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

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5 **Daniel Kozák[1*], **Martin Mikoláš[1,2], Marek Svitok[3,4], Radek Bače[1], Yoan Paillet[5], Laurent Larrieu[6],

6 Thomas A. Nagel[1,7], Krešimir Begovič[1], Vojtěch Čada[1], Abdulla Diku[8], Michal Frankovič[1], Pavel

7 Janda[1], Ondrej Kameniar[1], Srđan Keren[9], Peter Kjučukov[1], Jana Lábusová[1], Thomas Langbehn[1], Jakub

8 Málek[1], Stjepan Mikac[10], Robert C. Morrissey[1], Markéta Nováková[1], Jonathan S. Schurrman[1], Kristýna

9 Svobodová[1], Michal Synek[1], Marius Teodosiu[11,12], Elvin Toromani[13], Volodymyr Trotsiuk[1,14,15,16], Lucie

10 Vítková[1] Miroslav Svoboda[1]

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12 **These authors contributed equally to the work

13

14 [1] *Czech University of Life Sciences Prague, Faculty of Forestry and Wood Sciences, Kamýcká 129,*

15 *Praha 6 – Suchdol 16521, Czech Republic*

16 [2] *PRALES, Odtrnovie 563, 013 22 Rosina, Slovakia*

17 [3] *Department of Biology and General Ecology, Faculty of Ecology and Environmental Sciences,*

18 *Technical University in Zvolen, Masaryka 24, 96053 Zvolen, Slovakia*

19 [4] *Department of Ecosystem Biology, Faculty of Science, University of South Bohemia, Branišovská 1760,*

20 *37005 České Budějovice, Czech Republic*

21 [5] *Irstea, UR EFNO, Domaine des Barres, 45290 Nogent-sur-Vernisson, France*

22 [6] *INRA, UMR1201 DYNAFOR, Chemin de Borde Rouge, Auzeville, CS 52627, 31326 Castanet Tolosan*

23 *Cedex, France; laurent.larrieu@inra.fr; and CRPFOcc, 7 chemin de la Lacade, 31320 Auzeville*

24 *Tolosane, France*

25 [7] *Department of Forestry and Renewable Forest Resources, Biotechnical Faculty, University of*

26 *Ljubljana, 1000 Ljubljana, Slovenia*

27 [8] *PSEDA-ILIRIA organization, Tirana 1000, Albania*

28 9 *Department of Biometry and Forest Productivity, Faculty of Forestry, University of Agriculture in*

29 *Krakow, al. 29-Listopada 46, 31-425 Krakow, Poland*

30 10 *University of Zagreb, Forestry Faculty, Department of Forest Ecology and Silviculture,*

31 *Svetošimunska 25, 10002, Zagreb, Croatia*

32 11 *"Marin Drăcea" National Research-Development Institute in Forestry, Station Câmpulung*

33 *Moldovenesc, Calea Bucovinei 73b, 725100 Câmpulung Moldovenesc, Suceava, Romania*

34 12 *Ștefan cel Mare University of Suceava, Universităţii 13, 720229 Suceava, Romania*

35 13 *Agricultural University of Tirana, Faculty of Forestry Sciences, 1029 Koder-Kamez, Albania*

36 14 *Swiss Federal Institute for Forest, Snow and Landscape Research WSL, CH-8903 Birmensdorf,*

37 *Switzerland*

38 15 *SwissForestLab, CH-8903 Birmensdorf, Switzerland*

39 16 *Institute of Agricultural Sciences, ETH Zurich, CH-8092 Zurich, Switzerland*

45 *Corresponding author at: Czech University of Life Sciences Prague, Faculty of Forestry and Wood

46 Sciences, Kamýcká 129, Praha 6 – Suchdol 16521, Czech Republic.

47 E-mail address: kozakd@fld.czu.cz (D. Kozák)

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

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

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

1. Introduction

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

2. Material and methods

2.1 Study area and site selection

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

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

In the Carpathians, the Slovakia Havešová (HAV) study site was located in the Bukovské Mountains. Havešová lies within Poloniny National Park and it is part of the UNESCO World Heritage - Primeval Beech Forests of the Carpathians and the Ancient Beech Forests of Germany. In Romania, the selected study forests, Bistra Valley (BIS), Crivia (CRI), and Paulic (PAU), were located in the Maramures Mountains, which are formally protected within Maramures Natural Park, located on the 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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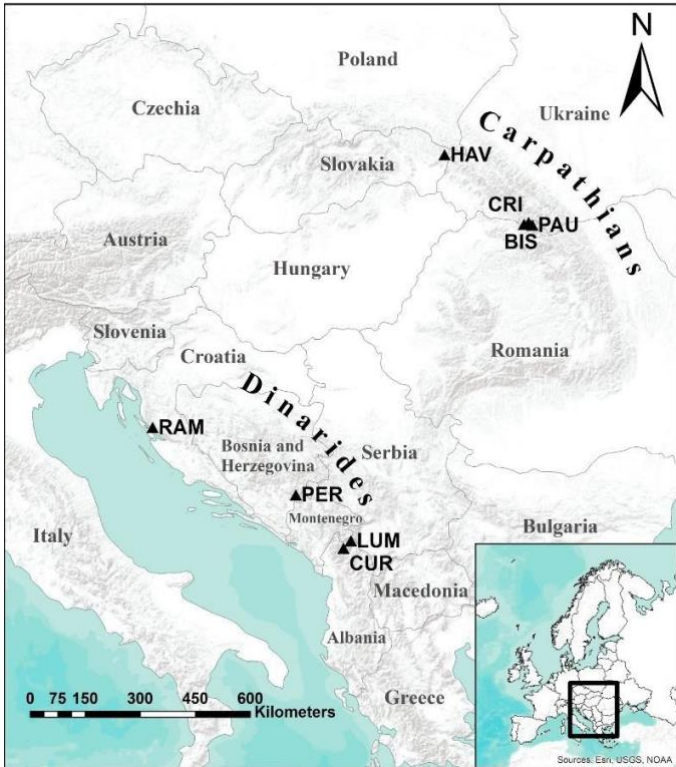
178   **Figure 1**. Locations of primary forest study areas in the Carpathians and Dinarides

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
	Dinarides										
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
	Carpathians										
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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2.2 Stand structural data

For the selection of permanent study plots, a polygon network (10 ha each) was created using the ArcView 9.3 Environment (ESRI ArcGIS, 2011). Within each 10-ha polygon we generated a random point to establish sampling points where we established two plots. The paired plots consisted of two 1,500 m2 circular plots (radius of 21.85 m); each plot center was located 40 m in opposite directions from the random sample point and parallel to the slope contour (Appendix 1). We established 146 permanent research plots nested within 73 pairs of plots across 8 forest stands. For each tree with diameter at breast height (DBH) $\geq$ 6 cm, the status of all trees (live or snag), tree species, and TreM presence/absence were recorded.

2.3 TreM data

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

2.4 TreM characteristics

Diversity and density measures of TreMs were quantified for each sample plot. To reflect the diversity of TreM types, diversity was defined in terms of the number of TreM types occurring within the plot. Alpha diversity was defined as the average number of TreM types per tree in a given plot. Because the number of trees varied widely among plots (27–277 trees per plot), gamma diversity was 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$_{-1}$) and Dinarides (289.3 bearing-trees ha$_{-1}$). The

253 average density of TreM-bearing trees for all stands was 277.8 TreM-bearing trees ha$_{-1}$. Epiphytes (128.8

254 bearing-trees ha$_{-1}$), bark characteristics (101.2 bearing-trees ha$_{-1}$), base cavities (65.2 bearing-trees ha$_{-1}$

255 $_{1}$), and non-woodpecker cavities (41.3 bearing-trees ha$_{-1}$) had the highest TreM densities in both regions

256 (Table 2). The lowest densities were observed for outgrowths (9.9 bearing-trees ha$_{-1}$) and dendrothelms

257 (4.6 bearing-trees ha$_{-1}$). In the Carpathians, bark characteristics (112.7 bearing-trees ha$_{-1}$) and base

258 cavities (98.9 bearing-trees ha$_{-1}$) had the highest densities, and dendrothelms (1.6 bearing-trees ha$_{-1}$) had

259 the lowest density. The Dinarides were characterized by high TreM densities of epiphytes (168.7

260 bearing-trees ha$_{-1}$) and non-woodpecker cavities (48.7 bearing-trees ha$_{-1}$), and low densities of patches

261 with exudates (8.6 bearing-trees ha$_{-1}$), outgrowths (7 bearing-trees ha$_{-1}$), and broken tops (10.1 bearing-

262 trees ha$_{-1}$).

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 ~ 23–25%).

273 The contribution of stands to the observed variation was less obvious, but still important (ICC ~ 9–14%),

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^{-1} 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**

Summary of GLMMs relating diversity (alpha, beta, gamma) and density of microhabitats to fixed and random effects. Likelihood ratio test statistics (χ^2),

probabilities (p), semi-partial marginal determination coefficients (R_{2m} [%]), and intra-class correlation coefficients (ICC [%]) are displayed. Significant

positive/negative partial relationships (r) are designated by +/- signs, respectively; inequality signs are used for comparisons between Carpathians (C) and

Dinarides (D). Model parameters were considered significant at 5% and are highlighted in bold.

| | Fixed effects | | | | | | | | | | | | | | | | Random effects | | | | | | | | |
| | Tree species richness | | | | RMS DBH | | | | Proportion of snags | | | | Region | | | | Stand | | | Paired plots | | | Plot | | |
Model	χ^2	p	R_{2m}	r	χ^2	p	R_{2m}	r	χ^2	p	R_{2m}	r	χ^2	p	R_{2m}	r	χ^2	p	ICC	χ^2	p	ICC	χ^2	p	ICC
Alpha diversity	**6.3**	**0.0121**	**0.6**	+	**64.3**	**< 0.0001**	**12.2**	+	**41.8**	**< 0.0001**	**7.2**	+	0.3	0.6152	1.4		**8.6**	**0.0034**	**9.4**	**84.3**	**< 0.0001**	**23.0**	**107.9**	**< 0.0001**	**48.0**
Beta diversity	**9.9**	**0.0016**	**2.2**	+	1.5	0.2223	< 0.1		**12.4**	**0.0004**	**4.6**	+	2.8	0.0962	9.0		2.2	0.1395	11.7	**64.3**	**< 0.0001**	**24.3**	**74.5**	**< 0.0001**	**42.1**
Gamma diversity	**10.5**	**0.0012**	**0.2**	+	**52.9**	**< 0.0001**	**13.2**	+	**16.5**	**0.0001**	**2.6**	+	1.0	0.3176	5.5		**11.8**	**0.0006**	**13.6**	**62.9**	**< 0.0001**	**25.2**	**63.5**	**< 0.0001**	**36.5**
Density																									
All microhabitats	**10.6**	**0.0011**	**7.3**	+	< 0.1	0.8353	< 0.1		**29.7**	**< 0.0001**	**14.4**	+	0.1	0.7811	< 0.1		**4.7**	**0.0294**	**5.7**	**100.9**	**< 0.0001**	**33.8**	**85.7**	**< 0.0001**	**44.0**
Crown deadwood	0.4	0.5135	0.2		**15.2**	**0.0001**	**7.2**	-	**4.4**	**0.0367**	**1.9**	+	0.1	0.7995	< 0.1		**8.1**	**0.0044**	**12.0**	3.5	0.0601	18.0	0.0	0.9708	0.0
Broken tops	**4.3**	**0.0376**	**< 0.1**	+	**5.6**	**0.0181**	**1.5**	-	1.0	0.3063	< 0.1		3.2	0.0727	13.9		**10.3**	**0.0013**	**19.7**	**50.0**	**< 0.0001**	**26.3**	**28.2**	**< 0.0001**	**32.8**
Conks of fungi	0.4	0.5268	< 0.1		**15.3**	**0.0001**	**7.4**	+	**11.8**	**0.0006**	**6.1**	+	**5.6**	**0.0178**	**13.3**	**C > D**	**5.4**	**0.0203**	**18.3**	**10.5**	**0.0012**	**12.6**	**15.6**	**0.0001**	**41.1**
Woodpecker cavities	0.1	0.7610	0.0		< 0.1	1.0000	< 0.1		**21.5**	**< 0.0001**	**9.9**	+	0.1	0.6993	0.8		**8.4**	**0.0038**	**11.7**	**60.6**	**< 0.0001**	**29.5**	**50.1**	**< 0.0001**	**39.4**
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		**6.6**	**0.0103**	**10.3**	**29.7**	**< 0.0001**	**14.8**	**55.7**	**< 0.0001**	**56.2**
Base cavities	0.2	0.6821	0.7		**6.4**	**0.0112**	**4.6**	+	3.1	0.0769	4.8		0.8	0.3585	5.7		**18.9**	**< 0.0001**	**18.7**	**14.0**	**0.0002**	**17.3**	2.9	0.0910	40.6
Bark characteristics	0.8	0.3864	0.4		1.3	0.2631	< 0.1		**50.9**	**< 0.0001**	**18.8**	+	0.8	0.3583	2.1		**5.4**	**0.0206**	**7.1**	**70.6**	**< 0.0001**	**25.8**	**99.3**	**< 0.0001**	**50.6**
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	**26.0**	**< 0.0001**	**16.0**	**32.2**	**< 0.0001**	**62.6**
Outgrowth	0.1	0.7428	0.7		**7.0**	**0.0082**	**1.6**	+	**7.6**	**0.0058**	**1.2**	-	3.8	0.0507	8.3		3.7	0.0529	13.6	**20.3**	**< 0.0001**	**22.4**	**12.5**	**0.0004**	**31.3**
Patches with exudates	**10.2**	**0.0014**	**4.3**	+	0.3	0.6099	< 0.1		**4.7**	**0.0299**	**1.2**	+	1.6	0.2124	8.1		**22.5**	**< 0.0001**	**25.8**	**53.4**	**< 0.0001**	**17.8**	**66.8**	**< 0.0001**	**40.3**
Epiphytes	**11.4**	**0.0007**	**8.9**	+	**5.4**	**0.0204**	**0.5**	+	0.5	0.4768	0.9		**6.4**	**0.0116**	**13.9**	**C < D**	< 0.1	0.9968	5.6	**51.1**	**< 0.0001**	**37.1**	**19.9**	**< 0.0001**	**27.6**
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	**42.2**	**< 0.0001**	**26.0**	**35.6**	**< 0.0001**	**33.2**
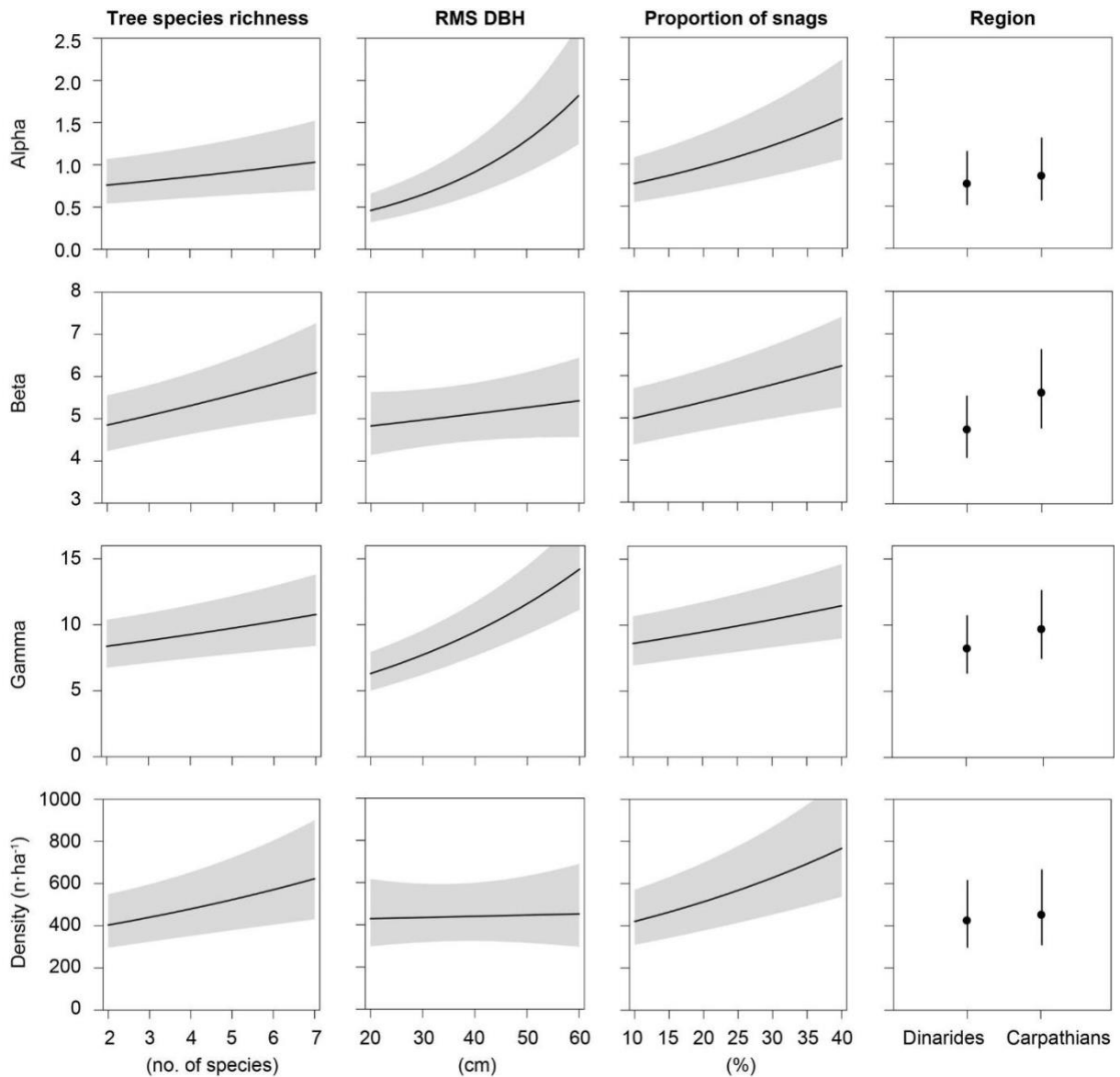
Figure 2. Effect plots showing the results of GLMMs testing for the effect of tree species richness, RMS DBH, proportion of snags, and region on diversity (alpha, beta and gamma) and density of TreMs. Predicted values (lines, circles) are displayed along with 95% confidence intervals (gray polygons, error bars).

4. Discussion

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.

414

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

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

References

Bates, D., Machler, M., Bolker, B.M., Walker, S.C., 2015. Fitting Linear Mixed-Effects Models using lme4. J. Stat. Softw. 67, 1–48. https://doi.org/10.18637/jss.v067.i01

Bauhus, J., 2009. Silviculture for old-growth attributes. For. Ecol. Manage. 258, 525–537. https:// doi.org/10.1016/j.foreco.2009.01.053

Blondel, J., 2005. Bois mort et cavités: leur rôle pour l'avifaune cavicole. Vallauri D, André J, Dodelin B, Eynard-Machet R, Rambaud D, Bois mort et à cavités: une clé pour des forêts vivantes. Lavoisier, Paris, 137-144.

464   Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., White, J.-S.S.,

465   2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol. Evol.

466   24, 127–135. https://doi.org/10.1016/j.tree.2008.10.008

467   Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K., Ellison, A.M., Chao, A.,

468   Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K., Ellison, A.M., 2014. Rarefaction and

469   extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies.

470   Ecological Monographs 84, 45-67. Stable URL : http://www.jstor.org/stable/43187596

471   Commarmot, B., Brändli, U.-B., Hamor, F., Lavnyy, V., 2013. Inventory of the Largest Primeval Beech

472   Forest in Europe. A Swiss-Ukrainian Scientific Adventure.

473   Courbaud, B., Pupin, C., Letort, A., Cabanettes, A., Larrieu, L., 2017. Modelling the probability of

474   microhabitat formation on trees using cross-sectional data. *Methods Ecol. Evol.*, *8*(10), 1347-1359.

475   https://doi.org/10.1111/ijlh.12426

476   Ding, Y., Liu, G., Zang, R., Zhang, J., Lu, X., Huang, J., 2016. Distribution of vascular epiphytes along

477   a tropical elevational gradient: Disentangling abiotic and biotic determinants. Sci. Rep. 6. https://doi.org/

478   10.1038/srep19706

479   ESRI ArcGIS, 2011. "Release 10." *Redlands, CA: Environmental Systems Research Institute* 437.

480   Hansen, M.C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D.,

481   Stehman, S. V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O.,

482   Townshend, J.R.G., 2013. High-resolution global maps of 21st-century forest cover change. Science

483   (80-.). 342, 850–853. https://doi.org/10.1126/science.1244693

484   Hunter, Jr., M.L., 1999. Maintaining biodiversity in Forest Ecosystems. Cambridge Univ. Press. https://

485   doi.org/10.1046/j.1365-2664.1999.00459-3.x

486   Jackson, J.A., Jackson, B.J.S., 2004. Ecological Relationships Between Fungi and Woodpecker Cavity

487   Sites. Condor 106, 37. https://doi.org/10.1650/7483

488   Keren, S., Diaci, J., 2018. Comparing the quantity and structure of deadwood in selection managed and

489   old-growth forests in South-East Europe. Forests 9, 1–16. https://doi.org/10.3390/f9020076

490   Keren, S., Diaci, J., Motta, R., Govedar, Z., 2017. Stand structural complexity of mixed old-growth and

491   adjacent selection forests in the Dinaric Mountains of Bosnia and Herzegovina. For. Ecol. Manage. 400,

492   531–541. https://doi.org/10.1016/j.foreco.2017.06.009

493   Kraus, D., Krumm, F., 2013. Integrative approaches as an opportunity for the conservation of forest

494   biodiversity, European Forest Institute.

495   Larrieu, L., Cabanettes, A., 2012. Species, live status, and diameter are important tree features for

496   diversity and abundance of tree microhabitats in subnatural montane beech–fir forests. Can. J. For. Res.

497   42, 1433–1445. https://doi.org/10.1139/x2012-077

498   Larrieu, L., Cabanettes, A., Brin, A., Bouget, C., Deconchat, M., 2014a. Tree microhabitats at the stand

499   scale in montane beech-fir forests: Practical information for taxa conservation in forestry. Eur. J. For.

500   Res. 133, 355–367. https://doi.org/10.1007/s10342-013-0767-1

501   Larrieu, L., Cabanettes, A., Delarue, A., 2012. Impact of silviculture on dead wood and on the

502   distribution and frequency of tree microhabitats in montane beech-fir forests of the Pyrenees. Eur. J.

503   For. Res. 131, 773–786. https://doi.org/10.1007/s10342-011-0551-z

504   Larrieu, L., Cabanettes, A., Gonin, P., Lachat, T., Paillet, Y., Winter, S., Bouget, C., Deconchat, M.,

505   2014b. Deadwood and tree microhabitat dynamics in unharvested temperate mountain mixed forests: A

506   life-cycle approach to biodiversity monitoring. For. Ecol. Manage. 334, 163–173. https://doi.org/

507   10.1016/j.foreco.2014.09.007

508   Larrieu, L., Paillet, Y., Winter, S., Bütler, R., Kraus, D., Krumm, F., Lachat, T., Michel, A.K., Regnery,

509   B., Vandekerkhove, K., 2018. Tree related microhabitats in temperate and Mediterranean European

510   forests: A hierarchical typology for inventory standardization. Ecol. Indic. 84, 194–207. https://doi.org/

511   10.1016/j.ecolind.2017.08.051

512   Lindenmayer, D.B., Franklin, J.F., Fischer, J., 2006. General management principles and a checklist of

513   strategies to guide forest biodiversity conservation. Biol. Conserv. 131, 433–445. https://doi.org/

514   10.1016/j.biocon.2006.02.019

515   McCullagh, P., Nelder, J. A., 1989. Generalized Linear Models, 2nd. edition. Chapman and Hall/CRC,
516   USA.

517   Meigs, G.W., Morrissey, R.C., Bače, R., Chaskovskyy, O., Čada, V., Després, T., Donato, D.C., Janda,
518   P., Lábusová, J., Seedre, M., Mikoláš, M., Nagel, T.A., Schurman, J.S., Synek, M., Teodosiu, M.,
519   Trotsiuk, V., Vítková, L., Svoboda, M., 2017. More ways than one: Mixed-severity disturbance regimes
520   foster structural complexity via multiple developmental pathways. For. Ecol. Manage. 406, 410–426.
521   https://doi.org/10.1016/j.foreco.2017.07.051

522   Meschede, A., Heller, K.G. ,2003. Ecologie et protection des chauvessouris en milieu forestier. MHN
523   de Genéve. Le Rhinolophe 16:1–248.

524   Meyer, P., Tabaku, V., von Lupke, B., 2003. Structural characteristics of Albanian beech (Fagus
525   sylvatica L.) virgin forests - Deductions for semi-natural forestry. Forstwissenschaftliches Cent. 122,
526   47–58. https://doi.org/10.1046/j.1439-0337.2003.02041.x

527   Michel, A. K., Winter, S., 2009. Tree microhabitat structures as indicators of biodiversity in Douglas-
528   fir forests of different stand ages and management histories in the Pacific Northwest, USA. For. Ecol.
529   Manage. 257(6), 1453-1464. https://doi.org/10.1016/j.foreco.2008.11.027

530   Mori, A.S., Kitagawa, R., 2014. Retention forestry as a major paradigm for safeguarding forest
531   biodiversity in productive landscapes: A global meta-analysis. Biol. Conserv. 175, 65–73. https://
532   doi.org/10.1016/j.biocon.2014.04.016

533   Nagel, T.A., Firm, D., Pisek, R., Mihelic, T., Hladnik, D., de Groot, M., Rozenbergar, D., 2017a.
534   Evaluating the influence of integrative forest management on old-growth habitat structures in a
535   temperate forest region. Biol. Conserv. 216, 101–107. https://doi.org/10.1016/j.biocon.2017.10.008

536   Nagel, T.A., Mikac, S., Dolinar, M., Klopcic, M., Keren, S., Svoboda, M., Diaci, J., Boncina, A., Paulic,
537   V., 2017b. The natural disturbance regime in forests of the Dinaric Mountains: A synthesis of evidence.
538   For. Ecol. Manage. 388, 29–42. https://doi.org/10.1016/j.foreco.2016.07.047

539   Nakagawa, S., Johnson, P.C.D., Schielzeth, H., 2017. The coefficient of determination R2 and intra-

540   class correlation coefficient from generalized linear mixed-effects models revisited and expanded. J. R.

541   Soc. Interface 14, 20170213. https://doi.org/10.1098/rsif.2017.0213

542   Paillet, Y., Archaux, F., Boulanger, V., Debaive, N., Fuhr, M., Gilg, O., Gosselin, F., Guilbert, E., 2017.

543   Snags and large trees drive higher tree microhabitat densities in strict forest reserves. For. Ecol. Manage.

544   389, 176–186. https://doi.org/10.1016/j.foreco.2016.12.014

545   Parviainen, J., 2005. Virgin and natural forests in the temperate zone of Europe. For. Snow Landsc. Res.

546   79, 9–18.

547   Peterken, G.F., 1996. Natural woodland: ecology and conservation in northern temperate regions,

548   Cambridge University Press.

549   R Core Team, 2017. R: A language and environment for statistical computing. R Foundation for

550   Statistical Computing, Vienna, Austria.

551   Ray-Mukherjee, J., Nimon, K., Mukherjee, S., Morris, D.W., Slotow, R., Hamer, M., 2014. Using

552   commonality analysis in multiple regressions: A tool to decompose regression effects in the face of

553   multicollinearity. Methods Ecol. Evol. 5, 320–328. https://doi.org/10.1111/2041-210X.12166

554   Regnery, B., Couvet, D., Kubarek, L., Kerbiriou, C., 2013a. Tree microhabitats as indicators of bird and

555   bat communities in Mediterranean forests 34, 221–230. https://doi.org/10.1016/j.ecolind.2013.05.003

556   Regnery, B., Paillet, Y., Couvet, D., Kerbiriou, C., 2013b. Forest Ecology and Management Which

557   factors influence the occurrence and density of tree microhabitats in Mediterranean oak forests ? 295,

558   118–125.

559   Remm, J., Lõhmus, A., 2011. Tree cavities in forests - The broad distribution pattern of a keystone

560   structure for biodiversity. For. Ecol. Manage. 262, 579-85. https://doi.org/10.1016/j.foreco.2011.04.028

561
562   Sabatini, F.M., Burrascano, S., Keeton, W.S., Levers, CH., Lindner, M., Potzchner, F., Verkerk, P.J.,

563   Bauhus, J., Buchwald, E., Chaskovsky, O., Debaive, N., Horváth, F., Garbarino, M., Grigoriadis, N.,

564   Lombardi, F., Duarte, I.M., Meyer, P., Midteng, R., Mikac, S., Mikoláš, M., Motta, R., Mozgeris, G.,

565   Nunes, L., Panayotov, M., Ódor, P., Ruete, A., Simovski, B., Stillhard, J., Svoboda, M., Szwagrzyk, J.,

566   Tikkanen, O.P., Volosyanchuk, R., Vrska, T., Zlatanov, T., Kuemmerle, T., 2018. . Where are Europe's

567   last primary forests? Divers. Distrib. 00:1–14. https://doi.org/10.1111/ddi.12778

568   Schurman, J.S., Trotsiuk, V., Bače, R., Čada, V., Fraver, S., Janda, P., Kulakowski, D., Lábusová, J.,

569   Mikoláš, M., Nagel, T.A, Seidl, R., Synek, M., Svobodová, K., Chaskovskyy, O., Teodosiu, M.,

570   Svoboda, M., 2018. Large-scale disturbance legacies and the climate sensitivity of primary Picea abies

571   forests. *Global change biology*. https://doi.org/10.1111/gcb.14041

572   Siitonen, J., 2012. Microhabitats, in: Biodiversity in Dead Wood. pp. 150–182. https://doi.org/10.1017/

573   CBO9781139025843.008

574   Standovár, T., Kenderes, K., 2003. A review on natural stand dynamics in beechwoods of east central

575   Europe. Appl. Ecol. Environ. Res. 1, 19–46.

576   Van Oldenborgh, G.J., Drijfhout, S., Van Ulden, A., Haarsma, R., Sterl, A., Severijns, C., Hazeleger,

577   W., Dijkstra, H., 2009. Western Europe is warming much faster than expected. Clim. Past 5, 1–12.

578   https://doi.org/10.5194/cp-5-1-2009

579   Veen, P., Fanta, J., Raev, I., Biriş, I.A., de Smidt, J., Maes, B., 2010. Virgin forests in Romania and

580   Bulgaria: Results of two national inventory projects and their implications for protection. Biodivers.

581   Conserv. 19, 1805–1819. https://doi.org/10.1007/s10531-010-9804-2

582   Vuidot, A., Paillet, Y., Archaux, F., Gosselin, F., 2011. Influence of tree characteristics and forest

583   management on tree microhabitats. Biol. Conserv. 144, 441–450. https://doi.org/10.1016/

584   j.biocon.2010.09.030

585   Whittaker, R.H., 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecol. Monogr.

586   https://doi.org/10.2307/1943563

587   Winter, S., 2015. Association of tree and plot characteristics with microhabitat formation in European

588   beech and Douglas-fir forests. Eur. J. Forest. Res. 134, 335–347. https://doi.org/10.1007/s10342-014-

589   0855-x

590   Winter, S., Möller, G.C., 2008. Microhabitats in lowland beech forests as monitoring tool for nature

591   conservation. For. Ecol. Manage. 255, 1251–1261. https://doi.org/10.1016/j.foreco.2007.10.029

592   Zahner, V., Sikora, L.,Pasinelli, G. 2012. Heart rot as a key factor for cavity tree selection in the black

593   woodpecker. For. Ecol. Manage. 271, 98-103.

594   Zeibig, A., Diaci, J., Wagner, S. 2005. Gap disturbance patterns of a Fagus sylvatica virgin forest

595   remnant in the mountain vegetation belt of Slovenia. For. Snow Landsc. Res. 79, 69-80.

596

597

598

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600

601

602

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604

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606
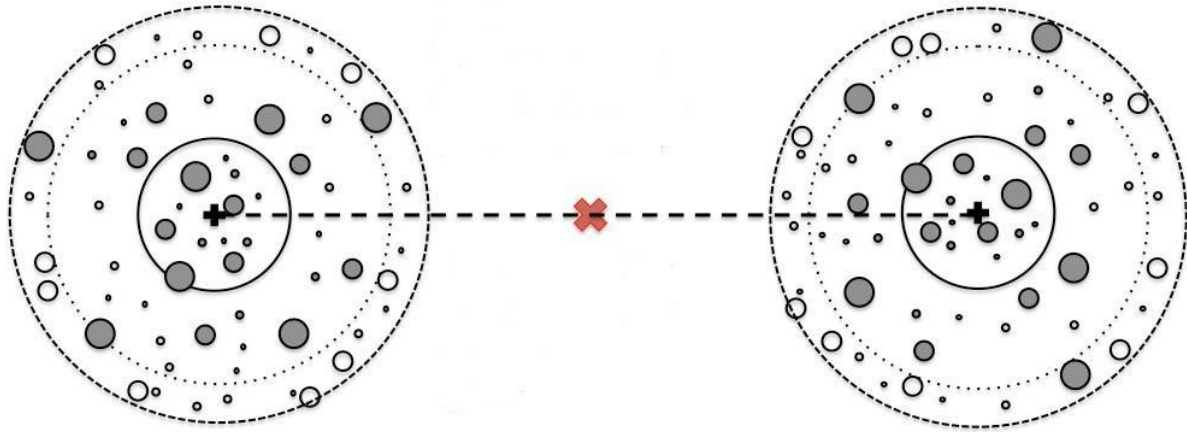
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613   **Appendices**

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Appendix 1

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

used to locate the pair of circular sample plots.

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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-1 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

			N									
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

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