# Species, live status, and diameter are important tree features for diversity and abundance of tree microhabitats in subnatural montane beech–fir forests1

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# Species, live status, and diameter are important tree features for diversity and abundance of tree microhabitats in subnatural montane beech–fir forests[1]

## Laurent Larrieu and Alain Cabanettes

**Abstract:** Because quantitative data on the distribution of whole microhabitat sets are still lacking to indirectly assess taxonomic biodiversity in forests, we studied the distribution of seven key microhabitat types in 10 montane European beech (*Fagus sylvatica* L.) – silver fir (*Abies alba* Mill.) forests (Pyrénées, France) that had not been harvested for several decades. We examined 2105 live trees and 526 snags. Frequencies of cavities and dendrothelms were significantly higher on live beech than on fir. Sap runs were strictly found on live fir. Frequencies of cracks and saproxylic fungi were significantly higher on snags than on live trees. Seventy percent of live beeches but only 18% of firs carried one or more microhabitats. For both beech and fir and for each microhabitat type, we found, using the recursive partitioning method, one to three diameter thresholds that each corresponded to a significant change in the probability of microhabitat presence. When considering the whole microhabitat set, the most significant diameter thresholds were 42, 60, 73, and 89 cm for beech and 99 cm for fir. We suggest that forest managers conserve (*i*) mixed stands and (*ii*) beech with a diameter at breast height >90 cm and fir >100 cm. These rules should be adapted for each forest ecosystem.

**Résumé :** Étant donné qu'il n'y a pas encore de données quantitatives sur la distribution d'ensembles complets de microhabitats qui permettraient d'obtenir une évaluation indirecte de la biodiversité dans les forêts, nous avons étudié la distribution de sept types clés de microhabitats dans 10 forêts montagnardes (Pyrénées, France) de hêtre (*Fagus sylvatica* L.) et de sapin (*Abies alba* Mill.) qui n'ont pas été récoltées depuis plusieurs décennies. Nous avons examiné 2 105 arbres vivants et 526 chicots. La fréquence des cavités et des dendrotelmes était significativement plus élevée sur les tiges vivantes de hêtre que sur le sapin. Des écoulements de sève ont été observés uniquement sur les tiges vivantes de sapin. La fréquence des fentes et des champignons saproxyliques était significativement plus élevée sur les chicots que sur les arbres vivants. Il y avait au moins un microhabitat sur 70% des hêtres mais sur seulement 18% des sapins. Tant sur le hêtre que sur le sapin et pour chaque type de microhabitat, nous avons trouvé, à l'aide d'une méthode de partitionnement récursif, entre un et trois diamètres seuils. Chaque diamètre seuil correspondait à un changement significatif dans la probabilité de la présence d'un microhabitat. Lorsqu'on tient compte de l'ensemble complet des microhabitats, les diamètres seuils les plus importants sont 42, 60, 73 et 89 cm chez le hêtre et 99 cm chez le sapin. Nous suggérons que les gestionnaires forestiers conservent (*i*) des peuplements mixtes ainsi que (*ii*) les hêtres et les sapins dont le diamètre à hauteur de poitrine est respectivement plus grand que 90 et 100 cm. Ces règles devraient être adaptées pour chaque écosystème forestier.

[Traduit par la Rédaction]

## Introduction

Using only a few species to assess taxonomic biodiversity in forest ecosystems is not satisfactory and it is rather preferable to use whole taxonomic groups (Lindenmayer and Franklin 2002). Further, direct bioindicator records are very expensive and require taxonomic specialists (Puumalainen et al. 2003). Most importantly, the relationships between indicator taxa and total biodiversity are not yet well established (Lindenmayer et al. 2000; McElhinny et al. 2005). Therefore, forest managers need alternative approaches to assess biodiversity in forests. Lindenmayer et al. (2000) suggested using structure-based variables as indirect biodiversity indicators. Indicators based on key structural factors have been shown to be a practical and efficient way to ensure that taxonomic biodiversity is taken into account in current forest management (Larsson 2001). Similarly, Tews et al. (2004) proposed using "crucial keystone structures", such as dead wood, for biodiversity management. Lindenmayer et al. (2006) pub-

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lished a checklist of strategies to guide forest biodiversity conservation that encompasses the maintenance of key elements of stand structural complexity.

Tree microhabitats (such as cavities or cracks) are key components of forest stands (Michel and Winter 2009) because they host a wide taxonomic biodiversity (Speight 1989). So, they are relevant and practical proxies to assess taxonomic biodiversity at the stand scale (Winter and Möller 2008). Several authors have demonstrated the important role of very large trees (Ranius and Jansson 2000; Grove 2002; Branquart et al. 2005; Bauhus et al. 2009), tree species (Gosselin and Larroussinie 2004), and snags (Jonsell and Weslien 2003) on taxonomic biodiversity. However, in most types of forest, few data are available regarding the distribution of tree microhabitats in natural stands and the links between tree species, diameter, status (live tree or snag), and microhabitat occurrence.

To improve our knowledge of the distribution of tree microhabitats in natural forests, and particularly to better understand the role of tree species and tree diameter on microhabitat occurrence, we observed tree microhabitats in montane European beech (*Fagus sylvatica* L.) – silver fir (*Abies alba* Mill.) forests that had not been logged for at least 60 years. Beech–fir forest is a common forest community, present in most of the European mountain ranges, and has a great economic and ecological importance. It is also a mixed forest where biocenoses partially differ between broadleaved trees and conifers (Nascimbene et al. 2009).

We chose a set of seven microhabitat types that seem to be very important for taxonomic diversity in forests because the associated taxonomic groups are numerous and varied or very specific: empty cavities, cavities with mould, sporophores of saproxylic fungi, dendrothelms (water-filled holes in the wood), sap runs, missing bark, and cracks. Empty cavities are used for protection against bad weather conditions or predators by more than 25% of vertebrate species in northeastern North American forests (DeGraaf and Shigo 1985). Moreover, in France, 41% of forest birds are cavity-dwelling species (Blondel 2005). Cavities with mould are inhabited by arthropods (Ranius 2002) and create favorable conditions for epiphyte species of conservation concern (Fritz and Heilmann-Clausen 2010). Sporophores of saproxylic fungi support a varied insect fauna (Dajoz 2007), especially when they are tough (polypores s.l.) or pulpy (e.g., oyster fungi). Some parasitic fungi also use saproxylic fungi as a resource (Lisiewska 1992). Dendrothelm-dwelling species are not numerous (Dajoz 2007) but very specialized (Kitching 1971). Sap runs host syrphid larvae (Speight et al. 2010) and are used by the adults of several Coleoptera species (Alexander 2002). Cracks are important microhabitats for spiders (Stanska et al. 2010), birds (Cramp 1980), flat bugs (Heiss and Pericart 2007), and bats (Pénicaud 2000). Cavities, cracks, and missing bark are indicators of natural forests (Michel and Winter 2009; Remm and Lõhmus 2011).

This paper aims at (*i*) evaluating the role in terms of supply of microhabitats of the tree species that compose beech–fir forests independently of their relative abundance and (*ii*) identifying critical diameter thresholds for both microhabitat abundance and diversity. Then, in the context of sustainable management practices, we suggest some practical recommen-

dations and a management strategy to conserve microhabitats.

## Materials and methods

### Studied forests and sampling design

The 10 studied forests (Table 1) are situated in the central Pyrénées mountain range (Fig. 1) and have not been logged for more than 60–100 years. They are natural habitats of beech–fir forest (Bardat et al. 2004). However, stands host a very variable proportion of fir, which is directly linked to historic human intervention that favored beech at the expense of fir (Métailié 2001). For the analysis, we pooled all of the studied forests because local conditions of fertility were not markedly different and we did not sample forests growing in extreme conditions of infertility (e.g., site with PODZOSOL). Observations were carried out in 2008 and 2009 on a sample of 62 plots, 2105 live trees, and 526 snags (Table 1). Although the leaf canopy may hinder observations, all of the plots were set up in summer because these sites are covered by snow for a large part of the year. Because of the presence of leaves, we expected an underestimation of the number of microhabitats on beech and on the other broadleaved species. For the evergreen species such as fir or common yew (*Taxus baccata* L.), data taken in the vegetation period or in winter are more easily comparable.

### Measurements and observation of microhabitats

Plots were circular and of variable sizes set up using the No. 1 strip (return angle of 1/50) of a Bitterlich relascope (Pardé and Bouchon 1988). This device uses a constant angle. The measurement errors due to terrain slope are automatically corrected by the relascope, which is very practical in the mountains. The use of a relascope allows a high sampling rate of large trees that are richer in microhabitats (Winter and Möller 2008; Larrieu et al. 2011). Plot locations were positioned approximately on a map before the field phase in relation to accessibility. Then, the precise locations of plots were established in relation to topographical constraints (such as cliffs) and plot centres were always a minimum of 100 m apart. Trees were observed individually. We noted the status (live tree or snag), identified the tree to species level, and measured the diameter on the outside of the bark at breast height (dbh) to the nearest centimetre when the diameter exceeded 5 cm. We carefully examined the trunk from the ground to the top of the tree to note microhabitats hosted on the visible part of the trunk both beneath and within the tree crown. We recorded a set of seven microhabitats types as follows. (*i*) "Empty" cavities with an entrance above 3 cm in width. We did not use a device such as a camera mounted on a telescopic pole to ensure the cavity volume. Therefore, we pooled in this category all woodpecker breeding holes, holes made by woodpeckers when feeding and deep enough to host a vertebrate, deep cavities formed between roots, and also natural cavities low enough on the tree to enable verification that they were empty and that they were not at a stage where mould could develop. (*ii*) Cavities with mould. We pooled in this category the other natural cavities and cavities with mould with an entrance above 3 cm in width and also missing bark patches with an area above 100 cm$^2$ with wood in a decay stage of more than 3 (in reference to a scale with

**Table 1.** Main characteristics of the studied European beech (*Fagus sylvatica*) – silver fir (*Abies alba*) forests and sampling design.

| Forest | Vegetation level | Dominant tree species | History | Studied area per forest (ha) | No. of plots | No. of observed trees | No. of observed snags | Diameter at breast height (cm) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | Live beeches | Beech snags | Live firs | Fir snags |
| Plagnech de ton | Lower montane | Beech and fir | Not logged since 1900 | 23 | 10 | 332 | 93 | 15.9 | 11.1 | 8.0 | 22.3 |
| | | | | | | | | 62.9 | 53.4 | 44.4 | 70.4 |
| | | | | | | | | 127.3 | 95.5 | 124.1 | 109.8 |
| Reouère | Lower montane | Beech | Old pasture woodland not logged for more than 110 years | 43 | 8 | 295 | 40 | 11.1 | 8.0 | | |
| | | | | | | | | 67.0 | 53.1 | | |
| | | | | | | | | 152.8 | 162.3 | | |
| Auribareille | Lower montane | Fir | Never logged | 12 | 2 | 61 | 14 | 15.9 | 63.7 | 22.3 | 19.1 |
| | | | | | | | | 50.9 | 63.7 | 70.6 | 64.0 |
| | | | | | | | | 78.0 | 63.7 | 130.5 | 89.1 |
| Genie loungue | Lower montane | Beech | Not logged since 1900 | 16 | 5 | 122 | 14 | 21.6 | 11.8 | 47.4 | |
| | | | | | | | | 54.4 | 25.6 | 47.4 | |
| | | | | | | | | 114.6 | 33.1 | 47.4 | |
| Bugatet | Upper montane/subalpine | Fir | Not logged since 1908 | 18 | 5 | 185 | 36 | | | 7.0 | 22.9 |
| | | | | | | | | | | 49.2 | 68.0 |
| | | | | | | | | | | 111.4 | 140.1 |
| Barrada | Upper montane | Fir | Only logged once (1953) by selective logging | 13 | 5 | 221 | 63 | 11.1 | | 11.1 | 19.1 |
| | | | | | | | | 20.3 | | 58.6 | 61.2 |
| | | | | | | | | 25.5 | | 171.9 | 125.7 |
| Bosc nou | Upper montane/subalpine | Beech and fir | Never logged | 13 | 5 | 178 | 55 | 29.0 | | 9.5 | 21.6 |
| | | | | | | | | 36.1 | | 57.5 | 59.7 |
| | | | | | | | | 42.7 | | 114.6 | 101.9 |
| Es tucoulets | Upper montane | Beech and fir | Not logged since 1900 | 34 | 9 | 265 | 82 | 24.8 | 19.1 | 9.5 | 15.9 |
| | | | | | | | | 31.8 | 19.1 | 53.7 | 60.9 |
| | | | | | | | | 38.8 | 19.1 | 130.5 | 154.4 |
| Es piches | Upper montane | Beech and fir | Not logged since 1900 | 17 | 5 | 153 | 20 | 15.9 | 31.8 | 11.1 | 12.7 |
| | | | | | | | | 56.2 | 35.0 | 56.8 | 62.5 |
| | | | | | | | | 95.5 | 38.2 | 135.3 | 124.1 |
| Ouderou | Upper montane | Fir | Old pasture woodland not logged for more than 100 years | 25 | 8 | 293 | 109 | 14.3 | 12.7 | 10.2 | 13.0 |
| | | | | | | | | 36.0 | 28.2 | 65.9 | 65.4 |
| | | | | | | | | 78.0 | 60.5 | 135.9 | 133.7 |

**Note:** For diameters at breast height, the three values are successively the minimum, mean, and maximum.

**Fig. 1.** The 10 studied forests are situated on the northern slopes of the Pyrénées mountain range (the southwest of France).
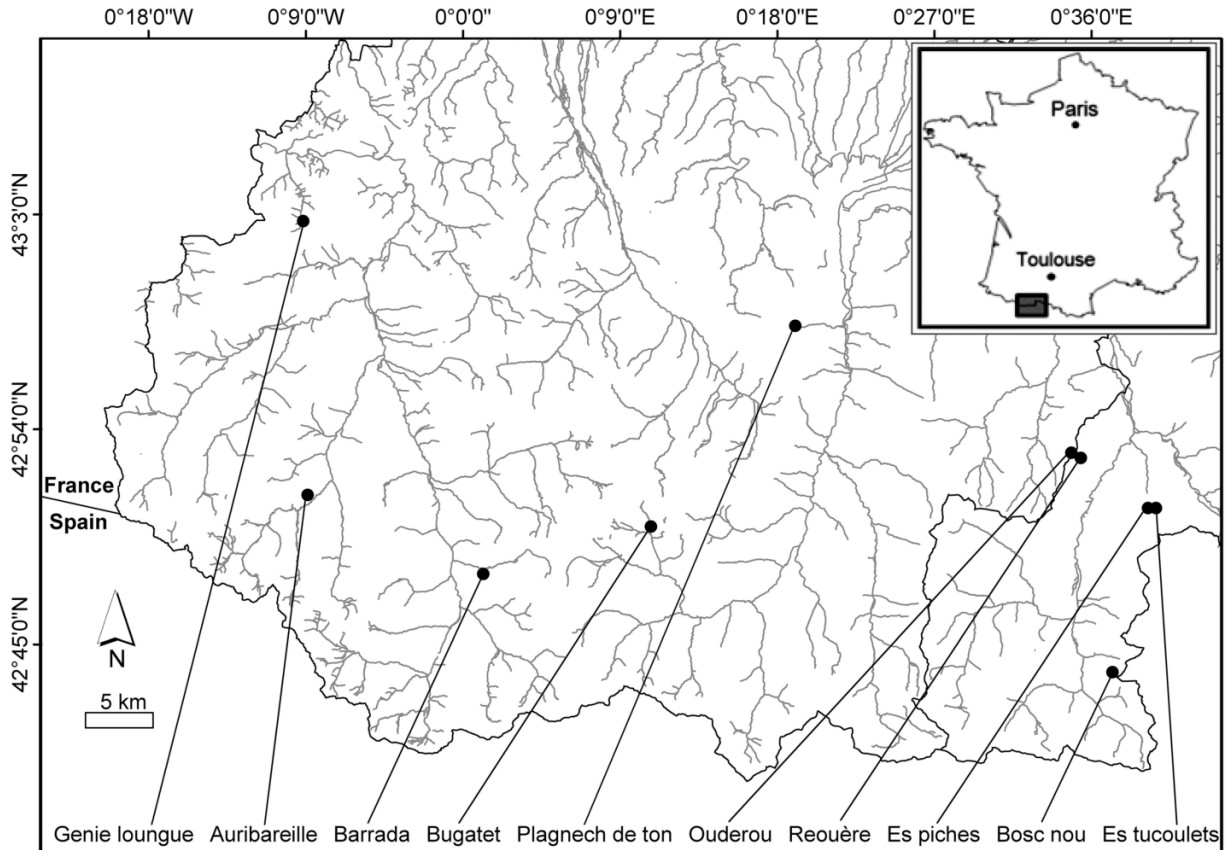


five steps: see Table S1[2] (describes in detail wood decay stages)). (*iii*) Sporophores of saproxylic fungi without taxonomic identification. We noted only tough fungi (polypores s.l.) or pulpy fungi (e.g., *Pleurotus ostreatus* (Jacq.) P. Kumm. 1871). (*iv*) Dendrothelms, when the entrance was more than 3 cm in width. In the dry period, observation of traces of water flow on the trunk allowed the diagnostic of inaccessible dendrothelms. (*v*) Sap runs with a minimal length of 10 cm. (*vi*) Missing bark (i.e., wood patches with bark loss) of at least 100 cm[2], with wood in a decay stage of less than 2. (*vii*) Cracks in the tree trunk with a width of 1–5 cm and situated over 1 m above the ground or bark in the process of peeling and that formed a shelter. Their importance for several species of bats (Meschede and Heller 2003) was the justification for pooling these two microhabitats and using these thresholds.

On each tree, we counted every microhabitat type as often as it appeared, except in the case of fungi, which were only noted as presence–absence.

Beech (658 live trees observed) and fir (1310 live trees observed) were the main tree species but we also observed 137 live trees of more than 10 secondary species (European mountain-ash (*Sorbus aucuparia* L.), European white birch (*Betula pendula* Roth), downy birch (*Betula pubescens* Ehrh.), European ash (*Fraxinus excelsior* L.), sweet cherry (*Prunus avium* (L.) L.), field maple (*Acer campestre* L.), Norway ample (*Acer platanoides* L.), common yew, largeleaf linden (*Tilia platyphyllos* Scop.), and *Salix* spp.). Secondary

species were pooled in the analysis because of their low number. Stand maturity allowed us to explore a large diameter gradient: 6–172 cm for fir, 11–153 cm for beech, and 5–95 cm for other species.

## Calculations and statistical procedures

The theoretical tree frequency per hectare was calculated by allocating the coefficient *N*, related to its diameter (*D*), to every tree observed in the relascope sampling (Pardé and Bouchon 1988):

$$ND = \pi 10^8 [\arctan(1/50)/\pi D]^2$$

where "arctan" is the trigonometrical "arctangent" function.

All statistical calculations were done using R software (R development Core Team 2007).

Basic data were measured and analyzed at the level of the individual tree: tree species, tree diameter, type, and number of microhabitats. However, the effect of tree species was tested using the average data per plot and per species. The role of the tree species in the supply of microhabitats was evaluated independently of their relative abundance.

Comparisons of frequencies, per species, of the trees that bear microhabitats and of frequencies of microhabitat co-occurrences per species were carried out using the $\chi^2$ test (Snedecor and Cochran 1971).

The hypothesis of independence between the three species categories (i.e., beech, fir, and the third that pooled all secon-

**Table 2.** Tree species (European beech (*Fagus sylvatica*), silver fir (*Abies alba*), and others) effect on microhabitat frequency: results for the comparison tests on live trees and snags (significant results in bold).

| Microhabitat | Tree status | All-categories comparison (*p*) | Pairwise comparison | *p* |
|---|---|---|---|---|
| Cavities with mould | Live trees | **<0.001** | **Beech/others** | **<0.001** |
| | | | fir/others | 0.841 |
| | | | **Fir/beech** | **<0.001** |
| Empty cavities | Live trees | **0.005** | **Beech/others** | **0.005** |
| | | | Fir/others | 0.503 |
| | | | Fir/beech | 0.161 |
| Saproxylic fungi | Live trees | 0.424 | Beech/others | 0.424 |
| | | | Fir/others | 0.779 |
| | | | Fir/beech | 0.871 |
| Dendrothelms | Live trees | **<0.001** | **Beech/others** | **<0.001** |
| | | | Fir/others | 0.978 |
| | | | **Fir/beech** | **<0.001** |
| Missing bark | Live trees | 0.988 | Beech/others | 0.976 |
| | | | Fir/others | 0.999 |
| | | | Fir/beech | 0.999 |
| Cracks | Live trees | 0.212 | Beech/others | 0.211 |
| | | | Fir/others | 0.688 |
| | | | Fir/beech | 0.733 |
| Sap runs | Live trees | <0.001 | Beech/others | 0.711 |
| | | | **Fir/others** | **0.002** |
| | | | **Fir/beech** | **<0.001** |
| Total | Live trees | **<0.001** | Beech/others | 0.366 |
| | | | **Fir/others** | **0.011** |
| | | | **Fir/beech** | **<0.001** |
| Empty cavities | Snags | **0.005** | Beech/others | 0.512 |
| | | | **Fir/others** | **0.001** |
| | | | **Fir/beech** | **0.005** |
| Saproxylic fungi | Snags | 0.48 | Beech/others | 0.569 |
| | | | Fir/others | 0.483 |
| | | | Fir/beech | 0.902 |
| Dendrothelms | Snags | 0.21 | Beech/others | 0.153 |
| | | | Fir/others | 0.633 |
| | | | Fir/beech | 1.000 |
| Cracks | Snags | **0.007** | Beech/others | 0.42 |
| | | | **Fir/others** | **0.007** |
| | | | **Fir/beech** | **0.04** |
| Total | Snags | **0.022** | Beech/others | 0.593 |
| | | | Fir/others | 0.064 |
| | | | **Fir/beech** | **0.022** |

**Note**: We distinguished three categories of tree species: beech alone, fir alone, and other tree species pooled. Values are *p* values from a $\chi^2$ test.

dary species) and the response variable (frequency of one or all microhabitats or frequency of microhabitat type) was assessed using multiple testing of resampled data (Hothorn et al. 2006). The response variable was analyzed as a rank variable. The *p* value obtained by this procedure was adjusted for multiple comparisons using a step-down max-T approach. In addition, for each response variable, a post hoc test (Tukey all-pair comparisons) was applied to assess the differences between each pair of categories. The corresponding *p* values were adjusted for all comparisons performed here. This analysis procedure is based on implementation of the above procedures in the add-on package "coin" (Hothorn and Hornik 2005).

The relation between microhabitat frequency and tree diameter was analyzed using tree-based regression and classification models. We tested the hypothesis that there is a threshold-based relation between the number of microhabitats and dbh because we found this kind of relation in a previous analysis of comparable data (Larrieu et al. 2011). These threshold values were calculated by recursive partitioning (Hothorn and Zeileis 2008). This approach allows simultaneous identification of a threshold and assessment of its significance by means of a statistical test procedure. The thresholds are derived from estimates of break points by means of maximally selected two-sample statistics. Their validity is judged by multiple test procedures. Once the data set is divided into

**Fig. 2.** Microhabitat frequency distributions split by species for live trees (European beech (*Fagus sylvatica*), silver fir (*Abies alba*), and others) (2.1) and snags (2.2) represented as boxplots. Each bar corresponds to the two interquartiles Q1 and Q3 of the distribution. The horizontal central line is the median. The length of the whiskers (broken lines) is $1.5 \times (Q3 - Q1)$. Outlying points are not represented. Different letters indicate significant differences between species. The deviations in the boxplots are based on average plot data.
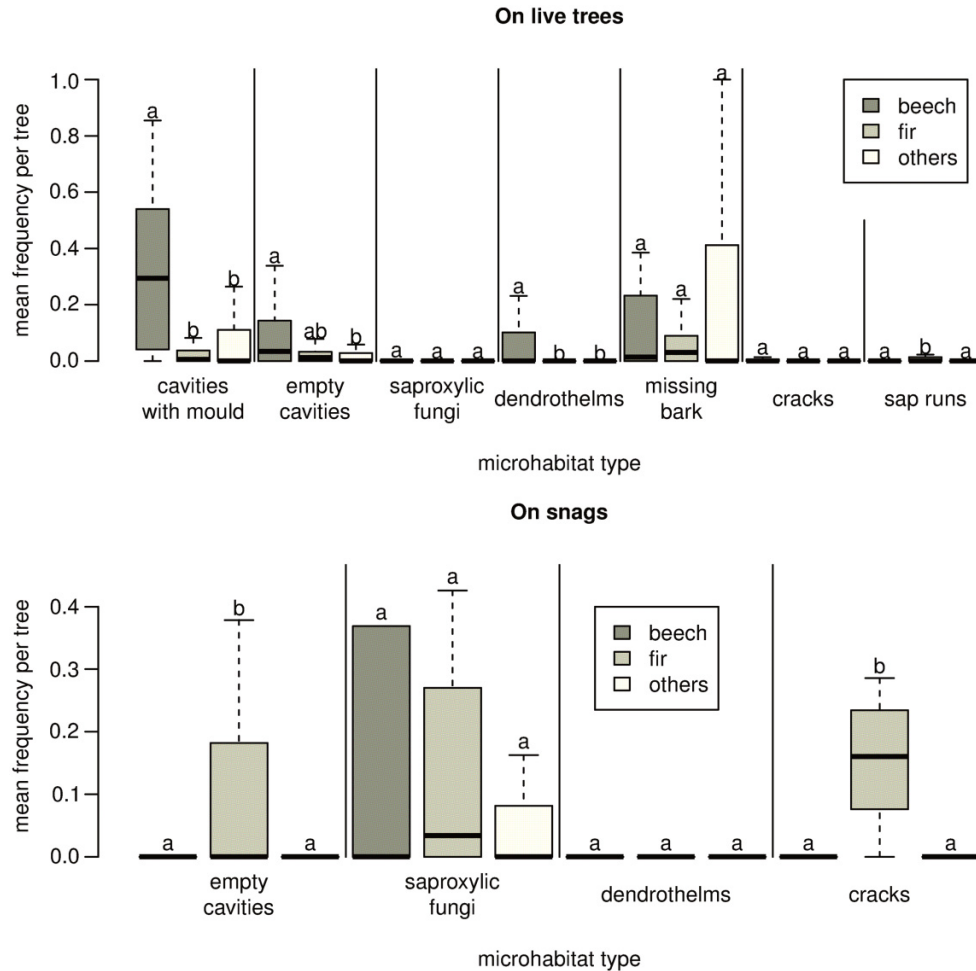
two subsets by the threshold with the highest explanatory power, each subset is evaluated for additional thresholds. This method provides a decision tree with *p* values for one or more critical thresholds. Based on 10 000 bootstrap samples, a confidence interval (at 80%) was calculated for all thresholds. The calculations were performed on "presence–absence" data using the add-on package "party" (Hothorn and Hornik 2006).

Furthermore, to make an explicit link with forest management practices, we also discuss our results by using "management diameter thresholds" that separate diameter categories used by all managers in French forestry to describe and manage stands. These management diameter thresholds are 20 cm $\leq$ small tree $\leq$ 25 cm, medium tree $\leq$50 cm, large tree $\leq$70 cm, and very large tree >70 cm (Bastien and Gauberville 2011).

## Results

### Tree species effect (live trees and snags)

***Tree species affects the occurrence of different microhabitat types and the total number of microhabitats per tree, independently of the relative densities of the different tree species***

The species of the live trees significantly affected the frequency of empty cavities, cavities with mould, dendrothelms, and sap runs (Table 2; Fig. 2). The first three microhabitats were mostly associated with beech, whereas sap runs were exclusively associated with fir. Secondary species played an intermediary role. The frequencies of saproxylic fungi, missing bark, and cracks were not related to tree species. On snags, in contrast, fir carried a higher quantity of empty cav-

**Fig. 3.** Total microhabitat distributions split by tree status and species (European beech (*Fagus sylvatica*), silver fir (*Abies alba*), and others). Each bar corresponds to the two interquartiles Q1 and Q3 of the distribution. The horizontal central line is the median. The length of the whiskers (broken lines) is 1.5 × (Q3 – Q1). Outlying points are not represented. Letters indicate if differences between species are statistically significant or not.
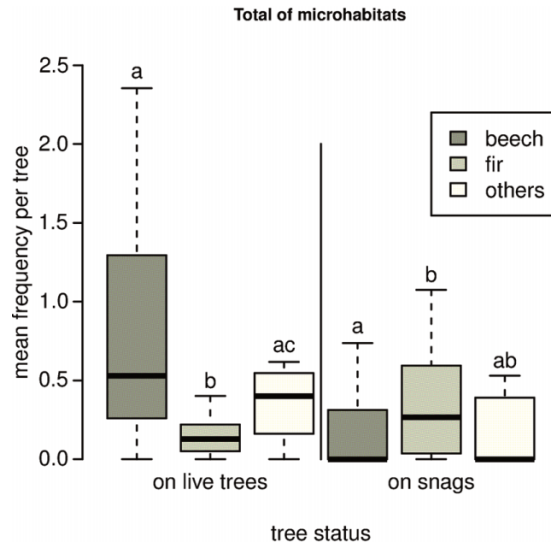


ities and cracks than beech. The frequencies of dendrothelms and saproxylic fungi were not influenced by snag tree species. Fir carried all microhabitat types (seven) whereas beech carried only a maximum of six.

In total, beech carried significantly more microhabitats than fir on live trees (Table 2; Fig. 2). Secondary species did not differ from beech and also carried significantly more microhabitats than fir. For snags, only fir differed from beech.

Beech and secondary species carried more than five times more microhabitats on live trees than on snags whereas fir carried twice as many microhabitats on snags than on live trees (Fig. 3).

### Tree species affects the density of microhabitat-bearing live trees

Seventy percent of the beech trees carried one or more microhabitats whereas we observed microhabitats on only 18% of firs. Others species carried as many microhabitats as beech (75%).

### Live tree species affects the conditional probability of occurrence of microhabitat types

The following microhabitat associations on a given tree were significantly more probable than random for both beech and fir (Table 3): (*i*) cavities with mould and missing bark and (*ii*) empty cavities, dendrothelms, and cracks. Concerning beech only, the following associations were found: (*i*) cavities with mould, empty cavities. and saproxylic fungi and (*ii*) saproxylic fungi and dendrothelms. On fir only, the following associations were significant: (*i*) empty cavities and saproxylic fungi, (*ii*) dendrothelms and missing bark, (*iii*) missing bark and cracks, and (*iv*) sap runs on the one hand and dendrothelms, missing bark, and cracks on the other hand.

## Tree diameter effects on microhabitat richness

### Tree diameter affects the presence of each microhabitat type

We found one to three significant diameter thresholds for each microhabitat type where the probability of its presence varied significantly (Table 4). Thresholds were less numerous in the fir data than in the beech data. Multiple thresholds correspond to microhabitats likely to occur more than once per tree (this was only the case for cavities, dendrothelms. and missing bark).

### Tree diameter affects the total number of microhabitats and the number of microhabitat types

For beech (Fig. 4 and Fig. 5), the four first diameter thresholds, which correspond to a gradual increase in the median of total numbers of microhabitats from zero to four, were significant and spaced at regular intervals (of roughly 15 cm). There was no significant threshold beyond four microhabitats per tree (between four and 16). For fir (Fig. 4 and Fig. 5), only the higher diameter threshold (99 cm) corresponded to a significant increase of the median number of microhabitats from zero to one. Beyond one microhabitat (between one and seven), we did not detect any significant threshold. For beech and fir, the first microhabitat occurred, respectively, at 41 and 60 cm dbh (median values).

Concerning the total number of microhabitat types per tree (Table 4): (*i*) for beech, only the two first thresholds (42 and 60 cm, similar to the thresholds for the total number of microhabitats per tree) significantly increased the median of the number of microhabitat types per tree from zero to one and then from one to two and (*ii*) for fir, the same threshold as for the total number of microhabitats per tree (99 cm) significantly increased the median from zero to one.

The proportion of microhabitat-bearing trees increased markedly with increasing diameter as specified for the management categories (Table 5). However, the shape of this relationship differed between tree species.

As dbh increased, the first microhabitat types that occurred on beech were cavities with mould and missing bark on small trees, then empty cavities, dendrothelms, and saproxylic fungi on medium trees, and finally cracks on large trees and very large trees. For fir, cavities and missing bark occurred on small trees, sap runs and cracks appeared on medium trees, and finally dendrothelms and saproxylic fungi on large trees and very large trees.

On average, when all the diameter categories were represented, a beech–fir stand carried 71 microhabitats/ha and a total of the seven microhabitat types. Large and very large trees carried 48% of the microhabitats.

## Discussion

Only a few papers describe the role of tree species and tree diameter for distribution patterns of a set of microhabitats. Indeed, in most cases, authors focused on only one microhabitat type. The most documented microhabitats are cavities (e.g., McClelland and Frissel 1975; Cline et al. 1980; Mannan et al. 1980; Fan et al. 2003*b*, 2005; Drapeau et al. 2005; Remm and Lõhmus 2011) and dendrothelms (Kitching 1971; Vaillant 1978; Schmidl et al. 2008). Due to this lack of available results, our work provides new insights on microhabitat key factors.

**Table 3.** Independence tests between microhabitat frequencies (microhabitat type co-occurrences).

| | Cavities with mould | Empty cavities | Saproxylic fungi | Dendrothelms | Missing bark | Cracks | Sap runs |
|---|---|---|---|---|---|---|---|
| Cavities with mould | — | **<0.000** | **0.010** | 0.09 | **0.007** | 0.56 | |
| Empty cavities | 0.44 | — | 0.75 | **0.01** | 0.2 | **0.011** | |
| Saproxylic fungi | 0.156 | **0.0015** | — | **0.017** | 0.58 | 0.96 | |
| Dendrothelms | 1 | **0.007** | 0.05 | — | 0.98 | 0.35 | |
| Missing bark | **<0.000** | 0.71 | 0.61 | **0.034** | — | 0.75 | |
| Cracks | 0.147 | **0.0005** | 1 | 1 | **<0.000** | — | |
| Sap runs | 0.23 | 0.71 | 1 | **0.011** | **0.0001** | **0.002** | — |

**Note**: Values are $p$ values from a $\chi^2$ test for European beech (*Fagus sylvatica*) and silver fir (*Abies alba*). Values above the diagonal concern beech and those below the diagonal concern fir. Results in bold indicate significant "positive" dependence between the two microhabitat types.

**Table 4.** Diameter thresholds and confidence intervals per tree species (European beech (*Fagus sylvatica*) and silver fir (*Abies alba*)), on live trees, for the presence of each microhabitat and their total or type frequencies.

| | Beech | | Fir | |
|---|---|---|---|---|
| Microhabitat | Threshold | Confidence interval | Threshold | Confidence interval |
| Cavities with mould | 41 | 33–51 | 65 | 47–81 |
| | **63** | **53–78** | **87** | **81–113** |
| | 79 | 75–88 | | |
| Empty cavities | 41 | 40–49 | 57 | 54–76 |
| | **65** | **48–88** | **94** | **64–99** |
| | 126 | 86–126 | | |
| Saproxylic fungi | **100** | **100–121** | **61** | **61–94** |
| Dendrothelms | 43 | 42–73 | **99** | **81–103** |
| | **86** | **60–93** | | |
| Missing bark | **110** | **72–110** | 47 | 31–75 |
| | | | **98** | **60–99** |
| Cracks | **72** | **72–81** | 100 | 86–102 |
| Sap runs | | | **76** | **74–102** |
| Total microhabitat frequency | 42 | 41–60 | *47* | *47–57* |
| | *60* | *44–60* | 81 | 67–81 |
| | *73* | **60–79** | **99** | **81–99** |
| | 89 | *80–107* | | |
| Microhabitat type frequency | 42 | 40–43 | 50 | 47–57 |
| | **60** | **59–67** | **81** | **80–99** |
| | 86 | 64–116 | 99 | 94–103 |

**Note**: The division level of the dichotomous branching is indicated as follows: bold, first level division in the set; regular, second level division of the two subsets; italic, third level division. All thresholds were statistically significant at $p < 0.05$.

## Role of the tree species on microhabitat distribution

### *Live beech and secondary species trees carried microhabitats more often than live fir and certain microhabitat types were associated with beech or fir, sometimes exclusively*

Tree species influences the number of different microhabitat types per tree as well as the occurrence of each microhabitat, and beech carries microhabitats more often than fir (Vuidot et al. 2011). In keeping with this, we showed that, at a given diameter, the proportion of microhabitat-bearing trees was mostly higher in beech and the other broadleaves species than in fir. However, we found that fir carried more microhabitat types than beech.

Beyond these general trends, each microhabitat shows particular variations.

The probability that a tree carries a cavity varies with tree species (Fan et al. 2003b). Remm and Lõhmus (2011) showed that cavity density is higher in deciduous forests than in mixed forests. McClelland and Frissel (1975), Cline et al. (1980), Mannan et al. (1980), as well as Drapeau et al. (2005) pointed out that cavities are rare in live conifers. However, Bull et al. (1997) revealed the important role of grand fir (*Abies grandis* (Douglas ex D. Don) Lindl.), western redcedar (*Thuja plicata* Donn ex D. Don), and western larch (*Larix occidentalis* Nutt.) in the supply of cavities for wildlife in forests dominated by conifers of the Columbia River basin (United States). On live trees, we found that cavities were mostly linked to beech. Trunk cavities result from woodpecker excavations or fungi colonization. Empty cavities are sometimes shaped by tree roots, more frequently when the slope is steep. Woodpeckers prefer broadleaved species

**Fig. 4.** Recursive partitioning tree for European beech (*Fagus sylvatica*) and silver fir (*Abies alba*) diameter at breast height (dbh) (cm) from total microhabitat frequency data. The *p* values indicate the level of statistical significance of each node and *n* indicates the numbers of trees per group. Only live trees. The difference between the two first box plots is linked to the number of outlying points that are merged.
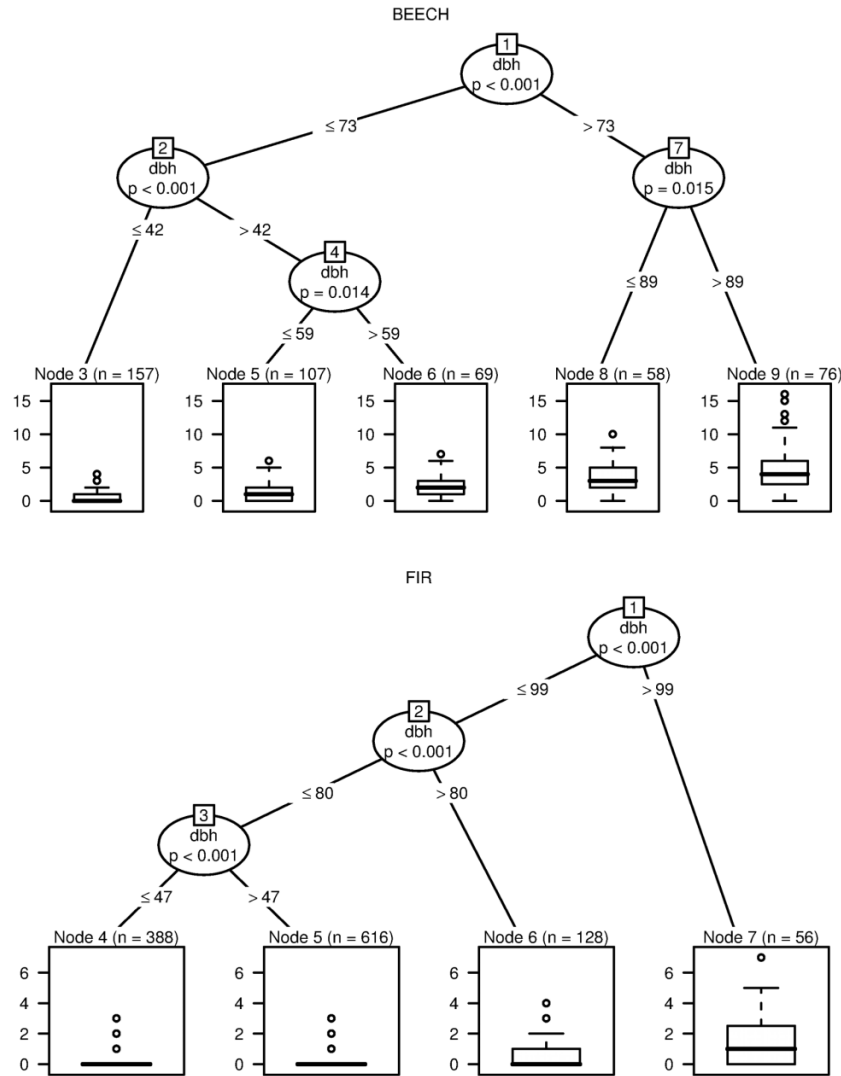


to construct their nest cavities because of resin runs in conifers (Cramp 1980). In deciduous riverine forests of Estonia, cavity occurrence is determined by tree species, with a strong preference for European aspen (*Populus tremula* L.) for woodpecker-excavated cavities and black alder (*Alnus glutinosa* (L.) Gaertn.) for cavities created by fungi (Remm et al. 2006).

We found that dendrothelms were mainly linked to beech and that fir rarely carries dendrothelms, in agreement with Vaillant (1978). Silver fir very exceptionally provides favorable conditions to create dendrothelms, probably because of a centripetal deterioration (the external layers rot quite quickly and fall off, while the heart resists much longer). Vaillant (1978) indicated in addition that beech and linden (*Tilia* spp.) carry dendrothelms more often than European white birch. Kitching (1971) indicated that dendrothelms occur most abundantly in European beech, but also occur in European ash, sycamore, birch, linden, and silver fir in the British Isles. Dendrothelms have been observed in other tree species: yellow poplar (*Liriodendron tulipifera* L.), horse

chestnut (*Aesculus hippocastanum* L.), European chestnut (*Castanea sativa* Mill.), European hornbeam (*Carpinus betulus* L.), durmast oak (*Quercus petraea* (Matt.) Liebl.), elms (*Ulmus* spp.), London plane (*Platanus* ×*hybrida* Brot.), northern red oak (*Quercus rubra* L.), and black alder (Vaillant 1978; Schmidl et al. 2008).

Although they are indicated on many genera present in montane beech–fir forests such as *Acer*, *Betula*, *Fagus*, *Fraxinus*, *Populus*, *Quercus*, *Tilia*, *Ulmus*, and *Salix* (Speight et al. 2010), sap runs were strictly linked to fir trees in our studied forests. We personally observed sap runs on beech in the Vosges Mountains (the northeast of France), but very rarely.

In spite of its thin bark, beech did not bear more missing bark than the other tree species, contrary to what we observed in managed beech–fir stands (Larrieu et al. 2011). In subnatural stands, missing bark forms mainly as fall scars of dying trees or stones on steep slopes. Missing bark that we observed on common yew mainly resulted from elk (*Cervus elaphus* Linnaeus, 1758) bark peeling occurring in winters

**Fig. 5.** Distribution for European beech (*Fagus sylvatica*) and silver fir (*Abies alba*) of the diameter at breast height (dbh) per number of microhabitats. The vertical lines correspond to the dbh thresholds that are statistically significant and correspond to an increase of a minimum of one unit in the median value for microhabitat number.
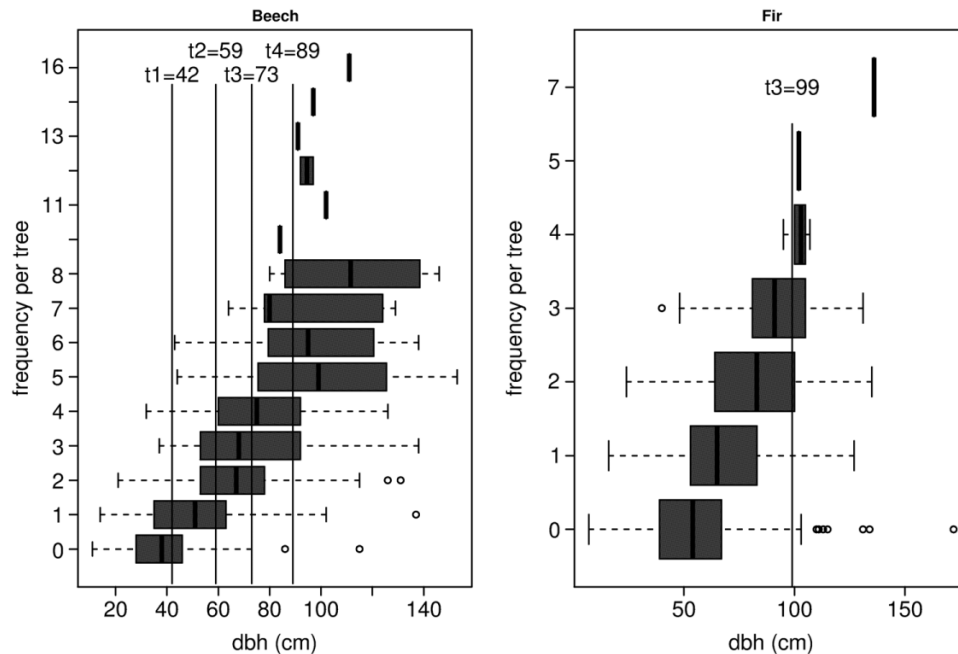


**Table 5.** Proportion of microhabitat-bearing trees (European beech (*Fagus sylvatica*) and silver fir (*Abies alba*)) per management diameter category.

| Management diameter category | % of microhabitat-bearing trees | |
| --- | --- | --- |
|  | Beech | Fir |
| Small trees (20 ≤ dbh < 25 cm) | 35 | 6 |
| Medium trees (25 ≤ dbh < 50 cm) | 43 | 9 |
| Large trees (50 ≤ dbh < 70 cm) | 78 | 21 |
| Very large trees |  |  |
|   dbh ≥ 70 cm | 92 | 32 |
|   dbh ≥ 89 cm | 99 |  |
|   dbh ≥ 99 cm |  | 70 |

**Note:** dbh, diameter at breast height.

with exceptionally great snowfalls (personal observation), in spite of the strong toxicity of the yew bark for animals (Cornevin 1887). We did not observe any significant association between missing bark and saproxylic fungi, although these bark injuries facilitate parasitic fungi colonization (Girompaire and Ballon 1992). This is all the more surprising for beech because its wood has a low resistance to fungi attacks (Keller 1986).

The association between empty cavities and saproxylic fungi was not significant in our beech data, probably because the main woodpecker species living in the study forests, black woodpecker (*Dryocopus martius* Linnaeus, 1758), dig holes in trees colonized by fungi but that are apparently healthy (Zahner et al. 2012), contrary to the other woodpecker species that dig their cavity nest in wood showing clear signs of decay (Cramp 1980).

The secondary species were rich in microhabitats but they did not play an important role because of their low abun-

dance in the stands, except for certain taxa that are strictly associated with a given tree species.

Beech and fir are complementary in their supply of microhabitats: beech provides quantity and fir may provide more diversity. Furthermore, the communities associated with a given microhabitat differ depending on whether the tree is a conifer or a broadleaved tree (Cramp 1980; Meschede and Heller 2003; Dajoz 2007; Speight et al. 2010).

### Snags and live trees were complementary in the supply of microhabitats (Fig. 2)

Vuidot et al. (2011) showed the important role that snags play in the supply of tree microhabitats by finding that snags carry almost twice as many microhabitats as live trees. However, Fan et al. (2003b) showed, on the contrary, that cavity abundance in the old-growth hardwood forests of the east-central United States is about twice the percentage for live trees than for snags. In fact, even though snags concentrate

certain microhabitats, particularly for fir in our data, their relatively low density could explain their low contribution in most stands.

In our data, cracks were linked to snags rather than to live trees. The cracks that we observed on fir snags were mostly in the form of bark in the process of peeling. One or 2 years after the death of a fir, bark fragments and peels off slightly. Before falling on the ground, this space under the bark lasts several years, offering shelter for medium-sized animals such as bats. Beech bark is very adhesive and peels off several years after the death of the tree, only in small fragments offering very little shelters to crack-dwelling mammals. However, this shelter can be used by other taxa, such as arboreal spiders (Chai and Liu 1998), flat bugs (Heiss and Pericart 2007), or beetles (Alexander 2002).

We also observed that snags carried sporophores of saproxylic fungi much more often than live trees. That said, a high hygrometry in dead wood is necessary for saprophyte fungi to develop carpophores, while lignicolous saprophyte fungi parasitizing weak trees are less dependent on atmospheric conditions.

### Role of tree diameter in microhabitat distribution

Winter and Möller (2008) found a strong link between the number of microhabitats and the diameter of the host tree. Vuidot et al. (2011) revealed that diameter is the main factor influencing the number and probability of occurrence of cavities, cracks, and missing bark. In Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) stands, the abundance of many bark microhabitats increased with tree diameter and several bark microhabitats were not observed in the smaller diameter classes (Michel et al. 2011). In a review, Fan et al. (2003a) concluded that cavity occurrence is strongly related to tree diameter. So, large trees are more favorable than smaller trees to cavity creation (DeGraaf and Shigo 1985). Dufour (2003) also showed a positive correlation between tree diameter and cavity occurrence. From Kitching (1971), dendrothelm density increases in beech trees with diameter above 50 cm.

Our results showed that the number of microhabitats per tree, and also the number of microhabitat types per tree, markedly increased with tree diameter. We found statistically significant diameter thresholds that could be used by forest managers. Most of these thresholds are situated above dbh = 50 cm (73% for beech and 90% for fir), which is used by forest managers, in most of the managed stands in the Pyrénées Mountains, as the diameter at which it is economically optimal to cut trees (ONF 2006). The harvest of the trees with dbh ≥ 50 cm significantly reduces the number of microhabitats per hectare by 48% and leads to the total elimination of one microhabitat out of six for beech and two microhabitats out of seven for fir.

### Practical recommendations to improve sustainable forestry

Beech and fir play complementary roles in the supply of microhabitat diversity. Secondary species (*Tilia* spp., *Acer* spp., *Betula* spp., etc.) are often scarce but often bear microhabitats. Furthermore, the broadleaved–conifer mixture (*i*) is the natural stand composition in most montane forests, (*ii*) facilitates management of a complex vertical structure that is favorable to several taxa (e.g., birds, Orthoptera), and (*iii*) is

a means to stabilize income for the small forest estates because the markets fluctuate and are sometimes favorable to broadleaved trees and sometimes favorable to conifers. In theory, we could also manage monospecific stands within a single landscape to achieve a high level of taxonomic biodiversity at the landscape scale. However, this approach is likely to provoke problems for species that are strictly associated with either broadleaved trees or conifers and that have a low dispersal capacity, as they may be unable to disperse across such a fragmented landscape. Thus, we suggest conserving mixed stands.

Very large trees play a significant role because they host all microhabitat types and the proportion of microhabitat-bearing trees is very high. We consider that current management diameter thresholds at 50 cm (lower limit of the large tree category) and 70 cm (lower limit of the very large tree category) are relevant with respect to microhabitats. Indeed, by taking into account the confidence intervals (CI) at 80%, we consider them equivalent to the significant thresholds that we found: respectively, 42 cm (CI 41–60 cm), 60 cm (CI 44–60 cm), and 73 cm (CI 60–79 cm) for beech and 47 cm (CI 47–57 cm) and 81 cm (CI 67–81 cm) for fir. We observed other diameter thresholds at 89 cm for beech (CI 80–107 cm) and 99 cm for fir (CI 81–99 cm) that are significant with respect to the number of microhabitats per tree and also to the number of microhabitat types per tree. Therefore, for forest management, we suggest creating a supplementary diameter category ("largest trees") with a lower limit at dbh = 90 cm for beech and at dbh = 100 cm for fir to better take into account the ecological role of these trees.

To promote the idea of "largest trees" category and thus to conserve microhabitat-bearing trees, we recommend developing silvicultural practices that allow, at the stand scale, a proportion of the trees to finish their complete natural cycle. The modeling of the microhabitat distribution at the stand level and the analysis of the abundant bibliography focusing on green retention trees will help us to work towards a consensual management strategy for mixed montane forests by fixing a proportion of trees to be conserved according to the stand characteristics.

The largest living trees seem to play a key role in all forest ecosystems. For example, they are key features from tropical (Grove 2002) to boreal (Martikainen et al. 2000) domains for the invertebrate assemblages. According to our results, conserving large trees and the diversity of tree species should help to manage taxonomic biodiversity in all forest ecosystems at the condition of defining the diameter thresholds and the role of each tree species in each ecosystem type.

# References

Alexander, K. 2002. The invertebrates of living and decaying timber in Britain and Ireland — a provisional annotated checklist. English Nature Research Reports No. 467. Department for Environment, Food and Rural Affairs and English Nature, Cranfield University at Silsoe, Bedfordshire, U.K.

Bardat, J., Bioret, F., Botineau, M., Boullet, V., Delpech, R., Géhu, J. M., Haury, J., Lacoste, A., Rameau, J.C., Royer, J.M., Roux, G., and Touffet, J. 2004. Prodrome des végétations de France. MNHN, Paris, France.

Bastien, Y., and Gauberville, C. (*Coordinators*). 2011. Vocabulaire forestier. Ecologie, gestion et conservation des espaces boisés. IDF, Paris, France.

Bauhus, J., Puettmann, K., and Messier, C. 2009. Silviculture for old-growth attributes. For. Ecol. Manage. **258**(4): 525–537. doi:10.1016/j.foreco.2009.01.053.

Blondel, J. 2005. Bois mort et à cavités: leur rôle pour l'avifaune cavicole. *In* Bois morts et à cavités: une clé pour des forêts vivantes. *Edited by* Vallauri et al. Tec et Doc Lavoisier, Paris, France. pp. 137–142.

Branquart, E., Vandekerkhove, K., Bourland, N., and Lecomte, H. 2005. Les arbres sur-âgés et le bois mort dans les forêts de Flandre, de Wallonie et du Grand-Duché de Luxembourg. *In* Bois mort et à cavités: une clé pour des forêts vivantes. *Edited by* Vallauri et al. Tec et Doc Lavoisier, Paris, France. pp. 19–29.

Bull, E.L., Parks, C.G., and Torgesen, T.R. 1997. Trees and logs important to wildlife in the interior Columbia River basin. U.S. For. Serv. Gen. Tech. Rep. PNW-391.

Chai, L.Y., and Liu, C.Y. 1998. Preliminary investigation report on the overwintering arthropod species in the cracks on stems of apple trees in the north of Henan. Acta Agric. Univ. Henanensis, **32**(1): 52–54.

Cline, S.P., Berg, A.B., and Wight, H.M. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. J. Wildl. Manage. **44**(4): 773–786. doi:10.2307/3808305.

Cornevin, C. 1887. Des plantes vénéneuses et des empoisonnements qu'elles déterminent. Institut National Agronomique, Paris, France.

Cramp, S. (*Coordinator*). 1980. Handbook of the birds of Europe, the Middle East and North Africa. The birds of the Western Palearctic. Oxford University Press, New York.

Dajoz, R. 2007. Les insectes des forêts. Rôle et diversité des insectes dans le milieu forestier. 2nd ed. Tec et Doc Lavoisier, Paris, France.

DeGraaf, R.M., and Shigo, A.L. 1985. Managing cavity trees for wildlife in the Northeast. U.S. Gen. Tech. Rep. NE-101.

Drapeau, P., Nappi, A., St Germain, M., and Angers, V.A. 2005. Les régimes naturels de perturbations, l'aménagement forestier et le bois mort dans la forêt boréale québécoise. *In* Bois mort et à cavités: une clé pour des forêts vivantes. *Edited by* Vallauri et al. Tec et Doc Lavoisier, Paris, France. pp. 46–54.

Dufour, D. 2003. Étude de l'influence du bois mort sur l'avifaune cavernicole en forêt feuillue. Mémoire de fin d'études. FUSAGx, Gembloux.

Fan, Z.F., Larsen, D.R., Shifley, S.R., and Thompson, F.R. 2003*a*. Estimating cavity tree abundance by stand age and basal area, Missouri, USA. For. Ecol. Manage. **179**(1–3): 231–242. doi:10.1016/S0378-1127(02)00522-4.

Fan, Z.F., Shifley, S.R., Spetich, M.A., Thompson, F.R., III, and Larsen, D.R. 2003*b*. Distribution of cavity trees in midwestern old-growth and second-growth forests. Can. J. For. Res. **33**(8): 1481–1494. doi:10.1139/x03-068.

Fan, Z.F., Shifley, S.R., Spetich, M.A., Thompson, F.R., and Larsen, D.R. 2005. Abundance and size distribution of cavity trees in second-growth and old-growth central hardwood forests. North. J. Appl. For. **22**(3): 162–169.

Fritz, O., and Heilmann-Clausen, J. 2010. Rot holes create key microhabitats for epiphytic lichens and bryophytes on beech (*Fagus sylvatica*). Biol. Conserv. **143**(4): 1008–1016. doi:10.1016/j.biocon.2010.01.016.

Girompaire, L., and Ballon, P. 1992. Conséquences de l'écorçage du Cerf élaphe dans le massif des Vosges alsaciennes [Results of barking by red deer in the Alsacian Vosges]. Rev. For. Fr. **44**(6): 501–511. doi:10.4267/2042/26354.

Gosselin, M., and Larroussinie, O. 2004. Biodiversité et gestion forestière: connaître pour préserver. Synthèse bibliographique. Cemagref, Nogent sur Vernisson, France.

Grove, S.J. 2002. Tree basal area and dead wood as surrogate indicators of saproxylic insect faunal integrity: a case study from the Australian lowland tropics. Ecol. Indic. **1**(3): 171–188. doi:10.1016/S1470-160X(01)00016-4.

Heiss, E., and Pericart, J. 2007. Hemiptères Aradidae Piesmatidae et Dipsocoromorphes euro-méditerranéens. Fédération Française des Sociétés de Sciences Naturelles, Paris, France.

Hothorn, T., and Hornik, K. 2005. The coin package, conditional inference procedure in a permutation tes-framework, 0.4-1. Available from http://CRAN.R-project.org.

Hothorn, T., and Hornik, K.Z.A. 2006. Party: a laboratory for recursive part(*y*)itioning. Available from http://CRAN.R-project.org.

Hothorn, T., and Zeileis, A. 2008. Generalizes maximally selected statistics. Biometrics, **64**(4): 1263–1269. doi:10.1111/j.1541-0420.2008.00995.x. PMID:18325074.

Hothorn, T., Hornik, K., Van de Wiel, M.A., and Zeileis, A. 2006. A Legosystem for conditional inference. Am. Stat. **60**(3): 257–263. doi:10.1198/000313006X118430.

Jonsell, M., and Weslien, J. 2003. Felled or standing retained wood — it makes a difference for saproxylic beetles. For. Ecol. Manage. **175**(1–3): 425–435. doi:10.1016/S0378-1127(02)00143-3.

Keller, R. 1986. Identification et classement des bois français. ENGREF, Nancy, France.

Kitching, R.L. 1971. An ecological study of water-filled tree-holes and their position in the woodland ecosystem. J. Anim. Ecol. **40**(2): 281–302. doi:10.2307/3247.

Larrieu, L., Cabanettes, A., and Delarue, A. 2011. Impact of silviculture on dead wood and on the distribution and frequency of tree microhabitats in montane beech–fir forests of the Pyrenees. Eur. J. For. Res. **131**(3): 773–786. doi:10.1007/s10342-011-0551-z.

Larsson, T.B. (*Compiler*). 2001. Biodiversity evaluation tools for European forests. Ecol. Bull. **50**: 75–81.

Lindenmayer, B., and Franklin, J.F. 2002. Conserving forest biodiversity; a comprehensive multiscaled approach. Island Press, Washington, D.C.

Lindenmayer, D.B., Margules, C.R., and Botkin, D.B. 2000. Indicators of biodiversity for ecologically sustainable forest management. Conserv. Biol. **14**(4): 941–950. doi:10.1046/j.1523-1739.2000.98533.x.

Lindenmayer, D.B., Franklin, J.F., and Fischer, J. 2006. General management principles and a checklist of strategies to guide forest biodiversity conservation. Biol. Conserv. **131**(3): 433–445. doi:10.1016/j.biocon.2006.02.019.

Lisiewska, M. 1992. Macrofungi on special substrates. *In* Fungi in vegetation science. *Edited by* W. Winterhoff. Kluwer, the Netherlands. pp. 151–182.

Mannan, R.W., Meslow, E.C., and Wight, H.M. 1980. Use of snags by birds in Douglas-fir forests, western Oregon. J. Wildl. Manage. **44**(4): 787–797. doi:10.2307/3808306.

Martikainen, P., Siitonen, J., Punttila, P., Kaila, L., and Rauh, J. 2000. Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. Biol. Conserv. **94**(2): 199–209. doi:10.1016/S0006-3207(99)00175-5.

McClelland, B.R., and Frissell, S.S. 1975. Identifying forest snags useful for hole-nesting birds. J. For. **73**(7): 414–417.

McElhinny, C., Gibbons, P., Brack, C., and Bauhus, J. 2005. Forest and woodland stand structural complexity: its definition and measurement. For. Ecol. Manage. **218**(1–3): 1–24. doi:10.1016/j.foreco.2005.08.034.

Meschede, A., and Heller, K.G. 2003. Écologie et protection des chauves-souris en milieu forestier. Le Rhinolophe, **16**.

Métailié, J.-P. 2001. Un patrimoine historico-environnemental: les forêts pastorales dans les Pyrénées. *In* Proceedings of "126 ème congrès des sociétés historiques et scientifiques", Toulouse, France. pp. 33–47.

Michel, A.K., and Winter, S. 2009. Tree microhabitat structures as indicators of biodiversity in Douglas-fir forests of different stand ages and management histories in the Pacific Northwest, USA. For. Ecol. Manage. **257**(6): 1453–1464. doi:10.1016/j.foreco.2008.11.027.

Michel, A.K., Winter, S., and Linde, A. 2011. The effect of tree dimension on the diversity of bark microhabitat structures and bark use in Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*). Can. J. For. Res. **41**(2): 300–308. doi:10.1139/X10-207.

Nascimbene, J., Marini, L., and Nimis, P.L. 2009. Influence of tree species on epiphytic macrolichens in temperate mixed forests of northern Italy. Can. J. For. Res. **39**(4): 785–791. doi:10.1139/X09-013.

ONF. 2006. Schéma régional d'aménagement des forêts pyrénéennes. ONF, Direction territoriale Sud-Ouest. Toulouse, France.

Pardé, J., and Bouchon, J. 1988. Dendrométrie. 2nd ed. ENGREF, Nancy, France.

Pénicaud, P. 2000. Chauves-souris arboricoles en Bretagne: typologie de 60 arbres-gîtes et éléments de l'écologie des espèces observées. Le Rhinolophe, **14**: 37–68.

Puumalainen, J., Kennedy, P., and Folving, S. 2003. Monitoring forest biodiversity: a European perspective with reference to temperate and boreal forest zone. J. Environ. Manage. **67**(1): 5–14. doi:10.1016/S0301-4797(02)00183-4. PMID:12659799.

R Development Core Team. 2007. R: a language and environment for statistical computing. Available from http://www.R-project.org.

Ranius, T. 2002. *Osmoderma eremita* as an indicator of species richness of beetles in tree hollows. Biodivers. Conserv. **11**(5): 931–941. doi:10.1023/A:1015364020043.

Ranius, T., and Jansson, N. 2000. The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. Biol. Conserv. **95**(1): 85–94. doi:10.1016/S0006-3207(00)00007-0.

Remm, J., and Lõhmus, A. 2011. Tree cavities in forests — the broad distribution pattern of a keystone structure for biodiversity. For. Ecol. Manage. **262**(4): 579–585. doi:10.1016/j.foreco.2011.04.028.

Remm, J., Lõhmus, A., and Remm, K. 2006. Tree cavities in riverine forests: what determines their occurrence and use by hole-nesting passerines? For. Ecol. Manage. **221**(1–3): 267–277. doi:10.1016/j.foreco.2005.10.015.

Schmidl, J., Sulzer, P., and Kitching, R.L. 2008. The insect assemblage in water filled tree-holes in a European temperate deciduous forest: community composition reflects structural, trophic and physicochemical factors. Hydrobiologia, **598**(1): 285–303. doi:10.1007/s10750-007-9163-5.

Snedecor, G.W., and Cochran, W. 1971. Méthodes statistiques. [Translated from English by H. Boelle and E. Camhaji.] ACTA, Paris, France.

Speight, M.C.D. 1989. Saproxylic invertebrates and their conservation. Rep. 42. Council of Europe, Strasbourg, France.

Speight, M.C.D., Castella, E., Sarthou, J.-P., and Monteil, C. 2010. Species accounts of European Syrphidae (Diptera). Syrph the Net, the database of European Syrphidae. Syrph the Net Publications, Dublin, Ireland.

Stanska, M., Rozwaka, R., and Kowalczyk, K. 2010. *Dipoena torva* (Thorell, 1875), spider living on tree stems. Lesne Prace Badawcze, **71**(2): 201–205.

Tews, J., Brose, U., Grimm, V., Tielborger, K., Wichmann, M.C., Schwager, M., and Jeltsch, F. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J. Biogeogr. **31**(1): 79–92. doi:10.1046/j.0305-0270.2003.00994.x.

Vaillant, F. 1978. Les *Systenus* et leur habitat dendrotelme (Dipt. Dolichopodidae). Bull. Soc. Entomol. Fr. **83**: 73–85.

Vuidot, A., Paillet, Y., Archaux, F., and Gosselin, F. 2011. Influence of tree characteristics and forest management on tree microhabitats. Biol. Conserv. **144**(1): 441–450. doi:10.1016/j.biocon.2010.09.030.

Winter, S., and Möller, G.C. 2008. Microhabitats in lowland beech forests as monitoring tool for nature conservation. For. Ecol. Manage. **255**(3–4): 1251–1261. doi:10.1016/j.foreco.2007.10.029.

Zahner, V., Sikora, L., and Pasinelli, G. 2012. Heart rot as a key factor for cavity tree selection in the black woodpecker. For. Ecol. Manage. **271**: 98–103. doi:10.1016/j.foreco.2012.01.041.