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Biologie et Ecologie pour la Forêt, l'Agronomie et l'Environnement
Spécialité

Forests and their environment

**Comparison of tree cavity abundance and characteristics
in managed and unmanaged Swedish boreal forest**

*Comparaison des densités et caractéristiques des cavités arboricoles en forêt
boréale suédoise aménagée et non aménagée*



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ABSTRACT

Tree cavities are major components of the forest ecosystem worldwide as they are required substrate for a large number of species. The present study aimed to provide new knowledge on cavity density and cavity tree characteristics in the Swedish boreal zone where little information exists on this subject. Assessing the impact of forest management on cavity availability was another main goal. My study was conducted in old forests around Umeå, in both managed and unmanaged stands. The mean cavity density in managed forest (1.2 ha^{-1}) was significantly lower than in unmanaged forests (2.5 ha^{-1}). Natural-decay cavities stood for 5.5% of the cavities, while the other 94.5% were excavated. This emphasizes the importance of primary cavity excavators for cavity supply in the Swedish boreal forest. Compared to their density in the forest, deciduous and dead trees were overrepresented as cavity trees. The different cavity densities could then be due to the fact that unmanaged forest presented a higher amount of dead trees and birch. As recorded in previous studies, aspens were overrepresented as cavity trees. My study highlights a negative effect of forest management on cavity availability. Therefore, management strategies should focus on increasing the amount of suitable excavation substrate, meaning standing dead trees and deciduous trees. Particular attention should be paid to the conservation and regeneration of aspen.

Substrats nécessaires à de nombreuses espèces, les cavités arboricoles sont des composantes majeures des écosystèmes forestiers dans le monde. Cette étude visait à apporter de nouvelles connaissances sur la densité de cavités et sur les caractéristiques des arbres à cavités en zone boréale suédoise où peu d'informations existent sur ce sujet. Un autre objectif était d'évaluer l'impact de la gestion forestière sur la disponibilité des cavités. Cette étude a été menée dans les forêts anciennes autour d'Umeå en peuplements aménagés et non aménagés. La densité moyenne de cavités en forêts aménagées (1.2 ha^{-1}) était significativement plus faible qu'en forêts non aménagées (2.5 ha^{-1}). Les cavités naturelles formées par décomposition représentaient 5.5% des cavités, tandis que les 94.5% restant étaient excavées. Ceci souligne l'importance des excavateurs primaires pour l'approvisionnement en cavités en forêt boréale suédoise. Comparativement à leur densité en forêt, les feuillus et arbres morts étaient surreprésentés parmi les arbres à cavités. La différence de densités de cavités pourrait ainsi être expliquée par le fait que les forêts non aménagées présentaient une plus grande quantité d'arbres morts et de bouleaux. Comme souligné dans de précédentes études, les peupliers trembles étaient surreprésentés parmi les arbres à cavités. Mon étude met en évidence un effet négatif de la gestion forestière sur la disponibilité des cavités. Par conséquent, les stratégies de gestion devraient se concentrer sur l'augmentation de la quantité de substrat approprié à l'excavation, soit les arbres morts et les feuillus. Une attention particulière devrait être octroyée à la conservation et la régénération de peupliers trembles.

INTRODUCTION

The boreal forest constitutes the largest continuous forest in the world and represents around one third of the world forested area. In Sweden, forests have been exploited by humans for centuries for different uses (e.g. tar production, charcoal, Larsson and Danell 2001). Large-scale forestry started around 150 years ago (Esseen et al. 1997), but greatest changes in forest composition happened with the arrival of modern forestry in the 1950's (Kruys et al. 2013, Lundmark et al. 2013). From then, forest policy changed from selective cutting to clearcutting, consisting in harvesting all or most of the trees in a defined area followed by planting or natural regeneration. Even-age stands and monocultural plantations are two examples of modern forestry outcomes in Sweden (Berg et al. 1994). This intensive management resulted in habitat loss, fragmentation, and modification of natural disturbance regimes (Esseen et al. 1997). The area of natural and old forests has considerably decreased (Mikusiński and Edenius 2006) to make way for young successional stages (Edenius and Elmberg 1996). Forest management has resulted in reduction of deciduous trees (Bjorse and Bradshaw 1998) and removal of dead and dying trees (Newton 1994, Straus et al. 2011). These major changes to forest ecosystems have resulted in habitat loss, associated with population declines in a large number of forest-dwelling species (Kouki et al. 2001). Among them, birds show a high sensitivity to habitat loss (Angelstam et Mikusinski 1994, Edenius and Elmberg 1996).

Cavity nesting birds depend on trees for roosting, breeding and for foraging substrate which make them sensitive to changes in forest structure, forest age and tree species composition (Imbeau et al. 2001). Obligate cavity nesters represent 5% of the avifauna in Europe and 4% in North America (Newton 1994) and up to 30 to 45 % of the avifauna when only consider forested systems (Blanc and Martin 2012).

Cavity users are divided in two main categories: *primary cavity excavators*, mainly woodpeckers (*Picidae*), which usually excavate one cavity per year, and *secondary cavity nesters* (e.g. some owls (*Strigidae*), ducks (*Anatidae*), tits (*Paridae*) and bats (*Chiroptera*)) which are dependent on cavities for roosting or nesting but cannot excavate themselves. Consequently, secondary cavity nesters are limited by the density of already available cavities which can be cavities excavated by primary excavators or cavities naturally formed by gradual wood decay process (Martin et al. 2004, Robles et al. 2011). Other species, as tits and nuthatches (*Sitta* spp.), belong to a group called *weak cavity excavators*. These species are able to excavate cavities in soft and decaying trees but they can also use natural-decay and already excavated cavities (Aitken et al. 2002). In North American forests, it is found that natural-decay cavities represent only a very small proportion of the usable cavities (Aitken and Martin 2007, Edworthy et al. 2012). Primary excavators are then often key species on which many other species rely on and they are very important for the entire cavity nester community (Drapeau et al. 2009). In most Swedish boreal forests, great spotted woodpecker (*Dendrocopos major*) and black woodpecker (*Dryocopus martius*) are the most important primary excavators. Both are generalist species, little affected by habitat alterations (Mikusiński et al. 2001). The great spotted woodpecker is the most important primary cavity excavator in the large part of the Fennoscandian boreal zone (Virkkala 2006), while black woodpecker is of major importance in Swedish boreal forest as it is the only excavator creating cavities big enough for large-bodied secondary users (Johnsson 1992).

Boreal Woodpeckers are known to rely principally on dead or decaying trees for cavity excavation (Drapeau et al. 2009). Deciduous trees, especially aspen (*Populus spp.*), are

preferred by many woodpeckers (Li and Martin 1991, Carlson et al. 1998, Drever and Martin 2010). In Sweden, intensive forest management decreases the amount of deciduous and dead trees and thereby reduces the supply of potential excavation substrates. Studies on cavity availability have already been conducted in North American forest (Peterson and Gauthier 1985, Rendell and Robertson 1989, Ouellet-Lapointe et al. 2012) and in European hemiboreal forests (Löhmus et al. 2005, Sandström 1992, Carlson et al. 1998). However, to my knowledge, no such study exists in the truly boreal zone of Europe, except a study by Pullinainen and Saari (2002) performed in subarctic environments at the very northern edge of the boreal zone. Therefore, there is an obvious lack of knowledge on cavity availability and characteristics in large parts of the European boreal zone.

The aim of this study was to compare cavity availability between managed and unmanaged old forests through estimating the true density of cavities with different characteristics, and determining the characteristics of trees with cavities in old boreal forests in Sweden.

MATERIALS AND METHODS

Study area

The study was conducted in 50 old forest stands (>100 years) within a radius of 30 km around Umeå (coordinates 63°49'30"N and 20°15'50"E), in Västerbotten county, Sweden (Figure 1). This area belongs to the middle boreal zone. The Swedish boreal forest is dominated by Scots pine, *Pinus sylvestris* and Norway spruce, *Picea abies* with occurrence of silver birch, *Betula pendula* and downy birch, *Betula pubescens* and less frequently trembling aspen, *Populus tremula* and willows, *Salix* sp.

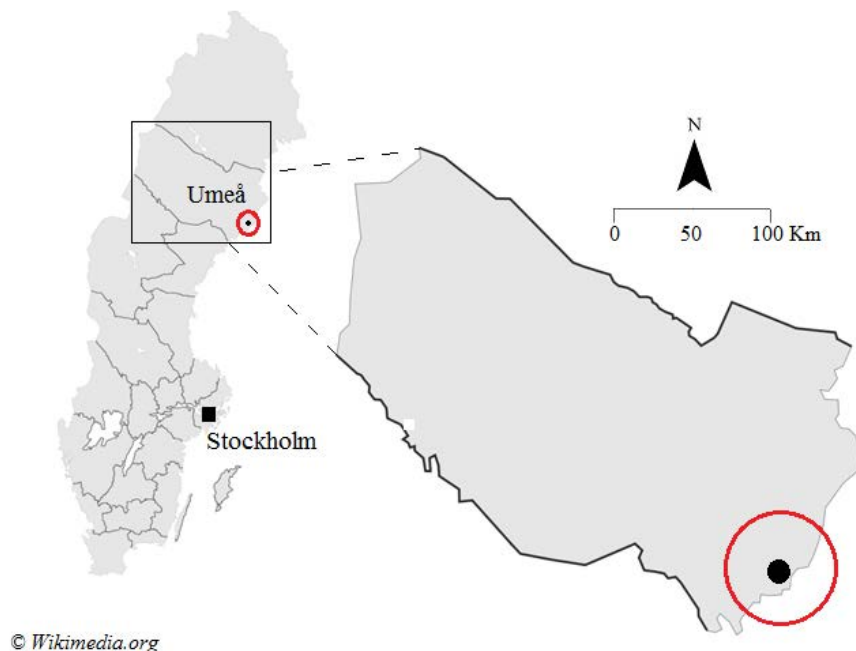


Figure 1. Map of Sweden with an enlarged image of the Västerbotten County. The red circle indicates the study area.

Study stand selection

I randomly selected 25 unmanaged stands and 25 managed stands in a 30 km radius buffer around Umeå. The radius of 30 km was chosen to contain enough managed and unmanaged stands fulfilling the selection criteria, and to be sufficiently small to minimize the time spent travelling from Umeå. Different datasets were used for the selection of unmanaged forests. Woodland key habitats data was obtained from the Swedish Forest Agency (Swedish Forest Agency 2012) while data on nature reserves and biotope protection areas came from the Swedish Environmental Protection Agency (Swedish Environmental Protection Agency 2014). These data do not include information on forest age. The kNN database (Reese et al. 2002) displays information on age of Swedish forests and was used in GIS to keep only forests older than 100 years. Since the kNN reference year was 2000 and my study was conducted in 2014, the selected forests had to be at least 86 years in the year 2000. Old managed forests were displayed as the kNN old forests layer minus the unmanaged selection.

The Swedish Forest Agency clear cut database was used to remove stands which were cut between 2000 and 2014. To minimize spatial dependency among study sites, all stands in the survey had to be at least 1 km away from each other. In the process some stands were divided in several parts and in these cases, the biggest fragment was kept in further analysis. All stands under one hectare were removed.

After searching for stands that met my criteria I remained with 79 and 53 managed and unmanaged stands respectively. From these 132 stands, I randomly selected 25 stands for each forest type (Figure 2). The mean area of the 25 unmanaged stands was 6.7 ha, varying between 1.0 ha to 63.3 ha. The 25 managed stands had a mean area of 4.8 ha, ranging from 1.0 to 17.6 ha. Approximately 90% of the surveyed area of managed stands was owned by private forest owners and 10% by industrial forestry companies.

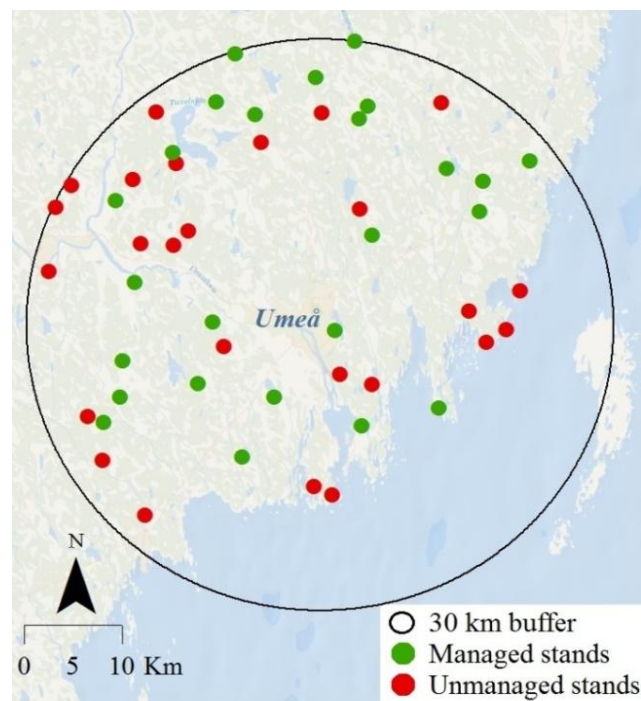


Figure 2. Map showing the study area and the selected stand locations. The 25 managed stands are represented by the green dots and the 25 unmanaged stands by the red ones. Source for background: Esri.

Sampling design for cavity survey

The cavity tree survey was carried out within circular sampling plots with an area of 0.2 ha (plot radius). The plots were distributed systematically within stands according to a grid pattern. A between-plot center distance of 50 m seemed too time consuming and a 100 m yielded too few plots, especially in the smallest stands. A between plot distance of 75 m was defined as a good compromise (Figure 3). In the biggest stands where the number of plots was too high, a maximum of 20 plots was randomly selected.

Some plots were expected to be on stand edges (Figure 3). The field surveyed allowed determining if the whole plot was inside an old forest or not. If the mean DBH (Diameter at Breast Height) of trees outside the edge was more than one-half of the mean DBH of the trees located on the inside, the whole plot area was surveyed. Otherwise, the part located outside was excluded from the plot. The proportion of the plot excluded was noted at the nearest 10 percent. This was done to determine more precisely the total area of forest surveyed.

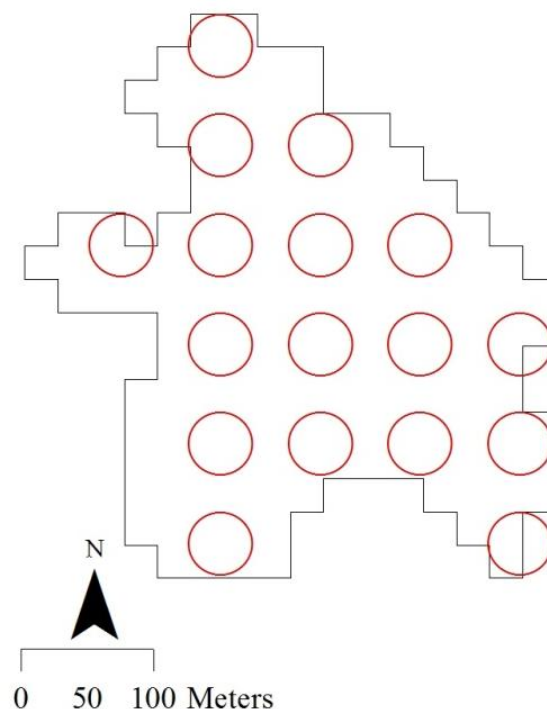


Figure 3. Example of the plot distribution within a managed stand. Black lines indicate the stand limits and the red circles the 0.2 ha plots.

I initially expected to survey a total of 418 plots; 218 in managed forests and 200 in unmanaged forests. At the end of the ocular cavity survey, 61 plots were considered as being outside of the old forest stands. A total of 175 plots were investigated in the managed forests and 185 plots in the unmanaged forests. The total surveyed area was 67.3 ha, 32.6 in managed forests and 34.7 ha in unmanaged forests.

Cavity survey

By using binoculars, I searched for cavities in all standing dead and living trees within the 0.2 ha plots. Each 0.2 ha plot was divided in two halves using a tape, or whenever possible, physical structures (rocks, dead trees, streams) as targets. Each half was investigated separately. The tree survey was conducted in a standardized fashion as follows: I started by standing in the middle of the plot and looking at every single tree towards the outer edge of the plot. Then I walked 10 to 15 m from the center to look at the same trees from the other side. After that, from the same distance, I looked again towards the outer edges of the plot. Finally, trees were scanned from the outer edge of the plot towards the center (Figure 4). The second plot half was surveyed by the other fieldworker.

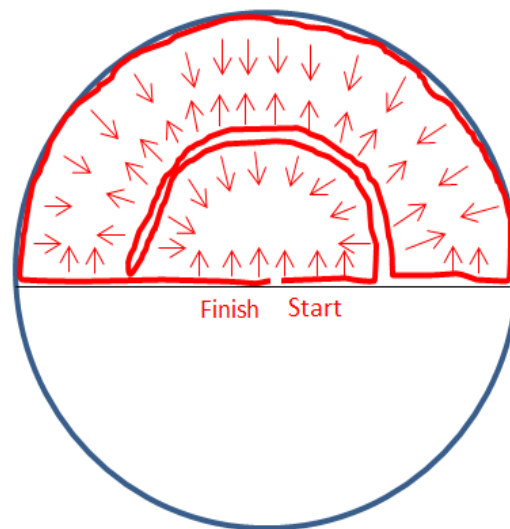


Figure 4. Path followed by one observer during the stage of cavity survey. The blue circle represents the 0.2 ha plot limits; the red line, the path of the observer and the red arrows, the direction towards which the observer looks at. Another observer follows the same path pattern in the second half.

For all the trees with presumed cavities, a GPS coordinate was taken by holding the GPS as close as possible to the tree trunk. For each suspected cavity tree an identity number was given. The tree species and the number of cavities were also recorded. The following information concerning cavities was noted: reachable from the ground, reachable with the 3 m ladder, reachable with the 6 m ladder, reachable with the telescopic pole or unreachable (Table 1). The presence of nest boxes and the approximate diameter of their entry hole were also recorded. The cavity survey conducted from the 20th of March to the 25th of April 2014 before the leafing out of the vegetation. The presence of leaves would have made difficult to observe cavities in deciduous trees as leaves would have reduced the visibility of the stem.

Table 1. Classification of the required equipment according to the height of the potential cavity during the observation of cavity trees.

Equipment required	Cavity Height (in m)
Reachable	0 – 1.8
3 m ladder	1.8 – 3.5
6 m ladder	3.2 – 6.5
Telescopic pole	6.5 – 11.5
Unreachable	> 11.5

Cavity checking and measurement

This second pass was performed from the 29th of April to the 23th of May.

A ground survey does not allow differentiating a true cavity (see the definition below) from a cavity not usable by animals (e.g. an incomplete excavation). This might lead to an overestimation of the number of true cavities (Ouellet-Lapointe et al. 2012). To estimate the true cavity density, all potential cavities found in the ground survey were checked. Each potential cavity was checked and classified as “false”, “usable”, “presumed usable”, or “unreachable”. To be considered as usable, a cavity had to be reachable directly from the ground or with a ladder and had to fulfill the following dimensions: 1) horizontal cavity depth and horizontal cavity width ≥ 6.0 cm; 2) entrance hole diameter ≥ 23 mm if circular or width ≥ 18 mm if slit-like; 3) bottom-top dimension ≥ 10.0 cm; 4) closed bottom; 5) no substantial amount of water in the cavity; 6) cavity bottom above ground level (e.g. not between roots); 7) cavity at least partly roofed, i.e. not an open “chimney”. The criteria 1 to 5 come from Van Balen et al. (1982). This study also stipulates that “the entrance should not be so large so the nest is exposed”. In the present survey, cavities with large entrance holes were not excluded as they may be useful for some species. When cavities were not reachable with the ladder, a camera on the top of a 10 m telescopic pole was used to check the inner cavity (Figure 5, picture a.). This method allowed verifying if a cavity could be defined as a presumed usable one. A presumable cavity should fulfill the following conditions: 1) diameter ≥ 23 mm (if circular) or a width ≥ 18 mm (if slit-like), estimated by comparing the size of the entrance hole with the camera diameter; 2) cavity at least partly roofed, i.e. not an open “chimney”; 3) the telescopic pole camera should penetrate at least 7 cm into the hole and be moveable sideways to ensure that the hole was not a cavity trial without an internal chamber, and the camera image should confirm that the cavity is usable (e.g. figure 5, picture b.). As with the cavity trees, an identity number was given to cavities belonging to the three last categories. If a tree had more than one cavity, the cavity number was given in order from the ground and up.

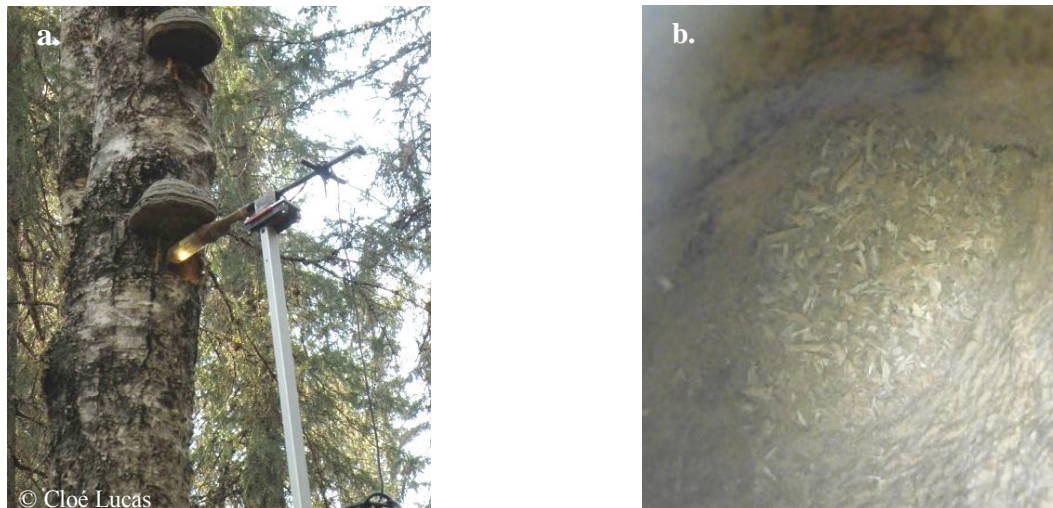


Figure 5. a) Cavity checking with the camera on the top of the telescopic pole. b) Inside view of the cavity using the camera.

All the suspected cavities which did not fulfill the criteria of the “usable” or “presumed usable” categories were categorized as “false cavities”. When cavities were not reachable even using the 10 m telescopic pole, they were called “unchecked”.

The following data were collected for cavities. The measurements identified by an asterisk (*) were only possible for cavities which were reachable directly from the ground or with the ladder, i.e. usable cavities according to the definition above.

- Vertical diameter of entrance hole.
- Horizontal diameter of entrance hole.
- Shape of entrance hole: round, oval, pear-shaped, slit/crack, rectangular, irregular.
- Aspect of entrance hole: direction of entrance hole.
- Excavating species (only if the bird was seen excavating).
- Height of the cavity entrance above ground.
- Bird-excavated cavity (Figure 6, pictures a. and b.) or natural decay cavity (Figure 6, picture d.).
- Fresh or old: for bird-excavated cavities, the cavity was recorded as fresh if it was excavated the present year; otherwise it was written as old.
- (*) Vertical cavity depth: from the lower lip of the hole to the bottom of the cavity.
- (*) Vertical cavity height: from the cavity roof to the lower lip of the entrance hole.
- (*) Horizontal cavity depth: length from the back of the cavity to the inside edge of the hole.
- (*) Lateral cavity width: widest dimension of the inside of the cavity measured at right angle from horizontal cavity depth.
- (*) DCH (diameter at cavity height): at the bottom of the cavity opening.
- It was noted if the cavity was a black woodpecker foraging excavation for carpenter ants or not (Figure 6, picture c.).



Figure 6. Four different cavities (a) excavated cavity. (b) Excavated cavity used by Eurasian nuthatch (*Sitta europae*) which reduced the original entrance hole with dried mud. (c) Black woodpecker feeding hole. (d) Natural cavity.

When a single cavity had more than one entrance hole, it was considered as one cavity and the measurements were based on the largest entrance hole.

Several properties were taken for each verified cavity tree. I recorded if the tree was dead or alive; if alive, its health (Appendix 1); if dead, its decay class (Hunter 1999); its status (full-height tree, naturally broken top or cut high stump); species, its total number of cavities. I also measured tree DBH; full tree height; height to the living crown (vertical distance from the level of the base of the tree to the lowest live branch); mean slope within 20 m from the tree; mean slope aspect within 20 m from the tree.

Forest characteristics

To allow linking cavity densities with forest stand characteristics, I measured trees and stumps within a circular subplot of 100 m² (radius 5.64 m) centered on each 0.2 ha plot. For

each standing tree with $DBH \geq 5$ cm (with midpoint of the stem section within 5.64 m from the plot center), I recorded its DBH, its species and its status (living, dead, or high-stump). Within the subplot, I also counted the number of low stumps with a diameter ≥ 10 cm. I also made a rough estimation of stump age by using a knife. Stumps were noted as “recent” if the blade penetrated less than 2 cm in the stump section. If the blade went deeper stumps were categorized as “old” (see Renvall 1995 for a detailed description).

Data analyses

To test for potential differences of tree species distribution and tree status (dead or alive) between the two management categories, I used Fisher exact test. The comparison between cavity trees DBH and mean subplot tree DBH was performed using a paired Wilcoxon test as the samples were non-normally distributed and dependent.

To compare cavity density between the managed and unmanaged forest stands, I used a Generalized Linear Mixed Model (GLMM) with a Poisson distribution. A zero inflated model was used because many plots had no cavity at all. I used the number of cavity in each plot as the response variable. Forest type (managed or unmanaged) and plot area were included as fixed factors. Stand identity was added as a random factor to account for the aggregation of the plots at stand level.

The area of the entrance holes was estimated using the formula of an ellipse area: $\pi \times \frac{1}{2} vd \times \frac{1}{2} hd$; where vd is the vertical diameter of the entrance hole and hd the vertical diameter of the entrance hole (figure 7). The inner cavity volume was approximated with the formula of an ellipsoid volume: $\frac{4}{3} \pi \times \frac{1}{2} (vcd + vch) \times \frac{1}{2} hcd \times \frac{1}{2} lcw$; where vcd is the vertical cavity depth, vch is the vertical cavity height, hcd the horizontal cavity depth and lcw is the lateral cavity width.

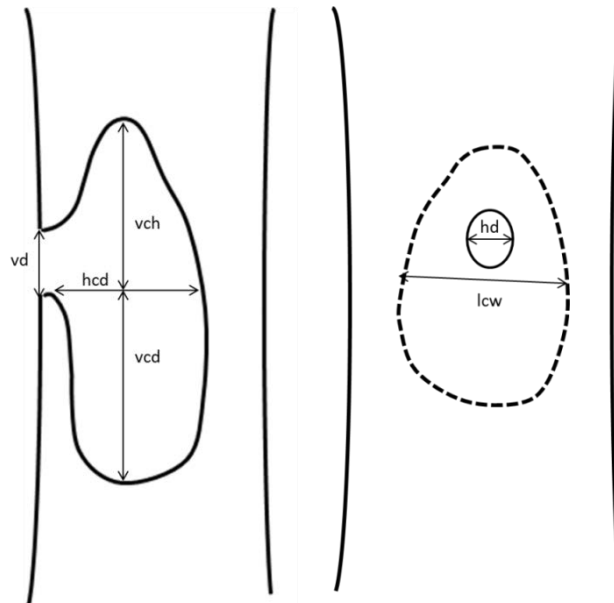


Figure 7. Measurement taken for each reachable cavity. vd : vertical diameter of entrance hole; hd : horizontal diameter of entrance hole; vcd : Vertical cavity depth; vch : Vertical cavity height; hcd : Horizontal cavity depth; lcw : Lateral cavity width. Domingo Gómez 2014.

Mann-Whitney U tests was used for continuous data, i.e. cavity tree DBH, height and height to living crown, entrance hole area, cavity volume, cavity height and DCH. The aim of these tests was to compare the potential differences between the managed and unmanaged forest stands. A Rayleigh test of uniformity was used to assess if the orientation of the entrance holes were randomly distributed or not.

All the analyses were performed in R version 3.0.3 (R Development Core Team 2014). The “glmmADMB” package (Fournier et al. 2012; Skaug et al. 2014) was used to fit the GLMM. The Rayleigh test was performed using the “circular” package (Agostinelli and Lund 2013).

RESULTS

Forest characteristics

Mean densities of 969 trees.ha⁻¹ and 1 030 trees.ha⁻¹ were found in the managed and unmanaged forests respectively. The tree species distribution in subplots differed significantly ($p < 0.0001$) between the managed and unmanaged forests. The principal differences lied in a higher density of birch and spruce in unmanaged forests than in the managed forests (Figure 8). The opposite trend was found for pine; higher density of pine in the managed forests. There was also a significantly ($p < 0.0001$) higher density of dead standing trees in the unmanaged forests.

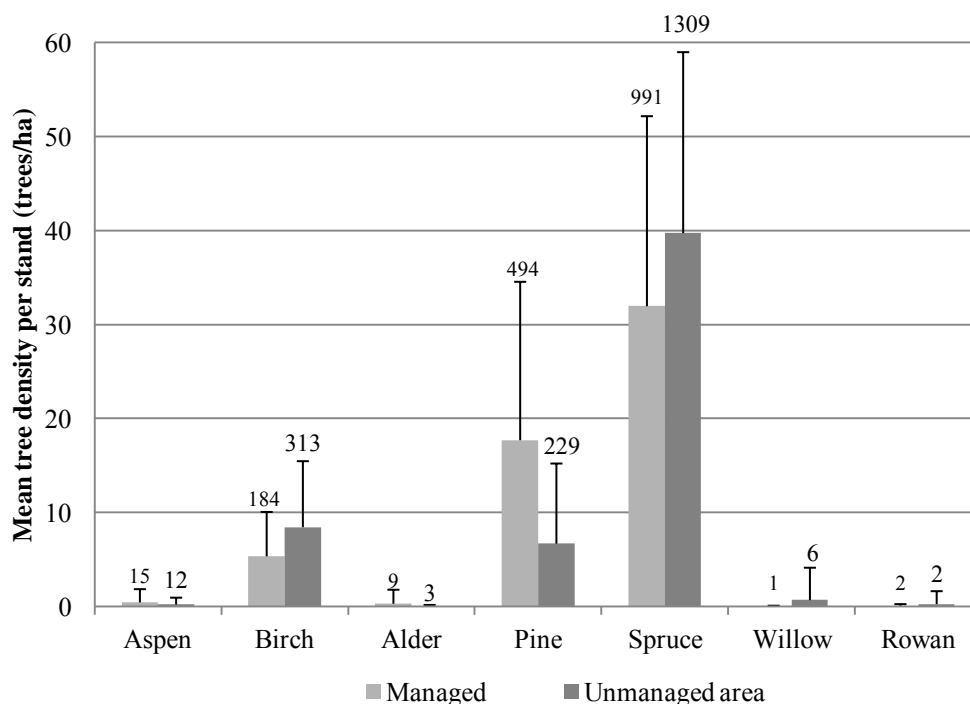


Figure 8. Mean tree density of each species in the 25 managed stands and the 25 unmanaged stands. Errors bars indicate the SD from the mean. The numbers above the bars indicates the number of trees recorded.

Cavity trees

Of the 118 presumed cavity trees found during the first pass, 85 turned out to be true cavity trees after the second part of the survey where the cavities were checked and measured. I also recorded 3 other cavity trees which remained unchecked due to unreachable cavities. The unchecked cavity trees represent only 3% of all the cavity trees and do not affect the results. I then decided to consider all 88 cavity trees in the results. I found 32 cavity trees in managed forests and 56 in unmanaged forests.

There was a mean density of 1.0 cavity trees per hectare (SD = 2.0) in the managed forests while in the unmanaged forests the mean density reached 1.6 cavity trees per hectare (SD = 2.8). The mean DBH of the cavity trees was 26.3 cm in the managed area and 27.4 cm in the unmanaged one (Table 2). Overall, the cavity tree DHB ranged between 10 and 47 cm. The mean cavity tree height was 11.7 m in the managed forests. Significantly smaller ($p = 0.013$), the mean cavity tree height in unmanaged forests was 9.1 m. The height to the living crown was only measurable for the living cavity trees. A number of 16 living cavity trees were found in managed forest with a mean height to the living crown of 8.2 m. In unmanaged forest, 15 living cavity trees presented a mean height to the living crown of 9.3 m. In managed forests, 50% of the cavity trees were alive, where in unmanaged forests; living trees represented 27% of the cavity trees. Dead naturally broken trees represent 64% of the cavity trees in the unmanaged stands and 41% of the cavity trees in managed stands.

Table 2. Mean dimensions of the cavity trees. Standard deviation is indicated in parenthesis. Height: total height of the tree (m); height live crown: height to the living crown (m).

	Managed				Unmanaged				p ⁽¹⁾
	Mean (SD)	Median	Range	n	Mean (SD)	Median	Range	n	
DBH (cm)	26.3 (7.6)	24.5	11.0-42.0	32	27.4 (8.2)	27	10.0-47.0	56	0.498
Cavity tree height (m)	11.7 (5.0)	11	1.7-19.8	32	9.1 (6.9)	6.5	1.2-25.6	56	0.013
Cavity tree height - living (m)	14.3 (4.1)	14.8	7.0-19.8	16	17.1 (6.7)	19.6	6.0-25.6	15	0.105
Cavity tree height - dead (m)	9.1 (4.5)	10.3	1.7-16.2	16	6.1 (4.1)	5	1.2-18.0	41	0.022
Height live crown (m)	8.2 (2.5)	8.4	3.1-11.8	16	9.3 (3.7)	9.8	2.0-14.5	15	0.384

⁽¹⁾ Mann-Whitney U test

In both management categories, a significant ($p < 0.0001$) difference was found between the species distribution of cavity trees and the species distribution of all available trees in the 0.01 ha subplots. In the managed area, aspen was the most common cavity tree (47% of all cavity trees in the managed forests) while at the same time it only constituted 0.1% of the trees in this forest type. Spruce and birch were the second most important species in the managed forests, with a proportion of 31% and 16% respectively (Figure 9). Like in the managed

forests, aspens were also overrepresented in the unmanaged forests (18% of the cavity trees but only 0.1% of all trees in the subplots). Spruce was still the most common cavity tree species (43% of all cavity trees in the unmanaged forests). The tree species distribution in the managed forests was found to be nearly significantly different ($p = 0.080$) from the one in the unmanaged forests (Figure 9).

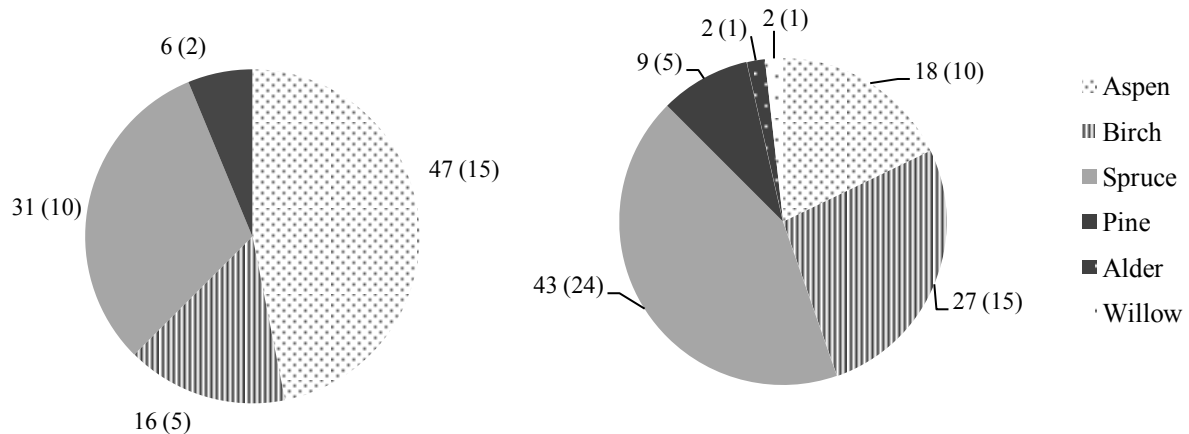


Figure 9 The percentage distribution of the cavity tree species in the managed forests (left) and the unmanaged forests (right). In parenthesis, the number of cavity trees found for each species.

Cavity trees in both forest types displayed a significantly higher proportion of dead trees than all available trees ($p < 0.0001$). Dead cavity trees were also found to be more common in the unmanaged forests than in the managed forests ($p = 0.038$). To be considered as usable, a cavity had to have a horizontal depth and a lateral width of at least 6 cm. Taking also into account the wall thickness, trees with a DBH below 10 were considered unlikely to hold cavities fulfilling these minimum size requirements. To compare the DBH of the cavity trees to the DBH of all the trees found in the subplot, I removed all the subplot trees with a DBH under 10 cm. This allowed keeping only trees which could potentially have cavities. The mean DBH of the remaining available trees (meaning the trees in the subplots) were 17.4 cm and 16.3 cm in the managed and unmanaged areas respectively. These mean DBH were significantly smaller than the mean cavity tree DBH for both forest types ($p < 0.0001$).

Cavities

In the first pass, 225 potential cavities were found. After checking, 117 (52%) were determinate as true and 11 (4.9%) remained unchecked. As for cavity trees, all the 128 cavities will be included in the analyses. A total of 40 cavities were recorded in managed forests while 88 were found in unmanaged forests. Cavities excavated by primary cavity nesters for breeding or roosting represented 79.7% of the cavities in both areas. Natural-decay cavities and black woodpecker feeding holes were represented respectively at 5.5% and 14.8%. In managed areas, the density of cavities was $1.2 \text{ cavities.ha}^{-1}$ and range from 0 to 10 cavities.ha^{-1} . The density was twice as high in the unmanaged area ($2.5 \text{ cavities.ha}^{-1}$; $p =$

0.020) and range from 0 to 8.6 cavities.ha⁻¹ (Table 3). I also calculate the densities of the cavities with large entrance holes. The mean diameters of black woodpecker entrance holes were chosen as the minimum dimensions for large entrance cavities. Therefore, the horizontal diameter had to be at least 7.6 cm and the vertical diameter 10.4 cm (Johnsson 1992).

Table 3. Mean cavity densities in the managed and unmanaged forests (SD in parenthesis).

	Managed			Unmanaged			p ⁽¹⁾
	Mean (SD)	Range	n	Mean (SD)	Range	n	
Mean density (cavities.ha ⁻¹)	1.2 (2.5)	0-10.0	40	2.5 (2.8)	0-8.6	88	0.020
Mean density of large entrance cavities (cavities.ha ⁻¹)	0.1 (0.3)	0-1.7	3	0.3 (0.9)	0-2.7	11	Too little sample size

⁽¹⁾ Generalized linear-mixed model Poisson distribution zero inflated

The above ground height of the cavities was measured for all 128 cavities found in the survey, including the unreachable ones. The mean height of the cavities in the managed forests did not differ from the mean height in the unmanaged forests ($p = 0.514$). The DCH, the area of the entrance hole and the volume of the cavity were only available for cavities directly reachable (with or without ladder), that is 21 cavities in the managed forests and 38 in the unmanaged forests. No significant difference was found between the two forest types in respect of these parameters (Table 4).

Table 4. Mean, SD and median of the cavity measurements. Height (height of the entrance hole above ground), DCH (diameter at Cavity Height), Entrance area (estimated area of the entrance hole) and Cavity volume (estimated volume within the cavity).

	Managed				Unmanaged				p ⁽¹⁾
	Mean (SD)	Median	Range	n	Mean (SD)	Median	Range	n	
Height (m)	4.4 (3.2)	4.3	0.1-10.8	40	4.2 (3.7)	3.4	0.1-14.6	88	0.514
DCH (cm)	27.7 (6.6)	29.0	14-35	22	30.5 (17.2)	27.0	9-82	38	0.466
Entrance area (cm ²)	64.7 (57.4)	36.9	19.4-263.9	22	76.2 (77.8)	38.6	8.9-354.6	40	0.825
Cavity volume (dm ³)	5.3 (11.5)	1.8	0.4-5.3	21	2.7 (3.5)	1.4	0.3-18.2	38	0.585

⁽¹⁾ Mann-Whitney U test

The orientations of the cavities' entrance holes did not differ from random ($p = 0.177$). The same trend was found after removing the 7 natural-decay cavities (non-woodpecker excavated cavities) ($p = 0.210$) and after removing both natural-decay cavities and the 19 black woodpecker feeding cavities (Figure 10, $p = 0.535$).

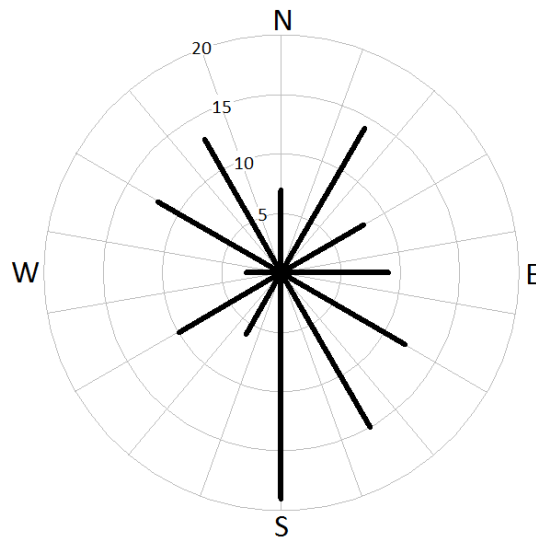


Figure 10. Orientation of the surveyed entrance holes (n = 102) after removing the natural-decay cavities and the black woodpecker feeding holes. The black lines show the number of cavities found within groups of 30 degrees intervals.

DISCUSSION

My results showed that in both management categories, aspen represented only 0.1% of all trees in the stands, while it represented 47% and 18% of the cavity trees in the managed and unmanaged stands, respectively. This result is consistent with numerous studies which identified aspen (*Populus tremula* in Europe and *Populus tremuloides* in North America) as the preferred cavity excavation substrate of cavity-nesting birds (Hagvar et al. 1990, Li and Martin 1991, Carlson et al. 1998, Drever and Martin 2010, Domingo Gómez 2014). Living aspens are susceptible to heartwood rot (Martin et al. 2004) which facilitate woodpecker excavation. With proportions of 50% and 73% in managed and unmanaged forests, respectively, dead trees (all species confounded) were also overrepresented as cavity trees. Dead trees are recognized to be favored by woodpeckers as decay makes them softer for cavity excavation than healthy living trees (Schepps et al. 1999).

Natural decay cavities represented only 5.5% of all the cavities found in my study. Similar results were also found in North American forests (Aitken and Martin 2007, Cockle et al. 2011, Ouellet-Lapointe et al. 2012) and in clearcut retention trees in the Swedish boreal zone (Domingo 2014). This finding is also consistent with Remm and Lõhmus (2011) suggestion that natural decay is not a significant agent of cavity formation in forest ecosystems where wood decay is slow, such as in boreal forests. In Swedish boreal forests, primary excavators are thus the main source of cavity formation. Therefore, woodpeckers are then a fundamental group on which secondary cavity nesters rely. In particular, the great spotted woodpecker and

black woodpecker could be considered as keystone species in the Swedish boreal forest as they are the most abundant primary excavators (see e.g. Johnsson 1992).

Checking the presumable cavities allowed determining that 52% of them were true cavities. A similar result was found by Domingo Gómez (2014), who found that around half of the cavity turned out to be true. As suggested by Ouellet-Lapointe et al. (2012), ground surveys will lead to a substantial overestimation of usable cavities. Thus, ground survey is fast and requires little equipment, but should be followed by cavity checking to accurately assess the true density of usable cavities.

I obtained a mean cavity density of 1.2 ha⁻¹ in the managed forest stands. The mean density in the unmanaged forest stands was 2.5 cavities ha⁻¹ which is more than twice as many. To my knowledge, only one other study on cavity availability has been conducted in the Swedish boreal zone. In this earlier study, Domingo Gómez (2014) found a density of 0.4 cavities ha⁻¹ in retention trees on clearcuts in the same region as the present study. All these results imply that cavity availability is heavily reduced in managed boreal forest compared to naturally-dynamic forest. In my study, the observed difference could be due to higher proportions of potential cavity trees in unmanaged stands. Indeed, dead trees, which represented high proportion of cavity trees, were more abundant in the unmanaged forest stands. The same pattern was found for birch and spruce.

The cavity density found in my study was higher than those found by Pulliainen and Saari (2002) (1.1 cavities.ha⁻¹ in Finnish subarctic forest) and by Lõhmus et al. (2005) (1.0 cavities.ha⁻¹ in Estonian hemiboreal forest). However, the densities obtained in my study remain within the lower range of most cavity densities reported in the literature for boreal and hemiboreal forests (Sandtröm 1992, Carlson et al. 1998, Bai et al. 2003, Ouellet-Lapointe et al. 2012). North American boreal forests are populated by a different composition of cavity tree species and excavators, but they also present broad ecological similarities with European boreal forests (Imbeau et al. 2001). Yet, the cavity density found in North American boreal forests by Ouellet-Lapointe et al. (2012) is five to ten times (11.2 cavities.ha⁻¹) higher than those found in my study. This may be explained by the fact that my study was conducted in a region with a much longer history of intensive forest management than in boreal North America (Imbeau et al. 2001). Indeed, in my study, most unmanaged stands have probably been subjected to some forms of selective loggings in the past. Even larger differences can be found between my results and the results found in Swedish hemiboreal forests; Sandström (1992) reported 15.2 cavities ha⁻¹ and Carlson et al. (1998) 60.4 cavities ha⁻¹. A reason for these differences could be that these studies were conducted in forests with a high abundance of deciduous trees and with higher productivity than in purely boreal forest. Moreover, woodpecker density and diversity is generally higher in hemiboreal than boreal forest (Ottoosson et al. 2012). Natural-decay cavities stood for more than half of all the cavities found in the two studies.

Cavity trees in managed forest stands were on average taller than in unmanaged forest stands. This is most probably due to the fact that all cavity trees were taken into account in this comparison. Indeed, if living and dead trees are treated separately, only dead cavity trees showed a height difference between the two management categories. Dead trees include naturally broken trees which are in general shorter than full-height trees. Naturally broken cavity trees are more abundant in the unmanaged than in the managed stands, respectively

64% and 41%. Cavity tree height difference might therefore be explained by the higher amount of naturally broken trees in unmanaged area. This result is not surprising as commercial forest management aims to minimize tree death in the forest.

Cavity-nesting species select cavities depending on their properties, e.g. height of the cavity, entrance hole diameter (Sandström 1991). Indeed, some cavity characteristics are particularly important as they directly affect the risk of predation (Nilsson 1984). No difference was found in the mean cavity characteristics between the two management categories in my study. However, even though no statistically significant differences were found in terms of mean cavity measurements, my results indicate that there might be a difference in the availability of large entrance cavities between managed and unmanaged forests. Cavities with large entrances are of particular importance since they provide breeding substrates for larger-bodied species of birds such as common goldeneye (*Bucephala clangula*) or Tengmalm owl (*Aegolius funereus*) (Johnsson 1992). Large entrance cavities were found in higher abundance in unmanaged forest stands, but the limited sample size did not allow performing statistical analyses.

My results suggest that forest management has a negative impact on cavity availability. Thus, it would be interesting to evaluate the impact of e.g. different thinning intensities on cavity density in managed stands. The density and the age class (recent or old) of low harvested stump could be a good indicator of this intensity. It may also allow finding if an unmanaged stand happened to be harvested in the past. In this study, the harvested stump data remained incomplete in several stands as the snow cover prevented recording stumps.

In my study I examined cavity density in old managed and unmanaged in Swedish boreal forest and cavity availability has previously been evaluated in retention trees in recent clearcuts (Domingo Gómez 2014), but no study have so far been conducted in intermediate successional stages. Future studies should focus on assessing cavity availability in young and middle-aged forests, i.e. forest stands that originated from clearcutting and which have been managed intensively for timber production. A study conducted by Stenbacka et al. (2010) in the Swedish boreal zone compared different successional stages and found that these intermediate stands were the ones with the lowest volume of dead wood. Low cavity tree density is then expected in these intermediate aged stands. Additional studies on nest occupancy and breeding success in Swedish boreal forests will be necessary to further assess the impact of forestry on cavity utilization. This could improve knowledge on cavity nesting birds in Swedish boreal forests and also on some mammals (e.g. bats, squirrels (*Sciuridae*), martens (*Mustelidae*) and invertebrates (e.g. red-listed beetles specialized on hollow trees)

To ensure a sufficient supply of cavities in forest, I suggest that conservation management should aim to protect suitable habitat for woodpecker species. As already suggested by other studies (Angelstam and Mikusinski 1994, Roberge et al. 2008), trees with large DBH and dead standing trees are of particular importance. Increasing the amount of deciduous trees and especially aspen should also be an objective of sustainable forest management and future set asides. Dead standing trees represent the majority of the cavity trees in my study, but retention of living trees is also fundamental as they represent a prerequisite for the recruitment and continuity of future cavities (Edworthy et al. 2012).

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APPENDIX 1. Tree health and decay class

Tree health (based on a protocol obtained from Kathy Martin (pers. comm. 2013))

- 1) *BT broken top*
- 2) *BF bracket fungus (= polypore)*
- 3) *BU burned trunk*
- 4) *RB rust broom (on SX or FD)*
- 5) *BI boring insect (can generally see their entry/exit holes/tunnels)*
- 6) *BN brown needles*
- 7) *TG trunk gall*
- 8) *MD mechanical damage (e.g. axe wound or scar from forestry operations)*
- 9) *AR antler rubbing (scars the bark, sometimes girdles the tree – this code also covers ‘cribbing’, or bark feeding)*
- 10) *BD beaver damage*
- 11) *BL bark blistering & seeping sap*
- 12) *SL split leader (= forked tree shape -- only applies to conifers)*
- 13) *UK unknown/undetermined*