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## Experimental warming interacts with soil moisture to discriminate plant responses in an ombrotrophic peatland

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4 **Experimental warming interacts with soil moisture to discriminate plant responses in an**  
5 **ombrotrophic peatland**

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7 **Running head: Experimental warming and plant responses**

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57 Keywords: climate change; vegetation, *Sphagnum*; OTC; temperature; drought; NDVI; point-  
58 intercept survey.

59

60

## 61 **ABSTRACT**

62

63 Question: A better understanding of the response of *Sphagnum* mosses and associated vascular  
64 plants to climate warming is relevant for predicting the carbon balance of peatlands in a warmer  
65 world. In peatland studies, open-top chambers (OTCs) have been used to investigate the effect on  
66 soil biogeochemical processes, but little information is available on the effects of OTCs on  
67 microclimate conditions and the associated response of plant community. We aimed to understand  
68 how simulated warming and differences in soil moisture affect overall vascular plant cover and  
69 individual plant species.

70 Methods and location: We used OTCs to measure the effect of a near-ground temperature  
71 increase (+ 1.5 °C on average) on vegetation dynamics in a peatland over 5 years (2008-2012). We  
72 performed this experiment in a *Sphagnum*-dominated peatland in the French Jura Mountains, in two  
73 adjacent areas (blocks) with different hydrological conditions – wet and dry. Microclimatic  
74 conditions and plant species abundance were monitored at peak biomass in years 1, 2, 3 and 5 and  
75 monthly during the plant-growing season in year 5.

76 Results: The response of plants to warming differed between vascular plants and bryophytes as  
77 well as among species within these groups and also varied in relation to soil moisture. *Andromeda*  
78 *polifolia* abundance responded positively to warming, while *Vaccinium oxycoccus* responded  
79 negatively and *Eriophorum vaginatum* showed a high resistance.

80 Conclusion: Depth of rooting of vascular plants appeared to control the response in plant  
81 abundance, while moss abundance depended on various other interacting factors, such as shading  
82 by the vascular plant community, precipitation and soil moisture.

83

84

85

## 86 INTRODUCTION

87 Peatlands are long-term sinks of atmospheric carbon (C) due to the accumulation of peat (Smith  
88 et al. 2004; Yu 2011). These ecosystems develop in areas that are hydrologically and climatically  
89 characterized by a net surplus of water, *i.e.* where precipitation exceeds evapotranspiration. As a  
90 consequence, prevailing soil anoxic conditions hamper microbial decomposition of organic matter  
91 (Holden 2005).

92 In ombrotrophic (= rain fed) peatlands of northern hemisphere, bryophytes of the genus  
93 *Sphagnum* (peat mosses) are generally the dominant plant species (Rydin & Jeglum 2006). Peat  
94 mosses produce litter with antimicrobial properties, which hampers microbial decomposition  
95 (Turetsky 2003; Hajek et al. 2011), leading to the build up of peat. Further, *Sphagnum* mosses can  
96 affect the abundance and the performance of associated vascular plants (van Breemen 1995;  
97 Dorrepaal et al. 2006) by regulating soil moisture, energy balance, soil temperature, and nutrient  
98 availability (Turetsky et al. 2012). Ultimately, the inter-specific competition between *Sphagnum*  
99 mosses and vascular plants controls peat accumulation because an increase of vascular plant  
100 abundance and in particular their shading effect can reduce *Sphagnum* growth (Heijmans et al.  
101 2002; Bragazza et al. 2013). Changes in the competitive balance between plant species of different  
102 growth forms has been shown to alter the C balance in peatlands (Kuiper et al. 2014), potentially by  
103 changes in the litter quality, which ultimately affects microbial decomposition (Bragazza et al.  
104 2007; Dorrepaal et al. 2007; Gogo et al. 2011).

105 Climate warming and associated extreme climatic events can be detrimental to *Sphagnum*  
106 mosses as, like all bryophytes, these plants cannot actively control their water balance and therefore  
107 rely on atmospheric precipitation to maintain suitable hydrological conditions (Robroek et al. 2007,  
108 Bragazza 2008; Nijp et al. 2014). Increased air temperature can increase evapotranspiration with  
109 direct negative effects on *Sphagnum* productivity (Skre & Oechel 1981; Gerdol 1995; Weltzin et al.  
110 2001), but with positive effects on vascular plant growth by drying out the top soil and enhancing  
111 soil oxygenation (Weltzin et al. 2000; Bragazza et al. 2013), to which plants of different functional  
112 types might respond differently (Kuiper et al. 2014). A better understanding of the response of  
113 *Sphagnum* mosses and associated vascular plants to climate warming is then relevant for predicting  
114 the C balance of peatlands in a warmer world. Indeed, a warmer climate has been reported to alter  
115 plant species abundance in peatlands, in particular favoring ericaceous dwarf shrubs (Weltzin et al.  
116 2003, Breeuver et al. 2009), which will affect soil biogeochemical processes (Bragazza et al. 2013).

117 Under field conditions, simulation of climate warming can be obtained by using passive  
118 warming open-top chambers (OTCs) (Marion 1997). Although OTCs are recognized to increase  
119 temperature consistent with general circulation models, they also affect a set of microclimatological  
120 variables such as moisture, light, snow accumulation and wind speed (Bokhorst et al. 2013). In  
121 peatland studies, OTCs have been reliably used to investigate the effect on soil biogeochemical  
122 processes (Dorrepaal et al. 2009, Huguet et al. 2013), but little information is available on the  
123 effects of OTCs on microclimate conditions and the associated response of plant species (Weltzin et  
124 al. 2003, Keuper et al. 2011; Delarue et al. 2013; Jassey et al. 2013).

125 In the present study we used OTCs to simulate an increase of soil and air temperature and we  
126 monitored changes in vegetation cover in a *Sphagnum*-dominated peatland over 5 years of  
127 experimental warming. We aimed to understand how species abundance and plant community  
128 composition responded to simulated warming and associated changes in soil moisture,

129 We hypothesized that the responses of plant will vary among functional types, more specifically  
130 that 1) vascular plants will respond to warming in accordance with their rooting depth, and 2)  
131 *Sphagnum* mosses will have a more complex response depending on the interaction between  
132 micrometeorological conditions and abundance of vascular plants.

133

## 134 MATERIAL AND METHODS

135

### 136 *Study site*

137 The study was performed on an undisturbed, ombrotrophic *Sphagnum*-dominated peatland  
138 situated in the Jura Mountains (The Forbonnet peatland, France, 46°49'35''N, 6°10'20''E, 840 m  
139 a.s.l). Climate is characterized by relatively cold winters (average temperature -1.4°C) and mild  
140 summers (average temperature 14.6°C), with annual mean temperature of 7.5°C and annual mean  
141 precipitation between 1300 and 1500 mm (Laggoun-Défarge et al. 2008).

142 Two areas (blocks) were selected based on their hydrological conditions. The first block  
143 (hereafter called 'wet') was a *Sphagnum*-dominated relatively flat area bordering a transitional poor  
144 fen, characterized by a moss cover dominated by *Sphagnum fallax*. Vascular plants such as  
145 *Eriophorum vaginatum* and *Andromeda polifolia* were recorded with low abundance, together with  
146 *Scheuchzeria palustris*, *Drosera rotundifolia* and *Vaccinium oxycoccus*. The second block  
147 (hereafter called 'dry') was directly adjacent to the first block in a slightly drier area and was  
148 characterized by a pattern of hummocks dominated by *Sphagnum magellanicum*, *V. oxycoccus*, *E.*  
149 *vaginatum* and *Calluna vulgaris*, and lawns with *S. fallax*, *Carex rostrata* and *A. polifolia*. Tree  
150 (*Pinus rotondata*) encroachment happens also in this dry block.

151

### 152 *Experimental design*

153 In April 2008, in both the dry and the wet block, six representative plots (3 × 3 m) were selected,  
154 which were then randomly allocated to either the control or the warming treatment (Laggoun-  
155 Défarge et al., 2008). Warming treatments were obtained by using open-top chambers (OTCs)  
156 (Aronson & McNulty, 2009). OTCs (transparent polycarbonate hexagonal chambers; 50 cm high,  
157 1.7 m top-width, 2.4 m base-width) allow quasi-natural transmittance of visible wavelengths, and  
158 minimize the transmittance of re-radiated infrared wavelengths (Marion et al., 1997). All OTCs  
159 were raised 10 cm above the peat surface to allow air circulation. The minimal (adjacent plots) and  
160 maximal (distant plots) distance between plots were *c.* 5 and 30 m, respectively.

161

#### 162 *Environmental monitoring*

163 From November 2008 to November 2012, peat temperature (7 cm below the moss carpet) and air  
164 temperature (at 10 cm above the moss carpet) were monitored at 30-minute intervals using  
165 thermocouple probes connected to a data logger (CR-1000 Campbell). Sensors were repositioned as  
166 necessary to keep height and depth of measurement constant despite moss carpet accumulation. In  
167 2012, these measurements were augmented with combined soil temperature/moisture sensors. In  
168 each block (wet/dry) and treatment (OTC/control) a randomly chosen plot was equipped with soil  
169 temperature-moisture probes (Decagon 5TM) at 3 cm and 5 cm depth. Furthermore, precipitation at  
170 the study site and water table depth in randomly chosen plot were continuously monitored by a  
171 meteorological station and sensors connected to the CR-1000 data logger.

172

#### 173 *Plant species abundance*

174 At peak biomass (July or August, depending on the year) in 2008, 2009, 2010 and 2012, plant  
175 species abundance was measured using the point-intercept frequency method (Jonasson 1988,  
176 Buttler 1992) in 50 × 50 cm subplots located in flat lawns. We used a Plexiglas frame with  
177 adjustable legs placed above a permanently marked subplot. A 20 holes ruler was moved along 20



178 different positions so as to obtain 400 measuring points on a regular grid. A metal pin (1 mm  
179 diameter) was lowered through each hole in the ruler and each contact of the pin with living  
180 vegetation and litter was recorded by species until the pin reached the *Sphagnum* surface. This field  
181 technique could account for three-dimensional biomass distribution because, at each point, each  
182 plant that was intercepted was recorded. The relative frequency of each species was then calculated.

183 To allow analyses on seasonal dynamics of plant species cover, during the growing season 2012  
184 (April - September), monthly pictures were taken from aforementioned subplots. In order to obtain  
185 high-resolution images, the subplots were divided into four 25 × 25 cm quadrats. For the digital  
186 image analysis, a grid of 100 points was laid on each 25 × 25 cm picture, after which the four grids  
187 were merged into a single 400 points grid-picture. Species overlaying the grid intersects were  
188 identified at 200% digital magnification. The relative frequency of each species was then calculated  
189 for each sampling date, as for the point-intercept method. Because we could not reliably distinguish  
190 *S. fallax* and *S. rubellum* in our point-intercept field measures and in the frequency analysis on  
191 photographs, we pooled these two species.

192

### 193 *Sphagnum height growth*

194 The cranked wire method (Clymo 1970) was used to measure *Sphagnum* growth. At the start of  
195 the 2011 and 2012 growing seasons (early April, after snow melt) cranked wires (5-10) were placed  
196 in each subplot. At the beginning of November, before snowfall, the length of the cranked wire  
197 above the moss surface was measured with a graduated pipe sliding down along the cranked wire  
198 and the average height of the *Sphagnum* capitula around the wire was calculated.

199

### 200 *Seasonality of plant community*

201 The normalized difference vegetation index (NDVI) was used as a phenological proxy and  
202 measured every fortnight between March and November 2012 using a portable spectroradiometer

203 sensor. This measure is also used as an indirect measure of bulk biomass (Soudani et al. 2012). The  
204 sensor was maintained at 50 cm above the moss carpet, which allowed obtaining a NDVI signal of  
205 the whole plant community, including the highest plants, while covering only the subplot surface. In  
206 each 50 × 50 cm subplot and for each campaign of sampling, 10 consecutive measures were taken  
207 according to a grid sampling design and then averaged to have a single NDVI value per plot. The  
208 NDVI measurements were performed under direct sunlight and with an umbrella to shadow the  
209 subplot.

210

### 211 *Statistical analysis*

212 Differences in vegetation between years (i.e. 2008, 2009, 2010, 2012) were analyzed using  
213 relative species frequency data obtained from the point-intercept method in the field, whereas  
214 seasonal trend of plant species cover during the 2012 growing season was analyzed with species  
215 relative frequency data obtained from the photographic image analysis. Analysis at species level  
216 was done with Linear Mixed Models, with treatment (OTC vs. control) and years (or months for the  
217 seasonal data set in 2012) as fixed factors, and years (or months) nested in plots and block as  
218 random factors. The same model was also used to test the block effect. *Sphagnum* growth was  
219 analyzed with Linear Mixed Models, with treatment and block as fixed factors, and location of  
220 growth measures within plots given as random nested factors. The model was also tested for each  
221 block separately. NDVI was also analyzed with Linear Mixed Model, with treatment and block as  
222 fixed factors, and dates nested in plots as random factors. Random effects on the intercept were  
223 used to correct the inflation of the residual degrees of freedom that would occur if repeated  
224 measurements within sites would have been used as true replicates (Pinheiro & Bates 2000). In  
225 addition, for NDVI, separate ANOVA's were performed for each block and date. Pearson's  
226 correlation coefficients were calculated and tested between NDVI signals and species frequencies.  
227 Differences in monthly means of differences in daily mean air and soil temperature were assessed

228 by ANOVA's. Comparisons of mean water level depth between blocks were done with Student t-  
229 tests. Data were log transformed prior to analysis. All statistical analyses were performed in R (R  
230 Core Team, 2014).

## 231 **Results**

232

233

### 234 *Micrometeorology*

235

236 In general, over the period 2009-2012, monthly air temperature in the OTCs was 0.2-1.5 °C  
237 higher than in the control plots ( $p < 0.05$ ). Interestingly, OTCs rarely affected significantly soil  
238 temperature, and when they did ( $p < 0.05$ ), the pattern was less clear, varying between a warming  
239 effect up to 0.3 °C in some cases, and a cooling effect up to -1 °C in some others (see also Delarue  
240 et al. 2011, 2014, 2015, Jassey et al. 2011). These effects of OTC on soil temperature were not  
241 related to the season, neither to block. Soil moisture and temperature measured in 2012 with  
242 Decagon sensors in a subset of 4 plots (dry control, dry OTC, wet control and wet OTC) indicate  
243 that soil temperature was slightly higher in OTCs this particular year (mean daily differences  
244 between OTC and control plots for soil temperature was +0.6 deg C in both blocks), and that  
245 moisture was slightly lower in OTC plots (mean daily differences between OTC and control plots  
246 for soil moisture were -0.011 and -0.067 (VWC) in dry and wet blocks, respectively).

247 Monthly cumulative rainfall during the period of *Sphagnum* growth measurements was higher in  
248 2012 (2108 mm) than in 2011 (1376 mm). Depth of water level fluctuated over time, but highest  
249 water levels were recorded during spring 2012. Mean water level during the measurement period of  
250 *Sphagnum* growth was significantly higher in 2012 than in 2011 (Student t-test;  $p = 0.002$  in dry,  
251  $p = 0.004$  in wet). Mean water level was also higher in the wet block than the dry block ( $p = 0.004$ ).

252

253

### 254 *Annual change in species abundance*

255

256 Considering all vascular plants, abundance (relative frequency) increased significantly with the  
257 OTC treatment (Figure 1). At species level, it appeared that with warming *A. polifolia* increased its  
258 abundance consistently in wet and dry blocks, whereas the abundance of *V. oxycoccus* decreased. *D.*  
259 *rotundifolia* abundance responded marginally to the OTC treatment whereas *E. vaginatum* did not  
260 respond significantly. Some other species responded contrastingly to the OTC treatment in the two  
261 blocks, for example *P. strictum* and *S. fallax+rubellum* increased their abundance in the dry block,  
262 whereas their abundance decreased or did not change in the wet block (treatment x block  $p=0.0367$   
263 and  $0.0767$ , respectively). Litter increased in the wet block, and decreased in the dry block  
264 (treatment x block  $p=0.0001$ ). Significant changes occurred also over time, with a decrease of  
265 abundance for *V. oxycoccus* and *S. fallax+rubellum*, and an increase for *E. vaginatum* and litter.

266 There was also a strong block effect related to the dry and wet situations in the bog ( $p<0.05$ ),  
267 except for *Drosera rotundifolia* for which the block effect was marginally significant, and for *Carex*  
268 *rostrata*, *C. limosa*, *Calluna vulgaris* and *Pinus rotundata* for which there was no significant block  
269 effect. *Vaccinium oxycoccus*, *D. rotundifolia*, *Scheuchzeria palustris*, and *Sphagnum*  
270 *fallax+rubellum* were more abundant in the wet block, whereas species such as *Andromeda*  
271 *polifolia*, *Eriophorum vaginatum* and *Polytrichum strictum* were more frequent in the dry block, or  
272 exclusively found in the latter one (*S. magellanicum*).

273

#### 274 *Monthly change in species abundance*

275 During the 2012 study season, total vascular plant abundance and, more specifically *Andromeda*  
276 *polifolia* frequency increased significantly in the OTCs (Figure 2). *Vaccinium oxycoccus* abundance  
277 decreased in the wet block (treatment x block  $p=0.0034$ ) whereas that of *Sphagnum*  
278 *fallax+rubellum* declined in the wet block, but increased in the dry block (treatment x block  
279  $p=0.008$ ). Litter increased in the wet block and decreased in the dry block (treatment x block  
280  $p=0,0001$ ). Significant changes occurred also over the seasons, with a decrease in abundance for *S.*

281 *magellanicum* (present only in the dry block) and litter, and an increase for *V. oxycoccus* and total  
282 vascular plants.

283

284 Sphagnum growth

285

286 The length increment of *Sphagnum* species differed between years, being higher in 2012 as  
287 compared to 2011 (Figure 3). In 2011, *Sphagnum* growth was significantly lower in the wet block,  
288 but warming did not affect length increment. In 2012, there were significant block and treatment  
289 effects as well as a cross effect, with increased moss growth in the warmed plots of the dry block  
290 ( $p=0.017$ ), whereas no-significant changes were observed in the wet block.

291

292 Normalized Difference Vegetation Index

293

294 The values of the NDVI taken under direct sunlight and in the shade were strongly correlated  
295 ( $R^2=0.83$ ), yet measurements at the start of the season (early May) were less correlated ( $R^2=0.49$ )  
296 than measurements close to the peak of biomass (mid-June;  $R^2=0.82$ ). The precision of the  
297 measurements was calculated as the mean difference between each pairwise measurement. It gives  
298 an error of 1.6% under sun and 2.0% in the shade. As such, we only used NDVI data from sun  
299 measurements in further analyses.

300 Throughout the season, OTCs increased the vegetation's NDVI signal ( $p=0.001$ ), yet the effect  
301 of OTCs differed between wet and dry blocks (block x treatment  $p=0.002$ ). In the dry block, the  
302 NDVI signal in the OTC exceeded the signal in control plots throughout the season (Figure 4a).  
303 Such difference was mainly significant at the beginning of the growing season, and marginally  
304 different in summer. In the wet block, however, the difference between OTC and control plots was  
305 less obvious, and occurred during a more limited time in summer (Figure 4b). NDVI was positively

306 correlated to vascular plant abundance ( $r=0.85$ ,  $p<0.001$ ), and negatively with litter ( $r=-0.60$ ,  
307  $p<0.001$ ). The correlation between NDVI and *Sphagnum* cover was negative ( $r=-0.24$ ,  $p<0.045$ ).

## 308 Discussion

### 309 *Effect of OTC on microclimate*

310 The observed OTC warming effect on near-ground air temperature was in the range of those  
311 found in other studies (e.g., Marion et al., 1997; Hollister & Webber, 2000; Dorrepaal et al. 2003;  
312 Sullivan et al., 2005). Yet, in accordance with Dabros et al. (2010), we observed OTCs to  
313 sometimes reduce soil temperature, which potentially results from increased evapotranspiration  
314 (Delarue et al. 2011).

315 Daily temperature fluctuations, minimum and maximum values and day or night means have all  
316 been shown to be affected by OTC warming (e.g. Marion et al. 1997; Dabros et al. 2010). A  
317 previous study at the same site revealed that daily soil temperature amplitudes were small but often  
318 significantly different between OTC's and control plots in winter months (Delarue et al. 2011). In  
319 summer months, amplitudes were larger, and even more so in OTCs as compared to control plots in  
320 April, May and June in the dry block (but differences were marginally or not significant), whereas  
321 an opposite trend appeared in the wet block. The additional sensors Decagon 5TM installed in 2012  
322 which integrate more soil volume might be more adapted to the very porous moss carpet than tiny  
323 thermocouples. Despite the absence of replication, it is reasonable to recognize that our OTCs had a  
324 slight warming effect on soils for the largest part of time, yet this effect has coincided with a slight  
325 reduction in soil volumetric water content. Indeed, Jassey et al. (2011) showed, in the same plots,  
326 that OTC treatment induced a significant decrease of *Sphagnum* water content in summer months.

327

### 328 *Effect of OTCs on vegetation*

329 We showed that warming differently influenced plant abundance (or frequency) depending

330 of the microclimatic conditions. Several species were found to respond either positively or  
331 negatively to warming. *A. polifolia* increased in abundance while *V. oxycoccus* decreased, and  
332 both *S. fallax+rubellum* and *P. strictum* responded positively to the OTC treatment in the dry block,  
333 and decreased or remained constant in the wet block. Among these species, the response of *A.*  
334 *polifolia* is key. This species has been shown to be sensitive to changes in environmental  
335 conditions such as snow cover and spring/summer warming (Aerts et al. 2006; Jassey et al.  
336 2013; Robroek et al. 2013). This species allocates about 98% of the total biomass belowground,  
337 concentrated in the 0-15 cm peat layer, with the bulk at 2.5-7.5 cm, and a continuous rooting  
338 system from recent vegetation down into the peat (Wallén 1986). Roots of *A. polifolia* may  
339 reach a depth of 45 cm (Flower-Ellis 1980 in: Jacquemart 1998) and fine roots form up to 24%  
340 of the total below ground biomass (Wallen 1986). *A. polifolia* might therefore be expected to have a  
341 somewhat deeper root system as compared to several other species in the bog and thus to be able to  
342 sustain growth when soil dries out at the surface. Differently, *V. oxycoccus* has a shallow root  
343 system hardly penetrating more than a few centimeters below the living parts of the moss layer  
344 (Jacquemart 1998). With its shallow roots, this species relies on the water-conducting capacity of  
345 the *Sphagnum* mosses for its water supply (Malmer et al. 1994), and indeed, a decrease of  
346 *Sphagnum* water content in the OTC treatment has been demonstrated by Jassey et al. (2011). A  
347 subsequent lowering of water table will also reduce the growth rate of *V. oxycoccus* through water  
348 stress (Malmer et al. 1994, Jacquemart 1998). Consequently, water table drawdown can hamper *V.*  
349 *oxycoccus* growth (Rodwell 1991), which seems to be optimal at water table depths of about 25-30  
350 cm (Gronskis & Snickovskis 1989 in: Jacquemart 1998).

351 Coriaceous leaves of *A. polifolia*, their silvery-glaucous lower surface and their revolute margins  
352 could indicate drought resistance (Barvaux 1958). But anatomical features of *V. oxycoccus* such as  
353 thick epicuticular waxes and stomata – present on the abaxial surface only (Warming 1908, 1912;  
354 Vander Kloet 1983) – are considered similar to those of desert plant characteristic to a high ability

355 to avoid drought (Jacquemart 1997). Drier soil might also promote ericoid mycorrhizal infection  
356 (Cullings 1996) and thus better access to nutrients in the soil, but this might equally apply to other  
357 Ericaceous present in the bog, such as *V. oxycoccus*.

358 An alternative explanation for the decrease of *V. oxycoccus* with OTC warming may come from  
359 direct nutrient resource competition (Malmer et al. 1994). This would be underpinned by our  
360 observation that in the dry block under OTC treatment, *S. fallax+rubellum* and *P. strictum*  
361 increased in abundance, and as such potentially cause nutrient limitation for *V. oxycoccus*. As,  
362 however, OTC warming coincided with a decrease in moisture content, a direct effect of moisture  
363 limitation on the shallow rooting *V. oxycoccus* cannot be ruled out.

364 The evidence of moisture limitation is supported by the lack of response to the OTC by *E.*  
365 *vaginatum*. This species is known to root deeply into the peat, up to 1.5 meters (Boggie et al 1958,  
366 Wein 1968), with roots having highest elongation rates at low soil temperatures (Shaver & Billings  
367 1977). Contrary to *A. polifolia* and *V. oxycoccus*, no vesicular-arbuscular mycorrhizas have been  
368 reported on *E. vaginatum* (Wein 1968). In warming experiment, no significant differences were  
369 reported for *E. vaginatum* root production between OTC's and control plots, albeit a tendency to  
370 higher production was observed (Sullivan & Welker 2005). We believe that the resistance of *E.*  
371 *vaginatum* is higher as compared to more shallow rooted species and that warming effect has to be  
372 expected on a longer term, as soil warms up at lower depth. Weltzin et al. (2003) found that within  
373 bog and fen communities, different life forms and species can respond differently to warming and  
374 water table manipulation. They showed that warming may lead to an increase in abundance of  
375 woody plants, as does lowering water table as a result of changes in rates of evapotranspiration  
376 (Gorham 1991). In the mires studied by Weltzin et al. (2003), in northeastern Minnesota,  
377 *Andromeda glaucophylla* responded mostly to the heat treatment, while other dominant shrubs  
378 (such as *Vaccinium oxycoccus*) did not, whereas graminoids decreased their cover. As observed by  
379 Weltzin et al. (2000), change in belowground biomass can be even more important. Our wet and dry



380 sites showed similar trends for vascular plants, but not for mosses. The better growth of some  
381 mosses in warmed plots might be transient since, on the long run, mosses will be out-competed by  
382 the concomitant increase of *Andromeda* shrubs. Overall, these observations could point to a  
383 different evolution of such contrasted dry and wet situations, as for “bog” and “fen” like facies  
384 (Weltzin et al. 2003), which ultimately is also conditioned by neighboring species (Sonesson et al.  
385 2002).

386 The increase of litter in the wet block and its decrease in the dry block under the OTC treatment  
387 does not follow the pattern of the abundance of total vascular plants, which could indicate that litter  
388 abundance is mainly driven by the differential decomposition rate in the dry and wet blocks.  
389 Nevertheless, this relationship between warming and decomposition is not straightforward (Aerts  
390 2006) and would deserve a proper litter decomposition experiment.

391 Moss length increment was also higher in the dry block in 2011, and was promoted by OTC  
392 warming in 2012 (Figure 3). In the dryer 2011 year, the higher cover of vascular plants, i.e.  
393 *Eriophorum* leaves in the dry block is the determinant factor for moss growth and might have had a  
394 facilitating effect on *S. fallax+rubellum* in limiting the drying out of the moss carpet (Grosvernier et  
395 al. 1994, Buttler et al. 1998). Instead, in the wetter year 2012, when water limitation was not critical  
396 and engendered an overall higher length increment, the warming effect by OTC's could promote  
397 further the moss growth in the dry block. Adaptive seasonal acclimation has been shown for *S.*  
398 *fallax*, as reflected by the maintenance of relatively high net photosynthetic rates to lower water  
399 contents and no response differences when plants were collected from different heights above the  
400 water table (Titus et al. 1983). In our study, we pooled *S. fallax* and *S. rubellum*, because we could  
401 not reliably distinguish these two species in our point-intercept field measures and in the frequency  
402 analysis on photographs. Nevertheless, some field sampling in the plots showed that *S. fallax* is by  
403 far the most frequent species and that *S. rubellum* occurs only on some very limited patches.  
404 Similarly to *S. fallax*, *S. rubellum* has been shown to adapt and maintain similar height increment at

405 different experimental water table depths (Robroek et al. 2007). Therefore, shading may be critical  
406 for the development of these mosses, mediating soil moisture and near ground temperature, which  
407 both are direct drivers of growth. Our results show that shading can facilitate growth in dry years,  
408 but when wetter years are combined with warmer conditions, in our case the OTC effect, this  
409 shading effect on growth is out-ruled by temperature. Nevertheless, a better length increment of  
410 *Sphagnum* might also, on the long run, change the structure of the moss carpet and consequently its  
411 moisture holding and transport capacity (Dorrepaal et al. 2003). Therefore, when analyzing long  
412 term-effect of global change, not only the change in species composition should be considered  
413 (Heijmans et al. 2008), but also the change of vegetation structure might be critical. The evolution  
414 of aboveground biomass over the seasons was well reflected in the NDVI, whose signal was also  
415 higher in OTC plots. Interestingly, it is also better correlated to vascular plants than to mosses,  
416 which explains the more obvious difference in the dry plot, where vascular plants are more  
417 abundant. Indeed, when mosses dry out temporarily in dry periods, which can be observed in the  
418 wet block where the moss carpet is less protected from wind, reflectance is lowered. Differentiating  
419 mosses from higher plants is critical in studying the carbon cycle of the boreal biome when using  
420 airborne remote sensing (Yan et al. 2014) since these plants play an important role in the soil energy  
421 balance (Beringer et al. 2001).

422

### 423 **Conclusion**

424 Our study on the response of plant cover to experimental warming in two contrasting  
425 hydrological peatland habitats – wet and dry – shows that experimental warming by OTC interacts  
426 with soil wetness, resulting in divergent responses of vascular plants and bryophytes. For vascular  
427 plants, the depth of rooting seems the key in determining the response of plant cover, whereas for  
428 mosses, the growth is under the dependence of various other interacting factors, such as shading,  
429 which contributes further to regulate the microclimate conditions in the moss carpet.

430

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For Review Only

628 **Captions to figures**

629

630 *Figure 1:* Changes of the relative frequencies of dominant plant species from 2008 to 2012 (no  
631 records in 2011) in the Forbonnet peatland (French Jura). Mean values (n=3) and standard error  
632 bars are given for dry (solid line) and wet (broken line) blocks, and for control (black line) and OTC  
633 (grey lines) plots. Significance of Linear Mixed Model is given for treatment effect (T) and for year  
634 effect (Y). Species that are not illustrated: *Carex pauciflora* (appeared in 2009 and then was only  
635 seen in one plot the years after), *Carex limosa* (appeared only in 3 plots in 2009), *Calluna vulgaris*  
636 (only in 2 different plots in different years), *Pinus rotundata* (only in one plot in one year).

637

638 *Figure 2:* Changes of the relative frequencies of species from April to September 2012 in the  
639 Forbonnet peatland (French Jura). Mean values (n=3) and standard error bars are given for dry  
640 (solid line) and wet (broken line) blocks, and for control (black line) and OTC (grey lines) plots.  
641 Significance of Linear Mixed Model is given for treatment (T) and month effect (M). Species that  
642 are not illustrated; with no significant differences: *Scheuchzeria palustris*, *Eriophorum vaginatum*,  
643 *Carex pauciflora*, *Carex rostrata*, *Drosera rotundifolia*, *Polytrichum strictum*; present only in one  
644 plot: *Calluna vulgaris*, *Carex pauciflora* and *Polytrichum strictum*.

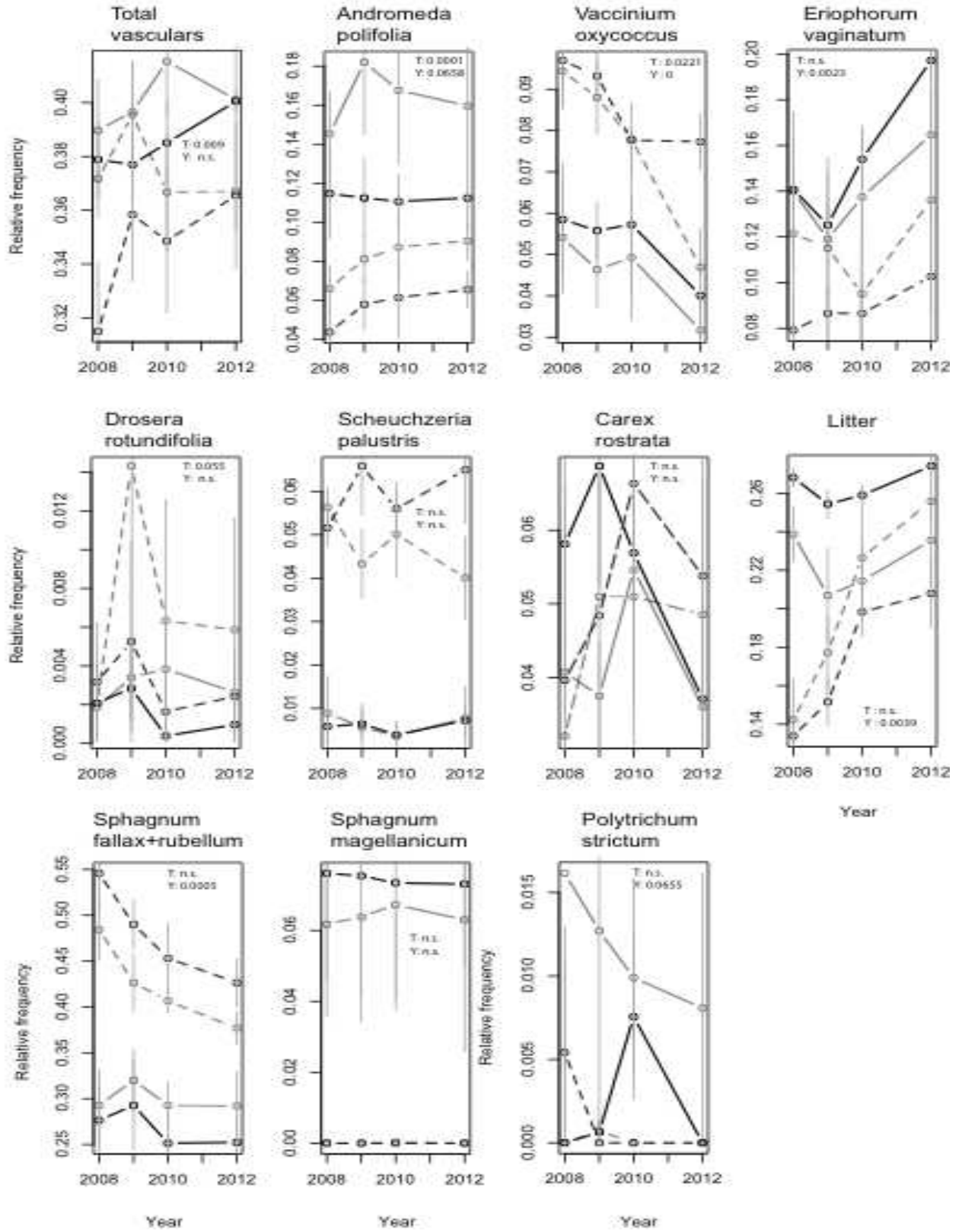
645

646 *Figure 3:* Length increment (mm) of *Sphagnum* mosses in the different treatments (OTC vs control)  
647 and blocks (dry vs wet) in 2011 (a: May 13 – November 27, n=60) and 2012 (b: March 30 –  
648 November 6, n=120) in the Forbonnet peatland (French Jura). Vertical bars represent standard  
649 errors. Scales of both graphs are different. Significance levels of Linear Mixed Model are given for  
650 block (B) and treatment effect (T), and for their interaction (B x T).

651

652 *Figure 4:* Normalised Difference Vegetation Index (NDVI) at plot scale in the dry (a) and wet (b)  
653 blocks in year 2012 in the Forbonnet peatland (French Jura). Curves represent mean values (n=3)  
654 for control (black) and OTC (grey) plots. Significance codes for ANOVA's are (\*\*\*) p<0.001 ; (\*\*)  
655 p<0.01 ; (\*) p<0.05 ; (.) p<0.1.

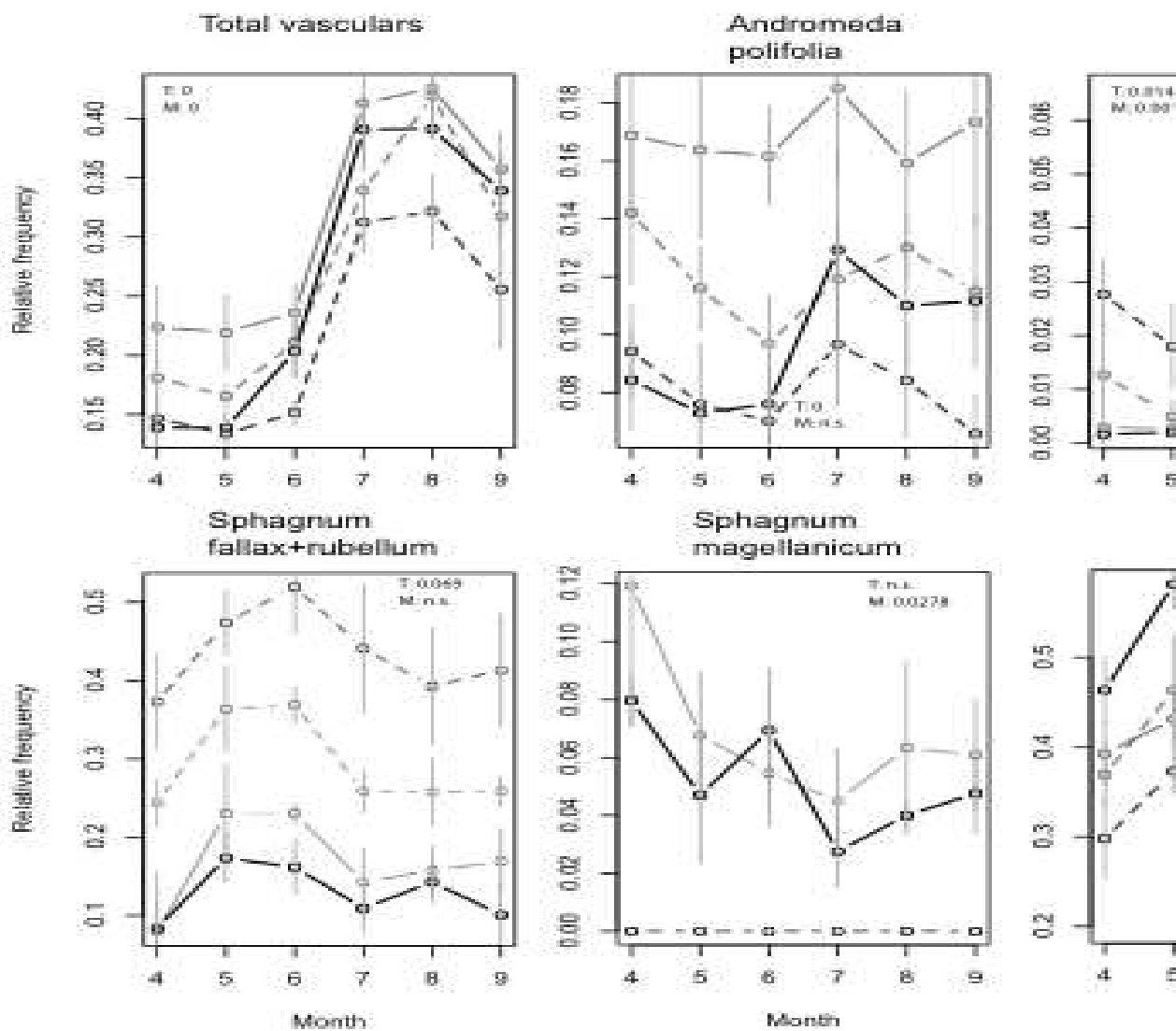
656



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658 Figure 1

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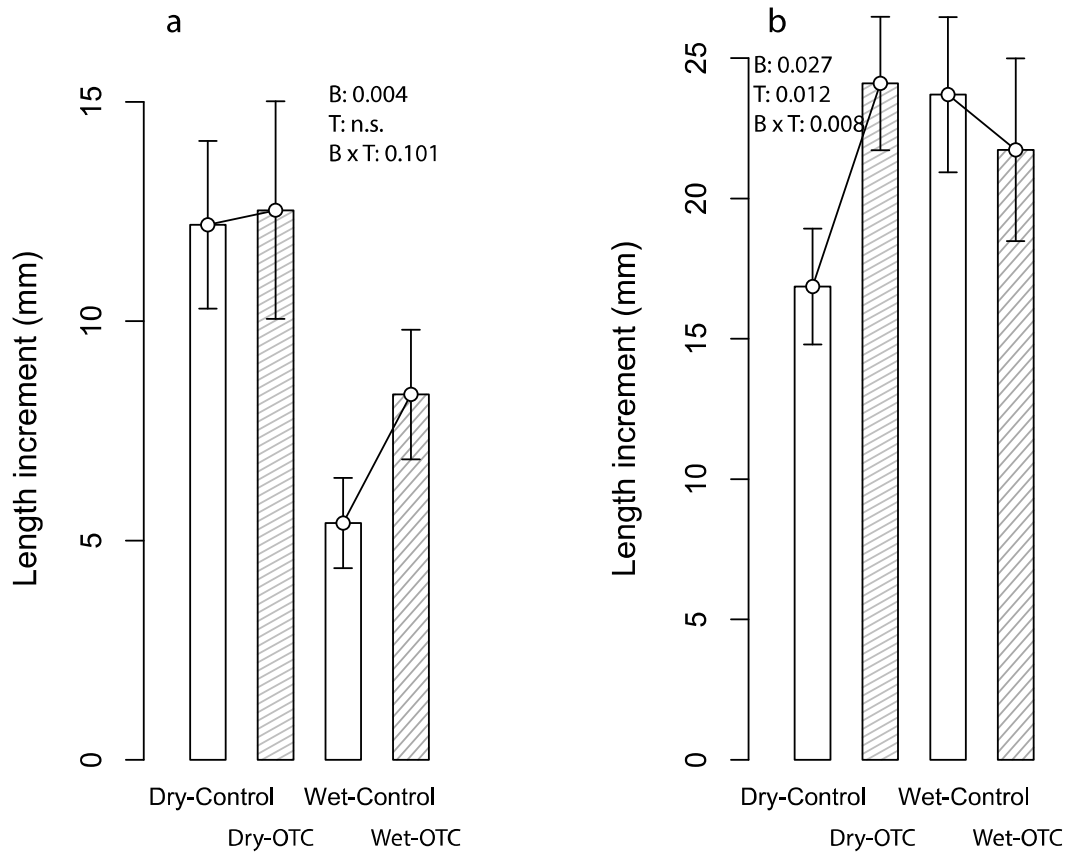
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664 *Figure 2*

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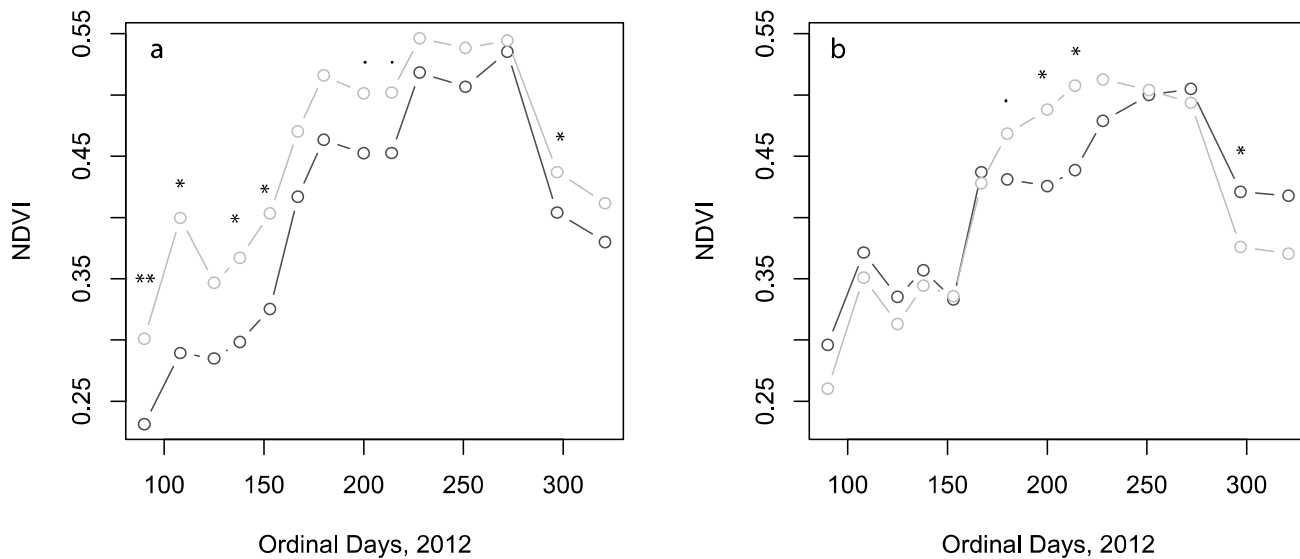
668 *Figure 3*

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674 *Figure 4*

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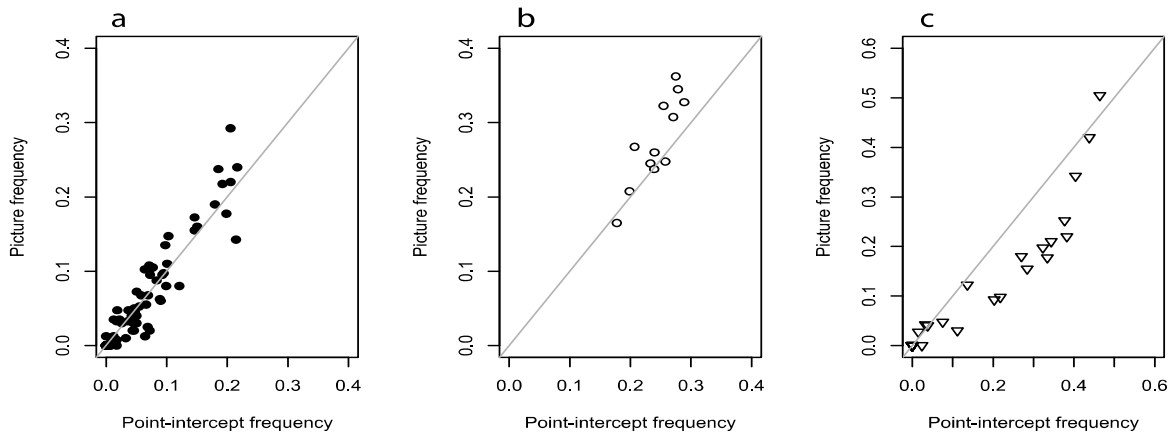
677 Electronic appendices

678

679 Supporting Information to the paper Buttler et al. 2015. Experimental warming interacts with soil  
680 moisture to discriminate plant responses in an ombrotrophic peatland. *Journal of Vegetation*  
681 *Science*. Appendix S1. Relationship between point-intercept frequency measures of vegetation and  
682 picture frequency analysis from the Forbonnet peatland (French Jura) for a: total vascular plants  
683 (Pearson  $r$ : 0.733,  $p < 0.01$ ), b: litter (Pearson  $r = 0.873$ ,  $p < 0.001$ ) and c: total Sphagnum and  
684 *Polytrichum strictum* (Pearson  $r = 0.942$ ,  $p < 0.001$ ).

685

686 The correlation between frequencies obtained by means of field point-intercepts and photographic  
687 analyses gives a good linear relation with vascular plants but shows an underestimation of mosses  
688 with the picture analysis. This is because leaves of vascular plants might hide the understory of  
689 mosses which than cannot be recorded in the one-layer photographic method, whereas in the field,  
690 the needle can hit more than one species or individual. This underestimation is mostly noticeable at  
691 intermediate moss cover, when vascular plants are most abundant. Conversely, the picture analysis  
692 overestimates litter when it is dense.



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