Effects of management and plant traits on tree-related microhabitats in second-growth stands of the Białowieża Forest

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Abstract

The study presents research conducted on Tree-related Microhabitats (TreM) in managed stands and nearly unmanaged stands in the Białowieża Forest (BF). A TreM is an above-ground structure that creates substrate, site or place for forest-dwelling species, and could be an important tool for assessing the level of biodiversity. The studied area has the same origin and comes after naturally regenerated clearcuts of the British company – "The Century European Timber Corporation" from 1924-1929, however it differs in management approach. Four plots were established in stands unmanaged over the last 30-40 years located in the Władysław Szafer's Landscape Reserve and another four in commercial forests managed by the Polish State Forests Enterprise.

The main hypothesis of the thesis is that trees in unmanaged forest are more abundant and richer in TreMs in comparison to managed stands with the same origin. Another assumption is that abundance and richness of TreMs increase with increasing DBH and depend on plant traits (light requirements and lifespan). Based on these traits the species were grouped into three categories: light-demanding, plastic and shade-tolerant species.

Data analysis was carried out in the R Studio Software 1.3.1073 and Microsoft Excel 2016. Main drivers of TreM abundance and richness were identified using generalized linear mixed models (GLMMs) with plot identity regarded as a random factor. Abundance was defined as the total number of TreMs per tree, while richness was calculated as a total number of TreM types per tree. The differences in abundance and richness overall and at TreM group level between managed and unmanaged stands were tested using nonparametric tests.

The results showed that TreM abundance and richness differ significantly between managed and unmanaged stands. Higher TreM abundance and richness occurred in unmanaged stands compared to stands of similar origin but with a longer history of silvicultural practices. In addition, the GLMM confirmed that the main drivers of TreM abundance and richness in the studied stands were the tree DBH and its plant trait category. TreM abundance and richness increased with the increase of tree DBH. Moreover, light-demanding trees were associated with the highest predicted values of TreM abundance and richness, regardless of the stand management.

The feasibility of the method used suggests that it could be widely used in forest management by locating and preserving trees containing TreMs. Retention of trees with higher TreM abundance and richness, notably large and light-demanding trees such as birch and aspen, is likely to be an important conservation action in managed forests.

Keywords: tree-related microhabitats, TreMs, Białowieża Forest, post-Century stands, second-growth forest

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Abbreviations

BA	Basal area
BF	Białowieża Forest
DBH	Diameter at breast height
TreM	Tree-related Microhabitat

1. Introduction

1.1 TreMs as a forest biodiversity indicator

Tree-related Microhabitats (TreMs) are an increasingly popular field of research among forest ecologists since they are a good indicator of biodiversity and a tool for habitat tree selection in forest ecosystems worldwide (Asbeck et al. 2021). Larrieu et al. (2018) defined a TreM as a “well delineated structure occurring on living and standing dead trees, that constitutes a particular and essential substrate or life site for species or species communities during at least a part of their life cycle to develop, feed, shelter or breed”.

Furthermore, Larrieu et al. (2018) proposed a hierarchical classification of TreMs that could be used both within research and applied forest management. They distinguished seven main forms of tree-related microhabitats: cavities, injuries, crown deadwood, excrescences, fungal fruiting bodies and slime moulds, epiphytic/epixylic structures and exudates. These general forms are further grouped into 15 groups and 47 types (Appendix 1, Table A5).

The occurrence of TreMs indicates that some of the tree structures form a habitat or constitute a special substrate for forest-dwelling species or species communities (Asbeck et al. 2021). TreMs are especially good indicators of mature and old-growth forests such as for instance the Białowieża Forest. It has been documented that higher number of TreMs occur in strict reserves and diverse, more complex forests that have not been managed for a long time (Paillet et al. 2017; Asbeck et al. 2022).

In Europe near-natural or structurally complex forests are currently scarce due to past and present forestry practices (Bengtsson et al. 2000). Silvicultural practices are often leading to simplified stand structure, where trees with high value for biodiversity are often unwanted by traditional forest managers, being considered to lower the timber production and economic benefits and are thus removed from stands (Larrieu et al. 2018; Kozák et al. 2018). Therefore, species depending on the old-growth structures, often found in forests with a high level of naturalness have been strongly affected by intensive commercial forest management (Kuuluvainen 2009).

A focus on TreMs may aid nature conservation efforts, especially in commercial stands which have been homogenised by forest management (Michel and Winter 2009). Retention of trees that bear TreMs during harvesting could improve biological diversity in managed forest stands (Lindenmayer et al. 2006; Gustafsson et al. 2012). Therefore, integrating TreM monitoring into silvicultural practices could be an important approach to maintain and assess biodiversity in Central Europe forests (Larrieu et al. 2018; Großmann et al. 2018; Asbeck et al. 2021).

Abundance and richness of TreMs are influenced by both tree characteristics: size (through the diameter at breast height – DBH), species and vitality; and stand characteristics: management history, forest type or stand structural complexity (Larrieu and Cabanettes 2012; Großmann et al. 2018; Asbeck et al. 2019). It has been proven that deciduous species provide more habitats than conifers, especially oak species (*Quercus robur* L. and *Quercus petraea* (Matt.) Liebl.), and that the largest living trees play an important role in TreM provisioning in forest ecosystems (Larrieu and Cabanettes 2012).

1.2 Hypotheses for the study

The main hypothesis of this thesis is that trees in unmanaged forest stands provide more and richer TreMs than in managed stands of the same origin (1).

A second hypothesis is that abundance and richness of tree-related microhabitats are dependent on tree life traits and increase with increasing tree DBH (2 and 3).

2. Materials and methods

2.1 Study area

This study was conducted in the Białowieża Forest (BF), located on the border area between Belarus and Poland (Fig. 1). BF in total covers 1 450 km^2 of which 600 km^2 is in Poland and the remaining 850 km^2 in Belarus. The climate of the study area has features of both a continental and an oceanic character. The long-term mean annual air temperature is 6.7 °C. The coldest month is January with an average of 4.6 °C below zero, and the warmest month is July with a mean temperature of 17.9 °C. Mean annual precipitation is ca. 640 mm and snow cover lasts for an average of 92 days.[1]

Figure 1. The location of the Białowieża Forest (courtesy of K. Bielak)

[1] The provided information is based on the long term data (1926-2015) from a meteorological station located in Białowieża (https://danepubliczne.imgw.pl)

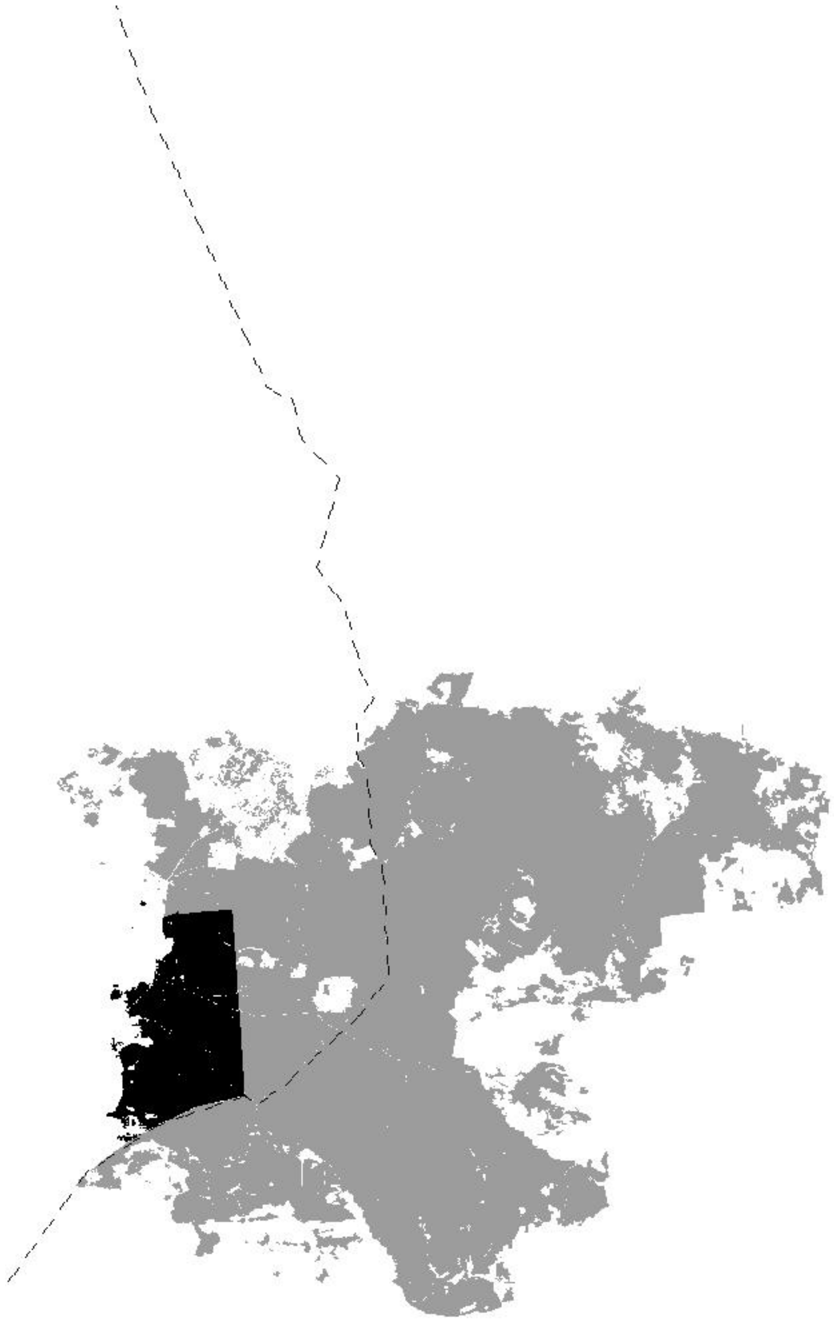

Figure 2. The area of conducted study. The Hajnówka Forest District marked with black (courtesy of K. Bielak)

2.2 Forest history background

BF avoided the intensive human population and commercial timber exploitation that occurred in most European forests as its woodlands served for centuries as widespread hunting area of the Lithuanian dukes, the Polish kings and the Russian czars from the 14th century until the beginning of the 20th century (Więcko 1984; Samojlik et al. 2013). Nevertheless, for centuries, wood in the Białowieża Primeval Forest has been a valued building and heating source for local inhabitants, and it was used for the production of potash, charcoal and tar.

From 1795 to 1914 the BF came under the control of the Russian partitioner, however the function as a hunting park still prevailed in this period. Afterward, in the First World War, the BF came under the German occupation (1915-1918). This time was marked by intensive management and large clearcuttings, mainly conducted for the needs of the occupier. During the German occupation 6 500 ha of stands with a total mass of approximately 2.6 million m^3 of wood were cut in the BF.[2] In the following years the economy boiled down to the elimination of the effects of over-exploitation and the acquisition of left trees and snags as a result of which about 1.2 million m^3 of wood was obtained (Więcko 1984). Moreover, according to the forest management plan carried out for the Białowieża Primeval Forest in 1921, around 1 700 ha of forest with a mass of 350 000 m^3 were cut with clearcuts.

On 17th of April 1924, a few years after the revival of the Polish state, the authorities of the Second Polish Republic signed an agreement with the British company "The Century Trust Ltd.", putting the BF into operation for 10 years with an annual allowable cut around 400 000 m^3.[3] Due to unreasonable management and late payments, the Polish government decided to terminate the contract, which turned out to be unfavourable and brought the State Treasury high losses. It is estimated that for five years "Century" harvested around 1 625 000 m^3 of wood (Mysiak 2020).

The results of exploitation by the British company are clearly visible today. Most of the clear-cut areas have been naturally regenerated. Nowadays, those second-growth stands are about 100 years old and because of the well-known stand history, they are useful for the study of tree-related microhabitats. Therefore, we decided to carry out our study based on eight selected second-growth forest stands that are located in the western part of the BF and under control of the Hajnówka Forest District (Fig. 2).

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[2] Forest management plan for the Białowieża Primeval Forest from 07.07.1933, p. 21.

[3] Agreement from 17.04.1924 signed between "The Century Trust Ltd." and the Ministry of Agriculture and State Goods in Poland on the exploitation of wood within the Białowieża Forest. Archive of New Files, Polska Spółka Drzewna "Century".

To test the main hypothesis about the effect of forest management (presence of silvicultural operations) on TreMs, two categories of stands were selected: stands unmanaged over the last 30-40 years (1) and stands commonly managed at present (2). The first category consists of 4 stands (forest compartments 386Ca, 387Ca, 387Da, 416Ab) that had only marginal management activity until the early 1990s, located in the Władysław Szafer's Landscape Reserve (Fig. 3), under protection since 1969. In the past, mainly Norway spruce trees attacked by bark beetles and dangerous trees along main roads (e.g. like from Hajnówka to Białowieża) were extracted. The second category is represented by 4 stands (414Bc, 415Ca, 442Da, 465Aa) that were managed in the past. Over the last 50 years standard thinnings were performed, usually once per 10 years. The thinning intensity was 10-15% (based on stand volume) and aimed at reduction of pioneer trees' share like aspen and birch in the favour mainly of oak and spruce as well as other long-lived tree species like lime (Bielak and Brzeziecki 2006).

All selected stands represent the same eutrophic forest site condition (Brunic Arenosols soil type of loamy sand) and are located relatively close to each other (maximum distance between stands is 2.8 km, Fig. 4).

2.3 Stand inventory

In autumn 2021, eight plots were established in the selected stands nearby the main road from Hajnówka to Białowieża. Each plot is 0.25 ha large (50 m x 50 m). The locations of the plots have been marked in the mLAS Inżynier application and loaded into the QGIS program.

When selecting the area for sampling, it was guided by the fact that the stands should be comparable with the same site conditions and located relatively close to each other. The sample area was marked by oak pickets located in the corner of every plot.

Figure 3. A stand in the compartment 416A b located in the Władysław Szafer's Landscape Reserve (W. Mysiak)

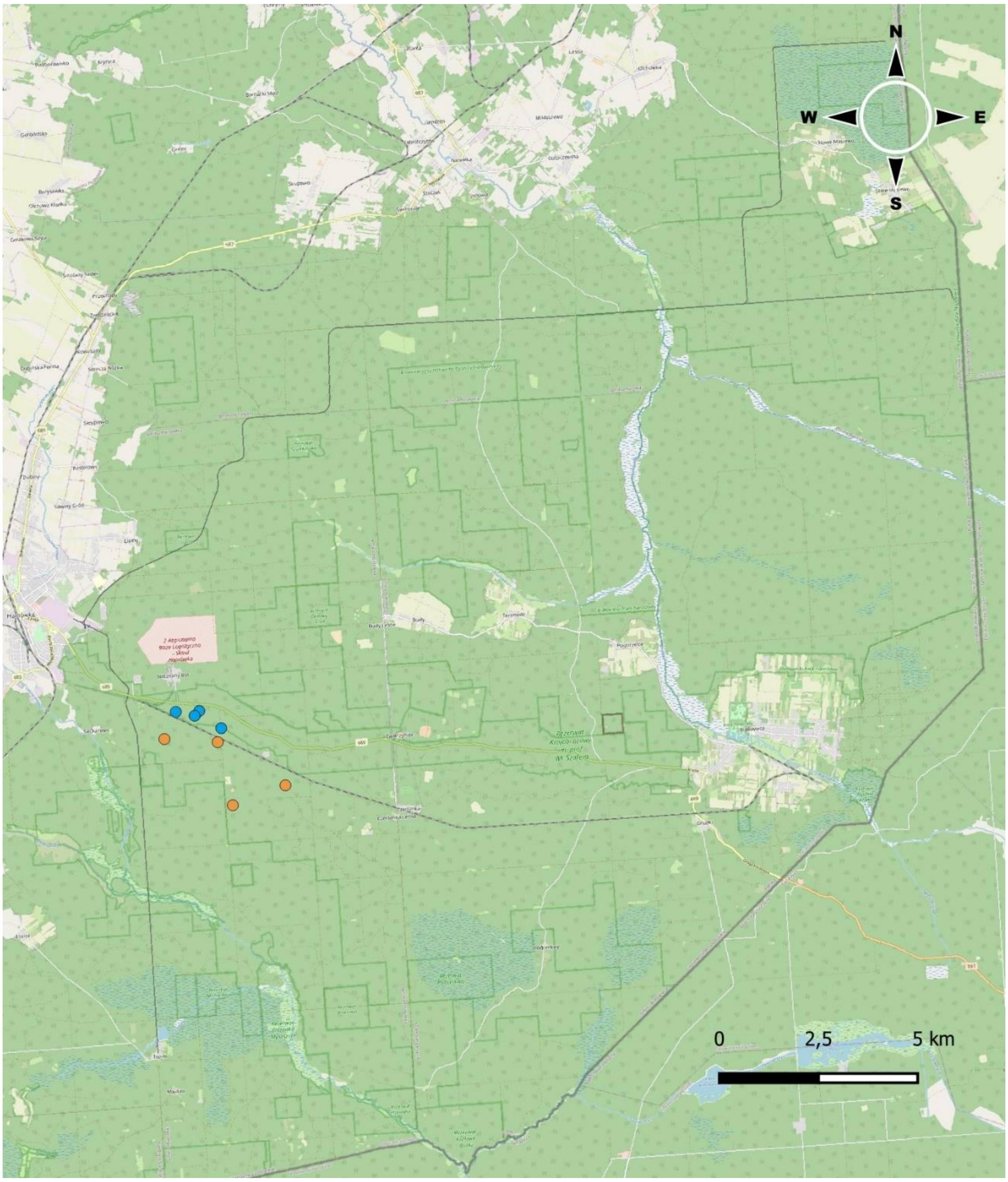

*Figure 4. A map with the locations of plots (QGIS). With **blue colour** are marked stands located in the Władysław Szafer's Landscape* Reserve*, which were slightly managed until the early 1990s (386Ca, 387Ca, 387Da, 416Ab); with **orange colour** are marked stands which have been regularly managed by thinnings for the last 50 years (414Bc, 415Ca, 442Da, 465Aa); **light green colour lines** – borders of the Władysław Szafer's Landscape Reserve and other* protected *areas.*

After selecting stands, activities related to tree measurements were started. The procedure was as follows:

1. Using tapes and poles, the plot was divided into five 10 m wide zones placed in the N-S direction, which was useful for tree numbering and orientation in the field.

2. All the trees were numbered with a waterproof pen after removing the top layer of bark (Fig. 6).
3. X and Y spatial coordinates of every tree were determined using the Field-Map (Fig. 5). Field-Map is a technology for field data collection and further processing (https://www.fieldmap.cz).
4. DBH was measured in two perpendicular directions using an electronic Haglöf caliper connected via Bluetooth with a field computer. The place of measurement was permanently marked in the form of scratches which left a scar on the tree.

Figure 5. A field computer Field-Map (W. Mysiak)

Figure 6. A numbered tree with scratched bark in the compartment 386Ca (W. Mysiak)

2.4 TreMs assessment

In March and April 2022 the TreMs were surveyed according to the protocol proposed by L. Larrieu (Appendix 1, Tab. A5). Using orientation maps created in QGIS (Fig. 8), the application ODK Collect (Fig. 7) and binoculars, I surveyed TreMs on living trees in every plot. The total number of assessed living trees was 672. The threshold diameter at the breast height for TreMs inventories was chosen to 20 cm as it is more likely that TreMs occur on larger trees. The chosen threshold also allowed to save time spent on the assessment. During data collection an observer using an orientation map helped me to follow the path in the right direction and pointed to the tree in order to not miss any of them. TreMs on two plots were assessed without helpers. Up to eight hours were spent on each plot. The first assessed plot (in the compartment 415Ca) was repeated due to overestimation and lack of experience.

The following steps were taken during the assessment:

1. I walked around the tree trunk once to check for TreMs from all directions from the root base, as Larrieu et al. (2018) suggested in their study.
2. After that I walked away several meters and looked up into the crown with binoculars. Sometimes I repeated the inspection to make sure nothing was missed.
3. I collected the data using the phone application ODK Collect and saved it on the server.
4. Finally, I took photos of trees with microhabitats.

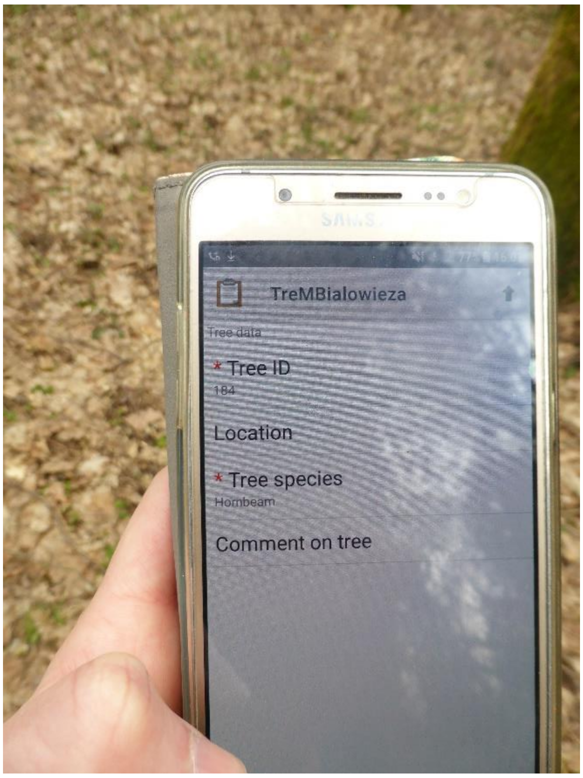

Figure 7. Application ODK Collect (W. Mysiak)

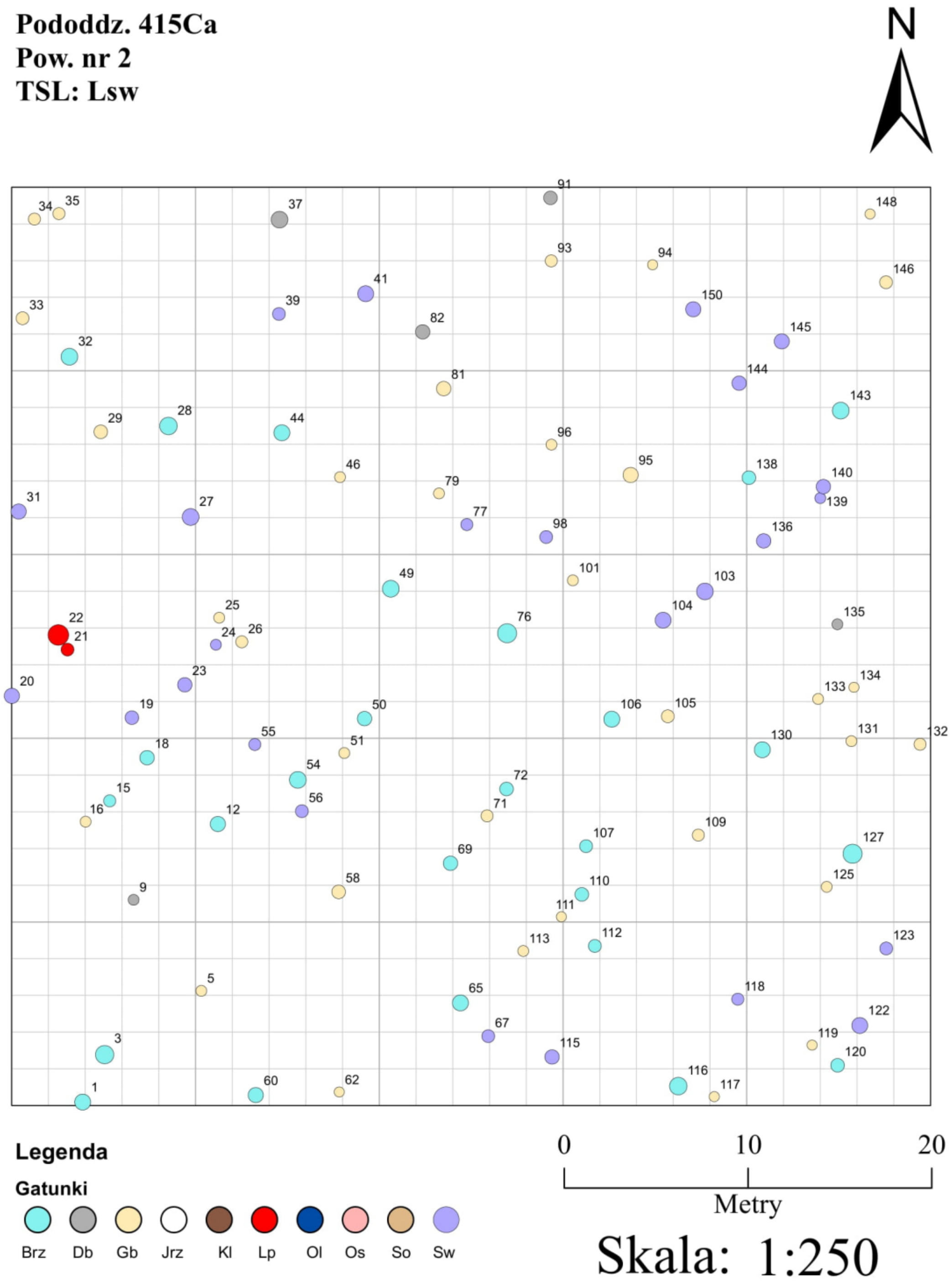

Figure 8. An example of an orientation map with numbered trees over 20 cm DBH in the compartment 415Ca created in QGIS. Species: Brz=birch, Db=oak, Gb=hornbeam, Kl=maple, Lp=lime, Os=aspen, Sw=spruce; Jrz, Ol, So (rowan, alder, pine) did not occur in the plots; scale 1:250 (courtesy of K. Bielak)

2.5 Traits of studied tree species

Tree species might be classified according to different habitat requirements, especially in terms of light. Birch (*Betula pendula* Roth) and aspen (*Populus tremula* L.) are light-demanding species in contrast to Norway maple (*Acer platanoides* L.), hornbeam (*Carpinus betulus* L.) and lime (*Tilia cordata* Mill.), which are shade-tolerant. Norway spruce (*Picea abies* (L.) H. Karst) shows a wide amplitude depending on the site conditions (Jaworski 2011). Pedunculate oak (*Quercus robur* L.) is generally light-demanding, but in the conditions of the BF tolerates some shade at its young stage (Bielak 2010), therefore it was classified as a plastic species.

I also think that lifespan could influence TreM composition. Since most of the trees in the plots have the same age (and same origin), it is expected that more TreMs are to be found on trees with a shorter lifespan as these started to decay and break first. Among these seven species, birch and aspen are relatively short-lived species in comparison to others (Brzeziecki 1991). The most long-lived species is pedunculate oak. Due to those similarities, I defined a new variable tree category which clusters the data in light-demanding, shade-tolerant and plastic species (Tab. 1).

Table 1. Tree categories according to light requirements and maximum lifespan in the conditions of the BF

	species	light requirements	max. lifespan in BF
Light-demanding	*Betula pendula* Roth	highly light-demanding	120
	Populus tremula L.	highly light-demanding	100
Plastic species	*Picea abies* (L.) H. Karst	wide amplitude (full light, half-shade, periodic shade)	300
	Quercus robur L.	light-demanding/shade-tolerant at young stage	500
Shade-tolerant	*Acer platanoides* L.	semi-shade tolerant	350
	Carpinus betulus L.	semi-shade tolerant	400
	Tilia cordata Mill.	shade tolerant	350

Note. Data based on publications of Brzeziecki (1991) and Jaworski (2011).

2.6 Data analysis

Data analysis was carried out in the R Studio Software 1.3.1073 (RStudio Team, 2020) and Microsoft Excel 2016. To avoid type I and II errors due to outliers, variance heterogeneity, missing values and collinearity, data was explored following Zuur et al. 2010 protocol (Appendix 2, Fig. A15). Main drivers of TreM abundance and richness were identified using generalized linear mixed models (GLMMs) with plot identity regarded as a random factor. This allows to avoid autocorrelation caused by trees belonging to the same sample plots (Dormann 2013).

Abundance was defined as the total number of TreMs per tree, while richness was calculated as the total of different TreM types per tree (Fig. 12). Because of the difficulty to correctly assess and count the insect galleries on the whole tree surface, insect galleries were included only in the TreM richness and not in the TreM abundance calculation. Significant differences in the average TreM abundance and richness between managed and unmanaged stands were tested using the nonparametric rank-based Kruskal–Wallis test (Tab. 4).

The GLMMs employed for TreM abundance and richness were based on count data with a negative distribution fitted for overdispersion. Data was divided according to the management type of the stands (managed/unmanaged) and models were considered according the formula:

TreM Abundance/Richness (Managed/Unmanaged) ~ DBH + Tree life trait category + (1|PlotID)

According to Table 1, the plant trait category variable represented the grouping of trees with similar plant traits:

1) light-demanding species (birch *Betula pendula* Roth and aspen *Populus tremula* L.),
2) plastic species (spruce *Picea abies* (L.) H. Karst and pedunculate oak *Quercus robur* L.),
3) shade-tolerant species (maple *Acer platanoides* L., hornbeam *Carpinus betulus* L. and lime *Tilia cordata* Mill.).

For these three categories share, minimum, maximum and mean value, and standard deviation of DBH were calculated (Tab. 3).

The “glmmTMB” package was used to run the models (Brooks et al. 2017) and over-dispersion, zero-inflation and model performance for each management type based on residuals were tested with the “DHARMa” package (Hartig 2018). The final results of the models are described in Table 4 and Figure 13.

Models were plotted according to the DBH effect and its relationship to the tree categories with the packages “ggeffects” (Lüdecke 2018) and “ggplot” (Wickham 2016).

3. Results

3.1 General data on inventoried trees

In the studied plots the number of trees in managed stands was 334 whereas in unmanaged stands it was 338. The difference of the tree proportion between the two types of management is visible especially for lime, birch and hornbeam (Tab. 2). Hornbeam is the most common tree species in managed stands and birch is the most common in unmanaged stands (Fig. 9). Additionally, there are 20 lime trees in commercial stands, while in unmanaged stands there is only one lime tree.

Table 2. Number of trees in the study plots, according to management

Species	*Acer platanoides*	*Betula pendula*	*Carpinus betulus*	*Picea abies*	*Populus tremula*	*Quercus robur*	*Tilia cordata*
Managed (334)	1	94	130	44	5	40	20
Unmanaged (338)	0	147	91	54	2	43	1

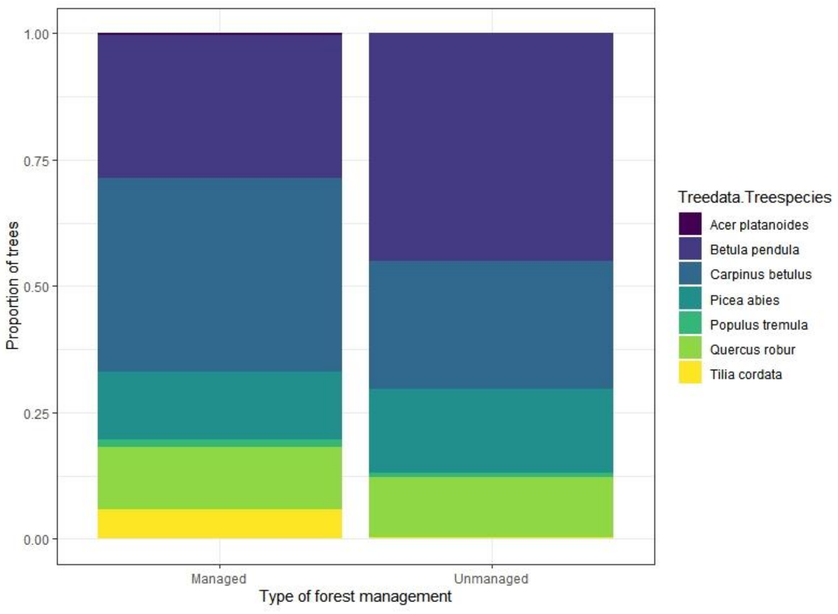

Figure 9. Share of tree species

Higher proportion of shade tolerant species is in managed stands (45.2%), while light-demanding species prevail in unmanaged stands (44.1%) (Tab. 3 and Appendix 2, Fig. A14). On the whole, the maximum value of DBH for managed stands is higher in comparison to unmanaged plots. The largest tree was found in the light-demanding category in a managed stand (707 mm). In unmanaged stands the shade-tolerant species have the lowest range of DBH (the maximum value is 430 mm). A similar pattern is present for the mean value of DBH.

Table 3. Main characteristics of the studied plots

		N	Share (%)	DBH [mm] Min.	Max.	Mean	SD
Managed (4 stands)	Light demanding	99	29.6%	212	707	390.0	100.9
	Plastic	84	25.2%	200	592	327.5	82.6
	Shade tolerant	151	45.2%	200	597	255.3	52.5
	Total	**334**					
Unmanaged (4 stands)	Light demanding	149	44.1%	200	574	357.1	81.3
	Plastic	97	28.7%	202	504.5	288.5	72.2
	Shade tolerant	92	27.2%	200	430	242.3	39.8
	Total	**338**					

The mean value of DBH and BA for both forest management types are similar (Fig. 10). In the managed stands very large trees are present, the largest is an aspen with DBH 707 mm. However, the study plots are comparable, because they do not differ significantly in terms of mean tree DBH and BA (DBH: W=9, p=0.89; BA: W=58339, p=0.45).

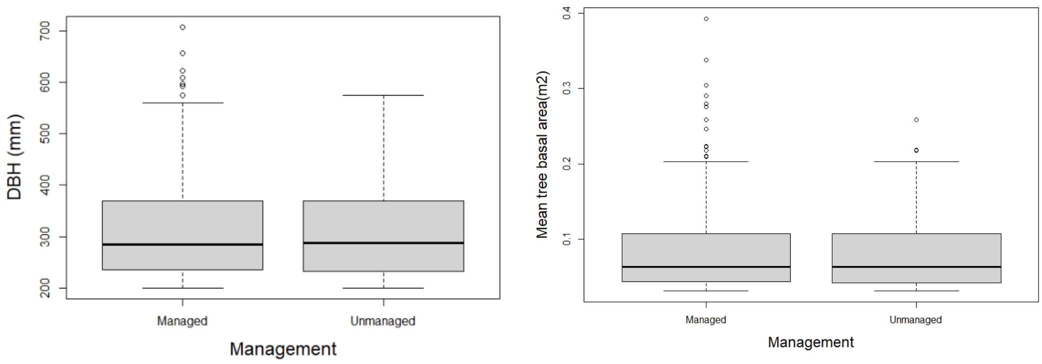

Figure 10. Tree DBH (left panel) and basal area (right panel) for different management types

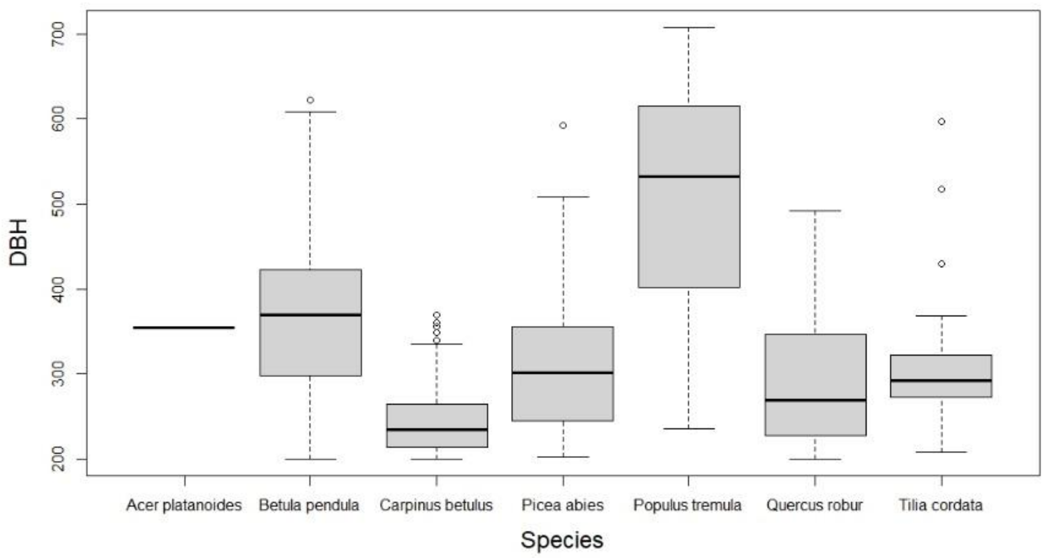

Figure 11. DBH distribution for different tree species in both stand types

The DBH distribution of the seven analyzed species is shown in Figure 11. The largest DBHs are specific to aspen trees while the lowest to hornbeams. Apart from aspens, birches are also characterized by high DBH values. Aspen trees have the widest DBH range, whereas the narrowest DBH range is found in hornbeams and limes.

3.2 TreM characteristics

The overall TreM abundance and richness differ significantly between managed and unmanaged stands. In addition, only two TreM groups (exposed sapwood and epiphytes) differ significantly between managed and unmanaged stands (Tab. 4).

Table 4. Comparison of TreM groups in managed and unmanaged stands of the BF

TreMs	Unmanaged stands	Managed stands	W	*P*-value
TreM abundance	**3.37**	**2.00**	**55115**	**0.01****
TreM richness	**1.10**	**0.92**	**56059**	**0.025****
Woodpecker cavities	0.03	0.02	62110	0.432
Rotholes	0.06	0.09	63011	0.2633
Concavities	0.08	0.06	62035	0.7576
Exposed sapwood	**0.70**	**0.22**	**59605**	**0.031****
Exposed sap- and heartwood	0.29	0.13	62756	0.3206
Crown deadwood	0.14	0.16	61901	0.9044
Burrs and cankers	0.02	0.01	61241	0.3602
Perennial fungi	0.07	0.04	61261	0.4951
Annual Fungi	0.01	0.02	62105	0.3711
Epiphytes	**1.77**	**1.04**	**51196**	**4.762e-06*****
Fresh Exudates	0.03	0.02	61440	0.667
Twig Tangles	0.01	0.01	61440	0.667

Note. Mean values per tree are provided. Statistical significance is marked in bold and with an asterisk.

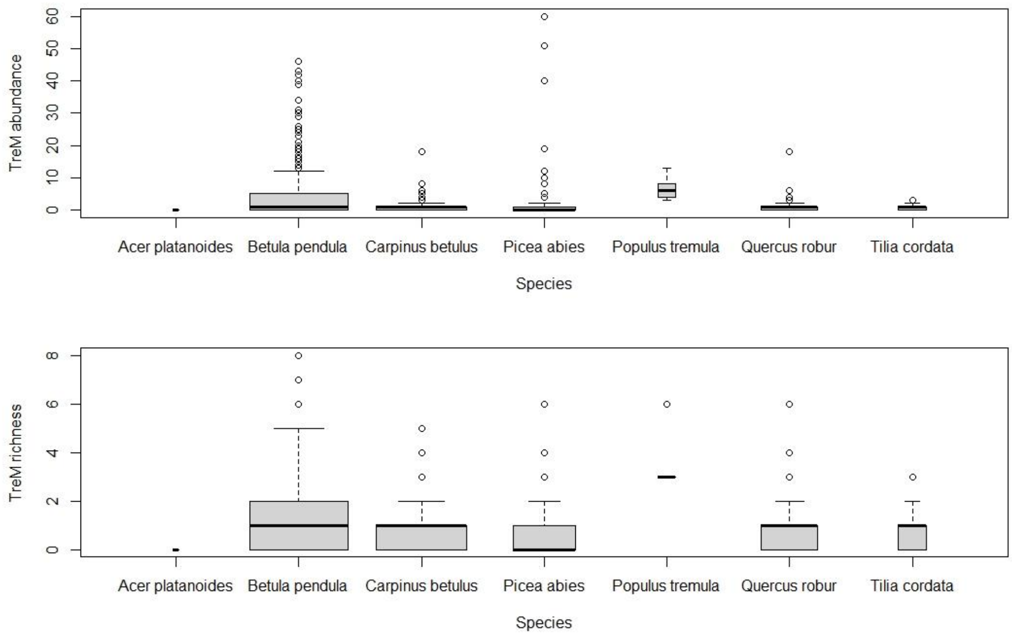

Figure 12. TreM abundance (upper panel) and TreM richness (lower panel) for each tree species in both managed and unmanaged stands

Moreover, TreM abundance and richness differ significantly among tree species (Abundance: χ^2 = 73.99, df= 6, $p < 0.001$; Richness: χ^2= 60.664, df = 6, $p <0.001$ in Fig. 12).

3.3 Predictors of TreM abundance and richness

The TreM patterns for TreM abundance and richness were similar for managed and unmanaged stands, but overall, TreM abundance was significantly higher in the unmanaged stands. The richness did not differ greatly between the two different management types (Appendix 2, Tab. A6).

Tree DBH was one of the main drivers of TreM abundance and richness in the BF, except for the TreM abundance in the managed stands, where the light-demanding trees category predicted the highest values. The light-demanding trees category was associated with the highest predicted values for both TreM abundance and richness regardless of the management type (Fig. 13).

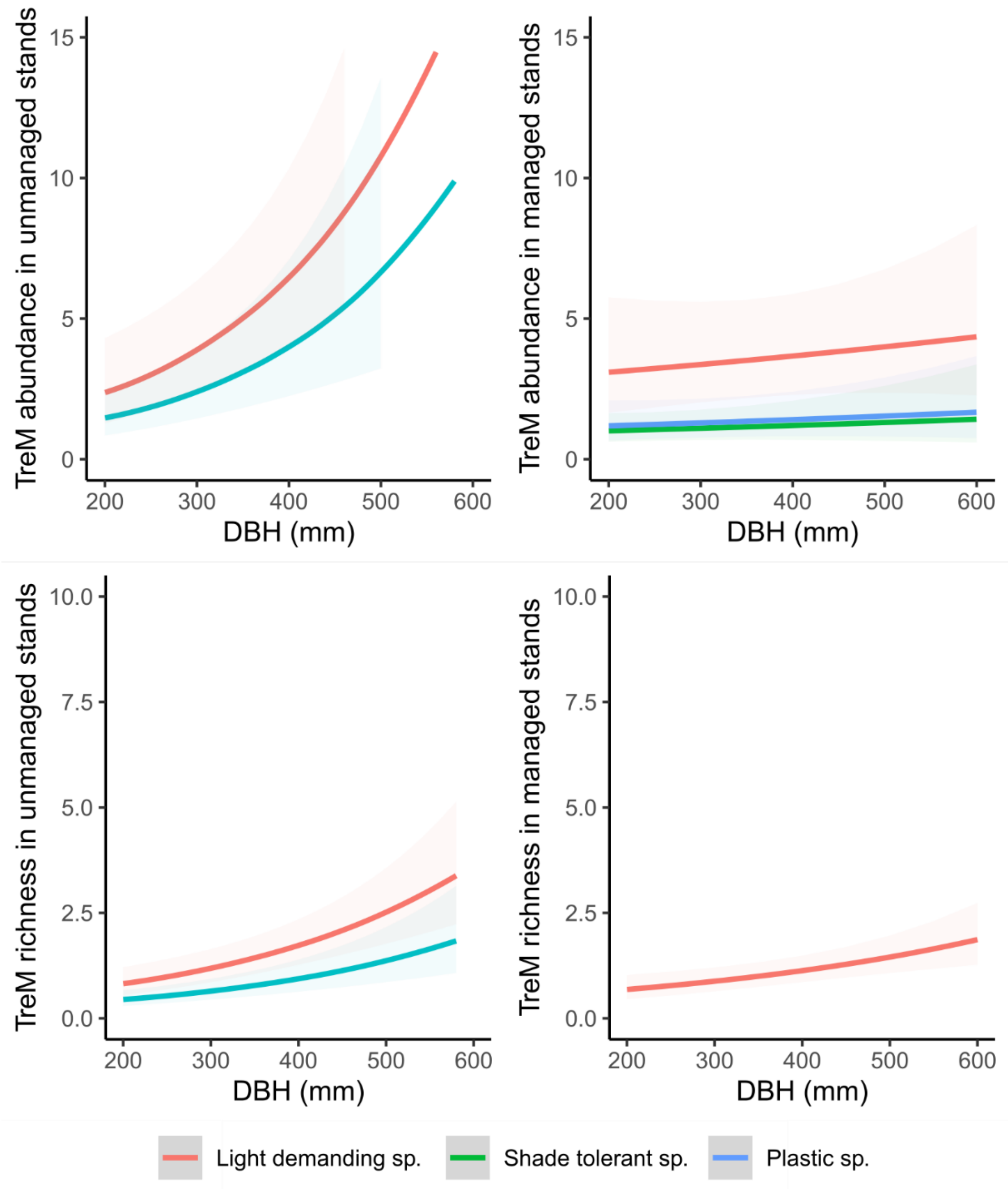

Figure 13. Estimated tree TreM abundance (upper) and richness (lower) in response to DBH of the surveyed trees belonging to different management types: unmanaged (left) and managed (right). Different colours and lines refer to the tree categories. Ribbons represent the 95% confidence intervals. Only significant tree categories predictors were included and DBH was significant in all cases, except for TreM abundance in managed stands

4. Discussion

4.1 The effect of forest management on TreM characteristics

My findings show that higher TreM abundance and richness occurred on trees in unmanaged stands compared to stands of similar origin, but with a longer history of silvicultural practices. This confirms the first hypothesis. The difference in the TreM abundance between trees from stands of different management types is greater than the difference in TreM richness. Most of the TreM groups, except for epiphytes and exposed sapwood, did not differ significantly between managed and unmanaged stands. Previous research has assessed the effect of management on TreM characteristics, but only studies in long-term unmanaged stands found significant differences (Asbeck et al. 2021; Asbeck et al. 2022).

The higher abundance of epiphytes on trees from the unmanaged stands can be attributed to the presence of mistletoes on birches, epiphytic bryophytes on hornbeams and oaks. As there are more birch trees in unmanaged stands (147) in comparison to managed stands (94), species composition could have influenced this result. In addition, this could also be attributed to a more closed canopy in the unmanaged stands. The tree density here is higher, thus the stands have a more closed canopy that maintains high humidity, low wind and prevents temperature fluctuations (Chen et al. 1999) that could facilitate the occurrence of epiphytes.

The second TreM with a significant difference for management type is exposed sapwood. The main goal of forest management practices is to produce good quality timber and thereby shape uniform stands without stem defects (Hansen et al. 1991). The potential TreM trees are therefore often removed at the early stage. Exposed sapwood (e.g. bark loss, fire scars, bark pocket and shelters) is more likely to be found in the unmanaged stands on the trees with lower vitality classes or little commercial value.

Increasing tree DBH leads to higher TreM abundance and richness in most of the cases. The results of the GLMM confirmed the hypothesis that TreM abundance and richness usually increases with larger tree DBH. This was expected as other studies have shown that DBH is a significant factor of TreM occurrence. This is either due to a larger surface area or due to the fact that larger trees are usually older and thus, TreMs had time to form and develop (Asbeck et al. 2021).

Interestingly, in my findings the TreM abundance in managed stands did not increase significantly with larger DBHs. This could be attributed to the effect of thinning operations which constantly removes dying trees, trees with injuries and defects, leaving behind trees with no or very few TreMs, regardless of their size.

4.2 Light demanding species predict the highest TreM abundance and richness

Referring to the second hypothesis, the light-demanding species trait category predicted the highest values for TreM abundance and richness, regardless of management type. This confirms that TreM abundance and richness are associated with species life traits. Furthermore, it is expected that due to their lifespan, light-demanding species age faster and therefore, their wood starts to break and decay faster than the wood of shade-tolerant species of the same age, allowing multiple TreMs to form.

The effect of tree species on TreM abundance and richness was not included in the predictions. However, from the tree data, it is worthy to highlight that even though there were only seven aspens in the research plots, they had various groups of TreMs: either woodpecker cavities, crown deadwood or fruiting body fungi. During the survey, it was noticed that the birch trees often bore decay branches or parts of stem. TreMs such as bark loss and insect galleries are more likely to appear on trees with decay wood. In addition, often forest dwelling species, such as woodpeckers prefer soft, decayed wood as a habitat or feeding site (Tozer et al. 2011; Blanc and Martin 2012).

On the other hand, given that stand history was similar for my studied stands and that “post-Century” stands are currently around 100 years old, birch and aspen are closer to the final stage of life cycle in comparison to other species such as oak, lime and hornbeam, which might also provide more TreMs in the future.

4.3 Conclusions

I conclude that management history affected TreM abundance and richness. The stands with a longer history of silvicultural practices have lower number and less diverse TreMs in comparison to the unmanaged forest.

The feasibility of the TreM approach used suggests that it could be widely used in forest management and close-to-nature silviculture by locating and preserving trees containing TreMs. Retention of trees with higher TreM abundance and richness, particularly large and light-demanding trees such as birch and aspen, could be an important conservation option in managed forests and a good compromise between ecology and economy in the forestry sector under climate and social changes. However, in order to maximise TreM variation and long-term provision retention trees should be chosen among all native tree species.

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Popular science summary

My research was carried out in north-eastern Poland in the Białowieża Forest, one of the most precious and rich in biodiversity forest. The aim of the thesis was to verify whether the type of forest management influences the occurrence of microhabitats on trees.

Microhabitats (so called TreMs) are tree-related structures that provide habitats for other organisms. Their occurrence may be conditioned by the size of a tree, its age, vitality, species or the availability of light. It is well studied that microhabitats are a good indicator of biodiversity in forests. For the purpose of my research, eight plots were established in the Białowieża Forest: four in managed forest stands where wood has been regularly extracted, and four in stands that have been left largely unmanaged since 1969 and protected as the Władysław Szafer's Landscape Reserve. It is worth mentioning that the stands, although managed by foresters in different ways, have the same origin. They come after cuttings done by the British company "Century" in 1924–1929 and were naturally regenerated.

The research showed that management history has an impact on the TreM abundance (total number of TreMs per tree) and richness (total of different TreM types per tree). More TreMs and more diverse types of TreMs occurred in unmanaged stands located in the landscape reserve. Additionally, I also tested the influence of diameter at breast height and individual species characteristics such as light requirements for TreM. Tree diameter at breast height was one of the main drivers of TreM occurrence. It means that bigger trees often have more TreMs. Moreover, light-demanding and short-lived species such as birch and aspen appeared to be more rich in TreMs.

The TreM survey method could be widely used by forest managers to preserve trees with TreMs. Retaining especially large birch and aspen trees contribute to improving biodiversity in commercial stands.

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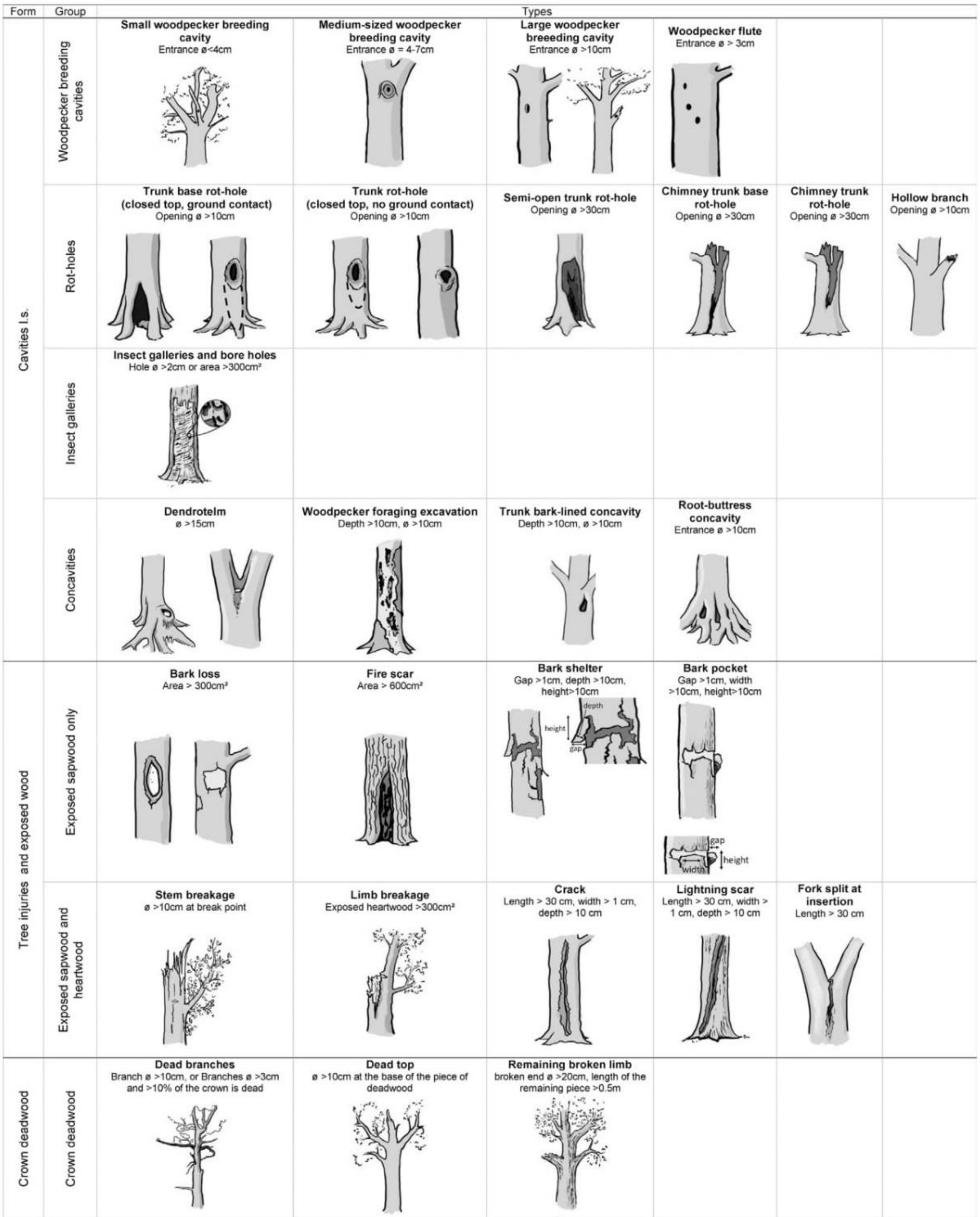
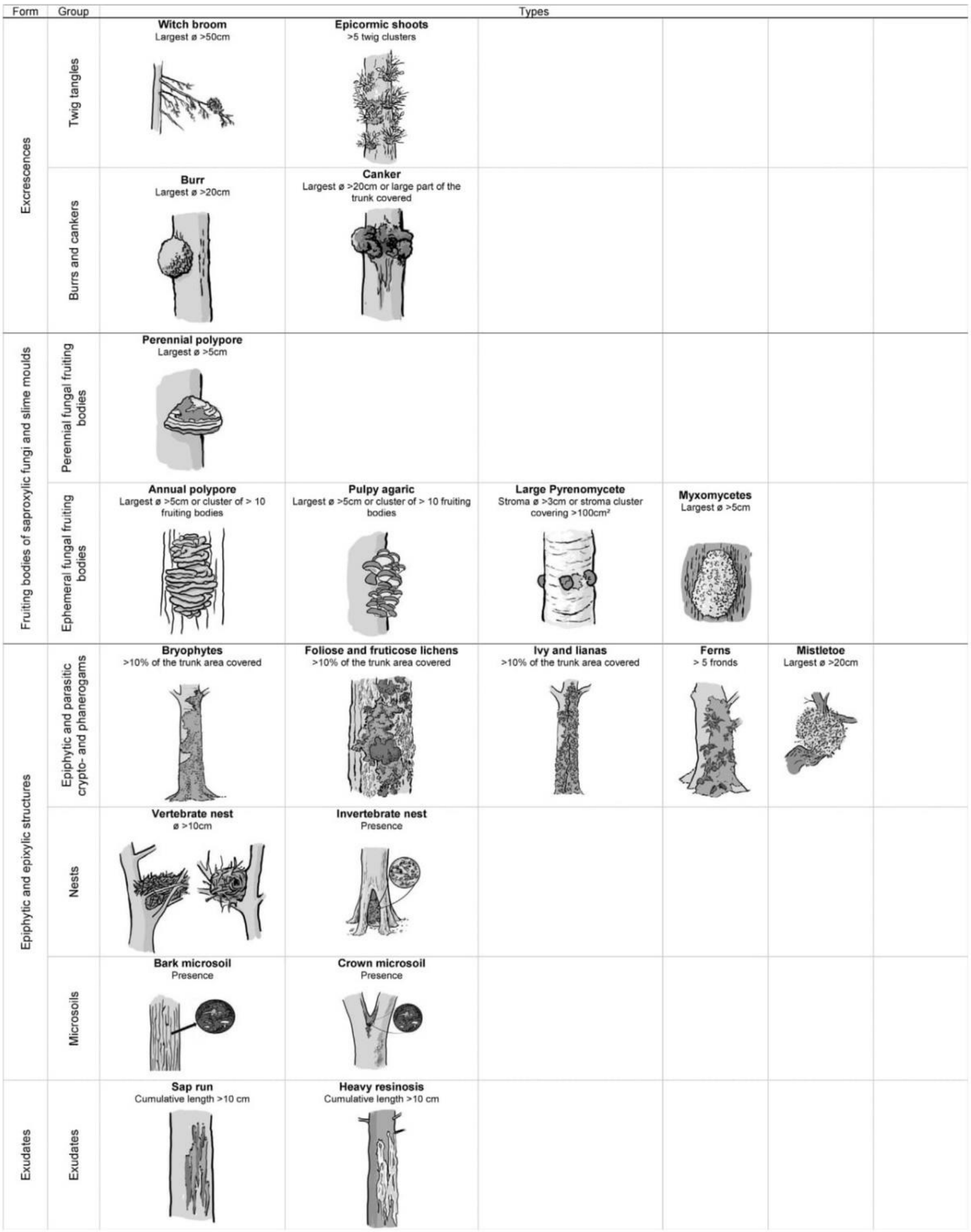
Appendix 1

Table A5. TreM hierarchical typology and inventory thresholds (Ø: diameter) in European temperate and Mediterranean forests



Form	Group	Types					
Cavities l.s.	Woodpecker breeding cavities	**Small woodpecker breeding cavity** Entrance ø<4cm	**Medium-sized woodpecker breeding cavity** Entrance ø = 4-7cm	**Large woodpecker breeeding cavity** Entrance ø >10cm	**Woodpecker flute** Entrance ø > 3cm		
	Rot-holes	**Trunk base rot-hole (closed top, ground contact)** Opening ø >10cm	**Trunk rot-hole (closed top, no ground contact)** Opening ø >10cm	**Semi-open trunk rot-hole** Opening ø >30cm	**Chimney trunk base rot-hole** Opening ø >30cm	**Chimney trunk rot-hole** Opening ø >30cm	**Hollow branch** Opening ø >10cm
	Insect galleries	**Insect galleries and bore holes** Hole ø >2cm or area >300cm^2					
	Concavities	**Dendrotelm** ø >15cm	**Woodpecker foraging excavation** Depth >10cm, ø >10cm	**Trunk bark-lined concavity** Depth >10cm, ø >10cm	**Root-buttress concavity** Entrance ø >10cm		
Tree injuries and exposed wood	Exposed sapwood only	**Bark loss** Area > 300cm^2	**Fire scar** Area > 600cm^2	**Bark shelter** Gap >1cm, depth >10cm, height>10cm	**Bark pocket** Gap >1cm, width >10cm, height>10cm		
	Exposed sapwood and heartwood	**Stem breakage** ø >10cm at break point	**Limb breakage** Exposed heartwood >300cm^2	**Crack** Length > 30 cm, width > 1 cm, depth > 10 cm	**Lightning scar** Length > 30 cm, width > 1 cm, depth > 10 cm	**Fork split at insertion** Length > 30 cm	
Crown deadwood	Crown deadwood	**Dead branches** Branch ø >10cm, or Branches ø >3cm and >10% of the crown is dead	**Dead top** ø >10cm at the base of the piece of deadwood	**Remaining broken limb** broken end ø >20cm, length of the remaining piece >0.5m			



Note. From Larrieu et al. 2018.

Appendix 2

Table A6. Results of the final generalized linear mixed models indicating the magnitude of influence and the significance of the predictors DBH and tree categories (light-demanding, plastic and shade-tolerant sp.)

		Intercept	**DBH [**mm]	**Tree categories**	
				Plastic	Shade tolerant
Unmanaged	TreM Abundance	-0.16	0.01***	-0.48*	-0.84***
	TreM Richness	-0.95**	<0.01***	-0.61***	0.13
Managed	TreM Abundance	0.96*	<0.01	-0.96***	-1.12***
	TreM Richness	-0.88**	<0.01***	-0.12	0.03

Note. Positive values show an increase in the TreM abundance or richness. The intercept represents the light-demanding species. Significance codes: '***' 0.001; '**' 0.01; '*' 0.05. All models were fitted with negative binomial distributions.

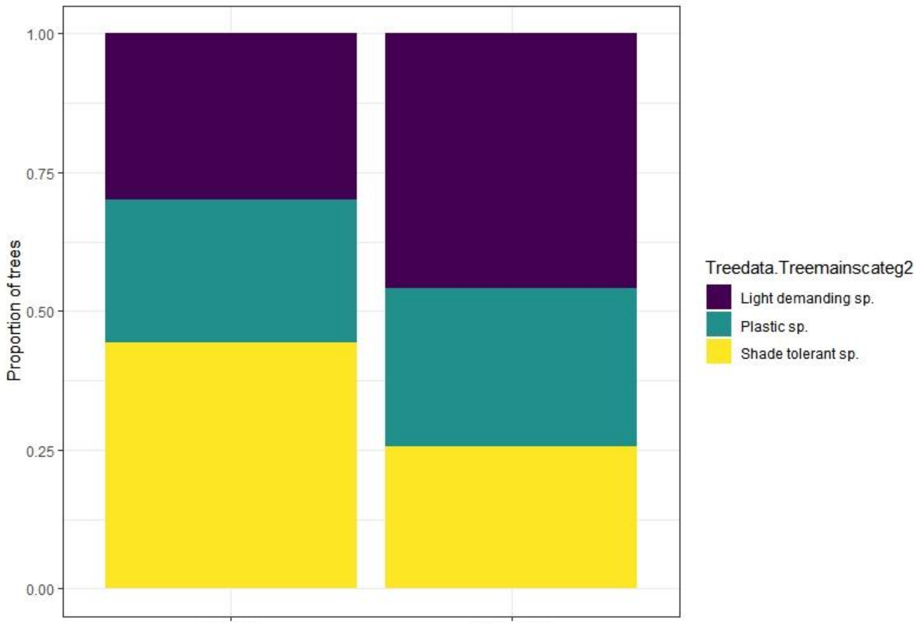


Figure A14. Share of different tree categories (trees clustered according to their life traits)

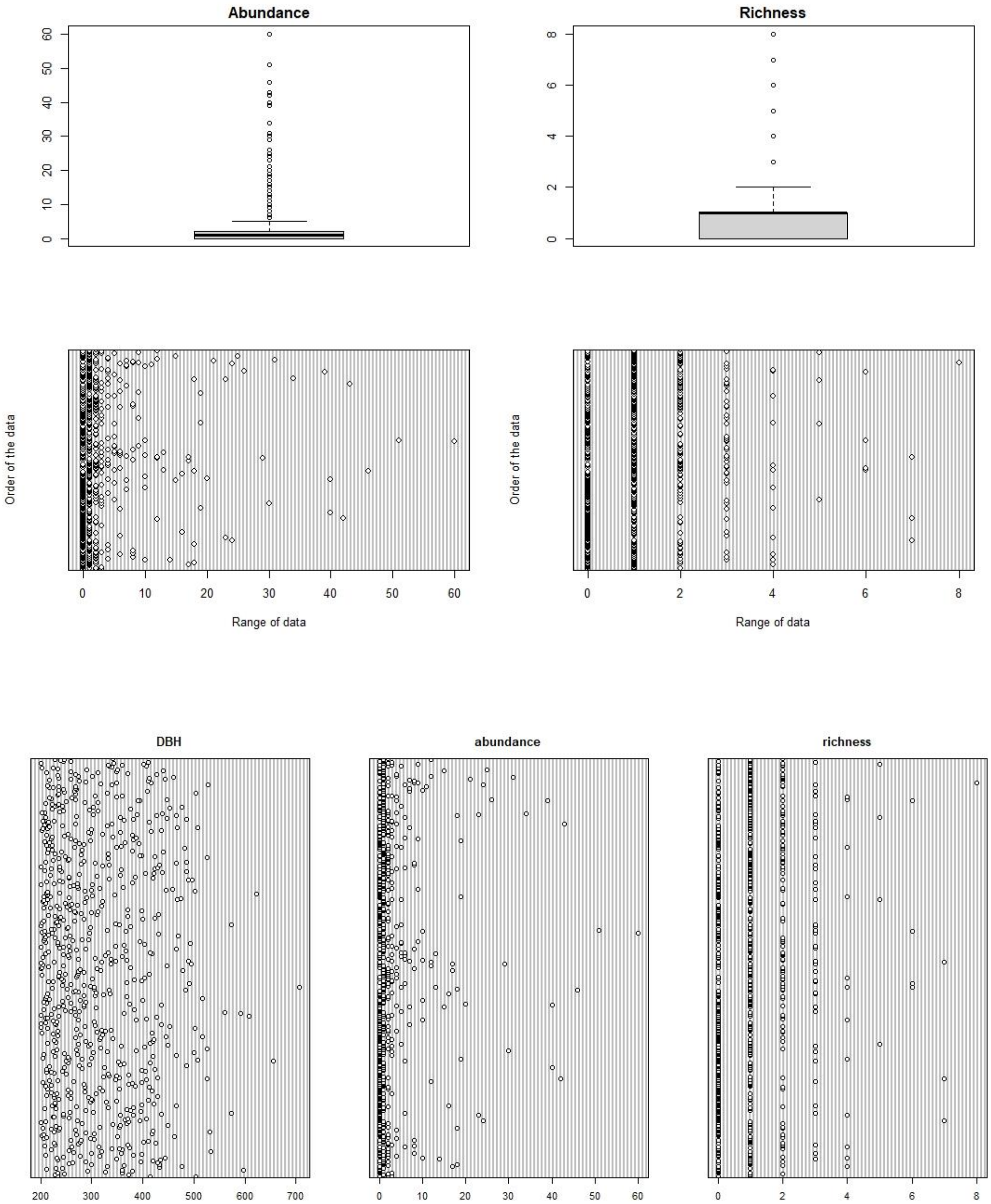


Figure A15. Descriptive statistics. Outliers and range of data

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