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Influence of tree characteristics and forest management on tree microhabitats

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ABSTRACT

Higher densities of tree microhabitats in unmanaged forests may explain biodiversity differences with managed forests. To better understand the determinants of this potential biodiversity indicator, we studied the influence of tree characteristics on a set of tree microhabitats (e.g. cavities, cracks, bark features) on 75 plots in managed and unmanaged French forests. We hypothesized that the number of different microhabitat types per tree and the occurrence of a given microhabitat type on a tree would be higher in unmanaged than in managed forests, and that this difference could be linked to individual tree characteristics: diameter, vitality and species. We show that unmanaged forests contained more trees likely to host microhabitats (i.e. large trees, snags) at the stand level. However, at the tree level, forest management did not influence microhabitats; only tree characteristics did: large trees and snags contained more microhabitats. The number and occurrence of microhabitats also varied with tree species: oaks and beech generally hosted more microhabitats, but occurrence of certain types of microhabitats was higher on fir and spruce. We conclude that, even though microhabitats are not equally distributed between managed and unmanaged forests, two trees with similar characteristics in similar site conditions have the same number and probability of occurrence of microhabitats, whatever the management type. In order to preserve biodiversity, foresters could reproduce unmanaged forest features in managed forests through the conservation of specific tree types (e.g. veteran trees, snags). Tree microhabitats could also be more often targeted in sustainable forest management monitoring.

1. Introduction

Since the Rio conference, integrating biodiversity concerns into management policies has been a priority (Secretariat of the Convention on Biological Diversity, 2006). However, management choices and political decisions related to biodiversity still tend to be based on "anecdote and myth" rather than scientific evidence (Sutherland et al., 2004). Forest management is no exception to the rule. Indeed, despite significant advances in the recent years (e.g. Lindenmayer et al., 2006; Smith et al., 2008), further research is still needed to provide well-documented and scientifically-based quantitative methods and indicators to assess sustainable forest management (Barbier et al., 2009). In addition, due to their key role in biodiversity conservation (Paillet et al., 2010), unmanaged forests may serve as references because they tend to have more complex tree composition and stratification, and more structures favourable to forest-dwelling species (Hunter, 1999; Peterken, 1996).

The term "microhabitat" encompasses several forest features that differ among authors: microhabitat s.l. are small substrates used by certain species, or groups of species, to grow, nest or forage (e.g. numerous bryophytes preferentially grow on deadwood logs, Fenton and Bergeron, 2008). Here we adopted a more restrictive definition and considered only tree microhabitats (hereafter referred to as "microhabitats"), which in our case encompass only microhabitats linked to living trees and snags (e.g. cavities, cracks, bark characteristics).

Lindenmayer et al. (2000) proposed using structure-based biodiversity indicators to assess forest management. In terms of indicator value, microhabitats have a complementary role compared to stand structure indicators such as deadwood volume: microhabitat indices could provide more precise information on taxa or ecological groups that use them for nesting, foraging or other functions (Michel and Winter, 2009; Winter and Moller, 2008), and could partly explain biodiversity variations between managed and unmanaged forests (Hansen et al., 1991; Norden and Appelqvist, 2001). Indeed, microhabitats are generally thought to be more abundant in unmanaged than in managed forests since forest management tends to reduce the number of trees susceptible to host microhabitats. Yet, compared to other typical structural features of unmanaged forests (e.g. dead wood, standing dead trees [snags] and veteran trees), microhabitats per se have rarely been studied. More specifically, few studies have tackled the ecological and management determinants of the abundance and richness of a set of microhabitats. In the framework of sustainable forest management,

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a better knowledge of the factors influencing microhabitats would allow forest managers to adopt scientifically-based practices to preserve biodiversity. In particular, it is crucial to better understand to what degree microhabitats are indirectly related to certain management practices (e.g. tree species composition) and how the type of management can influence them (Barbier et al., 2009).

To our knowledge, only Winter and Moller (2008), Michel and Winter (2009) have explored the link between microhabitats, management type and tree diameter. Following their work, we have hypothesized that the presence of microhabitats on a tree is influenced by either management or individual tree characteristics or a combination of both. We address this general hypothesis through quantitative analyses that include a larger set of tree characteristics than those studied by Winter and Moller (2008), Michel and Winter (2009), including senescence and tree species. We analyzed the combined effects of management and tree characteristics on the number of different microhabitat types per tree and the occurrence of a given microhabitat type on a tree (hereafter referred to respectively as "number" and "occurrence" of microhabitats).

2. Materials and methods

2.1. Study site descriptions and plot selection

We studied five French forests, two of which are situated in lowlands (Fontainebleau and Auberive) and three in mountain regions (Chartreuse, Vercors and Ventron). In the lowland forests, forest type was voluntarily limited to dominant beech (*Fagus sylvatica* L.) and oaks (*Quercus robur* L. and *Q. petraea* Liebl.), and in mountain forests to dominant beech, white fir (*Abies alba* Mill.) and Norway spruce (*Picea abies* (L.) Karst.). These forest types represent around 40% of the French forest cover (French Forestry Inventory data 2005–2008, www.ifn.fr). Each site contains a forest reserve where no management has occurred for a minimum of at least 10 years, and a maximum of more than 150 years (Table 1). Managed study plots were selected within a radius of 5 km around the forest reserve boundaries:

- in the two lowland forests, plots were drawn at random on a regular grid and paired, one within the managed zone, the other within the unmanaged zone so that each pair of plots shared the same soil conditions. Practically, this procedure of random plot selection ensured that plots located in managed forests were representative of a "mean" type of forest management of the forest;
- in the mountain forests, we chose plot pairs matched according to forest site and, to avoid elevation and aspect biases, we did not randomise.

A total of 75 plots were selected: most of the plots in unmanaged portions of the forest were matched with their equivalent in terms of forest site conditions in the managed portion of the same study site. However, due to field constraints, there were three more plots in managed forests than in unmanaged forests (without bias in terms of site conditions).

2.2. Environmental variables and stand structure

For practical reasons, the protocols used to describe the forest stand structure differed between lowland and mountain forests. We measured the diameter of living trees with a Diameter at Breast Height (DBH) of more than 20 cm in lowland forests (resp. more than 30 cm in mountain forests) and comprised within a fixed relascopic angle of 2% (resp. 3%). Practically, this means that a tree with a DBH of 60 cm was sampled at a maximum distance of 30 m distance from the centre of the plot (resp. 20 m) and accounted for a basal area of 1 m^2/ha (resp. 2.25 m^2/ha). Diameter and height of standing dead trees (snags) with a DBH of more than 30 cm were measured within a radius of 20 m (1257 m^2). Diameter, species and vitality (dead or alive) were noted for all 1252 trees (Table 2). In order to check how our results were potentially influenced by the incorporation of trees with DBH < 30 cm in lowland forests only, we restricted the dataset to trees with DBH > 30 cm. As these analyses largely provided much the same results, the results presented here concern the complete dataset.

2.3. Microhabitat inventory

We visually searched these 1252 trees for microhabitats and recorded the presence of each microhabitat type on each tree. To avoid observer effects, all the surveys were performed by one observer (Y.P.). We focused on 26 microhabitat types (Table 3), most of them were adapted from Winter and Moller (2008) and Michel and Winter (2009). Microhabitats 1–7 describe general tree features (mostly levels of canopy deadwood) whereas microhabitats 8–26 describe more local tree structures (microhabitats s.s.).

Percentage of dead wood in crowns was observed on living trees. Compared to Winter and Moller (2008), Michel and Winter (2009), we created three different categories of dead crown microhabitats (microhabitats 2–4, Table 3): 10–25%, 25–50% and >50% of dead crown. We also added three microhabitat types: "Tree crown remnants" (microhabitat 1) was only recorded on snags; Bryophytes and Ivy covers (microhabitats 25 and 26) were recorded when they covered more than 50% of the observed surface of the base or the trunk of the tree. These two microhabitats were added for their potential role as nesting and foraging sites for several species of birds and insects (see e.g. Mitchell, 1973).

2.4. Statistical analyses

We processed all the analyses with the R software v. 2.5.1 (R Development Core Team, 2007). Wilcoxon-tests were used to compare continuous stand characteristics and quasi-Poisson generalized linear models to compare count data stand variables.

We considered two response variables in our main analyses: "microhabitat number" corresponded to the number of different microhabitat types per tree; "occurrence" corresponded to the presence of a given microhabitat type on a tree. Five explanatory variables were tested in the models: management type (managed vs. unmanaged forests), site, tree species, diameter (continuous variable), and vitality (cf. Table 2 for the levels of each variable). We modelled the response of microhabitat number and occurrence of individual microhabitats with generalized linear mixed models (GLMM, Bolker et al., 2009), using the lmer function in the lme4 R package (with the default Laplace approximation to the log-likelihood). Indeed, GLMM can handle non-normally distributed data and incorporate random effects. Both aspects were important here: our data were either counts (microhabitat number) or binary data (presence/absence), for which the normal distribution was not appropriate. In addition, our sampling design was based on the survey of several trees within the same plot, which meant potentially higher similarity between trees in the same plot than between trees in different plots. We therefore included a Gaussian random "plot" effect to take this source of spatial autocorrelation into account. We compared several models for microhabitat number and occurrence responses to management type and tree characteristics:

[1] Null model.

[2–6] One-factor model: Management type, Diameter, Vitality, Site, Tree species.

Table 1
Study sites and stand characteristics of the studied sites. MAN = managed plots; UNM = unmanaged plots. Wilcoxon-tests: $^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$; $(*)\ p < 0.1$; n.s: non-significant result.

Site					
Site characteristics	Auberive	Fontainebleau	Chartreuse	Vercors	Ventron
Coordinates	47°47′N, 5°3′E	48°24′N, 2°42′E	45°20′N, 5°46′E	45°11 N, 5°30′E	47°56′N, 6°56′E
Mean elevation (m)	440	110	1280	1140	920
Substrate type	Calcareous	Acidic	Calcareous	Calcareous	Acidic
Time since abandonment (years)	40	>150	30	10	20
Surface area of unmanaged reserve (ha)	280	300	30	300	300
Forest type	Mixed beech-oak lowland forest	Mixed beech-oak lowland forest	Mixed beech-fir-spruce mountain forest	Mixed beech-fir-spruce mountain forest	Mixed beech-fir mountain forest

Stand characteristics		Auberive			Fontainebleau			Chartreuse			Vercors			Ventron			Total		
		MAN	UNM	p	MAN	UNM	p	MAN	UNM	p	MAN	UNM	p	MAN	UNM	p	MAN	UNM	p
Number of plots		12	11		13	12		5	5		5	5		4	3		39	36	
Mean basal area (m^{2s}/ha) (S.D.)		18.2 (2.9)	16.7 (6.6)	n.s	21.4 (5.2)	24.5 (6.2)	n.s	26.4 (5.8)	36.3 (5.5)	(*)	38.7 (9.2)	40.9 (5.0)	n.s	21.3 (4.9)	29.8 (7.3)	n.s	23.3 (8.2)	26.5 (10.5)	n.s
Mean snag volume (m^3/ha) (S.D.)		4.6 (7.3)	6.6 (7.9)	n.s	4.15 (8.6)	52.2 (42.7)	***	1.1 (2.5)	5.5 (6.0)	n.s	5.2 (7.2)	24.7 (39.7)	n.s	10.1 (4.7)	14.3 (17.2)	n.s	4.7 (7.2)	24.8 (34.8)	**
Mean log volume (m^3/ha) (S.D.)		14.5 (14.5)	38.0 (51.8)	n.s	14.2 (14.0)	123.2 (68.3)	***	40.1 (21.3)	26.3 (14.6)	n.s	14.8 (19.9)	60.7 (72.0)	n.s	37.4 (29.4)	17.4 (4.8)	n.s	20.1 (19.8)	66.2 (68.2)	***
Mean deadwood volume (m^3/ha) (S.D.)		19.2 (16.1)	44.5 (54.0)	n.s	18.4 (15.2)	175.4 (85.8)	***	41.2 (23.4)	31.9 (18.3)	n.s	20.1 (26.3)	85.5 (84.1)	(*)	47.5 (33.3)	31.7 (21.9)	n.s	24.8 (22.0)	91.0 (89.1)	***
Proportion of basal area represented by each dominant tree species (%)	Beech	44.5	49.1	n.s	40.2	74.9	***	4.0	38.5	***	16.3	35.9	n.s	21.4	31.1	n.s	31.9	52.9	***
	Oaks	30.4	27.9	n.s	49.5	12.4	**	–	–	–	–	–	–	–	–	–	25.8	12.7	n.s
	Fir and Spruce	–	–	–	–	–	–	92.1	38.5	*	74.3	48.1	n.s	52.0	45.0	n.s	16.2	11.8	n.s

Table 2
Number of trees in each category of variable comparing managed and unmanaged forests in France. Quasi-Poisson and quasi-likelihood GLM applied to plot level data: $^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$; $(*)\ p < 0.1$; n.s: non-significant result.

Variables	Levels	Managed	Unmanaged	Total	p
Vitality	Snags	14	46	60	***
	Living trees	612	580	1192	n.s.
Tree species	Oaks	224	107	331	*
	European Beech	201	363	564	**
	White fir and Norway spruce	138	96	234	n.s.
	Other species	63	60	123	n.s
Diameter classes	$20 \leqslant \text{DBH} < 47.5$	379	272	653	(*)
	$47{,}5 \leqslant \text{DBH} < 62.5$	158	158	316	n.s.
	$\text{DBH} \geqslant 62.5$	89	196	285	***

[7] Complete additive model: Management type + Diameter + Vitality + Site + Tree species.

[8] Management type + Diameter + Vitality + Site + Tree species + Tree species: Diameter.

[9] Management type + Diameter + Vitality + Site + Tree species + Management type: Diameter.

[10] Management type + Diameter + Vitality + Site + Tree species + Management type: Diameter + Management type: Site + Management type: Tree species.

We limited our choice of models to those that we assumed to be relevant to our investigation. Other models presented singularities, in particular the ones that interacted with vitality, and were impossible to compute. The selected models were developed as follows (see Appendix B and C for the parameters used in the models):

(i) Microhabitat number: we used quasi-likelihood methods, based on quasi-Poisson quasi-likelihood, to account for a dispersion of data that could be other than 1, the value for the Poisson distribution (McCullagh and Nelder, 1989). Models [1–10] were compared on the basis of their corrected Quasi Akaike Information Criterion (QAICc), a particular form of Akaike Information Criterion (AIC) adapted for the "quasi" distribution. The dispersion parameter of model [10] was chosen for all models (cf. Bolker et al., 2009). The model with the lowest QAICc was selected, except if simpler, nested models had a QAICc less than two points higher. To test the effects of each variable on the response variable, we used a multi-comparison test on the best model (R package: multcomp, function: glht). This test provided the effect of each variable and the significance of the different levels for each variable;

(ii) Microhabitat occurrence: for the 10 microhabitat types that occurred more than 40 times in our sample (1252 trees), we used binomial GLMM. Following the guidelines put forward by Harrell (2001) to avoid over-parameterization, we selected the models differently with respect to the frequency of observation for each microhabitat: for microhabitat types occurring less than 100 times in the dataset, we tested only the null and one-factor models [2–6]; for more frequent microhabitat types, we tested all ten models. These models were compared on the basis of their AICc, the small sample correction of the AIC. The model with the lowest AICc was chosen, except if simpler, nested models had an AIC less than 2 points higher. Some microhabitat types were rare (or even absent) for some levels of a variable, e.g. ivy was very scarce in mountain forests. In this case, high variances were associated to the estimates of the fixed effects. Contrary to the

Table 3
List of the 26 tree microhabitats sampled in managed and unmanaged plots. Microhabitats 1 to 7 represent general tree features while microhabitats 8 to 26 describe more specific tree structures (microhabitats s.s.).

Microhabitat type	Winter and Moller (2008)	Michel and Winter (2009)
1. Presence of the crown skeleton (snags only)		
2. Between 10% and 25% of dead crown: one or more main branches are dead. The living crown represents 75% of the former total crown	X (modified)	X (modified)
3. Between 25% and 50% of dead crown: one or more main branches are dead. The living crown represents between 50 and 75% of the former total crown	X (modified)	X (modified)
4.>50% the dead crown: one or more main branches are dead. The living crown seems to be < 50% of the former total crown	X (modified)	X (modified)
5. Broken stem: the primary crown is totally absent with or without presence of a secondary crown. Main parts of the tree stem are already dead with decomposing processes	X	X
6. Broken fork: complete fracture of one of the two forking branches; the loss of one forking branch results in a severe damage of the main stem	X	
7. Splintered stem: the split-up results in numerous scales (minimum 5) of wood > 50 cm long	X	X
8. Conks of fungi. Fruiting bodies, diameter > 5 cm.	X	X
9. Conks of fungi. Fruiting bodies > 5 cm in diameter or occur in 10 cm long cascades of smaller fruiting bodies	X	
10. Woodpecker cavities with > 2 cm aperture.	X	X
11. Non-woodpecker cavities with > 5 cm aperture: formed after injury, branch fall...		X
12. Cavity string: at least three woodpecker cavities in a stem with a maximum distance of two meters between two cavity entrances. Cavity strings are an important starting point for the development of deep and long lasting stem cavities.	X	X
13. Deep stem cavities: a tubular cavity in the base of the tree.	X	X
14. Deep stem cavities: a tubular cavity in the base of the tree with mould.	X	
15. Lightning scar: a crack caused by lightning; at least 3 m long and reaching the sapwood	X	
16. Cracks: cleft into the sapwood > 25 cm long along the stem and at least 2 cm deep in the sapwood	X	X
17. Bark pocket: space between loose bark and the sapwood with a minimum extension of 5 cm × 5 cm × 2 cm	X	X
18. Bark pocket with mould: same structure and size as 17. but with mould	X	X
19. Bark loss: patches with bark loss of at least 5 cm × 5 cm mainly caused by felling or natural falling of trees	X	
20. Bark burst: black burst of bark often with resin indicating injury/disease		X
21. Canker: proliferation of cell growth; irregular cellular growth on stems or branches, which is caused by bark-inhabiting fungi, viruses and bacteria. We recorded areas of canker > 10 cm in diameter	X	X
22. Witch broom: dense agglomeration of branches from a parasite or epicormic branching.		X
23. Heavy sap or resin: fresh heavy flow of sap or resin at least 30 cm long or > 5 flows of sap or resin of smaller size		X
24. Sap or resin drop: Only a few sap or resin drops indicating a minor injury		X
25. Bryophytes developed on > 50% of the base or trunk area		
26. Ivy developed on > 50% of the base or trunk area		

analyses on the number of microhabitat types, the multi-comparison tests described above were not available for probability of occurrence; we re-estimated the model parameters using Markov Chain Monte-Carlo fitting procedure (Hastings, 1970; Metropolis et al., 1953) to test the effects of each variable on the response variables (R-package: lme4, function: mcmcsamp). Using these a posteriori simulated values, we calculated the significant pairwise differences among the different levels of the explanatory variables (Gelman et al., 2004).

3. Results

3.1. Stand characteristics

Mean basal area tended to be higher in unmanaged than managed forests but did not significantly differ, except in Chartreuse (Table 1). Mean snag, log and total deadwood volumes were significantly higher in unmanaged forests, but at the site level, only differed significantly in Fontainebleau. The proportion of beech was significantly higher in unmanaged forests, notably in Fontainebleau and Chartreuse. The proportion of oaks was significantly higher in managed stands than in unmanaged stands in Fontainebleau, but for global results, did not differ between these two types of regimes. The same pattern was found for fir and spruce in the Chartreuse forest. Globally, the number of snags, trees with DBH $\geqslant$ 62.5 cm ($p < 0.001$) and beech trees ($p < 0.01$) was significantly higher in the unmanaged plots (Table 2). In contrast, oaks ($p < 0.01$) and trees with 20 $\leqslant$ DBH $\leqslant$ 47.5 cm ($p < 0.05$) were more numerous in managed forests.

3.2. Number of microhabitats per tree

The model with the lowest QAICc value was the complete additive model with the Diameter: Tree species interaction (model [8]; Appendix A). Site, tree species and vitality had a significant effect ($p < 0.001$) on the number of microhabitats. The number of microhabitats was significantly higher on the sites at Auberive (2.36 microhabitats per tree) and Chartreuse (2.24) than at Ventron (1.63) and Fontainebleau (1.28, Fig. 1). The Vercors site (1.94) had significantly more microhabitats than only one other site – Fontainebleau (Fig. 1). Surprisingly, once the model was corrected for tree characteristics and site effect, the number of microhabitats per tree in managed and unmanaged forests did not differ significantly ($p = 0.18$). Oaks had a significantly larger number of microhabitats per tree (2.66) than all three other tree species groups, including beech (2.23) (Fig. 1). Firs, spruces and "other species" had a significantly lower number of microhabitats (resp. 1.72 and 1.96) than beech but did not differ from each other. The number of microhabitats increased with diameter (Fig. 2), at a higher rate

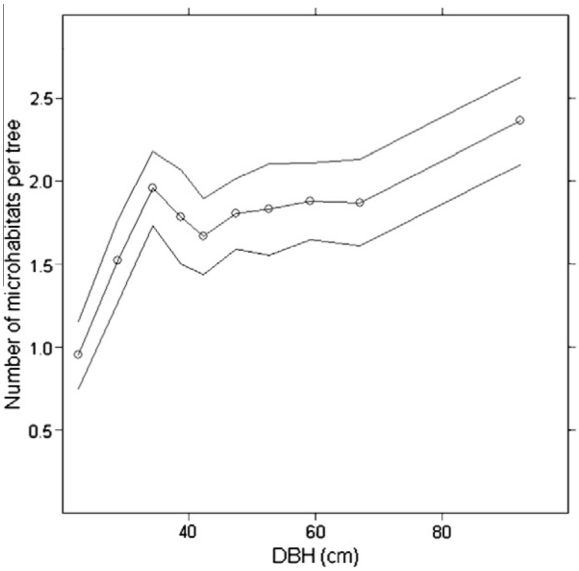

Fig. 2. Relationship between the number of microhabitats and diameter at breast height (DBH) based on raw data. Each open dot represents the mean value for 100 trees, grouped in ascending order of DBH. Upper and lower lines represent the 95% confidence intervals (see Harrell, 2001 for details on these types of graphical representations).

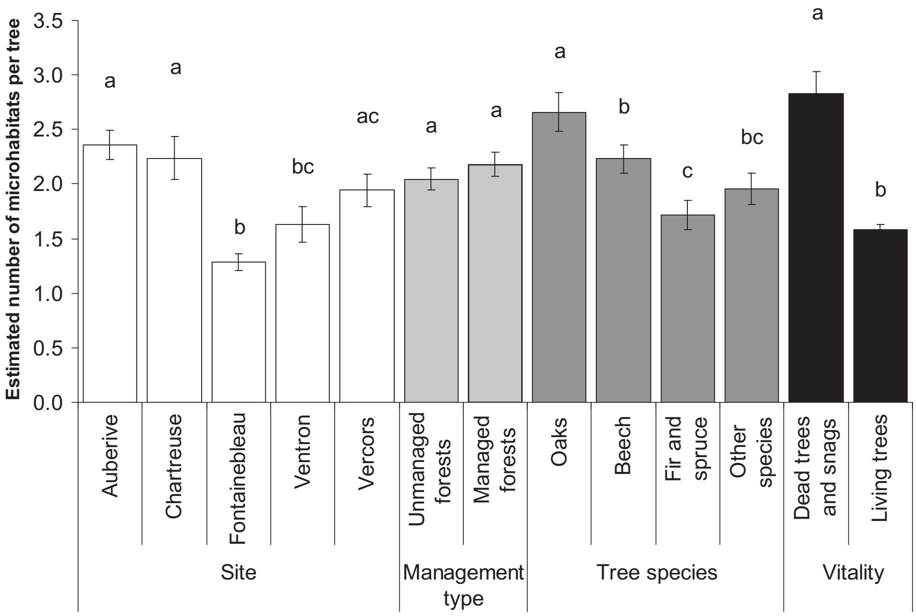

Fig. 1. Estimated number of microhabitats per tree derived from the selected generalized linear mixed effects model. Error bars are standard errors. Different letters indicate significantly different levels for a variable, assigned per group of variables (i.e. separately for Site, Management, Tree species and Vitality).

for beech than for oaks or for fir and spruce (Appendix B). Snags had a significantly higher number of microhabitats than living trees with almost twice as many microhabitats per tree (2.82 vs. 1.58).

3.3. Occurrence of microhabitat types

We modelled the occurrence of the following 10 microhabitat types: presence of ivy, non-woodpecker cavities, conks, woodpecker cavities, canker, dead crown (10–25%), cracks, bark pockets, bark losses and bryophytes (Table 4). At least one of the variables tested had an effect on the presence of the microhabitat types (i.e. the null model was never the best model) and no microhabitat type responded to management only (Table 4). The different models estimated the probability of occurrence of each microhabitat on a logit scale (Appendix C). The backward transformation of this probability to a linear scale presented below neglects the plot random effect.

Only presence of ivy responded to site: the highest frequency was observed for Auberive (14.3%) which significantly differed from Fontainebleau (2.9%). The probability of occurrence was nearly null at the three other sites. Presence of non-woodpecker cavities increased significantly with diameter. Presence of conks of fungi and woodpecker cavities best responded to tree vitality: the probability of occurrence was significantly higher on snags (respectively 21.2% and 29.9%) than on living trees (respectively 2.2% and 2.3%). Canker responded to tree species: the probability of occurrence was significantly higher on fir and spruce (15.9%) than on oaks and beech (resp. 1.7% and 0.8%) and nearly null for “other species”.

Presence of dead crown (10–25%) was significantly higher at Auberive and Fontainebleau than at Ventron. Chartreuse and Vercors did not differ from the other sites. The effects of management and diameter were not significant (the confidence interval included zero, see Appendix C). The highest probability of occurrence of dead crown was observed on oaks (35.4%), which significantly differed from “other species” (8.0%) and from beech (11.7%), but not from fir and spruce (14.3%).

Cracks differed between lowland and mountain sites: cracks were significantly more frequent in Chartreuse, Vercors and Ventron forests than in Auberive; the frequency of cracks in Fontainebleau was not significantly different from that of the other sites except Vercors. The effect of management was not significant, but cracks occurred significantly more often on snags than on living trees and on large trees than on small trees. The probability of occurrence of cracks was not significantly different among tree species.

The presence of bark pockets was significantly higher in Auberive than in Fontainebleau and Ventron. Chartreuse and Vercors did not differ from the other sites. Bark pockets occurred significantly more often in managed than in unmanaged forests and on snags than on living trees. Neither diameter nor tree species significantly influenced bark pocket occurrence.

Bark losses were significantly less frequent in Fontainebleau than in Auberive, Vercors and Chartreuse. No other difference between sites was detected. The probability of occurrence of bark losses tended to be higher in managed than in unmanaged forests. Snags had a significantly higher probability of occurrence of bark losses than living trees. Large-diameter trees generally had more bark losses than small trees, except for oaks. The frequency of occurrence of bark losses did not differ significantly among tree species.

The presence of bryophytes responded to the model with Tree species: Diameter interaction. The probability of occurrence of bryophytes was significantly lower in Fontainebleau than at all the other sites except for Vercors. The effect of management was not significant, whereas bryophytes were significantly more frequent on living than on dead trees. In addition, bryophytes were less often found on fir and spruce than on beech, oaks and other tree species. The presence of bryophytes increased with diameter at a higher rate for “other species” than for oaks or for fir and spruce.

4. Discussion

We showed that the number and occurrence of microhabitat types were mainly influenced by tree characteristics and that, surprisingly, once these characteristics were taken into account in our models, management generally had no effect on microhabitat indices. The density of large-diameter trees and snags favourable to microhabitats was higher in unmanaged than in managed forests, but two similar trees, whether in managed or unmanaged forests, had almost the same number and occurrence of microhabitat types.

Our findings confirm that snags have a predominant role in the availability of tree microhabitats, as earlier studies carried out in other biogeographic areas have emphasized (e.g. Bull et al., 1997; Nilsson et al., 2001). In our study, snags displayed almost twice as many microhabitats as living trees. During the tree senescence and decay process, favourable conditions for microhabitats are at work: softened and dried wood allows cavity builders to nest and forage more easily (woodpeckers, e.g. Rolstad et al., 2000;

Table 4
Model selection (GLMM with binomial distribution) by AICc for individual microhabitats. The number of degrees of freedom was that specified by the log-likelihood function (named logLik, Bolker et al., 2009). The model with the lowest AICc was chosen, except if simpler, nested models had an AICc less than 2 points higher. The AICc of the selected models are in bold characters.

Microhabitat type	Number of occurrences	[1] Null	[2] Site	[3] Management	[4] Diameter	[5] Vitality	[6] Tree species	[7] Complete additive	[8]	[9]	[10]
8. Conks of fungi	40	358	358	360	345	**326**	357	–	–	–	–
10. Woodpecker cavities	46	387	376	379	378	**341**	383	–	–	–	–
11. Non-woodpecker cavities	62	943	936	937	**912**	944	921	–	–	–	–
21. Canker	70	496	455	498	482	492	**435**	–	–	–	–
26. Ivy	96	582	**543**	583	572	582	552	–	–	–	–
16. Cracks	163	468	461	461	459	442	462	**403**	406	405	406
17. Bark pockets	127	785	785	785	787	757	783	**748**	748	750	746
2. Dead crown (10–25%)	246	1153	1126	1155	1153	–	1087	**1081**	1085	1083	1089
25. Bryophytes	485	1177	1120	1177	1179	1168	1095	1017	**1006**	1019	1005
19. Bark loss	530	1379	1337	1381	1351	1343	1367	1251	**1245**	1249	1257

Smith, 2007). These cavities are later suitable for use by other taxa, for example birds (Remm et al., 2006), bats (Kalcounis-Ruppell et al., 2005) and other mammals (Bull et al., 1997), bees (Westphal et al., 2008), as well as saproxylic organisms (Winter et al., 2005). Decaying bark, cracks and polypores increase the number of niches available for forest-dwelling species, such as bats and insects. Conks provide an important resource for mycetophagous insects and indirectly for their predators (e.g. Topp et al., 2006) and studies have shown correlations between the presence of conks and other taxa (e.g. birds, Jackson and Jackson, 2004; or saproxylic beetles, Jonsson and Jonsell, 1999).

Tree diameter also influences microhabitats. Our results confirmed a previously-observed trend (Michel and Winter, 2009; Winter and Moller, 2008): the larger the diameter of a tree, the higher the number of microhabitat types. Larger – and most of the time older – trees are more likely to have suffered injuries from harvesting operations or from natural disturbances (Bobiec, 2002; Boncina, 2000). In addition, larger trees appear to be more attractive to cavity builders because wood thickness provides buffered micro-climatic conditions inside the cavities for nesters (Boonman, 2000; Remm et al., 2006), although our analyses only partly confirmed this trend. In our study, diameter was the main factor influencing the number and probability of occurrence of the following microhabitats: presence of non-woodpecker cavities and – combined with other variables – cracks, bark losses and bryophytes.

Contrary to the previous studies (Michel and Winter, 2009; Winter and Moller, 2008), our results concerned mixed-forest types (i.e. beech-oak and beech–fir–spruce mixtures) and highlighted the fact that tree species also influence microhabitat number and occurrence. There were more microhabitats on oaks than on the other tree species and on beech than on fir and spruce. Oaks also had higher dead crown levels and beech had more cracks and higher bryophyte cover. However, canker was more frequent on fir and spruce and differences in microhabitats occurrence among tree species were not systematic (e.g. bark pockets and bark losses). Comparison of microhabitats among several tree species has rarely been studied except for a few reports in the United States (Bull et al., 1997; Parks et al., 1997). Our results made clear that the effect of tree diameter could vary among tree species: the increase in total number of microhabitats with tree diameter was stronger for beech and other tree species than for oaks or fir and spruce. More specifically, the increase in occurrences of bryophytes and bark loss with diameter was stronger for "other species" than for oaks (and fir and spruce in the case of bryophytes).

Presence of ivy was significantly influenced by site. Features and niches associated to ivy presence are particularly important for their role as foraging and nesting spots for certain birds and insects (Diptera, Lepidoptera) because ivy flowers and fruits in trees and not on the ground, and when other nectar and fruit resources are rare (Jacobs et al., 2009). More generally, most analyses with a sufficient number of occurrences revealed a strong and significant variation with site (Fig. 1, Appendix B and C).

Finally, our study of microhabitats at the tree level failed to highlight differences between managed and unmanaged forests, once tree characteristics were taken into account. The only exceptions were for bark characteristics that occurred more often in managed than in unmanaged forests. This particular effect is likely due to damage occurring during harvesting operations (Michel and Winter, 2009; Winter and Moller, 2008). However, if management type per se did not significantly influence tree-level microhabitats, the availability of trees rich in microhabitats (snags, large trees) was much higher in unmanaged than in managed forests. The fact that the unmanaged areas in our study had been managed in a relatively recent past may explain the limited impact of management at a tree scale. However, we found the same pattern in Fontainebleau where management stopped more than 150 years ago.

5. Implications for forest management

Our results raise questions about forest management strategies to be adopted for preserving microhabitats. We showed that trees in managed and unmanaged stands have the same levels of microhabitats once tree characteristics are taken into account. This result contrasts with those found in German beech forests by Winter and Moller (2008, Fig. 4), where beeches with similar diameters were poorer in microhabitats in managed than in unmanaged stands. One possible explanation could be that microhabitat-rich trees were more often harvested in Germany than in France. Specific management guidelines could therefore target microhabitat-based selective cutting to preserve biodiversity in managed forests by cutting microhabitat-poor trees while preserving microhabitat-rich trees. However, increasing the number of tree microhabitats could rely on other forest management strategies than those directly based on microhabitats. Management strategies could either target management abandonment and preservation of old growth forests (Parviainen et al., 2007), or focus on the retention, in managed forests, of microhabitat-rich tree types (large and veteran trees, snags and tree species such as oaks and beeches). The choice of a strategy will partly depend on the results of validation research. Indeed, using microhabitat-based indicators in sustainable management assessment still must be validated. First, potential observer effect, avoided in this study since the surveys were carried out by only one observer, should be tested. Second, the exhaustiveness of the list of microhabitats could be improved by conducting similar studies in ecological contexts other than temperate lowland and mountain forests, e.g. riparian and Mediterranean forests. Third, the cost of such surveys should be evaluated to keep forest monitoring cost-effective. Fourth, the spatial scale for recording such structural features should probably be optimized. Finally, the link between microhabitat type/abundance and biodiversity needs to be better assessed. Studies relating microhabitat characteristics to biodiversity data could provide a better knowledge of how species or species groups are linked to individual or groups of microhabitat types. This in turn is required to improve our knowledge of the potential ecological value of microhabitats and provide managers with guidelines for the appropriate density of microhabitats or microhabitat-rich tree types within stands (see e.g. Butler et al., 2004; Nilsson et al., 2002). These guidelines could finally be included in certification processes such as the Forest Stewardship Council (http://www.fsc.org) or the Pan-European Forest Certification (http://www.pefc.org).

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Appendix A. QAICc table for "number of microhabitats model selection

The QAICc of the selected model is in bold characters. Compared with Bolker et al. (2009), two modifications were incorporated: one degree of freedom was added for the dispersion parameter (Burnham and Anderson, 2002) and the scale parameter of the GLMM was squared (cf. https://stat.ethz.ch/pipermail/r-sig-mixed-models/2010q1/003345.html).

Microhabitat type	No of trees with at least 1 microhabitat	(M1) Null	(M2) Site	(M3) Management	(M4) Diameter	(M5) Vitality	(M6) Tree species	(M7) Complete additive	(M8)	(M9)	(M10)
Number of microhabitats	1041	1834	1799	1832	1707	1785	1804	1545	**1525**	1546	1542

Appendix B and C

Values of the estimates derived from generalized mixed effects models. Vitality and management type variables were centred: equalled 1 for snags and unmanaged stands and −1 otherwise. Diameter variable was manually standardized using the formula [diameter (in cm) −45)/30], to reach an interpretable nearly-standardized variable: an increase of 1 in the variable Diameter is therefore equivalent to an increase of 30 cm in the real diameter.

Appendix B. Number of microhabitat types. SE: standard error

Microhabitats	Explanatory variables	Levels	Mean value of the estimates	SE
Number of microhabitats	Tree species	Oaks	0.31	0.08
		Beech	0.13	0.07
		Fir and spruce	−0.13	0.09
	Management type		−0.03	0.02
	Vitality		0.29	0.03
	Sites	Auberive	0.92	0.08
		Chartreuse	0.86	0.10
		Fontainebleau	0.31	0.08
		Ventron	0.55	0.11
		Vercors	0.72	0.09
	Diameter: Tree species	Diameter: other species	0.54	0.10
		Diameter: oaks	0.24	0.05
		Diameter: beech	0.51	0.04
		Diameter: fir and spruce	0.24	0.07
	Random effect		−2.29	

Appendix C. Occurrence of microhabitat types per tree. SD: Monte-Carlo Markov Chain standard deviation

Microhabitats	Explanatory variables	Levels	Mean value of the estimates	SD	95% confidence intervals	
					−	+
8. Conks of fungi	Intercept		−2.55	0.19	−2.92	−2.20
	Vitality		1.24	0.19	0.86	1.59
	Random effect		−229.2	65.0	−357	−132
10. Woodpecker cavities	Intercept		−2.30	0.17	−2.64	−1.97
	Vitality		1.45	0.17	1.11	1.78
	Random effect		−124	42.2	−203	−41
11. Non-woodpeckers cavities	Intercept		−2.38	0.16	−2.70	−2.09
	Diameter		0.74	0.13	0.49	1.00
	Random effect		−0.55	0.41	−1.45	0.20
21. Canker	Tree species	Other species	−1664.55	946.36	−3171.97	−115.54
		Oaks	−4.05	0.46	−4.87	−3.19
		Beech	−4.76	0.48	−5.94	−3.91
		Fir and spruce	−1.66	0.31	−2.28	−1.07
	Random effect		0.46	0.38	−0.31	1.18
26. Ivy	Sites	Auberive	−1.79	0.28	−2.33	−1.26
		Chartreuse	−2374.83	1529.99	−5728.27	−171.11
		Fontainebleau	−3.52	0.41	−4.38	−2.83

Appendix C (*continued*)

Microhabitats	Explanatory variables	Levels	Mean value of the estimates	SD	95% confidence intervals	
					–	+
		Ventron	−3268.67	2345.35	−8482.53	−155.80
		Vercors	−2279.18	1666.21	−6415.44	−156.69
	Random effect		0.34	0.42	−0.50	1.11
16. Cracks	Tree species	Other species	−3.39	0.67	−4.70	−2.13
		Oaks	−4.33	0.73	−5.94	−3.00
		Beech	−2.87	0.50	−3.92	−1.95
		Fir and spruce	−4.84	0.67	−6.14	−3.59
	Management type		0.19	0.23	−0.25	0.65
	Vitality		1.33	0.22	0.89	1.81
	Sites	Chartreuse	2.29	0.75	0.78	3.74
		Fontainebleau	−0.29	0.64	−1.57	0.91
		Ventron	1.64	0.77	0.13	3.19
		Vercors	2.23	0.67	0.96	3.56
	Diameter		0.91	0.23	0.49	1.35
	Random effect		−1.38	3.14	−10.46	0.76
17. Bark pockets	Tree species	Other species	−1.22	0.48	−2.22	−0.28
		Oaks	−1.74	0.39	−2.51	−0.99
		Beech	−0.62	0.34	−1.29	0.07
		Fir and spruce	−0.75	0.59	−1.92	0.41
	Management type		−0.45	0.18	−0.84	−0.05
	Vitality		1.15	0.19	0.78	1.49
	Sites	Chartreuse	−1.30	0.76	−2.82	0.19
		Fontainebleau	−1.16	0.44	−2.03	−0.34
		Ventron	−2.22	0.91	−4.05	−0.55
		Vercors	−0.97	0.65	−2.65	0.31
	Diameter		0.34	0.21	−0.07	0.71
	Random effect		0.22	0.36	−0.55	0.86
2. Dead crown (10–25%)	Tree species	Other species	−2.44	0.44	−3.35	−1.61
		Oaks	−0.60	0.23	−1.08	−0.14
		Beech	−2.02	0.25	−2.53	−1.52
		Fir and spruce	−1.79	0.55	−2.86	−0.71
	Management type		0.15	0.14	−0.12	0.42
	Sites	Chartreuse	−1.13	0.65	−2.44	0.09
		Fontainebleau	0.44	0.29	−0.11	1.01
		Ventron	−3.19	1.31	−6.20	−1.05
		Vercors	−0.15	0.55	−1.26	0.88
	Diameter		0.01	0.14	−0.26	0.27
	Random effect		−0.68	0.42	−1.59	0.06
25. Bryophytes	Tree species	Other species	1.23	0.58	0.17	2.51
		Oaks	0.93	0.45	0.06	1.79
		Beech	1.34	0.45	0.49	2.29
		Fir and spruce	−1.53	0.62	−2.76	−0.33
	Vitality		−0.77	0.25	−1.29	−0.32
	Sites	Chartreuse	−1.01	0.71	−2.37	0.42
		Fontainebleau	−4.48	0.52	−5.57	−3.52
		Ventron	0.65	0.80	−0.88	2.29
		Vercors	−2.62	0.69	−3.95	−1.28
	Management type		0.17	0.21	−0.23	0.58
	Diameter		2.04	0.70	0.71	3.41
		Oaks: diameter	−2.17	0.79	−3.98	−0.77
		Beech: diameter	−1.35	0.73	−2.75	0.04
		Fir and spruce: diameter	−2.65	0.80	−4.38	−1.16
	Random effect		0.69	0.28	0.13	1.24
19. Bark loss	Tree species	Other species	1.25	0.44	0.38	2.12
		Oaks	2.17	0.38	1.42	2.94
		Beech	1.59	0.36	0.87	2.30
		Fir and spruce	1.12	0.51	0.15	2.13

(*continued on next page*)

Appendix C (*continued*)

Microhabitats	Explanatory variables	Levels	Mean value of the estimates	SD	95% confidence intervals	
					–	+
	Management type		−0.35	0.17	−0.67	−0.02
	Vitality		1.38	0.21	0.99	1.79
	Sites	Chartreuse	0.55	0.59	−0.60	1.71
		Fontainebleau	−2.73	0.42	−3.59	−1.92
		Ventron	−1.45	0.66	−2.77	−0.20
		Vercors	0.95	0.59	−0.21	2.13
	Diameter: Tree species	Diameter: other species	2.05	0.54	1.04	3.17
		Diameter: oaks	0.23	0.24	−0.25	0.69
		Diameter: beech	0.92	0.23	0.47	1.38
		Diameter: fir and spruce	1.11	0.32	0.50	1.75
	Random effect		0.37	0.26	−0.14	0.89

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