1 **Modern pollen-vegetation relationships in traditionally mown and**

2 **unmanaged boreal rich-fen communities in central Norway**

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16

20 **Abstract**

21 Knowledge of the relationship between vegetation and modern pollen deposition is necessary

22 to improve the interpretation of fossil pollen samples. We compared the cover of plant species

23 and the modern pollen deposition in surface moss samples in 49 plots in rich-fen vegetation

24 from the boreal vegetation zone in Norway in two areas (one oceanic and one more

25   continental). These rich fens were used for traditional hay cutting until ca. 1950. Three

26   management regimes are used: 1) biennial mowing 2) quadrennial mowing and 3) unmown.

27   The unmown areas were traditional hay fens, with no management since the 1950s. Of the 89

28   plant taxa and corresponding 65 taxa of pollen and spores, 29 and 22, respectively, were

29   sufficiently represented in both vegetation and as pollen, to allow direct comparisons of the

30   two data sets. Most of the plant and pollen taxa were found in the plots from both study areas

31   and in plots with different mowing frequency. Therefore, quantitative differences in

32   vegetation cover and pollen percentages were the main focus in this investigation of plant-

33   pollen relationships in mown and unmown vegetation. The relative difference in plant cover

34   was largest between biennially and unmown plots. 12 species showed a significant positive

35   correlation with difference in plant cover between mown and unmown areas ($p<0.05$;

36   Wilcoxon signed rank test), most pronounced for *Molinia caerulea* (most common in

37   unmown plots), and *Carex dioica* and *Thalictrum alpinum* (most common in mown plots). A

38   significant positive plant-pollen correlation (Spearman rank-correlation) was found for 10

39   pollen taxa. *Thalictrum alpinum* is a very good pollen indicator, and Cyperaceae,

40   *Eriophorum*-type and *Pedicularis*-type are good pollen indicators of mowing.

41   Poaceae/*Molinia caerulea* and *Succisa pratensis* are negatively correlated with mowing. The

42   impact of mowing on species composition was similar in both study areas. Mown and

43   unmown areas were differentiated in the vegetation data and could be identified by modern

44   pollen data. These results will improve the interpretation of past land-use practices using

45   pollen analysis of rich-fen vegetation.

46   **1. Introduction**

47   All over northern Europe fens have, for centuries, been important for production of hay for

48   winter fodder. The fertile infields were often of limited extent, so the outfields were of great

49   importance for haymaking, grazing and summer farming (e.g. Ellenberg, 1988; Hjelle et al.,

50   2012; Solem et al., 2012). This long-term regular harvesting has influenced the fens, turning

51   large areas into open semi-natural landscapes. The traditional use of the fens ceased many

52   decades ago in most countries in western and central Europe, including southern

53   Fennoscandia. In parts of central boreal Norway the traditional use of fens, including our

54   study areas, lasted until the 1950s (Moen, 1990; Tretvik and Krogstad, 1999).

55

56   Cultural landscapes leave contemporaneous traces in the form of pollen assemblages in

57   accumulating deposits. Pollen analysis is thus a widely used approach for reconstructing the

58   history of past cultural practices and landscapes (e.g. Berglund, 1991). Investigations of the

59   modern local plant-pollen relationship in areas with documented land-use regimes are a basis

60   for reconstructing these practices back in time. The taphonomy of pollen in modern moss

61   samples is comparable to pollen analytical data from peat cores. Pollen assemblages from

62   vegetation dominated by dwarf-shrubs, graminoids or herbs reflect local sources of non-tree

63   pollen (NAP) and thus small-scale vegetation variations (Hjelle, 1999a; Bunting 2003;

64   Bunting and Hjelle, 2010; Pardoe, 1996). The relationship between number of deposited

65   pollen grains and the corresponding plant cover is complex (e.g. Sugita, 1994), and the pollen

66   taphonomy must be taken into account when interpreting pollen assemblages (e.g. Fægri and

67   Iversen, 1989).

68

69   Mowing leads to disturbance and changes in available resources and competition between

70   species (Crawley, 1997; Grime, 2001). Species resilient to mowing will be favoured and

71   plants with low and rosette growth forms, with meristems close to the ground or clonal

72   growth, are tolerant to mowing (Klimešová et al., 2008). In addition, stress-tolerant species

73   are less affected by mowing (Grime, 2001; Øien & Moen, 2001). Thus mowing affects the

74   composition of vegetation and species abundance. For example the plant cover of *Thalictrum*

75 *alpinum* and several *Carex* and *Eriophorum* species increases with mowing in boreal fens

76 (Moen, 1995).

77

78 In order to reconstruct past vegetation communities from pollen data the relationship between

79 the vegetation community and the pollen produced and deposited within it must be known. If

80 good pollen–plant relationships exist and the plant community is reflecting a type of land use

81 today, pollen types/species may be identified as indicator taxa for that land-use (cf. Behre

82 1981). The present study aims to produce indicator taxa for mown fens which may be of

83 international value when interpreting pollen diagrams. Also the whole pollen assemblage may

84 be used in a comparative approach (Birks and Birks, 1980) to aid in the identification of past

85 vegetation communities or land-use practices. The results from the present study will be

86 combined with plant-pollen data from mown and grazed vegetation types in Western Norway

87 (Hjelle, 1999a) to form a larger data set. This data will aid the interpretation of possible land-

88 use practices (e.g. Gaillard et al., 1994; Hjelle, 1999b) for pollen diagrams from the rich fens

89 in Tågdalen and Sølendet. The data set should also be useful as part of future pollen–plant

90 databases, e.g. the European Pollen Database

91 (http://www.europeanpollendatabase.net/index.php).

92

93 The aim of the present study is to assess the modern pollen–plant relationships in rich fens in

94 two study areas. The areas are situated at the transition between the middle and northern

95 boreal vegetation zones, but in different vegetation sections (regional differences oceanity–

96 continentality, Moen 1999). Both study areas were used for traditional haymaking until ca.

97 1950. Regular mowing (with a scythe) of permanent plots was reintroduced in early 1970s

98 and they have been mown regularly for nearly 40 years. The plant communities vary between

99 the study areas, but with the same dominant species, where the impact of mowing on different

100   species is similar (Moen et al., 2012). Further, differences between mowing regimes and

101   unmown areas facilitate various species, giving mainly quantitative differences in plant cover

102   (Moen et al., 2012). We study the correlation between the plants growing in fen vegetation

103   and pollen deposited on a local scale. Three hypotheses are thus put forward: 1) There is a

104   close connection between the taxa in fen vegetation and local pollen deposition, 2) There are

105   small differences in local pollen–plant relationships between the two studied rich fens

106   (regional differences), and 3) Differences between mown and unmown vegetationcan be

107   detected from the contemporary pollen assemblages. The modern plant–pollen relationship in

108   fens will provide a basis for interpretations of palaeoecological investigations of past land-use

109   in the study areas.

110   **2. Study areas and plant communities**

111   The two study areas (Fig. 1) are both situated at the transition between the middle boreal and

112   northern boreal vegetation zones of central Norway (Moen, 1999). Tågdalen is an oceanic

113   inner-fjord area nature reserve and Sølendet is a continental nature reserve. Tågdalen is part of

114   the markedly oceanic vegetation section while Sølendet is situated on the transition between

115   the indifferent and slightly continental vegetation sections (sensu Moen, 1999). The 20

116   localities with 49 study plots presented in this paper were established as permanent plots 40

117   years ago, and vegetation and plant populations dynamics are described in a number of papers

118   (e.g. Moen, 1990, 1995, 2000; Aune et al., 1996; Moen et al., 1999, 2012, 2015; Øien and

119   Moen, 2001; Sletvold et al., 2010; Lyngstad et al., 2016). 10 localities are situated along a line

120   over a distance of 940 m in Tågdalen (Fig. 2a). In Sølendet the 10 localities are situated in an

121   area of just below 1 km^2 (Fig. 2b).

122

123   The duration of the growing season is similar in both areas, from the end of May until the first

124   part of September. Tågdalen has an oceanic climate with high annual precipitation and a

125 thick, long-lasting snow cover, while Sølendet has a more continental climate with less

126 precipitation and cold winters (Table 1). The distance between the study areas is 145 km. In

127 both areas calcareous Cambro-Silurian bedrock (Sigmond et al., 1984) is overlaid with base-

128 rich till (Follestad, 1995).

129

130 The dominant rich-fen vegetation at Tågdalen and Sølendet forms a mosaic with birch

131 woodland (*Betula pubescens*). Sloping fens (slope >3°) cover large areas. At Tågdalen the

132 slopes are between 3 and 12° and at Sølendet 3 to 5°. The depth of the underlying peat layer

133 exceeds 50 cm at Tågdalen, and 20 cm at Sølendet. The study areas have the same historical

134 land-use, where the traditional hay cutting declined during the 1930s, and ended in the 1950s.

135 Experimental scything (hereafter called mowing) of permanent plots started in 1973 and was

136 carried out in August, allowing flowering, seed production and dispersal to take place for

137 important species. The localities were established in homogenous fen areas, and the studied

138 plots have been mown regularly biennially or quadrennially since 1970s, or they have been

139 left unmown for ca. 60 years. The hay crop of the studied communities was estimated to about

140 110 g/m^2 and 140 g/m^2 (dry matter) in plots mown biennially and quadrennially, respectively

141 (Moen, 1990; Moen et al., 2015; Lyngstad et al., 2016). Biennial mowing represents the

142 traditional practice, where the harvest output was maximized in relation to labour invested.

143 Quadrennial mowing is a possible equivalent to the mowing frequency during periods of

144 extensive mowing, and during the period when hay-cutting was declining.

145

146 The terminology of mires follows the Fennoscandia tradition in mire ecology (*sensu* Sjörs,

147 1948), separating units related to the main local vegetation gradients. Rich fens are peat-

148 forming mire sites with characteristic vegetation dominated by brown mosses (e.g.

149 *Campylium stellatum*), and with base-rich water (pH above 6). Lawn communities of

extremely rich fen vegetation (Sjörs, 1948; Moen et al., 2012; Jiménez-Alfaro et al., 2013)

cover the study localities. Phytosociological analyses of the permanent study plots were

included in multivariate analyses of 134 rich fen plots from the two study areas (Moen et al.,

2012; the plots in this paper mainly belong to their communities II – IV). In the

phytosociological classification system (e.g. Dierssen, 1982; Rybniček, 1985), the studied

mires belong to the alliances Caricion davalianae Klinka 1934 at Tågdalen, and at Sølendet

Caricion atrofuscae Nordh. 1936. The mean number of species in plots with an area of 12.5

m^2 ranged between 30 and 37 (Table 2 and Supplementary A in Moen et al., 2012). The most

common vascular plant species in both areas are *Andromeda polifolia*, *Dactylorhiza* spp.,

Equisetum palustre, *Euphrasia wettsteinii*, *Parnassia palustris*, *Pinguicula vulgaris*,

Potentilla erecta, *Selaginella selaginoides*, *Succisa pratensis*, *Thalictrum alpinum*, *Tofieldia*

pusilla, *Carex dioca*, *C. flava*, *C. hostiana*, *C. lasiocarpa*, *C. panicea*, *C. rostrata*,

Eriophorum angustifolium, *E. latifolium*, *Molinia caerulea* and *Trichophorum cespitosum*.

The bottom layer was dominated by *Campylium stellatum*, with *Aneura pinguis*,

Barbilophozia rutheana, *Fissidens adianthoides*, *Gymnocolea borealis* and *Scorpidium*

cossonii occurring in all or a large majority of the plots. At Tågdalen the western/lowland

species *Drosera longifolia*, *Narthecium ossifragum* and *Schoenus ferrugineus* were present in

some plots. At Sølendet a number of alpine/inland species were present, the most common

being *Pedicularis oederi*, *Saxifraga aizoides* and *Kobresia simpliciuscula*.

3. Material and methods

3.1. Research design and vegetation plots

Ten localities with permanent experimental plots with and without mowing within each study

area in similar vegetation units of rich fens were chosen for the present research design (Fig.

3). Each locality consisted of two or more permanent plots of 2.5×5 m (total 49 plots). The

174 field work for this study was carried out in 2008. Inside each permanent plot one sample plot

175 of 1×1 m was placed in the centre, thus reducing potential edge effects. The minimum

176 distance from a sample plot to an area with different management regime was 0.75 m. The

177 minimum distance between the border of two sample plots was 1.5 m. Initial studies of

178 different sizes of sample plots (from 0.25 m^2 to 4 m^2) revealed that intermediate-sized plots of

179 1 m^2 were representative of the plant composition of the stand (e.g. Mueller-Dombois and

180 Ellenberg, 1974).

181

182 Three management regimes have been maintained since the 1970s: 1) biennial mowing, 2)

183 quadrennial mowing and 3) unmown since 1950s (Fig. 3). Management regimes 1) and 3)

184 were present in all investigated localities. Six localities at Tågdalen and three localities at

185 Sølendet included management regime 2). For management regime 1) mowing was done one

186 year prior to investigation of plant cover and sampling; for management regime 2) mowing

187 was done three years prior to investigation. The intensive mowing practice 1) represents the

188 traditional mowing, and 2) reflects extensive mowing.

189

190 Plant nomenclature follows Lid and Lid (2005) for vascular plants and Frisvoll et al. (1995)

191 for mosses (Table 2). The species cover was visually recorded using the following cover

192 classes [percent range of cover – cover class mean]: 1 [1-2 plants – 0,25%], 2 [0-1% – 0,5%],

193 3 [1-2,5% – 1,75%], 4 [2,5-5% – 3,75%], 5 [5-10% – 7,5%], 6 [10-20% – 15%], 7 [20-30% –

194 25%], 8 [30-40% – 35%] and so on up to 14. For each taxon the mean plant cover from each

195 management regime was calculated from the average of cover class means from all plots of

196 similar management regime (Table 3). Species recorded in the vegetation are equivalent to the

197 taxa included in "local terrestrial pollen" (see 3.3).

198   *3.2. Surface pollen sampling*

199   Moss polsters were collected from the sample plots as traps for pollen deposition (e.g. Hicks,

200   1977; Hjelle, 1998). Each moss sample consisted of five merged sub-samples, one from the

201   centre of the plot and four in each direction out from the centre and half way to the sample

202   plot border (Fig. 3). The result, a minimum distance of 1 m between a pollen sub-sample and

203   different land-use, reduces the risk of strong plot-edge effects. If moss was absent, sampling

204   was done as close as possible to these points. The modern analogue to a fossil sample from a

205   peat core is a single moss sample, but collecting several sub-samples reduce the potential

206   effect of outliers and of micro-scale differences in pollen content in moss polsters from

207   neighbouring samples (Pardoe, 1996; Hicks, 2001). Moss samples were collected in late July

208   2008. The moss sample consisted of the whole moss turf from the top down to the soil

209   surface. Thus several years of pollen deposition were probably included in the sample (e.g.

210   Mulder and Janssen, 1999; Pardoe et al., 2010), integrating observed year to year fluctuations

211   in fertility and pollen production (Hicks, 2001; Nielsen et al., 2010). Such samples are

212   comparable to the vegetation community when single-year effects can be evened out, as well

213   as to a peat pollen sample reflecting several years. By far the most frequently sampled moss

214   in all localities was *Campylium stellatum*. Among other common species were *Scorpidium*

215   *cossonii, Scorpidium scorpioides, Drepanocladus* spp. *and Sphagnum* spp.

216

217   *3.3. Pollen processing and analysis*

218   Moss samples were thoroughly rinsed through 450 µm sieves to remove the moss. Pollen

219   preparation of the material passing through the sieve followed standard methods, with KOH

220   and acetolysis (Fægri and Iversen, 1989), but without hydrofluoric acid treatment because the

221   minerogenic content was negligible in all samples. The residue was mounted in glycerol for

222   pollen counting. At least 500 terrestrial-plant pollen (range 563-1349) including more than

223   100 local terrestrial pollen (range 164-724) were counted per sample. Taxa were identified to

224   the lowest possible taxonomic level by the use of keys (Moe, 1974; Fægri and Iversen, 1989;

225   Moore et al., 1991; Beug, 2004) and the modern pollen reference collection at the University

226   of Bergen. Pollen data-analysis was made using TILIA (Grimm, 1990). When possible,

227   Cyperaceae pollen was identified to *Dulichium*-type, representing *Carex* spp., and

228   *Eriophorum*-type pollen (sensu Fægri and Iversen, 1989).

229

230   The percentage calculation sum is the sum of local terrestrial pollen ($\sum$ LP). The pollen

231   calculation sum for other pollen and microfossils is $\sum$P+X, where X is the microfossil in

232   question. Local terrestrial pollen and spores represent pollen and spores from taxa belonging

233   to the studied rich fen vegetation (e.g. Janssen, 1966). In this sense extra-local taxa are only or

234   mainly recorded as growing on nearby mineral soil, such as Ericaceae, *Calluna vulgaris*,

235   *Juniperus communis*, *Salix* spp. and *Betula* spp., which occur at low abundances or are absent

236   in the fen plots (Moen et al., 2012). Pollen from *Betula* spp. is mainly a part of the regional

237   pollen deposition, along with pollen from species not represented in the fen localities, like

238   *Pinus sylvestris*. As the yearly moss growth rates may vary between and within moss taxa, as

239   well as with mowing (Moen, 1995), the pollen trapping ability and concentration values will

240   not be directly comparable between samples. Therefore percentages based on the sum of local

241   pollen were used. The use of local terrestrial pollen as the calculation basis will minimize the

242   problems of absolute variations in extra-local and regional pollen related to percentage

243   calculations. Such variations are not related to the vegetation on the fen nor the local mowing.

244   *3.4. Data analyses*

245   In the data analysis comparing vegetation and pollen data, only the local terrestrial taxa are

246   included. A comparison of species occurrences and pollen data requires comparable

247   taxonomic groups. Therefore, the plant species were grouped according to the pollen taxa that

248   represent them. Analyses of some species were carried out for both single plant species and

249   for the corresponding palynological taxonomic groups, see Table 2.

250

251   *3.4.1. Gradients in the data - ordination*

252   Principal components analyses (PCA) implemented in CANOCO for Windows 4.5 (ter Braak

253   and Šmilauer, 2002) was used to ordinate the 49 vegetation plots according to the pollen taxa

254   they contained. Species centring with square-root transformed data was used. Species scores

255   were divided by their standard deviation to obtain inter-species correlations. Pollen

256   percentages (square-root transformed) from the same plots and taxa and the three

257   management regimes were added as passive samples and environmental variables,

258   respectively, and projected on the ordination diagram. The results were drawn using

259   Canodraw for Windows 4.5 (Fig. 4a and b).

260

261   *3.4.2. Paired comparisons from mown and unmown vegetation*

262   A paired test was carried out comparing the vegetation composition in pairs of mown-

263   unmown plots within each locality. The Wilcoxon signed rank test was used for the

264   nonparametric data to identify taxa with a statistically significant difference in mean

265   percentage plant cover between land-use regimes. It was run in R version 2.11.1 (R

266   Development Core Team, 2010). An exact Wilcoxon signed-rank test was chosen as the

267   grouped data-set has a potential for ties for the pairs. The data from Tågdalen and Sølendet

268   were analysed jointly providing a maximum of 20 pairs. Three sets of tests were run: 1) plots

269   from biennially mown and unmanaged plots, 2) Plots mown biennially and quadrennially, 3)

270   Plots mown quadrennially and unmown plots. Taxa with plant cover registrations in ≥ 6 plots

271   were included.

272

273   *3.4.3. Analyses of differences in species plant cover between management regimes*

274   The indices of difference (ID), equation (1), show whether and how often each taxon

275   increases, displays no change, or decreases in cover from the unmown to the mown pairs of

276   plots:

277    $(n_A(1)+n_B(0)+n_C(-1))(n_A+n_B+n_C)^{-1}$ ⇨ $(n_A-n_C)(n_A+n_B+n_C)^{-1}$ (1)

278   Where n_A is the number of pairs of plots where each taxon has larger vegetation cover in the

279   mown plot than in the unmown plot, n_B is the number of pairs of plots with no difference, and

280   n_C displays the number of pairs of plots where the taxa has lower vegetation cover in the

281   mown plot than in the unmown plot.

282

283   *3.4.4. Correlation between vegetation and pollen data*

284   To investigate whether plant cover is correlated with the corresponding pollen percentages in

285   the surface samples, the nonparametric Spearman rank-correlation coefficient, ρ (rho) (e.g.

286   Webb et al., 1978), was used to measure statistical dependence between pollen percentages

287   and plant cover for taxa in all plots for the three management regimes. The test was carried

288   out in R version 2.11.1 (R Development Core Team, 2010), examining the absolute

289   percentage differences of paired plots. The statistical significance level was set to 0.05. The

290   data-set of 49 plots from both Tågdalen and Sølendet was used. The correlation test was run

291   for only one study area when plant cover or pollen was absent from the other area. The tests

292   were run for all taxa recorded in ≥6 pairs of plots in each paired comparison.

293

294   *3.4.5. Indices of pollen association and representation*

295   Based on presence/absence data of vegetation and pollen from all investigated plots,

296   calculations of indices of association with coincidence (A), over-representation (O) and

297   under-representation (U) (Davis, 1984; Hjelle, 1997; Bunting, 2003; Mazier et al., 2006) were

298   made for each taxon. The definitions of the three indices are:

299     $A = B_0 (P_0 + P_1 + B_0)^{-1};$ $O = P_0 (P_0 + B_0)^{-1};$ $U = P_1 (P_1 + B_0)^{-1}$ (2)

300   where B_0 is the number of plots where the pollen or spore type and the associated taxon is

301   present, P_0 represents the number of plots where the pollen or spore type is recorded but this

302   taxon is not present in the vegetation, and P_1 is the number of plots where the pollen or spore

303   type is absent in the surface sample but the taxon is present in the vegetation. Based on the

304   indices, taxa were grouped into associations: strongly associated types (SAT, $A > 0.65$),

305   associated types (AT, A between 0.65 and 0.5), weakly associated types, (WAT, $A < 0.5$,

306   positive O and U), over-represented type (ORT, $A < 0.5$, $U = 0$), under-represented type (URT,

307     $A < 0.5$, $O = 0$) and unassociated type (UT, $A = 0$, positive O and U).

308   **4. Results**

309   89 plant species (77 vascular plant species and 12 moss species) were recorded from Tågdalen

310   and Sølendet. Taxa present in both the vegetation data-set and the pollen and spore analyses

311   were considered (Table 2). Thus 57 vascular plant taxa were represented in the pollen

312   assemblages and grouped into 26 pollen taxa (Table 2).

313

314   Taxa only recorded in the vegetation, like *Dactylorhiza* spp., *Equisetum* spp. and most moss

315   species, and taxa only identified in the pollen record, e.g. several tree species, were excluded.

316   *4.1. Vegetation data*

317   The most frequent species in both study areas were: *Trichophorum cespitosum* ssp.

318   *cespitosum, Thalictrum alpinum, Molinia caerulea, Potentilla erecta, Eriophorum latifolium,*

319   *Carex flava, C. panicea, C. rostrata* and *Succissa pratensis* (Table 3). *Molinia caerulea,*

320   *Thalictrum alpinum*, *Eriophorum latifolium, Betula nana* and several *Carex* taxa displayed a

321   large difference in plant cover between biennially mown and unmown plots (Table 3).

322

323   Twelve plant taxa had significantly different cover values in biennially mown and unmown

324   plots (Table 4 a). Highest cover values in biennially mown plots were found for: four *Carex*

325   species, *Thalictrum alpinum, Pinguicula vulgaris, Eriophorum latifolium*, *E. angustifolium*

326   and *Pedicularis palustris. Molinia caerulea* was much more abundant in unmown plots, and

327   this was the only plant taxon displaying a difference in plant cover between all the

328   management regimes. *Betula nana* and *Succisa pratensis* were more abundant in unmown

329   plots than in biennially mown plots. Combining the plant taxa into pollen groups resulted in

330   *Dulichium*-type (i.e. *Carex* spp.) displaying a difference in vegetation cover between all

331   management regimes, whereas *Eriophorum*, Cyperaceae and Poaceae only displayed a

332   difference between the two mown and the unmown plots (Table 4 b). The difference in plant

333   cover in biennially mown and unmown plots represented the main variation in plant cover in

334   fen vegetation (Table 4 a), most pronounced for *Molinia caerulea, Carex dioica* and

335   *Thalictrum alpinum*.

336   *4.2. Ordination of vegetation and pollen data*

337   The first two axes of the PCA-ordination of the 49 plots (Fig. 4) had eigenvalues of 0.25 and

338   0.23 respectively. The other axes had eigenvalues lower than 0.10 (not shown). The

339   vegetation samples representing different mowing frequencies were spread along the whole

340   range of the first axis (Fig. 4a), but were separated on the second axis, reflected in both the

341   dispersal of samples and the mean scores for the environmental variables. On axis 2 the

342   variable representing biennial mowing had a high negative mean score, while quadrennial

343   mowing had a small negative mean score and unmown had a high positive mean score. The

344   majority of pollen samples (passive data) had low scores on both axes. The pollen samples

345   showed a similar pattern as the vegetation samples, where the pollen samples from the

346   unmown plots to a large extent are separated from the plots with the two mowing frequencies,

347   most pronounced for unmown and biennially mown plots.

348

349   *Pedicularis*-type had a negative score on the first axis of the PCA ordination of plant taxa (as

350   pollen taxa groups, Fig. 4b) whereas *Potentilla erecta*, *Rhinanthus*-type and *Succisa pratensis*

351   had high scores. *Dulichium*-type, *Thalictrum*, Cyperaceae and *Eriophorum* had lowest scores

352   on the second axis whereas Poaceae had the highest score followed by *Sphagnum*.

353   *4.3. Pollen data in relation to management regimes*

354   Of the 65 palynological taxa found at Tågdalen and Sølendet, only 26 pollen and spore taxa

355   represented the investigated, contemporary vegetation (Table 2). Pollen taxa present in >4

356   plots are displayed in Table 5.

357

358   At Tågdalen *Thalictrum* and *Eriophorum*-type pollen had their largest pollen percentages in

359   mown plots, especially seen for *Thalictrum* in biennially mown plots in Tågdalen. Poaceae

360   and *Potentilla*-type had largest pollen percentages in unmown plots. *Dulichium*-type pollen

361   had largest pollen percentages in unmown plots, but in Tågdalen the differences are small.

362   Cyperaceae had generally small relative changes to no differences between management

363   regimes, and the standard error is large. *Succisa pratensis* had also small to no differences

364   between management regimes in Tågdalen, where at Sølendet the largest pollen percentages

365   were registered in unmown plots. *Pedicularis*-type pollen had a general low pollen presence.

366   The *Pedicularis*-type pollen percentages were slightly higher in biennially mown than in

367   unmown plots in Sølendet, and where absent in unmown plots in Tågdalen.

368

369   From Sølendet only three plots represent quadrennially mown fen, giving a potential for

370   uncertainties regarding the result. In Sølendet the pollen data does not always follow the trend

371   from Tågdalen, as for *Thalictrum* and Poaceae.

372

373   *4.4. Pollen-vegetation relationships*

374   Spearman rank-correlation coefficients relating plant cover to pollen percentages are

375   presented in Table 6, along with the indices of association and association types which reflect

376   relationships between presence/absence of plants and their pollen. As *Molinia caerulea*

377   formed the majority of the Poaceae plant cover (Table 3), both *M. caerulea* and Poaceae plant

378   cover were individually correlated to the Poaceae pollen data. *Eriophorum*-type pollen was

379   compared to both *Eriophorum* spp. and *Eriophorum*-type vegetation.

380

381   Most of the strongly associated plant-pollen types (SAT) and the associated plant-pollen type

382   (AT) had a statistically positive correlation between plant cover and pollen percentages (Table

383   6). These were Rosaceae, *Potentilla*–type, *Pedicularis*, *Thalictrum*/*Thalictrum alpinum*,

384   *Selaginella selaginoides*, *Eriophorum*-type/*Eriophorum* spp., Poaceae/*Molinia caerulea* and

385   Cyperaceae. *Succisa pratensis* and *Menyanthes trifoliata* had significant plant-pollen

386   correlations, but had weak associations with their corresponding pollen types as they

387   displayed a trend towards pollen under-representation.

388

389   The remaining taxa in Table 6 did not have a significant relationship between the vegetation

390   cover and pollen percentages. However, common species in the vegetation, such as Poaceae,

391   *Eriophorum* spp. and *Carex* spp., were also common in the pollen assemblages, reflected in a

392   strong association. Underrepresented taxa were insect pollinated species which were poorly

393   presented in the pollen assemblages, but they were present in the vegetation when present as

16

394   pollen, e.g. *Drosera rotundifolia*-type, *Bistorta vivipara*-type and *Saxifraga oppositifolia*-

395   type.

396   **5. Discussion**

397   Rich fen vegetation is widely distributed in Europe. Vegetation plots from our two study areas

398   are included in a European study, and are classified as boreal fens (Jiménez-Alfaro et al.,

399   2013, cluster 3a). The relationships between vegetation and pollen assemblages in our two fen

400   areas add to the database of surface-pollen samples from a variety of vegetation types and

401   land-use regimes (e.g. Gaillard et al., 1994; Hjelle, 1999a; Mazier et al., 2006; Ejarque et al.,

402   2011; Waller et al., 2017). These data contribute to modern-pollen studies and long-term

403   investigations. However, there are few studies that consider rich fens. An exception is the

404   nemoral rich fens of Waller et al. (2005, 2017) which include a number of species in common

405   with our studied fens; e.g. *Potentilla erecta*, *Carex nigra*, *C. panicea*, *C. rostrata* and *Molinia*

406   *caerulea*. These are among the most common species in our two study areas as well as in the

407   two study areas in southern and eastern England. The annually cut "Sedge fen" included in

408   Waller et al. (2017) has many features in common with our fens, and represent a community

409   with close relationship between vegetation and local pollen deposition.

410

411   Comparable to our study, Waller et al. (2017) found that nemoral rich fen vegetation subject

412   to different types of management, including different cutting regimes, produce distinctive

413   pollen signatures. Their study area is in nemoral vegetation zone, with somewhat different

414   plant communities and species, compared to our boreal rich sloping fens. Also, de Klerk et al.

415   (2017), in arctic fens, state that pollen deposition reflects vegetation, and that regional pollen

416   deposition relate to different biogeographical regions.

5.1. Plant cover and pollen deposition

The pollen recovery from moss samples is a measure of plant representation based on fertility and pollen production, and not only plant cover. However, there is a close connection between plant cover, plant biomass and flowering of a large number of species, as shown in the long-term population and vegetation studies in the two study areas (Moen, 1990, 1995; Aune et al., 1996; Lyngstad et al., 2016). Mowing leads to a reduction in above ground biomass and plant cover and a reduction in flowering for several tall-growing species, e.g. *Molinia caerulea* and shrubs (Table 3). A number of low growing species, with most of the above-ground biomass close to the surface (not reached by the scythe) increased in biomass, cover and flowering, e.g. *Thalictrum alpinum* and *Carex dioica*. Thus pollen recovery is regarded an approximation of plant cover of a taxon.

There can be a large variation in annual flowering, pollen production and pollen deposition between years (e.g. Hicks, 2001; Hättestrand et al., 2008), and several years of pollen deposition should be sampled (Pardoe et al., 2010). Although moss samples may contain only one or two years of pollen deposition (Räsänen et al., 2004), it is generally assumed that moss polsters contain several years of pollen deposition (Bunting et al., 2013). The annual pollen productivity for species of boreal trees such as *Pinus*, *Betula,* and *Picea* has been found to be related to summer temperature of the year prior to pollen emission (Autio and Hicks, 2004). Our moss samples were gathered in late July 2008. The meteorological stations in the two study areas recorded summer temperatures close to the 30-year normal for the summers 2007 and 2008 (Lyngstad et al., 2016). Both 2007 and 2008 were normal/good flowering years for most of the studied species; e.g. for *Eriophorum latifolium* (Lyngstad et al., 2016), indicating that even if only a few years are represented in the moss samples, the pollen data are probably representative.

442

443   The investigated plots are designed for vegetation studies (e.g. Lyngstad et al., 2016), where

444   different management regimes (and collected moss polsters) are very close, but still there

445   were differences between pollen assemblages taken 1-4 m apart. The differences in pollen

446   percentages corresponded well with the vegetation from different management regimes,

447   indicating that a substantial part of pollen was derived locally and that rich fens are suitable

448   for local-scale plant-pollen studies. Comparable studies have also demonstrated a strong

449   correspondence between local vegetation and pollen assemblages for herbs and dwarf-shrubs

450   (e.g. Pardoe, 1996; Hjelle, 1999a; Waller et al., 2017) and a relevant pollen source area (*sensu*

451   Sugita, 1994) of only a few meters is found within mire communities (Bunting 2003; Bunting

452   and Hjelle, 2010).

453   *5.2. Identification of management regimes by modern pollen assemblages*

454   Most plant species occurred in both study areas, and in plots with different mowing regimes.

455   Those with high cover in all plots were *Trichophorum cespitosum, Thalictrum alpinum* and

456   *Molinia caerulea*. Six other vascular plant species occurred in at least 80% of the plots: *Carex*

457   *dioica, C. panicea, Eriophorum angustifolium, E. latifolium, Potentilla erecta* and *Selaginella*

458   *selaginoides*. Many bryophytes occurred in the plots, e.g. the dominant and constant rich-fen

459   species *Campylium stellatum* and *Scorpidium cossonii* (Moen et al., 2012). Several rare

460   species distinguish between the fens of the two areas, leading to the classification of the

461   oceanic and the more continental fens in different alliances in the phytosociological system

462   (Moen et al., 2012). All of these species had low pollen percentages, and they are not included

463   in this discussion.

464

465   The differences in plant cover and pollen assemblages between the management regimes were

466   mainly quantitative. Earlier studies from these localities have shown that the variation in

467   vegetation cover of plots from similar land-use between localities can be larger than between

468   plots from different management regimes within the same locality, and that permanent plots

469   with different management regimes inside each locality belong to the same plant

470   community/vegetation cluster (Moen et al., 2012; Lyngstad et al., 2016). The differences

471   between vegetation plots from different managemental regimes were more pronounced than

472   the differences between pollen samples from these regimes (Fig. 4a). Generally, the plant

473   compositions in plots mown biennially and quadrennially were more similar than to unmown

474   vegetation (Fig. 4a and b), whereas this to a lesser degree was found for pollen data (Fig. 4a).

475   Similar results for plant cover were found in the same areas (e.g. Aune et al., 1996), as well as

476   for plant and pollen data from other studies of mown vegetation (e.g. Hjelle, 1999a).

477

478   Palynological studies of rich fens have received little attention in comparison to lakes and

479   raised bogs (Waller et al., 2017). Our results are a contribution to knowledge established in

480   earlier studies from fen vegetation (e.g. de Klerk et al., 2017; Waller et al., 2017)

481   demonstrating that fen vegetation produce distinctive pollen signatures with indicator taxa

482   and should be used also for palaeoecological studies.

483

484   To detect past types of land use and changes in land use by pollen analysis, taxa that show

485   responses to land use regimes, in the present case mowing, and have pollen deposition that

486   correlate with plant cover, must be identified. Here five groups of pollen taxa with different

487   potential for land-use reconstruction were identified (Table 7).

488

489   *5.2.1. Very good and good pollen indicators for managemental regimes*

490   In rich fens *Thalictrum* is sensitive to land-use changes, and the contemporary pollen

491   percentages correlate with the local plant cover. *Thalictrum alpinum* occurred in all plots,

492   with highest cover in biennially mown plots compared with unmown plots (Fig. 4b),

493   absolutely (Table 3) and relatively (Table 4a). This is in accordance with previous studies

494   from Sølendet, which also report increased biomass, cover and flowering with mowing

495   frequency (Moen, 1995; Aune et al., 1996). A difference in cover of *T. alpinum* between

496   biennially and quadrennially mown plots is not clear from this study. Its growing point is at

497   the soil surface and is little affected by mowing, so it becomes more abundant in mown fens

498   where competition is reduced. The effect of competition was demonstrated by Klanderud and

499   Totland (2005), who removed neighbouring vegetation in an alpine community and found

500   increases in the number and cover of leaves and reduction in the length of the flowering stems

501   of *T. alpinum.* However, *T. alpinum* is also present in grazed communitites in outfields, as in

502   Budalen, located between our two study areas (Austrheim et al. 1999), and without comparing

503   mown and grazed communities one cannot exclude *Thalictrum* as indicator of more than one

504   land-use practice. The strong association of the presence of both plant and pollen and absence

505   of pollen when plants are lacking, indicates a limited pollen-dispersal distance from these

506   plots with a minimum distance of 1 m. *T. alpinum* is wind dispersed, but dispersal can be

507   limited by the short flower stems. This means that *Thalictrum* pollen is a good indicator of

508   local plant presence, and an increase in plant cover can indicate land use like mowing (Table

509   7). Increased percentages of *Thalictrum* pollen in peat profiles have been used as an indicator

510   of mowing in vegetation history studies of rich fens in boreal areas of central Norway

511   (Gunnarsdóttir, 1999; Solem et al., 2012).

512

513   The interpretation of the pollen representation of Cyperaceae undiff. is more challenging. The

514   family is generally well adapted to mowing, although with variations and opposite trends for

515   single species, as for *Carex* species (Table 4 a) (e.g. Moen, 1990, 1995). Both mowing

516   regimes differed from unmown plots in total Cyperaceae plant-cover percentages, but the

517   differences between mowing intensities could not be detected in modern pollen samples. The

518   differences in the Cyperaceae pollen percentages between management regimes are small.

519   The strong plant-pollen correspondence from these closely situated plots suggests a limited

520   dispersal distance for Cyperaceae, which was reported by Bunting and Hjelle (2010) to be

521   between 1.5 and 3.5 m. The present investigation has shown the value of separating

522   *Dulichium*-type pollen, which in our area consists of *Carex* spp., from Cyperaceae undiff.

523   pollen.

524

525   *Eriophorum*-type pollen includes three *Eriophorum* species and two *Trichophorum* species.

526   *Eriophorum* spp. and *Trichophorum* spp. (included in Cyperaceae) were most abundant in

527   vegetation mown biennially (Fig. 4b). *E. angustifolium, E. vaginatum* and the more

528   widespread species *E. latifolium,* were well adapted to mowing, which also promoted

529   increased flowering according to Moen (1990, 1995), Aune et al. (1996) and Lyngstad et al.

530   (2016). *Trichophorum cespitosum* ssp. *cespitosum*, the dominant species in the rich fens, was

531   indifferent to mowing, as found in earlier studies (e.g. Moen, 1995; Aune et al., 1996) and the

532   difference between management regimes was relatively small.

533

534   There was a positive plant-pollen correlation between *Eriophorum*-type pollen and total

535   *Eriophorum* species, but not for the pollen type and all five individual species. Most of the

536   pollen type might be from *Eriophorum* if *Trichophorum* pollen deposition was reflecting the

537   small variation in *Trichophorum* vegetation cover. The difference in *Eriophorum* spp. plant

538   cover between the two mowing regimes and unmown plots could be detected from pollen

539   analysis, as found from other studies (Hjelle, 1998), indicating that *Eriophorum*-type pollen

540   should be separated from Cyperaceae undiff. if possible to increase its value in the

541   interpretation of past communities.

542

543   *Molinia caerulea* is the most abundant grass in the plots but the pollen taxon Poaceae can also

544   include *Deschampsia cespitosa, Festuca ovina* and *Nardus stricta*. *M. caerulea* is clearly

545   most abundant and very fertile in unmown plots (Moen, 1990, 1995; Aune et al., 1996). The

546   plant cover of *M. caerulea* decreased with the intensity of mowing, whereas the cover of

547   Poaceae only differed clearly between the mowing regimes and unmown plots (Table 3 and

548   4). The main reason for the decrease of *M. caerulea* in mown fens is the exposure of the

549   elongation zone to the mower (scythe), strongly reducing the plants. Under moist conditions

550   grazing also reduces plant cover of *M. caerulea* (Hume et al., 1999). In boreal shrub-

551   dominated plant communities and in areas with mowing every 5-10 years (Aune et al., 1996)

552   and in temperate tall-growing fen communities (Rowell et al., 1985) *M. caerulea* increases in

553   biomass and cover with mowing. On the generally nutrient-poor boreal fens *M. caerulea*

554   suffers from the removal of reserves by intensive cutting during a short growing season (Øien

555   and Moen, 2001). In more fertile localities, strong competitors like shrubs and tall herbs are

556   removed by mowing. In such areas, and under mowing with higher stubble, the *Molinia*

557   tussocks can develop. In addition, the fertility of *M. caerulea* is reduced in mown plots on

558   boreal rich fens (Moen, 1995). The modern Poaceae pollen percentages correlated with the

559   plant cover of *Molinia*, but not with all Poaceae species (Table 6). This indicates that most of

560   the Poaceae pollen originated from *M. caerulea*. *Molinia caerulea*/Poaceae displays a

561   difference in plant cover and pollen percentages between areas mown biennially and

562   quadrennially from Tågdalen, whereas the data from quadrennially mown areas in Sølendet

563   are few and difficult to interpret. Overall, mowing of the rich fens results in a reduction of

564   Poaceae plants and pollen and an increase of Cyperaceae plants and pollen. This is in

565   accordance with investigated fen communities in UK where Cyperaceae (including *Carex*

566   *nigra*, *C. panicea* and *C. rostrata*) have high values in intensively managed communities and

567 decrease with longer cutting rotation when Poaceae (including *Molinia*) increases (Waller et

568 al., 2017). The results from fens seem therefore to contrast to pollen assemblages from dry

569 meadows dominated by high Poaceae pollen values and relatively low values of Cyperaceae

570 (Hjelle, 1999a).

571

572 *Succisa pratensis* was present throughout the rich fens, with its largest cover in unmown

573 plots, as reported in Moen (1995) (Fig. 4b, Table 3 and 4). In other communities a decrease in

574 competition following mowing allows an increase in plant cover of *S. pratensis* (Moen 1995).

575 However, with relatively little competition in the boreal rich-fens the effect of reduced

576 biomass had an important impact on this species. In mesic to dry grasslands *S. pratensis*

577 increase in cover with grazing (Herben et al., 2006), making both vegetation type and type of

578 land use important for *S. pratensis* plant cover. The cover of *S. pratensis* in the plots was low

579 and the differences between management regimes were small. It is insect-pollinated and has a

580 limited dispersal distance (Hjelle, 1997, 1998), reflected also in this study by a strong plant-

581 pollen relationship, but with a tendency of being under-represented. This makes the species

582 suited for interpretation of local vegetation, but less important for differentiating the

583 investigated management regimes in the present study.

584

585 *Pedicularis*-type pollen included *Pedicularis palustris* and *P. sylvatica* at Tågdalen and

586 mainly *P. palustris* and *P. oederi*, in addition to the rare *P. sceptrum-carolinum* at Sølendet

587 (Moen, 1990, 2000). The pollen percentages of *Pedicularis*-type related well to the cover for

588 *Pedicularis* spp., possibly because *P. palustris* is the main pollen source as well as the main

589 plant in the studied vegetation. As an associated type *Pedicularis* species were common, but

590 not dominant in either vegetation or in pollen deposits. Both *Pedicularis* spp. and *P. palustris*

591 had greatest cover in mown plots, with a trend to greater abundance in quadrennially mown

592 plots. Only biennially mown and unmown plots displayed a difference even if the percent

593   values are small. Earlier studies (e.g. Moen, 1995) confirm this, along with increased

594   flowering frequency in mown plots. *Pedicularis* has a very low pollen representation, so even

595   small differences in pollen percentages may represent substantial differences in number of

596   plants between plots. *P. palustris* is a biennial species mainly occurring in mud bottoms and

597   carpets with a scattered field layer, i.e. localities with low competition. *P. oederi*, a common

598   species in lawns and open fen margins at Sølendet (Moen, 1990) occurred in only 11 of 49

599   plots. This species shows reduced plant biomass and lower flowering frequency in response to

600   mowing, especially intensive mowing, and is also reduced by abandonment during

601   succession. The pollen data showed a correlation with plant cover, in contrast to the usually

602   rare occurrence of *Pedicularis* in pollen diagrams. Bunting (2003) found no association

603   between plant and pollen in surface studies of heathland communities in UK. Our results

604   indicate that *P. palustris* has a larger potential of being recorded than the other species, which

605   may indicate that *Pedicularis* may be regarded as an indicator of mown fens.

606

607   There are short distances between areas of different land-use in the investigated plots. The

608   strong plant-pollen relationship and strong association of presence indicate a local pollen

609   source area of approximately 1 to a few meters for taxa defined as very good and good pollen

610   indicators for managemental regimes.

611

612   *5.2.2. Potential pollen and spore indicators for managemental regimes*

613   Within the homogenous rich-fen community a wide distribution of both plants and pollen

614   gave a high probability of association for many taxa (cf. Hjelle, 1997; Mazier et al., 2006).

615   However, for several of these taxa there was no identified plant response to different

616   managemental regimes. From other studies *Potentilla erecta* displays larger cover and

617   increased flowering in unmanaged plots compared to mown fens (Moen, 1995; Aune et al.,

618   1996). A reduction in plant cover of *P. erecta* has been documentet from grazed vegetation on

619   moist soil (Hulme et al., 1999). With the high cover, the relatively coarse resolution for

620   abundant taxa in the chosen cover scale (e.g. Bunting and Hjelle, 2010), and substantial

621   variations between and within managemental regimes, potential vegetation trends were not

622   identified in the present study (Fig. 4b). Rosaceae undifferentiated pollen correlated with *P.*

623   *erecta,* its only species in the vegetation, thus Rosaceae pollen was interpreted to mainly

624   representing *P. erecta*. With a good plant-pollen correlation *P. erecta* reflects local

625   vegetation, it is a good indicator of grazing (e.g. Hjelle, 1999; Mazier et al., 2006) and can, in

626   the present study, represent a pollen indicator type of open vegetation more than mowing.

627   High moisture levels might limit the plant cover of *P. erecta* on these rich fens, playing a

628   more important role in plant distribution than land use.

629

630   *Selaginella selaginoides* is known to be favoured in mown fens (Moen, 1995; Aune et al.,

631   1996). In the studied fens the spore recovery was a good indicator of its plant presence, but no

632   statistical relationship between plant cover and management regime has been identified. With

633   low percentages on the investigated fens, any trends have been difficult to decipher. There

634   was a tendency of increased plant presence with mowing from pairwise comparisons (Table 3

635   and 4), even if the general tendency in the plots is a slight decrease with mowing (Fig. 4b). If

636   its land-use response is identified from further studies, *S. selaginoides* could be an indicator-

637   type of mowing.

638

639   *5.2.3. Pollen types reflecting unidentified factors or not reflecting plant cover*

640   *Menyanthes trifoliata* was rare but still demonstrated a positive plant-pollen correlation on

641   these rich fens. Its main distribution on the fens was outside the investigated localities, in the

642   wettest places in the fens and in small lakes (Moen et al., 2012). However, in lawn and carpet

643   communities, the cover of *Menyanthes* increases and flowering decreases with mowing

644   (Moen et al. unpublished data).

645

646   Two sub-groups of pollen types not reflecting plant cover were identified:

647   a) Mowing regime affected the species cover, but there was no significant plant-pollen

648   correlation. The strong association between plant and pollen was due to their large abundance.

649   *Carex* species display a variety of plant responses to mowing regarding biomass, cover and

650   fertility (Moen, 1995). Several *Carex* species and the genus as a whole were most abundant in

651   mown plots (Fig. 4b; Moen, 1990; Aune et al., 1996). The low taxonomic precision of

652   *Dulichium*-type pollen and variations in pollen production within the genus (Randall et al.,

653   1986; Hjelle, 1998) were probable reasons for a lack of plant-pollen correlation. *Dulichium*-

654   type pollen has a potential in palaeoreconstruction if the plant-pollen relationship can be

655   interpreted locally. *Betula* species as a whole*,* and the main species *B. nana* and *B. pubescens*

656   were mainly found in relation to succession on the fen, along the margins and as surrounding

657   vegetation (e.g. Moen, 1990). The over-represented and variable pollen recovery from *Betula*

658   was probably from the extra-local and the regional vegetation. Thus *Betula* pollen has

659   limitations in reconstructing local vegetation, but an increase in pollen may indicate fen

660   succession and increased tree cover on extra-local and regional scales. The cover of *Drosera*

661   spp. at Tågdalen and *Pinguicula vulgaris* at Sølendet increased with mowing, as shown by

662   Moen (1995). As entomophilous and cleistogamous species, respectively, their strongly

663   under-represented and unassociated pollen document the presence of the plant, but they are

664   not suitable to represent variation in the vegetation.

665

666   b) The second sub-group includes taxa with no identified plant response to different land-use

667   and no plant-pollen correlation on the rich fens (Table 7). These were rare in this vegetation

27

668   type, but could be common in nearby herb and heather woodland (Moen, 1900, 2000). The

669   pollen might mainly be extra-local. These taxa are of limited value in local land-use

670   reconstructions in such boreal fens, but can be valuable in reconstructions of extra-local

671   vegetation, succession and fen dynamics.

672

673   Changes in climate and fen characteristics might change the effect mowing plays on single

674   taxa through time as well as geographically. Still, the ecological effect of mowing will be

675   similar for many taxa under various conditions, and thus comparable between regions (e.g.

676   Hjelle, 1999a).

677   **6. Conclusion**

678   The differences in plant cover between mown and unmanaged plant communities on the

679   boreal rich-fens were mainly quantitative, where the same taxa are present in the vegetation in

680   mown and unmown fens, but in varying amounts (Table 3). For several taxa managemental

681   regimes explained a substantial part of the plant-cover variation on the boreal rich-fens. The

682   relative changes of several taxa in the vegetation rather than the presence or absence of any

683   single pollen-indicator taxon indicate land-use changes on these fens.

684

685   A correlation between the plant cover of taxa constituting the majority of the vegetation on

686   the rich fen and their contemporary, deposited pollen on a local scale was documented. The

687   short distances between different managemental regimes in this study indicate a local pollen

688   source area from 1 and up to a few meters for important taxa in the mown fens, like

689   *Thalictrum alpinum*, Cyperaceae and *Succisa pratensis*. Thus, presences of their pollen in

690   peat samples can generally be assumed to reflect presence in the vegetation.

691

692   Modern pollen assemblages, with correlation to plant cover, display a difference in pollen

693   percentage between biennially mown and unmown vegetation. Further, several taxa have a

694   potential for indicating mowing quadrennially, even if the two mowing regimes are not

695   clearly separated in the present study. A modern pollen assemblage indicating mowing on

696   these rich fens has high percentages of *Thalictrum*, *Eriophorum*-type and Cyperaceae undiff.

697   pollen. *Pedicularis* pollen percentages are generally higher than in unmown vegetation, and

698   Poaceae (*Molinia caerulea*) and *Succisa pratensis* pollen percentages are lower than in

699   unmown vegetation. *Potentilla*-type and Rosaceae, pollen together representing *Potentilla*

700   *erecta*, decrease with mowing of the fens, whereas an increase in *Selaginella selaginoides*

701   spores potentially indicates mowing. In combination, these changes in pollen percentages

702   from such species can be considered a fingerprint for mowing regimes on rich fens. In other

703   vegetation types and under different land use, some of these species would display a different

704   combination of increase and decrease in plant cover and pollen deposition.

705

706   This study emphasises the importance of identification of pollen to as low a taxonomic level

707   as possible. The separation of *Eriophorum*- and *Dulichium*-type (i.e. *Carex* spp.) pollen from

708   Cyperaceae undiff. is essential as the two former, partly in different ways, are important taxa

709   in identifying land-use regimes.

710

711   This study has shown a close connection between taxa in fen vegetation and the local pollen

712   deposition in the two contrasting climate regimes (oceanic and continental) of the middle and

713   northern boreal vegetation zones, confirming hypothesis 1. Boreal rich-fens in the two areas

714   have the same dominant species and the same species producing the majority of the pollen,

715   supporting hypothesis 2. The difference between mown and unmown vegetation can be

716   detected from the contemporary pollen assemblages, particularly between biennial mown and

717 unmown vegetation, supporting hypothesis 3. In this study *Molinia caerulea*/Poaceae display

718 a difference in plant cover and pollen percentages between areas mown biennially and

719 quadrennially. This difference between biennially and quadrennially mown areas was not

720 identified for most taxa, and should be further investigated. The results from the present paper

721 contribute to a better understanding of vegetation-pollen relationships on rich fens and

722 separation of mown and unmown fens, based on pollen assemblages. Our findings will aid in

723 the interpretation of fossil pollen assemblages in terms of local land use on fens in the boreal

724 zone.

725

734 **References**

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895

896   Figure legends

897

898   Fig. 1. The location of the two study areas, Tågdalen in the inner fjord area and the inland

899   area Sølendet. Vegetation sections in central Norway after Moen (1999).

900

901   Fig. 2. The location of investigated localities in a) Tågdalen Nature Reserve and b) Sølendet

902   Nature Reserve. The reserves are marked with black solid borders. Numbering of the plots

903   follows the permanent plots in long-term studies from the reserves (Moen, 1990, 2000).

904

905   Fig. 3. Schematic presentation of a typical locality with permanent plots, investigated plots of

906   1 m^2 for the present study and collection points for moss samples. A= mown biennially, C=

907   mown quadrennially and B= unmown.

908

909   Fig. 4. PCA showing a) vegetation samples, pollen samples and environmental variables.

910   Pollen samples and environmental variables are treated as passive samples and variables

911   respectively. Veg. = vegetation samples, Pollen = pollen samples, 2nd = mown biennially, 4th

912   = mown quadrennially. Grey triangles = environmental variables, three mowing regimes, b)

913   plant species grouped into pollen taxa according to Table 2, based on 26 plots from Tågdalen

914   and 23 plots from Sølendet. Pollen types close to the center are not shown to increase

915   readability. Abbreviations: t = type, *Menyanthes tri = Menyanthes trifoliata*, *Saxifraga opp =*

916   *Saxifraga oppositifolia*.

917

O3 Highly oceanic section   O2 Markedly oceanic section   O1 Slightly oceanic section

OC Indifferent section   O1 Slightly continental section

918
919   Fig. 1.
920
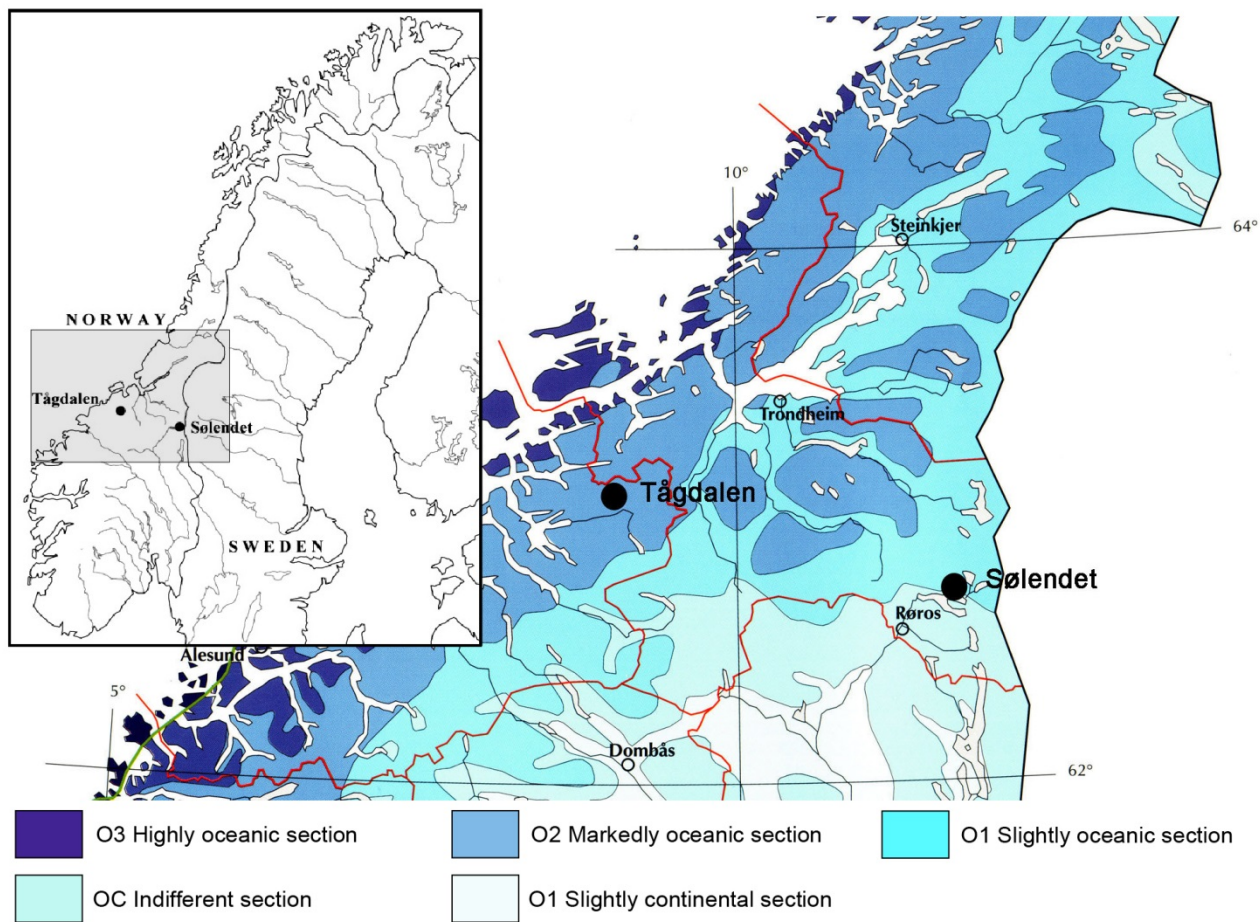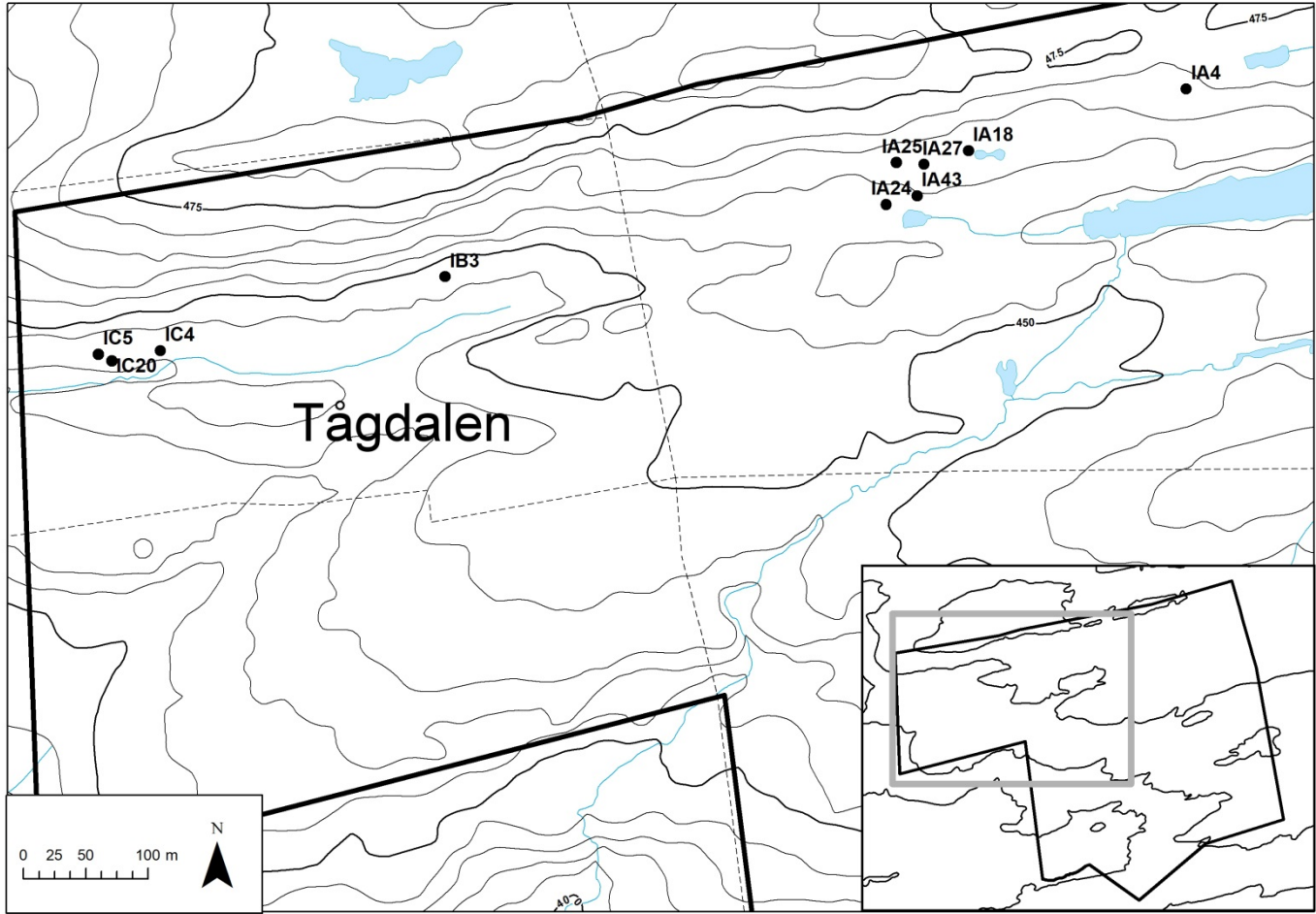
925 **Table 1**
926 Characteristics of the two study areas. Climatic data from Norwegian Meteorological Institute
927 (see Lyngstad et al., 2016, including Supplementary Material) for the study areas at Tågdalen
928 nature reserve and Sølendet nature reserve. Vegetation zones and sections after Moen (1999).
929

	Tågdalen	**Sølendet**
Latitude (N)	63°03'	62°40'
Longitude (E)	9°05'	11°50'
Altitude (m a.s.l.)	440-460	715-785
Mean annual precipitation (mm)	1583	637
Mean annual temperature (°C)	3.0	0.6
Mean July temperature (°C)	11.2	10.5
Mean January temperature (°C)	- 2.7	- 9.5
Vegetation zone	middle/ northern boreal	middle/ northern boreal
Vegetation section	markedly oceanic (O2)	indifferent (OC)/slightly oceanic (O1)

930
931

932 **Table 2**
933 The 26 pollen and spore taxa with their corresponding 57 plant species present in the studied
934 localities. Only taxa registered in both vegetation and pollen samples are included. T = pollen
935 or plant only present in Tågdalen; S = pollen or plant only present in Sølendet. Nomenclature
936 for pollen taxa follows Fægri and Iversen (1989), plant taxa follow Frisvoll et al. (1995) and
937 Lid and Lid (2005).

Pollen/spore taxa	Plant species in the vegetation plots
Anemone	*Anemone nemorosa*[T]
Asteraceae Cichorioideae	*Crepis paludosa*[S], *Leontodon autumnalis*[S]
Betula	*Betula nana, Betula nana* x *pubescens, Betula pubescens*
Bistorta vivipara-type	*Bistorta vivipara*
Calluna vulgaris	*Calluna vulgaris*[S]
Cyperaceae	*Carex* spp., *Eleocharis quinqueflora, Eriophorum* spp., *Kobresia simpliciuscula*[S], *Schoenus ferrugineus*[T], *Trichophorum* spp.,
Drosera rotundifolia-type[T]	*Drosera longifolia*[T] ,*Drosera rotundifolia,*
Dulichium-type	*Carex capillaris, Carex chordorrhiza*[T], *Carex dioica, Carex echinata, Carex flava, Carex flava* x *hostiana*[S], *Carex hostiana, Carex lasiocarpa, Carex limosa*[T],*Carex nigra, Carex panicea, Carex pauciflora*[T], *Carex rostrata, Carex vaginata*[S]
Ericaceae	*Andromeda polifolia, Calluna vulgaris*[S], *Erica tetralix*[T], *Vaccinium uliginosum* ssp. *uliginosum*
Eriophorum-type	*Eriophorum angustifolium, Eriophorum latifolium, Eriophorum vaginatum*[S], *Trichophorum alpinum, Trichophorum cespitosum* ssp. *cespitosum*
Galium-type[T]	*Galium boreale*
Juniperus communis	*Juniperus communis*
Menyanthes trifoliata[T]	*Menyanthes trifoliata*[T]
Pedicularis-type	*Pedicularis oederi*[S], *Pedicularis palustris*
Pinguicula-type[S]	*Pinguicula vulgaris*[S]
Poaceae	*Deschampsia cespitosa*[S], *Festuca ovina*[S], *Festuca vivipara*[T], *Molinia caerulea, Nardus stricta*
Potentilla-type	*Potentilla erecta*
Rhinanthus-type[S]	*Bartsia alpina*[S], *Euphrasia wettsteinii*
Rosaceae	*Potentilla erecta*
Salix[S]	*Salix glauca*[S]
Saxifraga oppositifolia-type	*Saxifraga aizoides*[S]
Selaginella selaginoides	*Selaginella selaginoides*
Solidago-type	*Solidago virgaurea*[S]
Sphagnum	*Sphagnum warnstorfii, Sphagnum* Section *Subsecunda*
Succisa pratensis	*Succisa pratensis*
Thalictrum	*Thalictrum alpinum*

938
939

Table 3

Number of plots with plant recorded (n), mean plant cover in vegetation plots based on 26 plots from Tågdalen (T) and 23 from Sølendet (S), and differences in cover between plots mown biennially (M2) and unmovn (U). [T] = only from Tågdalen; [S] = only from Sølendet; – = not present. The difference in % values displays absolute differences on a % scale between plots mown biennially and unmown plots.

Plant taxa	n	T, mean %	S, mean %	Difference in % values M2 – U (T & S)
Bartsia alpina	29	2.5	0.5	-1.6
Betula nana	16	0.01	2.9	-5.7
Bistorta vivipara	19	0.1	0.6	-0.5
Carex capillaris	20	0.7	0.8	0.3
Carex dioica	40	2.2	1.1	2.2
Carex echinata	9	0.7	0.01	2.1
Carex flava	35	2.6	6.1	5.9
Carex hostiana	22	4.3	0.01	4.9
Carex limosa[T]	25	2.8	–	2.4
Carex nigra	11	0.02	1.8	2.1
Carex panicea	48	2.2	4.0	1.2
Carex rostrata	30	3.1	2.3	4.8
Drosera longifolia[T]	13	2.0	–	4.0
Eriophorum angustifolium	43	0.7	0.8	0.9
Eriophorum latifolium	44	7.8	6.4	5.7
Eriophorum vaginatum[S]	10	–	0.3	-0.5
Euphrasia wettsteinii	25	0.8	1.4	0.0
Festuca ovina[S]	12	–	0.7	-0.7
Menyanthes trifoliata	9	0.4	1.6	-5.4
Molinia caerulea	49	8.3	7.4	-13.6
Pedicularis oederi[S]	11	–	0.5	-0.3
Pedicularis palustris	26	0.2	3.0	3.1
Pinguicula vulgaris	13	1.7	0.9	2.6
Potentilla erecta	44	9.2	5.2	0.4
Selaginella selaginoides	43	1.5	1.9	0.2
Succisa pratensis	32	3.5	1.6	-1.9
Thalictrum alpinum	49	10.8	13.9	10.6
Trichophorum alpinum	22	1.7	0.1	-0.4
Trichophorum cespitosum ssp. cespitosum	49	18.4	14.5	-1.9

Table 4
Results (p-values) from paired comparisons of differences in a) mean percentage cover of
plant taxa and b) sum of mean percentage cover of pollen taxa between management regimes
in Tågdalen and Sølendet using the Wilcoxon signed rank test. The test was run for plots
mown biennially and unmown plots (M2 & U), plots mown biennially and quadrennially (M2
& M4), and plots mown quadrennially and unmown plots (M4 & U). Numbers in bold display
values statistically significant at a 0.05-level. **--** = not enough plots to compute the test. The
rightmost column displays indices of difference (ID), range +1.0 to **-**1.0, between plots mown
biennially and unmown (M2 & U). Positive values refer to taxa with an increase in plant
cover with mowing, negative values vice versa.

	p-values			ID
a) Plant taxa	**M2 & U**	**M2 & M4**	**M4 & U**	**M2 & U**
Molinia caerulea	**<0.0001**	**0.047**	**0.010**	-0.95
Carex dioica	**<0.0001**	0.25	0.22	0.89
Thalictrum alpinum	**<0.0001**	0.50	0.06	0.90
Pinguicula vulgaris	**0.001**	**0.031**	0.38	0.65
Carex hostiana	**0.002**	0.50	0.06	1.00
Carex flava	**0.002**	>0.99	0.13	0.60
Eriophorum latifolium	**0.003**	0.50	0.06	0.72
Eriophorum angustifolium	**0.012**	0.06	0.13	0.44
Pedicularis palustris	**0.017**	>0.99	0.50	0.58
Betula nana	**0.027**	**--**	**--**	-0.60
Succisa pratensis	**0.036**	>0.99	>0.99	-0.38
Carex limosa[T]	**0.047**	>0.99	0.38	0.60
Carex echinata	0.06	**--**	**--**	0.83
Drosera longifolia[T]	0.06	>0.99	0.25	0.83
Bartsia alpina	0.18	0.63	0.25	-0.40
Carex nigra	0.19	**--**	**--**	0.50
Eriophorum vaginatum[S]	0.22	**--**	**--**	-0.57
Carex panicea	0.23	0.25	0.25	0.40
Bistorta vivipara	0.27	**--**	0.38	-0.40
Carex rostrata	0.31	0.06	>0.99	0.25
Trichophorum alpinum	0.34	0.31	0.63	-0.29
Festuca ovina[S]	0.38	**--**	**--**	-0.29
Trichophorum cespitosum ssp. cespitosum	0.44	0.38	0.50	-0.15
Menyanthes trifoliata	0.50	0.75	0.88	-0.25
Carex capillaris	0.67	**--**	**--**	0.10
Euphrasia wettsteinii	0.70	**--**	**--**	-0.07
Selaginella selaginoides	0.72	0.06	0.25	0.05
Potentilla erecta	0.87	0.13	0.31	0.11
Pedicularis oederi[S]	0.94	**--**	**--**	-0.17
b) Plant taxa in pollen taxa group				
Dulichium-type	**<0.0001**	**0.047**	**0.039**	1.00
Cyperaceae	**<0.0001**	0.06	**0.012**	1.00
Poaceae	**<0.0001**	0.09	**0.008**	-0.95
Eriophorum spp.	**0.002**	0.14	**0.039**	0.60
Betula	**0.002**	**--**	0.38	-0.69
Pedicularis-type	**0.023**	>0.99	0.13	0.38
Drosera.[T]	**0.031**	0.38	0.25	0.75

Eriophorum-type (incl. *Trichophorum)*	**0.040**	0.77	0.35	0.30

959 **Table 5**
960 Mean pollen percentages of local terrestrial pollen and spores from the two study areas,
961 Tågdalen and Sølendet, for each land-use regime. SE= standard error; n= number of samples.
962 * displays pollen taxa included in the local terrestrial pollen sum. Cyperaceae includes
963 *Dulichium*-type and *Eriophorum*-type, Ericaceae includes *Calluna vulgaris*, Rosaceae
964 includes *Potentilla*-type. *Menyanthes trifoliata*, Ericaceae, *Drosera rotundifolia*-type,
965 *Saxifraga oppositifolia*-type and *Galium*-type from Tågdalen and *Anemone, Saxifraga*
966 *oppositifolia*-type, *Bistorta vivipara*-type, *Pinguicula*-type and *Rhinanthus*-type from
967 Sølendet, were found in few plots and with low percentages and are not included.
968

Pollen/spore taxa	Mown biennially			Mown quadrennially			Unmown		
	n (of 10)	Mean %	SE	n (of 6)	Mean %	SE	n (of 10)	Mean %	SE
Tågdalen									
Cyperaceae	10	**80.0**	1.8	6	**78.2**	3.2	10	**80.8**	1.4
Betula	10	**32.7**	1.9	6	**29.7**	3.5	10	**29.1**	1.3
Dulichium-type*	10	**25.5**	1.3	6	**25.2**	1.6	10	**26.7**	2.4
Eriophorum-type*	10	**16.2**	0.6	6	**16.1**	2.3	10	**9.0**	1.3
Selaginella selaginoides	10	**15.1**	1.5	6	**11.0**	2.2	10	**17.4**	3.7
Poaceae*	10	**7.8**	0.5	6	**9.3**	1.2	10	**9.4**	0.7
*Thalictrum**	10	**4.8**	1.0	6	**5.9**	1.6	10	**3.2**	0.6
Rosaceae	9	**2.4**	0.5	6	**2.6**	0.4	10	**2.9**	0.3
Potentilla-type*	8	**1.4**	0.3	5	**2.0**	0.3	10	**2.5**	0.3
Juniperus communis	9	**0.9**	0.2	4	**0.5**	0.2	9	**0.7**	0.1
Sphagnum	7	**0.6**	0.2	5	**0.6**	0.1	7	**0.6**	0.2
Solidago-type*	3	**0.4**	0.2	1	**0.1**	0.1	3	**0.1**	0.05
*Succisa pratensis**	5	**0.2**	0.07	1	**0.2**	0.1	3	**0.2**	0.1
*Anemone**	4	**0.2**	0.08	1	**0.06**	0.04	4	**0.2**	0.07
Pedicularis-type*	3	**0.2**	0.09	3	**0.3**	0.1	0	**0**	0
Menyanthes trifoliata[T] *	1	**0.1**	0.03	1	**0.08**	0.05	2	**0.05**	0.03
Sølendet									
Cyperaceae	10	**78.5**	4.1	3	**90.4**	2.2	10	**83.7**	2.8
Betula	10	**32.4**	3.0	3	**18.2**	2.6	10	**30.2**	2.9
Eriophorum-type*	10	**28.9**	2.2	3	**35.9**	1.9	10	**14.9**	1.1
Selaginella selaginoides	10	**19.2**	3.1	3	**9.6**	1.2	10	**11.3**	1.8
Dulichium-type *	10	**18.4**	1.2	3	**21.6**	2.4	10	**24.4**	1.2
*Thalictrum**	10	**12.6**	3.9	3	**5.4**	2.6	10	**3.9**	1.1
Poaceae*	10	**4.6**	0.6	3	**2.7**	0.5	10	**7.2**	1.3
Juniperus communis	8	**1.0**	0.2	3	**0.5**	0.1	8	**0.6**	0.1
Pedicularis-type*	7	**0.6**	0.1	2	**0.6**	0.3	7	**0.4**	0.1
Asteraceae Cichorioideae[S]*	9	**0.5**	0.1	1	**0.1**	0.1	5	**0.5**	0.2
Sphagnum	6	**0.4**	0.1	3	**0.7**	0.2	10	**0.5**	0.1
Ericaceae	5	**0.3**	0.1	1	**0.2**	0.2	6	**0.3**	0.1
Calluna vulgaris	5	**0.3**	0.1	1	**0.2**	0.2	4	**0.2**	0.1
Salix[S]	6	**0.3**	0.1	2	**0.3**	0.1	7	**0.4**	0.1
Rosaceae	8	**1.0**	0.2	0	**0**	0	9	**2.1**	0.5
Potentilla-type*	7	**0.7**	0.2	0	**0**	0	9	**2.0**	0.5
Solidago-type*	4	**0.2**	0.1	0	**0**	0	4	**0.3**	0.1
*Succisa pratensis**	4	**0.2**	0.1	0	**0**	0	2	**0.6**	0.3

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970 **Table 6**
971 Correlation between plant cover (transformed to pollen taxa) percentages and pollen
972 percentages, and indices of association (A, U, O) based on presence/absence data.
973 Abbreviations: T = test only from Tågdalen; S = only from Sølendet; ρ(rho) = Spearman rank-
974 correlation coefficient. Correlation coefficient significant at p<0.05 in bold. The indices of
975 association were classified into SAT = strongly associated types, AT = associated types,
976 WAT = weakly associated types, ORT = over-represented type, URT = under-represented
977 type and UT = unassociated type. See section 3.4.5. for further description. *Anemone* (WAT),
978 *Calluna vulgaris* (ORT), *Juniperus communis* (WAT), *Salix* (UT) and *Solidago*-type (WAT)
979 were present in too few plots with plant or pollen to conduct the test.

Pollen taxon	ρ	A	U	O	Association
Rosaceae	**0.47**	0.83	0.11	0.07	SAT
Potentilla-type	**0.44**	0.8	0.16	0.05	SAT
Pedicularis-type	**0.43**	0.59	0.34	0.14	AT
Succisa pratensis	**0.43**	0.38	0.59	0.13	WAT
Thalictrum	**0.35**	1	0	0	SAT
Menyanthes trifoliata	**0.31**	0.25	0.67	0.5	WAT
Selaginella selaginoides	**0.30**	0.88	0	0.12	SAT
Eriophorum/Eriophorum spp.	**0.25**	0.98	0	0.02	SAT
Poaceae/*Molinia caerulea*	**0.25**	1	0	0	SAT
Cyperaceae	**0.24**	1	0	0	SAT
Drosera rotundifolia-type[T]	0.21	0.06	0.94	0	URT
Poaceae	0.20	1	0	0	SAT
Asteraceae Cichorioideae [S]	0.18	0.19	0.25	0.8	WAT
Bistorta vivipara-type[T]	0.11	0.06	0.94	0	URT
Betula	0.05	0.43	0	0.57	ORT
Rhinanthus-type[S]	0.04	0.13	0.87	0	URT
Ericaceae	0.02	0.19	0.74	0.57	WAT
Galium-type[T]	-0.05	0	1	1	UT
Sphagnum	-0.13	0.21	0.11	0.79	WAT
Dulichium-type	-0.16	1	0	0	SAT
Pinguicula-type[S]	-0.22	0	1	1	UT
Saxifraga oppositifolia-type	-0.96	0.13	0.88	0	URT
Eriophorum-type	-0.01	1	0	0	SAT

980

981 **Table 7**
982 Pollen indicator taxa for management regimes in boreal rich fens based on the results from the
983 Wilcoxon signed rank test (relationship between vegetation and management regime) and the
984 Spearman rank-correlation coefficient (relationship between plant and pollen percentages).
985 The effect of traditional mowing on the relative vegetation cover (plants expressed as pollen
986 taxa) in fens is displayed as: + positive effect of traditional mowing, • no effect, - negative
987 effect). Results from earlier studies in the study areas are displayed in brackets (after Moen,
988 1990, 1995; Moen et al., 1999); see text for further details.
989 *Pedicularis-type pollen mainly increases with mowing, but single species are reduced with
990 mowing.

Pollen-vegetation relationship	Pollen/spore taxa	Effect of mowing
Very good pollen indicator	*Thalictrum*	+
Good pollen indicators	Cyperaceae	+
	Eriophorum-type	+
	Poaceae	-
	Succisa pratensis	-
	Pedicularis-type	+*
Potential pollen indicators	*Potentilla*-type	(-)
	Rosaceae	(-)
	Selaginella selaginoides	(+)
Pollen type reflecting unidentified factors in present study	*Menyanthes trifoliata*	(+/•)
Pollen types reflecting plant cover in earlier studies	*Anemone*	
	Asteraceae Cichorioideae (*Leontodon* spp./*Crepis* spp.)	(+/-)
	Betula	(-)
	Bistorta vivipara-type	(+)
	Calluna vulgaris	(-)
	Dulichium-type	(+/•/-)
	Drosera rotundifolia-type	(+)
	Ericaceae	(-)
	Galium-type	
	Juniperus communis	(-)
	Pinguicula-type	(+)
	Rhinanthus-type (*Euphrasia* spp./*Bartsia* spp.)	(+)
	Salix	(+/-)
	Saxifraga oppositifolia-type	(+)
	Sphagnum	(-)
	Solidago-type	(-)

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