Above- and belowground community linkages in boreal peatlands

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Abstract In boreal peatlands, the aboveground (plant) and belowground (microbial) communities are acutely linked because the whole soil profile is partially decomposed plant matter (peat), and dictates the nutrients available to the belowground system. We characterized the aboveground and belowground communities in two boreal peatlands: a *Sphagnum*-dominated fen and a *Carex*-dominated fen. We link the plant and microbial communities by observing plant, litter and peat carbon and nitrogen values. The *Sphagnum*-dominated fen had greater plant diversity but provided low quality litter inputs (high carbon:nitrogen) that formed peat and that corresponded with greater fungi:bacteria and Gram-positive:Gram-negative bacteria microbial community compared to the *Carex*-dominated fen. The higher quality plant inputs in the *Carex*-dominated fen supported a 5 × greater microbial biomass that was also 2 × more active (as measure by CO_2 production). In this approach we highlight that peatlands and their component plant and microbial communities play-out along a common resource-spectrum that dictates 'fast' vs 'slow' carbon and nutrient cycling (i.e., a plant–soil interaction spectrum) that can, in turn, affect carbon storage potential. As peatland plant community composition is predicted to shift and decomposition rates are expected to increase under climate change, our work highlights the importance of understanding plant–soil microbial interactions.

Keywords Litter quality · Phospholipid fatty acid analysis · Community composition · *Sphagnum* mosses · *Carex* sedges

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Introduction

Traditionally, the aboveground (plant) and belowground (soil) communities have been studied in isolation from one another, yet a greater appreciation of the interconnectivity between the two has emerged over the last three decades (Schnitzer et al. 2011; Bardgett and van der Putten 2014). Aboveground plants provide organic carbon to the belowground consumers via plant litter (Hättenschwiler et al. 2005),

and belowground, plants provide important resources to root-associated organisms (i.e., the rhizosphere) (Porazinska et al. 2003; Brzostek et al. 2013). While belowground food webs are considered 'donor-controlled' suggesting limited or no ability of the soil community to regulate or feed back to aboveground plant communities (van der Heijden et al. 2008), plant communities are often associated with certain microbial communities. As such, recent perspectives suggest that above- and belowground communities are more tightly linked than previously thought (Porazinska et al. 2003; Eisenhauer 2012), and that both the above- and belowground community composition influence one another (Carlson et al. 2010; Shanmugam and Kingery 2018). However, the extent to which these above- and belowground pairings are causal (and bidirectional), or correlational (i.e., both plant and microbial communities are associated with resource gradients, independently) is under debate (Carlson et al. 2010; Orwin et al. 2010; Fan et al. 2015; Li et al. 2015).

There are various ways for plant species to acquire and allocate resources, presenting a long-standing trade-off paradigm in life history strategies (Grime 1977; Wright et al. 2004; Westoby and Wright 2006). Plant species are described to exist along a continuum of fast-growing, nutrient exploitative life history traits vs slow-growing, nutrient conservative life history traits that translate into differences in plant nutritional value for aboveground herbivores and litter quality for belowground decomposers (Grime 1977; Reich 2014). Litter is thus often described as either 'labile' or 'recalcitrant' where faster growing plants produce more nutrient-rich litter (mainly nitrogen (N)) that contains simpler carbon (C) compounds, and has lower C:N. This litter is considered to be higher quality, facilitating faster decomposition and nutrient cycling (Manzoni et al. 2010) (i.e., labile) because the C compounds are easier to decompose, and N is often the main limiting nutrient in terrestrial systems (Vitousek and Howarth 1991); however, there is evidence that peatlands may also be phosphorus limited (Wang and Moore 2014). On the other end of the spectrum, plants that are slow-growing, are typically conservative in their nutrient acquisition, often more heavily defended with structural compounds and secondary metabolites, and consequently produce more litter that has low N, complex C compounds, and higher C:N. This litter is considered

recalcitrant because this lower litter quality can lead to slower decomposition and nutrient cycling (Reich 2014). As soil microbial communities mineralize organic N from plant litter and make it bio-available for plant uptake, it can be hypothesized that microbial communities that have life history traits requiring more N will be paired with aboveground plant communities that have high quality, more labile (low C:N) litter, and vice versa.

Belowground, the microbial community also exists along a 'fast–slow' life history continuum. While both fungi and bacteria have the ability to use high quality, labile C substrates (Waldrop and Firestone 2004; de Vries and Caruso 2016), bacteria tend to outcompete fungi in this environment while the opposite is true under low quality, recalcitrant C, where fungi outcompete bacteria (Strickland et al. 2009a, b). As such, fungi are sometimes considered 'slow' C and nutrient cyclers that immobilize nutrients within long-lived biomass, while bacteria are considered 'fast' cyclers with nutrients turning over and being mineralized through bacterial cell metabolism and death (Joergensen and Wichern 2008; Strickland and Rousk 2010). Bacterial communities can be further classified as either Gram+ or Gram− bacteria and rather than differing across the 'fast–slow' dichotomy these groups differ in their preferred C source; Gram+ preferring soil organic matter derived C (i.e., microbially processed) and Gram− preferring plant derived C (Kramer and Gleixner 2008; Fanin et al. 2019).

Above- and belowground communities are particularly linked in peatlands because the whole soil profile is comprised of partially decomposed plant matter (peat) that largely dictates the nutrients available to the belowground microbial communities. Decomposition rates in peatlands are lower than the aboveground plant biomass production due to water saturation and often low temperatures (in boreal zones) such that aboveground plant C inputs are net sequestered in the soil as a build-up of peat. However, not all peatlands are equal in terms of decomposition rates, which also depends on hydrological regimes, nutrient inputs from ground water, and aboveground plant community composition. Peatlands exist on a continuum of hydrological connectivity and nutrient inputs (e.g., bogs, nutrient-poor fens to nutrient-rich fens). This continuum is also related to vegetation; bogs and nutrient-poor fens are typically dominated by *Sphagnum* mosses while, intermediate nutrient or

nutrient-rich fens are typically dominated by sedges (e.g., *Carex* spp.) (Rydin and Jeglum 2013). These two dominant plant functional types also represent the 'fast–slow' life history traits (Palozzi and Lindo 2017a) that are thought to affect the belowground microbial communities (Borga et al. 1994; Haynes et al. 2015) through different litter quality. *Sphagnum* mosses have more recalcitrant litter (low N, and high phenolics that mask cellulose and make tissue more resistant to microbial breakdown) compared to *Carex* sedges, and therefore *Sphagnum* peatlands are predicted to have slower nutrient cycling and differences in soil properties (Turetsky et al. 2008; Palozzi and Lindo 2017b). Peatland microbial communities contain high diversity of fungi (Asemaninejad et al. 2017) and bacteria, and less significantly archaea (Asemaninejad et al. 2019), where fungal and bacterial microorganisms are typically considered different functional groups because they differ in cell biomass and life history traits that leads to differences in decomposition dynamics. This 'fast–slow' dichotomy of both aboveground plants and belowground microbial communities has consequences for C sequestration and C release (dissolved organic C and CO_2) in peatland soils. Given predicted peatland plant shifts (Jassey et al. 2013; Dieleman et al. 2015; Bragazza et al. 2016) and increases in decomposition rates under climate change (Bond-Lamberty et al. 2018; Jenkinson et al. 1991), understanding plant–soil microbial interactions is of growing importance (Hagedorn et al. 2019).

Whether differences in microbial communities that stem from differences in aboveground plant community properties (e.g., plant litter quality) feed back to affect the plant community, and on what spatiotemporal scales is currently unknown (van der Heijden et al. 2008). Differences in the abundance of fungi and bacteria are thought to lead to different rates of C and nutrient cycling that can affect plant community composition. In this study, we characterize the aboveground plant community and the belowground microbial community in two boreal peatlands: an intermediate nutrient fen that is dominated by *Carex* sedges and a nutrient-poor fen dominated by *Sphagnum* mosses. Our objectives were to relate the above- and belowground communities by (1) examining the nutrient quality of the aboveground plant community, (2) the quality of the annual plant litter inputs to the belowground system, and (3) the quality of the peat in

which the microbial communities reside. As *Sphagnum* has conservative nutrient-use strategies, we predict that lower litter quality in the *Sphagnum*-dominated fen would correspond to a smaller and more fungal-dominated microbial community compared to the *Carex*-dominated fen that would produce higher litter quality and support a larger and more bacterial-dominated microbial community.

Materials and methods

Site description

The two fen sites chosen for this study are located near White River, Ontario, Canada (48°21′N, 84°20′W) where the mean annual precipitation is 980 mm and the mean annual temperature is 2.1 °C for the region (see Webster and McLaughlin (2010) for full site description). The two fens are approximately 2 km apart. One fen is dominated by *Sphagnum* mosses, has a nutrient-poor status, lower water table depth (median = 34 cm), and lower pH (median = 4.4) (Webster and McLaughlin 2010). The other fen is dominated by *Carex* sedges, has an intermediate nutrient status, higher water table depth (median = 17 cm), and higher pH (median = 5.5) (Webster and McLaughlin 2010). The *Sphagnum*-dominated fen is 4.5 ha, sparsely treed and is bounded by mixed wood forest and a small lake. The *Sphagnum*-dominated fen, as the name suggests, has a blanket of *Sphagnum* mosses (*S. magellanicum* Brid., *S. angustifolium* (C.E.P. Jensen ex Russow) C.E.O Jensen, *S. fuscum* (Schimp.) Klinggr., and *S. girgensohnii* (Russow)), is moderately covered by shrubs including Labrador tea (*Rhododendron groenlandicum* Oeder), leatherleaf (*Chamaedaphne calyculata* (L.) Moench), and lowbush blueberry (*Vaccinium angustifolium* Aiton), and is sparsely treed by black spruce (*Picea mariana* (Mill.) B.S.P.) and tamarack (*Larix laricina* (Du Roi) K. Koch). The *Carex*-dominated fen is larger (10.2 ha), mostly open and is surrounded by mixed coniferous forests with two small stream tributaries on the northern and southwestern edges. *Carex* spp. predominate the *Carex*-dominated fen vegetation where *C. stricta* Lam. grows in patches semi-isolated from *C. oligosperma* Michx., and *C. lasiocarpa*. Shrubs, *Chamaedaphne calyculata* and *Myrica gale* L. (sweet gale) in lesser amounts also

inhabit the *Carex*-dominated fen and *Sphagnum* mosses occur in sparse patches (see Palozzi and Lindo (2017a) for previous plant community description).

Aboveground plant sampling

The aboveground plant community was assessed in 0.25 m² plots ($n = 12$) from each fen during June, July, and August 2018, totaling 72 plots. Within each plot all aboveground plant biomass was destructively sampled by clipping at the root–shoot interface, sorted by species using the keys of Newmaster et al. (1997), and were dried at 60 °C for a minimum of 48 h. To determine *Sphagnum* spp. biomass, 5 cm² of *Sphagnum* carpet was collected and the photosynthetic shoots were retained as the sample, the biomass was then dried and multiplied by 25 to determine an estimate of *Sphagnum* biomass for each plot—the section collected was determined to be the best representation of the plot, in terms of species and density. We calculated plant richness, Shannon's diversity index (H'), and Pielou's evenness (J') based on the aboveground biomass calculated from each plot using the vegan package in R (Oksanen et al. 2018), where

$$H' = -\sum_{i=1}^{k} p_i \ln(p_i)$$

$$J' = \frac{-\sum_{i=1}^{k} p_i \ln(p_i)}{\ln(S)}$$

In these equations, p_i is the proportional aboveground biomass based on destructive sampling of each plant species and S is species richness.

The aboveground plant quality (i.e., %C and %N content, C:N) was assessed by collecting leaves from each species (photosynthetic shoots for moss species, based on Bond-Lamberty and Gower (2007)) from three randomly selected plots across all time points, where possible (Supplemental Information Table S1). Leaves and shoots for each species were ground using a stainless-steel blade grinder and homogenized within each plot. Leaves were analyzed for %C, %N, and C:N using a combustion analyzer (vario MAX cube Elementar CNS analyzer) with birch leaf (*Betula papyrifera* Marsh.) as the quality control. Subsequently the community-weighted mean (CWM) for each plant quality trait (i.e., %C, %N, C:N) was calculated for each of the 72 plots using the equation:

$$CWM_{\text{trait}} = \sum (p_i \times x_i)$$

where p_i is the proportional aboveground biomass based on destructive sampling of each plant species, while x_i is the trait value for that particular species to determine a composite quality value of %C, %N, and C:N for the entire community.

Plant litter and peat sampling

Litter traps were deployed at each fen to determine both quantity and quality of seasonal litter inputs to the soil system. Litter traps were constructed with a black mesh (1 mm) bottom, allowing moisture, but not plant litter through. At each fen, five 0.25 m² litter traps were deployed in August 2017, with litter collection in October 2017 (end of growing season), June 2018 (winter), and October 2018 (growing season); notably as *Sphagnum* is low lying, *Sphagnum* litter was excluded. The litter from each trap was dried at 60 °C for a minimum of 48 h to determine the total quantity of litter inputs. After drying and weighing the litter, the litter was ground and homogenized using a stainless-steel blade grinder, and analyzed for %C, %N, and C:N using a combustion autoanalyzer (vario MAX cube Elementar CNS analyzer) as described above.

Five surficial peat samples (top 5–10 cm, approximately 100 g) were collected from each fen in October 2017. A subsample of peat (15 g wet weight) was used to measure the moisture content gravimetrically. The soil was dried at 60 °C for one week and re-weighed after drying to determine the soil moisture content using the formula:

$$\% \text{ Moisture} = ((\text{g wet weight} - \text{g dry weight})/\text{g dry weight}) \times 100$$

Heterotrophic basal respiration was used as an estimate of microbial activity and was measured using a Licor Infrared Gas Analyzer (IRGA LI-8100A) with a Multiplexer unit (LI-8150). A 50 g wet weight subsample of peat was placed in 250 ml mason jars ($n = 5$ from each peatland site) wrapped with aluminum foil to ensure only heterotrophic basal respiration was measured. Respiration was measured over 12 h at room temperature; measurements for each

sample were averaged over 90 s for 30 min, with a 30 s purge of the headspace between measurements. Following, peat from each sample was dried, ground, and analyzed for %C, %N, and C:N using a combustion autoanalyzer (vario MAX cube Elementar CNS analyzer) as previously described. All remaining subsamples of peat were frozen at -80 °C and lyophilized for determination of the microbial community composition.

Phospholipid fatty acid analysis

The peat microbial community was characterized by phospholipid fatty acid (PLFA) analysis using methods modified from Quideau et al. (2016) and Buyer et al. (2010). All glassware used was rinsed with acetone and hexane, all reagents were ACS grade or higher, and only glass was used for all reagents. One blank and one duplicate were run for each fen. A 0.3 g subsample from each lyophilized peat sample was ground using a mortar and pestle for the *Carex*-dominated fen and a stainless-steel blade grinder for the *Sphagnum*-dominated fen. The PLFAs were then extracted using the Bligh and Dyer method, which consists of a 2:1:0.8 ratio of methanol:chloroform:0.15 M citrate buffer (Bligh and Dyer 1959). As peat samples are highly organic, 0.9 ml of chloroform was used for the *Carex*-dominated fen and 2.1 ml of chloroform was used for the *Sphagnum*-dominated fen, alongside an added citrate buffer as suggested by Frostegård and Bååth (1996) to extract more PLFAs when working with highly organic soils. The internal standard 19:0 PC (1,2-dinonadecanoyl-*sn*-glycero-3-phosphocholine) was added to each sample prior to PLFA extraction and subsequently used to calculate extraction efficacy. Samples were subsequently vortexed for 30 s, shaken for 2 h, and centrifuged for 1 h at 2500 rpm. The supernatant was removed and the Bligh and Dyer extractant procedure was repeated again on the peat samples to ensure thorough PLFA extraction. Chloroform (1.8 ml for *Carex*-dominated fen and 4.2 ml for *Sphagnum*-dominated fen) and citrate buffer (0.72 ml for *Carex*-dominated fen and 1.68 ml for *Sphagnum*-dominated fen) was added to the supernatant, and the samples were left for 12 h to separate.

Following separation, the upper aqueous layer was disposed of, and the lower organic phase was evaporated under N_2 gas in a hot water bath to accelerate

evaporation and prevent oxidation. Samples were re-dissolved in 2 ml of chloroform and PLFAs were separated from other fatty acids using a solid phase extraction column (50 mg silica gel SPE 96-well plate). Columns were conditioned with 1 ml of methanol and 1 ml of chloroform and the phospholipids were eluded with 0.5 ml of 5:5:1 methanol:chloroform:deionized water. The samples were again evaporated under N_2.

Methyl esters were added to the PLFAs using 0.5 ml of 1:1 methanol:toluene and 0.5 ml of methanolic potassium hydroxide. Samples were incubated for 15 min at 37 °C, cooled to room temperature, and 0.6 ml of hexane and 0.2 ml of chloroform were added to each sample. Samples were neutralized with 0.5 ml 1 M acetic acid, 0.8 ml deionized water was added, and samples were vortexed prior to being centrifuged at 2000 rpm for 5 min. The upper hexane layer was removed, and the extraction process was repeated with the lower layer (0.6 ml of hexane and 0.2 ml of chloroform). The upper hexane layer from the second extraction was added to the first and the organic phases were evaporated under N_2. All samples were subsequently re-dissolved in hexane and the fatty acid methyl esters were detected by gas chromatography (Agilent HP 6890 GC with an Agilent Ultra 2 column: 5% Phenyl Methyl Siloxane, Model: 19091B-102, Length: 25.0 m, Diameter: 200.00 microm, Thickness: 0.33) using flame ionization detector. The Sherlock software® (MIDI Inc.) was used to assign specific PLFAs into microbial groups, calculate total and microbial group biomass, and calculate percent biomass of the PLFA assigned to each microbial group (Supplementary Information Table S2). The MIDI software separated the PLFA microbial biomass into six microbial groups: arbuscular mycorrhiza fungi (AM fungi), fungi (all other fungi besides AM fungi), anaerobic bacteria, Gram-positive bacteria (Gram+), Gram-negative bacteria (Gram−), and actinomycetes.

Statistical analysis

Plant species richness, Shannon's diversity and Pielou's evenness were calculated in R (version 3.4.3) using the vegan package (Oksanen et al. 2018), and analyzed using a two-way ANOVA using fen and month as the main effects; because each plot was destructively sampled, all plots are considered independent. Aboveground plant quality was analyzed

using two-way MANOVA implemented in R to determine differences between the CWM of %C, %N, and C:N for the *Sphagnum*-dominated fen and *Carex*-dominated fen aboveground biomass, with fen and month as the main effects. Litter quantity was analyzed using a two-way repeated measures ANOVA and litter quality (%C, %N, and C:N) was analyzed using two-way repeated measures MANOVA in Statistica (version 7.0) with fen and time period (i.e., end of growing season, winter, and growing season) as the main effects (StatSoft Inc. 2004). To determine if each individual litter quality variable (%C, %N, and C:N) varied between sites, separate two-way repeated measures ANOVA were run. A one-way MANOVA was used to analyze peat quality (%C, %N, and C:N) with fen type as the main effect. The total biomass and biomass of each microbial group was analyzed using a one-way MANOVA with fen type as the main effect (version 3.4.3; R Development Core Team 2013). We calculated the overall fungal:bacterial (F:B) ratio and Gram+:Gram− ratio for each sample, and these were also included in the one-way MANOVA. However, actinomycetes biomass was not included in this analysis as the duplicate demonstrated > 70% variation.

To determine whether there were significant differences between either the aboveground plant community composition or the belowground microbial community, permutational multivariate ANOVA (PERMANOVA) based on Bray–Curtis dissimilarity was used, and results were visualized using a Non-metric multidimensional scaling (NMDS) ordination. The Bray–Curtis matrix consists of pairwise distances between each community (i.e., community dissimilarity), and the communities are plotted as points in non-metric multidimensional space with more dissimilar communities plotted farther away from one another in ordination space. Dissimilarities in composition between communities were examined for statistically significant differences between fens by comparing the distribution of dissimilarities using 1000 permutations. For the belowground microbial community any PLFA that contributed to less than 1% of the biomass across the five replicates was not included in the analysis. The adonis function in the vegan package in R (Oksanen et al. 2018) was used for the PERMANOVA and NMDS visualization. Finally, a Principal Components Analysis (PCA) using the vegan package in R was performed on the

belowground microbial community composition based on PLFA percentages (Oksanen et al. 2018). Site scores from the PCA were extracted for the two main axes and linear regressions that included all environmental variables (soil moisture, basal respiration, %C, %N, C:N of the peat) were used as explanatory variables to determine correlations between environmental variables and microbial community composition (i.e., PLFA percentages).

Results

Aboveground plants and litter

The *Sphagnum*-dominated fen demonstrated nearly $2 \times$ greater aboveground plant richness than the *Carex*-dominated fen $(F_{1,70} = 0.257.2, p < 0.001)$ (Fig. 1), and also had a significantly greater Shannon's diversity index but lower Pielou's evenness (Table 1). There were no significant differences among monthly sampling times for plant survey data (richness: $F_{2,70} = 0.065, p = 0.938$, diversity: $F_{2,70} = 0.485, p = 0.618$, evenness: $F_{2,70} = 0.549, p = 0.580$), and any difference between fen types was not affected by sampling time (i.e., interactive effects) (richness: $F_{2,70} = 2.775, p = 0.069$, diversity: $F_{2,70} = 0.944, p = 0.394$, evenness: $F_{2,70} = 0.051, p = 0.950$) although plant species richness was lowest during July in the *Sphagnum*-dominated fen and highest during July in the *Carex*-dominated fen. The
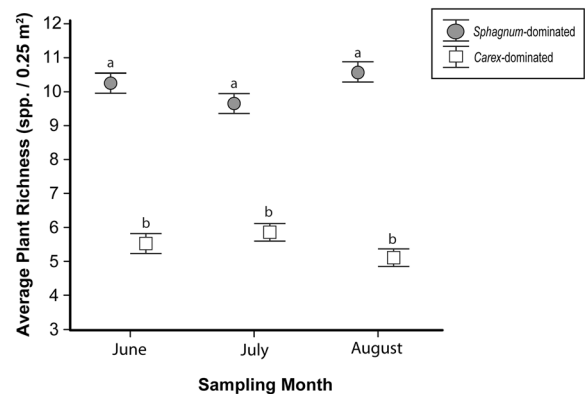
Fig. 1 Plant richness at both *the Sphagnum*-dominated fen *and Carex*-dominated fen across three sampling time points (June, July and August) during 2018. Letters denote significant differences using Tukey HSD post hoc comparisons and error bars are standard error

Table 1 Plant variables measured at two peatland sites in northern Ontario, Canada

	Sphagnum-dominated fen	*Carex*-dominated fen	$F_{(1,70)}$	p
Plant Shannon's diversity	1.46 ± 0.04	1.22 ± 0.04	17.07	**< 0.001**
Plant Pielou's evenness	0.63 ± 0.02	0.73 ± 0.02	15.46	**< 0.001**
Plant CWM C content (%)	47.89 ± 0.19	49.34 ± 0.21	25.80	**< 0.001**
Plant CWM N content (%)	1.18 ± 0.02	1.60 ± 0.04	115.39	**< 0.001**
Plant CWM C:N content	42.80 ± 0.51	33.83 ± 0.62	124.07	**< 0.001**

p-values in bold are deemed significant based on alpha < 0.05

Values are averages ± standard error. F & p values correspond to the main effect of fen corresponding to two-way ANOVAs for Shannon's diversity and Pielou's evenness and one-way MANOVAs for %C and %N

CWM community-weighted mean

differences in plant richness during July in the *Sphagnum*-dominated fen were driven by early seasonal small herbs such as *Maianthemum trifolium* (L.) Sloboda that decrease in abundance after June and *Carex* species such as *C. disperma* Dewey that increased in abundance during August (Fig. 1). The aboveground plant community was significantly different between the two fens (PERMANOVA: $F_{1,71} = 47.945$, $p = < 0.001$) (Fig. 2a), and shifts in the aboveground plant community were observed across the three sampling times ($F_{2,71} = 2.773$, $p = 0.005$). This shift in plant community during the growing season was more pronounced in the *Carex*-dominated fen, leading also to a significant fen-by-month interaction effect ($F_{1,71} = 3.293$, $p = 0.004$) (Fig. 2c, d).

The CWM for %C and %N of fresh plant material was significantly greater in the *Carex*-dominated fen compared to the *Sphagnum*-dominated fen (Table 1); however, there was a higher C:N in the *Sphagnum*-dominated fen compared to the *Carex*-dominated fen due to mosses, including *Sphagnum* species and *Pleurozium schreberi* (Brid.) Mitt., that had low %N, driving the high C:N ratio in *Sphagnum*-dominated fen. In the *Carex*-dominated fen, the abundant *Myrica gale* and lesser abundant *Salix pedicellaris* Pursh. had relatively high %N, driving the lower C:N values at that site. While there was variation in litter biomass across the three sampling periods (time main effect: $F_{2,16} = 4.79$, $p = 0.023$) that was mainly driven by the *Carex*-dominated fen where the highest litter biomass was collected after the growing season and the lowest biomass collected after the winter (Fig. 3a) (fen × time interaction: $F_{2,16} = 6.548$, $p = 0.008$), there was no difference in litter biomass between the two fens

(fen main effect: $F_{1,16} = 0.297$, $p = 0.601$). The overall repeated measures MANOVA model was significant for litter quality (%C, %N, C:N) across fens ($F_{1,16} = 427.7$, $p < 0.001$), sampling time ($F_{2,16} = 6.6$, $p = 0.024$), with a fen × time interaction ($F_{2,16} = 16.3$, $p = 0.002$). Litter quality (i.e., C:N) was lowest in *Sphagnum*-dominated fen litter collected at the end of the first growing season where C:N values were the highest of all litter collected (fen × time interaction: $F_{2,16} = 13.12$, $p < 0.001$), yet the *Sphagnum*-dominated fen litter had consistently higher C:N values compared to the *Carex*-dominated fen (fen main effect: $F_{1,8} = 379.60$, $p < 0.001$) (Fig. 3b). The C:N values of the litter were related to changes in both %C and %N across sampling times (%C time × fen interaction: $F_{2,16} = 19.10$, $p < 0.001$, %N time × fen interaction: $F_{2,16} = 18.43$, $p < 0.001$) (Fig. 3c, d). For instance, the high C:N values of litter at the *Sphagnum*-dominated fen during the end of the growing season (August-October) was not due to high %C but rather dramatically lower %N (Fig. 3c). In the *Carex*-dominated fen, high %N values were observed in the growing season accumulated litter (June–Oct), and low values of %C were observed during the winter accumulated litter (Oct–June) (Fig. 3d). Litter %C was consistently greater (%C fen main effect: $F_{1,8} = 49.13$, $p < 0.001$, %C time main effect: $F_{2,16} = 54.69$, $p < 0.001$) and %N consistently lower (%N fen main effect: $F_{1,8} = 308.37$, $p < 0.001$, %N time main effect: $F_{2,16} = 29.19$, $p < 0.001$) at the *Sphagnum*-dominated fen compared to the *Carex*-dominated fen.

Fig. 2 Compositional similarities of **a** aboveground plant communities ($n = 36$) and **b** belowground microbial communities ($n = 5$). Aboveground plant communities are based on aboveground biomass of individual plant species from 0.25 m² plots. Belowground microbial communities are based on PLFAs extracted from the top 5–10 cm of peat. Stress is 0.1 with $k = 2$ (number of dimensions) for the aboveground plant communities and 0.05 with $k = 2$ for the belowground microbial communities. Compositional similarities of **c** aboveground plant communities in the *Sphagnum*-dominated fen ($n = 36$) and **d** aboveground plant communities in the *Carex*-dominated fen ($n = 36$) across three sampling periods in 2018: June, July, and August. Aboveground plant communities are based on aboveground biomass of individual plant species from 0.25 m² plots. Stress is 0.24 with $k = 2$ (number of dimensions) for the *Sphagnum*-dominated fen and 0.16 with $k = 2$ for the *Carex*-dominated fen. The ellipses indicate 95% confidence intervals
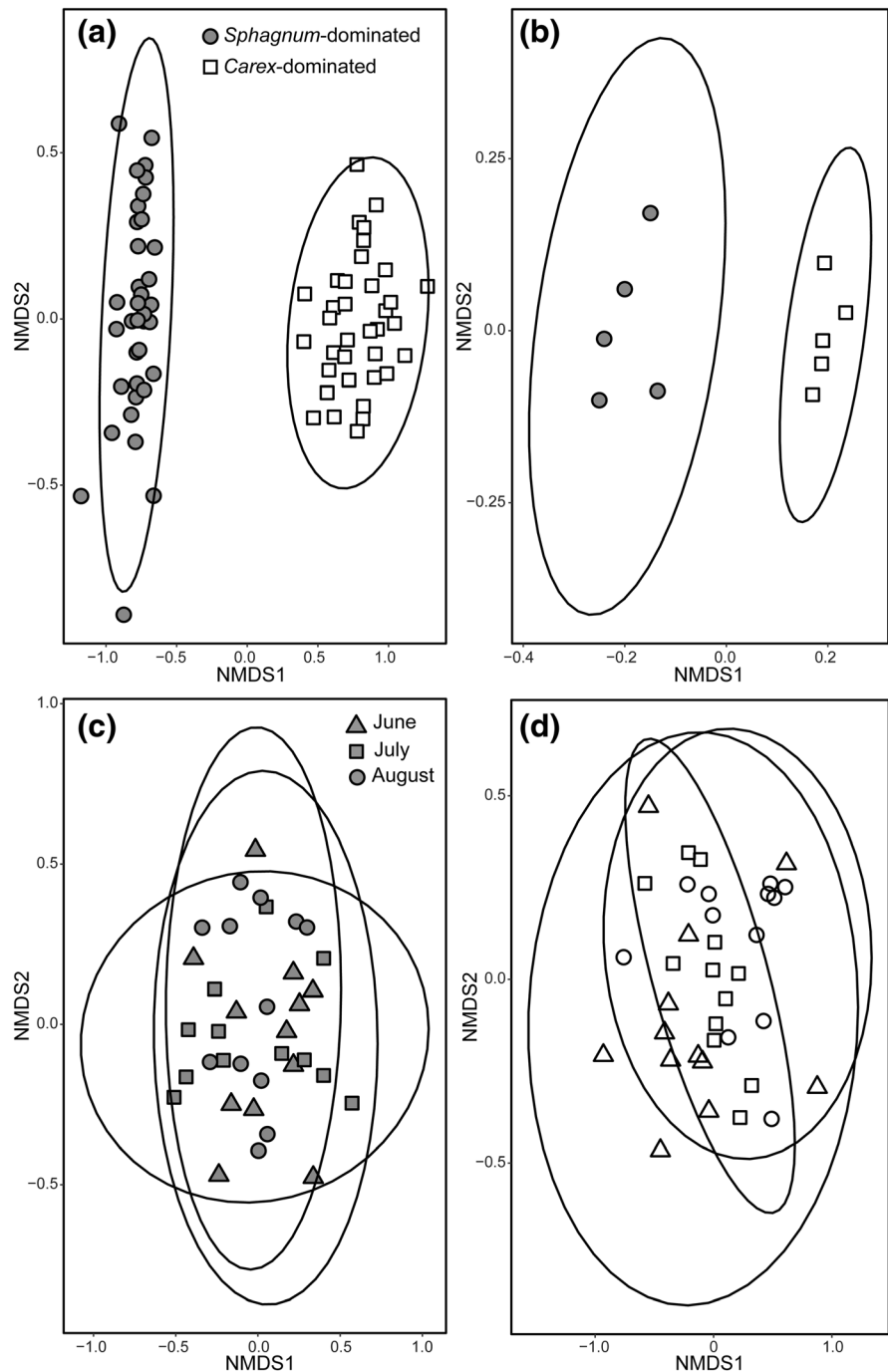
Peat quality and belowground microbial community

Belowground, the quality (i.e., %C, %N, C:N) of the peat mirrored the trends in the aboveground plant litter inputs from the litter traps and CWMs of the aboveground plant communities, where there was significantly greater %C, significantly lower %N, and significantly greater C:N (Table 2) in the *Sphagnum*-dominated fen compared to the *Carex*-dominated fen. The peat moisture content was significantly greater in the *Sphagnum*-dominated fen compared to the *Carex*-
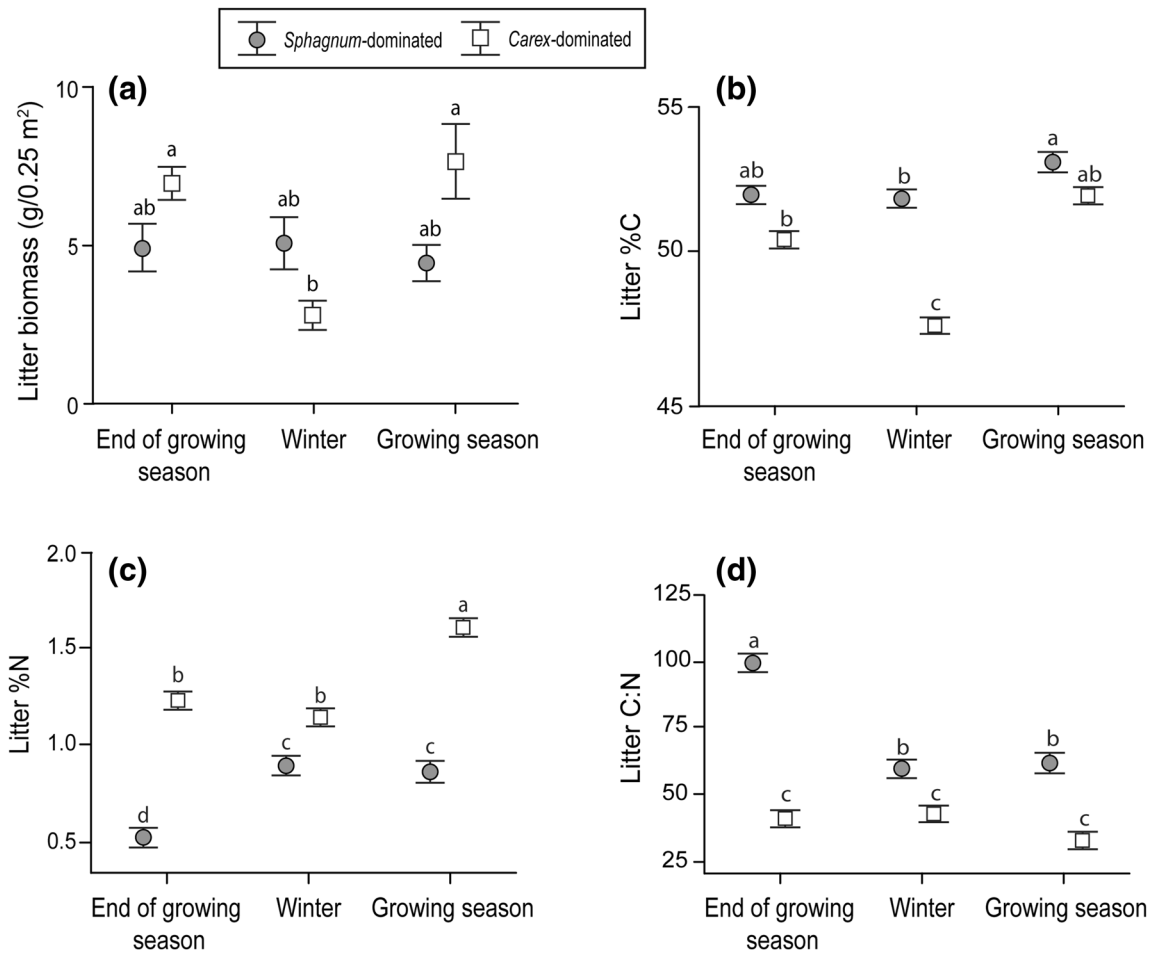
Fig. 3 **a** Litter biomass (g/0.25 m^2), **b** %C, **c** %N, and **d** C:N at both the *Sphagnum*-dominated fen and *Carex*-dominated fen across three sampling times: end of growing season, winter, and growing season. Letters denote significant differences after Tukey HSD post hoc comparisons and error bars are standard error

Table 2 Peat variables measured at two peatland sites in northern Ontario, Canada

	Sphagnum-dominated fen	*Carex*-dominated fen	$F_{(1,8)}$	p
Peat C content (%)	44.67 ± 0.22	40.56 ± 0.95	17.68	**0.003**
Peat N content (%)	0.844 ± 0.13	2.158 ± 0.05	92.43	**< 0.001**
Peat C:N content	57.25 ± 7.30	18.81 ± 0.26	22.73	**< 0.001**
Peat moisture content (%)	1117.28 ± 129.16	699.31 ± 46.55	9.27	**0.016**
Basal respiration (gCO$_2$/m^2/h)	0.040 ± 0.004	0.088 ± 0.015	8.74	**0.018**

p-values in bold are deemed significant based on alpha < 0.05

Values are averages ± standard error, and statistical F & p values correspond to main effect of fen. Peat %C, %N, and C:N results are based on one-way MANOVA. Peat moisture content and basal respiration results are based on one-way ANOVA

dominated fen, while basal respiration was 2 × greater in the *Carex*-dominated fen (Table 2). Overall microbial groups (fungi and bacteria) demonstrated biomass differences between fens with fungal-to-bacterial ratios (F:B) significantly greater in the *Sphagnum*-dominated fen compared to the *Carex*-dominated fen

($F_{1,8}$ = 164.93, p = < 0.001) (Fig. 4). While the *Sphagnum*-dominated fen had a greater fungal biomass, this was due to fungal groups such as

saprophytic fungi ($F_{1,8}$ = 47.10, p < 0.001), rather than arbuscular mycorrhizal (AM) fungi, which were more abundant in the *Carex*-dominated fen

Fig. 4 Boxplots of the total amount of PLFAs in the peat (nmol/g dry peat), the different microbial groups, (fungi include all fungal types excluding arbuscular mycorrhizal), the Gram-positive-to-Gram-negative ratio, and the fungi-to-bacteria ratio. All means are significantly different between the *Sphagnum*-dominated fen and *Carex*-dominated fen based on a one-way MANOVA
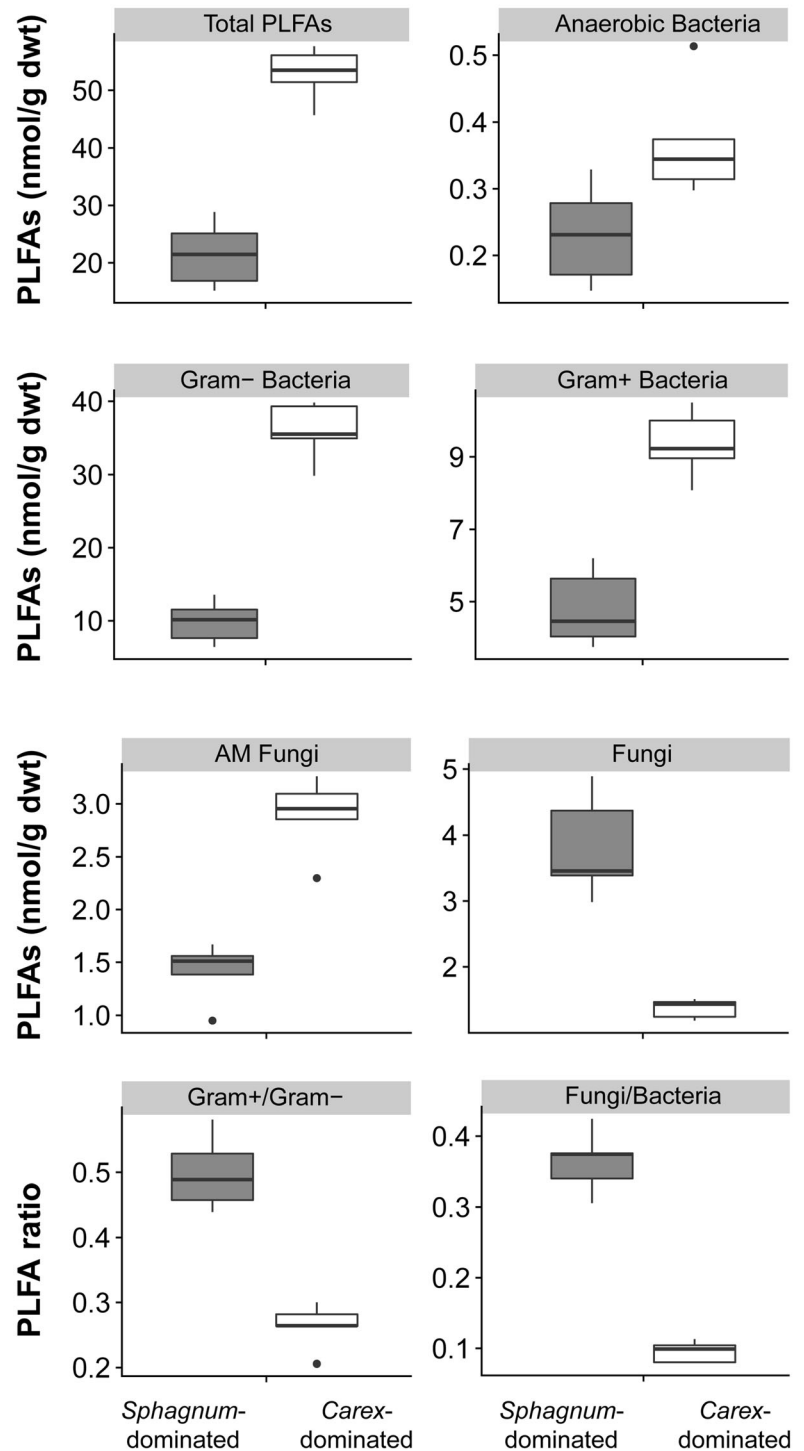
($F_{1,8} = 51.55$, $p < 0.001$). The *Sphagnum*-dominated fen also had significantly less overall PLFA biomass ($F_{1,8} = 91.81$, $p < 0.001$), and less anaerobic bacteria ($F_{1,8} = 7.28$, $p = 0.027$), Gram+ bacteria ($F_{1,8} = 51.62$, $p < 0.001$), and Gram− bacteria ($F_{1,8} = 138.5$, $p < 0.001$) than the *Carex*-dominated fen. However, the *Sphagnum*-dominated fen had a greater Gram+ bacteria:Gram− bacteria ratio ($F_{1,8} = 61.91$, $p < 0.001$) compared to the *Carex*-dominated fen (Fig. 4). Correspondingly, the belowground microbial community was highly dissimilar between the two fens (PERMANOVA: $F_{1,9} = 23.90$, $p = 0.007$) (Fig. 2b).

The relationship of specific PLFAs with peat %C and peat %N was revealed in the PCA, where the first PC axis (PC1) explained 45.93% of the total variance in PLFAs, and site scores were significantly related to peat %C ($R^2 = 0.983$, $p = 0.046$) and peat %N ($R^2 = 0.983$, $p = 0.008$) (Fig. 5). The positive PC1 values are associated with low %C values and high %N, while negative PC1 values are associated with high %C and low %N. The second PC axis (PC2) explained an additional 31.21% of the PLFA variance (first two PCA components combined explained 77.14% of the variance), but PC2 was not significantly related to any of the variables. The high %C and low %N peat from the *Sphagnum*-dominated fen was related to PLFA 16:0 (-0.39) (Gram+ bacteria) and 18:2ω6c (-0.45) (saprophytic fungi). The low %C and high %N peat from the *Carex*-dominated fen was characterized by PLFA 18:1ω7c (0.66) (Gram− bacteria). The 18:3ω6c (general fungi) and 10Me16:0 (actinomycetes) were found in highest abundance in a single *Sphagnum*-dominated fen sample; this sample also had higher moisture and higher N compared to the other four samples from the *Sphagnum*-dominated fen.

Fig. 5 Principal Components Analysis biplot for the belowground microbial communities based on the PLFAs ($n = 5$); only PLFAs with scores greater than 0.2 are shown. Positive PC1 values correspond to low %C and high %N and negative PC1 values correspond to high %C and low %N. PC2 values did not correspond to any of the measured environmental variables. 16:0 is a fatty acid associated with Gram+ bacteria, 18:3ω6c and 18:2ω6c corresponds with general fungi, 10Me16:0 corresponds with actinomycetes, 18:1ω7c corresponds with Gram− bacteria, i17:1ω10c corresponds to Gram− bacteria. The *Sphagnum*-dominated fen is indicated by gray circles and the *Carex*-dominated fen is indicated by white squares
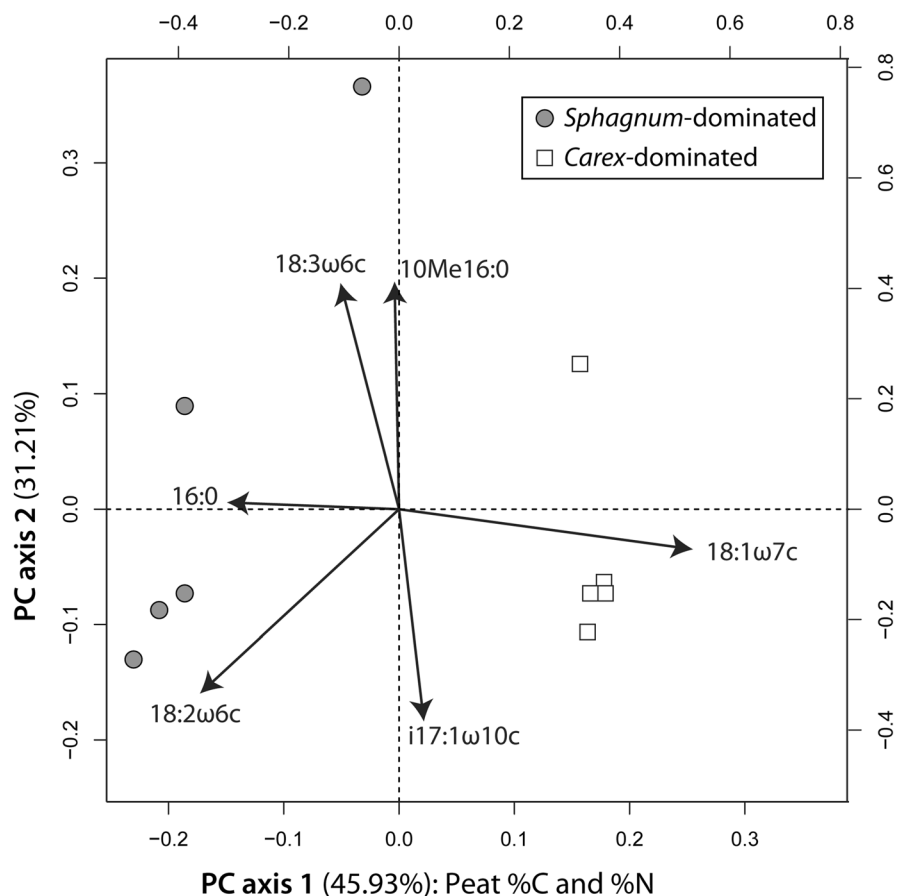
Discussion

The connection between the above- and belowground systems in boreal peatlands is innate because the peat in which the belowground community resides is composed of the partially decomposed aboveground plant community. For instance, root exudates and litter inputs (both quantity and quality) to belowground systems are dictated by the plant community composition (i.e., species richness, diversity and evenness, as well as specific plant species identities). Correspondingly, dominant vegetation types often have a positive feedback effect on belowground systems for both the microbial community composition as well as rates of carbon and nutrient turnover (i.e., a fast–slow continuum), that can more broadly be thought of as a *plant–soil interaction spectrum*. Dominant traits in plant communities that relate to resource acquisition and allocation lead to distinct inputs of litter quality, corresponding peat chemical profiles and microbial communities, and rates of nutrient cycling that correlate with dominant plant resource traits. We show that community-weighted means for plant traits reflecting resource allocation (i.e., %C, %N, and C:N values) turn into similar differences for litter inputs across our *Sphagnum*-dominated and *Carex*-dominated fens. We further show these differences persist in the composition of the peat, and that dominant microbial communities (i.e., fungal vs bacterial dominance) corresponds along this fast–slow continuum.

The *Sphagnum*-dominated and *Carex*-dominated fens differed greatly in terms of aboveground species richness, diversity and evenness, yet this higher plant richness and diversity found in the *Sphagnum*-dominated fen supported a microbial community half the size found in the *Carex*-dominated fen. This suggests that differences in the overall quality of plant litter inputs could be a more important predictor of microbial biomass (Wardle et al. 2004, 2006) than plant diversity per se, and lead to not only distinct microbial communities but also differences in total microbial biomass between these two sites (Wardle et al. 1997, 1999).

Plant traits such as short stature, low relative growth rates and longer life spans are typical of *Sphagnum* mosses making them more conservative in their nutrient requirements (Grime 1974; Grime et al. 1990) as evident by their low C:N in this study and others (Aerts et al. 2001; Turetsky 2003). However,

Carex sedges are able to efficiently capture resources such as nutrients, light and space due to their tall height and fast growth (Keddy et al. 1998). However, important differences were found in C and N for *Sphagnum* and *Carex* sampled at the two different sites that may also suggest extrinsic environmental factors play a role to modify this plant–soil interaction.

While in the *Sphagnum*-dominated fen the *Carex* spp. had higher %N than the *Sphagnum* spp., this was not quite as evident in the *Carex*-dominated fen where the *Carex* and *Sphagnum* spp. had more similar %N. Also, *Sphagnum* C:N was not consistent between the two sites driven by differences in %N, which was higher at the *Carex*-dominated fen with greater N availability, suggesting %N content is also environmentally dependent (Dorrepaal et al. 2005). An additional consideration is that *Sphagnum* mosses also have the ability to harbor N-fixing microorganisms (Vile et al. 2014) and wetter conditions, such as at the *Carex*-dominated fen, tend to support higher rates of N fixation (Živković et al. 2017). Similarly, the low litter values for C:N in the *Carex*-dominated fen appear to be driven by the shrub species *Myrica gale* and *Salix pedicellaris* (Bog willow), where *Myrica gale* is also well established to form N-fixing root nodules (Sprent et al. 1978; Schwintzer 1979; Skene et al. 2000) that may fix up to five times the amount of N contained in bulk precipitation (Schwintzer 1979).

Overall litter quality was significantly higher (low C:N) in the *Carex*-dominated fen compared to the *Sphagnum*-dominated fen. Yet we note that litter quality values presented here are conservative approximations given that our litter values underestimate contributions of *Sphagnum*, especially in the *Sphagnum*-dominated fen. Ericaceous shrubs such as *Chamaedaphne calyculata* and *Andromeda polifolia* also have low litter quality and contributed significantly to litter inputs in the *Sphagnum*-dominated fen (also see Del Giudice and Lindo 2017). This 'legacy' of the plants was further found in the peat (i.e., the *Carex*-dominated fen had greater %N and lower C:N) and absolute values of %N were even greater belowground in the *Carex*-dominated fen peat. Similarly, Palozzi and Lindo (2017a) found more biologically available N (NO_3^- and NH_4^+) in the *Carex*-dominated fen peat compared to the *Sphagnum*-dominated fen peat, which may be related to greater hydrological connectivity to ground water in the *Carex*-dominated

fen (Rydin and Jeglum 2013), rather than litter %N inputs.

Within the peat, differences in microbial biomass and microbial functional composition strongly relates to the resource allocation/turnover dichotomy. Fungi were dominant in the *Sphagnum*-dominated fen, including the PLFAs biomarkers associated with ectomycorrhiza, ericoid mycorrhiza, and saprophytic fungi, but not the arbuscular mycorrhiza. However, that the *Carex*-dominated fen was dominated by bacterial groups strongly suggests linkages with plant litter quality inputs as well as root resources. While *Sphagnum* mosses lack roots and therefore root associations with mycorrhiza, the *Sphagnum*-dominated fen contained several ericaceous shrubs (*Vaccinium angustifolium*, *Chamaedaphne calyculata*, *Kalmia polifolia* Wangenh., *Rhododendron groenlandicum*, *Andromeda polifolia*) that are known to form root associations with ericoid mycorrhiza, and trees (*Picea mariana*, *Larix laricina*) that form associations with ectomycorrhizal fungi (Thormann et al. 1999). Ectomycorrhizal and ericoid mycorrhizal fungi produce N-degrading enzymes allowing greater access to N sources compared to arbuscular mycorrhiza fungi (Averill et al. 2014), which could also correlate with the lower N availability observed by Palozzi and Lindo (2017a) in the *Sphagnum*-dominated fen (i.e., immobilized as fungal biomass). At the same time the greater arbuscular mycorrhizal biomass in the *Carex*-dominated fen may be the interplay between the plant community and hydrology. For instance, while there is discrepancy in the literature (Muthukumar et al. 2004), it appears that some *Carex* sedges may form associations with arbuscular mycorrhiza (Miller et al. 1999; Cornwell et al. 2001), and *Myrica gale* that is known to form associations with ectomycorrhiza may also form associations with arbuscular mycorrhiza (Skene et al. 2000). Arbuscular mycorrhiza fungi have been shown to increase in abundance under intermittent flooding conditions (Mentzer et al. (2006) using wet prairie soil), and the *Carex*-dominated fen is prone to intermittent water table levels at or above the soil surface (Webster and McLaughlin 2010). Ultimately, mycorrhizal associations are still poorly known and we are increasingly finding less specificity than previously thought where the same host species can show varying mycorrhizal associations, depending on habitat and other environmental conditions (Guillermo Bueno et al. 2019; Sun et al. 2019; Tedersoo et al. 2019).

More recalcitrant litter inputs to the *Sphagnum*-dominated fen include contributions from *Picea mariana* and ericaceous evergreen shrubs (*Andromeda polifolia*, *Chamaedaphne calyculata*, *Kalmia polifolia*) that make long-lived tissues, including woody stems and roots, and leaves covered with thick epicuticular waxes (Jacquemart 1998; Eckstein et al. 1999; Wright et al. 2004) that are composed of phenolics, lignin, and tannins. The polyphenolic compounds produce by *Sphagnum* mimics the compound structure of lignin and tannins (Verhoeven and Liefveld 1997) in addition to being nutrient poor, and contain antimicrobial properties (Mallegård et al. 2009) that is generally resistant to microbial breakdown (Turetsky 2003). All together explaining why the *Sphagnum*-dominated fen has more PLFA biomarkers associated with fungal groups that can breakdown these compounds using extracellular enzymes (Strickland and Rousk 2010). The high C:N of *Sphagnum* and the *Sphagnum*-dominated fen pairs well with the high C:N of fungi biomass, and is suggestive of fungi having lower nutrient demands compared to bacteria (Strickland and Rousk 2010; Waring et al. 2013).

Similarly, at the *Carex*-dominated fen, greater bacterial dominance can be attributed to the lower C:N and greater %N inputs from the aboveground plant community that provides a more N rich environment, and which pairs with the low C:N commonly associated with bacterial biomass (Strickland and Rousk 2010; Waring et al. 2013). Anaerobic bacteria were particularly more abundant at the *Carex*-dominated fen compared to the *Sphagnum*-dominated fen that may also be related to the hydrological regimes at these two fens. While the *Sphagnum*-dominated fen had greater moisture content at the peat surface, the *Sphagnum*-dominated fen has a lower water table; we would expect a greater concentration of anaerobic bacteria at closer proximity to the water table, which would suggest anaerobic bacteria may occur at greater peat depths in the *Sphagnum*-dominated fen (Asemaninejad et al. 2019) but occur near the surface in the *Carex*-dominated fen. Jaatinen et al. (2006) also found a strong relationship between water table depth and microbial community composition where a lower water table supported a more fungal-dominated community, whereas a higher water

table depth supported a more bacterial-dominated community.

It has been proposed that Gram+ use soil organic matter derived C (i.e., microbially processed) while Gram− use plant derived C that is considered to be a more labile source (Waldrop and Firestone 2004; Kramer and Gleixner 2008; Fanin et al. 2019); this is consistent with the plant inputs and PLFA results from our two sites. While both Gram+ and Gram− bacteria had greater biomass in the *Carex*-dominated fen, Gram+ PLFA marker 16:0 was associated with high peat %C and low peat %N, and the Gram− PLFA marker 18:1ω7c was associated with low peat %C and high peat %N in the PCA ordination. Correspondingly more labile (i.e., lower C:N and greater %N) plant inputs at the *Carex*-dominated fen was correlated with lower Gram+:Gram− values, similar to a comparative study of *Sphagnum* and *Carex* peatlands by Borga et al. (1994).

Higher Gram+:Gram− ratios have also been linked to lower soil respiration rates suggesting slower C cycling and subsequently greater C storage in soils (Whitaker et al. 2014), leading to the conclusion that the *Sphagnum*-dominated fen is potentially a greater C sink than the *Carex*-dominated fen. This is also supported by the greater fungal biomass at the *Sphagnum*-dominated fen as fungi demonstrate slower C processing compared to bacteria, and high F:B soils have been shown to contain greater amounts of soil organic matter and respire less, which supports this greater C sequestration potential (i.e., more C in soils and less lost as CO_2) (Malik et al. 2016). Even among the fungi, Averill et al. (2014) suggest that there could be more C stored in ecto- and ericoid mycorrhizal fungi-dominated soil compared to soils dominated by arbuscular mycorrhizae. These considerations of plant–soil interactions are especially relevant for understanding peatland C storage potential under climate change factors such as increased temperature and concomitant shifts in aboveground plant communities.

Determining linkages between plant and microbial communities for important C sequestering northern peatlands is imperative for predicting future climate scenarios, but is not currently incorporated into process-based models (e.g., DNDC) that are used to simulate the effects of vegetation, biogeochemistry, hydrology, and changes in climate and management on greenhouse gas fluxes. We highlight the conceptual links between plant and microbial communities in peatlands by exploring plant traits and peat quality. In this approach we highlight that peatlands and their component plant and microbial communities play-out along a common resource-spectrum that dictates 'fast' vs 'slow' carbon and nutrient cycling; the *plant–soil interaction spectrum*. In this study we also found that important environmental conditions such as site-specific hydrology can interact with this spectrum. While several studies highlight the link between peatland plant communities and differing plant traits such as litter quality (i.e., %C, %N, and C:N) (e.g., Dorrepaal et al. 2005 and Straková et al. 2010), both plant and microbial communities are strongly influenced by water table depth (among other environmental variables such as pH, nutrient content, bulk density) (see also Andersen et al. 2011; Palozzi and Lindo 2017a; Robroek et al. 2014; Szajdak et al. 2019). Our study emphasizes the feedbacks among these variables, yet also demonstrates the challenges in untangling causal and correlational links between plant and microbial communities and their environment.

Peatlands and in particular boreal peatlands, harbor slow decomposition rates making peatlands the largest terrestrial C store, storing 1/3 of the world's terrestrial C (Gorham 1991). Here, the vegetation, microbial, hydrological and nutritional continuum that our peatland sites represent provide a unique opportunity to understand the above- and belowground linkages related to predicted shift under climate warming. Whether nutrient availability, both in peat and plant litter (C:N), is a direct feedback between the microbial community and the plant community is still not entirely clear. However, what is clear is that climate-induced changes in plant communities will alter the nutrient content of litter inputs that will likely cascade to shifts in the microbial community (Jassey et al. 2013; Bragazza et al. 2015). Specifically, shifts under warming and elevated CO_2 from *Sphagnum*-dominated peatlands to vascular plant dominated communities (Jassey et al. 2013; Dieleman et al. 2015; Bragazza et al. 2016) and the consequent shifts in litter quality will lead to more bacterial-dominated peat communities that are thought to be less efficient at storing C than fungal-dominated communities.

Compliance with ethical standards

Conflicts of interest The authors declare that they have no conflict of interest.

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