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# *Acidity impacts on microbial diversity and litter decomposition for organic soils*

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**Title: Acidity impacts on microbial diversity and litter decomposition for organic soils.**

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**Abstract**

Background:

Dissolved organic carbon (DOC) concentrations have increased in soil solutions and surface waters over the past 30 years in acid sensitive areas of Europe and Northern America. This has been linked to recovery from acidification of soils with decreasing levels of atmospheric pollution. Whilst previous research has found pH related DOC solubility is a likely driver of increased DOC concentrations in surface waters, it is unclear whether increased DOC production from organic matter decomposition, due to more favourable pH conditions for biological activity, has also contributed to the rising trends in surface waters.

Aim:

We investigated how acidity impacts microbial communities, the decomposition of litter types common to acid-sensitive ecosystems, and the impact on DOC production.

Methods:

A decomposition study using litter bags and the Tea Bag Index was incorporated into an established acidity manipulation field experiment across two sites with contrasting acid deposition histories, and two characteristic soil types (peats and peaty podzols).

Results:

We found higher rates of litter decomposition in podzol soil than peat leading to higher DOC production and aromaticity, as indicated by absorbance properties. Acidity manipulations did not influence decomposition rates for most litter types, DOC production for any litter type, Tea Bag Index parameters (stabilisation factor and decomposition rate) or microbial diversity, for any site or soil type.

Conclusion:

Our study suggests that decomposition of aboveground-collected litter does not mediate acidity effects on DOC production, whilst soil type, and physiochemical soil responses to acidity, are more influential on DOC release from organic soils.

**Keywords**

DOC, Litter decomposition, Peat, Acid deposition, Organo-mineral, Tea Bag Index

**Introduction**

Dissolved organic carbon (DOC) concentrations in surface waters draining catchments dominated by organic soils have been increasing, since at least the 1980s, across large areas of Europe and North America (Evans et al., 2005, Monteith et al., 2007, Oulehle and Hruška, 2009, Couture et al., 2012, SanClements et al., 2012). Such significant increases in carbon fluxes have raised concerns over the stability of terrestrial carbon stocks (Freeman et al., 2001) and contributions to $CO_2$ emissions (Moody et al., 2013, Demars, 2019). In addition, a substantial proportion of potable water derives from catchments with organic soils in the UK, which also creates issues for the drinking water industry (Xu et al., 2020, Ritson et al., 2016). Understanding the drivers of increased DOC concentrations in surface waters requires detailed insight into the carbon cycling processes within these catchments and the factors regulating the production, mobility, and transport of DOC from soils to surface waters. Given the heterogeneity of soil types within catchments, it is also crucial to understand how regulating processes vary across dominant soil types to accurately capture the dynamics at the catchment scale.

There is now a substantial body of evidence suggesting that increasing DOC concentrations in acid sensitive catchments are due to recovery from acidification as a result of air pollution control policies that have driven a reduced deposition of acidifying pollutants. Solubility is dependant on solution pH, and so as soil pH increases with recovery from acidification, soil organic carbon (SOC) dissolves into solution, becoming DOC. This physio-chemical mechanism controlling DOC solubility is supported by field experiments (Evans et al., 2012, Oulehle et al., 2013, Evans et al., 2008a, Moldan et al., 2012, Ekström et al., 2011, Pschenyckyj et al., 2020), laboratory experiments (Clark et al., 2011, Palmer et al., 2013), modelling (Monteith et al., 2007, Rowe et al., 2014, Evans et al., 2008b, Sawicka et al., 2017) and numerous analyses of long-term data (Oulehle et al., 2017, Evans et al., 2006, SanClements et al., 2012, de Wit et al., 2007, Ukonmaanaho et al., 2014, Imtiazy et al., 2020, Meyer-Jacob et al., 2020).

However, high acidity has also been shown to affect biological activity, resulting in suppressed decomposition rates (Mulder et al., 2001, Sanger et al., 1993). Soil pH is highly correlated with microbial community structure (Griffiths et al., 2011), and is crucial to enzyme functioning (Fog, 1988), suggesting that microbial activities involved in DOC production and consumption may be impacted by changing acidity. Kang et al. (2018) found enzyme-mediated increases in organic matter decomposition and higher porewater DOC concentrations in soils with experimentally raised pH, and a ‘previously unrecognised biological mechanism’ for acidity-mediated increases in surface water DOC. In addition, the response of microbial communities to environmental change such as pH, over different time scales, has been identified as an important research gap where more work is required (Ritson et al., 2021). Therefore, further research is needed to explore a) peatland microbial

community and functional responses to acidity changes, and b) specifically, the extent to which increasing DOC concentrations may also be due to increased DOC production by organic matter decomposition with acidification recovery, which changes soil pH to more favourable conditions for biological activity (Andersson and Nilsson, 2001).

In addition to the uncertain effect of acidity change on biological processes, the role of different soil types in mediating the effects of acid deposition change on DOC export are not well understood. Several studies have however shown differences in DOC concentration and quality between peat and organo-mineral soils. While numerous studies show that DOC export is highest from peat soils (Billett et al., 2006, Aitkenhead et al., 1999, Dawson et al., 2011, Williamson et al., 2020, Sepp et al., 2019), the relationship between rates of DOC change and soil type is less clear. At a broad scale, DOC increases have tended to be greatest in catchments with high peat cover (Worrall et al., 2004, Monteith et al., 2007) but in many temperate and boreal landscapes these peat areas are intermingled with organo-mineral soils in better-drained areas. Studies that have examined DOC export at the scale of these individual contributing areas have tended to show that proportional increases in DOC are actually highest in those areas draining organo-mineral soils, rather than peatlands (Chapman et al., 2010, Fork et al., 2020). Higher sensitivity of DOC to pH change in organo-mineral versus peat soils has also been observed in both lab and field experiments (Clark et al., 2011, Evans et al., 2012), which has been attributed to greater exchangeable aluminium concentrations in organo-mineral soils, and/or to the buffering effect of sulphate reduction in waterlogged peat (Palmer et al., 2013).

The role of different soil properties between saturated peat and freely draining organo-mineral soils needs to be explored more fully. DOC in undrained and unforested catchments has been estimated to have a mean radiocarbon ($^{14}C$) age (i.e. time elapsed since the carbon was fixed from the atmosphere) of less than ten years, implying that it largely derives from fresh litter decomposition (Evans et al., 2007, Tipping et al., 2010, Aiken et al., 2014). Peat exerts a weak sorptive retention, and so DOC is easily transported, and as peat hydraulic conductivity is lower with depth, precipitation largely passes through the upper surface (Clark et al., 2008, Holden and Burt, 2003), as supported by correlations between DOC concentrations in surface layers of peat and DOC in stream water (Clark et al., 2008, Billett et al., 2006). In organo-mineral soils, DOC is flushed from the surface organic layer where sorption onto mineral surfaces is minimal, as hydrological flows shift from the mineral layer during times of high flow (Clark et al., 2007, Hood et al., 2006, Borken et al., 2011, Casper et al., 2003, Easthouse et al., 1992). As much DOC is transported from the surface layers of peat and organic soils, the input from litter decomposition plays a vital role in carbon dynamics and transport from upland organic catchments.

To investigate how acidity impacts the decomposition of litter types common to upland organic catchments, and the resulting effect on DOC production, a decomposition study was integrated into an established field experiment. The experiment, where acidity had been manipulated for several years, was conducted at two locations with contrasting pollution histories, encompassing both peat and organo-mineral soils at each location. Our objectives were to investigate the effect of acidity on microbial communities, litter decomposition, and the quantity and quality of DOC produced, and to assess how these responses varied by soil type.

## Methods

### Site description and experimental design

The established field experiment comprised of four replicated plot-scale experiments situated across two upland locations of the UK with contrasting historic and current rates of acid deposition. The first study location, Migneint (3°48.8' W, 52°59.6' N, 460 m a.s.l.), is in North Wales and represents a relatively undisturbed blanket peatland area with historically low levels of atmospheric nitrogen and sulphur pollution. During the experimental period (October 2015 to October 2016), average daily air temperature ranged from 4.4 to 20.1 °C (median 12.9 °C), with 234 rain days equating to 3516 mm of total rainfall (based on data obtained from a nearby weather station (Capel Curig), located 9 miles from the site). Soil temperature at 10cm depth ranged from 1 to 26.4 °C with a median of 9.8 °C (Met Office, 2016).

In contrast, the second study location, Peaknaze (Peak District, Northern England) (1°54.5' W, 53°28.3' N, 440 m a.s.l.), has experienced degradation of the ecosystem including *Sphagnum* loss and erosion, largely due to intensive land management and historically high levels of atmospheric pollution (Oulehle et al., 2013, Tallis, 1987, Carroll et al., 2009). Analysis of soils from the same experimental sites used for this study have shown soils from Peaknaze to be more acidic than Migneint soils (with a greater $H^+$ ion concentration of 3 % and 21 % for podzol and peat respectively) (Pschenyckyj et al., 2020). Based on meteorological data obtained from a nearby weather station (Buxton, 13 miles from the site), average daily air temperature ranged from -1.6 to 24.4 °C (median 9.7 °C), with fewer rain days (126) equating to 1043 mm of total rainfall during the experimental period. Soil temperature at 10cm depth ranged from -0.5 to 20 °C with a median of 8.8 °C (Met Office, 2016).

At each location, replicated acidity manipulation plots were established within two soil types; blanket peat (histosol) and peaty podzol (histic podzol) (FAO, 2015). These soils occur extensively in cool, humid temperate regions, and within the UK are among the commonest soils in the uplands. The dominant vegetation types at the peat sites are *Calluna vulgaris* and *Eriophorum vaginatum*

with some *Cladonia spp*. above a deep *Sphagnum* layer at the Migneint, whilst Peaknaze is dominated by *Eriophorum vaginatum*, *Calluna vulgaris* and *Vaccinium myrtillus* with widespread mosses largely consisting of *Pleurozium schreberi* and some *Caldonia spp.,* and large areas of bare peat. The Migneint podzol site is characterised by *Festuca ovina* and *Juncus squarrosus* with some *Galium saxatile, Eriophorum vaginatum* and *Calluna vulgaris*, as well as mosses such as *Polytrichum commune* and *Pleurozium schreberi.* The Peaknaze podzol site consists of *Festuca Ovina, Calluna vulgaris* and extensive *Vaccinium myrtillus,* with some *Eriophorum vaginatum* and *Juncus squarrosus*.

More information on the sites and experimental operation can be found in Evans et al. (2012) and Pschenyckyj et al. (2020). Previous work has focused on DOC dynamics in pore water (Evans et al., 2012), and litter and soil layers (Pschenyckyj et al., 2020). Here we build on the experiment further by investigating acidity effects on litter decomposition, a key process driving DOC production.

**Field experimental operation**

At each of the four experimental sites (termed Migneint Peat, Migneint Podzol, Peaknaze Peat, Peaknaze Podzol), there were twelve 9 $m^2$ plots, established in August 2007, comprising of four replicates of control, acid and alkaline treatments. Treatment solutions were applied monthly, initially from October 2008 until December 2012 (Evans et al., 2012), and for the purposes of this study, from January 2015 until October 2016 (Pschenyckyj et al., 2020). Additional information regarding treatment solutions can be found in Supplementary Figure 1.

Acid plots received a sulphur amendment of 50 kg $ha^{-1}$ $yr^{-1}$ at the podzol sites and 100 kg $ha^{-1}$ $yr^{-1}$ at the peat sites, the latter concentration being similar to the ambient deposition in the Peak District during the 1970s when sulphur deposition was at its peak. A prior trial determined the optimum doses needed to ensure measurable effects on pH (Evans et al., 2012). The $H_2SO_4$ solution was mixed with locally collected rainwater (20 L), with peat receiving a higher dose to account for the buffering effects of sulphate reduction and so achieving a similar pH change to the podzol soil. Following the same procedure, alkaline plots received a solution of sodium hydroxide (NaOH) and potassium hydroxide (KOH). Control plots received 20 L of rainwater only. A rinse was applied following pH treatment applications to ensure the treatment solution infiltrated into the soil and to minimise any direct toxicity effects on plant foliage. For acid plots this was 10 L of rainwater, and for alkaline plots the rinse involved a solution of magnesium chloride ($MgCl_2$) and calcium chloride ($CaCl_2$) to maintain base cation ratios similar to those observed in rainfall.

**Decomposition experiment**

Both litter bags and the Tea Bag Index were incorporated into the field experiment in order to investigate the effects of acidity on litter decomposition. The litter bag technique is commonly used as an indication of litter decomposition by measuring the mass loss of litter, which can be compared between litter types under different ambient or experimental conditions (Graça et al., 2005, Beyaert and Fox, 2007). The Tea Bag Index (Keuskamp et al., 2013) is a standardised method of measuring decomposition of established litter types, enabling comparison with other studies and experiments.

Litter samples were harvested at the end of the growing season during autumn (when- vascular plant death and DOC production from litter decomposition is at its greatest (Mastný et al., 2018)) and comprised of *Calluna vulgaris*, *Eriophorum vaginatum*, *Festuca ovina*, *Pleurozium schreberi* and *Sphagnum spp.*. These were categorised into two groups (Table 1). *Calluna* and *Eriophorum* litters (Group 1) are common in upland organic catchments and are present at all sites. Group 2 captures other dominant vegetation species specific to each of the four sites. For instance, *Festuca* is common at the podzol sites whilst bryophytes characterise peatland areas, with a distinction between the *Sphagnum* dominated Migneint site and *Pleurozium* dominating the degraded Peaknaze site.

Table 1: Summary of litter types buried at each site, and site abbreviations. All were harvested from the site where they were buried.

| Site | Site ID | Group 1 | Group 2 |
|---|---|---|---|
| Migneint Peat | M Peat | *Eriophorum, Calluna* | *Sphagnum* |
| Migneint Podzol | M Pod | *Eriophorum, Calluna* | *Festuca* |
| Peaknaze Peat | PN Peat | *Eriophorum, Calluna* | *Pleurozium* |
| Peaknaze Podzol | PN Pod | *Eriophorum, Calluna* | *Festuca* |

Vascular plants were collected as above-ground, recently senesced standing biomass, and bryophytes were collected as whole blocks, during September 2015. Samples were then sorted to remove other material and processed by cutting into 2 cm long pieces and homogenised. It is not possible to establish the starting point of decomposition for *Sphagnum* as this is a continuous process, so following protocols adopted by other studies (Aerts et al., 2001, Moore et al., 2007, Bragazza et al., 2007) the capitulum (2-4 cm below the tip) of each individual was removed, as this is likely to be living and photosynthesising. Therefore, only freshly senesced litter was used.

A commonly used pre-treatment procedure was applied to the samples (Moore et al., 2007, Bragazza et al., 2007). This involved air drying the samples to a constant mass at ambient lab temperature. The dry mass equivalent of 3 g of *Calluna*, *Eriophorum* and *Festuca*, and 1 g of *Sphagnum* and *Pleurozium* (a lower amount was used due to the low density of these species) were

added to the litter bags, all of which were buried at a depth of 5 cm in October 2015. Pre-sown 10 x 10 cm litter bags made of polyamide monofil were used (Filtrations Technik, Germany).

Mesh size has been found to significantly influence which community of decomposers the litter is exposed to based on faunal size classes (Bradford et al., 2002). A mesh size as small as 74 µm has been used for *Sphagnum* studies, and whilst this prevents the loss of litter pieces, it excludes many meso- and macro-faunal decomposers (Limpens and Berendse, 2003). Alternatively, much larger mesh sizes have been used such as 1-2 mm to encourage mesofauna decomposition (Moore et al., 2007, Latter et al., 1997), but there is a risk that litter may be lost, particularly *Sphagnum* which becomes dusty when dry. Therefore a mesh size of 0.5 mm was chosen to allow decomposers into the bag, whilst minimising loss of fine litter particles (Bragazza et al., 2007).

Bags were collected after 12 months of incubation and pH treatment applications, in October 2016. Once retrieved, litter bags were processed by removing all ingrown material and soil invertebrates, and the remaining litter was weighed. A cold-water extraction was then performed with a 1:20 litter to ultrapure water ratio, using a horizontal shaker for 24 hours, followed by centrifuging (15 minutes at 3500 rpm) and filtering through 0.45 µm cellulose membrane filter paper. The litter was then reweighed to establish a post-extraction weight and oven dried at 70 °C for 48 hours and weighed again for an oven dry mass. Bags were also incubated for 3, 6 and 9 months in control plots (*Calluna* and *Eriophorum*) during this period. Therefore mass loss of litter was measured quarterly over the year, the results of which are presented in Supplementary Figures 4-5.

The Tea Bag Index (Keuskamp et al., 2013) is a standardised method to establish a decomposition rate ($k_{TBI}$) and stabilisation factor ($S$) (see below) of soil which is comparable to other studies, and considered to be representative of other litter types (Duddigan et al., 2020). Two types of tea were buried in July 2016 (Green and Rooibos, both Lipton Tea Bags), which have contrasting decomposition rates. Green tea is more labile whilst Rooibos tea is more recalcitrant, meaning once the labile fraction of Green tea has been consumed by decomposers, the decomposition of the labile fraction of the more recalcitrant Rooibos tea still continues. Therefore, by comparing the mass loss, it is possible to estimate the decomposable fraction of Green tea and decomposition rate constant of Rooibos tea. From this the stabilisation factor of soil can be calculated, which represents the extent of organic matter stabilisation as labile material is transformed into more resistant forms, slowing decomposition. This method provides some standard measures of decomposition to compare the decomposition environment in different soils and under different acidity treatments.

Three sets of bags were incubated in each plot for 90 days, during which time they received three pH treatment applications. The bags were then retrieved in October 2016 and the mass loss was

established, allowing the decomposition rate ($k_{TBI}$) and stabilisation factor ($S$) to be calculated following the method outlined by Keuskamp et al. (2013). Soils were also sampled during this time from 0-10 cm depth and frozen in preparation for microbial analysis.

**Laboratory analysis**

Litter extracts were analysed for pH, electrical conductivity, DOC concentration, and specific absorbance at 254nm ($SUVA_{254}$). The DOC analysis of litter extracts are proxies for understanding DOC production, as commonly used in other studies (Mastný et al., 2018). The extracted DOC indicates the quantity and quality of DOC produced at the stage of decomposition reached after twelve months, whilst the mass loss of litter was used to indicate the amount of decomposition.

A Thermalox TC-TN analyser (Analystical Sciences, Ltd., UK) was used to measure the concentration of DOC (by subtracting the amount of total inorganic carbon (TIC) from the amount of total carbon (TC)). DOC concentrations were converted from mg $l^{-1}$ to mg DOC extracted per g of dry material. As a proxy measure of DOC quality, we used optical measures to define spectroscopic properties ($SUVA_{254}$). To do this, samples were diluted to less than 1 au, as determined by measuring absorbance at 240 nm. Ultraviolet (UV) visible absorbance spectra were then determined using UV transparent 96 well plates on a Spectromax M2e Microplate Reader (Molecular Devices, San Jose, CA) set to scan at wavelengths between 240 and 600 nm with a 1 nm increment. Data were converted to the equivalent value as if using a quartz cuvette, based on the corrections obtained by Peacock et al. (2014). $SUVA_{254}$ was then calculated by first converting the pathlength to m (by multiplying by 100), and then dividing the corrected absorbance value for a 1m pathlength at 254nm by the DOC concentration (mg $l^{-1}$) (Bowen et al., 2009, Weishaar et al., 2003). $SUVA_{254}$ has been identified as a proxy for measuring the aromatic fraction (Weishaar et al., 2003) and molecular weight (Chowdhury, 2013) of DOC, as it is strongly linked to the hydrophobic organic acid fraction of dissolved organic matter (DOM) (Spencer et al., 2012).

In addition, soils were oven dried at 60 °C for 24 hours to establish the soil moisture content at the time of litter bag retrieval (Table 2).

Table 2: Mean moisture content (% by weight) of soils collected from experimental plots.

| Site | M Peat | M Pod | PN Peat | PN Pod |
|---|---|---|---|---|
| Acid | 1317 | 239 | 496 | 252 |
| Control | 1382 | 267 | 659 | 334 |
| Alkaline | 1196 | 431 | 660 | 276 |

**Microbial community analysis**

DNA was extracted from 0.25 g of soil samples based on the manufacturer's instructions with a PowerSoil™ DNA isolation kit (MO BIO Laboratories, Carlsbad, CA). A two-step Polymerase Chain Reaction (PCR) was used for amplification of the V4 region of the 16S rRNA gene using the forward primer 515f (sequence GTGYCAGCMGCCGCGGTAA) and reverse primer 806rB (sequence GGACTACNVGGGTWTCTAAT) (Walters et al., 2016), creating amplicon fragments of approximately 380 base pairs. The PCR procedure is summarised in Supplementary Figure 2.

Following amplicon purification and normalisation (using the Applied Biosystems SequalPrep Normalization Plate (96) Kit (Thermo Fisher Scientific, USA)), DNA was diluted to 0.21 ng/ml using elution buffer from the normalisation kit, and vacuum concentrated from 400 µl to 40 µl. The DNA was cleaned using gel electrophoresis, followed by purification using the QIAquick Gel Extraction Kit (QIAGEN, Germany) instructions, and then analysed with Illumina MiSeq (Illumina, UK).

Bioinformatics were performed using R Statistical Software and the Dada2 package (Callahan et al., 2016) following the amplicon workflow: filtering; dereplication; sample inference; chimera identification; and merging of paired-end reads. During the first filtering step, forward and reverse reads were truncated based on the interpretation of quality profile plots. After truncation, readings with higher than expected errors were discarded. Identical sequences were then combined into 'unique sequences' during dereplication, which retains the quality information of each unique sequence to inform the error parameters. The sample inference step then applied the core sequence-variant inference algorithm to the data. Finally, forward and reverse reads which overlapped were merged. Chimeras were removed using the 'removeBimeraDenovo' function.

**Data analysis**

We used R statistical package to analyse data. Prior to using Analysis of Variance (ANOVA) statistical tests, data were assessed as to whether it met the assumptions of ANOVA, including normality and equal variance, and transformations were applied where necessary (Supplementary Table 2). When significance was apparent, a post hoc test was run using the 'Tukey HSD' function in R to confirm where significant differences occurred between groups. We used either two-way or one-way ANOVA tests depending on the factors and levels involved for different datasets (see Supplementary Figure 3).

Microbial data was analysed using Microbiome Analyst (http://www.microbiomeanalyst.ca) (Dhariwal et al., 2017). Firstly, samples with zero or low reads were removed manually. Once uploaded, the optimum filtering parameters which removed data noise whilst retaining key taxa were identified. Variables with low abundance features were removed and so features remaining

after the filtering step had a minimum count of two with 15% prevalence. This removed a total of 5147 low abundance features (873 remained). In order to address the variability within data and allow for biologically meaningful comparisons so that communities between groups could be compared, data was normalised by applying cumulative sum scaling (CSS) (Paulson et al., 2013, Weiss et al., 2017).

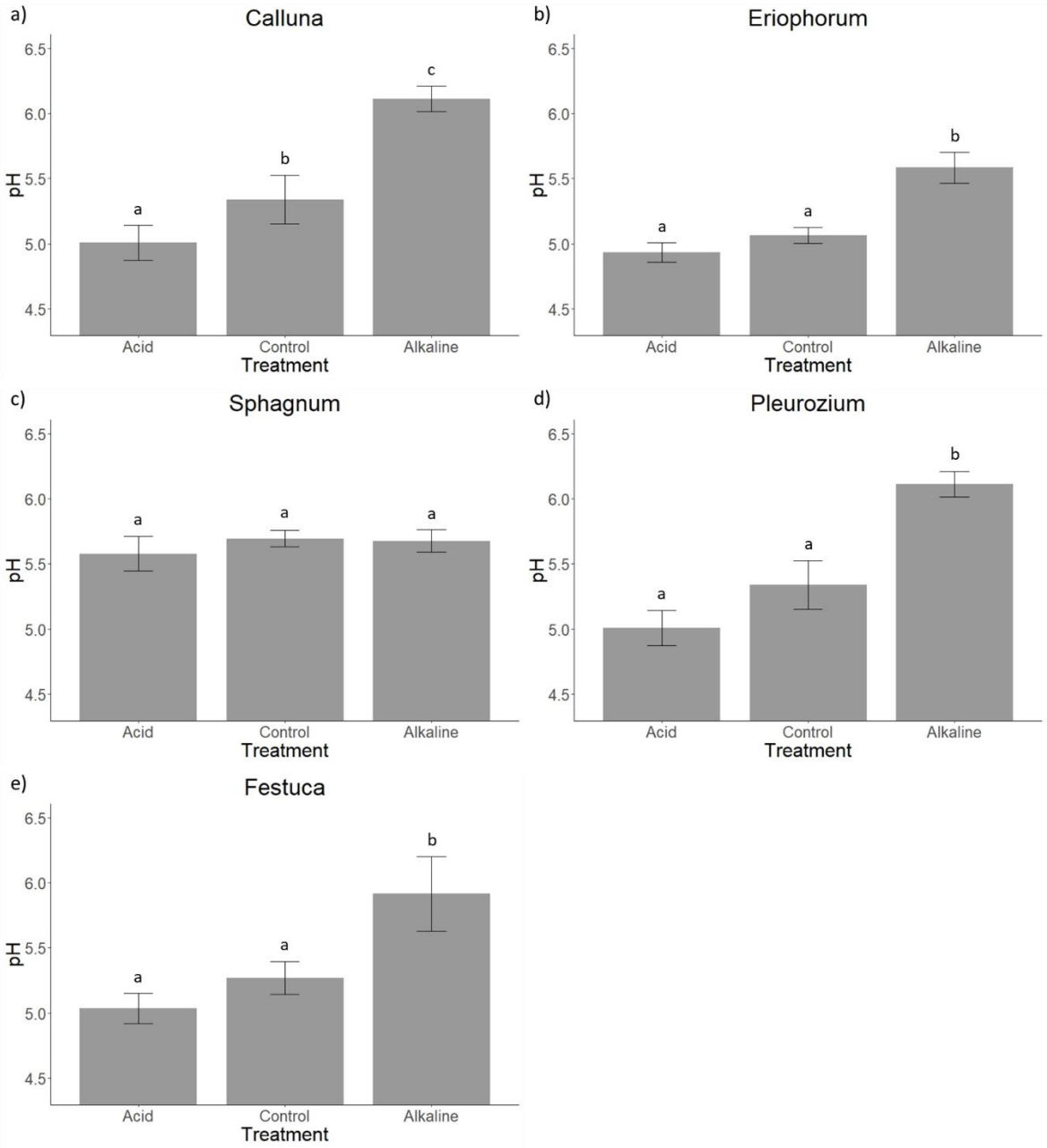
Alpha diversity indices (Shannon, Simpson's) and estimated richness (Chao1) were calculated at feature level in Microbiome Analyst, each reflecting a different element of alpha diversity. Chao1 estimates richness (Chao, 1984), Shannon's index estimates both richness and evenness of taxa (Ludwig and Reynolds, 1988), as does Simpson's, which reflects the probability of two individuals of the same taxa being randomly chosen (Simpson, 1949, Lemos et al., 2011). Changes in species diversity has been suggested to be specifically linked to changes in decomposition (Gessner et al., 2010). Therefore, alpha diversity was used as an indicator for understanding microbial community responses to environmental change, whilst decomposition was measured as an indicator of microbial soil ecosystem functional response.

Finally, correlations between litter bag data (extract pH, extract DOC and mass loss) were investigated for all litter types using Spearman's Rank correlation test. Relationships were also explored between diversity indices (Shannon, Simpson's) and estimated richness (Chao1), with mass loss and extract DOC, for *Calluna* and *Eriophorum* litters.

## Results

### Effectiveness of acidity treatments in changing sample pH

The litter extracts were more acidic when litter bags received acid treatments (ranging from pH 4.93-5.10, based on mean of plots for each litter type), and had a higher pH when they received alkaline treatments (pH 5.59-6.11) (Fig. 1). Differences were significant ($p<0.05$) when comparing acid with alkaline, and alkaline with control treatments, and when comparing acid treatment with the control for *Calluna*. The exception was *Sphagnum*, where the pH of extracts were similar regardless of pH treatment (pH ~5.60; $F_{2,8} = 0.35$, $p = 0.718$). Overall, these results demonstrate the persistence of the pH effect at the burial depth of the bags (~5 cm), consistent with findings from soil extracts and pore water samples taken at a similar depth (5-10 cm) over the same time period (see Supplementary Table 7 and Pschenyckyj et al. (2020)).




334

335 **Fig. 1** Mean pH of extracts from different litters (pooled for all sites) which received acid, alkaline
336 and control treatments (a) Calluna (N = 14-16 per treatment); (b) Eriophorum (N = 14-16); (c)
337 Sphagnum (N = 3-4); (d) Pleurozium (N = 4); (e) Festuca (N = 7-8). Differences in N relate to the
338 number of litter bags retrieved for each treatment. Letters signify where significant differences
339 occurred following post hoc analysis ($p < 0.05$). For full ANOVA results, see Supplementary Table 2.

340 **Effect of acidity on litter decomposition and DOC production**

341 Out of the Group 1 litters that were common to all sites (Table 1), the decomposition of *Eriophorum*
342 litter was significantly affected by pH treatments ($F_{2,31} = 3.74$**,** $p = 0.035$) (Fig. 2). Mass loss was 7%
343 lower when bags received acid treatments compared to alkaline treatments ($p = 0.029$), although

neither treatment was significantly different from the control (Supplementary Table 5). In contrast, the decomposition of *Calluna* litter was similar across all pH treatments ($F_{2,33}$ = 0.13, p = 0.877). There was also no significant interaction between pH treatments and sites (*Eriophorum* $F_{6,31}$ = 1.11, p = 0.379; *Calluna* $F_{6,33}$ = 1.72, p = 0.148), suggesting that the effect of pH treatment did not depend on location or soil type. In terms of the effect of acidity on the extracted DOC (a proxy for the DOC produced), pH treatments had no effect on the extracted DOC relative to the dry mass of litter, or on $SUVA_{254}$, for both *Eriophorum* and *Calluna*, and this was also found not to be dependent on location or soil type (Table 3; Supplementary Table 2). With respect to the Group 2 litters that were specific to each site (Table 1), acidity treatments had no significant effect on the decomposition of *Sphagnum* ($F_{2,8}$ = 1.92, p = 0.209), *Pleurozium* ($F_{2,9}$ = 1.50, p = 0.281) or *Festuca* ($F_{2,17}$ = 2.836, p = 0.087) litter after 12 months of incubation. In addition, pH treatments had no significant effect on the concentration of DOC extracted, or on DOC quality as indicated by the $SUVA_{254}$ value (Supplementary Table 2 and 6). Finally, no statistically significant (p = <0.05) and strong (rho = >0.06) relationship was found when comparing extract pH, extracted DOC, and mass loss, for litter bag data (Supplementary Table 9).

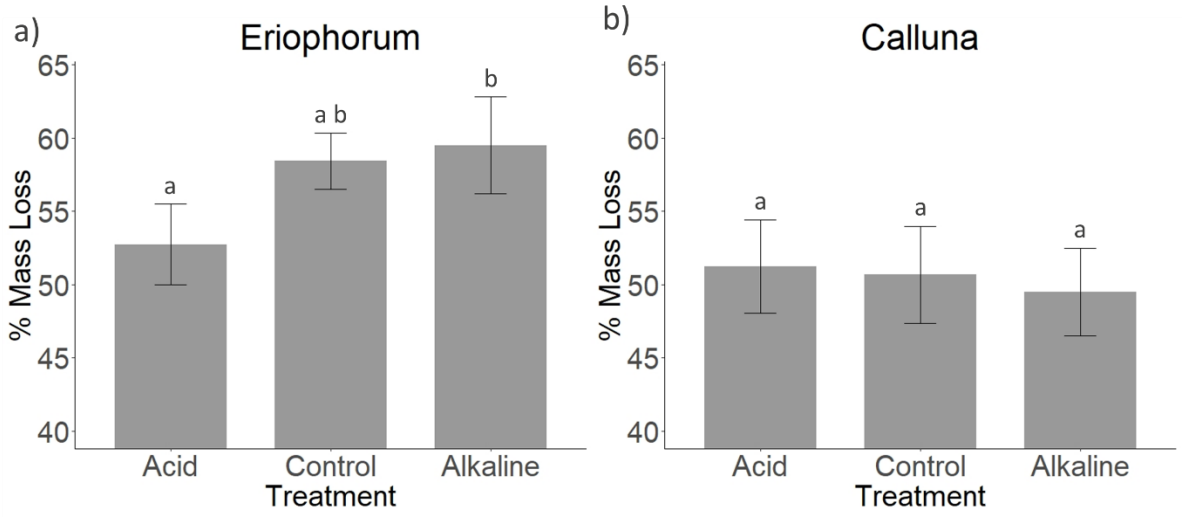


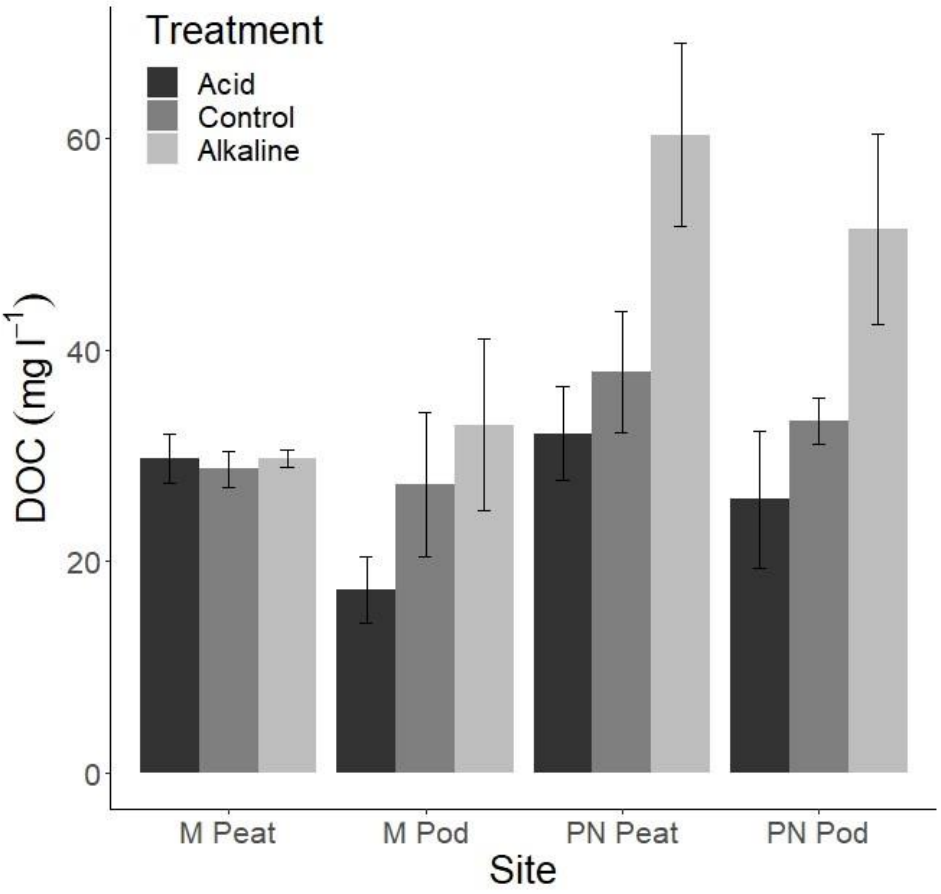

**Fig. 2** Mean percentage mass loss (pooled for all sites, N = 13-16 per treatment) of a) *Eriophorum* and b) *Calluna* litter after 12 months of incubation with different pH treatments. Error bars show standard error, whilst letters indicate where significant (p<0.05) differences occur.

Table 3: Mean and standard error (SE) of mass loss, DOC concentration per dry mass and $SUVA_{254}$ values for *Eriophorum* and *Calluna* litter extracts, incubated at different sites with different pH treatments. 'M' refers to Migneint, 'PN' refers to Peaknaze and 'pod' is podzol soil.

| | **Treatment** | ***Eriophorum*** | | | | ***Calluna*** | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | **M Peat** | **M Pod** | **PN Peat** | **PN Pod** | **M Peat** | **M Pod** | **PN Peat** | **PN Pod** |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Mass Loss (%)** | **Acid** | 50.22 | 60.26 | 41.35 | 59.14 | 43.93 | 50.39 | 41.02 | 66.90 |
| | SE | 1.66 | 5.88 | 4.03 | 4.39 | 3.38 | 2.98 | 4.69 | 0.71 |
| | **Control** | 51.68 | 58.98 | 51.10 | 65.09 | 53.27 | 49.33 | 36.48 | 67.78 |
| | SE | 3.86 | 2.51 | 1.87 | 1.76 | 5.18 | 2.21 | 2.47 | 2.21 |
| | **Alkaline** | 54.91 | 72.74 | 54.84 | 58.17 | 42.38 | 49.70 | 47.82 | 66.64 |
| | SE | 3.44 | 6.71 | 5.74 | 0.27 | 5.16 | 2.79 | 5.93 | 1.26 |
| **DOC (mg $g^{-1}$)** | **Acid** | 2.13 | 3.51 | 2.40 | 3.54 | 2.50 | 2.19 | 2.66 | 3.40 |
| | SE | 0.22 | 0.88 | 0.25 | 0.59 | 0.20 | 0.19 | 0.30 | 0.90 |
| | **Control** | 2.01 | 4.72 | 2.14 | 4.58 | 3.51 | 2.09 | 2.69 | 3.12 |
| | SE | 0.04 | 0.85 | 0.18 | 0.78 | 1.06 | 0.32 | 0.40 | 0.35 |
| | **Alkaline** | 2.02 | 2.54 | 2.97 | 2.94 | 2.94 | 1.50 | 2.73 | 3.36 |
| | SE | 0.14 | 0.42 | 0.72 | 0.24 | 0.48 | 0.16 | 0.39 | 1.16 |
| **$SUVA_{254}$ (L mg $C^{-1}$ $m^{-1}$)** | **Acid** | 2.06 | 2.79 | 1.55 | 3.05 | 1.06 | 2.35 | 1.21 | 1.88 |
| | SE | 0.19 | 0.19 | 0.45 | 0.10 | 0.14 | 0.05 | 0.17 | 0.30 |
| | **Control** | 1.87 | 2.75 | 2.32 | 2.78 | 1.45 | 1.83 | 1.15 | 1.76 |
| | SE | 0.45 | 0.12 | 0.28 | 0.30 | 0.10 | 0.19 | 0.13 | 0.12 |
| | **Alkaline** | 1.97 | 3.04 | 1.88 | 3.20 | 0.86 | 1.97 | 1.46 | 2.18 |
| | SE | 0.13 | 0.13 | 0.27 | 0.07 | 0.15 | 0.33 | 0.19 | 0.10 |

These results are in contrast to the pore water DOC sampled during the same month of harvesting the bags, which showed a response of DOC concentration to pH at all but one site (M Peat; Fig. 3). Significant comparisons of interest between treatment plots at each site was limited to PN Peat alkaline and acid plots only ($p = 0.047$), likely due to the fact this is based on a single sampling event.




371

372 **Fig. 3** Mean DOC concentration of pore water sampled from experimental plots during October
373 2016. Error bars show standard error (n=4).

374 Comparing decomposition and extract DOC between locations, *Calluna* litter in podzol control plots
375 decomposed 18% more at the acidic Peaknaze site when compared to the less acidic Migneint site (p
376 = <0.001) (Table 3). This was associated with 1.5 times more extractable DOC (p = 0.005). However,
377 the quality of DOC (using $SUVA_{254}$ as a proxy for this) did not vary between locations, and for
378 *Eriophorum* litter there were no differences in decomposition or extract DOC (both the
379 concentration per dry mass and $SUVA_{254}$) between experimental site locations (Supplementary Table
380 3).

381 Comparing soil types, we found that both *Calluna* (at Peaknaze) and *Eriophorum* (at Migneint and
382 Peaknaze) decomposed more in podzol soil and, for *Eriophorum*, this was associated with nearly
383 double the amount of DOC being extracted at >4.5 mg $g^{-1}$ (compared to ~2 mg $g^{-1}$ for litter incubated
384 in peat, based on mean of control plots). In addition, DOC extracted from litter incubated in podzol
385 soil was also found to be significantly more aromatic (as indicated by a larger $SUVA_{254}$ value) for both
386 litter types at both experimental locations (Supplementary Table 4). Therefore, after 12 months of

incubation, both decomposition of litter and extracted DOC were significantly lower in peats compared to podzols.

**Tea Bag Index**

Based on the tea bag decomposition results, the podzol soils had a lower *S* and greater $k_{TBI}$ value than the peat sites (Table 4). These differences were significant at Peaknaze (*S* p = <0.001; $k_{TBI}$ p = 0.028), but not at the Migneint site. Neither $k_{TBI}$ or *S* were affected by the acidity manipulations, regardless of location or soil type (Supplementary Table 2).

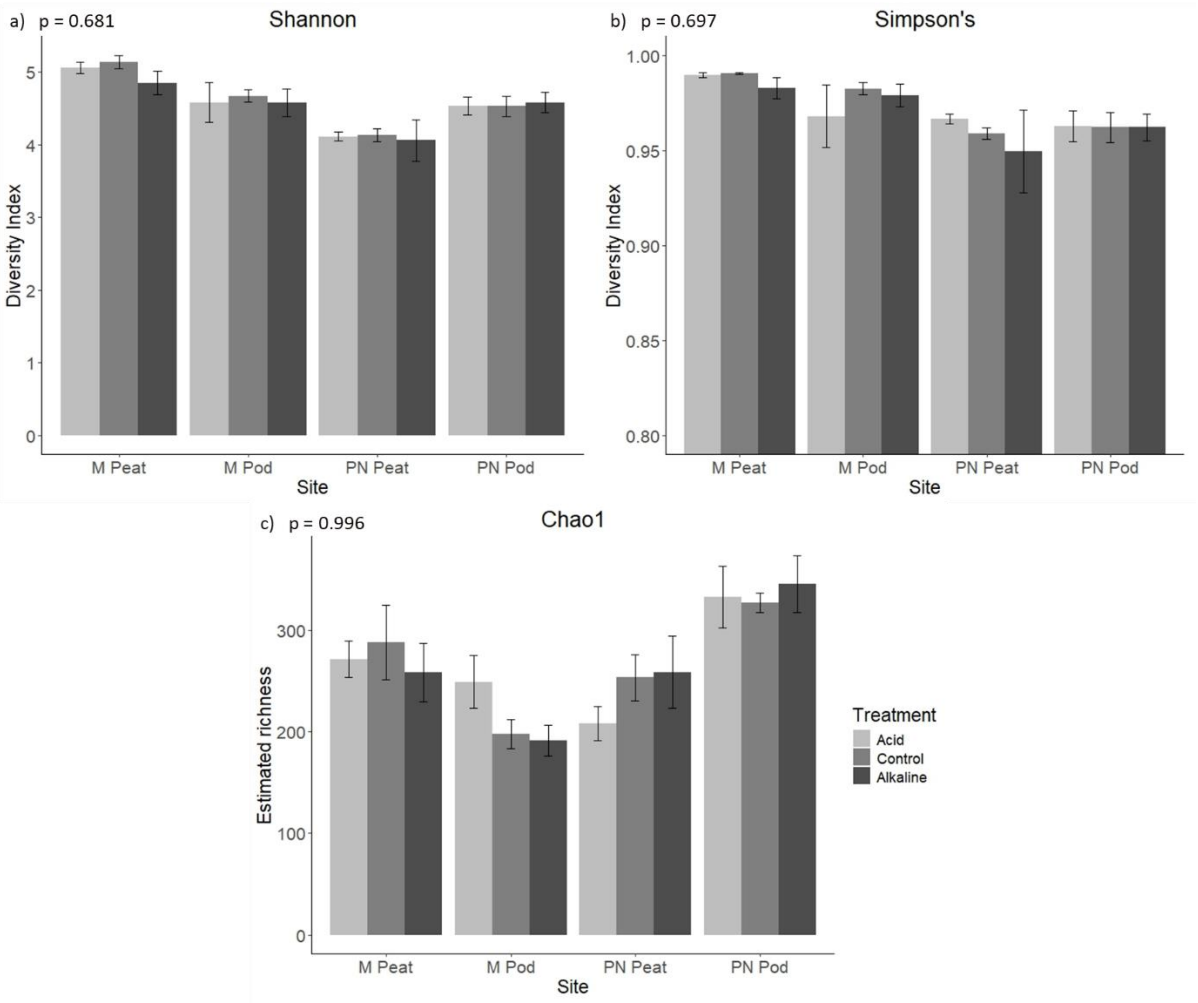
Table 4: Stabilisation factor (*S*) and decomposition rate ($k_{TBI}$) values, and standard error (SE, n=4) for different experimental sites and pH treatments.

| | Treatment | M Peat | M Pod | PN Peat | PN Pod |
|---|---|---|---|---|---|
| **Stabilisation Factor (*S*)** | **Acid** | 0.175 | 0.148 | 0.238 | 0.153 |
| | SE | 0.020 | 0.011 | 0.011 | 0.020 |
| | **Control** | 0.167 | 0.141 | 0.237 | 0.109 |
| | SE | 0.018 | 0.010 | 0.013 | 0.018 |
| | **Alkaline** | 0.170 | 0.139 | 0.229 | 0.127 |
| | SE | 0.013 | 0.010 | 0.017 | 0.021 |
| **Decomposition Rate ($k_{TBI}$)** | **Acid** | 0.012 | 0.015 | 0.011 | 0.013 |
| | SE | 0.000 | 0.001 | 0.000 | 0.001 |
| | **Control** | 0.012 | 0.012 | 0.011 | 0.013 |
| | SE | 0.000 | 0.001 | 0.001 | 0.001 |
| | **Alkaline** | 0.012 | 0.012 | 0.012 | 0.012 |
| | SE | 0.001 | 0.001 | 0.001 | 0.001 |

**Impact of acidity on microbial communities**

Bacterial and archaeal alpha diversity was found to be significantly different between experimental sites for estimated richness (Chao 1 $F_{3,34}$ = 12.433, p = <0.001) and both diversity indices (Shannon $F_{3,34}$ = 16.547, p = <0.001; Simpson's $F_{3,34}$ = 6.332, p = 0.001) (Fig. 4; Supplementary Table 8). Further analysis with Tukey's Post hoc showed a significant difference between peat sites for diversity indices (Shannon p = <0.001, Simpson's p = 0.002), with a higher diversity at Migneint Peat than at Peaknaze Peat. Estimated richness (Chao1) was found to be significantly different between podzol sites (p = <0.001), with greater richness at Peaknaze.

Microbial diversity differed between soil types at each site location based on Shannon index (Migneint p = 0.023; Peaknaze p = 0.01). However, results were inconsistent, with greater diversity for peat at Migneint compared to podzol, and the opposite at Peaknaze, whilst analysis of Simpson's index showed insignificant results (p = >0.05). Differences in estimated richness between soil types were only significant at Migneint (Chao1 p = 0.039), with greater richness in peat soil. In addition, acidity manipulations had no effect on microbial diversity or richness (Fig. 4). Finally, the treatment effect was found not to be dependent on-site location or soil type (p = >0.05) (Supplementary Table 8). When comparing alpha diversity and richness data, with extracted DOC and mass loss (for *Calluna* and *Eriophorum* litter bags), no significant relationships were found (Supplementary Table 10).




414

415 **Fig. 4** Mean values for a) Shannon index, b) Simpson's index and c) Chao1 estimated richness. Error
416 bars show standard error. ANOVA p value results comparing treatments are shown (for full results,
417 see Supplementary Table 8).

418 **Discussion**

419 **The effect of acidity on litter decomposition and DOC production**

420 There are few studies assessing the impact of acidity on litter decomposition, particularly in upland
421 organic soils. In this study, we found that mass loss did not differ between acidity treatments for any
422 litter type other than *Eriophorum*, which decomposed less with acid treatments and more with
423 alkaline treatments. Furthermore, the amount and quality of DOC extracted from litter, which
424 represents the DOC produced at 12 months of decomposition, did not differ between pH
425 treatments. However, it is important to note this is a snapshot in time, and so DOC production may
426 differ at different stages in decomposition (Soong et al., 2015). Regardless, these findings are in
427 contrast to pore water DOC concentrations, which evidenced an acidity response during the same

sampling month, and showed a significant response over the 13 month experimental period (Pschenyckyj et al., 2020).

Similarly to the litter bag results, TBI parameters (decomposition rate ($k_{TBI}$) and stabilisation of litter (*S*)) were also unaffected by acidity treatments. Additionally, soil microbial community diversity from soils sampled within the same experimental plots was found not to be impacted by acidity treatments. These results appear consistent with a previous assessment of respiration and enzyme activity for the same experiment, which also showed no evidence of biological responses to pH change (Oulehle et al., 2013). On the other hand, Kang et al. (2018) used phenol oxidase activity and microbial abundance data from these sites, as well as comparisons to more alkaline sites in Asia, to argue for a biological influence on DOC production.

As soil pH is crucial to enzyme functioning (Fog, 1988), and is highly correlated with microbial community structure (Griffiths et al., 2011), acidity may alter mechanisms involved in microbial decomposition of organic material. However, studies have shown contradictory results. Donnelly et al. (1990) found microbial biomass, lignin and cellulose decomposition to be unaffected by acidity in a forested environment, whilst leaf litter decomposition has been shown to be suppressed in acidified streams (Ferreira and Guérold, 2017). Suppressed decomposition of *Calluna* and *Eriophorum* litter has been observed in a peat monolith acidification experiment (Sanger et al., 1993), whilst no effects have been shown for *Sphagnum* in a poor fen environment (Rochefort et al., 1990). Both aerobic and anaerobic decomposition of glucose has been shown to be lower in the naturally acidic conditions of *Sphagnum* peat (4.3 pH units), compared to experimentally increased pH (6.8 pH units) (Bergman et al., 1999). In addition, Kluber et al. (2020) found that an increase in pH from 3.5 to 5.5 units altered microbial communities in deep peat (1.5-2 m depth) anaerobic microcosms, but this had no effect on $CH_4$ production suggesting methanogenic processes were not affected. As noted above, Kang et al. (2018) argued that pH effect on enzyme processes and microbial communities were contributing to DOC increases.

Our results suggest that changing acidity had little or no effect on litter decomposition and DOC production (using extracted DOC from litters as a proxy for this) at our experimental sites. It is possible that this apparent absence of effect could be because the change in pH was not of sufficient magnitude to drive detectable changes in biological processes, or confounded by environmental heterogeneity. However, measurements from pore water and soil extracts collected from the plots during the same sampling period showed that pH treatments had successfully altered pH at the depth at which bags were buried (Supplementary Table 7), with an average of half a pH unit difference between acid and alkaline plots (across all months and experimental sites) (Pschenyckyj et

al., 2020). With the exception of *Sphagnum*, the pH of water extracts from litter samples also reflected the pH treatments they received: extract pH was, on average, 0.21 units lower in acid versus control treatments and 0.55 units higher in alkaline versus control treatments. This magnitude of pH change is at least as large as the change in soil acidity that has occurred in response to decreasing acid deposition (Evans et al., 2012). In addition, Kang et al. (2018) observed differences in fungal abundances and phenol oxidase activity at these sites with changes in pH of <1 unit. Therefore, such acidity changes would be expected to have altered microbial community diversity and function, including decomposition rates, if biological processes were contributing to DOC increases as argued by Kang et al. (2018).

A possible reason behind the lack of litter decomposition response to acidity treatments observed may be methodological in relation to the litter incubation time. Some upland litter bag studies have been conducted over a period of two (Scheffer et al., 2001, Ward et al., 2015, Thormann et al., 2001) or three (Bragazza et al., 2010, Moore et al., 2007) years in similar environmental conditions. Bryophytes such as *Sphagnum* are consistently shown to have slow decomposition rates compared to other vegetation types (Pinsonneault et al., 2016, Ritson et al., 2014, Armstrong et al., 2012, Moore et al., 2007), likely due to the high phenolic content (Rasmussen et al., 1995), which suppresses biodegradation (Verhoeven and Toth, 1995, Fenner et al., 2004). In addition, Oulehle et al. (2018) detected a suppression effect of sulphuric acid treatments on teabag decomposition after 6 months of incubation in a forested podzol soil, whilst in this study we used three months of incubation. It is therefore possible that the labile fraction of green tea had not completely decomposed after three months, so that *S* may have been overestimated in peat, making it difficult to detect differences between pH treatment and soil types. Interestingly, MacDonald et al. (2018) also found no relationship between pH and $k_{TBI}$, but did find a negative correlation with *S*, after three months of incubation in a peatland environment. Therefore, while we found minimal effects, we cannot exclude the possibility that clearer effects might have emerged over longer time periods.

However, this would not explain the negligible effect on microbial diversity or richness, as the experimental plots received nearly six years of acidity manipulation treatments, which would be a sufficient period of time for microbial community responses to occur. Further work examining microbial communities (such as abundance and community composition) and functioning under each acid treatment is needed, including using different metrics to assess community responses, sequencing fungal communities, and investigating specific taxa. In addition, other environmental variables should be measured in order to disaggregate the full impacts of pH from other influencing factors, such as temperature at litter burial depth, a range of meteorological variables, water table depth, and soil moisture monitoring.

**How do litter decomposition and DOC production vary between peat and organo-mineral soils?**

Overall, litter decomposed more in podzol (with an average of 17% more mass lost) than in peat soil, resulting in 1.5 times more DOC being extracted after 12 months. Based on $SUVA_{254}$, DOC extracted from litter buried in podzols was also more aromatic. The greater DOC concentration and aromaticity of podzol litter extracts appears to be attributable due to the litter reaching a later decomposition stage than when incubated in peat, due to faster decomposition rates. Consistent with this finding, we previously observed higher DOC concentrations and $SUVA_{254}$ in extractions of in situ litter at the Migneint podzol versus peat sites (Pschenyckyj et al., 2020). These results are also supported by the TBI parameters, where peat had a lower $k_{TBI}$ and higher *S* value compared to podzol, suggesting that, as expected, decomposition rates are lower in peat with more stabilisation of the labile fraction of organic matter.

This difference in decomposition and DOC production between peat and podzol soils can be explained by differences in soil physical properties and functioning. Podzol soils are more freely draining allowing for more aerobic activity, whereas decomposition rates in peatlands are inhibited by anaerobic conditions (Swift et al., 1979, Keller et al., 2009). Better drainage results in net primary production of surface vegetation being greater for podzol soils compared to peat, and so there is a greater input of organic material from litter, which arguably could result in a more biologically active and primed microbial community, and therefore faster decomposition rates (Xiao et al., 2014, Kuzyakov et al., 2000). The higher rate of extracted DOC, indicating production, in podzol versus peat litter layers contrasts with the generally higher export of DOC from peat catchments noted earlier, which can be attributed to DOC adsorption in the mineral horizons of podzols (Jansen et al., 2005). This combination of high DOC production in the surface layer, along with subsurface retention, helps to explain the highly flow-dependent variation of DOC in headwaters draining podzolic catchments, and the very high peak DOC concentrations that can occur in these systems (Hinton et al., 1997, Stutter et al., 2012, Clark et al., 2008, Easthouse et al., 1992).

The differences in physical and chemical properties (and therefore microhabitats) will also result in, and be a result of, different microbial communities (Philippot et al., 2024), and may also explain differences in decomposition and DOC production between soils. Our results support this theory at Peaknaze, whereby microbial communities had a greater diversity (Shannon) in podzol soil compared to peat, which ties in with greater decomposition rates of litter (TBI and litter bags) and extracted DOC (indicating production), which was also more aromatic ($SUVA_{254}$) indicating more processing of DOC by soil microbes. However, the opposite is the case at Migneint, in which diversity (Shannon), as well as estimated richness (Chao1) were lower in podzol soil compared to peat, whilst

decomposition and extracted DOC were greater. One possible reason for the contrasting soil results between sites may be due to other limiting environmental variables on microbial functioning. These results also suggest that microbial diversity and richness are not sufficient metrics for understanding microbial functional responses to environmental change.

## Conclusion

We found negligible effects of changing acidity on litter decomposition, or extracted litter DOC indicating production, regardless of soil type, in either an acidity manipulation field experiment or when comparing two locations with contrasting ambient acidity levels. We also found no broad effects of acidity manipulation on microbial community alpha diversity, as indicated by Chao1 estimated richness, Shannon, and Simpson indices. These results are in contrast with strong evidence of a chemical solubility driven relationship between pH and DOC in several previous studies undertaken at the same experimental sites (Pschenyckyj et al., 2020, Evans et al., 2012). Together, these results suggest that the physiochemical response to changing acidity, and soil type, are more influential on DOC release from organic soils as opposed to the response of litter decomposition.

## Declarations

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**Author contributions:** All authors contributed to conceiving the ideas and designing methodology; CP, MB and JR were involved in laboratory work; CP collected and analysed the data with contributions from JC and CE in data interpretation; CP led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

**Data availability statement:** The datasets generated during and analysed during the current study are available in the EIDC repository https://doi.org/10.5285/3bd6397d-f0db-40c4-885a-95ca280a6683 (Pschenyckyj et al., 2021).

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