ASSESSING THE IMPACT OF PEAT EROSION ON GROWING SEASON CO_2 FLUXES BY COMPARING EROSIONAL PEAT PANS AND SURROUNDING VEGETATED HAGGS

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25 **FLUXES BY COMPARING EROSIONAL PEAT PANS AND SURROUNDING**

26 **VEGETATED HAGGS**

27 ## ABSTRACT

28 Peatlands are recognised as an important but vulnerable ecological resource.

29 Understanding the effects of existing damage, in this case erosion, enables more informed

30 land management decisions to be made. Over the growing seasons of 2013 and 2014

31 photosynthesis and ecosystem respiration were measured using closed chamber

32 techniques within vegetated haggs and erosional peat pans in Dartmoor National Park,

33 southwest England. Below-ground total and heterotrophic respiration were measured and

34 autotrophic respiration estimated from the vegetated haggs.

35 The mean water table was significantly higher in the peat pans than in the vegetated

36 haggs; because of this, and the switching from submerged to dry peat, there were

37 differences in vegetation composition, photosynthesis and ecosystem respiration. In the

38 peat pans photosynthetic CO_2 uptake and ecosystem respiration were greater than in the

39 vegetated haggs and strongly dependent on the depth to water table ($r^2 > 0.78$, $p < 0.001$).

40 Whilst in the vegetated haggs, photosynthesis and ecosystem respiration had the

41 strongest relationships with normalised difference vegetation index (NDVI) ($r^2 = 0.82$,

42 $p < 0.001$) and soil temperature at 15 cm depth ($r^2 = 0.77$, $p = 0.001$). Autotrophic and total

43 below-ground respiration in the vegetated haggs varied with soil temperature;

44 heterotrophic respiration increased as water tables fell. An empirically derived net

45 ecosystem model estimated that over the two growing seasons both the vegetated haggs

46 (29 and 20 gC m^{-2}; 95 % confidence intervals of -570 to 762 and -873 to 1105 gC m^{-2}) and

47 the peat pans (7 and 8 gC m^{-2}; 95 % confidence intervals of -147 to 465 and -136 to

48 436 gC m^{-2}) were most likely net CO_2 sources. This study suggests that not only the

49 visibly degraded bare peat pans but also the surrounding vegetated haggs are losing

carbon to the atmosphere, particularly during warmer and drier conditions, highlighting a need for ecohydrological restoration.

KEYWORDS

Photosynthesis; Ecosystem respiration; Heterotrophic respiration; peatland; carbon dioxide; blanket bog;

HIGHLIGHTS

- The effect of peatland erosion on CO_2 fluxes was studied to support land management
- Closed chamber measurements from blanket bog haggs and eroding peat pans, Dartmoor
- Peat pans were intermittently dry with less vegetation cover and species diversity
- P_G and R_{Eco} were driven by WTD in the pans and NDVI & soil temperature in the haggs
- Vegetated haggs & peat pans were growing season net CO_2 sources; carbon is being lost

1 INTRODUCTION

Peatlands are recognised as valuable ecological resources providing a range of ecosystem services including food provision, flood alleviation, drinking water supply, amenity value and carbon sequestration (Grand-Clement et al. 2013). However, many peatlands are damaged, putting these ecosystem services at risk (Holden et al. 2007). Projects aimed at restoring the ecohydrological functioning of mires are more likely to set realistic targets and succeed where the effects of existing damage are understood (Bonnett et al. 2009).

73   Blanket bogs form in cool (< 15 °C mean summer temperatures) and wet (>1000 mm rain
74   annually) conditions (Lindsay et al. 1988). They consist of multiple peat-forming
75   conditions (e.g. raised bogs, watershed mires, flushes etc.) which have spread
76   laterally and joined together smothering the underlying topography. As they rise
77   above the influence of groundwater they are dependent on precipitation for both water
78   and nutrients (Moore 1987) resulting in acidic nutrient poor conditions. In the UK,
79   ecohydrologically functioning blanket bogs are dominated by *Sphagnum* species
80   which maintain the water table at or above the ground surface (Clymo 1983; Evans et
81   al. 1999; Holden et al. 2011). The UK has 10-15 % of the world's blanket peat
82   resource (Tallis 1997) primarily located in upland areas, consequently they are
83   globally important.

84   Burning, grazing, deposition of atmospheric pollutants (Yeloff et al. 2006), thawing
85   permafrost (Schuur et al. 2008) and climate change (Stevenson et al. 1990) have all been
86   proposed as causes of peatland erosion. These can initiate a feedback loop where peat
87   erosion reduces vegetation cover leaving bare peat more susceptible to further erosion by
88   fluvial, aeolian and freeze-thaw processes forming erosional features (Bragg and Tallis
89   2001). These features are of great concern as they drain the peat, resulting in particulate
90   organic carbon losses downstream (Evans et al. 2006) and water table draw-down in the
91   surrounding vegetated areas (Daniels et al. 2008), altering vegetation composition and
92   CO_2 fluxes beyond their extent (Clay et al. 2012).

93   Lower water tables have been shown to alter the vegetation present away from *Sphagnum*
94   towards vascular plants such as *Molinia caerulea, Calluna vulgaris* and *Eriophorum*
95   species (Coulson et al. 1990; Bellamy et al. 2012). These species have larger and more
96   dynamic CO_2 fluxes (McNamara et al. 2008; Otieno et al. 2009) but are more readily
97   decomposed (Coulson and Butterfield 1978; Wallen 1993; Thormann et al. 1999) and
98   therefore contribute little to the long-term carbon store compared to *Sphagnum*.

99 Additionally vascular plants can have extensive root systems which may stimulate the

100 decomposition of more recalcitrant deeper peat (Fontaine et al. 2007).

101 To date, studies on CO_2 fluxes from eroding blanket bogs (McNamara et al. 2008; Clay et

102 al. 2012; Dixon et al. 2013; Rowson et al. 2013) have been focused in northern England

103 where erosional gullies are steeper, deeper and wider (up to 3 m) than the peat pans of

104 Dartmoor (up to 1.5 m wide and typically < 50 cm deep). It is unclear what initiated erosion

105 on Dartmoor but peat pans (shallow, sparsely vegetated, hydraulically-connected,

106 intermittently saturated depressions) and haggs (surrounding vegetated blocks) are

107 limited to flat areas with insufficient erosional energy for gullies to form. They expand as

108 the water level is lowered around the edges of the vegetated haggs destabilising the peat

109 (Luscombe, pers. comm. 2018).

110 The deep peats of Dartmoor store an estimated 13.1 Mt of carbon (Gatis et al. 2019) but

111 are vulnerable to climate change as they lie at the southern limit of the UK blanket bog

112 climatic envelope (Clark et al. 2010). This makes them invaluable as indicators of the

113 potential effects of climate change on other, more northerly, maritime peatlands.

114 Understanding the controls on CO_2 fluxes on Dartmoor may provide an indication of the

115 future for other deep peats as temperatures rise potentially initiating more erosion. The

116 aim of this study was to investigate the controls on CO_2 fluxes in peat haggs and peat

117 pans and quantify CO_2 fluxes from these landscape components.

118 ## 2 MATERIAL AND METHODS

119 ### 2.1 STUDY SITE

120 The study site is located in an area of degraded blanket bog in Dartmoor National Park

121 (Figure 1A and B), southwest England (50°36N, 3°57'W). At Princetown (Figure 1B) the

122 long-term average annual precipitation is 1974 mm and has a mean monthly temperature

123 range of 0.8 to 17.7 °C. The site lies at 515 m above sea level and is classified as National

124   Vegetation Classification class M17 *Scirpus cespitosus-Eriophorum vaginatum* blanket

125   mire (Rodwell 1991). Peat at the study site is estimated to be between 3.6 and 4.0 m thick

126   (Gatis et al. 2019) above the average for Dartmoor (0.81 m) (Parry et al. 2012). The study

127   site is within an extensive area of erosional peat pans and vegetated haggs (Figure 1C

128   and D). The areas is currently used for extensive sheep grazing.

2.2   NET CO_2 ECOSYSTEM EXCHANGE MEASUREMENTS

130   Net CO_2 Ecosystem Exchange (NEE) measurements were taken on 10 separate dates at

131   six locations in the vegetated haggs in a randomised pattern approximately every month

132   between 05/06/2013 and 20/09/2013 and 10/04/2014 and 10/09/2014. A 20 cm diameter,

133   50 cm tall Perspex collar was attached to the peat surface prior to each measurement

134   using silicon putty (Evo-Stick "Plumbers Mait", Stafford, UK), and subsequently removed

135   at the end of the measurement. The collar was 50 cm tall to allow for the expected mid-

136   summer vegetation height. The collar was not inserted into the peat as this severs fine

137   surface roots (Heinemeyer et al. 2011) and alters the hydrological and micro-

138   meteorological properties of the peat. Due to limited moss coverage it was possible to

139   ensure a good seal with the peat surface directly using silicon putty. A LiCOR-8100 infra-

140   red gas analyser (LiCOR, Lincoln, Nebraska) connected to a 8100-104C transparent

141   chamber (with a rubber gasket to ensure an airtight seal) measured variation in CO_2

142   concentrations every 2 seconds over 2 minutes concurrently with photosynthetic photon

143   flux density (PPFD) (LiCOR Li-190 Quantum Sensor). In order to limit the weight of

144   equipment carried to site it was not possible to control chamber temperature, therefore

145   temperature may have increased during the test potentially stressing the plants resulting

146   in an underestimate of photosynthesis. The variation in chamber temperature over the

147   tests ranged from 0.0 to 1.4 °C. To further limit this effect the chamber was removed

148   between measurements to restore ambient conditions.

149   In the peat pans CO_2 measurements were taken on 15 separate dates at six locations in

150   a randomised pattern approximately every two weeks (concurrent with soil respiration

151   measurements) from 29/05/2013 to 07/10/2013 and 14/04/2014 and 11/09/2014. The

152   8100-104C transparent chamber was too heavy to float so CO_2 concentration was

153   measured from a 16 cm diameter, 13 cm tall floating collars every 9 seconds over 90

154   seconds using an EGM-4 infra-red gas analyser and a transparent CPY-4 canopy

155   assimilation chamber (2.427l) (PP Systems, Hitchin) concurrently with chamber air

156   temperature and PPFD. No ebullition or sudden increases in CO_2 suggestive of ebullition

157   were observed so it is assumed CO_2 was not released via this mechanism. Measurement

158   of the same location via the two different methods resulted in an uncertainty of

159   0.2 µmol $m^{-2} s^{-1}$.

160   CO_2 measurements were taken on sunny days at 100, 60, 40, 10 and 0 % light levels

161   using a combination of shade cloths. It is acknowledged that shade cloths can

162   underestimate photosynthesis at low light levels compared to naturally low light conditions.

163   However, this seemed the most practical solution given the remoteness of the site and

164   labour availability. The net CO_2 exchange at each light level was calculated from the linear

165   change in chamber CO_2 concentration. Linear accumulation rates with an r^2 of less than

166   0.7 were discarded unless the maximum change in CO_2 concentration was ≤1 ppm in

167   which case a flux of 0 µmol $m^{-2} s^{-1}$ was assigned. Of the 1041 samples collected, 8 were

168   discarded from the vegetated haggs and 25 from the peat pans at this stage.

169   To account for variability in solar radiation between measurements, net CO_2 fluxes were

170   fitted to a hyperbolic light response curve (Equation 1) using a non-linear least-squares fit

171   across the different light levels measured for each plot for each month.

172   **Equation 1**

173
$$NEE = R_{\text{Eco}} - \frac{P_{max} . \text{PPFD}}{k + \text{PPFD}}$$

174   where NEE is the net CO_2 ecosystem exchange ($\mu mol\ m^{-2}\ s^{-1}$), P_{max} is the rate of light

175   saturated photosynthesis ($\mu mol\ m^{-2}\ s^{-1}$), k is the half-saturation constant of photosynthesis

176   (μmol photons $m^{-2}\ s^{-1}$), PPFD the incident photosynthetic photon flux density (PPFD)

177   (μmol Photons $m^{-2}\ s^{-1}$) and R_{Eco} ecosystem respiration ($\mu mol\ m^{-2}\ s^{-1}$). Only light response

178   curves with an $r^2 > 0.7$ were accepted therefore a further 11 and 171 measurements from

179   the vegetated haggs and peat pans respectively were discarded.

180   R_{Eco} was determined for each plot from each light response curve (one per sample day)

181   using equation 1. Photosynthesis and net ecosystem exchange were then determined for

182   a PPFD of 1000 μmol photons $m^{-2}\ s^{-1}$ (P_{G1000} and NEE_{1000}), the light saturated

183   photosynthesis rate, using Equation 1 and the parameters $P_{max,}$ and K previously

184   determined from each light response curve. As different PPFD meters were used in the

185   peat pans and vegetated haggs, a cross-calibration with a continuous (every 15 minute)

186   onsite global irradiation meter ($r^2>0.90$, n=284; Adcon, Klosterneuburg, Austria) was used

187   to ensure that fluxes were being standardised to the same light intensity.

188   ## 2.3 SOIL CO_2 EFFLUX MEASUREMENTS

189   At each vegetated hagg plot four Polyvinyl Chloride collars (16 cm diameter, 8 cm height)

190   were installed within 50 cm of the NEE plots (

191
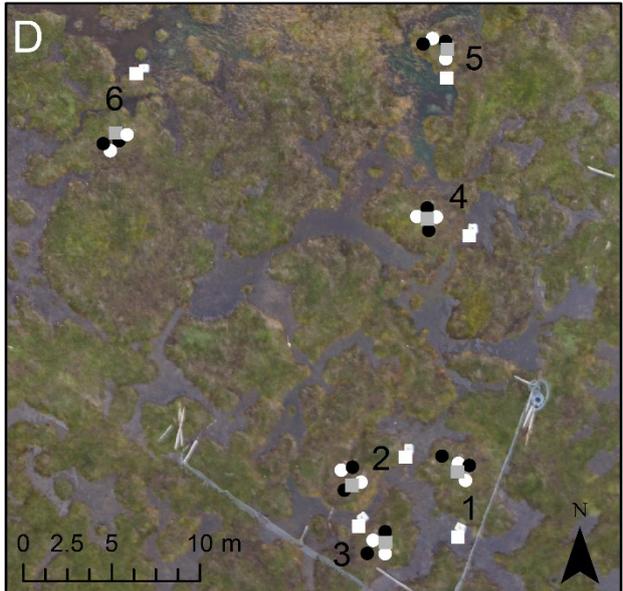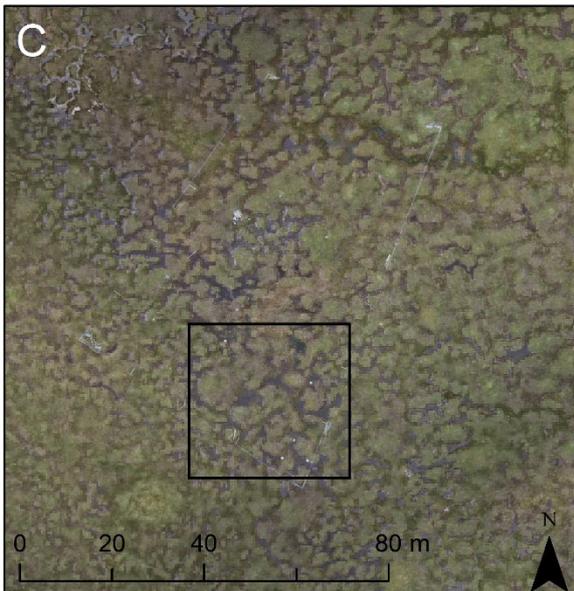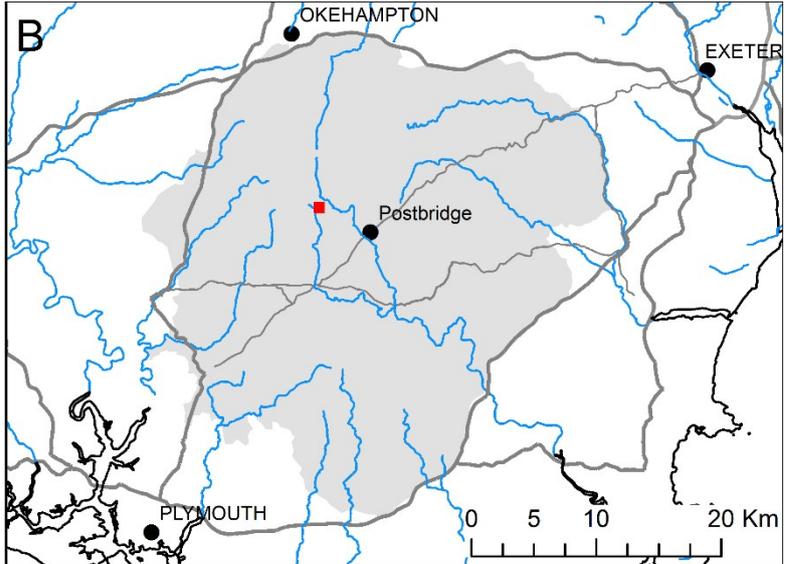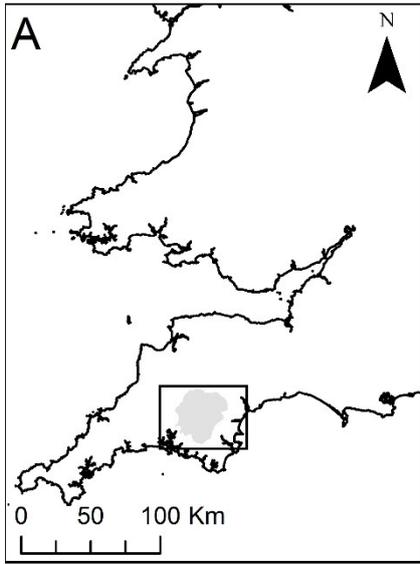
194   _{Figure 2}). These were sealed to the peat surface in March 2013 using non-setting putty

195   (Evo Stick "Plumbers Mait", Stafford, UK). All collars (n=24) had above-ground vegetation

196   removed by regular clipping so they measured below-ground fluxes only. In addition, 56

197   cm diameter, 20 cm deep trenches were cut around half the collars to exclude live roots

198   enabling measurement of the below-ground heterotrophic component. At each of six

199   plots, the two replicates of each treatment were averaged to produce a single value for

200   total soil (clipped) and heterotrophic soil (trenched and clipped) respiration. Repeated

201   trenching was used to prevent root re-growth, rather than a barrier, to minimise the effect

202   on the hydraulic properties of the peat.

203   Trenching and clipping were chosen as inexpensive, simple and established methods

204   subject to well documented uncertainties (Kuzyakov and Larionova 2005; Subke et al.

205   2006) such as severing roots which decompose leading to an overestimation of

206   heterotrophic respiration. Collars were installed 2 months prior to the start of sampling to

207   reduce disturbance effects.

208   Soil CO_2 flux measurements were taken on 17 separate dates in a randomised pattern

209   approximately every two weeks from 13/05/2013 to 1/11/2013 and 14/04/2014 to

210   11/09/2014. CO_2 flux was measured over 2 minutes using an EGM-4 infra-red gas

211   analyser and a CPY-4 canopy assimilation chamber (PP Systems, Hitchin, UK). The

212   autotrophic component of soil respiration was calculated from the difference between total

213   and heterotrophic soil respiration measured at each location for each sample round.

214   ## 2.4 AUXILIARY MEASUREMENTS

215   Concurrently with both NEE and soil CO_2 flux measurements soil temperature was

216   recorded down a single vertical profile at 5, 10, 15, 20, 25 and 30 cm (Electronic

217   Temperature Instruments, Worthing) below the peat surface in the vegetated haggs. In

218   both the peat pans and the vegetated haggs the water table depth below the peat surface

219   was measured using a ruler in a perforated tube. Water table depths were measured at

220 nearby dipwells automatically every 15 minutes with *in-situ* submersible water pressure
221 transducers (IMSL Geo100 Impress, UK). Soil temperature was continuously measured
222 at a depth of 15 cm every 15 minutes (Gemini Data Loggers, Chichester, UK) at vegetated
223 plot 4. Rainfall was measured using a tipping bucket rain gauge (0.2 mm tip, RT1, Adcon
224 Telemetry, Austria). Global irradiation was measured every 15 minutes (Adcon,
225 Klosterneuburg, Austria). Data gaps were filled in by correlation (r^2=0.91, p<0.001) to the
226 closest meteorological station, 18 km to the northwest and 340 m lower in elevation than
227 the study site; North Wyke (UK Meteorological Office 2012) (50°46'N 3°54'W).

2.5 VEGETATION COMPOSITION, SEASONAL DEVELOPMENT AND PRODUCTIVITY

2.5.1 Vegetation Composition and Productivity

231 Visual inspection of the area inside the NEE collars in August 2013 assessed the
232 percentage coverage of each species as well as total cover of bare ground, standing
233 water, herbs (forbs), grasses, sedges, non-*Sphagnum* moss and *Sphagnum* moss. The
234 number of species present at each location was counted to derive the species richness.
235 The Shannon Diversity Index (Shannon 1948) (Equation 2) and Inverse Simpson Diversity
236 Index (Simpson 1949) (Equation 3) were calculated; the first quantifies the uncertainty in
237 predicting the next species, whilst the second describes the richness of a community
238 increasing from 1, a community containing only one species.

239 **Equation 2**

$$Shannon\ Diversity\ Index = \sum_{i=1}^{n} P_i . lnP_i$$

241 **Equation 3**

$$Inverse\ Simpson\ Diversity\ Index = 1 \Big/ \frac{\sum N_i(N_i - 1)}{N(N-1)}$$

243   Where n is the number of species encountered and P_i the fraction of the entire population

244   made up of species I, N_i is the total area of species i present and N the total area of

245   vegetation.

246   Ellenberg's Moisture Indicator Values (Hill et al. 1999) were determined for each location.

247   Vascular species have been classified according to their ecological niche on a 12 point

248   scale ranging from 1 (extreme dryness) to 12 (submerged plants). The classification

249   values for the vascular species identified in this study were looked up and the average

250   value for the species present at each location was calculated.

251   Destructive samples were collected to measure annual net primary productivity (ANPP)

252   on 29/08/2013 and 07/08/2014. The timing was selected to coincide with flowering and

253   peak biomass of the dominant vegetation, *Molinia caerulea.* All green material in a 0.2 x

254   0.2 m area near the CO_2 collars (different location each year) was collected and oven

255   dried at 78°C to constant mass.

2.5.2 Vegetation Seasonal Development

257   Proxies for vegetation seasonal development were derived from Moderate Resolution

258   Imaging Spectoradiometer (MODIS). MOD15A2 fPAR (1000 x 1000 m resolution) and

259   MODIS9A1 surface reflectance (500 x 500 m resolution) were downloaded from USGS

260   Earth Explorer (http://earthexplorer.usgs.gov). The normalised difference vegetation

261   index was derived from bands 1 (Red) and 2 (near infra-red) of the surface reflectance

262   where NDVI = (Band 2 - Band 1) / (band 2 + Band 1).

263   Data were screened and poor-quality data (cloudy, high aerosol concentrations or poor

264   geometry) given a weighting of 0 and all other data a weighting of 1. To minimise variation

265   due to atmospheric conditions, illumination and observation geometry a third order Fourier

266   smoothing filter was applied. Points outside the 99 % confidence interval were excluded.

267   All remaining points (30 in 2013 and 23 in 2014) were then weighted equally and a Fourier

268   third order series fitted to form a continuous daily timeseries (Gatis et al. 2017).

2.6 SEASONAL NET CO$_2$ ECOSYSTEM EXCHANGE ESTIMATION

Seasonal NEE was modelled directly rather than modelling photosynthesis and ecosystem respiration separately and then combining them. Modelling the components separately requires the derivation of gross photosynthesis for each measurement based on the assumption that the full dark measurement represents ecosystem respiration. This adds additional uncertainty. As the closed chamber method measures NEE it was decided to work with these data directly. Given the binary nature of the system, NEE was parameterised for peat pans (n=398) and vegetated haggs (n=423) separately, using all the quality controlled closed chamber measurements collected at a range of light levels.

Linear, exponential, Arrhenius, Lloyd-Taylor and tolerance relationships were tested using combinations of NDVI, soil temperature at a range of depths and water table depths. The models selected had the greatest coefficient of regression, smallest root mean square errors and were the most parsimonious.

The NEE model for the vegetated haggs (Equation 4) had two components, the first is dependent on NDVI and the second shows an Arrhenius relationship with soil temperature at 15 cm, the soil depth with the greatest correlation with ecosystem respiration).
 Equation 4

$$NEE = \frac{P_{max}.NDVI.PPFD}{K + I} + a.exp^{-b/T_{15}}$$

The NEE model for the peat pan (Equation 5) is also made up of two components, the first is dependent on NDVI; the second is dependent on soil temperature at 15 cm depth and water table depth.

Equation 5

$$NEE = \frac{P_{max}.NDVI.PPFD}{K + I} + c.exp^{d.T_{15}}.exp^{f.WTD}$$

292 Where NEE is the net CO_2 ecosystem exchange (μmol m^{-2} s^{-1}), P_{max} is the rate of light

293 saturated photosynthesis (μmol m^{-2} s^{-1}), NDVI the normalised difference vegetation index,

294 PPFD the incident PPFD (μmol Photons m^{-2} s^{-1}), k the half-saturation constant of

295 photosynthesis (μmol photons m^{-2} s^{-1}), T_{15} soil temperature at a depth of 15 cm, a, b, c, d

296 and f (dimensionless) are coefficients.

297 An hourly timeseries of PPFD was created by correlating episodic measurements taken

298 concurrently with the flux measurements to global irradiation measured onsite (section

299 2.4). Water table depths and soil temperature measured every 15 minutes (section 2.4)

300 were averaged to produce hourly timeseries. The growing season was defined as from

301 the first three consecutive days with daily mean soil temperature > 10°C till the first three

302 consecutive days with daily soil temperature < 10°C as this is the temperature at which

303 root initiation and subsequent leaf growth occurs (Taylor et al. 2001).

304 Seasonal estimates were determined by the accumulation of hourly fluxes over the

305 duration of the growing season. Model confidence intervals (95 %) were determined from

306 the root mean squared error of modelled values compared to measured values. Input

307 parameter uncertainty was accounted for by using lower and upper 95 percentile values

308 in the model. These two sources of uncertainty were summed together for each hour over

309 the duration of the growing season. By convention CO_2 fluxes are reported relative to the

310 atmospheric pool so the peatland is a net CO_2 source if positive.

311 **2.7 STATISTICAL ANALYSIS**

312 To assess temporal and spatial variation in water table depth and soil temperature, a two-

313 way repeated measures ANOVA was carried out with time as the within subject factor and

314 landscape component (hagg or peat pan) as the between subject factor. To investigate

315 potential temporal controls on CO_2 fluxes, stepwise linear regressions were carried out on

316 photosynthesis at a PPFD of 1000 μmol photons m^{-2} s^{-1} (P_{G1000}), ecosystem respiration

317 (R_{Eco}) and total, heterotrophic and autotrophic below-ground respiration as measured and

14

318 natural log-transformed. The temporal variables tested were water table depth, soil

319 temperature at 5, 10, 15, 20, 25 and 30 cm, fPAR, NDVI, total PPFD in the preceding day

320 and hour, total rainfall on the day of measurement (Rain0) and preceding 1,7,14 and 28

321 days. Exponential, Arrhenius and Lloyd-Taylor relationships between below-ground

322 respiration and soil temperature at 5, 10, 15 20, 25 and 30 cm were also tested.

323 3 RESULTS

324 3.1 WATER TABLE DEPTH

325 Water tables were on average deeper and less variable in the vegetated haggs; mean of

326 9.1 ± 5.4 cm and varying from 28 cm below to 1 cm above ground level compared to a

327 mean of 7.1 ± 10.1 cm and varying between 23 cm below to 21 cm above ground level in

328 the   peat   pans   (
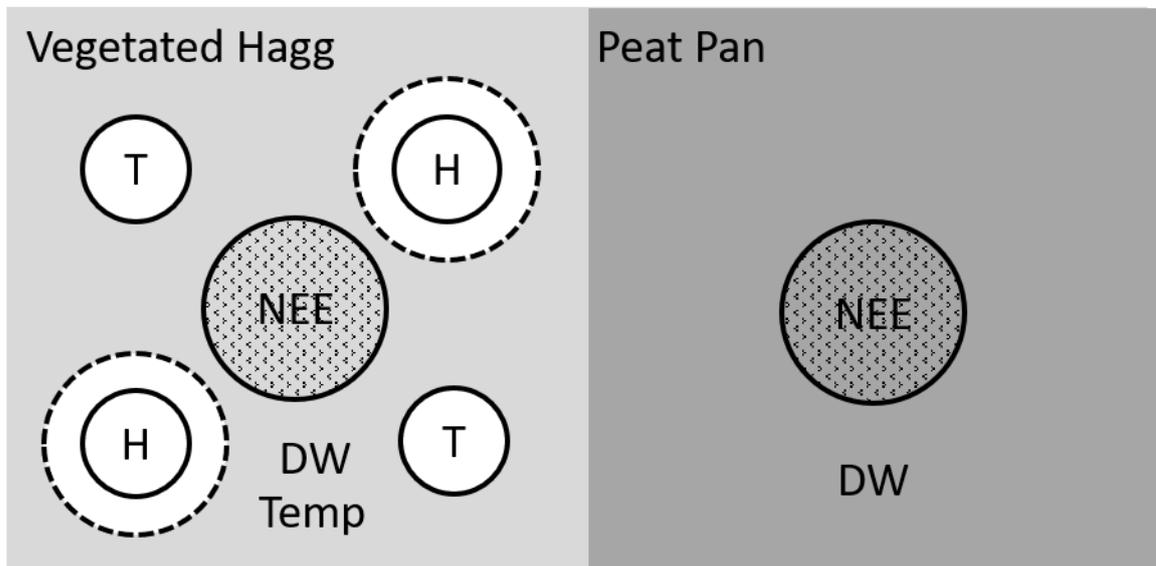
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330   _{Figure 3}). During the 2013 growing season water table depths fell to a maximum low in

331   July then rose again until late October 2013. Water table depths were generally higher in

332   2014 reaching a maximum in early June and a minimum in early July. Water tables

333   dropped below the ground surface at all plots within the peat pans in July 2013. However,

334   plots 5 and 6, which were located at a lower elevation than the other plots, had greater

335   standing water depth and were more often saturated than the other bare peat plots. Water

336   table depth varied significantly with time (two-way ANOVA $p<0.001$) and between haggs

337   and pans ($p=0.004$).

338   ## 3.2 VEGETATION COMPOSITION

339   *Molinia caerulea* was present in all vegetated NEE collars (8 to 50 % coverage) and was

340   the dominant vegetation in 5 out of 6 collars covering 20-50 %. In vegetated collar 6

341   *Narthecium ossifragum* was the most common species (50 %). *Erica tetralix* was the only

342   other species present in all collars (3 to 20 % coverage). In the peat pans either

343   *Eriophorum angustifolim* and/or *Sphagnum denticulatum* was present. A full species list

344   is provided in the supplementary material (Table 1). Shannon Diversity index, Inverse

Simpson diversity index, and species richness were all greater in the vegetated haggs (

Peat Pan / **Vegetated Hagg**

WTD (cm)

Legend:
- ············· 1
- ------- 2
- – – – 3
- ············· 4
- ------- 5
- – – – 6

X-axis labels: 01/05/13, 01/08/13, 01/11/13, 01/04/14, 01/07/14, 01/10/14
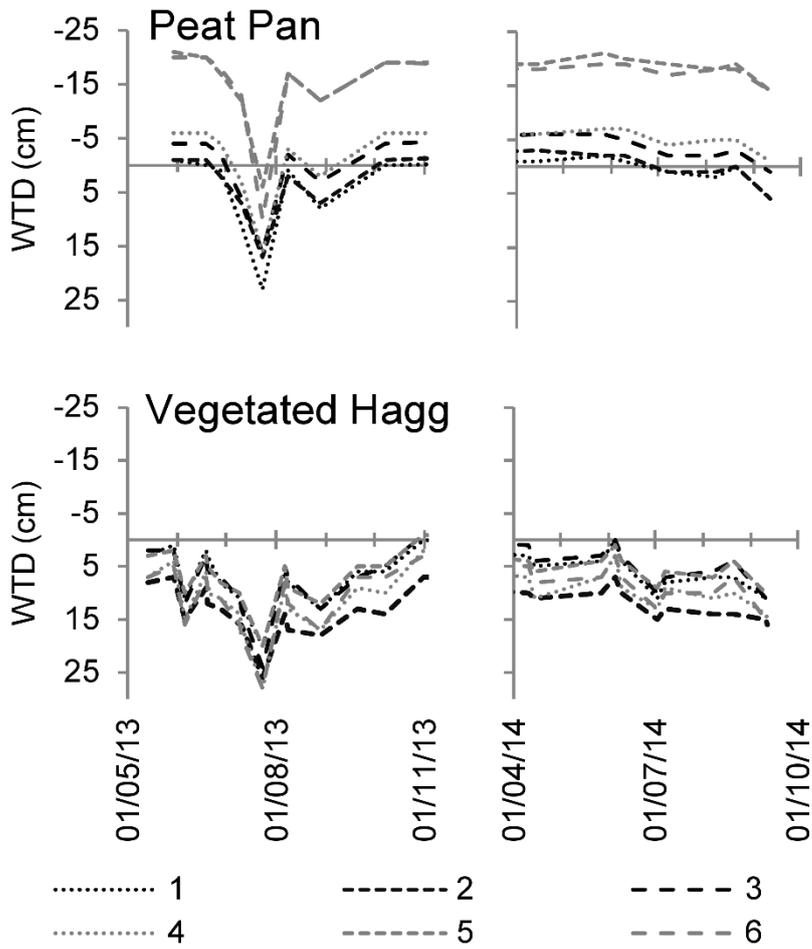
347   Figure **4**a, b & c). This is due to the presence of herbs, grasses and mosses in the

348   vegetated   haggs   but   not   in   the   peat   pans   (
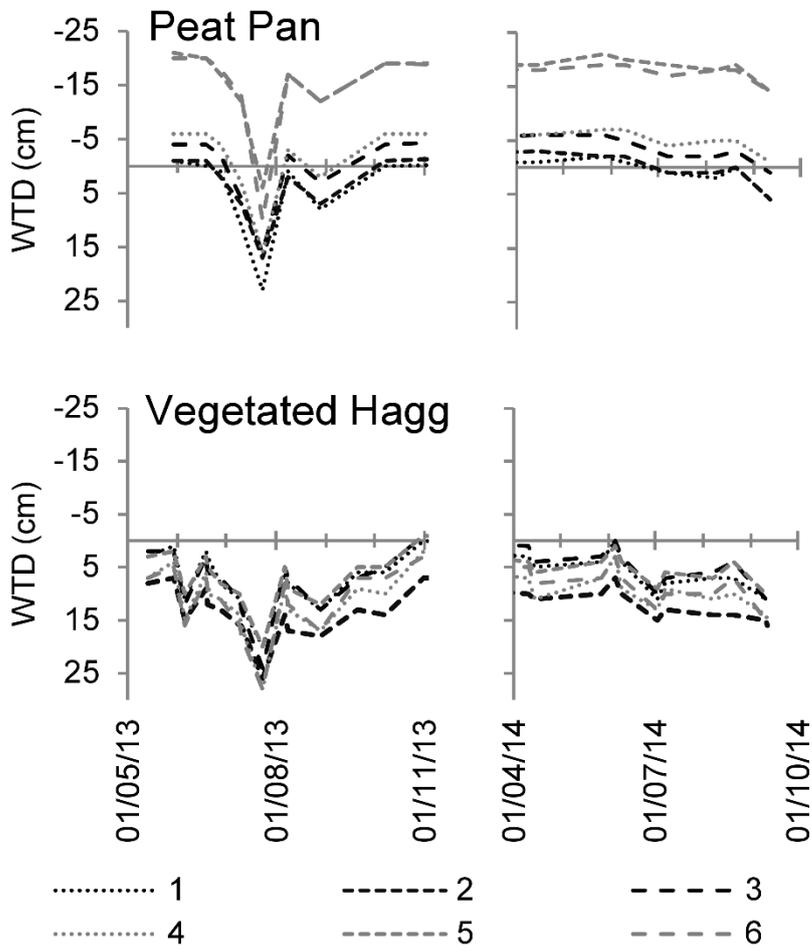
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350 Figure **4**f, g & i). Although there was some vegetation present in all collars, bare ground

351 and standing water were present in the peat pans but not the vegetated haggs (
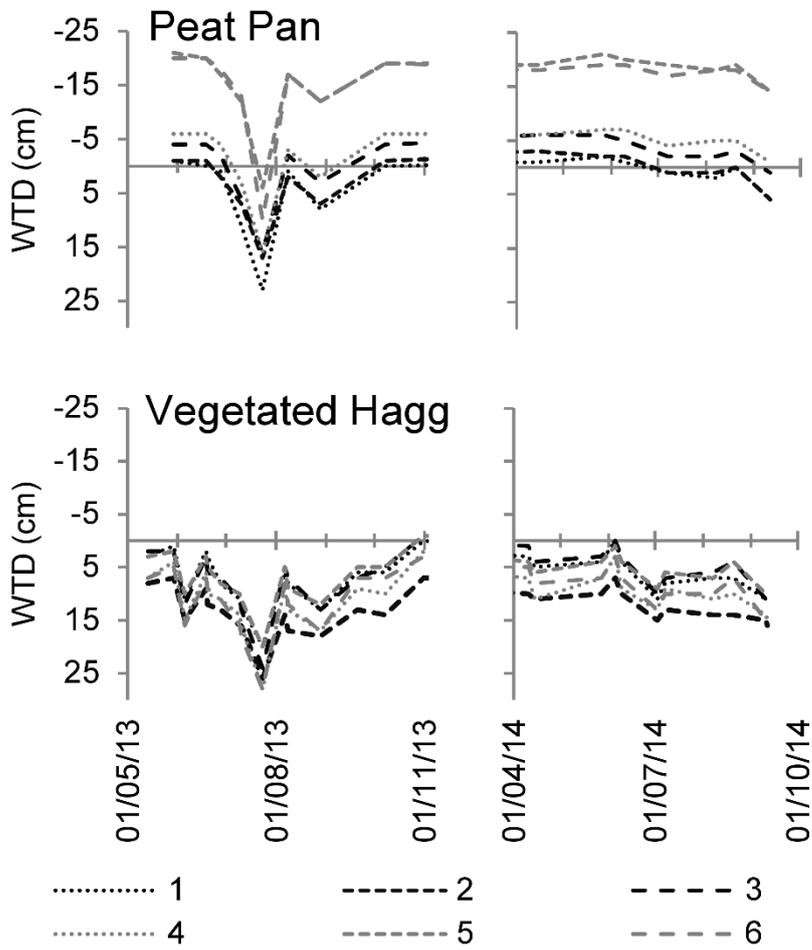

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353   Figure **4**k & l). Ellenberg's Moisture indicator values denoted the vegetated haggs were

354   damp and the peat pans wet and often water saturated as observed. In the vegetated

355   haggs above-ground annual net primary productivity (ANPP) was not significantly different

356   between 2013 (217 ±39 g m^{-2}) and 2014 (214 ±23 g m^{-2}). ANPP was not assessed for the

357   peat pans.

358   3.3 SEASONAL CO$_2$ FLUXES

359   Photosynthesis at a PPFD equivalent to 1000 µmol Photons m^{-2} s^{-1} (P$_{G1000}$) and ecosystem

360   respiration   (R$_{Eco}$)   followed   similar   seasonal   patterns   (
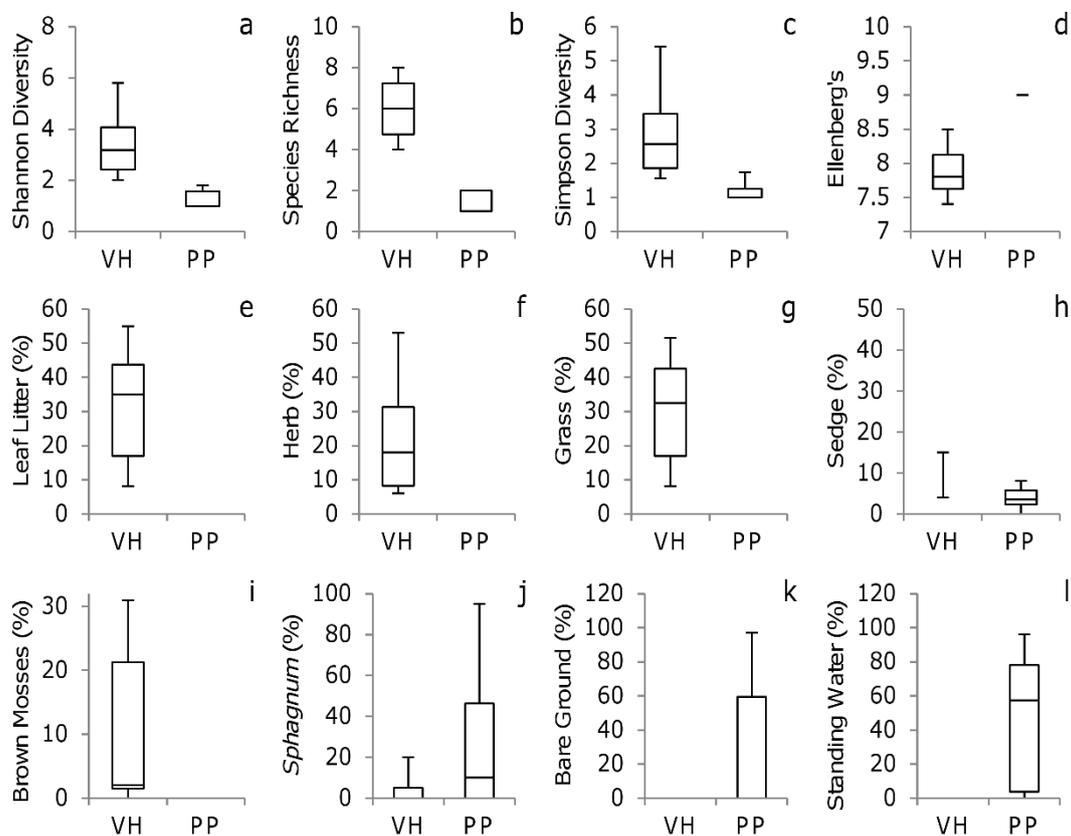

361

362   Figure **5**) in the vegetated haggs, with R_{Eco} and photosynthetic CO_2 uptake (P_{G1000})

363   increasing through late spring into summer. The greatest R_{Eco} was recorded in July 2014

364   (3.6 ± 0.9 µmol m^{-2} s^{-1}) whilst the greatest photosynthetic CO_2 uptake was measured in

365   September 2013 (-6.1 ± 2.2 µmol m^{-2} s^{-1}). Photosynthetic CO_2 uptake peaked towards the

366   end of the growing season (August and September) whilst R_{Eco} peaked in mid-summer

367   (July) reflecting seasonal temperature variation.

368   In the peat pans R_{Eco} and photosynthetic CO_2 uptake (P_{G1000}) were lower than in the

369   vegetated   haggs   (
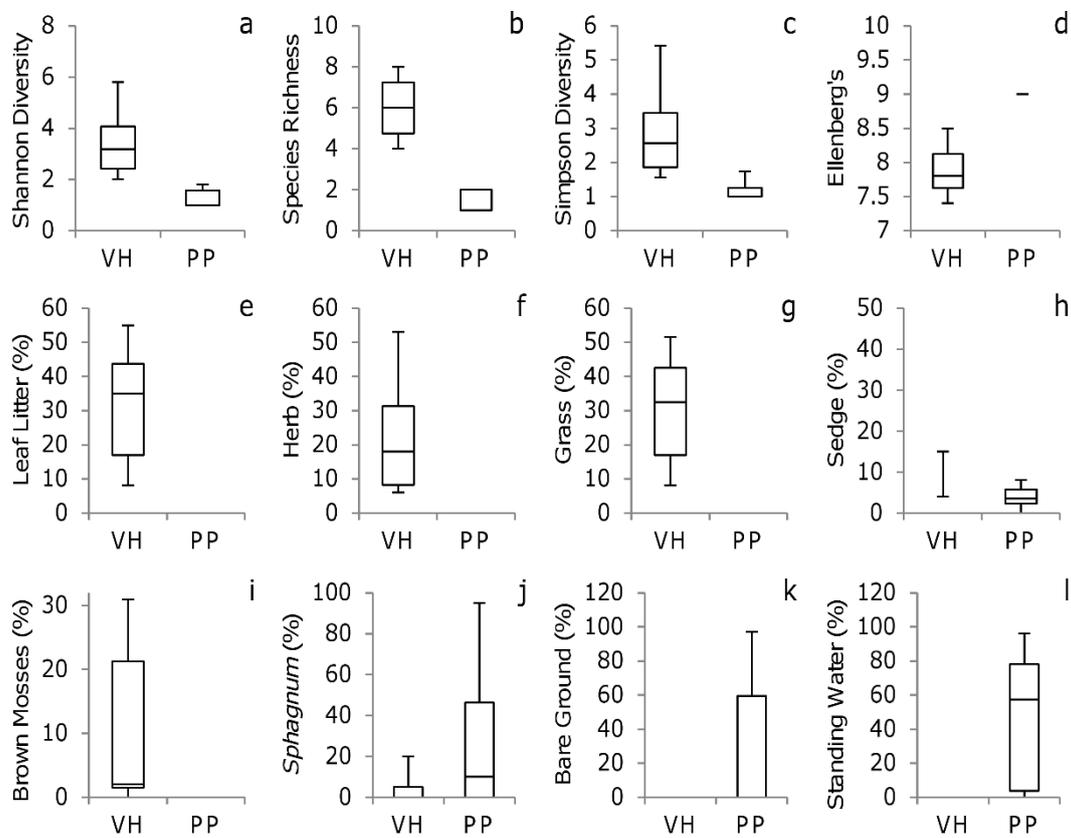
370

371   Figure **5**) except in July 2013 when there was a notable increase coinciding with low water

372   tables   (

Vegetated Hagg   Peat Pan

T   H

NEE   NEE

H   DW   T

DW   Temp
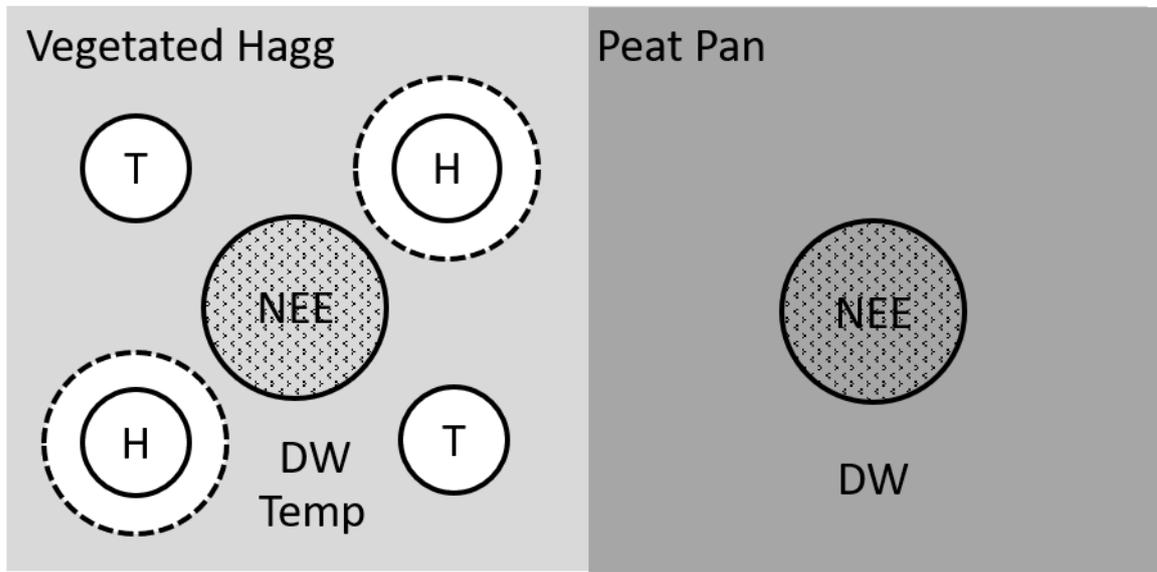
373

374   Figure 3). Neither P_{G1000} nor R_{Eco} showed a clear seasonal pattern.

375   Total and heterotrophic below-ground respiration in the vegetated haggs showed similar

376   seasonal patterns generally rising from mid-May to late-August then decreasing to late-

377   October in 2013 and rising from mid-April to mid-August in 2014 (
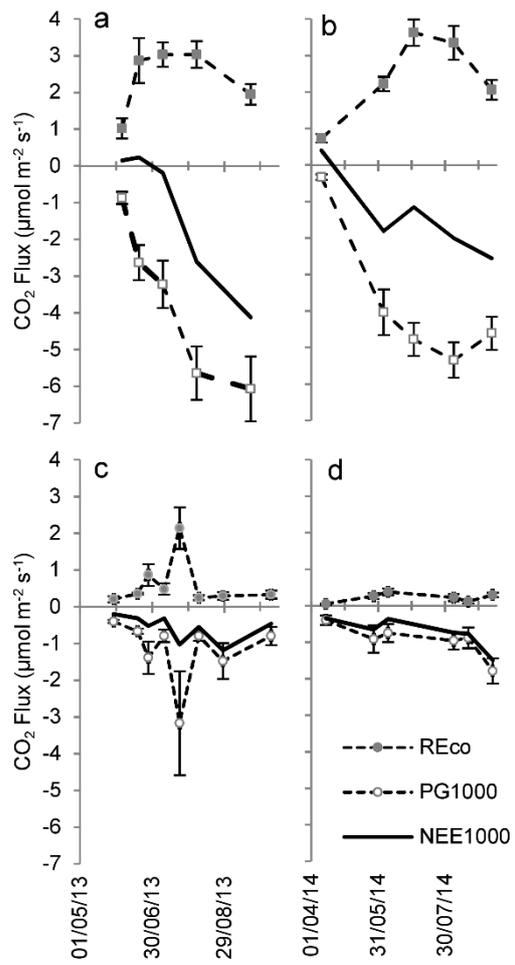
380   Figure **6**). There was noticeably greater respiration in July 2013 when the soil temperature

381   was greatest (17.6 °C), corresponding to the spike in photosynthetic CO_2 uptake and

382   ecosystem   respiration   observed   in   the   peat   pans   (
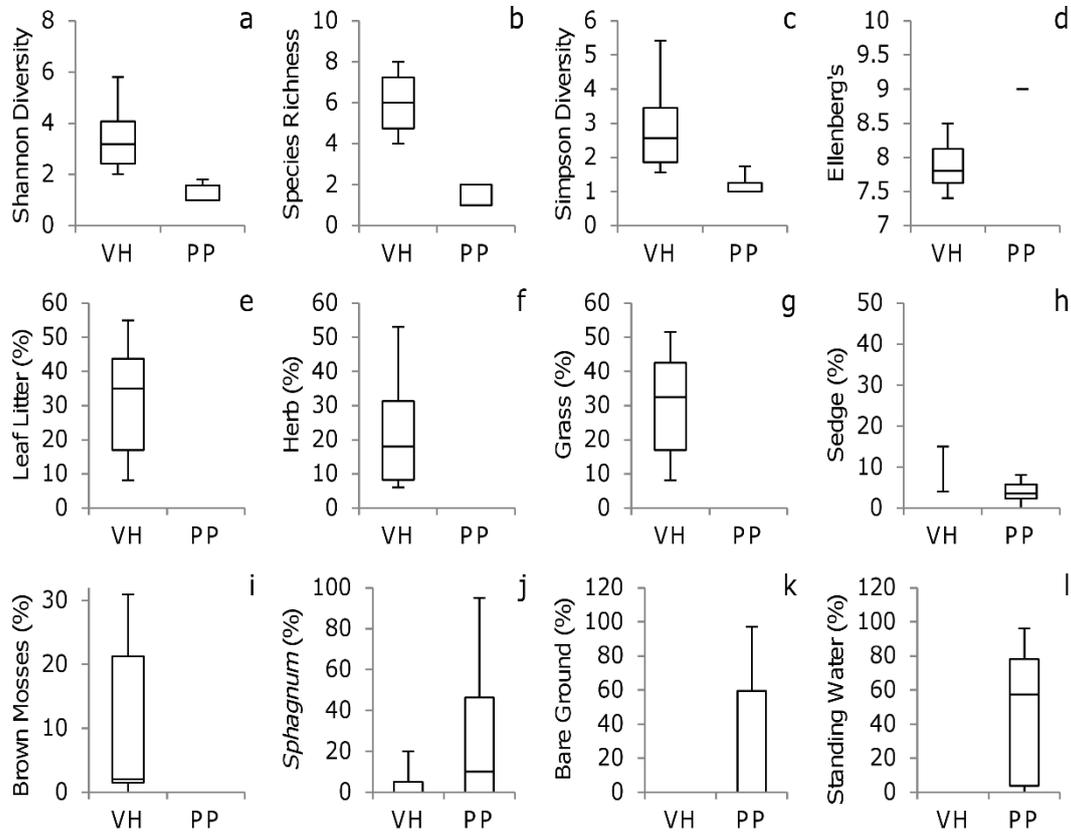
383

| 384 | Figure **5**c). Heterotrophic respiration was greater than autotrophic respiration except |

384 Figure **5**c). Heterotrophic respiration was greater than autotrophic respiration except

385 during October 2013 and July and August 2014.   The proportional contribution of

386 autotrophic respiration to total soil respiration varied between 1 and 66 % with the lowest

387 contributions occurring in May 2013 and April 2014 and greater contributions later in the

388 growing season. During the growing season autotrophic contributed on average 42 %.

389 ### 3.4 TEMPORAL CONTROLS ON CO_2 FLUXES

390 Ecosystem respiration and photosynthesis showed no significant relationships with water

391 table depth in the vegetated haggs (p>0.57) however, in the peat pans ecosystem

392 respiration and photosynthetic CO_2 uptake significantly increased when the water table

393 fell (Table 1).   This relationship was strongly driven by the high CO_2 fluxes (
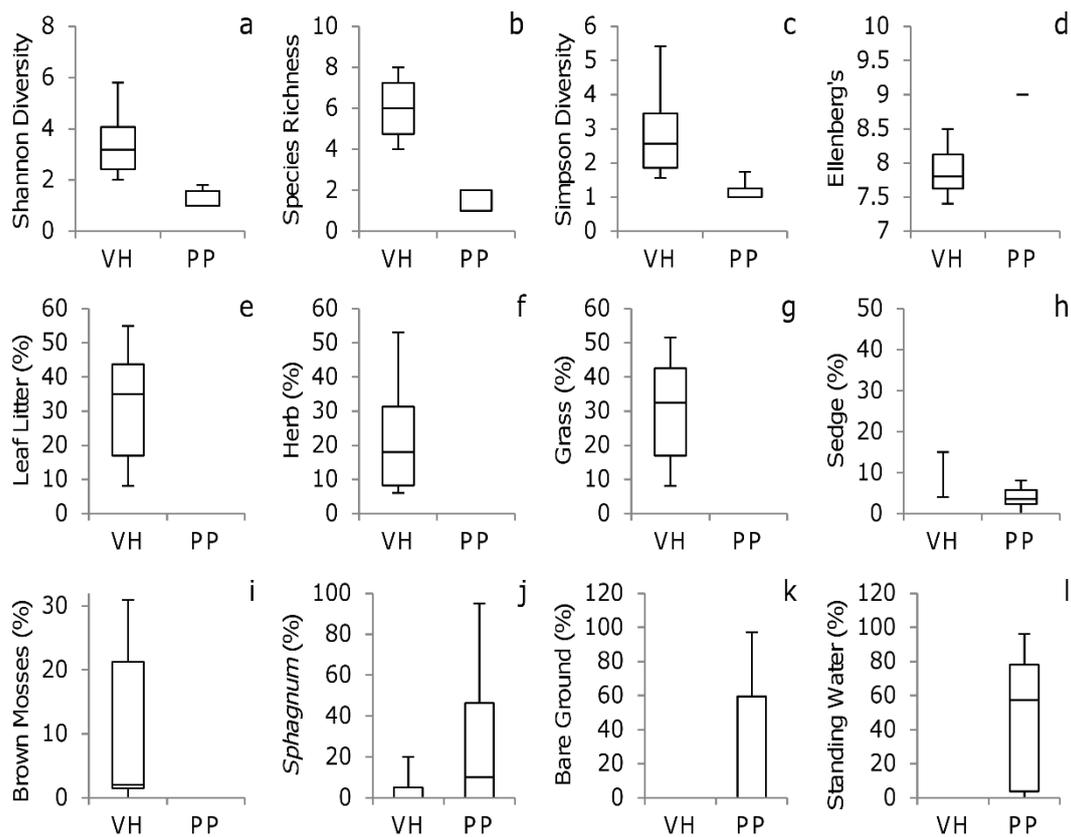
394

395 Figure **5**) and deep water tables in July 2013 (
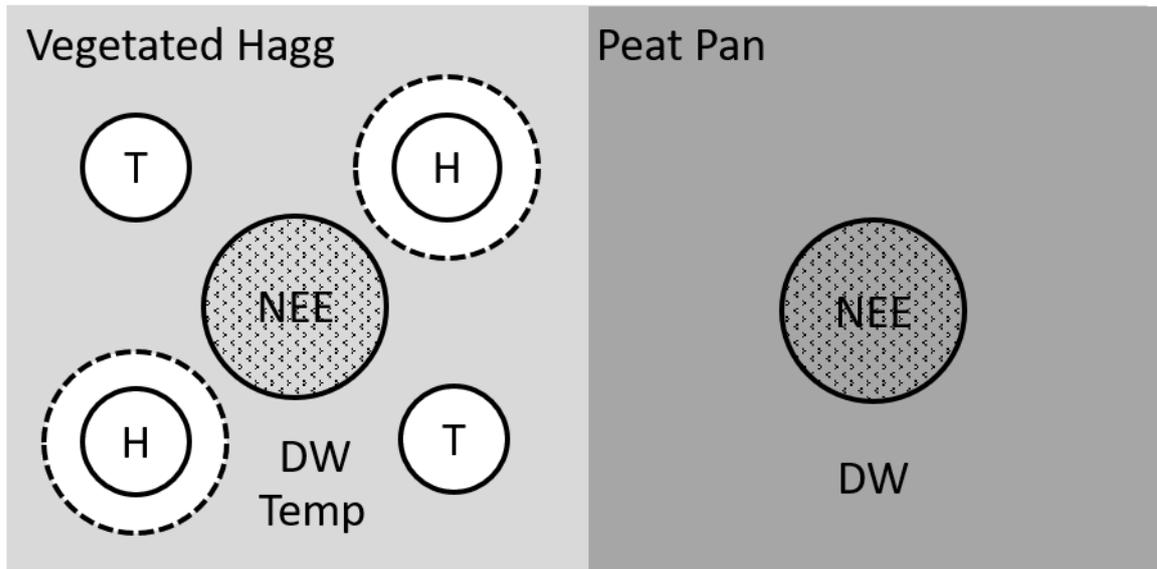
396

397   Figure 3). In the vegetated haggs photosynthetic CO_2 uptake showed the strongest

398   relationship with NDVI (Table 1), increasing when NDVI increased. Ecosystem respiration

399   showed a significant exponential relationship with soil temperature at a depth of 15 cm

400   (Table 1). Additional variables did not increase the coefficient of regression for

401   photosynthesis or ecosystem respiration in the vegetated haggs or peat pans.

402   Of the soil temperature depths measured, total and heterotrophic below-ground

403   respiration showed the strongest regression coefficients with an exponential function

404   dependent on soil temperature at a depth of 5 cm (Figure 7a & b) with respiration

405   increasing as temperature increased. Autotrophic respiration, although significantly

406   related to soil temperature at 5 cm (Figure 7c), showed the strongest exponential

407   relationship with soil temperature at 30 cm (Table 1, Figure 7e). Multiple regression

408   analysis indicated that water table depth was a stronger factor than soil temperature in

409   controlling heterotrophic respiration (Table 1). Adding total rainfall on the preceding day

410   increased the proportion of variability explained by 8 %. Total and autotrophic below-

411   ground respiration were also significantly related to water table depth (Figure 7a & e) with

412   higher respiration rates during dry conditions but their relationships with soil temperature

413   were dominant (Table 1).

3.5 SEASONAL NET CO_2 ECOSYSTEM EXCHANGE ESTIMATION

415   The model for the vegetated haggs (Equation 4, Table 2), based on all the CO_2 flux

416   measurements collected explained a greater proportion of the variability (76 %) than the

417   model (Equation 5, Table 2) for the peat pans (67 %) however, it also had greater root

418   mean square errors (Table 2). It can be seen that the model errors (Table 2) are large

419   when compared to P_{G1000} and R_{Eco} (Figure 5) resulting in great uncertainty in the seasonal

420   estimates (Table 3). It is estimated that it is most likely both the vegetated haggs and the

421   peat pans were net CO_2 sources over the 2013 and 2014 growing seasons (Table 3).

4 DISCUSSION

4.1 HAGGS AND PANS: A BINARY SYSTEM

4.1.1 Water Table Depths and Vegetation Composition

Average water table depth in the vegetated haggs (9.1±0.4 cm) was shallower than those

reported for inter-gully areas (23.4±8 cm) (McNamara et al. 2008) and upslope of drainage

ditches (19.8±0.38 cm) (Coulson et al. 1990) in *Calluna vulgaris* dominated British blanket

bogs.   In   addition,   peat   pans   were   frequently   inundated   (
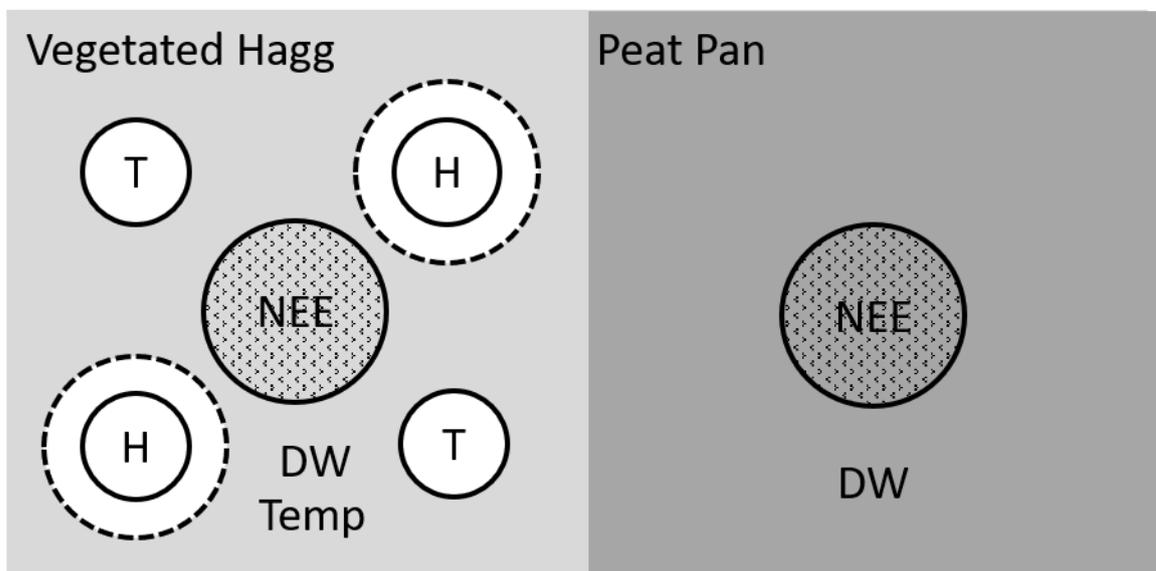
Figure 3) suggesting these peat pans function differently to both gullies (McNamara et al.

431   2008; Dixon et al. 2013) and drainage ditches (Cooper et al. 2014) where the water table

432   is more commonly below ground level except during storm events. It is likely the shallow

433   topographic gradients and poor connectivity between peat pans (Figure 1C) resulted in

434   less water table drawdown in the peat pans when compared to both erosional gullies and

435   drainage ditches (Parry et al. 2014). Despite this, hydrological monitoring at this site has

436   shown that in the vegetated haggs the water table drops lower adjacent to the peat pans

437   than further away (Luscombe, pers. comm. 2018). *Sphagnum* cover was <20 % in the

438   vegetated haggs whilst cover of grasses and herbs reached 53 and 50 % respectively (
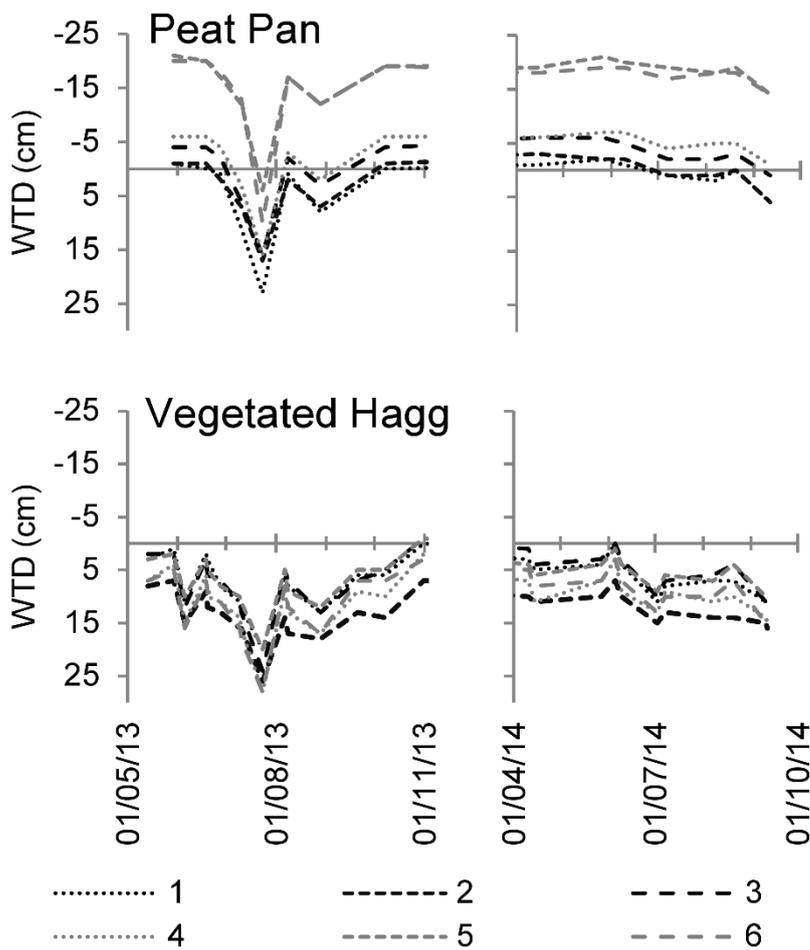
439

440   Figure **4**f, g & j) further indicating the deterioration of ecohydrological function in the

441   vegetated haggs.

442   Vegetation   in   the   peat   pans   was   sparse   (
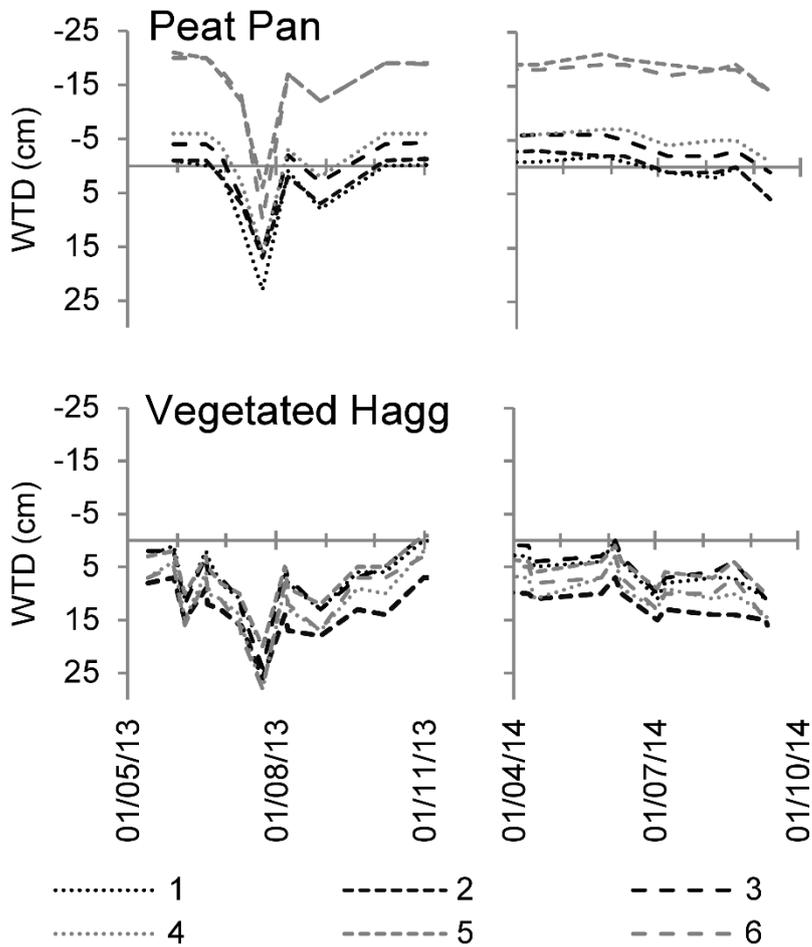
443

444   Figure **4**). This could be because active erosion (Foulds and Warburton 2007) removed

445   peat preventing a continuous vegetation cover from developing (Ingram 1967).   In

446   addition,   intermittent   dry   conditions   (

447
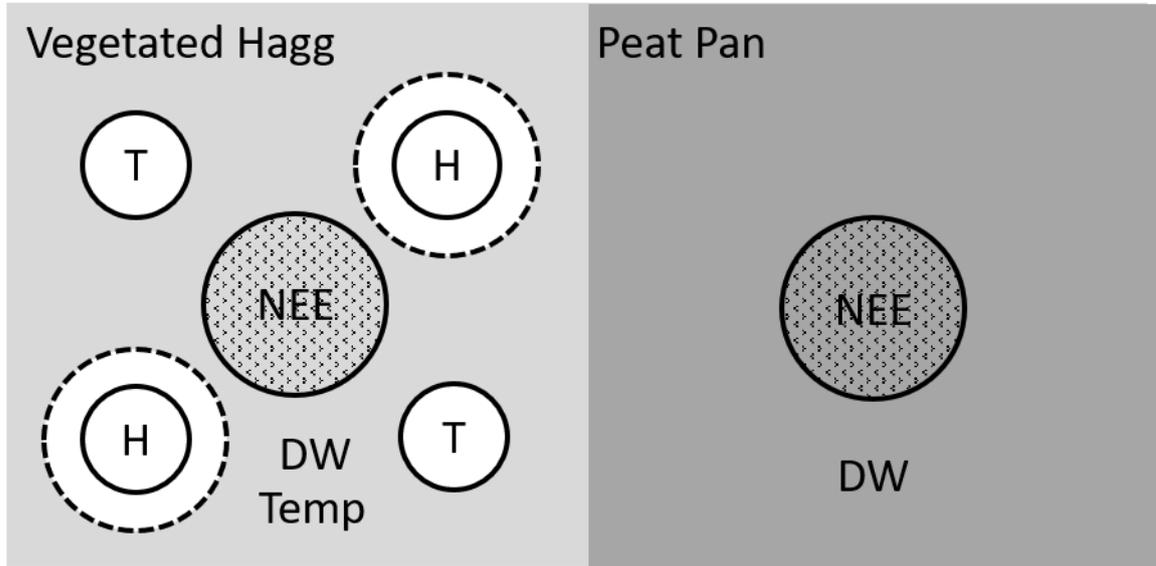
Figure 3) may have made re-colonisation impossible for *Sphagnum* species (Price and

449 Whitehead 2001). *Eriophorum vaginatum* has been shown to recolonise gullies starting

450 from zones of redeposited peat (Crowe et al. 2008) and facilitate recolonization by other

451 species (Tuittila et al. 2000). On Dartmoor, in nearby areas where lower connectivity has

452 limited erosion and maintained more stable water tables, dense areas of *Eriophorum*

453 *angustifolim* have formed. This suggests that if erosion could be halted and water tables

454 stabilised then vegetation would be expected to recolonise these sparsely vegetated

455 areas.

4.1.2 CO$_2$ Fluxes

457 Photosynthetic CO$_2$ uptake and ecosystem respiration were lower in the peat pans than

458 in the vegetated haggs (

459
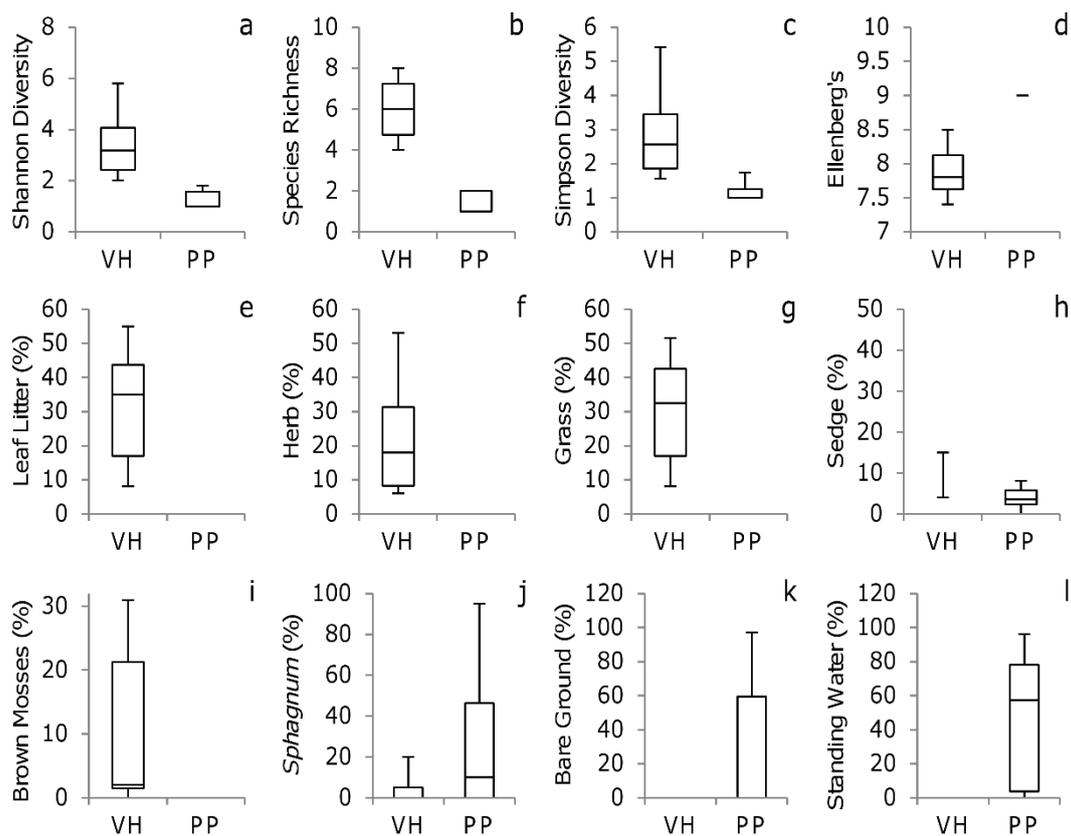
Figure **5**) even allowing for a 0.2 µmol m^{-2} s^{-1} uncertainty due to different CO_2 chambers

461   (15.7 l compared to 2.4 l) and analysers (Li-8100 compared to EGM-4) (section 2.2). This

462   difference was most likely driven by significant variation in vegetation diversity, species

463   richness   and   vegetation   cover   (
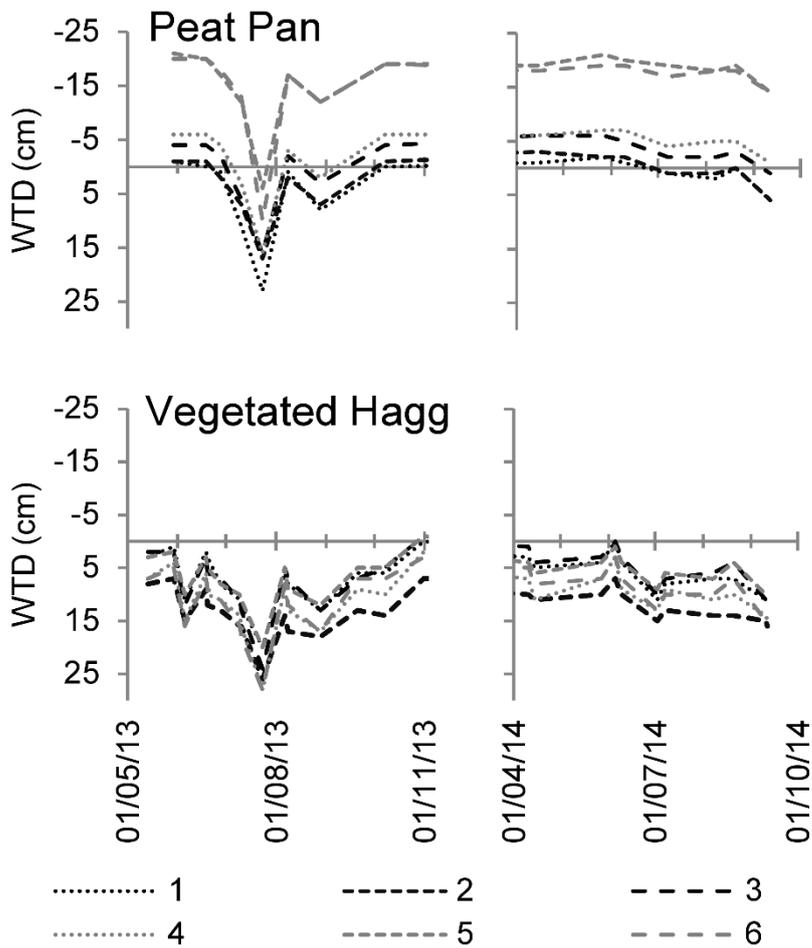
464

465   Figure   **4**)   due   to   different   water   table   depths   (
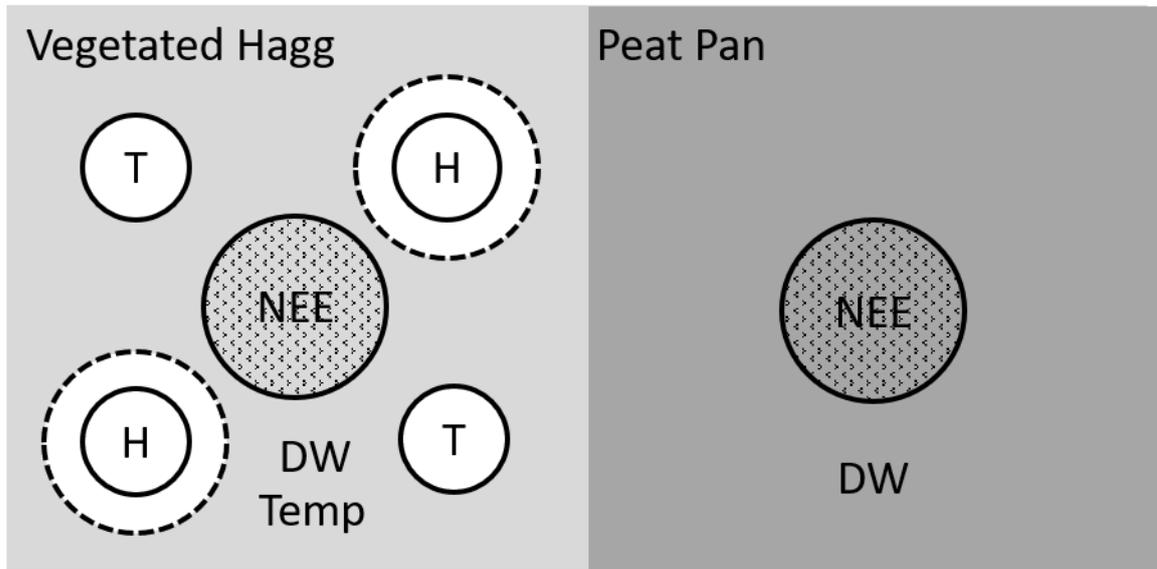
466

467   Figure 3).

468   Summer mean P_{G1000} (-1.0 µmol m^{-2} s^{-1}) from the peat pans was similar to an *Eriophorum*

469   *spp.*, *Vaccinium myrtillus* and bare peat naturally revegetating gully (-1.1

470   to -1.6 µmol m^{-2} s^{-1}) (Clay et al. 2012; Dixon et al. 2015) but photosynthetic CO_2 uptake

471   was less than a rewet cut-away *Eriophorum spp.* dominated peatland (-2.3 µmol m^{-2} s^{-1})

472   (Wilson et al. 2016) and much less than a rewet cut-away *Eriophorum spp.* tussock

473   (-15.5 µmol m^{-2} s^{-1}) (Tuittila et al. 1999). Given these annual results include large periods

474   with PPFD levels below saturation it can be seen that these peat pans have low primary

475   productivity even when compared to other damaged peatlands.

476   There was a notable spike in R_{Eco} in late July 2013 (2.1 µmol m^{-2} s^{-1}) (Figure 5) coincident

477   with warmer and drier conditions (Figure 3). Although notably higher than other values

478   recorded in this study, it is approximately half that reported for *Eriophorum vaginatum* in

479   a naturally revegetated erosional gully (4.1 µmol m^{-2} s^{-1}) (McNamara et al. 2008) under

480   similar water table and temperature conditions. Growing season mean ecosystem

481   respiration from the peat pans (0.5 µmol m^{-2} s^{-1}) was greater than annual (0.2 to

482   0.4 µmol m^{-2} s^{-1}) (Clay et al. 2012; Wilson et al. 2013; Dixon et al. 2015) and summer (0.04

483   µmol m^{-2} s^{-1}) (Tuittila et al. 1999) R_{Eco} rates for bare peat most likely due to some, albeit

484   sparse, vegetation cover. However, compared to annual mean R_{Eco} for an *Eriophorum*

485   *spp.* and bare peat channel floor (0.6 µmol m^{-2} s^{-1}) (Clay et al. 2012) and *Eriophorum spp.*

486   and *Sphagnum spp.* rewet cut-away peat (0.5 m^{-2} s^{-1}) (Wilson et al. 2016) the summer

487   mean R_{Eco} from the peat pans seems low. Again this probably reflects variation in

488   vegetation cover and low primary productivity rather than differences in water tables

489   directly, as the rewet peatland was wetter (-9.5 to -15.5 cm) (Wilson et al. 2016) than this

490   study and the natural channel (13.9 cm) (Clay et al. 2012) drier.

491   Maximum R_{Eco} in the vegetated haggs (3.6 µmol m^{-2} s^{-1}) was similar to August R_{Eco} from

492   Moor House, a *Calluna vulgaris, Eriophorum vaginatum* and *Sphagnum spp.* upland

493   blanket bog, (3.3 to 3.4 μmol m^{-2} s^{-1}) (Hardie et al. 2009; Lloyd 2010). Summer mean

494   R_{Eco} (2.4 μmol m^{-2} s^{-1}) was smaller than for a *Vaccinium spp., Eriophorum vaginatum,*

495   *Molinia caerulea* and *Calluna vulgaris* upland bog (3.1 μmol m^{-2} s^{-1}) (Urbanová et al. 2012)

496   however, the mean water table was deeper in this drained bog (19.5 cm).

497   Heterotrophic respiration rates (
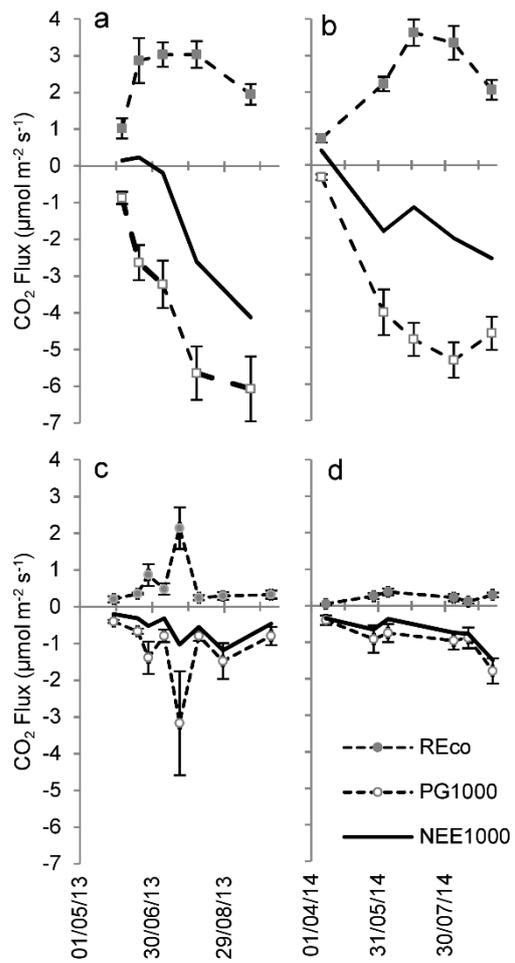
500   Figure **6**) were generally lower on Dartmoor (mean and maximum of 0.8 and

501   2.7 µmol m^{-2} s^{-1}) compared to those from August and September at Moor House (1.0 to

502   1.7 µmol m^{-2} s^{-1} (Hardie et al. 2009; Heinemeyer et al. 2011). This is surprising given the

503   difference in water table depths; 0 to 8 cm at Moor House (Hardie et al. 2009) compared

504   to -1 to 28 cm in this study. It is possible variation in leaf litter quality (Ward et al. 2010)

505   and quantity affected heterotrophic respiration rates. However, as the two studies at Moor

506   House were based on only four sample events there is insufficient data to fully understand

507   these differences.

508   Clipping and trenching severs roots which decompose leading to an overestimation of

509   heterotrophic respiration (Kuzyakov and Larionova 2005; Subke et al. 2006) and therefore

510   an underestimation of autotrophic respiration. Collars were installed 2 months prior to the

511   start of sampling to reduce disturbance effects and the data do not show a systematic

512   decrease in the proportion of heterotrophic respiration over time (Figure 6) suggesting the

513   effects were minimal.

514   Summer mean P_{G1000} (3.8 µmol m^{-2} s^{-1}) in the vegetated haggs was similar to summer

515   mean photosynthesis for a *Vaccinium spp., Eriophorum vaginatum, Molinia caerulea* and

516   *Calluna vulgaris* upland bog (-4.2 µmol m^{-2} s^{-1}) (Urbanová et al. 2012), however this

517   includes periods with lower PPFD so it is difficult to compare these values. Maximum

518   photosynthetic CO_2 uptake (P_{G1000}) (-6.1 µmol m^{-2} s^{-1}) in this study was greater than

519   maximum potential photosynthesis (P_{max}) from *Calluna vulgaris, Erica tetralix, Molinia*

520   *caerulea* and *Sphagnum spp.* hummocks in Irish blanket bog (-4.2 µmol m^{-2} s^{-1}) (Laine et

521   al. 2006) but less than those reported for a *Calluna vulgaris, Eriophorum vaginatum* and

522   *Sphagnum spp.* upland blanket bog (Moorhouse (-16.3 to -16.9 µmol m^{-2} s^{-1}) (Lloyd 2010).

523   The bogs in these studies had similar vegetation to this study (*Molinia caerulea, Erica*

524   *Tetralix, Eriophorum angustifolium, Calluna vulgaris*) but given the sensitivity of

525   photosynthesis to vegetation composition it is likely much of this variation is due to

526   differences in the vegetation community present. However, above-ground annual net

primary productivity was greater at Moor House, (approximately 300 g m^{-2}) (Ward et al.

528   2007) than Dartmoor (214±23 g m^{-2} in 2014) so the greater rates of photosynthesis may

529   also in part be due to greater biomass, reflecting more optimum growing conditions.

530   The summer maximum photosynthetic CO_2 uptake (P_{G1000}) and R_{Eco} measured in this

531   study   (
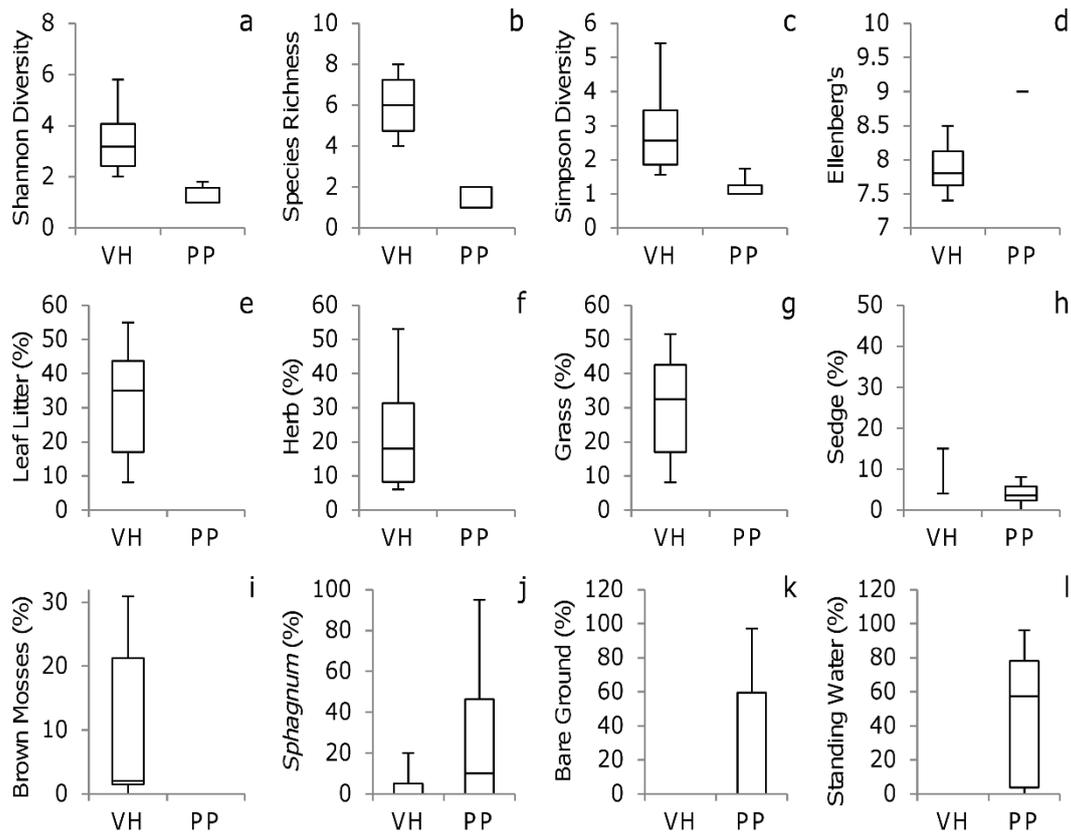
532

533   Figure **5**a & b) were lower than those found on Exmoor (-23.1 and 10.9 µmol m^{-2} s^{-1}

534   respectively) (Gatis 2015), an upland also located within the south west of England. On

535   Exmoor *Molinia caerulea* is more dominant and grows taller (up to 60 cm) than on

536   Dartmoor (up to 20 cm). This is reflected in greater above-ground annual net primary

537   productivity (ANPP); 517±30 g m^{-2} on Exmoor. A greater quantity of leaf litter resulting

538   from greater ANPP may also explain the higher rates of heterotrophic respiration on

539   Exmoor (1.5 ±0.1 µmol m^{-2} s^{-1}) (Gatis 2015) where peat thickness is shallower (<0.56 m).

540   As high rates of photosynthesis have been found to increase autotrophic respiration

541   (Subke et al. 2006) the difference in photosynthetic rates observed between these moors

542   may explain the lower average autotrophic respiration rates from Dartmoor (
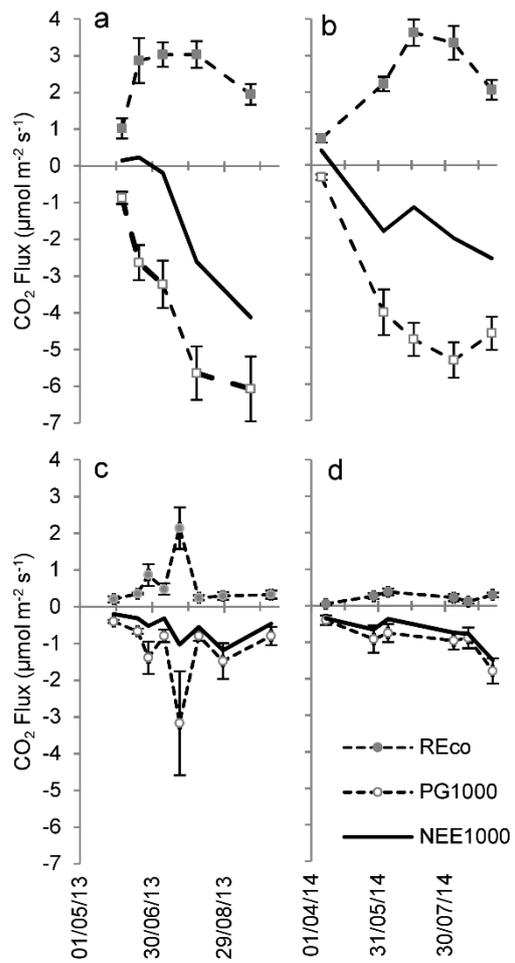
543

544

545   Figure **6**) than Exmoor (1.3 ± 0.2 µmol m^{-2} s^{-1}). No other values for autotrophic respiration

546   could be found for comparison in this region, reflecting the large uncertainty in measuring

547   autotrophic respiration (Subke et al. 2006).

548   4.2   DRIVERS OF TEMPORAL VARIATION IN CO_2 FLUXES

549   In the vegetated haggs and peat pans, photosynthetic uptake at 1000 µmol Photons m^{-}

550   ^{2} s^{-1} became significantly greater during periods of higher NDVI (Table 1). Photosynthesis

551   has been related to vegetation seasonal development measured by NDVI in northern

552   peatlands (up to 71 % of variation explained) (Kross et al. 2013), NDVI in alpine

553   grasslands (71 % of variation explained) (Rossini et al. 2012), leaf area (Nieveen et al.

554   1998; Street et al. 2007; Otieno et al. 2009), vegetative green area (Riutta et al. 2007;

555   Urbanová et al. 2012) and leaf biomass (Bubier et al. 2003). In the peat pans P_{G1000}

556   showed no significant relationship with NDVI most likely due to the minimal vegetation

557   cover.

558   In the peat pans, both ecosystem respiration and P_{G1000} (Table 1) showed the strongest

559   relationships with water table depth. Photosynthetic CO_2 uptake increased in the peat

560   pans during dry periods (Table 1). Although *Eriophorum angustifolium* is a wetland

561   species, evolved to live in waterlogged conditions, vegetation often close stomata in

562   response to raised water tables, limiting gases exchange through the leaf surface

563   (Pezeshki 2001). Photosynthetic uptake from *Eriophorum vaginatum* plots has been

564   found to increase as water levels fall from 16.8 cm to a maximum at 14.6 cm below ground

565   surface (Riutta et al. 2007). Where *Eriophorum spp.* plots were submerged following re-

566   wetting of a cut-over peatland, vegetation cover initially decreased before increasing in

567   the second year following re-wetting (Tuittila et al. 1999) suggesting *Eriophorum spp.* can

568   adapt to submerged conditions but not instantaneously.

569   Water table depth has commonly been found to influence ecosystem respiration (Tuittila

570   et al. 1999; Laine et al. 2006, 2007; Riutta et al. 2007; Wilson et al. 2007, 2013; Soini et

al. 2010) with greater respiration occurring during drier conditions. Lowering the water table increases the depth to which oxygen can diffuse, thus enabling more rapid aerobic heterotrophic respiration to occur (Clymo 1983; Moore and Dalva 1993). In addition, greater rates of photosynthetic CO_2 uptake and consequently autotrophic respiration also occurred during periods with lower water tables.

Total, heterotrophic and autotrophic below-ground respiration all showed significant exponential increase with soil temperature at 5 cm (Figure 7a, b & c). Soil temperature measurements from shallower depths have been shown to be better predictors of respiration (Lafleur et al. 2005; Lloyd 2010) especially when the proportion of autotrophic respiration is greater, although autotrophic respiration showed the strongest exponential relationship with soil temperature at 30 cm; the deepest depth measured in this study (Table 1). Perhaps reflecting a mix of autotrophic and heterotrophic sources, ecosystem respiration showed the strongest exponential relationship with soil temperature at 15 cm. This is similar to the depth found by Updegraff *et al.* (2001) but deeper than other studies which found air temperature (Schneider et al. 2012); an average of air temperature and soil temperature at 20 cm (Laine et al. 2006); soil temperature at 5 cm (Bubier et al. 2003; Lund et al. 2007; Wilson et al. 2007) and 10 cm (Blodau et al. 2007; Otieno et al. 2009; Lloyd 2010) to have the strongest relationships.

Soil temperature and water table depths commonly co-vary and interact to amplify effects on below-ground respiration. For example, warm and dry conditions are often concurrent, with both conditions increasing rates of below-ground respiration (Figure 7). Water table depths did show a significant relationship with total, heterotrophic and autotrophic soil respiration (Figure 7) indicating respiration increased during periods of lower water tables. However, multiple regressions indicated that soil temperature was the primary control on below-ground autotrophic and total soil respiration suggesting the apparent relationship with water table depth may have been due to co-variation of water table depths and soil temperature.

598 Water table depth was the strongest control on heterotrophic respiration possibly due to

599 increased aerobic heterotrophic respiration (Clymo 1983; Moore and Dalva 1993) and

600 enhanced gas diffusion through oxygenated peat (Blodau and Moore 2003). Although

601 below-ground respiration varied with water table, ecosystem respiration did not (Table 1)

602 possibly due to different drivers affecting the multiple respiration sources that contribute

603 to ecosystem respiration. This is consistent with other studies that have found

604 temperature to be the main control on ecosystem respiration under wet conditions

605 (Updegraff et al. 2001; Bubier et al. 2003) and within *Molinia caerulea* dominated systems

606 (Nieveen et al. 1998) but in contrast to studies that found water level to have the strongest

607 control over respiration (Silvola et al. 1996) or a small but significant effect (Lafleur et al.

608 2005; Otieno et al. 2009).

609 4.3 SEASONAL NET CO_2 ECOSYSTEM EXCHANGE

610 Given the sparse vegetation cover (Figure 4) it was unsurprising that the peat pans were

611 gaseous CO_2 (Table 3) as well as aquatic carbon sources (Malone, pers. comm. 2018)

612 over the growing season. NEE fluxes (0.1 gCO_2 m^{-2} d^{-1}) were lower than those observed

613 for bare Canadian cut-over peat (0.6 to 2.1 gCO_2 m^{-2} d^{-1}) (Waddington et al. 2010) and

614 *Eriophorum spp.* tussock and inter-tussock plots in a Finnish cut-over peatland (0.3 to 1.2

615 gCO_2 m^{-2} d^{-1}) (Tuittila et al. 1999). This might be due to the limited vegetation cover as a

616 closed *Eriophorum spp.* cover has been found to be a smaller net CO_2 source (or even a

617 net CO_2 sink) compared to a non-vegetated surface under the same environmental

618 conditions (Tuittila et al. 1999).

619 It was unexpected that the vegetated plots were a greater net CO_2 source over the growing

620 season (Table 3) given the greater vegetation cover (Figure 4). However, Hardie et al.

621 (2009) found 37-35 % of summer ecosystem respiration flux to be from soil (R_{BG-ToT})

622 suggesting 63-66 % was from the vegetation so although the vegetated haggs had greater

623 photosynthesis much of this would be rapidly re-released. In addition, root exudates add

624   fresh organic matter to the subsurface stimulating microbes to decompose more

625   recalcitrant peat (Fontaine et al. 2007). This would be enhanced by deeper water table

626   depths in the vegetated haggs (Figure 3) allowing oxygen to penetrate deeper into the

627   peat resulting in increased decomposition (Silvola et al. 1996).

628   Other studies in a range of peatlands have also reported vegetated plots to be growing

629   season net CO_2 sources (Tuittila et al. 1999; Waddington et al. 2010; Urbanová et al.

630   2012; Strack and Zuback 2013). During measurements all sites were net CO_2 sinks,

631   however, these were collected during bright, daytime conditions. It should be noted that

632   this model assumes the dependency of ecosystem respiration on temperature is the same

633   in the day and night. Daily variation in autotrophic respiration (and primed heterotrophic

634   respiration) has been shown to result in significant differences between day and night R_{Eco}

635   at the same temperatures (Juszczak et al. 2012; Wohlfahrt and Galvagno 2017).

636   Therefore, it is most likely ecosystem respiration is overestimated by this model. In

637   addition, shade cloths underestimate photosynthesis at low light levels compared to

638   naturally low light conditions and a lack of temperature control within the chamber may

639   have resulted in plant stress also underestimating photosynthesis. Consequently, this

640   experimental design is biased towards overestimating CO_2 release.

641   The models explained 76 % of the variability in observed NEE in the vegetated haggs and

642   67 % in the peat pans (Table 2) however, the root mean square errors are large in

643   comparison to P_{G1000} and R_{Eco} fluxes observed (Figure 5). This has resulted in

644   uncertainties many times larger than seasonal NEE estimates (Table 3). This uncertainty

645   consists of both natural variability which is known to be significant when using multiple

646   plots (Laine et al. 2009) and uncertainty associated with modelling. It has been shown

647   that different treatment of closed chamber data can result in variation in estimated NEE of

648   0.25 gCO_2 m^{-2} d^{-1} over annual estimates (Huth et al. 2017) sufficient to change the

649   estimate of ecosystem exchange from a net CO_2 source to a net CO_2 sink. Accepting this

650   uncertainty, the models suggest both landscape components are losing carbon with

651   greater loss from the haggs even with a greater vegetation cover.

652   Given, that in this study, NEE was modelled for the growing season only, when the

653   majority of carbon uptake occurs, Dartmoor would be expected to be a larger source over

654   the whole year. This suggests peat pan formation and expansion has altered the

655   ecohydrological functioning of the whole mire not just the eroded pan areas, altering the

656   balance of CO_2 uptake and release towards carbon loss. Ecohydrological restoration is

657   required to prevent further carbon loss and promote a return to carbon sequestration.

658   In the UK restoration schemes have blocked erosional gullies using a combination of

659   materials (peat, wood, stone, plastic piling and heather bales) to slow water flow, trap

660   sediment and raise local water tables (Parry et al. 2014). This would be expected to halt

661   the expansion of the peat pans and encourage peat deposition behind dams which should

662   provide zones for colonisation by pioneering species such as *Eriophorum spp.* (Crowe et

663   al. 2008) which may facilitate recolonization by other species (Tuittila et al. 2000). In rewet

664   cut-away peatlands high and stable water tables have been found to rapidly increase

665   *Eriophorum spp.* cover but also shift *Eriophorum spp.* dominated plots towards growing

666   season net CO_2 sinks (Tuittila et al. 1999; Waddington et al. 2010). In the vegetated haggs

667   the response would be expected to vary with vegetation type (Komulainen et al. 1999)

668   with raised water tables reducing respiration but also possibly photosynthesis. It should

669   be noted that this study has focused on CO_2, raising water tables has been shown to

670   increase the release of CH_4 particularly in areas of open water (Best and Jacobs 1997;

671   Komulainen et al. 1998; Strack and Zuback 2013; Cooper et al. 2014; Wilson et al. 2016).

672   However, in the longer-term, higher and more stable water tables might alter the

673   vegetation present towards those associated with wetter conditions (Bellamy et al. 2012)

674   and carbon sequestration.

5 CONCLUSION

This study aimed to investigate the spatial and temporal controls on CO_2 fluxes in a climatically marginal, eroding blanket bog and to quantify CO_2 fluxes from these landscape components. Understanding the effects of existing damage and the potential effects of restoration should enable more informed management choices to be made.

The water table was significantly higher in the peat pans than in the vegetated haggs resulting in clear differences in vegetation composition and productivity which lead to significant differences in photosynthesis and ecosystem respiration between these landscape components. CO_2 fluxes in the peat pans were dominated by changes in water table depths whilst photosynthesis in the drier vegetated haggs was related to normalised difference vegetation index (a proxy for vegetation seasonal development). Although ecosystem respiration was strongly related to temperature, heterotrophic below-ground respiration significantly decreased as water tables rose suggesting higher, more stable water tables may reduce the peat being respired. An empirically derived net CO_2 ecosystem exchange model suggests that over the growing seasons studied the drier vegetated haggs were a greater net CO_2 source than the peat pans despite greater vegetation cover.

Peat pan formation and expansion has affected the ecohydrological functioning of the whole mire not just the eroded pan areas. This demonstrates the need to limit the spread of bare peat pans to protect the biodiversity of the mire, prevent further loss of stored carbon and promote a return to carbon sequestration.

702 **DATA ACCESS**

703   The research data supporting this publication are openly available from the University of

704   Exeter's institutional repository at: https://doi.org/10.24378/exe.1143.

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930

931 **Table 1 Most significant variables from stepwise multiple regression analysis of temporal controls on**

932 **average CO_2 fluxes; photosynthesis at 1000 μmol Photons m^{-2} s^{-1} (P_{G1000}), ecosystem respiration (R_{Eco}),**

933 **total (BGR_{Tot}), heterotrophic (BGR_{Het}) and autotrophic (BGR_{Aut}) below-ground respiration.**

Landscape Component	CO_2 Flux	Variable		Coefficient		P	r^2
		1	2	1	2		
Vegetated	P_{G1000} (n=10)	NDVI		-8.951		<0.001	0.82
	LnR_{Eco} (n=14)	T15		0.172		0.001	0.77
Peat	P_{G1000} (n=10)	WTD		-0.111		<0.001	0.87
	R_{Eco} (n=14)	WTD		0.077		<0.001	0.78
Vegetated	$LnBGR_{Tot}$ (n=17)	T5		0.21		<0.001	0.72
	BGR_{Het} (n=17)	WTD	Rain1	0.125	0.084	<0.001	0.75
	$LnBGR_{Aut}$ (n=17)	T30		0.474		<0.001	0.69

Input variables: water table depth (WTD), soil temperature and natural log-transformed soil temperature at 5, 10, 15, 20, 25 and 30 cm, fraction of photosynthetically active radiation (fPAR), Normalised Difference Vegetation Index (NDVI), total PPFD in the preceding day and hour, total rainfall on the day of measurement (Rain0) and preceding 1,7,14 and 28 days.

934

935

936 **Table 2 Sample number (n), regression coefficient (r^2), root mean squared error (RMSE) and coefficient**

937 **estimates (standard errors) used in net CO_2 ecosystem exchange models (Equation 4 and 5)**

		Vegetated Hagg	Peat Pan
n		423	398
r^2		0.76	0.67
RMSE (umol m^{-2} s^{-1})		1.39	0.37
Coefficient estimate (standard error)	P_{max}	-13.05 (0.67)	-2.25 (0.19)
	K	1299.27 (241.05)	2606.31 (649.86)
	a or c	11.49 (1.98)	0.05 (0.02)
	b or d	19.49 (2.31)	0.15 (0.03)
	f	.	0.06 (0.01)

938

939

940

Table 3 Estimated seasonal CO$_2$ flux. Positive values indicate the ecosystem is a net CO$_2$ source to

the atmosphere.

Growing Season		CO$_2$ Flux (g C m^{-2})	95 % Confidence Interval
06/06/2013 to 28/10/2013	Vegetated Haggs	29	-570 to 762
	Peat Pans	7	-147 to 465
16/05/2014 to 12/10/2014	Vegetated Haggs	20	-873 to 1105
	Peat Pans	8	-136 to 436

944   Figure 1. Location of A, Dartmoor National Park (shaded area) within the south west of England, B, Study site

945   (red square) within the national park (grey), C, the study site (black square) within an area of erosion, and D, the

946   arrangement of plots and monitoring equipment; vegetated (grey squares) and bare (white squares) net CO_2

947   ecosystem exchange and total (white circles) and heterotrophic (black circle) below ground respiration. In panels

948   C and D the green vegetated areas are the vegetated haggs and the grey, watery areas are the peat pans.

949
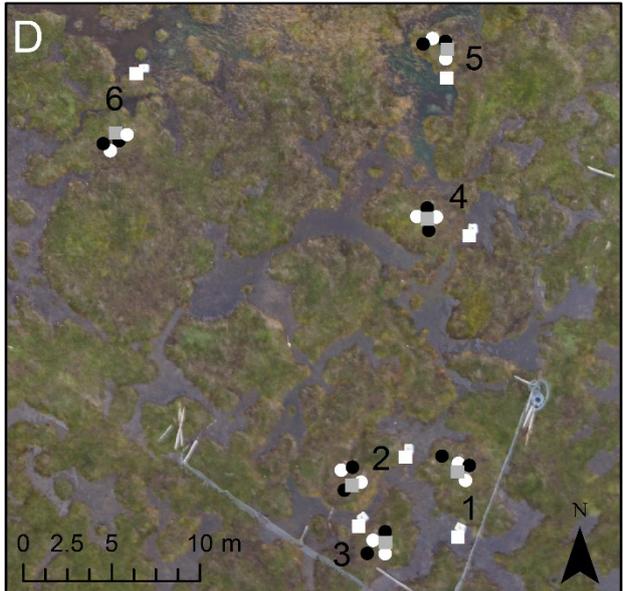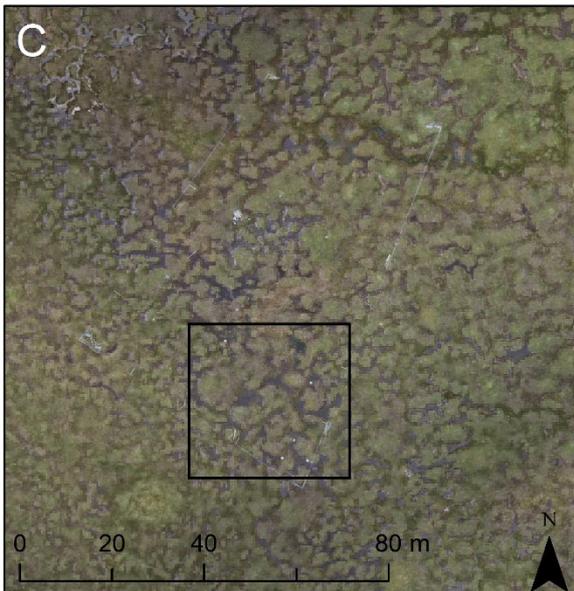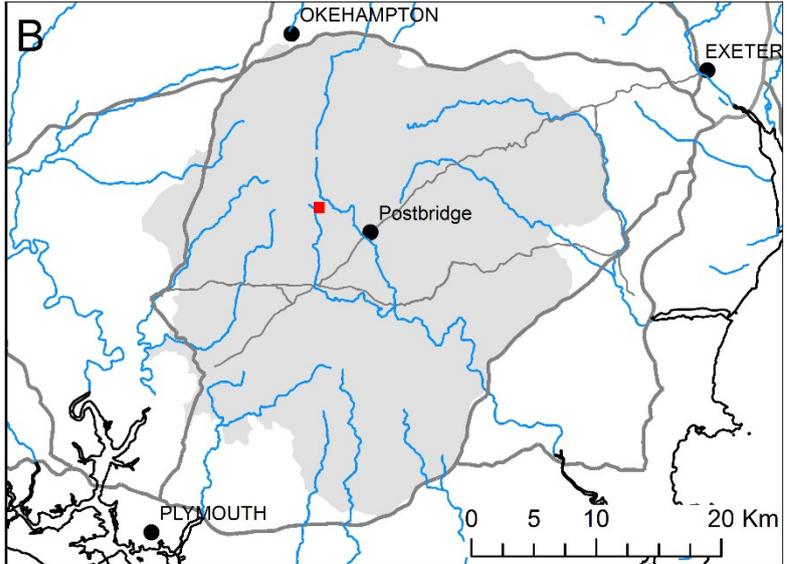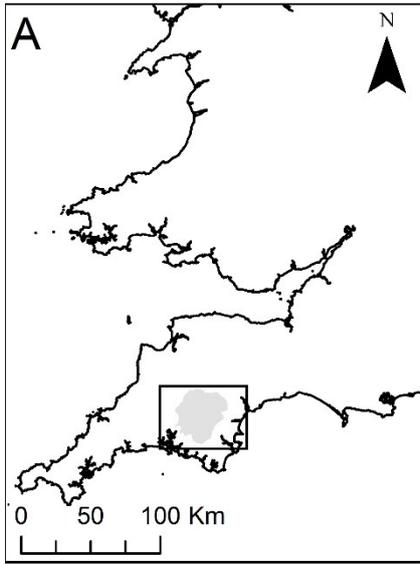
952   Figure 2 Schematic equipment layout. Perspex net ecosystem exchange collar (NEE) co-located with dipwell

953   (DW) in both the vegetated haggs and peat pans. In the vegetated haggs polyvinyl chloride collars were also

954   located measuring total (T) and heterotrophic (H) below ground respiration.

955
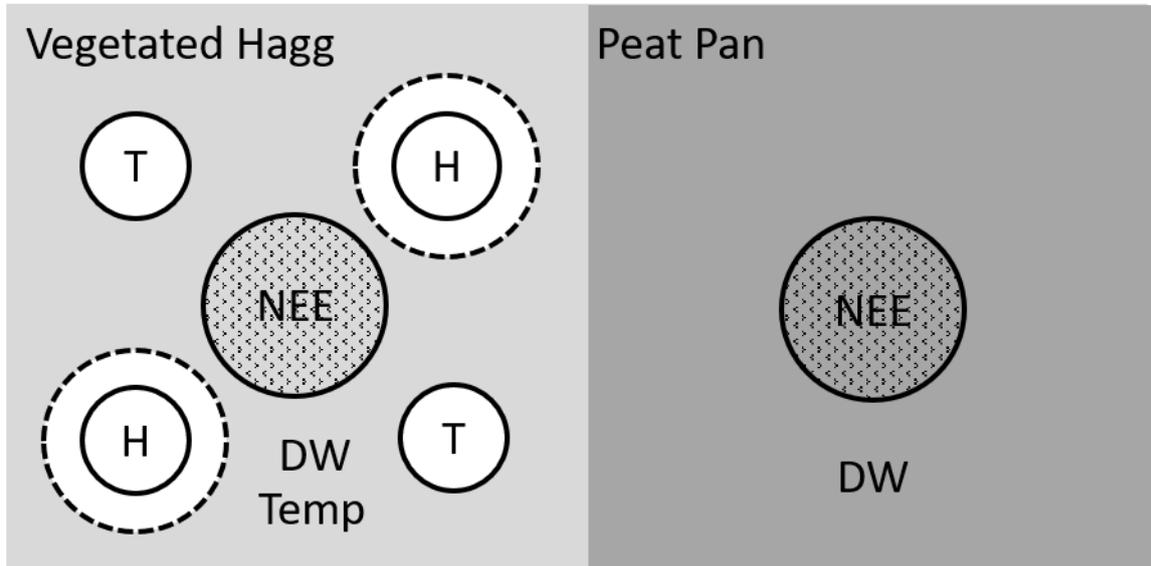
Figure 3 Water table depth (cm below ground level) in the peat pans (top) and vegetated haggs (bottom) over the

957 2013 and 2014 growing seasons the six replicate plots within the study site (Figure 1D)

958

61
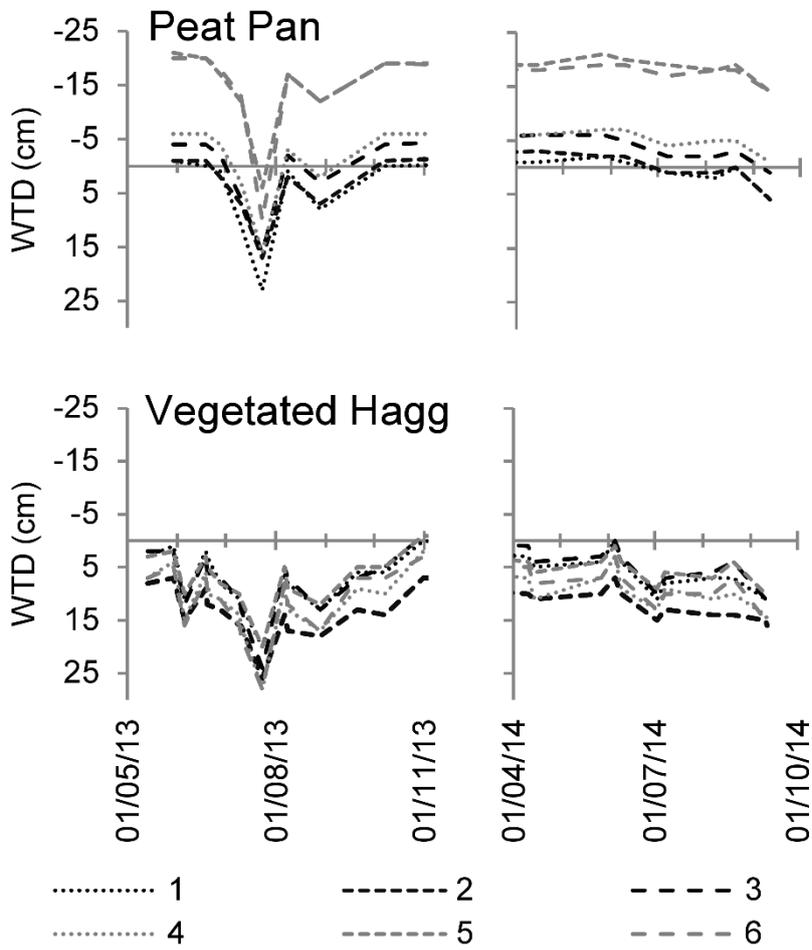
Figure 4 Comparison of vegetation composition indices between the vegetated haggs (VH) (n=6) and the peat

pans (PP) (n=6). Error bars reach the maximum and minimum recorded values. The vertical box extends from the

25th to the 75th percentile with a horizontal line at the 50th percentile.
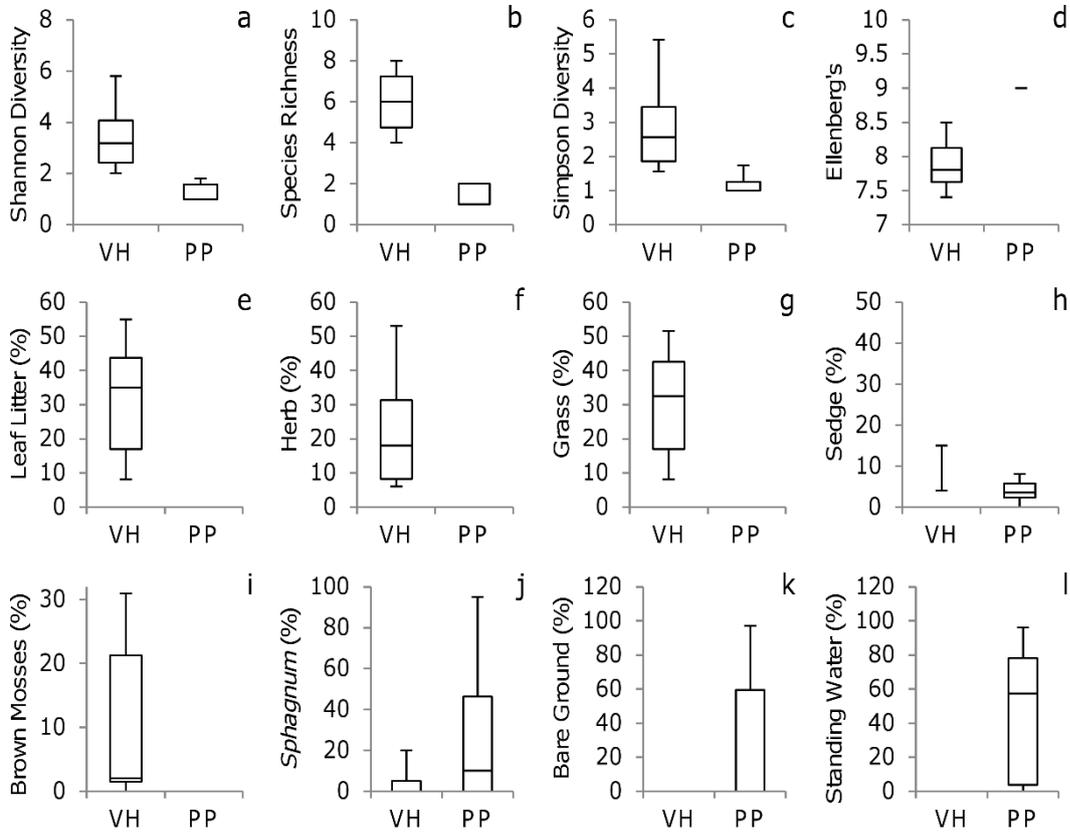
963 Figure 5 Seasonal variation in ecosystem respiration and photosynthesis and net ecosystem exchange at

964 1000 μmol Photons m^{-2} s^{-1} in the vegetated haggs (a & b) and peat pans (c & d) (μmol m^{-2} s^{-1}), error bars are 1

965 standard error, n=6.

966
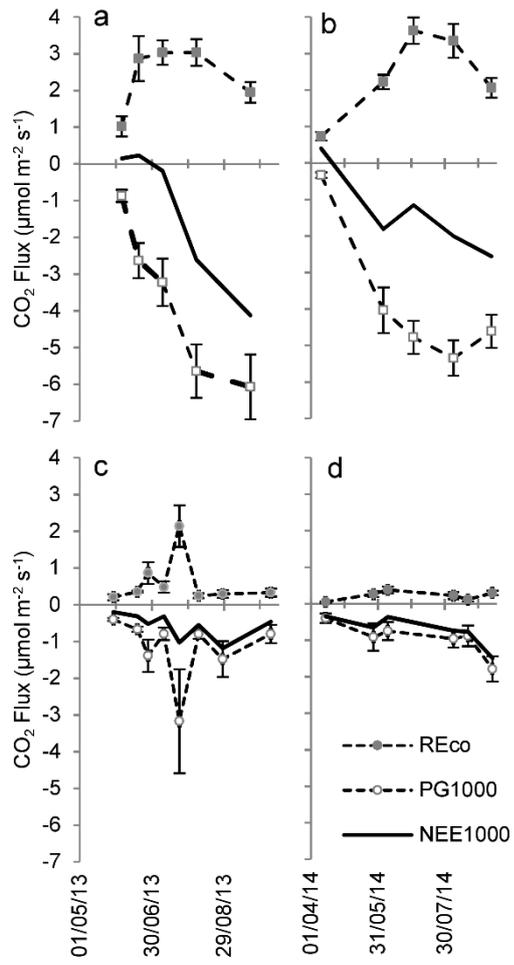
969 Figure 6 Seasonal variation in mean total and heterotrophic soil respiration rates (n=6) (μmol m^{-2} s^{-1}). Error bars

970 are 1 standard error.
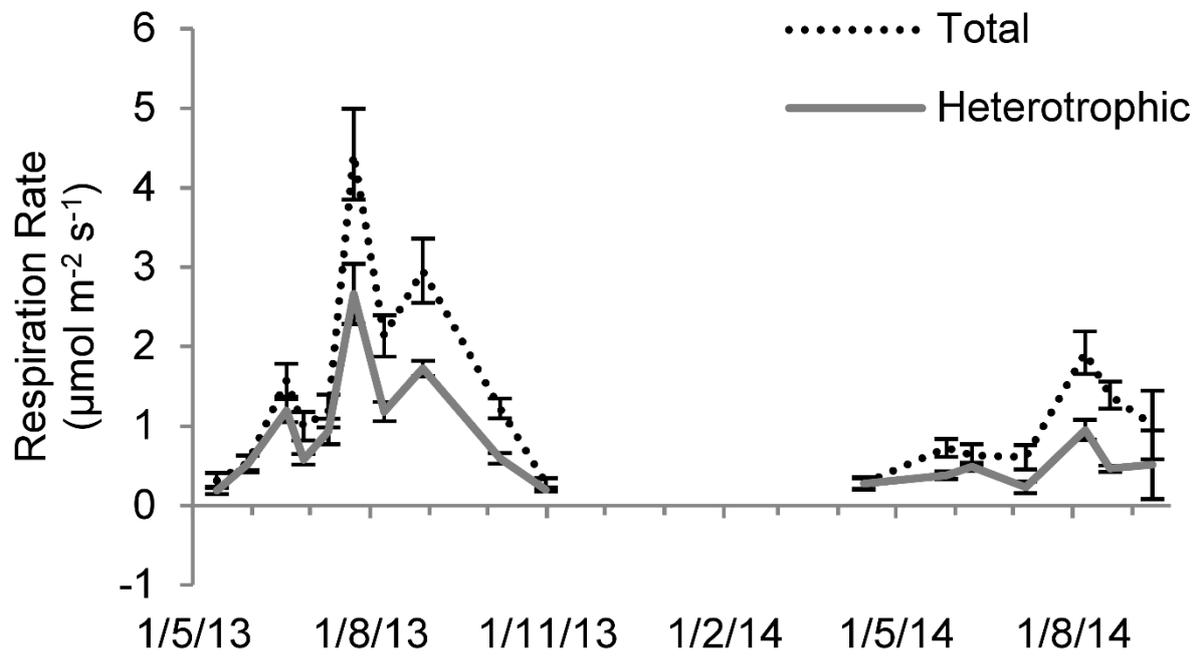
971

972   Figure 7 Temporal relationship between soil temperature (°C) at a depth of 5 cm (a, b & c) or water table depth (cm

973   below ground surface) (d, e & f) and total (a & d), heterotrophic (b & e) and autotrophic (c & f) below-ground

974   respiration from the vegetated haggs (n=6). p<0.001.

975
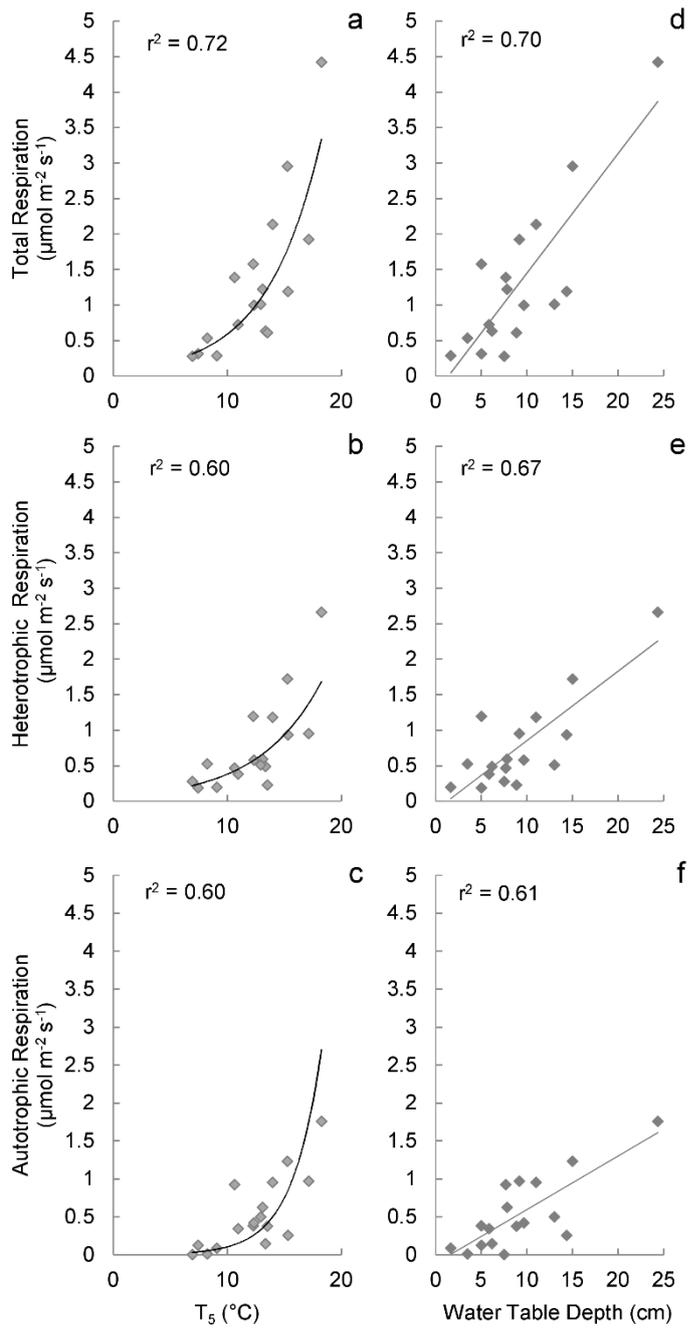
Supplementary Material Table 1 Percentage cover of species observed at sites (1-6) in vegetated haggs and peat pans

Species	Vegetated Haggs						Peat Pan					
	1	2	3	4	5	6	1	2	3	4	5	6
Calluna vulgaris	1	5	3	5								
Drosera rotundifolia		1										
Erica tetralix	4	7	20	15	8	3						
Narthecium ossifragum						50						
Polygala serpyllifolia	1			4	1							
Molinia caerulea	30	40	50	20	35	8						
Trichophorum cespitosum	30			4								
Eriophorum angustifolium		5	1	8	2	2	3	3	4	5		8
Campylopus introflexus	1	1										
Hypnum cupressiforme	30	1		18	2							
Racometrium langinosum			2									
Sphagnum capillifolium/rubellum		20										
Sphagnum denticulatum										30	95	20
Bare Ground	8	20	40	30	35	40	97	47				
Standing Water								50	96	65	5	72

982   Supplementary Material Figure 1 Modelled net ecosystem exchange (CO_2 μmolm^{-2}s^{-1}) against measured net

983   ecosystem exchange (CO_2 μmolm^{-2}s^{-1}) and model residuals (CO_2 μmolm^{-2}s^{-1}) against modelled net ecosystem

984   exchange (CO_2 μmolm^{-2}s^{-1}) for the vegetated haggs and peat pans.

Vegetated Haggs

$r^2 = 0.76$

Peat Pans

$r^2 = 0.67$

985