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ORIGINAL PAPER

Impact of silviculture on dead wood and on the distribution and frequency of tree microhabitats in montane beech-fir forests of the Pyrenees

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Abstract In forest ecosystems, the level of biodiversity is strongly linked to dead wood and tree microhabitats. To evaluate the influence of current forest management on the availability of dead wood and on the abundance and distribution of microhabitats, we studied the volume and diversity of dead wood objects and the distribution and frequency of cavities, dendrothelms, cracks, bark losses and sporophores of saproxylic fungi in montane beech-fir stands. We compared stands unmanaged for 50 or 100 years with continuously managed stands. A total of 1,204 live trees and 460 dead wood objects were observed. Total dead wood volume, snag volume and microhabitat diversity were lower in the managed stands, but the total number of microhabitats per ha was not significantly different between managed and unmanaged stands. Cavities were always the most frequent microhabitat and cracks the least frequent. Dendrothelm and bark loss were favored by management. Beech (*Fagus sylvatica*) carried many more microhabitats than silver fir *(Abies alba*), especially cavities, dendrothelms and bark losses. Fir very scarcely formed dendrothelms. Secondary tree species played an important role by providing cracks and bark losses. The proportion of microhabitat-bearing trees increased dramatically above circumference thresholds of 225 cm for beech and 215 cm for fir. Firs with a circumference of less than 135 cm did not carry microhabitats. In order to conserve microhabitat-providing trees and to increase the volume of dead wood in managed stands, we recommend conserving trees that finish their natural cycle over 10–20% of the surface area.

Keywords Dead wood · Cavity · Crack · Dendrothelm · Bark loss · Girth threshold

Introduction

Forests are complex terrestrial ecosystems (Rameau et al. 2000; Gosselin and Laroussinie 2004; Dajoz 2007), and a large part of this complexity is linked to woody plants, living or dead (Maser et al. 1984; McMinn and Crossley 1996; Vallauri et al. 2002; Dajoz 2007), and in particular to the heterogeneity provided by tree microhabitats (Winter and Möller 2008; Michel and Winter 2009). Because more than 25% of forest species are saproxylic organisms (Stokland et al. 2004; Bobiec et al. 2005) in boreal and temperate forests, the level of biodiversity is strongly linked to dead wood and tree microhabitats which are key structural attributes of old-growth forests (Bauhus et al. 2009).

As is the case for all temperate forests in Europe, the montane forests of the Pyrenees have been impacted by a high level of anthropization due to thousands of years of livestock-herding (Métailié 1984) and through the high demand in terms of energy for industry during the XVIIIth

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and XIXth centuries (Wonoroff 1984; Davasse 1992; Métailié 2001). Today, the main goal of the owners of Pyrenean forests is the production of saw timber. The current management of montane beech-fir forests in the Pyrenees consists of carrying out selective cuts, every 10–20 years on average, to improve the overall commercial quality of the wood produced. Thinning removes the trees: (1) which exceed the economic girth limit, (2) which have characteristics that reduce the quality of their wood (e.g., a lot of big knots, woodpecker cavities, saproxylic fungi), (3) whose remaining life expectancy is estimated as inferior to the cutting interval, and (4) disseminated tree species or those whose wood has little commercial value, in favor of beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.). Generally, thinning removes a fairly low number of stems (on average only 10–30% of the total number of trees), but mostly focuses on large trees.

The impact of these forestry methods on the biodiversity of montane forest ecosystems is little documented, as the references currently available mostly concern the boreal context (Fridman and Walheim 2000; Darveau and Desrochers 2001; Siitonen 2001), the forests of the North-West coast of the USA (e.g., Maser et al. 1984), or the tropical forests of Australia (Grove 2002a, b). However, the make-up of these forests, their dynamics and the forestry methods used in these zones are very different from those that occur in the montane forests of Europe. Almost all of the studies currently available have described the impact of forestry on biodiversity using bio-indicators such as Carabidae Coleoptera (Du Bus de Warnaffe and Lebrun 2004), saproxylic Coleoptera (Martikainen et al. 2000), mammals (Carey et al. 1999; Loeb 1999), saprophytic fungi (Sippola and Renvall 1999; Norsted et al. 2001), birds (Martikainen et al. 1998; Moning and Müller 2008, 2009), molluscs (Moning and Müller 2009) or lichens (Moning et al. 2009; Moning and Müller 2009). However, biodiversity assessment in forests using bio-indicator tools is very expensive and requires taxonomic specialists. Therefore, this approach cannot be used as a routine method for forest managers, and the focus on tree microhabitats as a proxy of taxonomic biodiversity is recommended (Winter and Möller 2008). However, relatively few studies that link forest structure and biodiversity are currently available. The majority of studies have focused on dead wood and its marked contribution to the level of biodiversity observed in forests (Harmon et al. 1986; Samuelsson et al. 1994; Darveau and Desrochers 2001; Norden et al. 2004; Odor et al. 2006). The most studied tree microhabitats are cavities (Healy et al. 1989; Fan et al. 2003; Branquart and Liégeois 2005). Deconchat (1994) pointed out the important role of mature trees as a source of biodiversity, and Nilsson et al. (2002) showed the positive effect of the presence of mature trees on the presence of endangered taxa. Gilg (2004) affirmed that "forestry methods, by taking away dead wood, destroy more than half of the microhabitats present in a natural forest." Winter and Möller (2008) observed microhabitats in lowland pure beech forests and Michel and Winter (2009) studied microhabitats in Douglas-fir forests.

However, to our knowledge, microhabitats in mixed beech-fir forests of Europe have not yet been studied despite the fact that this is a forest type with great economic and ecological importance, existing in most of the European mountain ranges.

Furthermore, the respective contribution of the different tree species in terms of the supply of microhabitats has not generally been looked at. Finally, the types of microhabitats carried by mature trees have not generally been specified.

In this study, besides dead wood, we focused on a set of five microhabitats: cavities, cracks, dendrothelms (water filled holes in the wood), bark loss and sporophores of saproxylic fungi; we studied these elements in stands that have been unmanaged for more than 50 years or more than 100 years, as well as in continuous managed stands, within montane beech-fir forests of the central Pyrenees. These five microhabitats seem to be very important for taxonomic diversity in forests because the associated taxonomic groups are numerous and varied (Table 5 in supplementary material), or very specific. Cavities are used for protection against bad weather conditions or predators for more than 25% of vertebrate species in the north-eastern North American forests (DeGraaf and Shigo 1985; Healy et al. 1989) and in France, 41% of forest birds are cavity-dwelling species (Blondel 2005). Furthermore, cavities, cracks and bark loss are the indicators of natural forests (Michel and Winter 2009). Dendrothelm-dwelling species are not numerous, but very specialized: there are only 14 species in Europe, but six of them are specifically associated with dendrothelms (Kitching 1971). Sporophores of saproxylic fungi support a varied entomofauna (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; Ellis and Ellis 1998). Even though sporophores of fungi are not representative of the strict spatial distribution of the species (Schmit and Lodge 2005), nor of the quantity of mycelium and the number of individuals (Richard et al. 2005), a high abundance of sporophores of saproxylic species has significance because it can be correlated with the presence of rare species (Bässler and Müller 2010) and a lot of insects live in the sporophores (Dajoz 2007).

This paper aims to: (1) evaluate the influence of silvicultural practices and time since logging on dead wood and on the abundance and distribution of these five tree microhabitats; (2) evaluate the role of the different tree species in terms of the supply of microhabitats, independently of their abundance; (3) identify critical girth tree thresholds for microhabitat presence.

We discuss the results in the context of sustainable management practices and then we propose a management strategy that could help to conserve a variety of tree microhabitats and dead wood objects in commercial stands.

Materials and methods

Study area

The stands studied are situated in the foothills of the central Pyrenees (WGS 84, Lat/Lon: 43°N/0.34°E). The dominant substrata are alkaline rocks of the Mesozoic, but older acid rocks may be observed very locally (Barrère et al. 1982, 1984; Ternet et al. 1995, 1996). The mesoclimate is of an Atlantic montane type, which is fairly harsh. Dominant winds are westerly and the position of the first mountain slopes provokes high rainfall (more than 1,500 mm/year on average). This precipitation falls partly in the form of snow, but also as mist. The topoclimates linked to exposition, slope and confinement are strongly contrasted. The conditions of the sites are overall very favorable to the growth of native tree species, at least up to the altitude of 1,500 m.

Characteristics of stands observed and samples used

All the stands studied are natural habitats of beech-fir forest (Bardat et al. 2004). However, the sylvofacies hosts a very variable proportion of fir, which is directly due to past management, with a high level of anthropization generally favoring beech at the expense of fir (Métaillé 2001). These stands are all located at an altitude of between 950 and 1,100 m, which corresponds to the Lower Montane bioclimatic zone in the Pyrenees.

We studied four zones for three levels of time since logging (Fig. 1). "BF-reference" contains the more mature beech-fir stands with no logging since 1900. "B-cable" contains stands dominated by beech, in a zone logged by a gravity cable technique in 1960 and unmanaged since. We distinguished two modalities in the group of stands logged up until the present day: "B-managed" and "F-managed" contain stands respectively dominated by beech and fir and logged 2 or 3 times in the last 20 years (see Fig. 5 and Fig. 6 in supplementary material). All the managed stands were under the control of the same manager.

Observations were carried out between 2003 and 2005 on a sample of 40 plots (Table 1). All plots were set up based on an approach of relascope sampling using the no 1 strip (with a return angle of 1/50) of a Bitterlich relascope

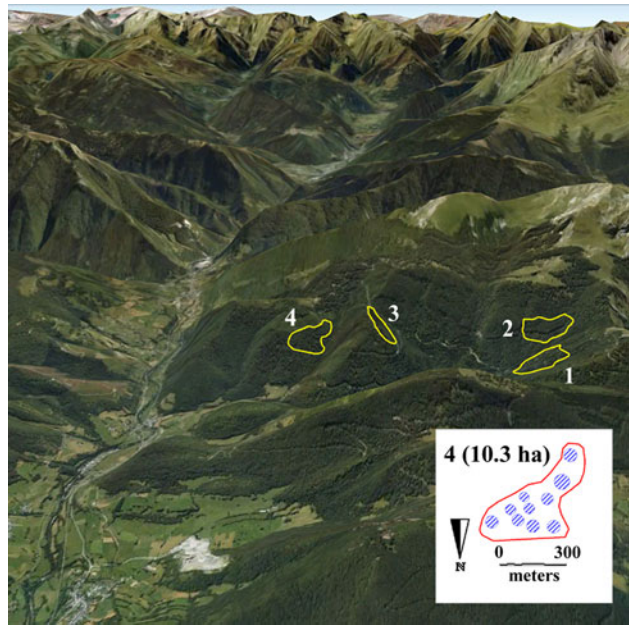

Fig. 1 Localization of the stands. *1*: BF-reference stands; *2*: B-cable stands; *3*: F-managed stands; *4*: B-managed stands. The zoom shows the spatial repartition of plots (*black-hatched* areas) within the B-managed zone

(Bitterlich 1984; Pardé and Bouchon 1988; Rondeux 1993). This device enables the production of a stand inventory using a constant angle. The error due to terrain slope is automatically corrected for by the device, which is very practical in the mountains. The use of a relascope leads to a high sampling rate of mature trees a priori richer in microhabitats (Winter and Möller 2008), but a high level of imprecision in the density of smaller trees, which seem to play a less important role in estimates of microhabitat richness. As the relascope sampling of fallen coarse woody debris is very sensitive to surveyor judgement (Ringvall and Stahl 1999), all the observations were carried out by the same operator.

To incorporate correctly the variability of each management category, each one of them was sampled with 9–11 plots. The plot surface was 0.3 ha on average and the distance between two plots was, at least, 100 m (Fig. 1; Table 1).

Measurements and observation of microhabitats

One thousand two hundred and four live trees and 460 dead wood objects were observed individually. All the live trees included in the relascope sampling were identified to species level and measured for the circumference on the outside of the bark, at breast height, to the nearest centimetre, without the notion of minimum girth being taken into account. Then, by going around the whole tree, we carefully examined the trunk from the ground to the crown to note the microhabitats hosted on the visible part of the

Table 1 Study design. The surface of the sampled area per modality is the sum of the plot surfaces, estimated with the distance between the plot center and the most distant tree observed

Modality	Number of plots	Total area sampled (ha)	Number of live trees observed	Numbers of dead wood items observed
BF-reference	10	4,684	371	84
B-cable	9	2,130	286	124
B-managed	10	2,386	280	73
F-managed	11	3,292	267	179
Total	40	12,492	1,204	460

trunk. Logs were grouped with snags and were not included in the stand basal area. In the case of standing dead wood, we distinguished "high stumps," when the dead part of the tree had a height of between 0.5 and 1.5 m, from "snags," whose height exceeded 1.5 m. In the unmanaged stands, high stumps corresponded to snags in a state of ultimate decay. All dead wood items were identified and measured in length and in girth beyond a circumference of 60 cm at the smallest extremity. The circumference was measured in the middle for logs and snags of under 4 m, at the cut for high stumps, and at breast height for snags of over 4 m, with the circumference being measured along the outside of the bark when this was present. Dying or dead trees were classed on a saproxylation scale of 6 levels (see Table 6 in supplementary material). For the large dead wood objects that showed a certain heterogeneity in the level of decay, the decay stage noted corresponded to the stage most present (in terms of volume) on the observed item. We used the French management girth classes: circumference at breast height (CBH) 65 cm $\leq$ Small Tree $\leq$ 85 cm; Medium Tree $\leq$ 150 cm; Large Tree $\leq$ 210 cm; Very Large Tree $>$ 210 cm.

In addition to the dead wood, we observed the following microhabitats, both on alive and dead trees. We defined the microhabitats partly with thresholds.

1. Cavities, with a distinction between "empty" cavities and cavities with wood mould (in a decay stage of more than 3). Cavities were not observed on logs. We distinguished the cavities situated at less than 0.5 m from the ground because logging does not remove them.
2. Cracks in the tree trunk, of a width of between 1 and 5 cm and situated over 1 m from the ground, in the wood or in the form of bark in the process of peeling. Bats were the benchmark for these thresholds (Meschede and Heller 2003).
3. Dendrothelms, when the orifice diameter was more than 3 cm.
4. Sporophores of saproxylic fungi (without taxonomic identification). Each tree or item of wood inventoried was classed in relation to the presence or not of sporophores, without estimating their numbers. In connection with the dates of observations, the great majority of fungi noted were species that produce perennial sporophores (Polypores *sl.*).
5. Patches with bark loss of at least 10 cm $\times$ 10 cm, only on live or dying trees. Wood was in a decay stage of less than 2.

We focused on microhabitats borne by the living trees because they are directly concerned by forest management. For the role of the tree species to the supply of microhabitats, we focused on BF-reference stands to avoid interaction between the effects of tree species and management.

Calculations and statistical procedures

The theoretical number of trees per hectare was calculated by allocating to every tree observed in the relascope sampling the coefficient N_C, in relation to its circumference (C): $N_C = \pi\ 10^8\ [\mathrm{ArcTan}(1/50)/C]^2$ (Pardé and Bouchon 1988).

The volumes of the stumps, snags smaller than 4 m and dead wood items on the ground were calculated by considering them as cylinders. The volume of standing wood was estimated using Schaeffer's cubage rates (Schaeffer 1949). Dead wood was expressed in $m^3\ ha^{-1}$ and also in % of total wood volume (dead + alive) to take into account the level of productivity of the habitat (Sippola et al. 1998). The proportion of snags was calculated because is a pertinent indicator of stand maturity (Gonin 1988).

For the variables expressed per surface unit, we analyzed the sum per plot. On the other hand, to analyze the relations with the girth (thresholds), we used individual variables of each observed tree.

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

Comparisons of frequencies of tree-bearing microhabitats per species were carried out with the chi-square test (Snedecor and Cochran 1971). The test of Kruskal–Wallis (Sprent 1992) was used to compare the number of stump cavities and the number of trunk cavities. The data on dead wood volume were analyzed with analysis of variance.

For the relation between numbers of microhabitats and tree girth, we used tree-based regression and classification models. Threshold values were calculated by recursive partitioning (Lausen and Schumacher 1992; Hothorn and Lausen 2003; 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 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 (80%) was calculated for all thresholds. The calculations were performed on "presence–absence" data, using the add-on package "party" (Hothorn et al. 2006b). The girth thresholds were calculated only for BF-reference stands (1) to only use data that were independent of management, (2) to observe a wide gradient in terms of tree girth, given that very large trees are rare in managed stands.

The global hypothesis of independence between the four stand categories and the response variable (number of one or all microhabitats) was assessed using multiple testing of re-sampled data (Westfall and Young 1993; Hothorn et al. 2006a). The P value obtained by this procedure was adjusted for multiple comparisons utilizing 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 also 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).

Results

Dead wood and microhabitats

All stands had less than 58 m^3/ha of dead wood per ha (Fig. 2). The average total volume of dead wood reached between 1.8 and 11% of the total volume of wood (live + dead). The total volume of dead wood was lower in the managed stands (B-managed stands and F-managed stands together) than in the unmanaged stands (BF-reference stands and B-cable stands together) ($F = 18$, $P < 0.001$), and the significant difference between the means of the two

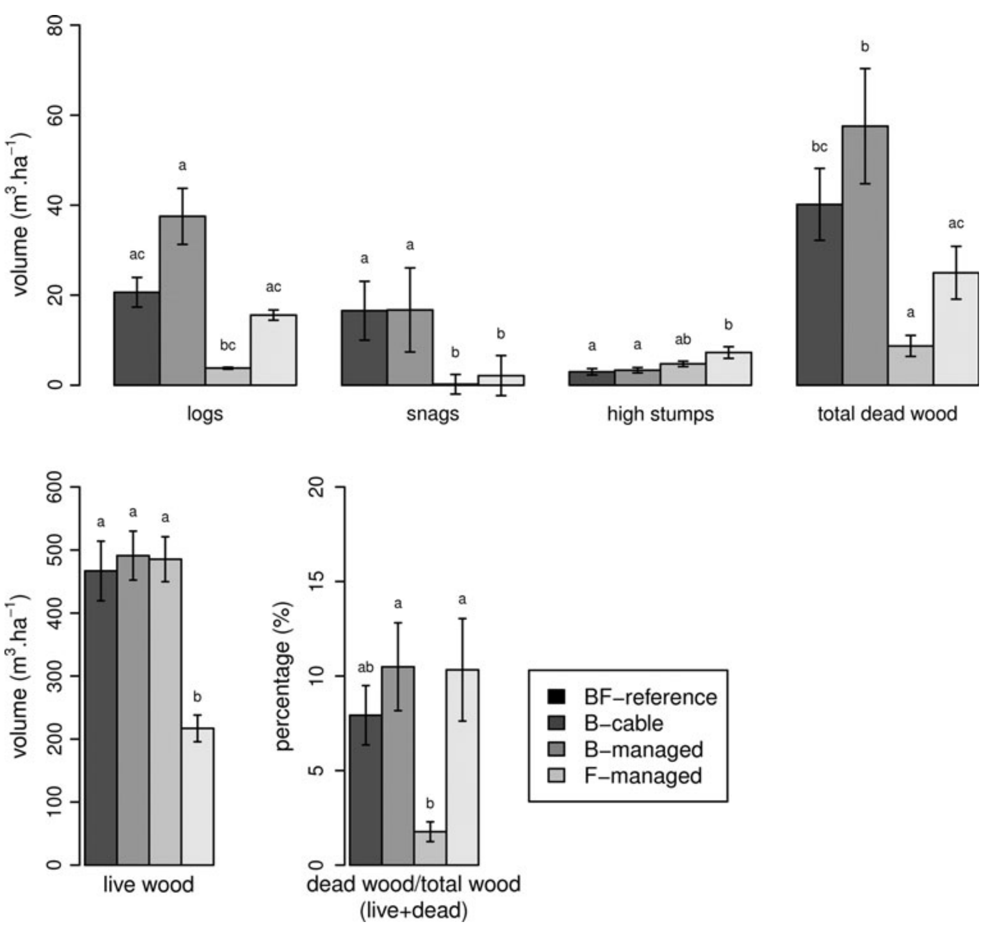

Fig. 2 Distribution of dead wood per type of support and quantification in relation to live wood (Montane beech-fir forests in central Pyrenees). *Vertical lines* indicate the standard error and *letters* indicate significant differences

modalities was evaluated to 5.2 m^3 ha^{-1} (Tukey-test $t = 4.3, P < 0.001$). Nevertheless, we observed 25 m^3 ha^{-1} in F-managed stands. Logs generally dominated the dead wood volume, but the volumes of logs and snags did not differ significantly in the BF-reference stands. In managed stands, the standing dead wood was mainly represented by high stumps: 54 and 29%, respectively, for B-managed stands and F-managed stands. We observed an almost complete absence of snags in B-managed stands.

Patterns of the distribution of decay stages of dead wood were very different between unmanaged and managed stands (Fig. 3 and see also Table 7 in supplementary material). BF-reference stands showed quite a high presence of dying trees (stage 0.5) and the main decay stage was the 4th. B-cable curve culminated in decay stage 2. Managed stands did not include the dying tree stage and showed a curve culminating in stage 2 or 3. In B-managed stands, only the stages of decay 3 and 4 occurred in the field.

Beech and fir showed almost the same profiles of decay.

Considering live trees only, beech carried more microhabitats than fir, especially in terms of cavities ($P < 0.001$), dendrothelms ($P < 0.001$) and bark losses ($P < 0.001$). Fir formed dendrothelms very scarcely (Table 2). In B-reference stands, the secondary tree species (*Acer* spp., *Prunus avium*, *Taxus baccata* and *Tilia platyphyllos*), in spite of their low densities, had an important role in providing microhabitats, particularly for cracks and bark loss.

Cavities were always by far the most frequent microhabitat and cracks the least frequent (6% of microhabitat-bearing trees in the BF-reference stands).

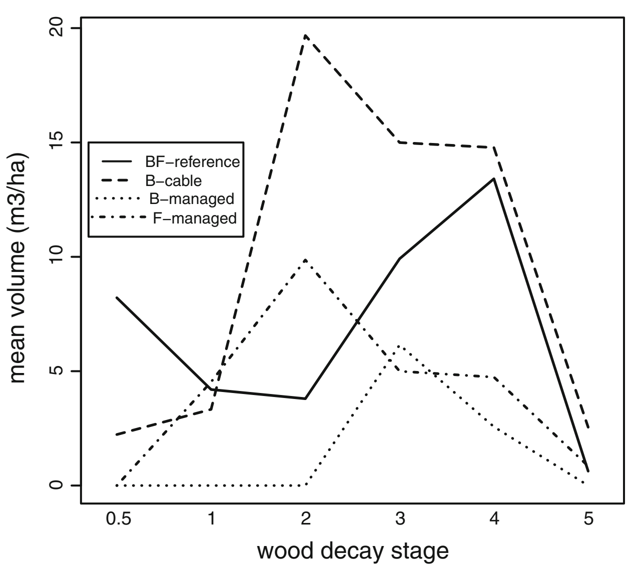

Fig. 3 Distribution of dead wood volume per decay stage. (Montane beech-fir forests in central Pyrenees)

In the BF-reference stands, 29% of the trees bearing microhabitats and almost 90% of the trees bearing saproxylic fungi were standing dead wood.

The comparison of the stand types showed significant differences for microhabitat density of dendrothelms, cracks, saproxylic fungi and bark losses (Tables 2, 3). Cracks were not observed in the F-managed stands and were mainly linked to the deciduous tree species. Cracks observed on standing dead trees were mostly in the form of bark in the process of peeling. The number of live trees that carried saproxylic fungi was very low (0.3 per ha) in the B-managed stands. We noted also a reduction in the trunk cavity number in managed stands, but the difference was not significant. Management led to a reduction in abundance of these three microhabitats. Dendrothelms and bark losses were more numerous in stands dominated by beech. B-managed stands offered more microhabitats than F-managed ones.

In B-reference stands, the cavities were as numerous on the trunk as at the foot of the tree ($P = 0.5$, NS). Cavities with decaying wood represented more than 70% of the cavities observed. There was less than four empty trunk cavities per ha. More than 80% of the cavities were borne by live trees.

Tree circumference thresholds

There were significant thresholds for the CBH at 225 cm for beech (80% confidence interval: 205–239 cm) and at 135 and 215 cm for fir (80% confidence intervals, respectively: 135–170 and 135–230 cm) (Fig. 4 and see also Fig. 7 and Fig. 8 in supplementary material). Fir did not bear microhabitats if the CBH was below 135 cm. Beech carried on average twice as many microhabitats when CBH $\geq$225 cm; in this case, beech carried on average almost one microhabitat per tree. When CBH $\geq$225 cm, beech carried on average twice as many microhabitats as fir.

Considering the usual circumference classes used in French forestry, beech provided microhabitats in all circumference classes, whereas fir did not provide microhabitats in the Small tree class (CBH $\leq$85 cm; Table 4).

Discussion

Dead wood

Gonin showed in 1988 that montane beech-fir forests have a natural cycle of 300–400 years. This cycle is made up of five phases: “rejuvenation,” “initial,” “optimal,” “terminal” and “decline.” This latter phase is characterized by high volumes of dead and live wood and an aggregated distribution of very large dead trees. The results of dead

Table 2 Distribution of tree bearing microhabitats per species and per microhabitat in the stands (montane beech-fir stands, central Pyrenees)

Microhabitat	Beech	Fir	Other tree species	Live trees	Standing dead trees	All trees
BF-reference						
Cavities	37.41 (85.8%)	4.12 (9.4%)	2.08 (4.8%)	35.11 (80.5%)	8.50 (19.5%)	43.61
Dendrothelms	8.39 (99.9%)	0 (0%)	0.05 (0.1%)	7.70 (91.2%)	0.74 (8.8%)	8.44
Cracks	1.39 (29%)	0.78 (16%)	2.66 (55%)	3.96 (82.0%)	0.87 (18.0%)	4.83
Fungi	12.03 (84.0%)	2.2 (16.0%)	0 (0%)	1.47 (10.3%)	12.85 (89.7%)	14.32
Bark losses	1.32 (12.5%)	0.74 (7.0%)	8.50 (80.5%)	9.69 (91.8%)	0.87 (8.2%)	10.56
Sub-total/ha[a]	60.54 (74.0%)	7.93 (9.7%)	13.29 (16.3%)	57.93 (70.9%)	23.83 (29.1%)	81.76
Dead wood (m^3/ha)	11.79 (29.4%)	25.67 (63.9%)	2.70 (6.7%)	–	–	40.16
B-cable						
Cavities	46.7 (96.1%)	1.92 (3.9%)	0 (0%)	48.6 (100%)	0 (0%)	48.64
Dendrothelms	17.83 (100%)	0 (0%)	0 (0%)	17.8 (100%)	0 (0%)	17.83
Cracks	6.37 (100%)	0 (0%)	0 (0%)	4.32 (67.8%)	2.05 (32.2%)	6.37
Fungi	36.52 (97.6%)	0.88 (2.4%)	0 (0%)	8.86 (23.7%)	28.54 (76.3%)	37.40
Bark losses	71.01 (45.3%)	3.30 (2.1%)	82.51 (52.6%)	156.8 (100%)	0 (0%)	156.82
Sub-total/ha[a]	178.4 (66.8%)	6.1 (2.3%)	82.51 (30.9%)	236.38 (88.5%)	30.59 (11.5%)	267.06
Dead wood (m^3/ha)	52.38 (91.0%)	5.18 (9.0%)	0 (0%)	–	–	57.56
B-managed						
Cavities	43.14 (100%)	0 (0%)	0 (0%)	42.86 (99.4%)	0.28 (0.6%)	43.14
Dendrothelms	54.8 (100%)	0 (0%)	0 (0%)	54.8 (100%)	0 (0%)	54.8
Cracks	2.34 (100%)	0 (0%)	0 (0%)	2.34 (100%)	0 (0%)	2.34
Fungi	8.24 (89.6%)	0.96 (10.4%)	0 (0%)	0.35 (3.8%)	8.85 (96.2%)	9.20
Bark losses	73.83	0 (0%)	0 (0%)	73.8 (100%)	0 (0%)	73.83
Sub-total/ha[a]	182.3 (99.5%)	0.96 (0.5%)	0 (0%)	174.15 (95.0%)	9.13 (5.0%)	183.28
Dead wood (m^3/ha)	8.36 (95.9%)	0.36 (4.1%)	0	–	–	8.72
F-managed						
Cavities	25.53 (81.6%)	5.75 (18.4%)	0 (0%)	30.18 (96.5%)	1.09 (3.5%)	31.28
Dendrothelms	11.49 (99.6%)	0.05 (0.4%)	0 (0%)	9.4 (81.5%)	2.14 (18.5%)	11.54
Cracks	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
Fungi	10.87 (68.2%)	2.52 (15.8%)	2.5 (16.0%)	3.45 (21.7%)	12.48 (78.3%)	15.93
Bark losses	0 (0%)	9.33 (100%)	0 (0%)	9.3 (100%)	0 (0%)	9.33
Sub-total/ha[a]	47.89 (70.3%)	17.65 (25.9%)	2.54 (3.8%)	52.33 (76.9%)	15.67 (23.1%)	68.08
Dead wood (m^3/ha)	3.45	19.13	2.40	–	–	24.98

The first numbers are averages per hectare of the number of trees that carry the microhabitat and those in brackets represent the rate of participation of each species for the microhabitat

[a] This total includes the possibility that certain trees might host several types of microhabitat, which would have the effect of diminishing the number of host trees

Table 3 Impact of silviculture and dominant tree species on microhabitat abundance

	Trunk cavities	Cracks	Saproxylic fungi	Dendrothelms	Bark losses	Total
1-BF-reference	236^{a}	48^{ab}	1.5^{b}	84^{bc}	97^{a}	467^{ab}
2-B-cable	146^{a}	57^{a}	8.9^{ad}	194^{b}	684^{b}	$1,090^{a}$
3-B-managed	100^{a}	23^{ab}	0.3^{cd}	608^{a}	827^{b}	$1,559^{c}$
4-F-managed	142^{a}	0^{b}	3.5^{abcd}	127^{bc}	103^{a}	375^{b}

Stand comparisons were performed with a step-down max-T approach. Scores are linear statistic T values. Live trees only. (Montane beech-fir stands; central Pyrenees). Letters indicate significant differences

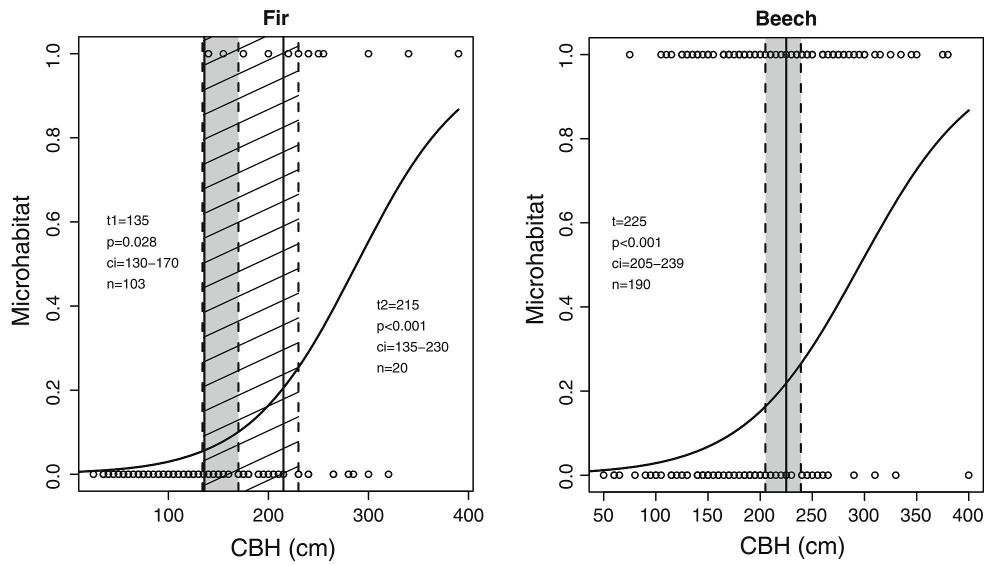

Fig. 4 Data distribution for CBH cm (*X*-axis) and presence/absence of microhabitats (*Y*-axis) for beech (*Fagus silvatica)* and fir (*Abies alba)* with logistic regression curves. BF-reference stands. The *black vertical lines* indicate the threshold values and the two *dotted vertical lines* the range of its 80% confidence intervals (two thresholds for the fir: *gray box* indicates the CI for $t = 135$ cm and the *hatched box* indicates the CI for 215 cm). *t* threshold value, *CI* confidence interval of the threshold value and *n* number of observed trees. Microhabitats on live trees only: cavities, sporophores of saproxylic fungi, dendrothelms, bark losses and cracks. (Montane beech-fir stands in central Pyrenees)

Table 4 Distribution of tree microhabitats (dead wood excluded) and host trees of microhabitats per category of girth

Category of girth	Beech			Silver Fir		
	N total/ha	% of host trees per girth category	% of host trees per stand	*N* total/ha	% of host trees per girth category	% of host trees per stand
Small trees	2.2	53.2	6.42	0	0	0
Medium trees	16.1	33.5	35.76	1.3	1.4	30.62
Large trees	12.6	43.9	30.38	1.2	1.3	29.67
Very large trees	12.4	70	27.45	1.9	2.1	39

Circumference at breast height (CBH): 65 cm $\leq$ Small Tree $\leq$ 85; Medium Tree $\leq$ 150; Large Tree $\leq$ 210; Very Large Tree > 210). Poles (CBH < 65 cm) are not taken into account. Results are expressed as: (1) total number of microhabitats per hectare, (2) relative abundance of the host trees in the girth category, (3) contribution of the girth category to the total number of host trees of the stand. (Montane beech-fir stands in central Pyrenees)

wood volumes (Fig. 2) and field observations showed an absence of the phase of "decline," even in BF-reference stands. It is probable that the long history of anthropization ended too recently to allow the tree communities to finish a complete natural cycle. The modal phase observed in B-cable stands is "terminal," whereas B-managed and F-managed are in an "optimal" phases: management is in the process of rejuvenating stands.

In all the stands that we studied, the volumes of dead wood were inferior to the data given in the literature for sub-natural forests (Christensen et al. 2005). If we express the results on dead wood in % of the total volume of wood (live + dead), Siitonen (2001) gives values much superior to the values that we found: 18–40% (on average 28%) for the forests of common spruce [*Picea abies* (L.) H. Karst.] and Scots pine (*Pinus sylvestris* L.), in keeping with Sippola (2001) who indicates 20–30% for Scandinavian forests. Bobiec et al. (2005) indicate a norm superior to 25% for unmanaged Central European forests. Continuing on from varied bibliographical sources, Gilg (2004) indicates average volumes of 20–40% (from 10 to 50% in extremes). The absence in the BF-reference stands of intense disturbance (storm damage, fire) throughout the last century may also have contributed to this low percentage of dead wood. Dead wood represented 11% of the total volume in the F-managed stands, while it represented only 1.8% in the B-managed stands. The predominance of fir in the F-managed stands explains this difference because, at the time of the last logging, only the stems of fir had a commercial value and industrial softwood was not removed. The volume of dead wood in the B-cable stands is partly linked with several windfall gaps. Nevertheless, only B-managed stands had a lower volume than the threshold range of 20–50 m^3 ha^{-1} revealed by Müller and Bütler (2010) for biodiversity conservation.

All authors point out the relative rarity of dead wood in the form of snags when compared with ground dead wood in very mature stands. Compiling a large amount of data on the forests of Fennoscandia and the North of Russia, Siitonen (2001) gives an average proportion of volume snags/total vol. dead wood as 30%. Muller and Liu (1991) state that, in the mixed forests of North America, snags represent 18% of total volume of dead wood. For Sippola (2001), in European boreal forests, 60–80% of total volume of dead wood is on the ground and only 18–35% is in the form of snags. Nilsson et al. (2002) give an average of 20–40% of volume of standing dead wood for the Polish forest of Bialowieza. Christensen et al. (2005) report that the ratio vol. snags/total vol. dead wood of an unmanaged European beech forest is 41% (22–60%). Dead wood in the form of snags measured in the BF-reference stands (41%) and in the B-cable stands (29%) are in agreement with these proportions (Table 2). On the other hand, the low amounts observed in B-managed (2.4%) and F-managed (8.5%) illustrates a strong effect of silviculture on dead wood proportions.

Christensen et al. (2005) point out that in a beech forest that was unmanaged for a long time, dead wood is to be found in all stages of decay, but we did not find any references giving the distribution of dead wood items per decay stage for the forests of Western Europe. The results obtained for the BF-reference stands are in keeping with the logic of the recycling of dead wood: the volume increased from stage 2 to stage 4 through simple increase in the duration of the stage itself (Maser et al. 1984) and numerous dying trees supplied the dead wood cycle. The volume at stage 5 was relatively low because this stage combines great difficulty in terms of observation with a reduction in volume due to loss in the contours of the piece of wood, as well as the dispersion of the heavily altered woody material. This final result is not in accordance with the observations of McMillan et al. (1977) who showed a volume at stage 5 much superior to the volume of each of the other stages in old stands of Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco]. This is certainly linked to the different behavior of the naturally durable wood of Douglas fir compared with the easily altered wood of beech and silver fir. The dead wood cycle was broken in the B-managed stands, and the main decay stage was linked to the last logging. The renewal in dead wood can be compromised by silviculture. The volume of the available dead wood may sometimes remains high when market conditions for wood are unfavorable to the extraction of certain low value products (e. g., industrial softwood), but the structure and the dynamics of the dead wood are dramatically disturbed.

Tree microhabitats

In the Pyrenees, a lot of mixed beech-fir forests were in the past transformed into pure beech forests. As beech is a much richer microhabitat provider than fir, this transformation increased the total supply of microhabitats per hectare. So, B-managed stands offered more microhabitats than F-managed ones, dominated by fir. But the comparison of beech and fir as regards organisms that are exclusively associated with one or the other tree species shows the importance of the biodiversity which is strictly associated with fir (Larrieu et al. 2010). Furthermore, a mixture of tree species is a guarantee of economic resilience because it is difficult to predict developments in the wood market.

With a total of 47 host trees ha^{-1} (Table 2), cavities were found on 61% of all microhabitat-bearing trees. Garrigue and Magdalou (2000) document 60 trees/ha with cavities in a protected nature reserve. Vallauri et al. (2002) think that at least one cavity per hectare is indispensable and that the optimum is about 10–20 cavity-bearing trees per hectare. Blondel (2005) thinks that the minimum for cavity-dwelling fauna is about 40 cavities/ha usable for birds, which is in keeping with the recommendations of Meschede and Heller (2003) for forest bats. The difference observed between beech and fir (fir only hosts 10% of the total number of cavities in BF-reference stands) is in keeping with the observations of Cline et al. (1980), Mannan et al. (1980) and McClelland and Frissell (1975) as well as Drapeau et al. (2005), who point out generally that cavities are rare in live conifers. Cavities are difficult to observe from the ground, and in deciduous trees, many small cavities are borne by big branches (Tillon 2006). This certainly leads to an underestimate of their number. In spite of trees bearing cavities being removed by thinning, reduction in the trunk cavity number in managed stands was not significant, maybe because this microhabitat is quickly renewed by woodpeckers and the fall of branches.

Dendrothelms were present in the BF-reference stands in only 10% of microhabitat-bearing trees. This result suggests that this microhabitat is quite rare in natural mixed forests, while it is a very frequent microhabitat in artificial beech forests in agricultural landscapes (Kitching 1971). Contrary to beech and maybe in connection with its mode of centripetal deterioration (the external layers rot quite quickly and fall off, while the heart resists much longer), the wood of silver fir only very exceptionally provides conditions favorable to the creation of dendrothelms. By creating surfaces which are subjected to decay, thinning favors the creation of the dendrothelms. Dendrothelms were more numerous in B-managed stands which combine high logging intensity with a predominance of beech. We could not find any references on the effect of dendrothelm densities on taxonomic biodiversity. We think that an increase in the dendrothelm frequency should not have a significant effect on taxonomic biodiversity because there are only a few dendrothelm-dwelling species and dendrothelms make up essentially one taxonomic group only.

In managed stands, logging creates bark losses at the foot of the trees, especially when the slope is steep. The thin bark of the beech facilitates bark loss. In B-cable stands, several windfall gaps and the construction of a forest road created numerous bark losses.

By trying to eliminate trees with characteristics that reduce the quality of their wood, current silvicultural practices reduce the number of microhabitats on live trees. Nevertheless, if a microhabitat is frequent initially (e.g., cavities), it does not disappear during the first thinning, as the forestry norms for harvesting levels are between 20 and 30% of live stems. However, certain microhabitats which are naturally infrequent, such as cracks, may be almost eradicated in one or two logging operations only. The only microhabitats favored by logging are dendrothelms and bark losses. Even if these fertile ecosystems provide a high yield in wood, the fairly short period of rotation between logging operations is certainly a limitation for the enrichment in microhabitats in managed stands.

The impact of management was not directly a reduction in the number of live trees hosting microhabitats. However, there was a trend to a reduction in the abundance of the trunk cavities, cracks and saproxylic fungi. On the contrary, dendrothelms and bark losses are encouraged by recent logging.

Tree circumference thresholds

Our data show clear threshold effects with a threshold of 225 cm circumference for beech and two thresholds, at 135 and 215 cm, for fir. Fan et al. (2003) indicate that there is a minimal girth tree threshold for bearing a cavity but they did not give any details about it, and they indicate that the probability of bearing cavities increases dramatically as tree circumference increases, without any indication of a significant threshold value. In the same way, Winter and Möller (2008) show that in beech forests which were unmanaged for more than 100 years, the number of microhabitats per tree is positively correlated with the girth of the tree, without any threshold effect. Dufour (2003) remarks too that there is an increase in the supply of cavities with circumference but identifies a threshold of 300 cm circumference, above which 1/3 of trees bear cavities. In stands dominated by sessile oak (*Quercus petraea* Liebl.), Tillon (2006) did not observe cavities in trees below a CBH of 38 cm and noted that the girth of cavity-bearing trees was significantly greater than that of trees without cavities. This very low threshold confirms that threshold values differ among tree species.

Considering the usual circumference classes used in French forestry, the increase in % of host trees that we observed concerns mainly the categories Large Tree and Very Large Tree (beech: +59% and fir: +62%). Because of differences of tree density per girth category, the total number of microhabitats per girth category is balanced in the categories Medium trees, Large trees and Very Large trees (Table 4).

Dufrêne et al. (2005) rather indicate an age threshold, pointing out that the availability of microhabitats becomes very high beyond 2/3 of the natural longevity of the tree species, which is approximately 200–250 years for beech and fir. In the context of average montane conditions of the central Pyrenees, a CBH = 220 cm corresponds roughly to an age of 200/250 years. Trees of this age support a great diversity of cavity-dwelling birds (Moning and Müller 2008), epiphytic lichens and molluscs (Moning and Müller 2009) in Bavarian montane forests.

Reconstitution of maturity in montane beech-fir forests

Although surveys of “sub-natural” forests have already been carried out in the Pyrenees using the discriminating criteria of a 50-year management-free period (Ponthus 1996), the characteristics of B-cable stands illustrate that 50 years is too short a period to allow the complete structural maturity of a stand. Indeed, natural stands have a more complex vertical structure, higher dendrological diversity in the bushy and arborescent strata, a higher proportion of Very Large trees and a bigger volume of dead wood, particularly in the form of snags (Greenberg et al. 1997; Nilsson et al. 2002; Christensen et al. 2005).

The characteristics of the BF-reference stands show that in the montane zone of the Pyrenees, more than 100 years without management is necessary to allow the return of a maturity close to that of natural stands.

These considerations are in keeping with the observations of Winter and Möller (2008).

Conclusion and suggestions to improve the current silviculture

Management of montane beech-fir stands reduces the total volume of dead wood and the snag volume, modifies the pattern of decay stages and also reduces the tree species diversity and the diversity of tree microhabitats.

We suggest managing montane mixed stands with an uneven-aged silvicultural system because it facilitates conservation of old-growth forests attributes which are necessary to conserve a wide range of species (Bauhus et al. 2009).

In Pyrenees forests, we are currently seeing the spread of a strategy of reduction in the girth of the largest logged trees, with the aim of increasing the supply to the wood industry and avoiding the depreciation of a high volume of wood. We have shown that in the montane beech-fir stands, the supply of microhabitats is strongly linked to the presence of large trees. It is indispensable to conserve permanently some trees with a CBH of more than 210 cm.

Silver fir hosts a specifically associated biodiversity (Nascimbene et al. 2009; Larrieu et al. 2010). As fir is a much poorer host for microhabitats than beech, it is necessary to favor a higher proportion of fir in the beech/fir mix to favor equal contributions of the tree species in terms of the supply in microhabitats. We suggest also conserving secondary tree species because they carry an associated taxonomic biodiversity.

We suggest that a beech-fir forest which is managed over the long term for the production of wood must consist of a unit made up of two sub-populations of trees. The first sub-population can be intensively managed with a short economic cycle (between 80 and 150 years) for wood production of quality, e.g., to avoid formation of red heartwood in beech wood. For the second sub-population, the natural sylvigenetic cycle should be respected to supply the microhabitats essential to a great part of forest biodiversity and also to increase the volume and the diversity of dead wood. Because it is important to assure the renewal of these attributes, a minimum of 10–20% of the surface area could be given over to the conservation or recruitment of trees with microhabitats (not including the area occupied by dead wood on the ground). This surface can be situated in a more or less aggregated manner, taking advantage of particular conditions such as rocks or steep slopes. To take into account the sometimes very low ability of certain taxa to spread (see for ex. Speight 1989; Ranius and Henin 2001; Dajoz 2007), care must also be taken to conserve biologically valuable trees which are isolated, to satisfy the necessity of a certain spatial continuity of microhabitats. This combination is recommended by Franklin et al. (1997). The microhabitat-bearing trees have generally little commercial value: a high proportion is waste wood and a high percentage is wood of pulp quality. In the context of montane forests, the cost of removing them is therefore often higher than their commercial value. Their preservation within the stand therefore improves the economic output of forestry stands. The surface area which is occupied and "non productive" may be counterbalanced by their high functional interest.

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