



Tree-related microhabitats in mixed hemiboreal forests

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Tree-related microhabitats in mixed hemiboreal forests.

Trädrelaterade microhabitat i hemiboreal blandskog.

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Keywords: TreMs, Tree-related Microhabitats, Hemiboreal forest, Mixed forest, Abundance, Richness

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Abstract

In more recent years, tree-related microhabitats (TreMs) have gained attention as an indicator of structural diversity. TreMs are morphological structures occurring on standing trees, dead or alive, that constitutes an important life site for a species. Most of the existing TreM studies have been performed in temperate broadleaved forests, temperate coniferous forests and mediterranean forests. However, there is a gap in the research about TreMs in the boreal and hemiboreal regions of northern Europe, and knowledge about TreM abundance and richness is very limited for the hemiboreal forest zone.

The aim of this thesis is to expand the knowledge about TreMs in the hemiboreal region of southern Sweden by looking at TreM richness and abundance at the tree level. A TreM inventory performed in southern Sweden showed that both TreM abundance and TreM richness was higher in broadleaved trees than in conifers, that tree species influence abundance and richness, and that both abundance and richness increase with diameter at breast height. A literature review of existing research from the temperate region was conducted and the results supported the findings of the TreM inventory. It is possible to conclude that TreM abundance and richness follow similar patterns in the hemiboreal region as in the temperate region.

Keywords: TreMs, Tree-related Microhabitats, Hemiboreal forest, Mixed forest, Abundance, Richness

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Abbreviations

C	Celsius
DBH	Diameter at breast height
df	Degrees of freedom
FTBA	Forest types for biodiversity assessment
NFIs	National forest inventories
TreM(s)	Tree-related microhabitat(s)
WoS	Web of science

1. Introduction

Forests cover almost a third of all land on earth (FAO 2020) and host 80% of all terrestrial biodiversity (World Commission on Forests and Sustainable Development 1999). Forests are a key natural resource that can act as a carbon sink and potentially reduce the impact of climate change (Harris et al. 2021). However, climate change, together with overexploitation, have caused significant degradation of forests, and biodiversity loss, worldwide (Puettmann et al. 2009). Because of anthropogenic impacts primary forests, which are remnants of forests without human influence, have become important references of natural ecosystems for restoring natural elements in production forests (Martin et al. 2022).

Biodiversity is the complex of species that constitute our world (Hancock n.d.). Three aspects of biodiversity that are widely recognised are composition, structure, and function (Larsson 2001). Factors that affect biodiversity have been further developed from these aspects and can be biotic, abiotic, or anthropogenic (Larsson 2001). Human induced change in our environment such as introduction of invasive species, climate change, pollution, and intensive cuttings pose a serious threat to biodiversity (Chirici et al. 2012). Climate change alters forest functioning and increases trees vulnerability to disturbances, whereas natural disturbances can decrease productivity, but at the same time, increase forest diversity (Witzell et al. 2022). Managing a rich species diversity is a key strategic move in combating the effects of climate change since species diversity can mimic natural forest structures and can reduce the risk of pest outbreaks through reducing the density of susceptible hosts (Witzell et al. 2022). Monocultures are a common way of yielding high timber production, but they support less biodiversity than mixed or natural forests (Gamfeldt et al. 2013; Witzell et al. 2022). Contrary, the use of mixed forests is a practical measure to increase diversity and mitigate the effects of climate change (Witzell et al. 2022) without compromising productivity (Schwarz & Bauhus 2019). Mixed forests are forest stands with two or more tree species (Merriam-Webster Dictionary n.d.). Structural traits such as canopy layers, patchiness and variations in tree density comprise a variety of different attributes that can contribute to structural diversity (Witzell et al. 2022). Tree species (compositional) diversity is the key attribute for forest diversity and can be described at different scales (alpha, beta, or gamma, Morris et al. 2014), but also through evenness and abundance

(Witzell et al. 2022). Tree species diversity is heavily affected by management practices, and selection of tree species has a serious effect on biodiversity (Witzell et al. 2022).

1.1 Biodiversity inventory

Due to its complexity, total biodiversity is complicated to measure, and the knowledge and resources needed to do so are very limited today (Larsson 2001). Biodiversity surveys are often focused on small taxonomic groups such as vascular plants or vertebrates because of practicality, although this limits its applicability (Martin et al. 2022). Acquiring reliable recordings of biota requires taxonomic experts and is expensive (Winter et al. 2008), therefore indirect methods of assessing biodiversity have been developed, especially for assessing species diversity (Larsson 2001).

An indirect method to assess biodiversity is the use of indicators. Indicators of biodiversity are defined as qualitative or quantitative structures that can be assessed, and when observed regularly can demonstrate trends (Winter et al. 2008). Although this definition is established, there is little available data for assessing indicators, and the consistency on an international level is absent (Winter et al. 2008). General forest structures and characteristics that can be used as indicators, which are thought to be essential for biodiversity, are horizontal and vertical forest structures, tree species composition, tree diameter, tree age, regeneration, and dead wood quantity and quality (Chirici et al 2012). Deadwood quantity and quality is recorded in many national forest inventories (NFIs) around Europe, and that data can be used to assess biodiversity (Winter et al. 2008). Another indirect method to assess biodiversity is forest types for biodiversity assessment (FTBAs, Larsson 2001). FTBA is a sectioning of European forests based on their structures, features and key factors that support forest biodiversity (Larsson 2001). In more recent years, tree-related microhabitats (TreMs) have gained attention as an indicator of structural diversity (Larrieu et al. 2018).

1.2 Tree-related microhabitats

TreMs are morphological structures occurring on standing trees, dead or alive, that constitutes an important life site for a species for parts of, or their whole, lifecycle (Larrieu et al. 2018). For many years TreMs has been studied individually as characteristics on trees related to biodiversity without any standardised typology or inventory methods (Larrieu et al. 2018). The definition and interpretation of what a

TreM is, and which features were recorded, varied between different studies which inhibited the comparison between studies (Larrieu et al. 2018). In 2018, Larrieu et al. developed clear definitions for what TreMs are and suggested a hierarchical list and methodology for recording TreMs for temperate and Mediterranean forests. Their aim was to provide a baseline for common application in monitoring TreMs to be able to compare future studies with each other (Larrieu et al. 2018). Larrieu et al. (2018) developed their TreM typology to have a strong relevance in morphology and strong connections to biodiversity.

TreMs can originate from both biotic and abiotic factors, and they can be tree-originating or caused by external agents (Larrieu et al. 2018). Tree-originating TreMs are composed only with material from the tree itself, on the contrary to TreMs caused by external agents where material is added. Tree-originating TreMs caused by biotic factors are for example insect galleries and woodpecker breeding cavities (Figure 1), and examples of tree-originating TreMs caused by abiotic factors are stem breakage caused by wind or fire scars (Larrieu et al. 2018). Examples of TreMs originating from external factors are nests and epiphytic or parasitic structures such as bryophytes or mistletoes (Larrieu et al. 2018). TreMs are ever changing and constantly developing structures and can therefore be considered short-lived (Larrieu et al. 2018). Winter & Möller (2008) found that trees with larger diameter at breast height (DBH) have a higher abundance of TreMs in unmanaged forests. Generally, larger or older trees are more likely to bear TreMs and broadleaves tend to host more, and a greater diversity of TreMs than conifers within the same DBH class (Martin et al. 2022).

TreMs constitute small, or parts of, habitats for specialised species and provide microclimatic conditions and substrates where specialised taxa forage, breed, or shelter (Larrieu et al. 2018). This highlights the link between TreMs and species and guilds (Larrieu et al. 2018). Some TreMs provide a more humid climate than the surrounding environment, while others provide a drier climate (Larrieu et al. 2018). Certain types of TreMs, mainly rot holes, can provide either a drier or a wetter environment depending on the surrounding conditions (Larrieu et al. 2018). By creating these small habitats TreMs contribute to internal heterogeneity within forest stands (Larrieu et al. 2018). A wide variety of organisms use TreMs in parts of their life cycle, such as insects, gastropods, arachnids, birds, mammals, amphibians and reptiles, lichens, bryophytes, and fungi. The taxonomic group that has the most known users of TreMs are arthropods (Larrieu et al. 2018). Other prominent users of TreMs are vertebrates (Larrieu et al. 2018). Wood decaying fungi utilises TreMs for colonisation entries as they provide important substrates for the fungi (Larrieu et al. 2018). The number of bryophytes and lichens that are specialised in TreMs are limited (Larrieu et al. 2018).

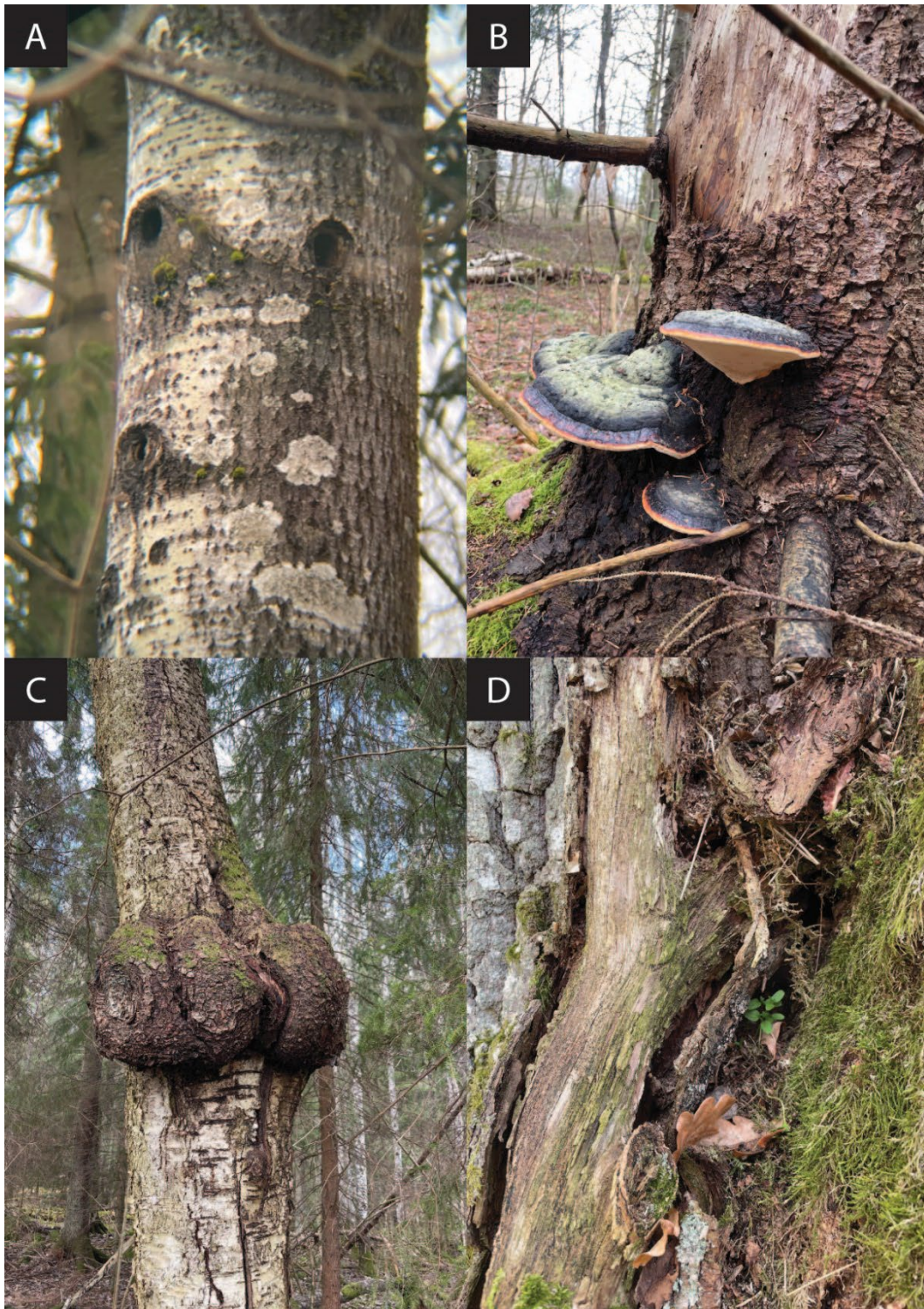


Figure 1. Three medium sized woodpecker breeding cavities on an aspen tree (A). Perennial polypores on a standing dead spruce (B). A big burr covering almost half of the circumference of the stem on a birch (C). Microsoil in a fork on an old oak, and bark loss (D).

1.3 Thesis aim

TreMs have been described as meaningful indicators of biodiversity at stand level (Larrieu et al. 2018). Most of the existing TreM studies have been performed in temperate broadleaved (or mixed) forests, temperate coniferous forests and mediterranean forests (Martin et al. 2022). However, there is a gap in the research about TreMs in the boreal and hemiboreal regions of northern Europe, and knowledge about TreM abundance and richness is very limited for the hemiboreal forest zone.

The aim of this thesis is to expand the knowledge about TreMs in the hemiboreal region of southern Sweden by looking at TreM richness and abundance at the tree level. The focus will be on continuous-cover mixed forests as a potentially diverse forest type that will allow for a comparison with existing literature.

1.3.1 Research question

How does tree species identity and size, described through DBH, affect the abundance and richness of TreMs? What relationship can be found between TreM types and tree species?

1.3.2 Hypotheses

The hypotheses are that (1) TreM types differ between tree species, (2) broadleaved trees host a higher number of TreMs than conifers and (3) larger trees have a higher number of TreMs.

1.3.3 Implementation and delimitations

This study will be conducted through data collection in the field together with data analyses and a literature review comparing the findings with existing findings from temperate forests. This study will only address mixed forests and will only use the data from four different study sites.

2. Methods

This study contains two different methods. An inventory of TreMs in the field and a literature review.

2.1 TreM inventory

Four different study sites were assessed: Slaka, Motala, Stöpen and Strakaskogen (Figure 2). These four sites are part of an established network of sample plots studying the effects on managed and unmanaged mixed forests. Each study site is composed of two stands, one managed through selective cutting and one unmanaged. The most common tree species are oaks (*Quercus* spp.), trembling aspen (*Populus tremula*), Norway spruce (*Picea abies*), and birches (both *Betula pendula* and *Betula pubescens*, hereafter grouped under birch).

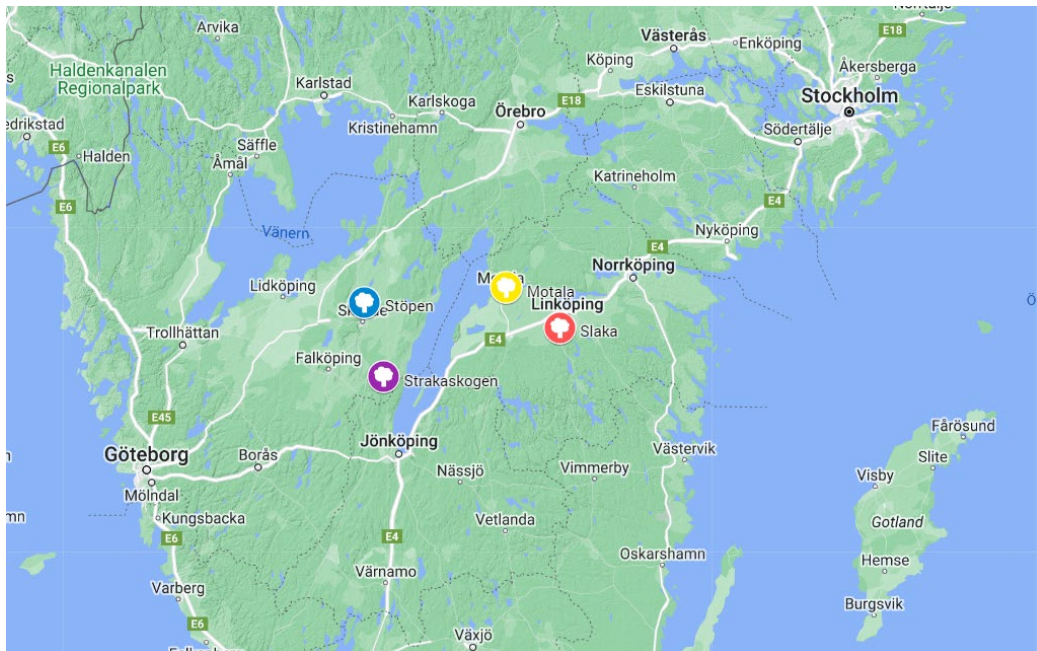


Figure 2. Map visualising the location of the four study sites: Slaka, Motala, Stöpen and Strakaskogen in southern Sweden. Slaka is marked with a red dot, Motala with yellow, Stöpen with blue, and Strakaskogen with purple. Kartdata ©2024 GeoBasis-DE/BKG (©2009), Google.

All study sites are located in southern Sweden, in the hemiboreal region. The hemiboreal region is a zone between the temperate and the boreal region (Skogsencyklopedin 2000). The main features in the hemiboreal region comes from the boreal forests, conifers are dominant, but patches of broadleaves break up the landscape (Skogsencyklopedin 2000). Common broadleaves in this region are oaks, birch and Norway maple (*Acer platanoides*). The climate in this region is characterised by cold winters and long warm summers (Skogsencyklopedin 2000). Mean temperature in winter (December to February) is around -1.4°C (SMHI 2021a), with an average precipitation of 121 mm (SMHI 2021b). In summer (May to September) the mean temperature is 14.4°C (SMHI 2021a), with an average precipitation of 308 mm (SMHI 2021b).

Larrieu et al. (2018) typology start at a general level with seven forms, then gets more specific with 15 groups which are further divided into 47 distinct types. The seven general forms were identified based on physiognomy and functional characteristics (Larrieu et al. 2018). These seven forms are (1) cavities, (2) injuries, (3) crown deadwood, (4) excrescences, (5) fungal fruiting bodies and slime moulds, (6) epiphytic and epixylic structures, and (7) exudates (Larrieu et al. 2018). The full hierarchical typology, including forms, groups, and types are presented in Appendix 1.

1. Cavities are different forms of holes and shelters created in the wood that provide buffered climatic conditions or nesting sites for many different taxa (Larrieu et al. 2018). Cavities can be created by cavity builders, like woodpeckers or saproxylic insects, decay processes, or morphological characteristics (Larrieu et al. 2018).
2. Injuries expose the trees sapwood, and in some cases also the heartwood, and are most often caused by mechanical damage such as limb breakage from wind, snow, or ice (Larrieu et al. 2018). Lightning strike or forest fires can also create injuries. This TreM form provides access for colonising taxa to enter the wood, and injuries can evolve to rot holes if the tree is not able to seal the wound (Larrieu et al. 2018).
3. Crown deadwood occurs in the crown when branches, and in some cases the top, have died and remain in the crown (Larrieu et al. 2018). The dead branches often create warm dry environments due to their position in the crown (Larrieu et al. 2018).
4. Excrescences are increased growth as a reaction to increased sunlight or parasitic or microbial intrusions on the stem (Larrieu et al. 2018). In Figure 1, picture C illustrates a burr which is a TreM type under the excrescences form.
5. Fungal fruiting bodies and slime moulds are the visible part of saproxylic fungi (Larrieu et al. 2018). They can be either perennial (Figure 1), lasting more than one year, or ephemeral, lasting less than a year.
6. Epiphytic and epixylic structures is a broad form that includes a wide variety of structures where the tree is a physical support on which the TreM grows or exists (Larrieu et al. 2018). The form includes different

organisms growing on the tree, like bryophytes or lichens, nests and microsoils that have developed from decaying organic material (Larrieu et al. 2018). Microsoils (Figure1) can occur in forks or flat areas in the crown as well as the trunk bark (Larrieu et al. 2018).

7. Exudates are created by sap runs or heavy resinosis (Larrieu et al. 2018).

The data collection was performed together with my supervisor, this is because reliable recordings of TreMs require a high level of expertise (Winter et al. 2008). Microhabitat inventories are particularly prone to observer effects (Paillet et al. 2015) because thresholds are assessed subjectively. Performing the data collection together with my supervisor also aims at minimising the observer effects. The inventory was conducted in late March before leaf flushing in accordance with Larrieu et al. (2018) recommendation to avoid leaves inhibiting the view of the canopy and minimise the risk of missing TreMs higher up in the canopies.

TreM data was collected in two sample plots, randomly selected, of variable sizes in each of the two stands at the four study sites by applying an angle-count sampling (a total of 16 sample plots). The angle-count sampling, also known as the Bitterlich approach, uses a relascope to choose sample trees and is commonly used for TreM inventories (Larrieu & Cabanettes 2012). When using angle-count sampling the trees are selected with a probability that is proportional to their size, allowing a high sampling rate of big trees that are richer in microhabitats (Winter & Möller 2008). All standing trees, dead or alive, were individually assessed following Larrieu et al. (2018) typology recording TreM types. The trunk of the trees was carefully observed from all angles both at a distance and close to the stem. Starting at a distance, the tree was observed from top to bottom to spot big obvious TreMs such as dead branches, dead top or bryophytes etc. Binoculars were used to assess the crown and the stem higher up towards the crown. Moving closer, smaller less obvious TreMs such as different types of rot holes and insect galleries were observed. Each TreM type was recorded as present or absent. Additionally, DBH was measured using a diameter measuring tape. For each tree species identity and status (dead or alive) was recorded. Since the inventory was performed in late March there were no leaves on the trees that could help with identification, thus tree species were determined looking at species specific traits such as bark and buds. A total of 236 trees of 12 different species were assessed. Five broadleaved species, hazel (*Corylus avellana*), European ash (*Fraxinus excelsior*), wild cherry (*Prunus avium*), goat willow (*Salix caprea*) and small-leaved lime (*Tilia cordata*) occurred at low frequencies and were therefore grouped under “other”.

Finally, TreM richness and abundance was calculated. TreM richness is defined as the number of different TreM groups on each tree and TreM abundance as the total number of TreM types on each tree.

Statistical analyses were made using R. As a preliminary analysis the Lilliefors (Kolmogorov-Smirnov) test was used, using the “*lillie.test*” function, to evaluate the datasets normality and see if a parametric or non-parametric analysis of variance would be applicable. The Lilliefors normality test showed that neither the TreM abundance nor richness in the dataset follow a normal distribution curve (the P-value was below 0.05), thus the non-parametric Kruskal-Wallis analysis of variance was used. The differences between tree species, status (dead or alive), and broadleaves versus conifers were analysed assessing total abundance, total richness, and occurrence of the five most common TreM types. For this the “*kruskal.test*” function was used. After this Dunn’s test was used for pairwise comparison between tree species using the “*dunn.test*” function in R. To test the relationship between DBH and abundance and richness of TreMs a regression analysis was performed with the “*lm*” function in R. The “*scatterplot*” function was used to visualise the results. Two regression analyses were performed, one with all tree species combined, and one with oaks, the most frequently occurring tree species.

2.2 Literature review

A systematic literature review was developed on the 10th of April 2024 using Web of Science’s (WoS) database core collection. The review began with defining relevant keywords. To target TreM studies performed in temperate forests of central Europe the words and phrases; TreMs, temperate forests and central Europe was chosen. To widen the search, and find more relevant sources, words of similar meaning that can be used interchangeably with the key words was added, e.g. TreM, tree related microhabitat, microhabitat etc. With the keywords and added words the final search string was developed:

TS = (TreM OR TreMs OR “tree related microhabitat” OR microhabitat*) AND (“temperate forests” OR “temperate zone*” OR temperate) AND (“central Europe” OR Europe OR Fennoscandia OR European)

This search string resulted in 127 hits. To find articles relevant for this study screening of titles, keywords, and abstracts was performed. To be able to compare my results with the existing literature the chosen articles must use the same or similar typology as used in the TreM inventory. All articles must also be written in English. The screening started with looking at the title and titles with associations to specific taxa were excluded. For the titles that did not include terms related to TreMs, the abstracts were screened to see if the articles were relevant. Articles that used modelling to assess TreMs were excluded to only include actual recordings of

TreMs. Additionally, articles that related TreM abundance to land tenure were also excluded since that is not relevant for the aim of this study. After full text screening two papers were excluded because they only presented results for one tree species. Three additional articles were added during the review process (Figure 3). The final number of selected articles was 12.

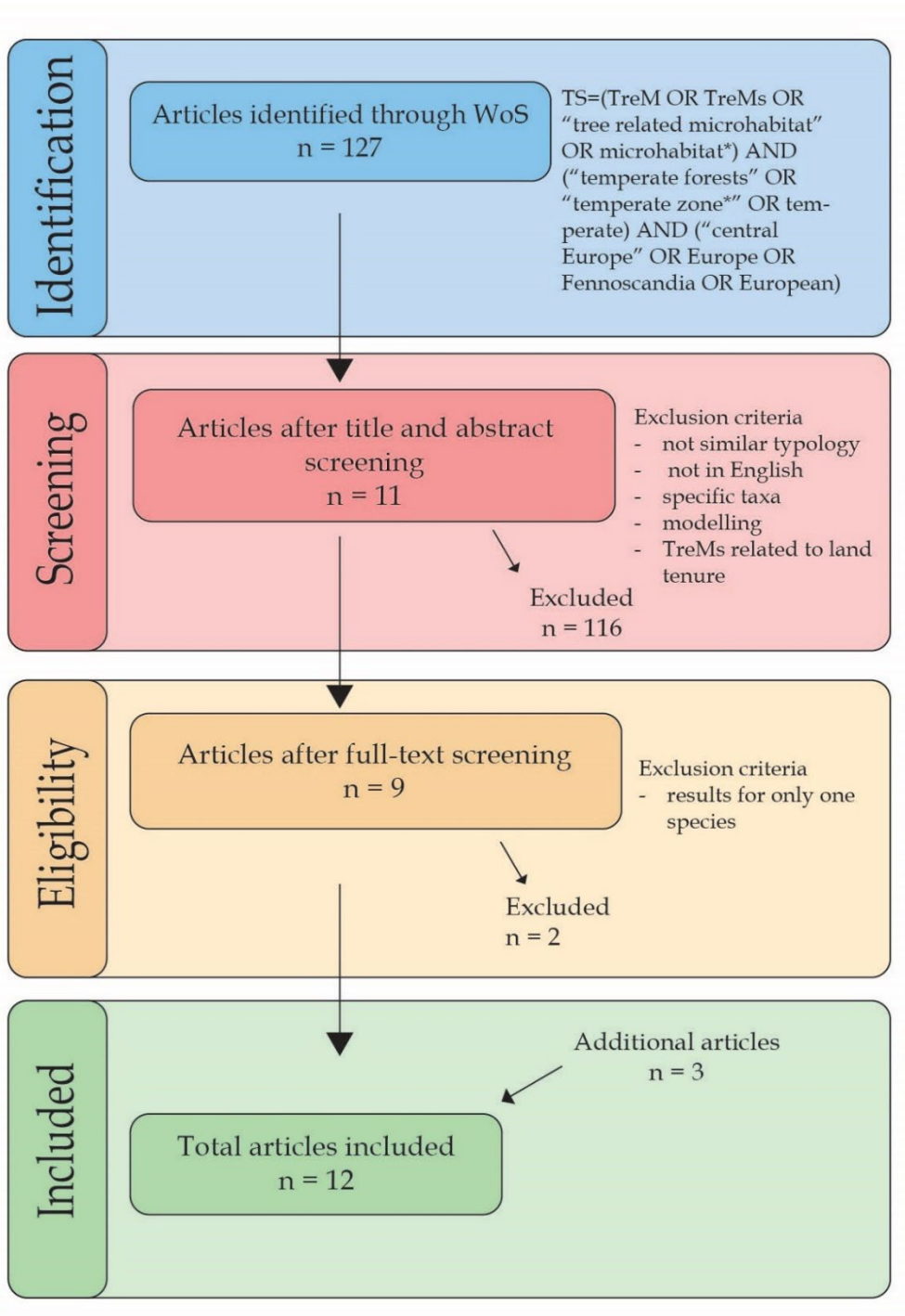


Figure 3. Flowchart visualising the systematic literature review process.

3. Results

3.1 TreM analysis

The most frequently occurring tree species was oaks with a total of 94 individuals (Table 1). Trembling aspen and Norway spruce were the second most frequent trees with 40 observations each. Ten out of the twelve observed tree species were broadleaves, and the two coniferous species were Norway spruce and Scots pine (*Pinus sylvestris*). Most of the assessed trees were living individuals, only eight out of 236 were standing dead trees. For the living trees the DBH varied from 9.1 cm up to 121 cm with most of the mean DBH spanning between 30 cm and 45 cm. The dead trees had a lower variation in DBH spanning between 20 cm and 58.8 cm, although their mean DBH had a bigger spread (Table 1). Within this study 28 out of the 47 TreM types were observed, 14 out of 15 groups and 6 out of the 7 forms (Appendix 1). The highest observed abundance on living trees was seven TreM types on one individual, whereas most of the mean values for abundances spanned between 2-2.5 TreMs per tree depending on the species. Figure 4 shows the mean TreM abundance for each tree species combining living and dead trees and Figure 5 shows mean TreM richness for each tree species combining living and dead trees. Dead trees hosted higher abundance of TreMs (3.5 to 5.3 on average, Figure 6), with 6 as the highest observed TreM abundance. The highest mean abundance for both living and dead trees was found in oaks with 3.0 and 5.3 TreMs per tree, respectively (Table 1). For living trees, the richness varied from zero to six, and for dead trees from two to five. Mean richness spanned between 1.1 – 2.6 for living trees. Dead trees also showed higher richness (TreMs from 3.5 – 4.7 different groups, Figure 7). The share of TreM bearing trees for each species varied from 71% of living Norway maple up to 100% for living birches, Scots pines, oaks, as well as dead trees.

Table 1. Number of samples trees, and their share, per species separating living and dead trees. Mean values are presented for DBH, TreM abundance, and TreM richness, including the standard deviation. Max and min observations are included. The last column described the amount of TreM bearing trees per species in percent.

Species	Living trees		DBH			Abundance			Richness			TreM bearing trees	
	N	%	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	N	%
Norway maple	7	3	28.8 ± 12.6	46.9	13.7	1.6 ± 1.3	3	0	1.4 ± 1.3	3	0	4	71
Birch	27	12	37.2 ± 12.9	63	16	2.5 ± 1.1	5	1	2.2 ± 0.9	5	1	27	100
Norway spruce	39	17	44.1 ± 18.0	75.5	9.1	1.1 ± 0.9	5	0	1.1 ± 0.9	4	0	29	74
Scots pine	4	2	43.8 ± 13.7	58.8	27.2	2.0 ± 0.8	3	1	1.5 ± 1.0	2	1	4	100
Trembling aspen	40	18	33.8 ± 11.6	60	11.1	2.1 ± 1.0	4	0	2.0 ± 1.0	4	0	39	98
Oak	91	40	45.5 ± 22.0	121	13.6	3.0 ± 1.5	7	1	2.6 ± 1.3	6	1	91	100
Rowan	12	5	25.4 ± 22.9	90	10	2.5 ± 2.1	7	0	2.3 ± 1.8	5	0	11	92
Other*	8	4	30.6 ± 17.6	68.6	13.4	2.5 ± 2.5	6	0	2.1 ± 2.0	5	0	6	75
Dead trees													
Birch	4	50	25.9 ± 6.1	36.1	20.0	3.5 ± 1.7	5	2	3.5 ± 1.7	5	2	4	100
Norway spruce	1	13	58.4			5.0			4.0			1	100
Oak	3	38	42.0 ± 5.7	48.6	38.2	5.3 ± 0.6	6	5	4.7 ± 0.6	5	4	3	100

*Other species include hazel (*Corylus avellana*), European ash (*Fraxinus excelsior*), wild cherry (*Prunus avium*), goat willow (*Salix caprea*) and small-leaved lime (*Tilia cordata*).

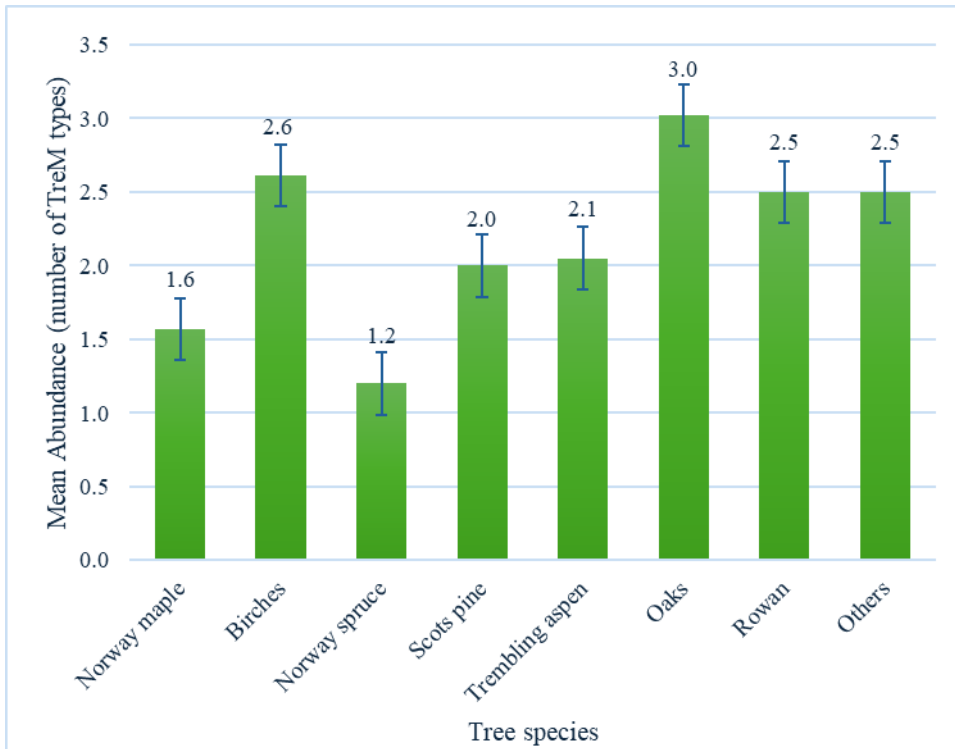


Figure 4. Mean TreM abundance for the different tree species combining dead and living trees, including standard error bars.

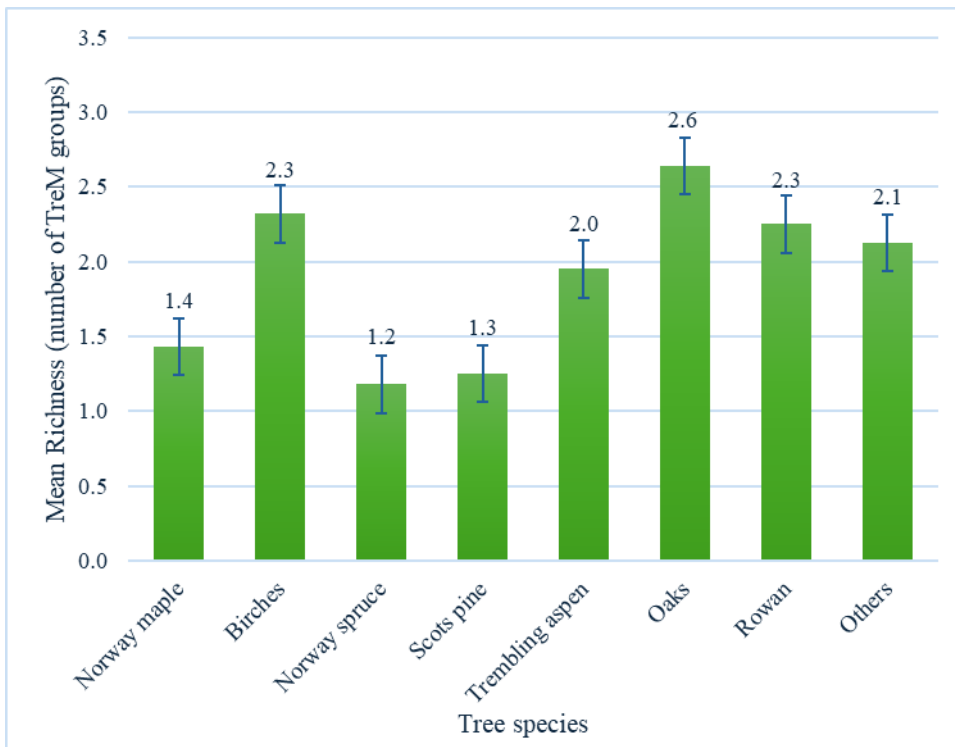


Figure 5. Mean TreM richness for the different tree species combining dead and living trees, including standard error bars.

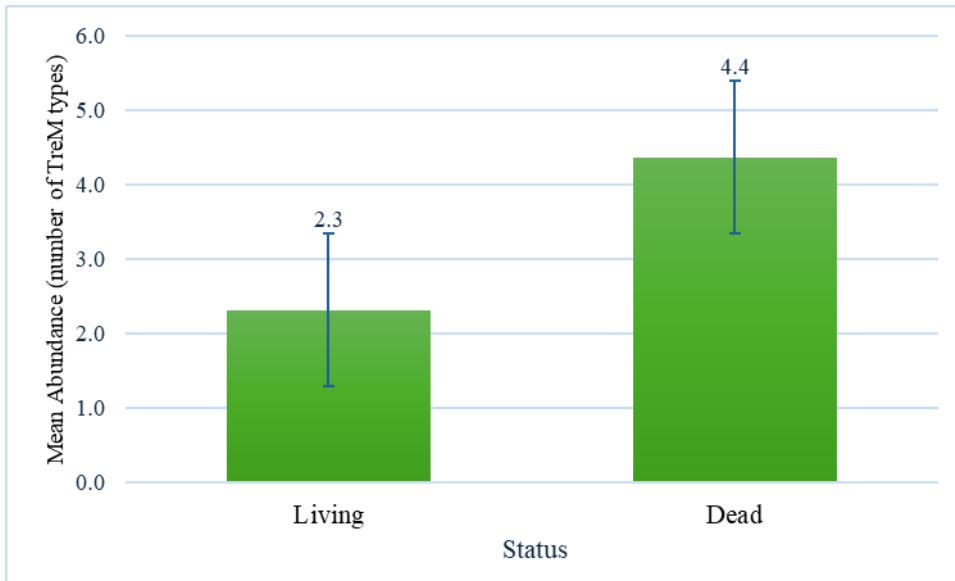


Figure 6. Mean TreM abundance for living and dead trees, including standard error bars.

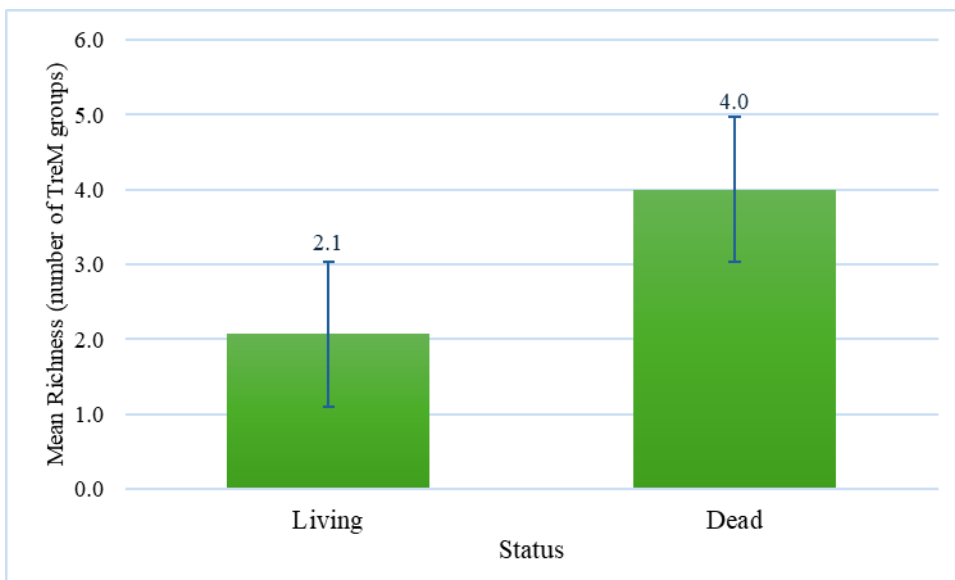


Figure 7. Mean TreM richness for living and dead trees, including standard error bars.

The analysis of variance showed that there are statistically significant differences in TreM abundance and richness between tree species (Table 2 and 3). For the five most common TreM types there was only significant differences between tree species for dead branches (Table 2). The pairwise comparison showed significant differences between tree species for abundance, richness, and dead branches (Table 3). The status, dead or alive, showed significant variance in abundance (Figure 6) and richness (Figure 7) as well as insect galleries. The difference between broadleaves and conifers were significant for abundance (Figure 8), richness (Figure 9), dead branches, and lichens (Table 2).

Table 2. Results from Kruskal-Wallis analysis of variance testing the differences between tree species, status, and broadleaves versus conifers assessing abundance and richness as well the five most common TreM types; dead branches, insect galleries, bark loss, bryophytes, and lichens. For each comparison the chi-squared, degrees of freedom (df) and P-value are shown. Significant values are marked in bold. N represents the number of observations for each TreM type.

	Abundance	Richness	Dead branches N=167	Insect galleries N=49	Bark loss N=58	Bryophytes N=64	Lichens N=59
Species	Chi-squared = 55.2 df. = 11 P-value < 0.001	Chi-squared = 48.1 df = 11 P-value < 0.001	Chi-squared = 52.9 df = 11 P-value < 0.001	Chi-squared = 9.4 df = 11 P-value = 0.589	Chi-squared = 9.4 df = 11 P-value = 0.587	Chi-squared = 5.4 df = 11 P-value = 0.912	Chi-squared = 18.0 df = 11 P-value = 0.081
Status	Chi-squared = 10.4 df = 1 P-value = 0.001	Chi-squared = 11.5 df = 1 P-value < 0.001	Chi-squared = 4.4 df = 1 P-value = 0.035	Chi-squared = 8.7 df = 1 P-value = 0.003	Chi-squared = 6.4 df = 1 P-value = 0.011	Chi-squared = 0.5 df = 1 P-value = 0.502	Chi-squared = 0 df = 1 P-value = 1
Broadleaves vs conifers	Chi-squared = 32.9 df = 1 P-value < 0.001	Chi-squared = 30.1 df = 1 P-value < 0.001	Chi-squared = 8.9 df = 1 P-value = 0.003	Chi-squared = 0.0 df = 1 P-value = 0.956	Chi-squared = 1.2 df = 1 P-value = 0.276	Chi-squared = 0.0 df = 1 P-value = 0.980	Chi-squared = 7.3 df = 1 P-value = 0.007

Table 3. Pairwise comparison of tree species assessing abundance (A), richness (R) and dead branches (DB). The table presents the P-values of each pairwise comparison were statistically significant values are bolded.

Species		Oak	Norway spruce	Trembling aspen	Birch	Rowan	Norway maple	Scots pine	European ash	Goat willow	Hazel	Small-leaved lime
Norway spruce	A	<0.000										
	R	<0.000										
	DB	<0.000										
Trembling aspen	A	0.001	0.001									
	R	0.008	0.001									
	DB	0.231	<0.000									
Birch	A	0.189	<0.000	0.056								
	R	0.187	<0.000	0.125								
	DB	<0.000	0.415	<0.000								
Rowan	A	0.060	0.009	0.396	0.195							
	R	0.083	0.016	0.457	0.241							
	DB	0.005	0.434	<0.000	0.377							
Norway maple	A	0.014	0.174	0.229	0.051	0.205						
	R	0.013	0.260	0.158	0.051	0.174						
	DB	0.008	0.402	0.004	0.452	0.371						
Scots pine	A	0.137	0.093	0.498	0.239	0.442	0.312					
	R	0.024	0.407	0.147	0.060	0.155	0.411					
	DB	0.276	0.014	0.377	0.012	0.029	0.023					

Continuation of Table 3.

Species		Oak	Norway spruce	Trembling aspen	Birch	Rowan	Norway maple	Scots pine	European ash	Goat willow	Hazel	Small-leaved lime
European ash	A	0.435	0.059	0.269	0.464	0.320	0.175	0.304				
	R	0.469	0.068	0.288	0.430	0.315	0.155	0.135				
	DB	0.133	0.470	0.099	0.442	0.500	0.423	0.103				
Goat willow	A	0.298	0.012	0.060	0.220	0.131	0.060	0.139	0.310			
	R	0.250	0.013	0.097	0.181	0.120	0.050	0.042	0.300			
	DB	0.133	0.470	0.099	0.442	0.500	0.423	0.103	0.500			
Hazel	A	0.298	0.114	0.400	0.394	0.450	0.272	0.418	0.396	0.224		
	R	0.273	0.167	0.485	0.367	0.495	0.293	0.252	0.353	0.180		
	DB	0.133	0.470	0.099	0.442	0.500	0.423	0.103	0.500	0.500		
Small-leaved lime	A	0.020	0.212	0.069	0.032	0.064	0.132	0.089	0.056	0.023	0.085	
	R	0.022	0.190	0.061	0.035	0.062	0.141	0.183	0.054	0.020	0.097	
	DB	0.030	0.152	0.023	0.165	0.146	0.190	0.025	0.185	0.185	0.185	
Wild cherry	A	0.020	0.212	0.069	0.032	0.064	0.132	0.089	0.056	0.131	0.085	0.500
	R	0.022	0.190	0.061	0.035	0.062	0.141	0.183	0.054	0.097	0.097	0.500
	DB	0.030	0.151	0.023	0.165	0.146	0.190	0.025	0.185	0.185	0.185	0.500

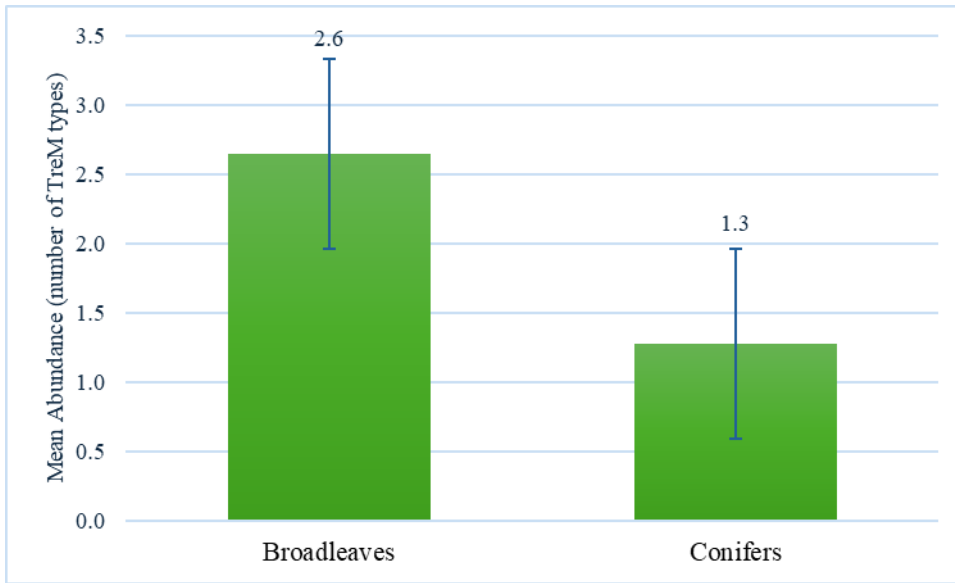


Figure 8. Mean TreM abundance for broadleaves and conifers, including standard error bars.

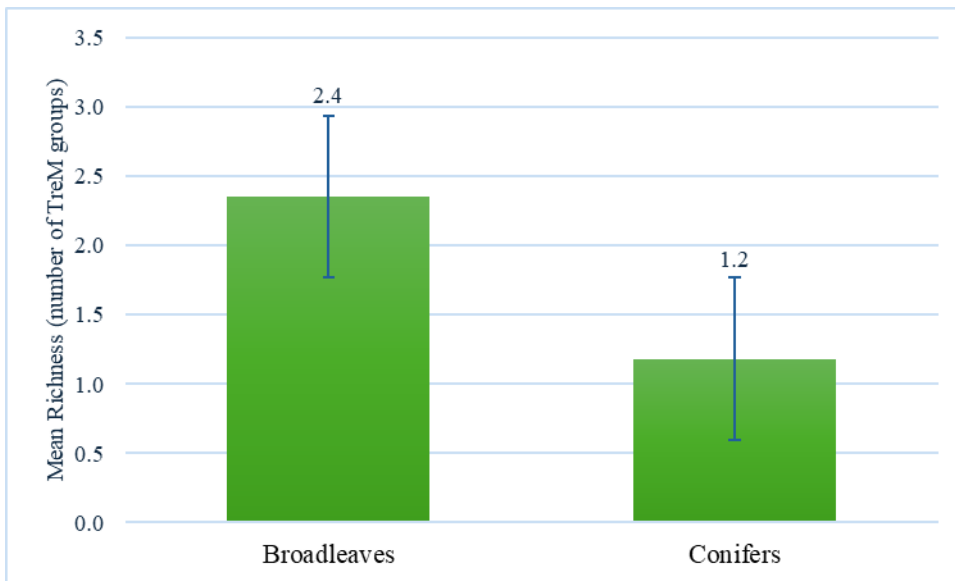


Figure 9. Mean TreM richness for broadleaves and conifers, including standard error bars.

The regression analysis for all tree species combined showed that TreM abundance and richness increased with DBH (Figure 10). For abundance, the slope of the regression line was 0.042 whereas for richness the slope was 0.033 suggesting that abundance increases more than richness with DBH. The P-values for both regressions shows that the results are significant (< 0.001 for both). For the most common species, oaks, the regression also showed that both abundance and richness increased with DBH (Figure 11). The slope for abundance was steeper than

the slope for richness at 0.041 versus 0.030, respectively. The P-values show that the regressions are significant (<0.001 for both).

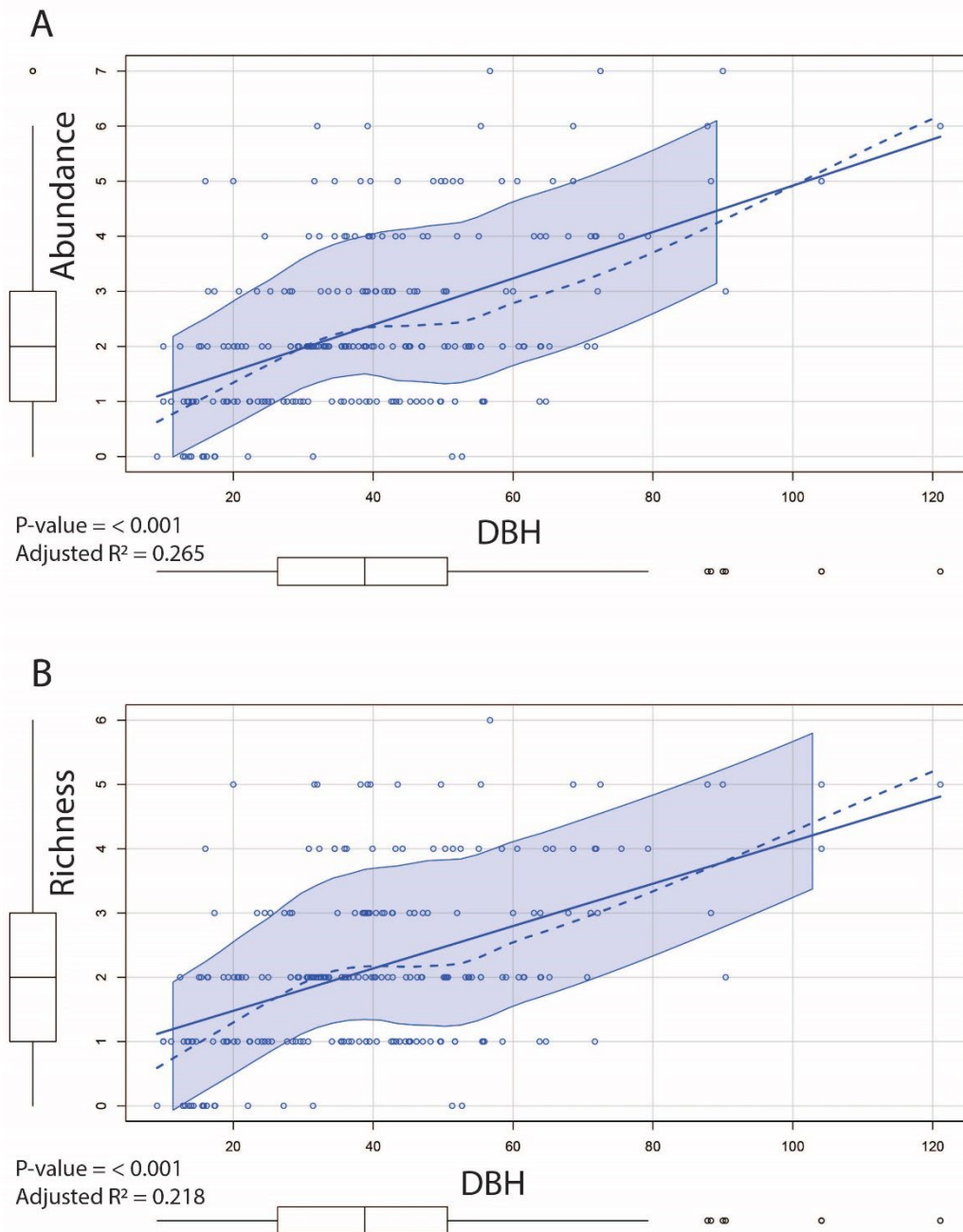


Figure 10. Regression analyses between tree DBH and TreM abundance (A) and TreM richness (B) for all tree species combined. Blue points represent individual trees. The solid blue line is the linear regression, for abundance (A) the function is $\text{abundance} = 0.042 * \text{DBH} + 0.71$, and for richness (B) the regression function is $\text{richness} = 0.033 * \text{DBH} + 0.82$. The dotted blue line is the smooth regression line that reflects the general patterns in the data. The light blue field represents the confidence interval (at 95%). Below each graph, their corresponding P-value and adjusted R^2 is presented. The box plots alongside the x- and y-axis represent the distribution of the data. The box represents the middle 50% of the data with the line visualising the median. The whiskers show the outer quartiles, and the circles represent outliers in the data.

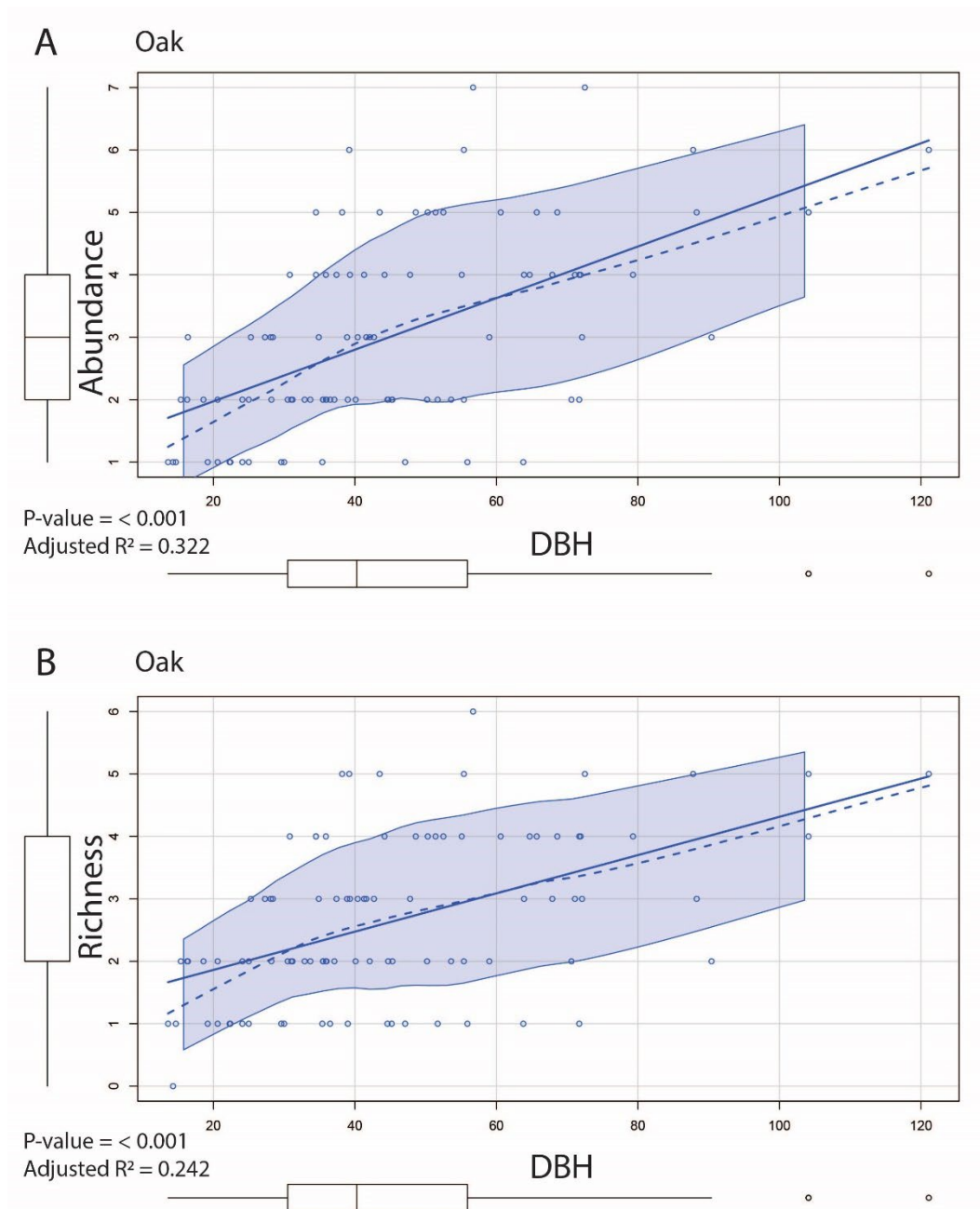


Figure 11. Regression analyses between tree DBH and TreM abundance (A) and TreM richness (B) for all oaks. Blue points represent individual trees. The solid blue line is the linear regression, for abundance (A) the function is $\text{abundance} = 0.041 \cdot \text{DBH} + 1.15$, and for richness (B) the regression function is $\text{richness} = 0.030 \cdot \text{DBH} + 1.25$. The dotted blue line is the smooth regression line that reflects the general patterns in the data. The light blue field represents the confidence interval (at 95%). Below each graph, their corresponding P-value and adjusted R² is presented. The box plots alongside the x- and y-axis represent the distribution of the data. The box represents the middle 50% of the data with the line visualising the median. The whiskers show the outer quartiles, and the circles represent outliers in the data.

3.2 Literature review results

A general consensus found during the literature review was that broadleaved trees host more TreMs than conifers (e.g. Asbeck et al. 2019; Kozák et al. 2023; Larrieu et al. 2012; Vuidot et al. 2010). For example, Przepióra & Ciach (2023) found that Norway spruce had lower TreM richness than pedunculate oak (*Quercus robur*) in the Białowieża forest. They also found that TreM diversity at stand level increased with the amount of hornbeam (*Carpinus betulus*) and decreased with the increasing amount of Norway spruce (Przepióra & Ciach 2023). Similarly, Spinu et al. (2022) found that living Norway spruce and silver fir (*Abies alba*) had lower abundance and richness of TreMs than European beech (*Fagus sylvatica*).

Species identity is another factor many articles have highlighted as differentiators in TreM assemblage (e.g. Larrieu & Cabanettes 2012; Larrieu et al. 2012; Vuidot et al. 2010). Larrieu & Cabanettes (2012) found that in the Pyrenees Mountain range certain TreM groups were mostly associated with certain tree species. Cavities, mouldy cavities, and dendrotelms were mostly found in European beech, and sap runs were exclusively associated with silver firs (Larrieu & Cabanettes 2012). Przepióra & Ciach (2022) observed that willows (*Salix* spp.) supported higher TreM richness than poplars (*Populus* spp.) in riparian forests, and that black poplar (*Populus nigra*) had higher richness than white poplar (*Populus alba*, Przepióra & Ciach 2022). Moreover, 15 of the studied TreM groups had a higher probability of occurrence in willows (e.g. cavities and injuries and wounds), while other groups had higher probability of occurrence in poplars (e.g. deformations, Przepióra & Ciach 2022).

When including species status, Spinu et al. (2022) found that concavities, woodpecker cavities, insect galleries, and exposed heart- and sapwood were mostly found on dead coniferous trees, whereas fungi were more related to dead beech trees. For living trees, broadleaved trees hosted more rot-holes, crown deadwood, nests and microsoils, and conifers showed the highest support of epiphytic structures, fresh exudates, burrs and cankers, and twig tangles (Spinu et al. 2022).

The most common attribute that was found to drive TreM occurrence was DBH (e.g. Asbeck et al. 2022; Przepióra & Ciach 2022; Przepióra & Ciach 2023; Spinu et al. 2022). TreM abundance and richness increase significantly with DBH, but DBH also affects the composition, different DBH classes host different TreM types and groups (Asbeck et al. 2019; Larrieu & Cabanettes 2012). For example, Vuidot et al. (2010) observed that TreM occurrence increased faster with DBH in broadleaves than in conifers.

Analysed articles and their main findings are presented in Table 4.

Table 4. Articles selected during the literature review presented with the study site, assessed tree species and main findings. Full references can be found in the reference list.

Reference	Study site	Species	Main findings
Asbeck et al. (2019)	Black Forest, Germany	Norway spruce (<i>P. abies</i>), European beech (<i>F. sylvatica</i>) and silver fir (<i>A. alba</i>)	Mean abundance: Norway spruce 2.5, European beech 3.6 and silver fir 2.8 Mean richness: Norway spruce 1.6, European beech 2.6 and silver fir 1.8
Asbeck et al. (2022)	Black Forest, Germany and Western and Southern Carpathians, Slovakia and Romania	Norway spruce (<i>P. abies</i>), European beech (<i>F. sylvatica</i>) and silver fir (<i>A. alba</i>)	Mean richness, managed forests: Norway spruce 1.6, European beech 1.9 and silver fir 1.9 Mean richness, primary forests: Norway spruce 3.0, European beech 3.2 and silver fir 2.8
Kozák et al. (2023)	Western and Southern Carpathians, Slovakia and Romania	Norway spruce (<i>P. abies</i>), European beech (<i>F. sylvatica</i>), silver fir (<i>A. alba</i>) and sycamore maple (<i>Acer pseudoplatanus</i>)	Tree age influenced TreM richness positively
Kozák et al. (2018)	Carpathians and Dinarides mountain ranges	European beech (<i>F. sylvatica</i>), silver fir (<i>A. alba</i>), maples (<i>Acer</i> spp.) and ashes (<i>Fraxinus</i> spp.)	Total TreM density per hectare 482.9
Larrieu & Cabanettes (2012)	Pyrénées mountain range	European beech (<i>F. sylvatica</i>) and silver fir (<i>A. alba</i>)	Beech had the highest frequency of TreMs, 0.5. Silver fir had 0.25
Larrieu et al. (2012)	Pyrénées mountain range	European beech (<i>F. sylvatica</i>) and silver fir (<i>A. alba</i>)	Beech carried more TreMs than firs.
Paillet et al. (2017)	Lowland and mountainous area of France	All standing trees, dead or alive. No specified species	TreM density in strict reserves was 23% higher than in managed forests. Total TreM density per hectare for managed forests was 175 and for strict reserves 215.
Przepióra & Ciach (2022)	Alongside the Vistula River in Poland	White willow (<i>Salix alba</i>), Crack willow (<i>Salix fragilis</i>), White poplar (<i>P. alba</i>), Black poplar (<i>P. nigra</i>) and Grey poplar (<i>Populus x canescens</i>)	Mean TreM abundance: White poplar 1.4, Black poplar 2.6, and Willows 2.9. Mean for all species combined 2.3
Przepióra & Ciach (2023)	Białowieża forest, Poland and Belarus	Small-leaves lime (<i>Tilia cordata</i>), European	Mean TreM abundance per tree was 3.1 and mean TreM density was 1378 TreMs per hectare

		hornbeam (<i>C. betulus</i>), Norway spruce (<i>P. abies</i>), Pedunculate oak (<i>Q. robur</i>) and Norway maple (<i>A. platanoides</i>)	
Spinu et al. (2022)	Southern Black Forest in Germany	Norway spruce (<i>P. abies</i>), European beech (<i>F. sylvatica</i>) and silver fir (<i>A. alba</i>)	Mean TreM abundance: Norway spruce 1.1, beech 2.3, silver fir 1.6 Mean TreM richness: Norway spruce 0.7, beech 1.4, silver fir 0.9
Vuidot et al. (2010)	Lowland and mountainous forests in France	European beech (<i>F. sylvatica</i>), oaks (<i>Q. robur</i> & <i>Quercus petraea</i>), Norway spruce (<i>P. abies</i>) and silver fir (<i>A. alba</i>)	Results showed that site, tree species and vitality had significant effect on number of microhabitats
Zemlerová et al. (2023)	Primary forests of the Carpathian mountain range in Slovakia and Romania	Norway spruce (<i>P. abies</i>) with admixes of silver fir (<i>A. alba</i>), rowan (<i>Sorbus aucuparia</i>), Scots pine (<i>P. sylvestris</i>), European beech (<i>F. sylvatica</i>) and birch (<i>Betula spp.</i>)	A significant relationship was found for living trees between disturbance severity and TreM group diversity, with increasing diversity with increasing severity

4. Discussion

Broadleaved trees are an important source of TreMs as shown by both the literature review and the field study I developed in southern Sweden. I observed that broadleaved trees host higher abundance of TreMs than coniferous trees in mixed-species forests, which is in accordance with Vuidot et al. (2010), Kozák et al. (2023), and Przepióra & Ciach (2023). This could be because of tree architecture, ontogenetic development (Larrieu et al. 2022) and physiological features, such as wood density and their response to intrusions. Conifers respond to injuries by releasing resin to heal their wound, which inhibits injuries from developing into TreMs. Moreover, woodpecker cavities are strongly associated with broadleaved trees (Larrieu & Cabanettes 2012) since resin prevents woodpeckers from carving their nests in conifers (Cramps 1980). My results from the TreM inventory showed that broadleaves had the highest abundance of TreMs and conifers the lowest, with the exception of Norway maple. A reason why Norway maple might have had lower abundance of TreMs than a coniferous species like Scots pine might be the size. Norway maples had a mean DBH of 28.8 cm, whereas pine had a mean DBH of 43.8 cm, and within the existing literature DBH is a common denominator for TreM abundance (e.g. Przepióra & Ciach 2023; Spinu et al. 2022; Asbeck et al. 2022). Both the results from the TreM inventory and the literature review supported the hypothesis that broadleaves host a higher number of TreM than conifers.

Richness of TreMs, as well as abundance, is shown to increase significantly with DBH (Asbeck et al. 2019; Larrieu & Cabanettes 2012). Large DBH indicates that the tree has been growing for a long time, which means it has been exposed to biotic and abiotic damages during an extended period of time, potentially developing into TreMs. Kozák et al. (2023) found that DBH was the most prominent driver of TreM richness, although tree age had a significant effect on certain TreM groups. DBH is often used as a proxy for tree age because these variables are, to some degree, related. However, their correlation depends on tree species, and they are not always interchangeable (Larrieu et al. 2022). In this study DBH was measured because of its ease to record and its strong correlation to TreM occurrence. However, some tree species can develop certain TreMs at small sizes. For example, in the Białowieża forest, Przepióra & Ciach (2023) found that both small-leaved lime and young hornbeam trees were important contributors to TreM diversity, despite their

small size. The regression analysis in this study showed that both abundance and richness increased with DBH, both for all tree species combined and for oaks. With this it is reasonable to conclude that the hypothesis that larger trees have a higher number of TreMs is supported.

Tree species identity influenced TreM assemblage and richness, both in temperate regions (e.g. Przepióra & Ciach 2023; Larrieu et al. 2012) and in the hemiboreal region of southern Sweden. Out of the five analysed TreM types, it was only dead branches that showed significant variation between tree species. Dead branches were present in most of the studied oaks (86%), and the occurrence of dead branches in oaks was significantly different from six other species. Since oak is a light-demanding species, big branches usually die because of light restrictions in the stand and stay in the crown a long time before falling down. At the plot scale, Przepióra & Ciach (2023) observed that total TreM richness in the Białowieża forest increased with higher abundance of hornbeam and decreased with the presence of Norway spruce. Contrary, Asbeck et al. (2019) found that coniferous forests hosted a higher abundance and richness of TreMs than mixed broadleaf-conifer forests. However, when excluding the most common TreM type (small buttress cavities) mixed broadleaf-conifer forests had highest abundance and richness of TreMs (Asbeck et al. 2019), suggesting that buttress cavities were highly associated with conifers. When studying riparian willow-poplar forests, Przepióra & Ciach (2022) found that cavities and injuries were more likely to occur in willows, whereas deformations were more common in poplars. The differences could originate from causal agents where willows might be more susceptible to tree-originating TreMs, such as limb breakage or cavity builders, and poplars are more susceptible to external causal agents, such as pests or pathogens, causing excrescences. Similarly, Spinu et al. (2022) identified patterns showing differences in TreM group assemblage between dead conifers and dead beech trees, as well as between living broadleaves and conifers. The pairwise comparison of tree species showed that oaks had significantly different abundance and richness from five other species, although the analysis of variance only found differences between tree species in one out of the five most common TreM types. However, both the literature review and the TreM analysis showed that TreM types, as well as abundance and richness, differ with tree species, and it is therefore possible to conclude that this hypothesis is supported.

Management regimes were found to also affect TreM occurrence (Asbeck et al. 2022; Larrieu et al. 2012; Paillet et al. 2017). Primary, or unmanaged forests, host a greater richness of TreMs than managed forests (Asbeck et al. 2022; Paillet et al., 2017). In addition to this, Larrieu et al. (2012) found that the management regimes had significant effect on TreM density, although the effect varied between tree

species. When comparing managed and unmanaged beech and fir stands Larrieu et al. (2012) observed that managed beech forests had higher TreM abundance than unmanaged silver fir stands, implying that species identity is a stronger driver of TreM abundance than management regimes. The study sites in southern Sweden are managed under a continuous-cover forest regime that is aimed at creating a forest structure closer to primary forests than to intensive management. Therefore, it can be expected to find TreM assemblages similar to unmanaged forests, or at least higher abundance of TreMs within these study sites, although this was not directly analysed in this study. Zemlerová et al. (2023) studied how time since the last natural disturbance affected TreM abundance and richness. They found that for living trees the highest abundance of TreMs were found directly after the disturbance and at late stages (u-shaped curve, Zemlerová et al. 2023). Within continuous-cover forestry, forest operations are performed at low intensity with short intervals. Considering Zemlerová et al. (2023) findings, it is reasonable to speculate that continuous-cover forestry would contribute to a higher TreM abundance and richness, mimicking small disturbances with short intervals.

4.1 Biodiversity and management implications

TreMs constitute an essential substrate for a variety of taxonomic groups, exhibiting significant relationships with their associated species (Larrieu et al. 2018). However, the link between TreM type and taxa is not always distinct (Martin et al. 2022), which can be positive in the sense that a TreM type can be used by generalist taxa and many different species. For instance, cavities can host over 100 different taxa, whereas other TreMs, like dendrothelms, host fewer but more specialised taxa (Martin et al. 2022). Because TreMs describe a wide variety of structures supporting many different species they are described as an important biodiversity indicator (Martin et al. 2022) that can be used on stand level. This study was performed in the hemiboreal region using a typology that is developed for temperate and Mediterranean forest. Although a wide variety of TreM types were found, the temperate and hemiboreal regions differs quite a bit. For the temperate region there is research showing connections between TreM types and specific taxa (Larrieu et al. 2018; Martin et al. 2022), but no such research is available for the hemiboreal region of southern Sweden. Therefore, further studies on what taxa is using TreMs in the hemiboreal region is needed for TreMs to be used as a reliable biodiversity indicator within this region.

There is a pressing need to elaborate biodiversity evaluation tools and standardised indicators that can be used both in NFIs and by forest managers at the operational level (Larsson 2001). Although NFIs aims to collect forest data that is useful for

silvicultural practices, some of the data can be used to evaluate deadwood and other biodiversity indicators (Winter et al. 2008). Most countries in Europe look at the same indicators in their NFIs but with different thresholds, which makes them not comparable with each other (Winter et al. 2008). Since NFIs are already established and conducted in many countries, an adoption of biodiversity indicators could potentially become the main component of a biodiversity monitoring network (Chirici et al. 2012).

The NFIs have potential to adopt indicators of biodiversity in their inventories, though this would require harmonised thresholds and assessment methods (Winter et al. 2008). Here, TreMs can be an easy-to-implement multitaxon indicator of the state of biodiversity (Martin et al. 2022). Although microhabitat inventories are particularly prone to observer bias (Paillet et al. 2015), actions to minimise this source of error are available. Paillet et al. (2015) suggests that TreM inventories should be performed by trained personnel and preferably in pairs when possible. Therefore, TreM inventory training programs could be useful to unify inventory methods. Moreover, the classification into general forms ($n = 7$), TreM groups ($n = 15$) and TreM types ($n = 47$) provides three hierarchical aggregation levels (grains) to be used differently depending on the aim of a given study, inventory, or monitoring process (Larrieu et al. 2018). For example, the general forms can easily be applied for quick scans and for selecting habitat trees during forest operations, and TreM types can be used in scientific studies. Groups can be used, for example, in general biodiversity surveys on small estates. The form grain is not fine enough for detailed monitoring, but thanks to the hierarchical structure, inventories with a finer grain can always be aggregated to a coarser level to merge different sources of information or compare different forests. Therefore, TreMs can be applied in different contexts and by different users, which shows their potential as a biodiversity indicator.

5. Conclusion

This study indicates that TreM richness and abundance in hemiboreal forests follow similar patterns as in temperate forests. Tree species identity is shown to have a strong effect on both abundance and richness, whereas DBH reveals a positive correlation with increasing size. Furthermore, variances in abundance and richness between broadleaves and conifers, as well as living and dead trees, was found. Specific patterns in TreM types have not been explained by tree species identity in this study, although differences in dead branches have been observed.

Further development of TreM inventory methods in mixed forests could greatly benefit management at stand level. Using TreMs as a selection basis for habitat, or retention trees could be an easily applicable method for forest managers and forest operators to integrate into their everyday professional practice.

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Appendix 1

Table explaining Larrieu et al. (2018) hierarchical TreM typology. Highlighted forms, groups and types are the ones observed within this study.

Forms N=7	Groups N=15	Types N=47
Cavities	Woodpecker breeding cavities	Small woodpecker breeding cavity
		Medium-sized woodpecker breeding cavity
		Large woodpecker breeding cavity
	Rot-holes	Woodpecker flute
		Trunk base rot-holes
		Trunk rot-hole
		Semi-open trunk rot-hole
		Chimney trunk base rot-hole
		Chimney trunk rot-hole
		Hollow branch
Insect galleries Concavities	Insect galleries and bore holes	
	Dendrotelm	
	Woodpecker nutritional cavities	
Injuries	Exposed sapwood only	Bark trunk concavity
		Root concavity
		Bark loss
	Exposed sap- and heartwood	Fire scar
		Bark shelter
		Bark pocket
		Stem breakage
		Limb breakage
		Crack
		Lightning scar
Fork split		
Crown deadwood	Crown deadwood	Dead branches
		Dead top

Excrescences	Twig tangles	Remnant of broken limb Witches broom
	Burrs and cankers	Epicormic shoots Burr Canker
Fungal fruiting bodies and slime moulds	Perennial fungal fruiting bodies	Perennial polypore
	Ephemeral fungal fruiting bodies	Annual polypore Pulp agaric Pyrenomycete Myxomycete
Epiphytic and epixylic structures	Epiphytic and parasitic crypto- and phanerogams	Bryophytes Lichens Ivy and lianas Ferns Mistletoe
		Vertebrate nest Invertebrate nest Bark microsoil Crown microsoil
Exudates	Exudates	Sap run Heavy resinosis

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