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

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A B S T R A C T

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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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