Soil Biology and Biochemistry

Microbial “hotspots” of organic matter decomposition in temperate peatlands are driven by spatial heterogeneity in abiotic conditions and not by vegetation structure

--Manuscript Draft--

Manuscript Number:	
Article Type:	Research Paper
Keywords:	Carbon, climate change, microbial communities, peatland habitats, plant functional type, spatio-temporal patterns
Corresponding Author:	Maria J.I. J.I. Briones, PhD Universidad de Vigo, Facultad de Biología Vigo, SPAIN
First Author:	Maria J.I. J.I. Briones, PhD
Order of Authors:	Maria J.I. J.I. Briones, PhD
	Raquel Juan-Ovejero
	Niall McNamara
	Nick Ostle
Manuscript Region of Origin:	SPAIN
Suggested Reviewers:	Richard Bardgett richard.bardgett@manchester.ac.uk Soil ecologist interested in understanding the role of interactions between plant and soil communities in regulating the structure and function of terrestrial ecosystems, and their response to global change
	Zoe Lindo zlindo@uwo.ca Aboveground-belowground approach for understanding the functional significance of biodiversity
	Christina Biasi christina.biasi@uef.fi soil ecologist interested in the microbial controls on greenhouse gas emissions, primarily in the Arctic

UNIVERSIDADE
DE VIGO

Prof. María Jesús Iglesias Briones

Tel. 986-812584; Fax: 986-812556
mbriones@uvigo.es

Please find enclosed our article entitled "**Microbial "hotspots" of organic matter decomposition in temperate peatlands are driven by spatial heterogeneity in abiotic conditions and not by vegetation structure**" submitted as a Research article to *Soil Biology and Biochemistry*.

Peatland soils are major global stores for carbon and whether they will release or build up these stores under climate change is a question of global significance. The role of soil biota and its interactions with the above-ground diversity in controlling soil carbon is absolutely critical, but remains totally ignored in current studies and models. Crucially, most of our understanding on the effects of climate changes on C stores comes from studies performed in the Arctic where non-vascular plants (namely, *Sphagnum* mosses) dominate. However, temperate peatlands (with other peat forming plant species) are currently undergoing a much more rapid retreat and pose serious risks in terms of GHG contribution than their northern counterparts due to their longer and warmer growing seasons.

Here we specifically tested if abiotic factors (soil temperature and soil moisture) are the major drivers of microbial community structure (PLFA) and C cycling in peatlands, while above-ground vegetation composition (plant functional types) acts as secondary modifier. We found that peat microbial communities were more strongly linked to local abiotic conditions than to the dominant above-ground vegetation and their responses determined C transformation pathways: the more aerobic and warmer conditions under shrubs accelerated fungal driven decomposition and CO_2 emissions, whereas decreases in Gram-negative bacteria under grasses promoted C losses as DOC. In the absence of these operating drivers, more C was retained (i.e. under mosses and sedges). Therefore, our study reveals that temperate peatlands should be considered 'ecosystem sentinels' for climate changes, acting as early-warnings indicators for climate-mediated impacts on the carbon cycle.

This knowledge is essential to gain a better understanding of the ecological linkages between above-ground and belowground communities (e.g. Bardgett & van der Putten 2014), and to decipher the mechanisms involved so we can build more realistic predictions on the direction and magnitude of the responses of these vulnerable ecosystems.

Sincerely,

Prof. M.J.I. Briones
On behalf of all co-authors

Highlights

- Peat microbial communities were more strongly linked to microclimatic conditions than to vegetation
- More aerobic and warmer soils under shrubs accelerated fungal driven decomposition and CO_2 emissions
- Decreases in Gram-negative bacteria under grasses promoted C losses as DOC
- In the absence of these operating drivers, more C was retained (i.e. under mosses and sedges)
- We propose temperate peatlands as 'ecosystem sentinels' for climate-mediated impacts on the C cycle

Title: Microbial "hotspots" of organic matter decomposition in temperate peatlands are driven by spatial heterogeneity in abiotic conditions and not by vegetation structure

Authors: Briones M.J.I.[1,2]*, Juan-Ovejero R.[1], McNamara N.P.[2], Ostle N.J.[3]

Affiliations:

[1]Departamento de Ecología e Biología Animal. Universidad de Vigo, 36310 Vigo, Spain

[2]UK Centre for Ecology & Hydrology, Lancaster Environment Centre, Lancaster LA1 4AP, UK

[3]Lancaster Environment Centre, Lancaster University, LEC Building, Lancaster LA1 4YQ, UK

***Corresponding author:**

M. J. I. Briones

Departamento de Ecología y Biología Animal. Universidad de Vigo. E-36310 Vigo (Pontevedra), Spain

Telephone: +34 986 812584

Fax: +34 986 812556

Email: mbriones@uvigo.es

Abstract

Climate change is triggering rapid shifts in plant communities and alterations in soil abiotic conditions in peatlands, with cascading effects on belowground decomposers and ecosystem C turnover. However, elucidating the dominant causal relationships between plant communities, soil biota and C fluxes in these vulnerable ecosystems requires a better understanding of the spatial-temporal variability of abiotic and biotic drivers. In this study we investigated the effects of biotic (plant functional types, PFTs) and abiotic factors (soil temperature and soil moisture) in determining dynamic patterns of soil microbial community structure and C cycling. Four representative temperate peatland habitats were selected based on their peat forming vegetation – an Atlantic wet heathland, two active blanket bogs with herbaceous plants (*Molinia caerulea* and *Eriophorum angustifolium*), and a transition mire dominated by *Sphagnum* mosses located along an altitudinal gradient to include the natural variations in soil temperature and water content regimes. We found that peat microbial communities were more strongly linked to local abiotic conditions than to the dominant above-ground vegetation. Aerobic conditions and warmer temperatures accelerated fungal driven decomposition and CO_2 emissions under shrubs, whereas decreases in Gram−negative bacteria promoted increased C losses under *Molinia*. These findings suggest that small spatial differences in abiotic conditions create local "hotspots" of organic matter decomposition under different PFTs. We propose that temperate peatlands should be considered as 'ecosystem sentinels' for climate change, acting as early-warning indicators of climate-carbon feedbacks.

Keywords: carbon, climate change, microbial communities, peatland habitats, plant functional type, spatio-temporal patterns

1. Introduction

The majority of the world's peatlands occur in boreal and temperate parts of the Northern Hemisphere where they cover around 3.5 million km^2 of land and store about 455 Gt of carbon (C), representing around 25% of all the soil C stored on earth (Moore, 2002). They are complex ecosystems, consisting of habitat mosaics containing plant species that form peat under high precipitation-low temperature climatic regimes that restrict decomposition, leading to carbon accumulation. Their plant communities are dominated by different functional types (PFTs) as defined by their growth forms (e.g. vascular woody plants, herbaceous forbs and graminoids and non-vacular plants including bryophytes; Dorrepaal, 2007). The PFTs supply a wide range of food sources (as litter and root exudates) to below-ground decomposers with cascading effects on ecosystem C turnover (De Deyn et al., 2008; Ward et al., 2015; Chen et al., 2016). In addition to nutrient inputs, the abiotic conditions are also key abiotic regulators of decomposer activities, with soil temperature and moisture determining anaerobic and aerobic processes (Cobb et al., 2017; Morton and Heinemeyer, 2019), and temperature defining the activation energy of biochemical reactions (Davidson and Janssens, 2006).

Consequently, climate change is expected to cause profound alterations in peatland hydrology that will increase rates of decomposition (Ise et al., 2008; Waddington et al., 2015). In addition, some projections forecast a functional shift in peatlands plant communities to favour vascular plants over mosses (e.g., Gallego-Sala and Prentice, 2013; Dieleman et al., 2015), which could exacerbate C losses (Walker et al., 2016; Robroek et al., 2016; Malhotra et al., 2020). As a result, concerns have risen about these critical C reservoirs becoming the largest natural global sources of C, with temperate peatlands being more likely to have a greater greenhouse gas contribution than their northern counterparts due to their longer and warmer growing seasons (Limpens et al., 2008; Teh et al., 2011).

When analysing the temperature sensitivity of peat C decomposition and potential feedbacks to climate change, the interactions between abiotic and biotic factors have been recognised as regulators of C cycling in these ecosystems (Briones et al., 2014; Armstrong et al., 2015; Juan-Ovejero et al., 2020). However, linking abiotic and biotic drivers of peatland C dynamics is challenged by the variability in plant-soil interactions even a small spatial scales. For example, in the particular case of peatlands, decomposition will vary through acrotelm and catotelm layers (Lunt et al., 2019), and as a result, the above- and below-ground phenologies are often unparallel (Schwieger et al., 2019). This could explain the contradictory responses reported in the literature, where certain PFTs have been found to strongly influence carbon dioxide (CO_2)

fluxes (Ward et al., 2013; Armstrong et al., 2015), whereas other studies concluded that abiotic factors are the main drivers of CO_2 production irrespective of PFTs (Preston et al., 2012; Haynes et al., 2015). Similarly, while some studies have detected correlative relationships between different PFTs and DOC (Armstrong et al., 2012), others have concluded that plant control on DOC release is indirect through their influence on soil fauna (Carrera et al., 2009; Juan-Ovejero et al., 2020).

Therefore, elucidating the dominant causal relationships between PFTs, soil biota and C fluxes in these ecosystems requires spatially and temporally extensive assessments of biotic and abiotic factors in field environments. Previous studies have shown that temporal variations of soil abiotic conditions across different PFTs result in profound alterations of soil mesofauna community structure as a consequence of their different ecophysiological adaptations to water table drawdown (Juan-Ovejero et al., 2019). However, there is a distinct lack of data on similar temporal changes in microbial community responses in such microhabitats, and the potential implications for the C sink/source function (see review by Zhong et al., 2020).

In this study, we aimed to disentangle the effects biotic (PFTs) and abiotic drivers (soil microclimatic conditions) on temperate peatland microbial community structure and C cycling. We selected four representative temperate peatland habitats based on their peat forming vegetation (Atlantic wet heathland (*Erica mackayana* and *Calluna vulgaris*), two active blanket bogs with herbaceous plants (*Molinia caerulea* and *Eriophorum angustifolium*), and a transition mire dominated by *Sphagnum* mosses) located at different elevations to include the natural altitudinal gradient in soil temperature and water content regimes (Bragazza et al., 2015). We hypothesized that distinct microbial communities will be associated with different PFTs (i.e., vascular vs. non-vascular), irrespective of their spatial location, in agreement with other studies linking peatland habitats to specific microbial taxa (Chroňáková et al., 2019). However, based on microbial responses to abiotic factors (e.g., Bragazza et al., 2015; Kumar et al., 2019), we also hypothesised that greater seasonal variations in temperature and moisture will determine changes in microbial community structure over time disregarding PFT. Finally, in addition to microclimatic conditions, litter quality differences among PFTs also drive microbial decomposition processes and accordingly, we expected a higher C turnover under a greater supply of more decomposable plant litter. *Sphagnum* mosses and shrubs have large concentrations of high molecular weight polyphenolic compounds they are very resistant to microbial attack (Hattenschwiler and Vitousek, 2000; Fenner and Freeman, 2011). Similarly, the cotton-grass *Eriophorum angustifolium* produces litter that is low in nutrient content than other vascular species and hence, its decomposition rates are similar to those of shrubs (Trinder et al.,

2008). In contrast, the graminoid *Molinia caerulea* is a fast growing grass that produces nutrient-rich litter (Certini et al., 2015; Kaštovská et al., 2018), proving a much greater supply of labile C to decomposers. Since previous modelling exercises have shown that C exports in these systems are abiotically mediated via direct and indirect effects on the mesofauna populations (Juan-Ovejero et al., 2020), we assessed if abiotic factors are also the major drivers of microbial decomposition, while above-ground vegetation composition acts as secondary modifier.

2. Materials and Methods

2.1. Peatland habitats

The study area is located in "Serra do Xistral'' (NW of the Iberian Peninsula) within the Atlantic Biogeographical Region. Data from the nearest meteorological station (Fragavella 43° 27" 16.56'' N, 7° 26" 46.5'' W; 710 m a.s.l.) indicate that the area is characterised by an oceanic climate, with a mean annual temperature of 10.5 °C (ranging from 6.0 °C in February to 16.0 °C in August) and annual rainfall of 1533 mm (spread throughout the year, but with lower rainfall between May and September (52-92 mm per month, on average) and a wet period between autumn and winter (134-227 mm per month, on average) in the 17 years prior to sampling. Similar temperature records were observed during the two years of study (2016 and 2017). However, 2017 was drier than 2016, with 25% less precipitation falling throughout the year (Fig. S1). This was due to the contrasting extreme rainfall values recorded in January of both years and the low precipitation records observed in July, September and October of 2017 compared with 2016 (Fig. S1).

Four different peatland habitats with functionally different plant communities (*sensu* Dorrepaal, 2007) were selected. Two of them were active blanket bogs (Nat-2000 7130) with herbaceous vascular plants: one dominated by the common cotton grass *Eriophorum angustifolium* and the endemic species of the Iberian NW *Carex durieuii* belonging to the Cyperaceae family (sedges) (43° 30' 12'' N, 7° 33' 02'' W; 970 m a.s.l.) and the other by the deciduous *Molinia caerulea*, a true grass belonging to the Poaceae family (43° 27' 36'' N, 7° 34' 12'' W; 960 m a.s.l.). The other two habitats were located in a valley (43° 26' 56'' N, 7° 33' 61'' W; 714 m a.s.l.): an Atlantic wet heathland Nat-2000 4020) where *Erica mackayana* but also *Calluna vulgaris* (woody vascular plants) colonize the drier fringes, and a transition mire (Nat-2000 7140) represented by pioneer communities associated with the existence of areas that receive a certain inflow of water, on which discontinuous tapestries of *Sphagnum* spp. are established (non-vascular) together with other hygrophilic plants (e.g. *Drosera* sp*., Rynchospora alba*). These sites, located in the north

146 west of Spain, represent the most southernmost location of these habitats within the Atlantic
147 Biogeographic Region and hence, likely to be most threatened by environmental changes. The
148 selection is also justified by the amount of exhaustive background information in the form of
149 flora inventories and habitat maps that is available (e.g. Izco Sevillano and Ramil-Rego, 2001;
150 Ramil-Rego and Izco, 2003; Rodríguez-Guitián et al., 2009; Cillero et al., 2016).

151

152 *2.2. Field sampling*

153 Intact peat samples were collected every two months at each peatland habitat during 2016 and
154 2017 (January to November; 12 samplings in total).

155 On each sampling occasion, to determine soil moisture at each habitat ten intact soil cores (PVC
156 pipes, 10 cm diameter x 10 cm depth) were randomly taken and oven-dried at 105 °C for 48 h
157 or until constant weight on re-weighing. Another subsample of fresh soil from each core was
158 freeze-dried and sieved (< 2 mm) and the total C and nitrogen contents determined by means
159 of a LECO elemental analyser (CN-2000, LECO Corp., St Joseph, MI).

160 Hourly soil temperature was recorded at 5 cm soil depth in each habitat for the duration of the
161 study using a temperature data logger (UA-002-08 HOBO). Due to temporal data acquisition
162 failures, 8% of temperature data were gap filled by triangulating temperature data from the
163 three nearest meteorological stations (for full details of the extrapolation procedure see Juan-
164 Ovejero et al., 2019).

165 Soil respiration was measured by inserting five PVC cylindrical collars (10 cm diameter × 10 cm
166 depth) into the soil (to a depth of 8 cm and approximately 2 cm remaining above the soil surface)
167 at each habitat on the first sampling occasion (January 2016), which remained in place for the
168 entire investigated period. We did this to avoid an overestimation of the soil CO_2 efflux
169 associated with perturbations due to the insertion of the PVC collars (Heinemeyer and
170 McNamara, 2011; Jovani-Sancho et al., 2017). We measured respiration rates ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$)
171 every two months (since March 2016) from all cores using a LI-8100 automated soil CO_2 flux
172 system (LI-COR Biosciences, Lincoln, Nebraska, USA) connected to a 10 cm survey chamber.

173 For DOC determinations, three additional intact soil cores of smaller size (PVC pipes, 5.5 cm
174 diameter × 10.5 cm depth) were also collected at each habitat on each sampling occasion. Soil
175 samples were leached by immersion in 200 ml of distilled water and draining under gravity
176 (Anderson and Ineson, 1982). The leachates were filtered (FilterLab® No. 1252, 7–9 μm pore
177 size) and frozen until analysis. Total dissolved organic C in the microbial extracts and leachates

was measured with a Shimadzu Total Organic Carbon Analyser (TOC-5000A) equipped with an autosampler ASI-V. The pH of the soil solutions was also measured using a Crison micropH 2000 and combination electrode.

Another set of three soil cores of the same size as before (PVC pipes, 5.5 cm diameter x 10.5 cm deep) were also taken from each peatland habitat on each sampling occasion, and frozen at -20 °C. These were subsequently freeze-dried (Christ alpha 1-4 LD Plus) and then sieved to 2 mm. Stones and roots were removed and the remaining soil was ball milled (Fritsch Planetary Mill Pulviresette 5) to a fine powder. Bulked subsamples of the 0-10 cm freeze-dried ground soil (≈ 1 g dry weight) were used for PLFA analyses to determine the microbial community structure under each system.

2.3. PLFA profiling

PLFA biomarkers were extracted as part of the total lipid extract of freeze-dried soil samples using a modified Bligh-Dyer extraction (White et al., 1979). Briefly, the method included three key steps: (i) lipid extraction using a single-phase chloroform mixture; (ii) lipid fractionation according to polarity (neutral lipids (hydrocarbons, free fatty acids and sterols), glycolipids and polar lipids (phospholipids)); and (iii) mild alkaline methanolysis of phospholipids to produce fatty acid methyl esters (FAMEs). Two blanks and two standards (C13:0 and C19:0) were used per batch of 21 samples for quality control assurance purposes.

Identification of PLFA's was carried out on a GC (Agilent Technologies 6890) fitted with a mass selective detector (Agilent technologies 5973). The straight-chain saturated fatty acids (14:0, 15:0, 16:0, 18:0 and 17:1ω8) were considered to be general bacterial markers (Willers et al., 2015). The terminal and mid-chain branched fatty acids 15:0i, 15:0a, 16:0i, 17:0i and 17:0a were used as indicators of Gram−positive bacteria (Whitaker et al., 2014) together with the branched saturated br17:0 and br18:0 (Seifert et al., 2011) and the methyl branched saturated fatty acid 7Me-17:0 (Willers et al., 2015). Cyclopropyl saturated (7 cyclic 17:0 and 7,8 cyclic C19:0) and monounsaturated fatty acids (16:1ω7, 16:1ω7, 18:1ω5 and 18:1ω7) were used as indicators of Gram−negative bacteria (Rinnan and Baath, 2009). The fatty acids 18:2ω6,9 was taken as indicator of fungi (Kaiser et al., 2010). Due to the poor correlation between 18:2ω6,9 and 18:1ω9 that makes the latter biomarker a poor indicator of fungi (Frostegård et al., 2011), this and two other monounsaturated fatty acids (16:1 and 19:1) were assigned to the “unspecific microbial biomarkers” category. Each identified PLFA was quantified as μg g^{-1} dwt soil. Total microbial

biomass was taken as the sum of all identified PLFA's (n = 23). See also Table S1 for the full list of PLFA markers used for taxonomic microbial groups and microbial indicators.

2.4. Statistical analyses

Data were checked for normality and homogeneity of variances using the Kolmogorov–Smirnov and Levene's tests, respectively, and transformed where necessary before running parametric analyses. We first tested for significant differences in microbial biomarker abundances between different PFTs across the whole study as well as per sampling date using ANOVA (Generalised Linear Model or GLM) followed by the Tukey's Studentized range tests. In addition, we used linear regression analyses to detect any potential relationships between the concentrations of the different PLFA biomarkers and the two independent variables (soil water content and soil temperature values) across PFTs. Both types of analyses were performed using SAS system v9.3 (SAS Institute, Cary, NC, USA, 2011).

Since biological responses to changes in the environment are nonlinear but unimodal, we also used Detrended Canonical Correspondence Analysis (DCCA) to identify the best set of response variables that explain the observed temporal patterns of variation in microbial community structure (ter Braak, 1986). Therefore, we analysed the relationships between the microbial communities and the environmental gradients in abiotic soil properties and C transformations (soil respiration and DOC exports) at each PFT. For these analyses, we combined existing data from 2016 and 2017 that showed a crucial role of direct and indirect effects of abiotic factors on the release of gaseous and aqueous C across the PFT's at our field sites (Juan-Ovejero et al., 2020; see also Table S2). The ordination result is displayed as a triplot, showing the optimum distribution of the microbial groups (points) along these environmental gradients (arrows) and PFTs as "centroids" (i.e. the (weighted) mean of response variables at a particular habitat). We further checked the variance inflation factor among selected variables to test the independence of the variables in the ordination space. Finally, the statistical significance of the relationship between the species and the whole set of environmental variables was tested using Monte Carlo permutation test. DCCA analyses were performed using the CANOCO software for Windows v4.5 (ter Braak and Šmilauer, 2002).

3. Results

3.1. Microbial community structure under different PFTs

Total PLFA biomarker abundance was significantly higher in the peat samples from the Atlantic wet heathland and the *Sphagnum* site (152.8±5.3 and 140.6±5.4 μg g^{-1}, respectively) than from the two blanket bogs (*Eriophorum*: 108.7±3.7 and *Molinia*: 105.4±4.2 μg g^{-1}; Table 1 and Fig. 1a).

However, microbial community structure was very similar across habitats, with bacteria being the most dominant group relative to total abundance (79-80%; Fig. 1b), and fungi representing the smallest proportion (< 3%; Fig. 1b). As a result, the Fungal:Bacteria (F:B) ratio was low across all four peatland habitats (0.02-0.03). Among the bacterial groups, Gram−negative biomarkers were significantly more abundant (35.9-40.1% of total PLFAs) than Gram−positive ones (23.6-28.5% of total PLFAs), and with general bacterial markers accounting for 16.2-18.3% of total PLFA concentrations (Fig. 1b). Consistently with total PLFA concentrations, these three PLFA groupings showed significantly lower values at the two blanket bogs (Fig. 1b and Table 1).

Further support for this clear distinction between upland and lowland valley bottom areas was found in the PLFA profiles (Fig. 2), which indicated that the concentrations of up to nine biomarkers were significantly higher in the samples from the two valley habitats than from the two blanket bogs, including the most abundant bacterial fatty acids (palmitic acid-C16:0, pentadecanoic acid-C15:0i, C18:1ω7, and 7,8Cy-C19:0; > 10 μg g^{-1}). However, the concentrations of other less well represented fatty acids allowed the separation between individual PFTs. Thus, peat samples collected from *Erica* dominated site had significantly higher concentrations of C16:0i, brC17:0, brC18:0, C16:1ω7, C17:1ω8, C19:1 and the fungal marker 18:2ω6,9; *Sphagnum* peat contained significantly more C14:0, C15:0a, and the least of C18:1ω5; *Molinia* was best characterised by the lowest concentrations of C15:0a and 7Cy-C17:0; *Eriophorum* had the lowest values of C16:0i, brC17:0, brC18:0, and 18:2ω6,9, but the highest ones of C16:1ω5 (Fig. 2).

3.2. *Abiotic regulation of microbial communities*

Monthly concentrations of total PLFAs indicated that, although the two valley habitats showed the highest PLFA concentrations during the 2 years-field study, the differences with the other two peatland habitats were mainly noticeable in 2017, in particular for the period from May to September (Fig. 3a). Despite the fact that a similar dry spell was observed from May to October of both sampled years at the study area (i.e. higher temperatures were coincidental with lower rainfall values), warmer ambient temperatures (above 12 ^{o}C) were recorded during those

months in 2017 than in 2016 (Fig. S1). Consequently, the peat soil was also significantly warmer at the two valley habitats (15.8 ^{o}C on average) than at the two upland ones (13.7 ^{o}C) in 2017 (Fig. S2). Similarly, the hot soil temperatures recorded in July 2016 at these two sites (19-20 ^{o}C; Fig. S2) also explain the significant increases in total PLFA concentrations observed in the peat samples collected from the lowest elevation (Fig. 3a). This finding was further supported by the significant positive relationship between total PLFA concentrations and soil temperature (Linear regression; p= 0.0104), which was not detected in the case of soil moisture.

A similar temporal pattern was observed for the Gram−positive bacteria (Fig. 3b), with the *Erica* site consistently showing the highest abundance of this bacterial group and the habitat dominated by *Molinia* the lowest values during the two investigated years. Interestingly, and for most of 2016, the peat under *Sphagnum* had concentrations of this bacterial group that were more similar to those recorded at the two blanket bogs than to those of the heathland (Fig. 3b). This was related to higher soil moisture contents being measured at these three sites compared to the heathland (Fig. S2); however, the negative relationship between Gram−positive bacteria and soil water content was only marginally significant (Linear regression; p = 0.0567).

In contrast, the abundance of Gram−negative bacteria showed a more variable pattern over time at all four habitats (Fig. 3c), and although the two blanket bogs were typically associated with lower concentrations of this PLFA grouping, the two other habitats showed marked fluctuations, especially in 2017. In particular, under *Sphagnum* mosses, significantly lower abundances of Gram−negative bacteria were observed in September of both years (Fig. 3c) that were mainly driven by decreases in the concentrations of the monosaturated fatty acid C16:1ω7 in response to increases in soil water content (Linear regression; $p < 0.0001$).

More marked abundance fluctuations with time were observed in the case of the fungal biomarker C18:2ω6,9, and even more so in the case of the two valley habitats (Fig. 3d). Unlike bacterial biomarkers, fungal abundances under *Sphagnum* were very similar to those measured under sedges except for September 2016, when the concentrations of this PLFA biomarker peaked and reached similar values to those observed in the heathland (Fig. 3d). Across the whole investigated period, the highest fungal abundance was observed in the drier and warmer soils from the *Erica* site, and significantly higher concentrations of this biomarker were found on most sampling occasions, when compared with the other three habitats, albeit few exceptions (i.e. January-2016, March and September of both years and November-2017; Fig. 3d). These rapid responses to changes in local abiotic conditions can be attributed to the strong negative relationship between fungi and soil moisture (Linear regression; $p < 0.0001$).

306

307 *3.3. Above-ground vegetation, below-ground microbial communities and C cycling*

308 The output from the canonical multivariate analysis (Fig. 4) revealed the existence of positive
309 relationships between PFTs, certain microbial PLFA groupings and indicators, and C turnover at
310 these four peatland habitats. The first ordination axis explained 50.2% of the species-
311 environment relation variance and was significant (Monte Carlo test: F-ratio = 8.452, P-value =
312 0.032). It confirmed the similarities between the two the valley habitats based on the microbial
313 community structure, by showing the highest bacterial dominance, and more specifically
314 Gram−negative bacteria, than the two upland habitats (*Molinia* and *Eriophorum*).

315 The second canonical axis accounted for 26.2% of the variance and revealed that the *Erica* site,
316 and to a less extent the *Molinia* habitat, could be differentiated from the other two peatland
317 habitats in terms of microclimatic conditions and C transformations. Accordingly, the warmer
318 and drier peat soils at the heathland, with the highest abundance of fungi and Gram−positive
319 bacteria, emitted more C as CO_2, whereas the soils under *Molinia* grasses with higher F:B and
320 Gpos:Gneg ratios were exporting C mainly as dissolved organic carbon (DOC). This contrasted
321 with the wetter soils under *Eriophorum* and *Spagnum* mosses that produced less acidic soil
322 solutions and retained more C (i.e., higher C:N ratio and lower C release; Fig. 4).

323

324 **4. Discussion**

325 *4.1. Linking habitat properties to below-ground microbial community structure*

326 The two-year field study showed that microbial communities were more strongly linked to local
327 soil abiotic conditions than to the dominant above-ground vegetation. These results contradict
328 previous studies concluding that different vascular plants are inhabited by unique microbial
329 communities (Chroňáková et al., 2019), but agree with those observations in tropical peatlands
330 where contrasting plant communities supported similar microbial communities (Girkin et al.,
331 2020).

332 The four peat soils investigated here had very similar edaphic characteristics (low bulk density,
333 high C content, low soil pH), but the peat under mosses had higher porosity (with the majority
334 being macropores) than the other three peat soils (Juan-Ovejero et al., 2019). This means that
335 water is able to move more freely within the peat matrix under the non-vascular plant
336 community but is more efficiently retained under the vascular vegetation, creating localised

differences in hydrology. In addition, the location of study sites at different altitudes provides an additional set of microclimatic conditions that shape these habitats. Accordingly, the two blanket bogs located at 960-970 m a.s.l. are subjected to more frequent precipitation and upslope fogs (Ramil-Rego et al., 2017), making them the most ombrotrophic habitats investigated. In contrast, the two habitats at the lowest elevation experienced slightly warmer soil temperatures (≈1.7 ^{o}C, on average across the two years) and more variable patterns in soil moisture due to greater microtopographical heterogeneity (i.e., the *Erica* heath colonises the drier hummocks and hence, are more disconnected from the water table, whereas the transition mire consisted of wetter flat lawns that are occasionally inundated).

Because of these microclimatic differences, a greater spatial dissimilarity in microbial community structure was expected across investigated sites. A shift in soil microbial community structure with altitude has been previously observed, with fungi, relative to bacteria, being less abundant at higher elevations (Bragazza et al., 2015) and, in agreement with this study, we also found an increasing abundance of fungi with improved soil oxygenation. This has been explained by the sensitivity of fungi to anoxic conditions (Jaatinen et al., 2007; Peltoniemi et al., 2009; Kwon et al. 2013; Lamit et al., 2017), which was corroborated by the negative relationship between fungi and peat water content observed here and in previous studies (Bragazza et al., 2015; Girkin et al., 2020). Fungal communities were low at all four investigated sites compared to other PLFA biomarkers, in particular when compared to bacteria, in agreement with previous observations (Briones et al., 2014); however, those habitats that experienced more often drier spells created more favourable conditions for their communities. This was the case of the Atlantic wet heath but also the blanket bog dominated by *Molinia caerulea*, where soil water contents below 75% were recorded on several months of both sampled years (Fig. S2).

The greatest bacterial dominance at the investigated sites is typical of temperate peatlands (Gilbert and Mitchell, 2006; Andersen et al., 2013; Briones et al., 2014; Chroňáková et al., 2019). Both Gram−positive and Gram−negative as well as general bacterial PLFA biomarkers were significantly more abundant in the peats under *Erica* and *Sphagnum* than in the two blanket bogs, which is in agreement with the suggestion that their abundance tends to decrease along the minerotrophic-ombrotrophic gradient (Jaatinen et al., 2007). Prokaryotes have been observed to respond more to local edaphic properties associated to specific habitats than fungi (Chroňáková et al., 2019), with pH, N and water table being the most influential factors controlling their communities (Waldrop et al., 2012; Kaštovská et al., 2018; Tian et al., 2019).

Due to the great similarities in soil pH and N content across our investigated sites, microclimatic conditions might have played a more determinant role in structuring soil bacteria communities under the different PFTs. The marked temporal variability shown by bacterial abundances during the investigated period indicates that their populations are strongly influenced by intra- and inter-annual fluctuations in soil temperature and moisture. Accordingly, the observed negative relationship between peat water content and Gram−negative bacteria has been previously reported (Balasooriya et al., 2008), whereas warmer peat temperatures seemed to decrease the abundance of Gram−positive bacteria (Bragazza et al., 2015), which suggest a better adaptability of the latter group to anaerobic soil conditions (e.g. Actinomycetes, the most abundant Gram-positive group are facultative anaerobes). However, their consistently greater abundance at the warmest and driest site during the investigated period does not support this latter conclusion. Furthermore, it has been suggested that the abundance of monounsaturated and saturated PLFAs in peat samples are indicative of the presence of aerobic and anaerobic eubacteria, respectively (Sundh et al., 1997) and, in our samples, monosaturated PLFAs were the most abundant biomarkers (46%), suggesting that aerobic bacteria dominated bacterial community composition at these sites. The fact that these changes in relative abundance of soil bacteria are context-dependent and driven by one or a few taxa (Naylor and Coleman-Derr, 2017) could also explain these discrepancies with the published literature.

4.2. Linking microbial community structure to C fluxes across different habitats

Because the four dominant plant species differed in their litter quality, we anticipated higher decomposition rates under vascular plants than under mosses, in agreement with previous studies (Ward et al., 2013; Walker et al., 2016), but more so under graminoids than under sedges and shrubs, due to higher N and lower polyphenolic contents in the litters (Ward et al., 2009, 2015; Bragazza et al. 2013) and enhanced microbial priming effects (Dieleman et al., 2017). Our results partly confirmed these findings with more DOC released from the peat under *Molinia*, and the highest respiration rates measured under *Erica*. This can be attributed not only to a more favourable abiotic environment for microbial activities (i.e. warmer temperatures and oxic conditions) at the Atlantic heathland, but also to the fact that the association of ericoid mycorrhizas to the hair roots of ericaceous shrubs can increase the supply of labile C to decomposers (Trinder et al., 2008). Furthermore, it has been shown that, in peatlands, increased aerobic conditions favour CO_2 over DOC as a metabolic end product (Freeman et al., 2004). Increased oxygen concentrations in the rhizosphere also remove the enzymatic latch preventing

C decomposition (Freeman et al., 2001, 2004; Fenner and Freeman, 2011; Dunn and Freeman, 2018) and together with warmer soil temperatures enhancing both microbial and root respiration could explain the higher CO_2 emissions observed under shrubs. From this, it is possible to anticipate that the expansion of shrubs in peatlands might not prevent microbial decomposition as suggested by some studies (Wang et al., 2015; Ward et al. 2015).

Interestingly, the larger C exports from shrub and graminoid dominated systems were also associated with increased abundances of fungi and Gram−positive bacteria under shrub and to higher F:B and Gpos:Gneg ratios under *Molinia*, suggesting that these three microbial groups and their relative abundances play a critical role in peatlands C cycling. High F:B ratios have been associated with the greatest temperature sensitivity of soil respiration (Briones et al., 2014) and consequently, under shrubs increased peat aeration led to a greater abundance of fungi relative to bacteria, whereas under graminoids the higher values of this ratio were caused by the overall decrease in total bacterial abundances. Similarly, the higher Gpos:Gneg ratio observed under shrubs and graminoids compared with the other habitats was a reflection of a higher abundance of Gram−positive bacteria in the case of the *Erica* site, but of a decreasing abundance of Gram−negative bacteria in the peat under *Molinia*. The lower abundances of Gram−negative bacteria correlated with increased DOC production, which contradicts previous observations (Bragazza et al., 2015). In addition, Fanin et al. (2019) suggested that Gpos:Gneg ratio has potential as a useful indicator of the relative C availability for soil bacterial communities in organic soils and accordingly, this ratio increases with decreasing labile C availability. This is because Gram−positive and Gram−negative bacteria use older C and fresh plant material, respectively, as substrates (Börjesson et al., 2012). Consequently, Gram−positive bacteria are more resilient under environmental stresses than Gram−negative bacteria and their numbers tend to increase in response to drought (Naylor and Coleman-Derr, 2019) and in nutrient-poor soils (Connon et al., 2007; Yuste et al., 2014; Mohammadipanah and Wink, 2016; Hartmann et al., 2017). Indeed, the Gram−positive and Gram−negative bacteria distinction overlaps with that of oligotrophic-copiotrophic since Gram−negative bacteria rely on labile C compounds, preferably in the form of plant root exudates (Balasooriya et al., 2014). However, in this study, higher Gpos:Gneg ratios did not correlate well with higher C:N ratios, which contradicts previous studies in boreal peatlands comparing a *Carex*-dominated fen and *a Sphagnum*-dominated fen (Lyons and Lindo, 2020) and the predictions from the proposed indicator (Fanin et al., 2019).

On the other hand, it has been shown that the anteiso fatty acids promote a more fluid membrane structure than the iso fatty acids, and that the bacteria producing these fatty acids modify their iso:anteiso ratio in response to temperature and pH stress (Zhang and Rock, 2008),

436 and anaerobic conditions (Weijers et al., 2006). The Gram−positive bacteria recorded in this
437 study showed higher values of the iso:anteiso ratio at the shrub and graminoid dominated
438 habitats than at the other two sites (with the lowest values being measured under *Sphagnum*
439 mosses; results not shown), indicating that no substantial amounts of anteiso fatty acids were
440 necessary for their growth at the two former habitats. Since soil temperature and pH cannot
441 explain these differences, less aerobic conditions is the most likely factor driving these
442 responses. The two habitats dominated by mosses and sedges were the wettest ones, with very
443 little soil moisture fluctuations during the investigated period. Their plant species are well
444 adapted to nearly constant waterlogging conditions, unlike shrubs and *Molinia caerulea* that
445 better develop in well-oxygenated soils, conditions favoured by local topography (i.e.,
446 hummocks for the shrub vegetation and the leeward orientation of the *Molinia* bog; Juan-
447 Ovejero et al., 2019).

448 Furthermore, improved peat aeration also influences the pH of the soil solution, with peat
449 oxidation decreasing the pH in the aerobic layer, and reductive reactions increasing the pH in
450 the anaerobic layer (Adamson et al. 2001; Loeb et al. 2008). In agreement with this finding, it
451 has been observed that warmer temperatures produce more acid soil solutions, whereas
452 increased peat wetness has the opposite effect (Carrera et al., 2011). Because less acid leachates
453 are linked to higher C exports as DOC (Jansen et al., 2003, 2005; Carrera et al., 2009, 2011), it is
454 possible to conclude that hydrology plays a crucial role in controlling C fluxes in these temperate
455 peatland soils.

456

457 **Conclusions**

458 Research to find common mechanisms that shape the diversity of above- and below-ground
459 plant-soil organisms have shown that community structure is governed by many interacting
460 factors (Bardgett and van der Putten, 2014). In temperate peatlands, local abiotic factors (such
461 as microtopography, soil temperature and pH, water and pore space availability, etc.) and
462 differences in local plant communities are expected to have a strong influence on soil
463 communities and C cycling. Despite the high heterogeneity in the peatland habitats included in
464 our study, we did not find that peat botanical origin was the main driver structuring microbial
465 communities, in contradiction with other studies (Girkin et al., 2020). Instead, changes in the
466 local abiotic environment, even at small spatial scales (namely, peat temperatures and aeration),
467 exerted a stronger influence on microbial community composition and temporal shifts in their
468 relative dominance. However, we could not confirm the contrasting relationships between

469 Gram−positive and Gram−negative with altitude (Bragazza et al., 2015; Kumar et al., 2019), nor
470 between Gram−negative bacteria and labile C availability (Balasooriya et al., 2014; Lyons and
471 Lindo, 2020), as observed patterns were better explained by their different ecological
472 requirements and stress tolerance to environmental changes.

473 Importantly, our results confirmed that certain microbial indicators, such as the F:B and
474 Gpos:Gneg ratios, are reliable proxies for C transformations in peatlands (Briones et al., 2014;
475 Fanin et al., 2019); however, careful interpretation of the changes in the abundances of both
476 fraction terms is required. While aerobic conditions and warmer temperatures accelerate fungal
477 driven decomposition and CO_2 emissions, decreases in Gram−negative bacteria might trigger
478 increased C losses in the soil solution, and hence creating local "hotspots" of organic matter
479 decomposition. Since it has been suggested that lowered water tables may pose more serious
480 risks to temperate peatlands than warmer temperatures under projected future climate
481 changes (Urbanová et al., 2013; Morton and Heinemeyer, 2019; Tiang et al., 2020), we propose
482 that these high sensitive systems should be considered as 'ecosystem sentinels' for climate
483 change-mediated impacts on the C cycle.

484

485 **Acknowledgements**

486 We are very grateful to Dr Annette Ryan (Lancaster University) for her valuable support with
487 PLFAs procedures and to Kelly Mason (UKCEH) for her advice on microbial biomarkers
488 assignation. This work was funded by a MINECO research grant (Ref. CGL2014-54861-R) and R.
489 Juan-Ovejero was supported by a PhD fellowship (FPI Programme, Ref. BES-2015-074461). MJIB
490 would also like to thank Xunta de Galicia (Ref. 10 PXIB 310 142 PR and CITACA Strategic
491 Partnership ED431E 2018/07) for funding the research visits made to the UK.

492

493 **References**

494 Adamson, J.K., Scott, W.A., Rowland, A.P., Beard, G.R., 2001. Ionic concentration in a blanket
495 peat bog in northern England and correlations with deposition and climate variables. *European*
496 *Journal of Soil Science, 52*, 69–79. https://doi.org/10.1046/j.1365-2389.2001.t01-1-00350.x

497 Andersen, R., Chapman, S.J., Artz, R.R.E., 2013. Microbial communities in natural and disturbed
498 peatlands: a review. *Soil Biology and Biochemistry, 57,* 979–994.
499 https://doi.org/10.1016/j.soilbio.2012.10.003

Anderson, J.M., Ineson, P., 1982. A soil microcosm system and its application to measurements of respiration and nutrient leaching. *Soil Biology and Biochemistry, 14*, 415–416. https://doi.org/10.1016/0038-0717(82)90015-3

Armstrong, A., Holden, J., Luxton, K., Quinton, J.N., 2012. Multi-scale relationship between peatland vegetation type and dissolved organic carbon concentration. *Ecological Engineering, 47*, 182–188. https://doi.org/10.1016/j.ecoleng.2012.06.027

Armstrong, A., Waldron, S., Ostle, N.J., Richardson, H., Whitaker, J., 2015. Biotic and abiotic factors interact to regulate northern peatland carbon cycling. *Ecosystems, 18,* 1395–1409. https://doi.org/10.1007/s10021-015-9907-4.

Balasooriya, W.K., Denef, K., Huygens, D., Boeckx, P., 2014. Translocation and turnover of rhizodeposit carbon within soil microbial communities of an extensive grassland ecosystem. *Plant and Soil, 376,* 61–73. https://doi.org/10.1007/s11104-012-1343-z

Balasooriya, W.K., Denef, K., Peters, J., Verhoest, N.E.C., Boeckx, P., 2008. Vegetation composition and soil microbial community structural changes along a wetland hydrological gradient. *Hydrology and Earth System Sciences, 12,* 277–291. https://doi.org/10.5194/hess-12-277-2008

Bardgett, R.D., Van Der Putten, W.H., 2014. Belowground biodiversity and ecosystem functioning. *Nature, 515*, 505–511. https://doi.org/10.1038/nature13855

Börjesson, G., Menichetti, L., Kirchmann, H., Kätterer, T. 2012. Soil microbial community structure affected by 53 years of nitrogen fertilisation and different organic amendments. *Biology and Fertility of Soils*, *48*, 245–257. https://doi.org/10.1007/s00374-011-0623-8

Bragazza, L., Bardgett, R.D., Mitchell, E.A.D., Buttler, A., 2015. Linking soil microbial communities to vascular plant abundance along a climate gradient. *New Phytologist, 205*, 1175–1182. https://doi.org/10.1111/nph.13116.

Bragazza, L., Parisod, J., Buttler, A., Bardgett, R.D., 2013. Biogeochemical plant-soil microbe feedback in response to climate warming in peatlands. *Nature Climate Change, 3,* 273–277. https://doi.org/10.1038/nclimate1781

Briones, M.J.I., McNamara, N.P., Poskitt, J., Crow, S.E., Ostle, N.J., 2014. Interactive biotic and abiotic regulators of soil carbon cycling: Evidence from controlled climate experiments on peatland and boreal soils. *Global Change Biology, 20*, 2971–2982. https://doi.org/10.1111/gcb.12585

Carrera, N., Barreal, M.E., Gallego, P.P., Briones, M.J.I., 2009. Soil invertebrates control peatland C fluxes in response to warming. *Functional Ecology, 23*, 637–648. https://doi.org/10.1111/j.1365-2435.2009.01560.x

Carrera, N., Barreal, M.E., Rodeiro, J., Briones, M.J.I., 2011. Interactive effects of temperature, soil moisture and enchytraeid activities on C losses from a peatland soil. *Pedobiologia, 54*, 291–299. https://doi.org/10.1016/j.pedobi.2011.07.002

Certini, G., Vestgarden, L.S., Forte, C., Tau Strand, L., 2015. Litter decomposition rate and soil organic matter quality in a patchwork heathland of southern Norway. *Soil, 1*, 207–216. https://doi.org/10.5194/soil-1-207-2015

Chen, D., Pan, Q., Bai, Y., Hu, S., Huang, J., Wang, Q., Naeem, S., Elser, J.J., Wu, J., Han, X., 2016. Effects of plant functional group loss on soil biota and net ecosystem exchange: a plant removal experiment in the Mongolian grassland. *Journal of Ecology, 104*, 734–743. https://doi.org/10.1111/1365-2745.12541

Chroňáková, A., Bárta, J., Kaštovská, E., Urbanová, Z., Picek, T., 2019. Spatial heterogeneity of belowground microbial communities linked to peatland microhabitats with different plant dominants. *FEMS Microbiology Ecology, 95*, fiz130. https://doi.org/10.1093/femsec/fiz130

Cillero, C., Díaz-Varela, R.A., Rubinos, M., Ramil-Rego, P., 2016. Assessment of anthropogenic pressures on South European Atlantic bogs (NW Spain) based on hydrochemical data. *Hydrobiologia, 774*, 137–154. https://doi.org/10.1007/s10750-016-2778-7

Cobb, A.R., Hoyt, A.M., Gandois, L., Eri, J., Dommain, R., Salim, K.A., Kai, F.M., Su'ut, N.S.H., Harvey, C.F., 2017. How temporal patterns in rainfall determine the geomorphology and carbon fluxes of tropical peatlands. *PNAS* 114, E5187–E5196. https://doi.org/10.1073/pnas.1701090114

Connon, S.A., Lester, E.D., Shafaat, H.S., Obenhuber, D.C., Ponce, A., 2007. Bacterial diversity in hyperarid Atacama Desert soils. *Journal of Geophysical Research Biogeosciences, 112*, G04S17. https://doi.org/10.1029/2006JG000311

Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature, 440*, 165–173. https://doi.org/10.1038/nature04514

De Deyn, G.B., Cornelissen, J.H.C., Bardgett, R.D., 2008. Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecology Letters, 11*, 516–531. https://doi.org/10.1111/j.1461-0248.2008.01164.x

562 Dieleman, C.M., Branfireun, B.A., Lindo, Z., 2017. Northern peatland carbon dynamics driven by
563 plant growth form — the role of graminoids. *Plant and Soil, 415*, 25–35.
564 https://doi.org/10.1007/s11104-016-3099-3

565 Dieleman, C.M., Branfireun, B.A., Mclaughlin, J.W., Lindo, Z., 2015. Climate change drives a shift
566 in peatland ecosystem plant community: implications for ecosystem function and stability.
567 *Global Change Biology, 21*, 388–395. https://doi.org/10.1111/gcb.12643

568 Dorrepaal, E., 2007. Are plant growth-form-based classifications useful in predicting northern
569 ecosystem carbon cycling feedbacks to climate change? *Journal of Ecology, 95*, 1167–1180.
570 https://doi.org/10.1111/j.1365-2745.2007.01294.x

571 Dunn, C., Freeman, C., 2018. The role of molecular weight in the enzyme-inhibiting effect of
572 phenolics: the significance in peatland carbon sequestration. *Ecological Engineering, 114*, 162–
573 166. https://doi.org/10.1016/j.ecoleng.2017.06.036

574 Elias, D.M.O., Rowe, R.L., Pereira, M.G., Stott, A.W., Barnes, C.J., Bending, G.D., McNamara, N.P.,
575 2017. Functional differences in the microbial processing of recent assimilates under two
576 contrasting perennial bioenergy plantations. *Soil Biology and Biochemistry, 114*, 248–262.
577 https://doi.org/10.1016/j.soilbio.2017.07.026.

578 Fanin, N., Kardol, P., Farrell, M., Nilsson, M.-C., Gundale, M.J., Wardle, D.A., 2019. The ratio of
579 Gram-positive to Gram-negative bacterial PLFA markers as an indicator of carbon availability in
580 organic soils. *Soil Biology and Biochemistry, 128*, 111–114.
581 https://doi.org/10.1016/j.soilbio.2018.10.010

582 Fenner, N., Freeman, C., 2011. Drought-induced carbon loss in peatlands. *Nature Geoscience, 4*,
583 895–900. https://doi.org/10.1038/ngeo1323

584 Freeman, C., Fenner, N., Ostle, N.J., Kang, H., Dowrick, D.J., Reynolds, B., Lock, M.A., Sleep, D.,
585 Hughes, S., Hudson, J., 2004. Export of dissolved organic carbon from peatlands under elevated
586 carbon dioxide levels. *Nature, 430*, 195–198. https://doi.org/ 10.1038/nature02707

587 Freeman, C., Ostle, N., Kang, H., 2001. An enzymic 'latch' on a global carbon store - A shortage
588 of oxygen locks up carbon in peatlands by restraining a single enzyme. *Nature, 409*, 149.
589 https://doi.org/10.1038/3505165

590 Frostegård, Å., Tunlid, A., Bååth, E., 2011. Use and misuse of PLFA measurements in soils. *Soil*
591 *Biology and Biochemistry, 43*, 1621–1625. https://doi.org/10.1016/j.soilbio.2010.11.021

592 Gallego-Sala, A.V., Prentice, C.I., 2013. Blanket peat biome endangered by climate change.
593 *Nature Climate Change, 3*, 152–155. https://doi.org/10.1038/nclimate1672.

594 Gilbert, D., Mitchell, E.A.D., 2006. Microbial diversity in *Sphagnum* peatlands. In: Martini I.P.,
595 Cortizas A.M., Chesworth W. (eds.). Peatlands: Evolution and Records of Environmental and
596 Climate Changes. *Developments in Earth Surface Processes, 13*, 287–318.
597 https://doi.org/10.1016/S0928-2025(06)09013-4

598 Girkin, N.T., Lopes dos Santos, R.A., Vane, C.H., Ostle, N., Turner, B.L., Sjögersten, S., 2020. Peat
599 properties, dominant vegetation type and microbial community structure in a tropical peatland.
600 *Wetlands, 40*, 1367–1377. https://doi.org/10.1007/s13157-020-01287-4

601 Hartmann, M., Brunner, I., Hagedorn, F., Bardgett, R.D., Stierli, B., Herzog, C., Chen, X., Zingg, A.,
602 Graf-Pannatier, E., Rigling, A., Frey, B., 2017. A decade of irrigation transforms the soil
603 microbiome of a semi-arid pine forest. *Molecular Ecology, 26*, 1190–1206.
604 https://doi.org/10.1111/mec.13995

605 Hattenschwiler, S., Vitousek, P.M., 2000. The role of polyphenols in terrestrial ecosystem
606 nutrient cycling. *Trends in Ecology and Evolution, 15*, 238–243. https://doi.org/10.1016/S0169-
607 5347(00)01861-9

608 Haynes, K.M., Preston, M.D., McLaughlin, J.W., Webster, K., Basiliko, N., 2015. Dissimilar
609 bacterial and fungal decomposer communities across rich to poor fen peatlands exhibit
610 functional redundancy. *Canadian Journal of Soil Science, 9*, 219–230.
611 https://doi.org/10.4141/cjss-2014-062

612 Heinemeyer, A., McNamara, N.P., 2011. Comparing the closed static versus the closed dynamic
613 chamber flux methodology: implications for soil respiration studies. *Plant and Soil, 346*, 145–
614 151. https://doi.org/10.1007/s11104-011-0804-0

615 Ise, T., Dunn, A.L, Wofsy, S.C., Moorcroft, P.R., 2008. High sensitivity of peat decomposition to
616 climate change through water-table feedback. *Nature Geoscience, 1*, 763–766.
617 https://doi.org/10.1038/ngeo331

618 Izco Sevillano, J., Ramil-Rego, P., 2001. Análisis y Valoración de la Sierra de O Xistral: un Modelo
619 de Aplicación de la Directiva Hábitat en Galicia. Xunta de Galicia. Consellería de Medio Ambiente.
620 Centro de Información e Tecnoloxía Ambiental, Santiago de Compostela.

621 Jaatinen, K., Fritze, H., Laine, J., Laiho, R., 2007. Effects of short- and long-term water-level
622 drawdown on the populations and activity of aerobic decomposers in a boreal peatland. *Global*
623 *Change Biology, 13*, 491–510. https://doi.org/10.1111/j.1365-2486.2006.01312.x

624 Jansen, B., Nierop, K.G.J., Verstraten, J.M., 2003. Mobility of Fe(II), Fe(III) and Al in acidic forest
625 soils mediated by dissolved organic matter: Influence of solution pH and metal/organic carbon
626 ratios. *Geoderma, 113*, 323–340. https://doi.org/10.1016/S0016-7061(02)00368-3

627 Jansen, B., Nierop, K.G.J., Verstraten, J.M., 2005. Mechanisms controlling the mobility of
628 dissolved organic matter, aluminium and iron in podzol B horizons. *European Journal of Soil*
629 *Science, 56*, 537–550. https://doi.org/10.1111/j.1365-2389.2004.00686.x

630 Jovani-Sancho, A.J., Cummins, T., Byrne, K.A., 2017. Collar insertion depth effects on soil
631 respiration in afforested peatlands. *Biology and Fertility of Soils, 53*, 677–689.
632 https://doi.org/10.1007/s00374-017-1210-4

633 Juan-Ovejero, R., Benito, E., Barreal, M.E., Rodeiro, J., Briones, M.J.I., 2019. Tolerance to
634 fluctuating water regimes drives changes in mesofauna community structure and vertical
635 stratification in peatlands. *Pedobiologia, 76*, 150571.
636 https://doi.org/10.1016/j.pedobi.2019.150571

637 Juan-Ovejero, R., Granjel, R.R., Ramil-Rego, P., Briones M.J.I., 2020. The interplay between
638 abiotic factors and below-ground biological interactions regulates carbon exports from
639 peatlands. *Geoderma, 368*, 114313. https://doi.org/10.1016/j.geoderma.2020.114313

640 Kaiser, C., Koranda, M., Kitzler, B., Fuchlueger, L., Schnecker, J., Schweiger, P., Rasche, F.,
641 Zechmeister-Boltenstern, S., Sessitsch, A., Richter, A., 2010. Belowground carbon allocation by
642 trees drives seasonal patterns of extracellular enzyme activities by altering microbial community
643 composition in a beech forest soil. *New Phytologist, 187*, 843–858.
644 https://doi.org/10.1111/j.1469-8137.2010.03321.x

645 Kaštovská, E., Straková, P., Edwards, K., Urbanová, Z., Bárta, J., Mastný, J., Šantrůčková, H.,
646 Picek, T., 2018. Cotton-grass and blueberry have opposite effect on peat characteristics and
647 nutrient transformation in peatland. *Ecosystems, 21*, 443–58. https://doi.org/10.1007/s10021-
648 017-0159-3

649 Kumar, S., Suyal, D.C., Yadav, A., Shouche, Y., Goel, R., 2019. Microbial diversity and soil
650 physiochemical characteristic of higher altitude. *PLoS One, 14*, e0213844.
651 https://doi.org/10.1371/journal.pone.0213844

652 Kwon, M.J., Haraguchi, A., Kang, H., 2013. Long-term water regime differentiates changes in
653 decomposition and microbial properties in tropical peat soils exposed to the short-term drought.
654 *Soil Biology and Biochemistry, 60*, 33–44. https://doi.org/10.1016/j.soilbio.2013.01.023

655 Lamit, L.J., Romanowicz, K.L., Potvin, L.R., Rivers, A.R., Singh, K., Lennon, J.T., Tringe, S.G., Kane,
656 E.S., Lilleskov, E.A., 2017. Patterns and drivers of fungal community depth stratification in
657 *Sphagnum* peat. *FEMS Microbiology Ecology, 93*, fix082. https://doi.org/10.1093/femsec/fix082

658 Loeb, R., Lamers, L.P.M., Roelofs, J.G.M., 2008. Effects of winter versus summer flooding and
659 subsequent desiccation on soil chemistry in a riverine hay meadow. *Geoderma, 145*, 84–90.
660 https://doi.org/10.1016/j.geoderma.2008.02.009

661 Limpens, J., Berendse, F., Blodau, C., Canadell, J.G., Freeman, C., Holden, J., Roulet, N., Rydin, H.,
662 Schaepman-Strub, G., 2008. Peatlands and the carbon cycle: from local processes to global
663 implications—a synthesis. *Biogeosciences, 5*, 1475–1491. https://doi.org/10.5194/bg-5-1475-
664 2008

665 Lunt, P.H., Fyfe, R.M., Tappin, A.D., 2019. Role of recent climate change on carbon sequestration
666 in peatland systems. *Science of The Total Environment, 667*, 348–358.
667 https://doi.org/10.1016/j.scitotenv.2019.02.239

668 Lyons, C.L., Lindo, Z., 2020. Above- and belowground community linkages in boreal peatlands.
669 *Plant Ecology, 221*, 615–632. https://doi.org/10.1007/s11258-020-01037-w

670 Malhotra, A., Brice, D.J., Childs, J., Graham, J.D., Hobbie, E.A., Stel, H.V., Feron, S.C., Hanson,
671 P.J., Iversen, C.M., 2020. Peatland warming strongly increases fine-root growth. *PNAS, 117*,
672 17627-17634. https://doi.org/10.1073/pnas.2003361117

673 Mohammadipanah, F., Wink, J., 2016. Actinobacteria from arid and desert habitats: diversity
674 and biological activity. *Frontiers in Microbiology, 6*, 1541.
675 https://doi.org/10.3389/fmicb.2015.01541

676 Moore, P.D., 2002. The future of cool temperate bogs. *Environmental Conservation, 29*, 3–20.
677 https://doi.org/10.1017/S0376892902000024

678 Morton, P.A., Heinemeyer, A., 2019. Bog breathing: the extent of peat shrinkage and expansion
679 on blanket bogs in relation to water table, heather management and dominant vegetation and
680 its implications for carbon stock assessments. *Wetlands Ecology and Management, 27*, 467–482.
681 https://doi.org/10.1007/s11273-019-09672-5

682 Naylor, D., Coleman-Derr, D., 2018. Drought stress and root-associated bacterial communities.
683 *Frontiers in Plant Science, 8*, 2223. https://doi.org/10.3389/fpls.2017.02223

684 Peltoniemi, K., Fritze, H., Laiho, R., 2009. Response of fungal and actinobacterial communities to
685 water-level drawdown in boreal peatland sites. *Soil Biology and Biochemistry, 41*, 1902–1914.
686 https://doi.org/10.1016/j.soilbio.2009.06.018

687 Preston, M.D., Smemo, K.A., McLaughlin, J.W., Basiliko, N., 2012. Peatland microbial
688 communities and decomposition processes in the James Bay Lowlands, Canada. *Frontiers in*
689 *Microbiology, 3*, 70. https://doi.org/10.3389/fmicb.2012.00070

690 Ramil-Rego, P., Izco Sevillano, J., 2003. Galician Wetlands Inventory. Dirección Xeral de
691 Conservación da Natureza. Xunta de Galicia.

692 Ramil-Rego, P., Gómez Orellana, L., Rodríguez-Guitián, M.A., López Castro, H., Real, C., Ferreiro
693 da Costa, J., Muñoz Sobrino, C., 2017. Tipología y sistemas de clasificación. In: Ramil-Rego P.,
694 Rodríguez Guitián M.A. (Eds.). Hábitats de Turbera en la Red Natura 2000. Diagnosis y Criterios
695 para su Conservación y Gestión en la Región Biogeográfica Atlántica. Horreum-Ibader, Lugo, pp.
696 29–148.

697 Rinnan, R., Baath, E., 2009. Differential utilization of carbon substrates by bacteria and fungi in
698 tundra soil. *Applied and Environmental Microbiology, 75*, 3611–3620.
699 https://doi.org/10.1128/AEM.02865-08.

700 Robroek, B., Albrecht, R., Hamard, S., Pulgarin, A., Bragazza, L., Buttler, A., Jassey, V.E.J., 2016.
701 Peatland vascular plant functional types affect dissolved organic matter chemistry. *Plant and*
702 *Soil, 407*, 135–143. https://doi.org/10.1007/s11104-015-2710-3

703 Rodríguez-Guitián, M.A., Ramil-Rego, P., Real, C., Díaz-Varela, R.A., Ferreiro Da Costa, J., Cillero,
704 C., 2009. Caracterización vegetacional de los complejos de turberas de cobertor activas del SW
705 europeo. In: Botánica Pirenaico-Cantábrica en el siglo XXI. Llamas F., Acedo C. (Eds.),
706 Publicaciones Universidad de León. 633–654.

707 SAS Institute Inc., 2011. Base SAS® 9.3 Procedures Guide. SAS Institute Inc., Cary.

708 Schwieger, S., Blume-Werry, G., Peters, B., Smiljanic, M., Kreyling, J., 2019. Patterns and drivers
709 in spring and autumn phenology differ above- and belowground in four ecosystems under the
710 same macroclimatic conditions. *Plant and Soil, 445*, 217–229. https://doi.org/10.1007/s11104-
711 019-04300-w

712 Seifert, A.G., Trumbore, S., Xu, X., Zhang, D., Kothe, E., Gleixner, G., 2011. Variable effects of
713 labile carbon on the carbon use of different microbial groups in black slate degradation.
714 *Geochimica et Cosmochimica Acta, 75*, 2557–2570. https://doi.org/10.1016/j.gca.2011.02.037

715 Sundh, I., Nilsson, M., Borgå, P., 1997. Variation in microbial community structure in two boreal
716 peatlands as determined by analysis of phospholipid fatty acid profiles. *Applied and*
717 *Environmental Microbiology, 63*, 1476–1482. https://doi.org/10.1128/aem.63.4.1476-
718 1482.1997

719 The, Y.A., Silver, W.L., Sonnentag, O., Detto, M., Kelly, M., Baldocchi, D.D., 2011. Large
720 greenhouse gas emissions from a temperate peatland pasture. *Ecosystems, 14*, 311–325.
721 https://doi.org/10.1007/s10021-011-9411-4

722 ter Braak, C.J.F., Šmilauer, P., 2002. CANOCO Reference Manual and CanoDraw for Windows
723 User's Guide: Software for Canonical Community Ordination (version 4.5). Biometris,
724 Wageningen.

725 Tian, W., Wang, H., Xiang, X., Wang, R., Xu, Y., 2019. Structural variations of bacterial community
726 driven by *Sphagnum* microhabitat differentiation in a subalpine peatland. *Frontiers in*
727 *Microbiology, 10*, 1661. https://doi.org/10.3389/fmicb.2019.01661

728 Tiang, J., Branfireun, B.A., Lindo, Z., 2020. Global change alters peatland carbon cycling through
729 plant biomass allocation. *Plant and Soil, 455*, 53–64. https://doi.org/10.1007/s11104-020-
730 04664-4

731 Trinder, C.J., Artz, R.R.E., Johnson, D., 2008. Contribution of plant photosynthate to soil
732 respiration and dissolved organic carbon in a naturally recolonising cutover peatland. *Soil*
733 *Biology and Biochemistry, 40*, 1622–1628. https://doi.org/10.1016/j.soilbio.2008.01.016

734 Urbanová, Z., Picek, T., Tuittila, E-S., 2013. Sensitivity of carbon gas fluxes to weather variability
735 on pristine, drained and rewetted temperate bogs. Mires and Peat, *11*, 04 (available online:
736 http://www.mires-and-peat.net/volumes/map11/map1104.php).

737 Waddington, J.M., Morris, P.J., Kettridge, N., Granath, G., Thompson, D.K., Moore, P.A., 2015.
738 Hydrological feedbacks in northern peatlands. *Ecohydrology, 8*, 113–127.
739 https://doi.org/10.1002/eco.1493

740 Waldrop, M.P., Harden, J.W., Turetsky, M.R. Petersen, D.G., McGuire, A.D., Briones, M.J.I.,
741 Churchill, A.C., Doctor, D.H., Pruett, L.E., 2012. Bacterial and enchytraeid abundance accelerate

742 soil carbon turnover along a lowland vegetation gradient in interior Alaska. *Soil Biology and*
743 *Biochemistry*, *50*, 188–198. https://doi.org/10.1016/j.soilbio.2012.02.032

744 Walker, T.N., Garnett, M.H., Ward, S.E., Oakley, S., Bardgett, R.D., Ostle, N.J., 2016. Vascular
745 plants promote ancient peatland carbon loss with climate warming. *Global Change Biology, 22*,
746 1880–1889. https://doi.org/10.1111/gcb.13213

747 Wang, H.J., Richardson, C.J., Ho, M.C., 2015. Dual controls on carbon loss during drought in
748 peatlands. *Nature Climate Change, 5*, 584–587. https://doi.org/10.1038/nclimate2643

749 Ward, S.E., Bardgett, R.D., McNamara, N.P., Ostle, N.J., 2009. Plant functional group identity
750 influences short-term peatland ecosystem carbon flux: evidence from a plant removal
751 experiment. *Functional Ecology, 23*, 454–462. https://doi.org/10.1111/j.1365-
752 2435.2008.01521.x

753 Ward, S.E., Orwin, K.H., Ostle, N.J., Briones, M.J.I., Thomson, B.C., Griffiths, R.I., Oakley, S., Quirk,
754 H., Bardgett, R.D., 2015. Vegetation exerts a greater control on litter decomposition than climate
755 warming in peatlands. *Ecology, 96*, 113–123. https://doi.org/10.1890/14-0292.1

756 Ward, S.E., Ostle, N.J., Oakley, S., Quirk, H., Henrys, P.A., Bardgett, R.D., 2013. Warming effects
757 on greenhouse gas fluxes in peatlands are modulated by vegetation composition. *Ecology*
758 *Letters, 16*, 1285–1293. https://doi.org/10.1111/ele.12167.

759 Weijers, J.W., Schouten, S, Hopmans, E.C., Geenevasen, J.A., David, O.R., Coleman, J.M., Pancost,
760 R.D., Sinninghe Damsté, J.S., 2006. Membrane lipids of mesophilic anaerobic bacteria thriving in
761 peats have typical archaeal traits. *Environmental Microbiology, 8*, 648–657.
762 https://doi.org/10.1111/j.1462-2920.2005.00941.x

763 Whitaker, J., Ostle, N., McNamara, N.P., Nottingham, A.T., Stott, A.W., Bardgett, R.D., Salinas,
764 N., Ccahuana, A.J.Q., Meir, P., 2014. Microbial carbon mineralization in tropical lowland and
765 montane forest soils of Peru. *Frontiers in Microbiology, 5*, 720.
766 https://doi.org/10.3389/fmicb.2014.00720.

767 White, D., Davis, W., Nickels, J., King, J., Bobbie, R., 1979. Determination of the sedimentary
768 microbial biomass by extractable lipid phosphate. *Oecologia, 40*, 51–62.
769 https://doi.org/10.1007/BF00388810.

770 Willers, C., Jansen van Rensburg, P.J., Claassens, S., 2015. Phospholipid fatty acid profiling of
771 microbial communities–a review of interpretations and recent applications. *Journal of Applied*
772 *Microbiology, 119*, 1207–1218. https://doi.org/10.1111/jam.12902

Yuste, J.C., Fernandez-Gonzalez, A.J., Fernandez-Lopez, M., Ogaya, R., Peñuelas, J., Sardans, J., Lloret, F., 2014. Strong functional stability of soil microbial communities under semiarid Mediterranean conditions and subjected to long-term shifts in baseline precipitation. *Soil Biology and Biochemistry, 69*, 223–233. https://doi.org/10.1016/j.soilbio.2013.10.045

Zhang, Y.-M., Rock, C.O., 2008. Membrane lipid homeostasis in bacteria. *Nature Reviews Microbiology, 6,* 222-33. https://doi.org/10.1038/nrmicro1839.

Zhong, Y., Jiang, M., Middleton, B.A., 2020. Effects of water level alteration on carbon cycling in peatlands. *Ecosystem Health and Sustainability, 6*, 1806113. https://doi.org/10.1080/20964129.2020.1806113

Table 1. Results from ANOVA for the temporal changes in PLFA biomarker abundance (μg g^{-1} dwt soil) at the investigated peatland habitats (Atlantic wet heath-*Erica mackayana*, transition mire-*Sphagnum* mosses, blanket bog-*Molinia caerulea* and blanket bog-*Eriophorum angustifolium*) during the investigated period (field sampling every two months in 2016 and 2017). Significance multivariate test on each factor and the interactions is Tukey's Studentized range test.

Source	*DF*	*F*	*P*
Total PLFA			
YEAR	1	62.73	<0.0001
MONTH	5	9.86	<0.0001
HABITAT	3	56.17	<0.0001
YEAR*HABITAT	3	3.56	0.0171
MONTH*HABITAT	15	1.77	0.0495
YEAR*MONTH*HABITAT	20	3.72	<0.0001
Fungi			
YEAR	1	0.05	0.8232
MONTH	5	7.59	<0.0001
HABITAT	3	99.16	<0.0001
YEAR*HABITAT	3	0.59	0.6244
MONTH*HABITAT	15	2.48	0.0041
YEAR*MONTH*HABITAT	20	4.11	<0.0001
Bacteria			
YEAR	1	68.81	<0.0001
MONTH	5	13.56	<0.0001
HABITAT	3	66.02	<0.0001
YEAR*HABITAT	3	2.87	0.0405
MONTH*HABITAT	15	2.07	0.0181
YEAR*MONTH*HABITAT	20	3.27	<0.0001
Gbacteria			
YEAR	1	64.5	<0.0001
MONTH	5	13.02	<0.0001
HABITAT	3	74.29	<0.0001
YEAR*HABITAT	3	4.96	0.0030
MONTH*HABITAT	15	2.23	0.0100
YEAR*MONTH*HABITAT	20	5.92	<0.0001
Gram positive			
YEAR	1	109.2	<0.0001
MONTH	5	16.48	<0.0001

HABITAT	3	110.92	<0.0001
YEAR*HABITAT	3	5.16	0.0024
MONTH*HABITAT	15	2.25	0.0094
YEAR*MONTH*HABITAT	20	3.81	<0.0001
Gram negative			
YEAR	1	37.44	<0.0001
MONTH	5	11.93	<0.0001
HABITAT	3	38.25	<0.0001
YEAR*HABITAT	3	1.52	0.2132
MONTH*HABITAT	15	3.26	0.0002
YEAR*MONTH*HABITAT	20	3.42	<0.0001
Unspecific			
YEAR	1	26.03	<0.0001
MONTH	5	2.74	0.0235
HABITAT	3	3.01	0.0340
YEAR*HABITAT	3	2.43	0.0700
MONTH*HABITAT	15	4.34	<0.0001
YEAR*MONTH*HABITAT	20	5.91	<0.0001
Fungal:Bacteria ratio			
YEAR	1	0.94	0.3336
MONTH	5	7.93	<0.0001
HABITAT	3	80.21	<0.0001
YEAR*HABITAT	3	0.77	0.5156
MONTH*HABITAT	15	2.39	0.0057
YEAR*MONTH*HABITAT	20	3.85	<0.0001
G+ve:G-ve ratio			
YEAR	1	12.11	0.0008
MONTH	5	6.84	<0.0001
HABITAT	3	38.05	<0.0001
YEAR*HABITAT	3	5.63	0.0013
MONTH*HABITAT	15	8.84	<0.0001
YEAR*MONTH*HABITAT	20	10.16	<0.0001

789

Figure legends

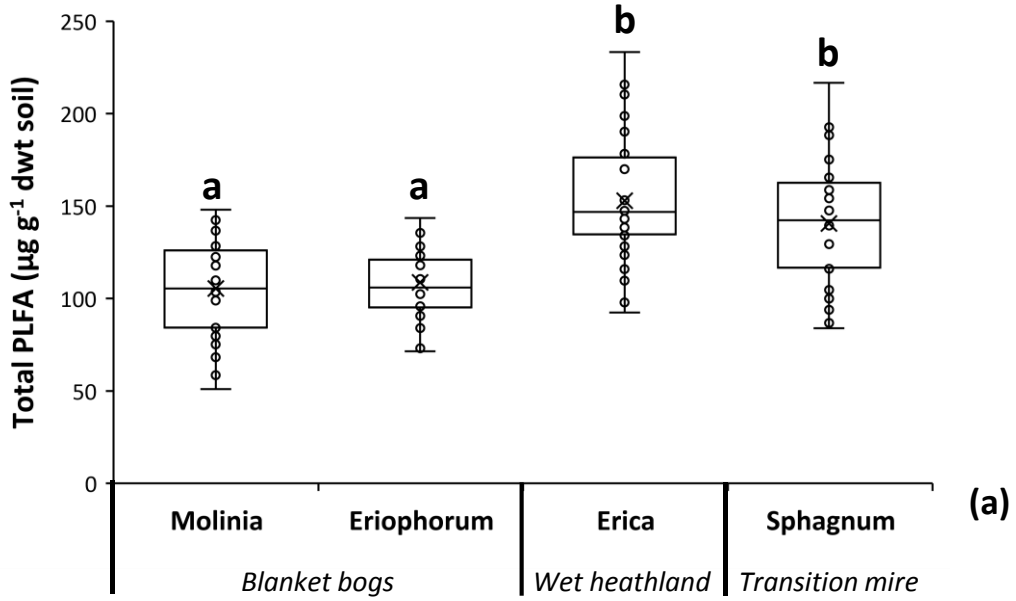
Figure 1. Total PLFA concentrations (a) and PLFA assigned to functional groups relative to total values (b) in the peat samples collected at the four peatland habitats dominated by different functional plant types (PFTs). Box plot charts show the median and quartiles (25th and 75th). Different letters indicate significant differences between PFTs per PLFA grouping.

Figure 2. PLFA biomarker abundance at the four peatland habitats dominated by different functional plant types (PFTs). Values are means ± standard errors and different letters indicate significant differences between PFTs per biomarker.

Figure 3. Temporal changes in the abundance of (a) total PLFA, (b) Gram−positive bacteria, (c) Gram−negative bacteria and (d) fungal biomarkers at each peatland habitat dominated by different functional plant types (PFTs) during the investigated period. Values are means ± standard errors and different letters indicate significant differences between PFTs per sampling time.

Figure 4. Detrended Canonical Correspondence Analysis (DCCA) triplot of microbial groupings and indicators (small black filled circles), environmental (arrows) and categorical variables (squares filled with different patterns to indicate peatland type (i.e. blanket bog, wet heathland and transition mire)) for the soil samples collected during the whole investigated period. Abbreviations: Total PLFAs (total PLFA), Total bacterial PLFAs (TBacteria); fungi PLFA (Fungi); Gram−positive bacterial PLFAs (Gpositive); Gram−negative bacterial PLFAs (Gnegative); General bacterial PLFAS (Gbacteria); Non-specific PLFAs (Unspecific), fungal to bacteria ratio (FB ratio), Gram−positive to Gram−negative ratio (G+:G- ratio), soil temperature (Soil T), soil moisture (Moisture), pH of the soil solution (pH leachates), carbon content (Carbon), CO_2 production (CO_2), dissolved organic carbon (DOC), ratio of C to N (C/N).

Figure 1


Total PLFA (µg g-1 dwt soil)
250
200
150
100
50
0
a
a
b
b
Molinia
Eriophorum
Erica
Sphagnum
Blanket bogs
Wet heathland
Transition mire
(a)

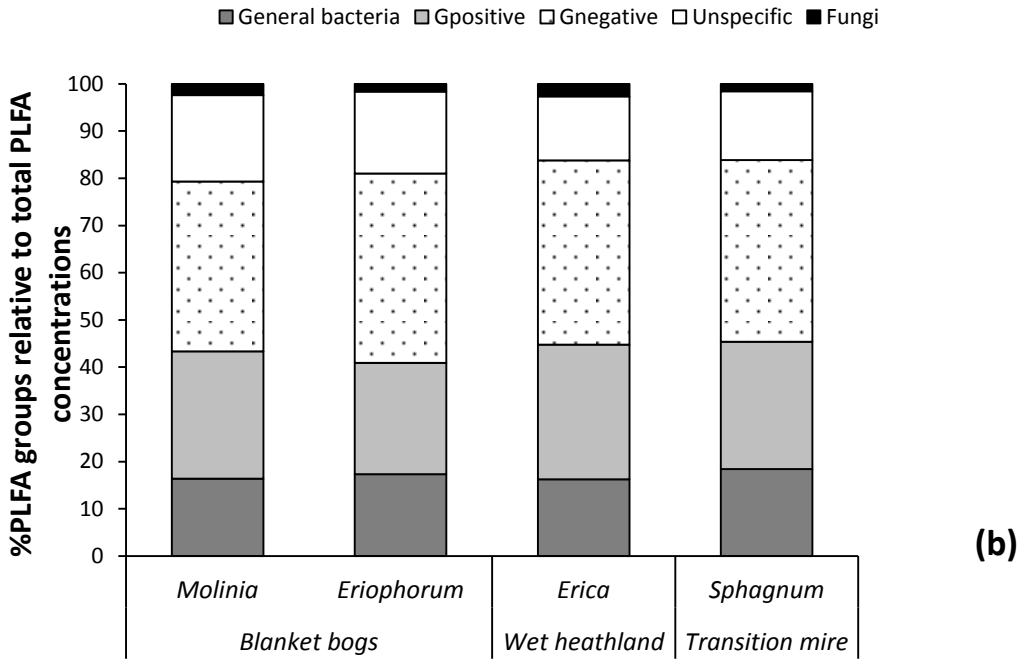

General bacteria
Gpositive
Gnegative
Unspecific
Fungi
%PLFA groups relative to total PLFA concentrations
100
90
80
70
60
50
40
30
20
10
0
Molinia
Eriophorum
Erica
Sphagnum
Blanket bogs
Wet heathland
Transition mire
(b)

Figure 2

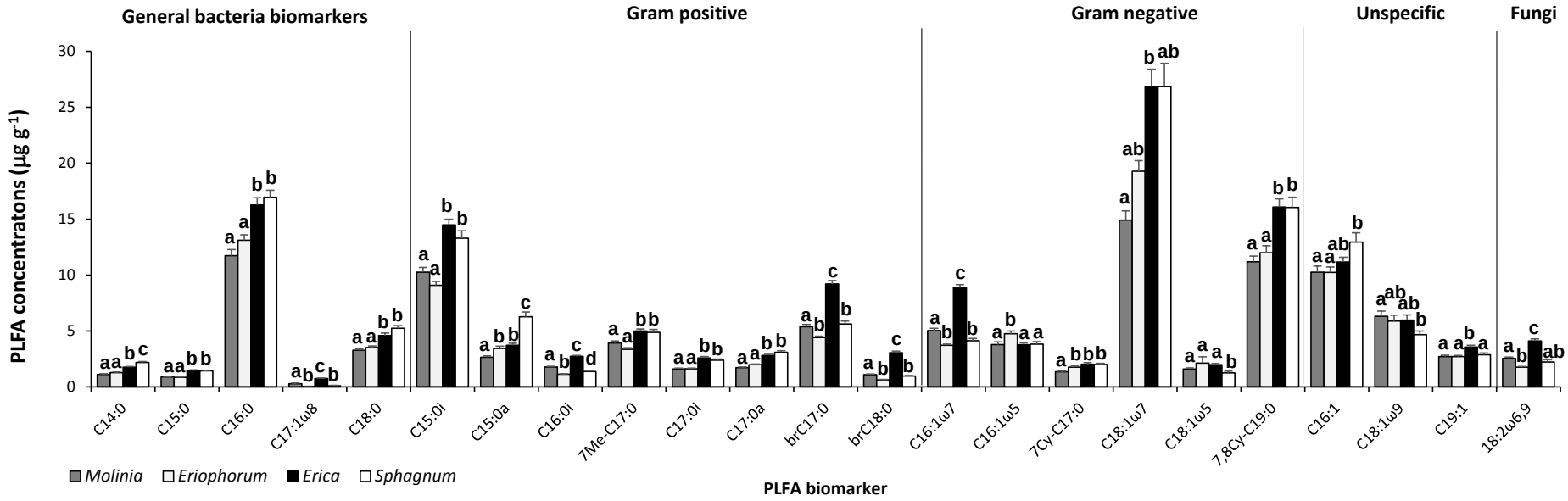

General bacteria biomarkers
Gram positive
Gram negative
Unspecific
Fungi
PLFA concentratons (μg g⁻¹)
30
25
20
15
10
5
0
C14:0
C15:0
C16:0
C17:1ω8
C18:0
C15:0i
C15:0a
C16:0i
7Me-C17:0
C17:0i
C17:0a
brC17:0
brC18:0
C16:1ω7
C16:1ω5
7Cy-C17:0
C18:1ω7
C18:1ω5
7,8Cy-C19:0
C16:1
C18:1ω9
C19:1
18:2ω6,9
Molinia
Eriophorum
Erica
Sphagnum
PLFA biomarker

Figure 3

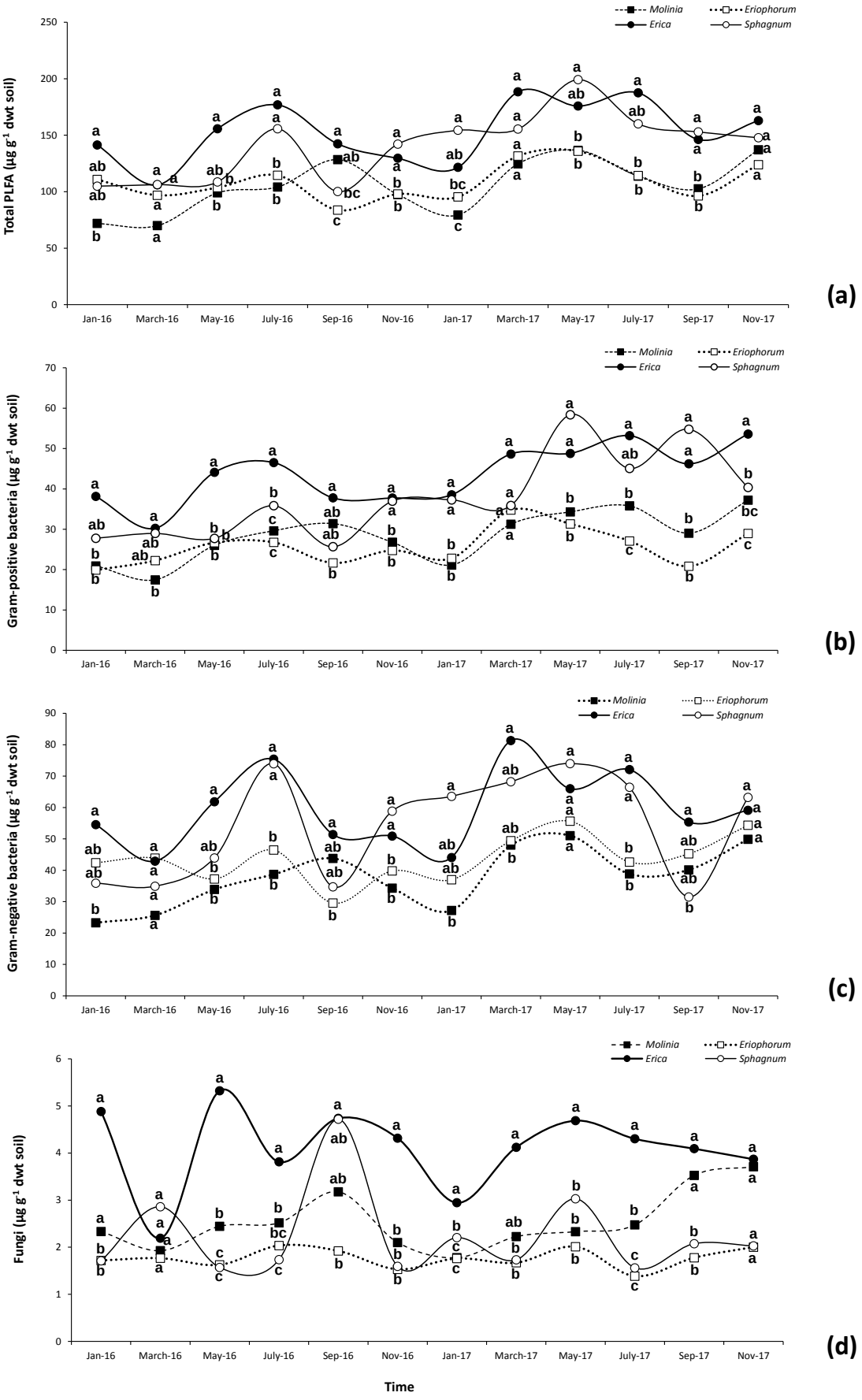
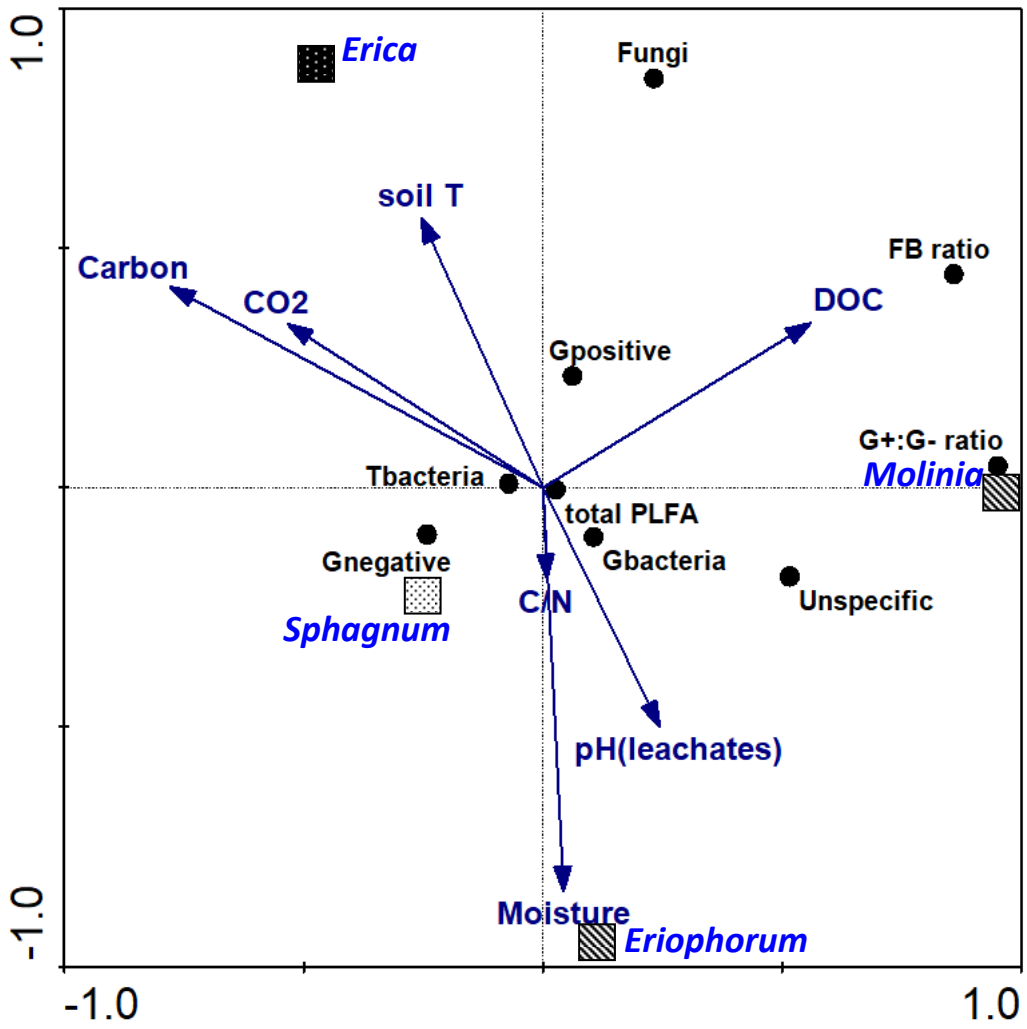

Molinia
Eriophorum
Erica
Sphagnum
Total PLFA (µg g-1 dwt soil)
Gram-positive bacteria (µg g-1 dwt soil)
Gram-negative bacteria (µg g-1 dwt soil)
Fungi (µg g-1 dwt soil)
Jan-16
March-16
May-16
July-16
Sep-16
Nov-16
Jan-17
March-17
May-17
July-17
Sep-17
Nov-17
Time
(a)
(b)
(c)
(d)

Figure 4


1.0
-1.0
-1.0
1.0
Erica
Fungi
soil T
Carbon
CO2
FB ratio
DOC
Gpositive
G+:G- ratio
Molinia
Tbacteria
total PLFA
Gnegative
Gbacteria
Unspecific
C/N
Sphagnum
pH(leachates)
Moisture
Eriophorum

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: