

Research

Deciphering the shifting role of intrinsic and extrinsic drivers on moss decomposition in peatlands over a 5-year period

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Bryophytes are largely responsible for globally significant carbon accumulation in peatland ecosystems. This accumulation is primarily caused by the slow decomposition of these mosses, which can be attributed to a combination of intrinsic (chemical) characteristics of decaying mosses and extrinsic (environmental) influences. Here we investigated the importance of intrinsic and extrinsic drivers of moss decomposition in peatlands and hypothesized that the early stages of decay will be driven primarily by intrinsic characteristics, while extrinsic drivers will become more important in the later phases of decomposition. We tested this hypothesis by placing litterbags of three moss types (*Sphagnum divinum*, *Sphagnum angustifolium/fallax* and *Polytrichum* sp.) into hummock and hollow microtopographies in a bog and a lawn microtopography in a nearby poor fen in northern Minnesota, USA. Decomposition was measured over a 5-year period and confirmed our hypothesis; while intrinsic and extrinsic variables were both important in driving decay rates over time, decay in the first year was primarily predicted by litter type, while extrinsic influences (e.g. peat temperature, moisture, nutrient limitation) that varied at peatland and microtopographic scales became more important by year 5. Though the nutrient (i.e. nitrogen [N] and phosphorus [P]) content of decaying mosses did not explain the variation in decay rates among litter types, analysis of N:P in moss litter suggested that litter-decaying microorganisms became increasingly P-limited over time. The majority of litter decomposition studies in peatlands are generally of short duration (< 3 years). Our study suggests that longer-term studies are needed to reveal the roles of multiple drivers of moss decay. Improving the mechanistic understanding of decomposition processes in peatlands will be critical to developing more robust representations of peatlands and their ecosystem processes in carbon and climate models.

Keywords: bog, boreal, bryophytes, decay, decomposition, feathermoss, microtopography, mosses, nutrients, poor fen, Sphagnum



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Introduction

One third of the Earth's soil carbon (C) is stored within peatlands (Gorham 1991). Comprising only about 3% of land surface, primarily in the boreal and temperate zones, peatlands are the most important C-sequestering terrestrial ecosystem on the planet (Gorham 1991, Page et al. 2011, Rydin and Jeglum 2013, Leifeld and Menichetti 2018). The recalcitrant nature of peatland C can largely be attributed to bryophytes (primarily *Sphagnum*) that thrive in these cold and nutrient-poor environments and that create acidic and waterlogged conditions unsuitable for rapid decomposition (Moore and Basiliko 2006, Finlayson and Milton 2018). The rate of primary production in peatlands exceeds the rate at which vegetative matter (i.e. litter) decomposes, allowing peat, and therefore C, to accumulate (Moore and Basiliko 2006, Graf and Rochefort 2009). Due to the important role of *Sphagnum* and of decomposition in regulating C accumulation in peatlands, understanding the drivers of moss decomposition in these systems is imperative to improving the accuracy of regional and global C cycle and climate change models.

Drivers of litter decomposition in peatlands can be organized into two categories: intrinsic and extrinsic. Intrinsic drivers include various chemical characteristics (e.g. phenolics, lignin, nutrients) and morphology/structure of the litter, while extrinsic drivers include external processes such as soil temperature and moisture, light and nutrient availability, and microbial community composition (Farrish and Grigal 1985, Moore et al. 2007, Laing et al. 2014). Many studies have investigated the intrinsic drivers of litter decomposition in peatlands and have found that a variety of chemical compounds (e.g. lignin-like phenolics, polymerized phenolics, cellulose and nutrients) can control litter decomposition, depending on the plant taxa studied (Johnson and Damman 1991, Verhoeven and Toth 1995, Belyea 1996, Scheffer et al. 2001, Turetsky et al. 2008, Graf and Rochefort 2009, Hájek 2009, Hagemann and Moroni 2015, Bengtsson et al. 2016, Barreto and Lindo 2018). For example, Bartsch and Moore (1985) found that mass loss among various peatland litter types (graminoids, shrubs, *Sphagnum*) was positively correlated with nitrogen, phosphorus and potassium content, and negatively correlated with cellulose and lignin content.

In peatlands, extrinsic factors and thus decomposition rates can vary across multiple spatial scales, from within peatlands to among peatlands (Clymo 1965, Bartsch and Moore 1985, Rochefort et al. 1990, Hogg et al. 1994, Scheffer et al. 2001, Moore et al. 2007). Specifically, peatland type has been shown to affect litter decay rates, with faster decomposition rates in groundwater-fed fens that are relatively richer in nutrients than in precipitation-fed, nutrient-poor bogs (Bayley et al. 2005, Moore et al. 2007, Yavitt et al. 2019). Extrinsic factors also vary at the microtopographic scale within peatlands, where higher-elevation, drier hummocks that rise above lower-elevation, wetter hollows and flat, mid-elevation lawns create differences in soil moisture, temperature and microbial community structure (Chapin and Slack

1979, Lindholm and Markkula 1984, Johnson and Damman 1991, 1993, Belyea 1996, Shi et al. 2015). When decomposition rates of the same *Sphagnum* species are measured in both hummocks and hollows, decay rates in hummocks are typically slower than in hollows (Belyea 1996, Turetsky et al. 2008, Hájek 2009). However, the effect of microtopography on moss decomposition is complicated because different moss species, each with different intrinsic characteristics, can generally be found in hummocks versus hollows, although overlap exists (Andrus et al. 1983, Luken 1985). In general, the decomposition rate of hummock mosses that decay in hummocks is usually slower than hollow mosses that decay in hollows (Belyea 1996, Turetsky et al. 2008, Hájek 2009, Bengtsson et al. 2016). This pattern has been suggested to primarily result from intrinsic differences in litter lability among hummock and hollow mosses and less-so due to extrinsic (environmental) differences between hummock and hollow microtopographic position (Johnson and Damman 1991, Belyea 1996, Hájek 2009, Bengtsson et al. 2016).

Though many short-term studies (≤ 3 years) focused on *Sphagnum* decomposition have reported litter quality as a better predictor of decay rates than extrinsic drivers (Johnson and Damman 1991, Belyea 1996, Scheffer et al. 2001, Turetsky et al. 2008, Graf and Rochefort 2009, Hájek 2009, Hagemann and Moroni 2015, Bengtsson et al. 2016), the importance of these drivers may change during the decomposition process. For instance, in a 23-year-long litter decomposition study in a bog, Latter et al. (1998) initially observed significant variation in mass loss across dominant vascular types, but these intrinsic differences were no longer present at the end of the study. In another example, Limpens and Berendse (2003) demonstrated that the decomposition of older portions of *Sphagnum* shoots generally had less intrinsic influence than the younger portions. Similarly, Hogg (1993) observed interspecific differences in the decay of young (green) *Sphagnum*, but these species-specific differences were no longer present in older, more decomposed organic matter. It can be hypothesized that the early phase of decomposition is mostly driven by intrinsic characteristics (Hogg 1993, Latter et al. 1998, Limpens and Berendse 2003), while extrinsic drivers may become more important in the later phase. However, decomposition studies that are carried out for long periods of time are rare (e.g. 84% of published litter-bag studies in temperate, boreal and subarctic regions were of 3 years duration or less; Moore et al. (2017)), making it difficult to test this hypothesis. To our knowledge, this hypothesis has not been explicitly tested for peatland mosses.

Our objective was to examine how intrinsic versus extrinsic drivers affect moss decay rates over 5 years in boreal peatlands in northern Minnesota, USA. We measured decay rates of three dominant moss types within two peatlands (an ombrotrophic bog and a nearby poor fen) and in two microtopographies in one peatland (hollows and hummocks in the bog). We expected that intrinsic litter quality would be a more important driver of early decomposition than extrinsic parameters represented in the different peatlands and microtopographies. We also predicted faster decay in the poor fen

and slower decay in the bog, and within the bog, slower decay in the drier hummocks than wetter hollows, especially in the later phase of decomposition.

Methods

Study sites

The boreal peatlands selected for this study are within the USDA Forest Service Marcell Experimental Forest (MEF), located in northcentral Minnesota, USA. With research and monitoring starting during the 1960s, the MEF has a long history of investigations on hydrological and biogeochemical processes of peatlands and surrounding watersheds (Sebestyen et al. 2021a). This area has a continental climate with warm, moist summers and cold, dry winters. Mean annual temperature is 3.5°C, with July monthly mean temperature of 18.9°C, and −15.0°C in January (data citation – Sebestyen et al. 2020a). The average annual precipitation is 78.7 cm (± 10.4 cm (SD)), roughly one-third of which occurs as snowfall (data citation – Sebestyen et al. 2020b). Snow accumulation generally begins in November and melts in March to April, though midwinter thaws are not uncommon. The MEF area is underlain by a glacial moraine and outwash deposits in low-elevation hills, and peatlands formed where ice-block depressions gradually filled with organic soils. The S1 Bog (47°30′17″N, 93°27′15″W) and Bog Lake Fen (47°30′19″N, 93°29′22″W) peatlands, which are the focus of this study, are located in the MEF South Unit approximately 2.5 km apart (Sebestyen et al. 2011a).

Vegetation of the 8.1-ha S1 ombrotrophic peat bog (hereafter referred to as the ‘bog’) is dominated by mosses, ericaceous shrubs (*Rhododendron groenlandicum*) and an overstory of trees, primarily *Picea mariana* (Pinaceae) and *Larix laricina* (Sebestyen et al. 2011a, Norby et al. 2019). Mosses in this bog are primarily *Sphagnum divinum* (sp. nov.) (formerly *Sphagnum magellanicum*; Kyrkjeeide et al. 2016, Hassel et al. 2018), *S. angustifolium*, *S. fallax* and *Polytrichum* sp., with lower abundances of *S. fuscum* and *Pleurozium schreberi* (Norby et al. 2019). Shrubs dominate the taller hummocks of the bog’s hummock–hollow microtopography. *Sphagnum angustifolium* and *S. divinum* tend to be found on hummocks while *S. fallax* dominates hollows in this bog, though each moss (including *Polytrichum*) grows in both hummock and hollow microtopographies (Norby et al. 2019). *Sphagnum angustifolium* and *S. fallax* are both within the subsection *Recurvum* and are nearly indistinguishable in the field (Vitt and Slack 1984). Because of the taxonomic similarity and difficulty in distinguishing *S. angustifolium* and *S. fallax*, we refer to them together as *S. angustifolium/fallax* (this same notation was used in another study in this same bog; Norby et al. 2019). Because of the predominance of the hummock–hollow microtopography across the bog, we used this peatland to investigate how moss decomposition varied at the microtopographic scale. The distribution of hummocks versus hollows in this bog was estimated at 67%

hummocks and 33% hollows using terrestrial laser scanning (data citation – Graham et al. 2019, Malhotra et al. 2020, Salmon et al. 2021). This bog has the greatest water table fluctuation compared to six other research peatlands on the MEF, with the historical record ranging from several centimeters above the surface to 1.4 m below the peat surface in hollows (Sebestyen et al. 2011a). Trees in the bog were harvested in two successive strip cuts in 1969 and in 1974 to determine the influence of harvesting and regeneration on water yield (Sebestyen and Verry 2011, Sebestyen et al. 2011b).

The Bog Lake Fen peatland is a 20-ha poor fen (hereafter referred to as the ‘poor fen’) with a slightly concave surface in cross section (Sebestyen et al. 2011a). The poor fen is predominantly open, with sparsely distributed, short-statured *L. laricina* among *Sphagnum* (*S. papillosum*, *S. angustifolium*) and *Polytrichum* mosses, arrow grass *Scheuchzeria palustris*, sedges *Rhynchospora alba*, bog rosemary *Andromeda glaucophylla*, pitcher plants *Sarracenia purpurea*, bog laurel *Kalmia polifolia* and leatherleaf *Chamaedaphne calyculata* (Dise et al. 2011). Water table fluctuation is less variable in the fens at the MEF, with a maximum depth of 0.7 m below the peat surface in this poor fen based on the historical record (Sebestyen et al. 2011a). This poor fen remains relatively wet with expansive lawns and some hummock–hollow microtopography.

Environmental measurements

Water table elevation, peat temperature and surface water chemistry were measured in the two study peatlands from 2014 through 2019 to characterize the physicochemical environment over the 5-year period that litterbags were deployed. Water table level was measured in a heated well in each peatland with a Belfort Instruments (Baltimore, MD, USA) FW-1 stripchart recorder. Recorded values were manually checked each week and daily maximum water level was recorded from stripcharts. Water level was then expressed as water table elevation (in m a.s.l.) (data citation – Sebestyen et al. 2020c). Water level data were also expressed as water depth relative to the peat surface in the bog and poor fen based on manual measurements of water level from each peatland. Water depth relative to the peat surface was measured at five locations in each peatland on one date, and the mean of these manual depth measurements was then converted to water table elevation (in m a.s.l.) using the water table elevation measured by the stripchart recorder on the measurement date. These data were also used to estimate the percentage of time that litterbags were submerged during the decomposition study. The litterbags were deployed vertically into the peat and so the percentage of time that both the tops and bottoms of the litterbags were submerged was calculated. We note that there is uncertainty in estimates of water table level relative to the peat surface due to natural variation in peat surface elevation across each peatland. An additional source of uncertainty is the location of litterbags relative to the water table level because mosses grew up over the litterbags over the 5-year incubation period.

Peat temperature was measured at a 5-cm depth below the hollow surface in both the bog and the poor fen. Peat

temperature at 5-cm depth was examined as this was the midpoint depth that litterbags were deployed in the peat. In the poor fen, peat temperature was measured approximately weekly using buried type-T thermocouples and read with a digital thermometer (data citation – Sebestyen et al. 2020d). In the bog, peat temperature was measured every 30 min using a multipoint thermistor probe (data citation – Hanson et al. 2015). The bog temperature data were subsampled so that temperature data from the same date/time stamps were analyzed from both peatlands (n=306 measurements per peatland). Temperature was also measured approximately 5 cm below the surface of a hummock in the bog every 30 min using a thermistor probe (data citation – Hanson et al. 2015) allowing for a comparison of temperature in a hummock and hollow. Temperature was only measured until 2018 in the hummock, and so temperature for the remainder of the study was estimated from a predictive relationship developed based on temperature measured in different, nearby hummock in the bog ($y = 0.89x - 0.1358$, $r^2 = 0.97$, $n = 1416$) (data citation – Hanson et al. 2016). Temperature data were reported as measured values (for weekly measurements in the poor fen and bog) or mean daily values (for hollow and hummock measurements), and also as cumulative values over the 5-year study.

Surface water chemistry samples were collected from the outlet stream of the bog and from an open pool of water in the poor fen (data citations – Sebestyen et al. 2021b, c). Samples were collected ~weekly from the bog and every two weeks from the poor fen unless the sampling sites were dry or frozen. Similar to the peat temperature data, surface water chemistry data were subsampled so that chemistry data from the same dates (within a week) were analyzed from both peatlands (n=100 measurements per peatland from 2014 through 2019). A suite of chemical analyses were completed on water samples using standard methods including pH, specific conductivity and anion (sulfate), cation (calcium, potassium, magnesium, sodium, aluminum, iron), nutrient (total nitrogen, total phosphorus) and total organic carbon concentrations (see Griffiths and Sebestyen 2016, Griffiths et al. 2019 for details).

Litterbag decomposition study

Three moss litter types were collected from the S1 bog in 2013 for the litterbag experiment: *Sphagnum divinum*, *S. angustifolium/fallax* and *Polytrichum* sp. These mosses were chosen because they are the predominant mosses in the study peatlands. *Polytrichum* sp. was also chosen because very few studies have measured the decay of *Polytrichum*. *Polytrichum* may increase relative to *Sphagnum* with warming and increased nitrogen deposition (Berendse et al. 2001, Bubier et al. 2007, Juutinen et al. 2016, Norby et al. 2019), and thus it is important to understand the decomposition dynamics of this understudied moss.

In collecting mosses for the decomposition study, the entire plant was pulled from the bog and the top ~1 cm (green moss; primarily the capitulum) was removed from *Sphagnum*. The senescing portion of the mosses (pale or brown in color) were also removed, leaving an approximately

8 cm length of pale green/brown moss to place into litterbags. Moss litter was air dried in the laboratory for several days (until the change in air-dried mass was < 10%) and then approximately 1 g (0.971 ± 0.028 g) of air-dried litter was placed into mesh bags (bag size 10 × 10 cm, mesh size 0.6 × 0.6 mm). The mesh size used in this study was similar to the average mesh size used in other moss decomposition studies in peatlands based on a literature survey (mean=0.65 mm; range=0.074–2.0 mm; n=18 studies). The initial air-dried mass of litter in each litterbag was recorded to the mg.

All three moss litter types were deployed in each of three hummocks and hollows in the bog and in three lawn sites in the poor fen. The three locations of each microtopography were considered replicates in this analysis and were located within ~15 m of each other. Litterbags were placed vertically into the moss layer in each location, with the top of the litterbag at the peat surface. Vertical placement was selected to imitate the orientation of moss growth and decomposition. Over the duration of the decomposition study, mosses grew up over the litterbags such that the litterbags were estimated to be ~5 cm below the moss surface after 5 years of incubation (based on a visual assessment during litterbag retrieval).

At each location, a total of nine litterbags were deployed; three of each litter type to be collected on three retrieval dates. The litterbags were deployed on 5 June 2014 (t=0 years), and one bag per litter type and replicate location was picked up on the same day to account for mass loss associated with handling/transport and also to estimate initial oven-dry mass for all litterbags (i.e. for air-dry to oven-dry conversion). Only two replicates of *Polytrichum* were used for this initial determination (two of the three locations had t=0 years litterbags) because not enough *Polytrichum* was collected to create a full set of litterbags. The subsequent litterbag retrievals occurred 1 and 5 years after initial deployment (on 16 June 2015 and 5 June 2019, respectively).

Laboratory analyses

After litterbags were retrieved from the field, all organic matter in each litterbag was removed and placed in a paper bag to air dry. All foreign material (e.g. roots that grew into the litterbags) was then carefully removed with forceps and the remaining moss litter was oven dried at 70°C for 24 h. Oven-dried samples were weighed (to the mg) to determine dry mass for calculation of decay rate (data citation – Shelley et al. 2021a). Samples were then pulverized with a grinder/tissue homogenizer to prepare samples for chemical analyses. Nitrogen (N) content of each sample was measured using an elemental combustion system, and phosphorus (P) content was analyzed using the persulfate digestion technique followed by flow injection analysis on an autoanalyzer. The N and P contents of all samples were above detection limits of the instruments. Nutrient contents of litter were expressed as percentages of sample dry mass (data citation – Shelley et al. 2021a), and the molar N:P was calculated. The mass of N and P in litter was also calculated by multiplying the % nutrient content by the litter dry mass remaining on each retrieval date.

Calculations and statistics

Environmental data (water table elevation, peat temperature, surface water chemistry) were summarized on an annual basis (i.e. annual range in water table elevation, mean annual peat temperature, annual range in peat temperature, mean annual pH, specific conductivity and solute concentrations) and these annual values ($n=6$ per peatland) were compared between the bog and poor fen or between the hummock and hollow using paired, two-tailed t-tests. Annual data were analyzed as this time scale corresponded to the temporal resolution of the decay rate data (measured at 1 and 5 years). The environmental data were also analyzed together using a principal components analysis (PCA) to characterize similarities and differences in environmental parameters between the two study peatlands. Water table elevation (in m a.s.l.) was not used in the PCA because of the inherent difference in elevation between the two peatlands. Instead, water table variation was calculated as the difference between the mean water table elevation over the measurement period (2014 through 2019) and water table elevation on each measurement date. Because the environmental data were collected at different frequencies and not all environmental variables were measured on the exact same date, data with a similar time stamp were aligned for use in the PCA (i.e. water chemistry sample collected within a week of the soil temperature and water table elevation measurements).

The decay rate of moss litter was estimated assuming a single exponential decay model, with the decay coefficient (k) as the slope of the natural log of percentage dry mass remaining versus duration (in days) that litterbags were deployed in the field. The decay coefficient was then converted from units of day^{-1} to years^{-1} . The decay coefficient was calculated separately for each litter type (*Polytrichum*, *S. divinum*, *S. angustifolium/fallax*), peatland/microtopographic position (hummock and hollow in the bog and lawn in the poor fen) and replicate location (1, 2, 3). Decay coefficients were calculated after 1 year (using data from years 0 and 1) and after 5 years of decomposition (using data from years 0, 1 and 5). We explored using a double exponential decay model, but opted to use the single exponential decay model for multiple reasons. Firstly, because we calculated decay coefficients for each unique combination of litter type, peatland/microtopography and replicate location, there were not enough data points ($n=3$) to solve the double exponential decay equation. Secondly, when decay coefficients were estimated for each unique litter type and peatland/microtopography combination across the three replicate locations ($n=9$) using both the single- and double-exponential decay models, the double-exponential decay rarely improved the model fit (based on the r^2), which is consistent with other studies (Thormann and Bayley 1997, Latter et al. 1998, Hobbie and Gough 2004, Hoyos-Santillan et al. 2015). Lastly, most litter decomposition studies in peatlands use the single exponential decay model, and thus decay coefficients calculated using this same model will be comparable to literature values (Moore et al. 2007).

We used repeated measures analysis of variance (RMANOVA) to examine the effect of extrinsic (peatland or

microtopography) and intrinsic (litter type) drivers on decay rate and litter chemistry over time. Because of the multiple spatial scales represented by the extrinsic drivers (i.e. peatland scale, microtopographic scale), and due to the unbalanced study design (i.e. two microtopographies in the bog versus one microtopography in the poor fen), the effects of peatland and microtopography were analyzed separately. A two-way RMANOVA was used to examine the effect of peatland and litter type on decay rate over time. For this analysis, a peatland-scaled decay rate was calculated for the bog whereby decay rates in hummocks and hollows were scaled up to one integrative decay rate. To calculate the peatland-scaled decay rate, the decay rates measured in each replicate hummock and hollow were averaged based on the distribution of hummocks (67%) and hollows (33%) in the bog (peatland decay rate = [hummock decay rate $\times$ 0.67] + [hollow decay rate $\times$ 0.33]). A two-way RMANOVA was also used to examine the effect of microtopography (hummock, hollow) and litter type on decay rate in the bog over time. Two-way RMANOVAs examined whether litter chemistry (%N, %P, N:P, N mass, P mass) varied over time, among litter types and between peatlands (or between hummocks and hollows in the bog). Peatland-scaled chemistry parameters for the bog were calculated in the same manner as decay rates.

Pearson's correlations were used to examine associations between decay rates and litter chemistry (%N, %P, N:P) and between chemical parameters (%N versus %P). The measured decay rates and litter chemistry values, not the peatland-scaled values, were used in the correlative analyses. Each litterbag had corresponding litter chemistry data (from years 0, 1 and 5) which allowed for these correlative analyses. In contrast, the same correspondence between decay rates and environmental data was lacking because environmental data were not measured at the microtopographic scale at which litterbags were incubated but instead were representative of the 'peatland' scale. Further, the temporal resolution of decay rate data (1 and 5 years) was too coarse relative to the environmental data to allow for meaningful correlative analyses. Because we were unable to conduct correlative analyses between decay rates and environmental variables, we instead focused on conducting analyses to compare environmental data between the two study peatlands (i.e. paired t-tests, PCA).

For all statistical analyses, data were natural-log transformed to meet parametric assumptions when necessary and analyzed using SigmaPlot ver. 14 and SYSTAT ver. 13.2 (Systat Software Inc.).

Results

Environmental data

Water table elevation was more variable in the bog than the poor fen over the study period with water table varying by 73 cm in the bog and by 39 cm in the poor fen from 2014 through 2019 (Supporting information). However, on an annual basis, the range in water table elevation was

similar in the bog (mean annual variation from 2014 through 2019 = 40 cm) and the poor fen (mean annual variation = 29 cm) (paired t-test, $t=2.26$, $p=0.07$). In the first year of the decomposition study, the water table elevation in the bog was generally lower than during the rest of the record, while the same lower water levels were not observed in the poor fen (Supporting information).

The water table in the poor fen was closer to the surface than in the bog (paired t-test, $t=4.76$, $p=0.005$; Fig. 1) such that litterbags in the poor fen were submerged more often than litterbags in the bog (Supporting information). Across the entire study period, the litterbags in the poor fen were submerged 43% (top of litterbags) to 76% (bottom of litterbags) of the time, while litterbags in the hollows of the bog were submerged 12% (top) to 49% (bottom) of the time (Supporting information). The water table was not high enough to submerge litterbags in the hummocks of the bog at any point during the study period (Fig. 1, Supporting information). Due to the lower water table elevation in the bog in the first year of the study, litterbags in the hollows were submerged less often than in the latter years, while a similar pattern was not observed in the poor fen (Supporting information).

Mean annual peat temperature measured 5 cm below the peat surface from 2014 through 2019 was higher in the bog (6.5°C) than the poor fen (6.1°C) (paired t-test, $t=3.54$, $p=0.02$). The annual range in soil temperature was larger in the poor fen (mean range from 2014 through 2019 = 21.3°C) than the bog (mean range = 17.7°C) (paired t-test, $t=3.80$, $p=0.01$). The larger temperature range in the poor fen reflected both higher maximum temperatures and

lower minimum temperatures compared to the bog (Fig. 2A). While there was a larger temperature range in the poor fen than in the bog, cumulative temperature was higher in the bog than the poor fen over the study duration (Supporting information; paired t-test, $t=4.80$, $p=0.005$).

Within the bog, hummock temperatures were more variable than hollow temperatures, with lower winter temperatures and higher summer temperatures in the hummock (Fig. 2B). On an annual basis, there was no difference in mean annual temperature between the hummock and hollow (paired t-test, $t=0.58$, $p=0.59$), but cumulative temperature was higher in the hollow than hummock (Supporting information; paired t-test, $t=3.21$, $p=0.02$).

There were some similarities and some differences in surface water chemistry in the bog versus the poor fen (Table 1). Sulfate and potassium concentrations and pH were similar in the bog and poor fen (paired t-tests, all $t \leq 2.44$, $p \geq 0.06$). In contrast, and contrary to expectations, specific conductivity and calcium, magnesium, sodium, aluminum, iron, total N, total P and total organic C concentrations were higher in the bog than the poor fen (paired t-tests, all $t \geq 4.44$, $p \leq 0.007$).

When environmental data were analyzed together in a PCA, differences between the bog and poor fen emerged, that were primarily driven by variation in surface water chemistry (Fig. 3, Table 2). The environmental characteristics of the two peatlands primarily separated along principal component axis 1 (PC1), which explained 50% of the variation, and reflected the higher specific conductivity and cation (calcium, magnesium, iron) and total organic carbon concentrations (Fig. 3, Table 2).

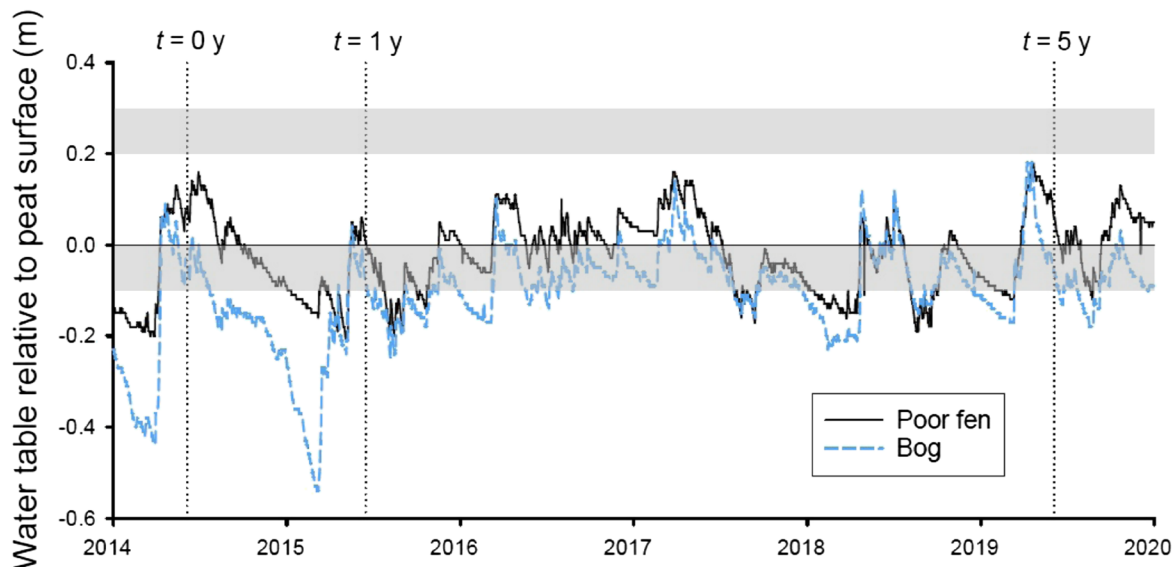


Figure 1. Daily water table level relative to the peat surface (m) in the bog (blue line) and the poor fen (black line) over the decomposition study (2014 through 2019). Vertical dotted lines show the litterbag deployment date ($t=0$ year), and the $t=1$ year and $t=5$ year pick up dates. The peat surface is indicated by a solid horizontal black line. Negative values indicate that the water table was below the peat surface while positive values indicate that the water table was above the peat surface. The estimated location of the litterbags in hollows in the bog and lawns in the poor fen (0 to -10 cm) and in the hummocks in the bog (20–30 cm) are shown in grey shading.

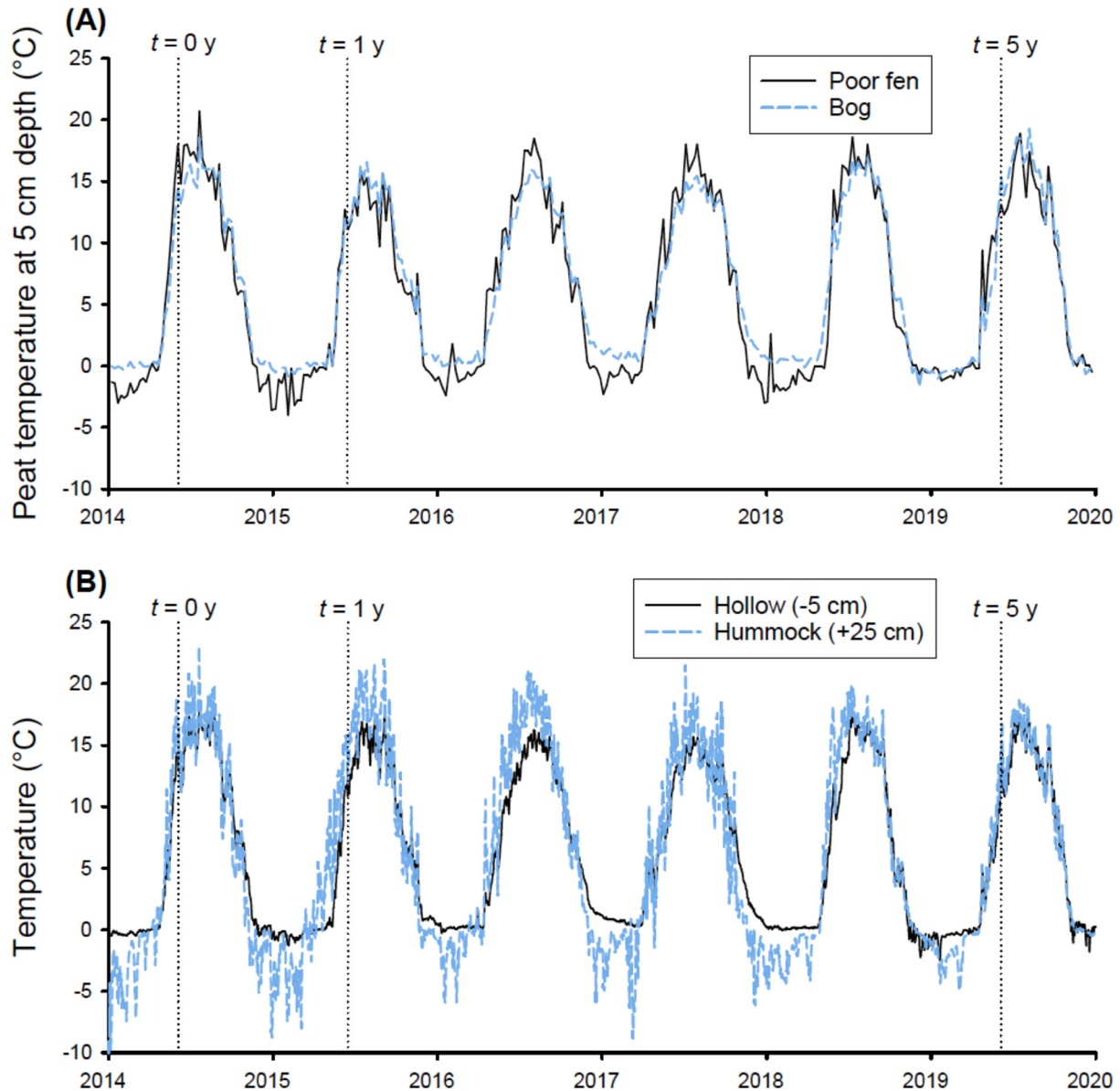


Figure 2. (A) Temperature measured 5 cm below the peat surface approximately every week in the bog (blue line) and poor fen (black line) over the decomposition study (2014 through 2019) and (B) mean daily temperature in a hollow (black line; 5 cm below the peat surface) and a hummock (blue line; 5 cm below the hummock surface/25 cm above the peat surface) over the study. Vertical dotted lines show the litterbag deployment date ($t=0$ year), and the $t=1$ year and $t=5$ year pick up dates.

Moss litter decomposition

The effect of intrinsic (moss type) and extrinsic (microtopography, peatland) drivers on decay rates varied over the 5-year decomposition period. Examination of peatland-scaled decay rates over time revealed significant differences in decay rates between peatlands (RMANOVA, $p=0.02$) and among litter types (RMANOVA, $p=0.01$), with no significant interaction (RMANOVA, $p=0.81$). When averaged across litter types, decay rates after 1 year were faster in the poor fen (mean $k=0.130 \text{ year}^{-1}$) than in the bog (mean $k=0.079 \text{ year}^{-1}$) (Fig. 4A). This same pattern was observed after 5 years but the difference in mean decay rates between peatlands was larger

(poor fen $k=0.189 \text{ year}^{-1}$, bog $k=0.073 \text{ year}^{-1}$) (Fig. 4B). After one year, the decay rate (averaged across peatlands) of *Polytrichum* was fastest (mean $k=0.181 \text{ year}^{-1}$) followed by *S. angustifolium/fallax* (mean $k=0.110 \text{ year}^{-1}$) and *S. divinum* (mean $k=0.021 \text{ year}^{-1}$) (Fig. 4A). In contrast, in year 5, decay of *S. angustifolium/fallax* was fastest (mean $k=0.176 \text{ year}^{-1}$) followed by *Polytrichum* (mean $k=0.144 \text{ year}^{-1}$) and then *S. divinum* (mean $k=0.073 \text{ year}^{-1}$) (Fig. 4B). Faster decay of *S. angustifolium/fallax* than *Polytrichum* in year 5 was primarily due to the fast decay rate of *S. angustifolium/fallax* in the poor fen (Fig. 4B). Specifically, the pattern of decay in the poor fen changed from year 1 (*Polytrichum* > *S. angustifolium/fallax* > *S. divinum*) to year 5 (*S. angustifolium/fallax* >

Table 1. Chemistry of surface water in the bog and poor fen. Values represent means (with standard deviations in brackets) across the sampling period (2014 through 2019). An asterisk indicates a significant difference ($p < 0.05$) in that chemistry parameter between the bog and poor fen based on a paired t-test.

Chemistry parameter	Bog	Poor fen
pH	3.7 (0.2)	3.7 (0.3)
Specific conductivity ($\mu\text{S cm}^{-1}$)*	46.2 (9.9)	27.8 (8.6)
Calcium (mg l^{-1})*	1.95 (0.52)	0.84 (0.41)
Potassium (mg l^{-1})	0.92 (0.80)	1.17 (0.80)
Magnesium (mg l^{-1})*	0.68 (0.16)	0.38 (0.18)
Sodium (mg l^{-1})*	1.03 (0.17)	0.67 (0.13)
Aluminum (mg l^{-1})*	0.40 (0.11)	0.11 (0.05)
Iron (mg l^{-1})*	1.30 (0.56)	0.60 (0.33)
Sulfate (mg l^{-1})	0.16 (0.24)	0.10 (0.07)
Total nitrogen (mg N l^{-1})*	0.80 (0.23)	0.60 (0.31)
Total phosphorus (mg P l^{-1})*	0.05 (0.03)	0.03 (0.02)
Total organic carbon (mg C l^{-1})*	58.4 (13.9)	32.3 (12.9)

Polytrichum > *S. divinum*) while the pattern was the same in both years in the bog (*Polytrichum* > *S. angustifolium/fallax* > *S. divinum*) (Fig. 4).

When comparing decay rates between hummocks and hollows in the bog over time, there were differences in decay

rates among litter types (RMANOVA, $p = 0.02$) and between microtopographies (RMANOVA, $p = 0.004$), with no significant interaction (RMANOVA, $p = 0.20$). After 1 year, decay rates were faster in the hummocks (mean $k = 0.101 \text{ year}^{-1}$) versus the hollows (mean $k = 0.033 \text{ year}^{-1}$) with negative decay rates for both *Sphagnum* litter types after 1 year in the hollows (i.e. mass gain) (Fig. 4A inset). In year 5, this pattern switched such that decay rates were faster in the hollows (mean $k = 0.102 \text{ year}^{-1}$) than in the hummocks (mean $k = 0.059 \text{ year}^{-1}$; Fig. 4B inset).

Moss litter chemistry

The peatland-scaled N content of litter varied significantly among litter types (RMANOVA, $p < 0.001$) and between peatlands (RMANOVA, $p = 0.02$) over time, with no significant interaction (RMANOVA, $p = 0.22$) (Fig. 5A). There was a general trend of increasing %N in *S. angustifolium/fallax* over time and in *S. divinum* from year 1 to 5; however, %N in *Polytrichum* was similar throughout the decomposition period. There were also differences in %N among moss types at the start of the experiment, with %N lowest in *S. angustifolium/fallax*, intermediate in *Polytrichum* and highest in *S. divinum* (Fig. 5A). However, as the decomposition

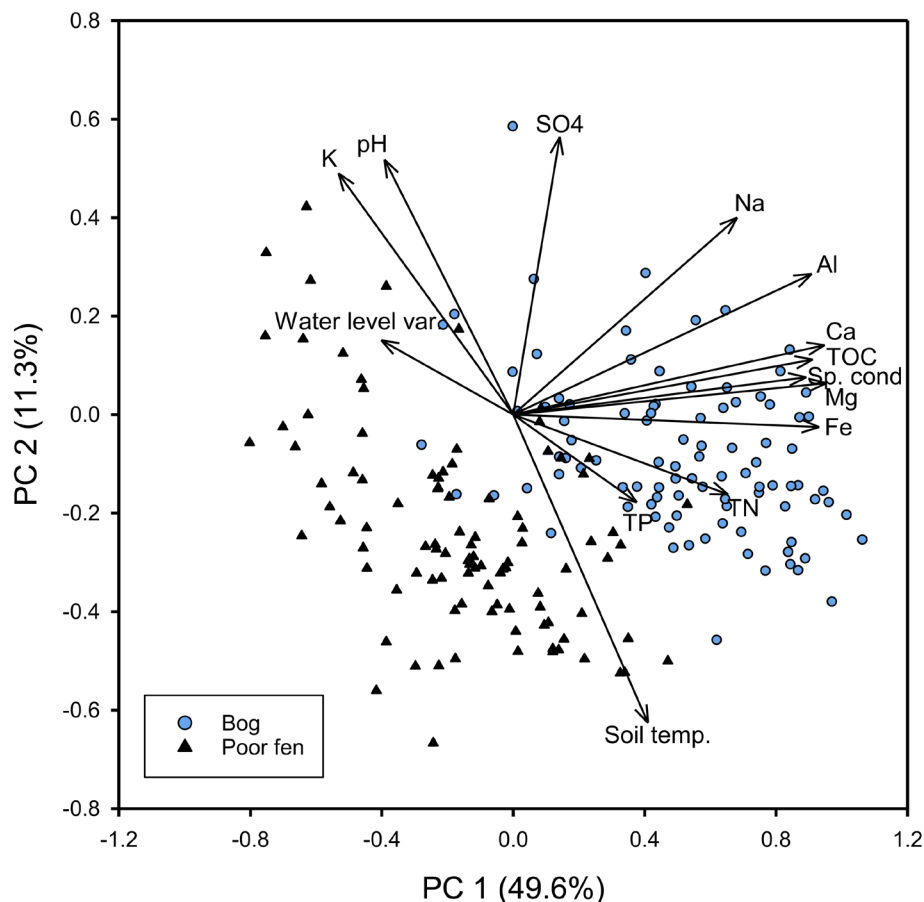


Figure 3. Principal components analysis of environmental variables in the bog (blue circles) and poor fen (black triangles). The environmental variables are component loadings and longer arrows correspond to stronger correlations with the closest axis. The factor scores for each measurement are indicated by the dots (triangles, circles).

Table 2. Component loadings from principal components analysis (PCA) of environmental variables (water level variation, soil temperature, surface water chemistry) in the bog and poor fen.

Parameters	PC1 (49.6%)	PC2 (11.3%)
pH	-0.39	0.52
Specific conductivity	0.89	0.08
Calcium	0.95	0.14
Potassium	-0.53	0.49
Magnesium	0.95	0.06
Sodium	0.68	0.40
Aluminum	0.91	0.29
Iron	0.93	-0.03
Sulfate	0.14	0.56
Total nitrogen	0.65	-0.16
Total phosphorus	0.38	-0.18
Total organic carbon	0.91	0.11
Soil temperature	0.41	-0.62
Water level variation	-0.40	0.15

process progressed, these differences became less apparent. In examining changes in %N of litter incubating in the bog versus the poor fen over time, %N was generally higher in the poor fen than the bog by year 5 (Fig. 5A). There were significant differences in N mass over the decomposition process both among litter types (RMANOVA, $p=0.001$) and between peatlands (RMANOVA, $p=0.002$) with no significant interaction (RMANOVA, $p=0.22$). In general, N mass in litter decreased over time, with larger decreases in the poor fen than the bog primarily reflecting mass loss rather than a change in %N (Supporting information).

Within the bog, the %N of litter incubated in hummocks was different than in hollows, but specific differences varied by moss litter type over time (RMANOVA, $p=0.04$); a similar interaction was found for N mass (RMANOVA, $p=0.009$). In general, %N of litter in hollows increased over time, but the same increase was not observed in hummocks (Fig. 5B). The mass of N in litter generally decreased over time except for the N mass of *S. divinum* in hollows, which increased over the decomposition period (Supporting information).

Variation in peatland-scaled P content of decomposing moss litter varied by moss type over time (RMANOVA, $p < 0.001$) (Fig. 5A). There was no significant effect of peatland over time (RMANOVA, $p=0.12$), nor a significant interaction (RMANOVA, $p=0.46$). The direction of the %P response over the decomposition process varied by moss type. In *Polytrichum*, %P decreased from year 0 to year 1 and then was similar between years 1 and 5. In contrast, %P in *S. angustifolium/fallax* increased after the first year and then was similar in year 5. Finally, %P in *S. divinum* was similar over the entire 5-year decomposition period (Fig. 5A). There were differences in %P among mosses at the start of the experiment, with lower %P in *S. angustifolium/fallax*, intermediate in *S. divinum* and highest in *Polytrichum* (Fig. 5A). Similar to N mass, there were significant differences in P mass among litter types (RMANOVA, $p < 0.001$) and between peatlands (RMANOVA, $p=0.005$) over the decomposition process with no significant interaction (RMANOVA, $p=0.49$). P

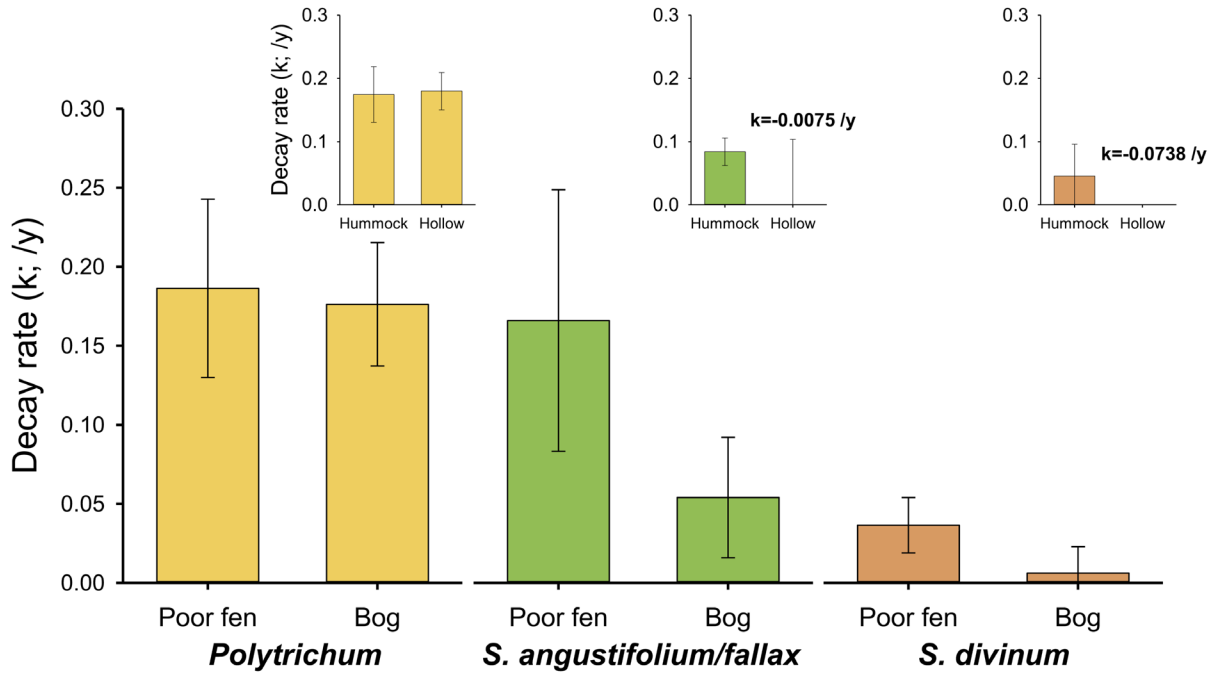
mass in litter generally decreased over time, with greater loss in the poor fen than in the bog (Supporting information).

In the bog, the %P of moss litter varied among moss types (RMANOVA, $p < 0.001$) and between hummocks and hollows (RMANOVA, $p < 0.001$) over the decomposition period. There was no significant interaction between microtopography and moss litter type over time (RMANOVA, $p=0.19$). In general, %P in moss litter was higher in hummocks than hollows at the start of the experiment, similar after 1 year, and lower in hummocks than hollows by year 5 (Fig. 5B). The mass of P in litter varied by both microtopography and litter type over time (RMANOVA, $p=0.049$) (Supporting information).

When examining the peatland-scaled N:P responses over the decomposition process, the effects of moss type (RMANOVA, $p < 0.001$) and peatland (RMANOVA, $p < 0.001$) were evident while there was no interaction between moss type and peatland (RMANOVA, $p=0.40$) (Fig. 5A). N:P increased over time (becoming more P-limited) in *Polytrichum* and also increased from years 0 and 1 to year 5 for both *S. divinum* and *S. angustifolium/fallax*, primarily due to responses in the poor fen (Fig. 5A). The initial N:P of *Polytrichum* was lower than that of *S. divinum* and *S. angustifolium/fallax*, while the N:P was similar for both *Sphagnum* types (Fig. 5A). As decomposition progressed, the N:P of the three moss types converged and were similar by year 5 (Fig. 5A). The trend in moss litter N:P over the decomposition period was more distinct in the poor fen than the bog, with a stronger increase in N:P in the poor fen over time (Fig. 5A). Within the bog, moss litter N:P varied by litter type over time (RMANOVA, $p < 0.001$), but there was no effect of microtopography (RMANOVA, $p=0.57$) nor a significant interaction (RMANOVA, $p=0.27$) (Fig. 5B).

There were no significant correlations between the decay rate measured over 1 year and %N or %P measured initially ($R=-0.20$, $p=0.60$ for %N; $R=0.07$, $p=0.86$ for %P) or after 1 year of decomposition ($R=0.44$, $p=0.24$ for %N; $R=-0.24$, $p=0.53$ for %P). There was a significant negative correlation between the decay rate measured after the first year and the initial N:P ($R=-0.76$, $p=0.02$), primarily reflecting the faster decomposition of *Polytrichum* which had a high %P and thus lower N:P. Similar patterns were observed with the decay rate measured after 5 years, with a lack of significant correlations with %N and %P measured initially ($R=-0.51$, $p=0.16$ for %N; $R=-0.23$, $p=0.58$ for %P), after 1 year ($R=-0.23$, $p=0.55$ for %N; $R=-0.62$, $p=0.07$ for %P) and after 5 years ($R=0.20$, $p=0.61$ for %N; $R=-0.42$, $p=0.26$ for %P). There was a positive correlation between the decay rate and N:P both measured at 5 years ($R=0.77$, $p=0.01$). Lastly, there was a positive correlation between initial %N and initial %P across moss litter types ($R=0.68$, $p=0.04$) that persisted in year 1 ($R=0.74$, $p=0.02$) and year 5 ($R=0.69$, $p=0.04$) (Fig. 6) although there was a shift in this relationship over time primarily reflecting the increasing %N in all litter types and secondarily the decreasing %P in *Polytrichum* litter over time.

(A) Decay rate after 1 year



(B) Decay rate after 5 years

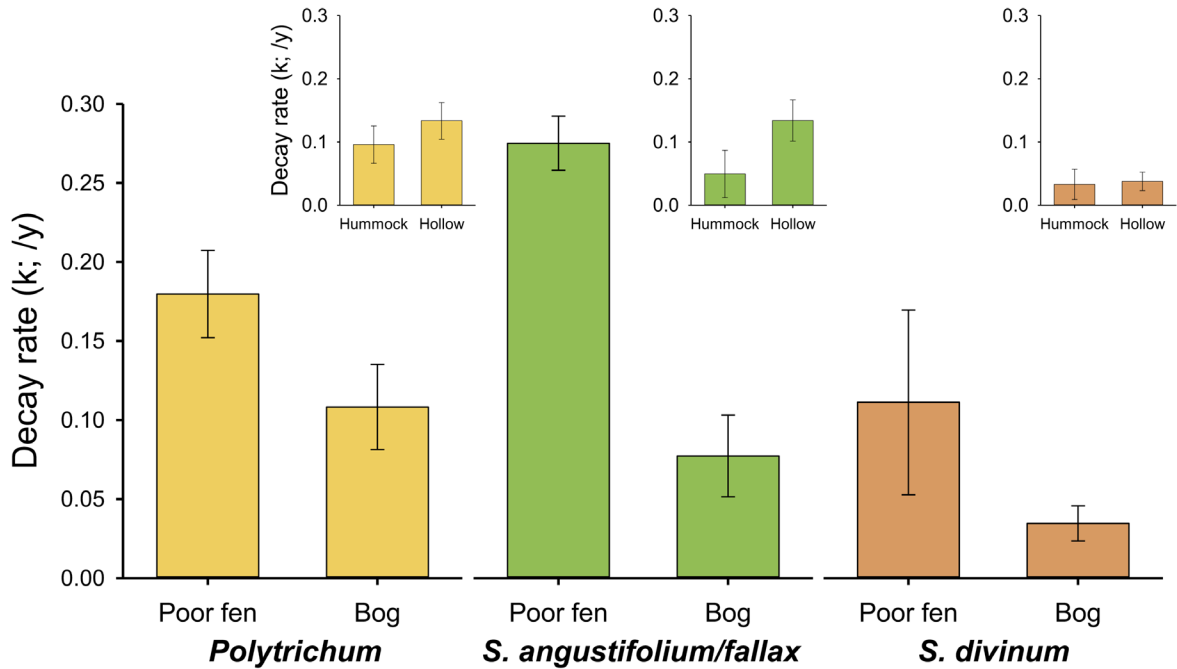


Figure 4. Mean decay rates ($\pm$ SD) of *Polytrichum* sp. (yellow bars), *Sphagnum angustifolium/fallax* (green bars) and *Sphagnum divinum* (orange bars) in the poor fen and the bog (large graphs) and in the hummock and hollow microtopographies in the bog (inset graphs) calculated (A) after 1 year of incubation and (B) after 5 years of incubation. The bog-scaled decay rates were calculated from measured decay rates in the hummock and hollow microtopographies and the percent cover of those two microtopographies in the bog. The scale of all y-axes is the same to facilitate comparison of decay rates among litter types, between peatlands and microtopographies, and over time.

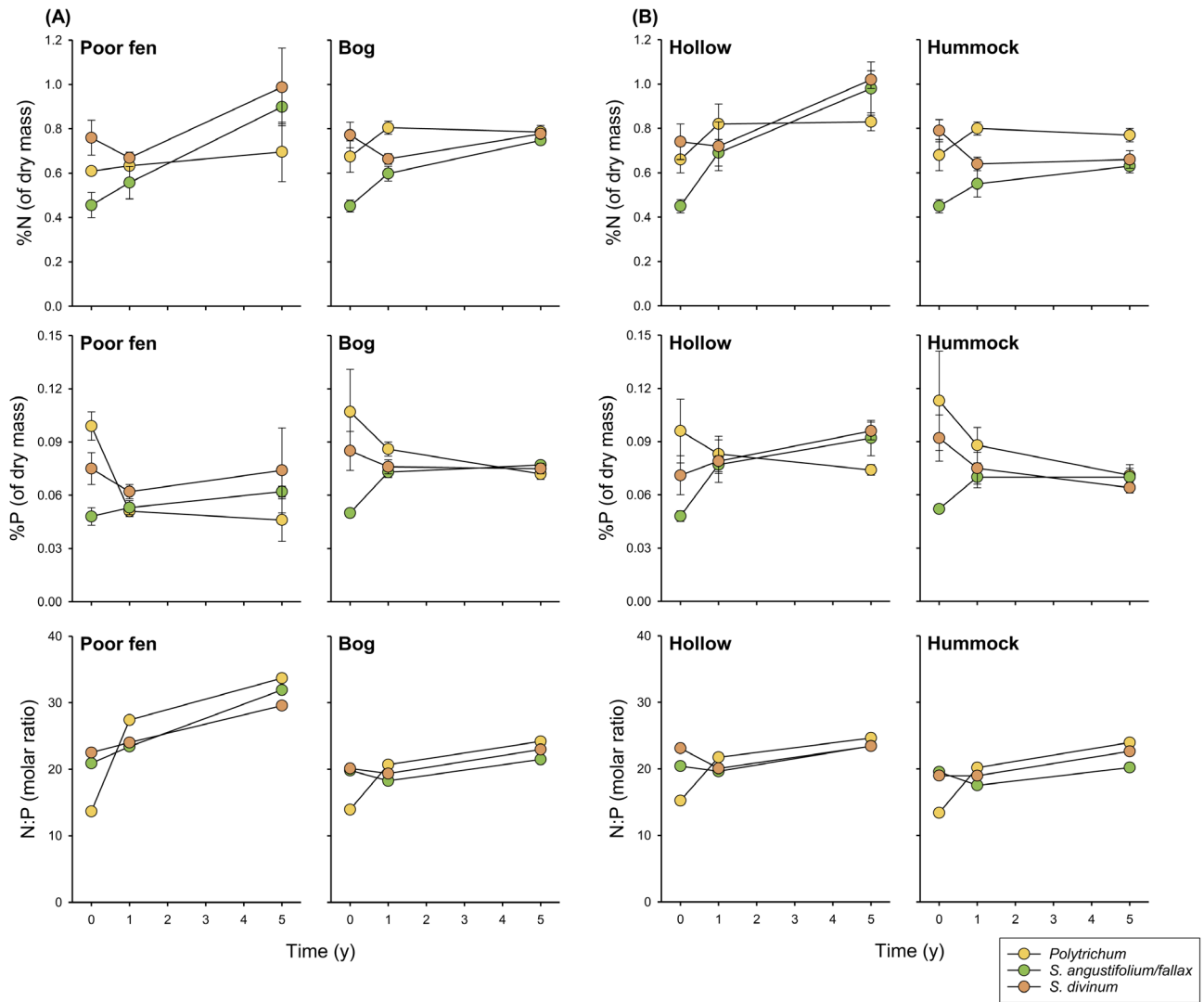


Figure 5. Temporal patterns in mean percentage nitrogen (top panels) and phosphorus (middle panels) content of dry mass ($\pm$ SD) and N:P (molar ratio; bottom panels) of *Polytrichum* sp. (yellow dots), *Sphagnum angustifolium/fallax* (green dots) and *Sphagnum divinum* (orange dots) in (A) the poor fen (left figures) and bog (right figures) and in (B) hollow (left figures) and hummock (right figures) microtopographies in the bog over the decomposition process (i.e. at 0, 1 and 5 years of incubation).

Discussion

In agreement with our predictions, decay rates were driven by intrinsic characteristics in the first year more so than extrinsic factors. However, there were still measurable extrinsic effects on decay rates in year 1, with faster decay in the poor fen than in the bog and faster decay in hummocks versus hollows. Intrinsic characteristics were the predominant driver of decomposition in part because the range in decay rates of the three moss types (from 0.181 year^{-1} for *Polytrichum* to 0.021 year^{-1} for *S. divinum*) was larger than the difference in decay rates between peatlands (poor fen: 0.130 year^{-1} ; bog: 0.079 year^{-1}) and between microtopographies (hummocks: 0.101 year^{-1} ; hollows: 0.033 year^{-1}). Our first-year results also agreed with the literature on moss decay rates in peatlands, which often finds that litter type predicts decay more than extrinsic drivers

(e.g. temperature, oxygen availability, nutrient availability, soil moisture) (Turetsky et al. 2008, Graf and Rochefort 2009, Hagemann and Moroni 2015, Barreto and Lindo 2018). A synthesis of moss decay in peatlands illustrates the large range in decay rates across taxa, with mean rates varying from 0.093 year^{-1} for *S. lindbergii* to 0.181 year^{-1} for *S. majus* (Fig. 7). However, there is also considerable variation in decay rates within a given moss species (Fig. 7), likely reflecting variation across locations (e.g. temperate versus boreal; Moore et al. 2007), peatland types (e.g. bog versus fen; Bayley et al. 2005, Moore et al. 2007, Yavitt et al. 2019), microtopographic positions (Johnson and Damman 1991, Latter et al. 1998, Turetsky et al. 2008, Hájek 2009, Bengtsson et al. 2016), as well as intraspecific variation in litter chemistry (Hogg et al. 1994, Chiapusio et al. 2018) and differences in methodology (e.g. incubation lengths in Fig. 7 ranged from 1 to 4 years).

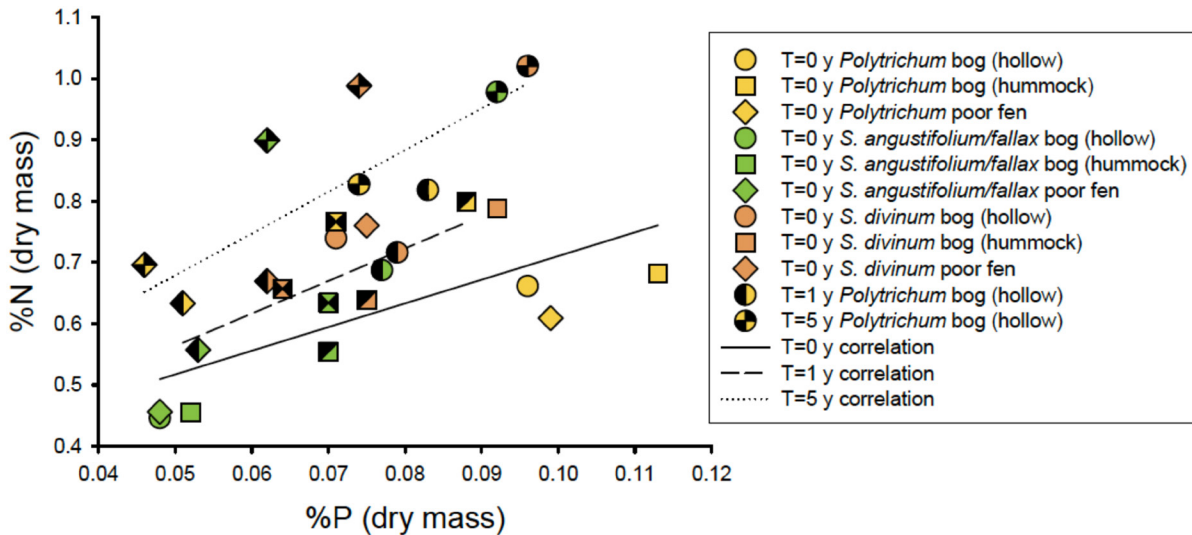


Figure 6. Positive correlations between %N (dry mass) and %P (dry mass) of *Polytrichum* sp. (yellow symbols), *Sphagnum angustifolium/fallax* (green symbols) and *Sphagnum divinum* (orange symbols) in hollow (circles) and hummock (squares) microtopographies in the bog and the lawn (diamonds) microtopography in the poor fen at 0 (open symbols), 1 (half-filled symbols) and 5 (quarter-filled symbols) years of incubation. Because the legend would display 27 separate symbols, the full set of symbols only for year 0 are shown as an example. There were significant correlations between %N and %P across litter types at the start of the experiment (year 0: $R=0.68$, $p=0.04$; slope=3.9; solid line), after 1 year ($R=0.74$, $p=0.02$; slope=5.3; dashed line) and after 5 years ($R=0.69$, $p=0.04$; slope=6.8; dotted line).

Interestingly, the 5-year decay rates for *S. angustifolium/fallax* measured in this study spanned the range of decay rates previously reported for both *S. angustifolium* and *S. fallax* (Fig. 7), illustrating the extent that extrinsic factors can also drive variation in decay rates. Some of the variation in decay rates of *S. angustifolium/fallax* may have resulted from the necessity of combining two *Sphagnum* species, each with different intrinsic characteristics, into one litter type in our analysis. However, combining these two moss species into the *S. angustifolium/fallax* litter type did not appear to lead to greater variation in decay rates compared to the other two mosses (i.e. standard deviations, reflecting variation among replicates, were similar across litter types; Fig. 4, 5). Our finding that decay rates were generally fastest for *Polytrichum* and *S. angustifolium/fallax* and slowest for *S. divinum* was consistent with the literature (Fig. 7). Interestingly, the decay rates for these three taxa were most similar and fell within the middle of the decay continuum of the 12 taxa summarized in Fig. 7. We also highlight a lack of published data on *Polytrichum* decay rates, especially when compared to *Sphagnum* (Fig. 7). We suggest that future studies on moss decomposition include *Polytrichum*, as it has been postulated that *Polytrichum* may prevail over *Sphagnum* under the drier conditions expected in peatlands with climate change (Roulet et al. 1992, Moore et al. 1998, Bubier et al. 2007, Norby et al. 2019).

Environmental drivers

Litter decomposition rates are often faster in fens than bogs (Bayley et al. 2005, Moore et al. 2007, Yavitt et al. 2019) in part due to greater nutrient availability in fen ecosystems (Bayley et al. 2005). In our study, the faster decay rates in the

poor fen did not seem to be driven by greater nutrient availability as surface water nutrient concentrations were higher in the bog than the poor fen. Greater demand for nutrients by litter-decaying microorganisms in the poor fen may have led to the more rapid decrease in the N and P mass of decaying litter in the poor fen versus the bog. While we observed differences in solute concentrations between the bog and poor fen, a previous study on the MEF found that porewater chemistry in these two peatlands was much more similar compared to a rich fen, which had higher concentrations of many solutes (Griffiths et al. 2019). Differences in soil moisture between the bog and poor fen may have also contributed to differences in decay rates between these two peatlands. High soil moisture and long periods of flooding can increase litter decay rates, likely because wetter conditions enhance litter fragmentation and leaching, and promote favorable microbial conditions (Zhang et al. 2019). In year 1 of our study, the water table in the poor fen was higher than in the bog, and this higher water table and the presumably greater soil moisture may have promoted decomposition. Lastly, peat temperature may have driven differences in litter decomposition between the poor fen and the bog. The annual range in peat temperature was larger in the poor fen than the bog and warmer summer peat temperatures in the poor fen may have promoted microbial activity and thus contributed to faster decay rates. However, both annual mean temperature and cumulative temperature were higher in the bog than the poor fen, making the role of temperature on litter decay unclear. Overall, the environmental data suggest that nutrient limitation, peat temperature and water availability may have affected the differential decay rates measured between the bog and poor fen in the first year.

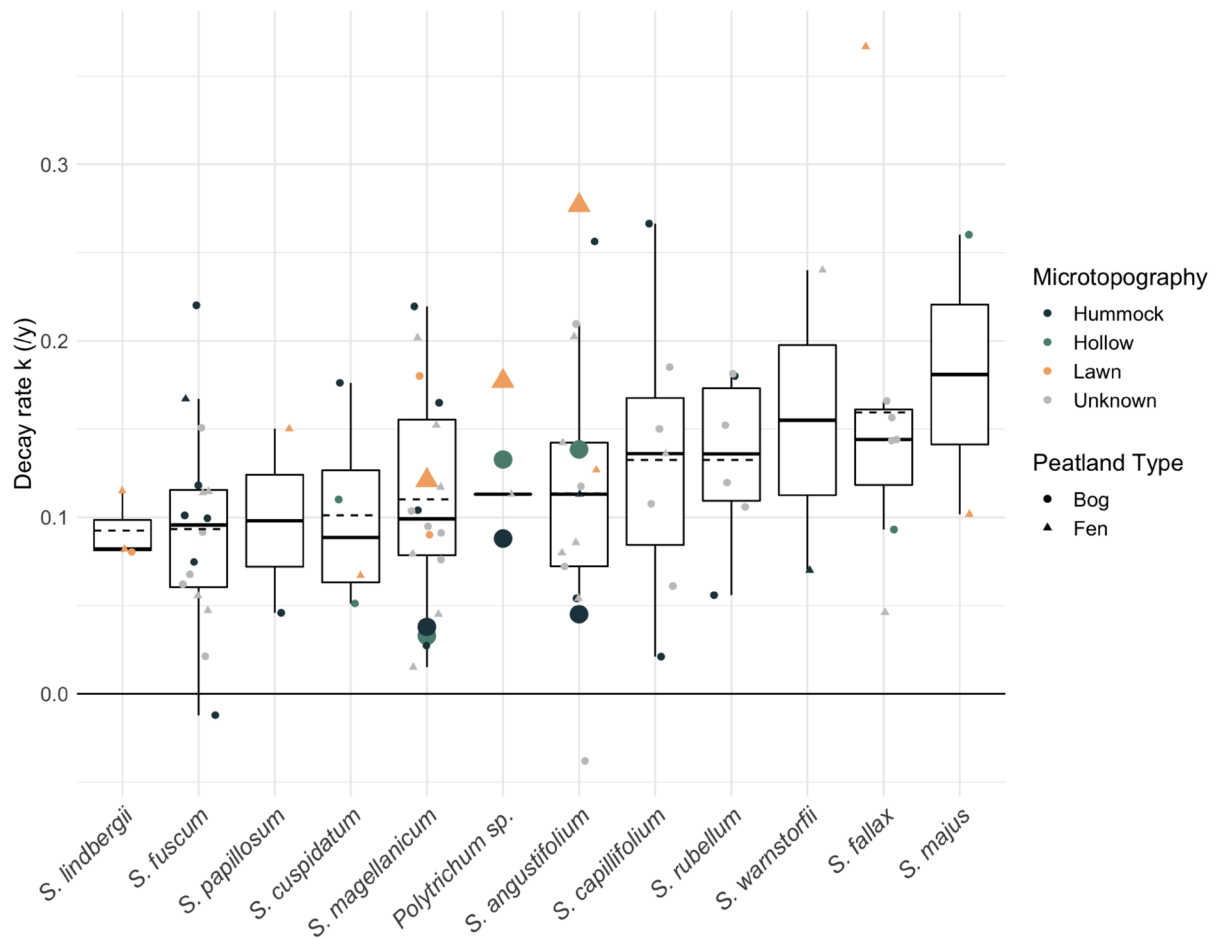


Figure 7. Summary of moss decay rates (k ; year⁻¹) from the literature (small symbols) and from this study (large symbols; 5-year data) that were measured in bogs (circles) or fens (triangles) and within those peatlands, in hollows (green), hummocks (black) or lawns (orange), or where the microtopography was not noted (grey). Box plots represent the mean (dotted line), median (solid line), 25th and 75th percentiles (edges of boxes) and 5th and 95th percentiles (whiskers). Decay rates of *S. angustifolium/fallax* from this study were included with literature data on *S. angustifolium*, and decay rates of *S. divinum* from this study were included with *S. magellanicum*. Decay rate data were extracted or were calculated from mass loss assuming an exponential decay from: Bartsch and Moore (1985), Lieffers (1988), Rochefort et al. (1990), Johnson and Damman (1991), Szumigalski and Bayley (1996), Limpens and Berendse (2003), Waddington et al. (2003), Thormann et al. (2004), Moore et al. (2007), Turetsky et al. (2008), Graf and Rochefort (2009), Hájek (2009), Bragazza et al. (2012), Tarvainen et al. (2013), Jiroušek et al. (2015), Bengtsson et al. (2016), Berube and Rochefort (2018), Mäkilä et al. (2018) and Nikonova et al. (2019).

After 5 years, extrinsic drivers appeared to play an increasingly important role in the decomposition of mosses. Specifically, after 1 year, the pattern of decay rates for the three moss types was consistent in the two peatlands, with faster decay of *Polytrichum* and *S. angustifolium/fallax* and slower decay of *S. divinum*. However, after 5 years, that same pattern in moss decay was only observed in the bog, while in the poor fen, decay of *S. angustifolium/fallax* was faster than *Polytrichum* and *S. divinum*. The differing pattern in decay in the bog versus the poor fen in year 5 suggests that extrinsic factors inherent to each peatland were acting on moss decomposition in different ways, although the exact mechanisms could not be resolved. Given that moss litter decay in peatlands is a slow process (i.e. dry-mass remaining after 5 years averaged 60% and ranged from 26% to 86%), longer measurement time frames are important for

understanding the implications of intrinsic versus extrinsic drivers of moss decay.

Decay rates also differed between hummocks and hollows in the bog with faster decay in hummocks than hollows in year 1 and the reverse pattern in year 5. While contrary to our hypothesis, the year 1 finding was consistent with another study at the MEF that found faster decay of *Sphagnum* peat cores in hummocks versus hollows after 1 year, possibly due to higher temperatures in hummocks versus hollows in summer (Farrish and Grigal 1985). In contrast, our year 5 finding of faster decay in hollows than hummocks was consistent with our hypothesis and similar to most published studies (Belyea 1996, Turetsky et al. 2008, Hájek 2009). Faster decomposition in hollows versus hummocks may have been due to the greater cumulative temperature measured in the hollow over the 5-year decomposition period. While temperature is

often positively correlated with decay rate, the effect of soil moisture on decomposition is typically unimodal, with soil moisture on either extreme (dry or saturated) resulting in the slowest decay and intermediate moisture conditions accelerating decomposition. For example, litter decay was fastest in or slightly above the zone of water table fluctuation, irrespective of *Sphagnum* species studied or microtopography, in a Scottish bog (Belyea 1996, Belyea and Clymo 2001). In this study, we estimated that the water table did not reach the height of litterbags deployed in the hummocks, suggesting that moisture was limiting decay in that microtopography. In summary, moss decay measurements revealed a shifting importance of intrinsic versus extrinsic drivers as the decomposition process progressed. This response was observed primarily in the fastest-decomposing mosses (*S. angustifolium/fallax* and *Polytrichum*), and less-so in the slower-decomposing moss (*S. divinum*). We hypothesize that if *S. divinum* decomposition was measured over a longer period, differences between microtopographic positions may become evident.

Moss litter chemistry

The nutrient content of litter exerts a strong influence on decay across a variety of litter types (e.g. mosses, graminoids and sedges) decomposing within wetland ecosystems (Aerts and de Caluwe 1997, Tao et al. 2019), but studies on *Sphagnum* decomposition in peatlands often find other chemical controls on decay rates (e.g. phenolics, lignin, carbohydrates; Bragazza et al. 2007, Moore et al. 2007, Turetsky et al. 2008). For example, phenolic content varies across *Sphagnum* species (Chiapusio et al. 2018), and phenolic compounds like *Sphagnum* acid may influence decay rates more so than N and P (Verhoeven and Toth 1995). The lack of effect of litter N and P on decay rates in this study and the multitude of chemical constituents that were found to affect decomposition in other studies highlights the chemical complexity of mosses that can influence decomposition. A fruitful area of future research might focus on examining how this array of chemical constituents changes and interacts over time to affect decay rates in multiple moss taxa in the same environmental setting as well as across different environmental conditions.

While moss litter chemistries measured in this study were generally not correlated with decay rates, patterns emerged that provided a more comprehensive understanding of moss decomposition. The %N of *Polytrichum* and *S. angustifolium/fallax* increased over time and may have reflected N that was immobilized by microorganisms colonizing the litter (Thormann and Bayley 1997, Moore et al. 2006). In contrast, the %N of *S. divinum* did not change over time, possibly because the slow decay corresponded with a slow colonization of microorganisms. The pattern in %P over time was different than %N: %P increased in *S. angustifolium/fallax*, decreased in *Polytrichum* and did not change in *S. divinum* over the 5-year period. The pattern in %P over time was related to the initial P content of the three moss types; *Polytrichum* had the highest initial P content and lost P while *S. angustifolium/fallax* had the lowest initial P content and gained P. This relationship

between initial P content and the change in %P over time, and a lack of a similar relationship with N content, was also found in an extensive study that examined the decay of 10 litter types in 18 upland forest sites across Canada (Moore et al. 2006). Peatland microorganisms and vegetation can be N-, P- or co-limited for N and P (Aerts et al. 1992, Verhoeven et al. 1996, Bedford et al. 1999, Hill et al. 2014, Lin et al. 2014, Wang et al. 2014, 2018, Pinsonneault et al. 2016) and our data suggest that P may have been more limiting than N for moss-decaying microorganisms. The initial N:P of all three mosses (14:1 for *Polytrichum*, 20:1 for *S. angustifolium/fallax*, 22:1 for *S. divinum*) was higher than global N:P estimates for soil microbial biomass (7:1 in Cleveland and Liptzin 2007, 6:1 in Xu et al. 2013), suggesting a greater demand for P than N by soil microbes in these peatlands. The N:P of decaying mosses also generally increased over time, suggesting a shift towards stronger P limitation throughout the 5-year study. Stronger P than N limitation in MEF peatlands was also observed in ecoenzymatic analyses of peat (Hill et al. 2014, Lin et al. 2014).

Summary

In our moss decomposition experiment, we found that intrinsic characteristics were a strong driver of decay in the first year and environmental extrinsic drivers played a larger role in decomposition by year 5. Our approach to measure decay rates at multiple time points over a relatively long period allowed us to examine how intrinsic versus extrinsic drivers changed over time. Even though our study measured moss decomposition over a longer time period than most (Moore et al. 2017), we still did not capture the full extent of decomposition in these peatlands. Thus, when feasible, future experiments should measure decay rates of peatland litter throughout the entire decomposition process. Ultimately, long-term measurements will result in more accurate rate estimates and will allow for a better understanding of the degree to which intrinsic versus extrinsic drivers influence decomposition, thus improving the representation of this important peatland ecosystem process in regional and global C cycle models.

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Author contributions

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Data availability statement

Data are available from multiple repositories. Datasets are cited in the manuscript as 'data citation' and includes the following citations: Graham et al. 2019, Hanson et al. 2015, Hanson et al. 2016, Sebestyen et al. 2020a, Sebestyen et al. 2020b, Sebestyen et al. 2020c, Sebestyen et al. 2020d, Sebestyen et al. 2021b, Shelley et al. 2021a.

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