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5 **ombrotrophic peatland**

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

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26 A.B., F.L.D, S.G. and E.M. conceived the experiment, B.R., V.J. and F.D. helped for vegetation and
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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. 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, Jaquemart 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

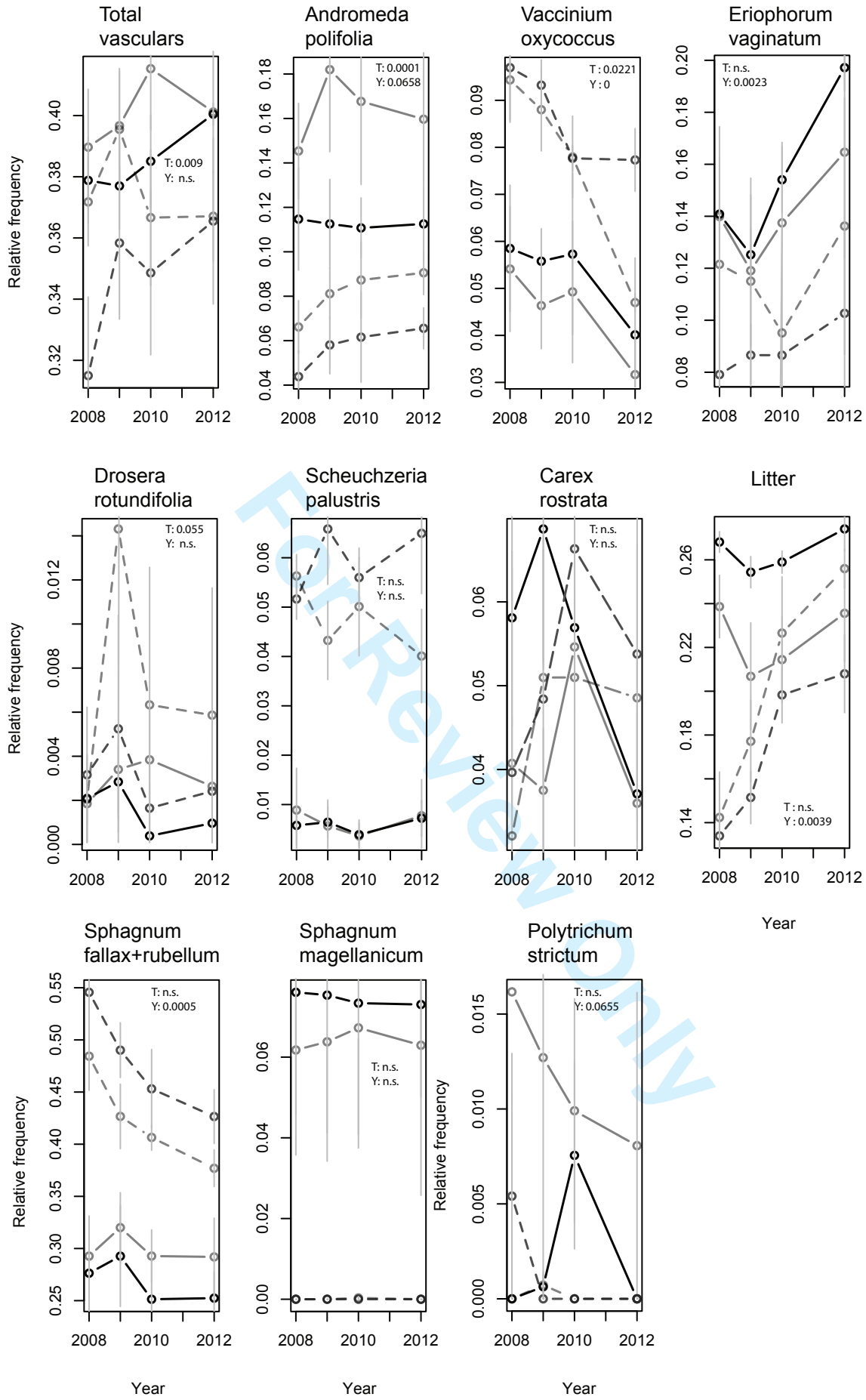
647 The correlation between frequencies obtained by means of field point-intercepts and photographic
648 analyses gives a good linear relation with vascular plants but shows an underestimation of mosses
649 with the picture analysis. This is because leaves of vascular plants might hide the understory 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

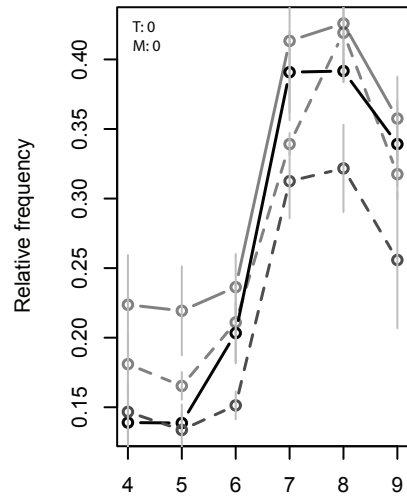
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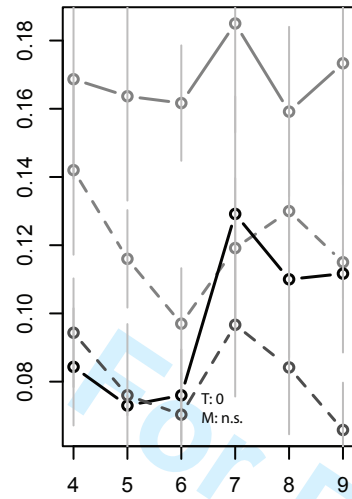
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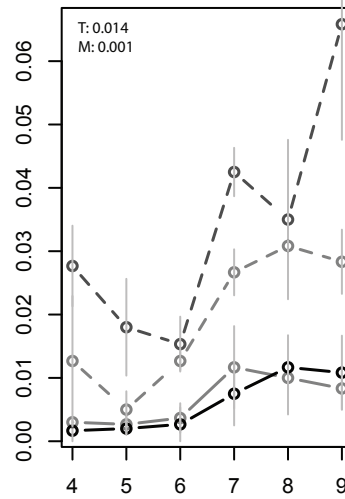
Total vasculars



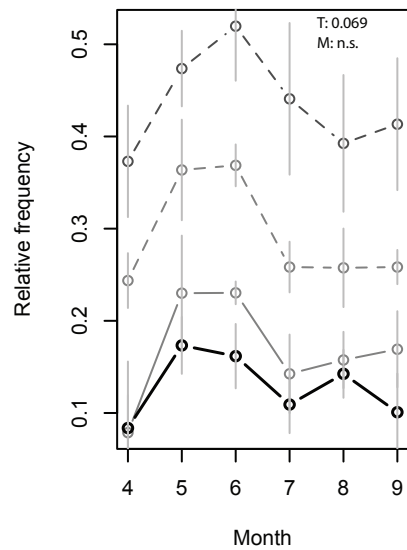
Andromeda polifolia



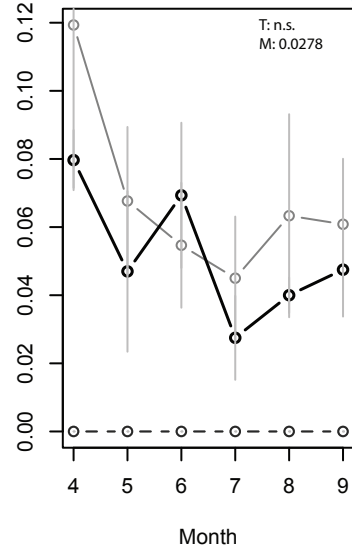
Vaccinium oxycoccus



Sphagnum fallax+rubellum



Sphagnum magellanicum



Litter

