

# **Bryophyte community composition as a function of environment in high-altitude peatlands of the Pocono Plateau**

A thesis presented to the faculty of Department of Biology at Villanova University

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By

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## BIOGRAPHICAL SKETCH

I was born in 1998 in Newark, Delaware. As a child, I was encouraged to find joy and wonder in the natural world, which undoubtedly led to my enduring love of plants. I attended the University of Delaware, majoring first in Wildlife Ecology and Conservation, and then adding a second major of Plant Science. While at UD, I discovered a passion for plant ecology and a particular fondness for mosses, which I believe are the unsung heroes of the plant kingdom. Shortly after graduating, I interviewed with Kel Wieder to see if I was a good match for his lab; I knew I was when I saw the enormous moss anatomy poster on his office wall.

Throughout my time at Villanova, I have honed my skills as a research biologist, and I am grateful to those who have inspired me. I look forward to publishing my work, to share what I have found with those who can use it to conserve our precious land.

While my next chapter is not yet clear, I am sure that moss will never be far from my mind.

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## ABSTRACT

Peatlands are wetlands that accumulate organic matter over time, in many cases by the action of an extensive bryophyte groundcover that facilitates inundation and resistance to decay. Despite the critical importance of bryophytes to ecosystem function, bryophyte community patterns in the Pocono Plateau of Pennsylvania had not previously been formally evaluated. Moreover, the relationship of these bryophyte communities to significant environmental factors had not been established. This is of particular concern given the isolation and vulnerability of individual peatlands in the Appalachians. Peatland bryophyte communities from three complexes were quantified along with canopy openness, depth to water table, peat depth, and numerous facets of porewater chemistry. Eight broad groupings of community types were described from shared bryoflora components. All three physical variables were found to be significantly correlated with community composition, and pH was found to be nearly correlated. Influence of the most prominent variable, canopy openness, suggests that community composition may be substantially impacted by woody encroachment. Uncommon communities, often dominated by state-imperiled *Sphagnum* species, were more strongly associated with high canopy openness and thus more at risk with increasing encroachment. Persistent losses of this kind could reduce species diversity and functional diversity of Pocono poor fens. Additionally, unexpectedly high base cation levels associated with proximity to major roadways provides insight into an anthropogenic threat that may affect peatlands near developed areas, a cause for concern as urbanization progresses.

## CHAPTER I: CONTEXT AND REVIEW OF CURRENT RESEARCH

### OVERVIEW

In a broad sense, peatlands are wetland ecosystems that accumulate partially decayed organic matter (peat), because the rate of organic matter production at the surface exceeding the rate of decomposition throughout the peat column over long periods of time (Wieder et al. 2006). The majority of peatland area (83 %) exists in boreal or subarctic regions, while temperate regions contain just 4 % of peatland area (Leifeld and Menichetti 2018). In North America, temperate peatlands are fewer, smaller, and more dispersed than their extensive boreal counterparts (Cameron 1968; Wieder et al. 1981). Perhaps because of their relatively small contribution by these metrics, temperate peatlands have been underrepresented in research, particularly in the context of global change (Wieder and Yavitt 1994; Schultheis et al. 2010; Cai and Yu 2011). However, the relative isolation of these peatlands as “ecological islands” increases the threat posed to their representative species by global change (Francl et al. 2004; Schultheis et al. 2010; Cartwright 2019). In northern U.S. states, peatlands support 7-13 % of the uncommon or rare flora despite occupying less than 0.1 % of the state area on average (Bedford and Godwin 2003). In the central Appalachians, there is low species similarity (high beta diversity) among these wetlands, and locally rare plants are sometimes restricted to only a few disjunct sites (Walbridge 1994). These insights contrast with the traditional view of peatlands as species-poor ecosystems, a misconception based in part upon a prevailing focus on vascular plants and consequent exclusion of bryophytes from consideration (Vitt et al. 1995; Newmaster

et al. 2005). Peatlands are often floristically and functionally dominated by mosses; thus, the significance of bryophytes therein must be underscored (Vitt 2006a).

In the temperate eastern U.S., peatlands are spatially concentrated in the Appalachian Highlands physiographic division (Cameron 1968; Halsey et al. 2000). Plant species diversity of the region is well documented (Franci et al. 2004; Thompson et al. 2012), but gaps remain in characterization of the plant communities – the associations of plants within the peatland ecosystems. In the glaciated Appalachian Plateaus of Pennsylvania, the composition and structure of peatland bryophyte communities have not been rigorously assessed (Schuette, pers. comm.). Moreover, a thorough understanding of the responses of bryophyte communities to global change is paramount in advancing the frontiers of bryophyte community ecology (Vitt 2006b). Mosses are particularly vulnerable to a changing environment, as their life history strategy and persistence are substantially reliant upon water availability (e.g., sexual reproduction requiring free water between gametangia; little to no ability to regulate hydrologic homeostasis); moreover, bryophytes are poorly adapted to compete with vascular plants (Hallingbäck and Tan 2014). Thus, it is critical not only to assess the community structures of Appalachian peatland bryophytes, but also to analyze their potential responses to global ecosystem change.

## **GENERAL ATTRIBUTES OF FENS**

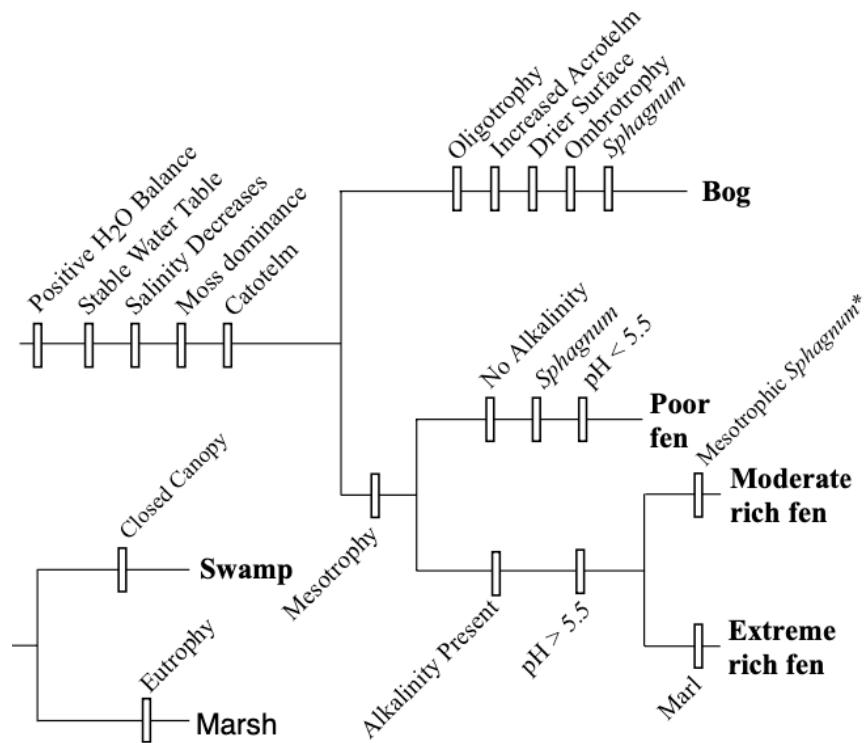
Peatlands may be broadly categorized into four types: marsh, swamp, bog, and fen. Classification into these types varies across disciplines and institutions, with each differentiated based on topography, hydrology, hydrochemistry, vegetation, ontogeny, climate, and substrate (Bridgham et al. 1996; Vitt 2006a). One of the most common

schemes stems from the Uppsala school of ecology and focuses on hydrochemical ontogeny (Gorham 1957; Bridgham et al. 1996). du Rietz (1954) characterizes bogs as ombrogenous (“rain-fed”), and fens as geogenous (“ground-fed”). These terms refer, respectively, to the development of bogs from water and nutrients derived solely from precipitation, in contrast to the development of fens primarily from ground or surface water sources (Vitt 2006a). Many central Appalachian peatlands are regarded as fens by this criterion, although they bear certain vegetational similarities to Canadian bogs (Wieder and Yavitt 1994; Francz et al. 2004; Cai and Yu 2011).

Fens can be further distinguished ontogenically by the source of geogenous waters, subdivided amongst soligenous, topogenous, and limnogenous origins. Soligenous sources involve the percolation of flowing water, particularly from seeps; topogenous sources include groundwater or stagnant surface water; and limnogenous sources are flood-derived, especially from floodwaters perpendicular to the direction of stream flow (du Rietz 1954; Bridgham et al. 1996; Vitt 2006a). All of these are nonetheless broadly grouped under the umbrella of geogeny.

In addition to geogenous origin, fens are characterized by continued minerotrophy, the acquisition of mineral nutrients from periodic contact with ground or surface water (du Rietz 1954; Vitt 2006a). The water source is variably enriched in base cations from the substrate, which also distinguishes fens along a nutrient gradient termed the poor fen-rich fen continuum (Zoltai and Vitt 1995; Bedford and Godwin 2003). Poor fens typically have a pH below 5.5, with little to no alkalinity (Figure 1.1) (Vitt, 2006b; Zoltai & Vitt, 1995). Moderate rich fens have greater alkalinity and a pH between 5.5 and 7.0, and extreme rich fens have a pH above 7.0 from even greater alkalinity.

Generally, inorganic nitrogen (N) occurs in low concentration in fen porewater, compared to concentrations in other soils (Gorham 1957; Limpens et al. 2006). Consequently, N is often limiting to plant growth in northern peatlands (Bridgham et al. 1996; Moore 2002). A considerable proportion of fen nitrogen input is from surface or groundwater rather than precipitation, although the ultimate source of these nutrients is partially confounded by the complexity of fluxes at large spatial scales (Limpens et al. 2006). Additionally, biological fixation of atmospheric diatomic nitrogen ( $N_2$ ) also has been a historically underestimated source of N in bogs and fens, and the resulting input can exceed that of deposition alone (Vile et al. 2014; Wieder et al. 2019, 2020). Phosphorus (P) occurs in even lower concentrations than N (Vitt and Chee 1990). In rich fens, N may



**Fig. 1.1.** A tree diagram showing sample criteria for distinguishing the four major groups of peatlands, and sub-classifications of fens. Adapted from Vitt (2006a).

be enriched relative to P, such that P is limiting (Walbridge and Navaratnam 2006), although some fens may be P-enriched by anthropogenic inputs (Bedford and Godwin 2003). Regardless, under natural conditions, macronutrients are scarce in fens, and gradients of micronutrients and macronutrients occur with relative independence to one another (Vitt and Chee 1990; Bedford and Godwin 2003).

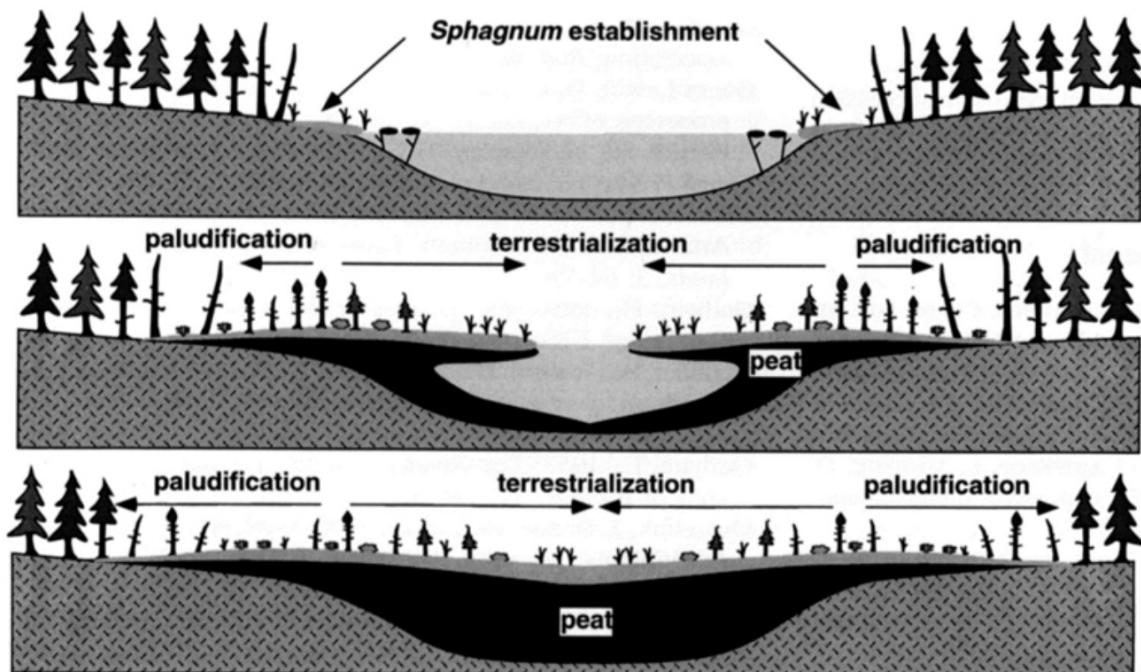
## **ROLE OF *SPHAGNUM***

Corollary to the poor-rich fen continuum of du Reitz (1954) are the floristic differences he described, particularly among the bryophytes that make up a considerable proportion of northern fen vegetation (Zoltai and Vitt 1995). Under this scheme, poor fen communities were regarded having low indicator species richness, being dominated by *Sphagnum*, and rich fen communities as having high indicator species richness and being dominated by brown mosses, an informal grouping of the true mosses (Bryopsida) (Vitt 2006a). Over time, a misconception has emerged that overall species richness (beyond that of indicator species) follows a similar pattern. However, overall species richness is highly variable among sites and is not always well predicted by the fen nutrient status (Vitt et al. 1995; Bridgman et al. 1996). Moreover, vascular plants were historically the focus of indicator species concepts for fens (Vitt et al. 1995). Peatland bryophytes also comprise indicator communities that vary along environmental gradients differently from vascular indicator communities. Such bryophyte communities are equally useful in the assessment of both past and present peatland succession and development (Gignac and Vitt 1994; Bedford and Godwin 2003).

In addition to the characteristic dominant *Sphagnum* layer in poor fens, moderate-rich fens often contain mesotrophic *Sphagnum* species, and rich fens may also contain *Sphagnum* in varying proportions (Vitt 2006a). This is particularly true in the temperate U.S., where moderate-rich fens can have a relatively high proportion of *Sphagnum* cover (Franc et al. 2004). *Sphagnum* are ecosystem engineers in the development and continued functioning of many fens (van Breeman 1995; Rydin et al. 2006; Vile et al. 2010). *Sphagnum* species possess multiple key traits that facilitate modification of peatlands: an ability to drive acidic and anoxic conditions, an ability to thrive in the resultant nutrient-poor environment, and the resistance of both live and dead tissues to decomposition (Rydin et al. 2006; Turetsky et al. 2008). The main physiological mechanism that enables this manipulation is an abundance of polyuronic acids in *Sphagnum* tissues (Clymo and Hayward 1982). These acids host cation exchange sites that reversibly bind nutrient cations from the surrounding water while releasing H<sup>+</sup>, thus acidifying peat interstitial waters. With a blanket of dominant *Sphagnum* and up to 30% uronic acid content by mass in each shoot, the acidification can be pronounced (Clymo 1963; Clymo and Hayward 1982; McKnight et al. 1985).

Acids both in tissues and in peat water also endow *Sphagnum* with a degree of decay resistance, particularly in later stages of decomposition (Clymo and Hayward 1982; Rydin et al. 2006). As healthy shoots die and decay, they are gradually buried by new growth. In the lower peat layers, conditions are too acidic and oxygen-poor for advanced degradation to occur (Clymo and Hayward 1982). The result is the characteristic vertical structure of peat profiles; the acrotelm is the upper layer rich in oxygen and active water flow, while the catotelm is the lower layer of semi-permanent water saturation with poorly

aerated organic matter (Ingram 1978; Kuhry and Turunen 2006). Ultimately, *Sphagnum* alters its surroundings to the extent that it functionally creates its own habitat (Rydin et al. 2006). Over large spatial and temporal scales, constant environmental manipulation by *Sphagnum* is a crux of peatland ecological processes. Colonization and expansion of *Sphagnum* are important in fen and bog succession, driving them towards drier, acidic, nutrient-poor conditions (Clymo and Hayward 1982; Bridgham et al. 1996; Kuhry and Turunen 2006). Gradual blanketing by *Sphagnum* was especially significant in terrestrializing small lakes and paludifying surrounding landforms (Figure 1.2) left behind by glacial retreat at the termination of the Pleistocene (Vitt & Slack, 1975; Halsey et al., 2000; Vitt, 2006b). Once mid-stage successional peatlands are formed, in the absence of disturbance, they form large carbon pools that remain relatively stable over long periods of

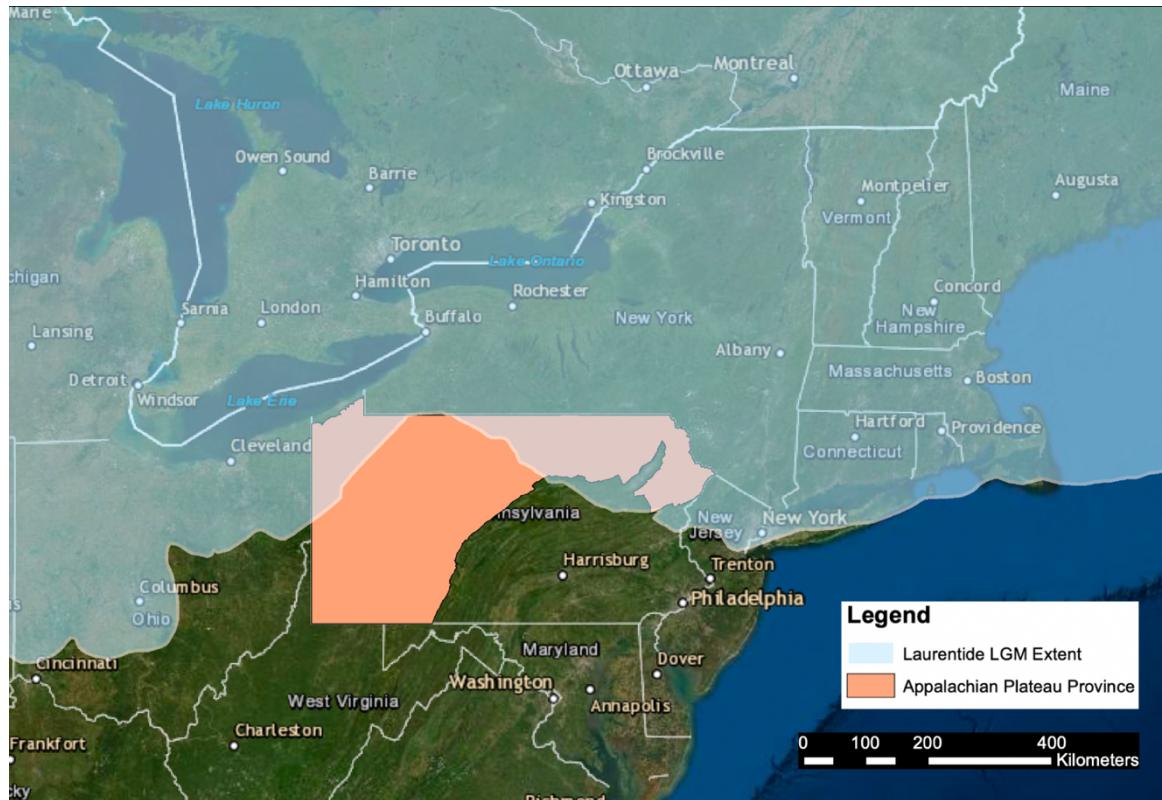


**Fig. 1.2.** Processes of *terrestrialization* – the infilling of a water body by progressive inward expansion of *Sphagnum* – and *paludification* – the outward expansion of *Sphagnum* leading to reduced cover of surrounding vegetation. From Klinger (1996).

time (Gorham 1991; Kuhry and Turunen 2006; Yu 2012). Out of all plant genera in northern temperate and boreal ecosystems, *Sphagnum* sequesters the greatest proportion of carbon, which contributes to enormous carbon sinks in peatland soils (Berendse et al. 2001). Globally, peatlands retain a third of the Earth's soil carbon, around 400-600 Gg, despite occupying less than 3% of total land area (Gorham 1991; Yu et al. 2010; Yu 2012). Although primary production is typically low, inhibition of decay by *Sphagnum* produces resistant organic carbon pools that may endure for tens of millennia.

## **FORMATION AND CHARACTERISTICS OF APPALACHIAN PEATLANDS**

Around 20 ka BP (thousand years before present), during the Last Glacial Maximum (LGM), much of the northern range of the Appalachians was covered by the Laurentide ice sheet (Dyke and Prest 1987). Towards the end of the Late Wisconsin glaciation (c. 18.5 ka BP), the ice sheet reached its southeastern limit (Figure 1.3) near the Pocono plateau in Pennsylvania (Dyke and Prest 1987). Flora around the ice sheet terminus primarily consisted of tundra communities of grasses, forbs, and bryophytes (Watts 1979). By about 18-16 ka BP, glacial retreat initiated along this southeastern boundary (Dyke and Prest 1987; Halsey et al. 2000). The result of this brief glaciation of the Pennsylvanian Appalachian Plateaus was a terminal moraine of hills and kettlehole basins, some of which formed shallow lakes (Cameron 1970). The favorable montane climate facilitated colonization of these lakes and lake basins by peatland bryophytes, some of which were already present in tundra communities (e.g., *Aulacomnium* spp. and *Drepanocladus* spp.) (Rigg & Strausbaugh, 1949; Watts, 1979; Vitt, 2006b). Primary formation of peatlands on moist glacial till also occurred to a limited extent (Cameron 1968, 1970; Kuhry and



**Fig. 1.3.** The extent of the Laurentide ice sheet during the Last Glacial Maximum (LGM) (pale blue) in the northeastern U.S. The ice sheet terminus aligned near the eastern boundaries of the Appalachian Plateau Province of Pennsylvania (orange). LGM Laurentide data courtesy of the University of Koeln; physiographic province data courtesy of Pennsylvania Department of Conservation of Natural Resources. Basemap from ESRI.

Turunen 2006). Development of significant peat deposits began by c. 9-13 ka BP (Wieder et al. 1981; Wieder and Yavitt 1994). In many of these sites, initial peat-forming bryophytes were likely brown mosses, some giving way to *Sphagnum* over the course of hydroseral succession (Kuhry and Turunen 2006; Cai and Yu 2011).

Comparisons of current vs. historical extents of Appalachian peatlands are complicated by gaps in information. Understanding of lateral expansion in eastern North American peatlands is a somewhat recent development compared to European models (Damman 1979; Anderson et al. 2003; Ireland and Booth 2011). In addition to

shortcomings in chronological data about the extents of individual peatlands, there are few reliable historical accounts of their distribution across larger scales. Early accounts up through the mid 20<sup>th</sup> century did not always distinguish peatlands among types, nor did they necessarily regard peatlands *en masse* as a unique category of wetland (Bedford and Godwin 2003).

Nonetheless, the physiographic heterogeneity of the Appalachian Plateau landscape compared to that of present-day boreal peatland complexes suggests that Appalachian peatlands have always been small and dispersed (Cameron 1968; Wieder and Yavitt 1994; Halsey et al. 2000). These peatlands have developed and persisted in the Appalachians owing to local conjunctions of cool, moist climate, heterogenous topography, and drainage-resistant substrate (Rigg and Strausbaugh 1949; Damman 1979; Schultheis et al. 2010). However, the overlap of such conditions favoring peat formation occurs sporadically across the landscape, isolating individual Appalachian peatlands from each other (Stewart and Nilsen 1993; Francz et al. 2004).

Appalachian Plateau peatlands are most aptly described as fens, based on their hydrologic regimes; however, their vegetation partially resembles boreal bogs (Stewart and Nilsen 1993; Wieder and Yavitt 1994; Francz et al. 2004); in this way they bear some similarity to the kettlehole “bogs” of the Great Lakes region (Vitt and Slack 1975). Likewise, Appalachian peatlands fall between the typical fen and bog classifications in terms of nutrient concentrations. They receive a greater proportion of nutrients from groundwater than any true ombrotrophic bog (Stewart and Nilsen 1993), but may not exhibit base cation enrichment to the same degree as boreal fens (Wieder 1985). In part, the lack of base cations reflects the nutrient-poor bedrock of shales and sandstones – and

glacial sediments from these bedrocks – that typically underlie impoverished fens in the northern U.S. (Cameron 1970; Bridgman et al. 1996). Additionally, a decrease in climatic moisture in the north-central Appalachians at c. 1.3 ka BP may have functioned as a recent allogeic force of succession (Cai and Yu 2011). Nonetheless, thinning of peat catotels among many Appalachian fens suggests a late stage of development with an equilibrium between production and decomposition (Damman 1979). With lower stocks of subsurface organic matter, carbon pools in these peatlands are generally smaller than those of boreal peatlands (Halsey et al. 2000; Leifeld and Menichetti 2018).

## BRYOPHYTE FLORISTICS OF APPALACHIAN PEATLANDS

Historically, many floristic assessments have disregarded bryophytes; in part, this is attributable to the use of incompatible sampling methodologies (Newmaster et al. 2005). In other cases, bryophytes have been intentionally excluded due to lack of available expertise, or a perception that they are an insignificant component of the flora (Pharo et al. 1999). Even among early studies of bryophytes in the Appalachians – including in eastern Pennsylvania – large groups of bryophyte specialists, such as *Sphagnum*, were sometimes excluded (Manuel 1975; Wallace and Reif 1983). The dominance of bryophytes in bogs and fens, however, has prompted thorough investigations in some areas (Vitt 2006b, a). While bryophyte community descriptions of the Pennsylvanian Appalachian Plateau are lacking, some basic inferences may be drawn from studies in other Appalachian peatlands.

The expansive continental peatland complexes of Canada have been the heart of North American peatland research, but north-central Appalachian peatlands differ considerably, not only in abiotic conditions, but also in their plant communities. The

dominance of *Sphagnum* in Appalachian fens is more typical of Canadian bogs rather than fens, although some intersection exists in poor fens. This comparison has likely contributed to the misnaming of several Appalachian fens as “bogs” despite their demonstrable minerotrophy (Wieder and Yavitt 1994). However, even among poor and moderate-rich fens in Canada, more oligotrophic-mesotrophic *Sphagnum* species can be a substantial component (Vitt 2006a). Some of these species (e.g., *S. fallax*, *S. russowii*) occur in both Canada and the eastern U.S., either in disjunction or as part of a continuous distribution (Vitt 2014).

The two regions also differ in the continuity of their communities. Among northern kettlehole peatlands, a concentric sequence of syntaxa from center to edge is typically observed (Vitt and Slack 1975). Appalachian peatlands instead form “irregular mosaic” patterns of vegetation (Wieder et al. 1981). Community distribution is nonetheless tied to similar environmental conditions between the two types, including pH and topography (Wieder et al. 1981; Vitt and Chee 1990; Walbridge 1994; Thompson et al. 2012). However, the resulting formations are not equivalent. Additionally, the role of microhabitats in community patterning has been well documented in Canada (Vitt et al. 1995; Vitt and Belland 1997) but has not been fully explored in Appalachian fens. Shade can also shape community patterns in peatlands (Belland and Vitt 1995; Graham et al. 2016), which may be particularly significant to those that are partially treed.

Fens comprise some of the most species-rich wetlands in the eastern U.S., harboring a diverse and unique bryoflora (Bedford and Godwin 2003). Bryophyte communities contain isolated populations of disjuncts, as well as locally rare species of conservation concern (Bedford and Godwin 2003; Schuette, unpubl. data). Moreover, some studies have

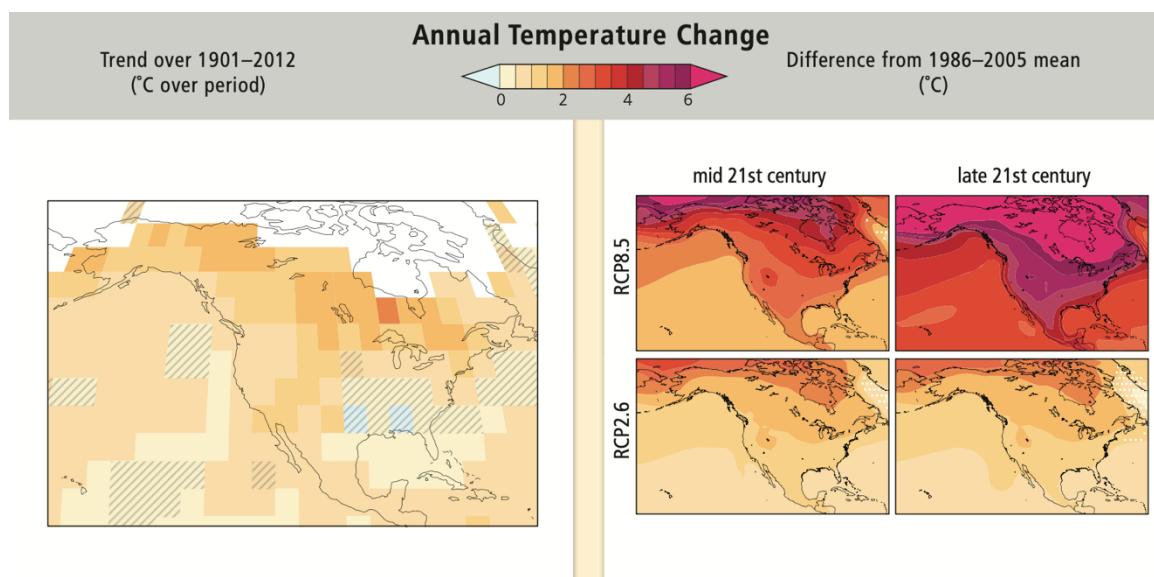
found no influence of individual fen size on species per unit area, in contrast to classical trends in species-area relationships (Franci et al. 2004). Walbridge's analysis (1994) of West Virginian peatlands noted that individual sites hosted unique assemblages, and while a few plant associations were nearly ubiquitous, roughly 40% of the species were found in only one of the studied sites. Collectively, these observations suggest that individual Appalachian peatlands, despite their generally small size, can be substantial, irreplaceable reservoirs of bryophyte biodiversity.

## GLOBAL CHANGE

### *Impacts of regional temperature and precipitation shifts*

Internationally, peatlands have been drawn into the spotlight of climate change, owing to their delicate balance between decomposition and production, and tight environmental controls on these processes (Gorham 1991). Degraded peatlands have increased decomposition and may become sources of carbon as CO<sub>2</sub> where they are usually sinks (Damman 1979; Leifeld and Menichetti 2018). Consistent net C losses from drained peatland soils highlight the importance of continued inundation to the inhibition of decay (Leifeld and Menichetti 2018). Where C losses pose a problem for broader C source-sink dynamics (Schultheis et al. 2010; Loisel et al. 2017), restoration and protection of peatlands may be seen as a prospective solution (Chimner et al. 2017; Leifeld and Menichetti 2018). Alternatively, with sufficient moisture, carbon pools in Appalachian peatlands could be naturally maintained by elongated growing seasons and enhanced primary production (Cai and Yu 2011).

Current climate trajectories in the north-central Appalachians show increasing annual precipitation and increasing annual temperature (Figure 1.4); climate forecasts under a range of emissions schemes suggest a long-term continuation of this pattern (Romero-Lankao et al. 2014; Dupigny-Giroux et al. 2018). These conditions could potentially reverse the autogenic succession of some peatlands, with increasing moisture availability, although this could be negated by a proportional increase in evapotranspiration (Kuhry and Turunen 2006; Cai and Yu 2011). Such a contingency is supported by the observation that as peatlands advance through succession, the influence of climate largely outweighs that of the landform or nutrient status (Damman 1979). The Pocono region specifically is likely to experience droughts with near annual frequency under high-emissions projections (Union of Concerned Scientists 2008; Pennsylvania Department of Environmental Protection 2021). Paleoclimate analysis of a Pennsylvania bog revealed that lateral expansion occurred episodically over the past millennium, initiating during or



**Fig. 1.4.** Past and projected future temperature changes in North America, from Romero-Lankao (2014). Annual temperatures in the Appalachian Plateau province have averaged a 1–2°C increase over the past century and are projected to increase an additional 1–5°C by the end of the 21<sup>st</sup> century.

immediately after multiyear droughts (Ireland and Booth 2011). Thus, changes in both the long-term averages and the variability of precipitation have implications for peatland function. Corresponding shifts in the dominant bryophyte species and communities could further have an indirect influence on autogenic succession (Clymo and Hayward 1982).

Bryophyte indicator communities can be a useful metric in gauging peatland development under the influence of a changing climate (Gignac and Vitt 1994). Distributions of indicator species overlap in actual space and niche space to form indicator communities (Vitt 2006b). Both individual species and their associations are critical in assessing functional peatland classification; even the poor-rich fen gradient itself is based in part upon the diversity of indicator species (Bedford and Godwin 2003; Vitt 2006a). The close interaction of ground-dwelling bryophytes with their substrate predisposes them to a sensitivity to even minute shifts in edaphic conditions (Vitt and Belland 1997). Further exploration of the indicator communities of Appalachian peatlands will inform our understanding of these unique ecosystems and aid in modeling the effects of climate change on their function.

#### *Nitrogen deposition and nutrient regimes*

Climate change-induced increases in nitrogen deposition may disrupt the nutrient-poor systems in which *Sphagnum* and other peatland bryophytes thrive (Moore 2002). Mineralization rates may also rise due to greater decomposition, placing dual pressure on oligotrophic specialists (Schultheis et al. 2010). The triphasic response framework accepted in European peatlands (Lamers et al. 2000) has not been supported by nitrogen experiments in a North American fen (Wieder et al. 2020). Wieder et al. (2020) suggest a

comparatively low critical load of  $3 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ , above which N cycling is disrupted and vascular plants may dominate assimilation of N. Declining *Sphagnum* growth and increasing vascular plant growth from nutrient regimes exacerbates the effect from climatic variables; with sufficient ecological momentum, vascular plants can effectively shade out bryophytes (Schultheis et al. 2010).

Inorganic N deposition has declined in the eastern U.S. in the last 35 years (Ackerman et al. 2019). Regulations on nitrogen emissions have limited sources of oxidized nitrogen, although reduced nitrogen has remained a prominent inorganic N component in the eastern U.S. from agricultural sources (Ackerman et al. 2019). Moreover, the historic role of the central Appalachians in coal extraction and use has contributed to previously high rates of nitrate deposition. Impacts of N enrichment on eastern North American bogs have been observed as recently as the past decade, and vegetation shifts may persist to present day (Bubier et al. 2007; Schultheis et al. 2010).

Besides increases in deposition, warming may increase the mineralization of organic N. Experimental warming leads to higher rates of nitrogen (N) mineralization, across many biomes and with many warming methods (Rustad et al. 2001). Temperature-driven increases in litter decomposition can release soluble N into the litter and eventually foster N mineralization as C:N ratio decreases (Limpens et al. 2006). Warmer peatlands may thus have larger labile N pools (Bridgham et al. 1998). However, the warming-nitrogen relationship is complicated by numerous, interconnected drivers that affect different processes or sinks of ecosystem N. In particular, the influence of precipitation and water table height cannot be ignored (Rustad et al. 2001; Keller et al. 2004). Additionally, the effects of warming-stimulated N release may be difficult to extricate from patterns of

anthropogenic N deposition. Nonetheless, the prospect of warming-driven N release presents an additional pathway for increased N in peatlands soils.

#### *Biotic shifts and woody encroachment*

The confluence of climate change and changing nutrient regimes may produce secondary effects in temperate peatlands. Among principal concerns is the decline or loss of bryophytes (He et al. 2016), especially *Sphagnum*. Moss declines are frequently accompanied by a progressive increase in the abundance of vascular plants, particularly woody plants, which may outcompete resident non-woody species or alter edaphic conditions such that the environment becomes unsuitable for bryophytes (Favreau et al. 2019; Beauregard et al. 2020; Langdon et al. 2020; McPartland et al. 2020). An innately poor adaptation to competition, combined with dependence on a narrow set of environmental conditions, strongly disadvantages bryophytes against vascular invaders (Hallingbäck and Tan 2014).

The reduction in available water is a significant abiotic driver of moss decline with warming. Water table drawdown can lead to widespread desiccation (Norby et al. 2019), for which *Sphagnum* has minimal long-term tolerance (Clymo 1973; Rydin 1985; Hájek 2014). Drawdown may affect bryophytes of hummocks (local high points in microtopography) more than those of hollows (local low points) (Eppinga et al. 2009; Norby et al. 2019). Following *in situ* drying, hummock species regenerate poorly in comparison to hollow species (Wagner and Titus 1984; Hájek 2014). However, hollow species typically have lower water holding capacity than hummock species, and thus greater potential for desiccation if water becomes inaccessible (Rydin 1985). Perhaps as a

consequence, hollows are more susceptible to fires than hummocks, and hollow bryophyte populations may be damaged more extensively (Benscoter and Wieder 2003; Benscoter et al. 2005). The resultant tradeoff indicates that *Sphagnum* species of both microhabitats are potentially vulnerable to desiccation events.

Water table drawdown can facilitate the colonization by woody plants. Lower water tables in hummocks generally favor the growth and survival of seedlings (Holmgren et al. 2015). Reduced inundation and the release from anoxic stress allows deeper and more extensive rooting (Poot and Lambers 2003) and enhances fine root growth (Malhotra et al. 2020). Woody plants also promote water table drawdown through increased evapotranspiration or canopy interception of precipitation (Eppinga et al. 2009). Although water table drawdown has variable impact across plant populations, models suggest that episodic drought alone is insufficient to create lasting changes to peatland communities. Heijmans et al. (2013) found that the reduction in evaporation from the moss surface following drought was greater than the gain in tree evapotranspiration, leading to a net reduction in ecosystem evapotranspiration following drought. The subsequent rise of the water table thus inhibited further tree colonization. Nonetheless, prolonged changes in water availability could have devastating impacts on peatlands bryoflora and foster woody encroachment.

Greater N turnover also generally favors the growth of woody plants rather than bryophytes (He et al. 2016; Maillard et al. 2021). In a *Sphagnum*-dominated system, high rates of ion exchange and resistance of moss tissues to decay limit the accessibility of N to woody plants (Turetsky et al. 2012). Some ericoid mycorrhizae access organic N pools directly, circumventing the need for mineralized N (Bragazza et al. 2013). The stimulation

of fine root growth by water table drawdown might enhance this capacity. Maillard et al. (2021) also observed a partial homogenization of microbial communities with warming – an increase in hummock-type decomposers that exploited the new abundance of N-rich substrates derived from ericoid mycorrhizae.

Positive feedbacks on woody encroachment further enable vascular plant dominance. As woody plant abundance increases, competition for light and nutrients between woody plants and bryophytes intensifies (Eppinga et al. 2009; Turetsky et al. 2012; Heijmans et al. 2013). In early seedling development, dense mats of bryophytes may impede germination or growth of vascular plants (Eppinga et al. 2009; Keuper et al. 2011); although Holmgren et al. (2015) suggest that higher moisture content in *Sphagnum* can promote germination. Once established, woody plants easily outcompete mosses, and have almost unrestricted control over light availability (Eppinga et al. 2009; Turetsky et al. 2012).

Encroachment frequently initiates through facilitation of woody plants by “pioneer” shrubs and trees. The ecotone between woodland and open peatlands is often bridged by areas where solitary or highly dispersed woody plants have retained a foothold on peat, usually on hummocks (Holmgren et al. 2015; Langdon et al. 2020). “Pioneers” can limit exposure of other seedlings to stressors, such as herbivory or desiccation (Bannister et al. 2020). Additionally, pioneers alter the surrounding soil conditions to be drier and more nutrient enriched, and thus favorable to other vascular colonizers (Holmgren et al. 2015). Pioneer facilitation is not confined to intraspecific interactions – unrelated woody plants may reap the benefits as well as conspecifics (Holmgren et al. 2015; Bannister et al. 2020). Eppinga et al. (2009) posit that bryophytes and vascular plants

exhibit “selfish” modification of their environment, promoting conditions suitable for their own functional group (and largely unsuitable for the other). Interspecific facilitation, and the gradual influx of facultative species, is likely critical in powering catastrophic shifts between alternate stable states (Scheffer et al. 2012) and may explain the success of woody encroachment following initial establishment of pioneers.

Implications of woody encroachment for plant communities are profound. A survey of 14 bogs in southeastern Canada found increased local species richness, functional richness, and beta diversity following tree encroachment, primarily due to colonization by facultative and shade-tolerant vascular plants (Favreau et al. 2019). Many such vascular invaders are non-native (Pellerin et al. 2021). In contrast to facultative colonizers, herbaceous and bryophyte peatland specialists decline in encroached peatlands (Warren et al. 2007; Pellerin et al. 2021; Saler and Jules 2021). Presumably, given the isolation of temperate peatlands, gamma diversity also decreases with successive encroachments. Hence, while site-scale diversity increases with woody plant dominance, diversity at higher scales plummets as threatened peatland specialists become extirpated.

## REFERENCES

- Ackerman D, Millet DB, Chen X (2019) Global estimates of inorganic nitrogen deposition across four decades. *Global Biogeochem Cy* 33:100–107.  
<https://doi.org/10.1029/2018GB005990>
- Anderson RL, Foster DR, Motzkin G (2003) Integrating lateral expansion into models of peatland development in temperate New England. *J Ecol* 91:68–76.  
<https://doi.org/10.1046/j.1365-2745.2003.00740.x>

Bannister JR, Travieso G, Galindo N, et al (2020) Shrub influences on seedling performance when restoring the slow-growing conifer *Pilgerodendron uviferum* in southern bog forests. Restor Ecol 28:396–407.  
<https://doi.org/10.1111/rec.13090>

Beauregard P, Lavoie M, Pellerin S (2020) Recent gray birch (*Betula populifolia*) encroachment in temperate peatlands of eastern North America. Wetlands 40:351–364. <https://doi.org/10.1007/s13157-019-01186-3>

Bedford BL, Godwin KS (2003) Fens of the United States: Distribution, characteristics, and scientific connection versus legal isolation. Wetlands 23:608–629.  
[https://doi.org/10.1672/0277-5212\(2003\)023\[0608:FOTUSD\]2.0.CO;2](https://doi.org/10.1672/0277-5212(2003)023[0608:FOTUSD]2.0.CO;2)

Belland RJ, Vitt DH (1995) Bryophyte vegetation patterns along environmental gradients in continental bogs. Écoscience 2:395–407.  
<https://doi.org/10.1080/11956860.1995.11682308>

Benscoter BW, Wieder RK, Vitt DH (2005) Linking microtopography with post-fire succession in bogs. Journal of Vegetation Science 16:453–460.  
<https://doi.org/10.1111/j.1654-1103.2005.tb02385.x>

Benscoter BW, Wieder RK (2003) Variability in organic matter lost by combustion in a boreal bog during the 2001 Chisholm fire. Can J For Res 33:2509–2513.  
<https://doi.org/10.1139/x03-162>

Berendse F, Van Breemen N, Rydin H, et al (2001) Raised atmospheric CO<sub>2</sub> levels and increased N deposition cause shifts in plant species composition and production in *Sphagnum* bogs. Glob Change Biol 7:591–598. <https://doi.org/10.1046/j.1365-2486.2001.00433.x>

Bragazza L, Parisod J, Buttler A, Bardgett RD (2013) Biogeochemical plant–soil microbe feedback in response to climate warming in peatlands. Nat Clim Change 3:273–277. <https://doi.org/10.1038/nclimate1781>

Bridgham SD, Pastor J, Janssens JA, et al (1996) Multiple limiting gradients in peatlands: A call for a new paradigm. Wetlands 16:45–65.  
<https://doi.org/10.1007/BF03160645>

Bridgham SD, Updegraff K, Pastor J (1998) Carbon, nitrogen, and phosphorus mineralization in northern wetlands. Ecology 79:1545–1561

Bubier JL, Moore TR, Bledzki LA (2007) Effects of nutrient addition on vegetation and carbon cycling in an ombrotrophic bog. *Glob Change Biol* 13:1168–1186.  
<https://doi.org/10.1111/j.1365-2486.2007.01346.x>

Cai S, Yu Z (2011) Response of a warm temperate peatland to Holocene climate change in northeastern Pennsylvania. *Quaternary Res* 75:531–540.  
<https://doi.org/10.1016/j.yqres.2011.01.003>

Cameron CC (1968) Peat. In: *Mineral Resources of the Appalachian Region*. United States Department of the Interior, Geological Survey, Washington, D.C., U.S.A., pp 136–145

Cameron CC (1970) Peat deposits of northeastern Pennsylvania. United States Department of the Interior, Geological Survey, Washington, D.C., U.S.A.

Cartwright J (2019) Ecological islands: conserving biodiversity hotspots in a changing climate. *Front Ecol Environ* 17:331–340. <https://doi.org/10.1002/fee.2058>

Chimner RA, Cooper DJ, Wurster FC, Rochefort L (2017) An overview of peatland restoration in North America: where are we after 25 years?: Peatland restoration in North America. *Restor Ecol* 25:283–292. <https://doi.org/10.1111/rec.12434>

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

Clymo RS (1973) The growth of *Sphagnum*: Some effects of environment. *J Ecol* 61:849–869. <https://doi.org/10.2307/2258654>

Clymo RS, Hayward PM (1982) The ecology of *Sphagnum*. In: Smith AJE (ed) *Bryophyte Ecology*. Springer Netherlands, Dordrecht, pp 229–289

Damman AWH (1979) Geographic patterns in peatland development in eastern North America. In: *Classification of peat and peatlands: proceedings of the International Symposium held in Hyytiälä, Finland, September 17-21, 1979*. International Peat Society, Helsinki, Finland, pp 42–57

du Rietz GE (1954) Die Mineralbodenwasserzeigergrenze als Grundlage einer natürlichen Zweigliederung der nord- und mitteleuropäischen Moore. *Vegetatio* 5:571–585

Dupigny-Giroux L-A, Mecray E, Lemcke-Stampone M, et al (2018) Chapter 18: Northeast. Impacts, risks, and adaptation in the United States: The Fourth National Climate Assessment, Volume II. U.S. Global Change Research Program

Dyke AS, Prest VK (1987) Late Wisconsinan and Holocene history of the Laurentide Ice Sheet. *Geogr Phys Quatern* 41:237–263. <https://doi.org/10.7202/032681ar>

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. <https://doi.org/10.1007/s11258-007-9309-6>

Favreau M, Pellerin S, Poulin M (2019) Tree encroachment induces biotic differentiation in *Sphagnum*-dominated bogs. *Wetlands* 39:841–852. <https://doi.org/10.1007/s13157-018-1122-6>

Franc KE, Ford WM, Castleberry SB (2004) Characterization of high elevation central Appalachian wetlands. U.S. Department of Agriculture, Forest Service, Northeastern Research Station, Newtown Square, PA

Gignac LD, Vitt DH (1994) Responses of northern peatlands to climate change: effects on bryophytes. *J Hattori Bot Lab* 75:119–132. [https://doi.org/10.18968/jhbl.75.0\\_119](https://doi.org/10.18968/jhbl.75.0_119)

Gorham E (1957) The development of peat lands. *Q Rev Biol* 32:145–166. <https://doi.org/10.1086/401755>

Gorham E (1991) Northern peatlands: Role in the carbon cycle and probable responses to climatic warming. *Ecol Appl* 1:182–195. <https://doi.org/10.2307/1941811>

Graham JA, Hartsock JA, Vitt DH, et al (2016) Linkages between spatio-temporal patterns of environmental factors and distribution of plant assemblages across a boreal peatland complex. *Boreas* 45:207–219. <https://doi.org/10.1111/bor.12151>

Hájek T (2014) Physiological ecology of peatland bryophytes. In: *Photosynthesis in Bryophytes and Early Land Plants*. Springer Netherlands, Dordrecht, pp 233–252

Hallingbäck T, Tan BC (2014) Past and present activities and future strategy of bryophyte conservation. *Phytotaxa* 9:266–274. <https://doi.org/10.11646/phytotaxa.9.1.15>

Halsey LA, Vitt DH, Gignac LD (2000) *Sphagnum*-dominated peatlands in North America since the Last Glacial Maximum: Their occurrence and extent. The Bryologist 103:334–352. [https://doi.org/10.1639/0007-2745\(2000\)103\[0334:SDPINA\]2.0.CO;2](https://doi.org/10.1639/0007-2745(2000)103[0334:SDPINA]2.0.CO;2)

He X, He KS, Hyvönen J (2016) Will bryophytes survive in a warming world? Perspect Plant Ecol 19:49–60. <https://doi.org/10.1016/j.ppees.2016.02.005>

Heijmans MMPD, van der Knaap YAM, Holmgren M, Limpens J (2013) Persistent versus transient tree encroachment of temperate peat bogs: Effects of climate warming and drought events. Glob Change Biol 19:2240–2250. <https://doi.org/10.1111/gcb.12202>

Holmgren M, Lin C-Y, Murillo JE, et al (2015) Positive shrub-tree interactions facilitate woody encroachment in boreal peatlands. J Ecol 103:58–66. <https://doi.org/10.1111/1365-2745.12331>

Ingram HAP (1978) Soil layers in mires: function and terminology. J Soil Sci 29:224–227. <https://doi.org/10.1111/j.1365-2389.1978.tb02053.x>

Ireland AW, Booth RK (2011) Hydroclimatic variability drives episodic expansion of a floating peat mat in a North American kettlehole basin. Ecology 92:11–18. <https://doi.org/10.1890/10-0770.1>

Keller JK, White JR, Bridgham SD, Pastor J (2004) Climate change effects on carbon and nitrogen mineralization in peatlands through changes in soil quality. Glob Change Biol 10:1053–1064. <https://doi.org/10.1111/j.1529-8817.2003.00785.x>

Keuper F, Dorrepaal E, Van Bodegom PM, et al (2011) A race for space? How *Sphagnum fuscum* stabilizes vegetation composition during long-term climate manipulations. Glob Change Biol 17:2162–2171. <https://doi.org/10.1111/j.1365-2486.2010.02377.x>

Kuhry P, Turunen J (2006) The postglacial development of boreal and subarctic peatlands. In: Wieder RK, Vitt DH (eds) Boreal Peatland Ecosystems. Springer Berlin Heidelberg, pp 26–46

Lamers LPM, Bobbink R, Roelofs JGM (2000) Natural nitrogen filter fails in polluted raised bogs. Glob Change Biol 6:583–586. <https://doi.org/10.1046/j.1365-2486.2000.00342.x>

Langdon SF, Dovciak M, Leopold DJ (2020) Tree encroachment varies by plant community in a large boreal peatland complex in the boreal-temperate ecotone of northeastern USA. *Wetlands* 40:2499–2511. <https://doi.org/10.1007/s13157-020-01319-z>

Leifeld J, Menichetti L (2018) The underappreciated potential of peatlands in global climate change mitigation strategies. *Nat Commun* 9:1071. <https://doi.org/10.1038/s41467-018-03406-6>

Limpens J, Heijmans M, Berendse F (2006) The nitrogen cycle in boreal peatlands. In: Wieder RK, Vitt DH (eds) *Boreal Peatland Ecosystems*. Springer Berlin Heidelberg, pp 195–230

Loisel J, van Bellen S, Pelletier L, et al (2017) Insights and issues with estimating northern peatland carbon stocks and fluxes since the Last Glacial Maximum. *Earth-Sci Rev* 165:59–80. <https://doi.org/10.1016/j.earscirev.2016.12.001>

Maillard F, Fernandez CW, Mundra S, et al (2021) Warming drives a ‘hummockification’ of microbial communities associated with decomposing mycorrhizal fungal necromass in peatlands. *New Phytologist* nph.17755. <https://doi.org/10.1111/nph.17755>

Malhotra A, Brice DJ, Childs J, et al (2020) Peatland warming strongly increases fine-root growth. *Proc Natl Acad Sci USA* 117:17627–17634. <https://doi.org/10.1073/pnas.2003361117>

Manuel MG (1975) Contribution to the bryoflora of Pennsylvania. *The Bryologist* 78:458–462. <https://doi.org/10.2307/3242170>

McKnight D, Thurman EM, Wershaw RL, Hemond H (1985) Biogeochemistry of aquatic humic substances in Thoreau’s Bog, Concord, Massachusetts. *Ecology* 66:1339–1352. <https://doi.org/10.2307/1939187>

McPartland MY, Montgomery RA, Hanson PJ, et al (2020) Vascular plant species response to warming and elevated carbon dioxide in a boreal peatland. *Environ Res Lett* 15:124066. <https://doi.org/10.1088/1748-9326/abc4fb>

Moore PD (2002) The future of cool temperate bogs. *Environ Conserv* 29:3–20. <https://doi.org/10.1017/S0376892902000024>

- Newmaster SG, Belland RJ, Arsenault A, et al (2005) The ones we left behind: Comparing plot sampling and floristic habitat sampling for estimating bryophyte diversity. *Divers Distrib* 11:57–72. <https://doi.org/10.1111/j.1366-9516.2005.00123.x>
- Norby RJ, Childs J, Hanson PJ, Warren JM (2019) Rapid loss of an ecosystem engineer: *Sphagnum* decline in an experimentally warmed bog. *Ecol Evol* 9:12571–12585. <https://doi.org/10.1002/ece3.5722>
- Pellerin S, Lavoie M, Talbot J (2021) Rapid broadleaved encroachment in a temperate bog induces species richness increase and compositional turnover. *Écoscience* 1–18. <https://doi.org/10.1080/11956860.2021.1907976>
- Pennsylvania Department of Environmental Protection (2021) Pennsylvania Climate Impacts Assessment 2021. Pennsylvania Department of Environmental Protection, Harrisburg, PA
- Pharo EJ, Beattie AJ, Binns D (1999) Vascular plant diversity as a surrogate for bryophyte and lichen diversity. *Conserv Biol* 13:282–292. <https://doi.org/10.1046/j.1523-1739.1999.013002282.x>
- Poot P, Lambers H (2003) Growth responses to waterlogging and drainage of woody *Hakea* (Proteaceae) seedlings, originating from contrasting habitats in south-western Australia. *Plant Soil* 253:57–70. <https://doi.org/10.1023/A:1024540621942>
- Rigg GB, Strausbaugh PD (1949) Some stages in the development of *Sphagnum* bogs in West Virginia. *Castanea* 14:129–148
- Romero-Lankao P, Smith JB, Davidson DJ, et al (2014) North America. In: Barros VR, Field CB, Dokken DJ, et al. (eds) Climate change 2014: Impacts, adaptation and vulnerability. Part B: Regional aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom, pp 1439–1498
- Rustad LE, Campbell JL, Marion GM, et al (2001) A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia* 126:543–562. <https://doi.org/10.1007/s004420000544>

Rydin H (1985) Effect of water level on desiccation of *Sphagnum* in relation to surrounding *Sphagna*. *Oikos* 45:374–379. <https://doi.org/10.2307/3565573>

Rydin H, Gunnarsson U, Sundberg S (2006) The role of *Sphagnum* in peatland development and persistence. In: Wieder RK, Vitt DH (eds) *Boreal Peatland Ecosystems*. Springer Berlin Heidelberg, pp 47–65

Saler JL, Jules ES (2021) Woody vegetation encroachment: A driver of herbaceous species diversity loss in a coastal fen. *Madroño* 68:9–19.  
<https://doi.org/10.3120/0024-9637-68.1.9>

Scheffer M, Hirota M, Holmgren M, et al (2012) Thresholds for boreal biome transitions. *Proc Natl Acad Sci USA* 109:21384–21389.  
<https://doi.org/10.1073/pnas.1219844110>

Schultheis EH, Hopfensperger KN, Brenner JC (2010) Potential impacts of climate change on *Sphagnum* bogs of the southern Appalachian Mountains. *Nat Area J* 30:417–424. <https://doi.org/10.3375/043.030.0407>

Stewart CN, Nilsen ET (1993) Association of edaphic factors and vegetation in several isolated Appalachian peat bogs. *B Torrey Bot Club* 120:128–135

Thompson Y, D'Angelo EM, Karathanasis AD, Sandefur BC (2012) Plant community composition as a function of geochemistry and hydrology in three Appalachian wetlands. *Ecohydrology* 5:389–400. <https://doi.org/10.1002/eco.228>

Turetsky MR, Bond-Lamberty B, Euskirchen E, et al (2012) The resilience and functional role of moss in boreal and arctic ecosystems. *New Phytologist* 196:49–67. <https://doi.org/10.1111/j.1469-8137.2012.04254.x>

Turetsky MR, Crow SE, Evans RJ, et al (2008) Trade-offs in resource allocation among moss species control decomposition in boreal peatlands. *J Ecol* 96:1297–1305.  
<https://doi.org/10.1111/j.1365-2745.2008.01438.x>

Union of Concerned Scientists (2008) Climate change in Pennsylvania: Impacts and solutions for the Keystone State. UCS Publications, Cambridge, MA, USA

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

Vile MA, Kelman Wieder R, Živković T, et al (2014) N<sub>2</sub>-fixation by methanotrophs sustains carbon and nitrogen accumulation in pristine peatlands. *Biogeochemistry* 121:317–328. <https://doi.org/10.1007/s10533-014-0019-6>

Vitt DH (2006a) Functional characteristics and indicators of boreal peatlands. In: Wieder RK, Vitt DH (eds) *Boreal Peatland Ecosystems*. Springer Berlin Heidelberg, pp 9–24

Vitt DH (2006b) Bryophyte community ecology: Going beyond description. *Lindbergia* 31:33–41

Vitt DH (2014) A key and review of bryophytes common in North American peatlands. *Evansia* 31:121–158. <https://doi.org/10.1639/079.031.0402>

Vitt DH, Belland RJ (1997) Attributes of rarity among Alberta mosses: Patterns and prediction of species diversity. *The Bryologist* 100:1–12

Vitt DH, Chee W-L (1990) The relationships of vegetation to surface water chemistry and peat chemistry in fens of Alberta, Canada. *Vegetatio* 89:87–106. <https://doi.org/10.1007/BF00032163>

Vitt DH, Li Y, Belland RJ (1995) Patterns of bryophyte diversity in peatlands of continental western Canada. *The Bryologist* 98:218–227. <https://doi.org/10.2307/3243306>

Vitt DH, Slack NG (1975) An analysis of the vegetation of *Sphagnum*-dominated kettle-hole bogs in relation to environmental gradients. *Can J Botany* 53:332–359. <https://doi.org/10.1139/b75-042>

Wagner DJ, Titus JE (1984) Comparative desiccation tolerance of two *Sphagnum* mosses. *Oecologia* 62:182–187. <https://doi.org/10.1007/BF00379011>

Walbridge MR (1994) Plant community composition and surface water chemistry of fen peatlands in West Virginia's Appalachian Plateau. *Water Air Soil Poll* 77:247–269

Walbridge MR, Navaratnam JA (2006) Phosphorus in boreal peatlands. In: Wieder RK, Vitt DH (eds) *Boreal Peatlands Ecosystems*. Springer Berlin Heidelberg, pp 231–258

Wallace RS, Reif CB (1983) *Sphagnum* species composition and distribution in the bogs of Nuangola Lake, Luzerne County, Pennsylvania. Proceedings of the Pennsylvania Academy of Science 57:143–146

Warren RJ, Rossell IM, Moorhead KK, Dan Pittillo J (2007) The influence of woody encroachment upon herbaceous vegetation in a southern Appalachian wetland complex. Am Midl Nat 157:39–51. [https://doi.org/10.1674/0003-0031\(2007\)157\[39:TIOWEU\]2.0.CO;2](https://doi.org/10.1674/0003-0031(2007)157[39:TIOWEU]2.0.CO;2)

Watts WA (1979) Late Quaternary vegetation of central Appalachia and the New Jersey Coastal Plain. Ecol Monogr 49:427–469. <https://doi.org/10.2307/1942471>

Wieder RK (1985) Peat and water chemistry at Big Run Bog, a peatland in the Appalachian Mountains of West Virginia, USA. Biogeochemistry 1:277–302. <https://doi.org/10.1007/BF02187203>

Wieder RK, McCormick AM, Lang GE (1981) Vegetational analysis of Big Run Bog, a nonglaciated *Sphagnum* bog in West Virginia. Castanea 46:16–29

Wieder RK, Vitt DH, Benscoter BW (2006) Peatlands and the boreal forest. In: Wieder RK, Vitt DH (eds) Boreal Peatland Ecosystems. Springer Berlin Heidelberg, pp 1–8

Wieder RK, Vitt DH, Vile MA, et al (2019) Experimental nitrogen addition alters structure and function of a boreal bog: critical load and thresholds revealed. Ecol Monogr 89:e01371. <https://doi.org/10.1002/ecm.1371>

Wieder RK, Vitt DH, Vile MA, et al (2020) Experimental nitrogen addition alters structure and function of a boreal poor fen: Implications for critical loads. Sci Total Environ 733:138619. <https://doi.org/10.1016/j.scitotenv.2020.138619>

Wieder RK, Yavitt JB (1994) Peatlands and global climate change: Insights from comparative studies of sites situated along a latitudinal gradient. Wetlands 14:229–238

Yu Z (2012) Northern peatland carbon stocks and dynamics: A review. Biogeosciences 9:4071–4085. <https://doi.org/10.5194/bg-9-4071-2012>

Yu Z, Loisel J, Brosseau DP, et al (2010) Global peatland dynamics since the Last Glacial Maximum. *Geophys Res Lett* 37:L13402.  
<https://doi.org/10.1029/2010GL043584>

Zoltai SC, Vitt DH (1995) Canadian wetlands: Environmental gradients and classification. *Vegetatio* 118:131–137

## CHAPTER II: BRYOPHYTE COMMUNITIES AND ENVIRONMENTAL RELATIONSHIPS

### INTRODUCTION

Peatlands of temperate regions represent only a small fraction of total peatland land area (Leifeld and Menichetti 2018). Nonetheless, the contribution of bogs and fens to biodiversity and ecosystem services in the temperate zone is irreplaceable. Though peatlands occupy less than 0.1 % of the area of northern U.S. states, they support 7-13 % of the uncommon or rare flora (Bedford and Godwin 2003). Peatland plants play a substantial role in maintaining peatland soil carbon stores, retaining and filtering runoff, and moderating local microclimates. However, the small size and dispersed configuration of Appalachian peatlands increases their vulnerability to global change factors. While flora of naturally fragmented habitats may be well adapted to cope with dispersal and reproductive limitations (Schöpke et al. 2019), stochastic events and biotic invasion still pose considerable threats to dispersed populations (Fischer and Lindenmayer 2007; Cartwright 2019). Moreover, in bogs and fens, the alleviation of stressors by global change can enable common, competition-adapted species to take hold and outcompete rarer, stress-adapted endemics (Cartwright 2019).

Identifying the responses of bryophyte communities to global change is a priority in advancing the frontiers of bryophyte community ecology (Vitt 2006b) and in conserving imperiled peatlands (Schultheis et al. 2010). Relating the composition and occurrence of communities to environmental gradients is a key first step towards predicting future patterns of distribution. In addition, quantifying current ecological relationships in temperate peatlands provides a model for the future of boreal peatlands with climate change

(Gignac and Vitt 1994; Wieder and Yavitt 1994). As boreal peatlands contain an estimated 400-600 Gg C in peat (Yu 2012; Leifeld and Menichetti 2018), including 178 Gg in boreal North America, it is critical to understand the structure and distribution of model temperate communities. For example, in temperate peatlands with broadleaf tree cover, understanding relationships of bryoflora to canopy cover offers insight about similar relationships in boreal peatlands as cold isotherms shift northwards and broadleaves become a greater constituent of boreal canopy (Turetsky et al. 2012; Kollas et al. 2014; Pinceloup et al. 2020).

In the northeastern U.S., moss-dominated peatlands are concentrated in the Appalachian highlands, where glaciated terrain and cool climate have favored the persistence of montane fens (Cameron 1968; Halsey et al. 2000). Although Appalachian peatlands are small and isolated, the flora are exceptionally diverse (Bedford and Godwin 2003; Thompson et al. 2012). In contrast to expected species-area relationships, the size of these wetlands is a poor predictor of plant diversity (Francz et al. 2004). The evenness of species diversity may be partially attributed to high rates of local endemism and corresponding beta diversity (Walbridge 1994). Despite thorough analyses of biodiversity of the region, gaps remain in understanding community structure, particularly among the bryophytes that dominate peatland groundcover.

## QUESTIONS AND HYPOTHESES

The overarching objective of this project was to characterize the bryophyte communities of peatlands in the Appalachian Plateau of Pennsylvania, and to relate the structure and occurrence of these communities to environmental variables. In doing so, I

aimed to provide insight about bryophyte ecology that would both fulfill scientific curiosity about temperate peatlands and provide applicable information for conservation of the studied peatlands. The detailed questions and hypotheses below outline the structure of my investigation and provide context for my findings.

*Q1: How are bryophyte communities structured? What species, in what proportions and arrangements, comprise them?*

Plant communities may be regarded as a function of two aspects: the species that constitute them (flora), and the structure that arises from the conformation of plants within the community (vegetation) (Vitt 2006b). Existing data from the peatland sites are sufficient to describe the bryoflora by species presence/absence, albeit limited to a single plot per site (Schuette, unpubl. data). However, a more complex understanding of the associations among the bryoflora, as well as the emergent structure, is lacking.

Hypotheses:

Q1, H1: Bryophyte communities will exhibit low within-site evenness; that is, one or two species will dominate/co-dominate, while other bryophytes will occur with low frequency.

Q1, H2: The dominant species of *Sphagnum* will not be consistent across an entire site, varying spatially.

Q1, H3: Bryophyte communities within sites will occur in a patchy distribution, with hydric, *Sphagnum*-dominated associations in locally inundated areas of the fens, and more mesic assemblages scattered throughout and along upland margins.

*Q2: How are communities distributed across environmental gradients within and between sites?*

Several characteristics tie bryophytes more closely to their environment than most vascular plants. These characteristics include small size, poikilohydric life strategy (inability to self-regulate to maintain hydrologic homeostasis), and the absence of a leaf cuticle and consequent absorption of nutrients directly through the leafy tissues. Traditional niche theory is not easily applied to *Sphagnum* because they engineer their own habitats (Rydin et al. 2006; Vile et al. 2010); however, *Sphagnum* species still occur along environmental gradients, partially due to interspecific competition amongst a diverse, narrowly adapted group. In contrast, most non-*Sphagnum* bryophytes cannot acidify their habitat to the same extent, and thus are distributed in a manner more consistent with traditional niche theory.

In a simplified Gleasonian view, species are distributed along environmental gradients. At the intersections of these distributions, communities are formed by characteristic interactions of these species. By quantifying species interactions, one can infer the significance of the contributing environmental factors and predict the response of community compositions to environmental change. However, because the composition of the bryophyte communities in this case is not known *a priori*, it is neither easy nor necessarily useful to anticipate how any given community will vary along specific gradients. Instead, I developed hypotheses about which factors will be significant overall: that is, which factors will potentially correlate with the greatest variation in bryophyte community composition.

Hypotheses:

Q2, H1: Among chemical factors, peatland porewater pH, as well as concentration of  $\text{Ca}^{2+}$  and  $\text{NH}_4^+$ , will correlate strongly with community composition.

Q2, H2: Among physical factors, canopy openness above the bryophyte layer and depth to water table will correlate strongly with community composition.

*Q3: What predictions can be made about how these bryophyte communities will react to global change?*

The response of bryophyte communities to global change is a topic of concern in peatland research (Vitt 2006b; Schultheis et al. 2010). Given the critical role played by *Sphagnum* and other peatland mosses in maintaining immense terrestrial carbon sinks, shifts in bryophyte communities, including loss of certain species, could have consequences for the global carbon budget. Simply identifying distinct bryophyte communities is an important first step (Loisel et al. 2017). With information about environmental gradients, one can model changes to these gradients aligning with predicted global change scenarios, to draw conclusions about potential future distributions of bryophyte communities. While temperate peatlands hold a comparatively small share of carbon as peat, the conclusions drawn from temperate peatlands potentially could be used in modelling interactions in boreal peatlands under climate change conditions (Wieder and Yavitt 1994).

Given the short time frame of this project, it was untenable to produce testable hypotheses about the impacts of global change. However, with robust data on bryophyte communities and environmental factors, it is possible to make generalized, qualitative predictions about how changes in the latter will affect the former; to that end, I developed an objective statement for this question in place of hypotheses.

**Objective:**

Q3, O1: I will characterize the relationships of bryophyte communities to environmental gradients such that I can make qualitative predictions about the relative vulnerability of communities to global change to help inform management decisions.

## METHODS

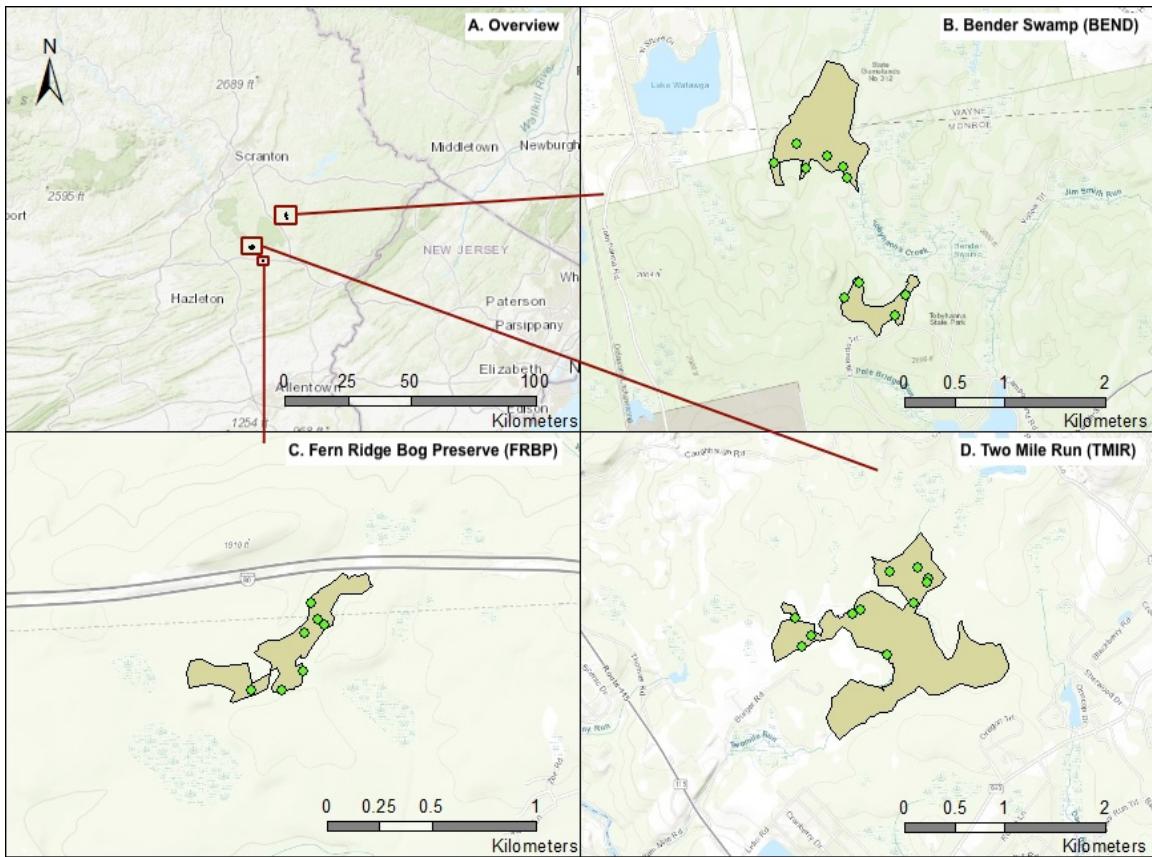
### *Study area*

The Glaciated Pocono Plateau Section (GPPS) of the Pocono Mountains is an elevated plateau in northeastern Pennsylvania forming part of the broader range of the Appalachian Mountains (Berg and Pennsylvania Bureau of Topographic and Geologic Survey 1989). The landform is characterized by wide, undulating hills, with an underlying bedrock of sandstone, siltstone, and shales. The regional climate is humid continental; temperatures range from mean annual highs of 13.3 °C to mean annual lows of 2.7 °C, and precipitation averages 1393 mm annually (PRISM Climate Group 2021). The region lies at the southern terminus of the Late Wisconsin glaciation, and favorable climate and physiography have contributed to the persistence of numerous peatlands within the GPPS.

Three peatland sites in the GPPS were selected with assistance from the Pennsylvania Natural Heritage Program (PNHP), which had previously established plots within all three sites to conduct analyses of vascular plant communities within the peatlands. Significant canopy species of the sites include red spruce (*Picea rubens*), red maple (*Acer rubrum*), birch (*Betula* spp.), blackgum (*Nyssa sylvatica*), eastern hemlock (*Tsuga canadensis*), and American larch (*Larix laricina*). Common understory shrubs include highbush blueberry (*Vaccinium corymbosum*), meadowsweet (*Spiraea* spp.), and/or leatherleaf (*Chamaedaphne calyculata* var. *angustifolia*).

Plot selection was conducted in ArcMap 10.8 (ESRI 2020), using shapefiles with vascular plant community classifications. Vascular plant communities were determined in previous work by the PNHP (Zimmerman et al. 2012). Within each site, 80 random plot centers were generated; between 8 and 16 plot centers were then selected semi-randomly, with the criterion that each vascular plant community polygon contain at least one plot. This process resulted in 40 total plots spanning 10 vascular plant community types. Several plots were inaccessible *in situ*, leaving 28 plots for sampling and data collection (Figure 2.1).

Field work was conducted in June-July 2021. At each plot, a 2-m transect was established by restricted randomization with a random number generator determining distance and direction from the point, as well as the orientation of the transect itself. Bryophyte community composition was assessed by the point-intercept method (Levy and Madden 1933; Goodall 1952; Jonasson 1988). While the relevé method with ocular assessment is commonly used in cover estimation, it is subject to bias by individual observers (Vitt et al. 2020). By comparison, the point-intercept method is more objective;



**Fig. 2.1.** Map showing the location of the three sites (tan) and their constituent plots (bright green). Note that frame C is at 2x scale relative to frames B and D.

moreover, it is statistically interchangeable with several similar methods, which is useful for meta-analysis and compatibility with future research (Godínez-Alvarez et al. 2009; Vitt et al. 2020).

#### *Sampling and field data collection*

A point frame was constructed, measuring 0.7 m with 11 evenly spaced pins offset by 5 cm. The frame was placed over the transect and species presence recorded by intersection with each pin. This process was repeated four times per transect, moving the point frame progressively further from one end of the transect to the next. The eleventh pin was not counted, but instead used as a placeholder to mark movement of the frame. The

resulting data were both retained as absolute frequency (counts of species) and transformed to cover proportions by dividing the absolute frequency by the total sampling intensity (40). For at least the first record of each species at each plot, a reference specimen was collected following protocols in Vanderpoorten et al. (2010), to confirm the *in situ* species determination.

Water samples were collected at each plot at the midpoint of each transect. If the transect midpoint was obstructed or the water table too low to easily take a sufficient sample, the nearest available location was used; in some upland plots, however, a sample could not be obtained at all. At each plot, a 10-cm diameter hole was excavated to the depth of saturation, and the depth recorded as an additional variable of interest. If the water table was not exposed at a depth of 8 in. (203 mm), the depth value was recorded as “NULL”, and no further collection was conducted. If the water table was exposed, a ~50 mL sample was collected from the exposed water tables by syringe filtration through Whatman grade 41 filter paper into acid-washed HDPE bottles. Samples were frozen within 8 hours of collection to preserve chemical integrity.

Peat depth was measured by a steel probe, which was inserted until touching mineral soil or another large obstruction. The position on the probe was temporarily marked, and the length from the tip to that mark measured to the nearest 1/16<sup>th</sup> inch. Measurements were then converted to mm for standardization. If the probe was completely submerged to the handle, the peat depth was recorded as >36 in. (>900 mm). This process was repeated three times at random points near the transect, taking care to avoid large trees or stones that could obstruct the probe. The resulting measurements were averaged.

Canopy openness was assessed with a convex spherical densiometer, held level at breast height. The surface grid was divided into 96 equal squares, and each square counted as either open or shaded. Four such measurements were taken, progressively facing each cardinal direction. The number of open squares was then summed across all 4 measurements and divided by 384 to yield the canopy openness proportion for the given plot.

#### *Water chemistry analyses*

Water samples were thawed, and aliquots extracted for chemical analyses. Ammonium-N concentration was measured by a Seal AA3 AutoAnalyzer, using the alkaline phenol method. Nitrate-N and sulfate-S were quantified on a DIONEX ICS 1500 ion chromatograph. Sodium, magnesium, potassium, and calcium ion concentrations were measured by inductively coupled plasma mass spectrometry (ICP-MS). pH and conductivity were measured by electrode, corrected to 20 °C using automatic temperature compensation. Reduced conductivity (RC) was then calculated by subtracting the H<sup>+</sup> contribution to total conductivity (Sjörs 1950). All ion concentrations were recorded in mg L<sup>-1</sup>. RC was recorded in µS cm<sup>-1</sup>.

#### *Bryophyte specimen analysis*

Reference bryophyte specimens were examined with light microscopy to confirm field identifications. Taxonomy and nomenclature followed Stotler and Crandall-Stotler (2017) for liverworts and Flora of North America (2007, 2014) for mosses, except for the

“*Sphagnum magellanicum*,” species complex, which followed Hassel et al. (2018). Several *Sphagnum* specimens were determined to species by Scott Schuette of PNHP.

#### *Calculations and statistics*

Prior to modeling, species that occurred in only one plot were removed. Although rare species removal in multivariate analysis remains hotly debated, the justification in this study is manifold. Rare species often add statistical noise without contributing substantially to comparisons of similarity between communities or relationships between environmental variables (Marchant 2002; Poos and Jackson 2012; Sgarbi et al. 2020); this is particularly true when using abundance data rather than presence-absence data (Sgarbi et al. 2020). Given the goal in the present study of characterizing broad groupings of assemblages, the “noise” from rare species arguably outweighs the value of including them. Common species are generally more useful in characterizing community similarities and patterns of diversity (Draper et al. 2019; Sgarbi et al. 2020). Among central Canadian bryophytes, Belland and Caners (2021) found no evidence that rare species differ from common species in their relationships to environmental variables. When rare species are included, a common means of accommodating differences in abundance is data transformation (Poos and Jackson 2012); however, while transformation is a suitable solution where rare species are infrequent but present in many sampling units, most transformations are arguably less effective where rare species are both infrequent and absent from most plots (and thus represented primarily by zeroes).

All statistical analyses were conducted in R 4.0.3 (R Core Team 2020), with some visualizations performed in JMP Pro 16 (SAS Institute Inc. 2021). A Bray-Curtis dissimilarity matrix was constructed from the remaining species counts by plot

(communities). Hierarchical agglomerative clustering was performed with *agnes* in the *cluster* package (Maechler et al. 2021); Ward's method (Ward 1963) as used for final clustering, as it produced the highest agglomerative coefficient from among the methods compared ( $AC = 0.9021$ ; c.f. Kaufman & Rousseeuw, 2005). Cluster differences in dissimilarity matrix space were assessed by analysis of similarities (ANOSIM) in the *vegan* package (Oksanen et al. 2020), using 999 permutations.

The community matrix was adjusted with Wisconsin double standardization and ordinated by non-metric multidimensional scaling (NMDS) with *metaMDS* in *vegan*, using Bray-Curtis dissimilarity with 999 permutations. Shepard plots were constructed to assess stress at different dimensionalities.

Environmental variables were scaled and converted to a Euclidean distance matrix. The resulting environmental matrix was correlated with the community matrix using a Mantel correlation test with Spearman's  $\rho$  with 9999 permutations. With a significant result of the overall matrix correlation, individual variables were then similarly transformed, and tests conducted for each.

For each site and for each community cluster, Pielou's evenness ( $J'$ : Pielou, 1966) was computed to assess the species abundance distributions.  $J'$  ranges from 0 (no evenness) to 1 (complete evenness).

All result maps were constructed in ArcMAP 10.8 (ESRI 2020).

## RESULTS

### *Bryophyte species and community structure*

Twenty-six bryophyte species were found across all sites. The bryoflora at each site characterized by a diverse array of *Sphagnum* species and common associates such as *Polytrichum commune* and *Pleurozium schreberi*, as well as several bryophytes typical of drier habitats such as *Hypnum imponens* and *Dicranum* spp. (Table 2.1). The most abundant species were *Sphagnum fallax* and *S. divinum*; however, other *Sphagnum* species were major constituents of certain sites, including less common *Sphagnum* such as *S. cuspidatum* or *S. flexuosum*. Several of the less frequent species were species of conservation concern in Pennsylvania; these included *Calliergonella cuspidata*, *Calypogeia integrifolia*, and *Sphagnum cuspidatum*, among others (Schuette, unpubl. data).

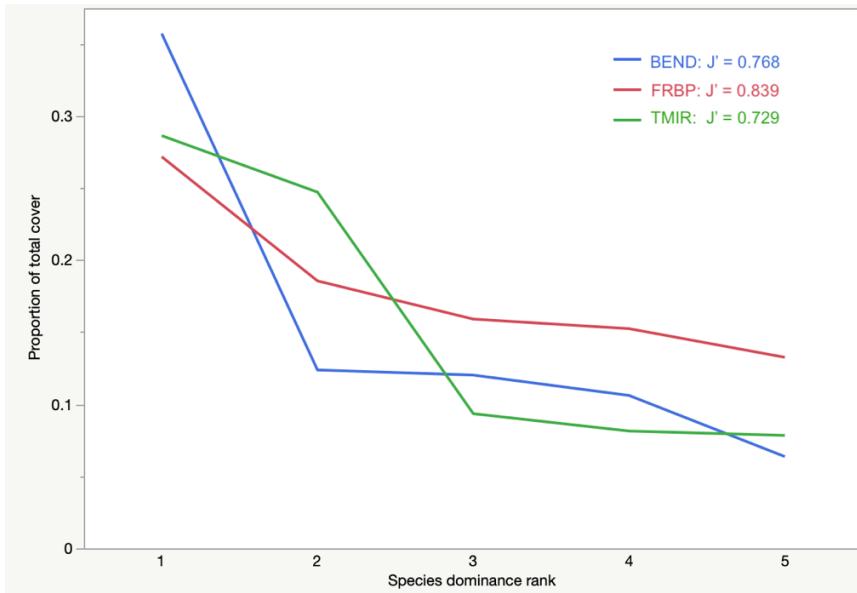
Bryophyte assemblages were typically dominated by a single majority species, accompanied by zero to five other species with lesser cover. Dominant species had an average cover of 31 – 60%, with the next most frequent species averaging 10 – 18% (Figure 2.2). Pielou's evenness was highest for Fern Ridge Bog (FRBP), with  $J' = 0.849$ . Bender Swamp (BEND) had  $J' = 0.768$ , while Two Mile Run (TMIR) was the least even with  $J' = 0.729$ .

*Sphagnum* spp. were the main component of most communities, although several plots were dominated by other mosses such as *Pleurozium schreberi* or *Hypnum imponens* (Figure 2.3). *S. fallax* was the most commonly dominant species, as the main component of eight of the 28 communities; it was also the most frequent species at each site (Table 2.1). *S. divinum* was nearly as common, dominating six communities. Nonetheless,

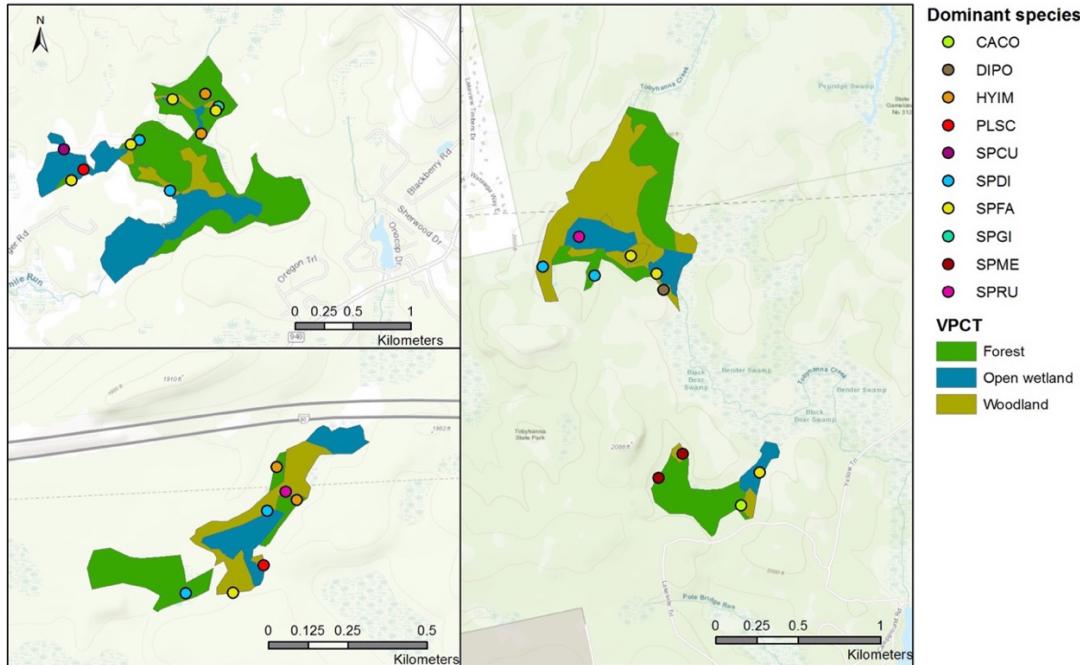
communities had considerable heterogeneity both in terms of constituent species and the proportions of those species. In some instances, the bryophyte layer was comprised entirely of a single species; in others, three or more species had relatively equal cover.

Species	Species code	Frequency by site			
		BEND	FRBP	TMIR	Overall
<i>Aulacomnium palustre</i>	AUPA	0	0	0.82	0.32
<i>Bazzania trilobata</i>	BATR	0.4	0	0.18	0.21
<i>Calliergon cordifolium</i>	CACO	1.2	0	0	0.43
<i>Calliergonella cuspidata</i>	CACU	0	0.14	0	0.04
<i>Calypogeia integrifistipula</i>	CAIN	0	0.57	0	0.14
<i>Dicranum montanum</i>	DIMO	0	0	0.18	0.07
<i>D. polysetum</i>	DIPO	1	0	0	0.36
<i>D. scoparium</i>	DISC	0	0.14	0.36	0.18
<i>Hypnum imponens</i>	HYIM	0.4	4	2.45	2.11
<i>Leucobryum glaucum</i>	LEGGL	0	0	0.09	0.04
<i>Odontoschisma sphagni</i>	ODSP	0.1	0	0	0.04
<i>Platygyrium repens</i>	PLRE	0	0	0.09	0.04
<i>Pleurozium schreberi</i>	PLSC	0	2.86	2.36	1.64
<i>Polytrichum commune</i>	POCO	3.4	1.29	1.64	2.18
<i>P. strictum</i>	POST	0.1	0	0.09	0.07
<i>Pseudobryum cinclidioides</i>	PSCI	0	0	0.27	0.11
<i>Rhizomnium appalachianum</i>	RHAP	0.3	0	0	0.11
<i>Sphagnum angustifolium</i>	SPAN	0	0	0.45	0.18
<i>S. cuspidatum</i>	SPCU	0	0	2.82	1.11
<i>S. divinum</i>	SPDI	3	3.43	7.45	4.86
<i>S. fallax</i>	SPFA	10.1	5.86	8.64	8.46
<i>S. flexuosum</i>	SPFL	1.6	0	0	0.57
<i>S. girgensohnii</i>	SPGI	1.3	0	2.18	1.32
<i>S. medium</i>	SPME	3.5	0	0	1.25
<i>S. russowii</i>	SPRU	1.8	3.29	0	1.46
<i>Tortella tortuosa</i>	TOTO	0.1	0	0.09	0.07
<b>Total abundance</b>		28.3	21.58	30.16	27.37

**Table 2.1.** Frequencies of sampled species at each site and in total.



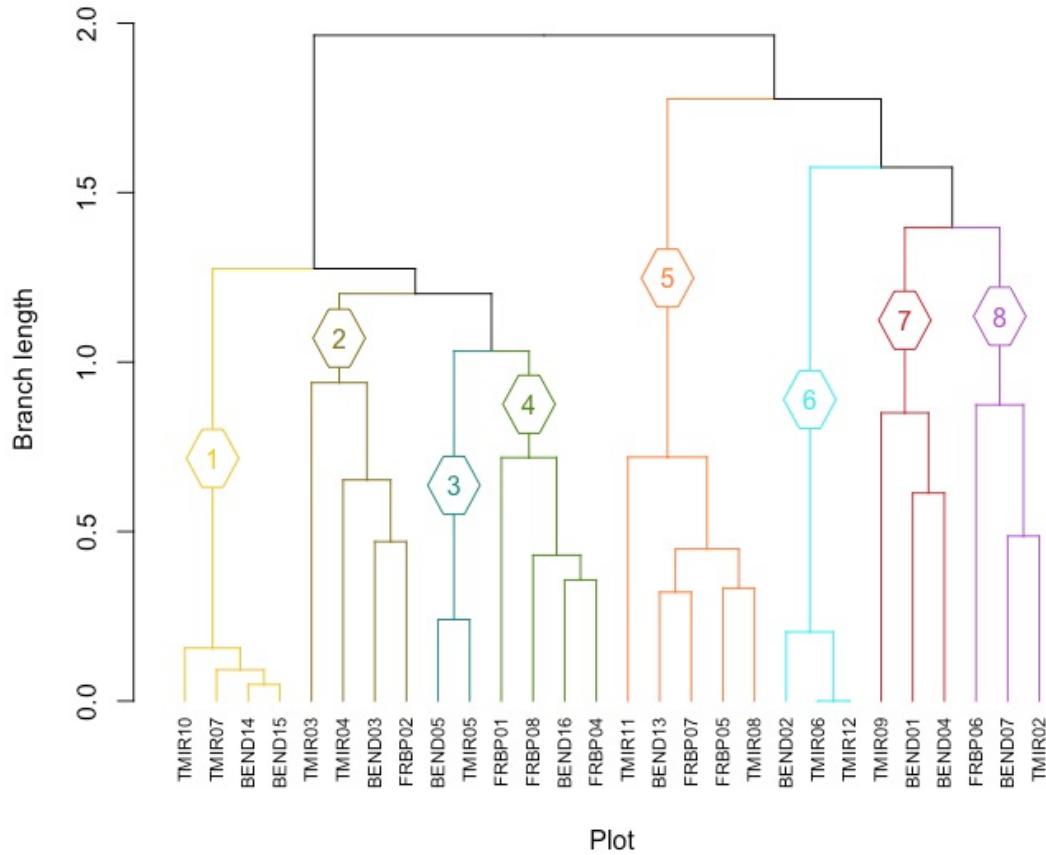
**Fig 2.2.** Species proportions of total cover, ordered from greatest to least for the three most frequent species at each plot. Proportions were averaged across plots within sites. Pielou's evenness ( $J'$ ) was computed for each site.



**Fig. 2.3.** Dominant bryophyte species at each plot. The dominant species is the species with the greatest proportion of total cover. Species codes: CACO = *Calliergon cordifolium*; DIPO = *Dicranum polysetum*; HYIM = *Hypnum imponens*; PLSC = *Pleurozium schreberi*; SPCU = *Sphagnum cuspidatum*; SPDI = *S. divinum*; SPFA = *S. fallax*; SPGI = *S. girgensohnii*; SPME = *S. medium*; SPRU = *S. russowii*. Vascular plant community type (VPCT) is also shown for reference.

Of the 26 species found across all sites, 12 were unique to a single sampled plot, and were thus excluded from clustering and ordination. Of the remaining 14, half were found at only two plots.

Eight broad community groups were determined from hierarchical agglomerative clustering (Figure 2.4). Groups consisted of 2-5 plots with similar bryoflora structure, described based on shared features (Table 2.2). ANOSIM of clusters was significant and



**Fig. 2.4.** Dendrogram derived from agglomerative hierarchical clustering performed on the bryophyte community matrix. Clustering used Ward's method (Ward, 1963), with an agglomerative coefficient (AC) of 0.9021. Groups are denoted by numbered hexagons, with constituent plots marked by branches in the corresponding color.

indicated strong separation of clusters in community matrix space ( $R = 0.8423$ ,  $p < 0.001$ ).

The two species that dominated most sites (*S. fallax* and *S. divinum*) were also defining constituents of five of the eight groups.

In terms of species composition, differences in *S. fallax* and *S. divinum* dominated groups (Groups 1-4 and Group 6) were attributable to both variation in frequency of the dominant *Sphagnum*, as well as variation in frequency of *Polytrichum commune* and *Pleurozium schreberi*. Group 6 communities contained the least of the latter two species, while Group 3 contained a small proportion of *P. commune*. Group 4 contained more *P. commune*, and occasional more mesic species including *P. schreberi*. Group 2 contained appreciably greater proportions of both *P. commune* and *P. schreberi* on average.

Among groups not dominated by *S. fallax* or *S. divinum*, Group 7 communities were least separated from the others, primarily from similar proportions of *Polytrichum commune*. Group 8 was more differentiated due to both dominance by unique *Sphagnum* spp. and the presence of *P. strictum* in place of *P. commune*. Group 5 was also strongly distinguished from other assemblages, as these communities were dominated by *Hypnum imponens* and typically lacked *Sphagnum* entirely. Additionally, *Dicranum* spp. were unique to Group 5, although their influence in the ordination was limited by the fact that two of the three documented *Dicranum* spp. occurred in only one plot each.

Evenness was lowest for Groups 1 and 6 (Table 2.2), each of which were characterized by nearly complete dominance of a single *Sphagnum* species. In contrast, evenness was highest for Groups 2 and 7, both of which typically showed co-dominance with numerous minor species.

Group number (from Fig. 2.4)	Description	Pielou's evenness ( $J'$ )
1	Completely or nearly monospecific layer of <i>Sphagnum fallax</i>	0.214
2	Generally dominated by <i>Pleurozium schreberi</i> or <i>S. fallax</i> , often with <i>Polytrichum commune</i>	0.818
3	<i>S. divinum</i> , with minor proportions of <i>Polytrichum commune</i> and sometimes <i>S. fallax</i>	0.729
4	Co-dominated by <i>S. divinum</i> and <i>S. fallax</i> , with minor proportions of other species	0.679
5	Generally dominated by <i>Hypnum imponens</i> , often with <i>Polytrichum commune</i> and <i>Dicranum</i> spp.	0.644
6	Completely or nearly monospecific layer of <i>S. divinum</i> ; rarely in nearly equal proportion with <i>Calliergon cordifolium</i>	0.418
7	Dominated by <i>S. medium</i> and/or <i>S. girgensohnii</i> , occasionally with other <i>Sphagnum</i> spp.	0.827
8	Dominated by either <i>S. russowii</i> or <i>S. cuspidatum</i> , often with a minor proportion of <i>Polytrichum strictum</i>	0.571

**Table 2.2.** Descriptions and evenness values of the eight bryophyte community groups identified from hierarchical agglomerative clustering. Each cluster consists of 2-5 plots with similar bryoflora structure. Pielou's evenness ( $J'$ ) was computed for each group.  $J'$  represents the distribution of relative abundances of species in a community, ranging from 0 (no evenness) to 1 (complete evenness).

Mean canopy openness ranged from 0 to 1, although only 25% of plots had an openness of  $>0.5$ . Openness was greatest in the shrub-dominated wetlands, and least in palustrine woodland and palustrine forest. Peat depth ranged from 101 to  $>900$  mm.

*Sphagnum*-dominated communities tended to have greater peat depth than those dominated by non-*Sphagnum* species. Depth to water table (DWT) varied from 0 to 170 mm, although at five plots, the water table was too low to measure (and water samples

could not be taken). DWT showed similar community patterns to peat depth, although the two did not co-vary (Figure AI in Appendix I).

Across all plots, pH ranged from 3.98 to 6.23. Open wetlands tended to have lower pH values, while higher pH values corresponded mostly to palustrine woodland. Palustrine woodland plots with the highest pH also had higher base cation concentration and reduced conductivity. Aside from these circumneutral plots, base cation concentrations had relatively low concentration and low variability. Sodium concentrations ranged from 1.955 – 55.599 mg L<sup>-1</sup>, but median concentration was 2.351 mg L<sup>-1</sup>. Similarly, potassium concentrations ranged from 0.189 – 5.098 mg L<sup>-1</sup> but had a median value of 0.533 mg L<sup>-1</sup>. Magnesium and calcium were less skewed; magnesium concentrations ranged from 0.101 – 1.047 mg L<sup>-1</sup>, with a median of 0.256 mg L<sup>-1</sup>, while calcium concentrations ranged from 0.179 – 4.855 mg L<sup>-1</sup>, with a median of 1.08 mg L<sup>-1</sup>.

Ammonium-N concentration averaged 0.14 mg L<sup>-1</sup>, varying from <0.01 to 0.49 mg L<sup>-1</sup>. Ammonium-N was lowest in wetlands – never exceeding 0.05 mg L<sup>-1</sup> – and highest in plots with spruce-dominated canopy. Nitrate-N concentration was lower on average than ammonium, with a mean concentration of 0.05 mg L<sup>-1</sup> and a range of 0.01 to 0.16 mg L<sup>-1</sup>. Sulfate-S concentrations averaged 0.26 mg L<sup>-1</sup> and ranged from 0.03 to 0.85 mg L<sup>-1</sup>. Sulfate-S was lowest in plots with high base cation concentration – among the base-enriched plots, the greatest concentration was 0.17 mg L<sup>-1</sup>.

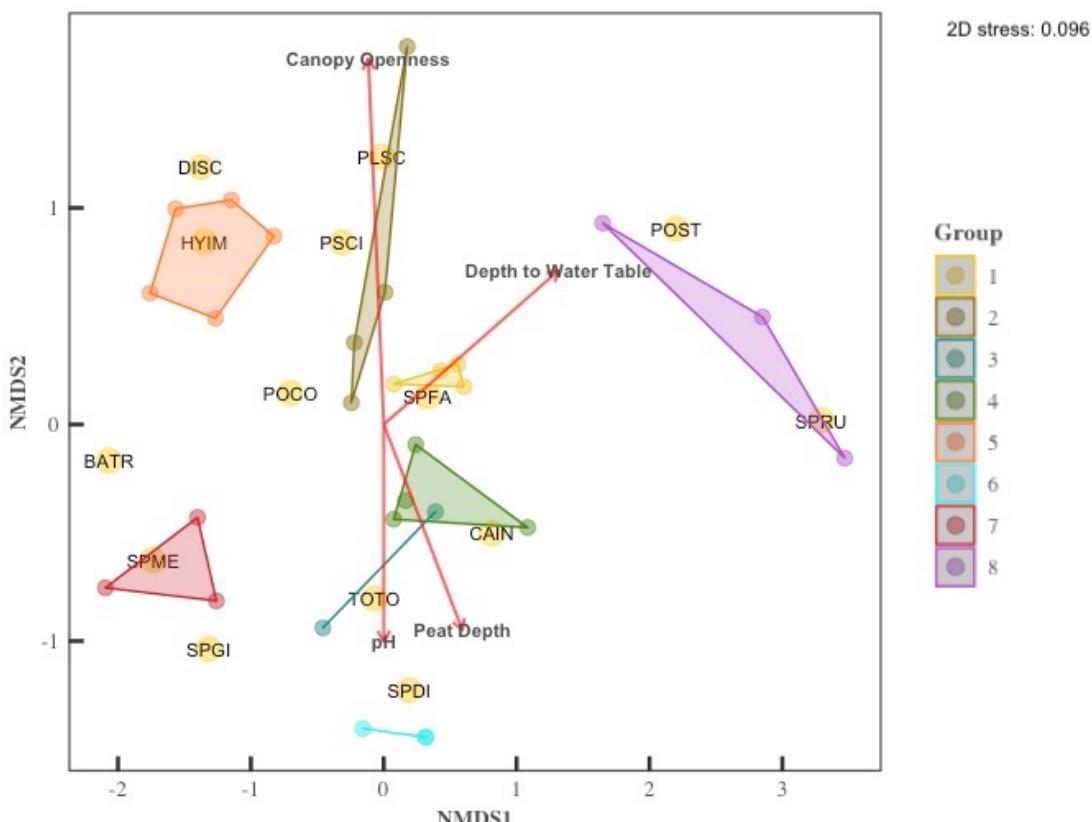
### *Ordination*

Ordination fit in two dimensions was good, with a 2D stress of 0.096 (Figure A2 in Appendix II). Community groups had little overlap in ordination space, consistent with the high  $R$  value from ANOSIM (Figure 2.5). On the NMDS1 axis, Groups 5 and 7 tended towards positive values. Generally, *SPFA* and *SPDI* dominated groups differed from one another along the NMDS1 axis, while other groups were separated along both axes. Among environmental factors, two factors had significant correlation ( $p < 0.05$ ) with the community dissimilarity matrix: canopy openness and peat depth (Table 2.3). pH had nearly significant correlation (Mantel  $r = 0.176$ ,  $p = 0.06$ ). Additionally, although DWT was not significantly correlated with the dissimilarity matrix (Mantel  $r = 0.038$ ,  $p = 0.269$ ), it was significantly correlated with the ordination ( $r^2 = 0.366$ ,  $p = 0.019$ ), as was canopy openness ( $r^2 = 0.468$ ,  $p = 0.004$ ).

On the ordination, canopy openness, pH, and peat depth covaried most strongly with the NMDS1 axis, while DWT covaried more strongly with the NMDS2 axis. In general, increasing NMDS1 values corresponded to increasing canopy openness (less shade), and to decreasing pH (increased acidity) and peat depth. Likewise, increasing NMDS2 values mostly corresponded to increasing depth to water table (lower water table).

## **DISCUSSION**

The overwhelming dominance of *Sphagnum* spp. across most plots is consistent with previous descriptions of Appalachian poor fen bryoflora (Bedford and Godwin 2003; Francel et al. 2004). *S. fallax* and *S. divinum* are both common constituents of North American poor fens and can form extensive lawns (Vitt 2014); indeed, Wieder



**Fig. 2.5.** NMDS ordination of plots, using a Wisconsin double-standardized matrix of Bray-Curtis dissimilarities. Community groups are indicated by color and enclosed by minimum convex polygons. Large gold points with text represent species scores. Red vectors represent significant environmental factors; vectors are scaled to the  $r^2$  of the correlation with the ordination for each factor. Species codes: BATR = *Bazzania trilobata*; CAIN = *Calypogeia integrifistipula*; DISC = *Dicranum scoparium*; HYIM = *Hypnum imponens*; PLSC = *Pleurozium schreberi*; POCO = *Polytrichum commune*; POST = *P. strictum*; PSCI = *Pseudobryum cinclidoides*; SPDI = *Sphagnum divinum*; SPFA = *S. fallax*; SPGI = *S. girgensohnii*; SPME = *S. medium*; SPRU = *S. russowii*; TOTO = *Tortella tortuosa*. Factor correlations: canopy openness (Ordination  $r^2 = 0.468$ ,  $p = 0.004$ ; Mantel  $r = 0.149$ ,  $p = 0.041$ ); depth to water table (Ordination  $r^2 = 0.366$ ,  $p = 0.019$ ; Mantel  $r = 0.038$ ,  $p = 0.269$ ); peat depth (Ordination  $r^2 = 0.205$ ,  $p = 0.175$ ; Mantel  $r = 0.178$ ,  $p = 0.005$ ); pH (Ordination  $r^2 = 0.164$ ,  $p = 0.223$ ; Mantel  $r = 0.178$ ,  $p = 0.06$ ).

Environmental factor	Ordination r <sup>2</sup>	p	Mantel r	p
Canopy openness	0.468	0.004**	0.149	0.041*
Peat depth	0.205	0.175	0.178	0.005**
Depth to water table	0.366	0.019*	0.038	0.269
pH	0.164	0.223	0.178	0.06^
Reduced conductivity	0.163	0.235	-0.031	0.57
NO <sub>3</sub> <sup>-</sup>	0.006	0.942	-0.112	0.837
NH <sub>4</sub> <sup>+</sup>	0.127	0.355	-0.011	0.504
SO <sub>4</sub> <sup>2-</sup>	0.137	0.291	-0.026	0.567
Na <sup>+</sup>	0.157	0.25	-0.011	0.507
Mg <sup>2+</sup>	0.276	0.1	0.044	0.311
K <sup>+</sup>	0.15	0.297	-0.059	0.68
Ca <sup>2+</sup>	0.227	0.139	0.026	0.386

**Table 2.3.** Correlation coefficients and significance values for environmental factors from correlation with the NMDS ordination, and Mantel correlation with the dissimilarity matrix.

<sup>^</sup> denotes 0.05 < p < 0.1; \* denotes 0.01 < p < 0.05; \*\* denotes p < 0.01.

and Yavitt (1994) describe the bryoflora of Big Run Bog, a well-studied Appalachian poor fen, as principally composed of *S. fallax* and *S. magellanicum* (the latter now *S. divinum* and *S. medium* in North America: see Chapter III).

The moderate-high evenness among sites reflects the pattern of one or two dominant species, usually *Sphagnum*, with a few other species as lesser components. Steel et al. (2004) suggest that low evenness in bryophyte communities compared to vascular plant communities reflects a “tail of minor species” in the abundance distribution. While the authors found a mean evenness of 0.31 at their sites, mean evenness in the present study was higher; this pattern could reflect greater competition in peatlands suppressing rare species, but it is more probably due to differences in sampling technique, as smaller sampling areas are likely to detect fewer species.

Nineteen of the 26 detected species were found at only one or two plots, indicating high plot-wise beta diversity (low similarity between plots) also consistent with prior descriptions of Appalachian peatlands (Walbridge 1994). Such high beta diversity may partially explain why so many groups were identified by hierarchical clustering from a relatively small number of plots, even without the inclusion of species unique to a single plot.

Among the seven more abundant species, two – aside from *S. fallax* and *S. divinum* – occurred in a broad range of groups. *Polytrichum commune* is a forest or peatland edge species in boreal North America (Vitt 2014; Graham et al. 2016) but seems to occupy a more generalist role in Pocono peatlands, occurring in six of the eight groups. Notably, though, *P. commune* was absent from Group 8, which had high overall canopy openness, indicating that the species may still be replaced by *P. strictum* in open wetlands. Like *P. commune*, *Pleurozium schreberi* is an abundant species of mature boreal forests (Hutchinson and Scott 1988; Whitehead and Gower 2001), but here occupied both closed and open canopy plots of three different community groups. However, depending on the exact limits of a “peatland edge”, many of the open sampled plots could still be considered edge habitat, as the small overall size and “irregular mosaic” pattern of Appalachian peatlands increases the proximity of most open patches to adjacent forest (Wieder et al. 1981).

Low overall pH and low base cation concentration in most sites is consistent with the “poor fen” description of many central Appalachian peatlands (Wieder and Yavitt 1994; Francel et al. 2004). However, a few sites, particularly in the northern section of Fern Ridge Bog Preserve (FRBP), had relatively elevated base cation concentration, pH, and

conductivity. The three sites with the highest base cation concentrations and conductivities were all within 0.65 km of I80, a major transcontinental highway that bisects northern PA. Runoff containing road salt and other dissolved ions can substantially impact peatland water chemistry (Wilcox 1986; Chimner et al. 2017). Although sodium concentrations in the affected plots was an order of magnitude below those reported in a severely salt-impacted bog in Indiana (Wilcox 1986), concentrations were still nearly 30-50x greater than the maximum value reported in Walbridge (1994) in West Virginian fens (~1.2 mg L<sup>-1</sup> vs. ~33-55 mg L<sup>-1</sup>). Calcium, magnesium, and potassium were within the ranges reported by Walbridge (1994) and within those from three Kentucky peatlands reported by Thompson et al. (2012). It is difficult to surmise if salinization from road runoff has had any long-term impacts on FRBP plots without a baseline comparison, but effects seen by Wilcox (1986) such as widespread tree mortality, *Sphagnum* decline, and invasion by cattails (*Typha* spp.) were not observed in FRBP. Walker et al. (2021) determined that exurban forested wetlands of the northeastern U.S. generally had increased base cation concentration from saline runoff, but remained below the threshold necessary to induce shifts in plant communities, consistent with observations in FRBP.

Ammonium-N in the present study was similar to or below concentrations from other Appalachian peatlands (Stewart and Nilsen 1993; Walbridge 1994), as was nitrate-N (Walbridge 1994; Thompson et al. 2012). In principle, low inorganic nitrogen could be attributed to declining N emissions from human activity in the Northeast over the past few decades (National Atmospheric Deposition Program 2000, 2020; Ackerman et al. 2019). In contrast to central Canadian peatlands, where biological nitrogen fixation (BNF) can account for a majority of N inputs (Vile et al. 2014), peatlands in eastern North America,

particularly those near urban-industrial centers, often have lower  $\delta^{15}\text{N}$  values associated with lower BNF rates (Živković et al. 2017). Declines in regional anthropogenic N emissions primarily represent increased regulation of oxidized rather than reduced nitrogen, as the latter is mostly derived from agricultural sources (Ackerman et al. 2019). Wet deposition of  $\text{NH}_4^+ \text{-N}$  alone in eastern Pennsylvania presently approaches the 3.0 kg/ha critical threshold proposed by Wieder et al. (2020) for Albertan poor fens (National Atmospheric Deposition Program 2020). As Wieder et al. (2020) detected substantial changes in *Sphagnum* abundance and plant community structure with increased nitrogen deposition, it is reasonable to suppose that anthropogenic N inputs have similarly affected Appalachian peatlands. Lack of apparent influence of N concentration on community composition observed in the present study may simply reflect the small spatio-temporal scale and relative homogeneity of N in porewater. Long-term N fertilization experiments could uncover effects of sustained high N deposition on Appalachian peatland communities.

Physical factors were more strongly correlated with community composition than chemical factors overall. Canopy openness, peat depth, and DWT were all variously related to the ordination and/or the community matrix itself. Peat depth is the most difficult to regard as an explanatory factor, as the causal link between peat depth and community composition is complicated by the fact that bryophytes directly influence peat depth. In any case, the strong correlation of peat depth by Mantel correlation, but weak correlation with the ordination, suggests that whatever variability is explained by peat depth is poorly represented in the ordination. Acrotelm depth can influence soil water holding capacity and

thus correlate with wetland indices (Franci et al. 2004), but missing data for upland sites in DWT measurements limit the ability to assess any such trend statistically.

Canopy openness and DWT are largely interrelated in principle. Shading reduces evaporation from the ground layer, while increased vascular plant presence (= increased shade) generally increases transpiration. In some cases, following vascular plant colonization of open areas, the magnitude of the former effect outweighs the latter, leading to net long-term reduction in evapotranspiration (Heijmans et al. 2013). Here, no covariance between canopy openness and DWT was detected (Figure A3 in Appendix III), which may also have been complicated by missing data from upland sites. However, separation of the factors is reflected in the NMDS ordination, which indicates divergent bearings of correlation, suggesting that the two factors explain different aspects of community variation. Moreover, in geogenous peatlands, DWT may be more closely related with proximity to streams or seeps than to canopy openness, depending on the proportion of porewater derived from precipitation.

Both canopy openness and DWT may be altered by woody encroachment, a growing threat to temperate North American peatlands (Cartwright 2019; Beauregard et al. 2020). As variation in precipitation increases and episodic drought becomes more frequent in eastern North America, water table drawdown may desiccate bryophytes and alleviate anoxic soil conditions that ordinarily impair the growth of vascular vegetation. While Heijmans et al. (2013) suggest that episodic droughts alone are insufficient to induce lasting state shifts, droughts may still allow woody plants to take hold and expand cover through facilitation. The corresponding increase in canopy cover also modifies the bryophyte microhabitat. This phenomenon may be more pronounced in Appalachian

peatlands than in boreal peatlands, as Appalachian peatlands have a greater proportion of tree cover from broadleaf trees and have smaller patch size with greater woodland edge.

Based on the ordination, a decrease in canopy openness corresponding to woody encroachment would favor *Sphagnum divinum*-dominated and Group 7 communities, and disfavor communities of Groups 2, 5 and 8. In particular, the species most associated with low canopy openness were *S. divinum* and *S. girgensohnii*, while *Pleurozium schreberi*, *Dicranum scoparium*, and *Polytrichum strictum* were most associated with high openness. Loss or reduction of open wetland bryophytes is concerning given the rarity and isolation of open patches, and the corresponding vulnerability of the bryoflora. While species such as *P. schreberi* and *D. scoparium* are sufficiently widespread in Pennsylvania to survive local extirpations, *P. strictum* is restricted to fewer habitats and is becoming increasingly threatened in the state (Schuette, unpubl. data). Other typically open wetland species such as *Sphagnum cuspidatum* and *S. russowii* are vulnerable or imperiled in PA.

Given the high floristic uniqueness and spatial isolation of Group 8 communities, loss or decline of these assemblages with woody encroachment would be a substantial blow to community diversity for Pocono peatlands. Bryophyte cover in general could decrease if, for example, other *Sphagnum*-dominated communities that replace Group 8 do not tolerate high canopy openness of broadleaf-enclosed wetlands during winter. While *Sphagnum divinum* appeared to tolerate a range of hydrologic conditions, it never occurred in plots with canopy openness > 0.35 and predominantly occupied spruce woodland, which suggest that *S. divinum* may not thrive in areas that receive seasonal exposure to strong sunlight. Presently, broadleaf woodland sites with moderate canopy openness were primarily red maple – highbush blueberry (*Acer rubrum* – *Vaccinium corymbosum*)

woodland with a bryophyte layer of Group 1 or Group 7, indicating that one or more of the associated *Sphagnum* species could instead exploit increasing broadleaf woodland habitat.

## CONCLUSIONS

Pocono peatlands match patterns of diversity observed in other Appalachian peatlands, with high beta diversity and moderate bryophyte evenness. Community composition was mostly associated with physical factors; except for pH, chemical factors did not significantly impact community composition across the studied sites, possibly because of low overall between-site and between-community variability observed in water chemistry. However, both physical and chemical factors highlighted threats from global change. The salinization of plots adjacent to a major roadway did not appear to have influenced plant communities, but increased sodium levels are a warning that proximity to roadways may be a risk factor for these peatlands. With climate change and woody encroachment functioning synergistically in temperate peatlands, communities with open wetland specialists such as *Polytrichum strictum* or *Sphagnum cuspidatum* are threatened, while shaded communities dominated by *Sphagnum divinum* or moderate-open woodland *Sphagnum* mats could expand. Long term monitoring of Appalachian peatland habitats and bryophyte communities is critical to informing management strategies that may protect vulnerable species and communities from extirpation.

## REFERENCES

- Ackerman D, Millet DB, Chen X (2019) Global estimates of inorganic nitrogen deposition across four decades. *Global Biogeochem Cy* 33:100–107.  
<https://doi.org/10.1029/2018GB005990>

Beauregard P, Lavoie M, Pellerin S (2020) Recent gray birch (*Betula populifolia*) encroachment in temperate peatlands of eastern North America. *Wetlands* 40:351–364. <https://doi.org/10.1007/s13157-019-01186-3>

Bedford BL, Godwin KS (2003) Fens of the United States: Distribution, characteristics, and scientific connection versus legal isolation. *Wetlands* 23:608–629. [https://doi.org/10.1672/0277-5212\(2003\)023\[0608:FOTUSD\]2.0.CO;2](https://doi.org/10.1672/0277-5212(2003)023[0608:FOTUSD]2.0.CO;2)

Belland RJ, Caners RT (2021) Patterns of rare moss diversity and distribution in Alberta. *Botany* 99:695–711. <https://doi.org/10.1139/cjb-2021-0018>

Berg TM, Pennsylvania Bureau of Topographic and Geologic Survey (1989)  
Physiographic provinces of Pennsylvania

Cameron CC (1968) Peat. In: Mineral Resources of the Appalachian Region. United States Department of the Interior, Geological Survey, Washington, D.C., U.S.A., pp 136–145

Cartwright J (2019) Ecological islands: conserving biodiversity hotspots in a changing climate. *Front Ecol Environ* 17:331–340. <https://doi.org/10.1002/fee.2058>

Chimner RA, Cooper DJ, Wurster FC, Rochefort L (2017) An overview of peatland restoration in North America: where are we after 25 years?: Peatland restoration in North America. *Restor Ecol* 25:283–292. <https://doi.org/10.1111/rec.12434>

Draper FC, Asner GP, Honorio Coronado EN, et al (2019) Dominant tree species drive beta diversity patterns in western Amazonia. *Ecology* 100:e02636. <https://doi.org/10.1002/ecy.2636>

ESRI (2020) ArcGIS Desktop. Version 10.8.1. Environmental Systems Research Institute, Redlands, CA

Fischer J, Lindenmayer DB (2007) Landscape modification and habitat fragmentation: a synthesis. *Global Ecol Biogeogr* 16:265–280. <https://doi.org/10.1111/j.1466-8238.2007.00287.x>

Flora of North America Editorial Committee (ed) (2007) Bryophyta, part 1. In: Flora of North America North of Mexico. Oxford University Press, New York, NY

Flora of North America Editorial Committee (ed) (2014) Bryophyta, part 2. In: Flora of North America North of Mexico. Oxford University Press, New York, NY

Franci KE, Ford WM, Castleberry SB (2004) Characterization of high elevation central Appalachian wetlands. U.S. Department of Agriculture, Forest Service, Northeastern Research Station, Newtown Square, PA

Gignac LD, Vitt DH (1994) Responses of northern peatlands to climate change: effects on bryophytes. *J Hattori Bot Lab* 75:119–132.  
[https://doi.org/10.18968/jhbl.75.0\\_119](https://doi.org/10.18968/jhbl.75.0_119)

Godínez-Alvarez H, Herrick JE, Mattocks M, et al (2009) Comparison of three vegetation monitoring methods: Their relative utility for ecological assessment and monitoring. *Ecol Indic* 9:1001–1008.  
<https://doi.org/10.1016/j.ecolind.2008.11.011>

Goodall DW (1952) Some considerations in the use of point quadrats for the analysis of vegetation. *Aust J Biol Sci* 5:1–41. <https://doi.org/10.1071/B19520001>

Graham JA, Hartsock JA, Vitt DH, et al (2016) Linkages between spatio-temporal patterns of environmental factors and distribution of plant assemblages across a boreal peatland complex. *Boreas* 45:207–219. <https://doi.org/10.1111/bor.12151>

Halsey LA, Vitt DH, Gignac LD (2000) *Sphagnum*-dominated peatlands in North America since the Last Glacial Maximum: Their occurrence and extent. *The Bryologist* 103:334–352. [https://doi.org/10.1639/0007-2745\(2000\)103\[0334:SDPINA\]2.0.CO;2](https://doi.org/10.1639/0007-2745(2000)103[0334:SDPINA]2.0.CO;2)

Hassel K, Kyrkjeeide MO, Yousefi N, et al (2018) *Sphagnum divinum* (*sp. nov.*) and *S. medium* Limpr. and their relationship to *S. magellanicum* Brid. J Bryol 40:197–222. <https://doi.org/10.1080/03736687.2018.1474424>

Heijmans MMPD, van der Knaap YAM, Holmgren M, Limpens J (2013) Persistent versus transient tree encroachment of temperate peat bogs: Effects of climate warming and drought events. Glob Change Biol 19:2240–2250.  
<https://doi.org/10.1111/gcb.12202>

Hutchinson TC, Scott MG (1988) The response of the feather moss, *Pleurozium schreberi*, to 5 years of simulated acid precipitation in the Canadian boreal forest. Can J Bot 66:82–88. <https://doi.org/10.1139/b88-012>

Jonasson S (1988) Evaluation of the point intercept method for the estimation of plant biomass. Oikos 52:101–106. <https://doi.org/10.2307/3565988>

Kaufman L, Rousseeuw PJ (2005) Finding groups in data: an introduction to cluster analysis. Wiley, Hoboken, New Jersey

Kollas C, Körner C, Randin CF (2014) Spring frost and growing season length co-control the cold range limits of broad-leaved trees. J Biogeogr 41:773–783.  
<https://doi.org/10.1111/jbi.12238>

Leifeld J, Menichetti L (2018) The underappreciated potential of peatlands in global climate change mitigation strategies. Nat Commun 9:1071.  
<https://doi.org/10.1038/s41467-018-03406-6>

Levy EB, Madden EA (1933) The point method for pasture analysis. New Zeal J Agr 46:267–279

Loisel J, van Bellen S, Pelletier L, et al (2017) Insights and issues with estimating northern peatland carbon stocks and fluxes since the Last Glacial Maximum. Earth-Sci Rev 165:59–80. <https://doi.org/10.1016/j.earscirev.2016.12.001>

Maechler M, Rousseeuw P, Struyf A, et al (2021) cluster: Cluster Analysis Basics and Extensions. Version 2.1.2

Marchant R (2002) Do rare species have any place in multivariate analysis for bioassessment? J N Am Benthol Soc 21:311–313.  
<https://doi.org/10.2307/1468417>

National Atmospheric Deposition Program (2000) 2000 Annual Summary. NADP Program Office, Illinois State Water Survey, Champaign, Illinois

National Atmospheric Deposition Program (2020) 2020 Annual Summary. NADP Program Office, Illinois State Water Survey, Champaign, Illinois

Oksanen J, Blanchet FG, Friendly M, et al (2020) vegan: Community Ecology Package. Version 2.5-7URL <https://CRAN.R-project.org/package=vegan>

Pielou EC (1966) The Measurement of Diversity in Different Types of Biological Collections. J Theoret Biol 13:131–144. [https://doi.org/10.1016/0022-5193\(66\)90013-0](https://doi.org/10.1016/0022-5193(66)90013-0)

Pinceloup N, Poulin M, Brice M-H, Pellerin S (2020) Vegetation changes in temperate ombrotrophic peatlands over a 35 year period. PLoS ONE 15:e0229146.  
<https://doi.org/10.1371/journal.pone.0229146>

Poos MS, Jackson DA (2012) Addressing the removal of rare species in multivariate bioassessments: The impact of methodological choices. Ecol Indic 18:82–90.  
<https://doi.org/10.1016/j.ecolind.2011.10.008>

PRISM Climate Group (2021) Monroe County 30-year normals, 1981 – 2010

R Core Team (2020) R: A language and environment for statistical computing. Version 4.0.3. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org>

Rydin H, Gunnarsson U, Sundberg S (2006) The role of *Sphagnum* in peatland development and persistence. In: Wieder RK, Vitt DH (eds) Boreal Peatland Ecosystems. Springer Berlin Heidelberg, pp 47–65

SAS Institute Inc. (2021) JMP Pro 16. Version 16.0.0. SAS Institute Inc., Cary, NC. URL <https://www.jmp.com/>

Schöpke B, Heinze J, Pätzig M, Heinken T (2019) Do dispersal traits of wetland plant species explain tolerance against isolation effects in naturally fragmented habitats? *Plant Ecol* 220:801–815. <https://doi.org/10.1007/s11258-019-00955-8>

Schlüter EH, Hopfensperger KN, Brenner JC (2010) Potential impacts of climate change on *Sphagnum* bogs of the southern Appalachian Mountains. *Nat Area J* 30:417–424. <https://doi.org/10.3375/043.030.0407>

Sgarbi LF, Bini LM, Heino J, et al (2020) Sampling effort and information quality provided by rare and common species in estimating assemblage structure. *Ecological Indicators* 110:105937. <https://doi.org/10.1016/j.ecolind.2019.105937>

Sjörs H (1950) On the Relation between Vegetation and Electrolytes in North Swedish Mire Waters. *Oikos* 2:241–258. <https://doi.org/10.2307/3564795>

Steel JB, Wilson JB, Anderson BJ, et al (2004) Are bryophyte communities different from higher-plant communities? Abundance relations. *Oikos* 104:479–486. <https://doi.org/10.1111/j.0030-1299.2004.12840.x>

Stewart CN, Nilsen ET (1993) Association of edaphic factors and vegetation in several isolated Appalachian peat bogs. *B Torrey Bot Club* 120:128–135

Stotler RE, Crandall-Stotler B (2017) A Synopsis of the Liverwort Flora of North America North of Mexico. *Ann Mo Bot Gard* 102:574–709. <https://doi.org/10.3417/2016027>

Thompson Y, D'Angelo EM, Karathanasis AD, Sandefur BC (2012) Plant community composition as a function of geochemistry and hydrology in three Appalachian wetlands. *Ecohydrology* 5:389–400. <https://doi.org/10.1002/eco.228>

Turetsky MR, Bond-Lamberty B, Euskirchen E, et al (2012) The resilience and functional role of moss in boreal and arctic ecosystems. *New Phytologist* 196:49–67. <https://doi.org/10.1111/j.1469-8137.2012.04254.x>

Vanderpoorten A, Papp B, Gradstein R (2010) Sampling of bryophytes. In: Eymann J, Degreef J, Häuser C, et al. (eds) Manual on field recording techniques and protocols for All Taxa Biodiversity Inventories and Monitoring. Royal Belgian Institute of Natural Sciences, pp 331–345

Vile MA, Kelman Wieder R, Živković T, et al (2014) N<sub>2</sub>-fixation by methanotrophs sustains carbon and nitrogen accumulation in pristine peatlands. *Biogeochemistry* 121:317–328. <https://doi.org/10.1007/s10533-014-0019-6>

Vile MA, Scott KD, Brault E, et al (2010) Living on the edge: The effects of drought on Canada's western boreal peatlands. In: Tuba Z, Slack NG, Stark LR (eds) *Bryophyte Ecology and Climate Change*. Cambridge University Press, Cambridge, pp 277–298

Vitt DH (2006) Bryophyte community ecology: Going beyond description. *Lindbergia* 31:33–41

Vitt DH (2014) A key and review of bryophytes common in North American peatlands. *Evansia* 31:121–158. <https://doi.org/10.1639/079.031.0402>

Vitt DH, House M, Kitchen S, Wieder RK (2020) A protocol for monitoring plant responses to changing nitrogen deposition regimes in Alberta bogs. *Environ Monit Assess* 192:743. <https://doi.org/10.1007/s10661-020-08645-z>

Walbridge MR (1994) Plant community composition and surface water chemistry of fen peatlands in West Virginia's Appalachian Plateau. *Water Air Soil Poll* 77:247–269

Ward JH (1963) Hierarchical Grouping to Optimize an Objective Function. *J Am Stat Assoc* 58:236–244. <https://doi.org/10.1080/01621459.1963.10500845>

Whitehead D, Gower ST (2001) Photosynthesis and light-use efficiency by plants in a Canadian boreal forest ecosystem. *Tree Physiol* 21:925–929.  
<https://doi.org/10.1093/treephys/21.12-13.925>

Wieder RK, McCormick AM, Lang GE (1981) Vegetational analysis of Big Run Bog, a nonglaciated *Sphagnum* bog in West Virginia. *Castanea* 46:16–29

Wieder RK, Vitt DH, Vile MA, et al (2020) Experimental nitrogen addition alters structure and function of a boreal poor fen: Implications for critical loads. *Sci Total Environ* 733:138619. <https://doi.org/10.1016/j.scitotenv.2020.138619>

Wieder RK, Yavitt JB (1994) Peatlands and global climate change: Insights from comparative studies of sites situated along a latitudinal gradient. *Wetlands* 14:229–238

Wilcox DA (1986) The effects of deicing salts on vegetation in Pinhook Bog, Indiana. *Can J Bot* 64:865–874. <https://doi.org/10.1139/b86-113>

Yu Z (2012) Northern peatland carbon stocks and dynamics: A review. *Biogeosciences* 9:4071–4085. <https://doi.org/10.5194/bg-9-4071-2012>

Zimmerman E, Davis T, Podniesinski G, et al (2012) Terrestrial and Palustrine Plant Communities of Pennsylvania, 2nd Edition. Pennsylvania Natural Heritage Program, Pennsylvania Department of Natural Resources, Harrisburg, PA

Živković T, Disney K, Moore TR (2017) Variations in nitrogen, phosphorus, and  $\delta^{15}\text{N}$  in *Sphagnum* mosses along a climatic and atmospheric deposition gradient in eastern Canada. *Botany* 95:829–839. <https://doi.org/10.1139/cjb-2016-0314>

## CHAPTER III: HABITAT PREFERENCES OF *SPHAGNUM DIVINUM* IN POCONO PEATLANDS

### INTRODUCTION

*Sphagnum* is a highly diverse, cosmopolitan genus of bryophytes that forms the foundation of most temperate and boreal peatlands (Clymo and Hayward 1982; Halsey et al. 2000; Rydin et al. 2006). One of the most widespread *Sphagnum* species is *S. magellanicum*, which occupies a circumboreal distribution with a disjunct population in the Southern Hemisphere (Kyrkjeeide et al. 2016). In North America, *S. magellanicum* is a major component of both temperate and boreal bogs and poor fens. In southern Canada, *S. magellanicum* dominates along with *S. angustifolium* and *S. fuscum* (Gignac and Vitt 1994), while in the northeastern U.S., it commonly occurs alone or with *S. fallax* (Wieder and Yavitt 1994; Cai and Yu 2011; Vitt 2014). Generally, *S. magellanicum* is more widespread towards the southern edge of its northern range, with abundance decreasing with higher latitude (Gignac and Vitt 1994). It is an important component of Appalachian peatland bryoflora and is known from the Pocono region (Manuel 1975; Cai and Yu 2011; Schuette and Krayesky 2014).

The near ubiquity of *S. magellanicum* in North American peatlands coincides with a broad niche space; the species has been variably described as typical of both hollows and hummocks (Vitt and Chee 1990; Vitt et al. 2020), as well as both forested and open areas (Yousefi et al. 2017). Recently, however, the broad niche space of *S. magellanicum* was hypothesized to actually reflect the presence of multiple cryptic species within the *S. magellanicum* concept (Kyrkjeeide et al. 2016; Yousefi et al. 2017). Because bryophytes often have few distinguishing morphological features, it can be difficult to differentiate

between closely-related but genetically distinct species (Kyrkjeeide et al. 2016). Following phylogenetic parsing, it was determined that *Sphagnum magellanicum* is three distinct species: *S. divinum* Flatberg & Hassel, *S. medium* Limpr., and *S. magellanicum* Brid. (Hassel et al. 2018). The latter occurs only in peatlands of the Southern Hemisphere; thus only *S. divinum* and *S. medium* are found naturally in the Northern Hemisphere.

*S. divinum* and *S. medium* are distinct morphologically, genetically, and ecologically. The two may be distinguished by branch length, leaf length, branch leaf arrangement, and, most conclusively, by the size, shape, and configuration of hyalocysts of the proximal end of the concave branch leaf surface (Yousefi et al. 2017; Hassel et al. 2018). While coloration is a potentially distinguishing feature, capitulum color corresponds strongly to habitat (Yousefi et al. 2017). *Sphagnum divinum* of shaded areas may lack red pigmentation entirely, while those of open areas (as well as *S. medium*) often have strong reddish pigmentation of the capitulum, a trait that was long used to distinguish *S. magellanicum* from the remainder of *Sphagnum* section *Sphagnum* in boreal peatlands (Vitt 2014).

Ostensibly, *S. divinum* and *S. medium* tend to inhabit different microhabitats and peatland types. *S. divinum* is characteristic of more shaded areas, particularly peatland edge and forested peatlands, and may inhabit ombrotrophic – mesotrophic peatlands (Yousefi et al. 2017; Hassel et al. 2018). *S. medium* is more typical of open expanses, and favors ombrotrophic settings, although it may also occur in poor fens. However, these habitat preferences have not yet been fully investigated (Hassel et al. 2018). Niche differentiation between the two species was primarily described from boreal specimens, despite that both are also common in temperate peatlands, which leaves gaps in information about niches at

the southern end of the *S. divinum*/*S. medium* range. For example, Hassel et al. (2018) indicate that “*S. magellanicum*” specimens examined from Pennsylvania were determined as *S. medium*, and did not examine a confirmed *S. divinum* specimen from the state, despite the present work identifying *S. divinum* as one of the most common species of Pocono poor fens (see Chapter 2). Moreover, microhabitat preferences assessed by Yousefi et al. (2017) were derived from experiments at a single ombrotrophic site; such preferences may not be the same in more oligotrophic peatlands. To expand understanding of the different habitat preferences of *Sphagnum divinum* and *Sphagnum medium*, I aimed to perform comparative analysis of species occurrence by location from three high elevation temperate peatlands in the Glaciated Pocono Plateau and to relate differences in occurrence to canopy cover and distance to forest edge.

## QUESTION AND HYPOTHESIS

*Q4: Are “Sphagnum magellanicum” in Pocono peatlands primarily S. divinum, S. medium, or some combination thereof? Do the habitat preferences of the present species align with those described in Hassel et al. (2018)?*

### Hypotheses:

Q4, H1: *S. divinum* will occur more broadly than *S. medium*. If and where *S. medium* occurs in the study sites, it will be a relatively minor component compared to *S. divinum*.

Q4, H2: My findings about the respective habitat preferences of the two species will be largely consistent with those described in Hassel et al. (2018); that is, *S. divinum* will be found along margins and areas of dense canopy cover

(low canopy openness), while *S. medium* will be found sparsely in central, open areas (high canopy openness).

## METHODS

Specimens of *Sphagnum divinum* and *Sphagnum medium* were collected and identified as described in Chapter 2. In determining *S. divinum* and *S. medium* to species, morphological features from Hassel et al. (2018) were used, as most other keys in print still recognize the species as one under *S. magellanicum*.

Preliminary results found ten plots containing *S. divinum* and two containing *S. medium*. Because *S. medium* was too infrequent to produce a reliable distribution for analysis, analytical methods were revised to assess only the habitat preference of *S. divinum*. Data of *S. divinum* abundance were transformed to presence/absence, as abundance may be influenced by interspecific interaction and is thus not necessarily indicative of the strength of habitat preference.

Geospatial polygons of vascular plant community type (VPCT) were obtained from the Pennsylvania Natural Heritage Program (described in Zimmerman et al., 2012). VPCTs were reclassified based on their broad category (forest, woodland, or open wetland) and boundaries were extracted. Distance to forest edge (DFE) was computed for each plot point, except those that were within forest polygons, for which the distance was recorded as 0. Canopy openness was reused from data collected in Chapter 2.

Using Shapiro-Wilk tests, both DFE and canopy openness were found to be non-normally distributed (DFE:  $W = 0.808$ ,  $p < 0.001$ ; canopy openness:  $W = 0.747$ ,  $p < 0.001$ ). Non-parametric tests were therefore deemed appropriate; one-sided two-sample Mann-

Whitney U-tests were conducted for both variables between the *S. divinum* presence and *S. divinum* absence plots, under the alternative hypotheses that DFE and canopy openness were both greater at absence plots. Hypotheses were based on descriptions in Yousefi et al. (2017) and Hassel et al. (2018).

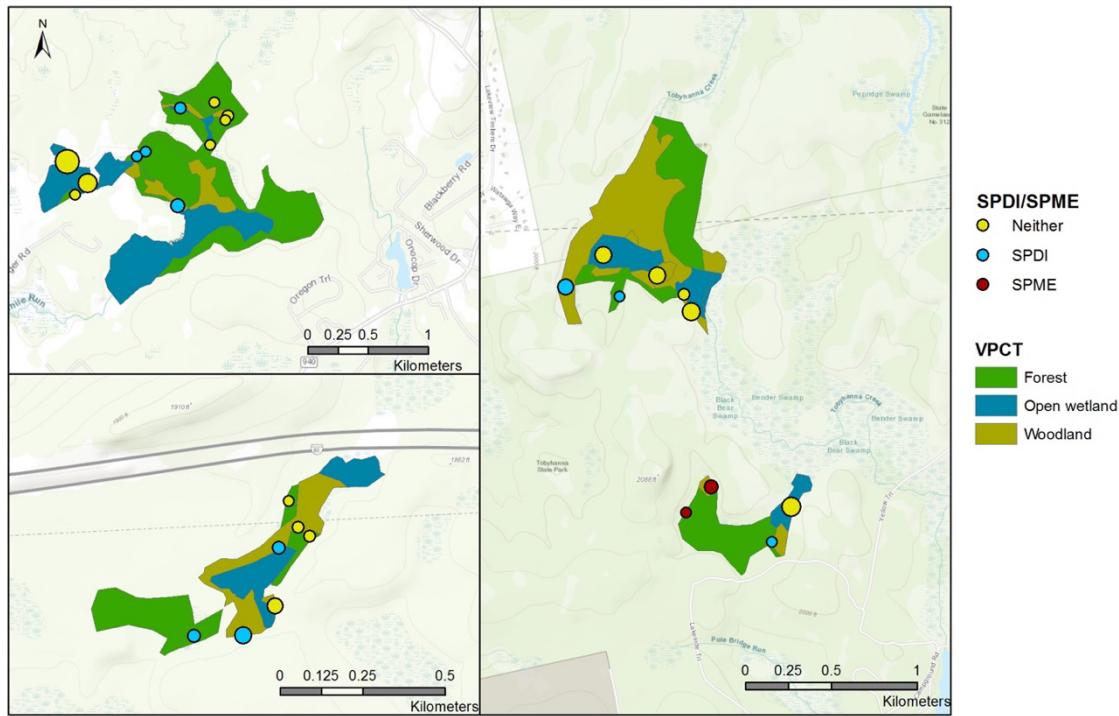
All statistical tests were conducted in R 4.0.3 (R Core Team 2020). All geospatial mapping was conducted in ArcMap 10.8 (ESRI 2020).

## RESULTS

Plots with *Sphagnum divinum* tended to occur in woodland or forest, as only one of the ten plots containing *S. divinum* was in open wetland (Figure 3.1). *S. medium* was found in one forest and one woodland plot. Plots with neither species occurred roughly evenly across all three VPCT types.

Distance to forest edge did not significantly differ between *S. divinum* present and *S. divinum* absent plots ( $W = 75.5$ ;  $p = 0.249$ ). While mean DFE was much lower for present plots, medians were roughly equal between present and absent plot distributions (Figure 3.2). Lowered medians with respect to means reflect the large number of zeroes in each distribution contributed from forest plots.

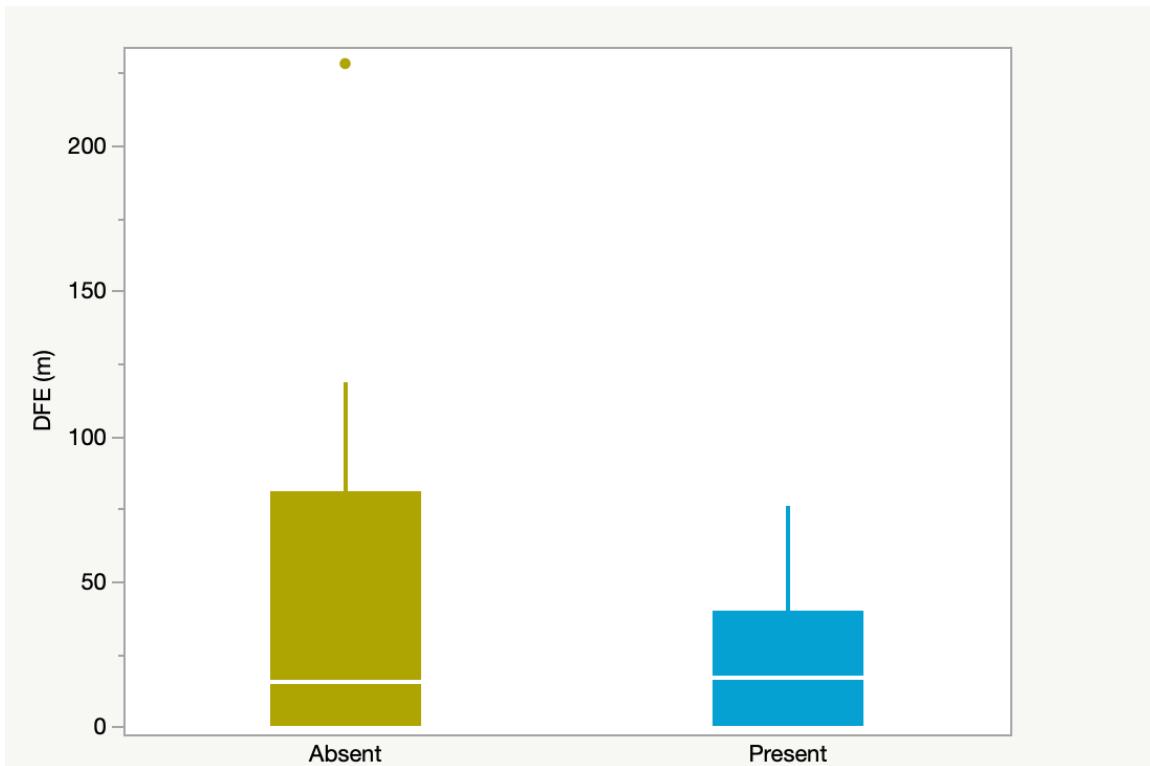
Canopy openness differed significantly between *S. divinum* present and *S. divinum* absent plots ( $W = 37$ ;  $p = 0.006$ ). On average, *S. divinum* present plots had much lower canopy openness than *S. divinum* absent (Figure 3.3).



**Fig. 3.1.** Plot maps showing the presence of *Sphagnum divinum* (SPDI), *Sphagnum medium* (SPME), or neither. Plot point size is scaled by the square root of the distance to forest edge (DFE), plus a constant to render low DFE points visible. Vascular plant community type (VPCT) is shown for comparison.

## DISCUSSION

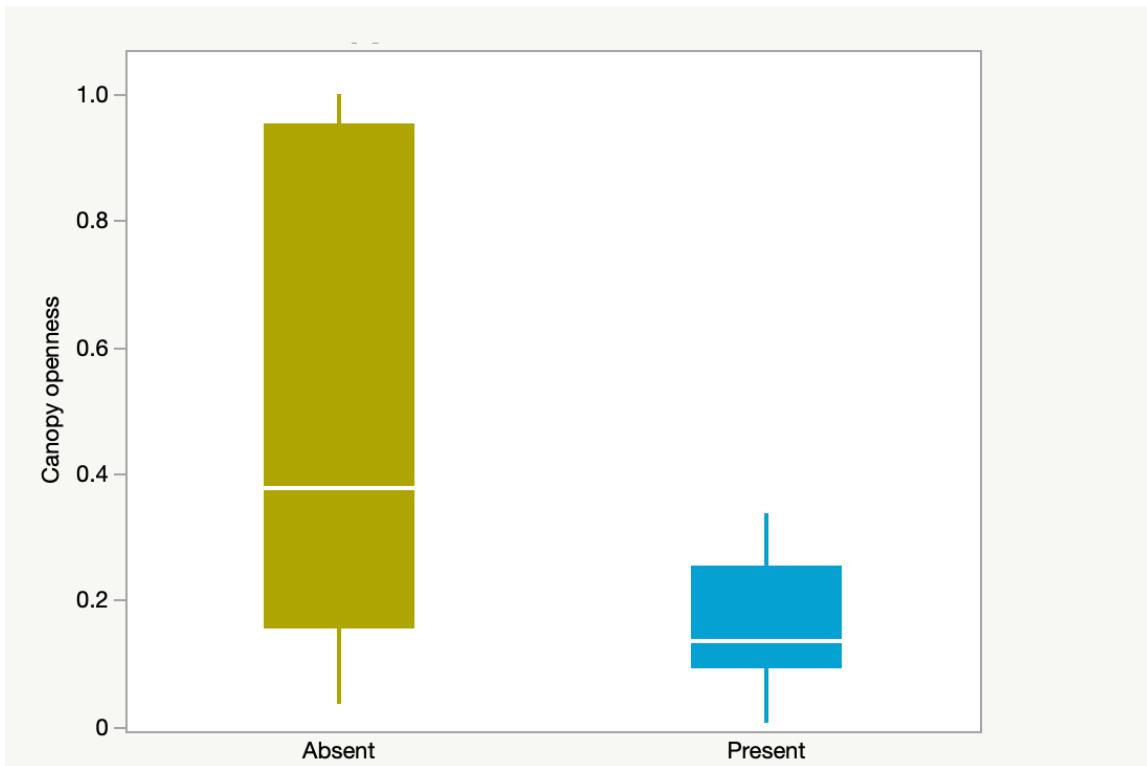
Observations that plots containing *Sphagnum divinum* tended to be in woodland or forest are consistent with descriptions in Hassel et al. (2018). The single open wetland plot with *S. divinum*, TMIR07, was moderately wooded by red maple (*Acer rubrum*) and had low overall openness compared to other open wetlands (0.336 for TMIR07 vs. 0.962 mean for all other open wetlands). Similarly, while *S. medium* occurred in woodland and forest, in contrast to descriptions from Hassel et al. (2018), the woodland plot (BEND04) had high canopy openness (= 0.94) and appeared dominated primarily by highbush blueberry



**Fig. 3.2.** Boxplots of DFE (distance to forest edge) in meters for *Sphagnum divinum* absent and *Sphagnum divinum* present plots. Upper and lower bounds of boxes represent the 75<sup>th</sup> and 25<sup>th</sup> percentiles, respectively; white lines through the center of each boxes represent medians. Whiskers extend to the maximum non-outlier values; outliers are represented by points. A one-sided, two-sample Mann-Whitney U-test was conducted and no significant difference in DFE was detected between presence and absence plots ( $W = 75.5$ ,  $p = 0.249$ ).

(*Vaccinium corymbosum*) and three-way sedge (*Dulichium arundinaceum*) rather than *Acer rubrum*, indicating that it may more closely approximate an open wetland rather than woodland.

Discrepancies between VPCT classes and observed vascular vegetation at plots may be reconciled as simple errors of precision; although plot points may be hypothetically located in a particular VPCT geospatial polygon, the correspondence of that polygon to the



**Fig. 3.3.** Boxplots of canopy openness for *Sphagnum divinum* absent and *Sphagnum divinum* present plots. Upper and lower bounds of boxes represent the 75<sup>th</sup> and 25<sup>th</sup> percentiles, respectively; white lines through the center of each boxes represent medians. Upper and lower whiskers extend to the maximum and minimum values, respectively. A one-sided, two-sample Mann-Whitney U-test was conducted and a significant difference was detected in canopy openness between presence and absence plots ( $W = 37$ ,  $p = 0.006$ ).

actual borders of certain habitats may be unreliable at proximity to boundaries. Additionally, as a discrete categorical variable, VPCT cannot account for ecotones at cross-class boundaries; discrepant plots such as BEND04 and TMIR07 may occupy these ecotones, and thus take on characteristics of multiple classes (Table A1 in Appendix IV).

The absence of a significant relationship between DFE and presence of *S. divinum* offers no supporting evidence for the previously described niche of *S. divinum*. However, the analysis was heavily swayed by the lack of *S. medium* and the resultant need to use presence-absence instead of *S. divinum* – *S. medium* for comparison. The absence group

included numerous non-SPDI communities such as Group 5 (see Chapter 2) that occupied forest and near-forest plots. While such plots may still be unsuitable habitat for *S. divinum*, this does not necessarily reduce their preference for forest and forest edge habitat. In other words, the occurrence of numerous forest plots without *S. divinum* is poor evidence against forest preference of *S. divinum*. Future work that includes sampling of more open, ombrotrophic sites might detect more *S. medium* and thus offer a more valuable, direct comparison.

Interestingly, despite the shortcomings of the presence-absence comparison, there was a strongly significant relationship between canopy openness and presence of *S. divinum*. This magnitude of this effect was pronounced, as the median openness of absent plots (= 0.375) exceeded even the maximum openness among present plots (= 0.336). This offers strong indication in support of descriptions of *S. divinum* as a predominantly shade-dwelling species.

## CONCLUSIONS

While habitat suitability based on distance to forest edge was inconclusive for *Sphagnum divinum*, canopy openness results clearly show that *S. divinum* occupies shaded areas preferentially within its temperate range, consistent with descriptions from boreal regions. Lack of *S. medium* at the sampled sites, which were mostly oligotrophic, hampered direct comparison of *S. medium* habitat preference to *S. divinum*. Future work in this region could include ombrotrophic wetlands to obtain a greater sample of *S. medium* and provide more conclusive evidence for niche differentiation between the two species.

## REFERENCES

- Cai S, Yu Z (2011) Response of a warm temperate peatland to Holocene climate change in northeastern Pennsylvania. *Quaternary Res* 75:531–540. <https://doi.org/10.1016/j.yqres.2011.01.003>
- Clymo RS, Hayward PM (1982) The ecology of *Sphagnum*. In: Smith AJE (ed) Bryophyte Ecology. Springer Netherlands, Dordrecht, pp 229–289
- ESRI (2020) ArcGIS Desktop. Version 10.8.1. Environmental Systems Research Institute, Redlands, CA
- Gignac LD, Vitt DH (1994) Responses of northern peatlands to climate change: effects on bryophytes. *J Hattori Bot Lab* 75:119–132. [https://doi.org/10.18968/jhbl.75.0\\_119](https://doi.org/10.18968/jhbl.75.0_119)
- Halsey LA, Vitt DH, Gignac LD (2000) *Sphagnum*-dominated peatlands in North America since the Last Glacial Maximum: Their occurrence and extent. *The Bryologist* 103:334–352. [https://doi.org/10.1639/0007-2745\(2000\)103\[0334:SDPINA\]2.0.CO;2](https://doi.org/10.1639/0007-2745(2000)103[0334:SDPINA]2.0.CO;2)
- Hassel K, Kyrkjeeide MO, Yousefi N, et al (2018) *Sphagnum divinum* (*sp. nov.*) and *S. medium* Limpr. and their relationship to *S. magellanicum* Brid. *J Bryol* 40:197–222. <https://doi.org/10.1080/03736687.2018.1474424>
- Kyrkjeeide MO, Hassel K, Flatberg KI, et al (2016) Spatial genetic structure of the abundant and widespread peatmoss *Sphagnum magellanicum* Brid. *PLoS ONE* 11:e0148447. <https://doi.org/10.1371/journal.pone.0148447>
- Manuel MG (1975) Contribution to the bryoflora of Pennsylvania. *The Bryologist* 78:458–462. <https://doi.org/10.2307/3242170>
- R Core Team (2020) R: A language and environment for statistical computing. Version 4.0.3. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org>
- Rydin H, Gunnarsson U, Sundberg S (2006) The role of *Sphagnum* in peatland development and persistence. In: Wieder RK, Vitt DH (eds) Boreal Peatland Ecosystems. Springer Berlin Heidelberg, pp 47–65

Schuette S, Krayesky DM (2014) A list of bryophytes for Wayne County, Pennsylvania. *Evansia* 31:25–30. <https://doi.org/10.1639/079.031.0104>

Vitt DH (2014) A key and review of bryophytes common in North American peatlands. *Evansia* 31:121–158. <https://doi.org/10.1639/079.031.0402>

Vitt DH, Chee W-L (1990) The relationships of vegetation to surface water chemistry and peat chemistry in fens of Alberta, Canada. *Vegetatio* 89:87–106. <https://doi.org/10.1007/BF00032163>

Vitt DH, House M, Kitchen S, Wieder RK (2020) A protocol for monitoring plant responses to changing nitrogen deposition regimes in Alberta bogs. *Environ Monit Assess* 192:743. <https://doi.org/10.1007/s10661-020-08645-z>

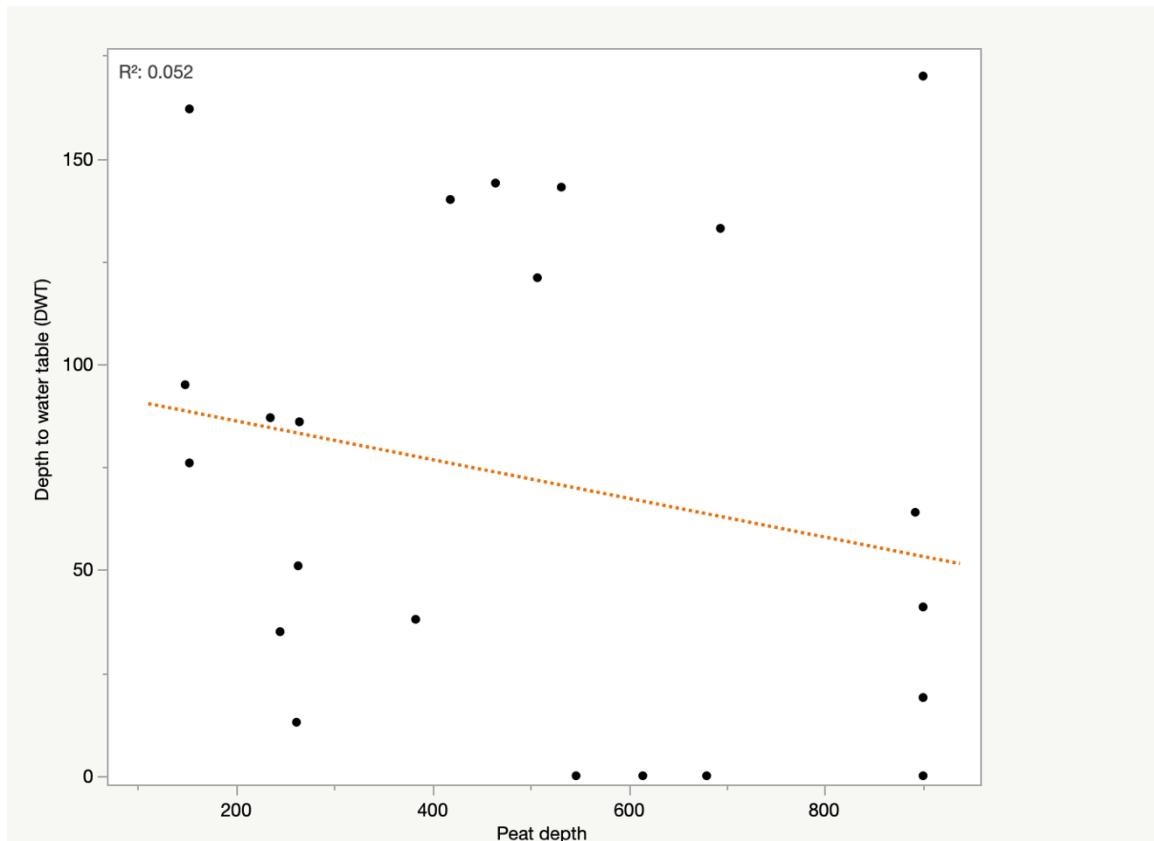
Wieder RK, Yavitt JB (1994) Peatlands and global climate change: Insights from comparative studies of sites situated along a latitudinal gradient. *Wetlands* 14:229–238

Yousefi N, Hassel K, Flatberg KI, et al (2017) Divergent evolution and niche differentiation within the common peatmoss *Sphagnum magellanicum*. *Am J Bot* 104:1060–1072. <https://doi.org/10.3732/ajb.1700163>

Zimmerman E, Davis T, Podniesinski G, et al (2012) Terrestrial and Palustrine Plant Communities of Pennsylvania, 2nd Edition. Pennsylvania Natural Heritage Program, Pennsylvania Department of Natural Resources, Harrisburg, PA

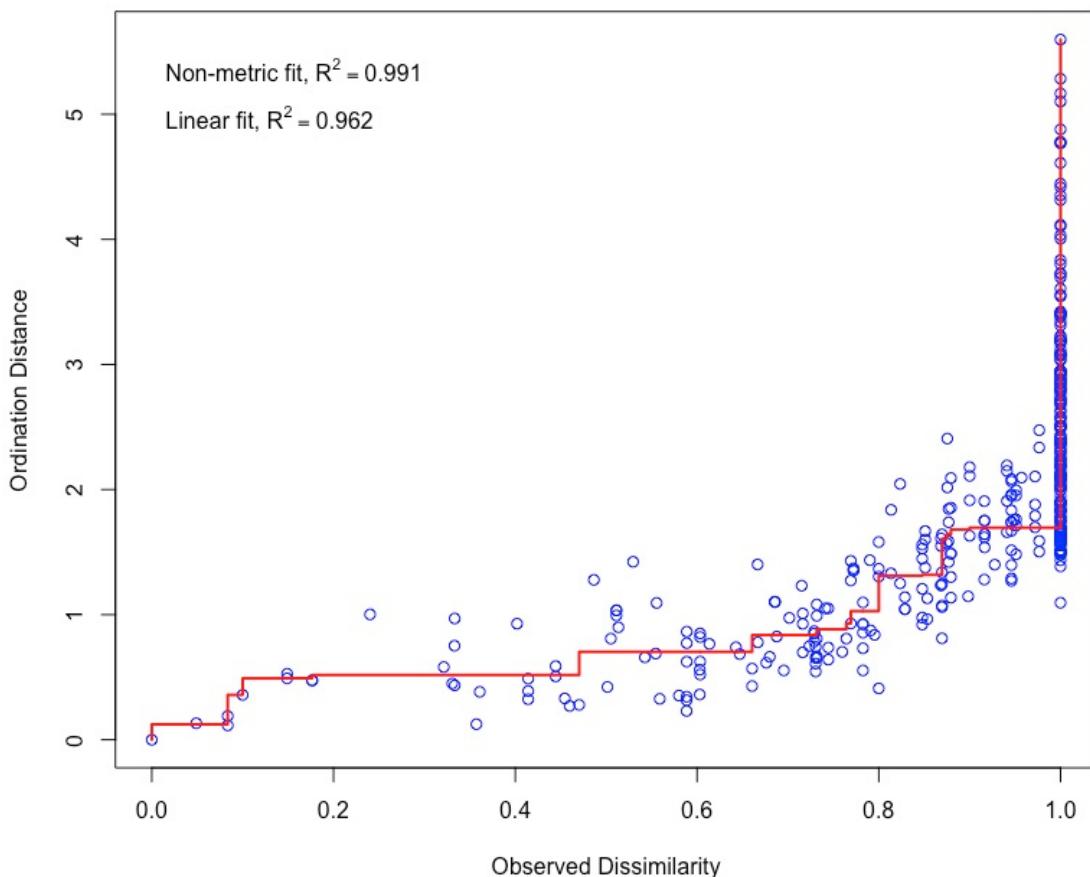
## APPENDICES

### Appendix I: Depth to water table (DWT) – peat depth covariance



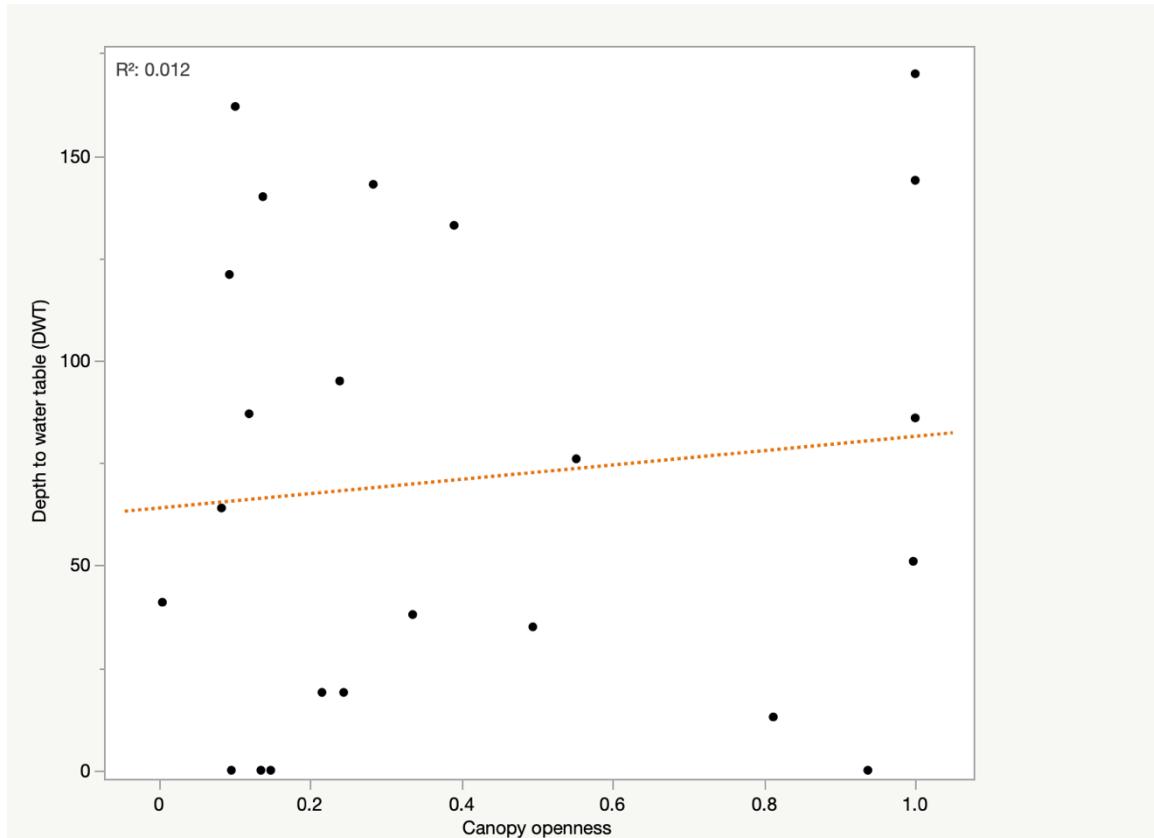
**Fig. A1.** Scatterplot of mean peat depth against depth to water table (DWT). Dashed orange line represents hypothetical linear fit. Low correlation coefficient ( $R^2 = 0.052$ ) suggests poor, if any, relationship between the two variables.

*Appendix II: NMDS ordination Shepard plot*



**Fig. A2.** Shepard plot of monotonic fit of pairwise comparisons between plots in community matrix space.

*Appendix III: Depth to water table (DWT) – canopy openness covariance*



**Fig. A3.** Scatterplot of canopy openness against depth to water table (DWT). Dashed orange line represents hypothetical linear fit. Low correlation coefficient ( $R^2 = 0.012$ ) suggests poor, if any, relationship between the two variables.

*Appendix IV: Ecological and physical characteristics of plots*

Plot	Dominant species	Group	Habitat	Mean canopy openness	Mean peat depth (mm)	DWT (mm)
BEND01	SPME	7	Forest	0.1354	680	0
BEND02	CACO	6	Woodland	0.1484	547	0
BEND03	SPFA	2	Wetland	0.8125	262	13
BEND04	SPME	7	Woodland	0.9375	615	0
BEND05	SPDI	3	Woodland	0.1198	235	87
BEND07	SPRU	8	Wetland	1.0000	>900	170
BEND13	DIPO	5	Woodland	0.1615	122	n.d.
BEND14	SPFA	1	Wetland	1.0000	465	144
BEND15	SPFA	1	Woodland	0.2161	>900	19
BEND16	SPDI	4	Forest	0.0938	507	121
FRBP01	SPFA	4	Woodland	0.0052	>900	41
FRBP02	PLSC	2	Woodland	0.1016	153	162
FRBP04	SPDI	4	Forest	0.2448	>900	19
FRBP05	HYIM	5	Forest	0.2734	101	n.d.
FRBP06	SPRU	8	Woodland	0.3906	694	133
FRBP07	HYIM	5	Forest	0.2396	149	95
FRBP08	SPFA	4	Woodland	0.0833	892	64
TMIR02	SPCU	8	Wetland	0.9974	264	51
TMIR03	PLSC	2	Wetland	1.0000	265	86
TMIR04	SPFA	2	Forest	0.1380	419	140
TMIR05	SPFA	3	Forest	0.2839	532	143
TMIR06	SPDI	6	Forest	0.2109	750	n.d.
TMIR07	SPFA	1	Wetland	0.3359	383	38
TMIR08	HYIM	5	Forest	0.0365	438	n.d.
TMIR09	SPGI	7	Woodland	0.4948	245	35
TMIR10	SPFA	1	Woodland	0.3594	247	n.d.
TMIR11	HYIM	5	Forest	0.5521	153	76
TMIR12	SPDI	6	Woodland	0.0964	>900	0

**Table A1.** Ecological and physical characteristics of plots. DWT indicates depth to water table; “n.d.” denotes no data, for plots for which no water was reached.

*Appendix V: Chemical characteristics of plots*

Plot	pH	RC	NO <sub>3</sub> <sup>-</sup>	NH <sub>4</sub> <sup>+</sup>	SO <sub>4</sub> <sup>2-</sup>	Na <sup>+</sup>	Mg <sup>2+</sup>	K <sup>+</sup>	Ca <sup>2+</sup>
BEND01	5.63	20.41	0.024	0.447	0.197	2.1804	0.3466	0.9179	1.3705
BEND02	4.41	17.64	0.023	0.257	0.080	2.2092	0.2557	0.4676	1.4470
BEND03	4.34	14.18	0.140	0.016	0.072	2.2665	0.2441	0.4004	1.1096
BEND04	5.21	17.78	0.029	0.060	0.482	1.9554	0.3976	0.4360	1.4618
BEND05	4.40	12.97	0.022	0.000	0.835	2.4075	0.1008	0.1888	0.2552
BEND07	4.11	15.72	0.030	0.051	0.046	2.2762	0.1602	0.4953	0.7897
BEND13									
BEND14	4.34	14.76	0.019	0.392	0.186	2.2568	0.1584	0.4075	0.3839
BEND15	4.32	14.43	0.054	0.136	0.154	2.4367	0.1685	0.6949	0.4415
BEND16	4.40	14.19	0.045	0.313	0.153	2.2862	0.1612	0.4420	0.3670
FRBP01	3.98	34.38	0.088	0.405	0.073	2.3739	0.3630	1.7837	1.6369
FRBP02									
FRBP04	4.00	228.14	0.031	0.131	0.033	33.1196	0.3596	1.1409	2.8048
FRBP05									
FRBP06	5.81	364.16	0.011	0.000	0.062	54.9461	0.3320	0.8969	4.6246
FRBP07									
FRBP08	6.23	378.29	0.018	0.000	0.033	55.5995	0.3573	1.0196	4.8550
TMIR02	4.36	43.63	0.020	0.000	0.170	2.3189	0.1357	5.0982	0.1839
TMIR03	4.08	13.51	0.043	0.000	0.210	2.5691	0.1374	0.5029	0.1791
TMIR04									
TMIR05	4.47	11.73	0.066	0.043	0.475	2.2080	0.1380	0.2657	0.2659
TMIR06	4.55		0.160	0.487	0.853	2.5874	0.3744	1.2686	1.0801
TMIR07	4.39	22.53	0.084	0.004	0.431	2.3509	0.3668	0.8773	0.7405
TMIR08									
TMIR09	5.35	17.93	0.023	0.019	0.282	2.2402	0.4389	0.3674	1.4943
TMIR10	4.10	12.06	0.030	0.000	0.599	3.0203	0.1518	0.5556	0.2092
TMIR11									
TMIR12	6.10	28.92	0.07	0.142	0.099	2.4878	1.0466	0.5335	3.1889

**Table A2.** Chemical characteristics of peat porewater by plot. RC denotes reduced conductivity and is measured in  $\mu\text{S}/\text{cm}$ ; all other measurements, except pH, are in  $\text{mg L}^{-1}$ . Blank rows correspond to plots from which no water sample was collected.

*Appendix VI: Species composition*

Plot	AUPA	BATR	CACO	CACU	CAIN	DIMO	DIPO	DISC	HYIM	LEGL	ODSP	PLRE
BEND01	0	4	0	0	0	0	0	0	0	0	0	0
BEND02	0	0	12	0	0	0	0	0	0	0	0	0
BEND03	0	0	0	0	0	0	0	0	0	0	0	0
BEND04	0	0	0	0	0	0	0	0	0	0	0	0
BEND05	0	0	0	0	0	0	0	0	0	0	0	0
BEND07	0	0	0	0	0	0	0	0	0	0	1	0
BEND13	0	0	0	0	0	0	10	0	3	0	0	0
BEND14	0	0	0	0	0	0	0	0	0	0	0	0
BEND15	0	0	0	0	0	0	0	0	0	0	0	0
BEND16	0	0	0	0	0	0	0	0	1	0	0	0
FRBP01	0	0	0	0	3	0	0	0	0	0	0	0
FRBP02	0	0	0	0	0	0	0	0	0	0	0	0
FRBP04	0	0	0	0	1	0	0	0	1	0	0	0
FRBP05	0	0	0	0	0	0	0	1	14	0	0	0
FRBP06	0	0	0	1	0	0	0	0	0	0	0	0
FRBP07	0	0	0	0	0	0	0	0	13	0	0	0
FRBP08	0	0	0	0	0	0	0	0	0	0	0	0
TMIR02	0	0	0	0	0	0	0	0	0	0	0	0
TMIR03	9	0	0	0	0	0	0	0	0	0	0	0
TMIR04	0	0	0	0	0	0	0	0	0	0	0	0
TMIR05	0	0	0	0	0	0	0	0	0	0	0	1
TMIR06	0	0	0	0	0	0	0	0	0	0	0	0
TMIR07	0	0	0	0	0	0	0	0	0	0	0	0
TMIR08	0	2	0	0	0	2	0	0	16	0	0	0
TMIR09	0	0	0	0	0	0	0	0	0	0	0	0
TMIR10	0	0	0	0	0	0	0	0	0	0	0	0
TMIR11	0	0	0	0	0	0	0	4	11	1	0	0
TMIR12	0	0	0	0	0	0	0	0	0	0	0	0

**Table A3.** Species frequencies for each plot. Species codes: AUPA = *Aulacomnium palustre*; BATR = *Bazzania trilobata*; CACO = *Calliergon cordifolium*; CACU = *Calliergonella cuspidata*; CAIN = *Calypogeia integristipula*; DIMO = *Dicranum montanum*; DIPO = *D. polysetum*; DISC = *D. scoparium*; HYIM = *Hypnum imponens*; LEGL = *Leucobryum glaucum*; ODSP = *Odontoschisma sphagni*; PLRE = *Platygyrium repens*.

*Appendix VI (cont.)*

Plot	PLSC	POCO	POST	PSCI	RHAP	SPAN	SPCU	SPDI	SPFA	SPFL	SPGI	SPME	SPRU	TOTO
BEND01	0	0	0	0	3	0	0	0	0	0	12	17	0	0
BEND02	0	0	0	0	0	0	0	7	0	0	1	0	0	0
BEND03	0	20	0	0	0	0	0	0	23	0	0	0	0	0
BEND04	0	6	0	0	0	0	0	0	0	16	0	18	0	0
BEND05	0	4	0	0	0	0	0	12	0	0	0	0	0	1
BEND07	0	0	1	0	0	0	0	0	0	0	0	0	18	0
BEND13	0	3	0	0	0	0	0	0	0	0	0	0	0	0
BEND14	0	1	0	0	0	0	0	0	34	0	0	0	0	0
BEND15	0	0	0	0	0	0	0	0	35	0	0	0	0	0
BEND16	0	0	0	0	0	0	0	11	9	0	0	0	0	0
FRBP01	0	0	0	0	0	0	0	8	9	0	0	0	4	0
FRBP02	12	6	0	0	0	0	0	0	11	0	0	0	0	0
FRBP04	1	0	0	0	0	0	0	12	10	0	0	0	0	0
FRBP05	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FRBP06	0	0	0	0	0	0	0	0	0	0	0	0	19	0
FRBP07	5	3	0	0	0	0	0	0	1	0	0	0	0	0
FRBP08	2	0	0	0	0	0	0	4	10	0	0	0	0	0
TMIR02	0	0	1	0	0	0	31	0	2	0	0	0	0	0
TMIR03	22	0	0	0	0	0	0	0	0	0	0	0	0	0
TMIR04	4	3	0	2	0	0	0	0	16	0	0	0	0	0
TMIR05	0	1	0	0	0	0	0	11	15	0	0	0	0	1
TMIR06	0	0	0	0	0	0	0	32	0	0	0	0	0	0
TMIR07	0	0	0	0	0	0	0	3	32	0	0	0	0	0
TMIR08	0	0	0	0	0	0	0	0	0	0	0	0	0	0
TMIR09	0	5	0	0	0	0	0	0	0	0	24	0	0	0
TMIR10	0	3	0	0	0	0	0	0	30	0	0	0	0	0
TMIR11	0	6	0	1	0	5	0	0	0	0	0	0	0	0
TMIR12	0	0	0	0	0	0	0	36	0	0	0	0	0	0

**Table A3 (cont.).** Species codes continued: PLSC = *Pleurozium schreberi*; POCO = *Polytrichum commune*; POST = *P. strictum*; PSCI = *Pseudobryum cinclidioides*; RHAP = *Rhizomnium appalachianum*; SPAN = *Sphagnum angustifolium*; SPCU = *S. cuspidataum*; SPDI = *S. divinum*; SPFA = *S. fallax*; SPFL = *S. flexuosum*; SPGI = *S. girgensohnii*; SPME = *S. medium*; SPRU = *S. russowii*; TOTO = *Tortella tortuosa*

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