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## Which factors influence the occurrence and density of tree microhabitats in Mediterranean oak forests?

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## ABSTRACT

Managed forests have the potential to promote tree microhabitats and hence to conserve the biodiversity, especially of birds, bats, and saproxylic insects, associated with such features. Although the value of tree microhabitats for biodiversity has been described, surprisingly, the factors that explain the occurrence and density of tree microhabitats in managed forests remain poorly known, especially in Mediterranean forests. To address this gap, we studied the occurrence and density of nine types of tree microhabitats inventoried in 1630 trees and 59 forest stands: canopy dead wood; woodpecker cavities; non-woodpecker cavities (with a distinction between lower, medium, and upper cavities); *Cerambyx* cavities; loose barks or cracks; conks of fungi; and ivy. Each tree was described according to the presence/absence of microhabitats as well as tree diameter, vitality, and species. In each stand, structural variables (basal area, stem density, log volume, stand height, diameter class distribution) and the time since last cutting (i.e., the number of years since the last cutting) were assessed. At the tree level, large-diameter trees, snags, and non-coniferous species supported a higher richness of microhabitats than trees of small diameter, living trees, and conifers. Holm oak (*Quercus ilex* L.), which is a typical species of Mediterranean forests, exhibited a particularly high ability to host microhabitats. Tree diameter was the best predictor of the occurrence of most microhabitats (7 out of 9). We studied co-occurrences among microhabitats, but our results indicated that microhabitat types served poorly as proxies of other microhabitats due to frequent but unspecific positive relationships. At the stand level, time since last cutting was the best predictor of density of microhabitat-bearing trees and the occurrence of most tree microhabitats. The density of microhabitat-bearing trees was approximately 13 times higher in older stands (>90 years post-cutting) than in recently cut stands (<30 years). To maintain biodiversity in forests, we suggest that managers conserve large trees and snags and preferentially use holm oaks for wood production. Silvicultural practices should include a long rotation period and favor harvesting by group selection to maintain forest stands with a time since last cutting >90 years.

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### 1. Introduction

In many parts of the world, forest managers have to balance wood production with biodiversity conservation over the long term (Secretariat of the Convention on Biological Diversity, 2010). Stand structure, the composition of tree species, deadwood volume and tree microhabitats (i.e., microhabitats that grow on trees) are important components of conserving biodiversity in forests (Grove, 2002; Hunter, 1999; Paillet et al., 2010). Many species depend on tree microhabitats for food, shelter and breeding habitat (Michel and Winter, 2009; Winter and Möller, 2008). For example, dead branches are food sources for saproxylic insects and fungi (Jonsell and

Nordlander, 2002; Vanderwel et al., 2006). Cavities provide habitats for breeding birds, mammals, and invertebrates but also lichens and bryophytes (Fritz and Heilmann-Clausen, 2010; Lučan et al., 2009; Parsons et al., 2003; Ranius, 2002). Many forest bats nest or roost behind cracked and loose bark (Pénicaud, 2000; Russo et al., 2004; Vonhof and Gwilliam, 2007). Other microhabitats, such as conks of fungi or ivy, are homes to insects and provide potential nesting and foraging sites for birds (Bässler et al., 2012; Dajor, 2005; Mitchell, 1973). Tree microhabitats support a large food web and may have an important role in the functioning of forest ecosystems (Aitken and Martin, 2007; Martin and Eadie, 1999). Some species linked to tree microhabitats are also of major concern for biodiversity conservation, such as some saproxylic insects (e.g., *Limonicus violaceus* – Goux and Brustel, 2011), birds (e.g., the White-backed Woodpecker *Dendrocopos leucotos* – Lehikoinen et al., 2011), and bats (e.g., *Barbastella barbastellus* – Russo et al., 2010).

Surprisingly, the links between trees, stand characteristics and tree microhabitats remain poorly explored compared to other

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research areas related to biodiversity indicators (Michel and Winter, 2009; Vuidot et al., 2011). Recently, several studies investigated the occurrence of tree microhabitats by comparing managed and unmanaged forests (Larrieu et al., 2012; Michel and Winter, 2009; Vuidot et al., 2011; Winter and Möller, 2008). However, the distinction between 'managed' and 'unmanaged' forests may involve a large array of silvicultural practices. For example, two managed forests may have contrasting management histories, leading to different structural characteristics and biodiversity levels (Bengtsson et al., 2000; Burger, 2009; Summerville, 2011).

Silvicultural practices tend to convert forests into simplified ecosystems (with reductions in species tree diversity, vertical stratification, and age structure) compared to unmanaged forests (Paillet et al., 2010). However, forest management also has the potential to maintain natural structural complexity and support the development of microhabitats (Bauhus et al., 2009; Larrieu et al., 2012). Although microhabitats are believed to play a key role in the conservation of biodiversity in managed forests (Michel and Winter, 2009; Winter and Möller, 2008), the factors that underlie their occurrence and density remain poorly known. To our knowledge, only Michel and Winter (2009) have explored the role of management history and stand structure in the occurrence of tree microhabitats in Douglas fir forests (USA). Yet, better understanding of the factors that allow the development of microhabitats in managed forests is of strong interest for managers and decision-makers, especially in Europe, where most forests are subject to silvicultural treatments (Bengtsson et al., 2000; Vanbergen et al., 2005).

The Mediterranean region is considered a priority area for biodiversity conservation (Cuttelod et al., 2008; MEA, 2005; Myers et al., 2000). Biodiversity conservation in Mediterranean forests is the subject of several research programs (see for example the ongoing program 'Mediterranean Integrated Studies at Regional And Local Scales' (MISTRALS, 2012); however, to our knowledge, research on the factors underlying the occurrence of tree microhabitats has never been conducted in Mediterranean forests (Vuidot et al., 2011).

The overall objective of our study is to test the effect of tree and stand characteristics (time since last cutting and stand structure) on the occurrence and density of tree microhabitats in managed forest stands in the Mediterranean region, specifically southern France. We distinguished between the tree and stand levels following the Vuidot et al. (2011) approach: at the tree level, the objectives were to (a) investigate the relationships between tree characteristics (species, vitality, and diameter) and tree microhabitats, and (b) determine co-occurrences among tree microhabitats. At the stand level (c), we examined the effects of time since last cutting (i.e., the number of years since the last cutting) and stand structure on the density of microhabitats. We showed that managed forests have the potential to conserve microhabitats, and we discuss measuring and promoting microhabitats from the perspective of forest managers.

## 2. Methods

### 2.1. Study area

The studied stands were located in southern France, in Saint-Paul-lès-Durance (44°41'16"N/5°42'30"E, surface area 1415 ha, mean altitude 300 m), Ribiers (44°13'55"N/5°21'26"E, area 126 ha, alt. 800 m), and Saint-Vincent-sur-Jabron (44°10'18"N/5°44'33"E, area 90 ha, alt. 850 m). Climate conditions were typical of the Mediterranean region with a long sun exposure (2500–2800 h annually) and warm summers (mean temperature in summer = 27 °C; annual mean = 12 °C) (Météo France, 2012). Annual precipitations averaged 750 mm, most of it occurring in autumn and winter. Summers are

characterized by long periods of drought (mean precipitation in summer = 70 mm) (Météo France, 2012).

Forests were dominated by pubescent oaks (*Quercus pubescens* Willd.) (37% of the total area), followed by mixed stands of pubescent-holm oaks (*Q. ilex* L.) (30% of the total area), stands of holm oaks (10%), and other types of stands (conifers, other deciduous, or a mixture of conifers-deciduous) (National Institute of the Geographic and Forest Information (IGN), 2012). *Q. pubescens* and *Q. ilex* forests represent approximately 40% of French Mediterranean forest cover (IGN, 2012). In average, stand basal area varied from 10 to 30 m<sup>2</sup>/ha and height from 5 to 15 m (data extracted from management plans). These stands were traditionally managed as coppices with standards, associating broadleaved coppices for fire wood, and standards for timber. Coppice was clear cut every 15 to more than 90 years. Forests of pubescent and holm oaks have a remarkable biodiversity value, especially *Q. ilex* forests which are listed as a habitat of community interest in the Appendix I of the Habitats Directive, i.e., the habitats that led to the establishment of the Natura 2000 network in European member states European Economic Community (EEC), 1992.

### 2.2. Microhabitat inventory

The survey of microhabitat-bearing trees was performed by the National Forest Office (Office National des Forêts, ONF) in 2009. All trees were exhaustively searched. In total, 1630 trees were inventoried and GPS-located within an area of 1631 ha.

Each tree was described according to three characteristics: species (holm oak, pubescent oak, other deciduous, and conifers), vitality (dead vs. alive), and diameter class for diameter measured at breast height (DBH) (six categories were defined by the ONF, see Table 1). The latter variable was later considered a semi-quantitative variable in the analyses, ranging from 1 (DBH between 0 and 32 cm) to 6 (DBH over 160 cm) (see Table 2).

The description of microhabitats followed a standardized protocol including 9 tree microhabitat types. For each tree, the presence/absence of every microhabitat was described. All microhabitats have a potential role in biodiversity as foraging, sheltering, and breeding sites (Gibbons and Lindenmayer, 2002; Winter and Möller, 2008):

- 1. Canopy dead wood, with a minimum threshold of 10% dead crown by volume.
- 2. Woodpecker cavities with >2 cm apertures.
- 3–5. Non-woodpecker cavities with >5 cm apertures. A distinction was made among 'lower cavities' (<0.5 m above the ground), 'medium cavities' (between 0.5 and 2 m above the ground), and 'upper cavities' (over 2 m above the ground).

**Table 1**

Tree characteristics and number of trees. The 'other deciduous' group included *Acer campestre*, *Acer monspessulanum*, *Sorbus aucuparia*, *Tilia platyphyllos*, *Prunus* sp., and *Populus* sp., and the 'conifers' group included *Pinus sylvestris*, *Pinus halepensis*, and *Juniperus* sp. (*Prunus*, *Populus*, and *Juniperus* species could not be identified at the species level during the field inventory).

Variables	Levels	Total
Species	Holm oak	834
	Pubescent oak	689
	Other deciduous	68
	Conifers	39
Vitality	Alive	1277
	Dead	353
Diameter class	0–32 cm	462
	32–64 cm	521
	64–96 cm	419
	96–128 cm	168
	128–160 cm	42
	Over 160 cm	16

**Table 2**  
Structural variables.

Structural variables	Mean	Std. error	Min.	Max.
Basal area (m <sup>2</sup> /ha)	11.46	0.65	1.29	32.99
Stem density (nb/ha)	686.36	46.57	77.85	1595.89
Log volume (m <sup>3</sup> /ha)	2.53	0.43	0.00	14.36
Stand height (m)	7.68	0.25	4.75	12.75
Diameter class distribution	0.28	0.04	0.00	1.15

- 6. Loose barks or cracks with a minimum width of 1 cm and over 1 m above the ground.
- 7. Conks of fungi with diameter >5 cm.
- 8. *Cerambyx* cavities (the endangered saproxylic beetle *Cerambyx cerdo* (Buse et al., 2007), included in Annex II of the UE 'Habitats' Directive, is the most abundant *Cerambyx* in the study area, but *C. miles* or *Cerambyx velutinus* may also be present).
- 9. Ivy (*Hedera helix*), with a minimum cover of 25% of the tree height.

Abundance of each microhabitat was also assessed by the ONF (see Appendix A for the scoring of microhabitats). From the abundance data, we calculated the total abundance (sum of the abundances of each microhabitat) and the diversity of microhabitats per tree (Shannon index on microhabitat abundances). However, we found that these metrics were multi-correlated (richness-abundance:  $r = 0.85$ ; richness-diversity:  $r = 0.96$ ; Appendix A). In the following analyses, we used microhabitats richness only which is the simpler metric, and allows more comparisons with other research (Larrieu and Cabanettes, 2012; Vuidot et al., 2011). Note that similar results were obtained when using abundance or diversity instead of richness (results not shown).

### 2.3. Stand characteristics

Stand characteristics were measured in a subset of 59 plots of 100 m radius following a stratified random sampling design (number of plots per site: Cadarache = 42, Ribiers = 10, Saint-Vincent-sur-Jabron = 7). Centers of plots were separated by at least 400 m so that no plots occurred in the same management unit. We covered 420 microhabitat-bearing trees along a gradient of density ranging from 0 to 27.07 microhabitat-bearing trees per ha (mean density per ha (standard error) = 2.27 (0.57)).

Each plot comprised 4 subplots of 15 m radius (1 at the center point of the plot and 3 at 50 m from the center point and equally distant from each other). We inventoried and measured the diameters at breast height (DBH) of all trees with DBH >5 cm (without distinctions between genet and ramet). Stand height was calculated as the mean tree height of the stand. Total log volume per plot was measured from downed woody debris with a diameter >5 cm using the volume formula:  $V = \pi/4 dL$ , where  $V$  = volume;  $d$  = mid-diameter; and  $L$  = length. From these measurements, we derived total basal area, stem density, and the diameter class distribution (calculated as the Shannon index of diameters per plot). These variables were chosen for their sensitivity to forest management practices (Bauhus et al., 2009; McElhinny et al., 2005). Each plot was classified a posteriori into 4 categories of time since last cutting (data extracted from the management plans of the ONF): 0–30 years ( $n = 27$  plots), 30–60 years ( $n = 10$ ), 60–90 years ( $n = 13$ ), and >90 years ( $n = 9$ ).

### 2.4. Statistical analyses

We considered several response variables depending on the level of analysis (tree vs. stand). At the tree level, we used the 'richness of microhabitats' (i.e., the number of tree microhabitat types per tree) and the 'occurrence of microhabitats' (i.e., the presence of a given tree microhabitat type on a tree). At the stand level,

we used the 'density of microhabitat-bearing trees' (i.e., the number of microhabitat-bearing trees per plot) and the 'density of microhabitats' (i.e., the number of tree microhabitats types per plot, calculated from the presence/absence of each microhabitat per tree – Larrieu and Cabanettes, 2012). Variables at the stand level were calculated as the sum of trees and microhabitats in each plot of 100 m radius (the same plots used for the description of stand characteristics).

We pooled the sites in the following analyses because they showed no significant differences among times since last cutting and no differences among stand structures (see Appendix B for statistical results), and they shared the same stand composition (IGN, 2012). However, we systematically considered spatial correlation structure in our analyses, hypothesizing that close trees or plots have a greater chance to share similar microhabitats due to similar abiotic conditions such as soil and microclimatic conditions (Michel and Winter, 2009). Thus, all models incorporated the equation  $x + y + x^2 + y^2$ , where  $x$  and  $y$  were the coordinates of microhabitat-bearing trees or the coordinates of the centers of the plots for plot-scale data (following the approach of Devictor et al., 2008; Doxa et al., 2010; Fortin and Dale, 2005). Note, however, that quite similar results were obtained without taking into account spatial correlation structure.

At the tree level ( $n = 1630$  trees), we tested the effect of tree characteristics (species, vitality, and diameter) on the richness of microhabitats using a logistic regression analysis (Generalized Linear Mixed (GLM) with a logarithmic link function) with a Poisson error distribution (richness of microhabitats was considered count data). We compared several models of different completeness (from simple models to complete models including all of the tree characteristics and interactions as explanatory variables) and selected the models with the lowest AIC to explain the significant effects of tree characteristics (Burnham and Anderson, 2002). We then investigated the influence of each tree characteristic on the occurrence of each microhabitat. We performed logistic regression analyses (GLM with a logit link) with a binomial error distribution (presence/absence of each microhabitat was the binary dependent variable) (Crawley, 2009). We also tested co-occurrences among microhabitats (i.e., we tested the influence of the occurrence of a microhabitat on another microhabitat) using logistic regression analysis to assess whether some microhabitats could be used as surrogates of other microhabitats.

At the stand level ( $n = 59$  plots), we examined the influence of stand characteristics (time since last cutting and structural variables: basal area, stem density, log volume, stand height, diameter class distribution) on the density of microhabitat-bearing trees and the density of microhabitats using logistic regression analyses with a Poisson error distribution. We constructed simple models (i.e., each stand characteristic was modeled separately) to avoid overparameterization (Crawley, 2009).  $P$ -values and estimates were corrected for over-dispersion according to Faraway (2006) approach. All analyses were performed using R statistical software v. 2.15.1 (R Development Core Team 2011).

## 3. Results

### 3.1. Influences of diameter, vitality and tree species on tree microhabitats

The model with the lowest AIC was the complete additive model without interactions (Appendix C). The richness of microhabitats per tree was influenced by diameter (GLM,  $F_{1,1618} = 236.58$ ,  $p < 0.001$ ), vitality (GLM,  $F_{1,1618} = 58.57$ ,  $p < 0.001$ ), and species (GLM,  $F_{3,1618} = 35.99$ ,  $p < 0.001$ ). We found a positive relationship between the tree diameter and the richness of microhabitats (slope estimate (SE) of the variable 'tree diameter' = 0.14 (0.01)). Living

trees supported a lower richness of microhabitats than snags (Fig. 1). We found that holm oaks had the highest richness of microhabitats (Fig. 1) but the lowest average tree diameter (mean tree diameter (SE): holm oaks = 1.85 (0.03), other deciduous = 2.31 (0.13), coniferous = 2.58 (0.15), pubescent oaks = 2.82 (0.04)). When grouping holm oaks, pubescent oaks, and other deciduous species as non-coniferous trees, we found that non-coniferous trees had a higher richness of microhabitats than conifers (GLM,  $F_{1,1620} = 14.69$ ,  $p < 0.001$ ).

We investigated which tree characteristics best explained the occurrence of each microhabitat. Tree diameter was the best predictor of the occurrence of 7 microhabitats (Table 3 – raw data are also presented in Appendix D): canopy dead wood, woodpecker cavities, lower cavities, upper cavities, loose barks or cracks, *Cerambyx* cavities, and ivy. The magnitude of the tree diameter-microhabitat relationship varied among the different microhabitats. Canopy dead wood and ivy were associated with the highest estimates (0.60 and 0.54, respectively) and lower and upper cavities the lowest estimates (0.25 and 0.26, respectively). Vitality was a less efficient predictor than diameter and species because models using vitality as explanatory variable were never selected. Tree species best explained 2 microhabitats (Table 3): medium cavities (with a minimum for conifers: estimate (SE) =  $-1.91$  (0.45)) and conks of fungi (with a maximum for conifers: estimate (SE) = 0.55 (0.35)).

### 3.2. Co-occurrences among microhabitat types

The most abundant microhabitats were canopy deadwood (89% of trees) and loose bark or cracks (77% of trees). These were followed by upper cavities (46%), medium cavities (43%), conks of fungi (33%), *Cerambyx* cavities (32%), lower cavities (26%), woodpecker cavities (17%), and ivy (7%).

We examined the co-occurrence among microhabitats. Canopy dead wood, woodpecker cavities, upper cavities, and *Cerambyx* cavities were all correlated with one another (comparisons among these microhabitats: all estimates  $> 0.5$  and  $p < 0.01$ ) (Table 4). Lower cavities only co-occurred with medium and *Cerambyx* cavities (medium cavities: estimate (SE) = 0.98 (0.12),  $p < 0.001$ ; *Cerambyx* cavities: estimate (SE) = 0.79 (0.12),  $p < 0.001$ ), but the latter were correlated with other microhabitats (medium cavities = 5 correlations, *Cerambyx* cavities = 6 correlations). Ivy exhibited a negative effect on medium cavities (estimate (SE) =  $-0.56$

(0.21),  $p = 0.007$ ) and conks of fungi (estimate (SE) =  $-0.53$  (0.23),  $p = 0.02$ ).

### 3.3. Effects of stand characteristics on the densities of tree microhabitats

We examined the effects of the stand characteristics on the density of microhabitat-bearing trees. Time since last cutting showed the lowest AIC and had a positive effect on the density of microhabitat-bearing trees (Table 5).

We then investigated the effect of stand characteristics on the density of each microhabitat (Appendix E). Models including time since last cutting showed the lowest AIC for 6 microhabitats (GLM): canopy dead wood ( $F_{3,51} = 6.27$ ,  $p = 0.001$ ), medium cavities ( $F_{3,51} = 3.55$ ,  $p = 0.02$ ), upper cavities ( $F_{3,51} = 5.64$ ,  $p = 0.002$ ), loose barks or cracks ( $F_{3,51} = 5.93$ ,  $p = 0.001$ ), conks of fungi ( $F_{3,51} = 5.94$ ,  $p = 0.001$ ), and *Cerambyx* cavities ( $F_{3,51} = 4.75$ ,  $p = 0.005$ ). Time since last cutting had a positive effect on all of these microhabitats. Stem density, log volume, and stand height best explained the density of lower cavities, woodpecker cavities, and ivy, respectively. Stem density exhibited a negative relationship with the density of lower cavities (GLM,  $F_{1,53} = 15.68$ ,  $p < 0.001$ ) (Fig. 2), and log volume and stand height were positively correlated with woodpecker cavities (GLM,  $F_{1,53} = 17.30$ ,  $p < 0.001$ ) and ivy (GLM,  $F_{1,53} = 5.63$ ,  $p = 0.02$ ), respectively.

## 4. Discussion

### 4.1. Influence of diameter, vitality and tree species on tree microhabitats

We found a positive relationship between tree diameter and the richness of microhabitats, which confirmed several previous observations in contrasting ecological contexts (Larrieu et al., 2012; Michel and Winter, 2009; Vuidot et al., 2011). However, this relationship may not be systematic, as Winter and Möller (2008) found no significant relationship in managed or recently unmanaged stands. Generally, it appears that larger trees host more microhabitats than smaller ones, most likely due to their longer lifespan and the higher probability of microhabitat-creating events (e.g., diseases, parasite attacks, climatic events, and harvesting damage – Vuidot et al., 2011). Diameter was also selected as the tree characteristic that best explained the occurrence of 7 microhabitats out of 9

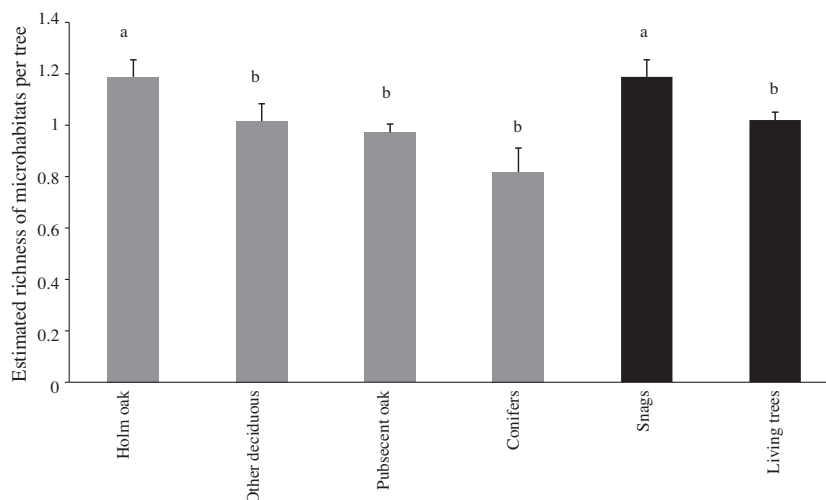


Fig. 1. Estimated richness of microhabitats per tree derived from the selected generalized linear model. Different letters indicate significantly different levels for a variable, assigned per group of variables (i.e., separately for tree species and vitality).

**Table 3**  
Occurrence of microhabitats as a function of tree characteristics (species, vitality, diameter). Table shows estimate values ( $\pm$ SE) and the  $p$ -values of the GLMs with binomial distribution and logit link applied to tree level data. Variables in brackets are intercepts of the models. The AIC of the selected models are in bold. Abbreviations: Pubes. oak = Pubescent oak, Other decid. = Other deciduous, Conif. = Conifers, Sna. = Snags, Liv. trees = Living trees, Int. = Intercept, Est. = Estimate.

Microhabitat type	Species			Vitality			Diameter							
	(Holm oak)	Pubes. oak	Other decid.	Conif.	AIC	$P$ -value	(Sna.)	Liv. trees	AIC	$P$ -value	(Int.)	Est.	AIC	$P$ -value
Canopy dead wood	1.16 (0.46)	0.91 (0.23)	0.74 (0.51)	0.28 (0.66)	1059.00	<0.001	2.25 (0.47)	-0.77 (0.26)	1064.30	0.001	0.65 (0.43)	0.60 (0.09)	<b>1028.50</b>	<0.001
Woodpecker cavities	-4.047 (0.28)	0.59 (0.15)	0.57 (0.34)	0.93 (0.36)	1353.00	<0.001	-3.51 (0.29)	-0.33 (0.15)	1362.80	0.03	-4.46 (0.31)	0.29 (0.06)	<b>1345.40</b>	<0.001
Lower cavities	-0.43 (0.26)	0.34 (0.13)	-0.17 (0.29)	-1.25 (0.54)	1826.40	0.007	-0.06 (0.27)	-0.62 (0.13)	1813.40	<0.001	-1.18 (0.28)	0.25 (0.05)	<b>1811.00</b>	<0.001
Medium cavities	0.55 (0.23)	-1.20 (0.12)	-0.91 (0.27)	-1.91 (0.45)	<b>2109.10</b>	<0.001	0.14 (0.23)	-0.25 (0.12)	2220.60	0.04	-0.12 (0.23)	0.02 (0.04)	2224.40	0.64
Upper cavities	-0.10 (0.23)	0.01 (0.12)	-0.06 (0.26)	-1.12 (0.40)	2161.40	0.02	-0.01 (0.24)	-0.09 (0.12)	2166.50	0.45	-0.69 (0.25)	0.26 (0.05)	<b>2136.90</b>	<0.001
Loose barks or cracks	1.46 (0.25)	0.40 (0.14)	0.42 (0.34)	-1.20 (0.34)	1714.90	<0.001	2.29 (0.28)	-0.73 (0.17)	1715.00	<0.001	0.80 (0.27)	0.45 (0.06)	<b>1678.40</b>	<0.001
Conks of fungi	0.85 (0.25)	-1.00 (0.13)	-1.13 (0.32)	0.55 (0.35)	<b>1900.00</b>	<0.001	-0.86 (0.25)	-0.49 (0.13)	1962.20	<0.001	-1.56 (0.26)	0.13 (0.05)	1969.60	0.006
<i>Cerambyx</i> cavities	-1.21 (0.24)	0.41 (0.12)	-1.34 (0.41)	0.30 (0.35)	1954.00	<0.001	-0.67 (0.25)	-0.36 (0.13)	1958.30	<0.001	-2.11 (0.26)	0.38 (0.05)	<b>1921.50</b>	<0.001
Ivy	-2.08 (2.20)	1.11 (0.25)	1.97 (0.36)	-0.16 (1.07)	753.43	<0.001	-0.14 (0.60)	0.19 (0.26)	787.81	0.45	-1.78 (0.57)	0.54 (0.08)	<b>746.01</b>	<0.001

(all microhabitats except medium cavities and conks of fungi). Comparatively, Vuidot et al. (2011) found that diameter was the primary factor influencing non-woodpecker cavities as well as, combined with other factors, bark losses and cracks. In our case, it appears that diameter explained the occurrence of more microhabitats than had been observed before. Thus, tree diameter may be a relevant indicator of the richness and the occurrence of microhabitats in Mediterranean broadleaf forests.

Snags were richer in microhabitats than living trees. This result was in line with the observations of Vuidot et al. (2011) and Larrieu and Cabanettes (2012) and confirmed the important role of snags in providing microhabitats compared to living trees. However, we showed that vitality had a lower contribution to the occurrence of microhabitats than species and diameter. Furthermore, independently of microhabitats, snags and living trees also provide different habitat qualities based on the differences between dead wood and living wood (Lassaue et al., 2011; Winter and Möller, 2008). Several bird species are dependent on dead trees for foraging, such as the White-Backed Woodpecker (*D. leucotos*) or the Lesser Spotted Woodpecker (*Dendrocopos minor*) (Olsson et al., 1992; Roberge et al., 2008; Stenberg, 1996). Many fungi and insects are also associated with dead substrates (Grove, 2002; Lassaue et al., 2011; Lonsdale et al., 2007); thus, microhabitats may not be the only factor driving biodiversity on snags.

The richness of microhabitats was higher in the non-coniferous trees (which were composed of 96% oaks) than in the coniferous trees. In our analyses, coniferous tree species were scarce compared to non-coniferous tree species (Table 1) and future studies should try to compensate this lack. However, our result confirms those of Vuidot et al. (2011), who showed that oaks in temperate lowland forests were more microhabitat-rich than other species. Surprisingly, holm oaks had the highest richness of microhabitats per tree but the lowest DBH among tree species. This reveals the ability of holm oaks to produce more microhabitats at a lower diameter than other species, but this may be due to the typical low growth rate of evergreen trees (Grime, 2002; Olet et al., 2009). An interesting perspective would be to assess tree age to compare microhabitat richness among species on an equivalent age basis, but to our knowledge, this information is not yet available. This may reflect the recent interest in microhabitats and also the fact that conducting dendrochronological measurements over a large sample of species and conditions remains costly. However, time since last cutting may be more accessible through management plans and provide interesting results at a stand level (see below).

#### 4.2. Co-occurrences among microhabitat types

Co-occurrences among microhabitats revealed variability among the different microhabitat types. Most relationships among microhabitats were positive, which meant that the presence of a given tree microhabitat tended to favor the presence of others (see also the results of Larrieu and Cabanettes, 2012). Four microhabitats were correlated with one another (canopy dead wood, woodpecker cavities, upper cavities, and *Cerambyx* cavities). The fact that woodpecker cavities were correlated to canopy dead wood is in line with the scientific literature, as most woodpecker species are linked to habitats with dying and dead wood (Roberge et al., 2008). Upper cavities (>2 m from the ground) also develop on old trees, which often bear canopy dead wood. We also found that the presence of loose barks or cracks was associated with the occurrence of *Cerambyx* cavities. This confirms the previously observed relationship detected by Buse et al. (2007) for *Cerambyx cerdo* in oaks. The only exception was observed for ivy, which was negatively correlated with the occurrence of medium cavities

**Table 4**  
Co-occurrences among microhabitats. Table shows estimate values ( $\pm$ SE) and the  $p$ -values of the GLMs with binomial distribution and logit link applied to tree level data. Abbreviations: Standing dw. = Standing dead wood, Woodpecker c. = Woodpecker cavities, Medium c. = Medium cavities, Bark loss & c. = Loose barks or cracks, *Cerambyx* c. = *Cerambyx* cavities.

Microhabitat type	Standing dw.	Woodpecker c.	Lower cavities	Medium c.	Upper cavities	Bark loss & c.	Conks of fungi	<i>Cerambyx</i> c.
Woodpecker cavities	1.91 (0.46) ***							
Lower cavities	0.01 (0.18) ns	−0.11 (0.16) ns						
Medium cavities	0.03 (0.16) ns	−0.17 (0.14) ns	0.98 (0.12) ***					
Upper cavities	0.64 (0.18) ***	0.64 (0.14) ***	0.02 (0.12) ns	0.19 (0.10) .				
Loose barks or cracks	1.11 (0.17) ***	0.13 (0.17) ns	0.14 (0.14) ns	0.32 (0.12) **	0.30 (0.13) *			
Conks of fungi	0.57 (0.19) **	0.29 (0.14) *	−0.12 (0.12) ns	0.29 (0.11) **	0.25 (0.11) *	0.13 (0.13) ns		
<i>Cerambyx</i> cavities	0.53 (0.20) **	0.75 (0.14) ***	0.79 (0.12) ***	0.38 (0.11) ***	0.54 (0.11) ***	0.50 (0.14) ***	0.07 (0.11) ns	
Ivy	1.02 (0.47) *	0.11 (0.27) ns	0.12 (0.22) ns	−0.56 (0.21) **	0.49 (0.20) *	0.43 (0.27) ns	−0.53 (0.23) *	−0.02 (0.21) ns

Significant codes: '.' =  $p < 0.1$ , 'ns' =  $p > 0.1$ .

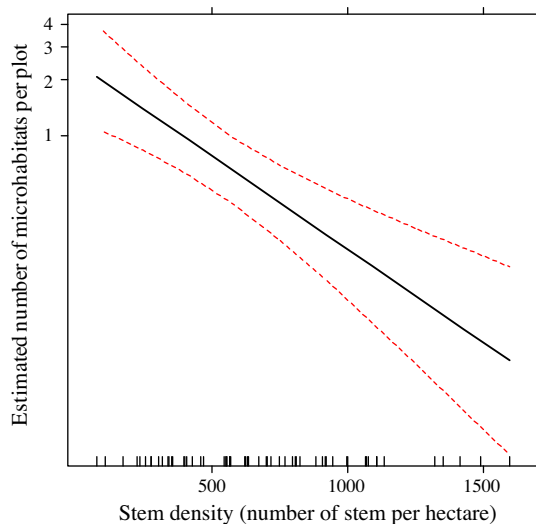
\*\*\*  $p < 0.001$ .

\*\*  $p < 0.01$ .

\*  $p < 0.05$ .

**Table 5**  
Influence of stand characteristics on the density of microhabitat-bearing trees. Table shows estimate values ( $\pm$ SE) and the  $p$ -values of the GLMs with Poisson distribution and log-link applied to stand level data. The lowest AIC is in bold.

Stand characteristic	Levels	Estimate (SE)	AIC	$P$ -value
Stem density		−0.001 (0.0007)	584.46	0.03
Basal area		−0.02 (0.04)	638.4	0.63
Log volume		0.05 (0.05)	626.78	0.29
Stand height		0.11 (0.09)	624.75	0.26
Vertical irregularity		1.49 (0.59)	577.65	0.01
Time since last cutting	(0–30 years)	3.48 (1.93)	<b>504.56</b>	0.001
	30–60 years	1.03 (0.62)		
	60–90 years	1.11 (0.58)		
	>90 years	2.15 (0.60)		



**Fig. 2.** Relationship between the stem density and the estimated number of microhabitats per plot. Upper and lower dotted lines represent the 95% confidence interval. Smoothed curves were obtained with the R package 'effects'.

and conks of fungi. Ivy foliage may create a physical barrier to the development of these microhabitats.

#### 4.3. Effects of stand characteristics on the densities of tree microhabitats

At the stand level, our results indicated that time since last cutting was the major factor to explain the density of microhabitat-

bearing trees. The density of microhabitat-bearing trees was almost 13 times higher in stands that were more than 90 years old since last cutting than in stands of 0–30 years post-cutting (densities of trees (SE): 0–30 years = 0.49 (0.16) trees ha<sup>−1</sup>; >90 years = 6.17 (1.92) trees ha<sup>−1</sup>). Time since last cutting was the best factor to explain the density of 6 microhabitats (canopy dead wood, loose barks or cracks, medium cavities, upper cavities, conks of fungi, and *Cerambyx* cavities). These results highlight the importance of time after forestry cutting in the development of tree microhabitats in forests (Lassauce et al., 2012), even over a relatively short time span, such as the one studied here.

Time is required for the development of decay processes and the creation of loose barks or cracks and canopy dead wood. For tree cavities, which are mostly created from mechanical damage by heat, lightning, or wind (Gibbons and Lindenmayer, 2002), time also plays a key role, as the probability of a stand or tree being affected by a significant event naturally increases with the time of exposure. We might expect that tree microhabitats that are plant- and animal-created (i.e., 'biodiversity-dependent microhabitats': woodpecker cavities, *Cerambyx* cavities, conks of fungi, and ivy) depend more on the type and the dynamic of biodiversity than old-growth attributes as such. Accordingly, woodpecker cavities and density of ivy were more sensitive to structural characteristics than time since last cutting. Most of the woodpecker species present in the study area search downed dead wood to forage for small beetles and larvae (e.g., *D. minor* or *Dendrocopos major*, see Roberge et al., 2008), and this could explain the positive effect of log volume on woodpecker cavities. The density of ivy was positively influenced by stand height. Ivy uses trees to develop, and height may be a critical variable for optimizing photosynthesis. However, conks of fungi and *Cerambyx* cavities were better explained by time since last cutting than by structural characteristics. Our results could not discriminate the spatial distribution of tree microhabitats from their origins ('biodiversity-independent microhabitats' vs. 'biodiversity-dependent microhabitats'), but further works with larger sample sizes and direct biodiversity measurements (e.g., assessments of the abundance and dynamics of fungi and *Cerambyx* populations) would be needed to strengthen these results.

An interesting perspective would be to consider the effect of the stand composition on the densities of tree microhabitats. Some species, and species groups, are sensitive to stand composition such as saproxylic beetles (Horak, 2011; Sama et al., 2011), whereas this effect on some others, such as birds, is more discussed (Wilson et al., 2010). However, the role of microhabitats in these differences of responses remains unknown. We could not analyze the effect of the stand composition on microhabitats (some stand compositions were underrepresented in our plots) but we encourage analyzing this effect in future research.

Although time since last cutting best predicted the density of microhabitat-bearing trees and most types of microhabitats, stem density and diameter class distribution also exhibited several significant relationships (see Table 5 and Appendix E: stem density showed a negative relationship with 7 microhabitats and diameter class distribution showed a positive relationship with 5 microhabitats). Because information about types of management is sometimes difficult to collect in private forests (Food and Agriculture Organization of the United Nations, 2010), which represent more than half of Europe's forests, stem density and diameter class distribution could be relevant proxies with which to assess global microhabitat densities in forests.

#### 4.4. Implications for biodiversity conservation and forest management

Despite growing interest in tree microhabitats as a potential biodiversity indicator, the factors that condition their presence at both the tree and stand levels remain poorly known, particularly for Mediterranean forests. Our results showed that some patterns observed at the tree level in temperate lowland and mountain forests (Larrieu and Cabanettes, 2012; Larrieu et al., 2012; Vuidot et al., 2011) were also confirmed in a Mediterranean context. In addition, even if the occurrences of tree microhabitats are relatively inter-correlated, none of the microhabitats we observed may accurately represent all of the others, so it appears important to observe them as a whole. Different tree microhabitats may represent different ecological niches for several taxa and thus constitute support for a diversity of species.

Measuring biodiversity is a key step in preventing further losses of biodiversity. Taxonomic measures to assess biodiversity may be time-consuming and highly subject to the knowledge of the observer and thus difficult to reproduce (Kallimanis et al., 2012; Prendergast et al., 1999). These inconveniences are non-negligible because they may introduce biases into biodiversity assessment, and they can limit initiatives of managers and policy-makers to assess and monitor biodiversity. Microhabitats have several advantages in term of measurements because they are simple (no specialized knowledge is required) and quick to measure (approximately 3 min per tree with the present protocol, including GPS location), and they provide a reliable measure of ecological niches for numerous forest species related to old-growth attributes. For example, woodpecker and upper cavities are reliable indicators of avian cavity nesters and bats such as *B. barbastellus*, several *Myotis* and *Nyctalus* species, and *Pipistrellus nathusii* that roost preferentially in these microhabitats (Lučan et al., 2009; Marnell and Presetnik, 2010; Roberge et al., 2008). However, an important point that also ought to be investigated is the potential observer effect (Vuidot et al., 2011). Observer effect might be low with this protocol, given the simplified list of tree microhabitats compared to other studies (Winter and Möller, 2008), but this still requires to be tested.

Our results indicated that tree and stand characteristics were reliable indicators of the richness, occurrence and density of microhabitats. These results suggest two possible approaches to be used when assessing biodiversity through microhabitats. A first approach could consist in roughly assessing the amount and types of microhabitats through the measure of two proxies: (i) time since last cutting (or if not available, stem density and/or diameter class distribution) and (ii) tree characteristics, especially tree diameters. A second approach could involve a finer assessment of microhabitats where specific microhabitats and more precise quantification are recorded. In both approaches, we provided a simple protocol, and we hope that our results will encourage managers to use tree microhabitats to assess biodiversity in forests.

Until recently, tree microhabitats were often considered as defects in wood production and silviculture. However, new standards

for sustainable forest management are expanding at an international level, such as Forest Management certifications brought about by the Forest Stewardship Council (FSC, 2012) or the Programme for the Endorsement of Forest Certification (PEFC, 2012), that could favorably take into account the presence of tree microhabitats. To meet rigorous standards of sustainability and biodiversity conservation, forest managers can allow the development of microhabitats by using tree species that best produce microhabitats, and they could conserve microhabitat-rich trees and stands. At the tree level, we showed that non-coniferous species, especially holm oak, which is a typical Mediterranean species, could be favored in Mediterranean forests rather than conifers. Snags and large trees should also be conserved because they support a high richness of microhabitats. At the stand level, we showed that the main factor favoring high densities of microhabitats was the time since last cutting, which was often more relevant than other stand characteristics. Thus, current silvicultural practices could favor harvesting and stand selection procedures that maintain some older stands since last cutting (Bauhus et al., 2009; Lassauce et al., 2012) with the aim of the global conservation of biodiversity. Economically, longer intervals between cuttings could be compensated for by the advantages of certifications over the short term (Blackman and Rivera, 2011; Stupak, 2011) and by social and ecological benefits over the longer term (Michel and Winter, 2009).

To conserve forest biodiversity, silvicultural practices need to balance the time scale of wood production with that of microhabitat creation. The next step in this research should include standardized and quantitative measures of biodiversity in relation to tree microhabitats (Vuidot et al., 2011), especially that of the birds, bats, and saproxylic insects that currently use tree microhabitats in their life cycles. These measures could provide a more comprehensive picture of critical ranges of microhabitats (with possible threshold values – Larrieu and Cabanettes, 2012; Larrieu et al., 2012) for preserving biodiversity in managed forests.

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#### Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2013.01.009>.

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