

Biodiversity and Conservation

Can large unmanaged trees replace ancient pollarded trees as habitats for lichenized fungi, non-lichenized fungi and bryophytes?

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Response to Reviewers:

Terminology changed to lichenized and non-lichenized species. It proved difficult to use 'other fungi' since it doesn't fit well when starting a sentence and to build sentences etc. I hope this is satisfactory.

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1 **Can large unmanaged trees replace ancient pollarded trees as habitats for lichenized fungi, non-**
2 **lichenized fungi and bryophytes?**

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8

9 **Abstract**

10 Management of ancient trees constitutes a major dilemma in the conservation of associated
11 biodiversity. While traditional methods are often advocated, such practices may incur considerable
12 costs and their effects have rarely been scientifically evaluated. We compared the communities of
13 lichenized fungi, non-lichenized fungi, and bryophytes among equal number of coarse previously
14 pollarded and unmanaged trees (n=340). On 400 *Ulmus glabra* and 280 *Fraxinus excelsior* trees at 62
15 sites in Norway, we found 209 lichenized fungi, 128 non-lichenized fungi, and 115 bryophytes.
16 Pollarded trees were richer in microhabitats than unmanaged trees and had significantly higher
17 richness of bryophytes (ash) and non-lichenized fungi (ash and elm), the latter increasing with the
18 availability of dead wood, cavities and coarse bark structure in pollarded trees. Further, the average
19 total number of red-listed species, and red-listed lichenized fungi separately, were significantly higher
20 on pollarded vs. unmanaged trees, with diversity related to trunk circumference, depth of bark fissures
21 and number of cavities. Our results underline the importance of microhabitats associated with old
22 trees, but we cannot establish with certainty the importance of pollarding *per se*. Since we did not find
23 any negative effect of canopy cover for community diversity, we assume that old trees with rich
24 epiphytic communities can develop without management intervention. The high share (37 out of 49)
25 of red-listed species occurring on unmanaged trees, and the fact that 11 red-listed species were found
26 exclusively on unmanaged trees, may further indicate that unmanaged trees can with time replace the
27 ancient pollarded trees as habitats for rich cryptogamic communities.

28 Keywords: Temperate deciduous forest; broad-leaf forest; wood-decaying fungi; bark-living fungi;
29 ecological restoration.

30

31 **1. Introduction**

32 Biodiversity conservation in abandoned agricultural landscapes often involves two main management
33 options, or combinations thereof: mimicking traditional management, or relying on natural disturbance
34 regimes (Götmark 2013). The choice of option depends on many factors, but decisions should be
35 evidence based (Bernes et al. 2015), and ideally consider the effects for several organism groups/taxa
36 to avoid taxonomic bias (Clark & May 2002). One case of traditional management that is often
37 advocated using either cultural/historical arguments or biodiversity arguments is pollarding of trees
38 (Read 1996; Höjer & Hultengren 2004; Lonsdale 2013).

39

40 Pollarding of temperate deciduous trees for leaf fodder was historically an important practice in the
41 subsistence farming economy in many regions of Europe (Sjölund & Jump 2013), Asia and north
42 Africa (Pankhurst 2013; Lang et al. 2015). Pollarding has probably been practiced in Europe since
43 prehistoric times (Bergendorff and Emanuelsson 1996). Nowadays, pollarding has been abandoned by
44 farmers in most of Europe (Castro et al. 2012; Read 1996; Moe & Botnen 1997, 2000; Mansion 2010;
45 Leppik et al. 2011; Sjölund & Jump 2013). In Norway it was common until about World War II
46 (Austad 1988). Pollarded trees are often of exceptional value for biodiversity (Nilsson et al. 1994;
47 Tønsberg et al. 1996; Moe & Botnen 1997, 2000; Timdal et al. 2010; Sebek et al. 2013). In many
48 regions, pollarded trees are currently the oldest existing trees, and ancient pollarded trees may function
49 as old-growth refugia for many epiphytic species (Nilsson et al. 1994). It is however unclear whether
50 the pollarding in itself is the crucial factor, or if the habitat qualities can be provided by unmanaged
51 trees as well with age.

52

53 Contrary to the earlier agricultural economy where leaves and branches from trees were an important
54 resource, it is today costly to continue the practice of pollarding. In Sweden alone, there are at least
55 700000 pollarded trees (Höjer & Hultengren 2004) and in Norway woodland with pollarded trees is
56 proposed as a selected habitat type in the Norwegian Nature Diversity Act. In both countries
57 landowners and other managers can apply for designated subsidies to re-pollard old trees, amounting

58 to substantial sums of money each year. The question arises: Should new trees be pollarded to replace
59 the old pollards as they die, or can aging unmanaged trees fill the same functions for biodiversity in
60 the future? In this study, we compare epiphytic communities on 1) previously pollarded *Ulmus glabra*
61 Huds. (elm) and *Fraxinus excelsior* L. (ash), with 2) the oldest available elm and ash trees that were
62 never pollarded. We choose to study elm and ash because both tree species host a rich associated
63 epiphytic funga and flora with many nationally red-listed species (Watson et al. 1988; Mitchell et al.
64 2014; Henriksen & Hilmo 2015). Both tree species are subject to severe diseases and red-listed in
65 Norway (Henriksen & Hilmo 2015). We ask the following research questions: 1) Do pollarded trees
66 and unmanaged trees differ in species richness of lichenized fungi, non-lichenized fungi, and
67 bryophytes? 2) What are the main tree characteristics responsible for the variation in species richness?
68 3) Do they differ in which species communities they support, with special emphasis on red-listed
69 species? We use the answers to these questions as a basis to discuss the suitability of restoration
70 pollarding as a biodiversity conservation measure.

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72

73 **2. Materials and Methods**

74 *2.1 Site selection*

75 To test whether pollarding is beneficial for biodiversity or not, pollarded and unmanaged trees of
76 similar age should be compared. This may however be a challenge since the currently oldest trees in
77 many areas were pollarded in the past, whereas younger trees were never pollarded (Sebek et al.
78 2013). We chose southern and western Norway as a study area since there are many thousands of
79 previously pollarded ash and elm trees as well as many large, but usually younger, unmanaged trees.
80 Old unmanaged trees can sometimes be found adjacent to pollarded trees, especially in steep and
81 inaccessible slopes. When possible, we surveyed an equal number (10) of trees of each category at the
82 same site. Because of the rarity of such sites, this was seldom possible, and we instead surveyed 10
83 trees of the respective category at separate but geographically adjacent and climatically similar sites.

84 We used the database of Norwegian high nature value areas Naturbase (www.naturbase.no;
85 Miljødirektoratet 2012) to select study sites. First, we narrowed the sample down to include all sites
86 with temperate deciduous trees (n = 2469). Secondly, we read through free text descriptions and
87 reduced the sample to include only sites with a high probability of containing at least 10 old elm or ash
88 trees (n = 355). Thirdly, we analysed these 355 sites according to regional climatic gradients (Moen
89 1999), and then made a stratified sample of totally 129 sites representing each vegetation zone. We
90 further narrowed down the selection by balancing the number of sites with pollarded and unmanaged
91 trees within each climatic region. From our final selection of 90 sites, we discarded 28 in the field
92 because of too few suitable trees (less than 10). The resulting 62 sites (Fig 1) were surveyed in 2012-
93 2014, six of these containing 10 + 10 trees, resulting in the total number of 68 surveyed tree groups of
94 ten trees each (App. A). The sites were used in the project ‘Old temperate deciduous trees – a hotspot
95 habitat’ and basic data and some preliminary results were presented in Norwegian in Nordén et al.
96 (2015)

97

98 [Insert Fig. 1.]

99

100 Within each vegetation zone an equal number of pollarded and unmanaged trees of each tree species
101 was surveyed (App. A). The sites were to some extent open woodland pastures, parks or churchyards,
102 but mainly closed semi-natural woodlands with an earlier history as woodland pastures (App. A). Six
103 sites with clearly ancient trees showed little evidence of human impact, including pollarding, and were
104 classified as natural woodland (App. A).

105

106 *2.2 Studied organisms*

107 The epiphytic communities on elm and ash in northern Europe are dominated by bryophytes and
108 lichenized fungi, including many red-listed species (Jönsson et al. 2011). In addition, many fungi with
109 various nutritional modes occur, viz. wood-decaying species, species growing on the bark of living

110 trees, tree pathogens, as well as lichenicolous or bryophilous species etc. These species are collectively
111 referred to as non-lichenized fungi below.

112

113 *2.3 Fieldwork*

114 At the 62 sites, we surveyed a total of 680 trees: 200 pollarded elms, 200 unmanaged elms, 140
115 pollarded ashes, and 140 unmanaged ashes. We selected trees at random whenever this was possible in
116 the often very steep terrain where accessibility was sometimes severely restricted by cliffs, overhangs,
117 and dangerous screes. At each site, we tried to cover the total area and variability of the site while
118 choosing the largest possible unmanaged trees with an elevation and exposition matching the
119 pollarded trees.

120 We tried to match the size of pollarded trees as much as possible, and all trees in both categories had a
121 breast height diameter of more than 40 cm. We identified previously pollarded trees as trees with the
122 main branches sprouting from a single, often enlarged, part of the trunk; showing signs that the upper
123 branches (usually 2-4 m above the ground) had been pruned at least once (see Sebek et al. 2013).
124 Trees with normal architecture we considered unmanaged. We excluded doubtful cases, for instance
125 cases where we suspected falling stones in steep screes could be the reason for the stunted growth-
126 form of trees.

127 For each tree we recorded tree circumference at breast height (1.3 m above ground), counted and
128 measured trunk cavities (whole trunk). We defined a trunk cavity as any space enlarging inwards from
129 the opening and at least as deep as it is broad. In addition, we recorded the percentage cover of dead
130 wood on the trunk surface, the percentage bryophyte cover on the north and south side of the trunk (up
131 to 2.0 m above ground), the maximum bark fissure depth, the amount of spruce trees close to the
132 studied trees, and the percentage of visible sky on the north and south side of the trees. We measured
133 the maximum bark fissure depth with a ruler, excluding cracks in the wood. This measure is a proxy
134 for the relative age of old trees (Ranius et al. 2008), and increases the number of microhabitats for
135 epiphytes (Paltto et al. 2011). We recorded the percentage of visible sky by standing with the back

136 close to the trunk and watching upwards at a 45 degrees angle. Before and during the fieldwork we
137 used printed photographs with counted pixels (with varying percentage visible sky) for calibration.
138 To survey species, two persons scrutinized the bark and exposed wood of each trunk with hand-held
139 illuminated 10 × lenses for about 30 minutes. We surveyed the entire area of the trees from 0.0–2.0 m,
140 including attached branches, but for bryophytes, we excluded the basal 10 cm of the trunk to avoid
141 ascending ground floor species. Epiphytic and epixylic species of lichenized fungi, non-lichenized
142 fungi and bryophytes were either noted in the field or collected for study in the laboratory. All
143 lichenized fungi were identified to species level by morphology and standard spot tests, except some
144 sterile species/genera that were treated collectively. Poorly developed sterile crusts were excluded
145 from the data (App. B).

146

147 *2.4 Data analysis*

148 We first investigated the difference between pollarded and unmanaged trees with respect to tree
149 characteristics (tree circumference, number of cavities, percentage cover of dead wood, maximum
150 bark fissure depth, and percentage bryophyte cover) and surroundings (percent visible sky). Because
151 we sampled several trees per site, we used mixed-effect models and included site as a random factor to
152 account for the spatial dependency of trees within sites. Pollarding and tree species were included as
153 predictor variables, as well as their interaction, to clarify differences between pollarded and
154 unmanaged trees across species. Restricted maximum likelihood (REML) was used for parameter
155 estimates. Significance was evaluated by use of likelihood-ratio tests with maximum likelihood (ML)
156 in a backwards stepwise selection procedure. Tree circumference, cover of dead wood and maximum
157 bark fissure depth were log-transformed prior to analyses to reduce heteroscedasticity. The number of
158 cavities was analysed with generalized linear mixed-effect models (GLMMs) with poisson distributed
159 errors.

160 As a second step we investigated the importance of pollarding and tree species for species richness.

161 We constructed generalized linear mixed-effect models with pollarding, tree species and their

162 interaction as predictor variables, and with site as a random factor. Models were fitted with poisson
163 distributed errors. Significance was evaluated by use of likelihood-ratio tests in a backwards stepwise
164 selection procedure.

165 Thirdly, to increase our understanding of important tree characteristics for species richness, we
166 explored the relationship between tree circumference, number of cavities, cover of dead wood, bark
167 fissure depth, and cover of bryophytes, and species richness of lichenized fungi, non-lichenized fungi,
168 and bryophytes. Tree species and pollarding (correlated to tree characteristics) were left out of this
169 analysis. We constructed a full model including all predictor variables and simplified the full model
170 using a backwards stepwise selection procedure with Chi-squared test and a significance level of $p <$
171 0.05 to keep a variable in the model. As the scale of the predictors varied considerably (Table 1), we
172 centred and scaled all predictor variables prior to analysis (Nakagawa and Cuthill 2007; Schielzeth
173 2010) and standardised the variables by one standard deviation, as recommended by Schielzeth
174 (2010). This facilitates the interpretation of the relative importance of the predictors in the model. All
175 models were constructed as GLMMs with poisson distributed errors and site included as a random
176 factor.

177 Separate models were constructed for total species richness, and for species richness of lichenized
178 fungi, non-lichenized fungi, and bryophytes. Similarly, models were constructed for total species
179 richness of red-listed species, and for species richness of red-listed lichenized fungi, and red-listed
180 non-lichenized fungi. For analyses of species richness of red-listed lichenized fungi and for the total
181 number of non-lichenized fungi we used poisson distributed errors and zero-inflated data due to the
182 many recordings of zero species.

183 To investigate variation in species composition, we ran detrended correspondence analysis (DCA; ter
184 Braak & Prentice 1988) on the species-tree-matrix, separately for each organism group. Only species
185 with presence on ≥ 5 trees were included. We investigated relationships between species composition,
186 represented as tree score along DCA axis 1 and 2, and tree characteristics (circumference, number of
187 cavities, dead wood, bark fissure depth, bryophyte cover, and visible sky) using Kendall's non-

188 parametric correlation coefficient τ . Linear mixed-effect models were constructed to investigate the
189 variation in species composition as a function of pollarding and tree species, including their
190 interaction, as predictor variables, and site as a random factor. Significance was evaluated by use of
191 likelihood-ratio tests with maximum likelihood (ML) in a backwards stepwise selection procedure.

192

193 Analyses were performed using R (R Core Team 2016) in RStudio v. 0.99.902 and the packages lme4
194 (Bates et al. 2015), glmmADMB (Fournier et al. 2012) and vegan (Oksanen et al. 2016).

195

196 **3. Results**

197 *3.1 Pollarded vs. unmanaged trees*

198 Pollarded trees were coarser, with more cavities, more dead wood and with deeper bark fissures than
199 unmanaged trees (Table 1, App. C). There were some differences between ash and elm trees (App. D):
200 elm trees were significantly coarser than ash trees (mean \pm standard deviation: 222.6 ± 81.4 vs. 203.4
201 ± 61.0 cm, respectively, $p = 0.009$), and the difference in cover of dead wood was smaller between
202 pollarded and unmanaged elm than ash trees (significant pollarding \times tree species interaction; $p =$
203 0.035 , App. D). Furthermore, there was a tendency for ash trees to be more exposed to light (the
204 percentage of visible sky higher) than elm trees, significant regarding the south side of the trees (ash:
205 $21.8 \pm 16.9\%$, elm: $16.1 \pm 12.4\%$, $p = 0.036$, App. D). There was no difference in the cover of
206 bryophytes among pollarded vs. unmanaged trees, or among tree species (App. D).

207

208 [Insert Table 1]

209

210 *3.2 Species richness*

211 We made in total 11758 records of 452 species: 209 lichenized fungi, 128 non-lichenized fungi, and
212 115 bryophytes (Appendix B). We found on average 17.6 species per ash tree (8.5 lichenized fungi,

213 1.2 non-lichenized fungi, and 7.9 bryophyte species), and 17.1 species per elm tree (7.1 lichenized
214 fungi, 1.8 non-lichenized fungi, and 8.2 bryophyte species).

215

216 Thirty-eight species of lichenized fungi (18%), 53 species of non-lichenized fungi (41%), and 26 species
217 of bryophytes (23%) occurred exclusively on pollarded trees. The corresponding numbers for species
218 only found on unmanaged trees were: lichenized fungi 65 species (31%), non-lichenized fungi 30 (23%),
219 and

220 bryophytes 24 (21%).

221

222 Total species richness was marginally higher on pollarded ash trees compared to unmanaged ash trees
223 but almost equal for elm (Figure 2, Table 3), and did not vary among tree species. Species richness of
224 lichenized fungi was higher on ash than on elm trees, but was not affected by pollarding. Species
225 richness of bryophytes (ash) and non-lichenized fungi (both ash and elm), on the other hand, were
226 significantly higher on pollarded compared to unmanaged trees. In addition, species richness of non-
227 lichenized fungi was significantly higher on elm compared to ash trees (Figure 2, Table 3).

228

229 [Insert Figure 2]

230

231 [Insert Table 3]

232

233

234 In the second analysis, excluding tree species and pollarding, species richness of lichenized fungi
235 increased with increasing depth of bark fissures. It also increased with bryophyte cover on the N side
236 of the trunk, but decreased with bryophyte cover on the S side of the trunk, with the relative
237 importance of the three predictors being similar (Table 4). Species richness of non-lichenized fungi
238 increased with depth of bark fissures, cover of dead wood and number of cavities, with the relative
239 importance ordered from bark fissure to number of cavities (Table 4). Species richness of bryophytes
240 increased with bryophyte cover on the N side of the trunk (Table 4).

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[Insert Table 4]

3.3 Red-listed species

A total of 951 records of 49 nationally red-listed species (Henriksen & Hilmo 2015) was made (App. B), including 33 lichenized fungal species (674 finds), 15 species of non-lichenized fungi (275 finds) and one bryophyte species (two finds). A total of 660 records of 38 red-listed species were made on pollarded trees, the corresponding figures for unmanaged trees trees being 291 records of 37 red-listed species (App. B). Twelve species (six lichenized fungi and six species of non-lichenized fungi) were found exclusively on pollarded trees, while 11 species (10 lichenized fungi and 1 non-lichenized fungal species) were found exclusively on unmanaged trees (App. B). The total number of red-listed species per ash tree was on average 1.02 (0.82 lichenized fungi, 0.20 non-lichenized fungi and 0.001 bryophyte species), and 1.65 on elm (1.11 lichenized fungi, 0.55 non-lichenized fungi and 0.0 bryophyte species).

The total number of red-listed species was significantly higher on pollarded vs. unmanaged trees, and on elm compared to ash trees (Table 5a). The same pattern was found when analysing red-listed lichenized fungi or non-lichenized fungi species separately. The richness of red-listed species increased significantly with trunk circumference, depth of bark fissures and number of cavities. When analysing red-listed lichenized fungi species separately, the same pattern was found, although the effect of circumference was only marginally significant (Table 5b). For red-listed non-lichenized fungi, bark fissure depth was the most important explanatory variable (Table 5b).

[Insert Table 5]

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3.4 Species composition

A total of 103 species of lichenized fungi, of which 18 red-listed, were present on ≥ 5 trees and were included in the analysis. There was a significant difference in lichenized fungi species composition related to tree species and pollarding (Fig. 3), with DCA axis 1 separating pollarded and unmanaged trees ($p < 0.001$) and DCA axis 2 separating elm and ash ($p < 0.001$, Fig. 3, Table 6). Kendall's tau correlation coefficients between ordination axes and the remaining tree variables showed that circumference, number of cavities, dead wood on trunk and bark fissure depth significantly affected species the composition of lichenized fungi, bryophytes and non-lichenized fungi (App. E).

[Insert Table 6]

[Insert Fig 3a, b]

A total of 69 species of bryophytes were present on ≥ 5 trees, none of which were red-listed. There was a significant difference in bryophyte species composition related to tree species and pollarding (Fig. 4, Table 6). DCA axis 1 separated both pollarded and unmanaged trees ($p = 0.010$) and elm from ash ($p = 0.031$), with a marginally significant interaction ($p = 0.070$, App. E), suggesting that there were larger differences in tree scores between pollarded and unmanaged ash than between pollarded and unmanaged elm (Fig. 4). DCA axis 2 showed a gradient in species composition related both to tree species ($p = 0.009$) and pollarding ($p < 0.001$).

[Insert Fig 4a, b]

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295

296 Only 33 species of non-lichenized fungi were present on ≥ 5 trees, with data from 476 trees. Seven of
297 these were red-listed. Many trees had only one species present, affecting the quality of the DCA. There
298 seemed to be a significant relationship between DCA axis 1 and tree species ($p < 0.001$), with elm
299 trees on the negative end and ash on the positive end of the axis (Fig. 5). There was a small significant
300 interaction between pollarding and tree species ($p = 0.039$), but no significant main effect of
301 pollarding ($p = 0.346$), suggesting that pollarding affect species composition of non-lichenized fungi
302 somewhat differently on elm and ash (App. E). We found no relationships between DCA axis 2 and
303 the predictors.

304

305 [Insert Fig 5a, b]

306

307

308 **4. Discussion**

309 Our study clearly shows that old elm and ash trees host species rich and diverse epiphytic
310 communities, which need to be considered in conservation and management plans. Several species
311 occurring in the western, oceanic, parts of Norway are also rare in the rest of Scandinavia and Europe.
312 Another fact that sets western Norway apart is that it is probably the last remaining tract in Europe
313 with a substantial population of old and coarse elm trees that are unaffected by the Dutch elm disease
314 (Solheim et al. 2011).

315

316 We found on average 8.5 lichenized fungi species per ash tree and 7.1 per elm tree. The number of
317 red-listed lichenized fungi species was on average 0.82 per ash tree and 1.11 per elm tree. Thor et al.
318 (2010) reported clearly higher numbers of lichenized fungi species per tree on old trees in wooded
319 meadows in SE Sweden (on average 19.8 on ash, and 22.2 on elm), but comparable numbers of red-
320 listed lichenized fungi species per tree (ash hosted on average 0.7 species, compared with on average

321 1.0 red-listed species per elm tree). The comparison indicates that while the general lichenized fungi
322 diversity may be lower in our mainly closed woodlands, the old elm and ash trees in Norway have a
323 high conservation value considering red-listed species. We also excluded some sterile crustose
324 lichenized fungi, which were included by Thor et al. (2010). In addition, our trees hosted several
325 bryophyte species (7.9 per ash tree and 8.2 per elm tree), probably related to the often oceanic or sub-
326 oceanic climate of our sites. The cover, and probably species richness, of bryophytes is lower in SE
327 Sweden, and the relative cover of lichenized fungi is larger (personal observation).

328 The pollarded trees had on average greater circumference, deeper bark fissures, more dead wood and
329 more cavities than the unmanaged trees. These features are consistent with a higher age of the
330 pollarded trees, a result of them being the only trees in the previous very intensively used agricultural
331 landscape (Moe & Botnen 1997, 2000). Our comparison of the two categories of trees is therefore
332 hampered by the lack of very old unmanaged trees. Nevertheless, we want to use our results to discuss
333 the mechanisms behind the observed patterns.

334

335 *4.1 Does pollarding favour high species richness of epiphytes?*

336 Pollarded trees had a higher total species richness of bryophytes and non-lichenized fungi. Our further
337 analysis indicated that at least the total species richness of non-lichenized fungi might benefit from the
338 increased availability of dead wood, cavities and coarse bark structure in pollarded trees. In addition,
339 the effect on bryophytes and non-lichenized fungi may be partly attributable to the size of the bark
340 area taking bark fissures into account, an aspect we did not address in our analysis. Deeper fissures
341 increase the total area of bark per tree trunk and it would be possible to estimate this effect, but to be
342 accurate it would probably require detailed and laborious mapping of the trunks. We assume that both
343 longer time for colonization, greater bark area, and particularly microhabitat availability, contribute to
344 the higher total species richness of bryophytes and non-lichenized fungi on pollarded trees. Higher age
345 is known to increase factors of importance for epiphytes such as bark pH, base cation ratio, porosity
346 and water holding capacity of the bark (Fritz et al. 2009; Mežaka et al. 2012), as well as time for
347 colonization.

348

349 The importance of microhabitats that develop with age is further supported by the results for
350 lichenized fungi. Total lichenized fungi species richness was not related to pollarding, but to tree
351 species, and to other microhabitat characteristics (e.g. bryophyte cover). However, the number of red-
352 listed species was significantly higher on the pollarded trees, particularly related to increased number
353 of cavities and maximum depth of bark fissures, but also related to trunk circumference. This result
354 further underlines the importance of microhabitats associated with high age of the trees. For instance,
355 seepage from stem wounds on old broadleaf trees may affect the microhabitat for lichenized fungi and
356 be crucial for certain rare lichenized fungi species (Fritz & Heilmann-Clausen 2010; Nordén et al.
357 2013).

358

359 Sebek et al. (2013) showed that old-growth microhabitats form more quickly on pollarded relatively
360 young *Salix* trees than on unmanaged trees. Tree cavities formed more readily in pollarded trees
361 making them more suitable for red-listed saproxylic beetles than unmanaged trees. We cannot confirm
362 or reject this hypothesis based on our study since the effects of pollarding in our material are difficult
363 to separate from the effects of high tree age. We do however find it reasonable to assume that
364 pollarding can speed up the formation of microhabitats, especially stem wounds and cavities, of
365 importance for certain species of wood-decaying fungi, and for lichenized fungi, and bryophytes (Fritz
366 & Heilmann-Clausen 2010). Consequently, one use for pollarding may be for ‘veteranization’ of
367 relatively young trees to produce trunk cavities and other microhabitats at an earlier age.

368

369 On the other hand, we cannot rule out that the same microhabitats would form with sufficient time also
370 without pollarding, especially in slopes with stones falling and injuring the trunks like at several of our
371 sites. Other microhabitats like deep bark fissures probably develop with age irrespective of pollarding.
372 The biggest tree in our dataset was an unmanaged elm (circumference 6.3 m), rich in microhabitats
373 and with high species richness, a very rare example which underlines the significance of tree age
374 regardless of pollarding. Re-pollarding of old trees (after a long halt in pollarding), or pollarding of old
375 trees with no previous pollarding may be associated with a risk. Drastic pollarding may lead to

376 increased, sometimes catastrophic, mortality (Vatne 2010; Lonsdale 2013), and their associated
377 lichenized fungi may be damaged (Vatne 2010). According to some authors, old trees should be (re-)
378 pollarded or subjected to crown-reduction to become less susceptible to breakage due to weight
379 imbalance, which would make them live longer than unmanaged trees (Moe & Botnen 1997, 2000;
380 Lonsdale 2013; Sjölund & Jump 2013). However, we found little evidence to corroborate this
381 hypothesis in the scientific literature.

382

383 *4.2 Species composition on pollarded and unmanaged trees*

384 Species compositions of lichenized fungi and bryophytes were both related to pollarding, and many
385 red-listed lichenized fungi species were mainly found on pollarded (older) trees. Together with tree
386 species, DCA 1 also represents a gradient of light availability in both cases since some typical light-
387 demanding lichenized fungi species from the *Parmelietum acetabuli* and *Xanthorion* communities
388 among the lichenized fungi, and several *Orthotrichum* species among the bryophytes (Barkman 1958)
389 are found to the right in the DCA charts.

390

391 For non-lichenized fungi, pollarding affected less and the communities on unmanaged (younger) trees
392 were apparently sub-sets of those on pollarded (older) trees, with most non-lichenized fungal species
393 being wood-decayers. These results may indicate that microhabitats developing with age are less
394 important for species composition of specialized non-lichenized fungi than for specialized lichenized
395 fungi and bryophytes.

396

397 The high number of species found exclusively on pollarded and unmanaged trees, respectively,
398 probably is a result of differences in microhabitats, with many lichenized fungi species on unmanaged
399 trees occurring on for example smooth bark (data not shown). The relatively high share of red-listed
400 species occurring on unmanaged trees (37 out of 49 species, including 11 species found exclusively on
401 unmanaged trees) may indicate that unmanaged trees can eventually replace the ancient pollarded trees
402 as habitat for rich epiphytic communities.

403

404 Non-lichenized fungi showed the strongest effect of dead wood and trunk cavities. However, among the
405 non-lichenized species found by us on living trunks mainly occur on fallen dead trees and no species is
406 unique to pollarded trees or even to old living trees (Hansen & Knudsen 1997, 2000; Knudsen &
407 Vesterholt 2012). We therefore surmise that pollarding is not crucial for the diversity of non-lichenized
408 fungi at our sites where dead wood is relatively common. Many of the bryophytes also have alternative
409 substrates, for example base-rich cliffs and boulders (Hallingbäck 2016), whereas most of the lichenized
410 fungi are strictly epiphytic (Smith et al. 2009).

411

412 *4.3 Conclusions and implications for management*

413 In the literature, the main threat to wooded meadows and their epiphytes is considered to be ceased
414 management leading to succession and closed woodland conditions (see Paltto et al. 2011, Johanson et
415 al. 2013 for epiphytes on *Quercus*, and Jönsson et al. 2011 for epiphytes on ash and elm). However,
416 we found little negative effect on the species communities of high crown cover (little visible sky in
417 summer). We suggest that the main threat is rather the risk that the old pollards will die before they are
418 replaced by other suitable trees in a closed forest close to the natural state. In cases where the age gap
419 between the old pollards and the re-growth trees is large, veteranization (pollarding of relatively young
420 trees) could be tried as a means to speed up microhabitat formation within reasonable distance from
421 source populations. In other cases, pollarding may not be necessary, and no intervention management
422 may be an option to sustain epiphyte populations.

423 Further studies should try to identify relict woodlands and there study the funga and flora and compare
424 it to ancient pollarded trees.

425

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427

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443

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445

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449

450 **7. References**

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562 Dutch Elm Disease on their Status. *The Lichenologist* 20: 327-352.

563

564 **Figures**

565

566

567 **Figure legends**

568

569 **Fig 1** Map of the 62 surveyed sites in Norway with climatic zones according to Moen (1999)

570

571 **Fig 2** Mean (\pm SE) number of species per tree on unmanaged and pollarded ash (*Fraxinus excelsior*)
572 and elm (*Ulmus glabra*) trees, totally, and of lichenized fungi, non-lichenized fungi and bryophytes
573 separately

574

575 **Fig 3a** DCA ordination plot of species composition of lichenized fungi on pollarded and unmanaged
576 trees of elm and ash **3b** DCA ordination of species. Some species names were slightly adjusted to
577 avoid overlap. Red-listed species in red. For full species names, see **App B**

578

579 **Fig 4a** DCA ordination plot of species composition of bryophytes on pollarded and unmanaged trees
580 of elm and ash **4b** DCA ordination of species. Some species names were slightly adjusted to avoid
581 overlap. Red-listed species in red. For full species names, see **App B**

582

583

584 **Fig 5a** DCA ordination plot of species composition of non-lichenized fungi on pollarded and
585 unmanaged trees of elm and ash. **5b** DCA ordination of species. Some species names were slightly
586 adjusted to avoid overlap. Red-listed species in red. For full species names, see **App B**

587

588

589 **Tables**

590

591 Table 1. Predictor variables collected for each sampled tree, with an explanation of the variable and
 592 mean \pm standard deviation for pollarded and unmanaged trees, pooled over tree species. Restricted
 593 maximum likelihood (REML), significance evaluated by likelihood-ratio tests with maximum
 594 likelihood (ML) in a backwards stepwise selection procedure. Tree circumference, cover of dead wood
 595 and maximum bark fissure depth log-transformed prior to analyses to reduce heteroscedasticity. The
 596 number of cavities was analysed with generalized linear mixed-effect models (GLMMs) with poisson
 597 distributed errors. * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Variable	Unit	Explanation	Value (mean \pm sd)
Circumference	cm	Measured at breast height (1.3 m above ground)	Poll.: 246.0 \pm 75.0 Unman.: 183.3 \pm 58.7 ***
Number of trunk cavities		Any hole enlarging inwards and at least as deep as broad	Poll.: 1.83 \pm 1.79 Unman.: 0.49 \pm 1.69 ***
Dead wood on trunk	%	Dead wood cover on trunk surface	Poll.: 4.6 \pm 10.6 Unman.: 2.2 \pm 5.8 ***
Bark fissure depth	mm	Maximum bark fissure depth	Poll.: 16.0 \pm 9.4 Unman.: 11.5 \pm 5.6 ***
Bryophyte cover – north	%	Percentage of bryophyte cover on the north side of the trunk	Poll.: 65.9 \pm 25.8 Unman.: 62.3 \pm 29.6
Bryophyte cover – south	%	Percentage of bryophyte cover on the south side of the trunk	Poll.: 43.2 \pm 28.7 Unman.: 47.4 \pm 30.3
Visible sky – north	%	Percentage of visible sky on the north side of the tree	Poll.: 20.4 \pm 15.1 Unman.: 17.0 \pm 15.8
Visible sky – south	%	Percentage of visible sky on the south side of the tree	Poll.: 19.7 \pm 13.9 Unman.: 17.2 \pm 13.9 *

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Table 3. Parameter estimates from GLMMs of species richness of all species (Total) and of each group separately as a function of pollarding, tree species and their interaction, n = 680 trees. Site (n = 62) was included as a random factor in all models. Models constructed with poisson distributed errors and site included as a random factor. Full model simplified using a backwards stepwise selection procedure with Chi-squared test and a significance level of $p < 0.05$ to keep a variable in the model, predictors centred and scaled, and variables standardized by one standard deviation. For analyses of species richness of non-lichenized fungi we used poisson distributed errors and zero-inflated data due to the many recordings of zero species. · $p \leq 0.10$, * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

<i>Parameter</i>	Total			Lichenized fungi			Non-lichenized fungi ^a			Bryophytes		
	<i>Est.</i>	<i>Std. dev.</i>	<i>p</i>	<i>Est.</i>	<i>Std. dev.</i>	<i>p</i>	<i>Est.</i>	<i>Std. dev.</i>	<i>p</i>	<i>Est.</i>	<i>Std. dev.</i>	<i>p</i>
Intercept	2.573	0.062		1.788	0.091		-2.113	0.270		1.928	0.077	
Pollarding	0.106	0.056	·	-0.013	0.084		0.835	0.319	*	0.172	0.073	*
Tree species – elm	0.015	0.072		-0.246	0.109	*	1.754	0.296	**	0.060	0.091	
Pollarding × tree species	-0.055	0.083		0.044	0.125		-0.576	0.364		-0.110	0.110	

610 ^aAnalysis of species richness of non-lichenized fungi with glmm with zero-inflation.

611

612 Table 4. Parameter estimates from GLMMs of species richness each group separately as a function of
613 tree characteristics. Only predictor variables with a significant contribution are included in the models.
614 Predictor variables were centred and scaled prior to analyses. n = 680 trees. Site (n = 62) was included
615 as a random factor in all models. Models constructed as GLMMs with poisson distributed errors and
616 site included as a random factor. Full model simplified using a backwards stepwise selection
617 procedure with Chi-squared test and a significance level of $p < 0.05$ to keep a variable in the model,
618 predictors centred and scaled, and variables standardized by one standard deviation. For analyses of
619 species richness of non-lichenized fungi we used poisson distributed errors and zero-inflated data due
620 to the many recordings of zero species. $\cdot p \leq 0.10$, * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

<i>Parameter</i>	Lichenized fungi			Non-lichenized fungi			Bryophytes		
	<i>Est.</i>	<i>Std. dev.</i>	<i>p</i>	<i>Est.</i>	<i>Std. dev.</i>	<i>p</i>	<i>Est.</i>	<i>Std. dev.</i>	<i>p</i>
Intercept	1.638	0.060		-0.875	0.142		2.021	0.047	
Dead wood				0.118	0.044	**			
No. of cavities				0.073	0.024	**			
Bark fissure depth	0.057	0.023	*	0.184	0.047	***			
Bryophyte cover N	-0.063	0.025	*				0.062	0.019	***
Bryophyte cover S	0.053	0.023	*						

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622

623 Table 5. a) Parameter estimates from GLMMs of species richness of all red-listed species (Total) and
624 of red-listed lichenized fungi and non-lichenized fungi as a function of pollarding, tree species and
625 their interaction. n = 680 trees. b) Parameter estimates from GLMMs of species richness of all red-
626 listed species (Total) and of red-listed lichenized fungi and non-lichenized fungi as a function of tree
627 characteristics. Only predictor variables with a significant contribution are included in the models.
628 Predictor variables were centred and scaled prior to analyses. Site (n = 62) was included as a random
629 factor in all models. GLMMs with poisson distributed errors and site included as a random factor. Full

630 model simplified using a backwards stepwise selection procedure with Chi-squared test and a
631 significance level of $p < 0.05$ to keep a variable in the model, predictors centred and scaled, and
632 variables standardized by one standard deviation. For analyses of species richness of non-lichenized
633 fungi we used poisson distributed errors and zero-inflated data due to the many recordings of zero
634 species. $\cdot p \leq 0.10$, $* p \leq 0.05$, $** p \leq 0.01$, $*** p \leq 0.001$.

a)	Total			Lichenized fungi ^a			Non-lichenized fungi a		
	<i>Est.</i>	<i>Std.</i> <i>dev.</i>	<i>p</i>	<i>Est.</i>	<i>Std.</i> <i>dev.</i>	<i>p</i>	<i>Est.</i>	<i>Std.</i> <i>dev.</i>	<i>p</i>
Intercept	-1.34 2	0.236		-1.96 0	0.288		-2.325	0.337	
Pollarding	0.695	0.274	***	0.801	0.330	***	0.632	0.412	
Tree species – elm	1.118	0.275	***	1.020	0.338	***	1.160	0.373	***
Pollarding × tree species	0.005	0.328		0.309	0.400		-0.276	0.476	
b)									
Intercept	-0.41 5	0.133		-1.00 2	0.161		-1.382	0.154	
Circumference	0.116	0.049	*	0.102	0.061		0.150	0.079	
No. of cavities	0.068	0.021	**	0.092	0.027	***			
Bark fissure depth	0.152	0.043	***	0.174	0.053	***	0.170	0.075	*

635 ^a Analysis glmm with zero-inflation.

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637

638 *Table 6.* Results of linear mixed-effect models of a) lichenized fungi, b) bryophyte, and c) non-
639 lichenized fungi species composition, recorded as tree score along DCA axis 1 and 2, as a function of
640 pollarding, tree species and the interaction between pollarding and tree species. Significance of

641 parameter estimates is evaluated with likelihood-ratio tests in a backwards stepwise selection
 642 procedure (see the main text for details). In all models *Fraxinus* and unmanaged are used as contrasts.
 643 Tree (n = 680) nested in site (n = 62) are included as random factors in all models.

644 a)

<i>Parameter</i>	<i>Estimate</i>	<i>Standard deviation</i>	<i>p</i>
<i>DCA 1</i>			
<i>Intercept</i>	0.433	0.140	
<i>Pollarding</i>	-0.519	0.118	< 0.001
<i>Tree species – elm</i>	-0.131	0.157	0.210
<i>Pollarding × tree species</i>	-0.193	0.173	0.257
<i>DCA 2</i>			
<i>Intercept</i>	-0.343	0.112	
<i>Pollarding</i>	0.059	0.096	0.121
<i>Tree species – elm</i>	0.746	0.126	< 0.001
<i>Pollarding × tree species</i>	0.120	0.140	0.382

645

646 b)

<i>Parameter</i>	<i>Estimate</i>	<i>Standard deviation</i>	<i>p</i>
<i>DCA 1</i>			
<i>Intercept</i>	0.063	0.116	
<i>Pollarding</i>	-0.257	0.082	0.010
<i>Tree species – elm</i>	0.212	0.118	0.031
<i>Pollarding × tree species</i>	0.221	0.122	0.070
<i>DCA 2</i>			
<i>Intercept</i>	0.354	0.084	
<i>Pollarding</i>	-0.404	0.084	< 0.001

<i>Tree species – elm</i>	–0.315	0.101	0.009
<i>Pollarding × tree species</i>	0.080	0.119	0.503

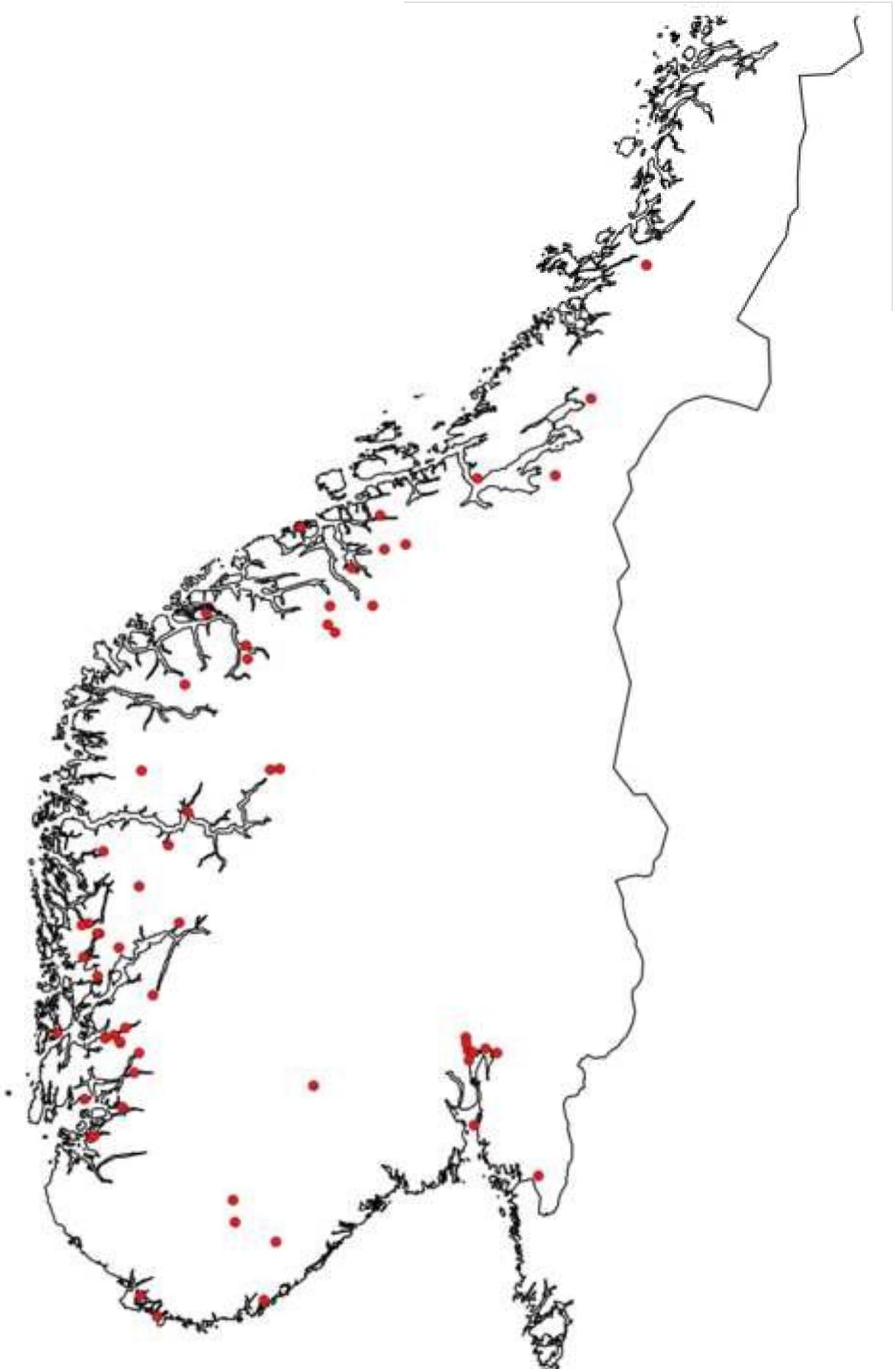
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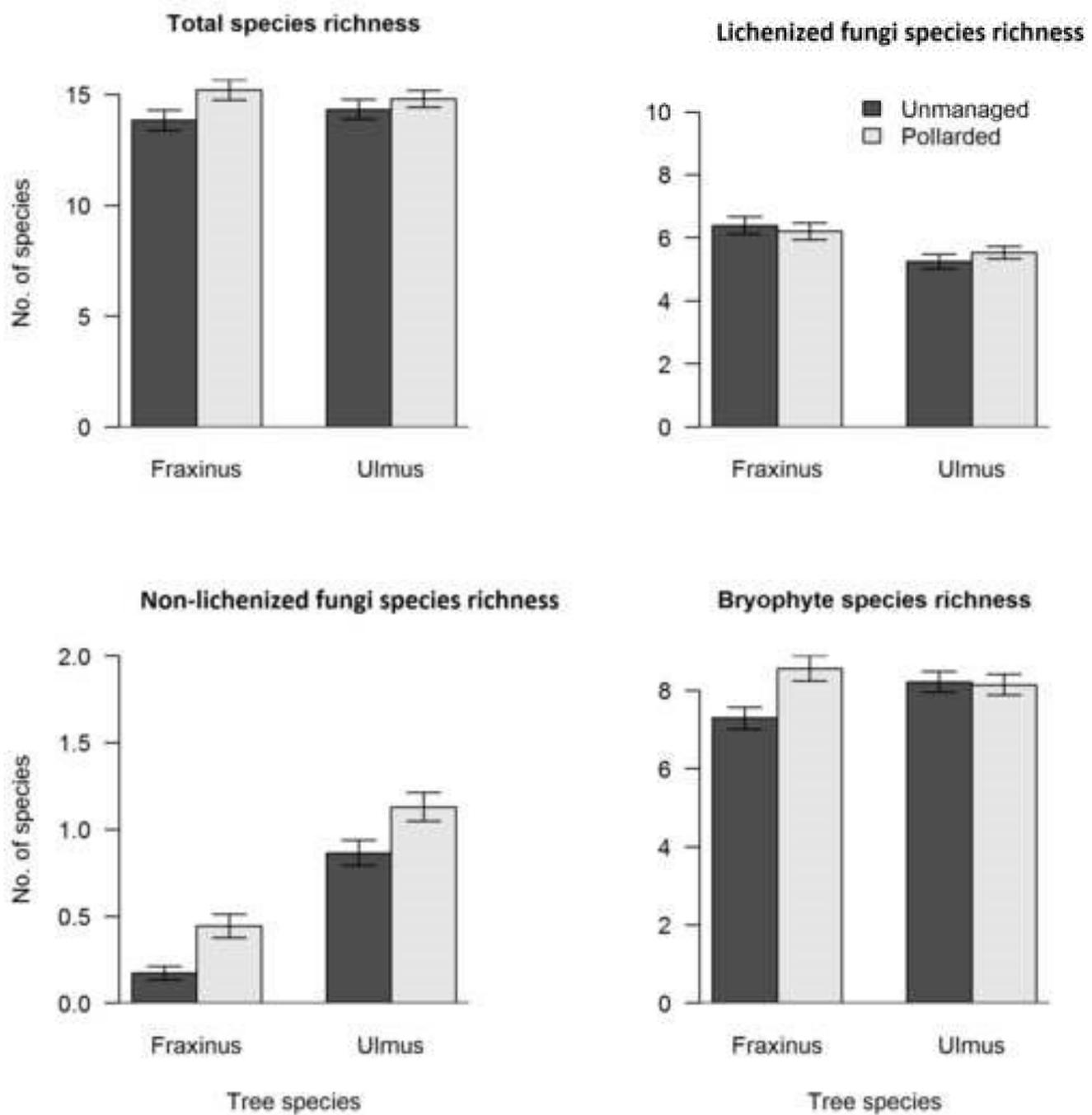
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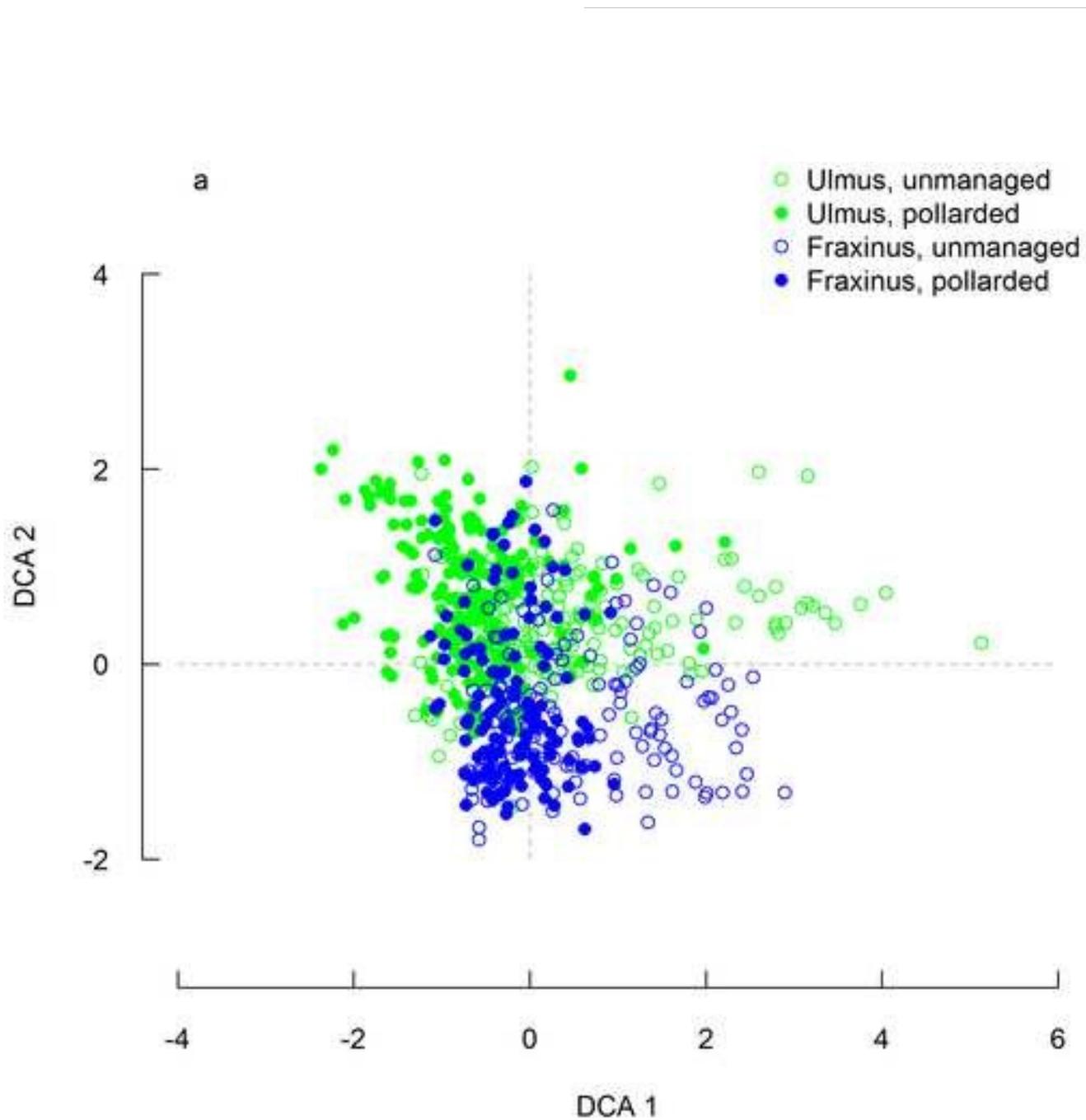
<i>Parameter</i>	<i>Estimate</i>	<i>Standard deviation</i>	<i>p</i>
<i>DCA 1</i>			
<i>Intercept</i>	2.167	0.147	
<i>Pollarding</i>	–0.156	0.172	0.346
<i>Tree species – elm</i>	–3.176	0.179	< 0.001
<i>Pollarding × tree species</i>	0.462	0.224	0.039
<i>DCA 2</i>			
<i>Intercept</i>	0.109	0.199	
<i>Pollarding</i>	–0.236	0.230	0.978
<i>Tree species – elm</i>	–0.231	0.242	0.885
<i>Pollarding × tree species</i>	0.393	0.300	0.223

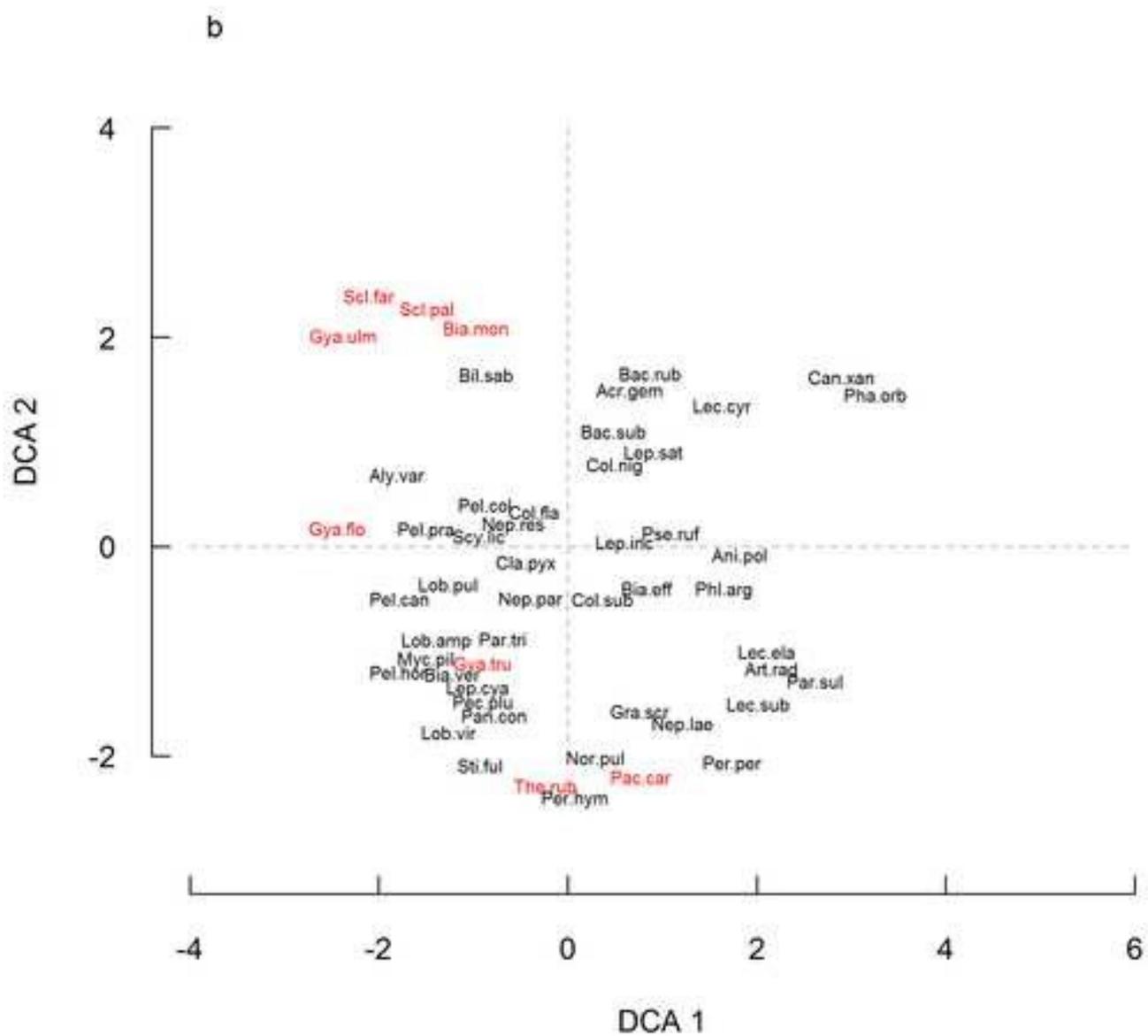
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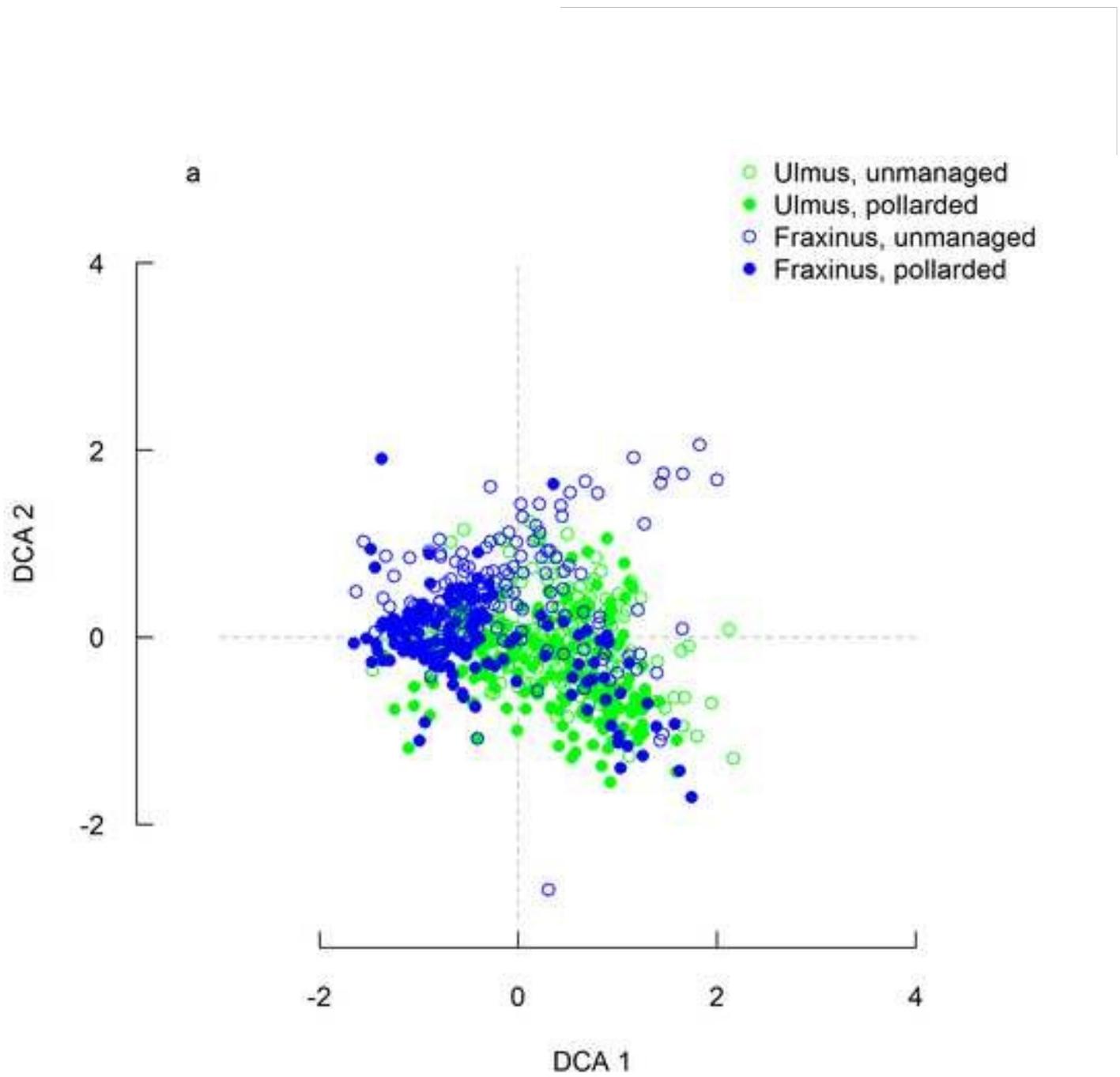
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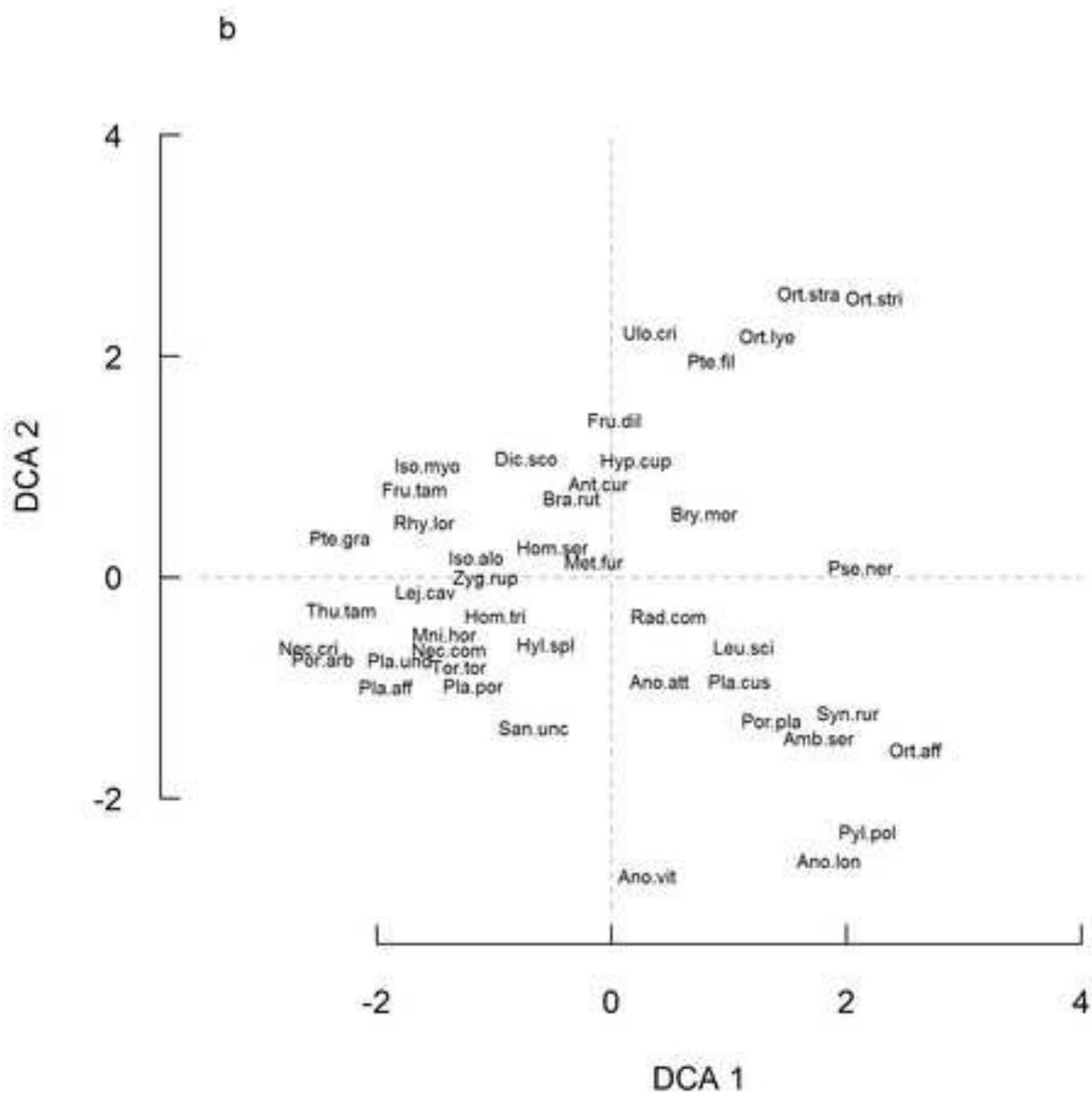


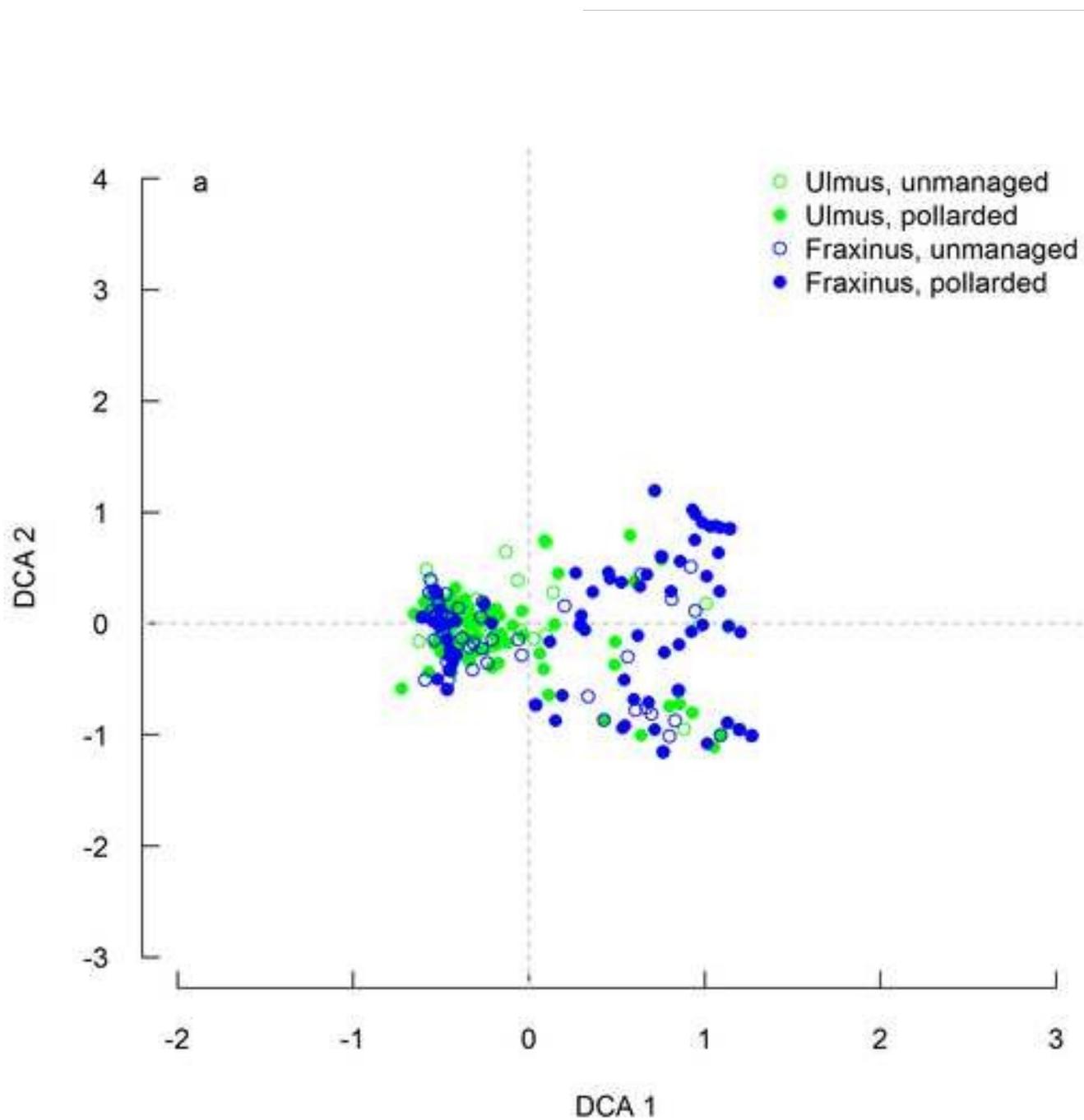


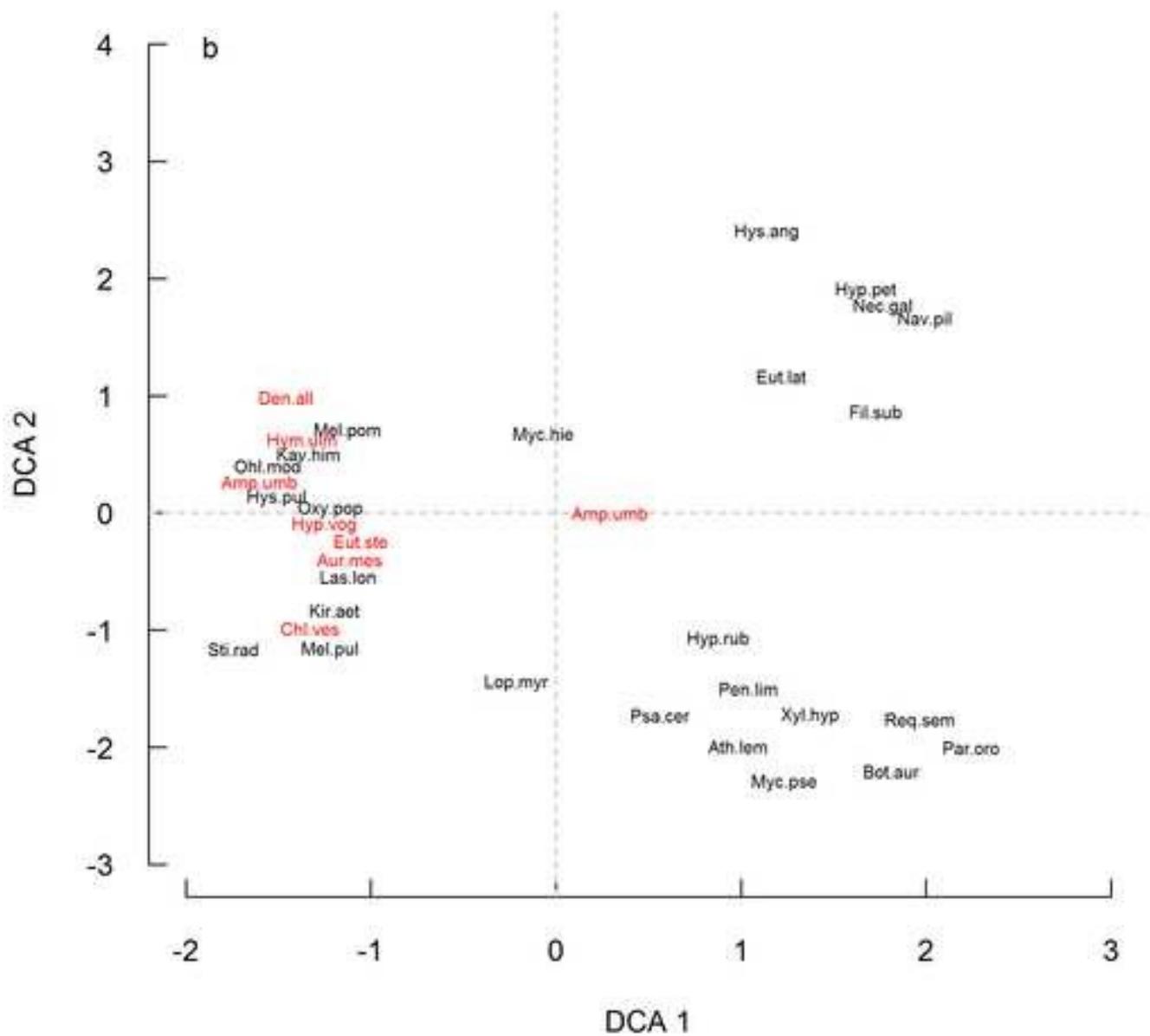










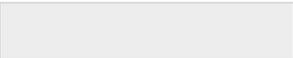


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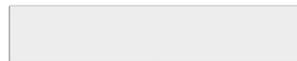


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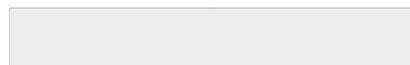
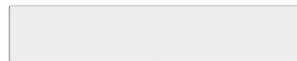


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