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Land ownership affects diversity and abundance of tree microhabitats in deciduous temperate forests

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ABSTRACT

Tree microhabitats – e.g. cavities, bark pockets or crown dead wood – have been described as key habitat elements, which are particularly important for birds, bats and xylobiont insects. They are therefore vital for promoting biodiversity in forest ecosystems. The occurrence of such tree microhabitats in forest stands is closely related to forest management. In Central European cultural landscapes, forest areas are subdivided into a mosaic of stands under different ownership types and owners vary in their forest management strategies and practices. However, little is known about the influence of forest ownership on the density and diversity of tree microhabitats in forest stands. In this study, we investigate tree microhabitats – categorised into 31 different tree microhabitat types – within forest stands in clusters of different ownership types. We compare small-scale private forests, municipal forests and state-owned forests in deciduous temperate forest ecosystems in south-western Germany. Our results reveal that the density of tree microhabitats per hectare is more than twice as high in small-scale private forests than in municipal or state-owned forests. Similarly, the diversity of tree microhabitats related to area is highest in small-scale private forests. Moreover, we found differences in tree microhabitat occurrences under the three ownership types at the single tree level. Besides ownership type, relevant indicators for tree microhabitats are basal area of forest stands as well as tree vitality and diameter. Within the study region, the share of tree microhabitats provided by small-scale private forests plays a substantive role for overall forest biodiversity. Management of publicly owned forests should promote a higher density and diversity of tree microhabitats to comply with goals of close-to-nature forest management approaches. In conclusion, we regard the type of forest ownership as a relevant driver of tree microhabitat occurrence. Ownership should therefore be considered in the design of policy frameworks and instruments which address the promotion of forest biodiversity.

1. Introduction

Forest management drives forest biodiversity (Putz et al., 2000). Negative consequences of forestry affect many species (e.g. Brunet et al., 2010; Lonsdale et al., 2008). This may in turn reduce quality of life because human well-being and biodiversity are closely related (Cardinale et al., 2012). On the other side, wood is needed as a regrowing resource for a wide range of human purposes. Against the backdrop of this conflict of interests, extended knowledge of the factors which influence forest biodiversity is required. One crucial link between forest management and forest biodiversity are tree microhabitats (TMHs). They are forest features which are strongly regulated by forest management and at the same time are a determining factor for forest biodiversity (Regnery et al., 2013a; Winter et al., 2005).

TMHs are referred to in the relevant literature as ‘special tree structures’ (Winter et al., 2005), ‘tree microhabitat structures’ (Michel and Winter, 2009), or ‘tree microhabitats’ (Larrieu and Cabanettes, 2012; Larrieu et al., 2012; Regnery et al., 2013a; Vuidot et al., 2011; Winter and Möller, 2008). TMHs such as tree holes, are determining factors of forest biodiversity (Michel and Winter, 2009). In France, 41% of forest-related birds are tree hole dwellers (Blondel, 2005). More than half of Germany’s bat species use tree roosts (Dietz, 2013). Decay holes create TMHs for rare epiphytic lichens and mosses (Fritz and Heilmann-Clausen, 2010). Many xylophilous insects depend on TMHs because of their specialization on dead wood, lignicolous fungi, mould or sap-runs.

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For other insect species, the tree nests of birds, bats or social insects are essential habitats (Köhler, 2000).

Diversity and density of TMHs are key attributes of biodiversity and are particularly present in old-growth forests. A higher number of species occur where TMHs are more abundant (Winter et al., 2005; Regnery et al., 2013a). TMHs have therefore been proposed as indicators for measuring forest ecosystem biodiversity (Michel and Winter, 2009). In Germany, forests are the second most widespread land cover type after agriculture (Bolte and Polley, 2006) and cover 31% of the land area (BMELV, 2005). Prior to human logging activities, 85–95% of the land surface had been covered by forest ecosystems (Korneck et al., 1998). Hence, forest structures and tree characteristics such as TMHs are of crucial significance for the conservation of large-scale biodiversity. National policy agendas have taken biodiversity requirements for forest management into account (e.g. BMUB, 2015).

The impact of land ownership on biodiversity has been revealed in previous studies, e.g. by Lovett-Doust et al. (2003), who revealed significantly greater rare-species richness on publicly owned land in comparison to private land in Canada. Schmithüsen and Hirsch (2010) summarised forest ownership data from 23 European countries and calculated that publicly owned forest lands represent 50.1% of all forests. Roughly 20% of German forests are state owned, 33% are owned by municipalities or other public bodies like churches and trusts and 47% are privately owned. Fifty-seven percent of the private forests in Germany are smaller than 20 ha (Depenheuer and Möhring, 2010). Private forest owners of large and medium-scale forests frequently have strong economic interests (Pickenpack, 2004). In contrast, small-scale forest owners vary more in their management objectives and are increasingly driven by recreation and nature conservation motives (Härdter, 2004). Small-scale private forests are frequently managed very extensively for firewood cutting or remain unexploited (Bieling, 2004).

In Germany and other European countries, public forests have been legally declared a public welfare good, which must be managed in a way that supports a multitude of goals, for example, maintaining recreation functions or serving as a model for biodiversity conservation (Schaich, 2013). However, public forest management has developed on the basis of a centuries-old tradition of timber production orientated management (Pistorius et al., 2012), which continues to shape forestry in the present (Schaich and Plieninger, 2013).

The influence of forest management on TMH density or diversity has rarely been studied (e.g. Larrieu et al., 2012; Vuidot et al., 2011; Winter et al., 2005). At the stand level, the time span since the last cutting has been suggested as a predictor of TMH density. 90 years old stands had almost 13 times higher TMH density than up to 30 years old stands (Regnery et al., 2013b). The relationship between forest ownership and TMH has, to our knowledge, not yet been studied. Information on the relationship between ownership, management and TMH provisioning is needed for the design of effective policies which aim to halt the loss of biodiversity or to promote more sustainable use of forest resources; especially if such policy frameworks are to be applicable to landscapes with different land ownership types.

We investigated the occurrence of tree microhabitats in adjacent broadleaf forest stands under three different forest ownership types – small-scale private forest, municipal forest and state forest – in the Swabian Alb Biosphere Reserve located in south-western Germany. Our main objective was to quantify to which extend forests under these distinct ownership types vary in terms of the density and composition of TMHs. Schaich and Plieninger (2013) found in the same region differing basal areas and differing diameter distribution when comparing forests of the three ownership types. Based on those findings we hypothesised: (1) The occurrence of TMHs on trees is influenced by the management approaches applied under different forms of forest ownership; (2) small-scale private forests in the Swabian Alb provide more TMHs than the publicly managed forests in the region; and (3) the diversity of TMHs is higher in small-scale private forests.

2. Material and methods

2.1. The study region Swabian Alb Biosphere Reserve

We collected data in the Swabian Alb Biosphere Reserve which is located in south-western Germany about 50 km south-east of Stuttgart (9°45′43–9°07′07 easting, 48°37′49–48°12′30 northing). It covers an area of about 85,300 ha and encompasses the lands of 29 municipalities which are subsumed within three administrative districts (Ministerium für Entwicklung und Ländlichen Raum, 2008). The region is predominantly rural and in 2005 the Biosphere Reserve had about 151,000 inhabitants (Ministerium für Entwicklung und Ländlichen Raum, 2012).

The elevation of the low mountain range Swabian Alb extends from 329 m to 872 m a.s.l. The vegetation is shaped by a subcontinental, cool-temperate climate and predominantly westwind weather conditions which result in annual perception between 750 mm and 1050 mm and annual mean temperatures between −1.5 °C in January and 15.9 °C in July (Fischer et al., 2010).

The topography is varied and frequently described as three distinct natural regions: (1) The *Albtrauf*, an escarpment area with steep slopes, rock faces, gorges and its foreland in the north of the Biosphere Reserve, followed southward by (2) the *Kuppenalb*, a plateau with highly variable relief at the small scale, and the southernmost area called (3) *Flächenalb* with a gently undulating topography, intersected by the Lauter and Schmiech rivers which flow into the nearby Donau. Soils are rich in clay and predominantly developed on Jurassic shell limestone (Fischer et al., 2010).

2.2. Forest vegetation

On a large scale, the potential natural vegetation type within the study area is beech (*Fagus sylvatica* L.) forests (Bohn et al., 2000). In many places, forest vegetation has been replaced by agriculture or settlements. Presently, forests cover about 37% of the Swabian Alb Biosphere Reserve (Regierungspräsidium Tübingen, 2007). Central Europe, as the centre of the beech (*Fagus sylvatica* L.) distribution, bears particular responsibility for beech forests.

The beech forests of the Swabian Alb Biosphere Reserve are frequently *Hordelymo-* or *Galio-odorati-Fagetum*. Moreover, many rare and protected forest types also occur there. Associations with *Acer pseudoplatanus* L., *Fraxinus excelsior* L. and *Ulmus glabra* Huds. thrive at particular locations with high humidity such as lower slopes and gorges, and associations with *Acer platanoides* L. and *Tilia cordata* Mill. or *Tilia platyphyllos* Scop. dominate on steep rocky screes with south-west aspect. Dry forest associations of *Carici-fagetum* or with *Quercus petreae* Liebl. and *Carpinus betulus* L. are locally distributed at hilltops, especially within the northern escarpment region (Reidel and Döler, 2006).

2.3. Definition of tree microhabitats

We defined 31 TMHs which are related to structural properties of trees or are associated species such as epiphytic plants, lichens and fungi (Table 1). They are structural features that perform particular functions for animal or plant species. A commonly occurring function is that of providing shelter against predators or weather (Gibbons and Lindenmayer, 2002). Another relevant function is the provision of access to food resources e.g. for xylobiont beetles (Köhler, 2000).

Table 1
Definitions of TMH categories, TMH occurrences per tree and group assignment.

Tree microhabitat	Occurrence per tree of the ownership type municipal	Occurrence per tree of the ownership type small-scale private	Occurrence per tree of the ownership type state	Definition	Group
Bird cavity	0.0023	0.0057	0.0047	Entrance Ø $\geqslant$ 2 cm	Cavities and pockets
Cavity string	0.0023	0.0014	0.0000	At least three woodpecker cavities within a distance of $\leqslant$2 m in each case	
Decay cavity (small) after loss of branch	0.0230	0.0298	0.0233	Opening Ø $\geqslant$ 5 cm	
Large stem cavity with mould	0.0023	0.0099	0.0047	Not at the base of the stem, volume at least 1000 cm^3, advanced decay	
Large stem cavity without mould	0	0.0028	0.0023	Not at the base of the stem, volume at least 1000 cm^3, e.g. decay proceeding upwards	
Cavity at stem base without mould	0.1977	0.2514	0.2023	Volume at least 1000 cm^3	
Cavity at stem base with mould	0.0368	0.0909	0.0349	Decay cavity, volume at least 1000 cm^3	
Bark pocket without mould	0.0161	0.0170	0.0093	At least 5 cm $*$ 5cm $*$ 2 cm	
Bark pocket with mould	0.0138	0.0099	0.0093	At least 5 cm $*$ 5 cm $*$ 2 cm	
Bark loss	0.1103	0.0781	0.1070	At least 5 cm $*$ 5 cm	Bark injuries
Bark injuries caused by woodpeckers	0.0046	0.0085	0.0023	At least 2 cm $*$ 3 cm or >10 small bark injuries	
Fomes fomentarius J. J. Kickx	0	0.0042	0	Conks	Fungi
Fomitopsis pinicola P. Karst	0	0.0014	0	Conks	
Other fungi	0.0067	0.0114	0.0093	Fruiting bodies $\geqslant$5 cm $*$ 5 cm or a string of fruiting bodies $\geqslant$10 cm	
Mosses	0.1310	0.2415	0.1558	Covering $\geqslant$20% of the stem	Epiphytes
Lichens	0.1908	0.3693	0.2116	Covering $\geqslant$20% of the stem	
Ivy (*Hedera helix L.*)	0.0023	0.0028	0.0023	Covering $\geqslant$20% of the stem	
Crown skeleton >50%	0.0069	0.0085	0.0047	>50% crown skeleton	Crown injuries
Crown skeleton min. 10%	0.0598	0.0554	0.0767	10–50% crown skeleton	
Broken stem/loss of crown	0	0	0	Broken stem without secondary crown	
$\geqslant$50% Crown loss	0.0023	0	0		
<50% Crown loss	0	0	0		
Secondary crown	0.0023	0.0043	0.0093	After loss of crown	
Broken fork	0.0115	0.0099	0.0070	One of two developed main stems lost	Stem and base injuries
Sap flow or resin flow	0.0092	0.0028	0.0093	Fresh flows, at least 30 cm long or >5 smaller flows	
Canker	0.0115	0.0099	0.0209	Ø $\geqslant$ 10 cm	
Lightning scar	0.0069	0.0028	0	At least 3 m long and reaching the sapwood	
Crack	0.0184	0.0440	0.0233	Length $\geqslant$ 25 cm, crack extending at least 2 cm into the sapwood	
Splintered stem	0.0069	0.0085	0.0070	Broken stem, at least 5 splinters of at least 50 cm in length	
Root plate	0.0046	0.0057	0.0023	Root plate Ø $\geqslant$ 1, 2 m	
Rejuvenation	0.0276	0.0810	0.0302	Rejuvenation from the stem base	

Existing TMH definitions have been adopted, as far as appropriate, from different authors (Michel and Winter, 2009; Regnery et al., 2013a; Winter et al., 2005; Winter and Möller, 2008; Vuidot et al., 2011) to facilitate comparisons with similar studies. Only recently several European authors published a common TMH typology (Kraus et al., 2016). Detailed information about functions of TMHs and links to biodiversity can be found e.g. in Larrieu (2014) or Köhler (2000).

2.4. Site selection and sampling procedure

We sampled a total of 108 plots with a horizontal size of 500 m^2 each, which accumulates to a sampled area of 5.4 ha. The plots were distributed over the entire extent of the Swabian Alb Biosphere Reserve in order to represent the different natural regions. In each natural region clusters of forest stands were identified that included the three ownership types – small-scale private, municipal, and state-owned forests – in close proximity. This sampling design was chosen in order to minimize confounding factors such as differences in microclimate or soil quality. Within each cluster one plot was randomly selected from each ownership type using a random walk procedure. Details of the sampling procedure and a map of the 36 sampling plot clusters in the Biosphere Reserve are provided in Schaich and Plieninger (2013).

The form of ownership was assigned based on 2011 data from the state land register. Small-scale private forest owners own up to 200 ha of forest, municipal forests are owned by municipalities, while state properties belong to the federal state of Baden-Württemberg (Schaich and Plieninger, 2013).

For each sampling plot we measured elevation, slope and exposure. The elevation of the plots spans from 420 m to 850 m a.s.l. Slopes of the plots are in the range from 1° to 33°. Additionally, we classified the sampling location as one of the following relief levels: crest, upper slope, mid-slope, lower slope or plain. We corrected plot radii for slope using the calculation $r_{slope} = \frac{r}{\sqrt{\cos a}}$. Pure or nearly pure spruce plantations were excluded from sampling.

2.5. Tree microhabitat inventory

At each sampling plot we investigated all living trees and standing dead trees with a DBH $\geqslant$ 20 cm. We examined the trees from nearby by walking around each of them and from a further distance to detect any of the 31 named TMHs. Each TMH was marked as either present or absent for each of the trees. Additionally, tree species and vitality (living or dead tree) was determined for each specimen. All in all, we recorded 16 different tree species in our case study area. European beech (*Fagus sylvatica* L.) was the dominant species and constituted 77.4% of all recorded trees. The percentage of beech differed across ownership types: 79.4% in small-scale private forests, 76.0% in state forests and 75.4% in municipal forests. TMH inventories are prone to observer effects (Paillet et al., 2015). Therefore, all data were collected by one observer (F.J.) to avoid bias.

2.6. Key indicators of stand structure

In the study region the forests of the three ownership types differ in terms of the stand structure (Schaich and Plieninger, 2013). Because the prior stand structure inventory was years ago we calculated the indicators based on our current measurements. The mean total basal area per plot is 20557.58 cm^2 (SD = 4791.61 cm^2) in small-scale private forests, 13818.23 cm^2 (SD = 3959.60 cm^2) in municipal forests and 13874.08 cm^2 (SD = 4719.26 cm^2) in state forests. The mean number of trees per 500 m^2 plot is 12.08 (SD = 4.47) in municipal forests, 20.17 (SD = 6.83) in small-scale private forests and 11.33 (SD = 4.15) trees in state forests. The mean basal area of standing dead trees per plot is 411.11 cm^2 (SD = 665.06 cm^2) on small-scale private plots, on municipally owned plots 182.26 cm^2 (SD = 439.94 cm^2) and on state owned plots 81.03 cm^2 (SD = 206.03 cm^2). The proportion of standing dead trees is 1.61% in municipal forests, 2.70% in small-scale private forests and 1.63% in state-owned forests. The maximum DBH of trees is 96 cm in small-scale private forests, 86 cm in municipal forests and 80 cm in state owned forests. The mean DBH is 37.51 cm (SD = 11.79 cm) in state forests, 36.28 cm (SD = 11.83) in municipal forests and 34.36 cm (SD = 10.78) in small-scale private forests.

2.7. Data analysis

We classified the 31 different types of TMHs in the six functional groups 'fungi', 'epiphytes', 'cavities and pockets', 'bark injuries', 'crown injuries' and 'stem and base injuries' (Table 1). For each of the five functional groups of TMHs we calculated the mean frequency per tree, whereby the occurrences of the TMHs assigned to each group were summarised. The software R 3.1.2 was used for statistical computing and visualisation (R development Core Team, 2015). The significance of differences between forests of the three ownership types was tested by applying Analysis of Variance (ANOVA). Subsequently, we conducted pairwise Tukey Post-hoc tests to find out for which pairs of ownership type a significant difference exists. To assess the role of forest ownership we analysed the data on two scales: (1) individual trees and (2) sampling plots of 500 m^2.

2.7.1. Tree scale

We fitted a general linear model (GLM) for TMH occurrence on a single tree as response which included the eventual predictors DBH, ownership type, vitality, tree species, elevation, exposure, slope, relief, plot basal area, maximum DBH on the same plot, number of tree-species on the same plot, number of dead trees on the same plot, cluster (group of three plots of different ownership types) and plot.

The predictors for which the GLM indicated significance ($p < 0.05$) were thereafter used in generalized linear mixed effects models (GLMERs) for TMH occurrence as response. For this purpose we used the function 'glmer' which is provided with the r-package lme4 (Bates et al., 2015). We scaled all included continuous predictors and took account for the nested sampling design by adding a random effect for the clustered plots to the GLMER. Furthermore the variable tree species was added as a random effect. We used several predictor combinations in order to find the lowest Akaike information criterion (AIC) and to allow for an evaluation of the predictor effects by comparing the resulting AICs. The number of variables in the models was considered when comparing models because AIC is a method of assessing model fit which penalises for the number of estimated parameters (Dziak et al., 2012)

The occurrence of TMHs is reported to depend on tree species (Larrieu and Cabanettes, 2012; Regnery et al., 2013b) and tree vitality (Larrieu and Cabanettes, 2012). We separated the expected effect of ownership type on TMH occurrence from the tree species effect and the vitality effect by further investigating only living trees of the tree species European beech (*Fagus sylvatica* L.). For the visualisation of the DBH and TMH relation on the tree level we used generalized additive model (GAM) predictions (Wood, 2011). Thereby all continuous predictor variables except DBH are set to the median value; the categorical factor 'relief' is not included (see Harrell, 2001: p 136).

2.7.2. Plot scale

Analogue to the analysis on the tree scale we computed as a first step at the plot-scale analysis a GLM for the occurrence sum of TMHs as response. Occurrence sum of TMHs on a plot is the sum of TMH presences per tree of all trees on the plot. The GLM included the supposed predictors 'ownership type', 'plot basal area', 'mean DBH', 'number of tree species', 'number of dead trees', 'elevation', 'exposure', 'slope', 'relief', and 'cluster-ID'. We used the predictors which were indicated as significant by the GLM for calculating GLMERs and incorporated 'cluster-ID' as random effect in order to account for the nested three-plot-cluster study design. The further steps were as previously described for GLMERs at the tree scale analysis. Finally we predicted TMH occurrence sum on the plot scale for the tree owner categories by a GLMER using the predictor 'plot basal area' and a random effect for 'cluster-ID'.

To evaluate the TMH diversity related to forest area we counted how many of the 31 TMH types (Table 1) occurred on a 500 m^2 plot at least once (TMH richness). Moreover – in order to weight the differing frequencies of distinct TMHs – we calculated Shannon Indices (Spellberg and Fedor, 2003) using the equation $H = -\sum_{i=1}^{n} pi * \ln pi$, with pi representing the share of one TMH type within all TMH occurrences on a plot.

For the analysis of the TMH richness and TMH Shannon index on the plot scale we used GLM and a LM for an overview of p-values for the variables. Hereby we used the predictors 'ownership type', 'plot basal area', 'mean DBH', 'max DBH', 'number of tree species', 'number of dead trees', 'number of trees', 'elevation', 'exposure', 'slope', 'relief', and 'cluster-ID'.

Subsequently we conducted GLMERs for TMH richness as response utilising a Poisson distribution and LMERs (gaussian distributed) for TMH Shannon index as response, respectively. In the GLMERs and LMRs we included predictors for which the GLM had indicated significance and added other factors which we assessed as being meaningful. Cluster-ID was added as random effect to the GLMERs and LMERs as to account for the nested plots. All continuous predictors are scaled. We modelled GLMERs and LMRs with different predictor combinations using full maximum likelihood estimation and evaluated the models and predictors by calculating AICs.

3. Results

3.1. TMHs on the tree scale

The survey recorded a total of 1569 trees and a total of 1800 TMHs. The average number of different TMHs per tree is 0.98 (SD = 1.19) in state-owned forests, 1.39 (SD = 1.45) in small-scale private forests and 0.92 (SD = 1.18) in municipal forests. An ANOVA revealed significant ($p < 0.05$) differences at $p < 0.001$ for the three different types of ownership. Subsequent Tukey post hoc tests found no significance in the comparison between state forests and municipal forests ($p = 0.73$), whereas comparing small-scale private forests with the other ownership types resulted in values which indicated significance in both cases ($p < 0.001$). The TMH occurrence per tree in small-scale private forests is 1.42 times as much as in state forests and 1.52 times as much as in municipal forests.

On living trees, TMHs are significantly ($p < 0.001$) more frequent in small-scale private forests than in municipal or in state owned forests (Fig. 1). In contrast, standing dead trees of the investigated ownership types have similar TMH occurrences.

The TMH classification in functional groups provides a more detailed insight. The analysis of the mean TMH diversity per tree revealed differences between the functional groups as well as between the ownership types within a functional group (Fig. 2).

Epiphytes are the most frequent type of tree-related microhabitats followed by cavities and pockets. In all three TMH groups for which the Tuckey post hoc test indicates significant differences between the ownership types TMHs are most frequent in small-scale private forests.

The GLM which included all supposed predictors showed a significant influence on TMH occurrence per tree for the ownership type small-scale private ($p < 0.001$), the variables 'DBH' ($p < 0.001$), 'vitality' ($p < 0.001$), 'tree species' ($p < 0.001$), 'slope' ($p < 0.001$), relief category 'lower slope' ($p = 0.035$), 'number of tree species on the same plot' ($p = 0.004$), 'number of dead trees on the same plot' ($p = 0.043$) and 'cluster ID' ($p = 0.002$). 'Elevation', 'exposure', 'plot basal area', 'maximum DBH on the plot' and 'plot ID' had no significant effect on TMH occurrence per tree.

At GLMERs for TMH occurrence on a tree as response the lowest AIC resulted when the model comprised 'DBH', 'vitality', 'ownership type', 'slope', and 'number of tree species on a plot'. For this model the AIC is 4047.2. Taking out one predictor worsens the model and increases the AIC by 169.3 when dropping 'vitality'. Dropping 'DBH' instead increases the AIC by 124.4, dropping 'ownership type' causes an AIC increase of 15.2, dropping 'number of tree species on a plot' increases the AIC by 7.7, and an AIC increase of 1.5 results when the variable 'slope' is dropped (Table 2).

The best GLMER indicates significance for the predictors 'ownership type small-scale private' ($p < 0.001$), 'vitality' ($p < 0.001$), 'DBH' ($p < 0.001$) and 'N-tree species on the same plot' ($p = 0.002$).

The GAM predictions (Wood, 2011) for solely living trees of the species European beech (*Fagus sylvatica* L.) show an increase of TMH numbers in line with larger DBH values in all studied forests. Small-scale private forests provide the highest number of TMHs across the entire DBH range. At the lower end of the DBH range, *Fagus sylvatica* L. in state forests provide the second highest

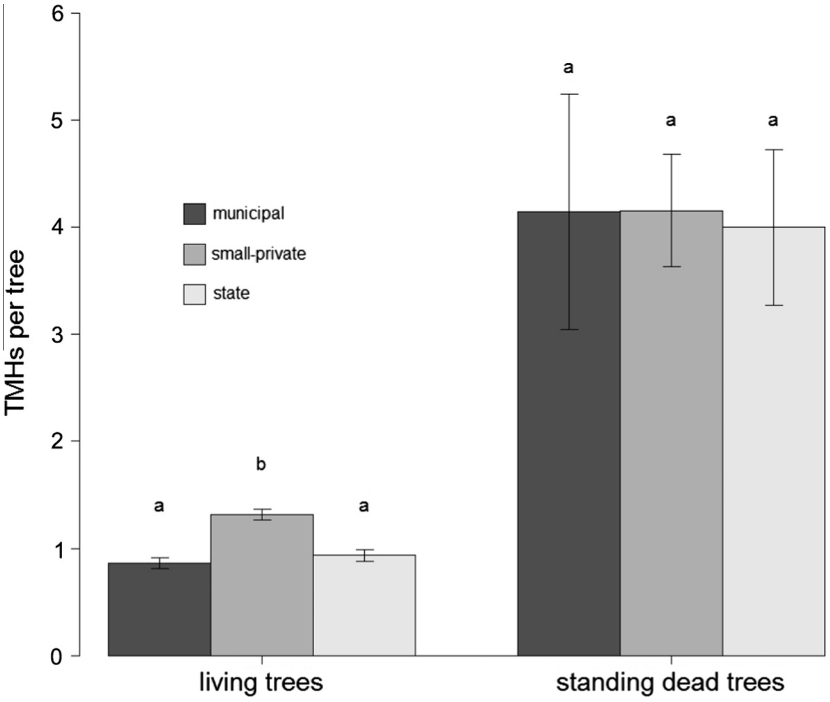

Fig. 1. Comparison of TMH occurrence on living or standing dead trees; mean and standard error of the mean (SEM). Different letters in a group indicate significant differences within the group (Tukey post hoc test; $p < 0.05$).

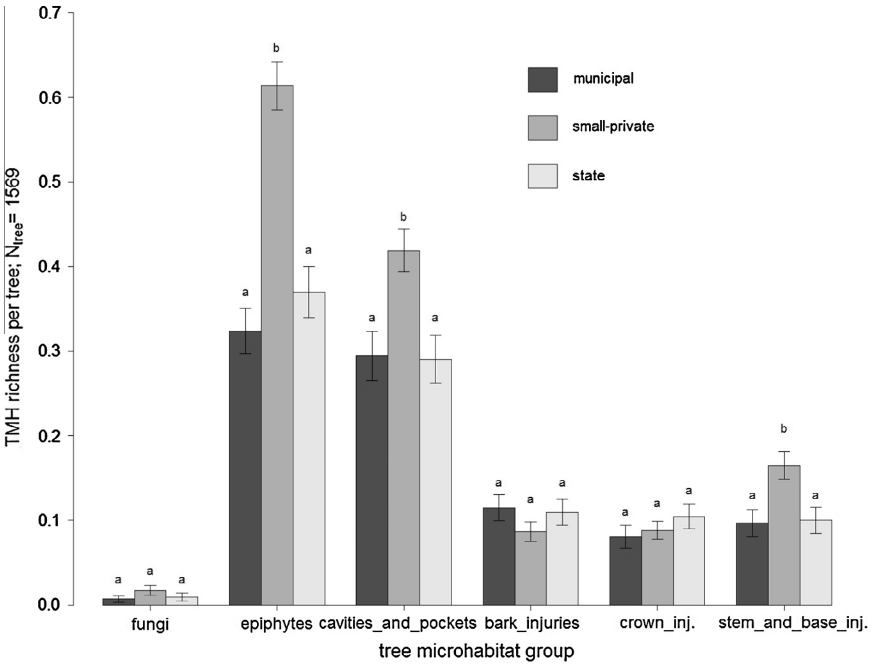

Fig. 2. TMHs per tree summarised in groups. Different letters in a group indicate significant differences within the group (Tukey post hoc test; $p < 0.05$).

Table 2
Fixed and random effects (RE) and AIC results of GMLERs for TMHs on the single tree scale (x = included effect; bold = model with the lowest AIC).

Owner ship type	Vitality	DBH	Slope	N-tree species on the plot	N-dead trees on the plot	Relief	Tree species (RE)	Cluster/plot (RE)	AIC
x	**x**	**x**	**x**	**x**			**x**	**x**	**4047.2**
x	x		x	x			x	x	4171.6
x		x	x	x			x	x	4216.5
	x	x	x	x			x	x	4062.4
x	x	x		x			x	x	4048.7
x	x	x	x				x	x	4054.9
	x	x	x	x		x	x	x	4058.8
x	x	x	x		x		x	x	4058.8

number of TMHs, but as DBH approaches 60 cm, the number of TMHs associated with this species is second highest in municipal forests (Fig. 3).

3.2. TMHs on the plot scale

3.2.1. TMH density

At a larger, plot-related scale, the differences between small-scale private forests and forests under municipal or state ownership are greater when compared to the single tree level. The sum of TMHs in small-scale private forests is more than twice as great compared to publicly owned forests. In municipal forests, the sum of all TMHs is 221.7 ha^{-1} (SD = 141.0), in small-scale private forests it is 558.3 ha^{-1} (SD = 365.4), and in state-owned forests it is 220.0 ha^{-1} (SD = 131.0). ANOVA and Tukey post hoc test show significant differences in pair wise comparisons between small-scale private forests and both types of publicly owned forests ($p < 0.001$), but not between municipal forests and state-owned forests.

The analysis of TMH groups reveals for all functional microhabitat groups that small-scale private forests have the highest density of microhabitats per hectare (Fig. 4 and Table 3). TMHs of the groups fungi, epiphytes, cavities and pockets, and base and stem injuries are in small-scale private forests more than twice as frequent in comparison to municipal forests or state owned forests.

In the comparison between small-scale private forests and municipal forests Tuckey post hoc tests reveal significant differences for 'fungi', 'epiphytes', 'cavities and pockets' and 'stem and base injuries'. The comparison between small-scale private forests and state-owned forests has the same result except for 'fungi'. In contrast, none of the TMH-groups had a p-value result which would indicate significant differences between state-owned forests and municipal forests.

The GLM for the TMH occurrence sum on plots as response shows significant effects of 'slope' ($p < 0.001$), 'plot basal area' ($p < 0.001$), 'ownership type' ($p < 0.001$), 'number of dead trees on the plot' ($p = 0.015$) and 'cluster-ID' ($p < 0.001$). The variables 'elevation', 'exposure', 'relief', 'number of tree species on the plot' and 'mean DBH' had p values above 0.05.

The lowest AIC results from the GLMER which uses 'plot basal area', 'ownership type', 'number of dead trees', 'slope' and 'mean DBH' (Table 4). Compared to the best model the AIC increases by 71.8 by if 'basal area' is removed, by 21.3 if 'ownership type' is removed, by 6.7 if 'slope' is removed, by 2.4 if 'mean DBH' is removed and by 1.3 if 'number of dead trees' is removed. If the predictors 'number of dead trees on the plot', 'slope' and 'mean DBH' are combined without adding 'basal area' or 'owner' the model AIC is much higher compared to models which include at least one of the latter predictors.

The GLMER predictions show an increase of TMHs when basal area increases for forests of all ownership types (Fig. 5). At the

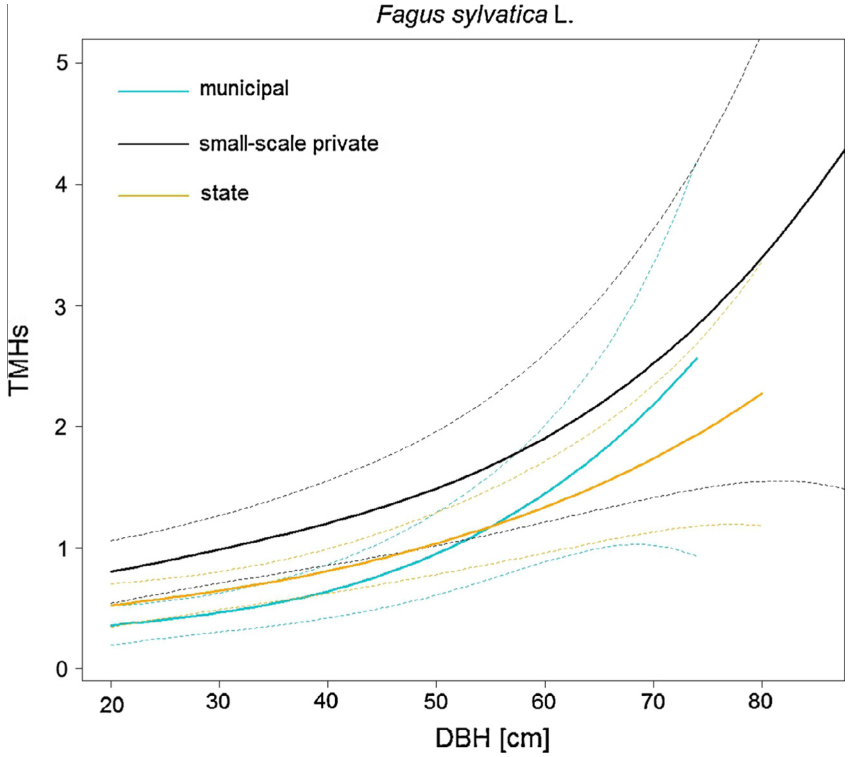

Fig. 3. Predicted number of TMHs per single tree for living European beech (*Fagus sylvatica* L.) (N = 1196) depending on DBH. For details on this kind of plot see Harrell, 2001: p 136.

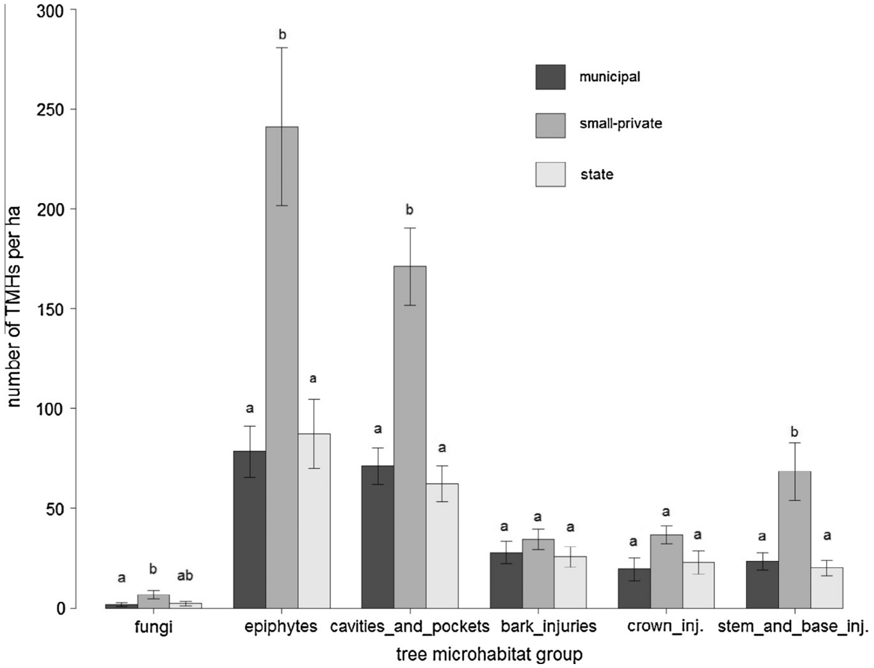

Fig. 4. Tree microhabitat density per hectare summarised in groups. Mean and SEM. Different letters in a group indicate significant differences within the group (Tukey post hoc test; $p < 0.05$).

Table 3
Mean and SD of TMH density per hectare. Tree microhabitats summarised in groups. $N_{TMH} = 1800$.

	Fungi	Epiphytes	Cavities and pockets	Bark injuries	Crown injuries	Stem and base injuries
Forest owner [TMH-number/ha; mean and SD]						
Municipal	1.67 (5.60)	78.33 (76.55)	71.11 (54.18)	27.78 (32.87)	19.44 (33.97)	23.33 (26.40)
Small-scale private	6.67 (1.64)	241.11 (237.31)	171.11 (116.47)	34.44 (30.84)	36.67 (27.26)	68.33 (87.16)
State	2.2 (6.37)	87.22 (103.11)	62.22 (53.83)	25.56 (30.09)	22.78 (35.18)	20.00 (23.90)
ANOVA [p]	0.0339	<0.001	<0.001	n.s.	n.s.	<0.001

Table 4
AIC results of GLMERs for the response TMH occurrence sum at the plot scale (x = included effect; bold = model with the lowest AIC).

Plot basal area	Owner ship type	Slope	Number of dead trees	Mean DBH	Cluster (RE)	AIC
x	**x**	**x**	**x**	**x**	**x**	**797.3**
x		x	x	x	x	818.6
	x	x	x	x	x	869.1
x	x	x	x		x	799.7
x	x		x	x	x	804.0
x	x	x		x	x	798.6
x	x				x	809.5
x	x			x	x	805.0
x		x	x		x	828.9
		x	x	x	x	1114.8
	x				x	889.6
x					x	865.8

same basal area value, small-scale private forests provide much more TMHs compared to municipal or state owned forests. At lower values of 'plot basal area' state forests provide more TMHs compared to municipal forests. Above basal area of about 14,000 cm^2 municipal forests provide more TMHs than state forests.

3.2.2. TMH diversity

The analysis of TMH diversity also shows significant differences between forests under the three different ownership types. The TMH diversity is highest in small-scale private forests (Fig. 6). This is also true with regards to occurrences of unique TMH types (TMH richness) as revealed by the Shannon Index. In both diversity measures the comparison between small-scale private and municipal forests and between small-scale private and state-owned forests results in significant values (Tukey post-hoc test, $p < 0.001$). In contrast, the comparison between the municipal and state ownership types does not show significant differences in the TMH diversity.

The GLM for TMH richness as response states only plot basal area as a significant predictor ($p = 0.013$). If 'plot basal area' is excluded 'ownership type small-private' is significant at $p = 0.012$. A comparison of GLMER AICs shows the lowest AIC for the GLMER which has the two predictors 'plot basal area' and 'ownership type' (Table 5). Adding 'ownership type' to 'plot basal area' improves the AIC more than the combination of other single predictors with 'basal area'. If the predictor 'ownership type' is combined with 'number of dead trees' the model performs better than in the case of the combination of 'plot basal area' with 'number of dead trees'. In contrast, 'plot basal area' combined with 'plot

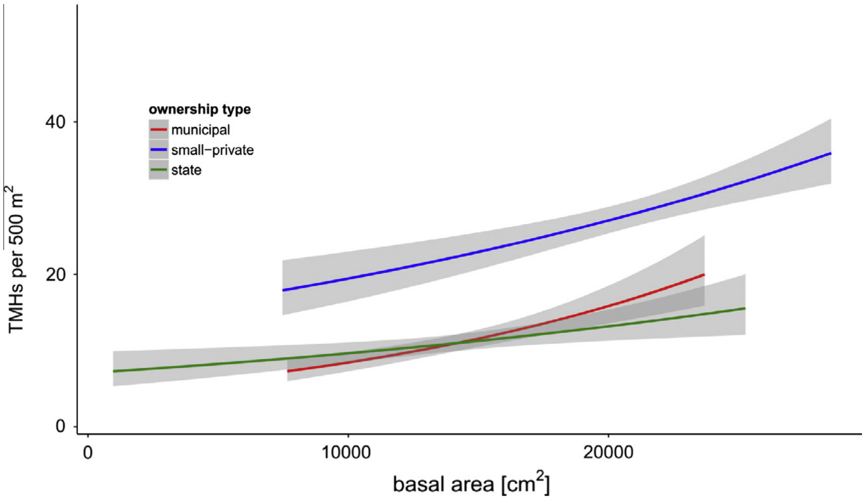

Fig. 5. GLMER predictions for TMH occurrence sum per 500 m^2 depending on basal area. GMLER using 'plot basal area' as predictor and 'cluster' as random effect.

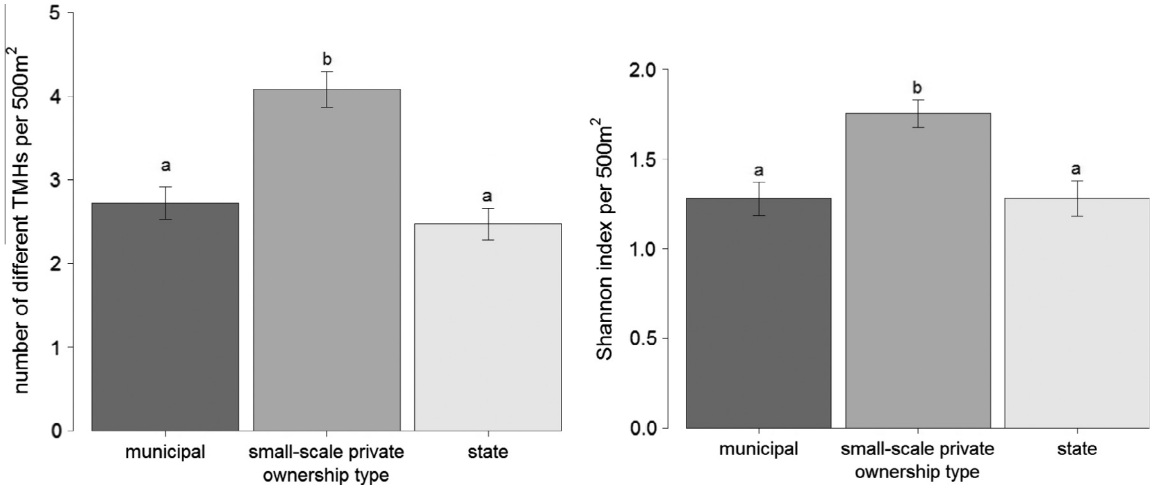

Fig. 6. Number of different tree microhabitat types (TMH richness) per 500 m^2 (left); Shannon index for TMHs on 500 m^2 plots (right). Different letters indicate significant differences (Tukey post hoc test; $p < 0.05$).

Table 5
AICs of GLMERs for unique TMHs (TMH richness) at the plot scale (x = included effect; bold = model with the lowest AIC).

Owner ship type	Plot basal area	Number of trees on the plot	Number of dead trees on the plot	Plot max DBH	Plot mean DBH	Cluster-ID (RE)	AIC
x	**x**					**x**	**373.61**
x			x			x	375.77
x				x		x	377.99
x					x	x	377.89
	x		x			x	378.48
	x			x		x	375.20
	x				x	x	374.66
x			x	x		x	379.96
	x		x	x		x	377.20
		x	x	x		x	377.97
			x	x		x	390.73

max DBH' or 'mean DBH' results in lower AICs as if 'ownership type' is combined with 'plot max DBH' or 'plot mean DBH'.

4. Discussion

4.1. Main findings

We analysed the indirect impact of forest ownership type on TMH occurrences and compared the importance of land ownership with that of biotic factors and abiotic landscape variables. Our main result is that forest ownership type has a strong effect on density and diversity of TMHs.

The results of the study support our three hypotheses. Small-scale private forests provide more TMHs per forest area, a higher TMH diversity and more TMHs per tree in comparison to municipal forests and state-owned forests. Municipal forests and state-owned forests do not differ significantly as regards TMHs.

4.1.1. Single tree scale

At the single tree level, the comparison of GLMER AICs suggests that tree vitality is the most relevant factor for TMH occurrences, followed by DBH. A higher number of TMHs on snags in comparison to living trees was also revealed by Regnery et al. (2013b). The relevance of the ownership type effect is on rank three. Adding the predictor 'ownership type' to the GLMER which already included the predictors 'vitality', 'DBH', 'slope' and 'number of tree species on the plot' improved the model AIC.

The GAM predictions for TMH occurrence on solely living trees of European beech confirm higher values at the entire DBH range for small-scale private forests in comparison to municipal forests or state owned forests. Bigger trees have more TMHs. This result is in accordance with earlier findings which describe a positive correlation between DBH and TMH occurrence (Larrieu and Cabanettes, 2012; Larrieu et al., 2012; Michel and Winter, 2009; Regnery et al., 2013b; Vuidot et al., 2011). A management effect was described by Winter and Möller (2008) who found increasing TMH occurrences in line with larger DBH in unmanaged forests, but not in managed forests or recently unmanaged forests.

However, at the single tree scale Vuidot et al. (2011) found no effect of management. This could be because of regionally different management rules or different forestry strategies such as regeneration, thinning and harvesting methods. In our study region, publicly managed beech stands are commonly thinned in periodic intervals, which is largely not the case in the extensively managed small-scale private forests.

Our analysis of the occurrence of TMH depending on DBH for solely living beech (*Fagus sylvatica L.*) as shown in Fig. 3 clearly underpins the hypothesis that management has an effect on TMH occurrences on the tree scale.

4.1.2. Plot scale

Forest ownership type shapes TMH occurrences on the plot scale via the basal area, diameter distribution and amount of dead trees. Our variable 'ownership type' integrates these parameters and includes ownership type effects which are not described by these stand-parameters.

At the plot level, the comparison of GLMER AICs suggests 'plot basal area' as the variable with the strongest effect on TMH density followed by 'ownership type'. 'Slope' is on rank three, 'mean DBH' on rank four and 'number of dead trees' on rank five.

At the single tree level, 'vitality' had the strongest effect on TMH occurrence. However, due to the small share of dead trees the variable 'dead trees per plot' was not ranked highly in the AIC-assessment of the importance of variables at the plot scale.

In terms of TMH diversity the combination of the predictors 'basal area' and 'ownership type' resulted in the better model fit than the combination of 'basal area' with 'mean DBH', 'max DBH' or 'number of dead trees'.

Small-scale private forests within the study region are less intensively exploited. This becomes obvious through a comparison of basal areas: 41.12 $m^2\,ha^{-1}$ in small-scale private forests, 27.64 $m^2\,ha^{-1}$ in municipal forests and 27.75 $m^2\,ha^{-1}$ in state-owned forests. The effect of forest management on TMHs at the area scale has been shown in previous studies (Michel and Winter, 2009; Vuidot et al., 2011; Winter and Möller, 2008; Winter et al., 2005).

4.2. Drivers

Most TMHs develop over time. The ownership type of forest properties has been persistent for more than 100 years in south-western Germany (Hasel, 1985). Hence, differences in the occurrence of TMHs which relate to the present ownership form can largely be associated with the corresponding management regime. In addition, old growth attributes could be developed in forests of all ownership types. In Germany, the historical deforestation reached its peak during the period of the years 1750–1850.

Small-scale private forests differ most from publicly managed forests in relation to the TMH groups 'epiphytes', 'cavities and pockets' and 'stem and base injuries'. Mosses and lichens are strikingly more abundant in small-scale private forests compared to municipal forests and state-owned forests. This can be explained, on the one hand, by higher and more constant air moisture due to larger basal area in small-scale private forests. On the other hand, the greater abundance of lichens points to longer periods of undisturbed development in apparently extensively managed or even unmanaged small-scale private forests. Lichens grow slowly, frequently only a few millimetres per year. Many of them need long periods of stable microclimates which are not present in intensively managed forests (Bradka et al., 2010).

Most bark injuries were observed below one meter stem height. They are presumably mostly the result of logging and wood transport activities during which moved stems and forestry machines graze the bark of trees in the work area. The intensively managed publicly owned forests had a higher number of bark injuries per tree. In contrast, on the plot scale small-scale private forests have the highest number of bark injuries. This can be explained by the higher number of trees per plot in small-scale private forests and the fact that besides manmade bark loss also natural caused injuries – e.g. bark loss caused by windfall of adjacent trees – contribute to the sum of this TMH type. The relevance of 'slope' for TMH density on the plot scale could reflect a less intensive management on steeper slopes as well as effects which are caused by erosion phenomena (e.g. more stem base cavities as a result of undermining or rock fall).

Three basic drivers of the reduced abundance of TMHs in the more intensively used publicly owned forests can be identified: (1) withdrawal of trees, (2) a shortened life span of the trees, and (3) silviculture and selected cutting as forestry encroachments. The withdrawal of trees is the most obvious driver. As each tree is a potential host of TMHs, each extraction represents a potential reduction of TMHs.

The second driver – the shortened life span of trees in managed forests (Jedicke, 2008) – reduces the probability of: injuries caused by external mechanical impacts; morphological responses to experienced weather extremes; and structure-forming biotic interactions e.g. with viruses, fungi or insects (Brechtel, 2002; Gibbons and Lindenmayer, 2002). The DBH of trees increases with increasing age. The negative effect of a shortened tree life span on TMHs in more intensively managed publicly owned forests is reflected in our results, specifically (1) in the high ranking of the DBH variable in the assessment of variable importance for single trees, and (2) in the high ranking of plot basal area in terms of variable importance at the plot scale and (3) in the correlation between increasing number of TMHs and increasing DBH in the generalized additive model.

Forestry – the third driver – shapes TMH development at several key stages: Species selection, regeneration method, thinning and DBH at logging. Business-oriented forestry measures focus on financial yield and promote trees that are free from sanitary risks and most highly rated in view of marketing properties such as timber quality (Klädtke and Abetz, 2001) and suitability for machine processing (Meschede and Heller, 2000). This approach is aimed at producing homogenous straight stems, free from defects, which implies a lack of TMHs. The effect of forestry measures is reflected in reduced occurrences of TMHs per tree and lower levels of TMHs related to DBH when comparing extensively used small-scale private forests with the more intensively used municipal forests or state-owned forests.

4.3. Links between ownership, forest management and tree microhabitats

Since the 1970s, close-to-nature forest management principles have been recognised under different terms as a guideline for sustainable forestry and adopted worldwide (Gamborg and Larsen, 2003). In the state forests of the study region, close-to-nature management has been the official forest management strategy since 1993 (MLR, 1993). Nevertheless, the applied forest management strongly reduces TMHs. Moreover, municipal forests and state-owned forests have been managed by the same state forest service for decades (Schaich and Plieninger, 2013). This may explain the similar results for TMH occurrences in forests under these ownership types.

In the same study site, Schaich and Plieninger (2013) found higher carbon storage, more structural diversity and larger amounts of lying dead wood in small-private forests compared to municipal and state-owned forests. State forests and communal forests have lower basal areas in comparison to small-scale private forests. In the publicly owned forests, selective shelterwood cutting aimed at stimulating natural regeneration and clear-away cutting to increase the growth of the remaining trees are common practice (Emborg, 1998; Schaich and Plieninger, 2013). The regeneration method targets dense sapling distribution with subsequent monopodial growth and natural loss of branches at the lower stem at young tree age. At higher tree age, stands are selectively thinned in periodic intervals where trees of lower quality are logged. Finally, both public ownership types aim for financial benefit and trees are used before the diameter increment gets too low or stem damages increase with advancing age. Consequently, there is a lack of TMHs. The small-scale private forests experienced most probably predominantly no controlled rejuvenation, remain largely unthinned and are only partly used for timber or firewood.

In terms of forest management, the owners of large forest properties are frequently motivated by economic considerations (Huntsinger et al., 2010; Pickenpack, 2004). In contrast, the motives of small-scale private owners are more diverse (Bieling, 2004; Dominguez and Shannon, 2011; Huntsinger et al., 1997) and besides economic aspects, recreation and nature conservation motives play an important role (Härdter, 2004). A high percentage of small-scale private forest owners live in cities (Ziegenspeck et al., 2004) and do not manage their forests at all or use them very extensively (Bieling, 2004). These factors contribute to the increased abundance of TMHs in small-scale private forests of the study region.

4.4. Implications

On the landscape scale of the Swabian Alb, small-scale private forests provide a high proportion of the overall supply of TMHs. This contribution is a crucial element of the landscape mosaic with the more open publicly owned forests. As the proportion of forest owners who are engaged in urban lifestyles has increased over the recent decades (Ziegenspeck et al., 2004), old growth attributes and TMHs within small private forests are likely to increase under constant framework conditions.

Expected higher demand for energy wood (Mantau and Saal, 2010) could jeopardise this development. Against the backdrop of climate change, potentials for fuel wood mobilisation from small-scale privately owned forests are being explored and incentive instruments are being developed or increasingly used. Examples include financial incentives for thinning, road construction or establishing forestry cooperatives (Plieninger et al., 2009; Verkerk et al., 2011). Such measures need to be harmonised with biodiversity goals and related financial efforts (Schaich and Plieninger, 2013).

The long-term provision of TMHs by small-scale private forest owners is not guaranteed. Future generations of small-scale forest owners could sell forest properties due to lost interest or because of financial constraints. An example offers the German agricultural sector which underwent a strong concentration of areas during the last decades (European Commission, 2016). However, as regards the German forestry sector a similar development is currently not observable. The amount of small-scale private forest owners which live an urban live style is increasing and the urban forest owners keep their forest property to fulfil non-materiel needs such as recovery, nature protection or pride (Ziegenspeck et al., 2004).

Studies of land ownership effects in other regions found less intensive land-use (Huntsinger et al., 1997) and more biodiversity (Lovett-Doust et al. 2003; Thomas et al., 1997) in state-owned lands compared to private lands. Forest biodiversity policies should consider which ownership types exist at the targeted region – e.g.

small-scale private or large-scale private – and tailor instruments according to the effect of each ownership type.

Populations of forest specialists are declining (Gregory et al., 2007). States have set aside forest areas as strict forest reserves which allow natural development of TMHs. But only 16.3% of the world's forests grow on formally protected lands (Morales-Hidalgo et al., 2015), which is not enough for long-term conservation success (Lindenmayer and Franklin, 2002). Because TMHs are key elements of forest biodiversity (e.g. Regnery et al., 2013a), a conceptual framework that would ensure sufficient availability of TMHs at the landscape scale and connectivity of populations is necessary (Lindenmayer et al. 2006). This framework needs to address all types of ownership which shape forests, be it through directives, incentives, or promotion of operative certifications.

Regarding resource-extracting forestry, our results suggest several approaches for promoting a greater abundance of TMHs: (1) an increased share of unused forest area, (2) longer rotation times and larger DBH-objectives respectively, (3) maintenance of higher basal area combined with less selective thinning (4) retention of trees with TMHs, and particularly those with many TMHs, (5) conservation of trees with large DBH as present or future TMH providers, (6) retention of standing dead trees. Using different combinations of these elements can foster forest variability at the landscape scale and promote biodiversity (Lindenmayer et al. 2006).

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