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Floristic and Environmental Characteristics of Sub-boreal Peatlands of Minnesota and Western Wisconsin

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Floristic and Environmental Characteristics of Sub-boreal Peatlands in Minnesota and Western Wisconsin

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ABSTRACT

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Advisor: Bradley J. Cook, Ph.D.

Peatland communities in the sub-boreal region of Minnesota and western Wisconsin were characterized by floristic composition, structure and environmental characteristics to determine the natural variation among peatland communities in the region and their shared associations with the boreal and temperate peatlands of North America. Floristic classification revealed five, distinct peatland community types, identified as *Sphagnum* Bogs, Herbaceous Fens, Forested Fens, Rich/Calcareous Fens and *Phalaris anrundinacea* – Dominated Peatlands. Differences among sub-boreal peatlands largely reflected changes in the significant indicator and dominant plant species identified, which were found to exhibit high fidelities to a particular peatland community type. Floristic variations among sub-boreal peatlands were observed to correlate with changes in pore-water chemistry along a strong pH-alkalinity gradient. Ordinal analysis by non-metric multidimensional scaling also indicated a strong community association with soil and pore-water chemistry, which reflected the geomorphic and hydrologic settings in which communities developed and the transitional nature of peatlands in the region. In addition, the broad physiological tolerance and invasive nature of *P. anrundinacea* was found to pose a substantial threat to the biodiversity and ecological functioning of sub-boreal peatland communities.

ACKNOWLEDGEMENTS

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CHAPTER 1

INTRODUCTION

Peatlands, commonly known as bogs and fens, are wetland communities characterized by an organic soil layer with the water table at or near the soil surface throughout the year (Moore and Bellamy 1974, Mitsch and Gosselink 2000). Peatlands primarily develop in areas associated with positive water balances (i.e., precipitation exceeds evapotranspiration), and where soil saturation and anaerobic conditions restrict microbial decomposition to rates far less than primary production (Vitt 1994). These conditions result in the accumulation of organic matter (colloquially known as "peat") to depths >40cm (Soil Survey Staff 1998, National Wetlands Working Group 1988), with depths >2m commonly observed (Gorham 1991). In most other wetland communities, the frequency and magnitude of hydrologic fluctuations, which strongly influence the depth and duration of aerobic conditions, create environments for greater microbial decomposition (Collins and Kuehl 2001), and limit accumulations to small quantities of highly decomposed organic matter (Zoltai and Vitt 1995). Low soil temperatures also decrease the rate of microbial decomposition (Boelter and Verry 1977, Collins and Kuehl 2001, Jenny 1950), which is reflected in the global distribution of peatland communities.

Peatlands are estimated to occupy between 2.97×10^6 km^2 (Matthews and Fung 1987) and 4.22×10^6 km^2 (Kivinen and Pakarinen 1981), making up roughly 3% of Earth's land surface (Gorham 1991), and representing over half of all wetlands worldwide (Bridgham et al. 2001). The distribution of peatland communities, however, is disproportionately concentrated in the northern latitudes, between 50 and 70°

(Aselmann and Crutzen 1989), where 95% of all wetland communities are classified as peatlands (Gorham 1991). In North America, peatland communities primarily occur in the boreal and sub-boreal regions (Figure 1), where cooler temperatures (Boelter and Verry 1977) and positive water balances facilitate extensive accumulations of organic matter (Vitt 1994 an Zoltai and Vitt 1995).

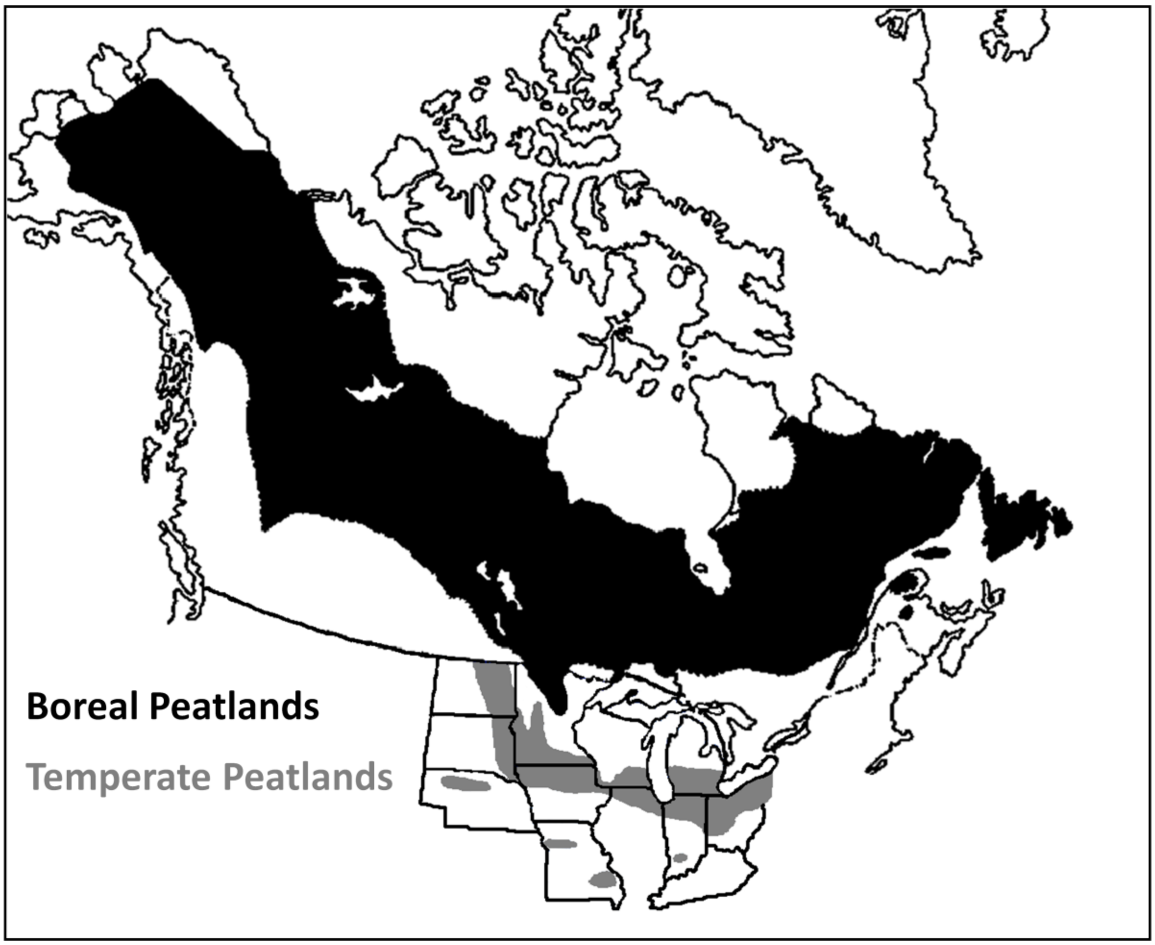

Figure 1 The distribution of peatland communities in North America is primarily concentrated across the boreal region, where climactic conditions facilitate organic matter accumulation. The occurrence of temperate peatlands is limited to areas of localized and sustained groundwater discharge. Figure was adapted from Glaser (1987) for the distribution of boreal peatlands and Amon et al. (2002) for the distribution of temperate peatlands in the United States.

In the continental interior of North America, peatland development initiated following the retreat of the Cordilleran ice sheet, between 4,700 and 8,000 years ago (Almendinger and Leete 1998a, Gorham et al. 2007). During this period, cool temperatures and slow moving glacial melt waters, which stagnated where substrate composition and landscape topography limited water movement, provided the climactic conditions, physical templates and stable hydrology necessary for organic matter accumulation (Boelter and Verry 1977). Peatlands, however, also occur in the temperate regions of North America (Carpenter 1995, Thompson 1993, Eggers and Reed 1997, MNDNR 2005b). In these regions, peatland communities are small, usually only a few hectares in size (Bedford and Godwin 2003), and occur in isolation where continuous hydrologic inputs, discharged as groundwater, maintain conditions necessary for organic matter accumulation (Almendinger and Leete 1998a, Amon et al. 2002). Distinctions between all peatland communities are based primarily on complex interactions between 1) landscape position, 2) organic matter accumulation and 3) the source and chemical composition of hydrologic inputs, which are reflected in the various methods by which peatlands are classified.

Historically, peatland classifications have grouped communities based on similarities in topography (Damman 1986, Glaser and Janssens 1986, Moore and Bellamy 1974), hydrology (von Post and Granlund 1926 [as cited in Bridgham et al. 1996], Moore and Bellamy 1974), water chemistry (Sjörs 1948 and Du Rietz 1949 [as cited in Bridgham et al. 1996]), nutrient availability (Du Rietz 1954 [as cited in Bridgham et al. 1996], Sjörs 1961, Moore and Bellamy 1974), floristic composition (Heinselman 1963, Gorham and Janssens 1992, Cowardin et al. 1979), and more recently, ecological function (Brinson 1993). These classifications reflect a progressive transition in peatland structure and floristic composition along multiple limiting gradients (Bridgham et al. 1996, Hájek et al. 2006, Økland et al. 2001), with distinctions among peatland communities derived from variations in the source and chemical composition of hydrologic inputs.

In terms of hydrologic classification, peatland communities are distinguished based on the dominant source of hydrologic inputs, which is directly related to landscape position and peatland topography (Moore and Bellamy 1974, National Wetlands Working Group 1988). In general, this variation is illustrated along a continuum, with bogs and fens representing endpoints (Figure 2). Hydrologically, fens are classified as minerogenous peatlands (Warner and Rubec 1997, Zoltai and Vitt 1995), in which soil saturation and anaerobic conditions are sustained by hydrologic sources other than precipitation (i.e., indirect hydrologic inputs), such as groundwater discharge and surface waters. Bogs, in contrast, are classified as ombrogenous peatlands, with hydrologic inputs exclusively derived from precipitation (i.e., direct hydrologic inputs).

In general, bogs develop from fens when the vertical accumulation of peat rises above the surrounding mineral soil (Ingram 1982), or when the downward hydraulic pressure from precipitation is greater than that of discharging groundwater (Siegel 1983, Siegel and Glaser 1987). Ultimately, both scenarios lead to the hydrologic isolation of bogs (Figure 2), and result in a dependence on precipitation to maintain soil saturation and anaerobic conditions. The point at which a fen transitions to a bog community, due to declining inputs of mineral-rich waters, is defined as the "mineral-soil-water-limit" (Du Rietz 1949 [as cited in Bridgham et al. 1996]). This transition has been shown to occur with as little as 10% hydrologic inputs from mineral-rich ground waters (Siegel 1983). However, few studies quantify hydrologic inputs sufficiently to classify peatland communities based on hydrologic source (Bridgham et al. 1996), much less accurately define regional variations. As a result, changes in pore-water chemistry are commonly used as surrogates to describe and classify peatland communities based on the relative influence and chemical composition of hydrologic inputs.

Similar to hydrologic classifications, water chemistry-based classifications primarily characterize the source of mineral nutrients (Sjörs 1948, Moore and Bellamy 1974, Warner and Rubec 1997). Fens, therefore, are defined as minerotrophic peatlands (i.e., mineral nourished), with nutrient inputs supplied from the mineral soils from which hydrologic inputs originate. In contrast, bogs are classified as ombrotrophic peatlands (i.e., rain nourished), with inputs of nutrients and major cations (e.g., Ca^{2+}, Mg^{2+}, Na^{+}, K^{+}) supplied only by precipitation. This intimate connection between the hydrologic and nutrient sources of peatland communities results in soil and pore-water chemistries of bogs and fens that largely reflect the chemical composition of their hydrologic inputs.

As peatland communities become increasingly isolated from mineral-rich water sources, due to the vertical accumulation of organic matter and changes in peatland topography, a sharp decline is observed in the supply of major cations (Figure 2) (Glaser 1987). This reduction in the supply of cations, combined with an increase in the organic content of peat, results in a significant decrease in the acidity of peatland soil and pore-water (Gorham 1957). Calcium concentrations are particularly important to the pore-water chemistry of peatland communities in that calcium contributes both to pore-water alkalinity and is directly related to pH through the buffering capacity of bicarbonates (Kemmers 1986, Glaser 1987). Inputs of calcium are often the result of discharging groundwater from calcium-rich substrates, such as limestone and dolomite (Almendinger and Leete 1998a, Grootjans et al. 2006). Additionally, locally important wind-blown inputs from calcium-rich glacial-till can contribute to the soil and pore-water chemistry of peatland communities (Gorham et al. 1984, Glaser 1987). In boreal region of northern Minnesota, calcium concentrations in fens can range from 3 to 45mg/l (Glaser et al. 1990). Whereas in the temperate region, calcium concentrations commonly exceed 100mg/l (Almendinger and Leete 1998b), and concentrations as high as 290mg/l have been observed in highly calcareous fens in the Midwest United States (Amon et al. 2002). In contrast, bogs are characterized by acidic pore-water chemistries, with pH levels generally <4.2, calcium concentrations <2mg/l and considerably lower total ionic concentrations (Glaser et al. 1990). The pore-water pH of fens, however, can range from mildly acidic to alkaline (4.5 to >8), dependent on the chemical composition of hydrologic inputs (Bedford and Godwin 2003). In boreal and sub-boreal peatlands, changes in pore-water pH and ionic concentrations are consistently observed to correlate with changes in the floristic composition of peatland communities (Sjörs 1950, Glaser 1987, Vitt and Chee 1990, Gorham and Janssens 1992, Wheeler and Proctor 2000). These consistent correlations have generated water chemistry-based classifications that define peatland communities along an acidity-alkalinity gradient (Moore and Bellamy 1974, Gorham and Janssens 1992, National Wetlands Working Group 1988).

The wide variations in soil and pore-water chemistries among peatland communities, particularly fens, are frequently described along a poor – rich gradient (Figure 2) (Zoltai and Vitt 1995, Vitt 2000). Poor fens are characterized by mildly acidic pore-water chemistries (pH = 4.5 – 5.5) and low ionic concentrations, whereas rich fens are characterized by slightly acidic to alkaline soil and pore-water chemistries (pH >6.0) and considerably higher ionic concentrations (Figure 2). The poor – rich gradient, however, does not necessarily reflect the nutrient status of peatland communities.

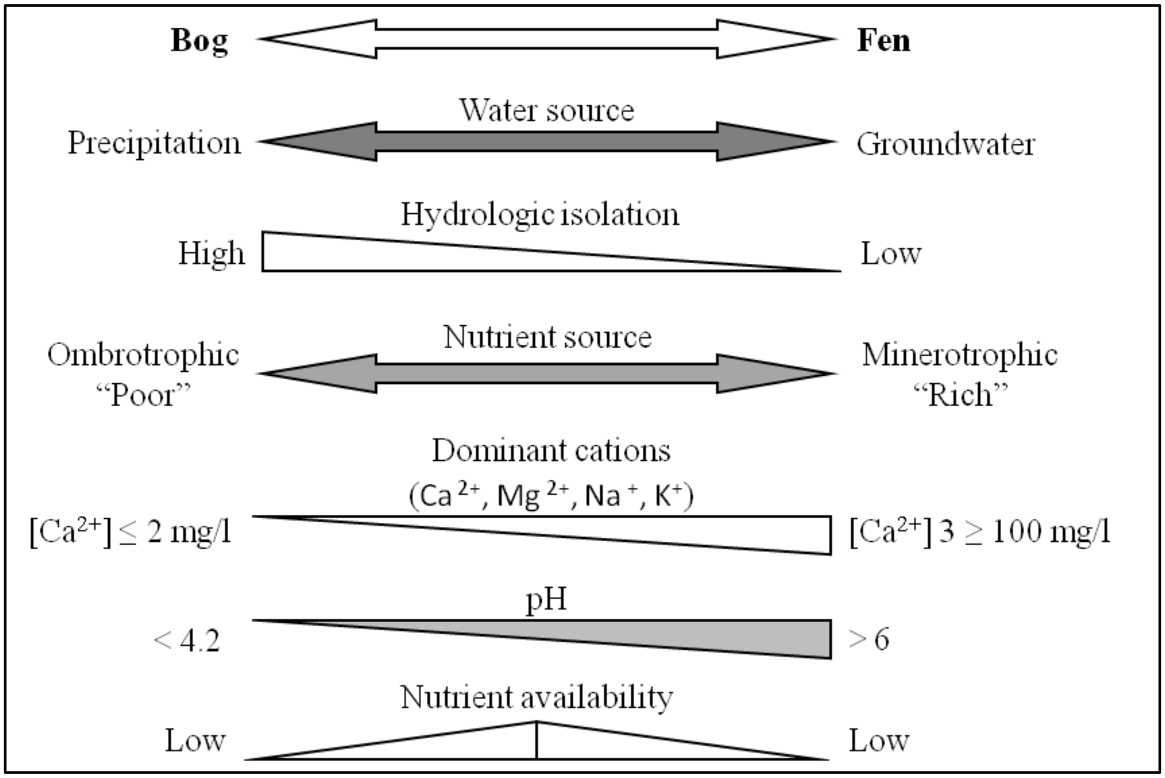

Figure 2 Variations in the floristic structure and ecological functions of peatland communities are commonly describe along multiple limiting gradients (Bridgham et al. 1996), which are primarily determined by the sources and chemical composition of hydrologic inputs.

Classification of the nutrient status of peatland communities is similar to that used for water bodies, with nutrient rich peatlands classified as eutrophic and nutrient poor peatlands are classified as oligotrophic (Weber 1908 [as cited in Bridgham et al. 1996], Warner and Rubec 1997). However, nutrient levels are not observed to increase directly with increasing pH and alkalinity (Figure 2). Nutrient levels tend to be the lowest in highly acidic and highly alkaline communities (Bridgham et al. 1996). The limiting nutrients most often associated with peatland communities are nitrogen and phosphorus (Bridgham et al. 1996). Nitrogen availability decreases as the organic content of peat increases, with bogs exhibiting the lowest levels of available nitrogen (Gorham 1957).

Phosphorus concentrations in bogs, although low, are sufficient to meet the physiological needs of the vegetation present (Chapin et al. 2004). In contrast, phosphorus deficiencies are common in extremely rich and calcareous peatlands, where significant accumulations of bicarbonate precipitate bind phosphorus in unusable forms (Boyer and Wheeler 1989, Almendinger and Leete 1998b). Although calcium deficiencies are common in terrestrial communities (Bolan et al. 2004), calcium is rarely a limiting nutrient in peatland communities (Clymo and Hayward 1982, Malmer 1986). In contrast, elevated calcium concentrations are toxic to many plant species (Clymo and Hayward 1982, Ingestad 1973 [as cited in Bridgham et al. 1996]), and can significantly limit the availability of other nutrients when present at elevated concentrations (Wheeler 1980, Boyer and Wheeler 1989). As such, nutrient availability peaks in the intermediate communities along the bog-fen continuum (Figure 2), with variations in floristic composition and structure among peatland communities significantly influenced by the availability of limiting nutrients and position along the pH-alkalinity gradient.

Floristic classifications define peatlands based on changes in floristic composition and structure, which primarily reflect changes in environmental conditions (i.e., water source, pH and nutrient availability) (Daniels 1978, Cowardin et al. 1979, Gorham and Janssens 1992, Vitt 1994). Similar to water-chemistry based classifications, floristic transitions among peatlands are generally defined along a pH-alkalinity gradient by an increased presence of fen-indicator plant species (Sjörs 1948, Gorham 1950, Du Rietz 1954 [as cited in Bridgham et al. 1996]). In general, fen-indicator species are associated with narrow distributions along environmental gradients (Sjörs 1948 and Gorham 1950), but rarely represent dominant species in peatland communities (Bridgham et al. 1996).

The presence of fen-indicator plant species is an indication of changes in the local environment conditions that allow colonization by species with greater nutrient and ionic requirements (Glaser et al. 1990), or can represent remnant species, which signify prior environmental conditions (Gorham and Janssens 1992). In contrast, dominant plant species in peatland communities distribute broadly along multiple environmental gradients (Glaser 1987), and often direct peatland development (Bridgham et al. 1996). This trend is most evident in the bimodal distribution of *Sphagnaecea* L. at low levels of pore-water pH and *Amblystegiacea* at higher pH levels (Gorham and Janssens 1992, Hájek et al. 2006), observed in the bryophyte-dominated (Zoltai and Vitt 1995) boreal peatlands of North America.

The application of floristic-based classifications, however, is generally limited to the areas for which the classifications were developed (Gore 1983), as fen-indicator and dominant species are largely "a matter of human convenience" (Bridgham et al. 1996). Nevertheless, plant species, which are commonly associated with peatlands, exhibit consistent adaptations in response to the specific environmental conditions in which they develop (Mitsch and Gosselink 2000). For example, plant adaptations, such as evergreenness, sclerophylly and nutrient translocation help limit nutrient loss in the acidic, nutrient poor environments characteristic of bogs. Specifically, multiple species of the *Ericaceae* (Heath) family have adapted the ability to acquire nitrogen from amino acids (Chapin et al. 1993) or ammonium (Bridgham et al. 1996) rather than nitrate. In addition, carnivorous plants, which are also commonly observed in bogs, trap and digest insects to offset nutrient deficiencies (Chapin and Pastor 1994). In contrast, peatland communities associated with high ionic concentrations generally are comprised of lowstature plant species and exhibit greater floristic diversity (Boyer and Wheeler 1989). Severe phosphorus limitations are suspected to influence this trend, which can hinder plant growth and prevent dominance by a few species. In addition, calcium-tolerant plant species (i.e., calciphiles) are characteristic of peatlands supplied with calcium-rich groundwater discharge (Almendinger and Leete 1998b, Eggers and Reed 1997).

In general, regionally specific differences in floristic composition and structure appear sufficient to define transitions between peatland communities along the multiple limiting gradients associated with the bog-fen continuum. However, many plant species that are common to peatland communities also occur in non-peat accumulating environments (Eggers and Reed 1997, Amon et al. 2002). In order to account for such similarities, various classification systems have adopted a hierarchical approach that defines communities based on increasingly similar characteristics (Warner and Rubec 1997, Zoltai and Vitt 1995, Cowardin et al. 1979).

In the United States, the most widely used hierarchical classification of wetland communities is the "Classification of Wetlands and Deepwater Habitats of the United States" (Cowardin et al. 1979); in which, peatlands are broadly defined by hydrology and floristic composition as non-tidal wetlands, dominated by trees, shrubs, herbaceous plants, mosses or lichens (i.e., Palustrine). Additional subclasses, dominance types and modifiers are used to distinguish peatlands from other wetland communities and define transitions among different peatland communities. In Canada, where peatlands represent a significantly greater portion of the landscape than that of the continental United States, a hierarchical approach is used that initially categorizes wetlands based on ontology (i.e., development), with peatlands broadly defined as either a bog or a fen. Further distinctions among bogs and fens are based on topography, water source, water chemistry and vegetation composition (Warner and Rubec 1997). A hierarchical classification of peatlands is advantageous in that it allows incorporation of multiple characteristics that can be used to distinguish a wide variety of community types across broad geographic extents. Development of a hierarchical classification, however, requires extensive knowledge of the geology, geomorphic settings, hydrologic settings and limiting gradients that influence the community structure and floristic composition of peatlands within the domain of the classification.

Most peatland classifications, as a result, are regionally oriented or focus on a specific peatland community type (i.e., bogs or fens) (Glaser and Janssens 1986, Amon et al. 2002). The advantage of regionally focused classifications is that they emphasize specific limiting gradients that influence variations in peatland structure and function. Alternatively, the usefulness of these classifications rarely extends beyond the region or peatland type for which it was intended, especially if the classification relies heavily on locally important floristic indicators. For example, peatlands in the temperate region of North America are distinguished from the expansive, boreal peatlands not only by their isolated distributions and reliance on groundwater inputs, but their chemical and physical composition as well as vegetation structure (Amon et al. 2002, Bridgham et al. 1996). Nevertheless, analyses of peatlands throughout the boreal and circum-boreal regions have revealed strong and consistent associations between peatland development (Moore and Bellamy 1974), topography (Moore and Bellamy 1974, Glaser and Janssens 1986 and National Wetlands Working Group 1988), vegetation structure (Cowardin et al. 1979) and environmental gradients (Sjörs 1948 and 1961, Du Rietz 1954 [as cited in Bridgham et al. 1996], Moore and Bellamy 1974).

In the continental interior of North America, peatlands characterize the extensive variation of climatic, geomorphic and hydrologic templates from which they develop. From the isolated temperate peatlands to the expansive peatland complexes of the boreal region, knowledge of this natural variation provides a foundation from which resource managers can effectively inventory, monitor and manage peatland ecosystems. The sub-boreal region of the continental interior is a transitional area, reflected in a north to south temperature gradient and an east to west precipitation gradient (Albert 1995). Peatland distribution also reflects these gradients, decreasing from north to south and from east to west (Wright 1972). Climatically, this region is defined as humid to sub-humid with precipitation increasing from west to east across the study area. Mean annual precipitation ranges from 29 to 33 inches, with roughly two-thirds occurring between the months of May and September (Wright 1972). The transitional nature of the region suggests sub-boreal peatlands will share characteristic features of both boreal and temperate peatlands. However, unlike boreal and temperate peatlands, less is known regarding the floristic and environmental characteristics associated with sub-boreal peatlands in the region. In addition, population densities and urban development are increasing at a higher pace in this region than surrounding areas (Hibbs 2000). As a result, peatlands in this region are subjected to increasing anthropogenic influences, which can, and often do result in alterations to the floristic composition, structure and environmental characteristics of peatland communities.

The objective of the current study was to classify and describe, in terms of floristic community and environmental characteristics, the natural variation of peatland communities in the sub-boreal region of Minnesota and western Wisconsin. Specifically, I set out to provide a floristically-based classification of peatlands in this region and a description of the limiting gradients that influence how these peatlands are structured. I hypothesized that sub-boreal peatlands would be structured along a strong pH-alkalinity gradient and would represent transitional communities, both in species composition and environmental characteristics, between the boreal and temperate peatland communities in the continental interior of North America.

CHAPTER 2

METHODS

Site Selection and Study Area

The primary objective of this study was to describe and characterize, in terms of floristic community and environmental characteristics, the natural variation of peatland communities in the sub-boreal region of Minnesota and western Wisconsin. Study sites were identified through a combination of aerial photography, published county soil surveys, peatlands listed in the *Field Guide to the Native Plant Communities of Minnesota* (MNDNR 2003b, MNDNR 2005a and MNDNR 2005b) and in consultation with wetland experts from multiple state and federal agencies. Study sites were selected to represent the natural variation of peatland communities in the study area with preference placed on sites occurring on public land for ease of access. Study sites were subjectively excluded from analysis if direct, geomorphic or hydrologic alterations were observed (e.g., soil removal, ditched, drained or flooded). In total, 56 study sites were located across 13 counties in Minnesota and 2 counties in Wisconsin (Figure 3).

Data Collection

Community Composition and Floristic Diversity

Characteristics of the floristic community, including plant species composition, abundance and an estimation of net primary productivity, were collected from 56 sites

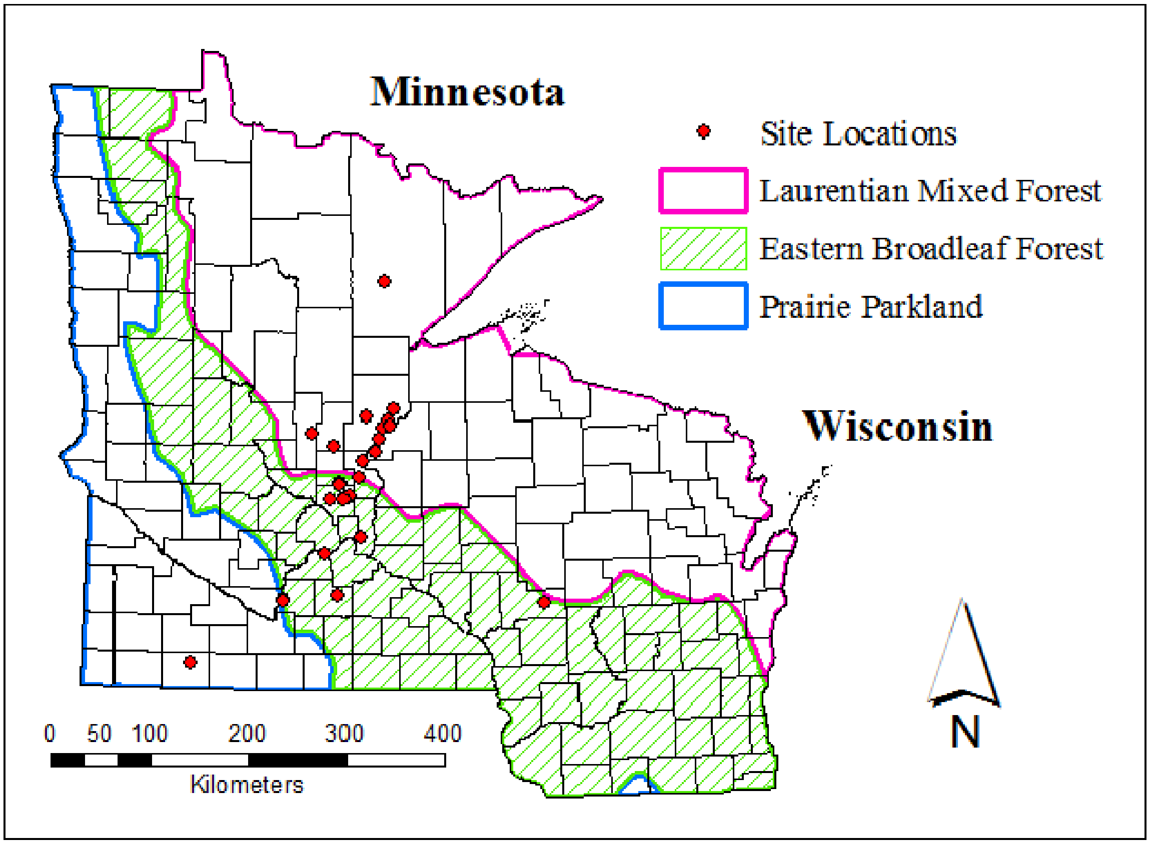

Figure 3 Fifty-six study sites were distributed across three ecological providences and located in 13 counties in Minnesota and 2 counties in Wisconsin. Study sites were selected to represent the known variation of natural peatland communities in the sub-boreal region of Minnesota and western Wisconsin.

during the 2008 – 2009 field seasons (May – October). All species, except bryophytes, were identified to the species level when possible. Bryophyte identification was limited to family associations, based on the bimodal distribution of *Sphagnaceae* and *Amblystegiaceae* in boreal peatland communities. Species composition and abundance data were collected based on a modified version of the Braun-Blanquet relevé method (MNDNR 2007) at multiple, strata-dependent spatial scales: 100m^2 for bryophyte and herbaceous strata and 400m^2 for shrub and tree strata. The herbaceous stratum encompassed all vascular plant species, woody climbers (e.g. *Rhus* L., *Parthenocissus* Planch. and *Vitis* L.), submerged or floating-leaved species (e.g. *Utricularia* L., *Potamogeton* L. and *Myriophyllum* L.) and seedling woody species <0.5m in height. The shrub stratum represented woody plant species between 0.5 – 2.0m in height, and the tree stratum represented woody plant species >2.0m in height. The bryophyte stratum accounted for all non-vascular vegetation (e.g., lichens and mosses). The intent of stratum designations was to provide a general description of peatland community structure. Sample plots were positioned to represent the dominant vegetation communities present at each site. Net primary productivity (g/m^2) of the herbaceous stratum was measured by a removal of aboveground biomass from three, randomly assigned $0.1m^2$ plots within the $100m^2$ plot at each study site. All samples of aboveground biomass were collected September 22 – October 16, 2008 and September 23 – 25, 2009. After removal, samples were dried to a constant mass at 60°C and weighed.

Pore-water Chemistry

Pore-water characteristics, including pH, electrical conductivity (EC) and water temperature, were measured *in situ* from perforated, closed-bottom wells. Pore-water was defined as near-surface water, within 10cm of the soil surface. Wells were constructed of 6.2cm PVC pipes, cut to lengths of 30cm. Fifty-six, 4mm perforations were evenly spaced around the circumference, from the bottom of the well to a height of 14cm. At sites with water tables within 10cm of the peat surface, wells were installed in three random locations in the $100m^2$ sample plots to a depth of 10cm below the soil surface. If variable microtopography was present (e.g., hummocks and hollows), wells were installed at the hummock base. After installation, wells were evacuated and allowed to equilibrate three times prior to *in situ* analysis and sample collection. *In situ* determination of pH, pore-water temperature and temperature compensated EC were recorded with YSI pH100 and YSI EC300 probes respectively. In addition, three 50ml pore-water samples were collected from each well for laboratory analysis. Collected samples were analyzed with an YSI 9500 photometer for total alkalinity (Ca^{2+}) and available phosphorus within 12 hours of collection.

At sites where water tables were greater than 10cm below the soil surface, soil cores were collected for laboratory analysis of extractable ions. Three soil cores were collected in each $100m^2$ plot to a depth of 10cm and preserved at 4°C prior to analysis. Extraction of ions was conducted in a water medium on air-dried and homogenized samples following the methods of Day et al. (1979). Post extraction, filtrate analysis was conducted in the same manner as pore-water analysis with EC values corrected for conductivity resulting from the disassociation of hydrogen ions (Peech 1965).

Soils

A description of the soil profile, which included soil color and texture, was recorded at each site. Soil profiles were described from samples collected using a Macaulay peat auger at thicknesses of 30 or 50cm. Within the profile, depths at which changes in soil color and/or soil texture occurred were recorded and described. Soil color (i.e., hue, value and chroma) was determined through comparison with Munsell soil charts. A modified version of the von Post method (ASTM 2000) was used to describe soil texture and as a qualitative determination of the degree or organic matter decomposition (von Post and Granlund 1926 [as cited in ASTM 2000]).

An additional three soil cores were collected for laboratory analysis of bulk density, organic matter content and carbonate content (calcium carbonate [$CaCO_3$]

equivalent). Bulk density was calculated per dry-weight (g) of sample volume collected (cm^3). Organic matter content and carbonate content were calculated by loss on ignition (LOI) (Bengtsson and Enell 2003, Heiri et al. 2001, Dean 1974) and reported as a percentage of dry-weight of the original sample. Organic matter content (LOI_{550}) was determined by heating a dry and ground sample of known mass (~3g) in a muffle furnace to a constant temperature of 550°C for 16 hours. Mass lost through organic matter combustion provides a good estimation of the organic carbon content of the soil samples (Dean 1974). Carbonate content (LOI_{940}) of the samples was estimated by a subsequent burning at 940°C (ca. 2 hours) (Bengtsson and Enell 2003). The change in mass between the first and second burning is proportional to the change in molecular mass associated with the breakdown of various carbonate complexes, and is strongly correlated with the carbonate content of clay-poor samples (Dean 1974).

Water-Table Depth

Water-table depth was measured in the perforated, closed-bottom wells used for pore-water sample collection. All measurements were taken in reference to the soil surface. If standing water was present, water-table depth was recorded as height above the soil surface. At sites with a water table greater than 10cm below the soil surface, depth to the water table was determined from unlined boreholes at intervals of 30 or 50cm until the water-table depth was determined.

Data Analysis

Data analysis was performed on mean floristic and environmental characteristics using SigmaPlot for Windows version 11.0 (Systat 2008). Results were considered significant at $\alpha = 0.95$ and are reported as *p*-values throughout. An one-way analysis of variance (ANOVA) was used to compare differences in species richness (alpha diversity) between the classified communities. However, no other variables met the assumptions of normality or equal variance. A non-parametric Kruskal–Wallis one-way ANOVA on ranks was used to compare differences in the remaining floristic community and environmental characteristics. Multiple pair-wise comparisons were performed using the Holm-Sidak (ANOVA) and Dunn's (ANOVA on ranks) methods when significant differences were detected ($p \leq 0.05$) between individual characteristics of the classified communities. All data is reported for each classified community type as variable means and one standard error.

Species diversity indices (gamma, alpha and beta) were calculated on the complete sample set of species identified for the sample population and optimum cluster level. Species diversity largely reflects the nutrient status of peatland communities, and is reflected by an increase in species diversity with an increase in hydrologic inputs form mineral-rich water sources (Bridgham et al. 1996). Total species richness (γ; gamma diversity) was measured as the total number of unique species. Alpha diversity (α) was calculated as mean species richness per site and estimated with the Shannon diversity index (Greig-Smith 1983). In addition, Whittaker's beta diversity (ß) was calculated to determine overall floristic similarity among sub-boreal peatlands (Whittaker 1972), and was used to correlate changes in floristic composition along environmental gradients.

Community Classification

Prior to community classification, 210 rare species, which occurred in less than three study sites, were removed from the community matrix, leaving 100 species in the herbaceous stratum, 25 species in the shrub stratum, 6 species in the canopy stratum and 3 bryophyte taxa for analysis. Removal of rare species is consistent with multivariate analysis and decreases noise associated with the chance occurrence of rare species across the landscape while increasing the detection of relationships between community structure and environmental variables (McCune and Grace 2002).

Floristic classification of the 56 study sites was conducted using PC-ORD software (McCune and Mefford 2006), and was based on species composition and abundance data. Specifically, study sites were classified by hierarchical agglomerative cluster analysis (Post and Sheperd 1974), which groups communities based on compositional similarity. The resulting dendrogram was structured such that the distance between study sites, and groups of study sites, decreases as the compositional similarity of floristic communities increases. Study sites were grouped using the Sørensen distance measure and a flexible beta linkage method (β = -0.25). The Sørensen distance measure is commonly used for community analysis (McCune and Grace 2002) and has been found to provide a robust representation of ecological distances (Faith et al. 1987). Linkage by flexible beta is a combinatorial method compatible with semi metric distance measures (i.e., Sørensen), providing similar results to Ward's method at β = -0.25 (McCune and Grace 2002). All study sites were retained for analysis, given that all study sites fell within the predefined level of variability, ±3 standard deviations, based on a frequency distribution of average distances.

Pruning a cluster analysis dendrogram presents a trade-off between within group homogeneity and the number of groups selected (McCune and Grace 2002). Indicator species analysis (ISA) provides an objective method by which the most informative cluster level is established based on indicator values of species at each cluster level (Dufrêne and Legendre 1997). Indicator values range from 0–100, and are calculated based on the relative frequency and relative abundance of each species for a particular cluster grouping and cluster level. An indicator value of 100 indicates complete fidelity of a species to a particular cluster grouping. The optimum cluster level is established by either the lowest mean *p*-value or the highest number of significant indicator species ($p \leq 0.05$) among cluster groupings.

Cluster groupings at the optimum cluster level were evaluated by Multi-Response Permutation Procedure (MRPP; Zimmerman et al. 1985) on the rank-transformed distance matrix. MRPP is a nonparametric procedure to test the hypothesis of no differences between average with-in group distances (McCune and Grace 2002). This is accomplished through calculation of weighted-mean, within group distances (delta; δ); a smaller δ indicates greater within group homogeneity. The probability (p) of achieving a smaller δ by chance is assessed by a randomized Monte Carlo procedure where study sites are reshuffled as to represent the total number of partitions while maintaining the species matrix constant. MRPP also calculates a test statistic (T) and chance-correlated within group agreement (A). T-values represent the separation among groups, with more negative values indicating greater separation, while A-values provide an indication of within group homogeneity, ranging between 0 and 1. An A-value of A=1 is obtained when all study sites within a group are identical.

Nonmetric multidimensional scaling (NMS; Mather 1976, Kruskal 1964) was performed to evaluate cluster analysis groupings and the relationships between community structure and environmental variables. A random starting configuration was used with the "slow and thorough" auto plot setting in PC-ORD (McCune and Mefford 2006). Dimensionality was assessed automatically based on reductions in stress as a function of dimensionality for real and randomized data. A final run was performed, with no step-down in dimensionality and a maximum of 100 iterations, to assess final stress and instability using coordinates from the dimension identified as having the lowest stress. In addition, ordination by detrended correspondence analysis (DCA; Hill and Gauch 1980) was performed to evaluate the reliability and consistency of results (Økland 2007). Percent variance was calculated after-the-fact (Sørensen for NMS and relative Euclidean for DCA) and represents the variation of Euclidean distances between study sites in ordinal space and the distances between study sites in the original *n*-dimensional space. Correlations between the ordinal scores of study sites and environmental variables were evaluated to assess changes in community structure along environmental gradients. MRPP, NMS, ISA and CA were all performed on raw abundance values with rare species removed prior to analysis.

CHAPTER 3

RESULTS

Floristic Classification

Five sub-boreal peatland community types were classified by cluster analysis based on similarities in floristic composition (Figure 4), four of which were identified along the bog-fen continuum as *Sphagnum* Bogs, Herbaceous Fens, Forested Fens and Rich/Calcareous Fens. The fifth sub-boreal peatland community type was characterized by the dominance of the invasive grass, reed canarygrass (*Phalaris arundinacea L.*), despite of the broader floristic variation present within the individual *Phalaris* – Dominated Peatland communities.

Table 1 MRPP (Multi-response Permutation Procedure [Zimerman et al. 1985]) pair-wise comparisons between the five classified peatland communities of Minnesota and western Wisconsin. All pair-wise comparisons were significantly different at the Bonferroni corrected α level of 0.005; Pa = Phalaris – Dominated, SB = Sphagnum Bogs, HF = Herbaceous Fens, FF = Forested Fens and RF = Rich/Calcareous Fens.

Pair-wise Comparisons			T	A	*P*-value
Pa	vs.	SB	-10.028	0.375	<0.001
Pa	vs.	HF	-7.035	0.301	<0.001
Pa	vs.	FF	-6.078	0.425	<0.001
Pa	vs.	RF	-8.236	0.268	<0.001
SB	vs.	HF	-13.217	0.342	<0.001
SB	vs.	FF	-10.034	0.331	<0.001
SB	vs.	RF	-18.756	0.475	<0.001
HF	vs.	FF	-8.238	0.306	<0.001
HF	vs.	RF	-13.849	0.335	<0.001
FF	vs.	RF	-10.810	0.305	<0.001

Floristic classification of the sub-boreal peatland communities was evaluated by Multi-response Permutation Procedure (MRPP; Zimmerman et al. 1985), which revealed high, within group homogeneity ($A = 0.614$, $T = -22.979$, $p < 0.001$), with significant pair-wise differences among between all peatland community types (Table 1). Classification of the sub-boreal peatland communities was also evaluated by Non-metric Multidimensional Scaling, which revealed distinct separations among the different peatland community types (Figure 5).

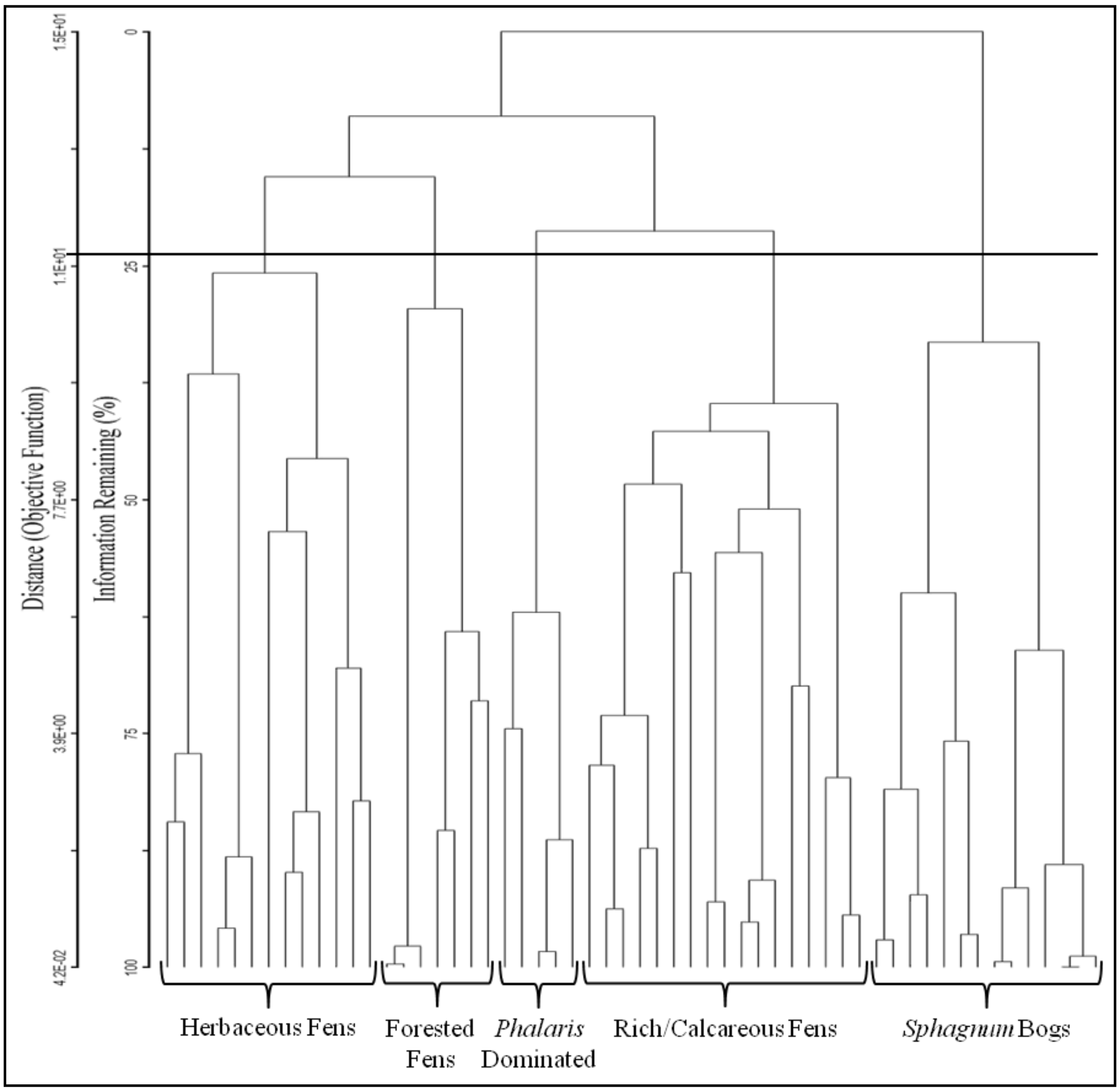

Figure 4 Cluster analysis dendrogram represented the community associations of the 56 sample sites and was scaled using the Wishart objective function (Wishart 1969). Approximately 23 percent information remained at the five – cluster level.

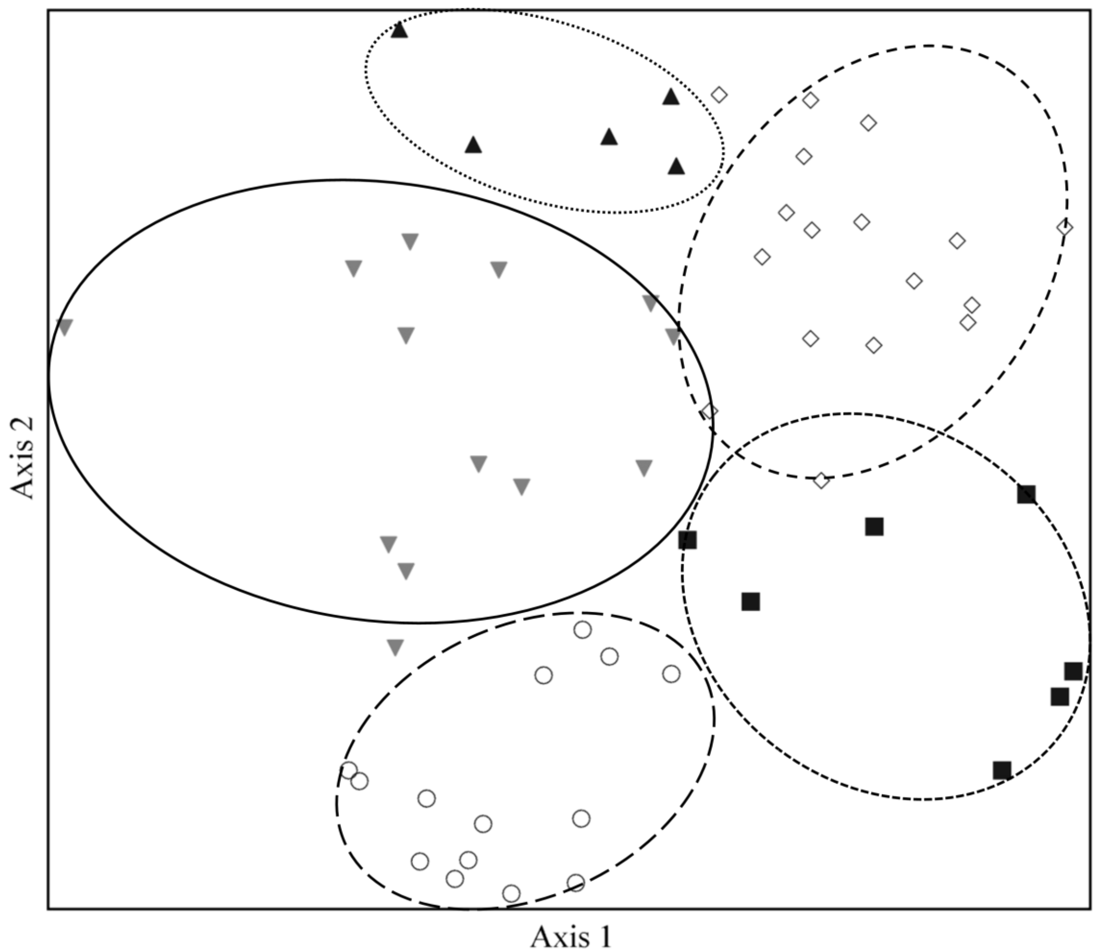

Figure 5 The final NMS ordination resulted from a stable 2-dimensional solution (final instability = 0.00019; number of iterations = 100) with moderately high, but acceptable final stress (final stress = 16.12331) (Kruskal 1964, Clarke 1993); *Phalaris* – Dominated = ▲, *Sphagnum* Bog = ○, Herbaceous Fen = ▼, Forested Fen = ■, and Rich/Calcareous Fen = ◊.

Environmental Characteristics

Pore-water Chemistry

Significant differences were detected among the different peatland community types for all measured environmental characteristics (Table 2). Analysis of mean pH revealed significant differences among the classified communities ($H_{pH} = 35.797$, $p < 0.001$), with significant pair-wise differences detected between multiple community types (Table 2). Similar results, as those observed for pH, were detected for EC and total alkalinity (Table 2). In addition, a consistent rank-order of pH, EC and total alkalinity variable means was observed among community types (i.e., *Sphagnum* Bogs < Herbaceous Fens < Forested Fens < *Phalaris* – Dominated Peatlands < Rich/Calcareous Fens), with the lowest values recorded in *Sphagnum* Bogs and the highest recorded in Rich/Calcareous Fens (pH: $H_{pH} = 35.797$, $p < 0.001$; $H_{\text{conductance}} = 18.499$, $p < 0.001$; $H_{\text{alkalinity}} = 29.627$, $p < 0.001$). Available phosphorus did not conform to this trend, but a significant difference was detected between *Phalaris* – Dominated Peatlands and Forested Fens ($H_{\text{phosphoorus}} = 9.609$, $p = 0.048$) (Table 2).

Table 2 Mean pore-water characteristics (S.E.) and Kruskal-Wallis ANOVA on Ranks *H*-statistic and *p*-values of the five sub-boreal peatland communities. Different letters denote significant differences among peatland community types (Dunn's Method, p <0.05). Significance labeled as: *p<0.05, **p<0.01; Pa = Phalaris – Dominated, SB = Sphagnum Bogs, HF = Herbaceous Fens, FF = Forested Fens and RF = Rich/Calcareous Fens.

	pH		Conductance (µS)		Total Alkalinity (mg/l)		Available Phosphorus (mg/l)	
	Mean (SE)	n	Mean (SE)	n	Mean (SE)	n	Mean (SE)	n
PH	6.5 (0.5)^{ac}	5	431.2 (134.6)^{ab}	5	194 (73)^{ac}	5	0.9 (0.2)	3
SB	4.4 (0.2)^{b}	12	112.1 (32.9)^{a}	12	17 (4)^{b}	12	1.5 (0.3)	12
HF	5.5 (0.2)^{ab}	13	208.4 (61.4)^{a}	13	42 (8)^{ab}	13	2.0 (0.4)	13
FF	6.1 (0.3)^{abc}	7	236.1 (57.2)^{ab}	7	77 (30)^{abc}	7	2.3 (0.4)	7
RF	7.1 (0.1)^{c}	16	500.9 (71.7)^{b}	16	222 (23)^{c}	16	1.7 (0.2)	13
H, *P*-value	36.797, <0.001**		18.499, <0.001**		29.627, <0.001**		9.609, 0.048*	

Soil Characteristics

No consistent group-by-variable trend was observed between the peatland community types and the physical characteristics of their organic soils (Table 3). However, the rank-order of mean bulk density paralleled the results observed for pH, EC and total alkalinity (Table 2). Mean soil bulk density was lowest in the *Sphagnum* Bog communities and highest in the *Phalaris* – Dominated Peatland communities ($H_{\text{bulk density}}$=13.548, p=0.009), but was not different among the other peatland community types. LOI_{550} revealed significant differences in the soil-organic matter content among sub-boreal peatland communities ($H_{\text{organic matter}}$=21.934, p<0.001), with multiple significant pair-wise differences detected (Table 3). LOI_{940} revealed significant differences in the soil-carbonate content of the sub-boreal peatland communities ($H_{\text{carbonate content}}$=32.360, p<0.001), with significant pair-wise differences between peatland Rich/Calcareous Fens, *Sphagnum* Bogs and Herbaceous Fens (Table 3). Significant differences in the mean water-table depth were also detected ($H_{\text{watertable depth}}$=14.295, p=0.006), with a significant pair-wise difference between Herbaceous Fens and *Sphagnum* Bogs (Figure 6).

Table 3 Mean soil characteristics, water-table depth (S.E.) and Kruskal-Wallis ANOVA on Ranks *H*-statistic and *p*-values of the five sub-boreal peatland communities. Different letters denote significant differences among peatland community types (Dunn's Method, p <0.05). Significance labeled as: *p<0.05, **p<0.01; Pa = *Phalaris* – Dominated, SB = *Sphagnum* Bogs, HF = Herbaceous Fens, FF = Forested Fens and RF = Rich/Calcareous Fens.

	Bulk density (g/cm^3)		LOI_{550} (% DW)		LOI_{940} (% DW)	
	Mean (SE)	n	Mean (SE)	n	Mean (SE)	n
PH	0.21 (0.06)	5	45.36 (14.42)^{b}	5	3.06 (1.38)^{ab}	5
SB	0.07 (0.01)	14	85.74 (1.39)^{a}	14	0.50 (0.08)^{a}	14
HF	0.12 (0.03)	13	56.55 (8.27)^{b}	13	0.69 (0.10)^{a}	13
FF	0.15 (0.03)	7	63.45 (6.94)^{ab}	7	1.38 (0.30)^{ab}	7
RF	0.18 (0.03)	17	53.66 (5.43)^{b}	17	9.78 (3.29)^{b}	17
H, *P*-value	13.548, <0.001**		21.843, <0.001**		32.360, <0.001**	

Community Characteristics

Herbaceous Productivity

Productivity of the herbaceous strata varied significantly among sub-boreal peatland communities ($H_{\text{productivity}}$ = 39.920, p < 0.001), and ranged from 88.9 g/m^2 in peatlands classified as Forested Fens, to 924.9 g/m^2 in *Phalaris* – Dominated Peatlands

(Figure 7). Significant pair-wise differences were observed between *Sphagnum* bogs, Forested Fens, and the other classified community types (Figure 7).

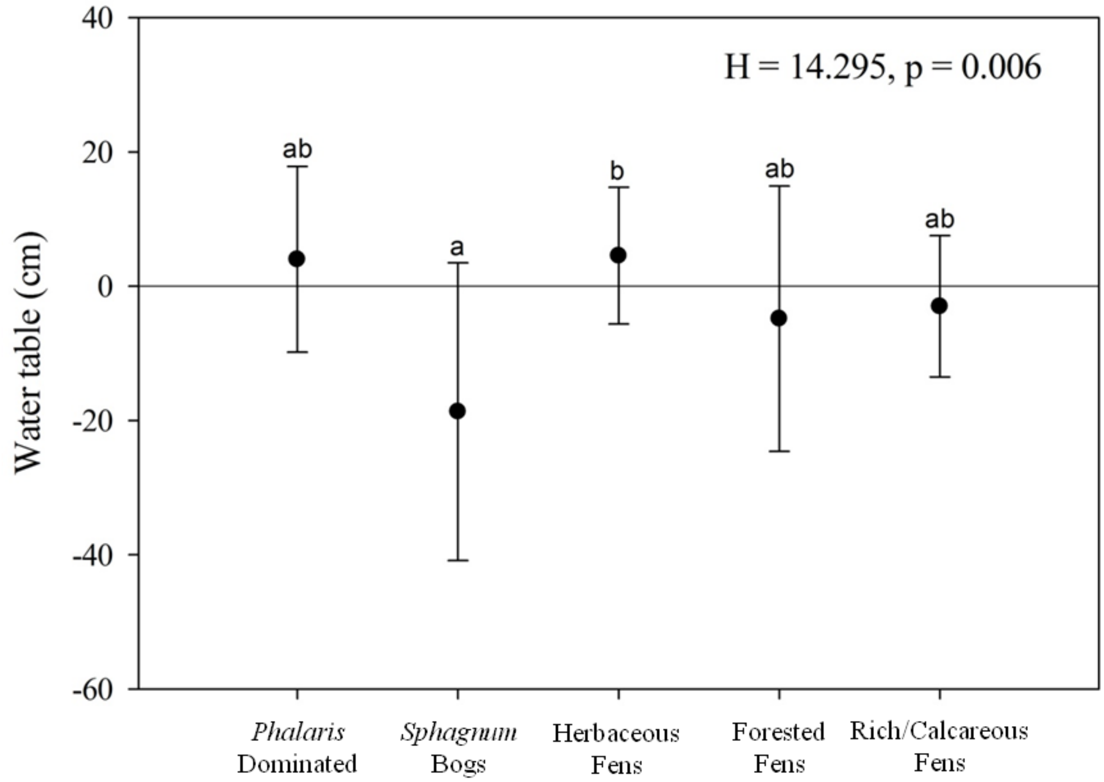

Figure 6 Mean water table depth, 95 percent confidence intervals, Kruskal–Wallis H statistic and *p*-value for the five sub-boreal peatland community types. Different letters denote pair-wise differences as determined by Dunn's Method.

Floristic Diversity and Indicator Species

Three hundred and forty-one plant species across four strata were identified from 56 sites during the 2008 and 2009 field seasons. The majority of the plant species, 273, occurred in the herbaceous stratum; 49 occurred in the shrub stratum and 15 in the canopy stratum. However, since each vascular plant species was also defined by the stratum or strata in which it occurred, only 297 unique vascular plant species were recorded in sub-boreal peatland communities. Nineteen of the 341 species were recorded in two different strata (i.e., herbaceous and shrub strata or shrub and canopy strata), and

10 species were recorded in the herbaceous, shrub and canopy strata. In addition, four families of bryophytes, *Sphagnaceae*, *Thudiaceae*, *Amblystegiaceae* and *Polytrichaceae*, and one family of liverworts, *Ricciacea*, were recorded in sub-boreal peatland communities.

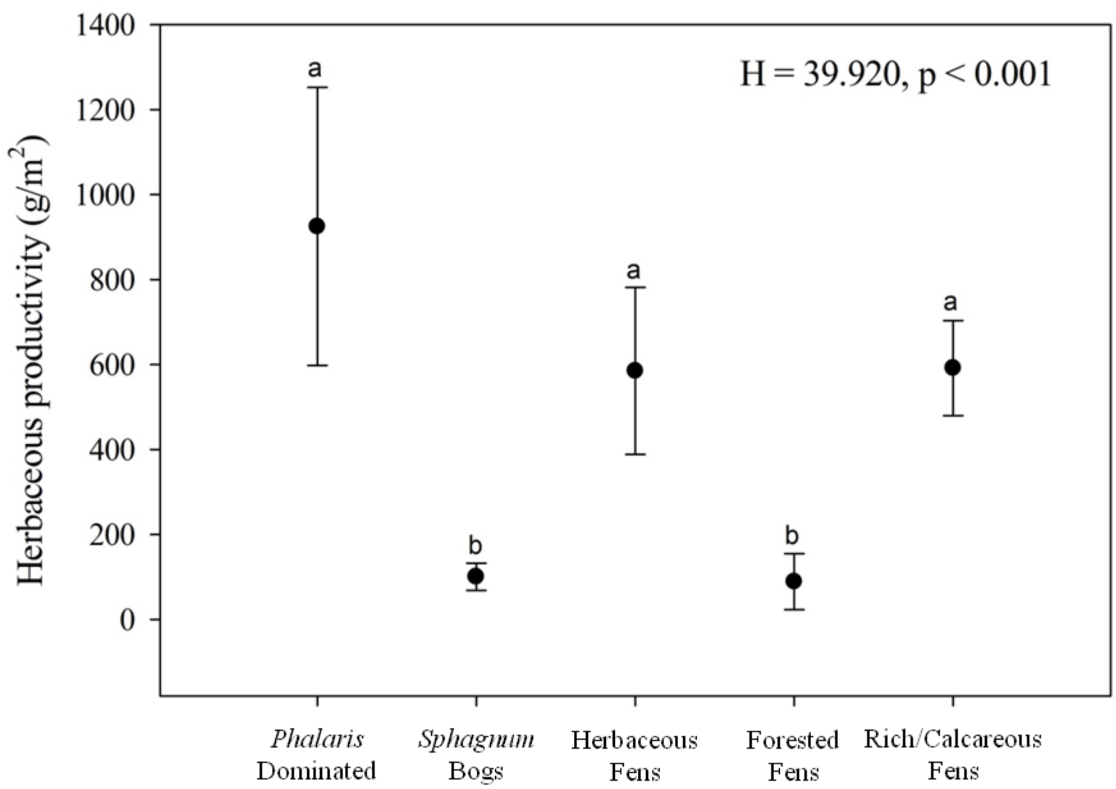

Figure 7 Mean productivity of the herbaceous strata, 95 percent confidence intervals, Kruskal–Wallis H statistic and *p*-value for the five sub-boreal peatland community types. Different letters denote pair-wise differences as determined by Dunn's Method.

Two-hundred five plant species (out of the 341species indentified) were defined as rare (having <3 occurrences among all sample sites), and represented roughly 60% of all species surveyed, with 122 species occurring only once. Eighteen species were considered "wide-spread", occurring in 20% or more sites. *Carex stricta* Lam. and *Calamagrostis canadensis* (Michx.) P. Beauv. were the most common species recorded, occurring in 43% and 45% of all sites, respectively. Species diversity was significantly different among sub-boreal peatland communities ($H_{Shannon's}$ = 19.728, p < 0.001) (Table 4). In addition, mean species richness differed among the classified peatland community types (F_{alpha} = 6.686, p < 0.001) with the highest mean species richness observed in Forested Fen communities (34 species), while the lowest mean species richness was observed in *Phalaris* – Dominated Peatlands (8 species) (Table 4). Similar trends were observed in the variation of both gamma diversity and beta diversity between the classified peatland communities (Table 4).

Table 4 Total and mean diversity indices (S.E.), Kruskal-Wallis ANOVA on Ranks H-statistic and ANOVA *F*-statistic (Alpha diversity only) and *p*-values of the five classified peatland communities of Minnesota and western Wisconsin. Different letters denote significant differences among peatland community types (Dunn's – Kruskal-Wallis and Holm-Sidak – ANOVA, *p* <0.05). Significance labeled as: *p<0.05, **p<0.01; Pa = Phalaris – Dominated, SB = Sphagnum Bogs, HF = Herbaceous Fens, FF = Forested Fens and RF = Rich/Calcareous Fens.

	n	Gamma	Alpha Mean (SE)	Shannon's Mean (SE)	Beta
All sample sites	56	341	20.4 (1.6)	2.66 (0.09)	15.8
Peatland Type					
PH	5	23	8.0 (0.3)[a]	1.89 (0.04)[a]	1.9
SB	14	83	15.3 (1.7)[ac]	2.43 (0.15)[ac]	4.4
HF	13	103	18.6 (2.2)[ac]	2.58 (0.21)[abc]	4.5
FF	7	133	34.1 (2.5)[b]	3.39 (0.07)[b]	2.9
RF	17	175	24.0 (3.6)[bc]	2.83 (0.17)[bc]	6.3
(*F*); *H*, *P*-value		-	(6.686), <0.001**	19.728, <0.001**	-

Sixty-nine plant species were identified as significant indicators ($p \leq 0.05$) (Dufrêne and Legendre 1997) of the five classified sub-boreal peatland community types (Table 5). Significant indicator species with high indicator values (IV) displayed fidelity to particular peatland community types (Dufrêne and Legendre 1997, McCune and Grace 2002), and were used to distinguish sub-boreal peatland communities based on floristic composition. Forested Fen communities possessed the greatest number of significant indicator species with 27, while only three significant indicator species were identified for *Phalaris* – Dominated Peatlands (Table 5).

Phalaris arundinacea – Dominated Peatlands (Type I)

Twenty-three plant species were observed in the *Phalaris* – Dominated Peatland communities (Appendix 1). Three species, *P. arundinacea* (IV = 76.7, *p* = 0.001), *Carex lacustris* Willd. (IV = 48.1, *p* = 0.005) and *C. canadensis* (IV = 32.7, *p* = 0.041), were identified as significant indicators with relative frequencies of 100, 80 and 80%, respectively (Table 5). Ten of the 23 total species identified in *Phalaris* – Dominated Peatlands were observed in at least four of the five sub-boreal peatland community types. *P. anrundinacea*, in addition to being the most significant indicator species of *Phalaris* – Dominated Peatlands, was recorded in four of the five classified peatland community types, with the exception of *Sphagnum* Bogs. Seven additional species occurred in four sub-boreal peatland community types (Table 5), and *C. lacustris*, and *C. canadensis,* were recorded in all five classified peatland community types. Herbaceous-stratum species represented 21 of the 23 species recorded in *Phalaris* – Dominated Peatlands. The two remaining species, *Salix petiolaris* Sm. and *Salix planifolia* Pursh, occurred in the shrub stratum, and were present in 20% of *Phalaris* – Dominated Peatlands (Appendix 1). Five of the 23 plant species observed in *Phalaris* – Dominated Peatlands were considered rare. Three species, *Polygonum persicaria* L., *Rorippa palustris* (L.) Besser and *Carex pellita* Muhl. ex Willd., were exclusively recorded in *Phalaris* – Dominated Peatlands.

Table 5 Indicator values (IV; Dufrene and Legendre 1997), *P*-values and percent relative frequencies of indicator plant species identified for the five classified sub-boreal peatland community types in Minnesota and western Wisconsin. Species are sorted by decreasing IV for each community type. **Bold** values indicate significant indicator plant species ($p \leq 0.05$).

				% Relative Frequency				
Species	Strata	IV	*P*-value	*Phalaris* Dominated	*Sphagnum* Bogs	Herbaceous Fens	Forested Fens	Rich/ Calcareous Fens
***Phalaris arundinacea* L.**	Herb.	**76.7**	**0.001**	**100**	0	15	14	35
***Carex lacustris* Willd.**	Herb.	**48.1**	**0.005**	**80**	7	8	14	18
***Calamagrostis canadensis* (Michx.) P. Beauv.**	Herb.	**32.7**	**0.041**	**80**	36	62	29	35
Carex L.	Herb.	20.3	0.123	40	0	8	43	12
Galium tinctorium (L.) Scop.	Herb.	14.1	0.218	20	0	8	14	6
Phragmites australis (Cav.) Trin. ex Steud.	Herb.	11.9	0.223	20	0	8	0	6
Typha latifolia L.	Herb.	16.3	0.231	40	0	23	0	24
Scirpus cyperinus (L.) Kunth	Herb.	15.3	0.255	40	21	15	0	6
***Sphagnaceae* L.**	Bryo.	**66.9**	**0.001**	0	**100**	46	29	6
Chamaedaphne calyculata* (L.) Moench var. *angustifolia	Shrub	**64.3**	**0.001**	0	**64**	0	0	0
***Picea mariana* (Mill.) BSP**	Shrub	**50**	**0.002**	0	**50**	0	0	0
***Vaccinium oxycoccos* L.**	Herb.	**50**	**0.002**	0	**50**	0	0	0
***Carex oligosperma* Michx.**	Herb.	**47**	**0.002**	0	**57**	8	0	0
***Ledum groenlandicum* Oeder**	Shrub	**42.9**	**0.004**	0	**43**	0	0	0
***Larix laricina* (Du Roi) K. Koch**	Can.	**38.9**	**0.006**	0	**57**	0	29	6
***Polytrichaceae* Hedw.**	Bryo.	**35.7**	**0.007**	0	**36**	0	0	0
***Eriophorum virginicum* L.**	Herb.	**35.7**	**0.008**	0	**36**	0	0	0
***Maianthemum trifolium* (L.) Sloboda**	Herb.	**33.6**	**0.011**	0	**36**	0	0	6
***Picea mariana* (Mill.) BSP**	Can.	**32.8**	**0.013**	0	**43**	0	14	0
Carex trisperma* Dewey var. *trisperma	Herb.	**32.8**	**0.014**	0	**43**	0	14	0
***Carex magellanica* Lam. ssp. *irrigua* (Wahlenb.) Hultén**	Herb.	**28.6**	**0.029**	0	**29**	0	0	0
Sarracenia purpurea* L. ssp. *purpurea	Herb.	**28.6**	**0.029**	0	**29**	0	0	0
***Larix laricina* (Du Roi) K. Koch**	Shrub	**25.9**	**0.032**	0	**29**	0	0	6

Table 5. Continued.

Species	Strata	IV	*P*-value	% Relative Frequency: *Phalaris* Dominated	*Sphagnum* Bogs	Herbaceous Fens	Forested Fens	Rich/ Calcareous Fens
***Vaccinium angustifolium* Aiton**	Shrub	**28.6**	**0.034**	0	**29**	0	0	0
Kalmia polifolia Wangenh.	Shrub	21.4	0.056	0	21	0	0	0
Vaccinium angustifolium Aiton	Herb.	21.4	0.07	0	21	0	0	0
Larix laricina (Du Roi) K. Koch	Herb.	21.4	0.078	0	21	0	0	0
Chamaedaphne calyculata (L.) Moench var. *angustifolia*	Herb.	18.6	0.088	0	21	8	0	0
Betula pumila L. var. *glandulifera* Regel	Shrub	21.3	0.13	0	43	23	14	12
Spiraea tomentosa L. var. *rosea*	Shrub	12.5	0.256	0	21	8	0	0
Drosera rotundifolia L. var. *rotundifolia*	Herb.	9.3	0.507	0	14	8	0	0
Betula papyrifera Marsh. var. *papyrifera*	Shrub	9.9	0.575	0	21	0	14	12
Dulichium arundinaceum (L.) Britton	Herb.	7.9	0.603	0	14	15	0	0
***Cicuta bulbifera* L.**	Herb.	**81.3**	**0.001**	0	0	**85**	0	6
***Carex lasiocarpa* Ehrh. var. *americana* Fernald**	Herb.	**65.8**	**0.001**	0	7	**69**	0	6
***Comarum palustre* L.**	Herb.	**46.2**	**0.002**	0	0	**46**	0	0
***Lysimachia thyrsiflora* L.**	Herb.	**47.8**	**0.003**	0	0	**54**	0	6
***Sagittaria latifolia* Willd.**	Herb.	**46.2**	**0.005**	0	0	**46**	0	0
***Bidens aristosa* (Michx.) Britton**	Herb.	**38.5**	**0.006**	0	0	**38**	0	0
***Spiraea alba* Du Roi**	Herb.	**30.8**	**0.011**	0	0	**31**	0	0
***Scutellaria galericulata* L.**	Herb.	**30.8**	**0.023**	0	0	**31**	0	0
***Triadenum fraseri* (Spach) Gleason**	Herb.	**30.8**	**0.026**	0	0	**31**	0	0
***Lemna minor* L.**	Herb.	**23.1**	**0.041**	0	0	**23**	0	0
***Polygonum sagittatum* L.**	Herb.	**25.6**	**0.046**	40	0	**46**	0	0
***Carex utriculata* Boott**	Herb.	**23.1**	**0.046**	0	0	**23**	0	0
Lythrum salicaria L.	Herb.	20.8	0.064	0	0	23	0	6
Rumex verticillatus L.	Herb.	20.1	0.087	0	0	31	14	0

Table 5. Continued.

Species	Strata	IV	*P*-value	% Relative Frequency *Phalaris* Dominated	*Sphagnum* Bogs	Herbaceous Fens	Forested Fens	Rich/Calcareous Fens
Carex stipata Muhl. ex Willd. var. *stipata*	Herb.	18.4	0.116	0	0	23	0	6
Salix petiolaris Sm.	Shrub	18.9	0.14	20	0	38	0	6
Thelypteris palustris Schott var. *pubescens* (G. Lawson) Fernald	Herb.	22.5	0.182	0	21	62	29	41
Lycopus uniflorus Michx.	Herb.	21.7	0.206	0	21	54	57	24
Lysimachia terrestris (L.) BSP	Herb.	10.5	0.335	0	7	15	0	0
Salix pyrifolia Anderson	Herb.	10.5	0.341	0	7	15	0	0
Typha angustifolia L.	Herb.	9.1	0.41	0	0	15	0	12
Polygonum amphibium L.	Herb.	8.7	0.525	0	0	15	0	6
Campanula aparinoides Pursh	Herb.	5.7	0.854	0	0	15	14	6
***Athyrium filix-femina* (L.) Roth ssp. *angustum* (Willd.) R.T. Clausen**	Herb.	**71.4**	**0.001**	0	0	0	**71**	0
Rubus pubescens* Raf. var. *pubescens	Herb.	**70**	**0.001**	0	0	8	**100**	35
Acer rubrum* L. var. *rubrum	Can.	**57.1**	**0.001**	0	0	0	**57**	0
Betula alleghaniensis* Britton var. *alleghaniensis	Can.	**57.1**	**0.001**	0	0	0	**57**	0
***Fraxinus nigra* Marsh.**	Can.	**57.1**	**0.001**	0	0	0	**57**	0
***Cornus canadensis* L.**	Herb.	**42.9**	**0.001**	0	0	0	**43**	0
***Corylus cornuta* Marsh.**	Shrub	**42.9**	**0.001**	0	0	0	**43**	0
***Maianthemum canadense* Desf.**	Herb.	**58.4**	**0.002**	0	7	0	**71**	0
***Fraxinus nigra* Marsh.**	Shrub	**57.1**	**0.002**	0	0	0	**57**	0
***Aralia nudicaulis* L.**	Herb.	**46.5**	**0.003**	0	7	0	**57**	6
***Glyceria striata* (Lam.) Hitchc.**	Herb.	**40.8**	**0.003**	0	0	0	**43**	6
Acer rubrum* L. var. *rubrum	Shrub	**45.2**	**0.004**	0	14	0	**57**	6
***Hydrocotyle americana* L.**	Herb.	**42.9**	**0.006**	0	0	0	**43**	0

Table 5. Continued.

Species	Strata	IV	*P*-value	% Relative Frequency *Phalaris* Dominated	*Sphagnum* Bogs	Herbaceous Fens	Forested Fens	Rich/ Calcareous Fens
***Thuja occidentalis* L.**	Can.	**42.9**	**0.006**	0	0	0	**43**	0
***Arisaema triphyllum* (L.) Schott**	Herb.	**40.1**	**0.007**	0	0	0	**43**	6
***Ulmus americana* L.**	Can.	**32.7**	**0.009**	0	0	0	**43**	12
***Impatiens capensis* Meerb.**	Herb.	**33.4**	**0.015**	0	0	15	**57**	29
***Viola cucullata* Aiton**	Herb.	**31.3**	**0.018**	20	0	0	**43**	12
Amblystegiaceae	Bryo.	**32.2**	**0.021**	0	0	23	**57**	18
***Amphicarpaea bracteata* (L.) Fernald**	Herb.	**25.1**	**0.022**	0	0	0	**29**	6
Trientalis borealis* Raf. ssp. *borealis	Herb.	**28.6**	**0.024**	0	21	0	**43**	0
***Ilex verticillata* (L.) A. Gary**	Shrub	**24.1**	**0.027**	0	0	8	**29**	6
Osmunda cinnamomea* L. var. *cinnamomea	Herb.	**30**	**0.029**	0	7	15	**43**	6
***Dryopteris carthusiana* (Vill.) H.P. Fuchs**	Herb.	**26.2**	**0.036**	0	21	0	**43**	6
***Viola* L.**	Herb.	**25.8**	**0.037**	20	0	15	**43**	6
***Galium triflorum* Michx.**	Herb.	**23.7**	**0.044**	0	0	0	**29**	6
***Onoclea sensibilis* L.**	Herb.	**28.8**	**0.045**	0	14	46	**57**	6
Cornus sericea L. ssp. *sericea*	Shrub	28.3	0.058	0	14	8	57	59
Viola macloskeyi Lloyed ssp. *pallens* (Banks ex Ging) M.S. Baker	Herb.	21.4	0.068	0	7	0	29	0
Rubus idaeus L. ssp. *strigosus* (Michx.) Focke	Herb.	21.5	0.098	0	14	8	43	29
Dryopteris cristata (L.) A. Gray	Herb.	20.4	0.128	0	21	23	43	0
Equisetum arvense L.	Herb.	16.9	0.169	20	0	0	29	18
Alnus incana ssp. *rugosa* (Du Roi) Clausen	Shrub	15.2	0.242	0	7	23	29	0
Equisetum fluviatile L.	Herb.	12.6	0.276	0	0	15	29	6
Ulmus americana L.	Shrub	10.9	0.336	0	0	0	14	12
Poa palustris L.	Herb.	8.2	0.513	0	7	0	14	12

Table 5. Continued.

Species	Strata	IV	*P*-value	% Relative Frequency: *Phalaris* Dominated	*Sphagnum* Bogs	Herbaceous Fens	Forested Fens	Rich/ Calcareous Fens
Ribes americanum Mill.	Shrub	7.3	0.667	0	0	8	14	6
Quercus rubra L.	Herb.	8.2	0.668	0	14	0	14	0
Parthenocissus Planch.	Herb.	6	0.820	0	0	8	14	12
***Carex stricta* Lam.**	Herb.	**63.4**	**0.001**	20	7	46	0	**94**
***Pycnanthemum virginianum* (L.) T. Dur. & B.D. Jacks. ex B.L. Rob & Fernald**	Herb.	**47.1**	**0.001**	0	0	0	0	**47**
***Eupatorium maculatum* L.**	Herb.	**49.5**	**0.002**	60	0	15	14	**88**
***Solidago gigantea* Aiton**	Herb.	**54.2**	**0.004**	20	0	0	14	**76**
***Symphyotrichum puniceum* (L.) A. Löve & D. Löve**	Herb.	**39.1**	**0.005**	0	0	15	43	**71**
***Cirsium muticum* Michx.**	Herb.	**41.2**	**0.008**	0	0	0	0	**41**
***Helianthus grosseserratus* M. Martens**	Herb.	**28**	**0.034**	20	0	0	0	**35**
Calamagrostis stricta* (Timm) Koeler ssp. *stricta	Herb.	**23.5**	**0.039**	0	0	0	0	**24**
***Salix discolor* Muhl.**	Shrub	**25.3**	**0.048**	0	0	8	0	**29**
***Frangula alnus* Mill.**	Shrub	**23.5**	**0.049**	0	0	0	0	**24**
Poa pratensis* L. ssp. *pratensis	Herb.	**23.5**	**0.050**	0	0	0	0	**24**
Lycopus americanus Muhl. ex W. Bartram	Herb.	23.5	0.055	0	0	0	0	24
Galium boreale L.	Herb.	23.5	0.061	0	0	0	0	24
Rhamnus cathartica L.	Shrub	23.5	0.063	0	0	0	0	24
Thalictrum dasycarpum Fisch. & Avé-Lall.	Herb.	23	0.080	0	0	8	14	35
Maianthemum stellatum (L.) Link	Herb.	17.6	0.086	0	0	0	0	18
Apocynum cannabinum L.	Herb.	17.6	0.090	0	0	0	0	18
Calystegia sepium (L.) R. Br.	Herb.	17.6	0.090	0	0	0	0	18
Acer negundo L.	Shrub	17.6	0.094	0	0	0	0	18
Pedicularis lanceolata Michx.	Herb.	17.6	0.094	0	0	0	0	18

Table 5. Continued.

Species	Strata	IV	*P*-value	% Relative Frequency: *Phalaris* Dominated	*Sphagnum* Bogs	Herbaceous Fens	Forested Fens	Rich/ Calcareous Fens
Oligoneuron riddellii (Frank ex Riddell) Rybd.	Herb.	17.6	0.096	0	0	0	0	18
Fraxinus pennsylvanica Marsh.	Shrub	17.6	0.098	0	0	0	0	18
Lathyrus palustris L.	Herb.	17.6	0.100	0	0	0	0	18
Oxypolis rigidior L. Raf.	Herb.	17.6	0.101	0	0	0	0	18
Carex tectanica Schkuhr	Herb.	17.6	0.103	0	0	0	0	18
Solidago canadensis L.	Herb.	17.6	0.103	0	0	0	0	18
Schoenoplectus acutus (Muhl. ex Bigelow) A. Löve & D. Löve var. *acutus*	Herb.	17.6	0.107	0	0	0	0	18
Salix bebbiana Sarg.	Shrub	17.6	0.114	0	0	0	0	18
Doellingeria umbellata (Mill.) Nees	Herb.	16	0.166	0	7	8	0	24
Asclepias incarnata L. ssp. *incarnata*	Herb.	14	0.183	0	0	8	0	18
Geum aleppicum Jacq.	Herb.	16.8	0.185	0	0	0	14	29
Symphyotrichum boreale (Torr. & A. Gray) A. Löve & D. Löve	Herb.	13.7	0.244	0	0	8	14	24
Bromus ciliatus L. var. *ciliatus*	Herb.	11	0.315	0	0	0	14	18
Agrostis gigantea Roth	Herb.	10.7	0.344	0	0	8	0	18
Eupatorium perfoliatum L. var. *perfoliatum*	Herb.	11.5	0.432	20	0	15	0	24
Caltha palustris L. var. *palustris*	Herb.	9.7	0.489	0	0	8	0	12
Carex interior L.H. Bailey	Herb.	7.7	0.602	0	0	8	0	12
Cornus racemosa Lam.	Shrub	7.9	0.605	0	0	0	14	12
Carex buxbaumii Wahlenb.	Herb.	7.1	0.840	0	0	8	0	12
Viburnum lentago L.	Shrub	7.1	0.848	0	0	8	0	12

Sphagnum Bogs (Type II)

Eighty-five species were recorded in the sub-boreal peatland communities classified as *Sphagnum* Bogs (Appendix 2). Sixteen species were identified as significant indicators (Table 5). Various species of the family *Sphagnaceae* L., genus *Sphagnum* L. (referred henceforth to as "*Sphagnum*") occurred with 100% relative frequency with an IV of 66.9 (p = 0.001). *Sphagnum* was also observed in four of the five classified sub-boreal peatland communities, with the exception of *Phalaris* – Dominated Peatlands. Twelve species were identified as significant indicators of *Sphagnum* Bogs (Table 5), three of which with IV's > 50. In addition, nine of the 12 significant indicator species were exclusively observed in *Sphagnum* Bogs (Table 5). Four indicator species, *Chamaedaphne calyculata* var. *angustifolia* (L.) Moench, *Picea mariana* (Miller) BSP. and *Vaccinium angustifolium* Aiton, were represented in multiple strata, while *Larix laricina* (DuRoi) K. Koch was observed in the herbaceous, shrub and tree strata. Eleven of the 83 species identified in *Sphagnum* Bogs were common throughout the 56 study sites; 36 species were classified as rare and 33 species were exclusively recorded in the sub-boreal peatlands classifies as *Sphagnum* Bogs (Appendix 2).

Herbaceous Fens (Type III)

One-hundred three plant species were recorded in the sub-boreal peatlands classified as Herbaceous Fens (Appendix 3). Twelve species, all from the herbaceous stratum, were identified as significant indicators (Table 5). Seven of the 12 significant indicator species were exclusively observed in Herbaceous Fens (Table 5). *Cicuta bulbifera* L. (IV = 81.3 p = 0.001), *Carex lasiocarpa* Ehrh. var. *americana* Fernald (IV =

65.8 *p* = 0.001) and *Lysimachia thrysiflora* L. (IV = 47.8 *p* = 0.003) were the most common significant indicator species, occurring with relative frequencies of 85, 69 and 54%, respectively (Table 5). *C. canadensis* also occurred with high relative frequency (62%), although not identified as a significant indicator of Herbaceous Fens. Locally abundant shrub populations were recorded in six of 13 peatland communities classified as Herbaceous Fens. However, the frequencies of occurrence were significantly less than herbaceous equivalents (Table 5). *S. petiolaris*, *Betula pumila* L. var. *glandulifera* Regel and *Alnus incana* (L.) ssp. *rugosa* (Du Roi) R.T. Clausen were the most common shrub species, all with relative frequencies <40%. Thirteen plant species were common across the 56 study sites, 36 were classified as rare and 33 species were exclusively recorded in peatland communities classified as Herbaceous Fens (Appendix 3).

Forested Fens (Type IV)

One-hundred thirty-three plant species were recorded in the sub-boreal peatland communities classified as Forested Fens (Appendix 4). Twenty-seven species were identified as significant indicators (Table 5), 10 of which were exclusive to Forested Fens. Five significant indicator species, *Acer rubrum* L. var. *rubrum* (IV = 57.1, *p* = 0.001), *Fraxinus nigra* Marsh. (IV = 57.1 *p* = 0.001), *Betula alleghaniensis* Britton var. *alleghaniensis* (IV = 57.1 *p* = 0.001), *Thuja ocidentalis* L. (IV = 49.2 *p* = 0.006) and *Ulmus americana* L. (IV = 32.7 *p* = 0.009), reflected the distinct tree stratum present in Forested Fens. Four of these five indicator species (all except *U. americana*) occurred exclusively in Forested Fen communities (Table 5). The most common significant indicators were *Rubus pubescens* Raf. var. *pubescens* (IV = 70.0 *p* = 0.001), *Maianthemum canadense* Desf. (IV = 58.4 *p* = 0.002) and *Athyrium filix-femina* (L.) Roth ssp. *angustum* (Willd.) R.T. Clausen (IV = 71.4 p = 0.001), all occurring at relative frequencies >70%, with *R. pubescens* var. *pubescens* present in all Forested Fen communities. Seventy-one species were classified as rare, 15 species were common among all study sites and 70 plant species were exclusively recorded in sub-boreal peatland communities classified as Forested Fens (Appendix 4).

Rich/Calcareous Fens (Type V)

One-hundred seventy-five plant species were recorded in the sub-boreal peatland communities classified as Rich/Calcareous Fens (Appendix 5). Eleven species were identified as significant indicators of Rich/Calcareous Fens (Table 5), five of which, *Pycnanthemum virginianum* (L.) Durand and Jackson (IV = 47.1, p = 0.001), *Cirsium muticum* Michaux (IV = 42.1, p = 0.008), *Poa pratensis* L. ssp. *pratensis* (IV = 23.5, p = 0.05), *Calamagrostis stricta* (Timm) Koeler ssp. *stricta* (IV = 23.5, p = 0.039) and *Frangula alnus* Mill. (IV = 23.5, p = 0.049), were exclusively recorded in Rich/Calcareous Fens (Table 5). Two of the 11 significant indicator species, *C. stricta* (IV = 63.4, p = 0.001) and *Eupatorium maculatum* L. (IV = 49.5, p = 0.002), were considered widespread across all 56 study sites and were observed in four of the five classified sub-boreal peatland communities (Table 5). *C. stricta* was the most common species recorded across all 56 study sites, and was also the most commonly recorded species in Rich/Calcareous Fens, occurring at a relative frequency of 94%. Two species from the shrub stratum were also identified as significant indicators, *Salix discolor* Muhl. (IV = 25.3, p = 0.048) and *F. alnus* (IV = 23.5, p = 0.049), occurring at 29 and 24% relative frequencies, respectively. Eighteen of the 175 plant species recorded in Rich/Calcareous Fens were common across all study sites and 92 species were classified as rare. In addition, 90 species were exclusively recorded in the sub-boreal peatland communities classified as Rich/Calcareous Fens (Appendix 5).

Table 6 Correlation coefficients (r), *p*-values and the number of study sites (N) used to calculate Spearman Rank Order correlations between NMS axis 1 and axis 2 ordinal scores and environmental and floristic characteristics. Significance labeled as: *p<0.05, **p<0.01.

		NMS axis 1		NMS axis 2	
Variable	N	r	*P*	r	*P*
pH	53	0.608**	<0.001	0.727**	<0.001
Electrical conductivity	53	0.464**	<0.001	0.619**	<0.001
Total alkalinity	53	0.573**	<0.001	0.692**	<0.001
Available phosphorus	48	0.193	0.19	0.007	0.96
Bulk density	53	0.333*	0.02	0.543**	<0.001
Von Post	51	0.344*	0.014	0.191	0.18
Peat depth	53	0.089	0.53	-0.152	0.28
LOI_{550}	51	-0.279*	0.05	-0.692**	<0.001
LOI_{940}	51	0.720**	<0.001	0.648**	<0.001
Depth to water table	55	0.056	0.68	0.266*	0.05
Herbaceous productivity	56	-0.00082	0.99	0.793**	<0.001
Species richness	56	0.544**	<0.001	-0.163	0.23
Shannon's diversity	56	0.539**	<0.001	-0.163	0.23

Ecological Gradients

The final ordinal arrangement explained a cumulative 64% of the observed structural variation between study sites, with 16% represented by axis 1 and 47% represented by axis 2 (Figure 8). The distribution of peatland communities in ordinal space reflected strong community association with pore-water chemistry, floristic diversity and the productivity of the herbaceous stratum (Figure 8). This was indicated by the strong and significant correlations detected between ordinal scores of study sites and the corresponding floristic and environmental characteristics (Table 6), in addition to the separations observed along axes 1 and 2 (Figure 8). The strongest correlations were between axis 2 and pH ($r^2 = 0.727$, $p < 0.001$) and herbaceous productivity ($r^2 = 0.793$, $p < 0.001$) (Table 6). Community distributions along axis 2 reflected a strong floristic gradient coincident with significant changes in pore-water pH and total alkalinity (Ca^{2+}) (Figure 8). In particular, the greatest separation along axis 2 was observed between the acidic and calcium poor environments of *Sphagnum* Bogs and the more alkaline and calcium rich environments of Rich/Calcareous Fens (Figure 8). Changes in floristic diversity and herbaceous productivity were inversely related along axis 1 (Figure 8), with positive correlations observed for floristic diversity indices and a negative correlation with herbaceous productivity (Table 6).

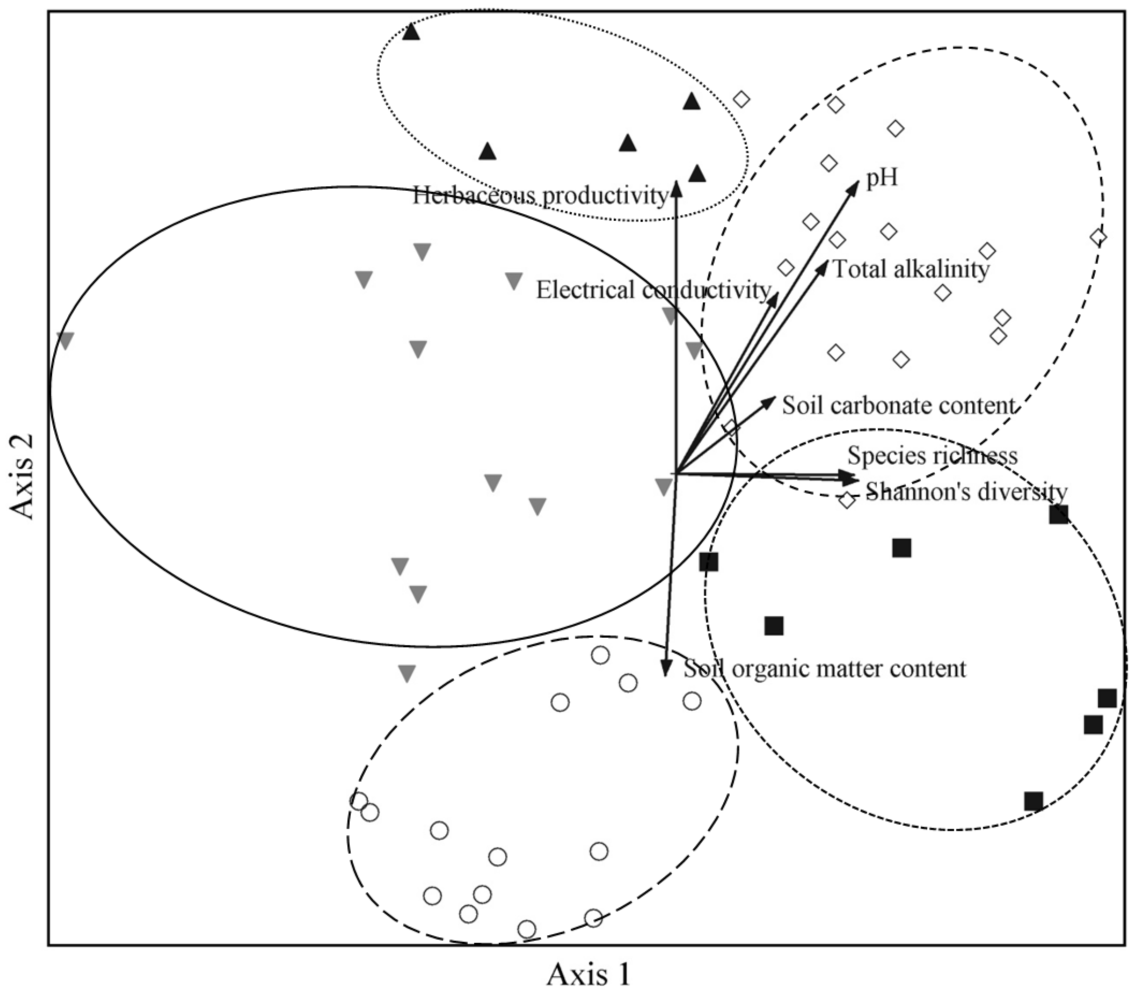

Figure 8 NMS ordination with joint – plot vectors that show the relationship between ordinal scores and measured environmental and community characteristics. The angle and length of joint – plot vectors represent the direction and strength of ecological gradients along which sub-boreal peatlands are structured. Peatland types represent cluster analysis groupings; *Phalaris* – Dominated = ▲, *Sphagnum* Bog = ○, Herbaceous Fen = ▼, Forested Fen = ■, and Rich/Calcareous Fen = ◊. The mean group values were used in place of missing environmental characteristics in order to construct joint plot vectors.

CHAPTER 4

DISCUSSION

The objective of this study was to characterize and describe the variation in floristic and environmental characteristics among sub-boreal peatlands in Minnesota and western Wisconsin. In addition, I set out to provide a classification of sub-boreal peatlands from which resources managers could accurately define, inventory and manage peatland communities in the region. I hypothesized that floristic variation among sub-boreal peatlands would correlate with a strong pH-alkalinity gradient, and sub-boreal peatlands would represent transitional communities, both in terms of floristic composition and environmental characteristics, between the boreal and temperate peatlands of the continental interior of North America.

Five distinct peatland community types were identified using multivariate analysis of 56 study sites located in the sub-boreal region of Minnesota and western Wisconsin. As hypothesized, the variation among sub-boreal peatlands significantly correlated with a strong pH-alkalinity gradient and reflected the commonly describe bog-fen continuum. Differences among the sub-boreal peatland community types were defined by changes in floristic composition and environmental characteristics. These changes also reflected a north to south climactic gradient, with sub-boreal peatlands representing a transitional link between the expansive boreal peatlands (Gorham 1991, Boelter and Verry 1977, Vitt 1994, Zoltai and Vitt 1995, Gorham et al. 2007, Glaser and Janssens 1986) and the isolated temperate peatlands (Carpenter 1995, Thompson 1993, Almendinger and Leete 1998a, Amon et al. 2002, Bedford and Godwin 2003). The results of this study complemented previous work conducted on peatland communities in North America, which had focus primarily on boreal peatlands and more recently temperate peatlands in the Midwest United States, by providing a description of the environmental and floristic characteristics associated with these transitional communities and the associations with their boreal and temperate counterparts. The classification presented can simplify peatland identification and facilitate peatland inventory in a region disproportionately affected by anthropogenic pressures through urban expansion and high population densities (Hibbs 2000). In addition, results indicated that sub-boreal peatlands are susceptible to invasion and dominance by the invasive grass, *Phalaris arundinacea*, which was found to substantially decrease floristic diversity. Changes in wetland structure, function and floristic composition have been attributed to *P. arundinacea* establishment throughout the Midwest United States (Galatowitsch et al. 1999), and this study highlighted the potential of *P. arundinacea* to affect the regional diversity of sub-boreal peatlands.

Peatland Classification

Floristic classification of sub-boreal peatlands revealed five distinct community types. The observed variations among sub-boreal peatlands reflected the commonly described bog-fen continuum, with *Sphagnum* Bogs and Rich/Calcareous Fens representing end-point communities along the continuum. Differences in environmental characteristics, particularly pore-water pH, total alkalinity, EC (Table 2) and soil carbonate content (Table 3), among the classified community types supported the floristic-based classification; and as hypothesized, variations among sub-boreal peatlands correlated with a strong pH-alkalinity gradient. Community transitions along a pH-alkalinity gradient are common among boreal peatlands in North America, and classifications frequently use pore-water chemistry to define transitions between peatland community types (Warner and Rubec 1997, Zoltai and Vitt 1995, Gorham and Janssens 1992, Glaser et al. 1990).

Other classifications of wetland communities in this region identify between nine (Eggers and Reed 1997) and 26 (MNDNR 2003a) different classes of native peatland communities based on differences in vegetation community structure and local environmental conditions. The results of this study, however, indicated that the floristic compositions and local environmental conditions among sub-boreal peatland communities did not vary within each community type such that greater divisions were necessary. One explanation for the reduced number of peatland community types identified is that the previous classifications included non-peat accumulating communities, which increased the floristic variation on which the classifications were based. As such, some vegetation communities, identified as peatlands, also were found to occur on mineral soils (Eggers and Reed 1997, MNDNR 2003a). In addition, the study area, although large, was limited to the sub-boreal region of Minnesota and western Wisconsin, which may have excluded other peatland communities found outside the study area. Nonetheless, broad variation was observed among the classified sub-boreal peatland community types, which was indicative of the large geographic extent of the study area and the dynamic nature of the glaciated landscape.

The majority of peatlands surveyed in this study were distributed near the border between two major Ecological Provenances (ECOMAP 1993) in the region, the

Laurentian Mixed Forest and the Eastern Broadleaf Forest (Figure 3). The Eastern Broadleaf Forest Provenance constitutes an area in which precipitation roughly equals evapotranspiration (Wright 1972), and is as an ecotone between the semiarid prairie and the semi-humid mixed deciduous-coniferous forested ecosystems in the region (Albert 1995). Similarly, this transitional nature was observed in the floristic and environmental characteristics of peatland communities surveyed in this study, as well as their spatial distribution in the region. In particular, the distribution of peatlands classified as *Sphagnum* Bogs was concentrated in the northern portion of the study domain. Similar peatland communities are common throughout northern Minnesota (Boelter and Verry 1977, Glaser 1987). In contrast, the peatland communities classified as Rich/Calcareous Fens were primarily distributed in the southern portion of the study domain, and were floristically and environmentally similar to the temperate peatlands of the continental interior of North America (Amon et al. 2002).

Environmental Characteristics

The range of variation observed in environmental characteristics (Table 2, Table 3 and Figure 6) indicated substantial differences among sub-boreal peatlands in the source and the chemical composition of hydrologic inputs. Previous studies have shown that a change in the source or chemical composition of hydrologic inputs is the primary factor that governs transitions between peatland community types (Moore and Bellamy 1974, Bridgham et al. 1996, Warner and Rubec 1997, Zoltai and Vitt 1995). In this study, no attempt was made to quantify hydrologic inputs; however, changes in pore-water chemistry are commonly used to infer changes in the chemical composition and relative source of hydrologic inputs (Sjörs 1950, Glaser 1987, Glaser et al. 1990).

This study showed that differences in mean pore-water chemistry (pH, total alkalinity and EC) were the primary environmental characteristics found to distinguish the different sub-boreal peatland community types (Table 2). Specifically, mean levels of pore-water pH, total alkalinity and EC exhibited an increasing trend from *Sphagnum* Bogs to Rich/Calcareous Fens (Table 2). The parallel relationship between changes in pore-water chemistry and transitions between peatland community types has been observed in boreal peatland communities throughout Europe (Du Rietz 1949 and Du Rietz 1954 [as cited in Bridgham et al. 1996], Sjörs 1961, Moore and Bellamy 1974, Sjörs 1950, Wheeler and Proctor 2000) and North America (Warner and Rubec 1997, Zoltai and Vitt 1995, Gorham and Janssens 1992); however, the point at which a transition is observed is often dependent on regionally specific environmental factors and floristic compositions of the peatland communities (Bridgham et al. 1996).

Sphagnum Bogs were distinguished from other sub-boreal peatland community types by a mean pore-water pH of 4.4 and mean total alkalinity of 17mg/l. In comparison however, the mean level of total alkalinity in *Sphagnum* Bogs was considerably higher than the level of <2mg/l reported for boreal bogs of northern Minnesota (Heinselman 1963, Glaser 1987, Glaser et al. 1990). The higher levels of mean total alkalinity, combined with a mean pH >4.2, indicated that *Sphagnum* Bogs were more similar, in terms of pore-water chemistry, to semi-ombrogenous or weakly minerotrophic peatlands of the boreal region (Heinselman 1963). Herbaceous Fens were weakly acidic peatlands, with pH a mean pH of 5.5 and mean total alkalinity of 42mg/l. As such, Herbaceous Fens were most similar to *Sphagnum* Bogs, in terms of environmental characteristics, than the other classified sub-boreal community types. The higher levels of total alkalinity and pore-water pH indicated that Herbaceous Fens received considerably greater hydrologic inputs from minerogenous water sources than *Sphagnum* Bogs, and represent the most acidic and ionic poor of fen peatlands in the sub-boreal region. *Phalaris* – Dominated Peatlands and Rich/Calcareous Fens were the most ion-rich of the classified sub-boreal peatland communities, with mean levels of total alkalinity >190mg/l (Table 2), which are consistent with those reported in calcareous fens of the Minnesota River Valley (Almendinger and Leete 1998b) and the temperate fens of the Midwest United States (Amon et al. 2002). Temperate fens are distinguished from their boreal counterparts by a direct dependence on sustained hydrologic inputs from groundwater discharge to facilitate organic matter accumulation (Bedford and Godwin 2003), and as a result, pore-water pH generally exceeds 7.0 with total alkalinity levels that range between 50 and 292mg/l (Amon et al. 2002). In the boreal region of Minnesota, extremely rich fens are defined by pH values >7.0 and total alkalinity levels >30 mg/l (Glaser 1987). All sub-boreal peatland communities, with the exception of *Sphagnum* bogs, exceeded total alkalinity levels of 30 mg/l. This may indicate that Herbaceous Fens and Forested Fens receive a greater proportion of hydrologic inputs from minerogenous water sources that originate from calcareous substrates (Vitt and Chee 1990, Glaser et al. 1990), which are common throughout central and southern Minnesota (Wright 1972), but considerably less than the high amounts observed in Rich/Calcareous Fens. Mean pore-water chemistries of Forested Fens were intermediate, but still exceeded the levels of extremely rich boreal fens. Although not analyzed, inputs of dissolved iron as iron ochre were recorded in many of the Forested Fen communities, which may have contributed to the elevated pore-water EC levels recorded while total alkalinity remained slightly above that observed in Herbaceous Fens (Table2).

Other environmental characteristics, including pore-water EC (Table 2), soil carbonate content and soil organic matter content (Table 3), were observed to co-vary with pore-water pH and total alkalinity (Table 2) and could be used to distinguish sub-boreal peatland community types. Water table depth (Figure 6) and available phosphorus (Table 2), although significantly different among peatland community types, were less useful in the classification of sub-boreal peatland communities due to variation among community types. However, mean water-table depths (Figure 6) provided an indication of water-table stability in sub-boreal peatlands, which have elsewhere been shown to be an important gradient along which peatlands are structured (Laitinen et al. 2008) Herbaceous Fens, Rich/Calcareous Fens and *Phalaris* – Dominated Peatlands exhibited the highest hydrologic stability among sub-boreal peatlands (Figure 6), with mean water-table depths of 4.5cm ± 4.7 in Herbaceous Fens, -3cm ± 5.0 in Rich/Calcareous Fens and 4.0cm ± 5.0 in *Phalaris* – Dominated Peatlands. In contrast, *Sphagnum* Bogs exhibited the greatest variation in mean water-table depth (-18cm ± 10.2). Variation in mean water-table depth was observed to decrease as climactic pressures increased from north to south. Peatlands in the southern portion of the study area experience an increased dependence on groundwater discharge to sustain organic matter accumulation. The low variation in water-table depths among Herbaceous Fens, Rich/Calcareous Fens and *Phalaris* – Dominated Peatlands was indicative of the stable hydrologic settings in which they occurred and constant hydrologic inputs from groundwater discharge, which supported the premise that the majority of sub-boreal peatlands were fen-classified communities. In contrast, inter-annual and intra-annual changes in water table depths are common in boreal peatland communities, with 1–2m drawdowns observed in the water tables of precipitation-dominated peatlands during periods of prolonged draught (Glaser et al. 1997). This suggested that *Sphagnum* Bogs in the sub-boreal region of Minnesota and western Wisconsin were, primarily, precipitation dominated peatlands, with only limited amounts of external hydrologic inputs.

Inter-annual and intra-annual variations in nutrient levels, particularly nitrogen and phosphorus, have been shown to occur in peatland communities and are not useful in the classification of peatland communities (Vitt et al. 1995b). Most surprisingly however, were the low levels of available phosphorus (0.9mg/l ± 0.2) observed in the *Phalaris* – Dominated sub-boreal Peatlands. *P. arundinacea* is an invasive grass species that is commonly associated with wetlands disturbed by nutrient enrichment and sediment deposition from agriculture (Green and Galatowitsch 2001, Green and Galatowitsch 2002, Werner and Zedler 2002). However, in this study none of the sub-boreal peatlands classified as *Phalaris* – Dominated were situated in agricultural landscapes. The low level of available phosphorus was more likely the result of bi-carbonates and phosphate complexes that immobilize phosphorus in areas associated with elevated bi-carbonate levels (Boyer and Wheeler 1989). In fact, three of the five *Phalaris* – Dominated sites were in located in the same peatland complexes as other communities classified as Rich/Calcareous Fens, with pH levels >7.0, total alkalinities >300mg/l and soil carbonate contents >3.0% of dry weight.

Floristic and Community Characteristics

Floristic differences among sub-boreal peatlands also reflected a strong pH-alkalinity gradient. In particular, changes in the relative frequencies of *Sphagnacea* and *Amblystegiacea* (Table 5) conformed to the bimodal distributions between *Sphagnacea* at low pH and *Amblystegiacea* at higher pH levels observed in boreal peatland communities (Gorham and Janssens 1992, Vitt et al. 1995a). The decrease in the relative frequency of *Sphagnum* with increasing pore-water pH also corresponded with the absence of calcium-tolerant *Sphagnum* species in extremely rich fen communities in central Europe (Hájek et al. 2006), with only one occurrence of *Sphagnum* recorded in the 17 study sites classified as Rich/Calcareous Fens. In contrast, the relative frequency of *Amblystegiaceae* species peaked in the Forested Fen communities at 57% (Table 5), with no occurrences recorded in *Sphagnum* Bogs. Other species, such as *Alnus incana* ssp. *rugosa* (Du Roi) Clausen, *C. stricta*, *C. lasiocarpa*, *Cladium mariscoides* (Muhl.) Torr, *Clintonia borealis* (Aiton) Raf., *Dasiphora fruticosa* (L.) Rydb. ssp. *floribunda* (Pursh) Kartesz, *Elocharis compressa* Sull, *Muhlenbergia glomerata* (Willd.) Trin. and *T. occidentalis*, among others, have been shown elsewhere to be minerotrophic indicator species (Jeglum 1991, Glaser et al. 1990 and Amon et al. 2002), and were all recorded with greater frequencies in fen-classified sub-boreal peatlands (Table 5).

Floristic variations among sub-boreal peatlands were defined, primarily, by significant indicator species, identified by indicator species analysis (Dufrêne and Legendre 1997). Many of which were exclusively found in a particular peatland community type (Table 5). Indicator plant species have traditionally been used in the classification of peatlands to define transitions between different floristic communities along environmental gradients (Locky et al. 2005, Zoltai and Vitt 1995, Glaser et al. 1990, MNDNR 2003a, Gorham and Janssens 1992). Similarly, indicator species identified in this study were associated with distinct environmental conditions. Unlike most studies, many of the indicator species identified were also found to be dominant species, and represented the prevailing vegetation stratum from which sub-boreal peatlands were defined.

Sphagnum Bogs were characterized by high relative frequencies of *Sphagnum* and other indicator species of nutrient poor and acidic environments associated with limited mineral-rich hydrologic inputs (e.g., *Picea mariana*, *Chamaedaphne calyculata* var. *angustifolia*, *Vaccinium oxycoccos* and *Carex oligosperma*). However, a number of species commonly regarded as minerotrophic or “fen” indicators (*Carex trisperma* Dewey var. *trisperma*, *Cladium mariscoides* (Muhl.) Torr., *Drosera rotundifolia* L. var. *rotundifolia* and *Rhamnus alnifolia* L'Hér) (Glaser et al. 1990) were observed in *Sphagnum* Bogs. Variation among *Sphagnum* Bogs reflected the presence or absence of a tree stratum. Tree canopies in *Sphagnum* Bogs were not as dense as those observed in Forested Fens, and were composed of solely of *P. negra* and *L. laricina*. Other classifications have characterized these communities as Open or Forested Bogs (Eggers and Reed 1997) and as acidic peatlands, with distinctions made between changes in the dominant floristic composition (e.g. Northern Open bog, Poor Tamarack – Black Spruce Swamp, Northern Spruce bog and Northern Poor Fen) (MNDNR 2003b). Regardless of how these communities are classified, all reflect the nutrient poor and acidic conditions associated with *Sphagnum* dominance, with a distinction between forested and open communities. This distinction was also observed among the sub-boreal Sphagnum Bogs;

however, the limited variation observed in this study did not support separate distinctions between the two communities.

Herbaceous Fens are common throughout the region, and as observed in ordinal analysis, span a large ecological distance (Figure 5). Significant indicator species characteristic of Herbaceous Fens primarily represented similarities in the herbaceous strata (Table 5), and were a reflection of stable hydrologic conditions with a positive mean water table (Figure 6). In the boreal region of northern Minnesota, these communities often occur as transitional communities between bogs and more nutrient-rich fen communities (Heinselman 1963). Isolated occurrences of *Sphagnum* Bogs were observed within larger complexes of Herbaceous Fen communities, which may indicate succession to *Sphagnum*-dominated peatlands in areas where inputs of precipitation offset climactic pressures. Variation within Herbaceous Fens also reflected an increase in the frequency of woody species, primarily *Alnus incana* ssp. *rugosa* and *Salix petiolaris*. In addition, other shrub-stratum species frequently observed included *Cornus sericea* L. ssp. *pallens* (Banks ex Ging), *S. discolor*, *Cornus racemosa* Lam., *Spirea tomentosa* L. var. *rosea*, *Betula pumila* L. var *glandulifera* Regel, and *Ribes americanum* Mill. (Appendix 3). Shrub-dominated peatlands are common throughout Minnesota and Wisconsin (Eggers and Reed 1997), and the lack of a distinct shrub-dominated peatland community type may indicate that this community type was not adequately sampled. Herbaceous species most frequently observed with greater shrub coverage were *Spirea alba*, *Triadenum fraseri* and *Carex utriculata*. Whereas higher frequencies of *Bidens aristosa* and *Carex lasiocarpa* var. *americana* were characteristic of the mostly herbaceous dominated communities of Herbaceous Fens. Increased hydrologic inputs, as evidenced by higher water tables, also were observed to alter the community composition of Herbaceous Fens, which resulted in a more marsh-like community structure with higher relative frequencies of *Lemna minor*, *Lythrum salicaria*, *Carex stipata* var. *stipata*, *Lysimachia thyrsiflora*, *Typha angustifolia* and *Sagittaria latifolia*. Although hydrologic alterations are common throughout Minnesota, the effect of elevated water tables was most evident in the Anoka Sand Plain, where hydrologic manipulations have converted extensive areas once dominated by *C. lasiocarpa* var. *americana* to marshes dominated by the invasive cattail species, *Typha angustifolia* (Rand 1953).

Forested Fens were characterized, primarily, by the presence of a dense tree stratum (Table 5). Forested peatlands of this type are predominantly found in the northern portions of the sub-boreal region (Eggers and Reed 1997), and have been classified as Wooded Swamps (Eggers and Reed 1997), and Forested Rich Peatlands (MNDNR 2003b, 2005a). In the boreal region of North America, similar communities are common and represent extremely-rich forested peatlands communities (Zoltai and Vitt 1995). In addition, these communities are known to occur, although infrequently, in the temperate region of the Midwest United States (Bedford and Godwin 2003). The indicator species that differentiated Forested Fens from other sub-boreal peatland communities were *Athyrium filix-femina* (L.) Roth ssp. *angustum* (Willd.) R.T. Clausen, *Rubus pubescens* Raf. var. *pubescens, Acer rubrum* L. var. *rubrum, Betula alleghaniensis* Britton var. *alleghaniensis, Fraxinus nigra* Marsh., *Maianthemum canadense* Desf., *Thuja occidentalis* L. and *Amblystegiaceae*. In addition to the high diversity observed within Forested Fens, considerable floristic variation was observed between forested sites with *Thuja occidentalis* and *Betula alleghaniensis* var. *alleghaniensis* as dominants, and sites primarily composed of *Ulmus americana*, *Acer rubrum* var. *rubrum, Fraxinus nigra* and *Larix laricina*. This distinction conforms to the classification of Eggers and Reed (1997), which differentiates coniferous from hardwood swamps. As indicated for *Sphagnum* Bogs, however, the variation among sub-boreal peatland communities was greater than that observed within Forested Fen communities. Therefore, no distinction was made between the different Forested Fen communities in this study.

The dominant composition and floristic structure of Rich/Calcareous Fens were differentiated from other sub-boreal peatland communities, primarily, by the presence of species adapted to high ionic concentrations, particularly bi-carbonates. Indicator species of high ionic concentrations identified in this study, which also are identified as indicators of Prairie Rich Fens and Prairie Extremely Rich Fens (MNDNR 2005b), included *Eupatorium maculatum* L., *Pyncanthemem virginian*, *Cirsium muticum* Michx. *Helianthus grosseserratus* M. Martens and *Calamagrotis stricta* (Timm) Koeler ssp. *stricta*. Other species not identified as indicator species, but are known to occur in calcareous or extremely rich fen communities, included *Lycopus americamis* Muhl. Ex W. Bartam, *Galium boreale* L., *Doellingeria umbellate* (Mill.) Nees and *Oxypolis rigidor* L. Raf. In addition, Rich/Calcareous Fens were found to support the highest number of endangered, threatened and species of special concern of all sub-boreal peatland communities. This may have been due to a combination of high ionic concentrations and limited habitat availability. Species recorded in Rich/Calcareous Fens, and are regarded as threatened in Minnesota, included *Carex sterilis* Willd., *Valeriana edulis* Nutt. Ex. Torr. & A. Gray var. *ciliate* (Torr. & A. Gray) Cronquest, *Cladium mariscoides* (Muhl.) Torr. and *Rhynchospora capillacea* Torr. Species of concern in Minnesota included

Lysimachia quadriflora Sims and *Rudbeckia triloba* L. var. *triloba*. One species recorded in Rich/Calcareous Fens, *Muhlenbergia richardsonis* (Trin.) Rydb, is listed as endangered in Wisconsin. In addition to being highly diverse ecosystems, Rich/Calcareous Fens exhibited considerable species turnover (Table 4). As such, none of the 13 significant indicator species identified were present in all Rich/Calcareous Fen communities (Table 5). *Carex stricta* was the most common species with 94 percent relative frequency, but its' occurrence was not limited to Rich/Calcareous Fen communities (Table 5). Floristic variation between Rich/Calcareous Fens illustrated the distinctions between rich and calcareous fens; however, as previously mentioned, the variation among sub-boreal community types was greater than the variation within the Rich/Calcareous Fen subtype. Similar to Herbaceous Fens, structural variations were observed within the Rich/Calcareous Fen communities. Shrub-stratum species are also common in highly calcareous peatlands in the region (MNDNR 2005b, Eggers and Reed 1997, Bedford and Godwin 2003), as was observed in this study (Appendix 5). Although primarily dominated by herbaceous-stratum species, a distinct shrub stratum, consisting of *S. discolor*, *F. alnus* and *Rhamnus cathartica* L., was frequently recorded in Rich/Calcareous Fen communities.

Phalaris – Dominated Peatlands reflect an ecological consequence of the presence of the invasive species, *P. anrundinacea*. *Phalaris anrundinacea* was found to occur across broad ranges of pH (5.17 – 7.83), total alkalinity (15 – 350mgl^{-1} [Ca^{2+}]) and water table depths (-53cm – +22cm), suggesting a wide physiological tolerance. Interpretation of the NMS ordination also indicated a successional trend associated with *P. anrundinacea* establishment and dominance (Figure 5). This most prominently affected

Rich/Calcareous Fens, from which, four significant indicator species were observed to occur in *Phalaris* – Dominated Peatlands (Table 5). The low species diversity and exclusion of native species, as observed in *Phalaris* – Dominated Peatlands (Table 4), has been observed in wetland communities throughout the Midwest United States due to aggressive nature of *P. arundinacea* and clonal expansion (Kercher et al. 2004, Kercher and Zedler 2004, Galatowitsch et al. 1999). Surprisingly, *Eupatorium maculartum* L. was observed at 60% relative frequency in *Phalaris* – Dominated Peatlands; whereas Kercher et al. (2004) observed competitive exclusion of this species due to shading in wet meadows in Wisconsin. It is difficult to determine the exact number of species excluded in *Phalaris* – Dominated Peatlands; however, since *Phalaris* – Dominated Peatlands are most similar to Rich/Calcareous Fens, in terms of environmental characteristics and floristic composition, the effect on species and peatland diversity are most likely significant.

Sub-boreal peatlands represent a floristically diverse set of communities, as indicated by the 341 species recorded. The high floristic diversity among sub-boreal peatlands was indicative of a transitional landscape, and supported the hypothesis that sub-boreal peatlands represent transitional communities between boreal and temperate peatlands. Transitional landscapes tend to support greater species diversity than either of the adjacent regions due to the overlapping distributions of regionally specific flora (Shmida and Wilson 1985). Peatlands in the boreal region of the continental interior of North America are floristically impoverished communities, particularly raised bogs, in which most communities support less than 20 vascular species (Glaser 1992). In the Red Lake peatlands of boreal Minnesota, which cover an estimated area of 1200 km^2, < 200 vascular species were recorded across seven major vegetation communities types (Wheeler et al. 1983). In contrast, temperate peatlands, which are considered distinctly different that their boreal counterparts, both in terms of environmental characteristics and floristic composition (Bridgham et al. 1996, Amon et al. 2002), are renowned for their high floristic diversity (Bedford and Godwin 2003), despite their geographic isolation and limited extent. The high beta diversity recorded among sub-boreal peatlands (Table 4) also supported the hypothesis that sub-boreal peatlands represent transitional communities between boreal and temperate peatlands. In this study, the strong pH-alkalinity gradient accounted for much of the species turnover observed among peatland communities, with changes in floristic diversity and composition strongly correlated (Table 6) with ordinal distribution of study sites (Figure 8). The increasing climactic pressures from north to south, however, cannot be overlooked as a major determinate in the distribution, composition and floristic structure of sub-boreal peatlands.

The results of this study complimented work previously done on peatland communities in North America by providing a description of the variation in floristic and environmental characteristics associated with peatlands that represent transitional communities between peatlands in the boreal and temperate regions of the continental interior of North America. In addition, this study highlighted the potential threat of *P. arundincacea* to the biodiversity of sub-boreal peatlands. Future research should continue to focus on the invasive mechanisms of *P. arundinacea* and its' impact on the floristic composition and structure of native peatland communities. Application of the purposed classification is most applicable to the northern portion of the sub-boreal region, where anthropogenic influences have not drastically altered the structure and ecological functions of peatland communities. To validate and further expand the application of the purposed classification into greater Wisconsin, Michigan and the Upper Peninsula of Michigan, floristic and environmental data should be collected from study sites that reflect the variation associated with the east-west precipitation gradient in the region. In addition, future research should attempt to quantify the contribution of microtopography to the floristic and environmental variation among sub-boreal peatland community types.

Appendix 1 Relative frequencies, total occurrence (TO), indicator values (IV) and *P*-values of the 23 plant species observed in *Phalaris* –Dominated Peatlands. Bold **species** were identified as significant indicators ($p \leq 0.05$) (Dufrene and Legendre 1997) of one of the five classified peatland community types, with the corresponding community types identified by bold **relative frequencies**. Species are sorted by decreasing relative frequency.

					% Relative Frequency				
Species	Strata	T.O.	IV	*P*-value	Phalaris Dominated	Sphagnum Bogs	Herbaceous Fens	Forested Fens	Rich/Calcareous Fens
***Phalaris arundinacea* L.**	Herb.	14	**76.7**	**0.001**	**100**	0	15	14	35
***Carex lacustris* Willd.**	Herb.	10	**48.1**	**0.005**	**80**	7	8	14	18
***Calamagrostis canadensis* (Michx.) P. Beauv.**	Herb.	25	**32.7**	**0.041**	**80**	36	62	29	35
***Eupatorium maculatum* L.**	Herb.	21	**49.5**	**0.002**	60	0	15	14	**88**
Carex pellita Muhl. ex Willd.	Herb.	2	-	-	40	0	0	0	0
***Polygonum sagittatum* L.**	Herb.	8	**25.6**	**0.046**	40	0	**46**	0	0
Carex L.	Herb.	8	20.3	0.123	40	0	8	43	12
Typha latifolia L.	Herb.	9	16.3	0.231	40	0	23	0	24
Scirpus cyperinus (L.) Kunth	Herb.	8	15.3	0.255	40	21	15	0	6
Polygonum persicaria L.	Herb.	1	-	-	20	0	0	0	0
Roripa palustris (L.) Besser	Herb.	1	-	-	20	0	0	0	0
Salix planifolia Pursh	Shrub	2	-	-	20	0	8	0	0
Symphyotrichum lanceolatum (Willd.) G.L. Nesom	Herb.	2	-	-	20	0	0	0	6
***Carex stricta* Lam.**	Herb.	24	**63.4**	**0.001**	20	7	46	0	**94**
***Solidago gigantea* Aiton**	Herb.	15	**54.2**	**0.004**	20	0	0	14	**76**
***Viola cucullata* Aiton**	Herb.	6	**31.3**	**0.018**	20	0	0	**43**	12
***Helianthus grosseserratus* M. Martens**	Herb.	7	**28**	**0.034**	20	0	0	0	**35**
***Viola* L.**	Herb.	7	**25.8**	**0.037**	20	0	15	**43**	6
Salix petiolaris Sm.	Shrub	7	18.9	0.14	20	0	38	0	6
Equisetum arvense L.	Herb.	6	16.9	0.169	20	0	0	29	18
Galium tinctorium (L.) Scop.	Herb.	4	14.1	0.218	20	0	8	14	6
Phragmites australis (Cav.) Trin. ex Steud.	Herb.	3	11.9	0.223	20	0	8	0	6
Eupatorium perfoliatum L. var. *perfoliatum*	Herb.	7	11.5	0.432	20	0	15	0	24

Appendix 2 Relative frequencies, total occurrence (TO), indicator values (IV) and *P*-values of the 83 plant species observed in sub-boreal peatlands classified as *Sphagnum* Bogs. Bold **species** were identified as significant indicators ($p \leq 0.05$) (Dufrene and Legendre 1997) for one of the five classified peatland community types, with the corresponding community types identified by bold **relative frequencies**. Species are sorted by decreasing relative frequency.

					% Relative Frequency				
Species	Strata	T.O.	IV	*P*-value	Phalaris Dominated	Sphagnum Bogs	Herbaceous Fens	Forested Fens	Rich/Calcareous Fens
***Sphagnaceae* L.**	Bryo.	23	**66.9**	**0.001**	0	**100**	46	29	6
Chamaedaphne calyculata* (L.) Moench var. *angustifolia	Shrub	9	**64.3**	**0.001**	0	**64**	0	0	0
***Carex oligosperma* Michx.**	Herb.	9	**47**	**0.002**	0	**57**	8	0	0
***Larix laricina* (Du Roi) K. Koch**	Can.	11	**38.9**	**0.006**	0	**57**	0	29	6
***Picea mariana* (Mill.) BSP**	Shrub	7	**50**	**0.002**	0	**50**	0	0	0
***Vaccinium oxycoccos* L.**	Herb.	7	**50**	**0.002**	0	**50**	0	0	0
***Ledum groenlandicum* Oeder**	Shrub	6	**42.9**	**0.004**	0	**43**	0	0	0
***Picea mariana* (Mill.) BSP**	Can.	7	**32.8**	**0.013**	0	**43**	0	14	0
Carex trisperma* Dewey var. *trisperma	Herb.	7	**32.8**	**0.014**	0	**43**	0	14	0
***Betula pumila* L. var. *glandulifera* Regel**	Shrub	12	21.3	0.13	0	43	23	14	12
***Polytrichaceae* Hedw.**	Bryo.	5	**35.7**	**0.007**	0	**36**	0	0	0
***Eriophorum virginicum* L.**	Herb.	5	**35.7**	**0.008**	0	**36**	0	0	0
***Maianthemum trifolium* (L.) Sloboda**	Herb.	6	**33.6**	**0.011**	0	**36**	0	0	6
***Calamagrostis canadensis* (Michx.) P. Beauv.**	Herb.	25	**32.7**	**0.041**	**80**	36	62	29	35
***Carex magellanica* Lam. ssp. *irrigua* (Wahlenb.) Hultén**	Herb.	4	**28.6**	**0.029**	0	**29**	0	0	0
Sarracenia purpurea* L. ssp. *purpurea	Herb.	4	**28.6**	**0.029**	0	**29**	0	0	0
***Vaccinium angustifolium* Aiton**	Shrub	4	**28.6**	**0.034**	0	**29**	0	0	0
***Larix laricina* (Du Roi) K. Koch**	Shrub	5	**25.9**	**0.032**	0	**29**	0	0	6
Trientalis borealis* Raf. ssp. *borealis	Herb.	6	**28.6**	**0.024**	0	21	0	**43**	0
***Dryopteris carthusiana* (Vill.) H.P. Fuchs**	Herb.	7	**26.2**	**0.036**	0	21	0	**43**	6
Thelypteris palustris Schott var. *pubescens* (G. Lawson) Fernald	Herb.	20	22.5	0.182	0	21	62	29	41
Lycopus uniflorus Michx.	Herb.	18	21.7	0.206	0	21	54	57	24
Kalmia polifolia Wangenh.	Shrub	3	21.4	0.056	0	21	0	0	0

Appendix 2. Continued.

Species	Strata	T.O.	IV	*P*-value	% Relative Frequency: Phalaris Dominated	Sphagnum Bogs	Herbaceous Fens	Forested Fens	Rich/Calcareous Fens
Vaccinium angustifolium Aiton	Herb.	3	21.4	0.07	0	21	0	0	0
Larix laricina (Du Roi) K. Koch	Herb.	3	21.4	0.078	0	21	0	0	0
Dryopteris cristata (L.) A. Gray	Herb.	9	20.4	0.128	0	21	23	43	0
Chamaedaphne calyculata (L.) Moench var. *angustifolia*	Herb.	4	18.6	0.088	0	21	8	0	0
Scirpus cyperinus (L.) Kunth	Herb.	8	15.3	0.255	40	21	15	0	6
Spiraea tomentosa L. var. *rosea*	Shrub	4	12.5	0.256	0	21	8	0	0
Betula papyrifera Marsh. var. *papyrifera*	Shrub	6	9.9	0.575	0	21	0	14	12
Andromeda polifolia L. var. *glaucophylla* (Link) DC.	Herb.	2	-	-	0	14	0	0	0
Andromeda polifolia L. var. *glaucophylla* (Link) DC.	Shrub	2	-	-	0	14	0	0	0
Eriophorum vaginatum L. var. spissum (Fernald) B. Boivin	Herb.	2	-	-	0	14	0	0	0
*Menyanthes trifo*liata L.	Herb.	2	-	-	0	14	0	0	0
Picea mariana (Mill.) BSP	Herb.	2	-	-	0	14	0	0	0
Acer rubrum* L. var. *rubrum	Shrub	7	**45.2**	**0.004**	0	14	0	**57**	6
***Onoclea sensibilis* L.**	Herb.	13	**28.8**	**0.045**	0	14	46	**57**	6
Cornus sericea L. ssp. *sericea*	Shrub	17	28.3	0.058	0	14	8	57	59
Rubus idaeus L. ssp. *strigosus* (Michx.) Focke	Herb.	11	21.5	0.098	0	14	8	43	29
Drosera rotundifolia L. var. *rotundifolia*	Herb.	3	9.3	0.507	0	14	8	0	0
Quercus rubra L.	Herb.	3	8.2	0.668	0	14	0	14	0
Dulichium arundinaceum (L.) Britton	Herb.	4	7.9	0.603	0	14	15	0	0
Abies balsamea (L.) Mill.	Herb.	1	-	-	0	7	0	0	0
Acer rubrum L. var. *rubrum*	Herb.	2	-	-	0	7	0	14	0
Agrostis scabra Willd.	Herb.	1	-	-	0	7	0	0	0
Betula pumila L. var. *glandulifera* Regel	Can.	2	-	-	0	7	0	0	6
Betula pumila L. var. *glandulifera* Regel	Herb.	2	-	-	0	7	8	0	0
Carex pauciflora Lightf.	Herb.	1	-	-	0	7	0	0	0

Appendix 2. Continued.

Species	Strata	T.O.	IV	*P*-value	% Relative Frequency: Phalaris Dominated	Sphagnum Bogs	Herbaceous Fens	Forested Fens	Rich/Calcareous Fens
Carex rostrata Stokes	Herb.	1	-	-	0	7	0	0	0
Cypripedium acaule Aiton	Herb.	1	-	-	0	7	0	0	0
Gaultheria hispidula (L.) Muhl. ex Bigelow	Herb.	1	-	-	0	7	0	0	0
Glyceria canadensis (Michx.) Trin.	Herb.	2	-	-	0	7	8	0	0
Iris L.	Herb.	1	-	-	0	7	0	0	0
Kalmia polifolia Wangenh.	Herb.	1	-	-	0	7	0	0	0
Ledum groenlandicum Oeder	Herb.	1	-	-	0	7	0	0	0
Nemopanthus mucronatus (L.) Loes.	Shrub	1	-	-	0	7	0	0	0
Osmunda claytoniana L.	Herb.	2	-	-	0	7	0	14	0
Osmunda regalis L var. *spectabilis* (Willd.) A. Gray	Herb.	2	-	-	0	7	0	14	0
Quercus macrocarpa Michx.	Herb.	1	-	-	0	7	0	0	0
Quercus rubra L.	Shrub	2	-	-	0	7	0	14	0
Rhamnus alnifolia L'Hér.	Shrub	1	-	-	0	7	0	0	0
Rubus arcticus (L.) ssp. *acaulis* (Michx.) Focke	Herb.	1	-	-	0	7	0	0	0
Rubus L.	Herb.	2	-	-	0	7	8	0	0
Salix pedicellaris Pursh	Shrub	2	-	-	0	7	8	0	0
Salix pyrifolia Anderson	Can.	1	-	-	0	7	0	0	0
Salix pyrifolia Anderson	Shrub	1	-	-	0	7	0	0	0
Spiraea alba Du Roi	Shrub	2	-	-	0	7	0	14	0
Toxicodendron vernix (L.) Kuntze	Shrub	2	-	-	0	7	0	0	6
Vaccinium macrocarpon Aiton	Herb.	1	-	-	0	7	0	0	0
Vaccinium myrtilloides Michx.	Shrub	1	-	-	0	7	0	0	0
***Carex lasiocarpa* Ehrh. var. *americana* Fernald**	Herb.	11	**65.8**	**0.001**	0	7	**69**	0	6
***Carex stricta* Lam.**	Herb.	24	**63.4**	**0.001**	20	7	46	0	**94**
***Maianthemum canadense* Desf.**	Herb.	6	**58.4**	**0.002**	0	7	0	**71**	0

Appendix 2. Continued.

					% Relative Frequency				
Species	Strata	T.O.	IV	*P*-value	Phalaris Dominated	Sphagnum Bogs	Herbaceous Fens	Forested Fens	Rich/Calcareous Fens
***Carex lacustris* Willd.**	Herb.	10	**48.1**	**0.005**	**80**	7	8	14	18
***Aralia nudicaulis* L.**	Herb.	6	**46.5**	**0.003**	0	7	0	**57**	6
Osmunda cinnamomea* L. var. *cinnamomea	Herb.	7	**30**	**0.029**	0	7	15	**43**	6
Viola macloskeyi Lloyed ssp. *pallens* (Banks ex Ging) M.S. Baker	Herb.	3	21.4	0.068	0	7	0	29	0
Doellingeria umbellata (Mill.) Nees	Herb.	6	16	0.166	0	7	8	0	24
Alnus incana ssp. *rugosa* (Du Roi) Clausen	Shrub	6	15.2	0.242	0	7	23	29	0
Spiraea tomentosa L. var. *rosea*	Herb.	4	14.3	0.182	0	7	23	0	0
Lysimachia terrestris (L.) BSP	Herb.	3	10.5	0.335	0	7	15	0	0
Salix pyrifolia Anderson	Herb.	3	10.5	0.341	0	7	15	0	0
Poa palustris L.	Herb.	4	8.2	0.513	0	7	0	14	12

Appendix 3 Relative frequencies, total occurrence (TO), indicator values (IV) and *P*-values of the 103 plant species observed in sub-boreal peatlands classified as Herbaceous Fens. Bolded **species** were identified as significant indicators ($p \leq 0.05$) (Dufrene and Legendre 1997) for one of the five classified peatland community types , with the corresponding community types identified by bold **relative frequencies**. Species are sorted by decreasing relative frequency.

					% Relative Frequency				
Species	Strata	T.O.	IV	*P*-value	Phalaris Dominated	Sphagnum Bogs	Herbaceous Fens	Forested Fens	Rich/Calcareous Fens
***Cicuta bulbifera* L.**	Herb.	12	**81.3**	**0.001**	0	0	**85**	0	6
***Carex lasiocarpa* Ehrh. var. *americana* Fernald**	Herb.	11	**65.8**	**0.001**	0	7	**69**	0	6
***Calamagrostis canadensis* (Michx.) P. Beauv.**	Herb.	25	**32.7**	**0.041**	**80**	36	62	29	35
Thelypteris palustris Schott var. *pubescens* (G. Lawson) Fernald	Herb.	20	22.5	0.182	0	21	62	29	41
***Lysimachia thyrsiflora* L.**	Herb.	8	**47.8**	**0.003**	0	0	**54**	0	6
Lycopus uniflorus Michx.	Herb.	18	21.7	0.206	0	21	54	57	24
***Sphagnaceae* L.**	Bryo.	23	**66.9**	**0.001**	0	**100**	46	29	6
***Carex stricta* Lam.**	Herb.	24	**63.4**	**0.001**	20	7	46	0	**94**
***Comarum palustre* L.**	Herb.	6	**46.2**	**0.002**	0	0	**46**	0	0
***Sagittaria latifolia* Willd.**	Herb.	6	**46.2**	**0.005**	0	0	**46**	0	0
***Onoclea sensibilis* L.**	Herb.	13	**28.8**	**0.045**	0	14	46	**57**	6
***Polygonum sagittatum* L.**	Herb.	8	**25.6**	**0.046**	40	0	**46**	0	0
***Bidens aristosa* (Michx.) Britton**	Herb.	5	**38.5**	**0.006**	0	0	**38**	0	0
Salix petiolaris Sm.	Shrub	7	18.9	0.14	20	0	38	0	6
***Spiraea alba* Du Roi**	Herb.	4	**30.8**	**0.011**	0	0	**31**	0	0
***Scutellaria galericulata* L.**	Herb.	4	**30.8**	**0.023**	0	0	**31**	0	0
***Triadenum fraseri* (Spach) Gleason**	Herb.	4	**30.8**	**0.026**	0	0	**31**	0	0
Rumex verticillatus L.	Herb.	5	20.1	0.087	0	0	31	14	0
Amblystegiaceae	Bryo.	10	**32.2**	**0.021**	0	0	23	**57**	18
***Lemna minor* L.**	Herb.	3	**23.1**	**0.041**	0	0	**23**	0	0
***Carex utriculata* Boott**	Herb.	3	**23.1**	**0.046**	0	0	**23**	0	0
Betula pumila L. var. *glandulifera* Regel	Shrub	12	21.3	0.13	0	43	23	14	12
Lythrum salicaria L.	Herb.	4	20.8	0.064	0	0	23	0	6

Appendix 3. Continued.

					% Relative Frequency				
Species	Strata	T.O.	IV	*P*-value	Phalaris Dominated	Sphagnum Bogs	Herbaceous Fens	Forested Fens	Rich/Calcareous Fens
Dryopteris cristata (L.) A. Gray	Herb.	9	20.4	0.128	0	21	23	43	0
Carex stipata Muhl. ex Willd. var. *stipata*	Herb.	4	18.4	0.116	0	0	23	0	6
Typha latifolia L.	Herb.	9	16.3	0.231	40	0	23	0	24
Alnus incana ssp. *rugosa* (Du Roi) Clausen	Shrub	6	15.2	0.242	0	7	23	29	0
Spiraea tomentosa L. var. *rosea*	Herb.	4	14.3	0.182	0	7	23	0	0
Bidens cernua L.	Herb.	2	-	-	0	0	15	0	0
Calla palustris L.	Herb.	2	-	-	0	0	15	0	0
Carex comosa Boott	Herb.	2	-	-	0	0	15	0	0
Epilobium leptophyllum Raf.	Herb.	2	-	-	0	0	15	0	0
Galium trifidum L. ssp. *trifidum*	Herb.	2	-	-	0	0	15	0	0
Rumex orbiculatus A. Gray	Herb.	2	-	-	0	0	15	0	0
Salix pedicellaris Pursh	Herb.	2	-	-	0	0	15	0	0
Salix petiolaris Sm.	Herb.	2	-	-	0	0	15	0	0
Typha L.	Herb.	2	-	-	0	0	15	0	0
Wolffia columbiana Karst.	Herb.	2	-	-	0	0	15	0	0
***Phalaris arundinacea* L.**	Herb.	14	**76.7**	**0.001**	**100**	0	15	14	35
***Eupatorium maculatum* L.**	Herb.	21	**49.5**	**0.002**	60	0	15	14	**88**
***Symphyotrichum puniceum* (L.) A. Löve & D. Löve**	Herb.	17	**39.1**	**0.005**	0	0	15	43	**71**
***Impatiens capensis* Meerb.**	Herb.	11	**33.4**	**0.015**	0	0	15	**57**	29
Osmunda cinnamomea* L. var. *cinnamomea	Herb.	7	**30**	**0.029**	0	7	15	**43**	6
***Viola* L.**	Herb.	7	**25.8**	**0.037**	20	0	15	**43**	6
Scirpus cyperinus (L.) Kunth	Herb.	8	15.3	0.255	40	21	15	0	6
Equisetum fluviatile L.	Herb.	5	12.6	0.276	0	0	15	29	6
Eupatorium perfoliatum L. var. *perfoliatum*	Herb.	7	11.5	0.432	20	0	15	0	24
Lysimachia terrestris (L.) BSP	Herb.	3	10.5	0.335	0	7	15	0	0

Appendix 3. Continued.

					% Relative Frequency				
Species	Strata	T.O.	IV	*P*-value	Phalaris Dominated	Sphagnum Bogs	Herbaceous Fens	Forested Fens	Rich/Calcareous Fens
Salix pyrifolia Anderson	Herb.	3	10.5	0.341	0	7	15	0	0
Typha angustifolia L.	Herb.	4	9.1	0.41	0	0	15	0	12
Polygonum amphibium L.	Herb.	3	8.7	0.525	0	0	15	0	6
Dulichium arundinaceum (L.) Britton	Herb.	4	7.9	0.603	0	14	15	0	0
Campanula aparinoides Pursh	Herb.	6	5.7	0.854	0	0	15	14	6
Acorus calamus L.	Herb.	1	-	-	0	0	8	0	0
Alisma subcordatum Raf.	Herb.	1	-	-	0	0	8	0	0
Alnus incana ssp. *rugosa* (Du Roi) Clausen	Herb.	1	-	-	0	0	8	0	0
Betula pumila L. var. *glandulifera* Regel	Herb.	2	-	-	0	7	8	0	0
Bidens frondosa L.	Herb.	1	-	-	0	0	8	0	0
Carex brunnescens (Pers.) Poir.	Herb.	1	-	-	0	0	8	0	0
Carex haydenii Dewey	Herb.	1	-	-	0	0	8	0	0
Equisetum hyemale L. var. *affine* (Engelm.) A.A. Eaton	Herb.	1	-	-	0	0	8	0	0
Erechtites hieraciifolia (L.) Raf. ex DC. var. *hieraciifolia*	Herb.	1	-	-	0	0	8	0	0
Euthamia graminifolia (L.) Nutt.	Herb.	2	-	-	0	0	8	0	6
Galium asprellum Michx.	Herb.	1	-	-	0	0	8	0	0
Glyceria canadensis (Michx.) Trin.	Herb.	2	-	-	0	7	8	0	0
Hypericum prolificum L.	Herb.	1	-	-	0	0	8	0	0
Polygonum hydropiper L.	Herb.	2	-	-	0	0	8	0	6
Ricciaceae	Bryo.	2	-	-	0	0	8	14	0
Rubus L.	Herb.	2	-	-	0	7	8	0	0
Rumex L.	Herb.	2	-	-	0	0	8	0	6
Sagittaria L.	Herb.	1	-	-	0	0	8	0	0
Salix discolor Muhl.	Herb.	2	-	-	0	0	8	0	6
Salix L.	Herb.	1	-	-	0	0	8	0	0

Appendix 3. Continued.

					% Relative Frequency				
Species	Strata	T.O.	IV	*P*-value	Phalaris Dominated	Sphagnum Bogs	Herbaceous Fens	Forested Fens	Rich/Calcareous Fens
Salix pedicellaris Pursh	Shrub	2	-	-	0	7	8	0	0
Salix planifolia Pursh	Shrub	2	-	-	20	0	8	0	0
Schoenoplectus fluviatilis (Torr.) M.T. Strong	Herb.	1	-	-	0	0	8	0	0
Symphyotrichum Nees spp.	Herb.	2	-	-	0	0	8	0	6
Typha×glauca Godr. (pro sp.) [*angustifolia×latifolia*]	Herb.	1	-	-	0	0	8	0	0
Rubus pubescens* Raf. var. *pubescens	Herb.	14	**70**	**0.001**	0	0	8	**100**	35
***Carex lacustris* Willd.**	Herb.	10	**48.1**	**0.005**	**80**	7	8	14	18
***Carex oligosperma* Michx.**	Herb.	9	**47**	**0.002**	0	**57**	8	0	0
Cornus sericea L. ssp. *sericea*	Shrub	17	28.3	0.058	0	14	8	57	59
***Salix discolor* Muhl.**	Shrub	6	**25.3**	**0.048**	0	0	8	0	**29**
***Ilex verticillata* (L.) A. Gary**	Shrub	4	**24.1**	**0.027**	0	0	8	**29**	6
Thalictrum dasycarpum Fisch. & Avé-Lall.	Herb.	8	23	0.08	0	0	8	14	35
Rubus idaeus L. ssp. *strigosus* (Michx.) Focke	Herb.	11	21.5	0.098	0	14	8	43	29
Carex L.	Herb.	8	20.3	0.123	40	0	8	43	12
Chamaedaphne calyculata (L.) Moench var. *angustifolia*	Herb.	4	18.6	0.088	0	21	8	0	0
Doellingeria umbellata (Mill.) Nees	Herb.	6	16	0.166	0	7	8	0	24
Galium tinctorium (L.) Scop.	Herb.	4	14.1	0.218	20	0	8	14	6
Asclepias incarnata L. ssp. *incarnata*	Herb.	4	14	0.183	0	0	8	0	18
Symphyotrichum boreale (Torr. & A. Gray) A. Löve & D. Löve	Herb.	6	13.7	0.244	0	0	8	14	24
Spiraea tomentosa L. var. *rosea*	Shrub	4	12.5	0.256	0	21	8	0	0
Phragmites australis (Cav.) Trin. ex Steud.	Herb.	3	11.9	0.223	20	0	8	0	6
Agrostis gigantea Roth	Herb.	4	10.7	0.344	0	0	8	0	18
Caltha palustris L. var. *palustris*	Herb.	3	9.7	0.489	0	0	8	0	12
Drosera rotundifolia L. var. *rotundifolia*	Herb.	3	9.3	0.507	0	14	8	0	0
Carex interior L.H. Bailey	Herb.	3	7.7	0.602	0	0	8	0	12

Appendix 3. Continued.

					% Relative Frequency				
Species	Strata	T.O.	IV	*P*-value	Phalaris Dominated	Sphagnum Bogs	Herbaceous Fens	Forested Fens	Rich/Calcareous Fens
Ribes americanum Mill.	Shrub	3	7.3	0.667	0	0	8	14	6
Carex buxbaumii Wahlenb.	Herb.	3	7.1	0.84	0	0	8	0	12
Viburnum lentago L.	Shrub	3	7.1	0.848	0	0	8	0	12
Parthenocissus Planch.	Herb.	4	6	0.82	0	0	8	14	12

Appendix 4 Relative frequencies, total occurrence (TO), indicator values (IV) and *P*-values of the 133 plant species observed in sub-boreal peatlands classified as Forested Fens. Bolded **species** were identified as significant indicators ($p \leq 0.05$) (Dufrene and Legendre 1997) for one of the five classified peatland community types , with the corresponding community types identified by bold **relative frequencies**. Species are sorted by decreasing relative frequency.

					% Relative Frequency				
Species	Strata	T.O.	IV	*P*-value	Phalaris Dominated	Sphagnum Bogs	Herbaceous Fens	Forested Fens	Rich/Calcareous Fens
Rubus pubescens* Raf. var. *pubescens	Herb.	14	**70**	**0.001**	0	0	8	**100**	35
***Athyrium filix-femina* (L.) Roth ssp. *angustum* (Willd.) R.T. Clausen**	Herb.	5	**71.4**	**0.001**	0	0	0	**71**	0
***Maianthemum canadense* Desf.**	Herb.	6	**58.4**	**0.002**	0	7	0	**71**	0
Acer rubrum* L. var. *rubrum	Can.	4	**57.1**	**0.001**	0	0	0	**57**	0
Betula alleghaniensis* Britton var. *alleghaniensis	Can.	4	**57.1**	**0.001**	0	0	0	**57**	0
***Fraxinus nigra* Marsh.**	Can.	4	**57.1**	**0.001**	0	0	0	**57**	0
***Fraxinus nigra* Marsh.**	Shrub	4	**57.1**	**0.002**	0	0	0	**57**	0
***Aralia nudicaulis* L.**	Herb.	6	**46.5**	**0.003**	0	7	0	**57**	6
Acer rubrum* L. var. *rubrum	Shrub	7	**45.2**	**0.004**	0	14	0	**57**	6
***Impatiens capensis* Meerb.**	Herb.	11	**33.4**	**0.015**	0	0	15	**57**	29
Amblystegiaceae	Bryo.	10	**32.2**	**0.021**	0	0	23	**57**	18
***Onoclea sensibilis* L.**	Herb.	13	**28.8**	**0.045**	0	14	46	**57**	6
Cornus sericea L. ssp. *sericea*	Shrub	17	28.3	0.058	0	14	8	57	59
Lycopus uniflorus Michx.	Herb.	18	21.7	0.206	0	21	54	57	24
***Cornus canadensis* L.**	Herb.	3	**42.9**	**0.001**	0	0	0	**43**	0
***Corylus cornuta* Marsh.**	Shrub	3	**42.9**	**0.001**	0	0	0	**43**	0
***Hydrocotyle americana* L.**	Herb.	3	**42.9**	**0.006**	0	0	0	**43**	0
***Thuja occidentalis* L.**	Can.	3	**42.9**	**0.006**	0	0	0	**43**	0
***Glyceria striata* (Lam.) Hitchc.**	Herb.	4	**40.8**	**0.003**	0	0	0	**43**	6
***Arisaema triphyllum* (L.) Schott**	Herb.	4	**40.1**	**0.007**	0	0	0	**43**	6
***Symphyotrichum puniceum* (L.) A. Löve & D. Löve**	Herb.	17	**39.1**	**0.005**	0	0	15	43	**71**
***Ulmus americana* L.**	Can.	5	**32.7**	**0.009**	0	0	0	**43**	12

Appendix 4. Continued.

Species	Strata	T.O.	IV	*P*-value	% Relative Frequency Phalaris Dominated	Sphagnum Bogs	Herbaceous Fens	Forested Fens	Rich/Calcareous Fens
***Viola cucullata* Aiton**	Herb.	6	**31.3**	**0.018**	20	0	0	**43**	12
Osmunda cinnamomea* L. var. *cinnamomea	Herb.	7	**30**	**0.029**	0	7	15	**43**	6
Trientalis borealis* Raf. ssp. *borealis	Herb.	6	**28.6**	**0.024**	0	21	0	**43**	0
***Dryopteris carthusiana* (Vill.) H.P. Fuchs**	Herb.	7	**26.2**	**0.036**	0	21	0	**43**	6
***Viola* L.**	Herb.	7	**25.8**	**0.037**	20	0	15	**43**	6
Rubus idaeus L. ssp. *strigosus* (Michx.) Focke	Herb.	11	21.5	0.098	0	14	8	43	29
Dryopteris cristata (L.) A. Gray	Herb.	9	20.4	0.128	0	21	23	43	0
Carex L.	Herb.	8	20.3	0.123	40	0	8	43	12
Betula alleghaniensis Britton var. *alleghaniensis*	Shrub	2	-	-	0	0	0	29	0
Carex leptalea Wahlenb. ssp. *leptalea*	Herb.	2	-	-	0	0	0	29	0
Circaea alpina L. ssp. *alpina*	Herb.	2	-	-	0	0	0	29	0
Clintonia borealis (Aiton) Raf.	Herb.	2	-	-	0	0	0	29	0
Coptis trifolia (L.) Salisb.	Herb.	2	-	-	0	0	0	29	0
Epilobium ciliatum Raf. ssp. *ciliatum*	Herb.	2	-	-	0	0	0	29	0
Fragaria virginiana Duchesne	Herb.	2	-	-	0	0	0	29	0
Fraxinus nigra Marsh.	Herb.	2	-	-	0	0	0	29	0
Laportea canadensis (L.) Weddell	Herb.	2	-	-	0	0	0	29	0
Mitella nuda L.	Herb.	2	-	-	0	0	0	29	0
Parthenocissus quinquefolia (L.) Planch.	Herb.	2	-	-	0	0	0	29	0
Phegopteris connectilis (Michx.) Watt	Herb.	2	-	-	0	0	0	29	0
Pilea fontana (Lunell) Rydb.	Herb.	2	-	-	0	0	0	29	0
Polygonum arifolium L.	Herb.	2	-	-	0	0	0	29	0
Symplocarpus foetidus (L.) Salisb. ex Nutt.	Herb.	2	-	-	0	0	0	29	0
Toxicodendron rydbergii (Small ex Rydb.) Greene	Herb.	2	-	-	0	0	0	29	0
***Sphagnaceae* L.**	Bryo.	23	**66.9**	**0.001**	0	**100**	46	29	6

Appendix 4. Continued.

Species	Strata	T.O.	IV	*P*-value	% Relative Frequency: Phalaris Dominated	Sphagnum Bogs	Herbaceous Fens	Forested Fens	Rich/Calcareous Fens
***Larix laricina* (Du Roi) K. Koch**	Can.	11	**38.9**	**0.006**	0	**57**	0	29	6
***Calamagrostis canadensis* (Michx.) P. Beauv.**	Herb.	25	**32.7**	**0.041**	**80**	36	62	29	35
***Amphicarpaea bracteata* (L.) Fernald**	Herb.	3	**25.1**	**0.022**	0	0	0	**29**	6
***Ilex verticillata* (L.) A. Gary**	Shrub	4	**24.1**	**0.027**	0	0	8	**29**	6
***Galium triflorum* Michx.**	Herb.	3	**23.7**	**0.044**	0	0	0	**29**	6
Thelypteris palustris Schott var. *pubescens* (G. Lawson) Fernald	Herb.	20	22.5	0.182	0	21	62	29	41
Viola macloskeyi Lloyed ssp. *pallens* (Banks ex Ging) M.S. Baker	Herb.	3	21.4	0.068	0	7	0	29	0
Equisetum arvense L.	Herb.	6	16.9	0.169	20	0	0	29	18
Alnus incana ssp. *rugosa* (Du Roi) Clausen	Shrub	6	15.2	0.242	0	7	23	29	0
Equisetum fluviatile L.	Herb.	5	12.6	0.276	0	0	15	29	6
Ricciaceae	Bryo.	2	-	-	0	0	8	14	0
Acer rubrum L. var. *rubrum*	Herb.	2	-	-	0	7	0	14	0
Acer spicatum Lam.	Herb.	1	-	-	0	0	0	14	0
Acer spicatum Lam.	Shrub	1	-	-	0	0	0	14	0
Actaea L.	Herb.	1	-	-	0	0	0	14	0
Anemone quinquefolia L. var. *bifolia* Farw.	Herb.	1	-	-	0	0	0	14	0
Betula papyrifera Marsh. var. *papyrifera*	Can.	1	-	-	0	0	0	14	0
Bidens L.	Herb.	1	-	-	0	0	0	14	0
Brachyelytrum aristosum (Michx.) Trel.	Herb.	1	-	-	0	0	0	14	0
Carex gracillima Schwein.	Herb.	1	-	-	0	0	0	14	0
Carex intumescens Rudge	Herb.	1	-	-	0	0	0	14	0
Carpinus caroliniana Walter ssp. *virginiana* (Marsh.) Furlow	Shrub	1	-	-	0	0	0	14	0
Cerastium fontanum Baumg. ssp. *vulgare* (Hartm.) Greuter & Burdet	Herb.	1	-	-	0	0	0	14	0

Appendix 4. Continued.

					% Relative Frequency				
Species	Strata	T.O.	IV	*P*-value	Phalaris Dominated	Sphagnum Bogs	Herbaceous Fens	Forested Fens	Rich/Calcareous Fens
Chelone glabra L.	Herb.	2	-	-	0	0	0	14	6
Cinna latifolia (Trevis. Ex Goepp.) Griseb.	Herb.	1	-	-	0	0	0	14	0
Corylus americana Walter	Herb.	1	-	-	0	0	0	14	0
Corylus americana Walter	Shrub	1	-	-	0	0	0	14	0
Cryptotaenia canadensis (L.) DC.	Herb.	1	-	-	0	0	0	14	0
Equisetum sylvaticum L.	Herb.	1	-	-	0	0	0	14	0
Eurybia macrophylla (L.) Cass.	Herb.	1	-	-	0	0	0	14	0
Galium L.	Herb.	1	-	-	0	0	0	14	0
Geum rivale L.	Herb.	1	-	-	0	0	0	14	0
Gymnocarpium dryopteris (L.) Newman	Herb.	1	-	-	0	0	0	14	0
Ilex verticillata (L.) A. Gary	Herb.	1	-	-	0	0	0	14	0
Lactuca biennis (Moench) Fernald	Herb.	1	-	-	0	0	0	14	0
Lonicera L.	Herb.	1	-	-	0	0	0	14	0
Matteuccia struthiopteris (L.) Todaro	Herb.	1	-	-	0	0	0	14	0
Mitella diphylla L.	Herb.	1	-	-	0	0	0	14	0
Osmorhiza claytonii (Michx.) C.B. Clarke	Herb.	1	-	-	0	0	0	14	0
Osmunda claytoniana L.	Herb.	2	-	-	0	7	0	14	0
Osmunda regalis L var. *spectabilis* (Willd.) A. Gray	Herb.	2	-	-	0	7	0	14	0
Parietaria pensylvanica Muhl. ex Willd.	Herb.	1	-	-	0	0	0	14	0
Petasites frigidus (L.) Fr. var. *palmatus* (Aiton) Cronquist	Herb.	1	-	-	0	0	0	14	0
Pilea pumila (L.) A. Gray var. *pumila*	Herb.	1	-	-	0	0	0	14	0
Pinus strobus L.	Can.	1	-	-	0	0	0	14	0
Quercus L. sp.	Shrub	1	-	-	0	0	0	14	0
Quercus rubra L.	Shrub	2	-	-	0	7	0	14	0
Ranunculus abortivus L.	Herb.	1	-	-	0	0	0	14	0

Appendix 4. Continued.

Species	Strata	T.O.	IV	*P*-value	% Relative Frequency Phalaris Dominated	Sphagnum Bogs	Herbaceous Fens	Forested Fens	Rich/Calcareous Fens
Ranunculus hispidus Michx.	Herb.	1	-	-	0	0	0	14	0
Ribes cynosbati L.	Herb.	1	-	-	0	0	0	14	0
Ribes hirtellum Michx.	Shrub	2	-	-	0	0	0	14	6
Rubus allegheniensis Porter var. *allegheniensis*	Herb.	1	-	-	0	0	0	14	0
Sambucus nigra L. ssp. *canadensis* (L.) R. Bolli	Herb.	1	-	-	0	0	0	14	0
Solidago flexicaulis L.	Herb.	1	-	-	0	0	0	14	0
Spiraea alba Du Roi	Shrub	2	-	-	0	7	0	14	0
Stellaria graminea L.	Herb.	1	-	-	0	0	0	14	0
Symphyotrichum lateriflorum (L.) A. Löve & D. Löve	Herb.	1	-	-	0	0	0	14	0
Thalictrum dioicum L.	Herb.	1	-	-	0	0	0	14	0
Thuidiaceae Schimp.	Bryo.	1	-	-	0	0	0	14	0
Tilia americana L. var. *americana*	Herb.	1	-	-	0	0	0	14	0
Tilia americana L. var. *americana*	Shrub	1	-	-	0	0	0	14	0
Toxicodendron radicans (L.) Kuntze ssp. *negundo* (Greene) Gillis	Herb.	2	-	-	0	0	0	14	6
Trillium grandiflorum (Michx.) Salisb.	Herb.	1	-	-	0	0	0	14	0
Ulmus americana L.	Herb.	2	-	-	0	0	0	14	6
Urtica dioica L. ssp. *gracilis* (Aiton) Seland.	Herb.	2	-	-	0	0	0	14	6
***Phalaris arundinacea* L.**	Herb.	14	**76.7**	**0.001**	**100**	0	15	14	35
***Solidago gigantea* Aiton**	Herb.	15	**54.2**	**0.004**	20	0	0	14	**76**
***Eupatorium maculatum* L.**	Herb.	21	**49.5**	**0.002**	60	0	15	14	**88**
***Carex lacustris* Willd.**	Herb.	10	**48.1**	**0.005**	**80**	7	8	14	18
Carex trisperma* Dewey var. *trisperma	Herb.	7	**32.8**	**0.014**	0	**43**	0	14	0
***Picea mariana* (Mill.) BSP**	Can.	7	**32.8**	**0.013**	0	**43**	0	14	0
Thalictrum dasycarpum Fisch. & Avé-Lall.	Herb.	8	23	0.08	0	0	8	14	35

Appendix 4. Continued.

Species	Strata	T.O.	IV	*P*-value	% Relative Frequency Phalaris Dominated	Sphagnum Bogs	Herbaceous Fens	Forested Fens	Rich/Calcareous Fens
Betula pumila L. var. *glandulifera* Regel	Shrub	12	21.3	0.13	0	43	23	14	12
Rumex verticillatus L.	Herb.	5	20.1	0.087	0	0	31	14	0
Geum aleppicum Jacq.	Herb.	6	16.8	0.185	0	0	0	14	29
Galium tinctorium (L.) Scop.	Herb.	4	14.1	0.218	20	0	8	14	6
Symphyotrichum boreale (Torr. & A. Gray) A. Löve & D. Löve	Herb.	6	13.7	0.244	0	0	8	14	24
Bromus ciliatus L. var. *ciliatus*	Herb.	4	11	0.315	0	0	0	14	18
Ulmus americana L.	Shrub	3	10.9	0.336	0	0	0	14	12
Betula papyrifera Marsh. var. *papyrifera*	Shrub	6	9.9	0.575	0	21	0	14	12
Poa palustris L.	Herb.	4	8.2	0.513	0	7	0	14	12
Quercus rubra L.	Herb.	3	8.2	0.668	0	14	0	14	0
Cornus racemosa Lam.	Shrub	3	7.9	0.605	0	0	0	14	12
Ribes americanum Mill.	Shrub	3	7.3	0.667	0	0	8	14	6
Parthenocissus Planch.	Herb.	4	6	0.82	0	0	8	14	12
Campanula aparinoides Pursh	Herb.	6	5.7	0.854	0	0	15	14	6

Appendix 5 Relative frequencies, total occurrence (TO), indicator values (IV) and *P*-values of the 175 plant species observed in sub-boreal peatlands classified as Rich/Calcareous Fens. . Bolded **species** were identified as significant indicators ($p \leq 0.05$) (Dufrene and Legendre 1997) for one of the five classified peatland community types, with the corresponding community types identified by bold **relative frequencies**. Species are sorted by decreasing relative frequency.

					% Relative Frequency				
Species	Strata	T.O.	IV	*P*-value	Phalaris Dominated	Sphagnum Bogs	Herbaceous Fens	Forested Fens	Rich/Calcareous Fens
Carex stricta **Lam.**	Herb.	24	**63.4**	**0.001**	20	7	46	0	**94**
Eupatorium maculatum **L.**	Herb.	21	**49.5**	**0.002**	60	0	15	14	**88**
Solidago gigantea **Aiton**	Herb.	15	**54.2**	**0.004**	20	0	0	14	**76**
Symphyotrichum puniceum **(L.) A. Löve & D. Löve**	Herb.	17	**39.1**	**0.005**	0	0	15	43	**71**
Cornus sericea L. ssp. *sericea*	Shrub	17	28.3	0.058	0	14	8	57	59
Pycnanthemum virginianum **(L.) T. Dur. & B.D. Jacks. ex B.L. Rob & Fernald**	Herb.	8	**47.1**	**0.001**	0	0	0	0	**47**
Cirsium muticum **Michx.**	Herb.	7	**41.2**	**0.008**	0	0	0	0	**41**
Thelypteris palustris Schott var. *pubescens* (G. Lawson) Fernald	Herb.	20	22.5	0.182	0	21	62	29	41
Phalaris arundinacea **L.**	Herb.	14	**76.7**	**0.001**	**100**	0	15	14	35
Rubus pubescens **Raf. var.** ***pubescens***	Herb.	14	**70**	**0.001**	0	0	8	**100**	35
Calamagrostis canadensis **(Michx.) P. Beauv.**	Herb.	25	**32.7**	**0.041**	**80**	36	62	29	35
Helianthus grosseserratus **M. Martens**	Herb.	7	**28**	**0.034**	20	0	0	0	**35**
Thalictrum dasycarpum Fisch. & Avé-Lall.	Herb.	8	23	0.08	0	0	8	14	35
Impatiens capensis **Meerb.**	Herb.	11	**33.4**	**0.015**	0	0	15	**57**	29
Salix discolor **Muhl.**	Shrub	6	**25.3**	**0.048**	0	0	8	0	**29**
Rubus idaeus L. ssp. *strigosus* (Michx.) Focke	Herb.	11	21.5	0.098	0	14	8	43	29
Geum aleppicum Jacq.	Herb.	6	16.8	0.185	0	0	0	14	29
Calamagrostis stricta **(Timm) Koeler ssp.** ***stricta***	Herb.	4	**23.5**	**0.039**	0	0	0	0	**24**
Frangula alnus **Mill.**	Shrub	4	**23.5**	**0.049**	0	0	0	0	**24**
Poa pratensis **L. ssp.** ***pratensis***	Herb.	4	**23.5**	**0.05**	0	0	0	0	**24**
Lycopus americanus Muhl. ex W. Bartram	Herb.	4	23.5	0.055	0	0	0	0	24
Galium boreale L.	Herb.	4	23.5	0.061	0	0	0	0	24

Appendix 5. Continued.

					% Relative Frequency				
Species	Strata	T.O.	IV	*P*-value	Phalaris Dominated	Sphagnum Bogs	Herbaceous Fens	Forested Fens	Rich/Calcareous Fens
Rhamnus cathartica L.	Shrub	4	23.5	0.063	0	0	0	0	24
Lycopus uniflorus Michx.	Herb.	18	21.7	0.206	0	21	54	57	24
Typha latifolia L.	Herb.	9	16.3	0.231	40	0	23	0	24
Doellingeria umbellata (Mill.) Nees	Herb.	6	16	0.166	0	7	8	0	24
Symphyotrichum boreale (Torr. & A. Gray) A. Löve & D. Löve	Herb.	6	13.7	0.244	0	0	8	14	24
Eupatorium perfoliatum L. var. *perfoliatum*	Herb.	7	11.5	0.432	20	0	15	0	24
***Carex lacustris* Willd.**	Herb.	10	**48.1**	**0.005**	**80**	7	8	14	18
Amblystegiaceae	Bryo.	10	**32.2**	**0.021**	0	0	23	**57**	18
Maianthemum stellatum (L.) Link	Herb.	3	17.6	0.086	0	0	0	0	18
Apocynum cannabinum L.	Herb.	3	17.6	0.09	0	0	0	0	18
Calystegia sepium (L.) R. Br.	Herb.	3	17.6	0.09	0	0	0	0	18
Acer negundo L.	Shrub	3	17.6	0.094	0	0	0	0	18
Pedicularis lanceolata Michx.	Herb.	3	17.6	0.094	0	0	0	0	18
Oligoneuron riddellii (Frank ex Riddell) Rybd.	Herb.	3	17.6	0.096	0	0	0	0	18
Fraxinus pennsylvanica Marsh.	Shrub	3	17.6	0.098	0	0	0	0	18
Lathyrus palustris L.	Herb.	3	17.6	0.1	0	0	0	0	18
Oxypolis rigidior L. Raf.	Herb.	3	17.6	0.101	0	0	0	0	18
Carex tectanica Schkuhr	Herb.	3	17.6	0.103	0	0	0	0	18
Solidago canadensis L.	Herb.	3	17.6	0.103	0	0	0	0	18
Schoenoplectus acutus (Muhl. ex Bigelow) A. Löve & D. Löve var. *acutus*	Herb.	3	17.6	0.107	0	0	0	0	18
Salix bebbiana Sarg.	Shrub	3	17.6	0.114	0	0	0	0	18
Equisetum arvense L.	Herb.	6	16.9	0.169	20	0	0	29	18
Asclepias incarnata L. ssp. *incarnata*	Herb.	4	14	0.183	0	0	8	0	18
Bromus ciliatus L. var. *ciliatus*	Herb.	4	11	0.315	0	0	0	14	18

Appendix 5. Continued.

					% Relative Frequency				
Species	Strata	T.O.	IV	*P*-value	Phalaris Dominated	Sphagnum Bogs	Herbaceous Fens	Forested Fens	Rich/Calcareous Fens
Agrostis gigantea Roth	Herb.	4	10.7	0.344	0	0	8	0	18
Amorpha fruticosa L.	Shrub	2	-	-	0	0	0	0	12
Andropogon gerardii Vitman	Herb.	2	-	-	0	0	0	0	12
Carex hystericina Muhl. ex Willd.	Herb.	2	-	-	0	0	0	0	12
Carex prairea Dewey ex Alph. Wood	Herb.	2	-	-	0	0	0	0	12
Carex sterilis Willd.	Herb.	2	-	-	0	0	0	0	12
Carex trichocarpa Muhl. ex Willd.	Herb.	2	-	-	0	0	0	0	12
Comandra umbellata (L.) Nutt. ssp. *umbellata*	Herb.	2	-	-	0	0	0	0	12
Cornus obliqua Raf.	Shrub	2	-	-	0	0	0	0	12
Eriophorum angustifolium Honck.	Herb.	2	-	-	0	0	0	0	12
Helenium autumnale L. var. *autumnale*	Herb.	2	-	-	0	0	0	0	12
Helianthus giganteus L.	Herb.	2	-	-	0	0	0	0	12
Hypoxis hirsuta (L.) Coville	Herb.	2	-	-	0	0	0	0	12
Liatris ligulistylis (A. Nelson) K. Schum.	Herb.	2	-	-	0	0	0	0	12
Lobelia siphilitica L. var. *ludoviciana* A. DC.	Herb.	2	-	-	0	0	0	0	12
Muhlenbergia frondosa (Poir.) Fernald	Herb.	2	-	-	0	0	0	0	12
Muhlenbergia glomerata (Willd.) Trin.	Herb.	2	-	-	0	0	0	0	12
Parnassia glauca Raf.	Herb.	2	-	-	0	0	0	0	12
Prenanthes alba L.	Herb.	2	-	-	0	0	0	0	12
Schoenoplectus tabernaemontani (C.C. Gmel.) Palla	Herb.	2	-	-	0	0	0	0	12
Scirpus atrovirens Willd.	Herb.	2	-	-	0	0	0	0	12
Silphium perfoliatum L. var. *perfoliatum*	Herb.	2	-	-	0	0	0	0	12
Solanum dulcamara L. var. *dulcamara*	Herb.	2	-	-	0	0	0	0	12
Spartina pectinata Bosc ex link	Herb.	2	-	-	0	0	0	0	12
Symphyotrichum novae-angliae (L.) G.L. Nesom	Herb.	2	-	-	0	0	0	0	12

Appendix 5. Continued.

Species	Strata	T.O.	IV	*P*-value	% Relative Frequency Phalaris Dominated	Sphagnum Bogs	Herbaceous Fens	Forested Fens	Rich/Calcareous Fens
Valeriana edulis Nutt. ex Torr. & A. Gray var. *ciliata* (Torr. & A. Gray) Cronquist	Herb.	2	-	-	0	0	0	0	12
Viola sororia Willd.	Herb.	2	-	-	0	0	0	0	12
Zizia aptera (A. Gray) Fernald	Herb.	2	-	-	0	0	0	0	12
***Ulmus americana* L.**	Can.	5	**32.7**	**0.009**	0	0	0	**43**	12
***Viola cucullata* Aiton**	Herb.	6	**31.3**	**0.018**	20	0	0	**43**	12
Betula pumila L. var. *glandulifera* Regel	Shrub	12	21.3	0.13	0	43	23	14	12
Carex L.	Herb.	8	20.3	0.123	40	0	8	43	12
Ulmus americana L.	Shrub	3	10.9	0.336	0	0	0	14	12
Betula papyrifera Marsh. var. *papyrifera*	Shrub	6	9.9	0.575	0	21	0	14	12
Caltha palustris L. var. *palustris*	Herb.	3	9.7	0.489	0	0	8	0	12
Typha angustifolia L.	Herb.	4	9.1	0.41	0	0	15	0	12
Poa palustris L.	Herb.	4	8.2	0.513	0	7	0	14	12
Cornus racemosa Lam.	Shrub	3	7.9	0.605	0	0	0	14	12
Carex interior L.H. Bailey	Herb.	3	7.7	0.602	0	0	8	0	12
Carex buxbaumii Wahlenb.	Herb.	3	7.1	0.84	0	0	8	0	12
Viburnum lentago L.	Shrub	3	7.1	0.848	0	0	8	0	12
Parthenocissus Planch.	Herb.	4	6	0.82	0	0	8	14	12
Acer ginnala Maxim.	Shrub	1	-	-	0	0	0	0	6
Acer saccharinum L.	Shrub	1	-	-	0	0	0	0	6
Ambrosia artemisiifolia L.	Herb.	1	-	-	0	0	0	0	6
Angelica atropurpurea L.	Herb.	1	-	-	0	0	0	0	6
Betula pumila L. var. *glandulifera* Regel	Can.	2	-	-	0	7	0	0	6
Cardamine bulbosa (Schreb. Ex Muhl.) BSP	Herb.	1	-	-	0	0	0	0	6
Carex aquatilis Wahlenb. var. *aquatilis*	Herb.	1	-	-	0	0	0	0	6

Appendix 5. Continued.

Species	Strata	T.O.	IV	*P*-value	% Relative Frequency: Phalaris Dominated	Sphagnum Bogs	Herbaceous Fens	Forested Fens	Rich/Calcareous Fens
Carex atherodes Spreng.	Herb.	1	-	-	0	0	0	0	6
Carex cristatella Britton	Herb.	1	-	-	0	0	0	0	6
Chelone glabra L.	Herb.	2	-	-	0	0	0	14	6
Cicuta maculata L.	Herb.	1	-	-	0	0	0	0	6
Cladium mariscoides (Muhl.) Torr.	Herb.	1	-	-	0	0	0	0	6
Cornus sericea L. ssp. *sericea*	Herb.	1	-	-	0	0	0	0	6
Dasiphora fruticosa (L.) Rydb. ssp. *floribunda* (Pursh) Kartesz	Herb.	1	-	-	0	0	0	0	6
Eleocharis compressa Sull.	Herb.	1	-	-	0	0	0	0	6
Euthamia graminifolia (L.) Nutt.	Herb.	2	-	-	0	0	8	0	6
Frangula alnus Mill.	Can.	1	-	-	0	0	0	0	6
Frangula alnus Mill.	Herb.	1	-	-	0	0	0	0	6
Galium aparine L.	Herb.	1	-	-	0	0	0	0	6
Gentiana andrewsii Griseb.	Herb.	1	-	-	0	0	0	0	6
Geum canadense Jacq.	Herb.	1	-	-	0	0	0	0	6
Geum macrophyllum Willd. var. *perincisum* (Rydb.) Raup	Herb.	1	-	-	0	0	0	0	6
Glyceria grandis S. Watson var. *grandis*	Herb.	1	-	-	0	0	0	0	6
Humulus lupulus L.	Herb.	1	-	-	0	0	0	0	6
Juncus nodosus L. var. *nodosus*	Herb.	1	-	-	0	0	0	0	6
Juniperus virginiana L. var. *virginiana*	Herb.	1	-	-	0	0	0	0	6
Lactuca L.	Herb.	1	-	-	0	0	0	0	6
Liatris Gaertn. ex Schreb.	Herb.	1	-	-	0	0	0	0	6
Lysimachia quadriflora Sims	Herb.	1	-	-	0	0	0	0	6
Muhlenbergia richardsonis (Trin.) Rydb.	Herb.	1	-	-	0	0	0	0	6
Packera aurea (L.) A. Löve & D. Löve	Herb.	1	-	-	0	0	0	0	6
Polygonum convolvulus L. var. *convolvulus*	Herb.	1	-	-	0	0	0	0	6

Appendix 5. Continued.

Species	Strata	T.O.	IV	*P*-value	% Relative Frequency: Phalaris Dominated	Sphagnum Bogs	Herbaceous Fens	Forested Fens	Rich/Calcareous Fens
Polygonum hydropiper L.	Herb.	2	-	-	0	0	8	0	6
Rhamnus cathartica L.	Can.	1	-	-	0	0	0	0	6
Rhamnus cathartica L.	Herb.	1	-	-	0	0	0	0	6
Rhynchospora capillacea Torr.	Herb.	1	-	-	0	0	0	0	6
Ribes hirtellum Michx.	Shrub	2	-	-	0	0	0	14	6
Rosa blanda Aiton	Herb.	1	-	-	0	0	0	0	6
Rudbeckia hirta L. var. *pulcherrima* Farw.	Herb.	1	-	-	0	0	0	0	6
Rudbeckia triloba L. var. *triloba*	Herb.	1	-	-	0	0	0	0	6
Rumex L.	Herb.	2	-	-	0	0	8	0	6
Salix discolor Muhl.	Herb.	2	-	-	0	0	8	0	6
Salix discolor Muhl.	Can.	1	-	-	0	0	0	0	6
Salix interior Rowlee	Can.	1	-	-	0	0	0	0	6
Salix interior Rowlee	Shrub	1	-	-	0	0	0	0	6
Schoenoplectus pungens (Vahl) Palla	Herb.	1	-	-	0	0	0	0	6
Symphyotrichum lanceolatum (Willd.) G.L. Nesom	Herb.	2	-	-	20	0	0	0	6
Symphyotrichum Nees spp.	Herb.	2	-	-	0	0	8	0	6
Toxicodendron radicans (L.) Kuntze ssp. *negundo* (Greene) Gillis	Herb.	2	-	-	0	0	0	14	6
Toxicodendron vernix (L.) Kuntze	Shrub	2	-	-	0	7	0	0	6
Ulmus americana L.	Herb.	2	-	-	0	0	0	14	6
Urtica dioica L. ssp. *gracilis* (Aiton) Seland.	Herb.	2	-	-	0	0	0	14	6
Viburnum opulus L. var. *americanum* Aiton	Shrub	1	-	-	0	0	0	0	6
Viola nephrophylla Greene	Herb.	1	-	-	0	0	0	0	6
Vitis riparia Michx.	Herb.	1	-	-	0	0	0	0	6
Zigadenus elegans Pursh ssp. *elegans*	Herb.	1	-	-	0	0	0	0	6

Appendix 5. Continued.

					% Relative Frequency				
Species	Strata	T.O.	IV	*P*-value	Phalaris Dominated	Sphagnum Bogs	Herbaceous Fens	Forested Fens	Rich/Calcareous Fens
Zizia aurea (L.) W.D.J. Koch	Herb.	1	-	-	0	0	0	0	6
Zizia W.D.J. Koch	Herb.	1	-	-	0	0	0	0	6
***Cicuta bulbifera* L.**	Herb.	12	**81.3**	**0.001**	0	0	**85**	0	6
***Sphagnaceae* L.**	Bryo.	23	**66.9**	**0.001**	0	**100**	46	29	6
***Carex lasiocarpa* Ehrh. var. *americana* Fernald**	Herb.	11	**65.8**	**0.001**	0	7	**69**	0	6
***Lysimachia thyrsiflora* L.**	Herb.	8	**47.8**	**0.003**	0	0	**54**	0	6
***Aralia nudicaulis* L.**	Herb.	6	**46.5**	**0.003**	0	7	0	**57**	6
Acer rubrum* L. var. *rubrum	Shrub	7	**45.2**	**0.004**	0	14	0	**57**	6
***Glyceria striata* (Lam.) Hitchc.**	Herb.	4	**40.8**	**0.003**	0	0	0	**43**	6
***Arisaema triphyllum* (L.) Schott**	Herb.	4	**40.1**	**0.007**	0	0	0	**43**	6
***Larix laricina* (Du Roi) K. Koch**	Can.	11	**38.9**	**0.006**	0	**57**	0	29	6
***Maianthemum trifolium* (L.) Sloboda**	Herb.	6	**33.6**	**0.011**	0	**36**	0	0	6
Osmunda cinnamomea* L. var. *cinnamomea	Herb.	7	**30**	**0.029**	0	7	15	**43**	6
***Onoclea sensibilis* L.**	Herb.	13	**28.8**	**0.045**	0	14	46	**57**	6
***Dryopteris carthusiana* (Vill.) H.P. Fuchs**	Herb.	7	**26.2**	**0.036**	0	21	0	**43**	6
***Larix laricina* (Du Roi) K. Koch**	Shrub	5	**25.9**	**0.032**	0	**29**	0	0	6
***Viola* L.**	Herb.	7	**25.8**	**0.037**	20	0	15	**43**	6
***Amphicarpaea bracteata* (L.) Fernald**	Herb.	3	**25.1**	**0.022**	0	0	0	**29**	6
***Ilex verticillata* (L.) A. Gary**	Shrub	4	**24.1**	**0.027**	0	0	8	**29**	6
***Galium triflorum* Michx.**	Herb.	3	**23.7**	**0.044**	0	0	0	**29**	6
Lythrum salicaria L.	Herb.	4	20.8	0.064	0	0	23	0	6
Salix petiolaris Sm.	Shrub	7	18.9	0.14	20	0	38	0	6
Carex stipata Muhl. ex Willd. var. *stipata*	Herb.	4	18.4	0.116	0	0	23	0	6
Scirpus cyperinus (L.) Kunth	Herb.	8	15.3	0.255	40	21	15	0	6
Galium tinctorium (L.) Scop.	Herb.	4	14.1	0.218	20	0	8	14	6

Appendix 5. Continued.

Species	Strata	T.O.	IV	*P*-value	% Relative Frequency: Phalaris Dominated	Sphagnum Bogs	Herbaceous Fens	Forested Fens	Rich/Calcareous Fens
Equisetum fluviatile L.	Herb.	5	12.6	0.276	0	0	15	29	6
Phragmites australis (Cav.) Trin. ex Steud.	Herb.	3	11.9	0.223	20	0	8	0	6
Polygonum amphibium L.	Herb.	3	8.7	0.525	0	0	15	0	6
Ribes americanum Mill.	Shrub	3	7.3	0.667	0	0	8	14	6
Campanula aparinoides Pursh	Herb.	6	5.7	0.854	0	0	15	14	6

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