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1 Annual gaseous carbon budgets of forest-to-bog restoration sites are strongly 2 determined by vegetation composition

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10

11 ABSTRACT

12

13 Large areas of naturally open peatland in western Europe were drained and planted with non-native

14 conifers in the twentieth century. Efforts are currently underway to restore many of these sites.

15 Ultimately, forest-to-bog restoration aims to bring back functional peatlands that can sequester

16 carbon but there is a lack of empirical evidence for whether current approaches are effective. Using a

17 chronosequence design, we compared the annual gaseous carbon balance of two forest-to-bog

18 restoration areas with an open area not subject to afforestation. A closed chamber method was used

19 to determine gas fluxes (Net Ecosystem Respiration, Gross Primary Productivity, Net Ecosystem

20 Exchange and methane) over a twelve-month period for locations spanning the range of peatland

21 microtopography and vegetation communities. Relationships between gas fluxes, vegetation/cover

22 and environmental factors were analysed and regression models used to estimate annual CO₂ and CH₄

23 budgets. During the study period, NEE estimates (total gaseous C expressed as CO₂-eq) showed a net

24 sink for the unafforested (-102 g C m⁻² yr⁻¹) and oldest (-131 g C m⁻² yr⁻¹) restoration area (17 years

25 post-restoration 'RES 17 YRS'), whilst the youngest restoration area (6 years post-restoration 'RES

26 6YRS'), was a net source (35 g C m⁻² yr⁻¹). We observed significantly higher CH₄ emissions from

27 restoration areas dominated by *Eriophorum angustifolium* compared with other peatland vegetation

28 types. Sampling points with higher cover of *Sphagnum* were found to be most effective for C

29 sequestration. Overall, vegetation composition/cover was observed to be an important factor

30 determining C emissions from forest-to-bog restoration areas. These results suggest that restoration
31 is effective in returning the carbon sink function of peatlands damaged by commercial forestry and -
32 depending on restoration techniques - timescales of more than 10 years may be required.

33 **KEYWORDS:** peatland, raised bog, carbon dioxide, methane, forestry, restoration

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41 INTRODUCTION

42

43 Peatlands only cover a small proportion (~3%) of Earth's surface (Xu et al., 2018), yet store about 500
44 ± 100 gigatons of carbon (GtC) (Gorham, 1991; Yu et al., 2010), representing an important stock (~25-
45 40%) of global soil carbon (Yu, 2012; Rydin and Jeglum, 2013; Cooper et al., 2014). Over millennia,
46 intact peatlands have had a net cooling effect on the global radiation balance through C sequestration
47 and storage (Frolking et al., 2011). However, when peatlands are drained, C can be released from peat
48 into the atmosphere through aerobic decomposition at far more rapid rates than it was accumulated
49 (Gorham 1991; Lindsay 2010). In northern temperate peatlands, it is currently uncertain whether
50 contemporary C accumulation rates offset C emissions from degraded peatlands (Billet et al., 2010).
51 Recent research suggests plant communities have potential to significantly affect C accumulation
52 (Mathijssen et al., 2019), and hence, the C sink function of ombrotrophic peatlands, i.e. raised bogs
53 and blanket bogs.

54

55 Peatland gaseous C dynamics are a balance of carbon dioxide (CO₂) uptake by plants during
56 photosynthesis (gross primary productivity, GPP) and CO₂ release through plant and soil respiration
57 (net ecosystem respiration, NER), and methane (CH₄) production and consumption. The
58 Intergovernmental Panel on Climate Change defined the global warming potential (GWP) of CH₄ over
59 a 100-year cycle and is reported to be 28 times greater than CO₂ (Myhre et al., 2013). Trade-offs
60 between the balance of CO₂ and CH₄ uptake and release have important climate implications, and
61 human actions can alter the greenhouse gas (GHG) balance in peatlands (Luo and Zhou, 2006; Dise
62 2009; Laine et al., 2019). Determining whether peatlands are functioning as a net C sink requires the
63 calculation of a C budget (or balance), which can be estimated by measuring fluxes of C exchanges at
64 land-atmosphere interface (Rowson et al., 2013) and export of dissolved organic C (DOC) into the
65 aquatic environment (for example, Worrall et al., 2011; Gaffney et al., 2018). Several studies have
66 calculated annual gaseous C budgets of peatlands degraded by human activity (for example, Strack

67 and Zuback, 2013; Worrall et al., 2009), with results strongly dependent on land-use and peatland
68 type (Hommeltenberg et al., 2014).

69

70 It is estimated that around 15 Mha of peatlands have been drained for forestry in the boreal and
71 temperate zones (Paavilainen and Päivänen, 1995). In the British Isles, afforestation of previously open
72 peatland was widespread in the late 20th century, and by the 1990's > 800,000 ha (circa 20%) was
73 afforested in the UK, and > 200,000 ha (circa 16%) in Ireland (Andersen et al., 2017). Whilst trees are
74 a natural component of many peatland ecosystems in continental climates (Hommeltenberg et al.,
75 2014), in more oceanic or colder climates most peatlands are treeless (Lindsay 2010; Payne and
76 Jessop, 2018a). In open peatlands, forestry requires the drainage of the peat surface before trees are
77 planted. Forestry practices in the UK often involved using closely spaced plough furrows between
78 deeper drainage systems, creating ridges sufficiently raised above the drained water table to
79 encourage tree establishment and survival. It is generally accepted that drainage of peatlands leads
80 to higher peat decomposition with substantial C losses to the atmosphere (Couwenberg, 2011), yet,
81 some studies have shown that forest drainage does not necessarily change a peatland from a C sink
82 to a C source (Minkkinen and Laine, 1998; Hommeltenberg et al., 2014). Net ecosystem exchange
83 (NEE) is used to determine the sink–source status of peatlands drained for forestry (Hommeltenberg
84 et al., 2014; Laine et al., 2019; Hambley et al., 2019).

85

86 Considerable investments have been made in the UK to restore peatland, including those damaged by
87 drainage and afforestation (Andersen et al., 2017; Payne et al., 2018a; Payne et al., 2018b).
88 Restoration of an afforested peatland typically involves the removal of trees and the blocking of
89 drainage ditches and/or plough furrows to raise the water table. Trials of different restoration
90 techniques are occurring rapidly, especially in Scotland, where older restoration techniques (e.g.
91 felling to waste where small trees are rolled into furrows, and only collector drains are blocked) are
92 being superseded by newer, more novel restoration practices (Hancock et al., 2018), such as whole

93 tree harvest, reprofiling, etc. All these techniques involve a significant initial disturbance. In the case
94 of forest-to-bog restoration, these efforts are largely driven by biodiversity incentives, to halt losses
95 associated with afforestation and habitat fragmentation (see Wilson et al., 2014). However, a key
96 question remains whether forest-to-bog restoration also deliver the climate benefits widely
97 associated with peatland restoration (Bonn et al., 2016).

98

99 Data on the C balance of forest-to-bog restoration sites are limited (Sloan et al., 2018), and in the UK,
100 research has focused on blanket bog (Hermans, 2018; Hambley et al., 2019; Hermans et al., 2019; Lees
101 et al., 2019). Despite some uncertainties, results of these studies demonstrate that forest-to-bog
102 restoration sites older than 15 years can have climate benefits, by storing more GHG's than they emit
103 (Hermans et al., 2019). However, apart from one study in Ireland (Rigney et al., 2018), there is
104 currently a lack of knowledge of whether forest-to-bog restoration can restore the C balance of raised
105 bog. Using an eddy covariance (EC) technique on blanket bog, Hambley et al (2019) report C sink
106 sixteen years post restoration and C source ten years post restoration, although this study did not
107 capture the CH₄ flux. In contrast, using a closed chamber technique, eight years post restoration,
108 Rigney et al (2018) found the C sink function in a raised bog in Ireland had not recovered to pre-
109 disturbance conditions. In their study, microsites dominated by *Cladonia* sp. and *Calluna* sp. were
110 reported to act as strong sinks for CO₂-C.

111

112 Vegetation is known to play an important role in the exchange of GHG's at the peatland surface of
113 restoration sites (Waddington and Day, 2007; Ward et al., 2009; Ward et al., 2013), but less is known
114 in relation to forest-to-bog restoration. Initial studies in Scotland have shown that the process of
115 forest-to-bog restoration and raising the water table creates a shift in vegetation communities, often
116 a dominance of sedges, particularly *Eriophorum angustifolium* (Hancock et al., 2018), with potential
117 for higher CH₄ emissions in the short term (Waddington and Day, 2007). Plant traits could also be a
118 co-driver of GHG fluxes of forest-to-bog restoration sites. For example, Konings et al (2019) found

119 intra-specific variation in plant species, specifically, significantly higher leaf area and chlorophyll
120 content in afforested and forest-to-bog sites compared with undisturbed open bog and suggested that
121 legacy effects of the forestry may persist even after vegetation communities have returned.

122

123 The aims of this paper are to present annual gaseous carbon budgets for a chronosequence of forest-
124 to-bog restoration areas of a raised bog and to compare these to unafforested open conditions, using
125 a space-for-time substitution approach (Pickett 1989; Walter et al., 2007). Our hypotheses were: 1)
126 Restoration of afforested peatlands returns the CO₂ sink function, 2) There will be a higher CH₄ efflux
127 from vegetation dominated by *Eriophorum angustifolium* and, 3) Annual net ecosystem exchange of
128 CO₂ and CH₄ (therefore total C sequestration) will be lower in the youngest restoration areas than
129 oldest and unafforested areas.

130

131 **METHODS**

132

133 **STUDY AREA**

134

135 Our study was conducted on a large raised bog complex spanning the border of England and Wales.

136 Fenns, Whixall and Bettisfield Mosses National Nature Reserve (52°92'24"N, 2°76'94"W) is a lowland
137 raised mire in the counties of Shropshire and Wrexham at an altitude of 72 m above sea level (Fig. 1).

138 The raised bog complex includes several distinct but inter-connected peat domes with peat initiation
139 occurring in the early Holocene (Hardy 1939; Turner, 1964). The site was drained during the 18th

140 century for commercial peat cutting, which persisted throughout the nineteenth and twentieth
141 centuries (see Leah et al., 1998). Commercial peat extraction ceased in 1990 when the site was

142 acquired by statutory nature conservation organisation the Nature Conservancy Council. Historically,
143 the site has also been managed for commercial forestry, particularly around the periphery of the site.

144 Marginal forestry plantings at our study areas were circa 1960 with Lodgepole pine *Pinus contorta*,
145 Norway spruce *Picea abies* and Scots pine *Pinus sylvestris* planted at 2 metre spacings. Since the late

146 1990's, management efforts have focused on removing existing plantations to reduce interception,

147 evapotranspiration, shading and tree seed sources combined with damming ditches to raise the water
148 table (Daniels *pers comms*). Monthly average air temperature ranges from 0.6°C (min) to 21.0°C (max)
149 and mean annual rainfall is 659.9 mm (1981 – 2010 average at Shawbury Meteorological Station, 22
150 km from the study site).

151 152 EXPERIMENTAL DESIGN

153
154 We focused on a chronosequence design considering non-afforested peatland and two phases of
155 restoration. In April 2015, a restoration chronosequence was identified, consisting: 1) trees planted in
156 ~1960 and removed in 1998 (17 years post-restoration – referred to as ‘RES 17YRS’), 2) trees planted
157 in ~1960 and removed in 2009 (6 years post-restoration – referred to as ‘RES 6YRS’), 3) control area
158 (no afforestation – referred to as ‘OPEN’). All study areas were adjacent and were not impacted by
159 historical peat cutting. Both afforested areas were planted with trees at the same time, using the same
160 practises and can be considered to have been equivalent prior to restoration. Restoration involved
161 whole tree removal (motor-manually felled), scrub control and brash removal coupled with damming
162 drainage systems to promote a high-water table. At the oldest restoration area (RES 17YRS) the trees
163 were manually carried off, whereas at the younger restoration area (RES 6YRS) trees were
164 mechanically removed. This is a different technique to mechanised harvesting because in both cases
165 it was whole tree removal rather than processing on site (Daniels *pers comms*).

166
167 Unafforested areas were characterised by hummock-hollow microtopography and supported typical
168 peatland plant species such as: *Sphagnum* spp., *Aulacomnium palustre*, *Vaccinium oxycoccos*, *Erica*
169 *tetralix* and *Eriophorum vaginatum*. Restoration areas were characterised by ridge-furrow
170 microtopography. Vegetation/cover in the oldest restoration areas were dominated by ericaceous
171 species such as: *Calluna vulgaris*, *Vaccinium oxycoccos* and *Erica tetralix* on the drier ridges with
172 *Eriophorum vaginatum* and *Sphagnum* spp., colonising the wetter furrows. In the youngest restoration
173 areas, ridges consisted of bare peat and brash (e.g. conifer needle litter and woody debris) with

174 *Calluna vulgaris* and furrows were colonised by *Eriophorum angustifolium* on bare peat and brash.
175 Photographs of the five main vegetation communities identified across the three study areas are
176 shown (Figs. 2a-e).

177 We established 7 sampling points ($n = 7$) distributed in hummock/ridge and hollow/furrow
178 microtopography in each study area to give a total of 21 sampling points. At each sampling point, PVC
179 gas chamber base rings, also referred to as collars (31.5 cm diameter and 10 cm height) and dipwells
180 were permanently installed to allow for repeated gas flux and water table measurements. Collars were
181 left for at least one month prior to gas flux measurements. Soil and air temperature loggers (HOBO
182 Pro v2 U23-00x) and water level loggers (HOBO U20L-0x) were installed in each of the three study
183 areas logging at one-hour intervals. Soil temperature loggers were installed at 5 cm depth. Hourly daily
184 air temperature and solar radiation data obtained from the UK meteorological office were used to
185 supplement the data logged data for modelling C fluxes.

186

187 VEGETATION COMPOSITION

188

189 Sampling points were surveyed in August 2015 at the peak biomass period using the line-point
190 intercept (LPI) method (Rochefort et al., 2013), and re-surveyed in August 2016 to assess vegetation
191 change. For this, a 50 x 50 cm frame was placed carefully over each collar and 25 measurements were
192 obtained at equal 5 cm intervals based on the number of species touches with a vertically-placed pin
193 (1 mm diameter). The LPI method was preferred over a percentage cover characterisation of the plant
194 species within the collars because it did not involve subjective estimates of plant cover. Furthermore,
195 this method is preferred to spatially assess the impact of restoration actions in the early stages post-
196 restoration (Rochefort et al 2013), which was the case in our youngest restoration area (RES 6YRS).
197 We averaged the plant species composition for both surveys for each sampling point and frequencies
198 (expressed as percentages) were calculated for each species, providing a quantitative measurement
199 of cover. The nomenclature follows Atherton et al. (2010) for mosses and Stace (2019) for vascular
200 plants.

201 CO₂ and CH₄ FLUX MEASUREMENTS
202

203 Sampling points were monitored during seventeen visits from June 2015 to June 2016 with
204 measurements taken between 1000 and 1600 hours. The closed chamber method (Alm et al., 2007;
205 Rowson et al., 2013; Goud et al., 2017) was used for surface exchange of CO₂ and CH₄. This method
206 involves circulating air between a transparent closed chamber and a gas analyser (Los Gatos Research
207 Greenhouse Gas Analyser Model 915-0011) which also measured ambient air temperature. The
208 chamber was fitted with a fan for headspace air mixing and a rubber seal was used to prevent the
209 exchange of gases between the chamber and the surrounding environment. Solar radiation was
210 measured using an Apogee Silicon Pyranometer (model SP-212-L).

211 We measured NEE and NER with GPP calculated from the difference (NEE – NER). NEE was measured
212 as the flux in light conditions and NER was measured by covering the chamber with a light
213 impermeable cover. Fluxes were monitored in real time which allowed measurements to be corrected
214 if equilibrium or a poor chamber seal was detected. Typically, light and dark measurements could be
215 taken in two minutes with a one-minute flush in between measurements until ambient concentrations
216 of CO₂ and CH₄ were reached. This study used the micro-meteorological sign convention which defines
217 a negative NEE as a C sink with positive NEE indicating a C source. Therefore, CO₂ taken in from the
218 atmosphere (via photosynthesis) is presented as a negative value, CO₂ emitted (via respiration) is
219 presented as a positive value. Gas fluxes were calculated and processed according to Dossa et al.
220 (2015), with slight modifications. Flux values were calculated based on the most linear change of CO₂
221 and CH₄ within the two-minute measurement period.

222 MODELLING ANNUAL CO₂ FLUXES

223 We modelled annual NER for each sampling point based on measured fluxes using the 2z + S model
224 (Rowson et al., 2013). When we did not have the data to parameterise the Rowson et al. (2013) model
225 (from June 2015 – September 2015 due to a delay installing the loggers), we adopted the widely used
226 Lloyd and Taylor (1994) model. The Lloyd and Taylor model accounted for twenty four percent of the

227 calculated annual NER budget whilst the Rowson model made up the largest proportion (~76%). The
228 Rowson et al (2013) model is an extension of the more widely used Lloyd and Taylor (1994) equation
229 based upon the Arrhenius relationship between soil temperature and measured NER. In addition, the
230 2z + S model links NER to plant function by accounting for the feedback between WTD, plant root
231 exudates, season (i.e. plant senescence) and respiration. Accounting for plant function in this way
232 improved the average R^2 from 0.66 to 0.79 (Figs. 3a and b) and reduced the standard error of the
233 estimate (SSE) from 0.01 to 0.006. Therefore, the model proposed by Rowson et al (2013) was deemed
234 more robust for modelling annual NER due to the better fit and lower error terms.

235 The parameters of the modelled NER (Rowson et al., 2013) derived for each sampling point were fitted
236 to temperature and WTD data, constants were identified using the generalised reduced gradient
237 (GRG2) nonlinear optimisation code (Lasdon et al., 1978), with 7 constants defined for each sampling
238 point. From each equation, the modelled values were plotted against the measured NER values. The
239 regression line for each sampling point had a relatively high coefficient of determination (range $R^2 =$
240 0.544 – 0.928). Having found no significant relationships between measured CO_2 flux and temperature
241 or solar irradiance, we modelled GPP based upon a second order (quadratic) polynomial relationship
242 with NER – a standard approach for modelling curvilinear regressions (Solkal and Rohlf, 2012). Solar
243 radiation data (MET office) was used to eliminate GPP fluxes in the absence of solar radiation.

244 MODELLING ANNUAL CH_4 FLUXES

245 The interpolation approach which linearly integrates fluxes between measurement periods (Green
246 and Baird, 2017) was adopted for CH_4 because, in contrast with other studies (e.g. Laine et al., 2007),
247 we found no significant relationships between measured CH_4 flux and soil/air temperature or WTD,
248 which eliminated the use of a modelling approach. We therefore calculated annual CH_4 flux based on
249 linear interpolation during the time periods between flux-chamber measurements (see Dise et al.,
250 1993). These values were then summed to predict the annual flux. GWP was calculated by converting
251 CH_4 fluxes to CO_2 equivalent emissions ($\text{CO}_2\text{-eq}$). For this, $\text{CO}_2\text{-eq}$ was determined by multiplying

252 annual CH₄ flux by a factor of 28, which is reported as the GWP of CH₄ over 100 years (Myhre et al.,
253 2013). The total gaseous C budget was calculated by summing the CH₄ CO₂-eq and CO₂ NEE values.

254 STATISTICAL ANALYSIS

255 Measured flux data (NER, GPP and NEE of CO₂ and CH₄) were compared between the three study areas
256 over the year. We used linear mixed models, fitted using restricted maximum likelihood (REML)
257 estimation of parameters, to analyse the effect of study area (restoration age), microtopography,
258 vegetation/cover and time of year on CO₂ fluxes (NEE, NER and GPP). Area, microtopography, and
259 time of year were included as categorical fixed factors, vegetation/cover was included as a random
260 factor and air temperature and WTD were included as covariates in all analyses. Solar radiation was
261 included for GPP and NEE.

262 For modelled flux data, one-way analysis of variance (ANOVA) was used to test for differences
263 between study areas, microtopography, collars and vegetation/cover. Differences between study
264 areas and vegetation/cover were analysed using Tukey post-hoc tests. The non-parametric Kruskal–
265 Wallis (KW) test was used for continuous data which did not satisfy the assumptions of normality and
266 homogeneity of variance after data transformation (as was the case for CH₄). All data were analysed
267 using statistical package IBM SPSS statistics (version 25).

268 **RESULTS**

269 270 SEASONAL TRENDS IN ENVIRONMENTAL VARIABLES

271
272 Water table depths for all three study areas showed variable seasonal patterns (Figs. 4a-c).
273 Restoration areas generally showed higher autumn/winter levels with high spring levels decreasing in
274 summer months. Water table position was closer to the peatland surface at the oldest restoration
275 area (RES 17YRS) compared with the unafforested area (OPEN). Temperature across all three study
276 areas followed a similar pattern (Fig. 4d) with a sharp decline in temperature in autumn 2015 and
277 gradually increasing from spring 2016.

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MEASURED GHG FLUXES

There was a clear annual cycle of CO₂ fluxes observed in all study areas and time of year was a significant factor in all CO₂ models, with significantly higher fluxes from June to October 2015. Linear mixed model analysis of net ecosystem CO₂ exchange showed that vegetation/cover, collar, time of year and microtopography were significant factors in CO₂ fluxes ($p = < 0.05$), but study area (restoration age) was not found to be a significant factor ($p = 0.945$) (Table 1). However, there was a significant interaction between study area and time of year which means patterns of uptake and release vary over the year between the three study areas. In all 3 study areas NEE of CO₂ was higher in hummock/ridge microtopography with lower water table and lower in furrows/hollows with high water table. NER of CO₂ followed a similar trend and was greater in hummock/ridge microtopography and was best explained by WTD and temperature. There was a significant interaction among study area and collar for NER of CO₂ which means that there is a significant factor within the collars which influences fluxes among the study areas and is perhaps a more important factor than restoration age.

In contrast with CO₂, CH₄ fluxes showed no clear annual cycle and time was not observed to be a significant factor ($\chi^2(16) = 4.656, p = 0.997$). Collar ($\chi^2(20) = 238.338, p < 0.001$) and microtopography ($\chi^2(1) = 85.40, p < 0.001$) were significant factors in CH₄ fluxes compared with study area ($\chi^2(2) = 5.227, p 0.073$), with highest emissions found in hollows/furrows with a high-water table and significantly lower fluxes observed from hummocks/ridges with a low water table. Vegetation/cover was observed to be the best predictor of CH₄ fluxes with higher fluxes observed from collars composed of *Eriophorum* species. Measured fluxes were not subject to further analyses and were used for modelling annual gaseous C budgets.

MODELLED GHG FLUXES & ANNUAL BUDGETS

305 The three study areas were net CO₂ sinks (Fig. 5a), with mean annual NEE of CO₂ ranging from -237 ±
306 153 g CO₂ m⁻² yr⁻¹ in the oldest restoration area to -154 ± 136 g CO₂ m⁻² yr⁻¹ in the youngest restoration
307 area. The oldest restoration area was a significantly stronger sink than the youngest restoration area
308 ($F_{2,195045} = 178.01, p < 0.001$) (Table 2), whilst no significant difference in NEE of CO₂ were found
309 between the youngest restoration area and the unafforested area ($p = 0.779$). Mean NER of CO₂ (Fig.
310 5b) was significantly greater in the unafforested area (857 ± 120 g CO₂ m⁻² yr⁻¹) than restoration areas
311 ($F_{2,195045} = 4778.67, p < 0.001$), lowest NER was found at the oldest restoration area (560 ± 102 g CO₂
312 m⁻² yr⁻¹). The unafforested area also had significantly greater GPP (-1015 ± 194 g CO₂ m⁻² yr⁻¹) than the
313 restoration areas ($F_{2,195045} = 659.74, p < 0.001$) (Fig. 5c).

314

315 In contrast with CO₂, all three study areas were CH₄ source (Fig. 5d), with mean emissions significantly
316 higher in the youngest restoration area (6.73 ± 3.27 g CH₄ m⁻² yr⁻¹) ($F_{2,195045} = 6318.75, p < 0.001$).
317 Lowest mean annual CH₄ emissions were found at the unafforested area (1.98 ± 0.55 g CH₄ m⁻² yr⁻¹).
318 When modelled annual CH₄ fluxes were converted to CO₂-eq, and included in the total gaseous C
319 budget, the unafforested and oldest restoration areas were C sinks (Fig. 5f), whereas the youngest
320 restoration area was an overall C source, estimated to be emitting on average 35 g C m⁻² yr⁻¹. Study
321 area, collar, microtopography and vegetation/cover were all significant factors on modelled fluxes
322 (NEE, NER and GPP of CO₂ and CH₄) (Table 2). Modelled CO₂ fluxes demonstrated that collars
323 distributed in hollows/furrows acted as a sink for atmospheric CO₂ whilst CH₄ emissions were
324 significantly greater in collars composed of *E. angustifolium* and bare peat in the youngest restoration
325 area.

326

327 VEGETATION CONTROLS

328

329 We categorised the mixed vegetation communities within each collar based on the dominant
330 vegetation/cover, these were: 1) *E. angustifolium* and bare peat/brash, 2) *Calluna vulgaris* and bare
331 peat/brash, 3) *Sphagnum* dominated, 4) *Sphagnum* and *E. vaginatum* dominated and 5) Ericaceous

332 shrubs and non-*Sphagnum* mosses (Table 3). We found vegetation significantly influenced all modelled
333 fluxes (Figs. 6a-d).

334

335 Our modelled results for NEE of CO₂ indicated that all vegetation groups were a net sink, the strongest
336 sink was the *Sphagnum* - *E. vaginatum* group sequestering -372 ± 214 g CO₂ m⁻² yr⁻¹. The mean NEE
337 flux of -0.04 g CO₂ m⁻² hr⁻¹ for the *Sphagnum* - *E. vaginatum* group was significantly greater than the
338 ericaceous shrub – non-*Sphagnum* moss group, which was estimated to sequester -0.013 g CO₂ m⁻² hr⁻¹
339 ¹ (Table 3). There were noticeable differences in fluxes between the groups that contained
340 aerenchymatous species, for instance, the mean NEE flux of CO₂ from *Sphagnum* - *E. vaginatum* was
341 significantly greater than *E. angustifolium* – bare peat/brash. NEE flux of CO₂ was significantly lower
342 in the *Sphagnum* dominated community than the ericaceous shrub – non-*Sphagnum* moss community
343 which showed the highest NEE flux of CO₂ to the atmosphere.

344

345 All vegetation communities were found to be a CH₄ source except for the bare peat/brash – *C. vulgaris*
346 community which was observed to be a negligible CH₄ sink (Table 3). The *E. angustifolium* – bare
347 peat/brash community showed the highest annual CH₄ emission (15.8 ± 1.84 g CH₄ m⁻² yr⁻¹) and was
348 significantly greater than the *Sphagnum* dominated community (0.96 ± 0.31 g CH₄ m⁻² yr⁻¹). The
349 calculation of CH₄ CO₂ equivalent clearly highlighted the vegetation controls on NEE CO₂eq, with *E.*
350 *angustifolium* – bare peat/brash becoming a relatively larger source of C in comparison with other
351 vegetation groups (Fig. 6f). This result had a noticeable influence on the calculation of the overall
352 annual C budget (CO₂ and CH₄ CO₂eq), all vegetation groups remained C sinks apart from the *E.*
353 *angustifolium* – bare peat/brash group which was estimated to emit on average 383 g C m⁻² yr⁻¹. The
354 *Sphagnum* - *E. vaginatum* group was the strongest sink sequestering on average -234 g C m⁻² yr⁻¹.

355

356

357 **DISCUSSION**

358 *DOES RESTORATION OF AFFORESTED PEATLANDS RESTORE THE CO₂ SINK FUNCTION?*

359

360 In the absence of longer time series data, we adopted a commonly used space-for-time substitution
361 approach (Pickett 1989; Walter et al., 2007) to compare early and more advanced stages of forest-to-
362 bog restoration. Our estimates of NEE of CO₂ suggests that forest-to-bog restoration is effective in
363 restoring the CO₂ sink function. Our findings show six- and seventeen-years post restoration, study
364 areas were functioning as net CO₂ sinks. We partially accepted our first hypothesis, although, did not
365 find the unafforested area to be a stronger sink compared with restoration areas.

366 These data add to the limited existing evidence base for UK peatland undergoing forest-to-bog
367 management and are the first such evidence for raised bog in the UK. In a study assessing the impacts
368 of forest-to-bog restoration in Northern Scotland, Hambley et al, (2019) found that restoration efforts
369 were successful in restoring the CO₂ sink function sixteen years post restoration, although, in contrast
370 with our findings, their youngest restoration area (10 years), was still a source, emitting 80 g CO₂ m⁻²
371 yr⁻¹. In comparison, our youngest restoration area (6 years) was estimated to sequester -154 g CO₂ m⁻²
372 yr⁻¹. A key difference was the technique employed in Hambley et al, (2019) study, specifically, the
373 sites had been “felled-to-waste” meaning that large amounts of brash remained on site and
374 contributed to the emission of CO₂. Further, differences in peatland types, i.e. raised versus blanket
375 bog and climatic condition at the time of the study may further explain the differences. After felling
376 of plantation forestry and re-wetting in Ireland, Rigney et al, (2018) found both blanket bog (8 years
377 after felling) and raised bog (3 years after felling) microsites were also CO₂ sources, suggesting
378 emissions were largely determined by plant community type, which varied along the water table
379 gradient.

380

381 We observed a strong positive correlation between GPP of CO₂ and soil respiration (Olajuyigbe et al.,
382 2012). Our results for GPP could suggest a potential legacy effect of previous conifer plantations and
383 forest-to-bog restoration practices on C fluxes, potentially altering the balance between autotrophic

384 and heterotrophic respiration (Olajuyigbe et al., 2012). For example, highly variable GPP estimates in
385 restoration areas could be explained by increased nutrient availability from initial fertilisation i.e.
386 phosphate and conifer felling/needle and brash decomposition (Gaffney et al., 2018). In other words,
387 higher nutrient availability in forest-to-bog restoration areas leads to increased plant growth and
388 production, and hence, higher rates of photosynthesis (e.g. Konings et al., 2019). Surprisingly, we
389 found NER of CO₂ significantly higher in open areas with no afforestation, with lowest NER of CO₂
390 observed in the oldest restoration area. Other large-scale studies on blanket bog have shown the
391 opposite, with annual NER of CO₂ lower in unafforested open sites compared to forest-to-bog
392 restoration sites (Hambley et al., 2019). Differences in NER could be explained by differences in WTD,
393 peatland type (i.e. blanket bog vs raised bog) and vegetation composition. For instance, lower NER at
394 the oldest restoration area is perhaps best explained by WTD which was closer to the surface
395 compared with the open areas. We found highest NER of CO₂ associated with ericaceous shrubs, which
396 were dominant at our reference (OPEN) areas. Whilst our 'OPEN' area has never been disturbed by
397 afforestation, it is worth noting that it is probably hydrologically degraded given the extent of the
398 surrounding disturbance.

399 Net Ecosystem Respiration is the second largest flux from terrestrial ecosystems, with rates expected
400 to increase with higher temperatures, potentially diminishing the CO₂ sink strength (Luo and Zhou,
401 2006). Importantly, we show improved accuracy in estimating NER flux by accounting for the feedback
402 between plant root exudates, season and NER, as well as temperature and WTD (Rowson et al., 2013).
403 The Lloyd and Taylor model (which made up twenty four percent of the calculated annual NER budget
404 reported here) tended to overestimate annual NER ($\sim 2400 \text{ CO}_2 \text{ g m}^{-2} \text{ yr}^{-1}$, (estimated from September
405 2015 – June 2016), compared with the Rowson et al, (2013) model. In this study, the main model
406 adopted to predict NER accounted for different NER production with varying peat depths, whilst also
407 accounting for season to prevent under-predicting NER over summer months and over-predicting NER
408 during winter months (Alm et al., 2007). We should state however that we cannot accurately say
409 whether our NER values are a product of decomposition of old peat and/or increased root respiration

410 and decomposition of fresh litter, because we did not distinguish between autotrophic and
411 heterotrophic respiration. A root trenching experiment carried out in forestry plantations on deep
412 peat has shown that newly created dead root biomass can contribute a significant proportion (~27%)
413 of the total soil CO₂ flux of forest plots in the first year of decomposition (Hermans, 2018), which could
414 be potentially contributing to the NER flux of CO₂ in the restoration areas in the present study.

415 Here we present an annual gaseous CO₂ budget (NEE, NER and GPP) of forest-to-bog restoration areas
416 and compare to unafforested conditions. It should be noted however that C can be released by other
417 pathways not measured in this study. For example, we did not quantify fluvial C fluxes: DOC,
418 particulate organic carbon, dissolved inorganic carbon and dissolved CO₂ (Worrall et al., 2009; Gaffney
419 et al., 2018; Payne and Jessop, 2018b). Quantification of fluvial C fluxes would be more appropriate at
420 the unafforested areas compared with restoration areas, where there are no obvious drains/water
421 flow due to the modified surface topography. Furthermore, we focused on the movement of two gases
422 CO₂ and CH₄, other GHG's e.g. nitrous oxide (N₂O) were not measured in this study. Whilst N₂O fluxes
423 can be substantial in peatlands (Couwenberg et al., 2011), other studies suggest N₂O emissions could
424 be smaller and less important than CO₂ and CH₄ in forest-to-bog restoration sites (Rigney et al., 2018,
425 Hermans et al., 2019). A further limitation of this study was that the collars had to be distributed within
426 proximity of each other due to the practicalities of using the equipment, for instance. it was not
427 possible to monitor twenty-one collars widely spread in a 6-hour time slot with travelling between
428 sites. It would also not be possible to have more areas with these restoration efforts because most of
429 the bog has been commercially extracted.

430 *THE INFLUENCE OF VEGETATION*

431
432 Our study indicated that vegetation was a stronger influence on all fluxes compared with time since
433 restoration. One possible explanation for this is that restoration of vegetation communities is unlikely
434 to be a linear process, and will vary spatially (Hancock et al., 2018). For instance, it has been reported
435 that forest-to-bog restoration may be more successful in the wetter furrows and stall in drier

436 microhabitats such as plough ridges and steeper slopes (Hancock et al., 2018). In this study comparison
437 of peatland vegetation groups showed that all vegetation groups were net sinks (CO₂ and CH₄ CO₂-eq),
438 except for vegetation composed of *Eriophorum angustifolium* on bare peat which was estimated to
439 emit $383 \pm 132 \text{ g C m}^{-2} \text{ yr}^{-1}$. This supports the idea that the relative proportion of the different plant
440 assemblages will have a strong influence on the net C emissions at the site scale (Gray et al., 2013).
441 Our findings of the influence of vegetation composition on fluxes in peatlands undergoing restoration
442 is reported in similar studies. For instance, Urbanová et al. (2012) conclude the C balance of pristine,
443 drained and bogs undergoing restoration had probably been determined by plant community type
444 which ultimately reflects long-term hydrology.

445

446 As we predicted, CH₄ emissions were significantly greater from the genus *Eriophorum* compared with
447 other vegetation groups, we therefore accepted our second hypothesis. Some studies have found CH₄
448 emissions increase post-restoration (Cooper et al., 2014), as a higher water table position results in
449 conditions conducive for enhanced methanogenesis and decreased CH₄ oxidation (Komulainen et al.,
450 1998). However, these effects are not always observed, and other studies have found no consistent
451 effect of drain blocking (Green et al., 2018) or forest-to-bog restoration (Hermans et al., 2019). Here,
452 we observed higher CH₄ emissions from *E. angustifolium* on bare peat compared with other mixed
453 vegetation communities including *Sphagnum* – *E. vaginatum* dominated community (Table 3). Frenzel
454 and Rudolf, (1998) show greater CH₄ emissions from tussocks of *E. vaginatum* compared with
455 *Sphagnum* lawns, suggesting that the lack of CH₄ oxidation associated with *Eriophorum* is one reason
456 for the high emission rate from peatlands. When these sedges dominate re-wetted peatlands, they
457 fuel methanogenesis by supplying labile C or suppress methanogenesis by transferring oxygen into the
458 rhizosphere through aerenchyma (Bubier 1995). The importance of plant-mediated CH₄ transport is a
459 well-known phenomenon in wetland plants (Bubier 1995; Frenzel and Rudolph, 1998).

460

461 At the plot scale, our results agree with previously published studies which show lower CH₄ emissions
462 from high hummocks with low water table and highest emissions in wetter areas with high sedge cover
463 (Kettunen et al., 2000; Couwenberg et al., 2011). In this study, we observed bare peat/brash – *C.*
464 *vulgaris* hummocks either not releasing CH₄ or functioning as small sinks, a similar trend was observed
465 in *Aulacomnium palustre* hummocks in the unafforested areas. Rigney et al, (2018) report hummock
466 vegetation types, for instance, *Cladonia-Calluna* hummocks acting as a strong sink for CO₂-C. In
467 accordance with these findings, Hartley et al (2015) report CH₄ uptake in drier ecosystems when
468 methanotrophic bacteria utilise CH₄ as their energy source and release CO₂. It is also worth noting the
469 known symbiotic relationship between *Sphagnum* and methanotrophs (Chen and Murrell, 2010). For
470 instance, in sampling points composed of *Sphagnum* there are more opportunities for methane
471 oxidation in the *Sphagnum* layer, in comparison with sampling points composed of non-*Sphagnum*
472 mosses and vascular plants.

473

474 Globally, one of the main goals of peatland restoration is to halt the C emissions associated with
475 degradation (Bonn et al., 2016). Ultimately, to return the C sink function means bringing back
476 conditions that lead to peat formation and for raised bogs, this involves encouraging the
477 establishment of peat-forming vegetation (Andersen et al., 2016). In contrast with other vegetation
478 groups studied, sampling points dominated by *Sphagnum* were shown to have relatively smaller effect
479 on fluxes (NEE, NER, GPP of CO₂ and CH₄). Mean NER of CO₂ from the *Sphagnum* dominated
480 community was low (Table 3), compared with vegetation composed of ericaceous shrubs and non-
481 *sphagnum* mosses. Therefore, our results agree with the suggestion made by Kivimäki et al (2008),
482 that reintroduction of *Sphagna* is recommended after the colonisation of vascular plants to speed up
483 the C sink function of peatlands under restoration. In terms of vascular plants, our findings agree with
484 other studies (Hancock et al., 2018), that *Eriophorum vaginatum* and *E. angustifolium* increase
485 markedly in forest-to-bog restoration areas, highlighting that *Eriophorum* taxa can promote peat
486 formation by reducing nutrient cycling and facilitating *Sphagnum* spread. Additionally, in order to

487 ensure *Sphagnum* survival in forest-to-bog restoration sites, it may be necessary to remove the
488 microtopographic differences i.e. plough ridges, in order to create a flat, moist surface conducive to
489 *Sphagnum* establishment and survival. In many blanket bogs impacted by afforestation, a technique
490 known as ground smoothing, where plough ridges are flattened, furrows are blocked and brash is
491 buried in the peat, is being trialled to achieve these conditions.

492

493 Numerous studies highlight the potential for vegetation to be used as a bioindicator (or proxy) for CO₂
494 and CH₄ fluxes in peatlands (Bubier 1995; Ward et al., 2009; Couwenberg et al., 2011; Urbanová et al.,
495 2012; Gray et al., 2013; Ward et al., 2013). Our results are partly consistent with Gray et al (2013),
496 who suggest that CO₂ uptake and turnover is greater for graminoids, however, our results do not fully
497 conform to the idea that the presence of dwarf-shrubs reduces C uptake and gross CO₂ fluxes. A
498 possible explanation for discrepancies in the literature could be because very few studies have
499 considered plant traits/functional groups and GHG fluxes in response to forest-to-bog restoration. In
500 a pilot study that aimed to begin to identify plant traits in sites undergoing forest-to-bog restoration,
501 Konings et al (2019) report that afforestation and restoration has led to greater specific leaf area and
502 chlorophyll content and lower leaf dry matter content. Recent research (Laine et al., 2019) also
503 suggests gas fluxes are not only primarily controlled by temperature and WTD, but also by leaf area.
504 Clearly, these relatively small yet significant changes in plant traits in forest-to-bog restoration sites
505 will have an impact on C fluxes and the overall C budget and require better understanding.

506

507 *IS TOTAL C SEQUESTRATION LOWER IN YOUNGER RESTORATION AREAS?*

508

509 Published studies reporting annual C budgets of forest-to-bog restoration sites in the UK have focused
510 on landscape-scale CO₂ emissions in blanket bog (e.g. Hambley et al., 2019; Lees et al., 2019), with
511 results suggesting the C balance of forest-to-bog restoration sites can be achieved between 5- and 10-
512 years post-restoration. However, these studies did not measure methane. Here we demonstrate the
513 importance of incorporating CH₄ measurements into annual estimates. In contrast to CO₂, CH₄

514 emissions were significantly greater in the youngest restoration area where *E. angustifolium* was
515 established in the wetter furrows. When methane fluxes were averaged for each study area, the
516 annual CH₄ flux in the youngest restoration area was almost a two-fold increase from CH₄ emissions
517 in the oldest restoration areas. Lowest CH₄ emissions were observed in areas not planted with trees.
518 Our interpolated CH₄ estimates were comparable to annual CH₄ emissions in other ombrotrophic
519 peatlands (see Dise et al., 1993; Laine et al., 2007). When these fluxes are expressed as CO₂-eq, the
520 oldest restoration area and unafforested area were a significantly stronger sink than the younger
521 restoration area as we had hypothesised.

522

523 The climate impact of peatlands has been the net result of reduced radiative forcing due to CO₂-C
524 uptake and storage as peat, and enhanced radiative forcing due to CH₄ emissions (Frolking and Roulet,
525 2007). Because the GWP of CH₄ for a 100-year time horizon is twenty-eight times greater than CO₂
526 (Myhre et al., 2013), increases in CH₄ emission from forest-to-bog restoration sites may offset
527 increased CO₂ sequestration. Our results here clearly demonstrate the GWP of forest-to-bog
528 restoration sites. Studies have shown that whilst CH₄ only represents a small (~1%) of the total C
529 emissions from peatlands undergoing restoration, in terms of GWP, CH₄ represented 14% of the total
530 CO₂ equivalent losses from the site (Waddington and Day, 2007). Our results are consistent with these
531 findings. It should also be noted however that peatlands are a natural source of CH₄ and can possibly
532 be a promising indication that key processes are returning. From a C management perspective, the
533 challenge is to design forest-to-bog restoration plans that do not create large hotspots of CH₄ (Cooper
534 et al., 2014), whilst also accepting that CH₄ emissions are inevitable. Importantly, novel restoration
535 techniques are currently being trialled across the UK for which there is little empirical evidence of
536 whether techniques promote *Sphagnum*. Clearly, if certain techniques promote the re-establishment
537 of *Sphagnum* whilst limiting the spread of *Eriophorum*, this might have more of a positive impact on
538 the C balance.

539 This study demonstrated that forest-to-bog restoration can be successful in restoring the GHG balance
540 over time. The advantage of the closed chamber approach used here is that it focuses on quantifying
541 the movement of different forms of carbon (i.e. CO₂ and CH₄) with differing greenhouse warming
542 potential, thus providing insights into the underlying mechanisms and complementing other
543 approaches such as stock-based approaches or eddy covariance (Payne et al., 2018; Hambley et al.,
544 2019). In terms of forest-to-bog restoration, future research should quantify flux measurements (such
545 as those reported here) from a range of sites and time periods, particularly targeting newer
546 restoration techniques that may result in different restoration trajectories. In doing so, this would
547 address the potential issue of pseudoreplication in the present study due to a shortage of forest-to-
548 bog restoration areas at our study site. Ideally, some sites should be established for long-term
549 monitoring such that space-for-time substitutions can eventually be replaced by time-series. We also
550 suggest that future work considers vegetation composition, plant traits and microtopography as an
551 integrator of processes controlling CO₂, and especially CH₄ emissions at forest-to-bog restoration sites.
552 Our findings support the suggestions reported by others (Gray et al., 2013; Urbanová et al, 2012;
553 Couwenberg et al., 2011), that robust predictive gas flux models can be derived from plant species
554 data, which can be used as indicators of a positive or negative C balance.

555
556 **CONCLUSION**

557
558 In this study, we predicted the annual gaseous C budget for forest-to-bog restoration areas and
559 compared to areas with no afforestation. From chamber-based CO₂ and CH₄ flux measurements, we
560 modelled NER and GPP, based on hydrological, temperature and light responses. We show that forest-
561 to-bog restoration can restore the C sink function, however, this is strongly dependent on vegetation
562 composition. In terms of vegetation most conducive to C sequestration, our findings suggest a ground
563 cover of *Sphagnum* with vascular plants could be most effective. Importantly, our results highlight the
564 necessity of incorporating vegetation composition as an integrator of processes controlling C fluxes in
565 forest-to-bog restoration sites. The development of models which predict fluxes based upon specific

566 vegetation (and/or plant traits) and representative vegetation communities would be extremely
567 useful for upscaling plot-scale measurements to landscape-scale.

568

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578

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