



Article

Stand Composition, Tree-Related Microhabitats and Birds—A Network of Relationships in a Managed Forest

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Abstract: Forest ecosystems contain many tree-related microhabitats (TreMs), which are used by various groups of organisms. Birds use TreMs for shelter, foraging and breeding. The abundance and variability of TreMs is related to tree stand composition and age. Over the last few centuries there has been a drastic decline in the structural and biological diversity of temperate forests over large areas of the Northern Hemisphere. These changes have reduced the diversity and quantity of TreMs. In this study we showed the relationships between stand composition, the abundance of TreMs, and the species richness of birds in a managed forest. We focused on TreMs that are important to birds: woodpecker breeding cavities, rot holes, dead branches, broken treetops, and perennial polypores. Our study was performed in a managed lowland temperate forest. In 94 plots (10 ha each) we made bird surveys and inventoried the stand composition and TreMs. Our results show that the tree stand composition of a managed forest affects the abundance of TreMs. The share of deciduous trees in the stand favors the occurrence of such TreMs as dead branches, rot holes and perennial polypores. The overall richness of bird species and the species richness of primary cavity nesters depended on the total basal area of oak, hornbeam and birch, whereas the species richness of secondary cavity nesters increased with the total basal area of birch and oak.

Keywords: tree-related microhabitats; deciduous trees; primary cavity nesters; secondary cavity nesters; temperate forest; forest management



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1. Introduction

Forest ecosystems contain many specific tree-related microhabitats (hereafter TreMs); examples include tree hollows, necroses, rotted places on trunks, stem shoots, bark cracks, dead canopy branches or upturned root plates [1,2]. The abundance of TreMs is positively related to the diversity of some species of vascular plants [3], fungi [4], invertebrates [5] and vertebrates [6,7]. They are key structures for biodiversity in both managed and protected forests [8,9].

Forest specialist birds, which spend most or all of their life cycle in forest habitats, use TreMs for shelter, foraging and breeding [10,11]. Birds may depend on TreMs in a direct way; examples include species that nest inside tree cavities [7,12]. Consequently, woodpecker breeding cavities, which are breeding sites for both primary and secondary cavity nesters, are among the most-studied TreMs [9]. Rot holes are another TreM well-known in the context of their relationship with birds. They arise as a result of mechanical damage and fungal activity, and serve as breeding places for secondary cavity nesters [13,14]. Birds may also depend indirectly on TreMs. Numerous arthropod species, which form a food base for birds, inhabit such TreMs as the rough and fissured bark of old trees, bark shelters and bark

pockets [15,16]. The significance of numerous other TreMs (e.g., dead branches, perennial polypores, broken treetops, trunk cracks) has not been studied in detail, but potentially they also positively affect bird abundance.

The abundance and variability of TreMs are strongly related to stand age, tree species composition and the presence of dying and dead trees [17,18]. The abundance of TreMs increases with tree aging. Older trees are richer in cavities, patches of bark loss, cracks, dead branches and broken tops [19]. Due to their morphology, anatomy and biology, particular tree species can promote or limit the occurrence of specific TreMs in forests. For example, deciduous trees such as poplar *Populus* spp., and willow *Salix* spp. with their softwood, have a large number of tree hollows carved out by woodpeckers [20]. Hornbeam *Carpinus betulus* trunks often have necroses and natural tree hollows [21]. Elm *Ulmus* spp. and lime *Tilia* spp. have numerous shoots at their trunk bases [22]. On the other hand, wood of coniferous trees (e.g., Scots pine *Pinus sylvestris*, European larch *Larix decidua*), with its numerous resin canals, limits the occurrence of necroses and natural hollows [23,24].

The structural and biological diversity of Europe's temperate forests has declined greatly over large areas in the last few centuries [25]. Forest management aimed at high timber production has been criticized for simplifying forest structure and reducing biological diversity [26]. These changes have reduced the diversity and quantity of TreMs. In consequence, the relation between the occurrence of TreMs and tree stand structure has been studied mostly in protected forests, where the higher diameter and lower vitality of trees have been identified as the main factors increasing the occurrence of TreMs [1,5,27,28]. In forests managed for timber, most studies have focused on the importance of habitat trees and less often on TreMs [29].

We wanted to know how tree species composition is related to the abundance of TreMs in relatively young stands of managed forest. Knowing this, we might be able to answer an important question: can forestry foster better conditions for bird species that rely on TreMs without lengthening stand rotation? Such an option would be most desirable, because extending the rotation period is a potentially expensive way to promote forest biodiversity [30], and in the near future the increasing demand for timber in some areas may also lead to shortening the rotation time [31].

Our main goal was to reveal relationships between stand composition, TreMs abundance and bird species richness in a forest managed for timber. We focused on five TreMs potentially related to birds and frequently present in managed forests: woodpecker breeding cavities, rot holes, dead branches, broken treetops and perennial polypores. We wanted to find out (1) how individual tree species determine the abundance of TreMs and (2) how the abundance of individual tree species affects the species richness of forest birds, especially that of primary and secondary cavity nesters.

2. Methods

2.1. Study Area

The study was conducted in the Niepołomice Forest (S Poland; 50°02' N/20°33' E; ~200 m a.s.l.), belonging to the lowland temperate forest zone. This forest complex, covering 106 km², is located about 20 km east of Kraków at the fork of the Vistula and Raba rivers. Since 2004, the whole Niepołomice Forest, with the surrounding meadows, is a Special Protected Area for Birds within the Natura 2000 system (Puszcza Niepołomicka, PLB120002). The forest hosts at least 17 breeding bird species from Annex I to Council Directive 79/409/EEC [32]. It is an important breeding site for the collared flycatcher *Ficedula albicollis*, middle spotted woodpecker *Dendrocoptes medius* and Ural owl *Strix uralensis*.

Two forest types dominate in the Niepołomice Forest: mixed oak–pine and hardwood oak–hornbeam, respectively covering 74 and 22% of the area. Patches of alder have developed in old riverbeds and small depressions. Scots pine *Pinus sylvestris* covers the largest area in this forest. Two oaks (pedunculate *Quercus robur*, sessile *Q. petraea*) and black alder *Alnus glutinosa* also have significant shares, and there are smaller shares of silver birch

Betula pendula, European beech *Fagus sylvatica*, European larch *Larix decidua* and hornbeam *Carpinus betulus* [33].

Most of the area of the Niepołomice Forest was wetland forest. To make the forested area more accessible, intensive melioration was carried out there from the mid-19th century until the 1930s. As a result of clear-cutting and artificial regeneration, deciduous stands were replaced with Scots pine monoculture over large areas. At present, most of the Niepołomice Forest (98.5%) is managed for timber. Forest management is based mainly on strip clear-cutting, group selection and artificial regeneration (mainly Scots pine and pedunculate oak). The average age of the tree stands is about 70 years; those older than 100 years cover about 15% of the whole forest [34]. A few fragments of the oldest forest are protected in six nature reserves established in the middle of the 20th century, but only two of them are under strict protection, without any tree felling. In addition, ten areas with representative forest habitats have been set aside since 2015 and excluded from timber extraction. Altogether, 1.5% of the forest area is protected.

2.2. Bird Surveys

In the Niepołomice Forest we set up 94 square plots (10 ha each, 316 × 316 m) situated within large individual management units (forest compartments). All plots were located in even-aged stands 60–100 years old, with tree cover of at least 90%, and created by artificial regeneration in the clear-cutting system. Given these criteria, the plots were regularly distributed throughout the studied forest.

In 2016, in each plot we determined the presence of all bird species during four surveys at two-week intervals from early April to late May, and recorded the observed birds, mainly singing males. In each survey we checked all plots over the course of 4–6 days. The observers walked zigzags (preset in a hand-carried GPS) to cover the whole area of each plot. All surveys were performed in the morning (06:00 to 11:00 CET) on days with no heavy rain or strong wind, and lasted 90 min per plot on average [35]. Nine observers participated in the ornithological surveys. To reduce any effect related to individual observers, they switched plots during successive surveys.

2.3. Inventory of Stand Composition and TreMs

Tree stand measurements and TreM inventories were done in the same year as the ornithological surveys. In each of the 94 plots we delineated nine subplots covering 500 m² each (20 × 25 m rectangles) distributed in a regular grid of 3 × 3 subplots. In each subplot we measured tree diameter at breast height (dbh), taking 20 cm as the lower threshold. For each of those 94 plots we calculated the total basal area of individual tree species in those nine subplots. Some closely related tree species were not distinguished when taking measurements; the species categories treated as single taxa in the analyses are oak (pedunculated and sessile), birch (silver and downy) and lime (small-leaved and large-leaved).

We used binoculars to observe and record the occurrence of TreMs important to birds on every tree measuring dbh > 20 cm. We took into account the TreMs potentially related to the presence of forest birds: woodpecker breeding cavities, rot holes, dead branches, broken treetops and perennial polypores. We limited the number of TreMs to the five most numerous ones in the studied forest. To facilitate comparisons with results from other studies, we defined the selected TreMs according to Larrieu et al.'s [18] hierarchical typology of TreMs in European temperate and Mediterranean forests. Woodpecker breeding cavities include breeding cavities of woodpeckers drilled in dead branches, in the insertions of broken-off branches, or on trunks. Rot holes include four types of trunk rot holes: trunk rot holes, semi-open trunk rot holes, chimney trunk rot holes and hollow branches (acc. [18]). For dead branches in canopies and broken treetops we set a minimum of 10 cm at the basal portion of the branch or at the broken treetop. Polypore fruiting bodies, irrespective of their size, were recorded.

To ensure the most complete detection of TreMs, each tree was carefully inspected from different sides and distances. In spite of this, some TreMs could be overlooked. To minimize the observer effect [36], all plots were searched for TreMs by the same two observers. One of them searched for TreMs in the tree crown and the second one for TreMs along trunks. The observations were made after the broadleaved trees had begun to shed their leaves, from October to January.

2.4. Data Analyses

Only the six most abundant tree taxa were included in the analysis: pine, oak, lime, hornbeam, alder and birch (given in descending order of abundance). To show the relationship between the occurrence of TreMs and tree species, we applied the chi-square test. It was assumed that under a random distribution the total number of occurrences of a TreM on a tree species is proportional to its abundance in all plots. The total basal area of all trees of a given taxon was used as a proxy for its abundance. The strength of the influence of individual tree species on the chi-square test result was expressed using Pearson's residuals.

To explain the richness of forest bird species we used generalized linear models (GLMs) with log link function [37]. TreMs were distributed non-randomly among tree species (see below), hence we focused our analyses of bird assemblages on tree species composition. The explanatory variables were basal area of pine, oak, hornbeam, lime, alder and birch. In the data exploration process, we checked for collinearity of all explanatory variables by calculating the variance inflation factors of each variable. During preliminary analyses, we found autocorrelation within the explanatory variables (TreMs and total basal area of tree species). Therefore, we did not model the dependence of forest birds on the TreMs and total basal area variables jointly. That is why we decided to use simpler analysis showing the dependence of TreMs on individual tree species. We included 42 bird species found during the four surveys in at least three plots. Within these groups of species, we distinguished two assemblages: primary and secondary cavity nesters (Appendix A). In the first analysis we used the overall number of bird species in the 10 ha plots as the response variable. For the response variables in the second and third analyses, we used the species richness of primary and secondary cavity nesters in the 10 ha plots. In our analyses, the global model and all the simpler (nested) models missing one or more terms were fitted in the MuMIn library [38]. We ranked the models based on AICc values to find the most parsimonious models. Models with ΔAICc values < 2 were taken as having similar support [39] and are presented in the results section. All data analyses employed R software in R 3.4.3 [40].

3. Results

3.1. Characteristics of Tree Stands

A total of 10,832 trees thicker than 20 cm (density 262 trees ha^{-1}), representing 21 species, were observed for TreMs in the 42.3 ha area (94 plots \times 9 subplots \times 500 m^2). Pine was the most abundant tree, accounting for almost half of all trees. Oak was the most abundant broadleaved tree. Four other broadleaved trees (hornbeam, lime, black alder, birch) occurred at density of more than five trees ha^{-1} . The mean diameter of all observed trees was 37 cm. Thickness differences between tree species were small. Oaks were the thickest and hornbeams the thinnest (Table 1).

Table 1. Characteristics of tree stands over all 94 plots.

Tree Species	N·ha ⁻¹	Diameter [cm]			
		Mean	Q1	Q2	Q3
<i>Pinus sylvestris</i>	126.1	37.1	32	37	42
<i>Quercus robur</i> and <i>Q. sessilis</i>	55.3	43.3	30	41	54
<i>Tilia cordata</i> and <i>T. platyphyllos</i>	25.8	33.1	23	29	39
<i>Carpinus betulus</i>	24.0	29.4	22	26	33
<i>Alnus glutinosa</i>	14.0	33.8	27	32	40
<i>Betula pendula</i> and <i>B. pubescens</i>	8.8	35.4	28	35	42
Other species *	8.1	32.1	23	29.5	36
All species	262.2	37.0	29	35	43

* Other species include *Acer pseudoplatanus*, *A. platanoides*, *Fagus sylvatica*, *Fraxinus excelsior*, *Larix decidua*, *Picea abies*, *Populus tremula*, *Sorbus aucuparia*, *Ulmus laevis*, *U. glabra* and *U. minor*.

3.2. Tree Species and TreMs

The total density of all TreMs was 46 ha⁻¹. Dead branches were the most abundant TreM, present on almost 13% of the observed trees. Other TreMs were much rarer, each occurring on less than 2% of the trees. The least abundant were broken treetops, occurring on less than 0.5% of the observed trees (Table 2).

Table 2. Number of TreMs in the studied tree stands.

Tree Species	Number of TreMs [N·ha ⁻¹]				
	Woodpecker Breeding Cavities	Rot Holes	Dead Branches	Broken Treetops	Perennial Polypores
<i>Pinus sylvestris</i>	0.57	0.21	3.33	0.24	1.91
<i>Quercus robur</i> and <i>Q. sessilis</i>	1.30	1.77	25.77	0.38	1.35
<i>Carpinus betulus</i>	0.05	1.44	1.18	0.09	0.59
<i>Tilia cordata</i> and <i>T. platyphyllos</i>	0.07	0.87	1.16	0.17	0.21
<i>Alnus glutinosa</i>	0.21	0.24	0.17	0.12	0.12
<i>Betula pendula</i> and <i>B. pubescens</i>	0.02	0.17	0.38	0.12	0.31
Other species *	0.19	0.07	1.09	0.12	0.19
All species	2.41	4.78	33.07	1.23	4.68

* Other species are the same as in Table 1.

Each TreM was distributed non-randomly between tree species (Table 3). Analysis of standardized residuals of the chi-square test showed that hornbeam had the strongest positive effect on the occurrence of natural hollows and perennial polypores, while oak had the strongest positive effect on the occurrence of woodpecker breeding cavities and dead branches. Birch showed a positive effect on the occurrence of broken treetops. In contrast, pine showed the strongest negative effects on the occurrence of most TreMs. Only polypores were slightly more negatively associated with lime and alder than with pine (Table 3).

Table 3. Pearson chi-square test residuals for dependence of TreMs on individual tree species.

TreMs	<i>Pinus sylvestris</i>	<i>Quercus robur</i> and <i>Q. sessilis</i>	<i>Carpinus betulus</i>	<i>Tilia cordata</i> and <i>T. platyphyllos</i>	<i>Alnus glutinosa</i>	<i>Betula pendula</i> and <i>B. pubescens</i>	Pearson X ² Statistic	p-Value
Rot holes	−8.791	1.380	13.157	6.551	0.659	0.368	284.9827	<0.001
Woodpecker breeding cavities	−3.015	4.564	−1.633	−1.512	2.500	−1.155	43.14035	<0.001
Dead branches	−19.592	31.770	−4.293	−4.714	−6.620	−4.320	1497.233	<0.001
Perennial polypores	−0.848	−0.512	3.328	−1.109	−1.061	2.858	21.92714	<0.0005
Broken treetops	−2.558	0.258	0.577	2.309	2.121	2.121	23.22503	<0.0003

3.3. Tree Species and Birds

Between 8 and 22 (mean \pm SE: 16 ± 3) forest bird species were recorded in the 10 ha plots (Appendix A). The species recorded most frequently were the great tit *Parus major* (100% of plots), common chaffinch *Fringilla coelebs* (99%), Eurasian nuthatch *Sitta europea* (97%), great spotted woodpecker *Dendrocopos major* (93%) and Eurasian blackcap *Sylvia atricapilla* (82%).

For predicting the overall richness of bird species, six of the 64 candidate models received equally high support ($\Delta\text{AICc} < 2$; Table 4). Oak, hornbeam and birch were most positively associated with forest bird species richness. Oak was present in all of the best models; hornbeam and birch were present in five of them. Pine and alder were also positively associated with the overall richness of forest bird species, but they were present in only one or two of the best models. Lime was present in one of the best models and showed negative relationships with forest bird species richness (Table 4; Figure 1).

For predicting the species richness of primary cavity nesters, nine of the 64 candidate models received equally high support ($\Delta\text{AICc} < 2$; Table 5). Oak and hornbeam were present in each of these best models, birch in five and alder in three of them. The species richness of primary cavity nesters increased with the total basal area of those trees. Pine and lime were present in five and two models, respectively, and showed negative relationships with the species richness of primary cavity nesters (Table 5; Figure 2).

For predicting the species richness of secondary cavity nesters, seven of the 64 candidate models received equally high support ($\Delta\text{AICc} < 2$; Table 6). Oak and birch were present in all of these best models, pine in four of them, lime and hornbeam in three, and all showed positive relationships with the species richness of secondary cavity nesters. Alder was not present in any of these best models (Table 6; Figure 3).

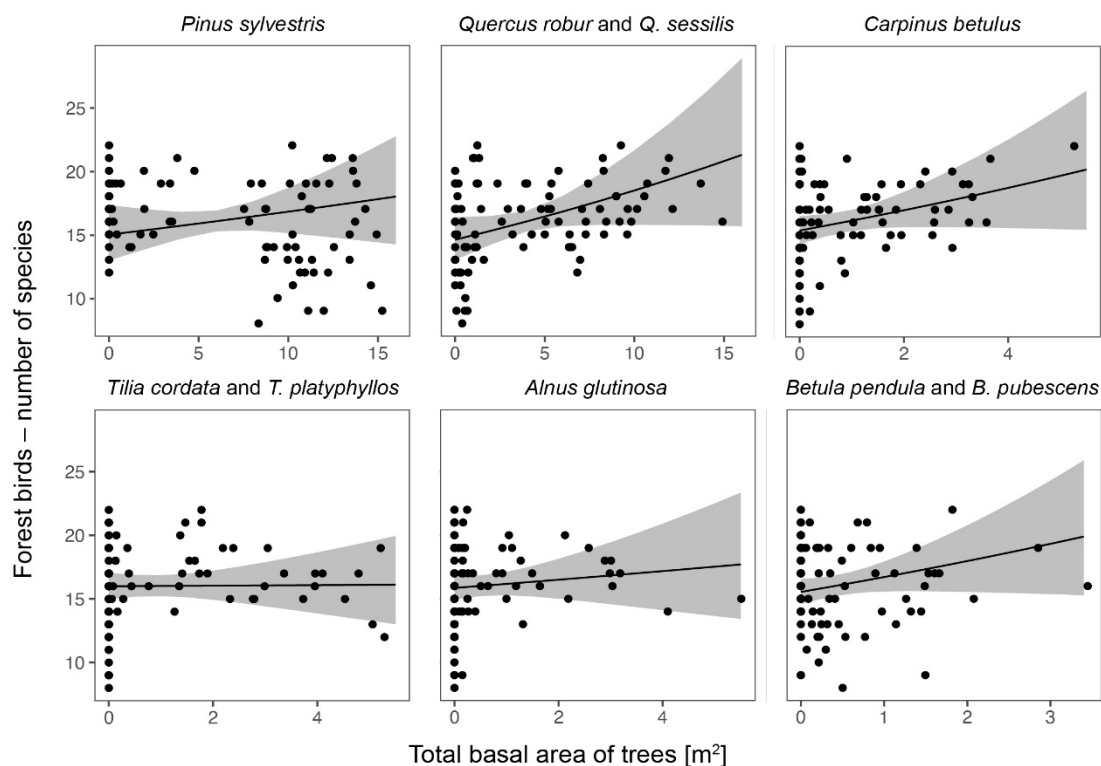


Figure 1. Relationships between species richness of forest birds (N/10 ha) and total basal area of trees thicker than 20 cm DBH ($\text{m}^2/0.45$ ha), estimated using generalized linear models (GLMs) with log link function (Table 4). Dots represent measured values, line—prediction, gray area—95% confidence interval for prediction.

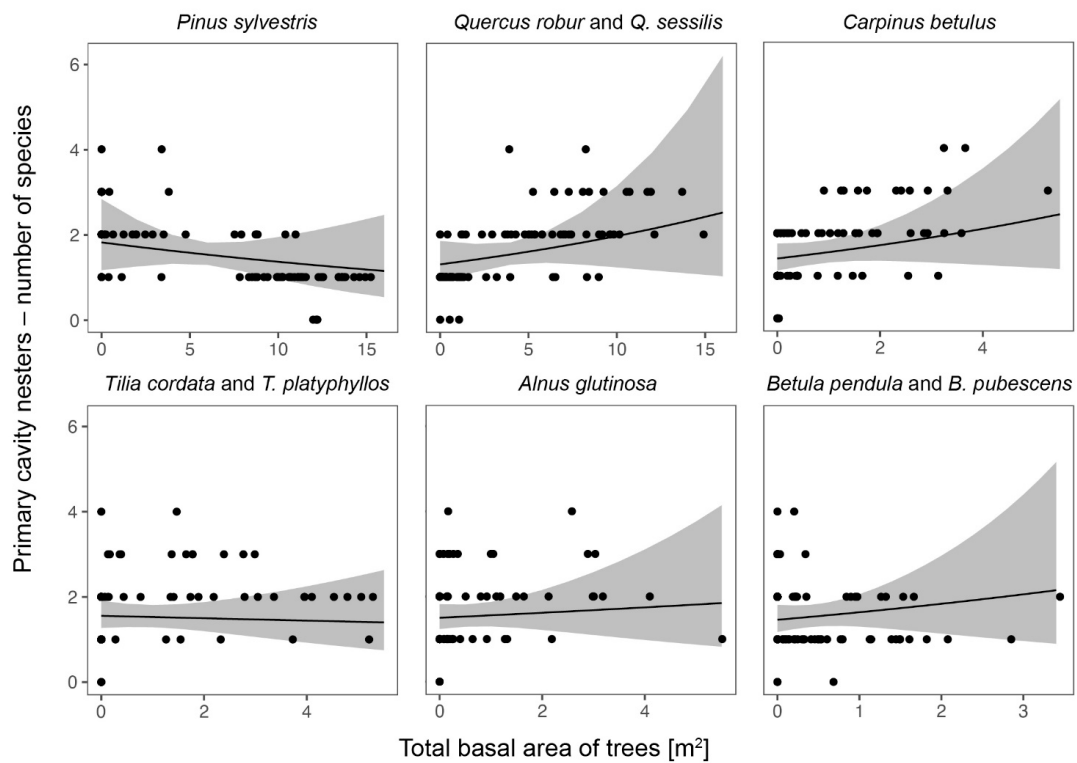


Figure 2. Relationships between species richness of primary cavity nesters (N/10 ha) and total basal area of trees thicker than 20 cm DBH (m²/0.45 ha), estimated using generalized linear models (GLMs) with log link function (Table 5). Dots represent measured values, line—prediction, gray area—95% confidence interval for prediction.

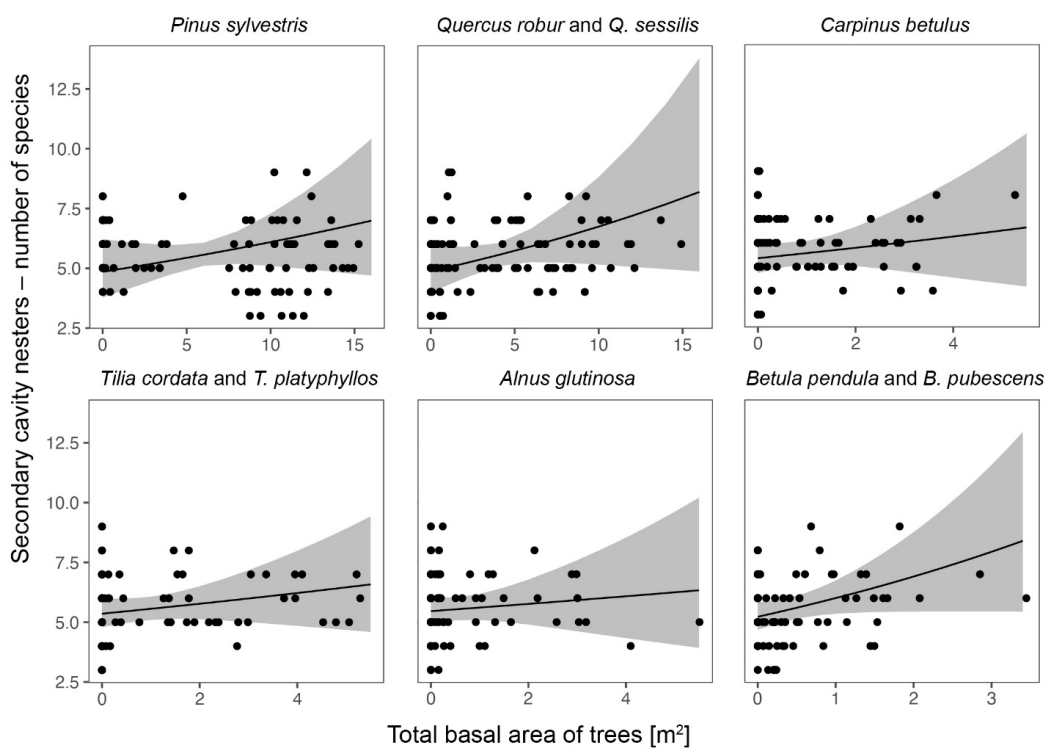


Figure 3. Relationships between species richness of secondary cavity nesters (N/10 ha) and total basal area of trees thicker than 20 cm DBH (m²/0.45 ha), estimated using generalized linear models (GLMs) with log link function (Table 6). Dots represent measured values, line—prediction, gray area—95% confidence interval for prediction.

Table 4. The highest-ranking models predicting species richness of forest birds in the studied forest based on (coefficients \pm 1 SE): total basal area of trees thicker than 20 cm DBH. The AICc weight (ω AICc) for a given model indicates the probability it is the most parsimonious model.

Model Rank	<i>Pinus sylvestris</i>	<i>Quercus robur</i> and <i>Q. sessilis</i>	<i>Carpinus betulus</i>	<i>Tilia cordata</i> and <i>T. platyphyllos</i>	<i>Alnus glutinosa</i>	<i>Betula pendula</i> and <i>B. pubescens</i>	Df	AICc	Δ AICc	ω AICc
	Coefficient \pm 1 SE									
1	-	0.01 \pm 0.01	0.03 \pm 0.03	-	-	0.06 \pm 0.04	5	472.5	0.00	0.121
2	0.01 \pm 0.01	0.02 \pm 0.01	0.05 \pm 0.03	-	-	0.07 \pm 0.04	6	473.0	0.048	0.095
3	-	0.01 \pm 0.01	0.04 \pm 0.03	-0.01 \pm 0.02	-	0.06 \pm 0.04	6	474.1	1.66	0.053
4	-	0.02 \pm 0.01	-	-	-	0.05 \pm 0.04	4	474.2	1.76	0.050
5	0.01 \pm 0.01	0.02 \pm 0.01	0.05 \pm 0.03	-	0.01 \pm 0.03	0.07 \pm 0.04	7	474.2	1.77	0.050
6	-	0.01 \pm 0.01	0.03 \pm 0.03	-	-	-	4	474.4	1.89	0.050

(-) the variable was not present in the model.

Table 5. The highest-ranking models predicting species richness of primary cavity nesters in the studied forest based on (coefficients \pm 1 SE): total basal area of trees thicker than 20 cm DBH. The AICc weight (ω AICc) for a given model indicates the probability it is the most parsimonious model.

Model Rank	<i>Pinus sylvestris</i>	<i>Quercus robur</i> and <i>Q. sessilis</i>	<i>Carpinus betulus</i>	<i>Tilia cordata</i> and <i>T. platyphyllos</i>	<i>Alnus glutinosa</i>	<i>Betula pendula</i> and <i>B. pubescens</i>	Df	AICc	Δ AICc	ω AICc
	Coefficient \pm 1 SE									
1	-	0.06 \pm 0.02	0.13 \pm 0.07	-	0.07 \pm 0.07	0.14 \pm 0.15	6	165.0	0.00	0.124
2	-	0.06 \pm 0.02	0.13 \pm 0.07	-	-	0.12 \pm 0.15	5	165.5	0.50	0.096
3	-0.03 \pm 0.03	0.04 \pm 0.04	0.01 \pm 0.08	-	-	0.11 \pm 0.14	6	165.8	0.83	0.082
4	-0.03 \pm 0.03	0.03 \pm 0.03	0.09 \pm 0.08	-	-	-	5	166.0	0.97	0.076
5	-0.04 \pm 0.03	0.03 \pm 0.03	0.09 \pm 0.08	-0.03 \pm 0.06	-	-	6	166.1	1.04	0.074
6	-	0.06 \pm 0.02	0.11 \pm 0.07	-	0.06 \pm 0.07	-	5	166.2	1.20	0.068
7	-	0.06 \pm 0.02	0.12 \pm 0.07	-	-	-	4	166.3	1.27	0.066
8	-0.02 \pm 0.03	0.04 \pm 0.04	0.10 \pm 0.08	-	0.04 \pm 0.08	0.12 \pm 0.15	7	166.6	1.60	0.056
9	-0.04 \pm 0.03	0.04 \pm 0.04	0.10 \pm 0.08	-0.03 \pm 0.06	-	0.10 \pm 0.15	7	166.6	1.61	0.055

(-) the variable was not present in the model.

Table 6. The highest-ranking models predicting species richness of secondary cavity nesters in the studied forest based on (coefficients \pm 1 SE): total basal area of trees thicker than 20 cm DBH. The AICc weight (ω AICc) for a given model indicates the probability it is the most parsimonious model.

Model Rank	<i>Pinus sylvestris</i>	<i>Quercus robur</i> and <i>Q. sessilis</i>	<i>Carpinus betulus</i>	<i>Tilia cordata</i> and <i>T. platyphyllos</i>	<i>Alnus glutinosa</i>	<i>Betula pendula</i> and <i>B. pubescens</i>	Df	AICc	Δ AICc	ω AICc
	Coefficient \pm 1 SE									
1	-	0.02 \pm 0.01	-	-	-	0.11 \pm 0.07	4	312.7	0.00	0.139
2	0.01 \pm 0.02	0.03 \pm 0.02	-	0.03 \pm 0.04	-	0.12 \pm 0.07	46	313.8	1.06	0.082
3	0.01 \pm 0.02	0.03 \pm 0.02	-	-	-	0.11 \pm 0.07	55	314.0	1.24	0.075
4	-	0.02 \pm 0.01	-	0.02 \pm 0.03	-	0.11 \pm 0.07	65	314.1	1.33	0.071
5	0.02 \pm 0.02	0.03 \pm 0.02	0.04 \pm 0.05	0.03 \pm 0.04	-	0.13 \pm 0.07	7	314.1	1.41	0.069
6	-	0.02 \pm 0.01	0.02 \pm 0.05	-	-	0.11 \pm 0.07	5	314.1	1.43	0.068
7	0.01 \pm 0.02	0.03 \pm 0.02	0.04 \pm 0.05	-	-	0.12 \pm 0.07	6	315.1	1.73	0.059

(-) the variable was not present in the model.

4. Discussion

Our study shows that TreMs of forests intensively managed for timber vary among tree species, and that tree species composition, especially of tree species with abundant TreMs, affected the species richness of birds. The occurrence of all studied TreMs correlated with the abundance of broadleaved species in the tree stand. The occurrence of dead branches and woodpecker breeding cavities was strongly and positively related with oak, while the occurrence of natural hollows and perennial polypores depended mostly on the abundance of hornbeam in stands. The occurrence of all five TreMs, on the other hand, was negatively related to the abundance of pine. Our work falls in line with earlier reports that

TreMs are more abundant on broadleaved than on coniferous trees [5,6,41]. Unlike most studies of TreMs, which have been conducted in unmanaged forests protected in nature reserves, our data were collected in managed mature stands 60–100 years of age, where the DBH of most trees was below 40 cm. Therefore the number of TreMs in our study was lower than in other studies done in those older stands [5,6,36,41].

Each TreM included in our study plays a different role for birds. Dead branches are excellent feeding sites and are also good places to find cavities [42]. They likely attract a large group of birds found in the studied forest, including the nuthatch *Sitta europaea*, treecreeper *Certhia* spp., and woodpeckers with more delicate beaks such as the European green woodpecker *Picus viridis* [43] and middle spotted woodpecker [13]. Trees with broken tops provide good nesting sites for cavity nesters [44,45]. Cavities and rot holes on trunks are valuable TreMs as foraging, shelter and nesting places for many forest bird species [6,12]. We distinguished woodpecker breeding cavities from rot holes, the former created by woodpeckers and the latter originating from wood rot [19]. The formation of rot hollows usually begins with the action of parasitic fungi, mostly polypores (Basidiomycota), which alter the properties of wood cells and soften the heartwood. Rot holes and the presence of perennial polypores, which are external indicators of wood decay, make it more likely that woodpeckers will carve out cavities [46,47].

The strong linkage between microhabitats and tree species resulted in a similarly strong relationship between bird species richness and stand species composition. The important trees for increasing the species richness of birds are oak, hornbeam and birch. Oak and hornbeam are important for primary cavity nesters, while oak and birch are most important for secondary cavity nesters. These statements should be treated with caution because the relationship between forests and birds is multifaceted. Of course, in addition to TreMs, forests provide birds with diverse foraging opportunities, and deciduous forests will provide a different set of food resources compared to coniferous forests [11].

Oak, both *Q. robur* and *Q. petraea*, is one of the trees having the most numerous microhabitats, especially hollows and dead branches [5,48]. Moreover, the fissured bark of oak, inhabited by a variety of invertebrates, is a preferred feeding place for numerous bird species [13,49]. Our results confirmed that oak has more thick and dead canopy branches and woodpecker breeding cavities than other tree species do. Large number of hollows in oak was probably related to the presence of a large number of dead branches in the crowns of older oaks. The woodpecker breeding cavities are carved mostly at the base of dead branches and directly on dead branches [50]. Besides showing such richness of microhabitats, oak was most strongly related to the overall richness of bird species as well as the richness of primary and secondary cavity nesters. Large oaks are key resources for the middle and great spotted woodpeckers and affect their nesting [46,51], space use [52] and occurrence [53]. In general, our results support the assertion that oak is one of the most important trees for maintaining biodiversity in Central European forests [29]. Because of its high economic value and wide ecological amplitude, it is also one of the most important broadleaved species in managed forests of the Central European lowlands [54]. However, due to the promotion of coniferous plantations in the past, its current share is half of what the natural environmental conditions potentially could sustain [55].

Hornbeam was only slightly behind oak in terms of microhabitat creation. In the forest we studied, natural hollows and perennial polypores were much more numerous on hornbeam than on other trees, but it had far fewer woodpecker breeding cavities and dead branches than oak did. The abundance of hornbeam was more positively related to the richness of primary cavity nesters than to that of secondary cavity nesters, and the overall richness of birds increased with the share of hornbeam. Similar results were obtained in oak–hornbeam forests of the Białowieża Forest, where hornbeam was most often used by birds for nesting, and where, for example, *Dendrocopos leucotos* and *D. medius* bred in hornbeam more often than in other trees [56]. This is due to specific characteristics of hornbeam trees. Hornbeam trunks and branches are rich in necroses [21]. They occur in fragments of damaged bark, phloem and xylem, and often they are infected by fungi and inhabited by

insects, which accelerate the development of wood rot and natural hollows [57]. Unlike oak, the economic value of hornbeam is less than its value for promoting TreMs abundance and bird species richness. Low commercial interest in this tree results in its low abundance in managed forests. In the past, hornbeam was used mainly for fuel, but recent changes in heating techniques have reduced interest in this species, so its share in managed forests can be expected to decline over time. Because of its low economic value, however, foresters often choose hornbeams for use as habitat trees [58]. Our findings suggest that such selection may be beneficial for forest biodiversity.

Both silver and downy birch were also positively associated with TreMs and bird species richness, positively affecting the occurrence of polypores and broken treetops, and the overall richness of bird species and secondary cavity nesters. In pine-dominated forest, birch is often the most numerous accompanying species; it contributes food resources for birds and increases nesting opportunities for cavity nesters. Among European tree species, the number of insect species associated with birch is among the highest [59]. Moreover, the very good insolation under birch crowns favors the growth of field-layer flowering plants, which support nectar feeders [60]. Both groups of insects furnish a feeding base for birds [61]. In young stands under 100 years old, naturally formed cavities are much more numerous on birch than on pine trees [62]. Our results indicate that while birch, like hornbeam, is of low commercial value, it is one of the most valuable trees for sustaining biodiversity. It is particularly valuable in young pine stands less than 100 years old, because TreMs appear on it much earlier than on pine trees.

Scots pine showed negative effects on the occurrence of all studied TreMs; the highest such effects were for dead branches and rot holes. This is attributable to its very resinous wood, which limits rotting, the formation of rot holes and fungal infection of trunks [63]. Only when pine stands reach 100–130 years of age do TreMs become more numerous [62]. In our study, the abundance of pine was positively associated with the number of all species and of secondary cavity nesters, but the effect was weaker than for oak, hornbeam and birch. Moreover, there was a marked negative association between its abundance and the occurrence of primary cavity nesters. This contradicts results given by Basile et al. [9] from mixed mountain forest; they found that pine trees were as preferred as beech trees, and more than other conifers. However, the pines with cavities in their study were almost twice as thick as in our study. In the forest we studied, most pine stands were younger than 90 years (short rotation time), so cavities were less likely to occur.

Forestry management decisions affect tree stand characteristics (species composition, age, size structure) and consequently can affect the abundance of TreMs. Our study of a managed lowland temperate forest of Central Europe suggests that forest management decisions that shape the tree stand composition and forest structure can have a great impact on the abundance of TreMs and the species richness of forest birds. Our work shows that individual tree species play different roles in the formation of the TreMs pool in mature stands, even in those younger than 100 years. For forestry, this means that the shares of species that contribute microhabitats should be maintained in these stands. This finding is especially important in view of the fact that in European countries the forests of this age cover much larger areas than older ones [64] and the recommended rotation age for most tree species is below 120 years [65,66]. Hence, the biodiversity of Europe's forests over large areas critically depends on the species composition of stands aged below 100 years. Increasing the shares of oak trees, in suitable habitats for them, would significantly increase the biodiversity of managed forests in Central Europe. This could be achieved primarily by increasing the share of oak at the expense of Scots pine, the species that least promotes the formation of microhabitats and bird richness in mature stands below 100 years old. An alternative strategy might be to allow pines to achieve greater ages. Our findings also suggest that increasing the shares of hornbeam and birch may benefit forest biodiversity. In managed forest, trees of lower commercial value, such as hornbeam and birch, should be promoted in management plans, in addition to other measures such as setting aside of old growth stands and retention of dead wood and living trees.

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Appendix A

Table A1. Breeding bird community of the Niepołomice Forest. Results of four surveys in 94 plots at two-week intervals from early April to late May 2016.

Species	Bird's Assemblage	Frequency (% of Plots)	
Great tit	<i>Parus major</i>	S	100
Common chaffinch	<i>Fringilla coelebs</i>	N	99
Eurasian nuthatch	<i>Sitta europaea</i>	S	97
Great spotted woodpecker	<i>Dendrocopos major</i>	P	93
Eurasian blackcap	<i>Sylvia atricapilla</i>	N	83
European robin	<i>Erithacus rubecula</i>	N	80
Eurasian blackbird	<i>Turdus merula</i>	N	78
Eurasian blue tit	<i>Cyanistes caeruleus</i>	S	74
Hawfinch	<i>Coccothraustes coccothraustes</i>	N	73
Eurasian jay	<i>Garrulus glandarius</i>	N	69
Common chiffchaff	<i>Phylloscopus collybita</i>	N	67
Eurasian wren	<i>Troglodytes troglodytes</i>	N	63
Collared flycatcher	<i>Ficedula albicollis</i>	S	62
Wood warbler	<i>Phylloscopus sibilatrix</i>	N	60
Middle spotted woodpecker	<i>Dendrocoptes medius</i>	P	51
European starling	<i>Sturnus vulgaris</i>	S	51
Coal tit	<i>Periparus ater</i>	S	49
Common wood-pigeon	<i>Columba palumbus</i>	N	38
Short-toed treecreeper	<i>Certhia brachydactyla</i>	S	38
Song thrush	<i>Turdus philomelos</i>	N	34
Eurasian treecreeper	<i>Certhia familiaris</i>	S	33
Willow warbler	<i>Phylloscopus trochilus</i>	N	24
Marsh tit	<i>Poecile palustris</i>	S	24
Common buzzard	<i>Buteo buteo</i>	N	24

Table A1. Cont.

	Species	Bird's Assemblage	Frequency (% of Plots)	
	Yellowhammer	<i>Emberiza citrinella</i>	N	21
	Crested tit	<i>Lophophanes cristatus</i>	S	18
	Eurasian golden oriole	<i>Oriolus oriolus</i>	N	15
	Goldcrest	<i>Regulus regulus</i>	N	14
	Tree pipit	<i>Anthus trivialis</i>	N	14
	Willow tit	<i>Parus (Poecile) montanus</i>	S	13
	Black woodpecker	<i>Dryocopus martius</i>	P	11
	Eurasian green woodpecker	<i>Picus viridis</i>	P	7
	Eurasian siskin	<i>Spinus spinus</i>	N	7
	Common cuckoo	<i>Cuculus canorus</i>	N	6
	Lesser spotted woodpecker	<i>Dryobates minor</i>	P	5
	Common raven	<i>Corvus corax</i>	N	4
	Long-tailed tit	<i>Aegithalos caudatus</i>	N	4
	Northern goshawk	<i>Accipiter gentilis</i>	N	4
	Gray-headed woodpecker	<i>Picus canus</i>	P	2
	European turtle-dove	<i>Streptopelia turtur</i>	N	2
	Common redstart	<i>Phoenicurus phoenicurus</i>	S	2
	Eurasian bullfinch	<i>Pyrrhula pyrrhula</i>	N	1

(P) primary cavity nester bird species, (S) secondary cavity nester bird species, (N) non-cavity nesting bird species.

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