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Temporal Development of Microhabitats on Living Habitat Trees in Temperate European Forests

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ABSTRACT

Tree-related microhabitats (TreMs) have been promoted as indicators of forest biodiversity and to guide conservation practices. Ensuring the provision of diverse TreMs in the long term is crucial for the survival of many forest-dwelling species. Yet, this task is challenging in the absence of information regarding TreM dynamics. We analysed the temporal development of TreMs on 11,569 living trees in temperate European forests. To identify drivers of change in TreM abundance and richness over a period of 3–12 years, we estimated the rates of TreM persistence and loss events at the tree-level using survival analysis methods: **persistence** was characterised by consistency and increment events (when TreM numbers were maintained or in-

creased) 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 revealed a highly dynamic TreM development on living habitat trees, particularly on large trees. While specific TreMs are prone to disappearing, irrespective of tree species or TreM groups, total TreM richness persists over a 12-year period. TreMs such as *crown deadwood*, *epiphytes* or *woodpecker cavities* are prone to decrease in the long term. However, large trees were more likely to maintain a certain degree of TreM richness. Increasing diameters resulted in high persistence rates in seven TreM groups and concomitantly low loss rates in four of them (*exposed sap- and heartwood*, *concavities*). Selecting habitat trees based on TreMs should consider the likelihood of TreMs being lost over time, to ensure the long-term provision of microhabitats for associated species.

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Author contributions A. P. Spînu and J. Bauhus developed the study design; A. P. Spînu, T. Asbeck, D. Kozak, M. Svoboda, M. Mikoláš, Y. Paillet collected the data and contributed to the interpretation of the results. A. P. Spînu and A. Nicolaie carried out the data analysis based on the analytical methodology designed by A. Nicolaie. A. P. 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.

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GRAPHICAL ABSTRACT



Key words: wildlife habitat conservation; survival analysis with competing risks; integrative forest management; tree-related microhabitats; TreM; tree cavity.

HIGHLIGHTS

- Assemblages of microhabitats remain diverse over time, especially on large trees.
- However, certain microhabitats may disappear over time.
- Retention of functionally different trees may secure the continuity of microhabitats.

INTRODUCTION

The retention of deadwood and habitat trees during silvicultural operations mitigates biodiversity loss in forests (Gustafsson and others 2012, 2020; Pastur and others 2020; Muys and others 2022). Follow-

ing forest disturbance, biological legacies can provide a life-boating function for species associated with their structures and substrate. The retention of habitat trees (large, old, living or dead trees with microhabitats, Bütler and others 2013) aims to ensure both spatial and temporal habitat continuity that cannot be provided by deadwood (Franklin and others 2000, 2012). Tree-related microhabitats (TreMs) are often used to identify and select high-quality habitat trees and are considered useful indicators of biodiversity in European and North American forests (Asbeck and others 2021a, b; Martin and others 2022; Larrieu and others 2022; Spînu and others 2022). 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 and others 2018). Some TreMs support forest-dwelling birds, rodents, bats, carnivores and invertebrates (for example, rot-holes: Goux and Brustel 2012; cavities: Bunnell and others 2013; Remm and Löhms 2011). Certain TreMs are critical for the survival of specialist species (for example, dendrotelmata for tree-hole breeding mosquitos: Kitching 1917; buttress cavities for salamander species: Basile and others 2017; tree hollows for the click and hermit beetles: Ranius and others 2002; Svensson and others 2004). Based on morphological characteristics and associated taxa, a typology of TreMs has been proposed (Larrieu and others 2018, Appendix 1). This typology contains 15 different groups such as *exposed sap- and heartwood* or *concavities*, which comprise 47, more precise, types as *stem and limb breakage*, *dendrotelms*. Tree dimensions, vitality status, species, age and stand management, as well as forest conditions and forest type are all important drivers of TreM occurrence and diversity (Michel and Winter 2009; Vuidot and others 2011; Winter and others 2015; Paillet and others 2017; Asbeck and others 2019; Larrieu and others 2014; Kozak and others 2023). Large, old broadleaved and/or dead standing trees in temperate forest commonly support the richest and most abundant TreMs.

TreM inventories are now included regularly in biodiversity surveys (for example, the Index of Biodiversity Potential in France: Larrieu and Gonin 2008; Gosselin and Larrieu 2020; Germany: Zeller and others 2022), in research projects (Martin and others 2022), and educational exercises (Cosyns and others 2020; Joa and Schraml 2020) and are promoted in integrative forest management

guidelines for the designation of habitat trees. Yet we have a limited understanding of the long-term implications of habitat tree selections based on TreMs.

Considering the temporal dynamics of TreMs, how their persistence and loss 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 break off (Basham 1991). Likewise, large rot-holes may persist as long as the habitat tree (Larrieu and others 2022), while the life of some living TreMs, such as fruiting bodies of saprotrophic agarics is no longer than a few days. The processes and events affecting TreM dynamics can be tree or stand specific. They can occur continuously (for example, tree senescence accompanied by the capacity to compartmentalize wounds and decay), regularly (for example, silvicultural operations) or occasionally (for example, natural disturbances). 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 and others 2006; Kahl and others 2017; Zemlerová and others 2023). For instance, *insect galleries* might occur often during the lifetime of a tree and can evolve into foraging cavities that subsequently might become rot-holes. TreMs such as *exposed sap- and heartwood* cannot form multiple times on a tree without causing its death (for example, a dead tree top or broken main fork). TreMs might persist longer on slow-growing hardwoods with low rates of decay and breakage in comparison to many conifers and fast-growing tree species (Körkjäs and others 2021). On the latter, TreMs usually form quicker and probably at higher rates (Körkjäs and others 2021; Spînu and others 2023). Additionally, depending on TreM size and the tree's capacity to inhibit the decaying fungus and form new wood, sealing the scars that are associated with certain TreMs, some tree species can fully overgrow TreMs after a few years or decades (Shigo 1984; Stoffel and Perret 2006; Smith 2015). While we do have some information on how different TreMs may develop in principle, there is little quantitative information on temporal dynamics of TreM that can guide conservation management. 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 and others 2022; Larrieu and others 2022).

While some studies have investigated the persistence of tree cavities, hollows or wounds affecting timber quality (Edworthy and others 2012; Lindenmayer and Wood 2010; Wesołowski and others 2011, 2012; Tavankar 2017, 2022), there is a lack of comprehensive longitudinal studies on the temporal dynamics of TreMs (Puverel and others 2019). This gap may be attributed to the scarcity of repeated inventories that assess TreMs on individual trees. Longitudinal data can help to understand the development of TreMs over time, which can inform an effective selection of habitat trees that ensures continuous provision of ecological niches.

Substantial progress in understanding temporal dynamics of TreMs has been made through a method developed by Courbaud and others (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 growth (Courbaud and others 2017, 2022; Jahed and others 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 and others 2023). This approach also assumes that TreMs never disappear from trees and trees never die, which does not reflect the reality of ecological processes. To overcome the limitations of this design in the evaluation of time-dependent outcomes, it is crucial to complement it with studies that have repeatedly recorded TreMs on the same trees (Lindenmayer and others 2011; Courbaud and others 2017; Asbeck and others 2023).

In this study, we merged different datasets with longitudinal TreM surveys from several regions in Europe. Following previous efforts (Courbaud and others 2017, 2020), we initiated a comprehensive investigation into the temporal development of microhabitats on living habitat trees, more likely to persist over the course of multiple inventories than dead trees. Once formed on a living tree, a TreM can either remain or be lost over a certain time interval. To quantify these two main trends, we assessed changes in TreM richness for 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). These two event types were summarized as **TreM persistence**; (3) TreM reduction (a decrease in TreMs), (4) TreM disappearance (the final number of TreMs is zero). These two event types were summarized as **TreM loss**.

We hypothesized that:

- a. **On living trees, 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**. Owing to the growth dynamics and low decay compartmentalization capacity of many European broadleaved species, we expect them to have a greater TreM turnover 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*. These TreMs may indicate tree vitality and thus the potential for development of subsequent TreMs.
- d. **Tree size is a significant driver of TreM dynamics and rates of both TreM persistence and TreM loss are highest on large trees**.

MATERIAL AND METHODS

Data Origin and Harmonization of TreM Classifications for Living Trees

Our study focused on the temporal TreM development on trees which were alive at the time of two subsequent surveys, with repeated TreM observations on 11,569 living trees belonging to 30 tree species. Longitudinal TreM data were more common on living trees than dead ones (Appendix 2a). In addition, TreM profiles differ significantly between dead and living trees (Spînu and others 2022) and targeting the latter ones facilitated a focused data interpretation and reduced possible errors from the data harmonization. The surveys concerned all trees, whether or not they bore TreMs initially. We used the availability of unique

datasets with repeated TreM surveys for an extensive study on temporal TreM development. These data were collected by three research and natural area management groups from different regions in Europe: France—Cateau and others 2024; Germany—Spînu and others 2022; Slovakia/Romania—Kozak and others 2023 (Figure 1). 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 the level of TreM groups based on a common typology (Larrieu and others 2018). We only retained TreM types that appeared in each classification and assigned them to 15 broader TreM groups proposed by Larrieu and others (2018), following a similar approach as other previous studies (Asbeck and others 2021b; Courbaud and others 2022). The TreM groups included: woodpecker cavities, rot-holes, insect galleries and bore holes, concavities, exposed sapwood and heartwood, crown deadwood, twig tangles, burrs and cankers, perennial and ephemeral fungal fruiting bodies, epiphytic or parasitic crypto- and phanerogams, nests, microsoils and fresh exudates. Specifics of the study areas, individual classifications and corresponding TreM groups are provided in Appendix 1.

The study plots were located in both managed and unmanaged mature stands, within a wide range of forest types. Most of the studied Central European sites were not affected by major disturbances, for example no major windthrows occurred between 2005 and 2020 in France. The rates of tree mortality in the period between the surveys in Germany were low in comparison with other European regions (Spînu 2023). In general terms, disturbances play an important role in shaping the structure and composition of primary forests from the Carpathian region, but few sites have been disturbed over the period covering the surveys used in our analysis (Janda and others 2017; Meigs and others 2018; Zemlerová and others 2023).

Owing to the small number of repeated observations in most TreM groups and of some tree species, the analyses could only be carried out 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 an overview of the distribution of TreM groups at tree level, for both surveys can be found in Appendix 2 and 3).

TreMs were inventoried between 2006 and 2021, with each living tree being surveyed twice within that interval. The time interval between the first

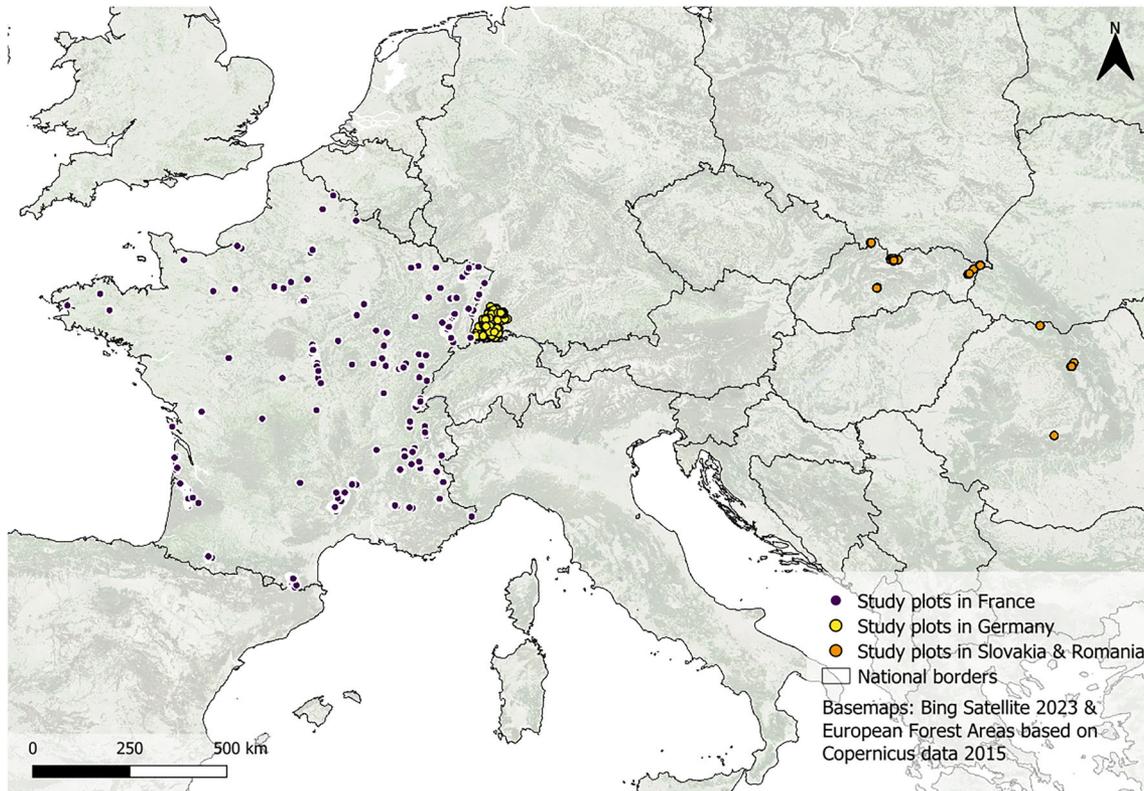


Figure 1. Location of the study areas.

Table 1. Overview of Timing of TreM Inventories and the Number of Habitat Trees Which Were Re-Surveyed

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

and the second survey, later called survey period, ranged between 3 and 12 years and differed between the different regions and studies (Table 1). The diameters at breast height (DBH at 1.3 m) 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 and 2018 m.a.s.l. European beech (*Fagus sylvatica* (L.), 33.9%), Norway spruce (*Picea abies* (L.), 19.5%) and silver fir (*Abies alba* (Mill.), 17.6%) were the main species. The main characteristics of TreM groups and corresponding living habitat trees are summarized in Table 2.

We conducted several data analyses to understand how temporal dynamics of TreMs on living habitat trees change over the course of a 12-year period. Firstly, we used a random forest analysis to describe overall TreM patterns. By means of survival analysis methods, we analyse the dynamics of TreMs on habitat trees to address hypotheses a, b and d. Additionally, a second random forest analysis was conducted to assess whether changes in TreM development were related variables describing living habitat trees at the first survey, such as DBH, altitude, and presence of specific TreM groups, in line with hypotheses c and d.

Description of the TreM Data

Habitat trees were defined as trees exhibiting the presence of at least one TreM at the first survey. The number of habitat trees was 4145, representing 35% of the total number of 11,569 living trees included in the study. The TreM counts followed a right-skewed distribution in each TreM group. The richness of TreMs for each tree and survey was calculated as the sum of TreM groups present on a tree (for example, crown deadwood, exposed sapwood, cavities). To gain a first impression of the data, we drew alluvial plots to visualise the number

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

of TreMs at each survey. Additionally, a random forest analysis was conducted to assess whether the presence of certain TreM groups predicted the overall TreM richness at both surveys (Breiman 2001). The independent variables considered in the analysis included tree DBH, altitude and presence of TreM groups. For the first survey, the predicted variables were log-transformed to improve the fit.

However, 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 without making prior assumptions about the

data. To assess the quality of predictions, we report variable importance lists, percentages of explained variance, and prediction errors. For this purpose, variables were ranked in terms of importance based on their impact in predicting the outcome (Appendices 5, 6). A variable was considered more important than another, if its removal from the prediction yielded an error larger than errors obtained through the removal of other variables. We conducted an additional random forest analysis to assess whether the change in TreM development related to variables describing 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 those TreM groups that predicted certain changes in TreM richness. Here, change was defined as the difference in TreM richness between the surveys.

Prediction and Modelling of TreM Dynamics

We used survival analysis methods to analyse the dynamics of TreMs on habitat trees, for both total TreM richness, as well as separately for each TreM group. The focus of our study was on habitat trees, trees which exhibited at the first survey at least one TreM (to model the presence of multiple 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 that can be referred to as competing risks. First, **TreM persistence** encompassed events where the number of TreMs remained the same (consistency events) or increased over time (increment events). Second, **TreM loss** represented events where the number of TreMs decreased (reduction events), potentially resulting in complete absence (disappearance events).

Further, we defined the time-to-event as the time of occurrence of an event and the type represents one of the four development events (consistency, increment, reduction, disappearance). The outcome was the combination of time-to-event (denoted by T) and type of event (denoted by D) variables, further referred to as (T, D) . The independent variables were tree DBH, altitude and the TreMs count at first survey (jointly denoted by \mathbf{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. For a tree with the covariate vector \mathbf{Z} , the type- j specific hazard was modelled as:

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

where $\lambda_{j,0}(t)$ is the baseline type-specific hazard and the vector β_j represents the covariates effects on type- j hazard. $\Lambda(u)$ represents the cumulative hazard function for the j th event at the time u . Tied events were dealt with by means of the Breslow correction.

Owing to the low number of *burrs and cankers*, *insect galleries*, and *nests* in the data set (< 20 observations), fitting Cox proportional hazards models was not adequate for these TreM groups. 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 event. 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 in the data source (for example, survey intervals) or between tree categories (broadleaves, conifers) was measured at the baseline survival level by allowing the estimation of survival curves to mold to each stratum (Appendix 4). Since *twig tangles* and *fresh exudates* were not recorded in older surveys, their average study interval of 3 years was the shortest of all TreM groups. The exact occurrence of events on a tree was likely not recorded at the exact time of occurrence but at the end of the inventory interval, during which it occurred. The scope of the analysis was to observe general patterns of change, as our

data and methods do not allow for the identification of the point in time when a change occurred.

All analyses were performed in R version 4.2.0 (R Core team 2021), using the *randomForest* (Liaw and Wiener 2002), *survival* (Therneau 2023) packages and represented graphically through the *ggplot2* (Wickham 2016) package.

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*, 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*. The percentage of explained variance for this random forest analysis reached 97.7% for the TreM richness in the first survey, and 96.3% in the second survey (Appendix 5). While some TreMs remained significant predictors of richness over time (*crown deadwood*, *exposed sap heartwood*, *annual* and *perennial fungi*), the ranking of other TreM groups decreased (*microsoils*, *fresh exudates*, *concavities*), being replaced by others TreM groups, such as *exposed sapwood* or *epiphytes* (Appendix 6). This observation was in line with the patterns provided 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 surveys indicated a trend of loss at the tree level for most TreM groups (Appendix 3).

Changes in TreM Richness at the Tree-Level

Throughout the study period, the incidences of TreM persistence events (increase and consistency) and loss events (reduction and disappearance) increased to reach a plateau (Figure 2, Appendix 7). The TreM richness showed similar cumulative incidence rates for persistence and loss events, irrespective of tree species group. Approximately 30% of the living habitat trees experienced consistency or increase events. Loss events accounted for approximately 40% of all events, while persistence represented 60% (Figure 2). The positive difference in frequency between persistence and loss events was higher in broadleaves than in conifers, with a 20% difference in cumulative incidence by the end of the survey period.

Temporal Changes at the TreM Group-Level

In contrast to TreM richness, losses represented the vast majority of events observed within each 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 tree category, to experience a 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 lowest values for *concavities* (52%) to the highest for *twig tangles* (88%), losses were consistently observed in all groups. *Crown deadwood*, *perennial fungi*, and *fresh exudates* were the least likely to be lost on 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 a slightly higher rate of increment were *concavities* in broadleaves, with an incidence rate of 40% by the end of the survey period. However, *woodpecker cavities*, *rot-holes*, *exposed sap- and heartwood* (broadleaved trees), *perennial fungi* (conifers), *epiphytes*, and *concavities* (both broadleaves and conifers) were groups that primarily experienced consistency, with an approximate incidence rate of 20% (Table 3, Figure 3).

Sufficient sample sizes to distinguish reduction and disappearance events were available for two groups, namely *crown 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).

Drivers of TreM Development

The results of the stratified Cox proportional hazard models indicated that the presence of certain TreMs at the first survey had an impact on hazard rates for five TreM groups. Specifically, the occurrence 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 second random forest analysis further supported the importance of *rot-holes*, *fresh exudates*, and *crown deadwood* as pre-

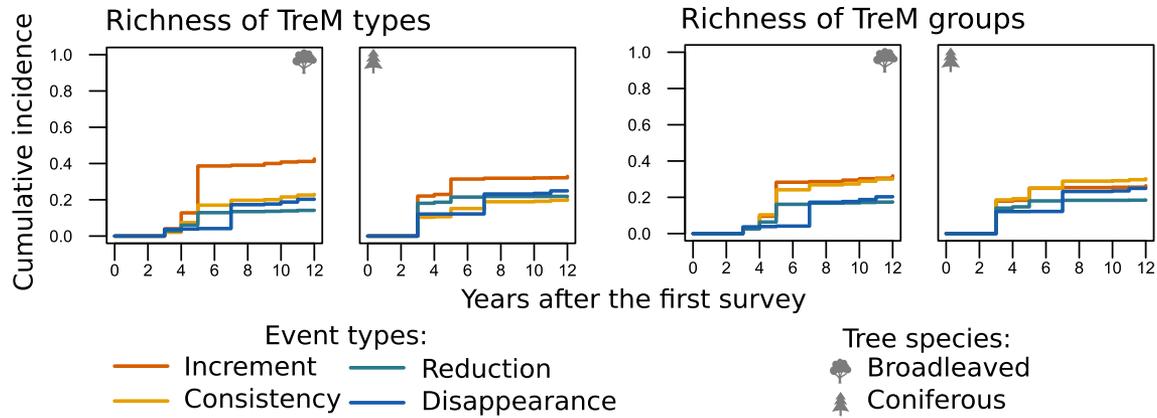


Figure 2. Cumulative incidence rates for all types of all events in the richness of TreMs at both type and group level, for each habitat tree since the first survey. Persistence events (increment, consistency) are marked in dark and light orange, while loss events (reduction, disappearance) are indicated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

dictors of the temporal changes in TreM richness (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*, and *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 loss in *woodpecker cavities*, *exposed sap- and heartwood*, *epiphytes*, and to lower rates of persistence for *rot-holes*. All events related to TreM richness showed lower rates with increasing altitude (Table 3).

DISCUSSION

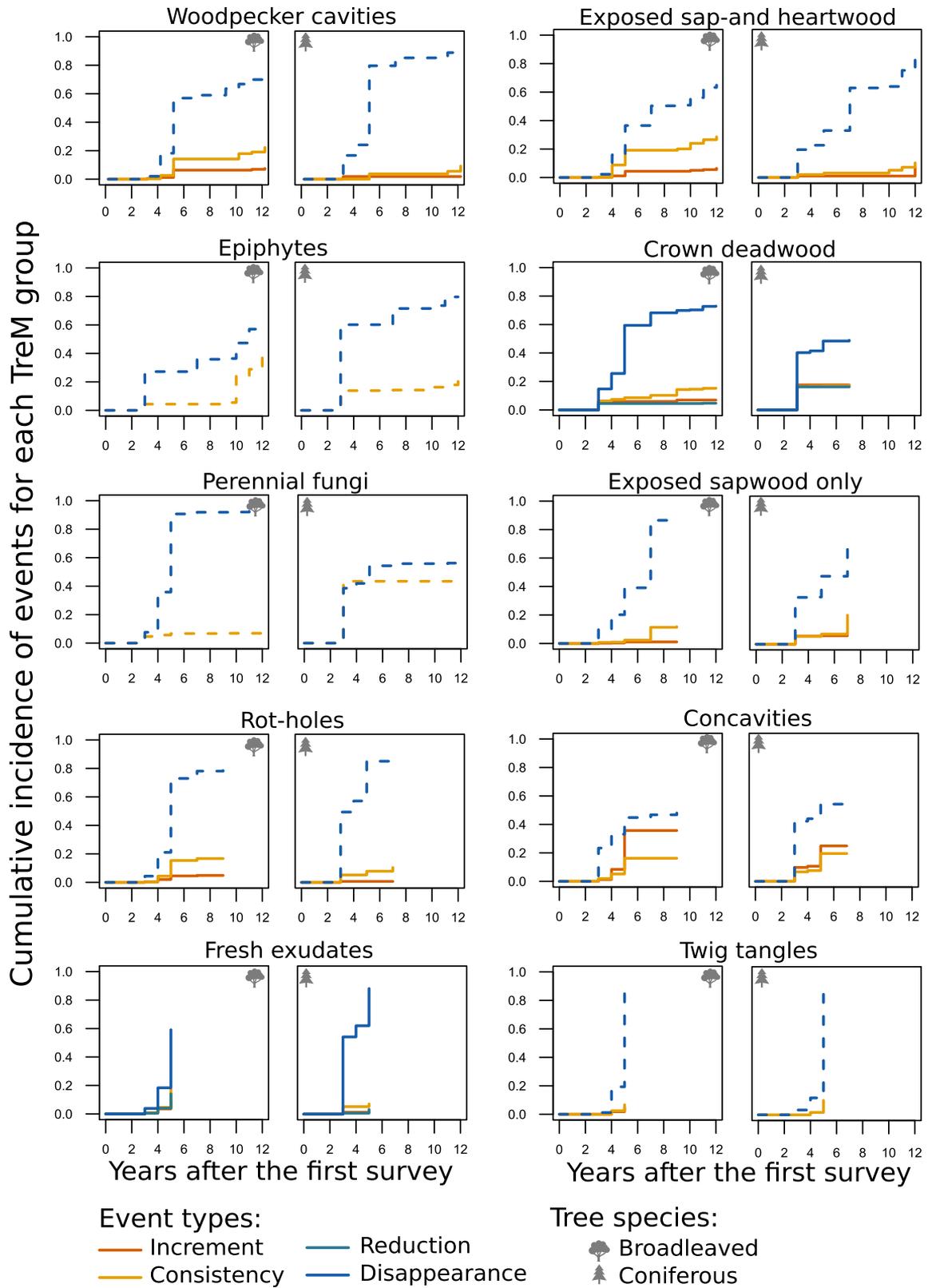
We studied the temporal dynamics of TreMs on a dataset comprising 11,569 living habitat trees distributed over four countries in Europe. Our study shows that TreM development on living habitat trees is highly dynamic, particularly on large trees, as tree dimension emerged as a driver of both TreM loss and persistence. The results indicate that, while TreM richness can persist in the long term, specific TreMs are prone to disappear on individual trees, irrespective of tree species or TreM group. Addi-

tionally, the presence of rot-holes, fresh exudates and crown deadwood on living trees could serve as indicators of subsequent changes in their TreM profile.

Balance Between TreM Persistence and Loss at the Tree-Level

We showed that the overall TreM richness remained stable over a period of 12 years at least. The processes of increment and consistency did not outweigh reduction and disappearance of TreMs, regardless of the tree species (Figure 2). However, broadleaved trees exhibited relatively higher rates of TreM increment compared to their loss. The resulting increase can be attributed to the 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, in comparison to *P. abies* thicker bark that protects a more flexible, softer xylem. This makes them more sensitive to mechanical impacts such as those caused by rockfalls, and lower capacity to seal wounds compared to species such as *P. abies* (Trappmann and Stoffel 2013). Additionally, the wood of *F. sylvatica* decays faster than that of *P. abies* (Kahl and others 2017). Thus, once formed, TreMs that are related to injuries or facilitate wood decay may lead to the subsequent formation of new TreMs. For instance, the formation rate of TreMs on *F. sylvatica* was found to be twice as high compared to conifers such as *A. alba* (Courbaud and others 2017).

However, the changes in the TreM data between surveys indicated a general balance between the formation of new TreMs and the loss of existing ones. For example, losses in *fresh exudates* and *con-*



◀ **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 the low number of recordings 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.

cavities were compensated by gains in *exposed sapwood* and *epiphytes*. The occurrence of living epiphytes can increase over time as a tree ages and its surface area expands, especially under favourable growth and dispersal conditions for bryophytes or lichens (Lie and others 2009; Asbeck and others 2021a, b; Kõrkjas and others 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 *P. sylvestris* has been observed in previous studies. Records show that indeed dead branches of those species can persist in the canopy for up to 10, and 6 years, respectively (Kahl and others 2017; Mäkinen 2002). Dead branches may persist even longer in broadleaved species such as *Quercus*, yet such data is scarce. TreMs associated with *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 and others 2021).

Certain TreM Groups are Prone to Decline or 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 habitat trees experienced losses in their TreM groups. The lowest rates of loss were found among *crown deadwood*, *perennial fungi*, and *exposed sapwood* on living conifers. This observation may be attributed to new occurrences of those TreMs, as responses of conifers to stress caused by recent episodes of drought events and bark beetle outbreaks (Senf and others 2018; Jakoby and others 2019). This pattern can also explain why TreMs such as *crown deadwood*, *fresh exudates*, and *rot-holes* were observed to predict future changes in TreM richness at the tree level. Crown dieback, increased resin production and bark loss are indicators of declining tree vitality

triggered by stress associated with recent extreme drought and subsequent bark-beetle outbreaks (Bouget and others 2019). Often, trees infested by bark beetles are colonised by perennial fungi such as *Fomitopsis pinicola* (Vogel and others 2017). These changes in tree vitality, characterised by elevated rates of wood decay and breakage, likely have an impact on TreM composition profile.

However, the underlying causes of apparent TreM loss are likely to vary among different TreM groups (see Table 4). Previous studies have examined the temporal development of *woodpecker cavities*, *rot-holes*, *fire scars*, as well as TreMs that affect timber quality (for example, Wesolowski 2011, 2012; Edworthy and others 2012; Tavankar and others 2017, 2019). The drivers of the temporal changes, particularly loss, across all TreM groups remain to be identified. While the loss of certain TreMs might seem straightforward and intuitive (for example, structures that naturally fall off or decay over time, such as *crown deadwood* or *ephemeral fungi*), the drivers behind loss processes can be diverse. For instance, the changes in TreMs linked to presence and activities of specific forest-dwelling species could be manifold (for example, *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 and Lindenmayer 2002; Siiton and Jonsson 2012). Concurrently, tree defence mechanisms may compartmentalise injuries by inhibiting wood-decaying fungi and sealing wounds, often associated with TreMs (Smith 2015). All the subsequent processes can alter the decay dynamics and shape the development of TreMs, eventually leading to their decline or disappearance.

Cavities have been reported to last approximately 10 years (Edworthy and others 2012; Edworthy and Martin 2013), with slightly shorter rates for excavated cavities than for non-excavated ones (Wesolowski 2011, 2012). Our findings align with these observations, as approximately 60% of the broadleaved trees 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, destruction by predators, decay and collapse of the walls, closure through growth of callus tissues (Wesolowski and Martin 2018). Similar causes can lead to loss of other TreMs too. For example, while large wounds may persist for up to

Table 3. Significant Results of the Cox Proportional Hazard 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

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

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

17 years, *exposed wood* patches and wounds of smaller sizes may be sealed successfully after 10 years depending on the extent of xylem and phloem injury (Vasaitis and others 2012; Tavankar and others 2017, 2019). The masking of wounds can contribute to the loss of TreMs, with a rate varying among tree species, with *P. abies* trees compartmentalising and closing scars at a faster rate than *A. alba* or *F. sylvatica* (Stoffel and others 2005; Trappmann and Stoffel 2013). A detailed overview of possible drivers of TreM loss among all groups is presented in Table 4.

Larger Trees have Highly Dynamic TreM Development Profile

Tree size played a significant role in the TreM development over the course of 3–12 years. In accordance with previous studies (Asbeck and others 2019; Paillet and others 2019; Courbaud and others 2022; Kozak and others 2023), our results support the notion that TreM composition becomes more diverse on trees during their growth. This phenomenon is attributed to the accelerated formation of new TreMs together with the accumulation of TreMs over time (Paillet and others 2019; Asbeck and others 2021a, b; Courbaud and others 2022). In our study, tree DBH appeared as an important driver of both TreM loss and persistence. The stability of TreMs on large trees was evident, as indicated by higher persistence rates of half of the TreM groups compared to smaller trees. Specifically, large trees lose less *exposed sap- and heartwood*, *perennial fungi*, *concavities*, and *fresh exudates*. This can be attributed to the ability of large trees to withstand breakage from wind or snow more successfully than smaller trees (Bragg and others 2002), resulting in fewer losses of TreMs specific to breakage processes (stem and limb breakage, cracks and splits). The presence of *fresh exudates* and *perennial fungi* on large trees may be linked to their susceptibility to stress induced by recent droughts and subsequent colonization by wood decaying fungi (Das and others 2016; Pfeifer and others 2011). However, the dynamics of TreMs on very large and old trees, reaching the stage of senescence, might show contrasting patterns due to advanced decay and breakage, important processes involved in TreM formation and drivers of TreM persistence (Edworthy and others 2012; Kőrckjas and others 2021). In our study, it was not possible to describe TreM dynamics on very large, old trees (over 80 cm in DBH) only, of which we had only a limited number in the data set.

Study Limitations and Research Needs

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 the TreMs was conducted to align with specific project objectives rather than capturing changes in TreMs. Thus, we could not record precisely the moment in time when an event occurred. The variations in survey periods from 3 to 12 years also limited site-specific comparisons and the evaluation of the effect of stand management, forest types, and growing conditions on TreM dynamics. Additionally, our analysis could capture only the dynamics of TreM groups. The stability in the TreM richness suggests increases in numbers of individual TreMs within each TreM group. 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 and others 2015). Nowadays, harmonized TreM typologies are widely available (Kraus and others 2016; Larrieu and others 2018). Thus, future studies may be able to provide more accurate and detailed insights into the development of specific TreMs and allow better understanding of how TreMs evolve, how they influence each other and develop into other TreMs. While the length of this study was sufficient to observe changes in many TreMs, longer periods between the surveys would allow the study of longer-lived microhabitats, such as rot-holes and exposed heartwood structures of large dimensions. Such information can further be implemented in dynamic forest models (Courbaud and others 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 only with living trees improved the statistical power by avoiding problems of 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 (Siitonen 2012). Because TreM composition and diversity differ between living and dead trees (Paillet and others 2019;

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 ($\varnothing \sim 4\text{--}10$ 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 and Meyer (2001), Günther and Hellmann (2005), Wesołowski (2011), Edworthy and others (2012), Smith (2015), Cockle and others (2017), Wesołowski & Martin (2018), Menkis and others (2022), Personal observations Mikusinski G., Nairn R
Exposed sap- and heartwood	Stem breakage ($\varnothing > 20$ 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 die-back** Wood breakage ** (e.g. falling of decayed branches that bear mistletoes or ivy) Removal through forest management (e.g. <i>Hedera helix</i>)	Bässler and others (2016), Nascimbene and others (2016), He and others (2016), Bilgili and others (2020), Zekhuis (2018)
Crown deadwood	Dead branches, top ($\varnothing > 10$ cm) Remaining broken limb ($\varnothing > 20$ 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)	Millington and Chaney (1973), Buse and others (2008), Spielmann and others (2013)
Perennial fungi	Fruiting bodies of perennial polypores ($\varnothing > 5$ cm)	Falling off ** Decay of fruiting bodies *** Breakage of decayed limbs with polypores **	Pouska and others (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 and others (2012), Tavankar and others (2017), (2022) Menkis and others (2022)
Rot-holes	Top-closed or semi-open trunk rot hole, hollow branch ($\varnothing > 10$ cm) Chimney trunk rot hole ($\varnothing > 30$ 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 and Heilmann-Clausen (2010), Edworthy and others 2012, Wesołowski and Martin (2018), Körkjäs and others 2021, Menkis and others (2022)

Table 4. continued

TreM group	Examples of TreM types	Potential drivers of TreM loss Probability of causing TreM loss: *** 'high', ** 'moderate'; * 'low'	References
Concavities	Dendrotelm ($\varnothing > 15$ cm) Woodpecker foraging excavation ($\varnothing > 10$ cm) Root buttress concavity ($\varnothing > 10$ cm)	Wood decay * Overgrowth by other plants * Evolving into another TreM (e.g. woodpecker-foraging wounds decay and form rot-holes)**	Edworthy and others 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 $\varnothing > 50$ cm Epicormic shoots > 5 twig clusters	Natural shedding ** Artificial pruning **	Evans (1985)

Spînu and others [2022](#)), we suggest further investigations on the dynamics of individual TreMs after tree death. This is particularly important in the context of increasing forest disturbances and high tree mortality rates (Seidl and others [2017](#)), which shape the occurrence of microhabitats on trees (Zemlerová and others [2023](#)), and likely their temporal development.

Our data contained recorded losses in certain TreM groups that are unlikely to disappear naturally 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.

In addition, while certain TreMs may be easily recovered due to quick and frequent formation, or even through artificial restoration, the loss of others such as large rot-holes, holds more significant implications for the species they host and need suitable management solutions. However, because we studied TreM dynamics only at the individual tree level, we cannot say how the overall provision of different microhabitats develops over time at the level of forest stands, where TreM dynamics are shaped by tree growth, changes in tree vitality and disturbances.

The retention of old, large trees with abundant and diverse TreMs has been recognised as a high-priority conservation strategy for enhancing the conservation value of European forests (Larsen and others [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 and Cabanettes [2012](#); Asbeck and others [2019](#); Vandekerkhove and others [2018](#)). Simulation studies have also suggested that retention of trees with no TreMs, particularly of short-lived tree species, can contribute to maintaining a continuous long-lasting habitat pool (Fan and others [2004](#); Courbaud and others [2017](#)). For future studies, it would be valuable to investigate the changes in TreMs on trees with various attributes, including different species, senescence stages, presence of decay, or other factors related to TreM development (Edworthy and others [2012](#); Larrieu and others [2022](#)).

CONCLUSIONS AND IMPLICATIONS FOR FUTURE FOREST MANAGEMENT

So far, the selection of habitat trees has focused on their current TreM occurrence without quantifying the impact of this practice for future habitat provisioning. 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 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 rare TreMs and additionally retain functionally different trees that provide diverse TreMs (for example, different tree species or vitality status). Biodiversity conservation can be promoted from the early stages of forest development and trees

with unusual shapes or defects that would normally be removed, could be retained and allowed to develop into habitat trees. 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 for retention of habitat trees.

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DATA AVAILABILITY

Data analysed during this study are provided in full within the published article.

Declarations

Conflict of interest The authors declare there are no competing interests.

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