



Assessing selected microhabitat types on living trees in Oriental beech (*Fagus orientalis* L.) dominated forests in Iran

Ameneh Khanalizadeh¹ · Javad Eshaghi Rad¹ · Ghavamodin Zahedi Amiri² · Habib Zare³ · Werner Rammer⁴ · Manfred J. Lexer⁴

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Abstract

• **Key message** On the selected sites in the investigated Oriental beech (*Fagus orientalis* L.) dominated forests in Iran with an extensive individual tree selection system, tree microhabitats (MH) are more influenced by tree level factors such as tree species and DBH than by plot level factors such as plot basal area or size and species diversity.

• **Context** Despite the ecological importance of tree microhabitats for biodiversity, there is a lack of information about the occurrence of microhabitat features in Hyrcanian forests in Northern Iran.

• **Aims** The aims of this study were to assess selected MH types on living trees in forests managed with an individual tree selection system and forests unmanaged since at least 30 years and to study the effect of tree and plot level factors on their occurrence.

• **Methods** A total of 120 circular sample plots were used to collect tree level microhabitat information at six different sites in Oriental beech forests in Iran. Pairs of managed and recently unmanaged forests were located at six sites. Generalized linear mixed models were employed to analyze (i) the effect of management on microhabitat occurrence, and (ii) to explain the occurrence of microhabitats at tree level.

• **Results** There was no significant difference in total number of assessed microhabitats per ha in forests managed with a low-intensity management regime with individual tree selection versus recently unmanaged forests (no management intervention for at least 30 years). Stem cavity with decay was by far the most frequent microhabitat type in managed (16.5 per ha) as well as in recently unmanaged forests (14.2 per ha). Hornbeam and oak trees have a higher probability to host microhabitats (bark loss, woodpecker cavity, and stem cavities) than the dominant oriental beech. Suppressed trees indicated by basal area of larger trees have a lower probability to show bark loss and conks of fungi.

• **Conclusion** Models of microhabitat occurrence on trees have potential to support the development of management guidelines to foster biodiversity.

Keywords Forest management · Tree microhabitats · Hyrcanian forests · Stem cavity · Individual tree selection system · Oriental beech

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✉ Javad Eshaghi Rad
j.eshagh@umia.ac.ir

¹ Department of Forestry, Faculty of Natural Resources, Urmia University, P.O. Box 165, Sero Blvd, Urmia, West Azarbayjan, Iran

² Faculty of Natural Resources, University of Tehran, Karaj, Iran

³ Research Institute of Forests and Rangelands, Nowshahr Botanical Garden, Agricultural Research, Education and Extension Organization, Areo, Tehran, Iran

⁴ Institute of Silviculture, University of Natural Resources and Life Sciences, Vienna (BOKU), Peter-Jordan-Straße 82, 1190 Vienna, Austria

1 Introduction

The maintenance and enhancement of biodiversity plays an important role within any framework of sustainable forest management (CIFOR 1999; Forest Europe 2009; FSC 2010; PEFC 2010; CBD 2010). The integration of biodiversity under the umbrella of sustainable forest management (SFM) is particularly important as it is increasingly clear that just setting aside some shares of forest area as strict conservation areas will not be sufficient to preserve the level of biological diversity that is required to maintain the “evolutionary potential” of forest ecosystems in a changing climate (e.g., Hunter 1999; Wintle and Lindenmayer 2008). Consequently, it is essential to provide guidelines for forest management to policy makers

and managers to support the development of policies and management concepts that integrate the maintenance of biological diversity in operational forest management. Indicators such as tree species composition and diversity, vertical stand structure, and deadwood quantity and quality have been frequently used to assess and monitor the level of biodiversity (Noss 1990; Gaston and Spicer 2004). While these approaches aim at the characterization of biodiversity in a holistic sense, the conservation of specific species may require the provision of targeted habitats. To characterize the habitat quality for specific species such as birds (Hodge and Peterken 1998), fungi (Tomaio et al. 2020), or ungulates (Heinze et al. 2011) indicator sets including, for instance, crown closure, large living trees, and large standing deadwood (Irauschek et al. 2017) have been used. Tree microhabitats, defined as peculiarities, that are not born by all trees (Larrieu et al. 2018), constitute another habitat component related to forest biodiversity (Grove 2002; Paillet et al. 2010; Stokland et al. 2012). Overall, microhabitat richness and diversity indicate taxonomic diversity which in turn supports food webs and are thus considered to play an important role for the functioning of forest ecosystems (Michel and Winter 2009). Several microhabitats are created by species themselves (e.g., woodpeckers and fungi) and others by natural factors such as wind, frost, or lightning strike and are then used by certain species (Gibbons and Lindenmayer 2002; Cockle et al. 2011).

Forest management controls species composition and dimensional diversity of trees via tending, thinning, and rejuvenation measures (e.g., Smith et al. 1997). Timber quality standards are negatively correlated with many microhabitat features such as conks and stem cavities. Thus, standard tending and thinning operations remove live trees which do not meet timber quality standards but compete with trees of better quality and thus reduce the number of trees that bear microhabitat structures. Although some studies do not report a clear signal of forest management on tree-related microhabitat density (e.g., Vuidot et al. 2011), in general, forests that have not been managed for a long time have a higher density of tree-related microhabitats (Winter and Möller 2008; Michel and Winter 2009; Paillet et al. 2017). Larrieu et al. (2017) emphasize that time since last management intervention correlates positively with microhabitat density. However, this relationship may not be continuous and linear. Thus, notwithstanding the overall importance of deadwood, microhabitats on live trees are supposed to constitute a critical link between forest management and forest biodiversity (Augustynczyk et al. 2019; Johann and Schaich 2016; Larrieu et al. 2012).

Focusing on individual tree level, the species, tree dimension, and stand structural characteristics such as stand density which characterize the neighborhood of a target tree have been reported to affect the occurrence of tree born microhabitats. For instance, Vuidot et al. (2011) found more microhabitats on large trees. Regnery et al. (2013) report in

their work on French forests that oak and beech generally bear more microhabitats compared to conifer species. For European beech and Douglas-fir forests, tree density influences the occurrence of microhabitats (Winter et al. 2015).

Temperate-mixed forests in the Hyrcanian region in northern Iran are one of the most important natural ecosystems with the highest economic value and a key role in the conservation of forest biodiversity in Iran. These forests are characterized by a heterogeneous stand structure, either horizontal or vertical (Sefedi et al. 2016). The most abundant characteristic tree species is *Fagus orientalis* L. Today, major shares of these Hyrcanian forests are managed with individual tree selection systems with interventions every 10 years intending to mimic natural gap dynamics processes. Despite the ecological importance of tree microhabitats for biodiversity, there is a lack of information about the impact of this management approach on tree microhabitat occurrence in Oriental beech (*Fagus orientalis* L.) dominated forests in Iran.

2 Objectives

To support the decision making process on sustainable management approaches for Hyrcanian forests, the aim of this paper is to compare microhabitat occurrence on live trees in managed and recently unmanaged Oriental beech (*Fagus orientalis* L.)-dominated forests in Iran.

Specifically, we address the following questions.

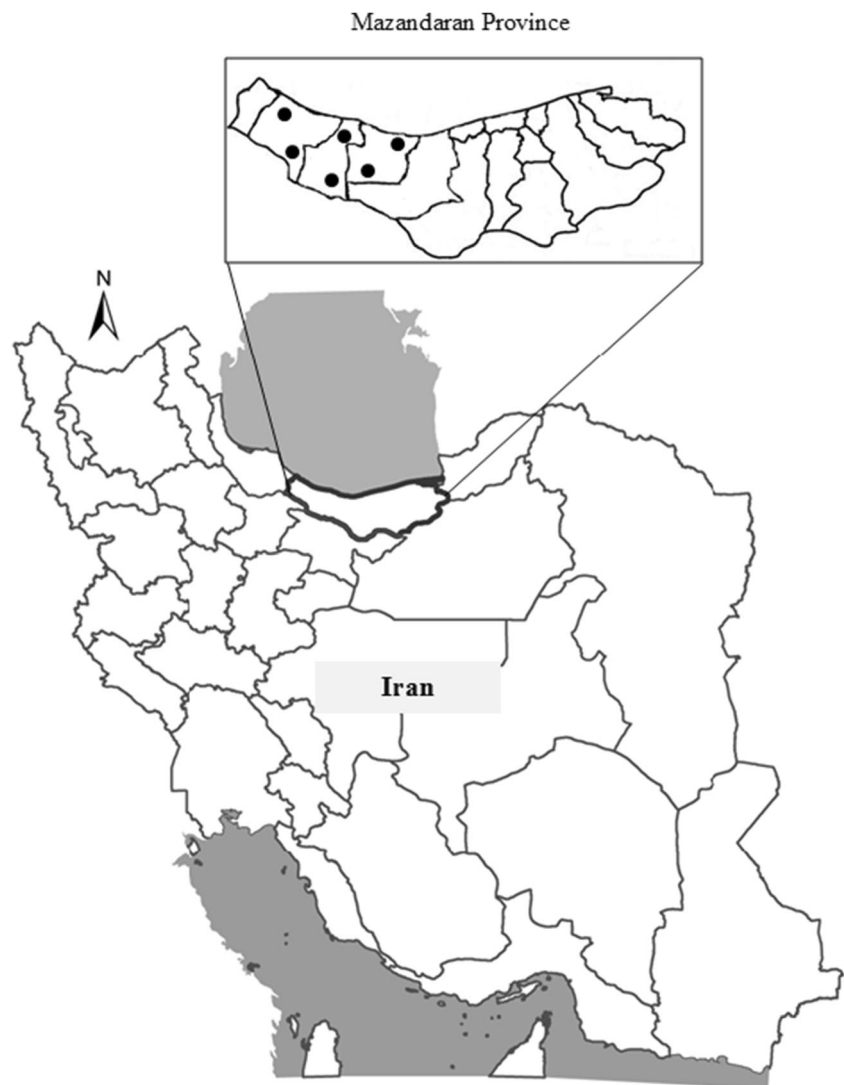
- (1) Does individual tree selection management in Oriental beech forests in Iran forests lead to a decrease in total densities of microhabitats on live trees?
- (2) Which tree and stand level factors influence the occurrence of microhabitats on live trees in Oriental beech forests in Iran?

3 Materials and methods

3.1 Study sites

The studied forests were located in the Hyrcanian forest zone in northern Iran, encompassing three lowland mixed forests (Dehga, Vashmerd, and Lakoobon) and three upland mixed forests (Jamand, Lalis, and Shirakones) (Fig. 1). The elevation ranged from 400 to 950 m for lowland and 1250 to 1850 m for upland sites. At all sites, the most abundant species were Oriental beech (*Fagus orientalis* L.) and hornbeam (*Carpinus betulus* L.) except for the Dehga site. At lowland sites, Ironwood (*Parrotia persica* DC. C.A. May) and Caucasian persimmon (*Diospyros lotus* L.) were major co-dominant species while in upland forests, alder (*Alnus*

Fig. 1 Location of study area within Iran. Black circles represent the six study sites



subcordata C. A. May) was the most abundant admixed species. The sites were selected so as to have similar site conditions and identical historical use practices for managed and unmanaged forests.

At each of the six sites, managed compartments (MAN) were compared to compartments that had not been managed since at least 30 years (NOM) (FRWO 2011). The management regime in the managed forests is a selection system where individual trees are selected for harvest that are either economically mature (i.e., large diameter) or of bad quality, thus hampering the development or ingrowth of trees with better quality in large dimension DBH classes. Interventions usually happen every 10 years. The annual allowable cut within this individual tree selection system as practiced in the Hyrcanian forests is usually 1% of standing volume (Marvie Mohadjer 2007). Standing volume in these forests is between 400 and 500 m³ ha⁻¹ (Sagheb-Talebi et al. 2004), resulting in harvested volume of 40–50 m³ ha⁻¹ in each intervention.

Planned forest management activities including the preparation of management plans in Hyrcanian region of northern Iran started in the 1940s after establishment of a governmental Forest Department. Also, forest management plans have been implemented only in 60% of these forests over the last 6 decades and consequently unmanaged and near natural forests do still exist in Hyrcanian forests of Iran (Sagheb-Talebi et al. 2005). In the beginning of this period, these forests partly have been managed by shelterwood systems for three decades but because of regeneration problems, this method was replaced by an individual tree selection system (Sagheb-Talebi et al. 2014). For our study, managed forests were selected from the forests in which the selection system has been used for at least 30 years (FRWO 2011). Recently, unmanaged forests that were selected for this study have not been subjected to any forest management activity for many years, even before the start of implementation of the individual tree selection regime more than 30 years ago. It is important to note that because of

lacking road networks and forest management plans before the 1960–1970s logging was very limited and traditional covering needs for local fuel and household uses only (Jourgholami and Majnounian 2013; Sagheb-Talebi et al. 2005). Table 1 shows some characteristics of the study sites.

3.2 Data collection

In each of the studied forests (3 upland and 3 lowland sites with recently unmanaged and managed compartments at each site), ten 0.1-ha circular plots were installed in managed (MAN) and unmanaged (NOM) compartments respectively, using a regular grid of 100 × 200-m spacing resulting in a total of 120 plots. On each plot, all living trees larger 7.5-cm diameter at breast height (DBH) were measured and species, DBH, and the frequency of a predefined set of microhabitat types were recorded. To record microhabitats, we walked around each living tree from nearby and from further distance of the tree and visually searched the trunk from the ground up to the canopy. Also, all of the measurements were carried out by one observer to avoid variability due to multiple observers.

Five pre-defined broad microhabitat types were used according to Winter and Möller (2008), Michel and Winter (2009), and Paillet et al. (2017) (Table 2). We focused on microhabitats which are common, have characteristic, and generally known for their relevant relationship with biodiversity of old growth forests. Also, most of the microhabitat types which were addressed in other studies were too scarce or related to coniferous species such as resin drops which do not exist in our studied forests.

3.3 Data preparation

For the 12 assessment entities (managed and recently unmanaged forests at 6 sites), the species composition was calculated based on basal area. The stem number per species ($n_{(i)}$ ha⁻¹) was calculated in 10 cm DBH categories.

At plot-level size diversity (D) was calculated based on Shannon's index of species diversity to consider the structural complexity at a plot. D was calculated from basal area shares of all trees in 10 cm DBH classes (N_{DBH}) where g_i is the basal

area in a DBH category and G is the total basal area on a plot (Eq. 1).

$$D = - \sum_{i=1}^{N_{DBH}} \frac{g_i}{G} \ln \left(\frac{g_i}{G} \right) \quad (1)$$

A widely used index to assess tree species diversity at the stand level is Shannon's entropy index, H (McElhinny et al. 2005, Neumann and Starlinger 2001), which takes into account the number of species in the stand and their relative abundance (Eq. 2). In the current study, basal area of a species was used with S the number of species and p_i as the ratio of the basal area of species (g_i) and G as the total basal area over all species. Plot level species diversity (SpD) is then calculated as the true diversity index (Jost 2006).

$$\text{SpD} = \exp(H) \quad (2)$$

$$H = - \sum_{i=1}^S p_i \ln(p_i)$$

Furthermore, as an indicator of competition by other trees on the plot, the basal area fraction of all trees larger than the target tree was calculated (BAL).

3.4 Statistical analyses

To compare managed against recently unmanaged forests, a generalized linear mixed model with a Poisson link function was used. Site and plot were defined as random factors to account for the pairing of managed and recently unmanaged plots at a site. Response variable was the number of microhabitats per plot; predictor variables were the mode of management and basal area. Based on exploratory analysis, tree species were grouped into the three categories "Quercus," "Carpinus," and "other species." Models were specified for each microhabitat type as well as for the aggregate including all microhabitats.

To account for the hierarchical structure of the data also at the tree level, generalized linear mixed models with a binomial link function were employed to analyze the fixed effects of tree species, DBH, and the plot level predictors BA (basal

Table 1 Characterization of the study sites (Forest, Range, and Watershed Organization 2011)

Forest sites	Mean temperature (°C)	Mean precipitation (mm)	Soil texture	Slope (%)	Aspect	Managed forest area (ha)	Unmanaged forest area (ha)
Dehga	15.2	980	Loam	15–25	N-NE	71	59
Vashmerd	12.7	1188	Loam	15–30	N-NW	34	58
Lakoobon	12.3	1093	Clay loam	20–35	NW-W	24.7	92
Jamand	10.4	753	Loam	20–35	NE-E	64	47
Lalis	8.7	731	Clay loam	15–35	NW-W	67	59
Shirakones	8.5	1087	Loam	20–30	NW-W	113	126

Table 2 Microhabitat types as defined for the current study

Microhabitat type	Description
Bark loss	Patches with bark loss of at least 5 cm × 5 cm mainly caused by felling or natural falling of trees
Woodpecker cavity	Woodpecker hole in the wood that indicates a cavity with a minimum diameter of 2 cm
Broken tree top	At least 50% of the tree crown has broken off
Conks of fungi	Fungi potentially indicating stem rot
Stem cavity with decay	Cavity at the base of the tree trunk or along the stem in an advanced decay stage and with mold.

area), BAL (basal area fraction of all trees larger than the target tree), D and SpD as well as the interaction terms of DBH with BA and BAL. The plot was defined as random factor to induce a correlation structure between observations at plots within the same site. Response variable were binary coded (0.1) occurrences of a specific microhabitat type on a tree. For the analysis stepwise backward, variable selection was used where in each iteration, the least significant predictor was dropped until all remaining predictors were significant at $p = 0.05$ level (Zuur et al. 2009). Before entering them into the model development routine, all continuous variables were scaled referring to mean = 0 and standard deviation = 1. Tree species were grouped into categories “*Quercus*,” “*Carpinus*,” and “other species.”

For each of the microhabitat type, a model was fitted. To assess the goodness of fit of the models’ sensitivity (i.e., the proportion of true positives) and specificity (i.e., the proportion of true negatives) were calculated from a confusion matrix. Furthermore, the area under the receiver operator characteristic curve (AUC) was used. AUC is the probability that a randomly selected observed positive event has a higher predicted probability value than a randomly selected observed negative event (Fawcett 2006).

The original parameter estimates for fixed effects were log odds of the scaled variables and had to be rescaled for interpretation. The impacts of the predictor variables in the models were assessed with partial effects plots. Partial effects measure the change in the expected value of predicted probability as a result of the change of a specific predictor variable while keeping all the other co-variables at a specific value. Here the median calculated from the available database was used. Log odds were transformed into probabilities of occurrence of a microhabitat type employing Eq. (3).

$$p(x) = \frac{\text{odds}(x)}{[1 + \text{odds}(x)]} \quad (3)$$

For statistical analyses, the `glmer` functions from the `lme4` package were used; variance inflation was analyzed with function `vif` from `car` package in R version 3.4.1 (Bates et al. 2015).

4 Results

4.1 Species composition and stand structure

Oriental beech had the highest basal area ($\text{m}^2 \text{ha}^{-1}$) except at the site Dehga where several other broadleaved species such as *Parrotia* and *Dyospyrus* were dominating the species composition in terms of basal area (Table 3).

The diameter distribution had a typical reversed J-shape in managed as well as recently unmanaged forests at all six sites (Fig. 2). On average, basal area in recently unmanaged forests was larger compared to managed forests except in Shirakones. In recently unmanaged forests, the number of very large trees (DBH > 80 cm) on average was higher than in managed forests (12.17 ± 1.68 trees per ha in managed forests, 20.17 ± 2.20 in unmanaged forests, difference is significant at $\alpha = 0.05$). Accordingly, due to a lower proportion of stand basal area from large-diameter trees and subsequently higher light levels in the canopy, the density of small trees (i.e., recruits) was larger in managed forests (293.50 ± 18.38 trees per ha with DBH < 80 cm in managed forests versus 238.33 ± 19.22 in unmanaged forests; difference is significant at $\alpha = 0.05$).

4.2 Microhabitats in managed and unmanaged forests

In total, 272 microhabitats of the five microhabitat types defined for this study (compare Table 2) were observed on 3382 measured trees over all sample plots. Stem cavity with decay was by far the most abundant microhabitat type in managed (16.5 occurrences per ha) as well as in recently unmanaged (14.2 per ha) forests (Fig. 3). The variation between the plots was huge. Subsequently, there was no significant difference between managed and recently unmanaged forests, neither at the level of individual microhabitat types nor in the total number of microhabitats (Table 4, Table 8 in the Annex). Basal area and species shares were not significant as predictor variables (Table 5).

Table 3 Tree species composition ($m^2 ha^{-1}$ basal area) at the six sites used in this study

Site	Management	Basal area ($m^2 ha^{-1}$)						Total
		Fagus	Acer	Alnus	Carpinus	Quercus	Other	
Dehga	Managed	0.00	0.00	9.32	7.99	4.20	13.1	34.66
Dehga	Unmanaged	0.20	0.03	7.34	17.76	4.78	4.80	34.91
Jamand	Managed	20.40	0.10	2.46	4.88	2.38	0.03	30.25
Jamand	Unmanaged	35.84	1.87	5.88	7.36	0.35	0.00	51.30
Lakoobon	Managed	20.23	3.83	0.00	3.00	0.00	0.75	27.81
Lakoobon	Unmanaged	33.15	3.52	0.00	2.87	0.00	1.47	41.02
Lalis	Managed	26.81	2.47	1.47	6.53	0.63	0.30	38.21
Lalis	Unmanaged	33.19	2.48	0.79	1.88	0.89	0.00	39.23
Shirakones	Managed	35.81	3.35	1.14	2.70	0.09	0.00	43.09
Shirakones	Unmanaged	36.21	0.36	2.21	0.74	0.00	0.02	39.54
Vashmerd	Managed	19.59	2.91	0.00	6.15	2.90	1.18	32.72
Vashmerd	Unmanaged	23.07	7.40	0.00	4.18	0.00	0.18	34.84

Fig. 2 Diameter distribution (stems per hectare in 10 cm DBH classes) in managed and recently unmanaged Hyrcanian forests at six sites (Filled circles represent mean value, $n=20$)

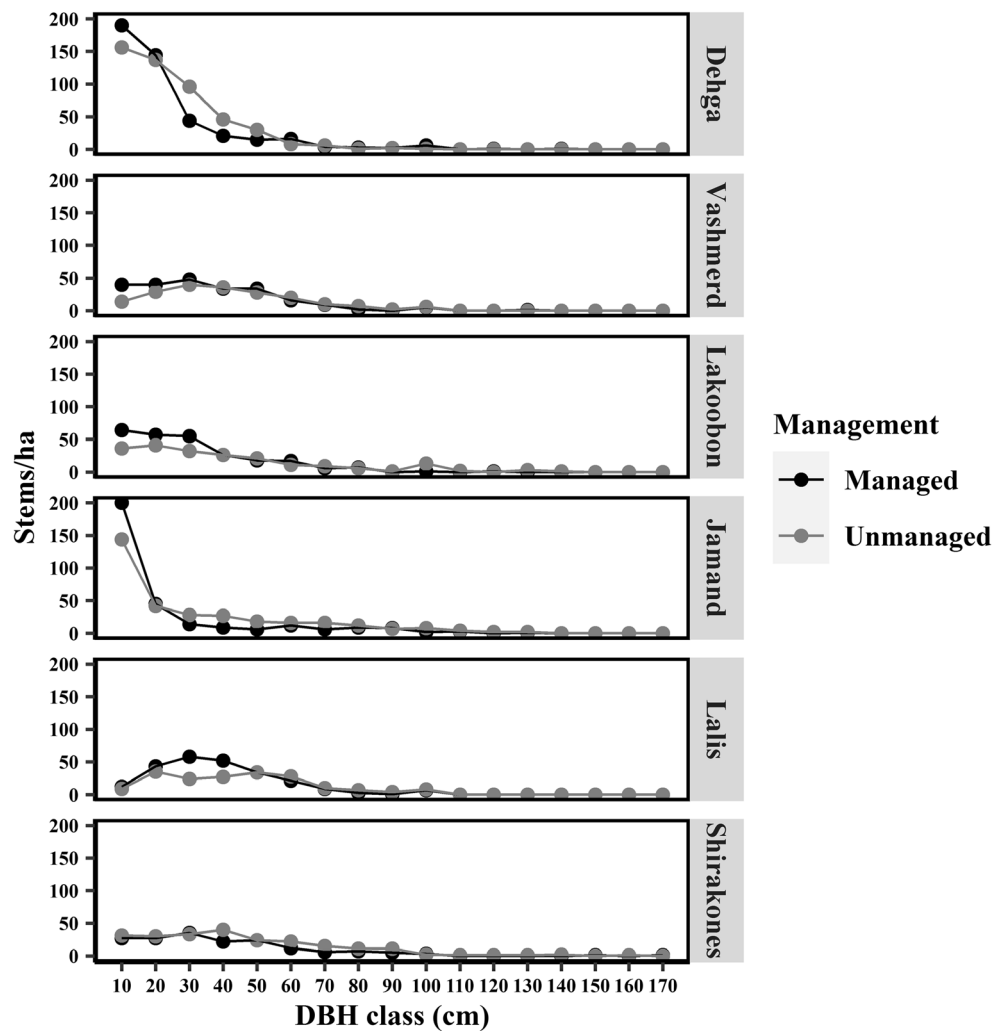
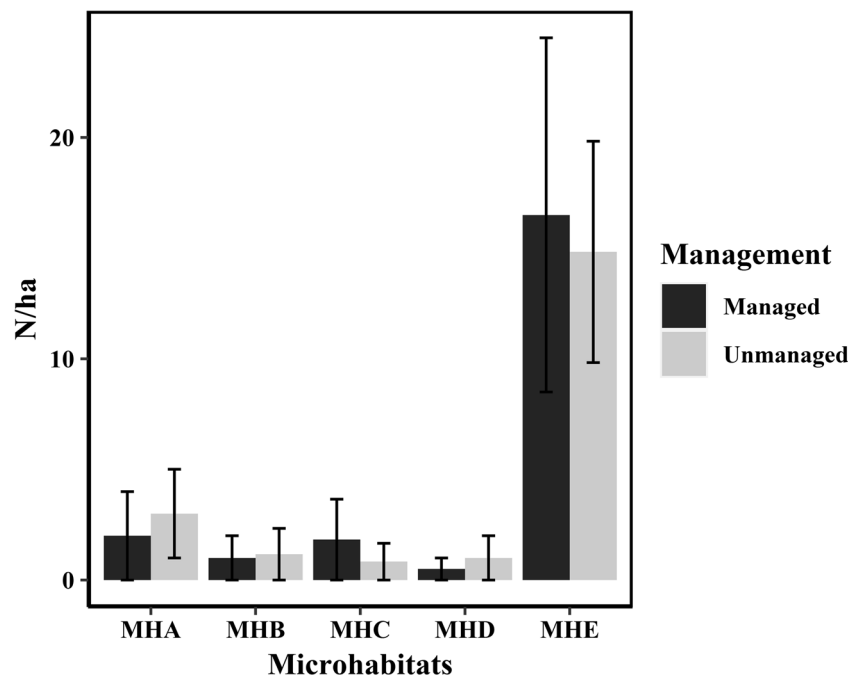


Fig. 3 Number of microhabitats per hectare in managed and recently unmanaged Hyrcanian forests (columns represent mean value, $n = 12$; whiskers represent standard deviation). MHA bark loss, MHB woodpecker cavity, MHC broken tree top, MHD conks of fungi, MHE stem cavity with decay



4.3 Microhabitat occurrence at tree level

The models for predicting the occurrence of microhabitat types at tree level are shown in Table 6, partial effects graphs in Figs. 4, 5, and 6. Overall, the models contain DBH, BA, BAL, Quercus, Carpinus, as well as the interaction term of DBH and BAL. D and SpD were not significant in any of the microhabitat models. The predicted probability of bark loss is higher in oak compared to other species and increases with BA. The higher the overtopping basal area, the lower is the probability of a bark loss (Fig. 4). In other words, a dominant oak tree in a forest with high basal area has the largest probability to show bark loss. The occurrence of conks and fungi is not significantly associated with any of the predictor variables. There is a slight but significant reduction of occurrence probability with increasing BAL (Fig. 4). Woodpecker cavities are most likely to occur at a large Carpinus tree (Fig. 5). Interesting is the model for the occurrence of broken tree tops. In general, the probability increases with DBH, indicating that the highest trees are most vulnerable to top breakage. However, the interaction term shows that beyond a certain

level of basal area density at a plot, the probability of top breakage starts to decrease (Fig. 5). This may be interpreted as an effect of collective stability within the tree population.

Not surprisingly, stem cavities with decay occur most likely on large trees, particularly on Carpinus and oak trees with minor effects of interacting plot basal area (Fig. 5).

Analysis of the confusion matrix from employing the fitted models to classify each tree as either bearing a specific microhabitat or not indicated reasonable behavior of the models (see Table 9 in Annex). Specificity of all models was high which means that most of the trees without a microhabitat were correctly classified. Sensitivity, meaning the correctly classified occurrences of microhabitats, was between 0.17 and 0.48. For conks of fungi, sensitivity was at a rather low value of 0.11.

AUC tells how good a model is in distinguishing between classes. The higher and closer AUC to 1.0, the better. An AUC of 0.5 tells that the model has no separation capacity at all. AUC values were calculated for models with and without random effects and indicated a reasonable predictive ability (Table 7).

Table 4 Significance of fixed effect “management” in generalized linear mixed models of microhabitat abundance after accounting for site and plot

Microhabitat type	$P(> Z)$
Bark loss	0.692
Woodpecker cavity	0.473
Broken tree top	0.294
Fungi	0.528
Stem cavity	0.311
All microhabitat types	0.527

Table 5 Mean value and min–max range of plot and tree level predictor variables used in the general linear mixed models analysis

Predictor variable	Mean	Min–max range
Diameter at breast height (DBH) (cm)	33.6	7.5–170
Basal area above (BAL) (–)	0.75	0–0.999
Plot basal area (BA) (m ²)	36.6	9.0–81.4
Species diversity (SD) (–)	2.3	– 1–4.5
Tree size diversity (spD) (–)	5.4	3.0–8.6

Table 6 Estimated model coefficients for the generalized linear mixed models for microhabitat occurrence. $P(>|Z|) < 0.05$. For microhabitat descriptions see Table 2

Predictor variable	bark loss		woodpecker cavity		broken tree top		Conks of fungi		stem cavity	
	Estimate	Std err	Estimate	Std err	Estimate	Std err	Estimate	Std err	Estimate	Std err
(Intercept)	- 5.4076	0.2774	- 7.8627	1.0276	- 7.9388	2.5720	- 6.2152	0.4126	- 3.5093	0.1421
DBH			0.0359	0.0097	0.0210	0.0089			0.0346	0.0031
BA	0.0397	0.0135								
DBH X BA					- 0.0020	0.0009			- 0.0005	0.0002
BAL	- 3.0866	0.5551					- 2.4862	0.9549		
Quercus	1.5289	0.5973							0.9390	0.4602
Carpinus			1.7134	0.6849					1.0014	0.1930

5 Discussion

Generally, biodiversity is composed of diversity within species, between species and of ecosystems (CBD 2010). Species diversity could be directly assessed (Puumalainen 2001). However, depending on the taxonomic group and the scale at which it is evaluated, such assessments are very resource intensive and time consuming. Instead, using tree microhabitat as indicators can provide proxy information about species which use such microhabitats in a rapid and cost-effective way (Michel and Winter 2009; Regnery et al. 2013). Since about one decade, studies have accumulated in the scientific literature that reports about microhabitat inventories in different forest types, comparative analysis of managed and unmanaged forests, as well as attempts to explain the occurrence of microhabitats at stand and tree level with various predictors, including ownership type (Johann and Schaich 2016), management regime (Vuidot et al. 2011), stand density and diversity (Grossman et al. 2018), and tree level attributes such as DBH, species, and tree vitality (Larrieu et al. 2014).

For temperate beech-dominated forests in Germany, which are ecologically comparable to Hyrcanian forests, Johann and Schaich (2016) report in state-owned beech forests the number of microhabitats per ha on living trees. Particularly, epiphytes and crown injuries added to microhabitat density in their study. These microhabitat types were not considered in our study because they were too scarce in our studied forests. If we recalculate microhabitat occurrence per tree for similar groups of microhabitat features, the densities for woodpecker cavities (0.00384 per tree), conks of fungi (0.00266 per tree), and stem cavities (0.0544 per tree) in our study are very similar to the findings of Johann and Schaich (2016) in state owned forests in Germany (0.0047, 0.0093, 0.0396). There were substantially less bark loss features in Hyrcanian forests, but more broken tree tops compared to the Central European beech forests.

While in general these comparative analyses confirm the order of magnitude of some major microhabitat types, it also points at a crucial problem when synthesizing findings from the literature. In many cases, differences in employed sets of microhabitats and their specific definitions defy a direct comparison between studies. The number of different microhabitat types that have been used in

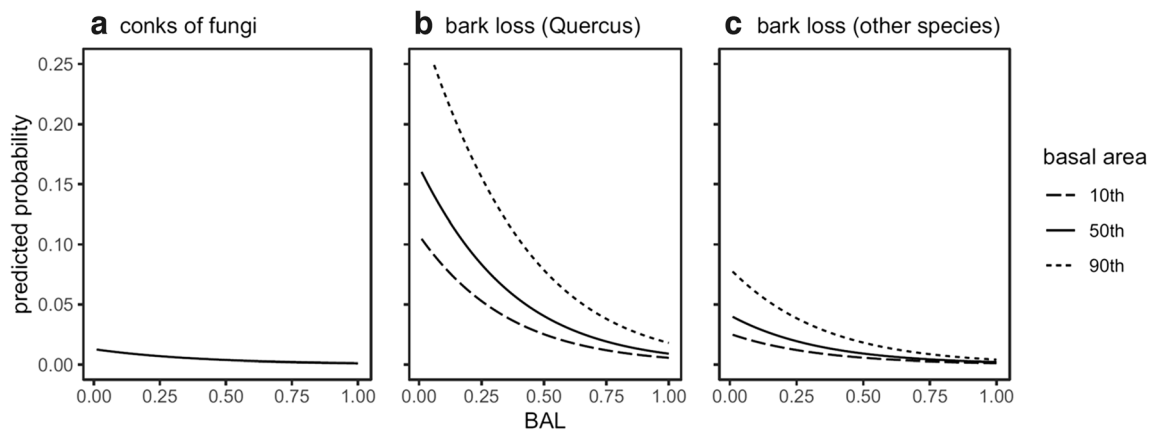
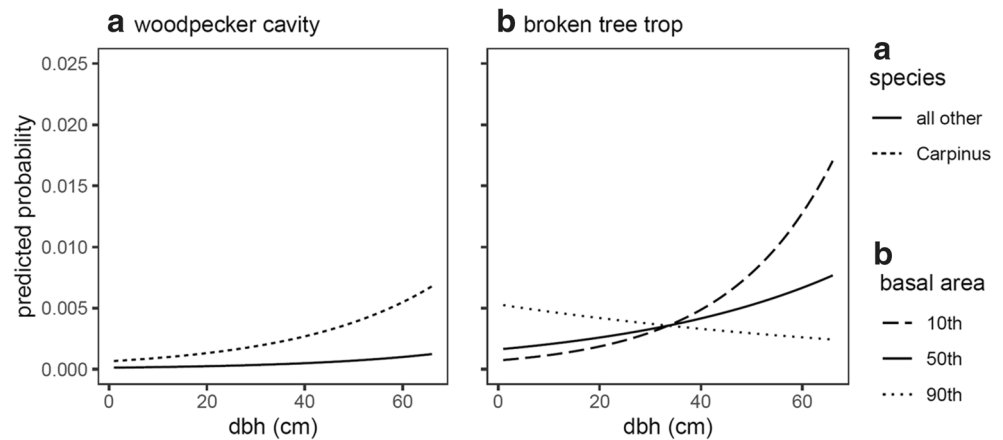


Fig. 4 Partial effects in the microhabitat models. Y-axis denotes the probability of occurrence of a microhabitat feature. X-axis denotes predictor variable BAL (basal area fraction larger than the target tree). **a**

Model for conks of fungi. **b, c** Model for bark loss. Probability of bark loss is shown at three levels of BA (basal area), in (B) incl. effect of *Quercus sp.*, in **c** all other species

Fig. 5 Partial effects in the microhabitat models. *Y*-axis denotes the probability of occurrence of a microhabitat type. *X*-axis denotes predictor variable DBH (tree diameter at 130 cm height). **a** Model for woodpecker cavity. **b** Model for broken tree top



recent studies varies greatly and includes, inter alia, seven (Ouin et al. 2015), nine (Larrieu et al. 2014), 13 (Grossman et al. 2018), 19 (Michel and Winter 2009), and 29 habitat types (Johann and Schaich 2016). An interesting result at forest level was that the density of non-woodpecker cavity in our study area (15.8 cavities per ha) was very similar to the global median density of non-woodpecker cavities which are estimated at 16 cavities per ha (Remm and Löhmus 2011).

Another crucial issue when comparing results of microhabitat studies is uncertainty in the measurement procedure itself. Some of the microhabitat types are difficult to assess in the field because specific features may evade direct detection, particularly when located higher up the trunk (compare definitions in Winter and Möller 2008).

Larrieu et al. (2018) propose a hierarchical typology of microhabitats in temperate and Mediterranean European forests with three levels of detail to make the microhabitat approach (i) easier to apply in operational forest management, and (ii) to make it easier to compare results from monitoring systems and scientific studies. In our study, we cover three out of seven microhabitat forms in Larrieu et al. (2018). The broken tree top habitat feature in our study may include the tree injuries and the crown deadwood forms. Excrescences, epiphytic, and

epixylic structures as well as exudates occur very rarely in Hyrcanian forests and may not have contributed to differentiate between managed and unmanaged forests. We definitely had a focus on cavities where we distinguished woodpecker cavities and rot holes at the group level of Larrieu et al. (2018). Main reason was that these microhabitat types are linked to high-species richness (e.g., Bouget et al. 2014; Winter and Möller 2008). However, we admit that knowledge on the relationship between microhabitat occurrence and related biodiversity remains incomplete at the moment.

What can be learned from our study? First, we did not find a significant difference in mean density of the investigated five MH types between managed and recently unmanaged forests. This is somehow surprising at first but can be explained by the similarity of the forests and their management history. In contrast, Michel and Winter (2009) found significant differences in microhabitat density along a gradient of management intensity. Paillet et al. (2017) showed that in French mountain forests, microhabitat density on living trees was significantly higher in strict forest reserves compared to managed forests. It is obvious that in unmanaged forest, “habitat trees” (i.e., large trees, old trees) occur more frequent than in managed forests due to common management guidelines which focus mainly on timber quality. However, Vuidot et al. (2011) found that at tree level, forest

Fig. 6 Partial effects in the microhabitat models. *Y*-axis denotes the probability of occurrence of a microhabitat type. *X*-axis denotes predictor variable DBH (tree diameter at 130 cm height). **a–c** Model for stem cavity. **b** Incl. effect of *Quercus* sp.. **c** Incl. effect of *Carpinus* sp.

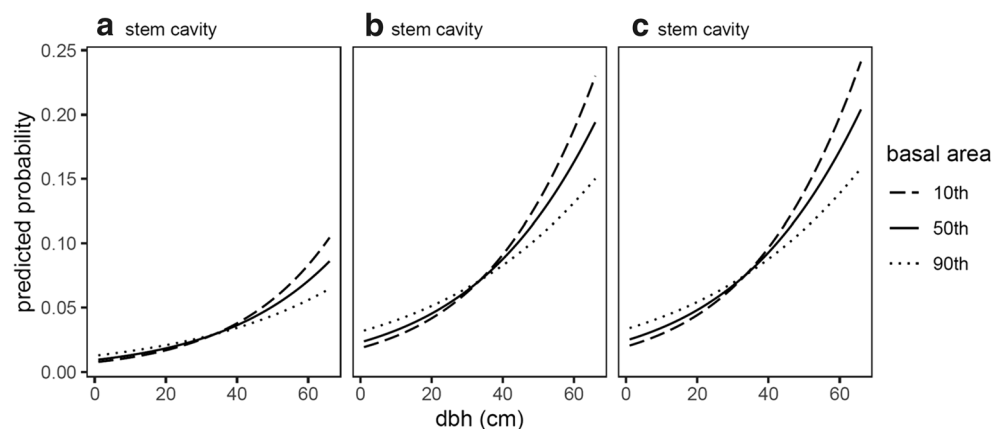


Table 7 AUC values for microhabitat models

Microhabitat type	AUC	
	Fixed and random effects	Fixed effects only
Bark loss	0.81	0.81
Woodpecker cavity	0.97	0.80
Broken tree top	0.97	0.60
Fungi	0.75	0.75
Stem cavity	0.81	0.76

management did not influence microhabitats. In German beech forests, microhabitats were more abundant in small private forests compared to municipal and state forests (Johann and Schaich 2016). It is well known (e.g., Anonymous 2015) that in small private ownerships in European forests, thinning intensity in general is much lower, thus leaving a higher number of habitat-bearing trees (e.g., trees with top breakage, cavities, conks of fungi, and bark loss) in the forest. An important issue is the definition of an “unmanaged” forest, given the long history of intense forest use in many parts of the world. Time since last harvesting can be considered an effective factor for microhabitat density. However, after setting a recently managed forest aside, it may take a long time for microhabitats to form and accumulate (Regnery et al. 2013). According to Larrieu et al. (2017) microhabitat density and diversity may also not develop linearly after management has stopped and some microhabitats may take as long as 50 years or more to develop.

Second, the low-intensity management regime with individual tree selection aiming primarily at mature and overmature trees, long harvest intervals, and low extraction intensity produces stand structures which are very similar to those in forests which had not been harvested since several decades at least (compare Fig. 2). Also, the fact that the management regime in Hyrcanian forests does not foresee thinning in a strict sense explains the similarity of microhabitat density in managed and unmanaged forests. Obviously, the share of “bad quality trees” in the harvests was quite low. Traditional thinning regimes may drastically reduce microhabitat-bearing trees by selecting trees for removal that do not meet timber quality standards. Due to target diameter harvesting in managed forests, very large trees are slightly more abundant in recently unmanaged forests while consequently small trees from the initiated regeneration in the harvest gaps are more frequent in managed forests.

A closer look at which factors explain the occurrence of microhabitats at the tree level can provide a guideline to biodiversity-oriented management. In Hyrcanian Oriental beech forests, tree species played a significant role for microhabitat occurrence. Hornbeam and oak trees had a much higher probability to bear microhabitats than the dominant oriental beech. Obviously, the mixture of broadleaves is important for microhabitat density. Tree species was also a significant predictor in other

studies (e.g., Grossman et al. 2018; Larrieu et al. 2014; Regnery et al. 2013; Larrieu and Cabanettes 2012). There is also agreement in many studies that increasing DBH is positively correlated with microhabitat occurrence (e.g., Larrieu et al. 2014; Ouin et al. 2015). Selected habitat features such as broken tree tops depend strongly on canopy structure and stem density and are thus heavily affected by the management regime. Dense populations of trees recruited into pole stage favor height growth in relation to diameter growth and are thus more prone to top breakage from snow and ice. Particularly in conifer stands, top breakage may produce breeding habitat for bark beetles and thus increase the risk of insect outbreaks. Thus, not all microhabitat features can be promoted equally in managed multi-purpose forests. However, targeted management regimes that aim at fostering microhabitats may accumulate habitat trees that very likely will bear microhabitat features such as woodpecker cavities and cavities and conks of fungi over time by leaving such trees on site.

6 Conclusion

After 30–50 years of no management, the similarity of recently unmanaged and managed Hyrcanian forests is somewhat surprising. However, the uncertainty in the management history in our studied forests, the low intensity harvests based on individual tree selection which presumably focused on the harvest of trees with reasonable timber quality, did not significantly affect microhabitat density over three decades. This also shows that simply using a general management approach as predictor of microhabitat density may not be specific enough but requires an operational guideline for harvest tree selection. Predictive models that indicate which trees in a forest are likely to bear and accumulate microhabitats over their life cycle can provide a useful support in shaping management guidelines.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Annex

Table 8 Average number of microhabitats per type per hectare in managed and recently unmanaged Hyrcanian forests at the six sites used in this study (Mean \pm Standard Error)

Site	Management	Bark loss	Woodpecker cavity	Broken tree tops	Fungi	Stem cavity	all microhabitat types
Dehga	Managed	4.00 \pm 1.63	0.00 \pm 0.00	1.00 \pm 1.00	0.00 \pm 0.00	32.00 \pm 4.16	37.00 \pm 4.95
Dehga	Unmanaged	4.00 \pm 1.63	5.00 \pm 3.07	1.00 \pm 1.00	3.00 \pm 1.53	25.00 \pm 5.42	38.00 \pm 8.92
Jamand	Managed	1.00 \pm 1.00	3.00 \pm 1.53	6.00 \pm 3.05	0.00 \pm 0.00	12.00 \pm 2.91	22.00 \pm 5.92
Jamand	Unmanaged	6.00 \pm 1.63	1.00 \pm 1.00	2.00 \pm 1.33	0.00 \pm 0.00	4.00 \pm 1.63	13.00 \pm 3.00
Lakoobon	Managed	0.00 \pm 0.00	1.00 \pm 1.00	3.00 \pm 1.53	1.00 \pm 1.00	13.00 \pm 3.00	18.00 \pm 3.59
Lakoobon	Unmanaged	0.00 \pm 0.00	1.00 \pm 1.00	2.00 \pm 1.33	0.00 \pm 0.00	15.00 \pm 3.07	18.00 \pm 4.42
Lalis	Managed	1.00 \pm 1.00	0.00 \pm 0.00	0.00 \pm 0.00	1.00 \pm 1.00	9.00 \pm 2.33	11.00 \pm 3.14
Lalis	Unmanaged	3.00 \pm 2.13	0.00 \pm 0.00	0.00 \pm 0.00	2.00 \pm 1.33	16.00 \pm 4.00	21.00 \pm 6.27
Shirakones	Managed	5.00 \pm 3.07	0.00 \pm 0.00	1.00 \pm 1.00	0.00 \pm 0.00	23.00 \pm 7.61	29.00 \pm 9.12
Shirakones	Unmanaged	3.00 \pm 2.13	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00	13.00 \pm 3.96	16.00 \pm 3.70
Vashmerd	Managed	1.00 \pm 1.00	2.00 \pm 1.33	0.00 \pm 0.00	1.00 \pm 1.00	10.00 \pm 2.98	14.00 \pm 4.27
Vashmerd	Unmanaged	2.00 \pm 1.33	0.00 \pm 0.00	0.00 \pm 0.00	1.00 \pm 1.00	13.00 \pm 2.60	16.00 \pm 3.05

Table 9 Confusion matrix for all tree level microhabitat models.

TP = true positive, FP = false positive, FN = false negative, TN = true negative. Specificity = TN/(TN + FP); Sensitivity = TP/(TP + FN), Accuracy = (TP + TN)/(TP + FP + TN + FN). No random effects included in predictions.

Model	TP	FP	FN	TN	Specificity	Sensitivity	Accuracy
A – bark loss	5	24	25	3328	0.99	0.17	0.98
B – woodpecker cavity	1	10	12	3359	0.99	0.08	0.99
C – broken tree top	2	22	14	3344	0.99	0.13	0.99
D – conks of fungi	3	249	6	3124	0.92	0.33	0.92
E – stem cavity	89	404	95	2794	0.87	0.48	0.85

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