

1 **Carbon stability in a Scottish lowland raised bog: Legacy effects of historical land use**
2 **and implications for global change**

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Accepted refereed manuscript of: Schimmel H, Braun M, Subke J, Amelung W & Bol R (2021) Carbon stability in a Scottish lowland raised bog: potential legacy effects of historical land use and implications for global change. *Soil Biology and Biochemistry*, 154, Art. No.: 108124. <https://doi.org/10.1016/j.soilbio.2020.108124>
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27 **Abstract**

28 Peatlands comprise major global stocks of soil organic carbon (SOC). Many degraded
29 peatlands are currently being restored, but little is known to which degree former
30 disturbances leave a 'legacy' in such restored peatlands, and subsequently how this impacts
31 their response to global change. Our aims were to investigate if after 20 years of restoration
32 (i) carbon stability may still be affected by the former land use and if (ii) restored peatlands
33 are less susceptible to nutrient input but (iii) more sensitive to temperature. We sampled the
34 top- and subsoil of a formerly drained, a previously drained and afforested part and an
35 unmanaged control site of a Scottish bog. We incubated peat from each part for
36 determination of basal respiration, nutrient limitation and temperature sensitivity (Q_{10}) of
37 aerobic peat degradation. Lowest respiration rates were identified at the afforested site while
38 nutrient addition had no significant effect on topsoil organic matter decomposition at all sites.
39 Q_{10} values were significantly higher in the topsoil (2.6 ± 0.3 to 2.8 ± 0.2) than in the subsoil.
40 For the subsoil, the drained site (2.0 ± 0.0) showed significantly lower Q_{10} values than the
41 afforested one (2.6 ± 0.6), while the control site had a Q_{10} of 2.1 ± 0.0 , indicating contrasting
42 temperature sensitivities of potential SOC losses following specific forms of disturbance.
43 Overall, our data indicate that afforestation left a legacy on potential subsoil SOC losses with
44 global warming. Such effects must be considered when integrating restored bogs into global
45 data bases on peatlands' responses to global change.

46 **Key words:** peatlands, carbon dioxide, restoration, Q_{10} , incubation, nutrient limitation

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52 **1. Introduction**

53 The anthropogenic use of peatlands enhances the emissions of carbon dioxide (CO₂)
54 through drainage and aeration of the peat. The aeration of naturally water saturated
55 conditions leads to increased decomposition of soil organic matter (SOM) and greenhouse
56 gas emissions, mainly in form of CO₂. The conversion of pristine peatlands to arable and
57 forested land accounts for 80% of the loss of peatlands worldwide (Joosten and
58 Couwenberg, 2008). In Scotland, the majority of disturbed peat soils are affected by drainage
59 and agricultural purposes, 17% of the deep peat soils (defined as > 40-50 cm depth;
60 Vanguelova et al., 2018) are afforested while less than 10% of the lowland raised bogs are in
61 a near-natural state (Artz et al., 2012; Vanguelova et al., 2018). Changes in soil chemical
62 properties through aeration and litter input impact the soil carbon (C) cycle. Aerobic
63 conditions favour microbial activity and enhance decay and thus, drive C emissions.

64 Pristine peatlands act as C sinks and store large amounts of C through the incomplete
65 decomposition of organic matter. Generally, the C balance of peatlands is slightly positive
66 with methane as the main C source. Drainage and usage shift the main emissions towards
67 CO₂, resulting in a net negative C balance (Parish et al., 2008). In the past 30 years, the
68 rising awareness of the negative effects of peatland use has led to more frequent restoration
69 efforts in order to regenerate peatlands as long-term C stores. However, the long-term
70 success of this restoration work is still uncertain, especially if different land uses have left
71 legacies in carbon stability, nutrient limitations and temperature sensitivity.

72 Peatland restoration efforts may alter the quality, i.e. stability of soil organic carbon (SOC) in
73 peat. Rewetting leads to a major deceleration of decomposition but former aeration can have
74 reduced substrate quality by enhanced decomposition of SOM (Clymo, 1984; Drollinger et
75 al., 2020). Nevertheless, Heller and Zeitz (2012) found that aerated and degraded peat
76 contains less stable SOM than pristine peat. Restoration can return peat properties close to
77 the natural state (Hermans et al., 2019), but how long it takes and how it affects the carbon
78 stability is largely unknown so far.

79 Even though restoration work attempts to restore the original functions of peatlands, former
80 land use might have changed nutrient statuses in these ecosystems. As bogs are one major
81 type of peatlands, they are in contrast to minerotrophic fens only rain-fed and thus, poor in
82 nutrients. Changes in nutrient availability through land use are likely to have a particular
83 influence here, as decomposition in pristine bogs is primarily limited by water saturation, a
84 low pH and low nutrient concentrations (Chapin et al., 2003; Lafleur et al., 2005; Moore et al.,
85 2008; Updegraff et al., 1995). However, aerated conditions and litter input through drainage
86 and afforestation favour nitrogen (N) and phosphorus (P) mineralisation and hence, higher
87 nutrient concentrations (Sundström et al., 2000; Wells and Williams, 1996). Especially under
88 afforestation additional fertilization increases N and P availability (Anderson, 2001) which can
89 remain high even several years after restoration (Gaffney et al., 2018; Konings et al., 2019).
90 An increase in nutrient concentrations might result in intensified microbial activity (Vitousek et
91 al., 2010) and thus, in higher decomposition rates (Silvola et al., 1985). How far management
92 has offset potential nutrient limitations and whether there is a legacy despite of restoration is
93 still uncertain. Due to the high atmospheric N deposition in Central Scotland, it is of particular
94 importance to examine potential shifts in nutrient limitations and their impact on
95 decomposition in restored and intact bogs.

96 Besides nutrient input, restored bogs have to cope with climate change and rising
97 temperatures. A warmer climate might promote C loss from bogs as microbial activity
98 increases with temperature, resulting in an intensified decomposition of SOM (Gregorich et
99 al., 2017; Zimmermann et al., 2009). As one third of the global soil carbon pool is stored in
100 peat, (Gorham, 1991), their sensitivity to temperature rise is of particular importance
101 (Davidson and Janssens, 2006). Sensitivity of soil respiration to temperature rise is often
102 indicated by the Q_{10} value, which gives the increase in soil respiration at a temperature rise
103 of 10°C (Kirschbaum, 1995). Previous studies showed that more recalcitrant SOM is more
104 sensitive to temperature than labile SOM (Bol et al., 2003; Hardie et al., 2011).
105 Anthropogenic use of bogs through drainage promotes decomposition and peat degradation,
106 resulting in an enrichment of stable and recalcitrant SOM moieties (Drollinger et al., 2020;

107 Tfailly et al., 2014). Waddington et al. (2001) showed that strongly decomposed SOM in a
108 cutover bog had higher Q_{10} values than intact bogs. Yet, how restoration affects the
109 temperature sensitivity of formerly used bogs remains largely unknown.

110 Understanding how restored bogs react to increasing loads of nutrients and to temperature
111 rise is important in predicting its response to global change. To elucidate the resilience of
112 restored bogs to such processes, the potential decomposition of SOM can be estimated via
113 the measurement of CO_2 emissions (Smirnova et al., 2014). The aim of this study was to
114 elucidate how anthropogenic disturbances and afterward restoration impact on the carbon
115 stability of the peat, especially regarding their response to nutrient inputs and temperature
116 rise. In detail, we hypothesize that after 20 years of restoration, carbon stability in restored
117 bogs remain altered compared to undisturbed bogs and that restored bogs are still less
118 sensitive to nutrient input but more sensitive to temperature rise. To test these hypotheses,
119 we analysed peat from a near-natural and restored lowland raised bog which was partly
120 drained or drained and afforested before restoration as well as undisturbed parts of the bog
121 and incubated the samples under different nutrient supplies and temperatures under
122 controlled conditions in the lab.

123

124 **2. Materials and Methods**

125 **2.1. Site description**

126 Peat cores were collected at the Flanders Moss National Nature Reserve in the Central Belt
127 of Scotland. It is located 15 km west of Stirling (56.159°N, 4.200°W) in a temperate oceanic
128 climate with an average annual precipitation of 1131 mm a^{-1} (1961-1990) and a mean annual
129 temperature of 9.3°C. Flanders Moss is a lowland raised ombrotrophic bog with a current
130 size of 860 ha of which 550 ha are in a near-natural condition. In the mid-1970s, a part of the
131 bog was drained and planted with conifers. Another 100 ha of the bog were drained in the
132 early 1980s. Restoration work at Flanders Moss started 1997 by removing planted conifers

133 and by damming the ditches. The stumps at the afforested site were mulched to level the
134 surface. The restoration measures of afforested sites depend on site conditions (Payne et al.,
135 2018) and mulching is one possibility to deal with stumps during restoration work. Other
136 possibilities are stump flipping and leaving stumps completely in the peat (Artz et al., 2018;
137 Forest Research, 2009). Since then management intends to restore the original structure
138 mainly by controlling the water table.

139

140 2.2. Sampling

141 Samples were taken in the southeast of the bog and in two different historical land use
142 systems in November 2018. Historical land uses were *Drainage* (only drained without any
143 further usage) and *Forestry* (drained and afforested). Additionally, one *Control* site without
144 management was sampled (Figure 1). At each system we sampled three independent
145 replicates, which were around 20 m apart from each other and not affected by surrounding
146 management. At the formerly drained site, samples were taken between ditches and more
147 than 3 m apart from a ditch. The different land uses were around 300 m apart from each
148 other. The formerly afforested site borders the woody edge of the bog; to exclude boundary
149 effects we sampled around 100 m away from the edge. Water table height at the date of
150 sampling was very close to the surface at all three sites (< 5 cm). We used a Russian Peat
151 Corer and sampled a depth of 1 m. The Russian Peat Corer is a half-cylindrical sampler for
152 soft sediments and water saturated samples, which gives semi-disturbed samples without
153 sediment loss during sampling (Pitkänen et al., 2011).

154

155 [Figure 1]

156

157 Cores were divided into six sections (0-10, 10-20, 20-40, 40-60, 60-80 and 80-100 cm) for
158 basic soil biochemical analysis. The topsoil of all 9 sites was additionally sampled using a

159 border spate. Peat samples from 0 – 10 cm (“topsoil”) and 40 – 60 cm (“subsoil”) were used
160 for the incubation experiment. These depths were chosen to compare two depths which were
161 both affected by drainage (drainage depth 70-80 cm) but have a different degree of
162 decomposition. Samples were kept cool until their transport to the laboratory at the University
163 of Bonn. Samples for incubation were stored at 4°C for one month while all other samples for
164 C, N and P contents were frozen for four months to maintain the status quo.

165

166 2.3. Soil analyses

167 The C and N content was determined for all sampled depths. To do so, the frozen samples
168 were defrosted at 4°C. For determination of the water content, 10 g of wet peat was oven-
169 dried at 105°C; remaining samples were oven-dried at 40°C and milled. The C and N
170 contents were determined on milled samples using a CN analyser (Elementar Vario Micro
171 Tube, Germany). Based on sample weight, water content and C content of the samples, the
172 C stock for the first meter depth was calculated. We are aware that this procedure might be
173 biased as the soil core extraction can compact the peat and that a loss of water from the
174 samples makes a sample volume measurement difficult. The calculated C stock is therefore
175 only an estimation which is used to indicate differences between sites.

176 The following soil analyses were only carried out with the samples chosen for incubation (0-
177 10 cm and 40-60 cm). The determination of the maximum water holding capacity (WHC_{max})
178 and the actual peat moisture was performed mainly after Alef and Nannipieri (1995), modified
179 by using 10 g wet peat instead of 20 g due to the low bulk density. The pH value was
180 measured by adding 1M KCl to 10 g wet peat until 25 ml suspension was obtained. The
181 degree of humification was determined using von Post humification index. Values range from
182 1 to 10 with 1 indicating no humification and 10 indicating completely humified peat (Ad-hoc-
183 AG Boden, 2005). Total P content was determined via aqua regia extraction. Extracts were
184 measured using inductively coupled plasma optical emission spectrometry (ICP-OES Ultima
185 2, Horiba Scientific, Japan). All described soil analyses were carried out in duplicates.

186

187 2.4. Soil Respiration Measurements

188 All incubation studies were carried out using a respirometer (Respicond VIII, Nordgren
189 Innovations AB, Sweden). Respicond VIII continuously measures every 60 min the CO₂
190 released from up to 94 samples. The plastic vessels are cylindrically shaped and have a
191 volume of 250 ml. Closed vessels are placed in a water bath with a constant temperature
192 which is covered by lid, enabling an incubation in the dark. Through decreases of electrical
193 conductivity in the potassium hydroxide solution (KOH), which traps released CO₂, the
194 respirometer measures the CO₂ release per hour in each vessel (Nordgren, 1988), based on
195 the following equation:

$$196 \quad (1) \text{ CO}_2 = A * \frac{C_{t0} - C_{t1}}{C_{t0}}$$

197 where A is a conductivity constant that depends on the molarity of the KOH solution, C_{t0} is
198 the conductance of the fresh KOH measured at the beginning of the incubation time, and C_{t1}
199 is the conductance at time t. Every incubation run was carried out with at least four blanks of
200 empty vessels.

201

202 2.4.1. *Nutrient addition*

203 To assess the impact of nutrient input on SOM stability, we added N and P to topsoil
204 samples (0-10 cm) in an incubation experiment. We here chose topsoil as nutrient input will
205 enter the bog from the surface. An equivalent of 4 g dry peat was brought to 60 % of its
206 WHC_{max} as this is reported to be an optimal soil moisture for incubation studies of peat
207 (Wang et al., 2010) and recommended by ISO 17155 (2012), avoiding completely anaerobic
208 conditions. We decided on 4 g dry peat as some samples had very low bulk densities and
209 high WHC_{max}, so that the maximum filling height to avoid O₂ limiting conditions was reached
210 with 4 g dry peat. Living plants and living organic material like large roots were removed from
211 the peat in order to avoid autotrophic respiration (Glatzel et al., 2004) and samples were put

212 into plastic vessels. The peat was incubated at 20°C to provide optimal conditions for
213 degradation. The respective ISO 16072 (2002) guideline recommends an incubation
214 temperature of 20-25°C. Also, Creamer et al. (2014) reported that, independent of the
215 geographical origin, samples incubated at 20°C showed a constant response while samples
216 incubated at lower temperatures showed large variations. The samples had three days to
217 equilibrate before nutrients were added. There were four different treatments with each three
218 replicates per sample:

219 1. Control without nutrient addition (blank treatment),

220 2. Nitrogen addition (N treatment),

221 3. Phosphorus addition (P treatment),

222 4. Nitrogen and phosphorus addition (NP treatment).

223 NH_4NO_3 was chosen as N source and KH_2PO_4 as P source. The amount of added N was
224 based on the annual atmospheric N deposition in Flanders Moss, which is $11.67 \text{ kg N a}^{-1} \text{ ha}^{-1}$
225 (average 2012-2014; Centre for Ecology and Hydrology, 2019). We took the fivefold amount
226 and added $0.5002 \text{ mg N g dry peat}^{-1}$ to ensure non-limited conditions. For an estimation of P
227 addition, an N:P ratio of 15:1 in the topsoil was assumed (Güsewell, 2004; Olde Venterink et
228 al., 2003; Wang and Moore, 2014). Based on the added N and to achieve a N:P ratio of 15:1,
229 $0.0333 \text{ mg P g dry peat}^{-1}$ were added. Nutrients were dissolved in deionized water and
230 added with 0.5 ml solution each. For the blank treatment without nutrient addition the
231 samples received 0.5 ml of deionized water. Nutrients were added twice. The first addition
232 was after 3 days equilibrium time, the second addition was after 26 days. Peat was
233 homogenized with a spoon after adding nutrients to distribute the nutrients evenly in the peat.
234 In total, peat was incubated for 45 days. During the experiment, the KOH was changed when
235 the half of the capacity of the KOH to trap CO_2 was reached. One sample (*Forestry*, P
236 treatment) had to be excluded from the experiment after 10 days because KOH solution got
237 into the sample when changing the lye.

238

239 *2.4.2. Temperature Rise*

240 For determination of Q_{10} values we incubated peat from 0-10 cm and 40-60 cm depth. Again,
241 an equivalent of 4 g of dry peat was rewetted to 60 % of its WHC_{max} with deionized water and
242 homogenized with a spoon. All samples were incubated with four replicates each. Samples
243 were preincubated at 5°C for three days to stabilize respiration and to level the effects of
244 water addition (Blagodatsky et al., 2000; Meyer et al., 2018). Temperature steps were 5, 10,
245 15, 20 and 25°C. The temperature was held for 24 h each and KOH was changed every 24
246 h. The first 12 h after heating and changing KOH solution were equilibration time for the
247 microorganisms to adapt to new circumstances. The subsequent 12 h were used as a
248 medium respiration and used for the calculation as the average CO_2 release per hour (Meyer
249 et al., 2018).

250

251 2.5. Data Analysis

252 The calculation of Q_{10} values was performed in R (version 4.0.3). The average soil
253 respiration per hour from the four vessels was used as the medium respiration rates for
254 further calculations. To calculate the relationship between soil respiration and temperature,
255 an exponential function was used. The equation (2) fits the soil respiration over the whole
256 temperature range, where SR_T is the soil respiration at a certain temperature, a and b are
257 fitted parameters and T is temperature:

$$258 \quad (2) \quad SR_T = a \times \exp^{b \times T}$$

259 By inserting b into the equation (3), the Q_{10} value is calculated as:

$$260 \quad (3) \quad Q_{10} = \exp^{10 \times b} \text{ (Meyer et al., 2018)}$$

261 Statistical analyses were performed in SigmaPlot (version 13.0). Normal distribution of the
262 data was tested using Shapiro-Wilk test, P value to reject normality was 0.05. Equal variance

263 was tested using Brown-Forsythe-Test, with a P value to reject of 0.05. When data did not
264 meet assumptions for normal distribution, data were log-transformed. Normally distributed
265 data with three groups were tested for significance with a one-way ANOVA. Samples which
266 were spatially dependent of each other were tested for significant differences with a
267 Repeated Measures ANOVA. To determine the influence of former land use and nutrients on
268 respiration rates, a two-way ANOVA was performed with normally distributed data. ANOVA
269 was followed by Holm-Sidak's post-hoc test. When comparing Q_{10} values of top- and subsoil
270 for significant differences, a paired t-test was conducted for normally distributed data.
271 Differences were considered significant for $p < 0.05$.

272

273 **3. Results**

274 **3.1. Peat characteristics**

275 Contents of total organic carbon (C_{org}) varied between 452.2 and 514.0 g kg⁻¹ soil and did not
276 differ significantly between sites (Appendix Table A.1). The control and the drained site
277 showed significantly higher C_{org} contents in subsoil layers than in the topsoil ($p < 0.05$) while
278 there were no significant differences between depths at the afforested site ($p > 0.05$). Total N
279 (N_{tot}) contents at the drained and afforested site were significantly higher in the topsoil than in
280 the subsoil ($p < 0.05$) while there were no significant differences between depths at the
281 control site. In 60-80 cm and 80-100 cm depth, the N_{tot} contents of both restored sites were
282 significantly lower than at the control site ($p < 0.05$). The C:N ratios ranged from 33.2 to 75.2
283 and increased with depth at the two restored sites ($p < 0.05$). Bulk densities varied between
284 0.04 g cm⁻³ and 0.21 g cm⁻³ and significantly decreased with depth at all three sites ($p < 0.05$)
285 but were not significantly different between sites. The upper 0-10 cm of the formerly
286 afforested site tended to have the highest values for the bulk density and for the C stock
287 (Appendix Table A.1).

288

314 Table 1: Mean accumulated mg CO₂ g dry peat⁻¹ after nutrient addition with standard deviation [n=3]. Nutrient
 315 treatments are coded as followed: Blank = no nutrient addition, N = Nitrogen addition, P = Phosphorus addition,
 316 NP = Nitrogen and phosphorus addition. Significant differences ($p < 0.05$) between sites are indicated by lower
 317 case letter (^a, ^b).

Treatment	Control	Drainage	Forestry
Blank	39.95 ± 28.3 ^a	34.32 ± 9.1 ^a	18.60 ± 5.5 ^b
N	33.78 ± 17.3 ^a	32.72 ± 15.4 ^a	12.20 ± 5.6 ^b
P	39.06 ± 24.3 ^a	40.85 ± 14.5 ^a	21.28 ± 7.2 ^b
NP	45.64 ± 33.9 ^a	32.92 ± 14.3 ^a	13.83 ± 4.2 ^b

318

319

320

321 3.4. Temperature dependence of carbon mineralization

322 In the topsoil, the aerobic CO₂ production was highest at the control site, increasing from
 323 11.9 ± 7.7 µg CO₂ g⁻¹ h⁻¹ at 5°C to 93.7 ± 45.7 µg CO₂ g⁻¹ h⁻¹ at 25°C, while the drained and
 324 the afforested site had lower respiration rates. The afforested site showed a higher
 325 temperature sensitivity with a Q₁₀ value of 2.8, however with no significant difference in Q₁₀
 326 with the other two sites ($p > 0.05$; Figure 3).

327

328 [Figure 3]

329

330 In the subsoil, respiration rates were significantly lower than in the topsoil ($p < 0.05$) by a
 331 factor of 3 to 10. Again, the control site had the highest CO₂ production, ranging from 3.6 ±
 332 0.6 µg CO₂ g⁻¹ h⁻¹ at 5°C to 21.8 ± 3.4 µg CO₂ g⁻¹ h⁻¹ at 25°C (Figure 3). Q₁₀ values of the
 333 control site showed no significant differences to both restored sites ($p < 0.05$), but the

334 drained site had significant lower values than the afforested site ($p < 0.05$). Generally, Q_{10}
335 values in the subsoil were significantly lower than in the topsoil ($p < 0.05$).

336

337 **4. Discussion**

338 4.1. Restoration effects on SOM decomposition

339 Anthropogenic use alters bog systems by aeration of the peat, resulting in an enhancement
340 of decomposition (Leifeld et al., 2012). Therefore, we assumed that drainage and
341 afforestation have changed SOM chemical properties and thus decomposition rates in
342 restored bogs compared to intact bogs. In both incubation experiments the afforested site
343 had the lowest respiration rates across all treatments, contrasting with higher CO_2 efflux at
344 the intact and the drained sites (Figure 2 and Table 1). Scanlon and Moore (2000) showed
345 that the degree of decomposition is the most important factor controlling CO_2 production.
346 Thus, the lower respiration rates at the afforested site might be caused by enhanced
347 decomposition under forest management in the past, leaving behind lower substrate quality
348 and elevated SOM recalcitrance (Bader et al., 2018; Wüst-Galley et al., 2016). Particularly,
349 young and labile SOM have presumably been lost in the course of management, thus
350 exposing more decomposed and recalcitrant peat at the surface (Leifeld et al., 2012). The
351 assumption of more decomposed topsoil peat at the restored sites is supported by the
352 relative enrichment of N and lower C:N ratio in the topsoil of the drained and the afforested
353 site, as generally a narrower C:N ratio indicates increased microbial activity and
354 mineralization (Krüger et al., 2015). Therefore, it can be assumed that the SOM of the
355 restored sites was more decomposed, presumably through aeration during management
356 (Bader et al., 2018). Also, the von Post humification index supports the theory that especially
357 afforestation has enhanced decomposition as the afforested site had the highest humification
358 values (Appendix Table A.2). In summary, past anthropogenic disturbance has likely
359 increased peat mineralisation and caused a lowered substrate quality, which renders the

360 current SOM more stable to decomposition than the fresh, undisturbed peat of the control
361 plots. This increased carbon stability may have also applied for the drained site, which was
362 not the case. There, differences in C stability could not be detected after 20 years of
363 restoration. Hence, we have to at least partly refute our initial hypothesis that usage of peat
364 still affects decomposition of restored bogs and thus assume additional effects from, e.g.,
365 altered litter quality and restoration practices.

366 There are several kinds of anthropogenic use of bog, which will presumably also influence
367 the effects and success of restoration. At Flanders Moss, sections of the bog were drained,
368 and some drained sections further afforested. Here, we observed a significant difference in
369 the respiration rates of both restored sites (Table 1). Under afforestation, there is additional
370 litter input from highly resistant wood-derived and lignin-rich material (Hermans et al., 2019;
371 Minkinen et al., 2008). Additionally, for restoration, roots and stumps were mulched and
372 mixed with surrounding peat and left in the peat body. These residues are more resistant to
373 decomposers and need higher activation energy for decomposition than labile organic
374 compounds (Kleber, 2010). In contrast to our results, Hermans et al. (2019) found no
375 differences in CO₂ production between shallow cores from restored forest-to-bog plots and
376 pristine bog plots, but higher a CO₂ efflux from an afforested bog. It indicates that restoration
377 has levelled the influence of former forest plantation regarding decomposition and CO₂
378 production. There, trees were felled and left in furrows but the peat was not mixed with the
379 stumps. Thus, at Flanders Moss we suspect that the impacts of the forest litter, and
380 particularly of the mulched stumps in the peat, contribute to the lower respiration rates of the
381 formerly afforested bog relative to intact or drained peat soils. Consequently, for the
382 afforested site we can confirm our hypothesis, i.e. that here the former usage changed
383 decomposition and even more than 20 years of restoration could not yet diminish these
384 effects. We conclude, that the legacy effect on SOM decomposition in bogs is mainly
385 dependent on the type of former usage.

386

387 4.2. Stability of SOM against increasing nutrient inputs in restored bogs

388 Bogs are naturally nutrient-poor ecosystems (Finlayson and Milton, 2016; Updegraff et al.,
389 1995) but anthropogenic disturbance and enhanced mineralization can increase nutrient
390 concentrations (Devito and Dillon, 1993; Gaffney et al., 2018). Therefore, it was suggested
391 that nutrient limitations might have been offset by past anthropogenic use and that
392 consequently, the intact site might show a higher susceptibility to nutrients than the restored
393 sites. In this study, however, the nutrient additions did not lead to significant changes in
394 respiration rates in either intact or restored sites. We observed that the mean values of all
395 three sites indicated slightly decreased respiration after N addition, which cannot be
396 statistically proven. Yet, this finding is consistent with literature evidences as a decrease in
397 respiration after N addition was also observed for forest litter and soils as well as for peat
398 soils (Aerts and Toet, 1997; Bowden et al., 2004; Mo et al., 2006), while also the opposite, an
399 increase in peat decomposition under higher N supply, has been reported (Bragazza et al.,
400 2006). According to the “microbial nitrogen mining” theory, decomposition might decline
401 when N is sufficiently available (Craine et al., 2007), because microorganisms do not need to
402 decompose recalcitrant material to access additional N sources. In this regard, the observed
403 but statistically not significant decreased respiration after N addition supports the microbial N
404 mining theory in that former N loads now provide a legacy in a way that increased
405 atmospheric N deposition reduces the need for N mining and therewith “stabilizes” OM
406 against rapid microbial mineralization.

407 High atmospheric N deposition in bogs dilutes P concentrations so that potentially shifts to P-
408 limitation can occur (Larmola et al., 2013). A shift from N- and P-co-limitation to P-limitation
409 was already observed in Central Europe and Eastern Canada, where atmospheric N
410 deposition negates N-limitation in bogs (Wang and Moore, 2014). Generally, our samples
411 showed large C:N:P ratios, which are based on data being affected by a high heterogeneity
412 in nutrient contents between samples (Appendix Table A.1 and Table A.2). This variation
413 might be caused by different predominant vegetation types during peat formation (Zhang et

414 al., 2017). Nevertheless, all samples show low P contents and large C:P ratios, thus, a P-
415 deficiency can be expected (Wang et al., 2014). The high N:P ratios of the incubated
416 samples confirm P-limited conditions, which occur at N:P ratios >20:1 (Güsewell, 2004;
417 Wang and Moore, 2014). Thus, we had expected an increase in respiration after P addition
418 (Wright and Reddy, 2007). However, the P addition had no significant effect on neither the
419 respiration rates of the intact nor of the restored sites compared to the blank treatment.
420 Consequently, these potential P-limited conditions are more reflected in P contents and
421 C:N:P ratios than in respiration rates upon P addition. We assume that all three sites are P-
422 limited regardless of their former land use, but that other factors like water saturation and
423 resulting anaerobic conditions influence decomposition more than this P-limitation.

424 The key factor that controls decomposition in peatlands is water saturation (Moore and
425 Knowles, 1989; Scanlon and Moore, 2000). Generally, O₂ availability is the main factor
426 determining CO₂ production (Fenner and Freeman, 2011; Philben et al., 2015). This
427 assumption is confirmed by the fact that several samples showed peaks in respiration after
428 venting the vessels, which indicate primarily O₂ limitation on decomposition in bog peat
429 (Appendix Figure B.1; values directly after venting the vessels are excluded from calculation
430 of respiration rates). Yet, these observations indicate that the height of the water table in the
431 analysed bog is more important for decomposition and CO₂ evolution than nutrient limitation.
432 This primary limitation in oxygen is likely to outweigh the secondary limitation in nutrients, as
433 the observed weak response to the added nutrients implies that decomposition is not
434 primarily nutrient-limited, because the microbial community of bogs might already be adapted
435 to nutrient-limited conditions (Hoyos-Santillan et al., 2018). As this seems to apply for the
436 intact as well as for the restored sites, we have to refute our stated hypothesis, that the intact
437 site shows a higher susceptibility to nutrient input. Future lab studies in this regard should
438 thus be performed under variable water levels.

439

4.3. Stability of SOM against temperature rise of restored bogs

440
441 To estimate potential feedback effects to climate change on the C balance of the restored
442 bogs we determined the temperature sensitivity of SOM decomposition. The carbon quality
443 temperature (CQT) hypothesis states that older and recalcitrant SOM is more sensitive to
444 temperature than younger SOM moieties (Bosatta and Ågren, 1999; Davidson and Janssens,
445 2006). However, beside age, SOM quality also depends on land use (Kögel-Knabner and
446 Amelung, 2014). Particularly drainage and afforestation can change SOM chemical
447 properties and enhance decomposition (Wüst-Galley et al., 2016), making the remaining OM
448 potentially more sensitive to temperature (Conant et al., 2008). This is in concordance with
449 our findings, as the formerly afforested site had Q_{10} values similar to values found in cutover
450 bogs (Waddington et al., 2001), which were in the subsoil significantly higher than those
451 found at the formerly drained site. The higher temperature sensitivity can be attributed to the
452 input and preservation of chemically recalcitrant litter in course of afforestation, resulting in
453 low substrate quality and highest C stability. Hence, drainage alone has left no legacy in
454 temperature sensitivity, while afforestation has stabilized both top- and subsoil against rapid
455 decomposition but in agreement with the CQT hypotheses it has also made the site more
456 sensitive to temperature rise, a legacy effect of former land use that remains detectable 20
457 years after restoration.

458 As temperature sensitivity is affected by SOM quality, it is also a function of soil depth. In
459 peatlands, SOM quality decreases with depth (Byrne and Farrell, 1997) and according to the
460 CQT theory, Q_{10} values and hence temperature sensitivity should increase with depth
461 (Hardie et al., 2011; Hiltunen et al., 2013; Waddington et al., 2001). However, this was not
462 confirmed in our study: the Q_{10} values of Flanders Moss were larger for the topsoil than for
463 the subsoil, both for the intact part of the bog and the restored sites. Boone et al. (1998)
464 found that soil Q_{10} was higher when roots were included in the measurement. The topsoil
465 peat in this study was slightly decomposed; yet, fine roots likely remained in the peat and
466 could thus have contributed to the higher Q_{10} values of topsoil.

467 There are other studies that did not find a depth and age dependency in temperature
468 sensitivity of SOM (Conen et al., 2006; Wang et al., 2010), and some studies even found a
469 higher temperature sensitivity of younger SOM (Bader et al., 2018; Christensen et al., 1999).
470 Bader et al. (2018) assigned higher Q_{10} values to intensive land use and remaining highly
471 decomposed topsoil peat after management. As discussed above, especially the afforested
472 site was disturbed intensively for afforestation and restoration but nevertheless, according to
473 the von Post humification index, the subsoil was more decomposed in all three sites than the
474 topsoil peat (Appendix Table A.2). Likely, the temperature sensitivity did not solely depend
475 on depth and quality of SOM but also on further factors like O_2 availability and nutrient status
476 (Davidson et al., 2006; Sihi et al., 2016; Szafranek-Nakonieczna and Stępniewska, 2014).

477

478 **5. Conclusion**

479 Anthropogenically modified peatlands are widely rewetted to restore their carbon sink
480 function and their natural resilience to environmental changes. The aim of this study was to
481 assess the effects of restoration in a Scottish bog that had been drained and partly further
482 afforested. We have to refute our initial hypothesis that both restored bogs showed a legacy
483 of former land use in carbon stability, nutrient limitations and temperature sensitivity
484 compared to intact bogs. Instead, the type of former land use and presumably the type of
485 restoration mainly determined the success of restoration. Whereby, SOM of the formerly
486 drained and afforested site was likely of lower quality and more stable against decomposition
487 but it was also more sensitive to temperature rise than in the intact and formerly drained bog.
488 More research is still needed to see how different restoration measures affect the restoration
489 of bogs and also to scale the findings for different levels of oxygen availability.

490

491 **Acknowledgement**

492 This project was funded by Geoverbund ABC/J. We also thank Scottish Natural Heritage for
493 enabling the sampling at Flanders Moss National Nature Reserve.

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Figure 1: Aerial photo of Flanders Moss National Nature Reserve with the three different sampling sites marked with different colours, indicating the former land uses (blue = control site; red = drained site; green = drained and afforested site) (Esri ArcMap 10.3.1).

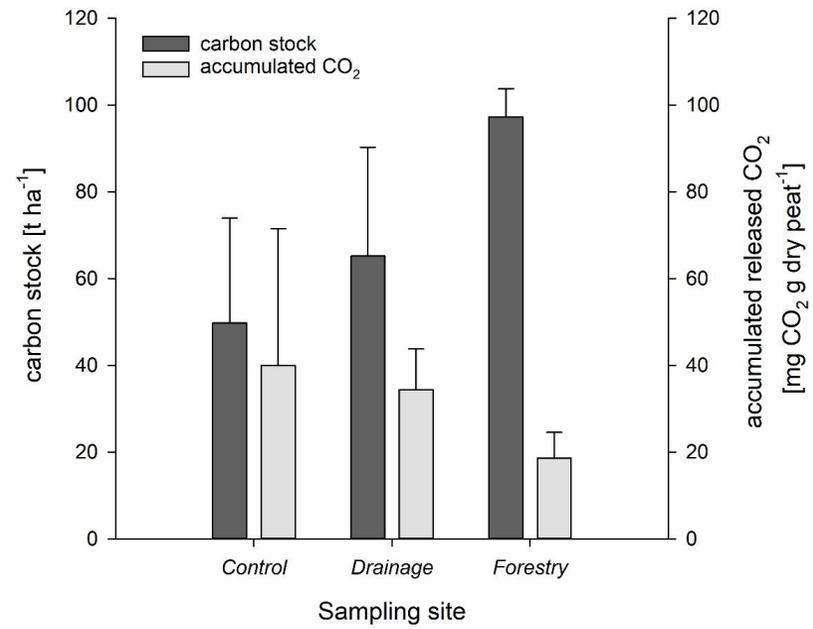


Figure 2: Comparison of the mean carbon stock [$n=3$] and mean accumulated basal respiration of the topsoil (0-10 cm) [$n=3$] with standard deviation.

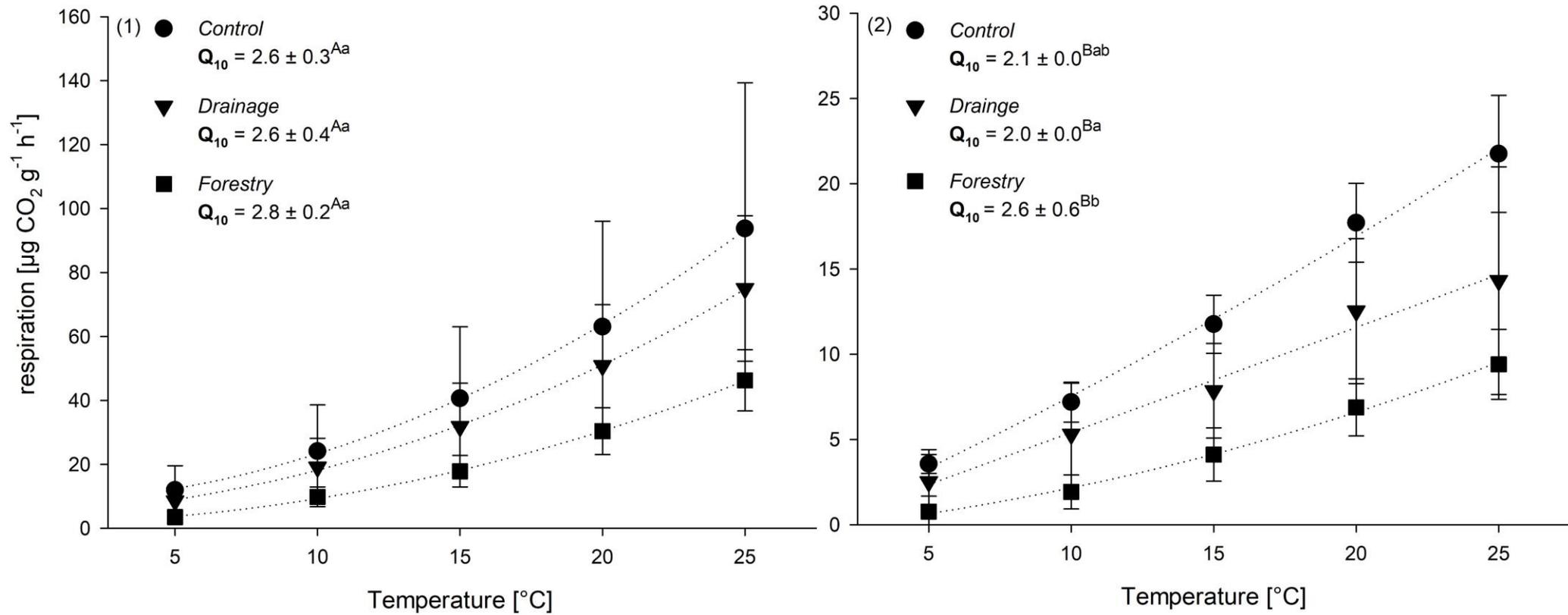


Figure 3: Mean hourly respiration per gram dry peat with increasing temperature of (1) the topsoil (0-10 cm) and (2) the subsoil (40-60 cm) with standard deviation and Q_{10} values (note the differences in y-axis scale). Significant differences ($p < 0.05$) in Q_{10} values between top- and subsoil are indicated by capital letter (A , B) and between sites within one depth are indicated by lower case letters (a , b).

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