Quality and temporal development of habitat trees and their microhabitats in temperate European forests

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> “…let us choose for ourselves our path in life, and let us try to strew that path with flowers.”
>
> Émilie du Châtelet,
> French natural philosopher and mathematician,
> 18th Century.

For my father, sister,
and my mother.
Always in my heart.

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To whoever reads this now, thank you for your interest.

Statement of originality

I hereby declare that this thesis has never been submitted, in the same or similar form, to another examination commission in Germany or another country for a degree. This thesis contains no material previously published or written by another person except where proper acknowledgement is made.

Andreea Petronela Spînu

Freiburg, 21st June 2023

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Statement of manuscripts

Four manuscripts were prepared for peer-reviewed publication in scientific journals and constitute individual chapters in this thesis:

- **Chapter II.** Spînu A.P., Asbeck T. & Bauhus J. (2022). Combined retention of large living and dead trees can improve provision of tree-related microhabitats in Central European montane forests. *European Journal of Forest Research* 141, 1105–1120 https://doi.org/10.1007/s10342-022-01493-1. Published;
- **Chapter III.** Spînu A.P., Mysiak W., Bauhus J., Bielak K. & Niklasson M. (2023). Short-lived, fast-growing species accelerate restoration of tree-related microhabitats in 50-year old reserves of Białowieża Forest, Poland. *Ecology and Evolution.* Published;
- **Chapter IV.** Spînu A.P., Nicolaie M.A., Asbeck T., Kozak D., Paillet Y., Cateau E., Mikoláš M., Svoboda M., Bauhus J. (2023) Temporal development of microhabitats on living habitat trees in temperate European forests. *Ecosystems*. Under review;
- **Chapter V.** Spînu A.P., Nairn T., Skiadaresis G., Denter M., Seifert T., Bauhus J. (2023) Mortality and growth patterns of habitat trees in continuous cover forests of Central Europe. In preparation.

Two additional and relevant publications have been developed during the course of this PhD project, but have not been included in the thesis because A. Spînu had only a moderate, not a major contribution to these manuscripts in the form of writing and literature review:

- Asbeck, T., Kozák, D., Spînu, A.P., … Svoboda M. (2022). Tree-Related Microhabitats Follow Similar Patterns but are More Diverse in Primary Compared to Managed Temperate Mountain Forests. *Ecosystems* 25, 712–726 https://doi.org/10.1007/s10021-021-00681-1. Published;
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Statement of contributions

Chapter II. A. Spînu collected the data, carried out the statistical analyses and wrote the manuscript with support from T. Asbeck and J. Bauhus; J. Bauhus designed the research layout; T. Asbeck provided statistical advice. All authors discussed the results and contributed to the final manuscript.

Chapter III. A. Spînu conceived the research layout and direction, carried out the statistical analyses and wrote the manuscript with support from J. Bauhus, K. Bielak and M. Niklasson; W. Mysiak collected the data; J. Bauhus contributed substantially in the result interpretation and manuscript direction; K. Bielak designed the study layout in the field, supervised the fieldwork and offered statistical support; M. Niklasson initiated the research, contributed to the study design and manuscript writing. J. Bauhus, K. Bielak and M. Niklasson contributed equally as last authors. All authors reviewed the results and approved the final manuscript.

Chapter IV. A. Spînu and J. Bauhus developed the study design; A. Spînu, T. Asbeck, D. Kozak, Y. Paillet collected the data and contributed to the interpretation of the results. A. Spînu and A. Nicolaie carried out the data analysis based on the analytical methodology designed by A. Nicolaie. A. Spînu was in charge of the overall direction and planning, manuscript writing with significant input from J. Bauhus. All authors contributed to the final manuscript.

Chapter V. A. Spînu and J. Bauhus conceived the ideas and design the methodology and study; A. Spînu and T. Nairn collected the data, carried out the laboratory work. A. Spînu and G. Skiadaresis performed the data analysis. A. Spînu lead the writing of the manuscript. All authors contributed critically to the draft and gave final approval for publication.

Summary

Background

The retention of habitat trees has been recently introduced as a biodiversity conservation practice in the multiple-use forests of temperate Europe. Habitat trees are commonly selected based on their microhabitats, such as woodpecker cavities or crown deadwood. Tree-related microhabitats or shortly TreMs, are structural features needed by many forest-dwelling species during different life stages. The occurrence of TreMs depends on various tree attributes, including size, vitality and species identity. Thus, TreM assemblages and associated forest-dwelling species will be affected by changes in tree communities such as those driven by increasing rates of climate change-related disturbances and tree mortality. However, current retention forestry approaches have been rather static, and do not consider the temporal dynamics of habitat trees and their TreMs.

Research objectives

The practical goal of this thesis was to provide an evidence-base for dynamic habitat tree selection in temperate European forests utilising data describing TreMs borne by functionally different trees, including both living and dead trees, as well as those with contrasting attributes and life-history traits. By investigating the persistence and loss of habitat trees and their TreMs, this research sought to provide empirical evidence that can inform the management and conservation of continuous and diverse habitat provisioning in forests.

The specific objectives were:

Chapter II. To investigate differences in TreM composition of living and dead habitat trees and to assess their complementarity in providing TreMs at the forest stand-level.

Chapter III. To compare the temporal development of TreMs on coexisting trees with contrasting life-history traits, in particular their successional character and resistance to decay and injuries, as influenced by management cessation.

Chapter IV. To assess the temporal dynamics of TreMs on living habitat trees from temperate European forests and examine the effect of tree dimension and species.

Chapter V. To quantify the mortality rates of habitat trees and detect early warning signs of drought-triggered tree mortality. In addition, this chapter aims to identify links between overall growth trends, vitality and TreM presence.

Study sites and methodology

To address the objective in **Chapter II**, TreM abundance, richness and composition were compared on living and dead trees. Data were collected from 133 one-hectare study plots in the Black Forest region, Germany, managed according to a continuous-cover approach. The dominant tree species were Norway spruce (*Picea abies* (L.) Karst), European beech (*Fagus sylvatica* L.) and Silver fir (*Abies alba* Mill.). The majority of the growing stock consisted of healthy, living trees, with few trees of lower vitality classes or diseased. Generalised linear mixed models were fitted to identify the main predictors of TreM abundance and richness. TreM composition was described using a bipartite network that clustered tree identities (a combination of tree species and vitality status) with similar TreMs into functional groups. The complementarity of habitat trees at plot-level was investigated by comparing different retention approaches based on various combinations of dead and living trees. Further, to understand the response of habitat trees of various species to extreme drought as well as the impact of microhabitats on their vitality (**Chapter V**), tree-ring data was collected from 32 plots, where mortality following the drought event in 2018 was observed through aerial images. The early signals of temporal changes in past growth of dead and living trees were compared using time-series metrics such as mean tree-ring width, first order autocorrelation, standard deviation and the temporal stability of tree growth. The relationships between TreM abundance, richness and growth trends were examined to identify whether past growth decline had an effect on the present TreM occurrence.

To be able to fulfil the objective of **Chapter III**, a comparative case-study was conducted in four managed and four set-aside 100-year-old second-growth stands (0.25 hectare each) originated from clearfelling in Białowieża Forest, Poland. This research examined the temporal development of TreMs on coexisting trees with contrasting life-history traits, in relation to changes in forest management approximately 50 years ago. The main predictors of TreM richness and abundance were identified by means of generalised linear mixed models.

The highly dynamic temporal development of TreMs was captured based on an original dataset describing TreMs borne by 11,569 living trees from temperate European forests (**Chapter IV**). Data were collected in France, Germany, Slovakia and Romania and comprised repeated TreM observations on trees belonging to 30 species. *F. sylvatica*, *P. abies* and *A. alba* were the main species. Data spanned from 2006 to 2021, with revisiting intervals from 3 to 12 years. The drivers of change in TreM richness, as well as the rates of TreM persistence and loss at tree-level, were investigated using survival analysis methods.

Results and discussion

The results of this thesis consistently demonstrate the importance of large trees for supporting abundant, diverse, unique and dynamic microhabitat profiles throughout their lifespan and following their death. However, this study emphasises that functionally different habitat trees can complement each other in TreM provisioning. For instance, while dead habitat trees of *A. alba* may have higher TreM abundance and richness compared to living broadleaves, their TreM composition differs significantly. Therefore, the overall richness of TreMs at stand-level can increase, particularly through the presence of decayed, large snags (**Chapter II**).

The temporal dynamics of habitat trees and their microhabitats also vary. The development of TreMs on habitat trees is highly dynamic and differs among conifers and broadleaves, as well as in relation to the capacity of trees to resist and heal wounds and their successional character (**Chapter III, IV**). At similar ages, irrespective of the forest management type, pioneer species generally support more and richer TreM assemblages than longer-lived, slower growing species like *Quercus*. However, longer-lived species play a crucial role by supporting certain TreMs, such as crown deadwood or concavities (**Chapter III**).

Although the richness of TreMs at tree level persists over time, specific TreM groups are susceptible to disappearing on living trees and following their death (**Chapter IV, II**). The presence of TreMs on trees does not contribute to tree mortality, which is rather associated with a long-term decline in growth rates, especially in conifers (**Chapter V**). That may lead to loss of TreMs associated with living trees, since changes in tree vitality status result in a different TreM composition (**Chapter II**).

Conclusion

This research advanced the understanding of the consequence of different approaches to habitat tree retention for forest biodiversity conservation in temperate European forests. To secure an ongoing provision of diverse habitat resources for forest-dwelling species, it is imperative to incorporate a diversified and dynamic approach within existing strategies of habitat tree retention. A combination of trees with different attributes, such as vitality status, compartmentalization capacity, successional character, form and shape, can provide diverse TreM assemblages. Additionally, consideration should be given to the likelihood of TreMs or the risk of the habitat tree itself being lost in the long term. This thesis underscores the importance of selecting as habitat trees, species adapted to climate change among both short- and long-lived tree species, to ensure a continuous and abundant supply of TreMs in the future.

Zusammenfassung

Hintergrund

Der Erhalt von Habitatbäumen wurde in letzter Zeit als praktische Maßnahme zur Sicherung der biologischen Vielfalt in bewirtschafteten, temperaten Wäldern Europas eingeführt. Habitatbäume werden in der Regel aufgrund ihrer Mikrohabitate, wie Spechthöhlen oder Kronentotholz, ausgewählt. Baumbezogene Mikrohabitate oder kurz TreMs (tree-related microhabitats) sind Strukturmerkmale, die von vielen waldbewohnenden Arten während verschiedener Lebensstadien benötigt werden. Das Vorkommen von TreMs hängt von verschiedenen Baumattributen ab, darunter Dimension, Vitalität und Art. Daher sind die Mikrohabitatausstattung und die damit verbundenen waldbewohnenden Arten von strukturellen und kompositionellen Veränderungen des Baumbestandes betroffen. Diese Veränderungen werden beispielsweise durch zunehmende, klimawandelbedingte Störungen und Baumsterben hervorgerufen. Die derzeitigen Ansätze für die Sicherstellung von Mikrohabitaten in den bewirtschafteten Wäldern waren jedoch eher statisch und berücksichtigten nicht die zeitlichen Dynamiken der Habitatbäume und der Entstehung und des Verschwindens ihrer TreMs.

Forschungsziele

Das praxisbezogene Ziel dieser Arbeit bestand darin, eine Evidenzgrundlage für die dynamische Habitatbaumauswahl in temperaten Wäldern Europas zu schaffen. Dazu wurden Daten zur Beschreibung von TreMs verwendet, die von funktionell unterschiedlichen Bäumen ausgehen, darunter sowohl lebende als auch tote Bäume sowie solche mit gegensätzlichen Eigenschaften und lebensgeschichtlichen Merkmalen. Durch die Untersuchung des Erhalts und Verlusts von Habitatbäumen und ihrer TreMs sollten empirische Erkenntnisse gewonnen werden, die für die Bewirtschaftung und Erhaltung eines kontinuierlichen und vielfältigen Habitatangebots in Wäldern genutzt werden können.

Die spezifischen Ziele waren:

Kapitel II. Untersuchung der Unterschiede in der Mikrohabitatzusammensetzung von lebenden und toten Habitatbäumen und Bewertung ihrer komplementären Bereitstellung von Mikrohabitaten auf Bestandesebene.

Kapitel III. Vergleich der zeitlichen Entwicklung von TreMs an koexistierenden Bäumen mit unterschiedlichen lebensgeschichtlichen Merkmalen, deren Vorkommen innerhalb der Waldsukzession und Widerstandsfähigkeit gegen bewirtschaftungsabhängige Verletzungen und Zerfall.

Kapitel IV. Bewertung der zeitlichen Dynamik von TreMs an lebenden Habitatbäumen aus gemäßigten europäischen Wäldern und Untersuchung der Auswirkungen von Baumgröße und -art.

Kapitel V. Quantifizierung der Mortalitätsraten von Habitatbäumen und Erkennung von Frühwarnzeichen für trockenheitsbedingtes Baumsterben. Darüber hinaus werden in diesem Kapitel Zusammenhänge zwischen allgemeinen Wachstumstrends, Vitalität und dem Vorhandensein von TreMs festgestellt.

Untersuchungsgebiete und Methodik

Um das in **Kapitel II** beschriebene Ziel zu erreichen, wurden die Häufigkeit, der Reichtum und die Zusammensetzung von TreMs an lebenden und toten Bäumen verglichen. Die Daten wurden auf 133 ein Hektar großen Untersuchungsflächen im Schwarzwald (Deutschland) erhoben, die nach dem Dauerwaldkonzept bewirtschaftet wurden. Die dominierenden Baumarten waren Fichte (*Picea abies* (L.) Karst), Rotbuche (*Fagus sylvatica* L.) und Weißtanne (*Abies alba* Mill.). Der überwiegende Teil des Bestandes setzte sich aus gesunden, lebenden Bäumen zusammen. Ein geringer Teil bestand aus kranken Bäumen und Bäumen der unteren Vitalitätsstufen. Es wurden generalisierte lineare gemischte Modelle angewandt, um die wichtigsten Prädiktoren für die Häufigkeit und den Reichtum von TreMs zu ermitteln. Die Mikrohabitatzusammensetzung wurde mit Hilfe eines bipartiten Netzwerks beschrieben, das Baumidentitäten (bestehend aus Baumart und Vitalitätsstatus) mit ähnlichen Mikrohabitaten zu funktionalen Gruppen zusammenfasste. Die Komplementarität der Habitatbäume auf Bestandsebene wurde durch den Vergleich verschiedener Retentionskonzepte auf der Grundlage verschiedener Kombinationen von toten und lebenden Bäumen untersucht. Um die Reaktion von Habitatbäumen verschiedener Arten auf extreme Trockenheit sowie die Auswirkungen von Mikrohabitaten auf ihre Vitalität zu verstehen (**Kapitel V**), wurden Jahrringdaten aus 32 Untersuchungsgebieten gesammelt, auf denen die Mortalität nach der Dürre im Jahr 2018 anhand von Luftbildern beobachtet wurde. Frühe Anzeichen für temporäre Wachstumsschwankungen bei toten und lebenden Bäumen wurden anhand von Zeitreihenmetriken wie der mittleren Jahrringbreite, der Autokorrelation erster Ordnung, der Standardabweichung und der zeitlichen Stabilität des Baumwachstums verglichen. Die Zusammenhänge zwischen der Häufigkeit sowie dem Reichtum von TreMs und der Baumwachstumsrate wurden untersucht, um festzustellen, ob ein verringertes Baumwachstum in der Vergangenheit einen Einfluss auf das gegenwärtige Vorkommen von TreMs hatte.

Um das Ziel von **Kapitel III** realisieren zu können, wurde eine vergleichende Fallstudie in vier bewirtschafteten und vier unbewirtschafteten 100-jährigen Sekundärwaldbeständen (jeweils 0,25 Hektar) durchgeführt, die aus Kahlschlägen im Białowieża-Wald in Polen hervorgegangen waren. Im Rahmen dieser

Untersuchung wurde die zeitliche Entwicklung von TreMs an Bäumen mit unterschiedlichen lebensgeschichtlichen Merkmalen im Zusammenhang mit den Veränderungen der Waldbewirtschaftung vor etwa 50 Jahren untersucht. Die wichtigsten Prädiktoren für den Reichtum und die Häufigkeit von Baummikrohabitaten wurden durch generalisierte lineare gemischte Modelle ermittelt. Die hoch dynamische zeitliche Entwicklung von TreMs wurde auf der Grundlage eines Datensatzes erfasst, der TreMs von 11569 lebenden Bäumen aus gemäßigten europäischen Wäldern beschreibt (**Kapitel IV**). Die Daten wurden in Frankreich, Deutschland, der Slowakei und Rumänien erhoben und umfassten wiederholte Mikrohabitatsbeobachtungen an Bäumen, die zu 30 verschiedenen Arten gehören. *F. sylvatica*, *P. abies* und *A. alba* waren die Hauptbaumarten. Die Aufzeichnungen reichten von 2006 bis 2021, mit Wiederholungsintervallen von 3 bis 12 Jahren. Die Ursachen für die Veränderung des Reichtums, der Verlustrate und der Dauerhaftigkeit von Mikrohabitaten auf Baumebene wurden mit Methoden der Überlebenszeitanalyse untersucht.

Ergebnisse und Diskussion

Die Ergebnisse dieser Arbeit zeigen durchgehend die Bedeutung von großen Bäumen für die Bereitstellung reichhaltiger, vielfältiger, einzigartiger und dynamischer Mikrohabitatprofile während ihrer gesamten Lebensdauer und nach ihrem Tod. Diese Studie hebt jedoch hervor, dass sich funktionell unterschiedliche Habitatbäume bei der Bereitstellung von TreMs gegenseitig ergänzen können. Während beispielsweise tote Habitatbäume von *A. alba* im Vergleich zu lebenden Laubbäumen eine höhere TreM-Abundanz und -Reichhaltigkeit aufweisen können, unterscheidet sich ihre TreM-Zusammensetzung erheblich. Daher kann der Gesamtreichtum an TreMs auf Bestandsebene zunehmen, insbesondere durch die Existenz von großen, stehenden, toten Habitatbäumen (**Kapitel II**).

Die zeitliche Dynamik von Habitatbäumen und ihren Mikrohabitaten variiert ebenfalls. Die Entwicklung von TreMs auf Habitatbäumen ist sehr dynamisch und unterscheidet sich zwischen Nadelbäumen und Laubbäumen. Zudem ist sie auch von der Widerstands- und Wundheilungsfähigkeit der Bäume und ihrem Sukzessionscharakter beeinflusst (**Kapitel III, IV**). Bei ähnlichem Alter und unabhängig von der Art der Waldbewirtschaftung weisen Pionierarten allgemein mehr und vielfältigere Mikrohabitate auf als langlebigere, langsamer wachsende Arten wie z.B. Quercus. Längerlebige Arten spielen jedoch eine entscheidende Rolle, indem sie bestimmte TreMs wie Kronentotholz oder Höhlungen begünstigen (**Kapitel III**).

Obwohl der TreM-Reichtum auf Baumebene im Laufe der Zeit bestehen bleibt, neigen bestimmte TreM-Gruppen dazu, auf lebenden Bäumen und nach deren Absterben zu verschwinden (**Kapitel IV, II**). Die Existenz von TreMs auf Bäumen trägt nicht zur Baumsterblichkeit bei, die vielmehr mit einem langfristigen Rückgang der Wachstumsraten, insbesondere bei Nadelbäumen, verbunden ist (**Kapitel V**). Dies kann zum Verlust von TreMs führen, die mit lebenden Bäumen in Verbindung stehen, da Veränderungen im Vitalitätsstatus der Bäume zu einer anderen TreM-Zusammensetzung führen (**Kapitel II**).

Schlussfolgerung

Die in dieser Dissertation dokumentierte Forschung hat das Verständnis für unterschiedliche Ansätze der Entwicklung und des Erhalts von Habitatbäumen für den Schutz der biologischen Vielfalt in europäischen Wäldern der gemäßigten Zonen verbessert. Um ein kontinuierliches und vielfältiges Angebot an Habitaten für die waldbewohnenden Arten zu gewährleisten, muss bei der Auswahl von Habitatbäumen im Rahmen bestehender Erhaltungsstrategien unbedingt ein dynamischer und diversifizierter Ansatz verfolgt werden. Eine Kombination von Bäumen mit verschiedenen Eigenschaften, wie zum Beispiel Vitalitätsstatus, Kompartimentierungskapazität, Sukzessionscharakter, Form und Gestalt, kann zu einer vielfältigen Mikrohabitatzusammensetzung führen. Diese Arbeit unterstreicht, wie wichtig es ist, sowohl unter den kurz- als auch unter den langlebigen Baumarten an den Klimawandel angepasste Arten als Habitatbäume auszuwählen, um auch in Zukunft ein kontinuierliches und vielfältiges Angebot an TreMs zu gewährleisten.

List of abbreviations:

- AIC = Akaike information criterion
- AR1 = first order autocorrelation (the correlation between adjacent tree ring widths)
- ConFoBi = “Conservation of forest biodiversity in multiple-use landscapes” Research Training Group
- DBH = diameter at breast height (diameter of a tree trunk or coppice branch, measured at 1.30 m height above the ground);
- GIS = geographic information systems, tools used to store, visualize and analyse geographic data;
- GLMM = generalised linear mixed models (statistical method);
- g_m= annual radial growth ratio of a tree;
- LIDAR = Light Detection and Ranging, a remote sensing method used to examine the surface of the Earth;
- SD = Standard Deviation, measure that quantifies the amount of variation; square root of the variance;
- TreM = Tree-related microhabitats (distinct structures on trees used by forest-dwelling organisms during their life cycle);

Symbols and measures:

- cm = centimetre
- dpi = dots per inch;
- ha = hectare (= 10.000 square meters);
- m^2 = square meter;
- m^2 ha^{-1} = square meter per ha;
- m.a.s.l. = meters above sea level;
- N ha^{-1} = number per ha;
- Ø = diameter

Key terms:

- Compartmentalization = tree defense mechanism to limit the loss of normal function and the spread of decay fungi introduced by wounding;
- Complementarity = elements which complete each other through their distinct characteristics;
- Dendro-ecological methods = scientific methods based on tree-ring patterns;
- Habitat tree = large, old, living or dead trees that provide habitats and refugia for forest-dwelling species;
- Radial growth = ability of a tree to grow outward from a central point;
- Senescence = natural process of aging and decline;
- Temporal stability of tree growth = the ratio between the mean tree-ring width and the standard deviation;
- TreM abundance = total number of individual TreMs;
- TreM richness = number of different TreM groups;
- TreM composition = the assemblage of TreMs;
- TreM persistence = temporal increment or consistency of TreM counts;
- TreM loss = temporal decline or disappearance of TreMs;
- Vitality status = living or dead tree;

I. General introduction

I.1. Past and future threats to biodiversity in European forests

On account of its value and manifold benefits, forest biodiversity contributes to human well-being (Piras et al., 2021; Piccolo et al., 2022). Under future changes in climate and disturbance regimes, promotion of biodiversity conservation is crucial to foster the creation of resilient and productive forest ecosystems, which can withstand environmental stress (Seidl et al., 2017) and recover naturally from it (Steffen et al., 2015; Seidl et al., 2016). Historically, habitat loss and overexploitation have emerged as major threats that resulted in global biodiversity loss (Brook et al., 2008). For instance, past forestry practices pursuing high levels of timber production have negatively impacted forest structure and reduced the quality and availability of habitats for forest-dwelling species, at both stand and landscape level (Gavin et al., 2021).

In Europe, due to past and presently high societal demands for natural resources, most forests are currently managed (Sabatini et al., 2020). Past commercial forestry with short production cycles has invariably simplified and homogenised the structure of managed forests, threatening the survival of many specialist or rare species (Bauhus et al., 2009; Puettmann et al., 2009). Although biodiversity-focused management strategies employed in recent decades have improved habitat quality, elements associated with old-growth stages or those emerging after natural disturbances are still scarce in managed European forests (Kraus & Krumm, 2013). Large, old trees with exceptional stem forms, deadwood in different decay stages, as well as specific habitats, such as open or disturbed forest patches, are critical for the viability of associated species communities (Bauhus et al., 2009; Gustafsson et al., 2012; Larsen et al., 2022). Furthermore, increased disturbances and mortality events occurred in Central European forests in recent decades (Lindner et al., 2014; Seidl et al., 2014; Millar & Stephenson, 2015), corresponding with the global trend of elevated stress from extreme heat, drought and pathogen attacks (Allen et al., 2015, 2010). These threats are anticipated to continue, leading to more severe and frequent impacts (Anderegg et al., 2015; Seidl et al., 2017). The health of European forests and associated biodiversity are, therefore, susceptible to significant effects caused by stress-induced mortality and changes in tree species distributions (Dyderski et al., 2018; Hanewinkel et al., 2013; Lindner et al., 2014).

While the multifunctional role of forests is recognised worldwide and in Europe, adaptive, biodiversity-focused management approaches have been implemented to address the forest biodiversity crisis (Bollmann & Braunisch 2013; Gustafsson et al., 2020; Muys et al., 2022), their suitability under climate change remains uncertain (Augustynczik et al., 2020).

I.2. Biodiversity-focused management approaches

Retention practices aim to improve the post-harvest conditions and to achieve temporal and spatial connectivity of key habitats in managed forests (Franklin et al., 2002; Gustafsson et al., 2012). Retention of specific areas and structural elements left in managed forests that reduce the negative impacts of timber harvesting on the viability of forest species communities, is suitable for both segregative (i.e. land sparing - Paul & Knoke, 2015) or integrative land-use (i.e. land sharing - Kraus & Krumm, 2013) (Figure 1).

Large national parks and reserves that safeguard rare, endangered habitat types and species, decouple production of timber from other forest services (Bollmann & Braunisch, 2013; Muys et al., 2022). Since forests with high degrees of naturalness are rare in Europe (Sabatini et al., 2018), cessation of silvicultural practices in formerly managed forests is also employed in restoration efforts. However, the time necessary for habitat restoration and consequently biodiversity recovery through set-aside approaches is likely long (Vandekerkhove et al., 2019). Temperate European forests are dominated by long-lived tree species such as *Fagus, Quercus* or *Abies* and the recovery of old-growth elements and associated taxa may take more than 100 years (Vandekerkhove et al., 2005; Paillet et al., 2015; Larrieu et al., 2017, 2019). The success of restoration also varies on the starting conditions (e.g. the degree of naturalness, connectivity), the approach employed (passive or active), and the species colonisation ability (Herrault et al., 2016; Boeraeve et al., 2018; Sabatini et al., 2020). For example, the recolonization by species with high dispersal ability, such as birds or fungi, can be prompt, while the slow-colonising species such as vascular plants may take much longer (Vanderkhove et al., 2010; Jackson & Sax, 2010).

Retention approaches are part of multi-scale conservation and may be implemented in various silvicultural systems (Gustafsson et al., 2013). Integrative solutions with conservation measures may support and complement segregative approaches at multiple time- and spatial scales by improving conservation value and climate resilience of the highly fragmented European landscape (Larsen et al., 2022). Habitat heterogeneity achieved through many small patches was proven to increase biodiversity at landscape scale (Riva & Fahrig, 2023). Additionally, fine-scale conservation practices resulting in higher quality of the dispersal corridors can promote a better landscape connectivity, species movement and gene flow between larger reserves and parks (Kraus & Krumm, 2013; Vandekerkhove et al., 2013).

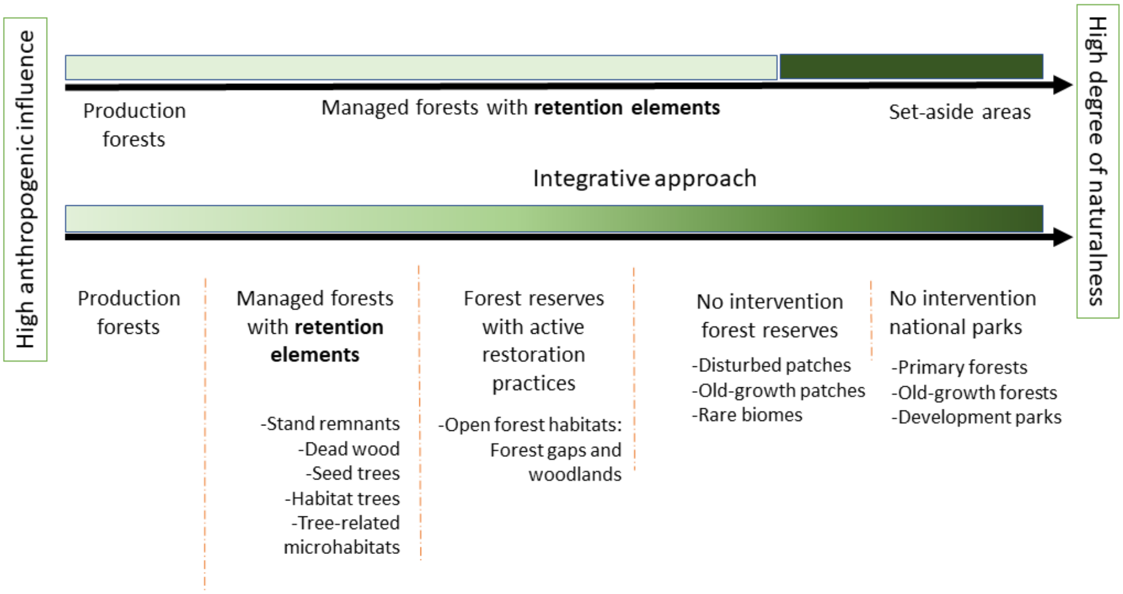


Figure 1. Retention elements within segregative and integrative forest management approaches. Conceptual design adapted from Bollmann & Braunisch, 2013; inspired by Muys et al., 2022.

Various biodiversity conservation approaches for forest management have been promoted, such as Continuous Cover Forestry, Natural Disturbances-Based Forest Management and Retention Forestry. Recently, the Closer-to-Nature concept was suggested as an “umbrella” term that recognises the benefits of those practices while providing an adapted direction to address biodiversity loss in European forests (Larsen et al., 2022). The first principle of Closer-to-Nature management emphasises the retention of deadwood, habitat trees and special habitats (Larsen et al., 2022). Special habitats, including disturbed patches, peatlands and rare biotopes around water bodies should be set aside to preserve their natural dynamics and associated taxa (Larsen et al., 2022; Muys et al., 2022). Although volumes of deadwood have improved over recent decades due to nature-based practices and increased disturbances (Pötzelsberger et al., 2021), the quality and functionality of the deadwood-related habitats still needs to be considered. For example, many specialised species rely on specific deadwood substrates, which remain scarce in European forests. For example, the endangered *Osmoderma eremita* hermit beetles prefer sun-exposed, decayed wood (Sebek et al., 2012), a limited type of substrate under present forest conditions. Similarly, while recently habitat trees have gained considerable attention as crucial elements of forest biodiversity conservation, an evidence-base considering their functionality for an effective selection has yet to be produced (Gustafsson et al., 2020; Martin et al., 2022; Asbeck et al., 2021).

I.3. Habitat tree retention in European forests

The conservation of habitat trees, which are large, typically old, living or dead standing trees, is of critical importance for the survival of many endangered and specialist forest species (Bütler et al., 2013). These trees serve as "life boats" and provide essential structures known as tree-related microhabitats (TreMs) that are vital for foraging, breeding, or nesting of forest organisms (Bütler et al., 2013; Larrieu et al., 2018; Gustafsson et al., 2020). The concept of habitat tree retention in multiple-use forests was derived from retention forestry, which originated in North America approximately 35 years ago. Retention forestry aims to address the limitations of clearfelling systems in sustaining forest species communities by maintaining structural elements during harvesting (Franklin et al., 1997; Rosenvald & Lõhmus, 2008; Gustafsson et al., 2012; Fedrowitz et al., 2014; Martínez Pastur et al., 2020). Biological legacies, i.e. structures and organisms that remain on site after natural disturbances, such as intact forest patches, living trees, standing and downed deadwood, are integral components of retention forestry and ensure habitat continuity in even-aged rotation forests (Franklin et al., 2002; Gustafsson et al., 2012).

In central Europe, the challenges associated with biodiversity conservation in continuous-cover forest management differ from those in clearfelling systems. Commonly, multiple-use forests exhibit complex structures with multiple layers, uneven-age distributions, and diverse tree species (Gustafsson et al., 2020). Although the stand canopy cover remains after harvesting, the lack of temporal and spatial connectivity of old-growth habitats poses a threat to associated forest-dwelling species (Gustafsson et al., 2020). Therefore, the deliberate retention of habitat trees and deadwood has become a recent management focus that complements existing conservation efforts and maintains populations of protected forest species (Bauhus et al., 2013). However, the availability of habitat trees is a concern for forest biodiversity conservation, since the occurrence of "giant", "ancient" or "veteran" trees in managed forests is limited (Larrieu & Cabanettes, 2012; Gustafsson et al., 2012). For instance, the density of habitat tree candidates, large individuals with diameter at breast height (DBH) over 70 cm, varied between 66 to 120 per 100 ha in national and regional forest inventories (Germany: 66 per 100ha; Belgium: 65 per 100 ha; Switzerland: 120 per 100 ha, Vandekerkhove et al., 2018). Traditionally, potential habitat trees would have been removed during thinning and stand improvement practices. Injured, weakened, malformed trees with high ecological value are often considered non-profitable and thus have been removed in early growth stages (Puettmann et al., 2009). While deadwood retention is rather straightforward, selecting living habitat trees may be difficult for practitioners, due to their low occurrence and the novelty of the practice in multiple-use forest management.

The use of TreMs in habitat tree selection is increasingly promoted in current retention forestry schemes in Central Europe (Asbeck et al., 2021). For example, in the *Old and dead wood* concept in Baden-Württemberg, Germany, practitioners are encouraged to retain large trees with bizarre forms and with presence of woodpecker cavities, large stem injuries, fruiting bodies of perennial fungi or broken forks (Asbeck et al., 2021; ForstBW, 2016).

However, the implementation of TreM surveys in practical forest management concepts and habitat tree selection is still developing and may not correspond yet to expert knowledge (Kraus et al., 2016; Larrieu et al., 2018). Therefore, conducting research that examines the spatial and temporal dynamics of habitat trees in providing diverse TreMs for forest-dwelling species may contribute significantly to informed decision-making in habitat tree selection.

I.4. Tree-related surveys – tools in assessing, promoting and improving forest biodiversity

TreMs are defined as distinct structures on living or dead standing trees, that provide essential substrates and resources for species communities during their life cycle to develop, feed, shelter or breed (Larrieu et al., 2018). TreM surveys were promoted as practical tools to assess and enhance forest biodiversity in European and North American forests (Asbeck et al., 2021; Martin et al., 2022; Larrieu et al., 2022). Harmonised definitions and field methodologies have been developed by a joint scientific effort to facilitate knowledge accessibility, generalisability and standardised research (Kraus et al., 2016; Larrieu et al., 2018). Current classifications distinguish seven forms with fifteen groups of TreMs, as follows:

- Cavities: woodpecker breeding cavities, rot-holes, concavities, insect galleries, and bore holes;
- Tree injuries and exposed wood: Exposed sapwood and/or exposed heartwood;
- Crown deadwood in different forms;
- Excrescences: twig tangles (witches broom), cankers, and burrs;
- Fruiting bodies of saproxylic fungi and slime moulds: perennial and ephemeral fungi fruiting bodies;
- Epiphytic, epixylic, and parasitic structures: epiphytic crypto- and phanerogams, nests of vertebrates and invertebrates, micro-soil (i.e. resulting from decay of lichens, mosses or leaf litter in either thick, old bark, or on horizontal limbs and forks for instance);
- Fresh exudates: sap run and heavy resinosis.

TreMs are considered to be valuable surrogate indicators of forest biodiversity due to their association with diverse species communities and their importance for the survival of endangered organisms (Larrieu et al., 2018, Asbeck et al., 2021). For example, certain TreMs, such as rot-holes and cavities, support rich communities of birds, rodents, bats, carnivores and invertebrates (Gouix & Brustel, 2012; Bunnell et al. 2013), while water-filled holes and tree hollows are vital in supporting specialist or low-diversity species, adapted to these TreMs (Kitching, 1917; Sebek et al., 2012) (Figure 2).

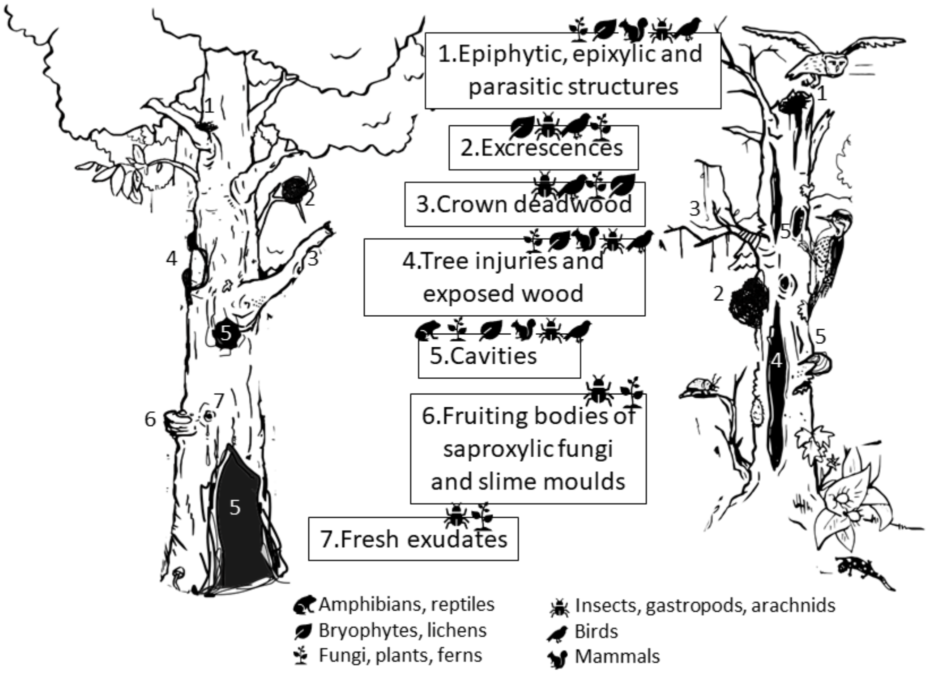


Figure 2. Tree-related microhabitats and associated taxa on living and dead habitat tree. Inspired and adapted from Martin et al., 2022; Storch et al., 2020.

The use of TreM monitoring offers multiple benefits in the context of assessing and restoring forest biodiversity (Gosselin & Larrieu, 2020; Zeller et al., 2022). There is also a strong practical advantage of using TreM surveys as user-friendly catalogues and identification guides are widely available (Larrieu et al., 2018; Joa et al., 2020). Thus, TreM surveys may be used to select and monitor the effectiveness of habitat tree retention in the medium to long term (Asbeck et al., 2021).

I.5. Drivers of TreM abundance and richness

The presence, abundance and richness of TreMs are influenced by a combination of environmental factors, stand conditions, and tree attributes (Michel & Winter 2009; Vuidot et al., 2011; Paillet et al., 2017; Kaufmann et al. 2018; Asbeck et al., 2019) (Figure 3). For instance, trees in unmanaged forests with high naturalness and structural complexity tend to exhibit higher TreM abundance and richness compared to managed stands (Larrieu et al., 2014a, b; Winter et al., 2015; Asbeck et al., 2019).

At the tree level, the size, vitality status (living or dead) and species are important factors influencing the occurrence of TreMs. Commonly, large, dead, broadleaved trees tend to bear a higher number and diversity of TreMs compared to smaller, living conifers (literature review by Asbeck et al., 2021). Only trees of exceptional dimensions may have all groups of TreMs (Larrieu et al., 2014). These patterns can be attributed to various factors such as the properties of the wood, crown structure, position in the canopy, and resistance to injuries and decay (Asbeck et al., 2019; 2021; Larrieu et al., 2018, 2022). The positive effect of large tree dimension relates to a larger surface area, advanced tree age and senescence, which can lead to the accumulation and persistence of TreMs over time (Puverel et al., 2019; Kõrkjas et al., 2021; Ranius et al., 2009; Kozak et al., 2023). Old individuals are likely to experience wood breakage and decay as their resistance to injuries and capacity to heal decreases with age (Larrieu et al., 2022). That allows the formation of multiple TreMs. At stand and site level, factors such as management, forest type, altitude have a significant impact on TreM occurrence and composition, with trees in mixed or primary forests supporting more diverse TreM assemblages than those in managed coniferous stands (Asbeck et al., 2021a, b).

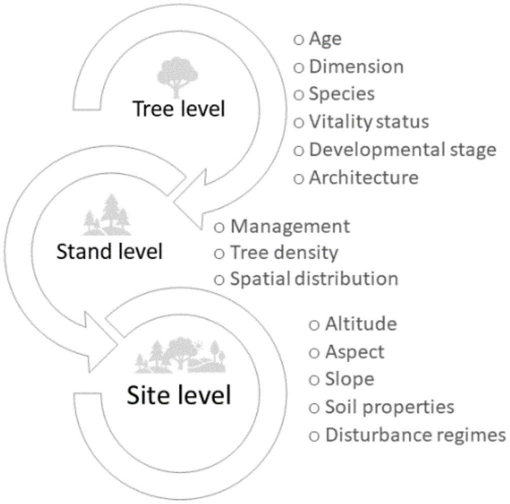


Figure 3. Drivers of tree-related microhabitat occurrence at different scales. Inspired by Asbeck et al., 2021; Martin et al., 2022; Larrieu et al. 2022.

Despite the clear differences in TreMs among trees of different status, species and senescence, the complementarity of habitat provisioning among trees of the same stand has not been studied. In many cases, selection of habitat trees has focused on individual characteristics such as size, status, species, or presence of a certain TreM (for example: Read 2000 in Britain; Land for Wildlife Queensland Note (2016) in Australia; Bütler et al., 2021 in Switzerland). Further, the temporal dynamics of habitat trees and their microhabitats once retained in managed temperate forests has not been studied or documented in Europe.

I.6. Temporal development of habitat trees and their microhabitats

Forest practitioners retain as habitat trees those trees that are large and have a high conservation value in order to provide continuous substrate resources in the long term. However, increasing disturbances and subsequent tree mortality expected in European forests will likely have an impact on habitat trees (Samaniego et al., 2018; Senf et al., 2020), as large trees are facing a global decline particularly due to drought and insect outbreaks (Vuidot et al., 2011; Winter et al., 2015; Bennett et al., 2015; Lindenmayer et al., 2012; Lindenmayer & Laurance, 2017). Increased heights and exposed crowns, which can result from retaining trees while removing their surrounding neighbours, enhance water-stress during drought events (Stovall et al., 2019; Grote et al., 2016). Under those conditions, tall habitat trees are also often vulnerable to insect attacks, such as bark beetles (Pfeifer et al., 2011). Additionally, the occurrence of certain TreMs that initiate wood decay such as injuries and wood exposure can further impact the vitality of habitat trees and increase mortality risks (Hunt & Etheridge, 1995).

A change in TreM composition will inevitable occur after tree death, which puts the associated structures and organisms linked to the living tree at risk. To address this, it is crucial to detect early warning signals of stress and mortality in habitat trees. This can be achieved by examining their temporal growth patterns (Bigler & Bugmann, 2004; Cailleret et al., 2016; Wunder et al., 2008). Dendro-ecological information obtained from tree-ring data, in combination with climate data and forest inventories, may be used to model and predict tree growth and mortality (Evans et al., 2017; Heilman et al., 2022). Growth models will allow selection of habitat trees with high longevity in stands or help estimate the time when new habitat trees should be selected to maintain those TreMs associated with living trees within the stand. Furthermore, understanding how TreM occurrence and composition at tree and stand-levels relate to tree mortality will inform other appropriate decisions regarding removal of trees for phytosanitary purposes.

Time series describing the development of TreMs on habitat trees are lacking. The persistence of only a few TreMs, such as woodpecker cavities, tree hollows or wounds (which decrease timber value), have been studied in the past (Edworthy et al., 2012; Lindemayer & Wood, 2010; Wesolowski et al., 2011, 2012; Tavankar 2017, 2022). However, there are no comprehensive analyses of temporal TreM dynamics based on longitudinal data (Courbaud et al., 2017, 2021). At the tree level, TreM development is likely not linear over time and differs greatly among tree species and TreM groups (Paillet et al., 2019). While some TreMs are transitory features on trees (e.g. bark pockets or saprotrophic agarics), others may persist for decades or centuries (e.g. rot-holes) (Larrieu et al., 2022). The formation and persistence of TreMs and the drivers involved are likely influenced by both tree- or stand-specific features. For example, TreMs might persist longer on slow-growing hardwoods with low rates of wood decay and breakage than in most conifers and fast-growing tree species (Cornwell et al., 2009; Smith et al., 2015; Kahl et al., 2017). On fast-growing species, TreMs usually form rapidly and likely, at high rates (Kõrkjas et al., 2021). The variability in TreM dynamics is further shaped by the rate at which events related to TreMs, occur. For example, tree senescence accompanied by the capacity of a tree to compartmentalize wounds and wood decay decreases with tree age (Smith et al., 2015). Other events might occur regularly (e.g. silvicultural operations) or occasionally (e.g. natural disturbances). Data describing the temporal development of both habitat trees and their TreMs are needed to provide an evidence-base for habitat tree selection that facilitates continuous habitat in the long term.

I.7. Provision of diverse habitats in the long term

Existing forest management approaches designed to promote biodiversity may not be suited to future climatic conditions (Augustynczik et al., 2019, 2020; Larsen et al., 2022). Forest management must secure a continuous and diverse habitat provision in the long term (Larsen et al., 2022). If this is approached through the cessation of management, it is important to estimate the time required to restore habitats for forest-dwelling species (Vandekerkhove, 2019). In retention practices that focus on habitat trees, it is pivotal to establish an evidence-base that can optimise the supply of TreMs, while considering the vulnerability of habitat trees to future increased environmental stress and mortality rates. Different trees, according to traits such as species, status, and senescence class, may support distinct TreM assemblages and respond differently to environmental and management changes. This calls for a dynamic management approach that also considers the effect of time on habitat trees and their associated TreMs. Understanding how habitat trees and their TreMs complement each other in terms of functionality will enhance and diversify current concepts of adaptive management in European multiple-use forests.

I.8. Study focus and research objectives

The practical objective of this thesis was to offer new directions for effective retention of valuable habitat tree in the multiple-use forests. This approach takes into account the dynamic nature of habitat provision over time. Previous studies have demonstrated that various tree attributes, such as dimension, species, status, and senescence stage, influence the occurrence of TreMs on trees. However, these patterns have typically been studied at a single point in time and often do not consider the interaction between different tree attributes. Given the anticipated increase in environmental stress in the future, it is crucial to recognise that the populations of both living habitat trees and their TreMs will undergo significant changes.

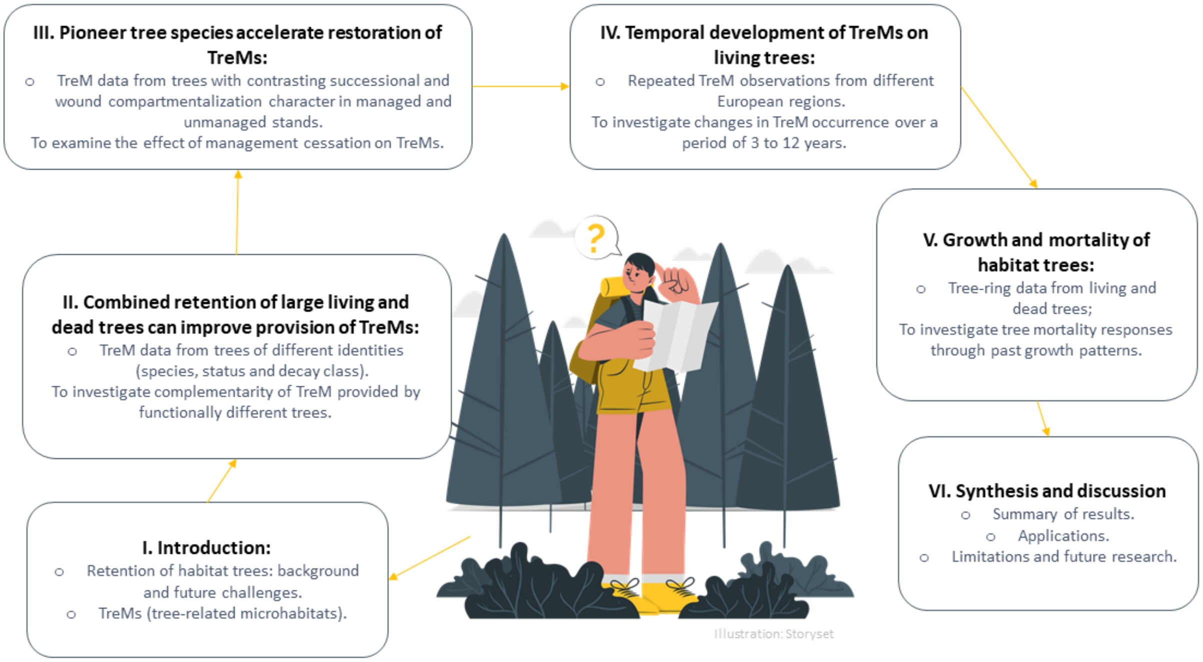
The aim of the study was to examine the differences and synergies among functionally different habitat trees, including both living and dead trees, as well as those with contrasting attributes and life-history traits. By investigating the persistence and loss of habitat trees and their TreMs, this research sought to provide empirical evidence that can inform the management and conservation of continuous and diverse habitat provisioning in forests.

The specific thesis objectives were:

- To investigate differences in TreM composition of living and dead habitat trees and to assess their complementarity in providing TreMs at the forest stand-level. **Chapter II**.
- To compare the temporal development of TreMs on coexisting trees with contrasting life-history traits, in particular their successional character and resistance to decay and injuries, as influenced by management cessation. **Chapter III**.
- To assess the temporal dynamics of TreMs on living habitat trees from temperate European forests and examine the influence of tree dimension and species. **Chapter IV**.
- To quantify the mortality rates of habitat trees and detect early warning signs of drought-triggered tree mortality in the Black Forest region. In addition, this chapter aims to identify links between overall growth trends and vitality of habitat trees, as well as the TreMs found on them. **Chapter V**.

I.9. Thesis outline

The thesis is structured in six chapters: a general introduction (**Chapter I**), four chapters with the main results that have been prepared and formatted for publication in peer reviewed journals (**Chapter II – V)** and a final discussion and synthesis (**Chapter VI**), as depicted in **Figure 4**.



I. Introduction:
- Retention of habitat trees: background and future challenges.
- TreMs (tree-related microhabitats).

II. Combined retention of large living and dead trees can improve provision of TreMs:
- TreM data from trees of different identities (species, status and decay class).

To investigate complementarity of TreM provided by functionally different trees.

III. Pioneer tree species accelerate restoration of TreMs:
- TreM data from trees with contrasting successional and wound compartmentalization character in managed and unmanaged stands.

To examine the effect of management cessation on TreMs.

IV. Temporal development of TreMs on living trees:
- Repeated TreM observations from different European regions.

To investigate changes in TreM occurrence over a period of 3 to 12 years.

V. Growth and mortality of habitat trees:
- Tree-ring data from living and dead trees;

To investigate tree mortality responses through past growth patterns.

VI. Synthesis and discussion
- Summary of results.
- Applications.
- Limitations and future research.

Illustration: Storyset

Figure 4. Thesis graphical outline

I.10. Study design and research framework

This subsection introduces the general research framework of the study. It outlines the study areas, overall approach and employed methodology (Figure 5). More detailed descriptions of the data collection and analysis specific to each chapter can be found in their respective sections.

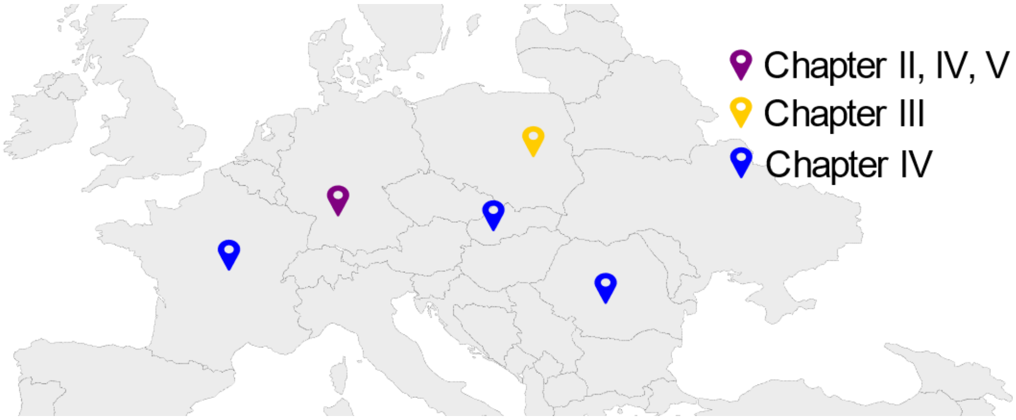


Figure 5. Location of the study plots in Europe.
Chapter II, IV, V: Germany; Chapter III: Poland; Chapter IV: France, Germany, Slovakia and Romania

I.10.1. A reference system: The Black Forest region

To ensure the applicability of the results to retention practices, a significant part of the research was conducted in a “real-world study system” that is relevant to temperate European multiple-use forests. The research area was defined within the framework of the interdisciplinary project “Conservation of forest biodiversity in multiple-use landscapes”, which specifically focused on the effects of retention practices for biodiversity conservation (Storch et al., 2020).

Chapter II and V were carried out in in the state-owned forests from the Black Forest region of south-west Germany (Latitude: 47.6°–48.3°N, Longitude: 7.7°–8.6°E, WGS 84; Altitudinal range between 500 and 1400 m.a.s.l.). This area may be considered a typical Central European mountain forest type that is managed under a close-to-nature paradigm, avoiding clearcutting, intensive soil preparation, use of fertilizers and herbicides (Bauhus et al., 2013; Larsen et al., 2022). Data were collected from 133 one-hectare plots within the study area. The dominant tree species were Norway spruce (*Picea abies* (L.) Karst), European beech (*Fagus sylvatica* L.) and Silver fir (*Abies alba* Mill.), in order of abundance. The selection of the plots was based on a gradient of forest cover in the surrounding 25 km^2, ranging from 50% to over 75% forest coverage as estimated by GIS raster data. The structural complexity of the plots was indicated by the occurrence of standing dead trees per plot, with an average of 34 per hectare, varying between 0 and 394. The majority of the growing stock consisted of healthy, living trees, with few trees of low vitality or diseased present.

I.10.2. A comparative study: Białowieża Forest

To be able to examine whether and how the cessation of forest management, which is increasingly adopted as an approach to biodiversity conservation, supports the restoration of TreMs, a comparative case-study was conducted in Białowieża Forest, Poland. The objective of **Chapter III** was to examine the temporal development of TreMs on coexisting trees with contrasting life-history traits, in relation to changes in forest management. TreM data were collected from four secondary forest stands located in the Władysław Szafer’s Forest Landscape Reserve (established in 1969) and four adjacent comparable stands with the same origin (clearfelling in 1920s), but under active management in the last 50 years. Most areas naturally regenerated with fast-growing, shade-intolerant tree species. Over time, shade-tolerant tree species appeared, dominating the regeneration up to the present. Such second-growth forest stands provided a unique opportunity to investigate the structural and functional differences among co-existing tree species with varying life history-traits.

I.10.3. Scaling-up: A joint study with TreM datasets from more European sites

Chapter IV aimed to capture the temporal dynamics of TreMs on living trees, by utilising an extensive, harmonised TreM dataset obtained from three European research and natural area managers groups. Data were collected in France, Germany, Slovakia and Romania and comprised repeated TreM observations on 11,569 living trees belonging to 30 species. The DBH ranged from 6 to 129 cm for broadleaved trees, and 7 to 142 cm for conifers. The trees were distributed across a wide range of altitudes, varying from 119 to 2128 m.a.s.l. for broadleaved, and 119 to 1931 m.a.s.l. for coniferous trees. European beech (*Fagus sylvatica*), Norway spruce (*Picea abies*) and Silver fir (*Abies alba*) were the main species. Data spanned from 2006 to 2021, with intervals between inventories ranging from 3 to 12 years.

Photo: Nolan Rappa

European beech and Norway spruce in the Black Forest.

II. Combined retention of large living and dead trees can improve provision of tree-related microhabitats in Central European montane forests.

Spînu A.P., Asbeck T. and Bauhus J. (2022).
Combined retention of large living and dead trees can improve provision of tree-related microhabitats in Central European montane forests. *European Journal of Forest Research*, 141, 1105–1120, https://doi.org/10.1007/s10342-022-01493-1. Published.

https://doi.org/10.1007/s10342-022-01493-1

Abstract

Retention of habitat trees is a common biodiversity conservation practice in continuous cover forests of temperate Europe. Commonly, living habitat trees are selected on the basis of their tree-related microhabitats (TreMs) such as cavities or crown deadwood. Owing to the increasing frequency and intensity of climate change related disturbances, habitat trees in particular are expected to experience increased mortality rates. This may impact the long-term provisioning of TreMs.

Here, we compared the TreM occurrence on living and dead trees to investigate whether dead trees support more and other TreMs than living trees. We also hypothesized that a combination of living and dead trees results in the most diverse stand-level TreM composition.

We surveyed the TreM composition of living and dead habitat trees in 133 one-hectare plots in the Black Forest region managed according to a continuous cover approach. We fitted generalized linear mixed models to identify the main predictors of TreM occurrence to predict their abundance and richness. Tree identity (as a combination of species and vitality status) and diameter were the main drivers of TreM abundance and richness, which were highest on dead *Abies alba*. Even though dead *A. alba* and *Picea abies* supported TreM numbers similar to those provided by large living trees, their TreM composition was significantly different. This suggests that dead trees cannot substitute the habitat functions of living habitat trees, but they can complement them to increase the overall stand-level TreM diversity, in particular through decayed, large snags.

Keywords

Biodiversity conservation, retention forestry, habitat tree, wildlife habitat, integrative forest management

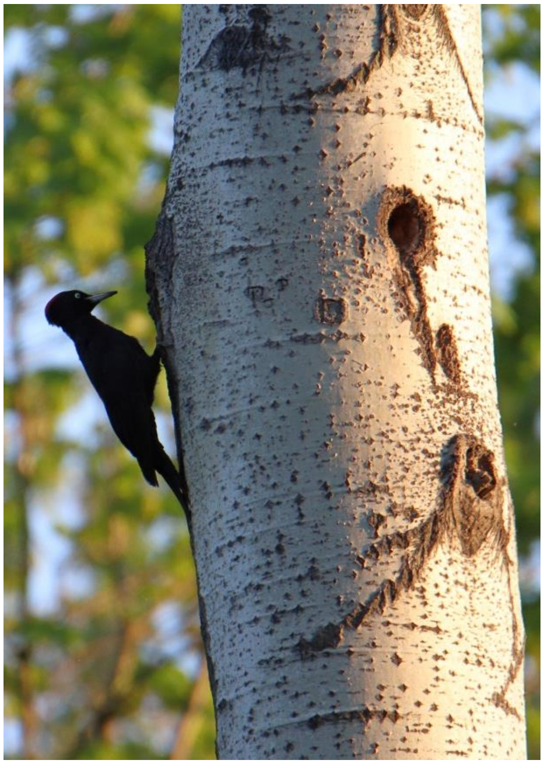


Photo: João Pereira

Black Woodpecker on an aspen tree.

III. Pioneer tree species accelerate restoration of tree-related microhabitats in 50-year old reserves of Białowieża Forest, Poland.

Spînu A.P., Mysiak W., Bauhus J., Bielak K. and Niklasson M. (2023). Pioneer tree species accelerate restoration of tree-related microhabitats in 50-year old reserves of Białowieża Forest, Poland. *Ecology and Evolution*. Published.

https://doi.org/10.1002/ece3.10238

Abstract

Retention of structural elements such as deadwood and habitat trees at the level of forest stands has been promoted to integrate biodiversity conservation into multiple-use forest management. The conservation value of habitat trees is largely determined by the presence, richness and abundance of tree-related microhabitats (TreMs). Since TreMs are often lacking in intensively managed forests, an important question of forest conservation is how the abundance and richness of TreMs may be effectively restored. Here we investigated whether the strict protection of forest through cessation of timber harvesting influenced TreM occurrence at tree- and stand level. For that purpose, we compared four managed and four set-aside stands (0.25 ha each) in the Białowieża Forest, with identical origin following clear-cuts approximately 100 years ago. We found that the abundance and richness of TreMs on living trees were not significantly different between stands that were either conventionally managed or where active forest management ceased 52 years ago. Yet, our analysis of TreMs on tree species with contrasting life-history traits revealed that short-lived, fast-growing species (pioneers) developed TreMs quicker than longer-lived, slower-growing species. Hence, tree species such as *Populus* or *Betula*, which supply abundant and diverse TreMs, can play an important role in accelerating habitat restoration.

Keywords

Biodiversity conservation, biodiversity indicator, closer-to-nature forest management, forest restoration, pioneer species, compartmentalization of decay.

Photo: Andreea Spînu

A short-lived microhabitat on decaying wood.

IV. Temporal development of microhabitats on living habitat trees in temperate European forests.

Spînu A.P., Nicolaie M. A., Asbeck T., Kozak D., Paillet Y., Cateau E., Mikoláš M., Svoboda M. and Bauhus J. (2023)
Temporal development of microhabitats on living habitat trees in temperate European forests. *Ecosystems.* Under review.

Abstract

Tree-related microhabitats (TreMs) have been promoted as indicators of forest biodiversity and to guide conservation practices. Ensuring a rich and diverse supply of TreMs in the long term is crucial for the viability of forest-dwelling species communities, yet challenging in the absence of information regarding their dynamics. Based on an original dataset describing TreMs borne by 11,569 trees, we provide first insights into the highly dynamic temporal development of TreMs on living habitat trees in temperate European forests. To identify drivers of change in TreM occurence and richness over a period of 3 to 12 years, we estimated the rates of TreM persistence and loss events at tree-level using survival analysis methods: **persistence** was characterised by consistency and increment events (when TreM numbers were maintained or increased) and **loss** was defined as a reduction in TreM numbers or their disappearance. Stratified Cox proportional hazards models were fitted for different TreM groups.

Our study describes a highly dynamic TreM development on living habitat trees, particularly on large trees. While TreM richness can persist over a 12-year period, specific TreMs are prone to disappearing, irrespective of tree species or TreM group. TreMs such as *crown deadwood, epiphytes* or *woodpecker cavities* are prone to be lost in the long term. However, large trees were more likely to maintain a stable overall TreM richness. Increasing diameters resulted in high persistence rates in seven TreM groups and concomitantly low loss rates in four of them.

Synthesis and applications. While TreM richness was relatively constant over time, particularly on large trees, high levels of loss processes were observed in most TreM groups. Selecting habitat trees based on TreMs should consider the likelihood of TreMs being lost over time, to ensure long-term provisioning of habitats for the TreM associated species.

Keywords

Wildlife habitat conservation, survival analysis with competing risks, integrative forest management, tree-related microhabitats (TreM), tree cavity.

Introduction

The retention of deadwood and habitat trees during silvicultural operations mitigates biodiversity loss in managed forests (Gustafsson et al., 2012, 2020; Martínez Pastur et al., 2020, Muys et al., 2022). By recognising how biological legacies (i.e. organisms, organic materials, and patterns persisting after natural disturbances) can provide a life-boating function for their associated species, retention of habitat trees (large, old, living or dead trees with microhabitats, Bütler et al. 2013) aims to ensure both spatial and temporal habitat continuity that cannot be provided solely by deadwood (Franklin et al., 2000, 2012). Tree-related microhabitats (TreMs) are increasingly used to identify and select high-quality habitat trees and are considered useful indicators of biodiversity in European and North American forests (Asbeck et al., 2021; Martin et al., 2022; Larrieu et al., 2022; Spînu et al., 2021). TreMs are defined as "distinct, well-delineated structures occurring on living or standing dead trees, that constitute a particular and essential substrate or life site for species during at least a part of their life cycle to develop, feed, shelter or breed" (Larrieu et al., 2018). Some TreMs support forest-dwelling birds, rodents, bats, carnivores and invertebrates (e.g. rot-holes: Gouix & Brustel, 2012; cavities: Bunnell et al., 2013; Remm & Lõhmus, 2011), others are critical for the survival of specialist species (e.g. dendrotelmata for tree-hole mosquitos: Kitching, 1917; buttress cavities for salamander species: Basile et al., 2017; tree hollows for the click and hermit beetles: Ranius et al., 2002; Svensson et al. 2004). Based on morphological characteristics and associated taxa, TreMs have been comprehensively delineated in 15 groups such as exposed sap- and heartwood or concavities and 47 types as stem and limb breakage, dendrotelms (Larrieu et al., 2018, Appendix 1). Tree dimension, vitality status, species, age and stand management, environmental conditions and forest type are all important drivers of TreM occurrence and diversity (Michel & Winter, 2009; Vuidot et al., 2011; Winter et al., 2015; Paillet et al., 2017; Asbeck et al., 2019; Larrieu et al., 2014; Kozak et al., 2023). Large, old broadleaved and/or dead standing trees in temperate forest support the richest and most abundant TreM assemblages.

TreM inventories are now included in biodiversity surveys (e.g. the Index of Biodiversity Potential in France: Larrieu & Gonin, 2008; Gosselin & Larrieu, 2020; Germany: Zeller et al., 2022; Swizerland: Tinner et al. 2012), research projects (Martin et al., 2022), and educational exercises (Cosyns et al., 2020; Joa et al., 2020) and are promoted in integrative forest management guidelines. Yet, we have a limited understanding of the dynamics of TreMs at multiple temporal scales and the long-term implications of habitat tree selections based on TreMs.

Considering how the persistence and loss of TreMs may affect habitat provisioning is crucial. Some TreMs are only a transitory feature of trees and thus represent ephemeral resource patches (Finn, 2001) and others can persist for decades or even centuries. For example, bark pockets last until the piece of bark providing shelter drops off, whereas dead branches might stay in the crown until they have sufficiently decayed to brake off (Basham, 1991). Likewise, large rot-holes may persist as long as the habitat tree (Larrieu et al., 2022), while the life of some living TreMs, such as fruiting bodies of saprotrophic agarics is no longer than a few days. The events affecting TreM dynamics can be tree- or stand-specific and can happen continuously (e.g. tree senescence accompanied the tree compartmentalisation capacity, to resist wounds and limit infections), regularly (e.g. silvicultural operations) or occasionally (e.g. natural disturbances, biotic agents like woodpeckers). While wood decay and breakage are processes occurring on all trees as they age, these events can happen at different rates as influenced by tree- and stand level attributes (Basham, 1991; Mäkinen, 2002; Schütz et al., 2006; Kahl et al., 2017; Zemlerová et al., 2023). For instance, insect galleries might occur often during the lifetime of a tree and can evolve into foraging cavities that subsequent with decay development, might become rot-holes. TreMs such as exposed sap- and heartwood cannot form multiple times on a tree without causing its death (e.g. a dead tree top or broken main fork). Generally, TreMs might persist longer on slow-growing hardwoods with rates of decay and breakage smaller in comparison to most conifers and fast-growing tree species (Cornwell et al., 2009; Smith, 2015; Kahl et al., 2017). On the latter, TreMs usually form quicker and probably at high rates (Kõrkjas et al., 2021). Additionally, depending on the size of the TreM and the tree capacity to inhibit decaying fungi and to form new wood sealing scars associated with TreMs, some tree species can fully overgrow TreMs after a few years or decades (Shigo, 1986; Stoffel & Perret, 2006; Smith, 2015). Given the variability in TreM dynamics, ensuring a constant, rich and diverse supply of TreMs to aid the populations of taxa dependent on them can be challenging for forest practitioners (Courbaud et al., 2021; Larrieu et al., 2022).

Although considerable research has focused on identifying the main drivers of TreM occurrence, limited knowledge exists regarding their temporal TreM dynamics. While some studies have investigated the persistence of tree cavities, hollows or wounds affecting timber quality (Edworthy et al., 2012; Lindenmayer & Wood, 2010; Wesołowski et al., 2011, 2012; Tavankar 2017, 2022), no comprehensive longitudinal studies on the temporal dynamics of TreMs exist (Courbaud et al., 2017, 2021). This gap may be attributed to the scarcity of repeated inventories assessing TreMs on individual trees. Long-term data can help to understand the development of TreM over time, which can further inform an effective selection of habitat trees that ensures continuous provision of resources.

Substantial progress has been made in understanding temporal dynamics of TreMs through a method developed by Courbaud et al. (2017). TreM formation rates were estimated based on TreM presence on living trees of different diameters. Studies using this adaptation of the survival and reliability theory, where increasing diameters in different trees are thought to represent tree development over time, indicated that

TreMs accumulate during tree dimensional growth (Courbaud et al., 2017, 2022; Jahed et al., 2020). However, the relationship between diameter, age and TreM occurrence may not be as direct and linear, as assumed, as both variables were shown to have distinct effects on TreM dynamics (Kozak et al., 2023). This approach also assumes that TreMs do not disappear from trees and tree mortality does not occur. To overcome the limitations of using cross-sectional designs in evaluation of time-dependent outcomes, it is crucial to complement them with studies based on repeated TreM observations (Lindenmayer et al., 2011; Courbaud et al., 2017; Asbeck et al., 2023).

In this study, we capitalised on the availability of a unique dataset with longitudinal TreM surveys from several regions in Europe. We initiated a comprehensive investigation into the temporal development of microhabitats on living habitat trees. Once formed on a living tree, a TreM can either persist or be lost over a certain time interval. To quantify these two main trends, we assessed changes in total TreM richness and for the occurrence of each TreM group over time. The change was defined as one of the following four event types, which are exclusive (do not happen at the same time on one individual tree):

(1) TreM increase (an increase in TreMs), (2) TreM consistency (no change occurs over time): **TreM persistence;**

(3) TreM reduction (a decrease in TreMs), (4) TreM disappearance (the final number of TreMs is zero): **TreM loss.**

Our specific hypotheses were:

a. **The processes of increase and consistency outweigh reduction and disappearance events of TreMs**, as TreMs are expected to accumulate on trees over time.
b. **Temporal TreM dynamics (persistence and loss rates) differ among tree species and across TreM groups.** Due to their morphology and low decay compartmentalization capacity in many European broadleaved species, we expect their TreM dynamics to be higher than in conifers (with both persistence and loss events occurring more frequently). Moreover, certain TreMs such as *exposed sapwood* and *crown deadwood* are probably short-lived and can decrease over time, while *rot-holes, exposed sap- and heartwood* are expected to persist over repeated inventories.
c. **Temporal dynamics of TreMs are influenced by presence of certain TreMs at the time of the first survey,** such as *fresh exudates*, *insect galleries*.
d. **Tree size is a significant driver of TreM development and rates of TreM persistence as well as TreM loss are highest on large trees.**

Material and methods

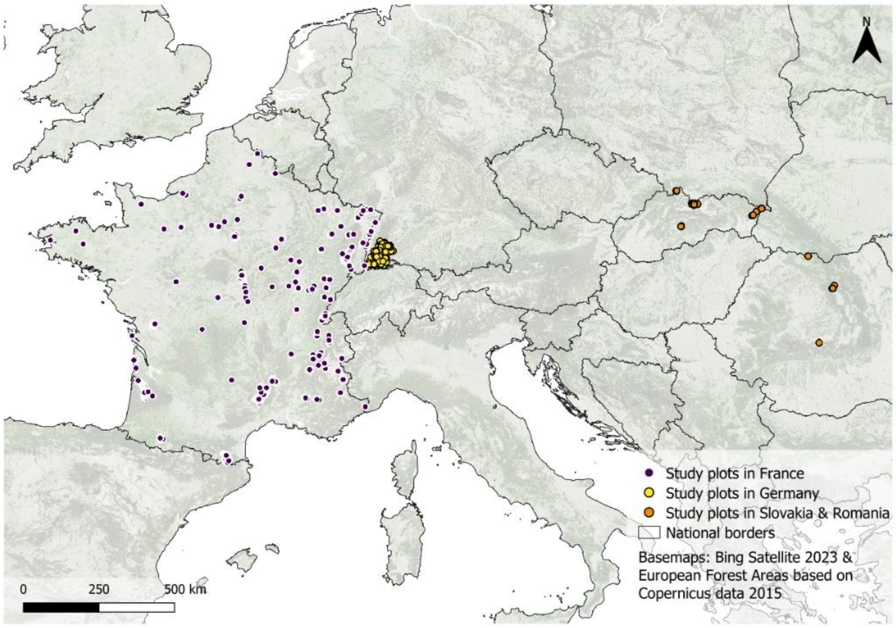


Figure 1. Location of the study areas.

Data origin and harmonization of TreM classifications for living trees

Our study focused on the temporal development of microhabitats on trees which were alive at the time of both surveys. We used the availability of datasets with repeated TreM surveys, comprising of TreM observations on 11,569 living trees from 30 species. These data were collected by three different European research and natural area managers groups. Each group used its own TreM description and field protocols (for examples, different size thresholds) and older inventories were carried out only at TreM group level. Despite this, we were able to harmonize the data at TreM-group level based on a common typology and included data at the level of TreM type if available (Larrieu et al., 2018). Specifics of the study areas, individual classifications and corresponding TreM groups were harmonised following a similar approach to Asbeck et al. (2021) and Courbaud et al. (2022) (details in Appendix 1). Owing to the small number of repeated observations in most TreM groups and of some tree species, we were able to carry out the analyses only at the level of tree species category (broadleaves - 57.6% and conifers - 42.4%), but not for individual tree species. Details on all tree species and overview of the distribution of TreM groups at tree level, for both surveys can be found in Appendix 2 & 3.

TreMs were inventoried between 2006 and 2021, with each tree being surveyed twice within that interval. If a tree was not alive anymore or not found at the second survey, it was excluded from the analysis. The time interval between the first and the second survey, later called survey period, ranges between 3 and 12 years (Table 1). The diameters (DBH) of habitat trees varied between 6 and 129 cm for broadleaves and 8 and 142 cm for conifers. The trees were located within a wide altitudinal range between 120 to 2018 m.a.s.l.. European beech (*Fagus sylvatica* (L.)), Norway spruce (*Picea abies* (L.)) and silver fir (*Abies alba* (Mill.)) were the main species, in this order of abundance. The main characteristics of TreM groups and corresponding living habitat trees are summarized in Table 2.

Table 1. Overview of timing of TreM inventories and the number of re-surveyed habitat trees (trees with at least one TreM).

	Number of habitat trees						
Year	2015	2016	2017	2018	2019	2020	2021
2006	220	289	568	320	0	0	0
2008	6072	0	0	0	0	0	0
2011	0	403	0	0	0	0	0
2015	0	0	0	71	256	1058	0
2016	0	0	0	0	1758	229	327

Description of the TreM data

The number of habitat trees, defined as trees exhibiting the presence of at least one TreM, was 4145. The TreM counts followed a right-skewed distribution in each TreM group with an overall shift in median values between surveys, specifically from 1 to 0. We calculated the richness of TreM types (47) and groups (15) for each tree and survey, as the total number of TreM types or groups present on a tree. To get a first impression of the data, alluvial plots were created to visualise the number of TreMs at each survey. Additionally, a random forest analysis was conducted to identify which TreM groups predicted the overall TreM richness at both surveys. The independent variables considered in the analysis included tree DBH, altitude and presence of TreM groups. For the first survey, the outcome variables were log-transformed to improve the fit, while log-transformation was not possible for the second survey due to presence of zero counts. We ran 1000 bootstrap samples and optimized the number of splits for each random forest on habitat trees, stratified by survey. This non-parametric approach allowed for the modelling of non-linear effects and complex interactions between predictors to perform accurate prediction without making prior assumptions about the data. We reported importance lists for variables, percentage of explained variance and prediction errors to assess the quality of predictions. Variables were ranked in terms of importance based on their impact in predicting the outcome. A variable was considered more important than another if its removal from the prediction yielded an error larger than obtained through the removal of the other variables. The percentage of explained variance reached 98.69% for richness of TreM types and 97.66% for TreM groups in the first survey, and 90.92% and 96.34% respectively in the second survey.

Table 2. Main characteristics of TreM groups and corresponding habitat trees.

TreM group	Total number of habitat trees	Broadleaved tree species			Coniferous tree species		
		Percentage of habitat trees (%)	DBH Mean±SD Min.-Max. (cm)	Altitude Mean±SD Min.-Max. (m.a.s.l.)	Percentage of habitat trees (%)	DBH Mean±SD Min.-Max. (cm)	Altitude Mean±SD Min.-Max. (m.a.s.l)
Woodpecker cavities	400	86.5	41.4±22 6.2-95.7	1169±429 120-2018	13.5	51.5±17 14.0-88.9	1255±318 130-1931
Exposed sap- and heartwood	530	81.7	39.1±25 6.6-127.3	1525±415 130-2018	18.3	43.0±20 8.0-82.0	1109±330 133-1868
Epiphytes	430	42.8	31.9±19 8.5-91.0	850±468 521-1358	57.2	49.8±18 8.0-137.0	883±419 521 - 1495
Crown deadwood	1062	45.9	40.1±24 6.0-123.0	854±360 547-1482	54.1	54.5±17 8.6-137.0	900±208 505-1399
Perennial fungi	847	68.5	40.6±26 6.0-128.0	935±313 132-1857	31.5	53.5±19 8.1-109.0	880±214 485-1857
Exposed sapwood only	1005	55.2	27.3±18 6.0-104.6	1003±297 512-1499	49.8	45.3±20 8.0-106.0	943±281 512-1431
Rot-holes	753	79.5	46.4±24 6.2-105.1	1015±203 129-1624	20.5	55.6±16 13.8-97.0	1006±285 505-1634
Concavities	369	39.6	51.4±25 7.5-128.0	897±168 535-1402	60.4	50.9±19 8.0-137.0	1176±319 546-1650
Fresh exudates	719	78.7	47.4±24 6.2-105.1	1015 ± 173 546-1634	21.3	55.9±17 13.8-97	976±283 505-1624
Twig tangles	552	89.3	56.7±21 7.0-127.3	1036±159 575-1624	10.7	59.3±15 19.2-92.6	1286±236 772-1613
Annual fungi	263	24.1	50.7±17 22.0-129	812±207 562-1386	75.9	58.4±16 27-111	895±180 505-1398
Burrs and cankers	2	0	-	-	100	52.13 39-60.0	1037 1003-1091
Insect galleries	87	29.88	48.7±20 22.0-128.0	764±170 903-170	70.11	56.4±14 33.0-92.0	903±170 546-1367
Nests	19	0	-	-	100	57±1 56.0-58.0	1122±17 1110-1135
Microsoils	192	28.1	48.4±19 21.0-128.0	774±166 535-1402	71.9	57.4±17 25.0-142.0	907±182 546-1368

Prediction and modelling of TreM dynamics

To analyse the dynamics of TreMs on habitat trees, we employed survival analysis methods at both the tree-level richness of TreMs, as well as the level of each of the fifteen TreM groups. The focus of our study was on habitat trees namely, trees that exhibited at the first survey at least one TreM (to model the joint presence of TreM groups by means of TreM richness) or a specific TreM group (to model at each TreM group level). We defined two main patterns of TreM development, consisting of mutually exclusive events than can be referred to as competing risks. **TreM persistence** encompassed events where the number of TreMs remained the same (consistency events) or increased over time (increment events). **TreM loss** represented events where the number of TreMs decreased (reduction events), potentially resulting in complete absence (disappearance events).

In our approach, we denote the time-to-event as the timing of occurrence of an event and the type represents one of the four development events (consistency, increment, reduction, disappearance). The outcome was the joint of time-to-event (denoted by T) and type of event (denoted by D) variables, further referred as (T, D). The independent variables were tree DBH, altitude and the TreM counts at first survey (jointly denoted by **Z** and referred as the covariate vector). Our aim was to model and estimate the type-specific cumulative incidence functions of (T,D):

$$F_j(t) = P(T \leq t, D = j),$$

Where P stands for probability and j stands for any event type out of the four events described above. The standard way of estimating is through the type-specific hazard rates:

$\lambda_j(t) = P(T = t, D = j | T \geq t)$, $\Lambda_j(t) = \sum_{u \leq t} \lambda_j(u)$.

We defined the survival function in the following way:

$$S(t) = P(T > t) = \exp\left(-\sum_j \Lambda_j(t)\right).$$

We fitted Cox proportional hazards models to each type-specific hazard, namely for a tree with covariate vector **Z** the type-j specific hazard was modelled as:

$\lambda_j(t|\boldsymbol{Z}) = \lambda_{j,0}(t)\exp(\beta_j \boldsymbol{Z})$,

where $\lambda_{j,0}(t)$ is the baseline type-specific hazard and the vector β_j represents the covariates effects on type-j hazard.

Models were not fitted for *burrs and cankers, insect galleries* and *nests* due to low number of observations (< 20). All four types of events were recorded only in two TreM groups: *crown deadwood* and *fresh exudates*. Other TreM groups exhibited no or a low number TreM reduction events. If the number of events was too low (< 20), the analysis was carried out at the level of the two main development patterns (TreM persistence and loss).

To overcome the issue of non-proportionality, we fitted stratified Cox proportional models at the hazard level. This was based on an exploratory analysis using the non-parametric Kaplan-Meier estimator, stratified by either tree categories or research sites. This approach implied that no effect was estimated for the stratifying variables, instead the difference between the Eastern and Western European samples was measured at the baseline hazard level by allowing the estimation of type-specific baseline hazards to mould to each stratum (Appendix 4). It is important to note that habitat trees were revisited at different intervals in the different regions and studies. *Twig tangles* and *fresh exudates* were not recorded in older surveys and thus their study interval was the shortest, of 3 years. The exact occurrence of the events on a tree may not have been recorded at the exact time of occurrence.

We conducted an additional random forest analysis to assess whether the change in TreM development related to parameters describing the living habitat trees at the first survey, such as DBH, altitude, and frequency of specific TreM groups. Similar to the methods used to describe the TreM data, we identified TreM groups that predicted certain changes in TreM richness. Change here was defined as the difference in TreM richness between the surveys. All analyses were performed in the RStudio software, version 4.2.0 (R Core team, 2021), by means of *randomForest* (Liaw & Wiener, 2002), *survival* (Therneau, 2023) and *ggplot2* (Wickham, 2016) packages.

Results

Data description

The top predictors for the richness of TreM groups at the first survey were *fresh exudates, microsoils, crown deadwood, concavities, exposed sap- and heartwood wood,* and *annual fungi,* in that order. At the second survey, the important predictors were *annual fungi, exposed sapwood only, crown deadwood, perennial fungi, epiphytes, exposed sap- and heartwood* and *twig tangles*. Some TreM groups remained significant predictors of richness over time (*crown deadwood, exposed sap heartwood, annual* and *perennial fungi*). Others, decreased in prediction significance (*microsoils, fresh exudates, concavities*) as replaced in rank by others groups, such as *exposed sapwood, epiphytes* (Appendix 5). This observation was in line with the impression yielded by alluvial plots, which showed that these top predictors were also the TreM groups with highest frequency of occurrence (Appendix 3). The differences in TreM occurrence between the surveys indicated a trend of loss for most TreM groups (Appendix 3).

The occurrence of events for different TreM groups varied in terms of intervals following the first survey. For TreMs such as *woodpecker cavities, exposed sap- and heartwood, epiphytes, crown deadwood,* and *perennial fungi*, the events were detected at intervals that varied from 3 to 12 years. The time interval decreased from 12 to 9 years for *exposed sapwood only, rot-holes* and *concavities*. The events in remaining TreM groups (*fresh exudates, twig tangles*) occurred between 3 and 5 years after the first survey (Table 3).

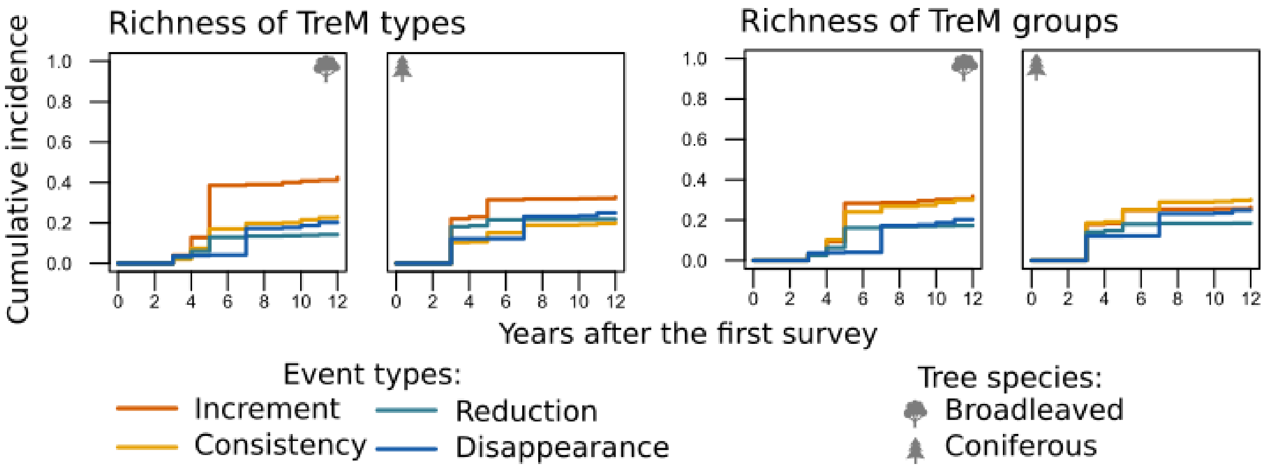


Figure 2. Cumulative incidence rates for all types of all events in the richness of TreMs at both type and group level, for each habitat tree since the first survey. Persistence (increment, consistency events) are marked in orange colour shades, while loss events (reduction, disappearance events) are represented by blue shades.

Changes in TreM richness at tree-level

Throughout the survey period, the processes of TreM persistence (increase and consistency events) and loss (reduction and disappearance event) reached a steady state at the tree level (Figure 2, Appendix 7). Richness of both TreM types and groups showed similar cumulative incidence rates for persistence and loss events, irrespective of tree species. Approximately 30% of the living habitat trees experienced increase events at the level of TreM type, as well as consistency or increase events at the TreM group level. Loss events accounted for approximately 40% of the overall events, while persistence represented 60%. Increment events in richness were more common for TreM types, while the distinction between event types was less pronounced for TreM groups (Figure 2). Among broadleaves, the difference in frequency between persistence and loss events was high, with up to a 20% difference in cumulative incidence by the end of the survey period, proportional to the TreM sample size.

Temporal changes at TreM group-level

Loss processes were the vast majority of events observed in all TreM groups, both on conifer and broadleaved habitat trees (Figure 3). Reduction and disappearance events exhibited the highest cumulative incidence rates throughout the survey period and showed the fastest increase in rates over time. On average, there was a cumulative incidence of over 70% in the sample population, irrespective of species, to experience loss in a TreM group by the end of the survey period. Although the cumulative rates of loss varied among TreM groups, ranging from the low values for *concavities* (52%) to the high for t*wig tangles* (88 %), loss processes were consistently observed in all groups. *Crown deadwood, perennial fungi*, *fresh exudates* were the least likely to be lost among conifers (Table 3, Figure 3).

Increment and consistency events were generally rare for most TreM groups, with a cumulative incidence of less than 10% and 20% respectively (Table 3, Figure 3) by the end of the survey period. The only TreM group that showed relatively high rates of increment were *concavities* in broadleaves, with an incidence rate of 40% by the end of the survey period. However, only *woodpecker cavities, rot-holes, exposed sap- and heartwood* (broadleaved trees), *perennial fungi* (conifers), *epiphytes and concavities* (both) experienced consistency, with an approximate incidence rate of 20% (Table 3, Figure 3).

Sufficient sample sizes for reduction and disappearance events were available for two groups, namely c*rown deadwood* and *fresh exudates.* The disappearance events showed incidence rates almost six times higher than TreM reduction by the end of survey period (Table 3, Figure 3).

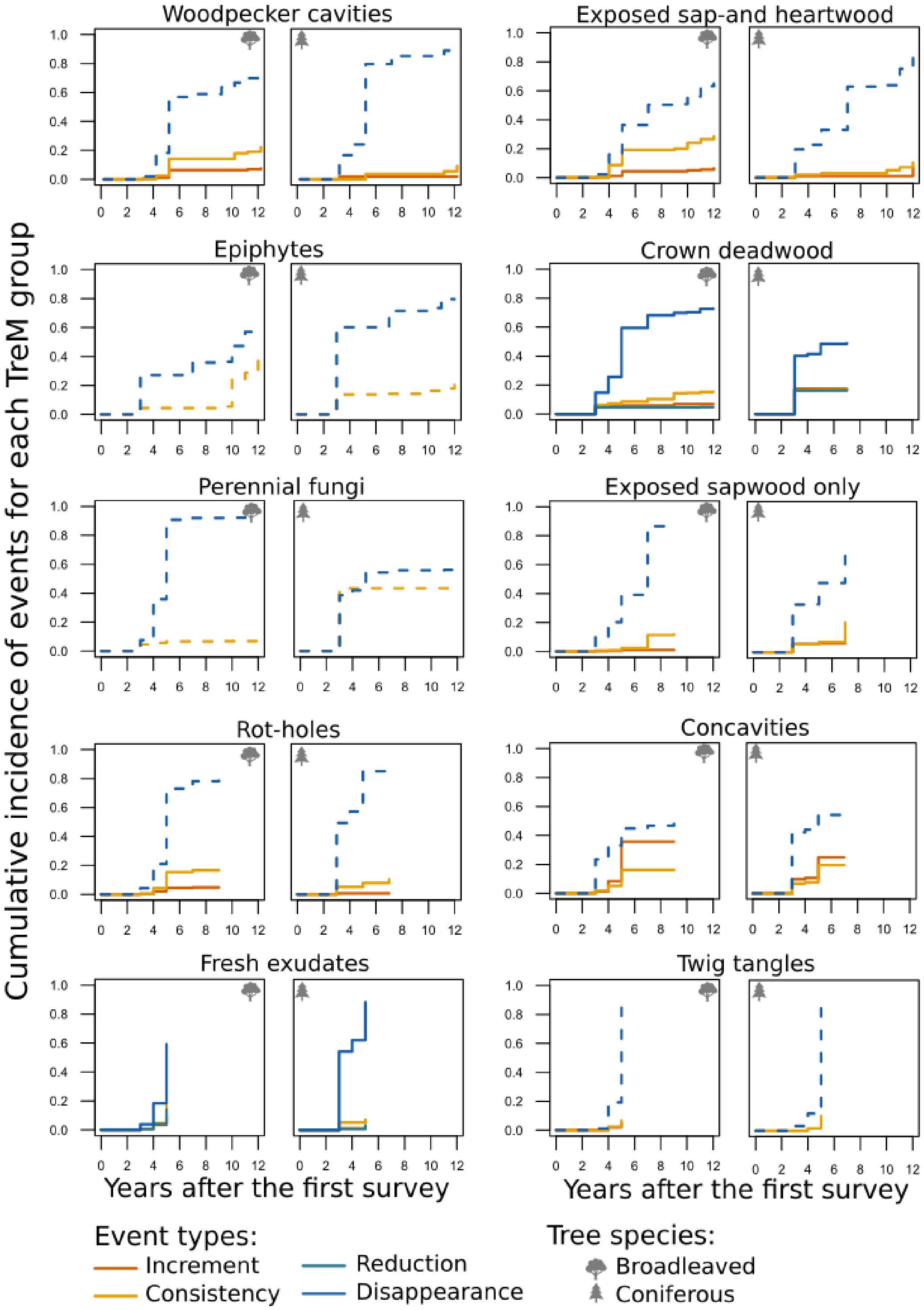


Figure 3. Cumulative incidence rates for all types of events in different TreM groups, since the first survey. Dashed lines represent events combined at the level of the two main development patterns due to too few observations at event type level. **Persistence** processes (increment and consistency events) are represented in orange shades. **Loss** processes (reduction and disappearance events) are shown in blue shades.

Drivers of TreM development

The results of the stratified Cox proportional hazards models indicated that presence of certain TreMs at the first survey had an impact on hazard rates for five TreM groups. Specifically, the availability of *exposed sap- and heartwood*, *crown deadwood, rot-holes, fresh exudates* and *twig tangles* at the beginning of the study increased the hazard rates for loss events. On the other hand, the presence of *fresh exudates* at the first survey had a negative effect on consistency and reduction events (Table 3). The random forest analysis further supported the importance of *rot-holes, fresh exudates* and *crown deadwood* as predictors of temporal changes in the richness of both TreM types and groups (Appendix 6).

Tree DBH was significantly associated with at least one type of event in most TreM groups, except for *woodpecker cavities*, *epiphytes* and *crown deadwood* (Table 3). Increasing tree DBH was associated with higher rates of persistence events (mostly increment) in seven TreM groups and overall TreM richness, while simultaneously leading to lower rates of loss events in three of those groups. The rates of both persistence and loss events increased with tree DBH for *twig tangles* and overall TreM richness. Tree DBH emerged as an important driver for loss events of *exposed sap- and heartwood, perennial fungi, concavities, fresh exudates, twig tangles*; with a negative effect in the first four categories and a positive effect in the last one (Table 3).

Altitude was associated with at least one type of event in four TreM groups and overall TreM richness. Higher altitude was linked to lower rates of *woodpecker cavities, exposed sap- and heartwood, epiphytes*, as well as lower rates of persistence for *rot-holes.* All events related to richness of both TreM types and groups showed lower rates with increasing altitude (Table 3).

Table 3. Significant results of the Cox proportional hazards models stratified by the interaction of tree species and sites, indicating the magnitude and significance of the risk factors (**DBH**, **altitude** and **the initial occurrence of the factor at the first survey**) on the persistence and loss events. The multivariate model^m (with all risk factors as main effects) is presented. Significant values above 1.00 indicating a positive effect (higher the risk factor, higher the event rate), which agreed with the verifying univariate models are illustrated with colour blue↑, opposite effects with colour grey↓. Results are detailed in Appendix 7.

<table>
<tr><th rowspan="2">TreM group</th><th rowspan="2">Period (years)</th><th rowspan="2">Risk factors</th><th colspan="3">Hazard rate for persistence events</th><th colspan="3">Hazard rate for loss events</th></tr>
<tr><th>Increment</th><th>Consistency</th><th>Cumulative incidence of trees that experience the event (%)</th><th>Reduction</th><th>Disappearance</th><th>Cumulative incidence of trees that experience the event (%)</th></tr>
<tr><td rowspan="3">Woodpecker cavities</td><td rowspan="3">12</td><td>DBH (cm)^m</td><td>-</td><td>-</td><td rowspan="3">27.3</td><td colspan="2">-</td><td rowspan="3">72.7</td></tr>
<tr><td>Altitude (m)^m</td><td>-</td><td>-</td><td colspan="2">↓***</td></tr>
<tr><td>Initial occurence^m</td><td>-</td><td>-</td><td colspan="2">-</td></tr>
<tr><td rowspan="3">Exposed sap- and heartwood</td><td rowspan="3">12</td><td>DBH (cm)^m</td><td>↑**</td><td>-</td><td rowspan="3">31.9</td><td colspan="2">↓**</td><td rowspan="3">68.1</td></tr>
<tr><td>Altitude (m)^m</td><td>-</td><td>-</td><td colspan="2">↓***</td></tr>
<tr><td>Initial occurence^m</td><td>-</td><td>-</td><td colspan="2">↑**</td></tr>
<tr><td rowspan="3">Epiphytes</td><td rowspan="3">12</td><td>DBH (cm)^m</td><td colspan="2">-</td><td rowspan="3">29.8</td><td colspan="2">-</td><td rowspan="3">70.2</td></tr>
<tr><td>Altitude (m)^m</td><td colspan="2">↓*</td><td colspan="2">↓***</td></tr>
<tr><td>Initial occurence^m</td><td colspan="2">-</td><td colspan="2">-</td></tr>
<tr><td rowspan="3">Crown deadwood</td><td rowspan="3">12</td><td>DBH (cm)^m</td><td>-</td><td>-</td><td rowspan="3">29.2</td><td>-</td><td>-</td><td rowspan="3">70.8</td></tr>
<tr><td>Altitude (m)^m</td><td>-</td><td>-</td><td>-</td><td>-</td></tr>
<tr><td>Initial occurence^m</td><td>↓***</td><td>-</td><td>↑***</td><td>-</td></tr>
<tr><td rowspan="2">Perennial fungi</td><td rowspan="2">12</td><td>DBH (cm)^m</td><td colspan="2">↑*</td><td rowspan="2">18.5</td><td colspan="2">↑*</td><td rowspan="2">81.5</td></tr>
<tr><td>Altitude (m)^m</td><td colspan="2">-</td><td colspan="2">-</td></tr>
<tr><td rowspan="3">Exposed sapwood</td><td rowspan="3">9</td><td>DBH (cm)^m</td><td>↑*</td><td>↑**</td><td rowspan="3">18.9</td><td colspan="2">-</td><td rowspan="3">81.1</td></tr>
<tr><td>Altitude (m)^m</td><td>-</td><td>-</td><td colspan="2">-</td></tr>
<tr><td>Initial occurence^m</td><td>-</td><td>-</td><td colspan="2">↑***</td></tr>
<tr><td rowspan="3">Rot-holes</td><td rowspan="3">9</td><td>DBH (cm)^m</td><td>↑***</td><td>-</td><td rowspan="3">19.4</td><td colspan="2">-</td><td rowspan="3">80.6</td></tr>
<tr><td>Altitude (m)^m</td><td>-</td><td>↓*</td><td colspan="2">-</td></tr>
<tr><td>Initial occurence^m</td><td>-</td><td>-</td><td colspan="2">↓***</td></tr>
<tr><td rowspan="3">Concavities</td><td rowspan="3">9</td><td>DBH (cm)^m</td><td>↑***</td><td>-</td><td rowspan="3">47.4</td><td colspan="2">↓*</td><td rowspan="3">52.5</td></tr>
<tr><td>Altitude (m)^m</td><td>-</td><td>-</td><td colspan="2">-</td></tr>
<tr><td>Initial occurence^m</td><td>-</td><td>-</td><td colspan="2">-</td></tr>
<tr><td rowspan="3">Fresh exudates</td><td rowspan="3">5</td><td>DBH (cm)^m</td><td>↑***</td><td>-</td><td rowspan="3">22.8</td><td>↓*</td><td>-</td><td rowspan="3">77.2</td></tr>
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<tr><td>Initial occurence^m</td><td>↓*</td><td>↓***</td><td>↑***</td><td>-</td></tr>
<tr><td rowspan="2">Twig tangles</td><td rowspan="2">5</td><td>DBH (cm)^m</td><td>↑***</td><td>-</td><td rowspan="2">11.4</td><td colspan="2">↑**</td><td rowspan="2">88.6</td></tr>
<tr><td>Altitude (m)^m</td><td>-</td><td>-</td><td colspan="2">-</td></tr>
<tr><td rowspan="2" colspan="2">Richness of TreM types</td><td>DBH (cm)^m</td><td>↑***</td><td>↓***</td><td rowspan="2">60.8</td><td>-</td><td>-</td><td rowspan="2">39.2</td></tr>
<tr><td>Altitude (m)^m</td><td>↓***</td><td>↓***</td><td>↓***</td><td>↓***</td></tr>
<tr><td rowspan="2" colspan="2">Richness of TreM groups</td><td>DBH (cm)^m</td><td>↑***</td><td>↓***</td><td rowspan="2">60.1</td><td>↑***</td><td>-</td><td rowspan="2">39.9</td></tr>
<tr><td>Altitude (m)^m</td><td>↓***</td><td>↓***</td><td>↓***</td><td>↓***</td></tr>
</table>

Significance codes: '***' p≤ 0.001; '**' p= 0.001 - 0.01; '*' p = 0.01 - 0.05.

Discussion

Our study describes a highly dynamic TreM development on living habitat trees, particularly on large trees. Our results indicate that, while TreM richness can persist in the long term, specific TreMs are prone to disappearing, irrespective of tree species or TreM group.

Balance of TreM persistence and loss at tree-level

The overall TreM assemblages were found to remain stable at the tree level over a period of 12 years. The processes of increment and consistency did not outweigh reduction and disappearance of TreMs, regardless of tree species. However, broadleaves exhibited relatively higher rates of TreM increment compared to their loss. The increase in TreMs on broadleaves can be attributed to their morphological and wood characteristics. Species such as *F. sylvatica* (the dominant broadleaved species in our study) have a hard xylem protected by a thin bark, making them sensitive to mechanical impacts and slow to seal wounds compared to species such as *P. abies* (Trappmann & Stoffel, 2013). Additionally, the wood of *F. sylvatica* decays faster than *P. abies* (Kahl et al., 2017). Thus, once formed, TreMs related to injuries or facilitating wood decay, may lead to the subsequent formation of new TreM types. For instance, the formation rate of TreMs on *F. sylvatica* was found to be twice as fast compared to conifers such as *A. alba* (Courbaud et al., 2017).

However, the changes in TreM data between the surveys indicated a general balance between formation of new TreMs and loss of existing ones, particularly predominance of *fresh exudates* and *concavities* was replaced by a dominance of *exposed sapwood* and *epiphytes.* The occurrence of living epiphytes can increase in the course of time, as trees age and their surface area expands, especially under favourable growth and dispersal conditions for bryophytes or lichens (Lie et al., 2009; Asbeck et al., 2021; Kõrkjas et al., 2021). *Crown deadwood* and *exposed sap- and heartwood*, which include dead branches of large diameters, dead tops, cracks and fissures, were present in similar shares at both surveys. The longevity of dead branches on decay-resistant tree species such as *P. menziesii* (Mirb.) Franco and *Pinus sylvestris* L. has been observed in previous studies. Dead branches can persist in the canopy for up to 10, and 6 years, respectively (Kahl et al., 2017; Mäkinen, 2002). However, TreM types associated with *to exposed sap- and heartwood*, such as broken tops or forks are less likely to disappear or occur repeatedly on a living tree without causing its death (Kõrkjas et al., 2021).

Individual TreMs are prone to disappear in the long term

Our results suggest that all TreM groups on living habitat trees are susceptible to long-term loss, regardless of tree species. The patterns of loss varied in frequency and incidence rates, but by the end of the study, more than half of the surveyed trees experienced loss in their TreM groups. *Crown deadwood, perennial fungi* and *exposed sapwood* were found to be less likely to decline or disappear from living conifers. This observation may be attributed to the response of conifers to stress caused by recent episodes of drought events and bark beetle outbreaks (Seidl et al., 2011; Senf et al., 2018; Jakoby et al., 2018). This phenomenon can also explain why TreMs such as *crown deadwood, fresh exudates, rot-holes* were observed to predict future changes in TreM richness at tree level. Crown dieback, increased resin production and bark alteration are indicators of declining tree vitality triggered by stress associated with recent extreme drought and subsequent bark-beetle outbreaks (Bouget et al., 2019). Often, trees infested by bark beetles are colonised by perennial fungi such as *Fomitopsis pinicola* (Vogel et al., 2017). Changes in tree vitality, characterised by elevated rates of wood decay and breakage, are likely to influence the composition of TreM assemblages.

The underlying causes of apparent TreM loss are likely to vary among different TreM groups. Previous studies have examined the temporal development of *woodpecker cavities*, *rot-holes*, *fire scars,* as well as of TreMs that affect timber quality (e.g. Wesołowski, 2011, 2012; Edworthy et al., 2012; Tavankar et al., 2017, 2019). However, the drivers of temporal changes, particularly loss, across all TreM groups remain to be identified. While the loss of certain TreMs might seem straightforward and intuitive (e.g. structures that naturally fall off or decay over time, such as *crown deadwood* or *perennial fungi*), the drivers behind loss processes can be diverse. For instance, changes in TreMs linked to presence and activities of specific forest-dwelling species could be manifold (e.g. *woodpecker cavities* or *rot-holes*). Cavities utilised by vertebrates, for example, are rich in nitrogen and attract invertebrate colonization, which may further excavate galleries, provide access for other organisms, and eventually lead to wood breakage and decay (Gibbons & Lindenmayer, 2002; Siiton & Jonsson, 2012). Concurrently, tree defence mechanisms compartmentalise injuries by inhibiting wood-decaying fungi and sealing wounds, often associated with TreMs (Smith, 2015). All subsequent processes can alter the decay dynamics and shape the development of TreMs, eventually leading to decline or disappearance.

Cavities have been reported to last approximately 10 years (Edworthy et al., 2012; Edworthy & Martin, 2013), with slightly shorter rates for excavated cavities than for non-excavated ones (Wesołowski, 2011, 2012). Our findings align with these observations, as approximately 60% of the broadleaves and 80% conifers experienced loss of *woodpecker cavities* over the 12-year study period. The loss of *woodpecker cavities* on living trees could be attributed to several biological drivers, such as breakage of branches and trunks with cavities, decay and collapse of the walls, closure through growth of callus tissues (Wesołowski & Martin, 2018). Similar causes can lead to loss of other TreMs. For example, while large wounds may persist for up to 17 years, *exposed wood* patches and wounds of smaller sizes may be sealed successfully in less than 10 years depending on the extent of xylem and phloem injury (Vasaitis et al., 2012; Tavankar et al., 2017; 2019). The masking of wounds can contribute to TreM loss, with rates varying among tree species. *P. abies* compartmentalise and close scars at a faster rate than *A. alba* or *F. sylvatica* trees (Stoffel et al., 2005; Trappmann & Stoffel, 2013). A detailed overview of possible drivers of TreM loss among all groups is presented in Table 4.

Our findings indicated losses in certain TreM groups that are unlikely to naturally disappear or increase over time on living trees, such as large rot-holes, stem and limb breakages, dead tops. It is thus essential to acknowledge the possibility of observer errors, which could have resulted in incorrect assessments of losses or increments in TreM occurrence. Certain TreMs might have been overlooked during the initial or subsequent survey, leading to inaccuracies in our data (Paillet et al. 2015). However, this effect cannot be fully disentangled, and we assumed that given the large sample size, it remains small compared to ecological processes.

Table 4. Potential drivers of TreM loss at group level.

TreM group	Examples of TreM types	Potential drivers of TreM loss Probability of causing TreM loss: *** 'high', ** 'moderate'; 'low'.	References
Woodpecker cavities	**Single cavities** (ø~4-10 cm); **Woodpecker "flute"** (a vertical string of cavities within a few meters)	Wood breakage ***(breaking of branches with small cavities, breakage of stem at the excavation point) Destruction** (by predators or woodpeckers) Decay, collapse of walls, often after rain water or sap flooding ** Closure through growth of callus tissue** Accumulation of debris inside the cavity ** Obstruction of entrance *	Meyer & Meyer, 2001 Günther & Hellmann, 2005 Wesołowski 2011 Edworthy et al., 2012 Smith, 2015 Cockle et al., 2017 Wesołowski & Martin, 2018 Menkis et al., 2022 Personal observations Mikusinski G., Nairn R.
Exposed sap- and heartwood	**Stem breakage** (ø>20 cm) **Limb breakage with heartwood exposed** (> 300 cm^2) **Crack, lightning scar** (length>30 cm; depth>10 cm) **Fork split at the intersection** (crack length >30 cm)	Decay * Alteration by birds, mammals, insects* Overgrowth by other plants * Wound covered through callus tissue** Evolving into another TreM* (e.g. stem breakage into chimney trunk rot-hole)	
Epiphytes	**Bryophytes, foliose and fruticose lichens.** **Ivy and lianas, ferns, mistletoe.** (>10% of the trunk area covered)	Falling off, climate-change related dieback** Wood breakage ** (e.g. falling of decayed branches that bear mistletoes or ivy) Removal through forest management (e.g. *Hedera helix*)	Bässler et al., 2015, Nascimbene et al., 2016 He et al., 2016 Bilgili et al, 2020 Zekhuis, 2018
Crown deadwood	**Dead branches, top** (ø > 10 cm) **Remaining broken limb** (ø >20 cm, length > 0,5 m)	Falling off, shedding with or without decay *** Evolving into another TreM ** (e.g. crown deadwood decays and forms branch hollows, rot-holes)	Milington & Chaney, 1973 Buse et al., 2008 Spielmann et al., 2013
Perennial fungi	**Fruiting bodies of perennial polypores** (ø >5 cm)	Falling off ** Decay of fruiting bodies *** Breakage of decayed limbs with polypores **	Pouska et al., 2011
Exposed sapwood	**Bark loss** (> 300 cm^2) **Fire scar** (> 600 cm^2) **Bark shelter, pocket** (height > 10 cm)	Falling off *** Closure of fire scars or wounds through callus tissue* Evolving into another TreM ** (e.g. a fire scar decays forming a rot-hole)	Vasaitis et al., 2012 Tavankar et al., 2017, 2022 Menkis et al., 2022
Rot-holes	**Top-closed or semi-open trunk rot hole, hollow branch** (ø > 10 cm) **Chimney trunk rot hole** (ø > 30 cm)	Wood decay * Alteration by birds, mammals, insects * Sealing of hollow branches * Evolving into another TreM* (e.g. hollow branch accumulates water, deepens and forms dendrotelms)	Fritz & Heilmann-Clausen, 2010 Edworthy, 2012 Wesołowski & Martin, 2018 Kõrkjas, 2021 Menkis et al., 2022
Concavities	**Dendrotelm** (ø > 15 cm) **Woodpecker foraging excavation** (ø > 10 cm) **Root buttress concavity** (ø > 10 cm)	Wood decay * Overgrowth by other plants * Evolving into another TreM (e.g. woodpecker-foraging wounds decay and form rot-holes)**	Edworthy, 2012 Gossner, 2018
Fresh exudates	**Fresh sap or resin run** (> 10 cm)	Drying-out *** Healing of wounds causing the exudates *** Cessation of biotic activity**	O'Hara, 2007 Smith, 2015
Twig tangles	**Witch broom** ø >50 cm **Epicormic shoots** > 5 twig clusters	Natural shedding ** Artificial pruning **	Evans, 1985

The way forward and study limitations

Our study allowed us to capture the manifold events involved in TreM development on living habitat trees across different European forest regions. However, our findings may be complemented by future studies, at finer temporal scale. Our analysis was likely influenced by different survey intervals as the re-survey of TreMs was conducted to align with specific project objectives rather than capturing precise event timings. Thus, we could not record precisely the moment in time when an event occurred. The variations in survey periods from 3 to 12 years limited as well site-specific comparisons and the evaluation of the effect of stand management, forest types, growing conditions on TreM dynamics. A targeted TreM study dedicated to quantify temporal changes in TreMs at tree species level, could better capture the underlying causes of TreM persistence and loss. The use of different, older typologies and subsequent simplifications as well as the observer bias are likely sources of inaccuracies in our study (Paillet et al. 2015). Nowadays, harmonized TreM typologies are widely available (Kraus et al., 2016; Larrieu et al. 2018). Thus, future studies may be able to provide more accurate and detailed insights into the development of specific TreM types and allow better understanding of how TreMs evolve and transform into one another. Such information may further be implemented in dynamic forest models that can inform an effective habitat tree selection (Courbaud et al., 2022).

We described TreM loss and persistence only on living habitat trees, exhibiting at least one TreM in the first survey. The decision to work with living trees derived from habitat retention approaches in Europe, which aim to provide a balanced supply of microhabitats associated with both living and habitat trees (Gustafson et al., 2020; Larsen et al., 2022). Understand how TreMs on living trees change over time is crucial for ensuring a continuous and varied provision of resources for species in temperate European forests. This approach improved the statistical power of our analysis by eliminating limitations related to zero-inflated data. However, we could not capture the formation of TreMs on individuals with no TreMs, nor describe how TreMs evolve after tree death. Certain TreMs, such as broken stems, forks, hollows, large areas or bark loss can affect tree vitality and potentially lead to subsequent tree mortality (Stokland et al., 2012). Since TreM composition and diversity differ between living and dead trees (Paillet et al., 2019; Spînu et al., 2021), we suggest further investigations on the dynamics of individual TreMs after tree death.

The retention of old, large trees with abundant and diverse TreMs has been recognised as a high-priority strategy for enhancing the conservation value of European forests (Larsen et al., 2022). However, such trees are often scarce in managed European forests and there may be a need to retain trees without TreMs and allow for TreM development over time (Larrieu & Cabanettes, 2012; Asbeck et al., 2019; Vandekerkhove et al., 2018). Simulation studies have also suggested that retention of trees with no TreMs, particularly short-lived species, can contribute to maintaining a continuous long-lasting habitat pool (Fan et al., 2004; Courbaud et al., 2017). For future studies, it would be valuable to investigate the changes in microhabitats on trees with various attributes, including different species, senescence stages, presence of decay, or other factors related to TreM development (Edworthy et al., 2012; Larrieu et al., 2022).

Conclusions and implications for future forest management

Our study provides a dynamic evidence-base for long-term habitat tree selection by analysing the temporal development of their microhabitats. So far, the selection of habitat trees has focused on their numbers without quantifying the impact of this practice for future provisioning of resources. Our findings show that although TreM richness was persistent at the tree level, TreMs in all groups were susceptible to disappearing in the long term. We therefore suggest a diversified and dynamic approach to habitat tree selection in order to secure a continuous supply of resources in the future. One key suggestion is to prioritise selection of trees with TreMs that are generally scarce in forests. Additionally, functionally different trees that provision diverse TreMs (e.g. different tree species, vitality statuses) may be retained. Biodiversity conservation can be promoted from the early stages of forest development and trees with unusual shapes or defects that would have been traditionally removed, could be retained on site and be allowed to develop into habitat trees (Puettmann et al., 2019). Further, the high rates of TreM losses over a 12-year period suggest that revisiting sites at regular intervals and monitoring TreM development of habitat trees might aid conservation efforts. Such practices are time consuming though and should be encouraged through financial incentives, as exemplified by a new grant in Germany, that provides support and motivation for habitat tree retention in managed forest stands (https://www.klimaanpassung-wald.de/hintergrund) or Natura 2000 contracts in France dedicated to maintaining habitat trees. Additionally, knowledge-exchange efforts between researchers and practitioners are crucial for consolidating the use of evidence-based retention strategies to achieve future positive socio- and ecological outcomes.

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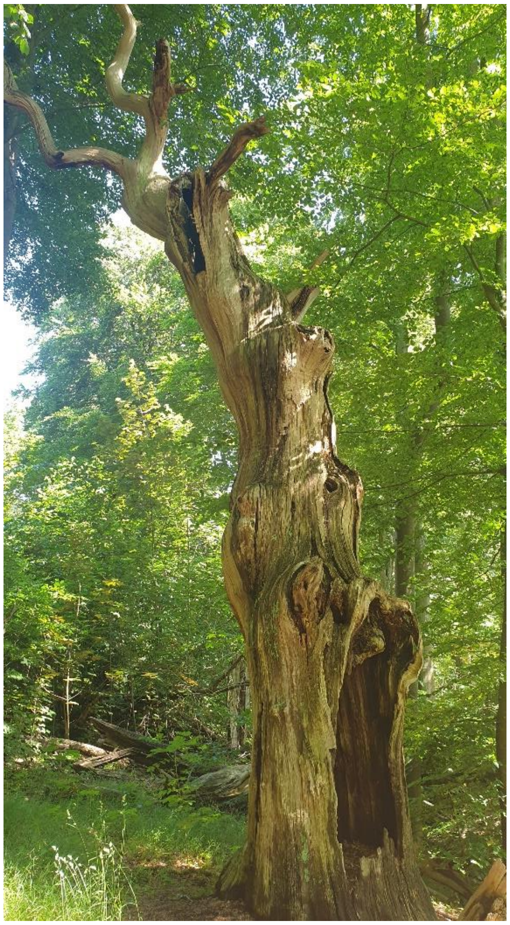


V. Mortality and growth patterns of habitat trees in continuous cover forests of Europe.

Photo: Andreea Spînu

Dead Scots pine - a habitat tree in Southern Sweden.

Spînu A.P., Nairn T., Skiadaresis G., Denter M., Seifert T. and Bauhus J. (2023)
Mortality and growth patterns of habitat trees in continuous cover forests of Europe.
In preparation.

Abstract

Habitat trees, namely large, old trees that support microhabitats, are retained as life-boats that supply resources for forest-dwelling species in managed Central European forests. Once selected, living habitat trees are expected to fulfil long-term ecological functioning. However, large trees are declining due to environmental stress caused by increasing drought events associated with climate change. The presence of tree-related microhabitats (TreMs) can also affect tree vitality and contribute to mortality risks. Thus, it is crucial to understand the response of habitat trees of various species to extreme drought, as well as the impact of TreM occurrence on tree vitality. This study investigated mortality rates and temporal growth patterns of habitat trees in continuous cover forests, using remote sensing images and tree-ring data. Our findings revealed relatively low mortality rates among habitat trees compared to other trees, with conifers being most susceptible to the drought event of 2018. No significant relationship was found between past growth patterns and the occurrence of TreMs. Irrespective of presence or absence of microhabitats, dead conifers trees exhibited a long-lasting growth decline and lower growth and variance prior to their death compared to surviving trees. Ongoing monitoring of growth responses is recommended to further understand the effect of retention forestry on growth of habitat trees. However, early warning signals were identified as potential predictors of habitat tree mortality. Dendro-ecological indices may thus be incorporated in forest growth models and could inform an effective selection of vital habitat trees in the future.

Keywords

Tree-related microhabitats, dendro-ecology, *Picea abies,* retention forestry, tree dynamics

Introduction

Central European forests have experienced increasing frequency and intensity of disturbances and tree mortality events in the past decades (Lindner et al., 2014; Millar and Stephenson, 2015; Seidl et al., 2014), aligning with the global trend of elevated stress levels resulting from heat, drought, and pathogen attacks (Allen et al., 2015, 2010). These threats are expected to persist under future climate change scenarios impacting the vitality of European forests (Anderegg et al., 2015; Seidl et al., 2017). Extensive mortality events and potential shifts in the distribution of tree species and associated taxa are expected to follow (Dyderski et al., 2018; Hanewinkel et al., 2013; Lindner et al., 2014). Consequently, forest management practices need to address the adaptation, mitigation and social dimensions of these climatic changes (Larsen et al., 2022). In order to compensate the historical loss of biodiversity in European forests, management alternatives are needed to minimise the negative impact of harvesting on the conservation of many forest-dwelling species, while considering climate change predictions (Gustafsson et al., 2020). In that regard, retention forestry has emerged as a novel approach, which aims to deliberately preserve biological legacies during harvesting, emulating the positive effects of natural disturbance regimes (Gustafsson et al., 2020, 2012). In recent years, enhancing species, structural and functional diversity, as well as habitat diversity have become crucial considerations in the management of the multiple-use forests in central Europe (Brang et al., 2014; Gustafsson et al., 2020; Storch et al., 2020). This has led to complementary practices such as retention of deadwood and habitat trees within managed forest stands (Bauhus et al., 2009; Gustafsson et al., 2020; Larsen et al., 2022).

Habitat trees are key elements of forest biodiversity that have garnered considerable attention in forest biodiversity conservation (Gustafsson et al., 2020; Larrieu et al., 2018; Kraus et al., 2016; Martin et al., 2022; Asbeck et al., 2021). These trees, typically old and large, serve as refugia for numerous endangered and specialist forest species by supporting tree-related microhabitats (TreMs). TreMs provide essential substrate that support various life processes, including feeding, breeding, and nesting (Larrieu et al., 2018). TreMs can be found on both living and dead trees and include a range of tree morphological structures such as cavities and deadwood, as well as epiphytic or parasitic organisms like mistletoe (*Viscum album*) and saproxylic fungi (Larrieu et al., 2018). Recent research has shown that habitat trees of different vitality statuses (living or dead), species, and life-history traits complement each other in providing TreMs, highlighting the importance of maintaining a combination of functionally different trees to achieve increased levels of TreM diversity and abundance at the stand level (Spînu et al., 2022, 2023). Although large living trees are known to have the most abundant and rich TreM assemblages (Asbeck et al., 2019; Paillet et al., 2019; Spînu et al., 2022), they have been facing a global decline (Lindenmayer et al., 2012).

Large trees are considered particularly susceptible to environmental stress, including drought and insect attacks (Bennett et al., 2015; Lindenmayer & Laurance, 2017). Their increased heights and exposed crowns can make them vulnerable to water deficits (Stovall et al., 2019; Forzieri et al., 2021), which can in turn result in reduced defence capacity against insect attacks (Pfeifer et al., 2011).

Ideally, forest practitioners should maintain a balance of living and dead habitat trees, as they are associated with distinct TreMs and taxa (Larrieu et al., 2018; Spînu et al., 2022). However, the relationship between TreM formation and vitality of living trees is bidirectional. TreMs such as cavities and injuries can impact the vitality of living habitat trees, potentially leading to their mortality as allowing fungi to penetrate and initiate wood-rot (Hunt & Etheridge, 1995). Conversely, dead trees in advanced stages of senescence are prone to breakage, wood decay and may facilitate TreM development, such as crown deadwood, exposed sap and heart-wood. Thus, understanding the early warning signals of tree mortality and their relation to TreM occurrence is crucial, particularly in the context of increased disturbances associated with climate change (Camarero et al., 2015; Senf et al., 2020). By selecting habitat trees with high longevity, retention practices could contribute to the maintenance of forest functioning and promote ecosystem recovery after disturbances, leading to increased levels of biodiversity (Asbeck et al., 2021; Bauhus et al., 2009). Additionally, information about the relationship between TreM occurrence and tree death will inform other relevant decisions regarding for example, the removal of trees for phytosanitary purposes.

Predicting tree mortality poses significant challenges and there is still a lack of reliable indicators that forecast mortality across different scales (McDowell et al., 2013; Trugman et al., 2021). The link between biotic mortality agents and the stress physiology of different trees is yet to be understood, as trees display distinct physiological interactions, including within-species trait variation, trait covariation, and trait–environment covariation (Trugman et al., 2021). However, several studies have successfully used temporal growth patterns in predicting tree stress and mortality (Bigler and Bugmann, 2004; Cailleret et al., 2016; Wunder et al., 2008). Temporal variations in radial stem growth were found to be reliable indicators of tree vitality and productivity (Dobbertin, 2005). Dendrochronological analysis, which provides precise measures of tree growth at an annual temporal resolution, is particularly valuable for exploring long-term and delayed effects of stress-induced mortality (Bigler et al., 2007; Dobbertin, 2005). Obtaining and analysing tree-ring data is relatively easy and affordable, allowing for the study of large numbers of trees, species and sites (Cailleret et al., 2019; Dobbertin, 2005).

Recent studies have highlighted various changes in growth patterns preceding tree mortality. Dead trees have been reported to exhibit lower radial growth rates compared to those that survived a drought event

(Bigler and Bugmann, 2004; Cailleret et al., 2016). In an extensive, long-term stand inventory in the south-eastern U.S. forests, 72% of trees displaying low growth rates before a drought event died within 10 years (Berdanier et al., 2016). These findings suggest that early signals of drought-triggered mortality can be identified and used as tools to predict tree death, although the tipping point at which trees become predisposed to dieback are likely species-specific (Bernadier et al., 2016; Cailleret et al., 2016; Camarero et al., 2015). Gymnosperms and shade- and drought-tolerant species consistently showed a strong and long-lasting decline in growth (Camarero et al., 2015; Cailleret et al. 2016). Several studies reported an increase in first-order autocorrelation and/or variance over time in the ring-width series of dead trees, indicating the potential value of these metrics for mortality prediction (Amoroso et al., 2012; Camarero et al., 2015; Cailleret et al., 2016). However, the inconsistency in results suggests that further research is required to understand the suitability of these methods as indicators of tree mortality (Cailleret et al., 2019; Herguido et al., 2016). The relationship between tree mortality and temporal radial growth patterns is not fully understood (Cailleret et al., 2017; Camarero et al., 2015). Gessler et al. (2018) recently proposed idealized types of long-term growth patterns and growth decline trajectories related to ‘hydraulic failure’ and ‘carbon starvation’, which combined with analyses of dual isotope (δ^13 C and δ^13 O) can indicate water-use efficiency in trees. Mortality risks could be predicted by using resistance, recovery and resilience indices calculated from tree ring widths and their relationship to past drought events (DeSoto et al., 2020).

The use of indicators derived from growth patterns can be used for forecasting when and where mortality events are likely to occur. Thus, by incorporating tree mortality probability, the vitality and longevity of habitat trees can be maintained for longer periods. While the significance of habitat trees for forest conservation has been recognised (Asbeck et al., 2021; Muys et al. 2022), there is a limited understanding of their mortality within the context of continuous cover forests, particularly due to the relatively recent practice of retention in temperate European forests.

The primary aim of this study was to investigate the mortality rates of habitat trees and detect early warning signs of tree mortality associated with drought in the Black Forest region. We aimed at identifying associations between overall tree growth trends, vitality, and the presence of TreMs. To achieve these aims, we formulated the following specific objectives and hypotheses:

1. Investigate habitat tree mortality rates using terrestrial inventory and aerial images before and after the 2018 drought event. We expected to observe high mortality rates among habitat trees, reflecting their vulnerability to drought stress.
2. Assess whether surviving habitat trees exhibit different temporal growth patterns compared to dead trees. Our hypothesis was that prior to death, dead trees would show lower mean annual growth rates compared to surviving trees. Additionally, we expected to observe distinct changes in growth autocorrelation, variance and stability in the years leading up to tree mortality.
3. Explore the relationship between growth patterns and the occurrence of microhabitats on habitat trees in the Black Forest region. We hypothesised that trees with decreasing growth rates show a higher richness of TreMs.

Materials and methods

Study area

The study was conducted in 133 one-hectare plots in the southern Black Forest Region, in Baden-Württemberg (Figure 1). The plots were selected as part of "Conservation of Forest Biodiversity" project (Storch et al., 2020) on the basis of two environmental gradients: landscape-scale forest connectivity, measuring forested land in the surrounding 25km^2 and plot-scale retention-related forest structure, including habitat trees and deadwood. The research area is characterised by low montane forests dominated by *Fagus sylvatica* L., *Abies alba* Mill. and *Picea abies* (L.) Karst. The geology is predominantly granite and gneiss and the macroclimate is influenced by the altitude range, which varies from 120 to 1,493 m.a.s.l.. Mean annual temperatures range from 4.0°C to 10.4°C, and mean annual precipitation ranges from 1500 to 2100 mm (Storch et al., 2020). The mean diameter at breast (1.3m height (DBH) per plot is 55cm, with a minimum of 37 cm and a maximum of 82 cm. Large trees with a DBH over 80 cm were scarce (Asbeck et al., 2019). While the plots management differed at the time of inventory, with 10 plots located in forest reserves, the management practices ceased only 25-50 years ago. The TreM occurrence on trees in reserves was not yet significantly different due to the persisting effect of past silvicultural practices (Spînu et al., 2022; Asbeck et al., 2019). The characteristics of the studied trees are presented in Table 1.

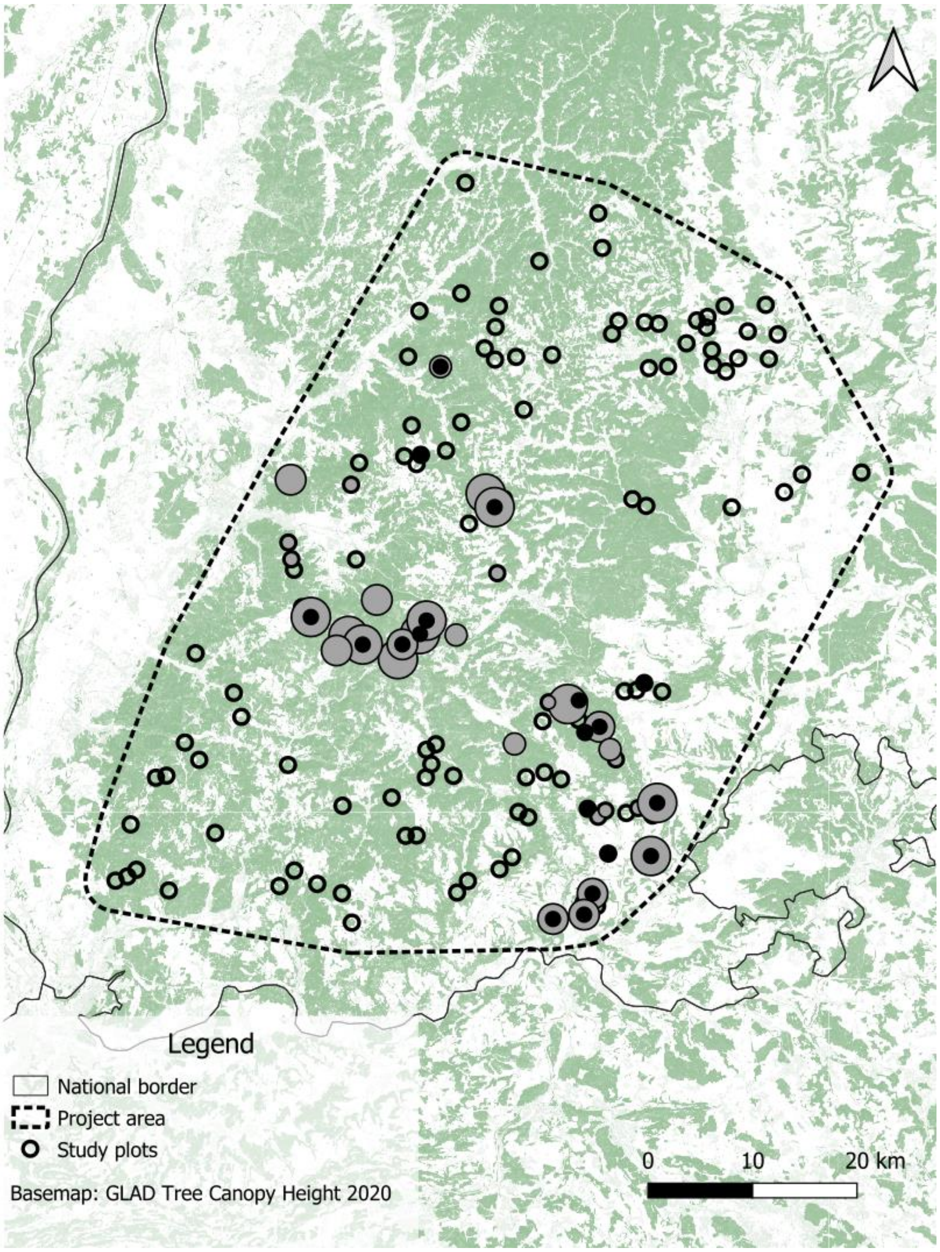


Figure 1. Study plots in southwest Germany. Rates of overall tree mortality in the subset plots are represented by ● (the symbol size increases with higher mortality rates). Study plots where habitat tree mortality was observed are marked with ⬤.

Table 1. Main attributes of the inventoried trees based on their vitality status (living or dead) and species.

Tree species	**N** of trees	**Total share** (%)	**DBH** (cm)				**Age** (years)				**AR1**	**SD**	**TreM abundance**				**TreM richness**			
			Mean	SD.	Min.	Max.	Mean	SD.	Min.	Max.			Mean	SD.	Min.	Max.	Mean	SD.	Min.	Max.
Living (N=185)																				
A. alba	57	30.8	74.17	14.5	27	111	121	32	49	238	0.81	7.79	3.5	3	0	23	1.7	1	0	5
P. abies	128	69.2	55.15	14.4	24	115	86	37	26	215	0.72	6.58	3.7	3	0	19	1.8	1.1	0	6
Dead (N= 45)																				
A. alba	10	77.7	53.75	20.3	30	94	118	48	46	192	0.75	1.10	6.0	7	0	24	2.1	1	0	5
P. abies	35	22.2	58.57	18.7	23	102	107	51	33	245	0.80	1.05	2.85	2	0	24	1.1	1	0	3

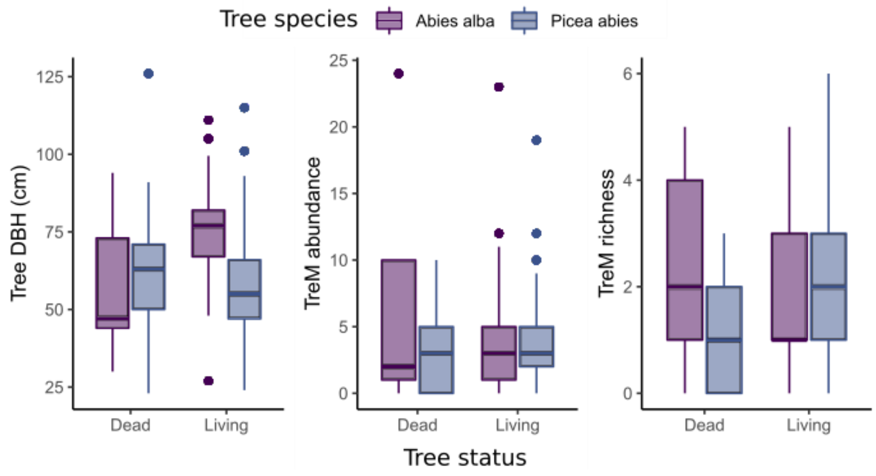


Figure 2. Differences in tree dimension (DBH) and TreM occurrence (abundance and richness) between living and dead trees of *A. abies* and *P. abies*.

Data collection

Recent tree mortality was determined though visual inspection. We counted only newly occurred dead trees based on visual cues such as tree crown colour, changes in tree form (broken, fallen or harvested) and signs of bark beetle presence. Local harvesting was permitted, but only for trees that were dying or dead. It was assumed that all removed trees were in a dying or dead state at the time of the data collection in 2019. The habitat trees in this study were previously selected by Asbeck et al. (2019) and have been since used in subsequent studies (Asbeck et al., 2019, 2021, 2021; Spînu et al., 2022; Basile et al., 2021; Hendel et al., 2023). These habitat trees were the largest 15 trees within each plot and considered the best candidates to support a diverse range of microhabitats. TreMs were recorded following the methodology outlined by Larrieu et al., 2018, which classifies TreMs in fifteen groups, such as woodpecker cavities, rot-holes and crown-deadwood.

Tree-ring data was collected from a subset of plots where recent tree mortality was observed based on aerial images (32 plots). The main three tree species surveyed were *P. abies*, *A. alba* and *F. sylvatica*, which accounted for 56.4%, 20% and 10.7% of trees sampled, respectively. During the spring and summer of 2020, a total of 79 living habitat trees and 61 recently dead trees (including the only five dead habitat trees found) were sampled. We considered recently dead trees those with a decay stage 1 or 2 adapted from Sippola and Renvall (1999), following the same approach used in Spînu et al. (2022) (Appendix 1a). Since only a small number of habitat trees were found dead (five out of 480 habitat trees), recently dead trees, not previously selected as habitat trees, were included in the analysis to enable a comparison of past growth between living and dead trees. In each plot, core samples were extracted at 1.3 m height using an increment-borer (Haglöf, Sweden) from a minimum of three living habitat trees and all available recently dead trees. The selection of the three living habitat trees for tree-ring analysis was based on a preliminary survey of TreMs that were considered to have an impact on tree vitality, such as cavities, bark loss and dendrotelms (Appendix 1b).

Sample preparation and dendrochronological methods

All core samples were air-dried and placed in wood mounts. Cores that were too decayed for analysis were discarded. Remaining samples (361) were secured to 5 mm-thick glass plates using self-adhesive cable concealers. Cores were cut perpendicular to the wood grain using an ultraprecise, single-point diamond flycutter, a novel method described in Spiecker et al. (2000). This method enables smooth surfaces without the need for sanding. The prepared samples were visually cross-dated using a binocular microscope (Speer, 2010) and afterwards scanned at 1,200 dpi (conifers) and 3,200 dpi (broadleaved tress) using the Epson Expression 1649XL flatbed colour image scanner. The tree ring widths were measured from the scanned images using WINDENDRO image analysis system (Regents Instruments, Quebec). The resulting tree-ring width series were visually and statistically crossdated using the functions corr.rwl.seg() and ccf.series.rwl() (Bunn, 2010) from the *dplR* package (Bunn, 2008) in R (R Core Team, 2021).

Data analysis

Data preparation and exploration

All data analyses were performed using R 1.4.1717. (R Core Team, 2021). Differences in tree attributes such as DBH, age, TreM abundance and richness based on tree status and species are presented in Figure 2 and Appendix 3. Tree age and DBH were correlated, so no conclusions were drawn regarding the relationship between tree age and TreM occurrence. Due to the limited number of dead broadleaved trees (four observations), data analyses to detect early signals of mortality in these species could not be conducted. Similarly, due to the scarcity of TreMs on *Pseudotsuga menziesii* trees, analyses were carried out only for *P. abies* and *A. alba*.

Habitat tree mortality was calculated as the ratio between the number of recently dead trees and total number of habitat trees (15 in each plot). To provide context to habitat tree mortality, aerial images before and after the drought event (2016, 2019) were visually inspected for plots where good-quality images were available (52) (Appendix 2). The tree mortality rate at the stand level was calculated as the ratio between the number of recently dead trees (identified visually from remote sensing images) and the total number of standing living trees.

Growth patterns and tipping points

Several studies have suggested that early warning signals of tree death can be detected through growth metrics associated with the proximity of trees to a tipping point (critical transition to a new state) (Cailleret et al., 2019; Dakos et al., 2012; Camarero et al., 2015). The annual growth ratios (g_m) for a mortality event between dead trees and surviving trees was calculated for their entire life (Berdanier & Clark, 2016; Cailleret et al., 2017). A lower growth rate for dying trees in comparison to surviving trees was indicated by a ratio below 1 (g_m <1). The tipping point we defined as the moment after which growth ratios were consistently below 1. To assess growth trends over time, we performed non-parametric Mann- Kendall tests for the period before and after the tipping point (30 years) as well as in the last years of growth (30 years). The Kendall rank correlation coefficient, also known as Kendall Tau, was used to quantify the strength and direction of the trend. The coefficient values range from -1 to 1, with positive values suggesting increasing growth and negative values, indicating declining growth.

Time-series metrics were used to analyse the temporal changes in growth patterns. These included mean tree ring width (*mean*, the average width of tree rings), first order autocorrelation (*AR1*, the correlation between adjacent tree ring widths), standard deviation (*SD,* the variability in tree ring widths), and temporal stability of tree growth (tree stability). Individual tree stability was defined as the ratio between the mean tree ring width and the standard deviation. The metrics were calculated for 20-year moving time windows. Further, we selected the windows in the period before and after the tipping point at individual tree-level. By calculating these metrics on an individual tree-level, it was possible to compare the growth trends between dead and surviving trees.

Tree growth patterns and TreM occurrence

We investigated the relationship between the TreM abundance, richness, and growth trends (Kendall Tau) as well as tree stability to identify whether past tree decline has an effect of the present occurrence of TreMs. We assessed these relationships by means of simple linear models. TreM abundance was calculated as the total number of individual TreMs per tree, while richness represented the number of different TreMs groups present on a tree (e.g. rot-holes, concavities, crown deadwood).

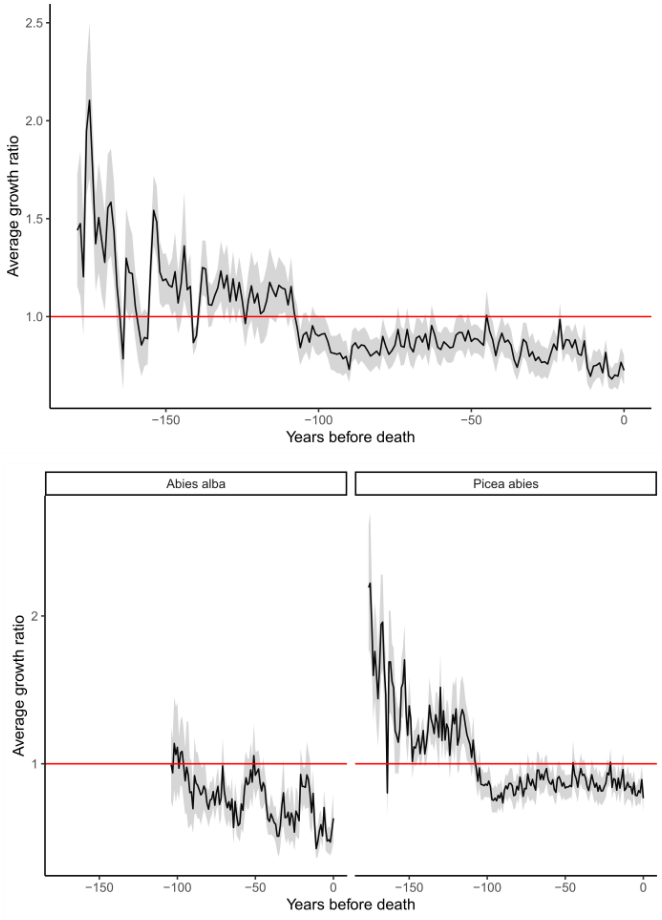


Figure 3. Temporal changes in growth ratio between dead and living (surviving) trees before the mortality for both tree species (upper panel) or separately (lower panel). Shaded areas represent the 95% confidence interval.

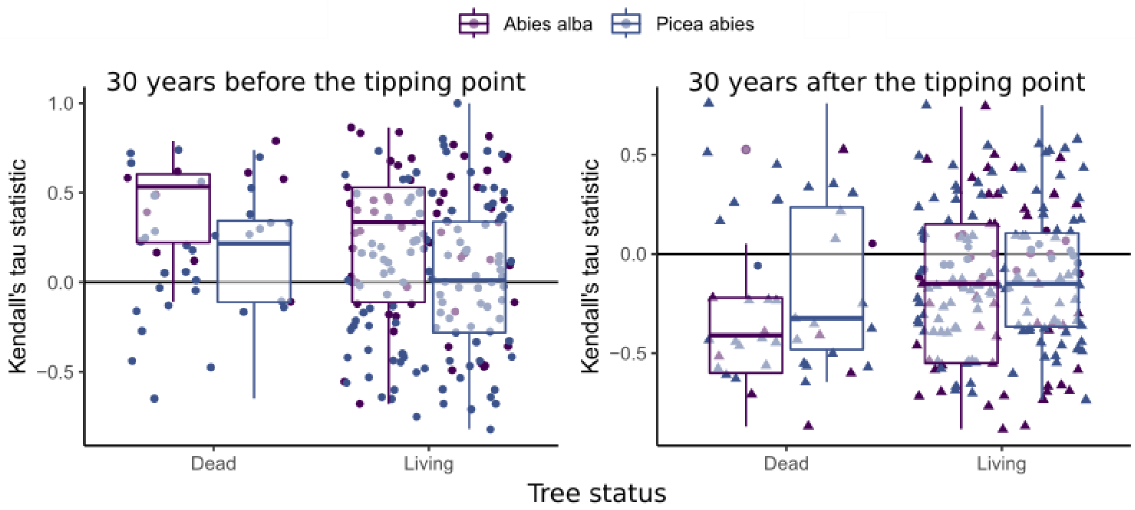
Results

Mortality rates and early warning signals

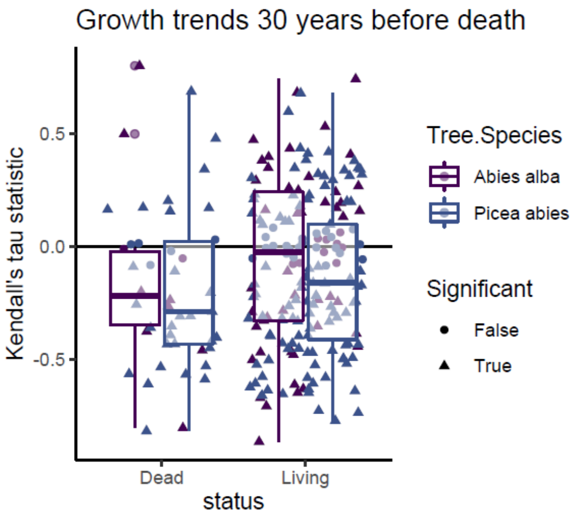
The results based on visual inspection of aerial images indicated that overall tree mortality rates were relatively low in the study plots. Mortality rates at the plot level were generally low, varying from 0.01 to 0.10%. In approximately 60 % of the plots, none of the habitat trees died following the drought event in 2018. In about one-third of the plots, only one tree out of 15 living habitat trees died. In less than 5% of the plots, higher mortality rates, ranging from 13 to 20% were observed among the surveyed habitat trees.

Tree characteristics and differences between dying and surviving trees

A total of 140 tree-ring series extracted from the 32 plots where tree mortality occurred were cross-dated. The earliest recorded growth year for a surviving tree was 1784, while for a dead tree it was 1831. Average age for the living trees was 131 (±33) years for *A. alba* and 103 (±41) years for *P. abies* trees (Table 1). Only surviving trees of *A. alba* had a significantly higher DBH compared to dead trees. Age and DBH were positively correlated for *P. abies*, while large trees of *A. alba* were not consistently the oldest trees (Appendix 3). The overall mean of growth rates differed significantly between dead and living trees, regardless of species. Average mean tree-ring width for living trees was 13.29± 48 for *A. alba* and 11.41 ±51 for *P. abies*, with lower values for dead trees, 1.87±1 for *A. alba* and 2.16±1 for *P. abies*. Dead trees exhibited reduced growth rates prior to death, indicated by growth ratios g_m below 1. This reduction in growth started approximately 100 years before the death for both for *P. abies* and *A. alba* (Figure 3). All trees, regardless of survival status, showed a decrease in growth after the tipping point (30 years) (Figure 4a). Clear differences between living and dead trees were also observed in terms of growth trends in the 30-year period before death or the sampling event for living trees (Figure 4b). Mean, standard deviation, autocorrelation and stability over the entire life of the trees, differed significantly between dead and living trees of *P. abies* and *A. alba* (Appendix 4). Moving mean and standard deviation were greater in living trees before and after the tipping point. Rolling autocorrelation and stability did not differ around the time of the tipping point. All growth metrics differed between the two tree categories, 30 years before the mortality event, with relatively higher values for living trees (Figures 5 and Appendix 6).



a.



b.

Figure 4. Differences in the growth trends before and after the tipping point (30 years) (a) and 30 years before the death event (b) between dead and living tree, according to their tree species.

TreM estimates and growth trends

The analysis of growth trends in *A. alba* and *P. abies* trees revealed that the decline in growth did not have a significant effect on the occurrence of TreMs. The Kendall Tau coefficient, which represents the growth trends, was not significantly related to the abundance or richness of TreMs, irrespective of tree species. The results showed that TreM abundance and richness were not related to any growth metrics (Figure 6, Appendix 5).

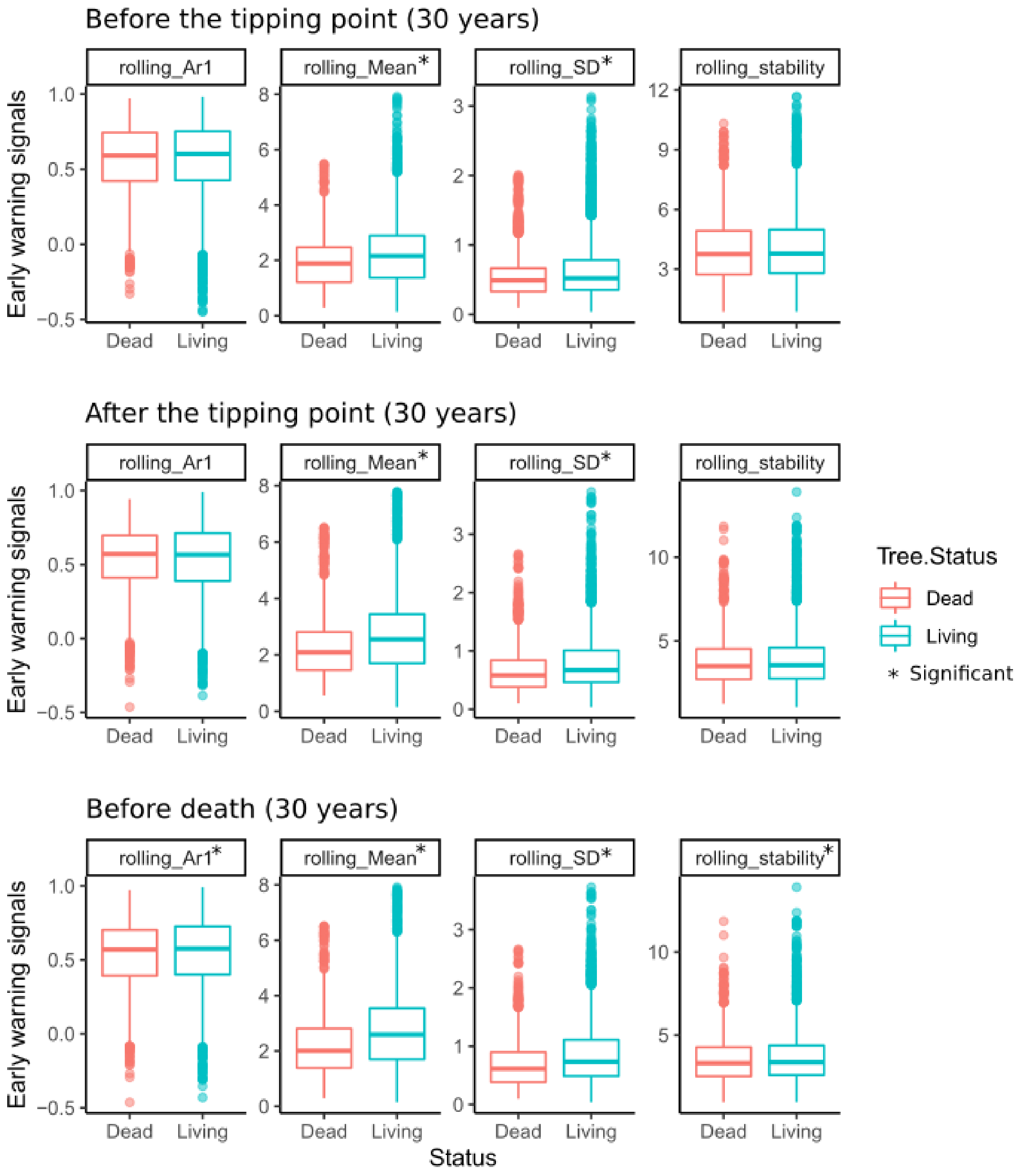
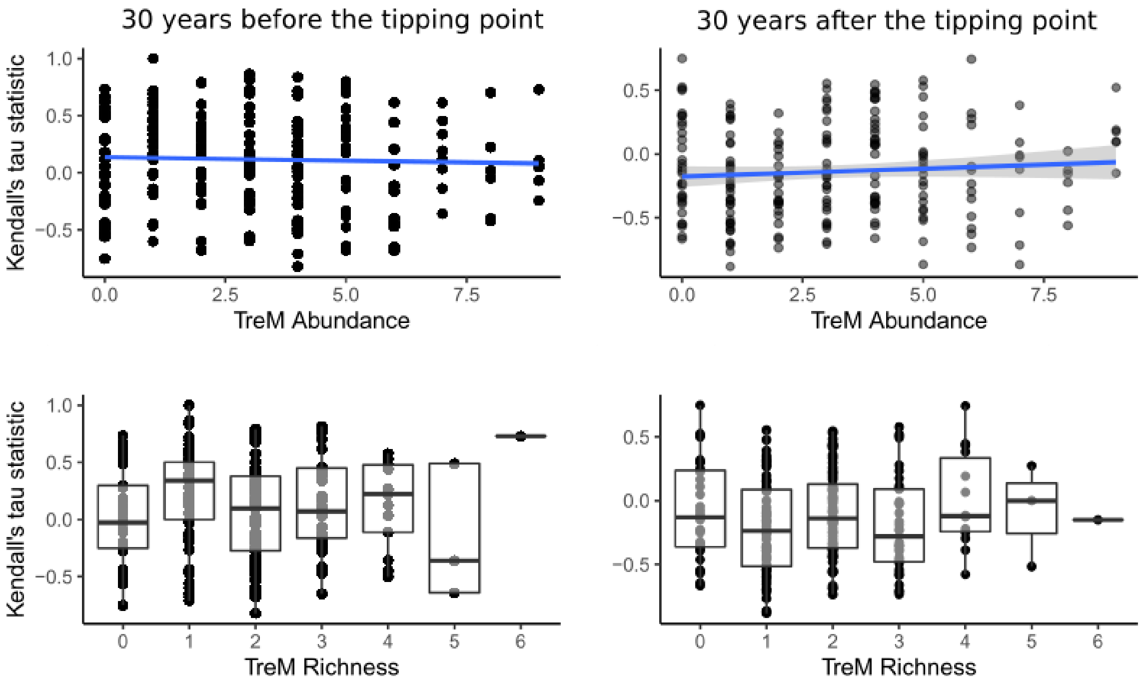
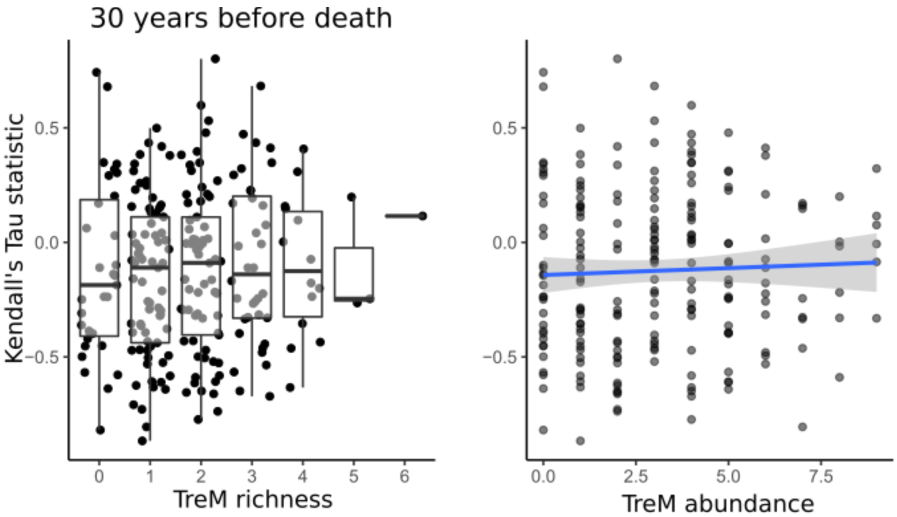


Figure 5. Temporal changes in time-series metrics of living and dead trees, irrespective of species: mean tree-ring width (mean), first order autocorrelation (AR1), standard deviation (SD), tree temporal growth stability (stability).



a.



b.

Figure 6. The relationship between TreM occurrence (richness and abundance) and growth trends 30 years before and after the tipping point (a) and 30 years before the mortality event (b).

Discussion

The mortality rates of habitat trees were not significantly different from other trees in the Black Forest region, following the severe drought event of 2018. Tree mortality was observed mostly among conifers. Analysing growth patterns of dead trees revealed a long-lasting decline, that started approximately 100 years prior to the mortality event for both *A. alba* and *P. abies.* We did not identify any relationship between the current occurrence of microhabitats and past growth patterns of the trees.

Low mortality rates among habitat trees and broadleaved species

The lack of differences in mortality rates between habitat trees (large trees that bear microhabitats) and other trees in the study, may be attributed to favorable growing conditions, including climate and site characteristics. Past management, such as thinning, may have contributed to the improved resistance and resilience of these trees (Lindenmayer & Laurence, 2017). While a few plots were in strict forests reserves, management ceased only 25 to 45 years ago. The majority of the plots were actively managed for timber production (Asbeck et al., 2019). The management practices targeted growth of healthy, large crop trees and could explain why dimensions of the *P. abies* trees, which were predominant in our study, did not vary significantly. Worldwide, numerous studies have indicated that large trees are at great risk of mortality under increasing environmental stress (Bennet et al., 2015; McDowell & Allen, 2015; Stovall et al., 2019). However, in this current study, although the habitat trees were the largest trees in the plots, only a few individuals exceeded 80 cm in DBH. Moreover, recent inventory data from Central Europe suggested that tree size had an effect on the growth reduction caused by the 2018 drought, only for *P. sylvestris* trees, not necessarily for other species (Thom et al., 2023).

Our analysis revealed differential mortality rates among tree species, with *F. sylvatica* exhibiting lower mortality rates compared to *P. abies* and *A. alba*. While conifers generally exhibit better recovery after a drought- induced decline, broadleaved trees show higher resistance (DeSoto et al., 2020). Dead conifers are thus, more likely to show sustained growth declines, if their ability to recover is impaired. This finding is congruent with recent inventory data from Central Europe, where Thom et al. (2023) reported that, although most tree species showed an annual growth decline of over 40% during the recent droughts, *P. abies* and *P. sylvestris* were more susceptible to drought than the common broadleaved tree species (*Fagus* and *Quercus* species). Similar results were found following the drought of 2013 (Pretzsch et al., 2020). This may relate to the drought-response of conifers, which close their stomata and downregulate photosynthesis, resulting in reduced secondary growth (Martinez-Sancho et al., 2017). In addition, the trees in our plots likely allocated resources away from growth towards resin production in response to bark-beetle outbreaks in the region (Kane & Kolb, 2010). Such growth compromises may have resulted in exhaustion of carbon resources (carbon starvation), particularly in drought-affected individuals that have experienced prolonged growth decline (Gessler et al., 2018).

Long-lasting decline in the growth of the dead trees

Among conifers, our analysis revealed a prolonged period of growth decline in dead trees compared to their living counterparts. The mean growth rates of dead trees were consistently lower than those of surviving trees throughout the majority of their life. After the tipping point, which occurred approximately 100 years before the mortality event, all trees experienced a decrease in growth, indicated by negative growth trends with the signal being more pronounced in trees that eventually died. Long-lasting decreasing growth trends have been previously associated with conifers and are indicative of a gradual loss in their ability to recover from environmental stress, particularly in the context of repeated drought events (Anderegg et al., 2015; Cailleret et al., 2017; DeSoto et al., 2020). The tipping point identified in our study aligns with the extreme drought event in 1921 (Erfurt et al., 2020). Tree-ring records from the region have also shown strong growth responses of *P. abies* and *A. alba* to subsequent drought years in 1976 and 2003 drought (Erfurt et al., 2020). This suggests that after repeated stress events, trees eventually reached a threshold where they could no longer sustain their vitality (Hartmann et al., 2015), most likely attributed to a combination of drought and beetle attacks that occurred in Central Europe in 2018 (Senf & Seidl, 2021).

Early warning signals

Our findings show that changes in certain growth metrics can be observed in dead trees as they approach the tipping point or the mortality event. An increase in mean, standard deviation and autocorrelation has been previously observed in various natural systems undergoing a transition to an alternate state (Scheffer et al., 2009). However, their effectiveness as early warning signals for predicting tree mortality has yielded mixed results. While this method has shown success for certain tree species such as *A. alba* and *Quercus petraea* (Camarero et al., 2015; Cailleret et al, 2016), it has not consistently indicated a change in autocorrelation across multiple coniferous and broadleaved species. Our study did not support the notion that autocorrelation and stability are indicators of tree mortality as trees approach the tipping point. However, variance has been observed as a reliable predictor around the time of the tipping point and before tree death, consistent with other studies on conifers (Cailleret et al., 2019). The changes in the growth stability predicted tree mortality 30 years before the event. The complex interactions between biotic and abiotic drivers, influenced by individual attributes and adaptation to stress, can significantly impact the overall growth signal and consequently affect growth metrics (Anderegg et al., 2015; Cailleret et al., 2019; Timofeeva et al., 2017). Given the findings above, it becomes evident that early growth signals detected in our study could be used to predict habitat tree mortality in the Black Forest region.

Growth patterns and occurrence of tree-related microhabitats

Our analysis did not find a relationship between past growth patterns and metrics with the current occurrence of TreMs. TreM abundance and richness was higher on dead trees compared to living ones, which aligns with findings from numerous other studies in this field (e.g. Larrieu et al., 2012; Paillet et al., 2017; Spînu et al., 2022). We cannot determine whether this pattern emerged after the mortality event or prior to it. However, TreM abundance and richness did not increase with growth decline, suggesting that TreMs might have formed after the death of the tree or just before, when the tree was weakened. This result may be attributed to increased rates of decay, breakage and associated TreM formation on dead trees. However, further investigations specifically focused on TreM dynamics on living, dying and dead trees are needed to gain a more comprehensive understanding of these processes.

The way forward

This study represents the first investigation into the mortality of habitat trees within managed continuous-cover forests in Europe. While the retention of habitat trees is a relatively recent practice, it is essential to consider the potential impact of future silvicultural practices on the development and mortality of these trees. Although the degree of change in the conditions prior and after harvesting is not as pronounced as in clearcutting systems, the growth of retained trees may still be influenced by factors such as canopy opening and stand density reduction. Future research should examine whether habitat trees in these systems benefit from harvesting operations, potentially gaining improved access to resources (Pretzsch et al., 2020). In contrast, habitat trees may face increased vulnerability to sudden exposure to environmental stress such as water deficits driven by higher radiation or wind breakages (Bennett et al., 2015). In clearcutting systems, it has been shown that post-harvesting, more than half of the retained trees may die, with highest rates observed among broadleaves (Bladon et al., 2008). After harvesting, the risks generally increase with increasing tree size (e.g. DBH) and broadleaves are more likely to die standing, while conifers such as *P. abies* are susceptible to windthrown (Bladon et al., 2008). Even though dead habitat trees are crucial for many saproxylic species (Runnel et al., 2013), the substrate resources provided by them differ when they are alive. The change of status from living to dead may have a significant impact on the viability of the associated species communities (Hämäläinen et al., 2014). Further studies, following the temporal development of habitat trees in continuous-cover forests even following their death, would be valuable for guiding future retention schemes. For instance, the decisions regarding spatial distribution of habitat tree or species choices may benefit from such research. Mortality risks could potentially be reduced if habitat trees are grouped or by combining mixed, climate-adapted species as habitat trees (Bladon et al., 2008; Pretzsch et al., 2020). Further, more research is needed to understand the effects of specific TreM assemblages on tree growth, as certain TreMs such as symbiotic fungi or mistletoe may disrupt water transportation and increase drought stress in habitat trees (Rigling et al., 2010; Durand-Gillmann et al., 2012).

Conclusion

This study provides evidence that habitat trees had lower mortality rates compared to average trees from managed continuous-cover forests in Europe. However, our findings suggest that conifer habitat trees such as *P. abies* and *A. alba* may be more vulnerable to future drought-induced stress than common European broadleaves (*F. sylvatica)*. Early warning signals such as mean growth and variance over time in the ring width series, could be used to effectively predict growth declines. The analysis of past growth patterns revealed a long decline, possibly triggered by previous drought events. Our study suggests that habitat trees that showed a slow recovery after the drought events may not be optimal candidates for provisioning TreMs associated with living tress. However, they could rapidly provide TreMs related to wood decay and breakage. These findings are valuable for developing management strategies aimed at ensuring the long-term vitality and longevity of habitat trees in managed forests.

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VI. Synthesis and discussion

VI.1. Quality and development of habitat trees and their microhabitats

This thesis provides the first evidence-base for diversified habitat tree selection in temperate forests, based on data describing TreMs borne by functionally-different trees at multiple points in time. The key findings are summarised in the following sections **(VI.1.1, VI.1.2)**. The synthesis presents the overarching linkages between the results and their application in forest management **(VI.2, VI.3)**. Strengths and limitations of the results and methods employed, as well as future outlooks on research are further discussed **(VI.4.)**.

VI.1.1. Quality of habitat trees and resources provided

A recurring finding in this thesis is that large trees support the highest abundance and richness of TreMs, but the patterns of habitat provisioning vary significantly among trees. The quality of the TreMs and consequently of habitat trees, is influenced not only by tree dimension, species identity or wood decay, but also by their interaction. This study suggests that habitat trees with different attributes complement, but cannot substitute one another in TreM provisioning. For example, while decayed, large snags of *A. alba* and *P. abies* may have higher TreM abundance and richness compared to living broadleaved trees, their TreM composition differs significantly **(Chapter II)**. Furthermore, specific TreMs, such as water-filled holes and stem and fork-level cracks are more closely associated with tree ontogeny and stem form rather than tree dimension **(Chapter III).** The variability among habitat trees extends to their temporal development. At similar ages, irrespective of the forest management, pioneer species support generally more and richer TreM assemblages than longer-lived, slower growing species that are more decay resistant and can successfully compartmentalize injuries (*Q. robur*). However, longer-lived species play a crucial role in providing specific TreMs, such as crown deadwood or concavities **(Chapter III)**.

The provision of diverse resources for species that depend on them can be enhanced through a combination of trees with different attributes, such as vitality status, compartmentalization capacity, successional character, form and shape.

VI.1.2. Temporal development of habitat trees and their microhabitats

This study revealed the highly dynamic temporal development of TreMs on habitat trees, particularly on trees of large dimensions (Figure 6). The formation and loss of TreMs vary in timing, magnitude, and frequency of TreM between coniferous and broadleaved species, as well as in relation to the compartmentalization capacity of trees and their successional character. In 100-year-old reserves and managed forests originating from clearfelling, TreMs formed more rapidly on pioneer trees like *Populus* and *Betula* compared to longer-lived species like *Quercus* **(Chapter III)**. Through longitudinal data obtained from repeated inventories on living trees, this study provides the first description of how TreMs change over time, highlighting a high rate of TreM loss over a 12-year period. While most TreM groups are likely to disappear in the long term, loss events occur earliest (after 3 years) for fresh exudates and twig tangles **(Chapter IV).** The presence of TreMs did not influence the vitality of habitat trees or contributed to their mortality. Tree mortality was rather associated to a long-decline in growth rates. Coniferous habitat trees face a higher risk of drought-induced mortality compared to broadleaved trees such as *Fagus sylvatica* in the Black Forest region **(Chapter V)**. The death of habitat trees may result in a different TreM composition. For instance, fresh exudates or bryophytes and fungi that are associated with the living trees might disappear **(Chapter II)**.

When selecting habitat trees based on the presence of TreMs, consideration should be given to the likelihood of TreM development and the risk of the habitat tree itself being lost in the long term. This thesis underscores the importance of selecting a combination of diverse habitat trees, including species adapted to climate change among both short- and long-lived tree species, to ensure a continuous and abundant supply of TreMs in the future.

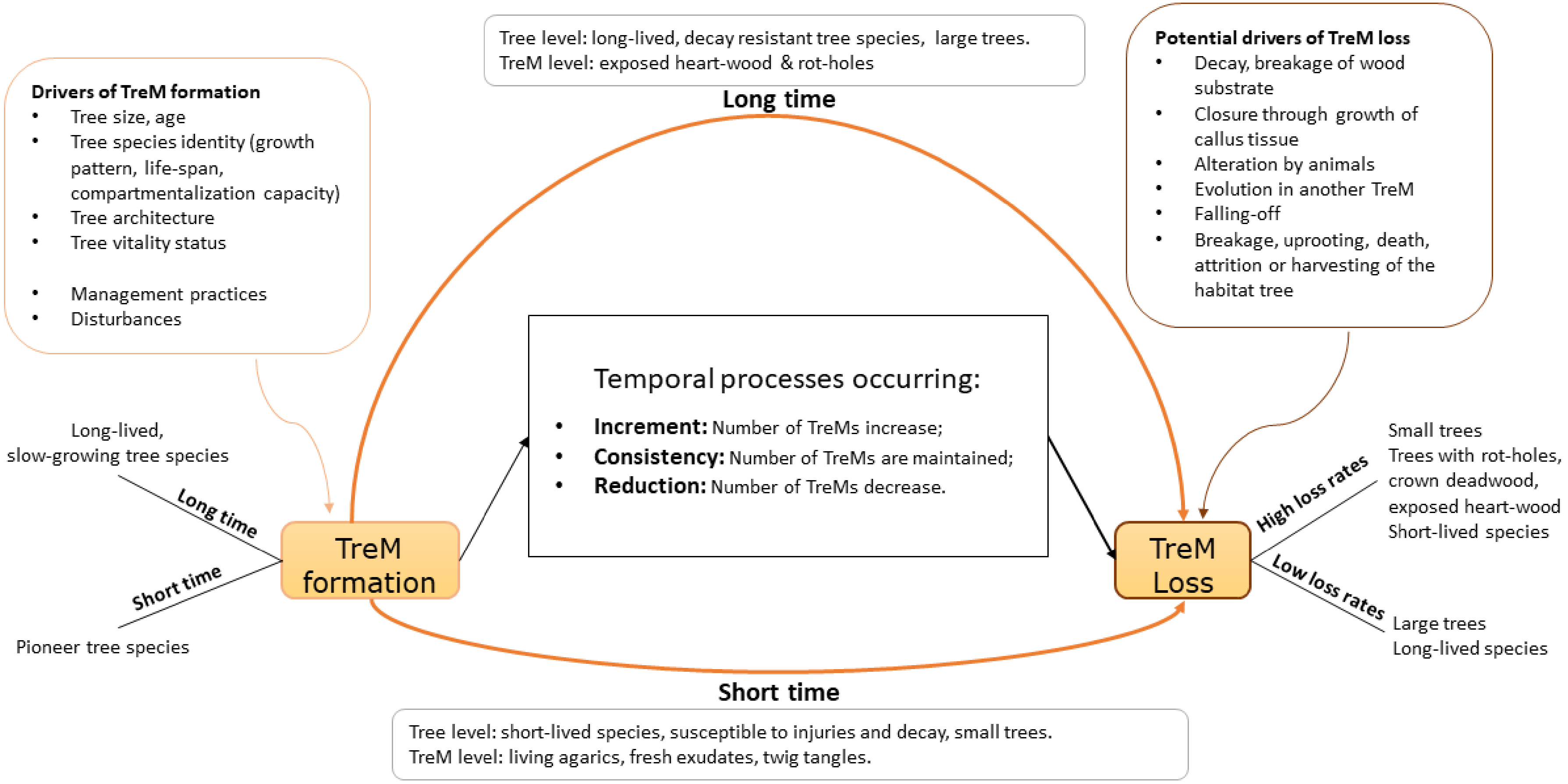


Figure 6. Conceptual development of microhabitats on living trees. Persistence and duration according to tree attributes and specific TreMs.

VI.2. Diversifying habitat tree retention

This thesis found that mortality rates among habitat trees were lower than average tree mortality rates, and the presence of TreMs did not affect tree vitality. However, it suggests that coniferous habitat trees may be more susceptible to future drought stress and subsequent insect outbreaks compared to broadleaved trees in the Black Forest region **(Chapter V)**. Therefore, in agreement with other studies, it may be assumed that if not salvaged, the deadwood volume of conifers such as *P. abies* or *A. alba* will continue to increase in the short to medium-term in forests of Central Europe (Seidl et al., 2017; Obladen et al., 2021; Pötzelsberger et al., 2021). The abundance of TreMs increases with advance decay stages and the composition of TreMs differs between *A. alba* and *P. abies*: woodpecker cavities, burrs and cankers found on *A. alba* and perennial fungi on *P. abies* **(Chapter II).** Under increased bark-beetle activity, TreMs such as insect galleries and bark structures (shelters, pockets) will be predominant on standing dead *P. abies* (Asbeck et al., 2023). While these types of habitats benefit several taxa (wild bees - Eckerter et al., 2021, bat species - Basile et al., 2020), sole retention of deadwood will not suffice for specialist organisms, when taking into consideration the temporal changes that occur on habitat trees.

The results of this study emphasise that the TreM composition of living trees differs significantly from that of dead trees, **(Chapter II)** and TreMs on both living and dead substrates may disappear over time **(Chapter IV).** Although not yet explored by other studies nor this current one, it may be assumed that due to breakage and attrition of dead habitat trees, TreMs present on those substrates will disappear. Therefore, retention practices should prioritise selection of trees with TreMs, not only to protect the TreMs associated with the current state of living trees, but also ensure a continuity in deadwood substrate with diverse attributes (e.g. diverse sizes, wood characteristics, decay stages, sun-exposure). This can be achieved by considering a combination of dead and living trees, long-lived and short-lived species, hardwood and softwood tree species of various ages, dimensions and ontogenic stages. For instance, pioneer species may accelerate restoration of TreMs, while longer-lasting trees accumulate more TreMs and provide diverse reserves for forest-dwelling species during trees lifetime and after their death **(Chapter II, III).** Large trees have been shown to harbour the most abundant and diverse TreM assemblages (Paillet et al., 2017,2019; Grossman et al., 2018; Kozak et al., 2023) and most dynamic TreM profile, as confirmed by this thesis. However, most TreMs, except for long-lasting ones (rot-holes, stem breakage, large injuries) change over time and disappear or evolve into other TreMs **(Chapter IV).** Additionally, to ensure secure future provisioning of TreMs associated with living trees, vital trees of species adapted to climate change can be included in retention schemes, regardless of their current TreM profile **(Chapter V)**.

This study found that dead trees exhibited a long-lasting decline in growth prior to death. However, the findings regarding tree mortality are limited to conifers due to the scarcity of dead broadleaved trees in the study area (Chapter V). Nonetheless, other studies have reported similar patterns of lower previous growth rates in dead trees of *F. sylvatica* compared to neighbouring surviving trees (Gillner et al., 2012; Camarero et al., 2018; Obladen et al., 2021). In the study region, the rates of *F. sylvatica* mortality were relatively low compared to drier regions, likely due to favourable site conditions and past management practices (Schuldt et al., 2020; Meyer et al., 2022). Similar low signals were detected for *F. sylvatica* in other managed sites under similar growing conditions after drought years in 2018 and 2019 (Meyer et al., 2022). However, *F. sylvatica* trees growing on dry sites with clay soils are negatively affected by recent extreme drought events (Obladen et al., 2021). Thinning practices and partial harvesting can benefit *F. sylvatica* trees by increasing their stem growth and enabling their survival during drought periods (Ammer, 2016; Pretzsch, 2005; Barna et al., 2010). Correspondingly, it may be assumed that habitat trees of *F. sylvatica* might benefit from releases through harvesting. On the contrary, sudden exposure to environmental stress, including increased evapotranspiration and susceptibility to wind and insect disturbances can be detrimental to very large trees (Bennet et al., 2015; Stovall et al., 2019). Additionally, although this study did not find a relationship between TreM occurrence and tree decline (Chapter V, similarly to Sebek et al., 2013; Grossmann et al., 2020), the presence of TreMs that may accelerate wood decay such as stem breakage or heartwood exposure could interact with the ability of trees to withstand environmental stress.

The current study provides valuable insights into mortality patterns of habitat trees, as influenced by drought and TreM presence and provides a comprehensive understanding of events and drivers influencing TreM dynamics, offering reliable recommendations for current retention schemes. The evidence-base established in this study considers the dynamic nature of TreMs and suggests that diversification of habitat trees is crucial for ensuring the availability of resources for forest-dwelling species in the long term. However, it is important to acknowledge that the success of this practice may vary depending on site conditions, such as tree species diversity and stand structural complexity. In even-aged managed forests, particularly those dominated by a single tree species, diversification of habitat trees can be challenging for practitioners. Implementing diversification strategies may also be influenced by factors such as economic feasibility and the availability of relevant information, especially in the case of private forest owners.

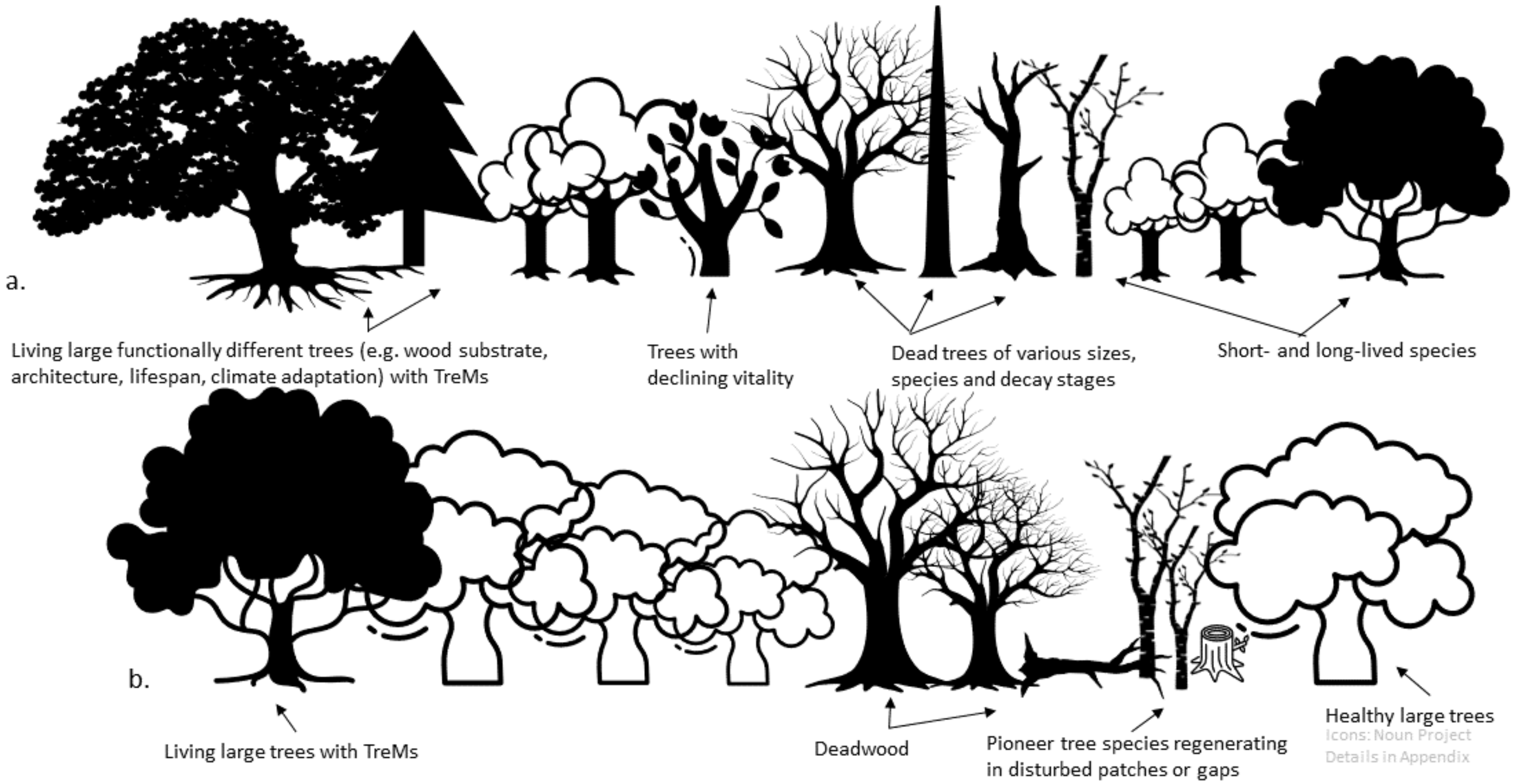
VI.3. Direct implications for forest management

Sustainable forest practices aim to address the conservation of biodiversity, the provision of ecosystem services taking into consideration the well-being of future generations (Kraus & Krumm, 2013; Larsen et al., 2022). The promotion of mixed-species and structurally complex stands can ensure both timber production and biodiversity protection, offering resistance and resilience in the face of future uncertainties linked to climate changes (Gamfeldt et al., 2013; Messier et al., 2021). Retention schemes should, therefore, align with the overall goals of promoting species and structural diversity in forest management and account for future temporal changes. In Europe, integrative forest management is implemented to resolve conflicting societal objectives within relatively small spatial scales, primarily driven by fragmented landscapes (Larsen et al., 2022). Thus, it is crucial that retention approaches suit the specific conditions of forest stand. In chapter VI.3., four distinct hypothetical forest stands and corresponding solutions to improve habitat tree retentions are presented, serving as examples of how the evidence-base established in this thesis may be utilised.

VI.3.1. Examples of diversified habitat tree selection

○ Reference stand with old-growth structures (Figure 7a)

In mature forests, particularly those characterised by a complex, multi-layered canopy structure and mixed-species composition, habitat tree retention can aim for the selection of a diverse range of functionally different trees. If present, trees harbouring diverse, abundant and/or rare TreMs should be protected to secure the availability of resources for forest-dwelling organisms in the present and near future (**Chapter II, IV**). Commonly, it has been observed that large, dead, broadleaved trees support the highest abundance and richness of TreMs (literature review by Asbeck et al., 2021, **Chapter II, III, IV**). Further, if such trees are scarce, the selection should focus on large living trees of different species and attributes to serve as future reserves. Suggested DBH thresholds are 86 cm for conifers and 70 cm for broadleaved trees (Grossmann et



Icons: Noun Project
Details in Appendix

Figure 7. Examples of diversification of habitat tree selection in forest stands with different conditions:

a. Structurally complex and mixed-species forest stand. Selection examples: identification of large trees exhibiting a diverse array of TreMs, considering the variation in wood characteristics, stem architecture, life-span, and resistance to injuries); inclusion of trees with different vitality statuses, such as living, declining, dead trees (upper figure).

b. Uneven-aged forest stand with long-living species (e.g. *Fagus sylvatica*). Selection examples: preservation of trees with existing TreMs; selection of healthy large trees with the potential to develop TreMs in the future; retention of deadwood and encouragement of pioneer tree species regeneration in disturbed patches (lower figure).

al., 2018). Encouraging a combination of coniferous and broadleaved tree species including long-lived ones with high compartmentalization capacity and short-lived ones with low compartmentalization capacity, is beneficial (Chapter II). However, if rare, specialist taxa are present, priority may be given to preserving the substrate needed for their survival, since those TreMs may disappear in the long-term (Chapter IV). Additionally, dead trees of various sizes, wood characteristics and decay stages are to be selected, especially if they do not pose any safety concerns for workers (Asbeck et al., 2019, Chapter II). In cases where most selected trees are senescent or over-mature and dead standing trees exhibit advanced decay, it is advisable to retain smaller, vital and declining trees to ensure a continuous supply of resources on both living and dead trees in the future (Chapter II, V) (Figure 7a).

Uneven-aged mature stand (Figure 7b)

A prevalent type of managed forests in Europe consists of multi-layered stands, often dominated by a single tree species such as *F. sylvatica*, *A. alba* or *P. abies*. For example, coniferous monoculture stands planted in the 19th and 20th centuries to address overexploitation and war devastation have since been converted into more complex stands, such as selection forests (Diaci, 2016; Pretzsch, 2019). The transformation of these stands has resulted in the development of uneven-aged forests with vertical diversity. However, the presence of old-growth elements such as large trees with numerous TreMs remains limited (Larrieu & Cabanettes, 2012; Asbeck et al., 2019; Vandekerkhove et al., 2018, Chapter II). In such cases, trees with large dimensions already present in the stands should be selected and allowed to grow and develop TreMs over time. Further, if gaps are present as a result of harvesting or natural disturbances, and regeneration has been established, special attention can be given to the young pioneer trees species (Chapter III). This current study emphasises how trees such as *P. tremula* and *B. pendula* can accelerate the provision of TreMs. This can be particularly beneficial when pioneer tree species are present in mature stands dominated by slow-growing species such as *F. sylvatica* and *Q. robur,* where passive habitat restoration processes may be extremely slow, often spanning more than 100 years - Chapter III, Vandekerkhove et al. 2005, Larrieu et al., 2017; 2019) (Figure 7b).

Even-aged mature stand consisting of a single tree species (Figure 8a)

In the case of even-aged stands, consisting of a single tree species, forest structure exhibits low variability, with most trees sharing attributes such as age or size. Forest management practices in these stands have historically focused on good-quality timber, leading to the removal of potential TreM-bearing trees such as low-quality trees, hazardous, forked, twisted, injured or diseased, as well as unwanted pioneer species (Puettmann et al., 2009, Chapter II, III). Consequently, suitable habitat trees, both living and dead may be lacking in such stands. Therefore, the selection of large living trees becomes crucial to allow for the formation of TreMs in the future. When the management objective is to accelerate restoration processes, active creation of TreMs can be employed, particularly considering that the majority of TreMs require a long time to develop naturally (Paillet et al., 2017; Bengtsson et al., 2012; Asbeck et al., 2023, **Chapter III**). Traditional practices such as pollarding or coppice played a significant role in the formation of TreMs, such as hollows or rot-holes (Ranius et al., 2009; Sebek et al., 2012). These practices, along with pruning which also initiate TreM formation, are no longer or rather limitedly used in gardens, urban forests or specific forest types (Sebek et al., 2012; Grossmann et al., 2020) (Figure 8a).

Experimental techniques have recently been employed at both the tree-level, such as the creation of specific TreMs through “tree veteranization” or the inoculation of trees with fungi (Bengtsson et al., 2012; Bednarz et al., 2013; Wainhouse & Boddy, 2022), as well as at the stand level, including topping and girdling of trees (Asbeck et al., 2023). It is important to note that excavated tree-holes tend to persist for a shorter duration compared to non-excavated ones (Wesolowski & Martin, 2018). Similarly, artificially created TreMs may also have shorter persistence than naturally formed ones, especially in young, small trees (**Chapter III**). In general, the artificial creation of TreMs and deadwood are time-consuming and should be approached with caution, as they can trigger insect outbreaks (Asbeck et al., 2023). These practices, should be carefully considered until further research can provide more clarity on their suitability for specific restoration objectives.

o Early stages of forest development (Figure 8b)

In the context of early stages of forest development, such as regeneration of large gaps or establishment of young plantations, it is important to consider the future habitat tree retention. Traditionally, potential habitat trees with unusual shapes or defects, as well as naturally regenerated pioneer species, have been removed during tending and thinning operations. However, an alternative approach involves retaining such trees within stands as potential habitat trees (Figure 8b). By preserving and selecting potential habitat trees, biodiversity conservation can be promoted from the early stages of forest development. Additionally, habitat tree selection should align with the changes in forest management practices. For example, given the expected changing climatic conditions, promoting the inclusion of drought-adapted tree species in retention schemes can enhance the adaptive capacity of the forest stands in the long term. This proactive, dynamic and diversified approach ensures provisioning of future reserves and supports the overall ecological integrity of the forest ecosystem (Figure 8b).

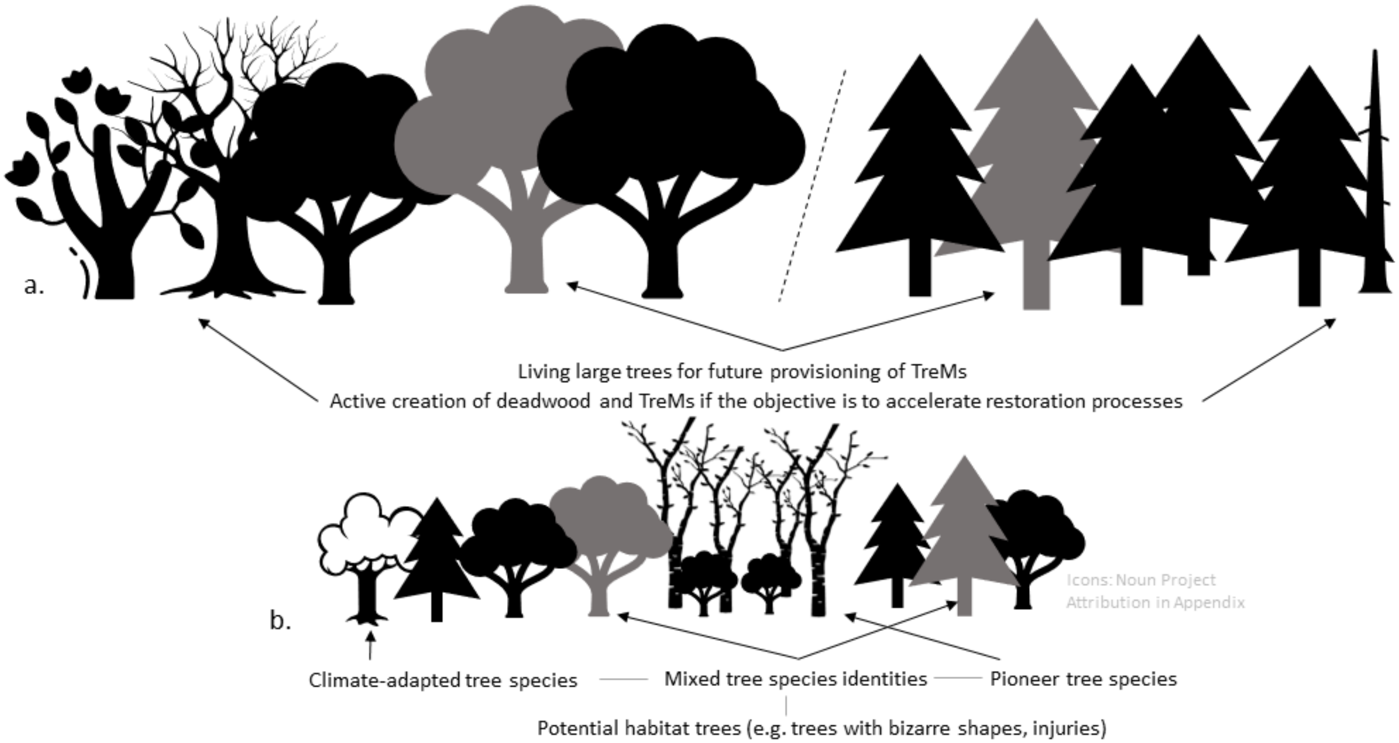


Figure 8. Examples of diversification of habitat tree selection in forest stands with different conditions:

a. Even-aged mature stand, single tree species. Selection examples: retention of living large trees that have the potential to develop TreMs in the future; enhancement of structural complexity through the creation of TreMs on living trees and incorporation of deadwood (upper figure).

b. Regeneration of large gaps or young stands. Selection examples: early-stage selection of potential habitat trees, such as trees with bizarre shapes or injuries; incorporation of different climate-adapted tree species in selection schemes; retention of naturally regenerated pioneer species as habitat trees (lower figure).

VI.3.2. Implementation

The successful implementation of a dynamic and diversified habitat tree retention approach is constrained by various factors. The selection of habitat trees in managed forests can lead to a reduction in harvesting volumes and profits, particularly when vital and large individuals are selected as habitat trees. Additionally, depending on the spatial arrangement of the selected trees, their location can affect stand access, workers safety, and future silvicultural operations. The calculation of costs associated with biodiversity conservation practices may be challenging (Hanley & Perrings, 2006; Paul et al., 2020), making it difficult to accurately assess their financial implications. Further, selection of habitat trees based on their TreM profile is also time-limited and -consuming. TreM surveys should be to carried out in the snow-and leaf-free periods, when the observer may visually asses the whole stem and crown of the tree, which may lead to additional costs.

While user-friendly catalogues, software applications and TreM co-occurrence lists are available (Kraus et al., 2016; Larrieu et al., 2021), forest owners and practitioners may still lack clear guidelines or training on how to effectively use these resources. For example, in the state forests of Baden Württemberg, practitioners are legally obliged to select habitat trees based on guidelines that follow the "Old- and deadwood concept" (ForstBW, 2016). The selection includes criteria such as the presence of specific TreM, including woodpecker cavities, stem injuries, fruiting bodies of fungi, lightning scars, or crown deadwood. In Germany, a new grant programme has been designed to financially incentivise biodiversity-friendly practices in forest management, requiring designation and maintenance of a minimum of five habitat trees or potential candidates per hectare (https://www.klimaanpassung-wald.de). However, such programmes do not provide any guidance on the selection of habitat trees. In order to obtain a balanced selection of trees that exhibit functional diversity, increased efforts for knowledge-transfer between researchers and practitioners are necessary. For instance, managers could benefit from educational and practical training aimed at improving their understanding of TreM surveys and diversified habitat tree selection in designated training forest plots, known as "marteloscopes" (Kraus et al., 2021; Joa et al., 2020). Knowledge-exchange efforts are crucial for consolidating the use of evidence-based retention strategies to achieve positive social and ecological outcomes (Gori et al., 1991; Chausson et al., 2020).

VI.4. Research limitations and future outlook

This thesis provides novel descriptions of TreM profiles and time-series analysis on trees with distinct functional characteristics. The findings of this research have direct practical applicability in the management of closer-to-nature forests in Europe. However, certain aspects related to the conservation value and development of habitat trees and TreMs could not be thoroughly examined or addressed within the scope of this study, but serve as opportunities for future research.

VI.4.1. Restricted data collection and analysis

Although the sample size of trees may have been sufficient, conducting an analysis at the TreM type level for all tree species, considering various developmental conditions (e.g. balanced sampling of tree decay classes, diversified tree species) was not feasible due to the overall scarcity of TreMs, particularly in managed forests. Further, the observations of TreM were predominantly characterised by low counts (zero, one, or two). In future, the retention of habitat trees in managed forests will facilitate TreM formation, allowing for in-depth investigations into the complex relationships between specific TreM occurrence and tree attributes. Such studies, combined with investigations into individual TreM development, could inform dynamic models and contribute to future decision-making regarding to more biodiversity-friendly strategies in multiple-use forests (Courbaud et al., 2022). However, collecting temporal observations of TreMs, especially those related to rare events, will pose challenges. While this thesis provided the first insights into the temporal changes of TreMs, the focus was primarily on living trees, as their selection presents greater challenges for practitioners compared to deadwood retention. Additionally, the description of the effects of TreM occurrence on tree vitality, and the impact of drought stress on habitat tree mortality were limited to conifers. Therefore, further studies investigating habitat tree mortality, following their development and observing changes in TreM assemblages following tree death will strengthen the dynamic evidence-base provided by this thesis.

VI.4.2. Biases and uncertainties in TreMs surveys

Nowadays, TreM typologies may be utilized to improve the comparability of TreM data (Larrieu et al., 2018; Kraus et al., 2016). However, observer bias can still influence TreM studies, particularly those collected by multiple observers, as in the case of Chapter IV (Paillet et al., 2015). Although remote-sensing techniques may offer more accurate and objective data collection and prediction, their high costs and time-consuming nature makes implementation at larger scales challenging (Rehush et al., 2018; Frey et at; 2020). Additionally, using a TreM typology designed for dead trees could lead to different results. By comparing the widely-used TreM classification (Larrieu et al., 2018) with a methodology that included TreMs relevant to local biodiversity, Kõrkjas (2021) highlighted the influence of the criteria itself on TreM estimates. The reliance of TreM abundance has its limitations as well, as count data are combined with presence/absence data in the existing catalogues (e.g. woodpecker cavities vs. lichen cover). Further, the typologies used might not reflect local conditions of biodiversity (et al., 2021). Owing to these limitations, TreMs might not be the "silver bullet" indicator (Asbeck et al., 2021), but are "promising, yet underused tools for biodiversity and nature conservation" (Martin et al., 2022). TreM surveys have been incorporated recently into studies quantifying forests biodiversity potential and could further be integrated into national forest inventory databases to address long-term ecological research questions (e.g. Hülsmann et al., 2017) or biodiversity assessments (Chirici et al., 2011). While the relationship between TreMs and species richness has generally yielded weak results (Paillet et al., 2018), the presence of large, old trees, presumed to have TreMs, has shown a positive correlation with species richness across different taxa (Zeller et al., 2023). This contrast may be due to an overall low number of TreMs found in European forests and a focus on biodiversity in general (Zeller et al., 2023). Studies targeting the relationship between specialised species and the quality and availability of associated TreMs have demonstrated strong connections, particularly for tree hollows or water-filled holes (Micó et al., 2017; Cuff et al., 2021). To improve habitat tree selection, further research should be carried out to establish causal relationships between TreMs and forest organisms. Some attempts have been made using trap cameras and environmental DNA analysis, allowing for the study of both dependent and visiting taxa (Kirsch et al., 2021; a collaboration derived from this thesis within the ConFoBi RTG: Shaw et al., 2023, in preparation).

It is also important to acknowledge that while this current study emphasises the significance of habitat trees and their TreMs for enhancing forest biodiversity in managed forests, other key elements should not be overlooked. For instance, the importance of lying deadwood has been recognised as crucial for the conservation of numerous saproxylic species, since this substrate decays at a faster rate and contains more moisture than standing dead wood (Merganičová et al, 2012; Paletto et al., 2012; Přívětivý et al., 2018). It would be interesting to investigate how TreMs change not only following tree death, but also throughout the subsequent stages of development as a lying log. Forest structural indices based on variables such as diversity of tree dimensions, decay stage, flowering and fructification need to be considered in future studies to capture habitat provisioning in multiple-use forests (Storch et al., 2018, 2023).

VI.5. Conclusion

This thesis uncovers how the occurrence and persistence of tree-related microhabitats are shaped by the complex interaction of tree attributes such as size, vitality, and species identity, and life-history traits. Large trees emerge as crucial elements, facilitating abundant, diverse, unique and dynamic TreM profiles throughout their lifetime and following their death. This study also underscores the complementarity of trees with contrasting attributes, such as life span, or capacity to withstand and recover from injuries or environmental stress. By shedding light on the dynamic nature of habitat trees and their TreMs, this research advanced the understanding of the consequence of habitat tree retention for forest biodiversity in temperate European Forests. To secure an ongoing and varied provision of resources for species inhabiting temperate European forests, it is imperative to apply dynamic and diversified approaches when selecting habitat trees within existing retention strategies.

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VII. Supplementary material

Supplementary material - Chapter four

Appendix 1a. Harmonisation and composition of TreM groups.

Harmonised TreM groups (Classification: Larrieu et al. 2018)	TreM types in Spinu and Paillet (Classification: EFI Catalogue)	TreM types in Kozak 1 (Classification CZU 1)	TreM types in Kozak 2 (methodology 2)
Woodpecker breeding cavities	CV 11-13, 15	11, 13	1, 2, 3, 4
Rot-holes	CV 21-30, CV 32-33	12, 17	5, 6, 7, 8, 9, 10
Insect galleries and bore holes	CV 51-52	NA	11
Concavities	CV 42, CV 44, CV 14, GR 12-13	15, 16, 20	12, 13, 14, 15
Exposed sapwood only	IN 11-14, IN 34, BA 11-12	51, 52, 64, 65	16, 17, 18, 19
Exposed sapwood and heartwood	IN 21-22, IN 24, IN 31-33	61, 62, 63	20, 21, 22, 23, 24
Crown deadwood	IN 23, DE 11-15	71, 72, 73, 74, 75	25, 26, 27
Twig tangles	GR 21-22	82	28, 29
Burrs and cankers	GR 31-32	81	30, 31
Perennial fungal fruiting bodies	EP 12	41, 42	32
Ephemeral fungal fruiting bodies and slime moulds	EP 11, EP 13-14, EP 21	NA	33, 34, 35, 36
Epiphytic or parasitic crypto- and phanerogams	EP 31-35	83, 84, 85	37, 38, 39, 40, 41
Nests	NE 11-21	NA	42, 43
Microsoils	OT 21-22	NA	44, 45
Fresh exudates	OT 11-12	31, 32	46, 47
Excluded TreMs	CV 31, CV 41, CV 43, GR 11, BA 21	14, 53	NA

Appendix 1b. Classification and description of tree-related microhabitats from Larrieu et al. 2018

Form	Group	Examples of TreM types
Cavities	Woodpecker cavities	Small woodpecker breeding cavity. Medium-sized woodpecker breeding cavity Large woodpecker breeding cavity Woodpecker "flute" (breeding cavity string)
	Rot-holes	Trunk base rot hole Trunk rot hole Semi-open trunk rot hole Chimney trunk base rot hole Chimney trunk rot hole Hollow branch
	Insect galleries and bore holes	Insect galleries and bore holes
	Concavities	Dendrotelm (phytotelmata, waterfilled hole) Woodpecker foraging excavation Trunk bark-lined concavity Root buttress concavity
Tree injuries and exposed wood	Exposed sapwood only	Bark loss Fire scar Bark shelter Bark pocket
	Exposed sapwood and heartwood	Stem breakage Limb breakage (heartwood exposed) Crack Lightning scar Fork split at the intersection
Crown deadwood	Crown deadwood	Dead branches Dead top Remaining broken limb
Excrescences	Twig tangles	Witch broom Epicormic shoots
	Burrs and cankers	Burrs and cankers
Fruiting bodies of saproxylic fungi and slime moulds	Perennial fungal fruiting bodies (life span> 1y)	Perennial polypore
	Ephemeral fungal fruiting bodies and slime moulds	Annual polypore Pulpy agaric Pyrenomycete Myxomycete
Epiphytic, epixylic and parasitic structures	Epiphytic or parasitic crypto- and phanerogams	Bryophytes Foliose and fruticose lichens Ivy and lianas Ferns Mistletoe
	Nests	Vertebrate nest Invertebrate nest
	Microsoils	Bark microsoil Crown microsoil
Fresh exudates	Fresh exudates	Sap run Heavy resinosis
7 forms	15 groups	47 types

Appendix 1c. Classification following EFI Catalogue (Kraus et al., 2016. Catalogue of tree microhabitats – Reference field list. Integrate+ Technical Paper. 16p)

Microhabitat type	Code	Description	Microhabitat type	Code	Description
Bark	BA11	Bark shelter, open bottom	Bark	BA12	Bark pocket, open top
Woodpecker cavity	CV11	Cavity entrance about ø = 4 cm	Woodpecker Cavity	CV14	ø ≥ 10 cm feeding hole
Woodpecker Cavity	CV12	Cavity entrance about ø = 5 - 6 cm w	Woodpecker Cavity	CV15	Woodpecker "flute“ /cavity string
Woodpecker Cavity	CV13	ø > 10 cm Woodpecker hole in the trunk			
Trunk/ mould cavity	CV21	ø ≥ 10 cm (ground contact)	Trunk/ mould cavity	CV24	ø ≥ 30 cm (no ground contact)
Trunk/ mould cavity	CV22	ø ≥ 30 cm (ground contact)	Trunk/ mould cavity	CV25	ø ≥ 30 cm / semi-open
Trunk/ mould cavity	CV23	ø ≥ 10 cm (no ground contact)	Trunk/ mould cavity	CV26	ø ≥ 30 cm /open top
Branch hole	CV32	ø ≥ 10 cm holes from breakage	Branch hole	CV33	Hollow branch, ø ≥ 10 cm
Dendrotelm	CV42	ø ≥ 15 cm / trunk base	Dendrotelm	CV44	ø ≥ 15 cm / crown
Insect gallery/bore holes	CV51	Gallery with single small bore holes	Insect gallery/bore holes	CV52	Large bore hole
Dead branch	DE11	ø 10 - 20 cm, ≥ 50 cm, sun exposed	Dead branch	DE12	ø > 20 cm, ≥ 50 cm, sun exposed
Dead branch	DE13	ø 10 - 20 cm, ≥ 50 cm, not sun exposed	Dead branch	DE14	ø > 20 cm, ≥ 50 cm, not sun exposed
Dead branch	DE15	Dead top ø ≥ 10 cm			
Fungi fruiting body	EP11	Annual polypores, ø > 5cm	Fungi fruiting body	EP13	Pulpy agaric, ø > 5 cm
Fungi fruiting body	EP12	Perennial polypores, ø > 10 cm	Fungi fruiting body	EP14	Large ascomycetes, ø > 5 cm
Myxomycetes	EP21	Myxomycetes, ø > 5 cm			

Epiphyte	EP31	Epiphytic bryophytes, > 25 % trunk	Epiphyte	EP34	Epiphytic ferns, > 5 fronds
Epiphyte	EP32	Epiphytic foliose/ lichens, > 25 % trunk	Epiphyte	EP35	Mistletoe in tree crown
Epiphyte	EP33	Lianas, coverage > 25 %,			
Root buttress cavity	GR12	ø ≥ 10 cm, natural cavity	Root buttress cavity	GR13	Trunk cleavage, length ≥ 30 cm
Witches broom	GR21	Witches broom, ø > 50 cm	Witches broom	GR22	Water sprout, dense epicormics
Canker or burr	GR31	Cancerous growth, ø > 20 cm	Canker and burr	GR32	Decayed canker, ø > 20 cm
Bark loss	IN 11	Bark loss 25- 600 cm2, decay stage < 3	Bark loss	IN13	Bark loss 25- 600 cm2, decay stage = 3
Bark loss	IN12	Bark loss >600 cm2, decay stage < 3	Bark loss	IN14	Bark loss >600 cm2, decay stage = 3
Exposed heartwood	IN21	Broken trunk, ø ≥ 20 cm at broken end	Exposed heartwood	IN23	Broken limb, ø ≥ 20 cm at broken end
Exposed heartwood	IN22	Broken tree crown /fork	Exposed heartwood	IN24	Splintered stem, ø ≥ 20 cm
Crack or scar	IN31	Length ≥ 30 cm	Crack or scar	IN33	Lightning scar
Crack or scar	IN32	Length ≥ 100 cm	Crack or scar	IN34	Fire scar, ≥ 600 cm^2
Nest	NE11	Large vertebrate nest, ø > 80 cm	Nest	NE21	Invertebrate nests in trunk
Nest	NE12	Small vertebrate nest, ø > 10 cm			
Sap and resin run	OT11	Sap flow, > 50 cm, fresh, deciduous	Sap and resin run	OT12	Resin flow /pockets, > 50 cm, coniferous
Micro soil	OT21	Crown micro soil	Micro soil	OT22	Bark micro soil

Appendix 1d. Classification following the methodology from D. Kozak, Czech University of Agricultural Sciences.

Methodology 1

10 - Cavities. Woodpecker breeding or feeding holes deep enough to host a vertebrate. Deep cavities formed between roots. Cavities with mould.
  - 11 - Woodpecker cavities with > 2 cm aperture.
  - 12 - Non-woodpecker cavities with > 5 cm aperture: formed after injury, branch fall.
  - 13 - Cavity string: at least three woodpecker cavities in a stem with a maximum distance of two meters between two cavity entrances. Cavity strings are an important starting point for the development of deep and long-lasting stem cavities.
  - 14 - Small cavities in the rings.
  - 15 - Deep stem cavities: a tubular cavity in the base of the tree.
  - 16 - Deep stem cavities: a tubular cavity in the base of the tree with mould.
  - 17 - Decayed hollow tree: a large cavity.

20 - Dendrotelms. Water-filled holes in wood.

30 - Sap runs. Both chronic and short-lived slime fluxes.
  - 31 - Sap or resin drop: Only a few sap or resin drops indicating a minor injury.
  - 32 - Heavy sap or resin: fresh heavy flow of sap or resin at least 30 cm long or > 5 flows of sap or resin of smaller size.

40 - Saproxylic fungi. Polypores s.l.
  - 41 - Conks of fungi. Fruiting bodies, diameter > 5 cm.
  - 42 - Conks of fungi. Fruiting bodies > 5 cm in diameter or occur in 10 cm long cascades of smaller fruiting bodies.

50 - Missing bark. Bare wood patches with bark loss and wood in a decay stage of less than 2.
  - 51 - Bark loss: patches with bark loss of at least 5 cm x 5 cm mainly caused by felling or natural falling of trees.
  - 52 - Bark burst: black burst of bark often with resin indicating injury/disease.
  - 53 - Gnaw + peeling by game: peeled bark or bark gnawed.

60 - Cracks and shelter bark. Cracks in the trunk wood. Peeling bark that forms a shelter.
  - 61 - Splintered stem: the split-up results in numerous scales (minimum 5) of wood > 50 cm long; caused by another tree fall etc.
  - 62 - Lightning scar: a crack caused by lightning; at least 3 m long and reaching the sapwood.
  - 63 - Cracks: cleft into the sapwood > 25 cm long along the stem and at least 2 cm deep in the sapwood.
  - 64 - Bark pocket: space between loose bark and the sapwood with a minimum extension of 5 cm x 5 cm x 2 cm.
  - 65 - Bark pocket with mould: same structure and size as 64 but with mould.

70 - Crown deadwood. Dead branches with a diameter > 5 cm located in the tree crown. Stem breakage.
  - 71 - Between 10% and 25% of dead crown: one or more main branches are dead. The living crown represents 75% of the former total crown.
  - 72 - Between 25% and 50% of dead crown: one or more main branches are dead. The living crown represents between 50 and 75% of the former total crown.
  - 73 - >50% the dead crown: one or more main branches are dead. The living crown seems to be <50% of the former total crown.
  - 74 - Broken stem: the primary crown is totally absent with or without presence of a secondary crown. Main parts of the tree stem are already dead with decomposing processes.
  - 75 - Broken fork: complete fracture of one of the two forking branches; the loss of one forking branch results in a severe damage of the main stem.

80 - Others.
  - 81 - Canker: proliferation of cell growth; irregular cellular growth on stems or branches, which is caused by bark-inhabiting fungi, viruses and bacteria. We will record areas of canker > 10 cm in diameter.
  - 82 - Witch broom: dense agglomeration of branches from a parasite or epicormic branching.
  - 83 - Bryophytes developed on > 50% of the base or trunk area.
  - 84 - Ivy developed on > 50% of the base or trunk area.

- 85 - Mistletoe

Methodology 2

1 - Small woodpecker breeding cavity (entrance diameter < 4cm): cavity entrance diameter < 4 cm, the breeding cavity of Dendrocopos minor is usually drilled in a dead branch.
2 - Medium-sized woodpecker breeding cavity (entrance diameter = 4-7 cm): round cavity entrance about diameter = 4-7 cm, the breeding cavities of the medium-sized woodpeckers are usually drilled into decaying wood (dead branch, snag, insertion of broken-off branches).
3 - Large woodpecker breeding cavity (entrance diameter > 10 cm): oval cavity entrance diameter > 10 cm, the breeding cavities of Dryocopus martius are usually drilled on the main part of the trunk.
4 - Woodpecker flute (entrance diameter > 3 cm): at least three woodpecker breeding cavities in line on the trunk, maximum distance of 2 m between two consecutive cavities.
5 - Trunk base rot-hole (closed top, ground contact, opening diameter > 10 cm): cavity chamber is completely protected from surrounding microclimate and rain, top-closed trunk cavity containing more or less mould (depending on its development stage), the cavity bottom has ground contact, note that the cavity entrance can be higher on the trunk.
6 - Trunk rot-hole (closed top, no ground contact, opening diameter > 10cm): top-closed trunk cavity containing more or less mould (depending on its development stage), the cavity bottom has no ground contact.
7 - Semi-open trunk rot-hole (opening diameter > 30 cm): cavity chamber is not completely protected from surrounding microclimate and rain may flow in, note that the cavity entrance can be higher up in the trunk.
8 - Chimney trunk base rot-hole (opening diameter > 30 cm): cavity in the trunk of the tree that is completely open at the top, often resulting from stem breakage, the cavity base reaches ground level, so the inner cavity is in direct contact with the soil.
9 - Chimney trunk rot-hole (opening diameter > 30 cm): cavity in the trunk of the tree that is completely open at the top, often resulting from stem breakage, the cavity base does not reach ground level, so the inner cavity is not in direct contact with the soil.
10 - Hollow branch (opening diameter > 10 cm): rot hole in a large branch, resulting in a tubular shelter, often horizontally oriented.
11 - Insect galleries and bore holes (hole diameter > 2 cm or area > 300 cm2): a bore hole network of xylophagous insects indicates a wood hole system, an insect gallery is a complex system of holes and chambers created by one or more insect species in the wood.
12 - Dendrotelm (diameter > 15 cm): cup-shaped concavity that, due to its form, retains water until it dries out by evaporation.
13 - Woodpecker foraging excavation (depth > 10 cm, diameter > 10 cm): concavity resulting from the foraging activities of woodpeckers, the excavation is conical - the entrance is larger than the interior.
14 - Trunk bark-lined concavity (depth > 10 cm, diameter > 10 cm): natural bark-lined concavity on the tree trunk, no mould.
15 - Root-buttress concavity (entrance diameter > 10 cm): natural bark-lined concavity at the base of the tree trunk formed by the tree roots and the soil, no mould (if so - see Trunk base rot hole).
16 - Bark loss (area > 300 cm2): loss of bark exposing sapwood (skinning caused e. g. by felling, skidding, natural tree fall, rock fall, rodents). Counts also on snags, but only such bark loss that were established during previous living stage of tree.
17 - Fire scar (area > 600 cm2): fire scars on the lower trunk, they usually have a triangular shape and are located at the base of the tree on the leeward side, fire scars are associated with charcoal and sometimes resin flow on exposed sapwood or bark.
18 - Bark shelter (gap > 1 cm, depth > 10 cm, height > 10 cm): space between peeled-off bark and sapwood forming a shelter (open at the bottom).
19 - Bark pocket (gap > 1 cm, width > 10 cm, height > 10 cm): space between peeled-off bark and sapwood forming a pocket (open at the top) possibly containing mould.
20 - Stem breakage (diameter > 10 cm at break point): the stem has broken off but the tree is still alive, the lower part of the deadwood is in contact with living wood with living wood with sap flow.
21 - Limb breakage (exposed heartwood > 300 cm2): exposed heartwood through limb or fork breakage, the wound is surrounded by living wood with sap flow.

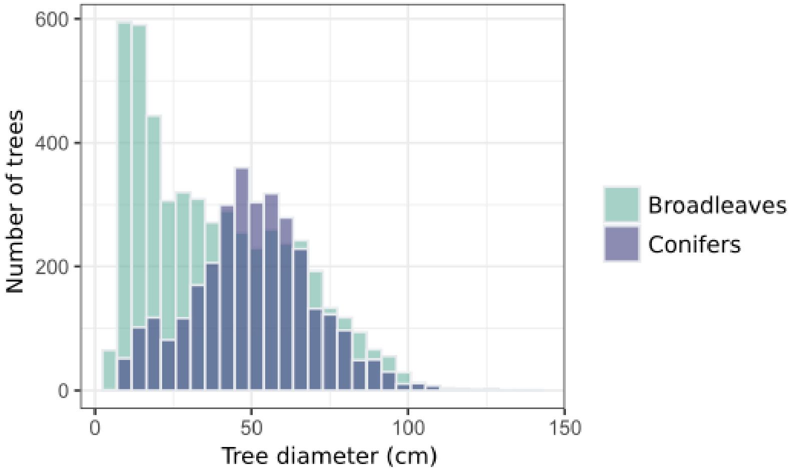
22 - Crack (length > 30 cm, width > 1 cm, depth > 10 cm): crack through the bark and the wood (if caused by lightning strike see Lightning scar).
23 - Lightning scar (length > 30 cm, width > 1 cm, depth > 10 cm): crack caused by lightning strike, usually spiraling around the tree with splintered wood present.
24 - Fork split at insertion (length > 30 cm): crack at the insertion of a fork, if one side of the fork has broken off, see Stem breakage).
25 - Dead branches (branch diameter > 10 cm, or branches diameter > 3 cm and > 10 % of the crown is dead): dead branches located in the canopy, conditions remain relatively shady.
26 - Dead top (diameter > 10 cm at the base of the piece of deadwood): the entire top of the tree is dead; the deadwood is sun-exposed.
27 - Remaining broken limb (broken end diameter > 20 cm, length of remaining piece > 0.5 m): a limb has broken off, the remaining end may be splintered, the injury does not affect the trunk (if so, see Stem breakage).
28 - Witch broom (largest diameter > 50 cm): dense agglomeration of twigs on branches.
29 - Epicormic shoots (> 5 twig clusters): dense agglomeration of twigs along the trunk.
30 - Burr (largest diameter > 20 cm): proliferation of cell growth with rough bark.
31 - Canker (largest diameter > 20 cm or large part of trunk covered): decayed canker, sapwood exposed, caused by e. g. Melampsorella caryophyllacerum, Nectria l. s.
32 - Perennial polypore (largest diameter > 5 cm): tough fruiting bodies of perennial polypores, showing distinct annual tube layers, main perennial genera Fomitopsis pp, Fomes, Perreniporia pp, Oxyporus, Ganoderma pp, Phellinus, Daedalea, Haploporus, Heterobasidion, Hexagonia, Laricifomes, Daedleopsis.
33 - Annual polypore (largest diameter > 5 cm or cluster of > 10 fruiting bodies): fruiting bodies of annual polypores, lasting several weeks, the European annual polypores have only one layer of tubes and are usually elastic and soft (no woody parts).
34 - Pulpy agaric (largest diameter > 5 cm or cluster of > 10 fruiting bodies): large, thick and pulpy or rather fleshy fruiting body of gill - bearing fungi (order Agaricales), e. g. Armillaria, Pleurotus, Pholiota, or large Pluteus species, the fruiting body generally remains several weeks.
35 - Large Pyrenomycete (stroma diameter > 3 cm or stroma cluster covering > 100 cm2): tough hemispheric dark fungi resembling a lump of coal.
36 - Myxomycetes (largest diameter > 5 cm): amoeboid slime mold which forms moving plasmodium, the plasmodium is gelatinous when fresh.
37 - Bryophytes (> 10 % of the trunk area covered): trunk covered by mosses and liverworts.
38 - Foliose and fruticose lichens (> 10 % of the trunk area covered): trunk covered by foliose or fruticose lichens.
39 - Ivy and lians (> 10 % of the trunk area covered): lianas and other climbing phanerogams (Hedera helix, Clematis vitalba, Lonicera periclimenum, Vitis vinifera).
40 - Ferns (> 5 fronds): ferns growing directly on a part of a tree (i. e. epiphyte).
41 - Mistletoe (largest diameter > 20 cm): hemiparasitic plants (Viscum spp., Arceuthobium oxycedri, Loranthus europaeus).
42 - Vertebrate nest (diameter > 10 cm): nest built by birds, dormice, mice or squirrels.
43 - Invertebrate nest (presence): larval nest of invertebrates e. g. Pine processionary moth Thaumetopoea pityocampa, wood ant Lasius fuliginosus or wild bees Apis melifera.
44 - Bark microsoil (presence): microsoil resulting from micro-pedogenesis of epiphytic mosses, lichens or algae and necrosed old, thick bark.
45 - Crown microsoil (presence): microsoil resulting from pedogenesis of debris and litter fallen from the crowns, often colonized by roots of the TreM bearing-tree, main positions - flat areas on limbs, forks, sometimes stem junctions of twin.
46 - Sap run (cumulative length > 10 cm): fresh significant flow of sap.
47 - Heavy resinosis (cumulative length > 10 cm): fresh significant flow of resin.

Appendix 2a. Proportion of surveyed living trees by species and data origin

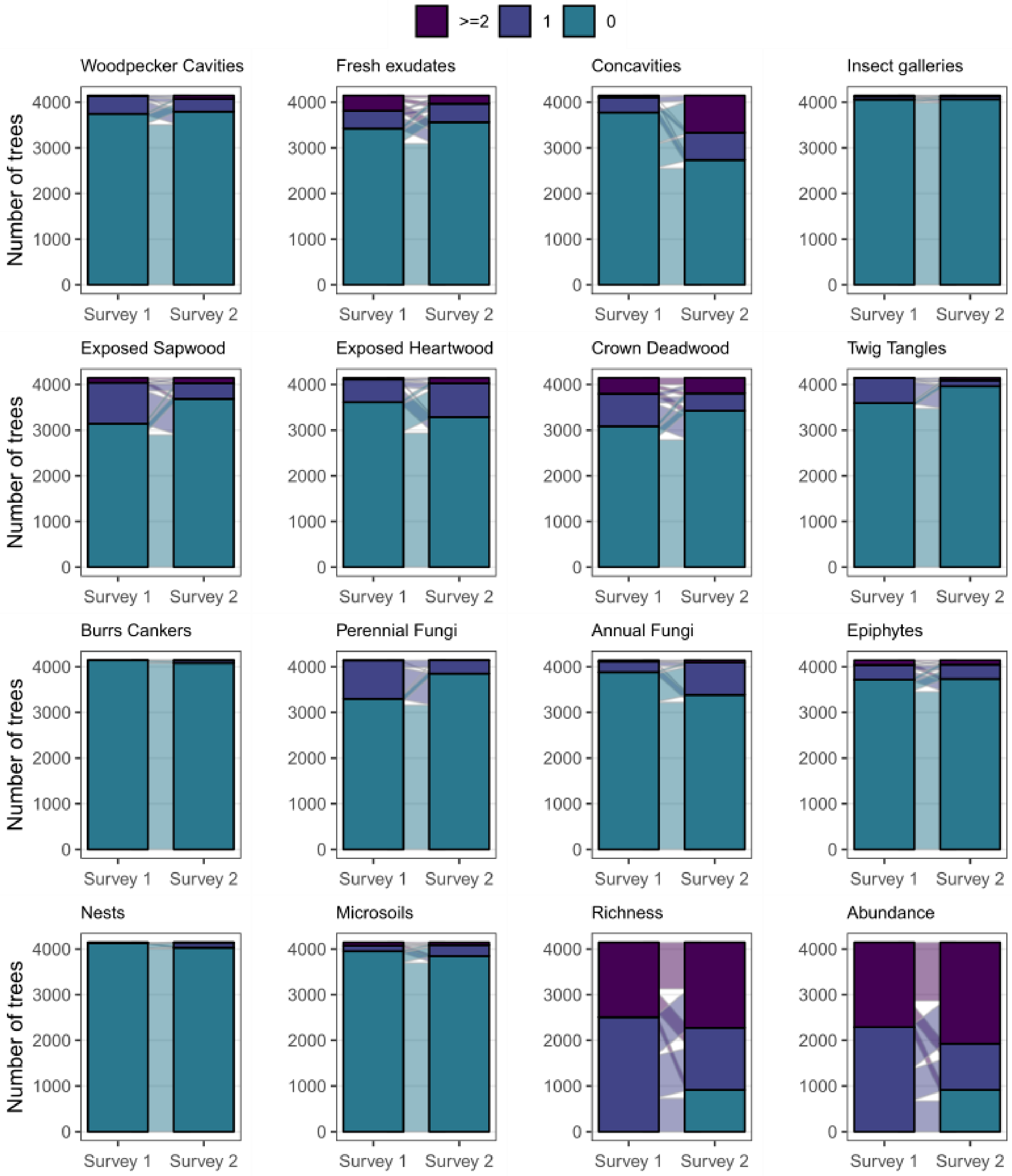
Tree species	Share (%)	Tree species	Share (%)
Abies alba	17.63	*Other conifers*	0.02
Acer campestre	0.22	*Picea abies*	19.56
Acer opalus	0.78	*Pinus sylvestris*	0.98
Acer platanoides	0.12	*Populus sp.*	0.05
Acer pseudoplatanus	5.16	*Pseudotsuga menziesii*	0.71
Betula sp.	3.32	*Quercus petraea*	0.42
Carpinus betulus	1.29	*Quercus robur*	0.17
Fagus sylvatica	33.98	*Quercus sp.*	0.75
Fraxinus sp.	2.04	*Salix sp.*	0.30
Ilex aquifolium	0.17	*Sorbus aria*	1.39
Laburnum anagyroides	0.35	*Sorbus aucuparia*	1.30
Larix decidua	0.25	*Tilia sp.*	1.06
Other broadleaves	0.14	*Ulmus sp.*	0.35

Data origin	Share (%)
France, Y. Paillet	70.4
Germany, A. Spinu	14.1
Eastern Europe, D. Kozak	15.5

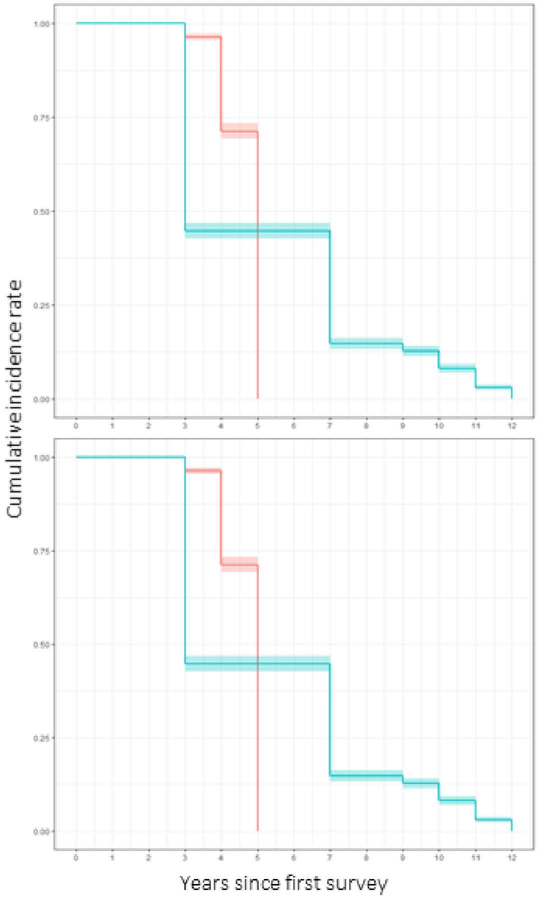
Appendix 2b. Distribution of habitat tree diameter.



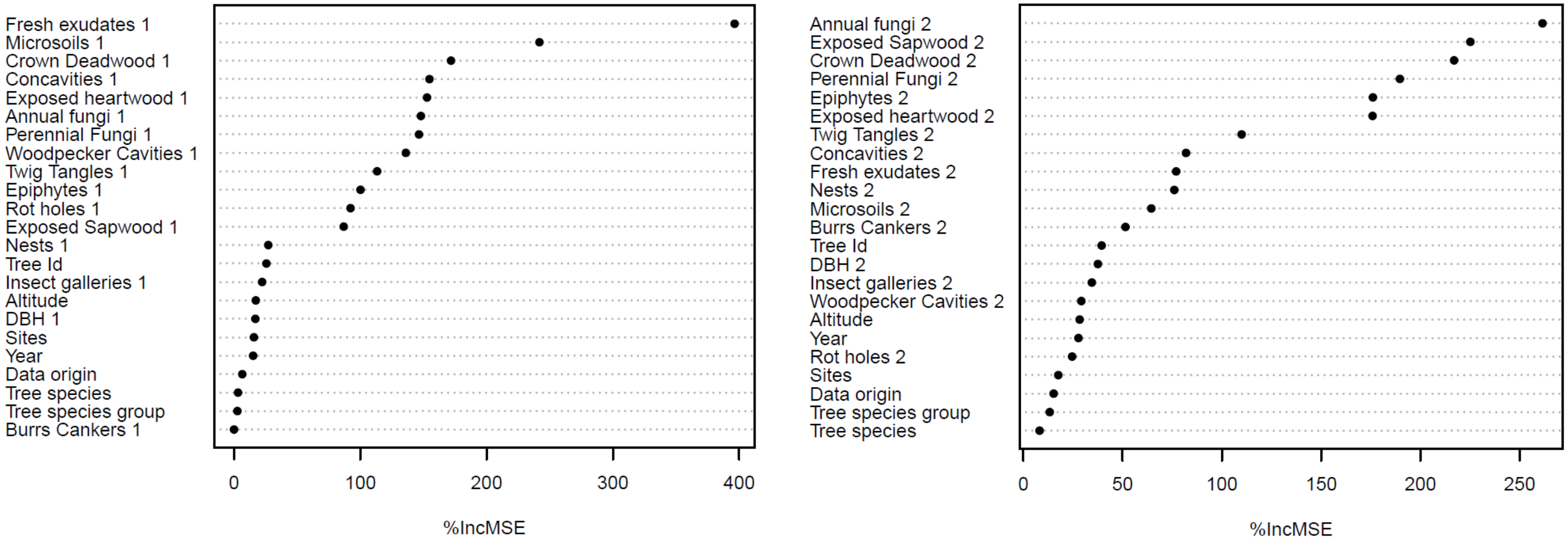
Appendix 3. Overview of changes in TreM occurrence at the first and second survey on all trees. Zero-counts are included.



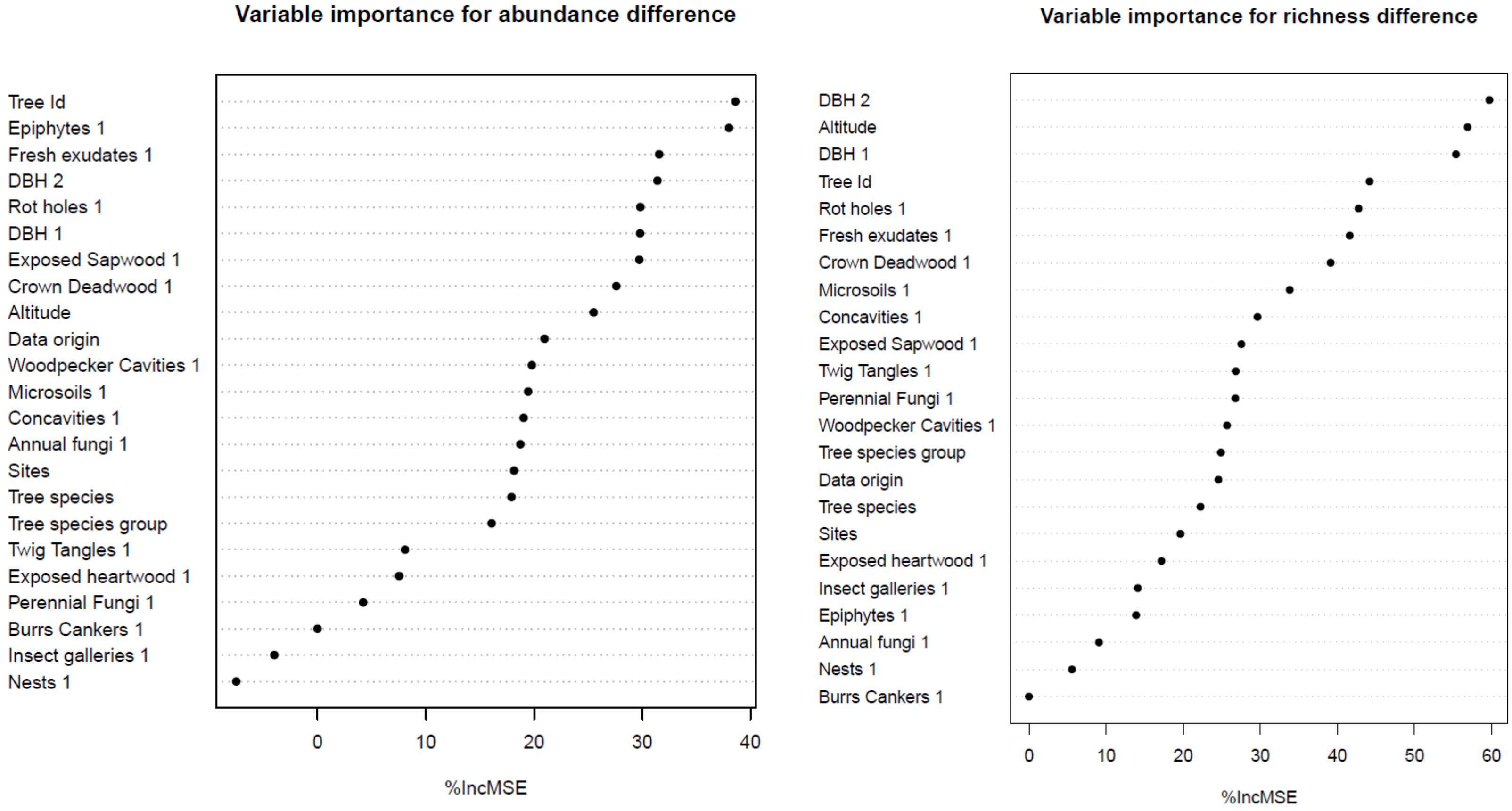
Appendix 4. Differences in the study design. Overall survival probability by sites (Western - blue and Eastern Europe- red) for richness of TreM types (upper panel) and groups (lower panel).



Appendix 5. Top predictors for the richness of TreM groups at the first (left) and the second survey (right). %IncMSE is the percentage of mean decrease accuracy, which is the loss in explained variance of the outcome, if the predictor was omitted from the model. Data from the first survey was log-transformed for a better fit.



Appendix 6. Ranking of top variables from the first survey predicting a change in richness of TreM types (left) and groups (right) at tree level. The larger a variable's percentage decrease in accuracy (here %IncMSE), the stronger a predictor that variable is."1,2" indicate the point in time when the variable was recorded.



Appendix 7. Characteristics of the TreM groups and overall estimates based on the event types

TreM group	Period in which events occurred (years)	Development pattern	Event type	Number of events	Cumulative incidence of living habitat trees that experienced the event by the end of the follow-up period (%)
Woodpecker cavities	12	Persistence	Increment	27	6.8
			Consistency	82	20.5
		Loss	Reduction	1	72.7
			Disappearance	290	
Exposed sap- and heartwood	12	Persistence	Increment	35	6.6
			Consistency	134	25.3
		Loss	Reduction	10	68.1
			Disappearance	351	
Epiphytes	12	Persistence	Increment	16	29.8
			Consistency	112	
		Loss	Reduction	18	70.2
			Disappearance	284	
Crown deadwood	12	Persistence	Increment	135	12.7
			Consistency	174	16.4
		Loss	Reduction	116	10.9
			Disappearance	637	60.0
Perennial fungi	12	Persistence	Increment	0	18.5
			Consistency	156	
		Loss	Reduction	0	81.5
			Disappearance	691	
Exposed sapwood only	9	Persistence	Increment	33	3.2
			Consistency	157	15.7
		Loss	Reduction	21	81.1
			Disappearance	794	
Rot-holes	9	Persistence	Increment	30	4.0
			Consistency	116	15.4
		Loss	Reduction	10	80.6
			Disappearance	597	
Concavities	9	Persistence	Increment	111	29.2
			Consistency	69	18.2
		Loss	Reduction	4	52.5
			Disappearance	195	
Fresh exudates	5	Persistence	Increment	53	7.4
			Consistency	111	15.4
		Loss	Reduction	85	11.8
			Disappearance	470	65.4
Twig tangles	5	Persistence	Increment	24	4.4
			Consistency	39	7.0
		Loss	Reduction	0	88.6
			Disappearance	489	
Richness of TreM types	5	Persistence	Increment	1610	38.8
			Consistency	910	22.0
		Loss	Reduction	710	17.1
			Disappearance	915	22.1
Richness of TreM groups	5	Persistence	Increment	1234	29.8
			Consistency	1258	30.3
		Loss	Reduction	738	17.8
			Disappearance	915	22.1

Appendix 8. Detailed results of the Cox proportional hazards models stratified by the interaction of tree genera and sites, indicating the magnitude and significance of the risk factors (**DBH**, **altitude** and **the initial occurrence of the factor at survey 1**) on the persistence and loss events. The multivariate model^{m} (with all risk factors as main effects) is presented. Significant values above 1.00 indicating a positive effect (higher the risk factor, higher the event rate), which agreed with the verifying univariate models^{u} are illustrated with colour blue, opposite effects with colour grey. Significance codes: '***' p≤ 0.001; '**' p= 0.001 - 0.01; '*' p = 0.01 - 0.05.

TreM group	Risk factors	Hazard rate for persistence events		Hazard rate for loss events	
		Increment	Consistency	Reduction	Disappearance
Woodpecker cavities	DBH (cm)^{m}	1.006 (0.989-1.023, p=0.468)	0.996 (0.986-1.006, p=0.442)	1.004 (0.999-1.009, p=0.144)	
	DBH (cm)^{u}	1.006 (0.990-1.024, p=0.451)	0.995 (0.985-1.006, p=0.395)	1.005 (1.000-1.011, p=0.048)	
	Altitude (m)^{m}	1.000 (0.998-1.003, p=0.745)	0.999 (0.998-1.001, p=0.337)	0.999 (0.999-1.000, p<0.001)***	
	Altitude (m)^{u}	1.000 (0.998-1.003, p=0.757)	0.999 (0.998-1.001, p=0.329)	0.999 (0.999-0.999, p<0.001)***	
	Initial occurence^{m}	1.317 (0.243-7.128, p=0.749)	0.702 (0.095-5.206, p=0.729)	1.181 (0.710-1.965, p=0.521)	
	Initial occurence^{u}	1.340 (0.266-6.753, p=0.723)	0.641 (0.088-4.678, p=0.661)	1.370 (0.822-2.284, p=0.228)	
Exposed sap- and heartwood	DBH (cm)^{m}	1.022 (1.008-1.037, p=0.002)**	1.007 (1.000-1.015, p=0.060)	0.992 (0.986-0.997, p=0.002)**	
	DBH (cm)^{u}	1.024 (1.009-1.039, p=0.002)**	1.007 (1.000-1.015, p=0.056)	0.994 (0.989-0.999, p=0.023)*	
	Altitude (m)^{m}	0.998 (0.997-1.000, p=0.099)	0.999 (0.998-1.000, p=0.097)	0.998 (0.998-0.999, p<0.001)***	
	Altitude (m)^{u}	0.998 (0.997-1.000, p=0.055)	0.999 (0.998-1.000, p=0.078)	0.999 (0.998-0.999, p<0.001)***	
	Initial occurence^{m}	0.416 (0.061-2.853, p=0.372)	0.713 (0.343-1.485, p=0.367)	1.280 (1.065-1.537, p=0.008)**	
	Initial occurence^{u}	0.502 (0.073-3.448, p=0.483)	0.754 (0.362-1.570, p=0.450)	1.400 (1.159-1.692, p<0.001)***	
Epiphytes	DBH (cm)^{m}	1.005 (0.994-1.015, p=0.376)		1.003 (0.996-1.010, p=0.423)	
	DBH (cm)^{u}	1.010 (1.000-1.019, p=0.045)		1.018 (1.013-1.024, p<0.001)***	
	Altitude (m)^{m}	0.999 (0.998-1.000, p=0.010)*		0.998 (0.998-0.998, p<0.001)***	
	Altitude (m)^{u}	0.999 (0.998-1.000, p=0.013)*		0.998 (0.997-0.998, p<0.001)***	
	Initial occurence^{m}	0.664 (0.454-0.970, p=0.034)		1.048 (0.990-1.109, p=0.105)	
	Initial occurence^{u}	0.763 (0.541-1.077, p=0.124)		1.116 (1.061-1.173, p<0.001)***	
Crown deadwood	DBH (cm)^{m}	1.009 (0.999-1.019, p=0.064)	1.002 (0.994-1.011, p=0.567)	0.994 (0.981-1.006, p=0.317)	0.999 (0.995-1.002, p=0.496)
	DBH (cm)^{u}	1.010 (1.001-1.019, p=0.032)*	1.005 (0.998-1.013, p=0.172)	0.998 (0.987-1.009, p=0.679)	0.999 (0.995-1.002, p=0.511)
	Altitude (m)^{m}	1.000 (0.999-1.001, p=0.930)	1.000 (0.999-1.000, p=0.071)	1.000 (0.999-1.001, p=0.703)	1.000 (1.000-1.000, p=0.331)
	Altitude (m)^{u}	1.000 (0.999-1.000, p=0.591)	0.999 (0.999-1.000, p=0.030)*	1.001 (1.000-1.001, p=0.100)	1.000 (1.000-1.000, p=0.336)
	Initial occurence^{m}	0.728 (0.600-0.884, p=0.001)***	0.865 (0.730-1.024, p=0.093)	1.644 (1.507-1.793, p<0.001)***	0.904 (0.811-1.008, p=0.068)
	Initial occurence^{u}	0.740 (0.610-0.898, p=0.002)**	0.872 (0.737-1.031, p=0.109)	1.654 (1.522-1.798, p<0.001)***	0.915 (0.822-1.019, p=0.107)

Perennial fungi	DBH (cm)^m	1.011 (1.002-1.020, p=0.013)*		1.011 (1.002-1.020, p=0.013)*	
	DBH (cm)^u	1.012 (1.003-1.021, p=0.007)**		0.996 (0.993-0.999, p=0.008)**	
	Altitude (m)^m	1.000 (0.999-1.000, p=0.189)		1.000 (0.999-1.000, p=0.189)	
	Altitude (m)^u	0.999 (0.999-1.000, p=0.110)		1.000 (1.000-1.000, p=0.460)	
	Initial occurence^m	-		-	
	Initial occurence^u	-		-	
Exposed sapwood	DBH (cm)^m	1.022 (1.005-1.039, p=0.010)*	1.015 (1.005-1.026, p=0.003)**	1.004 (0.999-1.008, p=0.089)	
	DBH (cm)^u	1.023 (1.007-1.039, p=0.005)**	1.018 (1.010-1.026, p<0.001)***	1.005 (1.001-1.009, p=0.006)	
	Altitude (m)^m	1.000 (0.998-1.002, p=0.959)	1.000 (0.999-1.000, p=0.286)	1.000 (0.999-1.000, p=0.234)	
	Altitude (m)^u	1.000 (0.998-1.001, p=0.671)	0.999 (0.999-1.000, p=0.069)	1.000 (0.999-1.000, p=0.029)	
	Initial occurence^m	0.654 (0.369-1.158, p=0.145)	0.700 (0.403-1.216, p=0.206)	1.290 (1.194-1.395, p<0.001)***	
	Initial occurence^u	0.829 (0.501-1.372, p=0.466)	0.864 (0.528-1.414, p=0.561)	1.400 (1.301-1.507, p<0.001)***	
Rot-holes	DBH (cm)^m	1.037 (1.019-1.055, p<0.001)***	1.005 (0.997-1.013, p=0.193)	0.999 (0.996-1.003, p=0.668)	
	DBH (cm)^u	1.036 (1.020-1.053, p<0.001)***	1.007 (0.999-1.015, p=0.070)	1.000 (0.997-1.004, p=0.817)	
	Altitude (m)^m	1.000 (0.998-1.002, p=0.966)	0.999 (0.998-1.000, p=0.059)*	1.000 (0.999-1.000, p=0.131)	
	Altitude (m)^u	0.999 (0.997-1.001, p=0.182)	0.999 (0.998-1.000, p=0.021)*	1.000 (0.999-1.000, p=0.145)	
	Initial occurence^m	0.360 (0.051-2.528, p=0.304)	0.718 (0.332-1.550, p=0.399)	1.417 (1.174-1.711, p<0.001)***	
	Initial occurence^u	0.483 (0.071-3.311, p=0.459)	0.749 (0.348-1.614, p=0.461)	1.446 (1.198-1.745, p<0.001)***	
Concavities	DBH (cm)^m	1.022 (1.013-1.030, p<0.001)***	0.991 (0.980-1.002, p=0.112)	0.992 (0.984-0.999, p=0.030)*	
	DBH (cm)^u	1.022 (1.013-1.030, p<0.001)***	0.991 (0.979-1.002, p=0.113)	0.992 (0.984-0.999, p=0.032)*	
	Altitude (m)^m	1.000 (0.999-1.001, p=0.928)	0.999 (0.998-1.001, p=0.370)	1.000 (0.999-1.000, p=0.377)	
	Altitude (m)^u	1.022 (1.013-1.030, p<0.001)***	0.999 (0.998-1.001, p=0.366)	1.000 (0.999-1.000, p=0.398)	
	Initial occurence^m	0.997 (0.414-2.400, p=0.994)	1.068 (0.565-2.018, p=0.840)	1.021 (0.841-1.240, p=0.832)	
	Initial occurence^u	1.036 (0.438-2.452, p=0.936)	1.065 (0.567-2.000, p=0.844)	1.016 (0.838-1.232, p=0.870)	
Fresh exudates	DBH (cm)^m	1.021 (1.009-1.034, p=0.001)***	1.000 (0.992-1.008, p=0.950)	0.989 (0.980-0.998, p=0.017)*	1.000 (0.996-1.005, p=0.815)
	DBH (cm)^u	1.022 (1.010-1.034, p<0.001)***	1.003 (0.995-1.011, p=0.407)	0.989 (0.980-0.998, p=0.020)*	1.000 (0.996-1.005, p=0.840)
	Altitude (m)^m	1.001 (0.999-1.003, p=0.244)	1.000 (0.998-1.001, p=0.521)	0.999 (0.998-1.000, p=0.112)	1.000 (1.000-1.001, p=0.063)
	Altitude (m)^u	1.000 (0.999-1.002, p=0.671)	0.999 (0.998-1.001, p=0.362)	0.999 (0.998-1.001, p=0.418)	1.000 (1.000-1.001, p=0.095)
	Initial occurence^m	0.567 (0.337-0.953, p=0.032)*	0.403 (0.270-0.603, p<0.001)***	3.161 (2.460-4.061, p<0.001)***	0.896 (0.772-1.039, p=0.147)
	Initial occurence^u	0.501 (0.294-0.856, p=0.011)*	0.400 (0.268-0.596, p<0.001)***	3.082 (2.400-3.957, p<0.001)***	0.911 (0.787-1.054, p=0.209)

Twig tangles	DBH (cm)^{m}	1.050 (1.027-1.074, p<0.001)***		1.023 (1.007-1.040, p=0.005)**	
	DBH (cm)^{u}	1.046 (1.025-1.067, p<0.001)***		1.026 (1.010-1.042, p=0.001)***	
	Altitude (m)^{m}	1.001 (0.999-1.004, p=0.286)		0.999 (0.997-1.001, p=0.259)	
	Altitude (m)^{u}	1.000 (0.997-1.002, p=0.872)		0.998 (0.996-1.000, p=0.056)	
	Initial occurence^{m}	-		-	
	Initial occurence^{u}	-		-	
Richness of TreM types	DBH (cm)^{m}	1.015 (1.013-1.017, p<0.001)***	0.986 (0.982-0.989, p<0.001)***	1.004 (1.000-1.007, p=0.041)*	1.002 (0.998-1.005, p=0.367)
	DBH (cm)^{u}	1.012 (1.010-1.015, p<0.001)***	0.981 (0.978-0.985, p<0.001)***	1.000 (0.996-1.003, p=0.933)	0.991 (0.987-0.996, p<0.001)***
	Altitude (m)^{m}	0.999 (0.999-0.999, p<0.001)***	0.999 (0.999-1.000, p<0.001)***	0.999 (0.999-1.000, p<0.001)***	0.999 (0.999-0.999, p<0.001)***
	Altitude (m)^{u}	0.999 (0.999-1.000, p<0.001)***	0.999 (0.999-0.999, p<0.001)***	0.999 (0.999-1.000, p<0.001)***	0.999 (0.999-0.999, p<0.001)***
Richness of TreM groups	DBH (cm)^{m}	1.013 (1.010-1.015, p<0.001)***	0.995 (0.992-0.997, p<0.001)***	1.008 (1.005-1.011, p<0.001)***	1.002 (0.998-1.005, p=0.367)
	DBH (cm)^{u}	1.010 (1.008-1.013, p<0.001)***	0.991 (0.988-0.994, p<0.001)***	1.006 (1.002-1.009, p=0.001)***	0.991 (0.987-0.996, p<0.001)***
	Altitude (m)^{m}	0.999 (0.999-1.000, p<0.001)***	0.999 (0.999-0.999, p<0.001)***	0.999 (0.999-1.000, p<0.001)***	0.999 (0.999-0.999, p<0.001)***
	Altitude (m)^{u}	0.999 (0.999-1.000, p<0.001)***	0.999 (0.999-0.999, p<0.001)***	0.999 (0.999-1.000, p<0.001)***	0.999 (0.999-0.999, p<0.001)***

Supplementary material - Chapter four

Appendix 1a: Decay stage classification scheme for dead wood (or coarse woody debris) used to classify recently dead trees in this study, adapted from Sippola & Renvall (1999) and Puletti et al. (2019)

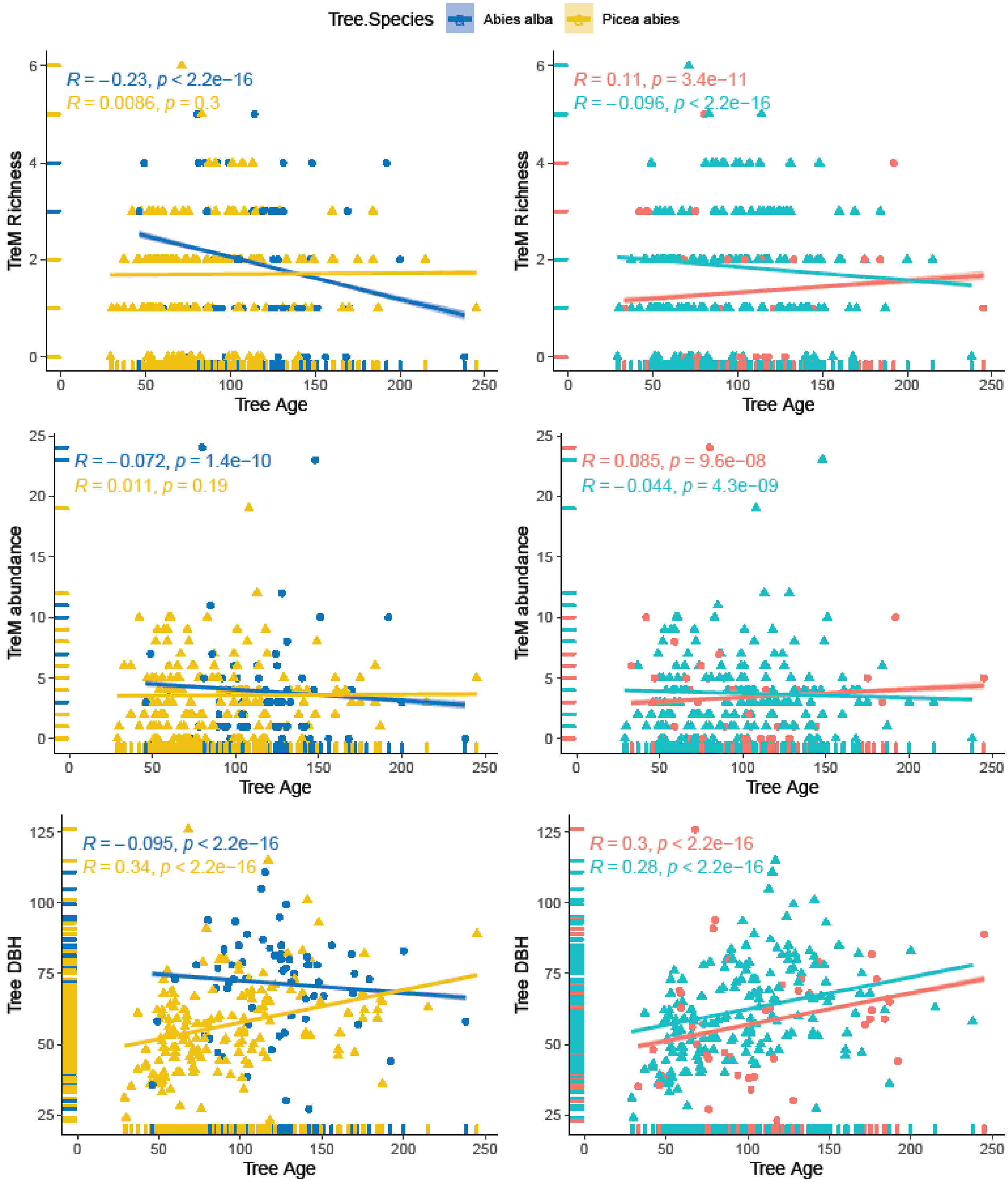
1	Recently dead or cut trunk/piece of wood; wood hard, bark and phloem fresh. Knife penetrates only a few mm into the wood
2	Wood hard, most of the bark left, but no fresh phloem present. Knife penetrates 1±2 cm into the wood
3	Wood partly decayed on the surface or in the centre (depending on tree species), usually large pieces of bark loosened or detached (pine logs). Knife penetrates
4	Most of the wood soft throughout, usually without bark (pine logs). The whole blade of the knife penetrates easily into the wood.
5	Wood very soft, disintegrates when lifted. Trunk covered by ground-layer mosses and lichens.

Appendix 1b: TreMs that were consider to be linked to declining tree vitality. Habitat trees that bear these TreMs were selected.

1	Woodpecker cavities
2	Trunk mould cavities
3	Branch holes
4	Dendrotelms
5	Insect galleries
6	Bark loss
7	Exposed heartwood
8	Cracks and scars
9	Large crown deadwood
10	Large root buttress cavity
11	Witches broom
12	Cankers and burrs
13	Fruiting bodies of fungi
14	Epiphytic or parasitic crypto- and phanerogams

Appendix 2. Example of visual detection of dead trees through aerial images (photo credit: Martin Denter)

Appendix 3. The relationship between tree age and other tree attributes (DBH, TreM occurrence) according to tree status (living or dead) and species (*A. alba, P. abies*).



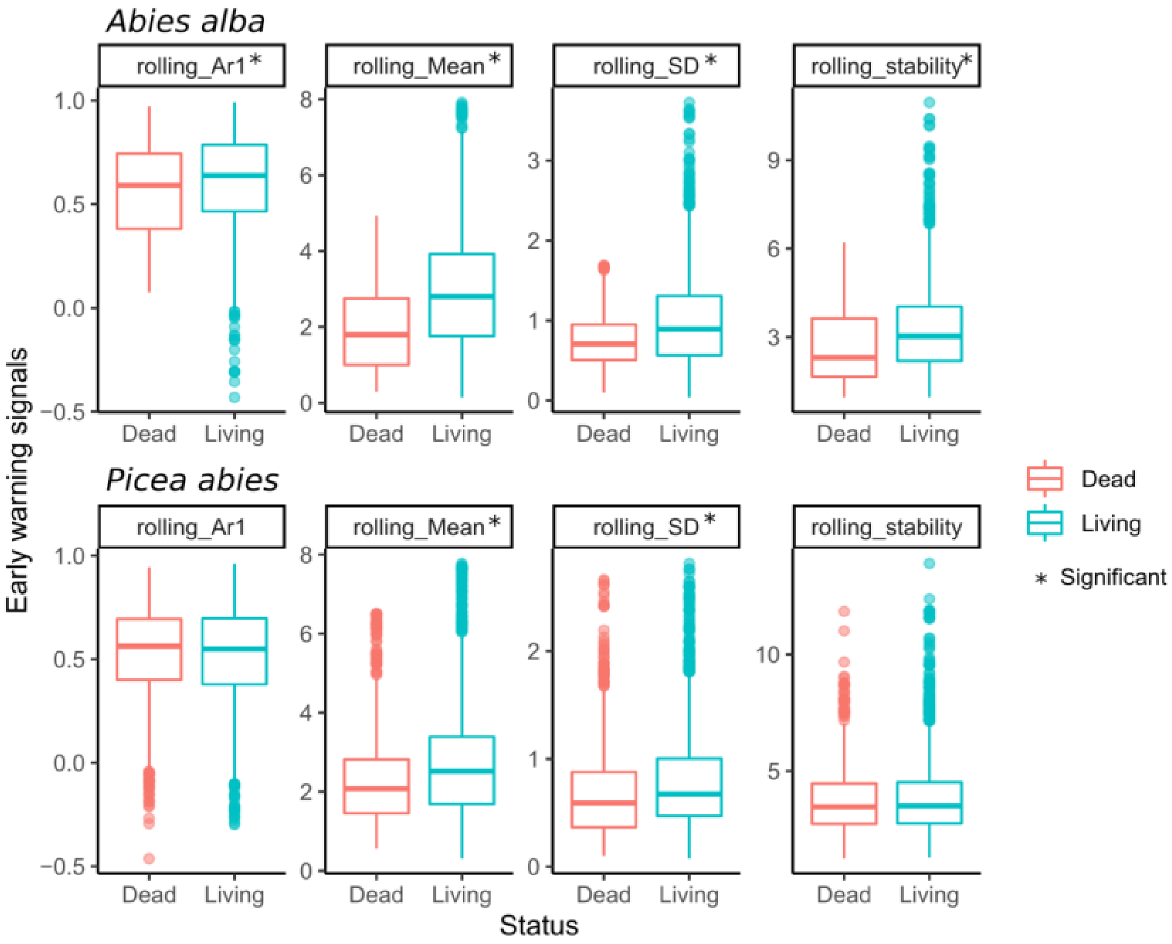
Appendix 4. Differences in growth metrics between living and dead trees over their entire lives.

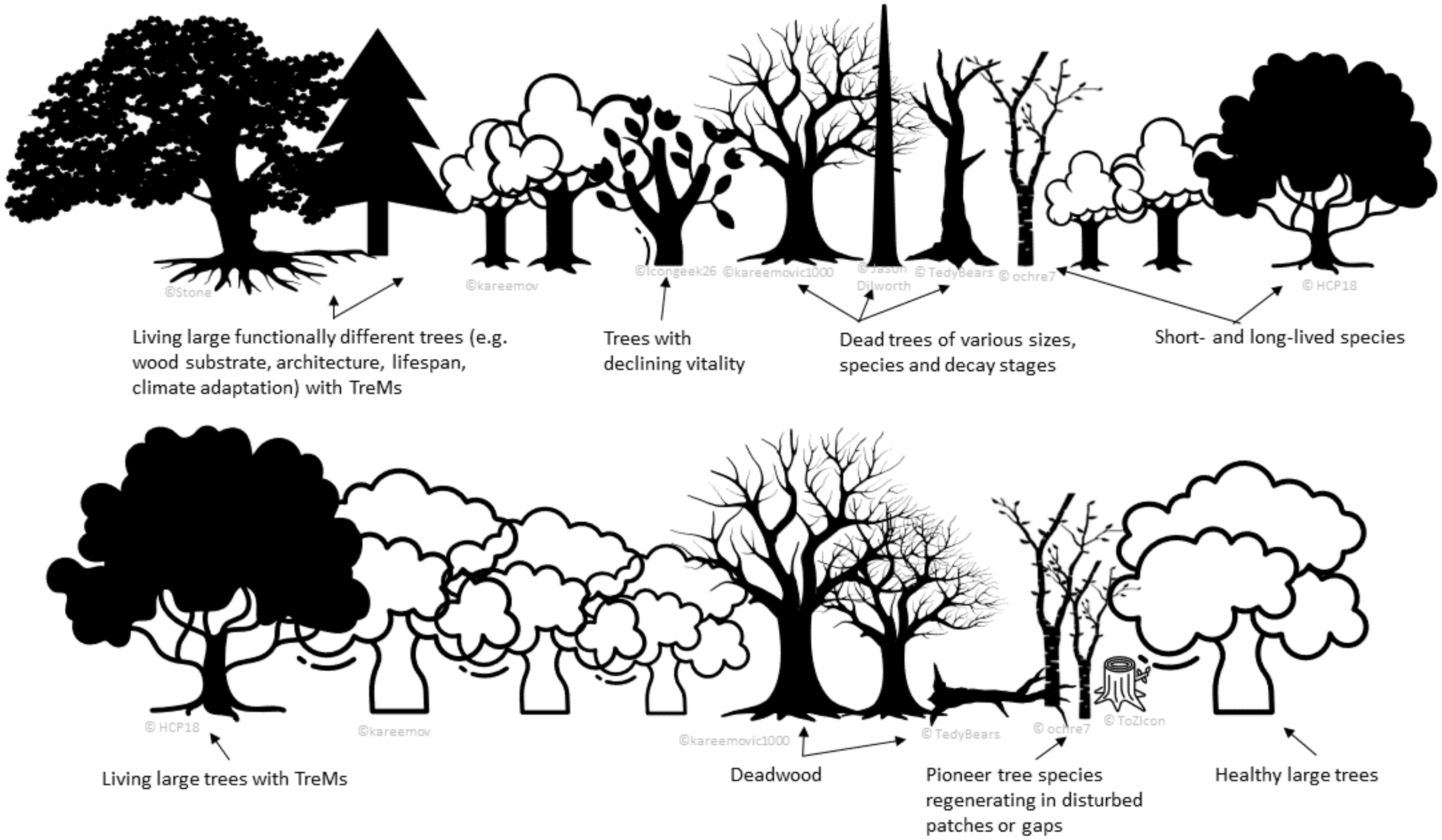
Growth metrics	Results of the Wilcoxon rank tests
Mean	W=31423801, p<0.001
Standard deviation	W=36270880, p<0.001
Autocorrelation	W=46834973, p<0.001
Stability	W=29144562, p=0.06

Appendix 5. Results of the simple linear regression models (TreM abundance/richness ~ mk_tau)

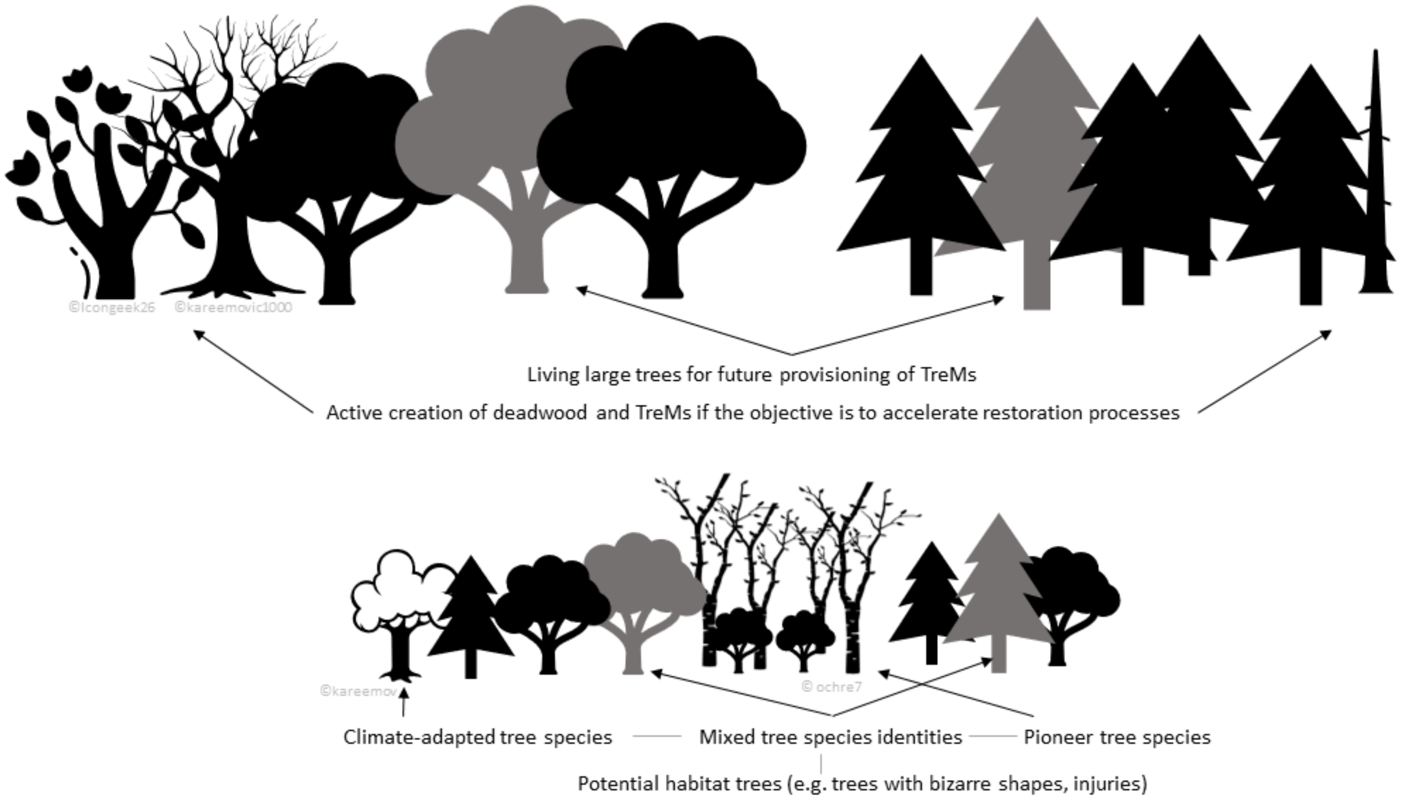
	Estimate		Std. Error		t value		Pr(>|t|)		R^2	F-statistic, p-value
	Intercept	mk_tau	Intercept	mk_tau	Intercept	mk_tau	Intercept	mk_tau		
30 years before tipping points										
TreM abundance										
Abies alba	3.5	1.5	0.6	1.4	5.2	1.1	<0.001	0.28	0.02	1.19, p=0.28
Picea abies	3.6	-0.3	0.2	0.6	14.4	-0.4	0.7	0.17	0.001	0.17, p=0.67
TreM richness										
Abies alba	1.9	-0.3	0.2	0.4	9.9	-0.8	<0.001	0.42	0.01	0.65, p=0.42
Picea abies	1.7	0.1	0.1	0.2	17.7	0.1	<0.001	0.92	<0.001	0.01, p=0.91
30 years after tipping points										
TreM abundance										
Abies alba	3.9	0.2	0.6	1.4	6.2	0.2	<0001	0.86	0.001	0.04, p=086
Picea abies	3.6	0.6	0.3	0.7	14.5	0.9	<0.001	0.35	0.005	0.85, p=0.36
TreM richness										
Abies alba	1.9	-0.1	0.2	0.4	9.9	-0.1	<0.001	0.99	<0.001	0.001, p=0.99
Picea abies	1.7	0.3	0.1	0.3	18.1	1.3	<0.001	0.31	0.006	1.059, p=0.31

Appendix 6. Temporal changes in time-series metrics of living and dead trees of *P. abies* and *A. alba:* mean tree-ring width (mean), first order autocorrelation (AR1), standard deviation (SD), tree stability (stability).





Appendix 1. Examples of diversification of habitat tree selection in forest stands with different conditions. Detailed copyright attribution



Appendix 2. Examples of diversification of habitat tree selection in forest stands with different conditions. Detailed copyright attribution