



Peatland Plant Functional Type Effects on Early Decomposition Indicators are Non-Pervasive, but Microhabitat Dependent

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Received: 4 April 2022 / Accepted: 13 October 2022 / Published online: 20 October 2022
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Abstract

Ombrotrophic peatlands are important long-term sinks for atmospheric carbon as plant productivity exceeds litter decomposition. Changes in plant community composition may alter decomposition rates through alterations in microbial communities and activity. Such plant community driven changes in decomposition rates may however differ between microhabitats. Nevertheless, the microhabitat-context-dependency of plant community composition effects on decomposition remains poorly understood. We used a long-term (> 10 year) plant removal experiment to study how vascular plant functional types (PFTs, i.e. graminoids and ericoids) influence decomposition processes in wet lawns and hummocks. We employed the Tea Bag Index (TBI) as an indicator for early litter decomposition and carbon stabilization and assessed the potential activity of five hydrolytic extracellular enzymes (EEAs) as indicators for microbial activity. PFT removal had no effect on the TBI decomposition rate constant (k), nor on the stabilization factor (S). Yet, k increased slightly when both PFTs were absent. In the lawns, we observed higher values of k and S as compared to hummocks. PFT composition influenced four out of five hydrolytic EEAs that can drive decomposition. Yet, this influence was non-pervasive and microhabitat dependent. In wet lawns, PFT removal generally increased enzyme activities, while opposite trends were detected in the hummocks. 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. This implies that potential consequences of vegetation changes on organic matter turnover, hence the peatland carbon sink function, cannot be generalized across peatland microhabitats.

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 is one of the best natural lines of defense 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 are undergoing 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.

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Ombrotrophic bogs often display distinct patterns in microhabitats that differ in their position along the water table: hummocks and wet lawns (sometimes also referred to as carpets). Hummocks are raised mounds where the peat-moss surface is relatively far from the water table, while the surface of wet lawns are situated closer to, and often move with, the water table (Rydin and Jeglum 2013). Moreover, the distance to the water table is known to influence decomposition (Wang et al. 2021; Górecki et al. 2021) and has been reported to greatly influence the microbial activity (Fisk et al. 2003; Jassey et al. 2018). Apart from being positioned differently along the water table, microhabitats differ in biotic community composition. Moreover, hummocks and wet lawns are each dominated by a distinct vegetation. The vascular plant community is comprised of two functional types, graminoids and ericoids, that differ in their mechanisms for nutrient acquisition (e.g. radial oxygen loss, mycorrhizal associations, rhizodeposition) (Gavazov et al. 2018; Kaštovská et al. 2018) and have a distinct effect of the composition of the microbial community (Martí et al. 2015) and its functionality (Bragazza et al. 2015; Robroek et al. 2015). Moreover, 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 (Bais et al. 2006; Kardol et al. 2010; Mastný et al. 2021). These litter deposits and root exudates serve as microbial substrates and stimulate microbial EEA and respiration with subsequent effects on decomposer community composition and consequential C cycling (Van der Heijden et al. 2008; De Deyn et al. 2008; Wiedermann et al. 2017). Hence, it is well established that plant functional types, and changes in their composition, can have considerable effects on decomposition processes (Johnson and Damman 1991; Ward et al. 2015; Zeh et al. 2020; Mastný et al. 2021).

Decomposition in peatlands is largely driven by soil microbial activity (Fenner et al. 2005; Preston et al. 2012; Briones et al. 2022). In peatlands, there is clear evidence that microbial community composition and activity is strongly dependent on abiotic conditions, including water table depth (Juszczak et al. 2013; Robroek et al. 2015; Jassey et al. 2018; Asemaninejad et al. 2019; Lamit et al. 2021). In addition to direct effect of abiotic condition of decomposition rates, decomposition can be affected indirectly through the composition of the plant community (Andersen et al. 2013; Ritson et al. 2021). Relationships between plant and microbial communities, in addition, can drastically alter in nature along enviro-climatic gradients (Robroek et al. 2021). What is more, warmer and drier conditions increase the abundance of graminoids and ericaceous shrubs in peatlands (Walker et al. 2006; Breeuwer et al. 2010; Antala et al. 2022; Malhotra et al. 2020). Hence, enviro-climatic change

is expected to have unprecedented impact on microbial community composition and activity and can potentially convert peatlands as global C sinks to sources of greenhouse gasses (Loisel et al. 2021).

Whether northern peatlands will remain to act as C sinks depends on the extent to which peatland plant communities and biological interactions respond to enviro-climatic change. Despite the recognized influence of PFTs and microhabitat on decomposition (Ward et al. 2015), their interactive effects are still unclear. Yet, studying the contribution of PFT on decomposition in the context of microhabitats could provide much needed insights into peatland carbon dynamics in the light of a warmer and drier future climate. Here, we investigate how alterations in vascular plant functional types in an ombrotrophic bog influence decomposition across two contrasting microhabitats in peatlands: hummocks and wet lawns. This work aims to address two specific objectives: to investigate the relative and interactive effect of vascular plant functional types and microhabitat on i) early decomposition by incubating standard substrates; and more specifically on ii) microbial activity by measuring the activity of five hydrolytic extracellular enzymes. We hypothesized that PFT composition and microhabitat affect decomposition and microbial activity. We postulate lawns to have higher hydrolytic enzyme activity compared to hummocks, which translates into increased decomposition rate but lower levels of stabilization of labile organic compounds. In addition, we expected that removal of graminoids and ericoids would decrease microbial activity leading to a decreased decomposition rate but increased organic C stabilization.

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 2011 we established a vascular plant removal experiment in a *Sphagnum*-dominated ombrotrophic bog comprising 80 experimental plots of 0.5 × 0.5 m (c.f. Robroek et al. 2015) that were equally divided over wet lawns (c.f. Rydin & Jeglum 2013; n = 40) and hummocks (n = 40). The bryophyte layer in the wet lawns was dominated by *Sphagnum cuspidatum* Ehrh. ex Hoffm. with sparse cover of *S. balticum* (Russow) C.E.O. Jensen, while the hummocks were largely covered by *S. medium* Limpr. and *S. rubellum* Wilson. The vascular plant cover in the wet lawns consisted of *Eriophorum vaginatum* L., *Trichophorum cespitosum* (L.) Hartm., *Rhynchospora alba* (L.) Vahl., *Vaccinium oxycoccos* L., *Erica tetralix* L. and *Andromeda polifolia* L. The hummock

vascular plant community mainly consisted of *E. vaginatum* L., *E. tetralix*, *V. oxycoccus*, *Calluna vulgaris* (L.) Hull and *A. polifolia*. Water tables in the wet lawns were close to (i.e. 1–3 cm below) the *Sphagnum* surface, and relatively stable throughout the year – even in dry periods – as the *Sphagnum* surface moves with apparent water table fluctuations. The water table in the hummocks is variable between 20 and 35 cm below the *Sphagnum* surface.

In each microhabitat (wet lawn and hummock) four plant functional group removal treatments – undisturbed control, graminoids removed (– Gram), ericoids removed (– Eric), ericoids + graminoids removed (– Gram / – Eric) – were established 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 was laid out in a randomized 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 ecology in situ (Díaz et al. 2003). During the summer of 2019, preceding the installation of standardized litter for this experiment (see below), we estimated the cover (%) for the vascular plant and *Sphagnum* community on a subset – i.e. 40 PFT removal plots (4 treatments × 2 microhabitat × 5 replicates) – using the pinpoint intercept method (Jonasson 1988) with a 100-point frame. At every point, a needle was lowered to the *Sphagnum* surface and all contacts with vascular plants were recorded, specifying taxonomic identity for each hit. Every point ended at the *Sphagnum* layer, resulting in each grid point to account for one individual of a certain *Sphagnum* species. Results from these surveys highlight that 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 (k) and Stabilization Factor (S)

We used the Tea Bag Index (TBI) method to estimate the role of vascular PFTs and microhabitat on early decomposition and organic matter stabilization in the peat. The TBI method makes use of commercially available green tea (EAN 8,722,700 05,552) and rooibos tea (EAN 8,722,700 188,438) with contrasting carbon fractions (Keuskamp et al. 2013). The TBI method is currently

widely applied (see also <http://www.teatime4science.org>) and has been proven to be suitable as a standard method to study the influence of environmental drivers on decomposition processes, as the tea and local litters were found to behave comparably (Didion et al. 2016; Macdonald et al. 2018; Duddigan et al. 2020). In July 2019, we buried a pair of tea bags (one green and one rooibos tea bag, accordingly labelled) 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 (48 h 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. The initial weight was taken as the average of ten unused tea bags for each type of tea.

We estimated the rate of early decomposition as constant k and the stabilization factor S following Keuskamp et al. (2013). While an estimation of k would require a time series, the TBI calculations make use of the contrasting litter quality of green tea and rooibos tea and are based on the two-step decomposition model by Wieder and Lang (1982), which assumes that labile compounds decompose faster than recalcitrant fractions. After two to three months incubation, the faster decomposing green tea will have lost its labile fraction, while in rooibos tea the most labile compounds are still being consumed. Based on the green tea mass loss S is calculated as:

$$S = 1 - a_g / H_g \quad (1)$$

S (Eq. 1) is defined by the ratio of actual decomposable fraction of green tea litter lost during incubation (a_g) to the expected fraction, namely the hydrolysable fraction ($H_g = 0.842 \text{ g g}^{-1}$) (Keuskamp et al. 2013). Hence, high values of S are thought to indicate a larger storage capacity of organic C attributable to local conditions (Fujii et al. 2017; Macdonald et al. 2018). Once S is determined, Eq. 2 can be used to determine the decomposable fraction of rooibos tea (a_r) using the chemically determined hydrolysable fraction of rooibos tea ($H_r = 0.552 \text{ g g}^{-1}$) (Keuskamp et al. 2013):

$$a_r = H_r(1 - S) \quad (2)$$

Assuming that the weight loss of the recalcitrant litter fraction during the incubation period is negligible (Berg and Meentemeyer 2002), k can be calculated as:

$$k = \ln \frac{a_r}{w_r - (1 - a_r)} \quad (3)$$

where, W_r is the fraction of rooibos tea remaining, t denotes incubation time (days). Thus, the final k value is an estimate of the early decomposition rate (day^{-1}).

Hydrolytic Enzyme Activity

The 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 \times 2 microhabitats \times 5 replicates) following Jasssey et al. (2011). In brief, 3 g homogenized fresh peat was added to 50 mL 0.1 M CaCl₂ solution with 0.05% Tween 80 and 20 g of polyvinylpyrrolidone and shaken at room temperature on a shaker for 90 min at 150 rpm. The mixture was centrifuged at 10,000 rpm for 5 min at 4 °C and the supernatant was filtered using Whatman GF/C of 1.2 μ m. Next, the filtrate was poured into a cellulose dialysis tube of 10–12 kDa molecular mass and then concentrated using polyethylene glycol. The concentrated solution was added to 10 mL 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-replicate assay wells (using opaque 96-well micro-plates) received 38 μ l of enzyme extract and 250 μ l of substrate. As a control, the same procedure was followed but with 38 μ l of inactivated enzyme extract. Incubation was performed in the dark at 25 °C for 3 h, after which the reactions were halted with 1 μ l of 0.5 M NaOH. Fluorescence intensity was measured spectrophotometrically at 365 nm excitation wavelength and 450 nm 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 wet lawns and hummocks was assessed by fitting a linear model with generalized least squares (gls) on the data from the control plots, using microhabitat as a fixed factor, and after testing for block effects. The addition of block as a random factor was not significant ($P > 0.05$) in any of the models and therefore

not included in downstream models. Likewise, the effects of the PFT removal treatment, microhabitat and their interaction on the early decomposition rate (k), labile carbon stabilization (S), and the activity of five hydrolytic enzymes (ALA, BG, NAG, PHOS, SUL) were tested by fitting gls models. Heterogeneity across PFT removal treatment and microhabitat in the k data was accounted for by using a VarComb variance structure in the model. All models were fitted with restricted maximum likelihood estimation (REML) and following the protocols outlined in Zuur et al. (2009). Residuals of the final model were analyzed for normality and homogeneity, with a Kolmogorov–Smirnov test and Levene’s test. All statistical analyses and visualizations were performed in the R software environment for statistical computing and graphics (version 4.1.2.)

Results

Decomposition Rate Constant and Stabilization Factor

Mass loss of the two types of litter (green tea and rooibos tea) differed between the wet lawn and hummock microhabitats ($P \leq 0.05$). The green tea in the hummocks lost $71.6\% \pm 0.04$ (mean \pm SD) of its initial weight, which was higher ($F_{1,72} = 30.59$, $P < 0.001$) than the $64.1\% \pm 0.07$ mass loss in the lawns. As expected, the mass loss from the rooibos tea bags was lower, but not significantly different ($F_{1,72} = 3.42$, $P = 0.068$) in the wet lawns ($20.1\% \pm 0.03$) as compared to the hummocks ($21.4\% \pm 0.03$). 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 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

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

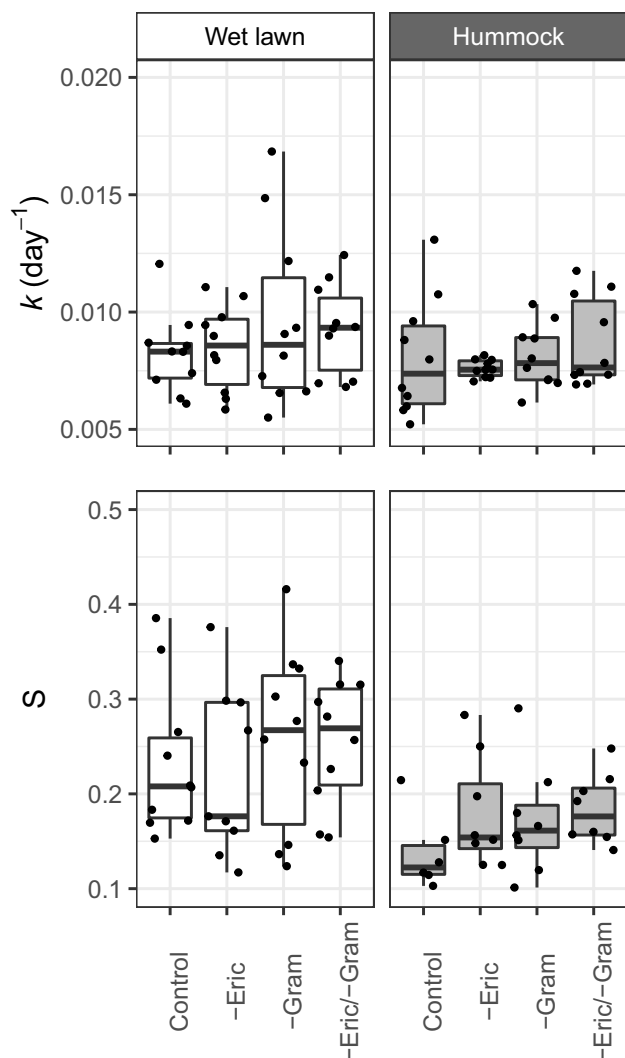


Fig. 1 Boxplots of the effects of vascular plant removal treatments and microhabitat (white panels = wet lawns, grey panels = hummocks) on decomposition rate constant (k [d^{-1}]) and organic matter stabilization factor (S), derived from mass loss data according to Eqs. 1–3 ($n=10$). Control = undisturbed control, - Gram = graminoids removed, - Eric = ericoids removed, - Eric / - Gram = ericoids + graminoids removed. Outputs for statistics are presented in text

ericoids (Fig. 1; - Gram / - Eric). The stabilization factor S , that is the potential of the labile fraction of the green tea litter to become stabilized, was higher in lawns than

hummocks ($F_{1,72} = 30.59, P \leq 0.001$). 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 increase slightly in the absence of vascular plants (- Gram / - Eric).

Hydrolytic Enzymatic Activity

To assess the relative and interactive effect of microhabitats and vascular PFT treatments on belowground enzyme activities, five hydrolytic EEA were measured. The hydrolytic enzyme activity of alanine-aminopeptidase (ALA), β -glucosidase (BG), and acid phosphomonoesterase (PHOS) seemed not to be affected by microhabitat. On the other hand β -glucosaminidase (NAG) activity was higher in lawns compared to hummocks, while sulfatase (SUL) activity was highest in the hummocks (Table 2, Fig. 2, Table S1). PFT removal treatment did not affect ALA activity, but the activities of the other enzymes did vary significantly between PFT removal treatments and were microhabitat dependent ($P < 0.05$, Table 2, Fig. 2). In lawns, the removal of all vascular PFTs (- Gram / - Eric) resulted in an increase in BG (22%), NAG (13%), PHOS (77%) and SUL (26%) activities compared to the control, while in the hummocks this resulted in a decrease in activities of BG (50%), NAG (46%), PHOS (30%) and SUL (48%) (Table S1). 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 shifts in the vegetation. While knowledge on the role of plant functional types (PFTs) on peatland processes is mounting (Ward et al. 2009; Lang et al. 2009; Rupp et al. 2019; Chroňáková et al. 2019), their influence in the context the microtopography in peatlands is less well understood. Here, we studied how plant functional types (graminoids and ericaceous shrubs) influence decomposition in two contrasting microhabitats (wet lawns and hummocks). Our results demonstrate that PFTs greatly influence

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 ($n=5$)

Variables	d.f	ALA		BG		NAG		PHOS		SUL	
		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

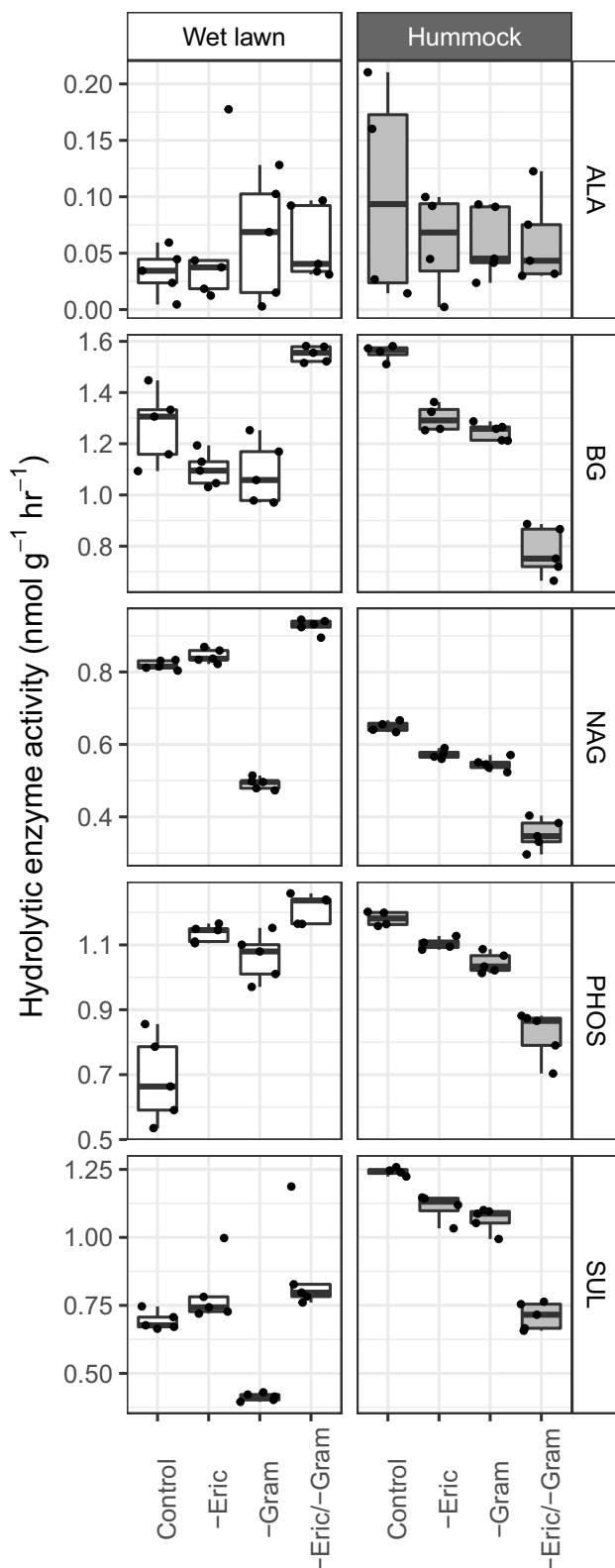


Fig. 2 Boxplots of the effects of vascular plant removal treatments and microhabitat (white panels = wet lawns, grey panels = hummocks) on the hydrolase activity of the enzymes alanine-aminopeptidase (ALA), β -glucosidase (BG), β -glucosaminidase (NAG), acid phosphomonoesterase (PHOS) and sulfatase (SUL) ($n=5$). Outputs for statistic are presented in Table 2

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 standardized indices for early decomposition (decomposition rate constant k and stabilization factor S), which only differed between lawns and hummocks.

Effects on Decomposition Rate Constant and Stabilization Factor

The lack of response of indices k and S to the plant removal treatments goes against our expectations. Yet, the values for k ($0.008 - 0.010 \text{ day}^{-1}$) and S ($0.118 - 0.256$) are in the range reported in other studies (Keuskamp et al. 2013; Macdonald et al. 2018; Górecki et al. 2021). Previous studies have documented the role of the plant community composition as well as spatial variation in microhabitats on below-ground decomposition processes (Dorrepaal 2007; Laiho 2006; Mäkilä et al. 2018; Ward et al. 2010, 2015). Also, previous research concluded that vegetation composition was the main driver for decomposition processes and C flux in peatlands (Basiliko et al. 2012; Linkosalmi et al. 2015). Shifts in the microbial community in response to the PFT removal treatments found earlier at the same experimental site (Robroek et al. 2015) make microbial adaptation a likely mechanism. While the responses of the enzymatic activity support this (as discussed below), our TBI results do not. Djukic et al. (2018) propose that microbial influence on decomposition may only become apparent in later stages of decomposition, during which more specialized microbes are responsible for the break-down of the recalcitrant compounds. This argument is supported by observations of Lin et al. (2020) who point out that microbial driven differences in decomposition, home-field advantage specifically, vary with incubation time and are stronger at later decomposition stages. Additionally, the TBI method relies on a standard substrate which is foreign in most ecosystems. While several studies conclude that the TBI method is suitable for replacing local litter for detecting responses to general decomposition drivers, such as temperature and precipitation (Didion et al. 2016; Duddigan et al. 2020; MacDonald et al. 2018), it may fail to pick-up local adaptation of the microbial community to specific litter inputs.

In our study, we found a significant influence of hummock-wet 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 stabilizing effect of the environment on the labile fraction of the litter. Both k and S values were significantly higher in lawns compared to hummocks. The combination of a higher k and S in lawns could indicate that high mass loss coincides with incomplete break-down,

during early decomposition and a higher potential for labile carbon to become stabilized within the ecosystem. Temperature and soil moisture are known to promote decomposition of green tea and rooibos tea (Fanin et al. 2020). At the experimental site, lawns are warmer than hummocks (Robroek et al. 2014), and the water table is closer to the surface. Earlier decomposition studies in peatlands recorded highest decomposition rates of litter placed in or just above the zone with fluctuating water levels (Belyea 1996), which explains the higher k values found in the lawns. Moreover, a higher proportion of fungal biomass to bacterial biomass in hummocks (Robroek et al. 2014) may result in a more complete break-down of litter and explain the higher S values, indicative of incomplete break-down, found in lawns. Further research on the decomposer community and litter chemistry during decomposition would be needed to confirm this.

Effects on Extracellular Enzyme Activity

In line with our hypothesis, the vascular plant functional community composition influenced belowground potential EEAs in contrasting microhabitats for four out of five hydrolytic enzymes. Previous findings from the same experiment demonstrated that removal of vascular plants results in distinct alteration of microbial community composition in the 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 wet lawn-hummock microhabitats are likely the result of 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). The higher vascular plant cover in hummocks was suggested to have resulted in a higher dependency of the microbial community on plant-derived substrates. Indeed, this may play a role in our observations as vascular plant cover in hummocks are twice as high as compared to lawns, with a more pronounced influence on belowground hydrolytic enzyme 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. In addition, drier hummocks are usually

nutrient poor environments due to dominance of recalcitrant shrubs. To meet the nutrient demands, soil microbes might produce more hydrolytic enzymes towards internal cues of nutrition stoichiometry (Allison and Vitousek 2004). 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) (Freeman et al. 2001; Blodau et al. 2004; Jungkunst et al. 2012). In lawns, the removal of all vascular PFTs resulted in a general increase in EEA. In other words, the presence of vascular plants seems to restrict belowground potential microbial EEAs. Previous research has shown 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 largely restricted by anaerobic conditions (Fisk et al. 2003). The combined removal of graminoid and ericoid plants increased hydrolase activity, which may be caused by the absence of shrub-derived phenolics (Wang et al. 2021). Interestingly, the removal of graminoids alone had a larger negative effect on hydrolytic enzyme activity in the wet lawns, particularly in NAG and SUL activities. As wet lawns are 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, this being more pronounced in the lawn microhabitat.

We found clear differences between microhabitats in the activities of hydrolytic enzymes, 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 the aerated zone of drained peat as compared to activities in the water-saturated zone. Contradicting these studies, we found that NAG activity was greater in lawn microhabitats, which are closer to the water table. This may be explained by the lawns being extraordinarily dry during the warm summer of 2019. This may have decreased the water table and improved the peat aeration (increased oxygen diffusion), resulting in enhanced NAG activity, as microbial necromass is rapidly mineralized by the extant microbial community under dry conditions. In contrast, we also observed that SUL activity was higher in hummocks than in lawns. It has been reported that sulphatase activity was stimulated due to enhanced nutrient mineralization upon water table drawdown. Furthermore, the vascular plant cover in hummocks was more than twice as high as that in lawns, which is likely reflected belowground and may have increased hydrolytic activity.

Conclusions

In response to global climate warming, vascular plant cover is expected to increase. 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, microhabitat controls 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 plant communities as well as hydrological conditions. Our results emphasize the need to focus on carbon dynamics of peatland ecosystem in the light of climate change, and particularly the role of changes in the plant community composition therein.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s13157-022-01626-7>.

Acknowledgements We 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 Lantbruksuniversitet Uppsala for support and logistics. Two anonymous reviews have much improved the manuscript

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.

Funding This work was financially supported by the Stiftelsen Anna och Gunnar Vidfelts for biologisk forskning (2018–024-Vidfelts fond). NeS was funded by a SPITFIRE PhD-studentship funded through NERC (NE/L002531/1).

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 corresponding author by request.

Declarations

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

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