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1 Dung fungi as an indicator of large herbivore dynamics in peatlands

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8 Declaration of interest: none

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10 Dung fungi as an indicator of large herbivore dynamics in peatlands

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13

14 Abstract

15 Coprophilous fungal spores (CFS) have gained prominence in palaeoecology as a proxy for
16 large herbivore dynamics. Dung availability is one of several factors that influences spore
17 abundance so it is unclear how closely CFS levels track herbivore biomass. This uncertainty is
18 particularly relevant in peat- and moorland, where grazing impacts are a recurring topic in
19 palaeoecology and source of tension in environmental management, and where the method
20 has yet to be tested. The current study used three ecological and conservation grazing
21 experiments in UK peat- and moorland to study modern and recent historic relationships
22 between grazing treatment and the abundance of three key CFS types and three pollen
23 disturbance indicators. A total of 78 surface samples and two short peat cores were
24 analysed. Dispersal distances are estimated to range from <10 m to tens of metres, based
25 on significantly lower CFS abundance in exclosed than grazed plots at two sites, and similar
26 CFS trends over the last century in short peats cores located 80 m apart at the third site. The
27 CFS signal thus represents activity in the surrounding landscape, despite predominantly local
28 dispersal. CFS abundance does not correspond with animal biomass when compared across
29 the three sites, however, and pollen disturbance indicators in the peat cores matched
30 recent historic grazing records more consistently than CFS abundance. Potential reasons for
31 these mismatches are discussed. Quantitative inferences about large herbivore abundance

32 from CFS in peatlands should therefore be made with caution and recommendations are
33 made for further testing of the method.

34

35 Keywords

36 Coprophilous fungi; non-pollen palynomorphs; Sporormiella; grazing disturbance

37

38 1.0 Introduction

39 Large herbivores influence the structure, diversity and functioning of many terrestrial
40 ecosystems. There is widespread concern over the ecological and socio-economic
41 consequences of significant declines in many large herbivore populations, as well as tension
42 over increasing herbivore numbers in other areas (Côté et al. 2004, Ripple et al. 2015).

43 However, it is difficult to predict what impact these changes in herbivore biomass will have
44 because data on animal populations are scarce over the long timescales associated with
45 ecological succession, nutrient cycles and climate change (Gordon et al. 2004, Malhi et al.
46 2016). Understanding the interactions between these factors is especially important in
47 periods of environmental change or stress, when herbivory may contribute to non-linear
48 vegetation responses (e.g. Gillson and Ekblom 2009, Dantas et al. 2016).

49 Palaeoecological data provide insights into ecosystem responses to changing disturbance
50 regimes over long timescales. Until relatively recently, palynology has been the most widely
51 used proxy for studying herbivory in sedimentary sequences. This is problematic, since
52 pollen is used to identify both grazing disturbance and its effects on plant communities, thus

53 adding potential circularity to causal arguments, whereas independent proxies would allow
54 a more rigorous assessment of cause and effect relationships. Coprophilous fungal spores
55 (CFS) have emerged as a proxy for large herbivore presence (Davis and Shafer 2006, Baker et
56 al. 2013). They have been used most often to infer the timing of megafaunal extinction (e.g.
57 Davis 1987, Burney et al. 2003, Gill et al. 2009, Froyd et al. 2014) and are increasingly being
58 used to understand what drives plant community dynamics over millennial timescales
59 (Jeffers et al. 2012, 2018, Ivory and Russell 2016). CFS can be analysed in the same samples
60 as pollen, making them a time-efficient addition to the palaeoecological tool-kit (Graf and
61 Chmura 2006).

62 Despite these advances, several studies suggest that the application of CFS in palaeoecology
63 may be outpacing validation of the method (Feranec et al. 2011). This is reflected in
64 contradictory recommendations about the interpretation of CFS signals: some studies
65 highlight the potential for CFS to provide a quantitative measure of herbivore population
66 size (Gill et al. 2013, Baker et al. 2016), while others urge caution because of our incomplete
67 understanding of the range of factors that may influence CFS abundance (Feranec et al.
68 2011, Dodson and Field 2018). A further gap in current knowledge arises because many
69 modern and palaeoecological studies of CFS have used lake sediments (Raper and Bush
70 2009, Parker and Williams 2012, Baker et al. 2016). There is less evidence from terrestrial
71 sediments to help interpret CFS signals from peat cores, even though peatlands are a key
72 source of palaeoenvironmental data (Payne et al. 2016, Gearey and Fyfe 2016) and were
73 important in early work on non-pollen palynomorphs (van Geel 1978). The small number of
74 CFS studies from peat- and moorlands suggest that CFS complement pollen, particularly
75 where high levels of grazing and browsing suppress pollen production (Räsänen et al. 2007,

76 Fyfe et al. 2008, Davies 2016). However, local hydrological conditions in wetlands may also
77 affect the CFS signal, so multiple drivers must be considered when interpreting changes in
78 the abundance of CFS in wetland sites (Wood and Wilmshurst 2012, Kamerling et al. 2017).
79 At present we therefore have an incomplete understanding of what controls spore
80 production, dispersal, deposition and taphonomy, and, consequently, how closely CFS
81 abundance tracks herbivory levels. More calibration and experimental studies are needed to
82 underpin inferences about large herbivore abundance from CFS in sedimentary and
83 archaeological contexts (Baker et al. 2016, Perrotti and van Asperen 2019).

84 The aim of this study is to examine CFS dispersal and taphonomy in relation to grazing
85 regimes in peat- and moorland ecosystems. It is important to understand the potential
86 indicator value of CFS in this setting because acidic and waterlogged conditions provide few
87 niches for the indicator taxa that are used in palynology to identify grazing disturbance,
88 many of which are characteristic of more minerogenic soils. As a result, pollen may be a
89 relatively insensitive indicator of local grazing disturbance in areas with extensive peat cover
90 (Davies and Tipping 2004). No previous methodological studies have explicitly compared
91 pollen with fungal spores in this setting. Legacies from historic grazing practices and
92 contemporary stocking regimes influence moorland diversity, erosion and carbon dynamics,
93 and animals are consequently a source of tension in moorland management (Holden et al.
94 2007, Worrall and Clay 2012, Swindles et al. 2016). Alternative and improved techniques for
95 detecting herbivores in peatlands could thus make a significant contribution to
96 understanding the long-term impacts of grazing on peatland function and resilience.

97 This exploratory study uses two long-term field-scale grazing experiments and one 'natural
98 experiment' on a conservation grazing site, all on peat- and moorland within the UK, to test

99 the quality of palaeoecological inference (Jackson 2012, Bakker et al. 2016). The study
100 addresses the following broad research questions: (1) can CFS be used as a grazing indicator
101 on peatlands, and (2) how do CFS compare with pollen as a grazing indicator? More
102 specifically in relation to question one, the study examines whether the abundance of CFS
103 can be used to differentiate between grazing treatments, and whether there is a
104 quantitative relationship between CFS abundance and large herbivore biomass. A multi-site
105 approach allows the study to investigate how consistent these relationships are across a
106 range of moorland ecosystems.

107

108 2.0 Study sites and methods

109 2.1 Study sites

110 The three study sites span a range of peat- and moorland habitats and grazing regimes (Fig.
111 1, Table 1). They were selected for the longevity of well-documented grazing regimes and
112 the existence of well-defined plots or compartments with different grazing treatments. This
113 allows treatment effects on CFS abundance and dispersal distances to be examined relative
114 to the size of the experimental plots. The experimental sites are part of the UK
115 Environmental Change Network, which offers long-term insights into ecological trends and
116 processes (Morecroft et al. 2009, Rose et al. 2016). The sites and established grazing
117 treatments are described before outlining the research design used in this study.

118 Moor House National Nature Reserve (NNR) is a 3800 ha upland mosaic of blanket peat and
119 acid grassland communities in the North Pennines, northern England (Eddy et al. 1969). Ten
120 experiments were established across the site between 1954 and 1972 to study the long-

121 term impacts of sheep (*Ovis aries*), grazing and burning on upland biodiversity and carbon
122 sequestration (Marrs et al. 1986, Garnett et al. 2000, Lee et al. 2013, Milligan et al. 2016).
123 All experiments consist of paired plots, with one from each pair fenced to exclude sheep
124 (i.e. exclosed) and the other left open to allow free-range grazing. Four of the experiments
125 were sampled in this study, all located on blanket peat (Table 1). The selected sites are 1.4-
126 2.5 km apart. Summer grazing intensities across the NNR have not remained constant over
127 time and also vary with vegetation type. Until 1972, average grazing intensity was
128 approximately 2.2 sheep/ha or 121 kg/ha (Rawes and Welch 1969). Densities were then
129 reduced to around 1.8 sheep/ha (100 kg/ha) and the current stocking density of 0.5
130 sheep/ha (28 kg/ha) was established in 2001 following an outbreak of Foot and Mouth
131 disease (Milligan et al. 2016, R. Rose, pers. comm.). The sampling sites, particularly Hard Hill
132 and Bog Hill, which have deeper blanket peat with heather-dominated cover, are less
133 attractive to grazers than neighbouring grassland. They are likely to have supported lower
134 herbivore densities, on the order of 0.1-0.3 sheep/ha, and been less affected by changes in
135 overall stocking density (Rawes and Welch 1969, Lee et al. 2013, Martin et al. 2013). Small
136 herbivores are also present, with a density of approximately 0.25 to 1.4 red grouse (*Lagopus*
137 *lagopus scoticus*)/ha (0.2-1.1 kg/ha) (R. Rose, pers. comm.). Numbers of wild deer (mainly
138 roe deer, *Capreolus capreolus*) are thought to be very low.

139 Glensaugh is a research station and hill farm located in upland Aberdeenshire, NE Scotland.
140 Four pairs of grazed and exclosed plots were established in 2005 in dry heathland as part of
141 a multi-site experiment to study the impact of woodland expansion onto *Calluna*-dominated
142 moorland, including the influence on soil properties and the role of herbivores (Mitchell et
143 al. 2007). The treatment and control plots are 10-20 m apart within a 14.66 ha fenced area

144 which is grazed by red deer stags (*Cervus elaphus*) at a density of 0.27 deer/ha. No other
145 herbivores are present within the deer enclosure.

146 Flanders Moss is a lowland raised bog located in central Scotland. This site forms a 'natural
147 experiment', since current management on one farm includes two grazing compartments
148 with different intensities of summer grazing by Shetland cattle, a comparatively small and
149 hardy breed. These comprise rush pasture on drained peat and remnant raised peat, with
150 estimated stocking densities of 2 and 0.5 cattle/ha, respectively. The pasture occupies land
151 that was drained and cleared of peat during the late eighteenth and nineteenth centuries
152 (Harrison 2008) and the current cattle grazing regime has been maintained for around 20
153 years. An adjacent area of the raised bog with no livestock grazing was also sampled for
154 comparison. The legacy of historical drainage combined with neighbouring afforestation is
155 leading to scrub encroachment. Conservation grazing on the peatland is intended primarily
156 to control this process, in combination with drain-blocking to raise the watertable. Wild
157 deer (mainly red deer) also have access to Flanders Moss, with densities to the east of the
158 study area estimated at 0.06-0.1 red deer/ha, which is high for a lowland agricultural setting
159 (Flanders Moss Deer Management Forum 2017).

160 After conversion to animal biomass/ha, the three sampling sites range support
161 comparatively low (Moor House), moderate (Glensaugh) and moderate to high herbivore
162 biomass levels (Flanders Moss) (Table 1). However, these estimates are low in comparison
163 with previous surface CFS studies, where values range from 118-136 kg/ha of bison (*Bison*
164 *bison*) (Gill et al. 2013) to 308-1863 kg/ha of cattle (*Bos taurus*), horse (*Equus ferus caballus*),
165 red deer and geese (*Anser anser*) (Baker et al. 2016). The grazing regimes in the present
166 study have varied ecological impacts. Deer herbivory at Glensaugh is restricting the growth

167 and recruitment of *Betula* (birch) and *Pinus sylvestris* (Scots pine) trees in planted sections
168 of the experimental plots, indicating that deer numbers are above regeneration limits
169 (Putman et al. 2011). At Moor House, sheep exclusion since the mid-twentieth century has
170 increased the abundance of *Calluna* and grazing-sensitive species on blanket peat (Rawes
171 1983). Relatively light summer grazing and sheep preference for grassland means that
172 current grazing levels on peat-dominated sites, like those in this study, are low enough to
173 enable the recovery of moorland taxa and recolonization of eroded peat, with limited
174 impact on plant species composition, diversity and carbon accumulation, although the
175 presence at Silverband of *Splachnum sphaericum*, which grows on herbivore dung, indicates
176 that grazing has some floristic impact (Garnett et al. 2000, Lee et al. 2013). This contrasts
177 with impacts on adjacent grassland communities, where grazing has contributed to a decline
178 in species diversity since the mid-twentieth century (Milligan et al. 2016). Less information is
179 available for Flanders Moss and on the effects of cattle grazing on peat, more generally,
180 although the need for manual tree seedling removal indicates that the current grazing and
181 hydrological regimes are not preventing continued colonisation. The impacts of wild deer on
182 Flanders Moss peat communities have been assessed as limited and localised, but there is
183 concern that deer impacts and the extent of bare ground are increasing (Laird 2014,
184 Flanders Moss Deer Management Forum 2017). Fungal and pollen signals for grazing will be
185 assessed within these varied ecological contexts.

186 2.2 Methodology and experimental design

187 Experimental plots and grazing compartments were sampled to assess whether spatial
188 variability in the CFS and pollen signals could be linked with the grazing regimes at the three
189 sites. In total, 78 samples were analysed, 24 each from Moor House and Glensaugh, and a

190 further 30 samples from Flanders Moss. At Moor House and Glensaugh, three surface moss
191 samples were taken from each of the four pairs of open (grazed) and fenced (exclosed)
192 plots, giving a total of 12 samples from each treatment at each location. Three samples
193 (replicates) were taken to examine variability within treatment plots. Each sample consisted
194 of three handfuls of moss from a c.1 m² area within the central area of each plot, and the
195 replicates were c.2 m apart. Samples consisted mainly of green parts of surface mosses,
196 with a preference for *Sphagnum* where this was available, but included a range of moss
197 species and occasionally litter when mosses were scarce. Since the grazing compartments
198 are larger at Flanders Moss, two 300-400 m perpendicular transects were laid out across the
199 rush pasture, cattle-grazed and livestock-free areas of raised peat (Fig. 1). Thirty samples
200 were collected along these transects, at 15 and 30 m intervals. Dominant vegetation cover
201 and any evidence of herbivory (dung, browsing on heaths, tracks) were recorded at each
202 sample location (Table A.1).

203 This research design does not allow CFS dispersal to be assessed over a range of distances,
204 since treatment effects and dispersal distances are estimated relative to fixed plot and
205 compartment sizes (cf. Gill et al. 2013), but the study provides a first approximation of the
206 source area and sensitivity of CFS to plot- and field-scale grazing patterns in peat- and
207 moorland communities. Short-distance variations in CFS abundance occur in both lake and
208 wetland sediments (Raper and Bush 2009, Kamerling et al. 2017), so multiple samples from
209 each treatment allow the extent of spatial replicability/variability to be assessed.

210 To compare indicator trends with known grazing history over the duration of the
211 experiment at Moor House, the longest-running of the three experiments, 50 cm deep peat
212 cores were extracted from one exclosed and one grazed plot on the Hard Hill site (Hard Hill

213 block A, Marrs et al. 1986) using a golf-hole corer. This allows an undisturbed sediment core
214 to be extracted from poorly humified, near-surface peat deposits. The peat cores were used
215 to assess temporal trends in the CFS signal over the 70 year duration of the experiment, and
216 to assess spatial differences in CFS representation between cores that are about 80 m apart
217 (cf. Edwards 1983).

218 Surface and core samples were analysed for pollen and selected non-pollen palynomorphs
219 (NPPs). Samples were processed using standard pollen analytical techniques, including
220 acetolysis but without hydrofluoric acid (Moore et al. 1991). Volumes were ~5-7 ml for
221 surface samples and ~1 ml for peat sediments. A minimum of 500 total land pollen grains
222 (TLP, excluding aquatic taxa, plant and fungal spores) was counted for each sample. Pollen
223 identification was based on standard pollen keys (Moore et al. 1991). Three coprophilous
224 fungal spore types were quantified on pollen slides. *Sporormiella* HdV-113, *Sordaria*-type
225 HdV-55A and *Podospora*-type HdV-368 have a strong, possibly obligate, preference for
226 dung, show a strong association with the presence of large herbivores and survive well
227 (Baker et al. 2013, van Asperen et al. 2016, Perrotti and van Asperen 2019). Fungal spore
228 nomenclature follows Miola (2012), although lab identifiers (e.g. HdV) are omitted in
229 subsequent text for brevity. Three pollen indicator taxa were selected, based on known
230 relationships with grazing disturbance: *Plantago lanceolata*, *Rumex* and *Urtica* (Sagar and
231 Harper 1964, Behre 1981, Bunting 2003). While not characteristic of moor and peatland
232 communities, these taxa are commonly used in peatland palaeoecology as indicators of
233 grazing in the landscape. In this study, they were more common than other herbaceous
234 pollen taxa. CFS and pollen abundance is expressed in relative (percentage of TLP) and

235 absolute terms (concentrations, based on the addition of *Lycopodium* tablets during sample
236 processing (Stockmarr 1971)).

237 Approximate chronologies for the peat cores were derived using spheroidal carbonaceous
238 particles (SCPs) which provide recent stratigraphic markers derived from fossil fuel
239 combustion. SCP concentrations on pollen slides were used to identify three key dating
240 horizons attributable to broad-scale changes in fossil fuel use over the last c.250 years: the
241 earliest appearance of SCPs (AD 1850 \pm 25), rapid rise (AD 1955 \pm 15) and peak
242 concentration (AD 1974 \pm 4) (Rose and Appleby 2005, Swindles 2010).

243 A Kruskal-Wallis chi-square test was used to assess whether there are statistically significant
244 relationships between grazing indicator abundance and grazing treatment. Response
245 variables included the CFS sum and the sum of three pollen grazing indicators, both
246 expressed as percentages (%TLP) and as concentrations (spores or pollen per cm³).

247 Ordination was used to understand the relationship between CFS and pollen grazing
248 indicators. The main patterns of variation in the combined pollen and NPP dataset were
249 identified using non-metric multidimensional scaling (NMDS) (similar results were obtained
250 using PCA with Hellinger transformation). A reduced dataset, including taxa present in \geq 4
251 samples only and excluding arboreal taxa, cereal-type pollen, aquatics or spores, was used
252 in order to focus on relationships between local, open ground pollen and fungal spore taxa.

253 Raw data from the reduced dataset were recalculated as proportions of the revised sum,
254 which consisted of pollen and fungal spores. *Podospora*-type was excluded since it did not
255 meet the selection criteria (presence in \geq 4 samples), whereas *Sporormiella*-type and
256 *Sordaria*-type were more frequently encountered at all sites. All analyses were implemented
257 in R, using default settings in the *vegan* package (R Core Development Team 2011).

258

259 3.0 Results

260 3.1 Treatment effects, dispersal distance and variability in indicator values

261 Coprophilous fungal spores were present in all samples. Average (mean and median) CFS
262 abundance is higher in grazed samples than enclosed plots and the ungrazed compartment
263 at Glensaugh and Flanders Moss (Fig. 2). A Kruskal-Wallis test indicates that CFS values are
264 significantly higher in grazed plots at Glensaugh when expressed as a concentration, and
265 significantly higher in both grazed compartments than on the ungrazed bog at Flanders
266 Moss for percentage and concentration values (Table 2). This suggests that, when expressed
267 as concentration abundance, CFS dispersal at Glensaugh is less than 10 m, which is the
268 distance from mid-plot (where samples were obtained) to the enclosure fence. At Flanders
269 Moss, the findings indicate that aggregate CFS abundance for each compartment can be
270 used to differentiate between grazed and ungrazed areas, using both CFS percentages and
271 concentrations. There are no significant differences in CFS values (relative or absolute)
272 between treatments at Moor House, suggesting that dispersal distances exceed plot size
273 (i.e. >4.5-15 m: the distance from the centre to the boundary of the plots). CFS abundance is
274 highly variable between plots and between sites (Fig. A.1-A.2, Table A.2). Average CFS
275 concentrations at Moor House are over four times higher than Glensaugh and more than 10
276 times higher than Flanders Moss (Fig. 2). This is in inverse order to estimated herbivore
277 biomass (Table 1).

278 The average abundance of pollen disturbance indicators is higher in grazed than ungrazed
279 samples at Moor House and Flanders Moss, but not at Glensaugh (Fig. 2, Table A.2). This

280 relationship is only statistically significant at Flanders Moss, where the percentage
281 abundance of pollen indicators is higher on the grazed than the ungrazed bog (Table 2, Fig.
282 A.2). Treatment differences are not significant at Moor House. Instead, the mean
283 abundance of pollen indicators in each of the four Moor House experiments corresponds
284 with vegetation type and relative palatability to sheep. Higher values occur in the sedge-
285 and grass-rich sites (Silverband, Troutbeckhead) and lower values are recorded in the
286 heather-dominated sites which are less preferred by sheep (Hard Hill, Bog Hill) (Grant et al.
287 1987, Williams et al. 2012) (Fig. A.1). Pollen indicator values therefore track vegetation type,
288 which is similar in the exclosed and grazed plots at each location, rather than treatment.
289 Similar to CFS, the site with the lowest grazer biomass (Moor House) has the highest
290 abundance of pollen indicators (Table 1, Fig. 2, Fig. A.1, Table A.2).

291 3.2 Comparison of CFS and pollen disturbance indicators: spatial and temporal relationships

292 CFS frequencies are often higher than pollen indicator values (Fig. 2: compare y-axis scales)
293 and they plot in different areas of ordination space in the NMDS (Fig. 4). At all sites, the
294 main gradient on ordination Axis 1 is between *Calluna* and *Poaceae* dominated samples or,
295 at Glensaugh, between denser and more open heather cover. At Moor House, this
296 differentiates the heather-dominated blanket peat plots (Hard Hill, Bog Hill) from the
297 *Eriophorum*-dominated plots (Troutbeckhead, Silverband). At Flanders Moss, the rush
298 pasture samples are differentiated from the raised bog plots by higher abundance of
299 herbaceous taxa. Treatments overlap at all sites, indicating that they do not have discrete
300 pollen (vegetation) assemblages. Pollen disturbance indicators, along with most herbaceous
301 pollen taxa, are associated with *Poaceae*, rather than *Calluna* and other heaths.

302 The position of the dung fungi varies between sites and taxa. *Sordaria* scores overlap with
303 *Poaceae* and other NAP at Moor House and Glensaugh, but it is positioned closer to the
304 heath pollen scores at Flanders Moss. *Sporormiella* is positioned towards the *Poaceae* and
305 other NAP scores at Glensaugh and Flanders Moss, but separated from all other taxa on Axis
306 2 at Moor House. *Podospora* was excluded due to infrequent occurrence.

307 The peat cores from the exclosed and grazed plots in Hard Hill experiment at Moor House
308 provide a comparison of indicators over time. The pollen disturbance indicators and CFS
309 show similar trends in both cores (Fig. 5), but the two proxies are not always in agreement.
310 There are two periods with higher or peak CFS values: the first around and after the start of
311 the experiment in 1954, dated by a steep rise in SCP values, and the second during the
312 1990s. Pollen indicator abundance is relatively high during the late nineteenth to mid-
313 twentieth centuries, with a peak in the decade after the experiment began, similar to CFS.
314 Pollen indicator values rise slightly in the grazed plot within the last two decades, but
315 remain low in the exclosure.

316

317 4.0 Discussion

318 This study provides the first evidence for CFS dispersal distances in peatland settings and
319 indicates a complex relationship between herbivory levels and the abundance of
320 coprophilous fungal spores in peat- and moorlands. The key factors that influence
321 relationships between the two proxies (CFS and pollen) and the grazing regimes are
322 discussed before evaluating the potential for and limits to quantitative interpretation of
323 dung fungi as a proxy for herbivory.

324 4.1 Understanding coprophilous fungal spore signals

325 In laboratory studies, spore discharge distances for dung fungi range from 10.5 cm
326 (*Sordaria*) to 20 cm (*Podospora*) (Ingold and Hadland 1959, Yafetto et al. 2008). Field-based
327 estimates of dispersal distance are therefore essential to understand how sensitive the CFS
328 signal is to local and landscape-scale grazing. The present results suggest that CFS dispersal
329 distances in peat- and moorlands range from <10 m at Glensaugh to tens of metres at
330 Flanders Moss and Moor House. This is true of both surface and peat core samples at Moor
331 House, where the non-significant treatment effects suggest that dispersal distances exceed
332 4.5-15 m, and similar CFS and pollen signals in two peat cores separated by 80 m indicate a
333 source area of at least this distance. These estimates are comparable with dispersal
334 distances established in previous surface sample studies from wet- and dry-land settings,
335 which range from <10 m from ponds in wet grassland (Baker et al. 2016) to 25-100 m from
336 Tauber traps in prairie grassland (Gill et al. 2013).

337 In this study, it is assumed that dispersal on air currents is the main mechanism for the
338 transport of fungal spores from fruiting bodies, which are produced on or near the ground,
339 to the mainly low-growing vegetation cover. Fungal spores can also be transported by water
340 (e.g. Raper and Bush 2009, Etienne et al. 2013). This is possible at Glensaugh, the only site in
341 the present study with pronounced slopes, but significant treatment differences suggest
342 that water-borne spore movement is limited on these well-vegetated slopes.

343 Treatment effects across the three sites were stronger for CFS than for pollen disturbance
344 indicators (Table 2). In part, this may be due to differences in source area between the two
345 proxies. For pollen, this includes local and background components (Jacobson and Bradshaw

346 1981). The indicator taxa used in this study are well-dispersed (Bunting 2003, Mazier et al.
347 2006) and likely to originate from acid grassland in the wider landscape owing to the limited
348 availability of suitable ecological niches within blanket peat. This is discussed below in
349 relation to the peat cores. Previous work indicates that high herbivore biomass at a
350 landscape level can lead to a significant background CFS component that is not related to
351 local herbivore distribution (Baker et al. 2016). Where grazer biomass in a landscape is low,
352 as is the case at the present study sites, it is therefore possible that the background
353 component of a CFS signal is small. This may mean that CFS and pollen signals represent
354 processes on different scales. Additional multi-site studies are needed to understand how
355 local and background components of the CFS signal change with herbivore abundance, since
356 this has implications for understanding ecological impacts and CFS thresholds for inferring
357 herbivore presence/absence.

358 At a local level, CFS peaks in some samples may reflect localised spore production and
359 dispersal around frequent use areas, such as animal tracks at Flanders Moss (samples 8, 25
360 and 26) and plots with path erosion and higher levels of tree browsing at Glensaugh (G1 and
361 G2) (Fig. 3, Fig. A.1-A.2). Previous studies have also noted high CFS values in terrestrial sites
362 where herbivores congregate or are corralled, indicating that CFS abundance depends on
363 both the size of the animal population and the duration of occupation (Davis and Shafer
364 2006, Parker and Williams 2012, Kamerling et al. 2017). The implications for identifying
365 thresholds to differentiate between grazed and ungrazed areas are discussed below.

366 Dispersal distance alone does not explain all patterns in CFS data, however, including large
367 differences in CFS abundance between sites and the inverse relationship between estimated
368 herbivore biomass and mean CFS values across the three sites (Table A.2). Mycological

369 studies indicate that fungal spore production is influenced by the quantity and quality of
370 dung as well as environmental conditions (Kuthubutheen and Webster 1986, Richardson
371 2001). In terms of dung type, the study sites are grazed by different herbivores, which will
372 influence their mycobiota, but it is not known if this influences CFS abundance in predictable
373 ways (Richardson 2001, van Asperen 2017). Small herbivore influence is considered below,
374 along with environmental and sampling considerations.

375 In this study, the highest mean CFS abundance and the lowest herbivore biomass occur at
376 Moor House. Small herbivore contributions may have increased CFS abundance here, since
377 red grouse dung was noted in some plots and enclosure fences do not exclude the birds
378 (Table A.1). Grouse numbers are low, but they are resident throughout the year, unlike
379 livestock, and so may contribute to CFS abundance and blur a plot-scale large herbivore
380 signal. Views about the relative CFS contribution from larger and smaller herbivores are
381 contradictory: Wood and Wilmshurst (2013) suggest that small herbivore contributions are
382 underestimated, while faecal and mycological studies show that dung from grouse and small
383 mammals is less abundant and less suitable for fungal growth than that from large
384 herbivores (Welch 1982, Richardson 2001). The role of small herbivores therefore remains
385 in need of further study.

386 Hydrological variability can also affect CFS signals and herbivore behaviour in wetlands, with
387 some evidence that in saturated sediments, *Sporormiella* abundance tracks hydrological
388 fluctuations rather than grazing levels (Wood and Wilmshurst 2012, Kamerling et al. 2017).
389 It is not possible to test directly for hydrological effects in this study, but plot-level CFS
390 values are highest at Moor House (with varied blanket peat conditions), followed by
391 Glensaugh (dry heath) and then Flanders Moss (dry peat and wet *Sphagnum* lawn). This cuts

392 across site-level differences in wetness and herbivore biomass (Fig. 2), suggesting that
393 factors other than wetness may be more significant determinants of CFS abundance.

394 The duration of sample accumulation and inter-annual variability in growing conditions
395 could also influence the fungal and pollen signals. Moss polsters are thought to represent
396 one to several years' worth of pollen and spore production, depending on species' growth
397 rates and growing conditions (Räsänen et al. 2004, Lisitsyna and Hicks 2014). Strong
398 differences in CFS and pollen values between the three study sites, especially in
399 concentrations (Fig. 2), could result from geographical differences in the moss species
400 sampled (Table A.1), relative moss growth rates and environmental conditions. The
401 relationship between sheep numbers and dung volume also breaks down when
402 measurements cover shorter periods (Rawes and Welch 1969). As a result, comparisons
403 between surface samples from different sites and extrapolation from surface samples to
404 sediments should be made with caution until temporal variability is better understood.

405 CFS studies that combine current and recent subfossil evidence in locations with
406 independent evidence for grazing levels could improve our understanding of how
407 transferable modern data are to sedimentary contexts. Few studies have taken this
408 approach (e.g. Cugny et al. 2010, Etienne et al. 2013). In the present study, temporal
409 averaging in the peat cores appears to reduce some of the 'noise' evident in the surface
410 samples. Each proxy shows a similar trend in both cores, which are 80 m apart, suggesting
411 that they provide a spatially-replicable signal from the surrounding landscape. This
412 reinforces the inference that CFS dispersal in surface samples exceeds plot sizes at Moor
413 House. Both indicators peak in the decade after the start of the experiment, during
414 maximum grazing levels, but a second CFS peak during the 1990s is weak (exclosure) or

415 absent (grazed plot) from the pollen record and does not match low stocking levels (Fig. 5).
416 Pollen therefore provides a more consistent match to grazing history. Divergent pollen and
417 fungal signals have been observed in previous studies, but in those cases, a combination of
418 high CFS values and low pollen indicator abundance was interpreted as reduced pollen
419 production under high grazing densities (Fyfe et al. 2008, Davies 2016). This is not the case
420 at Moor House, where stocking levels are low and grazing impacts are limited. Disparities
421 between CFS and non-pollen grazing indicators have also been observed in previous studies,
422 although the reasons for this are not always clear (Ortiz et al. 2016, Chepstow-Lusty et al.
423 2019), while other records show strong and consistent correlations between palynological
424 and fungal indicator values (e.g. Wood et al. 2016). This emphasises the need for further
425 methodological testing and the value of a combined surface and historic approach.

426 4.2 Implications and recommendations for the use of dung fungi as a proxy for herbivory in 427 moor- and peatlands

428 Two key aims of this and previous surface studies have been to understand CFS dispersal
429 and to identify meaningful thresholds for inferring large herbivore presence. This study
430 reinforces previous evidence that the CFS signal in small-diameter sampling sites originates
431 from the surrounding tens of metres, but demonstrates that dispersal distance and CFS
432 abundance can vary between sites for reasons that are incompletely understood. In
433 previous research, a threshold of around 2% TLP has been suggested for identifying large
434 herbivore presence (Davis 1987, Feranec et al. 2011, Gill et al. 2013). It was not possible to
435 identify common thresholds in this study due to variations in CFS abundance between the
436 three sites and the poor match between CFS abundance and grazer biomass. These findings
437 reinforce existing results, which urge caution when transferring quantitative thresholds

438 between environmental settings, grazing regimes and time periods, and stress the
439 importance of testing how the quantification method affects inferred relationships between
440 CFS and herbivory (e.g. Baker et al. 2013, Wood and Wilmshurst 2013, Perrotti and van
441 Asperen 2019). The inverse relationship between CFS and herbivore abundance across the
442 three sites indicates that quantitative relationships between CFS and herbivore abundance
443 cannot be reliably inferred unless other taphonomic, environmental, behavioural and
444 husbandry factors which influence CFS abundance are also understood (e.g. Parker and
445 Williams 2012, Wood and Wilmshurst 2012).

446 Most CFS studies have focused on major transitions, such as megafaunal extinctions or
447 livestock introductions, but questions remain as to how closely CFS track more modest
448 changes in large herbivore abundance, such as those often associated with land-use change
449 and conservation management, or how they relate to ecological sensitivity and thresholds.
450 These are significant gaps in knowledge since CFS are being used to assess whether
451 changing levels of herbivory influence ecosystem dynamics (e.g. Lopez-Merino et al. 2011,
452 Jeffers et al. 2012, Guillemot et al. 2015). This study incorporated a range of grazing
453 densities (Table 1), but CFS abundance was not a good predictor of herbivore biomass or
454 ecological impact. Multi-year trapping studies using Tauber traps, moss polsters, surface
455 lake and peat sediment samples, similar to those used to understand pollen productivity
456 and calibrate pollen-vegetation models (Sugita et al. 2010, Poska 2013), are needed to
457 establish how variable spore production is for CFSs and NPPs in general, and how much
458 variability in influx can be explained by herbivore biomass. The influence of small herbivores
459 and entire herbivore communities on CFS abundance also merits further study (Feranec et
460 al. 2011, Wood et al. 2011, Baker et al. 2016).

461 The present findings indicate that dung fungi can track known historical changes in animal
462 abundance but may do so imperfectly (e.g. Gelorini et al. 2012, Kamerling et al. 2017,
463 Orbay-Cerrato et al. 2017). With the current state of knowledge, inferences about herbivore
464 impacts should be considered most reliable at high (peak) CFS values (Gelorini et al. 2012,
465 Raczka et al. 2016) since we cannot currently explain why multiple proxies are not always in
466 agreement regarding herbivore levels. Analysing dung fungi alongside other proxies of
467 animal presence, such as dung beetles, faecal biomarkers and other molecular indicators,
468 would improve our understanding of how reliably CFS track long-term herbivore dynamics
469 and their impacts (e.g. de Bruyn et al. 2011, Smith et al. 2014, Etienne et al. 2015, Ortiz et al.
470 2016, Zocatelli et al. 2017). More use could also be made of historical herbivore records and
471 ecological experiments to disentangle these relationships (Bradshaw and Mitchell 1999,
472 Davies and Watson 2007, Bakker et al. 2016).

473

474 5.0 Conclusions

475 Non-pollen palynomorphs, including coprophilous fungal spores, are becoming a standard
476 component of palaeoenvironmental studies (e.g. Chambers et al. 2012, Edwards et al. 2015,
477 Birks and Berglund 2018), but the evidence needed to inform our interpretation of fossil
478 data is at a relatively early stage of development. This study supports some previous
479 findings but also identifies significant gaps in knowledge. The current results reinforce
480 existing evidence that dispersal distances for CFS are predominantly local, around tens of
481 metres or less. This indicates that dung fungi provide a local indicator with a source area
482 smaller than many pollen types. However, the trends in CFS abundance over the last century

483 were similar in grazed and exclosed plots located 80 m apart, which suggests that CFS
484 signals are not too localised to represent activity in the surrounding area. This provides
485 increased confidence that dispersal and treatment relationships identified in surface
486 samples are applicable to sedimentary records and indicates that major trends may be
487 spatially replicable. Uncertainties remain though and the present findings indicate that
488 inferences from CFS about large herbivore abundance or biomass should be made with care.
489 In particular, the reasons for large differences in surface sample CFS abundance between
490 sites remain incompletely understood. Potential explanations include differences in large
491 herbivore type, levels of small herbivore dung, vegetation structure, moisture availability,
492 exposure and sampling factors (sample duration, inter-annual variability), in addition to
493 climatic and other larger-scale environmental variables.

494 A number of research directions are recommended. These include further modern
495 calibration studies that span a range of settings and gradient of grazing levels and ecological
496 impacts, from 'passive' to degrading or 'ecosystem engineering' levels of herbivory. This
497 would allow us to better understand how grazing intensity and ecosystem sensitivity affect
498 CFS and pollen signals. For instance, current evidence suggests that CFS abundance may be
499 more reliable at 'high' levels (e.g. Raczka et al. 2016), but what constitutes 'high' will vary
500 depending on the herbivore community, ecological sensitivity and broader environmental
501 factors influencing ecosystem productivity (Feranec et al. 2011, Barnosky et al. 2016). Multi-
502 year monitoring to understand inter-annual and inter-site variability, and studies of trends
503 over recent decades at sites with known animal densities would allow the influence of
504 herbivory and environment on CFS abundance to be more rigorously assessed. This creates
505 opportunities for multi-proxy studies, particularly where it is possible to add fungal analyses

506 to existing records to test interpretations using multiple lines of evidence or make fuller use
507 of ecological and 'natural' experiments (e.g. Bradshaw and Mitchell 1999, Mitchell 2005,
508 Bakker et al. 2016). With appropriate meta-data and archiving, this would help build a geo-
509 temporal network suitable for examining local and regional patterns in fungal spore
510 abundance to test more fully the quantitative potential and limitations of dung fungi as a
511 proxy for large herbivores.

512

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798 **Table 1.** Location and grazing regime at each sampling site. Estimated herbivore biomass is based on information from published literature or
799 supplied by site managers: 55 kg hill ewe, 190 kg hill red deer stag, 350-450 kg Shetland cattle

Site	Grid location and elevation	Plot size	Vegetation type & condition	Experimental grazing regime	Estimated animals/ha	Biomass (kg/ha)	Biomass (kg/ha/yr)	Relative biomass
Moor House – Troutbeckhead	NY 72236 31760, 680 m OD	14 x 24 m	<i>Eriophorum</i> blanket peat with gully erosion	Sheep, April to October	0.5	28	16	Low
Moor House – Silverband	NY 71059 30975, 690 m OD	16 x 26 m	<i>Eriophorum</i> blanket peat with bare peat	As above	0.25	14	8	Very low
Moor House – Hard Hill (Block A sampled)	NY 74300 33000, 590 m OD	30 x 30 m	Intact <i>Calluna-Eriophorum</i> blanket peat	As above	0.1-0.3	5.5-16.5	3.2-9.6	Very low
Moor House – Bog Hill	NY 76789 32869, 550 m OD	9 x 14 m	Intact <i>Calluna-Eriophorum</i> blanket peat	As above	0.2	11	6.4	Very low
Glensaugh (Calluna control plots samples)	NO675801, 230-300 m OD	20 x 100 m blocks with 18 x 15 m treatment plots	Dry <i>Calluna</i> heath on hillslope	Red deer stags, mid-November to mid-September	0.27	53	44.3	Medium
Flanders Moss rush pasture	NS 64820 98740, 15 m OD	8.7 ha	<i>Poaceae</i> -dominated pasture with <i>Juncus</i>	Shetland cows with calves, May to September	1.95	879	366	Very high
Flanders Moss raised bog (grazed)	NS 64810 98570, 20 m OD	14 ha	Raised peat mosaic including <i>Calluna</i> ,	Young Shetland cattle, June to August	0.5	175	43.8	Medium

	<i>Cyperaceae</i> and <i>Sphagnum</i> lawn						
Flanders Moss raised bog (ungrazed)	As above	No livestock	0	0	0	0	Nil

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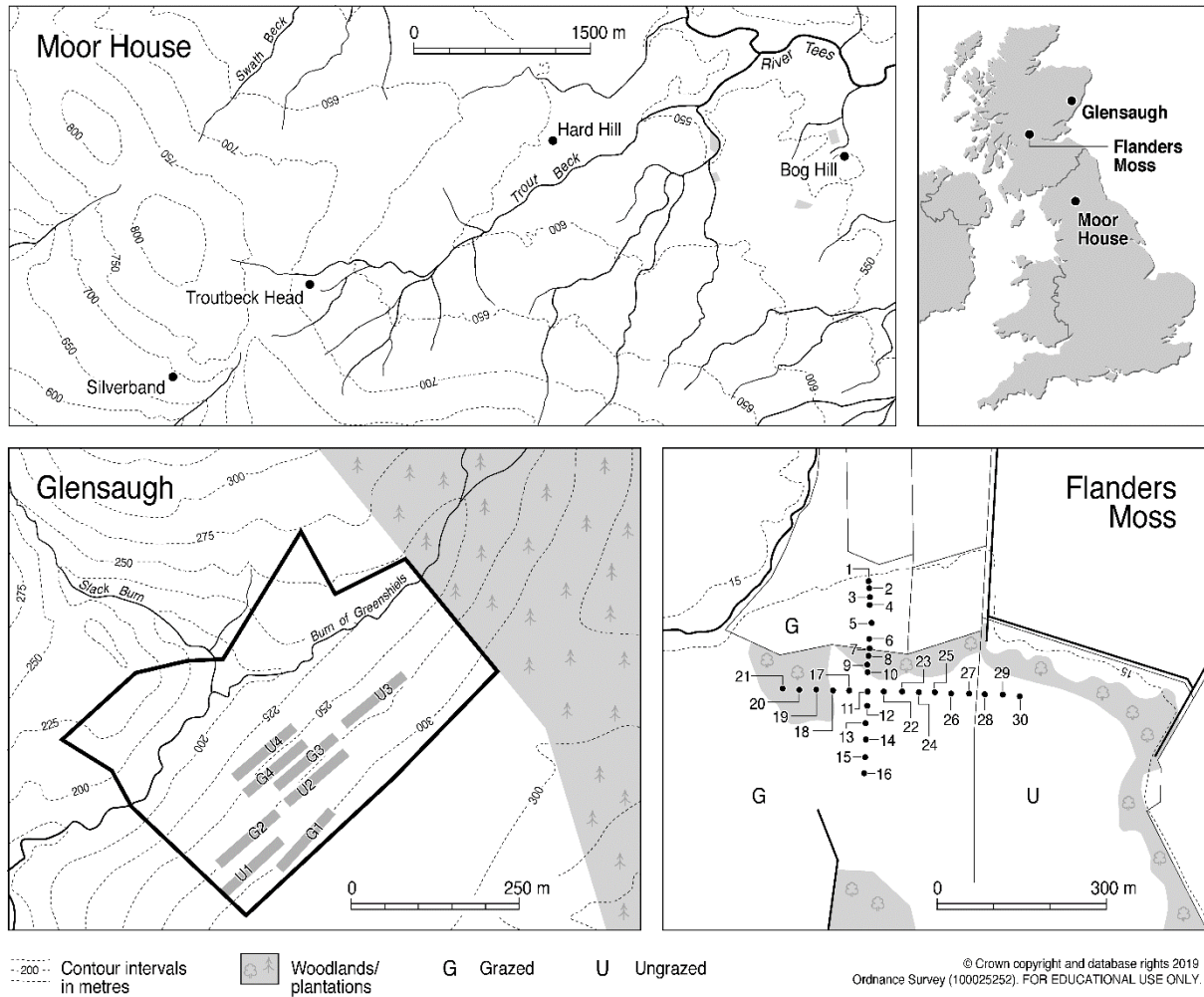
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802 **Table 2.** Kruskal-Wallis chi-squared test results for relationships between grazing treatment
 803 and indicator abundance. * indicates $p < 0.1$ and ** indicates $p < 0.05$. TLP = total land pollen,
 804 pollen grazing indicators = *Plantago lanceolata*, *Rumex* and *Urtica*

Site	Test and result
Moor House	CFS (%TLP): $\chi^2 = 0.2409$, df = 1, p-value = 0.6235
	CFS (spores/cm ³): $\chi^2 = 0.27$, df = 1, p-value = 0.6033
	Pollen indicators (%TLP): $\chi^2 = 0.9667$, df = 1, p-value = 0.3255
	Pollen indicators (grains/cm ³): $\chi^2 = 0.03$, df = 1, p-value = 0.8625
Glensaugh	CFS (%TLP): $\chi^2 = 2.2573$, df = 1, p-value = 0.133
	CFS (spores/cm ³): $\chi^2 = 3.4133$, df = 1, p-value = 0.06467*
	Pollen indicators (%TLP): $\chi^2 = 0.6115$, df = 1, p-value = 0.4342
Flanders Moss	Pollen indicators (grains/cm ³): $\chi^2 = 0.7017$, df = 1, p-value = 0.4022
	Grazed pasture vs. grazed bog:
	CFS (%TLP): $\chi^2 = 0.0769$, df = 1, p-value = 0.7815
	CFS (spores/cm ³): $\chi^2 = 0.0069$, df = 1, p-value = 0.9338
	Pollen indicators (%TLP): $\chi^2 = 1.7801$, df = 1, p-value = 0.1821
	Pollen indicators (grains/cm ³): $\chi^2 = 0.0927$, df = 1, p-value = 0.7608
	Grazed pasture vs. ungrazed bog:
	CFS (%TLP): $\chi^2 = 4.8348$, df = 1, p-value = 0.02789**
	CFS (spores/cm ³): $\chi^2 = 2.4083$, df = 1, p-value = 0.1207
	Pollen indicators (%TLP): $\chi^2 = 1.3146$, df = 1, p-value = 0.2516
	Pollen indicators (grains/cm ³): $\chi^2 = 0.1169$, df = 1, p-value = 0.732
	Grazed bog vs. ungrazed bog:
CFS (%TLP): $\chi^2 = 4.8238$, df = 1, p-value = 0.0280**	
CFS (spores/cm ³): $\chi^2 = 3.7532$, df = 1, p-value = 0.05271*	
Pollen indicators (%TLP): $\chi^2 = 3.0293$, df = 1, p-value = 0.08177*	
Pollen indicators (grains/cm ³): $\chi^2 = 0.3001$, df = 1, p-value = 0.5838	

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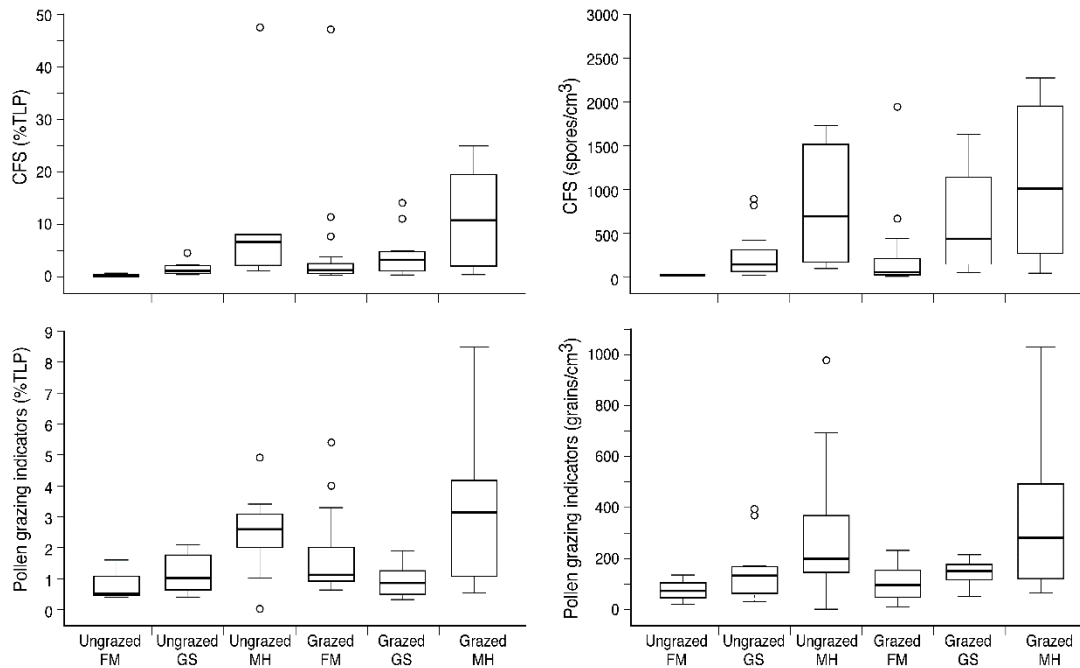
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Figure 1. Locations of study sites and plots. Each site includes ungrazed (fenced) and grazed

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(open) plots

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Figure 2. Boxplots showing the relative (percentage) and absolute (concentration)

813

abundance of (a) CFS and (b) pollen disturbance indicators in each grazing treatment at

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Moor House (MH), Glensaugh (GS) and Flanders Moss (FM). The data consist of 12 samples

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from grazed and ungrazed (exclosed) treatments, consisting of three samples from each site

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at MH and plot at GS (n=24 per site), and 7 pasture samples, 20 grazed bog and 3 ungrazed

817

bog samples (n=30) from FM. Each boxplot represents the median value (solid line), upper

818

(75%) and lower (25%) quartiles, two standard deviations (whiskers) and outliers (dots),

819

which are defined as values greater than $Q3 + 1.5 \cdot IQR$, where Q3 is the upper quartile and

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the interquartile range ($IQR = Q3 - Q1$). For legibility, the y-axis is truncated to exclude three

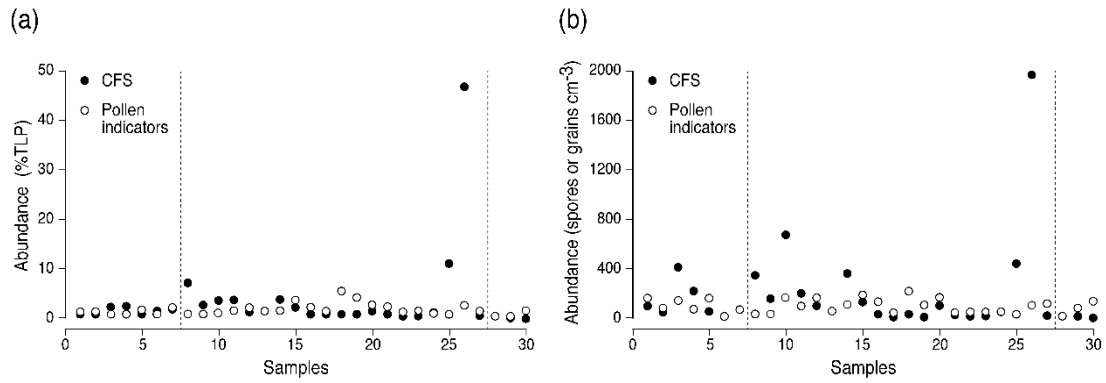
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very high CFS outliers at Moor House (two from grazed plots, one from an exclosed plot,

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with a maximum of 167% TLP, 22219 spores/cm³)

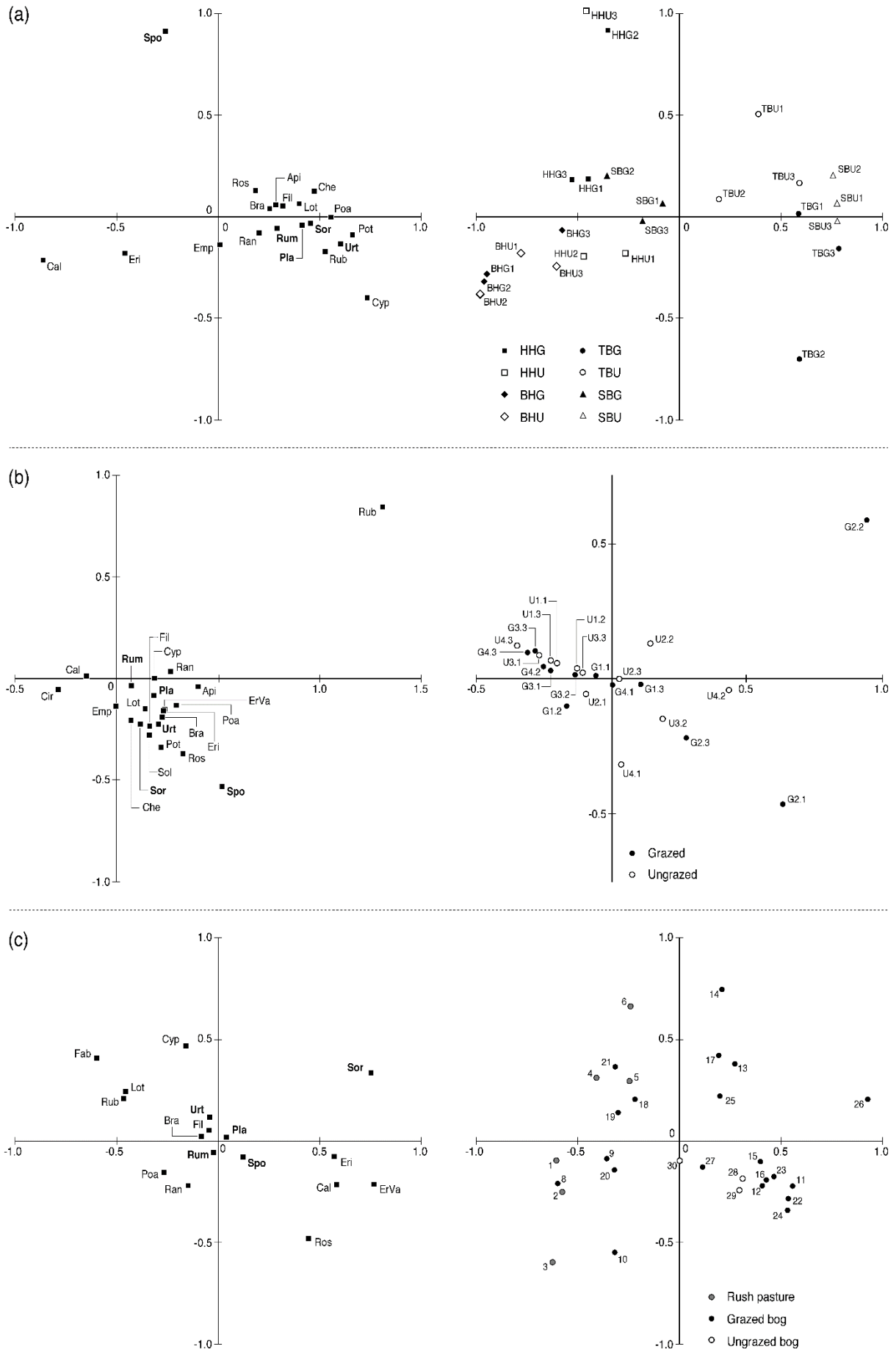
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825 **Figure 3.** Trends in CFS and pollen indicator values in each sample at Flanders Moss,
826 expressed as (a) percentages and (b) concentrations. Vertical dotted lines denote transitions
827 from rush pasture (samples 1-7) to grazed raised bog (samples 8-27) and ungrazed raised
828 bog (samples 28-30)

829



831 **Figure 4.** NMDS ordination results for (a) Moor House, (b) Glensaugh and (c) Flanders Moss.

832 U denotes ungrazed and G denotes grazed samples at Moor House and Glensaugh. See

833 Table 1 for abbreviations for Moor House sampling sites. Abbreviations: Api (*Apiaceae*), Bra

834 (*Brassicaceae*), Che (*Chenopodiaceae*), Cal (*Calluna vulgaris*), Cir (*Cirsium*-type), Emp

835 (*Empetrum nigrum*), ErVa (*Erica/Vaccinium*), Eri (other *Ericales*), Fab (*Fabaceae*), Fil

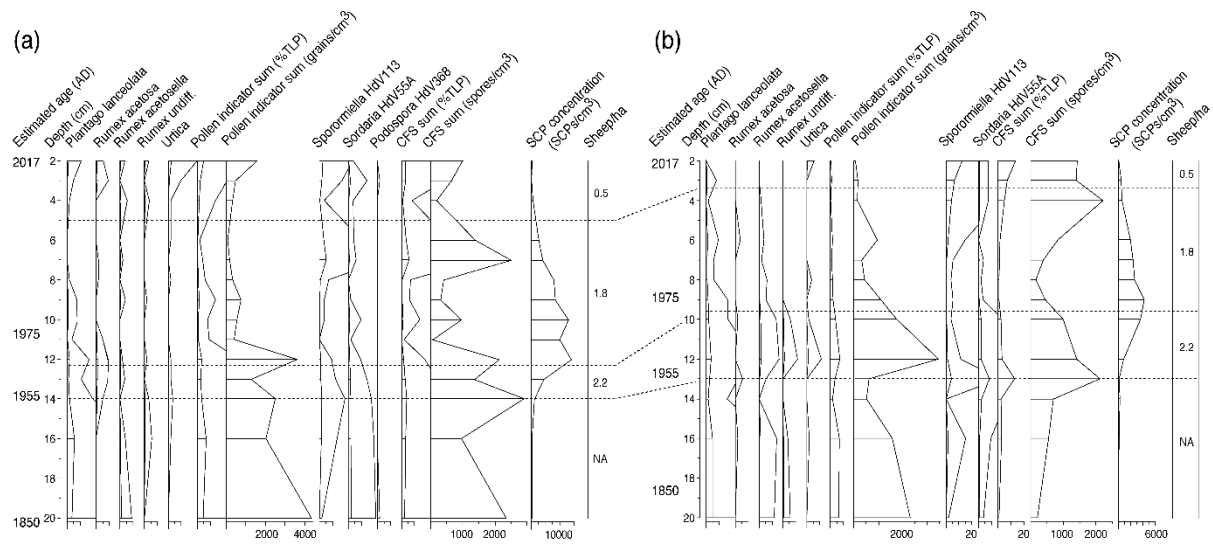
836 (*Filipendula*), Lot (*Lotus*-type), Pla (*Plantago lanceolata*), Poa (*Poaceae*), Pot (*Potentilla*-

837 type), Ran (*Ranunculus acris*-type), Ros (*Rosaceae*), Rub (*Rubiaceae*), Rum (*Rumex*), Sor

838 (*Sordaria*), Spo (*Sporormiella*), Urt (*Urtica*). Names of key pollen disturbance indicator taxa

839 and CFS are shown in bold for clarity

840



841

842 **Figure 5.** Grazing indicator trends over time in (a) grazed and (b) excluded plots at Moor

843 House (Hard Hill). Clear curves show x10 exaggeration for clarity and horizontal dotted lines

844 denote site-wide changes in grazing level