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

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5 **ombrotrophic peatland**

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

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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. Open-top chambers (OTCs) have been used to investigate the effect on soil biogeochemical  
66 processes in peatlands, but little information is available on the effects of OTCs on microclimate  
67 conditions and the associated response of plant community. We aimed to understand how simulated  
68 warming and differences in soil moisture affect plant species cover.

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

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

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

82

83

84

## 85 INTRODUCTION

86 Peatlands are long-term sinks of atmospheric carbon (C) due to the accumulation of peat (Yu  
87 2011). These ecosystems develop in areas that are hydrologically and climatically characterized by  
88 a net surplus of water. As a consequence, prevailing soil anoxic conditions hamper microbial  
89 decomposition of organic matter (Holden 2005).

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

102 Climate warming and associated extreme climatic events can be detrimental to *Sphagnum*  
103 mosses as, like all terrestrial bryophytes, these plants cannot actively control their water balance and

104 therefore rely on atmospheric precipitation to maintain suitable hydrological conditions (Robroek et  
105 al. 2007, Bragazza 2008; Nijp et al. 2014). Increased air temperature can increase  
106 evapotranspiration with direct negative effects on *Sphagnum* productivity (Gerdol 1995; Weltzin et  
107 al. 2001), but with positive effects on vascular plant growth by drying out the top soil and  
108 enhancing soil oxygenation (Weltzin et al. 2000; Bragazza et al. 2013), to which plants of different  
109 functional types might respond differently (Kuiper et al. 2014). A better understanding of the  
110 response of *Sphagnum* mosses and associated vascular plants to climate warming is then relevant  
111 for predicting the C balance of peatlands in a warmer world. Indeed, a warmer climate has been  
112 reported to alter plant species abundance in peatlands, in particular favoring ericaceous dwarf  
113 shrubs (Weltzin et al. 2003, Breeuwer et al. 2009), which will affect soil biogeochemical processes  
114 (Bragazza et al. 2013).

115 Under field conditions, simulation of climate warming can be obtained by using passive  
116 warming open-top chambers (OTCs) (Marion 1997). Although OTCs are recognized to increase  
117 temperature consistent with general circulation models, they also affect a set of microclimatological  
118 variables such as moisture, light, snow accumulation and wind speed (Bokhorst et al. 2013). In  
119 peatland studies, OTCs have been reliably used to investigate the effect on soil biogeochemical  
120 processes (Dorrepaal et al. 2009), but little information is available on the effects of OTCs on  
121 microclimate conditions and the associated response of plant species (Weltzin et al. 2003, Keuper et  
122 al. 2011; Delarue et al. 2014; Jassey et al. 2013).

123 In the present study we used OTCs to simulate increased soil and air temperature, and we  
124 monitored changes in vegetation cover in a *Sphagnum*-dominated peatland over five years of  
125 experimental warming. We aimed to understand how species abundance and plant community  
126 composition responded to simulated warming and associated changes in soil moisture. We  
127 hypothesized that plant responses will vary among functional types; and more specifically that 1)  
128 vascular plants will respond to warming according to their rooting depth, and 2) *Sphagnum* mosses

129 will have a more complex response depending on the interaction between micrometeorological  
130 conditions and abundance of vascular plants.

131

## 132 MATERIAL AND METHODS

133

### 134 *Study site*

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

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

150

### 151 *Experimental design*

152 In April 2008, in both the dry and the wet microhabitats, six representative plots (3 × 3 m) were  
153 selected, which were then randomly allocated to either the control or the warming treatment



154 (Laggoun-Défarge et al., 2008). Warming treatments were obtained by using open-top chambers  
155 (OTCs), which consisted of transparent polycarbonate hexagonal chambers (50 cm high, 1.7 m top-  
156 width, 2.4 m base-width). OTCs allow quasi-natural transmittance of visible wavelengths, and  
157 minimize the transmittance of re-radiated infrared wavelengths (Marion et al., 1997). All OTCs  
158 were raised 10 cm above the peat surface to allow air circulation. The minimal (adjacent plots) and  
159 maximal (distant plots) distance between plots were *c.* 5 and 30 m, respectively.

160

### 161 *Environmental monitoring*

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

171

### 172 *Plant species abundance*

173 At peak biomass (July or August, depending on the year) in 2008, 2009, 2010 and 2012, plant  
174 species abundance was measured using the point-intercept frequency method (Buttler 1992) in 50 ×  
175 50 cm subplots located in flat lawns. We used a Plexiglas frame with adjustable legs placed above a  
176 permanently marked subplot. A 20 holes ruler was moved along 20 different positions so as to  
177 obtain 400 measuring points on a regular grid. A metal pin (1 mm diameter) was lowered through  
178 each hole in the ruler and each contact of the pin with living vegetation and litter was recorded by

179 species until the pin reached the *Sphagnum* surface. This field technique could account for three-  
180 dimensional biomass distribution because, at each point, each plant that was intercepted was  
181 recorded. The relative frequency of each species was then calculated.

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

191

#### 192 *Sphagnum height growth*

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

198

#### 199 *Seasonality of plant community*

200 The normalized difference vegetation index (NDVI) was used as a phenological proxy and  
201 measured every fortnight between March and November 2012 using a portable spectroradiometer  
202 sensor. This measure is also used as an indirect measure of bulk biomass (Soudani et al. 2012). The  
203 sensor was maintained at 50 cm above the moss carpet, which allowed obtaining a NDVI signal of

204 the whole plant community, including the highest plants, while covering only the subplot surface. In  
205 each 50 × 50 cm subplot and for each campaign of sampling, 10 consecutive measures were taken  
206 according to a grid sampling design and then averaged to have a single NDVI value per plot. The  
207 NDVI measurements were performed under direct sunlight and with an umbrella to shadow the  
208 subplot.

209

### 210 *Statistical analysis*

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

228 with Student t-tests. Data were log transformed prior to analysis. All statistical analyses were  
229 performed in R (R Core Team, 2014).

## 230 Results

231

232

### 233 *Micrometeorology*

234

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

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

251

252

### 253 *Annual change in species abundance*

254

255 Considering all vascular plants, abundance (relative frequency) increased significantly with the  
256 OTC treatment (Figure 1). At species level, it appeared that with warming *A. polifolia* increased its

257 abundance consistently in wet and dry microhabitats, whereas the abundance of *V. oxycoccus*  
258 decreased. *D. rotundifolia* abundance responded marginally to the OTC treatment whereas *E.*  
259 *vaginatum* did not respond. Some other species responded contrastingly to the OTC treatment in the  
260 two microhabitats, for example *P. strictum* and *S. fallax+rubellum* increased their abundance in the  
261 dry microhabitat, whereas their abundance decreased or did not change in the wet microhabitat  
262 (treatment x block  $p=0.0367$  and  $0.0767$ , respectively). Litter increased in the wet microhabitat, and  
263 decreased in the dry microhabitat (treatment x block  $p=0.0001$ ). Significant changes occurred also  
264 over time, with a decrease of abundance for *V. oxycoccus* and *S. fallax+rubellum*, and an increase  
265 for *E. vaginatum* and litter.

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

273

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

275 During the 2012 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 microhabitat (treatment x block  $p=0.0034$ ) whereas that of *Sphagnum*  
278 *fallax+rubellum* declined in the wet microhabitat, but increased in the dry microhabitat (treatment x  
279 block  $p=0.008$ ). Litter increased in the wet microhabitat and decreased in the dry microhabitat  
280 (treatment x block  $p=0,0001$ ). Significant changes occurred also over the monthly course of 2012,

281 with a decrease in abundance for *S. magellanicum* (present only in the dry microhabitat) and litter,  
282 and an increase for *V. oxycoccus* and total 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  
288 microhabitat, but warming did not affect the length increment. In 2012, there were significant  
289 microhabitat and treatment effects as well as a cross effect, with increased moss growth in the  
290 warmed plots of the dry microhabitat ( $p=0.017$ ), whereas no-significant changes were observed in  
291 the wet microhabitat.

292

293 Normalized Difference Vegetation Index

294

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

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

307 NDVI was positively correlated to vascular plant abundance ( $r=0.85$ ,  $p<0.001$ ), and negatively with  
308 litter ( $r=-0.60$ ,  $p<0.001$ ). The correlation between NDVI and *Sphagnum* cover was negative ( $r=-$   
309  $0.24$ ,  $p<0.045$ ).

## 310 **Discussion**

### 311 *Effect of OTC on microclimate*

312 The observed OTC warming effect on near-ground air temperature was in the range of those  
313 found in other studies (e.g., Marion et al., 1997; Hollister & Webber, 2000; Dorrepaal et al. 2003;  
314 Sullivan et al., 2005, Walker et al. 2015). Yet, in accordance with Dabros et al. (2010), we observed  
315 that OTCs can reduce soil temperature, as a result of increased evapotranspiration (Delarue et al.  
316 2011). Daily temperature fluctuations, minimum and maximum values and day or night means have  
317 all been shown to be affected by OTC warming (e.g. Marion et al. 1997; Dabros et al. 2010). A  
318 previous study at the same site revealed that daily soil temperature amplitudes were smaller but  
319 often significantly different between OTC's and control plots in winter months (Delarue et al.  
320 2011). In summer months, amplitudes were larger, and even more so in OTCs as compared to  
321 control plots in April, May and June in the dry microhabitat (but differences were marginally or not  
322 significant), whilst an opposite trend appeared in the wet microhabitat. The additional Decagon  
323 sensors installed in 2012, which integrate more soil volume, might be more adapted to the very  
324 porous peat soil than tiny thermocouples. Despite the absence of replication, it is reasonable to  
325 recognize that our OTCs had a slight warming effect on soils for the largest part of time, yet this  
326 effect coincided with a slight reduction in soil volumetric water content as previously reported  
327 (Jassey et al. 2011)

328

### 329 *Effect of OTCs on vegetation*

330 We showed that experimental warming differently influenced plant abundance (or frequency),

331 depending on the underlying hydrological conditions and on individual species identity. *A. polifolia*  
332 increased in abundance while *V. oxycoccus* decreased, and both *S. fallax+rubellum* and *P. strictum*  
333 responded positively to the OTC treatment in the dry microhabitat, and decreased or remained  
334 constant in the wet microhabitat. Among these species, the response of *A. polifolia* is interesting.  
335 This species has been shown to be sensitive to changes in environmental conditions such as  
336 snow cover and spring/summer warming (Aerts et al. 2006; Jassey et al. 2013; Robroek et al.  
337 2013). It allocates about 98% of the total biomass belowground, concentrated in the 0-15 cm  
338 peat layer, with the bulk at 2.5-7.5 cm, and a continuous rooting system from recent vegetation  
339 down into the peat (Wallén 1986). Roots of *A. polifolia* may reach a depth of 45 cm (Jaquemart  
340 1998) and fine roots form up to 24% of the total below ground biomass (Wallen 1986). *A. polifolia*  
341 might therefore be expected to have a somewhat deeper root system as compared to several other  
342 species enabling the species to sustain growth when soil dries out at the surface. Differently, *V.*  
343 *oxycoccus* has a shallow root system hardly penetrating more than a few centimeters below the  
344 living parts of the moss layer (Jaquemart 1998). With its shallow roots, this species relies on the  
345 water-conducting capacity of the *Sphagnum* mosses for its water supply (Malmer et al. 1994).  
346 Indeed, a decrease of *Sphagnum* water content in the OTC treatment has been demonstrated by  
347 Jassey et al. (2011). A subsequent lowering of water table will also reduce the growth rate of *V.*  
348 *oxycoccus* through water stress (Malmer et al. 1994, Jacquemart 1998). Coriaceous leaves of *A.*  
349 *polifolia*, their silvery-glaucous lower surface and their revolute margins, could indicate drought  
350 resistance. But anatomical features of *V. oxycoccus* such as thick epicuticular waxes and stomata on  
351 the abaxial surface only are considered similar to those of desert plant characteristic to a high ability  
352 to avoid drought (Jaquemart 1997). Drier soil might also promote ericoid mycorrhizal infection  
353 (Cullings 1996) and thus better access to nutrients in the soil, but this might equally apply to other  
354 Ericaceous present in the bog, such as *V. oxycoccus*.



355 An alternative explanation for the decrease of *V. oxycoccus* with OTC warming may come from  
356 direct nutrient resource competition (Malmer et al. 1994), in particular with *A. polifolia*. Because,  
357 however, OTC warming coincided with a decrease in moisture content, a direct effect of moisture  
358 limitation on the shallow rooting *V. oxycoccus* cannot be ruled out. The evidence of moisture  
359 limitation is supported by the lack of response to the OTC by *E. vaginatum*. This species is known  
360 to root deeply into the peat, up to 1.5 meters, with roots having highest elongation rates at low soil  
361 temperatures (Shaver & Billings 1977). Contrary to *A. polifolia* and *V. oxycoccus*, no mycorrhizal  
362 association has been reported for *E. vaginatum*. In warming experiment, no significant differences  
363 were reported for *E. vaginatum* root production between OTC's and control plots, albeit a tendency  
364 to higher production was observed (Sullivan & Welker 2005). We believe that the resistance of *E.*  
365 *vaginatum* is higher as compared to more shallow rooted species, and that an effect of warming has  
366 to be expected on a longer term, as soil warms up at lower depth. Weltzin et al. (2003) found that  
367 within bog and fen communities, different life forms and species can respond differently to  
368 warming and water table manipulation. They showed that warming may lead to an increase in  
369 abundance of woody plants, as does lowering water table as a result of changes in rates of  
370 evapotranspiration. In the peatlands studied by Weltzin et al. (2003), *Andromeda glaucophylla*  
371 responded mostly to the heat treatment, while other dominant shrubs (such as *Vaccinium oxycoccus*)  
372 did not, whereas graminoids decreased their cover. As observed by Weltzin et al. (2000), change in  
373 belowground biomass can be even more important. Our wet and dry sites showed similar trends for  
374 vascular plants, but not for mosses. The better growth of some mosses in warmed plots might be  
375 transient since, on the long run, mosses will be out-competed by the concomitant increase of  
376 *Andromeda* shrubs. Overall, these observations could point to a different evolution of such  
377 contrasted dry and wet situations, as for "bog" and "fen" like facies (Weltzin et al. 2003).

378 The increase of litter in the wet microhabitat and its decrease in the dry microhabitat under the  
379 OTC treatment does not follow the pattern of the abundance of total vascular plants, which could

380 indicate that litter abundance is mainly driven by the differential decomposition rate in the dry and  
381 wet microhabitats. Nevertheless, this relationship between warming and decomposition is not  
382 straightforward (Aerts 2006) and would deserve a proper litter decomposition experiment.

383 Moss length increment was also higher in the dry microhabitat in 2011, and was promoted by  
384 OTC warming in 2012 (Figure 3). In the dryer 2011 year, the higher cover of vascular plants, i.e.  
385 *Eriophorum* leaves in the dry microhabitat is the determinant factor for moss growth and might  
386 have had a facilitating effect on *S. fallax+rubellum* in limiting the drying out of the moss carpet  
387 (Grosvernier et al. 1994, Buttler et al. 1998, Walker et al. 2015). Instead, in the wetter year 2012,  
388 when water limitation was not critical and engendered an overall higher length increment, the  
389 warming effect by OTC's could promote further the moss growth in the dry microhabitat. Adaptive  
390 seasonal acclimation has been shown for *S. fallax*, as reflected by the maintenance of relatively high  
391 net photosynthetic rates to lower water contents and no response differences when plants were  
392 collected from different heights above the water table (Titus et al. 1983). In our study, we pooled *S.*  
393 *fallax* and *S. rubellum*, because we could not reliably distinguish these two species in our point-  
394 intercept field measures and in the frequency analysis on photographs. Nevertheless, some field  
395 sampling in the plots showed that *S. fallax* is by far the most frequent species and that *S. rubellum*  
396 occurs only on some very limited patches. Similarly to *S. fallax*, *S. rubellum* has been shown to  
397 adapt and maintain similar height increment at different experimental water table depths (Robroek  
398 et al. 2007). Therefore, shading may be critical for the development of these mosses, mediating soil  
399 moisture and near ground temperature, which both are direct drivers of growth. Our results show  
400 that shading can facilitate growth in dry years, but when wetter years are combined with warmer  
401 conditions, in our case the OTC effect, this shading effect on growth is out-ruled by temperature.  
402 Nevertheless, a better length increment of *Sphagnum* might also, on the long run, change the  
403 structure of the moss carpet and consequently its moisture holding and transport capacity  
404 (Dorrepaal et al. 2003). Therefore, when analyzing long term-effect of global change, not only the

405 change in species composition should be considered (Heijmans et al. 2008), but also the change of  
406 vegetation structure might be critical. In their work, Walker et al. (2015) mentioned a mismatch in  
407 the growth responses of different plant functional types to simultaneous climate and vegetation  
408 change. This was due to the complexity of interacting factors between dwarf-shrubs, bryophytes  
409 and graminoids, suggesting that some functional types reflecting a direct response to increased air  
410 temperature, some others an indirect one.

411 The evolution of aboveground biomass over the seasons was well reflected in the NDVI, which  
412 was also higher in OTC plots. Interestingly, NDVI was also better correlated to vascular plants than  
413 to mosses, which explains the more obvious difference in the dry plot, where vascular plants are  
414 more abundant. Indeed, when mosses dry out temporarily in dry periods, which can be observed in  
415 the wet microhabitat where the moss carpet is less protected from wind, reflectance is lowered. This  
416 differentiation between mosses and higher plants is critical in studying the carbon cycle using  
417 airborne remote sensing (Yan et al. 2014).

418

#### 419 **Conclusion**

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

427

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590 **Captions to figures**

591

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

599

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

607

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

613

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

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620 *Figure 1*

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626 *Figure 2*

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629 *Figure 3*

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635 *Figure 4*

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638 Electronic appendices

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

646

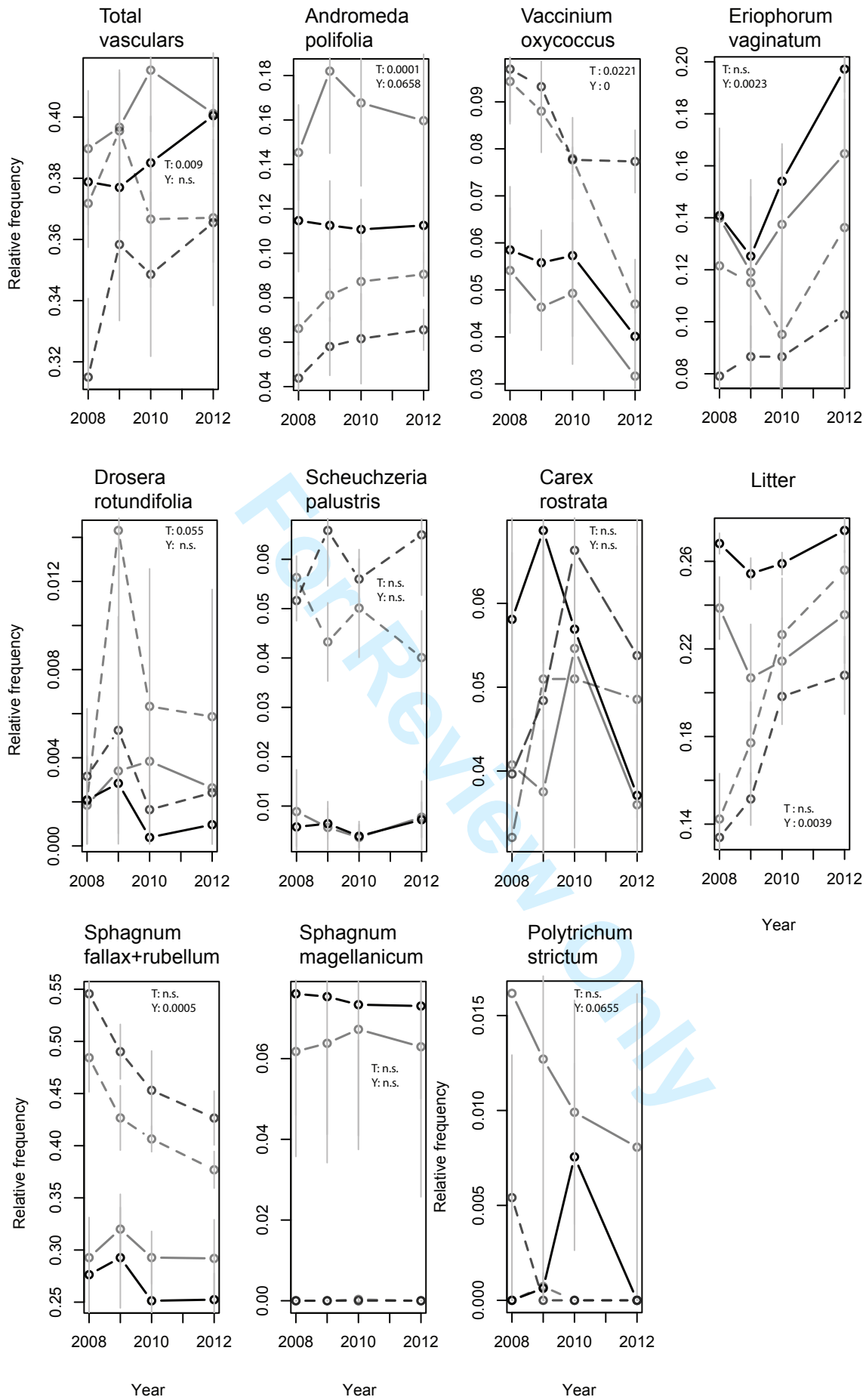
647 The correlation between frequencies obtained by means of field point-intercepts and photographic  
648 analyses gives a good linear relation with vascular plants but shows an underestimation of mosses  
649 with the picture analysis. This is because leaves of vascular plants might hide the understory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

654

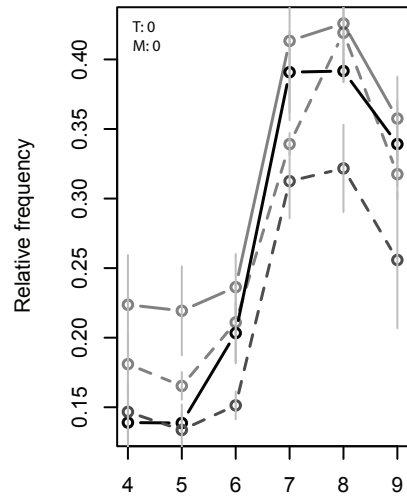
655

656

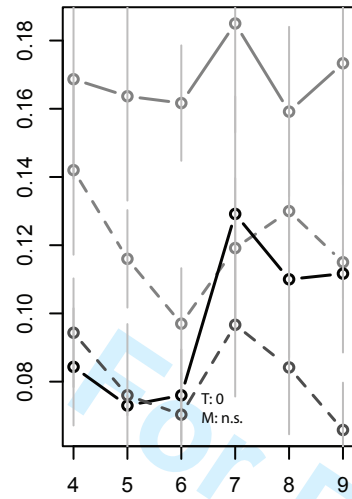
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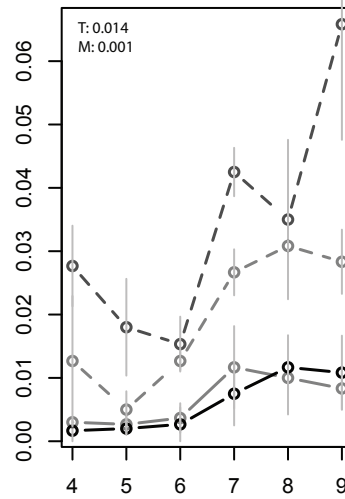
Total vasculars



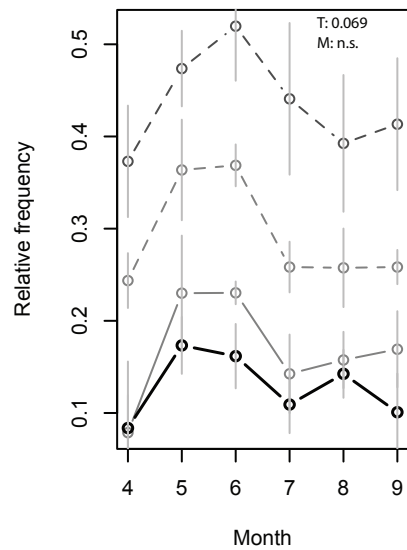
Andromeda polifolia



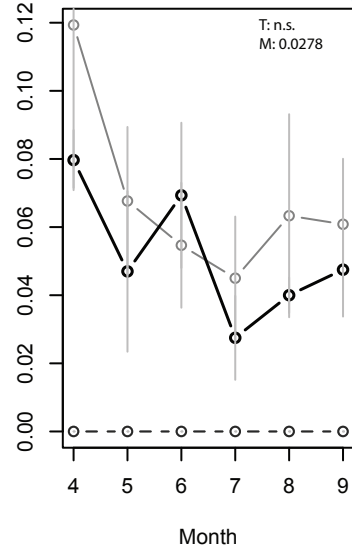
Vaccinium oxycoccus



Sphagnum fallax+rubellum



Sphagnum magellanicum



Litter

