

## Biodiversity and Conservation

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

--Manuscript Draft--

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

**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.



## 9    **Abstract**

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11    biodiversity. While traditional methods are often advocated, such practices may incur considerable  
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29    ecological restoration.

30

## 1. Introduction

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

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

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

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

## 2. Materials and Methods

### 2.1 Site selection

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

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

[Insert Fig. 1.]

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

## 2.2 Studied organisms

The epiphytic communities on elm and ash in northern Europe are dominated by bryophytes and lichenized fungi, including many red-listed species (Jönsson et al. 2011). In addition, many fungi with 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



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

#### *2.4 Data analysis*

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

As a second step we investigated the importance of pollarding and tree species for species richness. We constructed generalized linear mixed-effect models with pollarding, tree species and their

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

Thirdly, to increase our understanding of important tree characteristics for species richness, we explored the relationship between tree circumference, number of cavities, cover of dead wood, bark fissure depth, and cover of bryophytes, and species richness of lichenized fungi, non-lichenized fungi, and bryophytes. Tree species and pollarding (correlated to tree characteristics) were left out of this analysis. We constructed a full model including all predictor variables and simplified the full model 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. As the scale of the predictors varied considerably (Table 1), we centred and scaled all predictor variables prior to analysis (Nakagawa and Cuthill 2007; Schielzeth 2010) and standardised the variables by one standard deviation, as recommended by Schielzeth (2010). This facilitates the interpretation of the relative importance of the predictors in the model. All models were constructed as GLMMs with poisson distributed errors and site included as a random factor.

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

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

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

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

### 3. Results

#### 3.1 Pollarded vs. unmanaged trees

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

[Insert Table 1]

#### 3.2 Species richness

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

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

Thirty-eight species of lichenized fungi (18%), 53 species of non-lichenized fungi (41%), and 26 species of bryophytes (23%) occurred exclusively on pollarded trees. The corresponding numbers for species only found on unmanaged trees were: lichenized fungi 65 species (31%), non-lichenized fungi 30 (23%), and bryophytes 24 (21%).

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

[Insert Figure 2]

[Insert Table 3]

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

[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 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]

### 3.4 Species composition

A total of 103 species of lichenized fungi, of which 18 red-listed, were present on  $\geq 5$  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  $\geq 5$  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]

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

[Insert Fig 5a, b]

#### 4. Discussion

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

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

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

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

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

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

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

#### *4.2 Species composition on pollarded and unmanaged trees*

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

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

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

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

#### *4.3 Conclusions and implications for management*

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

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

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## Figures

### Figure legends

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

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

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

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

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

## Tables

Table 1. Predictor variables collected for each sampled tree, with an explanation of the variable and mean  $\pm$  standard deviation for pollarded and unmanaged trees, pooled over tree species. Restricted maximum likelihood (REML), significance evaluated by likelihood-ratio tests with maximum likelihood (ML) in a backwards stepwise selection procedure. Tree circumference, cover of dead wood and maximum bark fissure depth log-transformed prior to analyses to reduce heteroscedasticity. The number of cavities was analysed with generalized linear mixed-effect models (GLMMs) with poisson 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. ·  $p \leq 0.10$ , \*  $p \leq 0.05$ , \*\*  $p \leq 0.01$ , \*\*\*  $p \leq 0.001$ .

	Total			Lichenized fungi			Non-lichenized fungi <sup>a</sup>			Bryophytes		
<i>Parameter</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>	<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	

<sup>a</sup>Analysis of species richness of non-lichenized fungi with glmm with zero-inflation.

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Table 4. Parameter estimates from GLMMs of species richness each group separately as a function of tree characteristics. Only predictor variables with a significant contribution are included in the models. Predictor variables were centred and scaled prior to analyses. n = 680 trees. Site (n = 62) was included as a random factor in all models. Models constructed as GLMMs 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.  $\cdot p \leq 0.10$ , \*  $p \leq 0.05$ , \*\*  $p \leq 0.01$ , \*\*\*  $p \leq 0.001$ .

	Lichenized fungi			Non-lichenized fungi			Bryophytes		
<i>Parameter</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	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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Table 5. a) Parameter estimates from GLMMs of species richness of all red-listed species (Total) and of red-listed lichenized fungi and non-lichenized fungi as a function of pollarding, tree species and their interaction. n = 680 trees. b) Parameter estimates from GLMMs of species richness of all red-listed species (Total) and of red-listed lichenized fungi and non-lichenized fungi as a function of tree characteristics. Only predictor variables with a significant contribution are included in the models. Predictor variables were centred and scaled prior to analyses. Site (n = 62) was included as a random factor in all models. GLMMs 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.  $\cdot p \leq 0.10$ , \*  $p \leq 0.05$ , \*\*  $p \leq 0.01$ , \*\*\*  $p \leq 0.001$ .

a)	Total			Lichenized fungi <sup>a</sup>			Non-lichenized fungi <sup>a</sup>		
<i>Parameter</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	-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	$\cdot$
Tree species – elm	1.118	0.275	***	1.020	0.338	***	1.160	0.373	***
Pollarding $\times$ 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	$\cdot$	0.150	0.079	$\cdot$
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	*

<sup>a</sup> Analysis glmm with zero-inflation.

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

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

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

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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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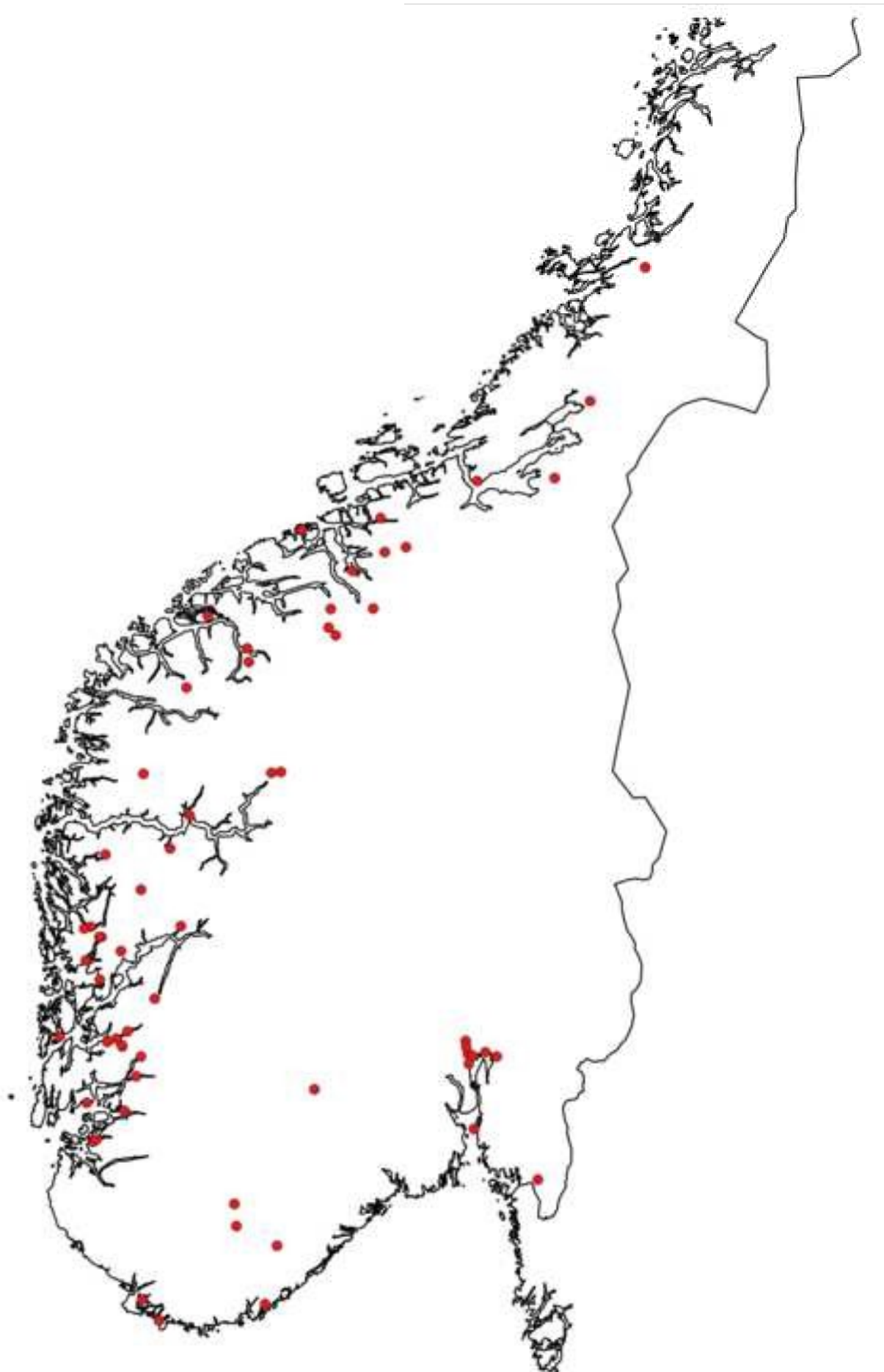
648 c)

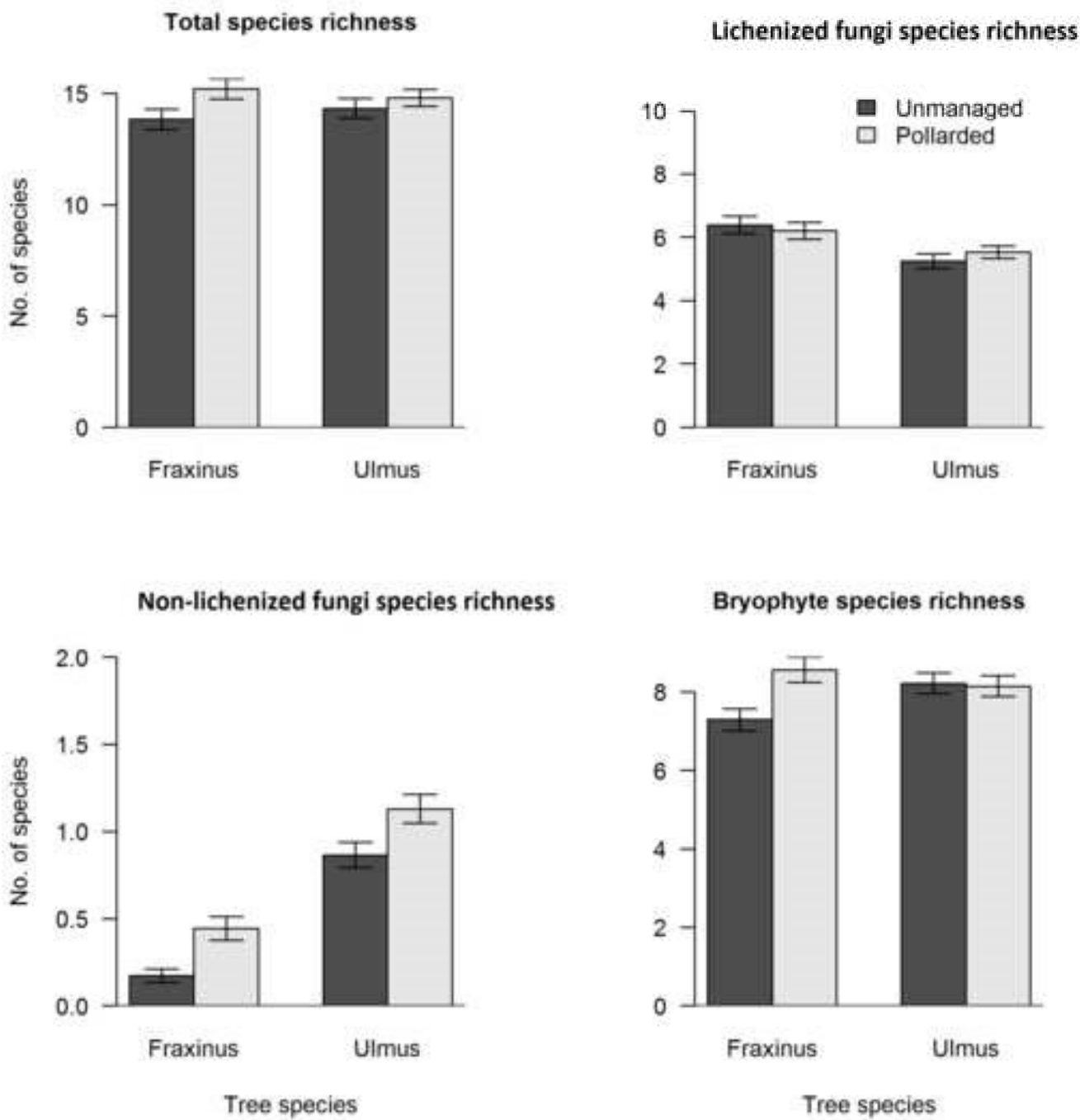
<i>Parameter</i>	<i>Estimate</i>	<i>Standard deviation</i>	<i>p</i>
<i>DCA 1</i>			
<i>Intercept</i>	2.167	0.147	
<i>Pollarding</i>	–0.156	0.172	0.346
<i>Tree species – elm</i>	–3.176	0.179	< 0.001
<i>Pollarding × tree species</i>	0.462	0.224	0.039
<i>DCA 2</i>			
<i>Intercept</i>	0.109	0.199	
<i>Pollarding</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

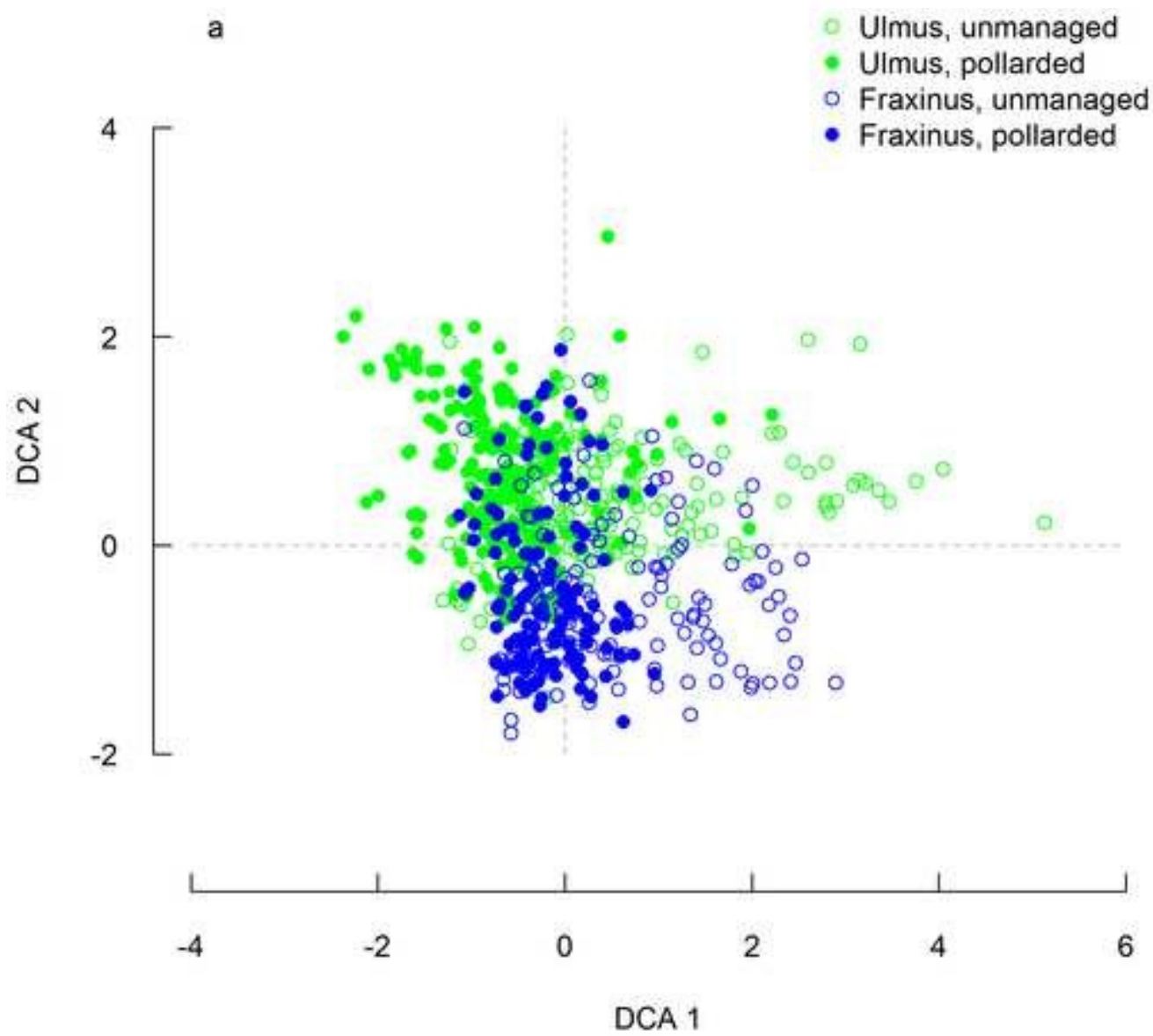
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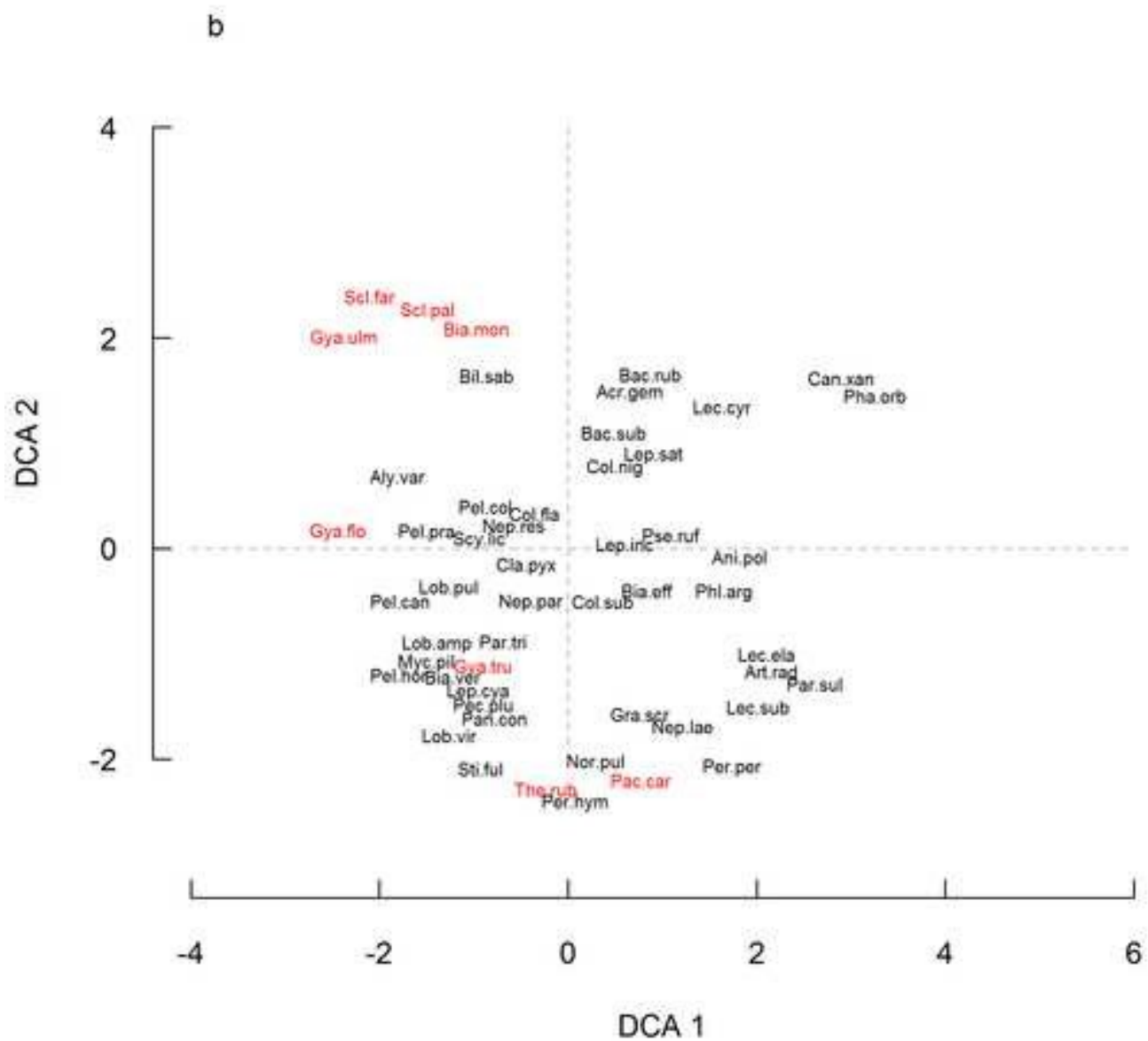
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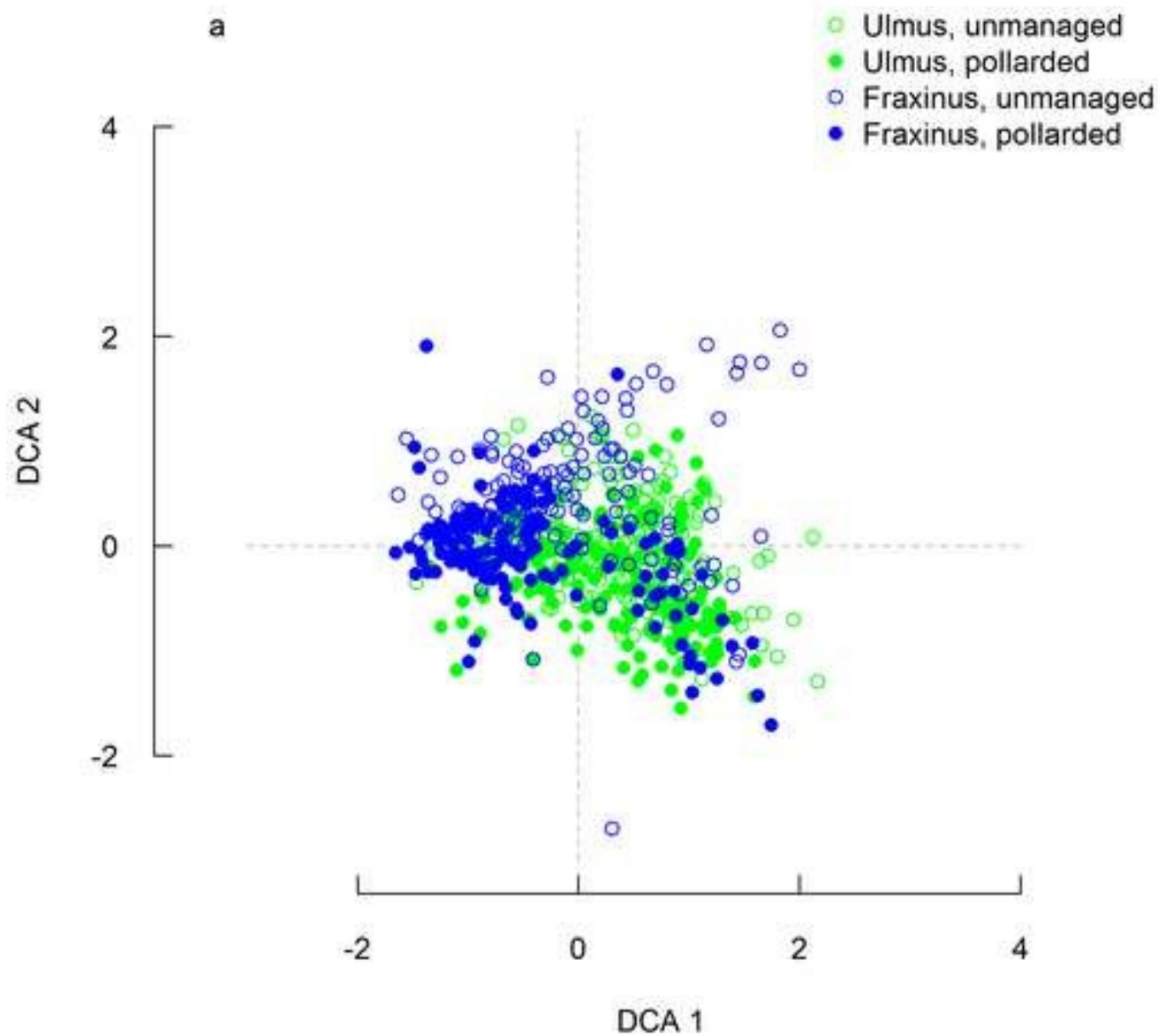


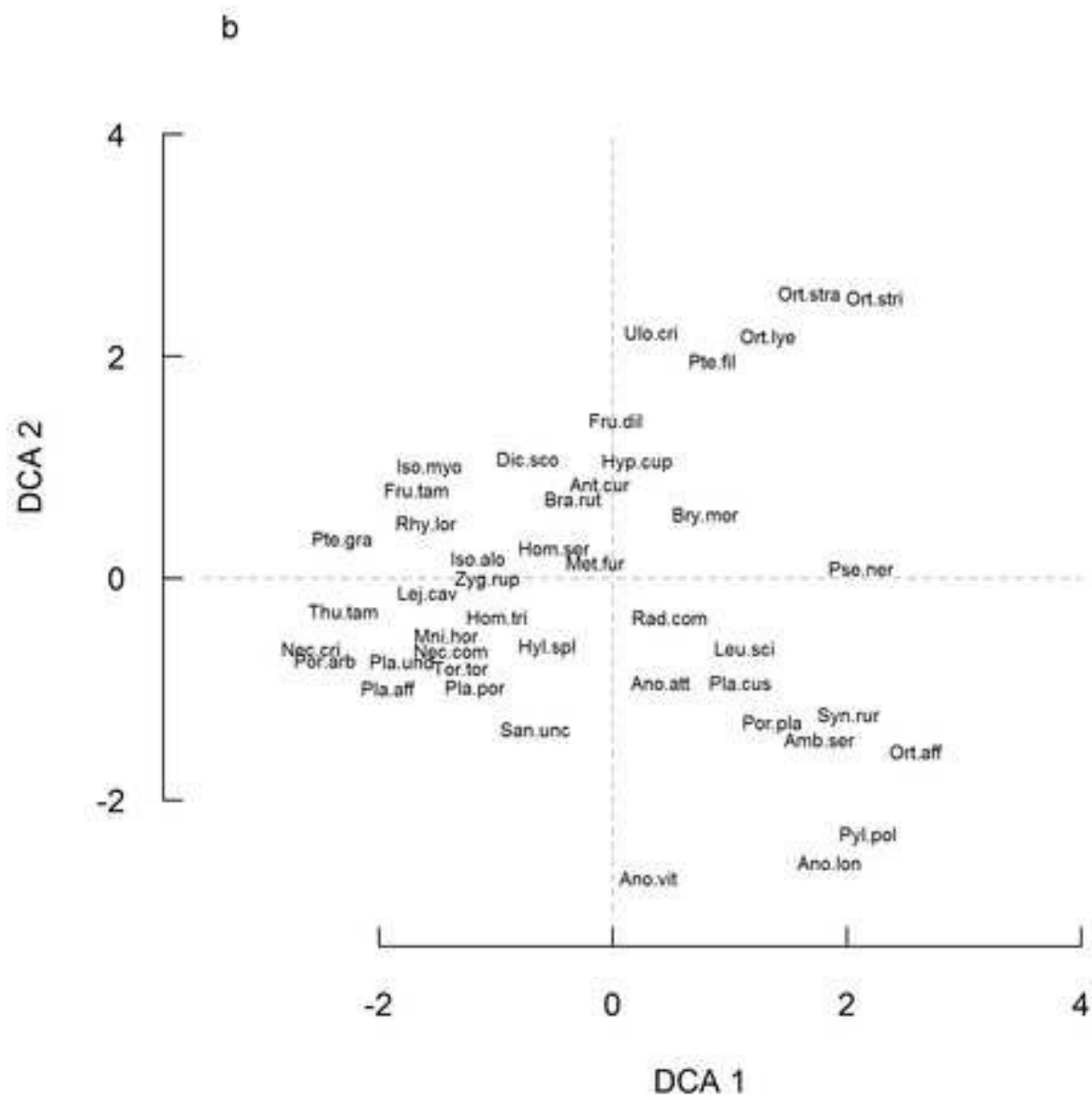


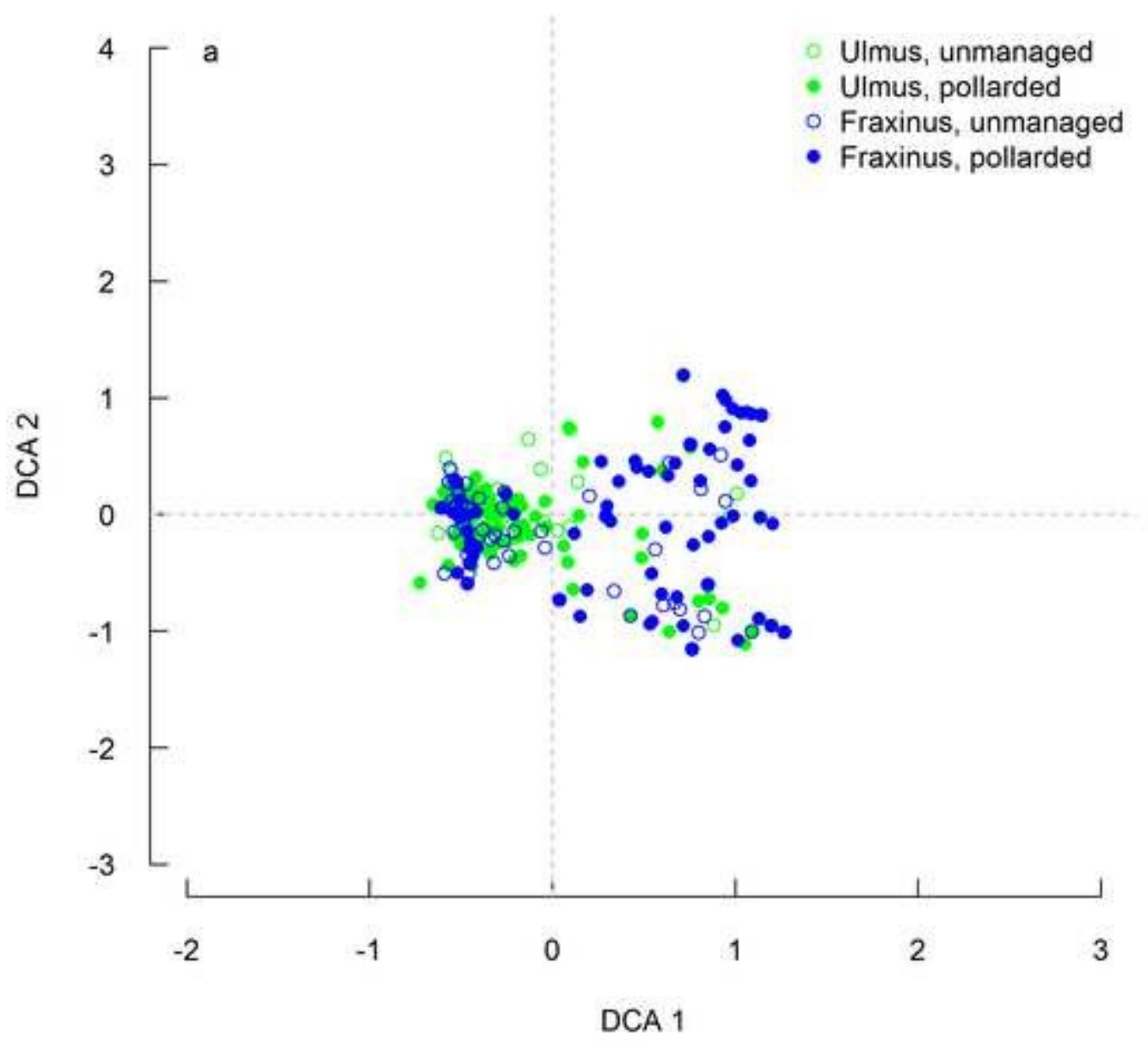


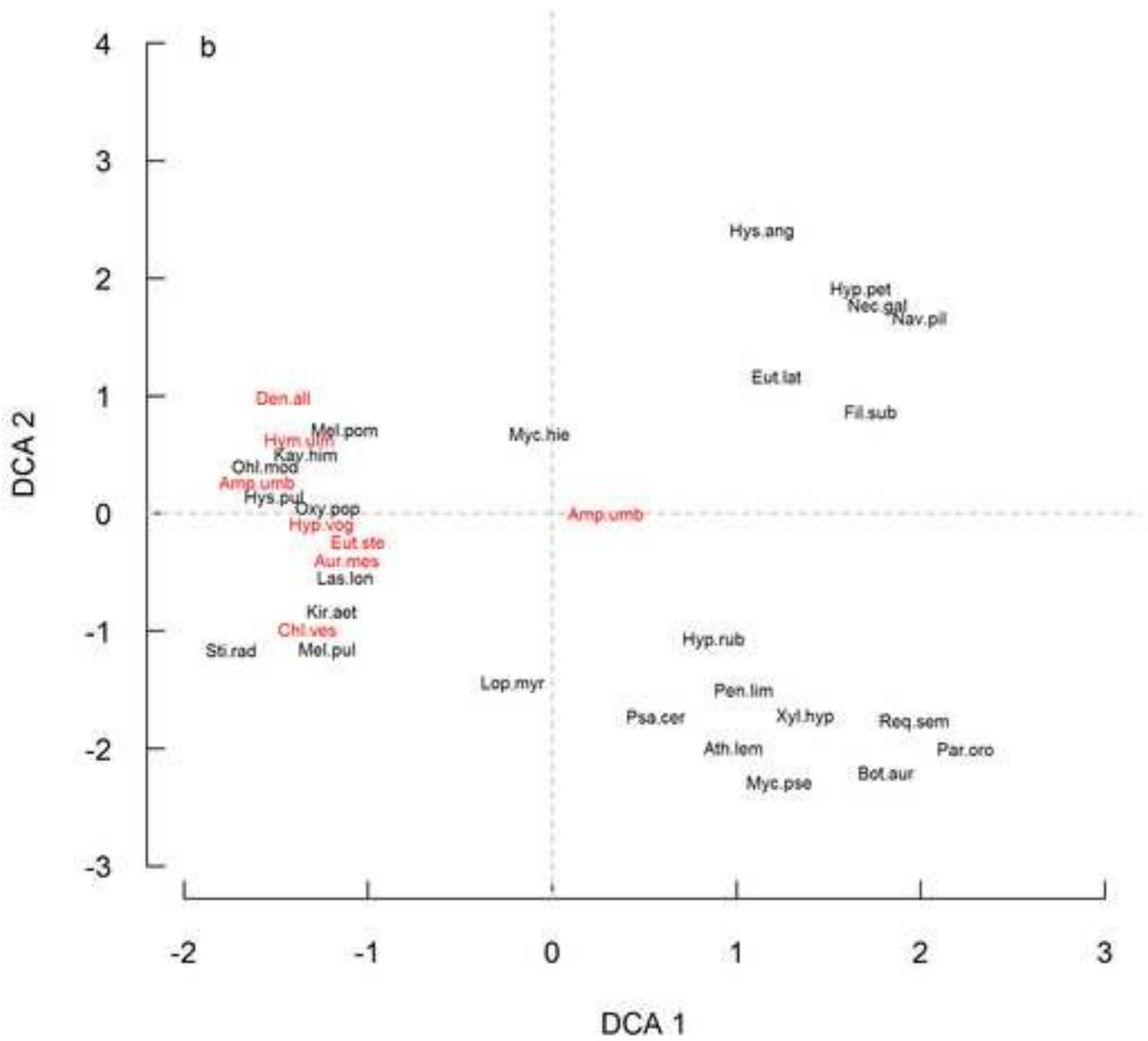














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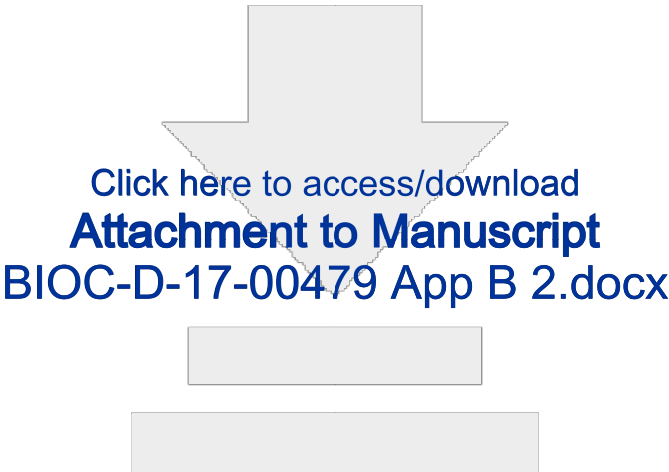
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