1 **Importance of conserving large and old trees to continuity of tree-related microhabitats**

2 **Abstract**

3 Protecting structural features, such as tree-related microhabitats (TreMs), is a cost-effective tool crucial

4 for biodiversity conservation applicable to large forested landscapes. While the development of TreMs

5 is influenced by tree diameter, species, and vitality, the relationships between tree age and TreM profile

6 remain poorly understood. Using a tree-ring based approach and a large dataset of 8038 trees, we

7 modeled the effects of tree age, diameter, and site quality on TreM richness and occurrence across some

8 of the most intact primary temperate forests in Europe, including mixed beech and spruce forest types.

9 We observed an overall increase in TreM richness on older and larger trees in both forest types. The

10 occurrence of specific TreM groups showed variable relationships with tree age and diameter, whereas

11 some TreM groups showed a stronger positive relationship with tree species and altitude. While many

12 TreM groups were positively associated with both tree age and diameter, only two TreM groups in

13 spruce stands reacted exclusively to tree age (insect galleries and exposed sapwood) without responding

14 to diameter. Thus, the retention of trees for conservation purposes based on tree diameter appears to be

15 a generally feasible approach with rather low risk of under-representation of TreMs. As greater tree age

16 and diameter showed positive effects on TreM development, placing a greater emphasis on both

17 conserving large trees and allowing them to reach older ages, for example through establishment of

18 conservation reserves, would better maintain the continuity of TreM resource and associated

19 biodiversity. However, this approach may face difficulties due to the widespread intensification of forest

20 management and global climate change.

21

22 **Article impact statement:** Conservation of habitat trees based on size, without considering tree age,

23 may impair landscape-level biodiversity potential

24

25 **Introduction**

Large and old trees play critical ecological roles such as carbon sequestration (Lutz et al., 2018) and habitat provisioning (Remm & Lohmus, 2011) and they are, therefore, often called "keystone structures" in forest ecosystems (Lindenmayer et al., 2014). Despite their importance, over the past century, global declines in mature and old forest areas and biodiversity related to habitat loss, along with fragmentation and overexploitation are causing increased concern among conservationists. Large old trees across the globe are in a steep decline, mainly due to preferential cutting in a variety of forest harvesting and land-use change context, causing serious threats to ecosystem integrity and biodiversity (Lindenmayer et al., 2012; Liu et al., 2022).

As complete biodiversity inventories typically are not feasible across forest landscapes due to time and economic constraints, scientists and forest managers in the past decade have focused on structural indicators of biodiversity, such as large trees, coarse woody debris, and canopy gaps (Gao et al., 2015; Burrascano et al., 2018). To quantify the potential of individual trees to host biodiversity, the concept of tree-related microhabitats (hereafter TreMs) was developed in recent years with standardized typologies for TreM assessment in order to ensure compatibility between different studies (Kraus et al., 2016; Larrieu et al., 2018). Here, we refer to TreMs as 'distinct, well-delineated structures occurring on living or standing dead trees, that constitute a particular and essential substrate or life site for species or species communities during at least a part of their life cycle to develop, feed, shelter or breed' (Larrieu et al., 2018). These include microhabitats such as cavities, tree injuries, exposed wood, fungal fruiting bodies or excrescences. Even though the relationship between TreM richness and forest biodiversity is relatively understudied, the occurrence of TreMs appears to be a suitable indicator for many taxa, such as certain insects, birds, and bats (Buse et al., 2007; Winter & Möller, 2008; Regnery et al., 2013; Paillet et al., 2018; Larrieu et al., 2019; Basile et al., 2020a).

Scientific understanding of TreM development and dynamics at the tree scale has increased substantially with the greater attention on TreMs (Paillet et al., 2019; Asbeck et al., 2021a). For instance, snags often contribute more to the TreM occurrence when compared to living trees, mostly due to decomposition and wood properties that favor the development of certain TreMs, such as cavities, breakages, and sloughing bark (Kõrkjas et al., 2021a). Another largely important factor is the tree diameter since the

occurrence and diversity of TreMs increases with larger tree diameter (Winter & Möller, 2008; Larrieu & Cabanettes, 2012; Paillet et al., 2019). Additionally, tree species influence type and rate of TreMs development, with broadleaved tree species generally accumulating TreMs to a greater extent than coniferous species (Larrieu & Cabanettes, 2012; Courbaud et al., 2017; Paillet et al., 2019; Krumm et al., 2020), and early-successional species tending to differ from mid- and late-successional species with higher formation of TreM types such as bark loss, crown deadwood, and rot holes on early successional species (Courbaud et al., 2021).

As TreMs typically take time to develop or often develop once a tree is sufficiently large (Michel et al., 2011; Courbaud et al., 2017), tree age may drive the occurrence of certain TreMs, like cavities, rot holes, and cracks. Tree age is often in a close relationship with tree size, but this relationship is not always straightforward as the largest trees are not always the oldest (Issartel & Coiffard, 2011; Hubau et al., 2019). Highly shade tolerant, suppressed trees can grow in the lower, shaded canopy strata for decades with relatively small diameter increments. Growth rates in suppressed trees can increase following mortality in the upper canopy and elevated light availability. This growth response is particularly true for long-lived and shade-tolerant species, such as European beech (*Fagus sylvatica* L.; Di Filippo et al., 2012) and silver fir (*Abies alba* Mill.; Pantic et al., 2015). In contrast, dominant canopy trees often grow faster and can reach large diameters without exceeding the life expectancy of understory conspecifics (Issartel & Coiffard, 2011; Pavlin et al., 2021). This effect can lead to substantially different TreM occurrence between large and old trees as certain conditions for TreM occurrence might relate to a large diameter but not necessarily to higher age and vice versa (Kõrkjas et al., 2021a).

There are limitations to derive TreM dynamics from studies carried out only in managed forests. The process of felling can cause tree damage and injuries which can lead to an increased occurrence of TreMs such as bark loss, dendrotelms, and resinosis (Michel et al., 2011; Larrieu & Cabanettes, 2012). In addition, most TreM groups have reduced formation rates in managed forests compared to unmanaged forests (Courbaud et al., 2021). Investigating TreM occurrences in forests that have never been managed or have not been managed for a long time provides a significant reference for understanding patterns of TreM development under natural conditions. Thus, primary forests represent the ultimate intact habitat

80 (Ulyshen et al., 2018) for biodiversity studies since they often contain an abundant and diverse array of

81 TreMs (Larrieu et al., 2014; Kozák et al., 2018; Jahed et al., 2020; Asbeck et al., 2021b).

82 In Europe, effects of tree age on TreM occurrence have mostly been studied within managed forest

83 stands of aspen (*Populus tremula* L.) or Norway spruce (*Picea abies* Karst.) (Kõrkjas et al., 2021b),

84 focusing only on specific TreM types, such as cavities or rot holes (Puverel et al., 2019; Fritz & Heilman-

85 Clausen, 2010). Consequently, the influence of tree age on TreM occurrence in primary forests (i.e.

86 never influenced by humans) is still relatively unknown.

87 To address this knowledge gap, we disentangled the effects of tree age and diameter on TreM occurrence

88 using dendrochronological methods using a large sample of trees (n = 8038) and study plots (n = 379)

89 across the geographic range of the Carpathian primary mixed beech and spruce forests. Here, we focused

90 on assessing the importance of tree age, diameter (Diameter at Breast Height, DBH), tree species, and

91 site quality on TreM occurrence at the tree scale. We used generalized mixed effect models to

92 differentiate the relative strength of these effects on overall TreM richness as well as on the occurrence

93 of specific TreM groups. Specifically, we asked to what extent (i) is TreM richness and occurrence

94 coincided with age and/or diameter of the trees, and (ii) are individual TreM groups related to tree age

95 and diameter differently in particular forest types?

96

97 **Methods**

98 **Study area**

99 The study area was restricted to primary forests in two regions: the western Carpathians (Slovakia) and

100 the southern Carpathians (Romania). The Carpathian Mountains support a substantial part of all

101 remaining primary forests in Europe (Sabatini et al., 2018, 2021; Mikoláš et al., 2019). We refer to

102 'primary forest' as a forest without signs of direct human impact and where natural disturbances are the

103 main driver of forest structure and composition (Barredo et al., 2021). The study forests were selected

104 based on previous inventories of primary forest remnants when available (e.g. Veen et al., 2010; Mikoláš

105 et al., 2019), and by searching the available archival information and historical data regarding the land

4

use history of these areas. During the initial field survey, all forests were inspected for various indicators

of naturalness (e.g. deadwood in various stages of decay, pit-and-mound topography, very large trees,

natural tree species composition), and for 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 (Mikoláš et

al., 2019).

We selected 379 plots in primary mixed beech (n = 133) and spruce (n = 246) mountain forests (Figure

1). Survey locations were based on an existing international network of permanent inventory plots

(REMOTE, https://www.remoteforests.org) that spans across primary forests in central, eastern and

southeastern Europe, and that are randomly distributed across various environmental and climatic

gradients. Due to possible differences in topography and climatic conditions within the two studied

forest types, which can influence differently the growth of the studied tree species as well as the

occurrence of certain TreM types (Asbeck et al., 2019; Paillet et al., 2019), we divided our data into two

subsets based on the forest type; i.e. mixed beech and spruce.

The dominant tree species in the mixed beech forests (montane zone) was European beech with

secondary species being mainly Norway spruce, silver fir (*Abies alba* Mill.), and sycamore (*Acer*

pseudoplatanus L.). Spruce forests (subalpine zone) were mostly dominated by Norway spruce with

minor admixture of other tree species, including rowan (*Sorbus aucuparia* L.), European beech, silver

fir, sycamore, and stone pine (*Pinus cembra* L.).

We collected field data to describe the tree and associated TreM characteristics during the vegetation

season of 2018 and 2019. All data were collected within 0.1 ha circular plots in spruce stands and 0.15

ha circular plots in mixed beech stands, corresponding to the extent of the original REMOTE plots.

TreMs and forest structure

Detailed inventory data were obtained to quantify forest structure and TreM occurrence across all study

plots. Tree characteristics were identified by precise mapping of all living trees using laser rangefinders

and customized software (Field-map; Monitoring and Mapping Solutions, Jílove u Prahy, Czech

Republic). As tree DBH has been recognized as an important factor for TreM occurrence (e.g. Paillet et

132   al., 2019), we measured DBH of all trees ≥ 6 cm at 1.3 m on the uphill side of the tree, and determined

133   ages for a subset of canopy trees based on increment core samples collected 1 m above the ground

134   surface. In the spruce forests, we collected an increment core from 25 random non-suppressed trees with

135   ≥ 10 cm DBH per plot. If the tree was rotten, it was replaced by a surrounding tree with similar DBH

136   (Janda et al., 2019). In the mixed beech forests, the trees were selected for coring based on hierarchy of

137   size classes in a circular nested plot design. All living trees up to 8 m from the plot center with ≥ 6 cm

138   DBH were cored, in addition to a quarter of all canopy and subcanopy trees with 10-20 cm DBH and all

139   trees ≥ 20 cm DBH up to 17.84 m from the plot center. All trees with ≥ 60 cm DBH were cored up to

140   21.85 m from the plot center (Pettit et al., 2021).

141   We identified occurrences of 47 distinct TreM types (Appendix 6) on all cored trees based on the

142   typology by Larrieu et al. (2018) and these types were pooled into 15 TreM groups described by the

143   same typology based on the similarities in their morphological characteristics and biodiversity

144   relevance. TreMs richness was defined as the number of different TreM types per tree and the occurrence

145   of TreM groups was set to 1 if at least one TreM type from the respective TreM group was present on a

146   tree and was set to 0 if none of the TreM types from the respective TreM group were present. All trees

147   were identified to species level. We only used four major tree species in the analyses, namely European

148   beech, silver fir, sycamore, and Norway spruce, due to the minor occurrence of other tree species in the

149   dataset. Trees that had not been cored, and the information about their age is thus unavailable, were

150   excluded from the final dataset.

151   **Tree age data**

152   Increment cores were dried in the laboratory and measured and cross-dated following standard

153   dendrochronological methods (Stokes & Smiley, 1968) in order to get accurate measures of the tree ages

154   and to avoid underestimation due to missing tree rings. Annual rings were measured to the nearest 0.01

155   mm using a stereomicroscope and a Lintab™ sliding-stage measuring device in conjunction with TSAP-

156   WIN™ software (http://www.rinntech.ds). Cores were first visually cross-dated using the marker year

157   approach (Yamaguchi, 1991), verified with CDendro software (Larsson, 2003), and then confirmed with

158   COFECHA™ software (Holmes, 1983). For cores that did not intersect the pith, the number of missing

159 rings was extrapolated from the curvature and average growth rates of the innermost rings (Duncan,

160 1989). We excluded all cores that had more than 20 estimated years missing or were of inadequate

161 quality due to rotten pith area, which did not allow us to properly measure and cross-date the samples

162 (Pavlin et al., 2021). This approach might lead to an underestimation of certain TreM types (such as

163 trunk rot holes) and the exclusion of TreM types which might cause difficulties during tree coring (e.g.

164 chimney trunk rot holes). Importantly, because we cored trees at 1 m of height, we did not consider the

165 number of tree rings required to reach 1 m, which could range from years to several decades for shade

166 tolerant species (Pantic et al., 2015).

Statistical analyses

168 We used generalized linear mixed models (GLMMs) to disentangle the effect of tree age and DBH on

169 the overall TreM richness and occurrence probability of TreM groups on trees in mixed beech and spruce

170 forest stands. First, we split the dataset into mixed beech forests data and spruce forests data and fitted

171 separate models to each forest type since we expected forest-specific responses of TreM characteristics.

172 The models involved several variables with fixed and random effects. A categorical explanatory variable

173 classifying tree species (variable Species with four levels: beech, spruce, fir, sycamore) was used in the

174 models of mixed beech forests as this forest type regularly supports multiple tree species that may bear

175 specific TreMs (Table 1). The categorical variable Species was not present in the spruce forest GLMMs

176 as there were only very few tree species present other than spruce. Therefore, we removed them from

177 the dataset. Moreover, we included site quality, namely altitude, terrain slope, and region as additional

178 fixed-effect variables to account for a possible confounding effect of environmental heterogeneity

179 among plots. Since the data were collected in a hierarchical sampling design (individual trees nested

180 within plots that were nested within stands), categorical indicators of plots and stands were used as

181 random effects in the GLMMs to avoid pseudoreplication.

182 The TreM richness data showed lower variability than expected under the unit mean-variance

183 relationship assumed in the Poisson distribution; dispersion parameter $\varphi = 0.8$ in mixed beech forests

184 and even less than 0.3 in spruce forests. Therefore, we fitted the TreM richness data by GLMMs with a

185 Conway-Maxwell-Poisson distribution which effectively handles underdispersion (Shmueli et al.,

186 2005). A zero-truncated Conway-Maxwell-Poisson distribution was used to fit TreM diversity in mixed

187 beech forests since these data completely lack zero values.

188 Presence/absence of 13 TreM groups (twig tangles and woodpecker cavities were excluded due to very

189 few observations) were fitted as binary outcomes to relate the probability of occurrence of individual

190 TreM groups with explanatory variables. GLMMs with binomial error distribution and logit link

191 function were employed for this task.

192 Our main aim was to separate the effect of tree age and DBH on TreM richness and their occurrence.

193 Those variables are often tightly related and using both in the same model might cause collinearity

194 problems and biased results. Therefore, we examined correlations between the tree age and DBH and

195 also variance inflation factors (VIF) of each variable in the models. Pairwise correlations were rather

196 moderate (spruce forests: $\rho = 0.47$, mixed beech forests: $\rho = 0.64$) and, importantly, no VIF exceeded

197 2.2 (Appendix 2 and 3) indicating that the models should not suffer from multicollinearity and the results

198 can be trusted (Quinn & Keough, 2002). The performance of each model was evaluated using diagnostic

199 plots of residuals; no considerable violation of the assumptions was observed (Appendix 4 and 5).

200 Likelihood ratio tests were used to examine statistical significance of individual fixed-effect terms and

201 also to test the significance of whole models comparing changes in deviance between full and null

202 models. Marginal pseudo-determination coefficients (R^2_m; Nakagawa & Schielzeth, 2013) were

203 quantified to assess the overall goodness-of-fit of the models. To compare the relative importance of

204 individual variables, we calculated semi-partial R^2_m based on commonality analysis (Ray-Mukherjee et

205 al., 2014). We also evaluated the models using a predictive approach that allows for independent

206 assessment of model performance. Root mean squared error (RMSE) and square root of Brier score

207 (BS) were used as measures of predictive performance of the TreM richness and binomial models,

208 respectively. Five-fold cross-validated RMSE and BS values were calculated to ensure unbiased

209 estimates of predictive performance (Kuhn & Johnson, 2013).

210 The analyses were performed in R 4.1.2 (R Core Team, 2021) using the packages DHARMa (Hartig,

211 2022), effects (Fox & Weisberg, 2019), ggplot2 (Wickham, 2016), glmmTMB (Brooks et al., 2017),

212 and performance (Lüdecke et al., 2021).

213

214 **Results**

215 Tree age positively influenced overall TreM richness in both studied forest types (Figure 2) and

216 significantly influenced the probability of occurrence of 4 out of 13 studied TreM groups in mixed beech

217 forests (Table 1) and 5 out of 13 TreM groups in spruce forests (Table 2). In spruce forests, the tree age

218 had relatively greater importance than diameter of the trees as quantified by partial R^2 (Table 2) and

219 standardized regression coefficients (Appendix 3) for the following TreM groups: insect galleries,

220 exposed sapwood, burrs and cankers (Appendix 7). In mixed beech forests, only one TreM group, i.e.

221 burrs and cankers, reached a higher magnitude of effect related with age rather than with the diameter

222 (Table 1, Appendix 2, Appendix 7).

223 Tree DBH was the most important predictor for overall TreM richness in both studied forest types

224 (Figure 2) and also positively influenced the probability of the occurrence of 8 out of 13 TreM groups

225 (Table 1 and 2). The effect of tree DBH was consistent across both forest types in almost all TreM

226 groups; the only exceptions were exposed sapwood and heartwood, and exudates (significant only in

227 mixed beech) and epiphytes (significant in spruce forests) (Appendix 2, 3 and 7).

228 Tree species, which were used as a predictor only in mixed beech forests, positively influenced overall

229 TreM richness and occurrence of all TreM groups except for insect galleries (Table 1). Broadleaved

230 species (European beech and sycamore) showed higher TreM richness than conifers (silver fir and

231 Norway spruce) (Figure 2).

232 Additionally, site quality had only a limited influence on TreM characteristics (Table 1 and 2). Altitude

233 showed a positive effect on the overall TreM richness in spruce forests (Figure 2) and was the most

234 important driving factor of the occurrence of epiphytes across both forest types. Terrain and slope had

235 only a minor effect; positively influenced the occurrence of epiphytes in spruce forests. Regional

236 differences were significantly manifested only in the occurrence of annual fungi in mixed beech forests

237 and insect galleries, crown deadwood, and exudates in spruce forests.

238

239 **Discussion**

240 The unprecedented rate of species extinctions, coupled with widely held expectations that the frequency

241 and intensity of landscape disturbances will increase with climate change and modify the age structure

242 of forests across the globe (Seidl & Turner, 2022) highlights the need to better understand how tree age

243 impacts habitat availability for forest biodiversity. Based on a unique dataset covering spruce and mixed

244 beech primary mountain forests across one of the largest remaining continuous forest ecosystems in

245 Europe - the Carpathians, we quantified the effects of tree age, diameter, species, and site quality on

246 TreM occurrence in natural landscapes to provide deeper insights for conservation emphasizing habitat

247 tree retention.

248 The older and larger trees benefited from higher overall TreM richness and showed increased occurrence

249 of almost all TreM groups with increasing age and diameter, suggesting the critical importance of old

250 trees for biodiversity conservation. Positive effect of increasing tree diameter on TreM richness and

251 occurrence is relatively well studied across different tree species (Paillet et al., 2019). In general, the

252 higher TreM richness among larger and older trees can be explained by higher susceptibility of such

253 trees to biotic or abiotic damage and by a longer lifespan leading to increased TreM development

254 (Larrieu et al., 2014; Asbeck et al., 2019; Kõrkjas et al., 2021b). Our results generally confirm mutual

255 substitutability of tree age and tree diameter for prediction of TreMs occurrence. Confirmation of mutual

256 substitutability between tree age and tree diameter should not lead to overlooking the positive effect of

257 tree longevity on TreMs richness. In this study, old trees indeed influenced the occurrence of specific

258 TreM groups, although only some TreMs (the insect galleries and exposed sapwood) were solely related

259 to tree age in spruce forests with strong regional effect. This trend among older spruce trees, prevalent

260 in western Carpathian region, might be connected to bark-beetle outbreaks in the previous decades (Senf

& Seidl, 2020), which may increase the likelihood of further colonization by other xylophagous insects (Hagge et al., 2019) due to a weakened defense system of older trees. Similarly, exposed sapwood (e.g. bark losses, pockets and shelters) occurred more likely on older trees probably due to longer exposure to damage and injuries or possibly because younger trees have a higher chance to heal the wound after an injury. Presence of TreMs caused by pathogens (burrs and cankers) was more likely to occur on older trees rather than on large ones in both forest types, which might be connected either to decreased efficiency of tree defense mechanisms against fungal, bacterial, and viral infections as trees grow older (Vasiatis, 2013) or due to longer exposure to these stressors. On the other hand, certain TreM groups more likely occur on older trees because of the time necessary for the development of these specific TreMs. One example is the rot holes originating from intrusions, lesions, and breakages, exposing sap and heartwood initiating wood decay; the fully evolved rot holes have thus a very long development time (Gouix et al., 2015). Our results supported the importance of tree age for rot holes occurrence across mixed beech forests. However, the magnitude of the effect was lower for tree age than for diameter. This pattern may result from the thresholds for rot holes opening (diameter of opening >10 cm or >30 cm based on the type of rot holes; see Appendix 6) which are applied when surveying TreMs with Larrieu et al. (2018) typology, with larger trees being more likely to form larger rot holes openings. Previously, the occurrence of rot holes on beech trees was related to low tree growth and not explicitly to the age or size of the tree (Fritz & Heilmann-Clausen, 2010). Even though we did not specifically focus on the effect of tree growth in this study, the described pattern of low growth and rot holes occurrence might be present in our data as well because the age of trees in temperate primary forests increases with longer periods of suppression where trees exhibit smaller growth rates (Pavlin et al., 2021). The variations in growth trends among individual trees might explain the development of certain TreMs but such analyses were out of scope of this study.

Many trees in our dataset exceeded more than 300 years of age and the oldest reached more than 500 years of age (Appendix 1). After trees of an advanced age die, they develop a diversity of TreMs over a long process of stem breakdown and bole decomposition in the standing dead tree, with time frame and TreM community composition dependent on tree species, decomposition rates, and other factors such

288   as stem snapping or uprooting. Consequently, TreM habitat provisioning may, in some cases, span

289   hundreds of years (van Pelt, 2007).

290   Besides tree age and size, tree species and site quality impacted the occurrence of several TreM groups.

291   For instance, in both forest types, the occurrence of epiphytes increased with altitude, which is in

292   accordance with other studies from European temperate forests and may be connected to higher

293   precipitation (Asbeck et al., 2019; Paillet et al., 2019). Moreover, from the four studied tree species,

294   sycamore exhibited increased occurrence of epiphytes, probably due to different bark characteristics,

295   such as water-holding capacity, roughness or chemical properties (Mitchell et al., 2021). Consistently

296   with other studies (Asbeck et al., 2019; Paillet et al., 2019) broadleaved species showed higher overall

297   TreM richness than conifers.

298   Strictly and permanently protected forest landscapes, such as biodiversity-rich primary forests, represent

299   an environment where trees are allowed to reach high ages and sizes and consequent TreM formation

300   (Pavlin et al., 2021; Liu et al., 2022; Asbeck et al., 2021b). Besides small-scale mortality factors such

301   as tree senescence, temperate primary forest dynamics are driven by natural disturbances. In the case of

302   the Carpathians, the most profound drivers are wind and bark-beetle outbreaks (Janda et al. 2017). Wind

303   damage may cause breakages of tree stems, limbs or branches, which might additionally damage

304   neighboring trees resulting in wounds and bark damage, with such events directly causing TreM

305   formation. Large trees might be more prone to damage, and allow for further TreM development as trees

306   get older (e.g. injuries can evolve to rot holes and cavities; Kõrkjas et al., 2021a). Moreover, biotic

307   agents such as woodpeckers, insects, or fungi are known to create certain TreMs or play an important

308   role in TreM development. For instance, cavities often appear after polypore emergence because of

309   changed wood properties (Courbaud et al., 2017), polypores are also known to co-occur with other

310   TreMs such as rot holes, cracks, and bark losses (Larrieu et al., 2021), and woodpeckers prefer to dig

311   their cavities on trees with a larger-than-average DBH (Basile et al., 2020b). Thus, the possibility of

312   TreM formation increases immensely with increasing age and diameter of the tree (Ranius et al., 2009;

313   Fritz & Heilmann-Clausen, 2010; Vuidot et al., 2011) significantly increasing the ecological value of

314   the tree (Bütler et al., 2020). Moreover, certain TreM formation processes are typical for old trees, such

as lower branches dying in the shade or the development of cavities from trunk wounds (Zheng et al., 2016). Increased size can make trees more prone to breakages of large limbs, treetops, or the formation of trunk injuries (Kõrkjas et al., 2021b). Although, in general, the tree age and diameter are closely correlated, the oldest trees are often not the largest trees in the primary forests, which results from the decreased growth rates of suppressed trees as opposed to the trees that grew fast in the open canopy and gained larger increments in a shorter time (Pavlin et al., 2021). This interesting pattern dependent on the growth trends of individual trees may thus result in different pathways of TreM formation between the old and large trees.

We present a widely applicable framework to improve conservation approaches based on selection of habitat trees. Besides other tree characteristics, integrating dendrochronological tree-ring measurements in surveys and selection of trees suitable for the creation of TreMs based on tree age might be vital to maintaining a full range of TreMs. This approach may help to identify the slow-growing (suppressed) trees with high potential to reach the highest ages and can help to avoid the deprivation of particular habitats. However, applying a dendrochronological approach might be time-consuming and expensive, and thus probably not possible to be applied everywhere, whereas habitat tree selection based on diameter can be routinely done during forest inventory. Alternatively, tree age estimation might be simplified by using methods based on visual characteristics (Handegard et al. 2021). Hence, the best way to reach the highest tree ages across the forest landscapes is the establishment of strict conservation areas (Liu et al., 2022). We argue that it might be difficult to reach the highest potential tree ages in conventionally managed stands and that integrative forest management approaches may not be sufficient to fulfill the maximum habitat potential for nature conservation across the landscapes unless complemented by a strict and permanent forest conservation (Muys et al., 2022).

While our statistical model and analyses relied on established approaches, our study has some limitations that warrant discussion. First, the oldest trees are often rotten, and extraction of the tree core and tree rings counting from heavily rotten trees is often impossible. Thus, such trees were omitted from the analyses, although they usually host a lot of TreMs. Therefore, the effect of age on TreMs occurrence could be even higher, if data from the potentially oldest, but rotten, trees were included. Second, larger

342   surface area of large trees makes the occurrence of TreM with specific size thresholds more likely than

343   on smaller trees. Third, we focused only on living trees within the study plots, even though living trees

344   host less TreMs than dead ones on average (Paillet et al., 2019; Asbeck et al., 2021a). This approach

345   helped us to better understand the important role of large and old trees and focus on improving

346   conservation approaches based on selection of habitat trees. However, as our results suggest, forests

347   must be allowed to attain older ages that would benefit the presence of standing dead and old trees in

348   the landscapes. Thus, we believe that our analyses produced results with a high degree of generality.

349

350   **Conclusion**

351   Global change factors have triggered a significant recent acceleration of tree mortality rates in forests

352   across Europe (Seidl & Turner, 2022). The effects of increasingly severe drought episodes, rising

353   temperatures, a climate-mediated intensification of natural disturbance, land clearing and wood harvest,

354   among other factors, are multiplicatively impacting tree demography and survival. These processes are

355   disproportionately affecting the persistence of the largest and oldest trees (Lindenmayer et al., 2012).

356   Remaining primary and intact forests support the largest proportion of the remaining large and old trees,

357   and these systems are the most threatened (IUCN, 2018). An awareness of the progressive and

358   accelerating loss of the largest trees has generated substantial research attention devoted to

359   understanding the consequences of these trends for ecosystem functioning. The largest trees are known

360   to disproportionately control the flux of carbon, nutrients, and energy in forests (Lutz et al., 2018). In

361   contrast, less is understood regarding the relative importance of individual tree size versus age for habitat

362   regulation and biodiversity potential. However, the largest trees are not necessarily the oldest (Pavlin et

363   al., 2021). In this study, we demonstrate that even if tree diameter and age are largely interchangeable

364   in their importance for temporal and spatial patterns in TreM richness and occurrence, they differ in the

365   effect on some specific TreMs. We show that particularly specialized TreM types emerge separately in

366   old vs. large trees, partly as a consequence of morphological differences that increase with time and age.

367   Consequently, the largest trees and the oldest trees differ, but synergistically support the integrity of

368   forest functioning, through the provisioning of specialized microhabitats, which, in turn, promote the

369 viability and persistence of dependent, niche-differentiated flora and fauna. Our findings may better

370 inform conservation efforts, suggesting a need to expand current strategies to also incorporate measures

371 that promote an explicit retention and protection of, both, large and old trees across divergent landscape

372 settings to stem current trends in biodiversity loss (Blicharska & Mikusiński, 2014, Lindenmayer et al.,

373 2014).

374

375 **Supporting Information**

376 Additional information is available online in the Supporting Information section at the end of the online

377 article. The authors are solely responsible for the content and functionality of these materials. Queries

378 (other than absence of the material) should be directed to the corresponding author.

379

380 **Literature cited**

381 Asbeck, T., Pyttel, P., Frey, J., & Bauhus, J. (2019). Predicting abundance and diversity of tree-related

382 microhabitats in Central European montane forests from common forest attributes. *Forest Ecology and*

383 *Management* 432, 400-408.

384

385 Asbeck, T., Großmann, J., Paillet, Y., Winiger, N., & Bauhus, J. (2021a). The use of tree-related

386 microhabitats as forest biodiversity indicators and to guide integrated forest management. *Current*

387 *Forestry Reports*, 1-10.

388

389 Asbeck, T., Kozák, D., Spînu, A.P., Mikoláš, M., Zemlerová, V., & Svoboda, M. (2021b). Tree-Related

390 Microhabitats Follow Similar Patterns but are More Diverse in Primary Compared to Managed

391 Temperate Mountain Forests. *Ecosystems*, 1-15.

392

393   Basile, M., Asbeck, T., Jonker, M., Knuff, A.K., Bauhus, J., Braunisch, V., Mikusiński, G., & Storch, I.

394   (2020a). What do tree-related microhabitats tell us about the abundance of forest-dwelling bats, birds,

395   and insects? *Journal Of Environmental Management*, 264, 110401.

396

397   Basile, M., Asbeck, T., Pacioni, C., Mikusiński, G., & Storch, I. (2020b). Woodpecker cavity

398   establishment in managed forests: relative rather than absolute tree size matters. *Wildlife Biology*, 1, 1-

399   9.

400

401   Barredo, J.I., Brailescu, C., Teller, A., Sabatini, F.M., Mauri, A., & Janouskova, K. (2021). Mapping

402   and assessment of primary and old-growth forests in Europe, Publications Office of the European Union,

403   Luxembourg.

404

405   Blicharska, M., & Mikusiński, G. (2014). Incorporating social and cultural significance of large old trees

406   in conservation policy. *Conservation Biology*, 28(6), 1558-1567.

407

408   Brooks, M.E., Kristensen, K., Van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J.,

409   Machler, M., & Bolker, B.M. (2017). glmmTMB Balances Speed and Flexibility Among Packages for

410   Zero-inflated Generalized Linear Mixed Modeling. *R Journal*, 9, 378-400.

411

412   Burrascano, S., De Andrade, R.B., Paillet, Y., Ódor, P., Antonini, G., Bouget, C., Campagnaro, T.,

413   Gosselin, F., Janssen, P., Persiani, A.M., Nascimbene, J., Sabatini, F.M., Stizia, T., & Blasi, C. (2018).

414   Congruence across taxa and spatial scales: Are we asking too much of species data?. *Global Ecology*

415   *and Biogeography*, 27(8), 980-990.

416

417   Buse, J., Schröder, B., & Assmann, T. (2007). Modelling habitat and spatial distribution of an

418   endangered longhorn beetle–a case study for saproxylic insect conservation. *Biological Conservation*,

419   137(3), 372-381.

420

16

421   Bütler, R., Lachat, T., Krumm, F., Kraus, D., & Larrieu, L. (2020). *Field Guide to Tree-related*

422   *Microhabitats. Descriptions and size limits for their inventory.* Birmensdorf. Swiss Federal Institute for

423   Forest, Snow and Landscape Research WSL., pp. 59.

424

425   Courbaud, B., Pupin, C., Letort, A., Cabanettes, A., & Larrieu, L. (2017). Modelling the probability of

426   microhabitat formation on trees using cross-sectional data. *Methods in Ecology and Evolution*, 8(10),

427   1347-1359.

428

429   Courbaud, B., Larrieu, L., Kozak, D., Kraus, D., Lachat, T., Ladet, S., Müller, J., Sagheb-Talebi, K.,

430   Schuck, A., Stillhard, J., Svoboda, M., & Zudin, S. (2022). Factors influencing the rate of formation of

431   tree-related microhabitats and implications for biodiversity conservation and forest management.

432   *Journal of Applied Ecology*, *59*(2), 492-503.

433

434   Di Filippo, A., Biondi, F., Maugeri, M., Schirone, B., & Piovesan, G. (2012). Bioclimate and growth

435   history affect beech lifespan in the Italian Alps and Apennines. *Global Change Biology*, 18, 960-972.

436

437   Duncan, R.P. (1989). An evaluation of errors in tree age estimates based on increment cores in kahikatea

438   (Dacrycarpus dacrydioides). *New Zealand Natural Sciences*, 16, 31–37.

439

440   Fox, J., & Weisberg, S. (2019). *An R Companion to Applied Regression, 3rd Edition*. Thousand Oaks,

441   CA.

442

443   Fritz, Ö., & Heilmann-Clausen, J. (2010). Rot holes create key microhabitats for epiphytic lichens and

444   bryophytes on beech (Fagus sylvatica). *Biological Conservation*, 143(4), 1008-1016.

445

446   Gao, T., Nielsen, A.B., & Hedblom, M. (2015). Reviewing the strength of evidence of biodiversity

447   indicators for forest ecosystems in Europe. *Ecological Indicators*, 57, 420-434.

448

449   Hagge, J., Bässler, C., Gruppe, A., Hoppe, B., Kellner, H., Krah, F.S., Müller, J., Siebold, S., Stengel,

450   E., & Thorn, S. (2019). Bark coverage shifts assembly processes of microbial decomposer communities

451   in dead wood. *Proceedings of the Royal Society B*, 286(1912), 20191744.

452

453   Handegard, E., Gjerde, I., Bollandsås, O.M., & Storaunet, K.O. (2021). Identifying old Norway spruce

454   and Scots pine trees by morphological traits and site characteristics. *Scandinavian Journal of Forest*

455   *Research*, 36(7-8), 550-562.

456

457   Hartig, F. (2022). DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression

458   Models. R package version 0.4.5.

459

460   Holmes, R.L. (1983). Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring*

461   *Bulletin*, 43, 69–75.

462

463   Hubau, W., De Mil, T., Van den Bulcke, J., Phillips, O.L., Angoboy Ilondea, B., Van Acker, J., Sullivan,

464   M.J.P., Nsenga, L., Toriambe, B., Couralet, C., Banin, L.F., Begne, S.K., Baker, T.R., Bourland, T.,

465   Chezeaux, E., Clark, C.J., Collins, M., Comiskey, J.A., Cuni-Sanchez, A., ... & Beeckman, H. (2019).

466   The persistence of carbon in the African forest understory. *Nature Plants*, 5(2), 133-140.

467

468   Issartel, J., & Coiffard, C. (2011). Extreme longevity in trees: live slow, die old?. *Oecologia*, 165(1), 1-

469   5.

470

471   IUCN. (2018). *Raising the profile of primary and intact forests*. https://www.iucn.org/

472

473   Jahed, R.R., Kavousi, M.R., Farashiani, M.E., Sagheb-Talebi, K., Babanezhad, M., Courbaud, B., Wirtz,

474   R., Müller, J., & Larrieu, L. (2020). A Comparison of the Formation Rates and Composition of Tree-

475   Related Microhabitats in Beech-Dominated Primeval Carpathian and Hyrcanian Forests. *Forests*, 11(2),

476   144.

477

478 Janda, P., Tepley, A.J., Schurman, J.S., Brabec, M., Nagel, T.A., Bače, R., Begovič, K., Chaskovskyy,

479 O., Čada, V., Dušátko, M., Frankovič, M., Kameniar, O., Kozák, D., Lábusová, J., Langbehn, T., Málek,

480 J., Mikoláš, M., Nováková, M.H., Svobodová, K., & Svoboda, M. (2019). Drivers of basal area variation

481 across primary late-successional Picea abies forests of the Carpathian Mountains. *Forest Ecology and*

482 *Management*, 435, 196-204.

483

484 Kraus, D., Bütler, R., Krumm, F., Lachat, T., Larrieu, L., Mergner, U., Paillet, Y., Schuck, A., & Winter,

485 S. (2016). *Catalogue of tree microhabitats: Reference field list*.

486

487 Krumm, F., Schuck, A., & Rigling, A. (eds). (2020). *How to balance forestry and biodiversity*

488 *conservation – A view across Europe*. European Forest Institute (EFI); Swiss Federal Institute for Forest,

489 Snow and Landscape Research (WSL), Birmensdorf, pp. 640.

490

491 Kozák, D., Mikoláš, M., Svitok, M., Bače, R., Paillet, Y., Larrieu, L., Nagel, T.A., Begovič, K., Čada,

492 V., Diku, A., Frankovič, M., Janda, P., Kameniar, O., Keren, S., Kjučukov, P., Lábusová, J., Langbehn,

493 T., Málek, J., Mikac, S., … & Svoboda, M. (2018). Profile of tree-related microhabitats in European

494 primary beech-dominated forests. *Forest Ecology and Management*, 429, 363-374.

495

496 Kõrkjas, M., Remm, L., & Lõhmus, A. (2021a). Development rates and persistence of the microhabitats

497 initiated by disease and injuries in live trees: A review. *Forest Ecology and Management*, 482, 118833.

498

499 Kõrkjas, M., Remm, L., & Lõhmus, A. (2021b). Tree-related microhabitats on live Populus tremula and

500 Picea abies in relation to tree age, diameter, and stand factors in Estonia. *European Journal of Forest*

501 *Research*, 140(5), 1227-1241.

502

503 Kuhn, M., & Johnson, K. (2013). *Applied Predictive Modeling*. Springer, NY

504

505   Larrieu, L., & Cabanettes, A. (2012). Species, live status, and diameter are important tree features for

506   diversity and abundance of tree microhabitats in subnatural montane beech–fir forests. *Canadian*

507   *Journal of Forest Research*, 42, 1433–1445.

508

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

510   (2014). Deadwood and tree-microhabitat dynamics in unmanaged temperate mountain mixed forests: A

511   life-cycle approach for biodiversity monitoring. *Forest Ecology and Management*, 334, 163–173.

512

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

514   B., & Vandekerkhove, K. (2018). Tree related microhabitats in temperate and Mediterranean European

515   forests: A hierarchical typology for inventory standardization. *Ecological Indicators*, 84, 194-207.

516

517   Larrieu, L., Gosselin, F., Archaux, F., Chevalier, R., Corriol, G., Dauffy-Richard, E., Deconchat, M.,

518   Gosselin, M., Ladet, S., Savoie, J.M., Tillon, L., & Bouget, C. (2019). Assessing the potential of routine

519   structural and dendrometric variables as potential habitat surrogates from multi-taxon data in European

520   temperate forests. *Ecological Indicators*, 104, 116–126

521

522   Larrieu, L., Cabanettes, A., Courbaud, B., Goulard, M., Heintz, W., Kozák, D., Kraus, D., Lachat, T.,

523   Ladet, S., Müller, J., Paillet, Y., Schuck, A., Stillhard, J., & Svoboda, M. (2021). Co-occurrence patterns

524   of tree-related microhabitats: A method to simplify routine monitoring. *Ecological Indicators*, 127,

525   107757.

526

527   Larsson, L.A. (2003). *CDendro: Cybis Dendro dating program*. Saltsjöbaden,Sweden: Cybis Elektronik

528   & Data AB.

529

530   Lindenmayer, D.B., Laurance, W.F., & Franklin, J.F. (2012). Global decline in large old trees. *Science*,

531   338(6112), 1305-1306.

532

533 Lindenmayer, D.B., Laurance, W.F., Franklin, J.F., Likens, G.E., Banks, S.C., Blanchard, W., Gibbons,

534 P., Ikin, K., Blair, D., McBurney, L., Manning, A.D., & Stein, J.A.R. (2014). New policies for old trees:

535 averting a global crisis in a keystone ecological structure. *Conservation Letters*, 7(1), 61-69.

536

537 Liu, J., Xia, S., Zeng, D., Liu, C., Li, Y., Yang, W., Yang, B., Zhang, J., Silk, F., & Lindenmayer, D. B.

538 (2022). Age and spatial distribution of the world's oldest trees. *Conservation Biology*, e13907.

539

540 Lorimer, C.G., & Frelich, L.E. (1989). A methodology for estimating canopy disturbance frequency and

541 intensity in dense temperate forests. *Canadian Journal of Forest Research*, 19, 651–663.

542

543 Lutz, J.A., Furniss, T.J., Johnson, D.J., Davies, S.J., Allen, D., Alonso, A., Anderson-Texeira, K.J.,

544 Andrade, A., Baltzer, A., Becker, K.M.L., Blomdahl, E.M., Bourg, N.A., Bunyavejchewin, S., Burslem,

545 D.F.RP., Cansler, C.A., Cao, K., Cao, M., Cárdenas, D., Chang, L.,... & Zimmerman, J.K. (2018). Global

546 importance of large-diameter trees. *Global Ecology and Biogeography*, 27(7), 849-864.

547

548 Lüdecke, D., Ben-Shachar, M.S., Patil, I., Waggoner, P., & Makowski, D. (2021). performance: An R

549 Package for Assessment, Comparison and Testing of Statistical Models. *Journal of Open Source*

550 *Software*, 6(60), 3139.

551

552 Michel, A.K., Winter, S., & Linde, A. (2011). The effect of tree dimension on the diversity of bark

553 microhabitat structures and bark use in Douglas-fir (Pseudotsuga menziesii var. menziesii). *Canadian*

554 *Journal of Forest Research*, 41(2), 300-308.

555

556 Mikoláš, M., Ujházy, K., Jasík, M., Wiezik, M., Gallay, I., Polák, P., Vysoký, J., Čiliak, M., Meigs,

557 G.W., Svoboda, M., Trotsiuk, V., & Keeton, W.S. (2019). Primary forest distribution and representation

558 in a Central European landscape: Results of a large-scale field-based census. *Forest Ecology and*

559 *Management*, 449, 117466.

560

561   Mitchell, R.J., Hewison, R.L., Beaton, J., & Douglass, J.R. (2021). Identifying substitute host tree

562   species for epiphytes: The relative importance of tree size and species, bark and site characteristics.

563   *Applied Vegetation Science*, 24(2) e12569.

564

565   Muys, B., Angelstam, P., Bauhus, J., Bouriaud, L., Jactel, H., Kraigher, H., Müller, J., Pettorelli, N.,

566   Pötzelsberger, E., Primmer, E., Svoboda, M., Thorsen, J.B., & Van Meerbeek, K. (2022). *Forest*

567   *Biodiversity in Europe*. From Science to Policy 13. European Forest Institute.

568

569   Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized

570   linear mixed-effects models. *Methods in Ecology and Evolution*, 4(2), 133-142.

571

572   Paillet, Y., Archaux, F., Du Puy, S., Bouget, C., Boulanger, V., Debaive, N., Gilg, O., Gosselin, F., &

573   Guilbert, E. (2018). The indicator side of tree microhabitats: a multi-taxon approach based on bats, birds

574   and saproxylic beetles. *Journal of Applied Ecology*, 55(5), 2147-2159.

575

576   Paillet, Y., Debaive, N., Archaux, F., Cateau, E., Gilg, O., & Guilbert, E. (2019). Nothing else matters?

577   Tree diameter and living status have more effects than biogeoclimatic context on microhabitat number

578   and occurrence: An analysis in French forest reserves. *PloS one*, 14(5).

579

580   Pantic, D., Medarevic, M., Dees, M., Borota, D., Tubic, B., Obradovic, S., Šljukic, B., Čukovic, D., &

581   Marinkovic, M. (2015). Analysis of the growth characteristics of a 450-year-old silver fir tree. *Archives*

582   *of Biological Sciences*, (1), 155-160

583

584   Pavlin, J., Nagel, T.A., Svitok, M., Pettit, J.L., Begović, K., Mikac, S., Dikku, A., Toromani, E.,

585   Panayotov, M., Zlatanov, T., Haruta, O., Dorog, S., Chaskovskyy, O., Mikoláš, M., Janda, P., Frankovič,

586   M., Rodrigo, R., Vostarek, O., Synek, M., … & Svoboda, M. (2021). Disturbance history is a key driver

587   of tree life span in temperate primary forests. *Journal of Vegetation Science*, 32(5), e13069.

588

Pettit, J.L., Pettit, J.M., Janda, P., Rydval, M., Čada, V., Schurman, J.S., Nagel, T.A., Bače, R., Saulnier, M., Hofmeister, J., Matula, R., Kozák, D., Frankovič, M., Turcu, D.O., Mikoláš, M., & Svoboda, M. (2021). Both Cyclone-induced and convective storms drive disturbance patterns in European primary beech forests. *Journal of Geophysical Research: Atmospheres*, 126(7), e2020JD033929.

Puverel, C., Abourachid, A., Böhmer, C., Leban, J.M., Svoboda, M., & Paillet, Y. (2019). This is my spot: What are the characteristics of the trees excavated by the Black Woodpecker? A case study in two managed French forests. *Forest Ecology and Management*, 453, 117621.

Quinn, G., & Keough, M. (2002). *Experimental Design and Data Analysis for Biologists*. Cambridge: Cambridge University Press.

Ranius, T., Svensson, G.P., Berg, N., Niklasson, M., & Larsson, M.C. (2009). The successional change of hollow oaks affects their suitability for an inhabiting beetle, Osmoderma eremita. *Annales Zoologici Fennici*, 46(3). 205-216.

Ray-Mukherjee, J., Nimon, K., Mukherjee, S., Morris, D.W., Slotow, R., & Hamer M. 2014. Using commonality analysis in multiple regressions: a tool to decompose regression effects in the face of multicollinearity. *Methods in Ecology and Evolution*, 5, 320-328.

R Core Team. (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/.

Regnery, B., Couvet, D., Kubarek, L., Julien, J.F., & Kerbiriou, C. (2013). Tree microhabitats as indicators of bird and bat communities in Mediterranean forests. *Ecological Indicators*, 34, 221–230.

Remm, J., & Lõhmus, A. (2011). Tree cavities in forests–the broad distribution pattern of a keystone structure for biodiversity. *Forest Ecology and Management*, 262(4), 579-585.

617

618 Sabatini, F.M., Burrascano, S., Keeton, W.S., Levers, C., Lindner, M., Pötzschner, F., Verkerk, J.P.,

619 Bauhus, J., Buchwald, E., Chaskovskyy, O., Debaive, N., Horváth, F., Garbarino, M., Grigoriadis, N.,

620 Lombardi, F., Duarte, I.M., Meyer, P., Midteng, R., Mikac, S., & ... Kuemmerle, T. (2018). Where are

621 Europe's last primary forests?. *Diversity and Distributions*, 24(10), 1426-1439.

622

623 Sabatini, F.M., Bluhm, H., Kun, Z., Aksenov, D., Atauri, J.A., Buchwald, E., Burrascano, S., Cateau,

624 E., Diku, A., Duarte, I.M., López, A.B.F., Garbarino, M., Grigoriadis, N., Horváth, F., Keren, S.,

625 Kitenberga, M., Kiš, A., Kraut, A., Ibisch, P.L., … & Kuemmerle, T. (2021). European primary forest

626 database v2. 0. *Scientific data*, 8(1), 1-14.

627

628 Seidl, R., & Turner, M.G. (2022). Post-disturbance reorganization of forest ecosystems in a changing

629 world. *Proceedings of the National Academy of Sciences*, 119(28), e2202190119.

630

631 Senf, C., & Seidl, R. (2021). Mapping the forest disturbance regimes of Europe. *Nature Sustainability*,

632 4(1), 63-70.

633

634 Shmueli, G., Minka, T.P., Kadane, J.B., Borle, S., & Boatwright, P. (2005) A useful distribution for

635 fitting discrete data: revival of the Conway-Maxwell-Poisson distribution. *Journal of the Royal*

636 *Statistical Society: Series C (Applied Statistics)*, 54 127–142.

637

638 Stokes, M.A., & Smiley, T.L. (1968). *Tree-ring dating*. Chicago, IL: University of Chicago Press.

639

640 Ulyshen, M.D., Ulyshen, M.D., & Koerner. (2018). *Saproxylic insects*. Springer.

641

642 van Pelt, R. (2007). *Identifying Mature and Old Forests in Western Washington*. Washington State

643 Department of Natural Resources. Olympia, WA.

644

645   Vasaitis, R. (2013). 10 Heart Rots, Sap Rots and Canker Rots. *Infectious forest diseases*, 197.

646

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

648   Bulgaria: results of two national inventory projects and their implications for protection. *Biodiversity*

649   *and Conservation*, 19(6), 1805-1819.

650

651   Vuidot, A., Paillet, Y., Archaux, F., & Gosselin, F. (2011). Influence of tree characteristics and forest

652   management on tree microhabitats. *Biological Conservation*, 144, 441-450.

653

654   Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York.

655

656   Winter, S., & Möller, G.C. (2008). Microhabitats in lowland beech forests as monitoring tool for nature

657   conservation. *Forest Ecology and Management*, 255(3-4), 1251-1261.

658

659   Yamaguchi, D.K. (1991). A simple method for cross-dating increment cores from living trees. *Canadian*

660   *Journal of Forest Research*, 21, 414– 416.

661

662   Zheng, Z., Zhang, S., Baskin, C., Baskin, J., Schaefer, D., Yang, X., & Yang, L. (2016). Hollows in

663   living trees develop slowly but considerably influence the estimate of forest biomass. *Functional*

664   *Ecology*, 30, 830–838.

665

666

667

668

669

670

671

Supporting Information

The supplementary material includes the following:

Appendix 1: Description of the main characteristics of the studied living trees in mixed beech and spruce forests.

Appendix 2: Details of the generalized linear mixed effect models testing the influence of tree characteristics (age, DBH, species) and site quality (altitude, slope, region) on the richness and occurrence of TreMs in mixed beech forests.

Appendix 3: Details of the generalized linear mixed effect models testing the influence of tree characteristics (age, DBH) and site quality (altitude, slope, region) on the richness and occurrence of TreMs in spruce forests.

Appendix 4: Diagnostic plots of residuals from the GLMMs on the richness and occurrence of TreMs in mixed beech forests.

Appendix 5: Diagnostic plots of residuals from the GLMMs on the richness and occurrence of TreMs in spruce forests.

Appendix 6: 47 Tree-related microhabitat (TreM) types based on the hierarchical typology of Larrieu et al. (2018).

Appendix 7: Effect plots showing the influence of tree age and DBH on the probability of TreMs occurrence in mixed beech forests and spruce forests.

Appendix 8: Table depicting the number of all trees and trees with respective TreM groups used for analyses for spruce and mixed beech forests.

Table 1: Results of the generalized linear mixed effect models testing the influence of tree characteristics (age, DBH, species) and site quality (altitude, slope, region) on richness and occurrence of TreMs in mixed beech forests. Table shows semi-partial R^2_m values and probabilities (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) for statistically significant model parameters. Overall R^2_m values and results of the whole model likelihood-ratio tests are displayed in the last column. Cross-validated RMSE values (TreM richness) and BS values (other characteristics) are given in squared brackets. For further details see Appendix 2.

TreM characteristics	Age	DBH	Species	Altitude	Slope	Region	Whole model
TreM richness	0.005 ***	0.063 ***	0.011 ***	-	-	-	0.160 [1.19] ***
Rot holes	<0.001 *	0.069 **	0.308 ***	-	-	-	0.398 [0.28] ***
Insect galleries	-	-	-	-	-	-	-
Concavities	0.003 **	0.069 ***	0.071 ***	-	-	0.006 *	0.313 [0.21] ***
Exposed sapwood	-	-	0.020 ***	-	-	-	0.035 [0.39] ***
Exposed sapwood & heartwood	-	0.011 *	0.048 **	-	-	-	0.066 [0.36] **
Crown deadwood	-	0.008 ***	0.026 ***	-	-	-	0.049 [0.21] ***
Burrs & cankers	0.020 ***	0.012 **	0.026 **	-	-	-	0.181 [0.43] ***
Perennial fungi	-	-	0.121 *	-	-	-	0.200 [0.24] **
Annual fungi	-	-	0.176 ***	-	-	0.050 *	0.226 [0.13] ***
Epiphytes	0.015 ***	0.015 ***	0.050 ***	0.038 **	-	-	0.180 [0.16] ***
Nests	-	0.033 ***	0.008 ***	-	-	-	0.107 [0.36] ***
Microsoils	-	0.086 ***	0.029 ***	0.031 *	-	-	0.213 [0.28] ***
Exudates	-	-	0.402 ***	-	-	-	0.503 [0.19] ***

Table 2: Results of the generalized linear mixed effect models testing the influence of tree characteristics (age, DBH) and site quality (altitude, slope, region) on richness and occurrence of TreMs in spruce forests. Table shows semi-partial p-values/(partial) marginal R^2_m values and probabilities (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) for statistically significant model parameters. Overall R^2_m values and results of the whole model likelihood-ratio tests are displayed in the last column. Cross-validated RMSE values (TreM richness) and BS values (other characteristics) are given in squared brackets. For further details see Appendix 3.

| TreM characteristics	Age	DBH	Altitude	Slope	Region	Whole model
TreM richness	0.002 ***	0.011***	0.007 **	-	-	0.057 [0.93] ***
Rot holes	-	0.013 *	-	-	-	0.047 [0.10] **
Insect galleries	0.008 ***	-	-	-	0.089 *	0.139 [0.19] ***
Concavities	0.002 *	0.065 ***	-	-	-	0.126 [0.38] ***
Exposed sapwood	0.005 **	-	-	-	-	0.024 [0.31] **
Exposed sapwood & heartwood	-	-	-	-	-	-
Crown deadwood	0.001 *	0.010 ***	-	-	0.099 **	0.138 [0.34] ***
Burrs & cankers	0.021 **	0.011 *	0.026 **	-	0.010 *	0.099 [0.15] ***
Perennial fungi	-	-	-	-	-	-
Annual fungi	-	0.004 *	-	-	-	0.014 [0.11] *
Epiphytes	-	-	0.101 ***	0.02 *	-	0.122 [0.39] ***
Nests	-	0.007 **	-	-	-	0.012 [0.07] *
Microsoils	-	0.040 ***	-	-	-	0.099 [0.12] ***
Exudates	-	0.007 ***	-	-	0.038 **	0.058 [0.42] ***
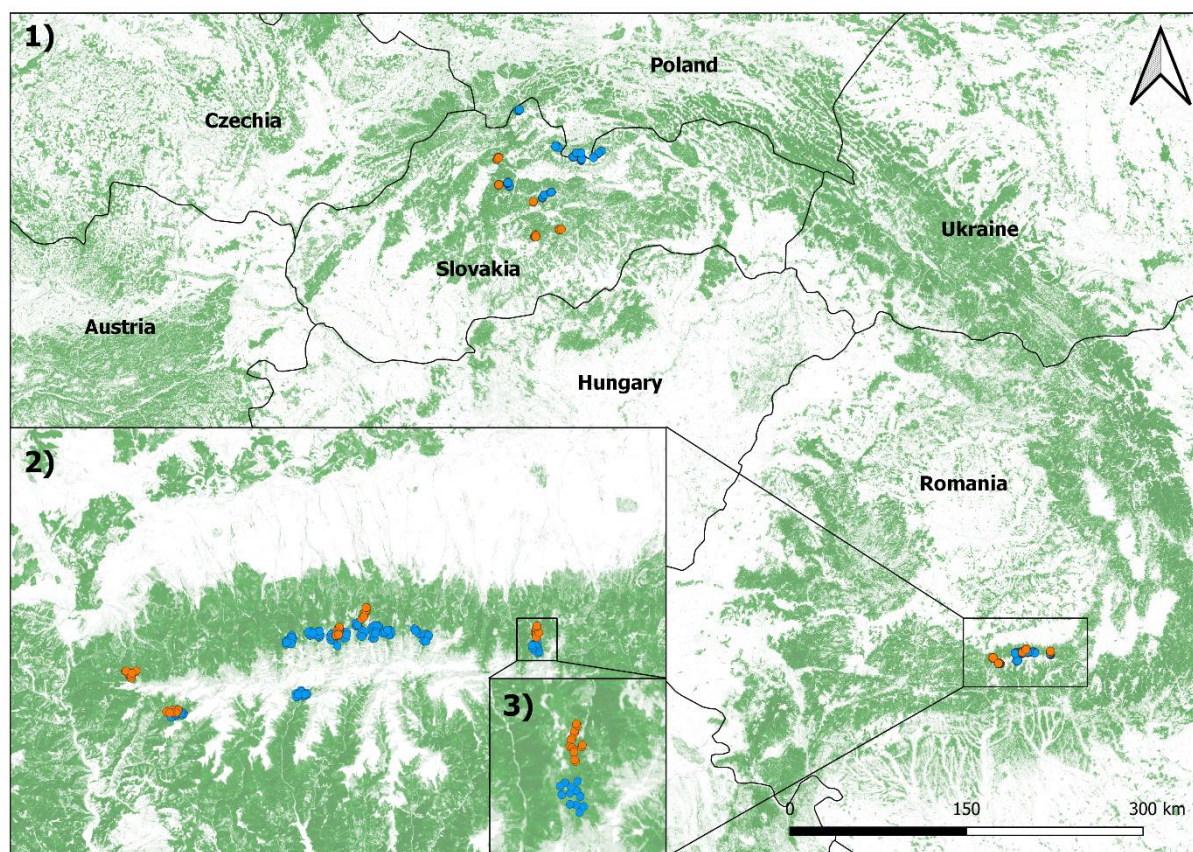
Figure 1: Distribution of the studied forests across Carpathian Mountains representing hierarchical sampling design (plots nested in forest stands nested in the regions). Study plots (orange color - mixed beech forests, blue color – spruce forests) are nested in landscape (1), regions (2), and forest stands (3).
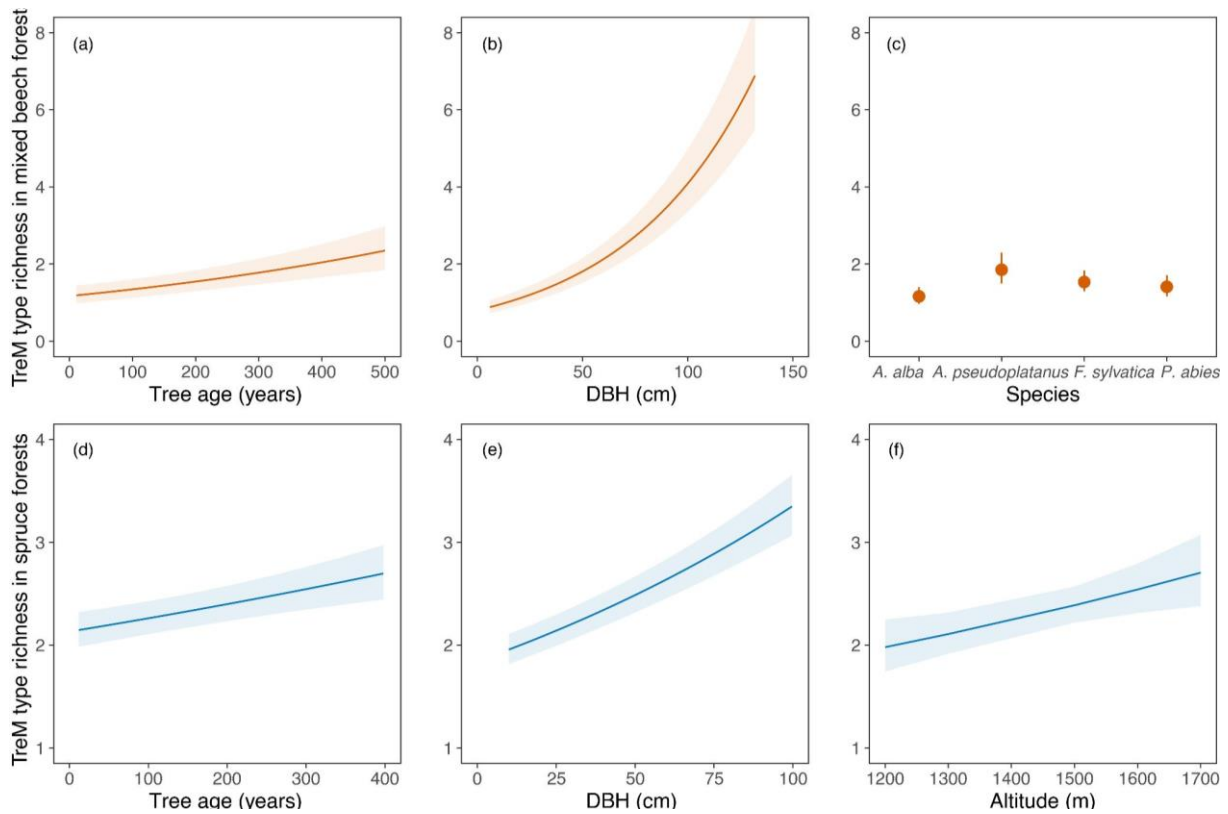
Figure 2: Significant effects of tree characteristics and site quality on richness of TreMs in mixed beech (a-c) and spruce forests (d-f). The effect plots show partial relationships between focal variables while keeping the other variables in the models constant. GLMM-based predictions (lines and dots) and their 95 % confidence intervals (bands and error bars) are displayed. For details of the models see Table 1 and 2 and Appendix 2 and 3.