Tree-related microhabitats are similar in mountain forests of Europe and North America and their occurrence may be explained by tree functional groups

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Abstract

Key message Drivers of the abundance and richness of tree-related microhabitats are similar in mountain forests of Europe and North America and their occurrence may be explained by tree functional groups.

Abstract A common approach to support forest-dwelling species in managed forests is to preserve valuable habitat trees. To assess the quality of habitat trees, a hierarchical typology of tree-related microhabitats (TreMs) is applied in the European context for inventory standardization. The first aim of this study was to evaluate whether it is possible to use this hierarchical typology as a standard protocol regardless of location, which is important for potentially standardizing future studies of TreMs, by testing whether the typology could be applied to the western North American mountain forests of Idaho. The second aim of the study was to analyse drivers that influence TreMs in forests of the region. Thirdly, we assessed whether the occurrence of TreMs could be explained by functional groups of trees across the western mountain forests of Idaho and Central European mountain forests, using TreM inventory data previously collected in the Black Forest, Germany. Abundance and richness of TreMs per tree were analyzed as a function of tree species, live status (dead vs. live trees), diameter at breast height (DBH), and site factors (latitude and altitude). Our results show that the TreM typology could be applied with slight modifications in the forests of Idaho. The abundance and richness of TreMs per tree increased with DBH. Snags offered more TreMs per tree than live trees. We were able to group tree species from the two continents in functional groups that were related to the occurrence of certain TreMs. Tree functional groups offer an opportunity to predict the role of certain tree species for habitat provision through TreMs. Combinations of trees from different functional groups could be used to optimize provisioning of TreMs within forest stands.

Keywords Tree-related microhabitats (TreMs) · Functional groups of tree species · Habitat tree selection

Abbreviations

DBH	Diameter at breast height
TreMs	Tree-related microhabitats
SD	Standard deviation
UIEF	University of Idaho Experimental Forest
HNEF	Herald Nokes Experimental Forest
GLMM	Generalized linear mixed models
SE	Standard error

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Introduction

Integrated biodiversity conservation through the retention of habitat trees in forests managed for timber production is increasingly adopted in Europe (Gustafsson et al. 2019). Habitat trees are large and old trees which provide key resources to support biodiversity and functions to enhance

ecosystem resilience (Bütler et al. 2013; Lindenmayer 2017). Habitat trees can provide resources for a wide array of organisms, including nesting sites (Gutzat and Dormann 2018), shelters (Basile et al. 2017) or feeding substrates (Müller et al. 2014). There may be different approaches and criteria to select habitat trees, including age or dimension or historical significance (Mölder et al. 2020). Here we selected habitat trees, based on their number and richness of specific microhabitats (Gustafsson et al. 2019). To assess the value of habitat trees for the provisioning of resources a typology of tree-related microhabitats (TreMs) has been developed for European forests (Larrieu et al. 2018). TreMs include a variety of structures, such as woodpecker cavities, mold cavities, or fungal fruiting bodies, which are beneficial for forest-dwelling species and biodiversity in general (Paillet et al. 2018). They include structures of biotic or abiotic origin and can constitute a synthesis of many other structural indicators (Larrieu et al. 2018). Earlier studies have shown that TreMs recorded following the hierarchical typology proposed by Larrieu et al. (2018) can partially explain the abundance and richness of bats, birds and saproxylic beetles (Regnery et al. 2013; Paillet et al. 2018; Basile et al. 2020) in European forests. Recently, the selection of habitat trees based on TreMs has been widely implemented in forest management throughout large parts of western Europe (Kraus and Krumm 2013; Forst 2015; Forstamt Thurgau 2017).

Although habitat trees are an important component of biodiversity conservation in North American forests (Michel and Winter 2009), retention forestry approaches can be very different from European practices. Whereas in North America clear-felling with variable retention of aggregates and single trees is a wide-spread regeneration method (Gustafsson et al. 2012), the retention of single habitat trees or small groups of trees in a forest stand matrix is more common in continuous-cover forests of Europe (Asbeck et al. 2020; Gustafsson et al. 2019). In addition to the different management approaches, the disturbance regimes between the two forest ecosystems, which are likely influencing the creation of TreMs (Larrieu et al. 2012), differ substantially. In North America, and especially in western mountain forests, fire is a dominant abiotic disturbance agent (Agee 1998). In contrast, the major natural abiotic disturbance in European forests are storms (Schelhaas et al. 2003; Seidl et al. 2011, 2017). Bark beetle outbreaks are common in conifer-dominated forests of both continents. In Europe, man-made disturbances are more frequent through repeated thinning interventions. Against this background, we analysed whether similar TreMs occur in mountain forests of North America and Europe and hence whether habitat trees might be characterized in a similar way.

There is a growing body of research on factors that drive the abundance and richness of TreMs in forests of Europe (Larrieu and Cabanettes 2012; Paillet et al. 2017; Asbeck

et al. 2019; Frey et al. 2020). In contrast, the concept of TreMs has received negligible attention in North America. There is a single study on TreMs in Douglass fir stands in the Pacific Northwest (Michel and Winter 2009) and one study from Eastern Canada (Maxence and Raymond 2019) as well as a few more that do not focus on a wide variety of TreMs or biodiversity conservation (e.g. Michel et al. 2011; Sheridan et al. 2013). In the prior study from the Pacific Northwest, management history had a strong effect on TreM abundance, which was lowest in stands with recent thinning and harvesting operations and highest in mature and old-growth stands (Michel and Winter 2009).

In the present study, we assessed whether the hierarchical typology of TreMs developed for European forests (Larrieu et al. 2018) could be applied to mountain forests of western North America. The approach by Michel and Winter (2009) provided a first step in the description of TreMs, and the methodology by Larrieu et al. (2018) expands upon the number and type of TreMs that can help characterize habitat trees. Evaluating whether it is possible to use this hierarchical typology as a standard protocol regardless of location is important for potentially standardizing future studies of TreMs and habitat trees. Additionally, this study is an essential step before evaluating the potential of TreMs as biodiversity indicators outside of the European context. While this study cannot give a full representation of biodiversity that is related to TreMs in the western mountains of Idaho, it serves as an indication whether the typology could be applied in its current form outside of Europe.

The second aim of the study was to identify driving factors for TreM abundance and richness in the western mountains of Idaho. The identification of driving factors that contribute to the provisioning of TreMs at the tree-level is crucial to inform forest managers on which trees to focus during retention operations (e.g. Larrieu et al. 2014). This might, for instance, lead to an increased retention of large trees that are decreasing globally or are absent in forests managed for timber production, even though they are essential for biodiversity conservation (Lindenmayer et al. 2012; Lindenmayer 2017) and have proven to support a disproportionately high abundance and richness of TreMs (Michel and Winter 2009; Larrieu and Cabanettes 2012; Paillet et al. 2017; Asbeck et al. 2019).

The third aim was to assess, whether the occurrence of TreMs could be explained by functional groups of trees across the mountain forests of Idaho and Central Europe, using TreM inventory data previously collected in the Black Forest, Germany. This goal focused on the functions that different tree species supply in forest ecosystems by providing TreMs (Larrieu and Cabanettes 2012; Paillet et al. 2019). Tree functional groups might offer an opportunity to predict the function of certain tree species for habitat provision through TreMs. We consider TreMs

as traits of particular tree species, following the definition that describes traits as “any morphological, physiological or phenological feature measurable at the individual (tree) level, without reference to the environment or any other level of organization” (Violle et al. 2007). An earlier study took a similar approach and grouped trees by ‘architectural traits’ into four functional groups (Poorter et al. 2006). Information on functional groups may, for example, be used to diversify habitat provision or to identify suitable replacement species, where native forest species are being lost.

Methods

Study site descriptions

The study sites were located in the western mountains of Idaho within an elevation range from 1000 to 1600 m above sea level (Fig. 1). The area spans over a latitudinal gradient from 44° to 48° North (Table 1). The mixed coniferous forests were dominated by western hemlock (*Tsuga heterophylla*) at higher elevations, and by western red cedar (*Thuja plicata*) at lower elevations (Cooper et al. 1991). All sites were in similar successional stages, mainly the mature phase of stand development, which is characterized by established natural regeneration, relatively large, live trees and patches

Fig. 1 Research area in the western mountains of Idaho, North America

Table 1 Description of study site including altitude, location and number of stems

Site	Altitude (m)	Location (DD)	Number of stems		SD	Forest type
			Total per research site	Mean number of stems per circular plot		
Coeur d'Alene National Forest	1223	47.72559, – 116.5074	119	23.8	10.1	Mixed coniferous
Herald Nokes Experimental Forest (McCall)	1562	44.89823, – 116.0691	55	11	3.4	Mixed coniferous
Ponderosa State Park (McCall)	1518	44.93904, – 116.0761	219	24.3	9	Pine dominated
St. Joe National Forest	1211	47.13875, – 116.0933	204	40.8	15.1	Mixed coniferous
University of Idaho Experimental Forest (Moscow)	1004	46.79958, – 116.8139	296	59.2	16.9	Mixed coniferous
Total	1304		893	30.8	19.2	

of multiple canopy layers as well as slow growth rates of the dominant trees which begin to approach their maximum height and crown width (Spies and Franklin 1996). In our data set, western hemlock is overall most abundant (29%), followed by western red cedar (22%) and Douglas fir (*Pseudotsuga menziesii*) (15%) (Table 2). The main disturbance was fire, and management can include fire suppression in some of the sites (Agee 1998). All of the forests surveyed in this study were managed for multiple uses. These uses included (but are not limited to) timber production and recreation. The University of Idaho Experimental Forest (Moscow) and Herald Nokes Experimental Forest (McCall) additionally served as sites where research is conducted to assess the effects of different silvicultural activities on forest processes.

TreM inventory and plot selection

At each study site, circular plots were placed at a minimum distance of 200 m from each other to optimise the accessibility and decrease the spatial autocorrelation. Visually assessed canopy cover > 30% and slope < 35° were criteria that guided plot distribution in the field. At each study site, we placed 5 circular plots (radius = 12 m) where all live and dead trees with a diameter at breast height (DBH) ≥ 7 cm were inventoried. We recorded tree species, DBH and the coordinates, including the altitude of each tree using an open-source software (Open-data kit) and handheld tablets. In the case of snags, we recorded broadleaved versus coniferous origin, because the identification of tree species in the field would have been difficult if not impossible in the majority of cases.

The TreM inventory (Trem groups = 15) followed the full catalogue of Larrieu et al. (2018). TreMs included in

the inventory are (for detailed description and abundance of TreMs types see appendix):

- Cavities: Woodpecker cavities, trunk and mold cavities, branch holes, dendrotelms (i.e. water-filled holes in the stem originating from natural growth) as well as insect galleries and boreholes;
- Injuries and wounds: bark loss or exposed sapwood, exposed heartwood or trunk and crown breakage, cracks and scars
- Bark: space between bark and sapwood forming a shelter or pocket, coarse structure
- Deadwood: dead branches and limbs or crown deadwood
- Deformation and growth form: root buttress cavities, witches broom, cankers and burrs
- Epiphytes: fruiting bodies of fungi, myxomycetes, epiphytic crypto- and phanerogams
- Nests: nests of vertebrates and invertebrates
- Other: sap and resin run, micro soil (i.e. resulting from the decay of lichens, mosses or leaf litter in either thick, old bark or on horizontal limbs and forks for instance)

The TreM inventory took place in late May to mid-June 2019 during the short time window between leaf-off and snow-free period in all research sites. Owing to the elevation range of study sites, conifers dominated most stands included in the inventory. All trees were inventoried by the same team of two observers (T.A. and M.B.) to reduce the observer bias (Paillet et al. 2015). We used binoculars to identify TreMs in the canopy region.

Data analyses

All data analyses were carried out using the R software (R Core Team 2016).

Table 2 Tree species composition in each study site and TreM composition by tree species. We report the mean TreM abundance per tree with standard deviation in brackets. Tree species: Douglas fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), mountain hemlock (*Tsuga mertensiana*), ponderosa pine (*Pinus ponderosa*), western hemlock (*Tsuga heterophylla*), western larch (*Larix occidentalis*), western paper birch (*Betula papyrifera*), western red cedar (*Thuja plicata*), western white pine (*Pinus monticola*)

	Broadleaf snag	Coniferous snag	Douglas fir	Engelmann spruce	Mountain hemlock	Other broad-leaf	Ponderosa pine	Western hemlock	Western larch	Western paper birch	Western red cedar	Western white pine
Species composition (% of number of stems)												
CAF	0.0	25.2	0.8	0.0	18.5	0.0	0.0	55.5	0.0	0.0	0.0	0.0
HNEF	0.3	17.6	6.8	0.0	0.0	0.0	0.3	5.1	11.2	1.0	57.8	0.0
PSP	0.0	7.3	18.2	0.0	0.0	0.0	27.3	47.3	0.0	0.0	0.0	0.0
SJF	0.0	10.1	44.8	4.6	0.0	0.9	14.2	23.7	1.8	0.0	0.0	0.0
UIEF	0.5	14.2	2.0	3.4	0.0	2.9	0.0	47.1	16.7	0.0	10.8	2.5
Total	0.2	15.3	14.9	1.9	2.5	0.9	5.3	28.6	8.0	0.3	21.6	0.6
Mean DBH (cm)	10	25.3 (20.4)	36 (21.5)	29 (11.2)	36.8 (18.8)	8.1 (1.2)	76 (35.1)	28.4 (17.2)	33.7 (14.5)	13.7 (2.9)	24 (15.7)	23.6 (19.3)
Woodpecker cavities (mean per tree (sd))	0	0.117 (0.79)	0.008 (0.09)	0	0	0	0.128 (0.44)	0.004 (0.06)	0	0	0.005 (0.07)	0
Rotholes (mean per tree (sd))	0	0.073 (0.26)	0	0	0	0	0.149 (0.74)	0.004 (0.06)	0.014 (0.12)	0	0.031 (0.17)	0
Insect galleries (mean per tree (sd))	0	0.474 (0.51)	0.038 (0.19)	0	0.045 (0.21)	0	0.064 (0.24)	0.012 (0.11)	0.028 (0.17)	0	0	0
Concavities (mean per tree (sd))	0	0.993 (2.89)	0.06 (0.40)	0.059 (0.24)	0.227 (0.52)	0.125 (0.33)	0.638 (1.85)	0.012 (0.14)	0.113 (0.52)	0	0.093 (0.53)	0
Exposed sapwood (mean per tree (sd))	0	1.847 (2.95)	0.098 (0.32)	0	0.091 (0.29)	0.125 (0.33)	0.745 (1.36)	0.067 (0.49)	0.183 (0.68)	0	0.109 (0.39)	0
Exposed heartwood (mean per tree (sd))	0	0.182 (0.42)	0.008 (0.09)	0	0.045 (0.21)	0	0	0.004 (0.06)	0	0	0.010 (0.1)	0
Crown deadwood (mean per tree (sd))	0	0.088 (0.55)	0.023 (0.15)	0	0	0	0.638 (1.12)	0	0.014 (0.12)	0	0	0
Twigs and tangles (mean per tree (sd))	0	0	0.038 (0.31)	0	0	0	0.043 (0.29)	0	0	0	0	0

Table 2 (continued)

	Broadleaf snag	Coniferous snag	Douglas fir	Engelmann spruce	Mountain hemlock	Other broad- leaf	Ponderosa pine	Western hemlock	Western larch	Western paper birch	Western red cedar	Western white pine
Burrs and cankers (mean per tree (sd))	0	0	0.015 (0.12)	0	0	0	0	0.004 (0.06)	0	0	0.005 (0.07)	0
Perennial polypores (mean per tree (sd))	1 (1)	0.139 (0.98)	0.008 (0.09)	0	0.136 (0.62)	0	0	0.008 (0.09)	0.169 (1.3)	0	0	0
Ephemeral polypores (mean per tree (sd))	1.5 (1.5)	0	0	0	0	0	0	0	0	0	0	0
Epiphytes (mean per tree (sd))	0	0.219 (0.41)	0.263 (0.44)	0	0.818 (0.39)	0.125 (0.33)	0.447 (0.50)	0.325 (0.47)	0.437 (0.5)	0.333 (0.47)	0.031 (0.17)	0.2 (0.4)
Nests (mean per tree (sd))	0	0.007 (0.09)	0.023 (0.26)	0	0	0	0	0	0	0	0.005 (0.07)	0
Microsoils (mean per tree (sd))	0	0.007 (0.09)	0	0	0	0	0	0.004 (0.06)	0	0	0.005 (0.07)	0
Fresh exudates (mean per tree (sd))	0	0	0.075 (0.32)	0	0	0	0	0	0.014 (0.12)	0	0	0

CAF Coeur d'Alene National Forest; HNEF Herald Nokes Experimental Forest; PSP Ponderosa State Park; S/F St. Joe National Forest; UIEF Moscow University of Idaho Experimental Forest

To identify drivers of TreM abundance and richness, we calibrated generalized linear mixed models (GLMM), including site as a random term. No spatial autocorrelation was found among sites when performing a Moran test on the model residuals. We built a global model for TreM abundance and richness by including the following predictor variables in the fixed term: DBH, tree species (including snags as one category), altitude and latitude. These predictors have all been described as strong determinants of TreM abundance and/or richness in Europe (Larrieu and Cabanettes 2012; Asbeck et al. 2019; Paillet et al. 2019). The abundance GLMM was built assuming a negative binomial error distribution to account for overdispersion; the GLMM for richness assumed a Poisson error distribution as there were no signs of overdispersion. To prevent over-parameterization we pooled broadleaved and coniferous snags. We also pooled mountain (*Tsuga mertensiana*) and western hemlock (*Tsuga heterophylla*). The few records of broadleaf trees ($N=11$) were also grouped. Due to the low number of observations of broadleaved trees in Idaho, we excluded them from the analyses. We performed a model selection by dropping non-significant predictors and focused on improving the Akaike information criterion (AIC). Lastly, we tested final model performance by checking residuals and diagnostics with the ‘DHARMA’ package (Hartig 2018). The same package was employed to check for spatial autocorrelation, over-dispersion and zero-inflation, while the GLMM were built with the R package ‘lme4’ (Bates et al. 2014).

To compare the provisioning of TreMs by tree species in mountain forests of Central Europe and Idaho, we used a complementary dataset from the Black Forest in southwestern Germany which contained 2621 trees with a mean DBH of 51 cm (Asbeck et al. 2019). In contrast to the dataset from Idaho, only living trees had been recorded (see Appendix for a comparison of TreM inventory between western mountains of Idaho and the Black Forest, Fig. S1). We considered the association of TreMs with tree species a bipartite network and aimed at clustering species that offer similar TreMs into functional groups. Bipartite networks, like other network types, can be divided into naturally occurring modules, identifiable with the modularity matrix method proposed by Newman (2006). Modularity measures were applied to a weighted version of our bipartite network, which takes the abundance of TreMs per tree species into account, using the method developed by Beckett (2016). The analysis was carried out using the ‘bipartite’ package (Dormann et al. 2018).

Results

Summary statistics of trees and TreMs in the study sites

Of the original 64 TreMs described in the protocol, 50 TreMs were found in the mountain forests of Idaho (see Appendix, Table S1). The most common TreMs were woodpecker feeding cavities, epiphytic lichens and exposed sapwood. Neither mould cavities and dendrotelms nor large ascomycetes were recorded at sampling sites. Further details on TreM occurrence are provided in the Appendix (Table S1).

TreM richness and abundance differed amongst tree species. Ponderosa pine, which was the largest tree species recorded, had the highest occurrence of woodpecker cavities and crown deadwood (Table 2). Conifer snags provided slightly fewer woodpecker cavities than live ponderosa pine but were the greatest provider of exposed sapwood TreMs (Table 2). The greatest abundance of epiphytes was found on mountain hemlock, which was represented in the data set only with a small number of individuals ($N=22$). However, several other species including western hemlock, ponderosa pine and western larch also supported substantial numbers of epiphytes (Table 2).

In addition, we observed two conspicuous structures, which have so far not received specific attention in the current typology: carpenter ant (genus *Camponotus* Mayr, 1861) cavities and galleries, as well as sap wells formed by sapsucking woodpeckers (*Sphyrapicus* spp.) (Fig. S2) (e.g. Walters et al. 2014). Carpenter ant cavities consist of small ($\varnothing < 1$ cm) to large ($\varnothing > 5$ cm) round holes in the main trunk, usually close to the ground. Sapsucker’s foraging holes, instead, consist of a regular pattern of small holes ($\varnothing < 1$ cm), which mostly just extend into the sapwood, often covering a large portion of the main stem.

Results of the models for abundance and richness

The GLMMs of abundance and richness of TreMs both agreed in the selection of predictors, retaining only tree species and DBH as significant predictors (Table 3). Latitude and altitude were not significant and subsequently omitted from the final model. In both models, regarding tree species, only snags and Engelmann spruce had a positive and negative significant effect, respectively (Fig. 2). In addition, western red cedar was marginally significant in the abundance model (Table 3). DBH had a positive and significant effect on both abundance and richness (Fig. 3), but overall smaller than tree species (Table 3).

Table 3 Estimated effects of standardised tree variables on TreM abundance and richness, according to the generalized linear mixed model assuming a negative binomial (abundance) or a Poisson error distribution (richness) as well as a site-level random effect

Variable	Estimate	SE	z value	Pr(> z)	Sign ^b
TreM abundance model					
Intercept	− 0.223	0.553	− 0.404	0.6865	.
Douglas fir	− 0.578	0.559	− 1.036	0.3003	.
Engelmann spruce	− 2.58	1.148	− 2.247	0.0247	*
Hemlock ^a	− 0.704	0.550	− 1.281	0.2002	.
Ponderosa pine	− 0.606	0.581	− 1.043	0.2970	.
Snag	1.433	0.542	2.642	0.0082	**
Western larch	0.081	0.558	0.146	0.8840	.
Western red cedar	− 0.973	0.563	− 1.730	0.0836	.
Western white pine	− 1.299	1.190	− 1.092	0.2749	.
DBH	0.721	0.044	16.330	< 2e-16	***
TreM richness model					
Intercept	− 0.549	0.523	− 1.049	0.2943	.
Douglas fir	− 0.114	0.520	− 0.219	0.8265	.
Engelmann spruce	− 2.196	1.118	− 1.964	0.0495	*
Hemlock ^a	− 0.417	0.511	− 0.817	0.4141	.
Ponderosa pine	− 0.054	0.537	− 0.101	0.9195	.
Snag	1.053	0.507	2.078	0.0377	*
Western larch	0.126	0.521	0.241	0.8095	.
Western red cedar	− 0.865	0.528	− 1.639	0.1012	.
Western white pine	− 1.023	1.118	− 0.915	0.3600	.
DBH	0.464	0.035	13.268	< 2e-16	***

^aHemlock = western hemlock and mountain hemlock

^bSignificance codes: '***' 0.001; '**' 0.01; '*' 0.05, '.' 0.1

Results of the tree-related microhabitat composition analysis

The results of the bipartite analyses of the abundance of TreMs per tree species for the Black Forest and the western mountain forests of Idaho indicate that four functional groups can be distinguished. The modularity matrix method identified these groups according to the associations between TreMs and tree species. One group, which is characterized by the occurrence of crown deadwood and woodpecker cavities comprises broadleaved species from the Black Forest and ponderosa pine and Scots pine (*Pinus sylvestris*). The second group consists of standing dead trees (snags) as well as western larch and western red cedar (Fig. 4), which are characterized by the occurrence of exposed sapwood (and heartwood) as well as perennial fungi. Silver fir, European larch, Douglas fir in North America and hemlock offer similar TreMs and can be grouped by epiphytes and other epiphytic structures such as twig tangles and nests. The last group consists of Engelmann and Norway spruce as well as Douglas fir in the Black Forest and is characterized by concavities (root buttress cavities, mainly) and fresh exudates

(resin run) (Fig. 4). The modules scored a likelihood of 0.33 with 100 iterations, which indicates a moderate level of grouping.

Discussion

Our field data from the western mountains of Idaho showed that the hierarchical typology of TreMs established in Europe could be adopted with slight changes to the forest ecosystem in the western mountains of Idaho. We identified similar drivers of TreM abundance and richness per tree at the Idaho study sites as found in earlier studies in Europe. Our results showed that if TreMs are considered as traits of tree species we could find four functional groups across continents.

Application of the hierarchical typology of tree-related microhabitats in western mountains of Idaho

Our goal was to assess whether the TreM inventory protocols developed in Europe (Larrieu et al. 2018) effectively captured TreM characteristics in western North American mountain forests. The purpose was not to evaluate the biodiversity associated with TreMs per se but rather to examine whether the existing TreM protocols can be applied to another forested region of the world with different disturbance and management regimes, as well as different species and communities. We found that the hierarchical typology of TreMs, which was developed for European forests, could indeed be applied to some North American forest types found in Idaho. The majority of TreMs included in the typology and all groups were present in the forests of Idaho (15 TreM groups out of 15).

However, we found indications that two conspicuous structures, which are either rare or absent in European forests, and which could be represented more explicitly in the current typology. The first one consists of the cavities and galleries excavated by carpenter ants. It could be argued that this structure belongs to the TreM “invertebrate nests”, yet the description does not specifically address carpenter ants and mentions the wood ant (*Lasius fuliginosus*) in contrast (Larrieu et al., 2018). We found this structure on lower stem sections of large trees, frequently ones that had fire scars, feeding holes of woodpeckers or other indication of softened wood. Carpenter ants tend to colonise decaying heartwood and dig galleries that can extend beyond the decaying wood (Sanders 1964). They colonise trees and stumps from bottom-up (Sanders 1964), hence they can benefit from events that damage the tree base, such as fire or root rot. Large stumps, logs or decayed tree section can host thousands of ants and larvae providing a key food resource for many

Fig. 2 Estimated mean **a** TreM abundance and **b** TreM richness with a 95% confidence interval for each tree species. The * indicates significant results. The effect is plotted by setting all other predictors to a mean value

forest organisms including woodpeckers (Rolstad et al. 1998; Weikel and Hayes 1999) and even large animals such as bears (Frank et al. 2015). In Europe, intensive forest management has been considered the cause of low average stocks of deadwood (Fridman and Walheim 2000; Vítková et al. 2018), which may be linked to the (perceived) absence of carpenter ants from central European forests managed for timber production. Carpenter ants, indeed, built their nests mostly in deadwood, namely stumps or wind-snapped trees, which have been attacked by rot (Véle and Horák 2019). The widespread practice of salvage logging in Europe (Müller et al. 2019) together with the abandonment of clearcutting might have resulted in the perceived decline of this species, especially the genus *Camponotus* (Véle et al. 2016). The current classification does not explicitly include carpenter ant cavities, although it recognizes generic insect galleries and the importance of woodpecker cavities for ants (Larrieu et al. 2018), thus the newly described TreM could either be more

explicitly added to the existing category or be described as a new category.

Another structure that could potentially augment the current typology is sap wells formed by sapsucking woodpeckers. Sapsuckers consist of four species of woodpeckers (genus *Sphyrapicus*, Baird, 1858) specialized in foraging on the sap of trees (Tate 1973). Their feeding activity can damage trees and increase crown or downed deadwood (Erdmann and Oberg 1974). Sap is a less common source of food for European woodpecker species, although it can be relevant for some species, such as the European three-toed woodpecker (Pakkala et al. 2018). In the European context, we are not aware of descriptions of the use of such sap wells by other taxa, possibly due to the rarity of these structures. However, they may be formed occasionally by for instance the middle-spotted woodpecker (Pasinelli and Hegelbach 1997). In contrast, the use of sap wells by hummingbirds for feeding has been reported in the North American context

Fig. 3 Estimated **a** abundance and **b** richness of TreMs in response to mean DBH of the inventoried trees in Idaho with a 95% confidence interval indicated by the light blue shades, the rugs at the bottom show the marginal distribution of the predictor. The effect is plotted by setting all other predictors to a mean value

Fig. 4 Functional groups of the bipartite network between TreMs and tree species of the western mountains of Idaho (US) and Black Forest (GER). The darker the squares the more associations were observed. The shades of blue provide for a relative comparison within a given tree species (by rows), but not over the whole matrix. The intensity of the blue refers thus to a 0–100% frequency of association of the tree species with the TreM group. For instance in snags, exposed sapwood is most abundant followed by concavities. Red boxes delineate the four groups

(Miller and Nero 1983). Other relationships that have been described relate sap wells to foraging activities of orange-crowned warblers (*Leiothlypis celata*), chipmunks and other sap feeders including wasps and butterflies (Daily et al. 1993). Therefore, we suggest that this structure needs to be adopted in a standardized TreM inventory protocol, at least for forest ecosystems where sapsucking woodpeckers are present.

Driving factors for the formation of tree-related microhabitats

In accordance with previous findings for European forests, abundance and richness of TreMs increased significantly and exponentially with increasing DBH (Larrieu and Cabanettes 2012; Asbeck et al. 2019; Paillet et al. 2019). In our study area, we recorded up to 26 TreMs from six different types on a single large tree, pointing to the disproportionally large importance of large trees for habitat provision. The increase in TreMs in larger trees is probably related to the increased surface area, processes driven by tree senescence, and the increasing probability with age to be damaged (by natural disturbances or harvesting activities) or colonized by other organisms such as epiphytes. For example, large trees support a more diverse flora of lichens and bryophytes (Kaufmann et al. 2018). As has been observed in Europe, snags offered significantly more TreMs when compared to living trees (Larrieu and Cabanettes 2012; Paillet et al. 2017). Snags provide a substrate for feeding or nesting such as large debarked parts of the trunk (TreM group of exposed sapwood), that are then exploited by woodpeckers, ants, and other excavating organisms, which in turn create the conditions for the establishment of additional TreMs.

Functional groups of tree species in western mountains of Idaho and the Black Forest

This part of the analyses was entirely exploratory and not driven by any specific hypotheses other than the assumption that tree species of the same genus might provide more similar TreMs compared to other genera. The information provided by this analysis might allow the development of more specific hypotheses regarding TreM formation and development in different tree species, focusing for instance on differences in the tree age when specific TreMs occur. The differences in provisioning of TreMs by tree species showed several similarities and discrepancies between North America and Europe. Broadleaved species of Europe were characterized by the more frequent occurrence of crown deadwood and woodpecker cavities than the companion coniferous species of the genera *Picea*, *Abies*, *Larix*, and *Pseudotsuga* (Vuidot et al. 2011; Larrieu and Cabanettes 2012; Großmann et al. 2018). Interestingly, both ponderosa pine from

North America and Scots pine from Europe belonged to the same functional group as European broadleaf species. This similarity is obviously unrelated to wood properties, and the same TreM such as crown deadwood would offer resources for distinctly different organisms between pines and broadleaves, as has been described for saproxylic wasps (Ulyshen et al. 2011). Also, the formation of woodpecker cavities in pines can result from processes (i.e. exposure to fire) (Farris and Zack 2005) that are not relevant in the studied broadleaved trees. The similarity, however, may be related to the longer production cycles on which pines and broadleaves are managed (120–160 years) when compared to the faster-growing conifer species (60–100 years). This may simply allow for the accumulation of more woodpecker cavities and crown deadwood.

Intriguingly, the only tree species occurring in both datasets, Douglas fir, which has been introduced in Germany more than a century ago, provides different kinds of TreMs in the two forest ecosystems. Owing to the more frequent occurrence of epiphytes in the western mountains of Idaho, Douglas fir from there is grouped with silver fir, European larch and hemlock. The only microhabitat of the epiphyte group found on Douglas fir in Idaho were lichens (total $N=227$, Tab.S1). The absence of an association of Douglas fir with epiphytes, and lichens in particular, in Europe may be for a number of reasons. Firstly, not all the lichen species that evolved in the western mountains of Idaho are present in Europe. Some species of the group of macrolichens are significantly related to Douglas fir in its natural range, as for instance *Hypogymnia imshaugii*, which is common in Europe as well, or *Platismatia glauca*, which does, to our knowledge, not occur in German forests (Sillett and Goslin 1999; Neitlich et al. 2003; Hauck 2005). Another contributing factor for the lower number of lichens on Douglas fir in Europe is that microclimatic conditions, air pollution, and the management history, which influence the occurrence of lichens (Nascimbene et al. 2013a, b; Ódor et al. 2013), differ between the two forest ecosystems. Similarly, western larch and European larch were associated with different TreMs. Western larch was grouped with snags and western red cedar in one functional group characterized by an abundance of perennial polypores and exposed sapwood. This is probably related to the management differences between the two forests. Since perennial fungi represent an obvious “defect” in terms of timber production, affected trees have a higher probability of removal in the intensively managed continuous-cover forests of Germany. However, it still needs further analyses to scrutinize whether similarities of trees in TreM abundance and richness might be generalized across biomes beyond species level e.g. using genus-level or other common traits as wood properties. The results presented here were not further specified on other driving factors such as management history that possibly explain these differences

in provisioning of TreMs on the species level (Johann and Schaich 2016; Paillet et al. 2017) to some extent. An analysis of common functional groups such as broadleaves versus conifers was limited by our study design since we did not include stands dominated by broadleaves in our inventory. The same holds true for an analysis of pioneer versus climax functional groups since we focused only on mature stands. These comparisons would certainly be the next step to compare the functional groups of trees in providing TreMs across continents.

Conclusions

The use of TreMs to assess habitat trees offers potential benefits in temperate mountain forests outside of Europe. Slight changes might be implemented in the current typology to improve its' application to North American forests. Further modifications to the current typology as described for North America may be necessary and need further testing for different forests with other genera, e.g. in the subtropics and tropics. However, whether direct links between TreMs and forest-dwelling species, as described for Europe (Paillet et al. 2018; Basile et al. 2020), can be found in the western mountains of Idaho needs to be evaluated in future.

This study provides a cross-continental assessment of the relationship between TreMs and tree species. Certain types of TreMs are associated with particular types of tree species. To increase the provisioning of TreMs in mixed forests, combinations of trees from different functional groups could be used. Nevertheless, a mechanistic understanding of relationships between TreM occurrence and tree species' traits, such as wood properties favoring fungal infection and the excavation of trees by woodpeckers (e.g. Puverel et al. 2019), is required to develop an a priori classification of trees into functional groups based on these relevant traits. This may be relevant in the case where new tree species are being introduced.

The type of management and the ecosystem attributes such as tree species composition and abundance of snags appears to influence the occurrence of TreMs. These influences need to be better understood to predict TreM development on different tree species. Overall, the TreM typology is a valuable tool for forest managers to evaluate the habitat resources provided by trees in the ecosystem and it could be applied to identify trees for retention purposes also outside Europe.

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Data availability The dataset from Idaho used and/or analysed during the current study are included in this published article [and its supplementary information files]. The dataset from the Black Forest has been published as supplementary information in Asbeck et al. (2019). <https://doi.org/10.1016/j.foreco.2018.09.043>

Compliance with ethical standards

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

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