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Vascular plant-mediated controls on atmospheric carbon assimilation and peat carbon decomposition under climate change

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34 **KEYWORDS**

35 climate warming, decomposition, ecosystem respiration, net ecosystem CO₂ exchange, peatlands,
36 rhizosphere priming, vascular plant biomass, elevation gradient

37

38 **Paper type: PRIMARY RESEARCH ARTICLE**

39 **Abstract**

40 Climate change can alter peatland plant community composition by promoting the growth of
41 vascular plants. How such vegetation change affects peatland carbon dynamics remains,
42 however, unclear. In order to assess the effect of vegetation change on carbon uptake and release,
43 we performed a vascular-plant removal experiment in two *Sphagnum*-dominated peatlands that
44 represent contrasting stages of natural vegetation succession along a climatic gradient. Periodic
45 measurements of net ecosystem CO₂ exchange revealed that vascular plants play a crucial role in
46 assuring the potential for net carbon uptake, particularly with a warmer climate. The presence of
47 vascular plants, however, also increased ecosystem respiration, and by using the seasonal
48 variation of respired CO₂ radiocarbon (bomb-¹⁴C) signature we demonstrate an enhanced
49 heterotrophic decomposition of peat carbon due to rhizosphere priming. The observed
50 rhizosphere priming of peat carbon decomposition was matched by more advanced humification
51 of dissolved organic matter, which remained apparent beyond the plant growing season. Our
52 results underline the relevance of rhizosphere priming in peatlands, especially when assessing the
53 future carbon sink function of peatlands undergoing a shift in vegetation community composition
54 in association with climate change.

55

56 INTRODUCTION

57 Peatlands are formed under climatic, hydrological and biological conditions that suppress the
58 decomposition of plant litter, resulting in the accumulation of organic matter as peat. The
59 imbalance between litter production and decomposition makes peatlands effective long-term
60 sinks of atmospheric carbon (Yu, 2012). Indeed, despite a distribution limited to c. 3% of the
61 Earth's land surface, peatlands contain c. 30% of its soil carbon (Yu, 2012). In northern
62 peatlands, *Sphagnum* mosses play a crucial role in peat accumulation due to the production of
63 litter particularly resistant to microbial decomposition (Hájek *et al.*, 2011). However, alteration of
64 the hydrological balance (Talbot *et al.*, 2014; Munir *et al.*, 2015), increase in nitrogen availability
65 (Bubier *et al.*, 2007; Juutinen *et al.*, 2010) and, more specifically, climate warming (Weltzin *et*
66 *al.*, 2000; Dieleman *et al.*, 2015) can promote the growth and cover of vascular plants in
67 peatlands. Such increase in the abundance of vascular plants can potentially reduce the
68 productivity of *Sphagnum* mosses due to, for example, lower light availability (Chong *et al.*,
69 2012) and increasing evapotranspiration (Hirano *et al.*, 2016). In addition, considering that the
70 decomposition rate of vascular plant litter is much faster than that of *Sphagnum* mosses
71 (Dorrepaal, 2007), it is crucial to clarify the role of a higher vascular plant biomass, particularly
72 with a warmer climate, with reference to the capability of the system to act as carbon sink
73 (Breeuwer *et al.*, 2010; Ward *et al.*, 2013; Wang *et al.*, 2015).

74 From a belowground biogeochemical perspective, the presence of vascular plants can supply
75 soil microbes with labile carbon substrates via rhizosphere exudates, providing additional energy
76 to invest in decomposition of old organic matter (Fontaine *et al.*, 2007; Schmidt *et al.*, 2011): a
77 process known as the priming effect (Kuzyakov, 2010). Nevertheless, it is still unknown whether
78 the priming effect in peatlands is directly linked to the abundance of vascular plants, and whether

79 the priming effect shows any seasonal trend, particularly in relation to plant phenology.
80 Answering these questions can help to better predict how climate warming will alter the carbon
81 cycle of northern latitude peatlands when vascular plants become more abundant (Dieleman *et*
82 *al.*, 2015) and the length of the growing season increases (Piao *et al.*, 2008).

83 To investigate the role of vascular plants in the seasonal net assimilation of atmospheric
84 carbon and in the decomposition of peat carbon under contrasting climatic conditions, we
85 performed a vascular plant-removal experiment in two *Sphagnum*-dominated peatlands that were
86 located at different elevations and thereby naturally differed in mean annual temperature,
87 growing season length and vascular plant abundance (Table 1). As such, the comparison of our
88 study sites should be interpreted as a space-for-time substitution (Blois *et al.*, 2013), whereby the
89 low elevation peatland represents the ecosystem state resulting from a natural response of
90 vegetation to warmer climate compared to the upslope site (Klaus, 2007). During a full growing
91 season, we periodically measured the net ecosystem CO₂ exchange (NEE), the ecosystem
92 respiration (R_{eco}) and its radiocarbon signature, and the humification degree of dissolved organic
93 matter in order to: 1) assess the role of vascular plants in assimilation of atmospheric CO₂
94 compared to *Sphagnum* mosses under contrasting climatic conditions; and 2) detect any temporal
95 link between the presence of vascular plants and enhanced decomposition of peat through
96 rhizosphere priming and the associated carbon release into both the atmosphere and pore water.

97

98 **MATERIAL AND METHODS**

99 **Study sites and experimental design**

100 We selected two *Sphagnum*-dominated peatlands located at 1035 m and 1885 m a.s.l. in
101 Switzerland (Table 1, Table S1). At both sites, dominant vascular plant species were *Eriophorum*

102 *vaginatum*, *Calluna vulgaris* and *Vaccinium* spp., whereas *Sphagnum magellanicum*, *S.*
103 *capillifolium* and *S. fallax* were the dominant peat moss species (Gavazov *et al.*, 2016). Peat
104 depth was estimated to be > 1.5 m.

105 At each site, six paired 40x40 cm plots were selected in midsummer 2013. To study the effect
106 of vascular plants on peat decomposition, we clipped the aboveground biomass of vascular plants
107 in half of the plots (-V treatment) without disturbing the moss layer, and left the belowground
108 roots to decompose until measurements commenced the following year (cf. Ward *et al.*, 2009;
109 Kuiper *et al.*, 2014). We started the field measurements after one year in order to allow the
110 decomposition of most living roots, in particular the most labile fine roots. Due to the low rate of
111 root decomposition in peatlands (Laiho *et al.*, 2004; Moore *et al.*, 2007), we are aware that root
112 biomass did not completely decompose after one year, but the delay of one year in field
113 measurements after biomass removal is, however, expected to have significantly reduced the
114 belowground carbon allocation and root exudation in clipped plots. Vascular plants were left
115 intact in paired control plots (+V treatment) so that our experimental set-up represents a paired-
116 plot design with three replicates. Individual plots were delimited by 10 cm high quadratic
117 stainless steel frames pushed to c. 5 cm depth in the living moss layer, which served as collars for
118 gas flux measurements (see below). At regular intervals during 2013, all plots were trenched
119 along the collars with a 30-cm long knife to avoid root colonisation. In the -V treatments vascular
120 plant regrowth was regularly clipped in 2013, whereas no or very limited regrowth was observed
121 in 2014. Because our primary aim was to study the biogeochemical role of vascular plants on
122 carbon cycling, we decided to limit any secondary effects associated with vascular plant removal
123 by shading the clipped plots (-V) with a UV-resistant mesh simulating the original vascular plant
124 cover as preliminarily measured by photosynthetically active radiation (PAR) extinction

125 underneath the canopy (60% and 30% at low and high elevation, respectively). By doing so, the
126 presence of a mesh avoided the desiccation of peat mosses, maintained the natural PAR intensity,
127 and avoided changes in soil microclimate. During gas exchange measurements this mesh was
128 instead used over the chamber to maintain the natural light intensity. Ancillary measurements of
129 soil temperature and soil water content in the clipped and control plots at both elevations
130 confirmed the suitability of this approach (Table S2).

131

132 **Plant biomass and cover estimations**

133 In each peatland, total aboveground vascular plant biomass was estimated by destructively
134 harvesting five random 25x25 cm quadrats at peak standing biomass in 2013. Vascular plant
135 cover within the experimental plots was estimated non-destructively with the point-intercept
136 method. In brief, a pin was lowered over the vegetation through a 40x40 cm grid with 361 holes
137 and the identity of the first intercepted plant was recorded. Species were attributed to one of the
138 existing five categories: graminoids, shrubs, forbs, *Sphagnum spp.* mosses and standing litter,
139 where the total surface cover equals 100%. Control plots (+V) as well as vascular plant removal
140 plots (-V) had 100% *Sphagnum* cover.

141

142 **CO₂ flux measurements**

143 In 2014, one year after the start of the vascular plant removal treatment, a series of monthly CO₂
144 flux measurements were carried out during the snow-free period at each peatland starting in mid-
145 April at 1035 m a.s.l. and in mid-June at 1885 m a.s.l. and lasting through to the end of October.
146 CO₂ fluxes at ecosystem level were measured using a custom made transparent (95% light
147 transmission) Plexiglas chamber (40x40 cm wide, 50 cm high) equipped with a diffusion infrared

148 gas analyser (GMP343, Vaisala, Finland) and a humidity-temperature probe (HMP57, Vaisala,
149 Finland). Air inside the chamber was mixed with a system of inbuilt computer fans. The chamber
150 had a rubber seal on the bottom and a small capped hole on the top which remained open when
151 the chamber was placed on the permanent stainless-steel collar to avoid pressurisation. Net
152 ecosystem CO₂ exchange (NEE) measurements were done in full light or and were immediately
153 followed by ecosystem respiration (R_{eco}) measurements for which the chamber was darkened
154 with a non-transparent cover. All flux measurements were carried out between 10 am and 12 am
155 local time, ensuring optimal photosynthetic conditions for both *Sphagnum* and vascular plants
156 (Bragazza *et al.*, 2016) with vapour-pressure deficit (VPD) below 1.5 kPa and PAR intensity
157 above the vegetation canopy between 1400 and 2100 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Each measurement lasted 1
158 minute in order to avoid excessive heat and humidity causing condensation inside the chamber.
159 The CO₂ flux was calculated as a linear change in concentration (ppm), taking into account
160 ambient atmospheric pressure and gas temperature. In this study, negative NEE represents a net
161 CO₂ assimilation by the plant community and the calculated gross ecosystem productivity (GEP)
162 was derived from the difference between R_{eco} and NEE.

163

164 **Radiocarbon analysis and age interpretation**

165 To determine the seasonal contribution of vascular plant-associated R_{eco}, we sampled respired
166 CO₂ for radiocarbon analysis in both the clipped and unclipped plots in July and at the end of
167 September 2014 (Table S3). We used a passive CO₂ sampling method to determine the
168 radiocarbon signature of ecosystem respiration (Garnett *et al.*, 2009). In brief, specific PVC
169 chambers (10 cm diameter, 10 cm height) connected to a zeolite molecular sieve cartridge (MSC)
170 were gas-tight mounted on collars of similar size pre-installed in 2013 in each plot at 7 cm depth.

171 Prior to sample collection, the atmospheric CO₂ in the chamber headspace was scrubbed by
172 pumping it at a constant rate (0.5 l min⁻¹) through a soda lime column for 10 min while
173 monitoring the concentration. The chambers were then left in place for 10 days until, based on
174 CO₂ production rates, a sufficient amount of CO₂ (i.e. ≥ 3 ml) was passively trapped on the
175 MSCs by diffusion without the use of an external pump. The trapped CO₂ was thermally
176 recovered (425 °C) while purging with high-purity nitrogen gas, converted to graphite by Fe/Zn
177 reduction and analysed by acceleration mass spectrometry (AMS) at the NERC Radiocarbon
178 Facility in Scotland, UK (Garnett & Murray, 2013). Subsamples of CO₂ were measured on a dual
179 inlet stable isotope mass spectrometer (Thermo Fisher Delta V) to determine their δ¹³C signature.

180 In addition, we evaluated the apparent carbon accumulation rate at the two peatlands by
181 splitting one 20-cm long peat core from each site into 5 cm segments. From these segments,
182 vascular plant remnants were removed, after which the carbon content, peat density and peat age
183 were determined (Table S4). After the combustion of these samples in a high-pressure bomb in
184 the presence of oxygen, CO₂ was converted to graphite as above. The peat age was estimated by
185 matching the ¹⁴C content with a known record (Levin *et al.*, 2013) of atmospheric ¹⁴CO₂ in order
186 to estimate the date of carbon fixation (Goodsite *et al.*, 2001) according to Cali-Bomb program
187 for post-bomb ¹⁴C samples (see Reimer *et al.*, 2004).

188 Following convention (Stuiver & Polach, 1977), all radiocarbon data were corrected for mass
189 dependent fractionation by normalising to δ¹³CVPDB values of -25‰ using the measured δ¹³C
190 values, and reported as %Modern with reference to the Oxalic Acid international radiocarbon
191 standard. These data (Table S3) were not subjected to further corrections for atmospheric air
192 contamination during chamber enclosure (Czimczik *et al.*, 2006; Natali *et al.*, 2011; Hartley *et*
193 *al.*, 2012; Hicks Pries *et al.*, 2013) as the fraction of atmospheric CO₂ in the recovered samples

194 proved low and subsequent ^{14}C corrections remained within the AMS measurement uncertainty
195 ($\pm 0.5\%$ Modern).

196 To distinguish between vascular plant-derived respiration and respiration from peat induced
197 by the presence of vascular plants (i.e. the rhizosphere priming effect), we made a common-
198 practice assumption that vascular plants respire contemporary carbon with a ^{14}C signature
199 identical to the current atmosphere (Subke *et al.*, 2011; Hartley *et al.*, 2012), whereas subsurface
200 peat respire older carbon (Hardie *et al.*, 2007), which has become very likely incorporated
201 during the post-1963 bomb- ^{14}C spike at our studied sites (Table S3). Experimental evidence from
202 peatlands dominated by herbaceous vegetation supports this assumption for vascular plant shoots
203 (Czimczik *et al.*, 2006; Hicks Pries *et al.*, 2013), and further indicates only a small contribution
204 of carbon fixed in the preceding year (i.e. up to 0.7 %Modern enrichment) for roots (Hicks Pries
205 *et al.*, 2013, 2015). A sensitivity analysis confirmed that our conclusions were robust regardless
206 of whether we used current year atmospheric ^{14}C values or those from the preceding year. We
207 used data from the nearby Jungfraujoch (53°20' N, 9°54' W, 3580 m a.s.l.) long-term atmospheric
208 ^{14}C monitoring station (Levin *et al.*, 2013) to calculate a mean seasonal value (June, July, August
209 and September) for the expected vascular plant-derived ^{14}C signature for the 2014 growing
210 season, which was 102.91 %Modern ^{14}C . Elevation differences between the study sites and the
211 ^{14}C monitoring station at the Jungfraujoch are expected not to affect the ^{14}C values due to
212 atmospheric mixing (Levin *et al.*, 2008). To this value, we compared the ^{14}C signature of the
213 vascular plant-associated respiration ($D_{\text{V_plant_associated}}$) in our experiment. Following Hardie *et al.*
214 (2009), the latter was calculated using a two pool mixing model:

$$215 \quad D_{\text{V_plant_associated}} = (D_{+V} \cdot R_{+V} - D_{-V} \cdot R_{-V}) / (R_{+V} - R_{-V})$$

216 where R represents the rate of ecosystem respiration measured on the day of chamber enclosure
217 and D its ^{14}C signature in plots with (+V) and without (-V) vascular plants. The vascular plant-
218 associated respiration in our experiment consisted of vascular plant-derived respiration and,
219 potentially, of vascular plant-induced peat respiration. A significant deviation in the calculated
220 ^{14}C signature of vascular plant associated respiration from that of the expected vascular plant-
221 derived ^{14}C signature (ambient atmosphere) was interpreted as an extra source of heterotrophic
222 peat respiration in the presence of vascular plants, i.e. the rhizosphere priming effect.

223

224 **Pore-water sampling and chemical analyses**

225 Representative pore-water samples were collected monthly during May-October 2014 from four
226 permanent microporous (0.20 μm) rhizons (Rhizosphere Research Products, The Netherlands)
227 installed in each plot at the rooting depth, i.e. from 5 to 15 cm below the surface. Concentration
228 of ammonium (NH_4^+) and nitrate (NO_3^-) were obtained colorimetrically on a continuous-flow
229 autoanalyser (SEAL Analytical, Germany), whereas total nitrogen (TN) and dissolved organic
230 carbon (DOC) were determined by combustion on a Shimadzu analyser (TOC-V CPHCTNM-1).
231 In order to characterise the quality of dissolved organic matter (DOM) and its level of
232 humification, lyophilised subsamples were analysed on a Frontier FT-NIR/MIR Spectrometer
233 (PerkinElmer, USA). The recorded spectra (4000 to 400 cm^{-1}) of diamond attenuated total
234 reflectance provide information on the DOM functional groups aliphatics (2943 cm^{-1} region),
235 carboxylic acids and aromatic esters (1720 cm^{-1} region), aromatics (1630 cm^{-1} region), lignins
236 (1510 cm^{-1} region), phenols (1420 cm^{-1} region), and polysaccharides (1090 cm^{-1} region)
237 (Niemeyer *et al.*, 1992; Biester *et al.*, 2014). During peat decomposition, substances enriched in
238 carboxylic, aromatic and phenolic groups accumulate with respect to labile polysaccharides,

239 thereby increasing the specific ratios between these moieties (Biester *et al.*, 2014). Commonly
240 referred to as humification indices, the ratios 2943/1090, 1720/1090, 1630/1090, 1510/1090,
241 1420/1090 can be used as an indication of the level of organic matter decomposition (Broder *et*
242 *al.*, 2012; Hodgkins *et al.*, 2014).

243

244 **Statistical analysis**

245 Data on seasonal CO₂ fluxes and pore-water chemistry were analysed as a paired-plot design for
246 the effect of vascular plant removal in each peatland. The hierarchical structure was coded in
247 R3.3 (R Core Team, 2016) as a linear mixed-effects model using the *nlme* package (Pinheiro *et*
248 *al.*, 2016), accounting for the spatial proximity of +V (control) and -V (clipped) pairs and the
249 repeated measurements in individual plots. Assumptions of normality and homoscedasticity of
250 the residuals in all final models were verified visually using diagnostic plots, and the simplest
251 models were retained by pooling non-significant interactions with the error term. Comparisons
252 between the radiocarbon signature of the atmosphere and the estimated vascular plant-associated
253 CO₂ were done in R using One Sample t-tests for each site and sampling date.

254

255 **RESULTS**

256 The main hydrological (water-table depth) and hydro-chemical (water pH and electrical
257 conductivity) parameters were comparable between the two peatlands and overall typical of
258 ombrotrophic peatlands, i.e. rain-fed bogs (Table 1). The main differences between the two sites
259 were related to climatic conditions and abundance of vascular plants, with characteristically
260 higher air temperature, lower precipitation and higher shrub biomass at low elevation (Table 1,
261 Table S1). Because the cover of peat mosses at plot level did not differ between the two sites

262 (100% at both sites), the study sites can be regarded as a natural climate change experiment
263 where the natural climatic gradient resulted in similar plant community composition, but with
264 different abundance of vascular plants in response to soil microclimate (Table 1, Table S2).

265 Overall, the net ecosystem exchange of atmospheric carbon (i.e., NEE) was weaker (i.e.
266 smaller sink capacity) at low elevation with warmer climatic conditions ($F_{1,4} = 15.5$, $P = 0.017$)
267 despite the larger vascular plant biomass (Fig. 1a). Nevertheless, in both peatlands the presence
268 of vascular plants (+V treatment) increased ($F_{1,35} = 19.4$, $P < 0.001$) the net CO₂ assimilation by
269 c. 50% compared to the treatment with *Sphagnum* mosses alone (-V treatment) (Fig. 1a).
270 Furthermore, at low elevation the absence of vascular plants prevented a net assimilation of
271 atmospheric carbon during most of the growing season (Fig. 1a).

272 During the peak of the growing season, vascular plants contributed to about 50% to gross
273 photosynthesis at both elevations (Fig. 1b) as indicated by the two-fold reduction of potential
274 gross ecosystem productivity (GEP) upon vascular plant removal ($F_{1,35} = 50.2$, $P < 0.001$).
275 Although vascular plant biomass was significantly larger at low elevation (Table 1), the GEP was
276 similar at both sites in the presence of vascular plants (+V). In the absence of vascular plants (-
277 V), GEP of *Sphagnum* mosses was also comparable between the two sites (Fig. 1b).

278 Overall, ecosystem respiration (R_{eco}) was slightly larger at low elevation as compared to high
279 elevation site ($F_{1,4} = 6.4$, $P = 0.064$) and at both sites the presence of vascular plants increased
280 R_{eco} ($F_{1,35} = 46.9$, $P < 0.001$) (Fig. 1c). By taking into account the CO₂ flux and the
281 corresponding ¹⁴C signature in plots with and without vascular plants, the two-pool mixing model
282 revealed that late in the growing season the vascular plant-associated respiration was more
283 enriched in bomb-¹⁴C than would be expected from autotrophic contributions alone at both low
284 ($t_{1,2} = 8.8$, $P = 0.006$) and high ($t_{1,2} = 2.7$, $P = 0.053$) elevation (Fig. 2). An enrichment in bomb-

285 ^{14}C likely occurred also during the peak of the growing season in July (Fig. 2); however, it was
286 masked by larger variability at both low ($t_{1,2} = 1.4$, $P = 0.153$) and high elevation ($t_{1,2} = 1.9$, $P =$
287 0.096).

288 On the basis of pore-water chemistry, the peatland at low elevation was characterized by a c.
289 30% greater concentration of dissolved organic carbon (DOC) (Table 1). Furthermore, the FT-IR
290 spectroscopy demonstrated that the presence of vascular plants (+V) was associated with a
291 consistently higher humification of dissolved organic matter in both peatlands. This was
292 indicated by higher concentrations of aliphatic, carboxylic, aromatic, lignin, and phenolic
293 compounds in proportion to more labile polysaccharides (Fig. 3).

294

295 **DISCUSSION**

296 Our net ecosystem exchange (NEE) measurements under optimal conditions and during the peak
297 of diurnal photosynthetic activity provide an objective assessment of the potential contribution of
298 vascular plants and *Sphagnum* mosses to the exchange of atmospheric CO_2 in the two contrasting
299 peatlands (Bahn *et al.*, 2009; Bragazza *et al.*, 2016). The NEE results demonstrate that the
300 presence of vascular plants is crucial to maintain high levels of net CO_2 assimilation in the two
301 peatlands during the growing season (Laine *et al.*, 2012; Ward *et al.*, 2013; Kuiper *et al.*, 2014).
302 *Sphagnum* mosses alone were much less efficient in offsetting ecosystem respiratory CO_2 losses
303 under warmer conditions. Concurrently, gross ecosystem productivity (GEP) in both peatlands
304 was much higher in the presence of vascular plants, in accordance with the higher photosynthetic
305 efficiency of vascular plants compared to mosses (Ward *et al.*, 2009; Armstrong *et al.*, 2015).
306 Despite the larger aboveground plant biomass at lower elevation, GEP was not significantly
307 different between the two peatlands, a result that can be at least partly explained by a larger

308 abundance of shrubs with a greater portion of ligneous, non-photosynthetic tissues at low
309 elevation (Table 1; Fig. S1) (Bubier *et al.*, 2003; Leppälä *et al.*, 2008; Juutinen *et al.*, 2010). On
310 the basis of our field measurements, *Sphagnum* mosses in the two peatlands contributed equally
311 to GEP per surface area, indicating that under suitable conditions of temperature and moisture the
312 photosynthetic potential was the same at both elevations even if the annual productivity can be
313 different (Bragazza *et al.*, 2013). Indeed, albeit a longer growing season (Fig. 1), both vascular
314 plants and *Sphagnum* mosses are likely to experience more limiting photosynthetic conditions at
315 lower elevation due to higher VPD values (Table 1).

316 The overall greater R_{eco} in the presence of vascular plants, particularly at low elevation, is
317 likely due to a higher contribution of autotrophic respiration, in line with: the larger vascular
318 plant biomass (Ward *et al.*, 2013; Kuiper *et al.*, 2014; Hicks Pries *et al.*, 2015), the corresponding
319 larger biomass of decomposing roots (Murphy *et al.*, 2009), as well as to an enhancement of
320 heterotrophic respiration, i.e. a boosting of microbial metabolism. The latter can be directly
321 stimulated by the improved soil physical conditions due to warmer climate (Updegraff *et al.*,
322 2001; Dorrepaal *et al.*, 2009; Conant *et al.*, 2011; Philben *et al.*, 2014) or indirectly promoted by
323 vascular plants through the rhizosphere priming. The two-pool mixing model, taking into account
324 the CO_2 efflux and the corresponding ^{14}C signature in plots with and without vascular plants at
325 each peatland, shows a consistent enrichment of vascular plant-associated respiration with older
326 carbon, a result that clearly indicates a stimulation of heterotrophic peat decomposition through
327 the rhizosphere priming effect (Hardie *et al.*, 2009; Basiliko *et al.*, 2012; Walker *et al.*, 2016).
328 Although we cannot exclude a contribution of residual decomposing roots to the priming (even
329 after one year of decomposition), if this should take place in the clipped plots it means that the

330 differences in the ^{14}C enrichment with the control plots would be still larger in total absence of
331 roots in the peat.

332 A sustained expression of the rhizosphere priming towards the end of the growing season is
333 intriguing because it indicates that the priming can still be active beyond the plant growing
334 season, i.e. when soil and air temperatures as well as GEP already decline (Fig. 1, Table S2). We
335 interpret this apparent temporal asynchrony between aboveground plant productivity and
336 belowground microbial decomposition as result of: i) the low thermal diffusivity of peat that
337 maintained favourable soil temperatures later into the growing season (Table S2), ii) the
338 preferential allocation of carbon resources by vascular plants to their roots well beyond their
339 aboveground senescence (Abramoff & Finzi, 2015; Blume-Werry *et al.*, 2016), and iii) the
340 leaching from fresh leaf litter (Singh *et al.*, 2014) providing soil microbes with labile carbon
341 substrates to access older organic matter (Qiao *et al.*, 2014).

342 On the basis of FT-IR spectroscopy, at both studied sites there was a higher humification
343 degree of dissolved organic matter in plots with intact vascular plants (Fig. 3), a result that seems
344 to reflect an enhanced microbial metabolism (Glatzel *et al.*, 2003; Höll *et al.*, 2009; Ward *et al.*,
345 2013; Lou *et al.*, 2014; Dieleman *et al.*, 2016). The removal of vascular plants is indeed expected
346 to reduce the availability of more labile, root-mediated carbon (Gogo *et al.*, 2011) that is used by
347 microbes for synthesising extracellular enzymes (Robroek *et al.*, 2016). Additionally, we observe
348 that warmer climatic conditions and larger vascular plant biomass are ultimately associated with a
349 larger release of dissolved organic carbon (DOC) in the peat soil at low elevation (Table 1). This
350 latter result points to the synergetic role of climate and vegetation in increasing the production
351 and release of DOC from peatlands (Neff & Hooper, 2002; Frey & Smith, 2005; Ward *et al.*,
352 2013; Kane *et al.*, 2014).

353 On the basis of the ^{14}C signature in the subsurface peat (Table 1), the estimated age of top 20
354 cm peat, particularly for the low elevation site, was in line with other studies (see e.g. Shotyk *et*
355 *al.*, 1997) suggesting a relatively recent peat accumulation, i.e. primarily after the bomb- ^{14}C peak
356 of 1963. We conclude that the carbon released by the priming effect was only a few decades old
357 (< 20 years) and stored above the mean water-table depth (Table 1). This observation highlights
358 the importance of water table in protecting peat from microbial decomposition (Ise *et al.*, 2008),
359 but also indicates the potential vulnerability of peat carbon if hydrological feedbacks to climate
360 change increase soil oxygenation (Waddington *et al.*, 2015) and, consequently, promote the
361 spreading of vascular plants (Dieleman *et al.*, 2015; Potvin *et al.*, 2015). The apparent rate of
362 carbon accumulation in the peat layers above the mean-water table depth approximated c. 90 g C
363 $\text{m}^{-2} \text{y}^{-1}$ for the low elevation site and c. $154 \text{ g C m}^{-2} \text{y}^{-1}$ for the high elevation site over a reference
364 period of 26-30 years for both sites, a result suggesting a lower carbon sink capacity of peatlands
365 at the lower end of their altitudinal distribution (Millar *et al.*, 2017). The effective annual
366 contribution of the rhizosphere priming to the observed difference in carbon accumulation rate in
367 relation to the dominant vascular plant functional types and their symbiotic microorganisms
368 remains an open question that deserves further attention (Gavazov *et al.*, 2016; Walker *et al.*,
369 2016; Sulman *et al.*, 2017).

370 Our CO_2 exchange measurements, whilst covering only a single growing season, show that the
371 presence of vascular plants is crucial to sustain high potential levels of net atmospheric carbon
372 assimilation in peatlands, particularly with warmer climate. Differently, *Sphagnum* mosses alone
373 could not keep pace with the observed higher ecosystem respiratory C-losses with warmer
374 climate. A sustained temporal expression of the rhizosphere priming effect, although deserving
375 further investigation (Luo *et al.*, 2016), suggests that the decomposition of older peat can be

376 promoted even beyond the plant growing season, so affecting the humification of peat and loss of
377 C in both gaseous and dissolved form. We argue that to accurately predict the future capacity of
378 peatlands to act as atmospheric carbon sinks the synergetic interactions among vegetation
379 dynamics, plant phenology and soil microbes must be taken into account, particularly if the
380 rhizosphere priming effect can be further stimulated in warmer soils (Zhu & Cheng, 2011),
381 thereby exerting a positive feedback to carbon emissions from organic rich soils.

382

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TABLE 1 Geographical location, climatic conditions for the year 2014 and the average for the period 2005-2013 (in brackets), cumulative hours of vapour-pressure deficit (VPD) and water-table depth during plant growing season 2014, vascular plant biomass and surface cover (%), pore-water chemistry, and estimated age of surface peat (with corresponding ^{14}C signature) at the two study sites. Aboveground plant biomass is the mean of 5 replicates for each site. Water table depth is the seasonal mean of continuous measurements collected in one representative piezometer during the plant growing season at each site. Plant cover estimates are mean (± 1 SE) of 3 replicates for each site. Pore-water chemistry is the seasonal mean (± 1 SE) of 3 replicates for each site as measured in the control plots where vascular plants were not clipped (+V treatment). Different superscripts indicate significant differences between the peatlands ($P < 0.05$). The age of the peat was calculated from a reference dataset of atmospheric ^{14}C measurements carried out at the Jungfraujoch station and refers to years before 2014.

	Praz Rodet	Hochrajen
Elevation (m a.s.l.)	1035	1885
Latitude and longitude	46°33'N, 6°10'E	46°36'N, 7°58'E
Mean annual air temperature (°C)	7.0 (6.2)	3.7 (3.3)
Mean annual precipitation (mm)	1219 (1264)	1427 (1372)
VPD > 1.5 kPa (hours)	150	53
Mean water-table depth (cm)	-17.8	-15.6
Total aboveground vascular plant biomass (g m^{-2})	160 ^a \pm 21	74 ^b \pm 7
Total vascular plant cover (%)	63.0 ^a \pm 2.0	35.4 ^b \pm 5.3
Graminoids (%)	26.5 ^a \pm 3.3	19.0 ^a \pm 3.4
Shrubs (%)	20.0 ^a \pm 2.6	8.3 ^b \pm 1.8
Forbs (%)	1.2 ^a \pm 0.5	1.8 ^a \pm 1.8
Standing litter (%)	15.2 ^a \pm 1.4	6.3 ^b \pm 1.9
Total moss cover (%)	100 ^a \pm 0.0	100 ^a \pm 0.0
pH	4.25 ^a \pm 0.02	4.37 ^a \pm 0.15
Conductivity ($\mu\text{S cm}^{-1}$)	31.03 ^a \pm 0.64	27.81 ^a \pm 7.34
Total N (mg l^{-1})	0.39 ^a \pm 0.03	0.30 ^b \pm 0.02
NH ₄ ⁺ (mg l^{-1})	0.018 ^a \pm 0.003	0.007 ^b \pm 0.002
NO ₃ ⁻ (mg l^{-1})	0.034 ^a \pm 0.002	0.032 ^a \pm 0.001
DOC (mg l^{-1})	22.14 ^a \pm 1.12	16.57 ^b \pm 1.53
Age at 5-10 cm (years / %Mod ¹⁴ C \pm 1 σ)	16 / 110.23 \pm 0.48	1 / 103.41 \pm 0.47
Age at 10-15 cm (years / %Mod ¹⁴ C \pm 1 σ)	30 / 120.75 \pm 0.53	16 / 110.01 \pm 0.48
Age at 15-20 cm (years / %Mod ¹⁴ C \pm 1 σ)	40 / 139.28 \pm 0.61	26 / 117.12 \pm 0.51

FIGURE CAPTIONS

Fig. 1 Seasonal dynamics of ecosystem CO₂ fluxes in relation to the presence or absence of vascular plants in two peatlands at different elevations. (a) Net ecosystem exchange (NEE), (b) Gross ecosystem productivity (GEP), (c) Ecosystem respiration (R_{eco}). The two peatlands were located at low (1035 m a.s.l.) and high elevation (1885 m a.s.l.) and two treatments were applied, i.e. mosses plus vascular plants present (+V, controls) or removal of vascular plants by clipping (-V, *Sphagnum* mosses alone). Panels on the left show the seasonal dynamics of mean values (± 1 SE, $n = 3$), whereas those on the right show the overall seasonal means (± 1 SE, $n = 3$). Asterisks indicate significant differences of mean CO₂ fluxes between treatments at each site and between elevations (*' = $P < 0.1$; * = $P < 0.05$; *** = $P < 0.001$). Negative values of NEE indicate a net assimilation of atmospheric CO₂.

Fig. 2 ¹⁴C content of ecosystem respired CO₂ associated with the presence of vascular plants in two peatlands at low and high elevations (1035 and 1885 m a.s.l., respectively) at peak biomass (July) and late in the growing season (end of September). Median and range ($n = 3$) of respired ¹⁴C-CO₂ associated with the presence of vascular plants (DV_plant_associated). Dotted line indicates the mean atmospheric ¹⁴C-CO₂ signature (102.91 ‰Modern) as measured in June, July, August and September 2014 at the Jungfraujoch atmospheric research station. Numbers beneath the dotted line are P -values from t-tests for differences of each date and elevation to this reference line. Significant differences ($P < 0.05$) are interpreted as a signal of plant-induced heterotrophic respiration of peat carbon through the rhizosphere priming effect.

Fig. 3 Mean seasonal values (± 1 SE, $n = 3$) of humification indices of dissolved organic matter based on FT-IR spectra. Pore-water samples were collected monthly from May through October 2014 in the two peatlands at low and high elevations (1035 and 1885 m a.s.l., respectively) in relation to the presence (+V) or absence (-V) of vascular plants. The selected functional groups are: aliphatics (2943 cm⁻¹ region), carboxylic acids and aromatic esters (1720 cm⁻¹ region), aromatics (1630 cm⁻¹ region), lignins (1510 cm⁻¹ region), phenols (1420 cm⁻¹ region) and they are expressed as a ratio to polysaccharides (1090 cm⁻¹ region). Significant differences between treatments are indicated with asterisks (*' = $P < 0.1$, * = $P < 0.05$, ** = $P < 0.01$; *** = $P < 0.001$), whereas no significant differences were observed between the two sites.





