



# Tree cavity patterns and implications for forest management in boreal Europe: A review

Aleksi Nirhamo<sup>\*</sup> , Jari Kouki

School of Forest Sciences, University of Eastern Finland, Joensuu, Finland

## ARTICLE INFO

### Keywords:

Fennoscandia  
Forest management  
Retention forestry  
Tree hollow

## ABSTRACT

Tree cavities are a common structural feature in forests with high importance to many forest-dwelling species. Cavity formation is affected by tree characteristics, wood-decaying fungi and excavating birds. Furthermore, cavity occurrence may be affected by habitat modifications resulting from forest management. Here, we review studies from boreal Europe on cavity formation patterns. We explore what kind of trees (in terms of species and vitality) are excavated by birds. We also assess how cavity formation processes are affected by forest management by reviewing studies that have compared the densities of cavities and cavity-nesting birds in managed and unmanaged forests. In total, we reviewed empirical results from 22 studies from the period 1939–2024.

Based on the reviewed studies, excavators can be divided into three groups depending on the types of trees they excavate: those that favor aspen, ranging from healthy to dead trees (four woodpecker species, of which two also frequently excavate pines), those that favor low-vitality or dead broadleaved trees, mainly birch (tits and two woodpecker species), and one species, three-toed woodpecker, that favors dead spruces. Overall, aspen is the most frequently excavated tree, and the majority of cavities are in low-vitality or dead trees. The densities of cavities or cavity-nesting birds was 1.7–4 times higher in unmanaged forests compared to managed forests. A lower frequency of trees suitable for excavation in managed forests is the most likely explanation for the observed difference.

To improve cavity availability in managed forests, regeneration and thinning practices should be adjusted to ensure the occurrence of dead or low-vitality broadleaved trees. Increased rotation lengths and tree retention practices can further increase the amount of trees suitable for excavation in managed forests.

## 1. Introduction

Cavities in trees are diverse in their structure, formation, and dynamics. They provide sites for breeding and sheltering for many taxa and, thus, are important to forest biodiversity (Gibbons and Lindenmayer, 2002). Tree cavities are a characteristic ecological feature of forests globally (Remm and Lõhmus, 2011), and they have lately received increasing attention through the study of tree-related microhabitats (Larrieu et al., 2018). Cavities are often formed by consecutive impacts of abiotic factors, decomposing fungi and excavating animals (Cockle et al., 2012). Cavity formation typically starts with a wound or injury that exposes the wood beneath the bark. Then, heart-rot fungi may access the exposed wood and begin its decomposition (Basham, 1958). Decay by fungi may alone form cavities, but cavity formation can be accelerated by excavating birds. Wood becoming softer from decay enables cavity excavation by birds (Martin et al., 2004; Cockle et al.,

2012; Zahner et al., 2012), although the capacity of excavating harder wood varies by species (Hågvar et al., 1990).

Tree properties affect cavity occurrence. Cavities are more frequent in some tree species than in others (Altamirano et al., 2017; Blakely et al., 2008; Cadieux et al., 2023; Niringiyimana et al., 2022; Ruggera et al., 2016; Takashima et al., 2021; Zheng et al., 2009). This is related to variation among tree species in capacity for defense against wood-decaying fungi, and in propensity for obtaining wood-exposing injuries. Since the likelihood of obtaining injuries that expose wood, or colonization by fungi through other means, increases with tree age, the occurrence of cavities increases with tree age (Gibbons et al., 2000; Ranius et al., 2009) or size (Fan et al., 2003; Blakely et al., 2008; Zheng et al., 2009; Cockle et al., 2012; Altamirano et al., 2017; Ibarra et al., 2020; Takashima et al., 2021; Niringiyimana et al., 2022). Additionally, cavities are common in standing dead trees that are usually softened by fungal decay and are easier to excavate. At the tree scale, standing dead

<sup>\*</sup> Corresponding author.

E-mail address: [aleksi.nirhamo@uef.fi](mailto:aleksi.nirhamo@uef.fi) (A. Nirhamo).

trees bear more cavities than living trees, yet, at the stand scale, more cavities are typically found in living trees because of the relatively low numbers of standing dead trees (Fan et al., 2003; Martin et al., 2004; Zheng et al., 2009; Zawadzka et al., 2016; Andersson et al., 2018).

A large portion of forests are managed for timber production by maintaining tree vitality and harvesting trees before they reach senescence. This changes tree species compositions, reduces deadwood volume, and truncates tree age distributions (Kuuluvainen, 2002; Siitonen et al., 2000). These impacts are expected to reduce cavity formation given that cavities are more frequently formed in older or dead trees and to certain tree species (see above). Thus, cavity formation and cavity-associated taxa may be influenced by forest management (Gibbons and Lindenmayer, 2002; Martin et al., 2004; Politi et al., 2010; Walankiewicz et al., 2014). Identifying the key factors of cavity dynamics can facilitate the reconciliation of cavity dynamics and forest management (Martin et al., 2004; Blanc and Walters, 2008; Cockle et al., 2012; Altamirano et al., 2017).

Here, we review research on cavity patterns in boreal European forests. Even though the dynamics of the forests in this region are known quite well, cavity patterns and dynamics have received scarce attention. In particular, any impacts that forest management may have on cavity occurrence have received very limited attention so far. We address two major research questions:

1. What kinds of trees are excavated by birds? We focus on two aspects: tree species and tree vitality.
2. What are the differences in the occurrence of cavities in managed and unmanaged forests? For this, we reviewed studies that have measured cavity occurrences directly, and supplemented these studies with data of cavity-nesting birds in managed and unmanaged forests.

Knowledge on the kinds of trees used for excavation by birds is central for understanding cavity dynamics, since cavity formation by tree decay alone is rare in the boreal zone (Remm and Löhmus, 2011). Our review mainly deals with birds because the majority of studies have focused on them. However, to highlight the significance of tree cavities for forest biodiversity in general, we preface our review with an overview of cavity-associated taxa.

## 2. Methods

### 2.1. Scope and definitions

This review focuses on boreal Europe as defined by Ahti et al. (1968). Thus, boreal Europe includes the Nordic countries (except Denmark and Iceland), the Baltic countries, and large parts of western Russia. European boreal forests are dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). Forests also often have a broadleaved component, consisting mainly of birches (*Betula pendula* and *B. pubescens*), aspen (*Populus tremula*) and alders (*Alnus incana* and *A. glutinosa*). The hemiboreal zone is a transition zone between the boreal and temperate zones. The hemiboreal zone contains conifer-dominated forests, broadleaved-dominated forests (including a higher diversity of trees such as *Quercus*, *Fraxinus*, *Tilia*, *Acer*, *Ulmus*), and mixed forests.

Most studies on cavities and associated diversity in boreal Europe originates from Estonia, Finland, Sweden and Norway. The majority of forests in these countries are managed, with even-aged rotation forestry as the prevailing silvicultural method. A rotation cycle consists of clearcutting, regeneration via planting (typically spruce or pine), and 1–3 thinnings from below before the next clearcut. The rotation length is 60–120 years depending on site conditions and geographical location.

For this review, we define a tree cavity as a hollow space inside the stem (or large branches) of a tree, with an opening of at least 2 cm in diameter. The size restriction is mainly to exclude small cavities made by

invertebrates, such as saproxylic beetles. Such small cavities may host some taxa but there is very limited data on them. Most studies on tree cavities have used a similar minimum size criterion for cavities, since vertebrate animals are unable to enter cavities smaller than that. We consider both cavities excavated by birds and those formed fully by decay.

We aimed to compile a full list of cavity-nesting birds breeding in boreal Europe. Cavity nesters are here defined as species that breed mainly in cavities in the stems (or branches) of trees. Thus, cavity nesters may use other types of nests, but the majority of breeding occurs in tree cavities. To determine which bird species are present in boreal Europe, we used the lists of the bird fauna of Finland, Sweden and Norway from the BirdLife Data Zone (BirdLife International, 2024a; BirdLife International, 2024b; BirdLife International, 2024c). This source also lists some species with very small ranges within boreal Europe, as well as species that have previously bred in the region but are currently absent. To determine cavity nesters, we used the list of cavity-nesting birds in Van der Hoek et al. (2017) as a starting point, and scoured literature on bird breeding biology to ensure that species listed by them match the definition of a cavity nester given above. While doing this, we emphasized studies from the boreal zone, and thus the classification of the species may not match their breeding biology in other regions.

### 2.2. Literature selection

To answer the study questions stated in the introduction, we aimed to cover all peer-reviewed publications where the relevant data had been collected in boreal Europe as defined in Section 2.1, and that contained information of:

1. The distribution of cavities excavated by a given excavator species into various tree species. A minimum of 15 excavations by a given excavator species had to have been recorded. These studies had also often recorded the status of the excavated trees (i.e., living, dead, or some description of reduced vitality; weakened, dying, decaying, etc.).
2. Differences in cavity density or the density of cavity-nesting birds between managed and unmanaged forests. Regarding bird studies, we summed and compared the observed densities of cavity-nesting birds (as listed in Section 3, and including species nesting in other tree-related microhabitats) in the two types of forest. Here, “managed forests” refer to those that are actively being modified for the purposes of timber production. “Unmanaged forests” mostly refers to forests with no management operations for several decades and where stand age is now significantly over the typical maximum rotation length. Exceptions to this are two studies which compared managed forests to forests of similar age under natural succession (Nilsson, 1979; Pass et al., 2022), and one study which compared salvage-logged post-fire sites to unintervened post-fire sites (Žmihorski et al., 2019).

Our initial literature searches proved that strictly defined search strings were an ineffective method of capturing studies that are useful in this context. This was primarily due to a small number of relevant publications and variable terminology. Thus, we chose a more non-systematic approach and compiled the publications by browsing studies available in online databases and reference lists in the original articles. There were no restrictions for publication year. However, some older publications in regional journals may have gone unnoticed if they were not available online. For the discussion section, we explored literature more broadly. The discussion is mainly based on publications from boreal Europe, but also on publications from other regions when they add insights to the research in boreal Europe. In total, this review summarizes the results of 22 studies.

**Table 1**

The cavity-nesting birds of boreal Europe. The list includes species for which primary nesting sites are tree cavities. Includes also five species that nest mainly in tree-related microhabitats that resemble cavities (see text). Species capable of excavating cavities are marked in the “Exc.” column. Compiled from the bird fauna of Finland, Sweden and Norway as listed in the BirdLife Data Zone (BirdLife International, 2024a; BirdLife International, 2024b; BirdLife International, 2024c).

Family	Exc.	Species	Common name
<b>True cavity-nesters</b>			
Anatidae		<i>Bucephala clangula</i>	Common goldeneye
Anatidae		<i>Mergellus albellus</i>	Smew
Anatidae		<i>Mergus merganser</i>	Goosander
Apodidae		<i>Apus aptus</i>	Common swift
Columbidae		<i>Columba oenas</i>	Stock dove
Coraciidae		<i>Coracias garrulus</i>	European roller
Corvidae		<i>Corvus monedula</i>	Eurasian jackdaw
Muscicapidae		<i>Ficedula albicollis</i>	Collared flycatcher
Muscicapidae		<i>Ficedula hypoleuca</i>	Pied flycatcher
Muscicapidae		<i>Phoenicurus phoenicurus</i>	Common redstart
Paridae		<i>Cyanistes caeruleus</i>	Eurasian blue tit
Paridae		<i>Cyanistes cyaneus</i>	Azure tit
Paridae	x	<i>Lophophanes cristatus</i>	Crested tit
Paridae		<i>Parus major</i>	Great tit
Paridae		<i>Periparus ater</i>	Coal tit
Paridae	x	<i>Poecile cinctus</i>	Siberian tit
Paridae	x	<i>Poecile montanus</i>	Willow tit
Paridae	x	<i>Poecile palustris</i>	Marsh tit
Passeridae		<i>Passer domesticus</i>	House sparrow
Passeridae		<i>Passer montanus</i>	Eurasian tree sparrow
Picidae	x	<i>Dendrocopos leucotos</i>	White-backed woodpecker
Picidae	x	<i>Dendrocopos major</i>	Great spotted woodpecker
Picidae	x	<i>Dryobates minor</i>	Lesser spotted woodpecker
Picidae	x	<i>Dryocopus martius</i>	Black woodpecker
Picidae		<i>Jynx torquilla</i>	Eurasian wryneck
Picidae	x	<i>Leiopicus medius</i>	Middle spotted woodpecker
Picidae	x	<i>Picoides tridactylus</i>	Three-toed woodpecker
Picidae	x	<i>Picus canus</i>	Grey-headed woodpecker
Picidae	x	<i>Picus viridis</i>	European green woodpecker
Sittidae		<i>Sitta europaea</i>	Eurasian nuthatch
Strigidae		<i>Aegolius funereus</i>	Boreal owl
Strigidae		<i>Glaucidium passerinum</i>	Eurasian pygmy owl
Strigidae		<i>Strix aluco</i>	Tawny owl
Strigidae		<i>Surnia ulula</i>	Northern hawk owl
Sturnidae		<i>Sturnus vulgaris</i>	Common starling
Tytonidae		<i>Tyto alba</i>	Common barn owl
Upupidae		<i>Upupa epops</i>	Common hoopoe
<b>Species nesting in other tree-related microhabitats</b>			
Certhiidae		<i>Certhia familiaris</i>	Eurasian treecreeper
Muscicapidae		<i>Ficedula parva</i>	Red-breasted flycatcher
Muscicapidae		<i>Muscicapa striata</i>	Spotted flycatcher
Strigidae		<i>Strix nebulosa</i>	Great grey owl
Strigidae		<i>Strix uralensis</i>	Ural owl

### 3. Cavity-associated taxa in boreal Europe

Thirty-seven species of birds that are currently breeding or have previously bred in Finland, Sweden or Norway are cavity-nesters (Table 1). In addition, 5 species nest in other tree-related microhabitats, i.e., beneath loose bark, in vertical crevices in trees, or in chimney cavities of broken-top snags. Cavity-nesting birds account for 14 % of the breeding bird fauna of boreal Europe. The proportion of cavity nesters is higher among forest-dwelling species. For example, in Finland, 80 breeding bird species are classified as having forests as their primary habitat (in the Finnish Biodiversity Information Facility), and of them, 25 (31 %) are cavity nesters. Van der Hoek et al. (2017) classified 18 % of bird species globally as cavity nesters. Out of the 295 breeding bird species of boreal Europe, they classified 58 (20 %) as cavity nesters. Thus, the proportion of cavity nesters among avifauna seems to be similar in boreal Europe as it is globally. We used a stricter definition for

cavity nesters than Van der Hoek et al. (2017) which is why Table 1 includes fewer species.

Among mammals, the Siberian flying squirrel, pine marten (Fig. 1b) and hazel dormouse nest primarily in cavities. In addition, a number of mammals use cavities infrequently or facultatively. Red squirrels, bank voles and yellow-necked mice can climb trees, and thus they frequently enter cavities, perhaps in search of food, but nest there only rarely (Czeszczewik et al., 2008; Yatsiuk, 2024). Stoats and weasels may prey on cavity nests (Nilsson, 1984). Most species of dormice (Gliridae) are arboreal and nest in cavities frequently, but garden dormouse seems to do so only rarely (Bertolino and Montezemolo, 2007). Several bat species use cavities for sheltering and breeding, but seem to be loosely associated with cavities, since many of them also use, e.g., human-made structures (Lučan et al., 2024). Furthermore, species that roost in trees may also roost beneath loose bark or in cracks in trees (i.e., “other tree-related microhabitats” as in Table 1; Dietz et al., 2018).

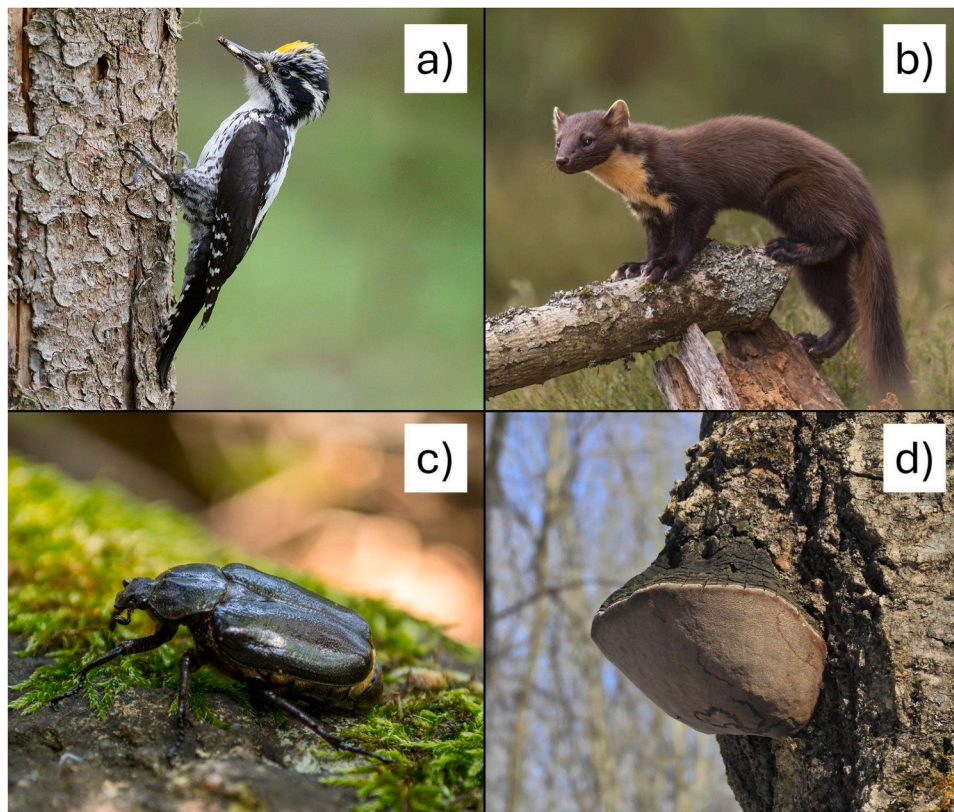
Many invertebrates are associated with tree cavities. They are mostly detritivorous or saproxylic species. Arthropods from 23 orders were found in the wood mould, i.e., organic matter accumulating on the bottoms of cavities, of 18 tree cavities in the USA (Park and Auerbach, 1954). Mites (Acarina) and springtails (Collembola) comprised most individuals, followed by beetles (Coleoptera) and flies and gnats (Diptera). The invertebrate community in wood mould has some resemblance to that in the soil. However, a study in hemiboreal Europe showed that the mite fauna in wood mould is distinct from that of soil and appears to include specialized species (Taylor and Ranius, 2014). Invertebrate communities of wood mould are mainly associated with old trees with large, long-lived cavities where wood mould has accumulated; in hemiboreal Europe, oak is a particularly favorable tree species for the occurrence of such cavities (Ranius et al., 2009; Ranius et al., 2009).

Beetles are the most extensively studied group of cavity-associated invertebrates. In a study in southern Sweden, 242 beetle species were trapped from 49 hollow trees representing four species (*Quercus*, *Tilia*, *Fraxinus*, *Acer*; (Milberg et al., 2014). Many of the beetle species in cavities are generalist saproxylic species, but the presence of several specialized species is also evident (Fig. 1c). Ranius and Jansson (2000) listed 30 saproxylic beetle species specialized to live in cavities in oaks. The specialized species are mainly associated with wood mould. Beetles within the cavities of broadleaved trees in the hemiboreal zone, especially oak, are relatively well-studied, but there are no studies concerning saproxylic beetles in tree cavities in more northern regions.

Many invertebrates are associated with the nests of vertebrates in tree cavities. These include ectoparasites of the nesters, species feeding on organic material accumulating in the nests (feathers, hair, carcasses of prey, excrement), and species that prey on other invertebrates in the nest. This group includes many taxa, but Diptera, Lepidoptera and Coleoptera have the highest numbers of individuals (Hanzelka et al., 2023). Hanzelka et al. (2023) identified 33 beetle species from 113 bird nests in cavities or nest boxes, and Ranius and Jansson (2000) reported 22 species found from hollow oaks to be associated with animal nests. There was little overlap in the species reported by these two studies. Cavity nests and open nests seem to be inhabited by partially different sets of invertebrate species (Hågvar, 1975).

Social insects may establish their nests inside tree cavities (Broughton et al., 2015). Minuscule tunnel-like cavities that are bored into wood by insects are outside of the definition of cavities used in this review. Nevertheless, it should be noted that many solitary bees and wasps nest in such cavities. About 5 % of all aculeate species in the Czech Republic (82 spp.) were considered cavity-nesters, and an additional 8 % of species (129 spp.) were considered facultative cavity-nesters (Bogusch and Horák, 2018).

When the opening is positioned so that rainfall enters and fills the cavity, and evaporation is low, cavities may become filled with water. Water-filled cavities host unique invertebrate assemblages, with flies and gnats (Diptera) in their larval stage as the most prominent



**Fig. 1.** Examples of cavity-associated species. a) Three-toed woodpecker excavates and forages from standing dead spruces. b) Pine marten is semi-arboreal, and nests in and seeks prey from cavities. c) Hermit beetle is a wood mould specialist, and aside from dispersal as adults, spends its life in hollow broadleaved trees, especially oak. d) *Phellinus tremulae* is the main cause of heart rot in aspen and a crucial enabler of cavity excavation. Photo credits: a) Timo Nirhamo, b) Caroline Legg, c) Oskar Gran, d) Rob Curtis. a) with permission from the author, b-d) under Creative Commons licenses.

component (Kitching, 2000; Petermann and Gossner, 2022). Water-filled cavities appear, however, to be rare in boreal Europe. We found no published research on invertebrates in water-filled cavities originating from boreal Europe.

## 4. Results

### 4.1. Trees excavated by birds

Excavators can be divided into three broad and somewhat overlapping groups based on their preferences for tree species (Table 2, Fig. 2). First, four species primarily excavate aspens: the great spotted, black, grey-headed and green woodpeckers. The first two of these also commonly excavate pines. All other excavators also excavate aspens at least occasionally. Second, the three-toed woodpecker mainly excavates spruces and is the only species to do so regularly. Third, the lesser spotted and white-backed woodpeckers and tits mainly excavate birches and alders. In a conifer-dominated southern boreal landscape, about half of woodpecker excavations were in aspen, and the rest were about evenly split between birch, pine and spruce (Pakkala et al., 2024). The great spotted woodpecker was the most prominent excavator, responsible of 66 % of excavations in managed forests, and 60 % in natural forests. The three-toed woodpecker was another fairly prominent excavator in natural forests (20 % of excavations; (Pakkala et al., 2024).

Not all studies reported whether excavated trees were dead or alive, and often low-vitality trees were not distinguished from healthy trees. Hågvar et al. (1990) did not present the precise distribution of excavations in tree vitality classes, but ranked seven woodpeckers based on the vitality of excavated trees, from highest to lowest vitality: black (mainly in healthy trees), green, great spotted, grey-headed (these three mainly in low-vitality trees), three-toed, white-backed, lesser spotted (these

three mainly in dead trees). Thus, from the three excavator groups delineated above, the second and third strongly favor dead or low-vitality trees (Table 2, Fig. 2). The species in the first group are capable of excavating healthy trees, but studies are inconclusive about their preferences between healthy, low-vitality and dead trees.

### 4.2. Densities of cavities and cavity-nesting birds in managed and unmanaged forests

We found only three studies in which the density of tree cavities was compared between managed and unmanaged forests in boreal Europe (Table 3). They found cavity density to be 2.1–3.7 times higher in unmanaged forests. In addition, ten studies gave information about assemblages of cavity-nesting birds in both managed and unmanaged forests in boreal Europe (Table 3). Population density was higher in unmanaged forests in all these studies, on average by a factor of 2.18 (Table 3). Species richness of cavity-nesting birds was, on average, about 30 % higher in unmanaged forests, and with no exception, the richness was either similar in unmanaged and managed forests or higher in unmanaged forests.

## 5. Discussion

### 5.1. Cavity formation

Bird species able to excavate cavities in boreal Europe appear to have clear preferences for the type of tree to excavate. The preferences are likely to be related to the strength of the excavators; standing dead alders and birches require the least strength, while healthy trees require the most (Hågvar et al., 1990). The black and great spotted woodpeckers are strong excavators and they often excavate healthy trees (Hågvar

**Table 2**

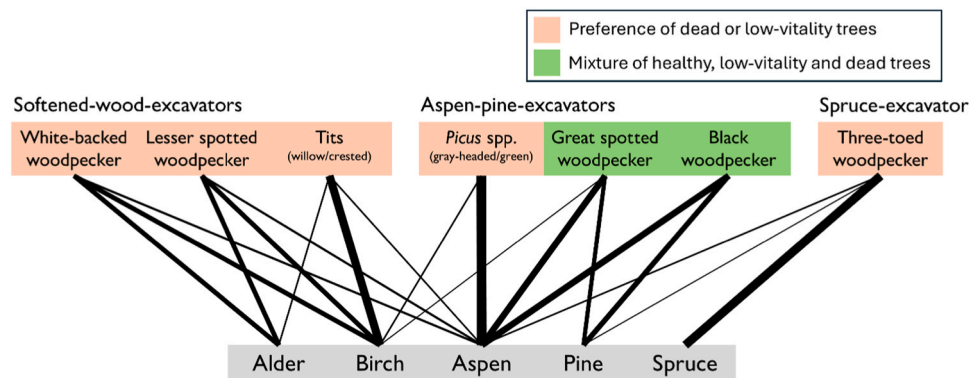
The distribution of cavity excavations or nestings by excavator species among tree species and tree vitality classes in studies from boreal Europe. ‘-’ means that no excavations or nestings in the tree species or vitality class in question were observed. ‘n/a’ means that the share of excavations or nestings in the tree species or vitality class in question was not reported precisely. Only cases with at least 15 observations are included here.

Excavator species	Number of observed excavations or nestings	Tree species						Tree vitality		
		Aspen	Birch	Alder	Pine	Spruce	Others	Healthy	Low vitality	Dead
<b>Great spotted woodpecker</b>										
(Pynnönen, 1939)	40	85 %	-	13 %	-	-	3 %	n/a	n/a	n/a
(Haapanen, 1965)	64	28 %	16 %	-	56 %	-	-	n/a	n/a	n/a
(Hågvar et al., 1990)	106	78 %	12 %	1 %	1 %	5 %	3 %	n/a	n/a	n/a
(Hansson, 1992)	66	68 %	12 %	-	3 %	8 %	9 %	n/a	n/a	n/a
<b>Black woodpecker</b>										
(Pynnönen, 1939)	18	89 %	6 %	-	6 %	-	-	n/a	n/a	n/a
(Haapanen, 1965)	18	11 %	-	-	89 %	-	-	n/a	n/a	n/a
(Hågvar et al., 1990)	102	66 %	2 %	-	32 %	-	-	n/a	n/a	n/a
(Johnsson et al., 1993)	173	74 %	n/a	n/a	13 %	n/a	n/a	88 %	n/a	12 %
(Rolstad et al., 2000)	457	60 %	4 %	1 %	33 %	3 %	-	78 %	n/a	22 %
<b>Grey-headed/green woodpecker</b>										
(Hågvar et al., 1990)	65	88 %	8 %	-	-	-	4 %	n/a	n/a	n/a
(Pakkala et al., 2020)	76	70 %	14 %	8 %	8 %	-	-	14 %	45 %	41 %
<b>Lesser spotted woodpecker</b>										
(Pynnönen, 1939)	19	11 %	47 %	42 %	-	-	-	n/a	n/a	n/a
(Hågvar et al., 1990)	50	40 %	34 %	26 %	-	-	-	n/a	n/a	n/a
(Pakkala et al., 2019)	106	18 %	37 %	43 %	-	-	2 %	-	21 %	79 %
<b>Three-toed woodpecker</b>										
(Pulliainen and Saari, 1989)	31	10 %	3 %	-	42 %	45 %	-	19 %	n/a	81 %
(Pakkala et al., 2018)	650	15 %	2 %	2 %	8 %	73 %	-	13 %	36 %	51 %
<b>White-backed woodpecker</b>										
(Krams, 1998)	31	19 %	26 %	48 %	-	-	6 %	32 %	16 %	52 %
<b>Tits</b>										
(Haapanen, 1965)	19	26 %	63 %	11 %	-	-	-	n/a	n/a	n/a
(Orell and Ojanen, 1983)	99	2 %	76 %	14 %	-	1 %	7 %	n/a	n/a	n/a
(Pakkala et al., 2024)	329	n/a	67 %	25 %	n/a	n/a	8 %	2 %	n/a	98 %
<b>All woodpeckers</b>										
(Pakkala et al., 2024)	2238	47 %	21 %	n/a	15 %	15 %	4 %	54 %	n/a	46 %

et al., 1990). Boreal European studies were inconclusive about their preference between healthy and low-vitality or dead trees. In coniferous forests in Poland, they excavated living and dead trees at a similar rate, although dead trees may have been slightly preferred (Hebda et al., 2017; Zawadzki, 2024). For the black woodpecker, it has been shown that nearly all excavated trees are affected by heart-rot fungi even if they have no superficial signs of reduced vitality (Zahner et al., 2012). It has also been suggested that the causative relation may be the opposite so that fungal colonization and the onset of heart rot is facilitated by bird excavations (Jusino et al., 2015). The preference of the great spotted and black woodpeckers between aspens and pines varied between studies. They probably excavate one or the other depending on which are better available; aspens in younger and mesic forests, and pines in older and xeric forests (Rolstad et al., 2000; Zawadzki, 2024). Also tree species

other than those in Table 2 and Fig. 2 are excavated, such as goat willow (*Salix caprea*) (Hågvar et al., 1990; Hansson, 1992; Pakkala et al., 2019). Goat willow assumably was very infrequent in the sites surveyed in various studies, and thus excavations were observed only rarely.

Excavators require a tree to be sufficiently large for cavity excavation. The requirements of different excavator species for tree size correlates roughly with the size of the excavator (Hågvar et al., 1990). Trees excavated by the smallest excavators, the lesser spotted woodpecker and tits, are most commonly 20–25 cm in diameter (Pakkala et al., 2019; Pakkala et al., 2024). The largest excavator, the black woodpecker, usually excavates trees that are larger than 40 cm (Hågvar et al., 1990; Rolstad et al., 2000; Pakkala et al., 2024; Zawadzki, 2024). Aspens and pines reached a size that is sufficient for cavity excavation by black woodpeckers at the age of 55 and 110 years, respectively (Rolstad et al.,



**Fig. 2.** Schematic connections between excavators and tree species. The thickness of the lines reflects how large a portion of the excavations by the given bird species is made in various tree species. Synthesised from data in Table 2.

**Table 3**

Cavity densities or population densities of cavity-nesting birds in managed and unmanaged forests. The columns 'Density difference' and 'Richness difference' indicate the multiplicative difference between unmanaged and managed forests, i.e., how many times higher density or richness was in unmanaged forests than in managed forests. Characterisation of forests is based on descriptions provided by the authors of the cited papers.

Sub-zone	Characterisation of managed forest	Characterisation of unmanaged forest	Density difference	Richness difference	Citation
<b>Cavity density</b>					
South boreal	Clearcut and planted, spruce-pine-dominated	Unmanaged for >70 years, spruce-pine-dominated	3.66		(Pakkala et al., 2024)
South boreal	Clearcut and planted, spruce-pine-dominated	Unmanaged for several decades, spruce-pine-dominated	2.18		(Andersson et al., 2018)
Hemiboreal	60–95 years old, thinned, mixed stands	Old-growth forests, mixed stands	2.10*		(Remm et al., 2008)
<b>Population density and species richness of cavity-nesting birds</b>					
Hemiboreal	30–70 years old, planted, spruce-dominated	>90 years old, unmanaged for at least 20 years, spruce-broadleaved dominated	3.94	1.58	(Pass et al., 2022)
Hemiboreal	80–100 years old, planted and thinned, spruce-dominated	30–120 years old, natural succession, broadleaved-dominated	2.99	1.25	(Nilsson, 1979)
North boreal	Thinned/shelterwood logged, pine-dominated	Natural forest, pine-dominated	2.35	1.00	(Virkkala, 1987)
Hemiboreal	60–95 years old, thinned, spruce-dominated	Old-growth forest, spruce-dominated	2.19	1.78	(Rosenvald et al., 2011)
Hemiboreal	60–95 years old, thinned, pine-dominated	Old-growth forest, pine-dominated	2.05	1.18	(Rosenvald et al., 2011)
Hemiboreal	55–80 years old, even-aged production forest	Conifer-dominated forest reserves, mostly >120 years old	2.04	1.33	(Lindbladh et al., 2019)
Hemiboreal	60–95 years old, thinned, broadleaved-dominated	Old-growth forest, broadleaved-dominated	1.94	1.15	(Rosenvald et al., 2011)
South boreal	Stand-replacing fire 1–2 years ago, salvage-logged	Stand-replacing fire 1–2 years ago, no intervention	1.92	1.42	(Žmihorski et al., 2019)
Hemiboreal	50–80 years old, production stand, broadleaved-dominated	Natural stand, broadleaved-dominated	1.73	1.45	(Felton et al., 2016)
Hemiboreal	30–70 years old, planted, spruce-dominated	30–70 years old, natural succession, broadleaved-dominated	1.69	1.00	(Pass et al., 2022)

\*Only includes cavities with entrances smaller than 5.5 cm in diameter.

2000; see also Zawadzki, 2024).

Most cavities in boreal forests are excavated by birds, and the proportion of decay-formed cavities is low (Remm et al., 2006; Andersson et al., 2018; Aitken and Martin, 2007). However, in some studies, up to about half of cavities were reported as decay-formed (Carlson, 1994; Carlson et al., 1998). Decay-formed cavities were reported to occur mainly in oak, aspen and black alder, and not in conifers (Carlson, 1994; Carlson et al., 1998; Remm et al., 2006). The scarcity of decay-formed cavities in the boreal zone is likely affected by the cold climate that causes the rate of decay by heart-rot fungi to be so low that cavities are formed by decay alone only rarely (Remm and Löhmus, 2011). Furthermore, the dominant conifers have high decay resistance. Decay-formed cavities are common in more southern biomes (Cockle et al., 2011), and accordingly, studies in which decay-formed cavities were reported in boreal Europe took place in the hemiboreal zone (Carlson, 1994; Carlson et al., 1998; Remm et al., 2006; see also Zawadzka et al., 2016).

Although cavities formed fully by decay are scarce in boreal Europe, heart-rot fungi have crucial roles in cavity formation since woodpeckers strongly favor dead or low-vitality trees that have been softened by fungi (Martin et al., 2004; Cockle et al., 2012; Zahner et al., 2012). Tree species differ markedly in the frequency and form of inner decay. Stem decay was found in over 90 % of aspens 100 years old or older (Tikka, 1956; Basham, 1958), and only in 4.4 % of living spruces averaging 200 years of age (Norokorpi, 1980). Correspondingly, aspens are excavated frequently, and spruces almost never, except by the three-toed woodpecker. Spruces are, however, occasionally affected by basal decay (27.2 % of trees; Norokorpi, 1980). This may explain the low height of excavations by three-toed woodpeckers in spruces (Hågvar et al., 1990; Pakkala et al., 2018). Fungi that are frequent agents of heart rot, such as *Phellinus tremulae* on aspen (Fig. 1d), should be considered keystone species of cavity dynamics. *Porodaedalea pini*, which affects pines, seems to have a significant role in the cavity dynamics of xeric forests, where tree species other than pine are scarce (Löhmus, 2016; see also Jusino

et al., 2015).

Most of the studies reviewed here were conducted in human-modified landscapes. Thus, there is a gap in research on cavity dynamics as a constituent of natural forest dynamics. Given the changes along natural forest succession in tree species composition and dead-wood volume (Angelstam and Kuuluvainen, 2004; Lilja et al., 2006), significant variation in cavity dynamics along natural succession is expected. Intermediate stages of natural succession are characterized by a high abundance of senescent and dead broadleaved trees (Angelstam and Kuuluvainen, 2004; Lilja et al., 2006), which could translate to a high rate of cavity excavation. Observations in Białowieża, Poland, indicate that cavity occurrence in conifer snags, particularly pine snags, may be high in late-successional forests (Walankiewicz et al., 2014).

## 5.2. Cavity persistence and secondary cavity nesters

After cavities are formed, they remain available for use by secondary cavity nesters until tree fall or breakage. Since a large portion of excavations are in dead or low-vitality trees, cavity persistence is usually short. Cavities in dead trees rarely persist for more than a decade (Wesołowski, 2011; Pakkala et al., 2018, 2019, 2021, 2022). Cavities in healthy trees persist for longer, at least up to a few decades (Wesołowski, 2011; Pakkala et al., 2021). An exception to these patterns are cavities in standing dead pines, which persist for much longer than cavities in standing dead trees of other species (Wesołowski, 2011). This is most likely explained by the exceptional longevity of standing dead pines (Rouvinen et al., 2002). The high persistence of cavities in standing dead pines may cause them to accumulate and reach high densities (Walankiewicz et al., 2014). In addition, exceptional cavity persistence has been observed in oaks in southern Sweden, with a median persistence of 87 years (Ranius et al., 2009). These old cavities in oaks are crucial for invertebrates associated with wood mould but may be unfavorable for vertebrate nesters.

Secondary nesters prefer recently excavated cavities. The occupancy

rate of cavities in the first three years of the lifespan of cavities was 30–60 %, and about 10 % in cavities older than 10 years (Pakkala et al., 2018, 2019, 2021; see also Johnsson et al., 1993; Hanzelka et al., 2023). Nesters probably avoid old cavities because their condition and stability has deteriorated due to decay and possible parasites and diseases after previous use. Secondary nesters use decay-formed cavities regularly if they are available and may even prefer them over excavated cavities (Carlson et al., 1998; Remm et al., 2006). The preference may be due to decay-formed cavities having slightly smaller entrances (Remm et al., 2006).

Most secondary nesting is by a small number of passerine species (Carlson et al., 1998; Remm et al., 2006; Pakkala et al., 2018, 2019, 2022). Many secondary nesters live in some specific habitats such as farmland (Johnsson et al., 1993; Berg, 2002) or near water (Pöysä and Pöysä, 2002), and thus have not been observed in studies conducted in forests. As the largest excavator of the region, the black woodpecker produces the largest cavities and has a special role as a provider of nest sites for large-bodied secondary cavity nesters (Johnsson et al., 1993; Brainerd et al., 1995).

### 5.3. Forest management and the density of cavities and cavity nester populations

Only a few studies had compared cavity density in managed and unmanaged forests in boreal Europe. These studies indicate that cavity formation is reduced by timber-oriented forest management (Remm et al., 2008; Andersson et al., 2018; Pakkala et al., 2024). Studies from other regions have shown similar patterns, although they represent different kinds of forests and management methods, such as selective logging (Pattanavibool and Edge, 1996; Politi et al., 2010; Ibarra et al., 2020; Oliveira et al., 2024). A Polish study, however, included forests and management methods that appear comparable to those in boreal Europe, and cavity density was almost four times higher in unmanaged forests (Walankiewicz et al., 2014). The extent of cavity density reduction in comparison to unmanaged counterparts appears to be determined by management intensity (Walankiewicz et al., 2014; Pakkala et al., 2024). The few studies comparing cavity density are supplemented by studies that examined bird assemblages in managed and unmanaged forests. They indicate similar differences in the density of cavity-nesting birds as the other studies in the density of cavities. Notably, managed forests were mainly represented by mature stands approaching the end of the rotation. In forests regenerating from previous clearing, forest age can affect cavity density significantly (Felton et al., 2016; Zawadzka et al., 2016; Oliveira et al., 2024). Young even-aged forests where trees are still too small for excavation may be assumed to have no cavities and thus very few cavity-nesting birds.

We identify three main mechanisms by which the even-aged silvicultural system used in boreal Europe is likely to reduce cavity formation. First, in natural succession, European boreal forests have a high proportion of broadleaved trees for the first 100–150 years (Angelstam and Kuuluvainen, 2004; Lilja et al., 2006). However, conifers are favored in forest management because of their higher commercial value. Thus, as managed forests are regenerated by planting conifers, they are dominated by conifers in which cavity formation is lower than in broadleaved trees. Second, thinning from below targets trees with reduced vitality (Tikkanen et al., 2012). Thus, thinning from below removes trees that are or are about to become favorable for cavity formation. Third, trees in managed forests are harvested at a low age compared to their maximum life span. The main reason for this is the decline of growth increment as trees reach a certain age (Roberge et al., 2016). Since the likelihood of cavity formation increases with tree age, the harvesting of trees before they reach senescence suppresses cavity formation.

These mechanistic explanations are supported by published studies, although it is rare for studies on cavities or cavity nesters to directly have addressed these factors. As the density of cavities or cavity nesters is

higher in older, unmanaged forests than in managed forests adhering to standard rotation lengths (Table 3), extended rotation lengths can be expected to have similar effects, with the magnitude of the effect depending on exactly how much the rotation lengths are extended. The density of cavity nesters was positively correlated with deadwood volume (Rosenvald et al., 2011; Felton et al., 2021), although the suppressive effect of thinning from below on deadwood formation was not addressed. Two studies found similar densities of cavity nesters in spruce-dominated and birch-dominated forests (Rosenvald et al., 2011; Felton et al., 2021). However, cavity density was higher in aspen-dominated than birch-dominated forests (Remm et al., 2006). Thus, an increasing share of aspens rather than birches within conifer-dominated forests would probably be more beneficial. In a North American study, the density of both excavators and secondary nesters increased with the share of aspen (Trzcinski et al., 2022). It is possible that an increasing share of broadleaved trees benefits cavity nesters only when that includes low-vitality or dead trees, as healthy broadleaved trees may be unsuitable for cavity formation.

Forest management may affect the densities of cavities and cavity nesters also through its effects on food supply to cavity nesters. Unmanaged forests can provide better food resources for excavators (Pettersson et al., 1995; Löhmus et al., 2010; Czeszczewik et al., 2013). All excavators and many secondary nesters are winter residents. Thus, their survival rate is largely dictated by food supply in winter, when resources are at their lowest (Pettersson et al., 1995; Lindén et al., 2011; Lehikoinen et al., 2024). Smaller populations of excavators in managed forests due to smaller food supplies would also lead to a lower cavity production rate. Thus, lower densities of cavities and cavity nesters in managed forests could be due to both smaller food supplies and low availability of trees suitable for excavation.

### 5.4. Improving cavity availability in managed forests

Installing artificial nest boxes that mimic tree cavities increases the amount of nesting sites for secondary cavity nesters, and thus may lead to larger populations (Pöysä and Pöysä, 2002; Löhmus and Remm, 2005; Mänd et al., 2009). There are, however, practical difficulties in conserving cavity-associated diversity with nest boxes. Nest boxes may require continuous maintenance, and once they become too degraded, they eventually need to be replaced. Additionally, conservation of cavity nesters would require supplying a variety of different types of nest boxes because of varied nest site requirements (e.g., entrance size and internal dimensions). Excavators do not use nest boxes, and some secondary nesters also avoid them (Löhmus and Remm 2005). Therefore, nest boxes cannot support all cavity-associated diversity, and their application for conservation in large areas may be impractical.

In retention forestry, a portion of trees is left unharvested. Retention forestry has been applied widely in boreal Europe and elsewhere since the 1990's (Gustafsson et al., 2012; Kuuluvainen et al., 2019). Retaining cavity-bearing trees and trees with high potential for later cavity formation could improve cavity availability in managed forests (Gibbons and Lindenmayer, 1996). The main challenge is that the tendency in retention forestry is that only a marginal portion of trees is retained (Gibbons and Lindenmayer, 1996; Kuuluvainen et al., 2019). Currently applied retention levels are unlikely to maintain cavity nester populations (Söderström, 2009). However, tree retention may be a cost-effective method for improving cavity availability if tree species with central roles in cavity dynamics are targeted (Drever and Martin, 2010; Cooke and Hannon, 2011; Andersson et al., 2018).

In a Swedish study, cavity density in clearcut sites with retained trees was one sixth of that in old-growth forests (Andersson et al., 2018). Cavity density on clearcut sites may be assumed to be strongly correlated with the number of retained trees, but is also affected by their species identity. Higher cavity density is expected when aspens and standing dead trees are retained (Andersson et al., 2018). Some species such as the black woodpecker readily nest in clearcut sites with retention

**Table 4**

An overview of the expected positive effects of various management adjustments on cavity formation. Assessed effects include those on the frequency of tree types important to cavity formation, and excavation rate by the groups of excavators delineated in Fig. 2. ‘++’ indicates an expected positive effect. ‘+’ indicates a partial or context-dependent positive effect. Under continuous cover forestry, ‘(-)’ indicates a potential positive effect through a better food supply.

	Natural regeneration	Lower thinning intensity	Increased rotation length	Retention forestry	Continuous cover forestry
Large, senescent trees			+	++	
Broadleaved trees	++	+		+	
Dead and dying trees		++	+	+	
Softened-wood-excavators	++	+	+	+	(+)
Aspen-pine-excavators	++	+	+	++	(+)
Spruce-excavator		+	+	+	

trees (Zawadzki and Sławski, 2023). Yet, cavity occupancy was lower in clearcut sites with retention trees than in uncut forests (23 % and 34 %, respectively; Carlson, 1994). Several species nested much less frequently in clearcut sites, where most nesting occurred within 50 m of uncut forest (Carlson, 1994). Regardless, cavity-nesting birds were observed more frequently in young forests with retention trees in comparison to similar stands without retention trees (Lindbladh et al., 2022), and their frequency increased with the number of retained trees (Söderström, 2009). Increased shelter from retention trees may have made birds less fearful of venturing into clearcut sites. More detailed studies on nesting (Carlson, 1994) and cavity occurrence (Andersson et al., 2018) are needed to understand the value of retention trees for cavity dynamics.

The creation of high stumps (or artificial snags) during harvests by removing the top but leaving the lowest few meters of the trunk intact is nowadays a common practice in boreal Europe. North American studies indicate that this practice is beneficial to cavity-nesting birds as cavity formation is frequent in high stumps (Walter and Maguire, 2005). However, excavators and secondary nesters appear to find high stumps usable only temporarily (Barry et al., 2018). It is unknown how readily birds in boreal Europe utilize high stumps. A Swedish study showed lower cavity occurrence in high stumps than in intact standing dead trees (Andersson et al., 2018).

Continuous cover forestry (i.e., uneven-aged management) based on recurrent thinning from above is an alternative to traditional rotation forestry that is based on cycles of planting, thinning from below, and clearcutting (Rautio et al., 2025). It is often portrayed as a more benign system for biodiversity. Gap cutting and thinning from above did not affect the occurrence of cavity-nesting birds (Versluijs et al., 2017; Versluijs et al., 2020). Therefore, the application of the harvesting methods of continuous cover forestry seems to not affect cavity nesters negatively. However, transitioning to cover continuous forestry does not ensure the preservation of species that require dead or large living trees (Koivula et al., 2025). Similarly, continuous cover forestry probably does not enable higher cavity availability in comparison to rotation forestry if the provision of trees suitable for cavity excavation is not given consideration. Thus, ensuring cavity availability in continuous cover forestry most likely requires the integration of retention practices. However, continuous cover forestry is a potentially favorable alternative to even-aged forestry for maintaining the food supplies of excavators (Lindén et al., 2011; Lehtikoinen et al., 2024).

## 6. Conclusions and management recommendations

Excavators present in boreal Europe have different preferences for the types of trees used for excavation. Overall, aspen is the most favored tree species, and most excavators preferentially or almost exclusively excavate dead or low-vitality trees. Based on the published studies, cavity formation is suppressed by timber-production oriented forest management. Across studies conducted in boreal Europe, the density of cavities or populations of cavity-nesting birds was 1.7–4 times higher in unmanaged than in managed forests. This effect is most prominent in the youngest and the most intensively managed forests where cavities are nearly absent. Assuming that the numbers of standing dead and low-vitality trees are low in managed forests, the capacity of the great

spotted and black woodpeckers to excavate healthy trees may be crucial.

We addressed only quantitative differences in cavities in managed and unmanaged forests, but there may also be relevant qualitative differences, e.g. by cavities in conifer snags being particularly abundant in some types of unmanaged forests (Walankiewicz et al., 2014). There are still important knowledge gaps regarding the relations between forest structure and the dynamics of cavities and cavity nester populations. Obtaining precise and reliable information may be very laborious, requiring several years of monitoring over large areas (e.g., Trzcinski et al., 2022; Pakkala et al., 2024).

To improve cavity availability in managed forests, based on the observed cavity patterns and excavator densities, several management options appear potentially applicable and useful (Table 4):

- Regeneration practices should be adjusted to ensure a larger share of broadleaved trees.
- Thinning intensity should be kept low enough to ensure the presence of low-vitality or standing dead trees.
- Rotation lengths should be increased for a higher frequency of senescent and sufficiently large trees.
- Retention forestry should be implemented in a way that the amount and tree species identity of retained trees are appropriate for maintaining the availability of trees suitable for excavation.

## CRediT authorship contribution statement

**Aleksi Nirhamo:** Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Jari Kouki:** Writing – review & editing, Supervision, Methodology, Conceptualization.

## Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Jari Kouki reports financial support was provided by Skogssällskapet. Editor-in-chief at Forest Ecology and Management - J.K. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Acknowledgements

The study was funded by Skogssällskapet (project “Tree cavities as indicators of nature conservation values in forest management, 2021-2028”, led by JK). We thank Philippe Fayt for inspiring discussions on the topic of this manuscript.

## Data availability

No data was used for the research described in the article.

## References

- Ahti, T., Hämet-Ahti, L., Jalas, J., 1968. Vegetation zones and their sections in northwestern Europe. *Ann. Bot. Fenn.* 5, 169–211.
- Aitken, K.E.H., Martin, K., 2007. The importance of excavators in hole-nesting communities: availability and use of natural tree holes in old mixed forests of western Canada. *J. Ornithol.* 148, 425–434.
- Altamirano, T., Ibarra, J.T., Martin, K., Bonacic, C., 2017. The conservation value of tree decay processes as a key driver structuring tree cavity nest webs in South American temperate rainforests. *Biodivers. Conserv.* 26, 2453–2472.
- Andersson, J., Gómez, E.D., Michon, S., Roberge, J.-M., 2018. Tree cavity densities and characteristics in managed and unmanaged Swedish boreal forest. *Scand. J. For. Res.* 33, 233–244.
- Angelstam, P., Kuuluvainen, T., 2004. Boreal forest disturbance regimes, successional dynamics and landscape structures: a European perspective. *Ecol. Bull.* 51, 117–136.
- Barry, A.M., Hagar, J.C., Rivers, J.W., 2018. Use of created snags by cavity-nesting birds across 25 years. *J. Wildl. Manag.* 82, 1376–1384.
- Basham, J.T., 1958. Decay of trembling aspen. *Can. J. Bot.* 36, 491–505.
- Berg, Å., 2002. Composition and diversity of bird communities in Swedish farmland–forest mosaic landscapes. *Bird Study* 49, 153–165.
- BirdLife International 2024a. Country profile: Finland. (<https://datazone.birdlife.org/country/finland>) Accessed on 14th November 2024.
- BirdLife International 2024b. Country profile: Sweden. (<https://datazone.birdlife.org/country/sweden>) Accessed on 14th November 2024.
- BirdLife International 2024c. Country profile: Norway. (<https://datazone.birdlife.org/country/norway>) Accessed on 14th November 2024.
- Bertolino, S., Montezemolo, N., 2007. Garden dormouse (*Eliomys quercinus*) nest site selection in an alpine habitat. *Ethol. Ecol. Evol.* 18, 51–60.
- Blakely, T.J., Jellyman, P.G., Holdaway, R.J., Young, L., Burrows, B., Duncan, P., Thirkettle, D., Simpson, J., Ewers, R.M., Didham, R.K., 2008. The abundance, distribution and structural characteristics of tree-holes in *Nothofagus* forest, New Zealand. *Austral Ecol.* 33, 963–974.
- Blanc, L.A., Walters, J.F., 2008. Cavity-nest webs in a longleaf pine ecosystem. *Condor* 110, 80–92.
- Bogusch, P., Horák, J., 2018. Saproxylic bees and wasps. In: Ulyshen, M.D. (Ed.), *Saproxylic Insects*. Springer, pp. 217–235.
- Brainerd, S.M., Helldin, J.-O., Lindström, E.R., Rolstad, E., Rolstad, J., Storch, I., 1995. Pine marten (*Martes martes*) selection of resting and denning sites in Scandinavian managed forests. *Ann. Zool. Fenn.* 32, 151–157.
- Broughton, R.K., Hebda, G., Maziarz, M., Smith, K.W., Smith, L., Hinsley, S.A., 2015. Nest-site competition between bumblebees (Bombidae), social wasps (Vespidae) and cavity-nesting birds in Britain and the Western Palearctic. *Bird Study* 62, 427–437.
- Cadioux, P., Drapeau, P., Ouellet-Lapointe, U., Leduc, A., Imbeau, L., Deschênes, R., Nappi, A., 2023. Old forest structural development drives complexity of nest webs in a naturally disturbed boreal mixedwood forest landscape. *Front. For. Glob. Change* 6, 1084696.
- Carlson, A., 1994. Cavity breeding birds and clearcuts. *Ornis Fenn.* 71, 120–122.
- Carlson, A., Sandström, U., Olsson, K., 1998. Availability and use of natural tree holes by cavity nesting birds in a Swedish deciduous forest. *Ardea* 86, 109–119.
- Cockle, K.L., Martin, K., Wesolowski, T., 2011. Woodpeckers, decay, and the future of cavity-nesting vertebrate communities worldwide. *Front. Ecol. Environ.* 9, 377–382.
- Cockle, K.L., Martin, K., Robledo, G., 2012. Linking fungi, trees, and hole-using birds in a Neotropical tree-cavity network: pathways of cavity production and implications for conservation. *For. Ecol. Manag.* 264, 210–219.
- Cooke, H.A., Hannon, S.J., 2011. Do aggregated harvests with structural retention conserve the cavity web of old upland forest in the boreal plains? *For. Ecol. Manag.* 261, 662–674.
- Czeczczewik, D., Walankiewicz, W., Stańska, M., 2008. Small mammals in nests of cavity-nesting birds: why should ornithologists study mammals? *Can. J. Zool.* 86, 286–293.
- Czeczczewik, D., Walankiewicz, W., Mitrus, C., Tumieli, T., Stański, T., Sahel, M., Bednarczyk, G., 2013. Importance of dead wood resources for woodpeckers in coniferous stands of the Białowieża Forest. *Bird Conserv. Int.* 23, 414–425.
- Dietz, M., Brombacher, M., Erasmy, M., Fenchuk, V., Simon, O., 2018. Bat community and roost site selection of tree-dwelling bats in a well-preserved European lowland forest. *Acta Chiropterologica* 20, 117–127.
- Drever, M.C., Martin, K., 2010. Response of woodpeckers to changes in forest health and harvest: Implications for conservation of avian biodiversity. *For. Ecol. Manag.* 259, 958–966.
- Fan, Z., Shifley, S.R., Spetich, M.A., Thompson, F.R., Larsen, D.R., 2003. Distribution of cavity trees in midwestern old-growth and second-growth forests. *Can. J. For. Res.* 33, 1481–1494.
- Felton, A., Hedwall, P.-O., Lindblad, M., Nyberg, T., Felton, A.M., Holmström, E., Wallin, I., Löf, M., Brunet, J., 2016. The biodiversity contribution of wood plantations: contrasting the bird communities of Sweden’s protected and production oak forests. *For. Ecol. Manag.* 365, 51–60.
- Felton, A., Hedwall, P.-O., Trubins, R., Lagerstedt, J., Felton, A., Lindblad, M., 2021. From mixtures to monocultures: bird assemblage responses along a production forest conifer-broadleaf gradient. *For. Ecol. Manag.* 119299
- Gibbons, P., Lindenmayer, D.B., 1996. Issues associated with the retention of hollow-bearing trees within eucalypt forests managed for wood production. *For. Ecol. Manag.* 83, 245–279.
- Gibbons, P., Lindenmayer, D.B., 2002. *Tree Hollows and Wildlife Conservation in Australia*. CSIRO Publishing.
- Gibbons, P., Lindenmayer, D.B., Barry, S.C., Tanton, M.T., 2000. Hollow formation in eucalypts from temperate forests in southeastern Australia. *Pac. Conserv. Biol.* 6, 218–228.
- Gustafsson, L., Baker, S.C., Bauhus, J., Beese, W.J., Brodie, A., Kouki, J., Lindenmayer, D. B., Löhmus, A., Martínez Pastur, G., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, W.J.A., Wayne, A., Franklin, J.F., 2012. Retention forestry to maintain multifunctional forests: a world perspective. *BioScience* 62, 633–645.
- Haapanen, A., 1965. Bird fauna of the Finnish forests in relation to forest succession. *I. Ann. Zool. Fenn.* 2, 153–196.
- Hågvar, S., 1975. Coleoptera in nests of birds of prey. *Nor. J. Entomol.* 22, 135–142.
- Hågvar, S., Hågvar, G., Mønness, E., 1990. Nest site selection in Norwegian woodpeckers. *Holarct. Ecol.* 13, 156–165.
- Hansson, L., 1992. Requirements by the Great Spotted Woodpecker *Dendrocopos major* for a suburban life. *Ornis Svec.* 2, 1–6.
- Hanzelka, J., Baroni, D., Laaksonen, T., 2023. Occupancy rates of excavated cavities and nest boxes in managed boreal forest in relation to forest structure. *Scand. J. For. Res.* 38, 367–379.
- Hanzelka, J., Baroni, D., Martikainen, P., Eeva, T., Laaksonen, T., 2023. Cavity-breeding birds create specific microhabitats for diverse arthropod communities in boreal forests. *Biodivers. Conserv.* 32, 3845–3874.
- Hebda, G., Wesolowski, T., Rowiński, P., 2017. Nest sites of a strong excavator, the Great Spotted Woodpecker *Dendrocopos major*, in a primeval forest. *Ardea* 105, 61–71.
- Ibarra, J.T., Novoa, F.J., Jaillar, H., Altamirano, T.A., 2020. Large trees and decay: suppliers of a keystone resource for cavity-using wildlife in old-growth and secondary Andean temperate forests. *Austral Ecol.* 45, 1135–1144.
- Johnsson, K., Nilsson, S.G., Tjernberg, M., 1993. Characteristics and utilization of old Black Woodpecker *Dryocopus martius* holes by hole-nesting species. *Ibis* 135, 410–416.
- Jusino, M.A., Lindner, D.L., Banik, M.T., Walters, J.F., 2015. Heart rot hotel: fungal communities in red-corked woodpecker excavations. *Fungal Ecol.* 14, 33–43.
- Kitching, R.L., 2000. *Food Webs and Container Habitats: The Natural History and Ecology of Phytotelmata*. Cambridge University Press.
- Koivula, M., Felton, A., Jönsson, M., Löfroth, T., Schei, F.H., Siitonen, J., Sjögren, J., 2025. Biodiversity. In: Rautio, P., Routa, J., Huuskonen, S., Holmström, E., Cedergren, J., Kuehne, K. (Eds.), *Continuous cover forestry in boreal Nordic countries*. Springer, Cham, pp. 195–220.
- Krams, I., 1998. Nest site selection of the White-backed Woodpecker *Dendrocopos leucotos* in the eastern part of Latvia. *Ornis Svec.* 8, 11–16.
- Kuuluvainen, T., 2002. Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. *Silva Fenn.* 36, 97–125.
- Kuuluvainen, T., Lindberg, H., Vanha-Majamaa, I., Keto-Tokoi, P., Punntila, P., 2019. Low-level retention forestry, certification, and biodiversity: case Finland. *Ecol. Process.* 8, 47.
- Larrieu, L., Paillet, Y., Winter, S., Büttler, R., Kraus, D., Krumm, F., Lachat, T., Michel, A. K., Regnery, B., Vandekerckhove, K., 2018. Tree related microhabitats in temperate and Mediterranean European forests: a hierarchical typology for inventory standardization. *Ecol. Indic.* 84, 194–207.
- Lehikoinen, A., Pakanen, V.-M., Kivinen, S., Kumpula, S., Lehto, V., Rytönen, S., Vatka, E., Virkkala, R., Orell, M., 2024. Population collapse of a common forest passerine in northern Europe as a consequence of habitat loss and decreased adult survival. *For. Ecol. Manag.* 572, 122283.
- Lilja, S., Wallenius, T., Kuuluvainen, T., 2006. Structure and development of old *Picea abies* forests in northern boreal Fennoscandia. *Écoscience* 13, 181–192.
- Lindblad, M., Petersson, L., Hedwall, P.-O., Trubins, R., Holmström, E., Felton, A., 2019. Consequences for bird diversity from a decrease in a foundation species—replacing Scots pine stands with Norway spruce in southern Sweden. *Reg. Environ. Change* 19, 1429–1440.
- Lindblad, M., Elmberg, J., Hedwall, P.-O., Holmström, E., Felton, A., 2022. Broadleaf retention benefits to bird diversity in mid-rotation conifer production stands. *For. Ecol. Manag.* 515, 120223.
- Lindén, A., Lehikoinen, A., Hokkanen, T., Väisänen, R.A., 2011. Modelling irruptions and population dynamics of the great spotted woodpecker – joint effects of density and cone crops. *Oikos* 120, 1065–1075.
- Löhmus, A., 2016. Habitat indicators for cavity-nesters: the polypore *Phellinus pini* in pine forests. *Ecol. Indic.* 66, 275–280.
- Löhmus, A., Kinks, R., Soon, M., 2010. The importance of dead-wood supply for woodpeckers in Estonia. *Balt. For.* 16, 76–86.
- Löhmus, A., Remm, J., 2005. Nest quality limits the number of hole-nesting passerines in their natural cavity-rich habitat. *Acta Oecol.* 27, 125–128.
- Lučan, R.K., Jor, T., Romportl, D., Morelli, F., 2024. Use of synanthropic roosts by bats in Europe and North America. *Mammal. Rev.* (EARLY VIEW).
- Mänd, R., Leivits, A., Leivits, M., Rodenhouse, N.L., 2009. Provision of nestboxes raises the breeding density of Great Tits *Parus major* equally in coniferous and deciduous woodland. *Ibis* 151, 487–492.
- Martin, K., Aitken, K.E.H., Wieben, K.L., 2004. Nest sites and nest webs for cavity-nesting communities in interior British Columbia, Canada: nest characteristics and niche partitioning. *Condor* 106, 5–19.
- Milberg, P., Bergman, K.-O., Johansson, H., Jansson, N., 2014. Low host-tree preferences among saproxylic beetles: a comparison of four deciduous species. *Insect Conserv. Divers.* 7, 508–522.
- Nilsson, S.G., 1979. Effect of forest management on the breeding bird community in southern Sweden. *Biol. Conserv.* 16, 135–143.
- Nilsson, S.G., 1984. The evolution of nest-site selection among hole-nesting birds: the importance of nest predation and competition. *Ornis Scand.* 15, 167–175.
- Niringiyimana, A., Nzarora, A., Twahirwa, J.C., van der Hoek, Y., 2022. Density and characteristics of tree cavities inside and outside Volcanoes National Park, Rwanda. *Ecol. Evol.* 12, e9461.
- Norokorpi, Y., 1980. Old Norway spruce stands, amount of decay and decay-causing microbes in northern Finland. *Commun. Inst. For. Fenn.* 97 (6), 1–77.

- Oliveira, C.D., Cornelius, C., Stouffer, P.C., Cockle, K.L., 2024. Secondary Amazon rainforest partially recovers tree cavities suitable for nesting birds in 18–34 years. *Ornithol. Appl.* 126, 1–11.
- Orell, M., Ojanen, M., 1983. Breeding biology and population dynamics of the willow tit *Parus montanus*. *Ann. Zool. Fenn.* 29, 99–114.
- Pakkala, T., Tiainen, J., Pakkala, H., Piha, M., Kouki, J., 2022. Dynamics of the cavities of grey-headed woodpeckers *Picus canus* reveal their long- and short-term ecological roles in boreal forests. *Acta Ornithol.* 56, 199–208.
- Pakkala, T., Tiainen, J., Piha, M., Kouki, J., 2018. Nest tree characteristics of the old-growth specialist Three-toed woodpecker *Picoides tridactylus*. *Ornis Fenn.* 95, 89–102.
- Pakkala, T., Tiainen, J., Piha, M., Kouki, J., 2018. Three-toed Woodpecker cavities in trees: a keystone structural feature in forests shows decadal persistence but only short-term benefit for secondary cavity-breeders. *For. Ecol. Manag.* 413, 70–75.
- Pakkala, T., Tiainen, J., Pakkala, H., Piha, M., Kouki, J., 2019. Nest tree characteristics of the Lesser Spotted Woodpecker (*Dendrocopos minor*) in boreal forest landscapes. *Ornis Fenn.* 96, 169–181.
- Pakkala, T., Tiainen, J., Piha, M., Kouki, J., 2019. Hole life: survival patterns and reuse of cavities made by the lesser spotted woodpecker *Dendrocopos minor*. *Ardea* 107, 173–181.
- Pakkala, T., Tiainen, J., Pakkala, H., Piha, M., Kouki, J., 2020. Nest tree characteristics of Grey-headed Woodpeckers (*Picus canus*) in boreal forests. *Ornis Fenn.* 97, 89–100.
- Pakkala, T., Tiainen, J., Pakkala, H., Piha, M., Kouki, J., 2021. Dynamics of the cavities of Grey-headed Woodpeckers *Picus canus* reveal their long- and short-term ecological roles in boreal forests. *Acta Ornithol.* 56, 199–208.
- Pakkala, T., Peltonen, A., Lindberg, H., Hjäältén, J., Kouki, J., 2024. The intensity of forest management affects the nest cavity production of woodpeckers and tits in mature boreal forests. *Eur. J. For. Res.* 143, 617–634.
- Park, A., Auerbach, S., 1954. Further study of the tree-hole complex with emphasis on quantitative aspects of the fauna. *Ecology* 35, 208–222.
- Pass, E., Kont, R., Löhmus, A., 2022. Spruce (*Picea abies* L.) planting leads post-clearcut bird assemblages to a novel successional pathway—a comparative study in hemiboreal mixed forests. *Ann. For. Sci.* 79, 20.
- Pattanavibool, A., Edge, W.D., 1996. Single-tree selection silviculture affects cavity resources in mixed deciduous forests in Thailand. *J. Wildl. Manag.* 60, 67–73.
- Petermann, J.S., Gossner, M.M., 2022. Aquatic islands in the sky: 100 years of research on water-filled tree holes. *Ecol. Evol.* 12, e9206.
- Pettersson, R.B., Ball, J.P., Renhorn, K.-E., Esseen, P.-A., Sjöberg, K., 1995. Invertebrate communities in boreal forest canopies as influenced by forestry and lichens with implications for passerine birds. *Biol. Conserv.* 74, 57–63.
- Politi, N., Hunter, M., Rivera, L., 2010. Availability of cavities for avian cavity nesters in selectively logged subtropical montane forests of the Andes. *For. Ecol. Manag.* 260, 893–906.
- Pöysä, H., Pöysä, S., 2002. Nest-site limitation and density dependence of reproductive output in the common goldeneye *Bucephala clangula*: implications for the management of cavity-nesting birds. *J. Appl. Ecol.* 39, 502–510.
- Pulliaainen, E., Saari, L., 1989. Tikkojen esiintymisestä ja pesinnästä Itäkaivassa on the occurrence and nesting of woodpeckers in northeastern Finland. *Kokko* 11, 14–17.
- Pynnönen, A., 1939. Beiträge zur Kenntnis der Biologie finnischer Spechte. I. Contributions to the knowledge of the biology of Finnish woodpeckers. *Ann. Zool. Soc. Zool. Bot. Fenn. Vanamo* 7 (2).
- Ranius, T., Jansson, N., 2000. The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. *Biol. Conserv.* 95, 85–94.
- Ranius, T., Niklasson, M., Berg, N., 2009. Development of tree hollows in pedunculate oak (*Quercus robur*). *For. Ecol. Manag.* 257, 303–310.
- Ranius, T., Svensson, G.P., Berg, N., Niklasson, M., Larsson, M.C., 2009. The successional change of hollow oaks affect their suitability for an inhabiting beetle, *Osmoderma eremita*. *Ann. Zool. Fenn.* 46, 205–215.
- Rautio, P., Routa, J., Huuskonen, S., Holmström, E., Cedergren, J., Kuehne, K., 2025. Continuous Cover Forestry in Boreal Nordic Countries. Springer, Cham.
- Remm, J., Löhmus, A., 2011. Tree cavities in forests – the broad distribution pattern of a keystone structure for biodiversity. *For. Ecol. Manag.* 262, 579–585.
- Remm, J., Löhmus, A., Remm, K., 2006. Tree cavities in riverine forests: what determines their occurrence and use by hole-nesting passerines? *For. Ecol. Manag.* 221, 267–277.
- Remm, J., Löhmus, A., Rosenvald, R., 2008. Density and diversity of hole-nesting passerines: dependence on the characteristics of cavities. *Acta Ornithol.* 43, 83–91.
- Roberge, J.-M., Laudon, H., Björkman, C., Ranius, T., Sandström, C., Felton, A., Sténs, A., Nordin, A., Granström, A., Widemo, F., Bergh, J., Sonesson, J., Stenlid, J., Lundmark, T., 2016. Socio-ecological implications of modifying rotation lengths in forestry. *Ambio* 45, S109–S123.
- Rolstad, J., Rolstad, E., Sæteren, Ø., 2000. Black woodpecker nest sites: characteristics, selection and reproductive success. *J. Wildl. Manag.* 64, 1053–1066.
- Rosenvald, R., Löhmus, A., Kraut, A., Remm, L., 2011. Bird communities in hemiboreal old-growth forests: the roles of food supply, stand structure, and site type. *For. Ecol. Manag.* 262, 1541–1550.
- Rouvinen, S., Kuuluvainen, T., Siitonen, J., 2002. Tree mortality in a *Pinus sylvestris* dominated boreal forest landscape in Vienansalo wilderness, eastern Fennoscandia. *Silva Fenn.* 36, 127–145.
- Ruggera, R.A., Schaaf, A.A., Vivanco, C.G., Politi, N., Rivera, L.O., 2016. Exploring nest webs in more detail to improve forest management. *For. Ecol. Manag.* 372, 93–100.
- Siitonen, J., Martikainen, P., Punttila, P., Rauh, J., 2000. Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. *For. Ecol. Manag.* 128, 211–225.
- Söderström, B., 2009. Effects of different levels of green- and dead-tree retention on hemi-boreal forest bird communities in Sweden. *For. Ecol. Manag.* 257, 215–222.
- Takashima, A., Nakanishi, A., Morishita, M., Abe, S., Saito, K., Kotaka, N., 2021. Tree-cavity formation in the mature subtropical forests of Yambaru, Okinawa Island. *J. For. Res.* 26, 410–418.
- Taylor, A.R., Ranius, T., 2014. Tree hollows harbour a specialised oribatid mite fauna. *J. Insect Conserv.* 18, 39–55.
- Tikka, P.S., 1956. Haapametsiköiden rakenteesta ja laadusta. II. Laatu. Structure and quality of open stands. II. Quality. *Commun. Inst. For. Fenn.* 45 (3), 1–54.
- Tikkanen, O.-P., Matero, J., Mönkkönen, M., Juutinen, A., Kouki, J., 2012. To thin or not to thin: bio-economic analysis of two alternative practices to increase amount of coarse woody debris in managed forests. *Eur. J. For. Res.* 131, 1411–1422.
- Trzcinski, M.K., Cockle, K.L., Norris, A.R., Edworthy, M., Wiebe, K.L., Martin, K., 2022. Woodpeckers and other excavators maintain the diversity of cavity-nesting vertebrates. *J. Animal Ecol.* 91, 1251–1265.
- Van der Hoek, Y., Gaona, G.V., Martin, K., 2017. The diversity, distribution and conservation status of the tree-cavity-nesting birds of the world. *Divers. Distrib.* 23, 1120–1131.
- Versluuis, M., Eggers, S., Hjäältén, J., Löfroth, T., Roberge, J.-M., 2017. Ecological restoration in boreal forest modifies the structure of bird assemblages. *For. Ecol. Manag.* 401, 75–88.
- Versluuis, M., Hekkala, A.-M., Lindberg, E., Lämäs, T., Hjäältén, J., 2020. Comparing the effects of even-aged thinning and selective felling on boreal forest birds. *For. Ecol. Manag.* 475, 118404.
- Virkkala, R., 1987. Effects of forest management on birds breeding in northern Finland. *Ann. Zool. Fenn.* 24, 281–294.
- Walankiewicz, W., Czeszczewik, D., Stanski, T., Sahel, M., Ruczyński, I., 2014. Tree cavity resources in spruce-pine managed and protected stands of the Białowieża forest, Poland. *Nat. Areas J.* 34, 423–428.
- Walter, S.T., Maguire, C.C., 2005. Snags, cavity-nesting birds, and silvicultural treatments in western Oregon. *J. Wildl. Manag.* 69, 1578–1591.
- Wesolowski, T., 2011. Lifespan of woodpecker-made holes in a primeval temperate forest: a thirty year study. *For. Ecol. Manag.* 262, 1846–1852.
- Yatsiuk, Y., 2024. The multi-functional use of large tree cavities by arboreal vertebrates in a temperate broadleaved forest of eastern Europe. *Ecol. Evol.* 14, e70521.
- Zahner, V., Sikora, L., Pasinelli, G., 2012. Heart rot as a key factor for cavity tree selection in the black woodpecker. *For. Ecol. Manag.* 271, 98–103.
- Zawadzka, D., Drozdowski, S., Zawadzki, G., Zawadzki, J., 2016. The availability of cavity trees along an age gradient in fresh pine forests. *Silva Fenn.* 50, 1441.
- Zawadzki, G., 2024. Nesting-tree preferences of the black woodpecker—the biggest cavity excavator in a conifer-dominated forests in Poland. *Can. J. For. Res.* 54, 305–314.
- Zawadzki, G., Stawski, M., 2023. Green tree retention as a conservation tool for the black woodpecker in managed forests. *For. Ecol. Manag.* 548, 121398.
- Zheng, Z., Zhang, S., Yang, G., Tang, Y., Baskin, J., Baskin, C., Yang, L., 2009. Abundance and distribution of cavity trees in an old-growth subtropical montane evergreen broad-leaved forest. *Can. J. For. Res.* 39, 2234–2245.
- Žmihorski, M., Hebda, G., Eggers, S., Månsson, J., Abrahamsson, T., Czeszczewik, D., Walankiewicz, W., Mikusiński, G., 2019. Early post-fire bird community in European boreal forest: comparing salvage-logged with non-intervention areas. *Glob. Ecol. Conserv.* 18, e00636.