ORIGINAL PAPER

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

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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

Introduction

The multifunctional role of forests is recognized worldwide, and in Europe, numerous integrative forest management approaches aim to balance potential conflicts between the goal of timber production and biodiversity conservation (Freer-Smith and Carnus 2008; Bollmann and Braunisch 2013; Kraus and Krumm 2013; FAO Report 2020; European Commission 2019). Commercial forestry with short production cycles has often simplified and homogenized forest structures. As a consequence, these forests often lack habitat for many forest-dwelling species especially those dependent on structural elements of old-growth forests (Ishii et al. 2004; Kuuluvainen 2009; Winter and Brambach 2011; Kraus and Krumm 2013; Fredowitz et al. 2014). In recent decades, retention forestry has been promoted to reduce the impacts of harvesting on many forest-dwelling species (Gustafsson et al. 2020). This forest management approach was introduced in North America about 35 years ago, but has also been practiced and researched in the context of clearcutting systems in regions such as Scandinavia and Australia (Gustafsson et al. 2012). One important element of retention forestry is biological legacies, i.e. structures and organisms that remain on site after disturbances to ensure habitat continuity for forest-dwelling species (Franklin et al. 2002; Gustafsson et al. 2012). Consequently, in uneven-aged, continuous cover forests of temperate Europe, the practice aims at enriching the conditions of the post-harvest ecosystem and achieving temporal and spatial connectivity of

key habitats by intentionally retaining deadwood and habitat trees (Gustafsson et al. 2020). Habitat trees are large living or dead standing individuals that already bear specific structures needed by many specialist species for parts of their life cycle for foraging, breeding, or nesting (Bütler et al. 2013; Larrieu et al. 2018). These structural features are called tree-related microhabitats (hereafter TreMs) and are essential for the structure and viability of forest communities and many associated species (for example: arthropods—Dajoz 2007; Stokland et al. 2012; bryophytes and lichens—Jahns 1989; Fritz and Heilmann-Clausen 2010; bird communities—Gossner et al. 2016; Gouix and Brustel 2012; Ranius 2002; Basile et al. 2020).

TreMs have not only been used as a proxy indicator of biodiversity in forests, but also as an efficient tool for habitat tree quality assessment and selection (Asbeck et al. 2019, 2021a; b; Larrieu et al. 2018). In the last decade, the concept of TreMs has been widely implemented in integrated conservation approaches through retention of habitat trees in managed Central European forests. Here, past management practices led to relatively low levels of standing deadwood and habitat trees owing to the constant removal of diseased, dying or old trees during thinning and traditional stand improvement practices. While deadwood retention is rather straightforward, the selection of suitable living habitat trees is increasingly based on TreMs in current schemes adopted in Germany, Austria, Switzerland, and France (Asbeck et al. 2021a, b).

Previous studies have shown that TreM abundance and richness are linked to both specific tree attributes [diameter at breast height (DBH), species, vitality status (live vs. dead trees)] (Michel and Winter 2009; Vuidot et al. 2011; Paillet et al. 2017; Kaufmann et al. 2018; Asbeck et al. 2019) as well as stand and environmental conditions (forest management, forest type, altitude) (Larrieu et al. 2014a, b; Winter et al. 2015; Asbeck et al. 2019). In temperate forests, broadleaved trees, large trees and dead standing trees were consistently found to bear more and richer TreMs than coniferous, small and living trees, respectively (Asbeck et al. 2021a, b). Only the largest trees supported all TreM types (Larrieu et al. 2014a, b). This can be attributed to a combination of factors related to species and vitality status: different wood properties, crown structure, position of the tree in the canopy, tree senescence (Asbeck et al. 2020, 2021a; b). Interestingly, the degree to which these tree attributes complement one another in terms of TreM abundance and richness at the stand level has not been studied so far.

Information on the combination of vitality status and tree species is valuable, since the selection of habitat trees has often focused on one of these attributes alone and never on their interaction (for example: Read 2000 in Britain; Land for Wildlife Queensland Note (2016) in Australia; Bütler et al. 2021 in Switzerland). Commonly, retaining large living

trees is one of the most straightforward approaches to provide TreMs at the stand level. However, large trees are facing global decline (Lindenmayer et al. 2012) and their increased size also makes them more susceptible to disturbances and environmental stress leading to mortality (Grote et al. 2016). Large trees suffer more than smaller ones from disturbances such as wind throw and drought-related water stress due to their greater heights and exposed crowns (Bennett et al. 2015; Stovall et al. 2019; Forzieri et al. 2021). Under high water stress, tall trees may also be more readily attacked by biotic agents, such as bark beetles (Pfeifer et al. 2011). Since a higher tree mortality is expected in European forests (Samaniego et al. 2018; Senf et al. 2020), information on how tree death affects the formation and dynamics of TreMs is valuable, also to support decisions about salvage harvesting or tree retention.

Biological, physical and chemical wood substrates are different not only among living trees, but also among dead trees of different decay stages (Herrmann et al. 2015; Kahl et al. 2017). The decay rate, which differs greatly among tree species, has an important role in snag dynamics (Cornwell et al. 2009) and likely a significant effect on TreM occurrence. For example, the low wood density of fast-growing species (*Populus, Betula* sp.) influences their susceptibility to breakage. This can result in branches and crowns falling earlier than in other hardwood species such as *Quercus* sp. (Basham 1991). In species preferred by wood-boring insects, tree decay is accelerated by excavated galleries (Rayner and Boddy 1988), often leading to the formation of ephemeral TreMs such as pockets and shelters under loosened bark. Moreover, higher carbohydrate and lower lignin levels in broadleaved trees cause higher decay rates when compared to conifers (Cornwell et al. 2009; Kahl et al. 2017). However, wood decay rates differ greatly among conifers. For example, *P. abies* logs decomposed 21 to 25 years faster than those of *A. alba* (Přívětivý et al. 2018). In addition, tree size has an effect on its wood decay dynamics. Larger trees, which have a smaller ratio of volume to surface area of wood exposed to colonization by wood decaying organisms, are expected to decompose slower than smaller trees (Mackensen et al. 2003; Vanderwel et al. 2006). Thus, deadwood of large trees and/or conifers are more likely to bear long-lived TreMs and greater abundance and richness of TreMs due to their longer persistence.

Although most studies on deadwood dynamics have focused on downed logs (Angers et al. 2012), we can assume that relative differences in decay rates among tree species remain similar in standing dead trees. However, it is likely that snags decay at a slower rate owing to the low degree of soil contact, which has been described as a primary driver of wood decomposition (Shorohova and Kapitsa 2014; Přívětivý et al. 2018). Yet, we do not know, how decay may influence provision of TreMs in snags.

Despite possible differences in habitat provision between dead and live large trees, the different microhabitat assemblages and how they complement each other have not been considered in current concepts of habitat tree retention in Central European forests. Yet, an evidence-based selection of living and dead trees to optimize microhabitat provision in managed forest is pivotal, especially since current forest management approaches for biodiversity conservation may become unsuitable under climate change (Augustynczik et al. 2019, 2020). Therefore, one important goal of our research was to offer practical recommendations for tree retention suitable for managed forests in Central Europe. The research objectives of our study 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. For that purpose, we compared TreM abundance, richness and composition on habitat trees of different species, vitality status (living or dead) and dimensions. In this study, we did not consider *species* and *vitality status* as two different factors, but combined them into *tree identity*. Our hypotheses were that:

1. TreM abundance, diversity and composition differ between different tree identities;
2. TreM abundance and richness differ between standing dead trees of different decay stages; they increase with decay stage and snag diameter;
3. The highest stand-level TreM abundance and richness can be achieved through combinations of trees with different identities.

Methods

Research area

The study was carried out within the project "Conservation of forest biodiversity in multiple-use landscapes" (Storch et al. 2020). The research area is located in the southern Black Forest (Latitude: 47.6°–48.3°N, Longitude: 7.7°–8.6°E, WGS 84) within an altitudinal range between 500 and 1400 m.a.s.l. (Fig. 1). Data were collected on 133 one-hectare plots, which were initially selected following a landscape gradient of forest cover in the surrounding 25 km^2 and a structural complexity gradient that was indicated by the number of standing dead trees per plot. The research plots are dominated by three tree species, Norway spruce (*Picea abies* (L.) Karst), European beech (*Fagus sylvatica* L.) and Silver fir (*Abies alba* Mill.), in this order of abundance. Healthy living trees were dominating the growing stock in the studied stands. Few trees of lower vitality classes, diseased or dying, were present in the study plots.

Forest management in the study area follows the prevailing paradigm of close-to-nature forest management, applied in many Central European forests, which generally avoids clearcutting, intensive soil preparation, use of fertilizers and herbicides (Bauhus et al. 2013; Larsen et al. 2022). Among the plots used for this study, the management intensity is variable, ranging from no interventions in six plots located in strict forest reserves, to more intensively managed forests (Asbeck et al. 2021a, b). In the latter, the proportion of tree volume that was harvested in recent decades can reach 80% of the theoretical maximum of the standing volume (Asbeck et al. 2021a, b). Even though a difference in TreM abundance and richness between managed and unmanaged forest stands can be expected (Paillet et al. 2017; Asbeck et al. 2021a, b), a previous study conducted on the same plots as used here showed that different forest management types did not have a significant effect on TreM abundance and richness on living habitat trees (Asbeck et al. 2019). The time since the management ceased (less than 50 years) appears to not have been long enough to see a difference yet in the TreM estimates between currently managed and unmanaged stands (see also Vuidot et al. 2011). The studied plots still show similar stand characteristics irrespective of their current management type.

Data collection

The TreM inventory followed the standardized typology of Larrieu et al. (2018). The typology includes 15 TreM groups that follow a hierarchy related to morphological characteristics and biodiversity relevance (Larrieu et al. 2018) (Appendix: Table 3). The TreMs were surveyed on the largest 15 living and, if possible, on 15 standing dead trees in each plot. The dead trees had a minimum DBH threshold of 20 cm and were selected in a random grid in the field to capture most of the variation of TreMs. In 18% of the plots, 15 dead trees were found, 10% of the plots had none and the rest had a variable number of dead trees (1–13) (Appendix: Table 4). The largest 15 living trees in each plot, which we regard as potential habitat trees, were pre-selected from LIDAR images based on their crown diameter, which is a strong determinant of stem diameter (here DBH) (e.g. Jucker et al. 2017). This method relates to the local guidelines for habitat tree selection (*The old- and dead wood concept,* Forst 2015) and was more time-efficient than a selection based on terrestrial inventory. Previous studies showed that TreM richness and abundance were strongly and positively related to DBH (Asbeck et al. 2021a, b). Hence, these 15 largest trees with a DBH ranging from 18 to 142 cm were the best candidates for habitat trees with many and diverse TreMs.

Living habitat trees were located in the field based on their GPS coordinates obtained from LIDAR images. TreMs,
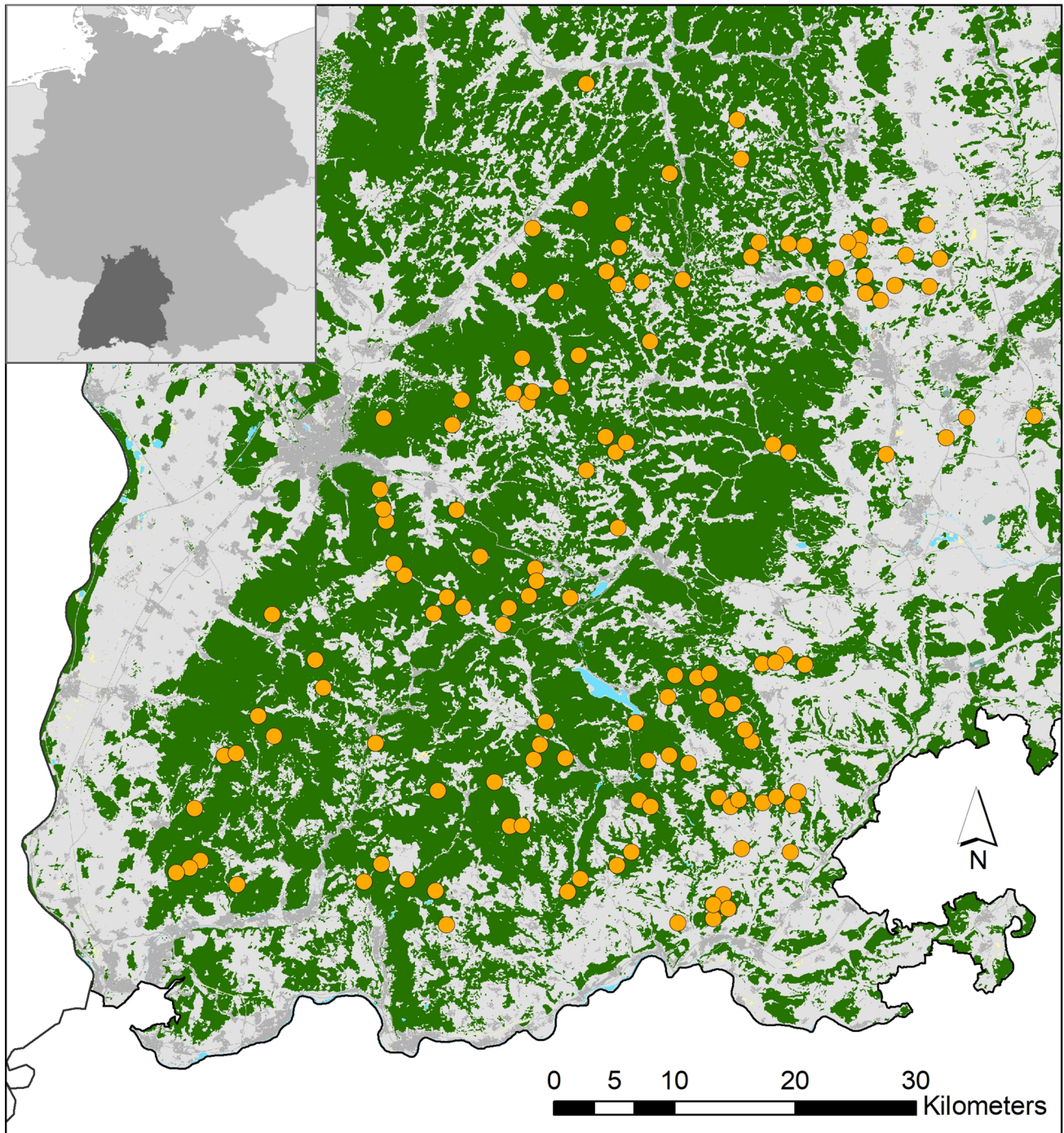
Fig. 1 Location of the 133 one-hectare plots in the Black Forest, Germany (insert) in the ConFobi study design (Storch et al. 2020)

tree DBH and species identity were recorded for all trees (living and dead). In addition, decay stages of dead trees were noted. The decay stage of standing dead trees was assessed in five classes adapted from Sippola and Renvall (1999) and Puletti et al. (2019): (1) hard wood, completely covered with bark, fresh phloem sometimes present; (2) wood mostly hard, most of the bark left, but no fresh phloem present; (3) wood is partly decayed on the surface or in the centre, large pieces of bark usually loosened or detached, branches still present; (4) most of the wood is soft, the central parts can remain hard, while the surface layers of the wood can be missing; (5) wood is very soft, usually covered by epiphytes. The presence of TreMs such as broken tops, crown deadwood or bark characteristics is often included

in classifications of standing deadwood. If such a classification were employed, provision of TreMs would not be independent from decay class in a statistical sense and could lead to biased results. Thus, we employed a methodology that classified dead wood solely on the wood decay stage to avoid this problem. Fieldwork was carried out during winter of 2019–2020 in the leafless and snow-free period. The TreM inventory was done by the same team of observers to minimize observer effects (Paillet et al. 2015). Binoculars were used to identify TreMs at greater tree heights. The main characteristics of the surveyed trees are summarized in Table 1.

Data analysis

All data analysis was processed with the R Studio Software 1.3.1073 (RStudio Team 2020). Preliminary data exploration was done following the protocol proposed by Zuur et al. (2010) to avoid type I and II errors by investigating outliers, heterogeneity of variance, collinearity, and missing values. TreM abundance was calculated as the total number per tree, whereas richness accounted for the number of different TreMs groups per tree (e.g. rot-holes, concavities, crown deadwood). To identify the main drivers of TreM abundance and richness across and within TreM categories, generalized linear mixed models (GLMMs) were used. Plot identity was included as a random factor to prevent autocorrelation of trees from the sample plots (Dormann 2013).

We defined a new variable *tree identity* that combined the variables *vitality status* and *tree species* since one is not independent from the other and their interaction can have a significant effect on TreM provisioning (e.g. dead *P. abies* or living *F. sylvatica*). The wood substrate of living and dead trees differs greatly between tree species (Cornwell et al.

2009). Owing to the small number of observations in some tree species and the difficulty to differentiate between different dead conifer species in advanced stages of decay, we could assign this variable only to living and dead *P. abies*, *F. sylvatica* and *A. alba*. Unidentified tree species were pooled into categories of other dead or living conifers and broad-leaved trees. Other broadleaved trees represented 3% of the total sample and included *Quercus petraea* (Matt.) Liebl*., Tilia cordata* Mill*., Acer platanoides* L*., A. pseudoplatanus* L*., Alnus glutinosa* L*., Betula pendula* Roth*, Fraxinus excelsior* L*., Prunus serotina* Erhr*., Populus tremula* L.. Other living conifers were *Pinus sylvestris* L*., Pseudotsuga menziesii* (Mirb.)*, Larix decidua* Mill. and *Abies grandis* Lindl., accounting for 14% of the total number of living trees.

We excluded insect galleries when calculating TreM abundance and from the TreM models, because it is practically not possible to assess from the ground the occurrence of this TreM over the whole tree surface, in particular not on snags. Microsoils, nests, twig tangles and crown deadwood were excluded from the statistical models for individual TreM groups since they were represented only by very few observations. Yet, they were considered in the statistical models for total TreM abundance and richness.

All models were based on count data with a negative binomial distribution that accounts for overdispersion. The only model which did not show signs of overdispersion was the GLMM for the TreM "burrs and cankers", which assumed a Poisson error distribution. Computation of models was done with the "glmmTMB" function of the "glmmTMB" package (Brooks et al. 2017). Model selection was done by dropping non-significant predictors in order to improve the Akaike information criterion (AIC) with the function "drop1" of the "stats" package of R. Overdispersion, zero-inflation and the performance of each model based on residuals were tested with the "DHARMa" package

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

Tree identity	N. of trees	Total share (%)	DBH (cm)				TreM abundance per tree			TreM richness per tree		
			Mean	SD	Min	Max	Mean	SD	Max	Mean	SD	Max
Living (N = 1804)												
Abies alba	332	12.07	47.85	17.2	24	142	1.6	2.5	23	0.9	0.9	5
Fagus sylvatica	392	14.25	42.11	15.8	19	120	2.3	3.4	35	1.4	1.2	7
Picea abies	753	27.38	42.02	14.1	19	115	1.1	1.9	19	0.7	0.8	6
Other coniferous sp.	262	9.53	36.10	14.9	23	102	1.1	2.2	14	2.1	1.6	4
Other deciduous sp.	80	2.91	32.75	15.8	17	88	2.8	2.7	17	1.9	1.3	5
Dead (N = 929)												
Abies alba	112	4.07	66.84	17.6	20	107	5.7	6.0	27	2.0	1.3	6
Fagus sylvatica	35	1.27	53.00	21.0	20	113	4.9	7.0	29	1.5	1.2	5
Picea abies	589	21.42	54.96	15.4	20	119	3.0	3.8	25	1.4	1.2	6
Other coniferous sp.	183	6.65	57.11	11.5	20	79	4.9	5.3	31	2.1	1.6	6
Other deciduous sp.	12	0.44	43.97	10.1	20	49	2.9	2.4	8	1.7	1.1	4

(Hartig 2018). All TreM models followed the initial formula: ~ *DBH + tree identity + (1|PlotID)*. The final models, after the backward stepwise selection, are summarized in Table 2. Plotting of models was performed with the "ggpredict" function of the "ggeffects" package, which shows the main effect of one predictor and sets all the others in relationship to it (Lüdecke 2018). Visualization was carried out with the "ggplot" package (Wickham 2016).

The association of TreMs with tree identities was investigated by using a bipartite network, clustering tree identities with similar TreMs into functional groups (e.g. Asbeck et al. 2020). This type of network is divided into modules, identified with a modularity matrix described by Newman (2006). By accounting for the TreM abundance per tree identity, the modularity measures are applied to a weighted version of the bipartite network (Beckett 2016). The analysis was performed with the R package "bipartite" (Dormann et al. 2018).

Nonparametric methods were employed to test whether TreM abundance and richness are significantly different for different decay classes and diameters of dead trees. We further investigated the effects of four different approaches of selecting habitat tree at the plot level. Here, we chose for each one-hectare plot the ten habitat trees with highest TreM richness and abundance following four different retention strategies. The number of ten habitat trees per ha is at the upper end of the currently practiced range of habitat retention in European forests (Gustafsson et al. 2020). In the first simulated retention approach, we selected a combination of five living and five dead habitat trees (trees that support TreMs). For the second and third approach, we focused on ten dead and, respectively, ten living habitat trees. The fourth approach represents a "reference" selection of ten habitat trees per plot with the overall highest abundance or highest richness of TreMs irrespective of their vitality status. Significant differences in the average TreM abundance and richness among the four retention approaches were tested using the nonparametric rank-based Kruskal–Wallis test with Dunn post-hoc tests (Dunn 1964). Figures were designed to be colour-blind friendly with the R package "viridis" (Garnier et al. 2021).

Results

Habitat tree level

The main drivers of the overall TreM abundance and richness were DBH and tree identity. Most of the TreM groups increased significantly with increasing DBH, but the interaction between DBH and TreM occurrence was not significant for exposed sapwood and epiphytes (Table 2). The GLMM model indicated that the tree identity with the highest

TreM richness and abundance was dead *A. alba.* Other living coniferous species such as *P. sylvestris, L. decidua, P. pseudotsuga* appeared to have the lowest TreM richness and abundance. In addition, other living broadleaved trees (excluding *F. sylvatica*) were significant only in the model of TreM abundance (Fig. 2, Table 2). The highest abundance of woodpecker cavities, burrs and cankers were found on dead *A. alba*, whereas the highest occurrence of rot-holes and exposed sap- and heartwood was predicted for other living conifers (Fig. 3, Table 2).

In dead trees, both TreM abundance and richness differed significantly among decay classes (Kruskal–Wallis test for TreM abundance ($\chi^2 = 72.422$, $df = 4$, p value < 0.0) and for TreM richness ($\chi^2 = 77.096$, $df = 4$, p value < 0.05) with highest values in decay classes 4 and 5 (Fig. 4, Appendix: Fig. 7). TreM abundance and richness on dead trees in more advanced decay classes increased with increasing DBH. Snags of *A. alba* had the highest mean DBH among dead trees, followed by other conifers that could not be identified to species level due to their advanced decay stage (Table 1). The average DBH of *P. abies* was 20 cm smaller than that of *A. alba*. Deciduous species other than *F. sylvatica* belonged to the smallest DBH category.

The bipartite analysis of the TreM composition distinguished four main functional groups within the matrix of TreM abundance and tree identity (Fig. 5, Appendix: Table 3). The first group was characterized by occurrence of woodpecker cavities, insect galleries, concavities, as well as exposed sap- and heartwood. This group of TreMs was mostly found on dead conifers. The second group consisted only of dead *F. sylvatica* and was characterized by the occurrence of fungi, both perennial and annual (Fig. 5). TreMs such as rot-holes, crown deadwood, nests and microsoils were mostly associated with living *F. sylvatica* and other broadleaves and conifers (excluding *A. alba* and *P. abies*). The last group, comprised of living *A. alba* and *P. abies*, supports most strongly the occurrence of epiphytes and other epiphytic structures, fresh exudates, burrs and cankers and twig tangles (Fig. 5).

Plot-level results

The four simulated retention strategies showed significant differences in TreM provision at the plot level. Selecting solely dead or living trees yielded the lowest abundance and richness of TreMs. The combined approach (five living and five dead habitat trees) yielded similar TreM abundance and the smallest reduction in TreM richness from the optimum level given by the reference selection of the ten trees with the overall highest abundance and richness of TreMs, irrespective of their status (Fig. 6, Appendix: Table 5).

Table 2 Results of the final generalized linear mixed models indicating the magnitude of influence and the significance of the predictors DBH and tree identities (dead/living and species)

| | Intercept | DBH (cm) | Tree identity | | | | | | | | |
| | | | Living | | | | | Dead | | | |
			P. abies	A. alba	Other conifers	Other deciduous	F. sylvatica	P. abies	F. sylvatica	Other conifers	Other deciduous
TreM abundance[b]	0.87***	0.02***	−1.69***	−1.55***	−1.70***	−0.68***	−1.04***	−0.53***	−0.04	0.10	−0.57
TreM richness[b]	0.18***	0.01***	−1.15***	−0.98***	−1.35***	−0.08	−0.41***	−0.32***	−0.20	0.18	−0.18
Woodpecker cavities[b]	−1.19***	0.01*	−4.94***	−21.4	−3.52***	−3.20**	−3.35***	−0.83***	−1.27*	−0.08	0.18
Rot-holes[b]	−3.31***	0.03***	−1.67***	−1.93***	−2.56***	1.21***	1.06***	−0.36	−0.51	−0.40	0.39
Concavities[b]	−0.35*	0.02***	−0.66***	−1.41***	−3.69***	−2.12***	−0.68**	−0.48***	−0.68**	−0.58***	−0.65
Exposed sapwood[b]	−1.26***	0.06	−1.14***	−0.93**	−0.75*	0.16	−0.05	0.08	−1.14	0.80**	0.21
Exposed sap- and heartwood[b]	−1.25***	0.01*	−3.31***	−3.70***	−2.83***	−1.05**	−1.44***	−0.23	0.44	−0.10	−0.34
Burrs and cankers[a]	−7.30***	0.02**	0.89	2.11*	−0.47	0.70	1.42	0.87	1.76	2.15	2.80
Perennial fungi[b]	−1.47***	2.14***	−2.41	−4.67***	−2.20	−2.07	−5.10***	−6.30*	4.9	−1.15**	−1.70
Annual fungi[b]	−5.11***	2.97**	−3.75***	−2.95*	−2.80*	−2.58	−2.12	1.01	−8.17	−2.74	−1.82
Epiphytes[b]	−3.53***	0.004	0.43	1.74***	−1.11*	1.86***	1.27***	−0.91**	−0.66	−0.92	−0.56
Fresh exudates[b]	−2.87***	–	1.96***	0.19	0.54	−21.08	−2.33**	0.56	−18.45	0.19	−15.07

Positive values show an increase in the group of tree-related microhabitats. The intercept represents the dead *Abies alba*

Significance codes: ***0.001; **0.01; *0.05

[a] A binomial distribution was used for burrs and cankers

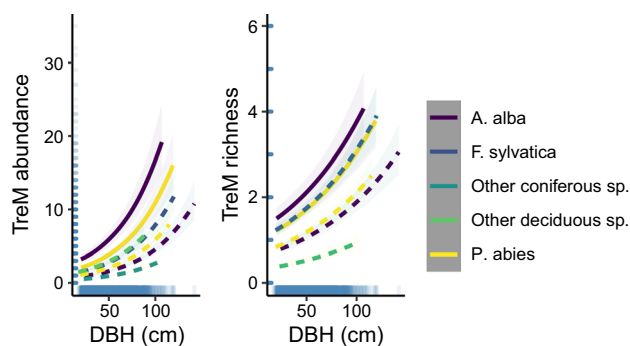[b] All models were fitted with negative binomial distributions

Fig. 2 Estimated TreM abundance (left) and richness (right) in response to DBH of the surveyed trees. Solid lines represent the dead, dotted lines the living trees and the colours refer to the tree species. Ribbons represent the 95% confidence intervals. Tree identities (species and vitality status) which were not significant in the models were not included in the graph

Discussion

Our results show that retention practices should take in consideration not only tree size and identity, which were important predictors of TreM abundance and richness, but also TreM composition. We identified four functional tree identity groups with distinctly different TreM associations. While dead *A. alba* trees provided the highest TreM abundance and richness, large living broadleaved trees supported distinct TreMs, not found on *A. alba*. In contrast to approaches that retain solely living or dead trees, retention of different tree identities not only assures complementary TreMs but provides also for an overall higher TreM abundance and richness.

Dead *Abies alba* provide many and diverse TreMs

Our results show that TreM abundance, richness and composition differed significantly among tree identities. Large dead *A. alba* carried the highest total abundance and richness of TreMs, almost twice the amount found on *F. sylvatica* and other broadleaved trees. Many previous studies found broadleaved trees to bear more and richer TreMs than conifers (Larrieu and Cabanettes 2012; Asbeck et al. 2019), but those results were reported for living trees only. The production time of *A. alba* in close-to-nature management is often longer than that of other species and the snags of *A. alba* were most likely of old large trees and in an advanced stage of decay. Snags of old *A. alba* trees are likely to persist for long periods owing to a combination of wood properties, a high mean DBH and possibly also a deep root system, which provides for anchorage in the soil. Debris of trees with larger
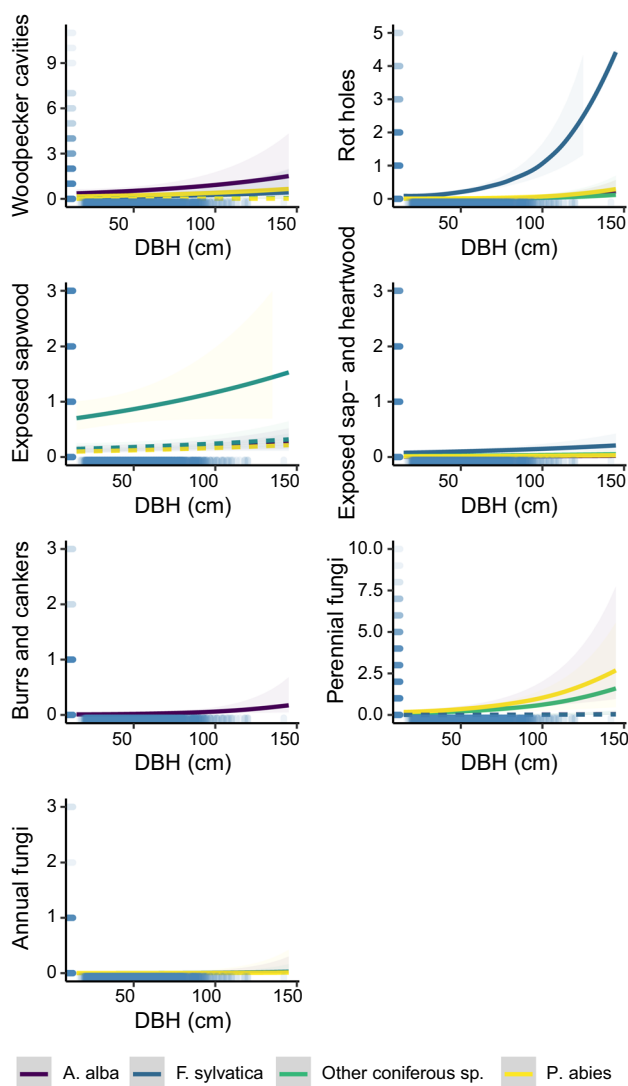

Fig. 3 Estimated abundance for TreM groups in response to the strongest predictors of the surveyed trees. Solid lines represent the dead, dotted lines represent the living trees and the colours refer to the tree species. Ribbons represent the 95% confidence intervals. Tree identities (status and species) which were not significant in the models were not included in the graph

dimensions shows in general a low decay rate (Vanderwel et al. 2006; Fravolini et al. 2018). This is related to a smaller surface to volume ratio which is exposed to mechanical and biological agents involved in decomposition, and a higher heartwood to sapwood ratio, where the heartwood is typically more decay resistant (Mackensen et al. 2003; Cornwell et al. 2009). Deadwood logs of *A. alba* decayed slower than those of *P. abies*, especially at cold sites (Přívětivý et al. 2018). Thus, snags of *A. alba* in this study may have persisted longer and accumulated TreMs that appeared both while trees were alive (burrs, cankers, twig tangles) and/or after their death (woodpecker cavities, concavities).
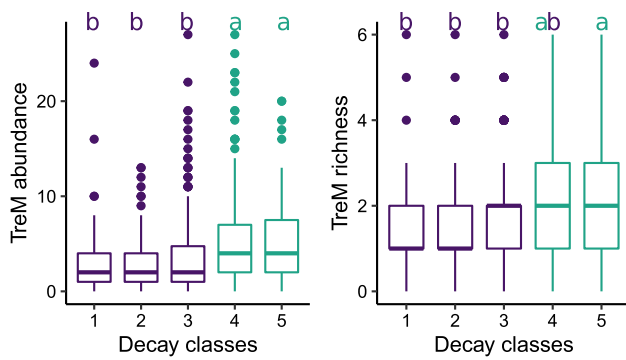
Fig. 4 Estimated mean of TreM abundance (left) and richness (right) of dead trees for each decay class in five categories from low (1) to high decay (5) with a 95% confidence interval

Dead *A. alba* supported also the highest occurrence of woodpecker cavities, which are some of the most important TreMs for biodiversity conservation in European forests (Larrieu et al. 2018). The high number of woodpecker cavities on dead *A. alba*, twice as many as on *F. sylvatica*, was contrary to our expectations since woodpeckers in their natural habitats are expected to prefer non-resinous wood (Schmidt and Czeschlik 2006; Tozer et al. 2011; Blanc and Martin 2012). Yet, in contrast to other conifers, wood of *A. alba* does not have primary resin ducts and glands (e.g. Metzler et al. 2012) and is thus more attractive to woodpeckers. However, many other studies have found high numbers of cavities in snags of *A. alba*, *P. abies* and *P. sylvestris* in

managed forests (Vuidot et al. 2011; Larrieu and Cabanettes 2012; Paillet et al. 2019). This is probably related to the lack of old living broadleaved trees that have dead branches or decayed parts of the stem with soft wood formed by fungal decomposition. Hardwood trees with presence of wood decaying fungi such as *Fomes fomentarius* are preferred by woodpeckers for cavity excavation, presumably to save energy (Rolstad et al. 2000; Zahner et al. 2012). Trees in managed forests are relatively young and since forest management commonly removes injured and decaying trees, large living hardwood trees with signs of decay are rare. Thus, the *A. alba* snags may fill an important gap as suitable trees for woodpecker cavities in these mixed mountain forests.

Our model predicted lowest numbers of TreMs for other living conifers, which is probably attributable to the presence of the introduced Douglas fir, *P. menziesii*. It has been shown that, even though the species is abundantly colonized by epiphytes in its natural range, individuals of *P. menziesii* do not support many TreMs in Central Europe (Asbeck et al. 2020). This species showed relatively low mortality rates, especially in the context of recent droughts (Eilmann and Rigling 2012) and its wood is characterized by a high decay resistance (Kahl et al. 2017). In addition, owing to its high growth rate, it is typically substantially younger than other tree species at a given tree diameter and hence has less time for the accumulation of TreMs until harvesting. Furthermore, fruiting bodies of perennial fungi were predicted to be abundant on snags of *P. abies*. This can be explained by

Fig. 5 Functional groups of the bipartite network between TreMs and different tree identities. The darker the squares the more associations of the species with a certain type of TreM were observed. The intensity of the colour blue provides for a relative comparison within a given tree identity (by rows), but not over the whole matrix. The colour intensity refers thus to a 0–100% frequency of association of the tree species with the TreM group. Red boxes delineate the functional groups (Dormann et al. 2021)
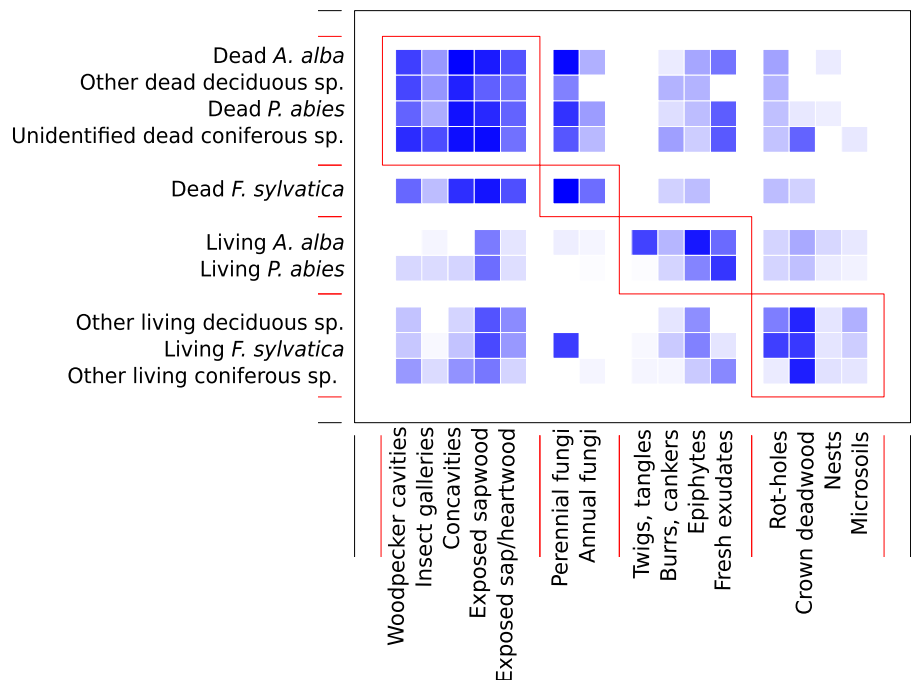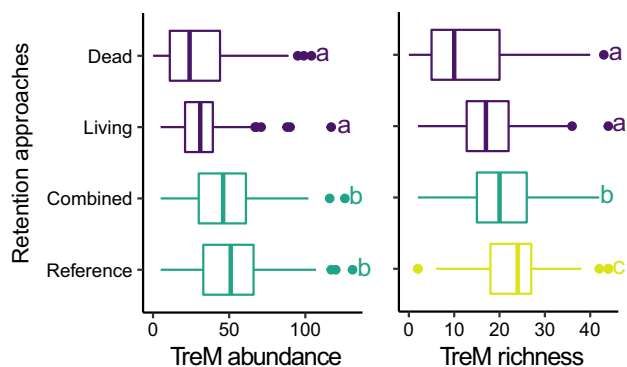
Fig. 6 The influence of different retention approaches of selecting ten potential habitat trees on mean abundance (left) and richness (right) of TreMs per one-ha plot: *Combined* (five living and five dead trees), *Dead* (ten dead trees), *Living* (ten living habitat trees), *Reference* (ten trees with the highest abundance or highest richness of TreMs irrespective of their vitality status)

the presence of *Fomitopsis pinicola,* a primary decay fungus which often colonizes dead trees infested by bark beetles (Vogel et al. 2017). Large areas of the Black Forest dominated by *P. abies* have been subjected to recent bark beetle outbreaks (FVA report, Baden-Württemberg 2020). The lack of other TreMs on dead spruce trees is likely attributable to the fact that the majority of these snags developed only recently (2–3 years since death) and were quite small. Thus, time may not have been sufficient to develop new TreMs specific to deadwood. Previous studies predicted the formation rate of TreMs on living trees (Courbaud et al. 2017, 2021), which increased with DBH for most of the TreM categories. However, reliable time series based on longitudinal observations are still needed to understand TreM development (formation and persistence) on both living and dead trees.

Living broadleaved trees have a distinct TreM composition

The bipartite network analysis of functional groups showed that trees of different identities supported distinct TreM groups. The main four functional groups of TreMs were related to tree genera, vitality status and thus similar wood properties. Similar results were found in a comparison of TreM composition between forest stands from North America and Central Europe (Asbeck et al. 2020). The only TreM group in our study that was found in equal abundance in both conifers and broadleaved trees is crown deadwood. This TreM may be related to the age of trees, their wood properties and crown shape. In the Black Forest region, stands of *P. sylvestris* and *F. sylvatica* are managed under longer

production cycles (120–160 years) than faster-growing conifer species such as *P. abies* or *P. menziesii* (60–100 years) (Asbeck et al. 2021a, b). Therefore, *F. sylvatica* and *P. sylvestris* (from the category of living coniferous species) are likely old, have more exposed crowns that lead to increased amounts of crown deadwood. Crown deadwood of *P. sylvestris* and *F. sylvatica* offers suitable resources for specific organisms (for example, saproxylic wasps, Ulyshen et al. 2011, and saproxylic beetles, Bouget et al. 2011) and could not be replaced by simply selecting dead conifers with an overall higher abundance and richness of TreMs. The most significant identities among the living trees for an increased TreM abundance were other broadleaved trees (such as *Quercus, Acer*, *Fraxinus* sp.) and *F. sylvatica* for TreM richness. This highlights the crucial role of living large broadleaved trees for supporting TreMs that are needed by many forest species (Stokland et al. 2012; Gossner et al. 2016; Basile et al. 2020; Kaufmann et al. 2021).

TreM abundance and richness in snags increased with decay class

TreM abundance and richness were higher on dead than on living trees and increased with advancing decay stages. Previous studies had shown that TreM abundance and richness increased with DBH of live habitat trees (Asbeck et al. 2019, 2021a, 2017; b; Großmann et al. 2018; Paillet et al. 2019). The positive effect of tree dimension on TreM occurrence was attributed to the indirect effect of tree age and life traits because this allows trees more time to accumulate TreMs (Asbeck et al. 2021a, b; Kõrkjas et al. 2021). The effect could also be a result of an increased surface area, suitable for specific TreMs (large cavities, epiphytes, long-lasting TreMs on larger snags that decay slowly). Here, we show that this relationship is also true for standing dead trees and thus confirms the importance of deadwood in large sizes and different decay classes in forests (Jonsell et al. 1998; Siitonen 2001; Merganičová et al., 2012). Whether the positive effect of DBH on TreM patterns is due to increased surface area or due to tree senescence (through age and growth patterns) remains to be analysed for snags in the Black Forest region.

Plot-level TreM provision can be optimized by retaining living and dead trees

Our plot-level analysis showed that retention of both dead and living habitat trees resulted in an overall better provision of TreMs than a sole focus on only living or dead

habitat trees. Retaining trees with the highest abundance and richness of TreMs irrespective of their status would be obviously the best approach, assuming that this superior result will persist into the medium- to long-term future. However, if retention is focused solely on living or dead habitat trees, a great number and types of TreMs could not be captured. Focusing only on dead trees would also carry the risk that TreMs may not be provided for long periods owing to the collapse or fall of snags. For example, the half-life of snags of congeneric *Picea mariana* and *Abies balsamea* species in the boreal forest was less than 20 years (Angers et al. 2010). The approach of combining both dead and living trees appears to provide abundant, rich and complementary TreMs with a longer time horizon.

Several aspects of design and methodology could be improved in future studies. In our study, the recording and quantification of some TreMs (such as insect galleries, deadwood) on dead trees were constrained by the standardized TreM catalogue and therefore some TreM groups could not be included in the data analysis. In addition, TreM surveys following the typology of Larrieu et al. (2018) are less suitable on dead trees in advanced decay classes, where certain TreMs can no longer be found. Using a TreM typology suitable for dead trees could lead to different results. By comparing the widely used typology of Larrieu et al. (2018) with a methodology that includes TreMs relevant to the local biodiversity, Kõrkjas et al. (2021) showed that the choice of the criteria itself affects the TreM estimates. The plots of our study were mostly located in managed forests, where there are typically few large dead trees, and living trees have an overall low average number of TreMs compared to unmanaged forests (Asbeck et al. 2021a, b). In particular, the sample size of dead broadleaved trees was small and fitting models for individual TreM groups were thus not possible due to the low number of observations. In addition, to separate clearly between the influence of the tree vitality status and species, adequate numbers of each combination of these two factors would need to be sampled.

Given these limitations, the recommended combined retention approach may be limited to Central European montane forests. Additional studies in lower altitude forests with higher abundance of dead deciduous trees would be needed to assess whether the combination of live and dead habitat trees provides for similar complementarity in TreM provision. In practice, in the studied plots and in many managed forests in Central Europe, standing deadwood

is generally in low amounts or not present (Vítková et al. 2018). While TreMs on dead standing trees complement those on large living habitat trees, snags should not be used to replace selection of live habitat trees or reduce their number. Both types of habitat trees support unique TreMs. Moreover, the increasing climate change-related mortality of large habitat trees (Bennett et al. 2015; Forzieri et al. 2021) will make it necessary to ensure retaining sufficient numbers to compensate for their attrition. Retention of dead trees could aid biodiversity conservation efforts, but it can also pose a greater operational health and safety hazard than retention of large living habitat trees. Therefore, location of dead trees to be retained within stands needs careful consideration to minimize risks for forest workers and people seeking recreation.

Conclusion

Our study shows that large trees of different species, vitality status and decay class complement, but cannot substitute one another in providing a rich and abundant array of TreMs at the plot level. For example, if in the future large broadleaved trees face high mortality rates, they could not be replaced by dead *A. alba* trees, even though they had the highest abundance and richness of TreMs.

This underlines the need for management to focus on the quality of habitat trees of different identities and functions for biodiversity conservation. So far, both habitat trees and their TreMs have been mostly accounted for in numbers rather than according to functionality and complementarity in applied retention approaches. The trade-off between retaining large living trees versus sufficient qualities and quantities of standing deadwood needs to be considered when disturbances increase the mortality of large trees. Our findings emphasize the need of selecting trees of different species and vitality status to achieve high TreM abundance and richness at the stand level and to retain unique TreMs. The larger these trees and snags, the higher are their TreM abundance and richness.

Appendix

See Tables 3, 4, and 5; Fig. 7

Table 3 Mean abundance of TreM groups among the inventoried trees

	Living					Dead				
	Abies alba	Fagus sylvatica	Picea abies	Other coniferous sp.	Other deciduous sp.	Abies alba	Fagus sylvatica	Picea abies	Other coniferous sp.	Other deciduous sp.
Woodpecker cavities	0	0.2	0.15	0.44	0.22	1.21	0.76	0.78	1.47	1.16
Rot-holes	0.16	1.21	0.16	0.09	0.59	0.36	0.24	0.23	0.22	0.29
Insect galleries	0.06	0.05	0.14	0.14	0	0.44	0.24	0.32	1.01	0.45
Concavities	0	0.22	0.16	0.46	0.16	4.58	1.46	2.44	2.51	1.64
Exposed sapwood only	0.62	1.08	0.68	0.63	0.94	1.69	1.95	1.62	2.53	0.79
Exposed sap-and heartwood	0.11	0.44	0.13	0.16	0.54	0.94	0.99	0.78	0.67	0.67
Crown deadwood	0.33	1.29	0.23	1.67	1.63	0	0.17	0.1	0.78	0
Twig tangles	1.18	0.05	0.04	0.06	0	0	0	0	0	0
Burrs, cankers	0.28	0.19	0.16	0.06	0.11	0.09	0.17	0.13	0.37	0.29
Perennial fungi	0.08	1.26	0	0	0	2.55	4.95	1.36	0.85	0.58
Annual fungi	0.06	0	0.04	0.06	0	0.31	0.68	0.42	0.27	0
Epiphytes	1.9	0.58	0.56	0.19	0.51	0.35	0.24	0.24	0.18	0.29
Nests	0.15	0.11	0.09	0.12	0.11	0.09	0	0.08	0	0
Microsoils	0.1	0.18	0.07	0.11	0.31	0	0	0	0.1	0
Fresh exudates	0.74	0.11	1.33	0.55	0	0.66	0	0.83	0	0.84

Table 4 Characteristics of the surveyed dead trees

Decay class	N	Total share (%)	Tree species					DBH (cm)			TreM abundance			TreM richness		
			Abies alba	Picea abies	Fagus sylvatica	Other coniferous sp.	Other deciduous sp.	Mean	SD	Max	Mean	SD	Max	Mean	SD	Max
1	59	7.01	13	36	2	7	1	44.41	17.22	94	3.22	4.09	24	1.51	1.26	6
2	146	17.34	16	100	7	22	1	41.81	15.56	89	2.75	2.87	13	1.42	1.22	6
3	350	41.57	37	237	15	58	3	39.58	13.92	113	3.50	3.92	27	1.59	1.19	6
4	236	28.03	28	155	9	39	5	42.97	16.21	110	4.52	5.02	27	2.10	1.25	6
5	51	6.05	14	33	0	3	1	42.60	15.08	79	5.60	5.31	20	1.94	1.27	6

Table 5 Comparison of TreM abundance and richness of different retention approaches

	Retention approach	Combined	Living	Dead
TreM abundance	Reference	24.82	110.92***	134.96***
	Combined		−86.10***	−110.15***
	Living			24.04
TreM richness	Reference	42.72*	94.96***	169.97***
	Combined		−52.23**	−127.26***
	Living			42.72*

Resulted ranks of the nonparametric rank-based Kruskal–Wallis test with Dunn post-hoc tests. Significance codes: ***0.001; **0.01; *0.05
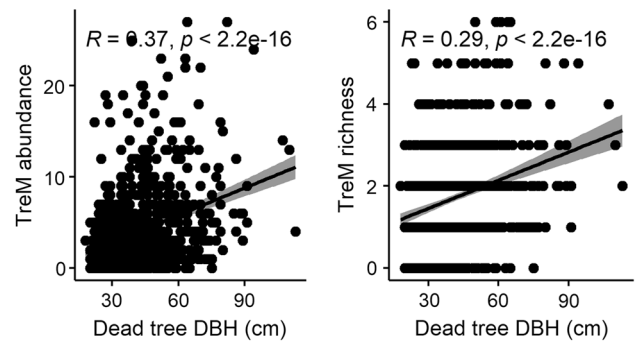
Fig. 7 Estimated abundance (left) and richness (right) for dead trees in response to their DBH. Ribbons represent the confidence intervals

Declarations

Conflicts of interest The authors declare that they have no conflict of interest.

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