


# Profile of tree-related microhabitats in European primary beech-dominated forests

## Journal Article

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48

## 49 **Abstract**

50 Tree-related microhabitats (TreMs) are important features for the conservation of biodiversity in forest  
51 ecosystems. Although other structural indicators of forest biodiversity have been extensively studied in  
52 recent decades, TreMs have often been overlooked, either due to the absence of a consensual definition  
53 or a lack of knowledge. Despite the increased number of TreM studies in the last decade, the role of  
54 drivers of TreM profile in primary forests and across different geographical regions is still unknown. To

55 evaluate the main drivers of TreM density and diversity, we conducted the first large-scale study of  
56 TreMs across European primary forests. We established 146 plots in eight primary forests dominated  
57 by European beech (*Fagus sylvatica* L.) in the Carpathian and Dinaric mountain ranges. Generalized  
58 linear mixed effect models were used to test the effect of local plot characteristics and spatial variability  
59 on the density and diversity (alpha, beta, and gamma) of TreMs. Total TreM density and diversity were  
60 significantly positively related with tree species richness and the proportion of snags. Root mean square  
61 tree diameters were significantly related to alpha and gamma diversity of TreMs. Both regions reached  
62 similarly high values of total TreM densities and total TreM densities and diversity were not  
63 significantly different between the two regions; however, we observed between the two regions  
64 significant differences in the densities of two TreM groups, conks of fungi and epiphytes. The density  
65 and diversity of TreMs were very high in beech-dominated mountain primary forests, but their  
66 occurrence and diversity was highly variable within the landscapes over relatively short spatial gradients  
67 (plot and stand levels). Understanding these profile provides a benchmark for further comparisons, such  
68 as with young forest reserves, or for improving forest management practices that promote biodiversity.

69 **Key words:** Biodiversity indicators, Old-growth, Mountain beech forest, TreMs, Snags, Habitat tree

70

## 71 **1. Introduction**

72

73 The natural development and the varied timing and intensity of disturbances within primary forests  
74 often results in high levels of structural heterogeneity (Bauhus et al., 2009). Certain structural elements,  
75 such as high volumes of accumulated standing and lying deadwood (Nagel et al., 2017a), large canopy  
76 (veteran) trees (Commarmot et al., 2013), and a diverse array of tree-related microhabitats (TreMs;  
77 Larrieu et al., 2018), are often abundant in primary forests. These structural elements are important  
78 features for the maintenance and conservation of biodiversity (Lindenmayer et al., 2006), and they are  
79 widely recognized as an important feature of conservation management plans (Kraus and Krumm,  
80 2013). Although structural indicators of forest biodiversity have been a major research topic in recent  
81 decades, TreMs have often been overlooked, either due to the absence of a consensual definition or a

82 lack of knowledge (Paillet et al., 2017). Larrieu et al. (2018) defined TreMs as a distinct, well-delineated  
83 structure occurring on living or standing dead trees that constitute a particular and essential substrate or  
84 life site for species or communities to develop, feed, shelter, or breed during at least a part of their life  
85 cycle. They are specific aboveground tree morphological singularities that are not found on every tree.  
86 The origins of TreMs encompass both endogenous modifications, caused by biotic and abiotic factors,  
87 such as intrusions, lesions, and breakages that expose sap and heartwood and initialize outgrowth  
88 structures and wood decay (saproxylic TreM), as well as exogenous elements that are physically linked  
89 to the tree (epixylic TreM).

90 Many recent TreM studies have largely been conducted in managed forests or forest reserves  
91 historically influenced by harvesting (e.g., Paillet et al., 2017; Regnery et al., 2013a; Vuidot et al., 2011),  
92 and studies have been largely restricted to a few distinct forest types in the Mediterranean, Western  
93 Europe, and the USA (Larrieu and Cabanettes, 2012; Michel and Winter, 2009; Regnery et al., 2013b;  
94 Winter et al., 2015). Forest management often encourages the production of uniform stands through the  
95 logging of high value trees and the removal of damaged or large trees with limited economic value.  
96 Conventional forest management systems sometimes create TreMs, such as dendrothelms or bark loss,  
97 due to damage during harvesting operations (Larrieu et al., 2012; Vuidot et al., 2011). However, most  
98 of the TreM types are typically removed or never develop (Paillet et al., 2017). It is widely documented  
99 that TreMs are more abundant and diverse in unmanaged stands (e.g., Paillet et al., 2017; Winter and  
100 Moller, 2008; Winter et al., 2015). The negative effects of forest management on the occurrence of  
101 TreMs can largely be explained by the lack of structural features and differences in tree species  
102 composition (Keren et al., 2017). Many of these structural components, such as snags and large trees,  
103 are considered to be important drivers of TreM diversity and abundance (Keren and Diaci, 2018; Larrieu  
104 and Cabanettes, 2012; Michel and Winter, 2009; Vuidot et al., 2011). Only a few studies have been  
105 conducted in forests that have developed naturally for at least a century (Larrieu et al., 2014a,b;  
106 Courbaud et al., 2017). Primary forests may serve as suitable reference points compared to forests with  
107 former management because they tend to have more complex structure and are thus more favorable for  
108 many forest-dwelling species (Hunter, 1999; Peterken, 1996).

109           The importance of studies carried out in primary forests has increasingly been recognized  
110 (Commarmot et al. 2013), however, the temperate forests of Europe have a complex land use history, as  
111 they have been used for a variety of purposes, such as for fuel wood, pasture, and timber extraction,  
112 since ancient times (Sabatini et al., 2018; Veen et al., 2010). Despite extensive forest exploitation in the  
113 middle ages and intensive commercial forest management more recently, large patches of primary  
114 forests were spared in some remote mountainous areas of central, eastern, and southeastern European  
115 countries (Veen et al., 2010). Within Europe, the southeastern European mountain ranges (Carpathians,  
116 Dinarides) contain some of the largest areas of well-preserved primary forests, primarily in old-growth  
117 stages of development, dominated by European beech (*Fagus sylvatica* L.)(Meyer et al., 2003;  
118 Standovár and Kenderes, 2003). There are currently few censuses of TreMs from primary forests  
119 because these forests are rare in Europe and they are usually located in remote mountain regions  
120 (Parviainen, 2005; Sabatini et al., 2018).

121           Despite the increased number of TreM studies in the last decade, the role of drivers of TreM  
122 densities and diversity is still unknown at the plot and stand scales across different geographical regions  
123 (Paillet et al., 2017). Differences in precipitation, temperature, topography, soils, and bedrock play an  
124 important role in the development of forest structure, and TreMs develop at differing rates (Paillet et al.,  
125 2017). Natural disturbance regimes are another important driver of stand structure in primary forests  
126 (Schurman et al., 2018), and studying remnants of primary forests may help us understand the spatial  
127 distribution of TreMs under natural conditions (Larrieu et al. 2018). External biotic factors, such as  
128 population dynamics of woodpeckers that create cavities, may also influence the production of certain  
129 TreMs (Remm and Löhmus 2011).

130           This study examines TreM profile from temperate primary forests dominated by European  
131 beech in two distinct mountainous regions – the Carpathians and Dinarides. Our objectives were: (i) to  
132 provide reference values of TreM density and diversity measures in mountainous mixed beech primary  
133 forests and (ii) to evaluate the importance of local plot structure and spatial variability for TreM density  
134 and diversity.

135

136 **2. Material and methods**

137 *2.1 Study area and site selection*

138 We refer to “primary forest” as a forest without signs of direct human impact (Figure 1, Table  
139 1), and where natural disturbances are the primary driver of forest structure and composition. These  
140 forests not only include old growth, but also the early seral stages of development. Potential study forests  
141 were selected using previous inventories of primary forest remnants when available (e.g., Veen et al.,  
142 2010), searching the available archival information, and historical data regarding the land use history of  
143 these areas. Almost all study forests are parts of formally protected areas (i.e., national parks, natural  
144 parks, strict forest reserves, UNESCO World Heritage sites), or they are proposed to soon be part of  
145 protected areas (i.e., Curai i Eperm, Ramino Korito). During the initial field surveys, all forests were  
146 inspected for various indicators of naturalness (e.g., coarse woody debris in various stages of decay, pit-  
147 and-mound topography, large trees, natural tree species composition) and signs of human impact; forests  
148 with evidence of past logging and grazing and those in close proximity (ca. 500 m) to formerly grazed  
149 areas were avoided. Preliminary dendrochronological analysis of selectively chosen tree cores from the  
150 study stands (30-40 trees per stand) revealed that a significant number of trees in each stand were older  
151 than 350 years, and one tree was even more than 450 years old (located at Perućica).

152 We selected four primary European beech-dominated mountain forests from both regions.  
153 Stands from the Carpathian Mountains spanned Slovakia and Romania, and those from the Dinarides  
154 were located in Croatia, Bosnia and Herzegovina, and Albania. The dominant tree species in these  
155 forests was European beech, mixed with mainly silver fir (*Abies alba* Mill.), maples (*Acer* spp. L.), and  
156 ashes (*Fraxinus* spp. L.).

157 In the Carpathians, the Slovakia Havešová (HAV) study site was located in the Bukovské  
158 Mountains. Havešová lies within Poloniny National Park and it is part of the UNESCO World Heritage  
159 - Primeval Beech Forests of the Carpathians and the Ancient Beech Forests of Germany. In Romania,  
160 the selected study forests, Bistra Valley (BIS), Crivia (CRI), and Paulic (PAU), were located in the  
161 Maramures Mountains, which are formally protected within Maramures Natural Park, located on the  
162 Romanian-Ukrainian border.

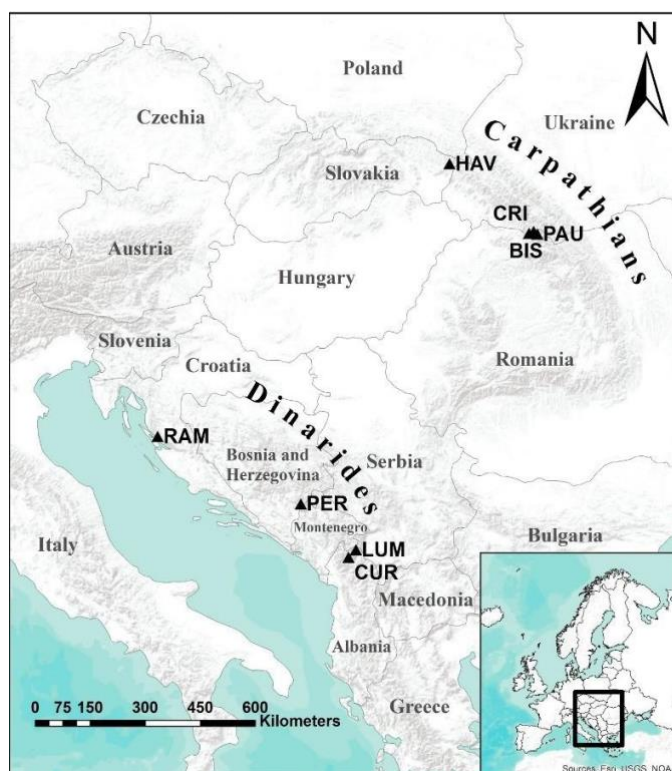
163 In the Dinarides, the Ramino Korito (RAM) study site is situated in Velebit Nature Park in the  
164 Velebit Mountains of Croatia. The Curraj i Eperm (CUR) and Lumi i Gashit (LUM) sites are part of  
165 Nikaj-Mërtur Regional Nature Park located in the Albanian Alps. Lumi i Gashit (Gashi River) is also  
166 part of the UNESCO World Heritage - Primeval Beech Forests of the Carpathians and Other Regions of  
167 Europe. The site in Bosnia and Herzegovina was located in the Perućica primary forest (PER), which is  
168 part of Sutjeska National Park.

169 There are broad environmental differences between our study sites of the Eastern Carpathians  
170 and the Dinarides that are important to point out (Table 1). The average annual precipitation and  
171 temperature are higher in the Dinaric region compared to the Carpathian sites. Bedrock in the Dinaric  
172 sites is primarily limestone, while in the Carpathians sites it is primarily flysch and gneiss. The sites in  
173 the Carpathians were also located on steeper slopes.

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**Figure 1.** Locations of primary forest study areas in the Carpathians and Dinarides





180 **Table 1**

181 Study stand characteristics from the Dinaric (CUR, LUM, PER, RAM) and Carpathian (CRI, HAV, BIS, PAU) mountain ranges. Climate characteristics were  
 182 obtained using the KNMI Climate Explorer (Oldenborgh et al., 2009). Mean temperature and mean annual precipitation were calculated using measurements  
 183 from 1901 to 2016.

Country	Forest	Number of plots	Elevation range (m a.s.l.)	Mean annual precipitation (mm)	Mean temperature range (°C)	Average slope (°)	DBH mean (DBH max) (cm)	Broadleaved-Coniferous ratio (%)	Snags (% from all trees)	Mean number of trees per ha (DBH > 6 cm)	Mean number of TreM-bearing trees per ha
<u>Dinarides</u>											
Albania	Curraj i Eperm (CUR)	14	1019-1287	1237	7.1-8.4	19.6	24.9 (124.1)	99:1	13	878	306.7
Albania	Lumi i Gashit (LUM)	14	1223-1682	1162	5.9-7.9	27.4	26.1 (135)	58:42	8	820	247.6
Bosnia	Perućica (PER)	48	1057-1450	1157	5-7.2	24.7	24.4 (134.5)	60:40	12	951	321.4
Croatia	Ramino Korito (RAM)	16	820-984	1299	8.1-8.9	15.4	32.1 (97.9)	91:9	16	518	281.6
<u>Carpathians</u>											
Romania	Crivia (CRI)	14	874-1147	862	4.2-5.6	34.7	28.1 (120)	77:23	7	533	311.4
Romania	Paulic (PAU)	12	942-1097	830	4.4-5.2	33.7	32.2 (163)	76:24	17	559	350.6
Romania	Bistra (BIS)	14	959-1154	830	4.1-5.1	35.4	32.2 (107.6)	69:31	9	477	176.7
Slovakia	Havešová (HAV)	14	615-710	815	6-6.5	23.4	25.5 (130)	100:0	13	572	226.7

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## 188 *2.2 Stand structural data*

189 For the selection of permanent study plots, a polygon network (10 ha each) was created using  
190 the ArcView 9.3 Environment (ESRI ArcGIS, 2011). Within each 10-ha polygon we generated a random  
191 point to establish sampling points where we established two plots. The paired plots consisted of two  
192 1,500 m<sup>2</sup> circular plots (radius of 21.85 m); each plot center was located 40 m in opposite directions  
193 from the random sample point and parallel to the slope contour (Appendix 1). We established 146  
194 permanent research plots nested within 73 pairs of plots across 8 forest stands. For each tree with  
195 diameter at breast height (DBH)  $\geq$  6 cm, the status of all trees (live or snag), tree species, and TreM  
196 presence/absence were recorded.

197

198

## 199 *2.3 TreM data*

200 For all study plots, each tree, including the stem and crown, was visually inspected for TreMs  
201 by two observers. Based on the typology of Vuidot et al. (2011), we created a list of 30 TreM types that  
202 we used to classify TreMs on our plots. All living trees with a DBH > 6 cm and snags located within the  
203 plots were searched for presence of TreMs (Appendix 2); we surveyed 13,640 living trees and snags in  
204 total. We arranged the TreM types into 12 groups for further analysis according to Paillet et al. (2017):  
205 crown deadwood, broken tops, conks of fungi, woodpecker cavities, non-woodpecker cavities, base  
206 cavities, bark characteristics, cracks, outgrowths, patches with exudates, epiphytes, and dendrothelms.  
207 All TreMs were surveyed in 2015 and 2016 during the period of June to September.

208

## 209 *2.4 TreM characteristics*

210 Diversity and density measures of TreMs were quantified for each sample plot. To reflect the  
211 diversity of TreM types, diversity was defined in terms of the number of TreM types occurring within  
212 the plot. Alpha diversity was defined as the average number of TreM types per tree in a given plot.  
213 Because the number of trees varied widely among plots (27–277 trees per plot), gamma diversity was  
214 calculated as the total number of TreM types per plot standardized by rarefaction to a common

215 abundance level ( $n = 27$  trees) to ensure comparability across plots (Chao et al., 2014). Beta diversity  
216 was defined as the ratio of gamma to alpha diversity, as originally proposed by Whittaker (1960); this  
217 ratio measures the degree to which TreM composition changes from tree to tree within a given plot.

218 To identify TreM densities, we used the index proposed by Paillet et al. (2017), i.e. the density  
219 of TreM-bearing trees, which allowed us to compare our results with other studies that used the same  
220 indices. Density of TreMs was quantified as the sum of TreM-bearing trees extrapolated to one hectare  
221 (Paillet et al., 2017). To determine the number of trees per plot bearing a given TreM type, each TreM  
222 type found on a tree was counted only once, even if it was present in greater numbers. Diversity and  
223 density measures were also calculated for several broad groups of TreM types (Table 2), in which case  
224 when we refer to density, it defines the density of trees bearing a particular TreM type. A major  
225 advantage of this sampling design was the minimal amount of time an observer needed to access  
226 TreMs in the field. Although we did not record the true abundance of all TreM types, our approach  
227 allowed us to compare our TreM data with other studies that used the same method (e.g., Paillet et  
228 al., 2017; Vuidot et al. 2011).

229

### 230 *2.5 Data analyses*

231 Generalized linear mixed models (GLMMs) were used to assess the effect of local plot structure  
232 and spatial variability on diversity and density characteristics of TreMs. Fixed effects included tree  
233 species richness (i.e., total number of tree species per plot), RMS DBH (root mean square diameter of  
234 trees at breast height in a given plot), proportion of snags (proportion of snags per plot versus total  
235 number of trees), and region (Dinarides and Carpathians). The random effects structure mirrored the  
236 spatial hierarchical nature of the sampling design, including plots nested within pairs of plots, which  
237 were nested within stands nested within regions. In the models of TreM density, the tree density per plot  
238 was treated as a nuisance variable to account for a trivial positive relationship between tree density and  
239 TreM density. Because diversity and density of TreMs are strictly positive and continuous variables, we  
240 used GLMMs with a gamma error distribution and log link function (McCullagh and Nelder, 1989).  
241 Model parameters were estimated using Laplace approximation and their significance was tested using

242 likelihood ratio tests (Bolker et al., 2009). There was no serious multicollinearity observed in the models  
243 (all VIFs < 2.3). To compare the relative importance of the fixed effects, we calculated semi-partial  
244 marginal determination coefficients ( $R_{2m}$ ; Nakagawa et al., 2017) derived from a commonality analysis  
245 (Ray-Mukherjee et al., 2014). The intraclass correlation coefficients (ICC) were used to quantify the  
246 proportion of variance explained by each of the hierarchical spatial levels. All analyses were performed  
247 in R language version 3.4.3 (R Core Team, 2017) using the lme4 library (Bates et al., 2015).

248

### 249 **3. Results**

#### 250 *3.1 Total TreM densities*

251 Total mean density of TreM-bearing trees (number of trees bearing at least one TreM) was  
252 similar in the Carpathians (266.4 bearing-trees ha<sup>-1</sup>) and Dinarides (289.3 bearing-trees ha<sup>-1</sup>). The  
253 average density of TreM-bearing trees for all stands was 277.8 TreM-bearing trees ha<sup>-1</sup>. Epiphytes (128.8  
254 bearing-trees ha<sup>-1</sup>), bark characteristics (101.2 bearing-trees ha<sup>-1</sup>), base cavities (65.2 bearing-trees ha<sup>-1</sup>),  
255 and non-woodpecker cavities (41.3 bearing-trees ha<sup>-1</sup>) had the highest TreM densities in both regions  
256 (Table 2). The lowest densities were observed for outgrowths (9.9 bearing-trees ha<sup>-1</sup>) and dendrothelms  
257 (4.6 bearing-trees ha<sup>-1</sup>). In the Carpathians, bark characteristics (112.7 bearing-trees ha<sup>-1</sup>) and base  
258 cavities (98.9 bearing-trees ha<sup>-1</sup>) had the highest densities, and dendrothelms (1.6 bearing-trees ha<sup>-1</sup>) had  
259 the lowest density. The Dinarides were characterized by high TreM densities of epiphytes (168.7  
260 bearing-trees ha<sup>-1</sup>) and non-woodpecker cavities (48.7 bearing-trees ha<sup>-1</sup>), and low densities of patches  
261 with exudates (8.6 bearing-trees ha<sup>-1</sup>), outgrowths (7 bearing-trees ha<sup>-1</sup>), and broken tops (10.1 bearing-  
262 trees ha<sup>-1</sup>).

263

#### 264 *3.2 Key factors to the diversity of TreMs*

265 Tree species richness, RMS DBH, and the proportion of snags showed significant relationships  
266 to TreM alpha diversity (i.e., the mean number of TreM types per tree), and gamma diversity (i.e., the  
267 total number of TreM types per plot; Table 3). All these habitat properties were positively correlated  
268 with the TreM diversity measures (Figure 2). RMS DBH displayed a relatively strong relationship with  
269 TreM alpha ( $R_{2m} = 12.2\%$ ) and gamma diversity ( $R_{2m} = 13.2\%$ ), but the effect of tree diversity was

270 rather negligible ( $R_{2m} \leq 0.6\%$ ). In contrast, beta diversity, the TreM turnover among trees, was  
271 unaffected by tree DBH. Considering spatial variability, alpha, beta, and gamma diversity of TreMs  
272 varied widely within paired plots ( $ICC > 35\%$ ) and also among pairs within stands ( $ICC \sim 23\text{--}25\%$ ).  
273 The contribution of stands to the observed variation was less obvious, but still important ( $ICC \sim 9\text{--}14\%$ ),  
274 with the exception of beta diversity, where the between-stand component of variance was not significant.  
275 We did not find any significant differences in TreM diversity between the Carpathians and Dinarides.

276

277

### 278 *3.3 Key factors to the density of TreMs*

279 Total density of TreMs was significantly and positively correlated with tree species richness  
280 and the proportion of snags in plots; RMS DBH showed no significant relationship with total TreM  
281 density (Figure 2). Total TreM density significantly varied among plots, pairs of plots, and stands, but  
282 there was no significant difference in overall TreM density between regions (Table 3).

283 The density of broken tops, patches with exudates, and epiphytes displayed a significant and  
284 positive relationship with tree species richness. RMS DBH was positively related with density of  
285 conks of fungi, base cavities, epiphytes, and outgrowths, and it was negatively related with crown  
286 deadwood and density of broken tops. The density of most TreMs was significantly correlated with the  
287 proportion of snags, both positively (crown deadwood, conks of fungi, woodpecker, bark  
288 characteristics, patches with exudates) and negatively (outgrowth). Significant differences between  
289 regions were observed for the density of conks of fungi and epiphytes; the first group showed higher  
290 densities in the Carpathians, while the latter group was higher in Dinarides. There was also a higher  
291 density of outgrowths and broken tops in the Carpathians, although the relationships were marginally  
292 non-significant (Table 3). These large-scale geographic trends were accompanied by high similarity of  
293 TreM densities among stands within regions (non-significant stand effects). In contrast, densities of  
294 the other TreM groups varied considerably at smaller spatial scales (plots, pairs of plots, stands), and  
295 consistent large-scale differences between regions were not evident.

296

297 **Table 2**

298 Tree-related microhabitat densities for different TreM groups for the Carpathian and Dinaric mountain ranges, including total, living trees, and snags. All  
 299 densities are presented as ha<sup>-1</sup> values.

TreM group	Total TreM density	Carpathians	Dinarides	Snags total	Snags Carpathians	Snags Dinarides	Living trees total	Living trees Carpathians	Living trees Dinarides
Crown deadwood	33.1	31.6	33.9	1.5	2.8	0.7	31.6	28.8	33.3
Broken tops	17.3	29.6	10.1	3.8	6.9	2.0	13.5	22.7	8.1
Conks of fungi	21.8	33.1	15.2	17.7	26.4	12.6	4.1	6.7	2.6
Woodpecker cavities	13.3	15.9	11.7	11.1	12.5	10.3	2.2	3.5	1.4
Non-woodpecker cavities	41.3	28.8	48.7	10.2	7.2	12.0	31.1	21.6	36.7
Base cavities	65.7	98.9	46.2	8.0	10.5	6.5	57.7	88.4	39.7
Bark characteristics	101.2	112.7	94.4	59.1	53.6	62.3	42.1	59.1	32.1
Cracks	30.3	23.7	34.2	7.9	10.4	6.4	22.5	13.3	27.8
Outgrowth	9.9	14.8	7.0	0.8	0.7	0.8	9.1	14.1	6.2
Patches with exudates	16.0	28.5	8.6	1.1	1.5	0.9	14.8	27.0	7.7
Epiphytes	128.8	60.7	168.7	15.8	11.5	18.3	113.0	49.3	150.4
Dendrothelms	4.2	1.6	5.8	0.2	0.0	0.3	4.1	1.6	5.5
SUM	482.9	480.0	484.6	137.1	144.0	133.0	345.8	336.0	351.6

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307 **Table 3**

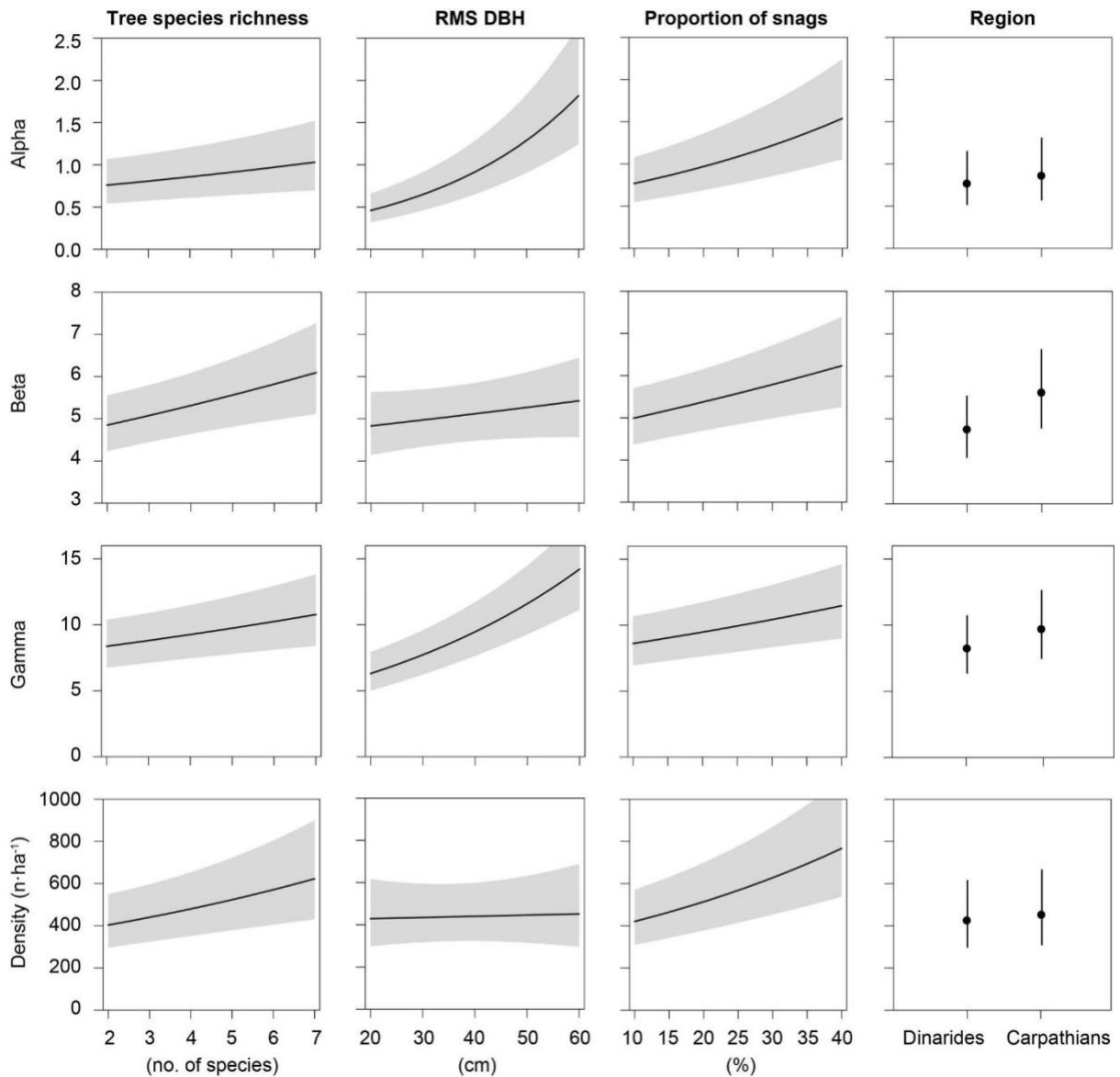
308 Summary of GLMMs relating diversity (alpha, beta, gamma) and density of microhabitats to fixed and random effects. Likelihood ratio test statistics ( $\chi^2$ ),  
309 probabilities (p), semi-partial marginal determination coefficients ( $R_{2m}$  [%]), and intra-class correlation coefficients (ICC [%]) are displayed. Significant  
310 positive/negative partial relationships (r) are designated by +/- signs, respectively; inequality signs are used for comparisons between Carpathians (C) and  
311 Dinarides (D). Model parameters were considered significant at 5% and are highlighted in bold.

Model	Fixed effects												Random effects												
	Tree species richness				RMS DBH				Proportion of snags				Region				Stand			Paired plots			Plot		
	$\chi^2$	p	$R_{2m}$	r	$\chi^2$	p	$R_{2m}$	r	$\chi^2$	p	$R_{2m}$	r	$\chi^2$	p	$R_{2m}$	r	$\chi^2$	p	ICC	$\chi^2$	p	ICC	$\chi^2$	p	ICC
Alpha diversity	<b>6.3</b>	<b>0.0121</b>	<b>0.6</b>	+	<b>64.3</b>	<b>&lt; 0.0001</b>	<b>12.2</b>	+	<b>41.8</b>	<b>&lt; 0.0001</b>	<b>7.2</b>	+	0.3	0.6152	1.4		<b>8.6</b>	<b>0.0034</b>	<b>9.4</b>	<b>84.3</b>	<b>&lt; 0.0001</b>	<b>23.0</b>	<b>107.9</b>	<b>&lt; 0.0001</b>	<b>48.0</b>
Beta diversity	<b>9.9</b>	<b>0.0016</b>	<b>2.2</b>	+	1.5	0.2223	< 0.1		<b>12.4</b>	<b>0.0004</b>	<b>4.6</b>	+	2.8	0.0962	9.0		2.2	0.1395	11.7	<b>64.3</b>	<b>&lt; 0.0001</b>	<b>24.3</b>	<b>74.5</b>	<b>&lt; 0.0001</b>	<b>42.1</b>
Gamma diversity	<b>10.5</b>	<b>0.0012</b>	<b>0.2</b>	+	<b>52.9</b>	<b>&lt; 0.0001</b>	<b>13.2</b>	+	<b>16.5</b>	<b>0.0001</b>	<b>2.6</b>	+	1.0	0.3176	5.5		<b>11.8</b>	<b>0.0006</b>	<b>13.6</b>	<b>62.9</b>	<b>&lt; 0.0001</b>	<b>25.2</b>	<b>63.5</b>	<b>&lt; 0.0001</b>	<b>36.5</b>
Density																									
All microhabitats	<b>10.6</b>	<b>0.0011</b>	<b>7.3</b>	+	< 0.1	0.8353	< 0.1		<b>29.7</b>	<b>&lt; 0.0001</b>	<b>14.4</b>	+	0.1	0.7811	< 0.1		<b>4.7</b>	<b>0.0294</b>	<b>5.7</b>	<b>100.9</b>	<b>&lt; 0.0001</b>	<b>33.8</b>	<b>85.7</b>	<b>&lt; 0.0001</b>	<b>44.0</b>
Crown deadwood	0.4	0.5135	0.2		<b>15.2</b>	<b>0.0001</b>	<b>7.2</b>	-	<b>4.4</b>	<b>0.0367</b>	<b>1.9</b>	+	0.1	0.7995	< 0.1		<b>8.1</b>	<b>0.0044</b>	<b>12.0</b>	3.5	0.0601	18.0	0.0	0.9708	0.0
Broken tops	<b>4.3</b>	<b>0.0376</b>	<b>&lt; 0.1</b>	+	<b>5.6</b>	<b>0.0181</b>	<b>1.5</b>	-	1.0	0.3063	< 0.1		3.2	0.0727	13.9		<b>10.3</b>	<b>0.0013</b>	<b>19.7</b>	<b>50.0</b>	<b>&lt; 0.0001</b>	<b>26.3</b>	<b>28.2</b>	<b>&lt; 0.0001</b>	<b>32.8</b>
Conks of fungi	0.4	0.5268	< 0.1		<b>15.3</b>	<b>0.0001</b>	<b>7.4</b>	+	<b>11.8</b>	<b>0.0006</b>	<b>6.1</b>	+	<b>5.6</b>	<b>0.0178</b>	<b>13.3</b>	<b>C &gt; D</b>	<b>5.4</b>	<b>0.0203</b>	<b>18.3</b>	<b>10.5</b>	<b>0.0012</b>	<b>12.6</b>	<b>15.6</b>	<b>0.0001</b>	<b>41.1</b>
Woodpecker cavities	0.1	0.7610	0.0		< 0.1	1.0000	< 0.1		<b>21.5</b>	<b>&lt; 0.0001</b>	<b>9.9</b>	+	0.1	0.6993	0.8		<b>8.4</b>	<b>0.0038</b>	<b>11.7</b>	<b>60.6</b>	<b>&lt; 0.0001</b>	<b>29.5</b>	<b>50.1</b>	<b>&lt; 0.0001</b>	<b>39.4</b>
Non-woodpecker cavit.	0.6	0.4444	1.4		0.8	0.3672	0.5		3.2	0.0715	2.1		2.2	0.1419	10.5		<b>6.6</b>	<b>0.0103</b>	<b>10.3</b>	<b>29.7</b>	<b>&lt; 0.0001</b>	<b>14.8</b>	<b>55.7</b>	<b>&lt; 0.0001</b>	<b>56.2</b>
Base cavities	0.2	0.6821	0.7		<b>6.4</b>	<b>0.0112</b>	<b>4.6</b>	+	3.1	0.0769	4.8		0.8	0.3585	5.7		<b>18.9</b>	<b>&lt; 0.0001</b>	<b>18.7</b>	<b>14.0</b>	<b>0.0002</b>	<b>17.3</b>	2.9	0.0910	40.6
Bark characteristics	0.8	0.3864	0.4		1.3	0.2631	< 0.1		<b>50.9</b>	<b>&lt; 0.0001</b>	<b>18.8</b>	+	0.8	0.3583	2.1		<b>5.4</b>	<b>0.0206</b>	<b>7.1</b>	<b>70.6</b>	<b>&lt; 0.0001</b>	<b>25.8</b>	<b>99.3</b>	<b>&lt; 0.0001</b>	<b>50.6</b>
Cracks	2.8	0.0932	3.4		< 0.1	0.8959	< 0.1		1.0	0.3172	0.9		1.5	0.2140	2.4		0.2	0.6855	1.6	<b>26.0</b>	<b>&lt; 0.0001</b>	<b>16.0</b>	<b>32.2</b>	<b>&lt; 0.0001</b>	<b>62.6</b>
Outgrowth	0.1	0.7428	0.7		<b>7.0</b>	<b>0.0082</b>	<b>1.6</b>	+	<b>7.6</b>	<b>0.0058</b>	<b>1.2</b>	-	3.8	0.0507	8.3		3.7	0.0529	13.6	<b>20.3</b>	<b>&lt; 0.0001</b>	<b>22.4</b>	<b>12.5</b>	<b>0.0004</b>	<b>31.3</b>
Patches with exudates	<b>10.2</b>	<b>0.0014</b>	<b>4.3</b>	+	0.3	0.6099	< 0.1		<b>4.7</b>	<b>0.0299</b>	<b>1.2</b>	+	1.6	0.2124	8.1		<b>22.5</b>	<b>&lt; 0.0001</b>	<b>25.8</b>	<b>53.4</b>	<b>&lt; 0.0001</b>	<b>17.8</b>	<b>66.8</b>	<b>&lt; 0.0001</b>	<b>40.3</b>
Epiphytes	<b>11.4</b>	<b>0.0007</b>	<b>8.9</b>	+	<b>5.4</b>	<b>0.0204</b>	<b>0.5</b>	+	0.5	0.4768	0.9		<b>6.4</b>	<b>0.0116</b>	<b>13.9</b>	<b>C &lt; D</b>	< 0.1	0.9968	5.6	<b>51.1</b>	<b>&lt; 0.0001</b>	<b>37.1</b>	<b>19.9</b>	<b>&lt; 0.0001</b>	<b>27.6</b>
Dendrothelms	< 0.1	0.9658	< 0.1		2.1	0.1446	1.0		2.5	0.1146	1.2		2.6	0.1098	6.9		1.3	0.2572	10.9	<b>42.2</b>	<b>&lt; 0.0001</b>	<b>26.0</b>	<b>35.6</b>	<b>&lt; 0.0001</b>	<b>33.2</b>

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315 **Figure 2.** Effect plots showing the results of GLMMs testing for the effect of tree species richness, RMS  
 316 DBH, proportion of snags, and region on diversity (alpha, beta and gamma) and density of TreMs.  
 317 Predicted values (lines, circles) are displayed along with 95% confidence intervals (gray polygons, error  
 318 bars).

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#### 322 4. Discussion

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Preserving the diversity of organisms that rely on specific forest structures is a key conservation challenge as forest management intensifies across the globe (Hansen et al., 2013; Mori and Kitagawa, 2014). Our assessment of TreM densities in primary forests provides a valuable benchmark for forest

326 managers and policy makers that seek to implement structures that will benefit a host of species of  
327 conservation concern (Vuidot et al., 2011). We performed the first quantitative TreM analyses and  
328 comparison of TreM diversity in primary mixed beech-dominated forests in two distinct mountainous  
329 regions — the Carpathians and Dinarides. The primary drivers of TreM density (number of trees bearing  
330 a particular TreM per hectare) and diversity (richness of TreM types) at the plot scale in these forests  
331 were structural characteristics, such as RMS DBH, tree species composition, and proportion of snags.  
332 Geographical distance between regions did not play an important role in TreM densities and diversity,  
333 either at the alpha, beta, or gamma levels. Our study highlights that TreM densities observed in the  
334 primary forests were significantly higher in comparison to densities presented in studies from managed  
335 forests (e.g., Larrieu et al. 2012; Paillet et al., 2017).

336 We observed a significant increase in total TreMs density and alpha and gamma diversity of  
337 TreM types with an increased proportion of snags and tree species richness. Several studies have already  
338 observed the importance of snags, large living trees, and different tree species for densities of TreM  
339 types (Larrieu and Cabanettes, 2012; Larrieu et al., 2014a; Vuidot et al., 2011). Tree diameter has also  
340 been recognized as an important factor in TreM dynamics across different forest types; it has been  
341 observed to influence the abundance of TreMs (Larrieu and Cabanettes, 2012), the diversity of TreM  
342 types (Larrieu et al. 2014a; Vuidot et al., 2011), or the occurrence of some TreM types, such as bark  
343 characteristics (Michel and Winter, 2009). Large diameter trees were also important in our study,  
344 especially for alpha and gamma diversity of TreMs, and densities of some TreM types. We did not find  
345 a significant relationship between DBH and total TreM density; most studies that observed a significant  
346 relationship between tree diameter and TreM used the DBH of the individual tree bearing the TreM. In  
347 contrast, we used RMS DBH of the trees on a plot, which likely introduced noise into the relationship  
348 given the mixed severity disturbance regimes of the region, and we also counted only one TreM type on  
349 each TreM-bearing tree, which may also further mask any relationship between diameter and density of  
350 TreMs. Tree species composition is another factor that has been observed to influence total TreM density  
351 and diversity (Larrieu and Cabanettes, 2012; Larrieu et al., 2014a; Vuidot et al., 2011). Tree species  
352 diversity has also been observed to positively influence densities of some specific TreMs, such as broken

353 tops, patches with exudates, and epiphytes. Patches with exudates, such as sap-runs and gummosis, are  
354 more likely to be found on deciduous trees (Siitonen, 2012), while the excurrent growth habit of conifers  
355 makes them more susceptible to broken tops. The proportion of snags had a significant effect on TreM  
356 diversity at the alpha, beta, and gamma levels, and also on the overall density of TreMs (Table 3).  
357 However, we observed that all TreM types were present within the living trees and snags as well, which  
358 may be due to partial mortality, whereby dead wood occurs on living trees, which is characteristic of  
359 very large trees (Siitonen, 2012) that could bear TreMs normally present on dead trees in managed  
360 forests (e.g., woodpecker feeding holes). Our findings emphasize the importance of snags in broadleaved  
361 stands because they promote increased TreM diversity and densities within beech-dominated primary  
362 forests. We also observed higher densities of certain TreM types that are rarer on living trees than on  
363 snags (woodpecker cavities, conks of fungi, and bark characteristics), which is consistent with the  
364 findings of Vuidot et al. (2011) and Larrieu and Cabanettes (2012) whereby the presence of conks of  
365 fungi and woodpecker cavities were significantly higher on snags than on living trees (Appendix 3).  
366 Woodpeckers generally prefer to nest and roost in snags, and fungi play an important role in the  
367 excavation of woodpecker cavities (Zahner et al. 2012), and woodpeckers are often suggested as a vector  
368 for the fungus (Jackson and Jackson, 2004). After the tree dies, the decay process promotes conditions  
369 that influence the occurrence of other TreM types, such as bark characteristics and non-woodpecker  
370 cavities (Vuidot et al., 2011). Although snags represented only 7-17 % of all trees per stand, they  
371 accounted for one-third of the density of all TreMs tallied in our study (Table 2). Our results generally  
372 agree with prior TreM research conducted in different regions, and it highlights the positive effects of  
373 high levels of structural heterogeneity (e.g., large trees, and high tree species richness and proportions  
374 of snags) to support a diverse array of TreMs. Finally, our results showed higher densities of TreMs  
375 associated with certain taxa compared to published conservation guidelines: a minimum of 40 cavities  
376 per hectare for the conservation of cavity dwelling birds (Blondel, 2005) or a network of 7 to 10 live  
377 cavity- or crack-bearing trees per hectare for bats (Meschede and Heller, 2003). Our data support these  
378 findings and demonstrate that the primary forests can reach very high TreM levels.

379           Here, we compared for the first time TreM densities and diversity between primary forests of  
380 the Carpathian and Dinarides mountain ranges. Although precipitation and temperature differ among

381 the regions (Table 1), we did not observe significant differences in total TreM densities or TreM  
382 diversity between the regions. Both of the regions had similarly high diversity values (Table 2).  
383 However, we observed significant differences in densities of several TreM types between the regions,  
384 including densities of conks of fungi and epiphytes (Table 3), which could potentially be influenced by  
385 large-scale climatic differences or soil properties (Ding et al., 2016). However, our results suggested  
386 significant variability between TreM densities and diversity on relatively small spatial gradients (stand  
387 and plot levels). We observed TreM densities almost two times greater than that of Paillet et al. (2017)  
388 in strict mixed mountain forest reserves of France (Table 2; Appendix 2). They determined that strict  
389 forest reserves had higher TreM densities, both total and individual densities, than comparable adjacent  
390 managed forests. This general trend has also been observed in several other European forests (Winter  
391 and Moller, 2008; Winter et al., 2015). Although Paillet et al. (2017) sampled strict forest reserves, the  
392 mean time since any previous harvesting was only 48 years; it is impossible to identify the structure of  
393 the stands at the beginning of the set-aside period or how intensively the stands were managed prior to  
394 their strict reserve designation. We analyzed TreMs exclusively from remote primary forests with very  
395 limited access, and it is likely that these stands were never managed; some of the oldest trees are more  
396 than 450 years old. Compared to the findings of Paillet et al. (2017), we observed the densities of broken  
397 tops was more than 10 times higher on average, and almost 20 times higher in the Carpathians. The  
398 higher densities of broken tops may be attributable to the natural disturbance regime that influences  
399 structural dynamics in primary forests (Meigs et al., 2017), as well as the high proportion of live trees  
400 bearing polypores, such as *Fomes fomentarius* or *Fomitopsis pinicola*, which make beech stems more  
401 prone to breakage (Zeibig et al., 2005). In addition, the tree dimensions, taller trees with larger primary  
402 branches, may be more prone to partial crown loss. Similar conclusions can be drawn for higher densities  
403 of other TreM groups. High volumes and diversity of deadwood, which are typical of primary forests  
404 (Nagel et al., 2017a), may influence the presence of conks of fungi and even woodpeckers (Jackson and  
405 Jackson, 2004). We also observed much higher densities of base cavities compared to Paillet et al.  
406 (2017); because large cavities take more time to develop, higher rates of occurrence on very old trees  
407 would be expected, thus many primary forests would have higher numbers of older trees with longer  
408 periods of time since the last severe disturbance (Siitonen et al., 2012). In contrast, we found lower

409 densities of outgrowths and bark characteristics in the Dinaric dataset compared to the French strict  
410 forest reserves (Paillet et al., 2017); outgrowths and bark characteristics tend to occur more frequently  
411 on oaks (*Quercus* spp.), firs (*Abies* spp.), and spruces (*Picea* spp.) compared to beech (Vuidot et al.,  
412 2011). However, higher densities of outgrowths and bark characteristics were found in the Carpathian  
413 dataset than in Dinarides dataset.

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## 415 **5. Conclusions**

416 We conducted the first assessment of tree-related microhabitats in beech-dominated primary forests of  
417 the Carpathian and Dinaric mountain ranges; these sites represent some of the last remnants of primary  
418 forests in Europe. Our study provides an empirical analysis of TreM variability and reference values  
419 from these primary forests, both of which will help inform forest managers, conservation strategies, and  
420 policy decisions. These reference values provide a means to assess the influence of forest management  
421 on TreM profile. However, our study sites represent a relatively small fraction of these two vast  
422 mountain ranges. To improve our understanding of TreM dynamics, we suggest a more thorough survey  
423 of primary forest study areas across the Dinaric and Carpathian Mountains, as well as other mountain  
424 ranges where similar forest types occur. Climate characteristics, topographical features, such as the  
425 presence of cliffs that can increase the occurrence of certain TreMs, such as bark loss, by rock falls, or  
426 biotic factors, such as woodpecker density (or diversity) or the presence of large ungulates, may also  
427 play an important role in the availability of TreMs. A potentially important driver of TreM density and  
428 diversity may be the natural disturbance regime that may play an important role in creation and  
429 maintenance of TreMs. Future research will include the analysis of disturbance history variables in  
430 relation to TreMs. In particular, a dendroecological approach could be used to link natural disturbance  
431 history with TreM diversity and density, and to assess how forest development influences the  
432 distribution of TreMs. Finally, our results show that primary forests maintain high TreM diversity, and  
433 that they may significantly contribute to the overall species diversity across forested landscapes.  
434 Although our paper did not directly compare primary forests with managed forests under similar  
435 environmental conditions, we also plan to establish plots in managed forests near primary forests in

436 future studies to better understand TreM dynamics and the critical role of protected areas to maintain  
437 and enhance biodiversity in our modern world.

438

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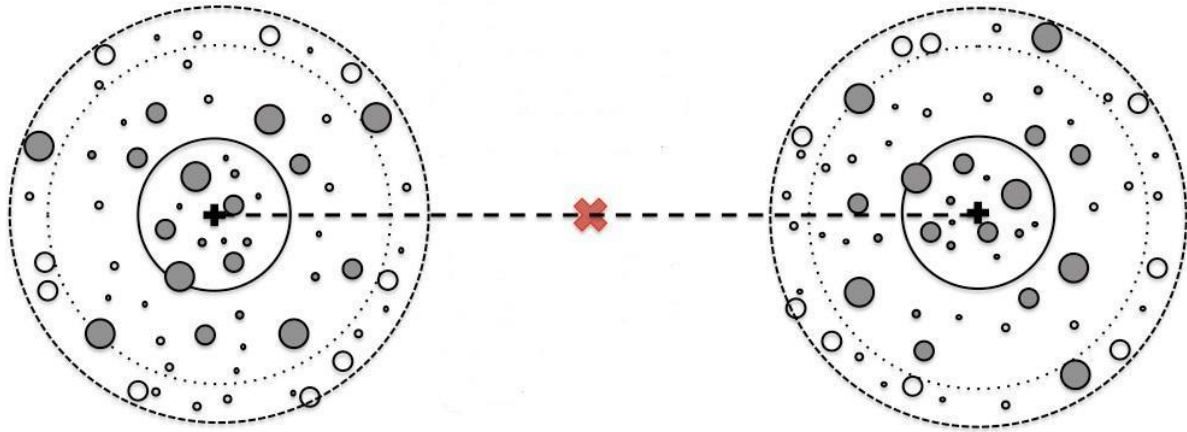
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613 **Appendices**

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616 **Appendix 1**

617 Example of the nested plot structure. The red cross indicates the randomly generated navigation point

618 used to locate the pair of circular sample plots.

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622 **Appendix 2**

623 Tree-related microhabitats densities for all surveyed TreM types for the Carpathian and Dinaric mountain ranges, including total, living trees, and snags. All  
 624 densities are presented as ha<sup>-1</sup> values.

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TreM group	Correlation with typology from Larrieu et al. 2018	TreM type	Total number of TreMs	Total TreM density	Total Carpathians	Total Dinarides	Total snags	Carpathians snags	Dinarides snags	Total living trees	Carpathians living trees	Dinarides living trees
Woodpecker cavities	X	Woodpecker cavities with >2cm aperture, woodpecker breeding or feeding holes	289	13.2	15.9	11.6	11.1	12.5	10.2	2.1	3.5	1.4
Non-woodpecker cavities	X(partially)	Non-woodpecker cavities with >5cm aperture anywhere on the trunk: formed after injury, branch fall	744	34.0	22.7	40.6	4.1	2.6	4.9	29.9	20.1	35.7
Non-woodpecker cavities	X	Cavity string: at least three woodpecker cavities in a stem with a maximum distance of two meters between two cavity entrances. Cavity strings are an important starting point for the development of deep and long lasting stem cavities	161	7.4	6.0	8.1	6.1	4.6	7.0	1.2	1.5	1.1
Woodpecker cavities		Shallow cavities in the bark arranged in a ring; usually woodpecker	2	0.1	0.0	0.1	0.0	0.0	0.1	0.0	0.0	0.1
Base cavities	X	Deep stem cavities: a tubular cavity in the base of the tree without mold	884	40.4	62.3	27.5	2.4	3.6	1.7	38.0	58.8	25.8
Base cavities	X	Deep stem cavities: a tubular cavity in the base of the tree with mold	525	24.0	35.9	17.0	5.4	6.8	4.6	18.6	29.1	12.4
Base cavities	X	Tree with hollow > 30 cm aperture	30	1.4	0.6	1.8	0.2	0.1	0.3	1.1	0.5	1.5
Dendrothelms	X	Dendrothelms with >5cm aperture. Water-filled holes in wood.	93	4.2	1.6	5.8	0.2	0.0	0.3	4.1	1.6	5.5
Patches with exudates	X	Sap or resin drop: Only a few sap or resin drops (shorter than 30 cm or <6	264	12.1	20.9	6.9	0.9	1.2	0.7	11.2	19.6	6.2

		flows) indicating a minor injury										
Patches with exudates	X	Heavy sap or resin: fresh heavy flow of sap or resin at least 30 cm long or >5 flows of sap or resin of smaller size	86	3.9	7.7	1.7	0.3	0.2	0.3	3.7	7.4	1.4
Conks of fungi	X(partially)	Conks of fungi (both perennial and annual; including agarics). Fruiting bodies, diameter >5 cm	285	13.0	18.0	10.1	10.1	13.6	8.0	2.9	4.4	2.0
Conks of fungi	X(partially)	Conks of fungi (both perennial and annual; including agarics). Fruiting bodies > 5 cm in diameter or occur in 10 cm long cascades of smaller fruiting bodies.	193	8.8	15.1	5.1	7.6	12.8	4.6	1.2	2.2	0.6
Bark characteristics	X	Bark loss: patches with bark loss of at least 5*5 cm mainly caused by felling, natural falling of trees and rock falls	1768	80.7	95.6	72.0	45.9	44.4	46.8	34.8	51.1	25.2
Bark characteristics	X(partially)	Bark burst: black burst of bark at least 2 cm wide often with resin indicating injury/disease	41	1.9	2.7	1.4	0.1	0.1	0.1	1.8	2.6	1.3
Bark characteristics		Gnaw and peeling by ungulates	20	0.9	1.5	0.6	0.3	0.1	0.4	0.6	1.4	0.1
Broken tops	X(partially)	Splintered stem: the split-up results in numerous scales (minimum 5) of wood > 50 cm long; caused by another tree fall etc.	70	3.2	4.2	2.6	2.1	3.0	1.5	1.1	1.2	1.1
Cracks	X	Lightning scar: a crack caused by lightning; at least 3 m long and reaching the sapwood	4	0.2	0.0	0.3	0.0	0.0	0.1	0.1	0.0	0.2
Cracks	X	Cracks: cleft into the sapwood >25 cm long along the stem and at least 2 cm deep in the sapwood	660	30.1	23.7	33.9	7.8	10.4	6.3	22.3	13.3	27.6
Bark characteristics	X	Bark pocket: space between loose bark and the sapwood with a minimum extension of 5*5*2 cm	357	16.3	11.4	19.2	11.9	7.7	14.4	4.4	3.7	4.8

Bark characteristics	X	Bark pocket with mold: same structure and size as Bark loss but with mold.	30	1.4	1.6	1.2	0.8	1.2	0.6	0.5	0.4	0.7
Crown deadwood	X(partially)	Between 10% and 25% of dead crown: one or more main branches are dead. The living crown represents 75% of the former total crown.	434	19.8	16.8	21.6	0.0	0.0	0.1	19.8	16.8	21.5
Crown deadwood	X(partially)	Between 25% and 50% of dead crown: one or more main branches are dead. The living crown represents between 50 and 75% of the former total crown.	127	5.8	6.8	5.2	0.0	0.0	0.1	5.8	6.8	5.1
Crown deadwood	X(partially)	More than 50% of dead crown: one or more main branches are dead. The living crown seems to be <50% of the former total crown.	163	7.4	8.0	7.1	1.4	2.8	0.5	6.1	5.2	6.6
Broken tops	X	Broken stem: the primary crown is totally absent with or without presence of a secondary crown. Main parts of the tree stem are already dead with decomposing processes.	265	12.1	25.1	4.5	1.7	4.0	0.4	10.4	21.1	4.1
Broken tops	X	Broken fork: complete fracture of one of the two forking branches; the loss of one forking branch results in a severe damage of the main stem.	44	2.0	0.4	3.0	0.0	0.0	0.0	2.0	0.4	3.0
Outgrowth	X	Canker: proliferation of cell growth; irregular cellular growth on stems or branches, which is caused by bark-inhabiting fungi, viruses and bacteria. We recorded areas of canker > 10 cm in diameter	211	9.6	14.7	6.7	0.8	0.7	0.8	8.9	14.0	5.9
Outgrowth	X	Witch broom: dense agglomeration of branches from a parasite or epicormic branching	6	0.3	0.1	0.4	0.0	0.0	0.0	0.3	0.1	0.4



Epiphytes	X	Bryophytes developed on >50% of the base or trunk area (height < 1 m)	2762	126.1	57.2	166.6	15.5	11.5	17.9	110.6	45.7	148.7
Epiphytes	X	Ivy developed on > 50% of the base or trunk area (height < 1 m)	18	0.8	0.0	1.3	0.2	0.0	0.4	0.6	0.0	0.9
Epiphytes	X	Mistletoe: presence of a hemiparasitic plants (e.g. Viscum spp., Arceuthobium oxycedri, Loranthus europaeus)	40	1.8	3.6	0.8	0.0	0.0	0.1	1.8	3.6	0.7
		SUM	10576	482.9	480.0	484.6	137.1	144.0	133.0	345.8	336.0	351.6

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632 **Appendix 3**

633 Comparison of densities of TreM groups between snags and living trees.

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### Densities of TreM groups

