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

Running head: Biotic and abiotic interactions and C cycling

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## Abstract

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

## Introduction

Northern peatland and boreal soils have been accumulating carbon for centuries (Limpens *et al.*, 2008). This retention capacity is the result of poor mineralisation rates due to the severe restrictions that cold and often wet climatic conditions impose on biotic activity. Global warming has, therefore, the potential to accelerate chemical transformations mediated by soil biota and to alter their C sink function. For example, observed increases in equinox temperatures in boreal forests over the last two decades show a trend towards an earlier autumn-to-winter carbon dioxide build-up, being associated to a greater increase of soil respiration over photosynthesis and offsetting the gains derived from earlier spring sequestration (Piao *et al.*, 2008). Similarly, rising temperatures have seen to alter bacterial and methanogen community structure and their relative ratios in peatlands, resulting in imbalance of $CO_2$ and $CH_4$ emissions (Kim *et al.,* 2012). In addition to C gas emissions, increased C losses, in the form of dissolved organic C, have been observed from peat soils (Freeman *et al.*, 2001a), which has been attributed to impaired microbial degradation coupled with increased plant inputs associated with global warming (Fenner *et al.*, 2007).

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

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

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

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

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

## Materials and methods

### *Soils*

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

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

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

Four cores, from each site, were used for analyses of initial soil moisture content, bulk density, total nutrient (C, N, P), $^{14}C$ content, microbial Phospholipid Fatty Acid biomarkers (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 20ºC.
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 10ºC and final enchytraeid
170 numbers determinations took place between February and June 2007.
171
172 *Gas measurements*
173 $CO_2$ 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). $CO_2$ 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 $CO_2$ (BOC, UK). $CO_2$ fluxes rates were calculated after applying linear regression analyses
180 to the $CO_2$ concentrations versus time data for each replicate core. $CO_2$ fluxes were
181 expressed on a per $m^2$ basis (Holland *et al.*, 1999).

182 The $Q_{10}$ values were calculated from the exponential model fitted to the $CO_2$ flux data
183 for the four incubation temperatures. The $Q_{10}$ is the proportional increase in respiration (R)
184 as the temperature increases by $10^0$C.

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

186 As the $Q_{10}$ only depends on the $a_1$ parameter the standard error of $Q_{10}$ was calculated
187 by:

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

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 $^{14}C$ 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 $^{14}C$ 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 $CO_2$ from combusted soil was converted to graphite on an iron catalyst using the hydrogen
201 reduction method (Vogel *et al.*, 1984) and the $^{14}C/^{12}C$ and $^{13}C/^{12}C$ ratios were measured by
202 accelerator mass spectrometry at the $^{14}$CHRONO Centre, Queen's University Belfast.

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

*Biotic community structure*

Microbial community biomass was also quantified with PLFA analyses. These biomarkers were extracted as part of the total lipid extract of freeze-dried soils (ca. 0.3 g dry weight) using a modified Bligh-Dyer extraction (White *et al.*, 1979; Crossman *et al*., 2004). PLFAs were quantified by the addition of a nonadecane standard of known concentration. GC analysis was carried out on an Agilent 6890 GC fitted with a CP-Sil 5CB fused silica capillary column (60 m x 0.32 mm ID; 0.25 μm film thickness). Carrier gas was hydrogen, and the flow was set to a constant velocity of 40 cm $sec^{-1}$. The temperature was raised, following an isothermal hold at 50°C for 2 min, to 150°C at 20 °C $min^{-1}$, then to 220°C at 3°C $min^{-1}$, followed by an increase to 340°C at 25°C $min^{-1}$ and a hold time of 5 min. Fatty acids were identified by retention time by comparison with previously identified samples and by gas chromatography-mass spectrometry on an Agilent 6890 GC connected to an Agilent 5973 Mass Selective Detector (GC conditions as above). Total PLFA concentration was calculated using all identified PLFAs. The Bacterial:Fungal ratio was calculated using the PLFA 18:2ω6,9 as an indicator of fungal biomass and the sum of 14 bacterial specific PLFAs identified as indicator of the bacterial biomass.

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

*Statistical analyses*

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

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

Linear correlations (Pearson correlation coefficient) were used to investigate the interdependence of the initial chemical and biological properties, $CO_2$ production B and $Q_{10}$ values as well as of final gas fluxes and enchytraeid data. In contrast, non-linear regressions (NLIN) were employed to describe the dependence of $CO_2$ fluxes with temperature at the end of the incubation period.

Final gas fluxes and enchytraeid numbers were not normally distributed but were approximately normal on the log scale. They were therefore log transformed either using $\log_{10}(n)$ or $\log_{10}(n+1)$ transformations. A general linear model (GLM) was fitted to the data (final $CO_2$ production and initial and final enchytraeid numbers) which included the effects of temperature, moisture, site from which the peat was obtained, and all two and three way interactions between these three experimental factors. In the case of enchytraeid numbers, the statistical analyses were then performed both with and without adjusting for initial

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

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

## Results

*Abiotic properties of the organic soil ecosystems*

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

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

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

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

*Biotic properties of the organic soil ecosystems*

The microbial communities in all soils were dominated by bacteria, especially in the peatland systems where the Bacteria:Fungi (B:F) ratio was significantly higher than in the boreal ones (ANOVA: $F_{1,9}$ = 15.76, $P$ = 0.0033). In contrast, fungi were more abundant in the boreal soils and best represented in the Swedish boreal systems (Fig. 1), although the differences were not significant. Furthermore, nutrient ratios exerted a strong influence on microbial communities and significant negative correlations were observed between total bacteria and C:P ratio (r = -0.62, $P$ = 0.0318) and between B:F and both C:P (r = -0.61, $P$ = 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 μmol $g^{-1}$ dry soil
309 against 15.27 μmol $g^{-1}$ 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 $CO_2$ production (mg $CO_2$-C $m^{-2}$ $h^{-1}$; $P > 0.05$). 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±0.20 *versus* 1.30±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±0.83 to 2.87±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 ($4^0$C) and $CO_2$ efflux rates gradually decreased with
338 increasing incubation temperatures (NLIN: $r^2 = 0.39$, $P < 0.0001$). Furthermore, more $CO_2$
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 4ºC. Additionally, different peat soils behaved differently (Table 3) and
342 the Scottish AUCH soil showed the lowest values of soil respiration (38.7 μg $CO_2$-C $m^{-2}$
343 $hr^{-1}$), 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 μg $CO_2$-C $m^{-2}$ $hr^{-1}$). 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 $CO_2$ 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 (> 15ºC) 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 4º and 15ºC temperatures stimulated $CO_2$ 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-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 $CO_2$ production, warming also had a negative effect on enchytraeid densities
369 (Table 4) and temperatures > 15ºC significantly decreased their populations numbers and
370 those soils incubated at 10ºC rendered the highest abundances (> 200,000 individuals.$m^{-2}$).
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 10ºC temperature treatment on enchytraeid reproduction
374 rates was reinforced (~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 20ºC; 66,000 and 86,000 individuals per square meter, respectively).

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

When considering the effects of both temperature and moisture treatments on each individual peat site (Fig. 4), it was obvious that the response was not uniform and that peat enchytraeid populations responded very differently to changes in the environmental conditions. Although in wetter soils survival success appeared better at lower temperatures (<10ºC; Fig. 4a), no significant effect of temperature on population sizes was found when the soils are saturated (Fig. 4a). In contrast, under drier conditions the animals seemed to prefer slightly warmer temperatures, with the exception of GDF where a significant decrease in population numbers was observed with increasing temperatures (Fig. 4b). Interestingly, enchytraeid numbers were positively linked to $CO_2$ production (n = 332; r = 0.12714, $P$ = 0.0205) and soils containing higher densities of these organisms emitted more $CO_2$ with wetter conditions exacerbating this effect (n = 164, r = 0.26103, $P$ = 0.0007).

## Discussion

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

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

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

In addition, the quality and nutrient characteristics of substrates also governs the accessibility of the SOM to soil biota and, hence, SOM turnover (Dungait *et al.*, 2012). This is a direct reflection of the control exerted by the dominant vegetation on the litter quantity and quality entering in the soil and, as a result, any alterations in the plant community composition, driven by changing temperature and moisture conditions, are expected to alter the quality of the organic matter (in terms of C:N ratios) susceptible to be decomposed (e.g. Meier & Bowman, 2008). For example, increased occurrence of periods with low water tables might result in a shift from mosses to ericoid shrubs species (Breeuwer *et al.*, 2009), which will have critical implications for SOM decomposition rates. This is due to ericoid and ectomycorrhizal fungi, which are particular abundant in 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 $CO_2$
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 $Q_{10}$ 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 $CO_2$ 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 $CO_2$ 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

mesofauna communities and a metric of soil C storage, with fungal dominated soils leading to greater C accumulation and bacteria possibly responsible for a greater turnover of recent labile substrates. In relation to this, rapidly cycling systems have been characterised as dominated by bacterial activity and enchytraeid grazing (Waldrop *et al.*, 2012) with our results showing that increased enchytraeid activity resulted in more $CO_2$ being emitted from peatland soils. However, the fact that we found more enchytraeids at the end of the experimental period than at the start of the experiment, when most of the labile substrates had been consumed, suggest that they were not only relying solely on these easily decomposable sources. Previous incubation studies have shown that if access to fresh/labile material is restricted or exhausted due to increasing competition pressures, enchytraeids can exploit more recalcitrant organic matter (Briones *et al.*, 2007a, 2010). However, lower quality organic matter puts severe restrictions on animal growth and therefore, in the field, their populations are usually concentrated in the upper topsoil layers where a wide range of food sources is available (Briones *et al.*, 2010). Additionally, enchytraeid reproduction rates have been linked to increasing temperatures (Standen *et al.*, 1973; Briones *et al.*, 1997), whereas their vertical distribution is determined by moisture (Briones *et al.*, 1997). Consequently, it is possible to suggest that, in our incubation study, wetter and mild temperatures (10-15ºC) provided the best range of environmental and nutrient conditions for enabling enchytraeids to grow.

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

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

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**Conflict of Interest**

The authors declare no conflict of interest.

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

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

**Table 3** Results from the GLM procedure for final soil respiration fluxes (μg $CO_2$-C $m^{-2}$ $hr^{-1}$) 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

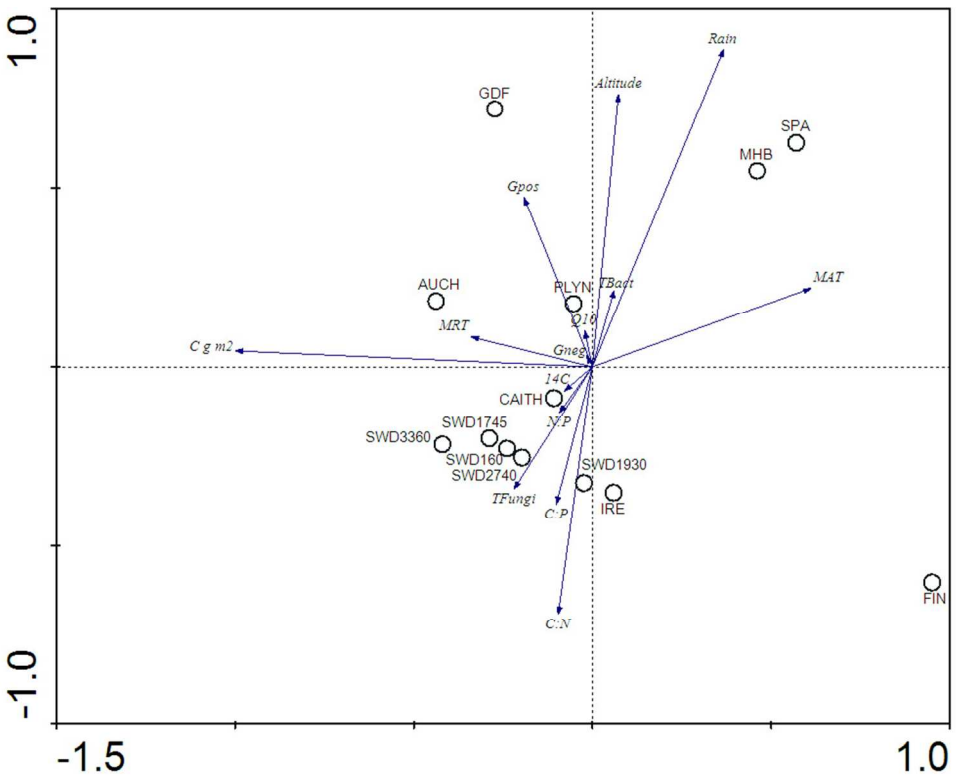
| Source | DF | Type I SS | Mean Square | F Value | Pr > F |
|---|---|---|---|---|---|
| SITE | 6 | 9.02929587 | 1.50488264 | 5.01 | <.0001 |
| TEMP | 3 | 11.79295155 | 3.93098385 | 13.08 | <.0001 |
| MC | 1 | 6.53577764 | 6.53577764 | 21.76 | <.0001 |
| SITE*TEMP | 18 | 36.09383463 | 2.00521303 | 6.67 | <.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.

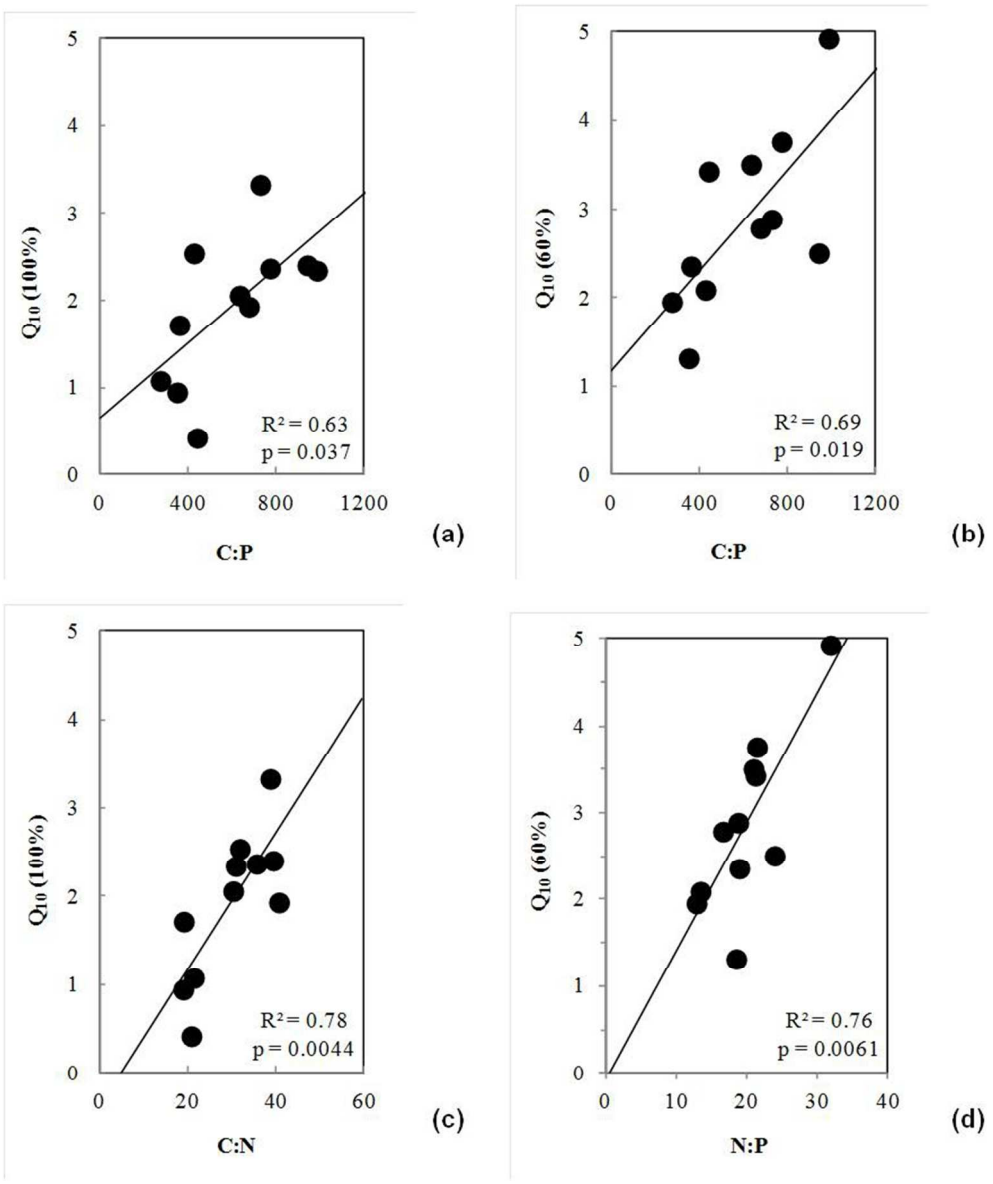
**Fig. 2** (**a**) Relationship between the temperature sensitivity of soil respiration ($Q_{10}$) and soil C:P ratio at field capacity moisture content. (**b**) Relationship between the temperature sensitivity of soil respiration ($Q_{10}$) and soil C:P ratio at 60% of field capacity moisture content. (**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 10ºC from each peatland soil previously incubated at 4, 10, 15 and 20ºC and two moisture levels (**a**) 100% WHC (**b**) 60% WHC. Values represent means ± standard errors with different letters indicating significant differences (Tukey-Kramer, $p < 0.05$) between temperature treatments.

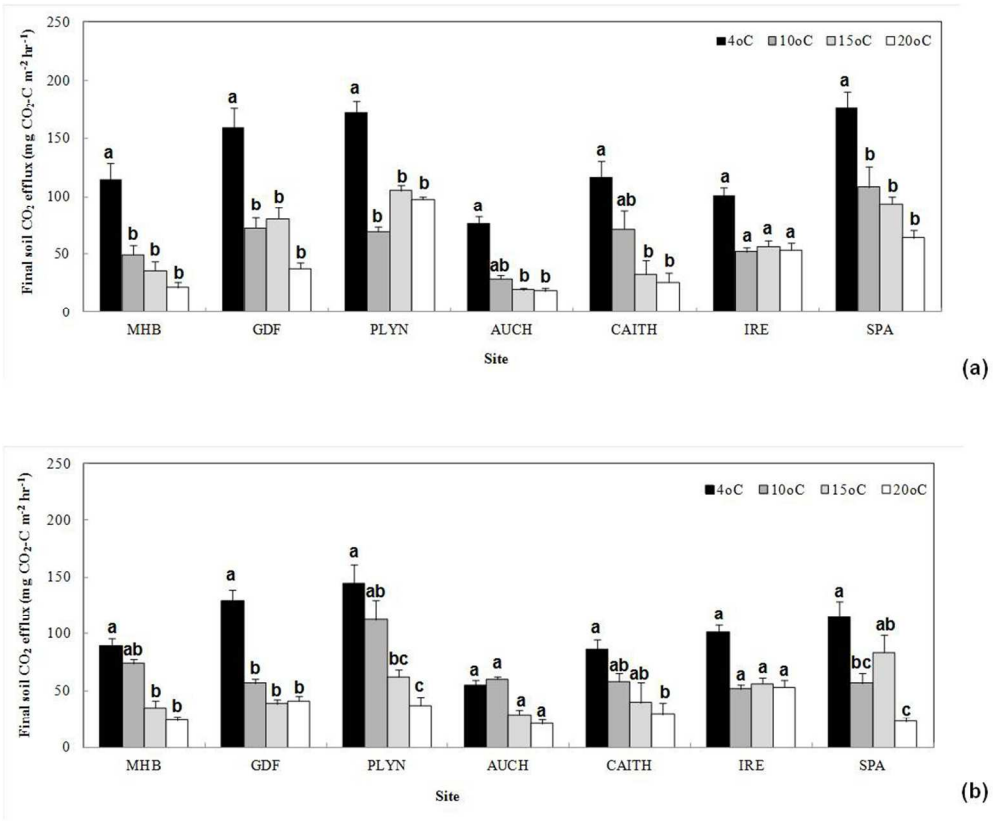
**Fig. 4** Final enchytraeid numbers from each peatland soil after being incubated at 4, 10, 15 and 20ºC and at two moisture levels (**a**) 100% WHC (**b**) 60% WHC. Values represent means ± standard errors with different letters indicating significant differences (Tukey-Kramer, $p < 0.05$) between temperature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



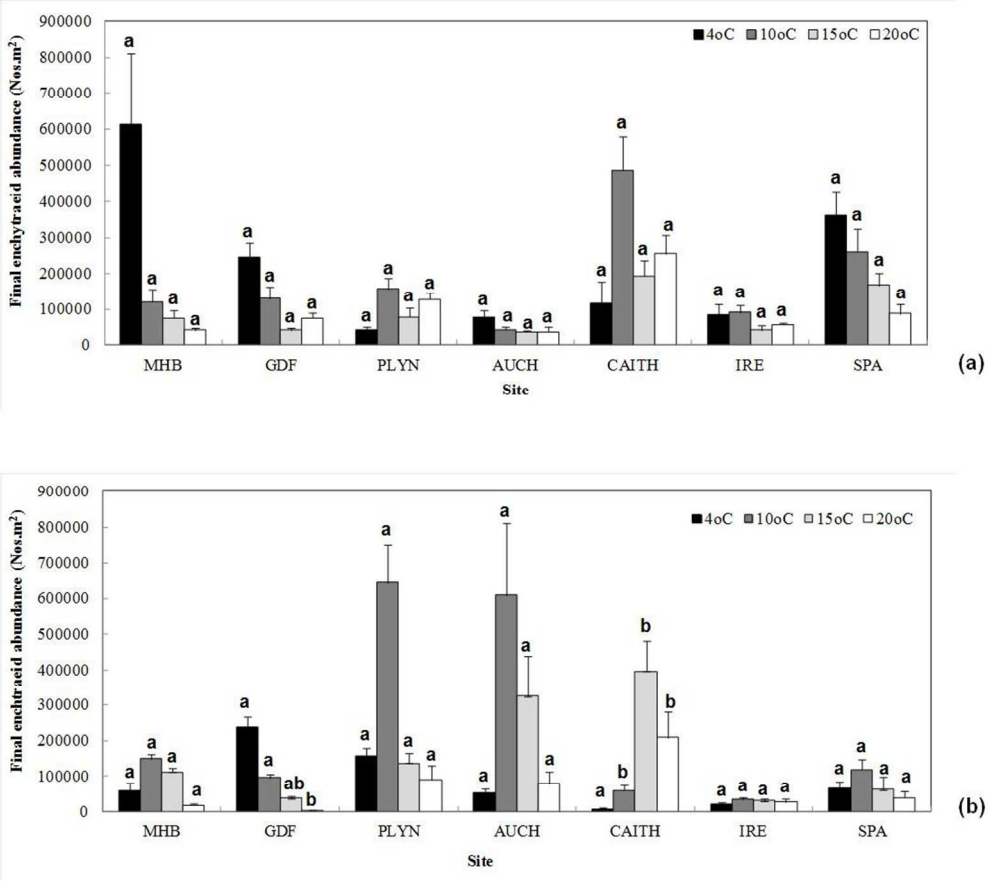

PCA biplot of the initial chemical and microbiological characteristics of the 6 boreal and 7 peatland sites investigated based on the first two axes.
361x294mm (72 x 72 DPI)




(a) Relationship between the temperature sensitivity of soil respiration (Q10) and soil C:P ratio at field capacity moisture content. (b) Relationship between the temperature sensitivity of soil respiration (Q10) and soil C:P ratio at 60% of field capacity moisture content. (c) Relationship between the temperature sensitivity of soil respiration (Q10) and soil C:N ratio at field capacity moisture content. (d) Relationship between the temperature sensitivity of soil respiration (Q10) and soil N:P ratio at 60% of field capacity moisture content.
150x176mm (150 x 150 DPI)




Final respiration fluxes at 10ºC from each peatland soil previously incubated at 4, 10, 15 and 20ºC and two moisture levels (a) 100% WHC (b) 60% WHC. Values represent means ± 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 20ºC and at two moisture levels (a) 100% WHC (b) 60% WHC. Values represent means ± standard errors with different letters indicating significant differences (Tukey-Kramer, $p < 0.05$) between temperature treatments.
184x162mm (150 x 150 DPI)