

1 **Old-growth forests with long continuity are essential for preserving rare**  
2 **wood-inhabiting fungi**

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11 **ABSTRACT**

12 The ongoing loss of Europe's old-growth forests urgently calls for further research that would  
13 improve our understanding of the impacts of habitat changes on native biodiversity. Studies  
14 disentangling the effects of habitat quantity, quality, and continuity on species diversity are  
15 rare, however, understanding the differences between these effects is crucial for forest  
16 management and conservation efforts. Here, we investigated the influence of habitat quantity,  
17 quality, and continuity on the total and red-listed species richness of wood-inhabiting fungi in  
18 old-growth mountain Norway spruce (*Picea abies* Karst.) forest in Central Europe. The  
19 fruitbody-based mycological survey was conducted on 30 permanent study plots of 1000 m<sup>2</sup>  
20 where structural characteristics of forest stands indicating habitat quantity (deadwood  
21 volumes) and quality (deadwood dimensions and decay stages) were recorded. The mean age  
22 of five oldest trees and the number of >250 years-old-trees (i.e., those that survived a probable  
23 logging activity about 250 years ago) were used as indicators of habitat continuity. The precise  
24 estimates of tree ages were gained by dendrochronological analyses of tree increment cores.  
25 Our results showed the total species richness of wood-inhabiting fungi to be best correlated  
26 with habitat quantity (volume of low snags and lying deadwood), while the red-listed species  
27 richness was best explained by habitat continuity indicated by the number of >250 years-old-  
28 trees. Our study provides novel evidence regarding uninterrupted habitat continuity being  
29 crucial in supporting rare fungal species. Old-growth stands as well as those stands with  
30 preserved habitat continuity should be prioritised for conservation. Habitat continuity supported

31 by retention forestry practices shall be also required in production forests. Our study shows that  
32 such decisions are likely to lead to positive effects that can persist for centuries.

33

34 **Key words:** Biological legacy, coarse woody debris, habitat amount, habitat loss, mountain  
35 spruce forest, saproxylic biodiversity.

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37

## 38 1. INTRODUCTION

39 Old-growth forests are known to harbour high biodiversity and are especially important for the  
40 occurrence of rare and endangered species confirming their importance for conservation goals  
41 (Tikkanen et al., 2006; Moning & Müller, 2009; Dittrich et al., 2014). Nevertheless, the area of  
42 old-growth and primary forests continues to decline and many stands highly valuable for  
43 biodiversity preservation still have insufficient protection (Mikoláš et al., 2019; Sabatini et al.,  
44 2018, 2020). The large-scale disturbances in Central European Norway spruce (*Picea abies*  
45 Karst.) forests also raise the question of the appropriate approach to biodiversity protection in  
46 the remaining mountain spruce forests. Although these forests are mostly located within  
47 protected areas, salvage logging is still applied after windthrows and bark beetle (*Ips*  
48 *typographus* L.) outbreaks in some areas.

49 The forest structure in the majority of European forests has been simplified and the habitat  
50 continuity was interrupted as a result of human activities over centuries (Hofmeister et al.,  
51 2019). This is especially the case of decreased quantity and quality of deadwood as the key  
52 habitat for saproxylic species (Seibold et al., 2015; Thorn et al., 2018). On the other hand,  
53 unmanaged forests provide structural attributes ensuring the highest diversity of fungi growing  
54 on deadwood as well as the presence of red-listed species (Bässler et al., 2012; Dvořák et al.,  
55 2017; Atrena et al., 2020; Tomao et al., 2020). To some extent, deadwood is a manageable  
56 characteristic of forest structure (Vítková et al., 2018). Deadwood quantity can be increased by  
57 management interventions relatively easily, unlike its quality (Hofmeister et al., 2015; Janssen  
58 et al., 2017). Understanding the role of these components, that are essential for biodiversity of  
59 saproxylic species, is therefore key for better-defined conservation management, clearer policy,  
60 and more refined decision-making.

61 Our study is focused on wood-inhabiting fungi since it is a representative group of saproxylic  
62 organisms with many roles in ecosystem functioning such as wood decomposition, nutrient and  
63 carbon cycling (Heilmann-Clausen & Boddy; 2005; Schwarze et al., 2000). Deadwood volume  
64 (indicating habitat quantity) is well known to affect communities of wood-inhabiting fungi  
65 (Heilmann-Clausen & Christensen, 2005; Bässler et al., 2012). However, the impact of  
66 deadwood decay stage on fungal communities (Renvall, 1995; Heilmann-Clausen &  
67 Christensen; Holec 2020) suggests that focusing purely on deadwood amounts may be  
68 insufficient particularly since habitat quality is also highly important for biodiversity of wood-  
69 inhabiting fungi. Fungal species colonising fresh deadwood are usually less affected by forest  
70 management compared to species present in later decay stages (Stokland et al., 2012; Halme et

71 al., 2013). Specialisation on deadwood in later decay stages and dependence on rare habitats is  
72 especially common among rare and endangered (red-listed) species (Odór et al., 2006; Nordén  
73 et al., 2013) that are principal for conservation goals.

74 Unlike the effect of habitat quantity and quality, the importance of habitat continuity (i.e. the  
75 degree to which the presence of the substrate was not temporally interrupted in the past) is still  
76 unclear. Fungi are generally considered to have an excellent ability to disperse spores, which  
77 should indicate low importance of long-term habitat continuity due to their ability to recolonise  
78 sites well (Ohlson et al., 1997; Nordén et al., 2014). However, some authors have found that  
79 the diversity of wood-inhabiting fungi in forests with interrupted continuity was lower  
80 compared to continuous natural forests (Bässler et al., 2012; Flensted et al., 2016). The lack of  
81 suitable habitats affecting the probability of establishment is considered a limiting factor in  
82 specialised species, especially since certain rare species, e.g. *Phlebia centrifuga* have a really  
83 low dispersal ability (Norros et al., 2012; Nordén et al., 2013). Studies on wood-inhabiting  
84 fungi distinguishing between the effects of habitat quantity, quality, and continuity are  
85 extremely rare since the quality and recent continuity of habitat (e.g., the presence of large  
86 and/or decayed deadwood) are correlated in forests. Therefore, further research is needed on  
87 this topic (see e.g., Bässler et al., 2012).

88 In this paper, we studied the effects of various forest stand characteristics on wood-inhabiting  
89 fungi diversity in old-growth mountain spruce forest in Central Europe, Czech Republic. The  
90 selected habitat quantity (deadwood volumes), quality (deadwood decay and sizes), and  
91 continuity (age of oldest trees) indicators were used to explain the total and red-listed species  
92 richness of wood-inhabiting fungi. We utilised a unique situation of well-preserved old-growth  
93 forest where the habitat continuity was interrupted by variably intensive forest management  
94 more than two centuries ago. This was well documented by a precise dendrochronological  
95 analysis showing the current variation in presence/absence of trees older than 250 years. The  
96 following hypotheses were tested: (1) the total species richness of wood-inhabiting fungi is best  
97 correlated with both habitat quantity and quality (e.g., Heilmann-Clausen & Christensen, 2005;  
98 Pouska et al., 2010), (2) red-listed species richness is mainly dependent on habitat quality (e.g.  
99 Tikkanen et al., 2006; Bässler et al., 2012), and (3) the habitat continuity plays a minor role  
100 compared to habitat quantity and quality (e.g., Ohlson et al., 1997; Nordén et al., 2014).

101

102

## 103 2. MATERIALS AND METHODS

### 104 2.1 Study area

105 The study was conducted in the north-eastern part of the Czech Republic in the mountains of  
106 Hrubý Jeseník with the study area situated mainly on the south-eastern and southern slopes of  
107 the ridge surrounding the peak of Praděd (Fig. 1). The elevation ranges between 1100 and 1360  
108 m a.s.l. The average annual temperature in the study area is approximately 3 °C and the average  
109 annual precipitation is around 1300 mm (Landscape atlas of the Czech Republic, 2009). The  
110 study area is located in the forest dominated by Norway spruce with a minor component of  
111 mountain ash (*Sorbus aucuparia* L.), sycamore maple (*Acer pseudoplatanus* L.) and, at  
112 relatively lower elevation, common beech (*Fagus sylvatica* L.). The study area is protected; i.e.  
113 located within three Nature Reserves.

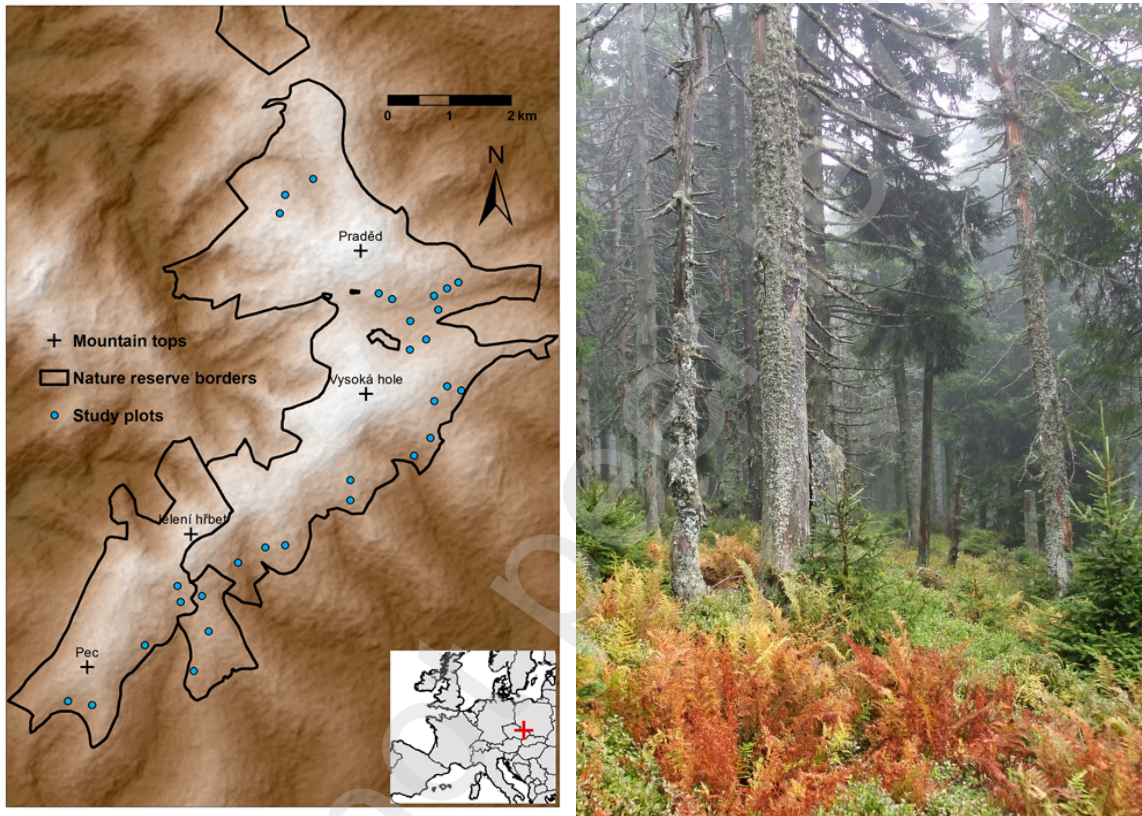
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### 115 2.2 Old-growth structure and forest stand history

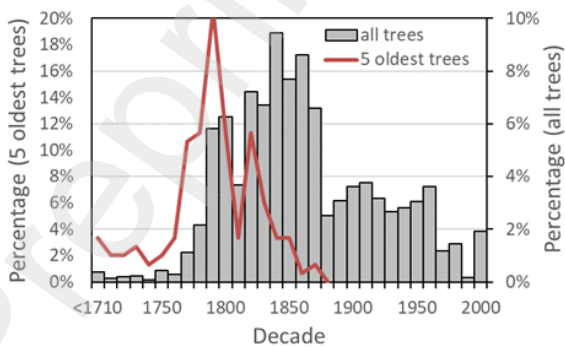
116 The study stands have an old-growth character as the oldest trees reached the age of more than  
117 195 years at all the study plots (tree ages were determined precisely by tree ring analysis, see  
118 below) with trees older than 140 years generally dominating the age distribution (Fig. 2). The  
119 average volume of the living trees was 268 m<sup>3</sup> ha<sup>-1</sup> and the average volume of deadwood  
120 (including all lying and standing deadwood above the diameter of 10 cm) was 135 m<sup>3</sup> ha<sup>-1</sup>.

121 The tree age distribution (Fig. 2) indicated an abrupt change in the studied forest at the end of  
122 18<sup>th</sup> century (approximately 1770 for the oldest trees per plot and around 1790 for all trees). We  
123 assume that the area was affected by a relatively large-scale disturbance (or combination of  
124 several disturbance events) during this period. Human logging was probably an important driver  
125 of the disturbance but natural events such as windstorms (Brázdil et al., 2004 provide evidence  
126 of windstorms in the 1770's, 1780's, and 1820's) or potential bark beetle outbreaks (e.g.,  
127 Temperli et al., 2013) could have also played a role. Three findings support the occurrence of  
128 logging activities in the late 18 century: (1) low proportion of trees older than 1770 in the current  
129 forest stands, i.e., low amount of former advanced regeneration (compared to e.g., Čada et al.,  
130 2016); (2) the attempt for forest logging in the north-eastern part of the study area as mentioned  
131 in the archival sources from 1754 (Hošek, 1982); and (3) young stands covering majority of the  
132 same area in 1803 as recorded in the historical forestry maps (Hošek, 1982). Hošek (1982)  
133 further suggested that the supposed logging was not spatially homogeneous and that seed trees  
134 were retained at a variable rate, which is also supported by our tree age analyses (Fig. 2). Tree

135 age structure is well synchronised between parts that were analysed using archival sources and  
 136 those that were not analysed. Therefore, we assumed that the habitat continuity of wood-  
 137 inhabiting fungi was interrupted in the study area around the end of the 18<sup>th</sup> century by logging  
 138 and wood extraction. The degree of habitat continuity interruption may correspond to the  
 139 presence/absence of >250-years-old trees that are currently growing in the studied stands.  
 140



141  
 142 **Fig. 1:** Study area location in the Czech Republic (Central Europe), plot locations within the  
 143 Nature Reserves, and an example of forest stand structure.



144  
 145  
 146 **Fig. 2:** The average age distributions of all and five oldest living trees on the study plots.

147

### 148 **2.3 Stand structure and age analysis**

149 The research was conducted on 30 permanent 1000 m<sup>2</sup> plots. Plots were placed randomly within  
150 cells of a grid of 500 x 500 m that covered the study area (i.e., one plot per approx. 25 ha). All  
151 standing trees (living and dead) with the DBH over 10 cm and all pieces of lying deadwood  
152 with the diameter over 10 cm at the thicker end and with the length greater than 1.5 m were  
153 recorded at each plot using FieldMap® technology (Monitoring and Mapping Solutions, Ltd.;

154 [www.fieldmap.cz](http://www.fieldmap.cz)).

155 Tree species, diameter, and tree height were recorded for each standing tree. Crown radius was  
156 recorded for all living trees. Substrate type was distinguished among dead standing trees as  
157 follows: standing trees (with no or crown breakage), high snags (with stem breakage and higher  
158 than 1.3 m), and low snags (lower than 1.3 m). The length and diameters at both ends were  
159 measured on lying deadwood (logs), and the tree species was identified. The diameter of the  
160 lying deadwood was expressed as the diameter at the thicker end. The degree of decomposition  
161 of standing and lying deadwood was estimated according to Sippola & Renvall (1999) using  
162 five classes: 1. recently dead tree with fresh phloem, 2. wood hard, with almost complete bark,  
163 knife penetrates 1-2 cm into the wood, 3. wood partly decayed, large pieces of bark can be  
164 missing, knife penetrates 3-5 cm, 4. wood softened with missing bark, the whole blade  
165 penetrates into the wood, 5. wood soft, disintegrated, covered by mosses.

166 The volume of each lying deadwood object was estimated using the truncated-cone volume  
167 equation. The volume of dead standing trees was estimated using their diameter and height  
168 based on the allometric equations. We used the equation of Korsuň (1961) for spruce and the  
169 equation of Zianis et al. (2005, equation 51) for beech, maple, and rowan. The height-diameter  
170 equations developed for each plot separately were applied to calculate the theoretical volume  
171 of the whole tree, which was reduced to an actual volume of snapped trees using the actual  
172 height and the reduction coefficient of Šmelko (2010).

173 Tree ring analysis of living trees was used to estimate the tree ages. An increment core was  
174 extracted 0.5 m above the ground for all living trees growing on a 1000 m<sup>2</sup> plot. It was necessary  
175 to core 25 dominant trees per plot; if an insufficient number of trees suitable for coring grew  
176 within the 1000 m<sup>2</sup> plot, additional trees were cored in the concentric circles around the plot.  
177 Furthermore, three old-looking trees located outside the plot were cored. Due to the variable  
178 amount of non-dominant trees and due to the 9 % of trees excluded from the analyses mostly

179 because of a rot, the final number of trees whose age was determined was between 25 and 105  
180 per plot (median 41, total amount was 1374). The cores were processed using standard  
181 dendrochronological techniques. The ring-width series were measured and cross-dated using a  
182 LINTAB sliding table and TsapWin software (RINNTECH, Heidelberg, Germany). In order to  
183 estimate the age of cores that did not intersect the pith, the curvature and the mean width of the  
184 five innermost rings were used to estimate the number of rings missing towards the pith. We  
185 did not correct for bias caused by coring height; therefore, what is referred to as ‘ages’ are not  
186 true ages but the number of years since individual trees reached the coring height.

187

## 188 **2.4 Fungal survey**

189 Mycological survey was based on fungal fruiting bodies growing on deadwood. The survey  
190 was conducted within the main fructification season of most fungal groups in the study area  
191 (i.e., late August to late September 2017). Each study plot was visited once by two mycologists  
192 that spent a maximum of 1.25 hours surveying each plot. After an initial inspection of the plot,  
193 deadwood objects for the survey were selected to reflect the overall variation of deadwood in  
194 the plot. We proceeded from the most abundant substrate type to the least represented. The  
195 objects were selected to cover the maximum possible combinations of substrate categories  
196 (lying log, dead standing tree, high snag, low snag), decay stage classes (1-5), diameter classes  
197 (10-24.9, 25-39.9, 40-55, >55 cm), and tree species present on the plot. Finally, we recorded  
198 fungi on a few objects of fine woody debris such as thin branches to include species preferring  
199 this substrate. We recorded all macromycetes (ascomycetes and basidiomycetes), i.e., the fungi  
200 with fruiting bodies visible with the naked eye, on selected deadwood objects. We included all  
201 trophic groups, even if some species do not directly decompose wood, they are a regular part  
202 of communities inhabiting deadwood, especially in higher stages of decomposition (e.g.  
203 Mäkipää et al., 2017). We did not record genera *Cortinarius* s.l., *Galerina* and small  
204 ascomycetes such as *Orbilina* and *Molisia*. Fungi were identified to the species level (or to the  
205 possible nearest taxonomic level) directly in the field or later in the lab using a microscope.  
206 Red-listed species were classified according to the IUCN categories as critically endangered,  
207 endangered, vulnerable, near threatened, and data deficient using the national red list (Holec &  
208 Beran, 2006).

209

210



## 211 2.5 Data analyses

212 Total species richness (the number of all species found on the plot) and red-listed species  
213 richness (the number of all red-listed species found on the plot) were used as the indicators of  
214 wood-inhabiting fungal diversity. We attempted to explain the variation in diversity by 13  
215 variables (Appendix, Table A.1 in Supplementary material) that were calculated from stand  
216 structure and age measurements. These variables presumably indicated habitat quantity  
217 (deadwood volumes), quality (deadwood decay and sizes), and/or continuity (ages of the oldest  
218 trees) of wood inhabiting fungi.

219 All the explanatory variables were first scaled to normal distribution to obtain comparable  
220 coefficient estimates and avoid issues with differences in scales. Generalised least squares  
221 models (GLS) were used to test the relationships, which allowed residuals to be correlated and  
222 to have unequal variance. These models also allowed us to correct for potential spatial  
223 autocorrelation of the data using the within-group correlation structure (we applied exponential  
224 spatial correlation). Plot elevation had a significant effect on total species richness (coefficient  
225 estimate = -1.87,  $p = 0.046$ ) and no effect on red-listed species richness ( $p = 0.429$ ). Therefore,  
226 elevation was included as the covariate in all the following models for total species richness but  
227 it was avoided in the models of red-listed species richness. First, we did a GLS model for each  
228 explanatory variable separately and evaluated its performance by p-values and AIC. Second,  
229 we attempted to select the best performing multiple variable model by backward selection  
230 starting with all the explanatory variables included. Competing models were compared using  
231 p-values, AIC, and ANOVA comparison. All the analyses were done in the R software (R Core  
232 Team, 2022) using the package *nlme* (Pinheiro et al., 2022).

233

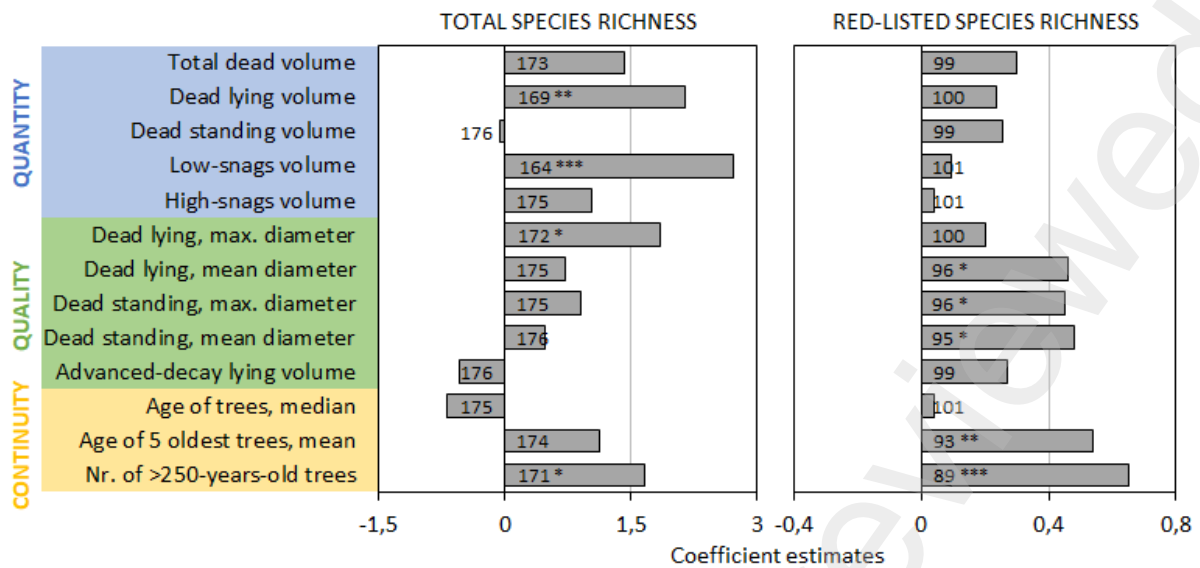
## 234 3. RESULTS

235 In total, we recorded 149 species (138 basidiomycetes and 11 ascomycetes) of wood-inhabiting  
236 fungi (Appendix, Table A.2). The total species richness of wood-inhabiting fungi varied  
237 between 12 and 31 species per plot. Lignicolous saprotrophs and saproparasites were the most  
238 represented trophic group (Appendix, Table A.2). The most frequently recorded species  
239 regarding both the number of records and the number of plots was *Fomitopsis pinicola*,  
240 common perennial polypore. We recorded 10 red-listed species (Appendix, Table A.2). Their  
241 richness per plot varied between 0 and 4. Five of those species belonged to threatened  
242 categories, i.e., critically endangered (*Globulicium hiemale*), endangered (*Antrodiella*

243 *citrinella*, *Hygroaster asterosporus*, *Hymenochaete fuliginosa*), or vulnerable (*Gymnopilus*  
244 *bellulus*). Apart from the red-listed species, several rare species of polypores (*Laetiporus*  
245 *montanus*, *Phellinus hartigii*) and resupinate corticioid fungi (*Dacryobolus sudans*,  
246 *Hastodontia hastata*, *Kneiffiella subalutacea*, *Litschauerella clematidis* or *Trechispora*  
247 *subsphaerospora*) were recorded during our study.

248 Variables indicating habitat quantity, i.e. the volume of lying deadwood and the volume of low  
249 snags were important for total species richness of wood-inhabiting fungi (Fig. 3, Table 2). The  
250 maximum diameter of lying deadwood was the only variable indicating habitat quality that was  
251 significant according to the simple models. However, it was excluded in multiple model  
252 selection probably due to its correlation with the volume of lying deadwood. The number of  
253 trees that were >250 years old (as a proxy of habitat continuity) had a particular effect on total  
254 species richness even though its effect was less strong compared to the volume of low snags  
255 and the volume of lying deadwood. All these three variables remained significant in the multiple  
256 variable model suggesting their relatively independent effect on total species richness (Fig. 4).  
257 Surprisingly, the total volume of deadwood was not significant for the total species richness.

258 The red-listed species richness of wood-inhabiting fungi was dominantly driven by variables  
259 indicating habitat continuity, i.e., the number of >250-years-old trees and the average age of  
260 the five oldest trees (these explanatory variables were correlated with the former performing  
261 generally better, Fig. 6). Some of the variables indicating habitat quality, such as the mean  
262 diameter of standing deadwood, the maximum diameter of standing deadwood, and the mean  
263 diameter of lying deadwood, were also significant in simple models for red-listed species  
264 richness. However, their effect was less strong compared to the number of >250-years-old trees  
265 and they were excluded from the multiple variable models (the mean diameter of standing  
266 deadwood could be considered marginally significant in multiple variable models; Table 2).  
267 These variables indicating habitat quality were partly correlated with habitat continuity  
268 variables, namely mean age of the five oldest trees (Fig. 6). The relationships of red-listed  
269 species richness to the most important variables are shown in Fig. 5.



270

271 **Fig. 3:** Comparison of the effects of different forest structural attributes on the total and red-  
 272 listed species richness as outputs of GLS models. The numbers by the columns and zero to three  
 273 asterisks indicate AIC and p-values (\* ~  $p < 0.05$ , \*\* ~  $p < 0.01$ , \*\*\* ~  $p < 0.001$ ), respectively.  
 274 The advanced-decay lying volume refers to the volume of lying deadwood of decay classes 4  
 275 and 5. The variables are sorted top-down based on their expected indication of quantity, through  
 276 quality, to continuity.

277

278

279 **Table 2:** The best performing multiple variable GLS models. Two competing models were  
 280 performing similarly for total species richness. One model that included just the number of  
 281 >250-years-old trees was selected for the red-listed species richness; adding the mean diameter  
 282 of the standing deadwood would cause the decrease of AIC just to 88, which was considered as  
 283 marginal.

284 **Total species richness =**

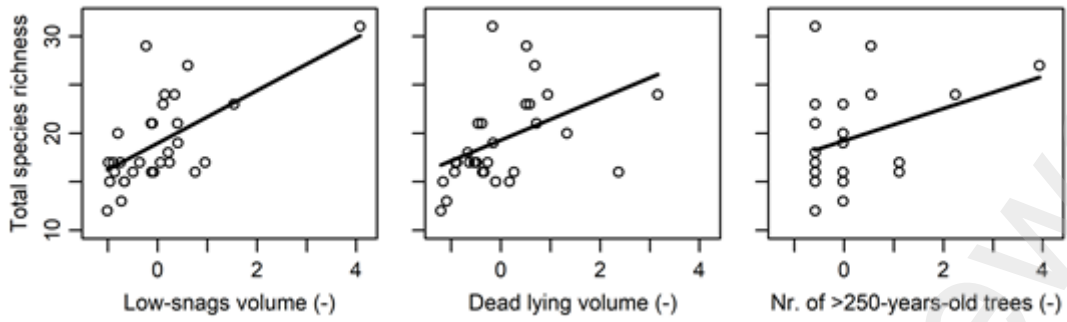
285  $19.0 - 0.8 \text{ elevation} + 2.4 \text{ low-snags volume} + 1.5 \text{ dead lying volume}; \text{ AIC } 160$

286  $19.0 - 0.8 \text{ elevation} + 2.6 \text{ low-snags volume} + 1.4 \text{ Nr. of } >250\text{-years-old trees}; \text{ AIC } 160$

287 **Red-listed species richness =**

288  $1.5 + 0.7 \text{ Nr. of } >250\text{-years-old trees}; \text{ AIC } 89$

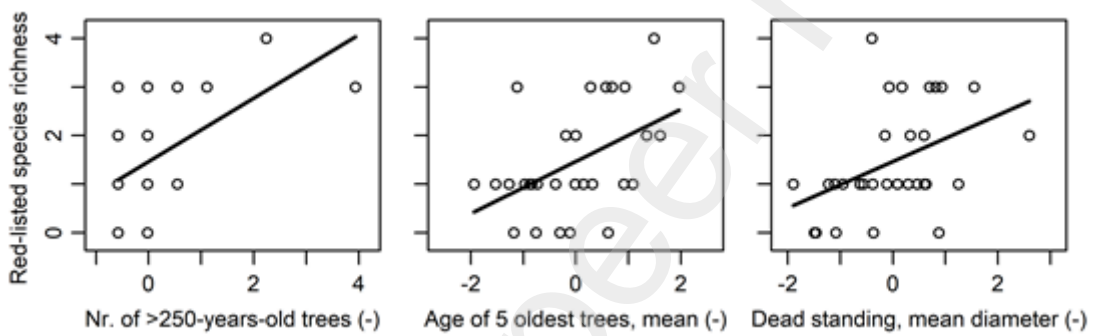
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290

291 **Fig. 4:** Relationships of the total species richness of wood-inhabiting fungi with selected stand  
 292 structural attributes.

293



294

295 **Fig. 5:** Relationships of the red-listed species richness with selected stand structural attributes.

296

297

	Total dead volume	Dead lying volume	Dead standing volume	Low-snags volume	High-snags volume	Dead lying, max. diameter	Dead lying, mean diameter	Dead standing, max. diameter	Dead standing, mean diameter	Advanced-decay lying volume	Age of trees, median	Age of 5 oldest trees, mean	Nr. of >250-years-old trees
Elevation	-0,16	-0,23	0,06	-0,26	0,03	-0,45*	-0,22	-0,18	-0,32	-0,13	0,20	-0,27	-0,20
<b>QUANTITY</b>													
Total dead volume		0,90***	0,62***	0,24	0,59***	0,51**	0,42*	0,25	0,25	0,55**	0,10	0,54**	0,29
Dead lying volume			0,23	0,23	0,60***	0,62***	0,51**	0,21	0,26	0,50**	0,09	0,55**	0,32
Dead standing volume				0,11	0,24	0,03	0,02	0,19	0,09	0,33	0,06	0,22	0,07
Low-snags volume					-0,08	0,30	0,11	0,22	0,19	-0,03	-0,53**	0,19	0,13
High-snags volume						0,07	0,12	<0,01	0,09	0,22	0,38*	0,29	0,04
<b>QUALITY</b>													
Dead lying, max. diameter							0,78***	0,43*	0,53**	0,33	-0,16	0,38	0,28
Dead lying, mean diameter								0,55***	0,75***	0,36	-0,09	0,45*	0,36
Dead standing, max. diameter									0,83***	0,10	-0,09	0,51**	0,17
Dead standing, mean diameter										0,11	0,02	0,58***	0,23
Advanced-decay lying volume											-0,18	0,39	0,08
<b>CONTINUITY</b>													
Age of trees, median												0,08	0,03
Age of 5 oldest trees, mean													0,68***

298

299 **Fig. 6:** Pearson correlations between the explanatory variables (\* ~  $p < 0.05$ , \*\* ~  $p < 0.01$ , \*\*\*  
300 ~  $p < 0.001$ ). The advanced-decay lying volume refers to the volume of lying deadwood of decay  
301 classes 4 and 5.

302

### 303 4. DISCUSSION

304 Using precise dendrochronological and structural data from mountain spruce old-growth forest,  
305 we confirmed our hypothesis that the total species richness of wood-inhabiting fungi was best  
306 correlated to habitat quantity, particularly to the volume of low snags and volume of lying  
307 deadwood. Surprisingly, the red-listed species richness was best explained by habitat  
308 continuity, which was indicated by the number of >250-years-old trees currently present on the  
309 study plot and related to possible logging activities that took place about 250 years ago. We  
310 provided novel evidence about the importance of habitat continuity (including continuity of  
311 specific structural attributes such as deadwood) for rare specialised fungal species.

312

#### 313 4.1 The effects of habitat quantity and quality

314 Our results supported the long-understood finding regarding importance of habitat quantity (i.e.  
315 the volume of deadwood) for fungal species richness on both deadwood-object and plot level  
316 (e.g. Heilmann-Clausen & Christensen, 2005, Bässler et al., 2012, Ferenčík et al., 2022). Higher  
317 habitat quantity allows for the presence of more individuals of organisms and, consequently,

318 more species. Additionally, higher habitat quantity is usually also associated with higher habitat  
319 diversity and more niches available for different species (Müller & Bütler, 2010). Regarding  
320 deadwood as a habitat for saproxylic species, higher habitat diversity usually means variation  
321 in deadwood sizes and decay stages (Müller & Bütler, 2010). Previous studies of wood-  
322 inhabiting fungi proved the dependency of species richness on deadwood diversity (Abrego &  
323 Salcedo 2013), including the importance of large deadwood objects (Heilmann-Clausen &  
324 Christensen, 2004; Pouska et al., 2010) and the presence of deadwood in advanced decay stages  
325 (Renvall, 1995; Heilmann-Clausen & Christensen, 2005; Holec 2020).

326 Our results did not prove habitat quality to be significant in relation to the total species richness  
327 on the plot level. However, many studies confirm its importance for fungal communities  
328 (Renvall, 1995; Pouska et al., 2010; Holec 2020). Deadwood of large dimensions and highly  
329 decayed deadwood are important for rare and specialised species (Renvall, 1995; Pouska et al.,  
330 2010), e.g., because they provide longer lasting habitat (Jönsson et al., 2008) and more stable  
331 microclimatic conditions (Pouska et al., 2016). The importance of habitat quality can also  
332 explain why abrupt increase of fresh and homogenous deadwood in previously managed forests  
333 does not necessarily lead to an increase in fungal diversity to the levels typical for old-growth  
334 forests (Bässler et al., 2012). Seemingly minor importance of habitat quality in our study could  
335 be explained by its correlation to parameters of habitat quantity, difficulties in its quantification  
336 at the plot level due to the specificity of the ecological requirements of individual species, or  
337 lower effect on total species richness compared to habitat quantity.

338 The volume of lying deadwood and the volume of low snags seemed to be the best habitat  
339 quantity predictors for total species richness of wood-inhabiting fungi. The total deadwood  
340 volume, and especially volume of dead standing trees, did not have a significant effect on  
341 species richness. The reason for this was apparently the low richness of species growing on  
342 relatively fresh standing dead trees without any breakage that comprised a significant portion  
343 of the dead standing volume and consequently total deadwood volume. It is to be noted that we  
344 only managed to record fungal fruiting bodies up to a height of about two metres on standing  
345 deadwood in relation to the volume of which the fungal species richness was analysed.  
346 Similarly, low species richness on fresh standing deadwood was found in other studies (e.g.  
347 Pouska et al., 2017). Dead standing trees, however, represent a specific substrate and are  
348 important for highly specialised species that are slow in colonisation (Niemelä et al., 2002).  
349 The effects of structural features such as fresh uprooted trees or high snags could have not been  
350 evaluated because of their low frequency in our dataset. In summary, our results show that the

351 effects of habitat quantity could partly include the effects of habitat quality since deadwood  
352 diameters and the volume of advanced-decay wood were correlated with the total volume of  
353 deadwood.

354

#### 355 **4.2 The effects of habitat continuity**

356 Our study belongs to very few studies that were able to relatively precisely quantify the habitat  
357 continuity in the conditions of old-growth forest and attempted to distinguish its effect on fungal  
358 species richness from the effect of habitat quality. We were able to utilise dendrochronological  
359 technique to precisely reconstruct the level of probable historical logging compared to previous  
360 studies which mostly used archival or map sources to obtain information about historical forest  
361 coverage (Heilmann-Clausen & Christensen, 2005; Halme et al., 2013, Hofmeister et al., 2019).  
362 Even though habitat continuity is mentioned in many studies, these studies often defined  
363 ‘continuity’ based on the quantity of specific structural attributes such as advanced-decay wood  
364 or large deadwood objects using the assumptions that it takes time to develop these structural  
365 attributes (Heilmann-Clausen & Christensen, 2005; Bässler et al., 2012). However, in our  
366 interpretation the present occurrence of these structural attributes rather define the current  
367 habitat quality than the habitat continuity *per se*. The effect of habitat continuity *per se* needs  
368 to be distinguished from the current habitat quality using the historical data that are indicative  
369 of past habitat presence or absence.

370 Using this approach, we were able to prove that habitat continuity (expressed by the number of  
371 >250-years-old trees or by the mean age of the five oldest trees) had the strongest effect on red-  
372 listed species richness in our study area. Age can be utilised as a relatively more independent  
373 indicator of forest continuity because we can speculate that the presence of living trees in the  
374 past (in the case of previously managed forest) may indicate that other forest structural attributes  
375 (deadwood) were also preserved during the historical periods or that some of the trees sharing  
376 similar life history died in the past and provided the continuity of the habitat. On the other hand,  
377 a full separation of the effect of habitat continuity and quality is likely impossible in  
378 observational studies. As shown in our results, some of the variables indicating habitat quality  
379 (e.g., diameters of dead trees) were still correlated to variables indicating habitat continuity  
380 (especially to the mean age of the five oldest trees). However, many of the variables were  
381 independent (especially the number of >250-years-old trees was weakly correlated to other  
382 variables). Thus, we tend to interpret the results showing the strongest statistical relationship of

383 red-listed species richness to the number of >250-years-old trees as an indication of potential  
384 causal relationship of red-listed species richness to habitat continuity *per se*.

385 The importance of habitat continuity for wood-inhabiting fungi richness is against the original  
386 expectation that the excellent dispersal ability of fungal spores should allow fungi to efficiently  
387 recolonise the sites with an interrupted continuity (Ohlson et al., 1997, Nordén et al., 2014).  
388 However, not only successful dispersal ability, but also the probability to establish and grow  
389 into the mycelium could be critical (Jonsson et al., 2005; Norros et al., 2012). Fungal spores  
390 likely have a very low establishment probability (in relation to spore viability or frequency of  
391 favourable conditions for establishment), which requires a large number of available spores for  
392 successful colonisation (Norros et al., 2012). Rare species with low population density and  
393 consequently low spore production have much lower colonisation ability compared to common  
394 species, particularly if dispersal ability of their spores is low (Norros et al., 2012). Low  
395 frequency of suitable habitat in a fragmented landscape makes successful colonisation even  
396 more difficult (Jonsson et al., 2005). Habitat continuity therefore shows to be crucial especially  
397 in the case of red-listed species, which highlights the need to consider its long-term effect in  
398 forest management practices.

399

#### 400 **4.3. Forest management implications**

401 The results of our study imply that habitat continuity should be valued in forest management,  
402 especially when considering wood-inhabiting fungi richness and the functions they provide. All  
403 of our study plots were likely affected by selective logging about 250 years ago to some degree  
404 but we assume that the logging intensity and retained structural variability (e.g., the amount of  
405 dead and living trees) varied. None to eight >250-years-old trees per plot were found currently  
406 growing in the forest with an increasing effect on the number of red-listed species. This suggests  
407 that the retention of trees during logging operations may help preserve ecosystem functions and  
408 diversity and that the positive effect will increase with increasing levels of retention. Long  
409 lasting effects suggest that forest management practices should consider a long-term  
410 perspective of several centuries when considering retention practices (that is much longer than  
411 the prevailing rotation periods of production forests). The importance of habitat continuity  
412 indicates that the conservation efforts should prioritise stands with higher degree of historical  
413 continuity (e.g., the absence of clearcutting and deforestation) as well as stands in their  
414 proximity as rare species likely have a limited ability to colonise new sites (Nordén et al. 2013).



415 Retention forestry practices supporting habitat continuity should be expanded to all forests.  
416 Habitat continuity and specific structural elements important for the survival of rare species,  
417 particularly heterogenous deadwood should be considered, for example, by adopting the  
418 minimum amount of trees or minimum volume of deadwood that would be retained in the forest  
419 (Vítková et al., 2018). The retention of living trees should be based on heterogeneity (i.e.  
420 various diameter, tree species, breakages), but generally, large old trees should be prioritised to  
421 enable the creation of large dimension deadwood, which is particularly missing in production  
422 forests and is especially important for rare species (Vítková et al., 2018). In addition, increasing  
423 log size also increases the species diversity (e.g., Heilmann-Clausen & Christensen, 2003).  
424 Concerning existing deadwood, its retention should be also based on covering variable  
425 substrates (uprooted trees, snags, lying logs in different decay stages and diameters) (Vítková  
426 et al., 2008). For example, retention of different log types (uprooted, broken) ensures  
427 establishment of specific communities, with logs broken in the stem base to be richer in red-  
428 listed species (Heilmann-Clausen & Christensen, 2003).

429 Creating a habitat suitable for red-listed species can take centuries and even in protected, but  
430 previously managed stands, the positive effect on diversity may not be visible for a long time  
431 (Blaser et al., 2013) as we have to consider both the time of the growth of a living tree to large  
432 dimensions and the time required for the decomposition process. This temporal lag in the  
433 development of required habitat quality along with long-term effects of management actions  
434 have to be acknowledged in forestry practice.

435

## 436 **CONCLUSIONS**

437 Habitat quantity expressed as the volume of lying deadwood or volume of low snags was the  
438 major driver of total species richness of wood-inhabiting fungi in our study. However, red-listed  
439 species richness was best related to habitat continuity expressed via the number of >250-years-  
440 old trees, i.e., trees that survived anthropogenic disturbance approximately 250 years ago. We  
441 provided novel evidence about the importance of habitat continuity (including continuity of  
442 specific structural attributes such as deadwood) for rare specialised fungal species. The sites  
443 with preserved habitat continuity should be prioritised for conservation. Preservation of habitat  
444 continuity using retention practices should be also required in production forests. Our study  
445 shows that such decisions may have effects that can last for centuries.

446

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454

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