Forest Ecology and Management 432 (2019) 400–408

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Predicting abundance and diversity of tree-related microhabitats in Central European montane forests from common forest attributes

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ABSTRACT

The continued provision of old-growth elements in forest landscapes is a critical factor for biodiversity conservation in Central Europe. A well-established method for predicting the potential of forests to maintain biodiversity is to quantify tree-related microhabitat structures (TreMs). Our aim was to predict the TreM abundance and diversity for collectives of TreM-bearing trees; here 15 large trees per plot that were preselected by the largest crown sizes using remote sensing information. TreMs were inventoried on 2085 living trees across 139 plots (each 1 ha) in montane forests of the Black Forest, southwest Germany according to a detailed catalogue comprising 64 different TreM structures. We tested the influence of forest management, forest cover in the surrounding landscape (25 km radius), forest type, the number of standing dead trees, altitude and mean diameter at breast height (DBH) on the abundance and diversity of TreMs on living trees. All plots are managed or have been recently (20–40 yrs) abandoned from management. Generalized linear models (GLM) were used to identify the drivers of abundance and diversity of TreMs. The abundance of TreMs borne by the 15 large trees per plot is greater on plots located at higher altitudes. Increasing mean DBH leads to significantly higher abundance and diversity of TreMs. Groups of TreM-bearing trees in monospecific coniferous forests have the highest abundance but those in mixed-coniferous-broadleaved forests have the greatest diversity of TreMs. The occurrences of 11 out of 64 specific TreM structures were related to forest management, forest type, altitude or mean DBH. Large branch holes and buttress cavities increased with mean DBH and were found more frequently in mixed-coniferous-broadleaved forests than in the other forest types. The abundance of epiphytes on TreM bearing trees increased with altitude. This study demonstrates that the average abundance and diversity of TreMs can be predicted with readily available forest attributes. Additionally, the occurrence of specific TreMs could be described with the variation in these selected forest attributes.

1. Introduction

The continued provision and retention of old-growth elements in managed forests has been identified as a critical factor for biodiversity conservation in Central Europe (Fedrowitz et al., 2014; Gustafsson et al., 2012; Mori et al., 2017; Roberge et al., 2015). Many species, in particular less mobile ones, are fully dependent on the maintenance or creation of specific structural elements exclusively found in old-growth forests (Bauhus et al., 2009). Besides the enrichment of forests with deadwood, the retention of future old-growth elements in the forest landscape focuses on habitat trees that provide relevant key structures for the conservation of forest biodiversity (Bouget et al., 2014a; Larrieu and Cabanettes, 2012; Michel and Winter, 2009; Winter and Möller, 2008). Habitat trees are usually large, old, dead or living trees bearing different types of TreM structures (Bütler et al., 2013). Several concepts for retention measures have been implemented recently. Most of these retention concepts aim to establish a network of old-growth structures within managed forests through the conservation of habitat trees (see e.g. the old - and deadwood concept in south-west Germany by (ForstBW, 2015). Usually habitat trees are left to their natural development, preferably in groups, to form biodiversity islands within a matrix of managed forest stands. This approach aims at delivering a greater availability and continuity of tree level habitats for all taxa depending on them. In several of these retention concepts, it remains to some degree unclear how to identify and locate the most valuable habitat trees worth retaining. One effective approach to identify them is through the inventory of TreMs, as for instance woodpecker cavities, crown deadwood or epiphytes (Bütler et al., 2013).

There is evidence that large trees provide a great share of TreMs and that tree species differ in the quantity and quality of TreMs provided at the tree scale (Michel and Winter, 2009; Paillet et al., 2017; Vuidot et al., 2011; Winter and Möller, 2008). As a forest stand is a collection of trees, the abundance and diversity of TreMs is thought to depend in addition to tree properties (diameter at breast height (DBH), species identity) also on stand characteristics (for instance structural complexity, forest type), which has been analyzed partly in earlier studies (Larrieu et al., 2014; Winter et al., 2015). The relationships between some specific species (or taxa) or TreMs, with different forest attributes

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https://doi.org/10.1016/j.foreco.2018.09.043
Received 6 June 2018; Received in revised form 18 September 2018; Accepted 22 September 2018

and characteristics is comparably well described. This includes, for example, lichens and their relation to forest maturity and forest cover (Baker et al., 2016b; Scheidegger and Stofer, 2015), parasitic wasps and their dependence on dead wood of specific tree species (Ulyshen et al., 2011) as well as saproxylic and ground-active beetles and their dependence on forest cover and open areas (Baker et al., 2016a; Bouget et al., 2014a). Thus, several TreMs as well as biotic agents possibly creating them might depend on specific conditions influenced by the proportion of forest cover in the surrounding landscape. As silvicultural management occurs typically at the stand scale, we analyzed the influence of management on this scale. The effect of management on TreM abundance has been analyzed, but the results remain inconclusive or depend on more detailed factors than management type in general (Johann and Schaich, 2016; Larrieu et al., 2012; Paillet et al., 2017; Vuidot et al., 2011). This indicates that it has not yet been systematically analyzed how the average TreM frequency and composition respond to forest attributes at spatial scales larger than stand-units. Here, we use a unique experimental design that aims to detect these relationships. This additional information on TreM development and persistence is urgently needed for evidence-based habitat tree selection, as so far there is just one approach of modelling the development of TreMs (Courbaud et al., 2017).

Hence, our specific research aims were to identify driving factors at the stand scale that allow the prediction of the average abundance and diversity of TreM structures for a collective of 15 large trees per hectare in montane forests. We hypothesized that:

- the abundance and diversity of TreMs can be explained by environmental factors including the degree of forest cover of the surrounding landscape (25 km radius), structural complexity expressed as standing dead trees that form canopy gaps, and altitude as a proxy of site conditions,
- the abundance and diversity of TreMs is higher in mixed conifer-broadleaved than in conifer forests and increases with time indicated by mean DBH in later stand developmental phases of managed stands,
- uneven-aged forests provide more TreMs than even-aged ones as well as strictly protected forests more than managed ones.

Moreover, we aimed at detecting the influences of the mentioned forest attributes on the occurrence of specific types of TreMs and their composition, which refers to the assemblage of TreMs for the collectives of 15 trees.

2. Methods

2.1. Research area and plot selection

The research area and plot selection took place within the project "Conservation of forest biodiversity in multiple-use landscapes" (ConFoBi, https://confobi.uni-freiburg.de/). Our research plots are distributed across the Black Forest in the federal state of Baden-Württemberg, south-west Germany (Fig. A.1). In total, we inventoried 139 plots of 1 ha size in temperate montane forests, dominated by Norway spruce *(Picea abies),* European beech (*Fagus sylvatica)* and silver fir (*Abies alba)*. All plots are located above 500 m altitude; the highest plots are around 1400 m above sea level (Tab. A.1). All plots are located in public forests.

The study design comprises a landscape and forest structure gradient. The landscape gradient refers to three categories of forest cover within a 25 km radius around the center of each plot: < 50%, 50–75% and > 75% forest coverage estimated by GIS raster data (state agency of spatial information and rural development of Baden-Württemberg (LGL)). The forest structure gradient refers to the number of standing dead trees per ha ranging from 0 to 21 per hectare. The plots were grouped by the number of standing dead trees (0, 1–9 and 10 or more), which were regarded as a surrogate for structural diversity due to the fact that they form small to large canopy gaps indicating horizontal structural heterogeneity (Aakala et al., 2008; Franklin and Van Pelt, 2004; McElhinny et al., 2005). Standing dead trees were identified by stereo photo-viewer technique. The nine possible combinations of forest cover and stand structure classes contained similar numbers of plots, first 135 plots were designated, but after initial inventory, several had to be moved. Still, the data of the additional plots was considered valuable and included in the analysis (N = 139). The plots do not contain forest roads, buildings and waterbodies and their maximum average slope is 35°.

Additional information about management of the study plots was derived from official forest inventory data provided by the state forest enterprise. Since we exclusively worked in state forests, we used this information that is more relevant to the stand-level than NFI data. Based on these data, we classified the plots into 'even-aged' (102 plots), 'uneven-aged' (17 plots), and 'mixed management' forests (14 plots) as well as 'strictly protected' forests (6 plots). The time since the last harvesting and management activities in the strictly protected forests ranges from 20 to 40 years. The category 'mixed management' applies to plots composed of multiple stands differing in the way they are managed (uneven- and even-aged management on spatially separated sub-units).

We identified three forest types within the research area from the inventory data: monospecific coniferous stands (7 plots) which are pure spruce stands. Mixed coniferous stands consisting of two or more coniferous species (50 plots) which are mainly spruce (*Picea abies*) mixed with silver fir (*Abies alba*), scots pine (*Pinus sylvestris*) or Douglas fir (*Pseudotsuga menziesii*). Lastly, mixed-coniferous-broadleaved forests (82 plots), where beech (*Fagus sylvatica*) is the main broadleaved species. However, this forest inventory information is partially based on estimates and may be up to 10 years old and therefore does not fully represent the real situation in the specific plots.

2.2. Inventory technique and data collection

We selected the 15 large trees per plot according to the largest crown sizes. The selection of sample trees followed a stepwise approach. First, we automatically delineated individual tree crowns of all trees in all 139 plots using the TreeVis software (Weinacker et al., 2004). The data basis for this procedure was a digital surface model (DSM) photogrammetrically generated from aerial images (40 cm ground sampling distance) and a digital terrain model (DTM) based on LIDAR flights. Thereafter, we identified the 15 trees per plot with the largest delineated crown areas to focus on trees with large DBH. The strong relationship between crown size and DBH has been tested at larges scale and proven to be significant (Jucker et al., 2017), also in our data set (see Tab. A.2 and Fig. A.2). In case we did not inventory the trees with the largest DBH in absolute terms, the possible changes in the results should be marginal as we summarized the mean DBH of the collectives. This procedure yielded a sample group of 2085 living trees in total (15 × 139).

The sample size of 15 trees is derived from the so called "*old- and dead wood concept*" that is applied to all state forests in the federal state of Baden-Württemberg (ForstBW, 2015). In this concept retention elements in the form of one group of 15 habitat trees selected for every three hectares is included. The sample trees were selected in order to gain an empirical base for analyzing the abundance and diversity of TreMs for these groups of trees. By selecting 15 large trees, we assumed additionally to capture most of the variation of TreMs in the plots.

A reference typology has been published recently to standardize TreM records (Larrieu et al., 2018). However, since our field records' were done before its publication, we used the catalogue designed for the EFI integrate + network (Kraus et al., 2016). This catalogue includes in total 64 TreMs that are grouped in the following eight categories (for detailed information as minimum sizes to be recorded see

Tab. A.3):

- Cavities: Woodpecker cavities, trunk and mould cavities, branch holes, dendrotelms as well as insect galleries and bore holes;
- Injuries and wounds: bark loss or exposed sapwood, exposed heartwood or trunk and crown breakage, cracks and scars
- Bark: space between bark and sapwood forming a shelter or pocket, coarse structure
- Deadwood: dead branches and limbs or crown deadwood
- Deformation and growth form: root buttress cavities, witches broom, cankers and burrs
- Epiphytes: fruiting bodies of fungi, myxomycetes, epiphytic crypto- and phanerogams
- Nests: nests of vertebrates and invertebrates
- Other: sap and resin run, micro soil

To locate the pre-selected sample trees in the field, we used a Garmin GPS tracker. For every sample tree, we measured and inventoried DBH, tree species and the TreMs. TreMs in the upper parts of trees including canopy branches were identified with binoculars. In order to prevent an observer effect (Paillet et al., 2015), all inventories were carried out by the same team of observers (T.A., F. Hauck, J. Großmann). Fieldwork was carried out in leafless and snow free periods between November 2016 and May 2017.

2.3. Statistical analysis

All statistical modelling was carried out with the R software package version 3.3.2 (R Core Team, 2016).

We analysed the sample coverage of TreMs of the 15 large trees per plot using the rarefaction approach (Hsieh et al., 2016), which includes an assessment of the sample completeness. To evaluate whether we captured the majority of the TreMs present per plot by selecting 15 trees, we analysed the TreMs found using the estimateD function in the iNext package (Hsieh et al., 2016).

Prior to model set-up we checked collinearities between the continuous predictors (Fig. A.3) with a correlation matrix using corrplot package (Wei et al., 2017) and the corrplot function. We checked correlations between categorical variables using Fisher's exact test with fisher.test function. There are no significant correlations between the categorical variables (Forest type ~ Management type, $p = 0.051$; Forest type ~ forest cover category, $p = 0.391$; Management type ~ forest cover category, $p = 0.389$).

At the plot scale, generalized linear regression models (GLM) were used to analyze the relationship between the response variables "average TreM abundance" as well as "TreM diversity" and the predictor variables *forest cover category, number of standing dead trees, management type, forest type,* and *altitude at plot level* and *mean DBH* of the 15 inventoried trees. Snags were used as continuous variable including the exact number per hectare. We did not include average tree age in the model because this information was not available for uneven-aged stands. Thus, we used mean DBH of the 15 inventoried trees as an indicator of stand development phase instead of stand age. The response variables represent count data, thus generalized models were used instead of simple linear regressions. Since both the predictor and the response variable were aggregated and applied at the plot (or group) level, autocorrelation between trees does not need to be considered in the models (Hurlbert, 1984). Thus, generalized linear models are preferred over generalized mixed models with random plot effects. We included interaction effects between DBH and the categorical variables forest cover category, management and forest type as well as altitude. In addition, we tested possible interactions of forest type with altitude. To find the best models we performed a backwards predictor selection, using step function. Selection criteria for the most suitable models are Akaike's information criterion (AIC), (Dormann, 2013) as well as distributions of residuals.

The TreM abundance per group of 15 trees was analyzed using the glm.nb function of the MASS package. The diversity of TreMs represents the sum of different TreM types per group of the inventoried 15 trees. We performed the analysis with the glm function using a Poisson distribution. To test the fit of the residuals as well as possible overdispersion of both models, the DHARMa package was used (Hartig, 2018).

Model 1: TreM abundance of 15 large trees

$$\text{TreM abundance}_{\text{per collective}} \sim \text{Mean DBH} * (\text{Forest cover category}|\text{Management type}|\text{Forest type}|\text{Altitude}) + \text{Altitude} * \text{Forest type} + \text{Number of standing dead trees}$$

Model 2: TreM diversity of 15 large trees

$$\text{TreM diversity}_{\text{per collective}} \sim \text{Mean DBH} * (\text{Forest cover category}|\text{Management type}|\text{Forest type}|\text{Altitude}) + \text{Altitude} * \text{Forest type} + \text{Number of standing dead trees}$$

Where * refers to interaction effects and | refers to "or", thus second order interactions between mean DBH and forest cover category, management type and forest type as well as altitude were included. In order to show the relative strengths of the effects we scaled the continuous predictors.

We tested the explanatory variables in the final models for collinearity with the generalized variance inflation factor (GVIF) using the vif function of the car package (Fox, 2018).

To test the validity of the models for prediction purposes, which is important for their application in actual forest management, we performed a cross validation with both models. The cross validation was performed by randomly splitting the data in two independent data sets (90% training, 10% test). To compare the results, we calculated the root mean square error (RMSE) and RMSE% for each data set and model and considered the residual plots of the test data.

To analyze the effects of *forest cover category, number of standing dead trees, management type, forest type, altitude* as well as *mean DBH* on occurrences of specific TreM types per plot, we used a statistical tool of the multivariate family. Multivariate models that can predict species abundances for different treatments (Wang et al., 2012) have recently been established in ecology. An adaptation of this tool to the current research question makes it possible to test the effects of the mentioned variables on the assemblage of the full set of TreMs as well as on the occurrence of specific TreMs per plot. An additional advantage of this approach is that correlations between TreMs are taken into account instead of performing the tests separately for each TreM, which would possibly result in detecting random significances. We used this model based approach that has been developed into the Mvabund package (David et al., 2017). The summary.manyglm function returns a summary of the multivariate terms in the model; additionally it displays univariate statistics that indicate for which specific dependent variables significances can be found.

3. Results

3.1. Raw inventory data at tree level

This data gives a general overview of the empirical raw data from the inventory summarized for the present tree species. At the level of individual trees, broadleaved species supplied both more and more diverse TreMs than conifers. There was no difference between Norway spruce (*Picea abies*) and silver fir (*Abies alba*) in abundance and diversity of TreMs (Table 1) despite a difference in mean DBH between the two species.

Table 1
Number of sampled trees per species, their share of the sample (N = 2085), average DBH per species, altitude and abundance and diversity of TreMs per tree and the respective standard deviation (SD).

			Mean (SD)			
Species	N	%	DBH (cm)	Altitude (m)	TreM abundance	TreM diversity
Picea abies	857	41.1	53.5 (13.5)	943 (174)	2.5 (2.6)	1.6 (1.1)
Fagus sylvatica	466	22.4	51.5 (15.0)	814 (192)	3.6 (3.3)	2.6 (2.0)
Abies alba	404	19.4	64.7 (16.2)	863 (147)	2.8 (2.8)	1.8 (1.2)
Pinus sylvestris	132	6.3	50.5 (9.8)	815 (118)	1.5 (1.7)	1.1 (1.1)
Pseudotsuga menziesii	92	4.4	66.1 (14.0)	742 (168)	1.2 (1.8)	0.9 (0.9)
Acer pseudoplatanus	49	2.4	44.0 (14.4)	907 (269)	2.9 (2.4)	2.6 (1.8)
Larix decidua	28	1.3	52.4 (9.8)	815 (197)	1.4 (1.3)	1.4 (1.2)
Fraxinus excelsior	26	1.2	40.5 (14.1)	741 (119)	1.6 (1.3)	1.5 (1.2)
Other species[*]	31	1.5	36.3 (16.0)	758 (47)	1.7 (1.6)	1.5 (1.3)
Total	2085	100	51.5 (13.6)	822 (159)	2.2 (2.1)	1.7 (1.3)

* Quercus petraea, Betula spp., Alnus glutinosa, Acer platanoides, Salix spp., Abies grandis, Ulmus glabra, Prunus avium, Tilia cordata, Populus tremula, Tilia platyphyllos.

3.2. Average TreM abundance and diversity

The rarefaction analysis showed that we found on average a sample cover of 81.1% per plot. Thus, by inventorying 15 large trees per hectare we captured most of the estimated maximum of TreMs.

The results from the backwards stepwise predictor selection of the generalized linear models are shown in Table 2.

The variance explained by these models for TreM abundance is 48% and for diversity 39%. The test for the generalized variance inflation factor showed clearly a non-collinearity of the predictors in the final models (Tab. A.4).

Forest type had a strong influence on TreM abundance and diversity. Pure spruce plots provided a higher abundance of TreMs than the other two forest types. In plots of the mixed-coniferous-broadleaved forest type, a higher abundance of TreMs was predicted than in mixed coniferous plots (Fig. 1a). The influence of forest types on the diversity of TreMs was different from the pattern observed for TreM abundance. Here, mixed-coniferous-broadleaved forests had a greater diversity of TreMs than the other two types (Fig. 1b). For both, abundance and diversity, the comparison between the different forest types stays constant when comparing identical DBH intervals (Fig. 1). We tested the influence of the most abundant TreM on this relationship by excluding it from the abundance model. When removing small buttress cavities (GR11, N = 1396), the relationship with the forest types changed and mixed-coniferous-broadleaved had the highest abundance of TreMs (Fig. A.4).

The abundance and diversity of TreMs increased significantly ($p < 0.001$) with increasing mean DBH (Fig. 2). The abundance of TreM structures reached more than 80 in collectives with a mean DBH of 80 cm. TreM diversity reached up to 16 different types at a mean DBH of 80 cm.

Table 2
Generalized linear model results for prediction of abundance and diversity of TreMs of 15 large trees per plot after stepwise backward predictor selection using scaled predictors.

Variable	Estimate	SE	p	Sign
TreM abundance model[a]				
Intercept	3.4235	0.0747	< 2e−16	***
Mixed-coniferous-broadleaved	0.3406	0.0714	1.81e−06	***
Pure-coniferous	0.414	0.1592	0.00933	**
Altitude	0.1052	0.0358	0.00331	**
Mean DBH	0.3119	0.0336	< 2e−16	***
TreM diversity model[b]				
Intercept	2.0804	0.0497	< 2e−16	***
Mixed-coniferous-broadleaved	0.3675	0.0589	4.51e−10	***
Pure-coniferous	0.0654	0.1432	0.648	
Mean DBH	0.0190	0.0028	5.81e−12	***

[a] GLM with negative binominal distribution.
[b] GLM with Poisson distribution.

Likewise the abundance of TreMs increased significantly ($p < 0.01$) with increasing altitude (Fig. 3). However, the altitude had no significant effect on the diversity of TreMs.

We observed no effect of forest cover as well as no relationship between the number of standing dead trees on the abundance and diversity of TreMs of the groups of inventoried trees. The four management categories, even-aged, uneven-aged, mixed management as well as strict protection were not selected in the final TreM abundance and diversity models, when performing a stepwise backward model selection. Moreover, the included interaction terms were dropped after the model selection.

3.2.1. Testing of models for prediction

The training data consisted of 126 plots and the independent test data of 13 plots. Our results indicated that the models could be applied to other data sets that are within the same data range (Table 3). For both abundance and diversity, the test data show a higher RMSE than the training data. This indicates that the model based on a 90% training data set does not fit as well to a 10% test data set in comparison to the training data. The difference between test and training data RMSE(%) indicates that the models for both abundance and diversity have a larger error in the test data. However, as the residual plots (Fig. A.5) indicate that the training data fits well to the test data set; we assume that the error difference is within acceptable limits.

3.3. Analysing the composition and occurrence of specific TreMs

Several of the predictor variables were significantly related to the composition and occurrence of TreMs, indicated by results of the multivariate model. Forest type had a significant effect on the composition of TreMs ($p = 0.003$), likewise the mean DBH ($p = 0.001$), altitude ($p = 0.001$) and the number of standing dead trees ($p = 0.027$). Strict protection ($p = 0.003$) and uneven-aged management ($p = 0.01$) showed a significant effect on the composition compared to even-aged management. The mixed management type as well as the percentage of forest cover surrounding the plots showed no influence on TreM composition in the multivariate analysis.

The modelled changes in the overall TreM composition do not include information on the direction of change in reference to the predictor variables. In contrast to that, when including univariate results, we were able to identify four predictors that explained the average abundance of 11 specific TreM types (Table 4) within the 15 large trees per plot. Several occurrences of TreMs increase in mixed-coniferous-broadleaved stands compared to mixed-coniferous and pure coniferous

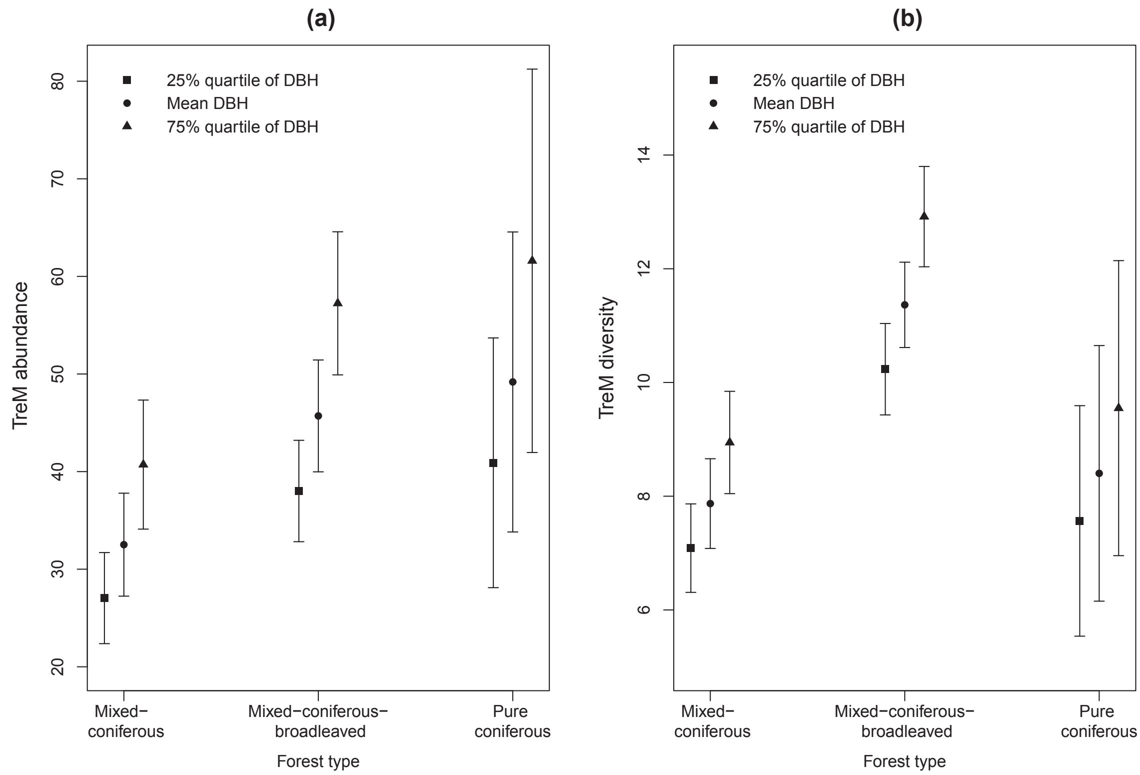

Fig. 1. Effect sizes from the modelled influence of the forest type in relation to different DBH intervals (25% quartile: 48.85 cm, mean: 55.28 cm, 75% quartile: 61.1 cm) on (a) the abundance and (b) the diversity of TreMs of 15 large trees per plot with a 95% confidence interval. In case of abundance, the altitude is kept at the mean for prediction.

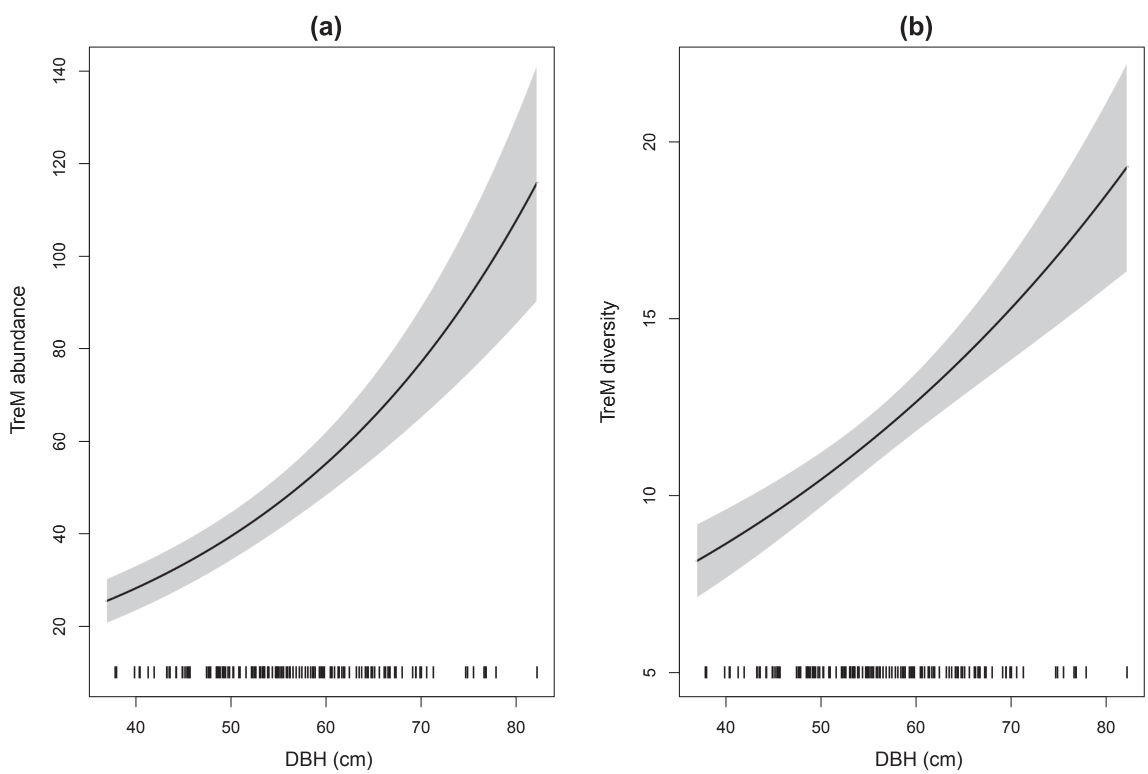

Fig. 2. Effect sizes from the modelled influence of mean DBH of the 15 inventoried trees on (a) the abundance and (b) the diversity of TreMs with a 95% confidence interval indicated by the grey bands, the rug plot at the bottom shows the marginal distribution of the numeric predictor.

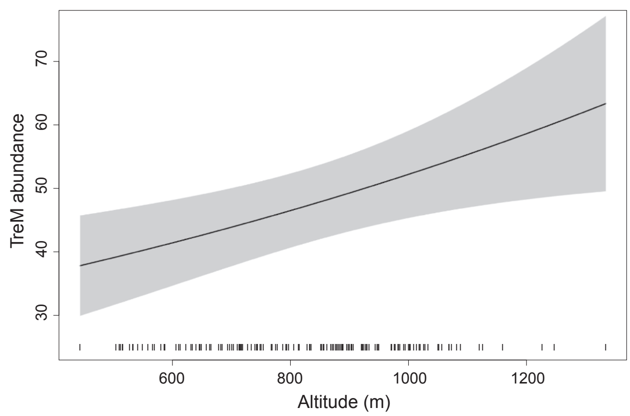

Fig. 3. Effect size from the modelled influence of the altitude of the plot centres on the abundance of TreMs with a 95% confidence interval indicated by the grey band, the rug plot at the bottom shows the marginal distribution of the numeric predictor.

Table 3
RMSE(%) comparison of test and training data for cross validation results from generalized linear models for TreM abundance and diversity.

Model and data set	RMSE	RMSE%
Abundance - training	16.3	39.9
Abundance - test	19.8	46.7
Diversity - training	3.3	32.2
Diversity - test	2.5	23.9

stands or in relation to average tree size. The occurrence of epiphytes increased with altitude. The occurrence of large crown dead wood in lower canopy parts (DE14) was significantly more frequent in strictly protected forests.

For the other predictors that were related to the overall composition of TreMs, no significant relationships could be found with occurrences of specific TreM types.

4. Discussion

TreM abundance, diversity and composition differed between the three forest types. Comparable effects of forest types were observed in previous studies (Bütler et al., 2004; Drever and Martin, 2010; Ulyshen et al., 2011). Unexpectedly, we found the greatest abundance of TreMs in pure spruce forests, although diversity was lower than in mixed-coniferous-broadleaved forests. This indicates that large quantities of few TreM types can be found in pure spruce stands. The somewhat counterintuitive result is strongly related to the most abundant TreM in this study, small buttress cavities (GR11). When excluding this type from the analysis, the abundance of TreMs was highest in mixed-coniferous-broadleaved stands. The frequent occurrence of small buttress cavities in pure spruce stands presumably refers to the flat rooting system of spruce that forms this kind of TreM. Moreover, a difference in the substrate between the forest types could play a role for the more frequent buttress cavities, but further analyses are required on this issue. Yet, small buttress cavities were not predicted to be significantly more abundant in pure spruce stands than in other forest types (Table 4), indicating that also groups of trees in broadleaved stands form abundantly small buttress cavities. In contrast to the abundance, the diversity of TreMs is clearly greatest in forests consisting of mixed-coniferous-broadleaved trees. This finding is in accordance with previous studies carried out in mixed montane forests in the French Pyrenees (Larrieu and Cabanettes, 2012). Our results indicate that the described relationships between the three different forest types stay constant when comparing different intervals of the mean DBH (Fig. 1). This means we can clearly distinguish a forest type and a DBH effect in our models.

The positive effect of mixed-coniferous-broadleaved forests on TreM composition indicates a larger variety of TreMs in these forests. We demonstrated the importance of the forest type on specific TreMs (e.g. small and large branch holes, dendrotelms, mosses on stems and crown dead wood). Previous studies have shown that mixed-species forests provide on average a higher level of ecosystem functions including provisioning of habitat for certain species groups (Gamfeldt et al., 2013; van der Plas et al., 2016). Our study demonstrates that an increased abundance and diversity of TreMs in mixtures of functionally different tree species groups (conifers vs. broadleaved) exists. This conclusion is supported by the fact that mixtures of functionally similar coniferous species, in this case mainly spruce and fir, did not show a greater abundance and diversity of TreMs when compared to monospecific spruce stands. Thus, in this forest region the mixture of coniferous with broadleaved tree species may be able to contribute to a higher biodiversity.

In accordance with other studies, that showed the increase in average abundance and diversity of TreMs with increasing tree size (Larrieu and Cabanettes, 2012; Michel and Winter, 2009; Winter and Möller, 2008) our study shows that this relationship holds true not only for individual trees but also for groups of large trees when using their mean diameter. However the range of mean DBH per plot was not as great as in other studies (min: 37 cm, mean: 55 cm, max: 82 cm) (Larrieu and Cabanettes, 2012), and very large individuals (DBH >

Table 4
Significance[a] of the effect of the predictors forest type, mean DBH of 15 large trees, altitude and management type on the abundance of individual TreM types including comparisons with categories or direction of change in relation to continuous predictor.[b]

TreM type	Average abundance per collective	Management[c]	Forest type[d]	Altitude	Mean DBH
CV31 – Small branch holes (5 cm)	1.6		PC < MC < MCB***		
CV32 – Large branch holes (10 cm)	0.28		PC < MC < MCB*		↑**
CV33 – Hollow branch (> 10 cm)	0.96		MC < PC < MCB***		
CV41 – Dendrotelms at trunk base (3 cm)	0.63		MC < PC < MCB**		
DE13 – Not sun exposed crown deadwood (10–20 cm)	1.66		MC < PC < MCB*		
DE14 – Not sun exposed crown deadwood (> 20 cm)	0.15	MM < EA < UE < SP*			
EP31 – Epiphytic bryophytes	2.24		PC < MC < MCB*	↓*	
EP32 – Epiphytic foliose and fruticose lichens	2.78			↑***	
EP35 – Mistletoe in tree crown	1.98			↓**	
GR11 – Small root buttress cavities (5 cm)	10.04		MC < PC < MCB**	↑**	↑***
GR12 – Large root buttress cavities (10 cm)	6.88			↑**	↑***

[a] $p < 0.001 = ^{***}$, $p < 0.01 = ^{**}$, $p < 0.05 = ^{*}$.
[b] ↑: Increase in TreM occurrence with increasing predictor or in respective category. ↓: Decrease in TreM occurrence with increasing predictor.
[c] MM: Mixed Management, EA: Even-aged, UE: Uneven-aged, SP: strict-protection.
[d] MC: Mixed-coniferous, PC: Pure-coniferous, MCB: Mixed-coniferous-broadleaved.

100 cm), that are known to bear dramatically more TreMs, were mostly lacking. In addition, we identified for the first time that individual TreM types such as large branch holes and root buttress cavities are directly related to the average diameter of groups of TreM-bearing trees. This result supports the notion that large trees are particularly important for forest biodiversity and need special attention in integrated conservation approaches (Bütler et al., 2013; Larrieu et al., 2014; Larrieu and Cabanettes, 2012; Lindenmayer, 2017; Lindenmayer et al., 2014) as they are often lacking in managed forests. Nevertheless, when aiming to conserve the full range of forest biodiversity all successional phases should be present on the larger landscape scale in managed forests (Hilmers et al., 2018). This includes also smaller tree dimensions that can provide particular TreMs (Großmann et al., 2018). In natural forests regeneration phases though are often combined with the presence of old-growth elements and differences in abundance and diversity of TreMs are not significant between regeneration and latest developmental phases (Larrieu et al., 2014).

The altitude of plots had a significant influence on the abundance of some TreMs such as root buttress cavities and epiphytic lichens that increased with elevation. As buttress cavities are the most abundant TreM and increase with altitude, the overall increase in abundance of TreMs with altitude is obviously caused by this type of TreM. However, we can only speculate about the underlying process that cause this trend with altitude. It may be caused by increasing rock fall or soil movement or other factors such as tree swaying that may lead to stronger development of buttresses in higher altitudes. Our results imply that neither DBH nor forest type, the two other predictors in the final abundance model, show a significant interaction with altitude. In contrast, mosses covering lower stem sections and mistletoes were more abundant at lower elevations. Thus the altitudinal influence may reflect the physiological niche (temperature, humidity, snow cover, air quality) of these epiphytic species, which sets them aside from the other types of TreMs. Since the occurrences of these epiphytic species were not influenced by management or DBH, this type of TreM should be relatively easy to maintain with different types and sizes of habitat trees. The same may not apply to particular epiphytic species that have more specific habitat requirements as for instance species of the fork moss family (e.g. *Dicranum viride*).

Much to our surprise, the strictly protected stands did not show a higher abundance or diversity of TreMs than conventionally managed ones. This might be explained by the fact that we considered exclusively living trees and no standing dead trees. A recent study showed that the density of snags is far more relevant than the TreMs on living trees for the difference in TreM abundance between strict reserves and managed stands (Paillet et al., 2017). Additionally, previous studies have shown that dead trees provide specific types of TreMs more frequently than living ones, for instance woodpecker cavities or cracks (Larrieu and Cabanettes, 2012; Vuidot et al., 2011) and our results underline that the number of standing dead trees influences the composition of TreMs on living trees. Thus, results from our study should not be misinterpreted in the sense that snags were not important for forest biodiversity. Their presence just does not influence the average abundance or diversity of TreMs on living trees occurring on the same plot. According to our results, standing dead trees are not a suitable indicator for assumed stand structural complexity that translates into abundances or diversity of TreMs on living trees.

The lack of differences between management types may be also attributable to the fact that management in all strictly protected forests had ceased only relatively recently (2–4 decades ago) and hence there was little opportunity for natural disturbances to shape these forests and thus the TreMs, which requires more time as pointed out by earlier studies (Bouget et al., 2014b). Further studies may show that management intensity, which can be quantified as a continuous variable (Kahl and Bauhus, 2014), is likely a better predictor for abundance and diversity of TreMs, when comparing these managed stands excluding strict-protected areas.

Regarding the composition of TreMs, except for forests with mixed management, all types of forest management differed significantly. This means that different types of silviculture have different effects on the processes that create specific TreMs, considering for instance light conditions or wounds (Larrieu et al., 2014) but not on the general TreM abundance or diversity. Only large diameter crown dead wood in the lower canopy was significantly more abundant in strict forest reserves than in the other management types. This may be a direct result of management interventions, which usually remove these trees in managed forests for the safety of workers and visitors, economic or silvicultural reasons. The removal of the large crown dead wood might as well represent a mere habit of forest workers.

Our study is to our knowledge the first to consider the landscape context for the occurrence of TreMs. It showed that the surrounding landscape does not influence the abundance, diversity or composition of TreMs. This is to some extent surprising as several of the processes that create TreMs, for example disturbance regimes or the activity of biotic agents such as fungi (Ruete et al., 2016), were assumed to differ due to the availability of forests in the landscape. At the selected landscape level, the sum of direct and indirect effects of forest cover was thought to be strong enough to be detectable, but the opposite was the case. Conversely, this might be attributable to the fact that the natural disturbance processes related to the forest cover are not pronounced enough due to their control by management activities. The absence of landscape effects on TreMs may be also related to a relatively low level of variability in landscape settings and/or the rather coarse categorization of the variable.

4.1. Management implications and outlook for the provisioning of future habitat trees

The models developed in this study, which predict the average abundance and diversity of TreM types based on several forest attributes can substantially enhance the prediction of habitat tree groups in mountain forests of Central Europe with similar forest composition and management history compared to the Black Forest. Suitable stands for habitat tree selection can be preselected based on forest inventory and remote sensing data. However, our models are not suited to predict the occurrence of specific TreMs, they solely indicate under which ecological and management circumstances some types of TreMs can be found more frequently. If other TreM types for which we did not find any relationships to forest attributes were to be conserved, they need to be assessed in field inventories. Still, we assume that the models benefit forest biodiversity conservation in comparable forest types also outside our specific research area.

Our study points to the importance of selecting functionally different species for habitat trees to provide a high abundance and diversity of TreMs. We showed that the maintenance of broadleaved trees in conifer-dominated forests could lead to an increase of TreMs. This is in accordance to the complementarity effect of tree species mixtures for the provisioning of TreMs as pointed out by earlier studies (e.g. Vuidot et al., 2011). We were able to identify some of the complementary TreMs in coniferous-broadleaved mixed stands such as small and large branch holes, dendrotelms, bryophytes and crown dead wood for the first time. Moreover, managed forests provide a similar number and diversity of TreMs regardless of the silvicultural system applied. To our knowledge, most attempts to generalize response patterns of forest dependent species groups in relation to management types in temperate forests remained unsuccessful. However, one recent case study showed a positive relation between regional species diversity and even-aged management in European beech stands covering developmental stages from 20 to 140 years (Schall et al. 2018). Based on the provisioning of TreMs in our study, uneven-aged management should not be understood as generally benefitting overall biodiversity. Hence, our results imply that not only in even-aged but also in uneven-aged management systems retention elements as large, functionally different trees are needed.

The lack of response of TreMs to the forest cover in surrounding landscapes suggests that there is no major reason to recommend specific locations or variation in density for habitat tree retention based on this attribute. However, our knowledge of the processes that shape TreMs at the landscape scale is still very poor. For instance, even if specific TreMs are present, this does not guarantee that they are used if the relevant taxa cannot disperse to them. Thus, especially selecting and locating those habitat trees that provide the highest abundance and diversity of TreMs requires more knowledge about their individual development.

Acknowledgements

This study was funded by the German Research Foundation (DFG), ConFoBi project number GRK 2123. Our field assistants F. Hauck and J. Grossmann provided valuable technical support. We thank the numerous public forest authorities involved for facilitating this research and the state agency of spatial information and rural development of Baden-Württemberg (LGL) for the provision of the DTM as well as the aerial images.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2018.09.043.

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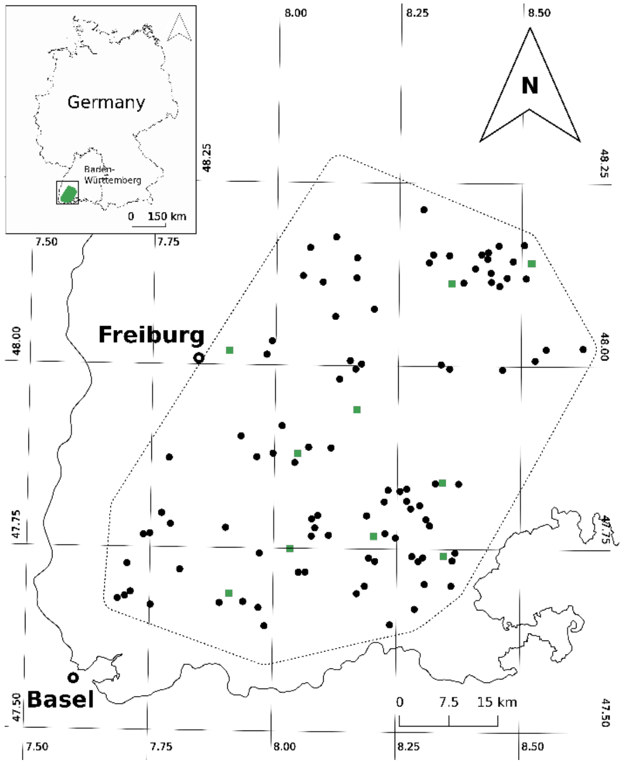
Supporting Information

Research area

Figure A.1 - Distribution of the research plots indicated by the black dots (final selection) and green dots (additionally inventoried plots).



Plot overview

Table A.1 - Overview of the plots inventoried including DBH, microhabitat abundance and richness, altitude, forest cover, number of standing dead trees, management type as well as forest type

Plot	*Mean DBH (cm) (SD)*	*Microhabitat abundance*	*Microhabitat richness*	*Altitude (m)*	*Forest cover (%)*	*Standing dead trees*	*Management*	*Forest type*
1	66.1 (19.7)	99	21	1247	>75	21	Strict-protection	Coniferous-broadleaved
2	53.1 (20.8)	49	16	873	>75	21	Uneven-aged	Mixed-coniferous
3	66.7 (17.2)	73	19	1226	>75	21	Strict-protection	Coniferous-broadleaved
4	51.0 (13.2)	95	11	833	>75	11	Even-aged	Coniferous-broadleaved
5	69.5 (21.3)	44	14	806	>75	10	Even-aged	Coniferous-broadleaved
7	43.5 (13.2)	47	14	1334	>75	21	Strict-protection	Coniferous-broadleaved
8	42.6 (10.1)	35	7	1295	>75	21	Mixed Management	Coniferous-broadleaved
9	55.4 (12.9)	34	10	716	>75	10	Even-aged	Coniferous-broadleaved
10	69.9 (16.4)	45	11	713	>75	10	Strict-protection	Coniferous-broadleaved
11	50.8 (9.4)	25	8	904	>75	5	Mixed Management	Mixed-coniferous
13	53.1 (12.7)	69	13	647	>75	10	Even-aged	Coniferous-broadleaved
14	57.8 (13.6)	21	10	512	>75	13	Even-aged	Coniferous-broadleaved
15	70.6 (11.5)	59	13	1069	>75	3	Even-aged	Coniferous-broadleaved
16	82.2 (23.2)	141	23	947	>75	3	Even-aged	Coniferous-broadleaved
17	61.4 (9.1)	71	9	1069	>75	5	Even-aged	Pure-coniferous
18	69.5 (14.3)	72	6	947	>75	3	Even-aged	Mixed-coniferous
19	57.2 (11.4)	72	16	1014	>75	3	Even-aged	Coniferous-broadleaved
20	59.6 (9.9)	52	8	992	>75	7	Even-aged	Mixed-coniferous
21	52.2 (10.8)	53	11	1088	>75	4	Even-aged	Coniferous-broadleaved
22	48.7 (10.6)	17	6	715	>75	4	Even-aged	Coniferous-broadleaved
23	48.9 (15.7)	32	8	906	>75	3	Even-aged	Coniferous-broadleaved
24	59.3 (9.8)	77	12	828	>75	3	Even-aged	Coniferous-broadleaved
25	55.1 (10.5)	32	8	920	>75	6	Even-aged	Mixed-coniferous

28	70.0 (11.6)	53	16	1026	>75	7	Even-aged	Coniferous-broadleaved
30	58.6 (9.4)	11	4	510	>75	0	Even-aged	Coniferous-broadleaved
31	43.6 (7.2)	21	10	541	>75	0	Even-aged	Coniferous-broadleaved
32	67.4 (9.0)	49	6	889	>75	0	Uneven-aged	Mixed-coniferous
33	53.5 (13.7)	39	9	985	>75	0	Even-aged	Mixed-coniferous
34	43.3 (7.2)	32	7	928	>75	0	Even-aged	Pure-coniferous
35	54.4 (5.5)	66	9	533	>75	0	Even-aged	Coniferous-broadleaved
36	44.9 (7.3)	34	6	1050	>75	0	Even-aged	Pure-coniferous
37	58.1 (8.2)	81	13	1056	>75	0	Even-aged	Coniferous-broadleaved
38	49.2 (14.2)	30	9	904	>75	0	Even-aged	Mixed-coniferous
39	66.3 (15.6)	76	13	649	>75	0	Even-aged	Coniferous-broadleaved
40	56.5 (11.5)	87	19	883	>75	0	Mixed Management	Coniferous-broadleaved
41	57.5 (10.3)	65	19	710	>75	0	Even-aged	Coniferous-broadleaved
44	61.3 (7.8)	35	10	835	>75	0	Mixed Management	Coniferous-broadleaved
45	54.0 (10.8)	34	8	587	<50	16	Even-aged	Coniferous-broadleaved
47	53.9 (19.3)	73	15	744	<50	11	Even-aged	Coniferous-broadleaved
48	54.7 (17.3)	52	13	704	<50	14	Even-aged	Coniferous-broadleaved
50	77.9 (18.5)	86	13	775	<50	10	Uneven-aged	Mixed-coniferous
53	64.2 (12.9)	36	6	950	<50	10	Uneven-aged	Mixed-coniferous
54	44.3 (21.1)	16	11	734	<50	10	Even-aged	Coniferous-broadleaved
55	58.4 (11.7)	32	10	767	<50	10	Mixed Management	Coniferous-broadleaved
56	53.1 (7.5)	28	11	443	<50	12	Mixed Management	Coniferous-broadleaved
57	58.7 (9.0)	41	10	640	<50	8	Even-aged	Coniferous-broadleaved
58	40.4 (20.9)	20	11	694	<50	10	Mixed Management	Coniferous-broadleaved
59	36.9 (10.0)	16	6	634	<50	10	Even-aged	Mixed-coniferous
60	56.9 (21.9)	29	13	613	<50	4	Even-aged	Mixed-coniferous
61	50.6 (8.0)	24	6	515	<50	4	Even-aged	Coniferous-broadleaved
62	61.9 (12.7)	21	5	976	<50	5	Even-aged	Coniferous-broadleaved
63	56.7 (14.5)	37	9	566	<50	2	Even-aged	Coniferous-broadleaved
64	48.8 (14.7)	49	15	717	<50	4	Even-aged	Coniferous-broadleaved
65	40.4 (16.8)	12	6	684	<50	4	Even-aged	Mixed-coniferous

67	49.4 (11.1)	18	7	740	<50	3	Even-aged	Mixed-coniferous
68	40.4 (18.3)	5	3	792	<50	4	Even-aged	Coniferous-broadleaved
69	64.4 (15.9)	43	10	794	<50	2	Even-aged	Mixed-coniferous
71	45.7 (6.4)	18	5	678	<50	2	Even-aged	Mixed-coniferous
72	51.6 (15.0)	25	4	713	<50	3	Even-aged	Mixed-coniferous
73	62.5 (18.0)	35	10	871	<50	4	Uneven-aged	Coniferous-broadleaved
74	37.8 (13.9)	20	10	586	<50	7	Even-aged	Coniferous-broadleaved
75	45.5 (11.6)	36	13	885	<50	0	Even-aged	Coniferous-broadleaved
76	53.3 (7.4)	39	13	504	<50	0	Even-aged	Coniferous-broadleaved
77	39.9 (6.1)	17	5	778	<50	0	Even-aged	Mixed-coniferous
78	61.7 (19.8)	67	20	697	<50	0	Mixed Management	Coniferous-broadleaved
79	63.2 (13.4)	64	16	922	<50	0	Even-aged	Mixed-coniferous
81	62.0 (14.1)	67	9	611	<50	0	Even-aged	Mixed-coniferous
83	48.6 (5.4)	61	10	971	<50	0	Even-aged	Coniferous-broadleaved
84	71.3 (12.8)	45	11	754	<50	0	Even-aged	Mixed-coniferous
85	53.5 (13.8)	28	12	769	<50	0	Even-aged	Mixed-coniferous
86	45.2 (4.2)	24	5	713	<50	0	Even-aged	Coniferous-broadleaved
87	49.3 (10.9)	76	6	1018	<50	0	Even-aged	Coniferous-broadleaved
89	74.9 (10.4)	28	9	701	<50	0	Even-aged	Mixed-coniferous
90	49.2 (18.1)	13	4	719	50 - 75	10	Even-aged	Mixed-coniferous
91	64.9 (17.7)	72	15	1082	50 - 75	10	Even-aged	Coniferous-broadleaved
92	52.5 (9.2)	49	10	606	50 - 75	16	Even-aged	Coniferous-broadleaved
93	64.8 (16.0)	46	14	665	50 - 75	14	Strict-protection	Coniferous-broadleaved
94	47.8 (14.9)	27	12	1000	50 - 75	21	Even-aged	Coniferous-broadleaved
95	46.3 (6.9)	44	10	881	50 - 75	17	Even-aged	Pure-coniferous
96	45.3 (9.0)	33	10	750	50 - 75	12	Uneven-aged	Coniferous-broadleaved
98	54.9 (8.2)	60	9	1120	50 - 75	10	Uneven-aged	Mixed-coniferous
100	55.4 (15.2)	18	5	1003	50 - 75	10	Mixed Management	Mixed-coniferous
101	74.7 (13.6)	40	10	986	50 - 75	15	Uneven-aged	Mixed-coniferous
102	52.3 (14.2)	16	6	877	50 - 75	12	Even-aged	Mixed-coniferous
103	41.3 (9.9)	17	6	841	50 - 75	12	Even-aged	Coniferous-broadleaved

104	49.1 (12.5)	37	14	580	50 - 75	18	Mixed Management	Coniferous-broadleaved
105	55.5 (9.0)	26	10	833	50 - 75	5	Even-aged	Coniferous-broadleaved
106	52.4 (16.8)	27	10	774	50 - 75	3	Even-aged	Coniferous-broadleaved
107	53.0 (16.8)	38	10	733	50 - 75	7	Even-aged	Mixed-coniferous
108	53.3 (10.2)	25	8	1126	50 - 75	4	Uneven-aged	Mixed-coniferous
109	63.5 (7.3)	47	12	888	50 - 75	3	Uneven-aged	Coniferous-broadleaved
110	43.3 (11.4)	36	7	930	50 - 75	6	Even-aged	Coniferous-broadleaved
111	60.6 (15.2)	58	12	682	50 - 75	5	Even-aged	Coniferous-broadleaved
112	56.5 (7.5)	72	7	1002	50 - 75	5	Even-aged	Mixed-coniferous
113	41.9 (7.4)	32	4	1160	50 - 75	6	Even-aged	Coniferous-broadleaved
114	76.6 (11.6)	48	12	516	50 - 75	5	Even-aged	Mixed-coniferous
116	56.2 (8.2)	35	8	1009	50 - 75	3	Even-aged	Pure-coniferous
117	52.8 (14.3)	23	13	857	50 - 75	6	Even-aged	Mixed-coniferous
118	76.8 (11.8)	77	19	657	50 - 75	4	Uneven-aged	Coniferous-broadleaved
119	67.2 (17.6)	48	16	887	50 - 75	4	Uneven-aged	Coniferous-broadleaved
120	47.9 (7.3)	25	10	623	50 - 75	0	Even-aged	Coniferous-broadleaved
121	56.2 (7.7)	29	12	632	50 - 75	0	Even-aged	Coniferous-broadleaved
122	56.0 (14.7)	30	13	527	50 - 75	0	Even-aged	Coniferous-broadleaved
123	53.4 (6.8)	38	9	646	50 - 75	0	Even-aged	Mixed-coniferous
124	52.6 (12.8)	35	10	929	50 - 75	0	Mixed Management	Coniferous-broadleaved
125	48.5 (13.2)	31	12	533	50 - 75	0	Even-aged	Coniferous-broadleaved
127	59.8 (9.6)	23	8	516	50 - 75	0	Even-aged	Mixed-coniferous
128	53.9 (12.1)	63	18	982	50 - 75	0	Even-aged	Coniferous-broadleaved
129	69.1 (12.8)	88	22	549	50 - 75	0	Even-aged	Coniferous-broadleaved
130	59.5 (11.2)	60	17	978	50 - 75	0	Even-aged	Coniferous-broadleaved
131	59.7 (12.0)	84	10	1033	50 - 75	0	Even-aged	Pure-coniferous
132	45.6 (5.7)	13	6	862	50 - 75	0	Mixed Management	Mixed-coniferous
133	63.8 (10.0)	80	23	743	50 - 75	0	Mixed Management	Coniferous-broadleaved
134	53.5 (12.2)	18	8	898	50 - 75	0	Even-aged	Mixed-coniferous
135	44.2 (7.0)	22	7	569	>75	12	Uneven-aged	Mixed-coniferous
137	66.5 (11.0)	25	7	815	50 - 75	2	Uneven-aged	Mixed-coniferous

138	55.8 (7.3)	34	6	853	50 - 75	2	Uneven-aged	Mixed-coniferous
139	65.1 (7.7)	33	10	856	50 - 75	2	Uneven-aged	Mixed-coniferous
140	49.7 (14.4)	8	5	744	<50	7	Even-aged	Mixed-coniferous
142	45.4 (9.1)	15	8	690	<50	3	Even-aged	Mixed-coniferous
144	49.2 (7.1)	19	10	879	50 - 75	0	Even-aged	Mixed-coniferous
147	55.2 (9.6)	30	7	839	50 - 75	3	Even-aged	Coniferous-broadleaved
148	54.9 (23.0)	29	7	831	50 - 75	0	Even-aged	Coniferous-broadleaved
149	60.5 (12.6)	40	10	933	50 - 75	0	Even-aged	Coniferous-broadleaved
150	55.0 (8.0)	39	9	983	50 - 75	4	Even-aged	Mixed-coniferous
151	60.9 (10.2)	20	5	851	50 - 75	10	Even-aged	Mixed-coniferous
152	53.6 (8.8)	45	7	994	>75	5	Even-aged	Mixed-coniferous
155	47.6 (9.1)	26	12	1073	>75	3	Uneven-aged	Coniferous-broadleaved
156	54.8 (12.9)	29	9	797	>75	11	Even-aged	Coniferous-broadleaved
158	61.3 (10.1)	30	12	1020	50 - 75	4	Even-aged	Coniferous-broadleaved
165	44.9 (12.1)	28	8	924	>75	12	Even-aged	Coniferous-broadleaved
167	42.2 (7.1)	12	3	813	>75	0	Even-aged	Mixed-coniferous
175	75.5 (18.5)	44	13	895	50 - 75	5	Even-aged	Coniferous-broadleaved
176	48.6 (7.7)	27	7	749	<50	0	Even-aged	Mixed-coniferous
177	47.4 (6.8)	29	6	972	<50	10	Even-aged	Pure-coniferous
178	49.9 (25.7)	36	14	663	<50	10	Strict-protection	Coniferous-broadleaved
179	50.3 (11.0)	23	10	1003	50 - 75	12	Even-aged	Mixed-coniferous
181	58.9 (16.0)	31	7	903	>75	4	Mixed Management	Coniferous-broadleaved
186	38.0 (8.1)	22	11	787	<50	5	Even-aged	Coniferous-broadleaved

Results from tree delineation

Figure A.2 - Relationship of the delineated crown diameter and estimated DBH from remote sensing data for all trees in the plots (N=22,732).

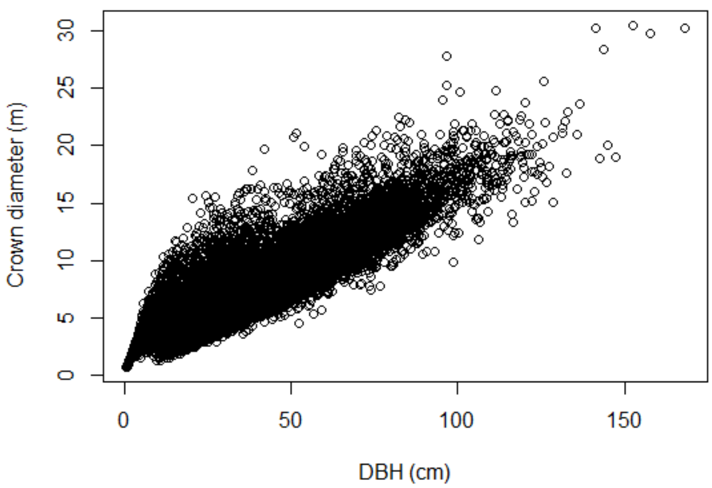


Table A.2 - Results of the delineated crown diameters and estimated DBH from tree delineation for all trees per plot (N=22,732).

Variable	*1st quartile (0.25)*	*Mean (0.5)*	*3rd quartile (0.75)*
Delineated crown diameter (m)	5.66	7.93	9.67
Estimated DBH (cm)	29.09	41.91	52.2

Correlation matrix continuous predictors

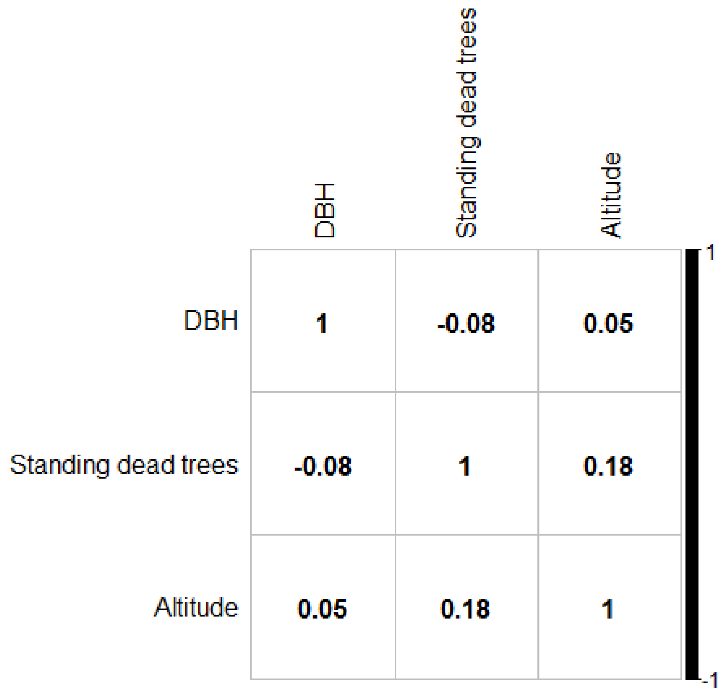


Figure A.3 - Correlation matrix of continuous predictors used for modelling indicating strengths of correlation with increasing values indicating increased correlations.

Inventory results

Table A.3 - Microhabitat type, detailed description and number of records from microhabitat inventory.

Microhabitat type	*Code*	*Description*	*N*
Bark	BA11	Bark shelter, open bottom	26
Bark	BA12	Bark pocket, open top	10
Bark	BA21	Coarse bark	119
Woodpecker cavity	CV11	Cavity entrance about ø = 4 cm	2
Woodpecker Cavity	CV12	Cavity entrance about ø = 5 - 6 cm w	9
Woodpecker Cavity	CV13	ø > 10 cm Woodpecker hole in the trunk	6
Woodpecker Cavity	CV14	ø ≥ 10 cm feeding hole	13
Woodpecker Cavity	CV15	Woodpecker "flute“ /cavity string	6
Trunk/ mould cavity	CV21	ø ≥ 10 cm (ground contact)	14
Trunk/ mould cavity	CV22	ø ≥ 30 cm (ground contact)	13
Trunk/ mould cavity	CV23	ø ≥ 10 cm (no ground contact)	21
Trunk/ mould cavity	CV24	ø ≥ 30 cm (no ground contact)	11
Trunk/ mould cavity	CV25	ø ≥ 30 cm / semi-open	4

Trunk/ mould cavity	CV26	ø ≥ 30 cm /open top	0
Branch hole	CV31	ø ≥ 5 cm, holes from breakage	222
Branch hole	CV32	ø ≥ 10 cm holes from breakage	39
Branch hole	CV33	Hollow branch, ø ≥ 10 cm	133
Dendrotelm	CV41	ø ≥ 3 cm / trunk base	88
Dendrotelm	CV42	ø ≥ 15 cm / trunk base	11
Dendrotelm	CV43	ø ≥ 5cm / crown	19
Dendrotelm	CV44	ø ≥ 15 cm / crown	6
Insect gallery/bore holes	CV51	Gallery with single small bore holes	4
Insect gallery/bore holes	CV52	Large bore hole	1
Dead branch	DE11	ø 10 - 20 cm, ≥ 50 cm, sun exposed	125
Dead branch	DE12	ø > 20 cm, ≥ 50 cm, sun exposed	7
Dead branch	DE13	ø 10 - 20 cm, ≥ 50 cm, not sun exposed	231
Dead branch	DE14	ø > 20 cm, ≥ 50 cm, not sun exposed	21
Dead branch	DE15	Dead top ø ≥ 10 cm	12
Fungi fruiting body	EP11	Annual polypores, ø > 5cm	2
Fungi fruiting body	EP12	Perennial polypores, ø > 10 cm	4
Fungi fruiting body	EP13	Pulpy agaric, ø > 5 cm	4
Fungi fruiting body	EP14	Large ascomycetes, ø > 5 cm	0
Myxomycetes	EP21	Myxomycetes, ø > 5 cm	1
Epiphyte	EP31	Epiphytic bryophytes, > 25 % trunk	311
Epiphyte	EP32	Epiphytic foliose/ lichens, > 25 % trunk	387
Epiphyte	EP33	Lianas, coverage > 25 %,	16
Epiphyte	EP34	Epiphytic ferns, > 5 fronds	5
Epiphyte	EP35	Mistletoe in tree crown	275
Root buttress cavity	GR11	ø ≥ 5 cm, natural cavity	1396
Root buttress cavity	GR12	ø ≥ 10 cm, natural cavity	956
Root buttress cavity	GR13	Trunk cleavage, length ≥ 30 cm	11
Witches broom	GR21	Witches broom, ø > 50 cm	72
Witches broom	GR22	Water sprout, dense epicormics	6
Canker or burr	GR31	Cancerous growth, ø > 20 cm	14
Canker and burr	GR32	Decayed canker, ø > 20 cm	25
Bark loss	IN 11	Bark loss 25- 600 cm2, decay stage < 3	255
Bark loss	IN12	Bark loss >600 cm2, decay stage < 3	63
Bark loss	IN13	Bark loss 25- 600 cm2, decay stage = 3	24
Bark loss	IN14	Bark loss >600 cm2, decay stage = 3	23
Exposed heartwood	IN21	Broken trunk, ø ≥ 20 cm at broken end	5
Exposed heartwood	IN22	Broken tree crown /fork	11
Exposed heartwood	IN23	Broken limb, ø ≥ 20 cm at broken end	19
Exposed heartwood	IN24	Splintered stem, ø ≥ 20 cm	0
Crack or scar	IN31	Length ≥ 30 cm	15
Crack or scar	IN32	Length ≥ 100 cm	13
Crack or scar	IN33	Lightning scar	2
Crack or scar	IN34	Fire scar, ≥ 600 cm²	0
Nest	NE11	Large vertebrate nest, ø > 80 cm	2
Nest	NE12	Small vertebrate nest, ø > 10 cm	40

Nest	NE21	Invertebrate nests in trunk	0
Sap and resin run	OT11	Sap flow, > 50 cm, fresh, deciduous	0
Sap and resin run	OT12	Resin flow /pockets, > 50 cm, coniferous	542
Micro soil	OT21	Crown micro soil	9
Micro soil	OT22	Bark micro soil	11

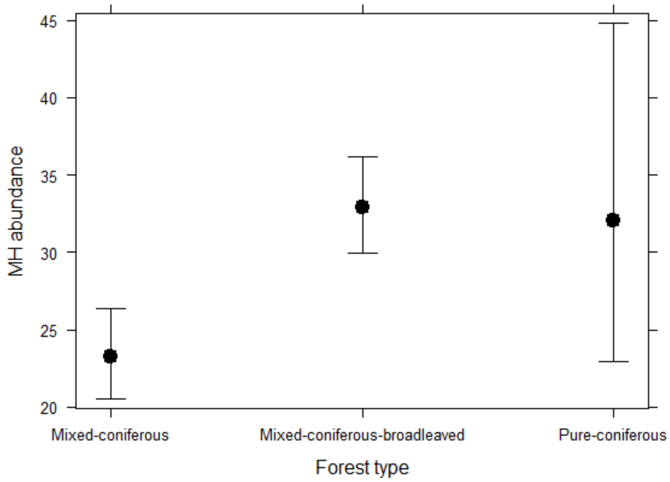


Figure A.4 - Effect sizes from the modeled influence of the forest type on the abundance of microhabitats excluding the most abundant microhabitat type (small buttress cavities, GR11) with a 95% confidence interval indicated by the bars.

Residual plots from cross validation

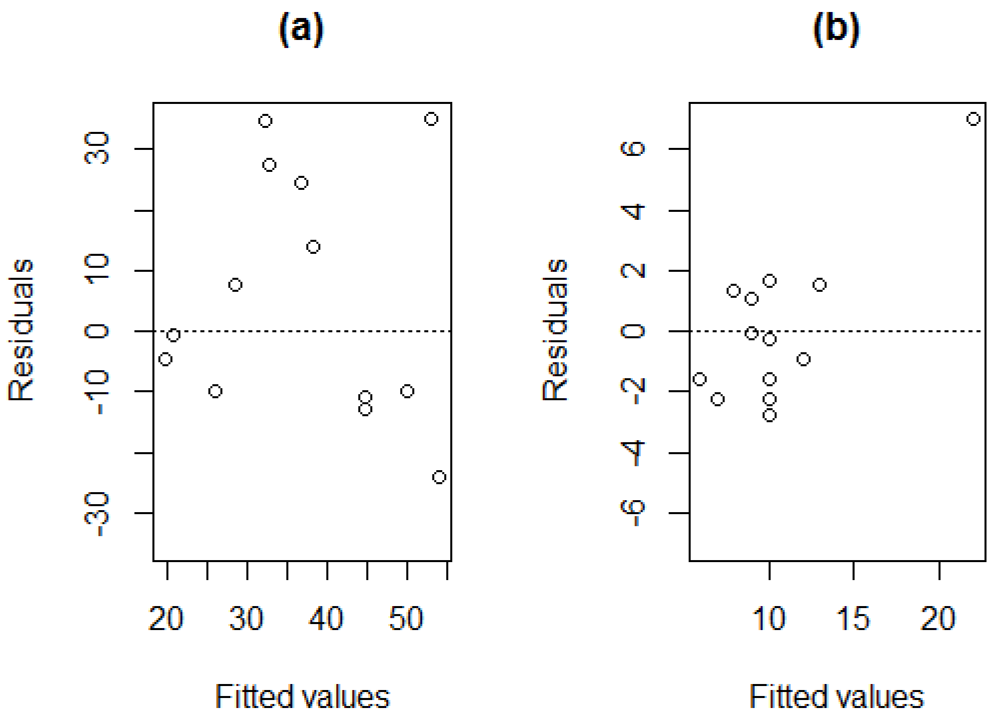


Figure A.5 - Residual plots showing residuals vs fitted values for a) abundance test data set and b) richness test data set.

Table A.4 - Results of variance inflation factor (VIF) test of final models to check for collinearity of predictors, with generalized variance-inflation factor (GVIF) and degrees of freedom (Df).

Variable	*GVIF*	*Df*	*GVIF^(1/(2*Df))*
TreM abundance model			
Forest type	1.206300	2	1.048006
Altitude	1.189586	1	1.090682
Mean DBH	1.049760	1	1.024578
TreM diversity model			
Forest type	1.010616	2	1.002644
Mean DBH	1.010616	1	1.005294