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1 Title: Interactive biotic and abiotic regulators of soil carbon cycling: evidence from  
2 controlled climate experiments on peatland and boreal soils

3 Running head: Biotic and abiotic interactions and C cycling

4  
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28

29 **Abstract**

30 Partially decomposed plant and animal remains have been accumulating in organic soils  
31 (i.e. >40% C content) for millennia, making them the largest terrestrial carbon store. There  
32 is growing concern that, in a warming world, soil biotic processing will accelerate and  
33 release greenhouse gases that further exacerbate climate change. However, the magnitude  
34 of this response remains uncertain as the constraints are abiotic, biotic and interactive.  
35 Here, we examined the influence of resource quality and biological activity on the  
36 temperature sensitivity of soil respiration under different soil moisture regimes. Organic  
37 soils were sampled from 13 boreal and peatland ecosystems located in the UK, Spain,  
38 Finland and Sweden, representing a natural resource quality range of C, N and P. They  
39 were incubated at 4 temperatures (4, 10, 15 and 20°C) at either 60% or 100% water holding  
40 capacity (WHC). Our results showed that chemical and biological properties play an  
41 important role in determining soil respiration responses to temperature and moisture  
42 changes. High soil C:P and C:N ratios were symptomatic of slow C turnover and long-term  
43 C accumulation. In boreal soils, low bacterial to fungal ratios were related to greater  
44 temperature sensitivity of respiration, which was amplified in drier conditions. This  
45 contrasted with peatland soils which were dominated by bacterial communities and  
46 enchytraeid grazing, resulting in a more rapid C turnover under warmer and wetter  
47 conditions. The unexpected acceleration of C mineralization under high moisture contents  
48 was possibly linked to the primarily role of fermented organic matter, instead of oxygen, in  
49 mediating microbial decomposition. We conclude that in order to improve C model  
50 simulations of soil respiration a better resolution of the interactions occurring between  
51 climate, resource quality and the decomposer community will be required.

52

53

54 **Introduction**

55 Northern peatland and boreal soils have been accumulating carbon for centuries (Limpens  
56 *et al.*, 2008). This retention capacity is the result of poor mineralisation rates due to the  
57 severe restrictions that cold and often wet climatic conditions impose on biotic activity.  
58 Global warming has, therefore, the potential to accelerate chemical transformations  
59 mediated by soil biota and to alter their C sink function. For example, observed increases  
60 in equinox temperatures in boreal forests over the last two decades show a trend towards  
61 an earlier autumn-to-winter carbon dioxide build-up, being associated to a greater increase  
62 of soil respiration over photosynthesis and offsetting the gains derived from earlier spring  
63 sequestration (Piao *et al.*, 2008). Similarly, rising temperatures have seen to alter bacterial  
64 and methanogen community structure and their relative ratios in peatlands, resulting in  
65 imbalance of CO<sub>2</sub> and CH<sub>4</sub> emissions (Kim *et al.*, 2012). In addition to C gas emissions,  
66 increased C losses, in the form of dissolved organic C, have been observed from peat soils  
67 (Freeman *et al.*, 2001a), which has been attributed to impaired microbial degradation  
68 coupled with increased plant inputs associated with global warming (Fenner *et al.*, 2007).

69 Besides climatic factors, spatial heterogeneity also plays an important role in  
70 determining the stability of soil organic matter (SOM), making the use of a single  
71 “average” Q<sub>10</sub> value an inaccurate approximation of the predictions of soil feedbacks to the  
72 climate system (Fierer *et al.*, 2006). This factor has not yet been taken into full  
73 consideration in many carbon-coupled Global Climate Models (GCMs) where a globally  
74 invariant Q<sub>10</sub> has been applied (e.g. Jones *et al.*, 2005). Indeed, the use of a variant Q<sub>10</sub>  
75 could amplify predicted soil respiration feedback to climate change by 25% (Zhou *et al.*,  
76 2009). This is particularly important for organic soils, including peats, with reported Q<sub>10</sub>'s  
77 that often exceed the global averaged model Q<sub>10</sub> of 2 (Chapman & Thurlow, 1998).  
78 Evidence from laboratory studies (Fierer *et al.*, 2006; Conant *et al.*, 2008) that confirm the

79 kinetic theory (Bosatta & Ågren, 1999), suggest that the temperature sensitivity of SOM  
80 decomposition is related to soil resource quality (such as nitrogen and lignin contents of  
81 plant residues; Melillo *et al.*, 1982). Moreover, there is growing evidence that variations in  
82 organic matter quality, including stoichiometric ratios of major elements (C, N and P), also  
83 act as important determinants of decomposition rates (Wardle *et al.*, 2004; Cleveland &  
84 Liptzin, 2007). Finally, it is expected that respiratory carbon losses from these C-rich  
85 systems will be exacerbated under drier and reduced water table conditions, which are  
86 predicted to occur under climate change (Jungkunst & Fiedler, 2007, Ise *et al.*, 2008).  
87 Therefore, accurately quantifying the respiratory  $Q_{10}$  value of organic soils, and its  
88 variability with resource quality and moisture, is critical for predicting the temperature  
89 sensitivity of soil carbon cycling.

90 Soil respiration is mediated by the soil biological community and therefore, a recurrent  
91 aspect highlighted in recent review studies is that there is not enough experimental  
92 information on the interactive effects between biological systems and atmospheric  
93 variables to predict how ecosystems will respond to global change (see overview by Long  
94 & Shekar, 2013). Early efforts have been made to incorporate soil microorganisms into  
95 carbon models (e.g. Moorhead & Sinsabaugh, 2006; Lawrence *et al.*, 2009); however, the  
96 challenge remains to include parameters of microbial function, diversity and evolution  
97 (Todd-Brown *et al.*, 2012). In relation to this, Amelung *et al.* (2008) emphasised the  
98 importance of microbial feeding niches, with fungi feeding on fresh plant material and  
99 gram-positive bacteria consuming both fresh and older SOM to accurately determine C  
100 stability. Consequently, it has been suggested that incorporation of microbial functional  
101 types into models will be needed to improve our predictions of the SOM response to global  
102 warming (see review by Schmidt *et al.*, 2011).

103 Similarly, despite a number of attempts to include soil invertebrates in C models (e.g.  
104 Osler & Sommerkorn, 2007; Wall *et al.*, 2008; Briones *et al.*, 2010), they are not well  
105 represented in GCM predictions. Different soil fauna groups are known to affect C and N  
106 pools by grazing on microbial communities (e.g. nematodes, enchytraeids and  
107 microarthropods) and by tunnelling and forming soil aggregates (enchytraeids and  
108 earthworms). This, in turn, has been shown to contribute to changes in soil N  
109 mineralisation (Osler & Sommerkorn, 2007), C cycling (Briones *et al.*, 2010) and litter  
110 chemistry during decomposition (Wickings *et al.*, 2012). An important reason for their  
111 exclusion has been associated with the difficulties in manipulating invertebrate animals  
112 experimentally across large geographic gradients (Wall *et al.*, 2008).

113 In this study, we investigated the impact of resource quality and biological communities  
114 on the temperature sensitivity of organic soil respiration under wet and dry moisture  
115 regimes. This was achieved in a controlled mesocosm incubation experiment with 13 soils  
116 from northern peatland and boreal ecosystems, representing a natural range of C, N and P  
117 at 4 temperatures (4, 10, 15 and 20°C) and two moisture regimes (60% or 100% WHC).  
118 Soil and biological properties and respiration rates were determined at two different time  
119 intervals to examine the importance of organic matter resource, microbial structure and  
120 mesofaunal abundance (enchytraeids) as predictors of long-term carbon turnover and short-  
121 term temperature sensitivity of soil decomposition processes (expressed as  $Q_{10}$ ).

122

## 123 **Materials and methods**

### 124 *Soils*

125 Intact soil cores (10 cm depth, 6.3 cm ID) were collected between June 2005 and February  
126 2006 from eight European peatlands and one Finish Boreal forest site, with further sets of  
127 soils obtained from five Swedish Boreal forested islands in July 2007.

128 The five UK peatlands were: (i) Moor House bog-MHB and Great Dun Fell-GDF, both  
129 included in the Moor House Nature Reserve (England), (ii) Plynlimon-PLYN (Wales), (iii)  
130 Auchencorth Moss-AUCH (Scotland) and (iv) Caithness-CAITH in the Forsinard Reserve  
131 (also in Scotland) and all had similar vegetation being *Sphagnum* spp., *Eriophorum* spp.,  
132 *Calluna vulgaris*. We also sampled a lowland raised bog with a soak system from Clara  
133 Bog in Ireland (IRE) and a “relic” peatland from Sierra do Xistral in NW Spain (SPA) with  
134 characteristic vegetation being *Eriophorum angustifolium*, *Carex durieui*, *Carex echinata*,  
135 *Molinia caerulea*, *Erica mackaiana* and *Calluna vulgaris*.

136 The six boreal forests were located in Finland and Sweden: the Finnish site (FIN) was  
137 dominated by hairy birch (*Betula pubescens*) and European spruce (*Picea abies*) with a  
138 characteristic understory of *Sphagnum angustifolium*, *S. girgensohnii*, *Polytrichum*  
139 *commune*, *Carex* sp., *Calamagrostis purpurea*, *Equisetum sylvaticum*, *Vaccinium myrtillus*,  
140 *V. vitis-idaea*. The five selected Swedish sites were located in an island archipelago in the  
141 northern boreal forest zone of Sweden, within two adjacent freshwater lakes—Lake  
142 Hornavan and Lake Uddjaure and were dominated by dwarf ericaceous shrubs *Vaccinium*  
143 *myrtillus*, *V. vitis-idaea* and *Empetrum hermaphroditum* with dominant trees being *Pinus*  
144 *sylvestris*, *Betula pubescens* and *Picea abies*. The specific composition of the vegetation  
145 for each of the Swedish locations is strongly influenced by historic natural lightning-  
146 induced wildfires (Wardle *et al.*, 2003) and the five soils selected for this study included a  
147 chronosequence since the last major fire (160 years after-SWD1960, 1745 years after-  
148 SWD1745, 1930 years after-SWD1930, 2470 years after-SWD2470 and 3360 years after-  
149 SWD3360).

150 Four cores, from each site, were used for analyses of initial soil moisture content, bulk  
151 density, total nutrient (C, N, P), <sup>14</sup>C content, microbial Phospholipid Fatty Acid biomarkers  
152 (PLFAs) and enchytraeid abundances. The remaining cores were stored in plastic bags at

153 4°C until temperature and moisture incubations began. This temperature was chosen to  
154 reduce metabolic rates (and thus minimise depletion of labile C pools) without the use of  
155 freezing.

156

### 157 *Experimental design*

158 The temperature incubations were started shortly after collection. Vegetation and litter  
159 were removed prior to experimentation. Incubations were made in 4 temperature controlled  
160 growth chambers located at CEH Lancaster which were programmed at 4, 10, 15 and 20°C.  
161 Twelve cores from each site were selected at random to be placed inside each of these  
162 chambers, half at 100% and 60% WHC, respectively. Soil moisture treatments were  
163 maintained by the addition of artificial low nutrient rainwater at regular intervals.

164 All cores were pre-incubated for 24 h (Swedish soils) or four months (remaining soils  
165 excepting IRE and CAITH) before initial measurements of soil respiration, which enabled  
166 the calculations of respiratory  $Q_{10}$  and the index of relative organic C quality (B) across the  
167 temperature range (4-20°C) and at each moisture treatment. Thereafter, the boreal Swedish  
168 soils were dismantled and incubation progressed with the remaining peatland soils for 16  
169 additional months when endpoint respiration measurements at 10°C and final enchytraeid  
170 numbers determinations took place between February and June 2007.

171

### 172 *Gas measurements*

173 CO<sub>2</sub> production rates were measured by sealing intact peat cores into gas tight incubation  
174 vessels (1.8 L), each with a rubber septum in the lid. Gas samples (9 mL) were taken 4-5  
175 times over a period of up to 4 hours during headspace closure and stored in 3.5 mL  
176 exetainer vials (Labco Ltd, UK). CO<sub>2</sub> concentrations were analysed using a Perkin Elmer  
177 Autosystem XL Gas Chromatograph (GC) fitted with a flame ionisation detector and



178 methaniser. Results were calibrated against a certified gas standard comprising 541 ppm  
 179 CO<sub>2</sub> (BOC, UK). CO<sub>2</sub> fluxes rates were calculated after applying linear regression analyses  
 180 to the CO<sub>2</sub> concentrations versus time data for each replicate core. CO<sub>2</sub> fluxes were  
 181 expressed on a per m<sup>2</sup> basis (Holland *et al.*, 1999).

182 The Q<sub>10</sub> values were calculated from the exponential model fitted to the CO<sub>2</sub> flux data  
 183 for the four incubation temperatures. The Q<sub>10</sub> is the proportional increase in respiration (R)  
 184 as the temperature increases by 10<sup>0</sup>C.

$$185 \quad Q_{10} = R(T + 10) / R(T) = R_1 e^{a_1(T+10)} / R_1 e^{a_1 T} = e^{a_1 10}$$

186 As the Q<sub>10</sub> only depends on the a<sub>1</sub> parameter the standard error of Q<sub>10</sub> was calculated  
 187 by:

$$188 \quad se(Q_{10}) = 10 * Q_{10} * se(a_1)$$

189 We also used the parameter B which provides an index of soil organic C bioavailability  
 190 from soils incubated under controlled conditions. It was calculated as the exponential fit  
 191 parameter describing the y-intercept of the first-order exponential equation relating  
 192 decomposition rate to temperature (Fierer *et al.*, 2006).

193

#### 194 *Total soil nutrient (C, N, P) and <sup>14</sup>C contents*

195 Carbon and nitrogen contents of freeze dried soil samples were measured on an Elementar  
 196 Vario EL elemental analyser and the determination of P was made colorimetrically using a  
 197 SEAL AQ2 discrete analyzer after aqua-pura digestion (Rowland & Grimshaw, 1985).

198 For <sup>14</sup>C analyses freeze-dried soil samples were individually loaded into quartz sample  
 199 tubes with 60 mg of pre-combusted CuO and a strip of Ag foil then sealed under vacuum.  
 200 CO<sub>2</sub> from combusted soil was converted to graphite on an iron catalyst using the hydrogen  
 201 reduction method (Vogel *et al.*, 1984) and the <sup>14</sup>C/<sup>12</sup>C and <sup>13</sup>C/<sup>12</sup>C ratios were measured by  
 202 accelerator mass spectrometry at the <sup>14</sup>CHRONO Centre, Queen's University Belfast.

203 Radiocarbon data are as  $F^{14}C$ , the fraction modern with the  $^{14}C/^{12}C$  ratio of oxalic acid  
204 corrected for decay since 1950 (Reimer *et al.*, 2004). The values were corrected for isotope  
205 fractionation using the AMS measured  $\delta^{13}C$ , which accounts for both natural and machine  
206 fractionation. Mean residence times (MRT) of carbon soil organic matter was calculated  
207 using a single pool steady-state model (Harkness *et al.*, 1986). The MRT was obtained by  
208 matching the measured and modelled  $\Delta^{14}C$  for the year in which the soil was sampled.  
209 Assumptions of the model were that C inputs equal C losses at each time step and the  $\Delta^{14}C$   
210 of inputs were equal to that of the atmosphere in the previous year.

211

212 *Biotic community structure*

213 Microbial community biomass was also quantified with PLFA analyses. These biomarkers  
214 were extracted as part of the total lipid extract of freeze-dried soils (ca. 0.3 g dry weight)  
215 using a modified Bligh-Dyer extraction (White *et al.*, 1979; Crossman *et al.*, 2004). PLFAs  
216 were quantified by the addition of a nonadecane standard of known concentration. GC  
217 analysis was carried out on an Agilent 6890 GC fitted with a CP-Sil 5CB fused silica  
218 capillary column (60 m x 0.32 mm ID; 0.25  $\mu$ m film thickness). Carrier gas was hydrogen,  
219 and the flow was set to a constant velocity of 40 cm sec<sup>-1</sup>. The temperature was raised,  
220 following an isothermal hold at 50°C for 2 min, to 150°C at 20 °C min<sup>-1</sup>, then to 220°C at  
221 3°C min<sup>-1</sup>, followed by an increase to 340°C at 25°C min<sup>-1</sup> and a hold time of 5 min. Fatty  
222 acids were identified by retention time by comparison with previously identified samples  
223 and by gas chromatography-mass spectrometry on an Agilent 6890 GC connected to an  
224 Agilent 5973 Mass Selective Detector (GC conditions as above). Total PLFA  
225 concentration was calculated using all identified PLFAs. The Bacterial:Fungal ratio was  
226 calculated using the PLFA 18:2 $\omega$ 6,9 as an indicator of fungal biomass and the sum of 14  
227 bacterial specific PLFAs identified as indicator of the bacterial biomass.

228 Because enchytraeid worms are a keystone mesofaunal group in peatlands (Briones *et*  
229 *al.*, 2007a), initial and final enchytraeid populations were determined from the peat cores  
230 only using the wet extraction method (O'Connor, 1955). Once extracted the animals were  
231 preserved in 70% alcohol and counted.

232

### 233 *Statistical analyses*

234 One-way ANOVA was used to determine the significance of the effects of pre-incubation  
235 time on gas fluxes and respiratory quotient calculations, and to test for differences of initial  
236 soil chemical and biological properties between boreal and peat soils between sites. The  
237 separation of means was determined using Tukey's Studentized range (HSD) test ( $\alpha =$   
238 0.05).

239 A Principal Component Analysis (PCA) was carried out to differentiate boreal and  
240 peatland soil samples based on their initial soil chemistry and microbiological properties.

241 Linear correlations (Pearson correlation coefficient) were used to investigate the  
242 interdependence of the initial chemical and biological properties, CO<sub>2</sub> production B and  
243 Q<sub>10</sub> values as well as of final gas fluxes and enchytraeid data. In contrast, non-linear  
244 regressions (NLIN) were employed to describe the dependence of CO<sub>2</sub> fluxes with  
245 temperature at the end of the incubation period.

246 Final gas fluxes and enchytraeid numbers were not normally distributed but were  
247 approximately normal on the log scale. They were therefore log transformed either using  
248 log<sub>10</sub>(n) or log<sub>10</sub>(n+1) transformations. A general linear model (GLM) was fitted to the data  
249 (final CO<sub>2</sub> production and initial and final enchytraeid numbers) which included the effects  
250 of temperature, moisture, site from which the peat was obtained, and all two and three way  
251 interactions between these three experimental factors. In the case of enchytraeid numbers,  
252 the statistical analyses were then performed both with and without adjusting for initial

253 values; however, the results were essentially the same for both analyses, and there was no  
254 significant correlation between initial and final numbers. Results are therefore presented  
255 only for analyses of final numbers without adjustment for initial values. Post analysis mean  
256 comparisons were made to test for significant differences between temperature and  
257 moisture treatments and the interaction made using the Tukey-Kramer test.

258 PCA analyses were performed using the CANOCO software for Windows v4.5 (ter  
259 Braak & Smilauer, 2002), whereas the remaining statistical analyses were performed on  
260 the data using SAS system v9.3 (SAS Institute, 2004).

261

## 262 **Results**

### 263 *Abiotic properties of the organic soil ecosystems*

264 The European climate gradient of selected sites included a wide range of mean annual  
265 temperature (MAT) and rainfall (MAR) regimes: from very cold (-0.3°C) and relatively dry  
266 (approx. 300 mm rainfall, on average) boreal forested Swedish islands to a warm and fairly  
267 wet blanket bog in Spain with MAT values of 11°C and annual precipitation of 1800 mm  
268 (Table 1). On average, the peatlands investigated here received nearly three times more  
269 rainfall than the boreal soils (ANOVA:  $F_{1,9} = 25.66$ ,  $P = 0.0007$ ); furthermore, at all  
270 locations, moisture contents (MC) were high and even the soil samples taken during the  
271 summer months were wet (> 75% of wet weight; Table 1).

272 Although all the soils investigated here are, by definition, organic soils, there was a  
273 wide variation in their carbon content (ranging from 21% to 55%; Table 1). Similarly,  
274 nutrient status was also highly variable across sites and thus, whereas the UK sites of GDF  
275 and PLYN contained the highest percentage of both nitrogen (>2.5%) and phosphorus  
276 (0.14%), the Spanish site showed low values of both elements (Table 1). However, despite  
277 the fact that no significant differences were detected in the elemental composition between

278 the two ecosystem types, C:N ratios in boreal soils were significantly higher (36 on  
279 average) than in the peatland sites (22 on average) (ANOVA:  $F_{1,9} = 24.85$ ,  $P = 0.0008$ ).  
280 Mean residence times (MRT), the net balance between carbon input and output from a soil,  
281 did not show any significant differences between peatlands and boreal forests and values  
282 were greater than 100 years in six of the investigated sites and between 5 and 53 years in  
283 the remaining ones (Table 1), suggesting that peat formation and accumulation are still  
284 dominant processes in these organic systems.

285 The output from PCA analyses identified the first component (absorbing 83.6% of the  
286 total explained variance) to be strongly related to the amount of C accumulated in the top  
287 10 cm (Fig. 1) and MAT and showed a clear gradient from the coolest Swedish boreal  
288 soils, GDF and AUCH storing the highest amount of C (between 5,700 and 7,334 g m<sup>2</sup> in  
289 the top 10 cm) to the soils containing less than 4,086 g C m<sup>2</sup> (MHB, SPA and FIN). The  
290 second component (absorbing 10.5% of the total variance) was positively related to rainfall  
291 values, altitude, and C:N and C:P ratios and clearly separated the upland wettest soils with  
292 the lowest nutrient availability from those with opposite properties (Fig. 1).

293

#### 294 *Biotic properties of the organic soil ecosystems*

295 The microbial communities in all soils were dominated by bacteria, especially in the  
296 peatland systems where the Bacteria:Fungi (B:F) ratio was significantly higher than in the  
297 boreal ones (ANOVA:  $F_{1,9} = 15.76$ ,  $P = 0.0033$ ). In contrast, fungi were more abundant in  
298 the boreal soils and best represented in the Swedish boreal systems (Fig. 1), although the  
299 differences were not significant. Furthermore, nutrient ratios exerted a strong influence on  
300 microbial communities and significant negative correlations were observed between total  
301 bacteria and C:P ratio ( $r = -0.62$ ,  $P = 0.0318$ ) and between B:F and both C:P ( $r = -0.61$ ,  $P =$   
302  $0.0355$ ) and C:N ratios ( $r = -0.81$ ,  $p = 0.0015$ ).

303 The range of peats considered here also supported different enchytraeid population  
304 numbers at the time of the sampling, with GDF concentrating the highest densities of these  
305 organisms (Table 2); however, only the differences with the Scottish bog (CAITH),  
306 containing the lowest densities of this key soil mesofaunal group, were significant  
307 (ANOVA:  $F_{6,20} = 4.93$ ,  $P = 0.003$ , Table 2). There was a contrasting difference in the  
308 abundance of gram-negative bacteria between these two sites ( $34.98 \mu\text{mol g}^{-1}$  dry soil  
309 against  $15.27 \mu\text{mol g}^{-1}$  dry soil), also corroborated by a significant positive relationship  
310 between enchytraeid numbers and this particular group of bacteria ( $r = 0.67$ ,  $P = 0.0239$ ).

311

### 312 *Controls on soil respiration and C turnover*

313 Pre-incubating the soil samples for different time periods after they have been collected did  
314 not have a significant effect of  $\text{CO}_2$  production ( $\text{mg CO}_2\text{-C m}^{-2} \text{h}^{-1}$ ;  $P > 0.05$ ). Overall, the  
315 peat soils respired nearly twice as much as the boreal ones at both moisture treatment  
316 levels, although the differences were not significant. However, the temperature sensitivity  
317 ( $Q_{10}$ ) of soil respiration in boreal soils at 100% WHC was significantly higher than in the  
318 peats ( $2.44 \pm 0.20$  versus  $1.30 \pm 0.33$ ; ANOVA:  $F_{1,9} = 9.83$ ,  $P = 0.0120$ ). Interestingly, there  
319 was a positive relationship between this respiratory coefficient and soil C:P ratio ( $r = 0.63$ ,  
320  $P = 0.0370$ ; Fig. 2a) and drying at 60% WHC exacerbated this effect ( $r = 0.69$ ,  $P = 0.0190$ ;  
321 Fig. 2b), with a 43% increase in average  $Q_{10}$  from  $1.92 \pm 0.83$  to  $2.87 \pm 1.0$  (ANOVA:  $F_{1,20} =$   
322  $5.75$ ,  $P = 0.026$ ). For waterlogged 100% WHC soils,  $Q_{10}$  was also positively related to soil  
323 C:N ratio ( $r = 0.78$ ,  $P = 0.0044$ ; Fig. 2c), whereas in the drier soils a positive relationship  
324 was found with N:P ratios ( $r = 0.76$ ,  $P = 0.0061$ ; Fig. 2d). We found that the greatest  
325 temperature sensitivity of respiration occurred in organic soils with the lowest B:F ratios,  
326 measured using PLFA, although this was significant for 100% WHC incubations only ( $r =$   
327  $-0.78$ ,  $P = 0.0046$ ). B:F ratios could be explained, in part, by the relationship with C:P

328 resource quality ( $r = -0.61$ ,  $P = 0.0355$ ) and C:N ( $r = -0.81$ ,  $P = 0.0015$ ), with greater  
329 fungal biomass in high C:P and C:N soils. MRT was not significantly related to quality (B)  
330 of organic carbon. With increasing quality, a decrease in the temperature sensitivity of soil  
331 respiration was observed for both 100% ( $r = -0.91$ ,  $P < 0.0001$ ) and 60% ( $r = -0.79$ ,  $P =$   
332  $0.0039$ ) WHC soils. Furthermore, carbon quality decreased with increased C:P ( $r = -0.70$ ,  
333  $P = 0.0154$ ) and C:N ratios ( $r = -0.73$ ,  $P = 0.0103$ ) for 100% WHC soils.

334 At the end of the experimental incubation period, both temperature and moisture (and  
335 their interactions) had a significant effect on the final respiration rates of the peatland soils,  
336 with the response being dependent on their original location (Table 3). Overall, they  
337 respired more at cold temperatures (4°C) and CO<sub>2</sub> efflux rates gradually decreased with  
338 increasing incubation temperatures (NLIN:  $r^2 = 0.39$ ,  $P < 0.0001$ ). Furthermore, more CO<sub>2</sub>  
339 was produced in wetter soils and drying the peat resulted in a 17.2% decrease in soil  
340 respiration ( $P < 0.0001$ ; Table 3); however, this effect was only significant when the soils  
341 were incubated at 4°C. Additionally, different peat soils behaved differently (Table 3) and  
342 the Scottish AUCH soil showed the lowest values of soil respiration (38.7  $\mu\text{g CO}_2\text{-C m}^{-2}$   
343  $\text{hr}^{-1}$ ), followed by the two peat bogs (MHB, IRE) and CAITH, whereas the three upland  
344 blanket peats (GDF, PLYN and SPA) showed the highest flux rates (ranging from 77 to  
345 100  $\mu\text{g CO}_2\text{-C m}^{-2} \text{hr}^{-1}$ ). These three sites were particularly sensitive to moisture changes  
346 and drying the peat resulted in 23.9, 19.7 and 37.2% decreases (respectively) in soil  
347 respiration, although the differences were only significant for the last two soils ( $P <$   
348  $0.0001$ ; Table 3).

349 When comparing sites at each temperature and moisture treatment (Fig. 3), it became  
350 clear that cold temperatures stimulated CO<sub>2</sub> emissions from waterlogged soils (Fig. 3a),  
351 with the differences with the rest of the temperature treatments being nearly always  
352 significant (with the exception of three sites: AUCH, CAITH and IRE; Fig. 3a). In

353 contrast, under reduced moisture conditions, although warmer ( $> 15^{\circ}\text{C}$ ) soils respired less  
354 C, the stimulating effect of low temperatures was less obvious (excepting GDF; Fig. 3b)  
355 and, in particular, one site (SPA) did not follow the general trend in the temperature  
356 response and both  $4^{\circ}$  and  $15^{\circ}\text{C}$  temperatures stimulated  $\text{CO}_2$  emissions.

357

#### 358 *Mesofauna differences and dynamics*

359 Peat origin, temperature, moisture conditions and all possible combinations of these factors  
360 also had a strong influence on the enchytraeid populations living in these soils (Table 4).  
361 The incubation treatments significantly increased their population numbers and more  
362 enchytraeids were extracted from the peat soils at the end of the 16 months incubation  
363 period than when they were collected in the field (GLM:  $t\text{-value} = 4.56$ ,  $P < 0.0001$ ).  
364 Although all the peat sites showed these increases in enchytraeid numbers, the differences  
365 between initial and final values were only significant for the Scottish site at CAITH where  
366 nearly forty times more enchytraeids were recorded when compared to the initial  
367 populations ( $P < 0.0001$ ).

368 Similar to  $\text{CO}_2$  production, warming also had a negative effect on enchytraeid densities  
369 (Table 4) and temperatures  $> 15^{\circ}\text{C}$  significantly decreased their populations numbers and  
370 those soils incubated at  $10^{\circ}\text{C}$  rendered the highest abundances ( $> 200,000$  individuals. $\text{m}^{-2}$ ).  
371 Furthermore, although drying the peat significantly decreased by 6% their overall  
372 population sizes ( $P < 0.0001$ ; Table 4), it was under these reduced moisture conditions  
373 when the positive effect of the  $10^{\circ}\text{C}$  temperature treatment on enchytraeid reproduction  
374 rates was reinforced ( $\sim 250,000$  individuals per square meter) and significantly contrasted  
375 with the lower densities observed at the two more extreme incubation temperatures ( $4$  and  
376  $20^{\circ}\text{C}$ ; 66,000 and 86,000 individuals per square meter, respectively).



377        Regardless of temperature and moisture content, four sites (MHB, PLYN, AUCH and  
378 CAITH) supported significantly more enchytraeids than IRE (Table 2). Altering the water  
379 content of the peat resulted in a great variability in the animal response, with either  
380 increases or decreases in enchytraeid densities; however, the differences between the two  
381 moisture treatments were only significant in the case of CAITH and SPA where reduced  
382 moisture contents led to significantly higher mortality rates (36 and 67% decrease in the  
383 population sizes, respectively).

384        When considering the effects of both temperature and moisture treatments on each  
385 individual peat site (Fig. 4), it was obvious that the response was not uniform and that peat  
386 enchytraeid populations responded very differently to changes in the environmental  
387 conditions. Although in wetter soils survival success appeared better at lower temperatures  
388 ( $<10^{\circ}\text{C}$ ; Fig. 4a), no significant effect of temperature on population sizes was found when  
389 the soils are saturated (Fig. 4a). In contrast, under drier conditions the animals seemed to  
390 prefer slightly warmer temperatures, with the exception of GDF where a significant  
391 decrease in population numbers was observed with increasing temperatures (Fig. 4b).  
392 Interestingly, enchytraeid numbers were positively linked to  $\text{CO}_2$  production ( $n = 332$ ;  $r =$   
393  $0.12714$ ,  $P = 0.0205$ ) and soils containing higher densities of these organisms emitted  
394 more  $\text{CO}_2$  with wetter conditions exacerbating this effect ( $n = 164$ ,  $r = 0.26103$ ,  $P =$   
395  $0.0007$ ).

396

## 397 **Discussion**

398        Currently, carbon coupled GCMs assume that soil organic matter decomposition is a first-  
399 order decay process, proportional to the size of the soil carbon pool and with soil chemical  
400 properties used as metrics to predict residence times (e.g. Thornton & Rosenbloom, 2005).  
401        Accordingly, the stability of organic soil C and its response to projected climate changes

402 has been directly correlated to the total carbon content of the soil (e.g. Bellamy *et al.*,  
403 2005), litter quality (e.g. Conant *et al.*, 2011) and the fresh supply of C entering into the  
404 system (e.g. Fontaine *et al.*, 2007). However, our incubation study demonstrates that the  
405 soil environment and its intrinsic chemical and biological characteristics are critical  
406 parameters for predicting C storage capacity.

407 It is widely accepted that temperature and precipitation patterns determine SOM  
408 decomposition across the globe (e.g. Bond-Lamberty & Thomson, 2010; Wu *et al.*, 2011),  
409 with soils located in historically cold climates having slower C turnover rates than those  
410 from the warmer climates (Hobbie *et al.*, 2000). There is, however, growing evidence that  
411 climate regimes influence soil biotic community structure and activity, with, for example,  
412 soil moisture being the primary global driver for the size of microbial biomass (Serna-  
413 Chavez *et al.*, 2013) and climate as a determinant of the distribution, abundance and  
414 ecology of enchytraeids and their vertical distribution in organic soils (Briones *et al.*,  
415 2007b).

416 In addition, the quality and nutrient characteristics of substrates also governs the  
417 accessibility of the SOM to soil biota and, hence, SOM turnover (Dungait *et al.*, 2012).  
418 This is a direct reflection of the control exerted by the dominant vegetation on the litter  
419 quantity and quality entering in the soil and, as a result, any alterations in the plant  
420 community composition, driven by changing temperature and moisture conditions, are  
421 expected to alter the quality of the organic matter (in terms of C:N ratios) susceptible to be  
422 decomposed (e.g. Meier & Bowman, 2008). For example, increased occurrence of periods  
423 with low water tables might result in a shift from mosses to ericoid shrubs species  
424 (Breeuwer *et al.*, 2009), which will have critical implications for SOM decomposition  
425 rates. This is due to ericoid and ectomycorrhizal fungi, which are particularly abundant in  
426 heathlands and boreal forests, being highly efficient at foraging for organic sources of N

427 and P and hence, restricting their access by the decomposer communities (Read *et al.*,  
428 2004) and contributing to C accumulation (Orwin *et al.*, 2011). Accordingly, our findings,  
429 from a wide range of organic soil ecosystems, provide further evidence of the importance  
430 of both abiotic and biotic factors in determining soil respiration responses to temperature  
431 and moisture changes, with each investigated soil responding differently to our climate  
432 manipulations, and soils exhibiting the highest C:P and C:N ratios being symptomatic of  
433 slow C turnover and long-term C accumulation.

434 The potential for chemical, climatic and biotic properties to influence our ability to  
435 predict how soil C cycling processes will respond to climate changes (Evans &  
436 Wallenstein, 2012) has prompted the need to model continuous changes in SOM dynamics  
437 (Lawrence *et al.*, 2009) to account for the interactions between abiotic conditions and  
438 microbial communities instead of assuming a quasi-steady-state (Schimel, 2001). For  
439 example, drying–rewetting events, commonly occurring in these organic systems (e.g. as  
440 result of permafrost melting and strong seasonality) can result in large pulses of soil CO<sub>2</sub>  
441 efflux which can have a strong temperature sensitivity and are probably driven by substrate  
442 quality (Chatterjee & Jenerette, 2011). In addition, the close coupling between enzymatic  
443 activities and temperature seasonal changes have seen to lead to more than one thermal  
444 optimum for the microbial communities (Fenner *et al.*, 2005) and could explain why our  
445 upland Spanish site did not follow the general observed trend in the temperature response  
446 of soil respiration.

447 Furthermore, our results also demonstrate that the greatest temperature sensitivity of  
448 respiration was observed in boreal soils with the lowest B:F ratios and nutrient availability  
449 (in terms of nutrient ratios) and the highest C storage capacity suggesting that future drying  
450 may further amplify the priming of soil organic matter decomposition (Ise *et al.*, 2008).  
451 Importantly, respiratory Q<sub>10</sub> decreased with increasing carbon quality (B) and was not

452 related to carbon MRT, confirming that mineralization of biologically resistant and less  
453 decomposable compounds is more climate sensitive than the mineralization of more labile  
454 substrates (Bosatta & Ågren, 1999). Indeed, boreal litter forest litter tends to be composed  
455 of phenol rich substrates which are prone to be resistant to decomposition (Nilsson *et al.*,  
456 2008); however, increased frequency of droughts could remove this restricting mechanism  
457 on biodegradation and result in vast amounts of CO<sub>2</sub> being released into the atmosphere  
458 (Freeman *et al.*, 2001b).

459 In addition, organic soil systems characterised by net C sequestration contain fungi  
460 dominated microbial communities with inputs from plants with conservative strategies (i.e.  
461 high C:N ratios and leaf dry matter content; see Grigulis *et al.*, 2013). The observation, in  
462 our study, of significant negative relationships between both total bacteria biomass and B:F  
463 ratios and nutrient ratios (C:P and C:N) add to evidence that nutrient limitation is the main  
464 factor controlling microbial community structure and activity. This is in agreement with  
465 recent meta-analyses studies (Waring *et al.*, 2013) showing that the differences in fungal  
466 and bacterial physiology can drive the relative abundance of these two groups (as B:F  
467 ratios) along environmental gradients. This is, in part, due to the low nutrient requirements  
468 of fungi and their conservative metabolic activities (Wardle *et al.*, 2004), explaining their  
469 presence in nutrient poor environments compared to bacteria which are more dependent on  
470 plant recent photoassimilates (Paterson *et al.*, 2007; Garcia-Pausas & Paterson, 2011).  
471 However, in those systems where mycorrhizal fungi are dominant, recently  
472 photosynthesised C can also be rapidly processed in response to increased plant  
473 photosynthetic rates, which results in a counteracting effect on C balance (Staddon *et al.*,  
474 2013). This could, therefore, explain why our forested systems, containing the highest  
475 fungal biomass, also had the highest C:N and C:P ratios.

476 In the case of peatland soils, our results showed an overall decline in soil respiration  
477 with increasing temperatures and reduced moisture contents, which could be explained by  
478 taking into consideration the strong sensitivity of enzymatic activities to climatically  
479 driven events and thus, summer droughts have seen to significantly reduce the phenol  
480 oxidase activity (Toberman *et al.*, 2008) and warmer temperatures to enhance the release  
481 of phenolic compounds (Freeman *et al.*, 2001a), all of which inhibit decomposition  
482 processes.

483 In contrast, the positive response of peat respiration to wet and cold conditions was  
484 unexpected and contradicts previous arguments that waterlogged soils with low oxygen  
485 availability microbial activities are restricted (Freeman *et al.*, 2001b). Recent evidence,  
486 however, suggests that, under aerobic conditions, fermented SOM takes over oxygen as  
487 both the electron provider and the electron acceptor for microbial activities, resulting in  
488 accelerate release of CO<sub>2</sub> from these soils (Keller & Takagi, 2013). From this, it could  
489 concluded that the importance of anaerobic decomposition in the climate feedbacks might  
490 be greater than assumed, at least for higher latitudes (Jungkunst & Fiedler, 2007).

491 Differences in C source preference (litter derived *versus* root-derived) have also been  
492 suggested as a potential driver for contrasting microbial activities between grassland and  
493 woody habitats (Crotty *et al.*, 2011). Therefore, it is also possible to conclude that our  
494 fungal-dominated boreal systems are reliant on litter inputs from low quality, slow  
495 decomposing coniferous tree species inputs which favour fungi, whereas increased root  
496 activity during the favourable temperature and moisture conditions promotes bacterial cell  
497 division and food-webs evident in peatland soils. The positive relationship found between  
498 enchytraeids and gram negative bacteria also confirms that bacteria are the main energy  
499 fuelling agents of invertebrate feeding activities in peatlands. The relative dominance of  
500 these two microbial groups is, therefore, indicative of preferential feeding activities of soil

501 mesofauna communities and a metric of soil C storage, with fungal dominated soils leading  
502 to greater C accumulation and bacteria possibly responsible for a greater turnover of recent  
503 labile substrates. In relation to this, rapidly cycling systems have been characterised as  
504 dominated by bacterial activity and enchytraeid grazing (Waldrop *et al.*, 2012) with our  
505 results showing that increased enchytraeid activity resulted in more CO<sub>2</sub> being emitted  
506 from peatland soils. However, the fact that we found more enchytraeids at the end of the  
507 experimental period than at the start of the experiment, when most of the labile substrates  
508 had been consumed, suggest that they were not only relying solely on these easily  
509 decomposable sources. Previous incubation studies have shown that if access to  
510 fresh/labile material is restricted or exhausted due to increasing competition pressures,  
511 enchytraeids can exploit more recalcitrant organic matter (Briones *et al.*, 2007a, 2010).  
512 However, lower quality organic matter puts severe restrictions on animal growth and  
513 therefore, in the field, their populations are usually concentrated in the upper topsoil layers  
514 where a wide range of food sources is available (Briones *et al.*, 2010). Additionally,  
515 enchytraeid reproduction rates have been linked to increasing temperatures (Standen *et al.*,  
516 1973; Briones *et al.*, 1997), whereas their vertical distribution is determined by moisture  
517 (Briones *et al.*, 1997). Consequently, it is possible to suggest that, in our incubation study,  
518 wetter and mild temperatures (10-15°C) provided the best range of environmental and  
519 nutrient conditions for enabling enchytraeids to grow.

520 Taken together, our findings suggest that integrative knowledge of ecological  
521 feedbacks, between resource stoichiometric (C, N and P) controls on soil decomposition,  
522 will improve predictions of organic soil respiration in response to climate change.  
523 Therefore, we conclude that a more realistic understanding of the mechanisms that govern  
524 C stability should incorporate three axes: climate, soil nutrient stoichiometry and biology

525 as well as their complex interactions. This, in turn, would improve models by reducing  
526 uncertainty in the climate sensitivity of SOM in C models (Schmidt *et al.*, 2011).

527

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537

### 538 **Conflict of Interest**

539 The authors declare no conflict of interest.

540

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**Table 1** Initial characteristics of the C-rich organic soils used in this study

Site	Habitat	Co-ordinates Latitude, Longitude	Altitude a.s.l. (m)	MAT (°C)	MAR (mm)	Sampling year	MC (%)	Bulk density (g cm <sup>-3</sup> )	%C	%N	%P	MRT Years
England-Moor House Bog	Peatland	54° 43' N, 2° 91' W	535	5.8	2048	2005	92.3	0.10	49.8	1.61	0.05	171.6
England-Great Dun Fell	Peatland	54° 65' N, 2° 45' W	848	3.9	1605	2005	82.8	0.15	48.8	2.56	0.14	52.9
Wales-Plynlimon	Peatland	52° 26' N, 3° 46' W	648	7.2	1000	2005	86.9	0.14	49.6	2.66	0.14	101.4
Scotland- Auchencorth	Peatland	55° 47' N, 3° 14' W	270	7.7	660	2005	84.2	0.17	50.5	2.38	0.11	101.9
Scotland- Caithness	Peatland	58° 08' N, 0° 36' W	100	8.0	939	2006	85.8	0.18	45.1	1.40	0.06	35.17
Ireland-Clara Bog	Peatland	53° 19' N, 7° 39' W	60	9.3	900	2005	87.5	0.09	50.5	1.61	0.03	12.59
Spain-Xistral	Peatland	42° 48' N, 8° 6' W	1039	11.0	1800	2005	76.7	0.17	21.7	1.01	0.08	5.9
Finland-Jyväskylä	Boreal Forest	62° 11' N, 25° 40' E	165	3.0	610	2005	92.2	0.07	47.3	1.49	0.11	10.4
SWD160	Boreal Forest	65° 58' N, 17° 49' E	431	-0.3	495	2007	76.8	0.12	55.6	1.39	0.07	124.4
SWD1745	Boreal Forest	65° 57' N, 17° 50' E	439	-0.3	495	2007	75.8	0.10	54.0	1.78	0.09	46.2
SWD1930	Boreal Forest	66° 02' N, 17° 45' E	425	-0.3	495	2007	76.0	0.12	54.6	1.37	0.08	39.6
SWD2740	Boreal Forest	65° 60' N, 17° 48' E	425	-0.3	495	2007	79.2	0.13	53.9	1.39	0.06	220
SWD3360	Boreal Forest	66° 01' N, 17° 45' E	426	-0.3	495	2007	77.0	0.12	54.5	1.54	0.07	120



**Table 2** Initial and final enchytraeid abundances (Nos. per square meter) collected from each of the peatland sites; data presented as means ( $\pm$  standard errors) with different letters indicating significant differences between sites (ANOVA, Tukey,  $p < 0.05$ )

Source	Initial numbers	Final numbers
MHB	24323.90 a (9540.88)	148572.68 ab (35383.02)
GDF	90042.48 a (18232.03)	108576.83 abc (14430.68)
PLYN	26732.98 a (5346.53)	180201.53 a (30133.55)
AUCH	17718.37 a (2058.02)	157224.63 ab (39466.03)
CAITH	5595.27 b (5090.39)	220411.51 ab (30229.16)
IRE	46549.58 a (23789.01)	47909.54 c (6129.61)
SPA	42613.63 a (3330.24)	152099.57 bc (20932.88)

**Table 3** Results from the GLM procedure for final soil respiration fluxes ( $\mu\text{g CO}_2\text{-C m}^{-2} \text{ hr}^{-1}$ ) from the investigated peatlands. Significance multivariate test on each factor and the interactions is Tukey-Kramer test. Abbreviations: TEMP = temperature, MC = moisture content

Source	DF	Type I SS	Mean Square	F Value	Pr > F
SITE	6	127623.4339	21270.5723	43.07	<.0001
TEMP	3	282409.1176	94136.3725	190.63	<.0001
MC	1	12784.6217	12784.6217	25.89	<.0001
SITE*TEMP	18	33131.2483	1840.6249	3.73	<.0001
SITE*MC	6	19399.2128	3233.2021	6.55	<.0001
MC*TEMP	3	9951.9586	3317.3195	6.72	0.0002
SITE*MC*TEMP	18	26619.2699	1478.8483	2.99	<.0001

**Table 4** Results from the GLM procedure for final enchytraeid numbers (Nos. per square meter) from the investigated peatlands. Significance multivariate test on each factor and the interactions is Tukey-Kramer test. For abbreviations see Table 3

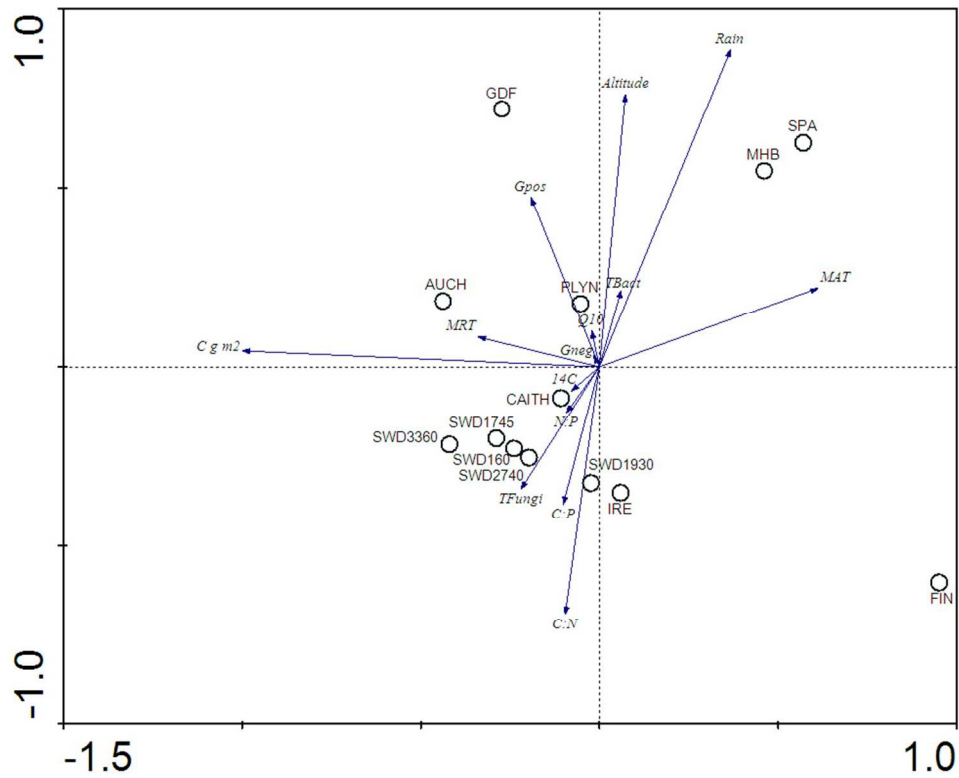
Source	DF	Type I SS	Mean Square	F Value	Pr > F
SITE	6	9.02929587	1.50488264	5.01	<.0001
TEMP	3	11.79295155	3.93098385	13.08	<.0001
MC	1	6.53577764	6.53577764	21.76	<.0001
SITE*TEMP	18	36.09383463	2.00521303	6.67	<.0001
SITE*MC	6	19.02129950	3.17021658	10.55	<.0001
MC*TEMP	3	6.39295105	2.13098368	7.09	0.0001
SITE*MC*TEMP	18	15.37711675	0.85428426	2.84	0.0001

**Fig. 1** PCA biplot of the initial chemical and microbiological characteristics of the 6 boreal and 7 peatland sites investigated based on the first two axes.

**Fig. 2 (a)** Relationship between the temperature sensitivity of soil respiration ( $Q_{10}$ ) and soil C:P ratio at field capacity moisture content. **(b)** Relationship between the temperature sensitivity of soil respiration ( $Q_{10}$ ) and soil C:P ratio at 60% of field capacity moisture content. **(c)** Relationship between the temperature sensitivity of soil respiration ( $Q_{10}$ ) and soil C:N ratio at field capacity moisture content. **(d)** Relationship between the temperature sensitivity of soil respiration ( $Q_{10}$ ) and soil N:P ratio at 60% of field capacity moisture content.

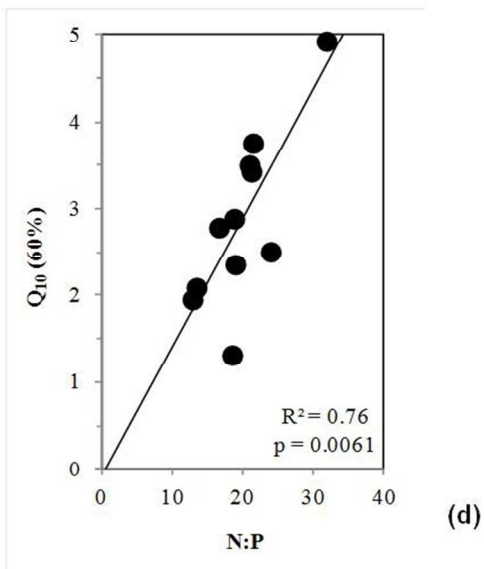
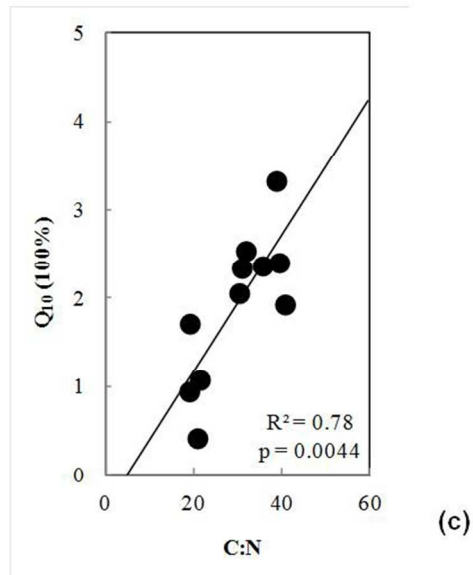
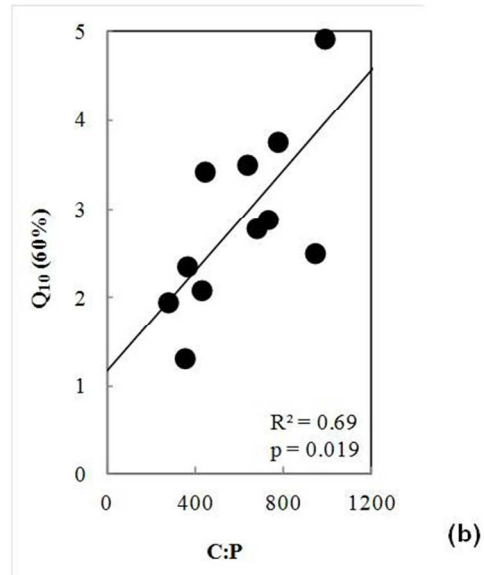
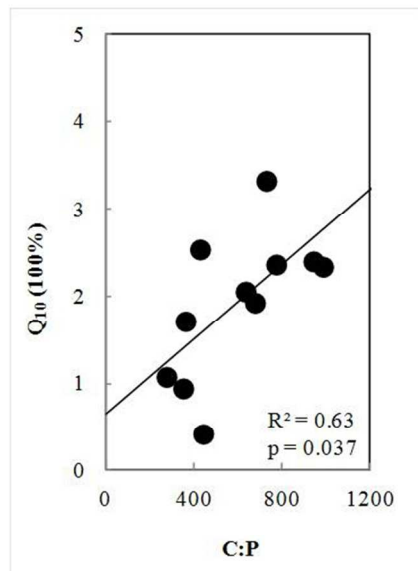
**Fig. 3** Final respiration fluxes at 10°C from each peatland soil previously incubated at 4, 10, 15 and 20°C and two moisture levels **(a)** 100% WHC **(b)** 60% WHC. Values represent means  $\pm$  standard errors with different letters indicating significant differences (Tukey-Kramer,  $p < 0.05$ ) between temperature treatments.

**Fig. 4** Final enchytraeid numbers from each peatland soil after being incubated at 4, 10, 15 and 20°C and at two moisture levels **(a)** 100% WHC **(b)** 60% WHC. Values represent means  $\pm$  standard errors with different letters indicating significant differences (Tukey-Kramer,  $p < 0.05$ ) between temperature treatments.

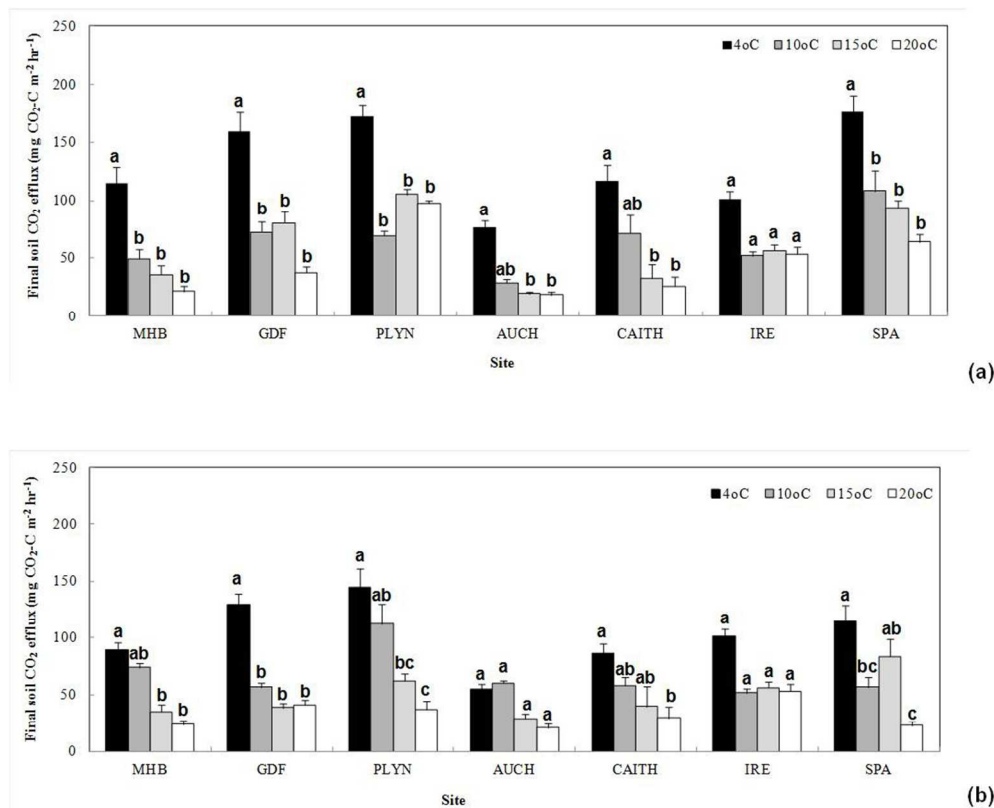


PCA biplot of the initial chemical and microbiological characteristics of the 6 boreal and 7 peatland sites investigated based on the first two axes.

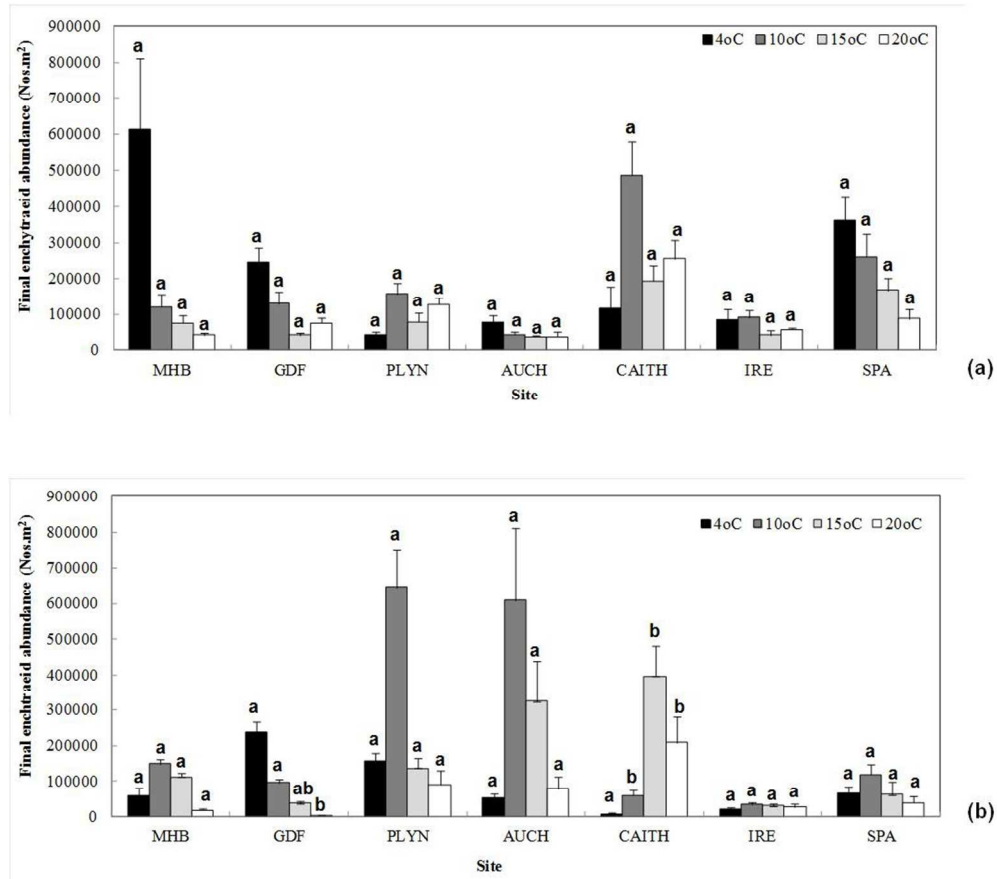
361x294mm (72 x 72 DPI)



(a) Relationship between the temperature sensitivity of soil respiration ( $Q_{10}$ ) and soil C:P ratio at field capacity moisture content. (b) Relationship between the temperature sensitivity of soil respiration ( $Q_{10}$ ) and soil C:P ratio at 60% of field capacity moisture content. (c) Relationship between the temperature sensitivity of soil respiration ( $Q_{10}$ ) and soil C:N ratio at field capacity moisture content. (d) Relationship between the temperature sensitivity of soil respiration ( $Q_{10}$ ) and soil N:P ratio at 60% of field capacity moisture content. 150x176mm (150 x 150 DPI)



Final respiration fluxes at 10°C from each peatland soil previously incubated at 4, 10, 15 and 20°C and two moisture levels (a) 100% WHC (b) 60% WHC. Values represent means  $\pm$  standard errors with different letters indicating significant differences (Tukey-Kramer,  $p < 0.05$ ) between temperature treatments.  
184x150mm (150 x 150 DPI)



Final enchytraeid numbers from each peatland soil after being incubated at 4, 10, 15 and 20°C and at two moisture levels (a) 100% WHC (b) 60% WHC. Values represent means  $\pm$  standard errors with different letters indicating significant differences (Tukey-Kramer,  $p < 0.05$ ) between temperature treatments.  
184x162mm (150 x 150 DPI)