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

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17 **Abstract**

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

27 (i) Cavity-trees would have lower wood density and display more conks of fungi than
28 control-trees;

29 (ii) The local environment of cavity-trees would be less crowded than those of the control
30 trees. In particular, the first branch would be higher up, and their first neighboring tree would
31 be further away from cavity-trees compared to control-trees;

32 (iii) Cavity-trees would display a higher number of other woodpecker cavities and more
33 saproxylic microhabitats than the control-trees.

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

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

43 **Keywords:** habitat tree; tree cavities; Tree Related Microhabitats; conservation; forest
44 management

45 **Introduction**

46 Forest biodiversity conservation relies on biodiversity-friendly practices in daily forest
47 management. Forest managers can preserve favorable elements such as ageing islands,
48 habitat trees, and standing and lying deadwood (Kraus and Krumm, 2013). Those elements
49 may in turn favor the presence of ecosystem-structuring species, for which it appears
50 necessary to understand and quantify the drivers in terms of conservation. Through cavity
51 excavation, woodpeckers are considered to be engineer species as they modify their
52 environment and provide new habitats for secondary cavity users (Jones *et al.*, 1994; Remm
53 and Löhmus, 2011). Primary excavators are therefore a target for the conservation of hole-
54 nesting assemblages because they can directly impact the abundance and diversity of many
55 other species (Wesołowski, 2011). Woodpecker species vary in their selection of trees in which
56 they excavate cavities ranging from live trees, decayed trees to dead trees (e.g. Martin, 2015).
57 The Black Woodpecker *Dryocopus martius* (Linnaeus, 1758) is the largest Eurasian
58 woodpecker species and the strongest excavator in Europe. It provides essential habitats for
59 a multitude of large, secondary cavity users (Johnsson *et al.*, 1993). With a home range
60 ranging from 200 ha to more than 1000 ha (Cuisin, 1986; Fernandez and Azkona, 1996; Bocca
61 *et al.*, 2007; Olano *et al.*, 2015), Black Woodpeckers require large patches of mature forest
62 (Garmendia *et al.*, 2006), though they are able to adapt to different forest landscape contexts
63 (Rolstad *et al.*, 2000; Angelstam *et al.*, 2002; Saporetti *et al.*, 2016). However, the drivers of
64 the Black Woodpecker's cavity excavation behavior are not fully understood yet, especially in
65 the context of managed temperate forests in Western Europe. Since Black Woodpeckers tend
66 to preferentially excavate living trees (Zahner *et al.*, 2012; Zawadzka and Zawadzki, 2017),
67 they may alter tree vitality and trigger senescence. Damaged trees could hence be easier for
68 other, weaker woodpeckers to excavate (Wesołowski, 2011), and may bear more wood-
69 decaying microhabitats – hereafter referred to as “saproxylic microhabitats” (Larrieu *et al.*,
70 2018). As engineer species, the Black Woodpecker may have numerous roles: the bird
71 provides holes for secondary cavity users and weakens healthy trees, which, in turn, triggers
72 the formation of other microhabitats. Additionally, since this bird plays a critical role in

73 determining community structure and in the conservation of a large number of co-occurring
74 species (Roberge and Angelstam, 2004), the Black Woodpecker is also an important umbrella
75 species (Garmendia *et al.*, 2006).

76 At the tree scale, Black Woodpecker cavity excavation could represent a trade-off
77 between the energy applied during excavation and the final cavity quality (time, resistance,
78 microclimate, predation risk). Black Woodpeckers may target tree whose characteristics
79 reduce excavation time thus minimizing the energy required. In North America, primary cavity
80 excavators preferentially choose trees with softer wood at the cavity height (Schepps *et al.*,
81 1999; Lorenz *et al.*, 2015). In particular, reciprocal positive relationships between fungi and
82 primary cavity excavators have been documented (Jackson and Jackson, 2004) since wood
83 decaying fungi soften wood (Conner *et al.*, 1976; Schwarze *et al.*, 2008). Like other primary
84 excavators, Black Woodpeckers may select heart-rotted trees thus reducing the energy
85 needed for excavation (Conner *et al.*, 1976; Zahner *et al.*, 2012). Moreover, selecting an
86 appropriate nest site that minimizes offspring, and adult, predation is important for bird fitness
87 (Lima, 2009). Black Woodpeckers seem to preferentially excavate straight trunks free of
88 branches, reducing predation risks (Cuisin, 1967; Rolstad *et al.*, 2000; Bocca *et al.*, 2007;
89 Zahner *et al.*, 2017). However, in western Europe, the studies documenting tree characteristics
90 favorable for the Black Woodpecker have rarely been carried out in forests used for wood
91 production. Furthermore, existing quantitative studies concern either other biomes, e.g. North
92 America, Scandinavia (Andersson *et al.*, 2018), or mature, primary forests (Wesołowski,
93 2011). Since forest managers already designate Black Woodpecker cavity-bearing trees as
94 habitat trees (Bütler *et al.*, 2013), our aim was to analyse specific characteristics of these trees
95 and indirectly assess their potential role for forest biodiversity (through the presence of tree
96 microhabitats, sensu Larrieu *et al.*, 2018). We therefore examined the role of tree-level factors
97 in Black Woodpecker cavity tree selection in two French managed forests. We compared the
98 characteristics of trees bearing at least one Black Woodpecker cavity (hereafter referred to as
99 “cavity-trees”) and trees devoid of Black Woodpecker cavities (hereafter referred to as “control-
100 trees”). We hypothesized that:

- 101 (i) Cavity-trees would have lower wood density and also display more conks than
102 control-trees;
- 103 (ii) The local environment of cavity-trees would be less crowded than those of the
104 control trees. In particular, the first branch would be higher up, and the first
105 neighboring tree would be further away from cavity-trees than from control-
106 trees;
- 107 (iii) Cavity-trees would display more cavities excavated by other woodpecker and
108 more saproxylic microhabitat than the control-trees.

109

110 **Materials and methods**

111 **Cavity-trees selection**

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

119

120 **Sampling design**

121 In Auberive, we preselected the 64 most recent (>2015) out of the total 223 cavities
122 because cavity-trees can break at the cavity location (Wesołowski, 2011) or heal (Colmant,
123 2003; Bouteaux Jean-Jacques; Dubois Michael, personal communications). In Loches, we
124 kept all 112 cavities since the inventory date was not available and no preselection was
125 possible. We then randomly selected the order in which the cavity-trees would be sampled. To
126 reduce spatial autocorrelation, we rejected cavity-trees which were within 400 m of each other

127 (Figure 1). In the field, we excluded dead trees and snags from our sample to avoid potential
128 confounding effects between tree vitality, wood density or microhabitats.

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

136

137 **Local forest structure description**

138 Each plot was centered around a cavity-tree. For each plot, we used a relascope (fixed
139 angle of 2%) to measure the basal area of small trees (DBH between 7.5 and 22.5 cm), medium
140 trees (DBH: 22.5 - 47.5 cm) and large trees (DBH:>47.5 cm), as well as the total basal area
141 (the sum of the three). Within a radius of 20 meters around the cavity-tree, we measured the
142 DBH and height of any dead standing trees (trees, snags or stumps) with a minimum DBH of
143 30 cm. We also measured the length and median diameter of lying dead logs with a minimum
144 median diameter of 30 cm. We used truncated cone volumes per ha to calculate standing and
145 lying deadwood volumes (Paillet *et al.*, 2015).

146

147 **Tree level measurements**

148 On the cavity-trees, we recorded cavity height (m) and orientation (gr), and visually
149 estimated cavity tilt (classified into four categories, Figure 2). For both cavity- and control-
150 trees, we measured tree DBH, total tree height and the height of the first occurring branch,
151 excluding epicormics shoots, as a proxy for the free-part of the trunk (hypsometer, Häglof's
152 Vertex IV). We also measured the distance to the nearest neighboring tree (DBH > 7.5cm,

153 threshold shared by forest inventories in Europe for tree recording, Gschwantner *et al.*, 2016)
154 as a proxy for vegetation clutter (Figure 2).

155 Using a manual auger, we sampled a wood core below the cavity of interest from the
156 trunk at breast height (1.30m); we sampled a similar core with the same orientation on the
157 paired control-tree. If the cavity-tree bore several Black Woodpecker cavities, we arbitrarily
158 chose the highest one to orient the coring (Figure 2). Each core aimed for the pith, but if we
159 missed it, the tree was not cored twice. For safety and practical reasons, we cored at breast
160 height and not at cavity height. It seems that Black Woodpeckers could detect and exploit
161 vertical density variations of a give tree (Conner *et al.*, 1976; Zahner *et al.*, 2012), but our aim
162 was to test whether excavated trees were overall less dense than a comparable neighboring
163 tree. We also assumed that wood density in beech was relatively homogeneous along the
164 trunk as shown by Longuetaud *et al.* (2016). Furthermore, managers can benefit from this
165 approach with management-linked data such as wood cores for increment assessments and
166 thus derive wood density more easily than at cavity height.

167 Finally, we recorded tree-related microhabitat abundance (47 types, see Table 5 in
168 Larrieu *et al.*, 2018) on both the cavity- and control-trees. Based on this abundance value, we
169 calculated the richness (number of types per tree) and abundance of saproxylic microhabitats
170 (32 types), grouped as follows: woodpecker cavities (excluding Black Woodpecker cavities),
171 woodpecker feeding holes, mould cavities, branch holes, insect galleries, water-filled holes,
172 bark pockets and shelters, injuries (exposed sapwood and exposed heartwood), conks of
173 fungi, exudates, dead crown and broken limbs. We also separately calculated other
174 woodpecker species cavity abundance.

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

179

180 **Wood density measurements and tree age estimation**

181 To determine wood density, the wood core samples were dried 24h at 103°C, then X-
182 ray scanned (General Electric BrightSpeed Excel medical tomograph, one image every
183 0.625mm along the cores) at the INRA Nancy (Xyloscience Platform) laboratory. We derived
184 density profiles from these images with the ImageJ software and the CalDenQB plug-in
185 (Longuetaud *et al.*, 2014; Leban *et al.*, 2016; Jacquin *et al.*, 2017; Leban *et al.*, 2017). We
186 calculated the mean density for each sampled core and, to assess whether density varied
187 along each profile, also calculated the means of each 5-cm-long section (n=6) along the wood
188 core samples from 0 cm (bark) to 30 cm (pith).

189 Finally, although age determination was not the primary aim of this study, the cores
190 allowed us to estimate tree age. We used a LintabTM sliding-stage measuring device
191 (Rinntech, Heidelberg) with a resolution of 0.01 mm to measure tree-ring widths. In the event
192 that the pith was missing from the core, we extrapolated the missing rings following Duncan's
193 (1989) method. We did not exclude cores for which a substantial part of the sample was
194 missing, but sensitivity analyses revealed that this did not significantly affect our results.
195 Finally, we used the COFECHA application (Holmes, 1983) to visually cross-date and verify
196 the cores.

197

198 **Statistical analyses**

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

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

205 We used generalized linear mixed-effect models (glmer function; lme4 package v1.1-
206 17; Bates *et al.*, 2014) to compare six response variables between cavity- and control-trees:

207 wood density (total and 5 cm lengths), first branch height, distance from the nearest
208 neighboring tree, other woodpecker cavity abundance, and saproxylic microhabitat richness
209 and abundance. Since the first three variables had positive continuous values, we chose the
210 Gamma error distribution with an identity link. For the last three variables, we chose the
211 Poisson error distribution with a log link since they are count variables. We added site
212 (Auberive *versus* Loches) as a fixed effect in interaction with tree type (cavity-trees *versus*
213 control-trees) to account for possible variations in the relationships with site. Finally, we added
214 a plot random effect on the intercept to account for the paired design. We first tested contrasts
215 for all the parameters (type, site and interaction) based on model predictors for each response
216 variable (`joint_tests` function; `emmeans` package v1.2.2; Russell, 2018). We then used
217 marginal post-hoc Tukey tests (`emmeans` function; `emmeans` package v1.2.2) to separately
218 compare estimated means between control- and cavity-trees by site.

219

220 **Results**

221 **Local environment and cavity-tree descriptions**

222 Auberive had a significantly higher mean elevation and steeper slopes than Loches.
223 Mean basal area was significantly higher in Loches than in Auberive, which was mostly
224 explained by a greater proportion of large trees (means = 14.1 and 8.6 m²/ha, respectively).
225 Basal area of medium and small trees did not significantly differ between sites. Mean volume
226 of deadwood near cavity-trees was not significantly different between sites (means = 20 and
227 24 m³/ha, respectively, Table 1).

228 All cavity-trees were beech (*Fagus sylvatica*) in Auberive; all but two (oak, *Quercus*
229 *petraea*) were beech in Loches. Cavity-tree DBH was not significantly different between
230 Loches and Auberive (mean = 51 and 55 cm, respectively). However, cavity-trees were
231 significantly taller in Loches than in Auberive (means = 33 and 27 m, respectively). Cavities
232 were located higher on the trees in Loches than in Auberive (means = 13 and 7 m, respectively)
233 and were also higher relatively to total tree height (means = 0.36 and 0.27, respectively, Table

234 1). Cavity entrance orientation (Supplementary materials, Figure S1) was never significantly
235 different from a uniform distribution (Rayleigh test, overall: $p=0.25$; Auberive: $p=0.88$; Loches:
236 $p=0.07$). All cavity entrance holes were vertical, except for four in Auberive which were tilted
237 downwards (between 0 and -30°).

238

239 **Comparison between cavity-trees and control-trees**

240 Mean wood density was 5% lower in cavity-trees than in control-trees (Figure 3A) in
241 Auberive ($p < 0.001$) but no significant difference was found in Loches ($p = 0.45$). When we
242 removed the 12 trees with heart rot from the dataset, cavity-tree wood density remained only
243 marginally lower than control-tree wood density ($p = 0.07$). Along wood core profiles, cavity-
244 tree wood density was significantly lower than in control-trees from 10 to 25 cm, but only in
245 Auberive (Table 2, supplementary materials Figure S2).

246 Tree age estimates did not differ between sites or between cavity- and control-trees;
247 only the interaction was significant ($p=0.013$) in the overall analysis. However, in Auberive,
248 cavity trees were significantly older than control trees (+6%, resp. 150.2 +/- SE 6.3 years, 141.2
249 +/- 6.2 years, $p=0.01$) while this was not the case in Loches (resp. 143.4 +/- 6.2 years, 146.6
250 +/- 6.2, $p=0.35$).

251 Cavity-trees had a higher first branch compared to control-trees (Figure 3B): 55%
252 higher in Auberive ($p < 0.001$) and 115% higher in Loches ($p < 0.001$). In Auberive, cavity-
253 trees had a more distant nearest neighbor than did the control-trees (Figure 3C): 45% further
254 away ($p = 0.002$), but there was no difference in Loches ($p = 0.96$).

255 Other woodpecker cavities were more numerous on cavity-trees compared to control-
256 trees (Figure 3D): 4500% more in Auberive ($p < 0.001$) and 500% more in Loches ($p = 0.001$).
257 Note that other woodpecker cavities were nearly absent on control-trees. Overall saproxylic
258 microhabitat richness tended to be higher on cavity-trees than on control-trees ($p < 0.1$; Figure
259 3E): 35% higher in Auberive ($p = 0.05$), but no difference in Loches ($p = 0.37$). Saproxylic
260 microhabitats were more abundant on cavity-trees compared to control-trees (Figure 3F): 60%

261 more in Auberive ($p < 0.001$) and 15% more in Loches ($p = 0.04$).

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

264

265 **Discussion**

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

270

271 **Black Woodpeckers minimize the energy they use for excavation**

272 We partially validated our first hypothesis: Black Woodpeckers did excavate trees with
273 a lower mean wood density, which tended to bear more signs of decay linked to fungi (either
274 conks or heart rot) compared to control-trees. In Auberive, radial wood density variations
275 revealed that cavity-trees were around 3% less dense than the control-trees in the 10-to-25
276 cm depth range (distance from bark). While we found no significant differences in Loches, the
277 core profiles revealed a lower mean wood density in cavity-trees than in control-trees
278 (Supplementary Materials, Fig. S2). In addition, we showed that these observed differences
279 were not related to tree age (Bouriaud *et al.*, 2004). These results are in accordance with
280 studies showing that North American primary cavity excavators select trees with softer interior
281 wood at the cavity height (Lorenz *et al.*, 2015). Primary cavity excavators probably face trade-
282 offs when selecting cavity-trees: excavating softer trees may reduce excavation time and the
283 amount of energy needed, which could give a selective advantage. Head and body movements
284 are confined during interior cavity excavation and this might force the birds to select trees with
285 soft interior wood (Lorenz *et al.*, 2015). On the other hand, lower wood density might increase
286 the risk of cavity-tree collapse during strong winds - decayed trees may more easily break than

287 healthy trees - leading primary cavity excavators to select trees with the maximum hardness
288 they are able to excavate, rather than the softer ones. Black Woodpeckers dig long-lasting
289 cavities (Wesołowski, 2011) and reuse them several years (Cuisin, 1986; Johnsson *et al.*,
290 1993; Colmant, 2003). They may therefore select trees with a slightly lower wood density to
291 facilitate their excavation work, but which are also healthy enough to live for a long time. In
292 terms of method, and contrary to Lorenz *et al.* (2015) who cored the trees at cavity height, we
293 cored at breast height (1.30 m), which may overestimate wood density. Coring near the cavity
294 may have allowed us to better detect signs of wood rot and revealed a stronger effect. Indeed,
295 woodpeckers may be able to detect areas of lesser wood density along the trunk (Schepps *et*
296 *al.*, 1999; Matsuoka, 2008; Zahner *et al.*, 2012). Still, we evidenced softer interior wood at 1.30
297 m in cavity-trees free of wood rot. Since beech wood density is relatively homogeneous along
298 the trunk (Longuetaud *et al.*, 2017), we assume that this comparison remains valid, but does
299 not provide an absolute estimate of the wood density Black Woodpeckers are capable to dig.
300 Density measures along the trunk would allow to have such an estimate.

301 We did not observe that cavity-trees bear more conks of fungi than control-trees. This
302 result did not confirmed the link between fungi and woodpecker cavities documented by other
303 authors (Conner *et al.*, 1976; Bull *et al.*, 1992; Welsh and Capen, 1992; Jackson and Jackson,
304 2004; Zahner *et al.*, 2012). However, as Conner *et al.* (1976) observed, cavity-trees do not
305 always have visible fungal fruiting bodies even when wood decay fungi are present; the low
306 detectability of conks may also explain why we did not validate our initial hypothesis. As
307 specified by e.g. Jackson and Jackson (2004), a tree may have be rotten inside for a long time
308 before exhibiting actual conks on the outside. This was partially confirmed in our study by the
309 trend towards a higher occurrence of heart-rot on cavity-trees. The use of DNA methods to
310 assess the actual presence of fungi seems more efficient – but also more labour-intensive –
311 than direct observation (Jusino *et al.*, 2014; Jusino *et al.*, 2016).

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

315

316 **Black woodpeckers minimize nest predation risk**

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

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

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

339 Indeed, as suggested by Cuisin (1967), isolated trees devoid of low branches could
340 facilitate aerial access to the cavity for adults and offspring flight when leaving the nest.
341 Moreover, the same tree characteristics could minimize predation risks. Using camera traps,

342 Zahner *et al.* (2017) showed that four predators visit inhabited Black Woodpeckers nest: the
343 Northern Goshawk (*Accipiter gentilis*), the Common Buzzard (*Buteo buteo*), the Great Spotted
344 Woodpecker (*Dendrocopos major*) and the Pine Marten (*Martes martes*). The Northern
345 Goshawk has seldom been seen extirpating young Black Woodpeckers from their nest (Cuisin,
346 1967), but the size of the cavity entrance and cavity depth can help prevent large raptors from
347 reaching the offspring (Zahner *et al.*, 2017). However, the Northern Goshawk, which prefers
348 to hunt in large patches of later-successional-stage forests, has been reported to predate adult
349 Black Woodpeckers (Cuisin, 1967; Widen, 1989; Mikusiński, 1995; Rolstad *et al.*, 2000). We
350 assume that Black Woodpeckers are more likely to avoid Goshawk predation when the cavity-
351 tree is more easily reachable, since it is potentially quicker to shelter when the cavity
352 environment is less crowded. The Pine Marten is the major Black Woodpecker nest predator
353 in Norway, Sweden and Germany (Nilsson *et al.*, 1991; Rolstad *et al.*, 2000; Zahner *et al.*,
354 2017). It has been seen extirpating young Black Woodpeckers from the nest (Cuisin, 1967)
355 and is known to revisit cavities (Sonerud, 1985), thus increasing predation risk in old cavities
356 (Nilsson *et al.*, 1991). The excavation of a new nest each year and the selection of higher
357 locations may reduce this risk (Nilsson, 1984; Johnsson *et al.*, 1993; Zahner *et al.*, 2017).
358 Moreover, our results are consistent with those of several other authors, who found that Black
359 Woodpeckers generally seem to locate nests along “branch-free trunks” (Colmant, 2003;
360 Bocca *et al.*, 2007), boles without branches for 10m (Rolstad *et al.*, 2000; Zahner *et al.*, 2012)
361 or boles without branches below the cavity (Cuisin, 1967; Pirovano and Zecca, 2014). These
362 authors assume that branches on the trunk, or those of neighboring trees, may serve as a
363 ladder that help predators, notably the Pine Marten, reaching the nest. Black Woodpeckers
364 could thus minimize offspring predation risk by selecting a safer tree, that is, one which is
365 relatively isolated with a branch-free trunk. Evidently, this explanation remains speculative and
366 e.g. video surveillance of nests sites would be necessary to confirm it (see e.g. Zahner *et al.*,
367 2017).

368

369 **Black woodpeckers as umbrella species: the role of microhabitats**

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

374 Black Woodpeckers are capable of excavating apparently healthy trees, and when they
375 do so, they could themselves be contributing to the tree decay process (Kosiński and Kempa,
376 2007; Zahner *et al.*, 2012; Zawadzka and Zawadzki, 2017), thus making the trees more
377 microhabitat-ready. This is the case for fungi, as shown in many studies other than ours (see
378 the review of Jackson and Jackson, 2004). Black Woodpecker cavities would decrease trees
379 health, induce its slow decay, indirectly causing more holes, bark and wood injuries and
380 deadwood. In comparison, other woodpeckers only excavate already decaying trees or target
381 dead branches borne by living trees: e.g. Pasinelli (2000); Kosiński and Kempa (2007) for the
382 middle spotted woodpecker; Wiktander *et al.* (2001) for the lesser spotted woodpecker. Black
383 Woodpeckers might be the first to degrade the trees, making them more suitable for weaker
384 primary excavators. To sum up, Black Woodpeckers, through the tree decaying process they
385 provoke, could be considered as an umbrella species linked to the supply of cavities available
386 to many secondary cavity users (Zahner *et al.*, 2017), increased microhabitat-dependent
387 biodiversity and other woodpecker excavation. These results suggest an additional umbrella-
388 species role for Black Woodpeckers through the supposed facilitation of tree microhabitats
389 formation, especially since recent research has linked microhabitats (including woodpecker
390 cavities) with bat and bird biodiversity (Paillet *et al.*, 2018). Black Woodpecker cavity-trees
391 have a higher potential regarding biodiversity than a comparable non-cavity trees, which
392 confirms their interest as habitat trees to be conserved in integrated forest management (Kraus
393 and Krumm, 2013)

394 Conversely, Black Woodpeckers could select trees already bearing microhabitats for
395 cavity excavation. This explanation is reversed in time and causality compared with the first
396 one. In this case, fungal microhabitats would first appear on a senescent tree, and only then

397 would Black Woodpeckers target that tree for excavation. We assume that this mechanism is
398 less probable since many cavity-trees in our study did not show any apparent signs of
399 senescence (but see Zahner *et al.*, 2012; Jusino *et al.*, 2016). However, to disentangle this
400 chicken-and-egg issue and to better understand the succession between microhabitats and
401 cavities ontogenesis, long-term monitoring in zones favored by the Black Woodpecker will be
402 necessary (Wesołowski *et al.*, 2010; Cockle *et al.*, 2011).

403

404 **Implications for forest management and Black woodpeckers' conservation**

405 We showed that Black Woodpecker cavity-trees are isolated large-diameter beech
406 trees free of low branches; this suggests that Black Woodpeckers tend to select trees based
407 on the energy required for cavity excavation and on predation risk. We confirmed our
408 hypothesis that Black Woodpeckers play a complementary umbrella role, by facilitating cavity
409 excavation for other woodpecker species and saproxylic microhabitat formation. Therefore,
410 this also confirms that Black Woodpecker cavity-trees have high conservation interest as
411 habitat trees (Office National des Forêts, 2010; Bütler *et al.*, 2013). To secure an abundance
412 of biodiversity-friendly, tree-borne microhabitats, preserving trees with Black Woodpeckers
413 cavities while favoring trees suitable for Black Woodpecker excavation where such trees are
414 rare seems appropriate. However, determining the threshold density for optimal conservation
415 remains beyond the scope of this study. Rolstad *et al.* (2000) propose preserving 1 tree /ha for
416 Black Woodpecker use while the French National Forest Service (Office National des Forêts,
417 2010) recommends preserving two living habitat trees/ha. Moreover, Black Woodpeckers
418 prefer to excavate new nests each year, probably to reduce offspring predation (Nilsson *et al.*,
419 1991), so it seems important to maintain a constant pool of favorable trees. In addition, suitable
420 cavity-trees should be scattered throughout the forest for two reasons. First, Black
421 Woodpeckers have large home ranges, so clustered cavity-trees would be used by the same
422 individual or pair and exclude other individuals by mere competition. Second, clustered cavity-
423 trees would be more sensitive to predation, which would reduce the efficiency of preserving

424 the habitat trees (Johnsson, 1993b).

425 Managers should keep in mind, however, that simply preserving a high quantity of
426 suitable cavity-trees scattered throughout the forest is likely to be insufficient to ensure the
427 presence of Black Woodpeckers. Obviously, the birds have other requirements, most notably
428 patches of mature forest, presence of open areas and access to deadwood (Garmendia *et al.*,
429 2006; Karimi *et al.*, 2018). Similarly, biodiversity conservation should probably not focus on
430 only one but several umbrella species (Lambeck, 1997; Roberge and Angelstam, 2004).
431 Nonetheless, in French lowland forests, it would undoubtedly be interesting to favor scattered
432 standing Beech trees with a minimum DBH of around 30 cm and a branch-free trunk, especially
433 in stands dominated by other, more commercially valuable, tree species such as oak. Since
434 Black Woodpecker cavities are relatively rare (e.g. 0.03-0.04/ha in our dataset, but see also
435 Kosiński *et al.*, 2004), applying this biodiversity-friendly practice would be an interesting
436 production-protection compromise in managed forests.

437

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601

602 Table 1. Main characteristics of the sampling sites (ONF, 2006, 2012), surrounding
 603 environment description and cavity-tree characteristics (n=28 plots for each site): means,
 604 standard errors (s.e.) and ranges (minimum-maximum). Basal area: small trees (Diameter at
 605 Breast Height [DBH] between 7.5 - 22.5 cm), medium trees (DBH: 22.5 - 47.5 cm) and large
 606 trees (DBH: > 47.5 cm). Relative cavity height: cavity height divided by total tree height. We
 607 used generalized linear models (Gamma error distributed with identity link) to compare
 608 variables between sites.

	Auberive		Loches		
Location	47° 47' 42" N, 5° 4' 57" E		47° 9' 16" N, 1° 4' 23" E		
Area (ha)	5 584		3 952		
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	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 ns
Basal area (m ² /ha)	Small	2.9 ± 0.4	2.2 ± 0.3	[0-6.5]	0.171 ns
	Medium	7.6 ± 0.6	8.5 ± 0.9	[2.5-24.5]	0.257 ns
	Large	8.6 ± 0.7	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]
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 ***

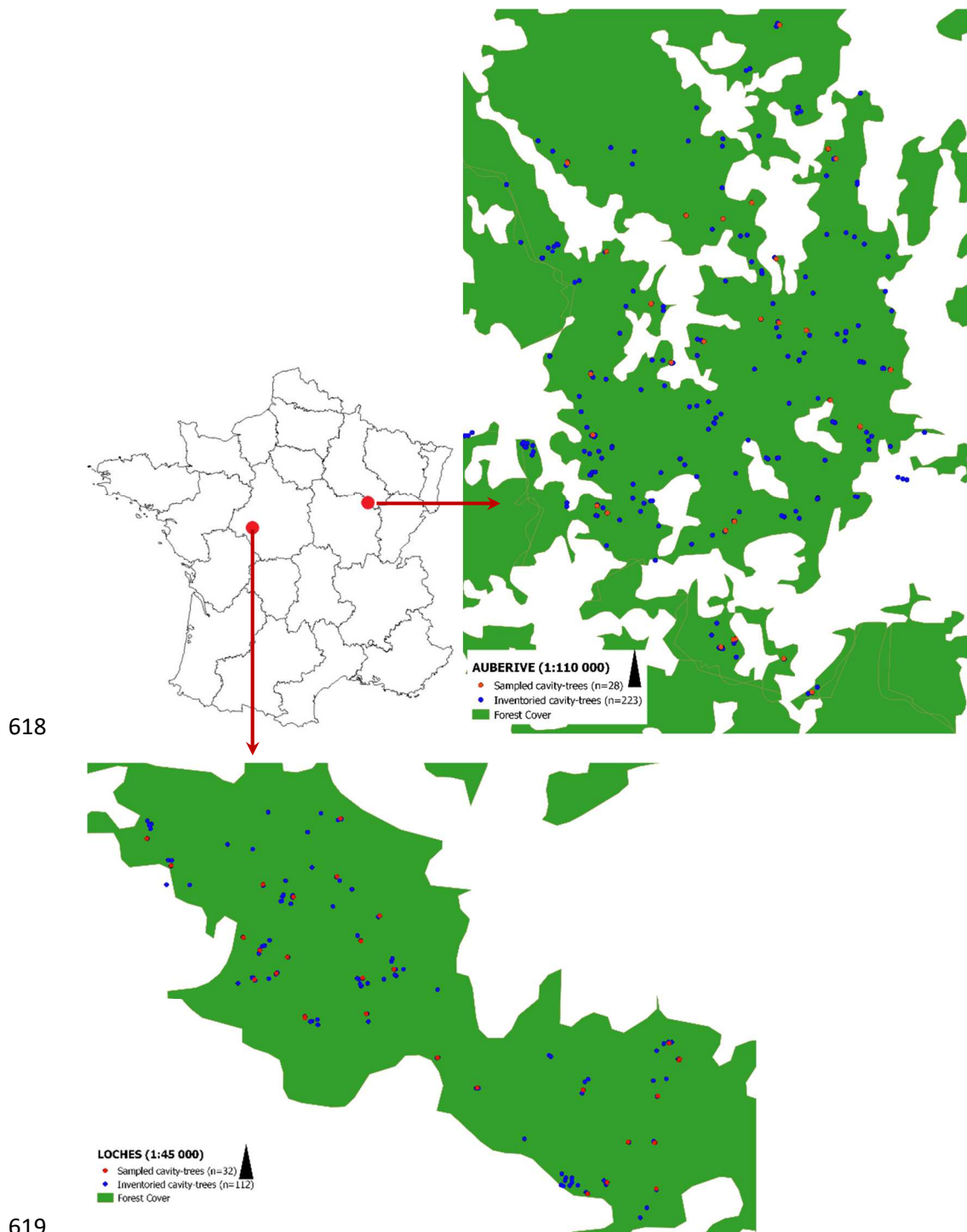
609

610 Table 2. Wood density comparisons (in percentage) between cavity- and control-trees based
 611 on estimates from generalized linear mixed models (Gamma error distribution). We compared
 612 means along wood core profiles every 5 cm from 0 (bark) to 30 (pith). Negative values indicate
 613 lower wood density for cavity-trees than control-trees. Stars show marginal Tukey test
 614 significance. Thresholds: (*) $p < 0.1$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

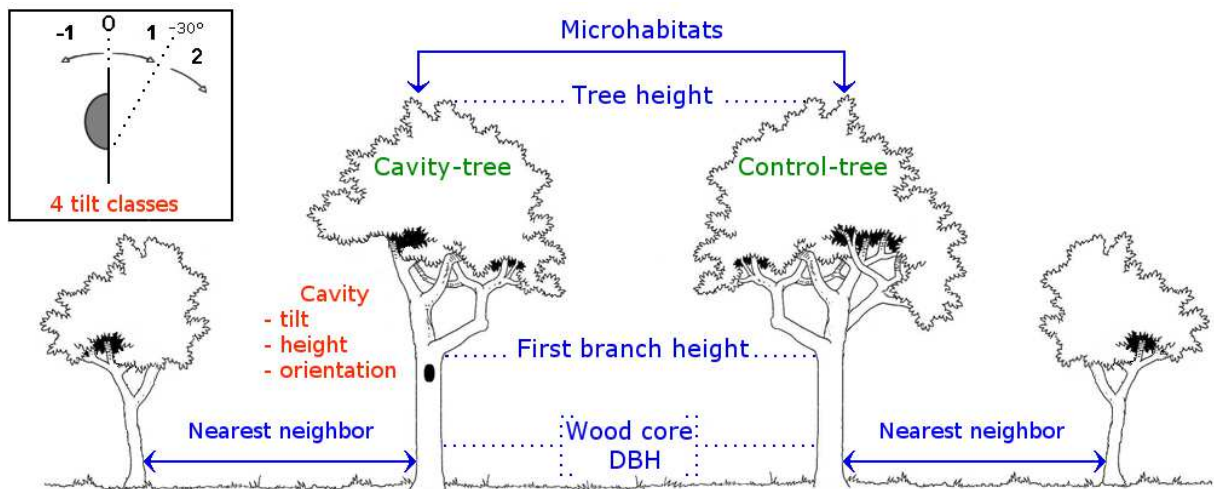
	Distance from bark					
	0-5 cm	5-10 cm	10-15 cm	15-20 cm	20-25 cm	25-30 cm
All trees (n=116)						
Auberive	- 1.86	- 1.94	- 3.25 (*)	- 3.59 (*)	- 6.13 *	+ 0.98
Loches	- 0.25	+ 0.15	+ 0.22	- 1.46	- 2.24	- 2.32
Trees without heart rot (n=104)						
Auberive	- 1.04	- 1.88	- 2.80	- 2.33	- 1.39	+ 3.47
Loches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

615

616 Figure 1. Sampling design maps of Auberive (top) and Loches (bottom). Blue dots represent
617 all recorded cavity-trees; red dots represent cavity-trees sampled in this study.



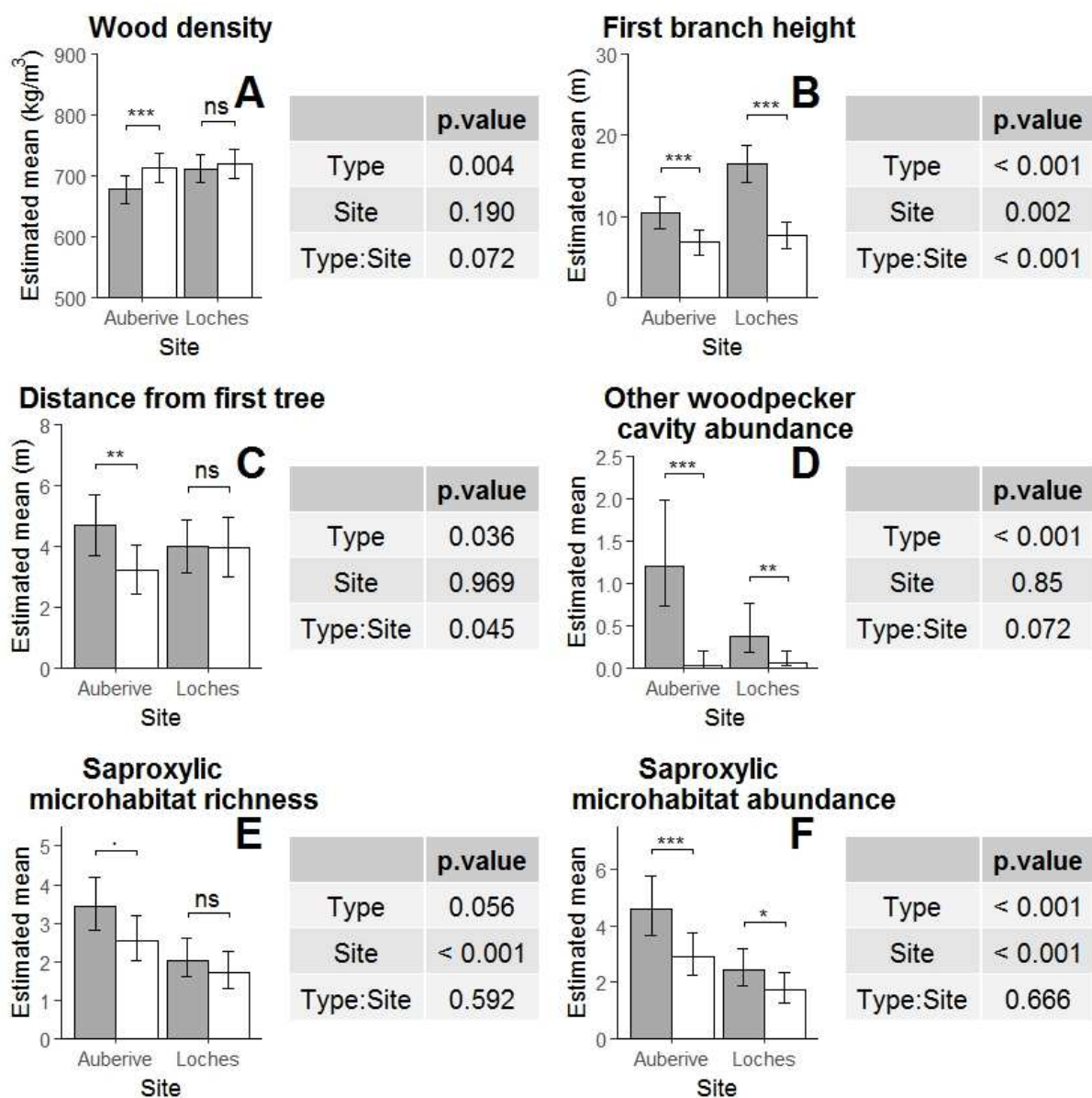
622 Figure 2. Tree-scale measurements comparing paired trees (green): cavity description (red)
 623 and comparable variables (blue). We paired a control-tree, the closest equivalent tree (same
 624 species and Diameter at Breast Height [DBH] \pm 10 cm), to each cavity-tree. The four classes
 625 of cavity tilt are shown in the top left box. We inventoried tree-related microhabitat richness
 626 and abundance following Larrieu et al.'s typology (2018). We sampled a wood core at breast
 627 height (1.30 m) for wood density and age measurements. We chose the nearest neighbor
 628 among all the surrounding trees with a DBH > 7.5cm.



629

630

631 Figure 3. Comparison of estimated means between cavity-trees (trees bearing at least one
 632 Black Woodpecker cavity, in grey) and control trees (trees without cavities, in white) based on
 633 generalized linear mixed models. A, B and C are Gamma error distributed models with identity
 634 links while D, E and F are Poisson error distributed models with log links (values were back-
 635 transformed). We added a random plot-level effect to the models to account for the paired
 636 design. Error bars represent 95% confidence intervals and stars show marginal Tukey test
 637 significance (thresholds: (*) $p < 0.1$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). Associated tables
 638 display the significance of each parameter in each model: Type (cavity- vs control-tree), Site
 639 (Auberive vs Loches) and Type:Site (the interaction between Type and Site).



640

641 **Supplementary materials**

642 Table S1. Occurrences of fungi and heart rot on all surveyed trees for both sites (Auberive and
 643 Loches) for trees bearing at least one Black Woodpecker cavity (cavity-trees) and trees without
 644 cavities (controls).

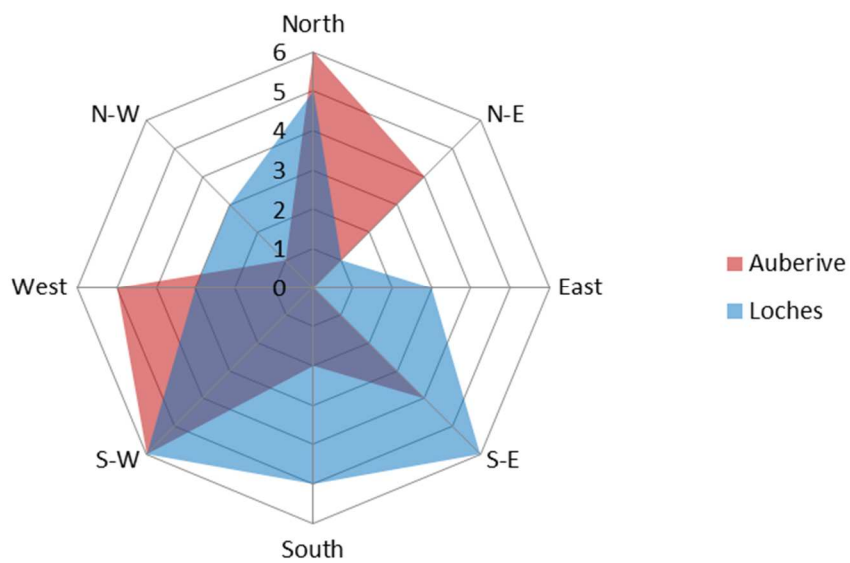
Tree type	Auberive		Loches	
	Cavity (n=28)	Control (n=28)	Cavity (n=32)	Control (n=28)
Fungi	1	4	0	0
Heart rot	7	2	2	1

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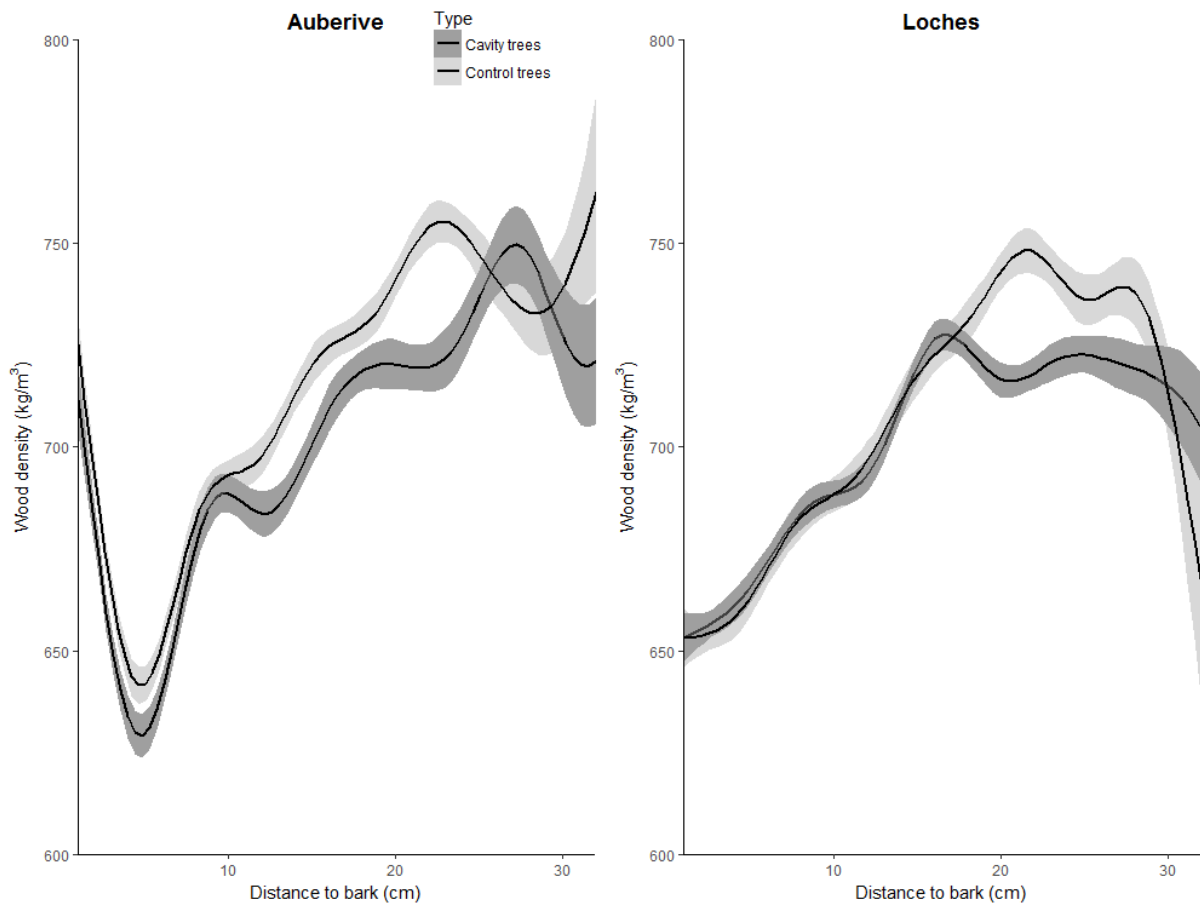
648 Figure S1. Black Woodpeckers cavity entrance hole orientation (n = 56). Cavities in Auberive
 649 are in red, and those in Loches in blue.



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651 Figure S2. Wood density profiles of trees bearing at least one Black Woodpecker cavity (cavity-
652 trees, in dark grey) and trees without any Black Woodpecker cavities (control-trees, in light
653 grey) in Auberive (left) and Loches (right). We used a generalized Additive Model (GAM) with
654 distance as a smoother. Error margins represent 95% confidence intervals.

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