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ORIGINAL PAPER

Evaluating retention forestry 10 years after its introduction in temperate forests regarding the provision of tree-related microhabitats and dead wood

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Abstract

The individual or grouped retention of habitat trees in managed multiple-use forests has become an approach used to protect biodiversity-related structural attributes typically found in old close-to-nature forests. This study focuses on the effect of one such retention approach in the managed forests of Baden-Württemberg, Germany, ten years after its introduction. Specifically, we asked: (1) How effective are habitat tree groups (HTGs) at providing large living trees (LLTs > 80 cm DBH), tree-related microhabitats (TreMs), and dead wood?, and (2) which tree and stand variables have the greatest influence on the occurrence of TreMs? For this purpose, we inventoried 326 HTGs and 94 reference plots in forests dominated by the most widely occurring native conifer and broadleaf tree species, silver fir (*Abies alba*) and European beech (*Fagus sylvatica*). In accordance with our hypotheses, LLTs and TreMs were significantly more abundant in HTGs than in reference plots in both forest types. More importantly, when retaining 5% of the forest area as HTGs (a common retention level), old forest attributes such as woodpecker cavities, rot-holes or exposed heartwood increased significantly at the stand level while the volume of LLTs almost tripled, and volume of snags increased by 25%. However, quantities of these two attributes remain below minimum thresholds recommended in the scientific literature. A conversion of 15–25% of the stand area into HTGs is needed to increase the stand level abundance of TreMs such as concavities, exposed sapwood, or crown dead wood significantly in the short term. At the single-tree level, tree diameter (DBH), tree species, vitality and neighborhood competition had a significant influence on modeled TreM abundance. At the stand level, TreM occurrence increased with stand age and amount of snags, whereas TreM richness declined with stand density. Ten years after introducing the retention approach, forest stands with HTGs comprised significantly more important structural attributes than those without. Selecting HTGs with high stand volume or low tree density that also include snags, a mix of tree species, LLTs, and some low-vitality habitat trees could further improve this practice.

Keywords Habitat tree · Tree microhabitat · Biodiversity · Retention forestry · Dead wood · Old-growth

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Introduction

Integrative approaches to conserve biodiversity in European forests managed for wood production have been developed to complement the small proportion of strictly protected areas such as the core areas of national parks (Bollmann and Braunisch 2013; Krumm et al. 2020). Retention forestry can facilitate integrating conservation into the management of multiple-use forest landscapes (e.g., Kraus and Krumm 2013; Gustafsson et al. 2020). In Central Europe, retention forestry typically encompasses setting aside small forest patches, habitat trees (also referred to as veteran trees, wildlife trees) and dead wood (Gustafsson et al. 2012; Kraus and Krumm 2013). Selection criteria for retention elements include the occurrence of endangered species or presence of characteristic old-growth structures (Bütler et al. 2013). Old-growth attributes, such as high stand volume, large living trees (LLTs), snags and downed dead wood or tree-related microhabitats (TreMs) (Bauhus et al. 2009; Oettel and Lapin 2021), correspond to the occurrence of certain groups of forest dwelling species, many of which are classified as rare or endangered (Lassauce et al. 2011; Regnery et al. 2013; e.g., Basile et al. 2020; Vogel et al. 2020). At the same time, the occurrence of rare TreMs as well as overall TreM abundance is strongly correlated to the occurrence of LLTs (DBH > 67.5 cm) (Paillet et al. 2017). This supports the use of minimum thresholds for the retention of certain structural elements for conservation purposes, for example for dead wood (e.g., Müller and Bütler 2010). Evidence-based recommendations do not exist for other structural elements such as TreMs and LLTs but information about their required densities within managed forests is needed to conserve and promote viable populations of forest dwelling species. The density of old-growth structures in natural settings may serve as an initial indication of reference values, but it cannot be adapted to forest management targets without further research. For example, Bobiec (1998) recorded an average of 10 LLTs (DBH > 80 cm) ha^{-1} in the Białowieża Forest national park. Similarly, a study in primeval beech forests in Ukraine reported an average of 8 to 12 LLTs ha^{-1} (Commarmot et al. 2013). Between 10 and 17 LLTs ha^{-1} is considered typical for Central European old-growth forests (Nilsson et al. 2002). In the primary European beech-dominated forests of the Carpathians and Dinaric mountains an average TreM-Abundance of 482.9 TreMs per hectare was found (Kozák et al. 2018). European beech (*Fagus sylvatica*) trees in primeval forests in Ukraine had a mean of 2 TreMs per beech tree (Jahed et al. 2020). An average richness of 3 TreMs per living tree was reported for the primary forests of the Western and Southern Carpathians (Asbeck et al. 2022).

In forest management guidelines, selection criteria for the retention of habitat trees or habitat tree groups (HTGs) are mostly based on TreM occurrence and tree diameter, but often remain unspecific (Großmann and Pyttel 2019; Asbeck et al. 2020a). German law requires the retention of trees with woodpecker cavities, mold-cavities, or large nests, while the retention of trees with stem breakage, lightning scars, or fungal fruiting bodies is optional (Großmann and Pyttel 2019). Although there is a long tradition of retaining habitat trees in Central Europe (Mölder et al. 2020), it was only in the last two decades that legislation and incentives were introduced to support this practice (Kraus and Krumm 2013; Borrass et al. 2017; Krumm et al. 2020). However, the effect of such retention programs has yet to be assessed. The purpose of this study is to address this gap.

In the absence of data on the occurrence of a wide range of forest dwelling species, the presence of certain structural elements including TreMs is often used as a surrogate to assess the effectiveness of retention patches such as HTGs (Asbeck et al. 2021). In this study, we analyzed the contribution of HTGs to the stand level provision of these structural elements. To further improve HTG selection, we also identified the tree and stand level factors with the greatest influence on TreM occurrence.

For example, European beech trees have been found to be richer in TreMs than silver firs (Larrieu et al. 2012). Accordingly, mixed-broadleaf-conifer forest stands harbor a greater number of, and more diverse TreMs than mixed-conifer or pure conifer stands (Asbeck et al. 2019). It was also found that TreM density and diversity increased with the number of tree species within forest stands (Kozák et al. 2018). We, therefore, assumed that tree species composition of HTGs is an important determinant of TreM abundance and richness.

Additionally, increasing stand density can have a negative effect on TreMs (Regnery et al. 2013; Winter et al. 2014) and the clustering of habitat trees does not promote stand-level TreM occurrence (Asbeck et al. 2020b). The retention of snags in HTGs may promote a richer and more diverse TreM composition, since snags bear significantly more, more diverse, and often different TreMs compared to living trees (Vuidot et al. 2011; Paillet et al. 2017; Spînu et al. 2022). We also assumed that the preferred retention of larger trees in HTGs would influence TreMs, as their abundance and richness are positively correlated to tree diameter (e.g., Asbeck et al. 2019).

In practice, the selection of HTGs typically focuses on trees that are already rich in TreMs or trees that are likely to form TreMs when retained, e.g., large trees and trees with declining vitality. Therefore, retained HTGs may immediately provide a greater number, and more diverse TreMs within these groups in comparison to the surrounding managed forests (Asbeck et al. 2020b). Hence any recorded differences between HTGs and reference plots in managed forests after a few years do not necessarily represent the process of TreM accumulation that will typically set in following cessation of forest management (Winter and Möller 2008; Larrieu et al. 2014; Paillet et al. 2017) but rather a difference in structural attributes between HTGs and the remaining stand at the time of selection. Therefore, the emphasis of our investigation was on the short-term contribution of existing HTGs on the stand-level provision of structural elements including TreMs in forests of Baden-Württemberg, Germany, 10 years after the introduction of the retention forestry approach (ForstBW 2010). We addressed the following questions:

(1) How effective are habitat tree groups (HTGs) at providing old forest structures, especially TreMs and dead wood?
(2) Which tree and plot variables have the greatest influence on the occurrence of TreMs?

Materials and methods

Project area

This study was conducted in the state forest of Baden-Württemberg, Germany (Fig. 1), where a retention forestry approach has been implemented since 2010. In the state forest, an average of 5 habitat trees per hectare are selected and retained, ideally aggregated to habitat tree groups (HTGs) of around 15 trees per 3 ha (ForstBW 2010, 2015). The selection of habitat trees is carried out by foresters, who should consider the presence of microhabitats such as crown-breakages, woodpecker cavities or hollows (ForstBW 2010; Lorek and Schmalfuß 2012). Ideally, HTGs after their selection represent the structurally rich parts of a forest stand (Fig. 2). Trees retained in HTGs are often of low timber quality. When selected, they are excluded from future harvesting, whereas similar trees outside of HTGs may be removed from the forest stand (ForstBW 2014). At the beginning of this study in 2018, 22,908 HTGs had been retained within the state forest (Tschöpe 2020). These HTGs are permanently marked and excluded from forest management practices. We randomly chose HTGs from two non-monospecific forest types dominated by either European beech *(Fagus sylvatica)* or silver fir (*Abies alba)*, both native tree species. The stands in which HTGs were located covered a gradient of age classes ranging from 0–20 to 180–200 years. Forest type (ForstBW 2014) and age class were derived from the state forest service (internal database). We sampled at least 16 HTGs per age class. The sampling method is detailed below (see *2.2 Inventory*). We sampled an additional circular reference plot ($r = 12.6$ m) at the same site with the same stand management history for every fourth HTG at 50 m distance in the surrounding managed forest stand, $N = 94$ in total. Since we could not establish a paired reference plot for every HTG, the reference plots were selected to capture the variability of stand structural conditions in each forest type stratum (beech and fir dominated forests) (see Fig. 2). The reference plots indicate what the stand structural conditions

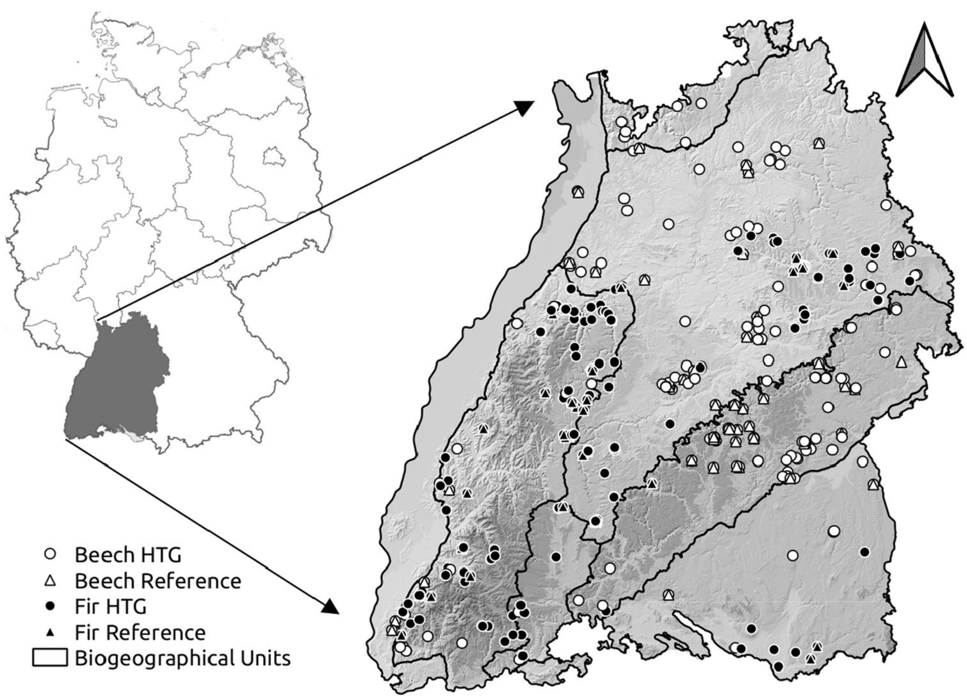


Fig. 1 Map of Baden-Württemberg, Germany with the sampled habitat tree groups (HTGs) for beech dominated (white fill) and fir dominated (black fill) forest stands. HTGs are represented by circles, reference plots by triangles. The background shows the elevation (the darker, the higher) (Landesanstalt für Umwelt, Messungen und Naturschutz Baden-Württemberg 2020). Solid black lines divide biogeographical units (Forstliche Versuchs- und Forschungsanstalt Baden-Württemberg 2020)

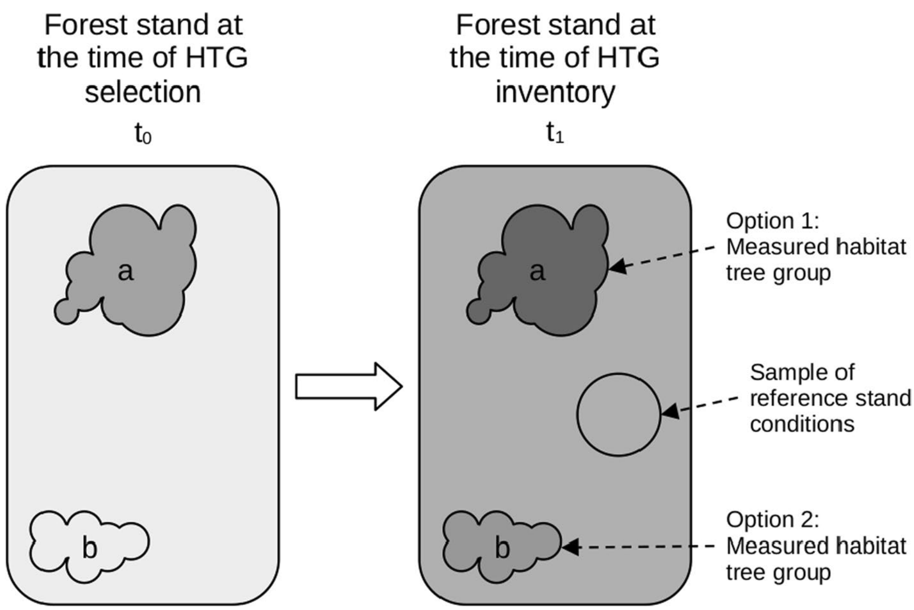


Fig. 2 Illustration of the problem of separating effects of temporal development versus effects of tree selection on attributes of habitat quality in habitat tree groups (HTGs) when based on a single inventory after a certain period since HTG selection. The darker the color the more habitat structures occur in the corresponding areas. The left side shows a forest stand at the time of HTG selection, where option "**a**" represents the selection of trees with above average expression of habitat attributes (indicated by darker color), whereas option "**b**" would represent a HTG with average stand condition (as indicated by the same color as the surrounding stand). The right side of the figure illustrates the sampling of the same stand x years after marking of HTGs. If at t_0, the HTG would have represented average stand conditions (option 2, "**b**"), the inventory at t_1 would depict only the actual development of habitat attributes over time. The increase in habitat quality in patch "**b**" would be the result of ongoing harvesting in the stand matrix and its exclusion inside the patch. In case of option 1, the conditions of habitat attributes in patch "**a**" at t_1 may be the result of both, previous selection of trees in the HTG with above average habitat attributes and the temporal development. Since option 1 would be the typical case, if the selection of HTGs followed standard procedure, our single inventory cannot disentangle the effects of selection and microhabitat development. This simple illustration also ignores the effect that the selection of habitat trees may have on the development of microhabitats, for example faster development on larger and senescent trees. The effect of temporal development can only be captured through a second inventory of HTGs

would be without the retention of HTGs, which does not indicate that the reference plots may not also contain the structural elements selected for in HTGs (Fig. 2). They also serve as a baseline for future assessments.

Inventory

The location and size of existing HTGs were provided by the state forest service's internal data base, which contains information about the number of trees in HTGs, the tree species and their vitality (living or dead) at the time of retention. Inventories of HTGs and reference plots took place in winter 2018/19 and 2019/2020 when deciduous trees had shed their leaves. Data collection was conducted in teams trained to avoid observer bias (Paillet et al. 2015). The HTGs sampled were retained between 2010 and 2018, with an estimated average retention time of 5 years (retained in 2013). HTGs retention time did not differ between beech and fir forests. To analyze the effect of forest stand characteristics on TreMs and other structural and old-growth attributes (following Bauhus et al. 2009) at the plot level, the following categorical and continuous variables were recorded: *crown closure* (dense, closed, intermediate, open, discontinuous), *stand development phase* (gap, regeneration, thicket-stage, pole-stage, timber stage, mature stage), *regeneration cover* (portion of the area covered with regeneration of trees and shrubs) and *stand layers* (single-layered, two-layered, all-aged). Within each HTG, a central point was marked from which the position of all structural elements (living trees, snags, downed dead wood and stumps) was determined by measuring the distance and azimuth. For individual trees, *species* and *diameter at breast height* (at 1.3 m, DBH) were recorded. Living trees were classified according to the IUFRO-tree-classification scheme: *height* (over-, middle-, understory), *vitality* (outstanding, normal, reduced), *growth trend* (ascending, steady, descending) and *crown length* (short = living crown < 0.25 of tree height, moderate = living crown = 0.25–0.5 of tree height, long = living crown > 0.5 of tree height, branches down to stem base). These variables are relevant to forest management practices and could be addressed in guidelines for habitat tree selection. We applied standardized sampling protocols for dead wood and TreM inventory to generate data that are comparable to those of other large-scale forest inventories (e.g.

National Forest Inventories). For dead wood, five different *decay classes* were surveyed. To be able to calculate dead wood volume, *height of snags* was estimated in 3 classes (1.3–5 m, 5.1–10 m, > 10 m) and for downed dead wood logs *length* (m) was measured. DBH was determined at 1.3 m from the ground level at the tree base. Stumps were defined as dead tree trunks lower than 1.3 m in height with a natural or artificial origin. Stump diameter was measured at a height of 0.3 m. For all living and dead trees, TreMs were inventoried following the classification of Larrieu et al. (2018) comprising 47 TreMs in 15 TreM-groups and 7 TreM-categories (Table 3). For countable microhabitats (e.g. woodpecker cavities or witches' brooms), we recorded the number of observations. For uncountable microhabitats (e.g. epiphytes) we recorded the presence (refers to 1) or absence (refers to 0). Further details about the sampling procedure are available in Großmann and Carlson (2021).

Data processing

Data were processed in R (version 4.0.3, R Core Team 2020). Species-specific tree heights and volumes were calculated using the allometric functions in the rBDAT-package (Vonderach et al. 2021). To derive tree crown projection areas, crown radii of living trees were calculated using the following equation based on DBH and species:

$$\text{Crown diameter} = (p0+p1*DBH)*(1-\exp(-((DBH)^{\wedge}p2))),$$

for which coefficients p0 to p3 are provided in Table 4 (Kahle 2004; Döbbeler et al. 2011; Albrecht et al. 2012). To facilitate upscaling and comparisons among HTGs and reference plots, we calculated the area covered by HTGs. For this purpose, local maps with Cartesian positions of all elements (living and dead trees) were produced for each plot (HTG and reference) (Fig. 10). We quantified the stand area occupied by HTGs as a polygon described by the outer limit of crown projection areas of peripheral living trees (Fig. 10). The 'stem-polygon' was defined as a concave hull around all elements, derived using the *concaveman* function (Gombin et al. 2020). The same procedure was applied to the reference plots to test how accurate this method is in comparison to conventional inventory methods with fixed-area plots. Compared to the fixed-area plots, we systematically underestimated the stand areas occupied by the habitat tree groups with the method described above. Accordingly, we systematically overestimated the area-based values (e.g., stand density or stocking volume). Thus, a correction factor of 1.277 was applied to determine the area occupied by HTGs (details are provided in Appendix A).

At the plot level, the measured number (n), basal area (m^2) and volumes (m^3) of all trees were used to calculate the total volume of standing trees, total volume of living trees, total dead wood volume, total snag volume, total volume of downed dead wood and total stump volume for both HTG and reference plots. Additional variables were calculated for living trees: species composition (number of different living species, Shannon-Diversity-Index using the *diversity* function from the vegan-package (Oksanen et al. 2019), mean species-mingling index, share of plot basal area occupied by conifers, share of plot basal area occupied by European oak species, mixture (only broadleaf, only conifers, broadleaf and conifers). The following variables characterizing old-growth attributes (Bauhus et al. 2009; Storch et al. 2018) were calculated: Amount and volume of large living trees (LLTs) referred to trees with a DBH greater than 80 cm (Bobiec 1998), mean decay class of dead wood, vertical heterogeneity (standard deviation (SD) of tree height within the plot), horizontal heterogeneity (SD of tree DBH within the plot), presence and diversity of TreMs. This was measured using TreM abundance and richness, i.e., TreM abundance refers to the total amount of TreMs on standing trees (living trees, snags) within the plot, TreM richness represents the mean number of different TreM-groups observed, the Shannon-Diversity Index was used to calculate TreM diversity. The Clark and Evans Aggregation Index (CE, Clark and Evans 1954) was used to test the effect of the spatial distribution of trees on TreMs. Each HTG's individual shape was accounted for using the *clarkevans* function from the spatstat R package (Baddeley et al. 2016). We also tested the effect of competition of neighboring trees on the occurrence of TreMs by calculating the competition metrics described below.

At the individual tree level, species identity and type (conifer vs. broadleaf) led to better TreM prediction. Conifer and broadleaf trees typically differ regarding the decay resistance of their wood (e.g., Cornwell et al. 2009), an important attribute for the development of TreMs. To account for species mixtures and competition effects on TreM occurrences on single trees, several variables were calculated: the Species-Mingling-Index (*M)*, the mean distance of neighboring trees (*meanDIST)*, the local basal area (*localBA)* and the *Hegyi competition index*. The Species-Mingling-Index considers how many of the three closest neighboring trees belong to different species than the subject tree (Pommerening 2002). It ranges from 0 (all four trees are the same species) to 1 (all four trees are different species). The competition metric *meanDIST* is the mean distance (m) of the four nearest neighboring trees (Kuehne et al. 2019). The local basal area (m^2) was calculated as the sum of the basal areas of all trees including the subject tree within a radius of 6 m around the subject tree (Kuehne et al. 2019). Trees closer than 6 m to the border of the plot were excluded from this calculation as not all competitors were known. Another distance dependent competition index based on Hegyi (1974) was calculated within the same 6 m radius.

To be able to compare the measured levels of the old-growth attributes (total dead wood volume, snag volume and number of LLTs), we used references and recommended thresholds from scientific literature. To support dead wood dependent biodiversity, dead wood volumes of 30–40 m^3 ha^{-1} in mixed-montane forests and 30–50 m^3 ha^{-1} in lowland oak–beech forests have been recommended (Müller and Bütler 2010). For specialized woodpeckers, recommended minimum snag volumes were 15–20 m^3 ha^{-1} (Angelstam et al. 2003; Bütler et al. 2004b, a). The mean dead wood volumes found in strict forest reserves (IUCN category IV) in Baden-Württemberg are 70 m^3 ha^{-1} (Table 10). During the last National Forest Inventory, the mean dead wood volume in the state forest of Baden-Württemberg was 34 m^3 ha^{-1} (Thünen Institut 2020). Densities of 10 to 17 large living trees per hectare (LLTs, DBH > 80 cm), are considered typical for Central European old-growth forests (Nilsson et al. 2002).

Statistical analysis

All statistical analyses and modeling were conducted in R (version 4.0.3, R Core Team 2020). Differences were considered significant for $p \leq 0.05$. As most of the variables were not normally distributed (Shapiro–Wilk Normality Test $p > 0.05$, *shapiro.test* function), we applied Wilcoxon Rank Sum tests (*wilcox.test* function).

To assess the effect of HTG retention on TreM provisioning in general terms, inventory data from HTGs ($N = 326$) were compared with the reference plots ($N = 94$), separately for beech and fir forests (Fig. 2). We used a subset of plots (the paired HTG and reference plots, $N = 87$ pairs), to assess the effect of HTG retention at the forest stand scale. For this step seven HTGs with less than five trees have been excluded, as extrapolation of small HTGs to stand level lead to extremely high and unbalanced values. In a second step, we created hypothetical stands of 1 ha size from each pair of HTGs and reference plots. To do so, we simulated inventory results for 1 ha with different HTG percentages (0 to 100%). To understand the role that retained HTGs play in providing certain structural elements at the stand level, we tested the mean values from 87 hypothetical stands at various proportions of HTGs (ranging from 0 to 100%) against the reference values (0% of HTG retention) allowing us to identify any significant contributions from the retained HTGs.

Effects on TreM abundance and richness at the single tree and at the plot level were identified by calculating Generalized-Linear-Mixed-Models (GLMM) with the glmer-function from the lme4-package (Bates et al. 2015). Both response variables were count data, thus we considered a Poisson distribution for the modeling procedure. Plot position was included as random effect to account for differences in local site and growing conditions. In a first step, we removed single or few occurrences of some categorical values in the predictor variables to avoid issues such as singular fits. At the single-tree level, species with $N < 20$ were excluded from the analysis. At the plot level, we only considered stands with *one*- and *two* canopy layers and only the *timber* and *mature* stand development phases. Therefore, age classes were regrouped into three broad classes with a more even distribution of observations (*up to 80*, *80 to 120*, *older than 120 years*). The Clark-Evan-Index (CE, spatial distribution of trees) was grouped into *clumped* (CE < 1), *randomly distributed* (CE = 1) and *evenly distributed* (CE > 1).

Only living trees were considered in our single-tree level models, because our aim was to investigate factors affecting TreM occurrence on living trees. Snags had a proportion of 4% of all inventoried standing trees. In the first step of the modeling process we fitted single predictor models and a null model (Tables 5 and 6). Then, all variables performing better than the null model were tested for collinearities (*varclus*-function from the Hmisc-package (Frank et al. 2020) and correlation (*pairs.panels*-function from the psych-package (Revelle 2020). In case variables correlated with each other, the one with the best-performing model according to the Akaike's-Information-Criterion (AIC) from the single predictor models was considered for further steps. Finally, to predict TreM abundance and richness at the plot and single-tree level, models with combinations of two, three, four and up to the full number of predictor variables were fitted, while considering possible interactions between predictors. All models were compared based on their AIC values. Models with the lowest AIC were considered best (Tables 7 and 8) and their performance was evaluated in more detail by testing for over- or under-dispersion, zero inflation and outlier performance using the DHARMa-package (Hartig 2020). In case of zero inflation modeling was repeated based on negative binomial distributions or a hurdle model was applied (glmmTMB-package) (Brooks et al. 2017).

Results

Habitat tree groups compared to managed forest

HTGs had an average size of 793 m^2 (median: 692 m^2), ranging from 59 to 4950 m^2. The number of trees in HTGs ranged from 1 to 125, with an average and median number of 15 and 12 trees per group, respectively. Tree volume (m^3 ha^{-1}) was about 20% higher in HTGs compared to reference plots from the surrounding forest, while stand density (trees ha^{-1}) in HTGs was less than half that of reference plots (Table 1). This difference was more pronounced in

Table 1 Mean values (standard deviation) from the inventoried habitat tree groups (HTG) and reference plots (Ref) for structural and old-growth attributes (following Bauhus et al. (2009))

Forest Type	Beech Forest			Fir Forest			Overall		
	HTG (N = 166)	Ref (N = 52)	Sig	HTG (N = 160)	Ref (N = 42)	Sig	HTG (N = 326)	Ref (N = 94)	Sig
Stand Density [N ha^{-1}]	163 (94)	491 (482)	***	250 (187)	457 (432)	***	206 (182)	476 (511)	***
Basal Area [m^2 ha^{-1}]	28.7 (14.6)	23.6 (13.7)	***	36.8 (13.8)	36.6 (11.9)	n.s	32.6 (14.4)	29.4 (13.8)	**
DBH [cm]	73.9 (16.9)	33.2 (14.7)	***	44.2 (14.3)	33.9 (10.9)	***	46.9 (16.3)	33.5 (13.1)	***
Old-Growth-Attributes									
Volume of Large Living Trees [m^3 ha^{-1}]	79.5 (188.0)	0.0 (0.0)	***	90.0 (197.9)	8.2 (37.9)	***	85.2 (193.1)	3.6 (25.4)	***
Occurrence of Large Living Trees [N ha^{-1}]	6.7 (16.0)	0.0 (0.0)	***	8.3 (17.2)	0.8 (3.8)	***	7.5 (16.6)	0.4 (2.5)	***
Stand Volume [m^3 ha^{-1}]	452.0 (146.2)	339.1 (140.9)	***	543.7 (200.0)	499.9 (159.8)	n.s	496.4 (179.1)	410.2 (169)	***
Total Dead Wood [m^3 ha^{-1}]	42.1 (71.8)	33.4 (45.3)	n.s	56.7 (85.1)	45.5 (38.8)	n.s	48.8 (78.3)	38.7 (42.8)	n.s
Snag Volume [m^3 ha^{-1}]	25.8 (64.7)	1.0 (4.6)	***	34.4 (68.3)	8.9 (20.0)	n.s	29.6 (66.1)	4.5 (14.2)	***
Downed Dead Wood Volume [m^3 ha^{-1}]	12.7 (30.4)	11.8 (23.0)	n.s	15.8 (33.1)	15.7 (21.2)	n.s	14.1 (31.5)	13.5 (22.2)	n.s
Stumps Volume [m^3 ha^{-1}]	3.6 (5.9)	20.6 (39.3)	***	7.1 (11.8)	23.5 (22.7)	***	5.4 (9.4)	21.9 (32.9)	***
Decayclass Distribution [Number of Decayclasses]	1.5 (1.1)	2.3 (1.1)	***	2.2 (1.2)	2.8 (1.1)	*	1.9 (1.2)	2.5 (1.1)	***
Vertical Variability [SD of Tree Height]	5.5 (3.3)	4.7 (2.7)	n.s	6.7 (3.4)	6.7 (2.8)	n.s	6.1 (3.4)	5.6 (2.9)	n.s
Size Variability [SD of DBH]	14.3 (7.1)	11.2 (6.1)	**	16.6 (8.1)	14.5 (5.9)	n.s	15.5 (7.7)	12.6 (6.2)	**
Spatial Heterogeneity [Clark Evans Index]	1.5 (0.5)	1.6 (0.6)	n.s	1.4 (0.5)	1.4 (0.2)	n.s	1.4 (0.5)	1.5 (0.5)	n.s
Presence of Advance Tree Regeneration [% of Plot Area]	51.9 (39.4)	54.0 (41.7)	n.s	28.6 (33.0)	31.8 (32.6)	n.s	40.4 (38.2)	44.2 (39.3)	n.s

Overall results and results for beech and fir forest are provided. P-values refer to results from the Wilcoxon-Rank-Sum-Tests between HTGs and reference plots (Significance levels (Sig.): n.s. = $p > 0.05$; * = $p \leq 0.05$; ** = $p \leq 0.01$; *** = $p \leq 0.001$)

beech forests. Mean basal area and mean DBH were higher in HTGs than in reference plots. In fir forests, the mean basal area of HTGs, which was generally higher than in beech forests, did not differ from reference plots (Table 1). Most old-growth attributes were significantly more abundant in HTGs compared to reference plots. On average, the mean abundance of large living trees (LLTs) was 18 times higher, and the volume of snags 6 times higher in HTGs than in reference plots. In both forest types, TreM abundance, diversity and richness were significantly higher in HTGs than in the surrounding forest (Table 2). This also held true for most TreM groups (Table 2) and single TreMs (Table 9). No significant differences between HTGs and reference plots were detected for downed and total dead wood, vertical variability, and spatial heterogeneity. The number of dead wood decay classes and stump volume were on average significantly higher in reference forest plots than in HTGs.

The comparison of three old-growth attributes measured in our study with values from the literature (Fig. 3) revealed that large living trees and snags occurred more frequently in HTGs, yet their overall occurrence was still low. The mean number of LLTs (DBH > 80 cm) in HTGs was significantly below the recommended 10 to 17 LLTs ha^{-1}. The median of LLTs was zero for both HTGs and reference plots. Mean total volume of downed dead wood and snags found in HTGs (43.7 m^3 ha^{-1}, stumps excluded) was below the recommended values as well as the average found in strict forest reserves in Baden-Württemberg (Fig. 3). Total dead wood volume in reference plots was 4 m^3 ha^{-1} above the average dead wood volume of 34 m^3 ha^{-1} recorded in the state forest of Baden-Württemberg in 2012 (Thünen Institut 2020). Values for total dead wood volume were highly variable, with a median below 20 m^3 ha^{-1} for HTGs and below 30 m^3 ha^{-1} for reference plots. The mean volume of snags in HTGs was significantly above the recommend 15–20 m^3 ha^{-1} for specialized woodpeckers and close to the average of 34 m^3 ha^{-1} in forest reserves. The volume of snags in reference plots was around the average of 4.9 m^3 ha^{-1} reported in the NFI (Fig. 3). However, 50% of HTGs and reference plots provided no snags.

Effect of habitat tree group retention at the stand level

To assess the short-term effect of HTG retention for providing desired structural elements at the stand level, we

Table 2 Mean values (standard deviation) from the inventoried habitat tree groups (HTG) and reference plots (Ref) for tree-related microhabitats (TreMs)

Forest Type	Beech Forest			Fir Forest			Overall		
	HTG (N=166)	Ref (N=52)	Sig	HTG (N=160)	Ref (N=42)	Sig	HTG (N=326)	Ref (N=94)	Sig
TreM Abundance [N ha^{-1}]	574.3 (435.1)	331.5 (262.3)	***	562.3 (460.3)	288.5 (303.3)	***	565.3 (445.2)	312.5 (280.4)	***
TreM Richness [N ha^{-1}] (Group, max. = 15)	4.6 (2.2)	2.2 (1.5)	***	4.4 (2.2)	2.8 (1.6)	***	4.5 (2.2)	2.4 (1.5)	***
TreM Groups									
Woodpecker-breeding Cavities [N ha^{-1}]	8.3 (18.0)	0.3 (1.9)	***	9.9 (50.5)	1.4 (6.4)	*	9.0 (37.3)	0.8 (4.5)	***
Rot-Holes [N ha^{-1}]	2.8 (7.5)	0.3 (2.5)	**	3.2 (9.0)	1.1 (5.1)	*	3.0 (8.2)	0.7 (3.9)	***
Insect Galleries [N ha^{-1}]	26.8 (65.6)	5.5 (17.2)	***	22.1 (35.1)	11.5 (32.2)	**	24.4 (52.6)	8.1 (25)	***
Concavities [N ha^{-1}]	3.3 (8.8)	0.3 (2.5)	**	1.1 (6.1)	0.4 (2.5)	n.s	2.2 (7.6)	0.4 (2.5)	**
Exposed Sapwood [N ha^{-1}]	50.3 (66.1)	23.8 (40.0)	***	44.2 (68.0)	22.0 (30.0)	*	47.1 (66.6)	23 (35.8)	***
Exposed Heartwood [N ha^{-1}]	10.9 (21.3)	12.3 (53.8)	*	12.3 (20.6)	12.5 (32.3)	n.s	11.5 (20.8)	12.4 (45.3)	*
Crown Dead wood [N ha^{-1}]	68.8 (71.5)	44.7 (53.7)	**	88.1 (131.5)	41.9 (100.6)	***	77.8 (104.9)	43.5 (77.5)	***
Twig Tangles [N ha^{-1}]	1.9 (16.5)	1.1 (8.0)	n.s	3.1 (11.0)	1.5 (5.5)	n.s	2.4 (14.0)	1.3 (6.9)	n.s
Burrs and Cankers [N ha^{-1}]	0.7 (3.0)	0.6 (3.1)	n.s	1.3 (6.2)	1.2 (8.0)	n.s	0.9 (4.8)	0.9 (5.8)	n.s
Perennial Fungal Fruiting Bodies [N ha^{-1}]	23.6 (96.7)	1.0 (7.3)	***	44.9 (111.0)	7.1 (32.2)	*	33.5 (103.6)	3.7 (22.1)	***
Ephemeral Fungal Fruiting Bodies [N ha^{-1}]	7.9 (36.1)	3.2 (16.5)	n.s	5.4 (25.2)	1.5 (7.7)	n.s	6.6 (31.0)	2.4 (13.3)	n.s
Epiphytic and Parasitic Crypto- and Phanerogams [N ha^{-1}]	21.2 (34.1)	22.5 (44.3)	n.s	42.6 (58.7)	24.4 (41.4)	*	31.6 (48.6)	23.4 (42.8)	**
Nests [N ha^{-1}]	4.9 (18.1)	2.0 (6.3)	n.s	4.4 (11.2)	7.7 (13.9)	n.s	4.6 (15)	4.5 (10.7)	n.s
Microsoils [N ha^{-1}]	1.1 (4.5)	0.3 (2.1)	n.s	2.2 (11.6)	0.9 (4.2)	n.s	1.6 (8.6)	0.6 (3.2)	n.s
Exudates [N ha^{-1}]	1.0 (4.8)	0.0 (0.0)	*	0.7 (3.3)	0.4 (2.6)	n.s	0.9 (4.1)	0.2 (1.7)	*

Overall results and results for beech and fir forest are provided. P-values refer to results from the Wilcoxon-Rank-Sum-Tests between HTGs and reference plots (Significance level (Sig.): n.s. = $p > 0.05$; * = $p \leq 0.05$; ** = $p \leq 0.01$; *** = $p \leq 0.001$)

analyzed the subset of our data containing the 87 pairs of HTGs and reference plots after a mean retention time of 5 years. When hypothetically retaining 5% of the stand, which would be the proportion typically occupied by an HTG, we detected a significant enrichment in the number and volume of LLTs (Fig. 4). At the same retention level, a positive effect can also be seen for *snag volume*. At 5% HTG retention, the mean abundance of *woodpecker-breeding cavities* increased in both beech and fir forests (Fig. 5). At the same level of retention, we found a significantly higher abundance of *insect-galleries, concavities, exposed heartwood, perennial fungal fruiting bodies* and *exudates* in beech forests and for both forest types combined. *Snag volume* was more than doubled on average, if 15% of stand area in beech forests were retained in HTGs (Fig. 4). In beech forests 20–40% of stand area retained in HTGs were needed to increase overall TreM abundance and richness significantly, whereas for fir forests 25% (TreM abundance) and 70% (TreM diversity) would be required (Fig. 4). To achieve a significant enrichment in specific TreMs, relatively large proportions of beech and fir forests, ranging between 25 and 85% would have to be retained in HTGs (Fig. 5). No effect on *downed dead wood* was observed with increasing the proportion of HTGs. A negative effect on total dead wood was observed, as stump volume decreased with increasing proportions of stand area in HTGs.

Factors influencing TreM occurrence

The occurrence of TreMs on single trees was best predicted by the variables *genus*, *DBH* and *vitality* for TreM richness (Fig. 6) and additionally by *competition (HEGYI)* for TreM abundance (Fig. 6). Other predictors such as *species mixture (M)* or other competition indices (*localBA, meanDIST*) had no significant effect on abundance and richness of TreMs on single trees. Tree *genus* in combination with *DBH* were the main drivers of TreM abundance (Fig. 6). For single trees, TreM abundance and richness were higher in broadleaves than in conifers (Fig. 6) and increased exponentially with *DBH*. Both high and low tree *vitality* lead to higher TreM abundance and richness compared to *average*

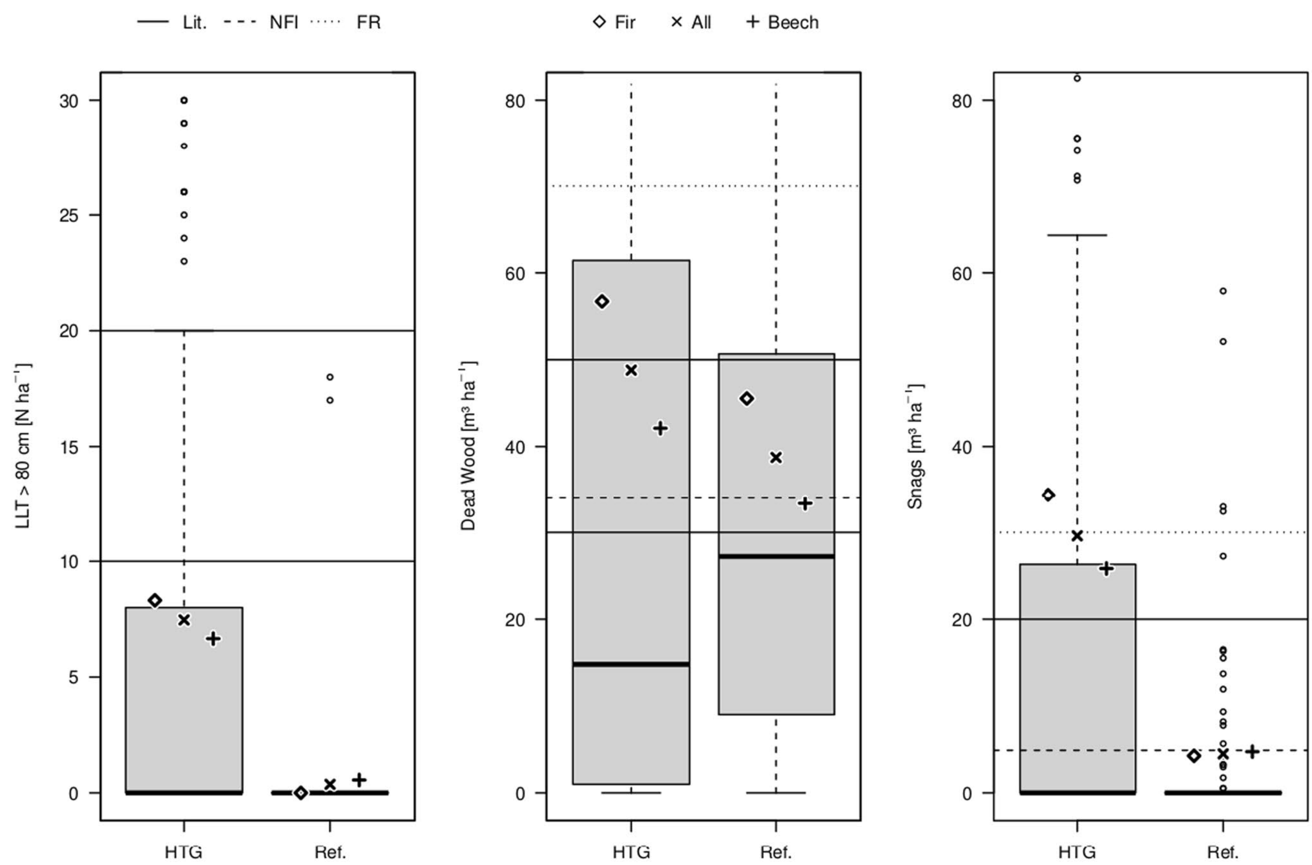


Fig. 3 The boxplots represent the number of Large Living Trees (LLTs > 80 cm DBH), total dead wood and snags in habitat tree groups (HTG) and reference plots (Ref.). The bold black line indicates the median, the box shows the interquartile range and the whiskers the 1.5 interquartile range. Additional symbols indicate the arithmetic mean values for all data (x), Fir forests (◇) and Beech forests (+). Horizontal lines provide comparisons for reference values from Literature (—— Lit.) (Angelstam et al. 2003; Bütler et al. 2004b, a; Müller and Bütler 2010), mean values from the German National Forest Inventory (- - -NFI) 2012 in the State Forest of Baden-Württemberg (Thünen Institut 2020) and Strict Forest Reserves (··· FR) in Baden-Württemberg (Appendix Table 10)

vitality (Fig. 6). Low vitality had a stronger influence than high vitality although the mean DBH of *high vitality* trees (64.5 cm (17.1) was significantly larger than in trees of *low vitality* (41.5 cm (21.2). Increased *competition* led to reduced TreM abundance (Fig. 6).

TreMs were significantly more abundant and diverse in forest stands with an average *age* over 80 years when compared to younger forest stands (Fig. 7). Higher *snag volume* resulted in higher TreM abundance and richness (Fig. 7). *Stand volume* also had a significantly positive influence on TreM abundance (Fig. 7). Forest stands of lower *density* were richer in TreMs compared to denser stands (Fig. 7).

Discussion

In this study, we aimed at assessing the effect of current retention forestry approaches with habitat tree groups (HTGs) in forests available for wood production. Since there are no widely agreed minimum thresholds for the retention of habitat trees or tree-related microhabitats, we employed an approach that aimed at quantifying stand proportions in HTGs that would be required to yield significantly higher quantities in desired structural attributes when compared to reference conditions in managed forests outside HTGs. We found that 5–15% of retained area in HTGs (in their current condition) was required to achieve significantly positive effects on the quantities of LLTs, dead wood and certain TreMs. These effects are attributable to (a) the initial selection of forest patches as HTG that bear more TreMs than the rest of the stand, (b) the protection of these trees from harvesting, and c) the temporal development of HTGs without subsequent removal of trees when compared to the forest matrix. Based on our inventory approach, we cannot quantify the proportional magnitude of these effects. The relatively strong differences of 20% in tree volume between HTGs and reference plots in beech forests given the short period since selection of HTGs, suggests that the effect of initial HTG selection was likely stronger than the effect of temporal development.

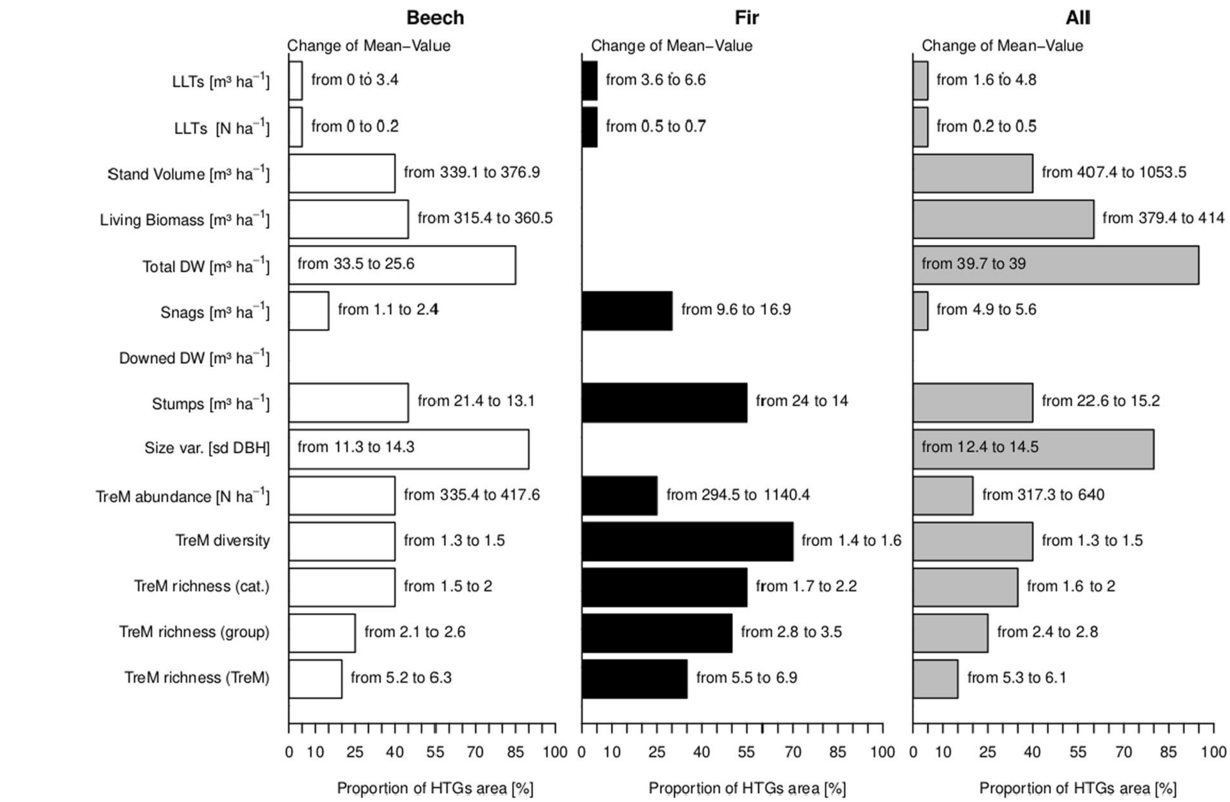


Fig. 4 The percentage of forest stand area in habitat tree groups (HTGs) needed to achieve a significant stand-level change in the expression of structural attributes in beech and fir dominated forest types and the combined data set (projected based on data collected in this study). The mean values range from '0% HTG retention' to the mean value of the proportion of HTGs area where a significant effect was detected

How effective is the current retention of habitat tree groups?

Ten years since the start of the systematic application of retention forestry in the state forests of Baden-Württemberg, the process of HTG selection led to the conservation of significantly more structural attributes such as dead wood, LLTs and TreMs in HTGs than in the reminder of managed forest stands. When projecting our findings to the forest stand level, 5% of forest area retained in HTGs led to an overall positive effect on rare TreMs, such as woodpecker cavities, rot-holes or exudates, as well as LLTs. More area in HTGs (10 to 40%) would be required to positively influence the occurrence of snags or TreM diversity.

Considering that the area of HTGs in the state forests of Baden-Württemberg corresponds to 2.6% of the total forest stand area, the effect of high LLT densities in HTGs at the stand level is quite small. HTGs give smaller trees a chance to grow to large dimensions in the future. This is an important finding as LLTs are not only of great ecological importance but also under high risk of decline worldwide (e.g., Lindenmayer and Laurance 2017). Current mean density of trees larger than 70 cm DBH was 14 trees ha^{-1} in HTGs in beech forests (data not shown). Assuming no mortality and an annual diameter growth rate of 4.5 mm/year for large beech trees (Vandekerkhove et al. 2018; Janík et al. 2018), the number of LLTs (DBH > = 80 cm) in beech forest HTGs would double in approximately 20 years. However, increased mortality due to climate change related disturbances may reduce this number (Walthert et al. 2021; Meyer et al. 2022). Average dead wood volumes in HTGs and reference plots were within the range of 30–50 m^3 ha^{-1} recommended for temperate forests (Müller and Bütler 2010). Dead wood volumes in conifer dominated stands tend to be higher than in broadleaf dominated forest stands (Oettel et al. 2020). Our study confirmed this result.

Our comparison of HTGs and reference plots in the surrounding forests suggests that the designation of HTGs can successfully protect LLTs. At the stand level, retaining only 5% of the stand area as HTGs would be required to achieve significant positive effects on the quantities of LLTs. The picture is somewhat different for dead wood, where average stand-level volumes were not significantly different between HTGs and reference areas and the total quantities were already above the recommended minimum value of 30 m^3 ha^{-1} (Müller and Bütler 2010). This indicates that

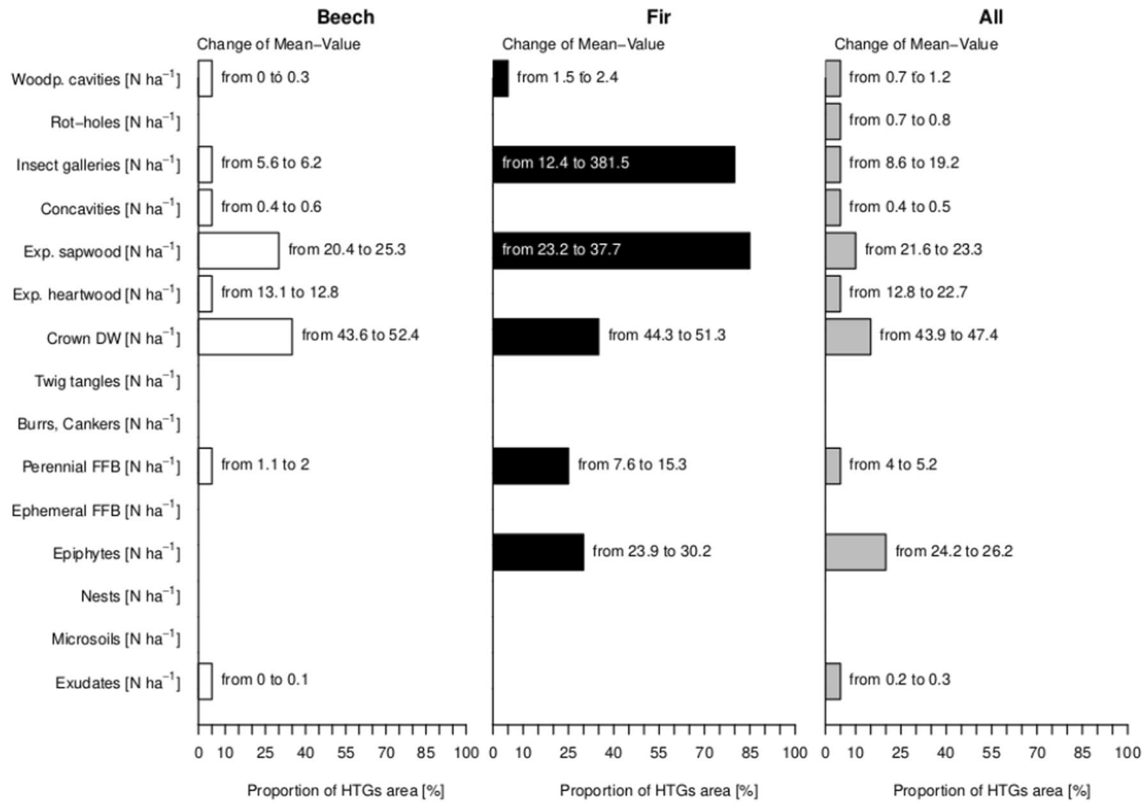
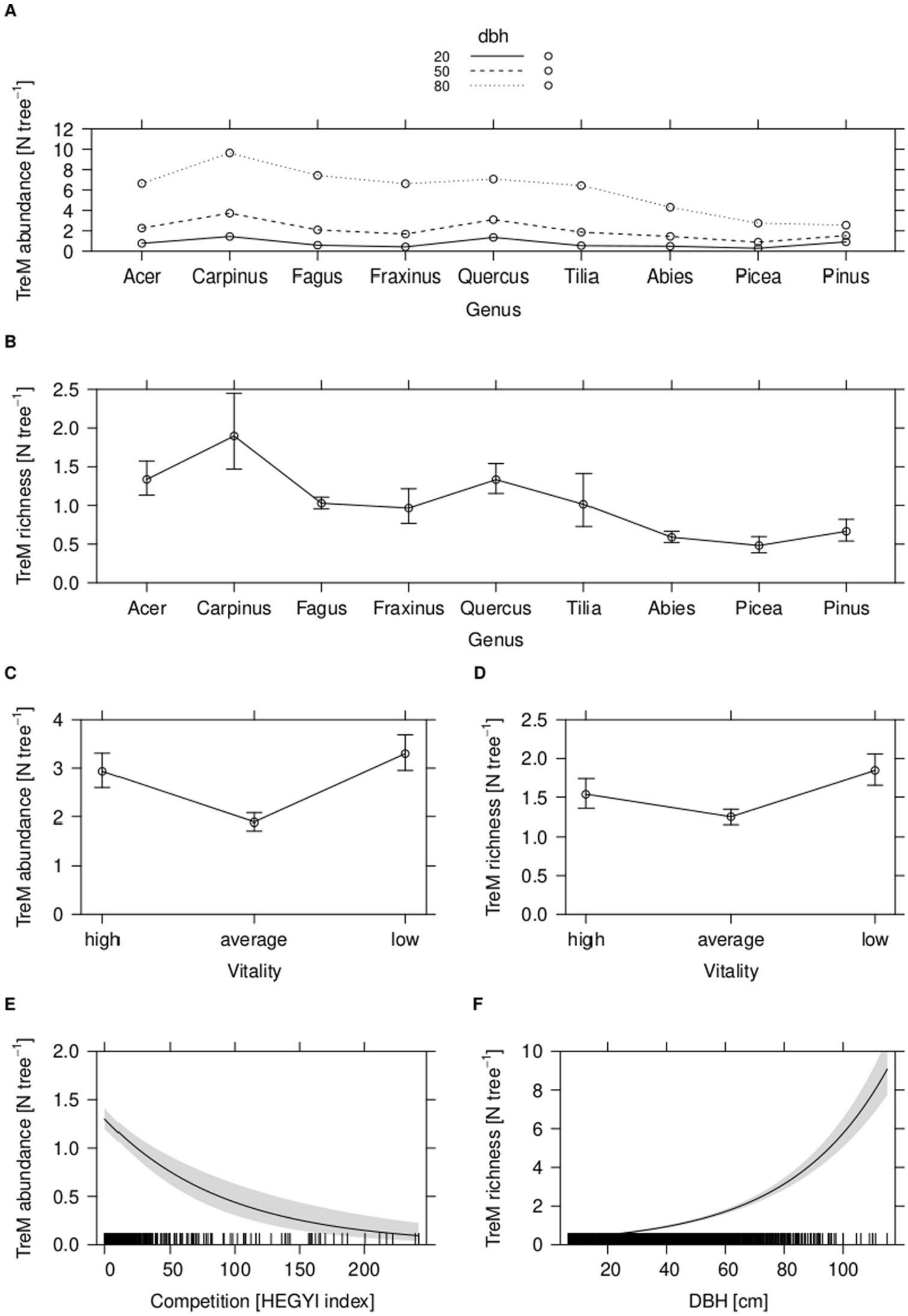


Fig. 5 The percentage of forest stand area in habitat tree groups (HTGs) needed to achieve a significant stand-level change in the occurrence of TreM groups in beech and fir dominated forest types and the combined data set (projected based on data collected in this study). The mean values refer to '0% HTG retention' to the mean value of the proportion of HTGs area where a significant effect was detected. LLTs = large living trees; DW = dead wood; Size var. = size variation; FFB = fungal fruiting body

the selection of HTGs places a stronger focus on LLTs than dead wood. However, more than 50% of total dead wood volume in managed forest stands were in the form of stumps, which are least important for the diversity of beetles and fungi compared to downed dead wood and snags (Uhl et al. 2022). The median of total dead wood volume in HTGs was below 20 m^3 ha^{-1} (Fig. 3), indicating that dead wood amount in many HTGs was quite low and substantially below the average. Snags occurrence was positively affected by retaining HTGs, although the average value was still below a recommended quantity of 20 m^3 ha^{-1} (Angelstam et al. 2003; Bütler et al. 2004b). The systematic retention of dead wood within HTGs in this context is relatively recent (since 2010, ForstBW 2010). The amount will likely increase in the future as the retained trees age and die naturally. Yet this process may be slow as has been shown for strict oak- and beech-dominated forest reserves in Europe that originated from managed forest, where median accumulation rates for dead wood ranged between 1.6 and 1.9 m^3 ha^{-1} a^{-1} (Vandekerkhove et al. 2009). In addition, extreme drought and heat from 2018 to 2020 led to an increase in dying and dead trees at many sites and in many different forest types (Taccoen et al. 2019; Schuldt et al. 2020). To what extent this has increased the input of dead wood in the types of forests investigated here, will be revealed in the results of the next national forest inventory of 2022. Where the quantities of dead wood remain considerably below desired levels, it may be advisable to create some dead wood artificially through girdling or toppling of trees to complement the slow natural accumulation process in HTGs and surrounding stands (Svensson et al. 2013; Toivanen et al. 2014; Seibold et al. 2015; Sandström et al. 2019; Uhl et al. 2022).

HTG retention is an appropriate approach to improve overall TreM richness, abundance and diversity within managed forest stands, and to provide and protect rare TreMs such as woodpecker cavities and rot-holes (Großmann et al. 2018; Asbeck et al. 2019). It should be kept in mind, that the calculated stand proportions in HTGs required for the provisioning of certain structural elements are based on their current condition. As HTGs change and continue to accumulate TreMs or lose certain structural elements (e.g., LLTs), these figures will change. Although the functional link between old-growth attributes and the occurrence of species that may depend on them has been demonstrated for some taxonomic groups (e.g., Basile et al. 2020), the mere occurrence of these structural elements does not translate

Fig. 6 Effect plots of TreM abundance (**A**, **C**, **E**) and richness (**B**, **D**, **F**) at the single-tree level for the best performing predictors. Whiskers and the gray line refer to the 95%-Confidence-Intervals. These are not provided for tree genus-DBH interactions to ensure the readability of the plot



directly into the co-occurrence of the species in question. Hence the effect of HTG retention on populations of forest dwelling species needs to be assessed in a next step.

HTGs are the smallest units in strict forest conservation measures (Kraus and Krumm 2013) in Baden-Württemberg, Germany. The retention of HTGs can protect structurally rich and ecologically valuable areas at the forest stand level (Götmark and Thorell 2003). At the landscape scale HTGs aim to supplement small and large forest reserves. Therefore, the ecological function of HTGs for nature conservation must be seen in the spatial context of larger strictly protected forest reserves, which are necessary from the point of view of conservation of species and processes (Abrego et al. 2015).

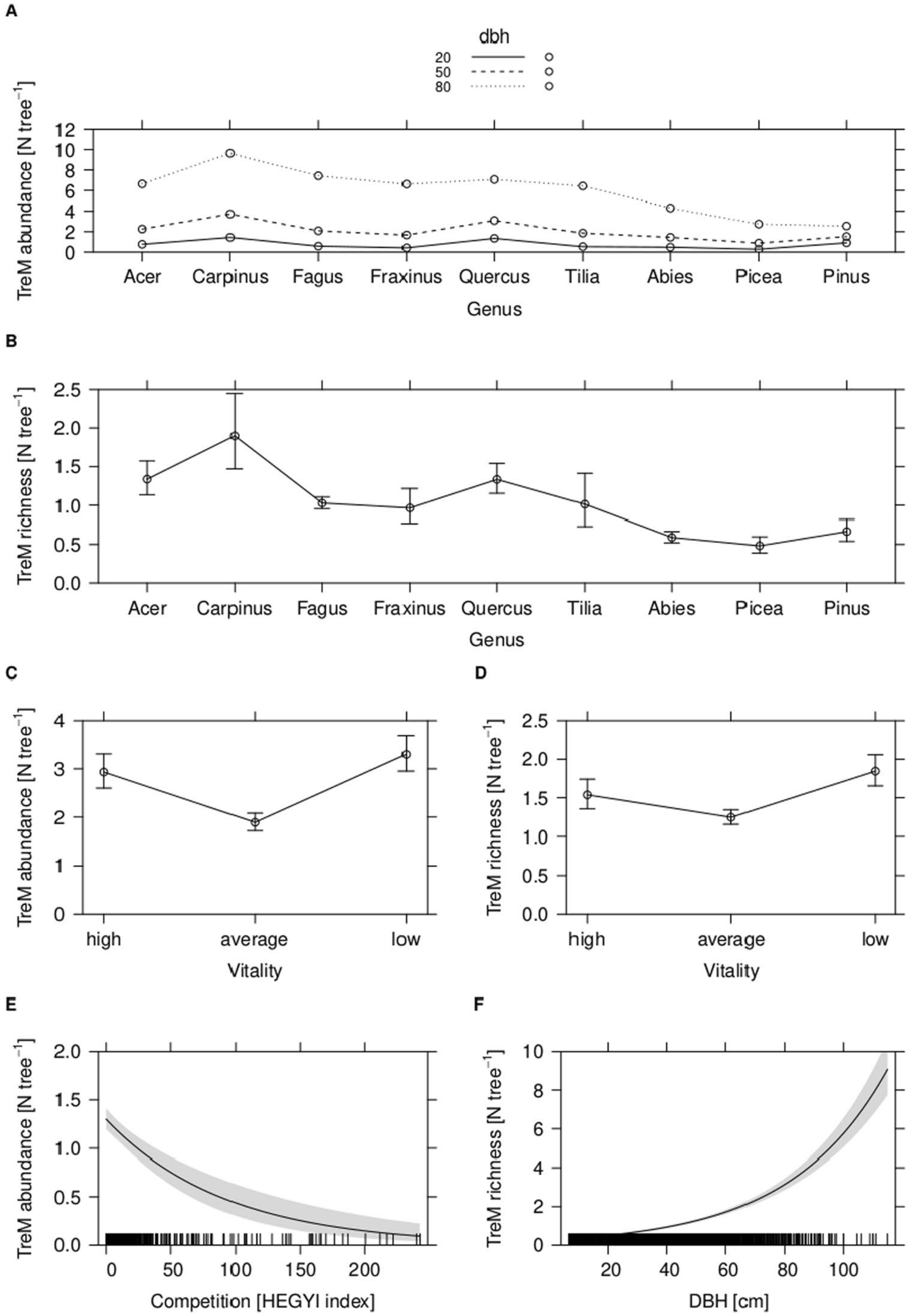


Fig. 7 Predicted effects on TreM abundance (**A**, **C**, **E**) and richness (**B**, **D**, **F**) at the plot level. Whiskers and the gray band refer to the 95%-Confidence-Intervals. Black rugs at the bottom represent the marginal distribution of the predictor

Optimizing TreM provision

Retention elements in temperate European forests under close-to-nature management are typically small (1–10 trees per ha, tree groups < 0.2 ha) compared to those in forest management systems with modified clear-cutting practice, where retention patch sizes may be greater than 1 ha) (Gustafsson et al. 2020). Owing to the relatively small sizes of HTGs inventoried in this study, the increase of TreM and amount of dead wood at the level of the stands, in which HTGs are embedded, is limited. Therefore, it is most important to protect existing structures while also considering factors that promote the future development of desired old-growth structures.

Factors supporting TreM occurrence at the plot level were increasing stand age, growing stock and snag volume as well as decreasing stand density (Fig. 7). Main predictors of TreM occurrence at the single-tree level were species, diameter, vitality and competition (Fig. 6). To provide many and diverse TreMs, forest patches with high levels of growing stock (Johann and Schaich 2016) should be preferentially selected for HTG retention. For the level of standing volume, lower density translates into larger trees, and potentially higher tree vitality (Rohner et al. 2021). Trees of higher vitality provide more TreMs compared to neighboring trees of average vitality (Winter et al. 2014; Großmann et al. 2018). At the same time, trees of low vitality also support high TreM abundance and richness (Fig. 6). Importantly, combinations of trees of different vitality are necessary to provide a variety of microhabitats: *exposed sapwood, twig tangles, fungal fruiting bodies* and *cavities* were more frequently associated with trees of reduced vitality, whereas *crown dead wood* and *concavities* occurred more frequently on trees of high vitality (see Supplementary Material). In addition, practitioners might include snags in HTGs to increase overall TreM abundance and diversity (e.g., Paillet

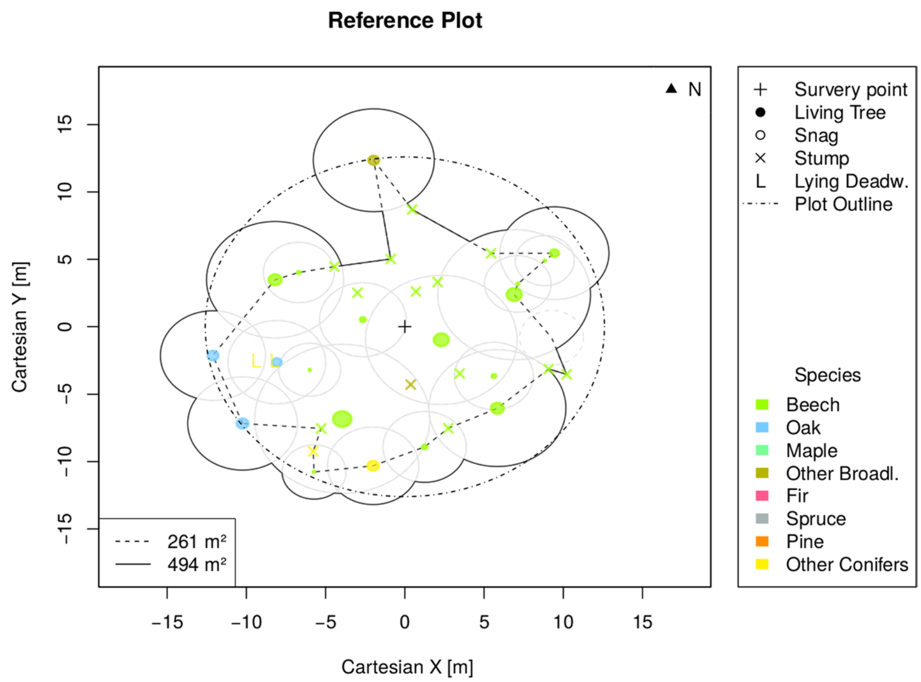


Fig. 8 Example of an inventoried Reference Plot with 12.6 m radius (dot dashed line) plotted in a Cartesian coordinate system. The stem icon's size represents the measured DBH scaled by a factor of 2. The light gray lines depict the calculated crown projection area

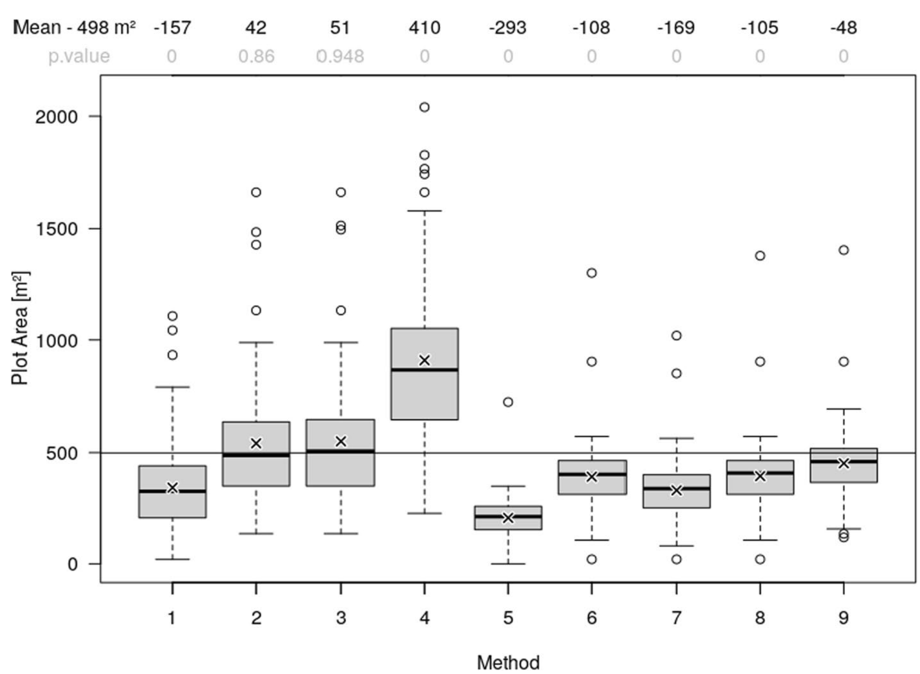


Fig. 9 Calculated areas for methods 1–9 as described above. The horizontal line represents the area of a circle used in classical inventories. The 'x' indicates the mean value for each method. The gray numbers above the boxplots show the *p*-values from a one-sided Wilcoxon-Rank-Sum Test for each method against the circular plot area. The black number refers to the difference of the mean and the circular plot area (498.76 m^2). Within the boxplot, the black line indicates the median, the box shows the interquartile range and the whiskers the 1.5 interquartile range

et al. 2017; Spînu et al. 2022). Regardless of vitality status and species, tree size matters for the provision of TreMs (Paillet et al. 2019). Thus, larger trees should be preferred for retention purposes. Although tree species mixture was not a significant final predictor of TreM occurrence in this study, we recommend including different species when selecting trees for HTGs since other studies found this to be important (Asbeck et al. 2019; Paillet et al. 2019). In addition, the same type of TreM can have different substrate properties on different tree species and thus actually provide different microhabitat conditions. Retaining a diversity of species as habitat trees also spreads the risk of their mortality, as they may respond differently to different types of disturbances.

Conclusion

Our study shows that the systematic retention of HTGs, helped to provide a locally higher occurrence of habitat structures, especially rare TreMs and snags. These effects were observed after short periods of less than 10 yrs (5 yrs on average). They have likely resulted to a larger extent from a) the selection of HTG that were richer in TreMs than the surrounding forest, b) the protection of these trees from harvesting, and c) to a smaller extent also from the temporal development of the structures quantified. Yet, this positive effect on forest structures at the stand scale needs to be confirmed for populations of forest dwelling species that rely on these structures. The small size of retention elements, their high variability and the gradual transition between managed and protected elements within forest stands are challenging for the evaluation of such integrative conservation approaches. It is obvious that the current retention of HTGs, of less than 5% of the area of managed forest stands cannot promote all types of structural elements at the stand scale. While the effectiveness of HTGs may increase with time through their natural maturation and the development of large trees with many and diverse TreMs, the anticipated increase in mortality rates of large trees may counteract this development. This study can serve as baseline to follow the dynamic development of HTGs, especially the TreMs, dead wood, or species related to old-growth structures. Continuing analysis of the differences between HTGs and reference plots can provide important information for payment schemes for nature conservation by contract

Appendix A

Our goal was to inventory the complete range of habitat tree groups (HTGs) which were already retained in forest practice. The HTGs sampled were of irregular shape and varying size (Fig. S10). To quantify characteristics of HTGs of different size in a comparable way on an area bases, we determined the area covered by each HTG. TWe adapted an existing approach to derive a HTG's stand area (see Aleff 2016). Based on the positions of trees and their DBH we estimated crown radii and derived the stands' area as described in the methods section. We tested 9 different possible methods of calculating the areas:

(1) Building the sum of the projection areas (gray solid lines) of **all living trees with DBH > 30 cm** without considering spatial overlap.
(2) Building the sum of the projection areas (gray solid lines) of **all living trees with DBH > 7 cm** without considering spatial overlap.
(3) Building the sum of the projection areas (gray solid lines) of living trees and hypothetical crown projection areas of **snags trees** (gray dashed lines) without considering spatial overlap.
(4) Building the sum of the projection areas (gray solid lines) of living trees and hypothetical crown projection areas of standing dead trees (gray dashed lines) and **stumps** without considering spatial overlap.
(5) Calculating the areas of the polygons connecting the outer **stems** (black dashed line).
(6) Calculating the areas of stem polygons (option 5) plus merged **crown projection areas of living trees**.
(7) Calculating the **crown projection area** of the plot (all crown projection areas merged).
(8) Calculating the stem polygon areas plus merged crown projection areas of living trees (option 7) and **hypothetical crown projection areas of snags**.
(9) Calculating the stem polygon areas plus merged crown projection areas of living trees, and hypothetical crown projection areas of snags and **stumps**.

We applied all of these methods to our reference plots ($N = 94$), which were inventoried based on a circular plot with 12.6 m radius, and an area of 498.76 m^2 (Fig. 8).

This showed that some methods underestimate and others overestimate the plot area compared to the circular area (Fig. 9). Underestimation of the plot area would lead to an overestimation of stand attribute such as stand density or volume and the opposite would happen, if the plot area was overestimated. This becomes problematic when comparing our findings to other studies and inventories. To us, method 6 and method 8 are most realistic, as they represent the projection area of HTGs best by considering the crown projection area as well as the area between the trees. However, both methods underestimated the plot area. Because the standard deviation of method 6 (158 m^2) was lower than that of method 8 (163 m^2), we calculated a correction factor based on the ratio of the true area and the mean area determined with method 6 (390 m^2): 498 m^2/390 m^2 = 1.277.

Appendix B

See Fig. 10 Tables 3, 4, 5, 6, 7, 8, 9, 10 and 11

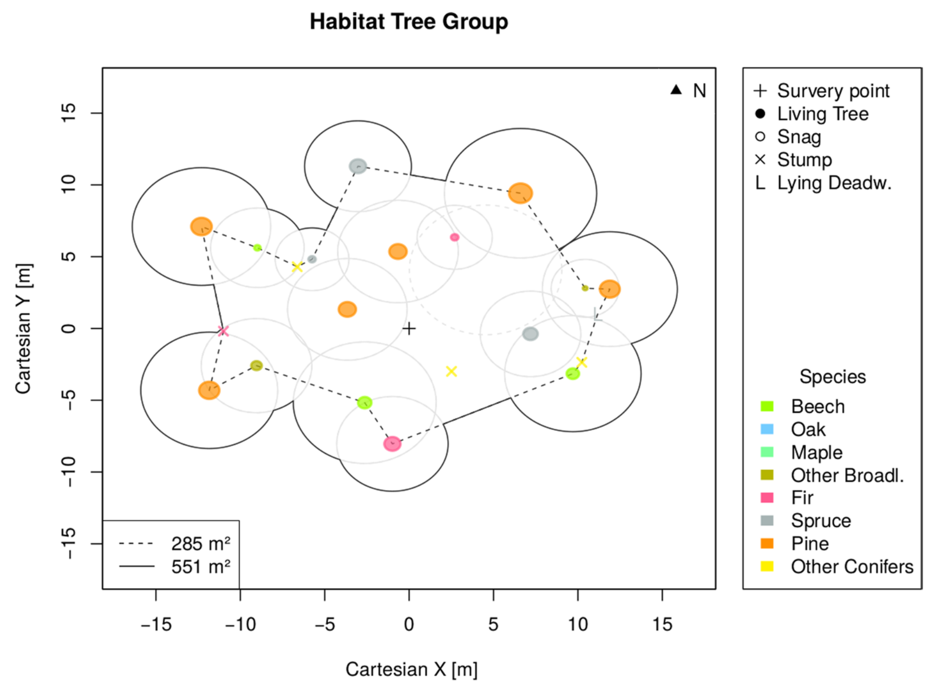


Fig. 10 Inventoried gabitat tree group plotted in a Cartesian coordinate system. The stem icon's size represents the measured DBH scaled by a factor of 2. The light gray lines depict the outline of the calculated crown projection area

Table 3 Catalog of tree-related microhabitats (after Larrieu et al. 2018)

TreM-Form	TreM-Group	TreM
Cavities	Woodpecker breeding cavities	Small, medium-sized, large woodpecker breeding cavities and cavity string
	Rot holes	Trunk base rot hole, trunk rot hole, semi-open trunk rot hole, chimney trunk base rot hole, chimney trunk rot hole, hollow branch
	Insect galleries and bore holes	Insect galleries and bore holes
	Concavities	Dendrotelm (phytotelmata, waterfilled hole), woodpecker foraging excavation, trunk bark-lined concavity, root buttress concavity
Tree injuries and exposed wood	Exposed sapwood only	Bark loss, fire scar, bark shelter, bark pocket
	Exposed sapwood and heartwood	Stem breakage, limb breakage (heartwood exposed), crack, lightning scar, fork split at the intersection
Crown dead wood	Crown dead wood	Dead branches, dead top, remaining broken limb
Excrescenes	Twig tangles	Witch broom, epicormic shoots
	Burrs and cankers	Burr, (decayed) Canker
Fruiting bodies of saproxylic fungi and slime molds	Perennial fungal fruiting bodies (life span > 1y)	Perennial polypore
	Ephemeral fungal fruiting bodies and slime molds	Annual polypore, pulpy agaric, pyrenomycete, myxomycete
Epiphytic, epixylic and parasitic structures	Epiphytic or parasitic crypto- and phanerogams	Bryophytes, foliose and fruticose lichens, ivy and lianas, ferns, mistletoe
	Nests	Vertebrate nest, invertebrate nest
	Microsoils	Bark microsoil, crown microsoil
Fresh exudates	Fresh exudates	Sap run, heavy resinosis

Table 4 Crown diameter = (p0 + p1*DBH)*(1 − exp(− ((DBH)^p2))). Coefficients of the formula to calculate tree crown diameter based on DBH, for details see section. Coefficients were modeled for different tree species based on inventory data

Tree species	Coefficients				Source
	p0	p1	p2	p3	
Fagus sylvatica	2.85739	0.14129	5.696	4.001	(Albrecht et al. 2012)
Picea abies	2.79563	0.07358	5.43234	1.34187	(Albrecht et al. 2012)
Abies alba	2.62495	0.08317	4.61778	1.64686	(Albrecht et al. 2012)
Pseudotsuga menziesii	1.65355	0.0901	1.0	1.9	(Albrecht et al. 2012)
Quercus spec	2.6618	0.1152	8.3381	1.4083	(Döbbeler et al. 2011)
Pinus sylvestris	1.2783	0.11388	8.70522	1.33944	(Döbbeler et al. 2011)
Carpinus betulus	3.002	0.1851	0.000001	1.0	(Döbbeler et al. 2011)
Fraxinus excelsior	17.372	−0.0646	45.371	1.238	(Döbbeler et al. 2011)
Acer spec	2.7916	0.134	2.7198	0.4197	(Döbbeler et al. 2011)
Larix decidua	3.6962	0.0762	21.8046	1.530	(Döbbeler et al. 2011)
Sorbus spec	2.227	0.121	5.332	2.261	(Kahle 2004)

Table 5 AIC values of single predictor models at the single-tree level for TreM abundance and TreM richness. For details see section

Variable	AIC-Value	
	TreM abundance	TreM richness
Hegyi-Index	13.353	91.82
DBH	17.163	12.244
Basal Area	17.583	12.489
Volume	17.712	12.527
Height	17.825	12.306
Layer	18.577	12.601
Species	19.834	13.070
Genus	19.852	13.065
Growth trend	19.887	13.067
Mean Distance	19.991	13.073
Vitality	20.032	13.095
Crownlength	20.062	13.081
Local Basal Area	20.098	13.199
Family	20.323	13.208
Order	20.333	13.206
NULL	20.354	13.242
Class	20.354	13.204
Species-Mingling	20.359	13.244

Table 6 AIC values of single-predictor models at the plot level for TreM abundance and TreM richness. For details see section

Variable	AIC-Value	
	TreM abundance	TreM richness
Snag volume	5.230	1.562
Stand phase	5.233	1.554
Stand volume	5.245	1.578
Basal area	5.247	1.582
Height SD	5.259	1.569
DBH SD	5.262	1.577
Share of conifers	5.267	1.575
Regeneration cover	5.271	1.593
LLT volume	5.272	1.589
LLT abundance	5.272	1.588
Age class	5.273	1.584
Clark & Evans Index	5.274	1.591
Stand layers	5.275	1.592
Stand density	5.275	1.588
Basal area share of oaks	5.275	1.592
NULL	5.276	1.591
Species diversity	5.277	1.585
Crown closure	5.278	1.594
Mean Species Mingling	5.278	1.588
Mixture	5.278	1.588
Species richness	5.281	1.579

Table 7 Variables of the best performing GLMM for TreM abundance and TreM richness at the plot level with Position as Random Effect. The 'X''s indicate which variables were included in which model

Variable	Age Class	Stand Development Phase	Stand Volume[m^3 ha^{-1}]	Snag Volume [m^3 ha^{-1}]	Stand Density [N ha^{-1}]	(1| Position)
TreM abundance	X	X	X	X		X
TreM richness	X	X		X	X	X

Table 8 Variables of the best-performing GLMM for TreM-Abundance and TreM-Richness for living trees with plot position as Random Effect. ":" indicates an interaction between variables

Variable	Genus	DBH [cm]	Vitality	HEGYI	DBH:Genus	(1| Position)
TreM abundance	X	X	X	X	X	X
TreM richness	X	X	X	X		X

Table 9 Mean values from the inventoried habitat tree groups (HTG) and reference plots (Ref) for tree-related microhabitats (TreMs)

Forest Type	Beech Forest			Fir Forest			Overall		
	HTG (*N* = 166)	Ref (*N* = 52)	Sig	HTG (*N* = 160)	Ref (*N* = 42)	Sig	HTG (*N* = 326)	Ref (*N* = 94)	Sig
TreM Diversity [Shannon-Index ha^{-1}]	2.0 (0.6)	1.3 (0.6)	***	1.8 (0.7)	1.4 (0.6)	***	1.9 (0.6)	1.3 (0.6)	***
TreM Richness (Category, max. = 7) [N ha^{-1}]	2.8 (1.2)	1.6 (1.0)	***	2.7 (1.2)	1.7 (1.1)	***	2.8 (1.2)	1.6 (1.0)	***
TreM Richness (TreM, max. = 47) [N ha^{-1}]	11.8 (5.5)	5.3 (3.4)	***	9.7 (5.2)	5.5 (3.0)	***	10.7 (5.4)	5.4 (3.2)	***
TreMs									
Small Woodpecker-breeding Cavities [N ha^{-1}]	8.3 (18.0)	0.3 (1.9)	***	9.9 (50.5)	1.4 (6.4)	*	9.0 (37.3)	0.8 (4.5)	***
Medium-sized Woodpecker-breeding Cavities [N ha^{-1}]	20.3 (36.0)	3.8 (26.0)	***	13.8 (38.1)	1.3 (5.5)	**	17.0 (36.9)	2.7 (19.7)	***
Large Woodpecker-breeding Cavities [N ha^{-1}]	4.1 (11.2)	0.0 (0.0)	***	3.8 (13.0)	0.0 (0.0)	*	3.9 (12.0)	0.0 (0.0)	***
Woodpecker Flute [N ha^{-1}]	5.8 (17.0)	0.7 (5.2)	***	4.0 (15.8)	0.4 (2.5)	n.s	4.9 (16.3)	0.6 (4.2)	***
Trunk Base Rot-hole [N ha^{-1}]	2.8 (7.5)	0.3 (2.5)	**	3.2 (9.0)	1.1 (5.1)	*	3.0 (8.2)	0.7 (3.9)	***
Trunk Rot-hole [N ha^{-1}]	5.7 (16.0)	3.4 (9.8)	n.s	4.2 (11.8)	0.9 (4.1)	*	5.1 (14.3)	2.3 (7.9)	*
Semi-open Trunk Rot-hole [N ha^{-1}]	1.8 (5.6)	0.0 (0.0)	**	2.2 (11.5)	0.1 (0.9)	n.s	2.0 (8.9)	0.1 (0.6)	**
Chimney Trunk Base Rot-hole [N ha^{-1}]	0.6 (6.0)	0.0 (0.0)	n.s	0.0 (0.0)	0.0 (0.0)	n.s	0.3 (4.3)	0.0 (0.0)	n.s
Chimney Trunk Rot-hole [N ha^{-1}]	1.6 (7.6)	0.0 (0.0)	*	0.6 (3.3)	0.1 (0.9)	n.s	1.1 (5.9)	0.1 (0.6)	*
Hollow Branch [N ha^{-1}]	11.4 (33.8)	6.6 (14.2)	n.s	5.0 (12.2)	0.9 (3.6)	*	8.3 (25.8)	4.1 (11.2)	*
Insect Galleries and Boreholes [N ha^{-1}]	26.8 (65.6)	5.5 (17.2)	***	22.1 (35.1)	11.5 (32.2)	**	24.4 (52.6)	8.1 (25.0)	***
Dendrotelm [N ha^{-1}]	3.3 (8.8)	0.3 (2.5)	**	1.1 (6.1)	0.4 (2.5)	n.s	2.2 (7.6)	0.4 (2.5)	**
Woodpecker Foraging Excavation [N ha^{-1}]	31.8 (66.7)	3.5 (16.4)	***	24.2 (57)	7.8 (27.7)	**	27.8 (61.8)	5.4 (22.1)	***
Trunk Bark-lined Concavity [N ha^{-1}]	5.0 (11.5)	1.7 (6.9)	**	1.5 (6.8)	1.0 (6.5)	n.s	3.3 (9.7)	1.4 (6.7)	**
Root-buttress Concavity [N ha^{-1}]	78.8 (100.3)	68.1 (86.1)	n.s	38.6 (48.9)	30.4 (68.2)	n.s	58.9 (81.7)	51.4 (80.5)	n.s
Bark Loss [N ha^{-1}]	50.3 (66.1)	23.8 (40.0)	***	44.2 (68.0)	22.0 (30.0)	*	47.1 (66.6)	23 (35.8)	***
Fire Scar [N ha^{-1}]	0.1 (1.0)	0.0 (0.0)	n.s	0.0 (0.0)	0.0 (0.0)	n.s	0.0 (0.7)	0.0 (0.0)	n.s

Table 9 (continued)

Forest Type	Beech Forest			Fir Forest			Overall		
	HTG (*N* = 166)	Ref (*N* = 52)	Sig	HTG (*N* = 160)	Ref (*N* = 42)	Sig	HTG (*N* = 326)	Ref (*N* = 94)	Sig
Bark Shelter [N ha^{-1}]	32.1 (79.1)	3.4 (10.2)	***	29.4 (88.5)	11.7 (36.7)	*	30.3 (83.2)	7.0 (25.7)	***
Bark Pocket [N ha^{-1}]	18.0 (63.5)	2.3 (7.8)	**	18.9 (67.4)	6.3 (22.6)	n.s	18.2 (64.8)	4.1 (16.2)	***
Stem Breakage [N ha^{-1}]	10.9 (21.3)	12.3 (53.8)	*	12.3 (20.6)	12.5 (32.3)	n.s	11.5 (20.8)	12.4 (45.3)	*
Limb Breakage [N ha^{-1}]	23.1 (37.6)	26.6 (49.1)	n.s	18.1 (37.9)	3.9 (15.8)	***	20.5 (37.5)	16.5 (39.6)	**
Crack [N ha^{-1}]	13.7 (31.7)	1.8 (6.9)	***	4.7 (11.8)	5.1 (14.6)	n.s	9.1 (24.3)	3.2 (11.1)	**
Lightning Scar [N ha^{-1}]	0.2 (1.7)	0.0 (0.0)	n.s	0.0 (0.0)	0.0 (0.0)	ns	0.1 (1.2)	0 (0)	n.s
Fork Split at Insertion [N ha^{-1}]	6.6 (13.5)	3.9 (15.6)	**	4.1 (13.5)	0.4 (2.6)	n.s	5.5 (13.6)	2.4 (11.9)	***
Dead Branches [N ha^{-1}]	68.8 (71.5)	44.7 (53.7)	**	88.1 (131.5)	41.9 (100.6)	***	77.8 (104.9)	43.5 (77.5)	***
Dead Top [N ha^{-1}]	15.7 (37.4)	19.9 (88.6)	**	8.5 (24.3)	4.6 (20.8)	*	12.0 (31.6)	13.1 (67.8)	***
Remaining Broken Limb [N ha^{-1}]	21.7 (37.8)	11.5 (28.7)	***	8 (20.9)	3.5 (11.5)	n.s	15 (31.4)	8 (23)	***
Whitch Broom [N ha^{-1}]	1.9 (16.5)	1.1 (8)	n.s	3.1 (11)	1.5 (5.5)	n.s	2.4 (14)	1.3 (6.9)	n.s
Epicormic Shoots [N ha^{-1}]	10.7 (31.9)	4.0 (11.9)	*	13.4 (34.6)	8.0 (18.0)	n.s	11.9 (33.0)	5.7 (14.9)	n.s
Burr [Nha^{-1}]	0.7 (3.0)	0.6 (3.1)	n.s	1.3 (6.2)	1.2 (8.0)	n.s	0.9 (4.8)	0.9 (5.8)	n.s
Canker [Nha^{-1}]	2.4 (10.0)	4.8 (35.2)	*	1.6 (5.4)	0.5 (3.4)	n.s	2.0 (8.0)	2.9 (26.3)	**
Perennial Polypore [N ha^{-1}]	23.6 (96.7)	1 (7.3)	***	44.9 (111)	7.1 (32.2)	*	33.5 (103.6)	3.7 (22.1)	***
Annual Polypore [N ha^{-1}]	7.9 (36.1)	3.2 (16.5)	n.s	5.4 (25.2)	1.5 (7.7)	n.s	6.6 (31)	2.4 (13.3)	n.s
Pulpy Agaric [N ha^{-1}]	5.8 (25.7)	0.0 (0.0)	*	4.1 (24.4)	2.5 (9.6)	n.s	4.9 (24.9)	1.1 (6.5)	n.s
Large Pyrenomycete [N ha^{-1}]	0.1 (1.0)	1.2 (4.9)	n.s	0.4 (2.3)	1.5 (9.7)	n.s	0.2 (1.8)	1.3 (7.4)	n.s
Myxomycetes [N ha^{-1}]	0.5 (4.0)	0.3 (2.1)	n.s	0.4 (3.4)	0.0 (0.0)	n.s	0.5 (3.7)	0.2 (1.5)	n.s
Bryophytes [N ha^{-1}]	21.2 (34.1)	22.5 (44.3)	n.s	42.6 (58.7)	24.4 (41.4)	*	31.6 (48.6)	23.4 (42.8)	**
Foliose and Fructiose Lichens [N ha^{-1}]	18.9 (36.7)	19.8 (43.7)	n.s	15.7 (36.4)	10.3 (26.7)	n.s	17.1 (36.3)	15.6 (37.3)	n.s
Ivy and Lianas [N ha^{-1}]	2.4 (9.1)	6 (25.3)	n.s	2.3 (9.4)	0 (0)	n.s	2.4 (9.2)	3.4 (19)	n.s
Ferns [N ha^{-1}]	0.3 (2.9)	0.3 (2.5)	n.s	0.1 (1.3)	0.2 (1.4)	n.s	0.2 (2.3)	0.3 (2.1)	n.s
Mistletoe [N ha^{-1}]	0.2 (1.9)	14.9 (105.1)	n.s	40.5 (116.6)	42.8 (149.6)	n.s	20.7 (85.4)	27.2 (126.7)	n.s
Vertebrate Nest [N ha^{-1}]	4.9 (18.1)	2 (6.3)	n.s	4.4 (11.2)	7.7 (13.9)	n.s	4.6 (15)	4.5 (10.7)	n.s
Invertebrate Nest [N ha^{-1}]	0.5 (5.0)	0.0 (0.0)	n.s	0.2 (2.5)	0.0 (0.0)	n.s	0.4 (3.9)	0.0 (0.0)	n.s
Bark Microsoil [N ha^{-1}]	1.1 (4.5)	0.3 (2.1)	n.s	2.2 (11.6)	0.9 (4.2)	n.s	1.6 (8.6)	0.6 (3.2)	n.s
Crown Microsoil [N ha^{-1}]	1.1 (4.5)	0.3 (2.1)	n.s	2.2 (11.6)	0.9 (4.2)	n.s	1.6 (8.6)	0.6 (3.2)	n.s
Sap Run [N ha^{-1}]	1.0 (4.8)	0.0 (0.0)	*	0.7 (3.3)	0.4 (2.6)	n.s	0.9 (4.1)	0.2 (1.7)	*
Heavy Resinosis [N ha^{-1}]	0.0 (0.4)	4.7 (18.2)	***	6.0 (16.9)	7.7 (20.2)	n.s	2.9 (12.1)	6.0 (19.1)	n.s

Overall results and results for beech and fir forest are provided. P-values refer to results from Wilcoxon-Rank-Sum-Tests between HTG and reference plots (n.s. = $p > 0.05$; * = $p \leq 0.05$; ** = $p \leq 0.01$; *** = $p \leq 0.001$)

Table 10 Overview of dead wood volumes in Strict Forest Reserve of Baden-Württemberg, Germany for beech-broadleaf and coniferous forest types

Strict Forest Reserve	Forest type	Inventory Year	Dead wood volume [m^3 ha^{-1}]			Source
			Snags	Downed	Total	
Zweribach	Beech-broadleaf	1999	21	42	63	(Keller and Riedel 2000)
Conventwald	Beech-broadleaf	1995	48	31	79	(Weber 2004)
Kohltal	Beech-broadleaf	2004	31	20	51	(Hauschuld 2007)
Rabensteig	Beech-broadleaf	1999	–	–	13	(Hüttl 2002)
Grubenhau	Beech-broadleaf	1986	51	91	142	(Labudda 1999a)
Scheibenfelsen	Beech-broadleaf	1998	15	11	26	(Abel and Riedel 2002)
Klebwald	Beech-broadleaf	2001	30	66	96	(Nowack 2005a)
Teufelsries	Spruce-coniferous	1995	14	61	75	(Kanke and Pisoke 1999)
Birkenkopf	Beech-broadleaf	1994	2	8	10	(Labudda 1999b)
Kesselgraben	Beech-broadleaf	1996	5	32	37	(Hoffmann and Ahrens 2004)
Buigen	Beech-broadleaf	1997	2	4	6	(Hüttl 2007)
Altspöck	Spruce-coniferous	2000	6	5	11	(Rudmann and Wolf 2007)
Eiberg	Spruce-coniferous	1998	6	11	17	(Ullrich 2000)
Bärlochkar	Spruce	1999	16	8	24	(Becker et al. 2007a)
Zimmeracker	Fir-coniferous	2001	39	93	132	(Nowack 2005b)
Stürmlesloch	Spruce-coniferous	2002	35	57	92	(Hüttl et al. 2007)
Röttlerwald	Beech-broadleaf	2001	–	–	151	(Wolf 2006)
Mietholz	Beech-broadleaf	2002	84	51	135	(Rudmann and Wolf 2006a)
Burghard	Beech-broadleaf	2004	8	45	53	(Rudmann and Wolf 2006b)
Ofenberg	Beech-broadleaf	2002	17	120	137	(Ullrich 2006)
Donntal	Beech-broadleaf	1998	9	14	23	(Becker et al. 2007b)
Stöffelberg-Pfullinger Berg	Beech-broadleaf	2004	3	9	12	(Ullrich 2007)
Sommerberg	Beech-broadleaf	1995	5	16	21	(Weber 1999)
Pfannenberg	Beech-broadleaf	1994	17	40	57	(Seiler 2001)
Hoher Ochsenkopf	Spruce-coniferous	1995	138	54	192	(Ahrens 2002)
Wilder See—Hornisgrinde	Spruce-coniferous	1996	126	39	165	(Wohlfahrt 2001)
	Mean values					*Sources [N]*
	Beech-broadleaf	1998	22	38	62	18
	Coniferous	1998	49	34	82	8
	total	**1998**	**30**	**39**	**70**	**26**

Table 11 Mean dead wood volume in the forests of Baden-Württemberg, Germany, according to the National Forest Inventory (Kändler et al. 2004; Thünen Institut 2020)

	Mean volume [m^3 ha^{-1}]	
	2002	2012
Snags	3	4.6
Downed dead wood	10.2	14.2
Stumps	5.7	9.7
other	0.2	0.2
Total	19.1	28.8

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Declarations

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