

MAARJA KÕRKJAS

Dynamics of tree-related
microhabitats in live forest trees
and its links with biodiversity



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Dynamics of tree-related microhabitats in
live forest trees and its links with biodiversity



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LIST OF ORIGINAL PUBLICATIONS

This thesis summarises the following papers, referred to in the thesis by their Roman numerals **I–III**. The author of this thesis is highlighted in bold type. All published papers are reprinted here with permission from the copyright owners. All photos in the thesis are by the author.

- I Kõrkjas, M.**, Remm, L., & Lõhmus, A. (2021). Development rates and persistence of the microhabitats initiated by disease and injuries in live trees: A review. *Forest Ecology and Management*, 482, 118833. <https://doi.org/10.1016/J.FORECO.2020.118833>
- II Kõrkjas, M.**, Remm, L., & Lõhmus, A. (2021). Tree-related microhabitats on live *Populus tremula* and *Picea abies* in relation to tree age, diameter, and stand factors in Estonia. *European Journal of Forest Research*, 140(5), 1227–1241. <https://doi.org/10.1007/S10342-021-01396-7>
- III Kõrkjas, M.**, Remm, L., Lõhmus, P., & Lõhmus, A. (2023). From tree-related microhabitats to ecosystem management: A tree-scale investigation in productive forests in Estonia. *Journal of Environmental Management*, 343, 118245. <https://doi.org/10.1016/J.JENVMAN.2023.118245>

Author’s contribution to the studies (‘ denotes a minor contribution, * a moderate contribution, ** a high contribution, *** a leading role).

	I	II	III
Original idea	*	‘	*
Study design	**	***	***
Data collection	***	***	***
Analysis and interpretation	**	***	***
Manuscript writing	**	***	***

1. INTRODUCTION

1.1. Linking forest condition, structural complexity, and biodiversity

Global biodiversity is estimated to be declining at elevated rates (Dornelas et al., 2023), perhaps – based on estimated extinction rates – even tens to hundreds of times faster than seen over the past 10 million years (IPBES, 2019). This is primarily driven by the expanding and intensifying influences of human activities (Halpern et al., 2019; Venter et al., 2016), which often cause habitat degradation and fragmentation (IPBES, 2019). Forests are crucial for maintaining biodiversity since roughly 75% of terrestrial plants, fungi, and animal species live in forests (FAO, 2020). While only 10% of all forests are designated for biodiversity protection, around 30% are used primarily for production, and the global forest area continues to decline (FAO, 2020). In Europe (excluding the Russian Federation), these proportions are similar, but 96% of the European forest area has management plans, which indicates an intention to manage forests sustainably (FAO, 2020). Severe climatic events, overexploitation, fires, pests, diseases, and invasive species can further disrupt forests, threatening biodiversity and ecosystem services like raw material provision and geochemical cycle regulation (FAO, 2020; Felipe-Lucia et al., 2020). Only 2.2% of European forests remain undisturbed by man (FOREST EUROPE, 2020).

Management-planning-related discussions on the forest condition, specifically in the sustainable forest management framework (Rametsteiner & Mayer, 2004), frequently include the concept of ‘forest health’. This complex, multifaceted and often subjective concept (Witzell et al., 2022) refers to the overall potential and resilience of the forest ecosystem (Burger, 2004; Witzell et al., 2022). Ecologically healthy forests are assumed to have a high structural and compositional complexity typical of naturally developed forests (Brocknerhoff et al., 2017). These properties are linked with biodiversity at all levels, indicating forest ecosystem functioning in soil fertility, primary production, nutrient recycling, pest control, etc. (Abas, 2023). Consequently, in those regions where clear-cutting is the dominant harvesting method, the resulting structurally simplified forests can be considered ‘unhealthy’ from an ecological perspective (Kuuluvainen, 2009; Zeller et al., 2023). The same applies to other interventions that reduce stand complexity, which is why the timber harvesting methods maintaining or even increasing forest structural diversity are of great interest (e.g., Maxence & Raymond, 2019; R uger et al., 2007). Specifically, a loss of slowly developing old-growth attributes and heterogeneity can reduce forest biodiversity and resilience to disturbances for extended periods (Zeller et al., 2023). Otherwise, transitional (semi-natural) forests may appear relatively ‘ecologically healthy’ and biodiverse in terms of plasticity to buffer natural or man-induced disturbances (Zeller et al., 2023). Nevertheless, semi-natural forests usually lack ecological continuity (forest communities could have been interrupted for multiple

tree generations) and could, thus, have ecosystem complexity and biodiversity levels below natural (e.g., Fritz et al., 2008).

Given the large scale of forest exploitation both globally and regionally, it is a worldwide sustainability challenge to reduce biodiversity loss and enhance the structural complexity of production forests (Kuuluvainen, 2009). Specifically, it has been suggested that retaining structural elements of natural forests at harvest supports environmental, economic, and cultural values in forestry (Lindenmayer et al., 2012). It could thus be a basis for ‘an ecologically healthy forest’. For example, preserving large old trees (‘habitat trees’) in forests not only supports biodiversity but could serve as an effective climate protection instrument as well (Hauck et al., 2023; Mildrexler et al., 2023).

1.2. Tree-related microhabitats as elements of forest complexity

The vast majority of an estimated 73,000 tree species on Earth form forests (Gatti et al., 2022). Trees are the defining structures of forests, but the exact mechanisms of how they support other species remain incompletely described. An apparently major mechanism is through tree-related microhabitats (TreMs). These are diverse structures on dead or live trees – such as cavities, witches’ brooms, exposed wood, bark cracks, and dead branches – that other organisms can use as substrates or for food, shelter or breeding. In this thesis, TreMs are defined according to Larrieu et al. (2018): “... *a distinct, well-delineated structure occurring on living or 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.*” TreM-bearing habitat trees could act as ‘small natural features’ that have disproportionately large ecological importance relative to their size and have potential as targets in sustainable forest management, especially in retention forestry (Hunter et al., 2017).

Larrieu et al. (2018) divided TreMs into seven main forms by morphology and inhabiting species: cavities; tree injuries; exposed wood; crown deadwood; excrescences; fruiting bodies of saproxylic fungi; epiphytic/epixylic/parasitic structures; and exudates. These add to forest ecosystem structural integrity and, for the reasons described above, are most diverse and abundant in old-growth forests (Asbeck et al., 2022). The question is, thus, how TreMs can and should be managed in production forests to serve landscape-scale biodiversity goals, e.g., to support rare and threatened species and to facilitate species dispersal (Baguette et al., 2013; Kraus & Krumm, 2013).

It is generally well known that TreMs provide habitat to birds, bats and arboreal mammals, invertebrates, small semi-aquatic organisms, and epiphytes (Basile et al., 2020; Ellis, 2012; Goldingay, 2012; Larrieu et al., 2018; Magyar et al., 2017; Paillet et al., 2018; Remm & Löhmus, 2011; Siitonen & Ranius, 2015). However, determining the exact set of species dependent on TreMs is challenging due to the complexity of ecological relationships and the various

interpretations of what defines a TreM. As an order of magnitude, it has been suggested that at least 18% of all bird species in the world are tree cavity-nesters, of which only about one-quarter can excavate their nest cavities (van der Hoek et al., 2017). Thus, the remaining species need cavities excavated by other birds or developed naturally due to decay processes. In a study conducted in Germany, where there are 107 mammal species (Butler, 2023), 11 have been found to visit water-filled holes, along with 17 birds and one amphibian species (Kirsch et al., 2021).

TreMs are dynamic and ever-changing structures. Natural forests typically have a rich supply of TreMs in all stages of development (due to trees in different age groups, with various decay stages and diversity in species) that could replace old collapsing TreMs. In principle, TreMs are caused by similar tree and environmental properties both in primary and managed forests (Asbeck et al., 2022). However, many TreM-creating processes in managed forests are interrupted by removing weaker trees during thinnings or large trees during final cuttings and by short rotation periods. As a result, TreMs in managed forests are often small and scarce and dominated by certain types, such as exposed wood, exudates, and dendrotelms, i.e., water-filled hollows (Asbeck et al., 2022; Larrieu et al., 2012, 2014). Several studies have shown that it takes several decades or even more than a century without logging to develop a TreM structure similar to old-growth natural forest (Ball et al., 1999; Courbaud et al., 2017; Fan et al., 2003; Larrieu et al., 2012).

It has been proposed that TreMs constitute an essential target for sustainable forest management, particularly while selecting habitat trees for retention (Courbaud et al., 2022). In the long term, however, retaining only TreM-bearing trees is not enough – it is also vital to promote trees where the likelihood of future TreM formation is high (Courbaud et al., 2022). According to Courbaud et al. (2022), some TreMs (exposed wood, deadwood, cracks and dendrotelms) are more prevalent on smaller trees. Given the usual strong correlation between tree size and age (e.g., Churski & Niklasson, 2010; but see Kuuluvainen et al., 2002 for comparison), this suggests that a mix of age cohorts is essential for maintaining TreM diversity. However, to construct predictive models for TreMs (and their functions) for forest planning, a deeper understanding of TreM development processes and rates is essential.

TreMs could also act as proxies in forest biodiversity monitoring under the assumption that these links are clear (Asbeck et al., 2021). This could enhance time- and cost-efficiency of the monitoring, particularly when compared with directly surveying rare, threatened, seasonal or inconspicuous forest species. Thus far, forest planning and simulation studies lack sufficient biodiversity indicators that would provide unbiased and comprehensive descriptions of its spatial and functional properties (Hunault-Fontbonne & Eyvindson, 2023). For example, improved biodiversity indicators should represent fauna, flora, and fungi kingdoms (by representative species across multiple groups), cover habitat persistence in addition to habitat quality and quantity, and consider the dynamic nature of habitat connectivity (Hunault-Fontbonne & Eyvindson, 2023).

Despite the relative ease of assessing, forecasting, and communicating these structural elements (Angelstam et al., 2001), TreMs beyond deadwood are poorly linked with biodiversity characteristics (Gao et al., 2015) and are underused for biodiversity monitoring purposes in forestry. Furthermore, understanding TreM lifecycles also helps predict the economic value of trees and model forest values for different harvesting scenarios. Notably, ‘mature’ forests are often defined by the age at which they transition from a productive phase to a stabilised tree mortality phase, characterised by the formation of TreMs and a subsequent decline in economic value.

1.3. Knowledge gaps

Despite the growing recognition of TreMs as essential components of forest biodiversity, significant knowledge gaps remain regarding their development, persistence, and ecological significance. For ecological planning (and other tree-condition-related questions), a quantitative synthesis of measured TreM development rates, time of presence, and their tree-scale and broader-scale modifiers is crucial.

For example, quantitative research is needed to understand how *the age and size of trees* affect TreM presence and characteristics. Such knowledge could help understand the impact of different silvicultural systems on TreM supply and their functions. A specific question is whether and how to incorporate tree age in predictive models of TreM pools (for diameter, see Courbaud et al., 2017). While TreM development takes time, the largest trees are often TreM-rich but not necessarily the oldest.

In parallel, *the variation* in how TreMs accumulate with age in different tree species and under various conditions needs further study. This variation affects the perspectives of predicting TreM stocks in space and time. More primarily, we still lack a clear understanding of the fundamental processes (TreM development pathways) involved in the formation, development, and persistence of most types of TreMs.

A whole set of questions is related to the links between TreMs and biodiversity. TreMs could act as biodiversity indicators (Basile et al., 2020; Larrieu et al., 2018; Martin et al., 2022; Paillet et al., 2018), but the link is often loose and variable (Asbeck et al., 2021; Paillet et al., 2018). Spatial factors to be considered include the scale (tree-, stand-, or broader scale) where we study these relationships and contextual effects. As an example of the latter, a single relatively poor TreM-bearing tree may have crucial habitat value in a (semi-)open landscape due to TreM-resource limitation but less so in an old-growth forest where multiple TreM-bearing trees are present.

Regarding forestry and conservation applications, the region plays a role, e.g., particular TreM size thresholds or management targets may not be applicable across vegetation zones (Martin et al., 2021). Little is known about the significance of inconspicuous TreMs such as bark deformations (e.g., bark shelters,

bark pockets formed by peeling bark), difficult-to-study TreMs such as witches' brooms, and rare TreMs such as dendrotelms. These TreMs are often unimportant from an economic perspective, but they may have high value for biodiversity (e.g., Bull et al., 1997; Kirsch et al., 2021). Overall, the usefulness of the TreM-based management approach needs to be clarified.

1.4. Aims and hypotheses

The broad purpose of this thesis was to investigate how trees develop their habitat value through TreM development in various circumstances. To advance the understanding of TreMs and their role in supporting forest biodiversity, the following approaches were selected and implemented in the three studies of this thesis:

1. **Review the published rates of development and loss of TreMs on live trees**, focusing on knowledge relevant to biodiversity conservation (**I**).
2. **Examine the relationship between tree age and TreM occurrence probability on live trees**, including the influence of potential effect modifiers, to better understand the temporal dynamics of TreM development (**II**).
3. **Compare the explanatory value of tree age and tree diameter at breast height (DBH) in predicting TreM occurrence on live trees** to support forest management planning that should balance the conservation of biodiversity (particularly through the preservation of TreMs and the identification of future TreM-rich trees) with sustainable timber production (**II**).
4. **Analyse tree-scale, age-independent contributions of TreMs to biodiversity variables of broader ecological importance** to better understand TreM-related conservation targets in managing production forests (**III**).

The specific hypotheses addressed using these approaches were as follows.

H1. TreM accumulation hypothesis: The diversity and abundance of TreMs increase monotonously as trees age and grow larger because of cumulative exposure in time to biotic and abiotic factors that promote TreM formation.

Rationale: Prolonged exposure to a myriad of ecological processes can create or modify microhabitats or accelerate their formation, notably:

- natural senescence: physiological decline associated with ageing, leading to structural changes (e.g., crown dieback, bark shedding) and increased susceptibility to degrading organisms (e.g., fungi, insects);
- physical damage: accumulation of injuries from, e.g., adjacent tree falls, lightning strikes, animal activity that creates wounds;

- pathogen and pest interactions: infections by, e.g., insects, fungi, and bacteria that cause disease, damage bark or wood structure or create cavities;
- abiotic factors: exposure to environmental stressors (e.g., drought, frost) that weaken the trees, break limbs or promote the formation of trunk cracks.

Alternatively, TreMs could accelerate tree loss, creating tree-scale trade-offs between TreM abundance and persistence.

H2. The hypothesis of tree species-specific constraints on TreM dynamics and ecological significance: Tree species identity plays a central role in shaping the occurrence, diversity, and ecological significance of TreMs by modulating their development, persistence, and the associated biodiversity they support. This modulation reflects complex interactions among tree species-specific traits, resource allocation strategies and other adaptations, as well as the ecology of organisms utilising TreMs on different tree species in their environments.

Rationale:

- Each tree species exhibits a unique suite of life history traits relevant in TreM formation (e.g., growth rate, wood density, bark thickness, branching architecture) and evolutionary adaptations that influence its susceptibility to damage, decay, and colonisation by organisms that create TreMs. These differences lead to distinct patterns of TreM occurrence, persistence, and diversity among tree species. For example, fast-growing species with soft wood, like the European aspen (*Populus tremula*), may be prone to decay processes leading to cavity formation through interactions with other species like woodpeckers and specific bracket fungi (Remm & Löhmus, 2011).
- The allocation of resources to growth, defence, and reproduction varies among tree species, influencing TreM development rate and persistence. Fast-growing species may invest more in growth, leading to rapid TreM formation and high TreM diversity, but also faster closure of small wounds.
- The biodiversity associated with TreMs is also affected by their other ecological preferences, which can be tree-species specific. Different taxa may exhibit varying affinities for tree species due to the substrate (bark, wood) chemistry and specific structures (e.g., needles, thorns, and spines; or even branch architecture), leading to tree species-specific patterns of TreM occurrence and biodiversity.

H3. Ecological-context dependency hypothesis: TreM development, persistence, and diversity are not solely determined by tree characteristics but also by a broader ecological and ecosystem-history context that affects the tree physiology, growth, and interactions with other organisms.

Rationale: Abiotic factors such as temperature, precipitation, and light availability affect tree growth, wound healing, and susceptibility to pathogens and pests. For example, warmer temperatures and higher moisture levels can accelerate fungal decay, promoting cavity formation. Drought stress can weaken trees and increase their vulnerability to damage. Both natural and anthropogenic disturbances and the stand origin (e.g., afforestation vs. natural regeneration) can influence TreM development. In a management context, thinning can create wounds, alter light availability, and modify competition dynamics for the trees retained. Stand origin can indirectly influence soil properties, TreM-promoting species composition (e.g., insects, fungi, birds), and disturbance regimes.

H4. TreM diversity-biodiversity hypothesis: A higher diversity of TreMs on a tree supports a greater diversity of inhabiting organisms and ecological relationships there.

Rationale: Different TreMs provide unique combinations of resources (e.g., food, shelter, breeding sites) and microclimatic conditions (e.g., temperature, humidity, light exposure), catering to the specific requirements of diverse species. For example, newly formed wounds may attract pioneer species, while older cavities may provide habitat for species that require stable and established microenvironments. Therefore, a greater diversity of TreMs can support a broader range of coexisting functional groups and trophic levels.

These four hypotheses were studied in live trees that constitute the main forest management targets and where TreMs function differently than in dead trees. TreMs on live trees have potentially higher longevity, better camouflage due to the tree foliage, and biologically, physically, and chemically different substrate conditions than TreMs on dead trees (Hooge et al., 1999; Spînu et al., 2022; Wiebe, 2001). The case studies (**II**, **III**) were based on two ecologically and economically distinct tree species: Norway spruce (*Picea abies*) – one of the most commercially valuable conifers in Europe (Caudullo et al., 2016), and aspen – a fast-growing deciduous species with a remarkably high biodiversity value (Rogers et al., 2020). The case studies were made at the individual tree level, including explicit measuring of the age of the trees. Most previous TreM occurrence and diversity studies have not directly focused on tree scale and have used generalised or indirect (diameter-derived) age estimates (Martin et al., 2022).

2. MATERIALS AND METHODS

2.1. Literature review (I)

The literature review examined empirical estimates of three time parameters associated with the development of TreMs in live trees: the *age of trees* at the onset of a functioning TreM, the *rate of change* in TreM size and quality, and the *persistence* of TreMs. The review addressed five distinct and common types of TreMs found globally, which only appear in trees after injury or disease: patches of exposed wood, tree cavities, bark pockets, dendrotelms, and witches' brooms. All these above-ground TreMs are structures of the tree itself, not other organisms attached to the tree.

The review considered primary studies (until 2019) that documented at least one of the following attributes of TreM development under untreated (uncured) conditions: (i) sequence and timing of the development stages, including size changes, colonisation by new inhabiting organisms, and emerging of new features; (ii) duration of the formation or rate of the changes; (iii) persistence of the habitat value of the TreM (also after the death of the tree); (iv) effect modifiers influencing the characteristics (i)–(iii), such as temperature, humidity, or their explicit combinations in contrasting sites. The literature was found through a basic search (in the Scopus database), follow-up scanning of the reference lists, and specific searches for poorly represented TreMs. The basic search terms included synonyms for the selected TreMs and various operational terms related to development processes. We excluded artificial wounding studies (drill wounding, branch pruning) since they can introduce processes with rates different from those of natural injuries. The consistency of inclusion was analysed based on abstracts by the author of this thesis and Liina Remm, indicating substantial agreement (Kappa tests, $k=0.7$). Potentially relevant articles were then evaluated for inclusion based on the full text.

In total, these searches yielded 71 papers, mainly from the temperate zone of Central Europe, and taking a forest management standpoint. Side cavities were the subject of 32 papers and exposed wood of 28 papers, while witches' brooms were only addressed in four papers, and dendrotelms and bark pocket development in one paper each. The process of TreM development that has received the most attention globally is the closure (with callus tissue or wood layer) of wounds caused by experimental procedures, ungulate bark-stripping, or timber harvesting (Table 2 in I). Wound closure is also the only TreM process well documented throughout its development, from initiation to loss. However, these studies typically address fungal decay from a wood industry perspective, and the effect of tree wounds on the habitat quality dynamics has not been evaluated.

Long-term monitoring of TreM persistence from detection or experimental creation until the loss is also rare. There were 12 such papers on exposed wood and 12 on side cavities, but only one on witches' brooms and none on dendrotelms or bark pockets. Some studies have examined TreM persistence from the perspective

of inhabiting species, with four papers tracking cavities from the first use to the loss for a focal species. Additionally, while several studies have compared TreM abundance in forests with different kinds of management, none have monitored the implementation of specific microhabitat management objectives. Moreover, research on decay expansion has almost exclusively focused on wound-related heart-rot, neglecting surface weathering and the spread of decay over exposed wood patches.

2.2. Case studies (II–III)

2.2.1. Study area and sampling design

Both case studies were carried out in 2018 in southeastern Estonia, in the European hemiboreal vegetation zone. The trees were sampled in 141 state-owned stands, primarily in Jõgeva, Tartu and Valga counties (Fig. 1). This study region is mostly an undulating lowland plain area below 200 m a.s.l., where forest lands cover 49% by area (of this 45% state-owned). Most forests are dominated by birch (*Betula* spp.) – 39% of stands; Scots pine (*Pinus sylvestris*) – 23%; or Norway spruce – 20%. Stands dominated by European aspen form 7% of the forests.

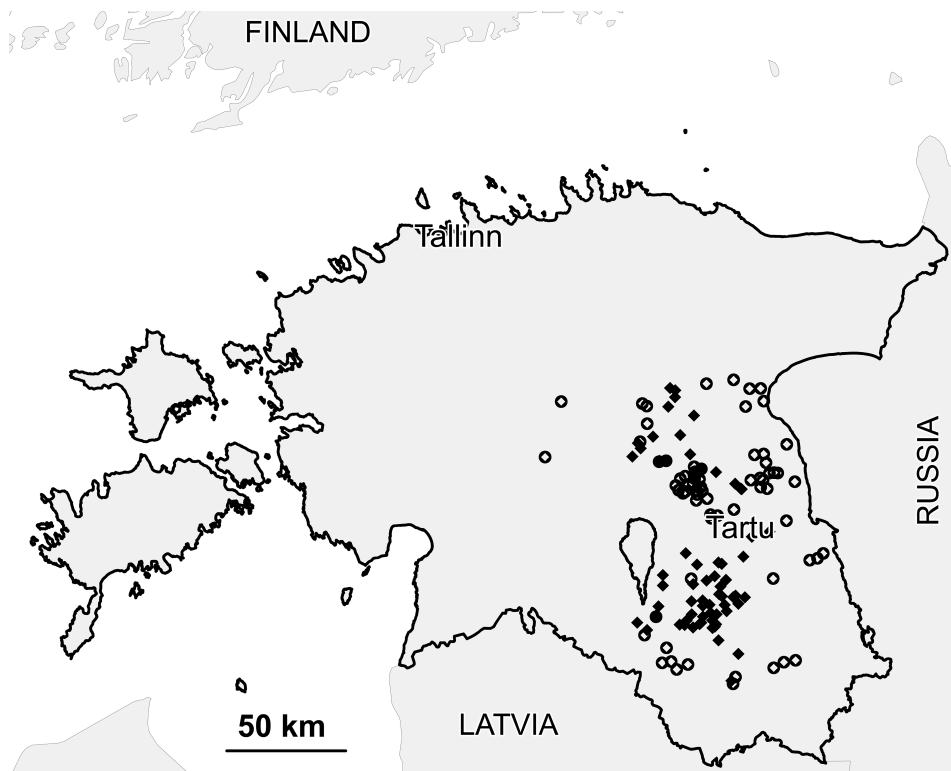


Fig. 1 Location of the studied stands in Estonia from II (diamond – *Hepatica* type; circles – *Filipendula* type)

The sampled stands were at least 20 years old and situated in mixed, mostly even-aged, forest stands representing two productive site conditions (*Hepatica* boreo-nemoral – on mesic soils; *Filipendula* paludifying – on moist soils). The stand characteristics recorded included whether they had been managed by partial cutting (mostly thinning) in the last 10 years (based on the Estonian forest notification database) and the stand origin based on historical maps (two classes: long-term forest lands and afforestation on former (semi)open sites). For such a three-factor design (Site type, Origin, and Management; see Table 2 in II), an age-class stratified random subset was drawn from the available stands within an 80 km radius of Tartu. The selection process involved using stand IDs (from the Estonian National Forest Registry) and a random number generator, with manual checks and additions to ensure the representation of all factor combinations.

2.2.2. Field surveys and laboratory techniques

Between March and May of 2018, the author conducted a field inventory of 469 live spruces and 446 aspens, totalling 915 trees. At least three spruces and three aspens were haphazardly sampled in each stand (except in 17 stands with fewer aspens or spruces). The presence of distinct TreMs in each sampled tree was recorded, following Larrieu et al.'s (2018) definition and hierarchical typology with adjustments considering the relevance to biodiversity in the study area (see Table 1 in I). The original protocol by Larrieu et al. (2018) was recorded in parallel for comparison. In total, 13 pre-defined TreM types were observed. All trees were cored for age determination by growth ring counting (see illustrations in Fig. 2, 3). The cores from 36 trees were problematic. Thus, the age data were available for 879 trees (451 spruces and 428 aspens).

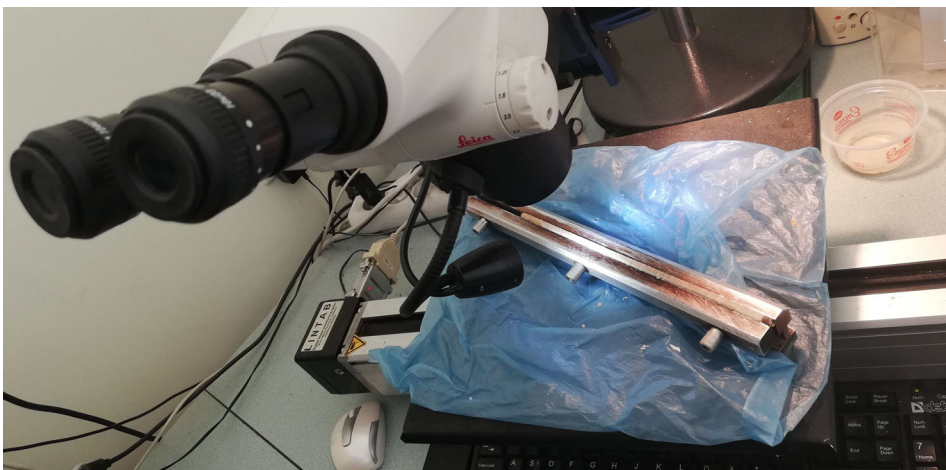


Fig. 2 Counting and measuring tree growth rings in the lab with Leica S4E stereomicroscope together with the measuring device Lintab, using TSAP-Win™ software in the Dendrochronology lab of the University of Tartu



Fig. 3 An illustration of an aspen core sample where the growth rings (indicated by the blue spots) are visible

To study TreM-related biodiversity (arthropods, gastropods, epiphytic lichens and bryophytes), the author conducted separate fieldwork between May 18 and August 15, 2018. Initially, a subset of 241 overstorey trees was selected: 123 spruces (aged 20–188 years) and 118 aspens (24–163 years) in 65 stands. The principle of stand selection for studying biodiversity was a wide range of tree (and stand) ages in various forest conditions.

For invertebrate sampling, cylindrical trunk traps (see an illustration in Fig. 4) were placed as close as possible to the most prominent TreM (0.3–2 m above ground) following a general design for catching invertebrates on woody substrates (e.g., Kaila, 1993). Twice per month during the three months, the animals caught were collected and stored in ethanol, and all the collectors were refilled with a fresh solution. Most of the laboratory work was carried out by the author, e.g., sorting and counting the collected organism material, assessing invertebrate prey volume by summing individuals of five size classes according to Rosenvald et al. (2011), and measuring the length of the longest arthropod in each sample. The collected snail specimens were identified to the species level by Liina Remm; some juveniles were left at a higher taxonomic level.



Fig. 4 A trunk trap positioned at a cavity with an old bird nest on spruce

Morphologically distinct lichens and bryophytes were collected from the same trunks up to 2 m from the ground, excluding the ground-dwellers spreading up to the lower trunk. The specimens were identified in the lab by Piret Lõhmus. While most taxa were identified at the species level, some bryophytes were analysed at the generic (e.g., *Plagiothecium*, *Thuidium*) or morpho-species level (e.g., *Brachythecium*) to reduce field sampling errors.

2.2.3. Data processing

The main approaches used in the case studies were statistical multi-factor models, which related tree- and stand-scale factors to the occurrence of TreMs (**II**) or, combined with TreMs diversity – to biodiversity variables (**III**). The key interests were TreM development and tree-dwelling biodiversity development over time (as identified in **I**) and whether TreM occurrence contributed to the biodiversity independently from tree age and size characteristics. Separate models were constructed for aspen and spruce, with stand identity always included as a random effect. Paper **II** also summarises the diversity of TreMs among tree age classes.

To study the effect of tree age and other key factors on TreM occurrence (a binomial dependent variable), generalised linear mixed-effects models (glmer) based on the logit-link function were used. Main analyses followed local TreM criteria (Table 1 in **II**), although alternative models based on stricter criteria (Larrieu et al., 2018) were also explored. To attain sufficient sample sizes, some closely related TreM categories were pooled (Table 1 in **II**).

The first step involved constructing Type III *full models* to evaluate TreM probability functions with tree age (a continuous variable) and three potential stand-scale effects (site type, stand origin, recent thinning – each comprising two categories). Only the linear effect of tree age was assessed for the TreMs present on 6–14 trees, and stand-scale effects were tested only for TreMs present on at least ten trees. If the sample size allowed, more complex effects were added, such as tree age squared (to analyse nonlinearity) and two-way interactions between stand-scale variables.

In the second step, the most informative explanatory models of TreM incidence for more frequent (present on at least ten trees) TreM types were extracted (*reduced models*). All possible factor combinations were considered, and the best models were identified based on the Akaike information criterion ($\Delta AIC < 2$). Another criterion was the statistical significance ($p < 0.05$) of all factors included (except in the main effects accompanying significant interaction terms). The subsequent interest was determining how the best models combined tree age or DBH as predictors, and square terms were included to account for non-linear relationships. Within each tree species \times age class, tree age and DBH had a weak correlation ($r = 0.04$ to 0.33) (**II**).

In the biodiversity study (**III**), the general form of the hypotheses tested was that the presence of one or several TreM categories (*TreM diversity*; see below) on a tree would affect a biodiversity feature. These models (lmer for continuous dependent variables; glmer negative binomial distribution for count data) thus followed a strict protocol to test for the significance of particular pre-defined factors, including potential confounding factors. A technique used was to add or remove other tree-scale variables to determine whether the TreM effect was independent of those variables. The trees were separately modelled by two age classes based on typical rotation ages in production forests for better management insights: spruces of 20–65 years vs. 65+ years old and aspens of 24–50 years vs. 50+ years old.

Regarding the TreM diversity index, the field records were interpreted as four TreM development processes (shown in Fig. 5 and listed in **III**), with the number of these processes present serving as the key independent variable. Among the trees studied, 44 spruces and 26 aspens showed no TreM processes, while 62 and 58 had a single process, and 17 and 34 had multiple processes, respectively. The four processes were:

- (i) Peculiarity – genetic predisposition and age-associated TreM types, e.g., buttress (i.e., bark-lined concavities formed by above-ground tree roots) and other concavities;
- (ii) Pathology – TreM types related to pathological processes, e.g., fungal fruiting bodies, crown deadwood;
- (iii) Injury – TreM types originated from factors like ungulate browsing, woodpecker cavitation, and falling neighbouring trees; and
- (iv) Emergent epiphyte cover – fruticose or foliose epiphyte cover that can host other species or compete for the trunk space, depending on the particular taxon.

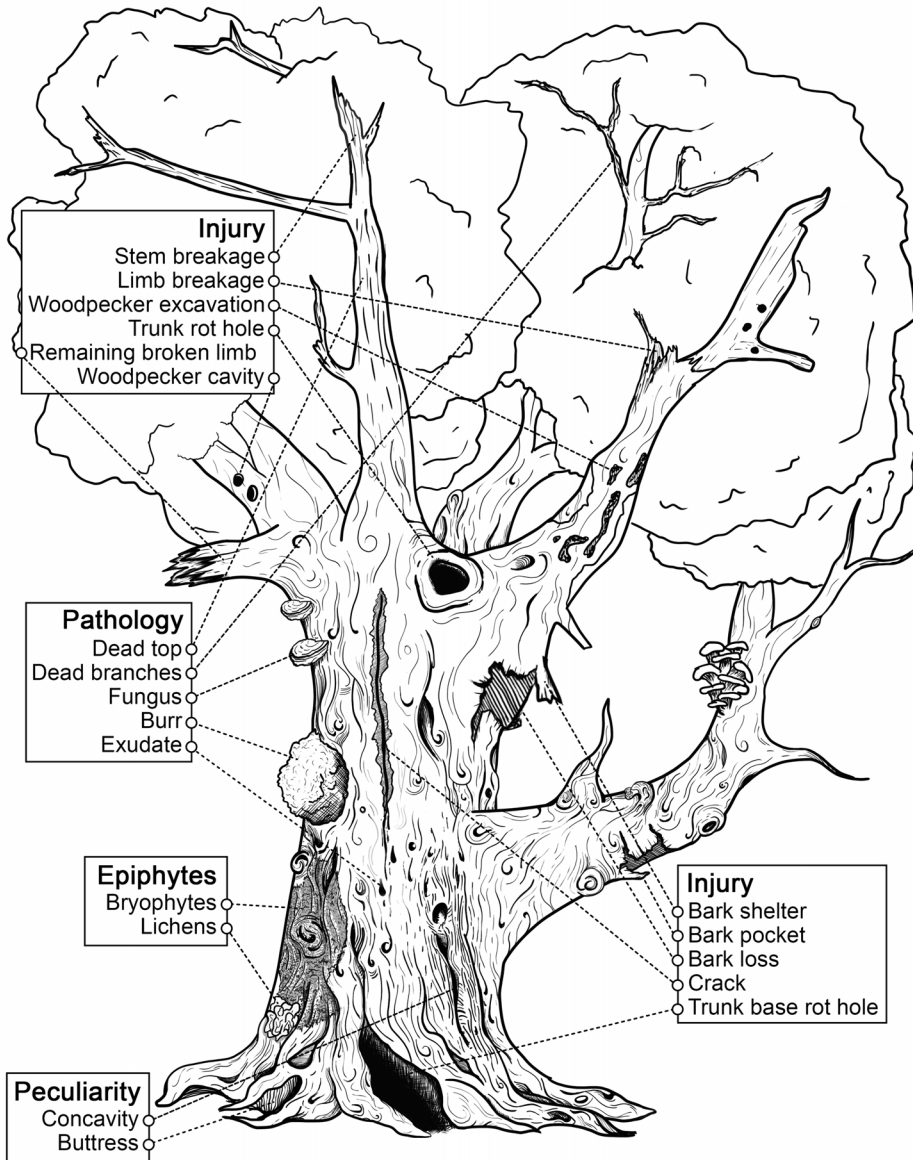


Fig. 5 The TreM types considered in III, and their categorisation into four development processes: peculiarity, pathology, injury, and emergent epiphyte cover. Artwork author: Arle Kõrkjas.

3. RESULTS

3.1. Current knowledge of TreM development and persistence (I)

The **development processes** of TreMs remain incompletely studied, but multiple time spans, tree- and stand-scale factors and alternative development pathways have been documented across studies. For example, expansion of decay (a key driver of cavity development) is slower radially than vertically; it increases with the initial wound width and depth (phloem damage); it may decrease with height from the ground; and it is enhanced by local precipitation. Additionally, tree species plays a significant role (often with manyfold differences in TreM development rates; e.g., Metzler et al., 2012), so that tree species distributions shape TreM distributions.

The decay of surface wounds into large hollows can last several decades or even a century, while side cavities can form due to rapid events such as excavation. The largest possible size of a hollow in a tree is mainly determined by the amount of heartwood, which increases as the tree grows. The likelihood of larger cavities (with an entrance diameter > 10 cm) tends to peak as trees approach an age of around 150 years. The depth of cavities may also change suddenly or gradually, and limited research suggests that this happens faster in subtropics than in boreal trees. There is only one report (Zheng et al., 2016) of the horizontal rate of cavity expansion, which is at least a magnitude smaller than vertical rates.

Natural loss of live-tree microhabitats primarily occurs through stem breakage and tree fall, but detailed studies have only been conducted on cavities and exposed wood. Less frequent causes of cavity loss include advanced decay, bark overgrowth, and animal destruction. Studies in the boreal zone and subtropics show that excavated cavities typically last for > 10 years, while in a temperate forest, excavated cavities lasted only 7–10 years and nonexcavated cavities 4–12 years (Wesołowski, 2011, 2012). Few comparisons across ecosystems exist, but one study showed that three-toed woodpecker (*Picoides tridactylus*) cavity persistence was shorter (7 years) in production forests avoided by the bird compared to preferred forests (11–12 years) (Hardenbol et al., 2019).

There is extensive literature on different factors affecting tree wound closure (Table 2 in I). On temperate trees, exposed wood patches (300–400 cm²) have persisted for 5–17 years. The factors increasing this time include: larger, deeper wounds and recurring injuries; trees with less healthy crown branches and slower diameter growth; altitude and stronger light competition. Optimal values for wound closure rates can be found for air temperature and the height of an exposed wood patch on a tree. In general, callus formation appears multiple times faster horizontally than vertically.

Tree species traits (notably wood density, growth rate, and fungal disease vulnerability) significantly influence the persistence of side cavities and exposed wood, and larger trees generally host more persistent cavities. For example, wood

density and decay resistance explain the observed disparity in the persistence of non-excavated side cavities in pedunculate oak (*Quercus robur*, 17 years) and aspen (5 years) (Wesołowski, 2012). In a more complex trade-off, slow-growing hardwood species may produce cavities later but with greater longevity.

While the longevity of TreMs (as defined by structure alone) is important, their ecological significance hinges on their **persistence as suitable habitats** for specific organisms. Cavity-nesting birds, for example, often exhibit preferences for recently formed cavities, but the actual time range can vary among species (e.g., Conner et al., 1998 vs. Mazgajski, 2007). However, such knowledge is fragmentary. For example, while some wood-inhabiting lichens exclusively colonise weathered wood, the duration of such specific microhabitats on live trees remains unstudied.

3.2. TreM occurrence patterns

The first TreMs to appear on young trees in Estonian forests were exudate (resin run on an 18-year-old spruce) and exposed sapwood (on a 20-year-old spruce and a 22-year-old aspen) (**II**). Similarly, the review suggests that exposed wood patches are also the first TreMs to appear on young trees in the temperate zone (**I**). The contribution of such early TreMs to forest habitat quality is potentially significant but uncertain: (i) there is significant variation in the subsequent processes, ranging from wound healing to tree mortality (Table 2 in **I**), (ii) the age-independent effect of TreM diversity on biodiversity was more frequent in young than in older trees (**III**).

TreM sets in spruces and aspens showed distinct age-related patterns. Aspens exhibited high incidences of fungal fruiting bodies (35%, mostly *Phellinus tremulae*; no fruiting bodies on spruces) and crown deadwood (50% of aspens vs. 7% of spruces), both emerged after the trees were ca. 30 years old (Table 3 in **II**). In contrast, spruces had frequent exudate exposure (resin run on 47% of spruces vs. sap run on 2% of aspens) and buttress concavities formed by their shallow roots (30% of spruces vs. 9% of aspens). Emergent epiphytic patches over 300 cm² (54% of aspens, 41% of spruces) were observed after about 30 years of age and mostly comprised bryophytes on aspens and lichens on spruces. Trees with sapwood exposure exceeded 10% in both tree species, but only four spruces had exposed heartwood.

The accumulation of TreMs in young to mid-aged trees was similar in both tree species, but after 80 years of age, aspens became substantially more TreM-rich than spruces (Fig. 2 in **II**). Among trees < 40 years old, almost two-thirds had no TreMs and one-third had only one TreM. For trees aged 40 to 79 years old, the proportions shifted to ca. 20% and 30%, respectively. For comparison, in temperate and subtropical zones worldwide, similar-sized TreMs of all other types except side cavities become regular already in trees < 50 years old (**I**). However, the estimated frequencies are sensitive to the size criteria used, particularly in young trees: 85% of trees < 40 years old had no TreMs meeting

the stricter Larrieu et al. (2018) criteria (II). Similarly, according to regional and Larrieu et al. (2018) criteria, only 2% versus 0.2% of the trees had at least five types of TreMs, respectively. The youngest of such TreM-rich trees were 51 years versus 79 years old.

The rarest TreMs in Estonian spruces and aspens were witches' brooms, bird or squirrel nests, and woodpecker cavities (II). Many TreM types were not found at all in the sample: large woodpecker cavities with entrances > 10 cm in diameter, hollow trunks with multiple connected entrances (woodpecker 'flutes'), semi-open trunk rot holes, broken trunks with 'chimney' tops, large hollow branches, dendrotelms, lightning or wildfire scars. Regarding cavities, these findings (Table 3 in II) are consistent with previous studies (I), which report small excavated and nonexcavated side cavities (entrance diameter > 2 cm) typically emerging in trees about 60 years old but remain rare in trees < 90 years old. Medium-sized cavities (entrance diameter < 5 cm) usually appear in trees that are over 90 years old, and large cavities (entrance diameter > 10 cm) appear in trees that are over 170 years old. In contrast, small dendrotelms and witches' brooms have been found even in stems < 20 years old in tropical and temperate zones (I).

In Estonia, the trees with rare TreM types (observed in < 15 trees of each species) exhibited at least 40% more TreM types overall than the average for tree species and the age group. The difference was particularly pronounced for rot holes (157%) and burrs (122%) in spruce and for woodpecker cavities in aspen (80%) (II).

3.3. Tree age and stand-scale effects on TreM probability (II)

The samples were sufficient to construct multifactor models for nine TreM types (14 full models; Table 1). Utilising the stricter criteria of Larrieu et al. (2018) qualitatively altered the outcomes of only two models (specified below). The **tree-age effects** (the primary interest) were variable but appeared in all 11 full models with significant factors. Additionally, univariate testing identified a statistically significant tree-age effect for spruce rothole (Table 1). Where possible to specify, the age effect was positive and linear (three full models; e.g., Fig. 6c) or, more frequently (six full models), an initial age-related increase in TreM probability levelled off or turned to a (usually non-significant) decline at an older age (e.g., Fig. 7a,b). One model (exposed sapwood in aspen) showed a convex relationship with tree age (Fig. 7c).

Two of the linear tree-age effects (crown deadwood in spruce and aspen heartwood) were supported by the AIC-based model selection, but the latter was even better explained by a linear effect of DBH. Also, the probability of spruce epiphytes was better explained by a nonlinear DBH function, which levelled off at DBH values > 50 cm (Fig. 8b).

Table 1 Aspen and spruce incidence of TreMs and factors influencing their presence. A revised version of the table originally published in **II** is presented here.

TreM type	Aspen ($n = 428$)		Spruce ($n = 451$)	
	No. of trees	Factors	No. of trees	Factors
<i>Cavities</i>				
Woodpecker cavity	5	–	0	–
Rothole	11/2	a	6/3	a*
Buttress concavity	40/24	aD	132/82	aDOt
Other concavity	23/7	D	12/2	D
<i>Injuries and dead wood</i>				
Tree exudate	8	*	210	D
Exposed sapwood	48/26	AT	72/27	A×M
Exposed heartwood	17/14	atD	4/0	–
Crown deadwood	213/204	AM	31/14	AD
<i>Emergent structures</i>				
Burr (trunk outgrowth)	9/5	*	2	–
Witches' broom	0	–	1	–
Stick nest	0	–	3	–
Epiphytic structure	230/30	A×TD	185/175	aD
Fungal fruiting bodies	149/143	AO×M	0	–

Notes Where two values are given, the first refers to locally adjusted (wider) size criteria of the TreM, and the second to the stricter Larrieu et al. (2018) criteria (see Table 1 in **II**). Significant factors ($p < 0.05$) are indicated by their initial letters, depending on inclusion in the best models (capital letters) or significance in full models only (lowercase letters): Age; Diameter at breast height; Origin (afforested vs. long-term forest); Management (thinned or not within ten years); Type (*Hepatica* vs. *Filipendula*). × denotes interaction term in addition to main effects; – refers to that no model was attempted due to small sample size; * indicates where only age effect was tested.

Nine significant **stand-scale effects** were observed in the full models, including one significant interaction (Table 1). Among them were four site-type effects: *Filipendula*-type forests had more epiphytic structures (Fig. 8a) and exposed sapwood in aspen (Fig. 7c), while the *Hepatica*-type had more frequently exhibited exposed heartwood in aspen and more buttress concavities in spruce. The latter were also more common in long-term forests than on afforested land (Fig. 6b). In recently thinned stands, aspens had less crown deadwood (Fig. 7a) and, on afforested sites, fewer fungal fruiting bodies (Fig. 7b). Interestingly, on aspens in afforested sites that had not been recently thinned, fungal fruiting bodies appeared even earlier and accumulated more rapidly than in long-term forest sites. In contrast, there was an earlier peak of spruce sapwood exposure in recently thinned than in unmanaged stands (Fig. 6a).

DBH predicted TreM occurrences more often than tree age. Among stable reduced models (six TreM types in both tree species), DBH was a significant factor in seven models compared to tree age in four models. Crown deadwood in spruce had age and DBH in alternative models, and epiphytic structures on aspens had both in the same model (Table 1).

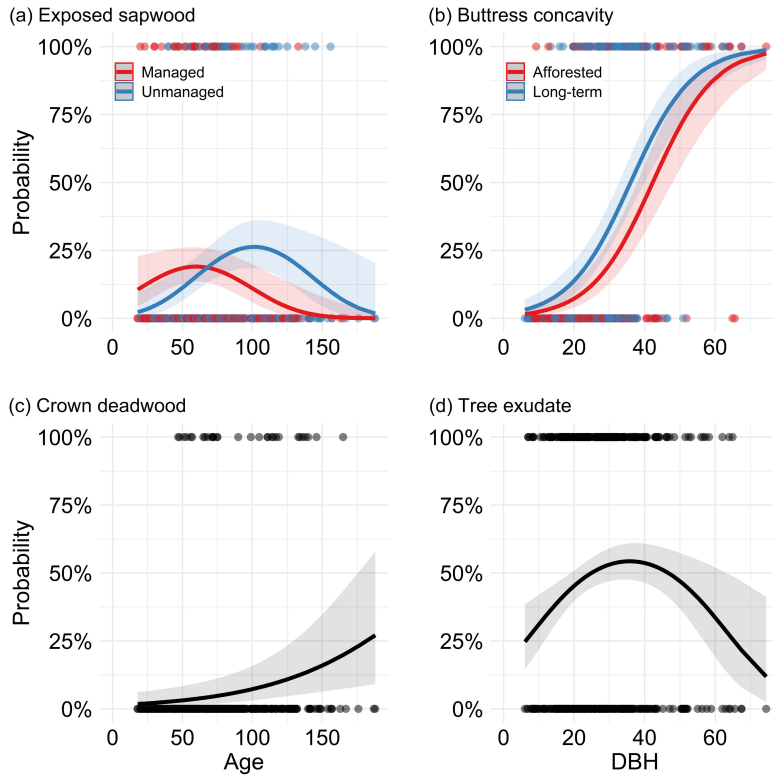


Fig. 6 Logistic probability curves with 95% confidence intervals for the best explanatory models of TreMs in spruce (tree age-based models on the left; diameter-based models on the right): the probability of exposed sapwood (a), buttress concavities (b), crown deadwood (c), and exudate (resin runs; d). Model (a) includes the interaction of tree age with recent management; model (b) includes the main effect of stand origin. Points depict the observed presence (top) and absence (bottom) values. Figure originally published in **II**.

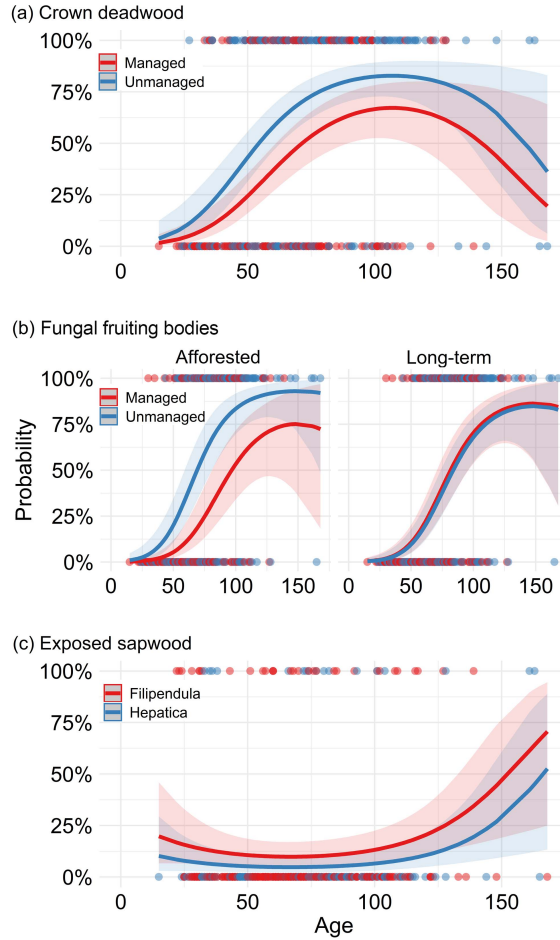


Fig. 7 Logistic probability curves with 95% confidence intervals for the best explanatory models of TreMs in aspen: the probability of crown deadwood (a), fungal fruiting bodies (b), and exposed sapwood (c). All the models comprise the square term of tree-age (x-axis) and stand-scale effects: site type (c), recent management (a), or its interaction with tree age (b). Points depict the observed presence (top) and absence (bottom) values. Figure originally published in **II**.

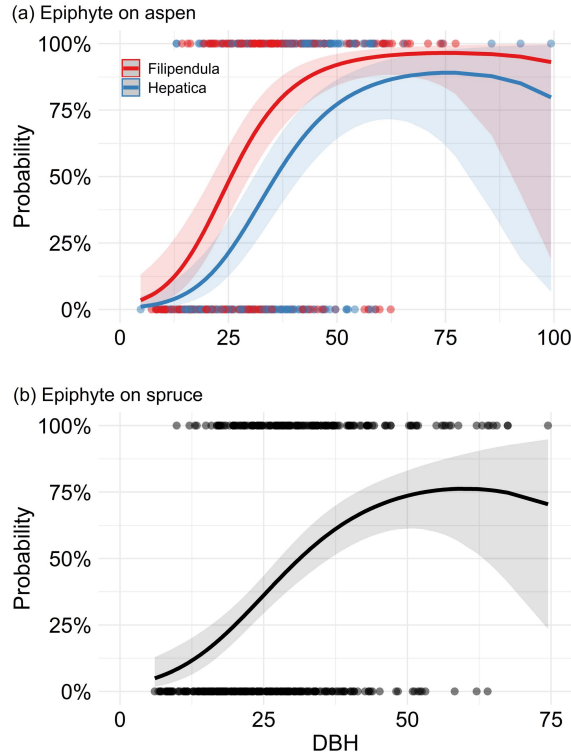


Fig. 8 Logistic probability curves with 95% confidence intervals for the best explanatory models of the probability of emergent epiphyte cover in aspen (a) and spruce (b). The models comprise nonlinear effects of diameter (DBH; x-axis), and (a) includes the main effect of site type. Points depict the observed presence (top) and absence (bottom) values. Figure originally published in II.

3.4. TreM diversity influence on tree-scale biodiversity (III)

The number of TreM development processes (an indicator of TreM diversity) had varying and generally weak effects on the measured biodiversity variables in both young and old trees. Among a total of 36 models, the TreM diversity effects were significant ($p < 0.05$) in only seven spruce and three aspen models. With the exception of beetle abundance in old spruces, all these significant effects were found in young trees, and seven were positive relationships. Most TreM diversity effects on biodiversity variables appeared only in one tree species, but epiphyte and, separately, bryophyte diversities increased in TreM-diverse young trees of both tree species, regardless of tree age (Fig. 9c,d).

Notably, several negative relationships between TreM diversity and biodiversity emerged, specifically on invertebrate variables and particularly after accounting for DBH (examples in Fig. 10b–d). Moreover, all positive effects in aspens disappeared when DBH was included in the model. In contrast, three apparent positive effects (beetle abundance, snail diversity, and epiphyte

diversity) persisted in young spruces. The negative TreM diversity effects on gastropod abundance in young aspens, beetle abundance in old spruces, and invertebrate prey volume in young spruces remained unaffected. However, the latter became weaker and appeared specifically related to tree injuries. Additionally, upon incorporating the strong positive effect of DBH, three more negative effects on invertebrate variables emerged in older trees.

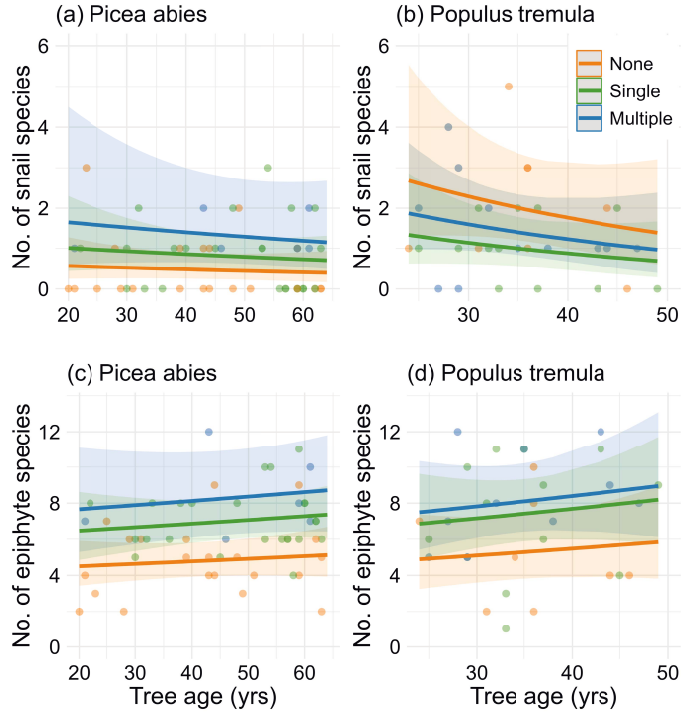


Fig. 9 Examples of tree species-specific (a, b – no. of snail species) and tree species independent (c, d – no. of epiphyte species) effects of TreM origin diversity (none, single, multiple processes) on biodiversity in young trees. The shaded areas depict 95% confidence intervals; see Table 3 in **III** for full models. Figure originally published in **III**.

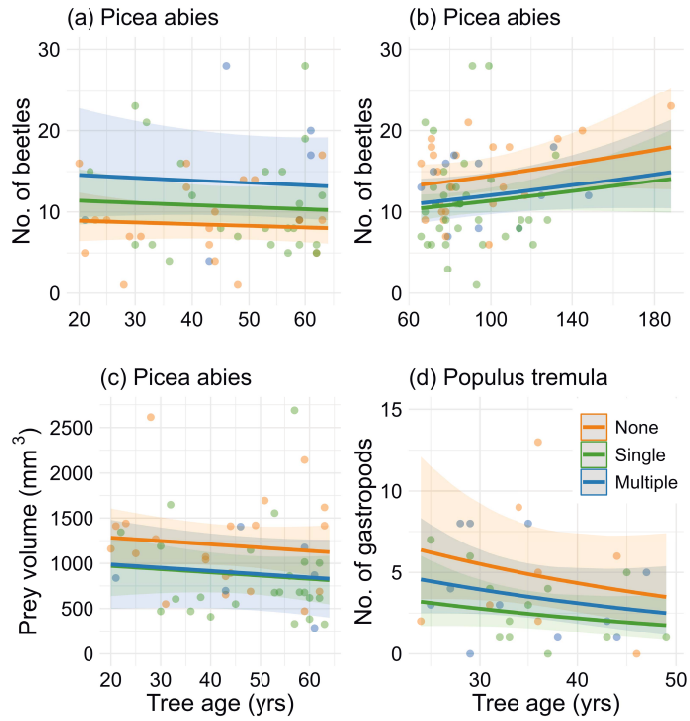


Fig. 10 The weak effects of tree age and TreM origin diversity (none, single, multiple processes) on invertebrate abundance. (a, b) An age class-dependent effect on beetle abundance in spruce. (c) Total volume of all invertebrates excluding Hymenoptera, beetles and shelled snails in young spruce. (d) Abundance of gastropods in young aspen. The shaded areas depict 95% confidence intervals; see Table 3 in **III** for full models. Figure originally published in **III**.

4. DISCUSSION

4.1. Complexity of tree- and stand-scale effects on TreM occurrence

4.1.1. Tree age and size

The results demonstrated complex relationships between tree age, diameter at breast height, and stand characteristics on TreM occurrence. In line with the TreM accumulation hypothesis (H1) stating that with time, TreM diversity and abundance increase, both tree age and tree diameter mostly influenced TreM presence positively. However, while tree age is often considered a key factor (I), the findings suggest that tree diameter is usually a better predictor of TreM occurrences in this study system (II). Previous studies reporting higher TreM diversities in larger trees (e.g. Asbeck et al., 2021; Kozák et al., 2023; Vuidot et al., 2011) often refer to that larger trees are mostly older but have not actually measured tree age.

One explanation is that larger trees offer more surface area for TreM development, regardless of age. This, particularly when combined with age, relates to a higher incidence of injuries from harvesting or natural disturbances (Bobiec, 2002). Additionally, larger trees often have a dominant crown position (Asbeck et al., 2021) and larger branches, which can influence TreM development (e.g., wind-induced breakage of large limbs; Hale et al., 2012). Also, woodpeckers may prefer larger trees for cavity excavation; these injuries may serve as starting points for various TreMs. Conversely, injury-related TreMs could be more common in younger trees (independent of harvesting operations) due to their vulnerability to physical damage (Courbaud et al., 2022).

Age-related effects that were evident in specific TreMs were often non-linear. A common (sigmoid) accumulation function (seen, for example, in buttress concavities, epiphytic structures, crown deadwood, and fungal fruiting bodies) rapidly increased in mid-aged trees but then slowed down. This has two explanations. First, while many TreMs are more likely in mature trees, there may also be counteracting factors in very old trees, such as loss of attraction for herbivores or a fraction of individuals with low genetic or environmental susceptibility to decay processes (Niemelä, 1974; Verbylaitė et al., 2015). Additionally, the occurrence metric itself does not reveal additions of TreMs per tree once they are present.

While the sigmoid functions support the TreM accumulation hypothesis (H1), the detected unimodal tree age or diameter relationships with TreM incidence probability (such as with spruce sapwood exposure and resin run, Fig 4a,d) reveal ecologically interesting variation. For example, herbivorous and wood-boring insects, as well as deer, may prefer to forage on mid-aged trees, which are growing rapidly and, thus, have abundant resources but whose defences may be weaker than those of the largest trees (Boone et al., 2011; Graf et al., 2012; Welch & Scott, 2017).

4.1.2. Tree species

The tree species constraints hypothesis (H2) was supported by the distinct TreM sets observed in aspens and spruces in Estonia (II), and it has further support from other studies. For example, sycamore trees (*Acer pseudoplatanus*) have been found to have a greater epiphyte cover than European beech (*Fagus sylvatica*), silver fir (*Abies alba*) or Norway spruce (Kozák et al., 2023), possibly because of their bark properties (Mitchell et al., 2021). Well-known are multiple differences between deciduous and coniferous trees and the susceptibility to decay in poplars (*Populus* spp.) (resulting in large rot holes, as noted by Larrieu et al., 2021), while, for example, oaks (*Quercus* spp.) have built-in protection against pathogens due to chemical and anatomical boundaries (Shigo, 1984). Tree species differences in TreM occurrences can become more complex over time, as evidenced by the differing TreM patterns between aspens and spruces after 80 years (II). These tree-scale successional dynamics of forest structural diversity have been insufficiently studied, and long-term surveys are essential for exploring their impact on biodiversity.

The same TreM types can function differently in different tree species due to chemical and physical substrate characteristics, the unique adaptations of the inhabiting organisms, as well as other resources the tree could provide (see also III). For instance, many ascomycetes are highly specialised to live on different exudates (mostly resin but also sap) that vary among tree species (Tuovila, 2013). Additionally, many insects (e.g., *Diptera*) are attracted to tree exudates, especially broadleaf sap (Luff & Wolton, 2016). In the Estonian study (II), the epiphytes that formed a TreM were mainly bryophytes on aspens and lichens on spruces. It has been found that tits (*Paridae*) use mosses for nest building (Wesołowski & Wierzcholska, 2018) but may depend on high lichen abundance while searching for invertebrate food in winter (Pettersson et al., 1995). Overall, these tree-species-related findings specify a broader-scale understanding of the importance of maintaining tree species diversity in forests to support biodiversity and a range of ecosystem functions (Gamfeldt et al., 2013).

4.1.3. Stand characteristics

The natural influence of stand characteristics on TreM occurrence patterns was evident in the site type effects. Thus, in moist (*Filipendula*-type) forests, aspen trees had more exposed sapwood and epiphyte cover compared to those in drier (*Hepatica*-type) forests (II). This was consistent with the risk of elk (*Alces alces*) browsing and moisture conditions affecting bryophytes, respectively (Vellak & Paal, 1999; Veeroja et al., 2018). Additionally, if more humid conditions inhibit the growth rate of trees (Sellin et al., 2017), wound closure may be delayed (Dujesiefken et al., 2005; Jones et al., 2019). Conversely, *Hepatica*-type forests favoured exposed heartwood in aspen and buttress concavities in spruce, which may be related to the higher prevalence of the fungal parasites there (e.g., Hanso & Hanso, 1999). Elsewhere, the appearance of spruce buttress concavities in

long-term forests might also be influenced by uneven terrain (Asbeck et al., 2019; Jahed et al., 2020).

Forest history, particularly recent thinnings, also emerged as a factor influencing TreM occurrence. While thinning seemed to reduce crown deadwood (Fig. 7a) and fungal fruiting bodies (on afforested sites) on aspen (Fig. 7b), it paradoxically led to an earlier peak in exposed sapwood (Fig. 6a) on spruce. This suggests that thinning operations, while removing already injured or otherwise unhealthy potentially TreM-bearing trees, might also temporarily increase the likelihood of injuries (either due to better access for elk, Randveer & Heikkilä, 1996, or mechanical damage).

However, when comparing afforested and long-term forests, sites that had not been thinned in recent years developed *Phellinus tremulae* fruiting bodies on aspen earlier and more rapidly in afforested forest sites (Fig. 7b). This rapid development of fruiting bodies is consistent with previous findings (Domański, 1983), highlighting the role of stress-related factors and soil conditions in fungal pathogen establishment (Koide et al., 2017). Similar impacts of other pathogens, such as *Heterobasidion* species, have been documented in former agricultural lands (Sierota, 2013).

4.2. TreM development on young trees

Two findings highlighted the importance of TreM formation in young trees, thus specifying the TreM accumulation hypothesis (H1; monotonous increase in TreM occurrence with tree age and size). The first finding was that certain TreMs, such as exposed wood, sap runs, buttress concavities, and occasionally dendrotelms and bark pockets, can emerge early in a tree's life (**I**, **II**). This suggests that some factors, such as injury and branch-loss probabilities, can specifically affect young trees. It is known that certain disturbances, like fires, animal grazing, insect damage, and logging, commonly affect young trees, also in production forests (**I**). However, their long-term contribution to live-tree TreMs remains unknown. Research on TreM persistence is scarce, particularly regarding how factors like healing processes and tree mortality influence their fate (**I**), along with the variability in TreM dynamics observed among tree species (**II**). For example, it remains unclear whether small wounds on young trees will eventually develop into large cavities or if the trees are lost before that. Nevertheless, the early-TreM-related mortality contributes to deadwood accumulation and thus supports saproxylic organisms (**II**; e.g., Nordén et al., 2004; Stokland et al., 2012).

The second finding was that TreM diversity affected tree-scale biodiversity predominantly in young trees (**III**). The definition of 'young' trees in **III** aligns with the standard logging age in Estonia, i.e., such trees are typical of managed forests. In such forests, these early TreMs could serve as "stepping stones" for species dispersal, facilitating movement between forest patches and potentially mitigating the negative impacts of forest fragmentation. The pronounced effect of TreM diversity on epiphyte diversity in young trees supports this view (**III**).

Particularly in retention systems, which also have legacy structures and species, young trees with early-forming TreMs could contribute to maintaining connectivity and gene flow between populations, thereby enhancing the resilience of forest ecosystems. Future studies could establish how young trees contribute to overall microhabitat diversity in forest stands and landscape mosaics over time.

In conclusion, while young forests harbour fewer and less diverse TreMs than older forests (II; Kozák et al., 2023), the young-tree TreMs may play distinct ecological roles and warrant management consideration, especially in the absence of old habitat trees. A more elaborate management question is how to combine the habitat trees and young TreM-bearing trees in partial harvests. Also, the young stands in the Estonian study area (II, III) typically contained older crop or habitat trees, reflecting recent clear-cutting practices, but the interactive roles of the older and younger trees were not addressed. One should also consider that young stands have other habitat differences from older forests, and their TreMs could thus support partly different sets of species. Variations in light availability, temperature fluctuations, and other factors such as plant species productivity, food web complexity, and nutrient fluxes could contribute to unique ecological contexts (Hilmers et al., 2018) that apparently could affect TreM use as well. Thus, TreMs in these environments could support pioneer species, accelerating forest recovery after disturbances (e.g., harvesting, wind storms, insect attacks, fire). Finally, rare TreM types may serve essential functions independently of the context, e.g., large owls may occur in very different forest stands provided cavity trees are present (Lõhmus, 2003).

4.3. TreM dynamics: state-of-the-art

TreMs exhibit complex and dynamic patterns of development and persistence. Studies on TreM development rates in live trees have been primarily focused on exposed wood and side cavities, particularly in commercially important conifers and hardwoods. This means that studies examining these structures as habitats, including their dynamics (particularly their formation, development and loss), remain limited. Research on decay expansion has almost exclusively focused on wound-related heart-rot, while studies on wood-surface weathering and radial spread of decay remain nearly absent (I). Nevertheless, the studies demonstrate that TreM development processes are affected by multiple factors, often in combination and possibly interacting. For example, lower wounds in trees tend to be more excessive and deeper due to logging operations (Tavankar et al., 2019; Tavankar & Bonyad, 2017; Vasiliauskas, 2001). However, Hecht et al. (2015) compared artificial wounds with an identical surface area and found that upper trunk wounds, often similar to those caused by felling, could be more susceptible to decay due to the upper parts being more prone to desiccation, allowing the decay fungi to enter. Additionally, the width of the wound relative to the tree's circumference can influence the callus formation rate (Neely, 1988), which may explain why wider wounds on the lower part of the trunk compared to the more

elongated wounds higher up as those in Hecht et al. (2015) study healed faster. In any case, slower healing gives time for exposed wood TreM development to be influenced by infection or insect activity. The complexity and limited understanding of TreM processes suggest that forestry practices may have significant unforeseen impacts on ecosystems. Therefore, a precautionary approach that prioritises the preservation of the natural TreM dynamics, to which forest species have likely adapted, is warranted.

The example of wound healing processes underscores the importance of considering both local (e.g., tree characteristics) and regional factors (e.g., climate) when studying TreM development and persistence to advance conservation efforts and sustainable forest management practices. Decay spread can significantly decrease the persistence of exposed-wood TreMs (Shibata & Torazawa, 2008), while stress can hinder wound healing along with slowing down tree growth. For instance (also in line with the ecological context dependency hypothesis H3), trees on sun-facing slopes or higher elevations may heal more slowly due to water scarcity during droughts (I). Furthermore, drying sapwood also makes trees vulnerable to fungal infections (Boddy & Rayner, 1983; Hecht et al., 2015). Evidence suggests that trees experiencing multiple stressors are more likely to develop more extensive scars from injuries (Jones et al., 2019). This indicates the complex interplay between tree physiology, environmental conditions, and disturbance agents in shaping TreM development. This complexity is further demonstrated in II, where the probability of TreM occurrence was influenced by a combination of tree- and stand-scale factors. Specifically, aspen exhibited a higher TreM diversity than spruce in older age classes, with possible explanations lying in differences in defence mechanisms and growth rate (II). Studies on tree health and TreMs consistently demonstrate in principle that the probability and rate of TreM development (and, to a lesser extent, persistence) vary significantly among tree species (I). While current research does not encompass all tree species and TreMs, grouping similar tree species can facilitate the application of this knowledge in practical models. However, due to the complexity of the processes involved, the dynamics of sapwood-related exposed-wood TreMs cannot be predicted reliably. Further research is needed to understand better the factors influencing tree wound healing, particularly in the context of changing environmental conditions and forest management.

This thesis reveals various persistence times for different TreM types, further shaped by tree species traits, environmental conditions, and disturbance regimes. Some individual TreMs, like excavated cavities, can persist for decades (perhaps even centuries), becoming “legacy structures” that span generations of trees. In contrast, others, like exposed wood patches, may be ephemeral, disappearing within a few years due to wound closure. Some tree species, with their durable wood and resistance to decay, such as oaks and pines (*Pinus* spp.), are more likely to support long-lasting TreMs, while others with softer wood, such as poplars and birches, may exhibit faster rates of wound closure or decay (I). When comparing broadleaves and conifers, the former typically gain more TreMs than they lose, probably due to differences in bark thickness and capacity to close wounds (Spînu

et al., 2024). This trend is supported by the findings of **II**, which showed that in Estonian forests, aspens exhibited a higher TreM diversity than spruces, but only after 80 years of age. However, while certain TreM types are prone to disappear over time (e.g., epiphytes, woodpecker cavities) and others are likely to persist (e.g., exposed wood, concavities), regardless of tree species, the overall TreM richness within a tree species may remain stable (Spînu et al., 2024). The dependence of TreM degradation rates on regional climate is poorly documented, but a couple of studies indicate that cavities deteriorate faster in subtropical than boreal trees (**I**), likely due to favourable conditions for year-round decay advancement and higher insect activity.

The slow-developing TreMs, such as large cavities in living trees, need special attention because they often conflict with current timber harvesting and safety practices (since these TreMs take a long time to develop, they are more likely to be lost due to forestry operations or other disturbances) (**I**). The conflict is exacerbated by the fact that such TreMs can be relatively scarce, especially in managed forests (**III**). This highlights the importance of preserving old, hollow trees and considering tree species that are more likely to develop cavities or other TreMs over time. However, because of the high variation in the development and persistence times, they can only be managed at larger scales based on persistence time distributions to account for stochasticity.

4.4. TreMs as biodiversity reservoirs: an uncertain relationship

The influence of the variety of TreM development processes (TreM origin diversity) on associated biodiversity revealed generally subtle, occasionally contradictory, and often group-specific effects. This contrasts with previous studies emphasising TreMs as forest biodiversity indicators (Martin et al., 2022). One potential explanation lies in the tree-scale approach of the current analysis compared to the pooling of TreM data across entire stands, which rarely accounts for confounding factors (Table 1 in **III**; Spina et al., 2024). It is also possible that the diversity of TreMs is more critical in certain tree species, ecosystems, or regions (especially in Central Europe, where it has been mostly studied and demonstrated so far; **I**; **III**) or for particular species groups. However, the results in **III** align with Asbeck et al. (2021) findings of unclear (landscape-scale) links between TreMs and species occurrence.

Among the studied variables, the most evident contribution of TreMs was found for tree-dwelling epiphytes (Table 2; **III**), which also create TreMs themselves (e.g., Larrieu et al., 2018; Mottl et al., 2019; Saeki et al., 2017). The resulting effect cascades could mediate TreM effects on other organisms like invertebrates and related ecological functions like nutrient cycling and water retention (Fenton et al., 2024; Larrieu et al., 2018). However, beetle abundance and shelled snail diversity in young spruces were also directly enhanced by TreM diversity (Table 2; Fig. 9, 10; **III**). This partially supports the TreM diversity-

biodiversity hypothesis (H4), demonstrating that the diversity of TreM origins (development processes) – likely reflecting diverse processes and resources – can positively influence the assemblages of these taxa. Notably, this contribution of TreMs to biodiversity variables was observed in young trees (discussed in section 4.2.).

Unexpectedly, several results also revealed such complex relationships where the effects of TreM diversity and invertebrates were negative, particularly when accounting for tree diameter (III). For instance, an analysis of prey abundance for birds in young spruces revealed a negative correlation with TreM diversity, independent of age (Table 2; Fig. 10c). This correlation was weakened when tree diameter was considered, and the negative effect was specifically linked to tree injuries (III). This suggests that tree injuries, either directly (e.g., reduced foliage) or indirectly (e.g., increased prevalence in shaded areas), may influence arthropod abundance. A similar pattern was observed for gastropods in young aspens (Table 2; Fig. 10d). In conclusion, TreM diversity may enhance invertebrate abundance and diversity by providing diverse food sources and shelter, but it can also suppress them through other mechanisms. For example, negative effects may arise due to TreMs supporting predators like *Arachnida* in more complex food webs.

4.5. Knowledge gaps and future directions

This thesis highlights three broad ecological knowledge gaps regarding TreMs in forests. First, the dynamics and ecological functioning have been studied only in a limited number of TreM types (mostly side cavities and exposed wood) and primarily in temperate forests (I). Expanding the range of TreMs, conditions, and a related study on biodiversity would enable us to develop a more complete understanding of the factors influencing TreM development, persistence, and ecological significance (Asbeck et al., 2021). This would allow us to analyse TreMs as an assemblage of habitat properties rather than individual structures and to make better-informed management decisions that consider the complexities documented here. For instance, we could better anticipate how TreMs might respond to future environmental changes, such as climate change, altered management practices or conservation interventions. Almost all research has studied the correlative relationship; few have actually measured TreM functioning (i.e., causality) (Asbeck et al., 2021). For some understudied TreM types (such as bark pockets, buttress concavities, dendrotelms, witches' brooms and fungal fruiting bodies), this may require developing new methodologies for their standard detection, monitoring, and establishing their ecological roles and relationships with other organisms.

Secondly, long-term monitoring initiatives are crucial for documenting, understanding and predicting the temporal dynamics of TreMs and their responses to environmental change, including climate change and disturbance from forest management practices (see also Lovell et al., 2023). The observed decline

in TreM abundance over a decade underscores the imperative for regular monitoring to track TreM development and inform the need for interventions to protect habitat trees (Spînu et al., 2024). TreMs could provide biodiversity change proxies for some ecosystems, but the current knowledge base is insufficient for that.

Third, while current research suggests that management practices can significantly alter TreM occurrence patterns, a more comprehensive understanding of these impacts is still needed. Further research, particularly field experiments, is essential to investigate the long-term effects, cumulative impacts, and indirect consequences of various management practices on TreM development, persistence, and ecological roles. This could include exploring the trade-offs among management objectives and implementing adaptive management strategies with regular monitoring to balance those potentially conflicting objectives.

The findings of this thesis further highlighted that the impact of TreMs on biodiversity is not uniform across taxa, containing complex interactions between TreM characteristics, species-specific requirements, and environmental context. To specifically manage TreMs for biodiversity, the following **research directions** can be highlighted:

- (i) **Methodological refinements:** Improve invertebrate survey methods to record their use, spatial distribution and interactions with specific TreMs. Conduct year-round surveys of whole trees to gain insights into the full range of TreM functions and their impact on biodiversity. For threatened species detection and investigation, other sampling designs might be more appropriate (e.g., around the species records rather than randomly among trees).
- (ii) **Mechanistic understanding:** Conduct manipulative experiments to isolate the effects of specific TreM characteristics on biodiversity, exploring mechanisms such as resource provision, predator-prey interactions, and microclimate regulation.
- (iii) **Context-specific effects:** Investigate the impact of TreMs in diverse forest ecosystems, particularly in regions with limited research, to identify factors (e.g., forest types, tree species, environmental conditions) that modulate TreM-biodiversity relationships.
- (iv) **Scale-dependent effects:** Conduct studies at different spatial scales (e.g., individual trees, stands, landscape) to assess the consistency of TreM effects on particular species and broader biodiversity. It is not self-evident that the same TreMs support broader ecosystem diversity and threatened species. Similarly, monitor TreM diversity and associated biodiversity over long time periods to understand the influence of forest succession, disturbance, and climate change.

4.6. Integrating TreMs into forest management

This thesis improves our knowledge of the practical biodiversity conservation value of TreMs in forest protection and management. Management decisions overall should be based on an understanding of the ecological roles of different TreM types, their interactions with specific taxa, and their long-term dynamics in forest ecosystems. In Estonia, the selection of retention trees at harvest considers microhabitats (trees with special features), but a specific treatment of TreMs in forestry practice has not been developed. At the same time, some TreMs are rare in the forest landscape, and ‘habitat trees’ with many microhabitats are very rare (II).

At the stand-scale, the density of trees bearing TreMs is generally an important driver of species richness for taxa such as saproxylic beetles, polypores, hoverflies, bats, and birds (Larrieu et al., 2018). However, in addition to positive effects, our data revealed some negative tree-scale effects of TreM origin diversity on invertebrate abundance variables (III). Thus, TreMs may make certain trees less attractive to specific organism groups. Consequently, species conservation cannot be replaced by TreM conservation, but overall protection of specific microhabitats is justified.

Based on this thesis, it can be argued that since different TreMs develop through distinct pathways and vary in their ecological significance (as well as in their economic impact), they should be addressed individually or grouped by similarity. Such a ‘multiple pathways’ approach would specify the selection of retention trees and is also relevant for the deliberate facilitation of TreMs essential for biodiversity (e.g., various cavities). It would require outlining the main alternatives and implementing relevant practices, for example by retaining trees with TreM potential during thinning operations, preserving wind-sensitive retention trees using retention groups and in continuous-cover forestry.

Thus, integrating TreMs and their associated biodiversity into forestry management should encompass not only current TreM-bearing trees but also the processes and temporal dynamics of TreM development and loss. This requires a shift from a static view of TreMs to a more dynamic perspective that considers their development trajectories and long-term potential to support biodiversity, as highlighted in this thesis. Until specific guidelines are developed through applied research, forestry operations should adhere to broad principles of precautionary and heterogeneous management, ensuring the presence of diverse TreMs on retention trees and set-asides, while allowing processes and events of TreM development at landscape scale.

Based on this thesis, the specific suggestions for forest managers are as follows:

- (i) **Prioritize retaining trees with rare TreMs:** In Estonia, these include large cavities and rot holes, dendrotelms, bird/animal nests, lightning and fire scars, and emergent epiphytes other than bryophytes and lichens. These often take a long time to develop. More specifically, a special focus should be on TreMs that are known to be important for threatened species in that specific area.

- (ii) **Assess the overall habitat value:** While common TreMs like bark injuries are important, evaluate the tree's overall contribution to habitat complexity within the specific stand. Consider the abundance and diversity of TreMs on the tree. When in doubt, err on the side of retaining trees with more diverse TreMs. The broader purpose is to retain a diverse TreM stock in a landscape.
- (iii) **Consider tree age and TreM diversity:**
 - a. In young forests (under 40 years), prioritize retaining trees with at least 3 different TreM types, especially if they support species of conservation concern.
 - b. In intermediate-aged forests (40–80 years), retain trees with at least 4 different TreM types.
 - c. In old forests (over 80 years), prioritize retaining trees with at least 5 different TreM types.
- (iv) **Focus on long-term habitat provision:** When assessing living trees, consider their potential to persist and provide TreMs for an extended period.
- (v) **Address TreM tree abundance:** Overall, to make assessments less time-consuming, specific guidelines should be developed to assess and retain priority TreMs (e.g., those mentioned in the first bullet) in a stand. Retention guidelines for priority TreMs could be consistent with existing practices for habitat tree retention, ensuring continuity in approach and minimum densities per area. In future, specific guidelines should also be developed for managing stands with an unusually high proportion of TreM-rich trees to balance ecological (e.g., maintaining TreM-associated species) and economic objectives (e.g., timber production).

5. CONCLUSIONS

This PhD thesis investigated the development, occurrence, and ecological significance of live tree TreMs (tree-related microhabitats – structures on trees that provide habitat for various organisms). The main contribution of the thesis is a focus on individual trees (as opposed to generalisations at stand-scale) with precise tree-age data. The key findings and conclusions were:

1. **TreM development and persistence** are complex processes influenced by tree age, size, species-specific biology, environmental conditions, and interacting organisms (especially pathogens).
 - a. The current knowledge is fragmented across study fields, and most studies focus on a few TreM types (side cavities, exposed wood) and ecosystems (temperate forests).
 - b. TreM development and decay rates vary significantly among tree species and ecosystems. While the growth of live tissue can vary tenfold, the decay of dead tissue can vary a hundredfold. The ecosystem-scale effects seem to be attributable to known ecological processes. Predicting the dynamics of TreMs might, therefore, be possible at broad scales by analysing the frequency and severity of pathogen and disturbances impacts and other natural processes.
 - c. Some TreMs, like cavities, can take decades to form; they persist longer in larger, slower-growing trees. In contrast, certain TreMs, such as exposed wood, sap runs, and buttress concavities, can emerge early in a tree's life.
 - d. While tree age is a significant factor for TreM presence, tree diameter at breast height often emerges as a stronger predictor and may refer to causal relationships with tree size. Thus, the TreM accumulation hypothesis was only partially supported.
2. **The relationship between TreM diversity and associated biodiversity** is contextual and depends on the taxon group, supporting the TreM diversity-biodiversity hypothesis only partially. At the tree scale, TreM diversity had a stronger effect on biodiversity in young trees than in old trees. However, the value of TreM-rich young trees for stand-scale biodiversity needs further assessment as a question separate from the conservation of old habitat trees. As an example of cascade effects, exposed wood and bark can serve as important habitats for epiphytes, which have additional contributions to forest biodiversity.
3. **The main implications for forest management and conservation** include:
 - a. maintaining a diversity of TreMs by promoting diverse tree species compositions, stand structures and disturbance regimes;
 - b. following retention forestry approaches, reducing salvage logging, and facilitating habitat tree development. An effective approach would be the

combination of the retention of TreMs already present as per the precautionary principle with long-term and broad-scale prediction and planning for the TreM development for the creation or formation of new ones;

- c. using TreM-based approaches as supplementary, not main conservation tools, given the overall weak independent TreM diversity effects found. This also applies to their indicator value since a snapshot estimate of TreM stocks may not accurately reflect their long-term importance;
- d. long-term monitoring studies to track TreM dynamics and their responses to environmental changes and management practices, and ecological research to better understand the ecological roles of TreMs and their causal interactions with forest organisms across multiple tree species, contexts, and scales. The variability of those interactions makes it challenging to develop universal management strategies for forest biodiversity. Instead, a more cautious and flexible approach that considers the unique characteristics of each forest is recommended.

SUMMARY IN ENGLISH

Forests are complex ecosystems that provide essential goods and services for humans. Maintaining their structural complexity is crucial for supporting biodiversity and the ecosystem functioning. This thesis focuses on tree-related microhabitats (TreMs) – structures like cavities and bark cracks that provide habitat for various organisms at the tree scale, thereby enhancing forest structural complexity and influencing biodiversity. TreMs are abundant in old-growth forests with diverse tree species and ages. However, managed forests often lack these features due to practices that remove old or weak trees and favour fewer tree species, disrupting natural TreM development processes.

This thesis addresses the need to explicitly understand TreM formation, persistence, and their specific impact on forest biota. By quantifying the TreM dynamics and their ecological significance, such research also aims to inform and improve forest management practices for enhanced biodiversity conservation. The question is how TreMs contribute to the habitat value of living trees across various forest conditions. The research involved three approaches: a literature review on TreM development processes (I), field studies examining the relationships between tree characteristics and TreM occurrence in Estonian forests (II), and an analysis of the association of TreMs with biodiversity indicators in the same Estonian setup (III). The field studies used two ecologically and phylogenetically distinct tree species as model systems: Norway spruce (*Picea abies*) and European aspen (*Populus tremula*).

The current knowledge about TreM dynamics is fragmented across study fields, and most studies focus on a few TreM types (side cavities, exposed wood) and ecosystems (temperate forests) (I). The thesis describes the complexity of TreM development as influenced by tree age, diameter, species, habitat conditions, and forest disturbances (I, II). As a general trend, TreM abundance increased with tree age and size, with tree diameter often having a greater predictive value than age (II). This could be due to the larger surface area of larger trees, which increases the probability of injuries and subsequent TreM development, but it may also involve complex biological mechanisms. Different tree species have different sets of TreMs that develop at varying rates (I, II). Aspen showed greater TreM diversity than spruce, especially in trees older than 80 years of age (II). This can be attributed to the varying resistance of tree species to diseases and injuries. It is also crucial to recognise that the same TreMs can hold different significance for biodiversity depending on the tree species (III). This is due to variations in chemical and physical properties between tree species, as well as the adaptations of organisms that colonise these TreMs.

Stand-level characteristics also influence TreM occurrence. Aspens in moist sites had more exposed sapwood and epiphytes, while those in drier sites had more exposed heartwood (II). Spruces in drier sites more frequently had buttress concavities (II). These differences can be linked to known ecological processes, such as differences in tree growth rates, variations in the spread of decay fungi,

and the variability of herbivore preferences under different growing conditions. Thinning reduced aspen fungal fruiting bodies and deadwood incidence but increased the probability of exposed wood in spruce (II), indicating that forest management practices can cause injuries that facilitate some TreMs.

The effect of TreMs diversity on biodiversity was generally weak and variable and mostly found in young trees (III). It is possible that TreMs are particularly important in specific tree species, ecosystems, or regions and only for certain groups of inhabitants. It can also be assumed that the results were influenced by a general scarcity of TreMs in Estonian forests (II). Clear positive relationships were found between TreM diversity and epiphyte diversity, which themselves create TreMs and, thereby, influence other organisms. TreM diversity also promoted beetle abundance and snail diversity in young spruces (III). However, negative relationships were also found, particularly for invertebrates. For example, invertebrate prey volume decreased with increasing TreM diversity in young spruces, likely due to the impact of tree injuries on arthropod abundance. Another negative relationship was found for gastropod abundance in young aspens (III). These findings suggest that while TreMs can promote invertebrate abundance and diversity by providing food and shelter resources, TreMs can also suppress their numbers through other mechanisms (for example, if TreMs also favour the abundance of predators). To clarify this, it would be necessary to examine more precisely (including over the long term) the ecological value and role of TreMs for selected groups of organisms (focal species) under various conditions.

These results have implications for forest management. Since TreMs have a variable effect on forest biota, they cannot replace species protection measures. The high uncertainty involved in TreM development and loss would be best addressed by following the precautionary principle in forest management, ensuring the presence of diverse TreMs in retained habitat trees and enabling microhabitat development processes at the landscape level. Recognising and promoting trees with a high probability of supporting TreMs in the future is crucial, particularly in the case of rare TreMs.

Overall, this thesis clarifies TreM dynamics and their role in supporting forest biodiversity, particularly in North European mixed forests. While the relationship between TreMs and biodiversity can be complex, this thesis highlights the need for long-term forest management planning that prioritises preserving natural TreM dynamics. By promoting diverse TreMs across various tree species and ages, forest management can contribute to the long-term health and resilience of forest ecosystems.

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SUMMARY IN ESTONIAN

Mikroelupaigad elusatel puudel, nende kujunemine, püsimine ja seos metsa elurikkusega

Arvestades metsade laialdast kasutust nii globaalselt kui ka piirkondlikult, on oluline hoida majandusmetsade struktuurilist keerukust. Näiteks toetab struktuurielementide säilitamine raie ajal (säilikmetsandus) metsades keskkonna-, majanduslikke ja kultuurilisi väärtusi. Suurte vanade puude (elupaigapuude) jätmise metsa suurendab bioloogilist mitmekesisust.

Käesolev doktoritöö uurib elusate puudega seotud mikroelupaikade (ingl *tree-related microhabitats*) näitel ühte peamist mehhanismi, mille kaudu puud toetavad metsa ülejäänud elurikkust ning sedakaudu metsaökosüsteemide keerukust. Sellised mikroelupaigad on puudel paiknevad struktuurid (nt õõnsused, koorepraod, paljandunud puit, kuivanud oksad), mida organismid kasutavad oma elutegevuse käigus toitumis-, varjumis- või sigimispaijana. Selliste struktuuride olemasolu määrab metsa kui elupaiga kvaliteedi näiteks paljudele lindudele, nahkhiirtele, imetajatele, selgrootutele, väikestele veeorganismidele ja epifüütidele. Mikroelupaikade suur mitmekesisus on iseloomulik eelkõige vanadele looduslikele metsadele, kus neid on erinevas kujunemisjärgus tänu puude vanuselisele, liigilisele ja kõduastmelisele mitmekesisusele. Looduslikult arenevates metsades asendavad kaduvaid mikroelupaiku järjepidevalt tekkivad uued. Majandusmetsades on aga nende tekkeprotsessid häiritud näiteks nõrgemate või suurte ja vanade puude eemaldamise, väheste puuliikide eelistamise või lühikeste raieringide tõttu. Seetõttu on mikroelupaiku seal vähem ja need on sageli vaid teatud (eelkõige vigastustest tulenevat) tüüpi, nagu näiteks vaigujooks ja paljandunud puit.

Kuigi üha enam nähakse mikroelupaikade olulisust seoses metsa elurikkuse kaitsega, on nende teket, püsimist ja ökoloogilist tähtsust puudutatav teadmine lünklik. Säätliku metsanduse ja looduskaitse planeerimiseks on vaja arvhinnanguid mikroelupaikade kujunemise kiiruse, püsivuse ning neid protsesse mõjutavate tegurite kohta nii puu kui ka metsa mastaabis. Näiteks selleks, et mõista metsakasvatussüsteemide mõju mikroelupaikadele, on vaja kvantitatiivseid uuringuid puude vanuse ja suuruse seostest mikroelupaikade esinemise ja omadustega. Samuti on mikroelupaikade esinemise prognoosimiseks oluline uurida, kuidas nende arv ajas muutub olenevalt puuliigist ja keskkonnatingimustest. Ebaselge on ka suurema osa mikroelupaikade kujunemisviis – pole teada, millised protsessid mõjutavad nende teket, arengut ja kestvust. Kuigi nad võiksid toimida elustiku indikaatoritena ja selle kaudu aidata teostada seiret, pole elustikuseosed piisavalt selged. Seega on vaja veel täpsemalt uurida mikroelupaikade kasutamise otstarbekust metsanduse ja looduskaitse planeerimisel.

Doktoritöö eesmärk oli uurida, kuidas puudega seotud mikroelupaigad kujundavad metsas elusate puude elupaigaväärtust. Täpsemalt oli eesmärk kirjeldada mikroelupaikade kujunemiseks kuluvat aega ja kujunemist mõjutavaid tegureid

(I, II); uurida, kuidas nende kujunemine toetab bioloogilist mitmekesisust (III); ning selgitada, kuidas saadud teadmisi kasutada metsaplaneerimises ja -majandamises (I–III). Selleks koostati kirjanduse ülevaade viie mikroelupaiga – paljandunud puit, puuõõnsused, kooretaskud, dendrotelmid (ehk vesilohud – aegajalt veega täituvad nõgusused) ja tuuleluuad – kujunemisest ja kadumisest (I); uuriti puu vanuse ja suuruse ning erinevate mikroelupaikade esinemise vahelisi seoseid Eesti metsades ning neid mõjutavaid tegureid (II); ning analüüsiti mikroelupaikade seost laiema ökoloogilise tähtsusega bioloogilise mitmekesisuse näitajatega (nt selgrootute hulk kui lindude toidubaas) (III).

Väliuuringud (II, III) põhinevad kahel ökoloogiliselt ja majanduslikult erineval puuliigil Eestis: harilikul kuusel (*Picea abies*) ja haaval (*Populus tremula*). Välitööde käigus kirjeldati rohkem kui 900 puu mikroelupaiku, võeti vanuse määramiseks puusüdamikku puurproov, koguti epifüüte ja püüti puudel liikuvaid selgrootuid. Andmete analüüsimiseks kasutati mitmefaktorilisi statistilisi mudeleid, mis seostasid puud (vanus, diameeter) ja puistut (kasvukohatüüp, päritolu, hiljutine harvendusraie) iseloomustavad tunnused mikroelupaikade esinemisega (II). Elurikkuse ja mikroelupaikade vahelise seose analüüsimiseks kaasati mudelitesse lisaks puu tunnustele ka mikroelupaikade mitmekesisuse tunnus (III).

Mikroelupaikade kujunemist ja püsimist puudel on äärmiselt vähe uuritud ja sedagi peamiselt paari mikroelupaiga osas: õõnsuste kui pesapaikade, ja puidupaljandite kui puu elujõulisust ja puiduväärtust kahandava vigastuse osas (I). Tulemused näitavad, et mikroelupaikade kujunemine eluspuudel on keeruline protsess, mida mõjutavad üheaegselt mitmed tegurid, sealhulgas puu vanus, diameeter, liik, kasvukohatingimused ja häiringud. Üldiselt suureneb mikroelupaikade arvukus puu vananedes ja kasvades, kuid see seos on enamasti mitte-lineaarne. Samuti selgus, et kuigi puu vanus on oluline tegur (I, II), on puu tüveläbimõõt tihti suurema ennustuväärtusega (II). Võib oletada, et põhjuseks on suurte puude suurem üldpind, mis omakorda suurendab vigastuste esinemise tõenäosust. Eri puuliikidel on erinevat tüüpi mikroelupaigad ja need kujunevad erineva kiirusega (I, II). Näiteks haava mikroelupaikade mitmekesisus on suurem kui kuusel, seda eriti vanematel – üle 80-aastastel – puudel (II). Selle põhjust saab seostada puuliikide erineva vastupanuvõimega haigustele ja vigastustele. Lisaks võib sama mikroelupaik eri puuliikidel olla elustikule eri mõjuga (III), ilmselt sõltuvalt keemilistest ja füüsikalistest tingimustest puul ning puid asustavate organismide kohastumustest.

Lisaks puu omadustele mõjutavad mikroelupaikade esinemist ka puistu tunnused. Näiteks niisketes kasvukohtades on haabadel rohkem paljandunud maltspuitu ja epifüüte, samas kui kuivemas kasvukohatüübis esineb neil enam paljandunud lülipuitu ning kuuskedel sagedamini jalami nõgususi (II). Selliseid erinevusi saab seostada teadaolevate ökoloogiliste protsessidega, milleks on näiteks puude kasvukiiruse, puiduseente asustustõenäosuse ja herbivooride eelistuste varieeruvus erinevates kasvutingimustes. Harvendusraie vähendab haabade võrastikes surnud puidu osakaalu ning seente (eeskätt haavataeliku, *Phellinus tremulae*) mitmeaastaseid viljakehi, kuid suurendab kuuskede paljandunud puidu

esinemistõenäosust (II). See kinnitab, et raiel võib olla positiivne mõju selliste mikroelupaikade tekkele, mis on seotud puu vigastustega.

Puu tasemel on mikroelupaikade mõju bioloogilisele mitmekesisusele üldiselt nõrk ja varieeruv ning enamasti seotud noorte (veel mitte raieküpsete) puudega (III). On võimalik, et mikroelupaigad on olulised eelkõige kindlatel puuliikidel, ökosüsteemides või regioonides ning vaid teatud liigirühmade jaoks. Samuti võib eeldada, et analüüsitulemusi mõjutab mikroelupaikade üldine vähesus uuritud Eesti majandusmetsades (II). Selge positiivne seos ilmnes mikroelupaikade mitmekesisuse ja epifüütide liigirikkuse vahel, kes omakorda moodustavad mikroelupaiku ning võivad sedakaudu mõjutada epifüütidest toituvaid ja neid pesamaterjalina kasutavaid loomi (nt selgrootuid, linde) ning ökoloogilisi aine- ringeid. Samuti seostus mikroelupaikade mitmekesisus positiivselt mardikate arvukuse ja kojaga tigude liigirikkusega noortel kuuskedel (III). Samas ilmnes ka negatiivseid seoseid, eriti selgrootute puhul (sealhulgas arvestades puu vanuse ja diameetri eraldiseisvat mõju). Näiteks lindude toidubaasina arvestatud lülijalgsete hulk vähenes noorte kuuskede mikroelupaikade mitmekesisuse suurenedes. See tendents võib olla seotud puu vigastustega, mis kas otseselt (nt lehes- tiku hõrenemine) või kaudselt (nt vigastuste sagedam esinemine varjulises paigas) võivad mõjutada lülijalgsete arvukust. Sarnane seos ilmnes ka tigude arvukuses noortel haabadel (III). Järelikult, kuigi mikroelupaigad võivad selg- rootute arvukust ja mitmekesisust toidu- ja varjeressurssi pakkudes suurendada, võivad need ka läbi teiste mehhanismide selgroogsete arvukust pärssida. Tarvis oleks täpsemalt (sh pikaajaliselt) uurida eluspuudega seotud mikroelupaikade ökoloogilist väärtust ja rolli kitsamatele organismirühmadele (nt suunisliikidele) erinevates tingimustes.

Metsade majandamine peaks arvestama mikroelupaikade kujunemise prot- sesse, pikaajalist dünaamikat ning ökoloogilist rolli. Et mikroelupaikadel on käesoleva doktoritöö tulemuste põhjal metsaelustikule varieeruv mõju, ei saa liikide kaitset asendada pelgalt mikroelupaikade kaitsega – vaja on eesmärgi- pärast ja liigirühma-spetsiifilist lähenemist. Sellise suure määramatuse puhul on põhjendatud metsade majandamisel järgida ettevaatusprintsipi ja heterogeense majandamise põhimõtteid, kaitsta mitme eri mikroelupaigaga säilikipuid ning luua võimalusi mikroelupaikade kujunemiseks maastiku tasandil. Aastakümnete perspektiivis ei piisa ainult mikroelupaigaga puude hoidmisest, tuleb kasvama jätta ka puid, millel on suur tõenäosus tulevikus mikroelupaiku kanda. See eeldab nihet staatiliselt vaatelt dünaamilisele maastikuplaneerimisele, mis arvestab mikroelupaikade kujunemise ja pikaajalise potentsiaaliga elurikkuse jaoks.

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PUBLICATIONS

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