

# Tree microhabitats as indicators of bird and bat communities in Mediterranean forests



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## ABSTRACT

Tree microhabitats (e.g., canopy deadwood, cavities, and loose bark) may play an important role in forest biodiversity conservation. Indeed, many species depend on tree microhabitats during their life-cycles for food, shelter, and breeding habitat. Although recent studies have developed a set of definitions and descriptions for tree microhabitats, the relationships between tree microhabitat inventory data and biodiversity remain poorly understood. In this study, we identified relationships among tree microhabitat variables (i.e., the density and diversity of microhabitat) and bird and bat metrics using data from 59 plots in 3 Mediterranean forest ecosystems in France. In each plot, 9 types of tree microhabitats were inventoried: canopy deadwood; woodpecker cavities; non-woodpecker cavities (divided into lower, medium, and upper cavities); *Cerambyx* cavities; loose bark or cracks; conks of fungi; and ivy. We also assessed structural characteristics (e.g., basal area, stand height), the time since last cutting (i.e., the number of years since the stand was last cut), the number of forest habitats, and the distance to the nearest road. We performed bird and bat inventories in the same plots and we used abundances and a number of bird and bat community indices (e.g., species richness, mean forest specialization). We found that variations in tree microhabitat (more specifically, variations in microhabitat diversity) were a major factor in explaining the abundance and community response of birds and bats. Bird species, including cavity-nesting birds, were most strongly affected by tree microhabitat diversity, while bat species were positively affected by both the diversity of the tree microhabitat and the density of cavities created by *Cerambyx* spp. Tree microhabitats were better predictors of bird and bat responses than other stand characteristics. Tree microhabitat characteristics provide a reliable measure of ecological niches in forest ecosystems and we propose that these microhabitats be used as indicators for assessing biodiversity in forests.

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## 1. Introduction

Since the Rio Conference in 1992, biodiversity conservation in forest ecosystems has received increasing political attention. Several international agreements (e.g., the Convention on Biological Diversity in 1993 and the pan-European Ministerial Conferences) have developed broad objectives for sustainable forest management, i.e., management that reconciles economic, social, and ecological functions. One of the challenges in pursuing these objectives is to identify relevant biodiversity indicators that indicate the status (e.g., population size, species composition, or biotic integrity), the trends, and the threats acting on biodiversity (Biodiversity Indicators Partnership, 2012). Recently, several authors proposed using structure-based indicators such as tree microhabitat to assess biodiversity levels in forests (Michel and

Winter, 2009; Winter and Möller, 2008). However, the sensitivity of biodiversity to tree microhabitats remains poorly understood (Vuidot et al., 2011).

Tree microhabitats (e.g., tree cavities, loose bark or cracks) are created by animals (e.g., woodpeckers, *Cerambyx* spp., fungi), and/or by mechanical damage from heat, lighting, or wind (Cockle et al., 2011; Gibbons and Lindenmayer, 2002). Many animal species depend on tree microhabitats to feed, shelter or breed (Larrieu et al., 2012; Michel and Winter, 2009; Winter and Möller, 2008). These microhabitats may also provide ecological niches for lichens and bryophytes (Fritz and Heilmann-Clausen, 2010), invertebrates (Ranius, 2002; Vanderwel et al., 2006), and vertebrates, especially birds and bats (Kroll et al., 2012; Lučan et al., 2009; Mahon et al., 2008).

When reviewing the scientific literature on tree microhabitats, we noted that (1) studies on microhabitats are scarce compared to studies on structure-based biodiversity indicators such as deadwood volume or vertical heterogeneity (Lassauce et al., 2011; McElhinny et al., 2005); (2) most literature focuses on particular species, especially threatened species (e.g., the White-backed

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Woodpecker (*Dendrocopos leucotos*) or the *Barbastella barbastellus* bat in Europe) (Lehikoinen et al., 2011; Russo et al., 2004) rather than on common species; and (3) few studies have been conducted at the community level (Fritz and Heilmann-Clausen, 2010; Kroll et al., 2012; Parsons et al., 2003). Indeed, only Winter and Möller (2008) have tested the relationship between a complete set of tree microhabitat inventory variables and a taxonomic group (threatened saproxylic beetles). Thus, the quantitative and functional relationships among tree microhabitat variables (i.e., the density and diversity of microhabitat) and most species and communities remain unknown.

Birds and bats are relevant groups for assessing the responses of biodiversity to tree microhabitat. Many birds feed and nest in forests, especially forest specialists that spend most or all their life-cycle in forest habitats (Archaux and Bakkaus, 2007; Mikusinski et al., 2001). Birds that live in forest habitats may either be indirectly dependent on tree habitats for the insects that use them or directly dependent on the habitats, as is the case for birds that nest inside microhabitats such as tree cavities and ivy. Many bats (e.g., *B. barbastella*, *Myotis nattereri*, *Rhinolophus ferrumequinum*, and *Plecotus auritus*) hunt forest insects (Arlettaz, 1999; Russo and Jones, 2003), and most of them (e.g., *B. barbastella*, *M. nattereri*) also roost and nest in tree cavities, cracks, or behind loose bark (Pénicaud, 2000; Russo et al., 2004). Moreover, because many birds and bats are at the top of food chains, they are good indicators of the quality of forest habitats and food webs (Ghadiri Khanaposhtani et al., 2012; Gunn and Hagan III, 2000).

The overall objective of our study was to test whether and how tree microhabitats can be used as biodiversity indicators. Specifically, we investigated the relationships between tree microhabitat variables (density and diversity) and bird and bat populations and communities in three managed forests in southern France. We distinguished between the species and community levels. At the species level, the objective was to determine the effects of the density and diversity of tree microhabitats on the abundance of bird and bat species. At the community level, we examined the effects of density and diversity of tree microhabitats on species richness, species diversity, and mean forest specialization. For birds, we also used the proportion of cavity-nesters and the community trophic index; for bats, we also used mean tree roost specialization. To determine whether tree microhabitats were relevant indicators of biodiversity, we compared tree microhabitats with more classical stand characteristics (i.e., basal area, stem density, stand height, diameter class distribution, deadwood volume, time since last cutting, number of habitats, and distance to the nearest road) as explanatory variables.

## 2. Methods

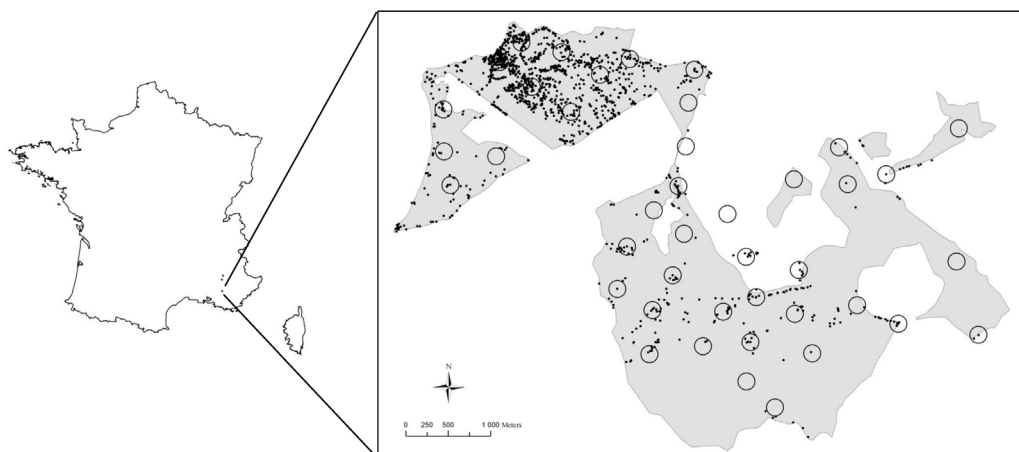
### 2.1. Study area and sampling design

The stands sampled in this study were located in southern France at Saint-Paul-lès-Durance (44°41'16" N, 5°42'30" E, 1415-ha forest area, mean altitude 300 m), Ribiers (44°13'55" N, 5°21'26" E, 126-ha forest area, mean altitude 800 m), and Saint-Vincent-sur-Jabron (44°10'18" N, 5°44'33" E, 90-ha forest area, mean altitude 850 m). Climate conditions were typical of the Mediterranean region with 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, and summers are characterized by long periods of drought (mean precipitation in summer = 70 mm) (Météo France, 2012). The stands were dominated by pubescent oaks (*Quercus pubescens* Willd.) and holm oaks (*Quercus ilex* L.) and were managed as coppice-with-standards systems, mainly for fuel wood production.

To assess the influence of tree microhabitat on biodiversity, we used a stratified random sampling design (Fig. 1). We sampled a total of 59 plots with a 100-m radius (the number of plots per site was 42 (Cadarache), 10 (Ribiers), and 7 (Saint-Vincent-sur-Jabron)). The plots represented a density gradient of microhabitat-bearing trees ranging from 0 to 27.07 microhabitat-bearing trees per ha and a diversity gradient of tree microhabitats (Table 2). The centers of the plots were separated by at least 400 m such that no plots were located within the same management unit. In addition, the distances between plots helped ensure that bird and bat individuals were not counted in more than one plot (National Museum of Natural History (MNHN), 2012). We used the same plots to record density and diversity of tree microhabitats, stand characteristics, and bird and bat inventory data.

### 2.2. Microhabitats and other environmental variables

The survey of tree microhabitats was performed by the National Forest Office (Office National des Forêts (ONF)) in 2009. Across the three sites (1631 total ha), all microhabitat-bearing trees were exhaustively searched and their locations were recorded. Each tree was carefully described by ONF staff according to a standardized protocol that included descriptions of 9 tree microhabitat types (presence/absence and abundance of microhabitat type were recorded) (see Table 1 for the description of tree microhabitat types). In total, 1630 microhabitat-bearing trees were inventoried and their locations were recorded with GPS. We sampled a subset of 420 microhabitat-bearing trees. In each plot we assessed (a)



**Fig. 1.** Location of the study sites and diagram of the sampling design. The box shows the sampling design at Saint-Paul-lès-Durance with the sampling plots (circles) and microhabitat-bearing trees (dots).

**Table 1**  
List of tree microhabitats.

Microhabitat type	Threshold	Abundance of microhabitats	Scoring
1. Canopy deadwood	>10% of dead crown in volume	Low volume; between 10% and 25% of dead crown	1
		Medium volume; between 25% and 50% of dead crown	2
		High volume; > 50% of dead crown	3
2. Upper cavities	>2 m from the ground and cavities with > 5 cm aperture	One macrocavity	1
		Two macrocavities	2
		Three macrocavities and more	3
3. Medium cavities	0.5 m <> 2 m from the ground and cavities with > 5 cm aperture	One macrocavity	1
		Two macrocavities	2
		Three macrocavities and more	3
4. Lower cavities	<0.5 m from the ground and cavities with > 5 cm aperture	One macrocavity	1
		Two macrocavities	2
		Three macrocavities and more	3
5. Woodpecker cavities	Cavities with > 2 cm aperture	One macrocavity	1
		Two macrocavities	2
		Three macrocavities and more	3
6. <i>Cerambyx</i> cavities	–	Cavity without sawdust at the foot of the tree	1
		Cavity with sawdust at the foot of the tree	2
7. Bark loss and cracks	>1 cm and > 1 m from the ground	Low bark loss and cracks on branches	1
		Bark loss and cracks on limb branches	2
		Bark loss and cracks on limb branches and on the trunk	3
8. Conks of fungi	Diameter > 5 cm	One individual	1
		Two individuals	2
		Three individuals and more	3
9. Ivy ( <i>Hedera helix</i> )	>25% of the tree height	Presence of ivy	1

the density of tree microhabitats, i.e., the abundance of microhabitats per plot based on scored values (Table 1); and (b) microhabitat diversity, i.e., the Shannon index calculated using the density of each microhabitat type per plot (Eq. (1)). All of the tree microhabitat types were expected to play a role in supporting biodiversity by serving as foraging, sheltering, or breeding sites (Gibbons and Lindenmayer, 2002; Winter and Möller, 2008).

In each plot we assessed stand characteristics. Each plot was comprised of 4 sub-plots with a 15-m radius that were arranged with 1 subplot at the center point of the plot and 3 subplots located 50 m from the center point at equal distances from each other. We measured diameter at breast height (DBH) for all trees with a DBH > 5 cm. From these measurements we calculated total basal area, stem density, and the diversity of diameter classes for each plot using the Shannon index (hereafter called 'diameter class distribution'). We also measured stand height (i.e., mean tree height) and deadwood volume. Deadwood volume was measured as the total volume of downed woody debris and snags with a

diameter > 5 cm using  $V = \pi/4dL$ , where  $V$  = volume,  $d$  = diameter at half-length, and  $L$  = length. Each plot was classified *a posteriori* into 4 categories of time since last cutting (using data extracted from ONF management plans) as follows: 0–30 years ( $n = 27$  plots), 30–60 years ( $n = 10$ ), 60–90 years ( $n = 13$ ), and > 90 years ( $n = 9$ ). Time since last cutting was later treated as a semi-quantitative variable in the analyses, ranging from 1 (time since last cutting = 0–30 years) to 4 (time since last cutting > 90 years). We assessed the number of habitats per plot using the Corine Biotope typology (Bissardon and Guibal, 1997). All the stand characteristics used in the study were chosen for their sensitivity to forest management practices and their links with biodiversity (Bauhus et al., 2009; Maes et al., 2011). Finally, we also assessed the distance of plots to the nearest road.

### 2.3. Bird and bat inventories

All bird counts were performed by the same person (Baptiste Regnery). Counts were carried out in each plot during two visits in

**Table 2**  
Tree microhabitats and stand characteristics in the plots.

Variable	Unit	Mean	SE	Min.	Max.
Tree microhabitats					
Microhabitat-bearing trees	nb/ha	2.27	0.57	0.00	27.07
Total tree microhabitats	score/ha	13.88	2.98	0.00	139.17
Diversity of tree microhabitats	–	1.09	0.10	0.00	2.09
Canopy deadwood	score/ha	3.66	0.77	0.00	32.48
Woodpecker cavities	score/ha	0.76	0.18	0.00	6.05
Upper cavities	score/ha	2.05	0.43	0.00	17.83
Medium cavities	score/ha	1.40	0.36	0.00	16.88
Lower cavities	score/ha	0.74	0.18	0.00	6.37
<i>Cerambyx</i> cavities	score/ha	1.15	0.25	0.00	9.24
Loose barks and cracks	score/ha	3.19	0.83	0.00	42.04
Conks of fungi	score/ha	0.86	0.27	0.00	14.01
Ivy	score/ha	0.08	0.03	0.00	1.27
Stand characteristics					
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
Deadwood 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
Time since last cutting	–	2.07	0.15	1.00	4.00
Number of habitats	–	1.71	0.11	1.00	4.00
Distance to the road	m	48.83	2.61	30	110

the spring (April 5–15 and May 31–June 13, 2011) to detect both early and late breeding birds, following the recommendations of the French Breeding Bird Survey (BBS) of the National Museum of Natural History (MNHN, 2012; Jiguet et al., 2012). Counts were performed at the same time of day (within 1–4 h after sunrise) and lasted 15 min each. Birds were mostly detected by their song because all of the plots were located in core forest habitats with low visibility. Individuals could be distinguished when several birds continuously sang at different locations in the plot. Flying birds were not included in the analyses because of the high level of uncertainty about habitat use by these individuals.

Bats were inventoried using standardized echolocation recordings (Stahlschmidt and Brühl, 2012). Echolocation calls were automatically detected using a Tranquility Transect Bat detector (Courtpan Design Ltd, UK) and recorded on a Zoom H2 digital recorder (Samson technologies, USA) at a sampling rate of 96 ks/s from both of the detector outputs (high frequency and time expansion). Bat activity was measured with the high frequency output, and the time expansion output was used only for species emitting echolocation calls > 48 kHz. The time expansion factor was set to 10, and sensitivity levels were set to enable the detection of echolocation calls while minimizing background noise due to wind or insects. All detectors were set at the same sensitivity level. In each plot, echolocation recordings were carried out in two visits corresponding to peaks in bat activity, following the recommendations of the French Bat Survey (BS) coordinated by the National Museum of Natural History (MNHN, 2012; also see Appendix A). The first visit occurred between June 9 and 22, 2011 during the period in which females are expected to give birth and feed their offspring. The second visit, occurring between September 21 and 29, 2011, corresponded to a period of intense activity prior to hibernation. Detectors were installed at the center of each plot (the same location used for the bird counts) and all echolocation calls were recorded for 30 min at the same time of day (within 2 h after sunset). Bat foraging activity was recorded only when weather conditions were favorable (no rain and temperatures higher than 12 °C). Calls were identified using Syrinx software and several identification keys (Arthur and Lemaire, 2009; Barataud, 2012). Some identifications were very difficult, especially for species from the genera *Plecotus* and *Myotis* (Barataud, 2012), so we grouped *Plecotus* calls together as *Plecotus* sp. and *Myotis* calls as *Myotis myotis/Myotis blythii* calls to avoid identification errors.

For the following analyses, bird abundance was defined as the number of individuals per species and bat abundance was defined as the number of echolocation calls per species, given that it was not possible to quantify the number of individuals (Barataud, 2012; Gorresen et al., 2008).

#### 2.4. Community indices

At the community level, we used species richness, species diversity, and mean forest specialization. We also used the following indicators: for birds, the proportion of cavity-nesters and the community trophic index (CTI) and for bats, the mean tree roost specialization. All community indices are listed in Table 3.

Species diversity was calculated using the Shannon index. The Shannon index reflects the number of different species in a community and simultaneously takes into account how evenly the individuals are distributed among those species (Lyashchevska and Farnsworth, 2012). For a given species richness, the value of species diversity is maximized when all species are equally abundant. It is calculated as follows:

$$H'_j = -\sum_{i=1}^n p_{ij} \ln p_{ij} \quad (1)$$

**Table 3**  
List of community indices.

Indicator	
Birds	Species richness
	Species diversity
	Mean forest habitat specialization
	Community trophic index
Bats	Proportion of cavity-nesters
	Species richness
	Species diversity
	Mean forest habitat specialization
	Mean tree roost specialization

where  $n$  is the total number of species recorded and  $p_{ij}$  is the proportion of individuals belonging to the species  $i$  in plot  $j$ .

Mean forest specialization was calculated as the arithmetic mean of the species specialization to forest habitat (SSF) weighted by the abundances following the approach of Julliard et al. (2006) (Eq. (2)). The SSF was the average density of a species in forest habitats divided by its average density in non-forest habitats. It was calculated using the French BBS (2001–2008) (Jiguet et al., 2012) and the French BS (2006–2012), which are the standards for volunteer-based monitoring of birds and bats, respectively (see Appendix A):

$$\text{mean forest specialization}_j = \frac{\sum_{i=1}^n a_{ij}(\text{SSF}_i)}{\sum_{i=1}^n a_{ij}} \quad (2)$$

where  $n$  is the total number of species recorded,  $a_{ij}$  is the abundance of individuals of species  $i$  in plot  $j$ , and  $\text{SSF}_i$  is the specialization index to forest habitat for species  $i$ .

Until now, the degree of habitat specialization for different species of bats has been based on expert knowledge, but here we used species and community indices from standardized monitoring methods. The SSF values used in this study were systematically referenced against the literature regarding forest-dependency gradients for bat species.

Mean tree roost specialization was the arithmetic mean of the species specialization to tree roosts (SSTR), weighted by the abundances. The SSTR was the dependence level of each species on tree roosts derived from data from the EUROBATs survey created by national experts in European countries (1 = low dependence, 2 = medium dependence, and 3 = high dependence) (Marnell and Presetnik, 2010). The SSTR discriminated among bat communities that had different proportions of individuals with specific specializations to tree roosts. We calculated the mean tree roost specialization with the same equation used for the mean forest specialization (see Eq. (2)).

The CTI was an indicator of the mean trophic level of bird communities (Mouysset et al., 2012). It was calculated from the species trophic index (STI), which was the sum of the proportion of each species' diet (available in *Birds of the Western Palearctic interactive*, 2006) weighted by a coefficient (1 for vegetables, 2 for invertebrates, 3 for vertebrates). The CTI was then calculated as the arithmetic mean of the species trophic index (STI) weighted by the abundances. We calculated the CTI with the same equation used for the mean forest specialization (see Eq. (2)).

The values of the species specializations (SSF, SSTR) and the species trophic indices (STI) for all bird and bat species in the study are described in Appendix B.

#### 2.5. Statistical analyses

In all models, the effects of tree microhabitat and stand characteristics were adjusted for temperature and time of sampling (for birds, time after sunrise; for bats, time after sunset). We pooled

the three sites because they showed no significant differences in tree microhabitat or stand characteristics (see Appendix C for statistical results) and they shared a similar stand composition (National Institute of the Geographic and Forest Information, 2012). However, we did systematically consider spatial correlation structure in our analyses, hypothesizing that plots that were close together were more likely to share similar ecological conditions due to similarities in the abiotic environment such as soil and microclimatic conditions (Michel and Winter, 2009). Thus, we incorporated the following equation into all of the models:  $x + y + x^2 + y^2 + x \times y$ , where  $x$  and  $y$  are the coordinates of the center of each plot (following the approach of Devictor et al., 2008; Doxa et al., 2010; Fortin and Dale, 2005). We considered all bird and bat counts in the models (i.e., both the first and the second sampling periods), and the effect of plot identity was assumed to be random.

At the species level, we used the abundance values for those species of birds and bats that were found in a minimum of 10 plots (birds = 22 species; bats = 5 species). We tested the effects of density and diversity of tree microhabitats on the abundance of bird and bat species using a generalized linear mixed model (GLMM) with a Poisson error distribution and a randomized effect of plot identity. To examine whether tree microhabitat affected the relative abundance of bird and bat species, we followed a two-step approach. First, we modeled the effects of each of the 12 tree microhabitat variables in 12 separate models (microhabitat-bearing trees, total density of tree microhabitats, diversity of tree microhabitats, and the density of each type of microhabitat) (Table 2). This approach allowed for testing the effects of each tree microhabitat type while avoiding overparameterization (Crawley, 2009). Second, we selected the model with the lowest Akaike information criterion (AIC) (we also confirmed these results using hierarchical partitioning methods and goodness of fits – see Appendices D and E). When the difference in the AIC among models was less than two points (Burnham and Anderson, 2002), we retained multiple models (AIC values can be found in Appendix F). At the community level, we tested the effect of density of tree microhabitats on the species richness of birds and bats using a GLMM with a Poisson error distribution (the values for species richness were treated as count data) and a randomized effect of plot identity (Crawley, 2009). We then investigated the effect of tree microhabitat density on the community indices using ordinary least squares regressions with a normal error distribution. To examine whether tree microhabitat type affected the abundance of bird and bat species, we used the same approach as that used for the species level analyses: we modeled the effects of tree microhabitat type using separate models and then selected the best model based on the AIC values.

Finally, we compared the AIC values for the models that used tree microhabitats as explanatory variables with the models that used stand characteristics (i.e., basal area, stem density, stand height, diameter class distribution, deadwood volume, time since last cutting, number of habitats, and distance to the nearest road (Table 2)) as explanatory variables to determine whether tree microhabitat or stand characteristics best explained biodiversity. In this final step, we wanted to know whether tree microhabitats were better indicators than stand characteristics.

To look for nonlinear relationships, we plotted the results of the corresponding general additive mixed model (GAMM) with tree characteristics or stand characteristics as smoothed terms. GAMM are analogous to GLMM but are able to handle nonlinear relationships between the response and predictive variables (Guisan et al., 2002; Zuur et al., 2009). Therefore, we reported the numerical results of the GLMM and the model plots for the GAMM. All analyses were performed using R statistical software v. 2.12.2.

### 3. Results

#### 3.1. Effects of tree microhabitats on species abundance

Our sampling design allowed to inventory 52 bird species (1552 individuals) and 16 bat species (6662 bat calls).

We tested the effects of the density and diversity of tree microhabitats on the abundance of bird species found in at least 10 plots ( $n = 22$  bird species, 1439 individuals). We found that the abundance values for 9 bird species were positively correlated with tree microhabitat variables (Table 4). The bird species included all of the cavity-nesting species (i.e., Great Tit (*Parus major*), Blue Tit (*Cyanistes caeruleus*), Short-toed Treecreeper (*Certhia brachydactyla*), Eurasian Nuthatch (*Sitta europaea*), European Crested Tit (*Lophophanes cristatus*), Great Spotted Woodpecker (*Dendrocopos major*), and European Green Woodpecker (*Picus viridis*)), in addition to the Long-tailed Tit (*Aegithalos caudatus*) and the Common Firecrest (*Regulus ignicapillus*). Surprisingly, the abundance of each of the cavity-nesters was best explained by the diversity of tree microhabitats rather than by the density of tree or woodpecker cavities. Only the European Goldfinch (*Carduelis carduelis*), which breeds in open or partially wooded lowlands, showed a negative relationship with one type of microhabitat (upper cavities) (Table 4).

Then, we tested for relationships among tree microhabitats variables and bat species abundance for bat species that were found in at least 10 plots. We analyzed the abundance of 5 bat species and 5760 echolocation calls. The abundance of Nathusius's Pipistrelle (*Pipistrellus nathusii*) and the Common Pipistrelle (*Pipistrellus pipistrellus*) were explained by tree microhabitat variables (Table 4). Nathusius's Pipistrelle was positively affected by tree microhabitat diversity and the common pipistrelle was positively correlated with three microhabitat variables ( $\Delta AIC < 2$ ): density of *Cerambyx* cavities, diversity of tree microhabitats, and volume of canopy deadwood. We did not find any significant results for Savi's Pipistrelle (*Hypsugo savii*), the Lesser noctule (*Nyctalus leisleri*), or Kuhl's Pipistrelle (*Pipistrellus kuhlii*).

#### 3.2. Effects of tree microhabitats on bird and bat community indices

All bird community indicators were positively affected by tree microhabitat diversity, except the community specialization index (Table 5). The highest slope estimates were obtained with bird richness (Fig. 2) and bird diversity as the response variables.

Bat species richness was positively affected by the variables in several models ( $\Delta AIC < 2$ ), and we were unable to select the best model. The models included the following variables: diversity of tree microhabitats (estimate (SE) = 0.28 (0.13),  $p = 0.03$ ) (Fig. 3), *Cerambyx* cavities (estimate = 0.11 (0.01),  $p = 0.01$ ), microhabitat-bearing trees (estimate = 0.05 (0.02),  $p = 0.02$ ), total density of tree microhabitats (estimate = 0.008 (0.04),  $p = 0.04$ ), canopy deadwood (estimate = 0.04 (0.02),  $p = 0.02$ ), and conks of fungi (estimate = 0.08 (0.04),  $p = 0.04$ ). Species diversity was explained by *Cerambyx* cavities (Table 5). We found no significant effects on the mean forest specialization or the mean tree roost specialization (Table 5).

#### 3.3. Comparison of tree microhabitats and other stand characteristics

We compared the AIC for models using tree microhabitats as explanatory variables with the AIC for models using other stand characteristics to assess the indicator potential of tree microhabitats.

At the species level, tree microhabitat variables were better predictors than other stand characteristics for most bird species (8 out

**Table 4**  
Model selection (GLMM with Poisson distribution) by AIC for the species-level models. The model with the lowest AIC was selected, except when another model had an AIC less than 2 points higher than the selected model (in brackets). For each selected model, the GLMM parameters (i.e., estimate, standard error, and *p*-value) are shown.

Species		Selected tree microhabitats		Selected stand characteristics		Best predictor
<b>Birds</b>						
Common Chaffinch	<i>Fringilla coelebs</i>	ns	ns	ns	Ns	ns
Tit	<i>Parus major</i>	Microhab. div.	0.57 (0.14) <sup>***</sup>	Dwd volume	0.06 (0.01) <sup>***</sup>	Tree microhabitat
Common Blackbird	<i>Turdus merula</i>	ns	ns	ns	ns	ns
Western Bonelli's Warbler	<i>Phylloscopus bonelli</i>	ns	ns	ns	ns	ns
European Robin	<i>Erithacus rubecula</i>	ns	ns	ns	ns	ns
Eurasian Blackcap	<i>Sylvia atricapilla</i>	ns	ns	ns	ns	ns
Common Chiffchaff	<i>Phylloscopus collybita</i>	ns	ns	ns	ns	ns
Blue Tit	<i>Cyanistes caeruleus</i>	Microhab. div.	1.11 (0.24) <sup>***</sup>	Diam. distrib.	1.97 (0.45) <sup>***</sup>	Tree microhabitat
Short-toed Treecreeper	<i>Certhia brachydactyla</i>	Microhab. div.	1.69 (0.33) <sup>***</sup>	Dwd volume (diam. distrib.)	0.08 (0.02) <sup>***</sup>	Tree microhabitat
Eurasian Jay	<i>Garrulus glandarius</i>	ns	ns	ns	ns	ns
Common Nightingale	<i>Luscinia megarhynchos</i>	ns	ns	ns	ns	ns
Eurasian Nuthatch	<i>Sitta europaea</i>	Microhab. div.	1.27 (0.32) <sup>***</sup>	Diam. distrib.	2.79 (0.55) <sup>***</sup>	Tree microhabitat
European Crested Tit	<i>Lophophanes cristatus</i>	Microhab. div.	1.26 (0.37) <sup>***</sup>	Stand height	0.39 (0.09) <sup>***</sup>	Tree microhabitat
Great Spotted Woodpecker	<i>Dendrocopos major</i>	Microhab. div.	1.82 (0.54) <sup>***</sup>	Dwd volume (diam. distrib.)	0.09 (0.03) <sup>**</sup>	Tree microhabitat
Long-tailed Tit	<i>Aegithalos caudatus</i>	Upper cavities	0.17 (0.06) <sup>**</sup>	ns	ns	Tree microhabitat
European Goldfinch	<i>Carduelis carduelis</i>	Upper cavities	−0.33 (0.14) <sup>*</sup>	Time since l.c.	−0.80 (0.24) <sup>***</sup>	Stand characteristic
European Green Woodpecker	<i>Picus viridis</i>	Microhab. div.	1.58 (0.66) <sup>*</sup>	Diam. distrib.	2.5 (0.9) <sup>**</sup>	Tree microhabitat
European Serin	<i>Serinus serinus</i>	ns	ns	ns	ns	ns
Subalpine Warbler	<i>Sylvia cantillans</i>	ns	ns	Dwd volume (stand height)	−0.29 (0.14) <sup>*</sup>	Stand characteristic
Common Wood Pigeon	<i>Columba palumbus</i>	ns	ns	Diam. distrib.	3.92 (1.56) <sup>*</sup>	Stand characteristic
Common Firecrest	<i>Regulus ignicapillus</i>	Microhab. div.	1.73 (0.89) <sup>*</sup>	Stand height	0.62 (0.17) <sup>***</sup>	Stand characteristic
Linnet	<i>Carduelis cannabina</i>	ns	ns	Stand height	−0.85 (0.34) <sup>*</sup>	Stand characteristic
<b>Bats</b>						
Savi's Pipistrelle	<i>Hypsugo savii</i>	ns	ns	ns	ns	ns
Lesser noctule	<i>Nyctalus leisleri</i>	ns	ns	ns	ns	ns
Kuhl's Pipistrelle	<i>Pipistrellus kuhlii</i>	ns	ns	ns	ns	ns
Nathusius's pipistrelle	<i>Pipistrellus nathusii</i>	Microhab. div.	2.02 (0.86) <sup>*</sup>	Dwd volume	0.19 (0.1) <sup>*</sup>	Tree microhabitat
Common Pipistrelle	<i>Pipistrellus pipistrellus</i>	Cer. cav. (microhab. div., canopy dwd.)	1.58 (0.46) <sup>***</sup>	Diam. distrib.	2.92 (1.39) <sup>*</sup>	Tree microhabitat

Microhab. div. = diversity of tree microhabitats, Cer. cav. = *Cerambyx* cavities, Canopy dwd. = canopy deadwood, Dwd volume = deadwood volume, Diam. distrib. = diameter class distribution, Time since l.c. = time since last cutting.

ns = non-significant test.

<sup>\*</sup> *p* < 0.05.

<sup>\*\*</sup> *p* < 0.01.

<sup>\*\*\*</sup> *p* < 0.001.

**Table 5**

Model selection (GLMM with Poisson distribution) by AIC for the community-level models. The model with the lowest AIC was selected, except when another model had an AIC less than 2 points higher than the selected model (in brackets). For each selected model, the GLMM parameters (i.e., estimate, standard error, and *p*-value) are shown.

Community index	Selected tree microhabitats		Selected stand characteristics		Best predictor
<b>Birds</b>					
Species richness	Microhab. div.	0.32 (0.05)***	Diam. distrib.	0.62 (0.13)***	Tree microhabitat
Species diversity	Microhab. div.	0.28 (0.03)***	Diam. distrib.	0.58 (0.13)***	Tree microhabitat
Proportion of cavity nesters	Microhab. div.	0.15 (0.01)***	Diam. distrib.	0.35 (0.06)***	Tree microhabitat
Mean forest specialization	Microhab. div.	0.13 (0.03)***	Stand Height	0.07 (0.01)***	Stand characteristic
Community Trophic Index	Microhab. div.	0.05 (0.01)***	Diam. distrib.	0.12 (0.04)**	Tree m./Stand char.
<b>Bats</b>					
Species richness	Cer. cavities (microhab. div./m.b-t./tot. t-m./canopy dwd/fungi)	0.12 (0.05)*	Basal area	−0.05 (0.02)†	Tree m./Stand char.
Species diversity	Cer. cavities	0.05 (0.02)†	ns	ns	Tree microhabitat
Mean forest specialization	ns	ns	ns	ns	ns
Mean tree roost specialization	ns	ns	ns	ns	ns

Microhab. div. = diversity of tree microhabitats, Diam. distrib. = diameter class distribution, Cer. cav. = *Cerambyx* cavities, M.b-t. = microhabitat-bearing tree, Tot. t-m. = total tree microhabitats, Canopy dwd. = canopy deadwood. Tree m./Stand char. = Tree microhabitat and stand characteristic ( $AIC_{\text{Tree microhabitats}} - AIC_{\text{Stand characteristic}} < 2$ ). ns = non-significant test.

†  $p < 0.05$ .

\*\*  $p < 0.01$ .

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

of 13 species were best explained by tree microhabitats (Table 4). Among the 5 species that showed a response to other stand characteristics, 3 species found in semi-open areas (European Goldfinch (*C. carduelis*), Subalpine Warbler (*Sylvia cantillans*) and Linnet (*Carduelis cannabina*)) showed a negative response to increased time since last cutting, deadwood volume, and stand height, respectively (Table 4). Among bats, the abundance of Nathusius's Pipistrelle was equally affected ( $\Delta AIC < 2$ ) by tree microhabitat variables (i.e., diversity of tree microhabitats) and other stand characteristics (i.e., deadwood volume). The abundance of the Common Pipistrelle was best explained by tree microhabitat variables (i.e., *Cerambyx* cavities).

At the community level, tree microhabitat variables were the best indicators for both bird and bat species (Table 5). For birds, the species richness, species diversity, and proportion of cavity-nesters were better explained by tree microhabitat variables (i.e., tree microhabitat diversity) than by other stand characteristics. The CTI was equally influenced by tree microhabitat variables (i.e., diversity of tree microhabitats) and other stand characteristics (i.e., diameter class distribution) ( $\Delta AIC < 2$ ). Only mean forest specialization was best explained by stand characteristics (i.e., stand height). For bats, the species richness was equally influenced by several tree microhabitat variables and one stand characteristic (i.e., basal area) ( $\Delta AIC < 2$ ). The species diversity was explained by tree microhabitat variables (i.e., density of *Cerambyx* cavities).

## 4. Discussion

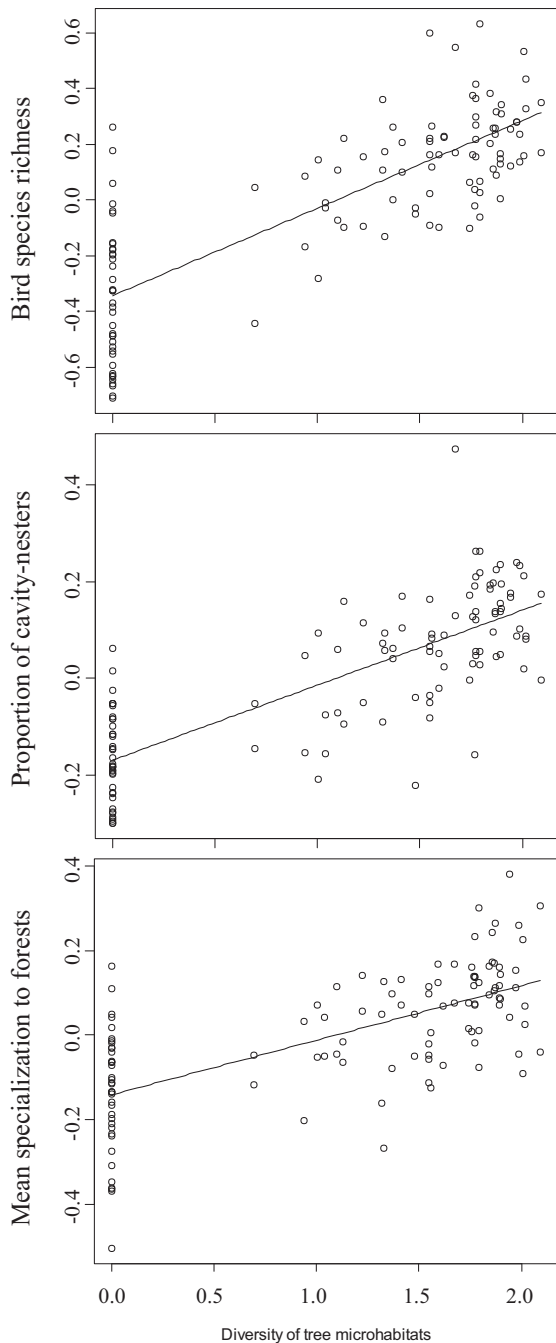
### 4.1. Effects of tree microhabitats on species abundance

Several studies have shown the importance of specific microhabitats for certain forest species, such as the amount of deadwood for woodpecker species (Bütler et al., 2004; Roberge et al., 2008), tree cavities for bird cavity-nesters (Martin et al., 2004), loose bark for the nesting or the resting places of bats (Vanhof and Gwilliam, 2007), or even the presence of fungi as a food resource for saproxylic beetles (Johansson et al., 2006). However, to our knowledge, this study is the first to correlate biodiversity (at the species and community levels) with in-depth forest inventory data on tree microhabitats. By comparing the effects of each tree microhabitat on species abundance, we found that diversity of microhabitat (a combination of the quantity and relative abundance of tree microhabitat types) was the most important factor for explaining bird and bat species abundance.

Among the birds in this study ( $n = 22$  species), 10 bird species, including all cavity-nesters in the study ( $n = 7$  species), showed a significant relationship with tree microhabitat. Surprisingly, our models showed that the cavity-nesting species were mainly affected by diversity of tree microhabitat rather than single tree cavities. However, after removing tree microhabitat diversity from the models, we found that upper cavities and woodpecker cavities best explained the abundance of cavity-nesting species (see the AIC values in Appendix G). This result is consistent with previous observations regarding the role of tree cavities (Aitken and Martin, 2007; Cockle et al., 2011; Martin et al., 2004). According to our results, cavities located high in the tree (upper cavities and woodpecker cavities) are important for cavity-nesters but the major factor determining the abundance of these species is the diversity of tree microhabitats.

Among the bats in this study ( $n = 5$  species), we found that Nathusius's pipistrelle (*P. nathusii*) and the Common Pipistrelle (*P. pipistrellus*) were positively affected by diversity of tree microhabitats (the Common Pipistrelle was also affected by *Cerambyx* cavities and canopy deadwood (Table 4)). Bat call recordings are often used to detect habitats that have available insects but that may be located several kilometers away from the bat roosts (Henry et al., 2002; Robinson and Stebbings, 1997). In forests, the insects themselves are associated with a variety of habitats, including tree microhabitats (Dietz et al., 2007; Gorresen et al., 2008; Jacobs et al., 2009). Thus, we expect that forest stands with a high diversity of tree microhabitats could be home to a more diverse, larger community of insects than those with a low diversity of tree microhabitats, although this hypothesis needs to be tested experimentally.

Tree microhabitat diversity was the most important factor explaining the abundance of many bird and bat species. We offer several explanations for these results. First, none of the bird and bat species in this study were strict specialists associated with a single tree microhabitat. Contrary to forest specialists that show very specific habitat interactions (e.g., plant–pollinator interactions involving one plant and one pollinator), European birds and bats use a wide array of tree microhabitats (Bull et al., 1997; Gibbons and Lindenmayer, 2002; Jones et al., 2009). For example, cavity-nesting birds use woodpecker cavities to nest but feed in other tree microhabitats (e.g., some birds feed on insects living in canopy deadwood or behind loose bark). Second, insectivorous birds and bats (all bats were insectivorous in this study), occupy high trophic levels. Therefore, their abundance in a given habitat depends on the quality and abundance of organisms at lower trophic levels (Gunn and Hagan III, 2000; Jones et al., 2009). A high diversity of tree microhabitats

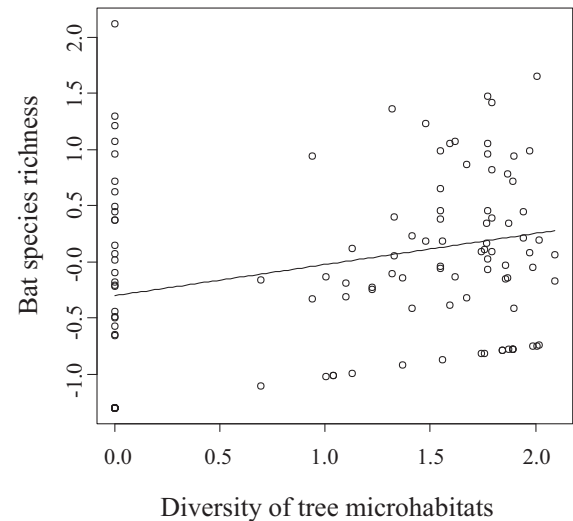


**Fig. 2.** Relationship between diversity of tree microhabitats and bird community indices: (a) species richness, (b) proportion of cavity-nesters, and (c) mean specialization of birds. Smoothed curves were obtained with generalized additive mixed models (GAMM) after accounting for spatial dependence among samples.

results in a variety of ecological niches and may play an important role in supporting forest food webs.

#### 4.2. Effects of tree microhabitats on bird and bat communities

Bird species richness and bird diversity were positively influenced by the diversity of tree microhabitats. These results are consistent with the niche theory, suggesting that a higher diversity of tree microhabitats allows for coexistence between species by increasing the spatial complexity of resources (Leibold, 1995; Pereira et al., 2012). However, in our study, bird species richness



**Fig. 3.** Relationship between diversity of tree microhabitats and bat species richness. Smoothed curves were obtained with generalized additive mixed models (GAMM) after accounting for spatial dependence among samples.

and bird diversity were not influenced by the number of forest habitats. Otherwise, all plots were located in wide forest landscapes hence we could not assess the effect of the heterogeneity at the landscape level. An interesting perspective would be to attempt to rank the importance of diversity at different spatial scales (from tree microhabitat to landscape level). Exploring these relationships is important to understand at which spatial scales birds and bats are the most sensitive to environmental changes, however this question would require another sampling design with plots distributed in different landscape contexts. The mean forest habitat specialization and the CTI were also positively affected by tree microhabitat diversity (Table 5). The increase in mean forest habitat specialization with higher tree microhabitat diversity could be explained by the presence of certain tree microhabitat types and associated attributes (e.g., deadwood, large trees) that are used by forest specialists (Tucker and Evans, 1997). Indeed, tree microhabitats mostly occur on large trees and snags (Michel and Winter, 2009; Regnery et al., 2013; Vuidot et al., 2011) that often have old-growth attributes or are found in the stand development stages typically sought after by bird forest specialists (Moning and Müller, 2008; Roberge et al., 2008). The increasing CTI revealed that stands with a high diversity of tree microhabitats have a higher mean trophic level compared to stands with a low diversity of tree microhabitats. In this study, the increase in the CTI was due to an increase in the proportion of insectivorous birds (only one raptor was identified among the 1552 recorded bird individuals). This result suggests that food webs are more complex in stands with a high diversity of tree microhabitats.

Bat richness and bat diversity were positively affected by the density of *Cerambyx* cavities, though bat richness was also influenced by the presence of other tree microhabitats and basal area (Table 5). *Cerambyx* cavities occur on sick, old or even dead trees (Buse et al., 2007) that can be home to many insect prey species. Another possible effect is the use of *Cerambyx* cavities by bats as tree roosts. Several observations of bat species using *Cerambyx* cavities as tree roosts have been reported from the French Mediterranean region (Pénicaud and Le Reste, 2011; Emmanuel Cosson, personal communication for *Pipistrellus* sp. and *N. leisleri*) but quantitative relationships between these microhabitats and their occupation by bats have not been performed until now.



#### 4.3. Comparison of tree microhabitats and other stand characteristics

Tree microhabitat variables were often better predictors of the abundance of bird and bat species when compared to other stand characteristics (Tables 4 and 5). The abundance of most bird species was better explained by tree microhabitat type than by other stand characteristics. However, 5 species were more sensitive to stand attributes than to tree microhabitat type (Table 4). Apart from the Common Firecrest, these species (European Goldfinch, Subalpine Warbler, Common Wood Pigeon, and Linnet) were non-specialists with regard to forest habitat and were either partial or total seed-eaters; therefore, their dependency on tree microhabitats was expected to be lower than that of specialist species. At the community level, birds and bats were most strongly affected by tree microhabitat type. Tree microhabitats are directly related to the ecological niches of forest species and play a key role in species' life-cycles compared to other stand characteristics.

#### 4.4. Implications for biodiversity assessment in forests

Understanding and measuring the factors that explain biodiversity in forest ecosystems remain challenging for researchers and practitioners. Surprisingly, the use of tree microhabitat inventory data to identify proxy variables for birds and bats in managed forests had never been tested until now (Michel and Winter, 2009; Regnery et al., 2013; Vuidot et al., 2011). In this study, we showed that variation in the density of tree microhabitats (more specifically, variation in microhabitat diversity) was a major factor that explains the abundance and community composition of birds and bats. These results have implications for biodiversity conservation for threatened species such as cavity-nesters (Monterrubio-Ricoa and Escalante-Pliegob, 2006) and forest specialists, whose populations are currently declining at the global scale (Gregory et al., 2007), and for common species and communities that play major roles in ecosystem functioning (Gaston, 2011). Our results also raise discussion about future biodiversity assessments in forests.

Currently, assessments of biodiversity in forests are based on species counts. This approach allows assessing species populations and conservation statuses, especially for threatened species for which precise counts may be required. However, species sampling methods can hardly be extended to all species in an ecosystem because they remain labor intensive and time-consuming (Winter and Möller, 2008). They may also be subject to many biases (e.g., identification limits, observer effects, economic constraints on sampling large areas) (Stahlschmidt and Brühl, 2012; Renwick et al., 2012). As a result, there is an increasing demand from policy makers and managers (e.g., ecologists conducting environmental impact assessments) to improve biodiversity assessments by incorporating relevant biodiversity indicators that are reliable and rapidly assessed. We suggest using tree microhabitats in a complementary manner to species sampling methods since they provide both an integrative and a perennial measurement of ecological potentialities (tree microhabitats do not need to be re-measured every year). The protocol used to describe tree microhabitats in this study has numerous advantages. First, it provides a specific description of tree microhabitat types, ensuring that the field methods are reproducible (see the description in Table 1). Second, the measurements do not depend on biological experts for species determination; in other words, anyone can perform an inventory of tree microhabitats. Third, tree microhabitat characteristics are rapidly measured (approximately 8 ha/h were performed in our study, including the time of detecting microhabitat-bearing trees and the description of tree microhabitats – 3 min per tree). Finally, measuring tree microhabitat characteristics is less seasonally dependent than performing taxonomic identifications. Tree microhabitats can be

identified throughout the year, but preferably in winter when the trees have lost their leaves. Performing inventories during winter could be an advantage for ecologists by helping alleviate pressure to complete other field inventories during spring and summer.

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#### Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolind.2013.05.003>.

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