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1   PFTs affect drought response in peatland

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3   Plant functional types define magnitude of drought response in peatland CO_2 exchange

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5   Jan J Kuiper[a,b], Wolf M Mooij[a,c], Luca Bragazza[d,e,f], Bjorn JM Robroek[b,d,e*]

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7   [a]*Department of Aquatic Ecology, Netherlands Institute of Ecology (NIOO-KNAW),*

8   *Wageningen, The Netherlands;* [b]*Ecology and Biodiversity Group, Institute of*

9   *Environmental Biology, Utrecht University, Utrecht, The Netherlands;* [c]*Aquatic Ecology*

10   *and Water Quality Management Group, Wageningen University, Wageningen, The*

11   *Netherlands;* [d]*École Polytechnique Fédérale de Lausanne (EPFL), School of*

12   *Architecture, Civil and Environmental Engineering (ENAC), Laboratory of Ecological*

13   *Systems (ECOS), station 2, CH-1015 Lausanne, Switzerland;* [e]*WSL - Swiss Federal*

14   *Institute for Forest, Snow and Landscape Research, Research Unit Community Ecology,*

15   *Site Lausanne, station 2, CH-1015 Lausanne, Switzerland;* [f]*University of Ferrara,*

16   *Department of Life Science and Biotechnologies, Corso Ercole I d'Este 32, Ferrara*

17   *44121, Italy.*

18

19   [*] Corresponding author: b.j.m.robroek@uu.nl

20

21   *Abstract.*   Peatlands are important sinks for atmospheric carbon (C), yet the role of

22   plant functional types (PFTs) for C sequestration under climatic perturbations is still

23   unclear. A plant removal experiment was used to study the importance of vascular PFTs

24   for the net ecosystem CO_2 exchange (NEE) during (i.e. resistance) and after (i.e.

25   recovery) an experimental drought. The removal of PFTs caused a decrease of NEE, but

26   the rate differed between microhabitats (i.e. hummocks and lawns) and the type of PFTs.

27   Ericoid removal had a large effect on NEE in hummocks, while in the lawns the

28   graminoids played a major role. The removal of PFTs did not affect the resistance or the

29   recovery after the experimental drought. We argue that the response of *Sphagnum* mosses

30   (the only PFT present in all treatments) to drought is dominant over that of coexisting

31   PFTs. However, we observed that the moment in time in which the system switched from

32   C sink to C source during the drought was controlled by the vascular PFTs. In the light of

33   climate change, the shifts in species composition or even the loss of certain PFTs are

34   expected to strongly affect the future C dynamics in response to environmental stress.

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36   *Key words: drought; net ecosystem CO_2 exchange; peatlands; plant functional types;*

37   *recovery; resistance; Sphagnum*

38

INTRODUCTION

39

40   The extensive amount of organic carbon (C) stored in northern peatlands has been

41   shown to be highly vulnerable to increasing soil temperature (Freeman et al. 2001a, Piao

42   et al. 2008, Dorrepaal et al. 2009) and decreasing soil moisture (Freeman et al. 2001b,

43   Fenner and Freeman 2011). In particular, prolonged periods of drought can significantly

44   impact the structure and the functioning of peatlands (Weltzin et al. 2003, Bragazza

45   2008) which then can (temporarily) shift from C sinks to C sources (Lafleur et al. 2003,

46   Lund et al. 2012). The adverse effects of drought on the peatland C balance may,

47   however, strongly depend on plant community composition (Johnson et al. 2011), and the

48   co-occurrence of species or plant functional types may help maintaining ecosystem

49   processes in response to disturbance (Mulder et al. 2001, Craine et al. 2012).

50   The role of plant species richness and diversity for the stability of ecosystems in

51   response to environmental changes is heavily debated (Loreau and de Mazancourt 2013).

52   Generally, high species diversity and high diversity in traits promotes non-additive

53   effects on ecosystem services due to complementarity, facilitation and competition

54   between species or species groups (Hooper et al. 2005, Dias et al. 2013). More evidence

55   is provided that species richness promotes the stability of ecosystem processes (Hector et

56   al. 2010, Isbell et al. 2011, Bloor and Bardgett 2012). Alternatively, the stability of

57   ecosystems is suggested to be mainly driven by the most dominant species, or species

58   group, and to be proportionate to the primary production of these species (Grime 1998).

59   Mosses of the genus *Sphagnum*, generally dominate ombrotrophic peatlands, or bogs,

60   and their decay-resistant litter makes the bulk of the stored peat (Hájek et al. 2011). Due

61   to their ability to modify their environment, *Sphagnum* mosses are considered typical

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62   *ecosystem engineers* (Rochefort 2000). Consequently, *Sphagnum* mosses reduce the

63   potential success of competing plant species (van Breemen 1995, Rydin and Jeglum

64   2006). Additionally, through their high polyphenol content *Sphagnum* mosses inhibit

65   microbial activity by which they control decomposition processes and thus the export of

66   C from peatlands (Bragazza and Freeman 2007). Vascular plant species, with different

67   functional traits, are typical inhabitants of bogs (Chapin et al. 1996, Dorrepaal et al.

68   2007), where plant communities are reported to be remarkably stable in terms of species

69   composition for long periods (Backéus 1972, Rydin and Barber 2001). Studies at species

70   level (Robroek et al. 2007, Otieno et al. 2009, Robroek et al. 2009), community level

71   (Alm et al. 1999, Bubier et al. 2003, Laine et al. 2007, Ward et al. 2009) and ecosystem

72   level (Deppe et al. 2010) revealed that biota play a decisive role in controlling peatland C

73   dynamics. The apparent protective role of vascular plant species on moss growth and C

74   uptake has previously been described. Photo inhibition of photosynthesis, for example,

75   under high irradiance has been reported to decrease under shading due to vascular plant

76   cover (Murray et al. 1989, 1993), and shading by vascular plants may additionally

77   decrease moss evaporation and protect the moss canopy from drying (Heijmans et al.

78   2004, McNeil and Waddingon 2003). Few studies, however, have explicitly studied the

79   role and function of different plant functional groups on peatland C uptake and its

80   robustness during summer drought.

81   In this study, we aim to elucidate the role of plant functional types in affecting C

82   fluxes in a peatland during a drought event. Specifically, we performed a plant removal

83   experiment in order to explore how two dominant plant functional types, i.e., ericoid

84   dwarf-shrubs and graminoids, can affect the resistance and the recovery of CO_2 uptake

85   during and after a drought event.

86

87   MATERIALS AND METHODS

88   *Field sampling and experimental set-up*

89   In November 2009, thirty-two intact peat cores (diameter 22 cm, depth 16 cm) were

90   collected from Tofte mose, Lille Vildmose Natural Park, Denmark (56°50'N, 10°15'E).

91   Half of the cores were taken from wet lawns, and half were taken from relatively dry

92   hummocks in order to include the two dominant microhabitats. All cores were

93   representative for the site and encompassed equal (i.e., within natural variation) amounts

94   of three plant functional types (PFTs): *Sphagnum* mosses, graminoids and evergreen

95   ericoid shrubs (Chapin et al. 1996). In the lawns, *Sphagnum cuspidatum* Ehrh. Ex Hoffm.

96   was the dominant moss species, while the vascular plant community consisted of the

97   graminoids *Eriophorum angustifolium* Honck. and *Rhynchospora alba* (L.), and the

98   ericoids *Erica tetralix* L.*, Vaccinium oxycoccus* L. and *Andromeda polifolia* L. In the

99   hummocks, *Sphagnum magellanicum* Brid. and *S. rubellum* Wils. dominate the peat moss

100   layer, while the vascular plant community consisted of the graminoid *Eriophorum*

101   *vaginatum* L., and the ericoids *E. tetralix, V. oxycoccus, A. polifolia, Empetrum nigrum*

102   L. and *Calluna vulgaris* (L.). The vascular plant cover ranged between 25-50% in both

103   microhabitats.

104   After extraction, the cores were carefully placed in plastic containers (hereafter

105   referred to as mesocosms), transported to Utrecht University, The Netherlands, and kept

106   in a growth room (20/18 °C [12/12 h; day/night], 70% RH, 400 ppm CO_2, 200 µmol m^{-2}

107   s^{-1} light intensity) for seven weeks to acclimate (*acclimation period*). Mesocosms were

108   watered twice a week, using artificial rainwater (Garrels and Christ 1965), which was

109   sprinkled over the vegetation to mimic an average precipitation of approximately 2 mm

110   day^{-1} (730 mm year^{-1}; *cf.* the region of Lille Vildmose NP; www.dmi.dk). Additionally,

111   water levels were kept constant at 2 cm and 10 cm below the *Sphagnum* capitula for

112   lawns and hummocks, respectively, by funneling artificial rainwater to the mesocosms.

113   One mesocosm became visibly infected with fungi and was removed from the

114   experiment, resulting in 31 mesocosms (16 hummocks, 15 lawns).

115   After the *acclimation period*, vascular plant functional type (PFT) composition was

116   manipulated by removing ericoids (E_{rem}), graminoids (G_{rem}), or both the PFTs so to leave

117   a pure *Sphagnum* stand (n = 4 for each treatments and microhabitat). Removal was

118   realized by clipping the above ground biomass flush to the moss layer (McLellan et al.

119   1995). An extra set of mesocosms was used a control treatment, but in order to take into

120   account the potential effects of the clipping procedure, about 20% of the ericoid and

121   graminoid cover was removed from the control mesocosms (Table 1). The period

122   between PFT removal and the drought event lasted four weeks (*pre-drought period*), and

123   was used to recover from the removal procedure. The second experimental period

124   entailed the actual drought event (*drought period*), during which the mesocosms were

125   allowed to dry out 'naturally'. After four weeks of drought, all mesocosms were rewetted

126   and allowed to recover (*recovery period*). Rainwater was added to completely submerge

127   the mesocosms over a one-night period, after which the water tables were brought back to

128   their initial levels and the original pre-drought watering regime was resumed. The process

129   of recovery was monitored for ten weeks. Throughout all the experimental periods, the

130   treatments were maintained by regular removal of regrown biomass.

131

132   *Carbon exchange measurements*

133   We used net ecosystem CO_2 exchange (NEE) measurements to approximate net

134   ecosystem productivity. Ecosystem respiration (R_e; autotrophic and heterotrophic) was

135   measured by darkening the chambers. Closed flux chambers (diameter 20 cm, height 29

136   cm, fitted with a circulating fan) were placed over the mesocosms to measure CO_2 fluxes

137   using an Innova Bruel Kjær BK 1302 photoacoustic multi gas analyzer (Bruel and Kjær,

138   type 1302, Denmark), connected to a multipoint sampler (CBISS MK2, 4-channel,

139   CBISS Ltd. England). During chamber closure, increment in air pressure in the chamber

140   headspace was avoided by a 10 mm opening at the top of the plastic container, which was

141   closed before any records were taken. The chambers made no contact with the vegetation

142   wherefore disturbance of pressure gradients across the soil-atmosphere interface was

143   avoided. Chamber measurements comprised five succeeding sampling points with an 8-

144   minute interval. NEE was measured weekly during the *pre-drought period* and every two

145   days during the *drought period*. During the *recovery period*, measurements were initially

146   performed every two days, but intensity was reduced at a later stage. R_e was measured

147   just before and after plant removal, and throughout the *drought period* and *recovery*

148   *period*. The ecological sign convention was used for the NEE and R_e data, so that positive

149   fluxes indicate CO_2 uptake and negative fluxes indicate CO_2 loss to the atmosphere.

150

151   *Calculations and Statistical Analyses*

152   NEE was calculated from the change in CO_2 concentration in the chamber headspace

153   with time, using an exponential non-linear function as proposed by Kutzbach et al.

154   (2007). We used the nls function in the *stats* package in R to fit the models to the first

155   four CO_2 readings of the individual time series. In general, the coefficients of

156   determination of the fitted models were very convenient (91% of the regressions showing

157   an $r^2 > 0.995$, n=940). The net CO_2 flux was then calculated for the time zero,

158   representing the flux at the start of the enclosure (see Appendix A for specifics). R_e was

159   determined by a linear regression over the five succeeding sampling points after

160   darkening the chambers.

161   The resistance to drought is the ability of the system to reduce the decrease of NEE

162   throughout the *drought period*. Here, the resistance was calculated, for each individual

163   mesocosm, as the slope of the linear regression through the NEE data-points over the

164   drought period. These regression parameters were also used to calculate the time when

165   NEE switched from positive to negative value (i.e., NEE = 0) for each individual

166   mesocosm. Similar to our measure of resistance, the recovery was calculated using the

167   slope through the NEE data-points over the *recovery period*. Since NEE values decreased

168   abruptly immediately after the recovery (data not shown), the use of a linear regression

169   would not be appropriate. To circumvent this problem, recovery was calculated using the

170   data collected one week after the start of the *recovery period*. Resilience was calculated

171   as the ratio of post-recovery to pre-drought NEE. As such, resilience combines resistance

172   and recovery and provides a measure of the extent to which the NEE has recovered to the

173   pre-drought level.

174   To test the influence of our treatments on net ecosystem exchange (NEE) and

175   ecosystem respiration (R_e), we used the generalized linear models (GLM) assuming a

176   Gaussian distribution of the data. We coded microhabitat (MH), ericoid removal (E_{rem})

177   and graminoid removal (G_{rem}) as binary factors and initially we tested the treatment effect

178   on NEE and R_e at three crucial moments during the experiment, i.e., just before the

179   initiation of the *drought period* (Pre-drought), at the end of the *drought period* (Post-

180   drought), and at the end of the *recovery period* (Post-rewetting). Similarly, we tested the

181   treatment effect on the resistance, recovery and resilience of the net ecosystem exchange.

182   As the amount of removed biomass can be considered as an explanatory factor, we

183   initially examined two models. The first model contained the factors MH, $E_{rem,}$ and $G_{rem,}$

184   while the second model considered the amount of 'biomass removed' as co-variable. The

185   goodness-of-fit in relation to the model complexity was evaluated by comparing values of

186   the corrected Akaike information criterion (AICc), using the selMod function in *pgirmess*

187   package in R (Giraudoux 2013). The model with the smallest AICc was selected, and

188   further analyses were performed using the ANOVA function and the F-statistic in the

189   *stats* package of R. The *lme* package in R (Pinheiro et al. 2011) was used to perform

190   repeated measures-ANOVA to determine the effects of E_{rem}, G_{rem} and MH on NEE

191   through the drought period and the recovery period. As microhabitats differed

192   significantly in their CO_2 exchange dynamics (significant MH effects, or MH $\times$ E_{rem} and

193   MH $\times$ G_{rem} interactions, see also Appendix C and D), these analyses were also performed

194   separately for the two microhabitats. All analyses were performed with the software R

195   2.15.2 (R Core Team 2012).

196

197   RESULTS

198   *Pre-drought period: the effect of vascular plant functional type removal*

199   To test the potential role of the amount of removed biomass in affecting net ecosystem

200   exchange (NEE) and ecosystem respiration (R_e), we examined the explanatory power of a

201   set of models with different complexities (see Appendix B). The amount of removed

202   biomass was rather important for the change in NEE and R_e before and after plant

203   functional type (PFT) removal. Therefore, the co-variable 'biomass removed' was always

204   taking into the potential models when testing for the effects on PFT removal in further

205   analyses.

206   Plant functional type (PFT) removal caused a decrease in pre-drought NEE, which

207   differed between the microhabitats in relation to the PFTs (Fig. 1A,B; Appendix C).

208   Indeed, in the lawns, graminoid removal reduced NEE (F = 16.9, $p \leq 0.01$). Ericoids

209   removal caused a reduction of NEE only in combination with graminoid removal (Ericoid

210   × Graminoid F = 3.5, $p = 0.09$). In the hummocks, ericoid removal resulted in a reduction

211   of NEE (F = 27.3, $p \leq 0.001$), whereas graminoid removal did not affect the NEE.

212   Including removed biomass in these GLM model did not enhance the explanatory power,

213   i.e. higher AICc (Appendix C).

214

215   *Drought period: the resistance to drought*

216   Net ecosystem exchange (NEE) and ecosystem respiration (R_e) decreased immediately

217   after the start of the experimental drought in all the mesocosms (Fig. 1 and 2). The

218   resistance to drought differed between microhabitats (Fig 3A,B, Table 2). The decrease of

219   NEE was faster in the lawns, resulting in lower post-drought NEE (Fig. 1; Appendix

220   C,D). In fact, lawns switched from CO_2 sinks (NEE > 0) to CO_2 sources (NEE < 0) earlier

221   than hummocks (Fig. 1 and. 3C,D, Table 2). The decrease of R_e was faster in the

222   hummocks (Fig. 2; Appendix D).

223   PFT removal did not significantly affect the resistance in both microhabitats (Table 2),

224   though in the lawn microhabitats graminoid removal seemed to slightly slow down the

225   decrease in NEE (F = 3.4, p = 0.09), and though not significant the removal of ericoids

226   seemed to slightly speed up the decrease of NEE. Nevertheless, PFT removal affected the

227   moment of the switch from CO_2 sink to CO_2 source in the two microhabitats (Fig. 3C,D,

228   Table 2). When analyzed separately it appears that in the lawn microhabitats, graminoid

229   removal caused an earlier switch of the ecosystem from CO_2 sink to CO_2 source (F =

230   14.4, $p \leq 0.01$), while in the hummock microhabitats ericoid removal enhanced such

231   switch, although not significantly (F = 3.9, p = 0.07).

232

233   *Recovery after, and resilience to drought*

234   Rewetting caused a sudden increase in CO_2 emission in all the mesocosms (data not

235   shown). After this initial 'desaturation respiration' (Gerdol et al. 1996), CO_2 uptake

236   recommenced relatively fast. On the whole, recovery was not influenced by the PFTs,

237   although mesocosms without ericoids seemed to recover faster (Fig. 3E,F, Table 2),

238   especially in the lawn microhabitats. Ecosystem resilience differed between microhabitats

239   (Table 2), and was higher in the hummocks (45 $\pm$ 6.3%) than in the lawns (25 $\pm$ 4.6%). In

240   both microhabitats, the PFT removal treatment did not affect the resilience of NEE (Table

241   2).

242

243 DISCUSSION

244   Using a plant removal experiment, we tested the role of vascular plant functional types

245 on short-term CO_2 fluxes in peatland in response to drought. Removal experiments are

246 useful to study the relation between plant functional types and ecosystem processes (Díaz

247 et al. 2003), although we acknowledge they have their limitations (Bret-Harte et al. 2004,

248 Ward et al. 2009, Gundale et al. 2010). Remaining plant roots, for example, may increase

249 ecosystem respiration (R_e), and concomitantly decrease net ecosystem exchange (NEE).

250 We, however, observed decreased R_e after vascular PFT removal, confirming the

251 contribution of vascular plant biomass to ecosystem respiration in peatlands (Bubier et al.

252 2003). Interestingly the decrease in NEE upon PFT removal was trait dependent and

253 different between lawns and hummocks. Indeed, decreased NEE in hummocks was

254 mainly caused by the removal of ericoids, whereas in lawns it was mainly caused by

255 graminoids removal (Fig. 1). The decrease in NEE due to plant removal can partly be

256 explained by the amount of removed biomass (Appendix B), yet the effects of PFT

257 removal and biomass removal are highly collinear, i.e. hummocks are dominated by

258 ericoids, while lawns are dominated by graminoids. Contrasting to our results, Ward et al.

259 (2009) did not find any change in NEE after ericoid or graminoid removal from a blanket

260 bog, due to an increase of both the gross C uptake and respiration rate. We argue that the

261 removal of the high cover (about 70%) of vascular plants in their experiment may have

262 stimulated the photosynthetic rates of the underlying moss layer. This apparent

263 "competitive release effect" (Wardle et al. 1999, Symstad and Tilman 2001) did not take

264 place in our experiment where the initial cover of vascular plants was much lower (25-

265 50%). Concurrently, negative effects of vascular plant cover on underlying mosses or soil

266   processes have been reported to occur mainly at dense vascular plant cover (Chapin and

267   Shaver 1985, Heijmans et al. 2002, Blok et al. 2011).

268   Our findings that NEE decreased with plant removal indicate an important role of

269   vascular plants and their corresponding traits in affecting NEE (McNeil and Waddington

270   2003), yet the overall aim of this study was to elucidate the role of PFTs on the resistance

271   of NEE to, and its recovery after an extreme summer drought. The decrease in NEE

272   during the drought period in all treatments, indicates an intrinsic sensitivity of peatlands

273   to drought (Cai et al. 2010, Fenner and Freeman 2011, Lund et al. 2012). Lawns were less

274   resistant to drought than hummocks (Fig. 3), supporting earlier findings of greater

275   resistance of hummock *Sphagnum* species to desiccation (Andrus 1986, Strack and Price

276   2009). While vascular plant species seem to be important in controlling levels of NEE,

277   they seem not to play an important role in mitigating the negative effect of drought on

278   NEE. This is surprising, as vascular plants can avoid desiccation during drought by

279   actively regulating their water content through morphological adaptations (roots, stomata,

280   vascular system). *Sphagnum* mosses are poikilohdyric and cannot actively control their

281   water contents. They can only tolerate drought through physiological responses, like

282   quenching its basal chlorophyll fluorescence (Hajek and Beckett 2008, Turetsky et al.

283   2012). Based on the absence of an effect of PFTs on the resistance to drought (Table 2),

284   we reason that the decrease of NEE is primarily controlled by the drought-induced

285   decrease of *Sphagnum* photosynthetic assimilation. Indeed, most mesocosms were visible

286   desiccated toward the end of the drought period (Robroek et al. 2009). Would we,

287   however, approach resistance as the ecosystems capacity to maintain positive CO_2 uptake

288   during drought (i.e. time to NEE $\leq$ 0), the presence of vascular plants becomes rather

289   important (Fig. 3). According to previous hypotheses from grassland studies (Wang et al.

290   2007, van Ruijven and Berendse 2009), the initial productivity (or NEE) and not the plant

291   functional type diversity *per se* then determines the resistance of the peatland to

292   environmental perturbations.

293   The observed recovery after drought resembles that already presented by Robroek et

294   al. (2009). They, however, report data from pure *Sphagnum* stands. Interestingly,

295   *Sphagnum* mosses are generally described as a drought intolerant genus, being very

296   sensitive to (repeated) desiccation (Gerdol et al. 1996, Schipperges and Rydin 1998) and

297   slow in their recovery after drought (Gerdol et al. 1996, Bragazza 2008). The faster

298   recovery observed in hummocks indicates a greater tolerance to desiccation of hummock

299   *Sphagnum* mosses (Hájek and Beckett 2008). Our results, however, show that after a ten-

300   week recovery period, CO_2 uptake returned only to <45% of the pre-drought perturbation

301   levels. Although our results indicate a relatively swift recovery of C uptake after a

302   drought, these results also indicate that a single drought can have a substantial impact on

303   the annual CO_2 budget (Alm et al. 1999). In fact, any cessation in carbon uptake can have

304   a strong effect on the annual C budget in peatlands (McNeil and Waddington 2003). The

305   size of this effect depends on the timing, the severity and the duration of the drought

306   (Lund et al. 2012).

307   The apparent absence of a crucial role for PFT composition on the resistance to, and

308   recovery after, a drought in peatlands, together with the response of net photosynthesis of

309   monospecific *Sphagnum* stands to drought (Robroek et al. 2009, Adkinson and

310   Humphreys 2011), indicate a dominant mechanistic role for the *Sphagnum* community.

311   Raised bogs have a rather low diversity and are characterized by the presence of a clear

312 ecosystem engineer, which may have a disproportionate influence on ecosystem

313 processes (Brown 1995, Polley et al. 2007). Consequently, *Sphagnum* mosses are largely

314 controlling the ecosystem C cycling. Such a strong effect displayed by a single group, has

315 been earlier reported as a possible explanation for the absence of diversity–ecosystem

316 functioning relationships (Hooper et al. 2005). As in peatlands, *Sphagnum* mosses have

317 the largest share of the aboveground green biomass in all plant communities (Laine et al.

318 2012), our results support Grime's biomass ratio hypothesis (Grime 1998), which states

319 that the effect of each species or plant functional group is proportional to its relative

320 biomass in the ecosystem.

321   Changes in short-term CO_2 fluxes due to drought are of relevance for the long-term C

322 budget of peatlands (Ward et al. 2009), especially if extreme drought events are expected

323 to occur more often (Dai 2012). Our study shows that vascular PFTs do not affect the

324 resistance of the peatland ecosystem to, nor the recovery after an experimental drought.

325 Nevertheless, vascular PFTs are important in controlling the net ecosystem productivity,

326 and thereby the moment the systems can switch from C sink to C source during a drought

327 event. As evidenced by our data, in both lawns and hummocks, the presence of vascular

328 plants secures the C sink function during drought events. In the light of climate change,

329 shifts in the species community composition or even the loss of certain PFTs can thus

330 have strong effects on future C dynamics in response to environmental stress.

331

332 ACKNOWLEDGMENTS

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532

533   SUPPLEMENTAL MATERIAL

534   APPENDIX A. Description on the exponential non-linear model used for calculating CO_2

535   fluxes from the mesocosms.

536   APPENDIX B. The effects of biomass removal on net ecosystem CO_2 exchange (NEE)

537   and ecosystem respiration (R_e).

538   APPENDIX C. Model test results for two models, one with and one without 'removed

539   biomass' as a factor.

540   APPENDIX D. Test results of the repeated measures-ANOVA on net ecosystem CO_2

541   exchange during the drought period.

542 **Table 1**   Amounts of removed vascular plant aboveground biomass (g dwt), and cover of the different plant functional types

543 (PFT) after biomass removal for the PFT removal treatments on the lawn and hummock microhabitats. Note that in the control

544 treatment part of the ericoid and graminoid aboveground biomass has been removed. Total evapotranspiration rates have been

545 calculated over the drought period; significant differences (Tukey's *post-hoc* test; $p \leq 0.05$) are indicated by different letters.

	Biomass removed (g dwt)	PFT cover after removal (%)				Total Evapotranspiration during the drought period (ml m^{-2})
Treatment		*Sphagnum*	Ericoids	Graminoids	Vascular plants	
Lawn						
Control	0.95 ± 0.3	100 ± 0	15.0 ± 3.5	15.0 ± 2.9	30.0 ± 3.5	67.53 ± 4.3[a]
E$_{rem}$	3.35 ± 0.9	100 ± 0	-	27.5 ± 3.2	27.5 ± 3.2	67.53 ± 4.3[a]
G$_{rem}$	0.54 ± 0.2	100 ± 0	17.5 ± 7.2	-	17.5 ± 7.2	59.30 ± 2.6[a]
E$_{rem}$ + G$_{rem}$	3.91 ± 0.3	100 ± 0	-	-	-	60.58 ± 4.3[a]
Hummock						
Control	1.93 ± 0.7	100 ± 0	20.8 ± 2.9	9.2 ± 2.5	30.0 ± 1.6	69.89 ± 2.5[ab]

E_{rem}	4.50 ± 0.7	100 ± 0	-	17.1 ± 3.0	17.1 ± 3.0	61.36 ± 1.7[a]
G_{rem}	0.12 ± 0.1	100 ± 0	21.3 ± 3.5	-	21.3 ± 3.5	72.64 ± 1.8[b]
$E_{rem} + G_{rem}$	5.26 ± 0.5	100 ± 0	-	-	-	65.24 ± 3.2[ab]

546

547

548 **Table 2** ANOVA results (F and *p*-values) for the interactive effects of microhabitat, ericoids removal and graminoid removal on

549 the resistance, time to NEE = 0, and recovery of net ecosystem CO_2 exchange. *p*-values in bold indicate significant values.

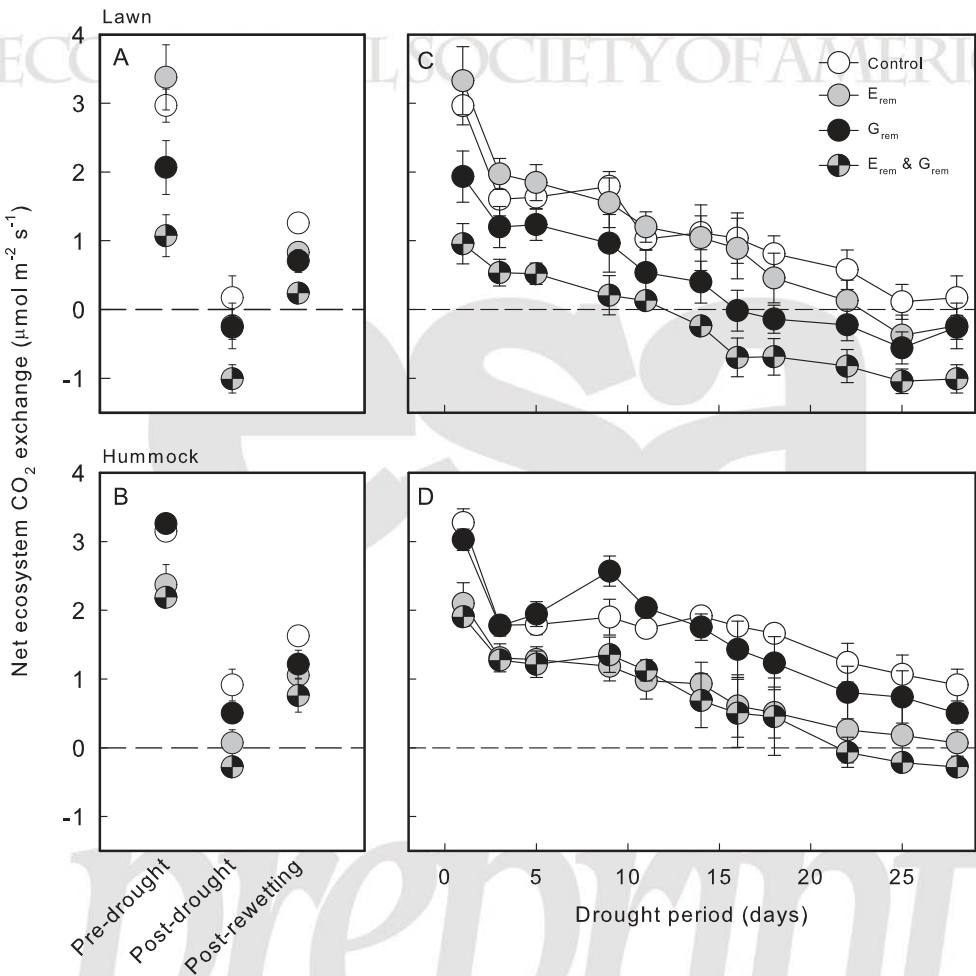|	Resistance NEE		NEE = 0		Recovery NEE		Resilience NEE	
	F	*p*	F	*p*	F	*p*	F	*p*
Microhabitat (MH)	7.1	**≤ 0.05**	11.6	**≤ 0.01**	0.5	0.48	0.6	0.44
E_{rem}	1.4	0.24	6.1	**≤ 0.05**	2.2	0.15	0.7	0.41
G_{rem}	0.0	1.00	4.5	**≤ 0.05**	0.4	0.51	0.9	0.34
MH : E_{rem}	0.5	0.49	1.3	0.26	0.0	0.9	0.0	0.91
MH : G_{rem}	4.9	**≤ 0.05**	0.1	0.78	0.0	0.94	0.5	0.47
E_{rem} : G_{rem}	2.1	0.16	0.1	0.77	0.3	0.59	0.5	0.48
MH : E_{rem} : G_{rem}	0.9	0.35	0.0	0.99	1.0	0.32	0.2	0.66

550

551

552   FIGURE LEGENDS

553   **Figure 1**   Comparison of net ecosystem exchange (± SEM) rates between the

554   different plant functional type removal at the pre-drought, post-drought, and post-

555   recovery period (A: lawns; B hummocks), as well as during the drought period (C: lawns;

556   D: hummocks). Negative values indicate net CO_2 loss. For statistics, see Appendix C and

557   D.

558

559   **Figure 2**   The effect of plant functional type removal on ecosystem respiration

560   during the drought period (A: lawns; B: hummocks). Negative values indicate net CO_2

561   loss. For statistics, see Appendix D.

562

563   **Figure 3**   The effect of plant functional type removal on the resistance (A, B), the

564   time to NEE = 0 (C, D), and the recovery (E, F) in the two microhabitats. For definitions,

565   see material and methods section.

Lawn

A

B

Hummock

C

D

Control
E_{rem}
G_{rem}
E_{rem} & G_{rem}

Net ecosystem CO_2 exchange (μmol m^{-2} s^{-1})

Pre-drought Post-drought Post-rewetting

Drought period (days)