



# Retention of tree-related microhabitats is more dependent on selection of habitat trees than their spatial distribution

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## Abstract

Habitat trees, which provide roosting, foraging and nesting for multiple taxa, are retained in managed forests to support biodiversity conservation. To what extent their spatial distribution influences provisioning of habitats has rarely been addressed. In this study, we investigated whether abundance and richness of tree-related microhabitats (TreMs) differ between habitat trees in clumped and dispersed distributions and whether the abundance of fifteen groups of TreMs is related to tree distribution patterns. To identify habitat trees, we quantified TreMs in temperate mountain forests of Germany. We determined clumping (the Clark–Evans index), size of the convex hull, diameter at breast height, as well as altitude, slope and aspect of sites for their possible influence on TreMs. We additionally determined the difference in TreM abundance and richness among four options of selecting five habitat trees per ha from 15 candidates: (a) the most clumped trees, (b) five randomly selected and dispersed trees, (c) the single tree with highest abundance or richness of TreMs and its four closest neighbors and (d) a “reference selection” of five trees with known highest abundance or richness of TreMs irrespective of their distribution. The degree of clumping and the size of the convex hull influenced neither the abundance nor richness of TreMs. The reference selection, option (d), contained more than twice the number of TreMs compared to the most clumped, (a), or random distributions, (b), of five habitat trees, while option (c) assumed an intermediate position. If the goal of habitat tree retention is to maximize stand-level abundance and richness of TreMs, then it is clearly more important to select habitat trees irrespective of their spatial pattern.

**Keywords** Clark–Evans index · Retention forestry · Size of convex hull · Tree-related microhabitats · Selection of habitat trees

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## Introduction

A global decline in large and old live trees as well as standing and fallen deadwood has been identified in most managed forests of the world (Müller and Bütler 2010; Lindenmayer et al. 2012). Factors that contribute to this decline in large old trees include intentional removal, increased mortality rates related to more severe disturbances such as drought or fire, and less recruitment (Lindenmayer et al. 2012; Pennisi 2019). This has led to the retention of structural elements as large trees, snags or deadwood in different silvicultural systems in many regions of the world to deliberately address the conservation of forest biodiversity (Gustafsson et al. 2012, 2019). In addition to maintaining patches of unharvested forest vegetation, these measures aim to provide specific habitats for forest-dwelling species. Habitat trees are commonly understood as very large, very old, dead or living microhabitat-bearing trees (Bütler et al.

2013; Mölder et al. 2020). One major unanswered question is the potential benefit of retaining live habitat trees in a clumped versus dispersed distribution of individual trees. It is an issue of great concern to forest ecologists and managers alike (ForstBW 2015; Larrieu et al. 2018). Clumping of habitat trees can offer advantages to forest management in terms of work safety, planning and documentation, and possibly longevity of retained trees. From a scientific point of view, this question is related to the habitat amount hypothesis that proposes that “species richness in equal-sized sample sites should increase with the total amount of habitat” (Fahrig 2013). To ensure minimum quantities of habitats required by forest-dwelling species, it is essential to quantify habitats retained by selecting trees in a clumped versus dispersed manner. We focus here on selection approaches to increase habitats rather than testing the hypothesis on species richness per se. To identify the most valuable live habitat trees to retain, the abundance and diversity of tree-related microhabitats (TreMs) is commonly used (Larrieu et al. 2014a, b; 2018; Winter and Möller 2008). A TreM is defined as “a distinct, well-delineated structure occurring on living or standing dead trees that constitutes a particular and essential substrate or life site for species or species communities during at least a part of their life cycle to develop, feed, shelter or breed” (Larrieu et al. 2018). Positive correlations between TreMs and several taxa such as bats, birds and to a lesser extent (saproxylic) insects have been shown in earlier studies (Paillet et al. 2018; Basile et al. 2020a), and TreMs are considered valuable biodiversity indicators (Gao et al. 2015). Specific correlations between taxa and TreMs have, for instance, been reported for rare aquatic organisms in water-filled holes in trees (Gossner et al. 2016), arthropod species inhabiting conks of tree-decaying fungi (Friess et al. 2019), as well as cavity nesting birds in tree hollows (Puverel et al. 2019). An overview of associations between TreMs and taxa has been provided by Larrieu et al. (2018).

### Earlier studies on clumping of habitat trees

Selecting retention trees in clumps and its effect on forest-dwelling taxa has been reported in the literature (Hazell and Gustafsson 1999; Sullivan and Sullivan 2001; Halpern et al. 2005; Löhmus et al. 2006; Preston and Harestad 2007). For example, clumped retention of trees has been shown to benefit one lichen species (Hazell and Gustafsson 1999) and one group of small mammals (Sullivan and Sullivan 2001). In a study that analyzed approaches for conserving a bird community similar to that found in closed forests, clump size was more important than the total number of retention trees preserved (Preston and Harestad 2007). However, these results were for specific taxonomic groups and from silvicultural systems that employed clearfelling. Thus, they do

not necessarily apply to selectively harvested forests where retained trees remain in a matrix of forest canopy.

### Retention of habitat trees in close-to-nature forest management

Close-to-nature forest management (CTNFM) is characterized by common principles including: (a) use of site-adapted tree species, typically of the natural forest vegetation, (b) promotion of mixed and structurally diverse forests, (c) avoidance of large canopy openings such as clear-cuts, (d) employment of natural processes such as natural regeneration, self-thinning and self-pruning and (e) silvicultural focus on individual trees rather than stands (Bauhus et al. 2013; Brang et al. 2014). Retaining trees in clumps has been advocated for conservation purposes in forests managed under CTNFM (Jedicke and Hakes 2006; ForstBW 2015). In addition to conservation, clumping of habitat trees is preferred over dispersed distributions to reduce safety hazards for forest workers and facilitate their mapping and monitoring. Selecting habitat trees can be difficult whenever there are no clear tree candidates based on tree attributes of dimension, age, decay stage or tree value such as known breeding sites. This is often the case in conventionally managed forests (Lindenmayer et al. 2012). However, as far as we know, there has not been any study that has tested spatial patterns of habitat trees in CTNFM although some work has been done on evaluating the possible effects of stand density or basal area on the abundance and diversity of TreMs (Regnery et al. 2013; Winter et al. 2015; Großmann et al. 2018). Whether to retain live habitat trees in a clumped versus dispersed distribution remains an important knowledge gap in CTNFM (Larrieu et al. 2018) and may be particularly relevant in temperate forests where both types of distribution are feasible from a management perspective.

The research questions in this study were whether:

- a Retention of live potential habitat trees in clumps provides a higher stand-level abundance and richness of TreMs than dispersed distributions of habitat trees selected randomly or based on TreM attributes;
- b Different groups of TreMs, due to the processes underlying their creation and development, are related to clumped or dispersed distributions of habitat trees; and
- c Attributes such as slope, aspect, tree species, DBH and altitude are drivers of TreM abundance and richness at the tree level.

### Expected spatial patterns of tree-related microhabitats

As in other studies (Larrieu et al. 2018), we assume that a variety of natural biotic and abiotic processes, such as

excavation of holes by woodpeckers, spread of fungal pathogens, bark beetle outbreaks or windthrow, as well as management activities are responsible for the development of different groups of TreMs (Table 1).

## Materials and methods

### Data collection

The data collection took place in 139 one-hectare forest plots located on state land in the Black Forest region (latitude: 47.6°–48.3° N, longitude: 7.7°–8.6° E, WGS 84). The plot selection followed a landscape gradient of forest cover in the 25 km<sup>2</sup> surrounding the plots and a gradient of structural complexity indicated by the number of standing dead trees per plot. For details of plot selection, see Storch et al. (2020). The majority of plots were managed for timber production ( $N=133$ ); six plots were in strict forest reserves where management had been abandoned 20–40 years ago. The main species among the inventoried trees were Norway spruce (*Picea abies* (L.)) (41%), European beech (*Fagus sylvatica* (L.)) (22%) and silver fir (*Abies alba* (Mill.)) (19%), accounting for more than 80% of the total. The TreM data were collected based on a detailed catalog proposed by Larrieu et al. (2018) which is based on earlier work by Kraus et al. (2016) (SI, Table A1).

A full inventory of all trees and their TreMs on all 139 one-hectare plots would have been beyond the capacity of this project. Instead, we inventoried the 15 largest trees per plot which had an average diameter at breast height (DBH) greater than 50 cm and occupied more than 15% of the area. Previous studies have shown that diversity and abundance of TreMs in these forests increase with tree dimension (e.g., Großmann et al. 2018). By selecting the 15 trees with the largest crown diameter per one-ha plot, we obtained a sample cover of 81.1% of types of TreMs per plot based on a rarefaction analysis (Asbeck et al. 2019). We recorded the position of all inventoried trees, their DBH, species and TreMs in the snow-free and leaf-free period between fall 2016 and spring 2017. We used binoculars to identify TreMs in the canopy. More detailed information on the data collection can be found in Asbeck et al. (2019). The corner points of each plot were used to determine the coordinates of all trees within each of the 139 plots. Additional data for each plot, including average slope and aspect, were obtained from GIS information.

### Statistical analyses

The Clark–Evans (CE) index of aggregation (Szmyt 2014) was used to quantify the degree of clumping of inventoried

trees. This single index value is based on distances between individuals within the populations and enables detection of complete spatial randomness. A CE index around 1 indicates trees are randomly distributed,  $CE > 1.0$  means trees are evenly spaced, and a value of  $CE < 1.0$  indicates clumped distributions of trees with increasing levels of aggregation as the index value declines. The Donnelly correction was used to correct for edge effects (Baddeley 2017). A Z-test was applied to test for a significant departure from complete spatial randomness (Szmyt 2014). The “spatstat package” in R (Baddeley 2017) was used for the analyses. The calculation of the size of the convex hull allowed us to evaluate the effect of maximum area covered by the 15 potential habitat trees on the abundance and richness of TreMs.

To evaluate possible spatial correlation among classes of TreMs, the inventory data were assigned to 15 different TreM groups as suggested by Larrieu et al. (2018). The abundance was calculated as the sum of TreMs per tree, and richness was the sum of different TreM groups per tree. To model the overall abundance and richness of TreMs as well as the TreM groups, we used generalized linear mixed models (GLMMs).

In combination with clumping and the size of the convex hull, we tested the effects of covariates such as slope, aspect and altitude on the abundance and richness of TreMs on individual trees. These covariates are potentially related to clumping of the trees and have not been tested yet for their influence on TreM abundance and richness per tree. The identification of drivers of TreM abundance and richness still deserves further attention as most studies have shown that DBH and tree species are the most important characteristics (e.g., Paillet et al. 2019). Slope and aspect (the cardinal direction the plot faces) are plot-level variables, whereas altitude was determined at the tree level. Tree DBH and species identity were included in the GLMMs as predictors. In addition to the three most common tree species, Norway spruce, European beech and silver fir, other species were summarized as “other broadleaf” and “other coniferous” to prevent over-parametrization, for possible correlations of the predictors see SI (Table A2, Table A3).

To prevent autocorrelation of trees within the same plot that might have more similar characteristics than trees in different plots (Dormann 2013), we included plot-identity as random factor. The computation of models was performed in R (R Core Team 2016). Since the abundance and richness data for TreMs were of count type, we built models with the “glmmTMB function” of the “glmmTMB package” (Brooks et al. 2017) with a negative binomial or the Conway–Maxwell Poisson (Sellers et al. 2012) distribution in case of overdispersion; a Poisson distribution was used in case there was no indication of under- or overdispersion. We used the default “log”-link function in all models (Brooks et al. 2017). For TreM richness, crown deadwood and epiphytes

**Table 1** Expected spatial patterns of the 15 TreM groups as described by Larrieu et al. (2018) including reference literature

TreM group	Description	Expected spatial pattern	Reason	Literature
Woodpecker breeding cavities	Entrance diameters ranging from small ( $\phi = 4$ cm) to large ( $\phi = 10$ cm)	Dispersed	Owing to territorial behavior and management activities that potentially limit the abundance of suitable nesting sites/trees	Newton (1994)
Rot holes	Trunk mold cavities, branch holes, semi-open trunks, hollow branches	Clumped	Decay processes create rot holes such as mold cavities. If these originate from soil borne pathogens, as <i>Heterobasidion annosum</i> which can spread through root contact, they will be clumped. Likewise, if cavities stem from the bark peeling activities of ungulates such as reed deer or moose, they will be clumped	Oliva and Colinas (2007), Remm and Löhmus (2011), Cockle et al. (2012), Büttler et al. (2013) and Gerhardt et al. (2013)
Insect galleries and bore holes	Galleries or single large bore holes	Species dependent (clumped in species that aggregate on weakened trees)	Depending on insect species responsible for galleries or bore holes	Seidl et al. (2016)
Concavities	Woodpecker feeding holes, dendrotelms, buttress cavities and trunk clefts from tree growth	Clumped	Morphological particularities can lead to concavities such as dendrotelms and buttress cavities. The latter can be influenced by geographic patterns such as altitude and might, therefore, occur in clumped trees present under these conditions	Asbeck et al. (2019)
Exposed sapwood only Exposed sapwood and heartwood Crown deadwood	Patches of bark loss in different stages of decay, bark pockets and shelter; Broken tree trunks and crowns, cracks and lightening scars; Broken branches, broken limbs	Clumped	Mechanical impact from wind, snow and harvesting can create TreMs grouped as exposed sapwood and heartwood and crown deadwood, which we assume to be more frequent in clumps due to the localized occurrence of such disturbance events. Regeneration density is not even, hence in patches with low density (as a result of competition with ground vegetation) trees with larger crowns that offer crown deadwood, exposed sapwood and heartwood will be found	Büttler et al. (2013) and Asbeck et al. (2019)

Table 1 (continued)

TreM group	Description	Expected spatial pattern	Reason	Literature
Twig tangles Burr and cankers	Witches broom or dense clusters of epicormic shoots; Cancerous growth or decayed cancer	Species dependent	Reactive growth, the creation of structures to isolate defective pathogens is possibly the underlying cause of burrs and cankers as well as twig tangles. The presence of these TreMs in clumped or dispersed trees would depend on the dispersal mechanisms of the respective pathogens	Larrieu et al. (2018) and Oliva and Colinas (2007)
Epiphytes	Epiphytic bryophytes, foliose and fruticose lichens, lianas ( <i>Hedera helix spp.</i> ), ferns, mistletoes	Clumped	Bryophytes, lichens, ferns and mistletoes depend firstly on the species being present, which in turn are mainly related to microclimate and site factors steering their development. However, habitat continuity is also an important determinant for the occurrence of some epiphytic species. Hence, these species may be clumped where that habitat continuity has been maintained, for example, through large and old trees	Moning and Müller (2009), Kriebitzsch et al. (2013), Nascimbene et al. (2013) and Kaufmann et al. (2018)
Nests	Large ( $\phi > 80$ cm) or small ( $\phi > 10$ cm) vertebrate nests	Species dependent	Depends on a number of factors, including the species' territorial or social behavior, the distance to predators' nests, as indicator of predation risk, and the forest type	Forsman et al. (2001)
Micro-soils	Accumulation of dead organic matter in the crown or on bark	Dispersed	The development of micro-soils in trees may depend on the presence of some particular growth forms of epiphytic mosses that facilitate the accumulation of dead organic matter; however, this process does not appear to be related to a clumped distribution	Fayle et al. (2009) and Lowman and Schowalter (2012)
Fruiting bodies of perennial and ephemeral fungi	$\phi > 5$ cm	Species dependent	Fungal fruiting bodies occur after decay, which is typically triggered through injuries, that has progressed for variable periods of time. Whether conks of fungi occur on clumped or dispersed trees depends on the species' dispersal mechanisms and predisposition of trees	Rayner and Boddy (1988) and Stenlid et al. (2001)

Table 1 (continued)

TreM group	Description	Expected spatial pattern	Reason	Literature
Fresh exudates	Sap or resin flow	Clumped	Fresh exudates such as heavy resin flow can occur following mechanical injuries or biotic processes such as severe bark beetle attacks, and they might, therefore, occur in more clumped situations	Seidl et al. (2016)

were signs of zero-inflation and were accounted for in the models. To test for under- and overdispersion as well as zero-inflation in the final models, we used the “DHARMA package” (Hartig 2018). We calculated the conditional as well as the marginal  $R^2$  as a measure of goodness-of-fit with the  $R^2$  function of the sjstats package (Lüdecke 2018a).

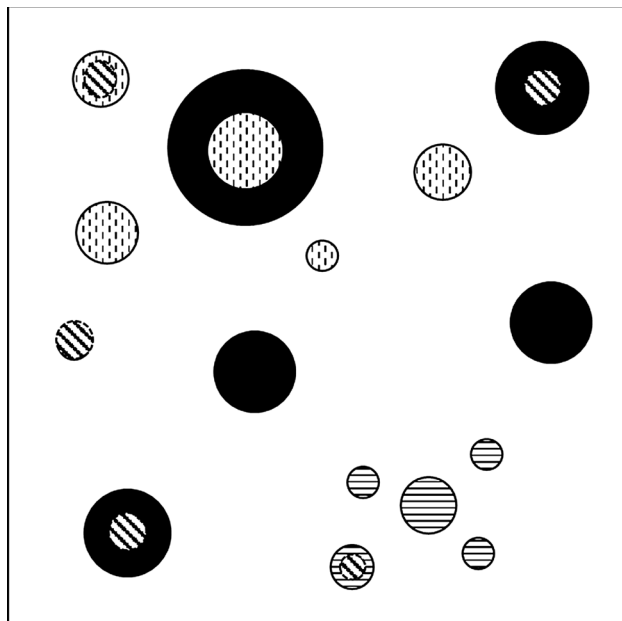
The full models consisted of these predictors:





- CE + size of the convex hull + DBH + tree species + altitude + slope + aspect + (1|PlotID)

Owing to the different scales, we adjusted the continuous predictors using the default setting of the scale function in *R*, which calculates the mean and the standard deviation (sd) of the predictor and then scales each element by those values by subtraction of the mean and dividing by the sd. For the mean and sd of the continuous predictors, see SI (Table A4). After initial model setup, we reduced the models until only significant predictors remained (stepwise backward selection). We re-run the final models with the unscaled data for plotting the effects of the significant predictors. We used the “ggpredict” function of the ggeffects package for plotting, which sets all other predictors, except the one for which the effect is shown, to the same value (Lüdecke 2018b). We included only TreM groups with more than 20 observations; hence, the groups “insect galleries,” “exposed sapwood and heartwood,” “perennial fungal fruiting bodies” and “ephemeral fungal fruiting bodies” were excluded.

### Comparison of tree-related microhabitat abundance and richness for four different approaches of habitat tree selection

We tested the effects of four different approaches of habitat tree selection from the 15 potential trees focusing on either TreM abundance or richness. Five habitat trees per hectare is the target number in management guidelines in state forests of the research area (ForstBW 2015). In the first approach, we selected the five most clumped trees out of the fifteen potential habitat trees per plot (Fig. 1). To select these five most clumped trees, we used the distance matrix of trees generated with the QGIS software. In the second approach, we randomly selected five trees leading to a dispersed distribution. The third approach, modeled after a method that could be employed in practical forest management to group trees, focused on the single habitat tree with either the highest abundance or the highest richness of TreMs per plot as the focal point of a cluster (Fig. 1). Hence, this tree and its four nearest neighbors were determined in QGIS using the distance matrix. In the fourth approach, we selected a “reference” set of five habitat trees with the highest abundance or the highest richness of



-  Most clumped trees
-  Five randomly selected, dispersed trees.
-  Four trees clumped around tree with highest abundance or richness of TreMs
-  Reference selection

**Fig. 1** Schematic illustration of the four approaches for selecting five trees per plot. The size of the circle indicates the abundance or richness of TreMs per tree. The habitat tree with the highest abundance or richness of TreMs (largest circle) is captured in selection approach three and four. The “reference selection” represents the maximum abundance or richness of TreMs that can possibly be achieved with five habitat trees, indicating how much TreM abundance and richness is reduced through the other selection approaches

TreMs (Fig. 1). In all cases, we expressed abundance as the sum of TreMs provided by the five trees and richness as the sum of different TreMs provided by the selected five trees. To test for significant differences in the mean of sums of TreM abundance and richness among the four approaches, we used the nonparametric Dunn test (Dunn 1964).

## Results

The mean TreM richness per tree was almost two, while 28% ( $N=589$ ) of all inventoried trees bore no TreMs (SI, Figure A1). The average frequency per tree varied

between 0.01 for rare TreM groups, such as woodpecker breeding cavities or micro-soils, and 0.52 for concavities (Table A1). The Clark–Evans index value varied from 0.36 to 1.04 indicating a considerable spread in the 15 potential habitat trees from heavily clumped to randomly dispersed trees across the plots. The variation in convex hull values from 0.24 to 0.93 ha underlines this spread in tree clumping (SI, Figure A2).

### Influence of spatial distribution of potential habitat trees on tree-related microhabitats

There was no significant influence of size of the convex hull or the Clark–Evans index of aggregation on the overall abundance and richness of TreMs. In addition, there was no influence of the tested spatial patterns on the individual TreM groups (Table 2).

The main drivers of overall TreM abundance and richness and of individual TreM groups were DBH and tree species (Fig. 2, Table 2). For instance, woodpecker cavities as well as rot holes are by far more abundant in beech and other broadleaf species than in conifers (Table 2). Some co-variables were significantly related to the provisioning of TreMs at the tree level (Table 2); however, they showed a lower magnitude of influence compared to tree species and DBH. The abundance of TreMs in some groups increased with the gradient of the slope. In addition, overall abundance and richness of TreMs as well as the abundance of concavities increased with altitude (Fig. 2, Table 2).

### Comparison of tree-related microhabitat abundance and richness for four different approaches of habitat tree selection

The four different approaches for selecting five habitat trees out of 15 potential trees yielded significant differences in group abundance and richness of TreMs (Fig. 3).

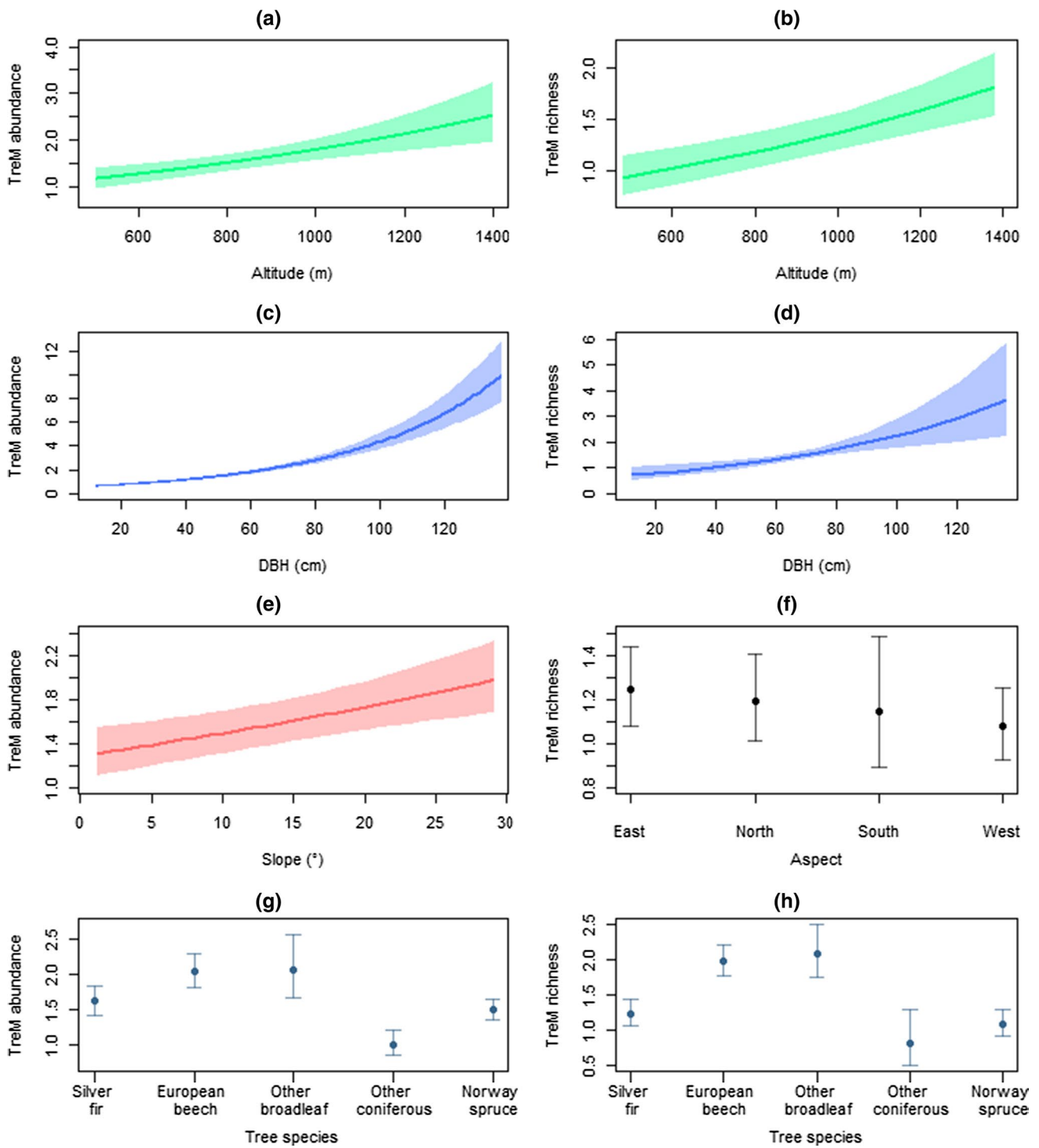
Selecting the five most clumped or randomly dispersed habitat trees yielded the lowest abundance and richness of TreMs. Selecting the individual tree with the highest abundance or richness of TreMs and its four closest neighbors resulted in less reduction of TreM abundance and richness from the optimum level represented by the reference selection. The reference approach where trees were selected solely on the basis of their abundance and richness provided a substantially higher abundance and richness of TreMs than the three other approaches.

**Table 2** Results of the final models after stepwise backward model selection showing significant predictors

	Intercept		Tree species							Aspect			R <sup>2</sup>	
	DBH		European beech	Other broadleaf	Other coniferous	Norway spruce	Altitude	Slope	North	South	West	Conditional	Marginal	
Overall TreM abundance	0.48***	0.34***	0.23**	0.25*	-0.47***	-0.08	0.15***	0.14***	-0.04	-0.08	-0.15*	0.34	0.2	
Overall TreM richness	0.22***	0.21***	0.46***	0.52***	-0.42***	-0.13*	0.13***					0.47	0.35	
Woodpecker cavities	-8.28***	0.61**	3.41**	3.14*	1.77	0.17						0.43	0.14	
Rot holes	-4.12***	0.46***	2.74***	2.57***	-0.47	-0.35						0.44	0.38	
Concavities	-1.62***	0.54***	0.76***	-0.66	-2.41***	0.93***	0.25**	0.23**	0.004	-0.20	-0.52*	0.6	0.45	
Exposed sapwood only	-2.21***	0.36***	0.75***	1.24***	0.63*	0.004						0.18	0.08	
Crown deadwood	-0.53	0.38***	0.15	1.19**	0.97*	0.04						0.52	0.32	
Twig tangles	-2.72***		-3.06***	-2.598**	-4.08***							0.52	0.28	
Burrs and cankers	-3.07***		-1.98***	-20.03	-2.63*			0.52**				0.79	0.78	
Epiphytes	0.396***		-1.65***	-1.46***	-3.02***			0.25**				0.9	0.54	
Nests	-3.44***	0.35*	-1.02*	-1.27	-0.61							0.26	0.16	
Micro-soils	-6.79***	0.91***	2.36**	4.11***	-18.13	-1.41						0.86	0.83	
Fresh exudates	-3.41***		-19.90	-19.46	0.498	2.62***	-0.30*					0.97	0.97	

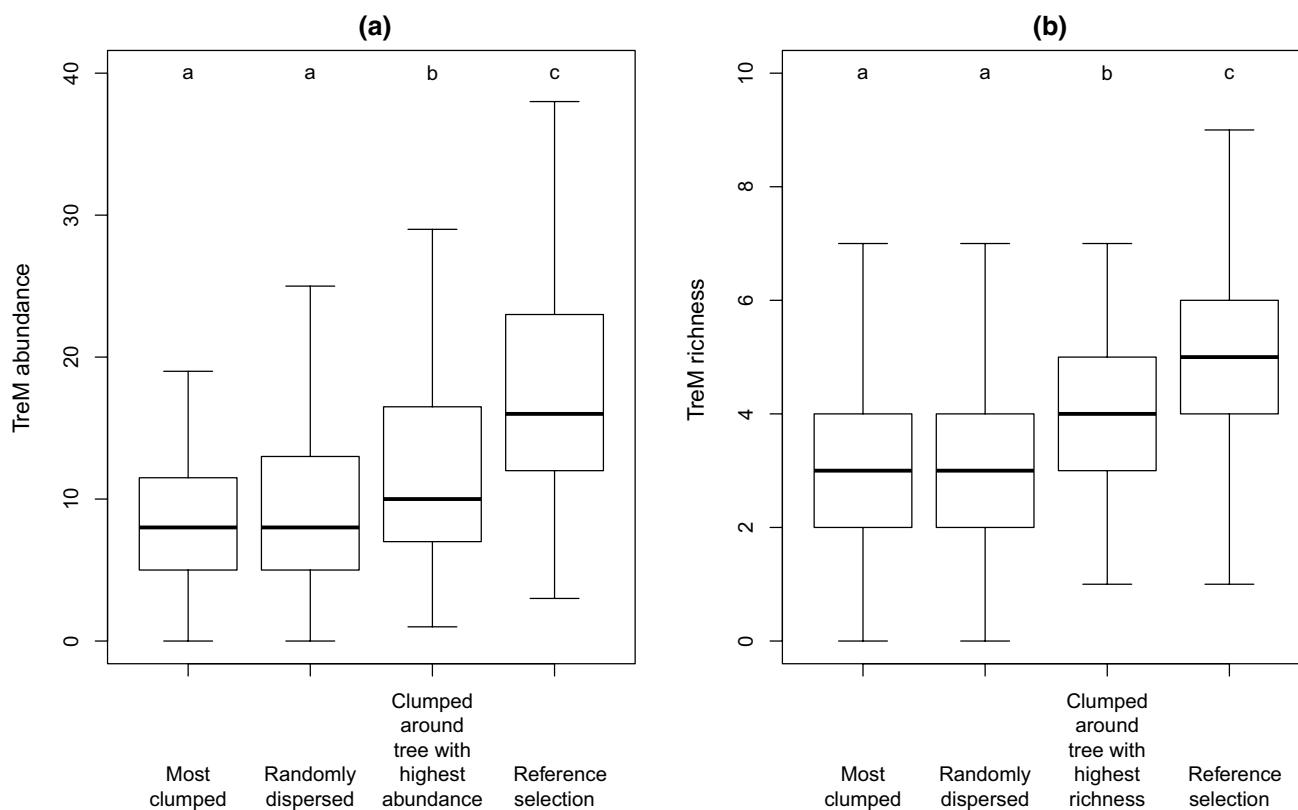
Significance codes: \*\*\*0.001; \*\*0.01; \*0.05. The results are displayed for scaled predictors so that the magnitude of the influence of each predictor is visible and positive values show an increase in the abundance or richness. The predictions of silver fir and east aspect are represented by in the intercept





**Fig. 2** Effect plots of the significant predictors from the GLMMs of TreM abundance (left panel) and TreM richness (right panel) per tree. The effect of altitude (a, b), DBH (c, d) and tree species (g, h) proved significant for both abundance and richness. Slope (e) was significant

for abundance, while aspect (f) was significant for richness. The light-colored band for the continuous predictors and the error bars for the categorical predictors indicate the 95% confidence interval



**Fig. 3** The influence of four different approaches of selecting 5 out of 15 potential habitat trees on mean **a** abundance and **b** richness of TreMs per 1-ha plot. Significant differences among groups have different letters ( $p < 0.05$ )

## Discussion

### Influence of spatial distribution of potential habitat trees on tree-related microhabitats

We found no influence of the spatial distribution of 15 large trees per hectare on the overall abundance and richness of TreMs at the tree level. DBH and tree species explained most of the differences in the overall abundance and richness of TreMs as well as the occurrence of certain TreM groups. The influence of these predictor variables is in agreement with results from a prior study at the plot-level (Asbeck et al. 2019). In addition, the higher richness of TreMs in broad-leaf trees is in line with findings of other studies (Larrieu and Cabanettes 2012; Paillet et al. 2019; Vuidot et al. 2011; Winter et al. 2015).

The finding that large trees supported a higher abundance and richness of TreMs in most of our models (9 out of 13) has been reported in similar studies in managed forests (Larrieu and Cabanettes 2012; Paillet et al. 2017). Recently, it has been shown that this trend also holds true in primary beech forests (Kozák et al. 2018).

There might be some indirect effects of the tree species linked to other predictors (Paillet et al. 2019). For instance,

a higher richness of TreMs was found on eastern compared to western slopes which might be related to the slightly greater number of beech trees found on these aspects (SI, Table A3). Yet, this difference is marginal and might not be the full explanation for the significance of the aspect. Changes in site conditions found on different aspects such as microclimatic conditions that determine the establishment of rot holes (Remm and Lõhmus 2011) might contribute as well to this result. As far as we know, only two other studies have tested the influence of aspect, and in both cases no significant relationship to provisioning of TreMs was found (Johann and Schaich 2016; Paillet et al. 2019). In addition to the effect of aspect, we found a greater richness of TreMs at higher altitudes and on steeper slopes. This may be the result of less intensive management on steeper slopes, where native forests escaped conversion to conifers (Johann and Schaich 2016). Since the slope effect was found for TreM groups that were often located in lower stem sections, e.g., concavities and rot holes, indicating that on these steeper slopes other drivers, such as rock falls, contribute to the formation of these TreMs (Paillet et al. 2017). In addition, trees with TreMs that may be considered “defects” from an optimal forest management perspective are perhaps less likely to be removed on steep slopes than on more gentle terrain.

Based on the above results, the second hypothesis that different groups of TreMs are related to clumped or dispersed distributions of large habitat trees cannot be accepted since spatial correlations were not found for any of the specific TreM groups. Consequently, to maximize stand-level provisioning of TreMs, selection of retention trees should focus on important tree characteristics such as microhabitat attribute or species and dimension (Larrieu et al. 2014a). Although this study focussed largely on dominant and co-dominant trees, had smaller and suppressed trees also been considered, different spatial patterns of TreMs might have been observed. At the same time, we do not believe that the processes that may lead to dispersed or clumped distributions of TreMs, as depicted in Table 1, would differ fundamentally between groups of habitat trees of more similar or more heterogeneous dimensions. However, the selection of habitat trees to increase or maintain abundance and richness of TreMs in managed forests commonly focusses on large individuals, which have proven to provide most of these structures (Larrieu and Cabanettes 2012; Paillet et al. 2017).

### Comparison of tree-related microhabitat abundance and richness for four different approaches of habitat tree selection

Our results show that the overall stand-level abundance and richness of TreMs were not related to spatial patterns at the scale of investigated plots when selecting 15 large trees per hectare, which offer a large sample cover of TreMs. This finding is supported by the comparison of the four approaches for selecting five habitat trees from 15 potential trees. The approaches of selecting the most clumped or randomly dispersed trees on a 1-ha plot showed a significantly lower abundance and richness of TreMs than the approaches of either selecting the one tree with highest TreM abundance or richness or selecting the five trees with highest abundance and richness of TreMs. To analyze the influence of the spatial configuration of habitat trees in a more detailed fashion, for instance, to directly test the habitat amount hypothesis (Fahrig 2013), future research would need to employ a different and more comprehensive approach. Ideally, one would analyze the actual use of all TreMs by taxonomic groups in trees of different dimensions and spatial settings, yet this would be highly labor intensive and extremely costly.

Any process that may potentially lead to spatial patterning of the abundance and richness of TreMs may be counteracted by the regular removal of trees with “defects” through forestry activities. The nonsignificant effect of clumping could be related to our selected plot size. Ideally, the influence of scattered and clumped distributions on TreMs should be analyzed over a wider gradient on contiguous areas of several hectares, which may better capture TreM forming processes, for example, related to the size of woodpeckers

territories (Basile et al. 2020b). To assess the spatial relationships in greater detail, variable numbers of trees, including smaller or suppressed trees, could be added; this was not possible in our design. Despite this limitation of plot size and tree numbers, our study still has clear implications for managed forests in temperate mountains in southwestern Germany and similar forests in other regions. The 1-ha plot size is common for many stands and within-stand patches at the scale at which canopy openings are planned and created through harvesting in CTNFM (Bauhus et al. 2013). Hence, the selection of habitat trees takes place at a relatively small spatial scale (typically < 3 ha), which also maintains habitat connectivity. In addition, retaining 5 habitat trees ha<sup>-1</sup>, the number we used to assess clumping effects, is a common management prescription in Central Europe (e.g., Gerst 2011). Often, these habitat trees are aggregated into groups of ca. 15 trees per 3 ha. At larger spatial scales, clumping of habitat structures may be achieved through other instruments of integrated conservation management such as temporal reserves to protect natural stand dynamics (Bollmann and Braunisch 2013). To determine the adequate spatial scale for these retention measures requires more research. Nevertheless, clumped patterns of retention even on small spatial scales might provide other benefits. For example, mortality of habitat trees may be lower in clumped than in dispersed distributions, if clumped trees provide protection against windthrow, as has been found in other studies (Aubry et al. 2009). Clumped distributions could offer certain microclimatic conditions required by some species (Maziarz et al. 2017). However, it is not clear, whether this is also the case in continuous cover forests, where retained habitat trees will be less exposed than in silvicultural systems employing clearfelling.

### Management recommendations for the retention of habitat trees

Based on our results, there is no indication that the spatial distribution of 15 large, potential habitat trees influences the abundance and richness of TreMs in the studied forests. At this stage, our recommendations are limited to the status quo of TreM abundance and richness in managed forests in a specific research area and cannot be applied to unmanaged forests. When selecting five habitat trees from 15 potential ones, simply clumping trees regardless of their TreM supply did not increase TreM abundance or richness over a randomly dispersed distribution. Clearly, the selection of habitat trees with the highest abundance and richness of TreMs is the best option to maximize TreMs at the time of selection in commercially mature managed forests. The approach of clumping trees around a “champion” habitat tree with many and diverse TreMs represents a compromise between these options.

The situation may be different in younger forests, where certain processes may create clumped distributions of TreMs on trees (e.g., bark peeling by large herbivores) that have not yet been disaggregated through thinning. In the absence of better information on long-term development of retained habitat trees, we therefore advise managers of mature continuous cover forests in temperate Europe to select live habitat trees on the basis of tree attributes and not only on distribution patterns.

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**Authors contribution** T.A. collected the data, prepared the statistical analyses and drafted the manuscript; J.B. designed the research layout; C.M. provided advice on the statistical analyses. All authors contributed to writing of the final manuscript.

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