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Plant functional types define magnitude of drought response in peatland CO₂ exchange

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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 CO₂ exchange

4

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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 CO₂ 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.

35
 36 *Key words: drought; net ecosystem CO₂ exchange; peatlands; plant functional types;*
 37 *recovery; resistance; Sphagnum*

38

39 INTRODUCTION

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

62 *ecosystem engineers* (Rocheft 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 Waddington 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 CO₂ 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 CO₂, 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 CO₂ 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 CO₂ fluxes
 137 using an Innova Bruel Kjaer BK 1302 photoacoustic multi gas analyzer (Bruel and Kjaer,
 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 CO₂ uptake and negative fluxes indicate CO₂ loss to the atmosphere.

150

151 *Calculations and Statistical Analyses*

152 NEE was calculated from the change in CO₂ 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 CO₂ 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 CO₂ 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 CO₂ exchange dynamics (significant MH effects, or MH × E_{rem} and
 193 MH × 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 \times 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 CO₂ sinks (NEE > 0) to CO₂ 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 CO₂ sink to CO₂ 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 CO₂ sink to CO₂ source (F =
 230 14.4, p ≤ 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 CO₂ emission in all the mesocosms (data not
 235 shown). After this initial ‘desaturation respiration’ (Gerdol et al. 1996), CO₂ 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 ± 6.3%) than in the lawns (25 ± 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 CO₂ fluxes in peatland in response to drought. Removal experiments are
 246 useful to study the relation between plant functional types and ecosystem processes (Diaz
 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 poikilohydric 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 CO₂ uptake
 288 during drought (i.e. time to NEE ≤ 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, CO₂ 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 CO₂ 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 CO₂ 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

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341

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533 SUPPLEMENTAL MATERIAL

534 APPENDIX A. Description on the exponential non-linear model used for calculating CO₂
 535 fluxes from the mesocosms.

536 APPENDIX B. The effects of biomass removal on net ecosystem CO₂ 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 CO₂
 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.

Treatment	Biomass removed (g dwt)	PFT cover after removal (%)				Total Evapotranspiration during the drought period (ml m ⁻²)
		<i>Sphagnum</i>	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}

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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 CO₂ exchange. *p*-values in bold indicate significant values.

	Resistance NEE		NEE = 0		Recovery NEE		Resilience NEE	
	F	<i>p</i>	F	<i>p</i>	F	<i>p</i>	F	<i>p</i>
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

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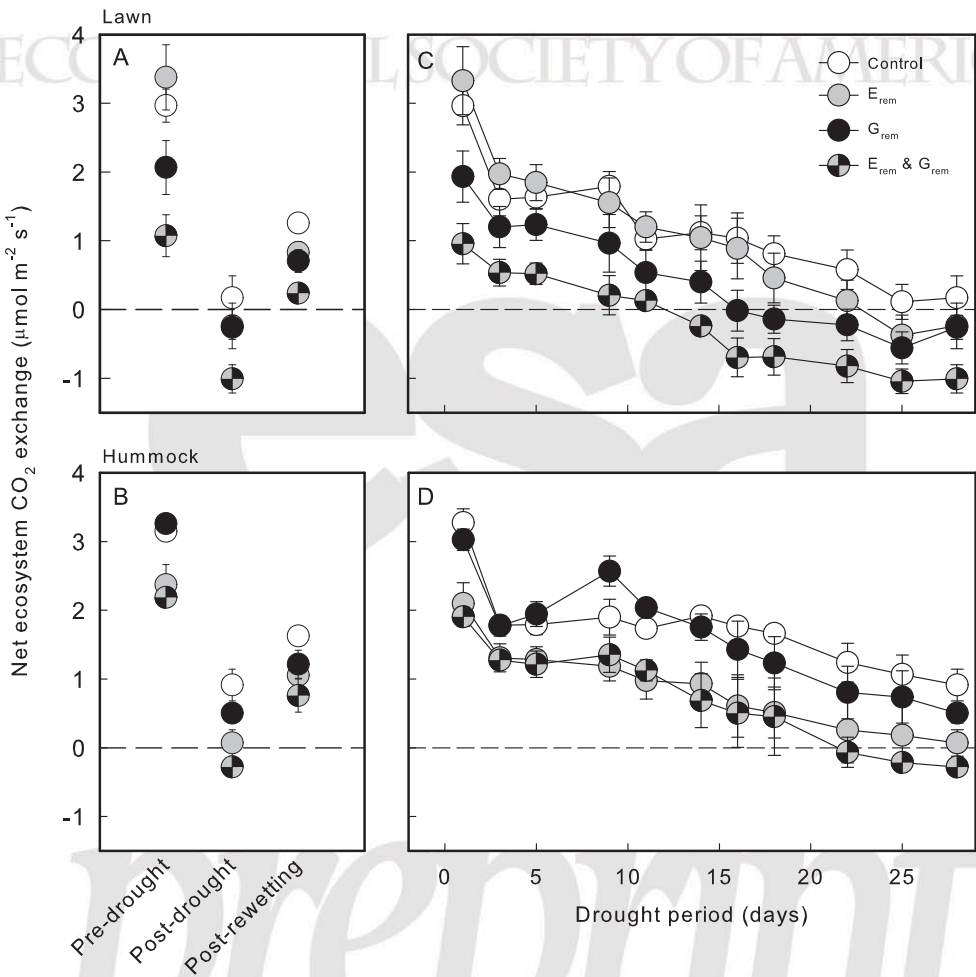
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552 FIGURE LEGENDS

553 **Figure 1** Comparison of net ecosystem exchange (\pm 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 CO₂ 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 CO₂
 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.



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