

This is my spot: What are the characteristics of the trees excavated by the Black Woodpecker? A case study in two managed French forests

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ABSTRACT

The Black Woodpecker (*Dryocopus martius* L.) is both an ecosystem engineer and an umbrella species: it has the capacity to modify its environment through cavity excavation, which in turn favors a large range of species that depend on cavities but are unable to dig them themselves (secondary cavity nesters). However, the factors driving cavity excavation by the Black woodpecker at the tree scale remain poorly known. We analyzed the characteristics of trees bearing Black Woodpecker cavities to assess the bird's local habitat requirements and their conservation potential as habitat trees. We compared the traits and characteristics of trees bearing Black Woodpecker cavities ($n = 60$) and control trees ($n = 56$) in two managed lowland broadleaf-dominated forests in France. We hypothesized that:

- (i) Cavity-trees would have lower wood density and display more conks of fungi than control-trees;
- (ii) The local environment of cavity-trees would be less crowded than those of the control trees. In particular, the first branch would be higher up, and their first neighboring tree would be further away from cavity-trees compared to control-trees;
- (iii) Cavity-trees would display a higher number of other woodpecker cavities and more saproxylic microhabitats than the control-trees.

We validated most of our hypotheses and showed that cavity trees differed significantly from their control counterparts. Black Woodpeckers excavate trees with softer wood and higher first branches in a less crowded environment, thus minimizing both the energy dedicated to cavity excavation and predation risk. Second, cavity-trees bear more microhabitats and play a complementary umbrella role than what was documented before. They also appear a good candidate for habitat-tree conservation.

In terms of biodiversity-friendly management measures, it would be beneficial to favor large isolated standing trees devoid of low branches (notably beech), especially in stands dominated by other tree species.

1. Introduction

Forest biodiversity conservation relies on biodiversity-friendly practices in daily forest management. Forest managers can preserve favorable elements such as ageing islands, habitat trees, and standing and lying deadwood (Kraus and Krumm, 2013). Those elements may in turn favor the presence of ecosystem-structuring species, for which it appears necessary to understand and quantify the drivers in terms of

conservation. Through cavity excavation, woodpeckers are considered to be engineer species as they modify their environment and provide new habitats for secondary cavity users (Jones et al., 1994; Remm and Löhms, 2011). Primary excavators are therefore a target for the conservation of hole-nesting assemblages because they can directly impact the abundance and diversity of many other species (Wesołowski, 2011). Woodpecker species vary in their selection of trees in which they excavate cavities ranging from live trees, decayed trees to dead trees (e.g.

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Table 1

Main characteristics of the sampling sites (ONF, 2006, 2012), surrounding environment description and cavity-tree characteristics ($n = 28$ plots for each site): means, standard errors (s.e.) and ranges (minimum-maximum). Basal area: small trees (Diameter at Breast Height [DBH] between 7.5 and 22.5 cm), medium trees (DBH: 22.5–47.5 cm) and large trees (DBH: > 47.5 cm). Relative cavity height: cavity height divided by total tree height. We used generalized linear models (Gamma error distributed with identity link) to compare variables between sites.

		Auberive		Loches		
Location		47° 47' 42" N, 5° 4' 57" E		47° 9' 16" N, 1° 4' 23" E		
Area (ha)		5584		3952		
Substrate		Limestone		Flint clay		
Management type		Uneven-aged		Even-aged		
Dominant tree species		<i>Fagus sylvatica</i> (56%) Other broadleaves (15%) <i>Quercus sp.</i> (13%)		<i>Quercus petraea</i> (92%)		
Total number of cavity trees		223 0.04 cav. /ha		112 0.03 cav. /ha		
		Mean ± s.e.	Range	Mean ± s.e.	Range	<i>p</i> value
Local environment						
Altitude (m)		425 ± 5	[370–458]	116 ± 3	[88–139]	< 0.001***
Slope (°)		10 ± 2	[0–26]	3 ± 1	[0–13]	0.001**
Deadwood (m ³ /ha)		20 ± 9	[0.4–232]	24 ± 9	[0.3–162]	0.942 ns
Basal area (m ² /ha)	Small	2.9 ± 0.4	[0–6.5]	2.2 ± 0.3	[0–6.5]	0.171 ns
	Medium	7.6 ± 0.6	[1–12]	8.5 ± 0.9	[2.5–24.5]	0.257 ns
	Large	8.6 ± 0.7	[1–15]	14.1 ± 1.2	[0–23.5]	0.001**
	Total	19.1 ± 0.5	[13.5–23.5]	24.7 ± 0.5	[18.5–30.5]	< 0.001***
Tree						
DBH (cm)		55 ± 2	[36–86]	51 ± 2	[31–64]	0.110 ns
Height (m)		27 ± 1	[18–35]	33 ± 1	[26–43]	< 0.001***
Cavity height (m)		7 ± 0.5	[3–15]	13 ± 0.6	[5–21]	< 0.001***
Relative cavity height		0.27 ± 0.02	[0.12–0.46]	0.39 ± 0.02	[0.19–0.56]	< 0.001***

Martin, 2015). The Black Woodpecker *Dryocopus martius* (Linnaeus, 1758) is the largest Eurasian woodpecker species and the strongest excavator in Europe. It provides essential habitats for a multitude of large, secondary cavity users (Johnsson et al., 1993). With a home range ranging from 200 ha to > 1000 ha (Cuisin, 1986; Fernandez and Azkona, 1996; Bocca et al., 2007; Olano et al., 2015), Black Woodpeckers require large patches of mature forest (Garmendia et al., 2006), though they are able to adapt to different forest landscape contexts (Rolstad et al., 2000; Angelstam et al., 2002; Saporetto et al., 2016). However, the drivers of the Black Woodpecker's cavity excavation behavior are not fully understood yet, especially in the context of managed temperate forests in Western Europe. Since Black Woodpeckers tend to preferentially excavate living trees (Zahner et al., 2012; Zawadzka and Zawadzki, 2017), they may alter tree vitality and trigger senescence. Damaged trees could hence be easier for other, weaker woodpeckers to excavate (Wesołowski, 2011), and may bear more wood-decaying microhabitats – hereafter referred to as “saproxylic microhabitats” (Larrieu et al., 2018). As engineer species, the Black Woodpecker may have numerous roles: the bird provides holes for secondary cavity users and weakens healthy trees, which, in turn, triggers the formation of other microhabitats. Additionally, since this bird plays a critical role in determining community structure and in the conservation of a large number of co-occurring species (Roberge and Angelstam, 2004), the Black Woodpecker is also an important umbrella species (Garmendia et al., 2006).

At the tree scale, Black Woodpecker cavity excavation could represent a trade-off between the energy applied during excavation and the final cavity quality (time, resistance, microclimate, predation risk). Black Woodpeckers may target tree whose characteristics reduce excavation time thus minimizing the energy required. In North America, primary cavity excavators preferentially choose trees with softer wood at the cavity height (Schepps et al., 1999; Lorenz et al., 2015). In particular, reciprocal positive relationships between fungi and primary cavity excavators have been documented (Jackson and Jackson, 2004)

since wood decaying fungi soften wood (Conner et al., 1976; Schwarze et al., 2008). Like other primary excavators, Black Woodpeckers may select heart-rotted trees thus reducing the energy needed for excavation (Conner et al., 1976; Zahner et al., 2012). Moreover, selecting an appropriate nest site that minimizes offspring, and adult, predation is important for bird fitness (Lima, 2009). Black Woodpeckers seem to preferentially excavate straight trunks free of branches, reducing predation risks (Cuisin, 1967; Rolstad et al., 2000; Bocca et al., 2007; Zahner et al., 2017). However, in western Europe, the studies documenting tree characteristics favorable for the Black Woodpecker have rarely been carried out in forests used for wood production. Furthermore, existing quantitative studies concern either other biomes, e.g. North America, Scandinavia (Andersson et al., 2018), or mature, primary forests (Wesołowski, 2011). Since forest managers already designate Black Woodpecker cavity-bearing trees as habitat trees (Bütler et al., 2013), our aim was to analyse specific characteristics of these trees and indirectly assess their potential role for forest biodiversity (through the presence of tree microhabitats, sensu Larrieu et al., 2018). We therefore examined the role of tree-level factors in Black Woodpecker cavity tree selection in two French managed forests. We compared the characteristics of trees bearing at least one Black Woodpecker cavity (hereafter referred to as “cavity-trees”) and trees devoid of Black Woodpecker cavities (hereafter referred to as “control-trees”). We hypothesized that:

- Cavity-trees would have lower wood density and also display more conks than control-trees;
- The local environment of cavity-trees would be less crowded than those of the control trees. In particular, the first branch would be higher up, and the first neighboring tree would be further away from cavity-trees than from control-trees;
- Cavity-trees would display more cavities excavated by other woodpeckers and more saproxylic microhabitat than the control-trees.

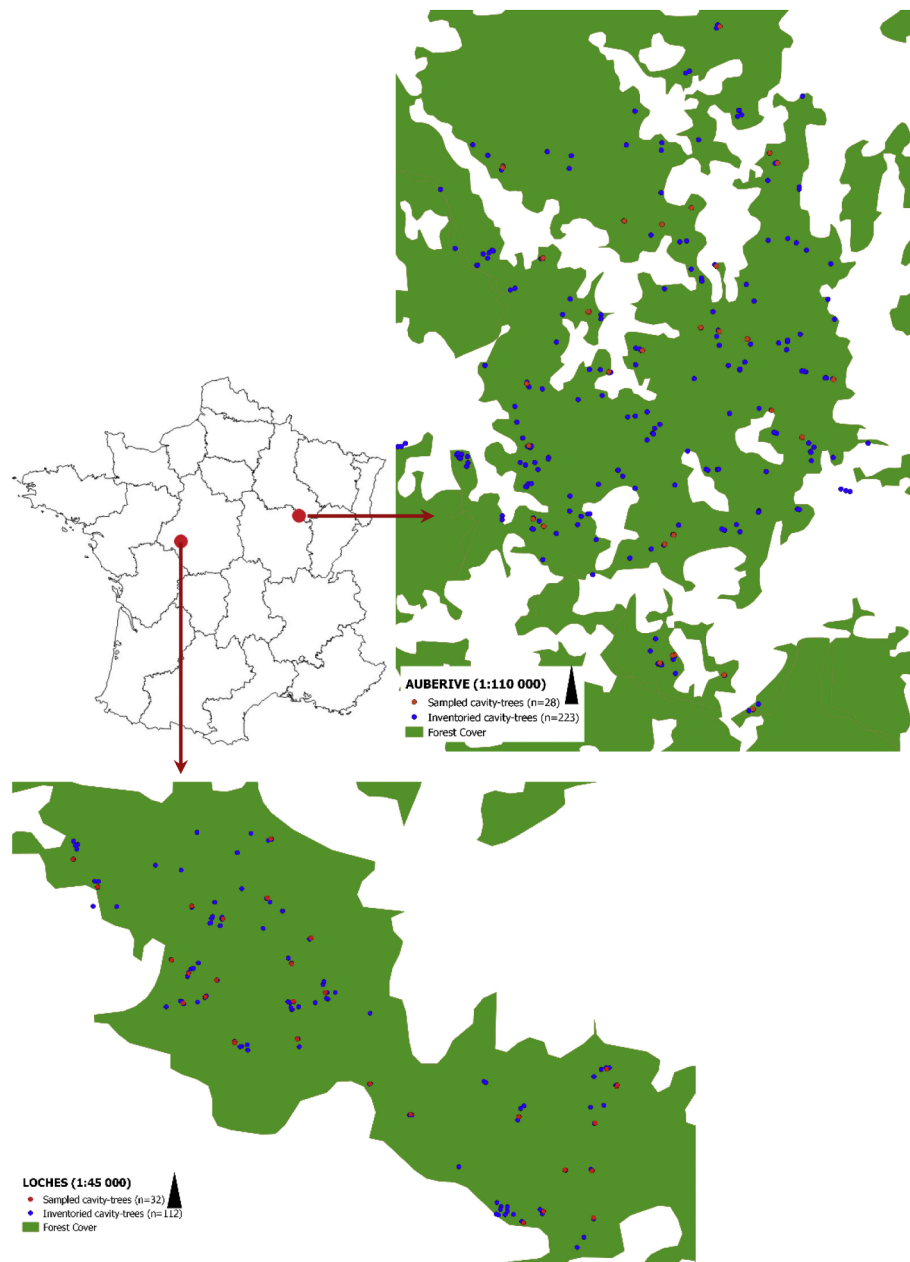


Fig. 1. Sampling design maps of Auberive (top) and Loches (bottom). Blue dots represent all recorded cavity-trees; red dots represent cavity-trees sampled in this study. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2. Materials and methods

2.1. Cavity-trees selection

We benefited from data for two managed broadleaf-dominated forest sites in France where Black Woodpecker cavities had been identified and mapped (Table 1, Fig. 1). In the Auberive forest, forest managers (French National Service, ONF) located 223 (0.04/ha) Black Woodpecker cavity-trees during tree selection operations between 2003 and 2018. In the Loches forest, a naturalist (Michael Dubois) located 112 (0.03/ha) Black Woodpecker cavity-trees between 2010 and 2018. Cavity use (nesting, roosting or abandoned) was not considered as long as the cavity had clearly been excavated by a Black Woodpecker (Larrieu et al., 2018).

2.2. Sampling design

In Auberive, we preselected the 64 most recent (> 2015) out of the total 223 cavities because cavity-trees can break at the cavity location (Wesołowski, 2011) or heal (Colmant, 2003; Boutteaux Jean-Jacques; Dubois Michael, personal communications). In Loches, we kept all 112 cavities since the inventory date was not available and no preselection was possible. We then randomly selected the order in which the cavity-trees would be sampled. To reduce spatial autocorrelation, we rejected cavity-trees which were within 400 m of each other (Fig. 1). In the field, we excluded dead trees and snags from our sample to avoid potential confounding effects between tree vitality, wood density or micro-habitats.

We paired each cavity-tree with a control-tree, the closest equivalent tree devoid of Black Woodpecker cavities (mean distance = 18 m). We selected each control-tree for the characteristics it shared with its paired cavity-tree (species and Diameter at Breast Height, DBH ± 10 cm). On four plots in Loches, we sampled an additional (unmapped) cavity-tree for the same control-tree, which gave us four triplets instead of pairs. As a result, we sampled 28 cavity-trees in Auberive, 32 in Loches, and 28 control-trees at each site. We performed the fieldwork in April 2018.

2.3. Local forest structure description

Each plot was centered around a cavity-tree. For each plot, we used a relascope (fixed angle of 2%) to measure the basal area of small trees (DBH between 7.5 and 22.5 cm), medium trees (DBH: 22.5–47.5 cm) and large trees (DBH: > 47.5 cm), as well as the total basal area (the sum of the three). Within a radius of 20 m around the cavity-tree, we measured the DBH and height of any dead standing trees (trees, snags or stumps) with a minimum DBH of 30 cm. We also measured the length and median diameter of lying dead logs with a minimum median diameter of 30 cm. We used truncated cone volumes per ha to calculate standing and lying deadwood volumes (Paillet et al., 2015).

2.4. Tree level measurements

On the cavity-trees, we recorded cavity height (m) and orientation (gr), and visually estimated cavity tilt (classified into four categories, Fig. 2). For both cavity- and control- trees, we measured tree DBH, total tree height and the height of the first occurring branch, excluding epicormics shoots, as a proxy for the free-part of the trunk (hypsometer, Håglof's Vertex IV). We also measured the distance to the nearest neighboring tree (DBH > 7.5 cm, threshold shared by forest inventories in Europe for tree recording, Gschwantner et al., 2016) as a proxy for vegetation clutter (Fig. 2).

Using a manual auger, we sampled a wood core below the cavity of interest from the trunk at breast height (1.30 m); we sampled a similar core with the same orientation on the paired control-tree. If the cavity-tree bore several Black Woodpecker cavities, we arbitrarily chose the highest one to orient the coring (Fig. 2). Each core aimed for the pith, but if we missed it, the tree was not cored twice. For safety and practical reasons, we cored at breast height and not at cavity height. It seems that

Black Woodpeckers could detect and exploit vertical density variations of a given tree (Conner et al., 1976; Zahner et al., 2012), but our aim was to test whether excavated trees were overall less dense than a comparable neighboring tree. We also assumed that wood density in beech was relatively homogeneous along the trunk as shown by Longuetaud et al. (2016). Furthermore, managers can benefit from this approach with management-linked data such as wood cores for increment assessments and thus derive wood density more easily than at cavity height.

Finally, we recorded tree-related microhabitat abundance (47 types, see Table 5 in Larrieu et al., 2018) on both the cavity- and control-trees. Based on this abundance value, we calculated the richness (number of types per tree) and abundance of saproxylic microhabitats (32 types), grouped as follows: woodpecker cavities (excluding Black Woodpecker cavities), woodpecker feeding holes, mould cavities, branch holes, insect galleries, water-filled holes, bark pockets and shelters, injuries (exposed sapwood and exposed heartwood), conks of fungi, exudates, dead crown and broken limbs. We also separately calculated other woodpecker species cavity abundance.

Although we recorded visible conks of fungi during the microhabitat inventories and heart rot on the wood core samples, there were not enough occurrences of these two traits to statistically test differences between cavity- and control-trees (Supplementary materials, Table S1).

2.5. Wood density measurements and tree age estimation

To determine wood density, the wood core samples were dried 24 h at 103 °C, then X-ray scanned (General Electric BrightSpeed Excel medical tomograph, one image every 0.625 mm along the cores) at the INRA Nancy (Xyloscience Platform) laboratory. We derived density profiles from these images with the ImageJ software and the CalDenQB plug-in (Longuetaud et al., 2014; Leban et al., 2016; Jacquin et al., 2017; Leban et al., 2017). We calculated the mean density for each sampled core and, to assess whether density varied along each profile, also calculated the means of each 5-cm-long section ($n = 6$) along the wood core samples from 0 cm (bark) to 30 cm (pith).

Finally, although age determination was not the primary aim of this study, the cores allowed us to estimate tree age. We used a LintabTM sliding-stage measuring device (Rinntech, Heidelberg) with a resolution of 0.01 mm to measure tree-ring widths. In the event that the pith was missing from the core, we extrapolated the missing rings following

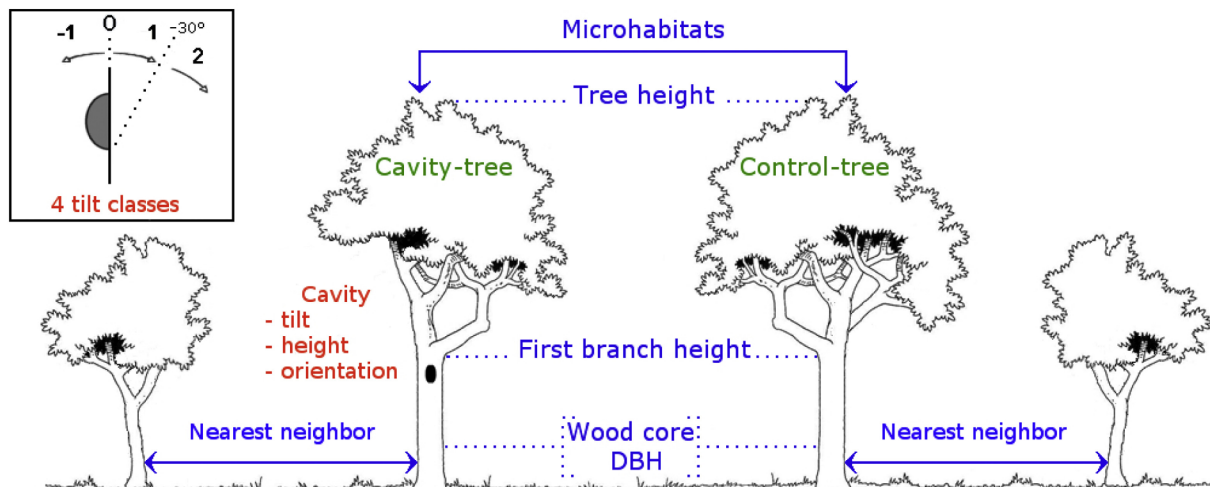


Fig. 2. Tree-scale measurements comparing paired trees (green): cavity description (red) and comparable variables (blue). We paired a control-tree, the closest equivalent tree (same species and Diameter at Breast Height [DBH] ± 10 cm), to each cavity-tree. The four classes of cavity tilt are shown in the top left box. We inventoried tree-related microhabitat richness and abundance following Larrieu et al.'s typology (2018). We sampled a wood core at breast height (1.30 m) for wood density and age measurements. We chose the nearest neighbor among all the surrounding trees with a DBH > 7.5 cm. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Duncan's (1989) method. We did not exclude cores for which a substantial part of the sample was missing, but sensitivity analyses revealed that this did not significantly affect our results. Finally, we used the COFECHA application (Holmes, 1983) to visually cross-date and verify the cores.

2.6. Statistical analyses

We processed all the analyses with the R software v. 3.4.3 (R Core Team, 2017).

We used generalized linear models (glm function) to compare the descriptive plot-level variables between the two sites. We chose the Gamma error distribution with an identity link since the variables had positive continuous values. We tested cavity orientation using the Rayleigh test of uniformity (circular package, Agostinelli and Lund, 2011). Tilt was not tested due to low variability (see below).

We used generalized linear mixed-effect models (glmer function; lme4 package v1.1–17; Bates et al., 2014) to compare six response variables between cavity- and control-trees: wood density (total and 5 cm lengths), first branch height, distance from the nearest neighboring tree, other woodpecker cavity abundance, and saproxylic microhabitat richness and abundance. Since the first three variables had positive continuous values, we chose the Gamma error distribution with an identity link. For the last three variables, we chose the Poisson error distribution with a log link since they are count variables. We added site (Auberive versus Loches) as a fixed effect in interaction with tree type (cavity-trees versus control-trees) to account for possible variations in the relationships with site. Finally, we added a plot random effect on the intercept to account for the paired design. We first tested contrasts for all the parameters (type, site and interaction) based on model predictors for each response variable (joint_tests function; emmeans package v1.2.2; Russell, 2018). We then used marginal post-hoc Tukey tests (emmeans function; emmeans package v1.2.2) to separately compare estimated means between control- and cavity-trees by site.

3. Results

3.1. Local environment and cavity-tree descriptions

Auberive had a significantly higher mean elevation and steeper slopes than Loches. Mean basal area was significantly higher in Loches than in Auberive, which was mostly explained by a greater proportion of large trees (means = 14.1 and 8.6 m²/ha, respectively). Basal area of medium and small trees did not significantly differ between sites. Mean volume of deadwood near cavity-trees was not significantly different between sites (means = 20 and 24 m³/ha, respectively, Table 1).

All cavity-trees were beech (*Fagus sylvatica*) in Auberive; all but two (oak, *Quercus petraea*) were beech in Loches. Cavity-tree DBH was not significantly different between Loches and Auberive (mean = 51 and 55 cm, respectively). However, cavity-trees were significantly taller in Loches than in Auberive (means = 33 and 27 m, respectively). Cavities were located higher on the trees in Loches than in Auberive (means = 13 and 7 m, respectively) and were also higher relatively to total tree height (means = 0.36 and 0.27, respectively, Table 1). Cavity entrance orientation (Supplementary materials, Fig. S1) was never significantly different from a uniform distribution (Rayleigh test, overall: $p = .25$; Auberive: $p = .88$; Loches: $p = .07$). All cavity entrance holes were vertical, except for four in Auberive which were tilted downwards (between 0 and -30°).

3.2. Comparison between cavity-trees and control-trees

Mean wood density was 5% lower in cavity-trees than in control-trees (Fig. 3A) in Auberive ($p < .001$) but no significant difference was found in Loches ($p = .45$). When we removed the 12 trees with heart rot

from the dataset, cavity-tree wood density remained only marginally lower than control-tree wood density ($p = .07$). Along wood core profiles, cavity-tree wood density was significantly lower than in control-trees from 10 to 25 cm, but only in Auberive (Table 2, supplementary materials Fig. S2).

Tree age estimates did not differ between sites or between cavity- and control-trees; only the interaction was significant ($p = .013$) in the overall analysis. However, in Auberive, cavity trees were significantly older than control trees (+6%, resp. 150.2 \pm SE 6.3 years, 141.2 \pm 6.2 years, $p = .01$) while this was not the case in Loches (resp. 143.4 \pm 6.2 years, 146.6 \pm 6.2, $p = .35$).

Cavity-trees had a higher first branch compared to control-trees (Fig. 3B): 55% higher in Auberive ($p < .001$) and 115% higher in Loches ($p < .001$). In Auberive, cavity-trees had a more distant nearest neighbor than did the control-trees (Fig. 3C): 45% further away ($p = .002$), but there was no difference in Loches ($p = .96$).

Other woodpecker cavities were more numerous on cavity-trees compared to control-trees (Fig. 3D): 4500% more in Auberive ($p < .001$) and 500% more in Loches ($p = .001$). Note that other woodpecker cavities were nearly absent on control-trees. Overall saproxylic microhabitat richness tended to be higher on cavity-trees than on control-trees ($p < .1$; Fig. 3E): 35% higher in Auberive ($p = .05$), but no difference in Loches ($p = .37$). Saproxylic microhabitats were more abundant on cavity-trees compared to control-trees (Fig. 3F): 60% more in Auberive ($p < .001$) and 15% more in Loches ($p = .04$).

Except for first branch height, all other differences between cavity- and control-trees had higher magnitudes and significance in Auberive than in Loches.

4. Discussion

We validated most of our hypotheses and showed that cavity-trees differed significantly from their control counterparts. Below we discuss two possible underlying ecological drivers of these differences: energy required for excavation and limitation of predation risk. We then suggest forest management implications based on our results.

4.1. Black Woodpeckers minimize the energy they use for excavation

We partially validated our first hypothesis: Black Woodpeckers did excavate trees with a lower mean wood density, which tended to bear more signs of decay linked to fungi (either conks or heart rot) compared to control-trees. In Auberive, radial wood density variations revealed that cavity-trees were around 3% less dense than the control-trees in the 10-to-25 cm depth range (distance from bark). While we found no significant differences in Loches, the core profiles revealed a lower mean wood density in cavity-trees than in control-trees (Supplementary Materials, Fig. S2). In addition, we showed that these observed differences were not related to tree age (Bouriaud et al., 2004). These results are in accordance with studies showing that North American primary cavity excavators select trees with softer interior wood at the cavity height (Lorenz et al., 2015). Primary cavity excavators probably face trade-offs when selecting cavity-trees: excavating softer trees may reduce excavation time and the amount of energy needed, which could give a selective advantage. Head and body movements are confined during interior cavity excavation and this might force the birds to select trees with soft interior wood (Lorenz et al., 2015). On the other hand, lower wood density might increase the risk of cavity-tree collapse during strong winds - decayed trees may more easily break than healthy trees - leading primary cavity excavators to select trees with the maximum hardness they are able to excavate, rather than the softer ones. Black Woodpeckers dig long-lasting cavities (Wesołowski, 2011) and reuse them several years (Cuisin, 1986; Johnsson et al., 1993; Colmant, 2003). They may therefore select trees with a slightly lower wood density to facilitate their excavation work, but which are also healthy

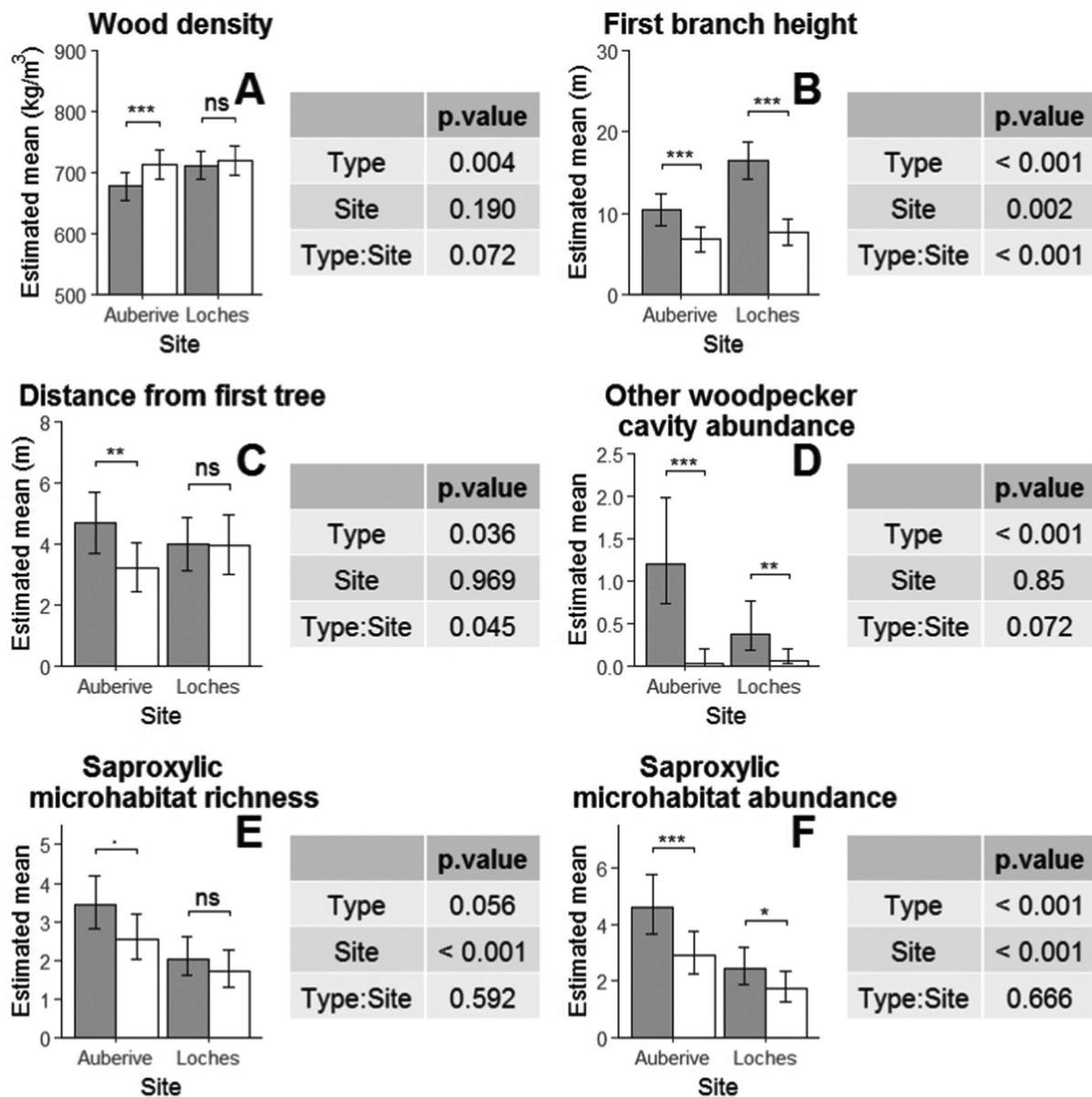


Fig. 3. Comparison of estimated means between cavity-trees (trees bearing at least one Black Woodpecker cavity, in grey) and control trees (trees without cavities, in white) based on generalized linear mixed models. A, B and C are Gamma error distributed models with identity links while D, E and F are Poisson error distributed models with log links (values were back-transformed). We added a random plot-level effect to the models to account for the paired design. Error bars represent 95% confidence intervals and stars show marginal Tukey test significance (thresholds: (*) $p < .1$; * $p < .05$; ** $p < .01$; *** $p < .001$). Associated tables display the significance of each parameter in each model: Type (cavity- vs control-tree), Site (Auberive vs Loches) and Type:Site (the interaction between Type and Site).

enough to live for a long time. In terms of method, and contrary to Lorenz et al. (2015) who cored the trees at cavity height, we cored at breast height (1.30 m), which may overestimate wood density. Coring near the cavity may have allowed us to better detect signs of wood rot and revealed a stronger effect. Indeed, woodpeckers may be able to detect areas of lesser wood density along the trunk (Schepps et al., 1999; Matsuoka, 2008; Zahner et al., 2012). Still, we evidenced softer interior wood at 1.30 m in cavity-trees free of wood rot. Since beech wood density is relatively homogeneous along the trunk (Longuetaud et al., 2017), we assume that this comparison remains valid, but does not provide an absolute estimate of the wood density Black Woodpeckers are capable to dig. Density measures along the trunk would allow to have such an estimate.

We did not observe that cavity-trees bear more conks of fungi than control-trees. This result did not confirmed the link between fungi and woodpecker cavities documented by other authors (Conner et al., 1976;

Bull et al., 1992; Welsh and Capen, 1992; Jackson and Jackson, 2004; Zahner et al., 2012). However, as Conner et al. (1976) observed, cavity-trees do not always have visible fungal fruiting bodies even when wood decay fungi are present; the low detectability of conks may also explain why we did not validate our initial hypothesis. As specified by e.g. Jackson and Jackson (2004), a tree may have been rotten inside for a long time before exhibiting actual conks on the outside. This was partially confirmed in our study by the trend towards a higher occurrence of heart-rot on cavity-trees. The use of DNA methods to assess the actual presence of fungi seems more efficient – but also more labour-intensive – than direct observation (Jusino et al., 2014, 2016).

To sum up, cavity-tree wood density selection seems a woodpecker species-dependent compromise. Trade-offs occur between excavation ability, time investment, and overall cavity-tree resistance and persistence (linked to cavity reuse by the species).

Table 2

Wood density comparisons (in percentage) between cavity- and control-trees based on estimates from generalized linear mixed models (Gamma error distribution).

	Distance from bark					
	0–5 cm	5–10 cm	10–15 cm	15–20 cm	20–25 cm	25–30 cm
All trees (n = 116)						
Auberive	–1.86	–1.94	–3.25 (*)	–3.59 (*)	–6.13 *	+ 0.98
Loches	–0.25	+ 0.15	+ 0.22	–1.46	–2.24	–2.32
Trees without heart rot (n = 104)						
Auberive	–1.04	–1.88	–2.80	–2.33	–1.39	+ 3.47
Loches	–1.25	–0.07	+ 0.23	–0.57	–2.34	–2.32

We compared means along wood core profiles every 5 cm from 0 (bark) to 30 (pith). Negative values indicate lower wood density for cavity-trees than control-trees. Stars show marginal Tukey test significance. Thresholds: (*) $p < .1$; * $p < .05$; ** $p < .01$; *** $p < .001$.

4.2. Black woodpeckers minimize nest predation risk

We validated our second hypothesis: we showed that the local environment of the cavity-trees was less crowded than that of the control-trees: cavity-trees were more isolated from other trees at the local scale and had higher first branches than the control-trees.

Our findings on distance to the closest neighbor refine studies which suggest Black Woodpeckers prefer to dig cavities in relatively open areas (Rolstad et al., 2000; Saporetti et al., 2016). This result seems to extend to the forest interior (a closed area at the stand scale), where Black woodpeckers preferentially chose trees standing apart from others (in an open area at the tree scale). Cavity-trees were significantly further away from their first neighbor only in Auberive, but the difference in response between the two sites could have several explanations. Firstly, even-aged management in Loches is likely to have equalized distances between trees. Secondly, we selected only recent cavities in Auberive but not in Loches, where neighboring trees might have grown since cavity excavation. However, the basal area of small trees was not significantly different between the two sites, which suggests that cavity trees were simply further apart from other trees than in Loches than in Auberive.

In Auberive, cavities were on average 2–3 m below the first branch (means = 7 and 9.8 m, respectively). In Loches, cavities were 2 m higher than in Auberive, but still lower on the trunk than the first branch (means = 13 and 15 m, respectively). These results confirm numerous observations elsewhere (Cuisin, 1967; Nilsson, 1984; Johnsson, 1993a; Rolstad et al., 2000; Colmant, 2003; Bocca et al., 2007; Pirovano and Zecca, 2014). To summarize, first branch height and distance to the closest neighboring tree appear to be factors of cavity-tree selection: a suitable Black Woodpecker cavity-tree has a trunk free of low branches and is relatively isolated.

Indeed, as suggested by Cuisin (1967), isolated trees devoid of low branches could facilitate aerial access to the cavity for adults and offspring flight when leaving the nest. Moreover, the same tree characteristics could minimize predation risks. Using camera traps, Zahner et al. (2017) showed that four predators visit inhabited Black Woodpeckers nest: the Northern Goshawk (*Accipiter gentilis*), the Common Buzzard (*Buteo buteo*), the Great Spotted Woodpecker (*Dendrocopos major*) and the Pine Marten (*Martes martes*). The Northern Goshawk has seldom been seen extirpating young Black Woodpeckers from their nest (Cuisin, 1967), but the size of the cavity entrance and cavity depth can help prevent large raptors from reaching the offspring (Zahner et al., 2017). However, the Northern Goshawk, which prefers to hunt in large patches of later-successional-stage forests, has been reported to predate adult Black Woodpeckers (Cuisin, 1967; Widen, 1989; Mikusiński, 1995; Rolstad et al., 2000). We assume that Black Woodpeckers are more likely to avoid Goshawk predation when the cavity-tree is more

easily reachable, since it is potentially quicker to shelter when the cavity environment is less crowded. The Pine Marten is the major Black Woodpecker nest predator in Norway, Sweden and Germany (Nilsson et al., 1991; Rolstad et al., 2000; Zahner et al., 2017). It has been seen extirpating young Black Woodpeckers from the nest (Cuisin, 1967) and is known to revisit cavities (Sonerud, 1985), thus increasing predation risk in old cavities (Nilsson et al., 1991). The excavation of a new nest each year and the selection of higher locations may reduce this risk (Nilsson, 1984; Johnsson et al., 1993; Zahner et al., 2017). Moreover, our results are consistent with those of several other authors, who found that Black Woodpeckers generally seem to locate nests along “branch-free trunks” (Colmant, 2003; Bocca et al., 2007), boles without branches for 10 m (Rolstad et al., 2000; Zahner et al., 2012) or boles without branches below the cavity (Cuisin, 1967; Pirovano and Zecca, 2014). These authors assume that branches on the trunk, or those of neighboring trees, may serve as a ladder that help predators, notably the Pine Marten, reaching the nest. Black Woodpeckers could thus minimize offspring predation risk by selecting a safer tree, that is, one which is relatively isolated with a branch-free trunk. Evidently, this explanation remains speculative and e.g. video surveillance of nests sites would be necessary to confirm it (see e.g. Zahner et al., 2017).

4.3. Black woodpeckers as umbrella species: the role of microhabitats

We validated our hypotheses linking Black Woodpecker cavities and other microhabitats; indeed, cavity-trees displayed significantly more other woodpecker cavities and saproxylic microhabitats than the control-trees. These results may have two opposing explanations.

Black Woodpeckers are capable of excavating apparently healthy trees, and when they do so, they could themselves be contributing to the tree decay process (Kosiński and Kempa, 2007; Zahner et al., 2012; Zawadzka and Zawadzki, 2017), thus making the trees more microhabitat-ready. This is the case for fungi, as shown in many studies other than ours (see the review of Jackson and Jackson, 2004). Black Woodpecker cavities would decrease trees health, induce its slow decay, indirectly causing more holes, bark and wood injuries and deadwood. In comparison, other woodpeckers only excavate already decaying trees or target dead branches borne by living trees: e.g. Pasinelli (2000); Kosiński and Kempa (2007) for the middle spotted woodpecker; Wiklander et al. (2001) for the lesser spotted woodpecker. Black Woodpeckers might be the first to degrade the trees, making them more suitable for weaker primary excavators. To sum up, Black Woodpeckers, through the tree decaying process they provoke, could be considered as an umbrella species linked to the supply of cavities available to many secondary cavity users (Zahner et al., 2017), increased microhabitat-dependent biodiversity and other woodpecker excavation. These results suggest an additional umbrella-species role for Black Woodpeckers through the supposed facilitation of tree microhabitats formation, especially since recent research has linked microhabitats (including woodpecker cavities) with bat and bird biodiversity (Paillet et al., 2018). Black Woodpecker cavity-trees have a higher potential regarding biodiversity than a comparable non-cavity trees, which confirms their interest as habitat trees to be conserved in integrated forest management (Kraus and Krumm, 2013).

Conversely, Black Woodpeckers could select trees already bearing microhabitats for cavity excavation. This explanation is reversed in time and causality compared with the first one. In this case, fungal microhabitats would first appear on a senescent tree, and only then would Black Woodpeckers target that tree for excavation. We assume that this mechanism is less probable since many cavity-trees in our study did not show any apparent signs of senescence (but see Zahner et al., 2012; Jusino et al., 2016). However, to disentangle this chicken-and-egg issue and to better understand the succession between microhabitats and cavities ontogenesis, long-term monitoring in zones favored by the Black Woodpecker will be necessary (Wesołowski et al., 2010; Cockle et al., 2011).

4.4. Implications for forest management and Black woodpeckers' conservation

We showed that Black Woodpecker cavity-trees are isolated large-diameter beech trees free of low branches; this suggests that Black Woodpeckers tend to select trees based on the energy required for cavity excavation and on predation risk. We confirmed our hypothesis that Black Woodpeckers play a complementary umbrella role, by facilitating cavity excavation for other woodpecker species and saproxylic microhabitat formation. Therefore, this also confirms that Black Woodpecker cavity-trees have high conservation interest as habitat trees (Office National des Forêts, 2010; Bütler et al., 2013). To secure an abundance of biodiversity-friendly, tree-borne microhabitats, preserving trees with Black Woodpeckers cavities while favoring trees suitable for Black Woodpecker excavation where such trees are rare seems appropriate. However, determining the threshold density for optimal conservation remains beyond the scope of this study. Rolstad et al. (2000) propose preserving 1 tree/ha for Black Woodpecker use while the French National Forest Service (Office National des Forêts, 2010) recommends preserving two living habitat trees/ha. Moreover, Black Woodpeckers prefer to excavate new nests each year, probably to reduce offspring predation (Nilsson et al., 1991), so it seems important to maintain a constant pool of favorable trees. In addition, suitable cavity-trees should be scattered throughout the forest for two reasons. First, Black Woodpeckers have large home ranges, so clustered cavity-trees would be used by the same individual or pair and exclude other individuals by mere competition. Second, clustered cavity-trees would be more sensitive to predation, which would reduce the efficiency of preserving the habitat trees (Johnsson, 1993b).

Managers should keep in mind, however, that simply preserving a high quantity of suitable cavity-trees scattered throughout the forest is likely to be insufficient to ensure the presence of Black Woodpeckers. Obviously, the birds have other requirements, most notably patches of mature forest, presence of open areas and access to deadwood (Garmendia et al., 2006; Karimi et al., 2018). Similarly, biodiversity conservation should probably not focus on only one but several umbrella species (Lambeck, 1997; Roberge and Angelstam, 2004). Nonetheless, in French lowland forests, it would undoubtedly be interesting to favor scattered standing Beech trees with a minimum DBH of around 30 cm and a branch-free trunk, especially in stands dominated by other, more commercially valuable, tree species such as oak. Since Black Woodpecker cavities are relatively rare (e.g. 0.03–0.04/ha in our dataset, but see also Kosiński et al., 2004), applying this biodiversity-friendly practice would be an interesting production-protection compromise in managed forests.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2019.117621>.

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