, decay, or excavations by animals (Carey, 1985; Fan et al., 2003a; Holloway et al., 2007).

Many animal species use tree cavities for dens and roosts because cavities offer shelter from weather and security from predators (Bull et al., 1992; Conner et al., 1975; Flemming et al., 1999; Martin et al., 2004; McComb, 2007). Cavity nesters may be particularly sensitive to timber harvesting (Gibbons and Lindenmayer, 2002; Titus, 1983; Wesolowski et al., 2005), especially secondary cavity nesters; i.e., species that use cavities created by primary cavity nesters (species such as woodpeckers that excavate their own cavities) or by wood decay following damage to a tree (McComb, 2007). To establish guidelines for maintaining cav-

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ity trees we need to understand the distribution of cavity trees and potential cavity trees at multiple spatial scales such as individual trees (species), stands, landscapes, and across forest regions (Cline et al., 1980; Gibbons, 1994; Morrison and Raphael, 1993; Raphael and Morrison, 1987).

Most Neotropical forest remnants are subject to timber harvesting and with increasing foreign investment and expanding demand for wood, logging will probably increase in the future (Bowles et al., 1998; FAO, 1993; Sugal and Mittermeier, 1999; Uhl et al., 1997). Sustainable forest management can meet economic interests of producers while assuring the conservation of biodiversity (Hunter, 1999). However, for sustainable management to succeed, clear guidelines should be articulated to make harvesting both economically and ecologically viable and thereby reduce pressures to convert forests into agricultural fields (Hartshorn, 1998).

Managing forests in a sustainable manner is particularly relevant in the subtropical montane forests of the Andes (hereafter, montane forests) because they are subject to intense timber management. These forests are especially important because they provide many ecosystem services (e.g., water for human consumption and agriculture irrigation), timber resources, and high levels of richness and endemism for several taxa (Grau and Brown, 1998). Since 2001, timber market values in Argentina have risen significantly, making logging more profitable (SAGPyA, 2005). However, if sustainable forest management guidelines are not adopted soon there is a risk of depleting the timber resource and driving the transformation of economically unproductive forests into agricultural fields, which are more profitable in the short term (Sanchez-Acosta and Vera, 2005). There is relatively little information on the ecology of most subtropical montane forests and virtually no information on the features important for cavity nesters. We do know that in the subtropical montane forest of northwestern Argentina more than 100 bird species are obligate or facultative cavity users (De la Peña, 1998).

This study has three objectives: (1) to examine some of the effects of logging on forest structure and composition; (2) to assess the abundance of tree cavities available to avian cavity nesters; and (3) to explore the factors associated with cavity tree abundance and develop models that can be used to predict how they affect the loss of cavities. This information will be useful in evaluating the effects of selective harvesting on tree cavity resources in the subtropical montane forest of the Andes and developing relevant management guidelines.

2. Materials and methods

2.1. Study area and design

Fieldwork was conducted in the subtropical montane forests of northwestern Argentina known as Southern Yungas or selva Tucumano-Boliviana (Cabrera, 1994). The piedmont forest is located in the lowest elevation gradient of the Yungas; i.e., from approximately 400 to 750 m above sea level. The cloud forest is found at the highest elevation of the forest between 1500 and 2200 m above sea level. Climate in both forest types is highly seasonal, and rainfall is concentrated (75–80%) during the summer (i.e., November–March). Annual rainfall averages ca. 800 mm in the piedmont and 1300 mm in the cloud forest (Brown et al., 2001). Mean annual temperature averages 21.1 °C for the piedmont forest and 11.7 °C in the cloud forest (Arias and Bianchi, 1996).

Most of the forestland (estimates range from 50 to 90%) in the piedmont region of northwestern Argentina has been transformed to agricultural fields (Brown and Malizia, 2004; Brown et al., 2001; Brown et al., 2002; Pacheco and Brown, 2006). Remnant piedmont forests are subject to extensive selective logging, essentially high grading that focuses primarily on 10 timber species (i.e., *Cedrela balansae*, *Amburana cearensis*, *Anadenanthera colubrina*, *Calycophilllum multiflorum*, *Phyllostilon rhamnoides*, *Astronium urundeuva*, *Tabebuia avellanedae*, *Myroxylon peruiferum*, *Cordia trichotoma*, and *Pterogyne nitens*). Cloud forest remnants are also subject to intense selective logging, primarily on one species (*Cedrela lilloi*), but occasionally on two others (i.e., *Podocarpus parlatorei* and *Juglans australis*).

The effect of selective logging was studied in a design that consisted of two treatments in piedmont and cloud forests of the subtropical montane forests of the Andes (Fig. 1): *harvested* forest with recent logging and *control* forests that have not been logged in for at least 30 years and represented the least disturbed conditions (in terms of tree species composition and forest structure) encountered during the pilot study (Delong and Kessler, 2000). Harvested sites had been logged regularly and represented current timber harvesting practices as undertaken throughout the region (Pablo Eliano–Director of the Northwestern Argentina Forester Association, personal communication); i.e., very selective based on large diameters and good condition of valuable timber species. Harvested sites were selected near a control site to minimize differences in tree species composition and forest structure and to maximize the possibility that the sites had been affected by the same large-scale natural disturbances. No logging occurred in the areas where we laid our transects, and therefore no cavity trees were lost due to logging. There is no information on the structure and composition of these forests before they were logged to allow before and after treatment comparisons. Each site comprises an area of ca. 100 ha. We selected six 100-ha sites in the piedmont forest: three harvested and three controls; and five 100-ha sites in the cloud forest: three harvested and two controls (in Argentina only two areas of the cloud forest have been cited as undisturbed, i.e., El Rey National Park and El Nogalar National Reserve (Grau and Brown, 1998), therefore we established one site in each of the mentioned reserves).

2.2. Forest and cavity sampling

At each site 20 circular plots of 0.05 ha were randomly placed, but at least 150 m apart. Within each plot, all trees >10 cm diameter at breast height (DBH) were identified, counted, and DBH measured. Snags (standing dead trees) of >10 cm DBH were counted and DBH measured but not identified to species. We also counted the number of stumps and measured their diameter at 50 cm from the ground.

At each site we established 20 variable-width, random direction, 300-m long transects that were at least 150 m apart. Cavity sampling was conducted during the dry season (from April to August) when many trees are leafless (piedmont forest is deciduous and cloud forest is semi-deciduous). We marked every cavity encountered that had a diameter entrance of more than 3 cm (the minimum diameter that the camera system could inspect, see below) and we measured the perpendicular distance from the transect to the tree cavity using distance sampling methodology (Buckland et al., 2001). Cavities were inspected with a camera system attached to a 15 m extendible pole (Richardson et al., 1999) to determine if they were "potentially usable" for avian cavity nesters (i.e., hollow chambers surrounded by sound wood [not collapsing wood] accessed by entrance holes with a floor to harbor an incubation chamber, and a roof that provided adequate protection) or "non-usable". This classification was based on our knowledge of cavities used by cavity-nesting birds (Politi et al., 2009). Non-usable cavities were generally either trial excavations by woodpeckers, or decay cavities that had either decayed to the degree that they were no longer usable, or not decayed enough to provide a cavity of sufficient size. In all cases they had similar cavity entrance dimensions

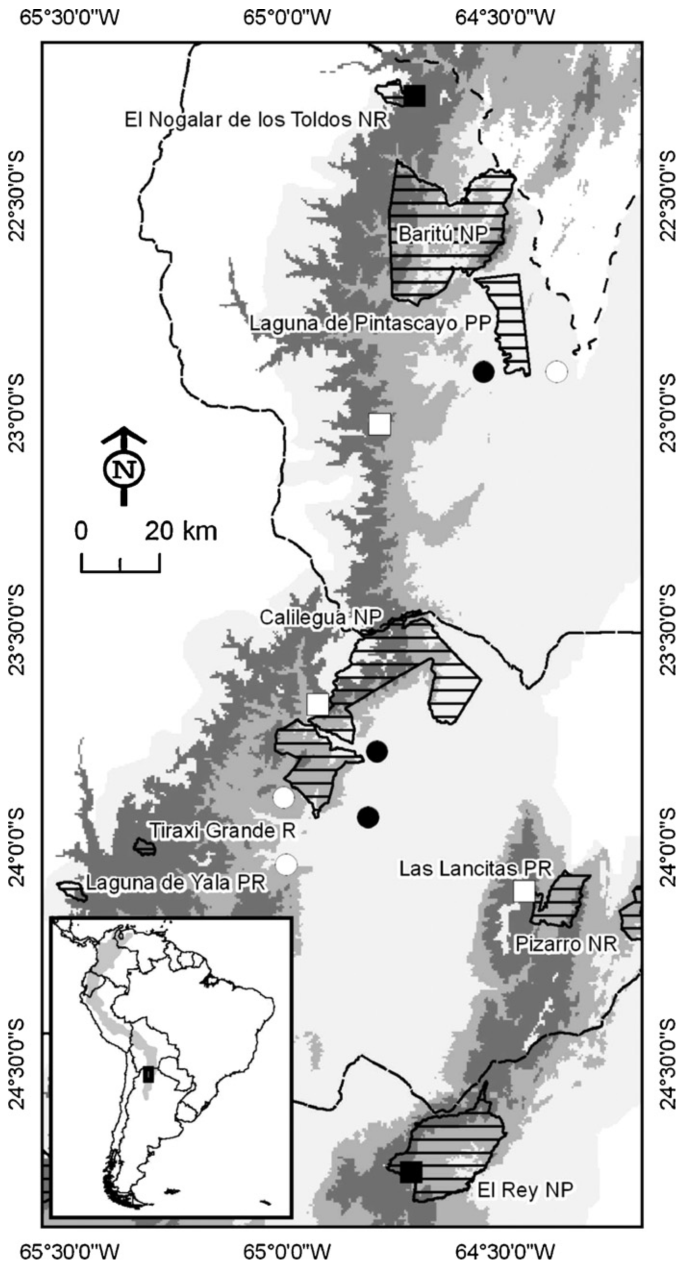

Fig. 1. Location of study sites in the subtropical montane forests of the Andes. Lightest gray (almost white) and circular symbols: piedmont forest; intermediate gray: montane forest of intermediate elevation that were not studied; darkest gray and square symbols: cloud forest; filled symbols: control sites; open symbols: harvested sites. Hatched areas represent protected areas; NP: National Park; NR: National Reserve; PP: Provincial Park; PR: Provincial Reserve. Left-bottom corner map shows (in gray) the distribution of subtropical and tropical montane forests of the Andes and the box shows the study area.

as usable cavities and thus could be mistaken for usable cavities in ground surveys that lacked direct inspection (Politi et al., 2009). We recorded tree species, DBH, tree height, tree condition (1: living with no signs of decay; 2: living with signs of decay; 3: dead), cavity height, tree diameter at cavity height (DCH), vertical and horizontal entrance diameter, diameter of the incubation chamber (Fig. 2), and origin of the cavity (i.e., excavated or decayed). We randomly selected one "potentially usable" cavity on each transect and made it the center of a 0.05 ha circular plot in which we recorded species, DBH, and condition for trees >10 cm DBH. We also recorded cavity and tree-level characteristics described above for non-usable cavities. We randomly selected one non-cavity tree from each transect

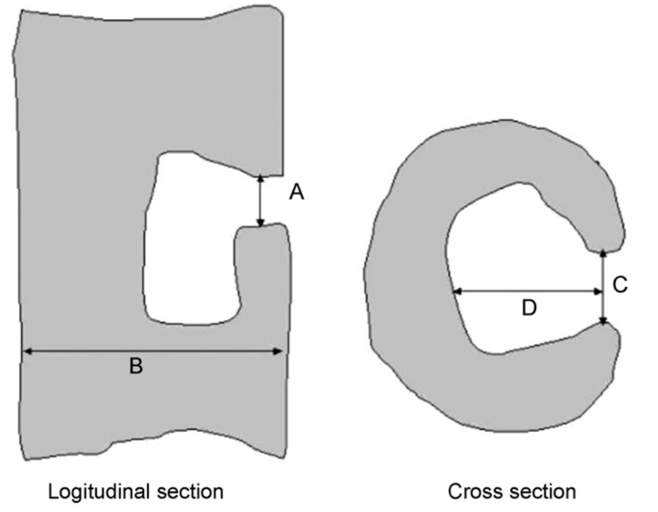

Fig. 2. Measurements taken from cavities. A: Entrance vertical diameter; B: tree diameter at cavity height (DCH); C: entrance horizontal diameter; D: internal cavity diameter.

and recorded and measured tree and stand-level characteristics described above. All cavities were revisited monthly during two breeding seasons (August to February 2005–2006 and 2006–2007) in two control sites and two harvested sites in the piedmont and one control and one harvested site in the cloud forest.

2.3. Data analysis

We calculated total number of individuals, number of species, stem density, basal area, and average DBH for total and valuable tree species and used Kolmogorov–Smirnov tests to assess differences between treatments. In addition, we analyzed the population structure of all tree species combined, individually for the most valuable timber tree species, snags, and stumps in each forest type. A Friedman test comparison of frequencies was conducted to check for differences in size distribution between treatments. We computed the importance value index (IVI) for each species by summing the relative density, relative frequency, and relative coverage for each species.

Cavity densities were analyzed following line-transect analysis guidelines and were modeled using the software Distance 5.0 (Buckland et al., 2001; Thomas et al., 2006). The model with the lowest Akaike's Information Criterion (AIC) was selected for each treatment and cavity category (Burnham and Anderson, 2002). The adequacy of the selected model for the perpendicular distances was assessed using a Kolmogorov–Smirnov test (Buckland et al., 2001).

Analysis of variance was used to compare tree DBH, tree height, cavity height, DCH, horizontal and vertical entrance diameter, and internal diameter among potentially usable cavity trees, non-usable cavity trees, and non-cavity trees and between treatments (i.e., harvested and control). The Tukey–Kramer multiple comparison procedure was used to examine differences among groups when the *F*-test was significant ($p < 0.05$).

We used logistic regression to estimate the probability of cavity occurrence at the tree level, comparing trees with cavities (1) and those without cavities (0) ($n = 82$ no n-cavity trees and 87 potentially usable cavity trees in the piedmont forest and 58 no n-cavity trees and 53 potentially usable cavity trees in the cloud forest). We included DBH, tree condition, and species as candidate predictor variables. Species and tree condition were categorical variables, represented by dummy variables in the analyses. Species with inadequate sample sizes were lumped into an "other species" class. We also included a variable that represented each of the most abundant tree species according to their decay status (i.e., Species × Condition), which was also categorical. All possible variables were included in the initial set of models. We carried out model selection in two stages, using Akaike's Information Criterion (AIC; Burnham and Anderson, 2002) to evaluate each candidate model. We first built the main effect models. Then, we compared candidate models by calculating the difference in AIC between each individual model and the model with the minimum AIC (i.e., ΔAIC). ΔAIC values were used to gauge the relative plausibility of models, where all models for which $\Delta AIC < 2$ have good support relative to each other (Burnham and Anderson, 2002). We also examined whether adding two-way interactions improved the main effect models. Only models that fit the data using the Hosmer–Lemeshow goodness-of-fit test are reported. The same approach described above was used to estimate the probability of cavity occurrence at the plot level, comparing plots with usable cavities (1) and without cavities (0) ($n = 120$ random plots and 87 plots with potentially usable cavity trees in the piedmont forest and 100 random plots and 53 plots with potentially usable cavity trees in the cloud forest). We included plot-level attributes (i.e., density, mean DBH, basal area, number of species) as candidate predictor variables.

Cavity loss rate was estimated by computing the number of usable cavities still available at the end of each of the two breeding seasons (20 months) and subtracting those from the number of available usable cavities at the beginning of the study period divided by the total number of cavities available. Stepwise logistic regression (Marsden, 1983; Press and Wilson, 1978) was used to assess the relative strength of each characteristic as a predictor of a cavity remaining available after 20 months (1), or of a usable cavity becoming unavailable (0). Cavity tree species, tree condition, DBH, tree height, cavity height, DCH, horizontal entrance diameter, vertical entrance diameter, internal diameter, and cavity origin were entered as independent variables. Species, tree condition, and cavity origin were categorical variables, represented by dummy variables in the analysis (Agresti, 1996). Species with inadequate sample sizes were lumped into an "other species" class. Species per decay status was also entered in the analysis (i.e., Species × Condition).

3. Results

3.1. Forest structure and composition

In the piedmont forest a total of 65 tree species were recorded in census plots (of which 58 were identified to species) and 30 species were found in the cloud forest. Control plots in the piedmont forest had significantly higher tree density (418 ± 133.4 individuals/ha vs. 334.6 ± 110.2 individuals/ha; K–S = 3.752, $p = 0.036$) and basal area than harvested plots (25.4 ± 9.2 m^2/ha vs. 15.6 ± 11 m^2/ha; K–S = 5.252, $p = 0.000$), but no difference was found in mean DBH (25 ± 5 cm vs. 26 ± 6 cm; K–S = 0.633, $p = 0.359$). No difference was found in density (426.28 ± 36.64 individuals/ha vs. 410.66 ± 26.14 individuals/ha; K–S = 1.118, $p = 0.999$), basal area (44.4 ± 9.26 m^2/ha vs. 35.94 ± 2.94 m^2/ha; K–S = 2.115, $p = 0.202$), or mean DBH (29.6 ± 6.4 cm vs. 28.7 ± 5.2 cm; K–S = 0.597, $p = 0.738$) between control and harvested plots in the cloud forest.

The density–size distributions in all sites were reverse-J shapes characteristic of uneven-aged forests (Figs. 3 and 4). The total size distribution was different between treatments in the piedmont forest (Friedman test: $\chi^2 = 76.63$, $p < 0.001$); small and intermediate-sized trees (<59 cm DBH) were more abundant in control sites, whereas harvested sites had more large trees (>70 cm DBH). The same pattern (i.e., small and intermediate-sized trees more abundant in control sites) characterized valuable timber species grouped in the piedmont forest (Fig. 3). Piedmont snags followed a typical reversed J distribution, while stumps peaked in the 40–49 cm class (Fig. 3).

No difference was found in overall size distribution between treatments in the cloud forest (Friedman test: $\chi^2 = 0.235$, $p > 0.05$) although collectively valuable timber species had curves that differed significantly between treatments, probably due to the significant decrease in *Cedrela lilloi* and *Juglans australis* in harvested sites (Fig. 4). *Cedrela lilloi* showed an irregular distribution in both treatments of the cloud forest (Fig. 4). Snags in the cloud forest followed a reverse J shape, and stumps peaked at >60 cm DBH class. Most of the dominant species found in both forest types were valuable timber species (Appendix A).

3.2. Cavity density, characteristics, and probability of occurrence

In both the piedmont and cloud forests, the estimated density of potentially usable cavities in control sites was significantly higher than in the harvested treatments (Table 1). The density of all cavities (usable plus non-usable) in the piedmont forest was significantly higher in control than in harvested treatments, but in the cloud forest it was significantly higher in harvested than in control treatments (Table 1).

In piedmont control sites, 42% of the potentially usable cavities were in *Calycophyllum multiflorum*, 25% in *Phyllostilon rhamnoides*, and 10% in snags (see Appendix A for a complete list of species that harbored cavities). In piedmont harvested sites, *Calycophyllum multiflorum* harbored 60% of the usable cavities; *Phyllostilon rhamnoides* and snags each harbored 12%. Overall, potentially usable cavities in piedmont control sites were mainly in the 30–50 cm DBH class, while piedmont harvested sites had many potentially usable cavities in trees >50 cm (Fig. 5).

In the cloud forest control sites, 35% of the potentially usable cavities were encountered in *Podocarpus parlatorei*, 25% in *Blepharocalyx gigantea*, and 24% in snags. In cloud forest harvested sites, *Podocarpus parlatorei* harbored 32% of the potentially usable cavities; *Ilex argentina* 36%; and snags 14%. Frequency of potentially usable cavities in cloud forest control sites increased with tree DBH, while harvested sites had many potentially usable cavities in intermediate classes (30–70 cm) (Fig. 5).

Potentially usable cavity trees in both treatments of both forest types had a greater DBH than non-cavity trees (Table 2). Usable cavities had a significantly greater tree height in control sites than in harvested sites of both forest types (Table 2). Generally, other cavity characteristics did not differ (Table 2).

When we compared stand-level characteristics of random plots with no n-cavity trees to plots with potentially usable cavity trees, we found no differences in either the piedmont or cloud forests. In both the piedmont and cloud forests, the best model for predicting the occurrence of a tree with a potentially usable cavity included two terms (DBH and species by tree condition) as the main effects (Appendix B). The probability of occurrence of potentially usable cavities in both the piedmont and cloud forests increased with DBH across all tree species and tree condition.

3.3. Usable cavity loss rate and probability of remaining available

In the control sites of the piedmont forest the average loss rate of potentially usable cavities was 23% per year (with a total decline of 44% after the end of the second year). The cavities in the 50–70 cm DBH class were the most likely to remain available (Table 3). In the harvested sites of the piedmont forest the loss of potentially usable cavities was 40% per year, was greatest in snags, and increased

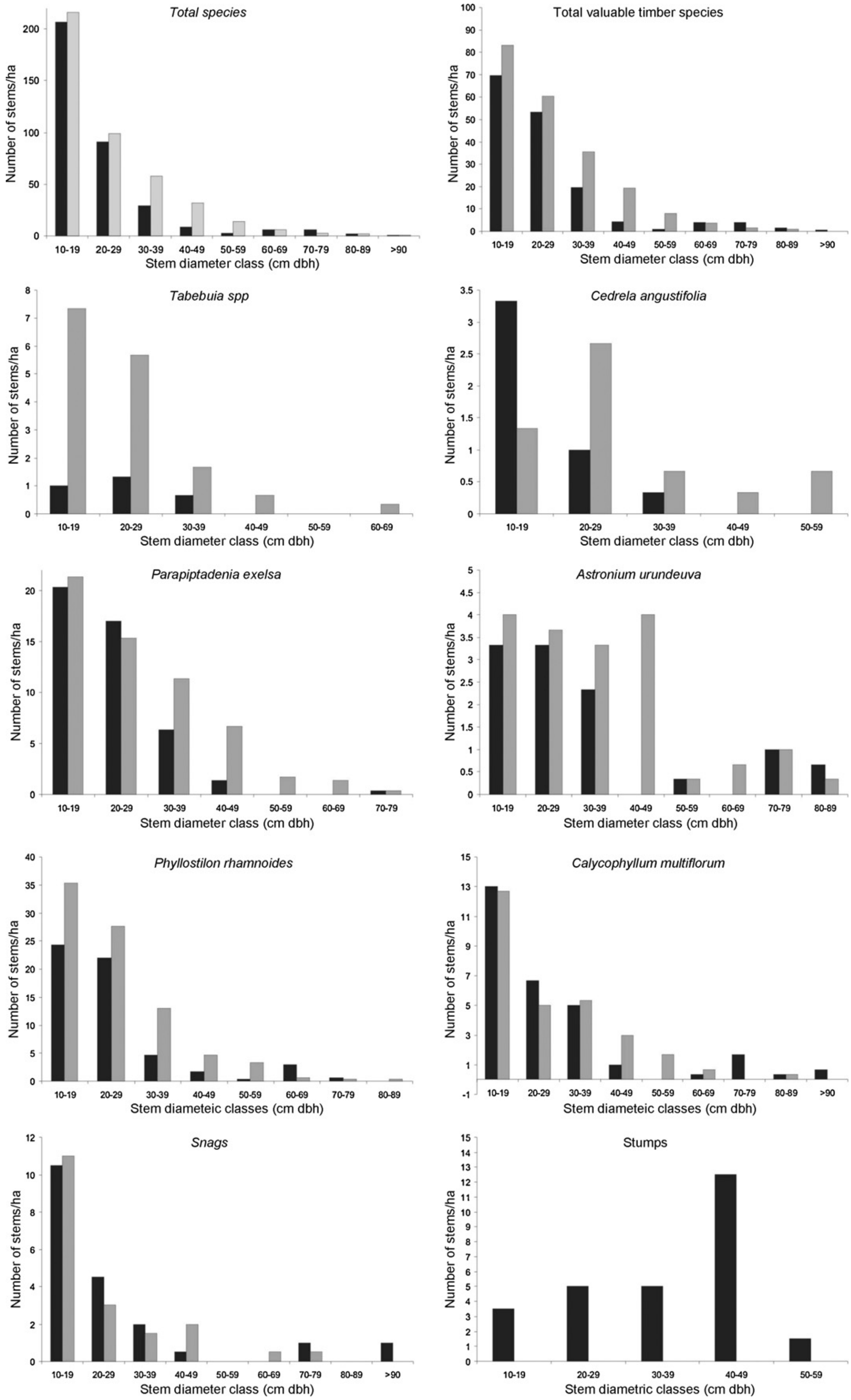

Fig. 3. Tree diameter distribution in 10 cm intervals for piedmont forests of northwestern Argentina (n = number of plots of 0.05 ha = 60). Black bars represent harvested sites, and gray control sites.

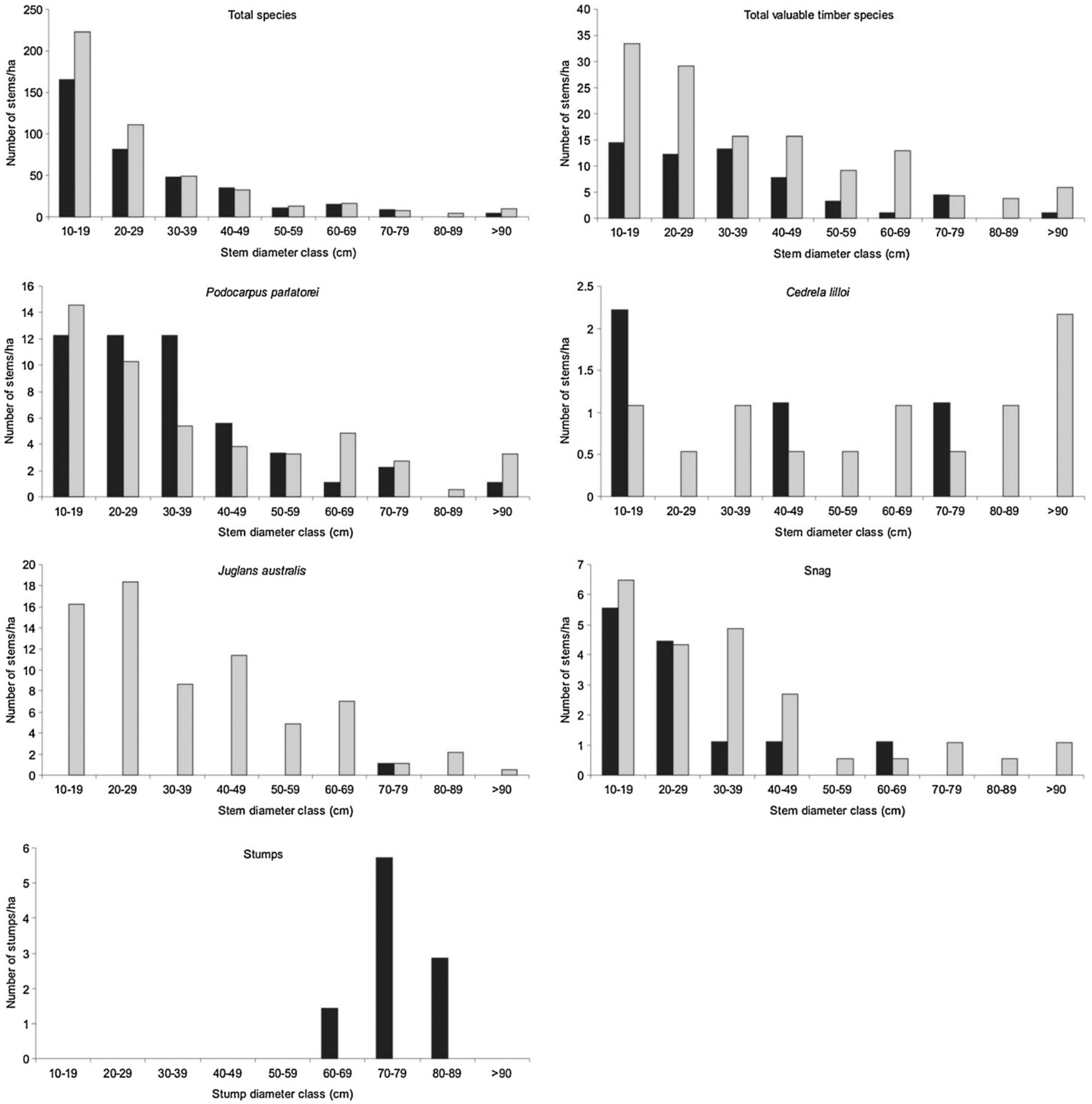

Fig. 4. Tree diameter distribution in 10 cm intervals for cloud forest. Black bars represent harvested sites (n = number of plots of 0.05 ha = 60), and gray control sites (n = 40).

as tree DBH increased (Table 3). The best model for predicting that a tree remained with an available cavity in the control site of the piedmont forest included two terms (DBH and tree condition) (Appendix B).

In the control sites of the cloud forest the loss rate was 33% per year (with a total decline of 57% after the end of the second year). In the harvested sites of the cloud forest there was a 27% loss of potentially usable cavities per year (with a total decline of 50% after the end of the second year). In both treatments potentially usable cavities in snags were more likely to remain available (Table 4). In the cloud forest, the model for predicting that a tree remained with an available cavity in the control site included two terms (DBH and tree condition) (Appendix B).

4. Discussion

In both piedmont and cloud forests we found differences between recently harvested sites and sites that were in relatively natural condition having not been logged for at least 30 years (our controls). We first discuss differences in forest structure and composition to provide a foundation for our primary focus, differences in cavity availability and rates of loss.

4.1. Forest structure and composition

In the piedmont, lower tree density and basal area in the harvested treatments probably reflected the effects of selective

Table 1
Estimates of density (tree cavities/ha) of total cavities and usable cavities at control and harvested sites in piedmont and cloud montane forests of the Andes (95% confidence limits in parentheses).

Forest	Site	Cavity	Density estimate	95% CI
Piedmont				
	Control (n = 60)	Total	13.62	(12.05, 15.40)
		Usable	4.12	(3.07, 5.53)
	Harvested (n = 60)	Total	3.24	(2.37, 4.42)
		Usable	0.51	(0.29, 0.89)
Cloud				
	Control (n = 40)	Total	12.80	(11.11, 14.75)
		Usable	3.91	(3.10, 4.95)
	Harvested (n = 60)	Total	18.02	(15.07, 21.54)
		Usable	1.64	(1.01, 2.67)

n = number of transects.

logging. The most profound differences occurred in the intermediate DBH classes of valuable timber species with fewer trees in harvested sites than controls (Fig. 3). In these forests there is a decrease in timber quality in over-mature individuals due to decay and loggers leave those trees (Eliano, personal communication). This is not good news for avian cavity nesters, because over-mature trees tend not to harbor usable cavities (Fig. 5), although these trees may provide other resources (e.g., foraging sites for woodpeckers) or cavities for other taxa (Hunter and Schmiegelow, 2011; McComb, 2007). Piedmont forest is characterized by mixed species composition and potentially common species are valuable timber trees, thus providing an opportunity to conduct sustainable timber management (Malizia, 2004; Politi, 2008). However, two factors work against the conservation of this forest (Brown and Grau, 1993; Brown and Malizia, 2004). First, almost flat terrain and short distances to paved roads make access relatively easy and lead to re-entering the forest too frequently. Second, land is leased to timber industries for short periods allowing loggers to deplete valuable timber stocks and then move to new areas with no effort to assure regeneration of valuable timber.

Basal area values in control cloud forest (44 m^2/ha) were similar to those found in other studies, while in harvested sites we found much higher values (36 m^2/ha) than in other studies (Brown et al., 2001; Pinazo and Gasparri, 2003). Our higher basal area figures in harvested forests could be related to the fact that we surveyed entire sites, rather than just harvested stands. Steep terrain and low accessibility confine logging operations to limited portions of this forest. Therefore, our figures for density and basal area are the result of averaging across plots with different degrees of logging intensity. In the cloud forest, trees >60 cm DBH were less common in harvested sites than in controls, probably because cloud forest trees are quite resistant to decay and thus large trees are still merchantable. Similarly, large snags (both deciduous and coniferous) were common in control sites, but rare in harvested sites (Fig. 4). Many large snags in the cloud forest are probably harvested because they remain merchantable.

4.2. Cavities

This is the first study to address cavity resources in Neotropical montane forests. We focused on cavity availability for avian cavity nesters because this group has been reported to be highly sensitive to timber harvesting effects in other temperate forests, such as in North America and Australia, and may require special management strategies (Drever et al., 2008; Drever and Martin, 2010; McComb and Lindenmayer, 1999; Newton, 1994) . In the Neotropics cavity-nesting species have received little attention (Cockle et al., 2008; Cornelius et al., 2008; Fimbel et al., 2001). This study indicates that in control sites of both forest types, trees with cavities (both usable and unusable) represented 3% of the total tree density (13.62 ± 0.87 cavities/ha in the piedmont forest and 12.80 ± 0.90 cavities/ha in the cloud forest). Globally, cavity densities vary widely among forests, although some of these differences can be attributed to different definitions of cavities and to the forest structure studied (for a literature review see Remm et al., 2006). Potentially usable cavities for avian cavity nesters are an uncommon feature in montane forests of northwestern Argentina (4.12 ± 0.61/ha in the control piedmont forest and 3.91 ± 0.46/ha in the control cloud forest). These values are comparable to those obtained in the Atlantic forest of Argentina (i.e., 4.6 ± 3.0 cavities/ha below 15 m height; Cockle et al., 2008). Usable cavities are limiting for many cavity-using species in other regions, although this finding is not a general rule because in many forests a high proportion of cavities remain unoccupied (Aitken and Martin, 2008; Brightsmith, 2005; Carey et al., 1997; Gibbons and Lindenmayer, 2002; Hartwig et al., 2004; Wesolowski, 2007).

In logged forests we found far fewer potentially usable cavities: in piedmont logged forest only 0.15% of the trees have a potentially usable cavity (0.51 ± 0.14 potentially usable cavities/ha) and in logged cloud forest the figure is 0.42% (1.64 ± 0.39 potentially usable cavities/ha). Moreover, the density of cavities found in this study is probably an overestimation of the actual number that are suitable for occupation by birds, since there are potentially other characteristics not considered in this paper that make a cavity unsuitable for occupation (e.g., social behavior, territoriality, etc.) (Aitken et al., 2002; Lindenmayer et al., 1990, 1993; Politi et al., 2009; Salinas-Melgoza et al., 2009). This could be the reason why, in a previous study in the area, Politi et al. (in preparation) detected significantly lower densities of cavity-nesting bird species in the harvested treatments of both forest types than in control sites. Other studies have shown that timber harvesting operations can significantly reduce the supply of cavities (Cockle et al., 2008; Cornelius et al., 2008; Dranzoa, 1998; Drever and Martin, 2010; Eyre et al., 2010; Johns, 1997; Kalina, 1989; Mahon et al., 2008; Marsden and Pilgrim, 2003; Politi et al., 2009).

Even more striking is the high loss rate of potentially usable cavities we documented in the 20 months we monitored cavities (from 23 to 40%/year, Tables 3 and 4). Four caveats are associated with these high values. First, these loss rates do not consider usable cavity recruitment, which might be high enough to balance loss. Second, these values take into account both the fall rate of trees that contain usable cavities, and the deterioration of cavities in trees that remain standing. Thirdly, usable cavity loss is only related to the loss for cavity-nesting birds, but the cavities may remain suitable for other taxa such as reptiles and invertebrates. Finally, monitoring of cavities was conducted for only 20 months, making it impossible to know the role of episodic disturbances that could make this loss rate higher or lower. In short, it is necessary to conduct long-term studies to follow cavity dynamics. The loss rates we documented are similar to another study of

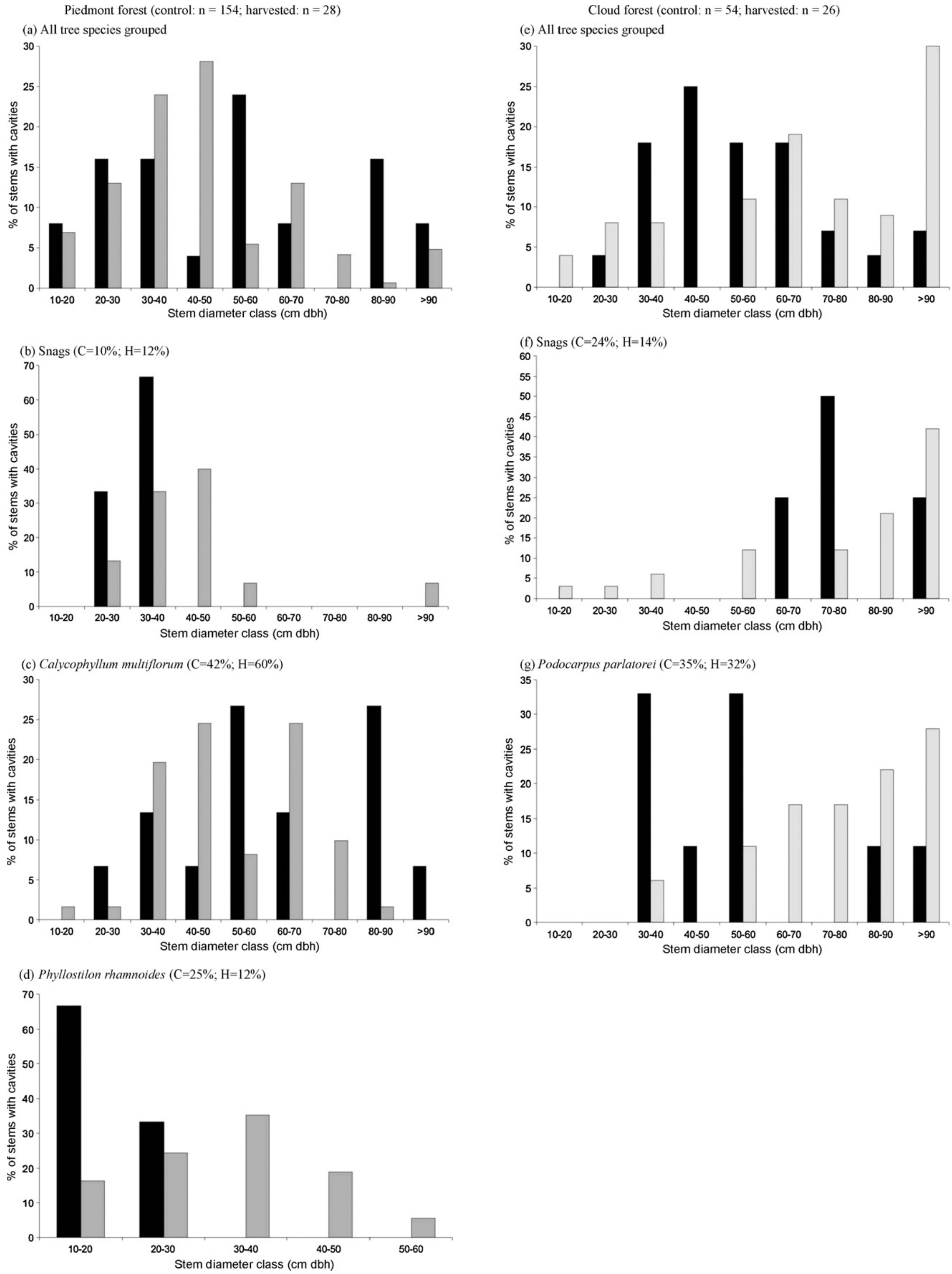

Fig. 5. Diameter class distribution for stems with potentially usable cavities. Abundance is expressed as a percent to facilitate comparison between harvested (black bars; H), and control (gray bars; C) plots. The percentages in parentheses following each category represent the total potentially usable cavities; *n* = number of usable cavities.

Table 2
Tree and cavity level characteristics (X ± SD) of usable, non-usable, and non-cavity trees in control and harvested sites in the piedmont and cloud forests.

Forest type	Characteristic	Control			Harvested		
		Usable cavities (n = 154)	Non-usable cavities (n = 28)	Trees without cavities (n = 20)	Usable cavities (n = 54)	Non-usable cavities (n = 26)	Trees without cavities (n = 20)
Piedmont							
	DBH (cm)	44.51 ± 22.64^{a}	48.55 ± 16.80^{a}	24.18 ± 9.40^{b}	50.56 ± 27.11^{a}	51.38 ± 22.15^{a}	19.76 ± 8.65^{b}
	DCH (cm)	33.11 ± 18.30	27.92 ± 14.89		29.90 ± 19.36	36.98 ± 34.94	
	Cavity height (m)	8.11 ± 3.53	7.92 ± 3.10		7.31 ± 3.08	6.62 ± 2.20	
	Tree height (m)	15.52 ± 5.13^{a}	16.46 ± 4.07^{a}		12.63 ± 4.40^{b}	13.48 ± 5.64^{b}	
	Horizontal entrance diameter (cm)	14 ± 26	10 ± 6		18 ± 15	20 ± 8	
	Vertical entrance diameter (cm)	22 ± 35^{a}	$24 \pm 19^{a,b}$		$36 \pm 54^{a,b}$	45 ± 45^{b}	
	Internal diameter (cm)	16 ± 9	13 ± 8		18 ± 13	17 ± 9	
Cloud							
	DBH (cm)	70.69 ± 25.84^{a}	$67.91 \pm 25.46^{a,b}$	23.93 ± 10.53^{b}	55.55 ± 19.63^{b}	49.87 ± 20.50^{b}	16.06 ± 0.04^{c}
	DCH (cm)	$44.09 \pm 23.39^{a,b}$	$47.21 \pm 24.53^{a,b}$		55.55 ± 47.62^{a}	25.84 ± 12.50^{b}	
	Cavity height (m)	9.89 ± 2.91^{a}	6.29 ± 2.31^{b}		6.81 ± 2.21^{b}	5.51 ± 1.91^{b}	
	Tree height (m)	22.88 ± 6.99^{a}	18.30 ± 7.22^{b}		12.60 ± 2.62^{c}	$13.14 \pm 3.52^{b,c}$	
	Horizontal entrance diameter (cm)	9 ± 5^{a}	$12 \pm 12^{a,b}$		17 ± 10^{b}	$11 \pm 5^{b,c}$	
	Vertical entrance diameter (cm)	14 ± 16^{a}	$24 \pm 24^{a,b}$		25 ± 19^{b}	$21 \pm 14^{a,b}$	
	Internal diameter (cm)	14 ± 5^{a}	12 ± 6^{a}		20 ± 8^{b}	11 ± 7^{a}	

Different superscript letters indicate significant differences within and between treatments and no letters indicate no significant differences within or between treatments with Kruskal–Wallis tests.

cavity loss that reported an average rate of cavity loss per year of 23% in a deciduous bottomland temperate forest in the United States (Sedgwick and Knopf, 1992). Most studies of cavity dynamics examine loss of whole cavity trees or snags (which varies between 3 and 8%/year), an approach that might overestimate the number of cavities suitable for nesting over time by assuming that cavities remain available until the tree falls (Aitken et al., 2002; Ball et al., 1999; Lindenmayer et al., 1997; Raphael and Morrison, 1987; Steeger and Dulisse, 2002). However, many usable cavities are available for shorter periods of time due to cavity deterioration (Sedgwick and Knopf, 1990); for example, the cavity entrance becoming too large, or the cavity compartment decomposing (see Politi et al., 2009 for characteristics used by avian cavity nesters). A high rate of usable cavity loss can be attributed to the high rates of wood decomposition in the tropics due to high temperatures and moisture (Jordan, 1986). Cavities are an avenue for fungal and invertebrate invasion and decomposition can deteriorate a cavity within a few months or years (Jackson and Jackson, 2004; Shigo, 1984). Interestingly, this study shows that rates of cavity loss differ between tree species and DBH classes because some tree species are more prone to decay processes and trees of greater DBH classes had more time exposed to decay agents (Remm et al., 2006). Also, it highlights that snags behave differently in the two forest types studied; in the piedmont forest, snags are more likely than live trees to lose potentially usable cavities, while in the cloud forest snags are more likely to retain potentially usable cavities. Snags > 20 cm DBH are less common in the piedmont than in the cloud forest (Politi, 2008), probably due to a higher fall rate that may be related to the fact that piedmont trees are tall and thin compared to cloud forest trees. The difference may also be related to temperature (i.e., piedmont forests are warmer and may have faster decomposition rates) and the durability of the wood in the piedmont vs. cloud forest tree species. Clearly, in order for the cavity tree resource to be sustained even in control areas, the rate of potentially usable cavity recruitment must balance the cavity loss, and this warrants further investigation to determine the role of woodpeckers in providing cavities and to identify disturbance events that lead to cavity formation.

This study provides information on the tree characteristics associated with cavity occurrence. This is particularly relevant because many avian cavity-nesting species have a narrow niche breadth using only a few species for nesting (Renton and Brightsmith, 2009). In the piedmont forest, large, decaying *Calycophyllum multiflorum* have a relatively greater probability of having potentially usable cavities, while in the cloud forest potentially usable cavities are disproportionably found in large, decaying *Blepharocalyx gigantea*. In both forest types, snags are also very likely to harbor a potentially usable cavity. The importance of snags as a source of potentially usable cavities has been long recognized (Adams and Morrison, 1993; Bull and Holthausen, 1993; Rosenberg et al., 1988; Sedgwick and Knopf, 1986). Despite the fact that potentially usable cavities are very likely to occur in snags, the majority of cavities occur in living trees because snags comprise a small portion (10%) of all standing trees in the montane forest of northwestern Argentina, as in many other tropical regions (Gibbs et al., 1993). As a result, the supply of live cavity trees is a key management consideration, both as present habitat and as future snags when trees die. To counter-balance the low availability of cavities in logged stands, since timber trees species are logged as soon as they reach commercial dimensions (30–40 cm DBH), it is necessary to retain an adequate number of these large trees to maintain cavity nesters in modified landscapes (Monterrubio-Rico et al., 2009).

Conserving adequate populations of *Calycophyllum multiflorum* and *Phyllostilon rhamnoides* should be relatively easy because they are dominant species and their wood is of low economic value (e.g.,

Table 3
Total number of usable cavities and percentage (% ±SD) of usable cavities that remained available during the study period (2005–2007) in the piedmont forest. In control sites, cavities were monitored for 20 months and in harvested sites for only one season. Cavities were grouped according to tree species and DBH classes.

	Tree species				DBH (cm) classes				
	Calycophyllum multiflorum	*Phyllostilon rhamnoides*	Snags of all species	Other species[a]	<30	31–50	51–70	>70	Total
Control									
Total cavities in 2005	66	41	23	24	33	84	26	11	154
% available at the end of each year[b]	83.07 ± 1.76	77.46 ± 2.62	56.74 ± 18.75	76.39 ± 1.96	73.86 ± 1.61	74.01 ± 1.97	80.96 ± 5.71	73.86 ± 1.61	76.97 ± 5.08
% available at the end of the second year	65.15	56.1	27.27	58.33	54.54	54.76	65.38	54.54	56.49
Harvested									
Total cavities in 2005	16	3	4	5	7	5	7	9	28
% available at the end of one year	56.25	100	50	60	71.43	60	57.14	33.33	60.71

[a] See Appendix A for a complete list of tree species that harbor usable cavities.
[b] Mean ±SD of the % of cavities that remained available after the end of each breeding season, in which cavities were monitored; i.e., 2006 and 2007.

Table 4
Total number of usable cavities and percentage (% ±SD) of usable cavities that remained available during the study period (2005–2007) in the cloud forest. Cavities were monitored for 20 months and grouped according to tree species and DBH classes.

	Tree species			DBH (cm) classes				
	Podocarpus parlatorei	Snags of all species	Other species[a]	10–30	31–50	51–70	>70	Total
Control								
Total cavities in 2005	18	13	16	6	5	16	27	54
% available at the end of each year[b]	66.92 ± 8.21	73.11 ± 26.25	67.08 ± 34.26	66.67 ± 47.14	70.83 ± 5.89	48.01 ± 29.33	77.38 ± 11.04	66.56 ± 18.48
% available at the end of the second year	44.44	50	39.13	33.33	50	18.75	59.26	42.59
Harvested								
Total cavities	9	14	3	2	11	9	4	26
% available at the end of each year[a]	69.44 ± 27.5	77.20 ± 22.15	66.67 ± 47.14	100	70.45 ± 28.93	63.18 ± 36.34	87.5 ± 17.68	73.24 ± 26.97
% available at the end of the second year	44.44	57.14	33.33	100	45.45	33.33	75	50

[a] See Appendix A for a complete list of tree species that harbor usable cavities.
[b] Mean ±SD of the % of cavities that remained available after the end of each breeding season, in which cavities were monitored; i.e., 2006 and 2007..

it is used for box frames, clothes hangers, broom sticks, etc.). In the cloud forest, implementing sustainable harvesting recommendations for *Podocarpus parlatorei* is harder due to the low density of mature trees, and slow growth rate (Blendinguer, 2006). It is listed in CITES I banning international trade, but no complementary measure has been implemented to regulate its internal commerce and the species is intensively removed in harvesting operations. *Blepharocalyx gigantea* was a very important tree species for pulp production and stocks have decreased throughout the montane forest, but now pulp is mainly derived from by-products of sugar cane, and current demand for this species, mainly for parquet floors, has declined (Pacheco and Brown, 2006).

4.3. Implications for forest management

This study shows that harvesting operations in the Neotropical montane forest can have a significant negative effect on the density of usable cavities. The lower number of potentially usable cavities in logged forest is not a simple function of the total number of stems extracted from the stand. For example, in control piedmont forests the tree density is 420 stems/ha and the usable cavity density is 4.12/ha, and extrapolating from these figures to harvested piedmont forest, where the tree density is 340, one would expect to find 3.34 usable cavities/ha. However, one finds 0.51 usable cavities/ha or six times less than the expected value. This greater decrease than expected could be explained by an overlap between those trees likely to harbor a usable cavity and those harvested. In particular, most harvested trees in the piedmont forest are in the intermediate (30–60 cm) DBH classes, which in this study were the most likely to harbor a usable cavity. Similarly, in the cloud forest the number of usable cavities found in harvested plots is half what one would predict based on the number of stems removed from the stand. In the cloud forest larger (>70 cm) DBH classes are the most intensively harvested and also are the ones that contain most of the usable cavities (Fig. 5). With the results from logistic regression models we can use the odds ratio (Appendix B) to estimate the number of trees that should be retained in logged stands to ensure a high probability of encountering potentially usable cavities. For example, at least 4.44 and 3.85 trees/ha of 50 cm DBH *Calycophyllum multiflorum* and snags, respectively, should be retained to ensure a 50% probability of potentially usable cavity occurrence per hectare. Although more information is needed to thoroughly understand cavity dynamics (Ball et al., 1999; Fan et al., 2003b; Ohmann et al., 1994; Remm et al., 2006; Spies et al., 1988), this study identifies some key characteristics that should be retained in working forests to assure the conservation of avian cavity nesters.

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Appendix A.

Importance value index (IVI) per species and snags of all species for treatments of each forest type and tree species that harbored a cavity in the subtropical montane forest of the Andes. IVI ranges from 0 to 300.

Forest type	Species	Control (n = 40)	Harvested (n = 60)	Cavity
Piedmont	*Phyllostilon rhamnoides*[a]	56.2	32.7	N
	Parapiptadenia excelsa[a]	36.8	23.7	U
	Calycophyllum multiflorum[a]	39.2	13.0	N
	Snag	16.1	15.2	N
	Astronium urundeuva[a]	15.3	10.2	N
	Ruprechtia laxiflora	15.2	13.5	N
	Saccellium lanceolatum	13.2	12.2	
	Trichilia hieronymi	8.4	14.6	
	Tabebuia spp.[a,b]	6.8	3.2	U
	Ceiba insignis	6.3	14.2	N
	Cedrela angustifolia= balansae[a]	3.6	2.6	U
	Schinopsis haenkeana			N
	Cordia trichotoma[a]			N
	Terminalia triflora			NU
	Amburana cearensis[a]			N
	Anadenanthera colubrina[a]			U
	Gleditsia amorphoides			U
	Myroxylon peruiferum[a]			U
	Pterogyne nitens			N
	Chlorophora tinctoria			U
	Fagara naranjillo			NU
	Allophylus edulis			NU
	Cupania vernalis			U
	Diaptenopterix sorbifolia			U
	Urera baccifera			N
	Urera caracasana			U

Forest type	Species	Control (n = 40)	Harvested (n = 60)	Cavity
Cloud	*Eugenia uniflora*	39.7	9.6	
	Allophylus edulis	31.9	0.0	NU
	Blepharocalyx salicifolius	30.5	7.6	N
	Podocarpus parlatorei[a]	25.0	36.4	N
	Snag	24.8	17.0	N
	Juglans australis[a]	24.5	5.3	NU
	Cinnamomum porphyria	23.7	11.9	U
	Cedrela lilloi[a]	21.6	9.7	N
	Prunus tucumanensis	11.8	36.1	U
	Ilex argentina	5.6	28.0	U
	Myrcianthes mato			U
	Myrcianthes pungens			NU

N: at least one tree had a cavity that was used as nest; U: at least one tree had a cavity that was classified as a usable cavity; NU: trees that had only non-usable cavities.

[a] Valuable timber species.

[b] *Tabebuia* was grouped to include two species *Tabebuia impetiginosa* and *Tabebuia lapacho*.

n = number of plots of 0.05 ha.

Appendix B.

AIC values for the top candidate models with effects for (a) potentially usable cavity occurrence when compared with non-cavity trees in the piedmont forest and cloud forest and (b) tree and cavity-level for cavities remaining available in control sites of the piedmont forest and cloud forest.

Forest type	Level	Variables	Generalized R^2	Hosmer–Lemeshow goodness-of-fit test ($\Pr > \chi^2$)[a]	AIC	ΔAIC
(a) Piedmont	Tree (n = 169)	SpeciesCondition + DBH + SpeciesCondition × DBH	0.55	0.83	102.84	
		Species + DBH + species × DBH	0.31	0.57	105.55	2.71
		Species + DBH	0.39	0.30	108.58	5.74
Cloud	Tree (n = 111)	SpeciesCondition + DBH	0.78	0.27	54.08	
		Condition + DBH	0.72	0.56	54.15	0.06
		Species + DBH + species × DBH	0.76	0.51	60.74	6.66
(b) Piedmont	Tree (n = 154)	Condition + DBH	0.81	0.12	207.47	
		Condition + tree height	0.69	0.13	207.62	0.15
		Condition + tree height + DBH	0.30	0.13	208.44	0.97
	Cavity (n = 154)	DCH + origin + HDE	0.14	0.08	209.94	2.47
		DCH + origin	0.23	0.09	210.55	3.08
		DCH + origin + HDE + DCH × origin	0.25	0.11	210.67	3.20
Cloud	Tree (n = 53)	Condition + DBH	0.36	0.17	70.66	
		Condition + tree height	0.13	0.09	71.08	0.42
		Condition + tree height + DBH	0.15	0.22	71.89	1.23
	Cavity (n = 53)	DCH + origin	0.06	0.10	73.99	3.33

Small values indicate a lack of fit of the model. SpeciesCondition: tree species categorized according to their decay condition. HDE: horizontal cavity entrance diameter. DCH: tree diameter at cavity height.

[a] Pr: predicted probability.

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