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Comparison of plant traits of sedges, shrubs and *Sphagnum* mosses between sites undergoing forest-to-bog restoration and near-natural open blanket bog: a pilot study

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SUMMARY

In the UK, the majority of peatlands have been damaged by drainage, agriculture, forestry plantations or erosion, compromising the ecosystem services they deliver including carbon sequestration. On the other hand, since the 1990s many projects have carried out a range of interventions to restore peatlands. In forest-to-bog restoration, tree removal and drain blocking lead to immediately visible changes. However, while some key plant species return within years, they may continue to exhibit differences in how they perform and interact with their environment. To investigate this, plant functional traits were measured and compared for *Calluna vulgaris*, *Erica tetralix*, *Eriophorum angustifolium*, *Eriophorum vaginatum*, *Sphagnum capillifolium* and *Sphagnum papillosum* collected in an open blanket bog, a forestry plantation and two forest-to-bog restoration sites in northern Scotland. Significantly lower specific leaf area and chlorophyll content, and higher leaf dry matter content, were found in the open bog site compared with plantation and forest-to-bog sites. This could be related to nutrient enrichment derived from brash and needle decomposition in the latter sites, suggesting a lasting effect of coniferous plantations even after decades of restoration management. Altered plant functional traits may have feedbacks on ecosystem processes such as litter decomposition and peat formation.

KEY WORDS: dwarf shrubs, *Eriophorum*, Flow Country, functional traits, peatland restoration

INTRODUCTION

Although peatlands cover less than 3 % of the land surface worldwide, they store approximately 455 Pg of carbon (1 Pg = 10¹⁵ g) which is roughly one-third of the total world pool of soil carbon (Gorham 1991, Loisel *et al.* 2014). Despite their importance as a soil carbon (C) store and their role in mitigating climate change, over 80 % of UK peatlands have been damaged over the years (Bain *et al.* 2011). Between 1945 and the late 1980s approximately 505,000 ha of peatland have been drained in the UK for forestry alone (Cannell *et al.* 1993). Following changes in the perception of the importance of peatlands for wildlife and carbon, several large restoration projects were initiated in the late 1990s. In order to raise the water table and to stimulate *Sphagnum* recovery and the growth of other key plant species on formerly afforested peatlands, many coniferous plantations have been removed and drains have been blocked (Andersen *et al.* 2016, Anderson *et al.* 2016).

Restoration is a long-term process. While the removal of trees and drain blocking lead to immediately visible changes, a number of legacy effects may persist and influence a range of ecosystem processes long after the restoration intervention is complete. For instance, in forest-to-bog sites, continued decomposition of needle litter and brash left on site has been shown to alter water chemistry for up to two decades and to lead to a significant rise in the concentration of plant nutrients (N, P) in pore water in the first five years following restoration (Gaffney 2017). The lower water table under forestry and associated exposure to oxic conditions enhance the mineralisation of nutrients (Sundström *et al.* 2000, Holden *et al.* 2004, Lunt *et al.* 2010) and can lead to significant changes in soil micro-organism communities (Creevy *et al.* 2017) as well as feedbacks on the nutrient cycle (Pennanen *et al.* 1999). In many systems including peatlands, changes in nutrient levels have also been shown to affect growth and various plant traits (Lavorel &

Garnier 2002, Chapin 2003, Gidman *et al.* 2006, Phoenix *et al.* 2006). In turn, plant traits can influence species interactions such as predation, mutualism and competition, and therefore possibly play a role in altering ecosystem processes (Lavorel & Garnier 2002, Chapin 2003, Bardgett *et al.* 2014). Studies have shown that some key species return following forest-to-bog restoration (Hancock *et al.* 2018). However, it is still unclear whether those species perform in the same way; in other words, if they display the same functional traits as their counterparts on natural blanket bog.

Two widely measured plant traits are specific leaf area (SLA, the ratio of leaf area to leaf dry mass) and leaf dry matter content (LDMC, the ratio of leaf dry mass to leaf fresh mass). SLA and LDMC are generally regarded as leading plant traits when it comes to understanding resource acquisition and distribution and, possibly, in predicting plant responses to nutrient stress (Wilson *et al.* 1999). Specifically, SLA reflects a trade-off between rapid production of biomass (high SLA) and conservation of nutrients (low SLA). Furthermore, high SLA leaves have been shown to be more vulnerable to herbivores and seem to be generally short-lived (Wilson *et al.* 1999, Pérez-Harguindeguy *et al.* 2013). Plants whose leaves have high SLA values seem to survive best in nutrient-rich environments, whereas plants with low SLA survive best in nutrient-poor environments. In contrast to SLA, plants with a high LDMC are relatively tough and are presumed to be more resistant to herbivory, while low LDMC can be associated with highly disturbed environments (Pérez-Harguindeguy *et al.* 2013). Apart from SLA and LDMC, other plant traits that are also related to environmental stress include leaf thickness and chlorophyll concentration (Carter & Knapp 2001).

Although there are many standardised methods for measuring these and other plant traits, due to different characteristics of plants and growth forms, not all methods might be suitable for measuring plant traits in peatland vegetation (Cornelissen *et al.* 2007). Here, we adapted methods of measuring plant traits for distinctive characteristics and growth forms of typical peatland vegetation. Our objective was to assess any potential legacy impact of forestry on plant function in forest-to-bog restoration sites. More specifically, we wanted to compare morphological traits and chlorophyll concentrations in species from three key peatland functional types (*Sphagnum* mosses, sedges and ericoid shrubs) collected from open blanket bog, afforested blanket bog and forest-to-bog restoration sites. We hypothesised that leaves of plants from restoration areas would display 1) higher SLA and lower LDMC and 2) higher

chlorophyll concentrations when compared to the open bog control, as a consequence of higher nutrient loads associated with forestry legacy and restoration management practices.

METHODS

Site description

This research was carried out in the Forsinard Flows National Nature Reserve (NNR; 58° 21' 42.6" N, 3° 53' 46.65" W) which lies within the Flow Country of Caithness and Sutherland in northern Scotland (Figure 1). The Flow Country has a temperate maritime climate with average annual precipitation 970.5 mm and mean annual temperature 11.4 °C (Kinbrace weather station 1981–2010; Hambley 2016). The reserve covers approximately 154 km² and consists of blanket bog, afforested bog with coniferous plantations established in the 1970s and 1980s, and a number of areas where forest-to-bog restoration has been carried out. Here we studied two restored areas (R19 and R13) as well as a natural open bog control (BOG) and a standing plantation on bog (FOR) (Figure 1). The restoration of R19 and R13 was initiated 19 and 13 years ago, respectively. In the following site descriptions, nomenclature of plant species follows Hill *et al.* (2004, 2007).

R19 (Talaheel) is the oldest restoration site in the NNR and covers an area of approximately 3.8 km² (Hambley 2016). This site was planted with a mixture of *Picea sitchensis* Bong. (Sitka spruce) and *Pinus contorta* Douglas ex Loudon (lodgepole pine) in 1981 before undergoing restoration in 1997/98. Due to poor growth, the trees were small enough to be felled by hand (chainsaw). They were then left to decompose on the site (Hambley 2016).

R13 (Lonielist) encompassed an area of approximately 2 km² and was planted in 1981 with a mix of *P. sitchensis* and *P. contorta* (Hambley 2016). As at Talaheel, the trees suffered from poor growth. However, the trees at Lonielist were older and, therefore, too big to be felled by hand. During 2003/04 the trees were felled by machinery and rolled into furrows (Hambley 2016, Gaffney 2017).

The BOG site (Cross Lochs) has never been planted and is actively sequestering carbon at rates within the range expected for blanket bogs (Levy & Gray 2015). Mosses (*Sphagnum* spp, *Racomitrium lanuginosum* Hewd), sedges and small shrubs dominate the vegetation, and the site is characterised by an extensive pool system.

The neighbouring Dyke plantation consists of both standing forestry and sites restored more

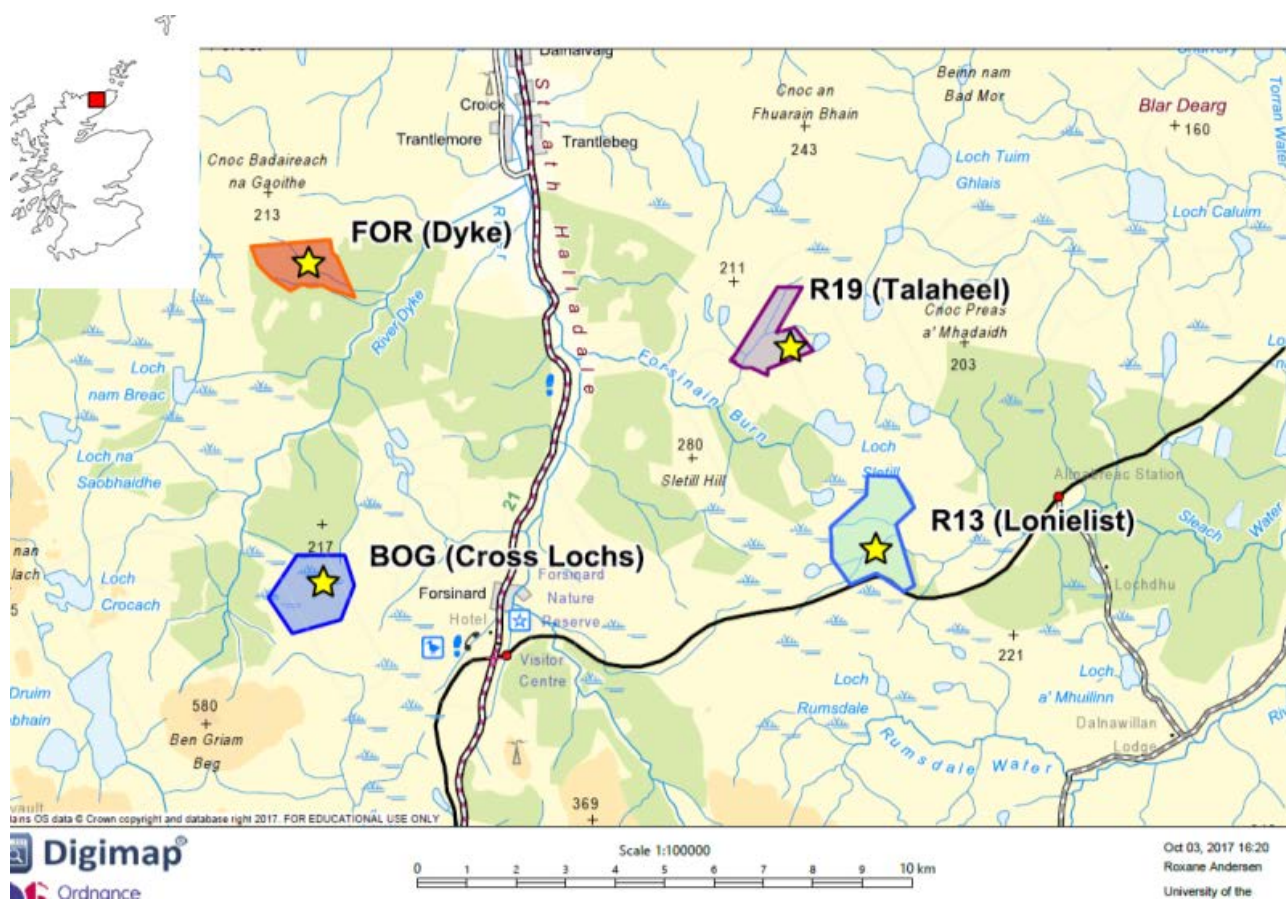


Figure 1. Map showing the four areas (BOG, R13, R19 and FOR) sampled for the study, with stars indicating location of eddy flux covariance tower for measuring GHG emissions. Insert shows location of the study area in Scotland.

recently (2014/15) (Gaffney 2017). For this research, FOR was situated in an area of standing coniferous trees in the north of Dyke and was used as a negative control. FOR is a typical example of Flow Country forestry on blanket bog, with a mixture of non-native *P. sitchensis* and *P. contorta*, planted between 1982 and 1989.

Sampling

In July 2017, 30 leaves of *Eriophorum angustifolium* L. and *Eriophorum vaginatum* L., 20 branches of *Calluna vulgaris* L. and *Erica tetralix* L. and 10 g of *Sphagnum capillifolium* (Ehrh.) Hedw. and *Sphagnum papillosum* Lindb. were collected in five random separate sampling areas within R19 and R13. The same collection was made in BOG, except that *E. angustifolium* was not found there. In addition, ten branches of *E. tetralix* and 20 leaves of *E. vaginatum* were collected in FOR (there was no *Sphagnum* or *E. angustifolium* under the canopy). Sampled areas were at least 50 m apart and in different blocks, i.e. separated by pools (BOG), by series of furrows or rides, or by areas that were not planted in R19, R13

and FOR), so were considered to be independent replicates. All the collected samples were placed in pre-labelled plastic ziplock bags and stored in a refrigerator at 4 °C until analyses were completed. The analyses were undertaken within days of collection.

Leaf destructive traits

SLA, LDMC, specific leaf mass (SLM) and leaf thickness were determined for *E. angustifolium*, *E. vaginatum*, *E. tetralix* and *C. vulgaris*. Leaf dry matter only was determined for the *Sphagnum* species. Leaves of *E. tetralix* were plucked using tweezers and 200 leaves were treated as one sample. Leaves that were damaged or not green in colour were discarded. Five replicate samples were scanned on a Canon CanoScan 4400F flat top scanner before being weighed. Leaf area was measured using the free open source software Easy-Leaf-Area (Easlon & Bloom 2014). The replicate samples were then oven dried at 60 °C for three days and weighed again. The same selection and measuring procedure was followed for *E. angustifolium* and *E. vaginatum*

leaves, except that one leaf was treated as one sample and ten replicates were used. From the gathered data, LDMC (mg g^{-1} ; dry mass/fresh mass), SLA ($\text{mm}^2 \text{mg}^{-1}$; leaf area/dry mass), SLM (mg mm^{-2} ; dry mass/leaf area) and leaf thickness (mm; fresh mass/leaf area) were calculated (Pérez-Harguindeguy *et al.* 2013). For *Sphagnum* spp. and *C. vulgaris* the capitula and a small (1 cm) terminal branch, respectively, were used to estimate dry matter content.

Chlorophyll

Chlorophyll a and b and total chlorophyll were determined for *E. angustifolium*, *E. vaginatum*, *E. tetralix* and *C. vulgaris*. Chlorophyll pigments were determined using a modification of the method described by Rajalakshmi & Banu (2015). One gram of fresh leaves was ground with 10 ml of 80 % acetone (aq) using a mortar and pestle. During grinding, another 10 ml of 80 % acetone (aq) was added to the sample. Extracts were filtered through a glass fibre plug and the absorbance measured at 645 and 663 nm. Samples with absorbance greater than 0.8 AU were diluted and measured again, and if necessary the process was repeated until absorbance was in the range 0.2–0.8 AU. The concentrations ($\mu\text{g ml}^{-1}$) of chlorophyll a, chlorophyll b and total chlorophyll in the final extracts were calculated using the following equations:

$$\text{Total chlorophyll} = 20.2(A_{645}) + 8.02(A_{663}) \quad [1]$$

$$\text{Chlorophyll a} = 12.7(A_{663}) - 2.69(A_{645}) \quad [2]$$

$$\text{Chlorophyll b} = 22.9(A_{645}) - 4.68(A_{663}) \quad [3]$$

Where samples had been diluted the calculated concentrations were multiplied by the dilution factor to give the concentration in the initial solution. Chlorophyll concentration was not measured on the leaves from FOR, as there was not enough material left after the other traits were measured. Chlorophyll was not determined for the *Sphagnum* samples.

Data analysis

Destructive traits and chlorophyll concentrations were compared across the four sites using MANOVA followed by Tukey tests. Log transformations were used where necessary but, where homoscedasticity could not be improved, non-parametric tests were employed, i.e. Kruskal Wallis and post-hoc Kruskal Nemenyi. All statistical analyses were performed in R v.3.4.4 (R Development Core Team 2017).

RESULTS

Leaf and plant traits

A significant effect ($p < 0.05$) of site type was found for *E. tetralix* and *E. vaginatum* LDMC, leaf thickness, mean leaf area (*E. vaginatum* only), SLA and SLM (Figure 2). *E. tetralix* leaves from BOG had a significantly higher LDMC than leaves from the other sites, which were all similar to each other. For *E. vaginatum*, leaves collected in R19 had the lowest dry matter content while all other sites had higher but similar values. *E. tetralix* leaves collected in FOR were significantly thinner than leaves from R13 and R19, which were of similar width to leaves from BOG. *E. vaginatum* leaves from FOR and R13 were similar and both were thinner than leaves from R19 and BOG. For both species, the mean SLA was highest in leaves collected from FOR, lowest in leaves from BOG, and intermediate in leaves from both R13 and R19. In contrast, leaves from BOG had the highest SLM, followed by R13 and R19, and the lowest SLM was found in FOR. No significant differences were found across sites for the LDMC of *C. vulgaris* (data not shown), and no significant differences were found between R19 and R13 for *E. angustifolium* (data not shown).

S. capillifolium from R19 contained the lowest dry matter content ($p < 0.05$), while capitula from BOG had the highest dry matter content ($p < 0.05$). *S. papillosum* from R13 contained the highest LDMC ($p < 0.05$), while no significant difference was found in LDMC between BOG and R19 (Figure 3).

Chlorophyll content

Site type significantly influenced the mean concentration of chlorophyll a, chlorophyll b and the total amount of chlorophyll in all the species studied ($p < 0.05$). More specifically, *E. tetralix* and *C. vulgaris* leaves from BOG had a significantly lower mean concentration of chlorophyll a and b, which also resulted in a significant lower mean concentration of total chlorophyll when compared with the leaves from R13. The concentration of chlorophyll a, b and the total concentration of chlorophyll in R19 was similar to R13 and BOG for *E. tetralix*, but higher for *C. vulgaris* (Figure 4). The leaves of *E. vaginatum* from R13 contained a significantly higher concentration of chlorophyll a when compared to R19, with intermediate values in BOG. For the total concentration, the pattern was $R13 \leq R19 \leq BOG$. For *E. angustifolium*, chlorophyll a, b and total chlorophyll concentration was higher in R19 than R13 ($p < 0.05$) (no data for BOG or FOR).

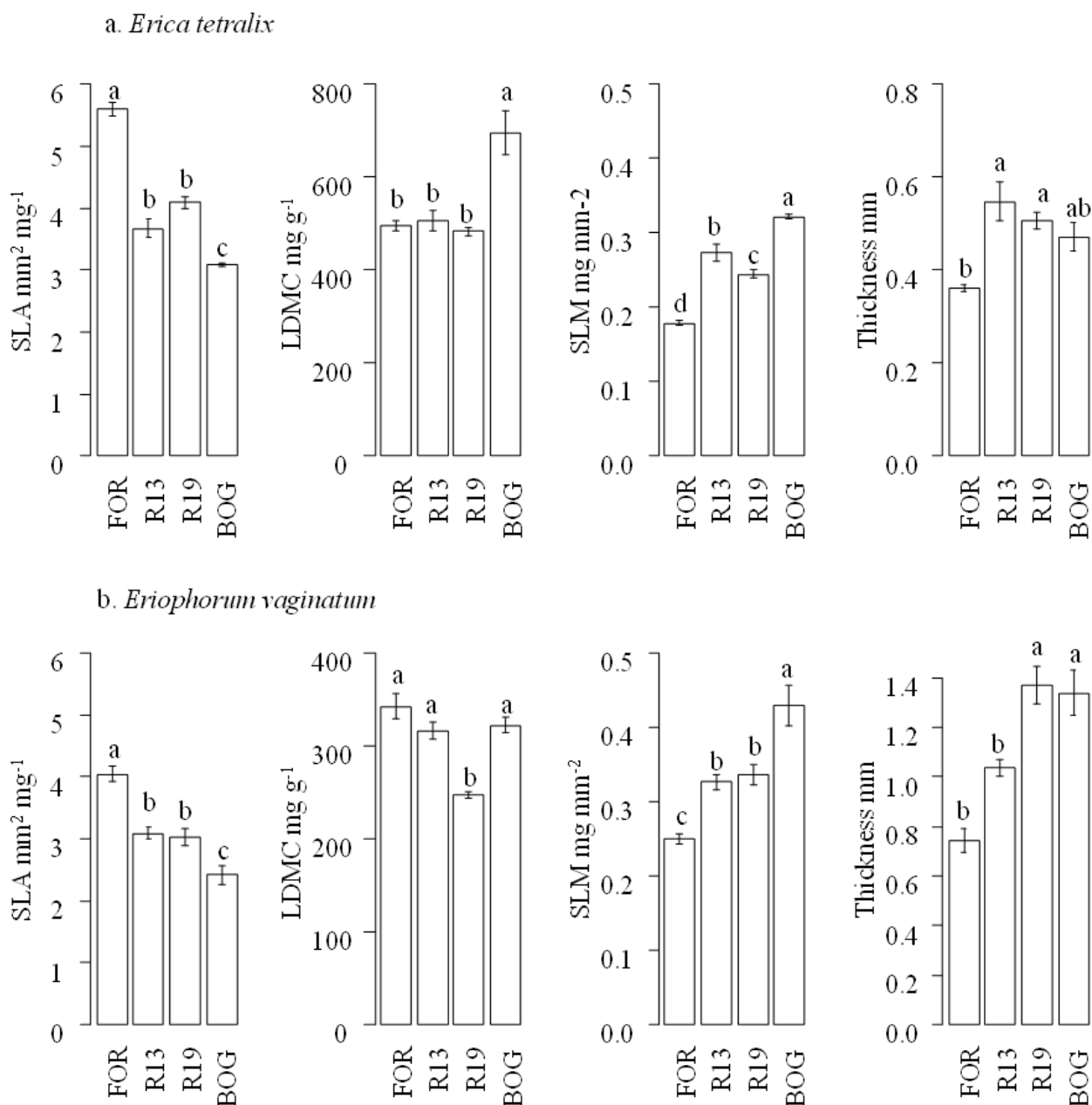


Figure 2. Mean and standard error values for destructive morphological traits measured for a) *Erica tetralix* (5 replicates, 200 leaves per replicate) and b) *Eriophorum vaginatum* (10 replicates, 1 leaf per replicate). SLA = Specific Leaf Area, LDMC = Leaf Dry Matter Content, SLM = Specific Leaf Mass; FOR = forested control, R13 = forest-to-bog restoration site aged 13 years, R19 = forest-to-bog site aged 19 years BOG = natural open blanket bog control. The letters above the bars indicate significant difference, i.e. for a given plant and trait; where the letters differ there was a significant effect of site ($p < 0.05$).

DISCUSSION

Some plant traits, such as SLA, can be directly linked to soil nutrient availability (Wilson *et al.* 1999, Diaz *et al.* 2004, Pérez-Harguindeguy *et al.* 2013). Similarly, chlorophyll concentration is known to be positively correlated with leaf nitrogen concentration (Jifon *et al.* 2005, Pérez-Harguindeguy *et al.* 2013). The BOG control site in Cross Lochs is a relatively

undisturbed blanket bog and is inherently a nutrient-poor environment, receiving water only from precipitation, consistent with the low SLA and low chlorophyll concentrations found in *E. vaginatum*, *E. tetralix* and *C. vulgaris*. In contrast, the initial fertilisation which took place when the trees were planted could be associated with more nutrient-rich soil conditions, contributing to higher SLAs in FOR. Previous research on these restored sites has shown

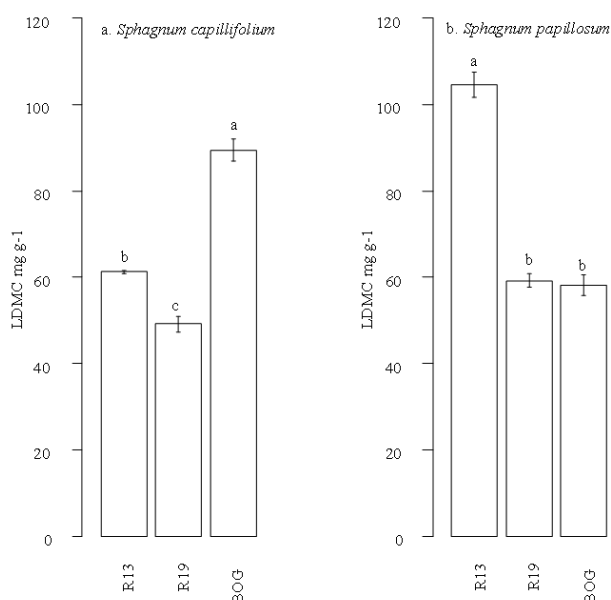


Figure 3. Mean and standard error ($n = 5$) values for destructive morphological traits measured for a) *Sphagnum capillifolium* and b) *Sphagnum papillosum*. LDMC = Leaf Dry Matter Content, BOG = open blanket bog control, R13 = forest-to-bog restoration site aged 13 years, R19 = forest-to-bog site aged 19 years. The letters above the bars indicate significant difference; i.e. for a given plant, where letters differ there was a significant effect of site ($p < 0.05$).

that, following sharp rises in levels of potassium (5-fold), phosphate (>40-fold) and ammonia (>5-fold) during the first ten years, nutrient concentrations decreased but remained higher than in open bog controls (Gaffney 2017). The increase in nutrients in restoration areas was attributed by the authors to conifer felling and needle and brash decomposition and has been observed in other studies (Moore *et al.* 2011, Asam *et al.* 2014).

With more nutrients available, plant species in forest-to-bog restoration areas can, therefore, invest in more growth (higher SLA) and photosynthesis (higher chlorophyll concentration) than their open bog counterparts. Increased nitrogen (N) availability in moorland and heathland has been shown to initially stimulate growth and flowering of *C. vulgaris* (Iason & Hester 1993, Carroll *et al.* 1999), but at high N dosages ($12 \text{ g m}^{-2} \text{ yr}^{-1}$) also had a long-term deleterious effect on the species itself and N-enriched litter impacted the underlying bryophyte community (Carroll *et al.* 1999). This generally lends support to our hypothesis that a lasting or legacy effect of previous coniferous plantations (needle litter) and forest-to-bog restoration practices (brash

left on site) could, through continued supply of nutrients in the soil water and litter, influence various plant traits across a range of common peatland plant species.

However, not all of the results can be explained solely by changes in nutrient availability. For instance, SLA and specific leaf dry matter can be highly variable between plants of the same species and even between leaves of the same plant (Wilson *et al.* 1999, Albert *et al.* 2010, Jung *et al.* 2010, Thuiller *et al.* 2010, Albert *et al.* 2011, Hulshof *et al.* 2013, Pérez-Harguindeguy *et al.* 2013); and because there is a strong correlation between SLA and leaf thickness and density, small differences in leaf thickness can cause significant changes in SLA (Wilson *et al.* 1999). The same authors showed how plants growing in shaded areas had higher SLA and thinner leaves than the same plants growing in the light. The shade created by canopy closure in the FOR site could, therefore, be another explanation as to why the leaves of *E. tetralix* and *E. vaginatum* growing in the Dyke forestry plantation had the highest SLA and lowest SLM.

Although LDMC is not as strongly correlated with soil fertility as SLA or chlorophyll concentration, it is easy to measure and, unlike SLA, less dependent on leaf thickness (Wilson *et al.* 1999, Shipley & Vu 2002, Pérez-Harguindeguy *et al.* 2013) and thus less influenced by shade. A low LDMC can be associated with productive and highly disturbed environments (Pérez-Harguindeguy *et al.* 2013). Following this, higher LDMC for *S. capillifolium* and *E. tetralix* in BOG would support the idea that R19 and R13 are more disturbed. Interestingly, these two species are generally associated with the driest microforms in bogs; and previous studies have shown that the driest microforms are the slowest to recover in forest-to-bog restoration sites (Hancock *et al.* 2018), possibly because they experienced greater drought-related stress. On the other hand, the pattern for *S. papillosum* and *E. vaginatum* is less conclusive. These two species are associated with wetter microforms, such as lawns and pool edges in bog or rewetted furrows in forest-to-bog restoration areas, and tend to be the first to recover following intervention (Hancock *et al.* 2018). In order to firm up these ideas, more species with different niche preferences, as well as more replicates from a range of sites, should be sampled alongside environmental variables such as water table or moisture regimes.

A clear difference in SLM can be seen in the leaves of *E. tetralix* and *E. vaginatum*. Leaves from FOR had the lowest SLM; however, like SLA, SLM is strongly correlated with leaf thickness and leaf density (Witkowski & Lamont 1991) and could

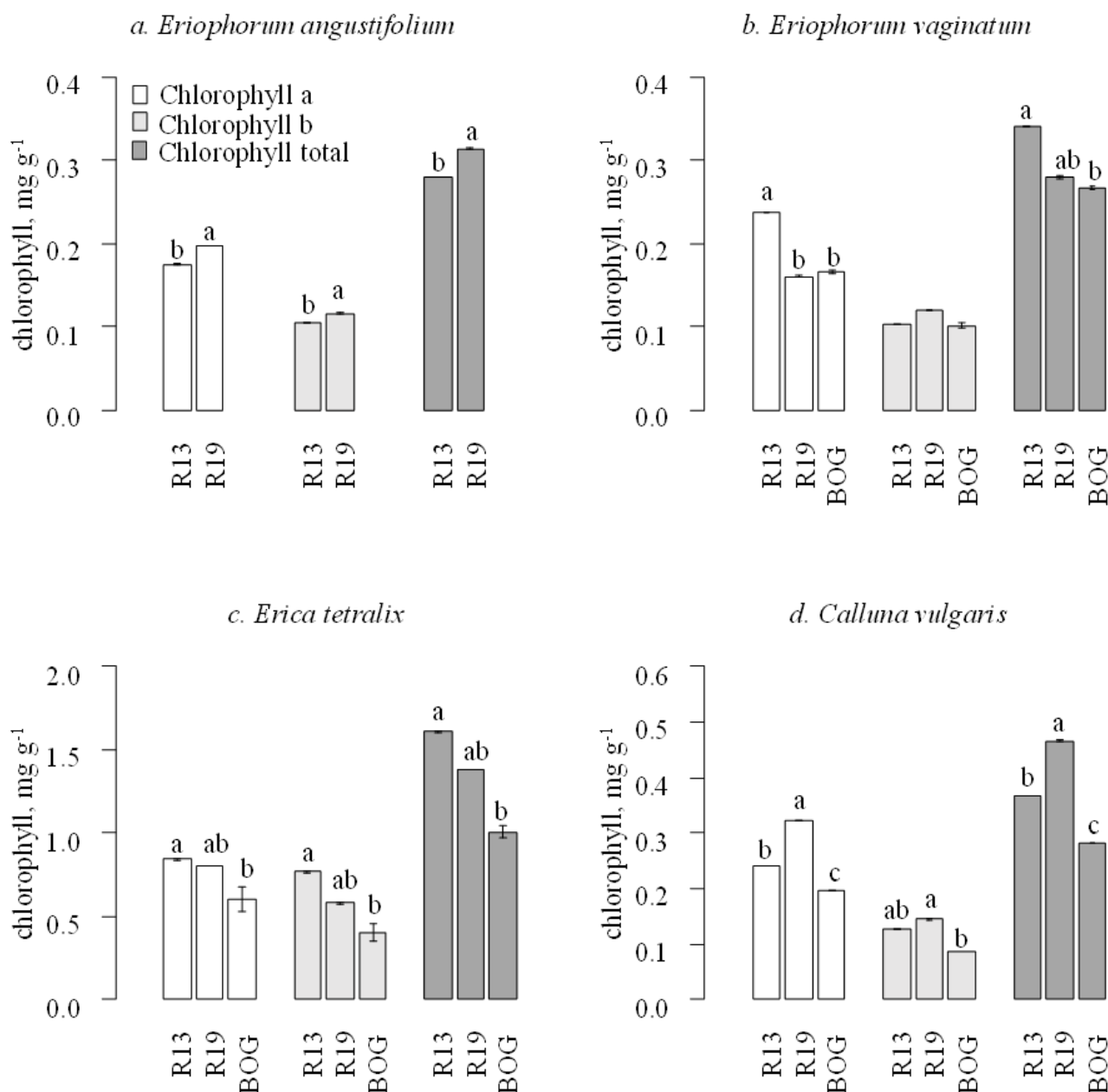


Figure 4. Mean and standard errors for chlorophyll concentrations ($n=3$) measured in leaves of a) *Eriophorum angustifolium*, b) *Eriophorum vaginatum*, c) *Erica tetralix* and d) *Calluna vulgaris*. R13 = forest-to-bog site aged 13 years; R19 = forest-to-bog site aged 19 years, BOG = open blanket bog control. The letters above the bars indicate significant differences, i.e. within a type of chlorophyll; where letters differ there was a significant effect of site. ($p < 0.05$).

similarly have been influenced by shade. SLM has been associated with carbon accumulation (Witkowski & Lamont 1991) and could be an important trait to analyse in peatlands in relation to C cycling and dynamics. In biomes with a short growing season and low nutrient availability like Scottish blanket bogs, soil carbon input is mainly derived from poor-quality litter produced by slow-growing, long-lived plants (Aerts & Chapin 2000) with high SLM. With leaves from R19 and R13

having lower SLM and higher chlorophyll concentrations than samples from BOG this suggests higher N inputs to these sites. As a result, leaves from R19 and R13 could be more easily decomposable than leaves from BOG, which have higher SLM and SLA and lower chlorophyll content (and therefore likely a higher C:N ratio) than samples from other locations. Changes in the decomposability of leaf litter could in turn influence processes like respiration. Interestingly, higher ecosystem respiration rates were

measured in both forest-to-bog restoration sites than in the BOG control using eddy flux covariance towers (Levy & Gray 2015, Hambley 2016).

Plant traits at similar sites can be used, in addition to climatic factors and soil chemical and physical properties, to predict variations in soil microbial community composition at the landscape scale; low SLA and leaf N being associated with fungal dominated microbial communities that are well adapted to decompose low-quality plant litter (de Vries *et al.* 2012, Bardgett *et al.* 2014). However, studies to date have generally compared contrasting ecosystems or plant communities. In the context of forest-to-bog restoration, where the comparison is between land uses within an ecosystem, they have the potential to further a better understanding of how relatively small yet significant changes in plant traits relate to potential changes in belowground structure and associated processes. Given that morphological traits can respond differently to a range of environmental drivers, directly measuring the C and N content and characterising the different compounds in the leaves would provide a robust way of determining how forestry legacy and restoration impact C sequestration through changes in litter quality, and linking it with plant traits (Aerts *et al.* 1995). Such research should involve measuring traits and properties from both aboveground and belowground structures, as shoot and root decomposability traits might not be directly related (Wardle *et al.* 1998, Craine *et al.* 2005) but both can influence key ecosystem processes (Bardgett *et al.* 2014).

In conclusion, our study identifies for the first time changes in plant traits that can be associated with disturbance and subsequent nutrient enrichment following forest-to-bog restoration. This pilot study also demonstrated that some routinely measured plant traits were not well suited to peatland plants. Notably, the minute leaves of *C. vulgaris* and *Sphagnum* spp. impeded the practical use of traditional leaf-based morphological traits. Nevertheless, the fact that we found significant differences in various plant traits across a range of plant functional types between forest-to-bog and control areas implies that it may be worth investing in future research to get more insight into the causes and consequences of these differences for ecosystem functioning. Other avenues to explore include the study of plant traits that may control carbon loss from soil via respiration, volatile organic compounds (VOCs), fire and leaching (Cornelissen *et al.* 1999, De Deyn *et al.* 2008), or the use of novel approaches that are not morphologically constrained such as metabolomics (Arbona *et al.* 2013).

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