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1           **EFFECTS OF LOCAL FOREST CONTINUITY ON THE DIVERSITY OF FUNGI ON**  
2   **STANDING DEAD PINES**

3  
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19

20 **ABSTRACT**

21 Human-induced fragmentation affects forest continuity, i.e. availability of a suitable habitat for the target  
22 species over a time period. The dependence of wood-inhabiting fungi on landscape level continuity has been  
23 well demonstrated, but the importance of local continuity has remained controversial. In this study, we  
24 explored the effects of local forest continuity (microhabitat and stand level) on the diversity of wood-  
25 inhabiting fungi on standing dead trunks of Scots pine (*Pinus sylvestris* L.). We studied species richness and  
26 community composition of decomposers and *Micarea* lichens on 70 trunks in 14 forests in central Finland  
27 that differed in their state of continuity. We used dendrochronological methods to assess the detailed history  
28 of each study trunk, i.e. the microhabitat continuity. The stand continuity was estimated as dead wood  
29 diversity and past management intensity (number of stumps). We recorded 107 species (91 decomposers, 16  
30 *Micarea* lichens), with a total of 510 occurrences. Using generalized linear mixed models, we found that  
31 none of the variables explained decomposer species richness, but that *Micarea* species richness was  
32 positively dependent on the time since tree death. Dead wood diversity was the most important variable  
33 determining the composition of decomposer communities. For *Micarea* lichens, the community composition  
34 was best explained by the combined effect of years from death, site and dead wood diversity. However, these  
35 effects were rather tentative. The results are in line with those of previous studies suggesting the restricted  
36 significance of local forest continuity for wood-inhabiting fungi. However, standing dead pines that have  
37 been available continuously over long periods seem to be important for species-rich communities of *Micarea*  
38 lichens. Rare specialists (e.g. on veteran trees) may be more sensitive to local continuity, and should be at the  
39 center of future research.

40

41 **Keywords:** dead wood continuity, decomposer, *Micarea*, microhabitat continuity, *Pinus sylvestris* L., stand  
42 continuity

43 **1. INTRODUCTION**

44 Intensive forestry activities have led to severe forest fragmentation throughout the globe (Riitters et  
45 al., 2000). The spatial aspects of fragmentation, such as decreased habitat amount, size, and  
46 connectivity are well known for a negative effect on biodiversity and ecosystems (Bengtsson et al.,  
47 2000; Fahrig, 2003). Temporal aspects of fragmentation, such as decreased habitat continuity, have  
48 been studied less than the spatial aspects, but have similarly been shown to have negative impacts  
49 on biodiversity (Nordén et al., 2014).

50 Forest continuity can be considered at local level where it relates to longevity of a single,  
51 available patch of suitable habitat for the target species or community, and where the scale of  
52 habitat patch is equivalent to one local population (Hanski, 2005; Nordén et al., 2014). With higher  
53 local continuity, higher species richness and larger variety of specialist species can occur as the  
54 colonization and/or breeding probability of species with establishment constraints, slow rates of  
55 establishment, development, or growth is enhanced (Esseen et al., 1997; Fritz et al., 2008; Nilsson  
56 and Baranowski, 1997; Nordén et al., 2014). The cause for higher species richness and larger  
57 variety of specialists may also be the emergence of special microhabitat types confined to late  
58 successional phases or larger diversity of different microhabitats. This is due to the absence of  
59 large-scale disturbances, which promotes the time-demanding development of these resources  
60 (Tibell, 1992; Sverdrup-Thygeson, 2001; Winter and Möller, 2008). Landscape level continuity, on  
61 the other hand, refers to a network of available habitat patches within a given region or landscape  
62 over time (Fritz et al., 2008; Hanski, 2005; Nordén et al., 2014). Here, the role of dispersal  
63 limitations increases when the landscape level continuity decreases (Nordén and Appelqvist, 2001).

64 Wood-inhabiting fungi are among the organism groups suffering most from the decreased  
65 landscape level forest continuity caused by fragmentation (Nordén et al., 2014; Flensted et al.,  
66 2016). The importance of this landscape level continuity for wood-inhabiting fungal diversity has  
67 been well demonstrated (Flensted et al., 2016; Gu et al., 2002; Junninen and Komonen, 2011; Paltto

68 et al., 2006; Ranius et al., 2008; Sverdrup-Thygeson and Lindenmayer, 2003). Apparently, the  
69 biological reason for this dependence is that some species of wood-inhabiting fungi are in fact  
70 dispersal limited (e.g. Norros et al., 2012), although species dependent on ephemeral habitats have a  
71 high dispersal ability in general (Herben et al., 1991).

72 The role of local continuity has remained less clear, compared to landscape level continuity.  
73 Stokland and Kauserud (2004) suggested that a polypore *Phellinus nigrolimitatus* cannot effectively  
74 colonize suitable trunks when the stand level dead wood continuity decreases. With epiphytic  
75 lichens, forest age and continuity appear to have a positive effect on their species richness and  
76 affect their community composition (Fritz et al., 2008). Also here, the increased colonization  
77 probability with increasing forest age and continuity was considered as the most probable  
78 explanation. On the other hand, several studies have detected no effects of local continuity (Groven  
79 et al., 2002; Rolstad et al., 2004; Sverdrup-Thygeson and Lindenmayer, 2003), and many studies  
80 have been criticized for not demonstrating the effect of continuity *per se* (Nordén and Appelqvist,  
81 2001; Nordén et al., 2014).

82 In their review, Junninen and Komonen (2011) deduced that boreal polypores are not affected  
83 by continuity on a stand scale in any way, and Nordén et al. (2014) concluded that local continuity  
84 does not have a significant effect on the diversity of fungi. Nevertheless, this generalization may be  
85 misleading; fungi encompass species with divergent ecological characteristics, with many of the  
86 species being habitat specialists, requiring dead wood in advanced stages of decay (Nordén et al.,  
87 2013). Moreover, studies have not focused on the smallest scale of local continuity, i.e. the detailed  
88 history of the microhabitats. Especially the standing dead coniferous trees may retain their qualities  
89 for decades, and therefore constitute a microhabitat with potentially high continuity. Considering  
90 ephemeral habitats in general, standing dead coniferous trees may be among the slowest constantly  
91 changing microhabitats (compared to more persistent abiotically determined microhabitats, such as  
92 those in soil).

93 In this study, we explored the effects of local forest continuity (microhabitat and stand level)  
94 on the communities of wood-inhabiting fungi. We studied fungal communities on standing dead  
95 wood of Scots pine (*Pinus sylvestris* L., hereafter pine) in 14 forests with varying state of  
96 continuity. We used trunk age parameters as estimates for microhabitat continuity, and estimated  
97 stand continuity as dead wood diversity and past management intensity. We focused on pine  
98 because the species is characterized by slow death and decay process (Niemelä et al., 2002;  
99 Siitonen, 2001). Specifically, we asked:

- 100 1. How does local forest continuity affect i) species richness and ii) community composition  
101 of wood-inhabiting fungi inhabiting standing dead pines?
- 102 2. How different scales of continuity (from microhabitat continuity to stand continuity)  
103 affect i) species richness and ii) community composition?
- 104 3. Are the effects of local continuity different for different fungal groups?

105

## 106 **2. MATERIALS AND METHODS**

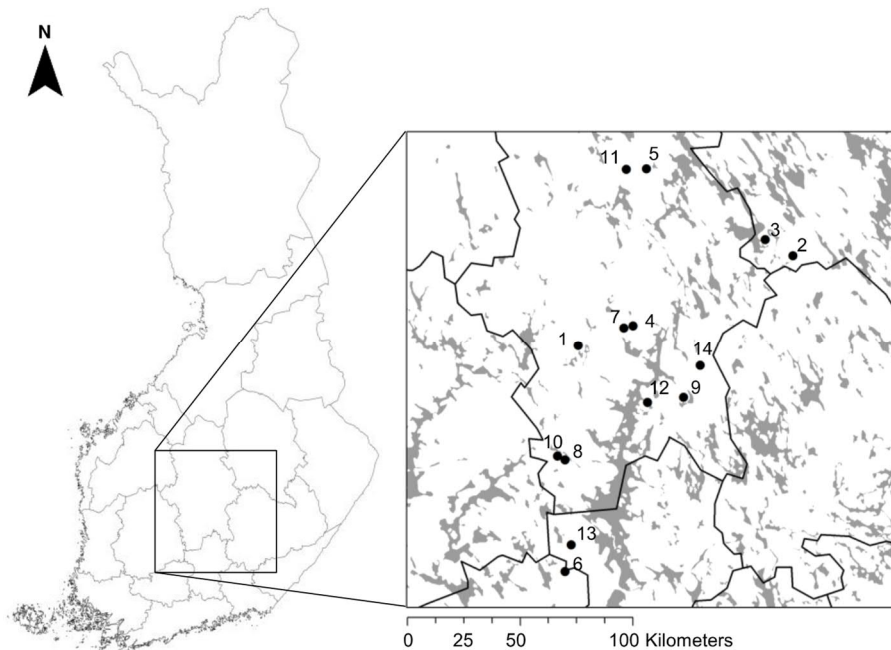
### 107 **2.1. Study sites and trunk selection**

108 Our 14 study forests (Table 1) were located in central Finland (Fig. 1), 12 of them being in the  
109 southern boreal zone, and two in the middle boreal zone (Ahti et al., 1968). In each forest, the study  
110 trunks were selected on a 10-m wide transect. Each transect was established 15 meters from the  
111 point of easiest access into the study stand. The direction of the transect was towards the center of  
112 the stand, except in smaller stands (< 100 m wide) where the transect followed the direction of the  
113 longest side of the stand. If the opposite side of a stand was met before trunks were surveyed, the  
114 transect was turned around and continued parallel to the first transect. The first five pine trunks  
115 within a transect that fulfilled the criteria of being 1) standing (leaning max. 45°) and dead, 2)  
116 trunks or high stumps ( $\geq 0.5$  m in height), and 3)  $\geq 7$  cm in diameter, were selected for sampling.

117 **Table 1.** Site information. Dominant tree species and mean age classes are derived from Natural Resources  
 118 Institute Finland, 2015.

	Site	Municipality	Dominant tree species	Mean age class
1	Hallinmäki	Jämsä	spruce	96–132
2	Ilmakkamäki	Suonenjoki	pine	56–65
3	Kalaja	Rautalampi	pine	62–71
4	Kirkkokangas	Muurame	spruce	85–109
5	Kivetty	Äänekoski	spruce	72–84
6	Kotinen	Hämeenlinna	spruce	75–89
7	Kuusimäki	Muurame	spruce	45–55
8	Latokuusikko	Kuhmoinen	spruce	88–108
9	Leivonmäki	Joutsa	pine	62–78
10	Lortikka	Kuhmoinen	spruce	70–80
11	Pyhä-Häkki	Saarijärvi	pine	101–144
12	Vaarunvuoret	Jyväskylä	spruce	62–72
13	Vesijako	Padasjoki	spruce	54–63
14	Vuorilampi	Toivakka	pine	45–55

119



120 **Fig. 1.** The map showing the regions of Finland and the locations of the study sites. Site names are presented  
 121 in Table 1. © National Land Survey of Finland 2016, 2017. [1.5-column fitting image]  
 122

123

## 124 2.2. Data collection and preparations

### 125 2.2.1. Species data

126 All decomposer fungi and *Micarea* lichens were recorded from each study trunk based on the  
 127 occurrence of fruit bodies. Sampling of *Micarea* and *Mycocaliciales* species was conducted in three  
 128 parts: October 2014, May–June 2015, and September 2015. Rest of the groups (agarics, corticioids,

129 discomycetes, jelly fungi, polypores, and pyrenomycetes) were sampled in separate surveys in  
130 August–September 2015. Agarics were sampled again during October 2015 to meet a better share  
131 of a local species community (their detectability is lower than in other groups, see Abrego et al.  
132 (2016) and Purhonen et al. (2016)). The trunks were carefully examined throughout from ground  
133 level up to a height of 1.8 meters. Species of *Mycocaliciales* were recorded only from sapwood, all  
134 other fungal groups also from bark. Fungi were identified to species in the field if possible.  
135 Otherwise, specimens were taken for later microscopical identification in the laboratory. Species  
136 nomenclature followed Coppins (1983), Czarnota (2007), and Czarnota and Guzow-Krzemínska  
137 (2010) with *Micarea* species, Tibell (1999) with species of *Mycocaliciales*, and Index Fungorum  
138 (Royal Botanic Gardens Kew et al., 2016) with the rest. If possible, identifications were made to  
139 species level, otherwise to genus level.

140 In the analyses, we used species level identifications. We also included genus level  
141 identifications that were different from the identified species of the same genus. We have  
142 thoroughly aimed at a similar taxonomic resolution throughout the data. In the case of  
143 taxonomically very poorly known groups of *Chaenothecopsis* and *Mycocalium*, several undescribed  
144 species were separated based on spore size, type and some other anatomical and chemical  
145 characters, and considered as distinct species. Also, some pyrenomycetes remained unidentified, but  
146 when it was possible to separate them from the rest of the detected species, they were considered as  
147 species in the analyses.

148

#### 149 2.2.2. Study trunk specific measures

150 Several variables were recorded for each study trunk in the field. These included coordinates,  
151 circumference at breast height (cm), height (m), decay stage (1–5), the proportion of surface not  
152 covered by bark (%) and the coverage of lichens (%). The circumference at breast height was  
153 converted to diameter, and it was used as an estimate of survey effort.



154 We also estimated the canopy openness around the trunks. Four fisheye photos were taken  
155 towards principal compass points while standing back against the trunk. The proportion of visible  
156 sky was calculated from each photo, using ImageJ (version 1.45s; Schneider et al., 2012). The final  
157 estimate for canopy openness was the mean of these four, trunk specific values.

158

### 159 2.2.3. Age and time since death of study trunks

160 We assigned each study trunk age and time since death, using dendrochronological methods. From  
161 each trunk, we extracted a cross-sectional sample disc, or a partial disc. When possible, the samples  
162 were extracted from the part of the trunk where bark was still present, to ensure we had the last  
163 growth ring. When bark or bark remnants were no longer present, we extracted the sample from  
164 where we subjectively estimated minimum ring erosion. In addition to the study trunks, we further  
165 extracted increment cores from five live trees within the vicinity of the study trunks at each site, for  
166 building a master chronology. In the laboratory, the samples were first dried, increment cores  
167 mounted to core mounts, and frail sample discs reinforced following Krusic and Hornbeck (1989;  
168 but in normal air pressure). Samples were sanded to make annual rings and ring borders clear and  
169 easily observable.

170 Tree rings were dated, using visual cross-dating (Yamaguchi, 1991), against the site-specific  
171 marker rings obtained from the live trees. The widths of the tree-rings in all samples were measured  
172 using WinDENDRO (Regent Instruments Inc., 2015), and the visual cross-dating results were  
173 statistically confirmed, using the COFECHA-software (Holmes, 1983). If the pith of the tree was  
174 missing (necessary for estimating the year of recruitment), we estimated the number of missing  
175 rings, using a pith locator (Speer, 2010).

176 The tree age at death (AAD) was calculated as the difference between the calendar year of the  
177 last ring, and the pith year. The years from death (YFD) was calculated as the difference between  
178 the sampling year (2015) and the cross-dated year of the last ring. In general, only trunks for which

179 both variables could be calculated were included in the analyses, but to increase the sample size, we  
180 subjectively estimated these variables for six of the trees where the presence of bark could not be  
181 ascertained but only a small number of rings were missing. Age at death and years from death for  
182 each trunk are presented in Table A.1 in Appendix A.

183

#### 184 2.2.4. Dead wood data

##### 185 2.2.4.1. Dead wood measurements

186 We collected a dead wood data to estimate the local dead wood continuity in the vicinity of each  
187 study trunk. Pieces of dead pine were recorded from four 10 m x 50 m transects, located in principal  
188 compass points around each study trunk. Transects to north and south begun at the trunk, and to  
189 west and east five meters from the trunk. If more than 10 meters of a transect was unfeasible to  
190 locate due to the position of the trunk, two transects were established to the opposite principal  
191 compass point. Otherwise the unfeasible part ( $> 10$  m) was turned  $90^\circ$  right. The transect was  
192 directed to a feasible half-cardinal point if it was not possible to establish a double transect to the  
193 opposite principal compass point.

194 We included all pieces of dead pine with a diameter of the wider end exceeding 10 cm, and  
195 fallen and standing dead wood with length or height  $\geq 1$  m. A piece of fallen dead wood was  
196 recorded only if its base was located inside the transect. The pieces were classified into categories  
197 of fallen and standing dead wood (including stumps formed by natural tree fall) and cut stumps. If  
198 the identification of tree species was uncertain due to the advanced decay stage, the piece was  
199 ignored.

200 For each piece of dead wood, the maximum diameter was measured. For standing and fallen  
201 dead wood, also the height (slant height measured with measuring tape if possible), minimum  
202 diameter and decay stage was recorded. A five-point decay stage estimation followed Renvall  
203 (1995).

204

205 2.2.4.2. Dead wood amount, diversity, and management intensity

206 Volumes were calculated for each recorded piece of fallen and standing dead wood, using the  
207 formula for truncated cone volume. We used the sum of volumes of standing and fallen dead wood  
208 in the four transects (total transect area was 1 ha) as the total dead wood volume ( $\text{m}^3 \text{ha}^{-1}$ ) on the  
209 site. The volumes of study trunks were added up to this estimate, calculated using the formula of  
210 right circular cone volume.

211 The stand continuity was described as diversity index for dead wood, calculated at the site  
212 level (Stokland, 2001). For the calculations, we constructed different dead wood types from the  
213 combinations of three variables: dead wood category (fallen/standing), canopy position (understory:  
214  $\varnothing < 30 \text{ cm}$ ; canopy:  $\varnothing \geq 30 \text{ cm}$ ), and decay stage (1–5). Altogether, there were 20 different dead  
215 wood types. The index used was Shannon’s diversity index (H) (Shannon and Weaver, 1949):

216 
$$H = - \sum_{i=1}^s p_i \ln p_i$$

217 where  $p_i$  is the number of dead wood pieces in a certain dead wood type  $i$  ( $n$ ) divided by the total  
218 amount of dead wood pieces ( $N$ ), and  $s$  is the number of different dead wood types.

219 We used the number of cut stumps per hectare within a site as a measure of forest  
220 management intensity, calculated as the sum of stumps recorded from all the transects (sampled  
221 area was 1 ha).

222

### 223 **2.3. Statistical methods**

224 All analyses were conducted at trunk level separately for decomposers and *Micarea* lichens, and  
225 they were performed using R (version 3.3.2; R Core Team, 2016). Dead wood diversity and  
226 management intensity were the explanatory variables representing stand continuity, and age at death  
227 and years from death represented microhabitat continuity. Dead wood diversity was chosen instead  
228 of the dead wood amount as it presumably describes continuity better. Also, diameter and canopy

229 openness were used to account for variation in survey effort and microclimate (Pouska et al.,  
230 2016b), respectively. Every explanatory variable was standardized to mean  $0 \pm 1$  SE. Trunks with  
231 missing values in any of the measured variables were omitted from the analyses.

232 Before the analyses, correlations between explanatory variables were inspected. Tree diameter  
233 and age at death correlated strongly (Table A.2 in Appendix A). Age at death was thought to be a  
234 more meaningful descriptor of microhabitat continuity of the trunks than diameter, and therefore it  
235 was chosen for the analyses of species richness.

236 A Generalized Linear Mixed Model (GLMM,  $n = 52$ ) with a Poisson distribution and a log-  
237 linear link function was used to study which environmental variables best explained species  
238 richness of wood-inhabiting fungi (function “glmer” from the package “lme4” by Bates et al.,  
239 2016). Site and trunk identities were included into the models as hierarchically structured random  
240 effects by nesting the trunks within sites. The analysis was always started with a full model  
241 including all explanatory variables. Then, the model was simplified by removing the least  
242 significant variable from the model until only one variable remained. A model with the lowest AIC  
243 value was chosen.

244 We used Bioenv-analysis to study the effects of environmental variables on the community  
245 composition (function “bioenv” from the package “vegan” by Oksanen et al., 2017). First, we  
246 calculated binary Bray-Curtis dissimilarities for the pairs of communities from the presence-  
247 absence transformed species data. All species with only one occurrence and trunks with only one  
248 occurring species were excluded from the analyses. In the community data for decomposers, there  
249 were 36 species and 48 trunks, and for *Micarea* lichens, 12 species and 33 trunks. We performed  
250 Bioenv-analysis to find the best subset of environmental variables (calculated as Euclidean  
251 distances) having the highest Spearman rank correlation with the community dissimilarities. To  
252 visualize the effects of environmental variables on the community composition, we conducted

253 Nonmetric Multidimensional Scaling (NMDS) with binary Bray-Curtis dissimilarities (function  
254 “metaMDS” from “vegan”). Finally, we chose the best two-dimensional solutions.

255 We also performed analyses on the responses of 14 individual species, namely those with  
256 high enough number of observations for reliable analyses. The methods considering these analyses,  
257 as well as their results are presented in Appendix B.

258

### 259 **3. RESULTS**

#### 260 **3.1. Species richness of wood-inhabiting fungi**

261 Altogether, 107 fungal species were identified with a total of 510 occurrences (Table A.3 in  
262 Appendix A). Out of these, 91 were decomposers and 16 *Micarea* lichens (the total number of  
263 detected species is somewhat higher than the number included in the analyses because we had to  
264 omit the communities for which some environmental variables could not be attained). The mean  
265 number of species per trunk was 4.9 for decomposers, and 2.4 for *Micarea* lichens (Table 2). 46 %  
266 of the species (n = 49) occurred only once in the data. 21 % (n = 23) of the species had over 5  
267 occurrences, and 15 % (n = 16) had over 10 occurrences. The 5 most common species were  
268 *Micarea melaena* (n = 45), *Glonium nitidum* (n = 33), *Micarea prasina* (n = 26), *Micarea misella* (n  
269 = 25), and Pyrenomycete sp. 4 (n = 23) (see Table A.3 in Appendix A for a full species list).

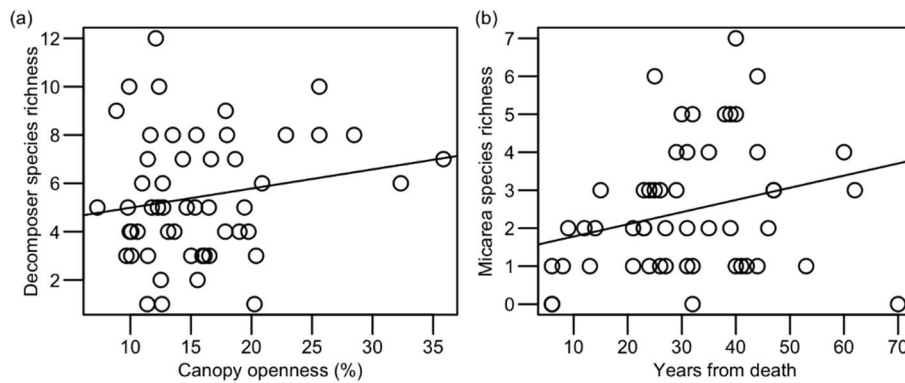
270 **Table 2.** Site information, showing site level means and standard deviations (in brackets) for stand and trunk  
 271 level variables (n for AAD and YFD indicated with upper index, for rest of the variables, n = 5 in all sites),  
 272 and means for all sites. The units used for variables are in brackets. Column label abbreviations: DW = dead  
 273 wood, stumps = management intensity, AAD = age at death, YFD = years from death,  $\phi$  = diameter, canopy  
 274 = canopy openness, dec./trunk = decomposer species richness, lic./trunk = *Micarea* species richness.  
 275

Site	Stand variables			Trunk variables					
	DW div.	Stumps (pc ha <sup>-1</sup> )	DW amount (m <sup>3</sup> ha <sup>-1</sup> )	AAD (y)	YFD (y)	$\phi$ (cm)	Canopy (%)	Dec./trunk	Lic./trunk
1 Hallinmäki	2.0	94	13.4	130.8 <sup>4</sup> (60.9)	25.8 <sup>4</sup> (25.7)	17.0 (3.0)	12.2 (2.1)	3.2 (1.8)	1.4 (1.7)
2 Ilmakkämäki	2.3	40	25.2	108.7 <sup>3</sup> (12.4)	19.0 <sup>3</sup> (9.6)	33.4 (21.2)	15.6 (4.7)	3.0 (3.2)	1.8 (0.8)
3 Kalaja	1.8	30	5.7	147.0 <sup>2</sup> (15.6)	12.0 <sup>2</sup> (4.2)	31.3 (13.3)	16.8 (4.4)	3.6 (1.8)	3.2 (1.3)
4 Kirkkokangas	1.6	73	68.5	277.1 <sup>5</sup> (42.5)	35.6 <sup>5</sup> (9.8)	48.7 (9.5)	14.0 (2.7)	6.0 (1.7)	3.6 (1.9)
5 Kivetty	1.6	19	6.9	98.2 <sup>5</sup> (10.4)	24.8 <sup>5</sup> (7.9)	15.9 (3.7)	16.5 (2.6)	8.4 (1.1)	1.6 (1.5)
6 Kotinen	1.8	26	33.0	236.7 <sup>3</sup> (30.6)	41.3 <sup>3</sup> (17.9)	29.2 (9.4)	14.3 (3.8)	3.0 (1.2)	2.6 (2.5)
7 Kuusimäki	2.3	16	20.2	147.3 <sup>3</sup> (16.6)	33.3 <sup>3</sup> (11.7)	27.0 (10.1)	14.7 (1.1)	4.6 (1.1)	2.0 (1.2)
8 Latokuusikko	1.8	36	15.1	166.8 <sup>4</sup> (28.6)	45.4 <sup>5</sup> (8.2)	28.9 (6.7)	20.3 (5.1)	4.6 (2.4)	2.8 (1.3)
9 Leivonmäki	2.1	106	14.4	111.0 <sup>3</sup> (13.5)	32.3 <sup>3</sup> (10.3)	30.0 (9.8)	14.9 (3.8)	5.8 (3.1)	1.8 (0.8)
10 Lortikka	1.9	71	3.3	154.8 <sup>4</sup> (67.0)	27.0 <sup>5</sup> (13.6)	26.8 (5.8)	30.3 (17.2)	4.8 (1.6)	2.0 (2.0)
11 Pyhä-Häkki	2.5	22	61.6	293.3 <sup>3</sup> (24.9)	43.3 <sup>4</sup> (27.0)	33.4 (12.0)	23.1 (5.5)	6.0 (2.9)	1.6 (1.7)
12 Vaarunvuoret	1.6	112	2.8	144.0 <sup>4</sup> (11.0)	31.8 <sup>4</sup> (16.7)	24.4 (9.9)	11.8 (1.3)	4.8 (1.9)	2.6 (1.1)
13 Vesijako	2.4	38	25.4	147.0 <sup>5</sup> (38.9)	29.8 <sup>5</sup> (14.4)	33.7 (7.8)	12.6 (4.7)	5.2 (4.1)	2.8 (2.7)
14 Vuorilampi	2.2	69	22.3	82.8 <sup>4</sup> (4.8)	29.0 <sup>4</sup> (7.1)	23.8 (12.4)	11.2 (2.9)	5.2 (2.4)	4.0 (1.4)
<b>All sites</b>	2.0 (0.3)	53.7 (32.3)	22.7 (19.5)	159.9 <sup>52</sup> (70.0)	31.5 <sup>55</sup> (15.3)	28.8 (12.3)	16.3 (7.3)	4.9 (2.5)	2.4 (1.7)

276  
 277 None of the variables entered into the GLMM model affected the decomposer species  
 278 richness (Table 3), and canopy openness was the only variable remaining in the final model (Table  
 279 3; Fig. 2a). For *Micarea* lichens, species richness was positively dependent on years from death  
 280 (Table 3; Fig. 2b). It was the only variable included in the final model (Table 3).

281 **Table 3.** Results from GLMM analysis for species richness of decomposers and *Micarea* lichens (n = 52 for  
 282 both datasets). Cells show estimates (B), standard errors (SE), z values, and statistical significances (P).  
 283 Variables having a statistically significant effect are bolded. The units used for variables are in brackets.  
 284 Abbreviations: canopy = canopy openness, YFD = years from death.

		B	SE	z value	P
<b>Decomposers</b>	<b>(Intercept)</b>	1.68	0.08	21.72	< 0.001
	Canopy (%)	0.08	0.08	1.05	0.295
<b>Micarea lichens</b>	<b>(Intercept)</b>	0.85	0.11	7.43	< 0.001
	<b>YFD (y)</b>	0.20	0.10	1.98	0.048



287  
 288 **Fig. 2.** Responses of (a) decomposer species richness to canopy openness and (b) *Micarea* species richness  
 289 to the number of years from death. Each dot represents species richness on one trunk. Figures are presented  
 290 only for variables included in the final models. [1.5-column fitting image]

291  
 292 **3.2. Community composition of wood-inhabiting fungi**

293 The community composition of decomposers was best explained by dead wood diversity (Table 4;  
 294 Fig. 3a). In NMDS, communities in the sites with the lowest dead wood diversities were located  
 295 closer to each other in the center of the ordination space while communities in sites with higher  
 296 dead wood diversities were more scattered (Fig. 3a). Years from death was the next fitted variable  
 297 but it did not increase the correlation between the community dissimilarities and environmental  
 298 distances (Table 4). Nevertheless, in NMDS communities on trunks with the least time since their  
 299 death had mainly negative values on both axes (Fig. 3b). With increasing time since tree death,  
 300 communities tended to be located closer to the upper right corner of the ordination space (Fig. 3b).  
 301 The final stress level for the two-dimensional NMDS solution in Fig. 3a and 3b was 0.175.

302 The *Micarea* lichen community composition was most efficiently explained by the combined  
 303 effect of years from death, site and dead wood diversity (Table 4; Fig. 3c and 3d). In NMDS, time

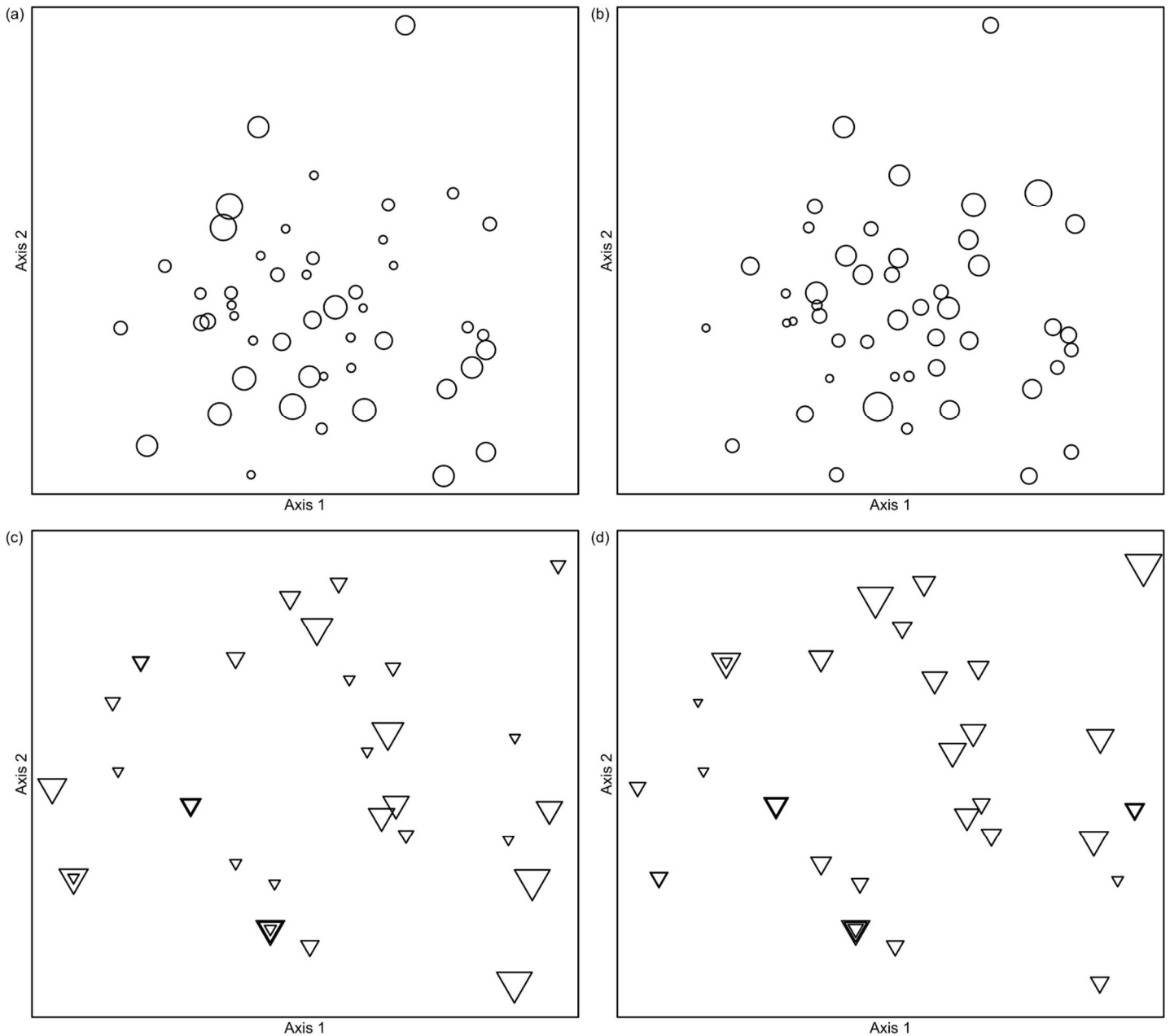
304 since tree death increased towards the upper right corner of the ordination space (Fig. 3d), and dead  
 305 wood diversity increased towards the lower right corner of the ordination space (Fig. 3c). However,  
 306 as adding site increased the correlation between the community dissimilarities and environmental  
 307 distances, the effect of years from death and dead wood diversity is not independent of site. The  
 308 final stress level for the two-dimensional NMDS solution in Fig. 3c and 3d was 0.175. Altogether,  
 309 the results for both decomposers and *Micarea* lichens should be interpreted with caution due to the  
 310 low correlations in the Bioenv analyses.

311 **Table 4.** Results from Bioenv analyses of environmental variables affecting community composition of  
 312 decomposers and *Micarea* lichens. Correlations are Spearman rank correlations between the community  
 313 dissimilarities and environmental distances. Abbreviations: DW = dead wood, YFD = years from death,  
 314 AAD = age at death, Stumps = management intensity, Canopy = canopy openness.

315

<b>Decomposers</b>		
Size	Variables	Correlation
<b>1</b>	<b>DW diversity</b>	<b>0.128</b>
2	DW diversity, YFD	0.120
3	DW diversity, YFD, Site	0.109
4	DW diversity, YFD, Site, Diameter	0.099
5	DW diversity, YFD, Site, Diameter, AAD	0.078
6	DW diversity, YFD, Site, Diameter, AAD, Stumps	0.049
7	DW diversity, YFD, Site, Diameter, AAD, Stumps, Canopy	-0.011
<b>Micarea lichens</b>		
Size	Variables	Correlation
1	YFD	0.126
2	YFD, Site	0.168
<b>3</b>	<b>YFD, Site, DW diversity</b>	<b>0.195</b>
4	YFD, Site, DW diversity, Stumps	0.177
5	YFD, Site, DW diversity, Stumps, AAD	0.160
6	YFD, Site, DW diversity, Stumps, AAD, Canopy	0.142
7	YFD, Site, DW diversity, Stumps, AAD, Canopy, Diameter	0.081





316 **Fig. 3.** NMSD representing the differences in community structure between the communities of decomposers  
 317 (a–b; circles) and *Micarea* lichens (c–d; triangles) observed in the study. One symbol represents one  
 318 community occurring on one trunk. The size of a symbol represents the magnitude of dead wood diversity in  
 319 Fig. 3a and 3c, and the number of years from death in Fig. 3b and 3d. The size of a symbol grows with  
 320 increasing values of the variables. Stress level for both solutions is 0.175. [2-column fitting image]  
 321

322 In our analyses on the 14 individual species, four species were statistically significantly  
 323 affected by some of the variables (Table B.1 in Appendix B). Local continuity explained the  
 324 presence of the species both positively and negatively. For the rest, the final models did not include

325 any statistically significant variables. All results considering individual species are presented in  
326 Appendix B.

327

## 328 **4. DISCUSSION**

### 329 **4.1. Effects of stand continuity**

330 Decomposers and *Micarea* lichens were affected by stand continuity through modest changes in the  
331 community composition that were driven by dead wood diversity. Communities of decomposers  
332 were more similar among sites with low dead wood diversity and differentiated when dead wood  
333 diversity increased. This might be because the communities in sites with low dead wood diversity  
334 might have more shared generalist species, able to survive in sites with more homogenous dead  
335 wood resources and thus, occurring more evenly across the landscapes (Nordén et al., 2013). With  
336 increasing dead wood diversity, sites can host more unique species assemblages including also  
337 specialists (Abrego and Salcedo, 2013; Nordén et al., 2013). Similar, although weaker trend  
338 occurred with *Micarea* lichens.

339 The species richness of decomposers or *Micarea* lichens was not affected by dead wood  
340 diversity or management intensity. Increased dead wood diversity should contribute to a higher  
341 amount of available resources and niches (Siitonen, 2001; Stokland et al., 2012), and its positive  
342 effect on species richness of wood-inhabiting fungi has been demonstrated in previous studies (e.g.,  
343 Hottola et al., 2009; Penttilä et al., 2004; Similä et al., 2006). Also, the negative effects of  
344 management intensity have been widely reported (e.g., Arnstadt et al., 2016; Bader et al., 1995).

345 In studies where all dead wood diversity (including also different tree species) has been  
346 measured to reflect the stand continuity, and the species richness has been measured from all of the  
347 material contributing to the dead wood diversity, it is very logical that clear positive correlations  
348 occur between species richness and stand continuity (see for example Hottola et al., 2009; Penttilä  
349 et al., 2004; Similä et al., 2006). Thus, it is worth emphasizing that as we measured only the dead

350 wood diversity of pine, and recorded the fungal species richness only from the selected standing  
351 dead trees, such correlation might be more difficult to find. However, we argue that if such a  
352 correlation would be found it would truly reflect the species dependence on stand continuity, not  
353 just that more diverse substrate pool has more diverse species pool.

354 Species interactions might also play its part in the absence of a positive relationship between  
355 species richness and stand continuity. Heilmann-Clausen and Christensen (2005) found that the  
356 species richness of wood-inhabiting fungi on an individual tree was negatively affected by dead  
357 wood continuity (estimated as the proportion of strongly decayed logs). They suggested competitive  
358 exclusion to be one of the possible explanations: highly competitive specialists replace the early  
359 successional, non-specialist species in sites with high dead wood continuity. Thus, the species  
360 richness it not necessarily higher in the high continuity stands compared to stands with lower  
361 continuity, but can show no trends or even be lower.

362 In addition, the sites were located in or in the vicinity of conservation areas and thus, at least  
363 some natural forests were located in the proximity of sites. The variation in dead wood diversity and  
364 management intensity might not have been sufficient to reveal all existing trends. Moreover,  
365 management intensity of the sites was relatively low compared to the average managed forests in  
366 the area. In a study by Penttilä et al. (2004), dead wood diversity and management intensity induced  
367 a clear trend in polypore community composition when they compared communities in managed  
368 and old-growth forests. They recorded 400–500 stumps in managed stands, whereas the most  
369 managed site in this study included only 112 cut stumps per hectare.

370 The fact that stand continuity did not have a strong effect on decomposers and *Micarea*  
371 lichens gives indirect evidence that they are not dispersal limited at such fine spatial scales. In fact,  
372 it has been suggested that pine inhabiting fungi would be less affected by forest management than  
373 species specialized in e.g. spruce due to their better dispersal abilities (Stokland and Larsson, 2011).  
374 Stokland and Larsson (2011) hypothesized that this could be due to the different selection pressures

375 in pine forests that experience forest fires and have lower input rates of dead wood than spruce  
376 forests. Thus, the sites may support viable metacommunities of these pine-inhabiting species if  
377 landscape level continuity is high. However, on rare specialist species, dispersal limitations might  
378 occur already at small spatial scales (Norros et al., 2012).

379

#### 380 **4.2. Effects of microhabitat continuity**

381 *Micarea* species richness increased with time since tree death. Microhabitat continuity could be  
382 more important for *Micarea* lichens than stand continuity due to their slow rates of growth and  
383 establishment (Nordén et al., 2014; Stenroos et al., 2011). With increasing time since tree death  
384 there is more time available for colonization (Johansson et al., 2007), and new suitable  
385 microhabitats, such as decorticated wood appear (Renvall, 1995). The result also fits well with the  
386 hypothesis of species time relationship (Rosenzweig, 1995), especially because competitive  
387 exclusion has been suggested to be rare in lichens (Lawrey, 1991; Uliczka and Angelstam, 1999).

388 Species richness of decomposers was not affected by time since tree death. Previous studies  
389 have demonstrated an increase in species richness of wood-inhabiting fungi from initial decay  
390 stages to intermediate ones (Arnstadt et al., 2016; Renvall, 1995), and with time since tree death  
391 (Heilmann-Clausen, 2001). This pattern could result from changes in the tree quality (e.g. bark  
392 exfoliation (Renvall, 1995), and decreasing wood density in standing dead trees (Saint-Germain et  
393 al., 2007)), and from the emergence of late successional species (Høiland and Bendiksen, 1997). In  
394 the present study, the trunks with the longest time since their death probably included many kelo  
395 trees, i.e. standing dead trees characterized by slow death that makes the trunk very resistant to  
396 decay (Niemelä et al., 2002). Since kelos are utilized by a limited set of specialist species (Niemelä  
397 et al., 2002; Stokland et al., 2012), species richness might not increase linearly with time.  
398 Additionally, increasing competition with increasing habitat patch age might explain our result  
399 (Nordén and Appelqvist, 2001).

400 Community composition of both decomposers and *Micarea* lichens was slightly dependent on  
401 time since tree death. Communities on recently died trunks probably share certain (pioneer) species  
402 that inhabit the freshly dead wood (Niemelä et al., 1995; Renvall, 1995). Later on, fungal  
403 succession takes place with proceeding decomposition (Rajala et al., 2012; Stokland et al., 2012)  
404 and thus, different species of wood-inhabiting fungi should occur at different times after the tree  
405 death (Niemelä et al., 1995; Heilmann-Clausen, 2001). Trends in the community composition could  
406 have been stronger if more trunks at the end of the decomposition range could have been included  
407 in the analyses. The trunks for which the year of death could not be determined due to the erosion  
408 of the outermost tree rings were likely the oldest but had to be excluded from our analyses.

409 Tree age at death did not affect either of the studied fungal groups. This indicates that it might  
410 be important only for few species if any. The opposite was hypothesized as, for example, the  
411 community composition of dead wood might be affected by the longevity of infection history  
412 during the tree lifespan (Heilmann-Clausen and Christensen, 2004). Similar to the tree age at death,  
413 trunk diameter did not affect the communities of wood-inhabiting fungi. Several studies focusing on  
414 downed dead wood have reported the opposite (e.g., Høiland and Bendiksen, 1997; Renvall, 1995).  
415 However, our results are in accordance with the results by Pouska et al. (2016a) that showed no  
416 effect of diameter on wood-inhabiting fungal communities on standing dead Norway spruces. They  
417 suggested that diameter interacts with several other, more important trunk characteristics (e.g. trunk  
418 temperature and moisture) than diameter *per se*.

419 Also canopy openness did not affect wood-inhabiting fungal communities. Sun exposure may  
420 affect community composition of wood-inhabiting fungi (Heilmann-Clausen, 2001), and lichens  
421 have been shown to respond positively to increasing canopy openness (Marmor et al., 2012;  
422 Uliczka and Angelstam, 1999). Our results could be explained by milder edge effect in natural  
423 forest edges (Ruete et al., 2016) that were characteristic for our study sites. Moreover, canopy

424 openness might be positively related to stand age, and thus light availability would not limit lichen  
425 communities in older stands (Bäcklund et al., 2016).

426

### 427 **4.3. Conclusions**

428 In the conservation areas of central Finland, wood-inhabiting fungal diversity was not significantly  
429 affected by local forest continuity. The results indicate that on a stand scale, other environmental  
430 filters and stochastic processes underlie the patterns of wood-inhabiting fungal diversity on standing  
431 dead pines. Although some species would depend on the continuous supply of dead wood and old  
432 trees, they seem not to be limited by dispersal, and can find these suitable habitats within the  
433 surrounding landscapes, underlining the importance of landscape level continuity.

434 The results demonstrated the importance of old, standing dead trees for species-rich  
435 communities of *Micarea* lichens. Conservation strategies concerning these species should aim to  
436 increase the local number of old trees that die and decay naturally. To achieve this, approaches of  
437 retention forestry should be applied in managed forests (Gustafsson et al., 2012; Lindenmayer et al.,  
438 2012). However, increasing the number of veteran trees in forest landscapes requires extending the  
439 time-frames of strategies that are currently applied in forest management (Lindenmayer et al.,  
440 2014).

441 The explicit relationship between local continuity and rare species remained unsolved. These  
442 species might be more sensitive to local continuity than common species when taking into  
443 consideration e.g. their highly specialized habitat use (Nordén et al., 2013). Therefore, rare and red-  
444 listed species should be at the center of future research on local continuity to be able to guide the  
445 required conservation actions, and to maintain these species also locally.

446

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455

456 **APPENDIX A.** Supplementary tables (Table A.1–A.3).

457 **APPENDIX B.** Responses of individual species

458

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