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ORIGINAL PAPER

The intensity of forest management affects the nest cavity production of woodpeckers and tits in mature boreal forests

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Abstract

Cavities made by birds are an important microhabitat for many taxa in forests. Long-term dynamics of cavity patterns and the effect of forest management on cavities are, however, largely unknown. We studied cavity production, measured as nest cavity production rates (CPR = no. of new cavities/km^2/year), of woodpeckers and tits in forests with different management intensity in southern Finland, based on a data from 37 years. Forests were divided into managed, seminatural and natural stands. The data covered 56 forest stands with the total area of 1690 ha. Stands were inventoried annually for new cavities. The total numbers of woodpecker and tit cavities were 2238 and 329, respectively. There were large differences in CPRs between forest stands with different management intensity. For woodpeckers, the CPR was highest in natural forests (5.7) and lowest in managed forests (1.5). For the tit species, the respective numbers were 0.9 and 0.3. The CPRs of different cavity-making bird species and cavity tree characteristics (e.g. tree condition and species) were consistent, suggesting that different cavity-makers benefit from similar forest and tree characteristics. The results also suggest that forests managed with currently prevailing methods limit the production of cavities. To promote cavities, the results from this and other studies suggest that managed forests should include more features of natural forests, such as more diverse tree species and within-stand structural variability distribution (tree-level heterogeneity), larger amount of decayed wood, more retention trees and snags and longer rotation periods.

Keywords Tree cavity · Forest management · Forestry history · Boreal forest · Woodpecker · Tit · Forest microhabitat

Introduction

Tree microhabitat is a discrete part of living or dead tree that creates a distinct habitat or environment for an assemblage of forest-dwelling species (Stokland et al. 2012; Larrieu et al. 2022). Cavities in trees are among the most conspicuous microhabitats in forests. Cavities have an important role as nesting, roosting or resting site and overwintering place for many vertebrates, and they also host many different invertebrates and fungi (Siitonen and Jonsson 2012; Edworthy and Martin 2014; Wesołowski and Martin 2018; Cockle et al. 2019). While some cavities can be formed directly by wood breakage and the following decay process (see details in, e.g. Speight 1989; Schwarze et al. 2000; Jusino et al. 2015; Kõrkjas et al. 2021), considerable part, 85–98% (Aitken & Martin 2007; Andersson et al. 2018), of tree cavities inboreal forests are made by birds—woodpeckers and tits—that excavate cavities for their nesting sites. These cavities are used by several species after the primary cavity-maker (e.g. Johnsson et al. 1993; Pulliainen and Saari 2002; Bai et al. 2003; Pakkala et al. 2018a, 2019a, 2022). Potentially, tree cavities could be used as an indicator for forest biodiversity, but the patterns and dynamics of cavity occurrence are poorly understood so far (Bednarz et al. 2004; van der Hoek 2020; Larrieu et al. 2022).

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Forest management always modifies the structural properties of forests, and management may influence the availability of suitable cavity trees and the cavity density. Cavity density appears to be often higher in unmanaged than in managed forests (e.g. Remm and Lõhmus 2011; Andersson et al. 2018). In managed forests, trees are younger and “healthier” and usually harvested before reaching old age (Henttonen et al. 2019; Mönkkönen et al. 2022). Besides affecting age structure of trees, management may influence cavity availability by changing tree species composition (Henneberg et al. 2021). For instance, deciduous trees are often preferred as nest cavity trees, but the number of deciduous trees is often lower in conifer-dominated managed forests (Felton et al. 2021), possibly resulting in lower cavity density when compared to natural forests of similar type. In Fennoscandia and many other parts of the boreal region, silviculture is mainly based on coniferous even-aged stands with short rotation period leading to forests with relatively small trees (Burton et al. 2003; Lindenmayer and Franklin 2002). This type of management can also affect the occurrence of cavities as it tends to promote trees that are not preferred for cavity-makers and cavity-breeders (Wesołowski 2012; Edworthy and Martin 2013; Basile et al. 2020). Generally, the highest cavity densities have been reported from old-growth, mixed or deciduous forests with many large sized trees (Remm and Lõhmus 2011).

There are several studies about the characteristics of cavity trees from boreal areas (see Wesołowski and Martin 2018; Pakkala et al. 2018c, 2019b, 2020), but studies that have analysed the occurrence of cavities and their dynamics for longer periods are still relatively rare (e.g. Wesołowski 2011, 2012; Edworthy et al. 2012, 2018; Edworthy and Martin 2013; Pakkala et al. 2018a, 2019a, 2022; Hardenbol et al. 2019). Also, the effects of intensive forest management on cavities are poorly understood. Additionally, even though clear-cut based silviculture aims at simple cohort structured forests, its intensity and the specific management methods can vary widely. Such variation can be caused by management actions such as extending the rotation periods, leaving retention trees, increasing the number of deciduous trees, and modifying the thinning intensity or timing (e.g. Franklin et al. 1997; Gustafsson et al. 2012; Schall and Ammer 2013; Gossner et al. 2014). While the modifications of silvicultural systems are potentially an efficient tool to affect those forest characteristics that are related to cavity occurrence, it is largely unknown how such modifications will affect different cavity-making species. Thus, there is an urgent need to understand how cavities are produced under varying silvicultural regimes, and if there are specific structural characteristics in forests that could be promoted to maintain populations of cavity-making species and thus general cavity availability also for other cavity-associated taxa.

In this study, we focus on the connections between forest management and the occurrence of bird-made nest cavities. The following questions will be explored:

1. Do cavity production rates by cavity-making species groups (woodpeckers and tits) in mature forest stands differ between forest stands with similar forest type but different management intensity?
2. How do cavity production rates differ between these forest stands in various cavity-making species and of cavities in various types of cavity trees?
3. Is the variation in cavity production rates of forest stands correlated between various cavity-making species or cavity tree species? Is the correlation different within forest stand classes compared to correlation in total data?

Study area, material, and methods

Study area and forest bird inventories

The study was conducted in southern Finland (around 61°15′ N, 25°03′ E) in an area of 170 km^2 within the southern boreal vegetation zone (Ahti et al. 1968). The area is dominated by coniferous and mixed forests on mineral soils, but the forest landscape is a mosaic of stands of different ages, patches of peatland forests, and small lakes. The study area includes both actively managed (about 80% of the total area) and protected or set-aside forests (20%). Breeding forest birds were inventoried over a 37-year period (1986–2022) within the area, including territory mapping, searching for nests, and monitoring cavity trees and cavities of cavity-nesting species (see Pakkala 2012; Pakkala et al. 2006, 2014, 2017, 2018b, 2019a, 2020, 2022). All cavity data were gathered by the author TP. Additional help in territory mapping, searching for nests of cavity-nesting birds and information of cavity trees and cavities during 1986–1997 and 2003–2008 was provided by ornithologists who took part in other breeding bird studies within the area. Detailed information of the cavity inventory method is given below in section "Cavity inventory method".

Selection and delineation of forest stands

Our aim was to find sets of forest stands with same age-class and forest type, but which differed in forest management intensity that could be used to classify them. We had to focus only on forests that were more than 60 years old, because forest stands that represent different management intensity classes were only found in mature forest age-class. For instance, due to active fire suppression and salvage loggings, there are practically no natural post-disturbance young forests in the study region, and they are very rare also elsewhere in Finland (Kouki et al. 2001). Moreover, mature forest stands in our study area consisted predominantly (ca. 70% of forests) of mesic spruce-dominated *Myrtillus* type (MT) and more fertile *Oxalis-Myrtillus* type [OMT; see Cajander (194) for the classification of Finnish forest types], and we restricted our study to these types of forests.

We defined the suitable forest stands with the help of national forest inventory (NFI) data provided by National Resources Institute Finland, aerial photographs of the study region and digital topographic maps, both provided by the National Land Survey of Finland, and on-site definition of the age-class and forest type of the forest stands done by the author TP during the cavity inventories in 1986–2022. The delineation of forest stands was then digitized manually with QGIS-program. To harmonize the comparison between forest stands and to avoid possible biases caused by small stand area and edge effects, we set a minimum area of 20 ha for the studied forest stands and excluded stands that were very narrow and showed high edge-to-interior ratio. In addition, we checked that the areas of the forest stands were generally of the same order of magnitude; the largest stands were divided to smaller units to achieve the criteria. Besides OMT-MT types of forests, small patches of mature spruce-dominated swamps [see Laine et al. (2012) for the classification of Finnish peatland types] were occasionally located within and around of forest stands.

Classification of forest management intensity

We divided the selected forest stands into three forest management intensity classes: (1) managed, (2) seminatural, and (3) natural forest stands. The division was based on studying in detail chronological aerial photographs and topographic maps of the selected forest stands covering the time periods of 1948–2022 (photographs) and 1965–2022 (maps). This study was complemented by information of on-site visual assessments of the forest stands during the cavity inventories in 1986–2022 and other information of the forest management history of the study area [especially Tuominen (1990) and Seppo Tuominen pers. comm.]. The silvicultural system in the managed forests is based on clear-cutting, planting or sowing, and repeated thinning. Similar silvicultural methods have been widely applied in Finland and in many other parts of boreal forests from 1950's to present. The selected managed stands included forests under active and continuous timber-production oriented forestry with areas of old clearcuts and saplings seen in their early phases in late 1940's and early 1950's in aerial photographs. In later periods, thinning was detected in aerial photographs and recorded in field observations within these forest stands. The class of natural stands included mostly protected forests and two set aside stands in managed forests, which had been practically unmanaged at least from late 1940's or early 1950's (e.g. Tuominen 1990) and that did not show marks of clear-felling in their history. As judged from old aerial photographs and topographic maps, in some natural forest stands, new narrow forest roads were built at the borders of the areas and some small areas of spruce-dominated swamps were ditched during 20–40 years before the beginning of the cavity inventory period. The seminatural stands consisted of forests which used to be managed but did not fulfil the above criteria of natural forests. Seminatural stands were usually left unmanaged 15–20 years before the beginning of the cavity inventory period, but there were small sections in some stands, which were managed just before and even during the set-aside time. As in natural stands, ditching of small spruce-dominated swamps was also accomplished in some seminatural stands.

The classification was not straightforward, and the selected forest stands rather formed a continuum in forest management intensity than three clearly separate classes. We nevertheless regard the classification to "managed" and "natural" classes solid because their history or status could be verified. The "seminatural" class was more problematic but the stands in this class are all set-asides or otherwise devoid of regular management indicating that they maintained some "naturalness" and biodiversity values. Nevertheless, we do not expect that this class can be used to assess the effect of any specific management operation during a rotation period, because the class was quite heterogenous in terms of their specific management actions and exact timings. Instead, we assume that this class shows overall how a recent reduction in management intensity compared with actively managed forest stands could influence the cavity patterns.

Cavity inventory method

Cavities in the forest stands were inventoried during 1986–2022. Cavity inventories were focussed on new cavities made during each study year. Territories of cavity-making bird species, especially woodpeckers, were surveyed in studied forest stands during the early breeding season in April to early May by the mapping method (Enemar 1959; Tomiałojć 1980; Pakkala and Väisänen 2000). The method is based on repeated visits to study sites, to detect established breeding territories. Based on the field observations of the cavity-making birds during territory mapping visits, nest cavities were searched for in each of the studied forest stands until early July. Moreover, old cavity trees and cavities found in the previous study years were also systematically checked during the territory mapping work or in nest cavity searches (Pakkala 2012; Pakkala et al. 2017, 2018b).

For each cavity tree, tree species, tree condition (dead/living) and size (DBH; at 1.3 m height) at the cavity excavation year were measured and the cavity-making bird species was recorded. The age-class and type of the forest (see above) at the cavity site were also defined and recorded. The cavities were made by six woodpecker and two tit species: the Black Woodpecker (BW) *Dryocopus martius*, the Great Spotted Woodpecker (GSW) *Dendrocopos major*, the Lesser Spotted Woodpecker (LSW) *D. minor*, the White-backed Woodpecker (WBW) *D. leucotos*, the Three-toed Woodpecker (TTW) *Picoides tridactylus*, the Grey-headed Woodpecker (GHW) *Picus canus,* the Willow Tit (WT) *Poecile montanus* and the Crested Tit (CT) *Lophophanes cristatus*.

We expect that the efficiency of annual cavity inventories was relatively similar in each woodpecker species, because of the standardized and effective inventory method including the systematic field check of old cavity trees, and so the cavity numbers are comparable between woodpecker species. However, the efficiency in tit cavity inventories was lower than in those of woodpeckers, mainly due to lower detectability of both tit cavities and nests compared with those of woodpecker: the tits breed early in spring and in less distinct trees compared with woodpeckers, and they are less noisy than woodpeckers during the nestling period. We therefore handled woodpeckers and tits separately in our analyses.

Cavity data and cavity production rate (CPR)

For the cavity data, all fresh, completed and actively used nest cavities were included (see Pakkala et al. 2017, 2018b, for the definition). We thus included only those cavities in which the cavity-making species started nesting in the first year of the cavity. By this restriction, we avoided the common problem in cavity inventories with initiated, but not completed cavities, which are relatively abundant also in our study area, but the status of which is difficult to define by ground checks (Wesołowski 2001; Ouellet-Lapointe et al. 2012; Andersson et al. 2018). On the other hand, cavity-making species do not make a new cavity every year, and e.g. in our study area the use of old cavities instead of excavating a new one varied between 5 and 50% depending on the species (Pakkala et al. 2017, 2019a, 2022; Pakkala unpublished data). Thus, a single annual survey of new cavities in a forest area is not an accurate measure of the quality of the respective area for the cavity-making species. However, in a long-term monitoring of cavities, as in this study, we can combine the annual numbers of new cavities in a forest area from a relatively long period, e.g. from annual inventories over 20 years to represent the more general cavity production potential of that area.

To standardize the cavity numbers to allow comparisons between areas, we define here the cavity production rate (CPR) as the mean number of the annually produced new nest cavities per km^2 of forest area. The CPR can thus be considered as the standardized (long-term) cavity production potential of a forest area, and we used the mean number of annually detected new cavities calculated from the data for the estimate of CPR in forest stands in our study. We calculated CPRs for individual forest stands, and, respectively, for the forest management intensity classes, cavity tree species and species groups, and cavity trees with various condition.

In total, the cavity data used in this study consisted of 56 forest stands with the total area of 1690 ha and mean area of 31 ha. The total numbers of woodpecker and tit cavities were 2238 and 329, respectively (Table 1).

Numerical analyses

Cavity production rates

CPRs were compared between forest stands in different management intensity classes. In woodpeckers, we analysed CPRs of all woodpecker species, the cavities of the three most common single species, namely the GSW, TTW and BW, and a combined set of the three less abundant species, the LSW, WBW and GHW. We also compared the CPRs in dead and in living cavity trees and in the most common single cavity tree species. i.e. in European aspen *Populus tremula*, in birch *Betula* spp., in Scots pine *Pinus sylvestris*, and in Norway spruce *Picea abies*, and in the group of six less abundant cavity tree species.

The sample size of cavities made by tits was much smaller than the sample size of cavities made by woodpeckers (see Table 1), and only the combined data of WT and CT were used in CPR calculations. The CPRs in total data, in dead and in living cavity trees were compared between forest stand classes as well as CPRs in the two most common cavity tree species, birch and grey alder *Alnus incana* and in the group of five less abundant cavity tree species.

The distributions of cavity production rates were often leptokurtic and/or positively skewed, and we therefore used Kruskal–Wallis tests to compare cavity production rates

Table 1 Studied stands and the cavity data in the three forest management classes

	Forest management intensity class			Total
	Managed	Seminatural	Natural	
Total area, ha	644	586	460	1690
Number of stands	22	21	13	56
Mean area, ha	29	28	35	31
Range, ha	20–61	20–57	23–53	20–61
Mean no. of annual cavity inventories for each class	28	33	34	31
Total no. of woodpecker cavities	303	904	1031	2238
Total no. of tit cavities	60	130	139	329

between different groups. In post hoc comparisons between pairs after a significant result, Dunn's test with Bonferroni correction was used. All statistical analyses in this study were conducted with IBM SPSS Statistics Version 27.

Differences and similarities between forest management intensity classes based on cavity production rates

The aim was to study how different forest management intensity classes differ in CPRs based on cavity-making species or cavity tree species, and which independent variables are the most important in separating the classes. We studied possible differences and similarities in cavity production rates between forest management intensity classes by linear discriminant analysis (LDA). We used separately two sets of data with the forest class as the dependent variable: (1) CPRs of woodpeckers divided to four classes: GSW, TTW, BW, and a combined set of CPRs of the three less abundant woodpecker species, and (2) CPRs of cavities in different cavity tree species divided to five classes: aspen, birch, Scots pine, Norway spruce, and a combined set of CPRs of cavities in six less abundant cavity tree species as the independent variables.

Dependencies of cavity production rates: total correlation and correlations between and within forest stand groups

We studied correlations of CPRs with a set of different cases including central groups of cavity-making species and characteristics of cavity trees. Correlations of CPRs were measured between all cavities of woodpecker and tit species, between woodpecker cavities in dead and in living trees, between GSW cavities and cavities of other woodpecker species, and between woodpecker cavities in aspen and in other tree species. In addition to investigate the strength of correlations, we focussed on comparing correlations of CPRs in total data and within forest stand classes to get a more accurate view of correlation patterns in CPRs. Spearman's rank-order correlation was applied to test dependence of cavity production rates between various groups.

Cavity tree size

To compare the cavity tree sizes (DBH) between various types of forest stands, we selected a set of cavity trees which would be comprehensive in relation to different cavity size classes. Thus, the set consisted of cavity trees of the BW (big cavities), of the GSW (medium-sized cavities) and of tits (small cavities). The cavity tree size was compared separately in each cavity size class. One-way analysis of variance (AOV) was used to compare cavity tree size (DBH) between groups. In post hoc comparisons between pairs after a significant result, Tukey's test was used.

Results

Cavity production rates and the intensity of forest management

Woodpecker cavities

Cavity production rates (CPRs) of all woodpecker-made cavities depended on the intensity of forest management. The median annual CPRs were 5.7 cavities per km^2 in natural and 4.3 in seminatural, but only 1.5 in managed forest stands. In pairwise tests, the managed stand class differed from the other two classes, which did not differ from each other (Table 2; Fig. 1a). Similar patterns were observed also in CPRs of GSW and of TTW, and in CPR in a combined set of cavies of the less abundant woodpecker species (GHW, LSW and WBW). The CPRs in BW, however, did not differ between forest stand classes (Table 2; Fig. 1b).

Moreover, considering the studied cavity tree characteristics of woodpeckers (tree condition and species), results in CPRs were similar: the CPRs were smaller in managed forest stands compared with those in natural and seminatural stands, which did not differ from each other (Table 3; Fig. 1c). This pattern was observed in CPRs of woodpecker cavities in living, in dead trees as well as in aspen, in birch, in Norway spruce, and in a combined set of cavities in other, less abundant tree species (Table 3; Fig. 1d). The only exception of this result was the CPR pattern observed in cavities in Scots pine: there was a general difference in CPRs between forest stands, but as CPRs were higher in natural forest stands compared with the other two classes, the CPRs in managed and in seminatural stands did not differ from each other (Table 3; Fig. 1d). Of the different tree species groups, living trees in general had higher CPRs compared with dead trees, and deciduous trees had higher CPRs than coniferous trees. Among the deciduous trees, aspen was clearly most common cavity tree species (Table 3; Fig. 1).

Tit cavities

Tit cavities showed a similar general pattern as woodpecker cavities: there was a difference in CPRs of all tit cavities between forest stands with different forest management intensity (Table 4; Fig. 2a). The median annual CPRs were lower, 0.33 cavities per km^2, in managed areas compared with natural (0.92) or seminatural (0.71) areas; the latter two types did not differ significantly from each other. The CPR of tits was clearly higher in dead trees, only 2% of the cavities were made in living trees. Deciduous trees

Table 2 Cavity production rates (CPRs) of woodpecker cavities in forest stands with different forest management intensity

Management intensity class Pairwise comparison	Managed (M) M vs. N	Seminatural (S) S vs. M	Natural (N) N vs. S	Test statistics
All woodpecker species, n	303	897	1038	
CPR, Median	1.53	4.27	5.70	$H=34.2$; $p<0.001$
Pairwise difference	$p<0.001$	$p<0.001$	$p=0.32$	
Great spotted woodpecker, n	241	627	703	
CPR, median	1.19	3.22	4.10	$H=33.3$; $p<0.001$
Pairwise difference	$p<0.001$	$p<0.001$	$p=0.20$	
Black woodpecker, n	25	69	59	
CPR, median	0.12	0.23	0.23	$H=4.08$; $p=0.13$
Pairwise difference	–	–	–	
Three-toed woodpecker, n	33	175	237	
CPR, median	0.00	0.72	1.44	$H=30.7$; $p<0.001$
Pairwise difference	$p<0.001$	$p<0.001$	$p=0.30$	
GHW+WBW+LSW, n	4	26	39	
CPR, median	0.00	0.00	0.00	$H=8.67$; $p=0.013$
Pairwise difference	$p=0.033$	$p=0.045$	$p>0.99$	

CPRs of all cavities, of cavities of the most common woodpecker species, and of cavities of the group of less abundant woodpecker species (GHW, WBW and LSW) are presented. Test statistics (H) show the results of Kruskal–Wallis's test between management intensity groups with the respective p-values. In the case of a significant general difference, Bonferroni-corrected a posteriori pairwise differences (p-values) based on Dunn's test are shown

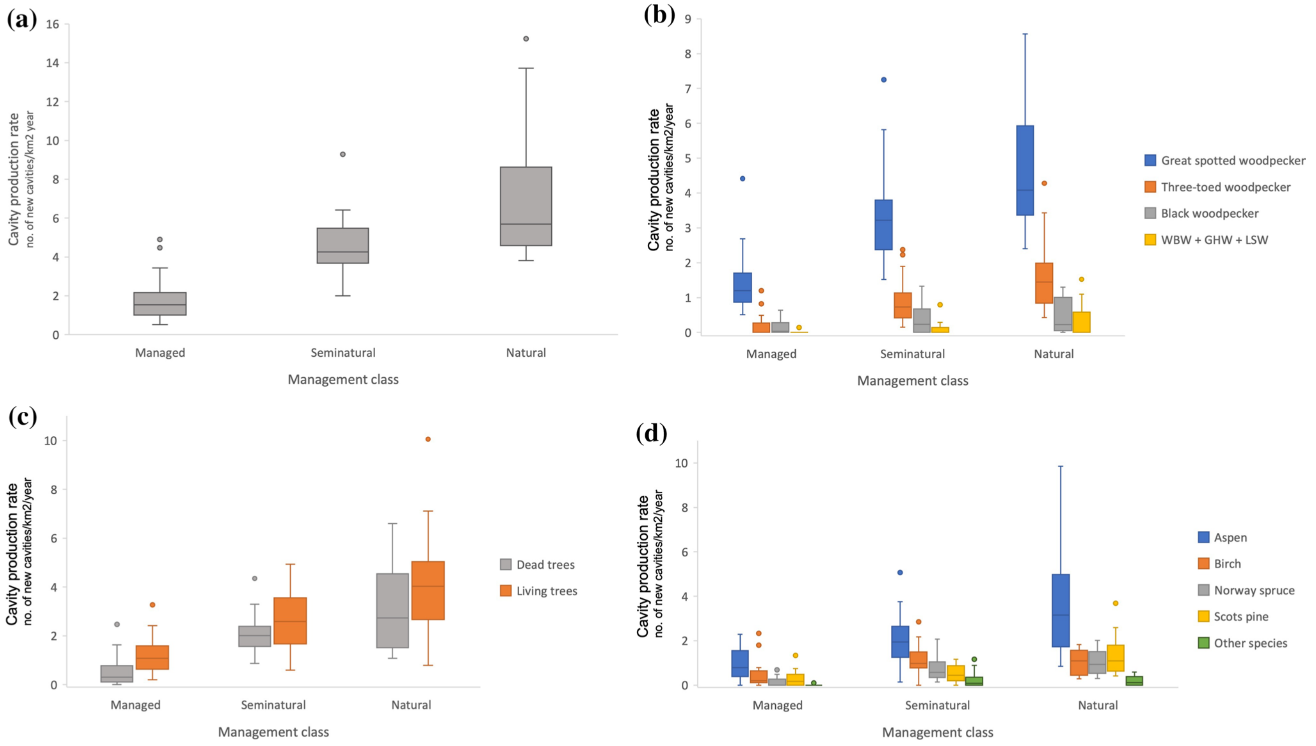

Fig. 1 Cavity production rates (CPR, no. of new cavities/km^2/year) of woodpecker species and of cavities in various types of trees in forest stands with separate management intensity class: **a** all woodpecker species; **b** separate woodpecker species (Great Spotted Woodpecker, Three-toed Woodpecker, Black Woodpecker, and a combined group of three less abundant woodpecker species WBW, GHW, LSW); **c** woodpecker cavities in dead and living trees; and **d** woodpecker cavities in separate tree species (aspen, birch, Norway spruce, Scots pine, and a combined group of six less abundant cavity tree species). Box & whisker-plots show the median, the interquartile range, minimum, maximum and the outliers. Outliers are values that are more than 1.5 times the distance of the interquartile range from the quartile 1 (below) or 3 (above)

Table 3 Cavity production rates (CPRs) of woodpecker cavities in the three management classes and in living and dead trees, in deciduous and coniferous trees, in most common cavity tree species, and in the group of less abundant tree species are presented

Management intensity class	Managed (M)	Seminatural (S)	Natural (N)	Test statistics
Pairwise comparison	M vs. N	S vs. M	N vs. S	
Living trees, n	200	475	528	
CPR, median	1.08	2.54	3.36	$H=22.1$; $p<0.001$
Pairwise difference	$p<0.001$	$p=0.02$	$p=0.54$	
Dead trees, n	103	422	510	
CPR, median	0.31	2.16	2.88	$H=33.4$; $p<0.001$
Pairwise difference	$p<0.001$	$p<0.001$	$p=0.80$	
Deciduous trees, n	225	635	700	
CPR, median	1.26	2.99	3.97	$\mathrm{H}=31.1$; $\mathrm{p}<0.001$
Pairwise difference	$p<0.001$	$p<0.001$	$p=0.84$	
Coniferous trees, n	78	262	338	
CPR, median	0.30	1.33	2.02	$H=28.8$; $p<0.001$
Pairwise difference	$p<0.001$	$p=0.001$	$p=0.19$	
Aspen, n	145	384	527	
CPR, median	0.78	1.94	3.15	$\mathrm{H}=23.0$; $\mathrm{p}<0.001$
Pairwise difference	$p<0.001$	$p=0.03$	$p=0.31$	
Birch, n	84	220	174	
CPR, median	0.19	0.98	1.10	$H=18.4$; $p<0.001$
Pairwise difference	$p=0.003$	$p<0.001$	$p>0.99$	
Scots pine, n	49	100	188	
CPR, median	0.17	0.46	1.09	$H=19.6$; $p<0.001$
Pairwise difference	$p<0.001$	$p=0.31$	$p=0.009$	
Norway spruce, n	29	155	152	
CPR, median	0.00	0.58	0.93	$H=28.2$; $p<0.001$
Pairwise difference	$p<0.001$	$p<0.001$	$p=0.88$	
Other tree species, n	4	53	29	
CPR, median	0.00	0.09	0.12	$H=11.6$; $p=0.003$
Pairwise difference	$p=0.02$	$p=0.01$	$p>0.99$	

Test statistics (H) show the results of Kruskal–Wallis's test between management intensity groups with the respective p-values. In the case of a significant general difference, Bonferroni-corrected a posteriori pairwise differences (p-values) based on Dunn's test are shown

were also more common cavity trees (94%) than conifers (Fig. 2b). Birch and grey alder were the most common cavity trees for tits. For both these tree species, the CPRs were smaller in managed forest stands compared with those in natural and seminatural stands, which did not differ from each other (Table 4; Fig. 2c).

Differences and similarities between forest stand classes based on cavity production rates

We used the linear discriminant analysis (LDA) to study the differences and similarities in the three forest stand classes with different management intensity in relation to the cavity production rates (CPRs). Two models were applied with the data sets of CPRs of a) separate woodpecker species (GSW, TTW, BW, and a combined group of three less abundant woodpecker species) and b) woodpecker cavities in separate tree species (aspen, birch, Scots pine, and a combined group of six less abundant cavity tree species) (Fig. 3).

In (a), the first discriminant function explained 96.8% of total variance (Wilks' lambda test $p<0.001$) and the second function 3.2% ($p=0.51$) with the CPRs of GSW and TTW (positive, first function) being the most important discriminant factors between the groups (Fig. 3a). The model classified correctly 71.4% of all data cases, the respective percentages within classes being in managed 86.4%, in seminatural 76.2%, and in natural stands 38.5%.

In (b), the first discriminant function explained 77.5% of total variance (Wilks' lambda test $p<0.001$) and the second function 22.5% ($p=0.03$) with the CPRs of birch and Norway spruce (positive, first function) and Scots pine (negative, second function) being the most important discriminant factors between the groups (Fig. 3b). The model classified correctly 73.2% of all data cases, the respective

Table 4 Cavity production rates (CPRs) of tit cavities in forest stands with different forest management intensity

Management intensity class	Managed (M)	Seminatural (S)	Natural (N)	Test statistics
Pairwise comparison	M vs. N	S vs. M	N vs. S	
Tit cavities, n	60	130	139	
CPR, median	0.33	0.70	0.92	$H = 29.8$; $p < 0.001$
Pairwise difference	$p < 0.001$	$p < 0.001$	$p = 0.26$	
Dead trees, n	58	128	137	
CPR, median	0.32	0.67	0.86	$H = 29.5$; $p < 0.001$
Pairwise difference	$p < 0.001$	$p < 0.001$	$p = 0.25$	
Deciduous trees, n	56	128	126	
CPR, median	0.30	0.67	0.91	$H = 31.4$; $p < 0.001$
Pairwise difference	$p < 0.001$	$p < 0.001$	$p = 0.26$	
Birch, n	45	88	87	
CPR, median	0.23	0.43	0.63	$H = 19.3$; $p < 0.001$
Pairwise difference	$p < 0.001$	$p = 0.002$	$p > 0.99$	
Grey alder, n	10	32	39	
CPR, median	0.0	0.14	0.29	$H = 23.7$; $p < 0.001$
Pairwise difference	$p < 0.001$	$p = 0.004$	$p = 0.20$	

CPRs of all cavities, cavities in dead trees and in deciduous trees as well as in birches and in grey alders are presented. Test statistics (*H*) show the results of Kruskal–Wallis's test between management intensity groups with the respective *p*-values. In the case of a significant general difference, Bonferroni-corrected a posteriori pairwise differences (*p*-values) based on Dunn's test are shown

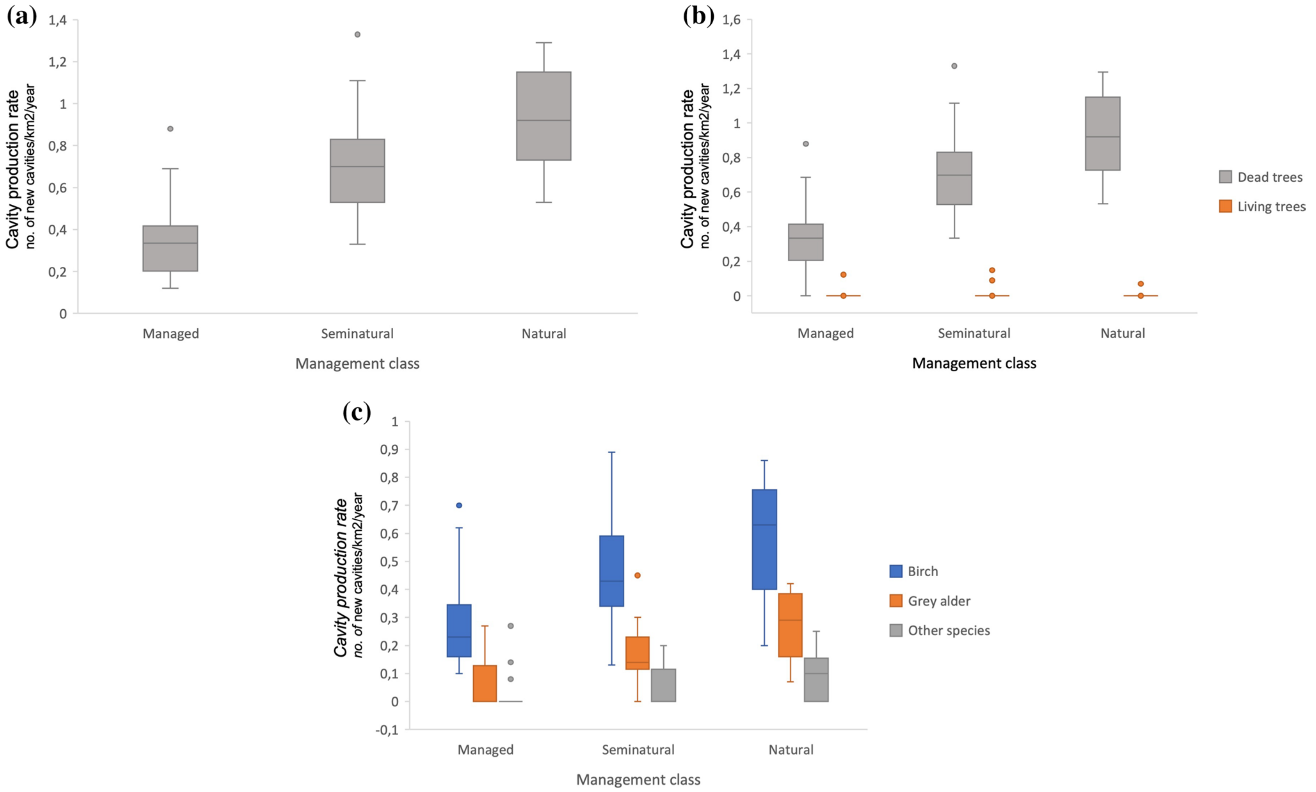

Fig. 2 Cavity production rates (CPR, no. of new cavities/km^2/year) of tits and of cavities in various types of trees in forest stands with different management intensity: **a** all tit species; **b** tit cavities in dead and living trees; and **c** tit cavities in separate tree species (birch, grey alder, and a combined group of five less abundant cavity tree species). Box & Whisker -plots show the median, the interquartile range, minimum, maximum and the outliers. Outliers are values that are more than 1.5 times the distance of the interquartile range from the quartile 1 (below) or 3 (above)

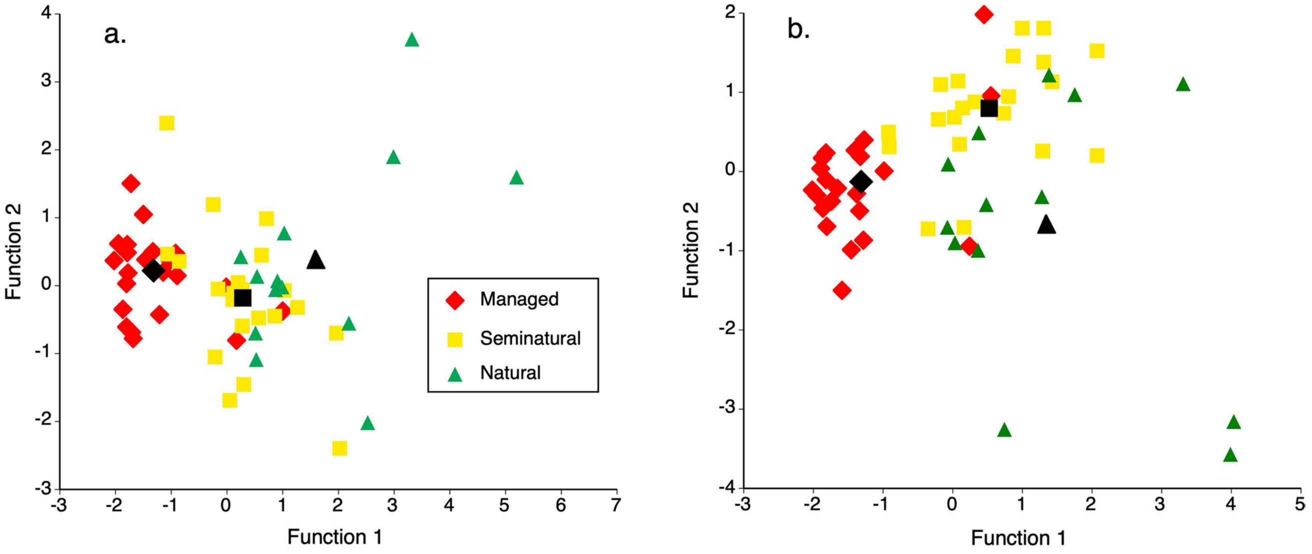

Fig. 3 Results of the linear discriminant analysis (LDA) of the three forest stand classes with different management intensity in relation to the cavity production rates (CPRs, no. of new cavities/km^2/year) of **a** separate woodpecker species (Great Spotted Woodpecker, Three-toed Woodpecker, Black Woodpecker, and a combined group of three less abundant woodpecker species) and **b** woodpecker cavities in separate tree species (aspen, birch, Scots pine, and a combined group of six less abundant cavity tree species). Forest stand classes and group centroids are shown with different symbols explained in panels. The group centroids are shown with the correspondingly shaped black symbol

percentages within classes being in managed 86.4%, in seminatural 81%, and in natural stands 38.5%.

As seen also from Fig. 3, the managed stand class differed from the other two classes. The classes of seminatural and natural stands overlapped in relation to the CPRs of both woodpecker and cavity tree species. In both cases (a) and (b), there was relatively large variation in the natural stand class, and it was difficult to classify its cases properly.

Bivariate correlations of cavity production rates in total data and within forest stand groups

We studied four cases of bivariate correlations of CPRs and focussed on the comparison of the total correlation and correlations within the three forest stand groups (Table 5). There were significant positive correlations in the CPRs of cavities in total data (n = 56) in all four cases: between all woodpecker- and tit-made cavities ($r_s = 0.77$, $p < 0.001$; Fig. 4a; Table 5), between woodpecker cavities in dead

Table 5 Comparisons of total and within group correlations of cavity production rates (CPRs)

Management intensity class	Total	Managed	Seminatural	Natural	
No. of forest stands	56	22	21	13	
Correlations of CPRs	Test statistics				Within groups, mean
All WP vs. all tit cavities	$r_s = 0.77$, $p < 0.001$	$r_s = 0.63$, $p = 0.002$	$r_s = 0.40$, $p = 0.07$	$r_s = 0.54$, $p = 0.06$	$r_s = 0.52$
Dead vs. living WP cavity trees	$r_s = 0.53$, $p < 0.001$	$r_s = -0.03$, $p = 0.88$	$r_s = 0.10$, $p = 0.65$	$r_s = 0.29$, $p = 0.34$	$r_s = 0.12$
GSW vs. other WP cavities	$r_s = 0.66$, $p < 0.001$	$r_s = 0.69$, $p < 0.001$	$r_s = -0.21$, $p = 0.37$	$r_s = 0.71$, $p = 0.07$	$r_s = 0.40$
Aspen vs. other WP cavity trees	$r_s = 0.53$, $p < 0.001$	$r_s = -0.15$, $p = 0.51$	$r_s = 0.28$, $p = 0.23$	$r_s = 0.36$, $p = 0.23$	$r_s = 0.16$
All cases, mean	$r_s = 0.62$	$r_s = 0.29$	$r_s = 0.14$	$r_s = 0.48$	$r_s = 0.30$
All cases, range	0.53–0.77	− 0.15–0.69	− 0.21–0.40	0.29–0.71	

Four cases of pairwise correlation results are presented (WP = woodpecker). Test statistics show the values of Spearman's rank order correlation coefficients (r_s) and the respective *p*-values of total correlations and within group correlations in the three forest stand classes. Mean values for within correlations in each case are also presented, as well as the respective mean values and ranges of all cases. Note the different correlation patterns observed in various cases, the large variation of correlation coefficient values in within group cases and the general difference in correlation coefficient values between the total correlation and within group correlations

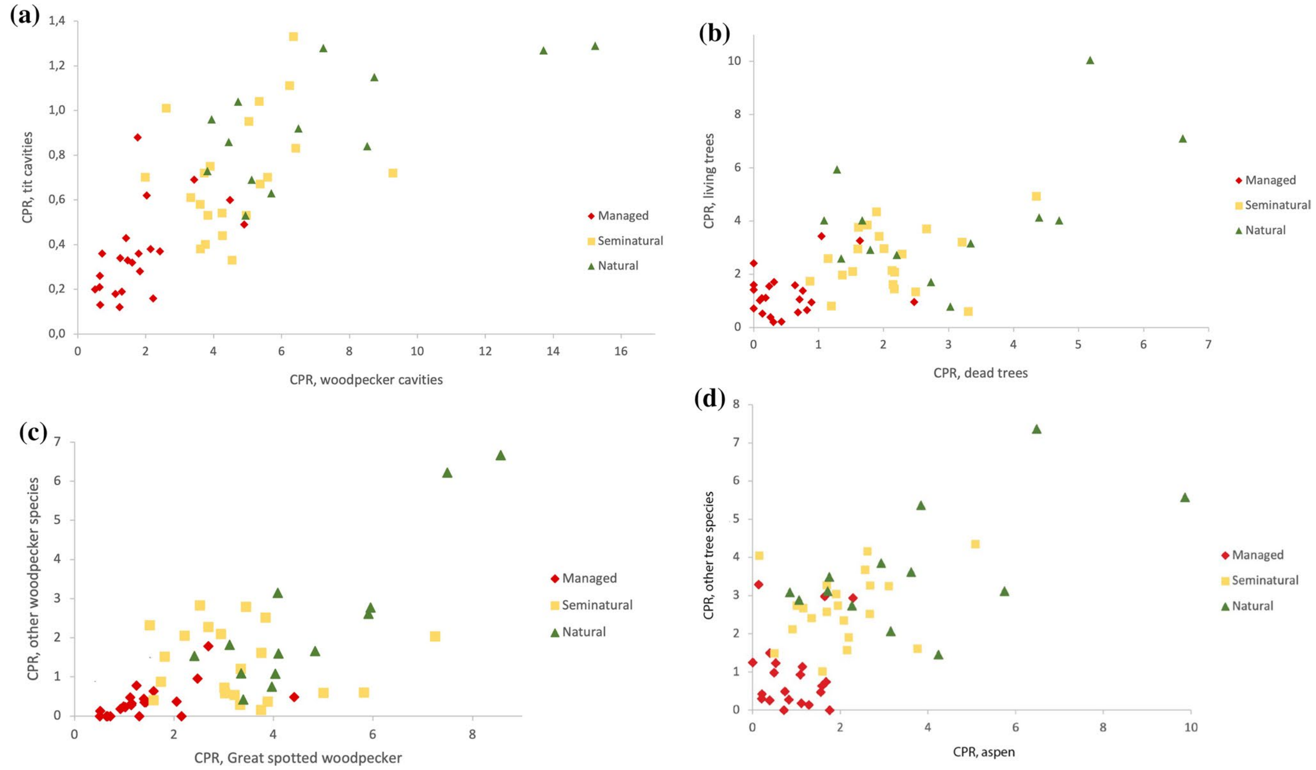

Fig. 4 Bivariate correlations between cavity production rates (CPRs, no. of new cavities/km^2/year) of: **a** woodpecker and tit cavities; **b** dead and living cavity trees of woodpeckers; **c** cavities of the Great Spotted Woodpecker and other woodpecker species; and **d** cavities in aspen and in other cavity tree species. Forest stands with different management intensity are shown in different symbols explained in each panel

and in living trees ($r_s = 0.53$, $p < 0.001$; Fig. 4b; Table 5), between cavities made by GSW and those by other woodpecker species ($r_s = 0.66$, $p < 0.001$; Fig. 4c; Table 5), and between woodpecker cavities in aspen and in other tree species ($r_s = 0.53$, $p < 0.001$; Fig. 4d; Table 5).

While the pattern of total correlations was quite coherent, there was much variation in the respective patterns of correlations within forest stands, both within and between the various cases (Table 5; Figs. 4a–d). Generally, the correlations within forest stands were smaller (mean $r_s = 0.30$, only two significant ($p < 0.05$) of all 12 cases) than the respective values in the total data (mean $r_s = 0.62$, all cases significant).

Table 6 Cavity tree sizes (DBH) of black woodpecker, great spotted woodpecker and tit species in forest stands with different management intensity

Management intensity class	DBH (cm), mean ± SD (n)			Test statistics
	Managed (M)	Seminatural (S)	Natural (N)	
Black woodpecker	55.6 ± 9.0 (25)	53.2 ± 10.3 (71)	55.1 ± 9.3 (57)	$F = 0.855$; $p = 0.43$
Pairwise difference	–	–	–	
Great spotted woodpecker	39.8 ± 7.4 (241)	37.6 ± 7.3 (627)	38.8 ± 7.4 (703)	$F = 9.10$; $p < 0.001$
Pairwise difference	M vs. N	S vs. M	N vs. S	
	$p = 0.15$	$p < 0.001$	$p = 0.009$	
Tit species	22.0 ± 5.6 (60)	21.2 ± 5.1 (130)	22.4 ± 6.4 (139)	$F = 1.45$; $p = 0.24$
Pairwise difference	–	–	–	

Mean values ± standard deviation (SD) in each group with sample size in brackets are presented. Test statistics (F) show the results of one-way AOV between the three groups with the respective p-values. In the case of a significant general tree size difference, a posteriori pairwise differences (p-values) based on Tukey test are shown

Cavity tree size

There were no differences in cavity tree size (DBH) in BW or in tit cavities between stands with different forest management (Table 6). However, GSW cavities were in smaller trees in seminatural stands compared with those of natural and managed stands, which did not differ from each other in cavity tree size (Table 6).

Discussion

The main finding of our study was that the cavity production rate (CPR) depended on the intensity of forest management in mature spruce-dominated forests (study question 1). This pattern was evident for cavities made by woodpecker species and cavities made by tit species. The greatest difference in CPR, three and fourfold, was detected between natural and managed forest stands, but also the semi-natural stands maintained higher cavity production than managed forests. This suggests that cavity production recovers in a relatively short time after the management intensity is lowered.

Generally, the CPRs of separate cavity-producer species and species groups were positively correlated and followed similar trends across the three forest management intensity classes (study questions 2 and 3). This indicates that management intensity affects similarly most cavity-producers. The correlations were mostly stronger between than within different management intensity classes. Thus, possibly similar general differences in structural characteristics of forests between management intensity classes were important for most cavity-making species. However, based on the results of the discriminant analysis, the natural forest stands showed much more variation in CPRs of separate cavity-making bird species and cavity tree species compared with seminatural and especially managed forest stands, which were quite similar to each other.

The higher production of cavities in natural forests was expected and is supported by results from earlier studies that have suggested that old and natural forests—e.g. in comparison to younger or intensively managed forests—maintain structural characteristics that appear more suitable for cavity-making (Remm and Lõhmus 2011; Andersson et al. 2018) or for cavity-making species in general in boreal forests (Angelstam and Mikusiński 1994). These characteristics likely include the amount of dead wood, the number of large trees, the proportion of deciduous trees, and spatial heterogeneity with small openings. Compared to previous studies that mostly document only the total cavity amounts or densities, our study can reveal the roles of separate cavity-makers and tree-level characteristics when explaining the differences in cavity patterns between natural and managed forests in our study sites.

A few issues seem to be especially noteworthy in our results when explaining the major findings: (1) the key role of the Great Spotted Woodpecker as the main cavity producer in all management classes, (2) the key role of aspen as the most important cavity tree species for woodpeckers in all management classes, and (3) the importance of damaged, weakened, and dead trees as well as the size variation of the cavity trees for woodpeckers and tits. We discuss these aspects in more detail below as they all are connected to the management implications of our main findings.

The Great Spotted Woodpecker is the key cavity-maker

The Great Spotted Woodpecker (GSW) was the dominant cavity-maker in all forest management intensity classes and produced 72–78% of all woodpecker cavities in separate forest management intensity classes. The GSW is clearly the key species in maintaining cavity availability in the mature moist spruce-dominated and mixed forests.

GSW is the most generalist Eurasian woodpecker species and flexible in its habitat needs, foraging behaviour, diet, and cavity tree selection, and the most abundant woodpecker species in Eurasian boreal forests (Pynnönen 1939; Glutz von Blotzheim and Bauer 1980; Cramp 1985; Glue and Boswell 1994; Michalek and Miettinen 2003). The major role of the GSW in cavity production can probably be attributed to its overall abundance but also to its ability to use widely different types of trees as cavity-trees. GSW is a strong excavator, and it can make its cavity in healthy, weakened, or dead trees, including coniferous and deciduous trees (Michalek and Miettinen 2003; Hebda et al. 2017).

The CPRs of GSW were significantly lower in our managed forest stands compared with seminatural and natural stands, and the CPRs in natural stands were also higher than in seminatural stands. This pattern may at first glance seem somewhat unclear as GSW can use also living trees for its cavities, and such trees should be abundantly available also in managed forests. However, also GSW uses often weakened, but living trees and injured and dead tree spots in otherwise healthy trees for cavity excavation (Glue and Boswell 1994; Kosiński and Winiecki 2004; Pasinelli 2007; Smith 2007; Fetisov 2017; Stański et al. 2020), which was also commonly observed in our study plots. In addition to dead trees, such tree types may not be common in intensively managed forests. However, based on our field experience, it is usually difficult to estimate the numbers of trees suitable or unsuitable for GSW cavities in various types of boreal forests (at least in mature age-class) and estimate if the availability of suitable cavity trees is a limiting factor for the GSW.

For the GSW, other aspects besides nest tree availability can be important in its breeding habitats. The abundance of edible insects for the GSW is possibly higher in more heterogenous natural forests with large trees and with more suitable microhabitats for different insect species and with more individuals compared with managed forests (Bouget and Duelli 2004; Fayt 2004; Vehviläinen et al. 2007; Stokland et al. 2012; Rappa et al. 2020). Thus, the high CPRs of GSW in natural forests compared with managed ones can at least partly be explained also by the better availability of food resources in natural forests, which allows for larger densities and higher CPRs of GSW territories in these forests.

Another aspect also indicates that food resources have a greater impact than the availability of suitable cavity trees on the observed CPR-values of GSW. GSW populations are known for their relatively large fluctuations in population numbers, especially in boreal forests (Glutz von Blotzheim and Bauer 1980; Cramp 1985; Michalek and Miettinen 2003). These fluctuations are driven by variations in cone crops of the two major coniferous tree species, the Scots pine and especially Norway spruce (Lindén et al. 2011). Also in our study plots, high breeding density years of GSW population were observed after good cone crop years. In the peak years, the annual CPR values were sometimes several times higher than the median values we observed. These unusually high annual CPR values were observed in all forest management intensity classes, but the relative effect of good seed crop years on annual CPR values appeared to be smaller in natural forest stands compared with other forest management intensity classes (Pakkala unpublished data). The observed pattern indicates that food resources have important effect on CPRs of the GSW, and it also suggests that the availability of suitable cavity trees is not a limiting factor for GSW at least at average population density levels in our study area. The relatively small difference observed in peak CPRs in natural areas compared with their typically (high) median CPRs may indicate that at least in some of these areas the densities of GWSs were already often near the “saturation” level, and due to, e.g. the territorial system, there were not so many vacant spaces for extra territories with their nest cavity trees.

The role of GSW as a key cavity maker in boreal forests is facilitated also by its wide habitat spectre. Based on our unpublished records from the study area of 170 km^2, 81% of all detected ca. 7200 woodpecker nest cavities covering all forest types and age-classes was excavated by GSW during the study period of 37 years (Pakkala et al. unpublished data). Moreover, the persistence times of GSW cavities, together with BW cavities, are generally much longer compared with cavities of tits and other woodpecker species (Meyer and Meyer 2001; Günther and Hellmann 2005; Wesołowski 2011; Pakkala et al. 2018a, 2019a, 2022; Hardenbol et al. 2019). Thus, GSW cavities are numerically the most important nest cavities for a variety of cavity-associated species in boreal forests. Consequently, the continuous availability of GSW cavities in reasonable densities should be a prime target in forest management options that aim to maintain cavity availability.

Aspen is the key cavity tree species for woodpeckers in moist spruce-dominated mature forests

In our study, aspen was the most common cavity tree species of woodpeckers; the percentages of aspen of total CPRs were 45–55% in forest stands with different management intensity. Aspen was the dominant cavity tree species in GSW, BW and GHW, but for other cavity-making species the most common cavity trees were birch (LSW, WBW, tits) or Norway spruce (TTW).

Aspen (*Populus* spp.) is known to be the key cavity tree genus for woodpeckers in boreal forests [see reviews of Remm and Lõhmus (2011) and Wesołowski and Martin (2018)]. For example, Martin et al. (2004) found that over 90% of the cavities was excavated in aspen while aspen made up only 10–15% of trees in the forest landscape. Moreover, Andersson et al. (2018) detected that aspen had the highest probability of containing excavated cavities among the four common tree species they studied (aspen, birch, Norway spruce and Scots pine) both in managed and unmanaged boreal forests.

Aspen trees have structural features that make them particularly suitable for cavity trees: the wood material is relatively soft for cavity excavation while the outer layer of the tree is rigid enough to sustain and protect the cavity (e.g. Short 1979; Jackson and Jackson 2004; Losin et al. 2006; Lorenz et al. 2015). Furthermore, saproxylic fungi, especially the aspen bracket *Phellinus tremulae*, modify further the inner parts of the tree trunk more suitable for woodpecker cavities in aspen (Jackson and Jackson 2004; Losin et al. 2006; Hart and Hart 2001; Blanc and Martin 2012).

The importance of aspen as a cavity tree is mediated especially by GSW and BW, which are the most important species making middle-size (GSW; see chapter above) and large cavities (BW; Johnsson et al. 1993; Pouttu 1985; Rolstad et al. 2000) in Eurasian boreal forests. The maintenance of aspen trees as admixtures in managed forests should thus be one of the key management options to facilitate availability of suitable cavity trees.

Finally, we note that the role of aspen as a cavity tree is probably most pronounced in the moist mature spruce-dominated forests that we studied. In other prevailing forest site types in boreal Fennoscandia where dominant trees are, e.g. pines or birches, we do not expect to see similar patterns because aspens are naturally less common in these forest types. Importantly, such forests cover large tracts in Fennoscandia. Among all detected woodpecker cavities in mature pine forests in our 170 km^2 study area, cavities in aspen made up only 8% while cavities in Scots pine made up 83%.

Respectively, in mature peatland forests, the percentage of woodpecker cavities in aspen was 6% and the most common cavity tree was birch (44%; Pakkala et al. unpublished data). However, more studies are needed to provide comparable cavity data from other boreal forest regions and various forest site types with different tree species composition.

The importance of weakened and dead trees for cavity-making bird species

We detected more woodpecker cavities in living than in dead trees, whereas tits excavated their cavities predominantly in dead trees. The effect of the tree condition for woodpecker cavities is, however, not that straightforward. The four less common woodpecker species (TTW, GHW, WBW and LSW) excavated their cavities mostly in dead or dying trees (see also Pakkala et al. 2018c, 2019b, 2022). Even the strongest excavators, GSW and BW, commonly use weakened and injured, but still living trees (GSW: see above; BW: Rolstad et al. 2000; Zahner et al. 2012), in our study area typically aspens and Scots pines. Thus, the decaying and dead trees are important as nest trees for the total cavity-excavating species group, and presumably their relative significance increases with decreasing cavity excavating capacity of the species.

The weakest excavators, LSW and tits, are highly dependent on the availability of relatively small dead and softened trees, in boreal forests especially birches and alders, for their cavity trees (Cramp 1985; Cramp and Perrins 1993; Vatka et al. 2014; Pakkala et al. 2019b). However, tits, notably CT, and to a lesser extent WT, can also use old tit and woodpecker cavities, other types of natural cavities, and nest-boxes for breeding (Orell and Ojanen 1983; Ojanen and Orell 1985; Cramp and Perrins 1993; Pakkala unpublished data). Major declines have been detected in breeding WT and CT populations in Finland during the last decades although both species are still relatively abundant (Fraixedas et al. 2015; Virkkala et al. 2020). Based on a long-term WT study in northern Finland, Kumpula et al. (2023) showed that the decline observed also in their study was associated with the forest management activities (clearcut and thinning) within and around the study area, and they suggested that a major reason for the decline was the shortage of suitable cavity trees, particularly dead birches, for the WT in managed forest landscapes.

The importance of dead and decaying trees for cavity-making species is, however, not restricted only to their role as nest places. Dead trees are important resources for many invertebrates (e.g. Martikainen et al. 1999; Stokland et al. 2012) that, in turn, are main forage items for several woodpecker and tit species (Cramp 1985; Cramp and Perrins 1993). Since many cavity-making species are mostly non-migratory, it is expected that resources needed during harsh winter conditions can be crucial for them, so dead and decaying trees and the invertebrates they provide are probably an important resource especially for woodpeckers (Glutz von Blotzheim and Bauer 1980; Cramp 1985; Cramp and Perrins 1993).

Cavity tree sizes in different types of forests

We did not detect differences in sizes of cavity trees with big (BW) or small (tit) cavities between forest stands with different management intensity. The cavity trees with medium-sized (GSW) cavities were slightly smaller in seminatural stands compared with natural and managed ones, but this observed difference, although statistically significant because of large sample sizes, seems not to be ecologically important. We did not analyse the various factors (e.g. cavity tree species and condition), which have effects on the cavity tree size, but rather wanted to compare the general patterns in cavity tree sizes within the three main cavity size classes between natural, seminatural and managed forest stands. There was a slight (but insignificant) difference in CPRs of big (BW) cavities; the CPRs were larger in natural and seminatural stands compared with managed ones. In CPRs of small (tit) and medium-sized (GSW) cavities the CPRs were clearly smaller in managed forest stands compared with seminatural and natural stands, which did not differ from each other.

Our results of the observed cavity tree sizes indicate that there are assumingly strong species-specific preferences to search for trees optimal in size to excavate a suitable and if possible, safe cavity [see Winkler and Christie (2002), Wesołowski and Martin (2018)], independent of the forest management intensity and densities (or CPRs) of the cavity-making species. However, we did not have data on the availability of suitable cavity trees of various sizes in forests with different management intensity. Basile et al. (2020) detected that the probability of woodpeckers selecting cavity trees did not depend on individual tree diameter, but rather the deviation from the mean DBH of the respective forest stand. Woodpeckers seemed to prefer trees that were about 15–20 cm larger than the mean stand DBH (Basile et al. 2020), and Gutzat and Dormann (2018) observed a similar pattern in the nest site selection of secondary cavity nesting bird species in their meta-analysis of woodpecker-made and other natural cavities in boreal and temperate forests. These results stress the importance of variability in the potential cavity tree size; for example, in managed forest stands a situation with generally suitable mean DBH but with the lack of larger trees can lead to selection of suboptimal trees, to lowered densities of woodpecker species, and to lower CPRs in managed stands.

To sum, simultaneous availability of large, medium-sized and smaller trees is probably essential to sustain various cavity-making species and various other species using cavities of different size. However, more studies are needed about the importance of size distributions of potential cavity trees in various types of forests to implement this knowledge to practical forest management actions.

Remarks and prospects

While our study is based on a long-term and large dataset on species-level patterns, a few important aspects need remarks. First, it should be stressed that the availability of suitable cavity trees is only one factor that is important for the cavity-making bird species in boreal forests and thus also for the observed CPR values. As all cavity-making bird species in this study are resident (at least their core populations of old birds) and thus live year-round in or close to their breeding habitats, evidently the amount food is crucial for their persistence and, especially for the winter-time survival. However, important factors for cavity-making species in forest environments are often spatially correlated. For example, there are probably more good feeding microhabitats for cavity-making bird species in less managed forests, but these types of forests also usually have more weakened and dead trees suitable for cavity excavation. Spatiotemporal dynamics and territoriality of cavity-making species probably affect CPRs in many ways. Although we used CPR values as a sort of general quality measures for the various cavity-making bird species in forest stands with different management intensity, more studies are needed to estimate which components in forest environment are in fact critical for the species. Second, we did not analyse the characteristics of forest environments around the selected forest stands, areas likely to be important for the cavity-making birds inhabiting our study plots. In fact, typical breeding territories of several of our study species are larger than the forest stands in our data. Only GSW, WT and CT have generally smaller breeding territories than the median value of our study plots (Ekman 1979; Cramp 1985; Cramp and Perrins 1993; Michalek and Miettinen 1993; Karlsson 1994; Rolstad et al. 1995; Siffczyk et al. 2003). For the other cavity-making species, the sizes of study plots are approximately of the same size or slightly smaller (TTW, LSW; Cramp 1985; Höntsch 1996; Wiktander et al. 2001; Pakkala et al. 2002; Pechacek 2004; Pechacek and d'Oleire-Oltmanns 2004) or clearly smaller compared with their breeding territory sizes (BW, GHW, WBW; Cramp 1985; Tjernberg et al. 1993; Ahola 1995; Blume 1996; Rolstad et al. 2000; Campion et al. 2020; Pakkala et al. 2020). Outside the breeding season all above-mentioned species also use the surrounding forests. In the future studies, we urge for more of multiscale and spatial analyses that could reveal not only stand-level patterns but simultaneously also territory and landscape-level factors that are likely important for resident cavity-makers.

Finally, we faced challenges to assess the management intensity of forest stands, and this aspect requires more considerations in future studies to connect the cavity patterns to practical management operations. We classified forest stands into different management intensity classes mostly retrospectively, based on management history and age and including some subjectively assessed forest characteristics. The classification posed challenges due to long time periods, quite heterogeneous history in some of the study sites, and the lack of systematically archived documentation of the conducted forest management operations. The difficulty of properly defining the level of naturalness is common in forest ecology. There have been several attempts to define and measure naturalness or management intensity of forests that are comparable to our studied forest stands (e.g. Uotila et al. 2002; Schall and Ammer 2013; Gossner et al. 2014; Kunttu et al. 2015), but we still lack a widely applied method for this. In the future, we urge for better documentation of management history and intensity. Such data could be used to better address the effects of specific management operations and their timings on those structural properties that appeared to be important for cavity-birds in our results.

Conclusions and management implications

Our results show that bird-made tree cavity abundances depend on the intensity of forest management in spruce-dominated boreal forests. Above all, the intensive clear-cut based forestry with regular thinning affects the cavity production rate by reducing cavity production in mature forest phase only to about one-fourth of what the cavity production is in natural forests. In managed forests, trees are typically "healthier", which means that fewer weakened, injured and dead trees are available while such trees are commonly used for cavities. Also, forest management in our study region promotes coniferous trees that are less common as cavity trees compared with deciduous trees. Additionally, trees do not have a possibility to grow old and senesce due to short rotation periods in managed forests. Based on current observations, all these aspects are connected to cavity production rates in forests, which in turn is likely to have consequences to various forest species groups that are dependent on bird-made cavities.

However, the knowledge of detailed patterns of cavity dynamics and cavity production among separate cavity-making bird species and their host trees open new possibilities to facilitate cavities in managed forests. For example, the seminatural forests in our data set represent areas of recently lowered management intensity, and their cavity patterns appear to resemble respective patterns in natural forests in many aspects. This suggests that lowering the management intensity has a clear potential to improve cavity availability.

More specifically, three factors appear highly important. First, for the overall cavity availability, the role of the Great Spotted Woodpecker is of paramount importance. While the GSW appears quite flexible in its habitat and cavity tree use, we found evidence that also the GSW benefits from lowered management intensity. However, the mechanism for this is not entirely clear and it may be related more to food availability than to the availability of nest trees. Second, the deciduous tree admixture and especially the maintenance of larger aspen trees in spruce-dominated stands is highly beneficial for cavity-makers because the aspen appears to contribute largely to cavity production. Third, especially for the less common woodpecker species and the tit species that we studied, the availability of dead, weakened and injured deciduous trees (aspens and small- to medium-sized birches and alders) appears to be highly important. Promoting these three structural features in managed forests could contribute a major improvement for cavity-associated species. We anticipate that economic losses due to these modifications to forest management are likely to remain modest, and that there are good chances to address these aspects also in forests managed mainly for timber production.

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Authors' contributions All authors contributed to the study conception and design. Data collection and material preparation were performed by Timo Pakkala. Analyses were performed by Timo Pakkala and Anna Peltonen. The first draft of the manuscript was written by Jari Kouki and Timo Pakkala and all authors commented on the previous versions of the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials The datasets analysed during the current study are available from the author Timo Pakkala on reasonable request.

Declarations

Conflict of interest Authors declare no conflicts of interests or competing interests.

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