Abundance and distribution of cavity trees in an old-growth subtropical montane evergreen broad-leaved forest

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Abstract: We examined the relationship between the density of cavity trees and forest structure characteristics and explored the occurrence of cavity trees among different tree species and diameter breast height (DBH) size in a subtropical evergreen broad-leaved forest in the Ailao Mountains in southwestern China. Cavity trees accounted for 7.9% of living trees and 16.3% of dead trees. Average density of living cavity trees (86.3 trees·ha^{-1}) was 6.9 times that of dead cavity trees. Density of living cavity trees was positively correlated with the density of living trees. Cavity trees showed a skewed distribution among DBH classes that peaked at DBHs of 20–40 cm. Moreover, the probability that a living tree was cavity-bearing was logistically related to DBH. Overall, the likelihood of trees being cavity-bearing differed significantly among species. The proportions of cavity trees among the 23 species having more than 63 trees were positively related to the average DBH and to the largest DBH recorded for each species. We suggest that (1) living tree density is important in determining density of cavity trees and (2) differences in proportion of living cavity trees among species is caused mostly by differences in average DBH of each species.

Résumé : Nous avons examiné la relation entre la densité des arbres creux et les caractéristiques structurales de la forêt et nous avons étudié l'occurrence des arbres creux selon l'espèce et la dimension (DHP) des arbres dans une forêt feuillue sempervirente subtropicale située dans les monts Ailao, dans le sud-ouest de la Chine. Les arbres creux représentaient 7,9 % des arbres vivants et 16,3 % des arbres morts. La densité moyenne des arbres creux vivants (86,3 arbres·ha^{-1}) était 6,9 fois supérieure à celle des arbres creux morts. La densité des arbres creux vivants était positivement corrélée à celle des arbres vivants. La distribution de la densité des arbres creux vivants en fonction des classes de DHP était asymétrique et culminait avec les DHP de 20–40 cm. De plus, la probabilité qu'un arbre vivant soit creux était logistiquement reliée au DHP. Globalement, les chances qu'un arbre soit creux étaient significativement différentes selon l'espèce. La proportion d'arbres creux parmi les 23 espèces comptant plus de 63 arbres était positivement reliée au DHP moyen et au plus grand DHP observés chez chaque espèce. Nos résultats indiquent que (1) la densité des arbres vivants a un effet déterminant sur la densité des arbres creux et (2) les différences entre les espèces dans la proportion d'arbres creux vivants sont principalement dues aux différences entre le DHP moyen de chaque espèce.

[Traduit par la Rédaction]

Introduction

Cavity trees in forests are important places for wildlife to roost, nest, den, breed, feed and hide, and more importantly, to hibernate (Lindenmayer et al. 1990; Sedgeley 2001; Gibbons et al. 2002). Many studies have found that the abundance of cavity-bearing trees is an important factor regulating species richness and population density of hollow-dependent fauna (Lindenmayer et al. 1993; Gibbons and Lindenmayer 1996). Cavity trees play a significant role in maintaining forest biological diversity, and the abundance of cavity trees has become an important parameter in wildlife conservation and forest management (Gibbons and Lindenmayer 1996; Whitford and Williams 2002; McElhinny et al. 2006).

There is an increasing recognition of a shortage of large cavity trees in many forests globally (Lindenmayer et al. 2009). Consequently, retaining large cavity trees has become an important forest management strategy in terms of biodiversity conservation. Also, in reforestation, attempts have been made to increase biodiversity using cavity trees as framework species to provide nesting habitat for local fauna (Goosem and Tucker 1995). Studies on the abundance and distribution of cavity trees and examination of the relationship between the characteristics of tree species and their likelihood of being cavity-bearing can help with these practices.

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The number of cavity trees in a forest site is well reflected by the positive relationship between the likelihood of trees being cavity-bearing and tree density. The likelihood that trees are cavity-bearing is related to characteristics such as tree diameter breast height (DBH), age, species, health, and growth habit, as well as to site features such as stand basal area, slope, topographic position, and amount of rainfall (Lindenmayer et al. 1993; Whitford 2002; Fan et al. 2003). The effect of DBH on cavity tree occurrence has been shown for many forests, and the reason that large trees tend to be cavity-bearing is attributed to increasing age (Lindenmayer et al. 1993; Wormington and Lamb 1999; Wormington et al. 2003). The likelihood of trees being cavity-bearing differs among species (Fan et al. 2003; Harper et al. 2005). In natural forests, there is always a significant difference in tree size among species. Thus, the difference in the likelihood of trees being cavity-bearing among species is likely to be related to DBH (Wormington et al. 2003). However, in many studies the ability of trees to resist decay and termite attack (Traill 1991), apical dominance (Jacobs 1955; Lindenmayer et al. 1993; Lindenmayer et al. 2000), branching habit, morphological features and ability to occlude wounds (Lindenmayer et al. 1993; Wormington et al. 2003) were considered key factors determining the differences in cavity tree occurrence among species in a forest, and the effect of DBH was ignored. A few studies have compared the occurrence of cavity trees among different species of trees in the same DBH classes or examined the influence of tree size on cavity tree occurrence among species (Fan et al. 2003; Wormington et al. 2003; Harper et al. 2005). Thus, the effect of difference in DBH among species on occurrence of cavity trees is still not well understood.

Tree density, an important structural feature of forests (Franklin et al. 2002; Niklas et al. 2003), is affected by forest succession status (Kennard 2002), disturbance regimes (Cochrane and Schulze 1999), and slope position (Clark and Clark 2000). Many studies have also suggested that the abundance of cavity trees may be affected by the same factors (Fan et al. 2003; Harper et al. 2005), but this relationship between tree density and the abundance of cavity trees has not been investigated closely.

Although many studies have investigated the abundance and distribution pattern of cavity trees and their importance in forests, the majority of them were carried out in *Eucalyptus*-dominated forests in Australia or in temperate forests of North America and Europe (Gibbons and Lindenmayer 1996; Fan et al. 2003; Remm et al. 2006), with a few reports from other areas (Bai 2005; Boyle et al. 2008). In particular, rather limited studies have been conducted on cavity trees and their importance in subtropical evergreen broad-leaved forests (Severinghaus 2007). Since formation of cavity trees and their abundance and distribution in forests is expected to vary with climate, flora, and fauna of the region, we investigated cavity trees in subtropical evergreen broad-leaved forest of Yunnan Province, China.

The subtropical evergreen broad-leaved forest in China is distributed primarily between 22°N and 34°N, and is the largest and most diverse forest in the subtropical area of the world (Wu 1980; Song et al. 2005). As such, it plays an important role in the conservation of Chinese biological diversity. The evergreen broad-leaved forest in the Ailao Mountains of Yunnan Province was selected as the site to investigate cavity trees because it is an old-growth forest with high tree species richness and low human disturbance (Wu et al. 1987; He et al. 2000). Thus, the relationship between tree species and the likelihood that trees are cavity-bearing can be well examined in such a forest. The specific goals of our research were to (1) quantify abundance and patterns of distribution of cavity trees in the montane moist evergreen broad-leaved forest in the Ailao Mountains, (2) explore the relationship between forest characteristics and cavity tree abundance, (3) examine cavity tree occurrence in relation to tree species and DBH, and (4) compare cavity abundance of montane moist evergreen broad-leaved forest of the Ailao Mountains with that of other kinds of forests reported in the literature.

Methods

Study site and tree survey

The study area is located in Xujiaba (24°32′N, 101°01′E, 2470 m altitude) in the National Nature Reserve in the Ailao Mountains, Jingdong County, Yunnan Province, southwestern China (Fig. 1). The National Nature Reserve, with an area of 540 km^2, is one of the largest reserves of subtropical evergreen broad-leaved forest in China. It is situated in the Ailao Mountains, which extend continuously for about 400 km from north to south. Xujiaba is located on the north ridge, with altitudes ranging from 2400 to 2670 m, and the topography is characterized by gently sloping terrain. In the vicinity of Xujiaba, there is well-preserved old-growth evergreen broad-leaved forest that consists primarily of species of Fagaceae, Theaceae, Lauraceae, and Magnoliaceae (Wu et al. 1987). Meteorological observations during 1991–1995 at Ailaoshan Station for Subtropical Forest Ecosystem Studies at Xujiaba show that the mean annual temperature of the study area is 11.3 °C, with monthly mean temperatures varying from 5.4 °C in January to 15.6 °C in July. Accumulated annual temperature for ≥10 °C days is 3420 °C. Annual rainfall is 1931 mm, with distinctive dry and wet seasons. More than 85% of the annual rainfall occurs in the wet season, from May to October. Mean annual evaporation is 1486 mm, and annual mean humidity is 86% (Qiu 1998).

Six 1 ha plots were located at Shanmenkou, Bojiba, Sankeshu, and Guoditang near Xujiaba (Table 1). Each inventory plot was further divided into 100 subplots of 0.01 ha, with the purpose of conducting long-term observations of cavity tree dynamics. All trees in the plots with DBH ≥ 5 cm were tagged. Species, DBH, and status (living or dead) were recorded for each tree. Based on experience, leaves and bark of a tree were used to determine whether the tree was living or dead.

Cavity tree survey

The entrance size of a cavity in a tree, which relates to animal occupancy, is the main criterion for determining whether the tree is a cavity tree or not (Gibbons et al. 2002; Remm et al. 2006). An entrance size of 2–5 cm was the minimum size used in most studies (Fan et al. 2003; Wormington et al. 2003; Harper et al. 2005). In montane moist evergreen broad-leaved forest, it was difficult to search for cavities because of a large number of tall trees, low light level resulting from high tree density, dense

Fig. 1. Location of the study site in southwestern China.

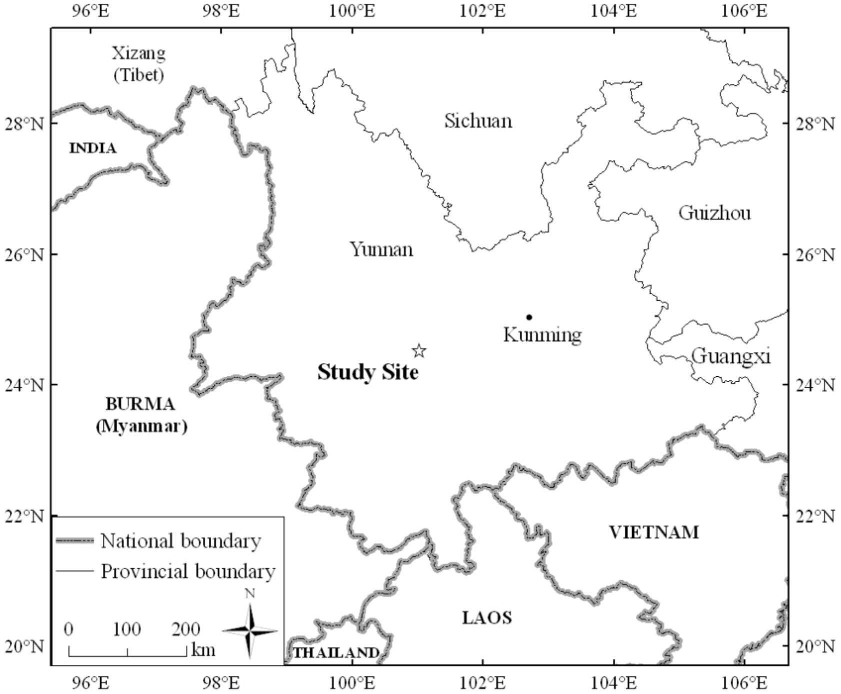


Table 1. Location and structural characteristics of trees in the six 1 ha plots.

Plots	Location	Altitude (m)	No. of living trees*	Max. tree DBH (cm)	Basal area (m^2)	No. of species	No. of dead trees*
1	24°32′25″N, 101°01′34″E	2455	1108	145.5	68.9	38	88
2	24°32′21″N, 101°01′36″E	2455	757	161.5	54.8	36	46
3	24°32′21″N, 101°01′40″E	2476	1754	156.3	70.1	41	163
4	24°31′53″N, 101°01′30″E	2536	676	241.3	71.5	30	48
5	24°31′51″N, 101°00′50″E	2513	1038	129.9	54.5	38	48
6	24°33′03″N, 101°01′20″E	2485	1203	149.3	58.3	44	68
	Mean		1089.3	164	63	37.8	76.8
	SE		156.9	16.1	3.3	1.9	18.5

*Trees with DBH ≥5 cm were included in the study.

canopy cover, and the presence of heavy epiphyte loads on trunks. As a result, we classified a tree as a cavity tree if it contained at least one cavity with a diameter ≥5 cm (diameter being the minimum vertical height and horizontal width of the entrance) (Harper et al. 2005), which could be easily seen during a search of the tree. Moreover, our survey was conducted between 0930 and 1630 on cloudless days for better visibility. All trees in our study were surveyed from ground level. The lower entrances were surveyed directly, while the higher entrances on trunks and branches were surveyed using binoculars (10 × 25). The trunk and branches of each tree were scanned carefully from different directions by four surveyors around the tree. The survey was carried out from April to June and from November to December of 2007.

Data analysis

To examine the distribution pattern of cavity trees, trees were assigned to one of eight DBH classes: ≥5–20, 20–40, 40–60, 60–80, 80–100, 10–120, 120–140, and ≥140 cm. Since a number of species had only a few trees and there were very few large trees in plots with DBH >80 cm, we used an interval of 20 cm instead of 10 cm for each DBH class (Gibbons et al. 2002).

We employed correlation, crosstabulation (χ^2 test), and binary logistical regression analyses (SPSS version 13.0 (SPSS Inc. 2004); Microsoft Office Excel 2000) to address the study objectives. To examine the relationship of cavity tree abundance with forest structure characteristics, we calculated the densities and proportions of living and dead cavity trees, living and dead trees, mean DBH, and basal area

Table 2. Abundance of cavity trees in the six 1 ha plots.

	Living cavity trees		Dead cavity trees		Total	
Plot	Density (stems·ha^{-1})	% of living trees	Density (stems·ha^{-1})	% of dead trees	Density (stems·ha^{-1})	% of total
1	86	7.8	16	18.2	102	8.5
2	58	7.7	12	26.1	70	8.7
3	144	8.2	17	10.4	161	8.4
4	63	9.3	9	18.8	72	9.9
5	98	9.4	9	18.8	107	9.9
6	69	5.7	12	17.6	81	6.4
Total	518	7.9	75	16.3	593	8.6
Mean ± SE	86.3±13.1	8.0±0.6	12.5±1.4	18.3±2.0	98.8±13.9	8.6±0.5

Table 3. Pearson's correlation coefficient (r) matrix for plot indicators.

	Living cavity tree density	Proportion of living cavity trees	Living tree density	Mean DBH of living trees
Proportion of living cavity trees	0.213			
Living tree density	**0.892***	–0.247		
Mean DBH of living trees	–0.808	0.190	**–0.875***	
Basal area of living trees	0.333	0.237	0.257	0.204

*Bolded values indicate significance at $p < 0.05$ (two-tailed Student's t test).

for each plot. Correlations were examined between the variables using SPSS version 13.0. Additionally, we used stepwise multiple regression analyses to explore relationships between density of living cavity trees and density, mean DBH, and basal area of all trees, with $\alpha \leq 0.05$ for inclusion (SPSS version 13.0).

To assess effects of tree species on the likelihood of trees being cavity-bearing, all trees were categorized according to species and DBH. We compared the occurrence of cavity trees among different species using crosstabulation analysis (SPSS version 13.0). Considering the large difference in tree size among different species, the relationships were further identified in each DBH class. The effect of the DBH class variable on the likelihood of trees being cavity-bearing was examined using the same procedures.

Binary logistic regression was used to construct models relating likelihood of living cavity tree occurrence to tree DBH. We fitted logistic regressions for each species expected to contain more than five individual cavity trees based on the average proportion of cavity trees. The general form of the model was

$$p = \frac{e^{a+b\mathrm{DBH}}}{1 + e^{a+b\mathrm{DBH}}}$$

where p is the estimated probability that trees are cavity-bearing.

Results

Forest structure

There were 30–44 tree species in each of the six plots, and the heights of canopy trees were approximately 25–30 m. Mean density of living trees (DBH ≥5 cm) was 1089 trees·ha^{-1}, and it differed greatly among plots (676–1754 trees·ha^{-1}) (Table 1). Large individuals of *Castanopsis wattii* A. Camus and *Lithocarpus xylocarpus* (Kurz) Markgr. were frequently recorded. The DBH of the largest trees in each plot ranged from 129.9 to 241.3 cm, indicating the old-growth state of the forest. Total basal areas in the six plots ranged from 54.5 to 71.5 m^{2}·ha^{-1}. Density of dead trees differed greatly (46–163 trees·ha^{-1}) among plots, with an average of 77 trees·ha^{-1} (Table 1).

Cavity tree density

We recorded 518 living and 75 dead cavity trees, accounting for 7.9% of the living trees (6536 trees) and 16.3% of the dead trees (461 trees) (Table 2). The average density of living and dead cavity trees was 98.8 trees·ha^{-1}. The proportion of living cavity trees ranged from 5.7% to 9.4%, and dead cavity trees from 10.4% to 26.1% (Table 2). However, the density of living cavity trees (86.3 trees·ha^{-1}) was nearly seven times that of dead cavity trees.

The density of living cavity trees was positively correlated with the density of living trees (r = 0.892, p = 0.017) (Table 3) and weakly negatively correlated with mean DBH (r = –0.808, p = 0.052). There was no significant correlation between density of living cavity trees and total tree basal area (r = 0.333, p = 0.519). Density of living trees was negatively related to mean DBH (r = –0.875, p = 0.022). There was a significant linear stepwise regression relationship between density of living cavity trees and density of total living trees ($y = 0.074x + 5.531$, $R^2 = 0.796$, p = 0.017), excluding the independent variables of mean DBH (p = 0.700) and basal area (p = 0.839), which did not contribute significantly to the model.

The proportion of living cavity trees was not significantly correlated with the density (r = –0.247, p = 0.637), mean DBH (r = 0.190, p = 0.719), or basal area (r = 0.237, p = 0.652) of living trees (Table 3).

Cavity tree distribution among DBH classes

The living cavity trees showed a skewed distribution among DBH classes, with a large number of cavity trees having DBHs from 20 to 40 cm (151 cavity trees, 29.2% of total cavity trees) (Fig. 2). The majority of living cavity trees (75.1%) had a DBH range of 5–60 cm. However, the proportion of living cavity tree occurrences increased as DBH increased. Only 2.7% of the trees with DBH 5–20 cm were cavity trees compared to 78.9% of trees in the 100–120 cm DBH class (Fig. 2). Trees in different DBH classes had a different probability of being cavity-bearing (χ^2 = 1286.1, df = 7, $p < 0.001$).

Although there was a low probability of trees with DBH 5–20 cm being cavity-bearing, they contributed nearly 23% of total cavity trees (119 stems) as a result of the large number of individuals in this size class. Furthermore, 28 of 2458 trees with DBH 5–10 cm were cavity trees (1.1%), accounting for 5.4% of the total number of cavity trees.

The size-class distribution of dead cavity trees was similar to that of living cavity trees. Dead cavity trees with DBH 20–40 cm were the most abundant (33, accounting for 44.0% of the total dead cavity trees) (Fig. 2). Dead cavity trees with DBH 5–40 cm accounted for 72% of the total dead cavity trees. The proportion of dead cavity trees was highest in the 60–80 cm DBH class (100%, Fig. 2). Dead trees in different DBH classes had a different probability of being cavity-bearing (χ^2 = 107.9, df = 5, $p < 0.001$).

Distribution of living cavity trees among all tree species

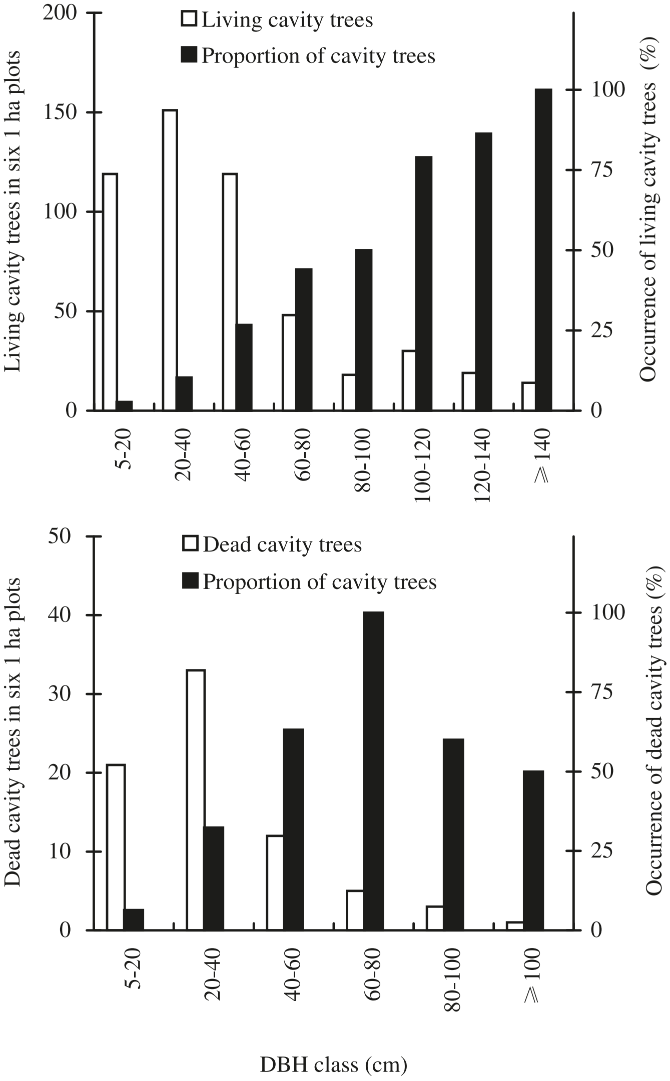
Fifty-eight tree species in the plots had at least one stem with DBH ≥5 cm, and the number of species varied greatly among the DBH classes (Table 4). *Vaccinium duclouxii* Hand.-Mazz. was the most abundant species, accounting for 13.8% of total stems. Seven species had only one stem each.

If there were fewer than 63 trees for a given species, the expected number of cavity trees would be less than 5, with 7.9% expected to have cavities. Thus, only 23 species having ≥63 trees (6070 total number of trees) were included in the χ^2 test. Among the 23 species, the proportions of cavity trees varied from 0% to 23.8%, with an average of 8%. Four species — *C. wattii*, *L. xylocarpus*, *Machilus yunnanensis* Lecomte, and *Lithocarpus hancei* (Bentham) Rehder — had a very high proportion of cavity tree occurrence (>17.2%), and all four were upper-canopy species with large individuals (Table 4). Other species with a high proportion of cavity trees also contained large individuals. Species with a much lower proportion (<3%) of cavity trees were those of the lower layer, except for *Machilus bombycina* King ex Hook.f., which is an upper-canopy species (Table 4).

The average proportions of cavity tree occurrence in the 5–20 cm DBH class among the 23 species was 3.0% (Table 4), and most species had no cavity individuals or only a low proportion in this DBH class.

Overall, the likelihood of trees being cavity-bearing differed significantly among species (χ^2 = 476.8, df = 22, $p < 0.001$). However, this difference was only detectable within trees with DBHs <60 cm (DBH 5–20 cm, χ^2 = 76.4, df = 22, $p < 0.001$; DBH 20–40 cm, χ^2 = 67.0, df = 22, $p < 0.001$; DBH 40–60 cm, χ^2 = 63.9, df = 17, $p < 0.001$). For trees with DBH ≥60 cm, there was no significant difference among species (DBH 60–80 cm, χ^2 = 7.391, df = 10, p = 0.688; DBH ≥80 cm, χ^2 = 4.285, df = 6, p = 0.638).

Fig. 2. Distribution of cavity trees within different DBH classes.



The proportions of cavity tree occurrence among the 23 species were significantly positively related to the mean DBH (r = 0.833, $p < 0.001$) and to the largest DBH recorded for each species (r = 0.879, $p < 0.001$). There was a positive correlation between the mean DBH and the largest DBH of species (r = 0.867, $p < 0.001$).

Effect of DBH on cavity occurrence in main species

For all the trees surveyed (5635 trees total), the occurrence of cavity trees was significantly logistically related to DBH ($p < 0.001$) (Table 5). Among the 23 species with more than 63 trees, 16 species showed a significant logistic correlation between the probability of trees being cavity-bearing and DBH (Table 5).

Figure 3 shows the change in likelihood of occurrence of cavity trees with increase in DBH. For the four predominant species in the upper canopy (height > 22 m, mean DBH > 30 cm), the logistic curves of *C. wattii*, *L. xylocarpus*, and *L. hancei* were similar and close to that of all species combined. However, *Schima noronhae* Reinw. ex Bl. Bijdr. showed a different pattern, with a much lower probability of cavity tree occurrence in all size classes (Fig. 3A). There

Table 4. Distribution of living cavity trees in DBH classes among main tree species.

						DBH class (cm)									
	Total					5–20		20–40		40–60		60–80		≥80	
Species	No. of trees	Mean DBH (cm)	Max. DBH (cm)	LCT	PLCT	No. of trees	PLCT	No. of trees	PLCT	No. of trees	PLCT	No. of trees	PLCT	No. of trees	PLCT
Castanopsis wattii	450	38.2	241.3	107	23.8	169	6.51	125	12.8	80	36.3	33	54.5	43	76.7
Lithocarpus xylocarpus	341	43.4	173.6	78	22.9	69	8.70	136	8.8	68	19.1	24	45.8	44	81.8
Machilus yunnanensis	177	20.7	92.2	32	18.1	124	4.03	29	34.5	12	66.7	8	62.5	4	100.0
Lithocarpus hancei	239	32.4	128.8	41	17.2	69	1.45	93	17.2	61	26.2	9	44.4	7	57.1
Michelia floribunda	82	21.7	71.6	10	12.2	47	4.26	27	22.2	7	28.6	1	0.0		
Manglietia insignis	239	23.0	101.9	28	11.7	110	3.64	107	15.9	19	26.3	2	50.0	1	100.0
Prunus undulata	92	14.3	58.2	10	10.9	74	8.11	16	18.8	2	50.0				
Schima noronhae	304	31.3	97.3	31	10.2	91	8.79	139	5.0	50	18.0	15	26.7	9	33.3
Ilex coralline	135	24.2	57	13	9.6	63	1.59	56	10.7	16	37.5				
Cyclobalanopsis stewardiana	108	23.9	69.1	9	8.3	47	6.38	49	6.1	9	22.2	3	33.3		
Ilex gintungensis	209	12.0	56.6	13	6.2	182	1.10	19	26.3	8	75.0				
Illicium macranthum	227	17.1	41.8	13	5.7	158	5.70	67	6.0	2	0.0				
Symplocos sumuntia	115	11.9	55	6	5.2	102	1.96	12	25.0	1	100.0				
Hartia sinensis	365	19.6	59.3	19	5.2	211	1.90	140	7.9	14	28.6				
Neolitsea polycarpa	78	24.2	63.2	4	5.1	35	0.00	30	6.7	12	16.7	1	0.0		
Eriobotrya bengalensis	268	12.3	70.6	13	4.9	240	2.50	26	23.1	1	0.0	1	100.0		
Rhododendron leptothrium	503	10.0	31.4	18	3.6	495	3.23	8	25.0						
Machilus bombycina	381	24.7	87.3	11	2.9	148	2.03	183	2.7	45	4.4	3	33.3	2	0.0
Symplocos anomala	127	9.9	26	3	2.4	126	2.38	1	0.0						
Camellia forrestii	414	7.8	21.8	7	1.7	412	1.70	2	0.0						
Eurya obliquifolia	234	8.7	34.6	3	1.3	232	1.29	2	0.0						
Vaccinium duclouxii	901	10.0	41.5	7	0.8	883	0.68	17	5.9	1	0.0				
Symplocos ramosissima	81	8.4	26.8	0	0.0	79	0.00	2	0.0						
Subtotal (23 species)	6070	19.6	241.3	476	8	4166	3.0	1286	12	408	31	100	41	110	64
Other 35 species	466	20.8	79.4	42	8.9	248	9.4	172	9.6	37	46.2	9	13.3		
Total (58 species)	6536	20.3	241.3	518	8.7	4414	6.8	1458	10.9	445	38.1	109	32.3	110	64

Note: LCT, living cavity trees; PLCT, percentage of living cavity trees in a species (i.e., (LCT/No. trees) × 100).

Table 5. Logistic regression models for cavity tree occurrence and DBH for each of 16 tree species and for all tree species combined.

Species		*B*	SE	*p*
Castanopsis wattii	DBH	0.039	0.005	<0.001
	Constant	–2.877	0.241	<0.001
Lithocarpus xylocarpus	DBH	0.047	0.006	<0.001
	Constant	–3.571	0.335	<0.001
Machilus yunnanensis	DBH	0.082	0.014	<0.001
	Constant	–3.649	0.458	<0.001
Lithocarpus hancei	DBH	0.040	0.009	<0.001
	Constant	–3.073	0.407	<0.001
Manglietia insignis	DBH	0.057	0.015	<0.001
	Constant	–3.535	0.485	<0.001
Schima noronhae	DBH	0.032	0.009	<0.001
	Constant	–3.346	0.405	<0.001
Ilex corallina	DBH	0.094	0.024	<0.001
	Constant	–5.104	0.930	<0.001
Cyclobalanopsis stewardiana	DBH	0.053	0.023	0.021
	Constant	–3.898	0.828	<0.001
Ilex gintungensis	DBH	0.146	0.027	<0.001
	Constant	–5.619	0.807	<0.001
Symplocos sumuntia	DBH	0.133	0.042	0.002
	Constant	–5.175	1.021	<0.001
Hartia sinensis	DBH	0.088	0.022	<0.001
	Constant	–4.986	0.656	<0.001
Neolitsea polycarpa	DBH	0.072	0.036	0.045
	Constant	–5.128	1.438	<0.001
Eriobotrya bengalensis	DBH	0.141	0.035	<0.001
	Constant	–5.195	0.710	<0.001
Rhododendron leptothrium	DBH	0.150	0.042	<0.001
	Constant	–4.995	0.591	<0.001
Machilus bombycina	DBH	0.039	0.018	0.031
	Constant	–4.640	0.674	<0.001
Camellia forrestii	DBH	0.188	0.095	0.047
	Constant	–5.695	1.001	<0.001
All 58 species combined	DBH	0.056	0.002	<0.001
	Constant	–3.973	0.091	<0.001

Note: The regression results for the other seven species (*Michelia floribunda*, *Prunus undulata*, *Illicium macranthum*, *Symplocos anomala*, *Eurya obliquifolia*, *Vaccinium duclouxii*, and *Symplocos ramosissima*) were not significant.

was no significant difference among *C. wattii*, *L. xylocarpus*, and *L. hancei* (χ^2 = 4.256, *p* = 0.119), but all of them differed from *S. noronhae* (χ^2 = 22.378, $p < 0.001$; χ^2 = 18.391, $p < 0.001$; χ^2 = 5.631, *p* = 0.018, respectively) (Table 6). Among the other seven species in the upper canopy (mean DBH 19–30 cm), *M. bombycina* had a different pattern from that of the other six species. Thus, a tree of this species had a low likelihood of being cavity-bearing across all DBH classes (Fig. 3B). There was a significant difference between *M. bombycina* and *M. yunnanensis* (χ^2 = 41.470, $p < 0.001$), *Cyclobalanopsis stewardiana* (A. Camus) Y.C. Hsu & H.W. Jen var. *longicaudata* Y.C. Hsu (χ^2 = 7.343, *p* = 0.007), *Manglietia insignis* (Wall.) Blume (χ^2 = 21.097, $p < 0.001$), and *Ilex corallina* Franchet (χ^2 = 11.485, *p* = 0.001) (Table 6). There were also some differences in cavity-producing ability among other species, especially between *M. yunnanensis* and some other tree species (Table 6).

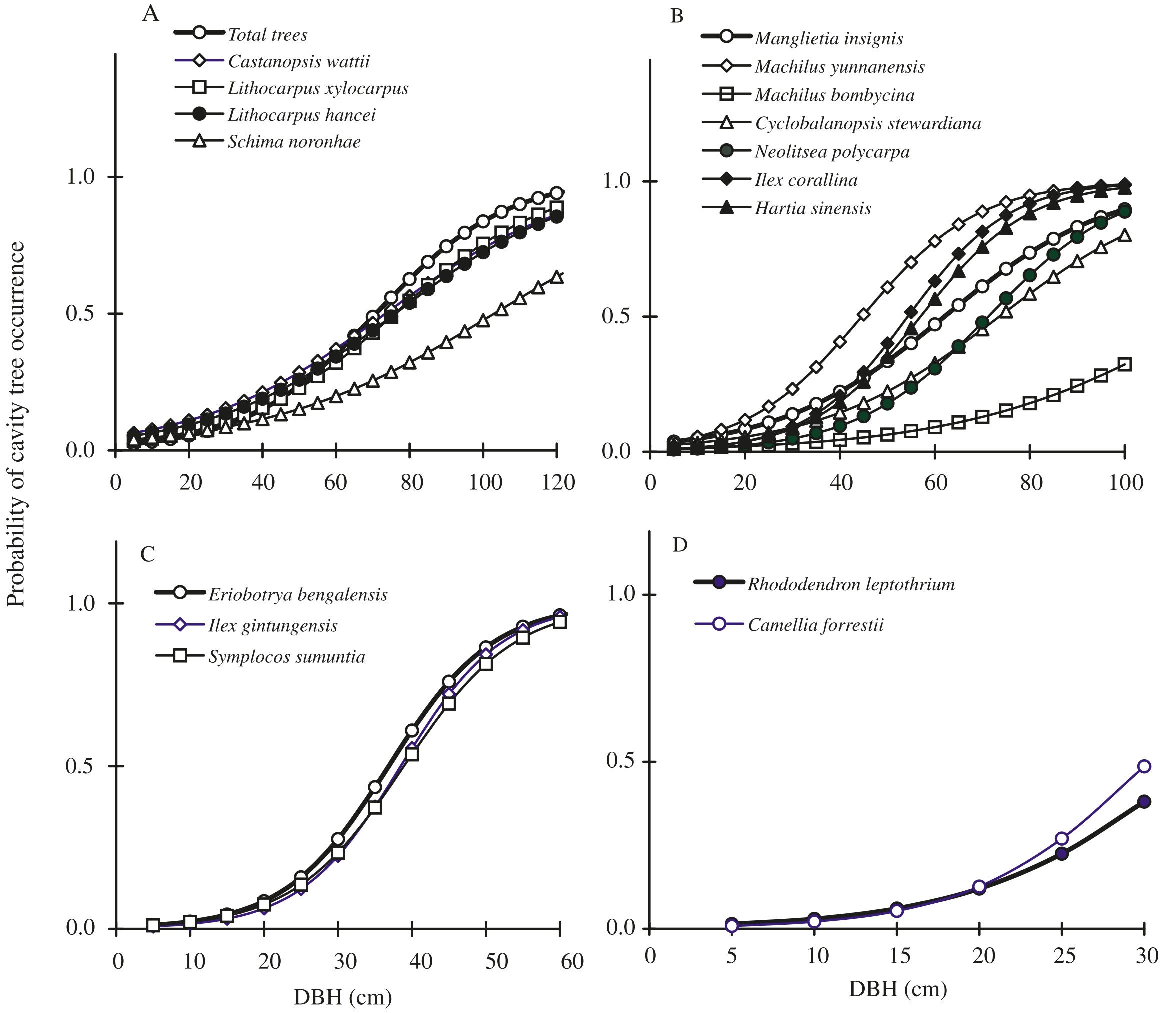
For the three middle-layer species (height 18–20 m, mean DBH 10–19 cm), *Eriobotrya bengalensis* Kurz, *Ilex gintungensis* H.W. Li ex Y.R. Li, and *Symplocos sumuntia* Buchanan-Hamilton ex D. Don, the logistic curves were similar (Fig. 3C), and there were no differences among the three species (χ^2 = 0.064, *p* = 0.969) (Table 6). In the lower-layer species (height about 10 m, mean DBH <10 cm), the likelihood of a tree of *Camellia forrestii* Cohen-Stuart and *Rhododendron leptothrium* I.B. Balfour & Forrest being cavity-bearing was similar in the low DBH class (Fig. 3D), A χ^2 test detected only a weak difference between them (χ^2 = 3.051, *p* = 0.081) (Table 6).

Discussion

Abundance of cavity trees in montane evergreen broad-leaved forest

Although several studies have reported abundance and distribution of cavity trees, it is difficult to compare our re-

Fig. 3. The probability of cavity tree occurrence by DBH for 16 tree species. Curves are based on the logistic regression models in Table 5.



sults with those of others because of different methods and different criteria used in cavity tree surveys. In some studies, only some of the main species of cavity trees were surveyed (Lindenmayer et al. 2000; Whitford 2002; Wormington et al. 2003). The minimum DBH for cavity trees also differed among studies; for example, minimum DBH was 10 cm in North America (Fan et al. 2003) and 20 cm in Australia (Wormington et al. 2003). Further, criteria for the entrance size of cavities also varied; for example, entrance size was ≥1 cm (Lindenmayer et al. 2000), ≥2 cm (Wormington et al. 2003), ≥2.5 cm (Fan et al. 2003; Boyle et al. 2008) and ≥5 cm (Harper et al. 2005). In only a few other studies (Fan et al. 2003; Boyle et al. 2008) have data for density of cavity trees (and not density of cavities) been presented.

To compare our results with those of Fan et al. (2003) and Boyle et al. (2008), we used densities of cavity trees with ≥10 cm DBH. The mean densities of living cavity trees and dead cavity trees (DBH ≥ 10 cm) in the forest of the Ailao Mountains were 82 and 12 trees·ha^{-1}, respectively (Table 7), both of which were higher than those in the temperate forests of North America (36–54 and 6–9 trees·ha^{-1}, respectively) (Table 7). Compared to tropical rain forest at La Selva (Table 7), forest in the Ailao Mountains had a higher density of living cavity trees. On the other hand, density of dead cavity trees was similar at La Selva and in the Ailao Mountains. Thus, the montane evergreen broad-leaved forest of the Ailao Mountains supported a much higher overall density of cavity trees than the temperate forests of North America and the tropical rain forest at La Selva.

Density of cavity trees and tree density

Our study showed that density of trees was a good indicator of the density of living cavity trees in a forest. This is supported by other studies in other forest types, for example, the temperate old-growth forests of the United States. Although densities of living trees with DBH ≥ 10 cm varied from 258 to 410 trees·ha^{-1} (Table 7) in Illinois, Indiana, and Missouri, the proportions of living cavity trees were nearly the same (13.2%–13.9%), indicating that density of trees is the key factor determining the density of cavity trees in these old-growth forests. In addition, the proportions of living cavity trees (12.1%) in the Ailao Mountains were similar to those of the temperate forests of North America (13.2%–13.9%) and the tropical rain forest of La Selva (10.8%). Furthermore, a significant correlation between the densities of living cavity trees and all trees across the five sites (Illinois, Indiana, Missouri, La Selva, and the Ailao Mountains) (r^2 = 0.947, p = 0.005, n = 5) suggests that the high density of

Table 6. Pearson's χ^2 tests of correlation of probability that 16 tree species are cavity-bearing.

	χ^2	Asymptotic *p*	Exact *p*
Schima noronhae × *Castanopsis wattii*	22.378	<0.001	<0.001
Schima noronhae × *Lithocarpus xylocarpus*	18.391	<0.001	<0.001
Schima noronhae × *Lithocarpus hancei*	5.631	0.018	0.021
Castanopsis wattii × *Lithocarpus xylocarpus* × *Lithocarpus hancei*	4.256	0.119	
Machilus bombycina × *Machilus yunnanensis*	41.470	<0.001	<0.001
Machilus bombycina × *Cyclobalanopsis stewardiana*	7.343	0.007	0.019
Machilus bombycina × *Neolitsea polycarpa*	1.372	0.241	0.272
Machilus bombycina × *Hartia sinensis*	3.323	0.068	0.087
Machilus bombycina × *Manglietia insignis*	21.097	<0.001	<0.001
Machilus bombycina × *Ilex corallina*	11.485	0.001	0.002
Machilus yunnanensis × *Hartia sinensis*	23.175	<0.001	<0.001
Machilus yunnanensis × *Neolitsea polycarpa*	7.490	0.006	0.006
Machilus yunnanensis × *Cyclobalanopsis stewardiana*	5.172	0.023	0.024
Machilus yunnanensis × *Manglietia insignis*	3.336	0.068	0.090
Machilus yunnanensis × *Ilex corallina*	4.430	0.035	0.050
Eriobotrya bengalensis × *Ilex gintungensis* × *Symplocos sumuntia*	0.064	0.969	
Rhododendron leptothrium × *Camellia forrestii*	3.051	0.081	0.103

Table 7. Comparison of density of cavity trees among forests in North America, La Selva, and the Ailao Mountains (DBH ≥ 10 cm).

Site	Plots	Plot area (ha)	Living cavity trees·ha^{-1} (%)	Dead cavity trees·ha^{-1} (%)	All living trees·ha^{-1}	All dead trees·ha^{-1}	Reference
Temperate							
Illinois	38	0.1	45 (13.2)	9 (27.3)	340	33	Fan et al. 2003
Indiana	166	0.1	36 (13.9)	6 (31.6)	258	19	Fan et al. 2003
Missouri	90	0.1	54 (13.2)	9 (24)	410	37	Fan et al. 2003
Tropical							
La Selva	24	0.01	58 (10.8)		542		Boyle et al. 2008
	12	0.5		11 (43.1)		26	
Subtropical							
Ailao Mountains	6	1.0	82 (12.1)	12 (22.0)	680	54	Present study

living cavity trees found in the forest of the Ailao Mountains might be due primarily to the higher density of living trees.

Density of cavity trees and mean DBH

In agreement with the results of many other studies, the likelihood of living trees of the Ailao Mountains being cavity-bearing increased with DBH. However, density of living cavity trees was slightly negatively correlated with mean DBH (Table 3). This means that the increase in large trees in the plots is likely the cause of the decrease in density of cavity trees, since tree density, an important factor affecting cavity tree density, was negatively related to mean DBH of trees (Table 3). The relationship of decrease in density with increase in mean DBH is well demonstrated in a broad spectrum of tree-dominated communities (Niklas et al. 2003). The likelihood of trees being cavity-bearing increased with age. However, the density of trees may decrease because of self-thinning (Niklas et al. 2003), which would lead to an overall decrease in density of cavity trees. With respect to cavity tree abundance, our study showed that the effect of increase in mean DBH did not compensate for the effect of decrease in tree density in the forest of the Ailao Mountains.

Relationship between DBH and cavity occurrence

The logistic relationship between the likelihood of cavity tree occurrence and DBH in our study has also been found in other studies (Fan et al. 2003; Harper et al. 2005). This relationship was considered to be the result of slow decomposition during cavity formation (Mackowski 1984; Gibbons and Lindenmayer 2002; Harper et al. 2005). Based on the positive relationship between DBH and ages of trees (Wormington et al. 2003), the larger the DBH the older the tree and the greater the chance that the tree may experience disturbance that causes trunk damage. The increased chance of damage, together with a longer period of decomposition of the broken part of the tree, are probably the main reasons for the increased probability of large trees producing a cavity (Lindenmayer et al. 2000; Ranius et al. 2009). The decomposition rate of dead wood in the tree cavity in the forest of the Ailao Mountains was much lower in the dry season (0.101 ± 0.012 mmol·kg^{-1}·s^{-1}) than in the rainy season (0.195 ± 0.011 mmol·kg^{-1}·s^{-1}) (Zhang and Zheng 2008). Water was likely to be one of the main factors regulating the decomposition of dead wood inside the cavities, since the water content in the dry season (0.592 ± 0.054 g H_2O·g^{-1}) was only 56% of that in the rainy season (Zhang and Zheng 2008). Although the Ailao Mountains forest is located in a subtropical area with high rainfall, the decomposition rate inside the cavities was lower than the average decay rate of coarse woody debris at 15 °C of forests in the transition zone (45°35′N, 84°43′W) between the northern hardwood and boreal forests of Michigan, USA (0.26 mmol·kg^{-1}·s^{-1}) (Gough et al. 2007). A very slow decomposition rate in cavities could be responsible for the low proportion of cavity trees in small DBH classes.

Small trees and criteria for cavity tree survey

The number of cavity trees in the Ailao Mountains with DBH 5–20 cm and even DBH 5–10 cm cannot be ignored because of the large number of trees in these small DBH classes, although the proportion of cavity trees in these size classes was low. Cavity trees with DBH 5–10 cm usually were individuals that resprouted after breakage of the main stem below a height of 1.3 m, and cavities were normally found on the old stumps. Thus, we believe that DBH ≥ 5 cm was a suitable size to use in surveying abundance of cavity trees in forests consisting of species that were very capable of resprouting.

Tree species and cavity trees

Our results showed that the mean DBH of a tree species in the old-growth forest of the Ailao Mountains is the key factor related to the difference in proportions of cavity trees among species; it explained 69% of the variation. However, in three classes of DBH < 60 cm, the likelihood of trees being cavity-bearing was significantly associated with species. This indicated that the differences in the likelihood of trees being cavity-bearing were influenced by different characteristics among species.

Of the four dominant species in the upper canopy with very large mean DBH, the likelihood of cavity tree occurrence was significantly higher in *C. wattii*, *L. xylocarpus*, and *L. hancei* (Fagaceae) than in *S. noronhae* (Table 4, Fig. 3A). Higher wood density, higher resprouting capacity, and more and thicker branches were more obvious in the three Fagaceae species than in *S. noronhae*. However, thinner branches and apical dominance of *S. noronhae* likely were responsible for the lower proportion of cavity trees of this species. In the two main species of Lauraceae, the proportion of cavity trees of *M. bombycina* was significantly lower than it was for *M. yunnanensis* despite the fact that the mean DBH of *M. bombycina* (24.7 cm) was higher than that of *M. yunnanensis* (20.7 cm). *Machilus yunnanensis* has thick branches, and stems of big trees usually resprout. On the other hand, *M. bombycina* has much stronger apical dominance and thin branches, and no resprouting trees have been seen. The difference in the likelihood of trees being cavity-bearing between the two species was also possibly due to branching and resprouting habit. Similar results have been obtained from investigations on cavity trees in other types of forests despite the different tree species composition (Lindenmayer et al. 1993, 2000; Wormington et al. 2003). The reason may be that injuries caused by small breakages (i.e., small branches) heal easily.

The influence of other characteristics such as hardness and chemical composition of the wood on the formation of cavity trees is little understood. Thus, it is necessary to survey more characteristics and more species to generally understand the causes of differences among species in formation of cavities.

Selection of cavity tree species

Our results showed that the expected size of a target species is an important indicator for its consideration as a framework species, because the proportion of cavity trees in different species was largely determined by the mean DBH and largest DBH of each species. Species with large DBH are more suitable to be used as a framework species. Large trees with cavities have been targeted as habitat providers for local fauna in forest management (Whitford and Williams 2002). However, the likelihood of a tree being cavity-bearing is also influenced by other intrinsic features of a species. Features such as apical dominance and branching habit may also affect cavity formation but are not discussed in many cavity tree studies because of the difficulties in surveying and lack of relevant methods (Fan et al. 2003; Boyle et al. 2008). Therefore, the information from cavity tree surveys is important in cavity tree management and in reforestation using framework species.

In the forest of the Ailao Mountains, some of the large tree species such as *C. wattii*, *L. xylocarpus*, and *L. hancei* had a higher proportion of cavity-bearing stems than small tree species such as *V. duclouxii* and *Symplocos anomala* Brand. They are potential candidates to be retained in the forest and to be used as framework species in reforestation.

Limitations of the study

In this study, the difference in cavity tree occurrence among species was examined for only 23 species, because of the small sample size of other species (<63 stems). A more robust analysis could be achieved if more plots were sampled or supplementary samplings of rare species were considered. Further, the abundance of cavity trees is also regulated by terrain, altitude, disturbance history, and rainfall (Lindenmayer et al. 1993; Whitford 2002). Larger and across-landscape surveys of cavity trees is desirable to address the importance of these physical, as well as biological, factors in the dynamics of cavity trees.

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