Peatland plant functional type effects on decomposition factors are non-pervasive, but microhabitat dependent

Najam e Sahar
University of Southampton
Bjorn JM Robroek (Bjorn.Robroek@ru.nl)
Radboud University Nijmegen: Radboud Universiteit https://orcid.org/0000-0002-6714-0652
Robert TE Mills
University of York
Marc G Dumont
University of Southampton
Janna M Barel
University of Eastern Finland: Ita-Suomen yliopisto

Research Article

Keywords: Decomposition, Extracellular Enzyme Activity, Microhabitat, Peatland, Plant functional types, Tea Bag Index (TBI)

Posted Date: April 4th, 2022

DOI: https://doi.org/10.21203/rs.3.rs-1514002/v1

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Najam e Sahar[1], Bjorn JM Robroek[1,2,*], Robert TE Mills[3], Marc G Dumont[1] and Janna M Barel[4]

Najam e Sahar, https://orcid.org/0000-0002-1338-730X
Bjorn JM Robroek, https://orcid.org/0000-0002-6714-0652
Robert TE Mills, https://orcid.org/0000-0002-5936-8737
Marc G Dumont, https://orcid.org/0000-0002-7347-8668
Janna M Barel, https://orcid.org/0000-0001-8520-8289

[1] School of Biological Sciences, Faculty of Natural and Environmental Sciences, Institute for Life Sciences, University of Southampton, Southampton SO17 1BJ, UK; [2] Aquatic Ecology & Environmental Biology, Radboud Institute for Biological and Environmental Sciences, Faculty of Science, Radboud University Nijmegen, AJ 6525 Nijmegen, The Netherlands; [3] Department of Environment & Geography, University of York, York YO10 5NG, UK; [4] School of Forest Sciences, University of Eastern Finland, Joensuu, Finland; [*] Corresponding author: bjorn.robroek@ru.nl; tel: +31 (0)24 3652860

Acknowledgements We would like to thank all staff of the Store Mosse National Park, notably Carina Härlin and Arne Andersson, for their logistic support and continuous input in discussions on the value of our work for peatland management and conservation. We are indebted to Länsstyrelsen i Jönköpings län for granting site access (permission 521-7195-2019/0617-01-101). We thank Mike Peacock at Sveriges Landbrukssniversitet Uppsala for funding and logistics.

Abstract

Despite their low primary production, ombrotrophic peatlands are important long-term sinks for atmospheric carbon due to even lower rates of litter decomposition. Litter decomposition can be affected by plant functional types (PFTs; Graminoids, Ericoids) and microhabitat (hummock, lawn), but the microhabitat context-dependency of PFT effects on decomposition processes remains poorly understood. We used a long-term (> 10 yr) plant removal experiment, in conjunction with the Tea Bag Index (TBI), to explore how PFT removal in both hummock and lawn microhabitats influence decomposition. In parallel, we assessed potential activity of five extracellular hydrolytic enzymes as proxies for microbial activity. Our results indicate that PFT removal had no effect on the TBI decomposition constant (*k*), nor on the stabilisation factor (S). Yet, *k* increased slightly when both PFTs were absent. In the lawns, we observed higher values of S as compared to hummocks. A similar trend was observed for the decomposition rate constant (*k*). PFT compostion influenced the potential hyrolytic EEAs underlying decomposition process, however this influence was non-pervasive and depended on microhabitat. Our results suggest an important role for vegetation change – through their influence on enzyme activity – along the lawn-hummock gradient in regulating decomposition processes in northern peatlands. Our results highlight it is important to monitor the interplay between plant functional type composition and microhabitat in order to understand decomposition processes in peatlands

Keywords Decomposition · Extracellular Enzyme Activity · Microhabitat · Peatland · Plant functional types· Tea Bag Index (TBI)

Introduction

Northern peatlands are important terrestrial carbon (C) stores that for millennia have accumulated non-decomposed plant material as peat (Gallego-Sala *et al*. 2018) and formed the organic C reservoirs that are currently estimated to hold 600-700Gt of carbon (Yu 2012; Ratcliffe *et al*. 2021). These values are equivalent to 25-30% of the global soil carbon stock (Gorham 1991). Peatlands are, therefore, key in regulating the global climate and their continued presence one of the best natural lines of defence against climate change. The peatland C sink function results from the production of decay-resistant plant litter, in combination with low average temperatures and waterlogged conditions that constrain microbial metabolic activity and lead to slow decomposition rates (Yu 2012). Currently, peatlands undergo rapid changes in enviro-climatic conditions that puts pressure on the ecological processes supporting their C sink function (Gallego-Sala *et al*. 2018; Swindles *et al*. 2019). To anticipate the impact of global change on peatland C dynamics it is essential we understand what drives the decomposition process.

Decomposition in peatlands is largely driven by soil microbial activity (Fenner, Freeman and Reynolds, 2005; Preston *et al*. 2012; Briones *et al*. 2022). Consequently, decomposition is influenced directly by abiotic factors such as hydrological conditions and temperature, and indirectly through the composition of the plant community (Weltzin *et al*. 2003; Robroek *et al*. 2021). Hence, enviro-climatic change is expected to have unprecedented impact on microbial decomposition (Didion *et al*. 2016) and can potentially convert peatlands global carbon sinks to sources of greenhouse gasses GHG (Loisel *et al*. 2021). Whether northern peatlands will remain to act as C sinks or become C sources depends on the extent to which peatland plant communities and biological interactions respond to enviro-climatic change. To date, much research has been undertaken on the

direct effects of global climate change on carbon dynamics in peatland, but indirect and interactive effects are less well understood.

Ombrotrophic bogs often display distinct patterns in microhabitats where hummocks – elongated/raised and well-aerated mounds – are alternated with wet depressions, lawns. These microhabitats are each dominated by a distinct community of *Sphagnum* mosses. The vascular plant community is comprised of two functional types, graminoids and ericoids, that differ in their mechanisms for nutrient acquirement (Kaštovská *et al*. 2018). Although both PFT types are found in both microhabitats, graminoids are prevalent in the wetter lawns, where they are associated with faster decomposition rates. This is because they produce relatively nutrient rich litter. Also, many of the graminoids in peatlands possess aerenchyma, sponge-like tissue forming open air canals in stem and roots, that promote the diffusion of oxygen to the roots and activates mineralization in anoxic peat through changes in microbial extracellular enzyme activity (EEA) (Bragazza *et al*. 2015; Robroek *et al*. 2015). In contrast, the drier hummocks are dominated by ericaceous shrubs that form a symbiotic association with ericoid mycorrhizal fungi. These species produce nutrient poor litter, rich in recalcitrant components, which possibly inhibits the decomposition process and associated C loss (Gadgil and Gadgil 1971; Read, Leake and Perez-Moreno 2004). It is well established that plant functional types can have considerable effects on decomposition (Johnson and Damman 1993; Mastný *et al*. 2021; Zeh *et al*. 2020). These vascular plant types shape belowground microbial communities and associated EEA (Robroek *et al*. 2015; Parvin *et al*., 2018) by providing different quality and quantity of litter (Hobbie 1992; Gartner and Cardon 2004; Handa *et al*. 2014) and various exudates released from roots (Bragazza *et al*. 2008; Kardol *et al*. 2010). These litter deposits and root exudates serve as microbial substrates and stimulate microbial EEA and respiration with subsequent effect on decomposer community composition and C cycling (Ayres, Dromph and Bardgett 2006; De Deyn, Cornelissen and Bardgett 2008; Haichar *et al*. 2008; Van Der Heijden, Bardgett and Van Straalen 2008; Wiedermann *et al*. 2017).

Apart from being different in composition of the plant community, microhabitats differ in hydrology which can greatly influence the microbial EEA (Jassey *et al*. 2018). Moreover, the depth of the water table is known to influence decomposition (Hilbert *et al*. 2000). For example, Radu and Duval (2018), reported that combined effect of precipitation frequency, water table level and different vascular PFTs on belowground processes, e.g. C cycling. In peatland ecosystems, microhabitats have been shown to affect the decomposition rates (Belyea 1996). Despite the recognized influence of PFTs and microhabitat on decomposition (Ward *et al*. 2015), their interactive effects are still unclear. What is more, warmer and drier conditions increase the abundance of graminoids and ericaceous shrubs in peatlands (Walker *et al*. 2006, 2015). It has been recently highlighted that widespread drying as a result of climate warming is alarming (Swindle *et al*. 2019), as that can have substantial consequences on peat carbon stock. Therefore, studying the contribution of PFT on decomposition in the context of hydrologically different microhabitats may provide much needed insights in peatland carbon dynamics in the light of a warmer and drier future climate.

Here, we investigate how alterations in vascular plant functional types influence the decomposition across two contrasting microhabitats in peatlands: dry hummocks and wet lawns. The aim of this work is to address two specific objectives: to investigate the relative and interactive effect of vascular plant functional types and microhabitat on i) decomposition rate constant (k) and stabilization factor (S) using standard substrate incubation (Keuskamp *et al*. 2013); and on ii) hydrolytic extracellular enzyme activity (EEAs) in an ombrotrophic bog. We hypothesized that PFT composition and microhabitat would affects decomposition and microbial activity. Hence,

we postulated lawns to have higher hydrolytic enzyme activity compared to hummocks, which translates to increased decomposition rate constant (*k*). In addition, we expected that selective removal of graminoids and ericoids would decrease the rate of decomposition rate constant (*k*) but increase stabilization factor (S) and altered microbial hydrolytic enzymatic activity.

Materials and Methods

Study area and experimental design

This work has been performed in the Store Mosse National Park (57°17'54 N, 14°00'39 E), the largest peatland complex in the south of Sweden and representative of ombrotrophic peatlands in the nemo-boreal zone. Specifically, in a *Sphagnum*-dominated ombrotrophic bog, a vascular plant removal experiment was established in June 2011 comprising 80 plots of 0.5 × 0.5 m (Robroek *et al*. 2015). Briefly, four plant functional group removal treatments – undisturbed control, graminoids removed (– Gram), ericoids removed (– Eric), ericoids + graminoids removed (– Gram / – Eric) – were established in lawn and hummock microhabitat by selectively clipping aboveground vegetation flush to the *Sphagnum* layer. Regrowth (roots included) was removed at least twice per year since the start of the treatments. The experiment is laid out in a randomised block design, with all treatments replicated ten times within block (4 PFT communities × 2 microhabitats × 10 blocks). This method allowed us to evaluate the influence of plant functional types on below ground ecological processes in their natural state (Díaz *et al*. 2003). During the summer of 2019, preceding the installation of the tea bags used for this experiment, we estimated cover (%) for the vascular plant community on a subset – i.e. 40 PFT removal plots (4 treatments x 2 microhabitat x 5 replicates).

Decomposition rate (*k*) and stabilization factor (S)

We used the Tea Bag Index (TBI) method to estimate the role of plant functional types composition and microhabitat on peat litter decomposition and organic matter stabilization in the peat. The TBI method makes use of commercially available green tea (EAN 8722700 05552) – high proportion of water soluble labile organic material – and red tea (EAN 8722700 188,438) – high proportion of acid insoluble polyphenolic material recalcitrant organic material (Keuskamp *et al*. 2013). In July 2019, we buried a pair of tea bags (one green and one red) in all plots. Tea bags were inserted vertically 10 cm apart and at a depth of *c*. 8 cm. The tea bags were recovered in September 2019 after an incubation time of 76 days. After initial air-drying, tea bags were oven-dried (48h at 60°C) in the laboratory, after which, adhered peat and roots were removed. Tea bags were then dried again, and the remaining tea was weighed. Following Keuskamp *et al* (2013), we estimated a decomposition rate (k) and an organic matter stabilization factor (S). Generally, *k* is linked to fast microbial litter breakdown, while S is associated to the transformation of fast-decomposing molecules into slow-decomposing molecules. Hence, high values of S are thought to indicate a larger storage capacity of organic matter, hence C storage (MacDonald *et al*. 2018; Fuji *et al*. 2017).

Hydrolytic enzyme activity

Activity of the decomposer community has a large influence on the decomposition of peat material (Preston *et al*. 2012). Therefore, we measured the activity of five hydrolytic enzymes (Table 1) in the rooting zone (0-15 cm) of 40 plots (4 treatments x 2 microhabitats x 5 replicates) following (Jassey *et al*. 2011). In brief, 3 g homogenized

wet peat was added to 50 mL 0.1 M $CaCl_2$ solution with 0.05 % Tween 80 and 20g polyvinylpolypyrrolidone and shaking at room temperature on shaker for 90 mins with 150 rpm. The mixture was centrifuged at 10,000rpm for 5 mins at 4°C and the supernatant was filtered using Whatman GF/C of 1.2µm. Next, the filtrate was poured into a cellulose dialysis tube of 10-12kDa molecular mass and then concentrated using polyethylene glycol. The concentrated solution was added to 10mL of phosphate buffer (pH 5.6) and divided into two equal aliquots. One aliquot – active enzyme extract – was stored at 4°C overnight, while the other aliquot – inactivated enzyme extract – was boiled for 3 h at 90°C. For each sample, four technical-replicates assay wells (using opaque 96-well micro-plates) received 38 µl of enzyme extract and 250 µl of substate. As a control, the same procedure was followed but with 38 µl inactivated enzyme extract. Incubation was performed in the dark at 25°C for 3h, after which the reactions were halted with 1 µl 0.5 M NaOH. Fluorescence intensity was measured spectrophotometrically at 365nm excitation wavelength and 450nm emission wavelength (BMG LABTECH Omega multidetector plate reader). Potential activity of hydrolytic enzymes was expressed as nmol of MUF/MUC released per gram of dry soil per hour (nmol g^{-1} h^{-1}).

Data analysis

Difference in vascular plant cover between lawns and hummocks was inspected by fitting linear model with generalized least squares (gls) on the data from the control plots, using microhabitat as a fixed factor. The effects of the PFT removal treatment, microhabitat and their interaction on the decomposition rate constant (*k*), the stabilisation factor (S), and the activity of five hydrolytic enzymes (ALA, BG, NAG, PHOS, SUL) were tested by fitting gls models. Heterogeneity in the *k* data was accounted for by using a VarComb variance structure in the model. All models were fitted with restricted maximum likelihood (REML). Residuals of the final model were analysed for normality and homogeneity, with Kolmogorov-Smirnov test and Levene's test. All statistical analysis and visualisation were performed with R, Version 3.1.0 (R Core Team 2018).

Results

Vascular plant cover

The PFT removal treatments were successful in creating distinct plant community compositions in the experimental plots (Supplementary Information Fig. S1). Noteworthy is that the natural vascular plant cover, hence the cover in the control plots, was twice as high in the hummocks (66%) as compared to the lawns (31%) ($F_{1,8}$ = 25.31, $P \leq 0.001$), primarily caused by the higher ericoid species abundance in the hummock plots. Consequently, the removal of ericoids or graminoids played out differently for the total vascular plant cover in hummocks and lawns (Fig. S1).

Decomposition rate constant and stabilization factor

The green tea bags in the hummocks lost 71.6% ± 0.04 (mean ± SD) which was significantly higher ($F_{1,72}$ = 30.59, $P < 0.001$) than the 64.1% ± 0.07 mass loss in the lawns. As expected, the mass loss from the rooibos tea bags was lower, but not significantly different ($F_{1,72}$ = 3.42, P = 0.068) between hummocks (21.4% ±0.03) and lawns (20.1% ± 0.03). We found no effect of PFT removal treatments on the mass loss of green tea ($F_{3,72}$ = 0.99, P = 0.403) or rooibos tea ($F_{3,72}$ = 0.35, P = 0.786).

The decomposition rate constant – k – was higher in lawns as compared to k-values in the hummock microhabitats ($F_{1,72}$ = 4.55, P = 0.036). PFT removal treatment did not influence k, neither as an overall effect ($F_{3,72}$ = 1.77, P = 0.160) nor in interaction with microhabitat ($F_{3,72}$ = 0.24, P = 0.864). Despite the non-significant PFT treatment results, k appeared to increase with the combined removal of graminoids and ericoids (Fig. 1; – Gram / – Eric). The potential of the labile fraction of the green tea litter to become stabilised, expressed as the stabilization factor (S), was higher in lawn microhabitats as compared to hummock microhabitats ($F_{1,72}$ = 30.59, $P \leq 0.001$). However, no effect of PFT removal on S was observed, neither as overall effect ($F_{3,71}$ = 0.99, P = 0.403) nor in interaction with microhabitat ($F_{3,72}$ = 0.79, P = 0.501). Nevertheless, S tended to slightly increase in the absence of vascular plants (Fig. 1; – Gram / – Eric).

Hydrolytic enzymatic activity

Hydrolytic enzyme activity of alanine-aminopeptidase (ALA), β-glucosidase (BG), and acid phosphomonoesterase (PHOS) seemed not to be affected by microhabitat. β-glucosaminidase (NAG) activity, on the other hand, was higher in lawns as compared to hummocks, while sulfatase (SUL) was higher in the hummocks (Table 2, Fig. 2, Table S2). PFT removal treatment did not affect ALA activity, but the activities of the other enzymes did vary significantly between PFT removal treatments ($P < 0.05$, Table 2, Fig. 2). These effects, however, were microhabitat dependent (Table 2, Fig. 2). In the lawns, the removal of all vascular PFTs (– Gram / – Eric) resulted in an increase in BG (22%), NAG (13%), PHOS (77%) and SUL (26%) activities (Table 2, Fig. 2), while in the hummocks this resulted in a decrease in activities of BG (100%), NAG (84%), PHOS (43%) and SUL (75%) (Table 2, Fig. 2). NAG and SUL activity in the lawns were lowest when only graminoids were removed (Fig. 2).

Discussion

Peatland ecosystems face changes in enviro-climatic conditions that may evoke both shifts in the vegetation as well as changes in hydrology. While evidence of the influence of plant functional types (PFTs) on peatland processes is mounting (Lang *et al*. 2009; Turetsky *et al*. 2012; Robroek *et al*. 2015; Zeh et al. 2022), and the link between hydrology and peatland carbon dynamics is well established (Chimner *et al*. 2017; Zhong *et al*. 2020), their combined effects are less well understood. Here, we study how plant functional types (graminoids and ericaceous shrubs) influence decomposition in contrasting microhabitats (lawns and hummocks). Our results highlight that PFTs greatly influence microbial metabolic processes (i.e. hydrolytic enzyme activity), and that this effect is microhabitat dependent. Despite these effects of PFTs on potential process rates, this result was not mirrored in broad decomposition indicators (decomposition rate constant (*k)* and stabilization factor (S)) which only differed between lawns and hummocks.

Effects on decomposition rate constant and stabilisation factor

Previous studies documented the role of the plant community composition and importance of ecohydrological on belowground decomposition processes (Laiho 2006; Dorrepaal 2007; Ward 2010; Ward *et al*. 2015). In contrast to our hypothesis and former findings about influence of PFT removal on decomposition process, we found no direct effect of PFTs on the decomposition rate constant k and stabilization factor (S) using TBI index. These results echo Wiedermann *et al*. (2017) who indicate no influence of PFTs on the decomposition rate constant and

stabilization factor. This agrees with previous research outputs concluding that vegetation community composition was the main driver for decomposition processes and C flux in peatlands (Basiliko *et al*. 2012; Linkosalmi *et al*. 2015). Ombrotrophic bogs, like the one this research has been performed in, are usually *Sphagnum* dominated. Hence, the peat is built up by *Sphagnum* remnants which are rather recalcitrant (Thormann 2006), and it can be envisaged that the microbial community has adapted to the nature of the recalcitrant carbon sources available. As such,

In our study, we found a significant influence of hummock-lawn microhabitat on the decomposition rate constant and stabilization factor. According to Keuskamp *et al.* (2013) and Fanin *et al.* (2020), *k* indicates early decomposition rates while S shows the stabilising effect of the environment on the labile fraction of the litter. Surprisingly, both *k* and S factor were significantly higher in lawns compared to hummocks. The combination of a higher *k* and S in lawns could indicate that high mass loss fast coincides with incomplete break-down, during early decomposition and a higher potential for labile carbon to become stabilised within the ecosystem. Indeed, Hoyos-Santillan *et al.* (2019) reported that water tables near the surface i.e lawns, where aerobic-anaerobic conditions are constantly changing with water table fluctuations, can result in enhancing C sequestration in lawns. The higher observed *k* in lawns may be a consequence of oxygenating of the soil profile by sedges, in particular, extra oxygenation provided by well-developed arechymatous tissues of *E. vaginatum,* which could promote decomposition of *Sphagnum* moss dominated peat (Roura-Carol and Freeman 1999; Greenup *et al*. 2000; Kaštovská 2018). Moreover, Zeh *et al.* (2020) found higher rates of decomposition under sedge coverage due to input of more easily decomposable, nutrient rich plant litter, which may have had an indirect stimulatory effect on our measurements. In addition, lawns undergo larger water table fluctuation, increasing the amount of nutrients for microbial activity, which could then stimulate decomposition (Belyea 1996; Oddi *et al*. 2019). Moreover, the unusually dry summer of 2019 could have impacted the results in our study: the lawns were exceptional dry, which created a thicker aerated layer and higher decomposition rates, while the drier conditions in hummocks could have limited the decomposition rates.

Effects on extracellular enzyme activity

The role of the vegetation on belowground microbial community structure and metabolic processes can result from established plant–microbe associations (Robroek *et al*. 2015). In addition, there are several mechanisms, such as rhizodeposition and rhizosphere oxygenation, which can directly influence ecosystem functioning (Wardle *et al*. 2004). Interestingly, in line with our hypothesis, altering vascular plant functional composition significantly influenced belowground potential EEAs in contrasting microhabitats for four out of five hydrolytic enzymes. Previous findings from the same experiment demonstrated that removal of PFT was associated with distinct microbial community composition in different microhabitats (Robroek *et al*. 2015). Moreover, Basiliko *et al*. (2013) and Matulich and Martiny (2015) link a change in microbial community composition to a shift in the activity of EEAs. The observed changes in EEAs under different PFT removal treatments in lawn-hummock microhabitats may thus have been mediated by shifts in microbial community composition.

The influence of vascular PFTs on hydrolase activity showed opposite effects in the two microhabitats. In hummocks, the removal of PFTs decreased hydrolytic enzyme activity, however in lawns PFT removal increased it, reflecting perhaps the direct effect of plant litter and rhizosphere inputs (or absence thereof). Earlier observations demonstrated lower overall potential microbial activity in hummocks than in lawns, while PFT

removal treatment effects were only observed in hummocks (Robroek *et al.* 2016). It was suggested that the higher vascular plant cover in hummocks may have resulted in a higher dependency of the microbial community on plant-derived substrates (Robroek *et al.* 2016). Indeed, this may play a role in our observations as vascular plant cover in hummocks are twice as great than in lawns, with a more pronounced influence on belowground hydrolytic activity in hummocks. As hummock's vascular plant cover enhanced the hydrolase activity of four out of five enzymes, this shows that microbial EEAs were greatly influenced by vegetation inputs (labile rhizosphere inputs) as well as distinct microhabitats. It has been shown already that aerobic microbial respiration is faster as compared to anaerobic microbial respiration, that requires a higher degree of microbial metabolic processes (potential EEAs) to fuel this aerobic respiration in oxic hummocks (Blodau *et al*. 2004; Freeman *et al*. 2001; Jungkunst *et al*. 2012). In lawns, almost all PFT removal increased EEA, in other words, presence of vascular plants restricts belowground potential microbial EEAs. Previous research from the same experiment showed that in hummocks with aerobic conditions, rhizosphere PFT inputs are essential source of substrate and metabolic energy for hydrolytic enzyme activities (Dieleman *et al*. 2017). However, in lawns, microbial activity is less dependent upon plant derived labial carbon compounds, which enhanced the EEAs activity in absence of PFTs (Robroek *et al*. 2016), which are consistent with our findings, combined removal of graminoid and ericoid plants increased hydrolase activity. Interestingly, removal of graminoids has more apparent effect on hydrolytic enzyme activity in lawns, and as result drastically declined, particularly in NAG and SUL activities. As wet lawns are permanently more anoxic as compared to hummocks and mostly dominated by the graminoid *Eriophorum vaginatum*, which possess aerenchymatic tissue (open air canals in stem and roots), this promotes the diffusion of oxygen to deep roots (Greenup *et al*. 2000). Absence of graminoids may therefore decrease microbial metabolism due to reduced peat oxygenation associated, this being more pronounced in the lawn microhabitat.

We found that the spatial variation in aerobic-anaerobic environments created by hummock-lawns microhabitats leads to significant differences in hydrolytic enzyme activities, which is consistent with other wetland studies (Parvin *et al*. 2018; Minick *et al*. 2019). Two out of five EEAs (NAG and SUL) showed significant difference in activities between hummock and lawns. Previous research has reported that drier hummocks had higher activity of NAG compared to wet lawns (Wang *et al*. 2021). In addition, Xu *et al*. (2021) reported that NAG activity was significantly higher in oxic zone of drained peat. Contradicting to these studies, we found that NAG activity was greater in lawns. This may be explained by as lawns being extraordinarily dry during the warm summer of 2019 which might improve the peat aeration (increased oxygen diffusion) by decreasing water table level, resulting in enhanced NAG activity, as microbial necromass is rapidly mineralised by the extant microbial community under dry conditions. Furthermore, lawns are usually abundant in aerenchymas graminoids, they are non-mycorrhizal, and transport oxygen into deep peat, which might enhance the metabolic efficiency of rhizosphere microbial communities. In contrast, we also observed that SUL activity was higher in drier hummocks than in wetter lawns. It has been reported that sulphatase activity was stimulated due to enhanced nutrient mineralization upon lowering the water table drawdown (Freeman *et al*. 1996; Kang and Freeman 1999). Furthermore, the vascular plant cover in hummocks was more than twice as high as that in lawns, which is likely reflected belowground and, may in-turn have increased hydrolytic activity. In addition, drier hummocks are usually nutrient poor environments due to dominance of recalcitrant shrubs. In order to meet the nutrient demands, soil microbes might produce more hydrolytic enzymes towards internal cues of nutrition stoichiometry (Allison and Vitousek 2004).

Conclusions

In response to global climate warming, vascular plant cover is expected to increase (Elmendorf *et al*. 2012). We highlight that the role of plant functional type composition is important for belowground decomposition processes through their impact on enzyme activity along with microhabitats. Our result indicate that vascular plants control microbial activity in peat with specific roles of plant functional types varying between lawns and hummocks. Moreover, microhabitats control over the decomposition process were more pronounced as compared to that of the vegetation. This shows that carbon turn-over in peatland ecosystems is vulnerable to changes in aboveground plant communities and hydrological conditions. Our results put emphasise the need of a re-focus on carbon dynamics of peatland ecosystem in the light of climate change, and particularity the role of changes in the plant community composition therein.

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Statements & Declarations

Funding This work was financially supported by the Stiftelsen Anna och Gunnar Vidfelts for biologisk forskning (2018-024-Vidfelts fond).

Competing Interests The authors have no relevant financial or non-financial interests to disclose.

Author Contributions NeS, BJMR and JB conceptualised the idea for this study, analysed the data and wrote the manuscript; MD and RTEM helped analysing the samples, and assisted in data analyses and manuscript writing.

Data Availability The dataset generated and analysed in this study are Data available through Archiving and Networked Services (DANS) EASY: https://doi.org/10.17026/dans-xnz-6dry. Code generated during the study is available from the first and/or the corresponding author by request.

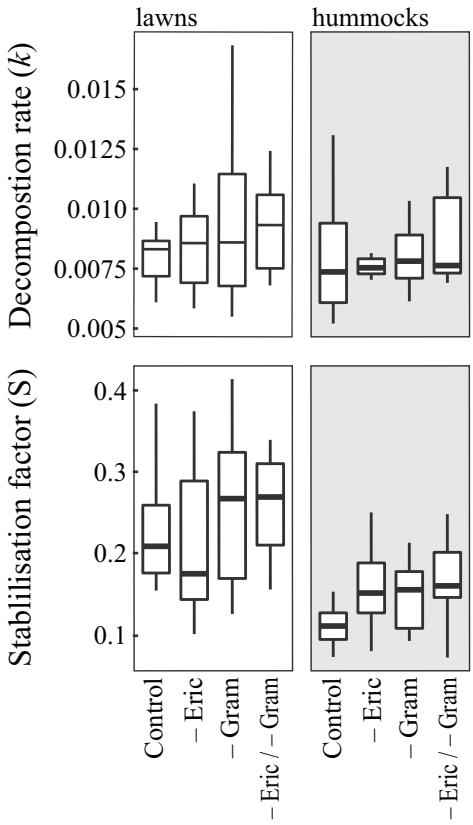
Table 1 Description of the peat extracellular enzymes, the substrates labelled with fluorophore methylcoumarin (MUC) or methylumbelliferone (MUB) used for the hydrolytic enzyme activity measurements.

Enzyme	**Abbr.**	**Substrate**	**Hydrolysis type**	**Targets**
Alanine-aminopeptidase	ALA	L-Alanine7-amido-4-MUC	N-acquisition	Oligopeptides
β-glucosidase	BG	β-D-glucoside-4-MUC	C-acquisition	Cellulose, starch and disaccharides
β-glucosaminidase	NAG	N-acetyl-β-D-glucosaminide-4-MUB	N-acquisition	Chitin
Acid phosphomonoesterase	PHOS	Phosphate-4-MUC	P-acquisition	Organic phosphorus
Sulfatase	SUL	Sulphate-4-MUB	S-acquisition	Organic sulphur

Table 2 Statistical analysis from the ANOVA, testing the influence of vascular plant functional type (PFT) removal treatment and microhabitat (MH) on the hydrolytic enzymes alanine-aminopeptidase (ALA), β-glucosidase (BG), β-glucosaminidase (NAG), acid phosphomonoesterase (PHOS) and sulfatase (SUL). Significant *P-values* ($P \leq 0.05$) are shown in bold values

Variables		ALA		BG		NAG		PHOS		SUL	
	d.f.	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
PFT	3	0.02	1.00	16.13	**≤ 0.001**	210.3	**≤ 0.001**	16.50	**< 0.001**	13.54	**≤ 0.001**
MH	1	0.90	0.35	2.88	0.10	1159.8	**≤ 0.001**	0.00	0.97	148.42	**≤ 0.001**
PFT : MH	3	1.03	0.39	84.53	**≤ 0.001**	355.3	**≤ 0.001**	69.85	**< 0.001**	45.32	**≤ 0.001**

494 **Figures**



495

496 **Fig. 1** Boxplots of the effects of vascular plant removal treatments and microhabitat (white panels = lawns, grey
497 panels = hummocks) on decomposition rate constant (*k*) and organic matter stabilization factor (S). Control =
498 undisturbed control, – Gram = graminoids removed, – Eric = ericoids removed, – Gram / – Eric = ericoids +
499 graminoids removed. Horizontal solid lines indicate median values; vertical bars show standard deviation.
500 Outputs for statistic are presented in text.

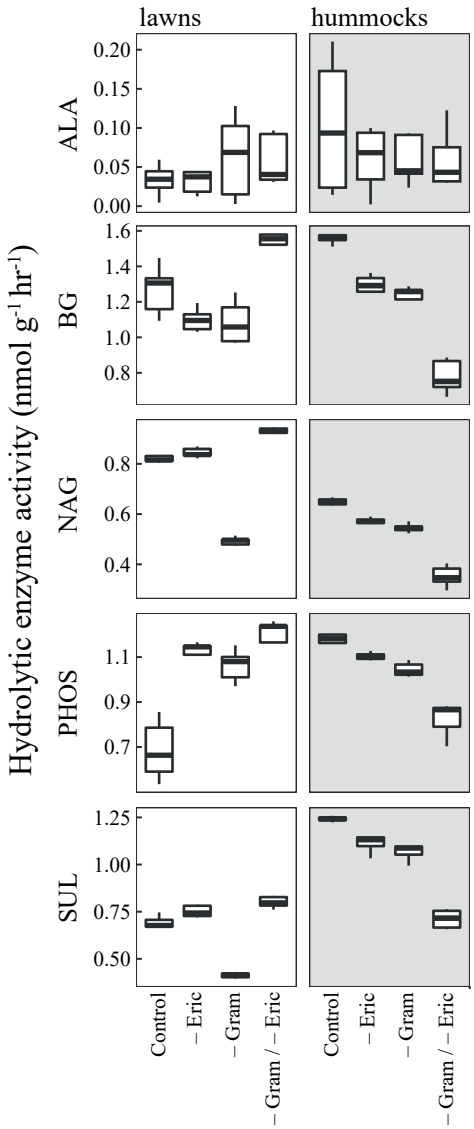
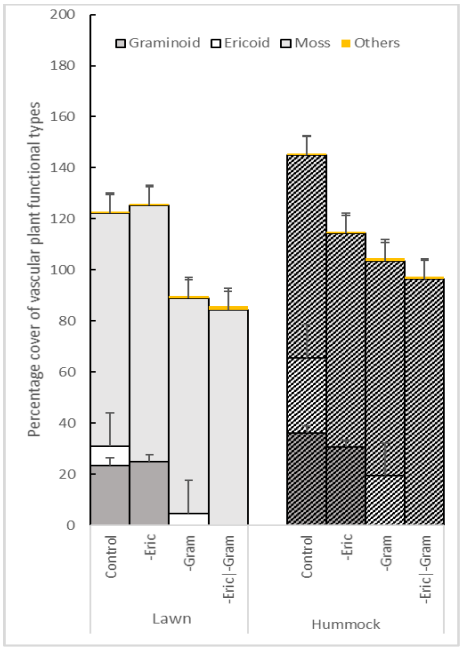


Fig. 2 Boxplots of the effects of vascular plant removal treatments and microhabitat (white panels = lawns, grey panels = hummocks) on the hydrolase activity of the enzymes alanine-aminopeptidase (ALA), β-glucosidase (BG), β-glucosaminidase (NAG), acid phosphomonoesterase (PHOS) and sulfatase (SUL). Horizontal solid lines indicate median values; vertical bars show standard deviation. Outputs for statistic are presented in Table 2.

Supplementary Information (SI)

Supplementary Table 1. Mean (SE) calculated values of decomposition rate, stabilization factor and five hydrolytic enzymes with standard error of mean for two microhabitats (hummocks and lawns) with different plant functional type communities. The standard error indicates variation in *k*, S and five enzymes within treatment plots

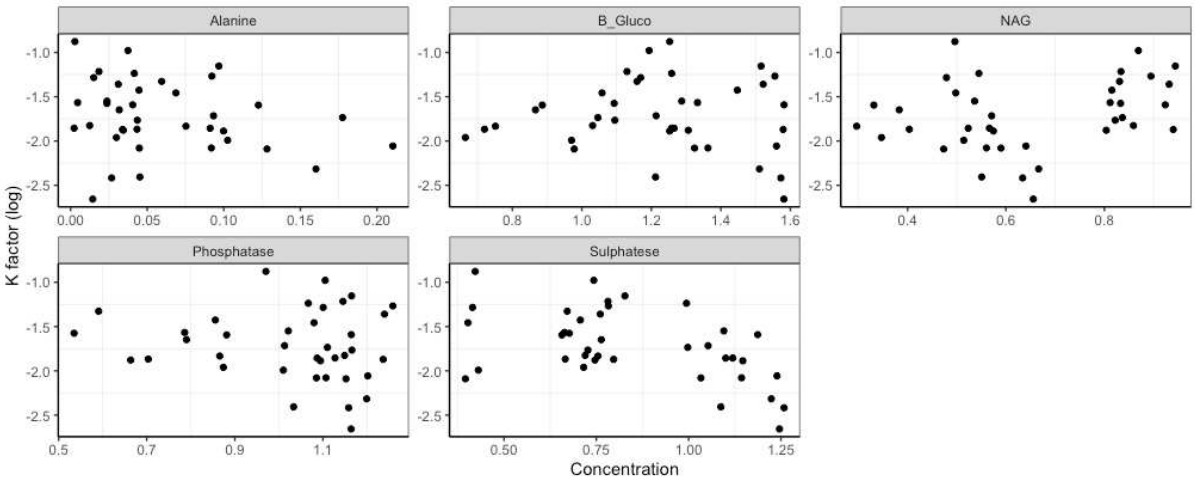
Parameters	Hummocks				Lawns			
	Control	*-Eric*	*-Gram*	*-Eric-Gram*	*Control*	*-Eric*	*-Gram*	*-Eric-Gram*
k (d^{-1})	0.0080 ±0.0024	0.0076 ±0.0004	0.0081 ±0.0013	0.0087 ±0.0018	0.0082 ±0.0016	0.0085 ±0.0017	0.0096 ±0.0036	0.0093 ±0.0018
S	0.1176 ±0.039	0.1609 ±0.062	0.1558 ±0.059	0.1628 ±0.052	0.2337 ±0.075	0.2098 ±0.088	0.2561 ±0.092	0.2548 ±0.063
ALA ($nmol\ g^{-1}\ h^{-1}$)	0.1029 ±0.084	0.0597 ±0.039	0.0590 ±0.028	0.0606 ±0.035	0.0635 ±0.049	0.0579 ±0.061	0.0589 ±0.029	0.0333 ±0.019
BG ($nmol\ g^{-1}\ h^{-1}$)	1.5563 ±0.027	1.2996 ±0.046	1.2474 ±0.030	0.7778 ±0.085	1.5509 ±0.028	1.0991 ±0.059	1.0858 ±0.110	1.0011 ±0.515
NAG ($nmol\ g^{-1}\ h^{-1}$)	0.6492 ±0.013	0.5727 ±0.011	0.5452 ±0.016	0.3522 ±0.038	0.9269 ±0.018	0.8442 ±0.017	0.8189 ±0.011	0.4922 0.015
PHO ($nmol\ g^{-1}\ h^{-1}$)	1.1809 ±0.020	1.1035 ±0.016	1.0443 ±0.028	0.8230 ±0.068	1.2130 ±0.040	1.1352 ±0.023	0.6863 ±0.119	1.0627 0.065
SUL ($nmol\ g^{-1}\ h^{-1}$)	0.7919 ±0.024	0.7429 ±0.024	0.6931 ±0.030	0.4130 ±0.013	1.2309 ±0.025	1.0881 ±0.061	1.0660 ±0.040	0.7113 0.044



511

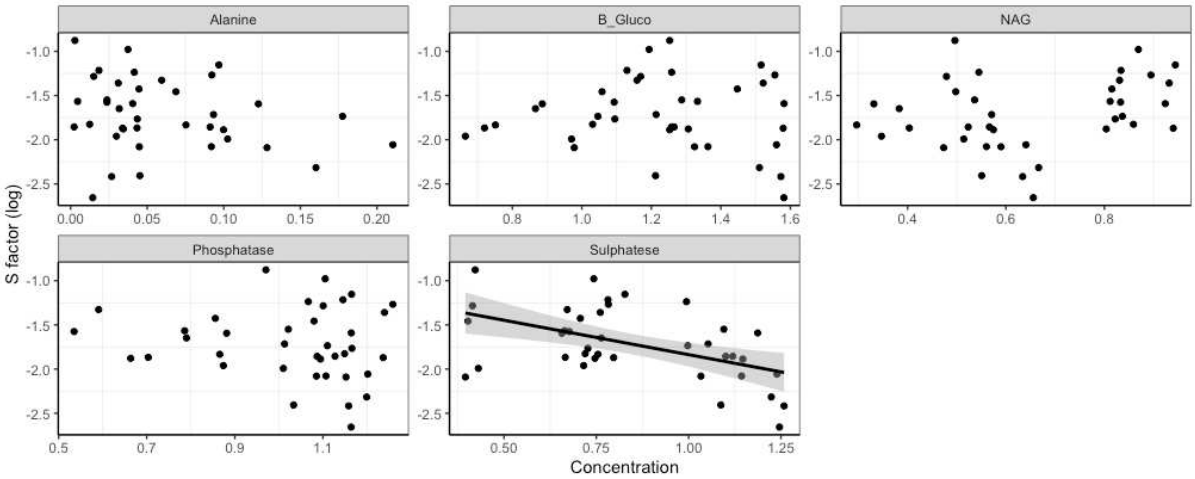
512 **Supplementary Fig. 1** Vascular plant cover (%) of different plant functional types in four plant removal
513 treatments in two microhabitats (lawns and hummock), black bars show standard deviations.

514



515

516 **Supplementary Fig. 2a** Linear regression relationship between decomposition rate constant (*k*) and five
517 hydrolytic enzymes. Dots shows individual plots.



518

519 **Supplementary Fig. 2b** Linear regression relationship between stabilization factor (S) and five hydrolytic
520 enzymes. Only SUL shows significant relationship hence linear model was applied. Dots shows individual plots.

Supplementary Files

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