Plant Soil (2017) 418:277–291
DOI 10.1007/s11104-017-3291-0

REGULAR ARTICLE

Boreal peat properties link to plant functional traits of ecosystem engineers

Julia E. Palozzi · **Zoë Lindo**

Received: 29 November 2016 / Accepted: 18 May 2017 / Published online: 30 May 2017

Abstract
Background and aims Plant species shape soil properties such as nutrient availability and carbon storage through functional traits. Understanding the role of plant functional traits, and the relationship between aboveground and belowground systems are especially important in boreal peatlands, which are important carbon sinks. *Sphagnum* as a key peat-forming bryophyte has long been considered an ecosystem engineer, whereas the engineering role of graminoids, also dominant in peatlands, has not traditionally been considered.
Methods We quantified vegetation community composition, plant functional traits, and peat properties in two peatland sites differing in dominant vegetation (*Sphagnum* mosses and *Carex* sedges), and link plant traits with peat properties using ordination.
Results We show that plant traits significantly explain many peat properties, including organochemicals that are indicators of decomposition dynamics. Specifically, *Carex*-dominated sites had larger amount of 'decomposition products' while a larger proportion of 'undecomposed materials' was observed in *Sphagnum*-dominated sites.
Conclusion Feedbacks in plant-soil systems are increasingly being recognised as drivers of ecosystem processes. In both peatland types, plant traits of the key ecosystem engineer drove properties of the belowground peat environment. Peat organochemical constituents between *Sphagnum*-dominated and *Carex*-dominated sites reveal differences in ecosystem function, and thus the conducive potential for carbon storage.

Keywords *Carex* · Decomposition · Ecosystem engineer · FTIR · Peatland · Plant functional traits · Plant-soil feedbacks · Organochemical properties · *Sphagnum*

Abbreviations

CWM	Community level weighted mean
FTIR	Fourier transform infrared spectroscopy
LDMC	Leaf dry matter content
LMA	Leaf mass per area
NMDS	Non-metric multidimensional scaling
SLA	Specific leaf area

Introduction

Understanding the structure and composition of plant communities (Cornwell and Ackerly 2009), and identifying mechanisms affecting variation in species distribution (Klironomos 2002), are major goals in community ecology (McGill et al. 2006). Plant community composition results from a series of abiotic and biotic filters (Garnier et al. 2016), where plant strategy (sensu

Responsible Editor: Jeff R. Powell.

Electronic supplementary material The online version of this article (doi:10.1007/s11104-017-3291-0) contains supplementary material, which is available to authorized users.

J. E. Palozzi · Z. Lindo (✉)
Department of Biology, The University of Western Ontario,
London, ON N6A 5B7, Canada
e-mail: zlindo@uwo.ca

Grime 1977) is put into a context of physiological tolerances and ecological trade-offs (Westoby and Wright 2006). However, an often-overlooked mechanism of community structure is the presence of certain organisms that exert a strong influence on the distribution of other species and the environment through ecosystem engineering. Ecosystem engineers are organisms that directly or indirectly influence the flow of resources for other species, and in doing so, modify, create and maintain habitat (sensu Jones et al. 1994). While all organisms to some degree engineer their environment (Wright and Jones 2006), some species disproportionately affect community organization and species abundance through strong environmental feedbacks that facilitates their own dominance and govern local scale patterns of species richness (Jones et al. 1997).

Plant ecosystem engineers generally modify their ecosystem by altering local abiotic factors, creating strong feedbacks between the aboveground plant community and the belowground soil environment that favour their own expansion. In doing so these ecosystem engineers can modify many core ecosystem properties, including soil moisture and pH, as well as nutrient availability. For instance, fast growing plants with high nutrient demands tend to produce nutrient-rich, labile litter that facilitates faster decomposition, and increases soil nutrient availability, while slow growing plants with low nutrient demands tend to produce nutrient-poor, recalcitrant, litter that facilitates slower nutrient cycling and reduces soil nutrient availability (Reich 2014). These life history trade-offs have more recently been placed within a trait-based approach to examining ecosystem engineering (Bouma et al. 2012; Emery and Rudgers 2014). Plant functional traits are any heritable physiological, morphological or phenological characteristic that influences fitness through plant growth, reproduction, or survival (sensu Garnier et al. 2016). Plant functional traits can be used to understand plant community structure (Dolédec et al. 1996), and can predict ecosystem functioning for a wide range of environments at various levels of spatial and biological organization (Shipley et al. 2016). Investigating plant functional traits is seen as a robust method in determining how plant composition, and the associated diversity among traits, can reveal underlying ecosystem-level processes attributed to ecosystem engineers (Petchey and Gaston 2002).

Understanding the role of plant functional traits, and the relationship between aboveground vegetation and belowground soil variables are especially important in boreal peatlands, where *Sphagnum* mosses have long been thought of as an ecosystem engineer (van Breemen 1995). *Sphagnum* is a key peat-forming bryophyte in boreal ecosystems. Slow growing and producing nutrient-poor litter, *Sphagnum* mosses facilitate large accumulations of peat that are important carbon sinks. Graminoid species (including sedges of the genus *Carex*) have not traditionally been considered ecosystem engineers (but see Crain and Bertness 2005), however, the distribution of both *Sphagnum* and *Carex* species is related to resource gradients (e.g. soil moisture, soil pH, nutrient availability) that largely affect the peat accumulation of the dominant peatland plant functional type (Rydin and Jeglum 2013). Thus both *Sphagnum*-moss spp. and *Carex*-sedge spp. may be considered ecosystem engineers as they are both linked to abiotic changes related to the chemical composition of living and dead plant material (Belyea and Clymo 2001; Crain and Bertness 2005).

A growing body of research demonstrates how peatland plant species shape peat properties such as nutrient availability (Aerts et al. 1999), dissolved organic carbon (Bragazza et al. 2016; Robroek et al. 2016), microbial community structure (Bragazza et al. 2013), acidity (Ehrenfeld et al. 2005) and moisture (Strack and Price 2009), yet links to the underlying plant functional traits remain relatively unexplored. Identifying links between peat properties and plant functional traits is critical for interpreting how changes to peat properties might affect peatland processes such as carbon and nutrient cycling (Jassey et al. 2013, 2014) with overall impacts to peatland function. Despite the growing popularity of utilizing plant functional traits in deciphering ecosystem engineering, the trait-based approach has not addressed engineering in boreal peatlands where *Sphagnum* and *Carex* species traits drive a tug-of-war over peatland moisture, pH and nutrients levels that ultimately dictate peat accumulation and therefore carbon storage.

In a mechanistically-based observational study we quantified vegetation community composition, plant functional traits, and peat-soil variables to elucidate engineering mechanisms driving plant community structure and carbon storage in two contrasting peatland sites differing in resource status and dominant plant growth form. Specifically, we ask 1) how do aboveground plant functional traits relate to belowground peat properties (community-level)?, and 2) how do the ecosystem engineers *Carex* and *Sphagnum* affect aboveground and belowground ecosystem properties in their respective site (species-level)? We use peat spectral organochemical properties and a series of statistical ordination techniques to explore the link between plant traits and peat quality, and explain how different plants can be linked to peat properties to help infer nutrient and decomposition dynamics.

Materials and methods

Study site

The study was conducted in August 2015 at a boreal peatland complex within the White River Experimental Watersheds, a long-term research area maintained by the Ontario Ministry of Natural Resources and Forestry near the city of White River, Ontario, Canada (48°21′N, 84°20′W). The region experiences a mean annual temperature of 2.1 °C and a mean annual precipitation of 980 mm (see McLaughlin and Webster 2010 for full site description). Within the peatland complex two study sites were established 2 km apart, one at a nutrient-poor fen dominated by *Sphagnum* mosses, and the second at a fen with intermediate nutrient availability, dominated by graminoids. For brevity these sites will be hence referred to as the '*Sphagnum*-dominated fen' and the '*Carex*-dominated fen' respectively.

The *Carex*-dominated fen (10.2 ha) is predominantly treeless, surrounded by coniferous forest with two main tributaries running along the northern and southwestern edges. The vegetation within this fen is dominated by *Carex* spp. sedges (*C. oligosperma* Michx., *C. stricta* Lam.) and ericaceous shrubs such as sweet gale (*Myrica gale* L.), and leatherleaf (*Chamadeaphne calyculata* (L.) Moench) with sporadic patches of *Sphagnum* moss spp. as the main bryophyte. The *Sphagnum*-dominated fen (4.5 ha) conversely is partially forested and is bounded by upland boreal forest and a lentic lake. The dominant vegetation of the *Sphagnum*-dominated fen includes *Sphagnum* moss spp. (*S. magellanicum* Brid., and *S. angustifolium* ((C. Jens. ex Russ.) C. Jens.) as the dominant ground cover, with low densities of leatherleaf and bog Labrador tea (*Rhododendron groenlandicum* Oeder), and sporadic black spruce (*Picea mariana* (Mill.) B.S.P.), and tamarack (*Larix laricina* (Du Roi) K. Koch).

Experimental design

Five 1 × 1 m plots were randomly selected from representative 25 × 25 m areas of both the *Sphagnum*-dominated and *Carex*-dominated fens. Within each site, the minimum distance between plots was 1 m, and the maximum distance between plots was 20 m. Vegetation surveys were performed in each 1 × 1 m plot to assess species richness as well as each species' percent cover. Plant species were identified in the field using Legasy (1995) and Newmaster et al. (1997). Species percent cover was measured using an adapted Braun-Blanquet scale by a single observer as recommended by Rochefort et al. (2013). Alongside plant species composition, nine functional traits were assessed using material collected from each species in every 1 × 1 m plot in accordance with Pérez-Harguindeguy et al. (2013). Surface peat samples (20 cm wide ×20 cm long ×25 cm deep) were collected alongside plant community and trait data from the north-facing side of each plot to assess 13 environmental variables. All peat monoliths were the same size and analyses were performed at the same depth within each. The depth chosen (25 cm) reflects the area in which most biological processes occur (Myers et al. 2012), as opposed to the rooting depth of any specific plant species.

To quantify functional traits, three upper, photosynthetically active leaves were collected from each vascular species (Pérez-Harguindeguy et al. 2013) while whole moss shoots (stem + capitulum) were collected from *Sphagnum* mosses (Bond-Lamberty and Gower 2007). Total plant height was also determined in the field at the time of leaf collection. The collected leaf and moss samples were then stored in plastic bags and kept cool and moist until further processing. In the lab, specific leaf area (SLA), wet and dry leaf weight, leaf area, leaf mass per area, as well as leaf C and N content were determined. Specific leaf area is defined as the one-sided leaf area (cm^2) divided by dry weight (g) and was determined by a digitally scanning the three leaves collected from each species at each plot. In the cases of mosses, photosynthetically active whole shoots were used as the functional analogue of a leaf as done by Bond-Lamberty and Gower (2007). Wet leaf weights were obtained before scanning and leaves were subsequently dried for 48 h at 60 °C to calculate the leaf dry matter content (LDMC), which represents the dry weight (mg) divided by the wet weight (g). Leaf area and leaf mass were obtained as plant traits from the calculations of SLA, and leaf mass per area (LMA) was calculated as the inverse of SLA.

Total C and N leaf concentrations were measured for 14 species using a combustion autoanalyser (vario MAX CN, Elementar) with glutamic acid as calibrant and birch leaf as the quality control. The same dried leaf samples that were used to determine SLA were ground using an electric grinder prior to analysis, however, species were pooled by site to obtain the minimum 0.2 g material required for analysis. Carbon-to-nitrogen ratios (C:N) were calculated using the total C and N values and treated as a separate plant functional trait.

Intact peat monoliths were collected manually using a key-hole saw, wrapped in aluminum foil and kept in a 4 °C fridge until processed. Litter biomass was determined from the surface of each peat monolith by weighing the dried (48 h at 60 °C) senesced vegetation. A 5 × 5 × 5 cm subsample of peat was extracted from the centre of each peat monolith for coarse root biomass (>2 mm diameter); roots were washed from surrounding peat matrix and oven dried at 60 °C for 48 h. Gravimetric moisture content was determined from another 5 × 5 × 5 cm of subsampled peat dried at 60 °C for 72 h. The same peat samples were further dried at 105 °C for 24 h before determining organic matter (carbon) content via loss-on-ignition (LOI) at 550 °C for 8 h (Chambers et al. 2011).

The pH of peat samples was determined using 2 g dry weight equivalent of fresh peat in 11 mL of distilled water using a calibrated glass probe. The filtrate of the pH sample was used to determine electrical conductance (EC) following vacuum filtration using Whatman #42 filters, and measured using a standard probe with a glass electrode. Available nutrients (PO_4^{3+}, NO_3^- and NH_4^+) were extracted from each peat sample by shaking 5 g dry weight equivalent of peat in 40 mL of Bray's Solution (dilute NH_4F in HCl), or 40 mL 2 N potassium chloride (KCl) for 1 h, respectively, followed by filtration through Whatman GF/A filter paper. Available PO_4^{3+} was analysed using the fluoride colourimetric method, while available NH_4^+ was measured by the indophenol-blue method and NO_3^- was measured by the hydrazine method on an AA3 autoanalyzer.

Heterotrophic (basal) respiration was determined for 35 g wet weight subsample of peat with a Licor multiplexer Infrared Gas Analyzer (IRGA LI-8100A and Multiplexer unit LI-8150) in 250 ml Mason jars with approximately 2 cm headspace. The quantified CO_2 flux values are expressed as mL CO_2 / g dry weight / h. Following basal respiration measurements, substrate induced respiration was performed to calculate microbial biomass. Samples were amended with 10 mg of glucose and respiration was measured for an additional 12 h. Microbial biomass (mg CO_2-C / g dry weight) was calculated according to Anderson and Domsch (1978) based on the lowest respiration rate (flux-CO_2) prior to the commencement of microbial growth:

$$\text{Microbial biomass} = 40.4 \times \text{flux}CO_2 + 0.37.$$

Metabolic quotient (qCO_2) was calculated as the basal respiration-to-biomass ratio. In doing so we quantify the amount of CO_2-C produced per unit microbial biomass C as a measure of microbial carbon resource use efficiency.

Lastly, Fourier transform infrared spectroscopy (FTIR) was performed on a 5 g dry weight equivalent subsample of the surface peat to characterise the organic chemical functional groups present in the peat. Fourier transform infrared spectroscopy identifies chemical compounds in peat through the use of the vibrational characteristics of structural chemical bonds (Artz et al. 2008), and can distinguish between carbohydrates, lignins, cellulose, fats, lipids and waxes. Generally, it is used as an indicator of organic matter quality or decompositional processes and the development of peat organic materials (Artz et al. 2008; Broder et al. 2012). Each subsample was extracted from an undisturbed section of the sampled peat monolith. Subsamples were freeze-dried and ground with an electric grinder prior to analysis. The FTIR spectra of 0.5 g homogenised peat sample were recorded using a Tensor 27 series (Bruker Optics Ltd., Milton, Ontario) equipped with a Golden Gate ATR sample loading system (Specac Inc., NJ, USA). Spectra were acquired by taking the average of 200 scans at 4 cm^{-1} resolution over the wave number range of 500–4000 cm^{-1}. To compare FTIR spectral differences in *Sphagnum*-dominated and *Carex*-dominated fen peat, means and 95% confidence intervals of the absorption intensities were calculated for all wave numbers. To compare decomposability of the different peats, humification indices were calculated from FTIR spectral data using ratios of absorption intensities of aromatic, aliphatic, carboxylic acid and phenolic moieties to polysaccharides, which reflect source plant material and decomposability through the relative proportions of complex substances to easily degradable compounds (Broder et al. 2012). Absorption peaks indicative of structural units in organic matter were used as indicators of peat organic matter quality and identified according to Niemeyer et al. (1992).

Data analysis

Plant community data was assessed for species richness (S), percent cover as sample abundances (N_0), Shannon's diversity (H), Simpson's diversity index (D) and Pielou's evenness (J) for each plot using the vegan package in R (R Development Core Team 2013; version 3.1.2). Plant trait data was normalised and used to calculate functional diversity indices (i.e. functional richness, evenness, divergence, dispersion, Rao's quadratic entropy) using the dbFD command in the FD package (Laliberté and Legendre 2010), to characterise the diversity of species traits among sampled plots. See Garnier et al. (2016) for full a description of indices used. We calculated the functional redundancy of each plots as the difference between Simpson's diversity (D) and Rao's quadratic entropy function (Q) (Pillar et al. 2013). Community weighted means (CWM) for each trait were also calculated for each plot, using:

$$\mathrm{CWM}_{\mathrm{trait}} = \Sigma(p_i \times x_i)$$

Where $\mathrm{CWM}_{\mathrm{trait}}$ is the CWM for trait x, p_i is the percent cover of species i in the community, and x_i is the trait value for the species i. One-way analysis of variance (ANOVA) was used to characterise and quantify the difference in mean values of plant, trait and peat-soil variables between these two specific fen sites.

To examine how *Sphagnum*-dominated and *Carex*-dominated fen sites were structured with respect to plant composition, and the composition of species traits, and peat-soil conditions, separate Bray-Curtis percent similarity matrices were constructed for plant community composition (30 species total), peat-soil variables, and plant species functional trait composition using the vegdist function in the vegan package of R. Dissimilarities were quantified using the adonis function to perform PERMANOVA. Simper analyses were also used to determine the contribution of individual species, peat variables or traits to the respective overall Bray-Curtis dissimilarity using the sim command in the vegan package (Clarke 1993). To examine how *Sphagnum*-dominated and *Carex*-dominated fen sites were functionally structured at the community-level with respect to plant composition and the composition of species traits, a percent similarity matrix (Bray-Curtis) was created examining trait similarity among the plant species. Dissimilarities were visualised using the metaMDS function to compute a non-metric multi-dimensional scaling (NMDS) ordination plot. In this ordination, the output presented becomes a representation of trait composition for each species. Thus data points that cluster close together represent species that have similar trait compositions, while data points that are further apart, represent species that differ in trait composition. Prior to analysis, species were assigned dominance to fen type based on the total abundance of that species at each site, with the criteria of at least 51% greater in abundance in one site or another. Differences in functional structure were assessed between fen types using the adonis function to perform PERMANOVA.

At the individual species-level we examine the species response to the environmental conditions across the fen sites using CCA, and the relationship of the traits with the environmental variables using RDA of CWMs (Kleyer et al. 2012). Also, to link characteristics of plant traits to the characteristics of the environment, we used the co-inertia analysis RLQ (R-mode Linked to Q-mode) (Dolédec et al. 1996) using all three data matrices: species × plot (L), plant trait × species (Q), and environmental variables × plot (R). Initial correspondence analysis (CA) was performed on the species × plot data, while principle components analysis (PCA) was performed on the plant trait × species, and environmental variables × plot data. Subsequently both environmental (R matrix) and trait (Q matrix) ordinations were constrained with species (L matrix) scores for the RLQ analysis using the dudi.pca command, and RLQ analysis was carried out with the rlq command in ade4, a support package for vegan (Dray and Dufour 2007). RLQ is thus performed via a double inertia analysis of two arrays (R and Q) with a link expressed by the contingency Table (L), where the rows of L (sites) corresponded to the rows of R (sites) and the columns of L (species) corresponded to the rows of Q (species) (Dray and Dufour 2007). Permutation tests (Monte Carlo, $n = 999$) were performed to test if whether sites (model 2), species (model 4), and sites and species (model 5) scores could be explained significantly by trait-environment relationships using the randtest function. The final RLQ product is presented as a three-way plot where species-trait-environment relationships are interpreted by correlating the spatial location of objects in the co-created plots.

Results

Comparison of site characteristics

Several peat-soil properties differed between the *Sphagnum*-dominated and *Carex*-dominated fen sites (Table 1); the *Carex*-dominated fen had characteristically higher pH, root biomass, metabolic quotient, and total available N than the *Sphagnum*-dominated fen, while the *Sphagnum*-dominated site had significantly greater vegetative biomass, moisture, and organic matter. Electrical conductivity, available phosphate, and microbial biomass were also greater in the *Sphagnum*-dominated site, but not significantly so (Table 1). In terms of plant functional trait CWMs, the *Carex*-dominated fen had greater leaf area, leaf mass, LDMC and height than the *Sphagnum*-dominated fen (Table 2). The average species richness, and diversity (Shannon's and Simpson's) were significantly greater in the *Sphagnum*-dominated nutrient poor fen compared to the *Carex*-dominated intermediate nutrient fen site (Table 3). Percent cover of vegetation was not significantly different between sites, but was mildly greater in the *Sphagnum*-dominated fen. Considering the functional diversity indices, the *Sphagnum*-dominated fen was found to have significantly greater functional richness and redundancy (Table 3).

The FTIR spectra varied among the two fen types, but both fens displayed absorption bands typical of humic substances (Fig. 1, Table 4). Peat from the *Sphagnum*-dominated fen had a significantly greater proportion of cellulose (wave number 3340 cm^{-1}), aliphatic structures (2920 cm^{-1} and 2850 cm^{-1}), carboxylic acids (1720 cm^{-1}), and long chain alkanes of aromatic structures (720 cm^{-1}). The *Carex*-dominated fen peat scored higher for aromatics (1650 cm^{-1}), lignin-like and phenolic structures (1515 cm^{-1}), proteinaceous compounds (1550 cm^{-1}), and alkyl groups at 1475 cm^{-1} representing plant wax. Polysaccharides (1030 cm^{-1}) and humic acids (1426 cm^{-1}), enhancers of decomposition rates and indicators of humification, respectively, were not significantly different between the fens. For the humification indices, the *Sphagnum*-dominated fen demonstrated greater aliphatic lipids and carboxylic acid moieties than the *Carex*-dominated fen, while the *Carex*-dominated fen had greater aromatic and phenolic index values (Table 4).

Composition similarity of site characteristics

Plant species community composition was highly dissimilar between *Sphagnum*-dominated and *Carex*-dominated fen sites ($F_{1,8} = 9.88$, $P = 0.001$, $R^2 = 0.553$) driven by *Carex stricta*, *M. gale*, and *C. oligosperma* as dominant species at the *Carex*-dominated fen, and *S. magellanicum* and *S. angustifolium* at the *Sphagnum*-dominated fen. The peat environment was also found to be significantly different between fen sites ($F_{1,8} = 5.99$, $P = 0.009$, $R^2 = 0.428$), explained by differences in organic matter content and electrical conductance. Examining the functional trait compositions of sampled plots, we also found high dissimilarity and a significant difference between fen types ($F_{1,8} = 6.29$, $P = 0.008$, $R^2 = 0.440$): differences in functional trait

Table 1 Summary of peat-soil environmental (plot) conditions of the *Sphagnum*-dominated and *Carex*-dominated sites located near White River, Ontario

Variable	*Carex*-dominated fen average (± SE)	*Sphagnum*-dominated fen average (± SE)	$F_{(1,8)}$	*P*
Vegetation biomass (g)	0.5 (0.2)	5.0 (1.6)	8.18	**0.021**
Litter biomass (g)	3.7 (1.8)	2.1 (0.7)	0.72	0.420
Root biomass (g/cm^3)	7.4 (1.6)	2.6 (0.5)	8.96	**0.017**
Moisture content (%)	87.8 (0.4)	90.1 (0.9)	6.37	**0.036**
Organic matter (%)	83.7 (3.6)	97.8 (0.3)	15.00	**0.005**
pH (in dH$_2$0)	5.4 (0.0)	4.8 (0.1)	64.27	**<0.001**
EC (dS/m)	73.2 (6.2)	80.5 (2.9)	1.12	0.320
PO_4^{+3} (mg/L)	1.2 (0.5)	4.4 (1.9)	2.76	0.136
NO_3^- (mg/L)	0.2 (0.1)	0.1 (0.0)	11.00	**0.011**
NH_4^+ (mg/L)	0.1 (0.1)	0.00 (0.0)	1.69	0.230
Basal respiration (mL CO$_2$/g dry weight/h)	0.1 (0.0)	0.1 (0.0)	1.99	0.196
Microbial biomass (mg CO$_2$-C/g dry weight)	3.2 (0.4)	5.0 (0.7)	4.67	0.063
Metabolic quotient	0.02 (0.0)	0.01 (0.0)	22.40	**0.002**

Table 2 Community weighted means (average ± SE) of plant functional traits collected from vegetation surveys performed at *Sphagnum*-dominated and *Carex*-dominated fen sites near White River Ontario, Canada

Trait	*Carex*-dominated fen average (± SE)	*Sphagnum*-dominated fen average (± SE)	$F_{(1,8)}$	P
Height (cm)	63.3 (4.59)	21.0 (2.33)	67.6	**< 0.001**
Leaf area (cm^2)	9.52 (1.03)	5.06 (0.45)	15.7	**0.004**
Leaf mass (mg)	76.02 (8.18)	32.41 (2.87)	25.3	**0.001**
SLA (cm^2/g)	138.6 (9.16)	154.2 (2.17)	2.75	0.136
LMA (mg/cm^2)	9.18 (0.51)	9.66 (0.50)	0.461	0.517
LDMC (mg/g)	422.87 (37.4)	303.4 (5.08)	10.0	**0.013**
Leaf C (%)*	47.9 (0.51)	49.1 (0.60)	2.32	0.166
Leaf N (%)*	1.53 (0.02)	1.52 (0.03)	0.087	0.775
Leaf C:N*	32.7 (0.42)	34.8 (1.65)	1.58	0.244

Bold denotes significant difference based on one-way analysis of variance

SLA specific leaf area, *LDMC* leaf dry matter content, *LMA* leaf mass per area

* denotes CWMs calculated with the 14 species that had C and N data; not all species could be included in C and N analyses due to insufficient material

composition were mainly driven by LDMC and plant height. However, when considering functional trait composition of the species, we find high similarity of trait composition for many species found across both fen locations (Fig. 2a). For example, the ericoid mycorrhizal shrub *C. calyculata* found in high abundance at the *Sphagnum*-dominated site and the arbuscular mycorrhizal shrub *M. gale* found in high densities at the *Carex*-dominated fen grouped closely together. This high overlap of many species found at both locations resulted in no significant difference in overall trait composition of plant species between fen sites ($F_{1,12}$ = 3.09, P = 0.105,

Table 3 Species and functional diversity indices of plant species and their traits measured during vegetation surveys of a nutrient poor (*Sphagnum*-dominated) and intermediate nutrient (*Carex*-dominated) fen sites in central Ontario, Canada

Diversity Index	*Carex*-dominated fen average (± SE)	*Sphagnum*-dominated Fen Average (± SE)	$F_{(1,8)}$	P
Species richness (S)	6.0 (1.1)	15.2 (1.2)	50.0	**<0.001**
Percent cover (N_0)	182.3 (20.7)	218.4 (18.5)	1.79	0.218
Shannon's diversity (H)	1.04 (0.11)	1.96 (0.07)	58.3	**<0.001**
Simpson's diversity (D)	0.59 (0.05)	0.82 (0.01)	22.4	**0.001**
Pielou's evenness (J)	0.61 (0.08)	0.72 (0.03)	1.83	0.213
Functional richness (FRic)*	2.06 (0.40)	16.9 (0.02)	1351	**< 0.001**
Functional evenness (FEve)*	0.50 (0.14)	0.59 (0.09)	0.273	0.615
Functional divergence (FDiv)*	0.89 (0.06)	0.79 (0.03)	2.12	0.185
Functional dispersion (FDis)*	1.96 (0.34)	2.49 (0.14)	2.06	0.189
Rao's quadratic entropy (Q)	0.32 (0.03)	0.41 (0.00)	9.66	0.015
Functional redundancy (D-Q)	0.26 (0.02)	0.42 (0.01)	33.4	**< 0.001**

Bold denotes significant difference based on one-way analysis of variance

FRic volume of functional space occupied by species in the community

FEve regularity of the distribution of trait abundances within functional space

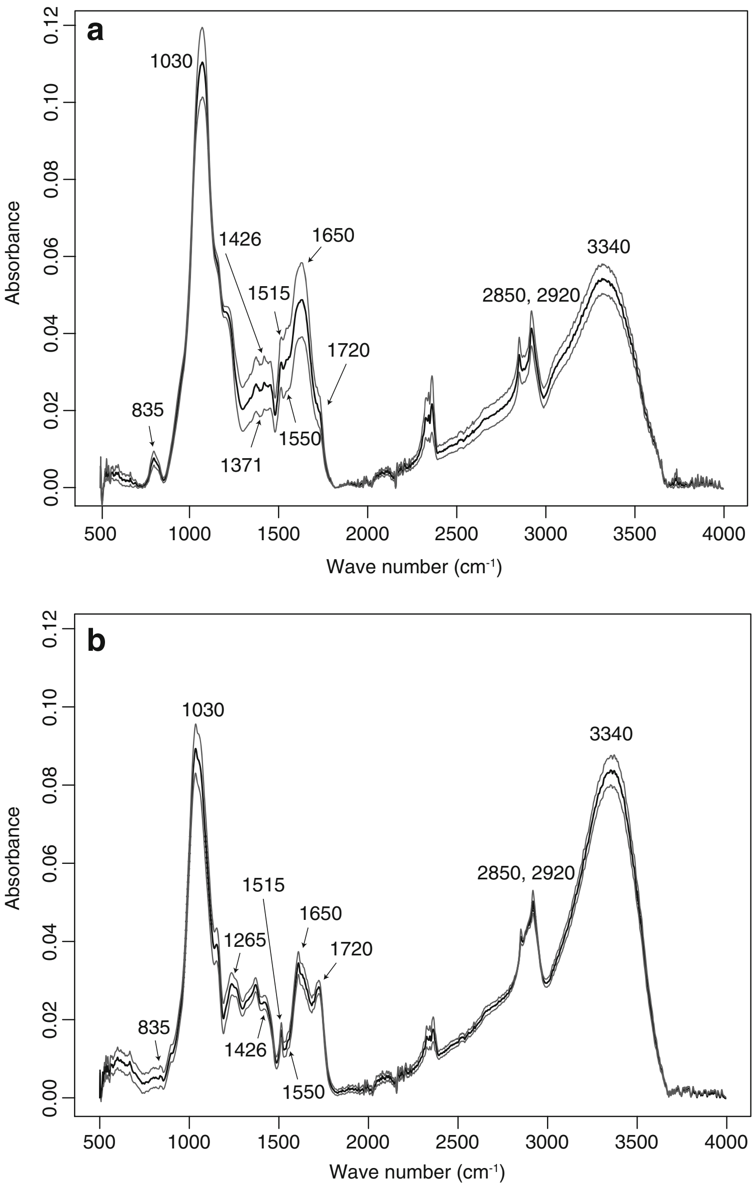
FDiv spread of distribution of trait abundances within functional space

FDis mean distance of each species and the centroid of all species in the community in multidimensional trait space

Q sum of distances between species weighted by relative abundance

* denotes indices that were calculated using the 14 species that had C and N data; not all species could be included in C and N analyses due to insufficient material

Fig. 1 Organochemical spectral properties (means ±95% confidence intervals) produced by Fourier transform infrared (FTIR) spectroscopy of a) *Carex*-dominated fen peat and b) *Sphagnum*-dominated fen peat collected near White River, Ontario, Canada. A list of peaks and associated compounds are found in Table 4



$R^2 = 0.205$). However, the species with greatest dissimilarity in trait composition were between *Sphagnum* spp. dominating at the *Sphagnum*-dominated fen and *Carex* spp. dominating at the *Carex*-dominated fen site. Traits driving the separation of *Sphagnum* species were high SLA values, while high leaf mass and low C:N was associated with the *Carex* species (Fig. 2a).

Species, trait, and environment relationships

At the individual species level, we found strong species-environment links with all plant species found in the *Sphagnum*-dominated fen plots clustering tightly, while the *Carex*-dominated fen plant species were more variable driven by the presence of *C. oligosperma* found in high abundance at a single plot, but not strongly associated with any specific environmental variable (Fig. 2b). The variance in the plant species response to environmental conditions explained by CCA axis 1 was 46.4% and demonstrates the separation between *Sphagnum*-dominated (positive values of axis 1) and *Carex*-dominated fen types (negative values of axis 1). Plant species found in the *Sphagnum*-dominated fen were associated with high moisture, greater microbial biomass, and higher peat-soil

Table 4 Mean (± SE) absorbance intensities and assigned absorbance bands for organic chemical compounds in a *Sphagnum*-dominated and *Carex*-dominated fen peat identified using Fourier transform infrared (FTIR) spectroscopy

Wave number (cm^{-1})	Compounds	*Carex*-dominated fen average (± SE)	*Sphagnum*-dominated fen average (± SE)	$F_{(1,8)}$	*P*
720	Long chain alkanes	0.001 (0.00)	0.005 (0.00)	12.2	**0.008**
835	Lignin	0.004 (0.01)	0.005 (0.00)	0.651	0.443
1030	Polysaccharides	0.092 (0.00)	0.089 (0.00)	0.639	0.447
1265	Lignin	0.027 (0.00)	0.028 (0.00)	0.122	0.736
1371	Phenolic (lignin) and aliphatics	0.027 (0.00)	0.029 (0.00)	0.351	0.570
1426	Humic acids (caryboxylate/carboxylic structures)	0.027 (0.00)	0.024 (0.00)	0.511	0.495
1450	Phenolic (lignin) and aliphatics	0.027 (0.00)	0.020 (0.00)	3.91	0.083
1475	Alkyl groups (waxes)	0.020 (0.00)	0.011 (0.00)	12.6	**0.007**
1515	Lignin-like/phenolic structures	0.033 (0.00)	0.017 (0.00)	20.1	**0.002**
1550	Proteinaceous	0.033 (0.00)	0.015 (0.00)	19.1	**0.002**
1650	Aromatics	0.046 (0.00)	0.029 (0.00)	14.0	**0.006**
1708	Free organic acids	0.022 (0.00)	0.027 (0.00)	4.31	0.068
1720	Carboxylic acids, aromatic esters	0.021 (0.00)	0.028 (0.00)	10.8	**0.011**
2850	Aliphatic fats, wax, lipids	0.035 (0.00)	0.041 (0.00)	7.27	**0.027**
2920	Aliphatic fats, wax, lipids	0.041 (0.00)	0.050 (0.00)	9.53	**0.015**
3340	Cellulose	0.054 (0.00)	0.083 (0.00)	125.5	**<0.000**
Humification indices					
1515/1030	Phenolic index	0.4 (0.1)	0.2 (0.0)	14.74	**0.005**
1650/1030	Aromatic index	0.6 (0.1)	0.4 (0.0)	7.82	**0.023**
1720/1030	Carboxylic acid index	0.2 (0.0)	0.3 (0.0)	11.47	**0.009**
2920/1030	Lipid index (aliphatics)	0.5 (0.0)	0.6 (0.0)	5.56	**0.046**

carbon content. *Carex* species (*C. stricta*, *C. lasiocarpa*) and the shrub sweet gale (*M. gale*) were associated with higher peat-soil nitrogen and pH, the presence of phenolics, and microbial activity (respiration). Axis 2 of the CCA ordination explained an addition 28.0%, which is attributed to the occurrence of *C. oligosperma* at a single plot. *Carex oligosperma* was not strongly associated with any specific environmental variable, but was positively associated with nitrate and pH, and negatively associated with peat-soil carbon content.

The first axes of the RLQ analysis explained 95.4% of the cross-matrix of species traits and environmental variables, separating peat-soil, plant species, and associated plant traits of the two fen types (Fig. 3). In all the RLQ biplots (Fig. 3a–c), the positive (right) side of the biplot is associated with the *Carex*-dominated fen sites, while the negative (left) side of the biplot is associated with the *Sphagnum*-dominated fen sites. Correlating the spatial location of the objects between the biplots can make relationships between environmental, species, and trait variables. The environmental data (R) axis 1 explained 46% variation with pH and nitrate (positive axis 1) and moisture and total carbon (negative axis 1), and four organochemical peat properties (aromatics and phenolics vs. cellulose, carboxylic acids) as main drivers separating the *Carex*-dominated and *Sphagnum*-dominated fens, respectively (Fig. 3a). The species data (L) was explained with cumulative 74% variation (axis 1: 46%, axis 2: 28%), with axis 1 being driven by *C. stricta* (positive values) vs. *Sphagnum* spp. (negative values) (Fig. 3b). For the results of the trait data (Q) axis 1 explained 90% of the trait variation, where height of the dominant vegetation was the main driver (Fig. 3c), and was strongly associated with the presence of *Carex* spp. (particularly *C. stricta*) found in the *Carex*-dominated fen. The initial ordinations used in the RLQ performed on the species × plot, environmental variables × plot, and trait × species data are provided in the supplementary information (Fig. S1a–c).

The Monte Carlo permutations of the variances explained by the RLQ analysis found that both sites and species were significantly explained by trait-environmental relationships (*P* = 0.010, *P* = 0.006). The model where both species and sites were combined was also significantly explained by trait-environment relationships (*P* = 0.004). The redundancy analysis

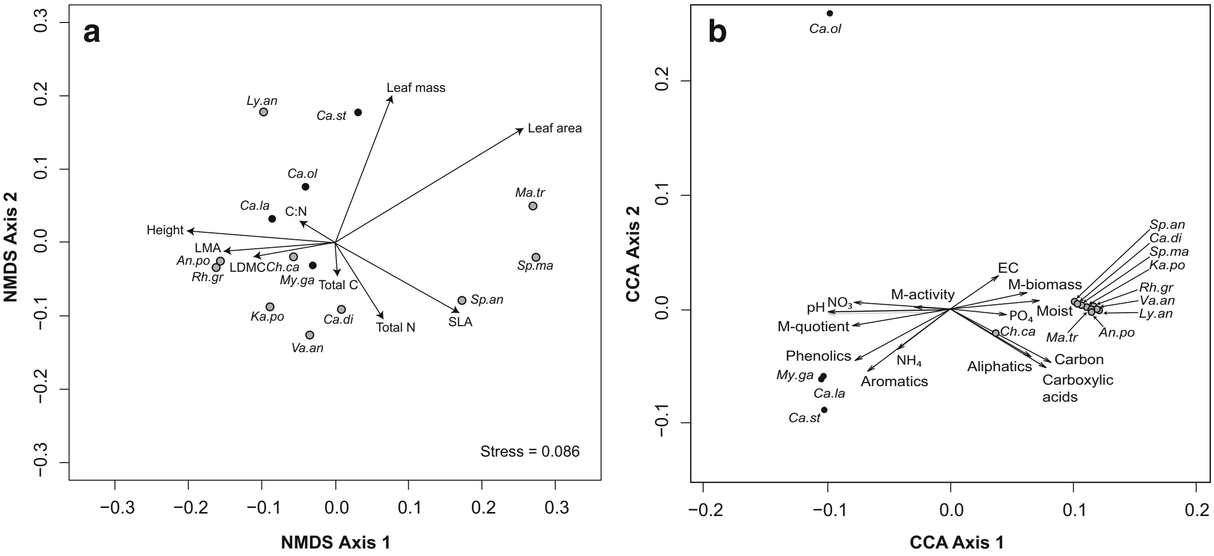


Fig. 2 Ordination biplots of (**a**) species-trait similarities and (**b**) species relationships to peat-soil environmental variables. (**a**) Non-metric multi-dimensional scaling (NMDS) plots showing trait similarity of species occurring in *Carex*-dominated intermediate and *Sphagnum*-dominated fen sites. Species designated with black circles are solely or predominantly found in the *Carex*-dominated fen site, while species designated with grey circles are solely or predominantly found in the *Sphagnum*-dominated site. (**b**) Canonical correspondence analysis (CCA) demonstrating the relationship between the peatland plant species and environmental variables across the two fen sites. Species codes are given in the caption of Fig. 3. Along axis 1 in this CCA, the positive (right) side of the biplot is associated with the *Sphagnum*-dominated fen sites, while the negative (left) side of the biplot is associated with the *Carex*-dominated fen sites. For axis 2, the *Sphagnum*-dominated fen sites (not shown for clarity) group closely with the environmental and plant variables, while a single plot within the *Carex*-dominated fen was associated with high abundance of *C. oligosperma*, but was not strongly associated with any specific environmental variable

(RDA) of trait CWMs and environmental variables demonstrated similar relationships to the RLQ (Fig. 4). The first axis representing a separation between *Sphagnum*-dominated and *Carex*-dominated fen types explained 44.8% of the variation in trait relationships with environmental conditions, while the second axis, explained 32.5% additional variation.

Discussion

In boreal peatlands, plants leave a legacy in partially decomposed plant material as peat. We show that plant traits of two different dominant plant functional types significantly explain much of the peat-soil environment, particularly numerous organochemicals that are indicators of decomposition dynamics. Using FTIR spectra we observed a dichotomy in peat constituents between the *Sphagnum*-dominated nutrient poor and the *Carex*-dominated intermediate nutrient fen sites, where the *Carex*-dominated fen had larger amount of 'decomposition products' while there was a larger proportion of 'undecomposed materials' (e.g. wax, cellulose) in the *Sphagnum*-dominated site. Furthermore, differences between the two sites were significantly explained by the RLQ relationship between plant traits and peat-soil variables, and that this trait-mediated environment was significantly explain by plant species composition at these sites driven by the dominant *Carex* and *Sphagnum* spp. This suggests that the dominant plant species traits exert influence on their environment (aboveground-to-belowground), and that these feedbacks between above- and belowground systems are reciprocal, as anticipated for ecosystem engineers.

Chemical composition of plant litter is important for the rate of litter decomposition and nutrient cycling. Chemical traits of leaves, mainly different nutrients (e.g. N) and carbon compounds (e.g. phenolics, carboxylic acids) interact directly or indirectly with the biotic and abiotic environment to modulate pH and nutrient levels. Specifically, we found differences in pH, organic matter and several organochemical properties of the peat that can be directly related to mechanisms underlying peat accumulation (or its inverse, decomposition). It is generally agreed that *Carex* litter decomposes more rapidly than *Sphagnum* litter due to more labile, water-

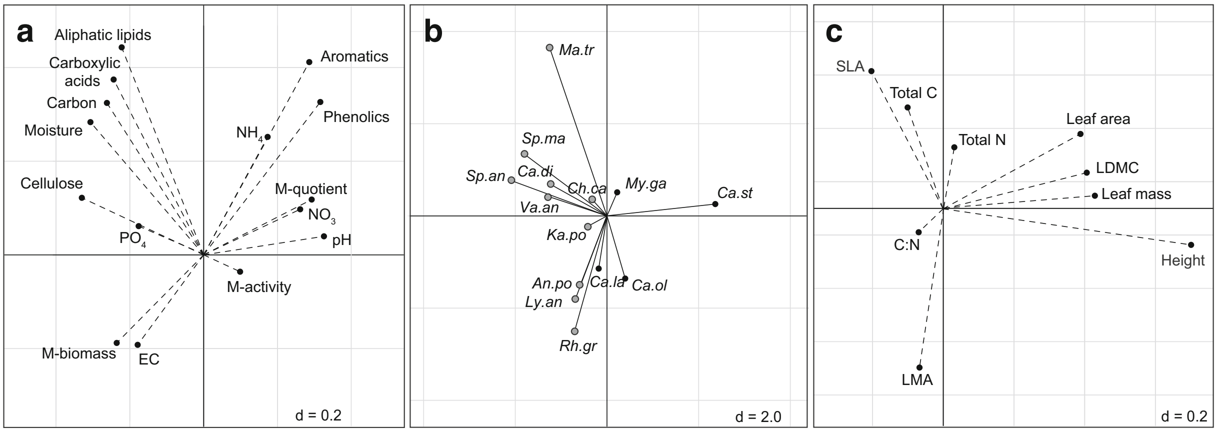
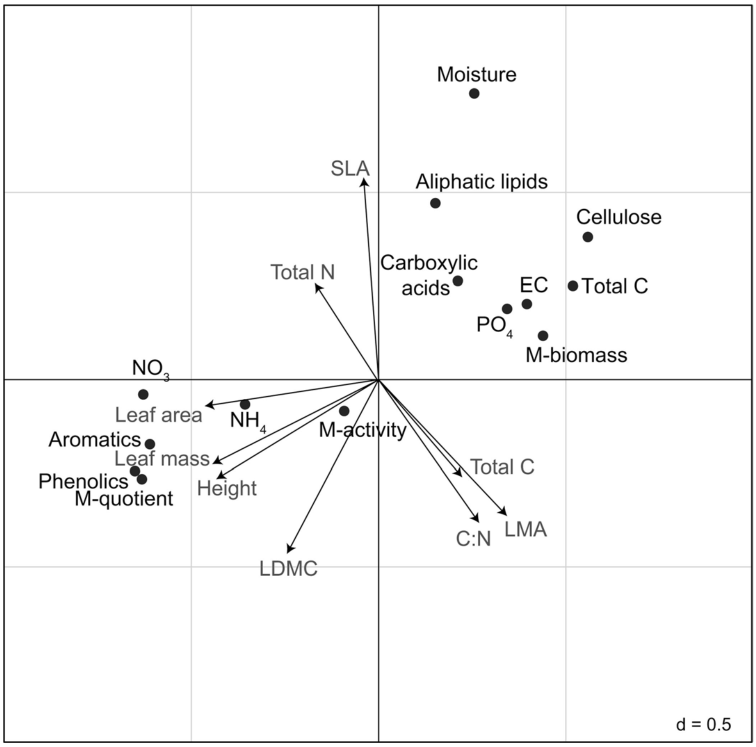


Fig. 3 RLQ ordination triplot showing relationships among (**a**) peat-soil conditions, (**b**) plant species, and (**c**) plant traits. Links can be made between peat variables, plant traits and species by correlating the spatial location of the objects between the plots. In all biplots, the positive (right) side of the biplot is associated with the *Carex*-dominated fen sites, while the negative (left) side of the biplot is associated with the *Sphagnum*-dominated fen sites. M-biomass, M-activity, and M-quotient represent the microbial biomass, respiration and metabolic quotient respectively. 'Carbon' represents organic matter as measured by Loss-on-Ignition. Species codes are as follows: An.po: *Andromeda polifolia*, Ca.di: *Carex disperma*, Ca.ol: *Carex oligosperma*, Ca.la: *Carex lasiocarpa*, Ca.st: *Carex stricta*, Ch.ca *Chamaedaphne calyculata*, Ka.po: *Kalmia polifolia*, Ly.an: *Lycopodium annotinum*, Ma.tr: *Maianthemum trifolium*, My.ga: *Myrica gale*, Rh.gr: *Rhododendron groenlandicum, Sp.an: Sphagnum angustifolium, Sp.ma: Sphagnum magellanicum*, Va.an: *Vaccinium angustifolium*. SLA = specific leaf area, LDMC = leaf dry matter content, LMA = leaf mass per area

soluble carbon compounds of the respective plant litter (Del Giudice and Lindo 2017). This points to enhanced nutrient cycling and availability, consistent with higher available nitrogen in peat from the *Carex*-dominated fen. However, we also observed greater utilization of organic materials within the belowground peat system through greater microbial carbon use efficiency (metabolic quotient). Recently it has been suggested that faster decomposition in *Carex*-dominated peatlands may be stimulated through priming effects of low molecular weight phenolics associated with root exudation (Fenner et al. 2007; Dieleman et al. 2016). The high phenolic compounds in peat observed at the *Carex*-dominated fen site is consistent with high root biomass in the peat, in addition to laboratory studies that correlated high phenolic compound concentrations with vascular plant expansion under experimental climate change scenarios in boreal peatlands (Robroek et al. 2016; Dieleman et al. 2016). Similarly, Scheffer et al. (2001) also observed peatland soluble phenolics to be much higher in litter of *Carex* species than that of *Sphagnum*. Our observation of high phenolics coincided with high LDMC as a functional trait in the RLQ analysis, and as LDMC is considered an indicator of leaf 'toughness' is likely also linked to the presence of ericaceous shrubs such as sweet gale at the *Carex*-dominated fen site. At the same time, LDMC is a trait that can be protective against wind, which is advantageous for *Carex*'s tall height.

While *Sphagnum* litter is typically nutrient poor (Hoorens et al. 2002), and litter C:N ratios are thought to be a predictor of long-term decomposition rates for peatland plants (Limpens and Berendse 2003), only minor differences between species C:N ratios were observed in this study. Rather the *Sphagnum*-dominated fen site scored higher in peat constituents for aliphatic lipids, and carboxylic acid groups that can be attributed to the presence of *Sphagnum*. *Sphagnum* have a strong lipid coating associated with their cell walls (van Breemen 1995), and is composed of polysaccharides possessing carboxylic acid groups, which are largely responsible for its acidic nature that facilitates an engineering of acidic environments (Eppinga et al. 2009). Compounds such as sphagnum acid (p-hydroxy-beta-(carboxymethyl)-cinnamic acid) can have a pathogenic effect on bacteria (Hájek et al. 2011) and anti-microbial properties (Verhoeven and Liefveld 1997), leading to reduced decomposition rates (Verhoeven and Toth 1995); yet our *Sphagnum*-dominated poor fen has greater microbial biomass (but lower metabolic quotient). However, the observed aliphatic lipids, fats and waxes may not be entirely resulting from the dominant *Sphagnum*. Ericaceous shrubs such as leatherleaf, *Andromeda polifolia* L. (bog rosemary), and *Kalmia polifolia* Wangenh. (bog laurel)

Fig. 4 Redundancy analysis (RDA) ordination biplot of peatland plant trait community-weighted means (CWMs) associated with peat-soil environmental variables (circles)



that were observed at the *Sphagnum*-dominated site have leaves that are covered with thick epicuticular waxes (Jacquemart 1998), and may contain a considerable amount of lipids (Pancost et al. 2002). The high abundance of pH-lowering chemical traits of *Sphagnum*, coupled with high proportions of cellulose in the FTIR spectra, point to relatively slower rates of decomposition at the *Sphagnum*-dominated fen, slower nutrient cycling, and enhanced C storage.

Spectroscopic techniques are being increasingly used to not only characterise constituents of peat (soil organic matter), but also infer peat forming process and decomposition at the micro-level scale (Heller et al. 2015). Belowground, the relative abundances of the chemical compounds identified by FTIR spectroscopy serve as a strong mechanistic link between plant traits (e.g. leaf chemical properties) and potentially ecosystem level processes (e.g. nutrient cycling). However, it is probably that some ecosystem engineering of the different belowground peat environments is generated through functional traits of the dominant species not measured in our study. For instance, it has long been known that *Sphagnum* possesses physical (morphological, structural and anatomical) traits that contribute to the engineering of wetness, acidic and nutrient levels in peatlands. *Sphagnum* branch and stem morphology mediate water transport upward by wicking water through the spaces between leaves, and branches and stem in the upper *Sphagnum* canopy (acrotelm) (Rydin and Jeglum 2013), but decrease water flow in subsurface peat when the finely porous tissue of lower *Sphagnum* canopy (catotelm) collapses leading to decreased hydraulic conductivity, anoxic environments and decreased decomposition rates (Belyea and Clymo 2001). *Sphagnum* has long been purported to acidify peat-soil conditions through acidic compounds within *Sphagnum* cell walls (e.g. uronic acids) (Painter 1983), which gives *Sphagnum* its high CEC and facilitates acidification (Clymo 1963). Similarly, physical and structural traits of *Carex* are shown to mitigate effects of anoxia through stratified litter accumulations that increase water flow thus reducing water-logging (Crain and Bertness 2005), and increasing pH as a result of increased hydrologic connectivity (Eppinga et al. 2009).

Among the species and functional diversity indices calculated, only species richness, functional richness, Rao's and functional redundancy differed between the two fen sites, with the *Sphagnum*-dominated fen being greater in all indices, and these indices being somewhat linked. Rao's describes the similarity (or dissimilarity) among species of a community in trait space while taking into consideration the diversity and abundances of the species (Botta-Dukát 2005); Rao's is therefore related to both species richness and functional redundancy. Functional redundancy could increase in a community with increasing species richness because of an expectation of increasing overlap of species functionality with another species (i.e. not all species are expected to be functionally unique). In highly diversity systems, high species richness may decrease the average functional dissimilarity among species, and reduce Rao values while increasing functional redundancy. However, this was not the case here, possibly because, while the *Sphagnum*-dominated fen was more than twice as species rich as the *Carex*-dominated fen, neither of these peatlands is considered highly diverse compared to many other terrestrial habitats. Furthermore, the different *Carex* spp. had greater variability in the traits we measured than the *Sphagnum* spp. that occurred at our sites.

While trait-environmental relationships explained differences among our peatland sites, sites were not generally different with respect to functionality at the community level. Rather, traits driving site differences were associated with the dominance of *Sphagnum* or *Carex* spp. Significant differences in overall peat-soil environments, plant species composition, and plant functional traits were driven by these dominant plant species. Despite low similarity of species composition between *Sphagnum*-dominated and *Carex*-dominated fen sites there was significant overlap of trait distribution among species observed in both the community-level ordination and many calculated functional indices, indicating that the same set of traits are being represented at both fen sites, and suggesting that the majority of non-dominant species share similar functional trait values between sites. Yet, impacts of both *Sphagnum* and *Carex* as ecosystem engineers become apparent when the fen sites are interpreted from a species-level functional perspective, where both taxonomically and functionally different plant communities dominated by *Carex* spp. or *Sphagnum* spp. were associated with differences in peat environments. Further to this, while *S. magellanicum* and *S. angustifolium* consistently plotted together in ordination space, it was primarily *C. stricta* that drove trait-environmental relationships in the *Carex*-dominated fen despite *C. oligosperma* and *C. lasiocarpa* also being present at this site. The congeneric *C. disperma* was the only *Carex* found at the *Sphagnum*-dominated site and functionally is quite distinct from the other *Carex* spp. in being much shorter with a fine rooting structure (see Supplementary Information Table S1).

Conclusion

Feedbacks in aboveground-belowground systems are increasingly being recognised as drivers of ecosystem processes (Wardle et al. 2004; Jassey et al. 2013). Understanding *Sphagnum* and *Carex* as ecosystem engineers of boreal peatlands will enhance our understanding of mechanisms underpinning peatland plant community dynamics. In both peatland types, aboveground plant traits of the key ecosystem engineer drove properties of the belowground peat environment. As relatively rapid shifts in peatland plant communities under future climate change conditions are expected, specifically from moss- to sedge-dominated plant communities (Dieleman et al. 2015), research should focus on the mechanistic link between plant traits (e.g. leaf chemical properties) and ecosystem level processes (e.g. carbon storage) that govern plant-soil feedbacks, as change at the ecosystem level will largely be mediated by key species, such as these ecosystem engineers. Belowground peat organochemical constituents between the nutrient-poor *Sphagnum*-dominated fen and the intermediate nutrient *Carex*-dominated fen sites helped reveal differences in decomposition rates and carbon use efficiency, and thus the potential for carbon storage.

Acknowledgements We are grateful for funding from the Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant program (ZL) and the Ontario Ministry of Research, Innovation and Science, Early Researcher Award (ZL). We thank Dr. J. McLaughlin (Ontario Ministry of Natural Resources and Forestry) for access to the White River, ON field site and his continued support with our research program. Many thanks to Maara Packalen, John Perron, and Sam Campagna for assistance in analyses performed at the Ontario Ministry of Natural Resources and Forestry in Sault Ste. Marie Ontario, to Aaron Craig for his assistance with analyses at Western, and Catherine Dieleman for comments on a previous version of this manuscript. We also thank Dr. Brian Branfireun, Mikhail Mack and Jing Tian for continued support.

References

Aerts R, Verhoeven JTA, Whigham DF (1999) Plant-mediated controls on nutrient cycling in temperate fens and bogs. Ecology 80:2170–2181. doi:10.1890/0012-9658(1999)080[2170:PMCONC]2.0.CO;2

Anderson JPE, Domsch KH (1978) A physiological method for the quantitative measurement of microbial biomass in soils. Soil Biol Biochem 10:215–221. doi:10.1016/0038-0717(78)90099-8

Artz RRE, Chapman SJ, Robertson AHJ, Poots JM, Laggoun-Défarge F, Gogo S, Comon L, Disnar JR, Francez AJ (2008)

FTIR spectroscopy can be used as a screening tool for organic matter quality in regenerating cutover peatlands. Soil Biol Biochem 40:515–527. doi:10.1016/j.soilbio.2007.09.019

Belyea LR, Clymo RS (2001) Feedback control on the rate of peat formation. Proc R Soc Lond [Biol] 268:1315–1321. doi:10.1098/rspb.2001.1665

Bond-Lamberty B, Gower ST (2007) Estimation of stand-level leaf area for boreal bryophytes. Oecol 151:584–592. doi:10.1007/s00442-006-0619-5

Botta-Dukát Z (2005) Rao's quadratic entropy as a measure of functional diversity based on multiple traits. J Veg Sci 16: 533–540. doi:10.1111/j.1654-1103.2005.tb02393.x

Bouma TJ, Temmerman S, van Duren LA, Martini E, Vandenbruwaene W, Callaghan DP, Balke T, Biermans G, Klaassen PC, Vam Steeg P, Dekker F, van de Koppel J, de Vries MB, PMJ H (2012) Organism traits determine the strength of scale-dependent bio-geomorphic feedbacks: a flume study on three intertidal plant species. Geomorphology 180–181:57–65. doi:10.1016/j.geomorph.2012.09.005

Bragazza L, Parisod J, Buttler A, Bardgett R (2013) Biogeochemical plant-soil microbe feedback in response to climate warming in peatlands. Nat Clim Chang 3:273–277. doi:10.1038/NCLIMATE1781

Bragazza L, Buttler A, Robroek BJM, Albrecht R, Zaccone C, Jassey VEJ, Signarbieux C (2016) Persistent high temperature and low precipitation reduce peat carbon accumulation. Glob Change Biol 22:4114–4123. doi:10.1111/gcb.13319

van Breemen N (1995) How *Sphagnum* bogs down other plants. Trends Ecol Evol 10:270–275. doi:10.1016/0169-5347(95)90007-1

Broder T, Blodau C, Biester H, Knorr KH (2012) Peat decomposition records in three pristine ombrotrophic bogs in southern Patagonia. Biogeosciences 9:1479–1491. doi:10.5194/bg-9-1479-2012

Chambers FM, Beilman D, Yu Z (2011) Methods for determining peat humification and for quantifying peat bulk density, organic matter and carbon content for palaeostudies of climate and peatland carbon dynamics. Mires Peat 7:1–10

Clarke KR (1993) Non-parametric multivariate analyses on changes in community structure. Aust J Ecol 18:117–143. doi:10.1111/j.1442-9993.1993.tb00438.x

Clymo RS (1963) Ion exchange in *Sphagnum* and its relation to bog ecology. Ann Bot (London) 27:309–324. doi:10.1093/oxfordjournals.aob.a083847

Cornwell WK, Ackerly DA (2009) Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. Ecol Monogr 79:109–126. doi:10.1890/07-1134.1

Crain CM, Bertness MD (2005) Community impacts of a tussock sedge: is ecosystem engineering important in benign habitats? Ecology 86:2695–2704. doi:10.1890/04-1517

Del Giudice R, Lindo Z (2017) Short-term leaching dynamics of three peatland plant species reveals how shifts in plant communities may affect decomposition processes. Geoderma 285:110–116. doi:10.1016/j.geoderma.201609028

Dieleman CM, Branfireun BA, McLaughlin JW, Lindo Z (2015) Climate change drives a shift in peatland ecosystem plant community: implications for ecosystem function and resilience. Glob Change Biol 21:388–395. doi:10.1111/gcb.12643

Dieleman CM, Branfireun BA, McLaughlin JW, Lindo Z (2016) Enhanced carbon release under future climate conditions in a peatland mesocosm experiment: the role of phenolic compounds. Plant Soil 400:81–91. doi:10.1007/s11104-015-2713-0

Dolédec S, Chessel D, Ter Braak CJF, Champely S (1996) Matching species traits to environmental variables: a new three-table ordination method. Environ Ecol Stat 3:143–166. doi:10.1007/BF02427859

Dray S, Dufour AB (2007) The ade4 package: implementing the duality diagram for ecologists. J stat Softw 22:1–20. doi:10.18637/jss.v022.i04

Ehrenfeld JG, Ravit B, Elgersma K (2005) Feedback in the plant-soil system. Annu Rev Environ Resour 30:75–115. doi:10.1146/annurev.energy.30.050504.144212

Emery SM, Rudgers JA (2014) Biotic and abiotic predictors of ecosystem engineering traits of the dune building grass, *Ammophila breviligulata*. Ecosphere 5:87. doi:10.1890/ES13-00331.1

Eppinga MB, Rietkerk M, Wassen MJ, De Ruiter PC (2009) Linking habitat modification to catastrophic shifts and vegetation patterns in bogs. Plant Ecol 200:53–68. doi:10.1007/s11258-007-9309-6

Fenner N, Ostle NJ, McNamara N, Sparks T, Harmens H, Reynolds B, Freeman C (2007) Elevated CO_2 effects on peatland plant community carbon dynamics and DOC production. Ecosystems 10:635–647. doi:10.1007/sl0021-007-9051-x

Garnier E, Navas ML, Grigulis K (2016) Plant functional diversity: organism traits, community structure and ecosystem properties. Oxford University Press, Oxford

Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am Nat 111:1169–1194. doi:10.1086/283244

Hájek T, Ballance S, Limpens J, Zijlstra M, Verhoeven JTA (2011) Cell-wall polysaccharides play an important role in decay resistance of *Sphagnum* and actively depressed decomposition in vitro. Biogeochemistry 103:45–57. doi:10.1007/s10533-010-9444-3

Heller C, Ellerbrock RH, Roßkopf N, Klingenfuß C, Zeitz J (2015) Soil organic matter characterization of temperate peatland soil with FTIR-spectroscopy: effects of mire type and drainage intensity. Eur J Soil Sci 66:847–858. doi:10.1111/ejss.12279

Hoorens B, Aerts R, Stroetenga M (2002) Litter quality and interactive effects in litter mixtures: more negative interactions under elevated CO_2? J Ecol 90:1009–1016. doi:10.1046/j.1365 2745.2002.00732.x

Jacquemart AL (1998) *Andromeda polifolia* L. J Ecol 86:527–541. doi:10.1046/j.1365 2745.1998.00274.x

Jassey VEJ, Chiapusio G, Binet P, Buttler A, Laggoun-Défarge F, Delarue F, Bernard N, Mitchell EA, Toussaint ML, France AJ, Gilbert D (2013) Glob Change Biol 19:811–823. doi:10.1111/gcb.12075

Jassey VEJ, Lamentowicz Ł, Robroek BJM, Gabka M, Rusińska A, Lamentowicz M (2014) Plant functional diversity drives niche-size-structure of dominant microbial consumers along a poor to extremely rich fen gradient. J Ecol 102:1150–1162. doi:10.1111/1365-2745.12288

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373–386. doi:10.2307/3545850

Jones CG, Lawton JH, Shachak M (1997) Positive and negative effects of organisms as physical ecosystem engineers.

Ecology 78:1946–1957. doi:10.1890/00129658(1997)078[1946:PANEOO]2.0.CO;2

Kleyer M, Dray S, de Bell F, Lepš J, Pakeman RJ, Strauss B, Thuiller W, Lavorel S (2012) Assessing species and community functional responses to environmental gradients: which multivariate methods? J Veg Sci 23:805–821. doi:10.1111/j.1654-1103.2012.01402.x

Klironomos JN (2002) Feedback with soil biota contributes to plant rarity and invasiveness in communities. Nature 417:67–70. doi:10.1038/417067a

Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. Ecology 91:299–305. doi:10.1890/08-2244.1

Legasy K (1995) Forest plants of northeastern Ontario. Lone Pine Press, Edmonton

Limpens J, Berendse F (2003) How litter quality affects mass loss and N loss from decomposing *Sphagnum*. Oikos 103:537–547. doi:10.1034/j.1600-0706.2003.12707.x

McGill BJ, Enquist BJ, Weiher E, Westoby M (2006) Rebuilding community ecology from functional traits. Trends Ecol Evol 21:178–185. doi:10.1016/j.tree.2006.02.002

McLaughlin JW, Webster KL (2010) Alkalinity and acidity cycling and fluxes in an intermediate fen peatland in northern Ontario. Biogeochemistry 99:143–155. doi:10.1007/s10533-009-9398-5

Myers B, Webster KL, McLaughlin JW, Basiliko N (2012) Microbial activity across a boreal peatland nutrient gradient: the role of fungi and bacteria. Wetl Ecol Manag 20:77–88. doi:10.1007/s11273-011-9242-2

Newmaster SG, Harris AG, Kershaw LJ (1997) Wetland plants of Ontario. Lone Pine Press, Edmonton

Niemeyer J, Chen Y, Bollag JM (1992) Characterization of humic acids, composts, and peat by diffuse reflectance Fourier-transform infrared spectroscopy. Soil Sci Soc Am J 56:135–140. doi:10.2136/sssaj1992.03615995005600010021x

Painter TJ (1983) Residues of D-*lyxo*-5-hexosulopyranuronic acid in *Sphagnum* holocellulose, and their role in cross-linking. Carbohydr Res 124:135–140. doi:10.1016/0008-6215(83)88373-6

Pancost RD, Baas M, van Geel B, Sinninghe Damste JS (2002) Biomarkers as proxies for plant inputs to peats: an example from a sub-boreal ombrotrophic bog. Org Geochem 33:675–690. doi:10.1016/S0146-6380(02)00048-7

Pérez-Harguindeguy N, Diaz S, Garnier E et al (2013) New handbook for standardized measurement of plant functional traits worldwide. Aust J Bot 61:167–234. doi:10.1071/BT02124

Petchey OL, Gaston KJ (2002) Functional diversity (FD), species richness and community composition. Ecol Lett 5:402–411. doi:10.1046/j.1461-0248.2002.00339.x

Pillar VD, Blanco CC, Müller SC, Sosinski EE, Joner F, Duarte LDS (2013) Functional redundancy and stability in plant communities. J Veg Sci 24:963–974. doi:10.1111/jvs.12047

R Development Core Team (2013) R: A Language and Environment for Statistical Computing. ISBN 3–900051–07-0. R Foundation for Statistical Computing, Vienna, Austria.

Reich PB (2014) The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. J Ecol 102:275–301. doi:10.1111/1365-2745.12211

Robroek BJM, Albrecht RJH, Hamard S, Pulgarin A, Bragazza L, Buttler A, Jassey VEJ (2016) Peatland vascular plant functional types affect dissolved organic matter chemistry. Plant Soil 407:135–143. doi:10.1007/s11104-015-2710-3

Rochefort L, Isselin-Nondedeu F, Boudreau S, Poulin M (2013) Comparing survey methods for monitoring vegetation change through time in a restored peatland. Wetl Ecol Manag 21:71–85. doi:10.1007/s11273-012-9280-4

Rydin K, Jeglum JK (2013) The biology of peatlands, 2nd edn. Oxford University Press, Oxford

Scheffer RA, van Logtestjin RSP, Vernhoeven JTA (2001) Decomposition of *Carex* and *Sphagnum* litter in two mesotrophic fens differing in dominant plant species. Oikos 92:44–54. doi:10.1034/j.1600-0706.2001.920106.x

Shipley B, de Bello F, Cornelissen JHC, Laliberté LDC, Reich PB (2016) Reinforcing loose foundation stones in trait-based plant ecology. Oceologia 180:923–931. doi:10.1007/s00442-016-3549-x

Strack M, Price J (2009) Moisture controls on carbon dioxide dynamics of peat-*Sphagnum* monoliths. Ecohydrology 2:34–41. doi:10.1002/eco.36

Verhoeven JTA, Liefveld WM (1997) The ecological significance of organochemical compounds in *Sphagnum*. Acta Bot Neerl 46:117–130. doi:10.1111/plb.1997.46.2.117

Verhoeven JTA, Toth E (1995) Decomposition of *Carex* and *Sphagnum* litter in fens: effect of litter quality and inhibition by living tissue homogenates. Soil Biol Biochem 3:271–275. doi:10.1016/0038-0717(94)00183-2

Wardle DA, Bardgett RD, Klironomos JN, Setälä H, van der Putten W, Wall DH (2004) Ecological linkages between aboveground and belowground biota. Science 304:1629–1633. doi:10.1126/science.1094875

Westoby M, Wright IJ (2006) Land-plant ecology on the basis of functional traits. Trends Ecol Evol 21:261–268. doi:10.1016/j.tree.2006.02.004

Wright JP, Jones CG (2006) The concept of organisms as ecosystem engineers ten years on: progress, limitations and challenges. Bioscience 56:203–209. doi:10.1641/0006-3568(2006)056[0203:TCOOAE]2.0.CO;2