

Article

Diversity and Determinants of Tree-Related Microhabitats in Hemiboreal Forests of Europe Based on National Forest Inventory Data

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Abstract

Tree-related microhabitats (TreMs) are small features on living or dead trees that offer habitat, shelter, breeding sites, or food for many organisms, making them useful indicators of forest-dwelling species. Despite increasing research on TreMs in Europe, most published studies have focused on temperate regions, leaving a relative paucity of data from hemiboreal forests. In our research, we aimed to fill the knowledge gap, offering insight into the occurrence patterns and factors influencing TreM diversity in the hemiboreal region. We analyzed data from the National Forest Inventory in Latvia, comprising information on 168,839 trees across 5653 sample plots. The most common TreMs were bark loss (6.1% of trees), bryophytes (2.6%), and perennial polypores (2.6%). TreMs occurred more frequently on deciduous than on coniferous trees, on larger trees (diameter at breast height more than 60 cm), and on dead trees compared to living ones. Forest type and signs of recent cutting also had significant effects on TreM richness at both the tree and plot scales, whereas forest protection status was significant only at the plot scale. TreMs such as buttress-root concavities and ivy or liana cover, which are common in temperate Europe, had a low relative occurrence in our study. The occurrence of specific TreM forms was strongly tree-species dependent: exudates were much more common on live *Picea abies* (4.0%) than on other species, whereas *Populus tremula* had a higher occurrence of fruiting bodies of saproxylic fungi and slime moulds (2.0%). The highest occurrence of crown deadwood was observed on *Quercus robur*. Overall, dead trees play a particularly important role, providing both a higher total number of TreMs and certain TreM types more frequently. Given their high TreM richness, dead and large trees represent important structural components supporting biodiversity in hemiboreal forests.

Keywords: TreMs; boreo-nemoral forests; forest monitoring; biodiversity indicators



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1. Introduction

Forests play a critical role in maintaining global biodiversity, harboring more than 80% of terrestrial species [1]. However, ongoing habitat loss, fragmentation, and intensive forest management practices are among the leading drivers of biodiversity decline in these ecosystems [2]. As global conservation priorities shift toward integrating biodiversity objectives into multifunctional landscapes, there is an increasing need for efficient tools to monitor and promote habitat quality in both protected and production forests. In this context, structural indicators have emerged as valuable proxies for ecological integrity and species richness [3]. Among these, tree-related microhabitats (TreMs) have received

growing attention as measurable, scalable, and management-relevant features that reflect key ecological processes [4,5]. The presence and diversity of TreMs have been shown to correlate with forest naturalness and continuity [6], making them a promising tool for integrating biodiversity considerations into forest management and conservation planning across both managed and unmanaged landscapes.

Tree-related microhabitats are small features found on living or dead trees that serve as habitats, nesting sites, shelters, or food sources for various organisms, including invertebrates, vertebrates, and epiphytic species [4]. Therefore, the presence of different TreMs might indicate that the tree is suitable for organisms that require the specific TreM. It is not only theoretical, but there has been evidence that the presence of particular TreMs is associated with higher taxa diversity of different organism groups, for example, tree cavities were associated with saproxylic beetles and bats [7], and trees with TreM epiphytic and epixylic structures did in fact host higher lichen species richness than trees without such TreM [8].

Numerous studies have shown that trees with larger diameters, deadwood (snags and logs), and broadleaf species support a greater diversity of tree-related microhabitats than smaller, living, or coniferous trees [9,10]. However, the relationship between tree diameter and TreM occurrence is not uniform across all TreM types; some features, such as bark loss or dendrotelms, may form more frequently on smaller trees [11]. While models often incorporate predictors such as diameter at breast height (DBH), tree species, vitality, and time since last harvest, recent findings suggest that plot-level context explains the greatest proportion of variation in TreM occurrence [12]. Additionally, environmental factors including slope, aspect, and elevation can significantly influence TreM formation patterns and should be integrated into predictive frameworks [10].

The rate of TreM formation varies across tree species, with pioneer species typically developing microhabitats more rapidly than slow-growing, long-lived species [13]. Courbaud et al. [11] introduced the concept of a “hazard rate” for first TreM formation—defined as the probability of a TreM forming on a tree previously without one during an infinitesimal DBH increment—which was found to increase with DBH for features like woodpecker cavities, rot holes, and root concavities. In contrast, TreMs such as bark loss or dendrotelms showed declining formation rates in very large trees. Studies in old-growth temperate forests further confirm that TreM richness tends to increase with tree age and size [14]. At the stand scale, however, TreM abundance is often higher at higher elevations and in monospecific coniferous forests, while the greatest diversity is typically observed in mixed coniferous–broadleaved stands [15].

Managed and unmanaged forests differ in several structural and ecological aspects. In this study, we use the term managed/unmanaged to refer to the presence or absence of forest management activities, whereas protected/unprotected refers to legal protection status and associated management restrictions. Although these categories may overlap, they are not equivalent. Primary forests typically contain a higher proportion of large, old living trees and snags, along with greater variability in DBH and tree age, contributing to more heterogeneous habitat conditions. These features are closely linked to increased TreM abundance, with trees in unmanaged forests generally supporting more microhabitats than those in intensively managed stands [9]. Spatial patterns of TreMs also differ, with unmanaged forests exhibiting more irregular and diverse distributions [16]. In even-aged, conifer-dominated production forests, the diversity of TreMs on retention trees increased with surrounding tree density, although the effects varied by TreM type—for example, crown deadwood and bryophytes were more frequent, while buttress-root concavities and lichens were less common [17]. Most TreM groups form less frequently in managed forests (harvested within the past 100 years) compared to unmanaged forests (no logging

for over a century), though dendrotelms were an exception to this trend [11]. Interestingly, Vuidot et al. [9] also reported that, when controlling for tree size and site conditions, management type alone did not significantly influence TreM occurrence—suggesting that forest structure may be a stronger driver than management per se. However, forest management activities can have a strong and direct influence on forest structure, especially under intensive practices such as clear-cutting [18]. Despite increases in research on TreMs in Europe, the majority of published studies have focused on temperate, Central and Southern European forests, leaving a relative paucity of data from Northern Europe and the Baltic region. For example, extensive TreM analyses have been conducted in primeval beech forests in the Carpathians [19], the Białowieża Forest in Poland [20], and mountain beech-dominated forests in the Carpathians [21]. In contrast, data from hemiboreal forests, such as those found in Latvia, remain rare, although see [22]. This geographic bias limits our understanding of how TreM richness and distribution respond to management and environmental gradients in northern forest ecosystems. Here, by analysing National Forest Inventory data from Latvia, we fill this gap by comparing TreM richness and identifying tree and site level drivers of TreM occurrence in a northern European context.

The aim of this study was to compare TreM richness between protected and unprotected forests, and to identify which factors best explain TreM occurrence at the tree level. To achieve this, we used a large dataset derived from the National Forest Inventory (NFI), comprising information on 168,839 trees across 5653 sample plots. To our knowledge, this is the first study in northern Europe to integrate TreM data into a national forest inventory framework, enabling a broad-scale, management-relevant analysis of TreM patterns. We hypothesized that (i) TreM richness would be higher in protected forests compared to unprotected ones, and (ii) TreM richness at the tree level would be significantly influenced by tree DBH, tree species, and tree status (alive or dead).

2. Materials and Methods

2.1. Study Area

This study was conducted in Latvia, a Northern European country located on the eastern coast of the Baltic Sea. Latvia lies within the hemiboreal forest zone, which represents a transitional region between the temperate broadleaf and boreal coniferous forest biomes [23]. In this zone, climatic conditions and species composition reflect both northern cold-tolerant and temperate broadleaf elements, resulting in mixed forest stands where boreal conifers (e.g., *Pinus sylvestris* and *Picea abies*) co-occur with temperate deciduous species (e.g., *Betula* sp., *Alnus* sp., *Quercus* sp., and *Tilia* sp.) across environmental gradients [24]. This mosaic of structural and compositional features contributes to high habitat heterogeneity and biodiversity compared to forests dominated solely by either boreal or temperate species [24]. In Latvia, the main forest management model is clear-cuts [25], with an average size of 0.94 ha [26] and at least five retention trees per ha according to government regulations [27].

The country's total land area is about 64,600 km², of which forests cover roughly 52% [28]. The climate is temperate and humid, characterized by relatively mild winters and cool summers, influenced by both maritime and continental air masses [29]. Mean annual precipitation ranges from 600 to 850 mm, while mean annual temperature varies from 4.5 °C in the east to 6.5 °C in the coastal regions [30].

2.2. Study Design

In total, 5653 evenly distributed sample plots were included in the analysis. These plots are part of the National Forest Inventory (NFI) network, ensuring systematic coverage across all forest types, age classes, and management categories throughout

Latvia to represent average values in the country. The spatial distribution of plots allows for a representative assessment of national-scale forest structure, composition, and environmental gradients.

The data for this study were obtained from the National Forest Inventory (NFI), which, in addition to measuring three standard forestry parameters, also included assessments of TreMs. The NFI plots are evenly distributed across the entire country according to a systematic sampling design that begins from a randomly selected starting point (Figure 1A). Sample plot tracts are arranged uniformly at 4×4 km intervals, following a layout that forms isosceles triangles (Figure 1B). Each tract contains four plots arranged at the vertices of a 250×250 m square (Figure 1C). The area of each circular sampling plot is 500 m^2 , within which for all of the trees with diameter at breast height (DBH) ≥ 14.1 cm, DBH was measured, as well as their condition (living, dead, cut, damaged, etc.) recorded. In a concentric subplot with the area of 100 m^2 , all trees with DBH ≥ 6.1 cm are measured, while in a 90° sector of the subplot (area of 25 m^2), all trees with DBH ≥ 2.1 cm are measured. Trees above the largest diameter threshold were measured across the entire area of the largest plot and recorded only once. In the intermediate and smallest nested plots, only additional trees within the respective smaller diameter classes were measured and added, while trees already measured in the larger plot were not re-recorded. To ensure even spatial and temporal coverage, one-fifth of all sample plots are surveyed annually, providing an unbiased distribution of fieldwork across Latvia.

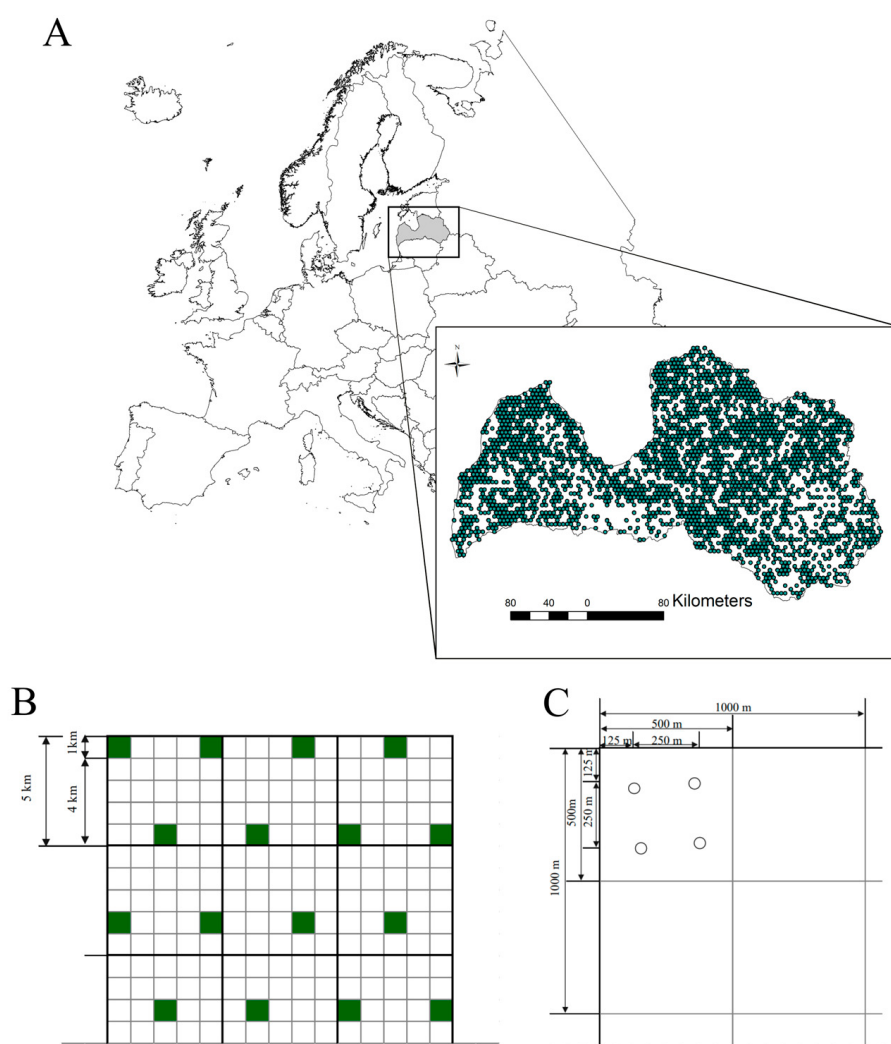


Figure 1. (A) Locations of sample plot tracts in Latvia; (B) Layout scheme of sample plot tracts [31]; (C) Layout scheme of sample plots within a sampling tract [31].

From all the NFI data we selected trees that were in forest stands or clearcuttings; therefore, in total 168,839 trees were selected across 5653 sample plots surveyed between 2019 and 2024. Assessment was carried out by NFI teams during the fieldwork season (normally between April 1 and October 31). Potential seasonal effects on TreM detectability (e.g., reduced visibility during the leaf-on period) were not specifically adjusted for. The NFI was conducted by five field teams. Before the survey period, all NFI teams received training on the recognition of TreMs and participated in a calibration meeting. Each tree was assessed by a single trained surveyor during the measurement of tree parameters: the lower part of the tree was inspected while measuring DBH, and the upper part of the tree, including the main trunk and major branches visible from the ground, was assessed during tree height measurement (without using binoculars). The dominant tree species in the sampled forests were *Pinus sylvestris* (present in 30.3% of plots), *Betula pendula* or *Betula pubescens* (28.2%), *Picea abies* (20.1%), *Populus tremula* (8.1%), *Alnus incana* (7.2%), and *Alnus glutinosa* (6.1%). The age of the dominant tree species ranged from 1 to 250 years, with two-thirds of the plots representing stands younger than 80 years. Across all plots, trees from 23 different taxa were recorded (Table 1). Approximately 16% of the measured trees were dead, including both snags and logs.

Alongside the tree measurements, TreMs were assessed on each measured tree using a classification originally developed by combining the approaches of Kraus et al. [5] and Larrieu et al. [4]. Although this methodology was established prior to the publication of Bütler et al. [32], it corresponds almost exactly to the TreMs classification proposed therein. Accordingly, all TreM types defined in Bütler et al. [32] were assessed in this study. In addition, two TreM categories not included in Bütler et al. [32] were recorded: splintered stems (*sensu* Kraus et al. [5]) and dead parts of the tree top, defined as dead branches with a diameter ≥ 3 cm accounting for more than 10% of the total crown. TreMs were assessed both on live and dead trees. However, on dead trees, crown deadwood was not assessed, and exudates were evaluated only on dead trees in decay stage I (wood hard).

Forest types at each plot were classified following the Latvian forest ecosystems classification system [33], which is based on soil characteristics and vegetation at tree stand maturity and expected regeneration. For data analysis, these forest types were grouped into five categories according to soil conditions: dry and mesic mineral soils, drained mineral soils, drained peat soils, wet mineral soils, and wet peat soils. Additionally, forest types were also grouped into five categories according to soil fertility: eutrophic soils, mesoeutrophic soils, mesotrophic soils, oligomesotrophic soils, oligotrophic soils. Based on management restrictions in force according to legislation in 2024, we classified all plots as either protected (prohibited final felling and thinning or any management activity) or unprotected (available for wood supply). Between 2018 and 2024, the protection status changed for 68 plots ($\approx 1.2\%$ of all plots), in all cases toward more stringent protection. Given the small proportion of affected plots, this is unlikely to influence the overall results. In total, 910 plots were designated as protected and 4743 as unprotected. However, the absence of management restrictions does not necessarily imply that management activities have occurred. Therefore, signs of recent cutting were recorded separately when stumps of anthropogenic origin indicated logging within the past 15 years (since beginning of NFI). Among unprotected forests, 1086 plots showed signs of recent cutting, whereas 85 plots did so in protected forests (in places where protection has started recently). Protected forests have significantly higher DBH (according to Wilcoxon test $W = 1,771,234,921$, $p < 0.001$) and a higher proportion of dead trees (according to Fisher's Exact Test odds ratio = 0.763, 95% CI = 0.738–0.788, $p < 0.001$) than unprotected forests.

Table 1. The number of studied trees in the study plots.

Tree Species	Total Number of Trees	Dead Trees (Snags and Logs)	Living Trees	Average of DBH *	Min DBH (cm)	Max DBH (cm) *
<i>Picea abies</i>	48,785	6718	42,067	18.8	2.1	90.5
<i>Betula</i> spp.	38,887	5438	33,449	17.8	2.1	79.9
<i>Pinus sylvestris</i>	36,499	5810	30,689	23.1	2.1	79.9
<i>Alnus incana</i>	15,858	3540	12,318	13.8	2.1	47
<i>Alnus glutinosa</i>	10,147	1303	8844	19.0	2.1	68
<i>Populus tremula</i>	8687	1437	7250	19.3	2.1	127.3
<i>Salix caprea</i>	2473	937	1536	16.4	2.1	64.1
<i>Quercus robur</i>	1644	174	1470	21.6	2.1	121
<i>Fraxinus excelsior</i>	1187	570	617	18.4	2.1	76
<i>Tilia cordata</i>	1168	66	1102	16.6	2.1	99.3
<i>Acer platanoides</i>	1020	18	1002	17.3	2.1	108.3
<i>Ulmus</i> spp.	551	100	451	18.9	2.1	65
<i>Sorbus aucuparia</i>	543	77	466	12.1	5.6	33.6
Undetectable	366	366		21.3	6.1	53
<i>Padus avium</i>	305	76	229	16.9	6.3	32.5
<i>Salix</i> spp.	291	120	171	15.2	2.1	84.7
deciduous tree	237	218	19	17.8	2.4	78.4
<i>Malus sylvestris</i>	81	9	72	18.3	2.1	40.1
<i>Larix</i> sp.	50	4	46	28.0	7.0	87.5
coniferous trees	25	25		18.7	8.8	35.5
<i>Pinus</i> spp.	18		18	4.5	2.2	9.2
<i>Prunus avium</i>	14		14	18.2	3.8	29.7
<i>Carpinus betulus</i>	3		3	12.7	10.3	14.2
<i>Juniperus communis</i>	3	2	1	14.8	7.4	25.3
<i>Fagus sylvatica</i>	2		2	21.6	15.3	27.9
<i>Populus</i> sp.	1		1	9.9	9.9	9.9

* For logs, DBH may refer to the diameter at the widest part when the log is a trunk fragment, and measuring at 1.3 m from the tree base is not possible.

2.3. Statistical Analysis

To estimate the weighted occurrence of each TreM type, we calculated the weighted proportion of trees on which it was observed. Each tree was assigned a weight corresponding to the number of trees it represents based on its diameter class and the subplot area in which it was measured. The weighted proportion (P) was then calculated as the sum of represented trees with the TreM divided by the total number of represented trees:

$$P = \frac{\sum_{j=1}^n w_j \cdot T_j}{\sum_{j=1}^n w_j}$$

where j indexes individual trees, w_j is the number of trees represented by tree j (based on subplot area and diameter class); $T_j = 1$, if tree j has the TreM, 0 otherwise.

This approach ensures that trees sampled in smaller subplots or representing fewer trees in their diameter class contribute proportionally to the plot-level estimate.

These calculations were performed separately for trees from protected and unprotected sites, as well as for trees with DBH > 14 cm and those with DBH ≤ 14 cm, reflecting both differences in measurement methodology and the need to assess potential differences in occurrence patterns between smaller and larger trees. Because the weights differ among individual trees, the weighted occurrence calculated for all trees combined is not a simple average of the occurrences in the DBH subsets. In some cases, this can result in the overall weighted occurrence being smaller than the weighted occurrences in both subsets. In addition, the proportion of trees with at least one TreM was also separately calculated for trees with DBH > 14 cm in the mature forest, where only mature stands eligible for final cutting were selected. In Latvia, the minimum allowable rotation age is regulated by legislation: 121 for *Quercus robur*, 101 years for *Pinus sylvestris*, 81 years for *Picea abies*, *Fraxinus excelsior*, *Tilia cordata*, *Ulmus glabra*, *Ulmus laevis*, *Acer platanoides*, 71 for *Betula pendula* and *Alnus glutinosa*, 41 for *Populus tremula* [34].

Linear mixed-effects models were fitted using the glmer function from the lme4 R package to assess the effects of tree- and stand-level variables on TreM aspects at the plot level.

Response variables:

- Presence of TreMs (at least one tree with at least one TreM; binary).
- Number of TreMs per plot (count).
- Proportion of trees with TreMs (proportion).
- Number of TreM forms per plot (count).

Explanatory (fixed) variables: signs of recent cutting (presence of stumps of anthropogenic origin after recent, <15 years, cuttings), management restrictions (with vs. without restrictions—protected/unprotected), forest type group, dominant tree species, sample plot tree species composition (single-species or mixed), and age of the dominant tree species.

Random effect: sampling team (the NFI team collecting data in each plot).

Model structure and error distributions:

- Count data (number of TreMs and number of TreM forms): Poisson distribution, log link.
- Proportion data: beta distribution, logit link.
- Presence/absence data: binomial distribution, logit link.

Significance testing: the significance of individual explanatory variables was assessed using model-derived *p*-values, with *p* < 0.05 considered statistically significant. To analyze effects at the tree level, only tree species represented by at least 500 trees were included. Generalized additive models (GAMs) from the mgcv R package were used to assess how tree- and stand-level variables influence the total number of TreMs per tree.

Response variable: total number of TreMs per tree (count).

Explanatory (fixed) variables: tree species, tree status (dead or alive), management restrictions, forest type, signs of recent cutting, DBH, tree species composition (mixed vs. single species), and tree species dominance (whether the tree represents the dominant species in the stand).

Random effect: sampling team.

Non-linear effects: DBH was included as a smooth term interacting with tree status (dead or alive), with basis dimension *k* = 4. Diagnostic checks confirmed the basis dimension was adequate (estimated effective degrees of freedom *k'* slightly lower than *k*), indicating no overfitting.

Model structure: Poisson error distribution with log link function. Separate GAMs with the same structure were also fitted for each tree species.

Significance testing: significance of explanatory variables was assessed using model-derived p -values, with $p < 0.05$ considered statistically significant.

All measured factors were included in the models to evaluate their effects explicitly. We tested multiple modeling frameworks (linear models, generalized linear models, and generalized additive models) and selected the approach that best accommodated the data structure, including non-linear relationships and random effects. No formal model selection or model averaging was applied, and all results are derived from the full models.

Spearman correlation was used to assess the relationship between the Shannon diversity index (H'), which accounts for both richness and relative abundance [35], calculated for tree species and for TreM forms at the plot level. The Shannon diversity index is calculated as follows:

$$H' = \sum_{i=1}^S p_i \ln(p_i)$$

where S is the number of species (or TreM forms), and p_i is the proportion of individuals belonging to species (or category) i .

All statistical tests were done in “R” v. 4.2.2. [36]. For data selection, analysis, and visualization following libraries were used: dplyr [37], ggplot2 [38], readxl [39], tidyr [40], lme4 [41], mgcv [42], ggeffects [43].

3. Results

3.1. Differences in TreM Occurrence on the Plot Level

At plot level, factors such as forest type according to soil fertility, management restrictions, dominant tree species, and age of dominant tree species had a significant effect on all analyzed aspects of TreMs—their presence, number of TreMs, proportion of trees with TreMs, as well as number of different forms of the TreMs (Table 2). However, signs of recent cutting did not significantly affect whether at least one TreM was present in a plot.

There was a statistically significant ($p < 0.001$) weak positive ($r = 0.31$) correlation between the Shannon index for tree species and the Shannon index for TreM forms on plot level (Figure 2).

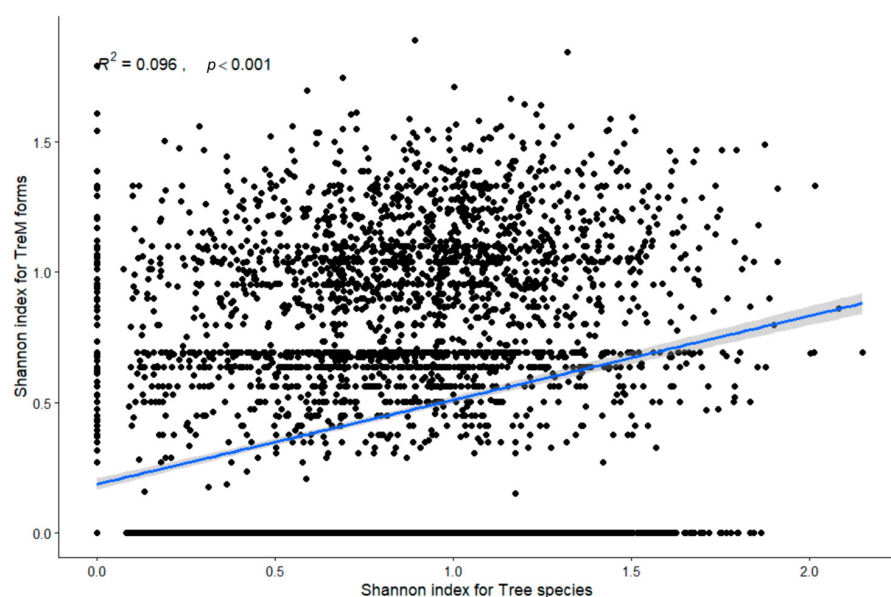


Figure 2. The relationship between the Shannon index for tree species and the Shannon index for TreM forms on plot level.

Table 2. Plot-level effects of forest management, forest type, and tree characteristics on TreM presence and diversity.

Fixed Effect	Presence of TreM		Number of TreMs		Proportion of Trees with TreM		Number of Forms of TreMs	
	Estimate	p-Value	Estimate	p-Value	Estimate	p-Value	Estimate	p-Value
Intercept	−1.16	<0.001	0.62	0.070	−1.77	<0.001	−0.22	0.397
Signs of recent cutting (ref = uncut)	<−0.001	0.991	−0.21	<0.001	0.11	0.004	−0.11	<0.001
Management restrictions (ref = no restrictions)	0.26	0.014	0.09	<0.001	0.12	0.006	0.06	0.031
Forest type according to soil conditions (ref = dry and mesic mineral soils)								
Drained mineral soils	0.31	0.004	−0.06	0.006	−0.01	0.816	0.02	0.634
Drained peat soils	0.44	<0.001	0.13	<0.001	0.10	0.063	0.05	0.205
Wet mineral soils	0.22	0.058	0.02	0.315	0.06	0.272	0.00	0.919
Wet peat soils	0.13	0.315	0.21	<0.001	0.08	0.227	0.02	0.661
Forest type according to soil fertility (ref = eutrophic soils)								
Mesoeutrophic soils	−0.22	0.073	−0.15	<0.001	−0.19	<0.001	−0.08	0.023
Mesotrophic soils	−0.19	0.213	−0.39	<0.001	−0.29	<0.001	−0.19	<0.001
Oligomesotrophic soils	−0.43	0.013	−0.54	<0.001	−0.38	<0.001	−0.29	<0.001
Oligotrophic soils	−1.10	<0.001	−1.00	<0.001	−0.62	<0.001	−0.71	<0.001
Dominant tree species (ref = <i>Pinus sylvestris</i>)								
<i>Picea abies</i>	0.76	<0.001	0.65	<0.001	0.40	<0.001	0.42	<0.001
<i>Betula</i> spp.	0.40	<0.001	0.59	<0.001	0.25	<0.001	0.41	<0.001
<i>Alnus glutinosa</i>	0.98	<0.001	0.83	<0.001	0.51	<0.001	0.59	<0.001
<i>Populus tremula</i>	0.78	<0.001	0.95	<0.001	0.51	<0.001	0.57	<0.001
<i>Alnus incana</i>	0.79	<0.001	0.86	<0.001	0.33	<0.001	0.55	<0.001
<i>Quercus robur</i>	−0.12	0.700	−0.11	0.134	0.04	0.853	−0.01	0.951
<i>Fraxinus excelsior</i>	2.00	0.072	0.94	<0.001	1.07	0.006	0.58	0.019
<i>Tilia cordata</i>	1.71	0.032	0.62	<0.001	1.03	<0.001	0.59	<0.001
<i>Ulmus</i> spp.	0.12	0.947	0.05	0.867	0.20	0.684	0.36	0.317
<i>Salix</i> spp.	1.30	0.240	0.68	<0.001	0.58	0.159	0.60	0.015
<i>Salix caprea</i>	0.93	0.043	0.91	<0.001	0.47	0.039	0.66	<0.001
<i>Acer platanoides</i>	0.06	0.391	−0.04	0.789	0.28	0.349	0.21	0.358
Tree species composition (ref = single-species forests)	0.39	<0.001	0.47	<0.001	0.04	0.306	0.39	<0.001
Age of dominant tree species	0.02	<0.001	0.52	<0.001	0.33	<0.001	0.40	<0.001

Table shows estimate values and p-values according to glmer results. Statistically significant values are highlighted in blue.

3.2. Occurrence of TreMs at the Tree Level

At least one TreM was found on 13.1% of all assessed trees and on 14.8% of trees with DBH greater than 14 cm. In addition, in mature forest stands, at least one TreM was present on 20% of trees with a DBH greater than 14 cm. Among all recorded TreMs, the most frequently observed were bark loss (3.8% of all trees and 6.7% of trees with DBH > 14 cm), bryophytes (1.4% and 3.0%), perennial polypores (1.2% and 2.8%), stem breakage (0.7% and 2.1%), and heavy resinosis (0.9% and 1.8%). TreMs such as chimney trunk rot-hole, lightning scar, myxomycetes (slime moulds), ferns, and mistletoe were among the least common ones (Table 3). For almost all TreM types, the occurrence on tree with DBH ≤ 14 cm was lower than on trees with DBH > 14 cm. There were differences in the frequency of the presence of

different types of TreMs between protected and non-protected forests, for most of TreMs being more frequent in protected forests. However, a few TreMs, as ivy and lianas (woody vines) and heavy resinosis, had higher occurrence in unprotected forests.

Table 3. Weighted occurrence of TreM types in protected and unprotected forests.

TreM Code	TreM Type	Occurrence on All Trees (% of All Trees in the Group)			Occurrence on Trees with $d \leq 14$ cm (%)			Occurrence on Trees with $d > 14$ cm (%)		
		Unprotected	Protected	All	Unprotected	Protected	All	Unprotected	Protected	All
c11	Small woodpecker breeding cavity ($d < 4$ cm)	0.004	0.023	0.007	0.001	0.010	0.003	0.014	0.051	0.021
c12	Medium-sized woodpecker breeding cavity ($d = 4\text{--}7$ cm)	0.014	0.023	0.016	0.001	0.000	0.001	0.057	0.071	0.062
c13	Large woodpecker breeding cavity ($d > 10$ cm)	0.003	0.009	0.004	0.001	0.000	0.001	0.007	0.028	0.012
c14	Woodpecker “Flute” (breeding cavity string)	0.009	0.017	0.010	0.006	0.000	0.005	0.018	0.051	0.025
c21	Trunk-base rot-hole (closed top, ground contact)	0.020	0.110	0.027	0.004	0.010	0.005	0.075	0.318	0.095
c22	Trunk rot-hole (closed top, no ground contact)	0.009	0.030	0.012	0.000	0.010	0.001	0.040	0.072	0.046
c23	Semi-open trunk rot hole	0.006	0.008	0.006	0.001	0.000	0.001	0.020	0.025	0.021
c24	Chimney trunk-base rot-hole (in contact with the ground)	0.002	0.004	0.002	0.000	0.000	0.000	0.008	0.013	0.009
c25	Chimney trunk rot-hole with no ground contact	0.000	0.011	0.002	0.000	0.010	0.001	0.001	0.011	0.003
c26	Hollow branch	0.003	0.003	0.003	0.000	0.000	0.000	0.011	0.008	0.011
c31	Insect galleries and bore holes (hole $d > 1$ cm)	0.007	0.010	0.007	0.004	0.000	0.004	0.014	0.030	0.017
c32	Insect galleries and bore holes (area > 300 cm ²)	0.016	0.033	0.018	0.004	0.020	0.006	0.056	0.059	0.057
c41	Dendrotelm	0.005	0.003	0.005	0.000	0.000	0.000	0.021	0.008	0.019
c42	Woodpecker foraging excavation	0.153	0.270	0.162	0.050	0.082	0.054	0.509	0.661	0.508
c43	Bark-lined trunk concavity	0.003	0.004	0.003	0.000	0.000	0.000	0.011	0.013	0.012
c44	Buttress-root concavity	0.150	0.239	0.162	0.013	0.031	0.015	0.624	0.670	0.633
b11	Bark loss	3.530	5.262	3.776	2.677	4.266	2.877	6.491	7.328	6.653
b12	Fire scar	0.004	0.008	0.005	0.001	0.010	0.003	0.014	0.004	0.012
b13	Bark shelter	0.258	0.564	0.301	0.144	0.338	0.168	0.652	1.035	0.726
b14	Bark pocket	0.109	0.322	0.156	0.048	0.194	0.067	0.320	0.586	0.443
b21	Stem breakage	0.690	1.049	0.741	0.273	0.542	0.307	2.138	2.099	2.131
b22	Limb breakage	0.011	0.015	0.012	0.001	0.000	0.001	0.045	0.047	0.045
b23	Crack	0.075	0.132	0.089	0.024	0.010	0.022	0.252	0.386	0.306
b24	Lightning scar	0.000	0.003	0.001	0.000	0.000	0.000	0.001	0.008	0.002
b25	Fork split at the intersection	0.018	0.032	0.017	0.004	0.000	0.004	0.065	0.098	0.059
b26	Splintered stem	0.029	0.069	0.034	0.003	0.020	0.005	0.117	0.170	0.128
d11	Dead branches	0.055	0.197	0.076	0.000	0.010	0.001	0.248	0.585	0.313
d12	Dead top	0.015	0.037	0.018	0.003	0.000	0.003	0.058	0.115	0.069
d13	Remnants of a broken limb	0.002	0.014	0.003	0.000	0.000	0.000	0.009	0.042	0.014
d14	Dead part of top	0.003	0.007	0.004	0.000	0.000	0.000	0.013	0.021	0.016

Table 3. Cont.

TreM Code	TreM Type	Occurrence on All Trees (% of All Trees in the Group)			Occurrence on Trees with $d \leq 14$ cm (%)			Occurrence on Trees with $d > 14$ cm (%)		
		Unprotected	Protected	All	Unprotected	Protected	All	Unprotected	Protected	All
e11	Witches' broom	0.002	0.010	0.003	0.000	0.000	0.000	0.008	0.030	0.014
e12	Epicormic shoots	0.003	0.014	0.004	0.000	0.000	0.000	0.012	0.042	0.016
e21	Burr	0.022	0.072	0.029	0.000	0.000	0.000	0.098	0.221	0.122
e22	Canker	0.016	0.045	0.021	0.001	0.020	0.004	0.065	0.096	0.074
f11	Perennial polypore	1.059	1.975	1.189	0.622	1.074	0.678	2.579	3.842	2.824
f21	Annual polypore	0.097	0.161	0.110	0.075	0.113	0.080	0.173	0.263	0.206
f22	Pulpy agaric	0.029	0.048	0.032	0.018	0.000	0.015	0.067	0.148	0.086
f23	Large pyrenomycete	0.005	0.004	0.005	0.004	0.000	0.004	0.008	0.013	0.009
f24	Myxomycetes (slime moulds)	0.003	0.007	0.004	0.003	0.010	0.004	0.004	0.000	0.003
a11	Bryophytes	1.329	2.015	1.426	0.896	1.289	0.946	2.832	3.520	2.966
a12	Foliose and fruticose lichens	0.156	0.171	0.158	0.115	0.102	0.113	0.299	0.314	0.302
a13	Ivy and lianas (woody vines)	0.016	0.000	0.013	0.016	0.000	0.014	0.015	0.000	0.010
a14	Ferns	0.001	0.000	0.001	0.000	0.000	0.000	0.006	0.000	0.004
a15	Mistletoe	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
a21	Vertebrate nest ($d > 50$ cm)	0.001	0.010	0.002	0.000	0.000	0.000	0.006	0.030	0.010
a22	Vertebrate nest ($d > 20$ cm)	0.004	0.014	0.006	0.000	0.000	0.000	0.019	0.042	0.024
a23	Vertebrate nest ($d > 10$ cm)	0.037	0.026	0.036	0.032	0.020	0.031	0.055	0.038	0.052
a24	Invertebrate nest	0.005	0.011	0.006	0.000	0.000	0.000	0.023	0.034	0.026
a31	Bark microsoil	0.008	0.006	0.007	0.004	0.000	0.004	0.019	0.017	0.019
a32	Crown microsoil	0.172	0.345	0.197	0.063	0.072	0.064	0.552	0.912	0.622
i11	Sap run	0.008	0.017	0.009	0.004	0.010	0.005	0.021	0.030	0.021
i12	Heavy resinosis	0.878	0.856	0.875	0.569	0.634	0.577	1.953	1.315	1.830

A three-color conditional-formatting scale was applied to the table, where cell color reflects the relative value: low values are shaded in red, intermediate values in white, and high values in blue.

3.3. Factors Affecting TreM Richness on the Tree Level

On the single tree level, the total number of TreMs was significantly affected by tree species, with *Sorbus aucuparia*, *Acer platanoides*, *Salix caprea*, *Populus tremula*, and *Quercus robur* hosting the highest number of TreMs (Table 4). In addition, factors as tree status (alive or dead), DBH, signs of recent cutting, tree species composition, and forest type also had a significant effect on the number of TreMs on a tree. However, management restrictions and tree species dominance had no significant effect on a tree level.

Table 4. Tree-level effects of tree species, tree status, management restrictions, forest type, and DBH on the presence of the total number of TreMs (response variable in the model).

Fixed Effect	Estimate	SE	Z Value	p-Value
Intercept	−1.06	0.26	−4.00	<0.001
Tree species (ref = <i>Pinus sylvestris</i>)				
<i>Picea abies</i>	0.33	0.02	15.69	<0.001
<i>Betula</i> spp.	0.28	0.02	12.95	<0.001
<i>Alnus glutinosa</i>	0.41	0.03	13.01	<0.001
<i>Populus tremula</i>	0.51	0.03	16.84	<0.001

Table 4. Cont.

Fixed Effect	Estimate	SE	Z Value	p-Value
<i>Alnus incana</i>	0.22	0.03	7.71	<0.001
<i>Quercus robur</i>	0.49	0.06	8.25	<0.001
<i>Fraxinus excelsior</i>	0.08	0.05	1.52	0.128
<i>Tilia cordata</i>	0.23	0.10	2.29	0.022
<i>Ulmus</i> spp.	0.13	0.10	1.31	0.19
<i>Salix caprea</i>	0.59	0.04	14.76	<0.001
<i>Acer platanoides</i>	0.60	0.11	5.39	<0.001
<i>Sorbus aucuparia</i>	0.80	0.10	7.75	<0.001
Alive tree (ref = dead tree)	−2.35	0.01	−175.60	<0.001
Management restrictions (ref = no restrictions)	0.02	0.02	1.084	0.278
Signs of recent cutting (ref = uncut)	−0.13	0.02	−6.82	<0.001
Forest type group according to soil condition (ref = dry and mesic mineral soils)				
Drained mineral soils	0.01	0.02	0.832	0.406
Drained peat soils	0.08	0.02	4.28	<0.001
Wet mineral soils	0.08	0.02	5.78	<0.001
Wet peat soils	0.12	0.02	5.78	<0.001
Forest type according to soil fertility (ref = eutrophic soils)				
Mesoeutrophic soils	−0.07	0.02	−3.94	<0.001
Mesotrophic soils	−0.09	0.03	−3.61	<0.001
Oligomesotrophic soils	−0.12	0.03	−3.86	<0.001
Oligotrophic soils	−0.09	0.05	−1.85	0.064
Tree species composition (ref = single-species forests)	0.14	0.02	6.65	<0.001
Tree species dominance (ref = tree from dominant tree species)	−0.01	0.01	−1.11	0.265
DBH	Chi.sq:	5370		<0.001

The table shows estimated values and *p*-values according to the GAM model results. Statistically significant values are highlighted in blue.

The number of TreMs was higher for dead trees compared to living trees for most of the compared species (Figure 3). The number of TreMs increases with increasing DBH for all the species; however, the pattern by which it changes differs. For example, a more rapid increase in the number of TreMs was for *Betula* spp., *Picea abies*, and *Pinus sylvestris* after DBH increased over 60 cm. While the increase in the number of TreMs seems gradual across all the included DBH ranges for *Tilia cordata* and *Acer platanoides* without having such a turning point.

Epiphytic and epixylic structures and tree injuries and exposed wood on live trees were more common on deciduous tree species compared to conifers (Table 5). Crown deadwood was more frequently on *Quercus robur* than on other species. Excrescences were similarly rare on all the compared species except from *Sorbus aucuparia*. However, exudates were quite rare on all the species except for *Picea abies*.

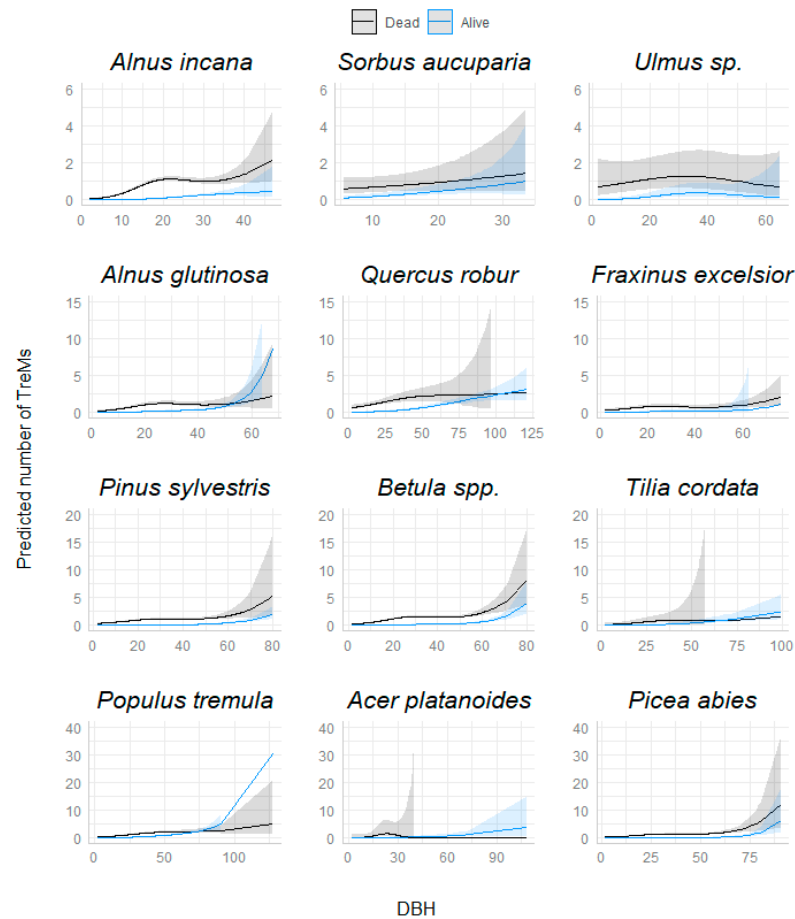


Figure 3. Predicted number of TreMs depending on tree DBH by tree species on alive and dead trees. Graphs showing GAM model results. NB! DBH scale is different by species.

Table 5. Weighted occurrence (% of trees) of different TreM forms by tree species on alive trees.

Tree Species	Epiphytic and Epixylic Structures	Tree Injuries and Exposed Wood	Cavities	Crown Deadwood	Excrescences	Fruiting Bodies of Saproxylic Fungi and Slime Moulds	Exudates
<i>Pinus sylvestris</i>	0.24	1.11	0.10	0.40	0.14	0.16	0.28
<i>Picea abies</i>	0.45	0.83	0.24	0.01	0.01	0.02	3.99
<i>Betula spp.</i>	0.66	0.36	0.39	0.04	0.11	0.23	0.05
<i>Alnus glutinosa</i>	2.39	0.47	1.10	0.07	0.08	0.22	0.00
<i>Populus tremula</i>	0.13	2.43	0.13	0.17	0.03	1.96	0.00
<i>Alnus incana</i>	0.38	0.41	0.12	0.07	0.03	0.11	0.00
<i>Quercus robur</i>	2.03	2.11	0.20	1.18	0.09	0.16	0.04
<i>Fraxinus excelsior</i>	0.31	0.36	0.16	0.16	0.00	0.10	0.00
<i>Tilia cordata</i>	1.56	0.46	0.17	0.14	0.00	0.07	0.00
<i>Ulmus spp.</i>	0.16	1.97	0.05	0.47	0.05	0.05	0.10
<i>Salix caprea</i>	1.27	4.89	0.50	0.25	0.06	0.73	0.01
<i>Acer platanoides</i>	0.99	1.25	0.18	0.23	0.02	0.16	0.00
<i>Sorbus aucuparia</i>	3.18	3.78	0.90	0.00	0.42	0.71	0.00

A three-color conditional-formatting scale was applied to the table, where cell color reflects the relative value: low values are shaded in red, intermediate values in white, and high values in blue.

While a higher proportion of dead trees compared to living trees had TreMs, epiphytic and epixylic structures, tree injuries, exposed wood, cavities, and fruiting bodies of saprox-

lytic fungi and slime moulds, the occurrence of excrescences and exudates was similarly low (Table 6). Approximately 15% of dead *Quercus robur* and 20% of dead *Fraxinus excelsior* trees had epiphytic and epixylic structures. Tree injuries and exposed wood were mostly recorded on *Pinus sylvestris* and *Ulmus* sp., while fruiting bodies of saproxylic fungi and slime moulds were most common on dead *Betula* spp. trees (21.5%).

Table 6. Weighted occurrence (% of trees) of different TreM forms by tree species on dead trees.

Tree Species	Epiphytic and Epixylic Structures	Tree Injuries and Exposed Wood	Cavities	Excrescences	Fruiting Bodies of Saproxylic Fungi and Slime Moulds	Exudates
<i>Pinus sylvestris</i>	8.88	48.88	1.66	0.04	1.81	0.04
<i>Picea abies</i>	8.57	30.80	0.71	0.00	2.61	0.30
<i>Betula</i> spp.	7.22	22.80	1.71	0.05	21.49	0.01
<i>Alnus glutinosa</i>	13.60	28.35	3.15	0.00	7.37	0.00
<i>Populus tremula</i>	5.51	21.76	1.20	0.05	4.28	0.00
<i>Alnus incana</i>	6.59	22.25	1.59	0.00	6.45	0.00
<i>Quercus robur</i>	15.40	40.55	1.34	0.00	4.93	0.00
<i>Fraxinus excelsior</i>	19.96	33.43	2.03	0.09	1.41	0.00
<i>Tilia cordata</i>	6.31	14.23	0.00	0.00	6.87	0.00
<i>Ulmus</i> spp.	6.28	76.90	1.86	0.00	3.16	0.00
<i>Salix caprea</i>	13.76	30.99	1.92	0.00	4.91	0.00
<i>Acer platanoides</i>	10.53	7.02	0.00	0.00	0.00	0.00
<i>Sorbus aucuparia</i>	14.00	16.64	0.00	0.00	4.57	0.00

A three-color conditional-formatting scale was applied to the table, where cell color reflects the relative value: low values are shaded in red, intermediate values in white, and high values in blue.

4. Discussion

TreMs serve as habitats, nesting sites, shelters, or food sources for various organisms, including invertebrates, vertebrates, and epiphytic species [4]. Although they have potentially important value in hosting various groups of species [7], TreM are not always abundant, and their occurrence can vary between regions and forest types. For example, in our study only 13.1% of all the trees and 14.8% of trees with DBH > 14 cm had at least one TreM. In contrast, in other studies, the proportion of trees has usually been higher like 23% of trees in mature production forests in Lithuania [22]. In our study selecting data from only mature stands and for trees with DBH > 14 cm, we had similar results, more specifically—20% of the trees had at least one TreM. The proportion of trees with TreMs is much greater in studies focused on potential habitat trees (DBH ≥ 50 cm) (72% trees with TreMs) or retention trees (61%) [44,45]. However, in our study, the most commonly found TreM was bark loss, which was found only on 6 to 7% of all the trees (Table 3), while the vast majority of TreM types were present on less than 1% of trees both in protected and unprotected forests.

The frequency of different TreM types in managed and natural forests in central Europe has been published by Bütler et al. [32]. Comparing to their results, we could suggest that there are slight differences in northern Europe. For example, buttress-root concavities and ivies and lianas were common in Switzerland [32] but had low relative occurrence in our study (Table 3). Smaller occurrence of buttress-root concavities in hemiboreal forests might be explained by the differences in tree species composition—this TreM is frequently recorded on *Fagus sylvatica* in terms of the number of individual TreMs (pieces) [46], which is a common species in central Europe but not a native species in most parts of northern Europe [47]. Similarly, ivies and lianas in central Europe might be represented by several

species, such as *Hedera* spp., *Humulus lupulus*, and *Clematis vitalba* for many of which northern Europe is out of their distribution area [48,49], while in Latvia this TreM type could be represented by *Hedera helix* or *Humulus lupulus*.

Although there are slight differences in the occurrence of particular TreMs in different parts of Europe, the overall factors influencing their richness seem to be the same as already found in previous studies—the total number of TreMs increases with larger DBH trees, and deciduous trees have a greater richness of TreMs than conifers (Table 4) [9,10]. The predicted number of TreMs for multiple species increased more rapidly after reaching a specific turning point of DBH value (Figure 3). It is also important to keep in mind that certain types of TreMs could even theoretically be present on trees starting from a certain diameter; for example, cavities of a certain size could not be present on trees of small sizes.

We also observed that some factors were significant only at the plot level, but not at the tree level—for example, management restrictions (Tables 2 and 4), which is expected because all trees within a plot share the same values for these attributes (e.g., forest type, management type). The higher number of TreMs and the greater proportion of trees bearing TreMs in protected forests are largely driven by stand-level characteristics—such as a higher abundance of large, old, and dead trees—that are more typical of unmanaged stands. In contrast, at the individual-tree level, management restrictions themselves did not significantly affect TreM richness, suggesting that similar tree-level patterns can also be found outside protected areas when comparable tree attributes are present. This finding indicates that the conservation of TreMs can be supported in production forests through retention of large trees and deadwood, highlighting that habitat-friendly management practices may complement protected areas in maintaining biodiversity. Also, Vuidot et al. [9] found that, when controlling for tree size and site conditions, management type alone did not significantly influence the occurrence of TreM. However, that might not always be true—management might also have an impact on the formation of a specific TreMs; for instance, Courbaud et al. [11] found that dendrotelm had higher formation rates in managed forests, which was explained by the fact that they often result from harvesting a tree on a twinstem or a coppice stump. In our study, site-specific factors such as recent cutting, forest type, and tree species composition significantly affected TreM abundance at both plot and tree scale (Tables 2 and 4), likely through their influence on stand structure, availability of large trees, and disturbance and decay processes. Similar studies have shown that plot-level context explains a large share of variation in TreM occurrence [12] and that topographic conditions can further influence TreM formation [10]. In Latvia, key plot-level variables such as forest type, dominant species, and management history are available from the National Forest Inventory and allow analyses like those presented here; however, finer-scale environmental variables (e.g., microtopography or microclimate) are not consistently recorded and could not be assessed in the present study. Tree species are an important factor influencing the biodiversity associated with trees, including epiphyte richness [50], invertebrate [51] and vertebrate [52] communities, and the diversity of tree-related microhabitats (TreMs), as discussed previously. Each tree species provides a specific set of conditions—for instance, through differences in bark chemistry (e.g., pH and nutrient content) [53], bark and wood structure (thickness, fissuring, porosity) [54,55], wood-decay dynamics [56], branching architecture and crown form [57]. These factors, in turn, influence the likelihood and nature of tree-related microhabitats (TreMs) forming on them. The results of our study clearly show that, for example, exudates are much more common on living *Picea abies* than on other tree species, while *Populus tremula* stands out with a higher occurrence of fruiting bodies of saproxylic fungi and slime molds, and the highest occurrence of crown deadwood was observed on *Quercus robur* (Table 5). Similar results were reported in the hemiboreal zone by Brazaityte et al. [22]. It is important to

highlight that some tree species are crucial for providing specific TreMs, even if they do not have the greatest overall TreM diversity, as seen in *Picea abies*. The differences between tree species might be the main reason why TreM diversity was significantly positively correlated to tree species diversity in the plot level (Figure 2). However, the differences among tree species are not important only on living trees, but also on dead trees; moreover, there are differences between alive and dead trees even within the same species (Tables 5 and 6).

Dead wood possesses unique physical and chemical properties that create specialized habitats, and it is widely recognized as a key component for maintaining biodiversity in forest ecosystems [58]. Our study shows that the total number of TreMs on dead wood is higher than on live trees for most of the compared tree species (Figure 3), which is consistent with the findings of Jansone et al. [45] on retention trees. It is important to note that crown deadwood was not assessed for snags and logs in our study (see Materials and Methods); therefore, the actual TreM richness on deadwood may be even higher than recorded. The higher occurrence of epiphytic and epixylic structures, exposed wood, and fruiting bodies of saproxylic fungi and slime moulds on dead trees reflects the key role of tree death and subsequent decay processes in TreM development. Dead wood provides stable substrates and microclimatic conditions that favour colonisation by saproxylic organisms, a pattern widely reported in forest ecosystems [59]. The particularly high occurrence of fungal and slime mould fruiting bodies on dead *Betula* spp. may be linked to its rapid decomposition and wood properties conducive to fungal growth [60], whereas the relatively small difference observed for *Populus tremula* suggests that this species can host such TreMs already on living trees due to internal decay [61]. Although we do not propose a specific deadwood volume threshold, our results support management practices that retain sufficient quantities and a diversity of deadwood types and tree species within managed forests, as such structural elements are crucial for sustaining TreM-associated biodiversity. The optimal amount of dead wood is likely to be context dependent, varying with forest type, stand structure, and management history.

The results from our study offer valuable insight into the occurrence patterns and factors influencing TreM diversity in the hemiboreal region, as our data included both managed and unmanaged forests across different age classes and a broad spatial (territorial) distribution of sampling plots across the country. However, it is important to note that in Latvia, since 1997, guidelines have required that old and wind-resistant trees, hollow trees, and trees with large bird nests be left in clearcuts, leaving a total of 5–10 trees per hectare [62]. Therefore, the TreM richness shown in this study for managed forests may differ from those in other hemiboreal forests that have been managed without such restrictions. In addition, several limitations should be considered when interpreting the data. For instance, the data collection period spanned from April 1 to October 31, which may have affected the TreMs that could be observed at specific times of the year. Certain features, such as fungi, might not have been registered due to seasonal constraints, and some TreMs in the tree crown may have been difficult to detect on leafy trees (e.g., in summer compared to early spring or late autumn). Fungal fruiting bodies are known to exhibit strong seasonal dynamics, with species richness and composition differing markedly among seasons and many taxa fruiting preferentially in spring or autumn rather than summer, which can lead to underestimation in seasonally restricted surveys [63,64]. Additionally, it is important to note that all TreM assessments were conducted as part of general forest inventories rather than with the explicit purpose of recording TreMs, which likely resulted in a lower probability of detection compared to studies focused specifically on TreM identification. However, the NFI method is designed such that the same plots will be remeasured every five years at approximately the same time of year (± 20 days), thereby providing the opportunity for future assessments of temporal trends in TreM dynamics.

5. Conclusions

TreMs such as buttress-root concavities and ivy or liana cover, which are common in temperate Europe, had a low relative occurrence in our study. TreMs were significantly more numerous, and occurred on a higher proportion of trees, in protected forests compared to unprotected forests, largely reflecting differences in stand structure. At the tree level, however, TreM richness did not differ between management regimes, indicating that tree-level drivers—such as tree size, species, and living status—are consistent across forest types. Overall, TreMs occurred more frequently on deciduous than on coniferous trees, on larger trees (with higher DBH), and on dead trees compared to living ones. The occurrence of specific TreM forms was strongly tree-species-dependent: exudates were much more common on live *Picea abies* than on other species, whereas *Populus tremula* had a higher occurrence of fruiting bodies of saproxylic fungi and slime moulds. The highest occurrence of crown deadwood was observed on *Quercus robur*. Overall, dead trees play a particularly important role, providing both a higher total number of TreMs and certain TreM types more frequently. Based on our findings, forest management should retain large living trees and deadwood, promote mixed-species stands, and consider tree-species-specific TreM patterns to improve the quantity and quality of TreMs and support forest biodiversity.

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Abbreviations

The following abbreviations are used in this manuscript:

DBH	Diameter at Breast Height
NFI	National Forest Inventory
TreMs	Tree-Related Microhabitats

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