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This is my spot: characteristics of trees bearing Black Woodpecker cavities

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Master thesis

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INTRODUCTION

Forest biodiversity conservation relies on biodiversity-friendly actions in daily forest management. Forest managers can preserve favorable elements such as ageing island, habitat trees, standing and lying deadwood (Kraus & Krumm, 2013). Those elements may in turn favor the presence of ecosystem-structuring species (e.g. engineer, keystone or umbrella species). Through cavity excavation, woodpeckers are considered forest engineers as they transform their environment and create new habitats used by cavity-dwelling organisms unable to excavate (secondary cavity users) (Jones, Lawton, & Shachak, 1994). Excavators are thus considered a top priority for the conservation of hole-nesting assemblages because they can directly impact the abundance and diversity of cavity users (Wesołowski, 2011). The Black Woodpecker *Dryocopus martius* (Linnaeus, 1758) is the largest Eurasian woodpecker species. It excavates the largest cavities in Europe and thus provides essential habitats for a multitude of secondary cavity users (Johnsson, Nilsson, & Tjernberg, 1993). Black Woodpeckers modify trunks of living trees, making them suitable habitat for more biodiversity. Damaged trees could be more disposed for other woodpecker excavation (Wesołowski, 2011) and more inclined to bear wood decaying microhabitats (thereafter, "saproxylic microhabitats"). The engineer role of Black Woodpeckers could then be multiple: creating holes for secondary cavity users and weaken trees which create microhabitats in chain effect. Since it plays a critical role in determining community structure, the Black Woodpecker is considered a keystone species (Johnsson, 1993; Kosiński, Bilińska, Dereziński, & Jeleń, 2010). In terms of conservation, its role of umbrella species has been documented (Garmendia, Cárcamo, & Schwendtner, 2006) and this species can be used as a tool to protect a large number of co-occurring species (Roberge & Angelstam, 2004).

Understanding and quantifying drivers of keystone or umbrella species presence is relevant to biodiversity conservation. With a vital area ranging from 200 ha to more than 1000 ha (Bocca, Carisio, & Rolando, 2007; Cuisin, 1967, 1986; Fernandez & Azkona, 1996; Olano et al., 2015), Black Woodpeckers are forest species capable to adapt to different landscapes as open and urban places. There are therefore regarded as habitat generalists (Angelstam et al., 2002; Cuisin, 1967; Rolstad, Rolstad, & Saeteren, 2000; Saporetti, Colaone, Guenzani, & Zarbo, 2016; Tjernberg, Johnsson, & Nilsson, 1993). They are also known to require large patches of mature forest (Garmendia et al., 2006). However, the drivers of Black Woodpeckers cavity excavation behavior are not fully understood; this organizes our problematic. Indeed, the presence of feeding substrates, suitable cavity trees and acceptable biotic interactions (intra and inter-specific competition, predation) constitute their suitable vital area (Figure 1). Feeding, nesting and roosting sites are specific habitat use that are spatially separated (Brambilla & Saporetti, 2014). Black Woodpeckers feed on ants and other insects (Rolstad, Majewski, & Rolstad, 1998) found on conifers, deadwood and open areas (Bocca et al., 2007; Brambilla & Saporetti, 2014; Mikusiński, 1995; Pirovano & Zecca, 2014). Nesting and roosting cavities are in the same habitat (Rolstad et al., 2000) which are broadleaf stands (Brambilla & Saporetti, 2014) and cavity trees selection relies on local and tree characteristics.

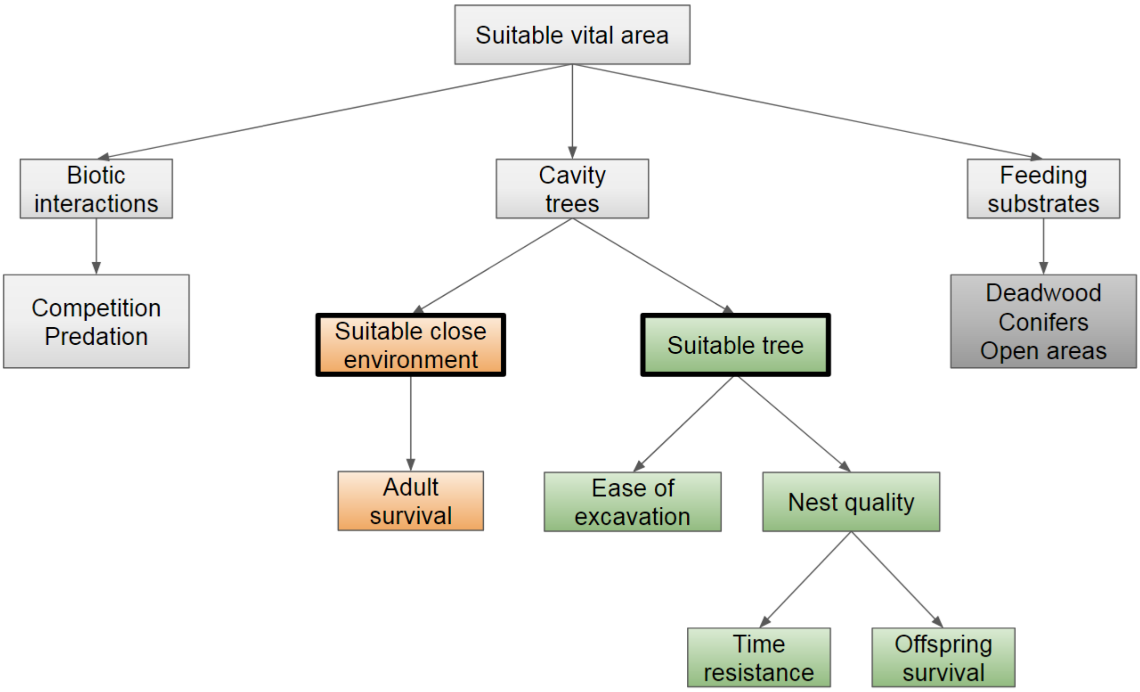


Figure 1. Factors influencing Black Woodpeckers presence at landscape scale (light grey). Factors influencing feeding substrates selection at local scale (dark grey) and the ones influencing cavity trees selection at local scale (orange) and tree scale (green). Bold borders indicate the focus of our work while boxes below represent presumed ecological mechanisms.

At the tree scale, Black Woodpeckers cavity tree selection is a trade-off among the energy applied during excavation and the cavity quality (time resistance, microclimate, predation risk). To minimize the energy applied, Black Woodpeckers may target tree characteristics which reduce excavation time. For instance, primary cavity excavators from North America excavate preferentially softer interior wood (Lorenz, Vierling, Johnson, & Fischer, 2015; Schepps et al., 1999), however wood density preferences have not been documented yet for Black Woodpeckers. Considering that wood decaying fungi soften the wood (Conner, Orson, & Adkisson, 1976; Schwarze, Spycher, & Fink, 2008), the reciprocal positive relationship between them and primary cavity excavators has been documented (Jackson & Jackson, 2004). Black Woodpeckers select heart rotted trees caused by wood decaying fungi in order to reduce their excavation time (Conner et al., 1976; Zahner, Sikora, & Pasinelli, 2012). As dead trees present a lower wood density than living trees (Harmon, Woodall, & Sexton, 2011), one could suppose that Black Woodpeckers would excavate preferentially dead trees. However documented preferences show that Black Woodpeckers can either dig living trees (Kosiński & Kempa, 2007; Zahner, Bauer, & Kaphegyi, 2017; Zahner et al., 2012) or dead trees (Rolstad et al., 2000). Moreover, the selection of an appropriate nest site location that minimizes offspring and adult predation is important for bird fitness (Lima, 2009). Black Woodpeckers excavate preferentially straight trunks free of branches, with the presumed explanation that it could reduce Pine Marten (*Martes martes*) predation (Bocca et al., 2007; Colmant, 2003; Cuisin, 1967; Déom, 2003; Rolstad et al., 2000; Zahner et al., 2017).

The local scale is between stand and tree scales: it is the close environment around a cavity tree. At the stand scale, Black Woodpeckers nest preferentially in open habitat (Rolstad et al., 2000) where there are few large trees (Saporetti et al., 2016) but Brambilla & Saporetti (2014) reveal woodland and broadleaves cover increase nesting suitability. It could be more relevant to look at Black Woodpeckers open area preference at the local scale, rather than at the stand scale. Open areas would facilitate cavity aerial access for Black Woodpeckers (Cuisin, 1967) and reduce predation risk (Cuisin, 1967; Mikusiński, 1995; Rolstad et al., 2000; Widen, 1989).

However, many European studies focusing on Black Woodpeckers cavity trees are expert descriptions from biologists and ecologists (few are from foresters) and quantitative studies concern on other biomes (North America, Scandinavia). The objective of this study was twofold: (1) we quantitatively described Black Woodpeckers cavity trees and their close environment (local scale description) in two French forests; (2) we examined the role of tree-level factors in Black Woodpeckers cavity tree selections. To do so, we compared tree-traits between trees bearing at least one Black Woodpeckers cavity (thereafter cavity-trees) and trees devoid of Black Woodpeckers cavity (thereafter control-trees). We hypothesized that:

(i) *Cavity-trees will have a lower wood density than control-trees.*
(ii) *There will be more fungal fruiting bodies on the exterior of cavity-trees compared to control-trees.*
(iii) *The first branch of cavity-trees will be higher compared to control-trees.*
(iv) *Cavity-trees first tree neighbor will be further away than control-trees first tree neighbor.*
(v) *Cavity-trees will welcome more cavities from other woodpecker species than control-trees.*
(vi) *There will be more wood saproxylic microhabitat richness and abundance on cavity-trees compared to control-trees.*

MATERIALS AND METHODS

1 - Cavity-trees

We benefited from opportunistic data of two French forest sites where Black Woodpeckers cavities have been searched and mapped (Table 1, Figure 2). In the forest of Auberive, forest managers (French National Service, ONF) have located 223 Black Woodpeckers cavity-trees during tree selection operations between 2003 and 2018. In the forest of Loches, a naturalist (Michael Dubois) has located 112 Black Woodpeckers cavity-trees between 2010 and 2018. We did not differentiate cavity use (nesting, roosting or abandoned) as long as it was dug by Black Woodpeckers. In either forest, our dataset was not an extensive survey but rather a sample of available cavities, which is not a problem for the analyses carried out in our study.

Table 1. Main characteristics of the sampling sites (ONF, 2006, 2012).

Sites	**Forest centroid coordinates**	**Dominant tree species**	**Area (ha)**	**Mean altitude (m)**	**Substrate**	**Management type**	**Known cavity trees**
Auberive	47° 47' 42.774" N 5° 4' 57.382" E	*Fagus sylvatica* (56%) Other broadleaves (15%) *Quercus sp.* (13%)	5 584	110	Limestone	Uneven-aged	223 0.04 cav. /ha
Loches	47° 9' 16.277" N 1° 4' 23.543" E	*Quercus petraea* (92%)	3 952	420	Flint clay	Even-aged	112 0.03 cav. /ha

2 - Field protocol

2.1 - Sampling design

For old records, trees can break at the cavity location (Wesołowski, 2011) or heal and close cavities (Colmant, 2003; personal communications Boutteaux Jean-Jacques; Dubois Michael). Searching for old excavated cavity-trees could lead to an obvious time loss during field trip. In Auberive, we selected recent inventories (>2015), thus we kept 63 recent cavity-trees out of 223. In Loches, we kept all inventories since the inventory date has not been recorded, which could induce a bias for some measurement. We draw cavity-trees at random to create a sampling order. To reduce spatial autocorrelation, we rejected cavity-trees which were closer than 400 m. When we did not find a cavity-tree, we processed to the next one in the random list (Figure 2). Even if Rolstad et al. (2000) considered dead trees as a selected tree type for Black Woodpeckers, we excluded dead cavity-trees from sampling because they could affect variables of interest. A dead cavity-tree related to a living control-tree would have modified wood density and microhabitat comparisons, as wood density decreases with tree death (Harmon et al., 2011), and as dead trees bear more microhabitats than living trees (Paillet, Debaive, et al., 2018). We controlled tree vitality to avoid a potential confound effect between tree vitality (which does not interest us) and wood density and microhabitats (which interest us).

For each cavity-tree, we paired a control-tree as the closest equivalent tree devoid of Black Woodpeckers cavity (maximum distance observed 66 m; mean = 18 m). We selected a control-tree with similar characteristics as the cavity-tree (species and Diameter at Breast Height (DBH) ± 10 cm). We controlled for the tree species and DBH because they could impact Black Woodpeckers choice (Mikusiński, 1995) and our objective was not to determine tree species and DBH preferences in this study. Moreover, tree species also greatly impacts wood density (Chave, Muller-landau, Baker, Easdale, & Webb, 2006). We controlled tree species to avoid a potential confound effect between tree species (which does not interest us) and wood density (which interest us).

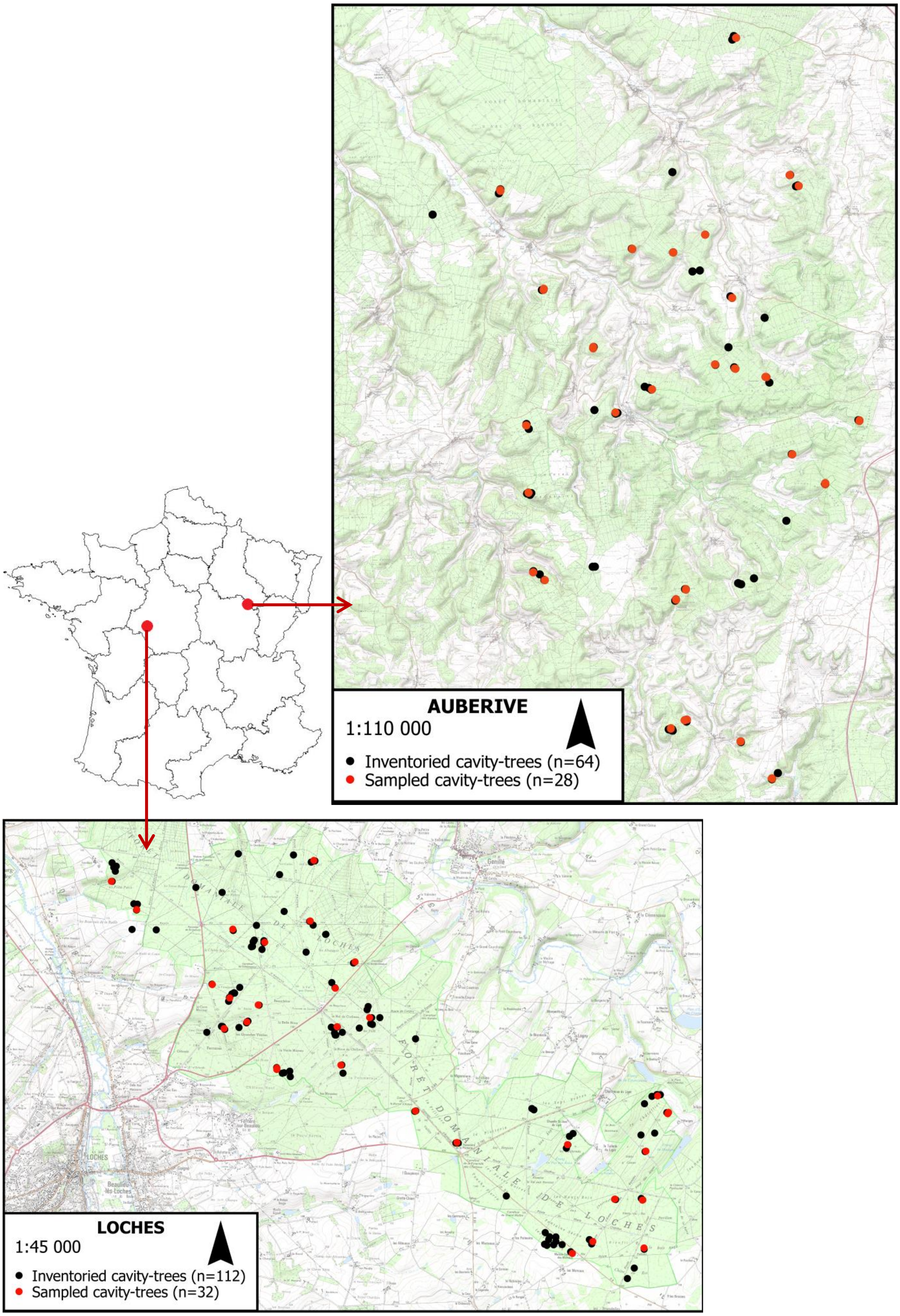


Figure 2. Sampling design maps of Auberive (up) and Loches (down). Black points show inventoried cavity-trees (only recent ones for Auberive) and sampled cavity-trees are displayed in red.

We did fieldwork in April 2018. We prospected for 32 cavity-trees in Auberive but selected 28 of them: 1 was broken; we did not find 2 of them and 1 cavity was closed. We prospected for 53 cavity-trees in Loches but selected 28 of them: 12 were broken, 5 were dead, we did not find 5 of them and 3 cavities were closed. On four plots, we discovered a second unidentified cavity-tree near the sampled one (within a 20 m radius). We decided to sample it as well, with the same control-tree, which gave us four triplets instead of pairs. As a result, we sampled 28 cavity-trees in Auberive and 32 in Loches. As there were more known cavity-trees in Auberive (223), the sampling effort was lower (12.5%) compared to Loches (28.6%). However, looking only at recent records only (>2015), the sampling effort was higher in Auberive (44.4%).

2.2 - Local forest structure

We evaluated basal area and deadwood volume once per paired trees. Indeed, as cavity-tree and control-tree were spatially close, those measurements could not differ much.

We measured basal area of small trees (DBH between 7.5 and 22.5 cm), medium trees (22.5 - 47.5 cm) and large trees (>47.5 cm), as well as total basal area (the sum of the previous basal areas) using a relascope (fixed angle of 2%).

Within a radius of 20 meters around the cavity-tree, we evaluated deadwood volume. We measured the DBH and height of dead standing trees (minimum DBH = 30 cm) and noted species whenever possible and type (tree, snag or stump). We also measured lying dead trees (logs, minimum median diameter = 30 cm) length and median diameter and noted species whenever possible. Afterwards, we estimated deadwood volume per hectare following Paillet et al. (2015) calculations.

2.3 - Tree level measurements

On cavity-trees, we recorded cavity height (m), orientation (gr), and tilt (4 qualitative classes estimated by eye). In further analyses, we used relative cavity height, which is the cavity height divided by the tree height, in order to compare cavity height between sites. On all trees, we measured DBH and using a hypsometer (HÄGLOF's Vertex IV) we evaluated tree height, first branch height, and the distance to the nearest neighbor (DBH > 7.5cm) as a proxy to vegetation clutter. Using a manual auger, we sampled a wood core (for wood density measurement) at breast height (1m30) below the cavity of interest, and in the same orientation on paired control-tree. If the cavity-tree bore several Black Woodpeckers cavities, we chose the highest one to determine the orientation of coring (Figure 3).

Finally, we recorded tree-related microhabitats richness (47 types) and abundance on cavity and control-trees following the typology of Larrieu et al. (2018). In further analyses, we used richness and abundance of saproxylic microhabitats (32 types): woodpecker cavities (excluding Black Woodpeckers 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 limb. We also separately looked at other woodpecker cavity abundance: lesser spotted woodpecker (*Dendrocopos minor*), middle spotted woodpecker (*Dendrocopos medius*), great spotted woodpecker (*Dendrocopos major*), european green woodpecker (*Picus viridis*) and grey-headed woodpecker (*Picus canus*) cavities, excluding Black Woodpeckers cavities.

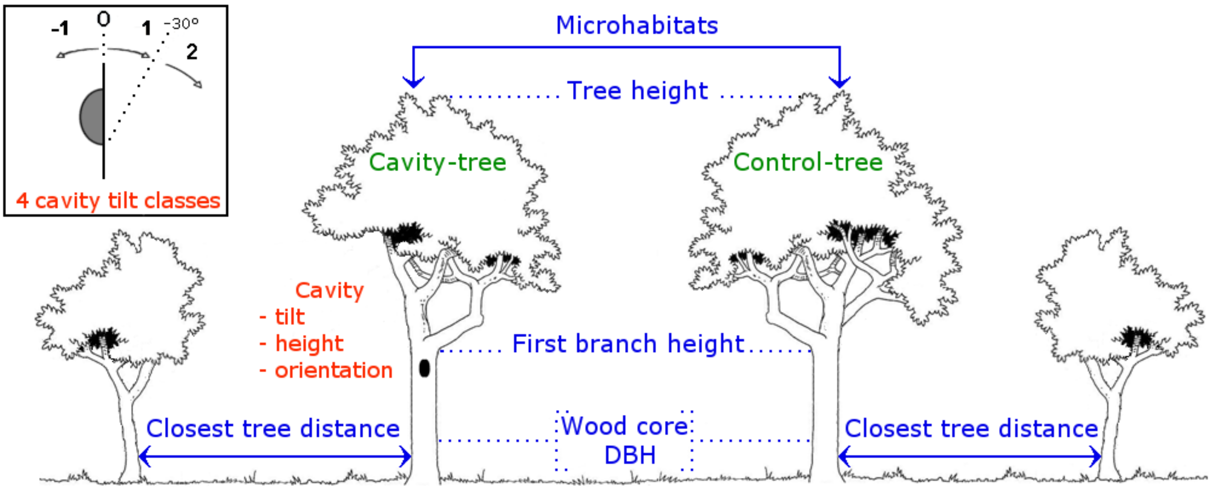


Figure 3. Tree scale measurements comparing paired trees (green): cavity description (red) and comparable variables (blue). We paired a control-tree as the closest equivalent tree to a cavity-tree (same species and DBH ± 10 cm). The fourth classes of cavity tilt are detailed in the top left box. We inventoried tree-related microhabitats richness and abundance following the typology of Larrieu et al. (2018). We sampled a wood core for wood density measurement at 1m30. We chose the nearest neighbor among all trees with a DBH > 7.5cm.

3 - Wood core samples treatment

To determine wood density, wood core samples were dried 24h at 103°C, and then X-ray scanned (medical tomograph type General Electric BrightSpeed Excel, precision each 0.625mm) at INRA Nancy (LERFoB laboratory) to produce pictures in levels of grey. We derived mean density values and density profiles from these pictures using ImageJ software and plug-in CalDenQB (Jacquin, Longuetaud, Leban, & Mothe, 2017; Leban et al., 2016, 2017; Longuetaud et al., 2014). For each core, we created a density profile based on measurements each 0.625 mm along the sample. We retained mean density as response variable of Black Woodpeckers cavity occurrence. We used density profiles to calculate means on 5 cm sections along wood core samples from 0 cm (bark) to 30 cm (pith) and we retained each mean per section as response variables of Black Woodpeckers cavity occurrence.

4 - Statistical analyses

We processed all the analyses with the R software v. 3.4.3 (R Core Team, 2017). We compared descriptive variables between the two sites using generalized linear models (glm function). We chose the Gamma error distribution with identity link since variables have positive continuous values.

We compared six response variables between cavity- and control-tree using generalized linear mixed-effect models (glmer function; lme4 package v1.1-17; Bates, Mächler, Bolker, & Walker, 2014). We analyzed the following response variables: wood density (total and each 5 cm), first branch height, distance from the nearest neighbor, other woodpecker cavity abundance, saproxylic microhabitat richness and abundance (Table 2). For the former three variables, we chose the Gamma error distribution with identity link since they have positive continuous values. For the latter three variables, we chose Poisson error distribution with 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 take into account possible variations of the relationships with site. We finally added a plot random effect on the intercept to account for the paired design. On those models, we first tested interaction contrast of all factors (type, site and interaction) based on model predictors for each response variable (joint_tests function; emmeans package v1.2.2; Russell, 2018). It is use to look at the variation of a variable (e.g. wood density) between control- and cavity-trees, and to look at the homogeneity of this variation between the two sites. Then, we compared estimated means between control- and cavity-trees separately by site using marginal post-hoc Tukey tests (emmeans function; emmeans package v1.2.2; Russell, 2018).

Table 2. Means, standard errors and ranges (minimum-maximum) of all six response variables measurements separated by sites (Auberive *versus* Loches) and tree type (cavity *versus* control). In addition to total mean, we separated wood density along wood core profile each 5 cm, from 0 (bark) to 30 (pith).

			Auberive		**Loches**	
		Tree type	**Mean ± s.e.**	**Range**	**Mean ± s.e.**	**Range**
Wood density (kg^{3}/m)	**TOTAL**	**Cavity**	680 ± 13	[551-776]	715 ± 10	[617-868]
		Control	712 ± 6	[665-799]	722 ± 11	[619-832]
	0-5 cm	**Cavity**	662 ± 10	[573-774]	657 ± 10	[563-776]
		Control	673 ± 9	[611-825]	656 ± 10	[574-820]
	5-10 cm	**Cavity**	665 ± 12	[456-749]	683 ± 11	[569-806]
		Control	676 ± 9	[604-826]	682 ± 15	[564-874]
	10-15 cm	**Cavity**	690 ± 15	[502-819]	706 ± 11	[602-857]
		Control	707 ± 8	[642-814]	703 ± 13	[600-911]
	15-20 cm	**Cavity**	715 ± 17	[497-893]	722 ± 11	[615-869]
		Control	734 ± 11	[646-885]	736 ± 14	[622-937]
	20-25 cm	**Cavity**	720 ± 25	[479-892]	721 ± 13	[596-855]
		Control	756 ± 15	[656-916]	742 ± 13	[602-866]
	25-30 cm	**Cavity**	742 ± 17	[640-865]	708 ± 12	[622-775]
		Control	741 ± 11	[682-824]	722 ± 21	[558-871]
First branch height (m)		**Cavity**	9.8 ± 0.7	[5.2-19.5]	15 ± 0.8	[2.5-22.6]
		Control	6.5 ± 0.5	[1.9-14.8]	8.2 ± 1	[0.7-19.9]
Nearest neighbor distance (m)		**Cavity**	4.2 ± 0.4	[0.7-6.9]	4.1 ± 0.4	[0.7-7.3]
		Control	3.6 ± 0.4	[0.2-7.3]	3.8 ± 0.4	[0.5-8.1]
Other woodpecker cavity abundance		**Cavity**	1.6 ± 0.3	[0-6]	0.8 ± 0.5	[0-15]
		Control	0.04 ± 0.04	[0-1]	0.14 ± 0.09	[0-2]
Saproxylic microhabitat richness		**Cavity**	3.4 ± 0.3	[1-7]	2 ± 0.2	[1-5]
		Control	2.5 ± 0.3	[0-6]	1.7 ± 0.2	[1-4]
Saproxylic microhabitat abundance		**Cavity**	4.9 ± 0.5	[1-11]	2.7 ± 0.6	[1-18]
		Control	3.1 ± 0.3	[0-7]	1.9 ± 0.2	[1-5]

RESULTS

1 - Local environment and cavity-tree descriptions

We first present raw descriptions of local environment and cavity-trees characteristics at two levels: the surrounding habitat and the tree level including tree and cavity descriptions (Table 3).

Auberive site has significant higher mean elevation and steeper slopes than Loches. Mean basal area is significantly higher in Loches than in Auberive, which is mostly explained by a greater proportion of large trees (means = 14.1 and 8.6 m²/ha, respectively). Basal area of medium trees and small trees are not significantly different between sites. Basal area ranges are larger in Loches than in Auberive (e.g. large trees basal area range is doubled at Loches). Mean volume of deadwood nearby cavity-trees is rather homogeneous between sites (means = 20 and 24 m^3/ha, respectively) but the range is twice as big in Auberive as in Loches (Table 3).

For sampled trees, in Auberive, beech (*Fagus sylvatica*) bears all Black Woodpeckers cavities while it is almost the case in Loches (only two are oaks *Quercus petraea*). Cavity-trees DBH is rather homogeneous between Loches and Auberive (means = 51 and 55 cm, respectively), although largest trees are found in Auberive. Conversely, cavity-trees are on average taller in Loches than in Auberive (means = 33 and 27 m, respectively), with equivalent range variations. Black Woodpeckers cavities are higher in trees in Loches than in Auberive (means = 13 and 7 m, respectively) and also higher relatively to tree height (relative cavity height means = 0.36 and 0.27, respectively). Variation ranges in cavity location on tree are quite large, with 12m difference between the lowest and the highest cavity in Auberive, and 16m difference in Loches (Table 3). At both sites, cavity entrance holes are rarely East or North-East oriented, and they tend to be more South oriented in Loches (Figure 4). All cavity entrance holes were vertical, except four in Auberive which were titled downwards (between 0 and -30°).

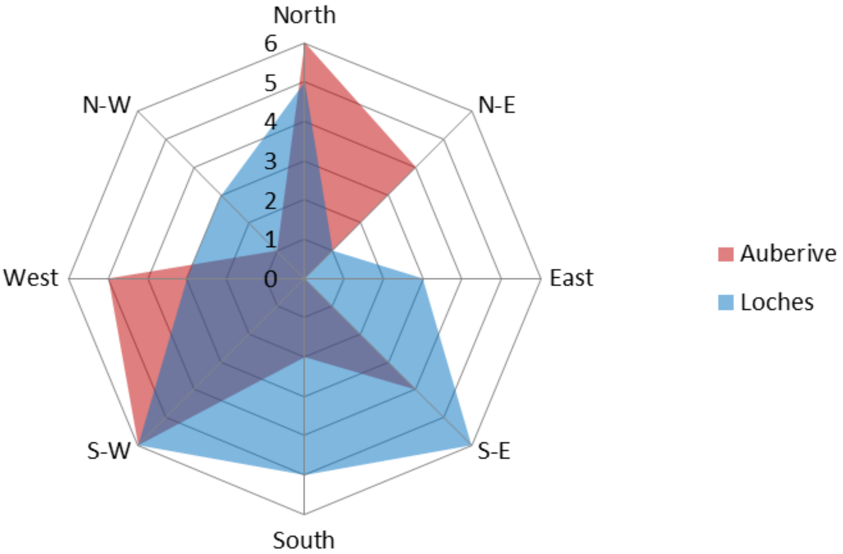


Figure 4. Occurrences of surveyed Black Woodpeckers cavity entrance hole orientation (n = 56). Occurrences of cavities from Auberive are displayed in red and from Loches in blue.

Table 3. Surveyed cavity-trees surrounding environment description and cavity-trees characteristics: means, standard errors and ranges (minimum-maximum). We divided basal area in three tree categories: S small (DBH between 7.5 - 22.5 cm), M medium (22.5 - 47.5 cm) and L large (> 47.5 cm). Relative cavity height is cavity height related to tree height. We compared variables between sites using generalized linear models (Gamma error distributed with identity link).

		Auberive (n = 28)		**Loches (n = 28)**		**Sites comparison**
		Mean ± s.e.	**Range**	**Mean ± s.e.**	**Range**	**p 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
Basal area (m^2/ha)	**S**	2.9 ± 0.4	[0-6.5]	2.2 ± 0.3	[0-6.5]	0.171
	M	7.6 ± 0.6	[1-12]	8.5 ± 0.9	[2.5-24.5]	0.257
	L	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 ***
TREES						
DBH (cm)		55 ± 2	[36-86]	51 ± 2	[31-64]	0.11
Tree 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 ***

2 - Comparison between cavity-trees and control-trees

We noted visible conks of fungi and heart rot, respectively during microhabitat observations and wood core samples. However, the few occurrences prevented us to statistically test appearance differences between cavity and control-trees (Table 4).

Table 4. Occurrences of fungi and heart rot on all surveyed trees in the two sites (Auberive and Loches), between trees carrying at least one Black Woodpecker cavity (cavity) and trees without any Black Woodpecker cavity (control).

	Auberive		**Loches**	
Tree type	**Cavity**	**Control**	**Cavity**	**Control**
Fungi	1	4	0	0
Heart rot	7	2	2	1

Hereafter, we compared estimated explanatory variables means between cavity-trees and control-trees, first overall and then for each site. Since our variables display different ranges, we used percentage of increase or decrease to compare their magnitude (see Figure 5 for absolute values).

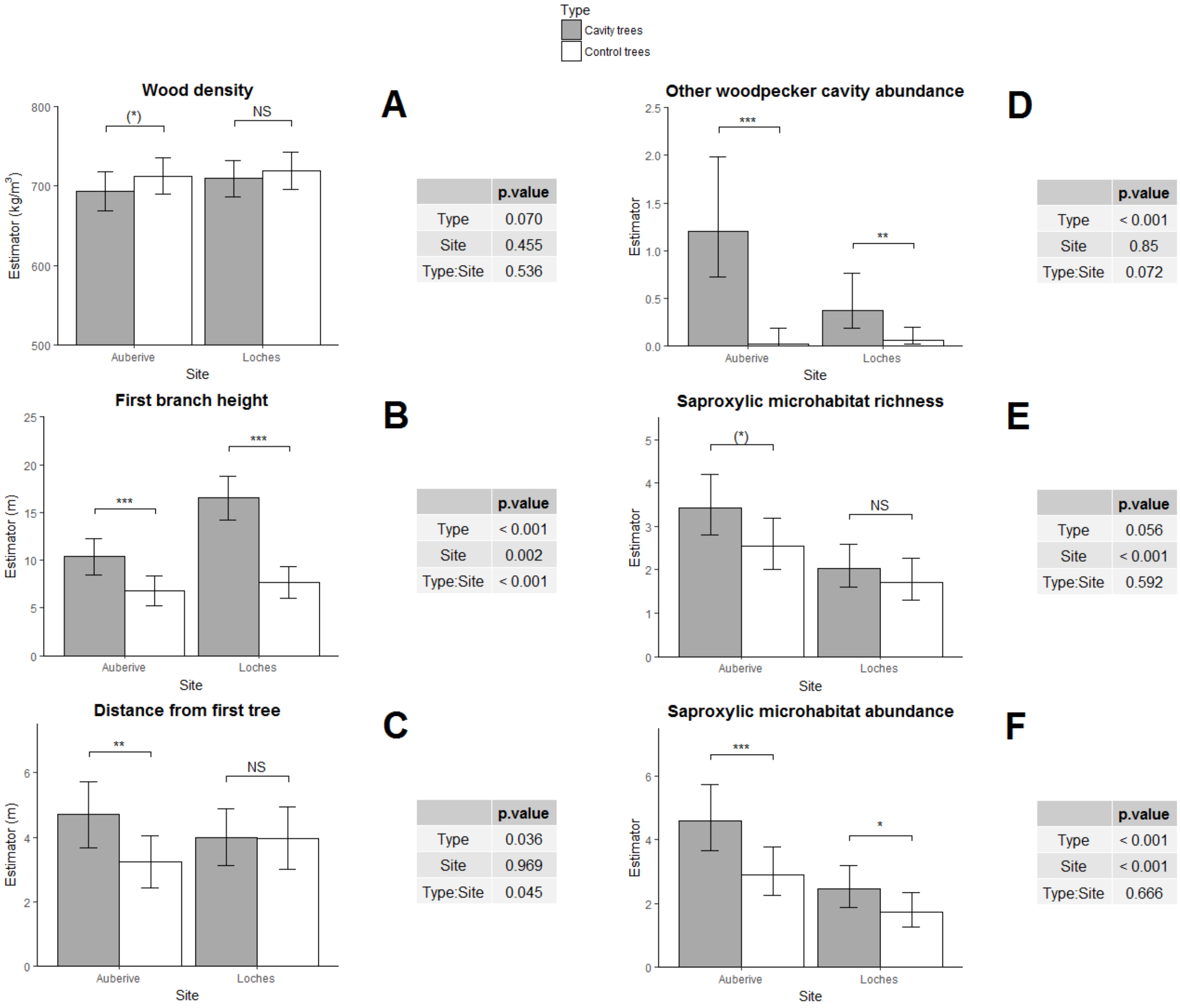
Globally, cavity-trees show a lower mean wood density than control-trees (Figure 5A). Wood density is 5% lower for cavity- than control-trees in Auberive ($p < 0.001$), but not different in Loches ($p = 0.45$). When we removed all 12 trees with heart rot from the dataset, cavity-trees wood density remained marginally lower than control-trees wood density ($p = 0.07$). Along wood core profiles, cavity-trees wood density was significantly lower than control-trees from 10 to 25 cm, only in Auberive (Figure 6, Table 5).

Generally, cavity-trees had a higher first branch compared to control-trees (Figure 5B). In Auberive, cavity-trees first branch was 55% higher than control-trees first branch (p <

0.001), and in Loches, this difference reaches 115% ($p < 0.001$). Overall, cavity-trees had a more distant nearest neighbor than control-trees (Figure 5C). The nearest neighbor of cavity-trees was 45% further away compared to the nearest neighbor of control-trees in Auberive ($p = 0.002$), whereas there was no difference between these distances in Loches ($p = 0.96$).

Overall, there were significantly more other woodpecker cavities on cavity-trees compared to control-trees (Figure 5D). Cavity-trees supported significantly 4500% more other woodpecker cavities than control-trees in Auberive ($p < 0.001$), and significantly 500% more in Loches ($p = 0.001$). Note that those high magnitudes are due to a quasi-absence of other woodpecker cavities occurrence in control. Globally, saproxylic microhabitats richness tend to be higher on cavity-trees than on control-trees ($p < 0.1$; Figure 5E). Cavity-trees tend to support 35% more wood decaying microhabitat richness than control-trees in Auberive ($p = 0.05$), but the richness was not different in Loches ($p = 0.37$). Generally, there were significantly more saproxylic microhabitats on cavity-trees compared to control-trees (Figure 5F). Cavity-trees supported significantly 60% more wood decaying microhabitats than control-trees in Auberive ($p < 0.001$), and only 15% more in Loches ($p = 0.04$).

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



A

	p.value
Type	0.070
Site	0.455
Type:Site	0.536

D

	p.value
Type	< 0.001
Site	0.85
Type:Site	0.072

B

	p.value
Type	< 0.001
Site	0.002
Type:Site	< 0.001

E

	p.value
Type	0.056
Site	< 0.001
Type:Site	0.592

C

	p.value
Type	0.036
Site	0.969
Type:Site	0.045

F

	p.value
Type	< 0.001
Site	< 0.001
Type:Site	0.666

Figure 5. Comparison of estimated mean (for six response variables) between trees supporting at least one Black Woodpecker cavity (cavity-trees, in grey) and trees without any Black Woodpecker cavity (control trees, in white) based on generalized linear mixed models. A, B and C are Gamma error distributed models with identity link while D, E and F are Poisson error distributed models (values were back transformed). We added a random plot-level effect to models to account for the paired design. Error bars represent 95% confidence interval and stars show marginal Tukey test significance (thresholds: (*) $p < 0.1$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). Associated tables display the contribution test of each factor for each model: Type (occurrence of a Black Woodpecker cavity in a tree), Site (Auberive *versus* Loches), and the interaction between Type and Site.

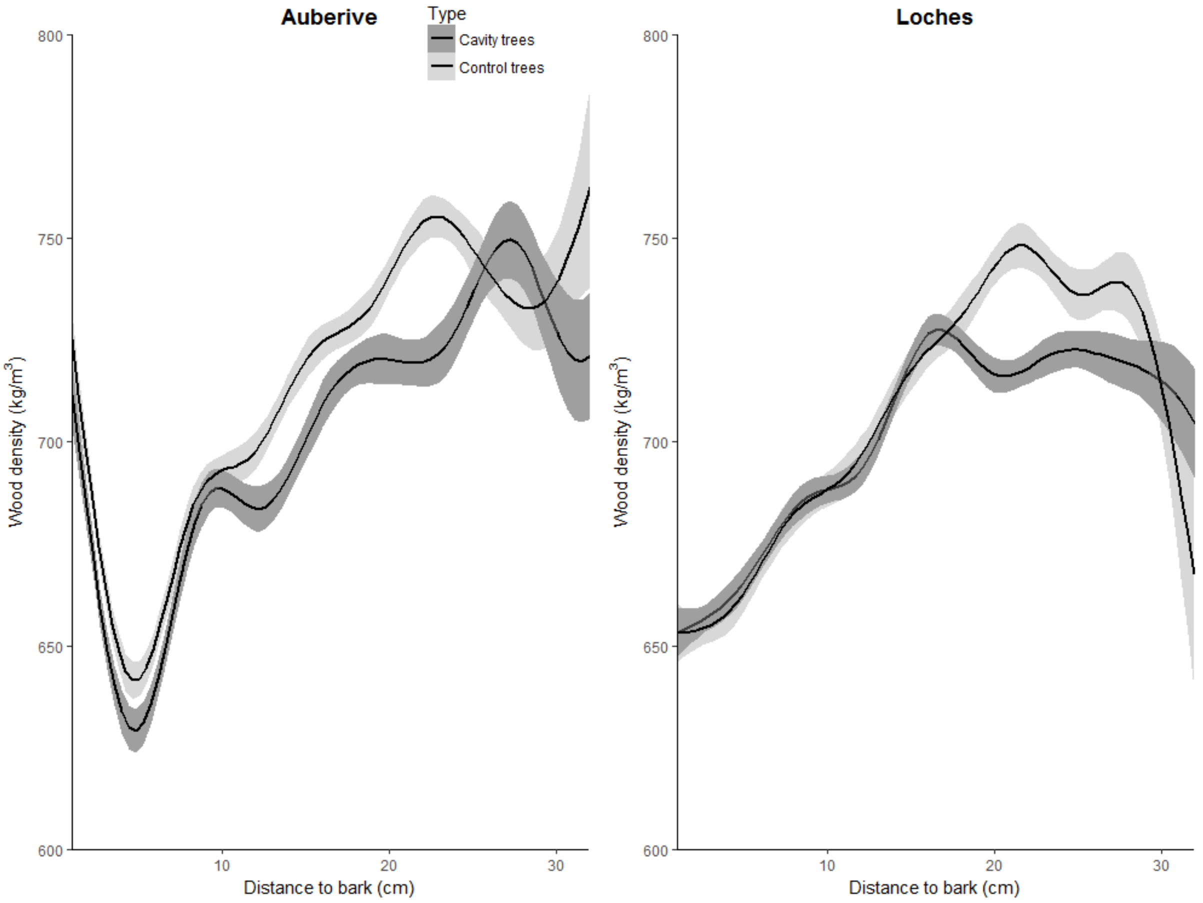


Figure 6. Wood density profiles of trees supporting at least one Black Woodpecker cavity (cavity-trees, in dark grey) and trees without any Black Woodpecker cavity (control trees, in light grey) in Auberive (left) and Loches (right). Error margins represent 95% confidence interval.

Table 5. Wood density comparisons in percentage between cavity-trees and control-trees considering based on estimates issued of generalized linear mixed models (Gamma error distribution). We compared means along wood core profiles each 5 cm from 0 (bark) to 30 (pith). Negative values signify lower wood density for cavity-trees than control-trees. Stars show marginal Tukey test significance (thresholds: (*) p < 0.1; * p < 0.05; ** p < 0.01; *** p < 0.001).

	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
WITHOUT HEART ROTTED TREES (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

DISCUSSION

We showed that Black Woodpeckers excavate trees that have globally different characteristics from the controls we chose. In this context, we discuss (1) cavity-trees distinctive characteristics and the engineering/umbrella role of Black Woodpeckers related to microhabitats, (2) descriptive measurements at tree and local scales and (3) we suggest biodiversity-friendly management actions.

1 - Black Woodpeckers cavity-tree specific characteristics (tree scale)

1.1 - Wood density

We validated our first hypothesis *(i)*: Black Woodpeckers excavate trees with a lower mean wood density compared to control-trees. Wood density is a determining factor during Black Woodpeckers cavity-tree selection, as it is for other primary cavity excavators (Lorenz et al., 2015). In Auberive, radial wood density variations reveal that cavity-trees are around 3% less dense than control-trees from 10 to 25 cm (bark distance). Even if we found no significant differences in Loches, profiles display a cavity-tree mean wood density lower than control-trees's, from 18 to 28 cm. These are in accordance with studies on North American primary cavity excavators which select interior soft wood trees. Four species excavate trees with a wood density 30% lower than random trees at 8 cm depth (means = 7 and 10 kg/m3, respectively; Schepps et al., 1999) and six species excavate trees with a wood density 66 % lower than random trees between 5 and 10 cm depth (means = 3 N/m and 9 N/m, respectively; Lorenz et al., 2015). The availability of these particularly soft interior trees is low in those two American studies, but primary cavity excavators still highly select them. For wood hardness, the maximum distance from bark measured is various among studies. Schepps et al. (1999) choose arbitrarily four locations at 2, 4, 6 and 8 cm depth. Lorenz et al. (2015) measured wood density at cavity height, and used cavity maximal depth (14 cm) to decide sampling length (15 cm). As we did not measure cavity depth, we sampled wood core the length of the tree's radius. It might be not the best choice since wood density measurement is not related to cavity depth. However, we still detected a particular softer in interior wood at 1m30 in cavity-trees. It might be explained because beech wood density at 1m30 is rather representative of the whole tree density (Longuetaud et al., 2017). Therefore we presume that this particular softer interior wood measured at 1m30 is also detected by Black Woodpeckers when excavating their cavity upper in the trunk. In that sense, Black Woodpeckers would select trees to excavate which possess, overall, a softer interior wood. Primary cavity excavators probably face trade-offs when selecting cavity-trees, depending on advantages and disadvantages given by a softer interior wood, as discussed in the following paragraphs.

Choosing softer trees may reduce excavation time and energy applied through excavation which could give a selective advantage. Primary cavity excavators may also select trees with the maximum hardness they are able to excavate. Head and body movements are confined during interior cavity excavation which might force them to select trees with soft interiors (Lorenz et al., 2015).

Conversely, a low wood density might increase the risk of cavity-tree collapse during strong winds: decayed trees may more easily break done than healthy trees. The Great Spotted Woodpecker selects soft trees with heart rot, however it does not reuse its cavities several consecutive years (Matsuoka, 2008). The selection of a cavity-tree wood density may depend on the potential reuse of the cavities. Black Woodpeckers dig long persistent cavities (Wesołowski, 2011) and reuse them several years (Colmant, 2003; Cuisin, 1986; Johnsson et al., 1993). Consecutive uses could explain the low difference between control-trees and cavity-trees density (only -6% at maximum). Black Woodpeckers could select healthy trees which are supposed to live for a long time with a little wood density reduction to facilitate their excavation. However, our results may overestimate cavity-trees wood density since we measured it at 1m30 from the ground and not at the height of the cavity. Sample the wood core near the cavity could have revealed a stronger effect. Indeed, vertical wood density weaknesses are used by woodpeckers (Matsuoka, 2008; Schepps et al., 1999; Zahner et al., 2012).

Moreover, softer wood may increase vulnerability to nest predators and thereby favor shorter nesting periods (Lorenz et al., 2015; Schepps et al., 1999). Again, this supports the idea that cavity-tree density selection is determined by cavity use. As a complement, wood density may directly or indirectly affect cavity microclimate, which could be a factor in the trade-off (Lorenz et al., 2015).

To conclude, cavity-tree wood density selection is a woodpecker species-dependent compromise. Trade-offs occur between excavation abilities, time investment, cavity-tree time resistance, cavity microclimate and predation risks (which can be related to nesting time). We suggest that future studies examine some of these trade-offs for several primary cavity excavators, for example the link between wood density and cavity microclimate or predation. We also suggest testing the differences between roosting and nesting cavities, as Black Woodpeckers reuse cavities, but still prefers to excavate a new nest each year in order to reduce offspring predation risk (Nilsson, Johnsson, & Tjernberg, 1991).

1.2 - Fungal fruiting body

We were not able test our second hypothesis *(ii)*: scarce observations of fungal fruiting bodies prevent us to analyze differences between cavity-trees and control-trees. This result is quite surprising according to the number of studies supporting the link between fungi and woodpecker cavities (Conner et al., 1976; Jackson & Jackson, 2004; Zahner et al., 2012). However, as Conner et al. (1976) observed, cavity-trees do not always display fungal fruiting bodies even when wood decay fungi are present. To better test this hypothesis we should searched for other wood decay fungi presence indication instead of fruiting bodies.

1.3 - Isolated trees free of low branches

We validated our two hypotheses concerning the factors that are supposed to minimize offspring and adult predation: *(iii)* cavity-trees have a higher first branch and *(iv)* a further closest neighbor compared to control-trees. First branch height can be related to cavity height. Mean cavity height at Loches is 13 m which is similar with values found in the literature (Table 6). Cavities are lower on average than first branch height (means = 13 and 15 m, respectively). In Auberive, cavity height is lower than in Loches (mean = 7 m) and still lower than cavity-trees first branch height (mean = 9.8 m). We conclude that Black Woodpeckers excavate their nests below the first branch, which confirms naturalistic observations (Bocca et al., 2007; Colmant, 2003; Cuisin, 1967; Déom, 2003; Johnsson, 1993; Nilsson, 1984; Pirovano & Zecca, 2014; Rolstad et al., 2000; Zahner et al., 2017, 2012). We also showed that cavity-trees are isolated from other at local scale: basal area is not apparently smaller, but targeted trees are apart from others in Auberive. This result is not shared in Loches, but the absence of response could have several explanations: even-aged management could have homogenized trees distances or neighbors might have grown up since cavity excavation because we did not know cavity-tree inventories date. Our findings from Auberive refine studies which suggest Black Woodpeckers prefer to dig cavities in open areas (Rolstad et al., 2000; Saporetti et al., 2016). Admittedly, we searched cavity-trees in forest only, which is not an open area, but we did not found cavity-trees in clearcuts or at edges. Our results support that Black Woodpeckers dig cavities in forests (close area at stand scale), but choose preferentially a tree locally apart from others (open area at tree scale). Therefore, the first branch height as well as the closest neighbor distance seems factors of selection during cavity-tree research. A suitable Black Woodpeckers cavity-tree has a trunk free of low branches and is relatively isolated. We presume underlying ecological processes which could guide this choice in the following paragraphs.

As suggested by Cuisin (1967), isolated trees devoid of low branches could facilitate adult aerial access to cavity and offspring flight from nesting cavity. Moreover, those tree characteristics could be linked to an anti-predator behavior. Zahner et al. (2017), using camera traps, 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*). Even if the Northern Goshawk can visit Black Woodpeckers nests and has seldom been seen pulling out young Black Woodpeckers from their nest (Cuisin, 1967), the size of the cavity entrance and cavity depth can limit large raptors to reach offspring (Zahner et al., 2017). However, the Northern Goshawk has been reported to also predate adult Black Woodpeckers (Cuisin, 1967; Mikusiński, 1995; Rolstad et al., 2000) and this species prefers to hunt in large patches of older successional stages (Widen, 1989). We could presume that Black Woodpeckers are more likely to avoid Goshawk hunting when the cavity-tree is easily reachable. Concerning offspring survival, the Great Spotted Woodpecker can predate Tits, Fly catchers and Blackcaps nests (Nilsson, 1984; Stevens, Anderson, Grice, Norris, & Butcher, 2008; Weidinger, 2009) but we found no indication of predation on Black Woodpeckers nests. The Pine Marten is considered as the major Black Woodpeckers nest predator in Norway, Sweden and Germany (Nilsson et al., 1991; Rolstad et al., 2000; Zahner et al., 2017). It has been seen to pull out young Black Woodpeckers from the nest (Cuisin, 1967) and is known to revisit cavities (Sonerud, 1985) which increases old cavities predation risks (Nilsson et al., 1991). The excavation of a new nest each year and the selection of a higher location may contribute to reduce this risk (Johnsson, 1993; Nilsson, 1984; Zahner et al., 2017). Moreover, different authors observed that Black Woodpeckers seem to choose “branch-free trunks”, either in general along the trunk (Bocca et al., 2007; Colmant, 2003), or bole without branches for 10 m (Rolstad et al., 2000; Zahner et al., 2012), or at least no branches below the cavity (Cuisin, 1967; Déom, 2003; Pirovano & Zecca, 2014). They assume that branches on the trunk, or those of neighboring trees, may serve as a ladder to the Pine Marten which may help it to reach nests. Black Woodpeckers could thus minimize offspring predation risk by selecting a tree of higher safety, which could be a relatively isolated tree which has a branch-free trunk.

We recommend future study that use camera traps on cavities, to also measure the part of the trunk which is free (using first branch height and closest neighbor distance or any other index). Once again, differentiating roosting from nesting cavities seems important, as anti-predator behaviors may vary between adult and offspring protection.

1.4 - Microhabitats

We validated our hypotheses on the link between Black Woodpeckers cavities and other microhabitats: *(v)* there are more cavities from other woodpecker species on Black Woodpeckers cavity-trees, as well as *(vi)* a higher richness and abundance of saproxylic microhabitats. As recent research links microhabitats (including woodpecker cavities) with bats and birds biodiversity (Paillet, Archaux, et al., 2018), Black Woodpeckers cavity-trees could potentially host a higher biodiversity than random trees. Correlations between Black Woodpeckers and microhabitats may have two explanations: the first is our explanation of predilection that suits the most literature and the second is alternative but we cannot exclude it with our design.

First, Black Woodpeckers could induce a change in trees when excavating them, making them more microhabitats-prone. Black Woodpeckers excavation behavior supplies forests in available cavities. Secondary cavity users are birds, e.g. Tengmalm's Owl (*Aegolius funereus*), Stock Dove (*Columba oenas*), and Jackdaw (*Corvus monedula*) (Johnsson et al., 1993) but also mammals, e.g. bats and rodents (Zahner et al., 2017). Nonetheless, we also presume Black Woodpeckers to facilitate other woodpecker excavation by degrading healthy trees. Since Black Woodpeckers are capable of excavating healthy trees, they could contributes to tree decay process (Kosiński & Kempa, 2007; Zahner et al., 2012; Zawadzka & Zawadzki, 2017). Moreover, excavation could reduce tree defenses and then help saproxylic microhabitats to colonize them, as it is the case for fungi in many studies (Jackson & Jackson, 2004). Black Woodpeckers cavities would decrease trees health and induce its slow degradation with more holes, bark injuries, wood injuries and dead parts. In that sense, Black Woodpeckers excavation behavior could be an initiating event that triggers the apparition of other microhabitats. In comparison, smaller woodpeckers excavate decaying trees (Kosiński & Kempa, 2007; Pasinelli, 2000 [middle spotted woodpecker]; Wiktander, Olsson, & Nilsson, 2001 [lesser spotted woodpecker]). To summarize, Black Woodpeckers would be an umbrella species through supplying available cavities, facilitating other woodpecker excavation and facilitating microhabitats-dependent biodiversity. These results emphasize a higher engineering/umbrella role of Black Woodpeckers than initially supposed.

Second, Black Woodpeckers could detect trees bearing microhabitats as suitable cavity-trees. This explanation is opposite in time and causality with the first one: microhabitats would first colonize a tree, and only after would Black Woodpeckers target this tree for excavation.

However those explanations will remain speculative until temporality between Black Woodpeckers excavation and microhabitats establishment is not explicitly studied. To test causality between Black Woodpeckers excavation behavior and presumed induced biodiversity, we could make microhabitat records and point counts near cavity-trees and control-trees during consecutive years. We could hypothesize that after excavation and over years, cavity-trees will slowly degrade, inducing an increase in microhabitat as well as in bird diversity and abundance.

1.5 - Conclusion

Comparing magnitudes of all tree traits, first branch height and other woodpecker cavities appear to be the most changing factors between control- and cavity-trees. Except for first branch height, all trees traits are more significant and/or display a higher magnitude in Auberive than in Loches. Further research is needed with many more sites to insure homogeneity of Black Woodpeckers cavity-tree preferences.

Excavator cavity-tree preferences are dependent on excavation capacities and cavity use, which comprise roosting or nesting, nesting duration and cavity reuse other years. In this sense, excavator cavity-tree preferences should be studied for each excavator species. Black Woodpeckers cavity-tree preferences are in that sense easy to analyze, since their cavities are easily identifiable by size and shape (oval, entrance holes > 10 cm) but it is different for middle sized cavities. They are excavated by several species, such as middle spotted woodpecker, great spotted woodpecker, European green woodpecker and grey-headed woodpecker. Gathering several species may convey to a conflated analyzes of several distinct niches, therefore searching for middle size cavity-tree characteristics could lead to non-sense.

2 - Local environment and cavity-tree descriptions

2.1 - Local scale

In our two sites, Black Woodpeckers excavate trees in stands displaying various basal areas, from 13.5 up to 30.5 m^3/ha. Auberive is an uneven-aged forest, thus basal area variations are smaller compared to Loches which is an even-aged forest. In Auberive, forest mean basal area (18 m^2/ha; ONF, 2012) is close to the one observed in the surroundings of cavity-trees (19 m^2/ha). In this site, we suppose Black Woodpeckers do not choose a tree to excavate according to basal area because of the large observed range, and because mean basal area around cavity-trees did not diverge from forest mean basal area. Mean basal area in Loches is harder to interpret (8.75 m^2/ha; ONF, 2006) because it takes clearcuts into account. However, we did not identify cavity-trees in clearcuts contrary to what was suggested by Rolstad et al. (2000) in Norway forests. We could have missed those trees since we do not work on trees excavated within the year and cavity-trees in clearcuts often break (Johnsson, 1993).

Deadwood volume around cavity-trees varied considerably, from 0 up to 232 m^3/ha. We thus hypothesize that Black Woodpeckers do not choose a tree to excavate according to surrounding deadwood volume. Deadwood availability favors the presence of Black Woodpeckers because it represents a feeding substrate (Hondong, 2016; Khanaposhtani, Najafabadi, Kaboli, Farashi, & Spiering, 2012; Mikusiński, 1997; Rolstad et al., 1998). However, feeding and cavity sites are spatially disjointed: nesting habitat is affected by cover of broadleaves and woodlands while patches of open habitat (grasslands), conifers and deadwood may increase foraging opportunities (Brambilla & Saporetti, 2014). To our knowledge, no study has analyzed if feeding and nesting sites are spatially separated because of their differences (open habitat and broadleaves cover are opposed) or because this separation is an advantage for Black Woodpeckers (deadwood abundance and broadleaves cover are not opposed). On one hand, choosing close feeding and nesting sites could be a selective advantage because it reduces foraging time. On the other hand, to feed near a cavity-tree could help predators to locate the cavity and increase predation risk.

2.2 - Tree scale

Our study supports that beech, in its natural range, is an important cavity-tree for Black Woodpeckers (Bocca et al., 2007; Colmant, 2003; Cuisin, 1967; Fernandez & Azkona, 1996; Kosiński et al., 2010; Mikusiński, 1995; Zahner et al., 2017), even in Loches where the forest is dominated by oak. Mean cavity-tree DBH and height are close to those found in other studies (Table 6). These similarities give the suspicion that Black Woodpeckers are a habitat specialist when selecting a cavity-tree (Pirovano & Zecca, 2014; Saporetti et al., 2016). To clarify if Black Woodpeckers are habitat generalists or specialists, we could summarize that they adapt to different vegetation cluttering within forests and excavate various tree species, but for cavity-trees they seem to have requirement (large size trees) and preferences (beech, straight trunk, free of low branches, locally apart from neighbor). Mean cavity heights varied between the two prospected sites but will be discussed below. Cavity entrances seem more South oriented in our study, whereas Zawadzka & Zawadzki (2017) and Colmant (2003) found a preference for East and North. However, in both study the preference is not significant. Cuisin (1967) reviewed known orientations and concluded that the determining factor was not cardinal direction but the presence of an open space in front of the cavity hole.

Table 6. Mean Black Woodpeckers cavity-trees DBH and height in our two sites (Auberive and Loches) and in other studies. Numbers of analyzed cavity-trees are specified in parentheses when possible.

	Auberive n = 28	**Loches** n = 32	**Zawadzka & Zawadzki** (2017) n = 150	**Pirovano & Zecca** (2014) n = 94	**Kosiński & Kempa** (2007) n = 14	**Poulsen** (2002)	
DBH (cm)	55	51	54	51	50	40 (Aspen)	50 (Scots pine)
Height (m)	27	33	30.5	X	29	X	X
Cavity height (m)	7	13	12.8	X	12.4	X	X

3 – Implications for forest management

To conclude, since Black Woodpeckers seem to excavate isolated large diameter beech free of low branches, our study supports that Black Woodpeckers are specialists for cavity-tree selections. We also presumed that Black Woodpeckers have a more important engineer role than previously proposed, through facilitation of other woodpecker excavation and other microhabitats formation. Therefore Black Woodpeckers cavity-trees have a conservation interest and can be considered as habitat trees (Bütler, Lachat, Larrieu, &

Paillet, 2013; ONF, 2010). To secure a high abundance of tree bearing microhabitats, we propose to preserve trees bearing Black Woodpeckers cavities, but also potential suitable cavity-trees for Black Woodpeckers to excavate new holes in.

It is important that many potential suitable cavity-trees are available; however determining the threshold density for optimal conservation remains beyond the scope of our study. Rolstad et al. (2000) propose to preserve 1 tree /ha for Black Woodpeckers use and ONF (2010) propose to preserve 2 habitat trees /ha. However cavity-trees are difficult to detect, thus those density could be underestimated. Moreover, Black Woodpeckers prefer to excavate new nests each year to reduce offspring predation (Nilsson et al., 1991), so it is important to frequently preserve new healthy trees. Besides, suitable cavity-trees have to be scattered in forest to preserve a Black Woodpecker population. First, Black Woodpeckers have a large size vital area, so clustered cavity-trees are used by the same individual or couple. Second, close cavity-trees are more subject to predation which would reduce the efficiency of habitat trees preservation (Johnsson, 1993).

Preserving scattered suitable cavity-trees in high quantity does not insure the presence of Black Woodpeckers, since this bird has also other requirement. In the same way, preserving one umbrella species is not sufficient to ensure maximum biodiversity. Indeed, an umbrella species is only linked with co-occurring species. Therefore, several umbrella species have to be considered to better preserve biodiversity (Lambeck, 1997; Roberge & Angelstam, 2004). To summarize our biodiversity-friendly management recommendations related to Black Woodpecker, in French forests we propose to preserve standing old beeches with a minimum DBH about 30 cm, a clear trunk (free of branches from the own tree and from neighbors), which are scattered in forest. Preserving those suitable cavity-trees have to be complementary with conserving broadleaves as well as conifers cover, presence of open areas and deadwood access (Garmendia et al., 2006).

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ABSTRACT

Through cavity excavation, the Black Woodpecker is a forest engineer and an umbrella species. We analyzed characteristics of trees bearing Black Woodpecker cavities to assess its local habitat preferences. In two French forests, we compared tree-traits between trees bearing Black Woodpecker cavity (n=60) and trees devoid of it (n=56). We hypothesized that Black Woodpecker cavity trees will *(i) have a lower wood density*; *(ii) bear more fungal fruiting bodies*; *(iii) have a taller first branch*; *(iv) have a further closest neighbor*; *(v) bear more other woodpeckers cavities*; *(vi) bear more richness and abundance of saproxylic microhabitats*. We validated most of our hypotheses and showed that cavity-trees differed significantly from their control counterparts according to analyzed factors. Among all, two factors appear important. First, Black Woodpeckers excavate trees with a higher first branch, which supports that they are specialists for cavity-tree selections. Second, cavity-trees bear more microhabitats, supporting a more important engineer role than previously proposed. In light of our results, it would be beneficial to keep up biodiversity-friendly management considering the following suggestions: In France, we recommend to preserve standing old Beeches with a trunk free of low branches and locally apart from others.

Keywords : habitat preference, tree cavities, microhabitat, conservation, forest management

RESUME

Le pic noir, ingénieur de l’écosystème lorsqu’il creuse des cavités, est une espèce parapluie. Nous cherchons les spécificités de ses arbres à cavité, dans le but d’analyser les préférences du pic noir. Dans deux forêts françaises, nous avons comparé les traits des arbres porteurs de cavités de pic noir (n=60) avec les traits d’arbres contrôles (n=56). Nous émettons les hypothèses suivantes : les arbres à cavités de pic noir *(i) présentent une plus faible densité de bois* ; *(ii) portent plus de champignons* ; *(iii) possèdent une première branche plus haute* ; *(iv) sont plus éloignés des voisins* ; *(v) supportent plus des cavités d’autres pics* ; *(vi) supportent une plus grande richesse et abondance de microhabitats*. Nous avons validé la plupart de nos hypothèses, et deux traits ressortent. Le pic noir creuse des arbres sans branches basses, validant son caractère spécialiste. De plus, ces arbres supportent de nombreux microhabitats, appuyant ainsi le caractère d’espèce parapluie du pic noir. A la lumière de nos résultats, il serait bénéfique de persévérer les efforts de gestion forestière pour la biodiversité, en prenant en compte les suggestions suivantes : en France, nous recommandons de préserver de vieux hêtres debout possédant un tronc dénué de branches (de l’arbre même, mais aussi ne présentant aucune gêne des branches des arbres voisins).

Mots-clés : habitat, arbres à cavités, microhabitat, conservation, gestion forestière